

A revision of the taxonomy of the blunt-hooked *Raillietiella*, pentastomid parasites of African, South-East-Asian and Indonesian lizards, with a description of a new species

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Summary

Three species of *Raillietiella* with blunt tips to the posterior hooks have been described from south-east Asia and Indonesia. However, we have established that two other species, *R. hemidactyli* from an Indian agamid lizard and *R. mabuiae* from an African skink, also possess blunt hooks but this fact is unaccountably not mentioned in early descriptions. The various species are distinguished by differences in body-length, or number of abdominal annuli and/or host and geographical distribution. Certain of the morphological characters overlap and some authors have considered the complex a single species. We have examined preserved material from a variety of sources, including type specimens, and by using comparative hook data and a standardized annulus counting procedure we show that at least three of the earlier described species are valid. A new species, *R. frenatus*, is described. An attempt is made to correct the various errors in identification that have crept into the more recent literature.

Introduction

Pentastomids of the genus *Raillietiella* with bluntly rounded tips to the posterior hooks and infecting small lizards form a natural grouping (Self, 1969). Three species have been formally described from south-east Asia and Indonesia: the first *R. gehyrae* (Bovien, 1927) from a Javan house gecko *Gehyra*

mutilata, differs from *R. hemidactyli* (Hett, 1934) from a Burmese gecko *Hemidactylus gleadovi* and an agamid lizard *Calotes versicolor*, principally in the number of abdominal annuli (Table I). The remaining species, *R. maculatus* from geckos and a skink in India, described by Rao & Hiregaudar (1959), is similar to *R. hemidactyli* but both sexes are comparatively small (Table I). Hett (1934) sought to erect a subgenus to accommodate all the species of *Raillietiella* possessing spindle-shaped bodies and large, but not necessarily blunt, posterior hooks, but this subdivision is not generally accepted (see Self, 1969).

The taxonomy of the above species appears straightforward but there are two more which possibly should be included in this group: these are *R. mabuiae* Heymons, 1922 and *R. geckonis* Dujardin, 1845.

Heymons (1922) described *R. mabuiae* from a West African skink *Mabuia sulcata*. We have examined the type specimen and the blunt posterior hook is plainly visible and yet, for some obscure reason, this is not mentioned in the type description nor in any of Heymon's subsequent reviews (Heymons, 1935; Heymons & Vitzthum, 1935). There are uncertainties regarding *R. geckonis*, first discovered by Dujardin (1845) in a Siamese gecko – possibly *Gecko verticillatus* according to Hett (1934). The type material is lost and this type description contains no specific mention of hook morphology. Hett (1924) found what she understandably claimed to be the same species in the same host in India (and also in another gecko

Hemidactylus flavoviridis) but nothing was added to its taxonomic status. Heymons (1939) later described the same species from an agamid lizard *Calotes versicolor* collected in Andhui, India. Our re-examination of this latter material has again revealed blunt posterior hooks, a feature which unaccountably elicited no comment from Heymons.

In short, there are four or five possible species, all relatively small (< 25 mm), all parasitizing small lizards and all separated by differences in body-length or number of abdominal annuli and/or host and geographical distribution. It should be noted however, that certain of these distinguishing characteristics (summarized in Table I) show varying degrees of overlap and, as Self (1969) has commented, there is some justification for considering them a single species.

Thus far, the story seems simple enough, but a number of more recent publications concerning the aforementioned 'species' have tended to obscure the picture (the salient points are summarized in Table II). For example, Dollfus & Canet (1954) described *R. hemidactyli* from Vietnamese geckos but their species has fewer annuli (according to their diagram p. 25) and the males are much smaller. *R. hebitihamata* (Self & Kuntz, 1960), another species from

small lizards taken on Lan Yü Island, Taiwan, was subsequently synonymized with *R. hemidactyli* (Self & Diaz, 1961). This species was also reported from *Hemidactylus mabuiae* in Puerto Rico (Self & Diaz, 1961) and in Africa (Fain, 1964).

The discovery of nymphal *Raillietiella*, tentatively identified as *R. hemidactyli*, in cockroaches in Singapore led to a study of the life-cycle (Rajamanickam & Lavoipierre, 1965; Lavoipierre & Lavoipierre, 1966; Lavoipierre & Rajamanickam, 1973). Three species of house gecko, *Hemidactylus frenatus*, *Cosymbotus platyurus* and *Gehyra mutilata* were found to be common definitive hosts. A recent ecological survey of *R. hemidactyli* in common house geckos in Sarawak has also implicated these hosts in the natural life-cycle and *Gecko monarchus* was added to the host list (Lim & Yong, 1977). Any comparison of the 'species' in Tables I and II reveals a number of inconsistencies, particularly in terms of overlapping diagnostic characters and hosts. Self (1969) could not establish consistent differences between specimens from India, Africa and Puerto Rico and considered all the blunt-hooked species as *R. gehyrae*, a theme later endorsed by Pence & Canaris (1973) in their comprehensive redescription of *R. gehyrae* from *Mabuya homalocephala* in Kenya (Table II).

Table I

Summary of morphological characteristics of blunt posterior hook *Raillietiella* based on type descriptions

<i>Raillietiella</i> sp.	Host	Locality	Female		Male		Author
			Body length (mm)	Number of body annuli	Body length (mm)	Number of body annuli	
<i>R. geckonis</i>	Siamese gecko?	Thailand	16-18	-	-	-	Dujardin, 1845* (After Shiple, 1898)
	<i>Calotes versicolor</i>	India	25	26-27	5	-	Heymons, 1939 (Redescription)
<i>R. mabuiae</i>	<i>Mabuya sulcata</i>	S.W. Africa	9-10	28	-	-	Heymons, 1922*
<i>R. gehyrae</i>	<i>Gehyra mutilata</i>	Java, Indonesia	13.5	21 or 22	-	-	Bovien, 1927
<i>R. hemidactyli</i>	<i>Calotes versicolor</i>	Burma	13-17	28-30	12-13	28-30	Hett, 1934
	<i>Hemidactylus gleadovi</i>						
<i>R. maculatus</i>	<i>H. maculatus</i>	India	7-12	about 30	2-3.5	about 30	Rao & Hiregaudar, 1959
	<i>H. lescheunaulte</i>						
	<i>Mabuya carinata</i>						

* The original descriptions do not mention the blunt posterior hook.

Table II

The morphological characteristics of blunt posterior hook *Raillietiella* (from various sources)

<i>Raillietiella</i> sp.	Host	Locality	Female		Male		Source
			Body length (mm)	Number of body annuli	Body length (mm)	Number of body annuli	
<i>R. hemidactyli</i>	<i>Hemidactylus frenatus</i> <i>Gehyra mutilata</i>	Vietnam	16.5	25*	3.0	24*	Dollfus & Canet, 1954
<i>R. hemidactyli</i> (= <i>R. hebiti-</i> <i>hamata</i>)	<i>H. frenatus</i> <i>Japalura swinhonis</i> <i>Mabuya longicaudata</i> <i>Gecko monarchus</i>	Lan Yü, Taiwan	13.0	29	3	29	Self & Kuntz, 1960
<i>R. hemidactyli</i>	<i>H. mabouia</i>	Congo	3.8–11	–	2.1–8.5	–	Fain, 1964
<i>R. hemidactyli</i>	<i>Calotes versicolor</i>	Thailand	10–16	25–27	3.5	–	Wingstrand, 1972
<i>R. gehyrae</i>	<i>Mabuya homalocephala</i>	Kenya	15–21 (17.8)	28–32 (30)	5.2–6.85	–	Pence & Canaris, 1973
<i>R. gehyrae</i>	<i>Calotes versicolor</i> <i>Gecko</i> sp. <i>Mabuya carinata</i>	India	18–23	23–33 (27)	4–6.5	24–25 (24)	Ramachandran, 1977

* Very approximate (counted from diagrams (Dollfus & Canet, 1954: Figs. 1 and 2)).

However, Ramachandran (1977) has reported differences in the accessory copulatory structures of male '*R. gehyrae*' derived from *Calotes versicolor*, *Mabuya carinata* and *Gecko* spp. collected in India and suggested that the synonymity proposed by Self (1969) warranted further critical study. Accordingly we have examined a number of blunt-hooked *Raillietiella* from various sources and we have used body-length, annulus number and, importantly, hook dimensions to rationalize the taxonomy of the assemblage. A new species is described.

Materials and methods

Sources: (i) The collection of Dr J.T. Self comprising mainly *R. frenatus* n. sp. from small lizards (mostly geckos) taken in the Philippine Islands, Kuala Lumpur (Malaysia) and Lan Yü Island (Taiwan) – all are preserved in 70% alcohol or on slides and are now deposited in the American Museum of Natural History (abbreviated, AMNH below).

(ii) *R. frenatus* n. sp. from freshly killed *Hemidactylus frenatus* imported from Kuching, Sarawak (Malaysia). These constitute a type series, deposited

in the British Museum (Natural History) (abbreviated BM(NH) below). The body-length of these specimens was measured after fixation in 70% alcohol.

(iii) *R. hemidactyli* Hett (1934) type specimen (slide mounted) from *Calotes versicolor* BM(NH) Reg. No. 1934.5. 18.11. Six mature females from *Calotes versicolor* from Madras, India, BM(NH) Reg. No. 1980.6.19. 20–24. One female and one male from *Calotes versicolor* from West Pakistan, BM(NH) Reg. No. 1980.6.30.1.2.

(iv) *R. geckonis* Dujardin (1845). Heymon's (1939) specimens from *Calotes versicolor* BM(NH) 1939.3.14.15–21.

(v) *R. mabouiae* Heymon's (1922) type specimen from *Mabuya sulcata*. Zoologisches Museum, Berlin (abbreviated ZMB) Reg. No. 17167.

(vi) *R. gehyrae* from *Gehyra mutilata* from Bandung, Java, Indonesia, BM(NH) Reg. No. 1980.6.19.14–16 and 1980.6.19.17–19.

Counting Abdominal Annuli: Counting the annuli is virtually impossible in slide mounted specimens and it is often difficult in alcohol-preserved specimens unless fixation is good. Annuli appear as elevated and discrete folds in the cuticle which form distinct

tyres around the abdomen (Figs. 1, 2, 3 and 4).

In the female, one annulus, which is usually indistinct on the ventral surface, lies immediately in front of the transverse slit marking the genital aperture which is situated on, or just in front of, the second annulus (Figs. 1A, 2A and 3). The last annulus can be visualized immediately in front of the bifid terminal segment (Figs. 1, 2, 3 and 4).

The genital aperture of the male is usually positioned between the second and third annuli but close to the second annulus (Fig. 2B).

Hook measurements: Hooks removed from one side of selected specimens using fine needles were trimmed of muscle and mounted directly in Hoyer's medium. A modification of Fain's (1964) convention for measuring hooks was used to alleviate difficulties in determining Fain's point C. The shank of the hook is hollow and open along the back: AB is the distance from the hook tip to a small lip or projection formed where the hollow back closes and BC is the distance from this point to the extremity of the flared base C (Fig. 5). Hooks were also measured in some whole-mounted slide specimens. Hook measurements are given in microns throughout.

Specimens used for SEM observations were either subjected to prolonged fixation in 70% alcohol, or fixed in 4.0% glutaraldehyde and washed in buffer etc., before being critical point dried.

Results

At least four species are recognized, one hitherto undescribed.

General description

Female: The body-length of mature females ranges from 12–23 mm. The body is fusiform or cigar-shaped, flattened ventrally and rounded dorsally and is widest at about one third along its length (Figs. 1A, 2, 3 and 4). The abdomen is conspicuously annulated; each annulus is a raised tyre of cuticle, often thickened and elevated into

pads at the ventro-lateral margins (Fig. 1A). Inter-annular sensory papillae, which appear as small conical elevations of the cuticle, are also present on the ventro-lateral margin (Figs. 1A, 2A and 3A, 3B). The cephalothorax is trapezoid and the mouth, which is subterminal and triangular, is flanked by two pairs of frontal papillae which carry an array of small sensillae. Dorsal papillae, situated on the dorsal cephalothorax at the level of the first hook pair, are prominent knob-like structures which project posteriorly (Fig. 1B). The anterior hook pair are sharp tipped and contrast markedly with posterior hook pair which are approximately two and a half times larger with bluntly rounded tips (Figs. 1A and 2A). Hooks are surrounded by fleshy, so-called, parapodial lobes; a lateral pair, furnished with many knob-like sensory papillae (Fig. 1B), flank the hook which is often retracted into the median lobe which acts as a sort of hook guard (Fig. 1B). The ventral slit of the genital pore is associated with the second abdominal annulus, though in some specimens it lies between annuli 2 and 3 (Figs. 1A and 2A). The anus opens on the terminal segment between a pair of divergent conical lobes (Fig. 1C).

Males: Males are invariably much smaller than females having a maximum length of 6.5 mm but are broadly similar in shape. However, the abdomen is more strongly tapered towards the caudal extremity (Fig. 2B). The genital opening is usually associated with the second abdominal annulus.

The posterior hooks of the male are less blunt than those of the female (Fig. 2C) and they are twice as big as the sharp-tipped anterior pair.

The species

(i) *Raillietiella mabuiiae* (Heymons, 1922)

Host: *Mabuya sulcata*

Locality: South West Africa

Female: Type specimen (ZMB 17167)

This specimen, already described by Heymons (1922, 1935) and Heymons & Vitzthum (1935) is 8 mm long and has 30 annuli (not 28). The specimen is an immature female and the swollen terminal lobes, previously thought to be an important diagnostic criterion, appear to be a fixation artefact.

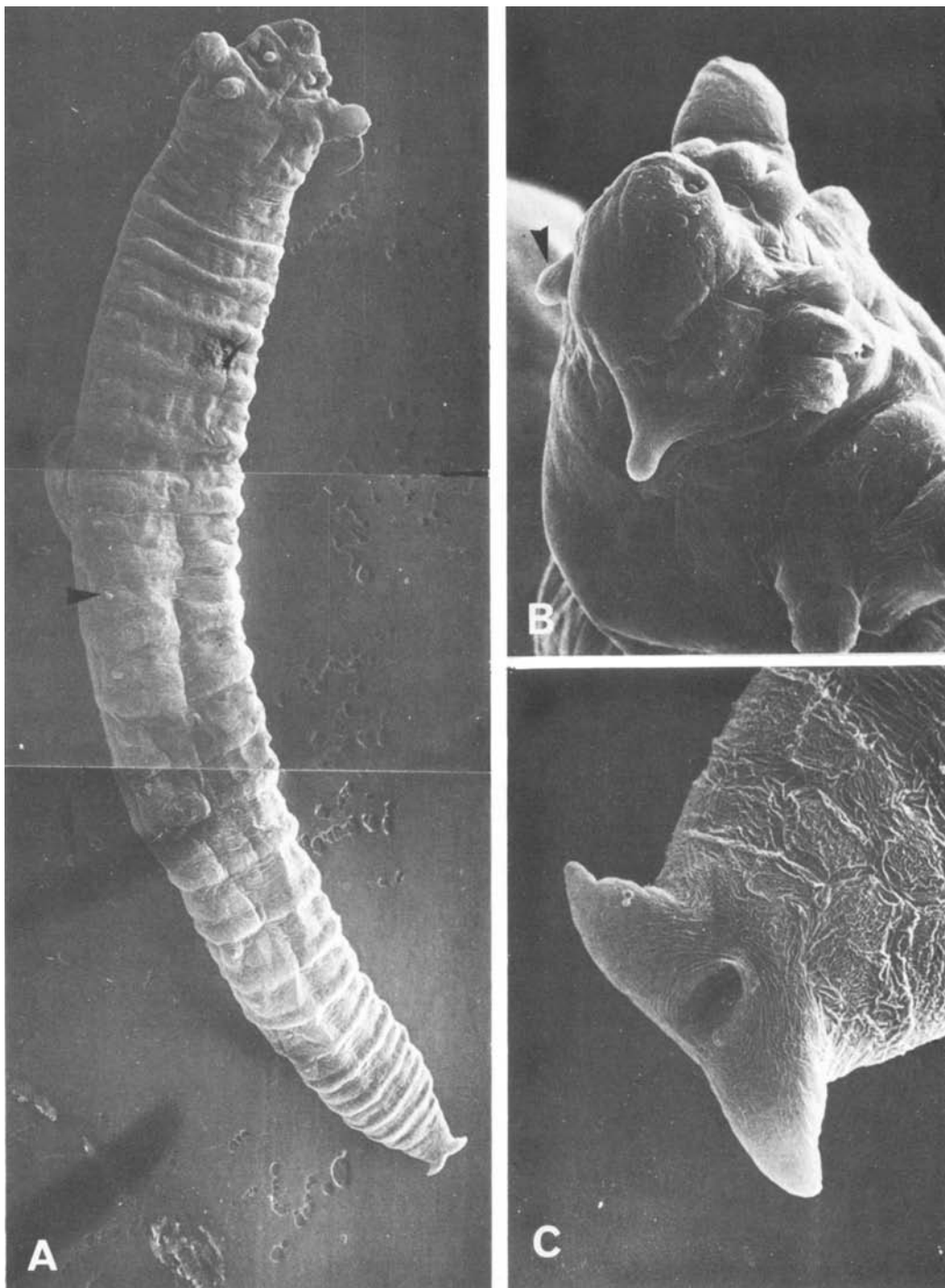


Fig. 1. *Raillietiella frenatus* n.sp.

1A. A stereoscan of an entire female from the ventral aspect showing the cigar-shaped body. The abdominal annuli are clearly shown and a series of lateral papillae, situated between the abdominal annuli, are visible down the left hand side (arrow). The genital pore is just visible as a slit-like aperture. $\times 18.5$.

1B. Detail of the head of a female from an anterior/lateral aspect showing the terminal mouth, at the apex of a small conical snout. The mouth is flanked by two minute pairs of frontal papillae. The large peg-like dorsal papillae are clearly visible (arrow) at the level of the first hook pair. The latter are covered by a fleshy median lobe surrounded by a pair of parapodial lobes which are studded with an array of small lumps; these probably represent sensory papillae. A single large median lobe covering a blunt hook is visible (top). $\times 75$.

1C. A view of the caudal region showing the anus opening between the divergent terminal lobes. $\times 140$.

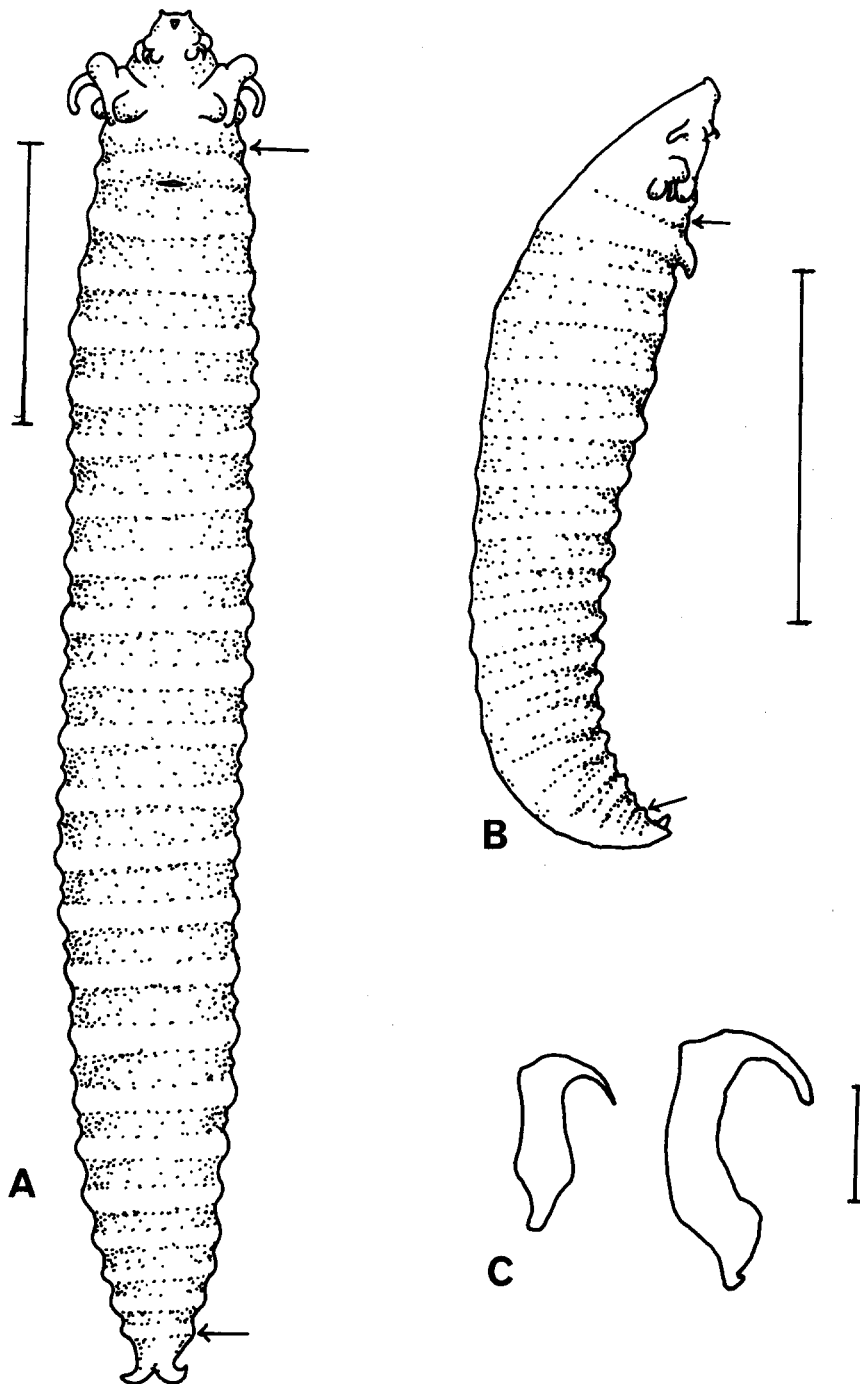


Fig. 2A. Ventral view of a holotype female BM(NH) 1980.6.19.1 of *Raillietiella frenatus* n.sp. The arrows indicate annuli 1 and 24 and the genital pore is associated with the second annulus. The median and parapodial lobes of both hook pairs are shown. Lateral papillae are small bumps between the abdominal annuli. (Scale bar = 2 mm).

2B. A lateral view of a paratype male BM(NH) 1980.6.19.8-12. Arrows indicate annuli 1 and 19. The genital pore, opening at the end of a posteriorly reflected projection, is associated with the second annulus (scale bar = 2 mm).

2C. The anterior and posterior hooks of the male drawn to the same scale. The posterior hook is more slender and less bluntly rounded than that of the female (Fig. 9). (Scale bar = 100 μ m).

The cuticle on the ventral surface bulges between annuli and there may be lateral abdominal papillae present. A smaller, poorly preserved male specimen measures about 3 mm in length.

We have examined specimens taken from *Mabuya homalocephala* in Kenya – described as *R. gehyrae* by Pence & Canaris (1973) – which appear close to *R. mabuiae*. The specimens (donated by Canaris) comprise two females, 17 and 18 mm long with 30 and 31 annuli respectively (hooks from the 17 mm specimen measure: anterior hook AB 127 BC 250, posterior hook AB 314 BC 446) and four males, 6–6.5 mm long with 21–23 annuli (the annuli of males were considered uncountable by Pence & Canaris). One male dissected: anterior hook AB 88 BC 176, posterior hooks AB 147 BC 255.

(ii) *Raillietiella gehyrae* (Bovien, 1927) (Figs. 4 and 9).

Host: Gehyra mutilata

Locality: Bandung, Java, Indonesia

Females: (N = 5) BM(NH) 1980.6.19.14–16 and 1980.6.19.17–19.

Our specimens correspond in every detail with Bovien's (1927) perfunctory type description and we have no doubt that we are describing the same species. The five female specimens are mature and measure 8 to 9.5 mm in length and 2 mm maximum width, with 21–22 annuli. The species is very distinctive because the cephalothorax is small compared to the wide, barrel-shaped abdomen and this, together with the attenuated terminal segment, gives the worm a pronounced fusiform shape (Fig. 4A). Hooks, dissected from four females are much smaller than those of related species (Fig. 5). Their dimensions are: anterior hooks AB 109, 98, 113, 113, BC 150, 176, 200, 190; posterior hooks AB 145, 167, 188, 198, BC 213, 235, 287, 296 respectively.

The ventral surface is flattened in contrast to the rounded dorsal surface and small lateral papillae are present between annuli.

Male: (N = 3) BM(NH) 1980.6.30.3

Slide mounted in Hoyer's medium. Length 3.5 mm, annuli too indistinct to count. Hook measurements are: anterior hook AB 69, BC 108; posterior hooks, AB 98, BC 157. Two other males, also

mounted in Hoyer's medium, measure 3.3 and 4.0 mm. Hook measurements are: anterior hooks AB 55, 63, BC 118, 110; posterior hooks AB 80, 95, BC 147, 140 respectively.

(iii) *Raillietiella hemidactyli* Hett, 1934 (Table III, Figs. 3A, 3B; 5)

Females: (N = 12), all from *Calotes versicolor* and comprising:

1. Type specimen, slide mounted female (BM (NH) 1934.5.18.11 from Burma.

2. Six specimens, all formalin-fixed *in situ*, from Madras, India – most of these specimens are contracted BM(NH) 1980.6.19.20–24.

3. Four specimens, one, 23 mm long, previously described in detail by Heymons (1939) as *R. geckonis* BM(NH) 1939.3.14.15–21.

4. A single slide-mounted specimen BM(NH) 1980.6.30.1 from West Pakistan.

The principal morphological characteristics are presented in Table III. Hooks removed from certain specimens (Fig. 5) form a tight cluster of values which are intermediate between *R. gehyrae* and *R. frenatus* n.sp.

Males: Only three males were observed intact and these measured 5 mm in length. Annuli, counted on a single specimen, totalled about 23 (Table III). A single slide-mounted specimen from Pakistan measured 6 mm in length: annulus number was counted from a photograph after the slide had been projected through an enlarger. Annuli totalled about 23. Hook measurements are summarized in Table III.

(iv) *Raillietiella frenatus* n.sp. (Table IV, Figs. 1, 2 and 5).

Diagnosis based on 27 females and 20 males (12 of these comprise the type series), recovered from *Hemidactylus frenatus* collected at Kuching, Sarawak, Malaysia. Specimens were either formalin fixed *in situ* or recovered live and fixed immediately in 70% alcohol.

Other specimens, previously described as *Raillietiella hebitiamata* (= *R. hemidactyli*) by Self & Kuntz (1960) (Table II), from small lizards (including *H. frenatus*), are also included within this

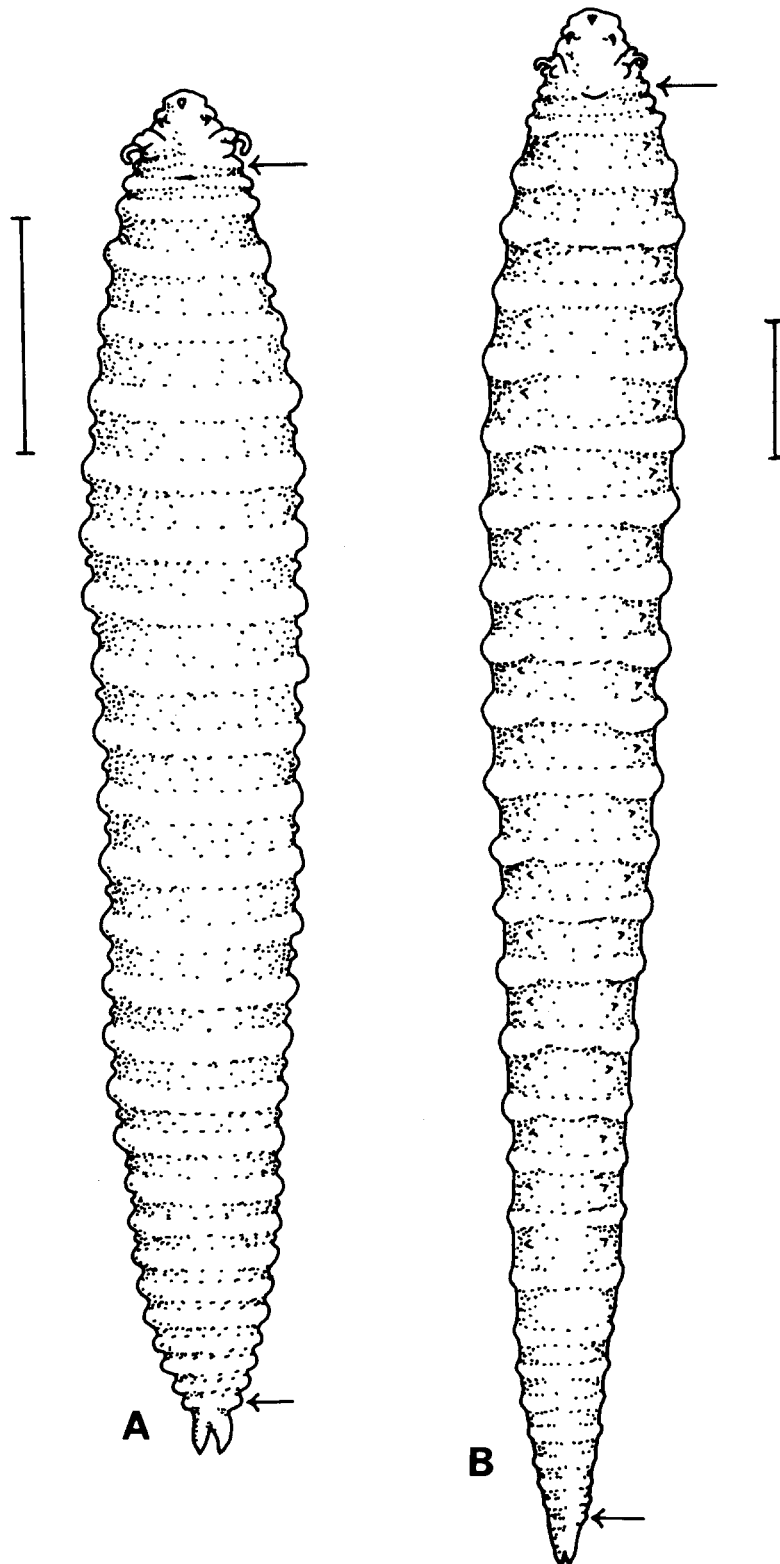


Fig. 3. Two adult females of *Raillietiella hemidactyli* (Hett, 1934, both from *Calotes versicolor*.

3A. An 11 mm specimen from Madras BM(NH) 1980.6.19.20-24, formalin fixed *in situ*. Arrows indicate annuli 1 and 27. (Scale bar = 2 mm).

3B. A 23 mm long specimen, previously identified by Heymons (1939) as *R. geckonis*. Arrows indicate annuli 1 and 29. (Scale bar = 2 mm).

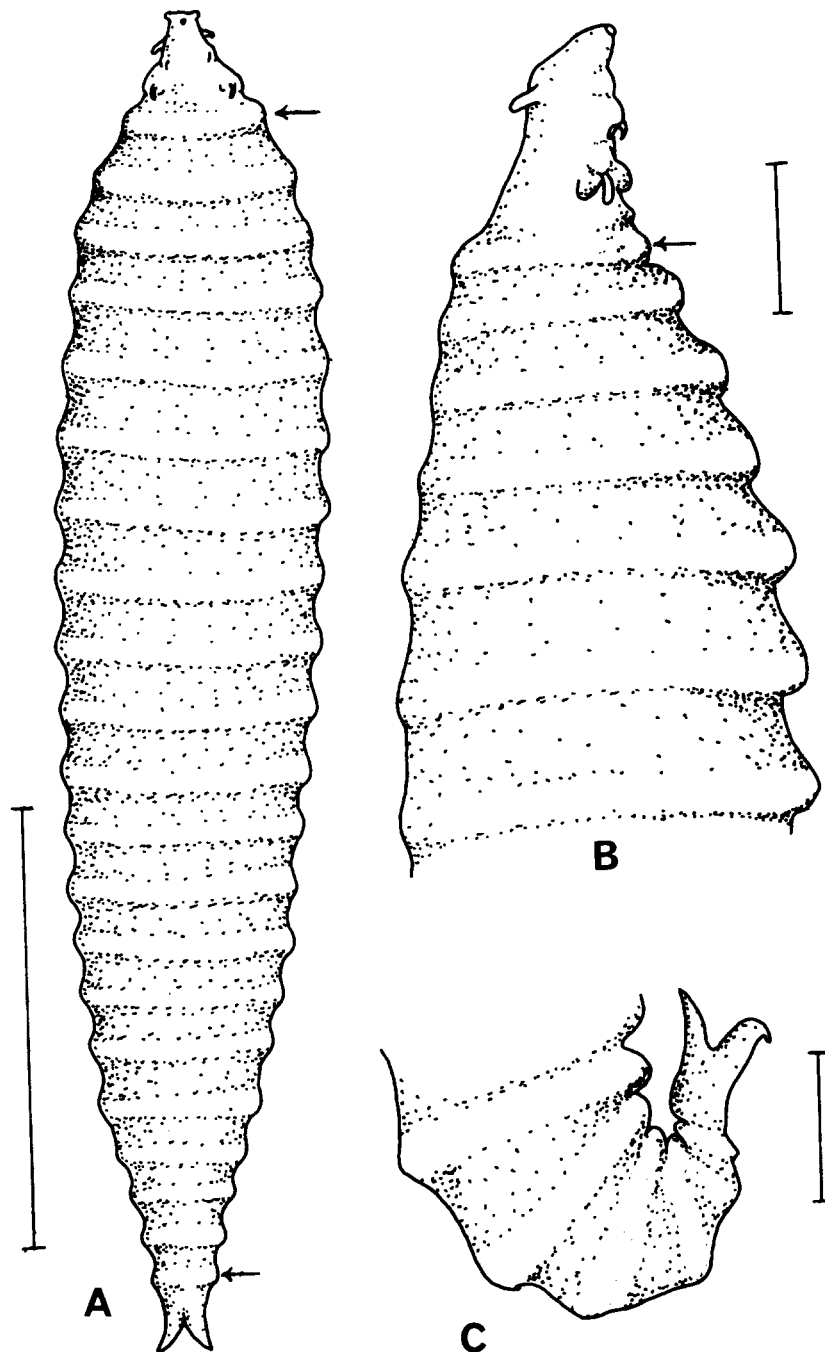


Fig. 4. An adult female of *Raillietiella gehyrae* Bovien, 1927 from *Gehyra mutilata* taken at Bandung, Java. BM(NH) 1980.6.19.14–16.
 4A. A ventral view showing the distinctive features of the species: the cephalothorax is small compared to the massive barrel-shaped abdomen. The lobes surrounding the hooks are relatively inconspicuous. Arrows indicate annuli 1 and 21. (Scale bar = 3 mm).
 4B. A lateral view of the anterior region showing the prominent, backwards-projecting dorsal papillae. The annuli are raised on the ventral surface (Scale bar = 1 mm).
 4C. Detail of the caudal extremity showing the small, bifid terminal segment. (Scale bar = 1 mm).

taxon. Their hosts, geographical distribution and morphological characteristics are summarized in Table IV.

Holotype female BM(NH) 1980.6.19.1: 12 mm long, 24 annuli (Fig. 2A).

Paratype females BM(NH) 1980.6.19.2–17: (N = 6) 9–13 mm long (\bar{x} = 10) with 24–26 annuli (\bar{x} = 25)

Paratype males BM(NH) 1980.6.19.8–12: (N = 5) 3.0–4.0 mm (\bar{x} = 3.4) long with 18 or 19 annuli (Fig. 2B).

A number of other specimens were measured. They were either slide-mounted, sectioned for electron-microscopy or mounted for scanning electron microscopy. We have retained this material and the principal morphological characteristics are:

Females: (N = 27) 5.5–14.5 mm long (\bar{x} = 11) with 23–27 annuli (\bar{x} = 24). The external features of

this species are very similar to *R. mabuiae* but there are fewer annuli.

Body flattened ventrally and rounded dorsally and distinctly cigar-shaped (Figs. 1 and 2) although some specimens are more tapered over the posterior third of the abdomen. Cephalothorax small and triangular. Mouth triangular, subterminal and flanked by two pairs of small frontal papillae which carry various small sensillae. Dorsal papillae very prominent (Fig. 1B). Genital opening on the second annulus or between annuli 2 and 3. Lobes on terminal segment strongly divergent (Figs. 1C and 2A).

Males: (N = 6) 2.0–4.5 mm long (\bar{x} = 3.8), 17–19 annuli (\bar{x} = 19) Cephalothorax similar to that of female, body markedly fusiform, strongly tapered posteriorly, terminal lobes divergent, genital pore on second annulus (Fig. 2B).

Table III

The morphological characteristics (where known) and the hook dimensions of *Raillietiella hemidactyli* from *Calotes versicolor*

Sex	Museum registration number	Locality	Body length (mm)	Number of body annuli	Hook dimensions (μm)			
					Anterior hook		Posterior hook	
					AB	BC	AB	BC
♀	BM(NH) 1934.5.18.11 Type specimen in slide form	Burma	16	28–30 ⁺	–	–	296	445
♀	BM(NH) 1939.3.14.15 1939.3.14.21	Andhui, India	7.5	28	78	147	108	186
			17 approx.	–	78	196	167	323
			17	28	–	265	265	421
			23	29	108	255	284	441
♀	BM(NH) 1980.6.19.20–24	adras, India	11*	26	118	225	225	412
			11*	26	118	206	265	421
			12*	27	98	206	265	421
			12.5*	26	98	225	294	451
♀	BM(NH) 1980.6.30.1 in the slide form	West Pakistan	22.5	30	147	225	304	470
♂	BM(NH) 1939.3.14.16–20	Andhui, India	5	–	–	–	–	–
			5	23	–	–	–	–
			fragmented	–	–	108	98	186
			fragmented	–	59	127	108	176
♂	BM(NH) 1980.6.30.2 (slide)	West Pakistan	6	23	59	147	118	206

⁺ According to Hett (1934) (annuli uncountable from the slide mounted specimen)

* Formalin fixed *in situ* and therefore contracted.

Table IV
The principal morphological characteristics of *Raillietiella frenatus* n.sp. from various localities. Mean values are given in parentheses

Sex	Host	Locality	Source and registration number	Number of specimens examined	Body length (mm)	Number of body annuli	Hook dimensions in μm					
							Anterior			Posterior		
							AB	BC	BC	AB	BC	
♀	<i>Hemidactylus frenatus</i>	Kuching, (Sarawak) Malaysia	BM(NH) 1980.6.19. 2-17 (part)	2	3.5 and 4	—	49 and 54	128	99 and 148	168 and 207		
♀				3	5-8 (6.2)*	25	108-118 (112)	188-196 (191)	316-343 (328)	425-464 (447)		
♀				7	11-12 (10.7)	23-27 (24)	68-128 (103)	176-217 (199)	264-382 (318)	343-519 (458)		
♀		Malaysia	AMNH 415	1	2	—	59	108	127	196		
♀				2	4.9 and 6.8	25 approx.	—	176	314 and 363	451 and 490		
♀		Philippine Islands	AMNH 411, 414, 416	3	2-5 (3)	20 and 22	—	93-147 (119)	70-186 (125)	140-294 (213)		
♀				1	11.5	27	127	196	343	490		
♀		Lan Yü Taiwan	Slide AMNH 423	3	12	—	118-127 (121)	206-255 (239)	353-402 (374)	509-578 (532)		
♀		Taiwan	Slide AMNH 423	1	7	—	78	137	176	294		
♀		South Vietnam	Slide AMNH 422	1	12.5	—	127	235	353	500		
♀	Gecko?	Thailand	BM(NH) 1980.6.19.13	3	11-11.5 (11.2)	23-25 (24)	108 and 127	206-225 (216)	333-392 (372)	480-549 (519)		
♀	<i>Japalura swinhonis</i>	Taiwan	Slide AMNH 421	3	5-12 (9.7)	25	78898 (85)	147-225 (193)	176-353 (285)	294-490 (421)		
♀	<i>Mabiya longicaudata</i>	Lan Yü Taiwan	AMNH 420	1	5.3	—	88	176	343	431		
♂	<i>Hemidactylus frenatus</i>	Kuching (Sarawak) Malaysia	BM(NH) 1980.6.19. 8-12 (part)	5	2.5-4.0	18-19 (19)	49-68 (55)	78-118 (105)	80-147 (106)	140-206 (165)		
♂	<i>Japalura swinhonis</i>	Taiwan	Slide AMNH 421	2	4.5 and 6	—	55 and 59	125 and 118	110 and 127	200 and 206		

* Formalin fixed *in situ* therefore contracted.

Comparison of the hooks of the four described Raillietiella species (Fig. 5):

Body size is not well correlated with hook size, probably because of inconsistencies in fixation combined with allometric growth. For example, we have found that living *R. frenatus* n.sp., removed from freshly killed geckos and fixed immediately in 70% alcohol, increase in length by an average of 50% whereas worms fixed *in situ* do not expand. Whenever possible we removed hooks only from fully gravid females – these have a distended uterus containing fully infective larvae (i.e. with well-formed hooks and penetratioapparatus) and these were assumed to be beyond the terminal moult. However, the diffuse nature of the cluster groups (Fig. 5) suggests that some immature females were also measured. Nevertheless, for reasons outlined below we consider hook data an invaluable aid in specific diagnosis.

The anterior hooks are much smaller than the posterior pair and are of little use in separating species. However, the posterior hook dimensions AB and BC plotted against each other reveal three distinct cluster groups which show considerable variation within each group but no overlap between groups. We regard the cluster group as the diagnostic criterion, rather than any of the individual data points it contains, and on this basis *R. gehyrae*, *R. hemidactyli* and *R. frenatus* n. sp. are well separated. The single data point for *R. mabuiae* is intermediate between the last two species and until more specimens are available it cannot be definitely distinguished by this technique.

Discussion

Hett (1924) pointed out that abdominal annuli are of great value inspecific diagnosis since they are more or less constant for each species but, for a variety of reasons, it is impossible to depend on this feature alone. Particularly in blunt-hooked *Raillietiella*, the first two annuli of the female are often difficult to detect, but careful observation reveals that the genital pore is normally associated with the second annulus. Despite our standardized counting

procedure there is considerable intraspecific variation which means that observations of large numbers of specimens are needed before interspecific differences are manifest. As Self & Kuntz (1957) commented, annulus number becomes a confusing specific character when the number in different species are close.

As already mentioned, body dimensions are also very variable and are considerably influenced by the method of fixation employed (Giglioli, 1927; Riley & Self, in press) and clearly, since this study utilized specimens from various sources and fixed in various ways (though mostly in 70% alcohol), body-length is not an infallible diagnostic criterion.

Esslinger (1962) used certain sclerotized structures, including the hooks, to separate the various nymphal stages of *Porocephalus crotali* and Riley & Self (1979, 1981, in press) used comparative hook data to separate closely related *Porocephalus*, *Kiri-cephalus* and *Armillifer* spp. Fain (1964) also demonstrated that hook size could separate the various instars of a blunt-hooked *Raillietiella* sp. (incorrectly called *R. hemidactyli* – see Fig. 2 and below), recovered from the African lizard *Hemidactylus mabouia*. Clearly hook size is unaffected by fixation and this character, together with annulus number (and, to a lesser extent, body size) can separate four blunt-hooked *Raillietiella* spp.

Although Bovien's (1927) original description of *R. gehyrae* was based on a single female he remarked that the cephalothorax was small compared to the abdomen and that the annuli numbered 21 or 22. Our specimens, from the same host taken on the same island, fits this description perfectly and the hooks are much smaller than those of related species (Fig. 5). The validity of *R. gehyrae* is thus confirmed and the strategy of Self (1969), Pence & Canaris (1973) and Ramachandran (1977) of grouping all the blunt-hooked species as *R. gehyrae* is clearly in error and should be abandoned.

Now to *R. mabuiae* (Heymons, 1922) from an African skink. The type specimen is immature and therefore its length (8 mm) is unimportant and its swollen terminal lobes, previously considered an important diagnostic criterion, seem to be a fixation artefact: the variability of the terminal lobes was

demonstrated by Mahon (1954) in *R. amphiboluri*. It does however possess 30 annuli and blunt posterior hooks although why this latter character went unnoticed by Heymons is strange. On the available evidence we consider the specimens described in considerable detail by Pence & Canaris (1973) – the salient features of their description are summarized in Table II – from an African skink *Mabuya homalocephala*, as *R. mabuiae*. In terms of its hook size, it is close to *R. frenatus* (meanwhile accepting that little significance can be attached to a single measurement) but differences in annulus number readily separate these species. *R. mabuiae* is close to *R. hemidactyli* in most respects but since each inhabit very different zoogeographical regions and infest lizards from different families (Agamidae and Scincidae) it is unlikely that they represent a single species. *R. mabuiae* is therefore a parasite of African lizards of the family Scincidae.

R. frenatus n. sp. is readily distinguished from *R. hemidactyli*, being smaller with fewer annuli, but

having larger hooks (Fig. 5). It appears to be the same species as that described as *R. hemidactyli* by Dollfus & Canet (1954) and Self & Kuntz (1960) (Tables II and IV). It is therefore, principally a parasite of lizards of the family Gekkonidae: *Hemidactylus frenatus*; *Gehyra mutilata*; *Gecko monachus*. According to Self & Kuntz (1960) it also occurs in the skink *Mabuya longicaudata* and the agamid lizard *Japalura swinhonis*. This remains a possibility – we have examined some of these specimens but most are unfortunately slide-mounted or very poorly preserved which renders abdominal annulus counts impossible, but their hooks are close to *R. frenatus*. *R. frenatus*, and not *R. hemidactyli*, also appears to be the subject of the life-cycle studies of Lavoipierre & Lavoipierre (1966) and Lavoipierre & Rajamanickam (1973) (see the introduction) in which case the house gecko *Cosymbotus platyurus* is yet another host. Aspects of the ecology of this species have been studied by Lim & Yong (1977).

R. hemidactyli is the source of a good deal of confusion, mainly because of the great variation in size (Table III) and there could be well more than one species in this complex. However, this must remain speculative until more specimens are available. The specimens examined here, which include the type specimen, are all from the agamid lizard *Calotes versicolor* and, from the point of view of female hook dimensions, they form a fairly homogeneous assemblage (Fig. 5). There is no justification for Heymon's claim (1939) that this species is *R. geckonis* (Dujardin, 1845). His apocryphal portrayal of the species (Heymons, 1939, p. 677) depicts a sharp posterior hook and the dorsal lobe of the parapodium, which is in fact the hook, as bluntly rounded! There is strong circumstantial evidence to suggest that at least some of the so-called *R. gehyrae* of Ramachandran (1977) (Table II), which has an unusually wide range in annulus number and a broad host spectrum, may also be *R. hemidactyli*.

Another problem with *R. hemidactyli* is that the males, as originally described by Hett (1934), are unusually large (12–13 mm), almost twice as long as other described males (Tables I and II). They also

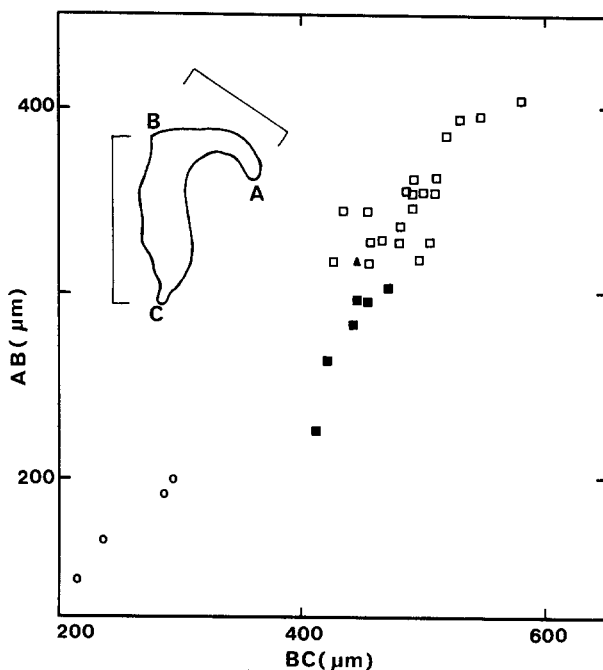


Fig. 5. A graph of the posterior hook dimensions AB and BC of *R. gehyrae* (○), *R. hemidactyli* (■), *R. frenatus* n.sp. (□) and *R. mabuiae* (?) from *Mabuya homalocephala* (▲). These data are disposed into three diffuse cluster groups which separate the first three species since there is no overlap between groups. *R. mabuiae* is not distinguished by this technique.

possess 29 annuli compared to our counts of 23 annuli (Table III). This leads us to suspect that Hett was in fact describing immature females – a mistake easily made in cephalobaenids since the genital pore is anterior in both sexes. This hypothesis is endorsed by the observations of Wingstrand (1972); he examined literally hundreds of males, from a large number of *Calotes* lizards, and these measured 3.5–4 mm in length (Table II). The wide size range of females as exemplified at one extreme by our specimens from Madras (< 12.5 mm) and Wingstrands' (1972) specimens from Thailand (10–16 mm) contrast markedly with those from India and Pakistan which measure up to 23 mm in length (Tables II and III). As mentioned above, there is the possibility of more than one species infecting a single host species, a situation not without precedent (Self & Kuntz, 1957; Riley & Self, in press).

R. maculatus Rao & Hiregauder, 1959 may be another valid species. It parasitizes a gecko and a skink, is small, and both sexes possess about 30 annuli. We have examined a few slide-mounted specimens from *Mabuya carinata* from India (thus no data are available regarding annulus number) and the hook dimensions are identical to those of *R. frenatus* n. sp. If, therefore, the annulus number (as recorded by Rao & Hiregaudar) is genuinely 30, this is likely to be a valid species.

Finally, the *R. hemidactyli* of Fain (1964) from *Hemidactylus mabouia* in Africa (Table II) is almost certainly misidentified. We have recalculated the hook dimensions given by Fain (Fain, 1964; Figs. 13–15 and Table 3) to fit our parameters AB and BC and the values are close to *R. frenatus* (Fig. 5). The species apparently occurs in the same host in Puerto Rico where it was introduced from Africa (Self & Diaz, 1961). At present, we suspect that this is another blunt-hooked species, but we shall have more to say about the New World species in a later communication.

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