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A redescription of *Chabaudus leberrei* (Bain & Philippon, 1969) (Nematoda: Seuratoidea) from *Xenopus* spp. in Swaziland

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Abstract

Chabaudus leberrei (Bain & Philippon, 1969) is redescribed from the pipid anurans *Xenopus muelleri* (Peters) and *X. laevis laevis* (Daudin) (new host records) in northern Swaziland, based on light and scanning electron microscope studies. The six anterior protuberances characteristic of the genus *Chabaudus* Inglis & Ogden, 1965, are, in *C. leberrei*, formed by bipartite lamellae associated with the internal margins of the three lips. Intraspecific variation in the number and disposition of male caudal papillae and in the development of the cephalic vesicle is documented.

Introduction

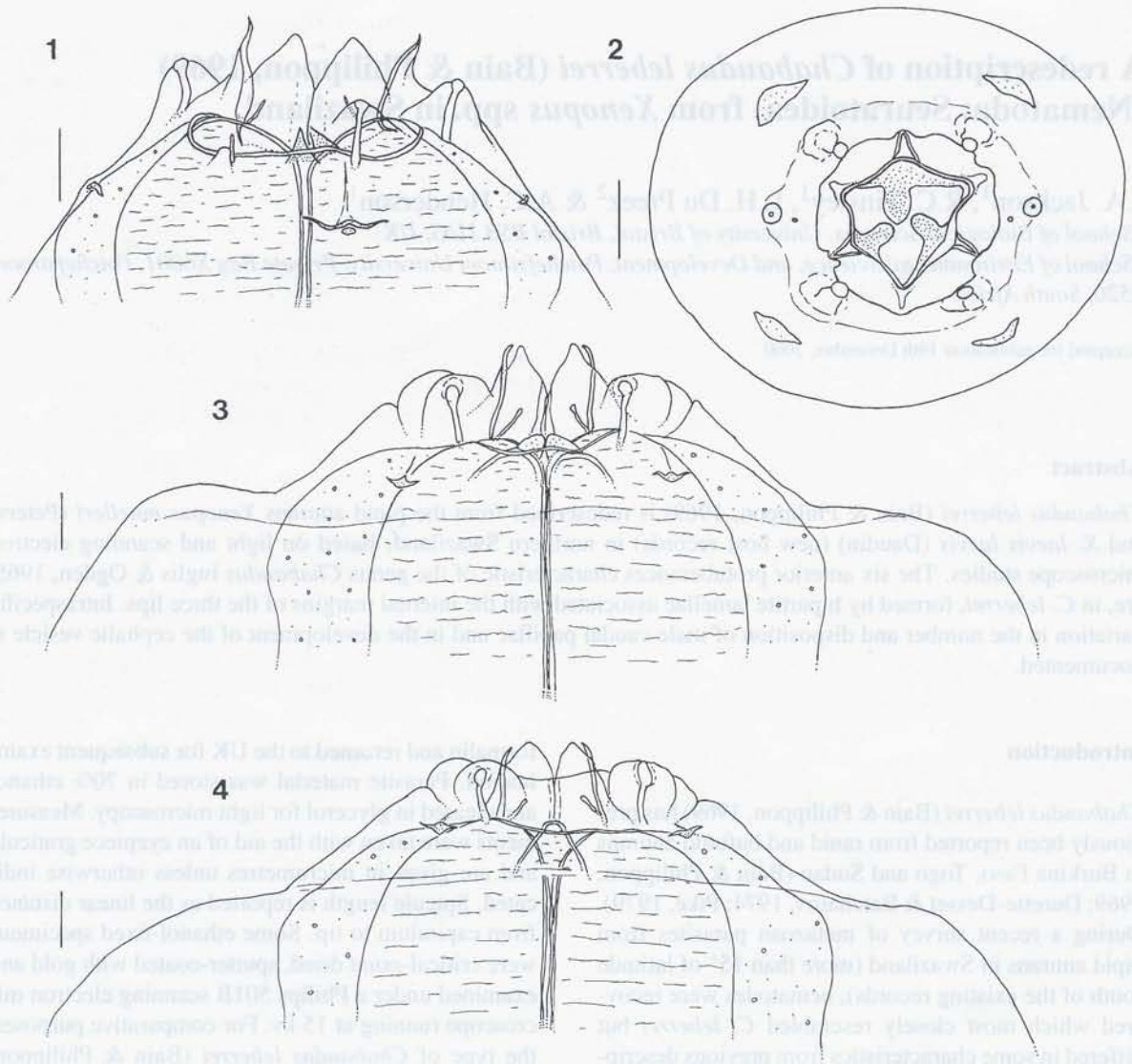
Chabaudus leberrei (Bain & Philippon, 1969) has previously been reported from ranid and bufonid anurans in Burkina Faso, Togo and Sudan (Bain & Philippon, 1969; Durette-Desset & Batcharov, 1974; Pike, 1979). During a recent survey of metazoan parasites from pipid anurans in Swaziland (more than 15° of latitude south of the existing records), nematodes were recovered which most closely resembled *C. leberrei* but differed in some characteristics from previous descriptions of this species. The present study aims to document the morphology of the Swazi specimens (based on light and scanning electron microscope studies) and establish their taxonomic status.

Materials and methods

Six *Xenopus muelleri* (Peters) and two *X. laevis laevis* (Daudin) were collected from pools alongside the Tshaneni/Mliba road, northern Swaziland on 11th December, 1999. Specimens were returned live to the laboratory in Bloemfontein, RSA. Here two of six *X. muelleri* specimens were dissected (within 72 hours post-capture) and nematodes recovered fixed in hot 70% ethanol. The remaining hosts were fixed in 10% formalin and returned to the UK for subsequent examination. Parasite material was stored in 70% ethanol and cleared in glycerol for light microscopy. Measurements were taken with the aid of an eyepiece graticule and are given in micrometres unless otherwise indicated. Spicule length is reported as the linear distance from capitulum to tip. Some ethanol-fixed specimens were critical-point dried, sputter-coated with gold and examined under a Philips 501B scanning electron microscope running at 15 kv. For comparative purposes, the type of *Chabaudus leberrei* (Bain & Philippon, 1969) Baker, 1987 (=*Gendria leberrei*) was borrowed from the Museum National d'Histoire Naturelle, Paris (specimen no. MNHN 142 NN).

Chabaudus leberrei (Bain & Philippon, 1969)

Previous records: (As *Gendria leberrei*.) River Leraba, at Dagoidougou, Burkina Faso in *Bufo regularis* Reuss (type-host and locality, Bain & Philippon, 1969); Lomé, Togo in *Rana occipitalis* (Günther) (Durette-Desset & Batcharov, 1974); Khartoum, Sudan in *R. occipitalis* (see Pike, 1979).
New host and geographical records: *Xenopus muelleri* (Peters) and *X. laevis laevis* (Daudin) at disused quarry next to Tshaneni/Mliba road, Swaziland (25°59′25″S,



Figures 1–4. Anterior morphology of *Chabaudus leberrei* (Bain & Philippon, 1969) from *Xenopus muelleri*. 1-4. Cephalic region (♀). 1. Sublateral view. 2. Apical view (note: position of inner labial papillae obscured by buccal lamellae). 3. Ventral view. 4. Dorsal view. *Scale-bars*: 10μ. (3-4. Specimen with apical region retracted, forming shallow concavity in anterior surface of cephalic vesicle.)

31°44′22″E). Altitude 320m.
Infection levels: 2/2 *X. l. laevis* infected (mean abundance 7.5, intensity 5-10); 5/6 *X. muelleri* infected (mean abundance 5.8, intensity 0-22).
Site: Lower intestine and rectum.
Ecological data: Hosts were recovered on 11th December, 1999 from two small adjacent pools, approximately 15 × 15 and 3 × 10m, both with dense marginal vegetation. *X. l. laevis* were taken in the same traps as *X. muelleri*.
Material studied: 27 specimens from *X. muelleri* (14♂, 13♀) and 11 (5♂, 6♀) from *X. l. laevis*.

Description (Figures 1-4, 6-18)

General. Long, slender worms with bulbous cephalic region. Triangular oral opening delimited by 3 bipartite lamella-like formations (=buccal lamellae) forming inner margins of cephalic labia and giving appearance of 6 apical protuberances. Six inner and 6 outer labial papillae, equally spaced in lateral, subdorsal and subventral sectors. Inner labial papillae overlying bases of buccal lamellae. Lateral outer labial papillae reduced, lying centripetal, and just ventral to, amphids. Four crescent-like cephalic papillae, 2

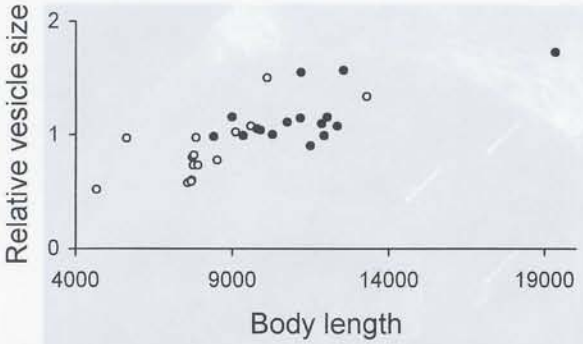


Figure 5. Scatterplot of relative cephalic vesicle size (distance of cephalic vesicle posterior margin from anterior of worm: distance of nerve-ring from anterior of worm) against body length in male (○) and female (●) *Chabaudus leberrei* (Bain & Philippon, 1969). Plotted data were significantly correlated for both males (r=0.72, n=15, P<0.01) and females (r=0.69, n=16, P<0.01).

ventrolateral, 2 dorsolateral, each with filamentous process extending anteriorly to near base of corresponding outer labial papilla. Base of buccal cavity guarded by 2 subventral onchia and larger dorsal onchium. Well-developed cephalic vesicle arising on marked subcuticular collar anteriorly (giving anterior region bulbous appearance), showing marked positive allometry relative to other forebody characters (Figure 5). Subcuticular cross-section markedly attenuated in region underlying cephalic vesicle. Lateral alae continuous with posterior margin of cephalic vesicle and extending to just posterior of deirids. Oesophagus divided into anterior and posterior sections by valve at level of nerve-ring; basal region of posterior section glandular, containing further valve-like formation.

Female. Measurements based on gravid worms, 10 from *X. muelleri*, 6 from *X. l. laevis* (data in parentheses); ranges precede means.

Body 8.39-19.34, 11.32 (8.98-12.54, 11.34) mm long, 165-421, 223 (210-268, 242) wide. Oesophagus total length 423-503, 457 (454-514, 484); anterior region 173-214, 192 (194-212, 200). Cephalic vesicle extending 163-348, 207 (196-323, 242) from anterior. Nerve-ring 168-201, 188 (170-206, 190), deirids 364-496, 411 (359-485, 427) and excretory pore 390-548, 443 (387-488, 455) from anterior end. Anterior ovary (with blind end in anterior half of body) reflexed twice anteriorly, then extending posteriorly beyond level of vulva to unite with oviduct (Figure 7). Posterior ovary (blind end in posterior half of body) reflexed once in posterior and once in anterior region of body, connecting with oviduct anterior to level of vulva. Uteri becoming constricted and uniting just anterior to level of vulva, connecting to genital opening via straight, muscular ovejector. Vulval opening 4.97-10.96, 6.71 (5.03-7.38, 6.55) mm, or 57-65, 59% (54-60, 58%) of total body length, from anterior, marked by external protuberance. Tail 165-263, 199 (170-258, 222) long, tapering gradually from level of anus, markedly attenuated in posterior third and terminating in tiny spine (distal extremity of tail sometimes partly eroded). Some specimens bearing 1-2 pairs of ventral papillae in mid-tail region (comparable to male caudal papillae). Phasmids 65-92, 79 (66-117, 100) from tail tip. Eggs thin-shelled, 54-59, 56 × 43-52, 46 (54-57, 56 × 44-46, 45); contents cleaved in distal regions of uteri.

Male. Measurements and counts based on adult worms, 9 from *X. muelleri*, 5 from *X. l. laevis* (data in parentheses); ranges precede means.

Body 7.58-13.29, 8.43 (5.61-10.10, 8.45) mm long, 156-297, 190 (173-256, 203) wide. Oesophagus total length 408-436, 417 (405-462, 439); anterior region 165-186, 174 (178-199, 190). Cephalic vesicle extending 98-243, 138 (168-271, 199) from anterior. Nerve-ring 164-191, 177 (173-183, 180), deirids 330-449, 383 (310-447, 406) and excretory pore 358-467, 404 (338-495, 439) from anterior end. Caudal region with ventrad curvature. Ventral caudal musculature prominent: posterior muscle series obliquely orientated (extending postero-ventrally towards mid-line from lateral attachments) in area between pseudosucker and posterior 1/3 of tail; 19-26, 21.4 (18-23, 21.2) right-hand and 18-27, 23.4 (14-22, 19.2) left-hand blocks anterior to anus. Sucker-like formation (= pseudosucker) 356-546, 408 (356-501, 452) anterior to anus, composed of 9-16, 12.6 (8-14, 11.8) right-hand and 9-16, 12.4 (11-14, 12.2) left-hand lateral muscle blocks radiating from ventral attachments in mid-line. Pseudosucker not associated with permanent surface feature in specimens examined by SEM. Spicules complex, subequal, bluntly pointed; left 188-219, 205 (201-253, 228); right 183-214, 203 (188-276, 231) long. Gubernaculum 23-31, 27 (26-34, 30) long. Subventral pre-anal papillae variable in number and disposition (see below): 4-7 (5-7) per side; anteriormost 584-893, 713 (541-950, 744) forward of anus. Large, ventral unpaired papilla in mid-line, 26-77, 52 (52-90, 72) anterior to anus. One pair of lateral papillae at, or just posterior to, level of anus. Four more posterior postanal papilla pairs, variably arranged (see below): first (counting from anus) 10-36, 26 (15-46, 30), second 57-83, 64 (46-98, 64), third 65-105, 80

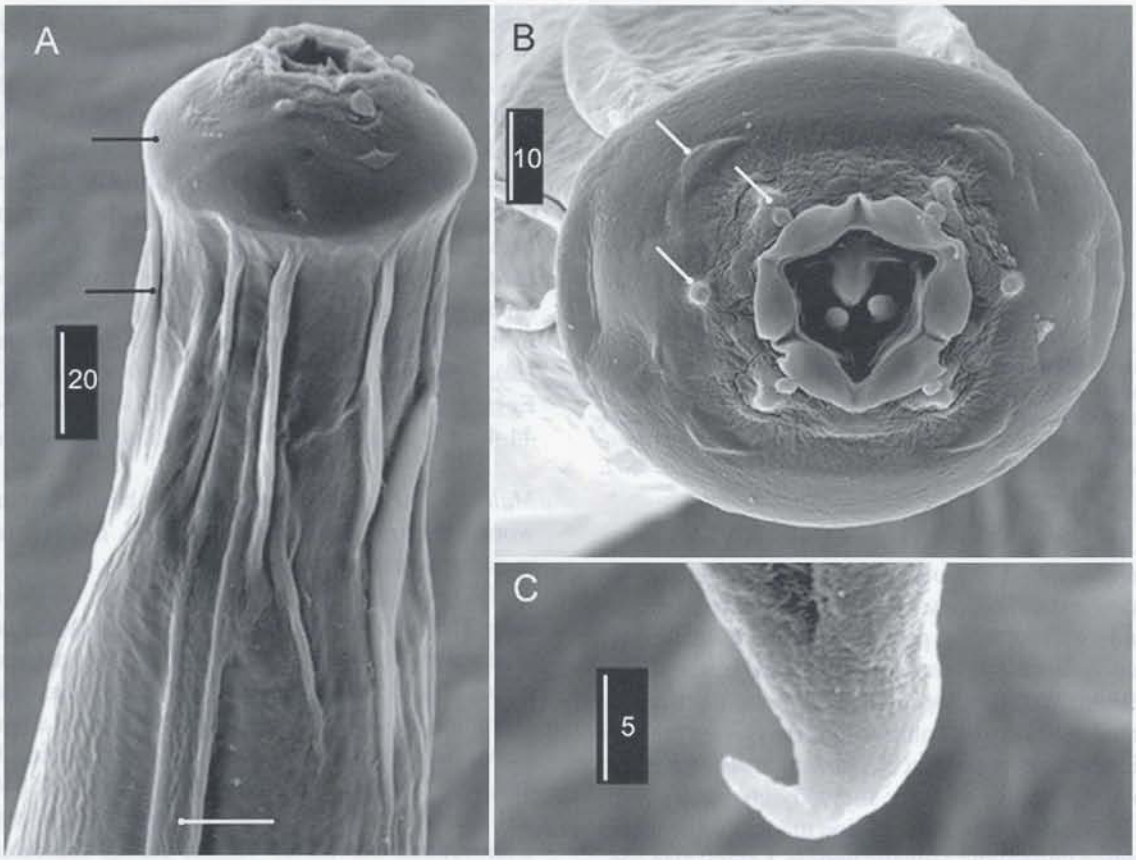


Figure 6. Scanning electron micrographs of *Chabaudus leberrei* (Bain & Philippon, 1969) (♀) from *Xenopus muelleri*. A. Anterior, lateral view, with cephalic vesicle and lateral ala collapsed by SEM preparation; pointers indicate: subcuticular collar (top), folds formed by collapsed cephalic vesicle (middle), collapsed lateral ala (bottom). B. Cephalic region, apical view; pointers indicate: cephalic papilla (top), subdorsal outer labial papilla (middle), amphid (bottom); note: position of inner labial papillae obscured by buccal lamellae. C. Tail tip.

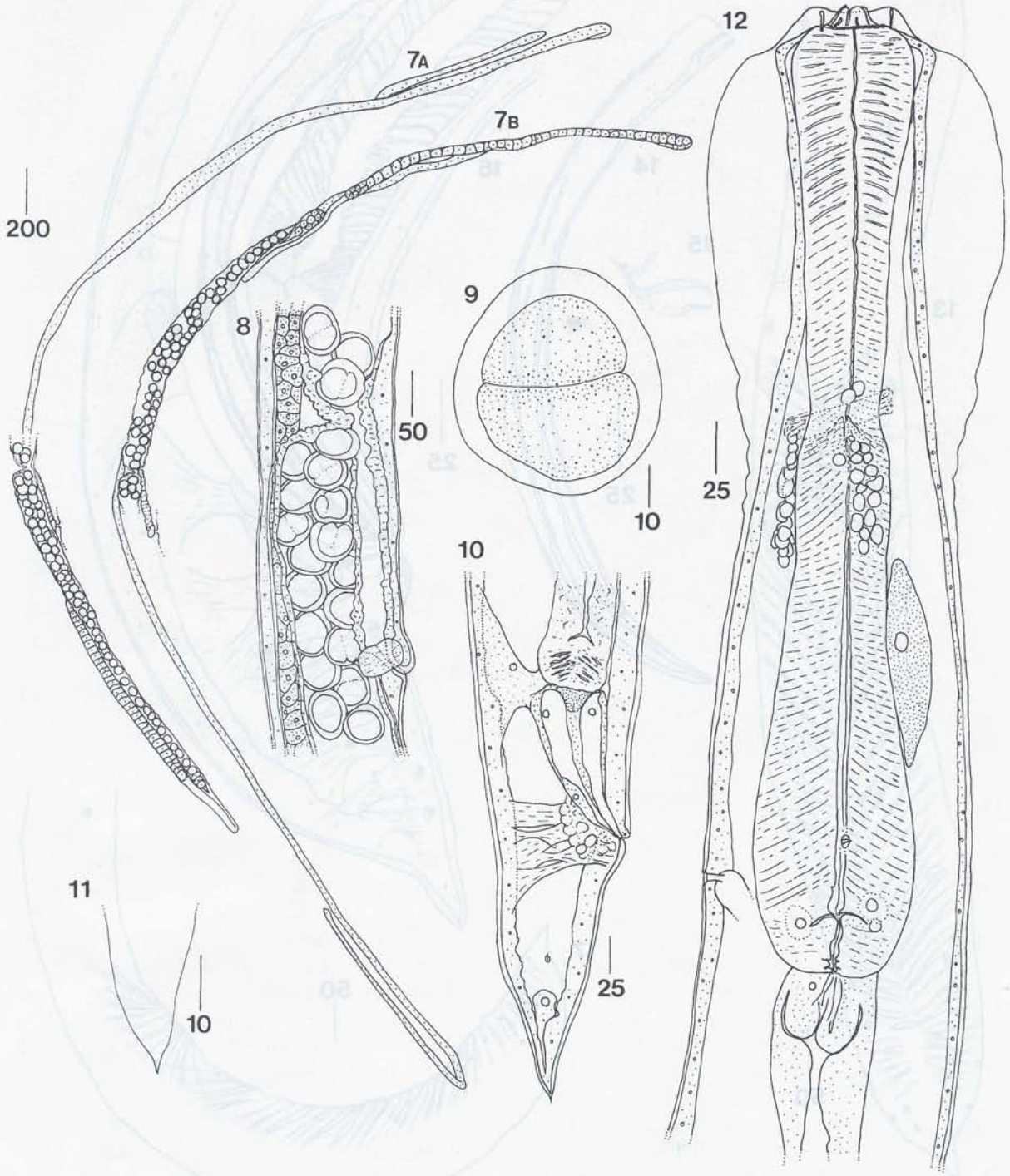
(65-126, 92) and fourth 72-112, 84 (95-157, 120) from level of anus. Phasmids 72-112, 84 (72-129, 91) from tail tip. Tail 147-170, 155 (164-219, 186) long, attenuated in posterior third and terminating in tiny spine.

Variation in male caudal papilla pattern

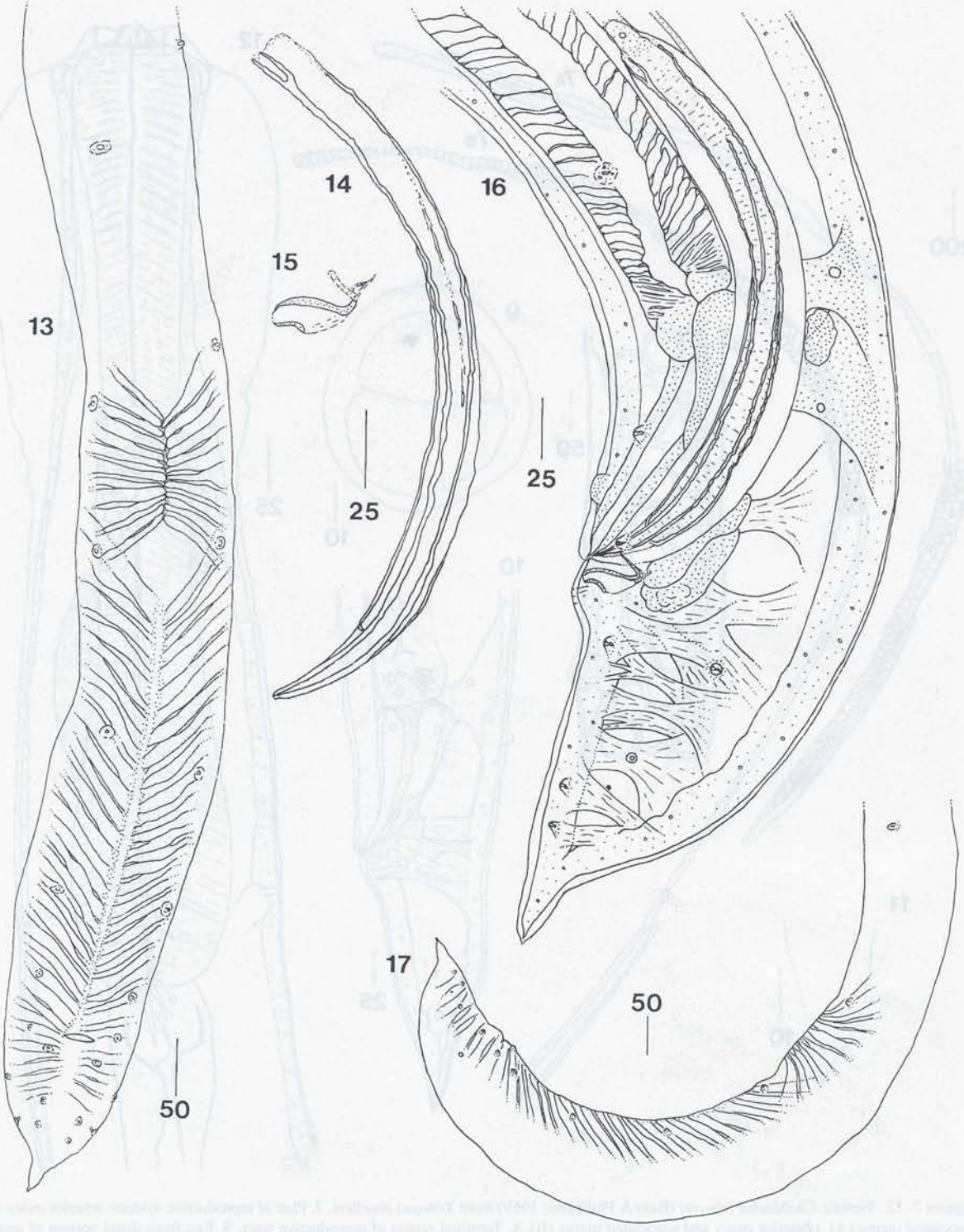
Two dispositions of male postanal papillae were observed. One pair was always present near the level of the anus in a lateral position. Other postanal papillae were arranged either in a ventral row of 4, or with one (the third counting from the anus) displaced laterally (Figure 18). The latter distribution was most common, occurring on both sides in 17/19 specimens examined in detail (4 from *X. l. laevis*, 13 from *X. muelleri*). The alternative configuration occurred on both sides in one male (from *X. muelleri*) and on one side in another (from *X. l. laevis*). Between 4 and 7 pre-anal papillae (Figure 19) were found per side (10-14 per worm), sometimes arranged asymmetrically, with a maximum difference of 2 between sides. There was a tendency for the first 2 papilla pairs anterior to the anus to be in close proximity. However, the distribution of remaining pre-anal papillae was inconsistent, and, where numbers differed between worms, the homology of particular papilla pairs (or asymmetrically distributed papillae) was unclear (Figure 19). Pre-anal papilla distribution was not related to host identity: the range of distributions found in specimens from *X. muelleri* being inclusive of the patterns observed in those from *X. l. laevis*.

Discussion

Chabaudus leberrei was originally described (as *Gendria leberrei*) on the basis of a single specimen from *Bufo regularis* in Burkina Faso (Bain & Philippon, 1969) and redescribed from *Rana occipitalis* in Togo



Figures 7–12. Female *Chabaudus leberrei* (Bain & Philippon, 1969) from *Xenopus muelleri*. 7. Plan of reproductive system: anterior ovary and associated uterus (A), posterior ovary and associated uterus (B). 8. Terminal region of reproductive tract. 9. Egg from distal portion of uterus. 10. Tail, lateral view. 11. Tip of tail. 12. Anterior, lateral view. Scale-bars with length indicated below.



Figures 13–17. Male *Chabaudus leberrei* (Bain & Philippon, 1969) from *Xenopus muelleri*. 13. Caudal region, ventral view. 14. Spicule. 15. Gubernaculum. 16-17. Caudal region, lateral views. Scale-bars with length indicated below or above.

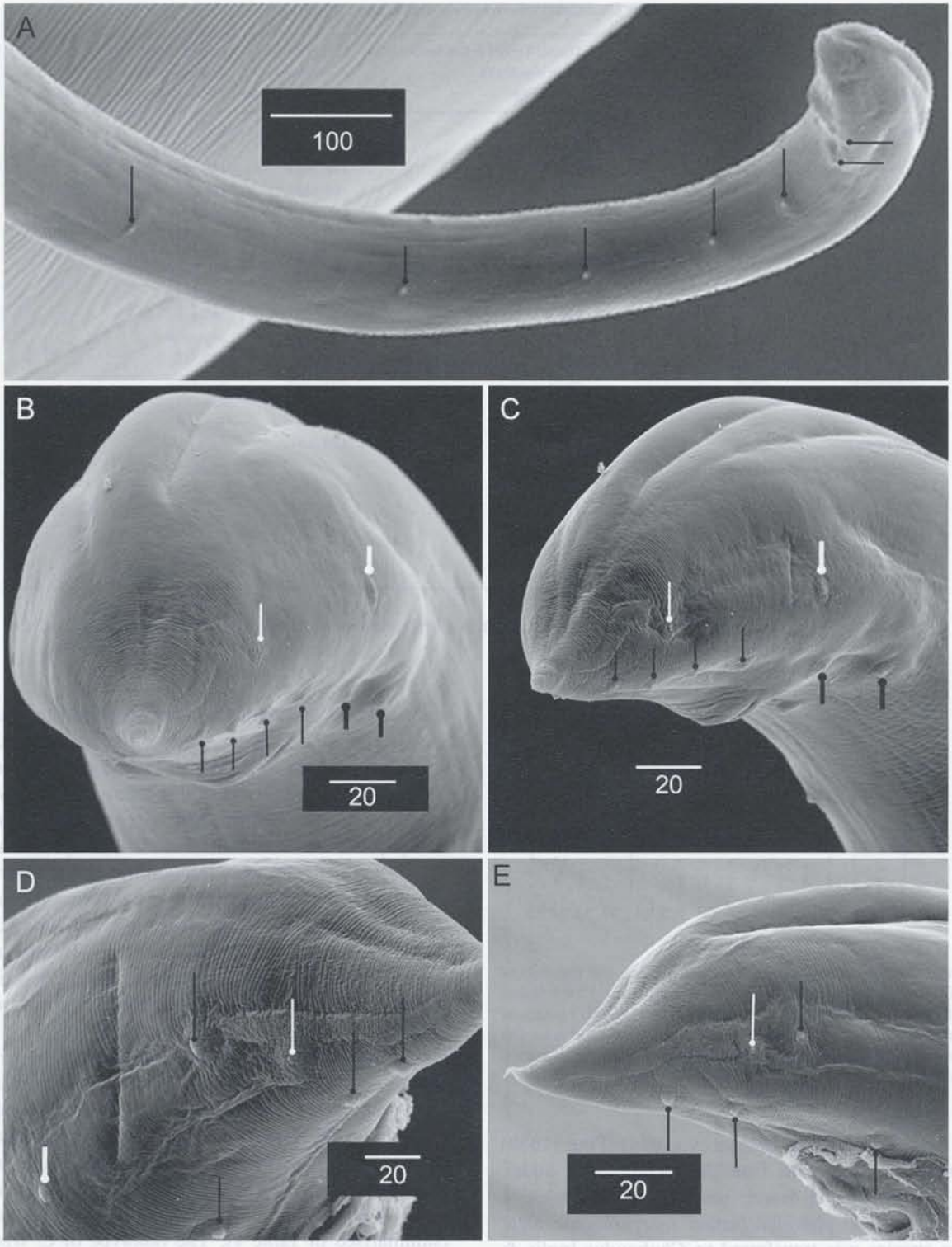


Figure 18. Scanning electron micrographs of *Chabaudus leberrei* (Bain & Philippon, 1969) (♂) from *Xenopus muelleri*. A. Caudal region, subventral view; pointers indicate pre-anal papillae. B-C. Tail. Pointers indicate: ventral row of four postanal papillae (pointer tip: •), posterior pre-anal papillae (●), phasmid (○), anterior lateral postanal papilla (○). B. Subapical view. C. Lateral view. D-E. Tail of specimen with different disposition of postanal papillae (homologous papilla pairs identified as for B-C). Note: one pair of postanal papillae is displaced laterally.

Table 1. Morphometric ranges reported for *Chabaudus leberrei* (Bain & Philippon, 1969).

Author	Bain & Philippon (1969)	Durette-Desset & Batcharov (1974)	Pike (1979)	Present study
Host	*Bufo regularis*	*Rana occipitalis*	*R. occipitalis*	*Xenopus* spp.[1]
Locality	Dagoidougou, Burkina Faso	Lomé, Togo	Khartoum, Sudan	Tshaneni-Mliba road, Swaziland
Body length (mm)	9.4♂	13.35♂	10.00-14.58♂	5.61-13.29♂
		16.90♀	12.11-18.42♀	8.39-19.34♀
Body width	190♂	250♂	140-260♂	156-297♂
		350♀	160-240♀	165-421♀
Cephalic vesicle length	110♂			98-271♂
				163-348♀
Nerve-ring*	190♂	180♂	150-200♂	164-191♂
		135♀	170-220♀	168-206♀
Deirids*	455♂	485♂		330-449♂
		280♀		359-496♀
Excretory pore*	510♂	485♂	350-430♂	338-495♂
		275♀	400-500♀	387-548♀
Oesophagus	565♂	485♂	380-550♂	405-462♂
		290♀	410-480♀	423-514♀
Spicules	340	270	220-270	183-276
Vulva (mm)*		7.10	4.64-6.84	4.97-10.96
Egg length		60		54-60
Egg width		40		43-52
Tail	180♂	180♂	110-210♂	147-219♂
		240♀	130-190♀	165-263♀
n	1♂	1♂	10♂	14♂
		1♀	8♀	16♀

*Distance from anterior end.

[1]Overall ranges for specimens from *Xenopus muelleri* (fixed in hot 70% ethanol or dissected from formalin-fixed hosts) and *X. laevis laevis* (dissected from formalin-fixed hosts).

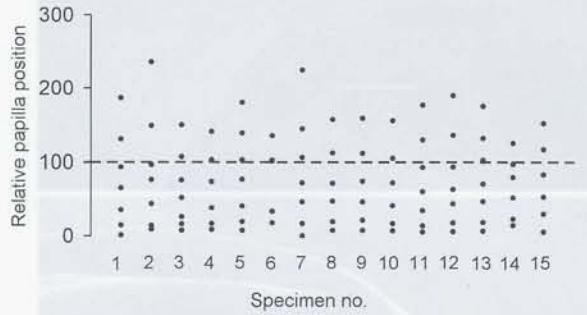


Figure 19. Variation of pre-anal papilla number and distribution in *Chabaudus leberrei*. Lateral papilla disposition in 15 specimens (1-10 from *Xenopus muelleri*, 11-15 from *X. laevis laevis*): positions relative to anus given as percentage of distance between anus and posterior edge of pseudosucker. Dashed line indicates pseudosucker position.

by Durette-Desset & Batcharov (1974). Pike (1979) considered specimens from *R. occipitalis* in Sudan to conform to the description by Durette-Desset & Batcharov and provided further morphometric data. The species was transferred to *Chabaudus* Inglis & Ogden, 1965 by Baker (1987). Specimens from *Xenopus* spp. in Swaziland fall outside the previously reported variation in *C. leberrei* due to the presence of anterior lateral alae and four to seven subventral male pre-anal papillae per side. Anterior alae were recorded as absent by Bain & Philippon (1969) and not mentioned by Durette-Desset & Batcharov (1974), who respectively described five and six pairs of male pre-anal papillae. A rexamination of the type-specimen of *C. leberrei* (MNHN 142 NN) confirmed that anterior lateral alae are present, and that the pattern of caudal papillae falls within the range observed during this study. Potentially significant differences are also apparent amongst morphometric data for *C. leberrei* in the literature, and between these existing records and material studied here. The single female measured by Durette-Desset & Batcharov (1974) may have been an abnormal specimen or even have belonged to a different species. When compared to the smaller male from the same study, and to other reported material of either sex, it had a much shorter oesophagus and more anterior nerve-ring, deirids and excretory pore (Bain & Philippon, 1969; Pike, 1979; present study) (summarised in Table 1). The holotype of *C. leberrei* (see Bain & Philippon, 1969) was described with a longer oesophagus and spicules than other material subsequently identified with this taxon (Table 1).

However, new observations on the type-specimen suggest that disparities could have arisen from the exact nature of the measurements used in different studies. Spicule length, if taken as the linear tip to capitulum distance (rather than a curvilinear measurement), is 219 (personal observation), falling within the ranges reported elsewhere (Table 1). The oesophagus is estimated (allowing for fragmentation of the holotype and excluding the posterior projection at the junction with the intestine) to have measured less than 500 from anterior end to base (personal observation), also comparable with other records. There was some host-related morphometric variation in material from the two *Xenopus* species. In particular, some males from *X. l. laevis* possessed much longer spicules than any specimens from *X. muelleri*. However, overlap in this and all other morphometric and qualitative characters was substantial, and the overall range of variation for specimens from both hosts was inclusive, or near inclusive, of the pattern occurring in the *C. leberrei* type (personal observations). The present record, therefore, extends the known range of this species southwards by over 15° of latitude and establishes its ability to infect representatives of a third anuran family (pipids).

Two potentially useful taxonomic characters demonstrated significant intraspecific variation in *C. leberrei*. The extent of the cephalic vesicle (Figure 5) shows strong positive allometry relative to other forebody characters. In smaller worms the vesicle terminates short of the nerve-ring, but may extend well beyond this level in larger specimens. Considerable variation was also noted in the disposition and number of male caudal papillae (Figures 13, 16-19), and one or two pairs of ventral postanal papillae were variably present or absent in females. The six nominal species of *Chabaudus* (see Baker, 1987) have all been described with six anterior lip-like formations (or equivalent structures) (Bain & Philippon, 1969; Inglis & Ogden, 1965; Puylaert, 1970; Le-Van-Hoa & Pham-Ngoc-Khue, 1971; Durette-Desset & Batcharov, 1974; Afonso Roque, 1981). Chabaud (1978) referred to an oral opening with three bi-lobed lips. Present observations confirm that the inner margins of the three lips in *C. leberrei* are formed by bipartite lamella-like structures, giving the appearance of six anterior protuberances (see Figures 1-4, 6A,B). These formations are a key diagnostic feature of *Chabaudus* (see Baker, 1987), but have not previously been characterised by SEM.

Acknowledgements

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