

Evolutionary relationships, host range and geographical distribution of *Camallanus* Railliet & Henry, 1915 species (Nematoda: Camallaninae) from clawed toads of the genus *Xenopus* (Anura: Pipidae)

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Abstract

Representatives of the genus *Camallanus* Railliet & Henry, 1915 occur mainly in teleost fishes, although a significant number of species have also been recorded from anuran amphibians. The taxonomy, host range, geographical distribution and phylogenetic relationships of *Camallanus* spp. from African clawed toads (*Xenopus* spp.) are reviewed. Besides *C. kaapstaadi* Southwell & Kirshner, 1937, which shows a widespread distribution in sub-Saharan Africa and occurs in *X. laevis* subspecies, *X. wittei*, *X. fraseri*-like toads, *X. borealis* and *X. muelleri*, three new species were found: *C. siluranae* n. sp. from *X. tropicalis* in west Africa, *C. macrocephalus* n. sp. from *X. borealis* in Kenya, and *C. xenopodis* n. sp. from *X. laevis laevis* in South Africa and *X. borealis* in Kenya. *C. johni* Yeh, 1960 described from *Xenopus* sp. in Tanzania is considered a *species inquirenda*. *C. kaapstaadi* and *C. macrocephalus* are very closely related and both occur in the oesophagus of their hosts, unlike other *Camallanus* spp. which are found in the intestine or more rarely the stomach. Some of the unusual morphological features of these species may be an adaptation to attachment in the oesophagus. The host of *C. siluranae*, *X. tropicalis*, belongs to a separate species group (as has been established by recent molecular and cytological studies) to those of *C. kaapstaadi*, *C. macrocephalus* and *C. xenopodis*. Morphological affinities suggest that *Camallanus* spp. from clawed toads are not monophyletic with those from other amphibians and that *C. siluranae* is distantly related to, and probably not monophyletic with the remaining species from clawed toads. The *Camallanus* fauna of *Xenopus* spp. may thus be derived from at least two independent colonisations, of different host clades, by parasite lineages occurring in teleost fishes.

Introduction

The genus *Camallanus* Railliet & Henry, 1915 contains many nominal species, occurring mostly in teleost fishes (Stromberg & Crites, 1974; Petter, 1979), but also in anurans (Akram, 1987; Baker, 1987). Durette-Desset & Batcharov (1974) considered the possibility that *Camallanus* spp. from amphibians might form a distinct grouping characterised by: (1) the presence of a distal process of the right spicule; (2) grouping together of the first three pairs of postcloacal papillae in males; (3) a pre-equatorial vulva; and (4) a mode of reproduction in which larvae develop to the first stage *in utero*. However, these character states occur in some fish parasites and none of the first three features is found in all of the species from amphibians (Durette-Desset & Batcharov, 1974). Petter (1979) concluded

that monophyly is unlikely in forms from Asian ranids and bufonids due to the presence in some of beaded buccal capsule ridges, which also occur in certain lineages from fish.

Two *Camallanus* spp. have been described from African clawed toads: *C. kaapstaadi* Southwell & Kirshner, 1937 from *Xenopus laevis* in South Africa and *C. johni* Yeh, 1960 from *Xenopus* sp. in Tanzania. However, little information exists on the geographical occurrence or host range of these parasites amongst the many *Xenopus* spp. from Africa. *C. kaapstaadi* was recorded from *X. muelleri* in Nigeria by Avery (1971), while Thurston (1970) reported *C. johni* in *X. laevis* from Zimbabwe and *Xenopus* sp. from Uganda and Nigeria. Tinsley *et al.* (1979) also noted the presence of *Camallanus* sp. in *X. wittei* from central Africa.

This study aims to review the taxonomic status, geographical distribution, host range and phylogenetic relationships of *Camallanus* spp. from clawed toads.

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. *Camallanus* spp. were teased from the host mucosa with needles and fixed in hot 70% ethanol. Other specimens were obtained from the dissection of hosts 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 (except where otherwise stated), either by conventional light microscopy or Nomarski differential interference microscopy. All measurements were taken with an ocular micrometer and are given in micrometres. Specimens to be examined by scanning electron microscopy (SEM) were fixed in hot 70% ethanol, dehydrated through a series of ethanols, critical point dried and sputter coated with gold.

Material

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. Mierste); 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. Type-specimens, examined as part of this study, which were placed by the original authors in the helminthological collections of the London School of Hygiene and Tropical Medicine or Liverpool School of Tropical Medicine, are now curated by the International Institute of Parasitology, St Albans.

The following specimens were examined for comparative purposes: *C. mazabukae* Kung, 1948, type-specimens (1 male, 1 female; 1 slide), International Institute of Parasitology, no. 9; *C. dimitrovi* Durette-Desset & Batcharov, 1974, 5 specimens, BM 1988.1638-1652; *C. baylisi* Karve, 1930, 2 specimens, BM 1964.1412-1413 and 2 specimens BM 1964.2134-2136.

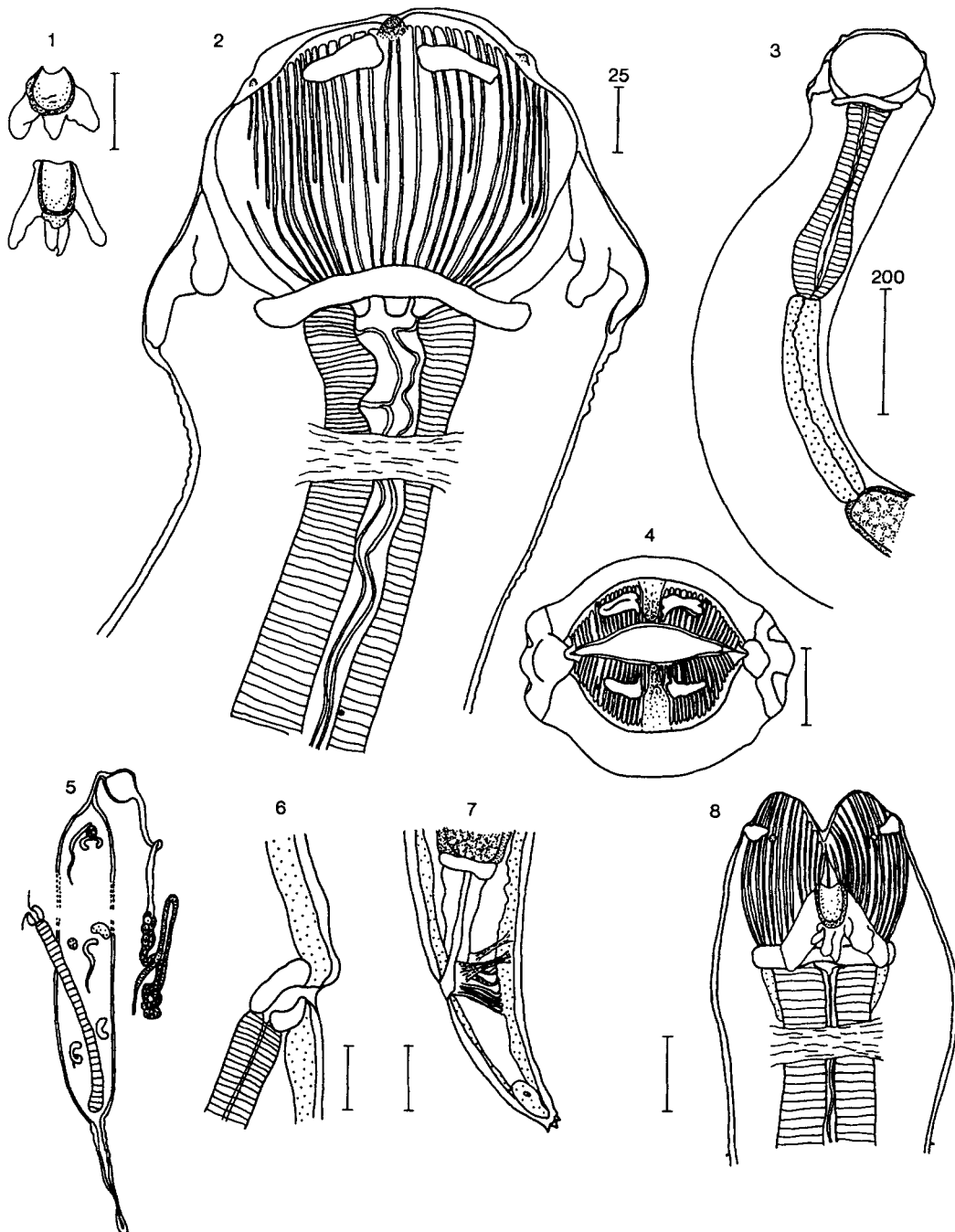
Host Identification

Xenopus spp. closely related to *X. fraseri* Boulenger are separated by characters including chromosome number and mating call: it is, therefore, often difficult to distinguish them 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. ruwenzoriensis* Tymowska & Fischberg. It was not possible to ascertain the chromosome number of *X. fraseri*-like toads from the present study, which are here referred to as *X. fraseri* aff. *X. tropicalis*-like toads also include cryptic, polyploid species. However, individuals from Togo and Ivory Coast (chromosome number not determined) and diploid individuals from Nigeria are referred to *X. tropicalis* (Gray) (see Loumont, 1984).

Camallanus kaapstaadi Southwell & Kirshner, 1937 (Figs 1–13, 45–46)

Type-host and locality: *Xenopus laevis* (Daudin) from Capetown, 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 *X. laevis* (subspecies unspecified): Mt. Salinda, Zimbabwe (reported as *Camallanus johni* Yeh, 1960, see Thurston (1970)) (2). From *X. muelleri* (Peters): northern Nigeria (Avery, 1971) (3). From *X. wittei* Tinsley, Kobel & Fischberg: Mukaka, Rwanda (recorded as *Camallanus* sp. by Tinsley *et al.* (1979)) (4), host from a type-locality for *X. wittei*. From *Xenopus* sp.:



Figs 1–8. Female *Camallanus kaapstaadi* Southwell & Kirshner, 1937 from *Xenopus laevis* at Cape, South Africa. 1. Ventral (above) and dorsal (below) tridents. 2–3. Anterior, lateral view. 4. Anterior, apical view. 5. Reproductive system (schematic, not to scale). 6. Terminal region of reproductive tract. 7. Tail. 8. Anterior, dorsal view. Scale-bars: 50 μ m, unless otherwise indicated.

Kajansi, near Kampala, Uganda (reported as *C. johni*, see Thurston (1970); host probably *X. l. victorianus* Ahl, see Tinsley (1973)) (5); Queen Elizabeth National Park, western Uganda (reported as *C. johni*, see Thurston (1970)) (6); Ogbomosho, Nigeria (reported as *C. johni*, see Thurston (1970)) (7).

Other hosts and localities: From *X. laevis* (subspecies unspecified): Samuru, Zaria, Nigeria (8). From *X. l. laevis*: Cape flats, South Africa (9); South Africa (10); Umtata, Transkei (11); Transvaal (exact locality unknown), South Africa (12); Mukuvisi river, Cranborne, Harare, Zimbabwe (13). From *X. l. victorianus* Ahl (new host record): Kagera, Rwanda (14); Kigali, Rwanda (15); Mutwanga, Zaire (16); Bulengo, L. Kivu, Zaire (17); Kaimesi area, Kenya (18); Eldoret-Item road (24 km west of Eldoret), Kenya (19). From *X. l. bunyoniensis* Loveridge (new host record): L. Bulera, Rwanda (20); L. Chahafi, Kigezi, Uganda (21). From *X. l. sudanensis* Perret (new host record): Sir, Cameroon (22); Jebel Marra, Sudan (23). From *X. l. poweri* Hewitt (new host record): Mukana marsh (near Lusinga), Zaire (24); Lufwa river, Lusinga, Zaire (25). From *X. muelleri* (Peters): Gueme, Cameroon (26); Sir, Cameroon (27); Niamtougou, Togo (28); Namoundjoga, Togo (29); Moba, Zaire (30); L. Moero area, Zaire (31); Kiambi, Zaire (32); Dika, Nepoko, Zaire (33); Zanzibar, Zanzibar Island, Tanzania (34); Kariba, Zimbabwe (35). From *X. fraseri* Boulenger aff. (new host record): Lula, Kasai Province, Zaire (36). From *X. borealis* Parker (new host record): Eldoret-Item road (24km west of Eldoret) (37).

Site: Oesophagus.

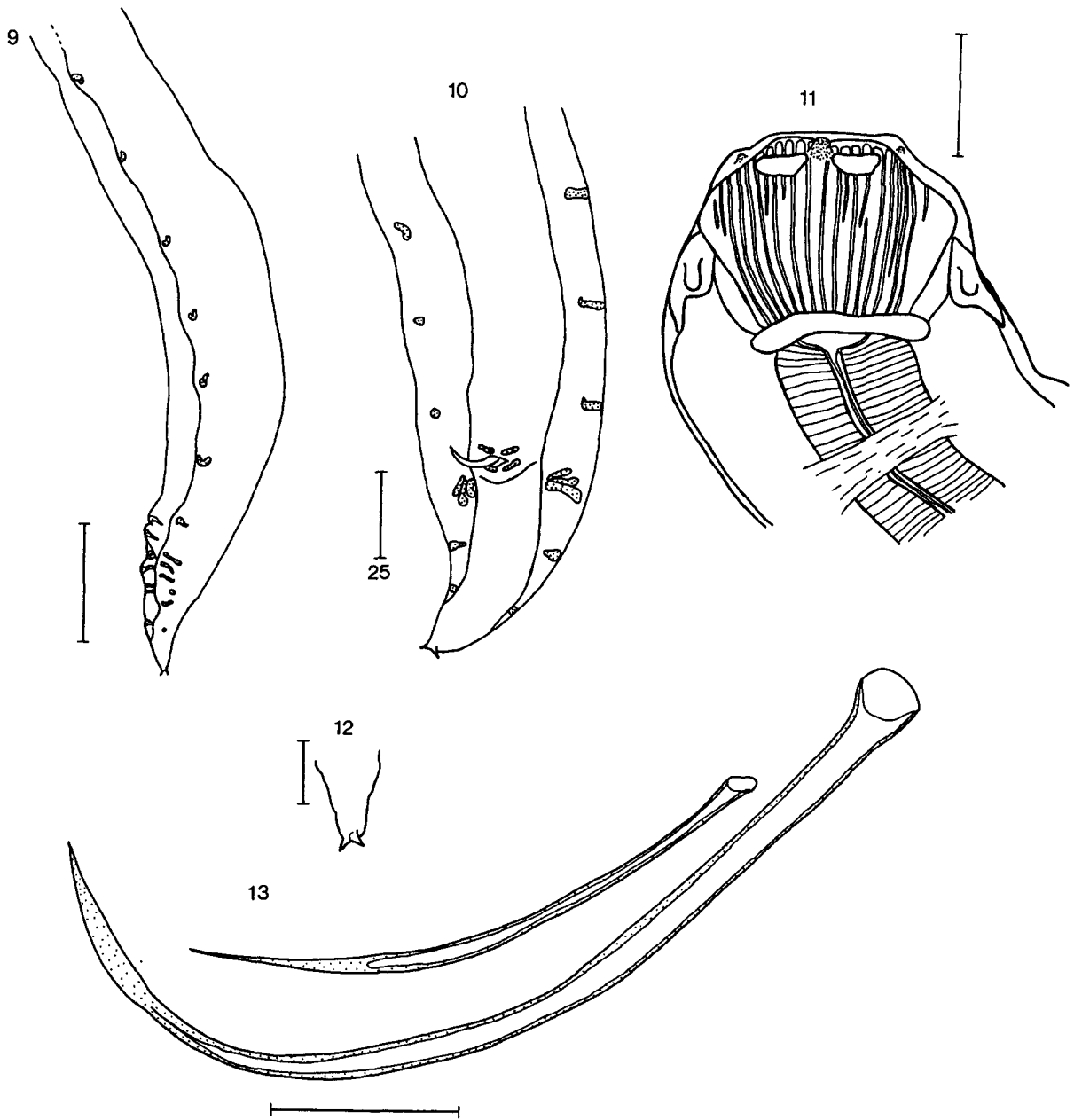
Material studied

Paratypes of *C. kaapstaadi*, International Institute of Parasitology, no.26 (originally deposited in helminthological collection of Liverpool School of Tropical Medicine) (1); 3 specimens BM 1968.40, (2); 8 specimens, P, (3); 1 specimen, P, (4); 2 specimens BM 1968.42, (5); 4 specimens BM 1968.39, (6); 3 specimens BM 1968.41, (7); 5 specimens BM 1975.2105-2110, (8); 50 specimens, F, hosts imported to UK, October, 1971 (9); 1 specimen BM 1975.891, (10); 18 specimens, F, hosts coll. P. Denny, August, 1988 (11); 8 specimens, F, hosts imported to UK January, 1976 (12); 30 specimens, F, coll. V. Clarke during 1989 (13); 2 specimens, P, hosts coll. RCT August, 1975 (14); 38 specimens, F, hosts coll. H. Hinkel, April, 1992 (15); 1 specimen, P, from hosts MRAC B-117656-117660, (16); 5 specimens MRAC 34.339, 1 specimen MRAC 34.340, 3 specimens MRAC 34.622,

1 specimen MRAC 34.627, (17); 921 specimens, P, hosts coll. M. Simmonds, September, 1982 (18); 33 specimens, P, host coll. M. Simmonds, September, 1982 (19); 1 specimen, P, host coll. RCT, August, 1975 (20); 1 specimen, P, host coll. RCT, August, 1975 (21); 167 specimens, P, hosts from RUCA 125, 126 and 127, (22); 31 specimens, P, from hosts ZFMK 39980-39981, ZFMK 39984-39985 and ZFMK 39989, (23); 6 specimens, P, from hosts MRAC B-64451-64460, (24); 55 specimens, P, from hosts MRAC B-64690-64699, (25); 30 specimens, P, hosts from RUCA 1.8, (26); 352 specimens, P, hosts from RUCA 125 and 127, (27); 13 specimens, P, hosts from RUCA 1094, (28); 11 specimens MRAC 34.733, 9 specimens MRAC 34.734, 5 specimens MRAC 34.735, (28); 66 specimens, P, hosts from RUCA 1139, 1211, 1236 and 1243, (29); 3 specimens MRAC 34.685, 3 specimens MRAC 34.686, 4 specimens MRAC 34.687, 1 specimen MRAC 34.690, 9 specimens MRAC 34.691, 14 specimens MRAC 34.727, 4 specimens MRAC 34.729, 1 specimen MRAC 34.730, 3 specimens MRAC 34.740, 6 specimens MRAC 34.741, 19 specimens MRAC 34.742, 6 specimens MRAC 34.745, 3 specimens MRAC 34.746, 4 specimens MRAC 34.750, 7 specimens MRAC 34.751, 2 specimens MRAC 34.752, 6 specimens MRAC 34.753, 5 specimens MRAC 34.754, 5 specimens MRAC 34.755, 8 specimens MRAC 34.756, (29); 1 specimen MRAC 34.595, 1 specimen MRAC 34.600, (30); uncounted specimens MRAC 33.680, 1 specimen MRAC 33.682, (31); 5 specimens MRAC 34.564, 1 specimen MRAC 34.568, (32); 2 specimens MRAC 33.683, 22 specimens MRAC 33.685, 1 specimen MRAC 34.569, (33); 2 specimens MRAC 34.585, 2 specimens MRAC 34.588, 12 specimens MRAC 34.590, (34); 10 specimens, F, hosts coll. V. Clarke April, 1991 (35); 3 specimens MRAC 33.662, (36); 15 specimens, P, hosts coll. M. Simmonds, September, 1982 (37).

Description

Measurements and counts provided in the text are based on specimens from Cape, South Africa: range precedes mean (in parentheses) for morphometric characters; other data on morphometric variation are given in Table I. The reproductive state of females described below and in Table I ranged from those with an empty uterus or only a few embryos *in utero* to specimens packed with embryos and developing or fully developed first stage larvae.



Figs 9–13. Male *Camallanus kaapstaadi* Southwell & Kirshner, 1937 from *Xenopus laevis laevis* at Cape, South Africa. 9. Caudal region, lateral view. 10. Caudal region, ventral view. 11. Anterior, lateral view. 12. Terminal region of tail. 13. Spicules. Scale-bars: 50 μ m, unless otherwise indicated.

General. Small worms. Lateral valves of buccal capsule with smooth internal ridges; most ridges complete, extending from anterior margin of valve to posterior edge. Four large, sclerotised plates situated on external surface of valves near their anterior margin. Four submedian cephalic papillae. Buccal capsule delimited

posteriorly by narrow basal ring. Dorsal trident usually larger than ventral trident, both distinctly trifid. Cephalic region slightly tilted in dorsoventral plane, towards ventral side.

Table 1. Morphometric variation (mean and range in micrometres) in *Camallanus kaapstaadi* Southwell & Kirshner, 1937.

Host	<i>Xenopus laevis laevis</i>		<i>X. muelleri</i>	
	Cape, South Africa		Bolgatanga, Ghana	
Sex	Female ¹	Male	Female ¹	Male
n	29	25	25	20
Length	3,000	2,250	2,460	1,960
	1,170–4,170	1,390–2,680	1,670–3,050	1,540–2,440
Width	240	143	217	155
	87–447	96–183	163–288	108–186
Buccal capsule valve	94 × 127	67 × 88	98 × 148	66 × 93
	69–100 × 98–163	57–76 × 78–104	80–109 × 139–159	59–76 × 81–103
Dorsal trident	78	57	75	57
	54–102	47–67	56–104	48–69
Ventral trident	67	50	57	46
	48–80	41–69	44–78	37–55
Muscular oesophagus	303	219	241	200
	193–371	172–256	203–277	181–227
Glandular oesophagus	394	279	249	198
	174–490	200–383	185–306	152–265
Vulva (%) ²	61		61	
	57–66		55–64	
Right spicule		273		232
		205–353		191–265
Tail	119	72	114	56
	54–216	46–89	83–148	46–65

¹Adult worms with and without larvae *in utero*.

²Distance from anterior of worm as a percentage of body length.

Females. Body robust. Number of ridges on each buccal capsule valve: 19–26 complete, 4–15 incomplete, 28–37 in total ($n = 10$). Basal ring 5–11 (8), $n = 28$, long. Nerve-ring and deirids 157–196 (178), $n = 10$ and 272–311 (292), $n = 10$ from anterior of worm, respectively. Ovary level with glandular oesophagus. Oviduct communicating with main body of uterus via short, dilated, seminal receptacle-like region. Tubular uterus containing developing embryos and larvae in mature specimens, reaching anteriorly to level of muscular oesophagus and rarely adjoining buccal capsule, extending into final quarter of body before becoming constricted to thin, blind-ending tubule. Post-equatorial vulva opening posterior to distinct projection of body wall. Vagina with very short, thick-walled distal portion and very long, muscular, posteriorly-directed proximal portion, meeting uterus just anterior to constriction. Tail conical, terminating in 3 mucrons.

Males. Smaller and thinner than females. Number of ridges on each buccal capsule valve: 19–26 complete, 6–16 incomplete, 26–37 in total ($n = 10$). Basal ring 4–9 (6), $n = 20$ long. Nerve-ring and deirids 119–139 (124), $n = 14$ and 193–259 (213), $n = 13$ from anterior of worm, respectively. Thin, sinuous testis present at level of glandular oesophagus and just posterior to this. Seven pairs of lateral, pedunculate pre-cloacal papillae extending onto caudal alae, posterior-most pair smaller and more ventral than preceding pairs. Two pairs of sessile ad-cloacal papillae flanking cloacal opening, one anteriorly, one posteriorly. Six pairs of lateral post-cloacal papillae: 3 large, pedunculate pairs located, in a group, immediately posterior to level of cloaca, two in particularly close association; further 2 pairs of papillae situated half way between level of cloaca and tip of tail, one large and pedunculate, other very small, anterolateral to larger pair; isolated pair of papillae, small, situated towards end of tail. Right spicule well developed, slightly expanded at proximal end; point

simple. Left spicule weakly developed, inconspicuous, 148-164 (155), $n = 5$ long; point simple. Tail conical, terminating in 2 small, latero-ventrally directed spines.

Remarks

C. johni Yeh, 1960 shows certain similarities to *C. kaapstaadi*. The pattern of male caudal papillae in the former is similar to that described here, and in both species the cephalic region is slightly twisted towards the ventral side, an unusual feature amongst representatives of *Camallanus*. There are a comparable number of longitudinal ridges on the female buccal capsule of these forms, but a slightly lower number in males of *C. johni* (21). The body measurements for both sexes quoted by Yeh (1960) are within the range for *C. kaapstaadi*. Three morphological differences which remain are: the tail of female *C. johni*, which bears four rather than three mucrons, the left spicule in male *C. johni*, which was described as short, broad and gubernaculum-like, and the ventral trident of this species, which is indistinctly branched. Forms showing these features were not encountered during the present study. Although the host of *C. johni* was identified only as *Xenopus* sp., the type-locality, in Tanzania, probably limits its identity to *X. laevis* or *X. muelleri* (see Loumont [1984] for information on clawed toad geographical distributions). Present specimens from the oesophagus of both *X. muelleri* and *X. laevis* correspond to *C. kaapstaadi*. However, no material was available from near the type-locality, and Yeh (1960) gave the site of infection for *C. johni* as the intestine. Examination of type specimens for *C. johni* was not possible as these are not present in the collection to which they were assigned by Yeh (1960) (the helminthological collection of the London School of Hygiene and Tropical medicine, which is now curated by the International Institute of Parasitology) and cannot be traced (Dr L. Gibbons, personal communication). Specimens reported as *C. johni* from Uganda, Nigeria and Zimbabwe by Thurston (1970), and examined as part of this study, were comparable in all characters with *C. kaapstaadi*. Given the absence of type-material, it is impossible to make definite conclusions about the taxonomic status of *C. johni* which is considered a *species inquirenda*.

Camallanus macrocephalus n. sp. (Figs 14-25,44)

Type-host and locality: *Xenopus borealis* Parker from Mumias, Kenya.

Site: Oesophagus.

Material studied

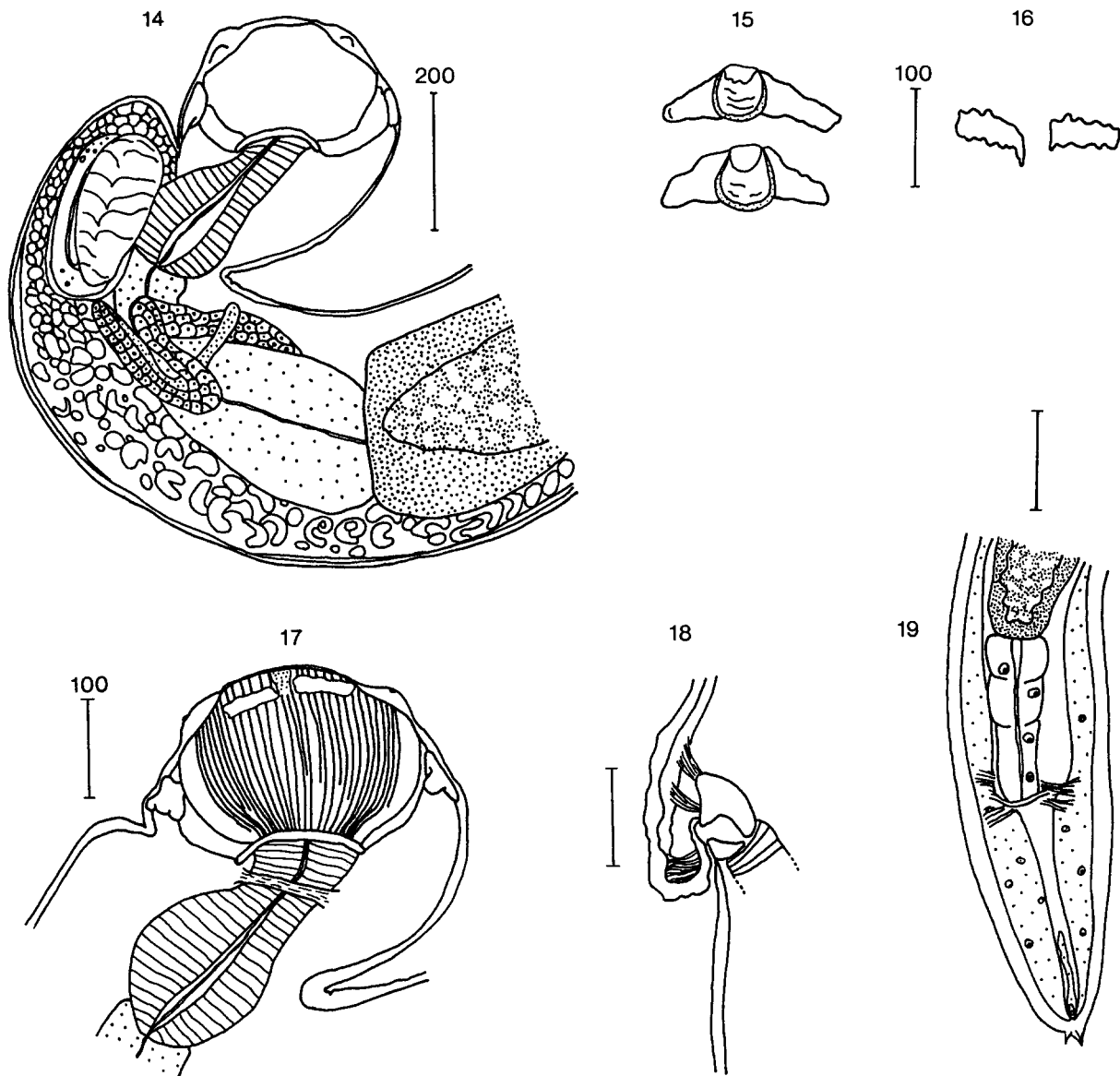
Holotype (female) BM 1993.5151, allotype (male) BM 1993.5152 and 6 paratypes (3 female, 3 male) BM 1993.5153-5158, F; 11 non-type specimens (6 female, 5 male) from type-locality, F. In all cases hosts coll. D. Yager, December, 1981.

Description

General. Small worms. Lateral valves of buccal capsule with smooth internal ridges; most ridges complete, extending from anterior margin of valve to posterior edge. Four large, sclerotised plates situated on external surface of valves near their anterior margin. Four submedian cephalic papillae. Buccal capsule delimited posteriorly by narrow basal ring. Cephalic region tilted in dorsoventral plane, towards ventral side.

Female. Measurements of holotype precede sample range and mean (in parentheses) for all specimens studied (reproductive state ranged from the presence of only a few embryos *in utero* to specimens packed with embryos and developing or fully-developed first stage larvae).

Very robust body; length 2,710, 2,130-3,560 (2,840), $n = 10$, width 326, 303-426 (355), $n = 10$. Buccal capsule massive, lateral valve 160, 139-180 (156), $n = 10$ long by 243, 243-261 (251), $n = 10$ wide (one valve sometimes overlaps other anteriorly in paratypes and non-type material). Number of longitudinal ridges on each buccal capsule valve: 29, 28-37, $n = 10$ complete, 6, 2-11, $n = 9$ incomplete, 35, 32-47, $n = 9$ in total. Cephalic region strongly tilted in dorsoventral plane, with marked ventral fold in body wall just posterior to buccal capsule. Basal ring 15, 9-15 (11), $n = 9$ long. Trident lacking middle process. Dorsal trident 85, 65-100 (82), $n = 10$ and ventral trident 91, 65-111 (86), $n = 10$ long. Nerve-ring and deirids 219, 213-272 (237), $n = 8$ and 248, 248-357 (303), $n = 8$ from anterior of worm, respectively. Muscular oesophagus 250, 242-285 (260), $n = 9$ and glandular oesophagus 350, 270-470 (380), $n = 6$ long. Ovary level with glandular oesophagus. Oviduct communicating with main body of uterus via short, dilate, seminal



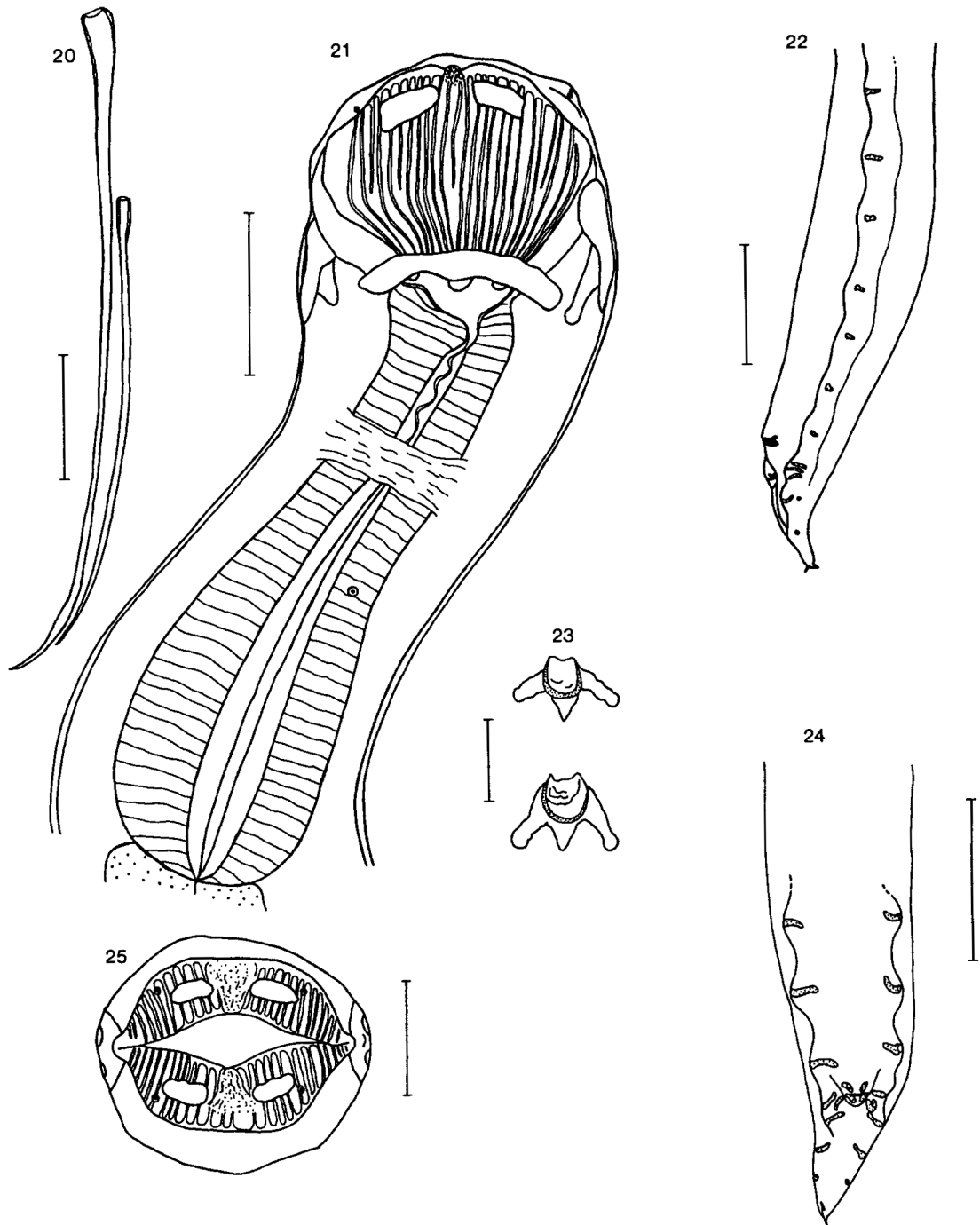
Figs 14–19. Female *Camallanus macrocephalus* n. sp. from *Xenopus borealis* in Kenya. 14. Anterior, lateral view. 15. Dorsal (above) and ventral (below) tridents. 16. Submedian sclerotized plates associated with buccal capsule valve (view from above). 17. Anterior, lateral view (holotype). 18. Terminal region of reproductive tract. 19. Tail. Scale-bars: 50 μm, unless otherwise indicated.

receptacle-like region. Uterus containing developing embryos and larvae, extending anteriorly as far as ventral fold of body wall and reaching into final quarter of body. Vulva postequatorial, 53, 53–63 (58)%, n = 10 of total body length from anterior, opening posterior to distinct projection of body wall. Vagina with very short, thick-walled distal portion and very long, muscular, posteriorly-directed proximal portion. Tail

conical, 117, 111–148 (130), n = 9 long, terminating in 3 mucrons.

Male. Measurements of allotype precede sample range and mean (in parentheses) for all specimens studied.

Smaller and thinner than females; body length 1,390, 1,390–2,390 (1,970), n = 9, width 83, 83–139 (153), n = 8. Cephalic region slightly tilted in



Figs 20–25. Male *Camallanus macrocephalus* n. sp. from *Xenopus borealis* in Kenya. 20. Spicules (allotype). 21. Anterior, lateral view (allotype). 22. Caudal region, lateral view (allotype). 23. Dorsal (above) and ventral (below) tridents. 24. Caudal region, ventral view (allotype). 25. Anterior, apical view. Scale-bars: 50 μ m.

dorso-ventral plane. Lateral valve of buccal capsule 57, 57–83 (70), $n = 9$ long by 85, 85–102 (95), $n = 9$ wide. Number of longitudinal ridges on each buccal capsule valve: 18, 18–23, $n = 9$ complete, 7, 6–14, $n = 7$ incomplete, 25, 25–33, $n = 7$ in total. Basal ring 7, 6–7 (7), $n = 9$ long. Dorsal and ventral tridents distinctly trifid, respectively 43, 37–54 (46), $n = 9$ and 41, 41–54 (45), $n = 9$ long. Nerve-ring and deirids 117, 117–154 (134), $n = 7$ and 148, 148–228 (192), $n = 7$ from anterior end of worm, respectively. Muscular oesophagus 209, 187–237 (210), $n = 9$ and glandular oesophagus 178, 178–243 (222), $n = 7$ long. Seven pairs of lateral, pedunculate precloacal papillae extending onto caudal alae; posterior-most pair smaller and more ventral than preceding pairs. Two pairs of sessile adcloacal papillae flanking cloacal opening, one anterior, one posterior. Six pairs of lateral post-cloacal papillae: 3 large, pedunculate pairs located, in a group, immediately posterior to level of cloaca, 2 in particularly close association; further 2 pairs of papillae situated half way between level of cloaca and tip of tail, one large and pedunculate, other very small, lateral to larger pair; isolated pair of papillae, small, situated towards end of tail. Right spicule well developed, slightly expanded at proximal end, 272, 272–331 (305), $n = 6$ long, point simple. Left spicule weakly developed and inconspicuous, 148, 148–158 (153), $n = 2$ long, point simple. Tail conical, 56, 51–78 (61), $n = 9$ long, terminating in 2 small, latero-ventrally directed spines.

Remarks

C. macrocephalus n. sp. is closely related to *C. kaapstaadi*, but may clearly be distinguished from this (see Fig. 26), and all other *Camallanus* spp., by the relatively great size of the buccal capsule valves in females. Female *C. macrocephalus* are also characterised by tridents without a middle process and an exaggerated ventral tilting of the cephalic region, to a degree which is unique amongst representatives of *Camallanus*. Body width is greater and total number of buccal capsule valve ridges relatively higher in females when compared to *C. kaapstaadi*, however, there is some overlap in both characters. Males of *C. kaapstaadi* and *C. macrocephalus* cannot reliably be distinguished by any qualitative feature or morphometric character. All of the female camallanines recovered from host samples at the type-locality were *C. macrocephalus*, and it is therefore assumed that the males from this site must belong to the same species.

Camallanus siluranae n. sp. (Figs 27–37, 42)

Type-host and locality: *Xenopus tropicalis* (Gray), from MRAC B-109221-109230, collected at Cavally river, Sahibly, Ivory Coast.

Other hosts and localities: From *X. tropicalis*: Ebeva, Togo (1); Nigeria (exact locality unknown) (2).

Site: Intestine.

Material studied

(MRAC Registration numbers of type-series to be added) Holotype (female), allotype (male), 5 paratypes (3 female, 2 male), and 6 non-type specimens (4 female, 2 male), P; 5 specimens, P, hosts from RUCA 1371, (1); 21 specimens (11 of these mounted in Canada balsam), F, hosts imported to UK, February, 1986 (2).

Description

General. Long, thin worms. Cephalic region not tilted towards ventral side. Buccal capsule with kite-shaped lateral valves. Internal ridges of buccal capsule valves smooth anteriorly but slightly beaded posteriorly (although not in all specimens). Most ridges complete, extending from anterior margin of each valve to posterior edge. Four thin, sclerotised plates situated on external surface of valves near their anterior margin. Four submedian cephalic papillae. Buccal capsule delimited posteriorly by narrow basal ring. Tridents subequal, large in proportion to capsule size, distinctly trifid.

Female Measurements of holotype given in text; data on morphometric variation are provided in Table II, based on specimens which ranged in reproductive state from those with empty uterus to worms containing many embryos and developing or fully-developed first-stage larvae.

Much larger than males, body length 24,700, width 447. Lateral valve of buccal capsule valve 78 long by 93 wide, bearing 10 complete and 6 incomplete longitudinal ridges (16 in total). Dorsal trident 115 and ventral trident 113 long. Basal ring 9 long. Nerve-ring 157 from anterior of worm. Muscular oesophagus 341 and glandular oesophagus 591 long. Vulva pre-equatorial, 28% of total body length from anterior extremity. Vulval opening delimited by 2 slightly elevated transverse lips. Vagina with very short, thick-walled distal portion and long, muscular, posteriorly-directed proximal portion. Uterus containing developing embryos and

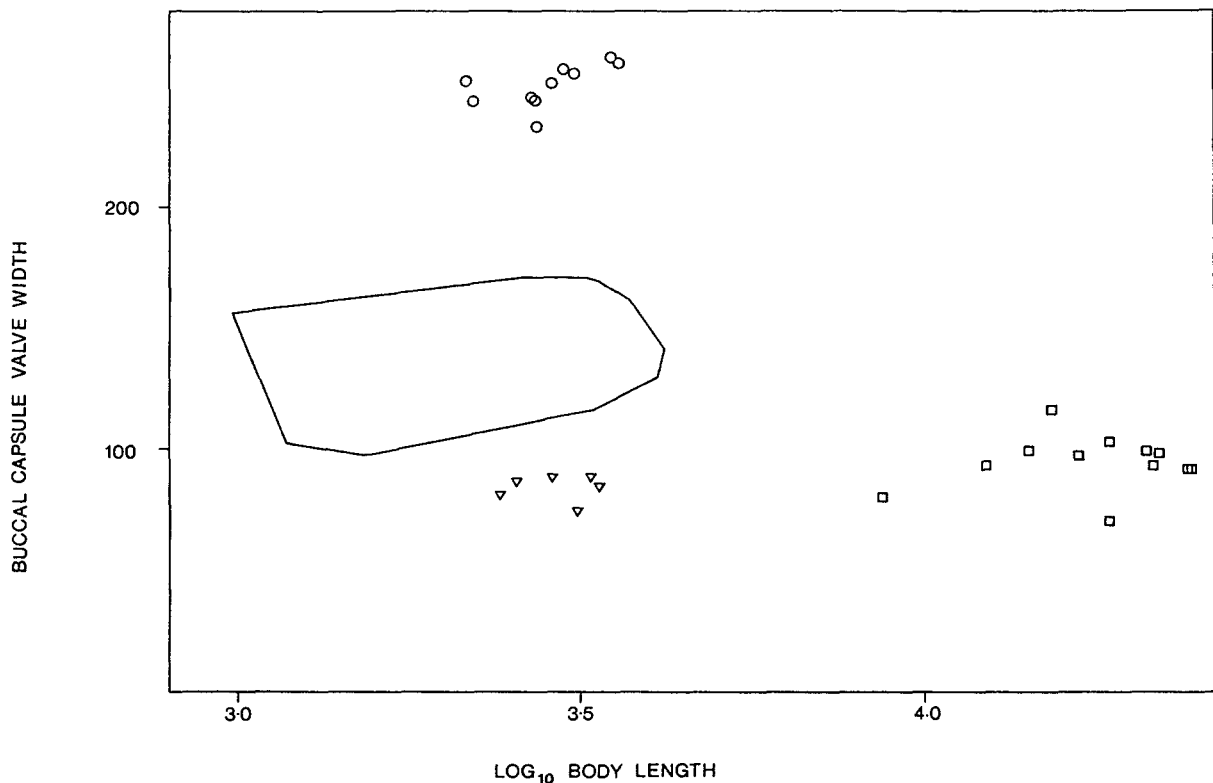


Fig. 26. Scatterplot of buccal capsule valve width vs \log_{10} body length for *Camallanus* spp. occurring in clawed toads. Scatter of individuals for *C. kaapstaadi* ($n = 104$) represented by minimally enclosing convex polygon; \circ , *C. macrocephalus*; ∇ , *C. xenopodis*; \square , *C. siluranae*.

larvae, extending from level of muscular oesophagus to just short of tail. Tail thin, 424 long, ending bluntly; mucrons absent.

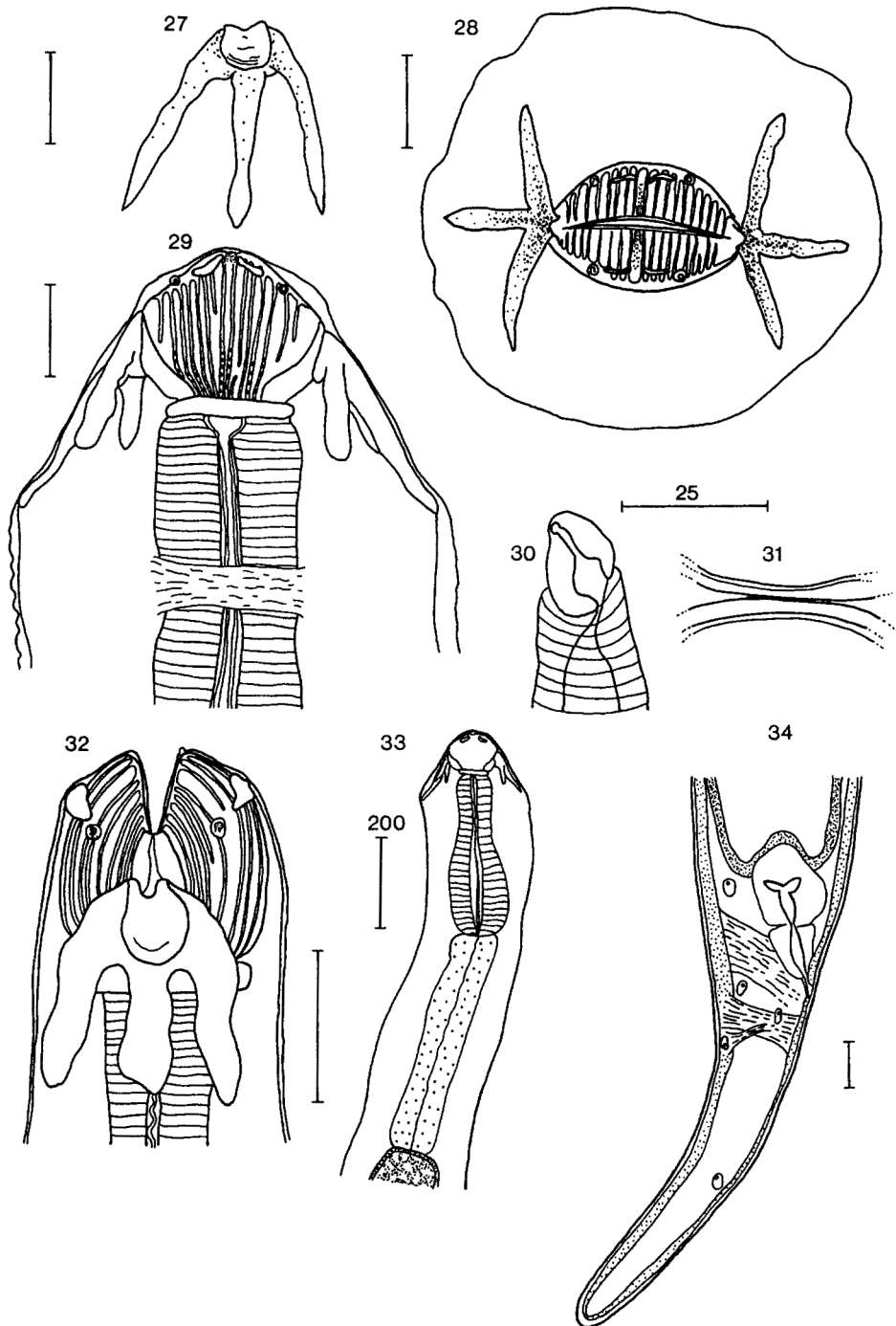
Male. Measurements of allotype given in text; data on morphometric variation are provided in Table II.

Body length 6,570, width 197. Lateral valve of buccal capsule 70 long by 78 wide, bearing 9 complete and 6 incomplete longitudinal ridges (15 in total). Dorsal trident 74 and ventral trident 81 long. Basal ring 9 long. Nerve-ring 139 from anterior of worm. Muscular oesophagus 289 and glandular oesophagus 374 long. Seven pairs of lateral, pedunculate precloacal papillae extending onto caudal alae; alae expanded into sucker-like formation at level of anterior pair of precloacal papillae. Two pairs of sessile adcloacal papillae flanking cloacal opening, one anterior, one posterior. Six pairs of lateral postcloacal papillae: 3 large, pedunculate pairs arising very close together and extending onto caudal alae just posterior to level of cloaca, one pair much longer than and lateral to other 2; further 2 pairs c. $\frac{1}{3}$ – $\frac{1}{2}$ distance between cloaca and end of

tail, more ventral pair larger and pedunculate; isolated pair of papillae, small, situated towards end of tail. Right spicule well developed with simple point, tapering gradually from proximal end, 313 in length. Left spicule similar in form to right but shorter, 148 in length. Tail tapering sharply from anterior third, ending bluntly, without spines, 100 long.

Remarks

No *Camallanus* species presents the same combination of characters as found in *C. siluranae* n. sp. This form is easily differentiated from *C. kaapstaadi*, *C. macrocephalus* (see Fig. 26) and *C. johnei* by its small buccal capsule with fewer longitudinal ridges, well-developed tridents, much greater body length, pre-equatorial vulva, and tail lacking mucrons (in females) and terminal spines (in males). *C. siluranae* shows closest affinities to *C. longicaudatus* Moravec, 1973 and *C. kirandensis* Baylis, 1928 from African fishes, but can immediately be distinguished from the former by a much shorter female tail and from the latter by a lower num-



Figs 27–34. Female *Camallanus siluranae* n. sp. from *Xenopus tropicalis* (specimens from Ivory Coast unless otherwise stated). 27. Trident. 28. Anterior, apical view (specimen from Ebeva, Togo). 29. Anterior, lateral view (holotype). 30. Terminal region of reproductive tract (specimen from Nigeria). 31. Vulva, surface view (specimen from Nigeria). 32. Anterior, dorsal view (specimen from Nigeria). 33. Anterior lateral view (holotype). 34. Tail (holotype). Scale-bars: 50 μ m; unless otherwise indicated.

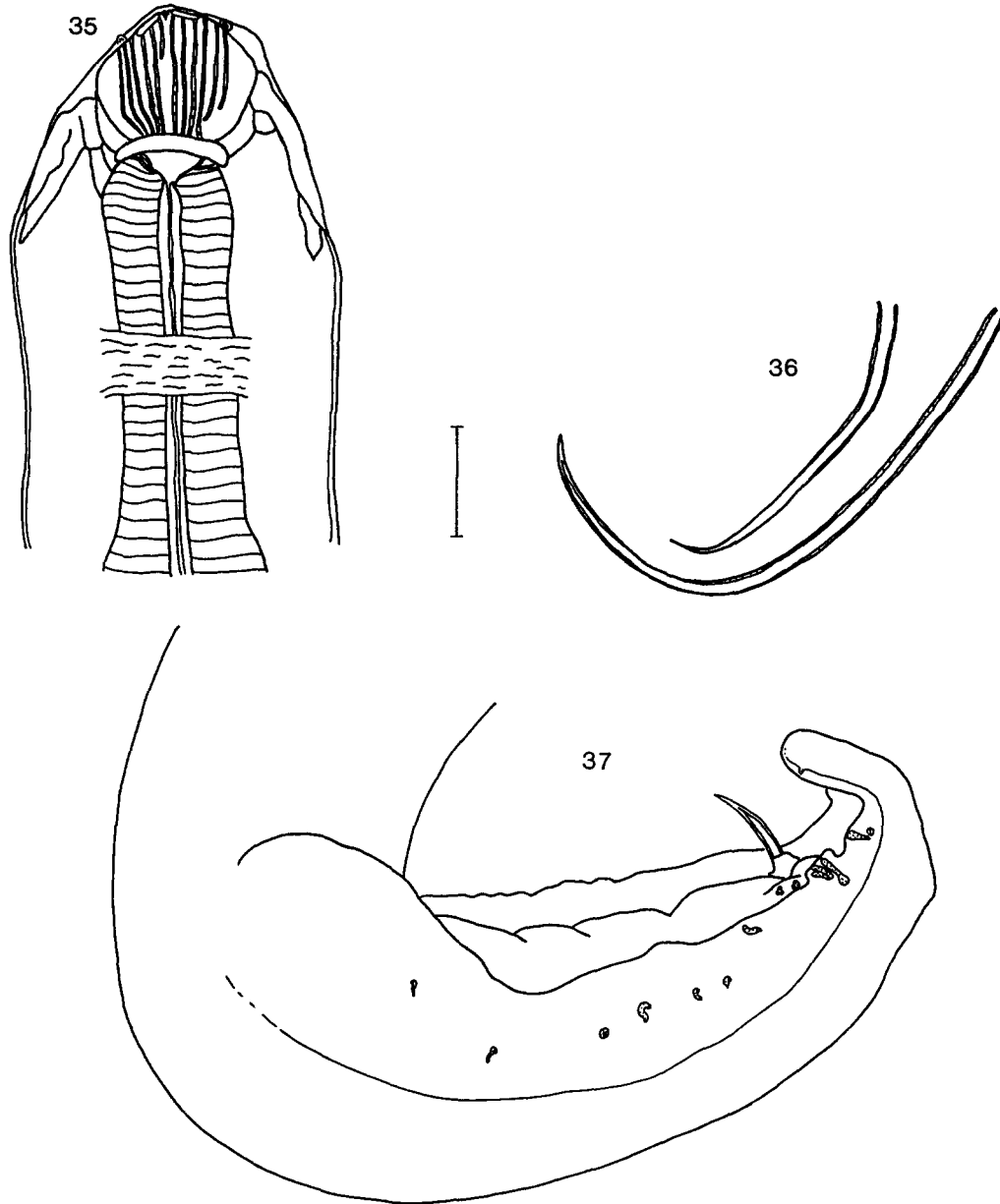
Table II. Morphometric variation (in micrometres) in *Camallanus siluranae* n. sp. from *Xenopus tropicalis*. Sample means given above ranges, with sample size in parentheses.

Locality Sex	Sahibly, Ivory Coast		Ebeva, Togo		Nigeria	
	Male	Female	Male	Female	Male ³	Female ³
Length	5,910 (5)	22,400 (7)	5,790 (4)	19,000 (1)	5,480 (10, 7)	16,600 (9, 4)
	4,720–7,000	12,400–26,900	5,350–6,250		3,830–6,760	8,700–22,400
Width	173 (5)	377 (7)	182 (4)	273 (1)	128 (3, 0)	157 (4, 0)
	143–197	258–447	152–235		106–144	133–194
Buccal capsule valve length	68 (5)	78 (7)	68 (4)	70 (1)	65 (10, 7)	77 (10, 4)
	65–70	70–85	65–74		48–78	54–102
Buccal capsule valve width	82 (5)	93 (4)	78 (2)	81 (1)	78 (10, 7)	97 (7, 4)
	78–90	93–94	76–80		54–93	76–117
No. of incomplete ridges on buccal capsule valve	5–9 (5)	5–8 (3)	4–10 (3)	8 (1)	2–8 (10, 7)	2–7 (7, 4)
No. of complete ridges on buccal capsule valve	9–11 (5)	8–11 (3)	7–9 (3)	8 (1)	7–13 (10, 7)	9–11 (7, 4)
Total number of ridges	14–18 (5)	14–18 (4)	13–17 (3)	16 (1)	12–17 (10, 7)	13–18 (7, 4)
	9 (5)	10 (5)	8 (4)	10 (1)	7 (10, 7)	7 (6, 0)
Basal ring	7–11	9–11	6–10		5–7	6–7
Dorsal trident	81 (5)	113 (4)	90 (4)	109 (1)	68 (10, 7)	76 (10, 4)
	76–96	106–123	80–108		44–81	74–104
Ventral trident	87 (5)	107 (5)	87 (4)	98 (1)	69 (10, 7)	78 (9, 4)
	81–97	87–102	77–104		39–85	70–103
Nerve-ring ¹	152 (5)	177 (5)	140 (4)	143 (1)	149 (7, 4)	149 (4, 0)
	139–167	157–206	124–157		93–191	137–157
Deirid ¹	271 (2)	303 (1)	239 (2)	278 (1)	–	343 (1, 0)
	246–296		220–257			
Muscular oesophagus	290 (5)	344 (7)	271 (4)	339 (1)	262 (10, 7)	305 (10, 4)
	280–303	333–364	261–280		157–318	233–394
Glandular oesophagus	392 (5)	533 (7)	335 (4)	426 (1)	288 (10, 7)	369 (10, 4)
	364–426	485–591	303–356		198–348	285–511
Vulva (%) ²		34 (7)		36 (1)		42 (6, 4)
		28–45				35–46
Right spicule	286 (5)		265 (4)		138 (3, 0)	
	263–313		261–267		122–157	
Left spicule	137 (3)		153 (4)		110 (1, 0)	
	109–154		144–167			
Tail	99 (5)	440 (7)	99 (3)	292 (1)	68 (11, 7)	230 (8, 4)
	74–117	346–484	87–109		37–98	178–341

¹Distance from anterior of worm.²Distance from anterior of worm as a percentage of body length.³Some specimens mounted in Canada balsam; number of these measured for each character follows total sample size.Females all adult with and without larvae *in utero*.

ber of buccal capsule valve ridges. Of the remaining African species, it is distinguished from *C. ctenopomae* Vassiliades & Petter, 1972 by much shorter male spicules, from *C. chelonius* Baker, 1983 and *C. dimitrovi* Durette-Desset & Batcharov, 1974 by the

absence of a complex distal tip of the right spicule and from *C. multiruga* Walton, 1932 by exhibiting smaller buccal capsule valves. In some specimens slight beading of ridges on the posterior surface of the buccal capsule valves was observed. *C. ctenopomae* Vassiliades



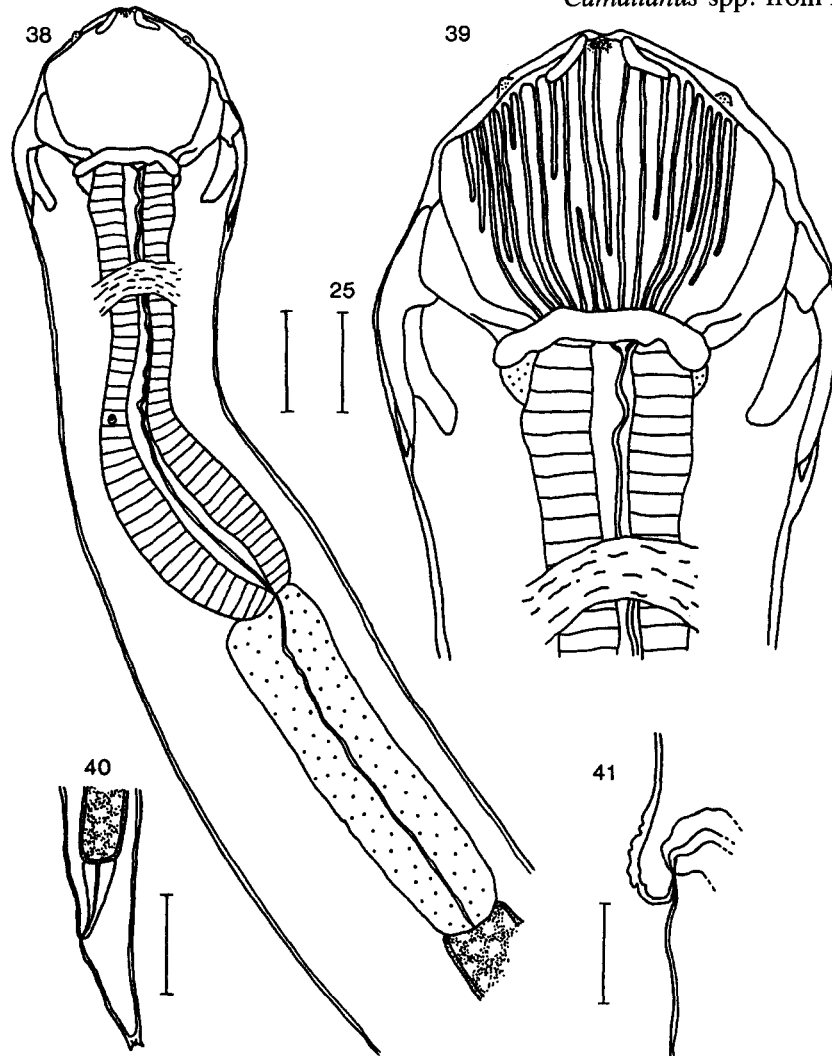
Figs 35–37. Male *Camallanus siluranae* n. sp. from Ivory Coast *Xenopus tropicalis*. 35. Anterior, lateral view (allotype). 36. Spicules (allotype). 37. Caudal region, lateroventral view (allotype). Scale-bar: 50 μ m.

& Petter, 1972 is the only other African representative of *Camallanus* which shows beaded buccal capsule ridges; however, in this species the beading is very well defined (Vassiliades & Petter, 1972) and not restricted to posterior regions of the buccal capsule.

***Camallanus xenopodis* n. sp.** (Figs 38–41,43)

Type-host and locality: *Xenopus laevis laevis* (Daudin) from Transvaal, South Africa (exact locality unknown).

Other record: From *X l. laevis*: South Africa (1). From *X. borealis* Parker: Chemenail-Nandi road, Kenya (2).



Figs 38–41. Female *Camallanus xenopodis* n. sp. from *Xenopus laevis laevis* in the Transvaal, South Africa. 38–39. Anterior, lateral view (holotype). 40. Tail (holotype). 41. Terminal region of reproductive tract (holotype). Scale-bars: 50 μ m; unless otherwise indicated.

Site: Intestine.

Material studied

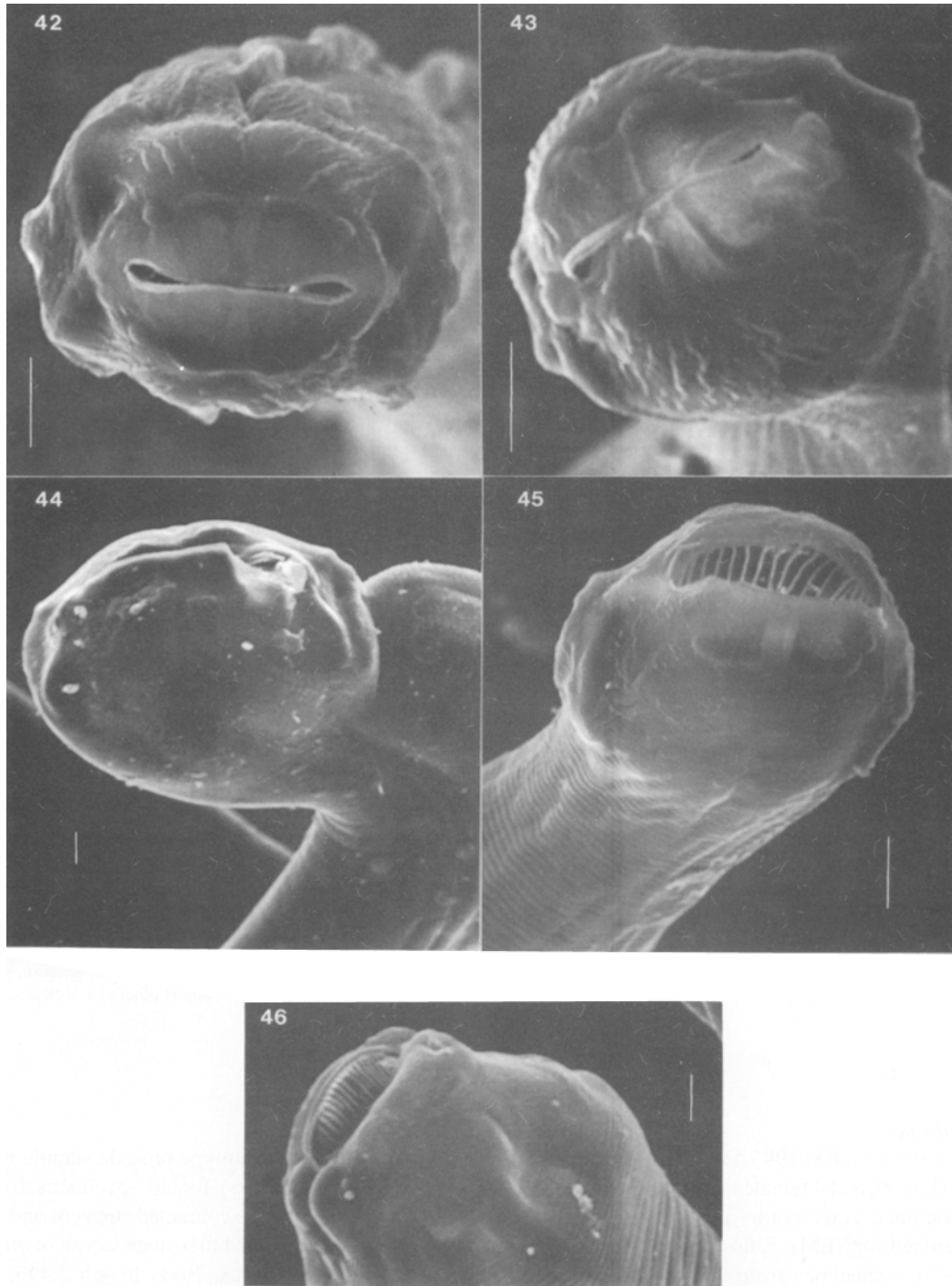
Holotype (female) BM 1993.5159, 1 paratype (female) BM 1993.5160, and 4 female non-type specimens (initially examined as temporary mounts in glycerine but then prepared for SEM), F, hosts imported to UK January, 1976; 1 specimen from vial containing "*Procamallanus slomei*", BM 1975.892, (1); 1 specimen, P, host coll. M.Simmonds, September, 1982 (2).

Description

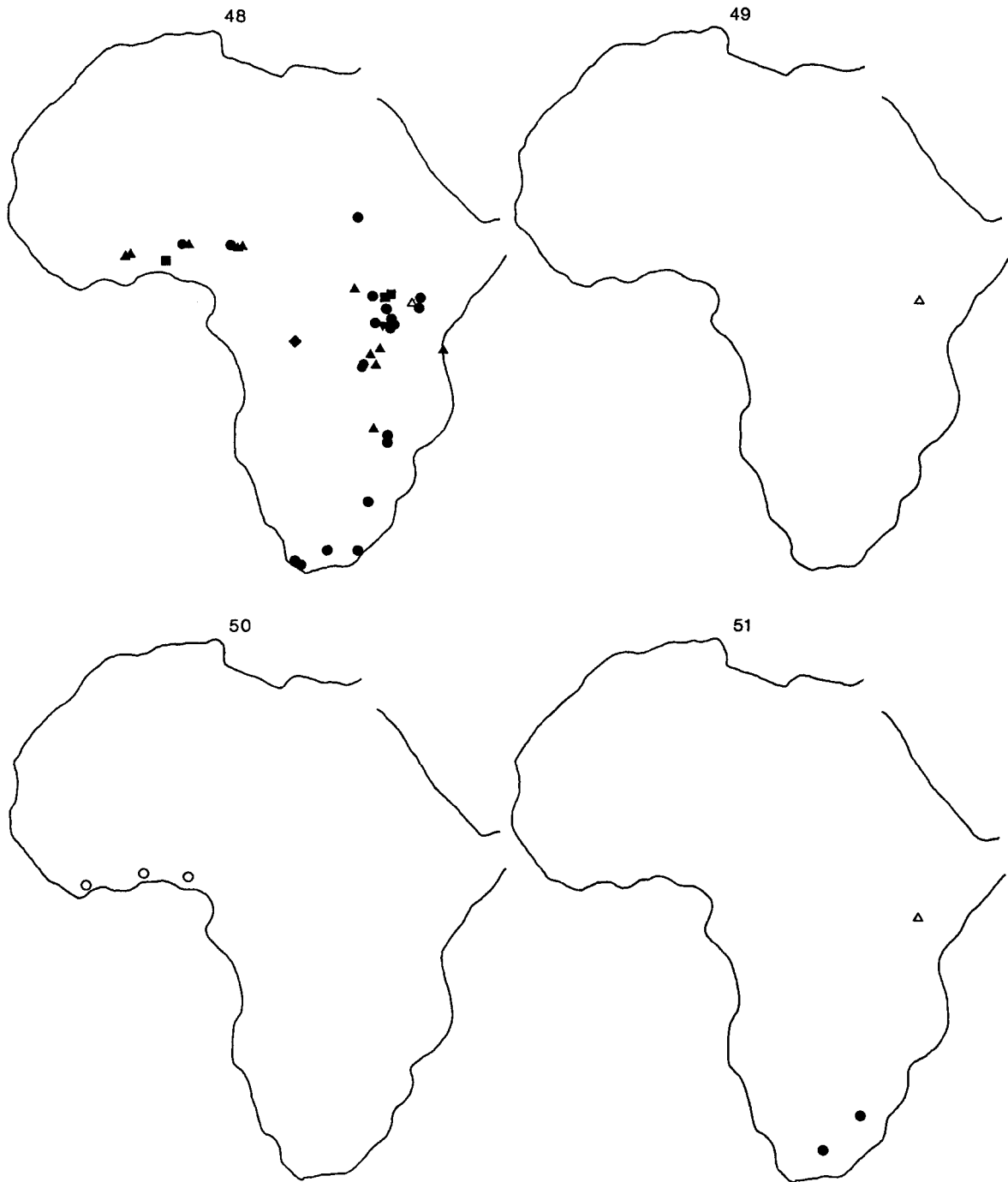
Female

Measurements of holotype precede sample range and mean (in parentheses) for all specimens from type-locality (n = 6) (these contained embryos and developing or fully-developed first stage larvae *in utero*).

Small, thin worms. Body length 2,490, 2,410–3,350 (2,920), width 121, 113–135 (121). Cephalic region not tilted towards ventral side. Small buccal capsule, lateral valve 67, 59–77 (70) long by 86, 74–89 (83) wide, bearing smooth, internal longitudinal ridges: 11, 11–16 complete ridges extending from anterior margin of each valve to posterior edge, 11, 4–11 incomplete



Figs 42–46. Scanning electron micrographs of the anterior of *Camallanus* spp. from clawed toads. 42. Female *C. siluranae* n. sp. 43. Female *C. xenopodis* n. sp. 44. Female *C. macrocephalus* n. sp. 45–46. *C. kaapstaadi* Southwell & Kirshner, 1937. 45. Male. 46. Female. *Scale-bars:* 25 μ m.



Figs 48–51. Host and geographical distribution of *Camallanus* spp. from clawed toads. Host taxa: ●, *Xenopus laevis* subspecies; ▲, *X. muelleri*; △, *X. borealis*; ▼, *X. wittei*; ◆, *X. fraseri* aff.; ○, *X. tropicalis*; ■, *Xenopus* sp. 48. *C. kaapstaadi*. 49. *C. macrocephalus*. 50. *C. siluranae*. 51. *C. xenopodis*.

Table III. Nominal species of *Camallanus*¹ from non-pipid amphibians.

Species	Host(s)	Locality
<i>C. baylisi</i> Karve, 1930	<i>Rana tigerina</i>	India
<i>C. ranae</i> Khera, 1954	<i>R. cyanophlyctis</i>	India
<i>C. nodulosus</i> Gupta, 1959	<i>R. cyanophlyctis</i>	Bangladesh
<i>C. thapari</i> Gupta, 1959	<i>R. tigerina</i>	Bangladesh
<i>C. cynophlyctis</i> Sahay, 1966	<i>R. cyanophlyctis</i>	India
<i>C. bufonis</i> Agrawal, 1967	<i>Bufo</i> sp.	India
<i>C. inglisi</i> Agrawal, 1967	<i>R. tigerina</i>	India
<i>C. tigrinis</i> Johnson, 1969	<i>R. tigerina</i>	India
<i>C. mujibia</i> (Bashirullah & Khan, 1972)	<i>R. cyanophlyctis</i>	Bangladesh
<i>C. alatae</i> Nama & Jain, 1974	<i>R. tigerina</i>	India
<i>C. vlastimili</i> Arya, 1984	<i>R. cyanophlyctis</i>	India
<i>C. pipientis</i> Walton, 1935	<i>R. pipiens</i>	USA
<i>C. multilineatus</i> Kung, 1948	<i>R. catesbeiana</i> ²	? ²
<i>C. mazabukae</i> Kung, 1948	"bullfrog"	South Africa
<i>C. multiruga</i> Walton, 1932	"frog"	West Africa
<i>C. dimitrovi</i> Durette-Desset & Batcharov, 1974	<i>R. occipitalis</i>	Togo
	<i>R. galamensis</i>	

¹Except for *C. nigrescens* (Linstow, 1906), which is of uncertain status and unknown geographical origin (Baker, 1987), all named species are listed; some of the Asian forms are likely to be synonymous (Akram, 1987).

²This species was reported from a captive host at London Zoo and is therefore of uncertain origin (Baker, 1987).

ridges, 22, 15-22 in total. Four thin, sclerotised plates situated on external surface of valves near their anterior margin. Four conspicuous submedian cephalic papillae. Buccal capsule delimited posteriorly by narrow basal ring, 8, 7-10 (8) long. Tridents subequal, large in proportion to capsule size, distinctly trifid; dorsal trident 65, 61-79 (71) and ventral trident 61, 56-73 (67) long. Nerve-ring and deirids 139 and 208 from anterior of worm, respectively. Muscular oesophagus 226, 211-272 (241) and glandular oesophagus 196, 181-272 (235) long. Vulva post-equatorial, 57, 50-57 (54)% of total body length from anterior of worm, associated with distinct projection of body wall. Vagina with very short, thick-walled distal portion and long, muscular, posteriorly-directed proximal portion. Uterus containing developing embryos and larvae. Tail conical, 61, 59-94 (74) long, terminating in 3 mucrons.

Remarks

Although no male specimens were recovered, female *C. xenopodis* n. sp. differ from *C. kaapstaadi*, *C. macrocephalus* and *C. johni* in possessing a relatively

thinner body, smaller buccal capsule valves with fewer longitudinal ridges and a cephalic region which is not tilted towards the ventral side. They most closely resemble *C. mazabukae* Kung, 1948, from an unidentified South African "bullfrog": this species exhibits similar buccal capsule structures to *C. xenopodis* with comparable numbers of lateral valve ridges (Kung, 1948; personal observation). Both forms occupy an intestinal site of infection. However, Kung (1948) described five mucrons on the tail of female *C. mazabukae*, whereas only three are found in *C. xenopodis*. Examination of *C. mazabukae* type-specimens, which are prepared in a permanent mount and are in poor condition, confirmed the presence of at least four mucrons. *C. xenopodis* differs from *C. siluranae* in having shorter tridents, the presence of terminal spines on the female tail, a post-equatorial vulval opening which is guarded anteriorly by a projection of the body wall, and by its much smaller body size. The combination of female characters shown by *C. xenopodis* is sufficient to differentiate this species from all other members of the genus. Amongst representatives of *Camallanus* from non-pipid amphibians, it is distinguished from

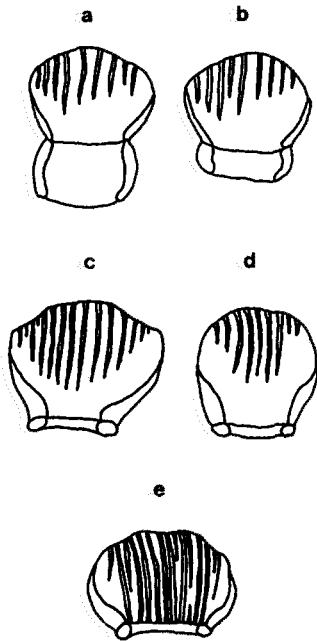


Fig. 47. Buccal capsule valve morphology in the Camallaninae: a. *Paracamallanus* spp. b. Primitive *Camallanus* spp. from Asian fishes; c–d. Most *Camallanus* spp. from amphibians and some species from fish; e. *Camallanus* spp. from clawed toads, a few other amphibian species and remaining forms occurring in fish.

all Asian forms, and the African *C. multiruga* and *C. dimitrovi* (see Table III), by the presence of buccal capsule valves with most ridges extending posteriorly to the basal ring. It can be separated from the remaining amphibian species (*C. pipientis* Walton, 1935 and *C. multilineatus* Kung, 1948), and all other African species, by the small body size of mature females.

Discussion

Two species of *Camallanus*, *C. kaapstaadi* and *C. macrocephalus* n. sp. are found in the oesophagus of clawed toads. As other representatives of the genus typically inhabit the host intestine (for examples see Ivashkin *et al.*, 1971), or in a few cases stomach, it is likely that infection of this site is a derived characteristic. Like other camallanids, *C. kaapstaadi* and *C. macrocephalus* attach to the host mucosa by means of their buccal structures. However, the surface of the host oesophagus is highly contractile and may be more subject to abrasion by ingested material, e.g. during swallowing of bulky prey items, than more posterior regions of the alimentary canal. Ventral tilting of the

cephalic region in *C. macrocephalus* and *C. kaapstaadi*, which is particularly marked in females, may allow the body to lie flat against the surface of the gut wall. In addition to this, the relatively large buccal capsule (in females) and short body length of these species when compared to most intestinal camallanines (for examples see Ivashkin *et al.*, 1971), may facilitate secure attachment and reduced obstructiveness.

Hypotheses concerning evolutionary relationships amongst the Camallaninae Railliet & Henry, 1915 are largely based on the degree to which the adult buccal capsule retains larval characteristics (Stromberg & Crites, 1974; Petter, 1979). In third-stage larvae of this group there is a distinct posterior chamber of the buccal capsule (Campana-Rouget, 1961; Moravec, 1969, 1974), which remains very well developed in adult *Paracamallanus* York & Maplestone, 1926 species and may be represented by the basal ring in members of *Camallanus*. *Paracamallanus* spp. and Asian *Camallanus* spp. with wide basal rings (Stromberg & Crites, 1974; Petter, 1979) have thus been considered to be primitive due to the retention of larval characteristics (the ontogenetic criterion, see Wiley, 1981). In these camallanines the buccal capsule ridges do not reach the posterior edge of the lateral valves, a condition which is also found in most forms from amphibians (including *C. dimitrovi* and *C. multiruga* from Africa) (see Fig. 47). However, representatives of *Camallanus* from *Xenopus* spp. all show ridges extending to the posterior margins of the lateral valves, as do some derived lineages (with narrow basal rings) from fish hosts. The same is also true for *C. mazabukae*, from a South African "bullfrog", and *C. multilineatus* Kung, 1948, which was recorded at London Zoo from a North American ranid and is of uncertain geographical origin (Baker, 1987). The distribution of the above character state suggests that a clade (or clades), which gave rise to species of *Camallanus* from clawed toads, probably diverged from a group parasitic in fishes independently of most forms occurring in other African and Asian amphibians. This is supported by the fact that males of *C. kaapstaadi*, *C. macrocephalus* and *C. siluranae* (the male of *C. xenopodis* is unknown) all lack the distal process of the right spicule found in several species from other amphibians. These include *C. dimitrovi*, *C. pipientis* Walton, 1935 and some *C. baylisi*-like forms from ranids and bufonids on the Indian subcontinent. A complex right spicule point was also described for *C. mazabukae* (see Kung, 1948), but examination of the type-specimen, which is whole-mounted and poorly cleared, does not allow this fact to be confirmed.

C. kaapstaadi shows a very wide geographical range, occurring in *X. laevis* subspecies from South Africa, Rwanda, Uganda, Kenya and Sudan, *X. muelleri* from Tanzania, Ghana and Togo, and both hosts from Zimbabwe, Zaire, Cameroon and Nigeria (see Fig. 48). *X. laevis* and *X. muelleri* are typically found in water bodies from savanna, scrubland or similar open habitats, but *C. kaapstaadi* also infects the highland species *X. borealis* from Kenya, *X. wittei* from montane forest in Rwanda, and in one case was found in a lowland rain forest-dwelling host, *X. fraseri* aff., from Zaire. Other *Camallanus* spp. from clawed toads show more restricted or patchy distributions: *C. macrocephalus* was only recorded at one site in Kenya, from *X. borealis*; *C. xenopodis* occurred in *X. l. laevis* and *X. borealis* in South Africa and Kenya, respectively; while *C. siluranae* was limited to *X. tropicalis*-like clawed toads from lowland rain forest in west Africa (see Figs 48-51).

Females of *C. xenopodis* and *C. mazabukae* resemble *C. kaapstaadi* and *C. macrocephalus* in a relatively short body length, the presence of mucrons and a postequatorial vulva guarded by a projection of the body wall. With respect to the position of the vulva and presence or absence of beaded buccal capsule ridges, mucrons on the female tail and terminal spines on the male tail, both *C. siluranae* and *C. kaapstaadi*-like forms resemble different groups of *Camallanus* spp. more closely than each other (for examples see Petter, 1979). *C. kaapstaadi*, *C. macrocephalus* and *C. siluranae* all share the same pattern of postcloacal papillae: six pairs arranged in groups of three and two pairs with one isolated pair near the end of the tail. However, a similar condition with five or six postcloacal papillae, is found in many *Camallanus* spp. from fish or amphibians, and the primitive *Paracamallanus cyathopharynx* (Baylis, 1923) (see Moravec, 1974). This character state is thus likely to be plesiomorphic and its shared presence in *Camallanus* spp. from clawed toads does not imply monophyly. The male of *C. xenopodis* is unknown, while the male type-specimen of *C. mazabukae* is in poor condition but appears to show the same pattern of postcloacal papillae as described above (personal observation.)

Based on morphological evidence it is suggested that the *Camallanus* fauna of clawed toads arose from at least two separate colonisations, probably by fish parasites, with one giving rise to *C. siluranae* and the other to *C. kaapstaadi*, *C. macrocephalus* and perhaps *C. xenopodis*. *C. mazabukae* from an unidentified South African frog (probably *Pyxicephalus adspersus*,

see Baker, 1987) shows affinities to the latter group, especially *C. xenopodis*, suggesting this clade may also have invaded other amphibian hosts. Two main groupings of clawed toads have been distinguished by molecular and cytogenetic studies (Graf & Fischberg, 1986; Carr *et al.*, 1987; Tymowska, 1991). One, containing *X. tropicalis*, the host of *C. siluranae*, shows chromosome numbers of $2n = 20$ or 40 , while chromosome number in the other grouping (hosts of *C. kaapstaadi*-like species) is $2n = 36$ or multiples of this (see Tymowska, 1991). Both major clades of clawed toads may therefore have been "captured" (Chabaud, 1981), separately, by different lineages of *Camallanus*. As *Xenopus* spp. are fully aquatic and feed underwater (Tinsley, 1981) host transfers of camallanids originally specific to fishes may have been favoured by the ecological similarity of the hosts involved.

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References

- Akram, M. (1987) Revision of the genus *Camallanus* Railliet and Henry, 1915 (Nematoda, Camallanidae) parasitic in amphibians and key to the species. *Karachi University Journal of Science*, **15**, 87-93.
- Avery, R.A. (1971) A preliminary list of parasites collected from reptiles and amphibians in northern Nigeria. *British Journal of Herpetology*, **4**, 217-219.
- Baker, M. (1987) A synopsis of the Nematoda parasitic in amphibians and reptiles. *Occasional Papers in Biology, Memorial University of Newfoundland*, **11**, 325 pp.
- Campana-Rouget, Y. (1961) Remarques sur le cycle évolutif de *Camallanus lacustris* (Zoega, 1776) et la phylogénie des Camallanidae. *Annales de Parasitologie Humaine et Comparée*, **36**, 425-434.
- Carr, S.M., Brothers, A.J. & Wilson, A.C. (1987) Evolutionary inferences from restriction maps of mitochondrial DNA from nine taxa of *Xenopus* frogs. *Evolution*, **41**, 176-188.

- Chabaud, A.G. (1981) Host range and evolution of nematode parasites of vertebrates. *Parasitology*, **82**, 169–170.
- Durette-Desset, M.-C. & Batcharov, G. (1974) Deux nematodes d'amphibiens du Togo. *Annales de Parasitologie Humaine et Comparée*, **49**, 567–576.
- Frost, D.R. (1985) *Amphibian species of the world*. Lawrence, Kansas: Allen Press and The Association of Systematics Collections, 732 pp.
- Graf, J.-D., & Fischberg, M. (1986) Albumin evolution in polyploid species of the genus *Xenopus*. *Biochemical Genetics*, **24**, 821–837.
- Ivashkin, V.M., Sobolev, A.A. & Khromova, L.A. (1971) *Camallanata of animals and man and the diseases caused by them*. *Osnovy Nematologii*, **22**, 388 pp. (In Russian; English edition; Jerusalem: IPST, 1977, 381 pp.)
- Kung, C.C. (1948) On some new species of spirurids from terrestrial vertebrates, with notes on *Habronema mansioni*, *Physaloptera paradoxa* and *Hartertia zuluensis*. *Journal of Helminthology*, **22**, 141–164.
- Loumont, C. (1984) Current distribution of the genus *Xenopus* in Africa and future prospects. *Revue Suisse de Zoologie*, **91**, 725–746.
- Moravec, F. (1969) Observations on the development of *Camallanus lacustris* (Zoega, 1776) (Nematoda: Camallanidae). *Vestník Československé Společnosti Zoologické*, **33**, 15–33.
- Moravec, F. (1974) The development of *Paracamallanus cyathopharynx* (Baylis, 1923) (Nematoda: Camallanidae). *Folia Parasitologica*, **21**, 333–343.
- Petter, A.J. (1979) Essai de classification de la sous-famille des Camallaninae (Nematoda, Camallanidae). *Bulletin du Museum National d'Histoire Naturelle*, Paris, 4^e ser., **1**, sect A., 991–1008.
- Southwell, T. & Kirshner, A. (1937) On some parasitic worms found in *Xenopus laevis*, the South African clawed toad. *Annals of Tropical Medicine and Parasitology*, **31**, 245–266.
- Stromberg, P.C. & Crites, J.L. (1974) Specialization, body volume, and geographical distribution of Camallanidae (Nematoda). *Systematic Zoology*, **23**, 189–201.
- Thurston, J.P. (1970) Studies on some Protozoa and helminth parasites of *Xenopus*, the African clawed toad. *Revue de Zoologie et de Botanique Africaines*, **82**, 349–369.
- Tinsley, R.C. (1973) Observations on Polystomatidae (Monogeneoidea) from east Africa with a description of *Polystoma makreri* n. sp. *Zeitschrift für Parasitenkunde*, **42**, 251–263.
- Tinsley, R.C. (1981) The evidence from parasite relationships for the evolutionary status of *Xenopus* (Anura: Pipidae). *Monitore Zoologico Italiano*, (N.S) Suppl., **15**, 367–385.
- Tinsley, R.C., Kobel, H.R. and Fischberg, M. (1979) The biology and systematics of a new species of *Xenopus* (Anura: Pipidae) from the highlands of central Africa. *Journal of Zoology, London*, **188**, 69–102.
- Tymowska, J. (1991) Polyploidy and cytogenetic variation in frogs of the genus *Xenopus*. In: Green, D.M & Sessions, S.K. (Eds) *Amphibian cytogenetics and evolution*. London: Academic Press, pp. 259–297.
- Vassiliades, G. & Petter, A.J. (1972) *Camallanus ctenopomae* n. sp. (Nematoda; Camallanidae), parasite de *Ctenopoma kingsleyae* Gunther (poisson; Anabantidae) au Senegal. *Annales de Parasitologie Humaine et Comparée*, **47**, 383–389.
- Wiley, E.O. (1981) *Phylogenetics: the theory and practice of phylogenetic systematics*. New York: Wiley, 439 pp.
- Yeh, L.-S. (1960) On *Camallanus johni* sp. nov. collected from *Xenopus* in Tanganyika Territory. *Journal of Helminthology*, **34**, 103–106.