

Krzysztof ZDZITOWIECKI

Institute of Parasitology, Polish Academy of Sciences,
ul. L. Pasteura 3. S.p. 153. 00-973 Warszawa, POLAND

Acanthocephala of the Antarctic*

ABSTRACT: The paper comprises the review of all 23 known valid species along with synonyms and polytomic keys based on morphological features. Mature specimens of 8 species occur in fishes, 4 in birds, 11 in mammals. Each species settles in a definite section of the digestive tract. The structure of a population is dependent upon the time which has passed since the moment of invasion and the intensity of infestation. Acanthocephalans can be found in hosts all the year round, but incomplete seasonality of the occurrence of 2 fish parasites has been recorded. Fish parasites show wide specificity in relation to the hosts mentioned while bird and mammal parasites specificity is narrow. The majority of acanthocephalan species have circumpolar distribution but only 3 have been found inside the polar circle and the other 7 are common in the environs of subcontinental archipelagoes. Acanthocephalans do not yield precedence as far as the diversity of species and infestation intensity are concerned in the Antarctic to other groups of parasite helminths. Their great importance results from their mass occurrence in the vertebrates which are the focus of man's practical interests — fishes, seals and whales.

Key words: Antarctic *Acanthocephala*; biology, key, distribution, specificity.

1. Introduction

The data concerned with internal parasites of Antarctic vertebrates hitherto obtained are scattered in the publications issued in many countries. This also refers to acanthocephalans, a group of parasites, which has attracted relatively little attention, though the first Antarctic species were described by Linstow as far back as 1892. The overwhelming majority of publications were limited to morphological and faunistical problems. They have been taken into account in the systematical review, which is the first chapter of the present paper. Only Holloway and Spence (1980)

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devoted a comprehensive study to the ecology of fish parasites caught in the McMurdo Sound, with an exhaustive description of acanthocephalans.

The description of the material collected by the present author in H. Arctowski's Research Station in South Shetlands (preliminary studies during the foundation of the station in 1977, all year studies in 1979) gave several unexpected results. Comprehensive findings are contained in the papers which are quoted in the respective chapters of the present paper. The examinations were a part of a program financed by Polish Academy of Sciences (PAN) and coordinated by Institute of Ecology PAN, concerned with functioning of Antarctic ecosystems. Special emphasis was put on the animal parasites utilized by man for economic purposes, mainly fishes. Antarctic acanthocephalans, the subject of the present study, were the least known group of parasite helminths until quite recently. The aim of this study is to sum all knowledge of Antarctic acanthocephalans accumulated so far, with a part of problems described solely on the basis of the author's data as they have not been taken into consideration in the studies conducted in the Antarctic up till now.

Mature acanthocephalans are the parasites of digestive tract in vertebrates. In the Antarctic they occur in fishes, birds and mammals. The present author personally collected the parasites harbouring in the hosts belonging to the above classes but among mammals he had an opportunity of examining only seals and fur seals. The author got acquainted with acanthocephalans occurring in whales, *Bolbosoma* spp, only on the basis of a part of the collection from the British Museum (Natural History) in London and on the basis of publications. Several problems dealing with morphology, systematics and specificity of *Bolbosoma* spp are unclear and require a revision of a global scope. For this reason the data included in the present paper dealing with acanthocephalans of the genus *Bolbosoma* are less comprehensive than those dealing with other genera.

The first question which arose during the study of the data included in the publications was concerned with the determination of the Antarctic borders. It is generally assumed that Antarctic convergence line is a geographical border of the Antarctic (Fig. 1.). It is a narrow belt where Antarctic cold surface waters merge with a several degrees warmer Subantarctic surface waters. Antarctic convergence line runs in waves about 60°S in the Pacific and about 50°S in the Atlantic and the Indian Ocean. The borders of flora and fauna ranges, which are the basis for distinguishing of phyto- and zoogeographical regions, subregions and provinces are not identical with the Antarctic convergence line. The disputable question is an assignment of South Georgia province and the subregion Kerguelen to the Antarctic or the Subantarctic. The specialists in the field of mammals and birds (Bonner and Laws 1964, Watson 1971) include these into the

Table I

Polytomic key for determination of Antarctic *Echinorhynchoidea*, fish parasites

Species	Somatic armature	Proboscis length (mm)		Proboscis length/width	Proboscis armature ¹	No. of rows of hooks	No. of hooks in row	The longest hook length (μm)		Cement glands		Embryophores length (μm)
		♂	♀					♂	♀	number	arrangement ¹	
<i>Aspersentis austrinus</i>	+	0.47—0.63	0.51—0.72	1.65—2.30	3	13—16	7—11	106—135	119—149	6	2	60—88
<i>Heterosentis heteracanthus</i>	+	0.22—0.25	0.26	1.35—1.64	2	10	4—5	57—60	73—76	6	2	
<i>Metacanthocephalus campbelli</i>	—	0.54—0.61	0.64—0.68	2.05—2.94	1	13—15	8—10	73—80	76—86	8	2	106—148
<i>Metacanthocephalus rennicki</i>	—	0.30—0.36	0.31—0.42	1.28—1.91	1	12—13	5—6	65—71	74—83	8	2	79—92
<i>Metacanthocephalus johnstoni</i>	—	0.43—0.55	0.49—0.60	1.69—2.67	1	12—17	5—8	71—86	79—96	8	2	88—108
<i>Metacanthocephalus dalmori</i>	—	0.30—0.40	0.33—0.44	1.18—1.68	1	11—16	4—6	54—73	64—77	8	2	97—124
<i>Echinorhynchus nototheniae</i>	—	0.82—0.84		3.03—3.16	1	19	12—13	65—66		6	1	
<i>Echinorhynchus</i> (s.l.) <i>zanclohrynchi</i>	—	circa 0.7	circa 1.0		1	14—16	10—12					circa 60

¹ Explanations of numeral designations of descriptive features, see an introduction to the systematical review and figs. 2—3.

Table II

Polytomic key for determination of Antarctic *Polymorphaeidea*, bird and mammal parasites

Species	Shape and armature of trunk ¹	Extent of somatic armature (% of trunk length)		Fore-trunk length (% of trunk length)		Proboscis shape ¹	Proboscis length (mm)		No. of rows of hooks	No. of hooks in row (basal ones)	The longest hooks site ¹	The longest hook length (μm)		No. of genital spines (if separated from somatic ones)		Female genital pore site ¹	Cement glands		Embryophores length (μm)
		♂	♀	♂	♀		♂	♀				♂	♀	♂	♀		number	shape ¹	
<i>Profilicollis antarcticus</i>	1	16—24	19			1	0.86—1.56	1.01	18—22	7—9 (4—5)	4	71—74	80	0	0	2	4	1	
<i>Corynosoma baylisi</i>	4		65—70		circa 50	2		0.82—0.90	16	circa 10 (4—5)	3		92—98		0—1	1	6	2	87—101
<i>Corynosoma clavatum</i>	4		circa 50		circa 50	2		0.63—0.71	14—16	10—11 (4—5)	3		79—83		0—few	1	6	2	68—80
<i>Corynosoma shackletoni</i>	3		100		100	2	0.88—1.05	1.01—1.12	15—17	7—10 (2—4)	3	130—144	137—156			2	6	2	100—117
<i>Corynosoma arctocephali</i>	4	55—60	58—69	51—56	48—57	2	0.73—0.88	0.82—1.00	19—22	10—14 (3—5)	2, 3	66—76	71—86	circa 150	0—circa 100	1	6	2	126—159
<i>Corynosoma australe</i>	3, 4	74—83	81—91	52—62	52—62	2	0.55—0.65	0.55—0.73	16—19	11—15 (2—4)	2, 3	44—51	43—56	11—28	20—40	2	6	2	66—82
<i>Corynosoma bullosum</i>	4	33—54	28—38	30—40	20—32	2	0.91—1.43	1.11—1.33	15—18	10—15 (2—4)	1	89—117	99—120	80—250	3—120	1	6	1	107—125
<i>Corynosoma evae</i>	4	61—69	63—69	57—64	55—61	2	0.63—0.72	0.61—0.79	20—24	11—13 (3—4)	3	57—63	61—73	40—60	0	1	6	2	103—127
<i>Corynosoma hamanni</i>	3	100	100	54—71	59—80	2	1.00—1.16	1.07—1.28	18—22	12—16 (2—4)	2	77—98	81—99			3	6	2	155—202
<i>Corynosoma hannaie</i>	3	100	96—99	58	53—58	2	0.59	0.65—0.68	22	12—13 (4—6)	3	75	80—82			1	6	2	105—130
<i>Corynosoma pseudohamanni</i>	3	100	100	56—59	67—85	2	0.80—0.93	0.80—1.00	18—22	10—14 (1—3)	2	67—79	64—81			1	6	2	92—120
<i>Bolbosoma balaenae</i>	2		circa 2		circa 4	3		circa 1	24	8— (1—2)				0	0	1		1	150
<i>Bolbosoma brevicolle</i>	2		circa 5		circa 9	3	0.51—0.57	0.54—0.60	20—22	circa 7 (1)	2		113	0	0	1	6	1	118—131
<i>Bolbosoma hamiltoni</i>	2		circa 5		circa 6	3		circa 0.9	26	7—8 (1—2)	2			0	0	1		1	112—137
<i>Bolbosoma turbinella australis</i>	2		circa 10		circa 15	3	0.52—0.62	0.53—0.68	20—24	6—8 (0—1)	2	64—79	78—87	0	0	1	6	1	132—167

¹ Explanations of numeral designations of descriptive features, see an introduction to the systematical review and figs. 4—8.

Subantarctic, and Andriashev (1965) on the basis of fish fauna to the Antarctic. The present author decided that he should take into consideration at least the whole area contained inside the Antarctic convergence line. Within this area, there are all member islands of the South Georgia province and the island Heard, which is situated in the Kerguelen subregion. Drawing the border line across the subregion is out of question. In view of the fact that the vast majority of life cycles of the Antarctic acanthocephalans proceed with the use of fishes as either paratenic or definitive hosts, the present author assumed, after Andriashev (op. cit.) that the whole Kerguelen subregion belongs to the Antarctic, including the environs of the islands Kerguelen, Prince Edward and Macquarie, situated outside the Antarctic convergence line.

2. Systematic review of acanthocephalans

All acanthocephalans recorded, hitherto, in the Antarctic belong to the order *Palaeacanthocephala* Meyer, 1931. In fishes, the representatives of 4 families from the *Echinorhynchoidea* superfamily occur whereas in birds and mammals the representatives of *Polymorphidae* family from the *Polymorphoidea* superfamily. From among the latter ones, the representatives of one genus (*Corynosoma*) can be found in hosts belonging to both classes of warm-blooded vertebrates, the representatives of remaining genera occur in the hosts belonging to one of those classes. Many species from the *Polymorphoidea* superfamily (including probably almost all occurring in the Antarctic) use fishes as paratenic hosts—a link of life cycle going between intermediate host and definitive one. In paratenic hosts there is no development of parasites but they are expecting in the incysted form (in the case of acanthocephalans usually in the abdominal cavity) for the consumption of paratenic host by the definitive one.

In the systematic review the author divided acanthocephalans into 3 groups according to the systematical membership of definitive hosts, which is to say, into the parasites of fishes, birds and mammals. In the tabulated polytomic keys, fish parasites are presented in table I, bird and mammal parasites in only one table II, and that has been done for two reasons: close relationship of acanthocephalans parasitizing in those hosts and the occurrence of juvenile forms of several species in the same paratenic hosts—fishes. The features described in the key enable to determine both mature and juvenile specimens. In the two keys, measurable, countable and descriptive features are included. In the case of descriptive features, the tables contain numeral designations corresponding to various variants of a certain feature. The designations are as follows:

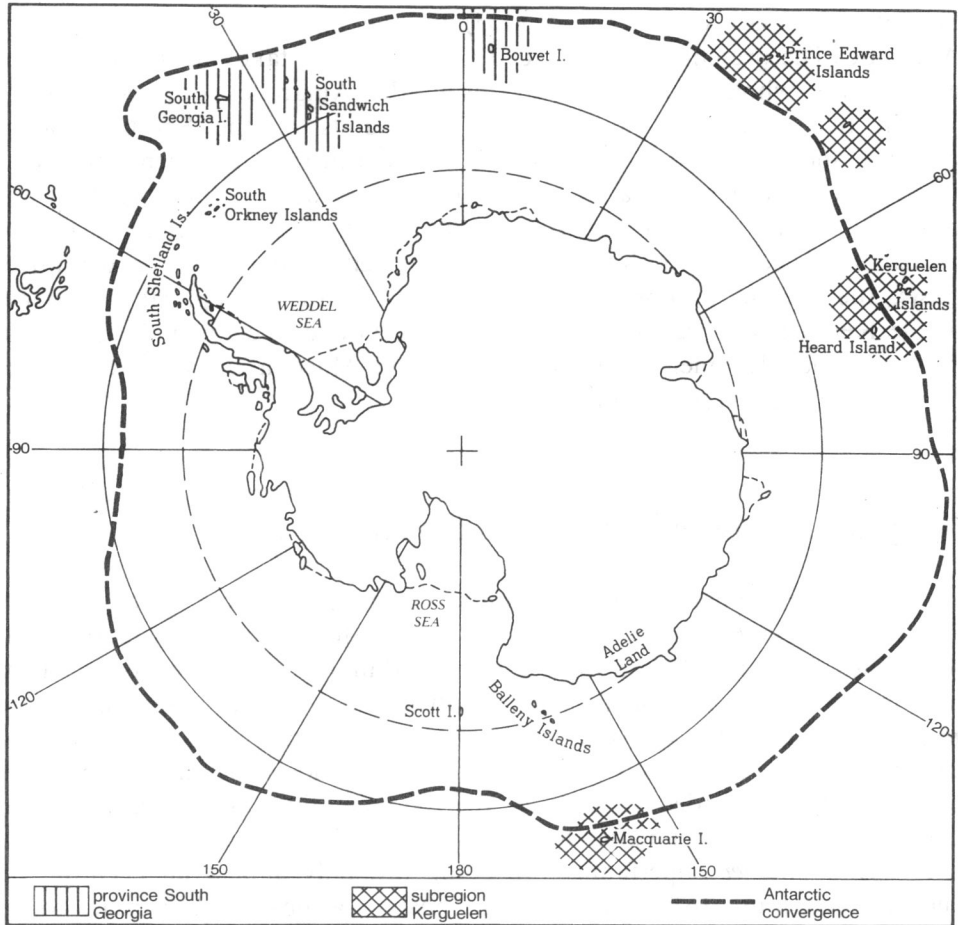


Fig. 1. The Antarctic. Antarctic convergence line according to Watson (1971).

I. For the key determining fish parasites (*Echinorhynchoidea*):

Proboscis armature.

1. Hooks approximately of identical structure, at the proboscis base — possibly slightly less developed, with roots partially reduced (Fig. 2a).
2. Hooks of two kinds — large distal and the remaining ones distinctly smaller with lack of dorso-ventral dissymmetry (Fig. 2b).
3. Distinct dorso-ventral dissymmetry of proboscis armature, hooks much larger on the ventral side (Fig. 2c).

Arrangement of cement glands.

1. Glands arranged in approximately linear way along trunk axis (Fig. 3a).
2. Glands in compact substance (Fig. 3b).

II. For the key determining bird and mammal parasites (*Polymorphoidea*):

Shape and armature of trunk.

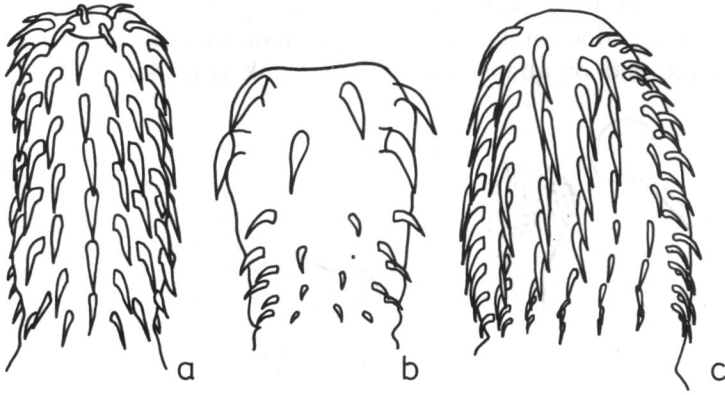


Fig. 2. Types of proboscis armature of Antarctic *Echinorhynchoidea*. a — *M. johnstoni* (1); b — *H. heteracanthus* (2); c — *A. austrinus* (3).

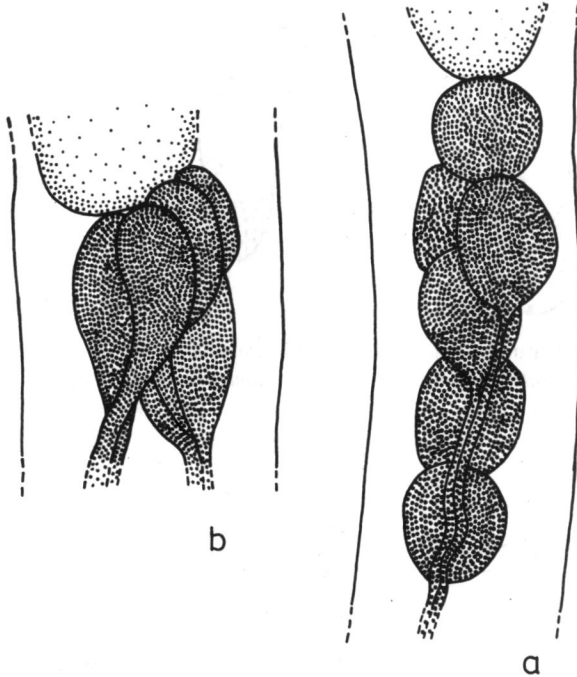


Fig. 3. Arrangement of cement glands in males of Antarctic *Echinorhynchoidea*. a — *E. nototeniae* (1); b — *M. johnstoni* (2).

1. The fore-trunk not swollen into bulbus, extent of somatic armature similar along dorsal side and ventral side, lack of genital armature (Fig. 4a).
2. At the fore-trunk, bulbus separated from the hind-trunk with a pronounced narrowing, somatic armature covers one annular area at the fore-trunk, lack of genital armature (Fig. 4b).

3. Bulbus at the fore-trunk not separated with a narrowing, the dorsal side armature does not reach further than bulbus, at the ventral side reaches the end or almost the end of trunk (Fig. 4c).

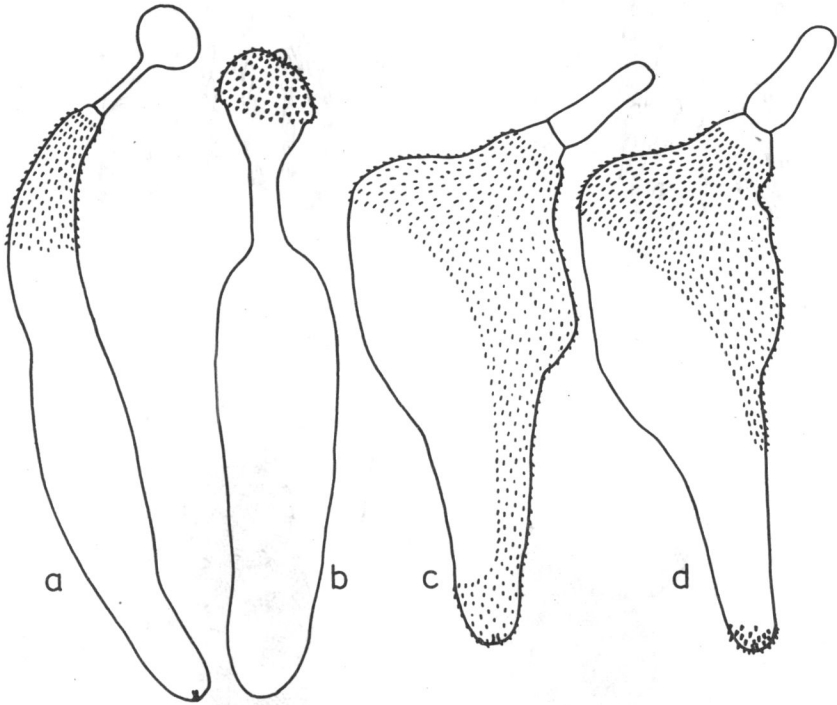


Fig. 4. Shape and armature of trunk of Antarctic *Polymorphidae*. a — *P. antarcticus*, male (1); b — *B. turbinella australis*, female (2); c — *C. hamanni*, male (3); d — *C. evae*, male (4).

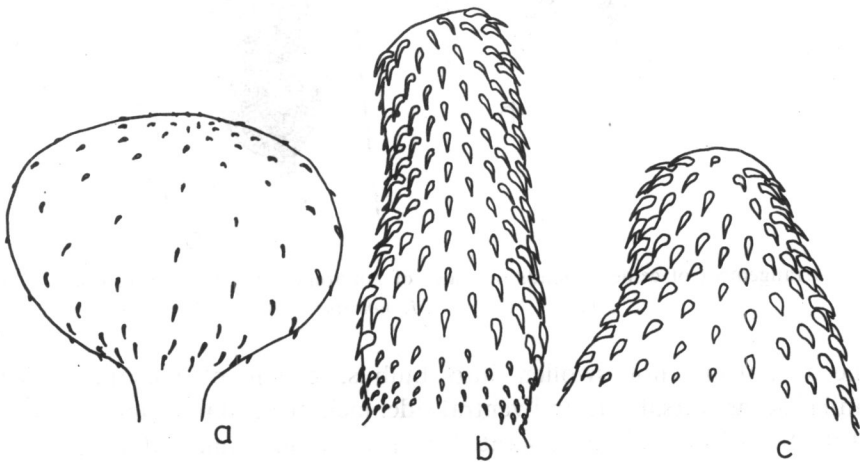


Fig. 5. Proboscis shape of Antarctic *Polymorphidae*. a — *P. antarcticus* (1); b — *C. evae* (2); c — *B. turbinella australis* (3).

4. Bulbus at the fore-trunk not separated with a narrowing, on the dorsal side the extent of armature smaller than that on the ventral side, somatic armature does not reach the end of trunk, genital armature (in some species developed, not in all specimens) separated from somatic armature with an area lacking spines (Fig. 4d).

Proboscis shape.

1. Spherical (Fig. 5a).
2. Approximately cylindrical with variously developed swelling in front of the base (Fig. 5b).



Fig. 6. Rows of proboscis hooks of Antarctic *Polymorphidae* (the longest hooks site). a—*C. bullosum* (1); b—*C. hamanni* (2); c—*C. hanna*e (3); d—*P. antarcticus* (4).

3. The maximum width of the proboscis at the base, gradually growing narrower on the anterior part of the proboscis (Fig. 5c).

The longest proboscis hooks site.

1. Distal (Fig. 6a).

2. Subdistal (Fig. 6b).
3. Prebasal (Fig. 6c).
4. Basal (the longest hooks have roots reduced or directed towards the front) (Fig. 6d).

Female genital pore site.

1. Approximately terminal (Fig. 7a).
2. Clearly displaced onto the dorsal side (Fig. 7b).
3. At the bottom of the hollow between two lateral-folds of the tegument (Fig. 7c).

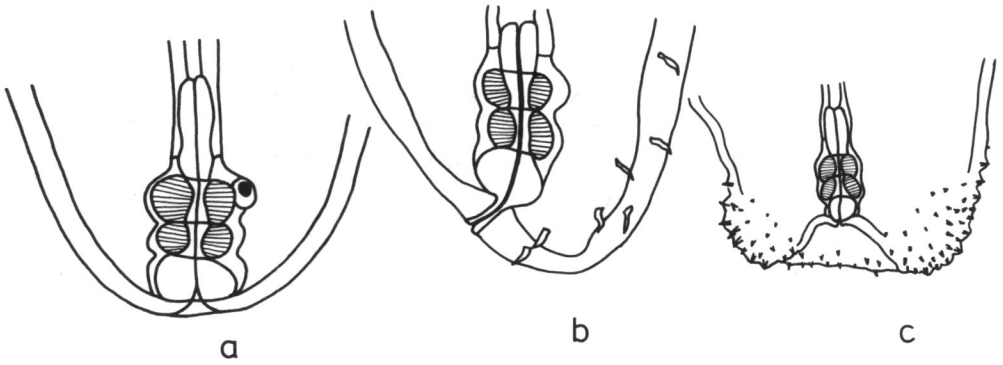


Fig. 7. Female genital pore site in Antarctic *Polymorphidae*. a — *C. evae* (1); b — *C. shackletoni*, on lateral side (2); c — *C. hamanni* on the dorsal side (3).

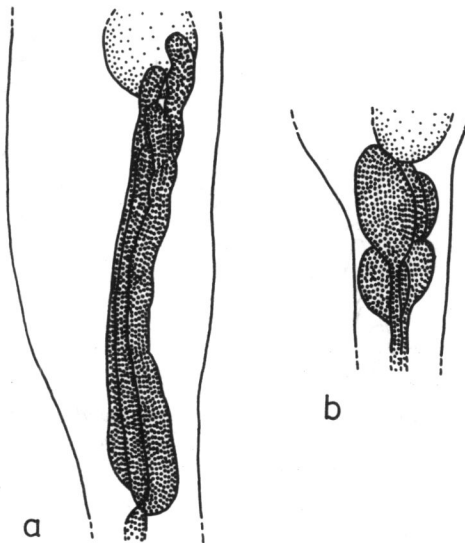


Fig. 8. Cement glands shape in males of Antarctic *Polymorphidae*. a — *P. antarcticus* (1); b — *C. arctcephali* (2).

Cement glands shape.

1. Tubular (Fig. 8a).
2. Pear-shaped (Fig. 8b).

In the majority of cases the data contained in the keys come from the author's own studies already published or just in press. Only in four cases (*E. zancloerhynchi*, *C. clavatum*, *B. balaenae*, *B. hamiltoni*) the author had no opportunity of personal acquaintance with the representatives of the species mentioned in the keys.

In the systematic review, only the species found in the Antarctic have been taken into account. It should be anticipated that in the future the list will also include other species of the genus *Bolbosoma* since their definitive hosts (proper species of whales) occur in the Antarctic and from the data given in the available studies (Skrjabin 1970, 1975, 1978) it does not follow unequivocally whether parasites were found only in the whales examined in the Subantarctic or in the Antarctic as well. A few other species of different genera (fish, bird and *Pinnipedia* parasites) were found in the Subantarctic in the hosts that also occur or might visit the Antarctic (Van Cleave 1937, Szidat 1950, Johnston and Edmonds 1953, Zdzitowiecki 1986b).

2.1. Fish parasites

Family: *Aspersentidae*

1. *Aspersentis austrinus* Van Cleave, 1929.

Synonyms: *A. wheeleri* (Baylis, 1929); *A. megarhynchus* (Linstow, 1892) Golvan, 1960 nec *Echinorhynchus megarhynchus* Linstow, 1892; *Heteracanthocephalus hureaui* Dollfus, 1965.

Definitive hosts — *Nototheniidae*: *Notothenia acuta*, *N. coriiceps coriiceps*, *N. coriiceps neglecta*, *N. cyanobranca*, *N. gibberifrons*, *N. myzops*, *N. nudifrons*, *N. rossi marmorata*, *N. rossi rossi*, *Trematomus bernacchii*, *T. hansonii*, *T. newnesi*; *Bathydraconidae*: *Parachaenichthys charcoti*, *P. georgianus*; *Chaenichthyidae*: *Chaenichthys rhinocerotus*, *Chaenocephalus aceratus*. Important notice: species "*Trematomus notothenia*" being noted as a type host does not exist. Van Cleave (1929) described *A. austrinus* on the basis of acanthocephalans collected from unprecisely determined fish belonging to the genus *Trematomus* or *Notothenia*.

Habitat: males mainly in the posterior part of small intestine, females mainly in large intestine, not numerous specimens in other parts of digestive tract (Zdzitowiecki 1981, Zdzitowiecki and Rokosz 1985).

Locality: South Shetlands, South Georgia, Heard, Kerguelen, Crozet, Macquarie (Van Cleave 1929, Baylis 1929, Joyeux and Baer 1954, Edmonds 1955, 1957; Dollfus 1965, Szidat and Graefe 1967, 1968;

Golvan 1969, Zdzitowiecki 1978, 1981, 1986e; Zdzitowiecki and Rokosz 1985).

The data given in the key according to Zdzitowiecki (1981).

Family: *Arhythmacanthidae*

2. *Heterosentis heteracanthus* (Linstow, 1896).

Definitive hosts — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. gibberifrons*, *N. rossi marmorata*; *Bathydraconidae*: *Parachaenichthys georgianus*; outside the Antarctic — *Atherinidae*: *Chirostoma microlepidotus*.

Habitat: The posterior part of small intestine and large intestine.

Locality: South Shetlands, South Georgia (Zdzitowiecki 1984a, 1986d, 1986e) and outside the Antarctic — Strait of Magellan (Linstow 1896, Van Cleave 1931, Meyer 1931).

The data given in the key according to Zdzitowiecki (1984a). It is not known whether the fish species given above are the right definitive hosts (mature females have not been found).

Family: *Leptorhynchoididae*

3. *Metacanthocephalus campbelli* (Leiper et Atkinson, 1914).

Synonyms: *Metacanthocephalus* sp. 2 Zdzitowiecki (1978).

Definitive hosts — *Nototheniidae*: *Trematomus bernacchii*, *T. borchgrevinki* (?), *T. centronotus*, *T. eulepidotus*, *Notothenia coriiceps coriiceps* (?); *Bathydraconidae*: *Parachaenichthys charcoti*; *Zoarcidae*: *Rhigophila dearboni*.

Habitat: small intestine.

Locality: McMurdo Sound, Adeliae Land, South Shetlands, South Orkneys (Leiper and Atkinson 1914, 1915; Johnston and Best 1937, Holloway and Spence 1974, 1980; Zdzitowiecki 1978a, 1983, 1986d, 1986e).

The data given in the key according to Zdzitowiecki (1983).

4. *Metacanthocephalus rennicki* (Leiper et Atkinson, 1914).

Synonyms: *Echinorhynchus debenhami* Leiper et Atkinson, 1914.

Definitive hosts — *Nototheniidae*: *Trematomus bernacchii*, *T. eulepidotus* (?), *Notothenia coriiceps coriiceps* (?).

Habitat: intestine, stomach (?).

Locality: McMurdo Sound, and (the correctness of the determination undependable) Adeliae Land, Weddell Sea (Leiper and Atkinson 1914, 1915; Johnston and Best 1937, Kock and others 1984).

The data given in the key according to the redescription of typical specimens from the McMurdo Sound (Zdzitowiecki 1983).

5. *Metacanthocephalus johnstoni* Zdzitowiecki, 1983.

Synonyms: *Leptorhynchoides campbelli* (Leiper et Atkinson, 1914) sensu Johnston and Best (1937) pro parte; *M. campbelli* sensu Zdzitowiecki (1978) nec Leiper et Atkinson (1914).

Definitive hosts — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. cori-*

iceps coriiceps (?), *N. gibberifrons*, *N. nudifrons*, *N. rossi marmorata*, *Trematomus bernacchii*, *T. hansonii*, *T. newnesi*; *Bathydraconidae*: *Parachaenichthys georgianus*; *Chaenichthyidae*: *Champscephalus gunnari*.

Habitat — mainly pyloric caeca and the anterior part of small intestine, not numerous specimens in other parts of digestive tract (Zdzitowiecki 1983, 1986d).

Locality: South Shetlands, South Georgia, Adeliae Land (Zdzitowiecki 1978a, 1983, 1986d, 1986e; Johnston and Best 1937).

The data given in the key according to Zdzitowiecki (1983).

6. *Metacanthocephalus dalmori* Zdzitowiecki, 1983.

Synonyms: *Metacanthocephalus* sp. 1 Zdzitowiecki (1978).

Definitive hosts — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. gibberifrons*, *N. nudifrons*, *N. rossi marmorata*, *Trematomus bernacchii*, *T. newnesi*; *Bathydraconidae*: *Parachaenichthys charcoti*; *Chaenichthyidae*: *Chaenocephalus aceratus*, *Chionodraco rastrospinosus*.

Habitat: mainly small intestine, not numerous specimens in pyloric caeca and large intestine (Zdzitowiecki 1983, 1986d).

Locality: South Shetlands (Zdzitowiecki 1978a, 1983, 1986d).

The data given in the key according to Zdzitowiecki (1983).

Family: *Echinorhynchidae*

7. *Echinorhynchus nototheniae* Zdzitowiecki, 1986.

Definitive hosts — *Nototheniidae*: *Notothenia coriiceps neglecta*, *Trematomus hansonii*.

Habitat: small intestine (the posterior part).

Locality: South Shetlands (Zdzitowiecki 1986a, 1986d).

The data given in the key according to Zdzitowiecki (1986a) on the basis of two males. It is not clear whether the fish species given above are the right hosts.

8. *Echinorhynchus* (sensu lato) *zanclorhynchi* Johnston et Best, 1937.

Definitive hosts — *Congiopodidae*: *Zanclorhynchus spinifer*.

Habitat: stomach.

Locality: Macquarie (Johnston and Best 1937, Edmonds 1957).

The data given in the key according to Johnston and Best (1937) and Edmonds (1957). There is a lack of a good description in the studies available; the published data are based on three badly preserved specimens. The generic status of this species is undetermined.

Besides the species mentioned above, there have been other acanthocephalans recorded in the Antarctic, which cannot be precisely determined because of the incompleteness of the descriptions and/or a bad state of the materials. Some of them at least are probably identical with well described species. The present author restricts himself to the presentation of their list:

1. *Echinorhynchus* (s. l.) *megarhynchus* Linstow, 1892.
2. *Echinorhynchus* sp. Linstow (1892).
3. *Echinorhynchus* sp. Baylis (1929).
4. *Hypechinorhynchus magellanicus* in Szidat (1965), Szidat and Graefe (1967, 1968) nec Szidat (1950).
5. *Echinorhynchus* sp. Kagei and Watanuki (1975).
6. *Metacanthocephalus* sp. Zdzitowiecki (1986e).

2.2. Bird parasites

Family: *Polymorphidae*

1. *Profilicollis antarcticus* Zdzitowiecki, 1985.

Definitive hosts (? unsuitable): *Chionis alba*.

Habitat: ileum, caecum.

Locality: South Shetlands (Zdzitowiecki 1985a).

The data given in the key according to Zdzitowiecki (1985a) based on not large material — 7 males and one immature female.

2. *Corynosoma baylisi* Zdzitowiecki, 1986.

Synonyms: *Corynosoma* sp. Zdzitowiecki (1985).

Right definitive hosts: *Chionis alba* and outside the Antarctic — *Phalacrocorax albiventer*.

Habitat: ileum.

Locality: South Shetlands (Zdzitowiecki 1985a, 1986c) and outside the Antarctic — Patagonia (Zdzitowiecki 1986c).

The data given in the key (by Zdzitowiecki 1985a, 1986c) based on not large material — 3 mature females partially contracted. One of these has been collected in the Antarctic, two in Patagonia.

3. *Corynosoma clavatum* Goss, 1940.

Right definitive hosts: *Phalacrocorax atriceps nivalis*, *Ph. atriceps traversi*, *Ph. verrucosus* and outside the Antarctic — *Ph. varius*, *Ph. ater*, *Ph. colensoi*, *Microcarbo melanoleucus*.

Habitat: intestine.

Paratenic hosts: fishes — outside the Antarctic — *Platycephalus fuscus*.

Locality: Heard, Kerguelen, Macquarie (Edmonds 1955, 1957) and outside the Antarctic — South and West Australia, the environs of New Zealand — islands Auckland and Campbell (Goss 1940, Johnston and Best 1942, Johnston and Edmonds 1952, 1953).

The data given in the key according to Goss (1940) and Johnston and Edmonds (1952, 1953).

4. *Corynosoma shackletoni* Zdzitowiecki, 1978.

Synonyms: *Corynosoma* sp. Zdzitowiecki (1978).

Right definitive hosts: *Pygoscelis papua*.

Unsuitable definitive hosts: *Larus dominicanus*.

Habitat: ileum.

Paratenic hosts: fishes — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. rossi marmorata*; *Bathydraconidae*: *Parachaenichthys charcoti*, *P. georgianus*; *Chaenichthyidae*: *Chaenocephalus aceratus*.

Locality: South Shetlands, South Georgia (Zdzitowiecki 1978a, 1978b, 1978c, 1985a, 1985b).

The data given in the key according to Zdzitowiecki (1978b, 1985a).

Moreover, in the Antarctic birds two forms belonging to undetermined species have been found, possibly identical with any of the above mentioned species:

1. *Corynosoma* sp. Edmonds (1955).
2. *Acanthocephala* gen. sp. Downes, Ealey, Gwynn and Young (1959).

In the digestive tracts of birds the occurrence of juvenile acanthocephalans usually harbouring in the Antarctic mammals has been recorded (they have probably been freshly freed from the cysts contained in the consumed fishes);

1. *Corynosoma hamanni* (Linstow, 1892).

Accidental hosts: *Chionis alba* (Jones and Williams 1969, Williams and others 1974), *Phalacrocorax atriceps* (Zdzitowiecki 1978, 1985a).

2. *Corynosoma pseudohamanni* Zdzitowiecki, 1984.

Accidental hosts: *Phalacrocorax atriceps* (Zdzitowiecki 1985a).

2.3. Mammal parasites

Family: *Polymorphidae*.

1. *Corynosoma arctocephali* Zdzitowiecki, 1984.

Synonyms: *C. singulare* Skryabin et Nikolsky, 1971 pro parte.

Right definitive hosts: *Arctocephalus gazella*, *Hydrurga leptonyx*.

Unsuitable definitive hosts: *Lobodon carcinophagus*.

Habitat: ileum and large intestine, sporadically jejunum.

Paratenic hosts: fishes — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. rossi marmorata*; *Bathydraconidae*: *Parachaenichthys charcoti*, *P. georgianus*; *Chaenichthyidae*: *Chaenocephalus aceratus*.

Locality: South Shetlands, South Georgia, Ross's Sea (Skrjabin and Nikol'skij 1971, Nikol'skij 1974, Zdzitowiecki 1978a, 1978c, 1984b, 1985b, 1985c).

The data given in the key according to Zdzitowiecki (1984b).

2. *Corynosoma australe* Johnston, 1937.

Right definitive hosts: *Hydrurga leptonyx* and outside the Antarctic — *Neophoca cinerea*, *Otaria hookeri*.

Habitat: jejunum and ileum.

Paratenic hosts: fishes — outside the Antarctic *Genypterus chilensis*.

Locality: South Shetlands (Zdzitowiecki 1984b) and outside the Antarctic — South Australia, the environs of New Zealand — islands Auckland and Campbell, Chile (Johnston 1937b, Johnston and Edmonds 1953, Vergara and George-Nascimento 1982), South Africa (unpublished materials in the British Museum Natural History, information received in the letter from dr D. Gibson).

The data given in the key according to Zdzitowiecki (1984b).

3. *Corynosoma bullosum* (Linstow, 1892).

Synonyms: *C. mirabile* Skrjabin, 1966; *C. singulare* Skrjabin et Nikolsky, 1971 pro parte.

Right definitive hosts: *Mirounga leonina* and outside the Antarctic *M. angustirostris* (provided that the parasites determination is correct).

Unsuitable definitive hosts: *Lobodon carcinophagus*, *Leptonychotes weddelli*, *Hydrurga leptonyx*, *Physeter catodon*.

Habitat: jejunum, ileum and large intestine.

Paratenic hosts: fishes — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. gibberifrons*, *N. nudifrons*, *N. rossi marmorata*, *Trematomus bernacchii*, *T. hansonii*, *Dissostichus eleginoides*; *Bathydraconidae*: *Parachaenichthys charcoti*, *P. georgianus*; *Chaenichthyidae*: *Chaenocephalus aceratus*, *Chionodraco rastrospinosus*, *Cryodraco antarcticus*; *Harpagiferidae* (undetermined species); *Liparidae*: *Paraliparis* sp.

Locality: South Georgia, South Shetlands, Heard, Crozet, Macquarie, Weddell's Sea, Ross's Sea (Linstow 1892, Baylis 1929, Edmonds 1955, 1957; Skrjabin 1966, Nikol'skij 1970, 1974; Skrjabin and Nikol'skij 1971, Zdzitowiecki 1978a, 1978c, 1984b, 1985b, 1985c, 1986e), and outside the Antarctic — environs of New Zealand — islands Auckland and Campbell (Johnston and Edmonds 1953), California (Schmidt and Dailey 1971; the author is not certain whether the parasite determination has been correct, there is a lack of morphological data in the quoted paper).

The data given in the key according to Zdzitowiecki (1985c).

4. *Corynosoma evae* Zdzitowiecki, 1984.

Synonyms: *C. singulare* sensu Zdzitowiecki (1978) nec Skryabin et Nikolsky (1971) pro parte.

Right definitive hosts: *Hydrurga leptonyx* and outside the Antarctic *Otaria flavescens*.

Habitat: jejunum and ileum.

Paratenic hosts: fishes — *Bathydraconidae*: *Parachaenichthys georgianus*.

Locality: South Shetlands, South Georgia (Zdzitowiecki 1978a, 1978c, 1984b) and outside the Antarctic — Falkland Islands (Zdzitowiecki 1986b).

The data given in the key according to Zdzitowiecki (1984b).

5. *Corynosoma hamanni* (Linstow, 1892).

Synonyms: *C. antarcticum* (Rennie, 1906); *C. siphon* Railliet et Henry, 1907; *C. pacificum* Nikolskij, 1974.

Right definitive hosts: *Hydrurga leptonyx*, *Leptonychotes weddelli*, *Ommatophoca rossi* (?).

Unsuitable definitive hosts: *Lobodon carcinophagus* (note: juvenile specimens have been recorded in birds, see the passage "Bird parasites").

Habitat: pyloric part of stomach, duodenum, the anterior part of jejunum, not numerous specimens in the further sections of intestines (Zdzitowiecki 1984b).

Paratenic hosts: fishes — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. gibberifrons*, *N. nudifrons*, *N. rossi marmorata*, *T. bernacchii*, *T. borchgrevinki* (?), *T. centronotus* (?), *T. hansonii*, *T. newnesi*; *Bathydraconidae*: *Para-chaenichthys charcoti*, *P. georgianus*; *Chaenichthyidae*: *Chaenocephalus aceratus*, *Chionodraco rastrospinosus*, *Cryodraco antarcticus*; *Zoarcidae*: *Rhigophila dearborni* (?).

Locality (note: the data are partly uncertain and so are the data referring to the hosts' list. A part of the data is related to *C. pseudohamanni*, a species recently described by the author and not distinguished before from *C. hamanni*. There is a lack of undoubted data on the occurrence of *C. hamanni* sensu stricto inside the polar circle): circumpolarly — the coasts and the seas around the Antarctic continent, South Shetlands, South Orkneys, South Georgia (Linstow 1892, Rennie 1906, Railliet and Henry 1907, Leiper and Atkinson 1914, 1915; Baylis 1929, Johnston and Best 1937, Edmonds 1957, Golvan 1959, Holloway 1965a, 1965b, 1966, 1967; Holloway and others 1966, Holloway and Bier 1967, Holloway and Nickol 1970, Holloway and Spence 1980, Nickol and Holloway 1970, Nikol'skij 1970, 1974; Markowski 1971, Kamegai and Ichihara 1973, Zdzitowiecki 1978a, 1978c, 1984c, 1985b, 1986e).

The data given in the key according to Zdzitowiecki (1984c). Note: a very accurate description of *C. hamanni* made by Nickol and Holloway (1968) and Holloway and Nickol (1970) deals mainly with *C. pseudohamanni*. According to Zdzitowiecki (1984c) *C. hamanni* was in the minority if any in the quoted material.

6. *Corynosoma hanna* Zdzitowiecki, 1984.

Right definitive hosts: *Hydrurga leptonyx*.

Habitat: large intestine.

Locality: South Shetlands (Zdzitowiecki 1984b).

The data given in the key (by Zdzitowiecki 1984b) are based on not large material — 1 male and 2 females.

7. *Corynosoma pseudohamanni* Zdzitowiecki, 1984.

Synonyms: *C. hamanni* of various authors nec Linstow (1892) pro

parte; *C. antarcticum* sensu Johnston and Best (1937) nec Rennie (1906) pro parte.

Right definitive hosts: *Leptonychotes weddelli*, *Hydrurga leptonyx*, *Lobodon carcinophagus*.

Unsuitable definitive hosts: *Mirounga leonina*, *Arctocephalus gazella* (note: juvenile specimens have been recorded in birds, see: the passage "Bird parasites").

Habitat: jejunum, ileum and large intestine (Zdzitowiecki 1984c).

Paratenic hosts: fishes — *Nototheniidae*: *Notothenia coriiceps neglecta*, *N. gibberifrons*, *N. nudifrons*, *N. rossi marmorata*, *Trematomus bernacchii*, *T. hansonii*, *T. newnesi*, *Dissostichus eleginoides*; *Bathydraconidae*: *Parachaenichthys charcoti*; *Chaenichthyidae*: *Chaenocephalus aceratus*, *Champscephalus gunnari*, *Chionodraco rastrospinosus*, *Cryodraco antarcticus*; *Harpagiferidae*: *Harpagifer bispinis*.

Locality: South Shetlands (Zdzitowiecki 1984c, 1985b), along the south coast of the Weddell Sea (Zdzitowiecki and Plötz, unpublished data), the McMurdo Sound (Zdzitowiecki 1984c on the basis of the data by Nickol and Holloway 1968 and Holloway and Nickol 1970) and probably circumpolarly in the environs of the Antarctic continent. A part of the data concerned with *C. hamanni* is in fact related to *C. pseudohamanni*, see Zdzitowiecki (1984c). *C. pseudohamanni* is likely to be a more southern species than *C. hamanni* and does not occur in the environs of the archipelagoes far away from the continent, situated north of 60°S.

The data given in the key according to Zdzitowiecki (1984c). The cited paper contains a comprehensive differential diagnosis with *C. hamanni*.

8. *Bolbosoma balaenae* (Gmelin, 1790).

Synonyms: *Sipunculus lendix* Phipps, 1774; *B. porrigens* (Rudolphi, 1819).

Definitive hosts: *Balaenoptera physalus*, *B. borealis* (the locality in the Antarctic is not certain) and outside the Antarctic — other species of whales. It is uncertain which species of whales are right hosts and which unsuitable hosts.

Locality: environs of Balleny Islands and Scott Island (Skrjabin 1978) and outside the Antarctic — environs of Australia, New Zealand, North Pacific and South Atlantic (Van Cleave 1953, Petročenko 1958, Skrjabin 1975, 1978).

The data given in the key according to Meyer (1933) based on non-Antarctic materials. An important morphological feature which has not been taken into account is the number of spine rows on the fore-trunk (bulbus) amounting to 6. In other species of the genus *Bolbosoma* found in the Antarctic about or over 20 spine rows occur on the bulbus.

9. *Bolbosoma brevicolle* (Malm, 1867).

Right definitive hosts: *Balaenoptera musculus*. Outside the Antarctic noted also in other species of whales. It is not known which of them are the right and which are the unsuitable hosts.

Unsuitable definitive hosts: *Balaenoptera borealis*.

Habitat: small intestine and large intestine.

Locality: South Shetlands, South Georgia (Baylis 1929, Zdzitowiecki unpublished data) and outside the Antarctic — environs of South Africa and North Atlantic (Baylis 1929, Zdzitowiecki unpublished data and the data of various authors contained in the monographs — see: Meyer 1933, Petročenko 1958, Yamaguti 1963).

The data given in the key according to Zdzitowiecki (unpublished data). Note: material determination is temporary. The descriptions of the species contained in the papers published so far are incomplete. Some of the data of different authors are incompatible (see: the cited above monographs). Baylis (1929) determined the parasites from *B. musculus* as *B. brevicolle*, which were gathered, among other places, in the environs of South Georgia, without giving any description. The present author's data are concerned with the specimens determined by Baylis and determined by the author to be identical with the mentioned ones. From the same host species Skrjabin (1959) described a new species *B. paramuschiri*. The author's data are compatible with the description of this species. Ascertaining of identity or separateness of the both species requires redescription of typical materials of *B. brevicolle*. Provisorily the author has not changed the designations made by Baylis (op. cit.) and as a consequence of this he used an identical name for the newly-determined materials.

10. *Bolbosoma hamiltoni* Baylis, 1929.

Right definitive hosts: *Balaenoptera physalus*, ? *B. musculus* (it is not clear whether it is the right host).

Habitat: probably intestine (in the original description there is a lack of data).

Locality: South Georgia (Baylis 1929).

The data given in the key (by Baylis 1929) based on not large material — 1 male and few females.

11. *Bolbosoma turbinella australis* Skrjabin, 1972.

Synonyms: *B. turbinella* (Diesing, 1851) of various authors pro parte — specimens originating from the south hemisphere.

Right definitive hosts: *Balaenoptera borealis schlegeli*.

Unsuitable definitive hosts: outside the Antarctic *Eubalaena glacialis australis*.

Habitat: intestine.

Locality: South Georgia and circumpolarly in the whole marine Antarctic

(Baylis 1929, Skrjabin 1972, 1975, Zdzitowiecki unpublished data) and outside the Antarctic — all oceans in the south hemisphere (Baylis 1929, Leiper and Atkinson 1914, 1915, Skrjabin 1972, 1975; Zdzitowiecki unpublished data).

The data given in the key according to Skrjabin (1972) and Zdzitowiecki (unpublished data).

Besides the acanthocephalans determined by the authors of the cited papers or liable to identification on the basis of the data available, several authors (Szidat 1965, Szidat and Graefe 1967, 1968, Tomo and Stadler 1973, Siegel 1980) gave information about the occurrence of incysted acanthocephalans, determined as *Corynosoma* sp., in fishes, in the environs of South Shetlands and neighbouring archipelagoes. In this area, incysted acanthocephalans belonging to five species with a quantitative dominance of *C. pseudohamanni* and *C. hamanni* (Zdzitowiecki 1985b) have been recorded.

3. Habitat in definitive hosts

All species of acanthocephalans described till now are at the mature stage parasites of digestive tract, mainly intestine. In the majority of earlier reports on the occurrence of acanthocephalans in the Antarctic, there is a lack of data on the habitat or they are restricted to the statement that parasites occur in intestine, or even in a more general way — in digestive tract. In few cases stomach was given as a typical habitat.

The author's field explorations proved that each of the examined species of Antarctic acanthocephalans settles mainly in a determined section of digestive tract. Not numerous specimens are also found in different sections, particularly frequently in the case of mass infestation. That is compatible with the data contained in the studies concerned with other areas and species (Kennedy and Lord 1982).

Using statistical methods the author carried out detailed researches on three fish parasites most commonly found in the environs of South Shetlands (Zdzitowiecki 1981, 1983, 1986d; Zdzitowiecki and Rokosz 1985). They settle in three successive sections of intestine: *Metacanthocephalus johnstoni* — pyloric caeca and the anterior part of small intestine, *M. dalmori* — small intestine, *Aspersentis austrinus* — the posterior part of small intestine and large intestine. In the case of *A. austrinus* it also turned out that males are located more anteriorly (mainly in small intestine) and females more posteriorly (mainly in large intestine). For the remaining two species such regularity has not been found.

The comparison of the distribution of gravid and immature females

in intestine has not revealed the backward movement of gravid females, which was described in the case of several species in the northern hemisphere (Bauer and Nikol'skaja 1957, Awachie 1966, Valtonen 1980 and others). Most of gravid females of *M. johnstoni* occur in pyloric caeca, i.e. more anteriorly than the majority of immature females which mostly settle in small intestine. That can be caused by the movement of fertilized females forwards or attaining a complete maturity by a larger per cent of females located in pyloric caeca than those located in small intestine (Zdzitowiecki 1986d).

The remaining 3 fish parasites (occurring in small numbers) found by the author in situ, *M. campbelli*, *Heterosentis heteracanthus* and *Echinorhynchus nototheniae*, mainly settle in the posterior half of small intestine. For *E. zancloerhynchi* Johnston and Best (1937) gave stomach as a place of location. However, they had to do with one specimen only and it is not clear if such habitat is normal.

The data concerned with the habitat of Antarctic bird parasites are scarce. All 3 species found by the author, *Corynosoma shackletoni*, *C. baylisi*, *Profilicollis antarcticus*, settle in ileum, mainly on the proximity of its end. The representatives of the latter were also found in caecum (Zdzitowiecki 1985a).

From among Antarctic mammal parasites, fairly precise data, although not so detailed as those related to fish parasites, were given by the author (Zdzitowiecki 1984b, 1984c, 1985c) for seven species of the genus *Corynosoma* settling in seals and fur seals. It has turned out that one species, *C. hamanni*, occurs in pyloric part of stomach, in duodenum and in first short section of jejunum. Four species, *C. pseudohamanni*, *C. bullosum*, *C. australe* and *C. evae*, occur through the whole length of small intestine, except its beginning. One species, *C. arctocephali*, occur in the posterior part of ileum, and another one, *C. hanna*, exclusively in large intestine. In addition, it should be noted that not numerous specimens of the species mentioned above have been found more posteriorly, away from the typical places of habitat (with an obvious exception of *C. hanna*) but they have not been found in the sections of digestive tract situated more anteriorly.

In the studies available there is a lack of precise data for all Antarctic species of acanthocephalans which have not been mentioned in this passage.

4. The structure of acanthocephalan populations in definitive hosts

Under the commonly accepted assumption that the numbers of males and females are equal among juvenile acanthocephalans infesting definitive hosts, it can also be assumed that in the case of fresh infestation sex

ratio should be similar. From the studies of many authors on non-Antarctic materials (Awachie 1966, Amin 1975, Amin and Burrows 1977, Valtonen 1980 and others), it follows that males remain in definitive hosts for a shorter time than females. Proportional indicator of males' participation is used for the purpose of determining the occurrence of fresh infestations at a certain time or in a certain area. In general, females are more numerous in right definitive hosts. In author's Antarctic investigations it has been ascertained that females outnumber males in all hosts' species in which females of a certain species of acanthocephalans can attain a complete maturity (contain mature embryophores). A considerable dominance of males and not numerous females not containing, as a rule, mature embryophores indicate that parasites have been found in an unsuitable host (see e.g. *H. heteracanthus*, *E. nototheniae*, *P. antarcticus*).

For the studies on the influence of the season of the year upon the infestation of definitive hosts, females' age structure and, in practice, their content of embryophores of various degree of maturity are most often taken into consideration (op. cit.). The occurrence of high percentage of females not containing embryophores but only ovarian balls in a sample under investigation indicates that parasites originating from fresh infestations are in the majority. A high percentage of females containing embryophores indicate that infestations are of a relatively long standing (specific time data are usually unknown).

In the author's studies on the common Antarctic fish parasites interesting regularities have been observed. In the case of *A. austrinus*, occurring in main definitive hosts usually in masses (infestations of several dozens or more specimens), with less numerous infestations the percentage of gravid females has been higher and the percentage of males lower than in the case of more numerous infestations (Zdzitowiecki and Rokosz 1985). The result has met the expectations. Older infestations have been, on the average, less numerous as a result of a gradual hosts' freeing themselves from parasites, males in the first place.

However, in the case of another species, *M. johnstoni*, with a similar percentage share of males, a highly significant statistical difference in the share of gravid females in favour of the hosts more numerously infested has been found (Zdzitowiecki 1986d). But *M. johnstoni* infestations are much less numerous than *A. austrinus*, usually of the order of a few specimens only. Under these conditions, the author has interpreted the received, slightly surprising result as follows. With low intensity of infestation (below 10 specimens) many females of *M. johnstoni* do not meet a male in the intestine, do not get fertilized and thus cannot contain mature embryophores (the accepted criterium of maturity). Hence, irrespective of the time of habitation in definitive hosts and the acquired size,

unfertilized females remain in the class "immature females" and the percentage of gravid females gets lower.

5. Seasonality

In the studies of all other authors, there is a lack of data relating to the seasonality of the occurrence of parasites in the Antarctic. The only research of this kind was carried out by the present author in South Shetlands. In this area, situated 500 km to the north from the south polar circle, the phenomenon of polar night does not occur. The shortest day has about 5 hours, in winter the sun rises a few degrees above the horizon line. From the studies carried out by M. Lipski (M.Sc.) from the Institute of Ecology, Polish Academy of Sciences (see: Zdzitowiecki 1985b), it appears that water salinity is practically constant all year round and the water temperature of the Admiralty Bay ranges within very narrow limits (-1.8°C to 1.7°C on the surface, in deeper places the variations are even smaller). The Bay generally freezes over in winter for the period of about 3—4 months. During author's one year (1979) studies a permanent ice sheet was not formed, only drifting pack ice occurred.

Under these conditions the author recorded the occurrence of all common species of acanthocephalans during the whole period of studies. Both gravid and immature females were found, which indicates the occurrence of fresh infestations all year round. With the use of statistical methods the occurrence of three common fish parasites *A. austrinus*, *M. johnstoni* and *M. dalmori* was thoroughly examined (Zdzitowiecki and Rokosz 1985, Zdzitowiecki 1986d). The prevalence of infestations, mean hosts' infestation and the structure of parasite population were analyzed. The main object of the studies was one host species, *Notothenia coriiceps neglecta*, although the data from other host species were also taken into account. It was found that the majority of fresh infestations of the examined host species by *A. austrinus* occurred in winter, whereas by *M. dalmori* in summer (incomplete seasonality). In the case of *M. johnstoni*, seasonality of infestation has not been recorded.

6. Remarks on the biology of acanthocephalans

All acanthocephalans hitherto recorded in the Antarctic are the representatives of the order *Palaeacanthocephala*. For the acanthocephalans of this order, arthropods, most often crustaceans, rarely insects (Golvan 1969),

are intermediate hosts. In the majority of cases, definitive hosts get infested by consuming infested intermediate hosts. A part of species (including most of Antarctic bird and mammal parasites) has paratenic hosts. In the Antarctic, acanthocephalans in intermediate hosts have not been found so far, and the attempt to infest them by way of experiment was not successful, either (Holloway and Bier 1967). The known life cycles of the species closely related with the Antarctic ones indicate that crustaceans, most probably *Amphipoda*, are potential intermediate hosts. Several authors (Szidat 1950, 1965, Tomo and Stadler 1973, Holloway and Spence 1980) suggested various crustaceans to play the role of intermediate hosts on the basis of the contents of digestive tracts of fishes, definitive or paratenic hosts of different acanthocephalan species.

The author (Zdzitowiecki 1985b, 1986d; Zdzitowiecki and Rokosz 1985) pointed out the dependence of fish infestations on their behaviour. It appeared that fishes consuming demersal crustaceans (mainly *Amphipoda*) are most often definitive hosts. In the same fishes, incysted young forms of bird and mammal parasites often occur. But the largest accumulation of juvenile forms occurs in demersal predatory fishes. In the author's opinion, they accumulate there gradually through consuming smaller infested fishes. Thus, paratenic hosting can be of two stages or of many stages and life cycles proceed then according to a pattern: intermediate host (crustacean) — I paratenic host (small fish feeding on crustaceans) — II paratenic host (predatory fish) — definitive host (bird or mammal). The occurrence of II paratenic host is facultative. The life cycles of the species harbouring in fishes at mature stage proceed according to a simple pattern: intermediate host (crustacean) — definitive host (fish). The analysis of the infestation of demersal fish species has shown the dependence of the occurrence of different acanthocephalan species on the depth at which the described fishes were caught (Zdzitowiecki op. cit.). It has been suggested that intermediate hosts of different acanthocephalan species (demersal crustaceans) occur in the area under study (South Shetlands) at depths, feasible for approximate determination, identical with the depths at which infested fishes were caught. Common acanthocephalan species have been divided into 4 groups, according to depth at which, in the author's opinion, fishes get infested.

I — to about 10 m — probably *C. shackletoni*.

II — to about 30—50 m — *A. austrinus*, *M. johnstoni*, *C. hamanni*, probably *C. arctocephali*.

III — from about 30—50 m to about 100 m — *M. dalmori*, *C. pseudohamanni*.

IV — about 100 m and deeper — *C. bullosum*.

The author has not recorded the dependence of infestation on fish sex. Fishes of all examined sizes have got infested. In the case of one fish

species, *N. coriiceps neglecta*, it has been recorded that *M. johnstoni* occurs more often and in greater numbers in young fishes, *M. dalmori* mainly in older fishes, and *A. austrinus* settles in fishes of all examined sizes in the same degree. Acanthocephalans, for which fishes serve as paratenic hosts, break from intestine through the internal wall to abdominal cavity and remain there in the incysted form till the death of a hosts. Infestation grows as host gets older and larger. Fish infestation by *Corynosoma* spp. in the Admiralty Bay in South Shetlands is extraordinarily strong, which is influenced by the presence of the massively infested definitive hosts — seals (Zdzitowiecki 1985b, 1986d).

The length of time required for attaining maturity and the duration of living in definitive hosts by Antarctic acanthocephalans are not known.

7. Specificity

As it has already been pointed out, acanthocephalans settle in 3 kinds of hosts: intermediate, paratenic and definitive. In the Antarctic, they were found only in paratenic and definitive hosts whereas intermediate hosts are still not known.

In the paratenic hosts (in the Antarctic, these are only fishes) juvenile acanthocephalans, in a short time, break from intestine through the internal wall to abdominal cavity where they get incysted. Under these conditions, not only species specificity has not been recorded but even host's family and infestation are determined by the behaviour of intermediate and paratenic hosts. From among Antarctic acanthocephalans, the representatives of the genus *Corynosoma* and *Bolbosoma* have paratenic hosts, but only the former have been found in this category of hosts in the Antarctic. Their paratenic hosts are fishes from at least five families, *Nototheniidae*, *Chaenichthyidae*, *Bathydraconidae*, *Harpagiferidae* and *Zoarcidae*, and probably from a larger number of families as well. Infestations often affect many species and nothing indicates the occurrence of the specificity phenomenon in relation to any families (Holloway and Bier 1967, Holloway and Spence 1980, Zdzitowiecki 1985b).

Mutual relations in the systems parasite—definitive host are much closer and all known parasites show narrower or broader specificity in relation to definitive hosts. Besides right definitive, hosts, in which parasites develop fully and procreate, they also settle in unsuitable hosts. In the course of the studies of Antarctic acanthocephalans, the author usually found male parasites in such hosts, and if females were encountered, they were not numerous and did not contain mature or even developing embryophores. Since in the majority of the papers by various authors,

it has not been said whether the recorded Antarctic acanthocephalans in various hosts have been fully mature or not, the author is forced to base mainly on the results of his own studies.

Common acanthocephalans, fish parasites, have a wide range of hosts in the Antarctic. The occurrence of fully mature females of *A. austrinus*, *M. campbelli*, *M. johnstoni* and *M. dalmori* has been recorded by the author in fishes belonging to two or three families grouped in superfamily *Notothenioidea* (see Systematical review). According to Holloway and Spence (1974, 1980), *M. campbelli* is also found in fishes from family *Zoarcidae*, which is systematically far from *Notothenioidea*. In the author's opinion, the correctness of determining parasites by the authors mentioned above requires confirmation. They assumed that in the Antarctic only one representative of the genus (they used genus name *Leptorhynchoides*) occurs, and in 1983, other species were described (Zdzitowiecki 1983). At any rate, the available data indicate that specificity of *A. austrinus* and Antarctic *Metacanthocephalus* spp. is not narrower than that of a superfamily.

Unlike the species mentioned above, *E. zanclorhynchi* is known to have only one host species, *Zanclorhynchus spinifer*, which can be caused by the lack of wider examination in the environs of the Macquarie Island. Gravid females of *H. heteracanthus* and *E. nototheniae* have not been found till now. All so far known definitive hosts of these species are probably unsuitable.

The representatives of the genus *Corynosoma* parasitize in aquatic birds and in mammals (a larger number of species), with each class of hosts having its own characteristic parasite species; specimens found in the representatives of other class than the right one are immature (Van Cleave 1953). In the Antarctic, it has been recorded that in birds two species of seal parasites occur, *C. hamanni* and *C. pseudohamanni* (Jones and Williams 1969, Williams and others 1974, Holloway and Spence 1980, Zdzitowiecki 1978c, 1985a). All specimens found by the author were juvenile. The sizes of parasites and the degree of development of gonads were identical with those recorded in the specimens collected in paratenic hosts. The recorded infestations were probably very fresh and the parasites would have been removed from the digestive tract in a short time.

Among three species of the genus *Corynosoma*, attaining sexual maturity in Antarctic birds, two show relatively narrow specificity. *C. clavatum* occurs in several species of cormorants, and *C. shackletoni* in one species of penguin, *Pygoscelis papua*. Although the latter was also found in a gull, *Larus dominicanus*, but in this host only a single male parasite was found (Zdzitowiecki 1978b). The third species, *C. baylisi* occurs in

Patagonia in cormorants and in the Antarctic a mature female was found in the representative of the order *Larilimicolae*, *Chionis alba*, which is rather surprising. The only representative of the genus *Profilicollis* (*P. antarcticus*) recorded in Antarctic birds (*Ch. alba*), has been probably found in unsuitable hosts, which can be assumed since no gravid females were observed (Zdzitowiecki 1985a).

Seven species of the genus *Corynosoma* have been recorded in Antarctic seals and fur seals. In most of host species, a complete development is attained by 1–2 parasite species. *Leopard seal*, *Hydrurga leptonyx* (*Phocidae*), turned out to be an exception. In this host, the author has found gravid females of six species *Corynosoma* spp. (except *C. bullosum*), including the species occurring also in the hosts belonging to a different family (*Otariidae*), namely *C. arctocephali*, *C. australe* and *C. evae*. *C. bullosum* attains full maturity exclusively in the representatives of the genus *Mirounga*, though males and immature females have been also found in other seals, and even in sperm whales. On the basis of the specimens collected in sperm whales, Skrjabin (1966) described a distinct species, *C. mirabile*, which turned out to be identical with *C. bullosum* (Zdzitowiecki 1985c).

It should be noted, at the same time, that the specificity of *Corynosoma* spp. in relation to different hosts cannot result from the lack of contacts between parasites and the hosts other than the right ones. In the area of the author's main studies (South Shetlands), paratenic hosts are massively infested, and the infestations are miscellaneous. Thus, the selection of parasites takes place in the digestive tract of definitive hosts and is determined by physiological factors, which are not necessarily connected with the affinity existing among definitive hosts (surprising susceptibility of leopard seal and *Chionis alba*, among birds, to the infestations caused by the parasites occurring in systematically distant hosts).

The available data concerned with the specificity of the representatives of the genus *Bolbosoma* are difficult to interpret. The lists of the hosts of different species are almost identical, many records are probably based on incorrect determinations or on finding of immature parasites in unsuitable hosts. Baylis (1929) and Skrjabin (1972) stress that they have found mature females *B. turbinella* only in one host species, *Balaenoptera borealis*. The author believes that other species should also have a narrow range of hosts. In the Antarctic, several representatives of the genus *Bolbosoma* have been recorded in two host species at most, and, in each case, gravid females have probably been found in one species (Baylis op. cit. in the case of *B. brevicolle* and *B. hamiltoni* does not say in which species of hosts he recorded mature females).

8. Geographical distribution

Parasitological studies have been carried out in the Antarctic in relatively small number of places and covered not large area, and in the majority of cases the materials collected by non-specialists for the purpose of different studies have been examined. Therefore, the data on the occurrence of parasites (not only acanthocephalans) in the most of the areas are incomplete. As far as acanthocephalans are concerned, the area most thoroughly examined, in the author's opinion, are South Shetlands (mainly the surroundings of "H. Arctowski" Research Station situated at the Admiralty Bay, on the King George's Island). Relatively a lot of data come from South Georgia and the McMurdo Sound (Ross Sea). The data from the islands situated in the subregion Kerguelen, South Orkneys and other areas seem absolutely accidental. However, several regularities concerned with geographical distribution of Antarctic acanthocephalans can be observed.

Whales parasites (except *B. balaenae*) and at least 8 species harbouring in other hosts, *C. hamanni*, *C. pseudohamanni*, *C. bullosum*, *C. australe*, *C. arctocephali*, *A. austrinus*, *M. campbelli*, *M. johnstoni* and probably *M. rennicki* occur circumpolarly. The cases of restricting the area of the occurrence to eastern or western Antarctic are very rare. The occurrence of *B. balaenae* was recorded by Skrjabin (1978) only in the environs of the Ross Sea and (outside the Antarctic) New Zealand. Cormorants' parasite, *C. clavatum*, which is widespread on the islands of the subregion Kerguelen (and to the north of them) is replaced in South Shetlands (and to the north of them) by a closely related species, *C. baylisi*. It seems possible that the area of the occurrence of fish parasite, *E. zanclorenchi*, is restricted to the environs of one island, Macquarie. Another fish parasite, *H. heteracanthus*, has been found only in the environs of various archipelagoes to the south of South America. A few other species have been described by the author from various hosts from the environs of South Shetlands, some of them also occur in the neighbouring areas. However, the author believes that regarding them as characteristic only for the Western Antarctic would be premature. The ascertainment of the occurrence of as many as 19 species of acanthocephalans in the environs of South Shetlands and South Georgia in comparison with 23 recorded in the whole Antarctic is an obvious result of far more accurate examinations of these areas compared with others.

The analysis of the occurrence of acanthocephalans in various latitudes enables to divide the species recorded in the Antarctic into 3 groups. Ist group comprises 3 species found inside the polar circle, but also occurring outside the polar circle. These are: *M. campbelli*, *M. rennicki*

and *C. pseudohamanni* (in the author's opinion, in the environs of the McMurdo Sound, not *C. hamanni* but *C. pseudohamanni* has been found, with a small admixture of *C. hamanni*, at most, see: Zdzitowiecki 1984c).

II-nd group comprises common species characteristic for the environs of the continent's coasts outside the polar circle and subcontinental archipelagoes such as South Shetlands and South Orkneys. Most of these species (except *M. dalmori*) also occur, often massively, in the environs of the islands situated in close proximity of Antarctic convergence line. The list includes 7 species: *M. johnstoni*, *M. dalmori*, *A. austrinus*, *C. bullosum*, *C. arctocephali*, *C. hamanni*, and *C. shackletoni*.

The remaining species belong to the III-rd group and are usually found in the surroundings of Antarctic convergence line on its both sides, i.e. in the province of South Georgia and the subregion Kerguelen, and also outside the Antarctic. The representatives of this group penetrate far into the Antarctic, but they do not occur commonly there. The author includes two species of rare occurrence in the third group tentatively. These are: *E. nototheniae* and *P. antarcticus*, described in the environs of South Shetlands and not found, so far, in other areas. The representatives of four species of the genus *Bolbosoma*, whale parasites, have been found in the Antarctic in definitive hosts exclusively. It is not known whether complete life cycles of these parasites can take place in the Antarctic, or whether infested whales only "carry" them in themselves from other areas. This view can be strengthened by the fact that the infestation extent of *Balaenoptera physalus* by *B. balaenae* was strongly reduced as the area under studies moved to the south, from the environs of Scott Island (Skrjabin 1978). Unquestionable representatives of the III-rd group are also 6 further species: *H. heteracanthus*, *C. baylisi*, *C. clavatum*, *C. australe*, *C. evae*, and *C. hannaе*.

A vast majority of Antarctic acanthocephalans do not occur in the northern hemisphere. The exceptions from this rule seemed to be, until recently, the cosmopolitan representatives of the genus *Bolbosoma*, whales parasites. But Skrjabin (1972) recorded the occurrence of serious morphological differences between the specimens belonging to the same species, but originating from different hemispheres, northern and southern hemisphere. He observed the greatest differences within the species *B. turbinella* and distinguished 2 subspecies — nominal in the northern hemisphere and *B. turbinella australis* in the southern hemisphere. The problem of systematic homogeneity of population of different species was left open.

Schmidt and Dailey (1971) stated that *C. bullosum* occurred in *Mirounga angustirostris*, the Californian relative of Antarctic host of this species, *M. leonina*. But the cited authors did not give any morphological analysis. Taking the geographical isolation of hosts into account, the

author believes that certain distinctive features of parasites can be anticipated, if not of specific then perhaps of a subspecific rank. As things are, the occurrence of *C. bullosum* in the northern hemisphere is considered uncertain. Such an opinion is supported by the fact that closely related pairs of species of the genus *Corynosoma* are known, out of which one occurs in mammals in the northern hemisphere, and the second in the southern hemisphere. These are *C. obtuscens* with *C. australe*, and *C. semerme* with *C. hanna*. Although it was stated that *C. semerme* occurred in the southern hemisphere (Meyer 1933, Johnston and Edmonds 1953, Grabda and Ślósarczyk 1981), but long ago Van Cleave (1953) and Golvan (1959) questioned the correctness of earlier determinations suggested the occurrence of a distinct species in the southern hemisphere.

Summing up, the present author has recorded the separateness of the fauna of Antarctic acanthocephalans from that of northern hemisphere, though in individual cases the separateness can be of lower rank than specific one.

9. The importance of acanthocephalans in the parasite fauna of the Antarctic

From among four main groups of helminths, internal parasites, acanthocephalans have the fewest species and are not the main focus of interest of most researchers. On the basis of the data contained in the publications up to 1975, it seemed that also in the Antarctic, they were of minor importance and were represented by few species. For instance, in the studies conducted within the framework of the program of British, Australian, and New Zealand Antarctic Research Expedition, 1929—1931, large publications were devoted to the descriptions of tens of species of *Digenea*, *Cestoda* and parasite *Nematoda* (Johnston and Mawson 1945, McEwin 1957, Prudhoe 1968, Prudhoe and Bray 1973). At the same time, 8 species of acanthocephalans were recorded, out of which only 5 in the Antarctic (Edmonds 1957). Similar proportions can be observed in other publications. Only Nikol'skij (1970) in his paper concerned with Antarctic parasites of seals recorded relatively large number of acanthocephalans, four in relation to only one species of *Digenea*, five species of *Nematoda* and indefinite number of *Cestoda*. The intensities of infestations by acanthocephalans ran into several thousands of specimens in one host. Deljamure (1955) had claimed before that only one species of acanthocephalans occurred in Antarctic seals.

The author's studies in South Shetlands (preliminary in 1977, all year examinations in 1979) revealed unexpectedly great importance of acanthoceph-

halans as Antarctic parasites of vertebrates, in respect of both the abundance of species and the intensity of infestations. Since the examinations conducted have not covered some groups of hosts (e.g. whales) and the data contained in the studies available are uncomparable because of the random character of the materials scientifically described, further considerations deal with South Shetlands only and the groups of hosts examined there by the author. Numerical data concerned with parasite groups other than acanthocephalans have not been published so far, except the description of some parasites collected during the preliminary studies (Zdzitowiecki 1978a, 1979; Szelenbaum-Cielecka and Zdzitowiecki 1978, Zdzitowiecki and Drózdź 1980, Cielecka and Zdzitowiecki 1981, Zdzitowiecki and Szelenbaum-Cielecka 1984).

9.1. Fish parasites

The studies covered, almost exclusively, the representatives of superfamily *Notothenioidea*. In the digestive tracts of fishes, mature specimens of acanthocephalans, belonging to 6 species were recorded. At the same time, 8 species of *Digenea* occurred, out of which 7 were recorded during the preliminary examinations (Zdzitowiecki 1978a, 1979), and the eighth, *Neolepidapedon trematomi*, during all year examinations. Not numerous mature *Cestoda* occurred only in rays (*Bathyraja* spp.), but the number of species has not been determined yet. 2 species of *Nematoda* were recorded. Moreover, in the digestive tracts and abdominal cavity, juvenile forms of five further species of acanthocephalans and the larvae of *Cestoda* and *Nematoda* (unknown number of species) occurred. As far as quantitative proportions are concerned, there were 37699 acanthocephalans in the number of 146740 of all parasites collected, which is 25.7%. The infestations of fishes by juvenile *Corynosoma* spp. were the strongest of all those recorded, so far, in the seas of the whole world. Similar intensity of infestation was only recorded in Ładoga Lake (Baryševa and Bauer 1957).

9.2. Bird parasites

If accidentally found juvenile mammal parasites are not to be taken into account, then only three species of acanthocephalans have been recorded in birds with the infestation intensity not exceeding few specimens. At the same time, not fewer than 3 species of *Digenea*, about 10 species of *Cestoda*, and at least 3 species of *Nematoda* occurred (the description of this material is not finished). Infestation intensities of *Cestoda* and *Nematoda* were often high, numbered by the hundred of specimens. Thus,

the importance of acanthocephalans in this group of hosts is marginal. This view is also supported by the fact that among juvenile acanthocephalans found in paratenic hosts (fishes), bird parasites constituted a small percentage, 0.24% (Zdzitowiecki 1985a).

9.3. Seal and fur seal parasites

In the Antarctic, in the digestive tracts of these hosts, only 1 species of *Digenea* (Johnston 1931, 1937a), 9 species of *Cestoda* (Markowski 1952) and 5 species of *Nematoda* (Nikol'skij 1970) were recorded. In the light of these facts, the number of seven species of acanthocephalans recorded by the present author in South Shetlands (the materials from other groups of parasites are not described) is impressive. Infestation intensities of leopard seals, Weddell seals, and elephant seals ran into thousands of specimens. However, it should be noted that the infestation intensities of two former host species by *Nematoda*, and particularly *Cestoda* were even higher and amounted to tens or even sometimes hundreds of thousands of parasites.

Summing up, the present author states that in South Shetlands the importance of acanthocephalans as fish and seal parasites does not yield precedence to that of other groups of parasite helminths. Only among bird parasites, the importance of acanthocephalans is marginal. At the present stage of studies, these statements cannot be applied to the whole Antarctic. In the environs of the McMurdo Sound (Ross Sea) only 2 species of acanthocephalans attaining maturity were recorded in fishes (Zdzitowiecki 1983) and 1 or 2 species in juvenile stage were found (Zdzitowiecki 1984c, on the basis of the data from the publications). At the same time, Holloway and Spence (1980) recorded in fishes in this area the occurrence of six species of *Digenea* and the larvae of *Cestoda* (plerocercoids of *Pseudophyllidea*, *Scolex pleuronectis* — juvenile *Tetraphyllidea*) and the larvae of *Nematoda* (*Contraeaecum* spp.) belonging to the unknown number of species. It cannot be excluded that the conditions controlling the Admiralty Bay (the main area under author's studies) are particularly favourable to massive infestations of vertebrates by acanthocephalans, which is a result of gathering of a considerable number of potential hosts of all development stages of these parasites in one, not large area. However, it is certain that also in other parts of the Antarctic, the importance of acanthocephalans is greater than it might be concluded from the data published so far.

From the practical point of view, it is crucial that the ranges of definitive and paratenic hosts massively conquered by acanthocephalans are

practically identical with the sphere of man's economic concern with Antarctic vertebrates. Almost all Antarctic species of acanthocephalans, at the juvenile stage, occur in abdominal cavity or, at the mature stage, in the digestive tract of fishes from the superfamily *Notothenioidea*. These are the very fishes which are the object of intensive fishing in the Antarctic by fishing fleets of several countries, including Polish ships.

At least 4 species of acanthocephalans (*Bolbosoma* spp.) occur in digestive tracts of whales, the other group of Antarctic vertebrates of great practical importance to man. Although the extent of whales' infestations is relatively low in the Antarctic, but the intensities happen to be very high, reaching thousands of parasites (Skrjabin 1975, 1978).

On the other hand, of great importance are the acanthocephalan species massively harbouring in some species of seals: Weddell seals, leopard seals and elephant seals. These are the representatives of the genus *Corynosoma*; their importance lies in the fact that juvenile forms of these very acanthocephalans occur massively in abdominal cavity of fishes. And particularly in those fishes which are large, mature and constitute the most valuable part of sea-fishing. Seals are definitive hosts and get infested by consuming fishes invaded by juvenile parasites. Life cycles of parasites are closed by demersal crustaceans, which consume acanthocephalans' embryophores excreted with feces by definitive hosts; crustaceans play the role of intermediate hosts in which larval forms of parasites develop and next get consumed by paratenic hosts — fishes.

Additional note

After the text has been delivered the author has received copies of three further publications. In the first one (Rodjuk G. N. 1984 — *Novye predstaviteli roda Metechinorhynchus (Acanthocephala) — parazitov ryb zapadnoj Antarktiki — Zool. Zh.*, 63: 1893—1896) two new species, *M. muraenolepisi* and *M. petrotschenkoi*, are described from fishes caught off South Georgia and South Shetlands. Both species mentioned are closely related to *E. nototheniae* but not identical with it.

Occurrence of cystacanths of undetermined acanthocephalans in amphipods is reported in other two articles (Bone D. G. 1972 — *Aspects of the biology of the Antarctic amphipod Bovallia gigantea Pfeffer at Signy Island, South Orkney Islands — Br. Antarct. Surv. Bull.*, No. 27: 105—122; Hoogesteger J. N., White M. G. 1981 — *Notes on parasite infestation of inshore fish at Signy Island, South Orkney Islands — Br. Antarct. Surv. Bull.*, No. 54: 23—31). In the last one aspects of infestation of common fishes (mainly *Notothenia neglecta* and *N. gibberifrons*) with larval nematodes and mature and juvenile acanthocephalans (determined with some doubts as *A. austrinus*, *C. hamanni* and *C. bullosum*) were investigated.

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understanding and self-control enabled the author to collect the necessary materials. The author wishes to thank all the colleagues of I-st and III-rd expedition to South Shetlands, too numerous to be mentioned here by names, for their help. Special thanks are due to Dr. D. I. Gibson for offering the possibility of getting acquainted with numerous comparative materials collected in the British Museum (Natural History) in London. The author is grateful to Assoc. Prof. B. Grabda-Kazubska for a patient reading of present and previous papers and for many valuable remarks.

10. Резюме

Настоящая работа является подведением итогов наших познаний об антарктических скребнях. Она содержит собственные материалы автора, собранные, главным образом, в окрестностях Южных Шетландских островов, а также данные из мировой литературы.

В Антарктике обнаружено до сих пор 23 не вызывающих сомнений вида скребней, в том числе 8 — это в зрелой стадии паразиты рыб: *Aspersentis austrinus*, *Heterosentis heteracanthus*, *Metacanthocephalus campbelli*, *M. rennicki*, *M. johnstoni*, *M. dalmori*, *Echinorhynchus nototheniae*, *E.* (s. l.) *zanclorhynchi*; 4 — птиц: *Profilicollis antarcticus*, *Corynosoma baylisi*, *C. clavatum*, *C. shackletoni*; 11 — млекопитающих: *Corynosoma arctocephali*, *C. australe*, *C. bullosum*, *C. evae*, *C. hamanni*, *C. hannaе*, *C. pseudohamanni*, *Bolbosoma balaenae*, *B. brevicollae*, *B. hamiltoni*, *B. turbinella australis*.

В работе представлен обзор всех выше упомянутых видов вместе с синонимикой, а также политоимические ключи, основанные на морфологических чертах. Кроме того, составлен список всех форм, которых невозможно было определить, исходя из доступных данных различных авторов.

Подробно рассмотрена локализация некоторых видов в пищеварительном тракте окончательных хозяев принимая во внимание половую структуру и возраст популяции паразитов. Отдельные виды обитают, главным образом, в определенных отрезках пищевого тракта, в других же отрезках выступают в небольшом количестве в случае массовой инвазии. Не обнаружено перемещения зрелых самок к задней пищевода что было замечено у многих видов на северном полушарии.

На примерах двух паразитов рыб обнаружена зависимость структуры популяции паразитов от интенсивности инвазии. В случае *A. austrinus*, выступающего обычно массовым образом при менее многочисленных инвазиях обнаружено большое процентное содержание зрелых самок и только немного самцов. Это свидетельствует об истечении довольно-таки длительного времени от момента инвазии, так как самцы удаляются из пищевого тракта раньше самок. В случае *M. johnstoni*, выступающего в небольшом количестве — обычно несколько особей больше зрелых самок обнаруживали при более многочисленных инвазиях. Это было вызвано фактом неоплодотворения многих самок которые при немногочисленных инвазиях не встретили самцов. Из этого следует, что при небольшой интенсивности заражения небольшое процентное содержание зрелых самок не свидетельствует о недавно происшедшей инвазии.

Все распространенные виды скребней выступают у своих хозяев в течение всего года, однако, неполная сезонность наблюдалась у двух паразитов рыб. *A. austrinus* является более многочисленным зимой, а *M. dalmori* — летом.

Исследования ограничивались до стадий развития, выступающих у хозяев паратенических и окончательных (промежуточные хозяева антарктических скребней не известны), однако на основе заражения придонных рыб, обитающих на различных глубинах, была выдвинута гипотеза относительно систематической принадлежности и мест пребывания промежуточных хозяев некоторых видов на Южных Шетландских островах.

Обнаружено отсутствие узкой специфичности представителей рода *Corynosoma* по отношению к паратеническим хозяевам — рыбам. Круг последних хозяев является широким в случае паразитов рыб (выступают эти же самые виды скребней у хозяев принадлежащих к нескольким семействам) и узким в случае паразитов птиц и млекопитающих (выступают отдельные виды скребней у немногих, обычно состоящих в близком родстве, хозяев).

Большинство антарктических скребней выступает циркумполярно, однако, некоторые виды являются характерными только для восточной или западной Антарктики. Из известных 23 видов только 3, *M. campbelli*, *M. rennicki* и *C. pseudohamanni*, найдены без сомнения в пределах Южного Полярного круга. Следующие 7, *M. johnstoni*, *M. dalmori*, *A. austrinus*, *C. bullosum*, *C. arctocephali*, *C. hamanni*, *C. shackletoni* широко распространены в окрестности субконтинентальных архипелагов, таких как Южные Шетландские острова. Остальные 13 видов выступают, главным образом, на границе Антарктики, вблизи линии антарктической конвергенции, или же за ее пределами.

Антарктическая фауна скребней отличается от фауны северного полушария, хотя в некоторых случаях (главным образом, у паразитов китообразных) эти различия внутривидовой, а не видовой степени.

В окрестностях Южных Шетландских островов многочисленные виды рыб и тюленей заражены скребнями массовым образом. Интенсивность инвазии и видовое разнообразие этих паразитов не уступает соответствующим показателям других групп гельминтов. В это же время значение скребней как паразитов антарктических птиц является второстепенным.

Практическое значение антарктических скребней заключается в их массовом выступлении у представителей тех групп позвоночных, которые находятся в сфере хозяйственного заинтересования человека, т.е. рыб, китообразных и тюленей. Самое большое значение имеют представители рода *Corynosoma*, выступающего в ювальной стадии у рыб, а половозрелой — у тюленей.

11. Streszczenie

Praca stanowi podsumowanie dotychczasowej wiedzy o antarktycznych kolecogłowach. Jest oparta na materiałach autora, zebranych głównie w okolicach Południowych Szetlandów, oraz na danych zawartych w światowym piśmiennictwie.

W Antarktyce zanotowano dotąd 23 pewne gatunki kolecogłowów, w tym 8 pasożytujących w stadium dojrzałym w rybach: *Aspersentis austrinus*, *Heterosentis heteracanthus*, *Metacanthocephalus campbelli*, *M. rennicki*, *M. johnstoni*, *M. dalmori*, *Echinorhynchus nototheniae*, *E.* (s. 1.) *zancloerhynchi*; 4 w ptakach: *Profilicollis antarcticus*, *Corynosoma baylisi*, *C. clavatum*, *C. shackletoni*; 11 w ssakach: *Corynosoma arctocephali*, *C. australe*, *C. bullosum*, *C. evae*, *C. hamanni*, *C. hanna*, *C. pseudohamanni*, *Bolbosoma balaenae*, *B. brevicollae*, *B. hamiltoni*, *B. turbinella australis*. Zamieszczono przegląd wszystkich powyższych gatunków wraz z synonimiką oraz klucze politomiczne oparte na cechach morfologicznych. Sporządzono listy wszystkich form niemożliwych do identyfikacji na podstawie dostępnych danych, które zostały zanotowane przez różnych autorów.

Omówiono szczegółową lokalizację niektórych gatunków w przewodzie pokarmowym żywicieli ostatecznych, z uwzględnieniem struktury płciowej i wiekowej populacji pasożytów. Poszczególne gatunki zasiedlają głównie określone odcinki przewodu pokarmowego, w innych odcinkach występują nielicznie w przypadkach masowych inwazji. Nie stwierdzono przemieszczania się dojrzałych samic ku tyłowi przewodu pokarmowego, co było notowane u wielu gatunków na półkuli północnej.

Na przykładach dwóch pasożytów ryb stwierdzono zależność struktury populacji pasożytów od intensywności inwazji. W przypadku *A. austrinus*, występującego zwykle masowo, przy mniej licznych inwazjach stwierdzono wysoki procentowy udział dojrzałych samic i niewiele samców. Świadczy to o upływie stosunkowo długiego okresu czasu od momentu inwazji, gdyż samce są usuwane z przewodu pokarmowego żywicieli ostatecznych wcześniej niż samice. W przypadku *M. johnstoni*, występującego nielicznie — zwykle po kilka osobników, stosunkowo więcej dojrzałych samic stwierdzano przy liczniejszych inwazjach. Było to spowodowane niezaplodnieniem wielu samic, które przy nielicznych inwazjach nie napotkały samców. Wynika z tego, że przy niskich intensywnościach zarażenia niski procentowy udział dojrzałych samic nie świadczy o niedawno zaszłej inwazji.

Wszystkie pospolite gatunki kolcogłów występują w żywicielach przez cały rok, ale stwierdzono niepełną sezonowość występowania dwóch pasożytów ryb. *A. austrinus* jest liczniejszy zimą, a *M. dalmori* latem.

Badania były ograniczone do postaci rozwojowych występujących w żywicielach paratenicznych i ostatecznych (żywiciele pośredni antarktycznych kolcogłów nie są znani), ale na podstawie zarażenia ryb występujących przydennie na różnych głębokościach wysunięto sugestie dotyczące przynależności systematycznej i miejsc bytowania żywicieli pośrednich niektórych gatunków na Południowych Szetlandach.

Stwierdzono brak wąskiej specyficzności przedstawicieli rodzaju *Corynosoma* w stosunku do żywicieli paratenicznych — ryb. Kręgi żywicieli ostatecznych są zróżnicowane, na ogół szerokie w przypadkach pasożytów ryb — występowanie tych samych gatunków kolcogłów u żywicieli należących do kilku rodzin, wąskie w przypadkach pasożytów ptaków i ssaków — występowanie poszczególnych gatunków kolcogłów u niewielu, na ogół blisko spokrewnionych żywicieli.

Większość antarktycznych kolcogłów występuje cirkumpolarnie, są jednak gatunki charakterystyczne tylko dla wschodniej albo zachodniej Antarktyki. Ze znanych 23-ech gatunków tylko 3, *M. campbelli*, *M. rennicki* i *C. pseudohamanni*, stwierdzono dotąd w sposób pewny wewnątrz południowego kręgu polarnego. Dalszych 7, *M. johnstoni*, *M. dalmori*, *A. austrinus*, *C. bullosum*, *C. arctocephali*, *C. hamanni*, *C. shackletoni*, występuje pospolicie w okolicach subkontynentalnych archipelagów, takich jak Południowe Szetlandy. Pozostałe 13 gatunków występuje głównie na krańcach Antarktyki, w pobliżu linii konwergencji antarktycznej oraz poza Antarktyką.

Antarktyczna fauna kolcogłów jest odrębna od fauny półkuli północnej, chociaż w niektórych przypadkach (głównie pasożyty waleni) odrębność może mieć rangę niższą niż gatunkowa.

W okolicach Południowych Szetlandów liczne gatunki ryb i fok są masowo zarażone przez kolcogłowy. Intensywności inwazji i różnicowanie gatunkowe tych pasożytów nie ustępują odpowiednim wskaźnikom dotyczącym innych grup robaków pasożytniczych. Natomiast znaczenie kolcogłów jako pasożytów antarktycznych ptaków jest marginalne.

Praktyczne znaczenie antarktycznych kolcogłów wynika z masowego występowania u przedstawicieli akurat tych grup kręgowców, które leżą w sferze gospodarczych zainteresowań człowieka, ryb, waleni i fok. Największe znaczenie mają przedstawiciele rodzaju *Corynosoma* występujący w stadium młodocianym w rybach i w stadium dojrzałym w fokach.

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