Some aspects of the morphology, population structure and larval biology of *Cephalochlamys namaquensis* (Cestoda: Diphyllidea), a parasite of the clawed toad, *Xenopus laevis*

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The morphology of *Cephalochlamys namaquensis* (Cohn 1906) Blanchard (1908), a diphyllid[a] cestode from the African clawed toad, *Xenopus laevis*, is examined with respect to variability reported in the literature. The parasite has a high prevalence of infection (68,9%) in the *X. laevis* population studied and shows a preference for attachment in the anterior duodenum. Approximately 76% of the worms recovered were juveniles. Coracidia had an LT50 of 6 h and transmission is thought to take place in darkness at the sediment/water interface. The copepod *Eucyclops gibsoni* serves as an intermediate host and it is suggested that chaoborid larvae may act as paratenic hosts.

Die morfologie van *Cephalochlamys namaquensis* (Cohn 1906) Blanchard (1908), 'n difiliede[a] sestode van die platanna *Xenopus laevis*, is ondersoek met verwysing na variasie wat in die literatuur voorkom. Die parasiet toon 'n hoë voorkoms van infeksie (68,9%) in die *X. laevis*-bevolking wat bestudeer is, met 'n voorkeur vir vashegting in die anterior duodenum. Ongeveer 76% van die wurms wat gevind is, was onvolwassenes. Corasidië het 'n LT50 van 6 uur gehad, en transmissie vind waarskynlik in die donker by die sediment/water-skeidingsvlak plaas. Die kopepodied *Eucyclops gibsoni* dien as 'n tussengasheer en daar word voorgestel dat chaoboriede larwes as parateniese gashere optree.

[a]Terminology following Wardle, McLeod & Radinovsky (1974)

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Cephalochlamys namaquensis is widely distributed in Africa and has been recorded several times from *Xenopus laevis* in southern Africa (Cohn 1906; Ortlepp 1926; Southwell & Kirshner 1937; Mettrick 1960,1963; Pritchard 1964; Thurston 1967; Macnae, Rock & Makowski 1973) and from *X. muelleri* in central Africa (Thurston 1967). In addition, it has been reported from *Rana angolensis* in Zimbabwe (Mettrick 1963) and *Pleurodeles poireti* from North Africa (Dollfus 1968 cited by Wardle, McLeod & Radinovsky 1974).

Considerable variation exists in the morphological descriptions of *C. namaquensis* and this has led in the past to some confusion regarding the taxonomy of the species. To date only Thurston (1967,1970) has discussed the biology of *C. namaquensis*. The present account therefore reviews the morphology of *C. namaquensis* and provides information on its population structure and larval biology.

Materials and Methods

The study site was the lower of three consecutive maturation ponds at Darvill Sewage Works, 6 km north of Pietermaritzburg (29°36'S / 30°24'E). *Xenopus laevis* was sampled using a box trap baited with ground beef and left overnight at a point 2–3 m from the bank. The zooplankton community of the ponds was sampled qualitatively with a 40 μm mesh plankton net.

Most toads were killed using chloroform, weighed, and the snout to cloaca measurement taken. Digestive tracts were removed, the duodenum and intestine opened longitudinally and all *C. namaquensis* collected, counted, and measured using a micrometer eyepiece (contracted lengths were normally used). Their attachment sites were recorded following Millard & Robinson (1955) as:

(a) anterior duodenum: the anterior half of the duodenum from the pyloric sphincter.
(b) posterior duodenum:remainder of the duodenum.
(c) intestine: from the posterior end of the duodenum to the cloaca, i.e. ileum and rectum.

Tapeworms were stained for morphological examination with Malzacher's stain (Pritchard & Kruse, 1982).

C. namaquensis egg output was measured by monitoring the eggs voided in the faeces of six toads kept individually in 0,5% amphibian saline for 48 h. The solution, which prevented hatching, was changed every 6 h and the egg counts were related to the worm loads determined after dissection.

In order to observe the vertical movement of newly hatched coracidia, approximately 2000 were released into a 1 ℓ measuring cylinder containing pond water and left undisturbed for 30 min. Three 5 ml samples were then taken with a pipette at each of three depths; 3 cm, 22 cm, and 42 cm respectively, and the number of coracidia per sample recorded. After 30 min this was repeated in the reverse order of depth so as to detect possible disturbance owing to the movement of the pipette. Four replicates were run in the light (60 W fluorescent tube) and four in the dark. Photometry was carried out at the maturation pond using a LI-COR L1-185B photometer in order to determine changes in light intensity with depth.

Results

Tapeworm morphology

Figure 1 shows a scolex and mature proglottid of *C. namaquensis*. The bilobed ovary is located at the posterior margin of the proglottid and occupies approximately one third of its width. The seminal receptacle and shell gland are anterior and anterolateral to the ovary respectively. The coiled uterus containing operculate, embryonated eggs is located medially and leads forward from the ovary to the uterine pore which may be left or right of the midline. The testes are in two lateral groups (2–7 in each group) anterior to the ovary between the uterus and the osmoregulatory ducts. The vitellaria are also in two groups located ventro-laterally to the osmoregulatory ducts and converging toward the ovary in the posterior of the proglottid. The genital pore is situated medially at the anterior end.

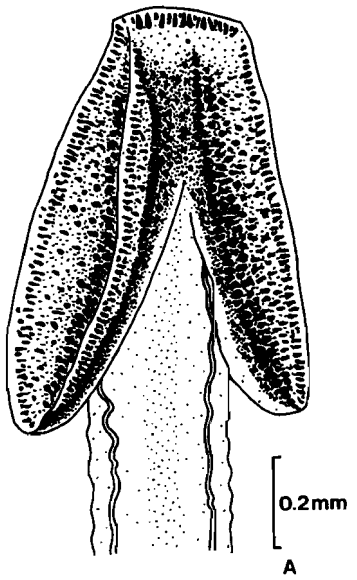

Figure 1(A) Scolex of mature *C. namaquensis* showing paired bothridia.

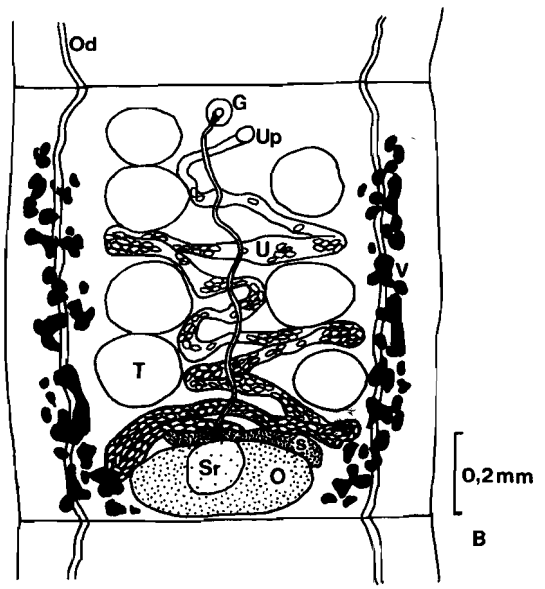

Figure 1(B) Mature proglottid of *C. namaquensis* showing ovary (O), seminal receptacle (Sr), shell gland (s), testes (T), vitellaria (V), uterus (U) containing eggs, uterine pore (Up), genital aperture (G) and osmoregulatory ducts (Od).

The largest tapeworm found in this study was approximately 115 mm long when extended, 90 mm when moderately relaxed, and 65 mm when contracted while the largest specimen recorded by Thurston (1967) was 60 mm in length when moderately relaxed and had a maximum extended length of 80 mm. Scolices of tapeworms ranged in size from 0,6–1,1 mm long by 0,4–0,7 mm wide and mature proglottids of 40-mm tapeworms measured 0,6 mm long by 1,3 mm wide when moderately relaxed. Table 1 compares the diagnostic features of the tapeworms examined in this study with those of *C. namaquensis* as reported by other workers. There are no demonstrable differences between present specimens and those described by other authors indicating that the species involved here is *Cephalochlamys namaquensis*.

C. namaquensis population structure

The prevalence of infection of *X. laevis* by *C. namaquensis* was 68,9% (62/90) and there was no significant difference between male and female toads ($\chi^2 = 3{,}14$; $n = 90$). A significant though low correlation,however, was found between toad size and mean tapeworm length per toad ($R^2 = 0{,}23$; $df = 28$; $p < 0{,}01$), but not between toad size and tapeworm burden ($p > 0{,}05$). Figure 2 illustrates the frequency distribution of *C. namaquensis* burdens in the *X. laevis* population. The median burden was three worms.

Table 2 shows that the most frequent attachment site for *C. namaquensis* scolices was the anterior duodenum. Where burdens were heavier than eight, worms were also found in the posterior duodenum and in burdens > 16, some occurred in the intestine as well.

Figure 3 shows the length/frequency distribution of 168 contracted *C. namaquensis* which, it should be noted, were approximately one third of their extended length when alive. There was a high frequency of occurrence of small tapeworms with progressively fewer large ones. Although eggs were present in the uteri of worms > 3,8 mm, all eggs from those < 6,4 mm were unembryonated. Embryonated eggs were, however, present in all tapeworms > 7,0 mm so that sexual maturity appears to be reached between 6,5–7,0 mm strobila length. The majority of the population (76,2%; 128/168) at the time of this study (May–July, 1986) therefore consisted of immature worms and the ratio of mature to immature tapeworms was 1:3,2 respectively.

Tapeworm egg output in the faeces was irregular, rising intermittently to high levels of up to 242 000 eggs/g. No significant correlation was found between egg output and tapeworm burden ($p > 0{,}05$).

Larval biology

The coracidia of *C. namaquensis* were short-lived (Figure 4). Mortality became evident after 4 h and

Table 1 Some morphological features of *C. namaquensis* from this and other studies

	This paper	Ortlepp (1926)	Mettrick (1960,1963)	Pritchard (1964)	Thurston (1967)	Dollfus (1968)*
Testis number per proglottid	4–12	–	12–15	4–20	3–23	14–20
Variability in testis no. between each side	1–3	–	–	1–3	–	–
Testis length (μm)	96–104	100–150	62–71	–	72–107	140
Testis width (μm)	80–95	66–82	–	–	57–94	–
Egg length (μm)	44–55	37	24	27–43	43–55	21,3–24
Egg width (μm)	31–38	26	16	21–32	29–35	12–14,6
Position of vitellaria relative to osmoregulatory ducts	Lateral & Ventral	Ventral	Lateral & Ventral	Lateral & Ventral	Lateral & Ventral	Lateral & Ventral

*Dollfus (1968) cited by Wardle, McLeod & Radinovsky (1974).

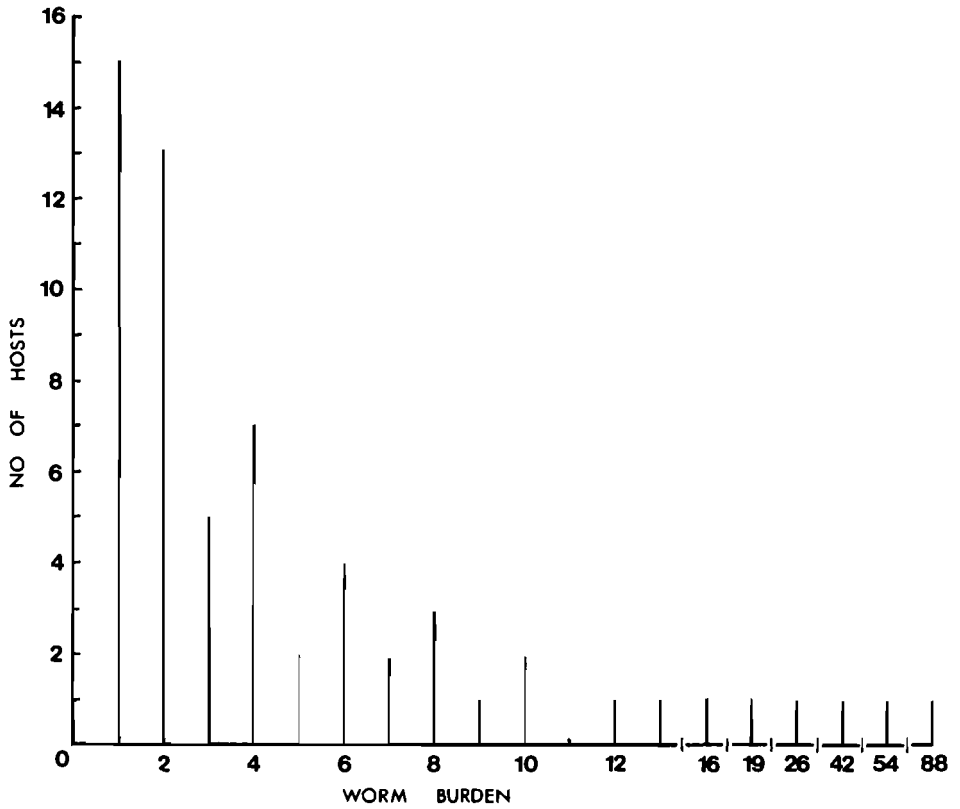

Figure 2 Frequency distribution of *C. namaquensis* burdens in *X. laevis*.

Table 2 Attachment sites of *C. namaquensis* (n = 340) from 37 infected *X. laevis*

	Anterior duodenum	Posterior duodenum	Intestine
Percentage of infected toads with tapeworms in each gut region	100	24,3	13,5
Total number and percentage (in brackets) of tapeworms attached in each gut region	258 (75,9)	58 (17,1)	24 (7,0)

increased dramatically thereafter to 100% at 10 h. The LT50 was 6 h.

The maturation pond in which naturally infected *X. laevis* were collected was shallow (depth 0,6 m) and turbid so that light penetration fell rapidly. Fifty per cent light extinction occurred at 15 cm depth and 100% at 50 cm. Under experimental conditions of both light and darkness the majority of coracidia released into a 45 cm deep measuring cylinder accumulated at the bottom (Figure 5). This suggests that in the natural habitat the coracidia would favour the sediment/water interface irrespective of the light intensity there.

The zooplankton community of the pond was examined in order to identify the likely intermediate hosts of *C. namaquensis*. This consisted predominantly

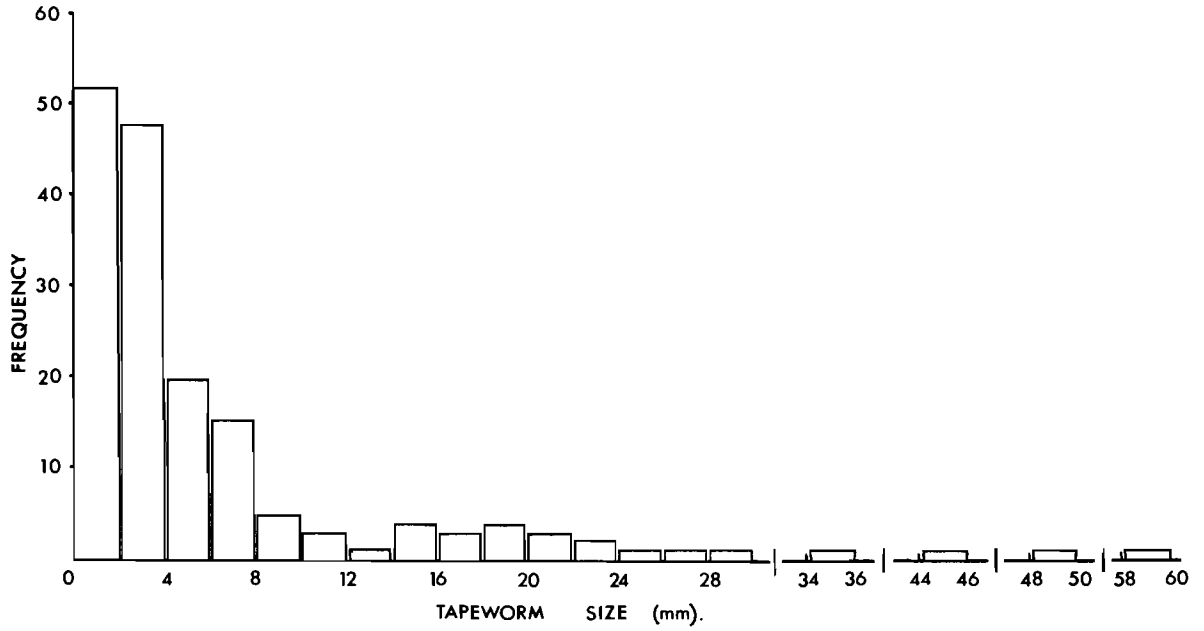

Figure 3 Size (length) frequency distribution of the *C. namaquensis* populution during the study (measurements made on contracted tapeworms).

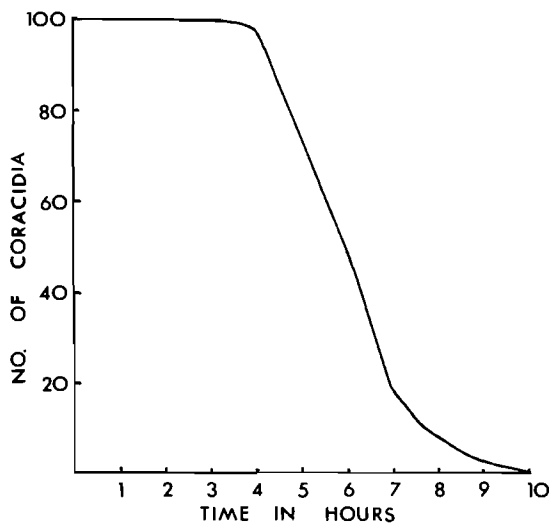

Figure 4 Survivorship of coracidia of *C. namaquensis*.

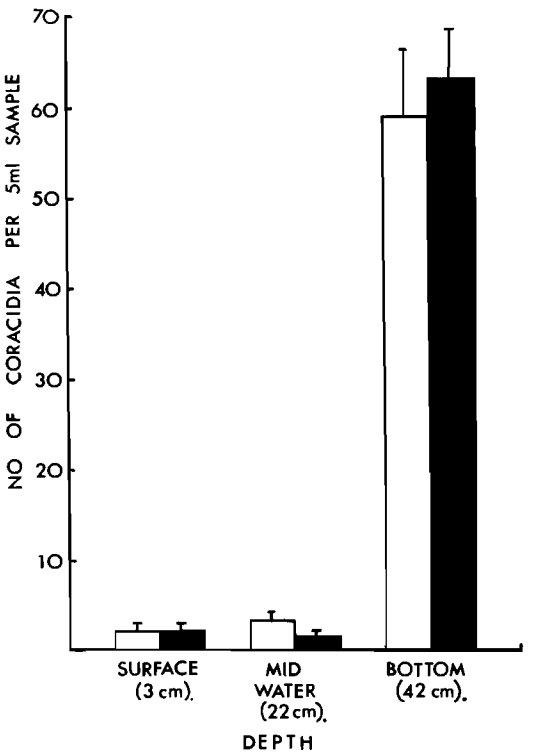

Figure 5 Mean number of coracidia per 5-ml sample (n = 8) of water at three depths in the 45 cm water column (bars above columns represent standard deviations).

of three species: the cladoceran *Daphnia pulex*, the cyclopoid copepod *Eucyclops gibsoni*, and dipteran larvae, *Chaoborus* spp. A few individuals of a second cyclopoid copepod, *Thermocyclops* sp., were also found. In an attempt to discover whether *E. gibsoni* could act as an intermediate host for *C. namaquensis*, the copepod was shown to become infected when exposed to coracidia but no quantitative data are available.

Discussion

Cephalochlamys namaquensis was described by Cohn (1906) as *Chlamydocephalus namaquensis* from *Xenopus laevis* collected in South West Africa (Namibia). Owing to preoccupation the genus was renamed *Cephalochlamys* by Blanchard (1908). Unaware of Cohn's (1906) description, Ortlepp (1926) described a similar cestode from *X. laevis* from Natal, South Africa, as *Dibothriocephalus xenopi*. Baylis (1934) and Southwell & Kirshner (1937) later synonymized *D. xenopi* with *C. namaquensis*, but Yamaguti (1959) considered Ortlepp's (1926) description of *D. xenopi* to differ from that of *C. namaquensis* and

proposed a new genus *Pseudocephalochlamys* with the species *P. xenopi*. Mettrick (1960,1963) subsequently recorded *C. namaquensis* from *X. laevis* and *Rana angolensis* in Rhodesia (Zimbabwe) and, like Pritchard (1964) and Thurston (1967,1970), rejected the genus *Pseudocephalochlamys*.

Variation in a number of taxonomically important features of the tapeworms examined during the present study has drawn attention to differences in the descriptions of *C. namaquensis* by other workers. Although there is a general agreement on the position and structure of the genital aperture, uterine pore, uterus, and the osmoregulatory ducts, variation occurs in other characters. Wardle & McLeod (1952) described the ovary as U-shaped but all other authors have reported it to be bilobed. The characters used by Yamaguti (1959) to differentiate *Cephalochlamys* and *Pseudocephalochlamys*, viz: position of yolk glands, number of testes and egg size, vary considerably in the descriptions of other workers and produce contradictory results when applied to the tapeworms examined in this study.

Vitellaria described and illustrated by previous workers vary from regular (spherical to ovoid) to irregular in shape and in position from lateral to ventral to the osmoregulatory ducts. In addition, some authors found the vitellaria to converge in the posterior of the proglottid and enter the post-ovarian area. Mettrick (1960) suggested that the position of the vitellaria might be affected by the degree of contraction of the worm and consequently could not be a reliable taxonomic feature.

According to the literature, the testes of *C. namaquensis* range from 3–26 per proglottid and in diameter from 57–150 μm. Thurston (1967), however, showed a statistically significant relationship between the nutritional state of the host and the number of testes per proglottid — they were more numerous in tapeworms of well-fed toads. This indicates that testis number too is not a satisfactory character to use for the identification of *C. namaquensis*. The size range of *C. namaquensis* eggs in this study was similar to that reported by Thurston (1967) but generally larger than those of other workers except Cohn (1906).

It is thus evident that there is considerable variability in a number of morphological characters of *C. namaquensis* which are held to be taxonomically important. The features examined in the present study fall within the range of descriptions given by other workers and agree best with the findings of Thurston (1967). So too, the prevalence of infection of *X. laevis* in this study was high (68,9%), but within the range recorded by other authors. Thurston (1967) found prevalences of 33–100% in *X. muelleri* from Uganda and of 22–89% in Kenya, Nigeria, and Zimbabwe. Macnae, Rock & Makowski (1973), however, found only 10–15% of the South African *X. laevis* to be infected. These were from the Cape and Transvaal, but not Natal.

Only two other amphibians have been found to host *C. namaquensis*. Mettrick (1963) reported a single *Rana angolensis* to be infected in Zimbabwe and Dollfus (1968) recorded two *C. namaquensis* from a specimen of *Pleurodeles poireti* in North Africa. It seems though that *X. laevis* and *X. muelleri* are the principal final hosts of *C. namaquensis*, probably because of their predominantly aquatic lifestyles. Apart from *Xenopus* spp., the only South African frogs to spend much of their time in water are a few *Rana* and *Phrynobatrachus* spp., and *Kassina maculata*. Unlike *Xenopus*, however, these species do not generally feed there. Since the copepod intermediate hosts of C. namaquensis are aquatic, amphibians which feed in water will be more disposed to infection than those which do not. With this in mind, it is interesting that *C. namaquensis* has not been recorded from other *Xenopus* species in Africa, and it would be well worth determining whether these congeneric species become infected.

Like many parasites, the distribution of *C. namaquensis* in the toad population is highly aggregated and seems to conform to the negative binomial pattern (Tinsley & Sweeting 1974; Stromberg, Toussant & Dubey 1978; Lemly & Esch 1984). Various mechanisms, including genetic, spatial, and behavioural factors can, however, generate such patterns (Stromberg *et al.* 1978; Anderson & May 1985). Infection is not self-limiting to a few parasites per host since some heavy infections were encountered in this study, with the largest being 88 worms from a single toad. Even higher burdens of 100 and 157 worms were reported from *X. laevis* by Cohn (1906) and Macnae *et al.* (1973) respectively. Thurston (1967) recorded 103 worms from a specimen of *X. muelleri*. Parasitologists have speculated as to the significance of these heavy burdens in the transmission of parasites and as a generalization, heavily infected hosts seem likely to be important because their egg output is highest. This is, however, complicated by density dependent checks on the growth and fecundity of the parasites.

Earlier workers examining relatively long-lived parasites have shown that older (larger) hosts have larger parasite burdens because they have been exposed to infection for longer periods than young hosts (Tinsley & Sweeting 1974; Stromberg *et al.* 1978). Thus the fact that no significant relationship was found between toad size (age) and tapeworm burden in the present study and that the correlation between toad size and tapeworm length (age) was low probably indicates that *C. namaquensis* do not survive much longer than 1–2 years. This means that the tapeworm burden of a toad will not be affected by the age of the toad except in its first two years — i.e. the period until the first tapeworm mortalities occur. Unfortunately, no toads of less than two years old (approx. 30 g) were examined in this study and no worm burden or prevalence data are available for them.

Interpretation of the population structure of *C. namaquensis* is difficult without a knowledge of its seasonal fluctuations as well as the worms' growth rate and life expectancy. Thurston (1967) found that *X. muelleri* did not become infected until metamorphosis, and yet a 1-g toad contained a mature tapeworm of 13 mm. This indicates that immature worms grow rapidly.

The occurrence of both small and large tapeworms in the same toad, and the fact that 76% of the present population comprised immature worms during the study period (late summer to midwinter) confirms the suggestion made earlier that these tapeworms survive for longer than 12 months. The high proportion of immatures and the presence of small tapeworms (< 5 mm) throughout the study shows that transmission occurred continually during the study period but that few of the small worms reach maturity. This may in some cases be due to the density dependent effects of crowding but may also reflect a high mortality amongst juvenile worms.

Only Macnae *et al.* (1973) have commented in any detail on attachment site selection by *C. namaquensis*. They noted that for infestations of < 6 worms, attachment near the pyloric sphincter was preferred, but that for larger worm loads there was no preference. This latter point is disputed in the present study since there is a trend to more distal attachment in the intestine with increasing worm burdens. The duodenum is, however, clearly the site of choice, presumably because large amounts of nutrients are available here before intestinal absorption occurs. It is also larger in diameter and has slightly larger folds than the intestine, thus providing a greater surface area for attachment.

The sporadic nature of *C. namaquensis* egg output probably explains the lack of any significant relationship between egg output and tapeworm burden. The eggs of *C. namaquensis* are embryonated upon release and are capable of hatching immediately. Operculate eggs of many pseudophyllids are dependent on light to trigger hatching (Rowan 1956; Hilliard 1960; Smyth 1963) but photometry at the study site showed that following defaecation by the host, the eggs of *C. namaquensis* would sink into darkness. Experiments revealed that the eggs hatched readily in both light and darkness as was found by Thurston (1967). Similarly, Hilliard (1960) showed that the eggs of some diphyllobothriid cestodes occurring in turbid habitats hatched almost as well in darkness as in light.

The coracidia of *C. namaquensis* are fast swimming (2 mm/s) in relation to those of diphyllobothriid cestodes and do so with a spiral motion similar to that of flagellate protozoans. The fastest swimming diphyllobothriid coracidia move at 1 mm/s while others are as slow as 1 mm in 33 s (Hilliard 1960). The longevity of *C. namaquensis* coracidia, however, is short when compared to diphyllobothriid coracidia which survive for between 10 h and 8 days at 20°C (Hilliard 1960). In this study coracidia selected to swim near the bottom of the water column and the fact that this was unaffected by light or darkness suggests that depth selection is unrelated to light attenuation. Nothing is known of the feeding behavior of *Eucyclops gibsoni* but it is likely (R.C. Hart pers. comm.) that they, in common with many cyclopoid copepods, will tend to accumulate at the sediment/water interface to feed on microorganisms including flagellate Protozoa. It is therefore probable that swimming near the substrate brings the coracidia into contact with feeding copepods, thereby increasing their chances of being ingested and promoting transmission. Following the ingestion of coracidia, procercoids were observed developing in the haemocoel of *E. gibsoni*. Thurston (1967) showed *Thermocyclops infrequens* to act as an intermediate host for *C. namaquensis* in Uganda but insufficient *Thermocyclops* were caught in the present study to determine whether they too could act as intermediate hosts. *Thermocyclops* spp. are, however, generally predatory (Fryer 1957) and it seems possible that many predatory copepods would be suitable intermediate hosts and that *C. namaquensis* makes use of different copepod species in different parts of its range.

Adult *Xenopus* are both predators and scavengers (Noble 1924; Passmore & Carruthers 1979; D.E. van Dijk pers. comm.) and although Inger & Marx (1961) found that dipteran larvae made up the largest single component of the diet of *X. laevis*, copepods made up a small portion. Chaoborid larvae occurred frequently in the diet of toads examined in this study but no copepods were found in stomach contents. This is in contrast with the findings of Thurston (1967) who concluded that crustaceans formed an important dietary item for post-metamorphosis *X. muelleri*. Considering their relative sizes, it is unlikely that copepods are a selected item in the diet of adult toads although this may be so in juveniles. *X. laevis* capture live prey by pouncing on them (D.E. van Dijk pers. comm.) and it is more likely that copepods are ingested accidentally. No second intermediate host was found but the existence of paratenic hosts in the life cycle of *C. namaquensis* seems possible. According to Chimney, Winner & Seilkop (1981), copepods form an important part of the diet of chaoborid larvae and since the latter occurred frequently in the stomach contents of toads in this study, they must be considered potential paratenic hosts for *C. namaquensis* here.

Conclusion

Variability occurred in some taxonomically important characters of *Cephalochlamys namaquensis* from this study with respect to the observations of other workers. These included the position and shape of vitellaria, the size and number of testes, the size of eggs and the shape of the ovary. *C. namaquensis* has a high prevalence of infection in *Xenopus laevis* and had a negative binominal type of distribution within the host population. Worms showed a preference for attachment in the anterior half of the toads' duodenum, followed by the posterior duodenum and intestine. Sexual maturity is reached at approximately 12 mm relaxed length. Egg output by *C. namaquensis* is high and no rhythm in egg release was evident. Hatched coracidia survive for 6 h on average and accumulate near the bottom of the water column. The copepod *Eucyclops gibsoni* became infected by coracidia of *C. namaquensis* and probably acts as an intermediate host.

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