

ALCATAENIA FRATERCULAE sp. n.
FROM THE HORNED PUFFIN,
FRATERCULA CORNICULATA (Naumann),
ALCATAENIA CERORHINCAE sp. n.
from the rhinoceros auklet, *Cerorhinca monocerata* (Pallas),
and *Alcataenia larina pacifica* ssp. n. (Cestoda : Dilepididae)
in the North Pacific basin

Eric P. HOBERG*

SUMMARY. Three Cestodes representing two species of the genus *Alcataenia* Spasskaia, 1971 and a subspecies of *Alcataenia larina* (Krabbe, 1869) are described. *Alcataenia fraterculae* sp. n. (Cestoda : Dilepididae) was found in horned puffins, *Fratercula corniculata* (Naumann), and other species of seabirds from localities in the western Aleutian Islands, Gulf of Alaska, Bering Sea, and Chukchi Sea. *Alcataenia cerorhincae* sp. n. is described from the rhinoceros auklet, *Cerorhinca monocerata* (Pallas) in the eastern North Pacific Ocean and western Aleutian Islands. *Alcataenia larina pacifica* ssp. n. is recognized from species of Laridae and other seabirds in the North Pacific Ocean, Sea of Okhotsk, Bering Sea and the region of the Arctic Ocean near Bering Strait. It is distinguished from *A. larina larina* (Krabbe, 1869) by a greater number of testes, a longer cirrus sac, and variation in the position of the genital ducts which may be either dorsal to or between the osmoregulatory canals. *A. fraterculae* and *A. cerorhincae* are most similar to *A. larina* and particularly to the North Pacific form *A. l. pacifica*. Generally specimens of *A. fraterculae* can be distinguished from the other taxa by larger rostellar hooks, a longer cirrus sac, and a combination of other characters. *A. fraterculae*, *A. cerorhincae*, and *A. l. pacifica* however represent a complex of cryptic species in which there is extensive overlap in some morphological characters. Results of a discriminant analysis among these nominal taxa were significant and, in combination with data about other morphological characters and host and geographic distribution, clearly indicated that these represent three species in the North Pacific basin.

***Alcataenia fraterculae* sp. n. du macareux cornu, *Fratercula corniculata* (Naumann), *Alcataenia cerorhincae* sp. n. du pingouin *Cerorhinca monocerata* (Pallas) et *Alcataenia larina pacifica* ssp. n. (Cestoda : Dilepididae) dans le bassin Nord Pacifique**

RÉSUMÉ. Trois Cestodes représentant 2 espèces du genre *Alcataenia* Spasskaia, 1971 et une sous-espèce d'*Alcataenia larina* (Krabbe, 1869) sont décrits : *A. fratercula* sp. n. (Cestode Dilepididae) a été trouvée chez les macareux *Fratercula corniculata* (Naumann) et d'autres espèces chez des oiseaux de mer de localités occidentales des Îles Aléoutiennes, du golfe d'Alaska et des mers de

* Wildlife Science, University of Washington, College of Forest Resources AR-10, Seattle, WA. 98195 USA.

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Bering et de Chukchi ; *A. cerorhincae* sp. n. est observée et décrite chez le pingouin *Cerorhinca monocerata* (Pallas) dans l'océan Nord Pacifique oriental et les Iles Aléoutiennes occidentales ; *A. larina pacifica* ssp. n. est découverte chez des espèces de Laridae et autres oiseaux de mer de l'océan Nord Pacifique, la mer d'Okotsk, la mer de Bering et l'océan Arctique proche du détroit de Bering. Elle se distingue de *A. larina larina* (Krabbe, 1869) par un plus grand nombre de testicules, une poche du cirre plus longue et des variations dans la position des conduits génitaux qui peuvent être soit dorsaux, soit entre les conduits osmo-régulateurs. *A. fraterculae* et *A. cerorhincae* sont très semblables à *A. larina*, en particulier à la forme Nord-Pacifique, *A. l. pacifica*. En général, les spécimens de *A. fraterculae* se distinguent des autres taxa par des crochets rostellaires plus grands, une poche du cirre plus longue et une association d'autres caractères. — *A. fraterculae*, *A. cerorhincae* et *A. l. pacifica* représentent toutefois un complexe d'espèces « occultes » chez lesquelles un grand nombre de caractères se chevauchent. Mais, les résultats d'une analyse discriminative chez ces taxa ont été significatifs, et, en association avec d'autres caractères morphologiques, l'hôte, la distribution géographique, ils indiquent clairement que l'on est bien en présence de 3 espèces valides du bassin Nord Pacifique.

Cestodes representing two previously undescribed species of the genus *Alcataenia* Spasskaia, 1971 were found in pelagic birds of the family Alcidae and other avian species in the eastern North Pacific Ocean and Bering Sea during the years 1975-1982. The first species was initially found in horned puffins, *Fratercula corniculata* (Naumann) collected at Buldir Island in the western Aleutian Islands in August, 1975 and subsequently at other localities in Alaska as indicated below. Additional specimens were collected from horned puffins, tufted puffins, *Fratercula cirrhata* (Pallas), a rhinoceros auklet, *Cerorhinca monocerata* (Pallas), a northern fulmar, *Fulmarus glacialis* (Linnaeus), and a common murre, *Uria aalge* (Pontoppidan), at Ugaiushak Island. At Kodiak Island, horned and tufted puffins, two slender-billed shearwaters, *Puffinus tenuirostris* (Temminck), and two black-legged kittiwakes, *Rissa tridactyla pollicaris* Ridgway were infected. At St. Paul (Pribilof Islands), St. Lawrence Island, St. Matthew Island, and Cape Thompson (L. G. Swartz, unpubl. data, 1960), only horned puffins were found to be infected. Crested auklets, *Aethia cristatella* (Pallas) were infected at Amchitka and Buldir Islands. Mature and gravid cestodes were found only in horned puffins and a single black-legged kittiwake. Specimens from birds of other species were always undeveloped or astrobilate.

Cestodes of the second species were found only in rhinoceros auklets : in a single bird collected September, 1982, and from 20 collected in July, 1981 at Destruction Island and Protection Island, in waters off Washington State. Additional specimens were collected from single birds at Forrester Island and at sea south of the western Aleutian Islands, Alaska. All had mature or gravid cestodes, with the exception of several birds from Washington, which had recently acquired infections.

During a continuing study of helminth parasites of seabirds, specimens of *Alcataenia larina* (Krabbe, 1869) were collected from black-legged kittiwakes, glaucous-winged gulls, *Larus glaucescens* (Naumann), and other avian species from localities in the North Pacific basin and Sea of Okhotsk. These specimens were distinct from the type series of *A. larina*, and from specimens of this species re-described by Baer (1956) from localities in the North Atlantic basin. Baer (1956) was the

first to suggest that North Pacific and North Atlantic populations of *A. larina* might be differentiated at the infraspecific level. Study of the present specimens from the North Pacific lend further support to this contention.

The specimens of *A. larina* from the North Pacific and Sea of Okhotsk were morphologically very similar to both undescribed species from alcids. In most cases it was difficult to distinguish these taxa by means of standard comparisons of various morphological characters. Consequently, a discriminant function analysis was conducted to determine the degree of dissimilarity among cestodes (mature or gravid) representing taxa from horned puffins, rhinoceros auklets, and forms of *A. larina* from the North Pacific, respectively (Fisher, 1936; Mayr, 1969; Wiley, 1981). The results of this analysis in conjunction with other morphological and distributional data support the concept of the occurrence in horned puffins, and rhinoceros auklets of discrete taxa of cestodes that differ morphologically from *A. larina*. In addition to descriptions of the two species, subspecies of *A. larina* in the North Atlantic and North Pacific are distinguished.

Methods and Materials

In Alaska, cestodes were generally collected alive and fixed in boiling 10 % formalin. Several birds from Alaska and those collected off of Washington State were frozen immediately after collection and necropsied later. All cestodes were prepared as whole mounts stained in Semichon's acetic carmine. Rostellar hooks from some specimens were mounted separately to ensure accuracy of measurements and determination of their form. In the following descriptions all measurements are given in micrometers unless stated otherwise. Ranges are followed by mean values in parentheses. Two hundred cestodes from horned puffins and other hosts were examined; the description of *Alcataenia fraterculae* sp. n. was based on 35 specimens mounted entire. One hundred mature specimens from rhinoceros auklets were examined; the description of *Alcataenia cerorhincae* sp. n. was based on 45 cestodes mounted entire.

Specimens of *A. larina* examined: 1) Krabbe's (1869) type series from *Rissa tridactyla* (Linnaeus) in Iceland: slides 84/50 (mount of rostellar hooks), 84/51 (2 entire specimens) and 84/59 (3 entire specimens) from the collections of the Muséum d'Histoire Naturelle, Genève. 2) Baer's (1956) specimens redescribed from *Rissa tridactyla* at Ivnaq, Greenland: slides 108/1 (rostellar hooks), 108/2 (eggs), and 108/3 (2 entire specimens) also from the collections of the Mus. d'Hist. Nat., Genève. 3) One hundred specimens from *Rissa tridactyla pollicaris*, *Larus glaucescens* and other species of seabirds from Buldir, Ugaiushak, Kodiak, and St. Matthew Islands, and 10 specimens collected by me from *R. t. pollicaris* in the Sea of Okhotsk near Magadan, USSR.

Discriminant function: Discriminant function analysis was conducted using the Biomedical Computer Program BMDP 7M (Dixon and Brown, 1979). Discriminant analyses were run in a stepwise fashion to include only those variables that contributed significantly to the discrimination (Partial $F < 4.0$).

Mature and gravid cestodes were grouped *a priori* according to host. Three groups representing *a priori* taxa were compared : 1) cestodes from *Fratercula corniculata* ; 2) cestodes from *Cerorhinca monocerata* ; 3) and specimens of *A. larina* from hosts in the North Pacific basin. The analysis was undertaken to determine if these three groups represented morphologically discrete taxa. Specimens of *A. larina* from the North Atlantic basin were not included, as the available sample was not sufficiently large. Among the three groups, only those specimens were used for which a complete set of data could be derived for all variables selected. The number of specimens representing each taxon in the analysis is as follows : 1) 27 *Alcataenia larina* from *Rissa tridactyla pollicaris* : 5 from the Sea of Okhotsk ; 10 from Buldir Island ; 11 from Ugaiushak Island ; and 1 from Kodiak Island. 2) 30 specimens of *Alcataenia fraterculae* sp. n. from *Fratercula corniculata* : 21 from Buldir Island ; 8 from Ugaiushak Island ; and 1 from Kodiak Island. 3) 25 specimens of *Alcataenia cerorhincae* sp. n. from *Cerorhinca monocerata* : 7 from the western Aleutian Islands ; 17 from Destruction and Protection Islands, Washington ; and 1 from the region of Grays Harbor Marine Canyon, off the north coast of Washington State.

Seven variables (morphological characters) were used in the discriminant analysis, viz., lengths of rostellar hooks, cirrus sac, vitelline gland, and seminal receptacle ; diameters of the Mehlis gland and testes ; and numbers of testes. Other potential characters, such as the overall dimensions of the strobila, diameter of the scolex and suckers, and dimensions of the embryophore and oncosphere were not used. The seven characters were chosen because they have diagnostic value, can be accurately measured, and are not generally influenced by contraction of the strobila unless it is extreme.

Certain problems were evident in developing data-sets for these variables. Cestodes, being polyzoic organisms, have a complete complement of reproductive organs in each proglottid. Any single proglottid, although an individual entity from the standpoint of reproductive function, is not completely representative of all mature proglottids that would occur as components of a single strobila. An entire strobila with scolex and hooks intact, and possessing mature and at least early gravid segments was regarded as a individual for the purposes of the analysis. Measurements of genital organs were taken only from mature segments. Mature proglottids are defined as those immediately anterior to the segment in which ova are first released into the uterus. Measurements were standardized by always examining segments (to a maximum of 15) immediately anterior from this point. Numerical values for measurements of cirrus sac, vitelline gland, seminal receptacle, Mehlis gland, and diameter of testes represent means from a series of a minimum of 5 mature proglottids in each strobila. As a single measurement could not be taken for each variable to represent an individual worm, a mean value was thought to be representative of measurements of these organs in a single strobila. The number of testes was determined in immature segments. In such segments, the developing testes are small and overlap is diminished. Accurate determination of the number of testes was not possible in mature segments of these cestodes. The length of the rostellar hooks is given as a mean for each scolex. The utilization of mean values for each variable allowed

recognition of a discrete measurement for each of the seven variables, and thus a complete data-set for each strobila.

When necessary, missing data were estimated from the infrapopulation mean for a particular variable (*i.e.*, values were based on a mean derived from the total population of cestodes examined from an individual host). Cestodes for which a complete data-set could not be derived were generally discarded from the analysis (*i.e.*, specimens with greater than three estimated variables).

Results

Alcataenia fraterculae sp. n. (*fig. 1-6*)

DESCRIPTION : Strobila 53-110 mm with up to 300 proglottids in gravid specimens. Maximum width in pregravid and gravid segments, 1.37-4.1 mm. Proglottids wider than long; strobila serrate. Neck 226-476 long by 392-690 wide. Scolex large, from 297 wide in immature or astrobilate specimens; 499-850 wide in mature specimens. Suckers from 120 in greater diameter in immature specimens; 270-357 in mature specimens. Rostellum 381-429 long by 166-214 wide at apex; armed with 20-26 hooks in two regularly alternating rows; 116-139 (125) long. Blade: handle ratio 1 : .75-1.11. Rostellar sheath 285-437 long, extending posteriad to mid-level of suckers. Ventral longitudinal excretory canals 21-48 in diameter, connected by transverse duct 6-12 in diameter; dorsal canals 12-21. Genital pores irregularly alternating. Genital atrium protrusible, appearing as sucker-like projection on lateral margin of segment. Genital ducts passing dorsal to osmoregulatory canals. Genital *Anlagen* visible immediately posterior to neck in 20th to 30th segment. Cirrus sac cylindrical, 259-572 (434) long by 39-78 (56) wide in mature segments; containing coiled vas deferens. Cirrus unarmed, 15-26 (20) in diameter. Vas deferens tightly coiled adjacent to poral excretory canals, extending posteriad and passing dorsal to seminal receptacle before splitting into numerous vas efferentia posterior to vitelline gland. Testes 27-61 (46) in number, discernable by 110th to 130th segment, occupying posterior half of segment between excretory canals; diameter 77-129 (102) in mature segments. Vagina 348-654 long, opening posterior to cirrus sac; extending mediad dorsal to ovary, expanding to form seminal receptacle 120-392 (217) long by 63-166 (101) wide, dorsal to ovary. Ovary ventral, highly lobed, 2 winged with small poral and larger antiporal wings; occupying anterior 1/2 of segment between excretory canals; overall 392-1.370 long by 178-416 wide. Vitelline gland dorsal, postovarian, slightly poral or median in center of segment, 202-464 (324) long by 60-214 (124) wide. Mehlis gland 61-101 (79) in diameter. Uterus arising dorsally from ootype, stem directed antero-ventrad and passing ventral to ovary; later forming laterally branching, highly lobed, flat reticulum with first ova appearing about 170th to 180th segment. In post-mature and early gravid segments uterus appears partitioned by trabeculae as walls of expanding tubular network become compressed. Gravid uterus, persistent and sacculate in

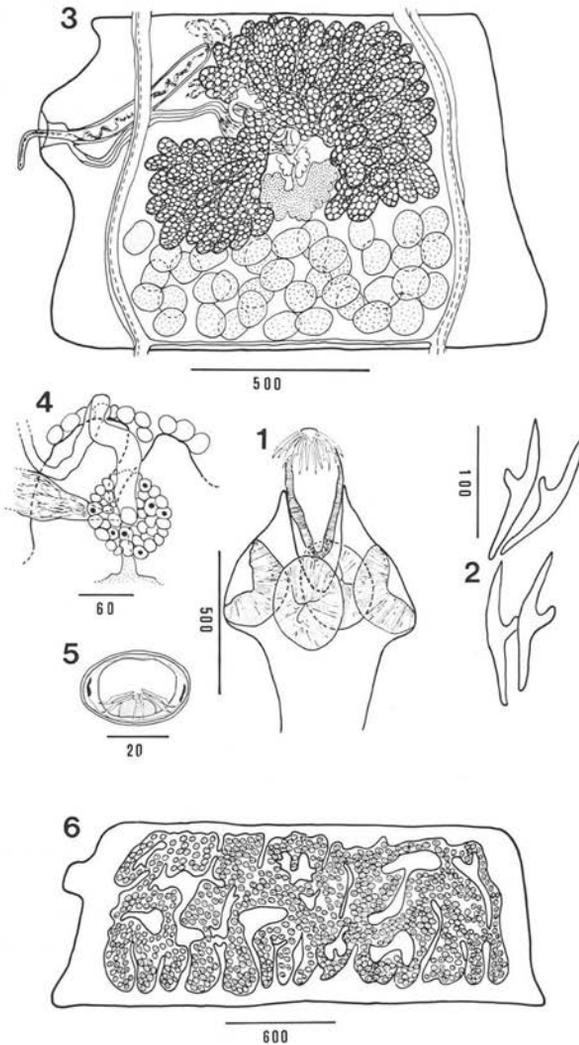


FIG. 1-6. — *Alcataenia fraterculae* sp. n. 1) Scolex. 2) Rostellar hooks. 3) Mature proglottid, ventral view. 4) Detail of ducts in the female reproductive system, dorsal view. 5) Embryophore and oncosphere. 6) Ventral view of early gravid proglottid showing detail of coarse reticulate uterus. All scales are in micrometers.

form, filling entire proglottid; finger-like projections extend through cortex ventrad and dorsad to level below tegument. Outer envelope of egg membranous, containing thick-walled embryophore 29-43 (36) long by 22-35 (26) wide. Oncosphere 21-32 (25) long by 16-24 (19) wide. Embryonic hooks 10-14 (12) long for lateral groups; 8-10 (9) for medial groups.

HOSTS : *Fratercula corniculata* (Naumann) (type). Also reported from *F. cirrhata*, *Cerorhinca monocerata*, *Uria aalge*, *Aethia cristatella*, *Rissa tridactyla pollicaris*, *Puffinus tenuirostris*, and *Fulmarus glacialis*.

LOCALITY : Buldir Island, Alaska (lat. 52° 21' N ; long. 175° 56' E.) (type). Also reported from Ugaiushak and Kodiak Islands in the Gulf of Alaska, Amchitka Island in the central Aleutian Islands, St. Paul (Pribilof Islands), St. Matthew, and St. Lawrence Islands in the Bering Sea, and Cape Thompson on the eastern shore of the Chukchi Sea.

HABITAT : Duodenum.

SPECIMENS : Holotype, USNM Helm. Coll. No. 77648, collected from the type host at Buldir Island, 21-VIII-1975. Paratype 1, USNM Helm. Coll. No. 77649, with same data as the holotype. Paratype 2, USNM Helm. Coll. No. 77649, from type host and locality, 18-VIII-1975. Paratype 3, USNM Helm. Coll. No. 77649 (2 slides, with hooks and strobila mounted separately), from type host and locality 14-VII-1975. Paratype 4, USNM Helm. Coll. No. 77650 (an astrobilate specimen), from *Fratercula cirrhata* at Ugaiushak Island, VI-1976. Paratype 5, USNM Helm. Coll. No. 77651, from type host at Ugaiushak Island, VI-1976.

ETYMOLOGY : The specific name *fraterculae* is derived from the generic name of the type host for this cestode.

Alcataenia cerorhincae sp. n. (fig. 7-10)

DESCRIPTION : Strobila 38-83 mm long, with maximum of 254 proglottids when gravid. Maximum width in pregravid and gravid segments 2.2-2.5 mm. Proglottids wider than long ; strobila serrate. Scolex large, 448-649 wide. Suckers 189-319 in greater diameter. Rostellum 283-484 long by 145-224 at apex ; armed with 21-24 hooks arranged in two regularly alternating rows ; 96-119 (108) long. Blade : handle ratio 1 : .67-1.33. Rostellar sheath 290-484 long, extending to level between suckers. Ventral longitudinal excretory canals 26-44 in diameter ; connected by transverse duct ; dorsal canals 14-17 in diameter. Genital pores irregularly alternating. Genital atrium protrusible appearing as a sucker-like projection on the lateral margin of segment. Genital ducts passing dorsal to osmoregulatory canals. Genital *Anlagen* visible by about 40th segment. Cirrus sac cylindrical, 145-348 (207) long by 32-73 (44) in mature segments ; containing coiled vas deferens. Cirrus unarmed, distally 9-17 in diameter ; proximally 20-26 ; up to 271-378 when fully extended. Vas deferens tightly coiled adjacent to poral osmoregulatory canals. Testes 32-68 (48) in number, discernable by 75th to 120 th segment, occupying posterior half of segment behind and to sides of female organs ; diameter 58-110 (70) in mature segments. Vagina 342-448 long, thick-walled, opening posterior to cirrus sac, extending mediad dorsal to ovary, expanding to form ovoid seminal receptacle 116-241 (158) long by 41-116 (71) wide. Ovary ventral, highly lobed, 2 winged, with small poral and larger antiporal wings ; occupying anterior 1/2 of segment between excretory canals ; overall 472-908 long by 118-295 wide. Vitelline gland highly lobed, median, 131-276 (203) long by 39-116 (69) wide. Mehlis gland 44-75 (62) in diameter. Uterus arising dorsally from

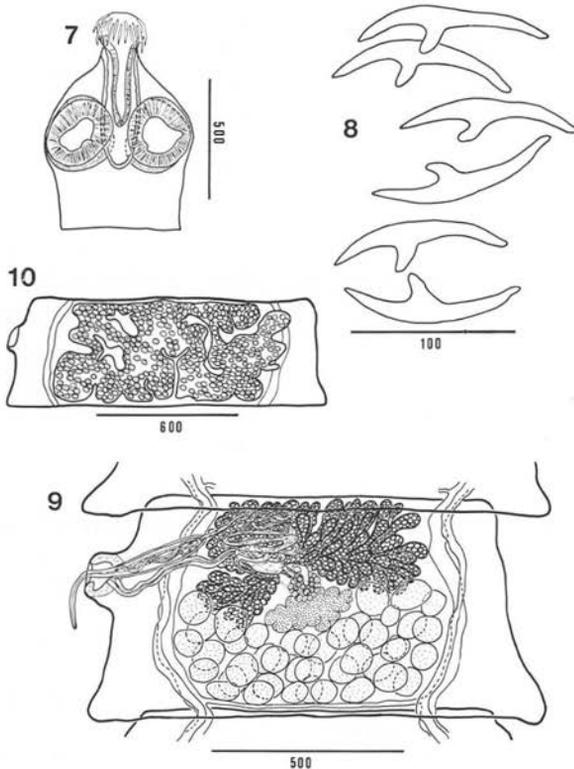


FIG. 7-10. — *Alcataenia cerorhincae* sp. n. 7) Scolex. 8) Rostellar hooks. 9) Mature proglottids, dorsal view. 10) Early gravid uterus, ventral view. All scales are in micrometers.

ootype, stem directed antero-ventrad, passing ventral to ovary; forming laterally branching, highly lobed, flat, coarse, reticulum; first ova appear about 155th to 190th segment. Gravid uterus persistent, sacculate in form, filling entire proglottid, lobes extending ventrad and dorsad through cortex to level of tegument. Outer egg envelope membranous, containing thick-walled embryophore 35-45 (38) long by 23-30 (28) wide. Oncosphere 21-30 (26) long by 16-21 (19) wide. Embryonic hooks 9.3-10.4 (10) for medial groups; 11.6-14 (13) for lateral groups.

HOSTS : *Cerorhinca monocerata* (Pallas), type and only known host.

LOCALITY : Grays Harbor Marine Canyon, at sea off the north coast of Washington (ca. lat. 46° 55' N., long. 124° 46' W.) (type). Also reported from Destruction Island and Protection Island, Washington, Forrester Island, Alaska, and at sea south of the western Aleutian Islands, Alaska (ca. lat. 50° 25' N.; long. 173° 52' E.).

SPECIMENS : Holotype, USNM Helm. Coll. No. 77652, from type host and locality, collected by D. R. Paulson, 8-IX-1982. Paratype 1, USNM Helm. Coll. No. 77653, collected at Protection Island by R. Fitzner, 21-VII-1981. Paratype 2, USNM Helm. Coll. No. 77654, from the western Aleutian Islands, 28-VI-1981.

HABITAT : duodenum.

ETYMOLOGY : The species name *cerorhincae* is derived from the generic name of the type and only known host for this cestode.

Alcataenia larina larina (Krabbe, 1869)

DESCRIPTION : Maximum length 30-37 mm, up to 1.37 mm wide. Rostellar hooks 20-23 in number ; 98-113 (107) long. Blade : handle ratio 1 : .64-.85. Genital ducts dorsal to osmoregulatory canals. Testes 16-30 in number. Cirrus sac 174-304 (237) long by 32-58 (44) wide. Vitelline gland 174-240 (198) long.

HOSTS : Species of Laridae.

LOCALITY : North Atlantic Basin.

Alcataenia larina pacifica ssp. n.

DESCRIPTION : Maximum length up to 92 mm by 2.0 mm in gravid specimens. Rostellar hooks 20-24 in number ; 87-111 (101) in length. Blade : handle ratio 1 : .48-.91. Genital ducts between or dorsal to osmoregulatory canals. Testes 27-59 (41). Cirrus sac 142-427 (330) long by 30-65 (48) wide. Vitelline gland 162-298 (261) long.

HOSTS : *Rissa tridactyla pollicaris* Ridgway (type). Also reported from *Rissa brevirostris* (Bruch), *Larus glaucescens*, *Fulmarus glacialis*, *Aethia cristatella* and *A. pygmaea* (Gmelin).

HABITAT : Duodenum.

LOCALITIES : Buldir Island, Alaska (lat. 52° 21' N. ; long. 175° 56' E.) (type). Also reported from Ugaiushak, Kodiak, St. Matthew, St. Paul (Pribilof Islands), and St. Lawrence Islands, and Point Barrow, Alaska, Also from the region near Magadan, USSR on the Sea of Okhotsk (ca. lat. 59° 35' N. ; 150° 45' E.).

SPECIMENS : Holotype, USNM Helm. Coll. No. 77655, from the type host and locality, 14-VIII-1975. Paratype 1, USNM Helm. Coll. No. 77656, with same data as holotype. Paratype 2, USNM Helm. Coll. No. 77657, from type host near Magadan, USSR, 17-VIII-1981, collected by A. Kondratiev.

ETYMOLOGY : The subspecific name *pacifica* indicates the distribution of this cestode in the North Pacific Ocean.

Discussion

There are seven species in the genus *Alcataenia* Spasskaia, 1971, viz., *A. campylacantha* (Krabbe, 1869) (type), *A. armillaris* (Rudolphi, 1810), *A. meinertzhageni* (Baer, 1956), and a recently described species (Hoberg, 1984) from seabirds of the

family Alcidae, and *A. larina* (Krabbe, 1869), *A. micracantha* (Krabbe, 1869), and *A. dominicanus* (Railliet and Henry, 1912) from birds of the family Laridae. The latter three species were formerly placed in *Rissotaenia* Spasskaia and Kolutolova, 1972, a genus that was recently reduced as a synonym of *Alcataenia* (Hoberg, 1984). *Alcataenia fraterculae* sp. n. and *A. cerorhincae* sp. n. are most similar to *A. larina* (Krabbe, 1869), a cestode that has a holarctic distribution and is host-specific in larids. The former two taxa are clearly distinguished from *A. larina larina* by larger size, greater numbers of testes, and a combination of other characters when compared to descriptions by Krabbe (1869), Joyeux and Baer (1954) (a redescription of Krabbe's type series), and Baer (1956). However specimens of both new species are difficult to distinguish from *A. larina pacifica* ssp. n. by standard morphological comparisons with descriptions of this North Pacific form published by Schiller (1951), Jurpalova and Spasskii (1971), and Spasskaia and Kolutolova (1972), and specimens collected by me at localities in the North Pacific basin. In *table I* characters that distinguish specimens of *A. fraterculae*, *A. cerorhincae*, *A. larina larina* (from a reexamination of Krabbe's and Baer's specimens) and *A. l. pacifica* are compared.

Specimens of *A. fraterculae* are generally larger than those of *A. cerorhincae* and *A. l. pacifica*. The length of the rostellar hooks 116-139 μm ($\bar{X} = 125$) distinguishes *A. fraterculae* from *A. cerorhincae* 96-119 μm ($\bar{X} = 108$) and *A. l. pacifica* 87-111 μm ($\bar{X} = 101$). The blade : handle ratios overlap in all three taxa, but only in specimens of *A. fraterculae* and *A. cerorhincae* was the handle longer than the blade. In *A. fraterculae* (mature segments) the length of the cirrus sac 259-572 μm ($\bar{X} = 434$) was substantially greater than that in *A. cerorhincae* 145-348 μm ($\bar{X} = 207$) and *A. l. pacifica* 142-427 μm ($\bar{X} = 330$). There were no apparent differences in the size and form of the scolex, numbers of rostellar hooks, number of testes, or dimensions of the embryophores and eggs among the three taxa. The position of the genital ducts, dorsal in *A. fraterculae* and *A. cerorhincae* appeared to be constant as opposed to the variable situation in specimens of *A. l. pacifica*.

The only other morphological characters which might be useful in differentiation of *A. fraterculae* from *A. cerorhincae* are the structure of the ovary, form of the genital atrium, and the degree of development of the vagina as it approaches the genital atrium (*fig. 3 and 9*). In specimens of *A. cerorhincae* the poral wing of the ovary is not as extensive and the individual lobes are apparently narrower and more elongate than those seen in representatives of *A. fraterculae*. The musculature of the genital atrium is also more strongly developed in specimens of the former species. The vagina is thick-walled throughout its entire length in representatives of *A. cerorhincae* while a thin-walled region is characteristic of the vagina distally as it enters the genital atrium in specimens of *A. fraterculae*. These differences are not absolute, as there is some degree of variation associated with these characters in both *A. fraterculae* and *A. cerorhincae*.

A. fraterculae is morphologically distinct from both *A. cerorhincae* and *A. l. pacifica*, however there is substantial overlap in the dimensions of most organs. This overlap might indicate that the three nominal species actually represent a single taxon with exceptionally broad morphological variation. Consequently a discriminant

TABLE I. — A comparison of diagnostic characters for *Alcataenia fraterculae* sp. n., *A. cerorhincae* sp. n. and *A. larina*.

	1	2	3	4	5	6	7
Length mm	30-37	80	20	50-62	92	38-83	110
Width mm	1.37	3.0	1.7	1.79-1.9	2.0	2.2-2.5	4.1
Hooks #	20-23	20-22	22	23-24	20-23	21-24	20-26
Hooks μ m	98-113 (107)	96-110	95-105	87-104 (95)	93-111 (101)	96-119 (108)	116-139 (125)
Blade : handle ratio	1: .64-.85	-----	1: .90	1: .57-.91	1: .48-.90	1: .67-1.33	1: .75-1.11
Position genital ducts	dorsal	between	between	dorsal	dorsal	dorsal	dorsal
Cirrus sac L	174-304 (237)	240-288	168-263	212-327 (276)	142-427 (330)	145-348 (207)	259-572 (434)
W μ m	32-58 (44)	72	45-50	44-64 (51)	30-65 (48)	32-73 (44)	39-78 (56)
Vitelline gland μ m	174-240 (198)	180	-----	162-296 (210)	202-298 (261)	131-276 (203)	202-464 (324)
Testes #	16-20 25-30* ≥ 20	30-40	35	40-52 (44)	27-59 (41)	32-68 (48)	27-61 (46)
Oncosphere L μ m	23-29 (25)	-----	33	27-32 (29)	24-27 (26)	21-30 (26)	21-32 (25)
W μ m	14-20 (18)	-----	28	22-28 (24)	18 (18)	16-21 (19)	16-24 (19)
Embryophore L μ m	31-41 (37)	-----	50	37-45 (41)	31-44 (37)	35-45 (38)	29-43 (36)
W μ m	23-30 (27)	32-36	45	25-35 (30)	21-31 (26)	23-30 (28)	22-35 (26)

1) *Alcataenia larina larina*. 2-5) *A. larina pacifica*. 6) *A. cerorhincae* sp. n. 7) *A. fraterculae* sp. n.

1) From a reexamination of Krabbe's (1869) type series, and specimens redescribed by Baer (1956) (data combined).
 2) Schiller (1951), St. Lawrence Island, Alaska. 3) Spasskaia and Kollitova (1972), western Bering Sea. 4) Hoberg (1981) Sea of Okhotsk, near Magadan, USSR. 5) Hoberg (1975-1982) Aleutian Islands, Bering Sea, and Gulf of Alaska.

* numbers of testes from Baer (1956).
 () mean values for measurements.

function analysis was conducted to examine this hypothesis. The results of the analysis between *A. fraterculae*, *A. cerorhincae* and *A. l. pacifica* were significant ($F = 69.253$; d.f. = 10 and 150; $p < .001$). A complete separation was achieved between *A. fraterculae* and the other taxa. There was minimal overlap between *A. cerorhincae* and *A. l. pacifica* (fig. 11; table II). Five of the seven variables contributed significantly to the discrimination; the length of rostellar hooks and length of the cirrus sac were most important. The analysis suggested that these nominal taxa represent a complex of three discrete but cryptic species. Data concerning host and geographic distribution presented below further support this contention.

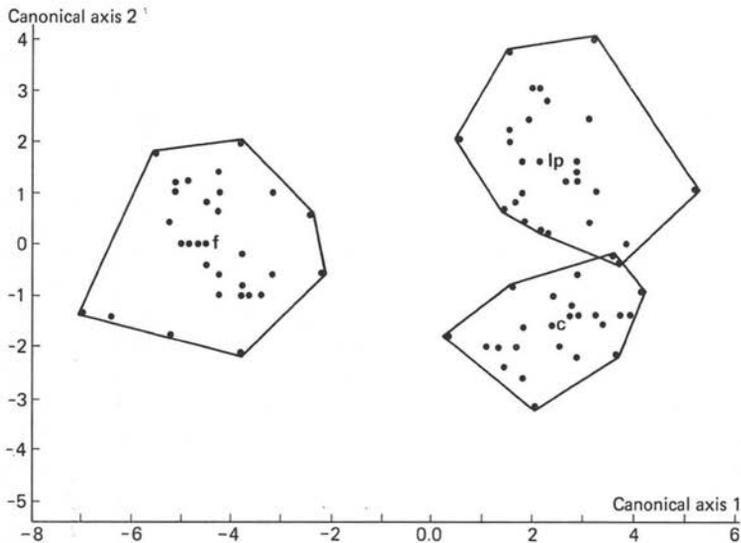


FIG. 11. — Canonical plot from discriminant function analysis for *Alcataenia fraterculae* sp. n. versus *Alcataenia cerorhincae* sp. n. versus *Alcataenia larina pacifica* ssp. n. Centroids are indicated for each: f = *A. fraterculae*; c = *A. cerorhincae*; and lp = *A. l. pacifica*.

Although other species of *Alcataenia* are known from alcids, none has previously been described from puffins, *Fratercula arctica* (Linnaeus), *F. corniculata*, *F. cirrhata*, and *Cerorhinca monocerata*. Belopol'skaia (1952) reported the cestode *Choanotaenia stercorarium* Baylis, 1919 from common puffins collected in the region of Murmansk in the Soviet Arctic, and Smetanina (1979) reported finding *A. larina* in *Cerorhinca monocerata* collected near Vladivostok, USSR.

Even though *A. fraterculae* has been reported from seven other avian species, it may be considered a host-specific cestode of the horned puffin as evidenced by complete development and egg production being recorded only in this host (according to existing data). Mature specimens of *A. fraterculae* have been found only in one of 121 black-legged kittiwakes collected in the North Pacific (Kodiak Island). Devel-

TABLE II. — Discriminant function computed for *A. l. pacifica* versus *A. fraterculae* versus *A. cerorhincae*.

Variable	Partial F	Character coefficients	
		First canonical Axis (X)	Second canonical Axis (Y)
Hook length	263.1562	-.20647	-.10344
Cirrus sac	64.3255	-.01538	.01041
Mehlis gland	8.1047	.00981	.07404
Vitelline gland	5.5951	.00565	-.00685
Testes #	4.4662	-.01319	-.08441
Constant		26.46968	7.71274

Overall F = 69.253 ; d.f. = 10 and 150 ; $p < .001$.

opment in these specimens appeared to be atypical. In one specimen the numbers of testes ranged from 0-40 ($\bar{X} = 13$) in early mature and mature segments and the cirrus sac was smaller 131-232 μm ($\bar{X} = 167 \mu\text{m}$) than might have been expected. Astrobilate cestodes or recently evaginated cysticercooids found in birds of other species were evidently indicative of new infections or developmental inhibition in hosts which were refractory to infection. In this regard, of 194 tufted puffins from the Aleutian Islands, Bering Sea and Gulf of Alaska, 23 were infected only with undeveloped specimens of *A. fraterculae*. Where other species of seabirds are sympatric with horned puffins during the breeding season, *A. fraterculae* could be acquired incidentally due to exploitation of the same prey-species (Sealy, 1973 ; Ainley and Sanger, 1979). Specimens identified as *A. larina* from common terns, *Sterna hirundo* Linnaeus, and long-tailed jaegers, *Stercorarius longicaudus* Vieillot, in the northern Sea of Okhotsk by Belogurov *et al.* (1968) are probably identical with *A. fraterculae* because of the length (120 μm) of their hooks.

A. cerorhincae is apparently a host-specific cestode of rhinoceros auklets. Although Smetanina (1979) reported finding *A. larina* in 3 of 5 auklets collected near Vladivostok (a description was not included) it seems likely that due to the similarity of *A. cerorhincae* and *A. l. pacifica* these specimens could represent the former. Cestodes indentical to *A. cerorhincae* have not been found in black-legged kittiwakes or horned puffins nor in other seabirds in regions where rhinoceros auklets and these other species are sympatric during the breeding season. Populations of rhinoceros auklets in the zone of sympatry with the primary hosts of *A. fraterculae* and *A. l. pacifica* in southern coastal Alaska and the Aleutian Islands are probably small and sporadically distributed (Sowls *et al.*, 1978). The largest populations of rhinoceros auklets are allopatric to those of horned puffins and black-legged kittiwakes during the breeding season, although there is likely to be substantial overlap due to post-breeding

dispersal during the winter. The life cycle of *A. cerorhincae* is apparently being completed during the breeding season of its host, in areas which are largely allopatric to the distribution of *A. fraterculae* and to a lesser extent to that of *A. l. pacifica*. This is indicated by newly-acquired infections in auklets that were collected in Washington State in July, 1981. Specimens of *A. cerorhincae* from the western Aleutians were from a single subadult bird collected far south of the islands in late June, 1981. It is possible that this bird was not local in origin (*i.e.* derived from a population breeding in the western Aleutians). This might indicate that the primary distribution of *A. cerorhincae* is parapatric to the geographic ranges occupied by *A. fraterculae* and *A. l. pacifica*, and thus to some extent is geographically isolated from the latter species.

The minimum geographic distributions (as indicated by locality of collection) of *A. fraterculae*, *A. cerorhincae*, and *A. l. pacifica* and their primary hosts are shown in figure 12. *Cerorhinca monocerata* (and probably *A. cerorhincae*) has an amphipacific, disjunct distribution, while *Fratercula corniculata* and *A. fraterculae* apparently have a Beringian-amphipacific distribution (Udvardy, 1979). *Rissa tridactyla* has a distribution similar to that of the horned puffin in the North Pacific basin. There are limited data concerning the host distribution of *A. larina* in the North Pacific. It is a characteristic parasite of kittiwakes and has been reported from a wide range of other species of larids (Matevosian, 1963). As a consequence the distribution of this

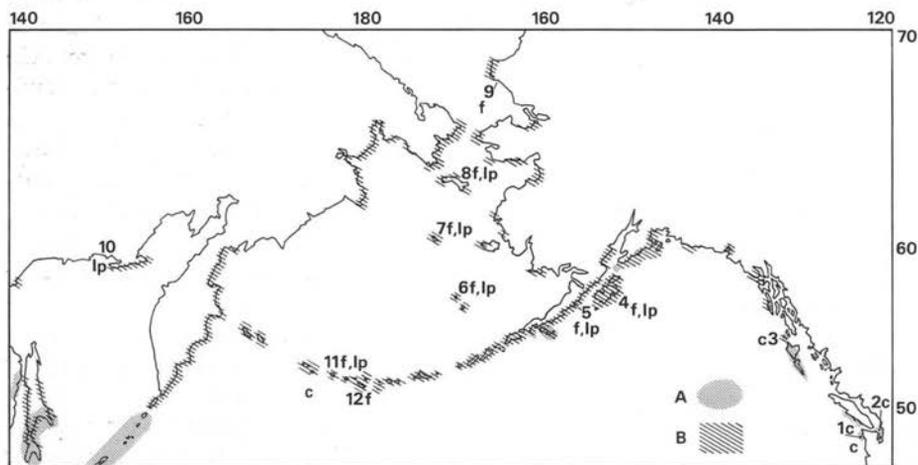


FIG. 12. — Collection localities for *Alcataenia fraterculae* sp. n. (f.), *Alcataenia cerorhincae* sp. n. (c), and *Alcataenia larina pacifica* ssp. n. (lp), and the approximate breeding distributions of their primary hosts. A) Distribution of *Cerorhinca monocerata*. B) Distribution of *Fratercula corniculata* and *Rissa tridactyla pollicaris*. Localities on the map are as follows: 1) Destruction Island, Washington; 2) Protection Island, Washington; 3) Forrester Island; 4) Kodiak Island; 5) Ugaiushak Island; 6) St. Paul Island (Pribilof Islands); 7) St. Matthew Island; 8) St. Lawrence Island; 9) Cape Thompson; 10) Magadan, USSR; 11) Buldir Island; 12) Amchitka Island. Point Barrow, Alaska, a collection locality for *A. l. pacifica* is not shown. Distributions of birds depicted in the figure are based on Dement'ev *et al.* (1951), Kozlova (1957), Sowls *et al.* (1978), and Manuwal and Campbell (1979).

cestode could extend much further south and substantially overlap with that of *A. cerorhincae*. However, based on observations of *A. larina pacifica* in other species of larids in Alaska, it is evident that *Rissa* spp. are probably a more typical host (Hoberg, unpubl. data). The distributions of *Fratercula corniculata* and *Rissa tri-dactyla* are parapatric with that of *Cerorhinca monocerata* with minimal overlap occurring in the Gulf of Alaska, possibly in the Aleutian Islands, and in the southern Sea of Okhotsk, northern Sea of Japan and along the coast of the USSR. *A. cerorhincae* and *A. fraterculae* are endemic to the North Pacific and appear most closely related to *A. l. pacifica*. This suggests that these host-specific parasites of puffins were independently derived from a *larina*-like cestode characteristic of larids. A more detailed treatment of this hypothesis and a discussion of the geographic relationships of these cestodes is in preparation.

The consistency of the form and size of rostellar hooks in specimens of *A. fraterculae* and *A. l. pacifica* in atypical and typical hosts suggests that the observed morphological differences between these species are not host-induced. This is further indicated by host distribution: specimens of *A. l. pacifica* and *A. fraterculae* occur only accidentally in birds other than larids and horned puffins, respectively. In hosts that are atypical for either species, normal development of the strobila is inhibited. Due to the apparent host-specificity of *A. l. pacifica* and *A. fraterculae* it is improbable that specimens of either species could develop to maturity in *Cerorhinca monocerata* but not in other species of alcids.

Baer (1956) noted the difference in some morphological characters between specimens of *A. larina* from the North Atlantic and those described by Schiller (1951) from St. Lawrence Island in the Bering Sea. Apparently, the rostellar hooks were identical but, according to Baer, specimens from the Pacific basin had a greater number of testes, and the genital ducts were between the osmoregulatory canals. Baer suggested that these groups of specimens might be distinguishable at the infra-specific level. Essential features of *A. l. larina* and *A. l. pacifica* are compared along with *A. fraterculae* and *A. cerorhincae* in table I. When comparing the two subspecies there are generally a greater number of testes, 27-59, in specimens of *A. l. pacifica*. The testes could not be accurately counted in Krabbe's or Baer's specimens, but in the former number at least ≥ 20 . The genital ducts are dorsal to the osmoregulatory canals as reported by Baer (1956) but apparently variable in position in specimens from the Pacific. In specimens of *A. l. pacifica* from the northern Bering Sea (Schiller, 1951), eastern Siberia (Iurpalova and Spasskii, 1971) and western Bering Sea (Spasskaia and Kolutolova, 1972) the ducts were between. In those from the Aleutian Islands, Gulf of Alaska, and Sea of Okhotsk they are dorsal to the canals. In addition to differences reported by Baer (1956) specimens of *A. l. pacifica* had a larger cirrus sac and vitelline gland. In specimens of *A. l. pacifica* the cirrus sac was 142-427 μm long ($\bar{X} = 330 \mu\text{m}$) and vitelline gland 202-298 μm long ($\bar{X} = 261$), which are substantially larger than those in Krabbe's and Baer's specimens of *A. l. larina* (174-304 μm , $\bar{X} = 237$; and 174-240 μm , $\bar{X} = 198$ respectively). Joyeux and Baer (1954) and Baer (1956) gave a smaller range of measurements for the cirrus sac, 266-274 μm and 240-288 μm respectively, than that found in the present reexamination.

Alcattaenia larina has not previously been reported from red-legged kittiwakes, *Rissa brevirostris*, glaucous-winged gulls, *Larus glaucescens*, northern fulmars, *Fulmarus glacialis*, and crested and whiskered auklets, *Aethia cristatella* and *A. pygmaea*. Two other species of alcids, black guillemots, *Cepphus grylle* (Linnaeus), and ancient murrelets, *Synthliboramphus antiquus* (Gmelin) have been reported as hosts for this species of cestode (Belopol'skaia, 1952 ; Smetanina, 1979). Species of larids, particularly black-legged kittiwakes and to a lesser extent other gulls are the typical hosts for *A. larina*.

The North Pacific form *A. l. pacifica* is distributionally and morphologically distinct from conspecifics in the Atlantic and in the Atlantic sector of the Arctic basin. There is at present only limited interchange (if any) via dispersal of larids through the Arctic basin. Kittiwakes which were infected with specimens of *A. l. pacifica* at Point Barrow, Alaska were non-breeding birds that had probably dispersed from the south through Bering Strait. The isolation of *A. larina* in the North Pacific, Arctic basin, and North Atlantic during the Pleistocene may have resulted in the morphological divergence which is observed. The philopatric relationships of the typical hosts of *A. l. pacifica* as well as those of *A. fraterculae* and *A. cerorhincae* would have tended to maintain isolation of parasites in particular geographic localities and thus may have been instrumental in speciation of this complex of cryptic taxa and responsible in some part, for the degree of host-specificity observed.

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