Host-specificity and distribution of cephalochlamydid cestodes: correlation with allopolyploid evolution of pipid anuran hosts

J. A. Jackson and R. C. Tinsley

School of Biological Sciences, University of Bristol, Bristol BS8 1UG, U.K.

Abstract

The taxonomy and distribution of cephalochlamydid cestodes are reviewed. This group is primarily specific to pipid anurans and occurs naturally across sub-Saharan Africa. *Paracephalochlamys* gen. nov. has two large lateral testes (sometimes doubled or absent on one side) on the anterior margin of each segment, while *Cephalochlamys* Blanchard, 1908 has three to 23 small testes scattered in lateral fields. *Paracephalochlamys papilionis* sp. nov. infects *Pseudhymenochirus merlini* in Sierra Leone. The distribution of *Cephalochlamys* species is inferred from the previous literature and numerous new records. *Cephalochlamys namaquensis* (Cohn, 1906) occurs in *Xenopus laevis laevis* in Namibia, South Africa, Lesotho and Zimbabwe, *X. l. poweri* (new host record) in Zambia and the Democratic Republic of Congo (D.R.C.), *X. l. victorianus* in Kenya, Uganda, Rwanda and D.R.C., *X. l. sudanensis* (new host record) in Cameroon and Sudan, and the ranid anuran, *Rana angolensis*, in Zimbabwe. Anthropogenic dispersal of *C. namaquensis*, together with *X. l. laevis*, has occurred to localities in the south-western United States and Isle of Wight, U.K. *Cephalochlamys compactus* sp. nov., differentiated from *C. namaquensis* by a less well developed median ovarian cavity and more compact vitellarium, occurs in *Xenopus muelleri* in Togo, Ghana, Nigeria, Cameroon, D.R.C., Zimbabwe and South Africa, *X. borealis* in Kenya, *X. clivii* in Ethiopia, *R. angolensis* in Ethiopia and *R. occipitalis* in Nigeria. *Cephalochlamys* representatives of uncertain specific status have been recorded in *X. gilli* (new host record) in South Africa, *X. pygmaeus* and *X. fraseri*-like hosts (new host records) in the D.R.C., *X. tropicalis* (new host record) in Nigeria and *R. occipitalis* in Gabon. Despite the ability of some species to infect distantly related amphibians, the distribution of cephalochlamydid taxa amongst their principal hosts, pipids, can be related to the allopolyploid evolution of this anuran family.

Key words: Cephalochlamydidae, *Xenopus*, allopolyploid, host-specificity, distribution

INTRODUCTION

The pseudophyllidean cestode family Cephalochlamydidae Yamaguti, 1959 occurs naturally in anuran amphibians in sub-Saharan Africa. Only one genus, *Cephalochlamys* Blanchard, 1908, is currently recognized (Bray, Jones & Andersen, 1995), which has been reported at localities from the tip of South Africa north to the Congo basin and West Africa. Previous records are mainly from pipids of the subgenus *Xenopus* (see Mettrick, 1960, 1963; Pritchard, 1964; Thurston, 1967, 1970; Dollfus, 1968; Fischthal & Asres, 1970; Avery, 1971; Macnae, Rock & Makowski, 1973; Tinsley, Kobel & Fischberg, 1979; Ferguson & Appleton, 1988), although cephalochlamydids have also been found in ranids on three occasions (Mettrick, 1963; Dollfus, 1968; Fischthal & Asres, 1970). In another instance,

Cephalochlamys namaquensis (Cohn, 1906), the only valid named species, was recovered from a captive urodele (Dollfus, 1968). It has also been recorded in an introduced population of *Xenopus laevis laevis* in the south-western United States (Lafferty & Page, 1997).

The present study is part of an extensive survey of metazoan parasites in pipid anurans from sub-Saharan Africa (Tinsley, 1981, 1996*a*; Fain & Tinsley, 1993; Tinsley & Jackson, 1995, 1998*a*; Jackson & Tinsley, 1995*a*,*b*, 1997, 1998*a*,*b*). It aims to review the taxonomy and distribution of cephalochlamydid cestodes occurring in these hosts. It also aims to correlate parasite distributions with known evolutionary events in the host group, which contains a remarkable series of polyploid species (Tymowska, 1991; Graf, 1996; Kobel, Loumont & Tinsley, 1996) that are believed to have arisen by interspecies hybridization (Kobel, 1996). Some

higher polyploids are sympatric with extant members of their parental lineages (Tinsley *et al.*, 1979; Tinsley, Loumont & Kobel, 1996). The distribution of parasites within this polyploid series might therefore provide insights into the influence of massive host genetic re-arrangement on the evolution of parasite host-specificity (Tinsley, 1996*a*; Tinsley & Jackson, 1998*b*). A preliminary analysis of the Cephalochlamydidae (without formal taxonomic statements) was presented in Tinsley (1996*a*). While the current work is a finalized version of this study, it is based on a very much larger set of material, which has led to revised conclusions in some instances.

MATERIALS AND METHODS

General

Hosts collected in the field were processed (as follows) in the country of origin or first imported to the U.K. by airfreight. Each was anaesthetized in a 0.2% MS222 (Sandoz) solution and pithed. The alimentary tract was removed and opened by a longitudinal slit while immersed in 0.6% saline. Worms were removed from the host's intestine and fixed under coverslip pressure in 4% formal saline. Other parasite specimens were recovered from hosts that had been fixed in the field (some of these were borrowed from museum collections). Whole worms were stained in alum carmine or methyl blue and mounted in Canada balsam; other material (from fixed hosts only) was embedded in wax, sectioned on a rotary microtome, stained in haematoxylin and eosin and mounted in DEPEX medium (Gurr). Measurements were taken under a light microscope (Nikon) fitted with an eye-piece scale and are given in microns.

Three categories of proglottid were measured: early proglottids with clearly differentiated ovaries and testes (S1); the first gravid proglottid (S2); heavily gravid proglottids (S3).

Material studied

The numbering of locality records in the text relates these records to the parasite specimens on which they are based. Worms fixed under coverslip pressure in 4% formal saline (F) or dissected from conserved hosts (P) are distinguished. The registration numbers of hosts are given for parasites which were obtained from conserved collections of clawed toads from the University of Antwerp (RUCA) (by permission of Professor J. Hulselmans), Zoologisches Forshungsinstitut und Museum Alexander Koenig, Bonn (ZFMK) (by permission of Dr W. Böhme) or Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC) (by permission of Dr D. Mierte). Other parasite specimens were borrowed from the latter museum (material collected by Dr F. A. Puylaert), the personal collection of Dr June Thurston (JT) (held at The Natural History Museum,

London), the United States National Parasite Collection (USNPC) and The Natural History Museum, London (NHM), at which institution type specimens and additional material from the present study have been deposited.

Host identification

Xenopus species of the *fraseri* Boulenger group (see Kobel *et al.*, 1996) are differentiated by characters including chromosome number and mating call and are often difficult to distinguish by morphological criteria alone. This is true of *Xenopus pygmaeus* Loumont, *Xenopus amieti* Kobel, Du Pasquier, Fischberg & Gloor, *Xenopus andrei* Loumont, *Xenopus boumbaensis* Loumont, and *Xenopus ruwenzoriensis* Tymowska & Fischberg. In cases where the identity of these toads is uncertain, they are recorded as *Xenopus fraseri*-like.

OBSERVATIONS

Cephalochlamydidae Yamaguti, 1959

Type genus

Cephalochlamys Blanchard, 1908

Other genera

Paracephalochlamys gen. nov.

Emended diagnosis

Cestoidea Rudolphi, 1808; Pseudophyllidea Carus, 1863. Scolex sagittate; two lanceolate to oval bothria, one dorsal, one ventral, continuous anteriorly with narrow, blunt-ending apical projection. Neck merging into segmented region of strobila: segmentation accompanying the early differentiation of sexual organs. Acraspedote. Longitudinal muscles in discrete bands forming single layer. Four medullary longitudinal excretory canals in dorsal and ventral pairs; ventral excretory canals wider, communicating in posterior region of each proglottid via narrow transverse duct. Genital pore ventral, in midline on anterior border of proglottid; genital atrium with muscular walls present. Protandrous. Testes in lateral fields, medullary, internal to longitudinal excretory canals, either: small, three to 23 per segment, subglobular to laterally elongate, scattered in subequal lateral groups, or, large, one to four per segment, pyriform, on anterior margin of segment. Dilated, convoluted vas deferens forming seminal vesicle in midline posterior to genital pore, with small, ovoid distal chamber in area immediately proximal to external opening (chamber surrounded by secretory

cells and forming prostatic complex). Male system opening on anterior surface of genital atrium through raised, muscular papilla. Ovary subglobular to laterally elongate, with variably developed median cavity encompassing proximal elements of the female reproductive system. Oviduct arising on margin of ovarian cavity, communicating in turn with small seminal receptacle just anterior to ovary (via a narrow duct) and common vitelline duct. Mehlis' gland in ovarian cavity, surrounding oötype. Sinuous vagina extending anteriorly from seminal receptacle, opening onto posterior surface of genital atrium. Uterus of gravid proglottid thrown into numerous transverse slings, internal to excretory canals, extending from level of ovary posteriorly to just short of anterior proglottid margin. Uterine pore located anteriorly, in midline or with slight lateral displacement, immediately posterior to genital pore. Vitelline follicles occurring in lateral series sometimes extending towards midline at posterior end of proglottid, medullary (but sometimes protruding between longitudinal muscle bands), in close association with excretory system: ventral and lateral to ventral longitudinal excretory canals. Eggs not visibly operculate in fixed material, ovoid: in mature proglottids, those in distal region of uterus either embryonated with membranous shell or thick-shelled, unembryonated. Parasitic in African Amphibia, principally pipids.

Remarks

The characters of this family were most recently reviewed by Bray *et al.* (1995). Their diagnosis is expanded here to include previously unknown variations found in the new genus described below. The location of the vitellarium is established to be essentially medullary, although vitelline follicles may sometimes protrude between the longitudinal muscle bands (see Fig. 6a, b).

Egg measurements in the literature for cephalochlamydids indicate a high degree of variability (Ferguson & Appleton, 1988). This may be because eggs in the distal portion of the uterus (in mature proglottids) are usually embryonated, with the developing coracidium enclosed in a thin, membranous shell which is frequently partially collapsed in fixed material. Smaller, thick-shelled eggs, which do not contain a developed embryo, sometimes also occur in the distal uterus of mature proglottids. Their biological significance is unclear, although they may simply be developing or non-viable stages.

Cephalochlamys Blanchard, 1908

Synonyms

Chlamydocephalus Cohn, 1906, *nec* Diesing, 1850, *nec* Schmarda, 1859; *Pseudocephalochlamys* Yamaguti, 1959.

Type-species

C. namaquensis (Cohn, 1906) Blanchard, 1908

Other species

C. compactus sp. nov.

Diagnosis

As for Cephalochlamydidae, except: testes always small, subglobular to laterally elongate, scattered in subequal lateral groups (three to 23 per segment).

Cephalochlamys namaquensis (Cohn, 1906) Blanchard, 1908

(Figs 1–2, 4a, 5b, 6b & 7a–i)

Synonyms

Chlamydocephalus namaquensis Cohn, 1906; *Dibothriocephalus xenopi*, Ortlepp, 1926; *Cephalochlamys xenopi* (Ortlepp, 1926) Baylis, 1934; *Pseudocephalochlamys xenopi* (Ortlepp, 1926) Yamaguti, 1959.

Type-host and locality

Xenopus (Xenopus) laevis (Daudin) at Angra Pequena, Namibia (formerly South West Africa) (Cohn (1906) cited in Dollfus (1968)) (locality suggests host subspecies *X. l. laevis*: see Tinsley, Loumont & Kobel (1996)).

Previously reported hosts and localities (natural populations)

From *X. laevis laevis* (all records as *X. laevis*, but localities suggest *laevis* as subspecies identity, see Tinsley *et al.* (1996)): northern Natal (recorded as *Dibothriocephalus xenopi*), Ortlepp (1926); Western Cape Province, Republic of South Africa (R.S.A.), Pritchard (1964) (1), Southwell & Kirshner (1937), Macnae *et al.* (1973); Transvaal, R.S.A., Thurston (1967) (2), Macnae *et al.* (1973); near Pietermaritzburg, KwaZulu-Natal, Ferguson & Appleton (1988); southern Zimbabwe, Mettrick (1960); Harare, Zimbabwe, Mettrick (1963); Mt Salinda, Melsetter District, Zimbabwe, Thurston (1967, 1970) (3). From *X. l. victorianus* Ahl: Costermansville, Democratic Republic of Congo (D.R.C.), Dollfus (1968). From *Xenopus* sp. (host reported as *X. muelleri* or *Xenopus* sp. (Thurston, 1967, 1970) but localities and dates of collection suggest identity as an *X. laevis* subspecies, see Tinsley (1973)): Kajansi, Kampala, Uganda, Thurston

(1967, 1970) (4); Queen Elizabeth Park, western Uganda, Thurston (1967, 1970) (5); L. Mutanda, Uganda, Thurston (1967, 1970) (6). From *Rana angolensis* Bocage: Harare, Zimbabwe, Mettrick (1963).

Previously reported hosts and localities (introduced populations)

From *X. l. laevis*: Santa Clara River estuary, Ventura County, California, U.S.A., Lafferty & Page (1997).

Other records (natural populations)

From *X. l. laevis*: Cape flats, Western Cape Province, R.S.A. (7); R.S.A. (exact locality unknown) (8); Transvaal (exact locality unknown), R.S.A. (9); Umtata, Eastern Cape Province, R.S.A. (10); La Letsie, Letseng, Lesotho (11); St Lucia, KwaZulu-Natal, R.S.A. (12); Mukuvisi River, Cranborne, Harare, Zimbabwe (13). From *X. l. victorianus* Ahl: Kisumu, Kenya (14); Kajansi, Uganda (15); Rutshuru, D.R.C. (16); Bulengo, L. Kivu, D.R.C. (17); Kigali, Rwanda (18); L. Bulera, Rwanda (19); Mutwanga, D.R.C. (20). From *X. l. poweri* Hewitt (new host record): Zambia (exact locality unknown) (21); Mukana marsh, near Lusinga, D.R.C. (22). From *X. l. sudanensis* Perret (new host record): Sir, Cameroon (23); Jebel Marra, Sudan (24). From *X. laevis* (subspecies unknown): L. Bunyonyi, Uganda (25). From '*Bufo*' sp.: locality unknown (26).

Other records (introduced populations)

From *X. l. laevis*: Sweetwater drainage system, San Diego County, California, U.S.A. (27); Placerita canyon, Los Angeles County, California, U.S.A. (28); Brighstone, Isle of Wight, U.K. (29).

Site

Intestine.

Material studied

Three specimens (1) USNPC 60149; seven specimens (2) JT; five specimens (3) JT; five specimens (4) JT; one specimen (5) JT; one specimen (6) JT; 30 specimens (7), P, hosts obtained from commercial imports, 1970–1990 (including NHM 1999.11.9.9–10); four specimens (8) NHM 1975.7.1.1; one specimen (8), F, host imported to U.K., January, 1976; six specimens (10), F, hosts coll. P. Denny, September, 1988; one specimen (11), P, host coll. J. Green, January, 1991; three specimens (12), F, coll. R. C. Tinsley and L. Du Preez, November, 1995; three specimens (13), F, coll. V. Clarke, 1989; three specimens (14) NHM 1984.6.4.5; 16 specimens
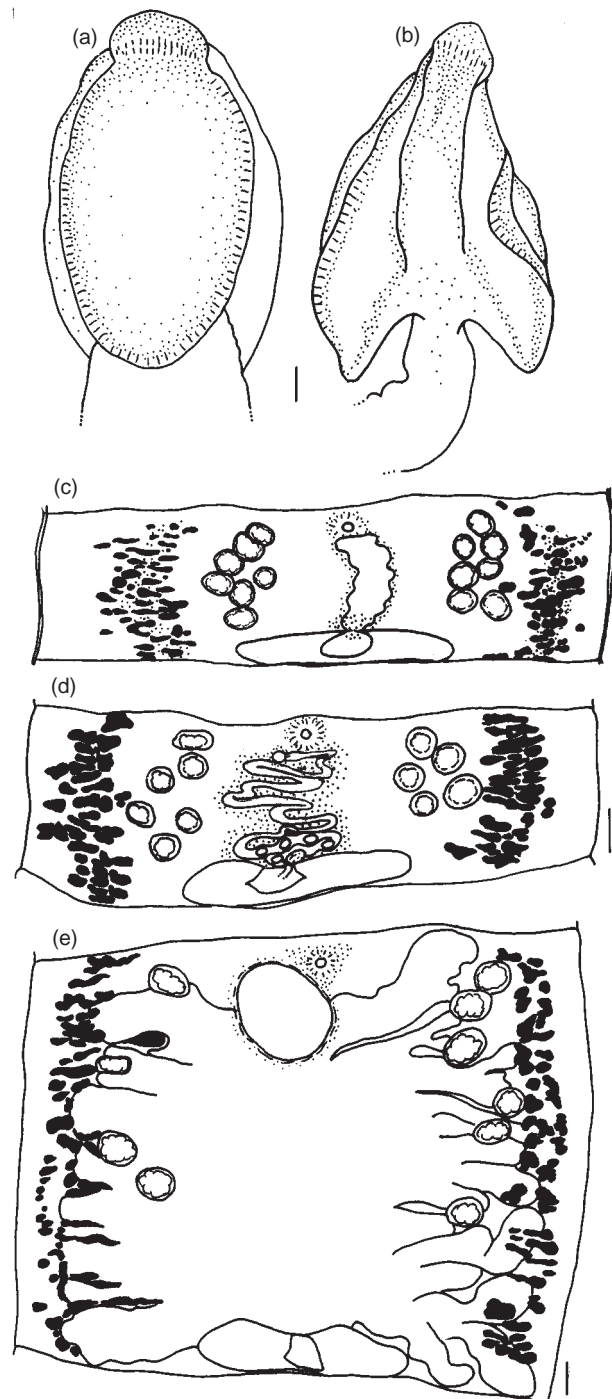

Fig. 1. *Cephalochlamys namaquensis* (Cohn, 1906) (ventral views unless otherwise indicated): (a) scolex; (b) scolex (lateral view); (c) early proglottid; (d) first gravid proglottid; (e) heavily gravid proglottid. Scale bars = 100 μm.

(15), F, coll. R. C. Tinsley, October, 1969; one specimen (16) MRAC 35.662; one specimen (17) MRAC 34.625; four specimens (18), F, hosts coll. H. Hinkel, November, 1992; two specimens (19), F, coll. R. C. Tinsley, August, 1975; one specimen (20), P, host from MRAC B117656–117660; three specimens (21), F, hosts coll. H. Monkonge, April, 1978; two specimens (22), P, host from MRAC B64451–64460; 38 specimens (23), P, hosts
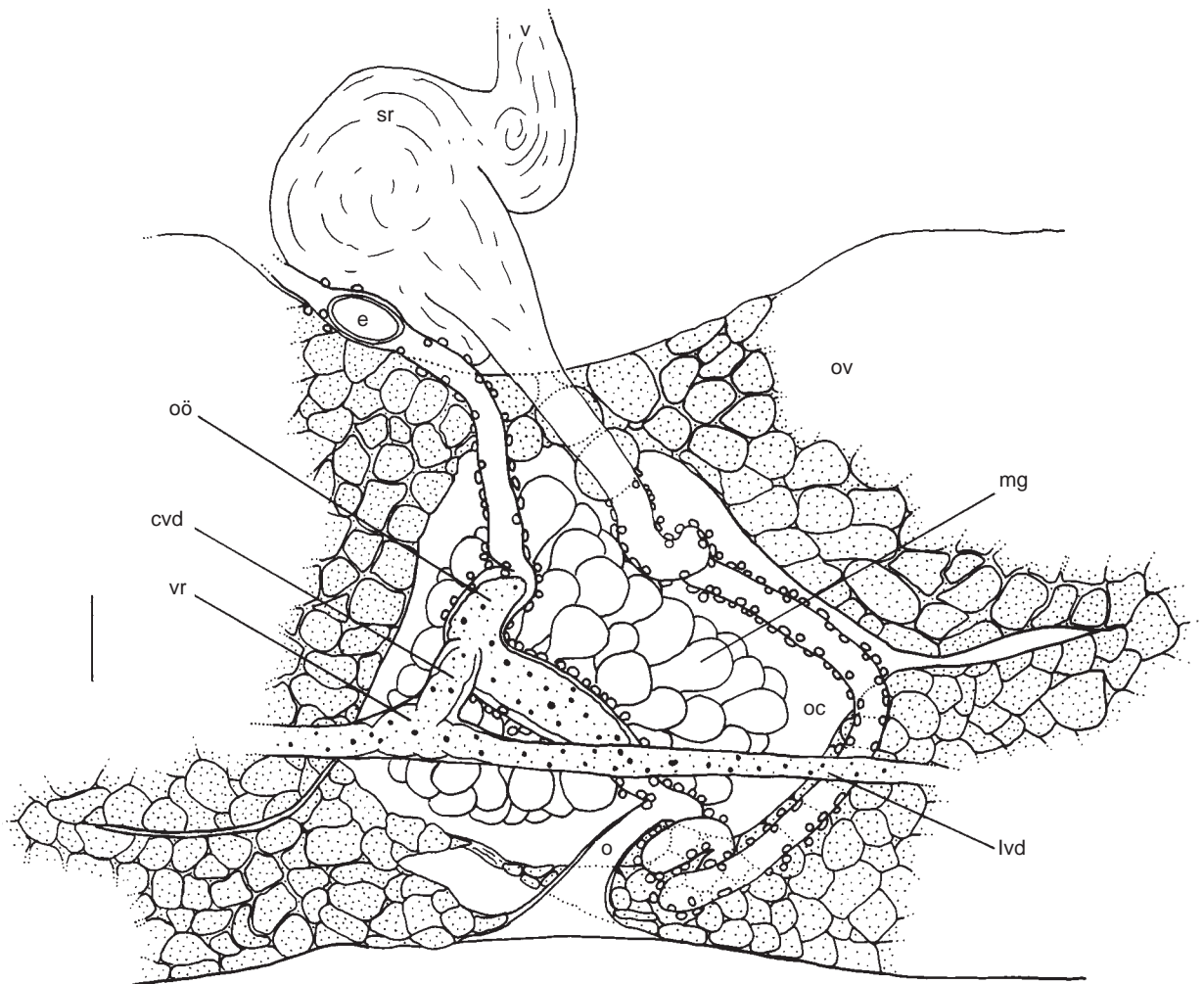
Fig. 2. *Cephalochlamys namaquensis* (Cohn, 1906) ovarian complex (ventral view). Proximal uterus and vagina passing dorsally over anterior margin of ovarian cavity. cvd, common vitelline duct; e, egg; lvd, lateral vitelline duct; mg, Mehlis' gland; o, oviduct; oc, ovarian cavity; oö, oötype; ov, ovary; sr, seminal receptacle; v, vagina; vr, vitelline reservoir. Scale bar = 10 μm.

from RUCA 125-126; 20 specimens (24), P, hosts from ZFMK 39980–39981, 39984–39985 and 39989; two specimens (25) NHM 1971.3.12.4–8; one specimen (26) NHM 1999.10.11.7; 20 specimens (27) (including NHM 1999.11.9.11–13), F, coll. R. C. Tinsley, June 1983 and June 1989; 20 specimens (28), F, coll. R. C. Tinsley, June 1990; one specimen (29), F, coll. R. C. Tinsley, September 1983.

Description

Morphometric and meristic data based on worms bearing gravid proglottids. Means and ranges (in parentheses) for material from Cape South Africa ($n = 6$) precede those for material from San Diego County, U.S.A. ($n = 5$).

With characters of genus. Scolex 889 (509–1333), 1022 (992–1452) long, apical projection 264 (189–358), 249 (172–288) wide. Total worm length 8730 (5920–10 280), 17 780 (9060–26 930); 34 (26–38), 47 (38–59)

proglottids. Testes scattered laterally, three to 23 per proglottid (based on material from all present localities), sometimes asymmetrically distributed in left and right fields (maximum difference of three; posterior extent increasing with testis number. Ovary subglobular to laterally elongate, with well-developed median ovarian cavity giving organ bilobed or horned appearance. Vitelline follicles showing extensive lateral scatter, sometimes protruding between longitudinal muscle bands. (Note on flattened material: due to the wide dispersion of the vitelline follicles, these are sometimes displaced to either side by pressure from the ventral excretory canal, if this is distended, giving the appearance of a 'double series' of follicles on each side.) Proglottid measurements: S1, 134 (76–265), 225 (91–567) long, 708 (431–889), 599 (265–815) wide, testis 32 (22–39), 40 (26–61) × 51 (36–61), 72 (67–88), ovary 27 (11–55), 42 (23–91) long, 239 (159–310), 223 (144–272) wide; S2, 324 (229–476), 369 (259–544) long, 836 (552–1074), 714 (280–982) wide, testis 61 (41–77), 64 (61–69) × 95 (72–121), 106 (96–113), ovary 62 (53–83), 76 (61–83) long, 380 (340–423), 314

Table 1. Host-specificity of sympatric *Cephalochlamys namaquensis* (Cohn, 1906) and *C. compactus* sp. nov. Samples from Sir area, Cameroon

Host	All cephalochlamydids[a]			No. identifiable specimens		
	Prevalence	Mean abundance	*n* (hosts)	*C. namaquensis*	*C. compactus*	*n* (parasites)
Xenopus muelleri	65%	1.3	20	0	14	26
X. laevis sudanensis	60%	1.9	20	24	0	38

[a] Infection statistics based on total numbers of worms (including specimens unidentifiable due to the absence of sufficiently developed proglottids).

(181–423) wide; S3, 596 (355–703), 812 (635–1056) long, 944 (665–1241), 1116 (982–1315) wide, testis 74 (60–95), 68 (56–80) × 109 (96–130), 113 (106–119), ovary 78 (57–102), 70 (45–91) long, 373 (257–476), 429 (340–567) wide. Unembryonated egg with thick, refractive shell, 23 (15–31), 20 (18–21) × 14 (10–19), 14 (11–16); embryonated egg with membranous shell from distal portion of uterus, 40 (37–42), 37 (36–37) × 24 (21–27), 22 (21–23), embryo 28 (23–32), 28 (23–30) × 17 (15–19), 16 (15–18).

Remarks

Amongst pipid species, material attributable to *C. namaquensis* was only found in *X. laevis*, although descriptions and figures in previous studies suggest it may occur naturally in ranids (Mettrick, 1963) and can infect urodeles in captivity (Dollfus, 1968; see also Tinsley, 1996*b*). A further specimen (NHM 1999.10.11.7, originally from the personal collection of J. Thurston) exists which was recovered from a '*Bufo*' sp. in unknown circumstances. Despite its ability to infect such distantly related amphibians, *C. namaquensis* shows a highly restricted distribution amongst African pipids. The basis of this specificity is unclear, but is not likely to arise from the simple two-host life-cycle (see below). Tinsley *et al*. (1979) showed that *C. namaquensis* is absent from *X. (Xenopus) wittei* Tinsley, Kobel & Fischberg and *X. (Xenopus) vestitus* Laurent in the western Rift Valley area (see also Tinsley, 1981, 1996*a*), despite the sympatric occurrence of infected *X. l. victorianus*. In the present study, samples of *X. vestitus* from western Uganda (L. Mutanda, *n* = 20) and *X. wittei* from Rwanda, Burundi and D.R.C. (*n* = 65, six localities) were also found to be uninfected with *Cephalochlamys* spp. Although *C. namaquensis* was present in *X. laevis* at localities throughout the range of this host, it has never been found in *X. muelleri* where these species are sympatric or parapatric in southern and central Africa (KwaZulu-Natal north to the D.R.C.). *Xenopus muelleri* was also uninfected with identifiable *C. namaquensis* specimens at Sir, Cameroon, where it was sympatric with infected *X. l. sudanensis* (see Table 1) (*C. namaquensis* can only be separated from the species which usually occurs in *X. muelleri* when sufficiently developed proglottids are present, see below).

Cephalochlamys namaquensis* has been introduced, together with *X. l. laevis*, to localities in the United States and western Europe. Lafferty & Page (1997) reported the species from the Santa Clara River estuary, California, while in the present study it was recorded from further sites in southern California and from the Isle of Wight, U.K.

Cephalochlamys compactus sp. nov.

(Figs 3, 4b, 5a, 6a & 7j–p)

Type-host and locality

Xenopus (Xenopus) muelleri (Peters) (western form, see Tinsley *et al*., 1996) at Bolgatanga, Ghana.

Previously reported hosts and localities

From *Xenopus (Xenopus) clivii* Peracca: Kebena River, Addis Ababa, Ethiopia (as *C. namaquensis*), Fischthal & Asres (1970) (1). From *Rana angolensis*: Sebeta River, Shoa Province, Addis Ababa, Ethiopia (as *C. namaquensis*), Fischthal & Asres (1970) (2).

Other records

From *X. muelleri* (western form): Namoundjoga, Togo (3); Niamtougou, Togo (4); Benin City, Nigeria (5); Sir, Cameroon (6); Gueme, Cameroon (7). From *X. muelleri* (eastern form, see Tinsley *et al*., 1996): Moba, D.R.C. (8); Kiembi, D.R.C. (9); Gangala na Bodio, D.R.C. (10); Marungu area, D.R.C. (11); L. Tanganyika, between Sengwe and Mwerase, D.R.C. (12); Kariba, Zimbabwe (13); Ndumu, KwaZulu-Natal, R.S.A. (14). From *X. (Xenopus) borealis* Parker: Nairobi, Kenya (15). From *Rana occipitalis* Günther: Warri, Nigeria (16).

Site

Intestine.

Material studied

Holotype, NHM 1999.11.8.1, one paratype, NHM 1999.11.8.2, and six non-type specimens from type-
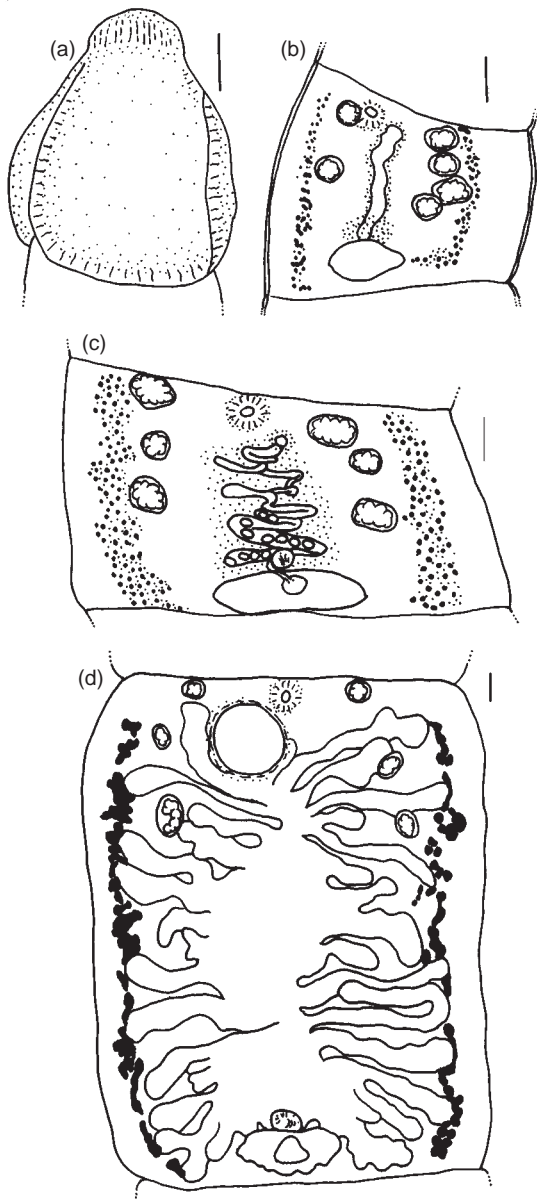
Fig. 3. *Cephalochlamys compactus* sp. nov. (ventral views): (a) scolex; (b) early proglottid; (c) first gravid proglottid; (d) heavily gravid proglottid. Scale bars = 100 μm

Fig. 4. Terminal genitalia of *Cephalochlamys* Blanchard, 1908 species (ventral views): (a) *C. namaquensis* (Cohn, 1906); (b) *C. compactus* sp. nov. mp, muscular papilla (male system); ga, genital atrium; gp, genital pore; pr, prostatic region; sv, seminal vesicle; v, vagina. Scale bars = 5 μm.

33.697–698; one specimen (12) MRAC 33.676; 12 specimens (13) (including NHM 1999.11.8.4), F, coll. V. Clarke, 1989 and 1991; nine specimens (14), F, coll. R. C. Tinsley and L. Du Preez, November, 1995; eight specimens (15) (including NHM 1999.11.8.5), F, hosts obtained from commercial imports, February, 1976 and April, 1981; one specimen (16) NHM 1988.10.26.8.

Description

Measurements for holotype followed by those for one paratype and one non-type specimen from type-locality bearing heavily gravid proglottids (in parentheses).

With characters of genus. Scolex 429 (416; 461) long, apical projection 160 (181; 294) wide. Total worm length 58 690 (28 598; 15 759); 73 + (52; 40) proglottids. Testes scattered laterally (but in non-type material sometimes occurring in a contiguous series, particularly in juvenile proglottids), four to eight per proglottid (three to 16 in material from all present localities), sometimes asymmetrically distributed in left and right fields (maximum difference of two); posterior extent increasing with testis number. Ovary subglobular to laterally elongate, median ovarian cavity only moderately developed giving organ compact appearance. Vitelline follicles showing limited lateral scatter. Proglottid measurements: S1, 429 (150; 181) long, 582 (509;

locality (including NHM 1999.11.8.3), F, coll. R. C. Tinsley, April, 1979. Four specimens (1) USNPC 70804; 19 specimens (2) USNPC 68106; five specimens (3), P, host from RUCA 1139; five specimens (3) MRAC 34.689, MRAC 34.743, MRAC 34.748–749; three specimens (4), P, host from RUCA 1094; two specimens (4) MRAC 34.731, MRAC 34.737; one specimen (5) NHM 1988.10.26.9; 25 specimens (6), P, host from RUCA 125 and 127; one specimen (7), P, host from RUCA 1.8; 13 specimens (8) MRAC 34.570, MRAC 34.593, MRAC 34.596–599, MRAC 34.601–602; 18 specimens (9) MRAC 34.558–560, MRAC 34.562–563, MRAC 34.566–567; three specimens (10) MRAC 34.579–580; three specimens (11) MRAC
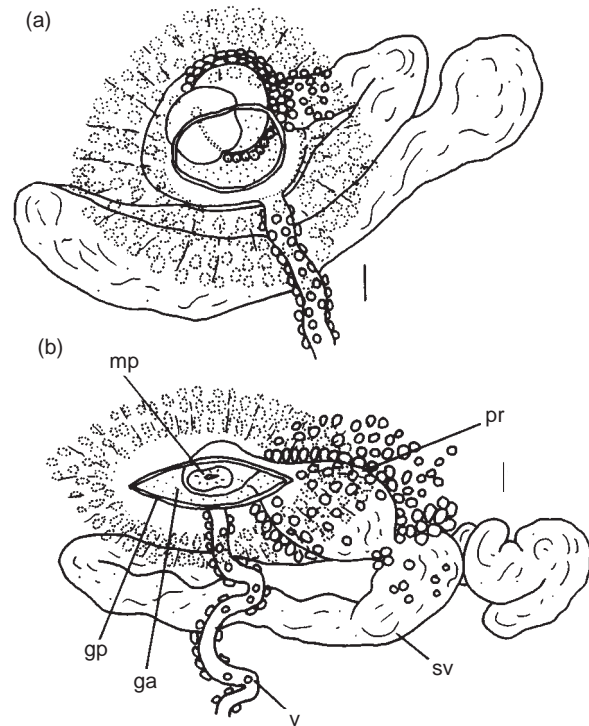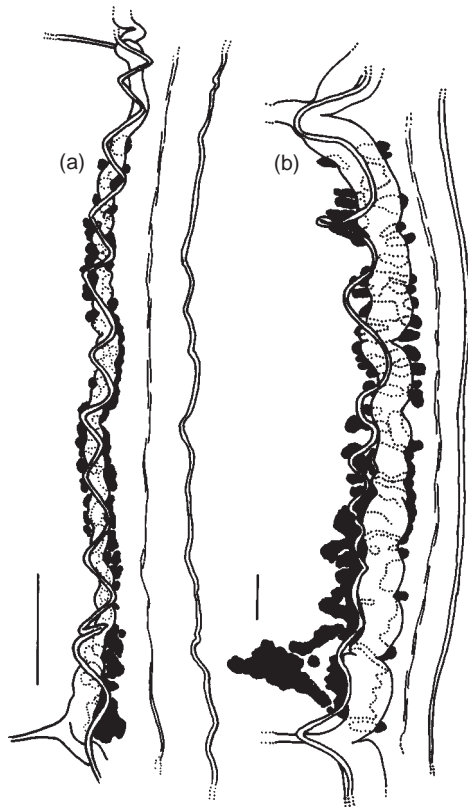
Fig. 5. Lateral excretory system, vitelline follicles and longitudinal muscle bands in *Cephalochlamys* Blanchard, 1908 species *(*dorsal views): (a) *C. compactus* sp. nov.; (b) *C. namaquensis* (Cohn, 1906). Scale bars = 100 μm.

Fig. 6. Lateral excretory system, vitelline follicles (solid) and longitudinal muscle bands (open) in *Cephalochlamys* Blanchard, 1908 species (transverse sections): (a) *C. compactus* sp. nov.; (b) *C. namaquensis* (Cohn, 1906). Scale bar = 100 μm.

406) wide, testes 39–66 (24–44; 26–39) × 49–87 (44–65; 49–62), ovary 90 (37; 34) long, 166 (138; 146) wide; S2, 493 (371; 298) long, 934 (960; 717) wide, testes 50–73 (49–73; –) × 66–105 (78–113; –), ovary 91 (89; 73) long, 341 (330; 310) wide; S3, 1857 (928; 698) long, 1460 (1524; 1114) wide, testes 62–102 (55–96; 55–81) × 65–141 (105–138; 99–149), ovary 163 (65; 49) long, 381 (352; 384) wide. Unembryonated egg with refractive shell 24 (26; 22) × 15 (14; 13); embryonated egg with membranous shell from distal portion of uterus 46 (36; 31) × 26 (19; 19), embryo 21 (31; 19) × 19 (15; 15).

Remarks

Cephalochlamys compactus lacks the great development of the median ovarian cavity which in *C. namaquensis* gives this organ a distinctive horned or bilobed appearance (see Fig. 7). Also, the lateral scatter of vitelline follicles (Fig. 5) is reduced in *C. compactus*, while *C. namaquensis* usually shows higher maximum numbers of testes per proglottid. However, the variation in testis number is continuous and could be influenced by host environmental factors (Thurston, 1967; Pappas & Leiby, 1986).

Like *C. namaquensis*, *C. compactus* can infect ranid hosts but only occurs in a subset of African pipids. It is a common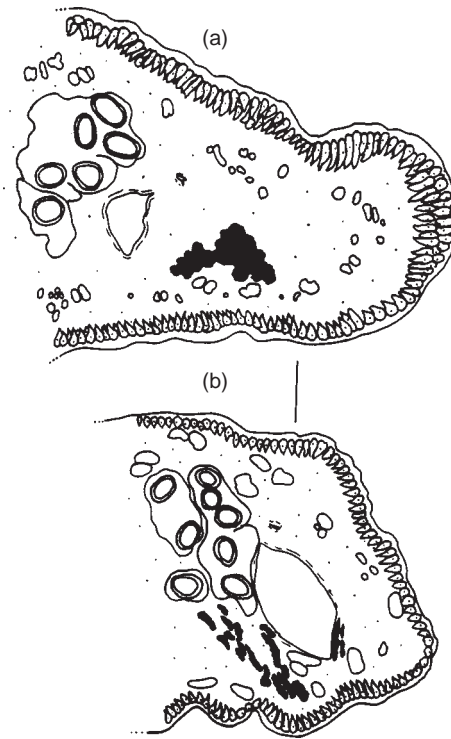 parasite of the *X. muelleri* species group and morphologically similar specimens of uncertain specific status also infect *X. fraseri* group hosts (see below). Adult *C. compactus* has never been found in any other pipids, including *X. laevis laevis* where this occurs in regional parapatry or sympatry with *X. muelleri* (KwaZulu-Natal north to southern D.R.C.). It was also not identified in *X. l. sudanensis* in the Sir area, Cameroon, where this toad subspecies is sympatric with infected *X. muelleri* (Table 1).

Given the host-specificity patterns observed in this study, the previous record of *C. namaquensis* from *X. muelleri* in western Africa (Avery, 1971) should be regarded as an undetermined *Cephalochlamys* sp.

Etymology

From the Latin *compactus* (= having been put together). Referring to the appearance of the ovary given its relatively poorly developed median cavity (see above).

Cephalochlamys sp. in *Xenopus gilli*

Host and locality

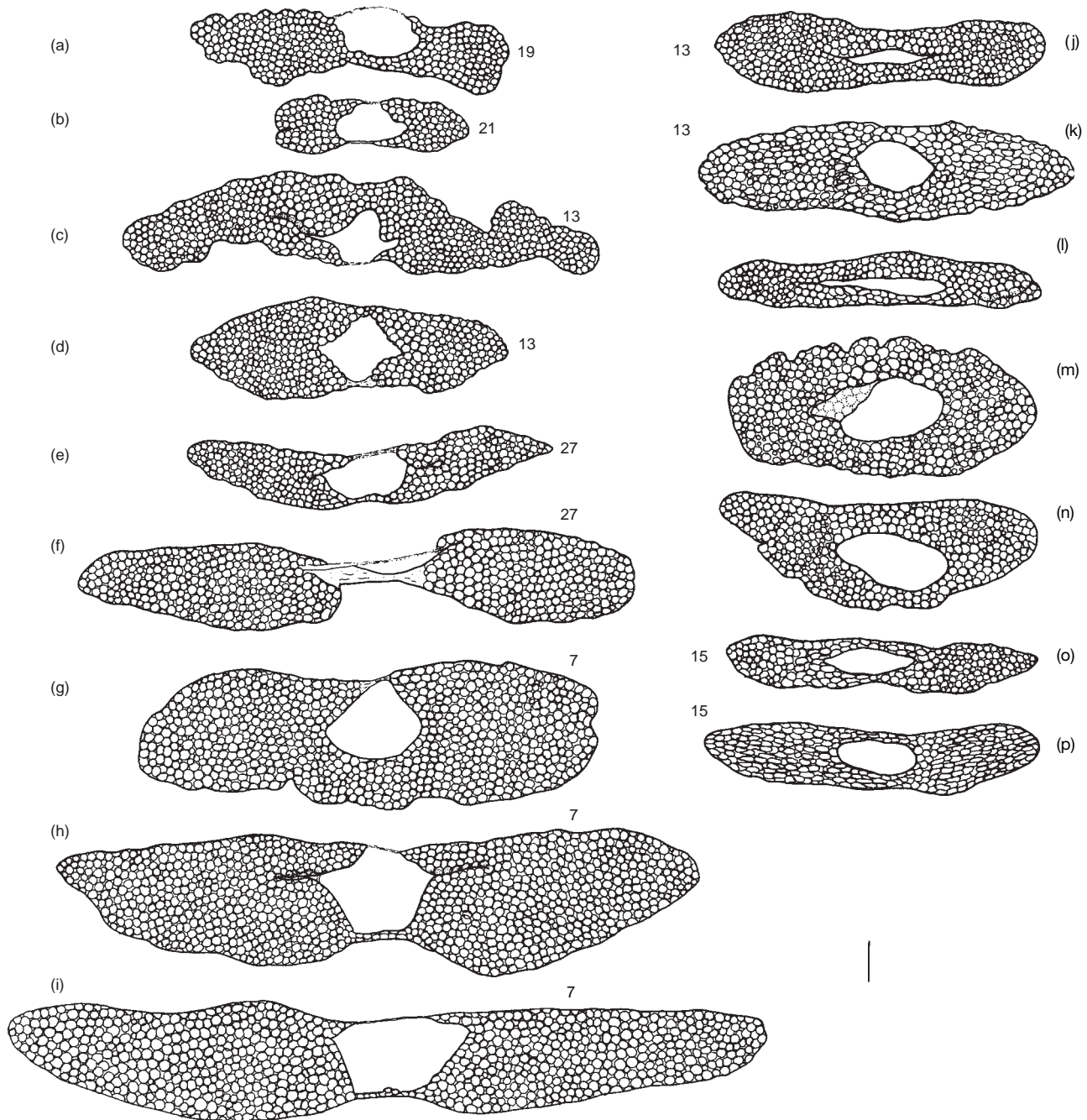*Xenopus (Xenopus) gilli* Rose & Hewitt at southwestern Cape Province, South Africa.

Fig. 7. Ovaries of *Cephalochlamys* Blanchard, 1908 species: (a–i) *C. namaquensis* (Cohn, 1906); (j–p) *C. compactus* sp. nov. (numbers correspond to host/locality records in text, unnumbered examples are from a type-locality). Scale bar = 50 μm.

Material studied

Two scolices and four immature proglottids, F, host coll. M. Simmonds, December 1983.

Morphological observations

Scolex 666–717 long, apical projection 214–224 wide. Total length 1016 ($n = 1$). Two to five testes in each lateral field (five to eight per proglottid) ($n = 4$ proglottids). Proglottid dimensions: S1 ($n = 1$), 230 long, 226 wide, testis 15–41 × 16–42, ovary 60 long, 110 wide.

Remarks

This material does not allow conclusive identification, but is most likely to belong to *C. namaquensis*. *Xenopus gilli* only occurs in a restricted area of south-western Cape, South Africa, where it is sympatric and may

hybridize (Kobel, Du Pasquier & Tinsley, 1981; Picker, Harrison & Wallace, 1996) with the closely related *X. laevis*, possibly with some degree of gene introgression (Kobel *et al.*, 1981). The latter species is the usual host of *C. namaquensis* and the only other *Xenopus* taxon to occur in this area (Tinsley *et al.*, 1996).

Cephalochlamys sp. in Xenopus fraseri group hosts

Hosts and localities

From *Xenopus (Xenopus) fraseri* Boulenger-like species: Boende, D.R.C. (1); Boteka, D.R.C. (2); Ebisha, near Irangi research station, D.R.C. (3). From *Xenopus (Xenopus) pygmaeus* Loumont: Kisangani, D.R.C. (4).

Material studied

One specimen (1), P, host from MRAC 75-035-B-0464-0468; four specimens (2), P, hosts from MRAC 85-030-B-0023-0032; five specimens (3), F, recovered in poor condition from recently dead host, coll. H. Hinkel, November 1992; two specimens (4), P, host from RUCA S(7) no.3243.

Morphological observations

Testes in anterior half of proglottids, sometimes forming a contiguous series: two to four in lateral fields (four to eight per proglottid). Ovary with moderately developed median cavity. Vitelline follicles in two compact lateral columns.

Remarks

These specimens differ from *C. namaquensis* in the same ways as *C. compactus*. However, conspecificity with the latter species cannot be assessed due to the poor quality of the material.

Cephalochlamys sp. in Xenopus tropicalis

Host and locality

Xenopus (Silurana) tropicalis (Gray) from Lagos area, Nigeria.

Material studied

One non-ovigerous specimen, F, host imported to U.K., March, 1986.

Morphological observations

Scolex 266 long, apical projection 92 wide. Total length 4370; 26 proglottids. Testes subrectangular, arranged in contiguous series, often extending to posterior region of proglottid: one to four in lateral fields (four to eight per proglottid). Ovary with moderately developed median cavity. Vitelline follicles in two compact lateral columns. Proglottid measurements: S1, 138 long, 496 wide, testes $32–52 \times 62–81$, ovary 41 long, 164 wide; last undistorted proglottid, 205 long, 570 wide, testes $32–45 \times 73–105$, ovary 52 long, 229 wide.

Remarks

This specimen most closely resembles *C. compactus*, juveniles of which sometimes show a comparable arrangement of the testes in contiguous series. However, as no gravid proglottids were present, its taxonomic status remains uncertain. It was the only example recovered from large numbers of *Silurana* hosts examined at localities throughout west Africa ($n = 172$ toads from 11 sites: same samples as studied in Tinsley & Jackson (1998*a*)). It may be that this pipid lineage is not usually parasitized by cephalochlamydids and that the present specimen represents a rare 'accidental' infection.

Cephalochlamys sp. of Dollfus (1968)

Host and locality

Rana occipitalis Günther at Ste Croix Eschiras, Gabon (Dollfus, 1968).

Remarks

A gravid specimen from *Rana occipitalis* was figured by Dollfus (1968) who noted that it might represent a distinct species from *C. namaquensis*, based on the distinctive arrangement of testes, in linear, contiguous (or near contiguous) series. Such a columnar arrangement of testes may occur in juvenile proglottids and more rarely in gravid proglottids of *C. compactus*. This pattern was also observed in *Cephalochlamys* sp. from *X. tropicalis* and *X. fraseri*-like hosts. However, in Dollfus's material the lateral series involved eight testes, while columns of two to four were observed in the present study. A *C. compactus* specimen from *R. occipitalis* in Nigeria (NHM 1988.10.26.8) showed testes which were contiguous but did not form linear series.

Cephalochlamys sp. in 'Xenopus sp.' (miscellaneous literature records)

Representatives of *Cephalochlamys* have been reported in unidentified *Xenopus* species by Thurston (1967, 1970)
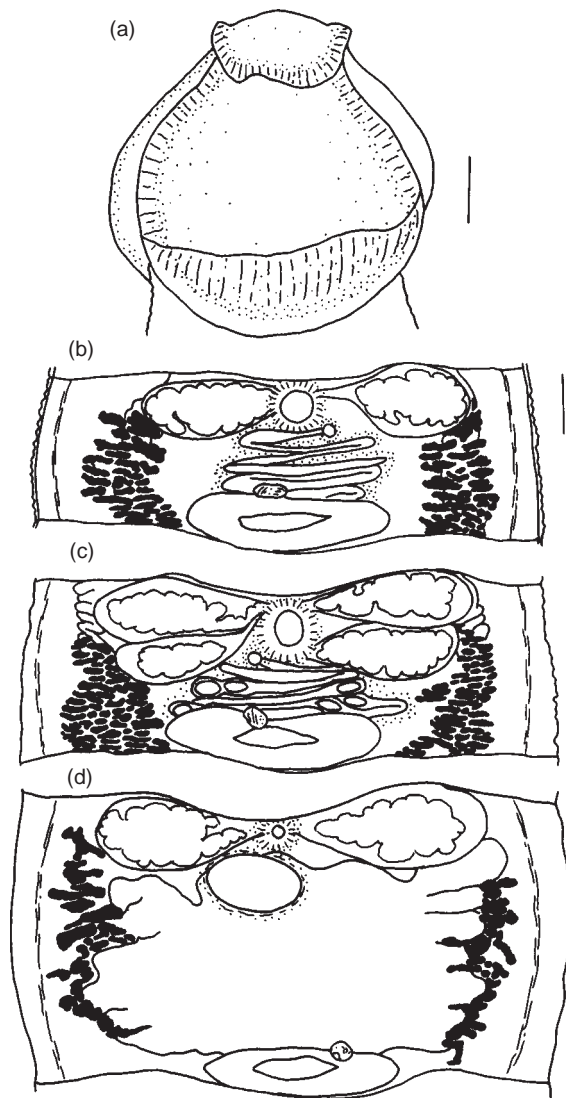
Fig. 8. *Paracephalochlamys papilionis* gen. nov., sp. nov. (ventral views): (a) scolex; (b) early proglottid; (c) first gravid proglottid; (d) heavily gravid proglottid. Scale bars = 50 μm.

at Ogbomosho (Nigeria) and Nairobi (Kenya), Baer & Fain (1961) at the Garamba National park (D.R.C.) and Baylis (1934) in western Uganda. These parasite specimens should now be considered of uncertain specific identity, although material from Ogbomosho (JT) resembles *C. compactus* (personal observation).

Paracephalochlamys gen. nov.

Diagnosis

As for Cephalochlamydidae, except: testes always very large, pyriform, arranged laterally on anterior margin of segment, usually two per segment (one on each side). Occasionally lateral testes doubled (on one or both sides), rarely testis absent on one side of segment.

Remarks

This genus is differentiated from *Cephalochlamys* by the number and form of the testes. These are very large in proportion to proglottid size, usually only two (but occasionally doubled on one or both sides), pyriform, and located on either side of the midline at the anterior border of each proglottid. Rarely the left or right testis is absent, or in mature proglottids both are atrophied.

Etymology

Implying a close relationship to *Cephalochlamys*.

Paracephalochlamys papilionis sp. nov. (Fig. 8)

Type-host and locality

Pseudhymenochirus merlini Chabanaud (Pipidae) at Komende, near Moyamba, Sierra Leone.

Other localities

From *P. merlini*: Periwahun village, near Komende, Sierra Leone (1); Kasewe forest reserve, Sierra Leone (2); Bradford, Sierra Leone (3).

Site

Intestine.

Material studied

Holotype NHM 1999.11.9.1, two paratypes NHM 1999.11.9.2–3 and five non-type specimens from type-locality, coll. R. C. Tinsley, March 1979. Thirty specimens (1), F, coll. R. C. Tinsley, April 1979 (including NHM 1999.11.9.4–6); 15 specimens (2), F, coll. R. C. Tinsley, March 1979 (including NHM 1999.11.9.7–8); 14 specimens (3), P, hosts coll. R. C. Tinsley, March 1979.

Description

Measurements and counts for holotype precede summary statistics (mean before range) for a sample of entire worms bearing heavily gravid proglottids (based on eight specimens unless otherwise stated: holotype, two paratypes, four from Periwahun, and two from Kasewe).

With characters of genus. Scolex 230 (312, 230–445) long, apical projection 106 (111, 83–146) wide. Total length 3550 (5410, 2530–11 690); 23 proglottids (26, 22–36) (but one fragmented specimen from Periwahun with

at least 44). Ovary laterally elongate (to subglobular in paratypes and non-type material), smooth (margins irregular in some paratypes and other material), with moderately developed median ovarian cavity. Proglottid measurements: S1, 76 (125, 76–262) long, 282 (320, 251–406) wide, testis 29 (38, 29–47) long, 53 (78, 53–110) wide, ovary 29 (35, 26–43) long, 89 (96, 70–131) wide; S2, 149 (215, 149–285) long, 445 (418, 323–499) wide, testis 52 (68, 52–78) long, 159 (133, 109–159) wide, ovary 45 (52, 42–65) long, 183 (154, 124–213) wide; S3, 378 (513, 339–691) long, 614 (548, 378–758) wide, testis 86 (94, 83–107) long, 207 (192, 149–243) wide (note: but testes sometimes atrophied in mature proglottids), ovary 62 (67, 57–93) long, 177 (171, 105–240) wide. Unembryonated egg with refractive shell, 26 (27, 24–30, $n = 6$) × 16 (16, 14–18, $n = 6$); embryonated egg with membranous shell from distal portion of uterus, 42 (44, 41–49) × 28 (30, 26–34), embryo 32 (30, 27–34) × 23 (21, 16–24).

Remarks

Paracephalochlamys papilionis was only found in *P. merlini*. This pipid is limited to lowland forest zones in Sierra Leone, Guinea and Guinea-Bissau (Frost, 1985) where it may occur in the same habitats as *X. tropicalis* (see Menzies, 1967; R. C. Tinsley, pers. obs.). Seventy-eight *X. tropicalis* examined from four localities in Sierra Leone were uninfected (based on samples studied by Tinsley & Jackson, 1998a), although only seven of these were from sites where it was possible to confirm the presence of *P. merlini* harbouring *P. papilionis*.

Etymology

From the Latin *papilionis* (= butterfly), suggested by the configuration of internal organs at the anterior of each proglottid.

DISCUSSION

Host-specificity and geographical distributions

Two genera and three species of cephalochlamydid cestode are recognized from pipids in sub-Saharan Africa. *Cephalochlamys namaquensis* occurs in *Xenopus (Xenopus) laevis laevis* in Namibia, South Africa, Lesotho and Zimbabwe, *X. l. victorianus* in D.R.C. (formerly Zaïre), Rwanda, Uganda and Kenya, *X. l. poweri* in D.R.C. and Zambia, and *X. l. sudanensis* in Cameroon and Sudan. Amongst pipids it has only been identified in *X. laevis*, although scolices recovered from *X. (X.) gilli* (a close relative of *X. laevis*, see Tymowska, 1991; Kobel *et al.*, 1996) may also belong to *C. namaquensis*. *Cephalochlamys compactus* is found in the western form of *X. (X.) muelleri* (see Tinsley *et al.*,

1996) in Ghana, Togo, Nigeria and Cameroon, in the eastern form of *X. muelleri* in D.R.C., Zimbabwe and South Africa, *X. (X.) borealis* in Kenya and *X. (X.) clivii* in Ethiopia. Both species have been recorded from ranid hosts in the field. *Cephalochlamys* specimens of undetermined specific status, but with closest affinities to *C. compactus*, were recovered from *X. (X.) fraseri*-like hosts and *X. (X.) pygmaeus* at localities in D.R.C. and *X. (Silurana) tropicalis* in Nigeria. As the latter record consisted of only one immature specimen, and cephalochlamydids have not otherwise been found in *Silurana* despite extensive investigations, these hosts may usually be uninfected. A distinct cephalochlamydid species of a new genus, *Paracephalochlamys papilionis*, occurs in *Pseudhymenochirus merlini* in Sierra Leone (the first record of a cephalochlamydid from a hymenochirine pipid).

Both *C. namaquensis* and *C. compactus* occupy geographical ranges extending over 40° of latitude in sub-Saharan Africa and including a wide variety of biotypes. In the case of *C. namaquensis* these range from the temperate Mediterranean climatic zone at the tip of South Africa to upland savanna at lower latitudes. *Cephalochlamys compactus* occurs in habitats bordering the Sahel zone of west Africa (in western *X. muelleri*), low altitude areas in east Africa (in eastern *X. muelleri*) and highland habitats in western Kenya *(X. borealis)* or Ethiopia (*X. clivii*). *Cephalochlamys* sp. in *Xenopus fraseri* group hosts and *P. papilionis* in *P. merlini* both occupy lowland forest biotypes in western Africa or the Congo basin. The occasional occurrence of cephalochlamydids in ranids (and infection of urodeles in captivity) shows that transfers to non-pipid hosts are possible. However, given the range of biotypes in which some species can exist and their restricted distributions amongst different pipid lines, it seems probable that the geographical distributions described above are primarily determined by associations with these phylogenetically distinct aquatic toads (Tinsley, 1996a). The importance of host-specificity is illustrated by the segregation of parasite populations where *X. laevis* (infected with *C. namaquensis*) and *X. muelleri* (infected with *C. compactus*) are sympatric or parapatric, and by the absence of *C. namaquensis* from *X. wittei* and *X. vestitus* in western Uganda (Tinsley, 1981, 1996a), despite the sympatric occurrence of this parasite in *X. l. victorianus*. The absence of mature infection in *Silurana* is despite sympatry with *Pseudhymenochirus merlini* (infected with *P. papilionis*) (Menzies, 1967; Frost, 1985; Jackson & Tinsley, 1998a) and *Xenopus fraseri* group species (infected with *Cephalochlamys* sp.) (Tinsley *et al.*, 1996) over broad geographical areas.

Cephalochlamys has a two-host transmission cycle with cyclopoid copepods as intermediate hosts (Thurston, 1970; Ferguson & Appleton, 1988). This reliance on a copepod intermediate clearly limits the potential to infect non-pipid anurans; whilst pipids primarily feed underwater, most other anurans are specialized terrestrial feeders (Tinsley *et al.*, 1996). Both of the ranid species which have been recorded as hosts,

R. angolensis and *R. occipitalis*, are relatively aquatic forms that might occasionally ingest prey contaminated with copepods (Tinsley, 1996*b*). Although an aquatic life-cycle can account for the common use of pipid hosts, the proximal mechanism for specificity between different pipid lines remains to be determined. It is unlikely to result from differential consumption of copepods by definitive hosts, as all African pipid groups can be assumed to include these crustaceans in their diet. Camallanid nematodes, which also use cyclopoids as intermediate hosts, have been found in every *Xenopus*, *Hymenochirus* and *Pseudhymenochirus* species that has been examined parasitologically (Jackson & Tinsley, 1995*a*,*b*, 1998*a*). Infection of different copepod species is also an unlikely mechanism, as the available evidence suggests that parasite specificity to these hosts is low. *Cephalochlamys namaquensis* has invaded habitats in the U.S.A. and U.K., where it must use indigenous species. The ability of this parasite to reach the procercoid stage in a variety of U.K. cyclopoids has also been confirmed experimentally. Narrow adaptation to the physiological or immunological characteristics of definitive host taxa could be responsible for the tendency of cephalochlamydids to infect certain pipids, however, this would entail that at least some *Cephalochlamys* species retain a seemingly paradoxical ability to infect ranids.

Evolutionary host–parasite relationships

The amphibian family Pipidae contains four extant genera: the neotropical *Pipa* and the African *Pseudhymenochirus*, *Hymenochirus* and *Xenopus*. *Xenopus* is recognized to comprise two main evolutionary lines (Tymowska, 1991; Graf, 1996; Kobel *et al.*, 1996; Kobel, Barandun & Thiébaud, 1998) which both contain polyploid species derived from interspecific hybridization (Kobel, 1996). These two lineages have most recently been recognized at the subgeneric level (Kobel *et al.*, 1996) and are respectively characterized by multiples of 20 (*Silurana*) or 18 (*Xenopus*) chromosomes. Molecular studies (Graf, 1996) support the monophyly of *Xenopus* and *Silurana*, whilst an alternative hypothesis (Cannatella & Trueb, 1988*a*,*b*), based on an anatomical analysis, suggests that *Silurana* is the sister group of the hymenochirines and *Pipa*, i.e. ((*Pipa* + hymenochirines) *Silurana*) (*Xenopus*). Whilst one *Silurana* species, *X. tropicalis*, is primitively diploid (as are the pipines and hymenochirines which have been studied), the subgenus *Xenopus* contains no extant diploid forms. Tetraploid representatives of this taxon fall into three species groupings (Kobel *et al.*, 1996) with affinities to *X. laevis* (*X. laevis* subspecies, *X. gilli*), *X. muelleri* (*X. muelleri*, *X. borealis*, *X. clivii*) or *X. fraseri* (including *X. pygmaeus*). Interbreeding within and between these lineages has, in turn, produced octoploid and dodecaploid species (Kobel *et al.*, 1998). The restricted distributions of cephalochlamydids amongst pipid groups suggest some degree of ecological specialization by the parasites with regard to different host lineages. Thus, *Paracephalochlamys* and *Cephalochlamys* spp. are specific to hymenochirines and to the subgenus *Xenopus*, respectively, whilst *C. namquensis* and *C. compactus* occur in different *Xenopus* species groups. Excluding accidental infections (see above), cephalochlamydids are probably absent from *Silurana*. This could be attributed either to their extinction in this host lineage or to a failure to colonize it over evolutionary time. *Cephalochlamys* spp. are also absent (Tinsley, 1981; present study) from the octoploid species *X. wittei* and *X. vestitus*, both of which are hypothetically derived from interspecies hybridization between tetraploid *Xenopus* lineages related to *X. laevis* and *X. fraseri* (see Tymowska, 1991; Kobel *et al.*, 1998). As cephalochlamydids occur in all tetraploid members of the subgenus *Xenopus* which have been examined (including *X. laevis*, *X. gilli*, *X. borealis*, *X. muelleri*, *X. fraseri*-like forms and *X. clivii*), it may be that the hybridization/polyploidization event giving rise to the octoploid species produced behavioural, physiological or immunological changes which protect them from infection (Tinsley, 1981; Tinsley, 1996*a*). Allopolyploid hybrids would have inherited the genes determining resistance or susceptibility to particular parasites from both parental hosts. It is probable that a proportion of genes have become silenced in ancient allopolyploid species (Kobel *et al.*, 1998), including some involved in host defences, such as MHC (Du Pasquier *et al.*, 1977) and immunoglobulin genes (Du Pasquier & Robert, 1996). The phenotype of susceptibility or resistance to particular parasites might then depend on the subset of genes expressed in the hybrids after such reorganizations have occurred. Recent experimental and field studies on the host specificity of monogenean platyhelminths from *X. wittei* and *X. vestitus* do suggest that they may have inherited resistance to some monogenean parasites found in the 'parental' *X. laevis* and *X. fraseri* groups but susceptibility to others (Jackson, Tinsley & Kigoolo, 1998; Tinsley & Jackson, 1998*b*). It is possible that the combination of 'parental' genes expressed by *X. wittei* and *X. vestitus* has provided resistance to the *Cephalochlamys* species from both parental hosts.

REFERENCES

Avery, R. A. (1971). A preliminary list of parasites collected from reptiles and amphibians in northern Nigeria. *Br. J. Herpetol.* **4**: 217–219.

Baer, J. G. & Fain, A. (1961). Cestodes. *Explor. Parc nat. Garamba Mission H. de Saeger* **21**: 1–10.

Baylis, H. A. (1934). Miscellaneous notes on parasitic worms. *Ann. Mag. Nat. Hist.* **13**: 223–228.

Bray, R. A., Jones, A. & Andersen, K. I. (1995). Order Pseudophyllidea. In *Keys to the cestode parasites of vertebrates*: 205–247. Khalil, L. F., Jones, A. & Bray, R. A. (Eds). Wallingford, U.K.: CAB International.

Cannatella, D. C. & Trueb, L. (1988*a*). Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zool. J. Linn. Soc.* **94**: 1–38.

Cannatella, D. C. & Trueb, L. (1988*b*). Evolution of pipoid frogs: morphology and phylogenetic relationships of *Pseudhymenochirus*. *J. Herpetol.* **22**: 439–456.

Dollfus, R. Ph. (1968). Présence insolite chez un urodele et en Afrique du nord d'un *Cephalochlamys* (Cestoda, Pseudophyllidea). *Bull. Mus. Natl Hist. Nat. Paris* **39**: 1192–1201.

Du Pasquier, L., Wilson, M. & Robert, J. (1996). The immune system of *Xenopus*: with special reference to B cell development and immunoglobulin genes. In *The biology of Xenopus*: 301–313. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Du Pasquier, L., Miggiano, V. C., Kobel, H. R. & Fischberg, M. (1977). The genetic control of histocompatibility reactions in natural and laboratory-made polyploid individuals of the clawed toad, *Xenopus*. *Immunogenetics* **5**: 129–141.

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. *J. Afr. Zool.* **107**: 513–517.

Ferguson, R. R. & Appleton, C. C. (1988). Some aspects of the morphology, population structure and larval biology of *Cephalochlamys namaquensis* (Cestoda: Diphyllidea), a parasite of the clawed toad, *Xenopus laevis*. *S. Afr. J. Zool.* **23**: 117–123.

Fischthal, J. H. & Asres, M. (1970). Two cestodes of amphibians from Ethiopia. *Proc. Helminthol. Soc. Wash.* **37**: 203–204.

Frost, D. R. (1985). *Amphibian species of the world*. Lawrence, KS: Allen Press & The Association of Systematic Collections.

Graf, J.-D. (1996). Molecular approaches to the phylogeny of *Xenopus*. In *The biology of Xenopus*: 379–389. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Jackson, J. A. & Tinsley, R. C. (1995*a*). Representatives of *Batrachocamallanus* n. g. (Nematoda: Procamallaninae) from *Xenopus* spp. (Anura: Pipidae): geographical distribution, host range and evolutionary relationships. *Syst. Parasitol.* **31**: 159–188.

Jackson, J. A. & Tinsley, R. C. (1995*b*). Evolutionary relationships, host range and geographical distribution of *Camallanus* Railliet & Henry, 1915 species (Nematoda: Camallaninae) from clawed toads of the genus *Xenopus* (Anura: Pipidae). *Syst. Parasitol.* **32**: 1–21.

Jackson, J. A. & Tinsley, R. C. (1997). The taxonomic status, host range and geographical distribution of *Dollfuschella* Vercammen-Grandjean, 1960 (Digenea: Halipeginae) from *Xenopus* spp. (Anura: Pipidae). *Syst. Parasitol.* **36**: 1–11.

Jackson, J. A. & Tinsley, R. C. (1998*a*). Hymenochirine anurans (Pipidae) as transport hosts in camallanid nematode life-cycles. *Syst. Parasitol.* **39**: 141–151.

Jackson, J. A. & Tinsley, R. C. (1998*b*). Paramphistome digeneans from *Xenopus* species (Pipidae) in Africa: taxonomy, host-specificity and biogeography. *Syst. Parasitol.* **40**: 143–160.

Jackson, J. A., Tinsley, R. C. & Kigoolo, S. (1998). Polyploidy and parasitic infection in *Xenopus* species from western Uganda. *Herpetol. J.* **8**: 19–22.

Kobel, H. R. (1996). Allopolyploid speciation. In *The biology of Xenopus*: 391–401. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Kobel, H. R., Barandun, B. & Thiébaud, Ch. H. (1998). Mitochondrial rDNA phylogeny in *Xenopus*. *Herpetol. J.* **8**: 13–17.

Kobel, H. R., Du Pasquier, L. & Tinsley, R. C. (1981). Natural hybridization and gene introgression between *Xenopus gilli* and *Xenopus laevis laevis* (Anura: Pipidae). *J. Zool. (Lond.)* **194**: 317–322.

Kobel, H. R., Loumont, C. & Tinsley, R. C. (1996). The extant species. In *The biology of Xenopus*: 9–33. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Lafferty, K. D. & Page, C. J. (1997). Predation on the endangered tidewater goby, *Eucyclogobius newberryi*, by the introduced African clawed frog, *Xenopus laevis*, with notes on the frog's parasites. *Copeia* **1997**: 589–592.

Macnae, W., Rock, L. & Makowski, M. (1973). Platyhelminths from the South African clawed toad, or Platanna (*Xenopus laevis*). *J. Helminthol.* **47**: 199–235.

Menzies, J. I. (1967). An ecological note on the frog *Pseudhymenochirus merlini* Chabanaud in Sierra Leone. *J. West Afr. Sci. Assoc.* **12**: 23–28.

Mettrick, D. F. (1960). Contributions to the helminth fauna of central Africa. II. Some cestodes of the order Pseudophyllidea recorded from southern Rhodesia. *Proc. Trans. Rhod. sci. Assoc.* **48**: 54–62.

Mettrick, D. F. (1963). Some cestodes of reptiles and amphibians from the Rhodesias. *Proc. zool. Soc. Lond.* **141**: 239–250.

Ortlepp, R. J. (1926). On a collection of helminths from a South African farm. *J. Helminthol.* **4**: 127–147.

Pappas, P. W. & Leiby, D. A. (1986). Variation in the sizes of eggs and oncospheres and the numbers and distributions of testes in the tapeworm, *Hymenolepis diminuta*. *J. Parasitol.* **72**: 383–391.

Picker, M. D., Harrison, J. A. & Wallace, D. (1996). Natural hybridisation between *Xenopus laevis laevis* and *X. gilli* in the south-western Cape Province, South Africa. In *The biology of Xenopus*: 61–71. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Pritchard, M. H. (1964). Notes on four helminths from the clawed toad, *Xenopus laevis* (Daudin), in South Africa. *Proc. Helminthol. Soc. Wash.* **31**: 121–128.

Southwell, T. & Kirshner, A. (1937). On some parasitic worms found in *Xenopus laevis*, the South African clawed toad. *Ann. trop. Med. Parasitol.* **31**: 245–265.

Thurston, J. P. (1967). The morphology and life-cycle of *Cephalochlamys namaquensis* (Cohn, 1906) (Cestoda: Pseudophyllidea) from *Xenopus muelleri* and *X. laevis*. *Parasitology* **57**: 187–200.

Thurston, J. P. (1970). Studies on some Protozoa and helminth parasites of *Xenopus*, the African clawed toad. *Rev. Zool. Bot. Afr.* **82**: 349–369

Tinsley, R. C. (1973). Observations on Polystomatidae (Monogenoidea) from east Africa with a description of *Polystoma makereri* sp. nov. *Z. Parasitenkd.* **42**: 251–263.

Tinsley, R. C. (1981). Interactions between *Xenopus* species (Anura: Pipidae). *Monit. zool. ital. Suppl.* **15**: 133–150.

Tinsley, R. C. (1996*a*). Evolutionary influences from host and parasite co-speciation. In *The biology of Xenopus*: 403–420. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Tinsley, R. C. (1996*b*). Parasites of *Xenopus*. In *The biology of Xenopus*: 233–261. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Tinsley, R. C. & Jackson, J. A. (1995). The genus *Oligolecithus* Vercammen-Grandjean (Digenea: Telorchiidae) from *Xenopus* spp. (Anura: Pipidae), with a description of *O. siluranae* sp. nov. from *X. tropicalis* (Gray) in Ghana. *Syst. Parasitol.* **32**: 131–140.

Tinsley, R. C. & Jackson, J. A. (1998*a*). Speciation of *Protopolystoma* Bychowsky, 1957 (Monogenea: Polystomatidae) in hosts

of the genus *Xenopus* (Anura: Pipidae). *Syst. Parasitol.* **40**: 93–141.

Tinsley, R. C. & Jackson, J. A. (1998*b*). Correlation of parasite speciation and specificity with host evolutionary relationships. *Int. J. Parasitol.* **28**: 1573–1582.

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. *J. Zool. (Lond.)* **188**: 69–102.

Tinsley, R. C., Loumont, C. & Kobel, H. R. (1996). Geographical distribution and ecology. In *The biology of Xenopus*: 35–59. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.

Tymowska, J. (1991). Polyploidy and cytogenetic variation in frogs of the genus *Xenopus*. In *Amphibian cytogenetics and evolution*: 259–297. Green, D. M. & Sessions, S. K. (Eds). London: Academic Press.