Systematic Parasitology **31**: 159–188, 1995.

Representatives of *Batrachocamallanus* n. g. (Nematoda: Procamallaninae) from *Xenopus* spp. (Anura: Pipidae): geographical distribution, host range and evolutionary relationships

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Accepted for publication 19th May, 1994

Abstract

The great majority of the Procamallaninae occur in teleosts from tropical regions; however, representatives of this group are also frequent parasites of aquatic clawed toads (*Xenopus* spp.) in Africa. The taxonomic status of procamallanines from different *Xenopus* spp. and their geographical distribution is reviewed. *Batrachocamallanus* n. g. is created to include forms from amphibians with large numbers of mucrons on the female tail and relatively small body size. *B. occidentalis* n. sp. and *B. siluranae* n. sp. are described, while *Procamallanus brevis* Kung, 1948, originally recorded from an unidentified African amphibian, is considered a synonym of *B. slomei* (Southwell & Kirshner, 1937) n. comb. Due to the presence of spiral thickenings on its buccal capsule, *B. xenopodis* (Baylis, 1929) n. comb. has previously been placed in the genus *Spirocamallanus* Olsen, 1952. However, this species shares the apomorphic presence of numerous mucrons on the female tail, and almost identical cephalic morphology, male caudal structures and female reproductive system with other procamallanines from clawed toads. This suggests that they represent a monophyletic grouping. There is also only limited morphometric differentiation between *B. xenopodis* and the other proposed representatives of *Batrachocamallanus* (supported by a multivariate analysis of male and female specimens), which further indicates a close relationship between them. Great variability in the presence and type of buccal capsule thickenings occurs within *Batrachocamallanus*. Members of this genus most closely resemble the African species *Procamallanus laeviconchus* (Wedl, 1862), which exhibits a smooth buccal capsule similar to that of *B. siluranae*. Buccal capsule thickenings of the remaining *Batrachocamallanus* spp. probably arose independently from those described in other procamallanines. Such characters may be evolutionarily unstable and an unsuitable basis for generic classification in this subfamily. Although *B. siluranae* is the only *Batrachocamallanus* species to occur in *X. tropicalis*-like hosts (which represent a separate lineage from other clawed toads), its distribution, and that of its congeners, may be determined more by host-independent ecological or biogeographical factors than by an association with host phylogeny. Thus, *B siluranae* occurs in *Xenopus* spp. from tropical rain forest (including those from other host lineages) while the other forms are typically found in savanna or montane forest, and in the cases of *B. slomei* and *B. xenopodis* at least, do not show narrow host specificity to particular clawed toad taxa. Although more than one *Batrachocamallanus* spp. were found in *X. laevis*, *X. muelleri* and *X. fraseri*-like clawed toads, co-existence at the same locality never occurred, perhaps indicating a high degree of interspecific ecological segregation.

Introduction

The Procamallaninae Yeh, 1960 are a species rich group, occurring mainly in teleost fish from tropical regions (Stromberg & Crites, 1974; Petter, 1979). Only three members of this subfamily have been described from amphibians, and two of these, *Procamallanus xenopodis* Baylis, 1929 and *P. slomei* Southwell & Kirshner, 1937 were found in clawed toads (*Xenopus* spp.). *P. brevis* Kung, 1948 was described from an African anuran identified only as a "bullfrog" (possibly *Pyxicephalus adspersus*, see Baker (1987)). Despite sharing certain unique apomorphic characteristics with *P. slomei* and *P. brevis* (see Petter, 1979), *xenopodis* has previously been assigned to *Spirocamallanus* Olsen, 1952, due to the presence of internal spiral thickenings

on its buccal capsule (Olsen, 1952). Only this character separates the latter genus from *Procamallanus* Baylis, 1923 (see Olsen, 1952; Yeh, 1960; Petter, 1979), although the validity of *Spirocamallanus* is accepted by most authors at the generic or subgeneric level (Pinto *et al.*, 1974; Moravec & Sey, 1988). Ali (1960) considered procamallanine buccal capsule thickenings to be an inadequate taxonomic criterion above species level due to their great variability in form. However, classification of *Procamallanus* spp. (Ali, 1956, 1960) into subgenera based on simple differences in spicule number and length does not produce natural groupings, and some of the supposed variation in these features may be due to inaccurate descriptions.

Neither *P. brevis* nor *P. slomei* has been recorded since their original descriptions, although *xenopodis* was reported from Uganda, Kenya and Zimbabwe by Thurston (1970), and Nigeria by Avery (1971), and Tinsley *et al.* (1979) noted the presence of *Spirocamallanus* sp. in *X. wittei* from Central Africa.

The aim of this study was to review the taxonomic status, geographical distribution, host range and phylogenetic relationships of the Procamallaninae from *Xenopus* spp.

Materials and methods

General

Hosts collected in the field and imported to the UK by air freight were anaesthetised in a 1:1000 MS222 (Sandoz) solution and pithed. The alimentary tract was removed and opened by a longitudinal slit while immersed in 0.6% saline. Worms were teased from the host mucosa with dissecting needles and fixed in hot 70% ethanol. Other specimens were obtained from the dissection of toads which had been killed and preserved in the field (in some cases these hosts were obtained from museum collections). Worms were cleared and examined as temporary mounts in glycerine, either by conventional light microscopy or Nomarski differential interference microscopy. All measurements were taken with an ocular micrometer and are given in micrometres. Specimens (also fixed in 70% ethanol) to be examined by scanning electron microscopy (SEM) were dehydrated through a series of ethanols, critical point dried and sputter coated with gold.

Morphometric analysis

In order to assess the degree of morphometric differentiation between procamallanines from *Xenopus* spp., principal components analysis was carried out on the covariance matrix of log-transformed morphometric characters for male and female worms. Analyses (performed using MINITAB release 6.1.1) were based on the following variables, measured from specimens fixed in hot 70% ethanol and cleared in glycerine: body length, body width, buccal capsule length, buccal capsule width, muscular oesophagus length, glandular oesophagus length, tail length, distance of vulva from anterior of worm (in females), and right spicule length (in males).

Materials

Where locality records in the text below are followed by a number in parentheses, this relates the record to the parasite specimens on which it was based. Details of these are reported in a separate "material studied" section, identified by the corresponding number (also in parentheses). The symbols F and P indicate whether worms collected as part of this study were fixed in hot 70% ethanol or dissected from preserved hosts, respectively. Some parasites were obtained, during this study, from collections of preserved *Xenopus* spp. kept at the University of Antwerp (by permission of Professor J.L.J. Hulselmans), the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (by permission of Dr W. Bohme), or from the Musée Royal de l'Afrique Centrale, Tervuren, Belgium (by permission of Dr D. Mierte); the collection numbers of these hosts are preceded by the abbreviations RUCA, ZFMK, and MRAC, respectively. Parasite collections from the latter museum are identified in the same way, while those from The Natural History Museum are denoted by the letters BM; all parasite specimens borrowed from the Musée Royal de l'Afrique Centrale were collected from preserved museum hosts by Dr F.A. Puylaert. Material studied here which was originally from the helminthological collections of the Liverpool School of Tropical Medicine and the London School of Hygiene and Tropical Medicine is now curated by the International Institute of Parasitology (IIP), St Albans.

Host identification

Xenopus spp. closely related to *X. fraseri* Boulenger are distinguished by characters including chromosome number and mating call and are often difficult to identify by morphological criteria alone (Frost, 1985). This is true of *X. pygmaeus* Loumont, *X. amieti* Kobel, du Pasquier, Fischberg & Gloor, *X andrei* Loumont, *X. boumbaensis* Loumont and *X. ruwen-*

zoriensis Tymowska & Fischberg. In cases where the identity of these *X. fraseri*-like toads is uncertain, they are referred to as *X. fraseri* aff. *X. tropicalis*-like toads (which also include cryptic, polyploid species) are referred to *X. tropicalis* (Gray) from localities to the west of Cameroon, *X. epitropicalis* Fischberg, Colombelli & Picard (a polyploid) at sites to the east of this (see Loumont, 1984) and *X. tropicalis* aff. for specimens from Cameroon from which chromosome number was not determined. Polyploid *X. tropicalis*-like specimens from Nigeria (possibly of a cryptic, undescribed species) are also identified as *X. tropicalis* aff. Toads morphologically similar to *X. wittei* Tinsley, Kobel & Fischberg are referred to as *X. wittei* aff., unless they were actually from the localities indicated by Tinsley *et al.* (1979) in the species description.

***Batrachocamallanus* n. g.**

Type-species: *B. xenopodis* (Baylis, 1929) n. comb.
Other species: *B. slomei* (Southwell & Kirshner, 1937) n. comb., *B. occidentalis* n. sp., *B. siluranae* n. sp.

Generic diagnosis
Camallanidae Railliet & Henry, 1915, Procamallaninae Yeh, 1960. Very small worms. Internal walls of buccal capsule smooth or with spiral, transverse or longitudinal thickenings. Female tail bearing numerous mucrons (5 or more). Parasitic in African amphibians.

Non-diagnostic generic characters
(Based on all known representatives of genus.) Mouth circular, delimited by thin membrane into which extend 6 labial papillae (2 lateral, 4 submedian). Four submedian cephalic papillae. Amphids lateral. Buccal capsule barrel-shaped to globose. Anterior margin of capsule with 6 equally spaced notches (2 lateral, 4 submedian). Posterior aperture of buccal capsule triangular in aspect. Three distinct processes projecting into buccal cavity from thickened rim at capsule base. Nerve-ring within anterior third of muscular oesophagus. Excretory pore approximately level with nerve ring or posterior to this (level with middle third of muscular oesophagus). Ovary approximately level with glandular oesophagus in females. Oviduct communicating with main body of uterus via short, dilate, seminal receptacle-like region. Uterus tubular, containing developing embryos and larvae in mature worms, extending into posterior quarter of body before becoming constricted into short, blind-ending tubule. Vulva approximately equatorial (usually slightly post-equatorial). Vagina with very short, thick-walled distal portion and very long, muscular, posteriorly-directed proximal portion, meeting uterus just anterior to constriction. Tail short. Males smaller and thinner than females. Tubular testis thin, sinuous, at level of oesophagus and just posterior to this. Caudal region of worm ventrally coiled, bearing well-developed alae. Pre-cloacal papillae 8–11, large, lateral, extending into each caudal ala, sometimes differing in number on left and right; posterior-most pair just anterior to, or level with cloaca. Right spicule longer and better developed than left; both with simple points. Three pairs of small, ventral papillae, one just anterior to, and 2 flanking cloacal opening. Tail short, blunt-ending. Six pairs of post-cloacal papillae occurring near end of tail: anterior 3 subventral, pedunculate; middle pair of group not reaching to edge of alae; 2 pairs lateral, anterior-most very large; one pair subterminal, tiny. Phasmids just ventral to largest pair of lateral post-cloacal papillae.

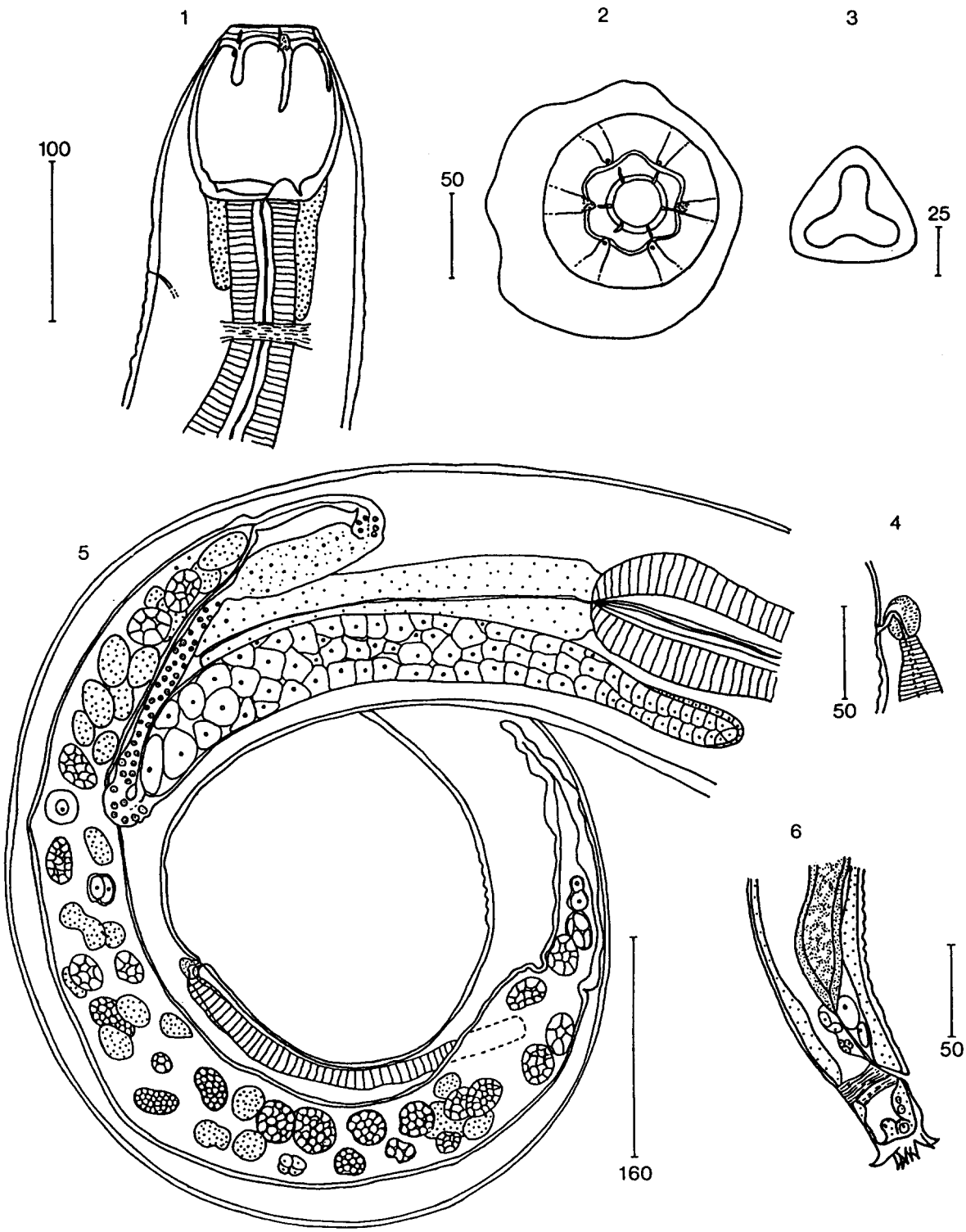
Remarks

Representatives of this group differ from other procamallanines in the large number of mucrons on the female tail (adults of other genera never exhibit more than three mucrons). They also have a comparatively very small maximum body size. All currently known procamallanines from amphibians may be referred to *Batrachocamallanus*.

***Batrachocamallanus slomei* (Southwell & Kirshner 1937) n. comb.** (Figs 1–11)

Syns: *Procamallanus slomei* Southwell & Kirshner, 1937; *P. brevis* Kung, 1948.

Type-host and locality: *Xenopus laevis* (Daudin) from Cape, South Africa (see Southwell & Kirshner, (1937)) (1); locality suggests host subspecies is *X. l. laevis* (Daudin) (see Loumont, 1984).
Previously published host and locality records: From a "bullfrog" in South Africa (Kung (1948), as *Procamallanus brevis*) (2). From *Xenopus* sp.: Nairobi, Kenya (Thurston (1970), reported as *Spirocamallanus xenopodis*) (3).
Other hosts and localities: *X. l. laevis*: South Africa (4); Umtata, Transkei (5); Mukuvisi river, Cranborne, Harare, Zimbabwe (6). *X. l. poweri* Hewitt (new host



Figs 1–6. Female *Batrachocamallanus slomei* (Southwell & Kirshner, 1937) n. comb. from *Xenopus laevis poweri* in Zaire. 1. Anterior, lateral view. 2. Anterior, apical view. 3. Transverse section through base of buccal capsule. 4. Terminal region of reproductive tract. 5. Reproductive system. 6. Tail.

record): River Lufwa (tributary of River Lufira), Lusinga, Zaire (7); Mukana marsh, near Lusinga, Zaire (8).
Site: Stomach.

Material studied
Procamallanus slomei paratypes, IIP, no. 25 (originally deposited in helminthological collection of Liverpool School of Tropical Medicine) (1); *P. brevis* "cotypes", IIP, no. 221 (originally deposited in helminthological collection of London School of Hygiene and Tropical Medicine) (2); 2 specimens, BM 1968.46, (3); 24 specimens, BM 1975.892, (4); 3 specimens, F, hosts coll. P. Denny, August 1988 (5); 40 specimens, F, coll. V. Clarke, during 1989 (6); 13 specimens, P, from hosts MRAC B64690-64699, (7); 8 specimens, P, from hosts MRAC B64451-64460, (8).

Description

General. With characters of genus. Buccal capsule showing smooth internal surfaces; marked thickening of capsule associated with anterior rim and extending posteriorly, in 6 longitudinal ridges (2 lateral, 4 submedian), approximately 20–50% of capsule length.

Females. Data on morphometric and meristic variation are given in Table I.

Deirids about level with nerve-ring or just posterior to this (level with middle third of muscular oesophagus). Vulva never marked by prominence of body wall. Tail terminating in crown of 6–12 mucrons.

Males. Data on morphometric and meristic variation not given in text are provided in Table II.

Deirids posterior to nerve-ring, level with middle third of muscular oesophagus. Nine or 10 precloacal papillae extending into each caudal ala. Left spicule approximately 40–50 long.

Remarks

Southwell & Kirshner (1937) who described *B. slomei* (as *Procamallanus slomei*) reported slightly greater body lengths than found in the present material (1,800–2,000 in males and 2,500–2,900 in females) (see Tables I and II). However, paratypes of *B. slomei* correspond to specimens from this study in all other characters (personal observation), and such size differences may be explained by ontogenetic or environmentally induced variation. Kung (1948) differentiated *Procamallanus brevis* from *B. slomei* by the presence of ventral adcloacal papillae, a differing number of postcloacal papillae and a more posterior vulva. Kung also noted the presence of a left spicule in his specimens and considered that this structure may have been overlooked in *B. slomei*. The occurrence of a poorly developed left spicule in *B. slomei* has been confirmed in the present study (see above), as has the presence of three adcloacal papillae, which were distributed as described by Kung for *P. brevis*. Comparison of *P. brevis* "cotypes" with *B. slomei* paratypes and material of the latter species from this study suggested that there were no significant differences in position of the vulva or arrangement of postcloacal caudal papillae. Although Kung (1948) reported only five to seven mucrons on the tail of female *P brevis*, the female "cotypes" examined as part of this study showed between six and 10 (n = 3), which is consistent with the range exhibited by *B. slomei*. *P. brevis* shows no morphological differences in these, or any other, characters to *B. slomei* and is therefore considered a synonym of this species.

Thurston (1970) reported *Spirocamallanus xenopodis* from *Xenopus* sp. at Nairobi, Kenya. However, an examination of two of the specimens upon which the record was based revealed their true identity as *B. slomei*.

***Batrachocamallanus siluranae* n. sp.** (Figs 12–22, 49–51, 53)

Type-host and locality: *X. tropicalis* (Gray) from Aburi, Ghana.
Other hosts and localities: *X tropicalis*: Bo, Sierra Leone (1); Njala, Sierra Leone (2); Sahibly, River Cavally, Ivory Coast (3); Bonna, Ivory coast (4); Ebeva, Togo (5); Misahohe, Togo (6); Nigeria (exact locality unknown) (7). *X tropicalis* aff.: Nigeria (*X. tropicalis*-like species with 2n = 40 chromosomes) (exact locality unknown) (8); Korup National Park, Cameroon (9). *X epitropicalis* Fischberg, Colombelli & Picard: Mabuba, Tshela, Zaire (10). *X pygmaeus* Loumont: Kisangani, Zaire (11); Zaire (exact locality unknown) (12). *X fraseri* Boulenger aff.: Boteka, Zaire (13); Mabuba, Tshela, Zaire (14); Lula, Kasai Province, Zaire (15); Boende, River Tshuapa, Zaire (16); Mieri, River Doume, Cameroon (17); Olonou, Cameroon (18); Kombetiko, Nguesse river, Cameroon (19).

Table I. Morphometric variation in female *Batrachocamallanus slomei* (Southwell& Kirshner, 1937) n. comb.

Host:	"Bullfrog"	*X. l. laevis**	*X. l. laevis*	*X. l. laevis*	*X. l. poweri*	*X. l. poweri*	*Xenopus* sp.**	
Locality:	South Africa (*P. brevis* "cotypes")	South Africa	Umtata, Transkei	Mukuvisi River, Zimbabwe	Lusinga, Zaire	Mukana, Zaire	Nairobi, Kenya	
			F	F	P	P		Overall range
Body length	1,930 (2)	1,810 (5)	1,540 (2)	1,670 (20)	1,320 (3)	2,080 (1)	1,690 (1)	
	1,780–2,080	1,550–2,210	1,510–1,570	1,330–2,080	1,170–1,410			1,170—2,210
Body width	142 (2)	123 (5)	130 (2)	187 (20)	142 (3)	212 (1)	161 (1)	
	117–167	100–136	102–157	139–235	131–150			100–235
Bucal capsule length	104 (2)	92 (5)	131 (2)	114 (20)	91 (3)	89 (1)	93 (1)	
	100–107	89–96	120–141	94–131	89–94			89–141
Buccal capsule width	93 (2)	86 (3)	99 (2)	103 (20)	84 (3)	89 (1)	82 (1)	
	91–95	83–89	93–106	93–124	83–87			82–124
Muscular oesophagus	198 (2)	210 (5)	197 (2)	212 (20)	214 (3)	241 (1)	208 (1)	
	176–220	187–227	189–205	176–242	206–219			176–242
Glandular oesophagus	223 (2)	263 (5)	242 (2)	223 (10)	215 (3)	293 (1)	269 (1)	
	202–243	250–280	205–280	185–304	213–219			185–304
Vulva***	54 (2)	53 (4)	63 (1)	54 (20)	51 (3)	52 (1)	60 (1)	
	54	51–57		48–61	49–53			48–63
Tail length	32 (2)	29 (4)	24 (1)	29 (20)	32 (2)	33 (1)	24 (1)	
	31–33	26–31		19–41	31–33			19–41
Mucron no.	6–10 (3)	6–8 (5)	7–8 (2)	8–10 (11)	8–12 (2)	8–10 (2)	6 (1)	6–12

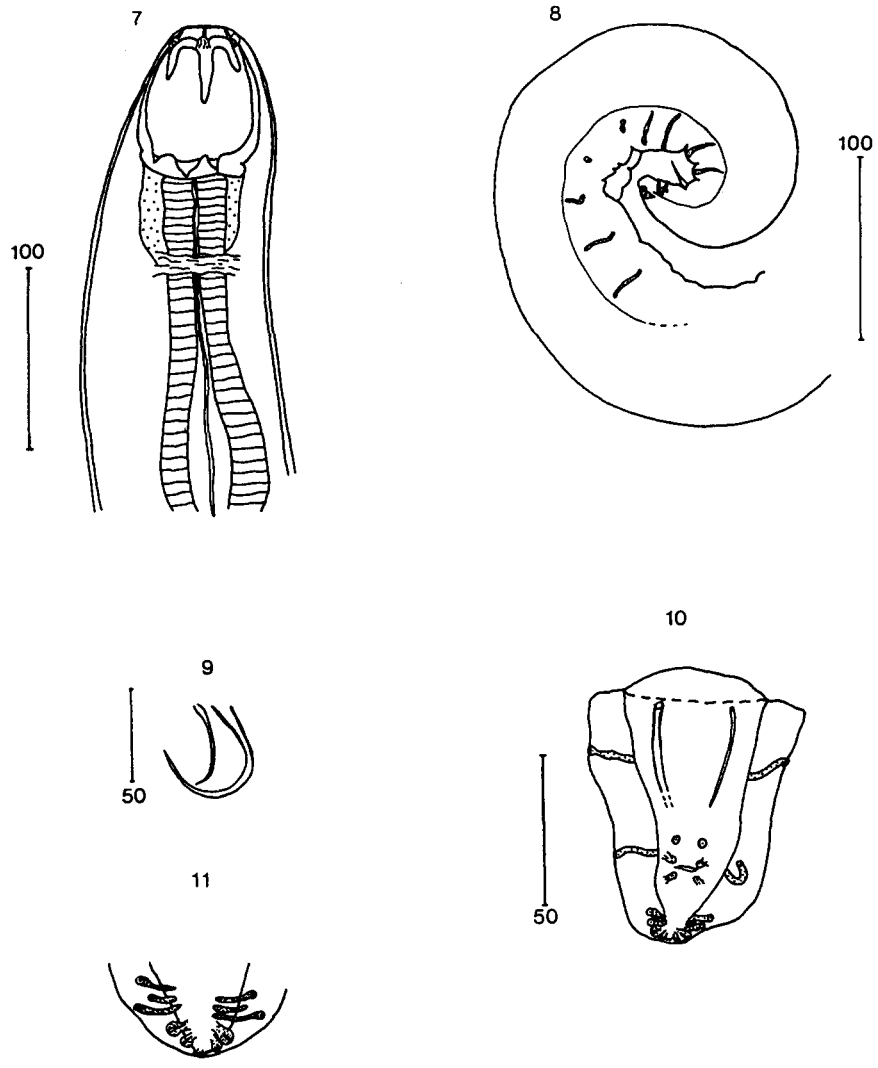
*BM 1975.892.

**BM 1968.46.

***Distance from anterior as a percentage of body length.

For material collected as part of the present study: F, fixed in hot 70% ethanol; P, dissected from preserved hosts.

Mean (with sample size in parentheses) given above range, except for mucron number for which range only is given.



Figs 7–11. Male *Batrachocamallanus slomei* (Southwell & Kirshner, 1937) n. comb. from *Xenopus laevis poweri* in Zaire. 7. Anterior, lateral view. 8. Caudal region, lateral view. 9. Spicules. 10. Caudal region, ventral view. 11. Distribution of postcloacal papillae, ventral view (schematic, not to scale).

Site: Stomach.

Material studied

Holotype (female) BM 1993.5121, allotype (male) BM 1993.5122, 12 paratypes (3 male, 9 female) BM 1993.5123-5134, and 10 non-type specimens from type-locality, F, coll. RCT, April, 1979; 13 specimens, P, hosts coll. RCT, April, 1979 (1); 4 specimens, P, hosts coll. RCT, March, 1979 (2); 5 specimens, P, from hosts MRAC B-109221-109230, (3); 3 specimens, F, hosts imported live to UK, 1989 (4); 15 specimens, P, hosts from RUCA 1371, (5); 1 specimen MRAC 34.667, 2 specimens MRAC 34.668, 1 specimen MRAC 34.669, 2 specimens MRAC 34.670, 3 specimens MRAC 34.671, (5); 12 specimens MRAC 34.666, (6); 78 specimens, F, hosts imported live to UK, February, 1986 (7); 11 specimens, F, hosts imported live to UK, February, 1986 (8); 8 specimens, P, hosts imported live to UK, 1988 (9); 6 specimens MRAC 33.668, uncounted specimens MRAC 33 670, 3 specimens MRAC 33.671, 3 specimens MRAC 33.672, (10); 44 specimens, P, hosts from RUCA S(7), (11); 4 specimens, F, hosts imported live to UK, September, 1985 (12); 14 specimens, P, from hosts MRAC 85-030-B-0023-0032, (13); 4 specimens MRAC 34.603, 6 specimens MRAC 34.604, 2 speci-

Table II. Morphometric variation in male *Batrachocamallanus slomei* (Southwell & Kirshner, 1937) n. comb.

Host:	"Bullfrog"	*X. l. laevis**	*X. l. laevis*	*X. l. poweri*	*Xenopus* sp.**	
Locality:	South Africa (*P. brevis* "cotype")	South Africa	Mukuvisi River, Zimbabwe	Lusinga, Zaire	Nairobi, Kenya	
			F	P		Overall range
Body length	1,780 (1)	1,700 (1)	1,390 (5)	1,400 (2)	1,780 (1)	
			1,090–1,920	1,370–1,420		1,090–1,920
Body width	117 (1)	102 (1)	121 (5)	111 (2)	121 (1)	
			106–136	100–121		100–136
Buccal capsule length	100 (1)	68 (1)	103 (5)	74 (2)	80 (1)	
			98–111	74		68–111
Buccal capsule width	91 (1)	59 (1)	79 (5)	67 (2)	63 (1)	
			74–85	63–70		59–91
Muscular oesophagus	144 (1)	191 (1)	192 (5)	205 (2)	199 (1)	
			141–241	190–220		141–241
Glandular oesophagus	182 (1)	242 (1)	215 (5)	216 (2)	–	
			160–270	189–242		160–270
Right spicule	80 (1)	80 (1)	82 (5)	95 (2)	74 (1)	
			63–100	94–95		63–100
Tail length	26 (1)	30 (1)	31 (5)	31 (1)	35 (1)	
			24–37			24–37
No. of pairs of precloacal papillae	10 (1)	9 (1)	9–10 (5)	9 (2)	9 (1)	9–10

*BM 1975. 892.
**BM 1968. 46.
For material collected as part of the present study: F, fixed in hot 70% ethanol; P, dissected from preserved hosts.
Mean (with sample size in parentheses) given above range, except for precloacal papilla number for which range only is given.

mens MRAC 34.605, 2 specimens MRAC 34.606, 1 specimen MRAC 34.608, 2 specimens MRAC 34.609, 1 specimen MRAC 34.612, (14); 16 specimens MRAC 33.662, uncounted specimens MRAC 33.663, 30 specimens MRAC 33.664, (15); 56 specimens, P, from hosts MRAC 75-035-B-0464-0468, (16); 9 specimens, P, from hosts MRAC 75-035-B-0850-0854, (16); 98 specimens, P, from hosts MRAC 76-014-B-0084- 0091, (17); 159 specimens, P, hosts from RUCA 1.269 and 1.279, (18); 29 specimens, P, from hosts MRAC 76-014-B-0151-0160, (19).

Description

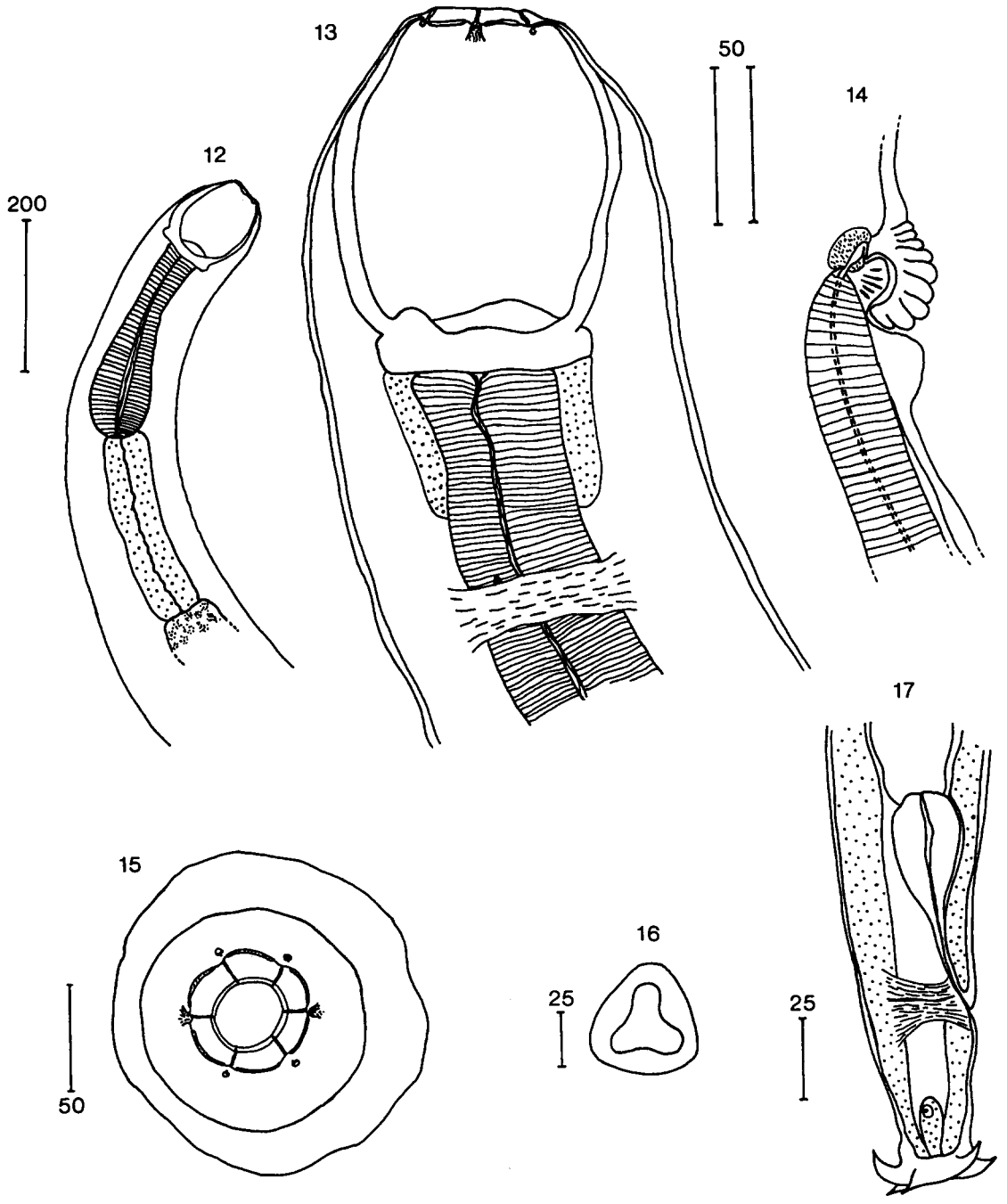
General. With characters of genus. Buccal capsule with smooth internal surfaces; capsule rim slightly thickened between notches; longitudinal thickenings absent.

Females. Measurements of holotype given in text; data on morphometric and meristic variation are provided in Table III.

Body length 3,950, width 228. Buccal capsule length 120, width 100. Muscular oesophagus 272 and glandular oesophagus 254 long. Nerve-ring 198 from anterior of worm; deirids approximately level with nerve-ring (or sometimes posterior to this and level with middle third of muscular oesophagus in paratypes and other material), 193 from anterior. Opening of vulva marked by distinct, rugose prominence of body wall, 49% of body length from anterior. Tail 56 long, terminating in crown of 5 mucrons.

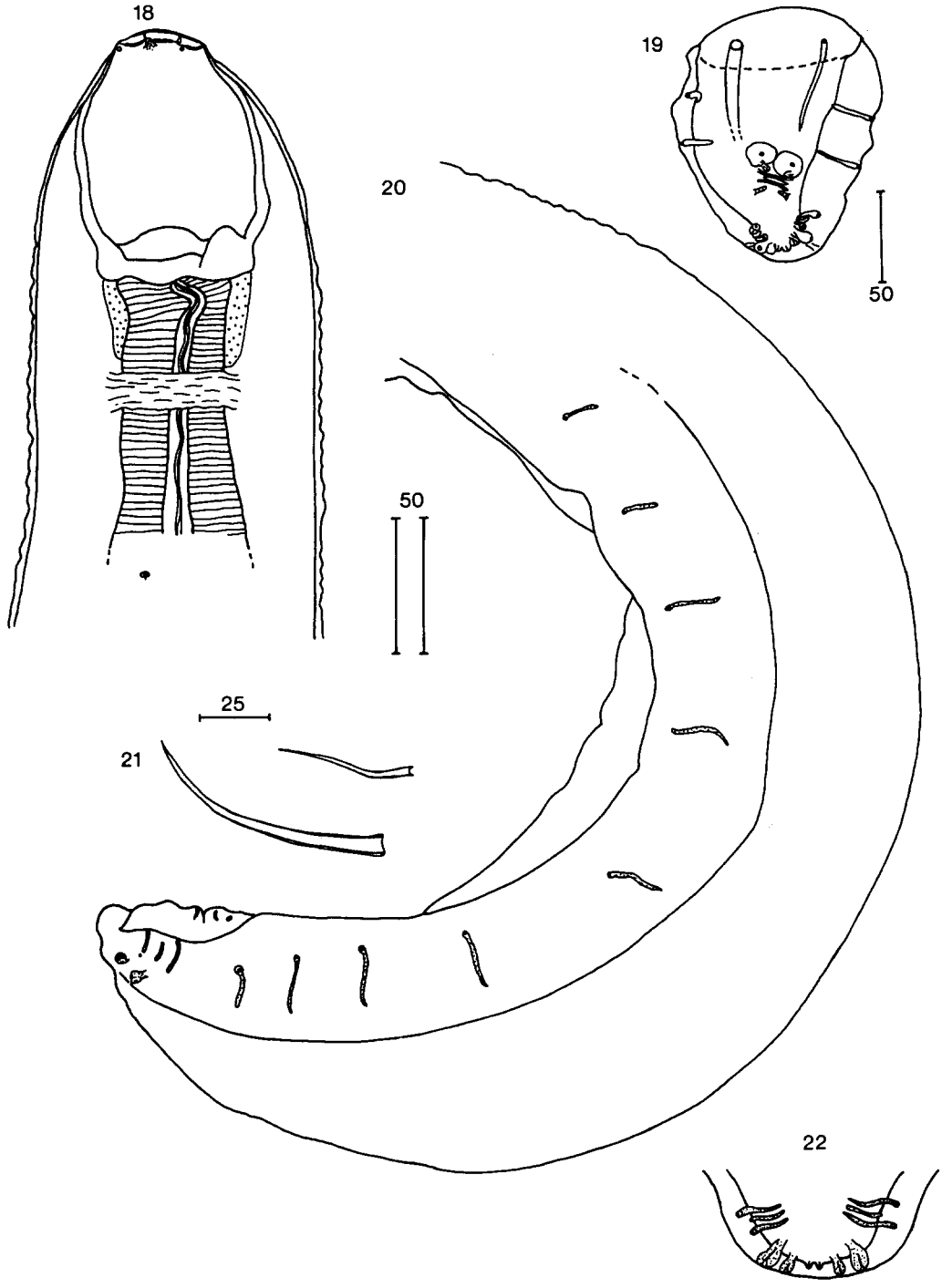
Males. Measurements of allotype given in text; data on morphometric and meristic variation not given in text are provided in Table IV

Body length 1,840, width 109. Buccal capsule length 81, width 67. Muscular oesophagus 210 and glandular oesophagus 211 long. Nerve-ring and excretory pore 120 and 163 from anterior of worm, respec-



Figs 12–17. Female *Batrachocamallanus siluranae* n. sp. from *Xenopus tropicalis* at Aburi, Ghana. 12, 13. Anterior, lateral view (holotype). 14. Terminal region of reproductive tract (holotype). 15. Anterior, apical view. 16. Transverse section through base of buccal capsule. 17. Tail (holotype).

tively. Deirids posterior to nerve-ring, level with middle third of muscular oesophagus, 193 from anterior of worm. Nine pedunculate, precloacal, papillae extending onto each caudal ala. (In paratypes and other material each ala with 9–11 precloacal papillae.) Right spicule 119 and left spicule approximately 50 long (in paratypes and other material approximately 50–80 long). Tail 35 long.



Figs 18–22. Male *Batrachocamallanus siluranae* n. sp. from *Xenopus tropicalis* at Aburi, Ghana. 18. Anterior lateral view (allotype). 19. Caudal region, ventral view. 20. Caudal region, lateral view (allotype). 21. Spicules (allotype). 22. Distribution of postcloacal papillae, ventral view (schematic, not to scale).

Table III. Morphometric variation in female *Batrachocamallanus siluranae* n. g., n. sp.

Host:	*X. tropicalis*	*X. tropicalis*	*X. tropicalis* aff.	*X. pygmaeus*	*X. fraseri* aff.	
Locality:	Aburi, Ghana	Nigeria	Korup, Cameroon	Zaire	Olonou, Cameroon	
	F	P	P	F	P	Overall range
Body length	2,860 (16)	2,080 (20)	3,510 (5)	3,100 (3)	3,090 (5)	
	1,130–5,000	1,310–3,940	2,800–4,410	2,540–4,200	2,810–3,490	1,130–5,000
Body width	179 (16)	153 (20)	213 (5)	177 (3)	315 (5)	
	93–284	94–273	174–278	139–226	287–326	93–326
Buccal capsule length	106 (16)	117 (20)	121 (5)	143 (3)	133 (5)	
	83–120	100–141	104–139	133–152	126–139	83–152
Buccal capsule width	97 (16)	101 (20)	109 (5)	121 (3)	136 (5)	
	76–109	80–135	107–113	119–122	131–144	76–144
Muscular oesophagus	262 (16)	268 (20)	303 (5)	250 (3)	308 (5)	
	197–318	220–333	258–356	227–289	284–333	197–356
Glandular oesophagus	233 (16)	223 (20)	315 (5)	238 (3)	296 (5)	
	157–333	189–250	289–356	197–273	256–324	157–356
Vulva*	51 (16)	50 (20)	46 (5)	48 (3)	46 (5)	
	45–60	43–56	44–47	47–51	43–50	43–60
Tail length	50 (15)	41 (20)	56 (5)	59 (3)	49 (5)	
	37–65	28–57	41–78	56–61	43–54	28–78
Mucron no.	5–7 (16)	5–7 (20)	5–7 (5)	5–6 (3)	6–8 (5)	5–8

*Distance from anterior as a percentage of body length.
For material collected as part of the present study: F, fixed in hot 70% ethanol; P, dissected from preserved hosts.
Mean (with sample size in parentheses) given above range, except for mucron number for which range only is given.

Remarks

This species may be distinguished from *B. slomei* by the absence of longitudinal thickenings in the anterior portion of the buccal capsule and from *B. xenopodis* by the absence of spiral thickenings on the inner surface of the buccal capsule. Females of *B. siluranae* n. sp. are also differentiated from other *Batrachocamallanus* spp. by the presence of a projection of the body wall in association with the vulva (see Figs 14, 50), greater maximum body size (irrespective of the manner of fixation) (see Table III) and smaller numbers of mucrons (see Fig. 23).

***Batrachocamallanus occidentalis* n. sp.** (Figs 24–34)

Type-host and locality: *Xenopus muelleri* (Peters) from Bolgatanga, Ghana.
Other hosts and localities: *X. muelleri*: Niamtogou, Togo (1); Namoundjoga, Togo (2); Faradje, Zaire (3); Dika, Zaire (4); Gangala na Bodio, Zaire (5); L. Tanganyika, between Sengwe and Mwerase, Zaire (6).
Site: Stomach.

Material studied
Holotype (female) BM 1993.5135, allotype (male) BM 1993.5136, 14 paratypes (4 male, 10 female) BM 1993.5137-5150, and 24 non-type specimens from type locality, F, coll. RCT, April, 1979; 4 specimens, P, hosts from RUCA 1094, (1); 7 specimens MRAC 34.733, 3 specimens MRAC 34.734, 3 specimens MRAC 34.735, 3 specimens MRAC 34.738, (1); 114 specimens, P, hosts from RUCA 1139, 1211, 1236 and 1243, (2); 58 specimens MRAC 34.685, 5 specimens MRAC 34.686, 9 specimens MRAC 34.687, 9 specimens MRAC 34.690, 1 specimen MRAC 34.691, 3 specimens MRAC 34.730, 26 specimens MRAC 34.742, 1 specimen MRAC 34.744, 36 specimens MRAC 34.745, 26 specimens MRAC 34.746, 7 specimens MRAC 34.747, 17 specimens MRAC 34.750, 6 specimens MRAC 34.751, 19 specimens MRAC 34.752, 2 specimens MRAC 34.753, 6 specimens MRAC 34.754, 9 specimens MRAC 34.755, 5

Table IV. Morphometric variation in male *Batrachocamallanus siluranae* n. g., n. sp.

Host:	*X. tropicalis*	*X. tropicalis*	*X. tropicalis* aff.	*X. pygmaeus*	*X. fraseri* aff.	
Locality:	Aburi, Ghana	Nigeria	Korup, Cameroon	Zaire	Olonou, Cameroon	
	F	F	P	F	P	Overall range
Body length	2,040 (8)	1,630 (40)	2,170 (3)	1,830 (2)	1,700 (4)	
	1,700–2,350	1,060–2,280	2,110–2,290	1,760–1,890	1,290–2,100	1,060–2,350
Body width	116 (8)	101 (40)	133 (3)	113 (2)	144 (5)	
	91–124	65–150	133	102–124	105–174	65–174
Buccal capsule length	88 (8)	115 (40)	100 (3)	120 (2)	97 (5)	
	80–93	112–118	98–104	115–124	90–113	80–124
Buccal capsule width	69 (8)	78 (40)	69 (3)	87 (2)	84 (5)	
	61–74	57–106	66–72	81–93	75–93	57–106
Muscular oesophagus	219 (8)	218 (40)	249 (3)	228 (2)	216 (5)	
	201–254	136–265	234–260	220–235	197–241	136–265
Glandular oesophagus	202 (8)	189 (40)	275 (3)	182 (1)	230 (5)	
	176–227	106–252	260–292		216–257	106–292
Right spicule	129 (8)	114 (12)	81 (3)	113 (2)	101 (4)	
	113–165	85–128	72–95	110–115	93–113	72–165
Tail length	39 (8)	32 (12)	38 (3)	32 (2)	37 (3)	
	33–43	28–37	38–39	30–33	33–40	28–43
No. of pairs of precloacal papillae	9–10 (8)	9–11 (12)	9 (2)	9 (2)	10–11 (3)	9–11

For material collected as part of the present study: F, fixed in hot 70% ethanol; P, dissected from preserved hosts.
Mean (with sample size in parentheses) given above range, except for precloacal papilla number for which range only is given.

specimens MRAC 34.756, (2); 5 specimens MRAC 34.573, 19 specimens MRAC 34.576, (3); 36 specimens MRAC 33.683, 8 specimens MRAC 33.684, 10 specimens MRAC 33.685, 1 specimen MRAC 34.569, (4); 27 specimens MRAC 34.577, 13 specimens MRAC 34.578, 17 specimens MRAC 34.581, (5); 25 specimens MRAC 33.677, (6).

Description

General. With characters of genus. Internal surfaces of buccal capsule bearing series of wide, transverse ridges which are more marked in anterior region; prominent thickening of capsule associated with anterior rim and extending posteriorly, in 6 longitudinal ridges (2 lateral, 4 submedian), approximately 30–60% of capsule length.

Females. Measurements of holotype precede range and mean (in parentheses) for a sample of specimens from type-locality (including all paratypes).

Body length 1,670, 1,210–2000 (1550) (n = 23), width 167, 106–242 (156) (n = 23). Buccal capsule length 76, 68–94 (79) (n = 23), width 81, 78–97 (82) (n = 23). Muscular oesophagus 212, 182–257 (213) (n = 23) and glandular oesophagus 211, 189–295 (231) (n = 21) long. Nerve-ring and excretory pore 139 and 154 from anterior of worm, respectively. Deirids posterior to nerve-ring, level with middle third of muscular oesophagus, 168 from anterior of worm. Vulva 52%, 49–59 (54)% (n = 23) of body length from anterior, not marked by prominence of body wall. Tail, 24, 19–35 (28) (n = 23) long, terminating in crown of 8 mucrons (7–9 in other material from type-locality, n = 20).

Males. Measurements of allotype precede range and mean (in parentheses) for a sample of specimens from the type-locality (including all paratypes). Body length 1,240, 1,070–1,480 (1,280) (n = 11), width 93, 72–104 (88) (n = 11). Buccal capsule length 57, 52–70 (60) (n = 11), width 54, 52–59 (56) (n = 11). Muscular oesophagus 174, 133–186 (162) (n = 11) and glandular oesophagus 197, 148–217 (176) (n = 11) long. Nerve-ring and excretory pore 109 and 124 from anterior of worm, respectively. Deirids posterior to nerve-ring, level with middle third of muscular oesophagus, 137

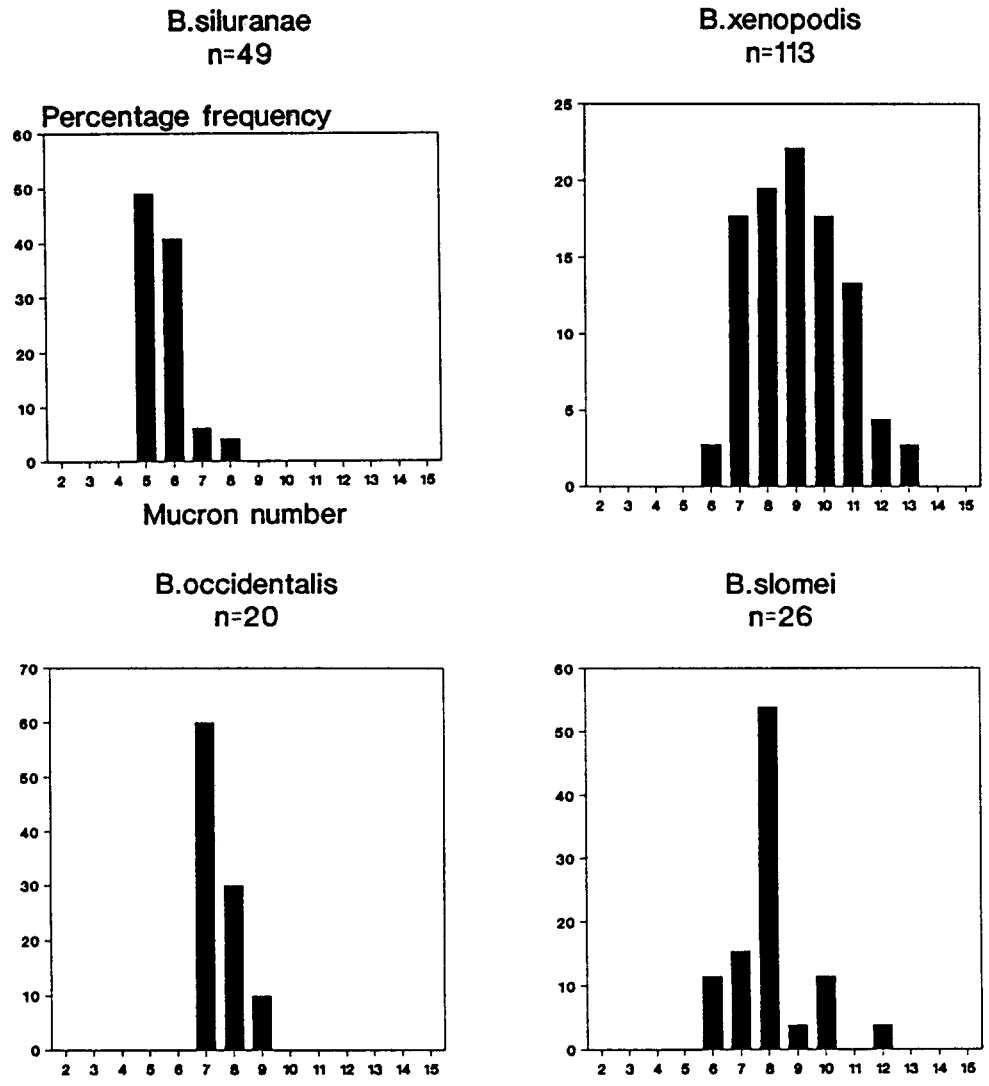


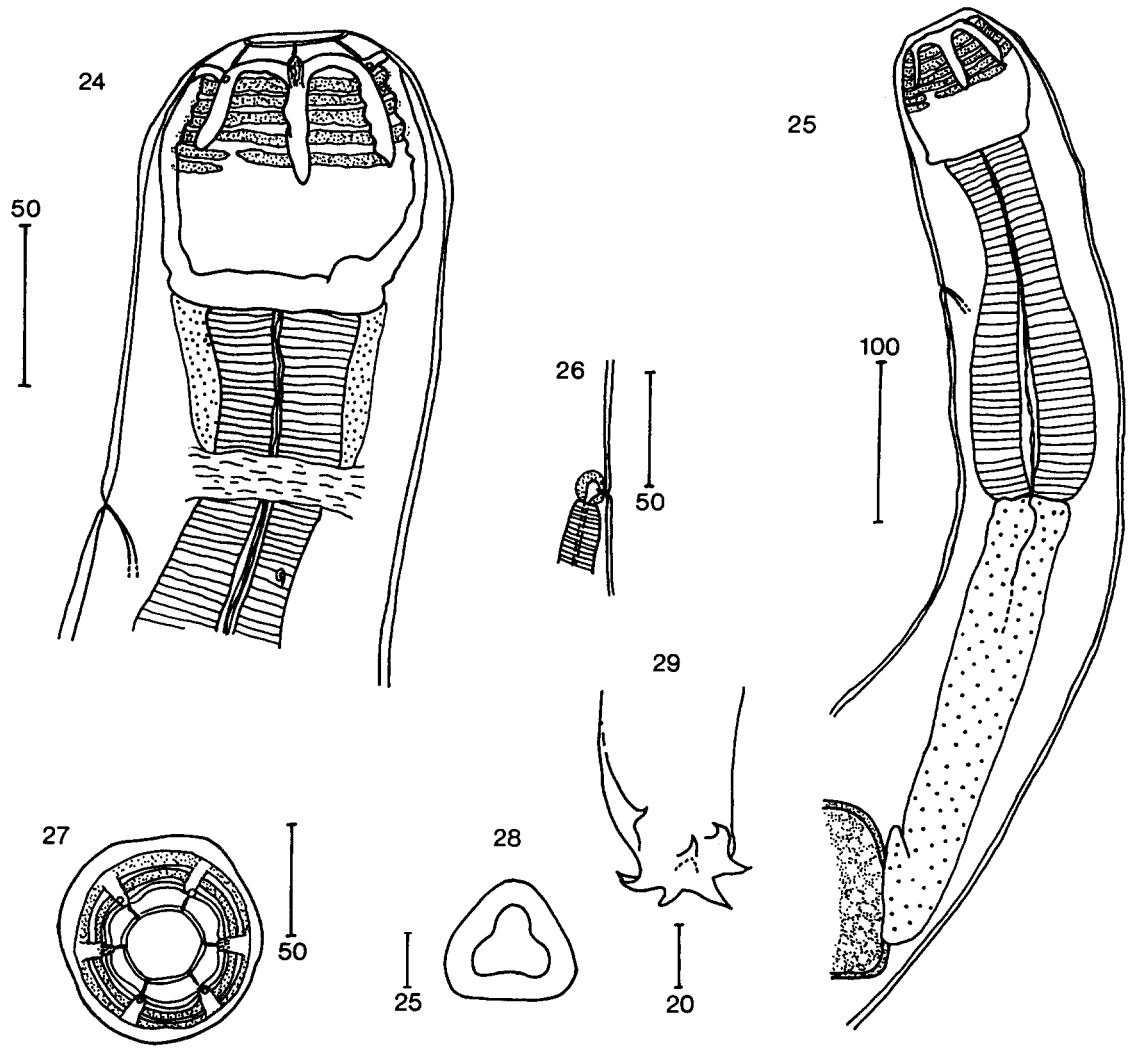
Fig 23. Frequency distribution of mucron number in females of *Batrachocamallanus* spp. (For each species, data from different localities pooled.)

from anterior of worm. Nine and 10 lateral, pedunculate, precloacal papillae extending onto right and left caudal alae, respectively (in paratypes and other material each ala also with 9–10 precloacal papillae.) Right spicule 67, 67–102 (87) (n = 11) and left spicule approximately 40–50 long (also in paratypes). Tail 30, 27–35 (30) (n = 11) long.

Remarks

Petter (1979) created *Onchocamallanus* for procamallanines with transverse thickenings on the inner surface of the buccal capsule and three distinct projections from the buccal capsule base. This genus is not accepted by some authors (Moravec & Sey, 1988), as intermediate conditions between transverse and spiral ridges are found in some species and many procamallanines, from diverse lineages, show tooth-like projections from the buccal capsule base.

The transverse ridges on the buccal capsule of *B. occidentalis* n. sp. are broad and relatively indistinct (see Fig. 24) when compared to the narrow, well-defined thickenings exhibited by *Spirocamallanus* or *Onchocamallanus*-like species (and *B. xenopodis*, see Figs 35, 37), and may have arisen independently.



Figs 24–29. Female *Batrachocamallanus occidentalis* n. sp. from *Xenopus muelleri* at Bolgatanga, Ghana. 24,25. Anterior, lateral view (holotype). 26. Terminal region of reproductive tract. 27. Anterior, apical view. 28. Transverse section through base of buccal capsule. 29. Tail (holotype).

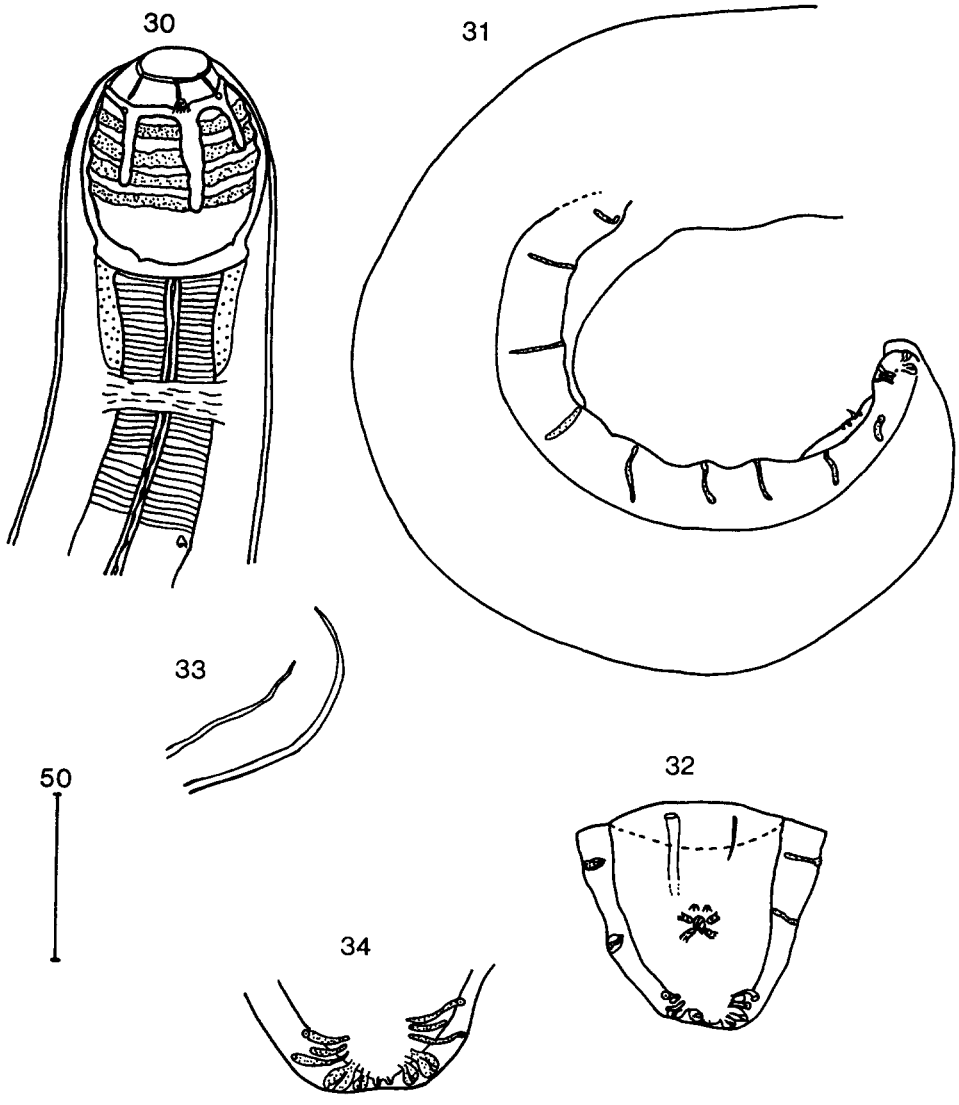
B. occidentalis n. sp. is distinguished from *B. slomei* by the presence of transverse internal thickenings and more greatly developed longitudinal thickenings of the buccal capsule. It differs from *B. siluranae* n. sp. in having a smaller maximum body length in females, no projection of the body wall associated with the vulva, larger numbers of mucrons (see Fig. 23) on the female tail, and the presence of transverse internal and longitudinal buccal capsule thickenings.

***Batrachocamallanus xenopodis* (Baylis, 1929) n. comb.** (Figs 35–48, 52)

Syns: *Procamallanus xenopodis* Baylis, 1929; *Spirocamallanus xenopodis* (Baylis, 1929) Olsen, 1952.

Type-host and locality: *Xenopus muelleri* (Peters) from Dar es Salaam, Tanzania (see Baylis, 1929) (1).

Previously published host and locality records: *X. muelleri*: northern Nigeria (Avery (1971), reported as *P. xenopodis*) (2); *X. laevis* (Daudin) (subspecies unspecified): Mt. Salinda, Zimbabwe (Thurston (1970), reported as *S. xenopodis*) (3). *X. wittei* Tinsley, Kobel & Fischberg: Kigezi district, Uganda (Tinsley



Figs 30–34. Male *Batrachocamallanus occidentalis* n. sp. from *Xenopus muelleri* at Bolgatanga, Ghana. 30. Anterior, lateral view (allotype). 31. Caudal region, lateral view (allotype). 32. Caudal region, ventral view. 33. Spicules (allotype). 34. Distribution of postcloacal papillae, ventral view (schematic, not to scale).

et al.. (1979), reported as *Spirocamallanus* sp.) (4). *Xenopus* sp.: L. Mutanda Uganda (Thurston (1970), reported as *S. xenopodis*; host probably *X. vestitus* Laurent, see Tinsley [1973]) (5); Queen Elizabeth National Park, Uganda (Thurston (1970), reported as *S. xenopodis*) (6).

Other hosts and localities: *X. muelleri*: Gueme, Cameroon (7); Sir, Cameroon (8); Kariba, Zimbabwe (9); L. Moero, Zaire (10); Mpala, L. Tanganyika, Zaire (11); Kiembi, Zaire (12); Zanzibar, Zanzibar Island, Tanzania (13). *X. l. victorianus* Ahl: Rutshuru, Zaire (14); Eldoret, Kenya (15); Chemenail-Nandi road, Kenya (16). *X. l. sudanensis* Perret (new host record): Sir, Cameroon (17); Jebel Marra, Sudan (18). *X. boreallis* Parker (new host record): Mumias, Kenya (19); Eldoret, Kenya (20); Chemenail-Nandi road, Kenya (21). *X. vestitus* Laurent: L. Mulehe and L. Mutanda, Uganda (22). *X. wittei*: Kasongwere, Zaire (23), hosts from the same site and collection date were included in the type series of *X. wittei* (see Tinsley *et al.*, 1979). *X. wittei* aff.: Cyamudongo, Rwanda (24); Bugarama valley, Rwanda (25); Kanudga, Rwanda (26); Butembo,

Zaire (27); Tora, Burundi (28). *X fraseri* Boulenger aff. (new host record): Ebisha, near Irangi research station, Zaire (29).
Site: Stomach.

Material studied
"Cotypes" of *Procamallanus xenopodis*, 2 specimens (1 male, 1 female) (1 slide), BM 1929.10.23.154, (1); 32 specimens (2); 4 specimens, BM 1968.45, (3); 6 specimens, P, (4); 1 specimen, BM 1968.44, (5); 2 specimens, BM 1968.47, (6); 120 specimens, P, hosts from RUCA 1.8, (7); 464 specimens, hosts from RUCA 125 and 127, (8); 14 specimens, F, hosts coll. V. Clarke, April, 1990 (9); uncounted specimens MRAC 33.680, 18 specimens MRAC 33.681, 9 specimens MRAC 33.682, (10); 15 specimens MRAC 33.678, (11); 22 specimens MRAC 34.561, 4 specimens MRAC 34.564, 2 specimens MRAC 34.568, (12); 22 specimens MRAC 34.582, 50 specimens MRAC 34.585, 18 specimens MRAC 34.588, 22 specimens MRAC 34.590, (13); 5 specimens MRAC 35.661, (14); 3 specimens, P, host coll. M. Simmonds, September, 1982 (15); 34 specimens, P, hosts coll. M. Simmonds, September, 1982 (16); 157 specimens, P, hosts from RUCA 125, 126 and 127, (17); 119 specimens, P, from hosts ZFMK 39980-81, ZFMK 39984-85 and ZFMK 39989, (18); 35 specimens, F, hosts coll. D. Yager, December, 1980 (19); 23 specimens, P, hosts coll. M. Simmonds, September, 1982 (20); 67 specimens, P, hosts coll. M. Simmonds, September, 1982 (21); 36 specimens, P, hosts coll. RCT, August, 1975 (22); 3 specimens MRAC 34.643, 2 specimens MRAC 34.644, 2 specimens MRAC 34.645, (23); 111 specimens, F, hosts coll. H. Hinkel, November, 1989 and December, 1991(24); 9 specimens, P, hosts coll. H. Hinkel, July, 1992 (25); 19 specimens, F, hosts coll. H. Hinkel, September, 1991 (26); 20 specimens, P, from hosts MRAC 75-027-B-0013-0022, (27); 31 specimens, P, from hosts MRAC 76-020-B-0072-0076, (28); 333 specimens, F, hosts coll. H. Hinkel, September, 1991 and December, 1991 (29).

Description

General. With characters of genus. Internal surfaces of buccal capsule bearing numerous oblique, narrow, internal thickenings, variable in length and arising irregularly; anterior rim of capsule not thickened, longitudinal thickenings absent.

Females. Data on morphometric and meristic variation are given in Table V.

Deirids at about same level as nerve-ring or posterior to this (level with middle third of muscular oesophagus). Opening of vulva not marked by prominence of body wall. Small region of heavy pigmentation associated with distal portion of vagina. Tail terminating in crown of 6–13 mucrons.

Males. Data on morphometric and meristic variation not given in text are provided in Table VI.

Deirids posterior to nerve-ring, level with middle third of muscular oesophagus. Eight to 11 precloacal papillae extending onto each caudal ala. Left spicule approximately 40–50 long.

Remarks

Mature female specimens of this species are here described for the first time, as those studied by Baylis (1929) were immature. Mean buccal capsule dimensions of *B. xenopodis* from *X. vestitus*, *X. wittei* aff. and *X. l. laevis* in the present study are comparatively greater than from other *Xenopus* spp. (see Tables V, VI). However, as variation is continuous and the specimens could not be distinguished in any other way, these differences are not considered to be of taxonomic significance. Some variability may also have resulted from differences in the method of fixation (see 'Materials & Methods' and Tables V, VI).

Procamallanine specimens from *Xenopus* sp. at Nairobi, Kenya, reported by Thurston (1970) as *S. xenopodis*, have been identified as *B. slomei* (see above).

The monophyly and relationships of *Batrachocamallanus*

All of the recognized procamallanine genera are distinguished primarily by variations in the presence and type of internal buccal capsule thickenings (Chabaud, 1975; Petter, 1979). *Procamallanus* exhibits smooth internal capsule walls, *Spirocamallanus* spiral ridges, *Malayocamallanus* Jothy & Fernando, 1971 irregular, longitudinal bands sometimes armed with denticles near their base, and *Onchocamallanus* Petter, 1979 transverse ridges. Moravec & Sey (1988) and Moravec & Scholz (1991) regarded *Spirocamallanus* as a subgenus of *Procamallanus* (and *Onchocamallanus* as a synonym of *Spirocamallanus*). These authors have also

Table V. Morphometric variation in female *Batrachocamallanus xenopodis* (Baylis, 1929) n. comb.

Host: Locality:	*X. muelleri* Northern Nigeria	*X. muelleri* Kariba, Zimbabwe F	*X. borealis* Mumias, Kenya F	*X. vestitus* L. Mutanda, Uganda P	*X. wittei* aff. Cyamudongo, Rwanda F	*X. wittei* L. Mulehe, Uganda P	*X. laevis** Mt. Salinda, Zimbabwe	*X. fraseri* aff. Ebisha, Zaire F	Overall range
Body length	1,400 (15)	1,500 (8)	1,230 (25)	1,470 (16)	2,170 (6)	1,500 (2)	1,450 (2)	1,420 (18)	
	1,020–1,820	1,050–2,070	780–1,590	920–1,930	1,910–2,670	1,450–1,550	1,240–1,670	1,090–1,720	780–2,670
Body width	161 (15)	196 (8)	158 (25)	217 (16)	206 (6)	147 (2)	132 (2)	144 (16)	
	93–242	160–289	94–222	96–294	176–280	141–152	116–148	120–163	93–294
Buccal capsule length	101 (15)	112 (8)	95 (25)	141 (16)	120 (6)	92 (2)	130 (2)	99 (20)	
	74–111	88–135	80–102	111–161	107–131	89–94	126–133	93–113	74–161
Buccal capsule width	88 (15)	104 (8)	91 (25)	142 (16)	125 (6)	98 (2)	116 (2)	95 (16)	
	70–98	91–120	78–114	117–200	109–148	94–102	115–117	91–106	70–200
Muscular oesophagus	209 (15)	241 (8)	204 (25)	230 (16)	309 (6)	204 (2)	207 (2)	225 (20)	
	167–242	203–326	174–254	189–272	280–326	167–242	193–220	189–283	167–326
Glandular oesophagus	213 (15)	211 (8)	204 (25)	223 (16)	308 (6)	204 (2)	178 (2)	216 (19)	
	167–242	163–287	144–254	136–258	278–333	182–227	167–189	168–261	136–333
Vulva**	54 (15)	52 (8)	54 (25)	52 (16)	55 (6)	58 (2)	52 (2)	55 (17)	
	50–58	46–60	47–63	40–62	47–58	57–59	46–58	49–64	40–64
Tail length	34 (15)	34 (8)	26 (25)	32 (16)	37 (6)	29 (2)	31 (2)	33 (19)	
	24–59	24–56	19–33	17–48	33–43	28–31	28–35	24–37	17–59
Mucron no.	7–12 (15)	9–13 (8)	7–11 (25)	7–11 (16)	6–10 (6)	8 (2)	11–13 (2)	7–13 (39)	6–13

*BM 1968.45.

**Distance from anterior as a percentage of body length.

For material collected as part of the present study: F, fixed in hot 70% ethanol; P, dissected from preserved hosts.

Mean (with sample size in parentheses) given above range, except for mucron number for which range only is given.

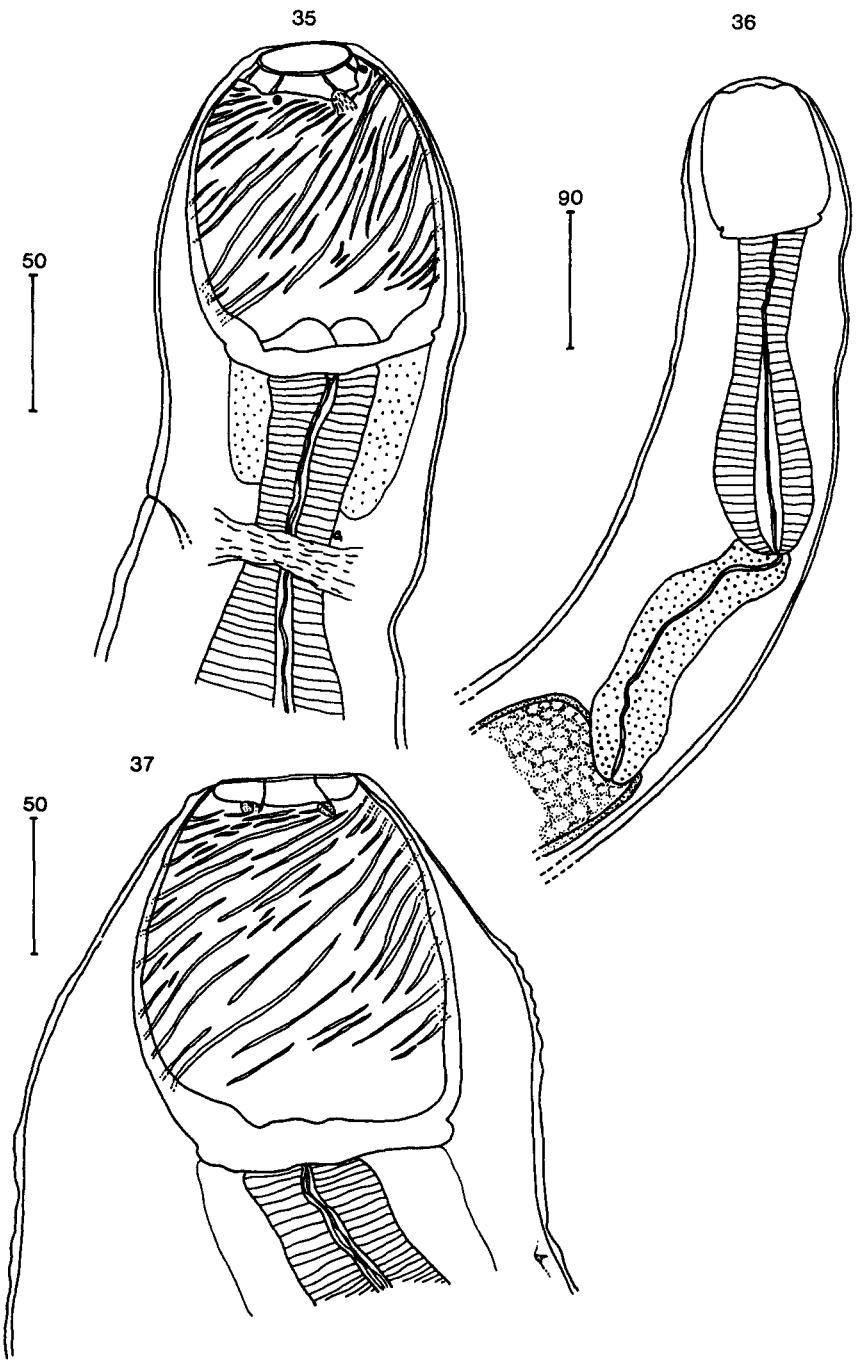
Table VI. Morphometric variation in male *Batrachocamallanus xenopodis* (Baylis, 1929) n. comb.

Host: Locality:	*X. muelleri* Northern Nigeria	*X. muelleri* Kariba, Zimbabwe F	*X. borealis* Mumias, Kenya F	*X. vestitus* L. Mutanda, Uganda P	*X. wittei* aff. Cyamudongo, Rwanda F	*X. fraseri* aff. Ebisha, Zaire F	*Xenopus* sp.* L. Mutanda, Uganda	Overall range
Body length	1,450 (8)	1,320 (11)	1,070 (10)	1,140 (10)	1,500 (14)	1,270 (23)	1,670 (1)	
	1,120–1,710	820–1,920	720–1,220	780–1,370	1,190–2,130	1,100–1,650		720–2,130
Body width	106 (8)	122 (11)	87 (10)	111 (10)	100 (13)	103 (23)	124 (1)	
	92–126	85–181	68–94	83–137	83–146	74–115		68–181
Buccal capsule length	81 (8)	78 (11)	85 (10)	106 (10)	96 (13)	82 (23)	102 (1)	
	72–93	74–83	78–93	78–135	80–107	72–93		72–135
Buccal capsule width	65 (8)	65 (11)	66 (10)	84 (10)	83 (13)	69 (23)	78 (1)	
	59–69	62–69	56–83	63–100	72–124	63–74		56–124
Muscular oesophagus	188 (8)	188 (9)	178 (10)	193 (10)	187 (13)	175 (23)	239 (1)	
	144–206	163–204	157–197	167–227	150–227	126–224		126–239
Glandular oesophagus	196 (8)	207 (9)	178 (10)	187 (10)	200 (13)	181 (23)	220 (1)	
	144–220	148–278	130–205	152–227	157–263	133–209		130–278
Right spicule	84 (8)	89 (11)	77 (3)	78 (8)	92 (12)	91 (23)	100 (1)	
	69–99	78–102	65–83	65–85	74–104	74–104		65–104
Tail length	31 (8)	31 (11)	22 (8)	28 (8)	28 (11)	26 (22)	37 (1)	
	28–33	26–39	17–28	24–35	24–31	20–31		17–39
No. of pairs of precloacal papillae	8–10 (8)	8–10 (11)	9 (8)	9 (8)	8–10 (12)	8–11 (30)	–	8–11

*BM 1968.44.

For material collected as part of the present study: F, fixed in hot 70% ethanol; P, dissected from preserved hosts.

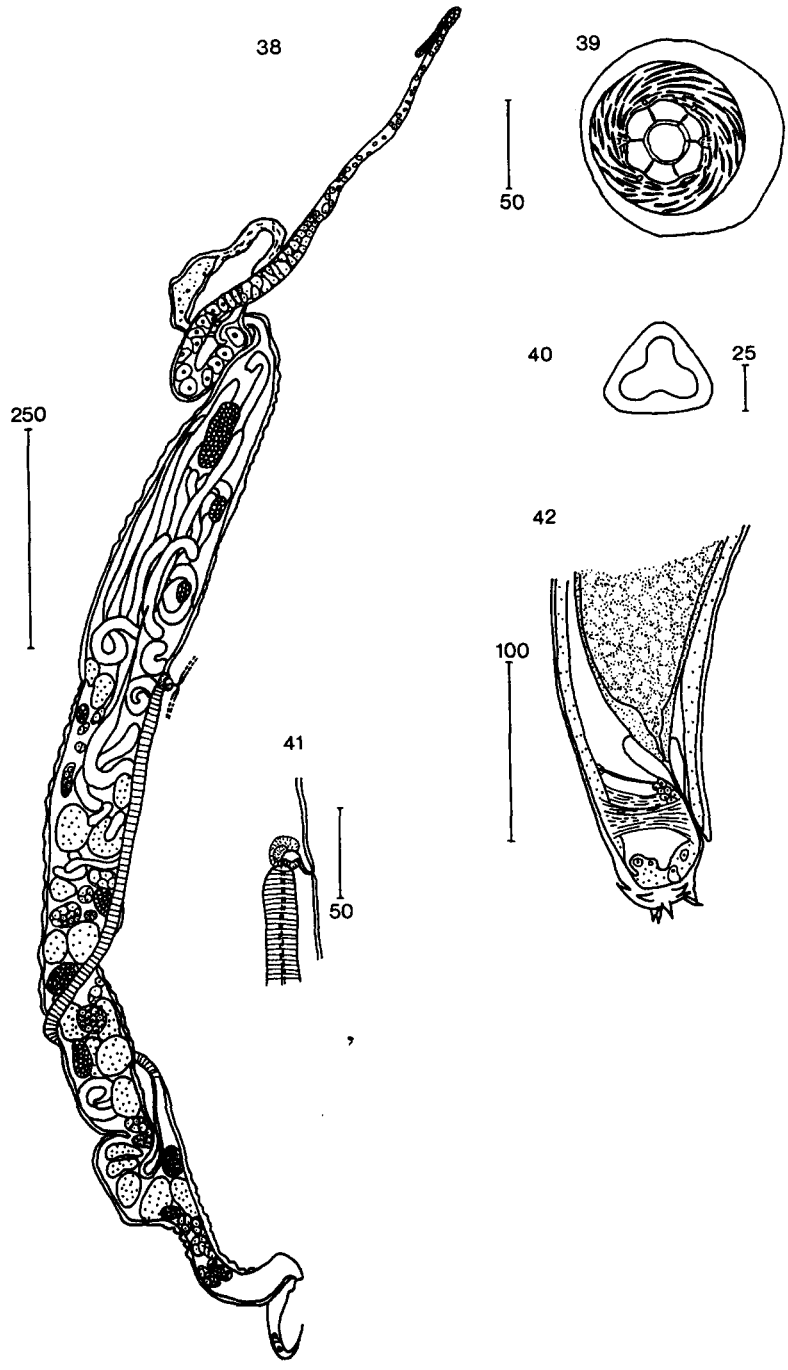
Mean (with sample size in parentheses) given above range, except for precloacal papilla number for which range only is given.



Figs 35–37. Female *Batrachocamallanus xenopodis* (Baylis, 1929) n. comb. 35,36. From *Xenopus fraseri* aff. at Ebisha, Zaire; anterior, lateral view. 37. From *X. vestitus* at L. Mutanda, Uganda; anterior, ventral view.

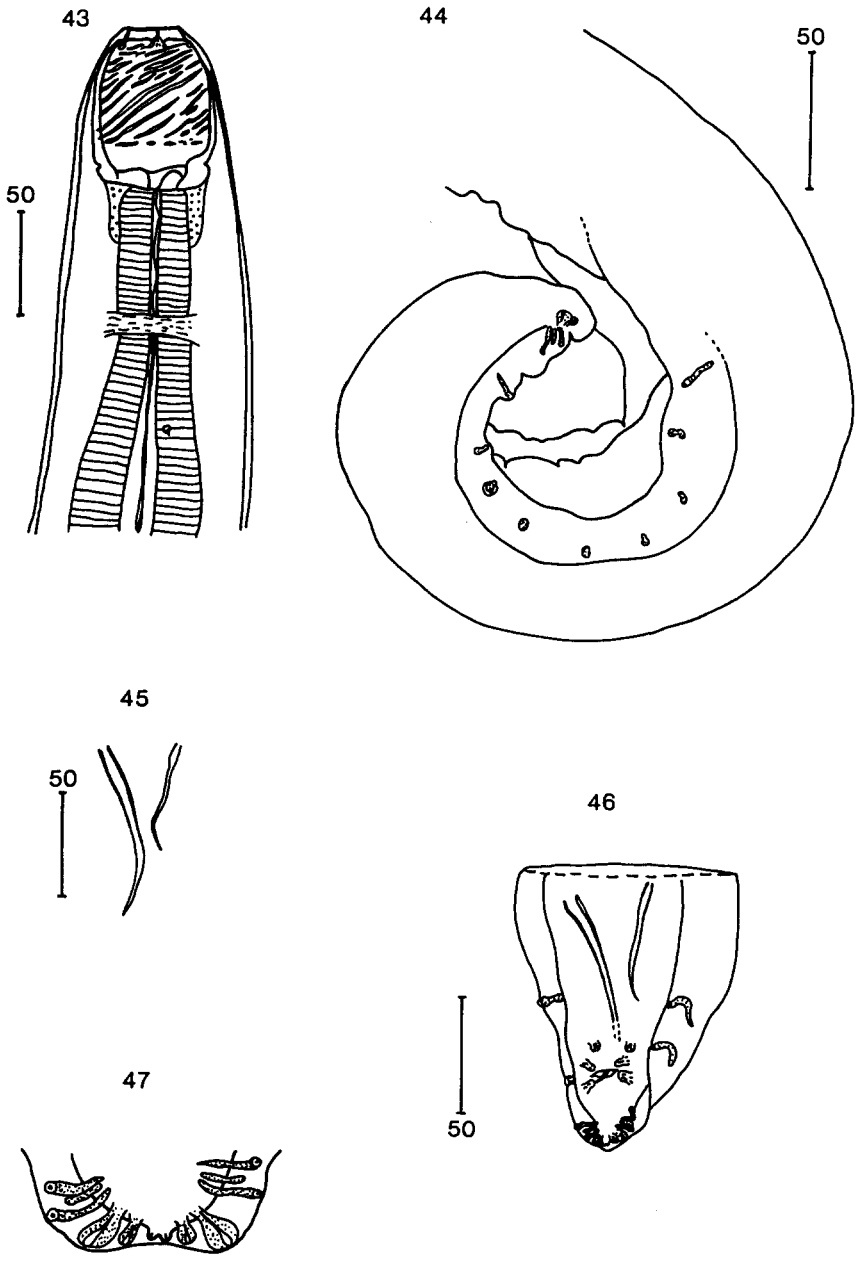
proposed two further *Procamallanus* subgenera: *Spirocamallanoides* Moravec & Sey, 1988, for species with spiral ridges in females only, and *Punctocamallanus* Moravec & Scholz, 1991 for *P. punctatus* Moravec & Scholz, 1991 in which the internal surface of the buccal capsule is ornamented with numerous punctations.

Within *Batrachocamallanus* different species exhibit spiral, transverse and longitudinal buccal cap-



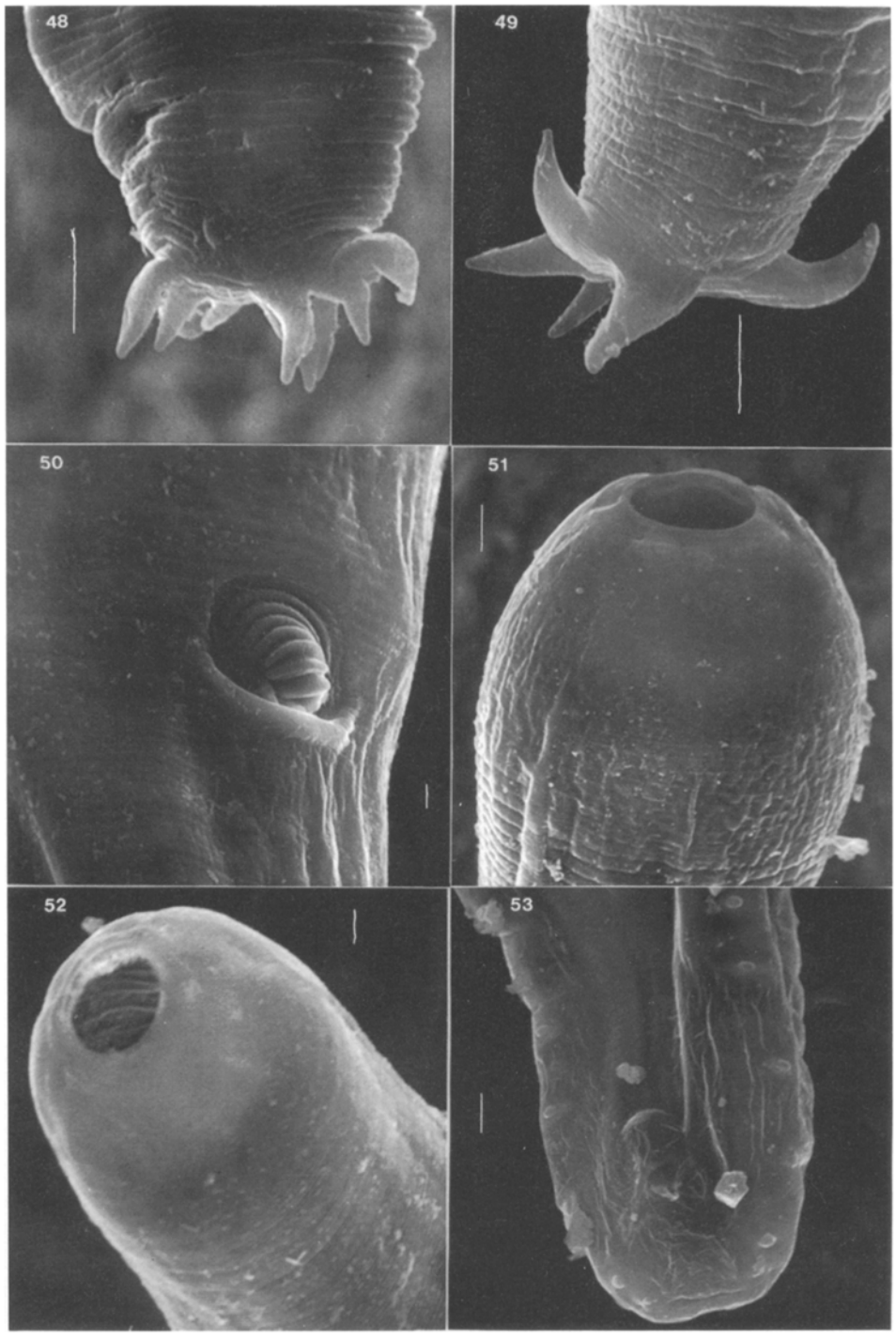
Figs 38–42. Female *Batrachocamallanus xenopodis* (Baylis, 1929) n. comb. from *Xenopus muelleri* at Gueme, Cameroon. 38. Reproductive system. 39. Anterior, apical view. 40. Transverse section through base of buccal capsule. 41. Terminal region of reproductive tract. 42. Tail.

sule thickenings. The transverse ridges of *B. occidentalis* and the longitudinal thickenings found in this species and *B. slomei* do not resemble those described for any other procamallanine. However, the spiral ridges on the buccal capsule of *B. xenopodis* are of similar form to those found in many *Spirocamallanus* spp., which has led to the placement of *xenopodis* within this genus (Olsen, 1952; Yeh, 1960). Such a classification



Figs 43–47. Male *Batrachocamallanus xenopodis* (Baylis, 1929) n. comb. from *Xenopus muelleri* at Gueme, Cameroon. 43. Anterior, lateral view. 44. Caudal region, lateral view. 45. Spicules. 46. Caudal region, ventral view. 47. Distribution of postcloacal papillae, ventral view (schematic, not to scale).

is not supported when variation in other characters is considered: the large number of mucrons on the female tail, relatively small body size, and the almost identical cephalic morphology, male caudal structures, and female reproductive system shown by the Procamallaninae from *Xenopus* spp. suggest they form a monophyletic group. While the descriptions of other procamallanines are sometimes inadequate, a high degree of variability in these characters is evident within the subfamily (see Petter (1979) and Ivashkin *et al.* (1971)). For instance, in no species has exactly the same pattern of male caudal papillae, as in representatives of



Figs 48–53. Scanning electron micrographs of *Batrachocamallanus* spp. 48. Female *B. xenopodis*, tail. 49–51. Female *B. siluranae*. 49. Tail 50. Vulva. 51. Anterior. 52. Female *B. xenopodis*, anterior. 53. Male *B. siluranae*, tail, ventral view. *Scale-bars*: 10 μm.

Batrachocamallanus, been described. This degree of similarity would be unlikely to arise by parallel evolution. Principal components analysis (see 'Materials and Methods') was used to assess the nature of morphometric variation between *Batrachocamallanus* spp. The first three principal components accounted for 82 and 89% of total variation in males and females, respectively (see Table VII). In both cases the character coefficients for the first principal component (PC1) were of the same sign, suggesting that it was strongly influenced by variation in body size (Bookstein *et al*, 1985). Amongst female specimens, *B. siluranae*, which reaches much greater maximum body length than other *Batrachocamallanus* spp., showed the greatest dispersion and differentiation along this component (see Fig. 54). The second (PC2) and third (PC3) principal components displayed both positive and negative character coefficients and might therefore reflect variation in shape (Bookstein *et al.*, 1985). Characters with large coefficients (and therefore influence) on PC2 were buccal capsule dimensions and tail length in males and body width and tail length in females, while PC3 showed high coefficients for buccal capsule dimensions in females, and body width, glandular oesophagus length, and right spicule length in males. Scatterplots of individual scores against the first three principal components suggested only a limited degree of interspecific differentiation in males and females (see Figs 54–55), due partly to PC1 (i.e. heavily influenced by body size), but also PC2 and PC3. Scatter against subsequent principal components (up to PC5) did not contribute significantly to the identification of groups. Male *B. siluranae* and particularly male *B. occidentalis* were discriminated to some degree from other forms along one combination of the first 3 principal components. A similar pattern was noticeable but less marked in females of these species. Neither male nor female *B. xenopodis* were differentiated as an isolated grouping relative to all of the other three forms (see Figs 54–55). The limited interspecific morphometric variability shown by procamallanines from clawed toads (despite striking variations in buccal capsule morphology within this assemblage) further supports their common origin, as very large morphometric differences are found between *Batrachocamallanus* spp. and other members of the Procamallaninae.

The greatest morphological resemblance to *Batrachocamallanus* is shown by the African species *Procamallanus laeviconchus* (Wedl, 1862) (based on a redescription by Moravec (1975)). Features of particular similarity are the arrangement of anterior papil-

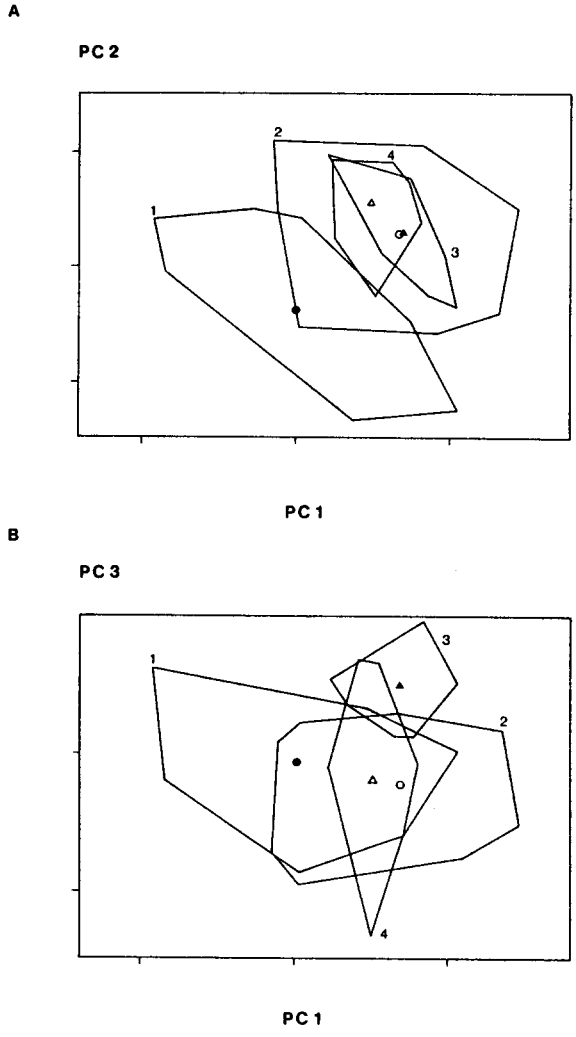


Fig 54. Principal component scores for *Batrachocamallanus* spp. (female specimens). A. PC2 *vs* PC1. B. PC3 *vs* PC1. Scatter of individuals represented by minimally enclosing convex polygons (polygon for each species identified by number), group centroids indicated by symbols: *B. siluranae*, n = 38 (●, 1); *B. xenopodis*, n = 55 (○, 2); *B. occidentalis*, n = 21 (▲, 3); *B. slomei*, n = 11 (△, 4).

lae, the presence of a posterior blind-ending process of the uterus, unequally developed spicules with simple points and the pattern of caudal papillae. Nine pairs of pedunculate papillae occur anterior to, or level with the cloaca in *P. laeviconchus* (8–11 are found in *Batrachocamallanus*), while three small adcloacal papillae and six postcloacal papillae are found on a relatively short tail (the same number as in *Batrachocamallanus*). Three of the postcloacal papillae in both *P. laeviconchus* and *Batrachocamallanus* are pedunculate and occur in a subventral group. However, *P.*

Table VII. Principal component analyses of 8 morphometric characters of male and female *Batrachocamallanus* spp.

	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	0.0209	0.0077	0.0059	0.0556	0.0114	0.0065
Percentage of total variation	49.8%	18.3%	14.1%	67.0%	13.7%	7.8%
Coefficients:						
Character						
body length	−0.51	0.21	0.07	−0.60	−0.02	0.32
body width	−0.32	0.22	−0.64	−0.25	0.74	−0.27
buccal capsule length	−0.34	−0.66	0.06	−0.16	−0.04	−0.60
buccal capsule width	−0.25	−0.45	−0.04	−0.15	0.15	−0.43
muscular oesophagus	−0.39	−0.10	−0.05	−0.24	−0.03	−0.14
glandular oesophagus	−0.29	0.04	−0.37	−0.18	0.26	0.12
anterior-vulva distance				−0.55	−0.01	0.35
right spicule	−0.35	0.07	0.63			
tail length	−0.32	0.51	0.21	−0.38	−0.59	−0.36

laeviconchus reaches much greater maximum body size (Moravec, 1975; Baylis, 1923) and shows only 3 mucrons on the female tail in adults (and 4 in the L3 larvae). The buccal capsule of this species is similar to that of *B. siluranae*, exhibiting smooth internal surfaces with a small degree of thickening at its anterior margin. *Batrachocamallanus* probably therefore evolved from an African lineage of *Procamallanus* with smooth buccal capsules. This would require that the various longitudinal and internal capsule thickenings exhibited by different members of the genus arose independently from those described in other procamallanines.

Phylogenetic analysis of Procamallaninae from *Xenopus* spp.

A phylogenetic analysis (Wiley, 1981) of character state variation amongst *Batrachocamallanus* spp. was carried out, based on two multistate and four binary characters (with eight apomorphic character states in total). As already argued above, it was assumed that *Batrachocamallanus* is monophyletic and evolved from African *P. laeviconchus*-like procamallanines with smooth buccal capsules. The distribution of character states on all possible cladograms was examined by hand (as only four taxa were involved) in order to find trees with the minimum number of character reversals and convergences. Characters were polarised by outgroup comparison (Watrous & Wheeler, 1981) with *P. laeviconchus* (redescribed by Moravec (1974, 1975)).

Characters

1. Anterior and longitudinal thickenings of buccal capsule.

   Plesiomorphic state (0): Anterior rim of capsule slightly thickened between notches; longitudinal thickenings absent (similar to *P. laeviconchus*).

   1: no anterior thickening; longitudinal thickenings absent.

   2: anterior rim of capsule thickened; longitudinal ridges present on anterior buccal capsule.

2. Thickenings on internal buccal capsule surface.

   0: absent (as in *P. laeviconchus*).

   1: spiral ridges present.

   2: transverse ridges present.

3. Mucron number (on female tail).

   0: few mucrons (sample ranges 5–8, mode 5 or 6) (3 in *P. laeviconchus* adults, 4 in L3 larvae).

   1: many mucrons (sample ranges 6–13, mode 7 or above).

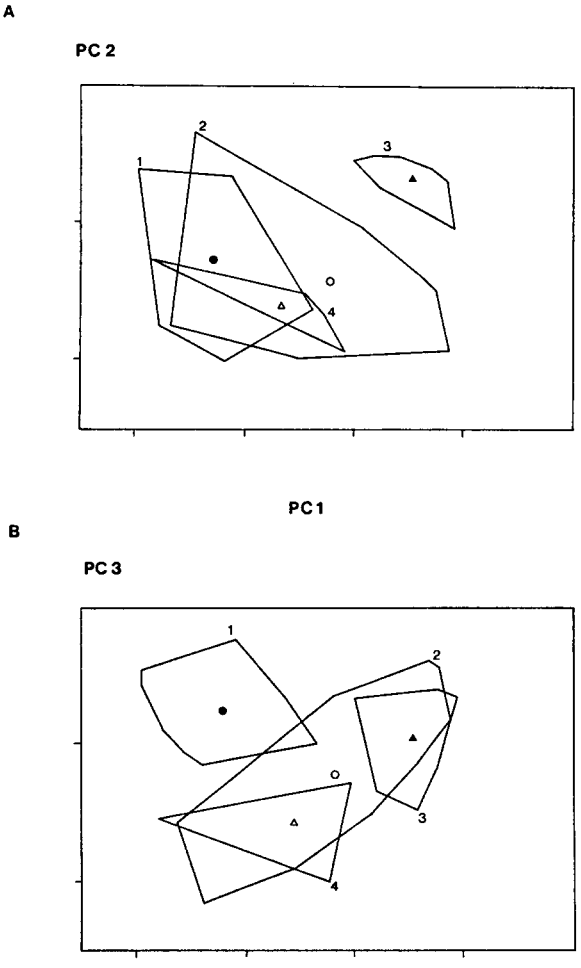


Fig 55. Principal component scores for *Batrachocamallanus* spp. (male specimens). A. PC2 *vs* PC1. B. PC3 *vs* PC1. Scatter of individuals represented by minimally enclosing convex polygons (polygon for each species identified by number), group centroids indicated by symbols: *B. siluranae*, n = 21 (●, 1); *B. xenopodis*, n = 45 (○, 2); *B. occidentalis*, n = 11 (▲, 3); *B. slomei*, n = 5 (△, 4).

4. Rugose projection of body wall associated with vulva.

   0: present (elevated lip reported in *P. laeviconchus*).

   1: absent.

5. Small area of heavy pigmentation associated with distal portion of vagina.

   0: absent (not reported in *P. laeviconchus* or other procamallanine species).

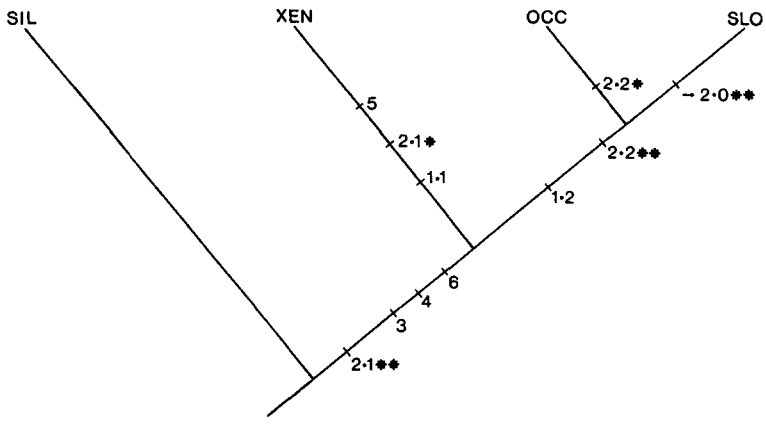
   1: present.

6. Female body length.

   0: maximum length over 4 mm (*P. laeviconchus* reaching up to 15 mm (Baylis, 1923)).

   1: never above 3 mm.

The different types of buccal capsule thickenings (anterior and longitudinal thickenings or internal ridges) are treated as two separate characters because their occurrence does not appear to be related. *Batrachocamallanus* spp. with longitudinal thickenings show both presence (*B. occidentalis*) and absence (*B. slomei*) of internal ridges (see Fig. 56), and the same is true for those lacking longitudinal thickenings. Similarly, some representatives of *Spirocamallanus* (with internal spiral ridges) and *Procamallanus* (no internal spiral ridges) from fishes show the presence of other types of capsule thickenings (for examples see Ivashkin *et al.* (1971)). It was presumed that states 1 and 2 of character 1 could not have evolved from each other, as this would involve a complex transition resulting in the secondary loss or gain of buccal capsule thickenings. However, no sequence of evolution was initially assumed for character 2. Fig. 56 represents the only possible cladogram which shows no convergences or reversals, provided spiral (character 2, state 1) and transverse ridges (character 2, state 2) arose independently (scheme C of Fig. 57), or a reversal to state 0 of character 2 is allowed (scheme B of Fig. 57). Trees in which a common origin for character states 1 and 2 of character 2 is assumed, and which do not show reversal in character 2, require convergence in the presence of longitudinal thickenings (character 1, state 2; see scheme A of Fig. 57). This is considered less likely (Fig. 57) because the longitudinal thickenings of *B. slomei* and *B. occidentalis* are of very similar structure, strongly supporting the monophyly of these species, whereas the internal spiral ridges of *B. xenopodis* and transverse thickenings shown by *B. occidentalis* are fundamentally different in nature (see above). The basal position of *B. siluranae* (see Fig. 56) is dependent on the assignment of plesiomorphic states to *B. siluranae*, and apomorphic states to other species, for the binary characters 3, 4 and 6. However, if these assumptions are not made, other relationships are possible between *B. siluranae*, *B. xenopodis* and the presumed sister species *B. slomei* and *B. occidentalis*.



Data matrix for phylogenetic analysis of *Batrachocamallanus* species

Character:	1	2	3	4	5	6
Group:						
B.siluranae	0	0	0	0	0	0
B.xenopodis	1	1	1	1	1	1
B.slomei	2	0	1	1	0	1
B.occidentalis	2	2	1	1	0	1

0 = plesiomorphic

Fig 56. Possible phylogenetic relationships of *Batrachocamallanus* spp. (taxa identified by first three letters of specific name), with data matrix upon which analysis was based. Transitions to apomorphic states are indicated by the character numbers (followed by the character state number for multistate characters); a reversal to the plesiomorphic state is indicated by an arrow. *Consistent with independent evolution of spiral (character 2, state 1) and transverse ridges (character 2, state 2) (see text, Fig. 57). **Consistent with common origin for spiral and transverse ridges, and the secondary loss of these in *B. slomei* lineage (see text, Fig. 57).

Discussion

A new genus, *Batrachocamallanus*, is created to include the Procamallaninae from African amphibians bearing a large number of mucrons on the female tail and with relatively small body size. Four species parasitic in clawed toads are recognised, these are: *B. siluranae* n. sp., *B. xenopodis* (Baylis, 1929) n. comb., *B. slomei* (Southwell & Kirshner 1937) n. comb. and *B. occidentalis* n. sp. *B. siluranae* (with a smooth buccal capsule) is considered the most plesiomorphic form, and may be the sister group to a clade including *B. xenopodis*, *B. slomei* and *B. occidentalis*. The monophyly of the latter two species is strongly supported by the presence in both of very similar longitudinal buccal capsule thickenings. Cytogenetic and molecular studies have revealed that clawed toads are represented by two distantly related lineages (Tymowska, 1991): one including *Xenopus tropicalis* and *X. epitropicalis*-like forms, and the other all remaining species. *B. siluranae* is the only member of *Batrachocamallanus* to occur in *X. tropicalis* and *X. epitropicalis*, while its congeners are restricted to other clawed toads. Thus, host evolutionary relationships might, to some extent, be reflected in the phylogeny of the parasite group. However, ecological and biogeographical factors, rather than associations with particular host taxa, may be the most important influence on the distribution of *Batrachocamallanus* spp. *B. siluranae* also occurs in *X. pygmaeus* and other *X. fraseri*-like forms which, in common with *X. tropicalis* and *X. epitropicalis*, inhabit lowland rain forest (Tinsley, 1981a; Loumont, 1984, 1986). It is found exclusively in this biotype (see Figs 58–61 for geographical distributions), from Sierra Leone in the west, to Zaire in the east. The only other representative of *Batrachocamallanus* to occur in any of the

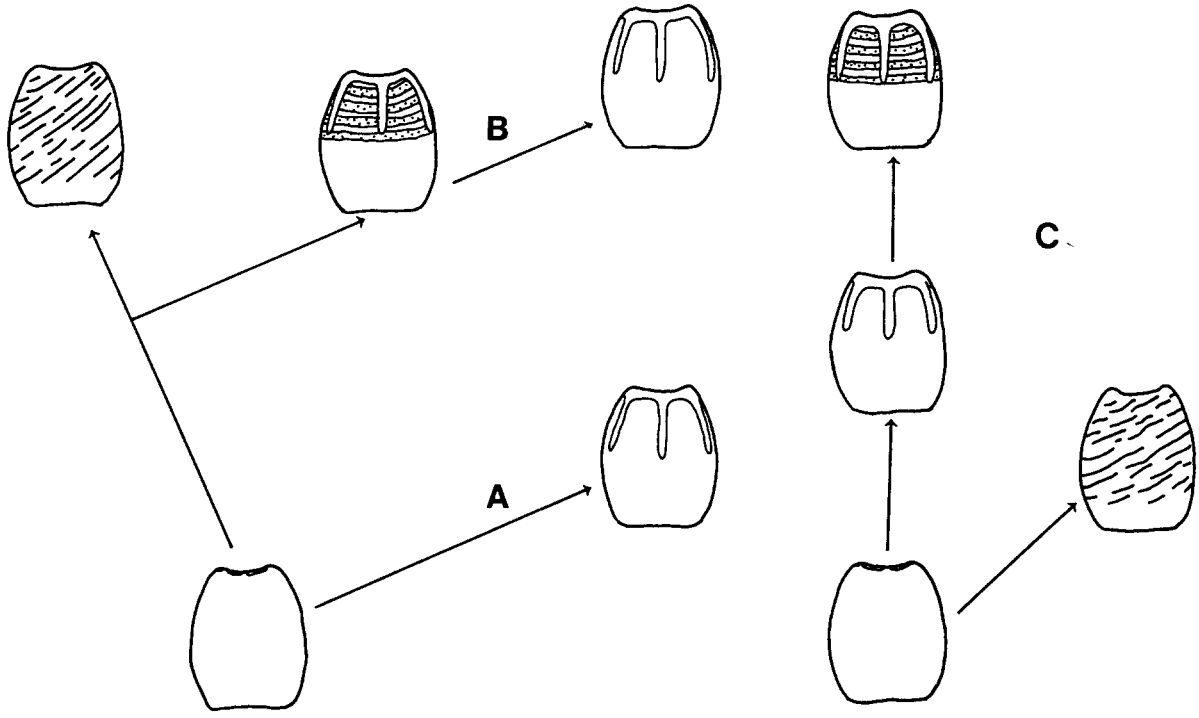
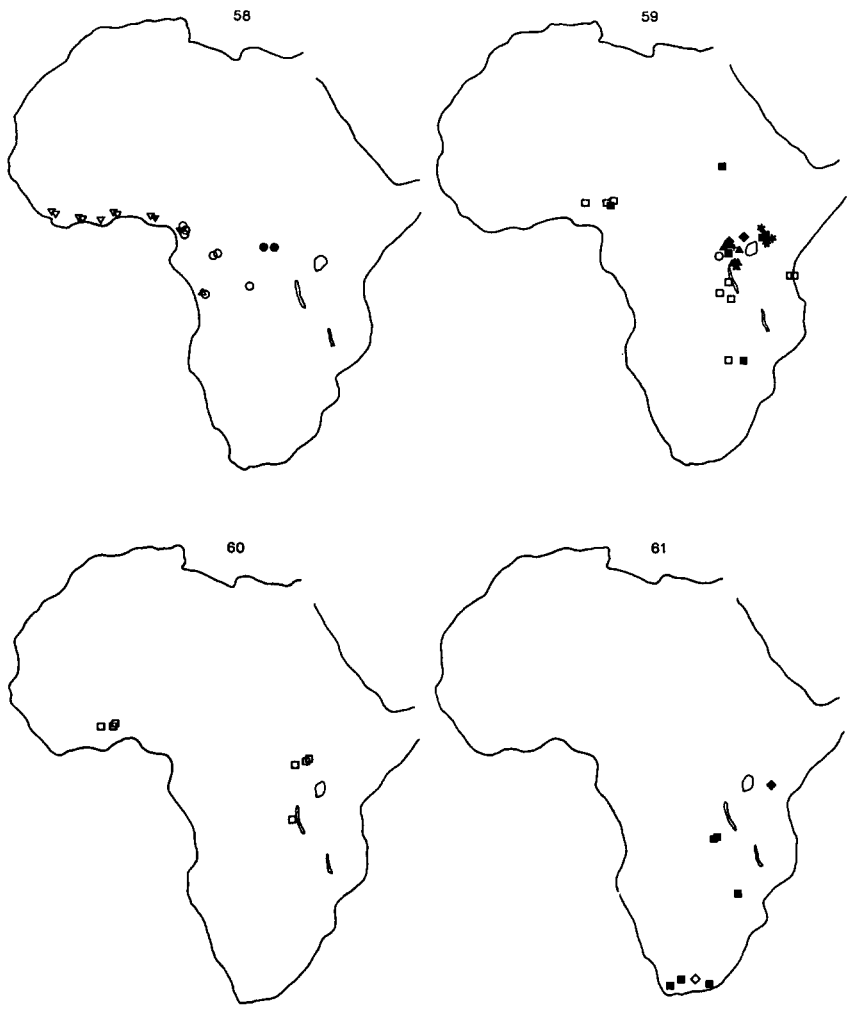


Fig 57. Alternative hypotheses for the sequence of evolution of buccal capsule thickenings in *Batrachocamallanus* requiring only one convergence or reversal (see text). A,B Spiral and transverse thicknenings of common origin. A. Independent evolution of longitudinal thickenings. B. Secondary loss of transverse thickenings. C. Independent evolution of spiral and transverse thickenings.

same hosts as *B. siluranae* is *B. xenopodis*, which was recorded from *X. fraseri* aff. at one lowland site in eastern Zaire. This locality is towards the eastern extreme of the rain forest habitat occupied by *B. siluranae* (and its usual hosts) and is close to central African areas where *B. xenopodis* is common in other *Xenopus* taxa (see Figs 58-59). *B. xenopodis* shows a particularly broad host and geographical distribution, occurring from Uganda, Rwanda, Burundi and eastern Zaire (in *X. l. victorianus*, *X. wittei*, *X. vestitus* and *X. muelleri*), to the Sudan (in *X. l. sudanensis*), Kenya (in *X. borealis* and *X. l. victorianus*), Tanzania and Zimbabwe (in *X. muelleri* and *X. laevis*); it is also found in *X. muelleri* and *X. l. sudanensis* from Cameroon and Nigeria. This distribution encompasses a range of ecological zones from highland forest (for *X. wittei* and *X. vestitus*) to savanna (for *X. muelleri* and *X. l. sudanensis*). *B. slomei* occurs in *X. laevis* subspecies from South Africa, Zimbabwe, and south eastern Zaire, and *Xenopus* sp. from Nairobi, Kenya. It can also infect non-pipid amphibians as its synonym, *Procamallanus brevis*, was described from a South African "bullfrog", possibly *Pyxicephalus adspersus* (see Baker, 1987). *B. occidentalis* is found in *X. muelleri* from Togo and Ghana, north eastern Zaire and the Lake Tanganyika area of Zaire. The present data suggest that the geographical distributions of some *Batrachocamallanus* spp. might overlap to some extent (see Figs 58–61), especially with *B. xenopodis* which has been recorded from hosts known to harbour either *B. occidentalis*, *B. slomei*, or *B. siluranae* at different sites. However, no concurrent infections (of the same host individual or at the same locality) were found during the present study, suggesting that members of this genus may show strict ecological segregation.

An analysis of the nature and distribution of buccal capsule thickening types amongst *Batrachocamallanus* spp. suggests that internal thickenings have arisen independently at least once, and possibly twice in this genus (see Figs 56–57). *Batrachocamallanus* spp. most closely resemble *Procamallanus laeviconchus* from African fishes and probably, therefore, evolved from an ancestral lineage with smooth buccal capsules. The buccal capsule of *B. siluranae* is similar to that of *P. laeviconchus*; however, in *B. xenopodis* this structure shows spiral, *Spirocamallanus*-like internal ridges, and in *B. occidentalis* transverse internal ridges of very different form. *B. slomei*, with no spiral



Figs 58–61. Host and geographical distribution of *Batrachocamallanus* spp. Host taxa: ■, *Xenopus laevis* subspecies; □, *X. muelleri*; ⁎, *X. borealis*; ▲, *X. wittei* or *X. wittei* aff.; +, *X. vestitus*; ○, *X. fraseri* aff; •, *X. pygmaeus*; △, *X. epitropicalis*; ▽, *X. tropicalis*; ▼, *X. tropicalis* aff.; ♦, *Xenopus* sp.; ◇, "bullfrog" (see text). 58. *B. siluranae*. 59. *B. xenopodis*. 60. *B. occidentalis*. 61. *B. slomei*.

or transverse internal ridges, and *B. occidentalis* are probably monophyletic, sharing unique longitudinal ridges absent in *B. xenopodis*. This suggests that spiral and transverse internal ridges may have evolved independently or that a secondary loss of internal ridges occurred in the lineage giving rise to *B. slomei* (see Fig. 57). The presence of buccal capsule thickenings may therefore show considerable evolutionary instability and in some cases be an inadequate criterion for generic separation (with consequences for the status of *Spirocamallanus*). As noted by Petter (1979), the Procamallaninae, including *B. xenopodis*, from African anurans do not show a close morphological relationship to *Spirocamallanus* spp. described from the same continent (*S. spiralis* (Baylis, 1923) and *S. mazabukae* Yeh, 1957). This further supports the independent evolution of *B. xenopodis* spiral ridges from those shown by *Spirocamallanus*-like forms with superficially similar buccal capsules. Amongst other procamallanines a marked degree of convergence in different characters, or the independent gain or secondary loss of spiral ridges, is required to explain the morphological similarity of some *Procamallanus* and *Spirocamallanus*-like species. For example, the South American *P. annipetterae* Kohn & Fernandes, 1988, exhibits great similarities in caudal morphology (Petter, 1990) to some of the *Spirocamallanus*-like forms which dominate the camallanid fauna of this continent

(Stromberg & Crites, 1974; Petter, 1979; Thatcher, 1991)). Similarly, *P. peraccuratus* Pinto, De Fabio, Noronha & Rolas, 1976, the only other South American procamallanine lacking internal ridges of the buccal capsule, displays similar spicule morphology to some *Spirocamallanus*-like Brazilian species (Pinto *et al.*, 1976; Petter, 1979). In one case from Asia, *P. siluri* Osmanov, 1964, the presence of spiral buccal capsule thickenings may vary between the sexes (Moravec & Sey, 1988).

P. laeviconchus, to which members of *Batrachocamallanus* are most closely related, inhabits more than 20 species of fish from five families and is widely distributed (Khalil, 1969; Khalil & Thurston, 1973; Moravec, 1974), occurring from the Nile to South Africa (Mashego & Saayman, 1981). Only one other *Procamallanus* species has been recorded from mainland Africa: *P. potamogale* Hugot, 1979, which shows close affinities to *P. laeviconchus* and was described from an otter shrew, *Potamogale velox* (see Hugot, 1979). The colonisation of clawed toads by a *Procamallanus*-like lineage may have been favoured by the ecological similarity of these amphibians, which show a fully aquatic lifestyle, to the more usual fish hosts of procamallanines (see Tinsley, 1981a). However, the distinctive morphology of the clade found in amphibians suggests that any "host jump" from fish is not recent.

Acknowledgements

We are grateful for research grants from NERC (GR3/6661 and GR9/632) and the Royal Society (to RCT) and The Systematics Association (to JAJ). We are also very grateful to the following for the supply of material which has made a major contribution to this study, including hosts or parasites collected during fieldwork in Africa and preserved museum specimens provided on loan: Dr R.A. Avery, Dr W. Bohme, Dr V. Clarke, Dr P. Denny, Dr L. Gibbons, Dr D.I. Gibson, Mrs E. Harris, Dr H. Hinkel, Professor J.L.J. Hulselmans, Mr M. Kazadi, Dr F.A. Puylaert, Mr M.P. Simmonds and Professor D.D. Yager.

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