

## SARCOTRETES (COPEPODA: PENNELLIDAE) PARASITIZING MYCTOPHID FISHES IN THE SOUTHERN OCEAN: NEW INFORMATION FROM SEABIRD DIET

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**ABSTRACT:** Copepods are common parasites of marine fishes, but little information is available on the biology of species that parasitize mesopelagic fishes in oceanic waters. In this study, we report the finding of large numbers of *Sarcotretes* spp. ( $n = 2,340$ ) in dietary samples of king penguins collected at Crozet and the Falklands Islands. Analysis of penguin food indicates that *S. scopeli* Jungersen parasitizes myctophid fishes, *Protomyctophum tenisoni* (Norman), in the southern Indian Ocean and *P. choriodon* Hulley in the southern Atlantic. It suggests that the much rarer *S. eristaliformis* (Brian) also parasitizes myctophids, but the host species of that copepod remains to be determined. The new data add significant information concerning the hosts and distribution of *Sarcotretes* spp. in the Southern Ocean and emphasize the usefulness of ichthyophagous predators in revealing valuable information on the biology of organisms that parasitize their prey.

Copepods are common parasites of marine fishes. They have been studied extensively in coastal and neritic waters, where they have become pests of fish species of commercial importance. However, little is known of the ecology of parasitic copepods of fishes in oceanic waters (Jones, 1998). One reason is that little information is available on many of their hosts, the fish living in the high seas, including the dominant Myctophidae and Gonostomatidae (Gjosaeter and Kawaguchi, 1980). Another reason is that the diversity of parasitic copepods of deep-sea pelagic fish is probably extremely low, with only 2 pennellids commonly recorded on a worldwide basis, i.e., *Cardiodectes medusaeus* (Wilson) primarily in the Pacific and *Sarcotretes scopeli* primarily in the Atlantic (Boxshall, 1998). To our knowledge, the latter species was not recorded either in the Indian Ocean or in the Southern Ocean (the marine area south of the Subtropical Front [STF]) (Boxshall, 1998; Rohde et al., 1998). However, 2 specimens of *S. eristaliformis*, the only other valid species of *Sarcotretes* (Hogans, 1988), were described from a fish, *Bathylagus* sp., caught in the Antarctic (Kabata and Gusev, 1966). According to Hogans (1988), the specimens were misidentified and should be referred to as *S. scopeli*.

During investigations on the feeding ecology of a large marine predator of the Southern Ocean, the king penguin *Aptenodytes patagonicus* Miller, numerous female parasitic copepods of *Sarcotretes* spp. were identified from food samples collected at Crozet Islands in the southern Indian Ocean (Cherel et al., 1993, 1996; Ridoux, 1994) and at the Falkland Islands in the southern Atlantic (Cherel et al., 2002). The deep-diver king penguin is a specialist myctophid eater (see review in Cherel et al., 2002), which targets its mesopelagic prey in the top 300 m of the water column in oceanic waters (Kooyman et al., 1992). This article details these unexpected findings and adds new biological and biogeographical information on *Sarcotretes* spp. in the Southern Ocean, using penguins as biological samplers of copepods that parasitize their prey.

### MATERIALS AND METHODS

Fieldwork was carried out on king penguins during the whole 1990 breeding season and during the winters of 1991 and 1992 at La Baie du Marin, Possession Island (46°25'S, 51°45'E; Crozet Archipelago),

and in February 2001 at Volunteer Beach, East Falkland (51°29'S, 57°50'W; Falkland Islands). Dietary samples were collected using the stomach-flushing method on randomly chosen adult king penguins returning ashore to feed their chicks. Food analysis was made in the laboratory according to Cherel and Ridoux (1992). Briefly, fresh remains were divided into broad prey classes (fish and cephalopods) that were weighed to calculate their proportion by fresh mass in the diet. Identification of prey relied almost entirely on the examination of otoliths and bones for fish, which were compared with material held in our own collection and by reference to the literature.

Because parasitic copepods are secondarily ingested with their hosts (fish, which are the primary prey of king penguins), they were not considered in the analysis by number of the penguin prey (Cherel et al., 1993, 1996, 2002). However, they were enumerated in each food sample. Most of the stomach contents were highly digested precluding, except in a few cases, the discovery of parasitic copepods still attached in situ to fish flesh. Instead, they were free in the samples. The exoskeleton was probably more resistant to digestion than fish remains, resulting in an accumulation of copepods with time in the penguins' stomachs.

### RESULTS

Fish dominated the diet of king penguins both by fresh mass and numerically in autumn (98.8 and 98.9%, respectively) and spring of 1990 (97.6 and 98.5%, respectively) at Crozet and in autumn of 2001 (99.1 and 98.0%, respectively) in the Falklands Islands. In winter, the proportion of squid increased by fresh mass (33.9%; results from the 3 winters pooled) and that of fish decreased (66.1%), but because of the large size of squid prey, fish was again the main prey numerically (92.8%) at Crozet Islands. At both localities and whatever the season, lanternfishes (family Myctophidae) were by far the major component of the fish diet, accounting for 75.9–99.7% of the total number of fish prey (Table I).

In total, 2,335 *S. scopeli* and 5 *S. eristaliformis* were identified from stomach contents of king penguins. Most of the specimens of *S. scopeli* ( $n = 2,020$ ) were found in 10 food samples from the Falkland Islands (Table I). All of them contained an amazing number of parasitic copepods (range, 71–381). The penguin diet was heavily dominated by the myctophid, *Protomyctophum choriodon*, which occurred in large numbers in all samples (range, 240–863). This, together with a few copepods still attached to fish flesh, indicates that *S. scopeli* was a parasite of *P. choriodon*. Using allometric equations between otolith and total lengths (Olsson and North, 1997), the mean size of *P. choriodon* was estimated to be  $87 \pm 5$  mm (73–102 mm,  $n = 294$ ). The mean total length (without egg

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TABLE I. Main myctophids (% of fish prey) and numbers of *Sarcotretes scopeli* found in the diet of king penguins at Crozet and the Falkland Islands.

Locality	Crozet					Falklands
	1990		1991	1992	2001	
	Year	Year				
Season	Autumn	Winter	Spring	Winter	Winter	Autumn
Food samples (n)	15	15	15	17	15	10
Fish (n)	5,444	739	5,910	1,781	2,437	4,611
Myctophids (%)	99.7	75.9	99.0	93.7	96.9	99.7
<i>Electrona carlsbergi</i>	25.2	<1.0	7.5	—	—	4.7
<i>Gymnoscopelus nicholsi</i>	—	4.9	3.1	6.8	2.8	2.3
<i>G. piabilis</i>	—	5.7	—	13.3	2.5	—
<i>Krefflichthys anderssoni</i>	72.5	2.2	41.8	29.1	17.0	4.9
<i>Lampichthys procerus</i>	—	8.0	—	3.2	17.0	—
<i>Metelectrona ventralis</i>	—	2.2	—	<1.0	1.9	—
<i>Protomyctophom bolini</i>	—	12.7	—	2.8	1.6	—
<i>P. choriodon</i>	<1.0	3.9	<1.0	<1.0	1.2	85.9
<i>P. tenisoni</i>	1.8	31.0	46.4	35.9	50.6	1.9
<i>S. scopeli</i> (n)	7	11	90	39	168	2,020
(n)*	3	8	85	32	158	2,020
(%)*	42.9	72.7	94.4	82.1	94.0	100.0

\* Associated with large numbers (n > 50) of *P. tenisoni* (Crozet) or *P. choriodon* (Falklands).

strings) of barely digested specimens of *S. scopeli* was  $19.3 \pm 2.5$  mm (15.2–25.2 mm, n = 30).

Overall, 315 *S. scopeli* were identified from 77 food samples of king penguins collected at the Crozet Islands. Most of them were found in spring of 1990 (n = 90) and winter of 1992 (n = 168), 2 periods during which the diet was overall dominated by the myctophids *P. tenisoni* (46% by number) and *Krefflichthys anderssoni* (42%) and *P. tenisoni* alone (51%), respectively. Interestingly, during both periods, specimens of *S. scopeli* mainly occurred (94%) in food samples containing large numbers of *P. tenisoni* (>50 individuals) and not of *K. anderssoni* or other fish (Table I). Conversely, only a few parasitic copepods were found in dietary samples during the season when *P. tenisoni* was a minor prey (see autumn of 1990, for example). This strongly suggests that the primary host of *S. scopeli* was *P. tenisoni*, even if the data cannot preclude that *S. scopeli* parasitized other fish species, but with a much lower prevalence.

Five specimens of *S. eristaliformis* were identified from the Crozet samples (none occurred in the Falkland Island samples). At present, the main feature distinguishing the 2 species of *Sarcotretes* is the larger size of *S. eristaliformis* (Hogans, 1988). Accordingly, its mean total length was  $38.1 \pm 4.2$  mm (33.8–42.3 mm, n = 4), i.e., they were about twice as long as *S. scopeli*. All specimens were collected in 1990, 2 in autumn (in 1 sample), 1 in winter, and 2 in spring (in 2 samples). The 4 dietary samples contained mainly myctophids (n = 174–773, >99% by number of fish prey) with a few other fish, mainly paraplepidids, having been identified (n = 1–3). The diversity of fish prey in the 4 samples precludes the identification of the species parasitized by *S. eristaliformis*, but because of their abundance it is likely that the hosts were myctophids.

Many aspects of the morphology of *S. eristaliformis*, including the limbs, have never been described. The head is similar to that of *S. scopeli* in having a pair of broad lateral processes. The oral cone and mouthparts are carried at the distal margin

of a well-developed, anteroventrally directed proboscis (Fig. 1A, B), which is over 1 mm in length. The paired antennules and antennae are located dorsally at the base of the proboscis. The long neck region is about the same length as the trunk and tapers gradually toward its junction with the trunk. On the dorsal surface, at its anterior extremity, the neck carries the 3 tergites (arrowed in Fig. 1A) of pedigerous somites 2–4 inclusive. In the same region, but on the ventral surface, are the swimming legs.

The antennules (Fig. 1C) are indistinctly segmented and carry numerous setae, some longer than the limb. The antenna is chelate (Fig. 1E), with the movable distal claw opposing a process on the inner margin of the robust middle segment. The claw carries a single fine seta proximally. The oral cone (Fig. 1D) has a deep marginal membrane encircling its opening, and it is furrowed, allowing it to shorten by telescoping. The mandible (Fig. 1D) is reduced to a simple stylet, and the maxillule carries 2 long apical setae plus a short seta on the outer lobe. The maxilla (Fig. 1F) has a single tooth on the syncoxa, and the basis is clawlike, terminating in a short row of spinules and a tapering element, which is bilaterally spinulose. The maxilliped is absent.

The first 2 pairs of swimming legs are biramous, and leg 3 is uniramous (lacking an endopod). Leg 1 has 2-segmented rami (Fig. 1G) with incomplete setation in the material available. No difference was noted from leg 1 setation in *S. scopeli*. Leg 4 is represented by a vestige located just posterior to leg 3 (Fig. 1H, arrowed in Fig. 1B). This appears to represent the intercoxal sclerite. No trace was found of leg 5.

## DISCUSSION

Knowledge of parasites of fish from the high seas, and especially from the Southern Ocean, is scarce (Jones, 1998; Rohde et al., 1998; Ho et al., 2003). This study adds significant information on parasitic copepods, i.e., *Sarcotretes* spp., in the

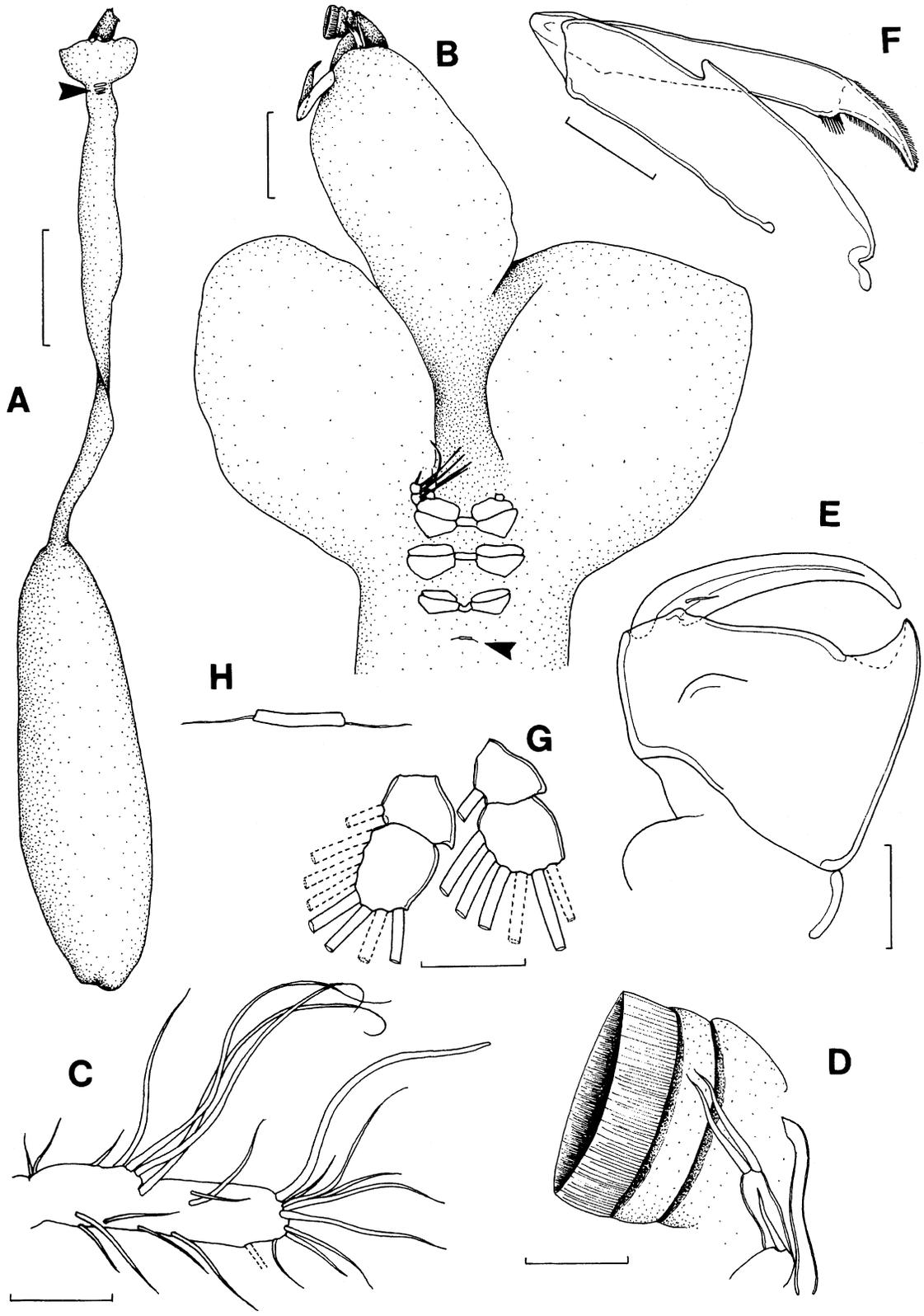


FIGURE 1. *Sarcotretes eristaliformis*: Adult female. (A) Habitus, dorsal view with free tergites of pedigerous somites 1 to 3 arrowed. Bar = 5 mm. (B) Holdfast, ventral view with vestige of intercoxal sclerite of leg 4 arrowed. Bar = 0.5 mm. (C) Antennule. (D) Mouth cone, maxillule and mandible, lateral view, in situ. (E) Antenna. (F) Maxilla. (G) Rami of leg 1 showing positions of missing setae. Bar = 100  $\mu$ m (C-G). (H) Vestige of leg 4.

Southern Ocean, on the basis of 1 of the largest collections of these parasites, which were found in dietary samples from king penguins. The data indicate that female *S. scopeli* parasitizes 2 species of myctophid fishes (*Protomyctophum*), *P. tenisoni* in the Indian Ocean and *P. choriodon* in the Atlantic. They also suggest that the much rarer *S. eristaliformis* also parasitizes myctophid fishes, but the hosts of that species remain to be determined.

Parasitic copepods of *Sarcotretes* spp. have not been recorded in numerous studies (but see Ridoux, 1994; Cherel et al., 2002), showing the importance of shoaling myctophids in the nutrition of seabirds and marine mammals from the Southern Ocean. The most likely explanations are: first, they were not recognized as parasitic copepods because of their highly modified morphology, and second, they were not considered as primary prey but as secondary prey ingested with their hosts and consequently are not included in food analysis. This study, nevertheless, demonstrated the usefulness of ichthyophagous predators in revealing information on the biology (biogeography, new host records) of organisms that parasitize their fish prey. Moreover, predation is probably higher on parasitized than on nonparasitized myctophids because it has been recently demonstrated that parasitized fish have a tendency to occupy the periphery of the shoals, where they are more at risk of capture (Ward et al., 2002).

*Sarcotretes* comprises only 2 valid species, *S. scopeli* and *S. eristaliformis*, the latter being twice the size of the former (Hogans, 1988). In addition to size, the 2 species of *Sarcotretes* can now be distinguished by body proportions. The neck of *S. eristaliformis* is as long as the trunk, whereas in *S. scopeli* the neck is typically shorter than the trunk. Differences in setation pattern of the antennule are not regarded as significant given the state of the material recovered from the dietary analysis. The maxilla of *S. eristaliformis* lacks the "large, hair-covered seta" described for *S. scopeli* by Hogans (1988). A seta in this position is not known in other pennellids, and its presence in *S. scopeli* could not be confirmed in the new material. The apical claw of *S. scopeli* is longer than in *S. eristaliformis* and is longitudinally grooved and ornamented with setules. The presence of free tergites on the dorsal surface of the neck has rarely been reported for *S. scopeli*, but they are present. The vestige of the fourth swimming leg was not observed in *S. scopeli*.

*Sarcotretes scopeli* is 1 of the 2 species of parasitic copepods that have been regularly reported from deep-sea pelagic fishes. The species exhibits a relatively low level of host specificity because it has been reported from 12 fishes representing 7 different families (see review in Boxshall, 1998). The main fish family was the Myctophidae, with 5 species involved. This study is in agreement with the view that *S. scopeli* is mainly a parasite of mesopelagic fish, and it adds 2 species as its recorded hosts, *P. tenisoni* in the southern Indian Ocean and *P. choriodon* in the southern Atlantic. The abundance of *S. scopeli* in oceanic waters surrounding the Falkland Islands conforms with the view that the species occurs primarily in the Atlantic (Boxshall, 1998). However, its occurrence in Crozet waters extends considerably the geographical range of *S. scopeli*, being, to our knowledge, the first record of the species in the Indian Ocean. This, together with its occurrence in the Pacific (Boxshall, 1998), suggests that *S. scopeli* has a worldwide distribution.

At Crozet Islands, king penguins forage in the vicinity of the Antarctic Polar Front (APF) in autumn and spring (Charrassin and Bost, 2001). In winter, their foraging trips reach Antarctic waters (Charrassin and Bost, 2001), but food given to their chicks was collected in the vicinity of the colonies at that time (Cherel et al., 1996). Consequently, most of their prey, and hence parasites of their prey, were caught in the Polar Frontal Zone (the area between the Subantarctic Front in the North and the APF in the South; Park and Gambéroni, 1997). Accordingly, *P. tenisoni* has a broadly Antarctic pattern (species living from the STF to south of the APF) and *P. choriodon* has a subantarctic pattern (species living between the STF and the APF) (Hulley, 1981). Thus both penguin foraging areas and host biogeography indicate that *S. scopeli* and *S. eristaliformis* occur in the northern part of the Southern Ocean, between the STF and the APF.

Assuming that the intensity of infection of fish by *S. scopeli* is 1.0 (Hogans, 1988) and that only *P. choriodon* and *P. tenisoni* were parasitized (but see below), the prevalence of the 2 fish species can be estimated. It amounts to 51.0% for *P. choriodon* at the Falklands and ranges from 3.3 to 13.6% for *P. tenisoni* at Crozet Islands. These values are probably overestimates because the exoskeleton of *S. scopeli* is more resistant to digestion than myctophid otoliths and bones, resulting in a differential accumulation of copepods versus fish remains with time in penguins' stomachs. Nevertheless, they suggest a high level of infection of *P. choriodon* in the southern Atlantic and indicate that the species is more heavily infected than *P. tenisoni* in the southern Indian Ocean. Such a high prevalence (56%) was previously described in *C. medusaeus*, the only other common pennellid that targets mesopelagic fishes, parasitizing the myctophid, *Diaphus theta*, off California (Perkins, 1983).

Some myctophid species (*Electrona carlsbergi*, *K. anderssoni*, *Gymnoscopelus nicholsi*, and *G. piabilis*) were identified in large numbers in king penguin food samples during this study, but they were found to be associated with no or only a few parasitic copepods. The data suggest, first, that these species are not parasitized or are parasitized with a low prevalence, and, second, that *S. scopeli* targets specifically myctophids of *Protomyctophum* spp. However, more information is needed to test that hypothesis because in this study copepods were not found attached to their hosts but were free in the food samples, thus precluding confirmation of whether all *S. scopeli* parasitized *Protomyctophum* spp. or if other myctophids were involved.

The same problem arises with the larger and rarer *S. eristaliformis*. Their hosts are not known, but analysis of penguin food samples strongly suggests that, similar to *S. scopeli*, they were parasites of myctophids. We recently identified a sixth specimen of that species. It was found again in a king penguin food sample that was collected at Crozet Islands in autumn of 2002, and again the main prey in the sample was various myctophids. *Sarcotretes eristaliformis* is known to parasitize deep-sea benthic fishes, not pelagic fishes (Hogans, 1988). Benthic fishes are very rare prey of king penguins in winter, and they were not found in its diet in autumn or spring (Cherel and Ridoux, 1992; Cherel et al., 1996). Hence, the presence of *S. eristaliformis* in king penguin food samples extends the host range of that rarely encountered parasitic copepod to include mesopelagic fishes of the Southern Ocean.

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