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The genus *Oligolecithus* Vercammen-Grandjean (Digenea: Telorchiidae) from *Xenopus* spp. (Anura: Pipidae), with a description of *O. siluranae* n. sp. from *X. tropicalis* (Gray) in Ghana

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Abstract

The taxonomy, host range and geographical distribution of *Oligolecithus* Vercammen-Grandjean, 1960, a genus of telorchiid digeneans from *Xenopus* spp. in Africa, is reviewed. *O. jonkershoekensis* Pritchard, 1964 is established as a junior synonym of *O. elianae* Vercammen-Grandjean, 1960, and *O. siluranae* n. sp. is described from *X. tropicalis* in Ghana. These two species are differentiated by variations in body length, testicular arrangement and ventral sucker width in proportion to body size. *O. elianae* occurs in *X. laevis laevis* from South Africa and Zimbabwe (new locality record), *X. l. poweri* from Zaire, *X. l. victorianus* from Zaire, Uganda and Rwanda (new locality record), *X. l. bunyoniensis* (new host record) from Uganda and *X. l. sudanensis* from Sudan (new host and locality record). It is also found in *X. wittei* from Uganda and Zaire and *X. vestitus* (new host record) from Uganda. The host of *O. siluranae* belongs to a separate species group within the genus *Xenopus* from the hosts of *O. elianae*; this "*tropicalis*" group is phylogenetically isolated, but it also occurs in a different biotype, lowland tropical rain forest, ecologically distinct from the other known host species.

Introduction

Two species of the telorchiid digenean genus *Oligolecithus* Vercammen-Grandjean, 1960 have been described: *O. elianae* Vercammen-Grandjean, 1960 and *O. jonkershoekensis* Pritchard, 1964. The latter is considered a junior synonym of *O. elianae* by some authors (Macnae *et al.*, 1973). Both are known only from southern and central Africa in subspecies of the African clawed toad *Xenopus laevis* (see Vercammen-Grandjean, 1960; Pritchard, 1964; Thurston, 1970 [but see also Tinsley, 1973]; Macnae *et al.*, 1973; Fischthal, 1977). In addition, Tinsley *et al.* (1979) reported *Oligolecithus* sp. from *X. wittei* in highland areas of central Africa. Prudhoe & Bray (1982) provided a generic diagnosis of *Oligolecithus* but did not consider the validity of the species. The present study aims to establish the specific status of material from different hosts and geographical areas.

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 transferred to the surface of a slide and fixed under coverslip pressure in 4% formal saline. Other specimens were obtained from the dissection of toads which had been killed and preserved in the field (in some cases these hosts were borrowed from museum collections). All material was stained in alum carmine, dehydrated along a series of ethanols, cleared in xylene and mounted in Canada balsam. Specimens were examined under a light microscope (Zeiss); measurements were taken with an ocular micrometer and are given in micrometres.

Materials
Where locality records 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 4% formal saline or dissected from preserved hosts, respectively.

Specimens borrowed from the collections of The Natural History Museum, London and the Musée Royal de l'Afrique Centrale, Tervuren, Belgium are identified by the abbreviations BM and MRAC, respectively (which precede individual specimen numbers).

***Oligolecithus elianae* Vercammen-Grandjean, 1960**
(Figs 1–2)
Syn. *O. jonkershoekensis* Pritchard, 1964.

Type-host and locality: *Xenopus laevis victorianus* Ahl from Bukavu, Kivu, Zaire (see Vercammen-Grandjean, 1960).
Previously published host and locality records: From *X. l. poweri* Hewitt: Kilwezi, Upemba Parc, Zaire (Fischthal, 1977) (1). From *X. l. laevis* (Daudin): Jonkershoek, Stellenbosch, South Africa (Pritchard [1964], reported as *O. jonkershoekensis*; Macnae *et al.* [1973]); Silvermine river, nr Fish Hoek, southern Cape Peninsula, South Africa (Macnae *et al.*, 1973); "western Cape", South Africa (Macnae *et al.*, 1973). From *X. wittei* Tinsley, Kobel & Fischberg: Butongo, Kigezi district, Uganda (Tinsley *et al.* [1979], reported as *Oligolecithus* sp.) (2); Kalondo, Mokoto, L. Ndalaga, Zaire (Fischthal [1977], host reported as *X. l. victorianus*, see below; locality reported as Kabondo, L. Ndaraga) (3). From *Xenopus* sp.: Kajansi, near Kampala, Uganda (Thurston [1970], host probably *X. l. victorianus*, see Tinsley [1973]) (4).
Other hosts and localities: From *X. l. victorianus*: Kampala area, Uganda (5); Kigali, Rwanda (6); L. Bulera, Rwanda (7). From *X. l. bunyoniensis* Loveridge (new host record): Bufundi, L. Bunyonyi, Uganda (8). From *X. l. laevis*: Umtata, Transkei (9); Cape flats, South Africa (10); Mukuvisi River, Cranborne, Harare, Zimbabwe (11). From *X. l. sudanensis* Perret (new host record): Jebel Marra, Sudan (12). From *X. laevis* (subspecies unknown): L. Bunyonyi, Uganda (13). From *X. vestitus* Laurent (new host record): L. Mulehe and L. Mutanda, Uganda (14).

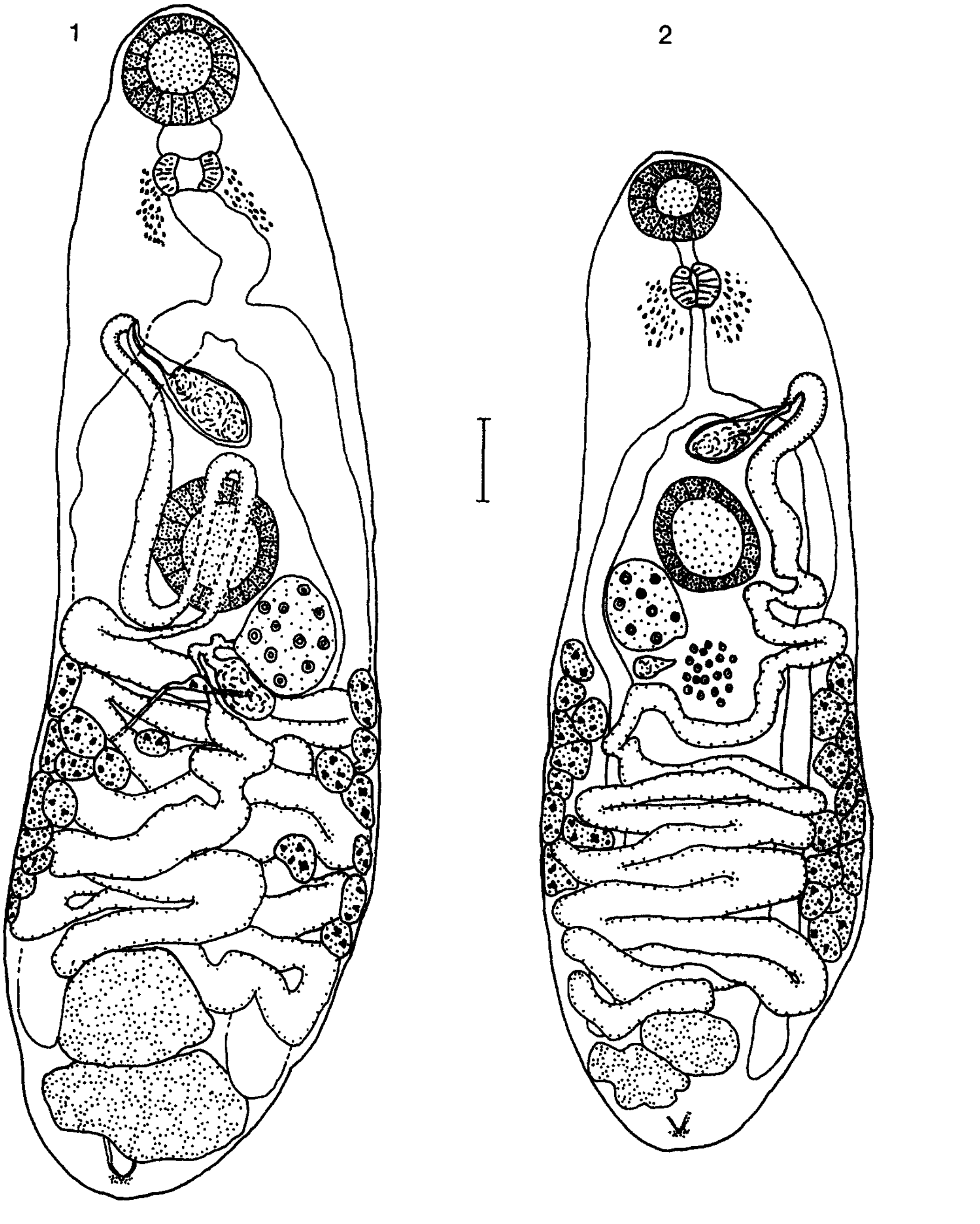
Material studied
Type-series of *O. elianae*: one specimen designated "type original naturel" (see Vercammen-Grandjean, 1960), MRAC 32.134; one specimen designated "type d'elevage" from an experimental infection (see Vercammen-Grandjean, 1960), MRAC 32.135; 85 specimens designated "paratypes" of *O. elianae*, MRAC 32.174-88 (41 slides), MRAC 32.561-81 (22 slides). Other material: one specimen (1), MRAC 33.703; 4 specimens (2), P; 24 specimens (3), MRAC 34.365 (one slide), MRAC 34.370 (5 slides), MRAC 34.373 (2 slides), MRAC 34.632 (4 slides), MRAC 34.635 (one slide), MRAC 34.637 (3 slides), MRAC 36.181 (one slide), MRAC 36.182 (one slide); 6 specimens (4), BM 1968.12.5.9 (one slide); 4 specimens (5), F, hosts coll. RCT, December, 1969; 3 specimens (6), F, hosts coll. H. Hinkel, imported into UK, April, 1992; 3 specimens (7), P, hosts coll. RCT, August, 1975; 2 specimens (8), P, from host BM 1935.10.10.281; 3 specimens (9), F, hosts coll. P. Denny, imported into UK, August, 1988; 2 specimens (10), F, coll. RCT, 1971, BM 1972.3.16.1-4 (2 slides); 8 specimens (10), F, hosts imported into UK, 1971; 30 specimens (11), F, coll. V. Clarke, during 1989; 7 specimens (12), P, obtained as part of this study from a preserved host in the collection of the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (by permission of Dr W. Bohme; host registration number: 39980); 2 specimens (13), BM 1971.3.12.23-26 (2 slides); 7 specimens (14), P, hosts coll. RCT, August, 1975.

Site of infection: Intestine.

*Description (*based on material fixed under coverslip pressure only*)*

Data on morphometric variation are summarised in Table I.

Small worms, never exceeding 2,400 in length. Body elongate to pyriform in shape. Tegumental spines dense anteriorly, becoming progressively more sparse posteriorly, disappearing in final quarter of body. Oral sucker subterminal. Pharynx preceded by very short prepharynx and flanked by densely-staining glandular cells. Oesophagus relatively long; caecal bifurcation 19-36% of body length from anterior. Caeca terminating at level of anterior or posterior testis. Ventral sucker 23-45% of body length from anterior. Oral/ventral sucker width ratio 1 : 0.94–1.81. Two testes arranged obliquely or in tandem, in posterior region of body, contiguous or separated by narrow inter-testicular space, smooth or with shallow lobes, subglobular to transversely elongate. Post-testicular space short. Cirrus-sac orientated obliquely, just anterior to ventral sucker (sometimes overlapping), ven-



Figs 1–2. *Oligolecithus elianae* Vercammen-Grandjean, 1960, whole specimens. 1. MRAC 32.135 ("type d'elevage") from *X. l. victorianus* at Kivu, Zaire, dorsal view (gut caeca omitted where dorsal to reproductive system). 2. From *X. l. victorianus* at Kajansi, Uganda, ventral view. *Scale-bar*: 100 μm.

tral to left caecum, containing distinct, coiled seminal vesicle, short pars prostatica and short ejaculatory duct. Genital pore ventral, sinistral to left caecum. Ovary subglobular to transversely elongate, dextral to mid-line, posterior to and sometimes overlapping posterior margin of ventral sucker. Oviduct arising from posterior or sinistral postero-lateral surface of ovary, exhibiting short proximal expansion then communicating successively with small, pear-shaped seminal receptacle and Laurer's canal opening at dorsal

Table I. Morphometric variation in *Oligolecithus elianae* Vercammen-Grandjean, 1960.

Host Locality	*Xenopus laevis victorianus* Kivu, Zaire[4]	 Kajansi, Uganda	*X. l. laevis* Cape, South Africa[5]	 Umtata, Transkei	 Mukuvisi River, Zimbabwe
Body length	1,350 (20)	1,030 (4)	1,160 (7)	780 (2)	1,690 (30)
	820–2,110	940–1,120	530–1,500	590–970	1,020–2,330
Body width	450 (20)	410 (4)	430 (8)	290 (2)	600 (30)
	310–610	380–440	350–520	240–340	300–770
Oral sucker width	144 (19)	133 (4)	122 (8)	114 (2)	147 (30)
	100–199	124–143	89–141	106–122	91–183
Prepharynx	40 (16)	15 (2)	31 (8)	–	24 (27)
	24–64	13–17	19–41		9–74
Distance anterior to caecal bifurcation[1]	25 (20)	25 (4)	29 (8)	30 (2)	23 (30)
	20–34	24–26	23–36	27–34	19–29
Distance anterior to ventral sucker[1]	35 (20)	35 (4)	39 (8)	35 (2)	31 (30)
	29–44	33–37	36–45	33–37	23–40
Cirrus-sac length	188 (19)	180 (4)	141 (8)	140 (2)	177 (30)
	126–256	156–198	74–263	127–152	104–228
Cirrus-sac width	67 (20)	53 (4)	51 (8)	43 (2)	55 (30)
	41–104	46–59	26–72	34–51	31–67
Ventral sucker width	178 (20)	153 (4)	138 (8)	131 (2)	203 (30)
	141–244	135–176	112–163	110–152	131–256
Sucker ratio	1 : 1.26 (19)	1 : 1.15 (4)	1 : 1.14 (8)	1 : 1.11 (2)	1 : 1.39 (30)
	1 : 0.97–1.55	1 : 1.09–1.23	1 : 0.94–1.37	1 : 0.96–1.25	1 : 1.13–1.81
Ovary length	117 (20)	97 (4)	110 (8)	89 (2)	122 (30)
	88–171	83–112	57–152	53–125	65–154
Ovary width	138 (20)	116 (4)	127 (8)	106 (2)	148 (30)
	106–205	91–131	100–154	100–112	74–196
Vitelline follicle number:					
left	10–13 (14)	11–14 (4)	11–15 (8)	11–12 (2)	9–16 (29)
right	8–11 (14)	7–10 (4)	9–13 (8)	8–9 (2)	8–10 (29)
Anterior testis:					
length	121 (19)	89 (4)	60 (7)	65 (2)	98 (29)
	63–178	67–109	39–83	53–76	56–146
width	190 (19)	172 (4)	132 (7)	134 (2)	183 (29)
	119–277	112–243	85–198	110–158	104–248

surface. Distal region of oviduct extending posteriorly, joined by common vitelline duct before developing into oötype surrounded by cells of Mehlis' gland. Vitelline follicles lateral, extracaecal or overlapping caeca ventrally, 7–13 in right field and 9–16 in left field, extending from level of ovary to three-quarters of distance between ovary and testis (rarely to level of anterior testis), exhibiting slightly greater extent on left than right hand side. Lateral vitelline ducts uniting dorsal to Mehlis' gland to form vitelline reservoir. Uterine coils occupying most of space between anterior testis and ovary, overlapping anterior margin of foremost testis and extending slightly past this level laterally. Anteriorly some uterine coils extending past ovary, terminating in metraterm lying alongside cirrus-sac. Eggs oval, 16–29 × 10–19. Excretory vesicle tubular at level of posterior testis; anterior portion not observed; excretory pore subterminal.

Table I. Continued.

Host	*Xenopus laevis victorianus*		*X. l. laevis*		
Locality	Kivu, Zaire[4]	Kajansi, Uganda	Cape, South Africa[5]	Umtata, Transkei	Mukuvisi River, Zimbabwe
Posterior testis:					
length	105 (19)	88 (4)	63 (7)	52 (2)	107 (28)
	52–167	63–126	52–76	32–72	57–181
width	221 (19)	169 (4)	136 (7)	135 (2)	217 (28)
	157–281	127–209	89–191	124–146	128–293
Inter-testis distance[2]	70, 20 (17)	75, 2 (4)	86, 2 (7)	100, – (2)	89, 10 (27)
	4–38				6–15
Posterior testis to extremity	75 (20)	27 (4)	23 (7)	34 (2)	85 (28)
	19–144	15–42	2–37	30–38	19–181
Egg length[3]	19–29 (13)	16–28 (4)	19–26 (5)	21–27 (3)	–
Egg width[3]	13–19 (13)	10–17 (4)	11–14 (5)	10–14 (3)	–

Mean given above range (except where otherwise indicated); sample size in parentheses. Material from present study fixed under coverslip pressure in 4% formal saline and mounted in Canada balsam.
[1]Distance given as percentage of body length.
[2]Percentage of specimens with contiguous testes precedes mean distance between non-contiguous testes (range given below); total sample size in parentheses.
[3]Range based on five eggs per parasite.
[4]Subsample from *O. elianae* type-series (data for ventral sucker position given in text are based on a larger sample).
[5]Including two specimens from BM 1972.3.16.1–4.

Remarks

The two species of *Oligolecithus* previously recognised were recorded from different subspecies of *X. laevis* at localities separated by nearly 4,000 km: *O. elianae* Vercammen-Grandjean, 1960 was described from *X. l. victorianus* at Kivu, Zaire, and *O. jonkershoekensis* Pritchard, 1964 from *X. l. laevis* in Cape Province, South Africa. Pritchard (1964) differentiated *jonkershoekensis* from *elianae* by the following characteristics: (1) a more anterior ventral sucker; (2) caeca not extending into post-testicular space; (3) vitelline follicles rarely extending to level of anterior testis margin; and (4) uterine coils extending to anterior margin of foremost testis (and slightly past this level laterally). Macnae *et al.* (1973) considered *O. jonkershoekensis* a synonym of *O. elianae* because some new material from Pritchard's type-locality was "consonant with Vercammen-Grandjean's specimens". The type series of *O. elianae* was examined as part of the present study. These worms show an arrangement of posterior uterine coils comparable to that indicated for *O. jonkershoekensis* by Pritchard (1964) and found in present material from *X. l. laevis* in South Africa. Variation in the distribution of vitelline follicles and the posterior extent of the gut caeca amongst Vercammen-Grandjean's specimens were also consistent with southern African representatives of *Oligolecithus* (present study; Pritchard, 1964): the specimen from an experimental infection ("type d'elevage", see Vercammen-Grandjean [1960], MRAC 32.135) was unusual (Fig. 1) in showing vitelline follicles extending almost to the level of the anterior testis. Pritchard (1964) stated that the ventral sucker of *O. jonkershoekensis* occurred at "about one-third body length from anterior end". In specimens from the *O. elianae* type-series, this structure is located 25–44% of body length from the anterior (mean = 34%, random sample, n = 38; personal observation). As *O. jonkershoekensis* cannot be distinguished by this, or any of the above characters, it is confirmed as a junior synonym of *O. elianae*.

Fischthal (1977) reported *O. elianae* from *X. l. victorianus* at Mokoto, Zaire, based on material obtained from hosts in the collections of the Musée Royal de l'Afrique Centrale, Tervuren, Belgium. However, all representatives of *Xenopus* from this locality in the Tervuren collections were assigned to *X. wittei* by Tinsley *et al.* (1979).

***Oligolecithus siluranae* n. sp.** (Figs 3–5)

Type-host and locality: *Xenopus tropicalis* (Gray) from Aburi, Ghana.

Material studied
Holotype BM 1994.9.26.1, 4 paratypes BM 1994.9.26.2–5, and 5 non-type specimens from type-locality, F, coll. RCT, April, 1979.

Site of infection: Intestine.

Description (based on specimens fixed under coverslip pressure)

Holotype measurements precede sample range and mean (in parentheses) for all available specimens (n = 10).

Body elongate; length 3,500, 2,480–3,500 (2,940), width 684, 555–760 (658), somewhat attenuated in region posterior to uterine coils. Tegumental spines dense anteriorly, becoming progressively more sparse posteriorly, disappearing in final quarter of body. Oral sucker subterminal, 177, 127–177 (164) wide. Pharynx 86, 56–96 (83) wide, preceded by very short prepharynx, 43, 10–43 (21) long, flanked by densely-staining pharyngeal glands. Oesophagus relatively long; caecal bifurcation 14, 10–16 (13)% of body length from anterior. Caeca extending past anterior testis, terminating at level of inter-testicular space. Ventral sucker 167, 144–182 (159) wide, 20, 20–27 (22)% of body length from anterior. Oral/ventral sucker width ratio 1 : 0.95, 0.90–1.13 (0.98). Two testes arranged in tandem at posterior end of body, separated by long inter-testicular space, 162, 46–167 (123), smooth, subglobular. Anterior testis 185, 185–251 (217) long, 324, 243–324 (266) wide; posterior testis 204, 160–239 (206) long, 300, 224–331 (266) wide. Post-testicular space long; distance from posterior testis to end of body 443, 152–443 (239). Cirrus-sac 200, 200–274 (237) long, 99, 84–99 (90) wide, orientated obliquely just anterior to ventral sucker (not overlapping), ventral to left caecum, containing distinct, coiled seminal vesicle, short pars prostatica and short ejaculatory duct. Genital pore ventral, sinistral to left caecum. Ovary subglobular to transversely elongate, 132, 125–168 (149) long, 276, 190–276 (225) wide, in mid-line or displaced slightly to right of this, posterior to ventral sucker. Oviduct arising from posterior surface of ovary, exhibiting short proximal expansion then communicating successively with small, ovoid seminal recepta-

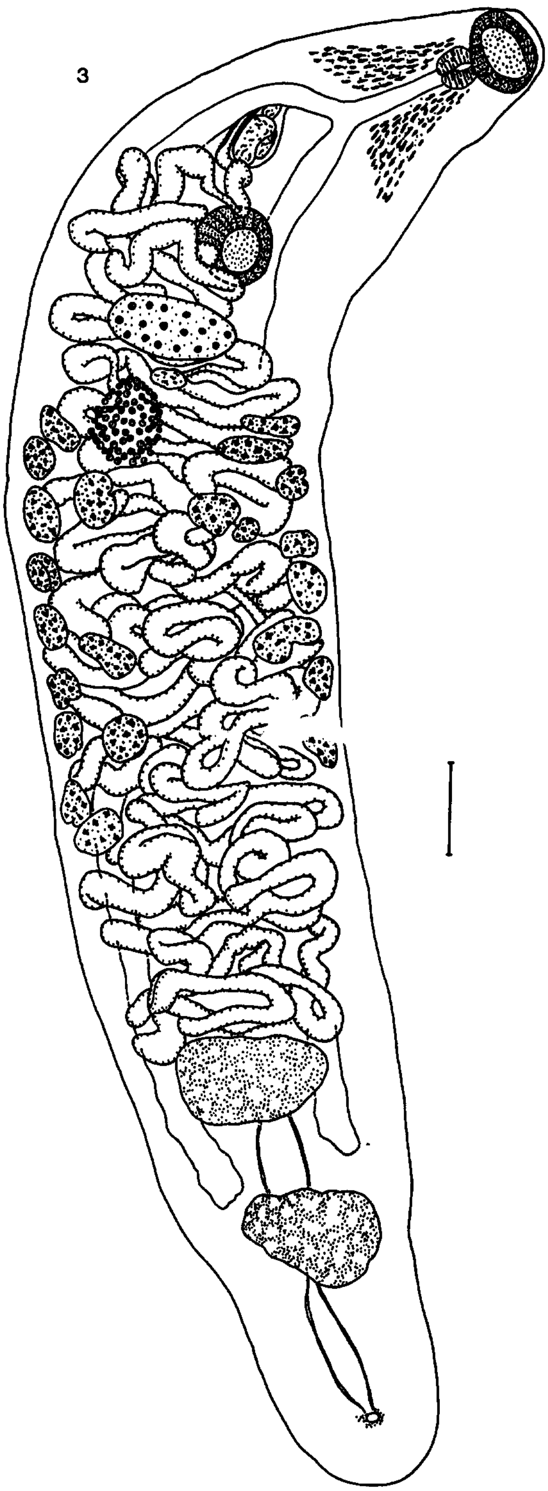


Fig. 3. *Oligolecithus siluranae* n. sp., holotype, dorsal view (gut caeca omitted where dorsal to reproductive system). *Scale-bar*: 200 μm.

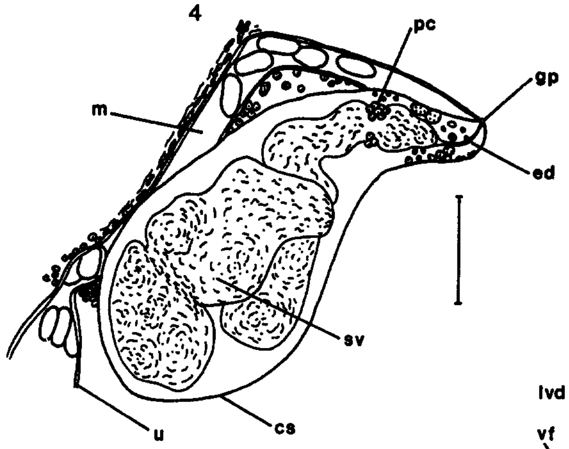
cle and Laurer's canal opening at dorsal surface. Distal region of oviduct extending posteriorly, joined by common vitelline duct before developing into oötype surrounded by cells of Mehlis' gland. Vitelline follicles well dispersed, lateral, extracaecal or overlapping caeca ventrally, 12, 11–13, in left field and 9, 7–10, in right field, extending from level of ovary to three-quarters of distance between ovary and anterior testis, showing slightly greater extent on left than right side. Lateral vitelline ducts uniting dorsal to Mehlis' gland to form vitelline reservoir. Long, convoluted uterus. Uterine coils occupying most of space between testes and ovary, overlapping anterior margin of first testis and extending slightly past this level laterally. Anteriorly some uterine coils extending past ovary, terminating in metraterm lying alongside cirrus-sac. Eggs oval, dimensions in holotype 18–21 × 10–13 (n = 10), in paratypes 14–23 × 8–15 (n = 10 from each of 9 specimens). Excretory vesicle tubular at level of testes; anterior region not observed; excretory pore subterminal.

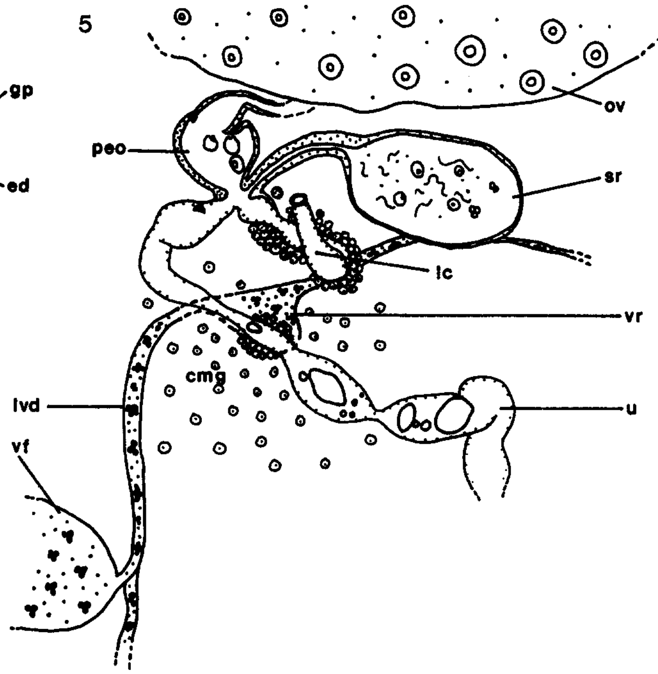
Remarks

O. siluranae n. sp. differs from *O. elianae* in body length, testicular arrangement and ventral sucker width in proportion to body size. It also shows more dispersed vitelline follicles and a longer, more convoluted uterus than *O. elianae*. In the present material, the maximum body length of the latter species (2,330) was outside the range for *O. siluranae* (2,480-3,500). This difference is unlikely to result from biased sampling of different growth stages, as large numbers of *O. elianae* were measured (n = 140, from all localities). Potential effects of different fixation techniques are excluded, since our samples include *siluranae* and *elianae* fixed under identical conditions. Although Macnae *et al.* (1973) reported *O. elianae* up to 3,000 in length from *X. l. laevis* in South Africa, their measurements were of live specimens which are highly extensible and do not allow comparison with fixed material (on which all the present data are based). The testes of *O. siluranae* are smooth, subglobular and always arranged in tandem, while those of *O. elianae* often show shallow lobes, vary from laterally elongate (by far the most frequent form) to subglobular, and may be arranged obliquely (most frequently) or in tandem. *O. siluranae* has very long inter-testicular and post-testicular spaces when compared to *O. elianae*, in which the testes are contiguous or separated by a very narrow space (see Table I). The ventral sucker width of *O. siluranae* falls within the range of variation for *O. elianae*. However, this structure is clearly smaller in proportion to body size (see Fig. 6): specimens of *O. elianae* over 1,800 long show larger ventral suckers than *O. siluranae* of much greater size. Both the caecal bifurcation and ventral sucker are relatively more anterior in *O. siluranae*, although there is some overlap with *O. elianae* in the latter character (see Table I).

Discussion

Two species of *Oligolecithus*, *O. elianae* Vercammen-Grandjean, 1960 and *O. siluranae* n. sp., are found in clawed toads. These forms are differentiated primarily by variation in body length, testicular arrangement and ventral sucker width in proportion to body size. Taxonomic conclusions from this study have been based, for the sake of uniformity, primarily on specimens fixed under coverslip pressure. This has enabled us to consider material representing a geographical range of 45 degrees of latitude (closely corresponding with the complete range of *Xenopus*) and specimens collected by a number of investigators. The degree of fixation pressure could, potentially, affect several of the characters recorded, including relative sizes of structures (the oral and ventral suckers, for instance) and the distance between organs (e.g. intertesticular space). We have carefully considered these potential effects: the differences between *elianae* and *siluranae* are too great to be determined by fixation. Recent molecular and cytological studies (see Tymowska [1991] for review) suggest that *X. tropicalis*, the host of *O. siluranae*, belongs to a different lineage of *Xenopus* spp. from the hosts of *O. elianae*. The latter are characterized by a chromosome number of 2n = 36 (*X. laevis*) or multiples of this (2n = 72 in *X. wittei* and *X. vestitus*), unlike *X. tropicalis* which belongs to a group of clawed toads showing 2n = 20 or 40 chromosomes (Tymowska, 1991). *O. elianae* shows a very widespread distribution (Fig. 7), occurring in southern (South Africa, Transkei and Zimbabwe) and central Africa (Zaire, Rwanda and Uganda), and as far north as Jebel Marra in Sudan. *O. siluranae*, however, was only recovered from one locality in Ghana. The hosts of *O. elianae* are found in a range of habitats, from wooded savanna (for some *X. laevis* subspecies) to montane forest (for *X. wittei* and *X. vestitus*), while *X. tropicalis* typically occurs in lowland tropical rain forest. *X. tropicalis* may show limited areas of co-occurrence with *X. laevis* at the margins of their distributions (see Tinsley, 1981)





Figs 4–5. *Oligolecithus siluranae* n. sp. 4. Terminal genitalia. 5. Ovarian complex. *Abbreviations*: cmg. cells of Mehlis' gland; cs, cirrus-sac; ed, ejaculatory duct; gp, genital pore; lc, Laurer's canal; m, metraterm; ov, ovary; pc, prostatic cells; peo, proximal expansion of oviduct; sr, seminal receptacle; sv, seminal vesicle; u, uterus; lvd, lateral vitelline duct; vf, vitelline follicle; vr, vitelline reservoir. *Scale-bar*: 50 μm.

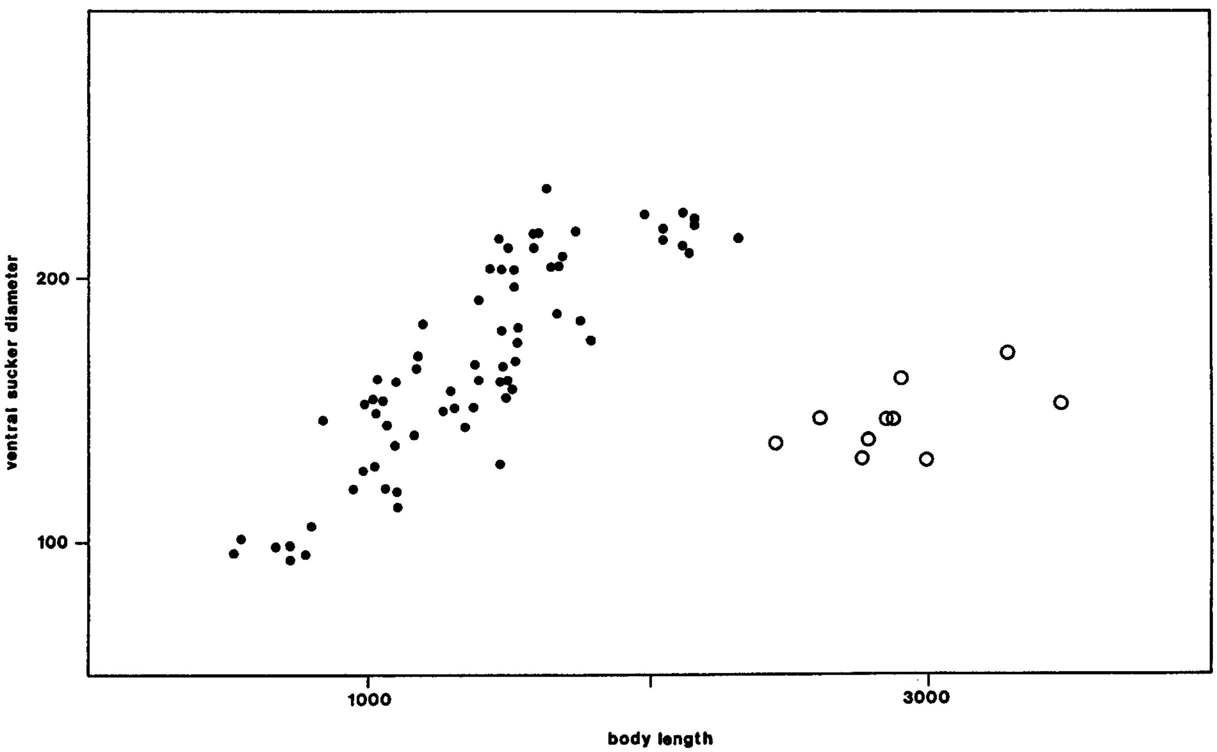


Fig. 6. Scatterplot of ventral sucker diameter against body length in *Oligolecithus* spp. Ventral sucker diameter = length + width/2. •, *O. elianae*; o, *O. siluranae*.

and is sympatric with *X. fraseri*-like forms, which show multiples of 2n = 36 chromosomes, over some of its range (Tinsley, 1981; Loumont, 1984, 1986). A series of studies (Fain & Tinsley, 1993; Jackson & Tinsley, 1995a,b, in prep.) have documented the extent of parallel speciation of *Xenopus* and a series of parasite groups. In some instances, there is close cospeciation involving parasites with both direct and indirect life-cycles. In the case of digeneans, speciation is likely to be influenced significantly by the molluscan host in the life-cycle. Discontinuities in the geographical distribution of particular snails may be a determining factor in the speciation of the parasite within its definitive host. For *Oligolecithus*, with a three-host life-cycle, speciation corresponds to a major separation of definitive host lineages, but also with differences in geographical distribution and in the habitat types in which transmission occurs. The occurrence of *Oligolecithus* spp. parallels the divergence in a series of other parasite groups from the 2n = 20 and 2n = 36 clades of *Xenopus*. This division is so profound and ancient that it may warrant generic separation of the hosts (Cannatella & Trueb, 1988) or perhaps subgeneric separation (Kobel, Loumont & Tinsley, in press). The speciation of *Oligolecithus* may therefore reflect phylogenetic specificity to the definitive host; however, the influence of other key ecological factors (including the effect of geographical variation in snail hosts) is unknown.

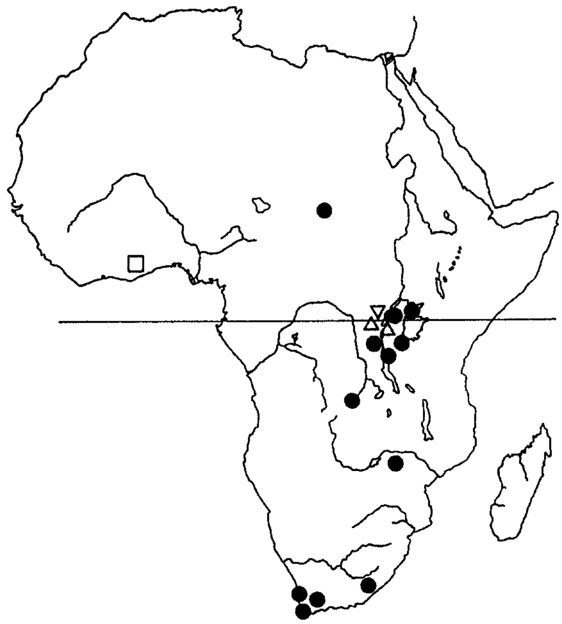


Fig. 7. Geographical distribution of *Oligolecithus* spp. □, *O. siluranae* n. sp. from *Xenopus tropicalis*. *O. elianae* from: •, *X. laevis* subspecies; Δ, *X. wittei*; ∇, *X. vestitus*.

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References

Cannatella, D.C. & Trueb, L. (1988) Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zoological Journal of the Linnean Society*, **94**, 1–38.

Fain, A. & Tinsley, R.C. (1993) A new *Xenopacarus* (Acari, Ereynetidae) from the nasal cavities of *Xenopus* sp. (*fraseri* group), with a discussion on the evolution host-parasite. *Revue de Zoologie Africaine*, **107**, 513–517.

Fischthal, J.H. (1977) Some digenetic trematodes of anurans from central and west Africa. *Revue de Zoologie et de Botanique Africaine*, **91**, 117–130.

Jackson, J.A. & Tinsley, R.C. (1995a) Representatives of *Batrachocamallanus* n. g. (Nematoda: Procamallaninae) from *Xenopus* species (Anura: Pipidae): geographical distribution, host range and evolutionary relationships. *Systematic Parasitology* (in press).

Jackson, J.A. & Tinsley, R.C. (1995b) Evolutionary relationships, host range and geographical distribution of *Camallanus* Railliet & Henry, 1915 species (Nematoda: Camallanidae) from clawed toads of the genus *Xenopus* (Anura: Pipidae). *Systematic Parasitology* (in press).

Kobel, H.R., Loumont, C. & Tinsley, R.C. (1995). The extant species. In: Tinsley, R.C. & Kobel, H.R. (Eds) *The biology of* Xenopus. Oxford: Oxford University Press. pp. 000-000.

Loumont, C. (1984) Current distribution of the genus *Xenopus* in Africa and future prospects. *Revue Suisse de Zoologie*, **91**, 725–746.

Loumont, C. (1986) *Xenopus pygmaeus*, a new diploid pipid frog from rain forest of equatorial Africa. *Revue Suisse de Zoologie*, **93**, 755–764.

Macnae, W., Rock, L. & Makowski, M. (1973) Platyhelminths from the South African clawed toad, or platanna (*Xenopus laevis*). *Journal of Helminthology*, **47**, 199–235.

Pritchard, M.H. (1964) Notes on four helminths from the clawed toad, *Xenopus laevis* (Daudin), in South Africa. *Proceedings of the Helminthological Society of Washington*, **31**, 121–128.

Prudhoe, S. & Bray, R.A. (1982) *Platyhelminth parasites of the Amphibia*. Oxford: Oxford University Press. 217 pp.

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 (Monogenoidea) from east Africa with a description of *Polystoma makereri* n. sp. *Zeitschrift für Parasitenkunde*, **42**, 251–263.

Tinsley, R.C. (1981) Interactions between *Xenopus* species (Anura Pipidae). *Monitore Zoologico Italiano*, (N.S) Suppl., **15**, 133–150.

Tinsley, R.C., Kobel, H.R. & 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.

Vercammen-Grandjean, P.H. (1960) Les trematodes du Lac Kivu sud (Vermes). *Annales du Musee Royal de l'Afrique Centrale, Tervuren* (N.S. 4°) *Sci. Zool.*, **5**, 1–171.