COPEPODS AND NEEDLEFISHES: A STUDY IN HOST-PARASITE RELATIONSHIPS

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ABSTRACT

A survey of museum material of the species of needlefishes (Belonidae) found 3,863 copepods of 31 species from 25 species of needlefishes. Twelve species of copepods are described as new; one is included in a new genus (*Acusicola*) of Ergasilidae. The new species are: *Ergasilus spatulus, E. argulus, E. coleus, E. semicoleus, E. inflatipes, Acusicola cunula, Paraergasilus remulus, Parabomolochus ensiculus, P. constrictus, P. sinensis, Nothobomolochus digitatus,* and *Colobomatus goodingi.* In addition, 11 previously described species are reported: *Ergasilus orientalis* Yamaguti, *Acusicola tenax* (Roberts), *Parabomolochus bellones* (Burmeister), *Nothobomolochus gibber* (Shiino), *Caligus tylosuri* (Rangnekar), *C. belones* Krøyer, *C. malabaricus* Pillai, *Caligodes laciniatus* (Krøyer), *Lernanthropus belones* Krøyer, *L. tylosuri* Richiardi, and *Lernaeolophus sultanus* (Milne-Edwards). Eight additional species were not named or described in detail because of insufficient material. The copepod fauna of each species of needlefish is listed separately after the taxonomic descriptions of the copepods.

Eight questions regarding needlefishes and their copepod parasites are considered:

(1) Host specificity. The ergasilid and bomolochid copepods show little host specificity; *Caligodes laciniatus, Lernanthropus belones,* and *L. tylosuri* are restricted to certain groups of needlefishes.

(2) Distributions. Maps of the ranges of the common species of copepods and their needlefish hosts show general agreement; however, *Colobomatus goodingi* is restricted to warmer waters than its hosts.

(3) Intraspecific variation in copepods. Total lengths of female *Caligodes laciniatus* and *Lernanthropus belones* were related to host species and geography, respectively. Lengths of setae in *Parabomolochus bellones* also varied geographically rather than by host species.

(4) Relative evolutionary rates. The four worldwide species of needlefishes appear to be more highly differentiated than the four worldwide species of copepods. One widespread copepod, *Parabomolochus bellones,* has given rise to *P. constrictus* in the eastern Pacific, whereas the needlefish hosts have differentiated to only the subspecific level.

(5) Effect of host size. Specialized copepods (those possessing holdfasts) are attached to needlefishes of larger than average size; generalized copepods that lack these adaptations are found on average-sized needlefishes.

(6) Competition between copepods. Individual needlefishes infested with several species of copepods have copepods living in different ecological niches on the host. Distributional evidence indicates that the widespread *Parabomolochus bellones* is being replaced in the Indo-West Pacific by *P. sinensis* and two species of *Nothobomolochus.*

(7) Variation in infestation in time and space. The relative infestation of Bahamian *Strongylura notata* with *Colobomatus goodingi* seems to be increasing. Geographic differences in infestation of widespread hosts were prominent in *Caligodes laciniatus, Lernanthropus tylosuri,* and *Colobomatus goodingi.*

(8) Nature of the symbiotic relationship. The copepods with holdfasts appear to be doing at least mechanical damage to their hosts; the bomolochids appear to be commensal or even mutualistic.

This paper is a cooperative undertaking by a specialist in a parasite group (Cressey) and one in the host group (Collette). Misidentification of host animals has marred most past attempts of parasitologists to analyze collection and literature data. Identifications of hosts have rarely been authoritative because only occasionally has a specialist for the hosts been consulted. We have not used literature records in our analysis because the resulting misidentifications in the literature cloud

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the analysis of host-parasite relations and because our material is so abundant. In this paper we present the results of our survey of the parasitic copepods found on the needlefishes (Belonidae). Cressey is responsible for the identifications and descriptions of the parasitic copepods, and Collette is responsible for the identifications of the hosts and most of the collection data. Both authors are responsible for the interpretations and analysis of data.

We believe a host specialist and a parasite specialist must work together to answer the questions we consider here. Data on host distribution, ecology, and evolution can then be integrated with parasite data. Only in this way can we solve some of the important problems concerning the biology and evolution of host and parasite.

We have considered the following questions about needlefishes and their copepod parasites:

1. To what extent are copepods host-specific?
2. How do the distributions of hosts and parasites compare?
3. Is intraspecific variation in copepods related to host influence, ecology, or geography?
4. What are the relative rates of evolution of host and parasite?
5. Do larger host individuals have a greater copepod fauna?
6. Is there competition among different species of parasites on the same hosts?
7. How do the relative infestations of a given host species by a given copepod species compare in time and space? (We use the word infestation as the appropriate term for an ectoparasite or commensal that is a nonmultiplying invader as opposed to a multiplying one.)
8. Are the copepods associated with needlefishes parasitic in the strict sense or are some of them commensal or mutualistic?

This paper consists of three major parts: first, a taxonomic description of copepods found on needlefishes; second, an account of the copepods we found on each species of needlefish; and third, a consideration of the questions posed above on the basis of the data presented in the first two sections.

We have not subjected our data to sophisticated statistical tests for several reasons. The needlefish material available in museum collections is strongly biased as regards such things as locality, number of specimens, and dates of collection. Then a further bias has been introduced by selecting certain needlefishes to examine. Ideally, one should plan a sampling program for needlefishes in time and space and then subsample the hosts, especially with regard to size. But we have used historic collections (or accumulations) so we believe it is preferable to present tabular summaries or graphs of what we found and then to try to explain the results. Our use of museum collections of needlefishes has certainly biased our results in one other respect—because many external forms are not firmly attached we have found far fewer external copepod parasites (such as *Caligus*) than we would have found on fresh material.

MATERIALS AND METHODS

The 28 species of epipelagic fishes composing the needlefish family Belonidae are found in fresh waters, estuaries, and marine habitats both inshore and offshore. Four species are worldwide; the other 24 species have more restricted distributions. Needlefishes vary in maximum body length from 42 mm. for the two neotenic South American fresh water species of *Belonion* to 950 mm. for the worldwide *Tylosurus acus*. While preparing a monograph on the Belonidae, Collette looked for copepods on 2,720 needlefishes from more than 800 collections. Copepods were found on all but three species—the rare South African *Petalichthys capensis*, of which only a single specimen was examined, and the two species of *Belonion*. The nomenclature used for the needlefishes in this paper is based on Collette and Berry (1965), Parin (1967), and Collette and Parin (1970).

The needlefishes examined for copepods are housed in most of the major fish collections in the world. Abbreviations of these collections are listed below. Full data on each host collection are not included in this paper but are available from Collette:

AMNH: American Museum of Natural History, New York, N.Y.
ANSP: Academy of Natural Sciences, Philadelphia, Pa.
BMNH: British Museum (Natural History), London, England
BOC: Bingham Oceanographic Collection, Peabody Museum, Yale University, New Haven, Conn.

CAS: California Academy of Sciences, San Francisco, Calif.
CBAT: Centro de Biologia Aquática Tropical, Lisboa, Portugal
CROA: Centres Recherches Océanographique, Abidjan, Côte d'Ivoire
CU: Cornell University, Ithaca, N.Y.
FMNH: Field Museum of Natural History, Chicago, Ill.
FSU: Florida State University, Tallahassee, Fla.
GCRL: Gulf Coast Research Laboratory, Ocean Springs, Miss.
HUJ: Hebrew University, Jerusalem, Israel
IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
ISFRS: Israel Sea Fisheries Research Station, Haifa, Israel
LACM: Los Angeles County Museum, Los Angeles, Calif.
MACN: Museo Argentina Ciencias Naturales, Buenos Aires, Argentina
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MMF: Museu Municipal do Funchal, Madeira
MNHN: Muséum National d'Histoire Naturelle, Paris, France
MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium
SAM: South African Museum, Cape Town, South Africa
SIO: Scripps Institution of Oceanography, La Jolla, Calif.
SU: Stanford University, Division of Systematic Biology, Stanford, Calif.
TU: Tulane University, New Orleans, La.
UCLA: University of California, Los Angeles, Calif.
UF: University of Florida, Gainesville, Fla.
UMML: University of Miami Marine Laboratory, Miami, Fla.
UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Mich.
UPR: University of Puerto Rico, Mayaguez, P.R.
USNM: U.S. National Museum, Washington, D.C.

Examination of these hosts yielded 488 collections of parasitic copepods containing 3,863 copepods (table 1). They represent 23 species (12 described for the first time herein) plus 8 more that were not described or assigned specific names because of the lack of sufficient material. All copepods are preserved in 70 percent ethyl alcohol and have been deposited in the USNM collections.

Type-specimens of the following copepod species were examined: *Caligus belones* Krøyer, *Lernanthropus belones* Krøyer, *Lernanthropus chlamydotes* Wilson, and *Caligodes megacephalus* Wilson.

In the formulas for spines and setae included in the descriptions, Roman numerals refer to spines and Arabic to setae.

The large numbers of copepods collected made it possible to evaluate statistically the variation of a particular character within each of three species: *Caligodes laciniatus*, *Parabomolochus bellones*, and *Lernanthropus tylosuri*. We compared host influence with geographical influence in these three species. We could have expanded such variational studies with our collections; however, this was not the primary purpose of the paper.

ACKNOWLEDGMENTS

We thank the curators of the many collections housing the needlefishes that we examined for copepods. Bruce Barrett picked copepods off many needlefishes while working as a volunteer in the summer of 1967. Robert Mathewson, Director of the Lerner Marine Laboratory, Bimini, Bahamas, and Jack Rudloe, Gulf Specimen Company, Panacea, Fla., sent us *Colobomatus*-infested specimens of *Strongylura notata* and *S. marina*. N. V. Parin, Institute of Oceanology, Moscow, sent us our first copepods from *Tylosurus choram*. Clyde S. Dawe, Laboratory of Pathology, National Cancer Institute, Bethesda, Md., provided us with a histopathological description of the *Colobomatus* swellings. Gerhard Gsell, also of the Laboratory of Pathology, prepared the photomicrographs (figs. 172–174). Mildred H. Carrington made the drawings of *S. notata* (fig. 170), *Caligodes* (fig. 146), and *Colobomatus* (fig. 171). Martin L. Wiley and Samuel Atsaides assisted with the statistical analyses. Thomas E. Bowman, Daniel M. Cohen, and Sneed B. Collard read the manuscript and made valuable suggestions.

TABLE 1.—*Summary of numbers of copepods found on each of the 28 species of needlefishes*

Needlefish species	Specimens examined	*Parabomolochus*				*Nothobomolochus*		*Caligodes lacinulatus*	*Lernanthropus*		*Colobomatus goodingi*	*Lernaeolophus sultanus*	*Caligus* spp.	*Ergasilus*						*Acusicola*		*Paraergasilus remulus*	Species of copepods	Copepods
		bellones	*constrictus*	*ensiculus*	*sinensis*	*gibber*	*digitatus*		*tylosuri*	*belones*				*spatulus*	*argulus*	*coleus*	*scmicoleus*	*orientalis*	*inflatipes*	*tenax*	*cunula*			
		Number																						
Ablennes hians	251	160	35	----	2	60	------	103	130	4	31	----	14	----	----	----	----	----	----	------	------	----	9	539
Belone belone	77	40	----	----	----	1	------	----	----	------	----	----	1	----	----	----	----	----	----	------	------	----	3	42
B. svetovidovi	15	1	----	----	----	4	------	----	----	------	----	----	----	----	----	----	----	----	----	------	------	----	2	5
Belonion apodion	15	----	----	----	----	------	------	----	----	------	----	----	----	----	----	----	----	----	----	------	------	----	0	0
B. dibranchodon	7	----	----	----	----	------	------	----	----	------	----	----	----	----	----	----	----	----	----	------	------	----	0	0
Lhotskia gavialoides	24	20	----	----	----	------	------	22	------	------	----	----	----	----	----	----	----	----	----	------	------	----	2	42
Petalichthys capensis	1	----	----	----	----	------	------	----	----	------	----	----	----	----	----	----	----	----	----	------	------	----	0	0
Platybelone argalus	487	48	65	----	----	157	------	1	1	2	----	----	72	----	----	----	----	----	----	------	------	----	7	346
Potamorrhaphis guianensis	63	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	9	----	------	------	----	1	9
Pseudotylosurus angusticeps	25	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	----	----	------	8	----	1	8
Strongylura anastomella	33	70	----	----	----	------	------	----	65	8	----	----	1	----	----	----	----	----	----	------	------	----	4	144
S. exilis	97	----	20	14	----	------	------	----	8	107	1	----	1	----	----	----	----	----	----	------	------	----	6	151
S. fluviatilis	33	----	----	----	----	------	------	----	------	------	----	----	----	----	58	----	----	----	----	------	------	----	1	58
S. incisa	75	6	----	----	----	------	------	----	1	16	----	----	3	----	----	----	----	19	----	------	------	----	5	45
S. krefftii	44	----	----	----	----	------	------	----	------	------	----	----	----	----	----	----	36	----	----	------	------	----	1	36
S. leiura	49	1	----	----	----	------	5	39	4	------	----	----	----	----	----	----	----	----	----	------	------	----	4	49
S. marina	316	119	----	----	----	------	------	----	5	172	6	1	----	23	----	----	----	----	----	203	------	----	7	529
S. notata	200	161	----	----	----	------	------	----	------	143	42	----	3	----	----	----	----	----	----	------	------	----	4	349
S. scapularis	38	----	15	139	----	------	------	----	------	12	----	----	----	----	48	----	----	----	----	------	------	----	4	214
S. senegalensis	27	5	----	----	----	------	------	----	------	------	----	----	----	----	----	----	----	----	62	------	------	----	2	67
S. strongylura	69	2	----	----	13	------	19	----	5	21	----	----	----	----	----	28	----	----	----	------	------	----	6	88
S. timucu	281	172	----	----	----	------	------	----	13	199	31	----	----	6	----	----	----	----	----	------	------	----	5	421
S. urvillii	21	1	----	----	----	------	------	----	1	------	----	----	1	----	----	4	----	----	----	------	------	----	4	7
Tylosurus acus	147	14	31	----	----	1	------	74	53	------	22	2	7	----	----	----	----	----	----	------	------	----	8	204
T. choram	18	----	----	----	----	------	------	7	1	------	----	----	1	----	----	----	----	----	----	------	------	----	3	9
T. crocodilus	212	25	12	----	----	12	1	128	185	------	57	----	17	----	----	----	----	----	----	------	------	----	8	437
T. punctulatus	31	----	----	----	----	------	3	----	2	5	----	----	----	----	----	----	----	----	----	------	------	----	3	10
Xenentodon cancila	65	----	----	----	----	------	------	----	------	------	----	----	----	----	----	51	----	----	----	------	------	3	2	54
Total number of specimens	2,721	845	178	153	15	235	28	374	474	689	190	3	121	29	106	83	36	28	62	203	8	3	XX	3,863
Total number of species	28	16	6	2	2	6	4	7	14	11	7	2	11	2	2	3	1	2	1	1	1	1	21+	XX

NEEDLEFISH COPEPODS

The accounts of the copepods found on needlefishes are arranged in three orders: Cyclopidea, Caligidea, and Philichthyidea.

Order Cyclopidea

Two families of cyclopid copepods were represented in the collections: Ergasilidae and Bomolochidae.

FAMILY ERGASILIDAE

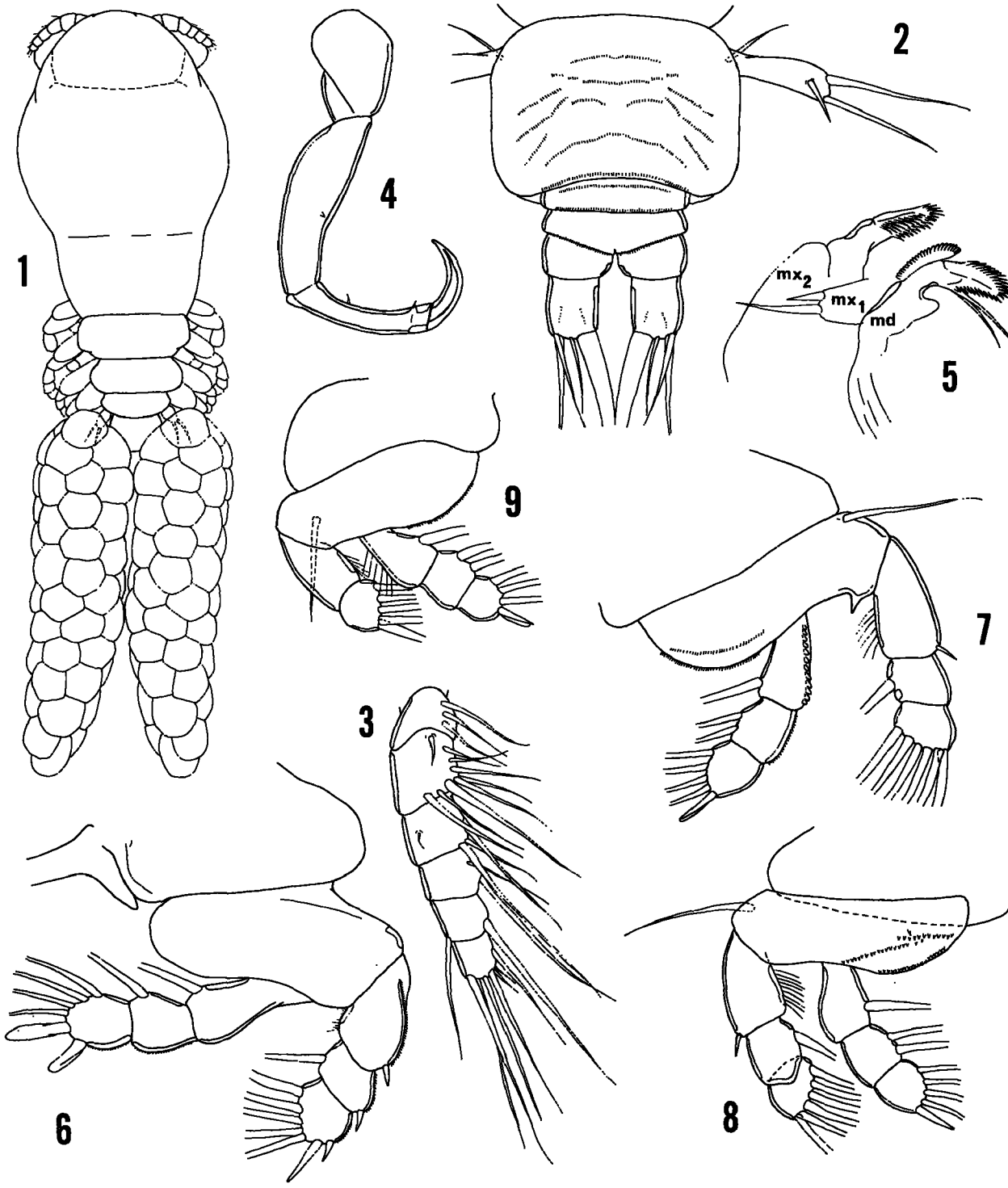
Eleven species of ergasilids were collected representing three genera; *Ergasilus*, *Paraergasilus*, and *Acusicola*, new genus. New species are described in each genus.

Ergasilus spatulus Cressey, New Species

Figures 1 to 9

Specimens studied.—Twenty-nine females from two collections from North America. The first collection containing the holotype female (USNM 125675) and 13 paratype females (USNM 125676) parasitic on the gill filaments of *Strongylura marina* (TU 6950) caught in Lake Pontchartrain, La. The second collection of six females is from the gill filaments of *S. timucu* and *S. marina* caught at Tortuguero, Costa Rica.

Female.—Body form as in figure 1. Total length 725 μ. Greatest width 363 μ measured at widest part of cephalon. First thoracic segment partially fused with head, composing cephalon. Cephalon 500 μ



FIGURES 1–9.—*Ergasilus spatulus*, new species, female. 1. Dorsal view. 2. Genital segment and abdomen including fifth leg, ventral view. 3. First antenna. 4. Second antenna. 5. Mouth parts (mandible, md; first maxilla, mx_1; second maxilla, mx_2). 6. First leg. 7. Second leg. 8. Third leg. 9. Fourth leg.

long, nearly 70 percent of total body length. Free thoracic segments, each succeeding one narrower than the one anterior to it. Genital segment (fig. 2) slightly wider than long (96 μ by 88 μ); rows of spinules on ventral surface as indicated in figure. Abdomen 3-segmented; each segment somewhat narrower than preceding one; terminal segment divided nearly entire length along medial anteroposterial line. Caudal rami nearly square (23 μ by 23 μ), with four terminal setae; innermost seta longest (190 μ) with base about half as wide as ramus.

First antenna (fig. 3) 6-segmented; all segments of nearly equal length, second slightly longer than others. Second antenna (fig. 4) in form of a claw; segments measure 89 μ, 221 μ, 118 μ, and 110 μ, respectively, devoid of ornamentation. Mouth parts (fig. 5) small and like other species of genus. Maxilliped absent.

Legs 1 to 4 biramose. Leg 1 (fig. 6) rami 3-segmented; two outer spines on endopod last segment spatulate. Leg 2 (fig. 7) rami 3-segmented; row of blunt spinules along outer edge of endopod first segment; spinelike process near inner edge of exopod on coxopod. Leg 3 (fig. 8) rami 3-segmented; coxopod with rows of spinules as indicated in figure. Leg 4 (fig. 9) exopod 2-segmented; endopod 3-segmented. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	I:0	0:1	I:0	0:1	I:0	0:1	0:0	0:1
Seg. 2.....	I:1	0:1	0:1	0:2	0:1	0:2	5	0:2
Seg. 3.....	II:5	II:4	6	I:4	6	I:4	---	I:3

Leg 5 (fig. 2) a well-developed free segment bearing two terminal setae, one shorter subterminal seta, and one seta near base. Leg 6 absent.

Egg sacs long (640 μ), containing 50 to 60 eggs.

Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *spatulus* is Latin for "a broad, flat tool" and refers to the nature of the endopod spines of leg 1.

Remarks.—This species may be separated from the other species of the genus by the row of spatulate spinules on the first endopod segment of leg 2 and by the broad spines on the last endopod segment of leg 1. This species appears to be very close to *Ergasilus arthrosis* Roberts.

Ergasilus argulus Cressey, New Species

Figures 10 to 16

Specimens studied.—Three collections containing 106 females from the Dagua River in Colombia, South America. The first collection containing the holotype female (USNM 125677) and 57 paratype females (USNM 125678) removed from the outer surface of the gill filaments of 5 *Strongylura fluviatilis* (CAS 11606). The other two collections from the gill filaments of *S. scapularis* caught in the mouth of the same river, 44 from 5 specimens (FMNH 59434–8) and 4 from 1 specimen (USNM 203520).

Female.—Body form as in figure 10. Total length 660 μ and greatest width 413 μ. Cephalon somewhat longer than wide (472 μ by 413 μ) with anterior portion subdivided. First thoracic segment fused with head. Width of free thoracic segments 218 μ, 160 μ, and 112 μ, respectively. Genital segment (fig. 11) 94 μ long and 106 μ wide with irregular row of spinules along posterior ventral border. Abdomen 3-segmented, each segment with row of spinules along posterior ventral border. Caudal rami nearly square, with four setae; longest seta 235 μ long; all setae sparsely plumose; short row of spinules on posterior ventral inner corner.

First antenna (fig. 12) 6-segmented; each segment with naked setae as in figure; segments measure 22 μ, 36 μ, 20 μ, 15 μ, 22 μ, and 18 μ in length, respectively. Second antenna (fig. 13) 4-segmented and in form of a claw; segments measure 195 μ, 384 μ, 295 μ, and 177 μ in length, respectively. Other mouth parts as in previous species. Maxillipeds absent.

Legs 1 to 4 biramose. Leg 1 (fig. 14) exopod 3-segmented; endopod 2-segmented; rami armed as in figure. Leg 2 (fig. 15) both rami 3-segmented, interpodal plate with row of prominent spinules along posterior border; both rami armed as in figure. Leg 3 same as leg 2. Leg 4 (fig. 16) exopod 2-segmented; endopod 3-segmented; rami armed as in figure; interpodal plate with spinules but less prominent than in legs 2 and 3. All setae on rami of legs 1 to 4 plumose. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	1:0	0:1	1:0	0:1	1:0	0:1	0:0	0:1
Seg. 2.....	0:1	II:5	0:1	0:2	0:1	0:2	I:5	0:2
Seg. 3.....	II:5	-----	I:6	I:4	I:6	I:4	------	4

Leg 5 (fig. 11) a small knob bearing two naked setae. Leg 6 absent.

Egg sacs about 400 μ long, containing 28 to 32 eggs.

Color in life unknown; preserved material with purplish opaque spots scattered along middorsal line of body.

Male.—Unknown.

Etymology.—The specific name *argulus* refers to the resemblance of the cephalon to the branchiuran genus *Argulus*.

Remarks.—This species may be separated from other species of the genus with spinules on the intercoxal plates by a combination of the shape of the cephalon, shape of the egg sacs, and the rows of broad spinules on the genital and abdominal segments.

***Ergasilus coleus* Cressey, New Species**

Figures 17 to 25

Specimens studied.—A single collection containing 4 females from *Strongylura urvillii* from the Philippines; three collections from *S. strongylura*, one with 4 females from Cagayan de Misamis, Mindanao, Philippines, one with 6 females from Sandakan Bay, Borneo, and one with 16 females from Porto Novo, Madras, India; two collections from *Xenentodon cancila*, one from USNM 149701 containing the holotype female (USNM 125679) and 10 paratype females (USNM 125680) from Travancore, India, and the other from SU 34948 with 40 females from Calcutta, India.

Female.—Body form as in figure 17. Total length 530 μ. Greatest width 210 μ. Cephalon subdivided; anterior portion bearing first and second antennae, posterior portion bearing mouth parts and first two thoracic legs. Thoracic segments bearing legs 3, 4, and 5 free. Genital segment (fig. 18) about twice as long as wide with thin wrinkled surface inconspicuously sclerotized. Abdomen 2-segmented; sclerotization heavier than in genital segment; articulation between segments obscure. Caudal rami small, nearly square, inner posterior corners produced to form stout spinelike processes; each ramus bearing three setae as indicated in figure.

First antenna (fig. 19) 6-segmented, armed as in figure. Second antenna (fig. 20) 4-segmented; first three segments enclosed in hyaline wrinkled sheath; claw of antenna free of sheath but piercing sheath of opposite second antenna as the two appendages encircle gill filament of host (sheath may provide soft surface for claw of opposite member to penetrate to secure copepod to host's gill). Mandible, first maxilla, and second maxilla (fig. 21) very small; mandible and second maxilla easily seen under oil immersion, but first maxilla reduced to a very small knob between these two and bearing a single short seta. Maxilliped absent.

Legs 1 to 4 biramose. Leg 1 (fig. 22) rami 3-segmented, outer distal spine on corner of exopod first segment very small. Leg 2 (fig. 23) rami 3-segmented; devoid of spines, setae arranged as in figure. Leg 3 (fig. 24) rami 3-segmented; devoid of spines as in leg 2, bearing one additional seta on exopod last segment; outer seta on endopod last segment short. Leg 4 (fig. 25) exopod 2-segmented; endopod 3-segmented; rami armed as in figure. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	0:0	0:1	0:0	0:1	0:0	0:1
Seg. 2	0:1	0:1	0:1	0:1	0:1	0:1	5	0:2
Seg. 3	II:5	II:3	4	5	5	4	.....	4

Leg 5 (see fig. 18) a free segment with two terminal setae and one seta near base (a subterminal seta could not be found). Segment bearing leg 5 fused with genital segment. Leg 6 absent.

Egg sac 480 μ long, bearing about 40 eggs.

Color in life unknown.

Male.—Unknown.

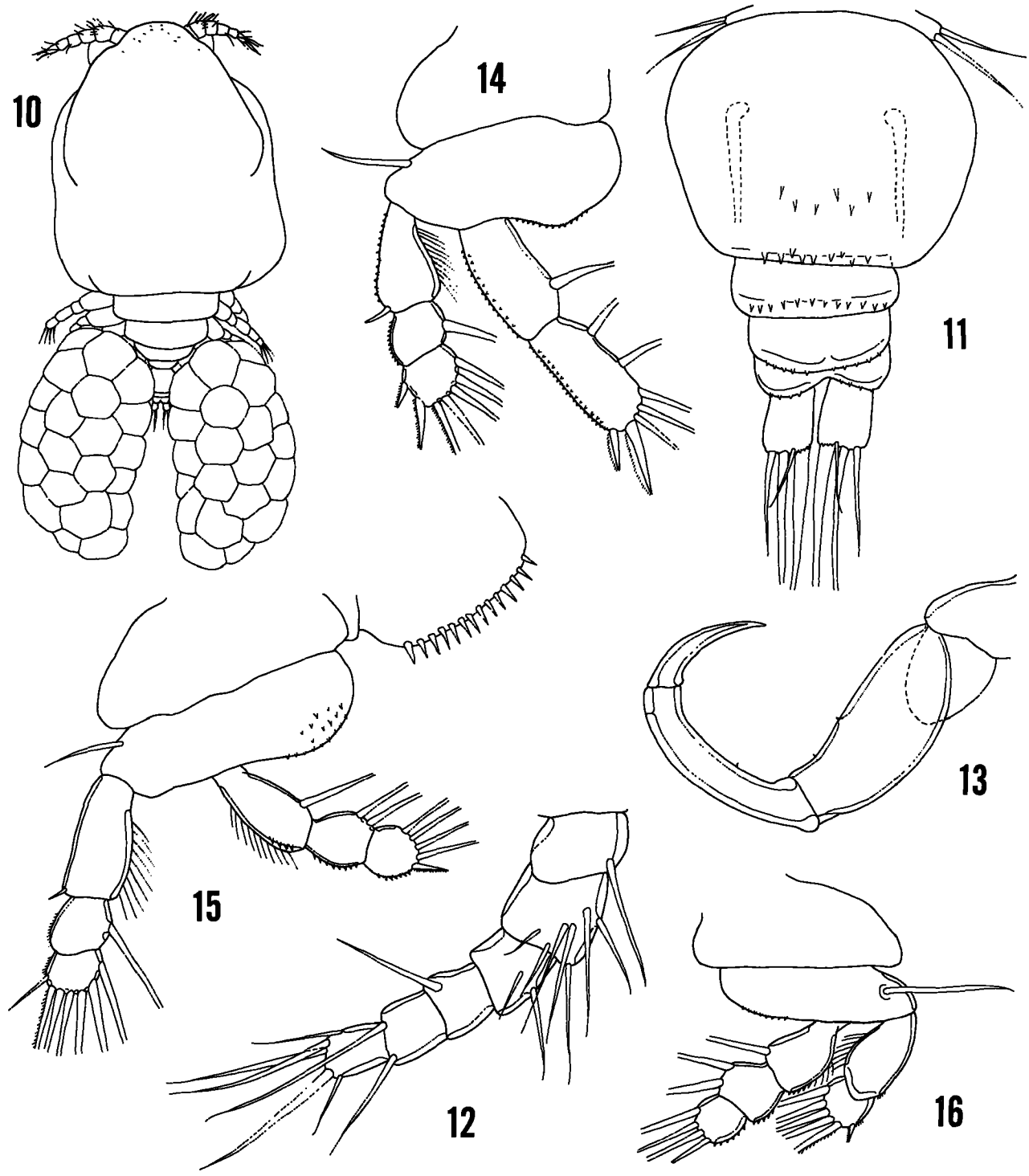
Etymology.—The specific name *coleus* is Latin for "sheath" and refers to the nature of the second antenna.

Remarks.—This species may be separated from all known species of *Ergasilus*, except *E. amplectens* Dogiel and Akhterov (1952) by the presence of the sheath surrounding the second antenna. It differs from *amplectens* by the nature of the genital segment; in *amplectens* the genital segment and abdomen are well defined, whereas in *coleus* the genital segment appears to be encased in a sheath similar to that on the second antenna.

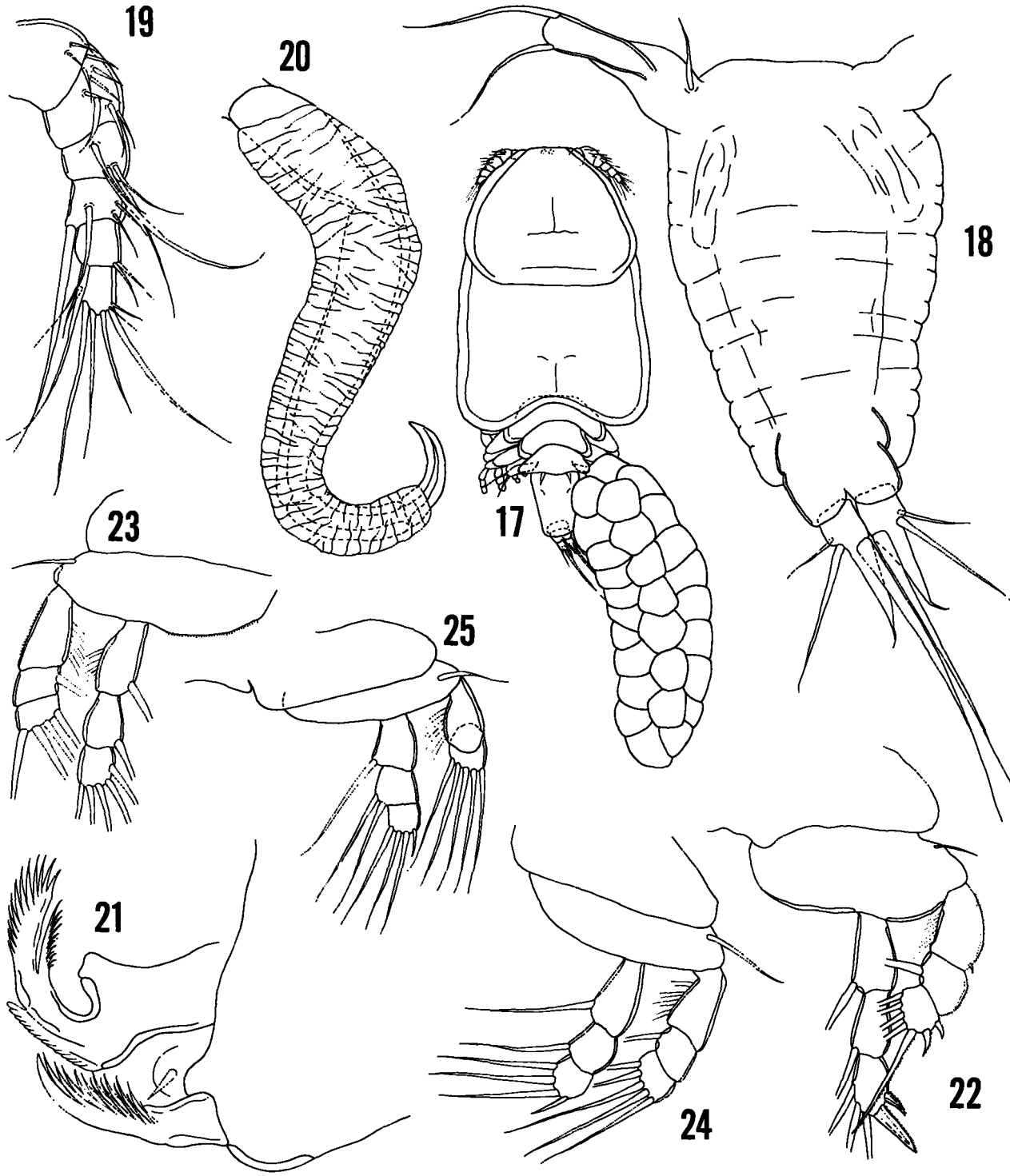
***Ergasilus semicoleus* Cressey, New Species**

Figures 26 to 32

Specimens studied.—A single collection from the gill filaments (mostly in upper branchial area—between demibranchs of 4th gill arch) of six *Strongylura krefftii* (USNM 173999) from a large



FIGURES 10–16.—*Ergasilus argulus*, new species, female. 10. Dorsal view. 11. Genital segment and abdomen, including fifth leg, ventral view. 12. First antenna. 13. Second antenna. 14. First leg. 15. Second leg. 16. Fourth leg.



FIGURES 17–25.—*Ergasilus coleus*, new species, female. 17. Dorsal view. 18. Genital segment and abdomen, including fifth leg, ventral view. 19. First antenna. 20. Second antenna. 21. Mouth parts. 22. First leg. 23. Second leg. 24. Third leg. 25. Fourth leg.

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billabong at Oenpalli on the Alligator River, Arnhem Land, Australia. Holotype female (USNM 125681) and 35 paratype females (USNM 125682).

Female.—Body form as in figure 26. Total length 725 μ. Greatest width 295 μ measured at widest part of posterior portion of cephalon. Cephalon subdivided as in *E. coleus*, but posterior lobe bearing mouth parts and first thoracic legs only. Thoracic segments bearing legs 2, 3, 4, and 5 free. Genital segment (fig. 27) as wide as long (81 μ by 81 μ). Abdomen 3-segmented, each segment somewhat narrower than preceding. Caudal rami short, inner distal corner produced to form stout spine-like process; each ramus with three additional setae.

First antenna (fig. 28) 6-segmented and armed as in figure. Second antenna (fig. 29) 4-segmented; second segment enveloped in a thin sheath, surface of sheath somewhat wrinkled in appearance (not as much as in *E. coleus*). Second antennae completely encircle a gill filament of host. Mouth parts as in previous species. Maxillipeds absent.

Legs 1 to 4 biramose. Leg 1 (fig. 30) rami 3-segmented, armed as in figure. Leg 2 (fig. 31) rami 3-segmented, armed as in figure. Leg 3 similar to leg 2 except last exopod segment with six setae and last endopod segment with four setae and one spine. Leg 4 (fig. 32) exopod 2-segmented; endopod 3-segmented, armed as in figure. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	I:0	0:0	I:0	0:0	I:0	0:0	I:0	0:1
Seg. 2.....	0:1	0:1	0:1	0:1	0:1	0:1	5	0:2
Seg. 3.....	II:6	II:5	5	I:3	I:4	6	.....	I:3

Leg 5 (see fig. 27) a free segment bearing two terminal setae—one subterminal and one near base of free segment. Leg 6 absent.

Egg sacs 500 μ long and containing 25 to 30 eggs.

Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *semicoleus* is Latin for "half sheath" and refers to the nature of the second antenna.

Remarks.—This species differs from all other known species in having half of the second antenna encased in a sheath. It seems to be closely related to *E. coleus* and *E. amplectens* based on the presence of this sheath and other characters common to all three species.

Ergasilus inflatipes Cressey, New Species

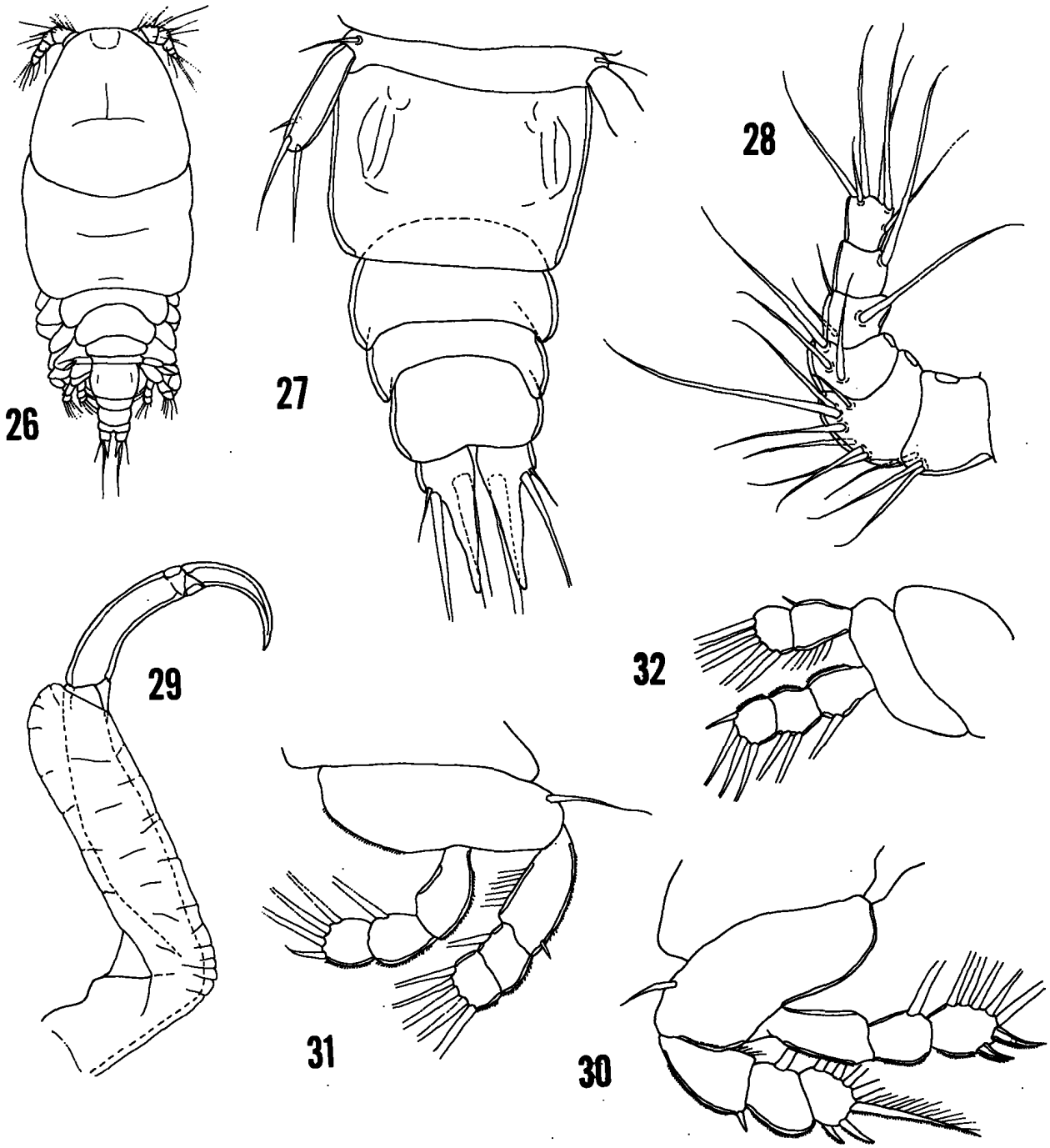
Figures 33 to 41

Specimens studied.—Three collections containing 28 females from *Strongylura senegalensis* from the Volta River, Ghana, and a single collection with 33 females from the same host from Ebzie Lagoon, Ivory Coast. Holotype female (USNM 125683) and 8 paratype females (USNM 125684) from one of the Ghana specimens.

Female.—Body form as in figure 33. Total length 625 μ. Greatest width 354 μ measured at widest part of cephalon. Cephalon not subdivided dorsally as in previous two species. Thoracic segments bearing legs 1 to 5 free, each one narrower than preceding segment. Genital segment (fig. 34) slightly wider than long (88 μ by 74 μ). Abdomen (fig. 34) 3-segmented; anterior two segments each with two interrupted transverse rows of spinules and last abdominal segment with a row of fine spinules along posterior border, all on ventral surface. Caudal rami short, about as wide as long and bearing four setae, innermost considerably longer and wider at base than other three.

First antenna (fig. 35) 6-segmented; first two segments incompletely divided, each segment armed as in figure with a plumose seta present on each of the last three segments. Second antenna (fig. 36) in shape of claw with no distinguishing characters. Mouth parts as in figure 37; mandible with single seta near base of terminal process; first maxilla a small lobe with three setae; second maxilla with single seta on terminal segment near base of spinose tip. Maxillipeds absent.

Legs 1 to 4 biramose. Leg 1 (fig. 38) rami 3-segmented, armed as in figure. Leg 2 (fig. 39) rami 3-segmented; coxopod with rows of fine spinules; rami with spines and setae as in figure. Leg 3 identical to leg 2. Leg 4 (fig. 40) exopod 2-segmented; endopod 3-segmented; rami armed as in figure. Leg 5 (fig. 41) with free segment bearing three setae, outer two plumose; single seta near base of free segment. Leg 6 absent.



FIGURES 26–32.—*Ergasilus semicoleus*, new species, female. 26. Dorsal view. 27. Genital segment and abdomen, including fifth leg, ventral view. 28. First antenna. 29. Second antenna. 30. First leg. 31. Second leg. 32. Fourth leg.

Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	1:0	0:1	1:0	0:1	1:0	0:0
Seg. 2	I:1	0:1	0:1	0:2	0:1	0:2	5	0:2
Seg. 3	II:5	II:4	6	I:4	6	I:4	---	I:2

Egg sacs long (650μ), containing about 40 eggs. Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *inflatipes* is Latin for "swollen foot" and refers to the shape of the fifth leg.

Remarks.—This species can be separated from all described species of the genus by the nature of the fifth leg. Yamaguti (1963, p. 28) stated that the first maxilla of *Ergasilus* has two setae; this species has three. It does not seem justifiable to erect a new genus on the basis of this character difference alone but *E. inflatipes* can apparently be further separated from all other species in the genus by this difference.

Ergasilus orientalis Yamaguti

Figure 42

Yamaguti (1939a, p. 393) described *Ergasilus orientalis* from *Acanthogobius flavimanus* (Gobiidae) and *Atherina bleekeri* (Atherinidae) from Japan. A single collection of 19 females of this species from 1 specimen of *Strongylura incisa* (USNM 174005) caught near the mouth of the Emerald River, Groote Eylandt, Arnhem Land, Australia, is reported here, plus a single collection of 9 females from *Potamorrhaphis guianensis* (MCZ 8788) from Gurupá, Brazil, near the mouth of the Amazon River.

Female.—The description provided by Yamaguti is adequate, and, except for a figure of an Australian female (fig. 42) and its measurements, no further description is given here.

Total length 790 μ. Greatest width 325 μ. Cephalon 590 μ long, 325 μ wide. Anterior portion of cephalon separate lobe measuring 230 μ by 230 μ. Egg sacs 725 μ long, containing 50 to 60 eggs.

Remarks.—No differences could be found between the two populations referred to *E. orientalis*. The South American population may represent a separate, apparently identical species.

Ergasilus Sp. A

A single female was collected from the gill filaments of *Strongylura marina* (USNM 114589) from Lake Yzabel, Guatemala; two additional females were collected from the gill filaments of *S. timucu* (USNM 114314) from 20 miles above the mouth of the Río Sarston on the Guatemala-British Honduras border. This copepod appears to be the same as the specimen described and figured by Thomsen (1949) as *E. lizae* from *Mugil braziliensis* from the Río de la Plata near Montevideo, Uruguay. Thomsen's material plus the three specimens reported here probably represents an undescribed species, but it seems best not to name it until more material is available and a complete description can be provided.

Ergasilus Sp. B

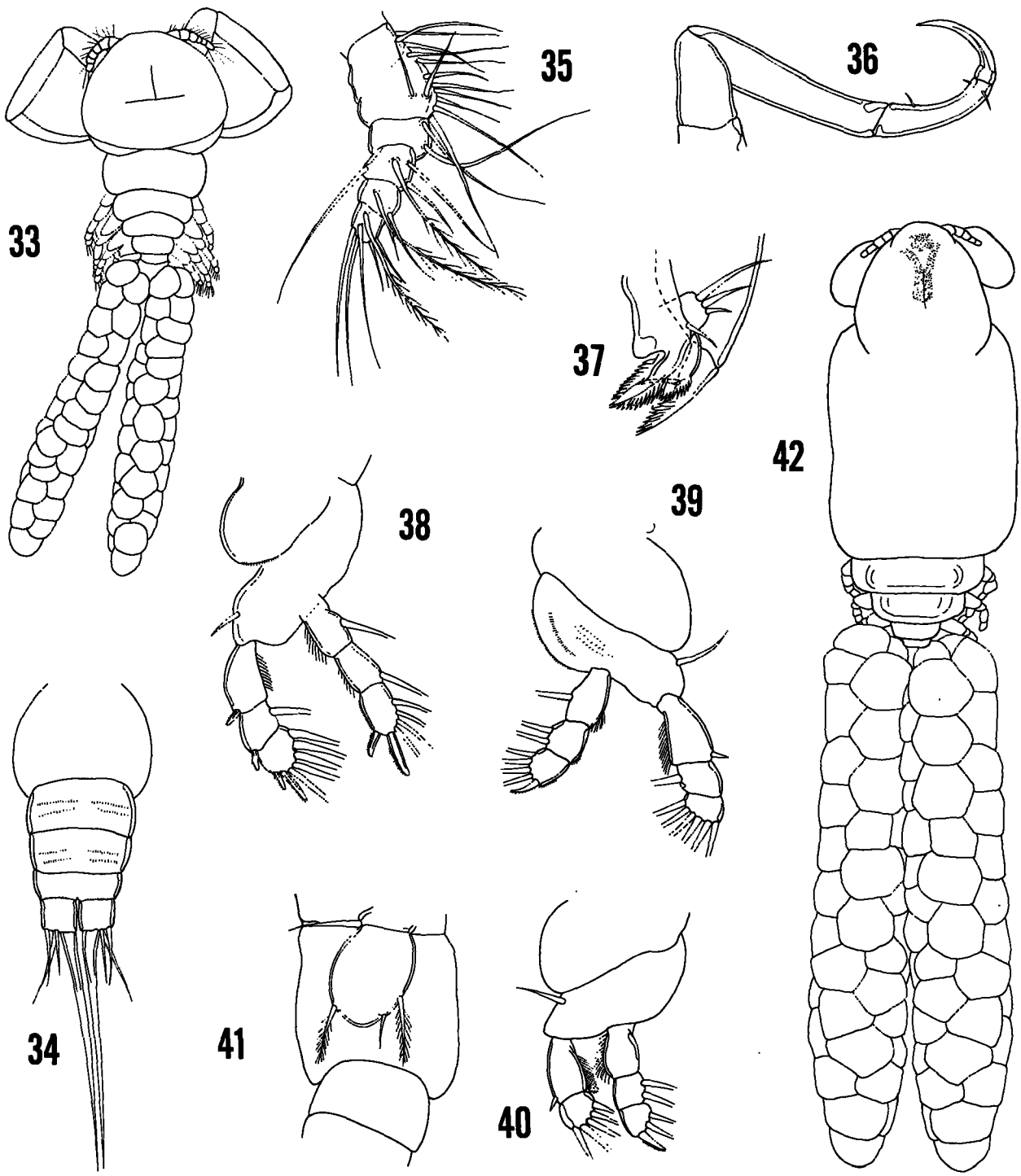
One female from the gill filaments of *Xenentodon cancila* (FMNH 58917) collected in Ceylon. It has not been described as a new species because only one specimen was available. The following characters were noted, however, and are presented to aid future workers.

This species is closely related to *Ergasilus coleus* and *E. semicoleus* described above. The second antenna is sheathed nearly its entire length, but the sheath is not as conspicuous as in *E. coleus*. The degree of segmentation of the abdomen is intermediate between the lack of segmentation in *E. coleus* and the well-defined segments of *E. semicoleus*. In the species discussed here, the three abdominal segments are separate; each of the posterior two segments has a single transverse row of spinules on its ventral surface. The genital segment bears two transverse rows of spinules on its ventral surface. The caudal rami are similar to those of *E. coleus* and *E. semicoleus*.

Ergasilus coleus also was collected from *Xenentodon* in India.

Acusicola Cressey, New Genus

Ergasilidae. Male unknown. Female: Thoracic segments bearing legs 1 to 4 free. Abdomen 3-segmented. First antenna 5-segmented. Second antenna 5-segmented; terminal three segments very short, combined length of all three about one-half length of second segment. Maxilliped absent. Legs 1 to 4 biramose; leg 1 endopod 2-segmented; leg 4 exopod 2-segmented; all other rami 3-segmented. Leg 5 a short papilla at the distal outer



FIGURES 33–42.—*Ergasilus* species. 33–41. *E. inflatipes*, new species, female. 33. Dorsal view. 34. Genital segment and abdomen, ventral view. 35. First antenna. 36. Second antenna. 37. Mouth parts. 38. First leg. 39. Second leg. 40. Fourth leg. 41. Fifth leg, lateral view. 42. *E. orientalis* Yamaguti, female, dorsal view.

border of genital segment bearing a single seta. Leg 6 absent.

Acusicola differs from all other known genera of ergasilids except *Paraergasilus*, *Ergasiloides*, and *Thersitina* by having a 5-segmented first antenna. It differs from *Ergasiloides* by having a 3-segmented abdomen (*Ergasiloides* has only one segment), from *Thersitina* by the presence of maxillipeds in *Thersitina*, and from *Paraergasilus* by the nature of the second antenna.

The generic name is Latin, *acus* for "needle" and *cola* for "inhabitant" and refers to the fact that the first two species of the genus are reported from needlefishes.

Type-species.—*Acusicola tenax*.

***Acusicola tenax* (Roberts)**

Figures 43 to 52

Specimens studied.—A single collection containing 203 females removed from the outer tips of the gill filaments (usually the upper filaments) of 17 *Strongylura marina* (UMMZ 143506) caught at Río de la Pasíon, Peten, Guatemala. An additional collection of two females from one *S. marina* caught at El Quiche, Guatemala.

Female.—Body form as in figure 43. Total length 800 μ; greatest width 225 μ. Thoracic segments bearing legs 1 to 4 separated from head. Thoracic segments decreasing in width from first to fourth. Genital segment about as wide as long (100 μ by 100 μ). Abdomen (fig. 44) 3-segmented; second and third segments only slightly narrower than preceding one. Caudal rami about twice as long as wide (44 μ by 21 μ), with three long terminal setae (longest about 175 μ long) and one short median one; patch of spiniforms on ventral surface near distal end of each ramus.

First antenna (fig. 45) 5-segmented; first segment longest (60 μ) with remaining four each about half as long, armed as in figure. Second antenna (fig. 46) 5-segmented; segments measure 103 μ, 325 μ, 60 μ, 60 μ, and 30 μ, respectively, and unarmed. Mandible (fig. 47) armed as in figure. First maxilla a small knob with two setae between mandible and second maxilla. Second maxilla (fig. 48) with brushlike tip.

Legs 1 to 4 biramose. Leg 1 (fig. 49) exopod 3-segmented, each segment with spinulose outer margins; endopod 2-segmented, each segment with spinulose outer margins and strong clawlike spine on end of terminal segment. Leg 2 (fig. 50) both rami 3-segmented; one spine on outer distal corner of exopod first segment, otherwise armed with setae as in figure. Leg 3 (fig. 51) both rami 3-segmented; spine on outer distal corner of exopod first segment plus weak spine at terminus of endopod, otherwise armed with setae as in figure. Leg 4 (fig. 52) exopod 2-segmented, outermost terminal seta unusually long and conspicuous; endopod 3-segmented with weak spine on outer corner of terminal segment, otherwise armed with setae as in figure.

Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	0:0	0:0
Seg. 2	0:1	I:4	0:1	0:2	0:1	0:2	4	0:2
Seg. 3	I:6	---	6	5	6	5	...	I:3

Leg 5 a small papilla bearing one seta near anterior outer corners of genital segment. Leg 6 absent.

Egg sac about 500 μ long, bearing 28 to 32 eggs.

Color in life unknown.

Male.—Unknown.

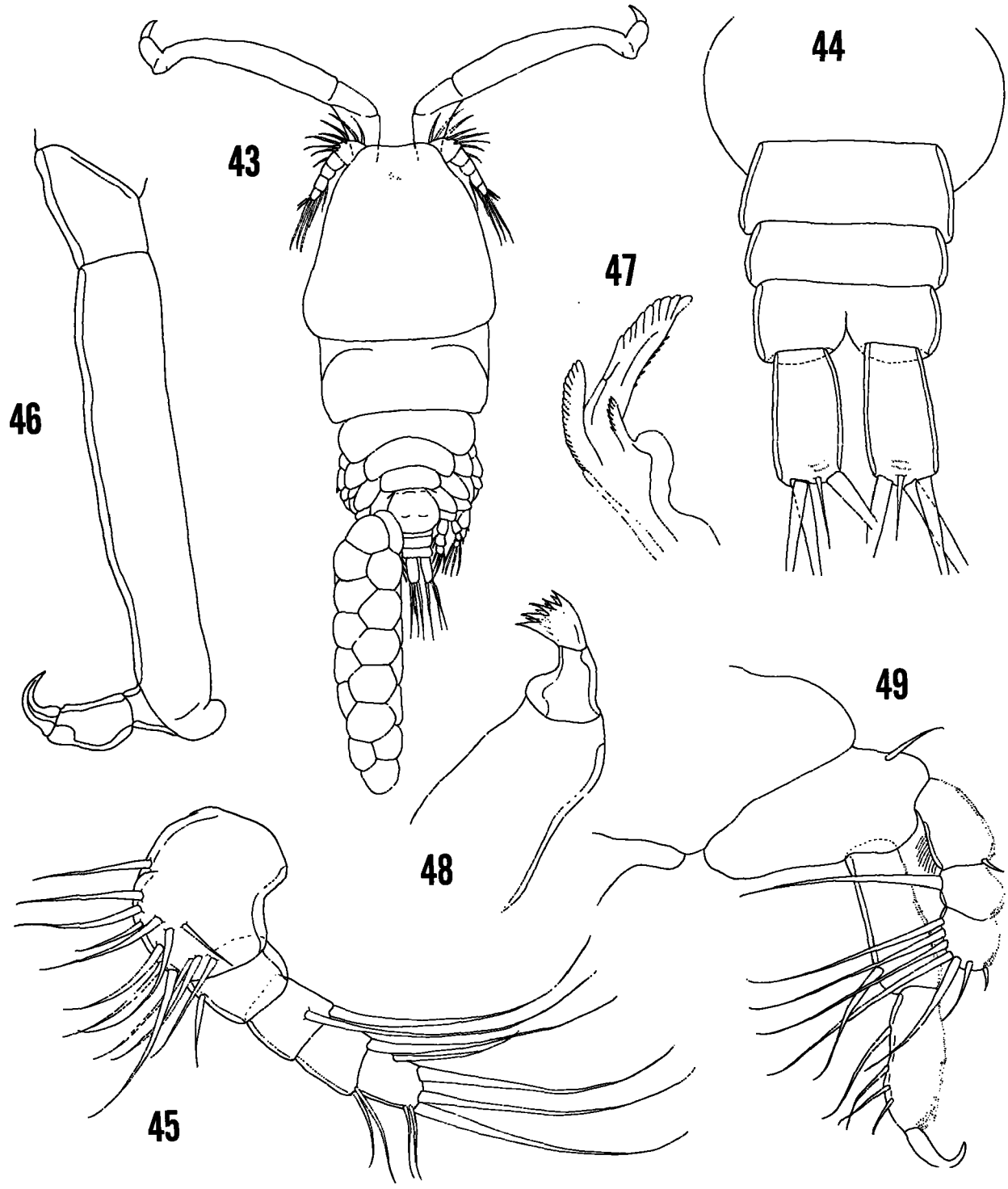
Remarks.—The copepods came from a freshwater population of *Strongylura* now referred to *S. marina* but possibly representing an undescribed form. *Acusicola tenax* was previously reported by Roberts (1965) from Texas as a parasite of *Pomoxis annularis*.

***Acusicola cunula* Cressey, New Species**

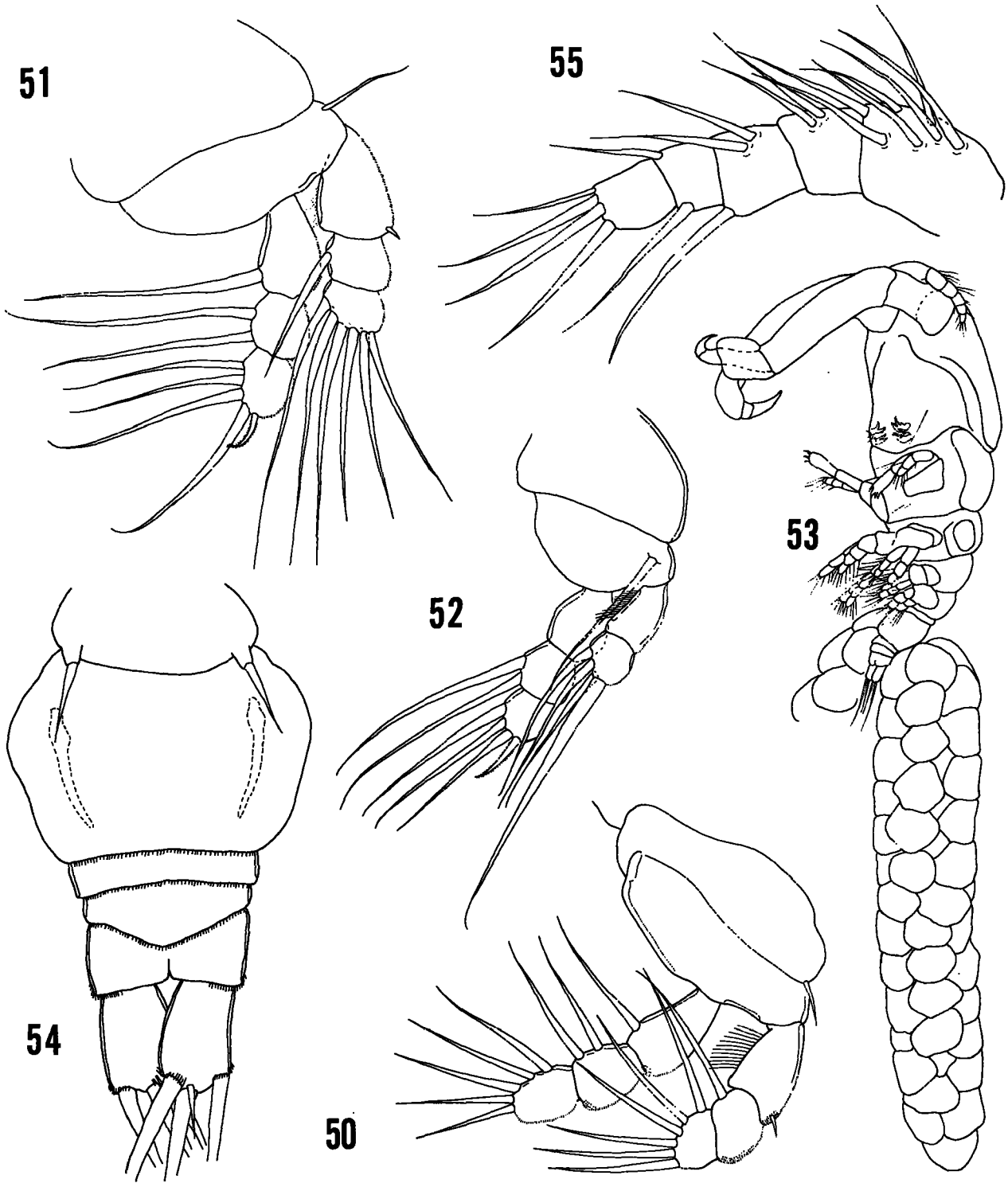
Figures 53 to 60

Specimens studied.—Eight females from two collections from the gill filaments of *Pseudotylosurus angusticeps* collected from Brazil. Holotype female (USNM 125687), two paratype females (USNM 125688) from a single host fish (MCZ 8797) collected at Porto do Moz, near the mouth of the Amazon River, Brazil. Exact locality data for second collection in Brazil (host fish—MCZ 8790) unknown, second collection contains six females.

Female.—Body form as in figure 53. Total length 652 μ. Greatest width 290 μ. Thoracic segments bearing legs 1 to 4 free. Genital segment (fig. 54) slightly wider than long. Abdomen 3-segmented; ventral posterior border with row of spinules on each segment, last segment row confined to outer corners. Caudal rami longer than wide (38 μ by 24 μ); rows of spinules on ventral



FIGURES 43–49.—*Acusicola tenax* female. 43. Dorsal view. 44. Genital segment and abdomen, ventral view. 45. First antenna. 46. Second antenna. 47. Mandible. 48. Second maxilla. 49. First leg.



FIGURES 50–55.—*Acusicola*, new genus. 50–52. *A. tenax* female (continued). 50. Second leg. 51. Third leg. 52. Fourth leg. 53–55. *A. cunula*, new species, female. 53. Lateral view. 54. Genital segment and abdomen, ventral view. 55. First antenna.

distal corners, otherwise armed as in previous species.

First antenna (fig. 55) 5-segmented; basal segment largest, remaining four all of about same length, armed as in figure. Second antenna (fig. 56) 5-segmented; second segment longer than other four combined, third segment with shieldlike process originating at base and surrounding entire inner surface of segment plus part of fourth segment, claw of antenna cradled in this shieldlike process. Mandible, first and second maxilla (fig. 57) similar to preceding species; maxilla larger than in *A. tenax*, with two setae. Maxilliped lacking.

Legs 1 to 4 biramose. Leg 1 (fig. 58) exopod 3-segmented, spine on outer distal corner of first segment and two spines on outer edge of last segment, otherwise armed with setae as in figure; endopod 2-segmented, two short spines on terminus of ramus, outer edge of both segments with numerous spinules, setae arranged as in figure. Leg 2 (fig. 59) rami 3-segmented; one spine on outer distal corner of exopod last segment, otherwise rami armed with setae as in figure. Leg 3 as leg 2. Leg 4 (fig. 60) exopod 2-segmented; endopod 3-segmented, with a spine on outer distal corner of terminal segment, otherwise rami with setae as in figure. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	0:0	0:1	0:0	0:1	0:0	0:1
Seg. 2	0:1	II:4	0:1	0:2	0:1	0:2	5	0:2
Seg. 3	II:5	----	I:6	5	I:6	5	----	I:3

Leg 5 (fig. 54) papilla with one seta near anterior corner of genital segment. Leg 6 absent.

Egg sac 945 μ long, containing about 50 eggs.

Color in life unknown.

Male.—Unknown.

Etymology.—The specific name *cunula* is Latin for "small cradle" referring to the cradlelike structure on the second antenna.

Remarks.—This species may be distinguished from *A. tenax* by the nature of the second antenna and the first leg. These two species may be further separated by the differences in the spine and seta formulas for legs 1 to 4.

***Paraergasilus remulus* Cressey, New Species**

Figures 61 to 70

Specimens studied.—A single collection from *Xenentodon cancila* (UMMZ 181174) collected in a tributary of Prek Andhor, Cambodia. Holotype female (USNM 125689) and one paratype female (USNM 125690) attached to upper inner surface of operculum (not on gill filaments) of host.

Female.—Body form as in figure 61. Total length 443 μ. Greatest width 153 μ. Thoracic segments bearing legs 2 to 4 free. Thoracic segment bearing leg 1 separated from cephalon, articulation weak giving appearance of segment being incorporated into cephalon. Thoracic segments bearing legs 2 to 4, each narrower than preceding segment. Genital segment (fig. 62) slightly wider than long (47.8 μ by 41.3 μ). Abdomen (fig. 62) 3-segmented, first two each with a row of spinules along the ventral posterior border as in figure. Caudal rami slightly longer than wide (16.5 μ by 14.7 μ), with four terminal setae, innermost considerably longer (90 μ) than other three and with a bulbous swelling about 20 μ from base; ventral surface of ramus with an interrupted row of spinules near base of setae.

First antenna (fig. 63) 5-segmented and armed with numerous delicate setae. Second antenna (fig. 64) 4-segmented; second segment with a short seta on outer distal corner; terminal segment with three long terminal setae and one short subterminal seta. Mandible (fig. 65), first maxilla (fig. 66), and second maxilla (fig. 67) very small; even at a magnification of 1,500x, it was difficult to make out details of these three appendages. Maxilliped absent.

Legs 1 to 4 biramose. Rami of legs 1, 2, and 3, 3-segmented. Leg 1 (fig. 68) coxopod with row of spinules; last segment of endopod bearing two broad spines in addition to four setae. Leg 2 (fig. 69) and leg 3 the same in appearance. Leg 4 (fig. 70) exopod 2-segmented, endopod 3-segmented; each armed as in figure. All setae on legs 1 to 4 plumose. Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	0:1	0:1	0:1	0:0	0:1	0:0	I:5	0:1
Seg. 3	II:4	II:4	6	I:4	6	I:4	---	I:3

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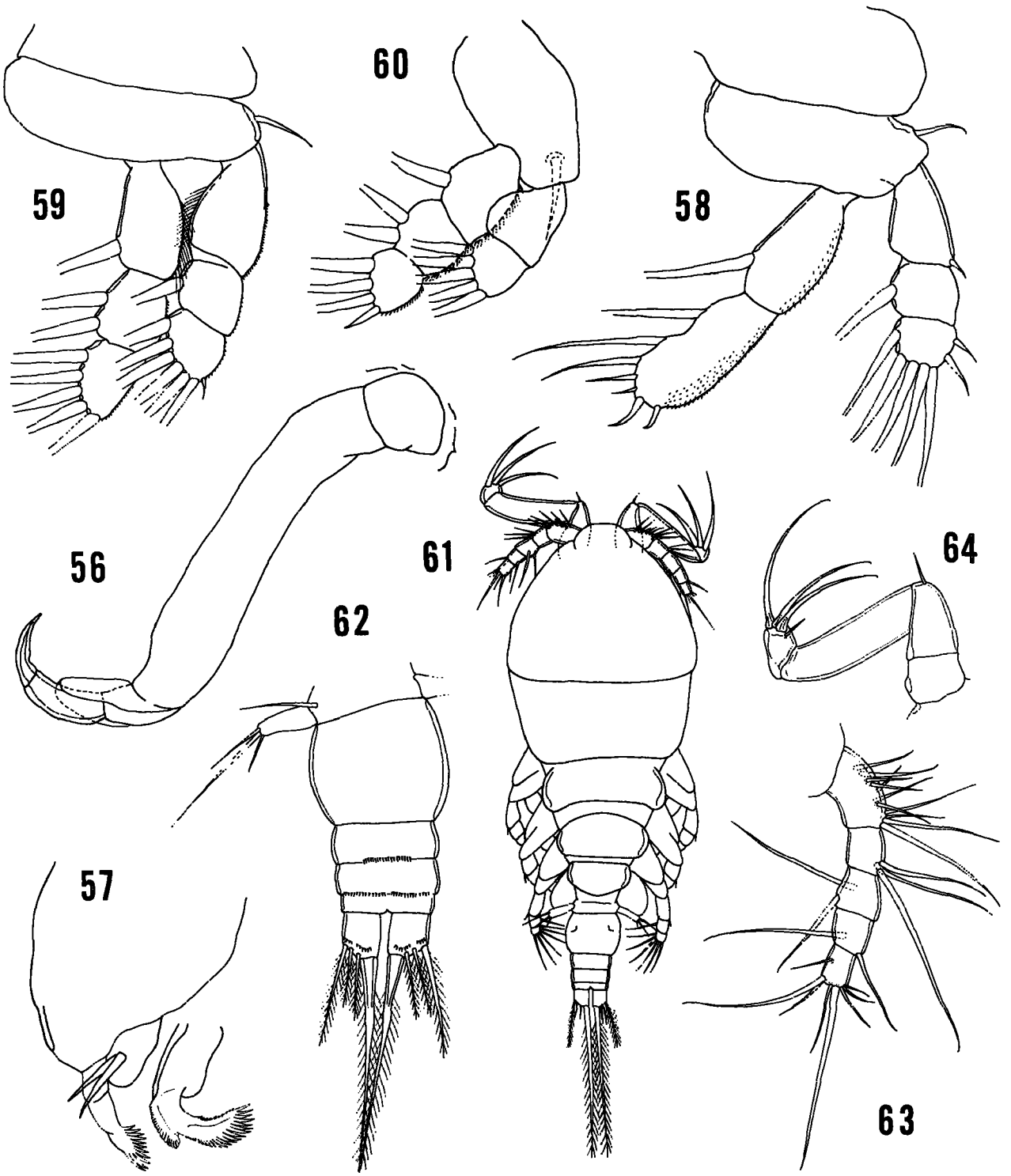


FIGURES 56–64.—*Acusicola*, new genus, and *Paraergasilus*. 59–60. *A. cunula*, new species, female (continued). 56. Second antenna. 57. Mouth parts. 58. First leg. 59. Second leg. 60. Fourth leg. 61–64. *P. remulus*, new species, female. 61. Dorsal view. 62. Genital segment and abdomen, ventral view. 63. First antenna. 64. Second antenna.

Leg 5 (see fig. 62) a free segment with three setae at its tip and an additional seta near its base on thoracic segment. Leg 6 absent.

No egg sacs present on material studied.

Male.—Unknown.

Etymology.—The specific name *remulus* is Latin for "oar" and refers to the nature of the broad spatulate spines on the tip of the endopod of leg 1.

Remarks.—This species may be distinguished from the six known species of *Paraergasilus* by the two broad spines on the tip of the endopod of leg 1. Fryer (1968) stated that *Paraergasilus* is probably restricted to the nasal sinuses of the hosts. The two specimens reported here were found attached beneath the operculum. The nasal fossae of all synentognath fishes are open pits so it would be difficult for any copepod to attach therein. In any event, it seems apparent that members of this genus are not found on the gills as Yamaguti (1963) has reported.

All known species of *Paraergasilus* have been collected from Asia or East Africa.

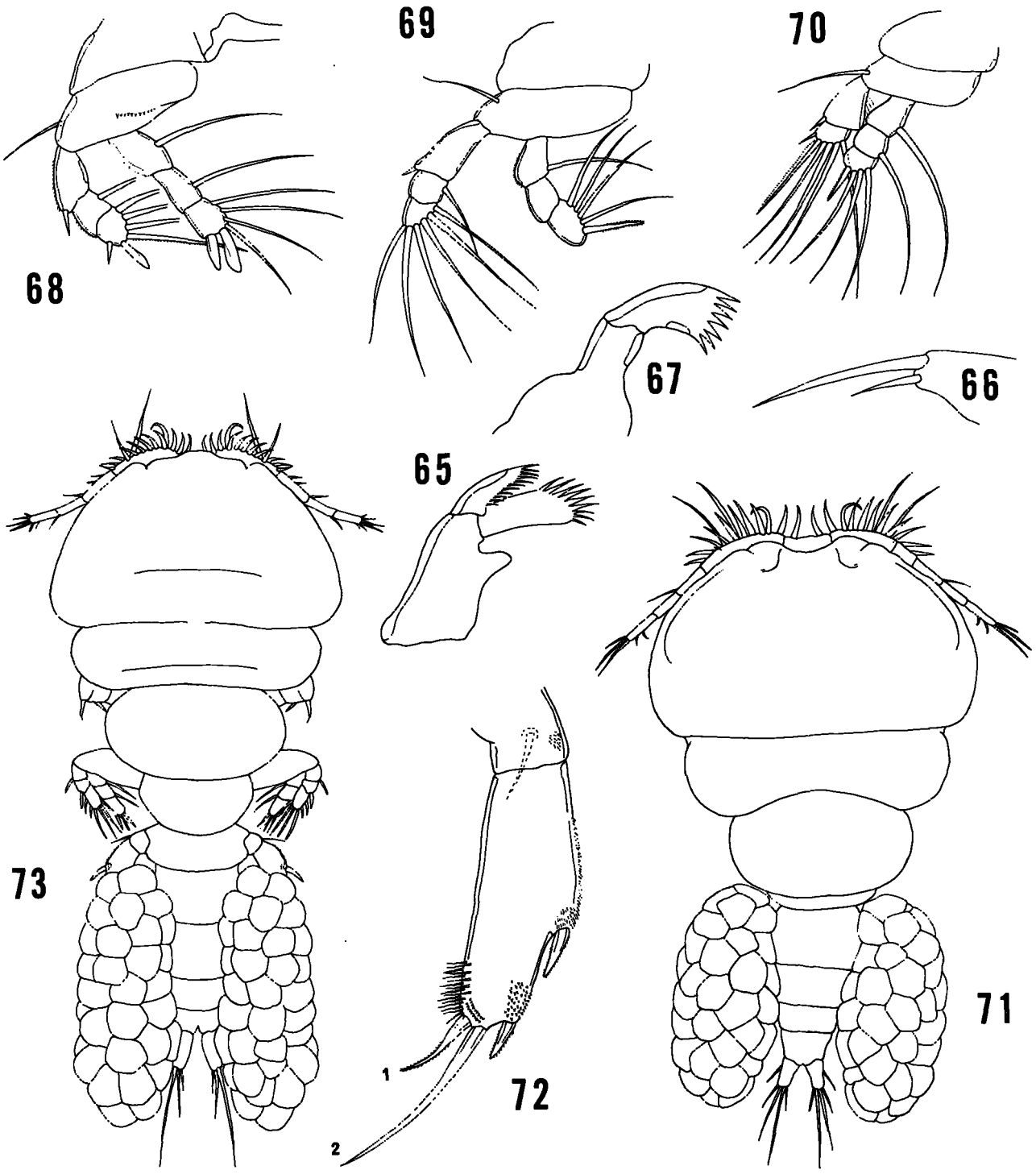
FAMILY BOMOLOCHIDAE

Six species of bomolochids were collected representing the genera *Parabomolochus* and *Nothobomolochus*. Four of the six species discussed are new.

Parabomolochus bellones (Burmeister)

Figures 71, 72

Specimens studied.—A total of 860 individuals from the gill chambers and oral valves of 16 species of hosts: *Ablennes hians* (gill chambers), Woods Hole, Mass.; Virginia coast (3 collections); north Florida; Florida Keys; Gulf of Mexico, lat. 28°30′ N., long. 88°45′ W. (2 collections); Haiti; British Honduras (3 collections); Padre Bank, Caribbean Sea; Grand Bahama Island; off North Brazil (2 collections); Gulf of Guinea (7 collections); Liberia; Persian Gulf; Natal, South Africa; Red Sea; Japan (4 collections); *Belone belone* (gill chambers), "Europe" (2 collections); Trieste; Venice, Italy (2 collections); Naples, Italy; Mediterranean Sea; Tunisia; Spain (2 collections); *Belone svetovidovi* (gill chambers), Genoa, Italy; *Platybelone argalus* (gill chambers), Puerto Rico (2 collections); Cuba; Gulf of Mexico, lat. 20°12′ N., long. 91°59′ W., Cay Arcas, Gulf of Mexico; Cumana, Venezuela; Saudi Arabia; *Strongylura anastomella* (gill chambers), Matsushima, Japan; "Japan" (5 collections); Yokohama, Japan (2 collections); Suruga Bay, Japan; Sea of Japan; Chiba Prefecture, Japan; Korea; *Strongylura leiura* (gill chambers), Hong Kong; *Strongylura incisa* (gill chambers), Philippine Islands (2 collections); *Strongylura marina* (gill chambers and oral valves), Martha's Vineyard, Mass.; Morehead City, N.C.; Beaufort, N.C. (4 collections); Southport, N.C.; St. Simons Island, Ga. (4 collections); Jekyll Island, Ga.; Amelia River, Fla.; Flagler Beach, Fla.; Key West, Fla.; Everglades Park, Fla.; Sanibel Island, Fla.; Alligator Harbor, Fla. (3 collections); Yucatan, Mexico; Panama (Atlantic); Cumana, Venezuela; Venezuela; Trinidad; *Strongylura notata* (gill chambers and oral valves), Sarasota, Fla. (4 collections); New Smyrna, Fla.; Banana River, Fla.; Key Biscayne, Fla. (7 collections); Matecumbe Key, Fla.; Bayport, Fla.; Alligator Harbor, Fla.; Pensacola, Fla.; Andros Island, Bahamas; Mujeres Island, Yucatan; Tampico, Mexico; Havana, Cuba (2 collections); Palisadoes, Jamaica; *Strongylura senegalensis* (gill chambers and oral valves), Ivory Coast (2 collections); Volta River, Ghana; *Strongylura strongylura* (gill chambers), Arnhem Land, Australia; *Strongylura timucu* (gill chambers), Sarasota, Fla.; Pensacola, Fla.; Placida, Fla.; Clearwater, Fla.; Monroe County, Fla.; Tampa Bay, Fla.; Key Biscayne, Fla. (2 collections); Sanibel Island, Fla.; Virgin Gorda Sound, Virgin Islands; Mayaguez, Puerto Rico; Laguna Rincon, Puerto Rico; Cabo Rojo, Puerto Rico; San Juan, Puerto Rico; Punta Arenas, Puerto Rico; Port-au-Prince, Haiti; Lazaretto, Jamaica; St. Thomas, Virgin Islands; New Providence, Bahamas; Ascension Bay, Yucatan; Progresso, Yucatan; Honduras; *Strongylura urvillii* (gill chambers), Philippine Islands; *Tylosurus acus* (gill chambers and oral valves), Gulf of Mexico, lat. 20°50′ N., long. 93°00′ W.; off North East Florida; Monroe County, Fla.; Honduras; Freetown, Sierra Leone; Gulf of Guinea; *Tylosurus crocodilus* (gill chambers), Sarasota, Fla.; Virginia Key, Fla.; U.S. Atlantic Coast; Havana, Cuba; Golfo de Lanaio, Venezuela; Venezuela; Delagoa Bay, Mozambique; Kenya; Mosios Islands, Burma; Kerala, India; *Lhotskia gavialoides* (oral valves), Botany Bay, Australia;



FIGURES 65–73.—*Paraergasilus* and *Parabomolochus*. 65–70. *Paraergasilus remulus*, new species, female (continued). 65. Mandible. 66. First maxilla. 67. Second maxilla. 68. First leg. 69. Second leg. 70. Fourth leg. 71–72. *Parabomolochus bellones* (Burmeister), female. 71. Dorsal view. 72. Fifth leg. 73. *Parabomolochus ensiculus*, new species, female, dorsal view.

"Australia"; Great Barrier Reef; Newcastle, Australia; New South Wales, Australia.

Remarks.—This species has been reported many times in the literature. Vervoort (1962) provided a good description with figures of the female; little additional description is necessary here. He, however, described and figured the exopod of leg 1 as 2-segmented; all of our specimens show this ramus to be 3-segmented and similar to the figure of leg 1 provided in the description of the following species.

We tested the variability of one taxonomic character—the relative lengths of the spines and setae on leg 5—in our large series of collections from a wide range of hosts and localities. It was apparent that the spines and setae are of taxonomic importance and that their relative lengths vary in *Parabomolochus bellones* as well as in other species. This variation in the four species of *Parabomolochus* considered in this paper is discussed in a later section.

Parabomolochus ensiculus Cressey, New Species

Figures 73 to 86

Specimens studied.—A total of 153 individuals from 14 collections from under the oral valves of two species of eastern Pacific needlefish hosts: *Strongylura exilis*, San Diego, Calif. (2 collections); Baja California (3 collections); Chame Point, Panama (gill cavity); Pachacamac Island, Peru; Peru; *Strongylura scapularis*, Balboa, Panama (2 collections); Manabi Province, Ecuador; Guyaquil, Ecuador; Point Pizarro, Peru; Western South America.

Holotype female (USNM 125691), allotype male (USNM 125692), and 33 paratypes (29 females, 4 males) (USNM 125693) from the oral valves of 5 *Strongylura scapularis* (USNM 84276) collected at Balboa, Panama.

Female.—Body form as in figure 73. Total length and greatest width of three specimens: 1,420μ by 520μ, 1,270μ by 600μ, 1,195μ by 480μ. Body form in general like that of *P. bellones*. Thoracic segments not inflated dorsally, not overlapping succeeding segments. Genital segment and abdomen as in *P. bellones*, except for the patch of spinules present on the last abdominal segment of *P. ensiculus*. Caudal rami (fig. 74) armed with setae as in *P. bellones* but different from that species by the presence of a prominent patch of spinules on the ventral surface of the posterior third of the ramus; rami of three specimens measure 133μ by 57μ, 129μ by 58μ, and 119μ by 46μ; slightly more than twice as long as wide (in *P. bellones* the rami are less than twice as long as wide, 100μ by 58μ).

First antenna (fig. 75) armed as in figure. Second antenna (fig. 75) as in *P. bellones*. Oral area as in figure 76. Labrum surface with two patches of scalelike processes and fine fringe on lateral border. Mandible broad, bladelike with small accessory process at tip. Paragnath finger-shaped with row of fringe. First maxilla with three stout plumose setae and a shorter naked one. Second maxilla (fig. 77) with two distal processes; shorter plumose, longer with heavy fringe. Maxilliped (fig. 75) with prominent lateral tooth on outer border of terminal hook as in *P. bellones*.

Legs 1 to 4 biramose, all rami 3-segmented. Leg 1 (fig. 78) exopod first segment with broad spine on outer distal corner, surface of spine striated; remainder of leg armed with spines and setae as in figure. Leg 2 (fig. 79) as in *P. bellones* except last segment of exopod with three outer spines (*P. bellones* has four), bases of setae swollen on first two segments of endopod. Leg 3 (fig. 80) and leg 4 (fig. 81) as in *P. bellones* except terminal spine on exopod of both legs proportionally longer in *P. ensiculus* The spine and seta formulas for legs 1 to 4 follow:

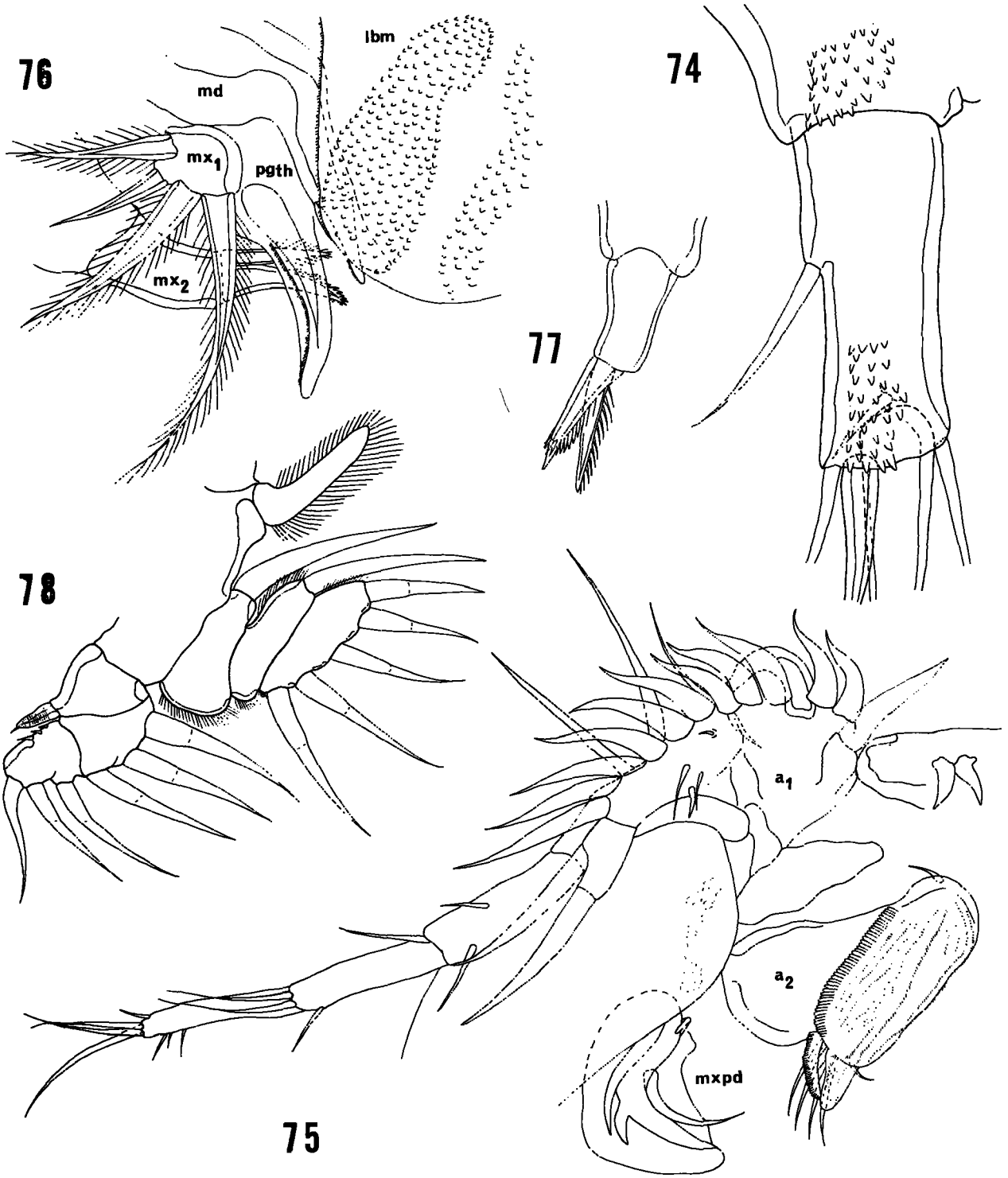
	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	0:3	0:1	I:1	0:2	I:1	0:1	I:1	0:1
Seg. 3	III:3	5	III:5	II:3	III:5	II:2	III:4	I:1:I

Leg 5 (fig. 82) 2-segmented; terminal segment with an outer prominent spine, two terminal broad spines separated by a median terminal seta, and patches of setules near bases of spines as in figure. Leg 6 absent.

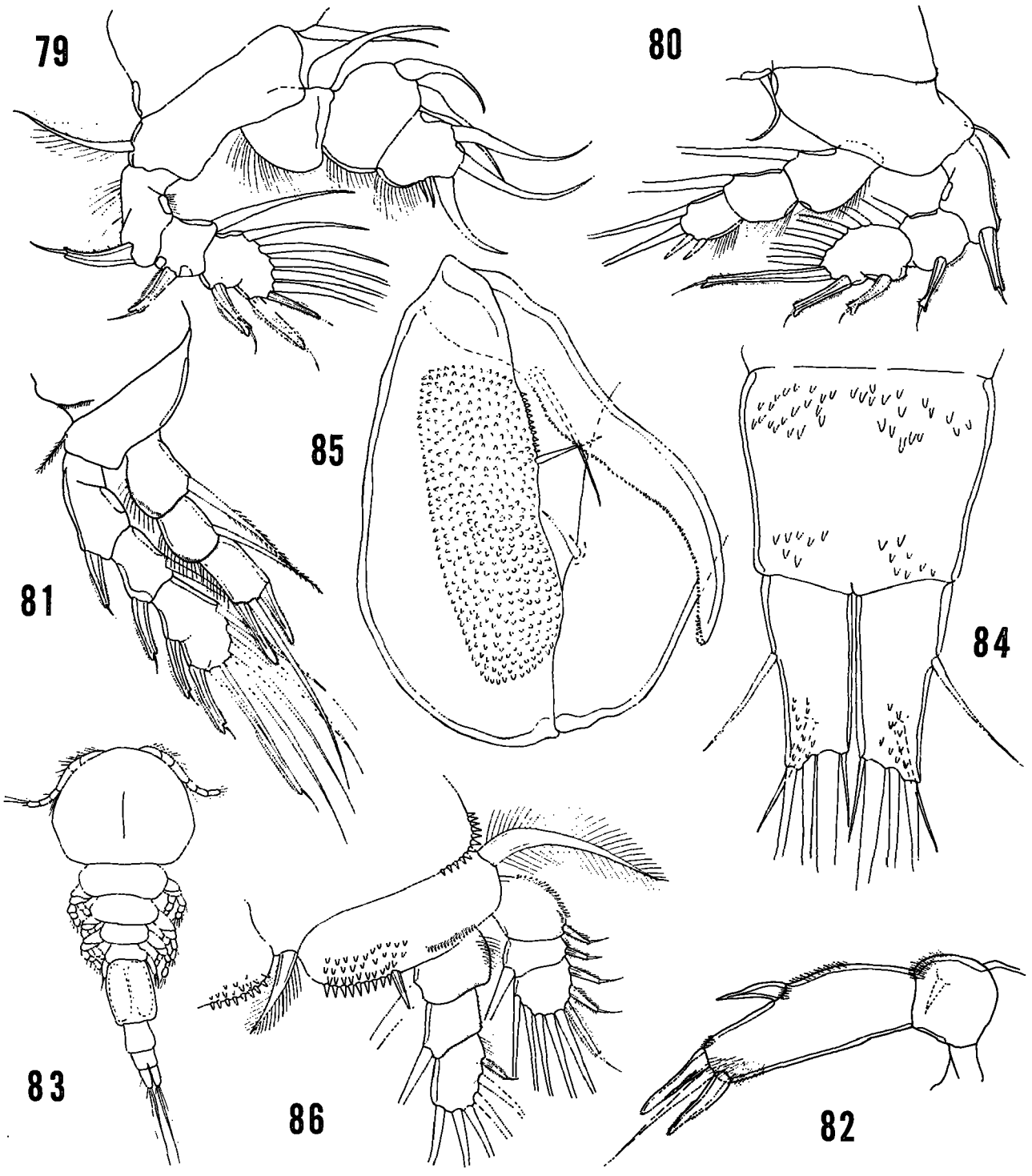
Egg sacs about 800 μ long, containing about 40 eggs.

Color in preserved specimens, cream.

Male.—Body form as in figure 83. Total length 1,116 μ. Greatest width 507 μ. Cephalon slightly wider than long (406 μ x 507 μ). Thoracic segments bearing legs 2 to 5 free, each narrower than the preceding segment. Similar to *P. bellones* in general body form. Last abdominal segment and caudal



FIGURES 74–78.—*Parabomolochus ensiculus*, new species, female (continued). 74. Caudal ramus, ventral view. 75. First antenna (a_1), second antenna (a_2), and maxilliped (mxpd). 76. Mouth parts (labrum, lbm; mandible, md; paragnath, pgth; first maxilla, mx_1; second maxilla, mx_2). 77. Tip of second maxilla. 78. First leg.



FIGURES 79–86.—*Parabomolochus ensiculus*, new species, female (continued). 79. Second leg. 80. Third leg. 81. Fourth leg. 82. Fifth leg. Same, male. 83. Dorsal view. 84. Caudal rami, ventral view. 85. Maxilliped. 86. First leg.

rami (fig. 84) with patches of broad spinules. Maxilliped (fig. 85) second segment with a large patch of spinules. Leg 1 (fig. 86) with patches of broad spinules on interpodal plate and basipod, otherwise armed as in *P. bellones*. Other appendages as in *P. bellones*.

Etymology.—The specific name *ensiculus*, Latin for "sword," refers to the terminal spines on the female 5th leg.

Remarks.—*P. ensiculus* can be separated from all other members of the genus by the spines on leg 5. This species is apparently restricted to the eastern Pacific Ocean and so far has been collected only from *Strongylura exilis* and *S. scapularis*, both hosts endemic to that area.

The male of this species can be separated from *P. bellones* only by the more prominent spinules on the interpodal plates, maxilliped, and basipod of leg 1 of *P. ensiculus*.

Parabomolochus constrictus Cressey, New Species

Figures 87 to 90

Specimens studied.—A total of 178 individuals from 32 collections from the gill chambers of 6 species of eastern Pacific needlefishes: *Ablennes hians*, Acapulco, Mexico; Panama Bay, Panama (2 collections); Ecuador; Cabo Blanco, Peru (2 collections); *Platybelone argalus*, Bahia Santa Maria, Baja California; Secas Island, Panama; Perlas Islands, Panama; Gulf of Panama; Galapagos Islands; Gulf of Guayaquil, Ecuador; *Strongylura scapularis*, Gulf of Nicoya, Costa Rica; Panama Canal Zone (3 collections); *Strongylura exilis*, Baja California (5 collections); Gulf of California; northern Peru; *Tylosurus acus*, Costa Rica (2 collections); Panama (2 collections); Colombia; Cabo Blanco, Peru; *Tylosurus crocodilus*, Tangola, Mexico; Cocos Islands; Panama (2 collections).

Holotype female (USNM 125694) and 43 paratype females (USNM 125695) from 13 specimens of *Platybelone argalus pterura* from the Gulf of Guayaquil, Ecuador.

Female.—Body form as in *P. ensiculus*. Total lengths and greatest widths of three specimens: 1,050 μ by 600 μ, 1,050 μ by 600 μ, 980 μ by 560 μ. Patches of fine spinules present on ventral surface of last abdominal segment and caudal rami (fig. 87). Caudal rami proportionally larger than in *P. ensiculus* and *P. bellones;* lengths and widths of the rami of three specimens are 152 μ by 74 μ, 143 μ by 73 μ, and 138 μ by 80 μ.

Cephalic appendages as in *P. ensiculus* with following exceptions: paragnath bladelike with fringe along posterior border and encircling tip; second maxilla (fig. 89) largest terminal spine with large patch of spinules, smaller spine with prominent spines on both edges; maxilliped (fig. 88) with small, blunt lateral tooth on outer border as compared to prominent pointed tooth present in both *P. bellones* and *P. ensiculus*. Surface of labrum with two patches of fine spinules.

Legs 1 to 4 as in *P. ensiculus*. Leg 5 (fig. 90) outer two spines on terminal segment pinched near tip; inner spine pinched near midpoint, distal half narrowed. Patches of spinules near bases of spines with finer spinules than those of *P. ensiculus*. Leg 6 absent.

Egg sacs as in *P. ensiculus*.

Color in preserved specimens, cream.

Male.—Unknown.

Etymology.—The specific name *constrictus* is Latin for "drawn together" and refers to the nature of the spines on the 5th leg of the female.

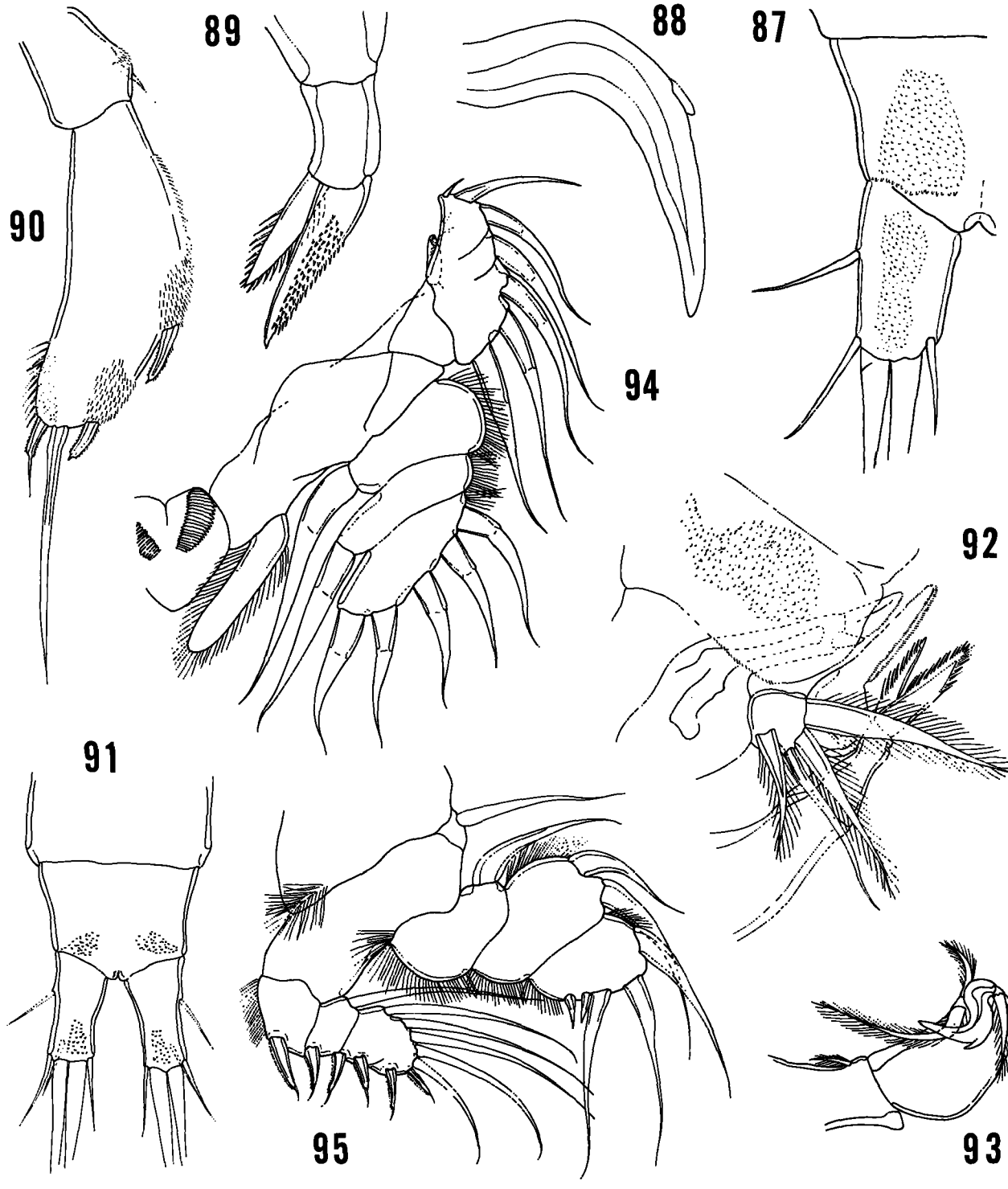
Remarks.—This species can be separated from all other known members of the genus by the nature of the 5th leg spines. It is described here from five species of needlefishes and is apparently endemic to the eastern Pacific Ocean.

Subsequent to this study, Cressey examined parasitic copepods collected by Edmund Hobson at La Jolla, Calif., from 30 species of inshore fishes. *Parabomolochus constrictus* was collected from one collection of each of the following hosts: Atherinidae, *Atherinops affinis* (Ayres); and Embiotocidae, *Micrometrus minimus* (Gibbons), *Phanerodon atripes* (Jordan and Gilbert), and *Rhacochilus vacca* (Girard). These additional hosts point out the "loose" host specificity in this species, and it is likely that bomolochids as a group are less host specific than most other parasitic copepods. In each of the California collections, only one copepod was collected from each individual.

Parabomolochus sinensis Cressey, New Species

Figures 91 to 98

Specimens studied.—Six collections containing 12 females and 1 male from the oral valves of *Strongylura strongylura* and a single collection containing 2 females from the upper oral valve of



FIGURES 87–95.—*Parabomolochus*. 87–90. *P. constrictus*, new species, female. 87. Caudal ramus, ventral view. 88. Claw of maxilliped. 89. Tip of second maxilla. 90. Fifth leg. 91–95. *P. sinensis*, new species, female. 91. Caudal rami, ventral view. 92. Mouth parts. 93. Maxilliped. 94. First leg. 95. Second leg.

Ablennes hians as follows: *Ablennes hians*, Batavia, Java; *Strongylura strongylura*, Fukien, China; Hong Kong (2 collections); Amoy, China (2 collections); Penang, Malaysia.

Holotype female (USNM 125696) and two paratype females (USNM 125697) from the oral valves of a *Strongylura strongylura* (ANSP 76986) from Hong Kong.

Female.—Body form as in *P. ensiculus*. Total length 2,100 μ. Greatest width 1,100 μ. Thoracic segments not inflated dorsally, not overlapping succeeding segments. Genital segment wider than long (207 μ by 325 μ). Abdomen 3-segmented; lengths of segments from anterior to posterior 106 μ, 65 μ, and 83 μ, respectively, last segment with ventral patches of spinules (see fig. 91) near outer distal corners (spinules not as conspicuous as in *P. ensiculus*). Caudal rami (fig. 91) about twice as long as wide (75 μ by 34 μ, 65 μ by 31 μ, 65 μ by 35 μ for three specimens); each with a ventral patch of spinules as indicated in figure.

First and second antennae as in *P. ensiculus*. Oral area as in figure 92; labrum with a patch of scalelike processes on each half (finer than those of *P. ensiculus*). Mandible with two terminal processes, inner process much shorter than outer. Paragnath bladelike, double row of fringe along posterior border. First maxilla with four long setae—three plumose, one naked. Second maxilla as in *P. ensiculus*. Maxilliped (fig. 93) with accessory process on claw; terminal segment with three plumose setae.

Legs 1 to 4 biramose, all rami (except leg 1 exopod) 3-segmented and all setae plumose. Leg 1 (fig. 94) exopod first segment with broad spine on outer distal corner, second segment with three small outer spines and six well-developed setae; endopod 3-segmented, first two segments each with an inner seta and terminal segment with five setae. Leg 2 (fig. 95) exopod, first segment with an outer spine, second segment with an outer spine and an inner seta, terminal segment with four outer spines (*P. ensiculus* has three) and five terminal to inner setae; endopod, first segment with an inner seta, second segment with two inner setae, terminal segment with two short outer spines and three terminal setae. Leg 3 (fig. 96) exopod, first two segments armed as in leg 2, terminal segment with three outer spines and five terminal to inner setae; endopod, first two segments each with an inner seta, terminal segment with two terminal setae and two short outer spines. Leg 4 (fig. 97) exopod, first two segments armed as in legs 2 and 3, last segment with three outer spines (terminal-most about twice the length of other two) and four terminal to inner setae; endopod, first two segments armed as in leg 3, last segment with an inner and an outer spine and a median terminal seta. Spine and seta formulas of legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	I:0	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	III:6	0:1	I:1	0:2	I:1	0:1	I:1	0:1
Seg. 3	-----	5	IV:5	II:3	III:5	II:2	III:4	I:1:I

Leg 5 (fig. 98) armed as in *P. ensiculus;* ratio of seta 1 to seta 2 less than in *P. bellones* or *P. ensiculus* (see Discussion). Leg 6 represented as two setae on lateral border of genital segment.

Egg sacs broken in the only specimens bearing them.

Color in preserved material, cream.

Male.—Unknown.

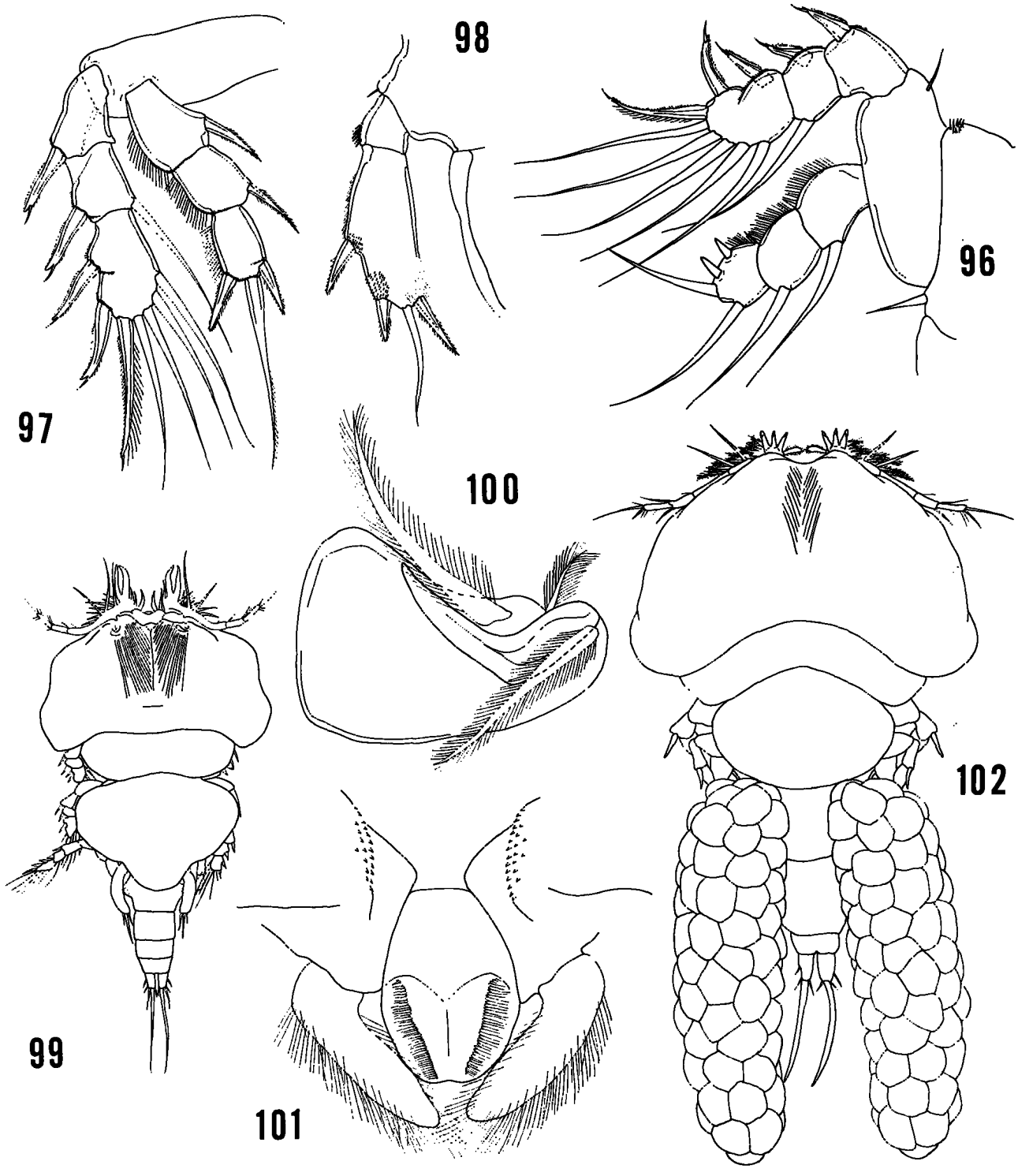
Etymology.—The specific name *sinensis* refers to the geographic area (China coast and environs) to which this species seems to be restricted.

Remarks.—This species can be separated from all species of the genus except *P. ensiculus*, *P. constrictus*, and *P. decapteri* Yamaguti by the patches of spinules on the ventral surface of the caudal rami and last abdominal segment. It can be separated from *P. constrictus* by the nature of the setae of leg 5. *P. ensiculus* has only three spines on the last exopod segment of leg 2, whereas *P. sinensis* has four; also the spinules on the caudal rami, abdomen, and labrum are much heavier in *P. ensiculus*. Finally, *P. sinensis* can be separated from *P. decapteri* by the presence of patches of spinules on the exopod segments of legs 2 to 4 of *P. decapteri* and their absence in *P. sinensis*.

***Nothobomolochus gibber* (Shiino)**

Figures 99 to 101

Specimens studied.—A total of 235 females from 20 collections from 6 species of hosts. From the Mediterranean and eastern Atlantic, collections were made from the following hosts and localities: *Belone belone*, Funchal, Madeira; *Belone svetovidovi*, Tunisia; Genoa, Italy; *Platybelone argalus*, Ascension and Annobon Islands, Gulf of Guinea. From the Indo-West Pacific, collections were made from the following hosts and localities: *Ablennes*



FIGURES 96–102.—*Parabomolochus* and *Nothobomolochus* species. 96–98. *P. sinensis*, new species, female (continued). 96. Third leg. 97. Fourth leg. 98. Fifth leg. 99–101. *N. gibber* (Shiino), female. 99. Dorsal view. 100. Maxilliped. 101. Area between coxopods of leg 1. 102. *N. digitatus*, new species, female, dorsal view.

hians, Andaman Islands, Bay of Bengal; Borneo; Torres Strait, northern Australia; Manila, Philippine Islands; Japan (2 collections); *Platybelone argalus*, Aldabra Island, Indian Ocean; Marshall Islands (4 collections); Tokelau Islands (2 collections); Fakaofo Atoll (2 collections); Christmas Island; Line Islands; Fanning Island; Rose Island, Samoan Islands; Apia, Samoa (2 collections); *Tylosurus acus*, Taiwan; *Tylosurus crocodilus*, Red Sea; Zanzibar; Seychelles Islands; Nosy Bé, Madagascar; Kerala, India; Cavite, Philippine Islands; Bellona Island, British Solomon Islands.

Female.—Body form as in figure 99 (after Shiino, 1957). This species was well described by Shiino (as *Bomolochus gibber*) in 1957, and additional notes were provided by Vervoort in 1962. No additional description is necessary here except to point out two characters not considered by the aforementioned authors which may have some taxonomic value: the maxilliped (fig. 100) terminal claw is angular, the distal half nearly at a right angle to the base, and the area between the coxopods of leg 1 (fig. 101) has a pad with surface corrugations as indicated in figure.

Remarks.—This species is common in the Indo-Pacific region and only occasionally found in the Mediterranean and eastern Atlantic.

***Nothobomolochus digitatus* Cressey, New Species**

Figures 102 to 112

Specimens studied.—Fourteen collections containing 28 females from four species of needlefishes, all from the Indo-West Pacific area as follows: *Strongylura leiura*, Gulf of Thailand; Panay, Philippines (2 collections); Java; *Strongylura strongylura*, Calicut, India; Bombay, India (3 collections); Malaysia (2 collections); Hong Kong; Australia; Philippines; *Tylosurus crocodilus*, British North Borneo; *Tylosurus punctulatus*, New Guinea.

Holotype female (USNM 125698) and two paratype females (USNM 125699) from a specimen of *Strongylura strongylura* (SU 32879) from Penang, Malaysia.

Female.—Body form as in figure 102. Total length 1,800 μ. Greatest width 1,200 μ. Caudal rami (fig. 103) longer than wide (66 μ by 44 μ) with one long terminal seta (413 μ), three subterminal short setae, and one lateral seta. First antenna (fig. 104) with three stout, modified setae of equal length on basal segment; each seta with a hyaline tip, other setae as in other members of the genus. Second antenna as in *P. gibber*. Labrum (fig. 105) with two rings of blunt spinules on surface. Mandible (fig. 106) terminating in two short bladelike processes, each with a fringe along one edge. Paragnath (fig. 107) with nine fingerlike terminal processes, each with a bulbous tip. In view of the striking difference between the paragnaths of *gibber* and *digitatus* this structure is of great interest and taxonomic importance. First maxilla (fig. 108) bearing three long plumose setae and a shorter naked one. Second maxilla (fig. 109) ending as a long bladelike process with a stout basal seta. Arrangement of mouth parts as in figure 105. Maxilliped (fig. 110) with terminal claw slightly recurved, not angular. Area between coxopods of leg 1 (fig. 111) with wreathlike fringe as in figure.

Spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1	III:6	0:1	I:0	0:1	I:0	0:1	I:0	0:1
Seg. 2	-----	0:1	I:1	0:2	I:1	0:1	I:1	0:0
Seg. 3	-----	5	IV:5	II:3	III:5	II:2	III:4	I:1:I

Leg 5 (fig. 112) similar to that of other members of the genus; two outer terminal spines with very fine spinules on inner margin, patch of spinules near base of terminal spines heavier than in *N. gibber*. Leg 6 absent.

Egg sacs about 1 mm. long and containing 60 to 75 eggs.

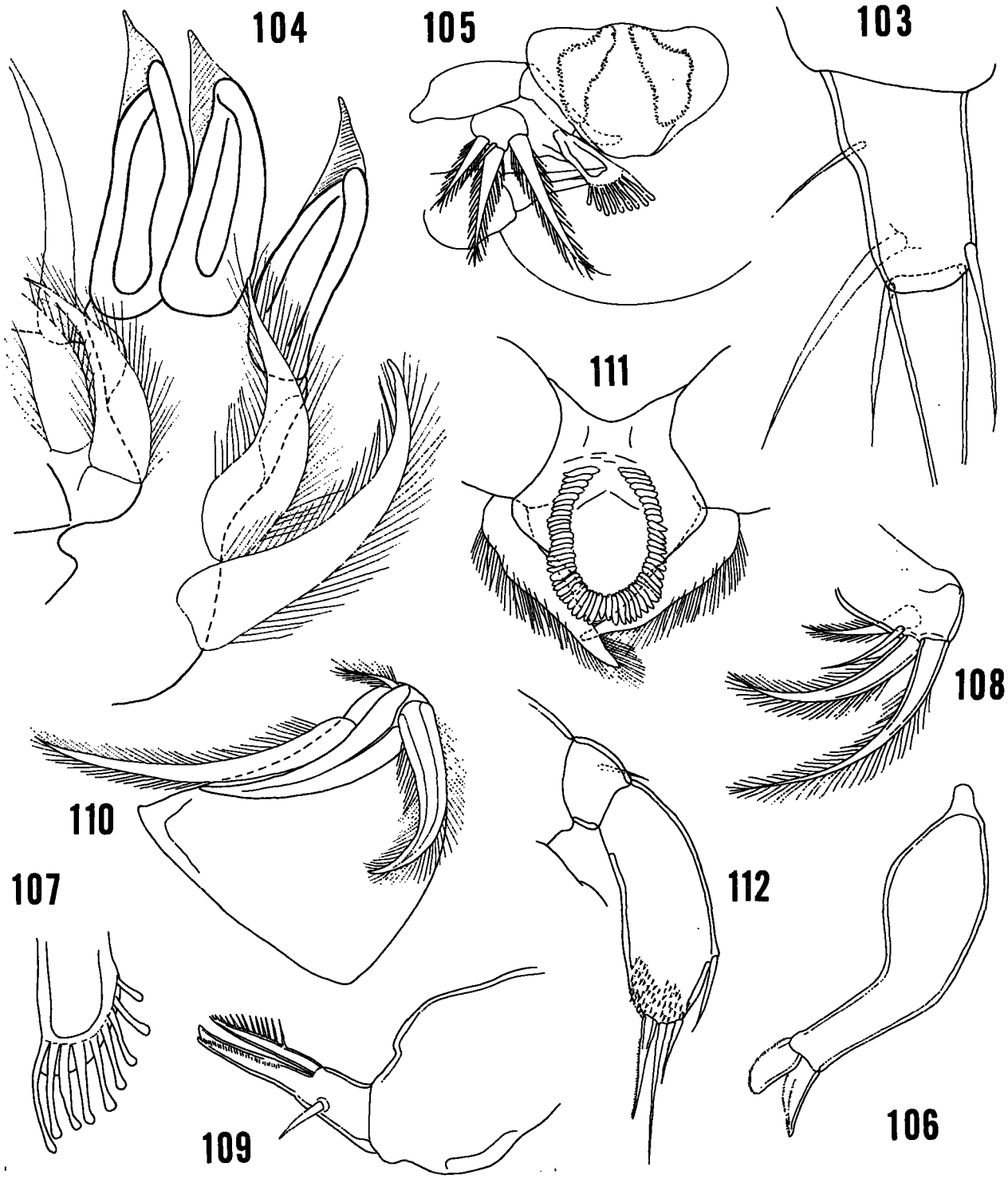
Color in preserved specimens, cream.

Male.—Unknown.

Etymology.—The word *digitatus* refers to the fingerlike processes on the paragnath.

Remarks.—This species can be separated from all other species except *N. saetiger* (Wilson) and *N. lateolabricus* (Yamaguti and Yamasu) by the nature of the first antenna: the three modified spines on the first segment are of equal length, whereas in all other species they are not. The new species can be separated from *N. saetiger* and *N. lateolabricus* by the nature of the paragnath. In *N. saetiger* and *N. lateolabricus* the paragnath is a bladelike structure, whereas in *N. digitatus* it bears nine fingerlike processes at its distal end.

This species is known only from Indo-West Pacific needlefishes.



FIGURES 103–112.—*Nothobomolochus digitatus*, new species, female (continued). 103. Caudal ramus, ventral view. 104. Base of first antenna. 105. Mouth parts. 106. Mandible. 107. Paragnath. 108. First maxilla. 109. Second maxilla. 110. Maxilliped. 111. Area between coxopods of leg 1. 112. Fifth leg.

Order Caligidea

Four families of caligoid copepods were collected from needlefishes: Caligidae, Anthosomatidae, Lernaeidae, and Lernaeoceridae.

FAMILY CALIGIDAE

Seven species of *Caligus* plus *Caligodes laciniatus* were collected.

Caligus tylosuri (Rangnekar)

Figures 113 to 116

Specimens studied.—Two collections from *Tylosurus crocodilus*, one from Leyte, Philippines, containing three females and one from North Borneo containing a single female; one collection from *Tylosurus acus melanotus* from Luzon, Philippines, containing a single male and one collection from *T. acus pacificus* from Bahia Palmas, Gulf of California, containing a single male.

This copepod was described by Rangnekar in 1956 and at that time assigned to the genus *Tuxophorus*. In 1961 Pillai transferred it to the genus *Caligus*. Rangnekar's primary reason for placing this copepod in *Tuxophorus* was the presence of small dorsal thoracic plates which she described from females in her collections. Pillai was unable to find these plates in his material and, thus, reassigned the species to *Caligus*. These plates could not be located on the specimens reported here.

This copepod has been described and figured by Rangnekar and Pillai so only a few points are added to the existing descriptions.

Female.—Body form as in figure 113. Total length and greatest width of the specimen from North Borneo 3.7 by 2.1 mm.; those from Leyte, Philippines 3.3 by 2.0 mm., 3.4 by 2.0 mm., and 3.5 by 2.1 mm.

Male.—Body form as in figure 114. Total length and greatest width of the specimen from Luzon, Philippines, 3.2 by 1.9 mm.; those from Gulf of California 2.9 by 1.7 mm. Abdomen (fig. 115) 2-segmented (not 1-segmented as stated by Rangnekar). Caudal rami (fig. 116) with six setae arranged as in figure.

The following points concerning the description should be corrected as follows. Rangnekar described the endopod of leg 3 as 2-segmented and stated "exo and endopods are well separated by a ciliated membrane." This "membrane" is actually the first endopod segment, thus the endopod is 3-segmented. The 5th and 6th legs described by Rangnekar are parts of leg 5—the anterior lobe represents the exopod and the posterior lobe the endopod. Leg 6 is represented by a single seta near the junction of the genital segment and abdomen.

Remarks.—This copepod seems to be restricted to needlefishes. It has thus far not been reported from the Atlantic Ocean.

Caligus belones Krøyer

Figure 117

Specimens studied.—A single collection containing 1 female from under the gill cover of a *Belone belone* taken in the Elbe River plus the type-specimens from *B. vulgaris* (=*B. belone*) borrowed from the Universitetets Zoologiske Museum (Copenhagen). A lectotype has been selected and deposited in the above museum. An additional collection from *P. argalus* containing 1 female and 1 male.

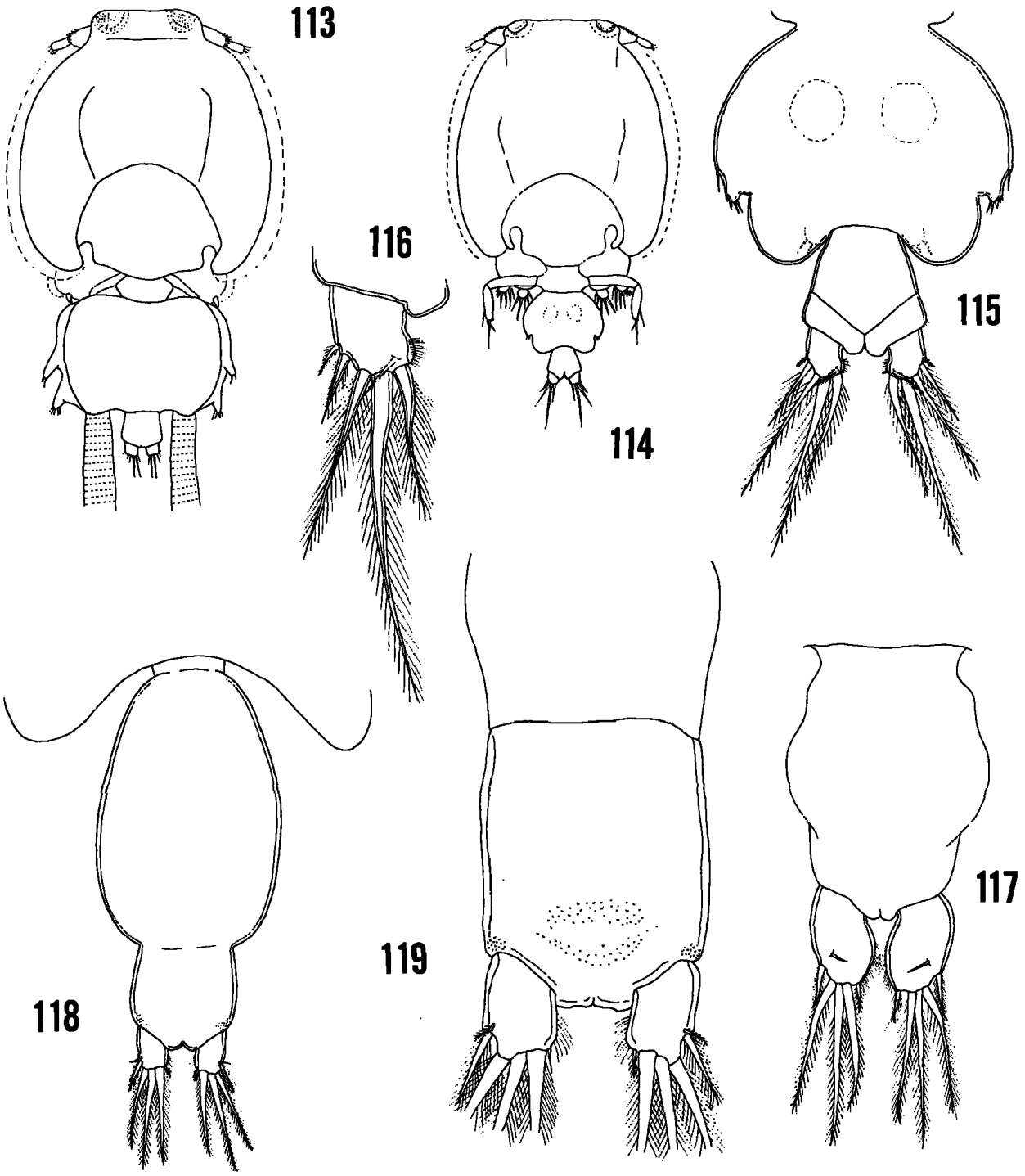
Total length and greatest width 5.7 by 2.1 mm. Abdomen (fig. 117) 1.1 mm. long and 1-segmented. Caudal rami large (384 μ by 266 μ), longer than wide; outermost of three longest setae bent inwardly, longest seta 650 μ long. Sternal furca spatulate, tines short. Leg 2 endopod with large patch of hairs on outer distal corner of first segment, rows of hairs on outer edge of second segment, small patch of hairs on third segment near junction of second and third segment. Leg 4 exopod 2-segmented with lateral spine and three terminal spines. Measurements of *B. belone* specimen.

The specimens assigned to *C. belones* from the dolphin *Coryphaena equisetis* by Wilson (1905) were described as a new species (*C. wilsoni*) by Delamare Deboutteville and Nuñes-Ruivo in 1958.

Caligus malabaricus Pillai

Figure 118

Specimens studied.—Two collections containing five females from *Ablennes hians* from Torres Strait off Northern Australia. Total length and greatest width of the specimens 4.13 by 1.42 mm., 4.13 by 1.35 mm., 3.90 by 1.27 mm., 3.75 by 1.35 mm., and 3.60 by 1.35 mm. In the largest specimen the genital segment is 1.27 by 1.12 mm. (longer than wide). The abdomen in this same specimen is 1.35 mm. long. Pillai (1961) provided a description with good figures of this species which he reported from *Tylosurus crocodilus* from India. In addition to his description it should be noted that the abdomen has a patch of spinules on the posterior corners as indicated in figure 118.



FIGURES 113–119.—*Caligus* species. 113–116. *C. tylosuri* (Rangnekar). 113. Female, dorsal view. 114. Male, dorsal view. 115. Female, genital segment and abdomen, ventral view. 116. Female, caudal ramus, ventral view. 117. *C. belones* Krøyer, female, abdomen and caudal rami, ventral view. 118. *C. malabaricus* Pillai, female, abdomen and caudal rami, ventral view. 119. *Caligus* species A, female, last abdominal segment and caudal rami, ventral view.

***Caligus* Species A to D**

Figures 119 to 132, Plate 1

In addition to the three species of *Caligus* reported above, the collections of copepods from needlefishes included four additional species of *Caligus*. These collections generally contained only one or two specimens of each species. Robert Parker, Fisheries Research Board of Canada, is currently revising the genus *Caligus*, and in view of his work we have not attempted to assign names, new or otherwise, to these remaining four species. Information is included here which may facilitate determination of the status of these species when the genus is better understood.

Caligus sp. A.—Four collections containing six females from the Gulf of Guinea, three from *Ablennes hians* and one from *Tylosurus acus*. Total length and greatest width 3.8 by 1.7 mm. Abdomen 2-segmented, posterior segment (fig. 119) with fine spinules on outer ventral corners and a patch on the medial-ventral surface as in figure. Caudal ramus 207 μ long and 124 μ wide, middle seta of longest three is 475 μ long. Sternal furca (figs. 120 and 121) spatulate, tines of furca (fig. 120) more divergent in specimen from *T. acus* than in those (fig. 121) from *A. hians*. Leg 2 endopod (fig. 122) with patch of six stout spines on outer distal corner of first segment, rows of stout, distally bent spines on outer border of second segment, and a few small spines near outer junction of second and third segments on third segment. Leg 4 exopod (fig. 123) 2-segmented; terminal segment 366 μ long with lateral spine 118 μ long, three terminal spines measure 242 μ, 148 μ, and 88 μ from innermost to outermost.

Caligus sp. B.—One collection containing four females from *Strongylura notata* from Sarasota, Fla., and another collection containing one female from *Tylosurus acus pacificus* from Cabo Blanco, Peru. Total length and greatest width of Florida specimen 3.8 by 1.9 mm. Total length and greatest width of Peru specimen 4.7 by 2.1 mm. Abdomen (fig. 124) 1-segmented, unornamented. Caudal rami longer than wide 324 μ by 236 μ; longest seta 680 μ. Sternal furca (fig. 125) spatulate. Leg 2 endopod (fig. 126) with patch of hairs on outer distal corner of first segment, rows of hairs on outer edge of second segment, and a patch of hairs on third segment. Leg 4 (fig. 127) exopod 2-segmented; terminal segment with no lateral spine, three terminal spines 254 μ, 195 μ, and 116 μ, respectively, each with a prominent basal hood.

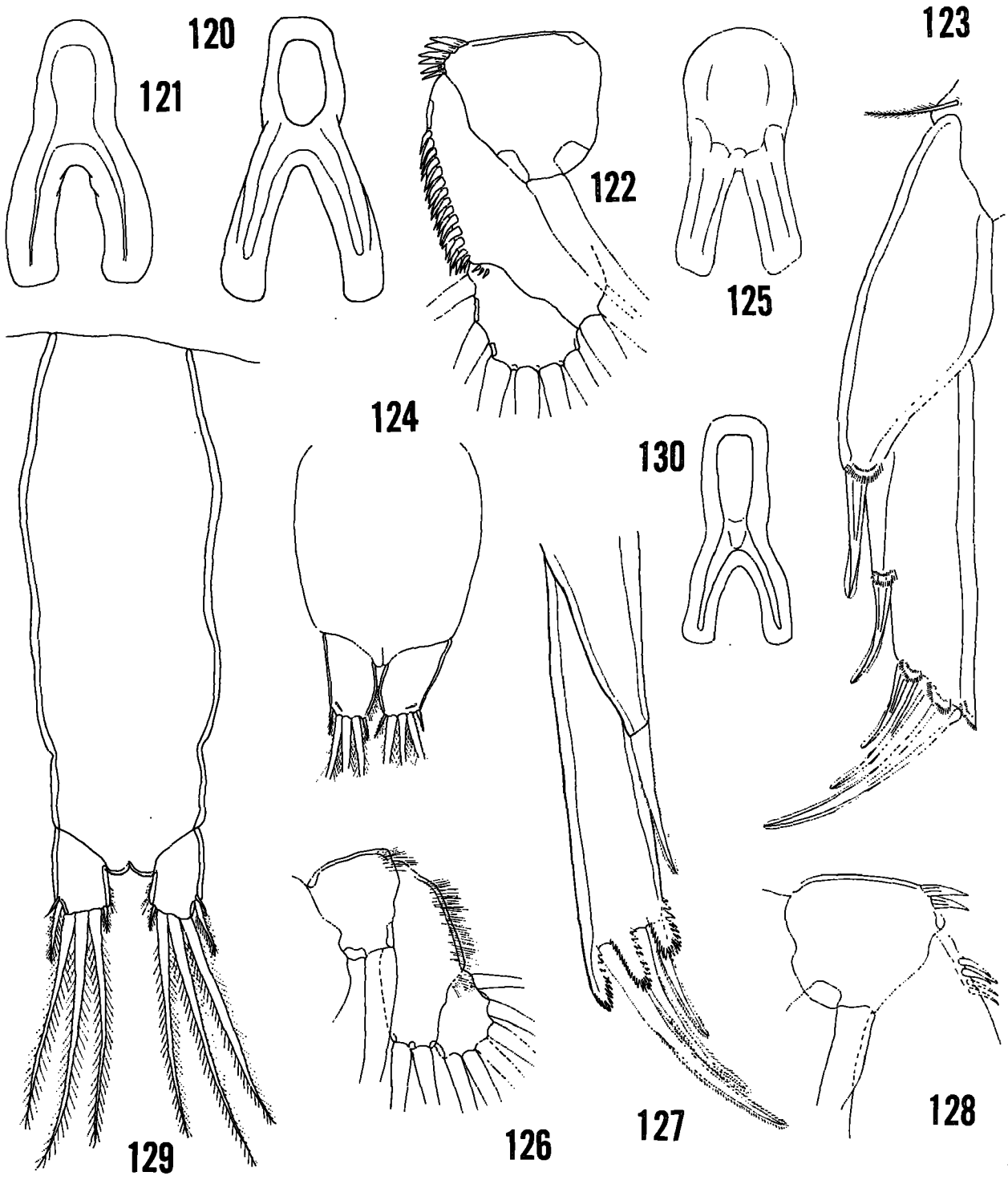
Caligus sp. C.—Two collections containing three females from *Tylosurus acus pacificus* and *T. crocodilus fodiator* from the Pacific side of Panama. Total length and greatest width 3.5 by 1.3 mm. This copepod is similar to *Caligus* sp. A in most respects including the presence of spinules on the ventral surface of the last abdominal segment. It differs from sp. A, however, in having only two prominent spines on the outer distal corner of the first endopod segment of leg 2 (fig. 128).

Caligus sp. D.—Two collections from the Philippines from *Strongylura incisa* and *S. urvillii*, each containing one female and a single collection containing one female from *Tylosurus choram* from the Red Sea. Total length and greatest width of specimen from *S. incisa*, 7.7 by 3.1 mm. Abdomen (fig. 129) 1-segmented and unarmed. Caudal rami small, slightly longer than wide (189 μ by 165 μ), longest seta 502 μ. Sternal furca (fig. 130) spatulate. Endopod of leg 2 (fig. 131) with patch of thin spines on outer corner of first segment, a row of thin spines along outer margin of second segment, and a few thin spines on third segment near outer basal corner. Leg 4 (fig. 132) exopod 2-segmented; terminal segment with a lateral spine, longest terminal spine about twice length of each of other two (230 μ).

***Caligodes laciniatus* (Krøyer)**

Figures 133 to 145, Plate 2

Specimens studied.—A total of 374 individuals from 94 collections from 7 host species. The host and locality data are provided below: *Ablennes hians*, off Pensacola, Fla.; Florida Keys; Padre Bank, Caribbean Sea; off Mississippi coast; off Surinam; off northern Brazil; Cape Verde Islands (2 collections); Gulf of Guinea (5 collections); off Sierra Leone (2 collections); Angola; Mauritius; Zanzibar; Japan (2 collections); Hawaii; off western Mexico (3 collections); off Peru (2 collections); *Strongylura leiura*, off Pondicherry, India; off Formosa; Philippines (3 collections); *Platybelone argalus*, Maldive Islands; *Lhotskia gavialoides*, off northern Australia (5 collections); *Tylosurus acus*, off southeast United States (5 collections); Gulf of Mexico (7 collections); Haiti; Virgin Islands; Gulf of Guinea; off Angola (2 collections); Philippines (4 collections); Japan;



FIGURES 120–130.—*Caligus* species. 120–123. *Caligus* species A, female (continued). 120. Sternal furca. 121. Sternal furca. 122. Endopod of second leg. 123. Fourth leg. 124–127. *Caligus* species B, female. 124. Abdomen and caudal rami, ventral view. 125. Sternal furca. 126. Endopod of second leg. 127. Last segment of fourth leg. 128. *Caligus* species C, female, first segment of second leg endopod. 129–130. *Caligus* species D, female. 129. Abdomen and caudal rami, ventral view. 130. Sternal furca.

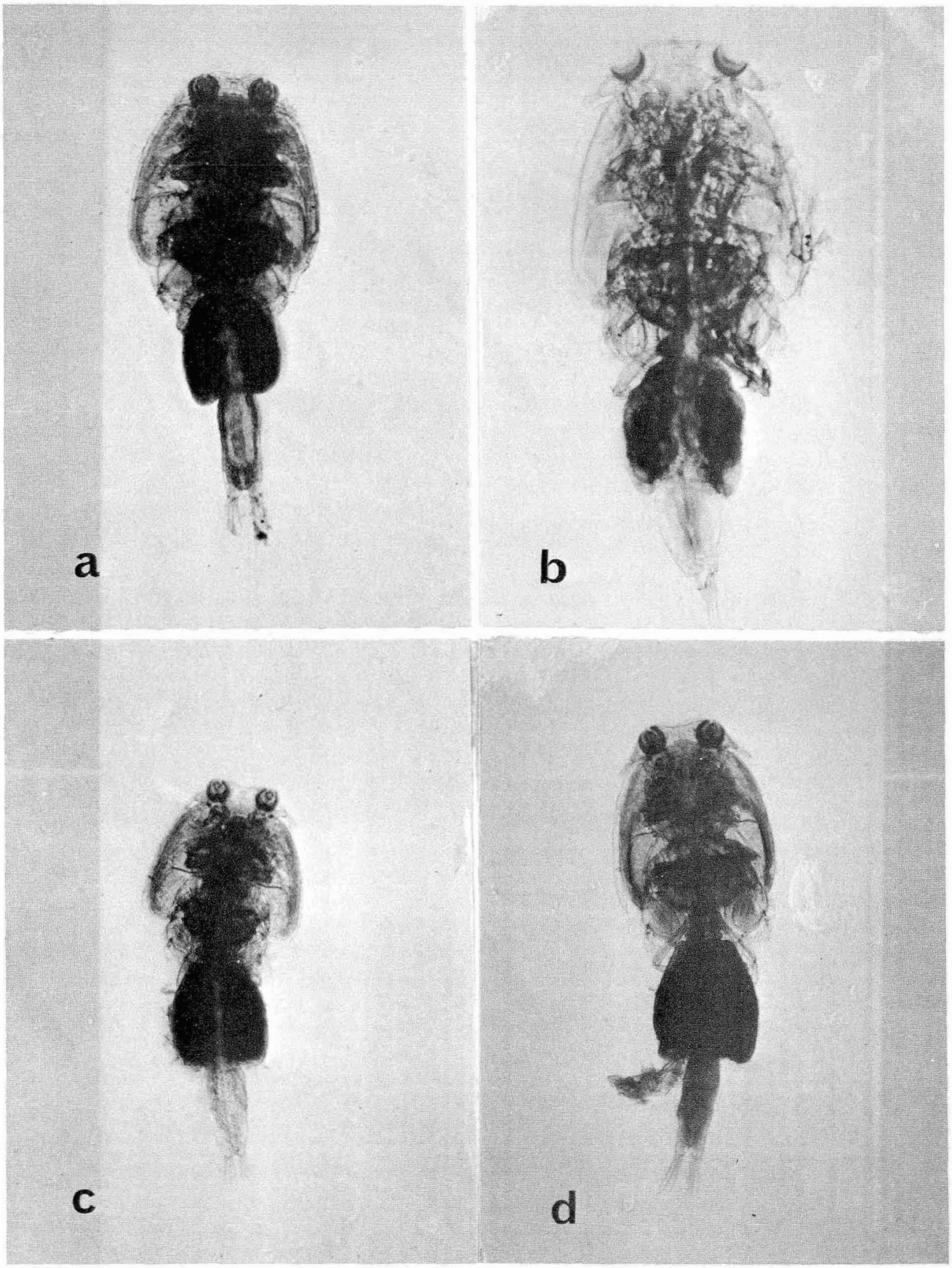


PLATE 1.—a. *Caligus* species A, female. b. *Caligus* species B, female. c. *Caligus* species C, female. d. *Caligus* species D, female.

Hawaii; Revillagigedos Islands, Mexico; Panama (Pacific); *Tylosurus crocodilus*, Matecumbe Key, Fla.; Cuba; Jamaica; Trinidad; off Venezuela; off Liberia; Gulf of Aden; Red Sea; off Zanzibar (2 collections); off Malagasy Republic (3 collections); Farquahar Island; Comores Islands; Aldabra Island; Mauritius; Seychelles Islands; Arabian Gulf; Ceylon; Madras, India; Singapore; Gulf of Thailand; Philippines; Samoa; Hawaii (2 collections); off west coast of Mexico (2 collections); off west coast of Panama; Cocos Islands (eastern Pacific); *Tylosurus choram*, Red Sea; Seychelles Islands.

Female.—Body form as in plate 2. Specimens examined had total lengths of 2.3 to 7.1 mm. (see Remarks). Greatest width in area of genital segment also varies but generally is not less than one-fourth or more than one-third of total length. In a form as variable as this, measurements of absolute size are not a reliable taxonomic character. Cephalon caligiform, about as wide as long. Lunules present. Thoracic segment bearing fourth legs free and in the form of a neck. Genital segment prominent, each posterior corner of segment has a long process that may or may not extend beyond end of abdomen. Abdomen 1-segmented, variable in length, and 5 to 7 times as long as wide. Caudal rami (fig. 133) small, bearing six setae, outermost and innermost naked, other plumose.

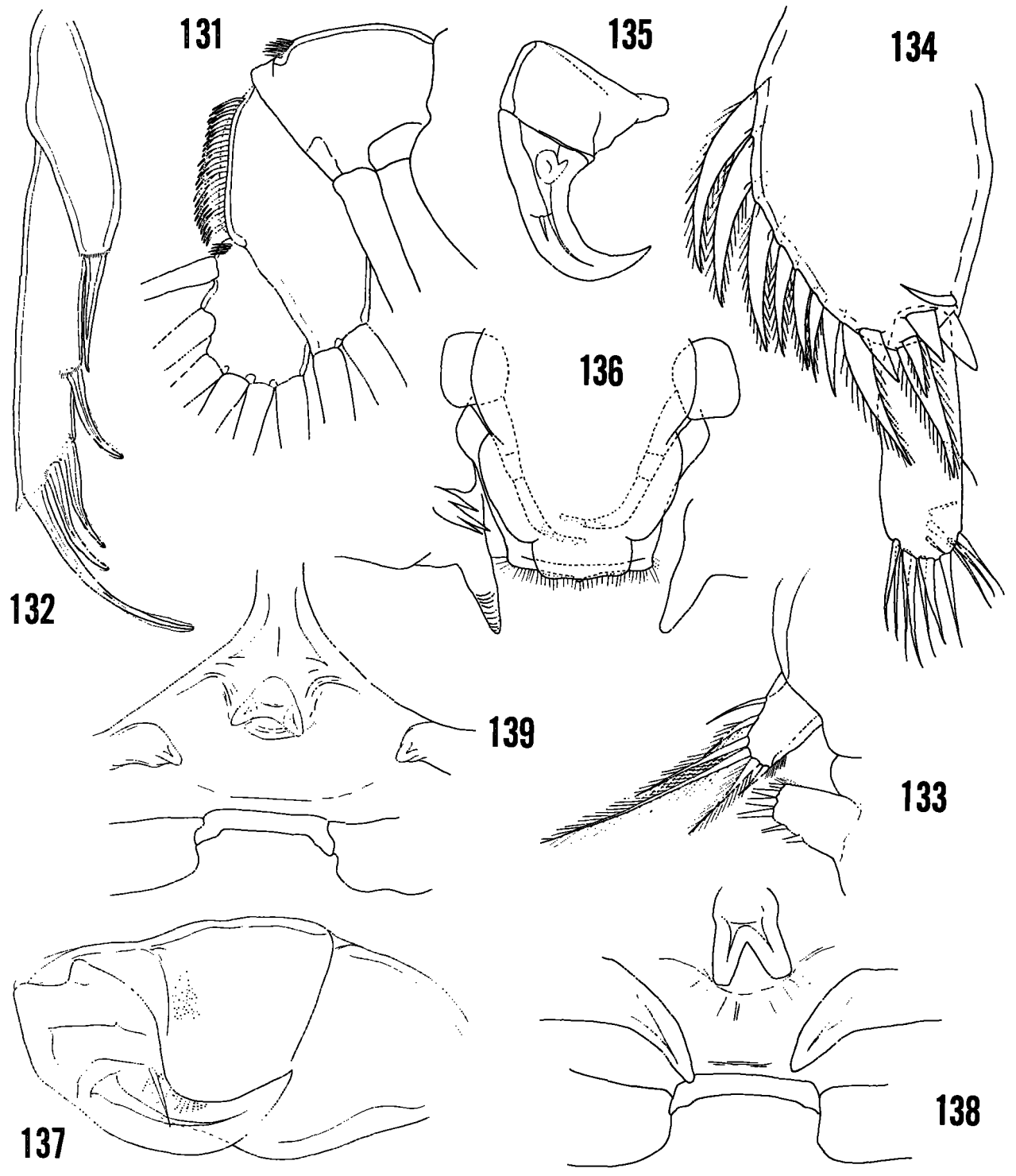
First antenna 2-segmented, armed with spines and setae as in figure 134. Second antenna (fig. 135) in form of a hook; terminal hook with two medium setae and accessory hooklike process near base. Mouthtube, mandible, and first maxilla (fig. 136) of usual caligoid form; first maxilla with three setae. Postoral processes present (fig. 136). Second maxilla of usual caligoid form, terminating in two plumose setae. Maxilliped (fig. 137) in form of a stout claw, terminal claw with patch of spinules and setae; patch of spinules present also on penultimate segment. Furca (figs. 138 and 139) usually spatulate but sometimes rounded at tips of spines (fig. 139). Accessory processes present on either side of furca and vary in length. Pillai (1961, p. 114) noted differences in development of these processes. Figures 138 and 139 show two extremes in development within the sample studied here—both from *Tylosurus acus acus* in the western Atlantic. Intermediate forms were common.

Legs 1 to 3 biramose. Leg 1 (fig. 140) exopod 2-segmented, first segment without spines and setae, second segment with three terminal spines and three inner setae; endopod 1-segmented, small, bearing two small terminal spines. Leg 2 (fig. 144) exopod 3-segmented, first two segments each with one inner seta and one small spine on outer distal corner, last segment bearing six setae and two spines; endopod 3-segmented, first segment with an inner seta, second segment with two inner setae and a spine on outer distal corner, terminal segment bearing five setae. Leg 3 (fig. 142) exopod 2-segmented, basal segment with prominent claw on outer distal corner, terminal segment bearing eight short setae; endopod 2-segmented, basal segment with one inner seta, terminal segment with four terminal setae. Leg 4 (fig. 143) uniramose; exopod with three segments, basal two segments each with short spine on outer distal corner, terminal segment with one long and two short spines. Leg 5 represented by one long process on each posterior corner of genital segment. Leg 6 absent. Egg strings uniseriate.

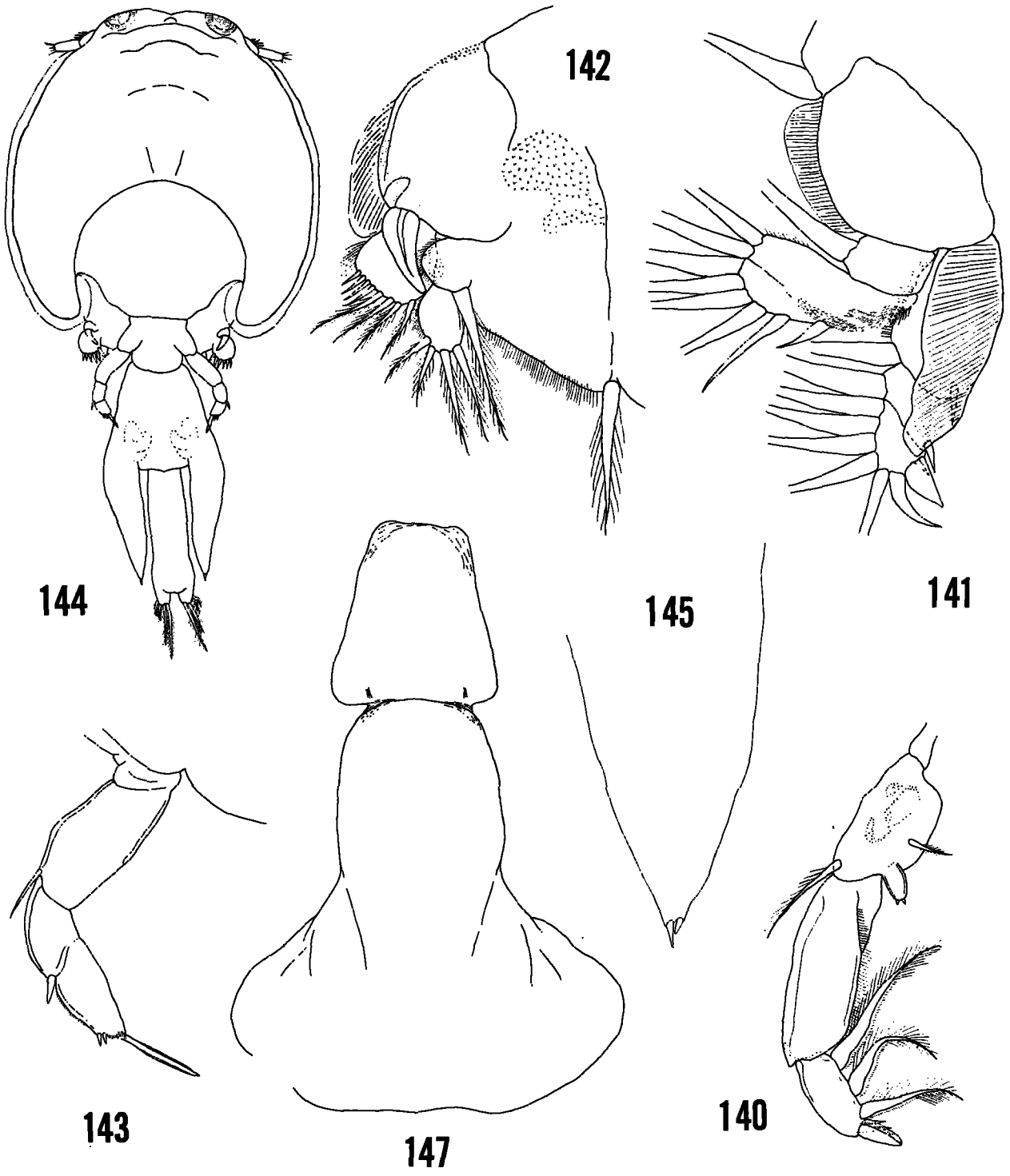
Immature female.—Body form as in figure 144. Total length 1.8 mm. Greatest width 0.82 mm. Appendages as in adult except for two spines at tip of leg 5 (fig. 145). The two immature forms are from *Tylosurus a. acus* from Honduras and *T. crocodilus* from Thailand.

Remarks.—The large sample of *C. laciniatus* studied here permits observations on size variation. Pillai (1961, p. 114) noted differences in lengths of adult females depending on host. On the basis of his collections from Indian Ocean needlefishes, he stated that those specimens from *Ablennes hians* were distinctly larger (9.8 mm.) than those from *Tylosurus crocodilus* (5.0 mm.). Kirtisinghe (1937, p. 441) noted that his specimens of this copepod from *Strongylura leiura* were larger (7.5 mm.) than those from *S. strongulura* (5.0 mm.). Nuñes-Ruivo (1962b) compared the relative lengths of four body divisions of seven females from a single *Ablennes hians* from Angola.

From the sample reported on here, 69 ovigerous females from 65 collections representing six host species were measured. Total lengths were measured from the anteriormost point on the cephalon to the end of the 5th legs. In most specimens the 5th legs extend slightly beyond the caudal rami. On the basis of these measurements, it is apparent



FIGURES 131–139.—*Caligus* and *Caligodes*. 131–132. *Caligus* species D, female (continued). 131. Endopod of second leg. 132. Fourth leg. 133–139. *Caligodes laciniatus* (Krøyer), female. 133. Caudal ramus, ventral view. 134. First antenna. 135. Second antenna. 136. Oral area. 137. Maxilliped. 138. Area of sternal furca. 139. Area of sternal furca.



FIGURES 140–145.—*Caligodes laciniatus* (Krøyer), female (continued). 140. First leg. 141. Second leg. 142. Third leg. 143. Fourth leg. 144. Dorsal view, immature female. 145. Fifth leg, immature female. 147. *Lernanthropus belones* Krøyer, female, dorsal view.

that size depends on the host (table 2). In addition to total length, we determined the proportional lengths of four main body divisions (cephalon, thorax, genital segment, and abdomen). The size of the cephalon varied the least from one host to another. The total length of the copepod was nearly seven times the length of the cephalon in specimens from *A. hians*, whereas in those from *T. crocodilus* the ratio was only 4.5 : 1. From other hosts the ratio was intermediate as follows: *T. acus*, 5.1 : 1; *Lhotskia gavialoides*, 5.3 : 1; and *S. leiura*, 5.9 : 1. These ratios suggest that the part of the copepod most affected by the host is the more posterior. Considering the habitat of this species (generally beneath the oral valve), the copepod may have to grow to lengths which permit anal respiration and elimination by extending that portion of the body beyond the edge of the oral valve, and permit egg strings to be exposed for proper oxygenation and larval escape. Figure 146 shows three specimens in place under the lower jaw oral valve of *Ablennes hians*.

TABLE 2.—*Total lengths of ovigerous female* Caligodes laciniatus, *by hosts and by areas*

Host and, in parentheses, its maximum body length (mm.)	Copepod total length												Average length, by host
	Atlantic				Indo-West Pacific				Eastern Pacific				
	Mm.				*Mm.*				*Mm.*				*Mm.*
Ablennes hians (725)	5.3	6.2			----------				5.3				
	5.3	6.8			----------				5.6				6.03
	5.4	6.9			----------				6.6				
	5.9	7.1			----------				----------				
Lhotskia gavialoides (665)	----------				3.9				----------				
	----------				4.5				----------				4.66
	----------				5.6				----------				
Strongylura leiura (501)	----------				4.1				----------				
	----------				4.2				----------				
	----------				4.3				----------				4.54
	----------				4.8				----------				
	----------				5.3				----------				
Tylosurus acus (950)	2.4	3.6			3.2				3.7				
	3.0	3.8			3.7				4.7				
	3.1	3.9			4.5				----------				
	3.2	4.1			----------				----------				3.77
	3.2	4.4			----------				----------				
	3.3	4.5			----------				----------				
	3.4	4.7			----------				----------				
	3.4	5.4			----------				----------				
Tylosurus crocodilus (860)	3.1	-----			2.3	3.2			3.4	3.8			
	3.4	-----			2.5	3.2			3.5	3.8			
	3.9	-----			2.6	3.4			3.6	3.8			
	4.3	-----			2.7	3.4			3.8	4.7			3.47
	4.4	-----			2.8	3.8			3.8	-----			
	----------				3.0	4.0			----------				
	----------				3.1	4.3			----------				
Tylosurus choram (415)	----------				2.9				----------				2.90
Average length, by area	4.36				3.70				4.29				

Geography does not seem to influence total length of the copepod except as it determines the distribution of the hosts (see table 2).

In a paper on the genus *Gloiopotes*, Cressey (1967) noted that the average size of the adult female *G. watsoni* depended on the host. Whether size differences are influenced primarily by the host or secondarily by the environment of the host cannot be determined at present, but the fact that the host influences the morphometrics of parasitic copepods is becoming more apparent. It is also obvious that the absolute size of parasitic copepods cannot be considered a reliable taxonomic character.

FAMILY ANTHOSOMATIDAE

Two species of *Lernanthropus* were collected. We have determined that only two species, *L. tylosuri* and *L. belones*, are found on needlefishes. Others described from needlefishes have been synonymized with these two.

Lernanthropus belones Krøyer

Figures 147 to 156, Plate 3 (a–c)

Lernanthropus chlamydotes Wilson, 1922, p. 48.

Specimens studied.—A total of 689 specimens, including both sexes, from 80 collections from 11 host species. A detailed list of these collections is provided below: *Ablennes hians*, Puerto Rico; *Platybelone argalus*, Bermuda (2 collections); *Strongylura anastomella*, Suruga Bay, Japan; *Strongylura exilis*, San Diego, Calif. (3 collections); Baja California (2 collections); Panama (Pacific); *Strongylura incisa*, Ebon Island, Marshall Islands (2 collections); Arnhem Land, Australia; Philippines (2 collections); Singapore (2 collections); Gilbert Islands; *Strongylura marina*, Beaufort, N.C.; Morehead City, N.C.; St. Simons Island, Ga. (3 collections); Florida, west coast (3 collections); Florida, east coast (2 collections); Venezuela; Trinidad; *Strongylura notata*, Florida, west coast (7 collections); Florida, east coast (3 collections); Andros Island, Bimini Island, Bahamas; Yucatan; Cuba (2 collections); Jamaica; *Strongylura scapularis*, Balboa, Canal Zone (2 collections); Guayaquil, Ecuador (2 collections); *Strongylura strongylura*, Bombay, India; Madras, India; Singapore; China; Philippines; *Strongylura timucu*, Florida, west coast (5 collections); Florida, east coast (3 collections); Bahamas (2 collections); Cuba; Jamaica (3 collections); Puerto Rico (4 collections); Virgin Islands (2 collections); Colon, Panama; Yucatan (2

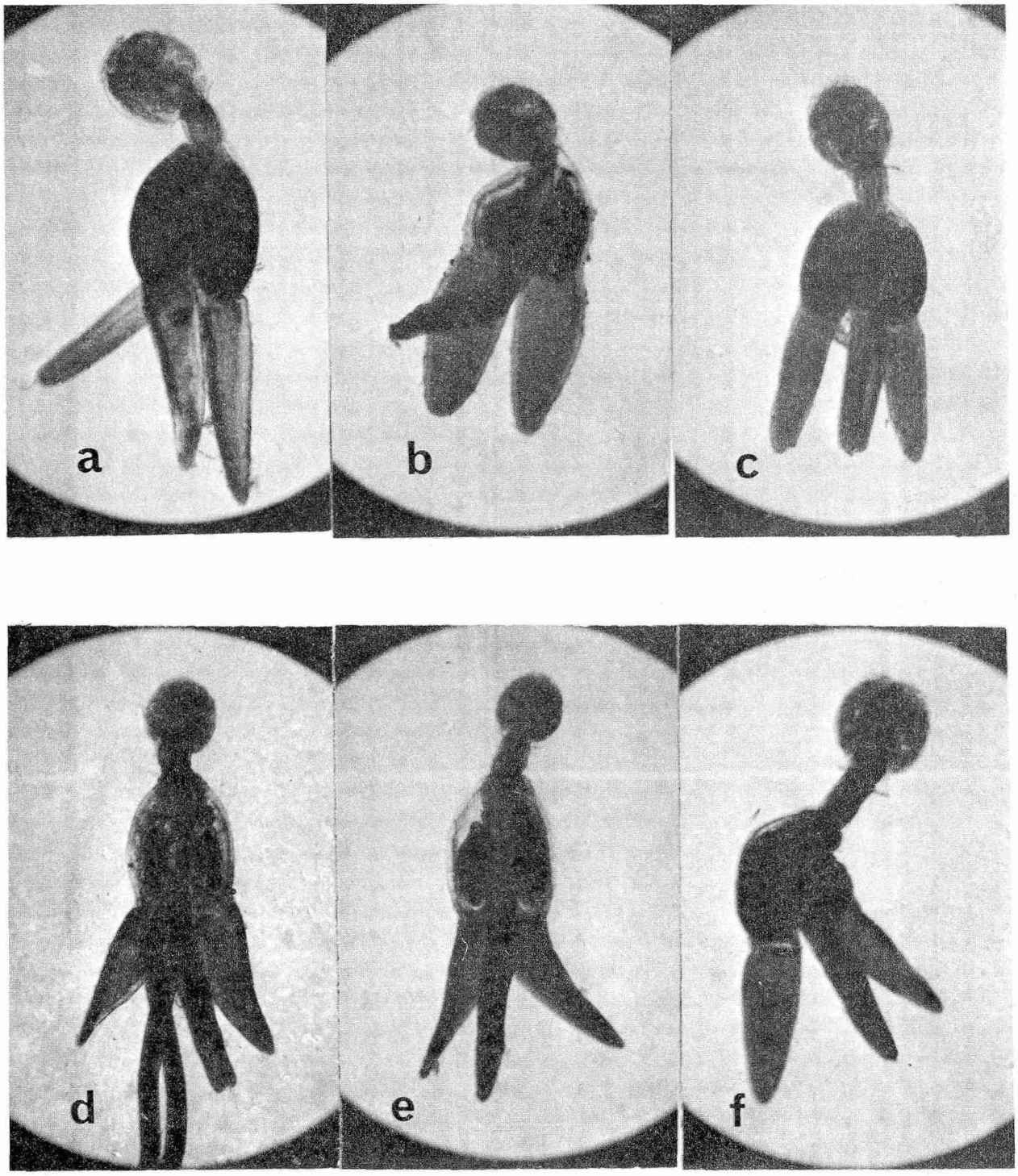


PLATE 2.—*Caligodes laciniatus* (Krøyer), female. a. From *Tylosurus acus* (Western Atlantic). b. From *Tylosurus acus* (Gulf of Mexico). c. From *Tylosurus acus* (Revillagigedo Islands). d. From *Ablennes hians* (Surinam). e. From *Ablennes hians* (Gulf of Guinea). f. From *Tylosurus crocodilus* (Jamaica).

collections); Honduras; Brazil (2 collections); *Tylosurus punctulatus*, Sandakan, Borneo.

Female.—Body form as in figure 147. Average total length 2.58 mm., based on 128 ovigerous females from six host species. Specimens from Pacific waters average larger (4.02 mm.) than those from the Atlantic (2.22 mm.). Most of our collections were from the Atlantic; if more material were available from the Pacific the average total length for all collections would be greater. The total length (in millimeters) of each adult female in 36 collections from six host species is presented below. Note that the variation between collections is greater than the variation within a collection.

Strongylura notata	2.19 (average).
Sarasota, Fla.	1.7, 1.8, 1.9, 1.9, 1.95.
Sarasota, Fla.	1.95, 2.0.
Sarasota, Fla.	3.0, 3.15, 3.15, 3.2, 3.3, 3.4.
Sarasota, Fla.	2.8, 2.8, 3.0, 3.0, 3.15.
Key Biscayne, Fla.	1.95, 2.0, 2.1.
Andros Island, Bahamas	1.65, 1.7.
Cuba	2.3, 2.4, 2.5, 2.6.
Yucatan	1.7, 1.95, 2.5.
Strongylura timucu	2.10 (average).
Sanibel Island, Fla.	1.5.
Sarasota, Fla.	1.7, 1.8, 1.9, 1.9, 1.9, 1.9, 2.0.
Cedar Keys, Fla.	1.6, 1.7, 1.7, 1.8, 2.1.
Key Biscayne, Fla.	2.2.
Key Biscayne, Fla.	1.95, 2.1, 2.1, 2.2.
Bahamas	2.0, 2.1, 2.2.
Bahamas	2.0, 2.3.
Yucatan	2.1, 2.25, 2.4, 2.4, 2.5.
Yucatan	2.1, 2.2, 2.3, 2.4, 2.7.
Puerto Rico	1.9, 2.2, 2.2.
Puerto Rico	2.2, 2.2, 2.25, 2.3.
Virgin Islands	1.9, 1.95, 2.2.
Colon, Panama	2.0.
Brazil	2.4, 2.5, 2.5.
Strongylura marina	2.44 (average).
Beaufort, N.C.	2.1, 2.3, 2.3, 2.3, 2.3, 2.5.
Beaufort, N.C.	2.9, 3.1, 3.3, 3.4, 3.4.
Beaufort, N.C.	2.6, 2.7, 2.8, 2.85, 2.9, 3.0.
Jekyll Island, Ga.	1.9, 1.9, 2.25, 2.4, 2.5.
Flagler Beach, Fla.	1.8, 2.0.
Amelia River, Fla.	1.65, 1.9, 1.9, 1.95.
Strongylura incisa	3.93 (average).
Marshall Islands	4.0, 4.2, 4.2, 4.4, 4.5.
Gilbert Islands	4.2.
Philippines	3.15.
Arnhem Land, Australia	2.8.
Strongylura exilis	4.08 (average).
San Diego, Calif.	2.5, 2.7.
San Diego, Calif.	3.6, 3.7, 3.75, 3.9, 4.5.
San Diego, Calif.	4.4, 4.5, 4.7, 4.9, 4.9, 4.95.
Strongylura scapularis	3.20 (average).
Balboa, Canal Zone	3.2, 3.2.

The mean total length clearly varies with the host or geographic area or both. Atlantic *L. belones* are generally shorter than those from the Pacific. The lengths are not always consistent within a geographic area, however. For example, the lengths of the copepods from four collections from *S. notata* from Sarasota, Fla., vary considerably from collection to collection; each collection was made in July–August but in different years (1965–68). Another example is the three collections from *S. exilis* from San Diego, Calif.

Cephalon about one-third total body length. Posterior corners without horns (fig. 147). No further description of the female is given here as the appendages are identical to those described for *L. cornutus* (=*L. tylosuri*) by Shiino (1965). Shiino stated that the armature of the second pair of legs differs in the two species but we could not find this difference in the collections of both species reported herein.

Male.—Body form as in figure 148 and plate 3. Total length of six specimens averages 1.53 mm. (1.10–2.18 mm.). Specimens from Pacific areas are larger (1.42, 1.42, 1.80, and 2.18 mm.) than those from the Atlantic (1.10 and 1.27 mm.). Cephalon slightly wider than long and composing about one-quarter total body length.

Second antenna (fig. 149) a simple claw, surface of segments covered with small pits. Mandible

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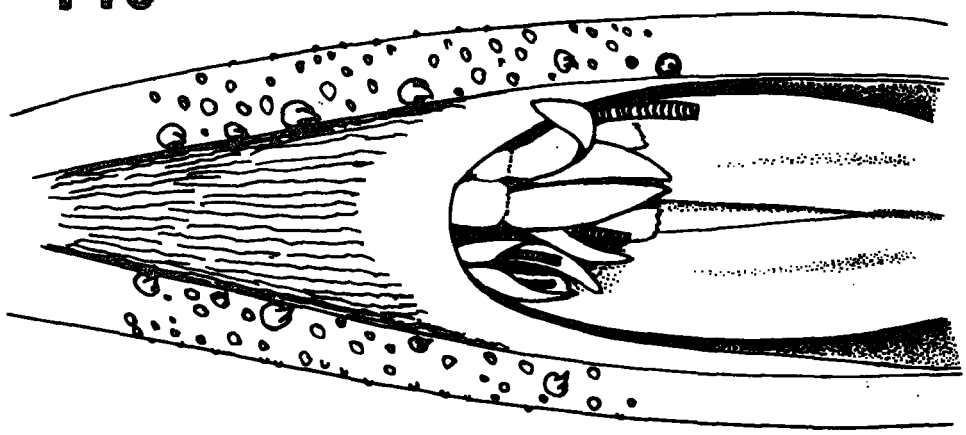


FIGURE 146.—Lower jaw of *Ablennes hians* showing three female *Caligodes lacintatus* attached beneath oral valve.

(fig. 150) of usual caligoid type with about six teeth. First maxilla (fig. 150) with inner posteriorly directed process near mouthtube and outer lobe bearing three setae. Second maxilla (fig. 151) with stout basal segment, distal two segments in form of a claw; tip of maxilla with rows of spinules (fig. 152).

Leg 1 (fig. 153) exopod 1-segmented with five broad distal spines, row of spinules near base of innermost spine; endopod 1-segmented bearing a single long seta and spinules scattered over distal half. Leg 2 (fig. 154) exopod 1-segmented with distal border bearing rows of spinules, posterior surface of segment with median ridge bearing spinules. Leg 3 in form of an elongate lateral process tipped by an area bearing several (6–10) short spines, spinose area sometimes knoblike. Leg 4 in form of an elongate process with bifurcated tip (figs. 155, 156), each arm of bifurcation bearing short spines at tip; as in leg 3 spinose area often knoblike, area between rami with shallow indentation.

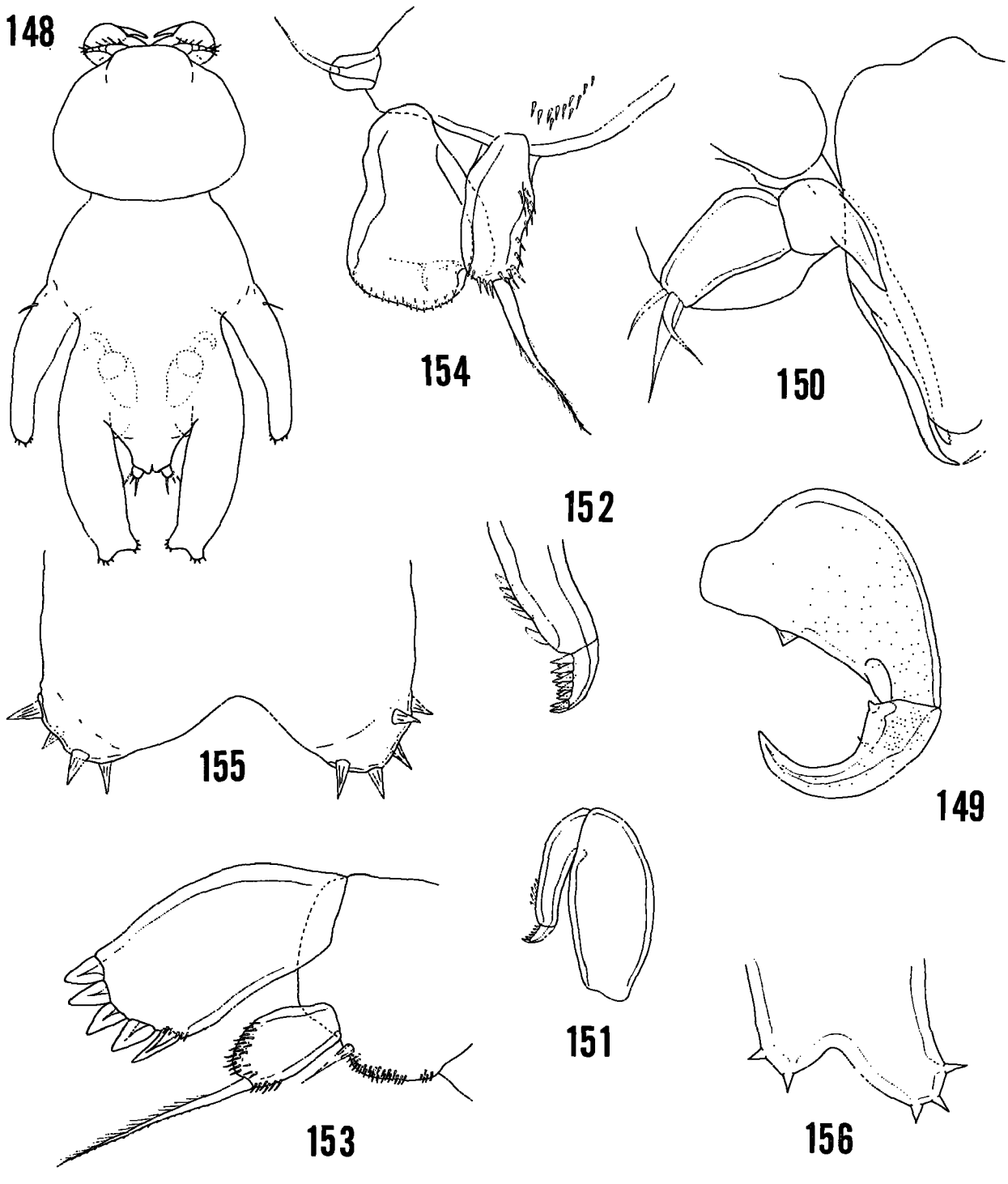
Remarks.—This species is closely related to *L. tylosuri* (= *cornutus*) also commonly found on needlefishes. A discussion of the characters used to separate these two species and of the host specificity of each follows the description of *L. tylosuri*.

***Lernanthropus tylosuri* Richiardi**

Figures 157 to 162, Plates 3(d-f), 4

Lernanthropus cornutus Kirtisinghe, 1937, p. 448.

Specimens studied.—A total of 474 specimens from 99 collections, including both sexes, from 14 host species. A detailed list of these collections is provided below: *Ablennes hians*, Woods Hole, Mass.; off Virginia coast; Haiti; Recife, Brazil; Gulf of Guinea (3 collections); Sierra Leone (3 collections); Mauritius; Philippines (2 collections); Japan (10 collections); Formosa; Marshall Islands; Hawaii; Gulf of California; Acapulco, Mexico; Panama (Pacific); Cabo Blanco, Peru; *Platybelone argalus*, Fernando Póo, Gulf of Guinea; *Strongylura leiura*, Persian Gulf; Philippines (2 collections); *Strongylura exilis*, Baja California; northern Peru; *Strongylura incisa*, Queensland, Australia; *Strongylura marina*, British Honduras; *Strongylura strongylura*, Malay Peninsula (2 collections); *Strongylura timucu*, Rio de Janeiro, Brazil; *Strongylura urvillii*, Philippine Islands; *Strongylura anastomella*, Japan (9 collections); Korea (2 collections); *Tylosurus acus*, Puerto Rico; Virgin Islands; Honduras; Sierra Leone; Angola (3 collections); Java; Philippines (2 collections); Revillagigedos Island, Mexico; Gulf of California; Acapulco, Mexico; Panama (Pacific); *Tylosurus choram*, Red Sea; *Tylosurus crocodilus*, Matecumbe Key, Fla.; U.S. east coast; Bahamas (3 collections); Venezuela (5 collections); Red Sea; Kenya; Zanzibar; Nosy Bé, Madagascar (3 collections); Mauritius; Seychelles; Gulf of Aden; Persian Gulf; Arabian Gulf; Ceylon; Kerala, India; Java; Singapore; Gulf of Thailand; North Borneo (3 collections); Philippines (3 collections); Japan; Marshall



FIGURES 148–156.—*Lernanthropus belones* Krøyer, male. 148. Dorsal view. 149. Second antenna. 150. Oral area. 151. Second maxilla. 152. Tip of second maxilla. 153. First leg. 154. Second leg. 155. Fourth leg. 156. Fourth leg.

Islands; Hawaii (2 collections); Matzatlan, Mexico; Panama (Pacific); *Tylosurus punctulatus*, Philippines (2 collections).

Female.—Body form as in plate 4 and figure 157. The female of this species was redescribed by Shiino (as *L. cornutus*) in 1965 so no further description is given here except as pertains to variation in the lateral cephalic processes. These processes, by which the females of this species can be separated from the preceding species, show great variation in development. However, little correlation could be found with host or locality regarding this variation. Plate 4 illustrates several examples of variation in this character. In a series of 52 specimens from as many collections the width of the cephalon across the lateral processes was compared with the length of the cephalon. Unlike *L. belones*, where the width of the cephalon at the posterior corners is less than or occasionally equal to the cephalon length, the width of the cephalon of *L. tylosuri* at this point, because of these processes, is significantly greater than the cephalon length. A summary of the measurements for the 52 collections is presented below.

The average widths, expressed as percentage of cephalon length to width, for four host species are as follows:

A. hians	66.7	(13 collections)
S. anastomella	76.5	(7 collections)
T. crocodilus	77.3	(28 collections)
T. acus	75.9	(9 collections)

The average widths, expressed as percentage of cephalon length to width, by geographical area are as follows:

Western Atlantic	73.4	(13 collections)
Eastern Atlantic	73.0	(6 collections)
Indian Ocean	79.4	(9 collections)
Central and western Pacific	74.5	(23 collections)
Eastern Pacific	77.3	(6 collections)

Male.—Body form as in figure 158 and plate 3. Total length 2.4 mm. (single specimen from *S. anastomella*—Japan). Cephalon wider than long (0.82 by 0.68 mm.) and making up about one-quarter of the body length. Caudal rami armed with four setae as indicated in figure 159. Appendages as in *L. belones* except for the following subtle differences. Tip of leg 3 (fig. 160) with the spine-bearing portion knoblike. End of leg 4 (figs. 161, 162) bifurcate (as in *L. belones*), each branch with knoblike tip bearing short spines; indentation between branches deeper than in *L. belones* (compare figs. 155 and 156 with 160 and 161).

Remarks.—*L. tylosuri* and *L. belones* are common on needlefishes. In the 146 collections of these species the two species of copepods were never found on the same host individual. The following list shows the frequency of each copepod species on each host species and demonstrates host specificity within each species of copepod (the numbers refer to numbers of collections):

	L. tylosuri	*L. belones*
Ablennes hians	12	1
Platybelone argalus	1	1
Strongylura exilis	0	4
S. incisa	1	7
S. leiura	3	0
S. marina	1	12
S. notata	0	15
S. scapularis	0	4
S. strongylura	2	4
S. urvillii	1	0
S. timucu	0	26
S. anastomella	9	0
Tylosurus acus	10	0
T. crocodilus	31	0
T. punctulatus	2	0

L. tylosuri clearly is common on *Ablennes hians*, *Strongylura leiura*, *S. anastomella*, and the species of *Tylosurus*, whereas *L. belones* is predominant on the other species of *Strongylura*.

FAMILY LERNAEIDAE

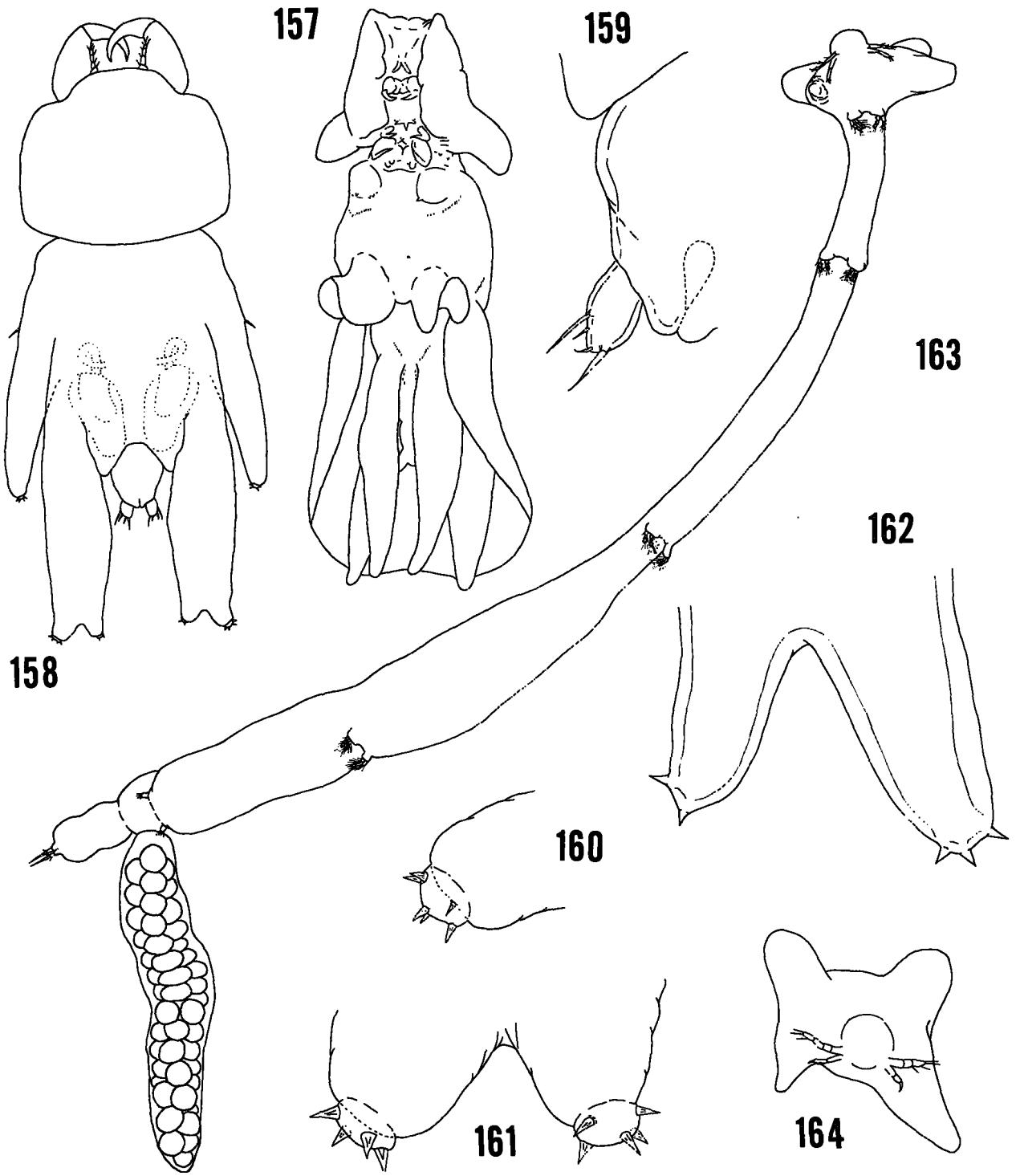
Two members of this family were collected, *Lernaea* sp. and *Lernaeenicus* sp. Neither of these is considered a specific parasite of needlefishes.

Lernaea Sp.

Figures 163, 164

A single ovigerous female (6.9 mm. long) was removed from the pit immediately behind the left pectoral fin of a *Xenentodon cancila* collected in an unknown fresh-water locality in southeast Asia.

The copepod may be an undescribed species but in view of the amount of variation which occurs within the species of this genus (see Ho, 1961) and the lack of locality data, description on the basis of a single specimen would be premature. Figures of the whole animal (fig. 163) and the anchoring apparatus (fig. 164) are provided. One of the horns seems to be deformed in this specimen.



FIGURES 157–164.—*Lernanthropus tylosuri* Richiardi and *Lernaca* species. 157–162. *L. tylosuri* female. 157. Ventral view, after Shiino. Same, male. 158. Dorsal view. 159. Caudal ramus, ventral view. 160. Third leg. 161. Fourth leg. 162. Fourth leg. 163–164. *Lernaea* species, female. 163. Ventral view. 164. Anterior end of body.

The spine and seta formulas for legs 1 to 4 follow:

	Leg 1		Leg 2		Leg 3		Leg 4	
	exo	end	exo	end	exo	end	exo	end
Seg. 1.....	I:1	0:1	I:1	0:1	I:1	0:1	I:1	0:1
Seg. 2.....	I:1	0:1	I:1	0:2	I:1	0:2	I:1	0:2
Seg. 3.....	II:5	II:4	III:5	II:4	III:5	II:4	III:5	II:3

On the basis of the shape of the anchor, the specimen seems to be closely related to *Lernaea composita* Wilson, 1924 described from the electric catfish, *Malapterus electricus*, in Egypt.

***Lernaeenicus* Sp.**

Specimens studied.—A single female embedded at the base of the pectoral fin of a specimen of *Tylosurus crocodilus* from Manila, Philippines.

FAMILY LERNAEOCERIDAE

***Lernaeolophus sultanus* (Milne-Edwards)**

Specimens studied.—One collection containing one immature female from the tongue of *Platybelone argalus trachura* taken at Ascension Island; one collection containing two females from the roof of the mouth of *Strongylura marina* collected off Belize, British Honduras; and one collection of two females from the roof of the mouth of *Tylosurus a. acus* from Haiti.

Remarks.—This copepod has been considered recently by Kabata (1968) so no further description is added here. His investigations showed this species to be a lernaeocerid and not a pennellid as thought by Yamaguti (1963). *L. sultanus* is not common on needlefishes, and they are probably not its preferred host. It has been previously reported from *Acanthocybium solandri*, *Caranx ascensionis*, *Istiophorus gladius*, *Haemulon plumieri*, *Maena vulgaris*, and two species of *Serranus*.

Order Philichthyidea

A single species of the family Philichthyidae was collected—a new species of *Colobomatus* from the cephalic canals of needlefishes.

FAMILY PHILICHTHYIDAE

***Colobomatus goodingi* Cressey and Collette, New Species**

Figures 165 to 174

Specimens studied.—Sixty-five collections from 7 host species containing 190 females as listed below: *Ablennes hians*, Cuba; Haiti; Sierra Leone (2 collections); Dahomey; Gabon; Torres Strait, Australia (2 collections); Acapulco, Mexico; Panama (Pacific); *Strongylura notata*, Sanibel Island, Fla.; Sarasota, Fla. (2 collections); Tampa Bay, Fla.; Alligator Harbor, Fla.; Key Biscayne, Fla. (3 collections); Bimini, Bahamas (2 collections); Providence Island, Caribbean Sea; *Strongylura marina*, west coast of Florida; Everglades Park, Fla.; Clearwater, Fla.; Alligator Harbor, Fla.; Panama City, Fla.; *Strongylura timucu*, west coast of Florida (2 collections); Haiti (2 collections); Puerto Rico (2 collections); Virgin Islands; Curaçao; *Strongylura exilis*, Panama (Pacific); *Tylosurus acus*, Gulf of Mexico (2 collections); Bahamas (2 collections); Angola (2 collections); Philippines; Acapulco, Mexico; Panama (Pacific); Cabo Blanco, Peru; *Tylosurus crocodilus*, Virginia Key, Fla.; Bahamas; Trinidad; Venezuela; Cameroons; Red Sea; Gulf of Aden; Madagascar (4 collections); Madras, India; Kerala, India; Ceylon; Java; Manila, Philippines; Marianas Islands; Solomon Islands; Marshall Islands; Panama (Pacific) (2 collections); Cocos Island (Eastern Pacific).

Holotype female (USNM 125700) and five paratype females (USNM 125701) from *Strongylura notata* from Bimini.

Female.—Body form as in figure 165. Total length based on an average of 28 ovigerous females from the four host species 4.4 mm. (2.7–7.1 mm.). Greatest width 1.9 mm. (0.82–2.78 mm.).

Cephalon with single lobe projecting anterior to first antenna (in all other species except *C. muraenae* this lobe is double). Three thoracic segments partially separated from each other posterior to cephalon, each segment only slightly wider than cephalon. Next following segment greatly expanded, each side bearing an anteriorly and posteriorly directed lobe; this segment composes about one-third total body length. The following segment with a lateral, well-developed lobe on each side. Three remaining segments (abdomen?) of about equal width and incompletely divided from each other, last segment with a posteriorly directed lobe projecting between caudal rami giving posterior portion of body a triramose appearance.

First antenna apparently 4-segmented, each segment bearing a few long setae; the total length of this appendage is only 26.5 μ. Because of its small

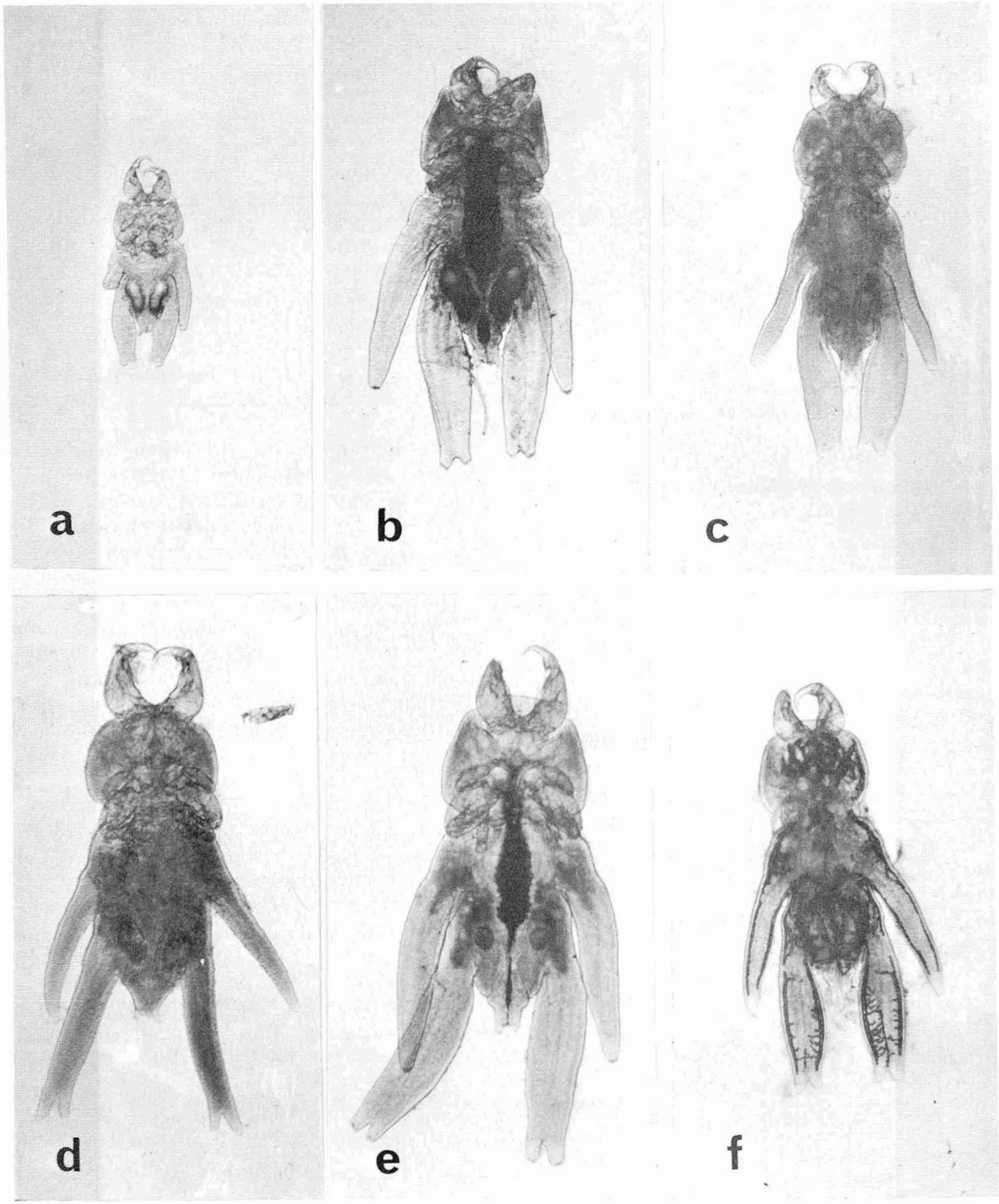


PLATE 3.—*Lernanthropus belones* Krøyer, male. a. From *Strongylura strongylura* (Bombay, India). b. From *Ablennes hians* (Puerto Rico). c. From *Strongylura exilis* (San Diego), *Lernanthropus tylosuri* Richiardi, male. d. From *Strongylura anastomella* (Japan). e. From *Ablennes hians* (Marshall Islands). f. From *Ablennes hians* (Philippines).

size it was not possible even with the highest magnification to see enough details to make an accurate drawing of this appendage (five specimens examined).

Remaining appendages consisting of mandible (fig. 166), first maxilla (fig. 167), and second maxilla (fig. 168) contained within the mouthtube. Figure 169 illustrates position of appendages within tube. All other appendages lacking. Egg sacs broken on all but one specimen; sacs held close to body on either side of abdomen (represented by dotted lines on fig. 165) and containing 50 to 75 eggs.

Color in life, cream.

Male.—Unknown.

Etymology.—This species is named for Richard Gooding who made preliminary examinations of this species and first recognized it as new.

Remarks.—This species can be separated from all other species of *Colobomatus* except *C. muraenae* by the two cephalic lobes present in the other species. It can be separated from *C. muraenae* by the presence of a posterior lobe between the caudal rami in the new species (no such lobe in *C. muraenae*).

Sites of infestation.—*Colobomatus goodingi* has been found in three of the major lateral line canals on the heads of needlefishes: preoperculomandibular (from the tip of the lower jaw posteriorly); interorbital (above each eye); and preorbital (short canal in front of eye). *C. goodingi* has occasionally been found on the upper jaw which does not appear to have a distinct branch of the lateral line system. The most common site of infestation (51 of 66) in *Strongylura notata* is the lower jaw, where a large easily visible swelling forms (fig. 171). The next most common site in *S. notata* is in the interorbital canal (11 of 66 sites). Only three infestation sites were on the upper jaw and one was in the preorbital canal. Similar swellings were present in infested *S. marina* and *S. timucu*.

No distinct capsule (fig. 171) such as is present in western Atlantic species of *Strongylura* was found in any specimens of *Tylosurus* or *Ablennes*. In *Ablennes*, expansion of the lateral line canal is usually internal and makes it very difficult to detect infested specimens; consequently, *C. goodingi* was at first thought to be confined to western Atlantic species of *Strongylura*.

Twenty-one of 24 Venezuelan specimens of *Tylosurus crocodilus* (132–300 mm. BL) were infested with *C. goodingi*. Of 46 sites, 37 were on the lower jaw (19 on the left and 18 on the right) and 9 were in the interorbital canal (4 on the left and 5 on the right). Three Bahamian and one Jamaican specimens each had an infestation site on the right side of the lower jaw. A specimen of *T. crocodilus* from Haiti had one small *C. goodingi* in the left interorbital canal and one on each side of the lower jaw.

Histopathology.—Seven *Colobomatus* lesions were examined in step-serial sections prepared from mandibles and maxillae of four *Strongylura notata* from Bimini. These tissues had been fixed in 4 percent formalin and were decalcified in 5 percent formic-citrate before sectioning. Staining was hematoxyline and eosin.

Reactions to the *Colobomatus* were variable, ranging from almost none (fig. 172) to a nearly complete obliteration of the involved lateral line canal by granulation tissue, inflammatory infiltrate, and, in some infestations, new bone formation (fig. 173). New bone formation was always orderly and showed no evidence of neoplastic transformation. In one example the formation could be related to fracture of an adjacent bone trabeculum. New bone formation was always associated with marked chronic osteitis or osteitis combined with microfracture.

The epithelium lining the canals occupied by *Colobomatus* was generally only a few cells thick, and the cells were extremely flat except where underlying inflammation was pronounced. In the latter situation, the epithelium was thickened and usually diffusely infiltrated by the cellular reaction.

The inflammatory infiltrates were composed mainly of lymphocytes and macrophages. Mononuclear eosinophils were moderately numerous, often forming small clusters. Occasionally, the granulation tissue contained fairly discrete granulomas, and the epithelioid cells within these granulomas contained deposits of eosinophilic material, possibly derived from phagocytosis of the necrotic ova commonly present within the cavity (fig. 174).

HOST-PARASITE LIST

The species of copepods collected from each species of needlefish are given in this section. The

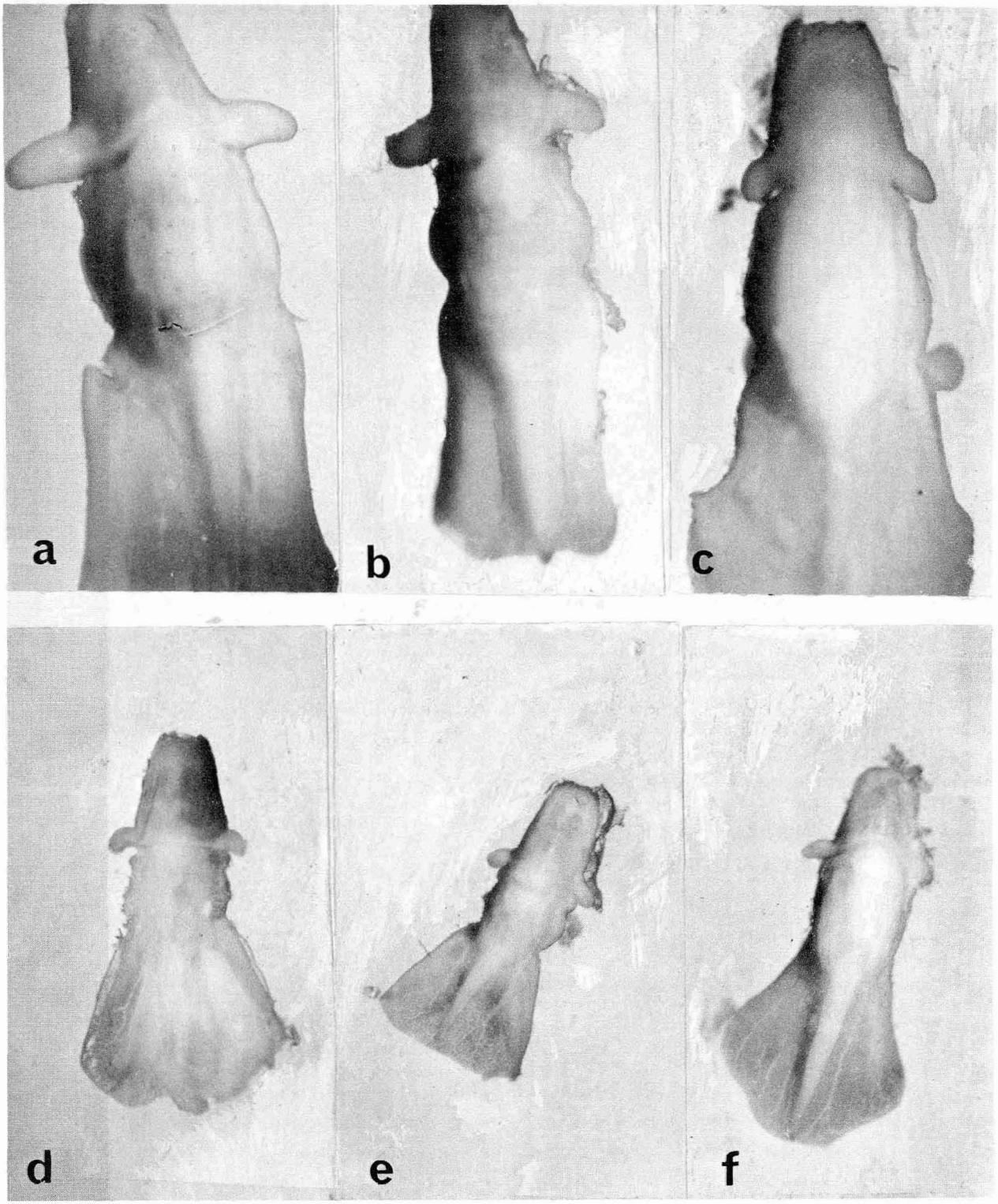
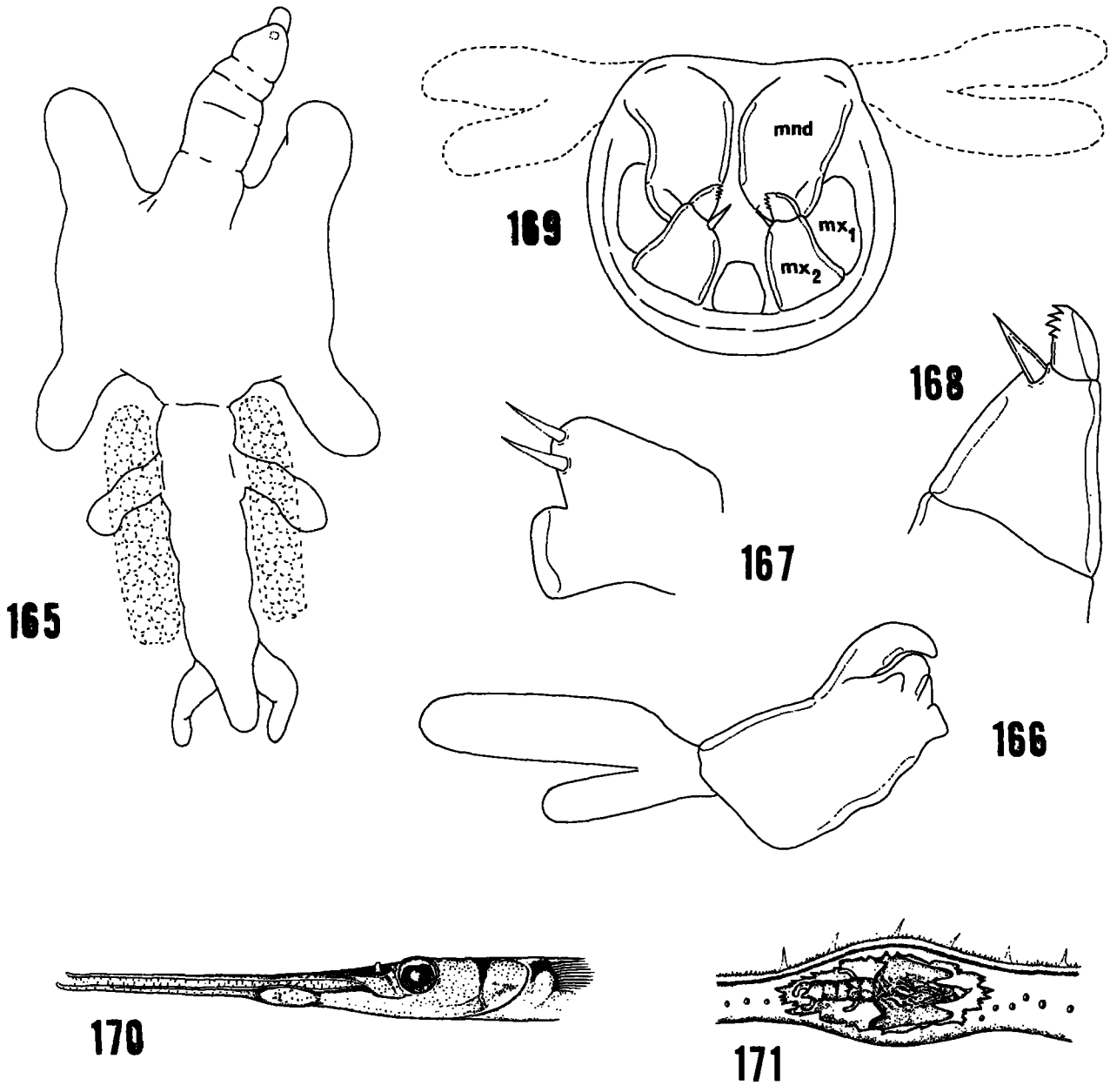


PLATE 4.—*Lernanthropus tylosuri* Richiardi, female. a. From *Ablennes hians* (Marshall Islands). b. From *Ablennes hians* (Gulf of Guinea). c. From *Strongylura anastomella* (Japan). d. From *Tylosurus acus* (Virgin Islands). e. From *Tylosurus crocodilus* (Venezuela). f. From *Tylosurus crocodilus* (Madagascar).



FIGURES 165–171.—*Colobomatus goodingi*, new species, female. 165. Dorsal view. 166. Mandible. 167. First maxilla. 168. Second maxilla. 169. Oral area. 170. Lateral view of head of *Strongylura notata* showing site of *Colobomatus* infestation on lower jaw. 171. *Colobomatus* site on lower jaw of *Strongylura notata* with covering of capsule removed.

needlefish species are listed alphabetically; the four worldwide species are further listed regionally, from the western Atlantic to the eastern Pacific. Total numbers of hosts examined, size range (in millimeters BL, body length, and SL, standard length, where possible), and brief description of host range are also included. The copepod lists include total numbers, sex, and general localities. Literature records are given following our material.

Ablennes hians (Valenciennes)

A large (maximum size 725 mm. BL) offshore marine needlefish found worldwide in tropical and subtropical seas (see fig. 175).

WESTERN ATLANTIC

81 specimens (83–630 mm. BL) from 30 collections.

Caligodes laciniatus, eight females from six specimens (200–240 mm. BL). Florida; Mississippi; Caribbean Sea; Surinam; Brazil.

Parabomolochus bellones, 12 males and 96 females from 31 specimens (169–535 mm. BL). Woods Hole, Mass.; Virginia; Florida; Mississippi; Grand Bahamas; Haiti; Caribbean Sea; Honduras; Recife, Brazil.

Lernanthropus tylosuri, six females and three males from four specimens (353–455 mm. BL). Woods Hole, Mass.; New Point, Va.; Port-au-Prince, Haiti; Recife, Brazil.

Lernanthropus belones, three males and one female from one specimen (459 mm. BL). Western Puerto Rico.

Colobomatus goodingi, two females from interorbital canals of two specimens (455–630 mm. BL). Cuba; Port-au-Prince, Haiti.

EASTERN ATLANTIC

37 specimens (132–530 mm. BL) from 17 collections.

Caligodes laciniatus, 58 females from nine specimens (207–530 mm. BL). Cape Verde Islands; Guinea; Sierra Leone; Ghana; Gabon; Angola.

Parabomolochus bellones, 1 male and 26 females from 17 specimens (132–530 mm. BL). Guinea; Sierra Leone; Ghana; Dahomey; Gabon.

Lernanthropus tylosuri, five females and one male from four specimens (418–530 mm. BL). Sierra Leone; Gabon.

Colobomatus goodingi, 15 females from 15 specimens (147–530 mm. BL). Sierra Leone; Dahomey; Gabon.

Caligus sp. A, two males and six females from four specimens (418–530 mm. BL). Sierra Leone; Gabon.

INDIAN OCEAN

31 specimens (84–725 mm. BL) from 13 collections.

Caligodes laciniatus, six females from two specimens (610–725 mm. BL). Mauritius; Zanzibar.

Lernanthropus tylosuri, 2 males and 10 females from 1 specimen (610 mm. BL). Mauritius.

Parabomolochus bellones, 4 males and 16 females from 6 specimens. Red Sea; Persian Gulf; Natal, South Africa.

Nothobomolochus gibber, one female from one specimen (311 mm. BL). Andaman Islands.

WEST AND CENTRAL PACIFIC

77 specimens (99–615 mm. BL) from 21 collections.

Caligodes laciniatus, three females from three specimens (305–470 mm. BL). Japan; Hawaii.

Lernanthropus tylosuri, 22 males and about 54 females from 16 specimens (295–615 mm. BL). Japan; Taiwan; Bikini, Marshall Islands; Philippine Islands; Hawaii.

Nothobomolochus gibber, 59 females from 29 specimens (192–374 mm. BL). Japan; Philippine Islands; Borneo; North Australia.

Parabomolochus bellones, five females from four specimens (286–449 mm. BL). Suruga Bay, Nagasaki, and Kobe, Japan; Djakarta, Java.

Parabomolochus sinensis, two females from one specimen (286 mm. BL). Djakarta, Java.

Colobomatus goodingi, 10 females from 9 specimens (226–278 mm. BL). Torres Strait, Australia.

Caligus sp. E, one male and five females from three specimens. Djakarta, Java; Torres Strait, Australia.

EASTERN PACIFIC

25 specimens (120–540 mm. BL) from 11 collections.

Caligodes laciniatus, 28 females from 8 specimens (252–540 mm. BL). Gulf of California; western Mexico; Cabo Blanco, Peru.

Lernanthropus tylosuri, 10 females and 17 males from 5 specimens (462–540 mm. BL). Gulf of California; western Mexico; Panama; Cabo Blanco, Peru.

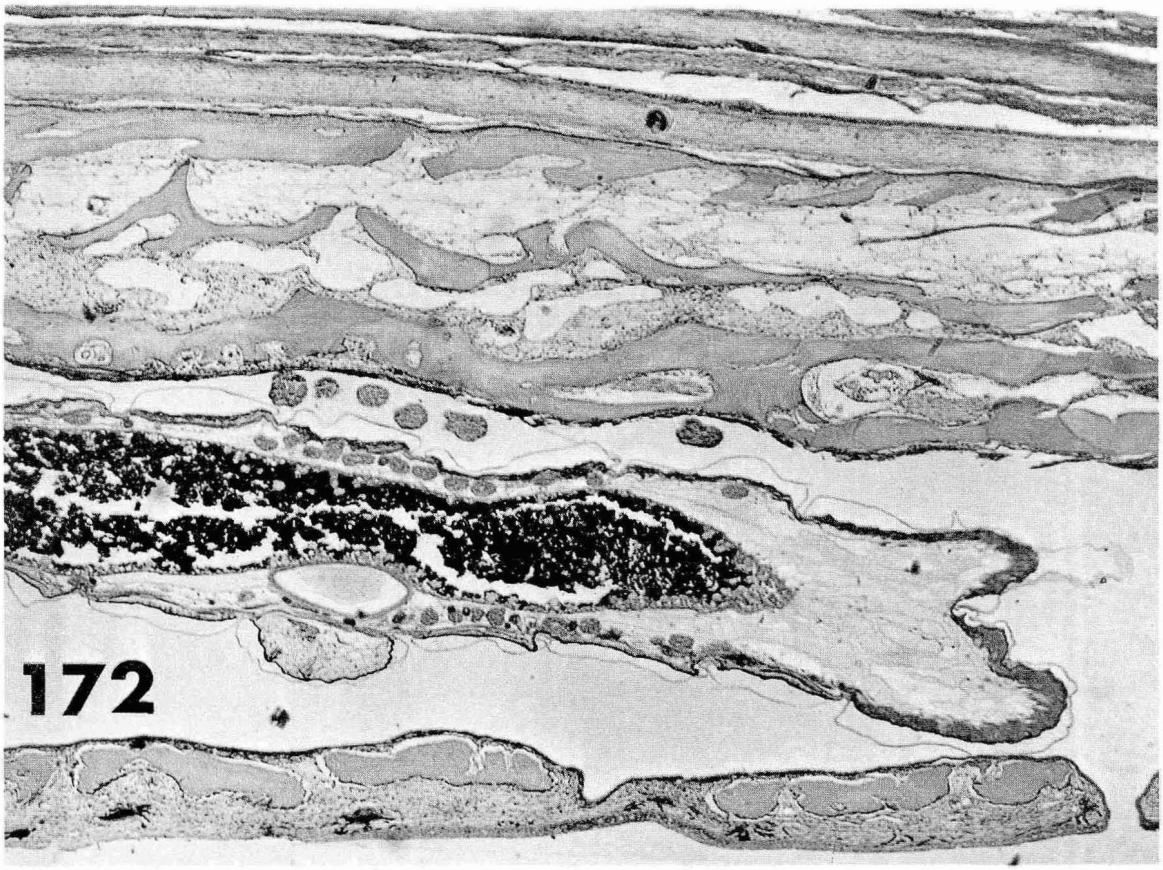


FIGURE 172.—*Colobomatus goodingi* within preoperculomandibular canal of *Strongylura notata*. Note absence of inflammation in the wall of the canal, and flat epithelium. No changes in bone. Several disintegrating ova lie between the *Colobomatus* and the canal wall. X 55, H and E.

Parabomolochus constrictus, about 35 females from 9 specimens (128–483 mm. BL). Acapulco, Mexico; Panama Bay; Cabo Blanco, Peru.

Colobomatus goodingi, four females from interorbital canals of three specimens (465–540 mm. BL). Acapulco and Mazatlan, Mexico; Panama.

Belone belone (Linnaeus)

A large (maximum size 537 mm. BL, 743 mm. SL) eastern Atlantic species known from the White Sea, Norway, and Iceland south through the North Sea and the Baltic Sea along the coasts of France and Spain to Madeira, the Azores, and the Canary Islands. Also found throughout most of the Mediterranean and Black Seas.

77 specimens (105–537 mm. BL) from 47 collections.

Parabomolochus bellones, 40 females from under gill covers and oral valves of 21 specimens (163–318 mm. BL). Mediterranean Sea: Trieste; Venice; Naples; Tunisia.

Caligus belones, one female from inside the lower jaw posterior to the oral valve of one specimen (300 mm. BL). Elbe River.

Nothobomolochus gibber, one female from under the gill cover of one specimen (239 mm. BL). Funchal, Madeira.

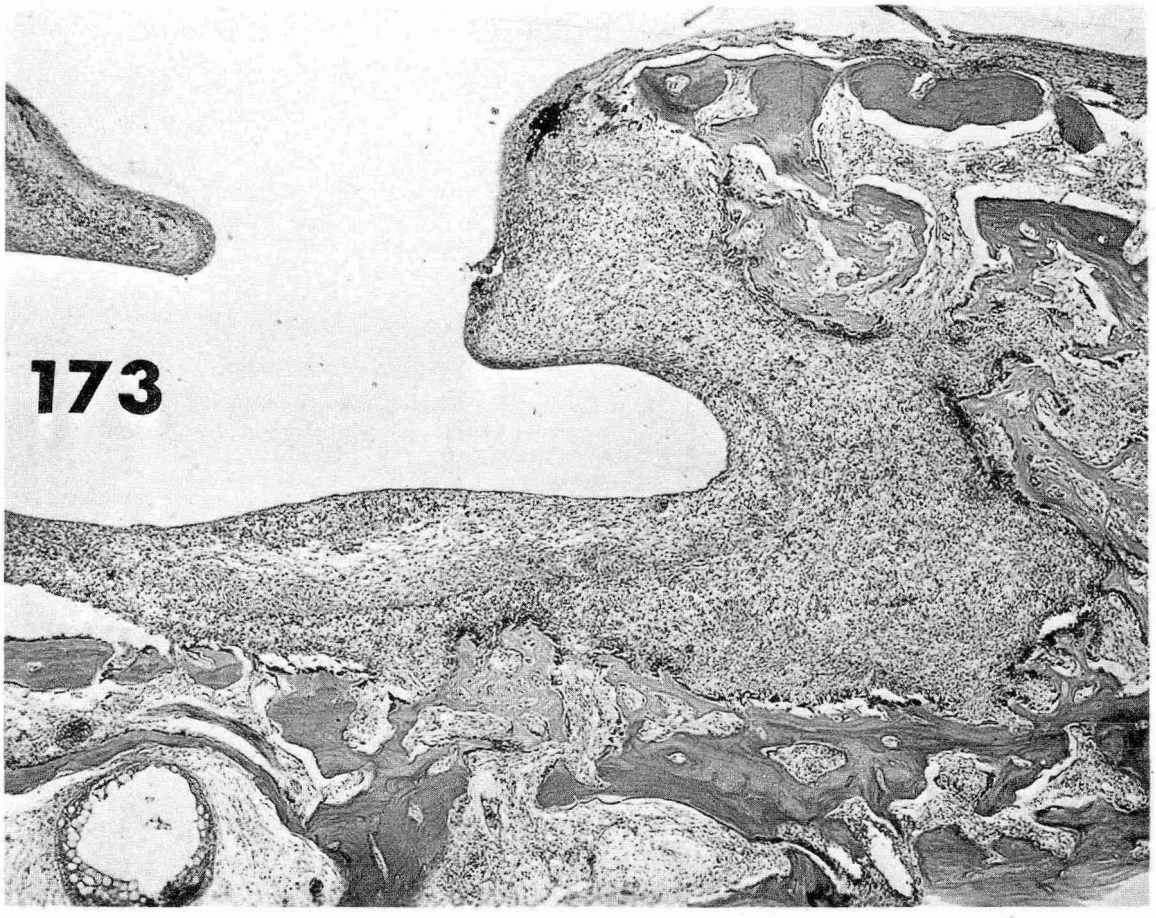


FIGURE 173.—*Colobomatus goodingi* within preoperculomandibular canal of *Strongylura notata*. Marked inflammatory reaction surrounding area occupied by *Colobomatus* before the copepod dropped out when the tissue block was cut. Note new bone formation in zone of osteitis. Ostium of canal is at right. X 55, H and E.

Belone svetovidovi Collette and Parin

A medium-sized (maximum size 320 mm. BL, 445 mm. SL) marine species known from the Mediterranean Sea and the Atlantic Coast of Spain.

15 specimens (145–320 mm. BL) from 4 collections.

Parabomolochus bellones, one female from one specimen (210 mm. BL). Genoa Bay, Italy.

Nothobomolochus gibber, one male and three females from three specimens (171–210 mm. BL). Genoa Bay, Italy; Gabes, Tunisia.

Belonion apodion Collette
Belonion dibranchodon Collette

These are the two smallest species of needlefishes (maximum sizes 42 and 38 mm. BL, respectively). They are found in tributaries of the Amazon and Orinoco Rivers in Brazil, Venezuela, and Bolivia.

No copepods were found in any of the specimens of either species: *B. apodion*, 15 (22.6–41.8 mm. BL); *B. dibranchodon*, 7 (27.1–38.2).

Lhotskia gavialoides (Castelnau)

A large (maximum size 665 mm. BL, 955 mm. SL) Australian marine species.

24 specimens (162–665 mm. BL) from 8 collections.

Caligodes laciniatus, 22 females from about 7 specimens (292–665 mm. BL). New South Wales, Australia.

Parabomolochus bellones, 20 females from 8 specimens (228–297 mm. BL). Great Barrier Reef and New South Wales, Australia.

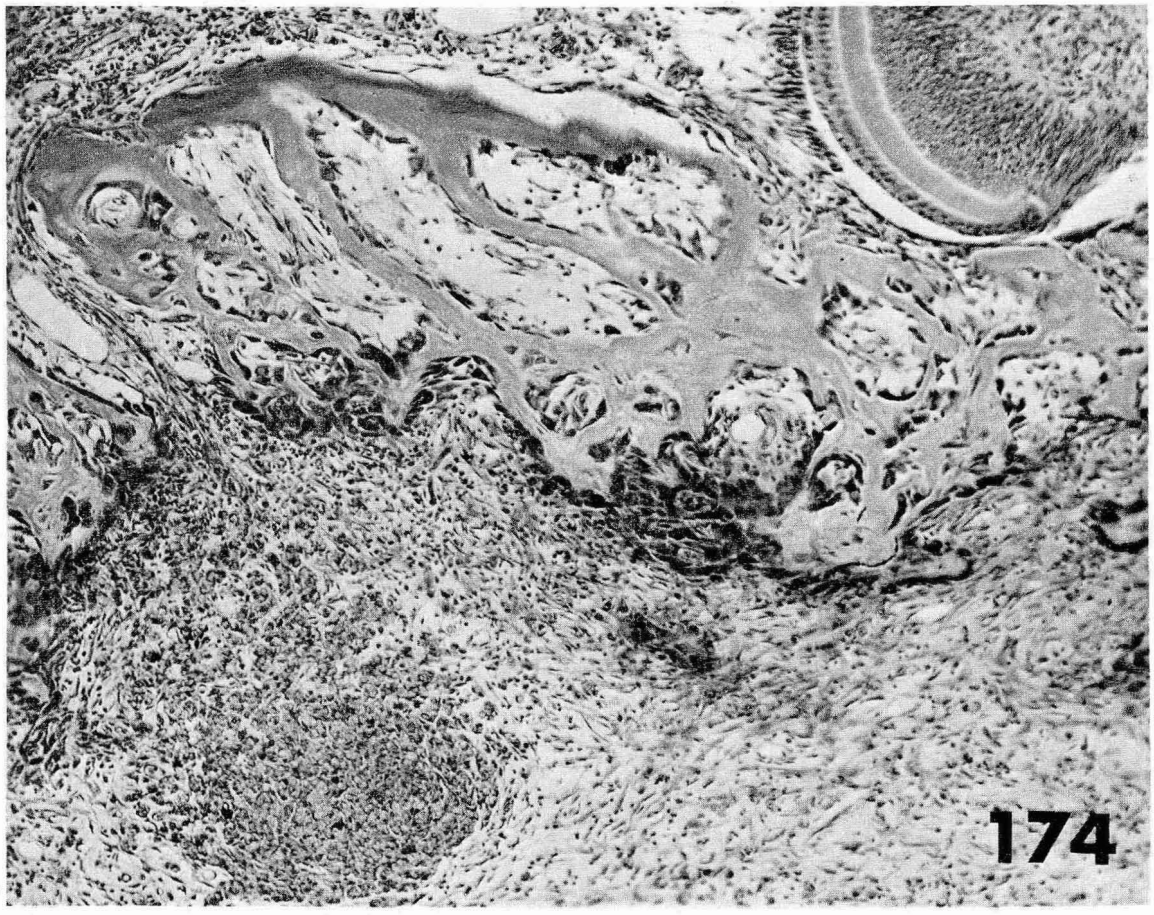


FIGURE 174.—*Colobomatus goodingi* within preoperculomandibular canal of *Strongylura notata*. A small granuloma adjacent to an area of new bone formation. Note hypertrophic osteoblasts at sites of bone formation. X 150, H and E.

Petalichthys capensis Regan

A medium-sized (maximum size 211 mm. BL) marine species known only from South Africa.

One specimen, 211 mm. BL.

No copepods.

Platybelone argalus (LeSueur)

A medium-sized (maximum size 300 mm. BL, 431+ mm. SL) polytypic worldwide marine species usually found around islands in tropical and subtropical seas (see fig. 176).

WESTERN ATLANTIC

146 specimens (90–248 mm. BL) from 31 collections.

Parabomolochus bellones, one male and 46 females from 15 specimens. Cay Arcas, Gulf of Mexico; Cuba; Puerto Rico; Cumana, Venezuela.

Caligus belones, one male and one female from two specimens. Cay Arcas, Gulf of Mexico; Navidad Bank, Caribbean Sea.

Lernanthropus belones, two males and one female from three specimens (164–248 mm. BL). Bermuda.

EASTERN ATLANTIC

129 specimens (144–287 mm. BL) from 21 collections around islands.

Caligus belones, many, mostly juveniles, from 54 specimens (161–287 mm. BL). Annobon, St. Helena, and Ascension Islands.

Lernanthropus tylosuri, one female from the gill filaments of one specimen. Fernando Póo.

Nothobomolochus gibber, two females from two specimens. Ascension and Annobon Islands.

INDIAN OCEAN

63 specimens (110–267 mm. BL) from 8 collections.

Nothobomolochus gibber, six females from three specimens (195–230 mm. BL). Aldabra Island.

Parabomolochus bellones, one female from one specimen (161 mm. BL). Saudi Arabia, Persian Gulf.

Caligodes laciniatus, one female from one specimen (198 mm. BL). Ari Atoll, Maldive Archipelago.

Caligus sp., six chalimus juveniles from pectoral fins of five specimens (184–231 mm. BL). Aldabra Island.

WEST AND CENTRAL PACIFIC

107 specimens (172–270 mm. BL) from 23 collections.

Nothobomolochus gibber, 149 females from about 57 specimens (174–238 mm. BL). Marshall, Tokelau, Christmas, Fanning, and Samoan Islands.

EASTERN PACIFIC

42 specimens (64–262 mm. BL) from 22 collections.

Parabomolochus constrictus, more than 65 females from 20 specimens. Baja California; Panama; Galapagos Islands; Guayaquil, Ecuador.

Caligus sp., from anal fin of one specimen (250 mm. BL). Baja California.

Potamorrhaphis guianensis (Schomburgk)

A small (maximum size 157 mm. BL, 232+ mm. SL) fresh-water species of eastern South America (see fig. 180).

63 specimens (67–157 mm. BL) from 13 collections.

Ergasilus orientalis, nine females from gill filaments of six specimens (115–157 mm. BL). Gurupá, near mouth of Amazon River, Brazil.

Pseudotylosurus angusticeps (Günther)

A medium-sized (maximum size 255 mm. BL, 379 mm. SL) South American fresh-water species (see fig. 180).

25 specimens (98–243 mm. BL) from 10 collections.

Acusicola cumula, eight females from gill filaments of two specimens. Amazon drainage, Brazil.

Strongylura anastomella (Valenciennes)

A large (maximum size 580 mm. BL, 805 mm. SL) marine species found in the northwestern Pacific—the Sea of Japan, Japan, Korea, and Formosa (see fig. 179).

33 specimens (128–580 mm. BL) from 18 collections.

Lernanthropus tylosuri, 10 males and 55 females from 15 specimens (285–580 mm. BL [average 390]). Japan; U.S.S.R.; Korea.

Lernanthropus belones, two females and six immature females from one specimen (430 mm. BL). Suruga Bay, Japan.

Parabomolochus bellones, 55 females from 14 specimens (227–474 mm. BL [average 344]). Japan; U.S.S.R.

Caligus sp., one female from one specimen. Boshu, Japan.

Strongylura exilis (Girard)

A large (maximum size 490 mm. BL, 715+ mm. SL) eastern Pacific marine species found from southern California to Peru and the Galapagos Islands (see fig. 179). Most closely related to the western Atlantic *S. marina*.

97 specimens (54–490 mm. BL) from 30 collections.

Parabomolochus ensiculus, 14 females from under oral valves of 13 specimens (89–363 mm. BL). San Diego, Calif.; Baja California; Chame Point, Panama; Peru.

Parabomolochus constrictus, 20 females from 9 specimens (155–367 mm. BL). Baja California; northern Peru.

Lernanthropus belones, 43 males and 64 females from 14 specimens (112–363 mm. BL). San Diego, Calif.; Baja California.

Lernanthropus tylosuri, three males and five females from four specimens (227–340 mm. BL). Baja California; northern Peru.

Colobomatus goodingi, one female from one specimen (415 mm. BL). Miraflores Lock, Canal Zone, Panama.

Caligus sp., one male from the mouth of one specimen (142 mm. BL). Gulf of Nicoya, Costa Rica.

Strongylura fluviatilis (Regan)

A medium-sized (maximum size 321 mm. BL, 517 mm. SL) fresh-water species found in the rivers of Ecuador and Colombia.

33 specimens (104–321 mm. BL) from 10 collections.

Ergasilus argulus, 58 females from gill filaments of 4 specimens (153–196 mm. BL). Dagua River mouth, Colombia.

Strongylura incisa (Valenciennes)

A medium-sized (maximum size about 450 mm. BL) marine species found from Ceylon, Malaysia, and Thailand through the Philippine Islands to the Marshall Islands, Gilbert Islands, Marianas Islands, Samoan Islands, Fiji Islands, and Palau Islands (see fig. 179).

75 specimens (59–450 mm. BL) from 42 collections.

Lernanthropus belones, 6 males and 10 females from 7 specimens (193–450 mm. BL). Marshall Islands; Gilbert Islands; Philippine Islands; Arnhem Land, Australia; Singapore.

Lernanthropus tylosuri, one female from one specimen (233 mm. BL). Great Barrier Reef, Australia.

Parabomolochus bellones, six females from two specimens (102–222 mm. BL). Philippine Islands.

Ergasilus orientalis, 19 females from 1 specimen (220 mm. BL). Emerald River at and near mouth, Arnhem Land, Australia.

Caligus sp. D, two females from two specimens (233–315 mm. BL). Great Barrier Reef, Australia; Philippine Islands.

Strongylura krefftii (Günther)

A medium-sized (maximum size 388 mm. BL, 735 mm. SL) fresh-water species found in northern Australia—Arnhem Land and Queensland.

44 specimens (21–388 mm. BL) from 7 collections.

Ergasilus semicoleus, 36 females on gill filaments of 6 specimens (207–325 mm. BL).

Large billabong at Oenpelli, Arnhem Land, Northern Territory, Australia.

Strongylura leiura (Bleeker)

A large (maximum size 501 mm. BL, 790 mm. SL) marine species most closely related to *S. anastomella*. Found from east Africa, the Persian Gulf, and India to Borneo, the Philippines, Australia, China, and Fiji (see fig. 179).

49 specimens (115–398 mm. BL) from 35 collections.

Caligoides laciniatus, 39 females from 5 specimens (171–313 mm. BL). Pondicherry, India; Philippine Islands; Formosa.

Lernanthropus tylosuri, four females from three specimens (171–280 mm. BL). Persian Gulf; Philippine Islands.

Nothobomolochus digitatus, five females from four specimens (171–229 mm. BL). Java; Gulf of Thailand; Philippine Islands.

Parabomolochus bellones, one female from oral valve of one specimen (387 mm. BL). Hong Kong.

Strongylura marina (Walbaum)

A medium-sized (maximum size 418 mm. BL, 640 mm. SL) marine species found in the western Atlantic from Massachusetts south to Rio de Janeiro (see fig. 179). Not found in the Bahamas or Antilles. Frequently runs long distances up fresh-water rivers.

316 specimens (43–418 mm. BL) from 100 collections.

Parabomolochus bellones, 3 males and 116 females from 53 specimens (55–300 mm. BL [average 149.5]). Massachusetts; North Carolina; Georgia; Key West; Everglades; western Florida; Yucatan; Panama; Trinidad; Venezuela.

Colobomatus goodingi, six females from cephalic lateral line canals of five or six specimens (171–260 mm. BL [average 216.8]). Clearwater, Fla., Everglades, Fla., western Florida.

Lernanthropus belones, 114 males and 58 females from 37 specimens (110–280 mm. BL). Beaufort, N.C.; St. Simons and Jekyll Islands, Ga.; Lemon Bay, Alligator Harbor, Clearwater, and Amelia River, Fla.; Trinidad; Venezuela.

Lernanthropus tylosuri, three males and two females from three specimens (296–410 mm. BL). Belize, British Honduras.

Lerneaolophus sultanus, one female from one specimen (368 mm. BL). Belize, British Honduras.

Ergasilus sp. A, one female from one specimen (418 mm. BL). Lake Yzabel, Guatemala.

Acusicola tenax, 203 females from 18 specimens (113–285 mm. BL). Usumacinta River, El Petén, Guatemala.

Ergasilus spatulus, 23 females from 5 specimens (129–272 mm. BL). Lake Pontchartrain, La.; Tortuguero, Costa Rica.

Argulidae, from one specimen, (230 mm. BL). Lake Pontchartrain, La.

Strongylura notata (Poey)

A medium-sized (maximum size 245 mm. BL, 411 mm. SL) western Atlantic marine species

found from southern Florida and the Bahamas to Cuba, Jamaica, Yucatan, and Honduras (see fig. 179).

About 200 specimens (29–245 mm. BL) from about 50 collections.

Colobomatus goodingi, from cephalic lateral line canals of 42 specimens (72–238 mm. BL [average 133.3]). Bimini, Bahamas; Tampa Bay, Cape Haze, Sanibel Island, and Key Biscayne, Fla.; Providence Island, Caribbean Sea.

Lernanthropus belones, 63 males and 78 females from about 50 specimens (87–245 mm. BL [average 151.0]). Bimini and Andros Is., Bahamas; Sanibel Island, Cape Haze, Sarasota, Pensacola, and Key Biscayne, Fla.; Florida Keys; Cuba; Jamaica; Yucatan.

Parabomolochus bellones, 3 males and 158 females from about 50 specimens (41–226 mm. BL [average 108.4]). Andros Island, Bahamas; Cape Haze, Sarasota, New Smyrna, Pensacola, Bayport, and Key Biscayne, Fla.; Florida Keys; Jamaica; Yucatan and Tampico, Mexico.

Caligus sp. B, four females from two specimens. Sarasota, Fla.

Strongylura scapularis (Jordan and Gilbert)

A medium-sized (maximum size 245 mm. BL, 385 mm. SL) eastern Pacific marine species found from Costa Rica to Ecuador (see fig. 179).

38 specimens (36–245 mm. BL) from 12 collections.

Lernanthropus belones, eight males and four females from four specimens (157–227 mm. BL). Canal Zone, Panama; Guyaquil, Ecuador.

Parabomolochus constrictus, 15 females from under opercles of about 7 specimens (64–148 mm. BL). Costa Rica; Canal Zone, Panama.

Parabomolochus ensiculus, 139 females from under oral valves of 21 specimens (59–235 mm. BL). Canal Zone, Panama; Ecuador; Peru.

Ergasilus argulus, 48 females from gill filaments of 6 specimens (187–245 mm. BL). Mouth of Dagua River, Colombia.

Strongylura senegalensis (Valenciennes)

A medium-sized (maximum size 263 mm. BL, 381 mm. SL) eastern Atlantic marine species found from Senegal through the Gulf of Guinea to Angola (see fig. 179). Sometimes enters rivers.

27 specimens (116–229 mm. BL) from 6 collections.

Parabomolochus bellones, five females from five specimens (143–175 mm. BL). Volta River at Ada, Ghana; Ebzie Lagoon, Ivory Coast.

Ergasilus inflatipes, 62 females from 17 specimens (129–218 mm. BL). Volta River at Ada, Ghana; Ebzie Lagoon, Ivory Coast.

Strongylura strongylura (van Hasselt)

A medium-sized (maximum size 233 mm. BL, 366+ mm. SL) estuarine species found along the coasts of India, southeast Asia, China, Borneo, the Philippines, and Australia (see fig. 179).

69 specimens (56–233 mm. BL) from 32 collections.

Parabomolochus bellones, two females from one or two specimens. Arnhem Land, Australia.

Parabomolochus sinensis, 12 females and 1 male from 7 specimens (78–166 mm. BL). Hong Kong; Amoy and Fukien, China; Penang, Malaysia.

Nothobomolochus digitatus, 19 females from 12 specimens (103–206 mm. BL). Bombay and Calicut, India; Penang, Malaysia; Hong Kong; Arnhem Land, Australia.

Lernanthropus belones, 11 males and 10 females from 9 specimens (145–255 mm. BL). Madras and Bombay, India; China; Singapore; Philippine Islands.

Lernanthropus tylosuri, two males and three females from six specimens (103–201 mm. BL). Penang, Malaysia.

Ergasilus coleus, 28 females from gill filaments of 6 specimens. Cagayan de Misamis, Mindanao, Philippine Islands; Sandakan Bay, Borneo; Porto Novo, Madras, India.

Strongylura timucu (Walbaum)

A medium-sized (maximum size 275 mm. BL, 418 mm. SL) western Atlantic marine species found in southern Florida, the West Indies, Central and South America south to Rio de Janeiro (see fig. 179). Frequently enters fresh water.

281 specimens (82–250 mm. BL) from 95 collections.

Colobomatus goodingi, 31 females from cephalic lateral line canals of 26 specimens (112–232 mm. BL [average 158.0]). Sarasota, Fla.;

Florida Keys; Haiti; Puerto Rico; Virgin Islands; Curaçao.

Lernanthropus belones, 76 males and 123 females from 72 specimens (93–250 mm. BL [average 170.9]). Bahamas; Cedar Keys, Lemon Bay, Sarasota, Clearwater, and Key Biscayne, Fla.; Cuba; Jamaica; Puerto Rico; Virgin Islands; Yucatan; Panama; Rio de Janeiro, Brazil.

Lernanthropus tylosuri, six males and seven females from one specimen (235 mm. BL). Rio de Janeiro, Brazil.

Parabomolochus bellones, about 22 males and 150 females from 80 specimens (49–250 mm. BL [average 158.2]). Everglades, Tampa Bay, Clearwater, Lemon Bay, Sarasota, Pensacola, Sanibel Island, and Key Biscayne, Fla.; Yucatan; Jamaica; Haiti; Puerto Rico; Virgin Islands.

Ergasilus spatulus, six females from four specimens (125–250 mm. BL). Tortuguero, Costa Rica.

Strongylura urvillii (Valenciennes)

A medium-sized (maximum size, 228 mm. BL, 386 mm. SL) western Pacific marine species known from the Philippines, New Hebrides, and East Indies (see fig. 179).

21 specimens (79–220 mm. BL) from 11 collections.

Lernanthropus tylosuri, one male from one specimen (136 mm. BL). Culion, Philippine Islands.

Caligus sp. D, one female from one specimen (220 mm. BL). Verde del Sur Island, Philippine Islands.

Parabomolochus bellones, one female from one specimen (168 mm. BL). Manila, Luzon, Philippine Islands.

Ergasilus coleus, four females from gill filaments of one specimen (130 mm. BL). Culion, Philippine Islands.

Tylosurus acus (Lacépède)

A large (maximum size 950 mm. BL, 1,285 mm. SL) worldwide polytypic marine species of tropical and subtropical waters (see fig. 177).

WESTERN ATLANTIC

***T. acus acus* (Lacépède)**

39 specimens (110–950 mm. BL) from 26 collections.

Caligodes laciniatus, 40 females and 1 male from oral valves of 17 specimens (178–516 mm. BL). Virginia; Florida; Bahamas; Gulf of Mexico; British Honduras; Haiti; Virgin Islands.

Lernanthropus tylosuri, three females and two males from gill filaments of three specimens (338–382 mm. BL). British Honduras; Puerto Rico; Virgin Islands.

Parabomolochus bellones, seven females and three males from four specimens (200–305 mm. BL). Florida; Gulf of Mexico; British Honduras.

Colobomatus goodingi, 10 females from 8 specimens (244–400 mm. BL). North Carolina; Gulf of Mexico; Bahamas; British Honduras.

Lernaeolophus sultanus, two females from roof of upper jaw of one head. Haiti.

MEDITERRANEAN SEA

***T. acus imperialis* (Rafinesque)**

23 specimens (200–443 mm. BL) from 5 collections. No copepods.

GULF OF GUINEA

***T. acus rafale* Collette and Parin**

21 specimens (201–570 mm. BL) from 15 collections.

Caligodes laciniatus, 15 females from 10 specimens (261–456 mm. BL). Freetown, Sierra Leone; Congo; Angola.

Lernanthropus tylosuri, a few males and about 15 females from 6 specimens (261–570 mm. BL). Freetown, Sierra Leone; Luanda, Lobito, and Baía Farta, Angola.

Parabomolochus bellones, four females from three specimens (240–356 mm. BL). Freetown, Sierra Leone; Congo.

Colobomatus goodingi, six females from three specimens (452–570 mm. BL). Lobito and Baía Farta, Angola.

Caligus sp. A, one female from one specimen (201 mm. BL). Freetown, Sierra Leone.

INDIAN OCEAN

***T. acus melanotus* (Bleeker)**

One specimen (342 mm. BL).

Caligodes laciniatus, several females from one specimen (342 mm. BL).

WESTERN AND CENTRAL PACIFIC

***T. acus melanotus* (Bleeker)**

33 specimens (281–610 mm. BL) from 21 collections.

Caligodes laciniatus, nine females from six specimens (415–610 mm. BL). Philippine Islands; Nagasaki, Japan; Hawaii.

Lernanthropus tylosuri, two males and two females from four specimens (384–463 mm. BL). Djakarta, Java; Philippine Islands.

Colobomatus goodingi, one female from preorbital canal of one specimen (415 mm. BL). Jolo, Philippine Islands.

Caligus tylosuri, one male and one female from under gill covers of two specimens (301–416 mm. BL). Luzon, Philippine Islands; Sea of Japan.

Nothobomolochus gibber, one female from one specimen (380 mm. BL). Taiwan.

EASTERN PACIFIC

***T. acus pacificus* (Steindachner)**

30 specimens (50–550 mm. BL) from 22 collections.

Caligodes laciniatus, nine females from four specimens (308–535 mm. BL). Revillagigedos Islands, Mexico; Piñas Bay, Panama; Cabo Blanco, Peru.

Lernanthropus tylosuri, 7 males and 19 females from 6 specimens (296–535 mm. BL). Revillagigedos Islands; Gulf of California; Acapulco, Mexico; Piñas Bay, Panama.

Parabomolochus constrictus, about 31 females from 8 specimens (112–339 mm. BL). Costa Rica; Panama; Colombia; Peru.

Colobomatus goodingi, five females from three specimens (296–535 mm. BL). Acapulco, Mexico; Piñas Bay, Panama; Cabo Blanco, Peru.

Caligus tylosuri, one male from dorsal fin of one specimen (470 mm. BL). Bahia Palmas, Gulf of California.

Caligus sp. B, one female from one specimen (316 mm. BL). Cabo Blanco, Peru.

Caligus sp. C, two females from the throat of one specimen (535 mm. BL). Piñas Bay, Panama.

Tylosurus choram (Rüppell)

A medium-sized (maximum size at least 415 mm. BL, 625 mm. SL) Indo-West Pacific species of marine needlefish.

Two specimens (250–260 mm. BL) from the Persian Gulf, 14 (95–415 mm. BL) from the Red Sea, 1 from the Seychelles Islands, and 1 from the eastern Mediterranean Sea (277 mm. BL).

Caligodes laciniatus, seven females from four specimens (277–400 mm. BL). Red Sea; Seychelles Islands.

Lernanthropus tylosuri, one female from one specimen (415 mm. BL). Red Sea.

Caligus sp. D, one female from one specimen (261 mm. BL). Red Sea.

Tylosurus crocodilus (Peron and Le Sueur)

A large (maximum size 860 mm. BL, 1,156 mm. SL) worldwide polytypic marine species of tropical and subtropical waters (see fig. 178).

WESTERN ATLANTIC

38+ specimens (88–480 mm. BL) from 19+ collections.

Caligodes laciniatus, 19 females from 7 specimens (205–480 mm. BL). Florida; Cuba; Jamaica; Trinidad; Venezuela.

Lernanthropus tylosuri, 40 females and 39 males from 20 specimens (135–420 mm. BL). Matecumbe Key, Fla.; Bahamas; Venezuela.

Parabomolochus bellones, 12 females and 5 males from 8 specimens (135–244 mm. BL). Virginia Key and Sarasota, Fla.; Havana, Cuba; Venezuela.

Colobomatus goodingi, 23 females from 18 specimens (180–477 mm. BL). Virginia Key, Fla.; Bahamas; Trinidad; Venezuela.

Caligus sp., four chalimus from fins of three specimens (112–235 mm. BL). Key Biscayne, Fla.; Golfo de Cariaco, Venezuela.

Argulidae, from one specimen. Sarasota, Fla.

GULF OF GUINEA

Four specimens (173–284 mm. BL) from four collections.

Caligodes laciniatus, one female from one specimen (284 mm. BL). Liberia.

Lernanthropus tylosuri, four females from one specimen (173 mm. BL). Fernando Póo.

Colobomatus goodingi, seven females from one specimen (215 mm. BL). Cameroons.

INDIAN OCEAN

70 specimens (72–500 mm. BL) from 45 collections.

Caligodes laciniatus, 54 females from 20 specimens (172–490 mm. BL). Seychelles and Comores Islands; Aldabra; Zanzibar; Madagascar; Mauritius; Gulf of Aden; Arabian Gulf; Persian Gulf; Gulf of Mannar, Ceylon.

Lernanthropus tylosuri, 11 males and 23 females from 16 specimens (172–450 mm. BL). Madagascar; Mauritius; Zanzibar; Kenya; Seychelles; Red Sea; Gulf of Aden; Arabian Gulf; Persian Gulf; Kerala, India; Ceylon.

Parabomolochus bellones, eight females from four specimens (175–217 mm. BL). Mozambique; Kenya; Kerala, India; Moscos Islands, Burma.

Nothobomolochus gibber, 10 females from 6 specimens (98–233 mm. BL). Madagascar; Zanzibar; Seychelles Islands; Red Sea; Kerala, India.

Colobomatus goodingi, 12 females from 10 specimens (157–446 mm. BL). Madagascar; Red Sea; Gulf of Aden; Kerala, India; Gulf of Mannar, Ceylon.

Caligus sp., seven juveniles on fins of three specimens (72–142 mm. BL). Shimoni, Kenya.

Caligus sp., one male in mouth of one specimen (105 mm. BL). Nosy Bé, Madagascar.

WESTERN AND CENTRAL PACIFIC

76 specimens (58–570 mm. BL) from 51 collections.

Caligodes laciniatus, 28 females from 6 specimens (254–565 mm. BL). Thailand; Singapore; Samoa; Philippine Islands; Hawaii.

Lernanthropus tylosuri, 14 males and 33 females from 15 specimens (150–440 mm. BL). Japan; Thailand; Singapore; Philippine Islands; Java; Borneo; Marshall Islands; Hawaii.

Nothobomolochus gibber, two females from two specimens (190–286 mm. BL). Bellona Island, Solomon Islands; Cavite, Philippine Islands.

Nothobomolochus pacificus, one female from one specimen (388 mm. BL). Sandakan, North Borneo.

Colobomatus goodingi, nine females from seven specimens (214–420 mm. BL). Java; Philippine Islands; Marianas Islands; Solomon Islands.

Caligus tylosuri, four females from two specimens (317–388 mm. BL). Leyte, Philippine Islands; Sandakan, North Borneo.

Lernaeenicus sp., one female from one specimen (252 mm. BL). Manila, Philippine Islands.

EASTERN PACIFIC

T. crocodilus fodiator Jordan and Gilbert

24 specimens (65–671 mm. BL) from 11 collections.

Caligodes laciniatus, 26 females from 6 specimens (262–450 mm. BL). Mexico; Cocos Islands; Panama Canal Zone.

Lernanthropus tylosuri, 2 males and 19 females from 5 specimens (303–515 mm. BL). Mazatlan, Mexico; Panama Canal Zone.

Parabomolochus constrictus, 12 females from 8 specimens (69–450 mm. BL). Mexico; Cocos Islands; Panama Canal Zone.

Colobomatus goodingi, six females from three specimens (161–570 mm. BL). Cocos Islands; Panama Canal Zone.

Caligus sp. C, one female from one specimen (535 mm. BL). Panama Canal Zone.

Tylosurus punctulatus (Günther)

A medium-sized (maximum size 385 mm. BL, 573 mm. SL) western Pacific marine species. Known from Malaya, the Philippines, Borneo, New Guinea, the Celebes, Australia, and the Solomon Islands.

31 specimens (87–385 mm. BL) from 22 collections.

Lernanthropus tylosuri, two females from two specimens (180–205 mm. BL). Culion and Luzon, Philippine Islands.

Lernanthropus belones, four females and one male from three specimens (235–269 mm. BL). Sandakan, North Borneo.

Nothobomolochus digitatus, three females from two specimens (110–130 mm. BL). New Guinea.

Xenentodon cancila (Hamilton-Buchanan)

A small (maximum size 169 mm. BL, 284 mm. SL) fresh-water species found in India, Ceylon, and southeast Asia (see fig. 180).

65 specimens (56–169 mm. BL) from 13 collections.

Ergasilus coleus, 51 females from gill filaments of 5 specimens (66–112 mm. BL). Travancore and Calcutta, India.

Paraergasilus remulus, three females from operculum of two specimens (111–112 mm. BL). Prek Andhor, Cambodia.

Ergasilus sp., one female from gill filaments of one specimen (119 mm. BL). Ceylon.

Ergasilidae, one female from gill filaments of one specimen (102 mm.). Sutlej River, Punjab, India.

Lernea sp., one female from behind left pectoral fin of one specimen. Locality unknown.

LITERATURE RECORDS OF NEEDLEFISH COPEPODS

As stated previously, we did not incorporate literature records into the data included in this paper. Because of the comprehensive nature of our collections we felt that they would add nothing of significance and might even add data based on misidentified parasites or hosts. To complete this report on needlefish copepods, however, we felt it desirable to cite those reports here (a few have already been cited elsewhere in this paper). We consider most of the recent records to be accurate. The records are listed by recorded host. Wherever possible we have included the corrected host or parasite name in parentheses.

***Ablennes anastomella* (=*Strongylura anastomella*)**

Lernanthropus cornutus: Shiino, 1965 (Japan; = *L. tylosuri*).

Ablennes hians

Bomolochus tumidus Shiino, 1959 (Sea of Japan; = *Nothobomolochus gibber*).

Pseudopetalus caudatus var. *rotundus* Pillai, 1962 (Trivandrum, S. India).

Lernanthropus cornutus: Shiino, 1965 (Japan; = *L. tylosuri*).

Caligodes laciniatus: Pillai, 1961 (Trivandrum, S. India); Nuñes-Ruivo, 1962a, 1962b (Baie de Moçâmedes, Angola).

***Belone acus* (=*B. belone*)**

Bomolochus belones: Brian, 1902 (Elba Island, Italy); Richiardi, 1880 (Italy); (=*Parabomolochus bellones*).

***Belone almeida* (=*Strongylura marina* or *S. timucu*)**

Lernanthropus belones Krøyer, 1863 (Brazil).

***Belone ardeola* (= *Strongylura marina*?)**

Bomolochus ardeolae Krøyer, 1863 (New Orleans, La.).

Artacolax ardeolae: Wilson, 1911 (= *B. ardeolae*).

***Belone bellone* (= *B. belone*)**

Parabomolochus bellones: Vervoort, 1962 (Holland).

Caligus belones: Delamare Deboutteville and Nuñes-Ruivo, 1958 (Mediterranean coast of France).

***Belone contrainii* (sic) (= *Tylosurus acus imperialis*)**

Caligodes laciniatus: Brian, 1902 (Genoa, Italy).

***Belone rostrata* (= *B. belone*)**

Bomolochus belones: Valle, 1880 (Adriatic Sea; = *Parabomolochus bellones*).

***Belone vulgaris* (= *B. belone*)**

Bomolochus bellones: Hartmann, 1870 (Mediterranean Sea); Brian, 1906 (Helgoland, Germany); (= *Parabomolochus bellones*).

Caligus belones Krøyer, 1863 (Denmark).

Metopocatacoteinus hirsutus Hesse, 1872 (France; = *Parabomolochus bellones*).

***Belone* Sp. (=*Strongylura* or *Tylosurus* Sp.)**

Sciaenophilus laciniatus Krøyer, 1863 (Mollucca Islands; =*Caligodes laciniatus*).

Caligodes laciniatus: Heller, 1868 (Indian Ocean).

***Belones* (sic) *platyura* (=*Platybelone argalus*)**

Nothobomolochus gibber: Lewis, 1968 (Eniwetok Atoll, Marshall Islands).

***Esox bellone* (=*Belone belone*)**

Bomolochus bellones Burmeister, 1833 (Helgoland, Germany).

***Lepisosteus osseus* (=*Tylosurus acus*?)**

Caligodes megacephalus Wilson, 1905 (Woods Hole, Mass.; =*C. laciniatus*).

***Strongylura acus* (=*Tylosurus acus*)**

Caligus schistonyx: Pearse, 1947 (3 chalimi; Beaufort, N.C.; = ?).

***Strongylura crocodila* (=*Tylosurus acus*?)**

Caligodes laciniatus: Capart, 1953 (Dakar); Capart, 1959 (Congo).

Lernanthropus cornutus: Capart, 1953 (Gorée, Sénégal); Delamare Deboutteville and Nuñes-Ruivo, 1954 (Gorée); (=*L. tylosuri*).

Strongylura leiura

Caligodes laciniatus: Kirtisinghe, 1937 (Ceylon).

Lernanthropus cornutus Kirtisinghe, 1937 (Ceylon; =*L. tylosuri*).

Strongylura notata

Lernanthropus chlamydotes: Bere, 1936 (Lemon Bay, Fla.; = *L. belones*).

Strongylura strongylura

Caligodes laciniatus: Kirtisinghe, 1937 (Ceylon).

Strongylura timucu (=*S. marina*?)

Bomolochus nitidus: Bere, 1936 (Lemon Bay, Fla.; =*Parabomolochus bellones*).

Lernanthropus chlamydotes: Bere, 1936 (Lemon Bay, Fla.; =*L. belones*).

Tylosurus acus

Tuxophorus caligodes Wilson, 1908 (chalimus: Beaufort, N.C.).

Tylosurus crocodilus

Caligus tylosuri: Pillai, 1961 (Vizhingom, S. India).

Caligus malabaricus Pillai, 1961 (Trivandrum, S. India).

Caligoides laciniatus: Pillai, 1961 (Trivandrum, S. India).

Lernanthropus cornutus Kirtisinghe, 1937 (Ceylon; =*L. tylosuri*).

Tylosurus giganteus (=*T. crocodilus*)

Bomolochus gibber Shiino, 1957 (Owase, Japan; =*Nothobomolochus gibber*).

Tylosurus imperialis (=*T. acus imperialis*)

Lernanthropus tylosuri Richiardi, 1880, 1885 (Italy).

Caligodes laciniatus: Brian, 1906 (Genoa, Italy).

Tylosurus incisus (=*Strongylura incisa*)

Lernanthropus cornutus: Kabata, 1962 (Gilbert and Ellice Islands; = *L. tylosuri*).

Tylosurus indicus (=*T. crocodilus*)

Nothobomolochus gibber: Vervoort, 1962 (Japan; based on Shiino, 1957).

Tylosurus marinus (=*Strongylura marina*)

Lepeophtheirus edwardsi: Wilson, 1905 (male; Woods Hole, Mass.); Wilson, 1908 (Beaufort, N.C.).

Tuxophorus caligodes Wilson, 1908 (8 chalimi; Beaufort, N.C.).

Bomolochus concinnus Wilson, 1911 (Beaufort, N.C.;=*Parabomolochus bellones*).

Lernanthropus chlamydotes Wilson, 1922 (Beaufort, N.C.;=*L. belones*).

Lernanthropus sp.: Linton, 1905 (Beaufort, N.C.; =*L. belones*).

Tylosurus schistomatorhynchus (=*Ablennes hians*)

Lernanthropus chlamydotes: Yamaguti, 1939b (Japan;=*L. tylosuri*).

Tylosurus strongylurus (=*Strongylura strongylura*)

Tuxophorus tylosuri Rangnekar, 1956 (Bombay;=*Caligus tylosuri*).

Caligodes laciniatus: Rangnekar, 1959 (Bombay).

HOST-PARASITE RELATIONSHIPS

Host Specificity

To answer the question, "Are needlefish copepods host specific?" we compared statistically the percentage infestation of the various species of needlefishes by different species of copepods. The analysis yielded little evidence of host specificity in the copepods of fresh-water needlefishes—the Ergasilidae (table 3). Rather, a given species of ergasilid is found on the fresh-water needlefishes in its range. Most ergasilids found on needlefishes are restricted to one host species because it is the only one available. When there are more hosts, they are utilized. *Ergasilus spatulus* is present on both *Strongylura marina* and *S. timucu* at Tortuguero, Costa Rica, but on only *S. marina* in Lake Pontchartrain, La., where it is the only needlefish present. *E. argulus* is found on *S. fluviatilis*, a fresh-water South American species of needlefish and also on *S. scapularis*, primarily a marine species, but taken with *S. fluviatilis* at the mouth of the Dagua River, Colombia. *E. coleus* was collected at several localities from *S. strongylura*, *S. urvillii*, and *Xenentodon cancila*. *X. cancila* is a fresh-water species, *S. strongylura* an estuarine species, and *S. urvillii* a primarily marine species.

The worldwide species of needlefishes (table 4) differ sharply in infestation between *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus* on the one hand, and *Platybelone argalus* on the other.

TABLE 3.—*Percentage of specimens of 12 fresh-water species of needlefishes (or fresh-water populations of marine species of* Strongylura) *infested by 11 species of ergasilid copepods*

Area, species, and number of specimens	*Ergasilus*							*Acusicola*		*Paraergasilus*
	spatulus	*argulus*	*coleus*	*semicoleus*	*inflatipes*	*orientalis*	sp. A	sp. B	*tenax*	*cunula*	*remulus*
	Percent										
North America:											
S. marina (190)	3						0.5		9		
S. timucu (18)	22						6				
South America:											
S. fluviatilis (33)		12									
S. scapularis (7)		86									
Potamorrhaphis (63)						10					
Pseudotylosurus (25)										8	
Africa:											
S. senegalensis (27)					59						
Asia:											
S. incisa (8)						13					
S. krefftii (44)				14							
S. strongylura (10)			50								
S. urvillii (3)			33								
Xenentodon (65)			8					2			3

TABLE 4.—*Percentage of specimens of four worldwide species of needlefishes infested by 10 species of copepods*

Species, area, and number of specimens	*Parabomolochus*			*Nothobomolochus*		*Caligodes laciniatus*	*Lernanthropus*		*Colobomatus goodingi*	*Caligus* spp.
	bellones	*constrictus*	*ensiculus*	*gibber*	*digitatus*		*tylosuri*	*belones*		
	Percent									
Ablennes hians;										
W. Atlantic (81)	38					2	0.5	0.1	0.2	
Gulf of Guinea (37)	46					24	11		41	11
Indian Ocean (31)	19			3		8	3			
W. Central Pacific (77)	5			38		3	21		12	4
E. Pacific (25)		36				32	20		12	
Tylosurus acus;										
W. Atlantic (39)	10					44	8		21	
Mediterranean (23)										
Gulf of Guinea (21)	14					48	29		14	5
Indo-W. Pacific (34)						24	9		3	6
E. Pacific (30)		27				10	20		10	10
Tylosurus crocodilus;										
W. Atlantic (38)	21					18	53		47	5
Gulf of Guinea (4)						25	25		25	
Indian Ocean (70)	6			9		29	21		14	6
W. Central Pacific (76)				3	1	8	20		9	3
E. Pacific (24)		33				25	21		13	4
Platybelone argalus;										
W. Atlantic (146)	10							1		1
E. Atlantic (129)				2			.8			42
Indian Ocean (62)	2			5		2				8
W. Central Pacific (107)				53						
E. Pacific (46)		43								

Three species of copepods are common on the first three species of needlefishes: *Caligodes laciniatus*, *Lernanthropus tylosuri*, and *Colobomatus goodingi*. There are only a few accidental records of *Caligodes* and *Lernanthropus* from *Platybelone* and none at all of *Colobomatus*. Yet all four species of needlefishes are commonly infested with *Parabomolochus bellones* or its eastern Pacific analog *P. constrictus*. Collette (in Collette and Parin, 1970) considered *Ablennes* and *Tylosurus* as closely related; the high incidence of *Caligodes*, *L. tylosuri*, and *Colobomatus* infestation in these genera could be considered as parasitological support for this view. Parin (in Collette and Parin, 1970), however, considered the similarities between *Ablennes* and *Tylosurus* as convergent evolution associated with occupation of a similar ecological niche. The parasitological data could be equally well applied to the support of this point of view.

Examination of the copepods associated with 16 other marine species of needlefishes (table 5) may help in deciding between the alternatives. *Caligodes* is found on one of the two other species of *Tylosurus*—*T. choram*. *Caligodes* is also found on *Lhotskia gavialoides*, a species placed in *Tylosurus* by Collette and Berry (1965) but referred to the monotypic *Lhotskia* by Parin (1967). The sixth species infested with *Caligodes*, *Strongylura leiura*, is the only member of its genus to be so infested. *S. leiura* is definitely not closely related to *Ablennes* or *Tylosurus*. Its only characters in common with the other *Caligodes* hosts are: large size (501 mm. BL compared to 665–950 mm. BL), wide distribution, and apparent intolerance of estuarine conditions. Thus, we conclude that *Caligodes* is not host-specific—it is associated with large, widely distributed, oceanic species of needlefishes.

The contrast is sharp among *Ablennes*, *Tylosurus acus*, and *T. crocodilus*, which are commonly infested with *Lernanthropus tylosuri*, and most of the species of *Strongylura*, which are usually infested with *L. belones*, particularly in the western Atlantic and eastern Pacific. The situation is confused in the Indo-West Pacific where nearly half of the *S. anastomella* examined were infested with *L. tylosuri*, and several other species of *Strongylura* have *L. belones*, or *L. tylosuri*, or both. *S. strongylura* has about an equal percentage of infestation of both species of *Lernanthropus*. The common character of *L. tylosuri* hosts is avoidance of estuarine areas. Most of the hosts are large offshore species as is true of *Caligodes* hosts. The common character of *L. belones* hosts is its likelihood of being taken in estuarine situations. We conclude that the reason for host differences between *L. belones* and *L. tylosuri* is that *L. belones* is euryhaline and *L. tylosuri* stenohaline.

Bomolochid copepods associated with needlefishes are apparently not host specific. Tables 4 and 5 show *Parabomolochus bellones* common on all seven species in four genera in the western Atlantic, on five of seven species in five genera in the eastern Atlantic, and on seven species of *Lhotskia* and *Strongylura* in the Indo-West Pacific. *P. bel-*

TABLE 5.—*Percentage of specimens of 16 marine species of needlefishes infested by 10 species of copepods*

Area, species, and number of specimens	*Parabomolochus*			*Nothobomolochus*	*Caligodes*	*Lernanthropus*		*Colobomatus*	*Caligus*
	bellones	*constrictus*	*ensiculus*	*gibber digitatus*	*laciniatus*	*tylosuri*	*belones*	*goodingi*	spp.
	Percent								
West Atlantic:									
S. marina (126)	42					2	29	5	
S. notata (200)	25						25	21	1
S. timucu (263)	30					.4	27	10	
East Atlantic:									
B. belone (77)	27			1					1
B. svetovidovi (15)	7			20					
S. senegalensis (27)	19								
Indo-West Pacific:									
L. gavialoides (24)	33				29	6			
S. anastomella (33)	42					45	3		3
S. leiura (49)	2			8	10	6			
S. incisa (67)	3					1	10		4
S. strongylura (59)	3			20		10	15		
S. urvillii (18)	6					6			6
T. choram (18)					22	6			6
T. punctulatus (31)				6		6	10		
East Pacific:									
S. exilis (97)		9	13			4	14	1	1
S. scapularis (31)		23	68				13		

lones is replaced by a derivative species in the eastern Pacific—*P. constrictus*. This copepod is abundant on all six eastern Pacific needlefishes and has also been found on four other species of inshore fishes in two different families. These two copepods seem to be found on whatever needlefish is available and may also occur on non-needlefish hosts.

Host-Parasite Distribution

To summarize the known distributions of needlefishes and their copepods and to contrast the distribution of a given species of needlefish with its associated copepods, 12 maps were prepared. Six maps (figs. 175–180) were made for the needlefishes: one for each of the four worldwide species (*Ablennes hians*, *Platybelone argalus*, *Tylosurus acus*, and *T. crocodilus*); one for the 11 marine species of *Strongylura;* and one for the fresh-water species of needlefishes and fresh-water populations of primarily marine species of *Strongylura.* Six maps (figs. 181–186) of copepod distributions were also made: *Caligodes laciniatus; Colobomatus goodingi; Lernanthropus belones* and *L. tylosuri;* the four species of *Parabomolochus; Nothobomolochus gibber* and *N. digitatus;* and the nine species of Ergasilidae. The needlefish maps are based on all of the specimens of needlefishes examined by Collette for his revisionary studies. The copepod maps are based on all of the copepods collected for this study. Not all of the needlefishes were examined for copepods so the needlefish maps have greater coverage than the copepod maps. Less abundant species of both needlefishes and copepods were not mapped. The 75° F. (23.9° C.) or 80° F. (26.7° C.) sea surface isotheres from Hutchins and Scharff (1947) are plotted on the 10 maps of marine species. These isotheres delimit the ranges remarkably well except along part of the mainland coasts where inshore species of *Strongylura* can move beyond the limits of the isothere.

In general, copepod distributions correspond to needlefish distributions. Most of the widely distributed species extend as far north and south as their hosts. There is, however, one striking exception: *Colobomatus goodingi* is restricted to warmer waters than its hosts—80° F. (26.7° C.) rather than 75° F. (23.9° C.) isotheres (Hutchins and Scharff, 1947). This difference is clearest in the western Atlantic where *Colobomatus* is confined to the region of the Gulf of Mexico and Caribbean Sea (lat. 10–30° N.—fig. 182). Although one of its primary hosts, *Strongylura notata* (fig. 179), has a similar restriction, other major hosts such as *S. marina*, *S. timucu*, and *T. crocodilus* (figs. 178, 179) range much farther to the north (past lat. 40° N.) and south (past lat. 20° S.).

Lernanthropus belones has an apparent gap in distribution (fig. 183). Both *L. belones* and *L. tylosuri* seem to be equally common throughout the world except for the eastern Atlantic and western Indian Oceans where we have found only *L. tylosuri.* We believe this break is primarily due to the lack of proper hosts for *L. belones* in these *Strongylura*-deficient regions. The eastern Atlan-

tic has only one species of *Strongylura*—*S. senegalensis*—and it is confined to the Gulf of Guinea. The western Indian Ocean has only one *Strongylura*—*S. leiura*—a large offshore species infested (rarely) with *L. tylosuri* and apparently never with *L. belones*. *L. belones* probably will be found to occur on *S. senegalensis*, so part of the distributional gap will be filled in. There does, however, appear to be a real gap in the distribution of *L. belones* that tends to divide the worldwide population. Perhaps detailed analysis of geographic variation in *L. belones* will provide morphological support for this geographical two-population hypothesis. The ovigerous females from the Atlantic and the Indo-West Pacific show a difference in total length (See discussion of intraspecific variation in copepods and fig. 187).

As has been noted previously, the widespread *Parabomolochus bellones* is replaced by two species in the eastern Pacific—the closely related *P. constrictus* and the more distantly related *P. ensiculus* (fig. 184). The Eastern Pacific Barrier, so important in blocking the distribution of shore fishes (Briggs, 1961), seems to operate as effectively within this genus of needlefish copepods.

Parabomolochus bellones appears to be in the process of being replaced in the eastern Indian and western Pacific Oceans by *P. sinensis* and the two species of *Nothobomolochus*. This replacement is partially apparent from a comparison of the distribution of *Parabomolochus* (fig. 184) with *Nothobomolochus* (fig. 185). In the western Pacific, *P. bellones* is common in Japan and Australia, between the 75° and 80° F. isotheres (23.9° C. and 26.7° C.—Hutchins and Scharff, 1947), whereas the other three bomolochids are common in the tropical waters. Relative abundance of *P. bellones* also differs from that of the other bomolochids (tables 4 and 5). *P. bellones* is very abundant in the western Atlantic (infestations ranging up to 42 percent). It is also equally abundant on most hosts in the Gulf of Guinea and Mediterranean Sea. However, *N. gibber* has largely replaced *P. bellones* on one host—*Belone svetovidovi*. In the Indo-West Pacific, *P. sinensis* and the two species of *Nothobomolochus* replace *P. bellones* on some hosts, particularly *Ablennes hians* and *Platybelone argalus* in the western and southern Pacific. Perhaps *P. sinensis* and the two species of *Nothobomolochus* evolved more recently and have begun to replace the older *Parabomolochus bellones* in the warmer parts of the Indo-West Pacific oceans.

The distributional maps of ergasilid copepods (fig. 186) and their fresh-water needlefish hosts (fig. 180) may also be compared. With one exception, the ranges of the host species are greater than those of their ergasilid copepods. The exception is the presence of what we have called *Ergasilus orientalis* on *Potamorrhaphis* in the Amazon Basin and on *Strongylura incisa* from Arnhem Land, Australia. We do not believe that this is a widespread species, but Cressey has been unable to discover any significant differences between the two populations; for the present we let this distributional pattern stand.

Probably the most widely distributed ergasilid copepod considered here is *Ergasilus coleus*. This copepod has been collected on three different hosts: the fresh-water *Xenentodon cancila* from India; the estuarine *Strongylura strongylura* from India, Borneo, and the Philippine Islands; and the primarily marine *S. urvillii* from the Philippines. This extensive distribution argues for either a greater degree of salt tolerance than is usually found in ergasilids or an old distributional pattern dating back to when the fresh waters of southeast Asia, Borneo, and the Philippines were connected, permitting the transfer of fresh-water fishes and their parasites.

Intraspecific Variation in Copepods

Studies were made of the variation in total length in *Caligodes laciniatus* and *Lernanthropus belones* and in relative lengths of two setae on leg 5 of *Parabomolochus bellones*.

As discussed under *Caligodes*, the total length of ovigerous females of this copepod varies widely. We analyzed this variation by host and by area (table 2). By area, the ranges and mean lengths were: Atlantic 2.4 to 7.1 (4.36), Indo-West Pacific 2.5 to 5.6 (3.70), and eastern Pacific 3.4 to 6.6 (4.29). By hosts, *Ablennes hians* stands out with by far the largest *Caligodes* 5.3 to 7.1 (6.03) compared to five other host species 2.4 to 5.6 (means 3.77–4.66). Although evidence is clear for differences in lengths of copepods by host species and not by geographic areas; we do not know if the host directly influences the growth of the copepod or whether the host's environment does so.

373-320 O—70——9

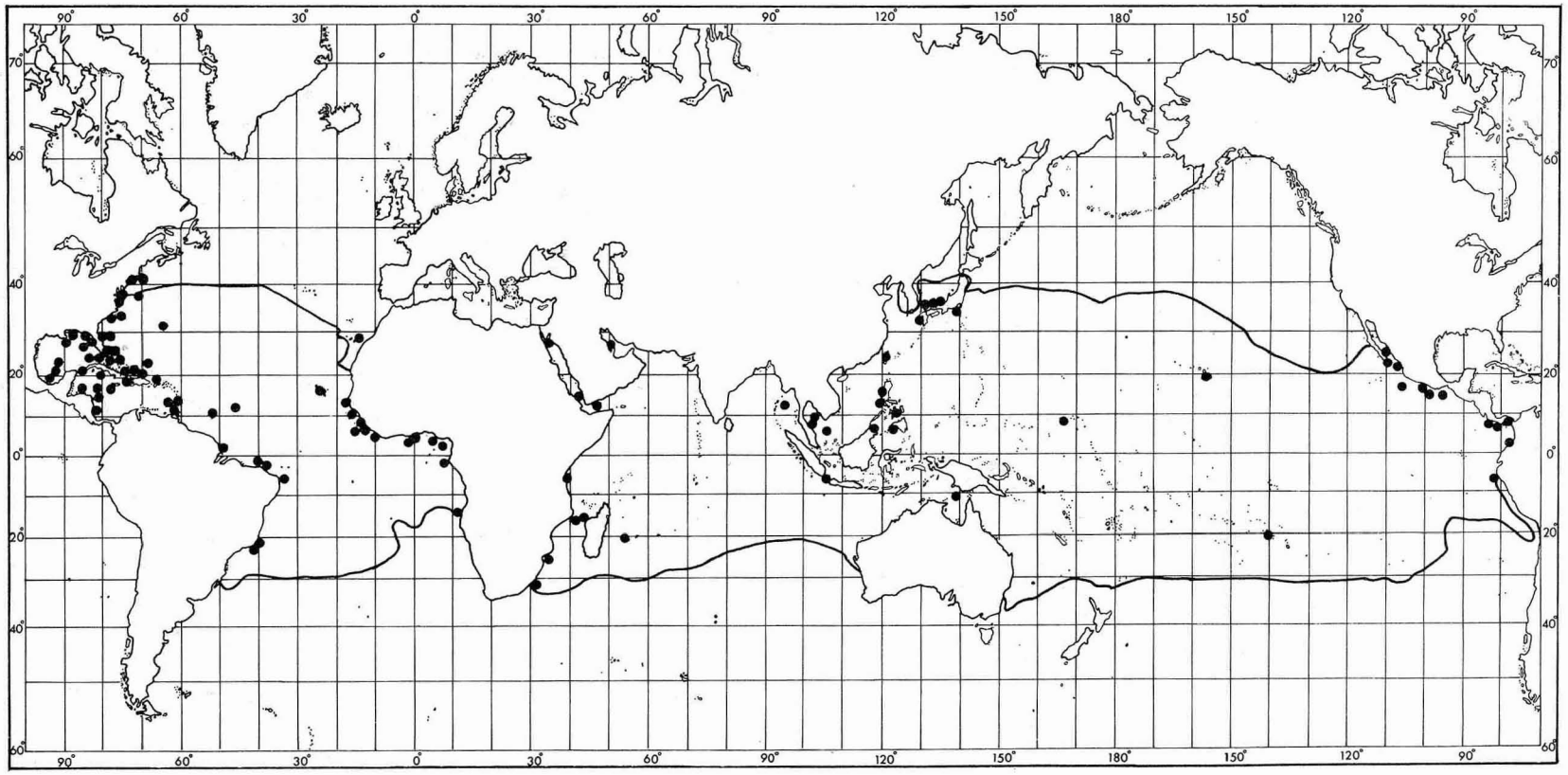


FIGURE 175.—Distribution of *Ablennes hians* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

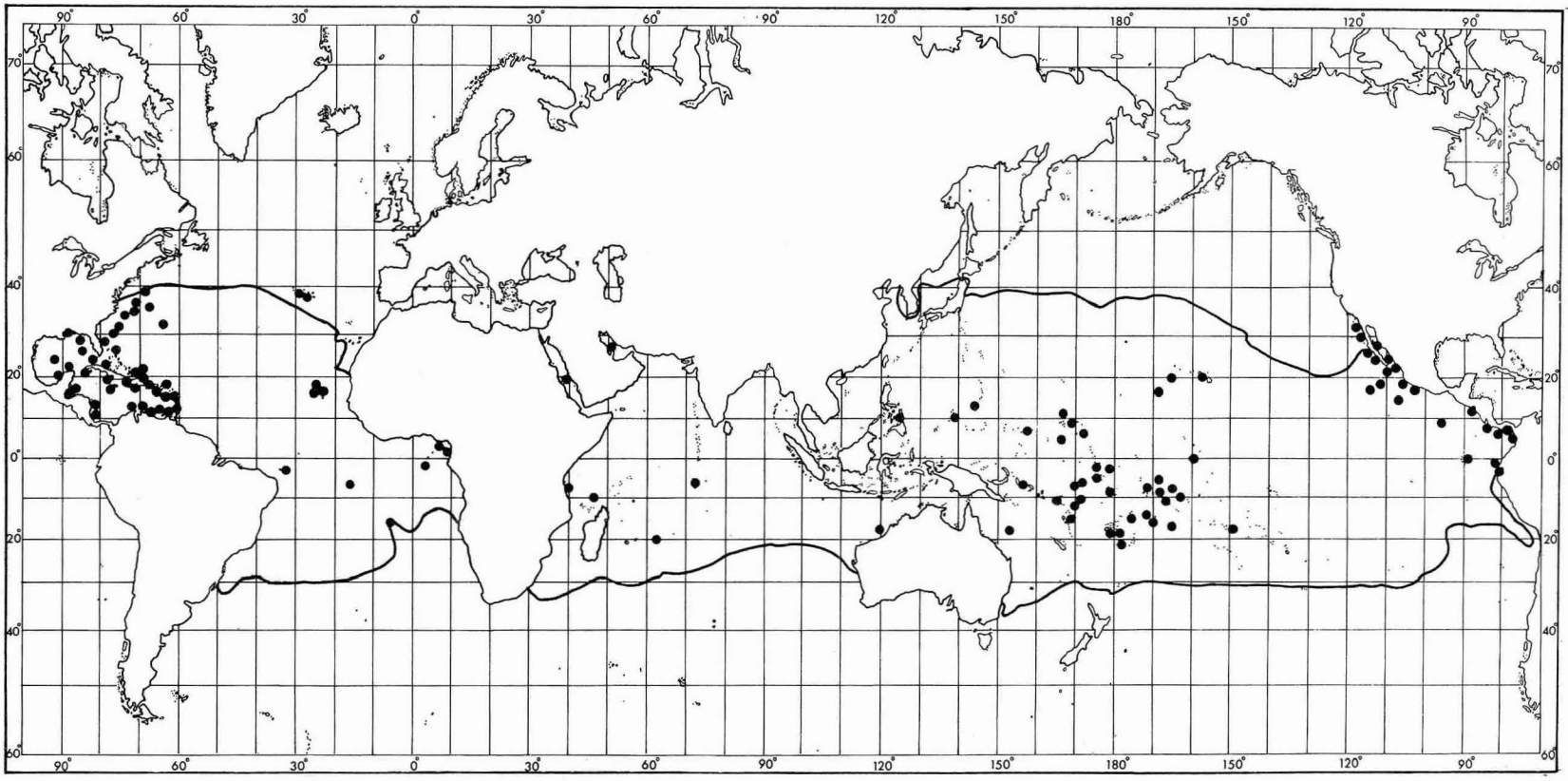


FIGURE 176.—Distribution of *Platybelone argalus* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

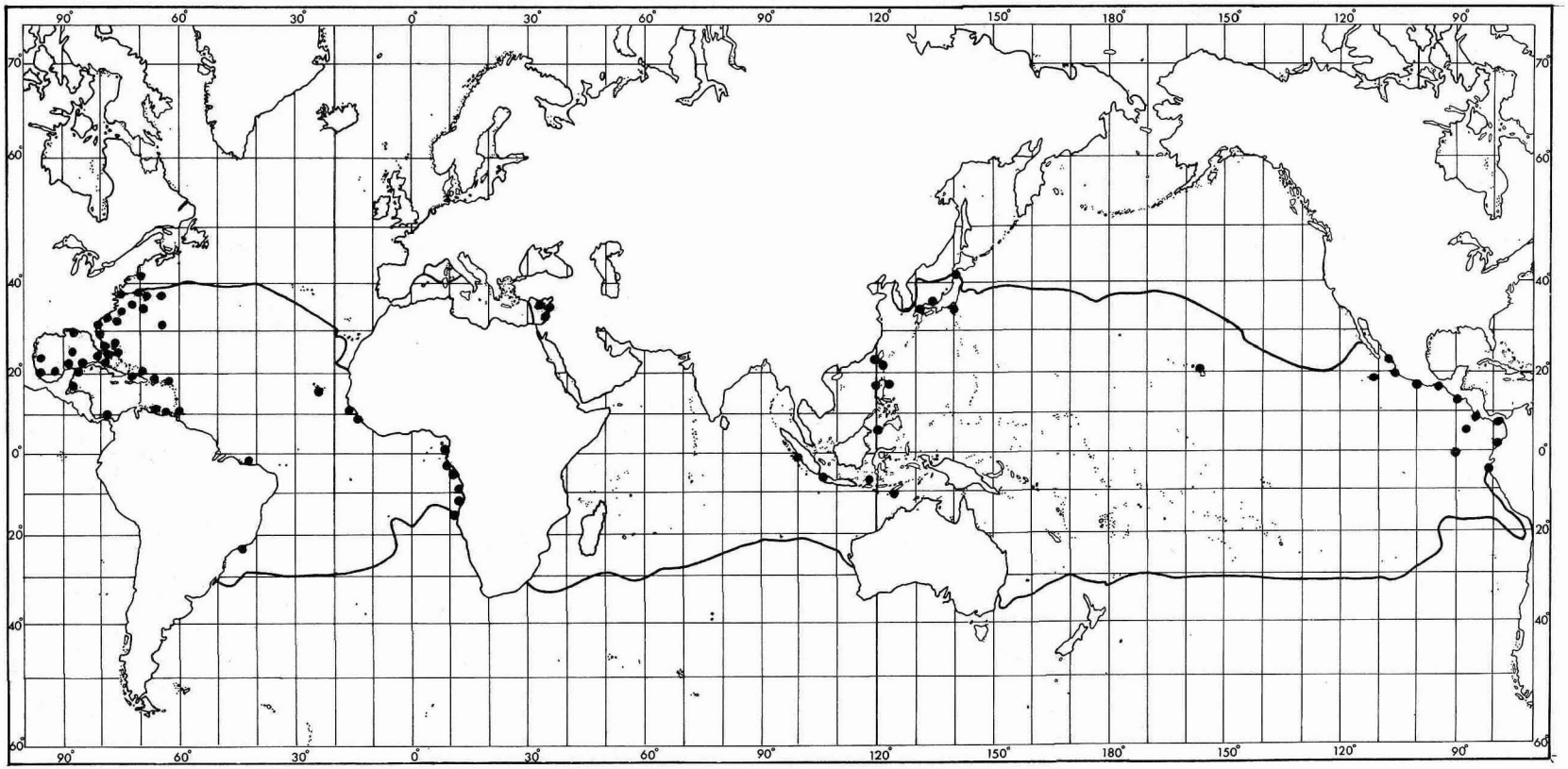


FIGURE 177.—Distribution of *Tylosurus acus* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

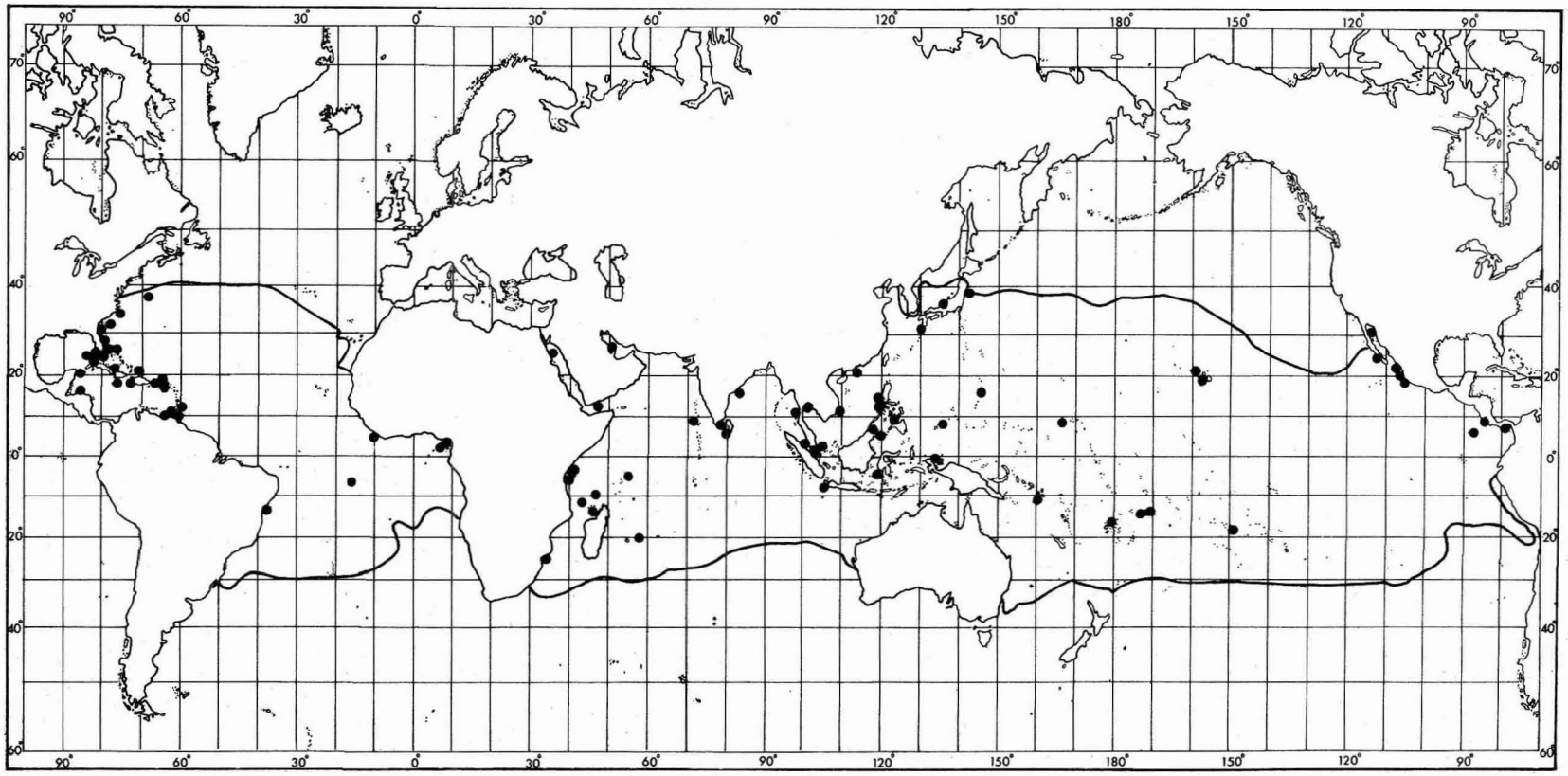


FIGURE 178.—Distribution of *Tylosurus crocodilus* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

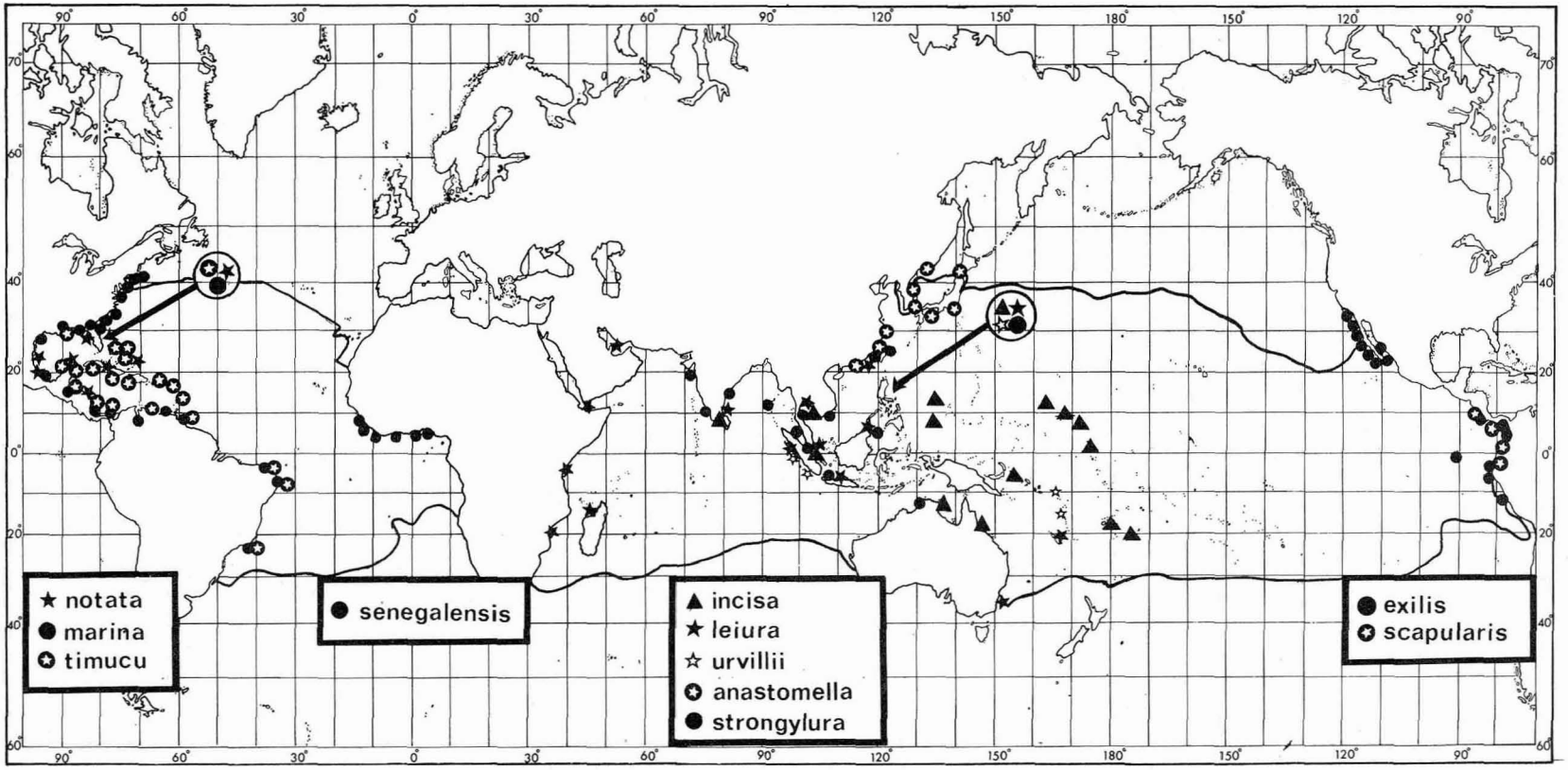


FIGURE 179.—Distribution of marine populations of 11 species of *Strongylura* based on specimens examined in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

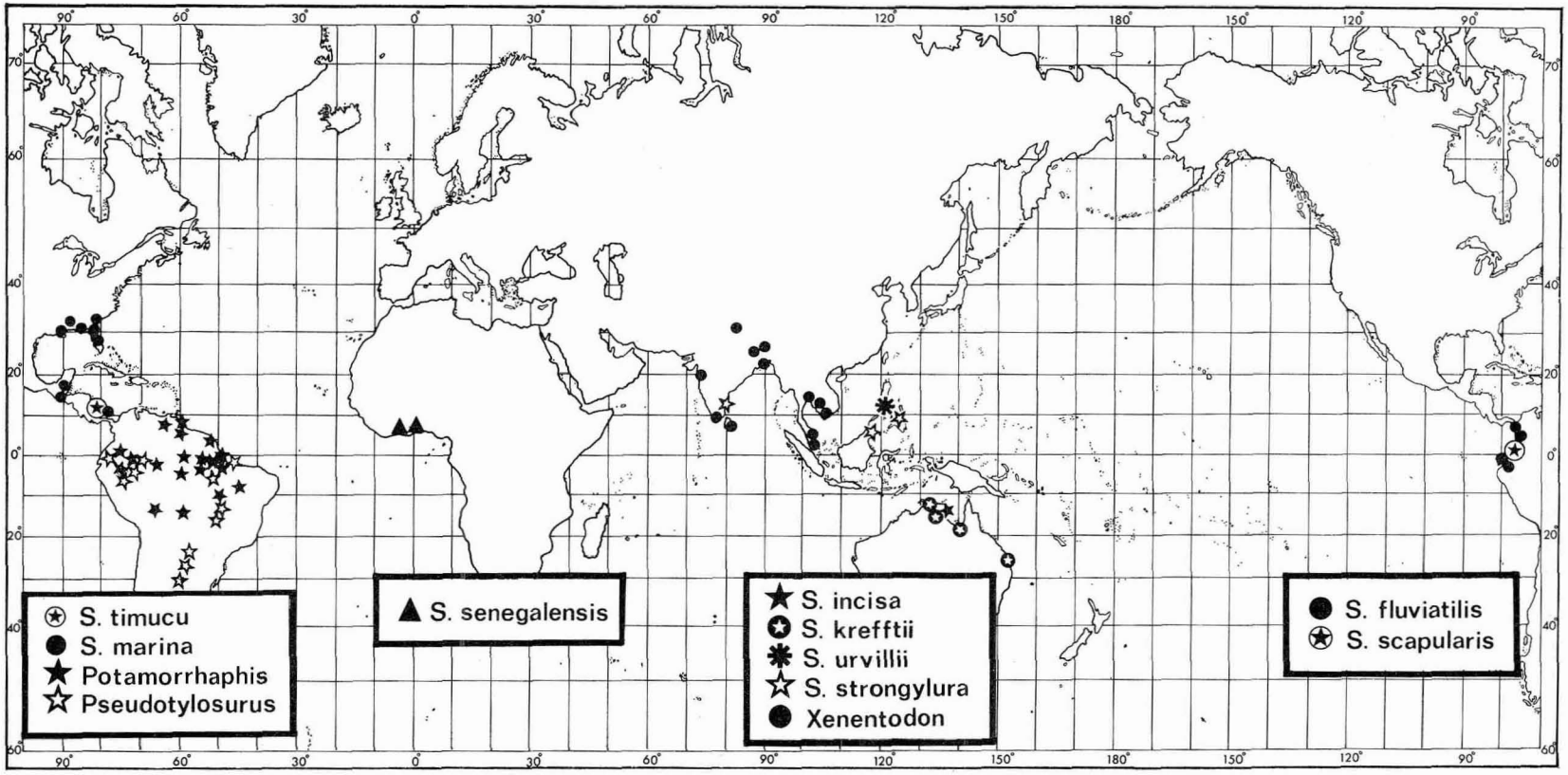


FIGURE 180.—Distribution of fresh-water needlefishes including fresh-water populations of *Strongylura* based on specimens examined.

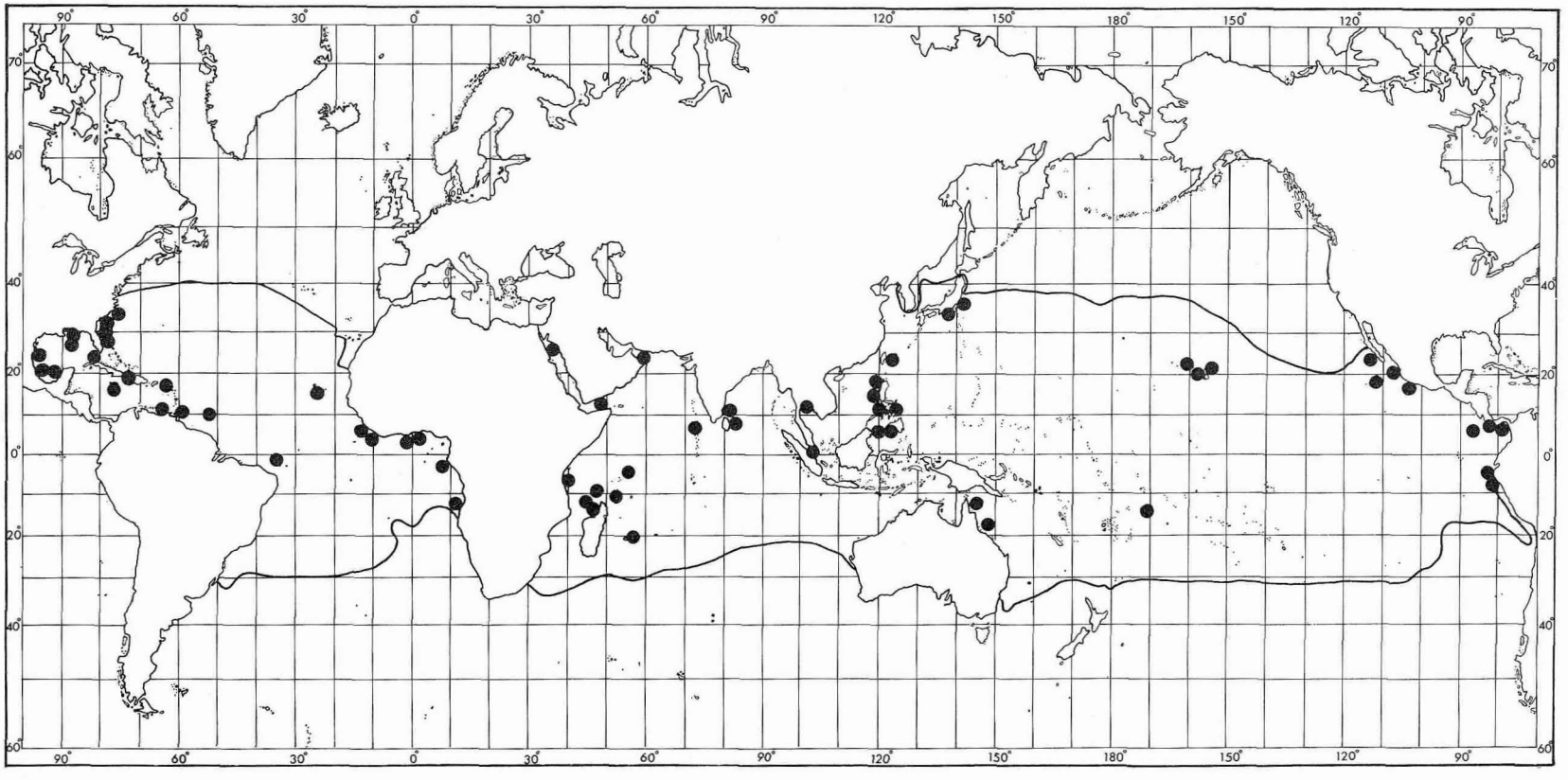


FIGURE 181.—Distribution of *Caligodes laciniatus* from needlefishes in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

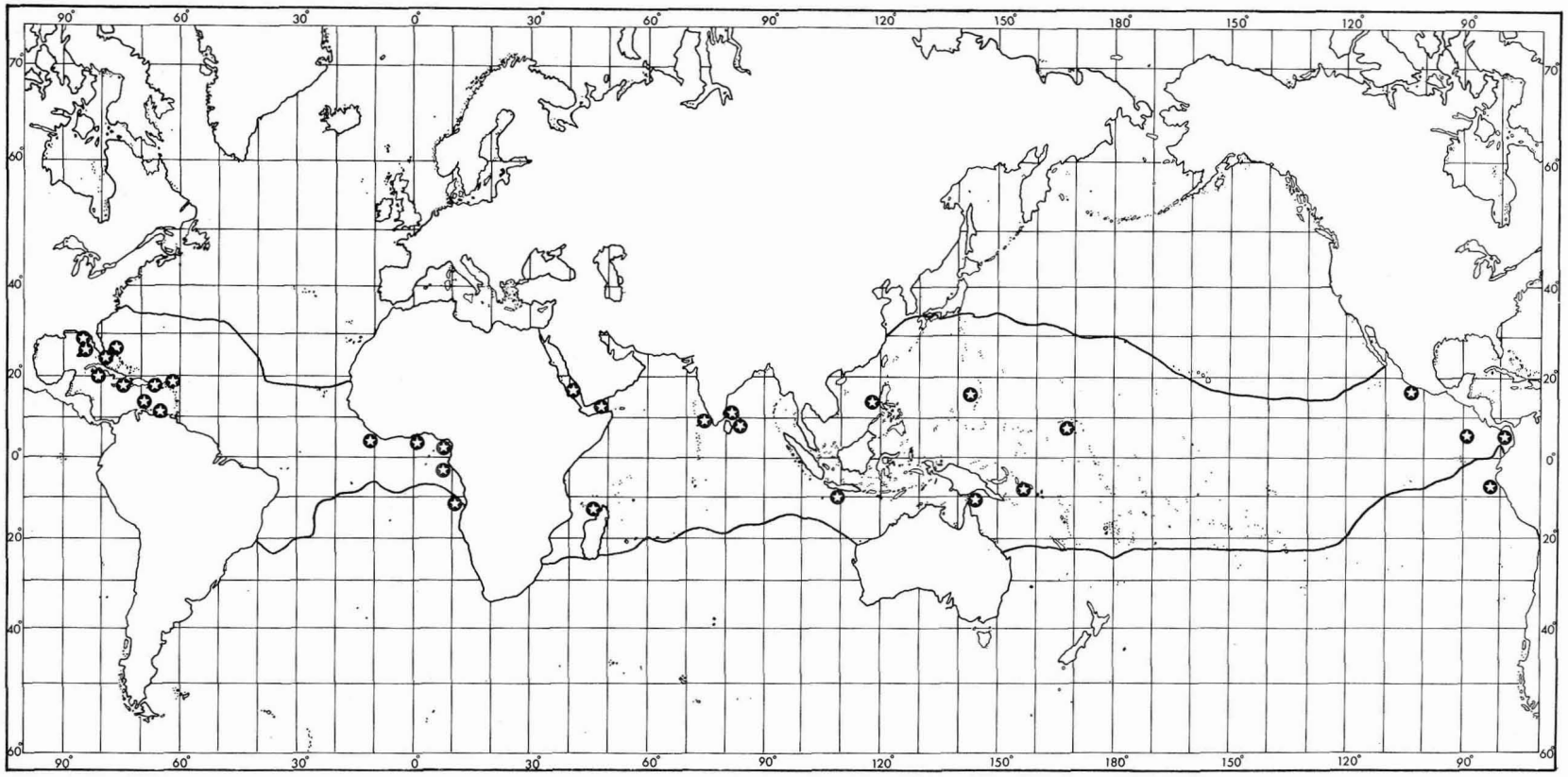


FIGURE 182.—Distribution of *Colobomatus goodingi* from needlefishes in relation to the 80° F. (26.7° C.) isothere from Hutchins and Scharff (1947).

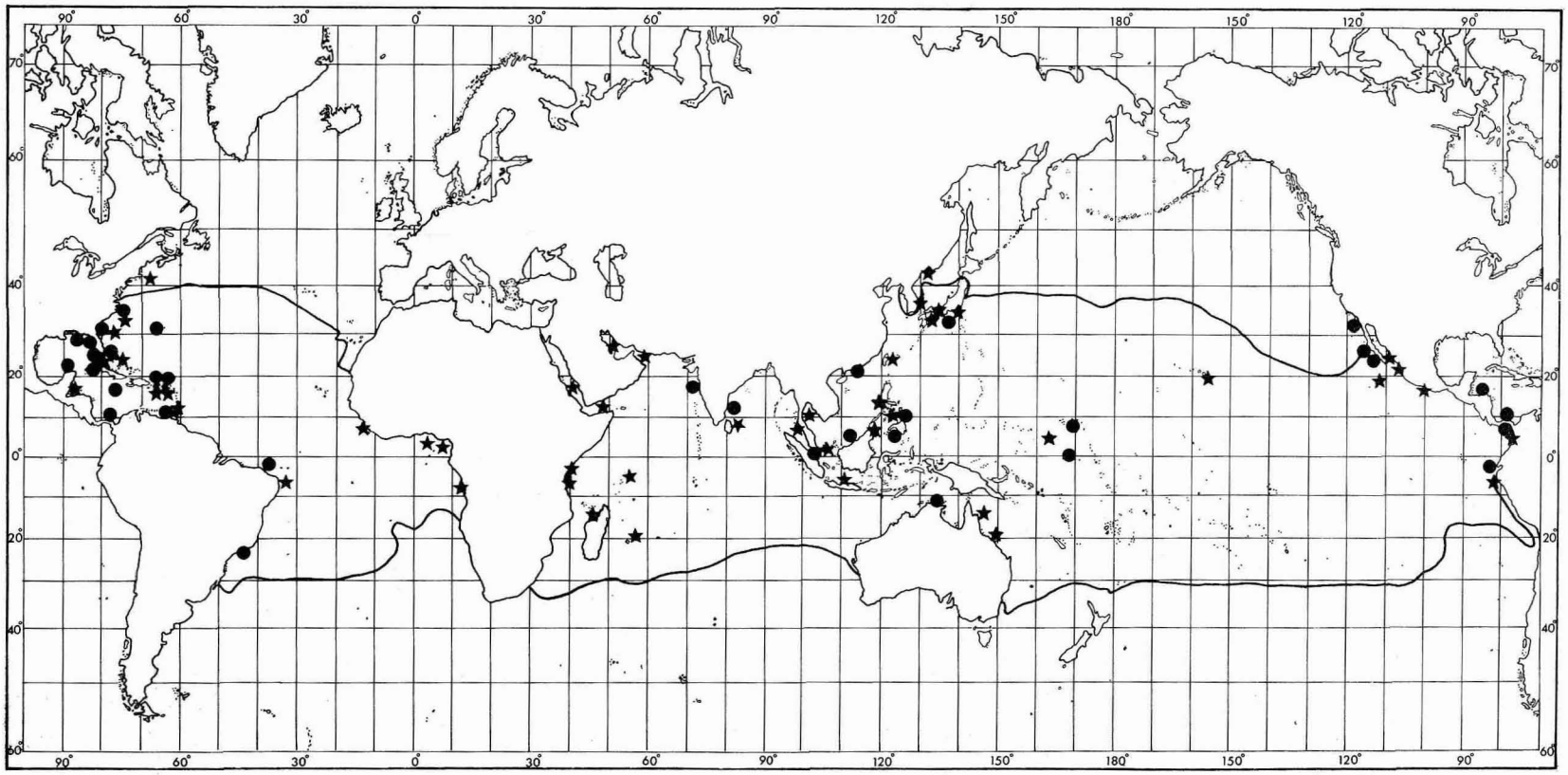


FIGURE 183.—Distribution of *Lernanthropus belones* (dots) and *L. tylosuri* (stars) from needlefishes in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947).

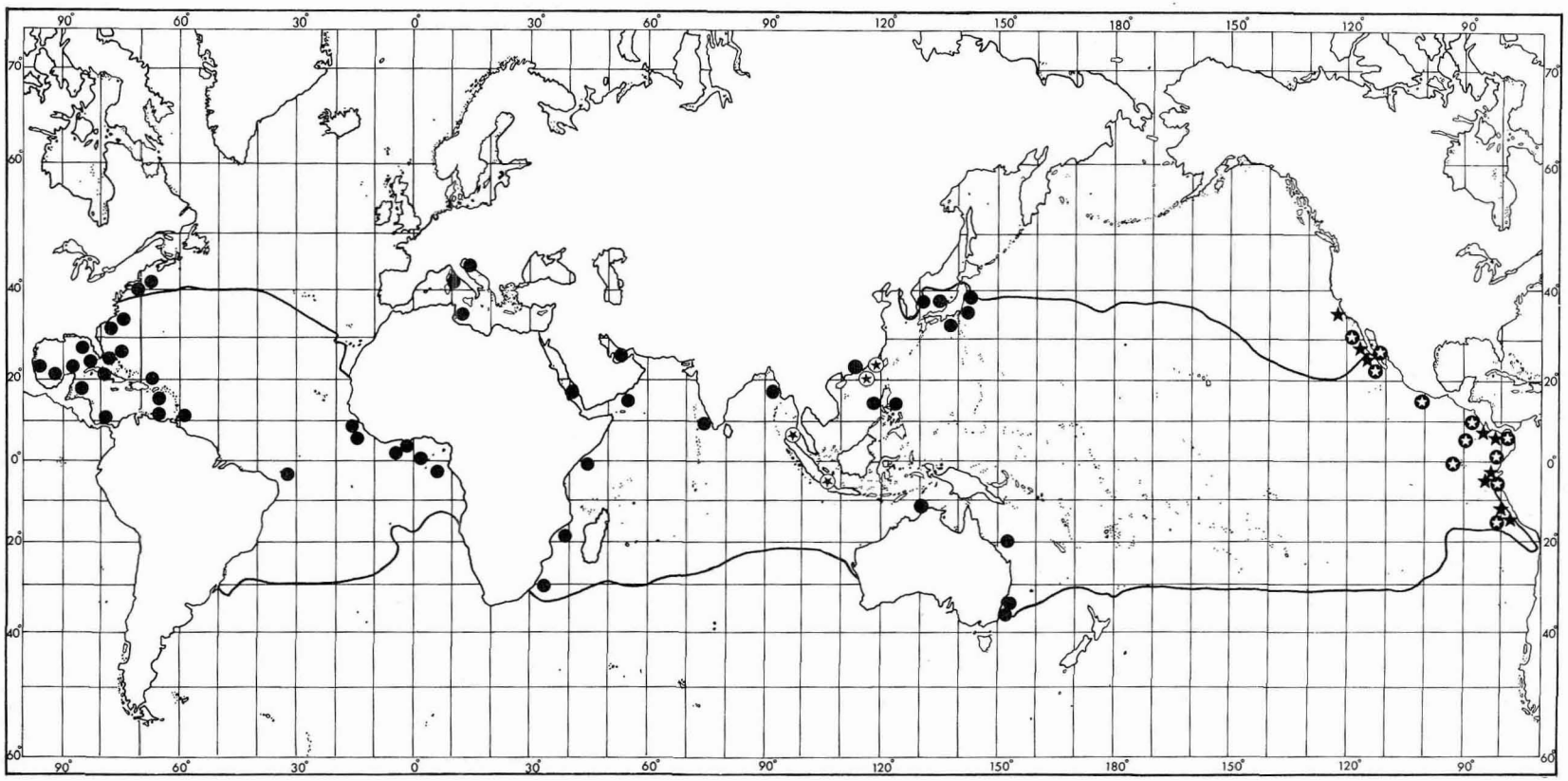


FIGURE 184.—Distribution of four species of *Parabomolochus* from needlefishes in relation to the 75° F. (23.9° C.) isothere from Hutchins and Scharff (1947). Dots—*P. bellones*, stars—*P. ensiculus*, stars in circles—*P. sinensis*, white stars (eastern Pacific)—*P. constrictus*.

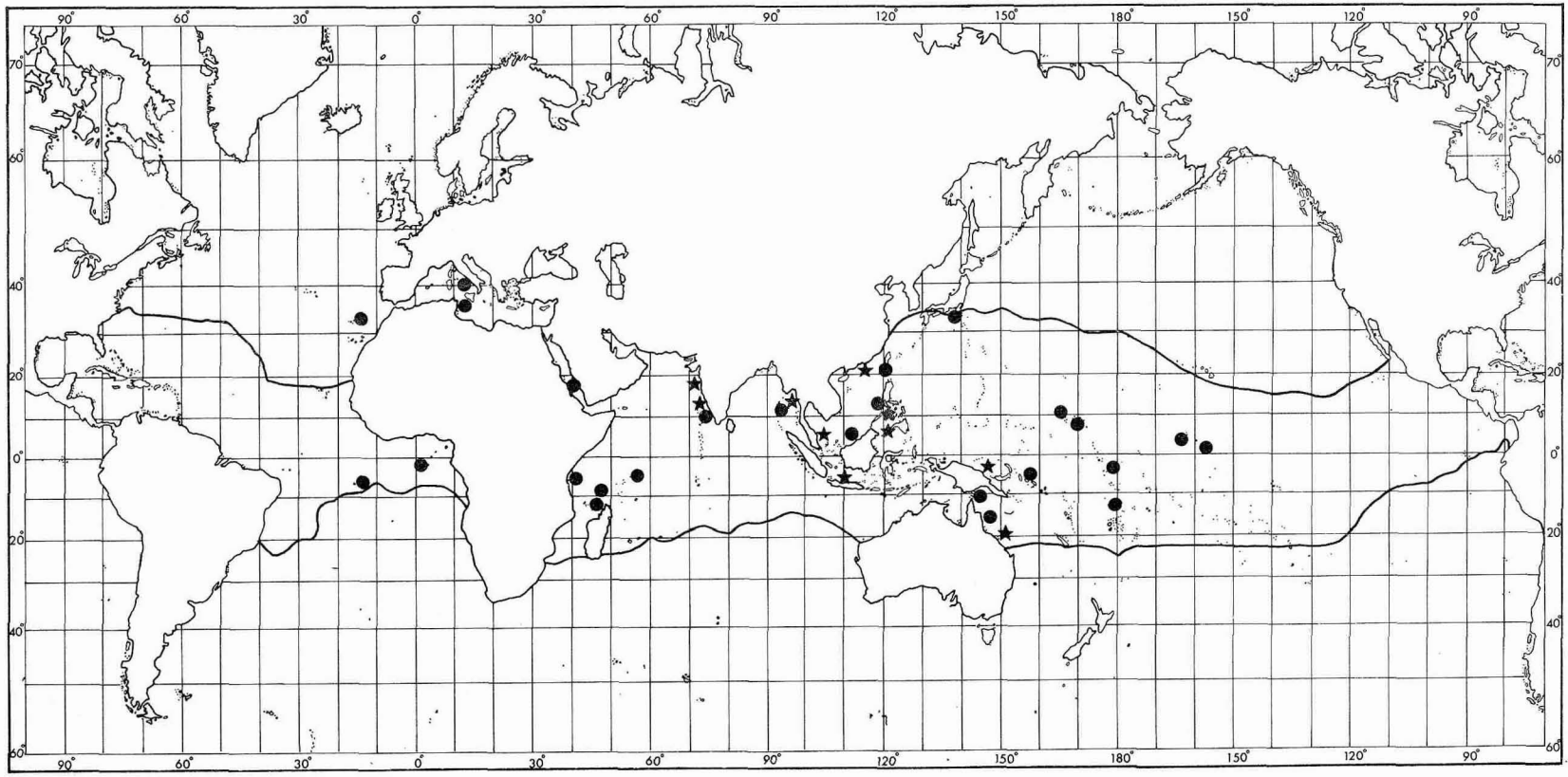


FIGURE 185.—Distribution of *Nothobomolochus gibber* (dots) and *N. digitatus* (stars) from needlefishes in relation to the 80° F. (26.7° C.) isothere from Hutchins and Scharff (1947).

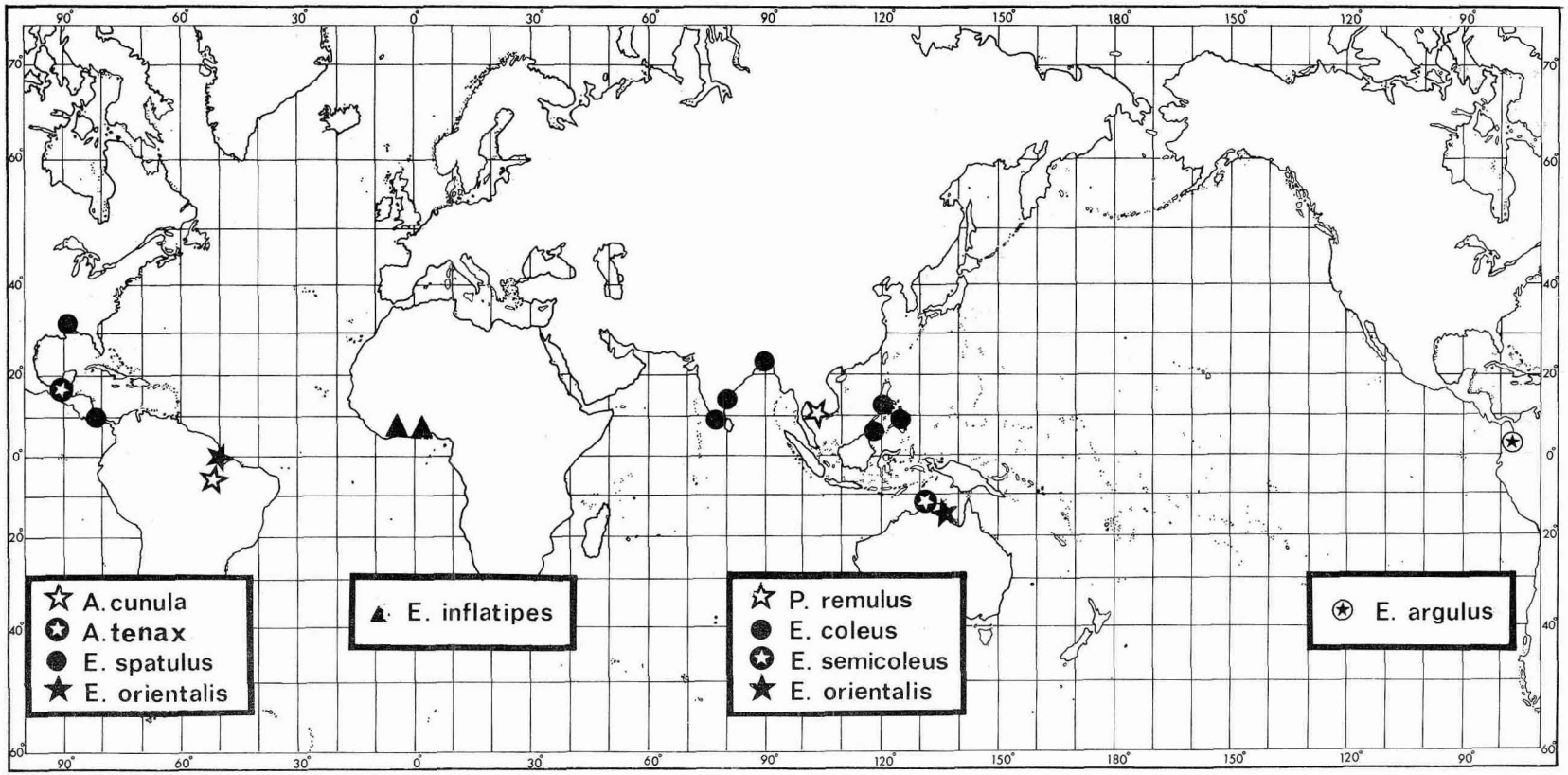


FIGURE 186.—Distribution of ergasilid copepods of the genera *Acusicola*, *Ergasilus*, and *Paraergasilus* from needlefishes.

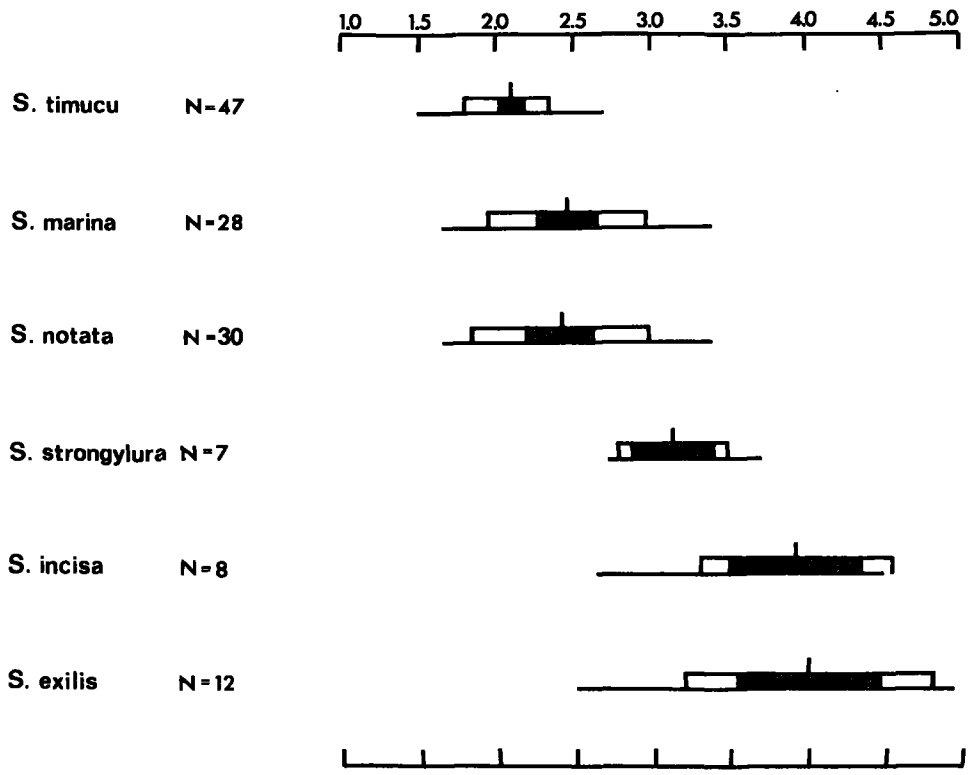


FIGURE 187.—Total length (in μ) of ovigerous female *Lernanthropus belones* from six species of *Strongylura* arranged from W. Atlantic east to E. Pacific. The horizontal line represents the range, the vertical line the mean, the filled-in rectangle two standard errors on each side of mean, and open rectangle one standard deviation on each side of mean.

The total length of ovigerous female *Lernanthropus belones* also varies: copepods from the three western Atlantic hosts are significantly smaller than those from the two Pacific hosts (fig. 187). *Strongylura strongylura* is geographically intermediate (Indo-West Pacific) and has intermediate-sized *L. belones*. The Pacific hosts (*S. incisa* and *S. exilis*) do reach a greater length than the other four species of hosts, but the possible host-parasite size correlation breaks down: *S. strongylura*, the smallest of the six host species, does not have the smallest copepods.

The relative lengths of the two setae on leg 5 in *Parabomolochus* have been examined by area (fig. 188) and by host (fig. 189). The first set of Hubbs-Perlmutter diagrams in each figure is of a sample of 50 *P. bellones* taken from one collection of *Strongylura notata* at Sarasota, Fla. This diagram gives a measure of the amount of variation to be expected in setae lengths of a single population from one host species at one time and place. The smaller ratio of seta 1 to 2 distinguishes the eastern Pacific *P. constrictus* from its probable ancestor *P. bellones*. The higher ratio distinguishes *P. sinensis* from either of these. The difference in the ratio is primarily due to the much greater length of seta 2 in *P. constrictus* and the shorter length of seta 2 coupled with a longer seta 1 in *P. sinensis*. Neither the absolute lengths of seta 1 and seta 2 nor their ratio varies significantly among the populations living on the three hosts of *P. constrictus* in the eastern Pacific Ocean. Variation is extensive, however, among populations of *P. bellones*. The populations in the five subareas of the western Atlantic all have similar absolute lengths of both setae, and their ratios are nearly identical. The Gulf of Guinea and Mediterranean populations have seta 1 somewhat longer, resulting in a significantly higher ratio of seta 1 to seta 2. Setae lengths differ among three western Pacific populations—Japan, Australia, and Philippines—but their ratios are nearly identical.

Thus, in *Caligodes laciniatus* at least, intraspecific variation in the copepod is related to host

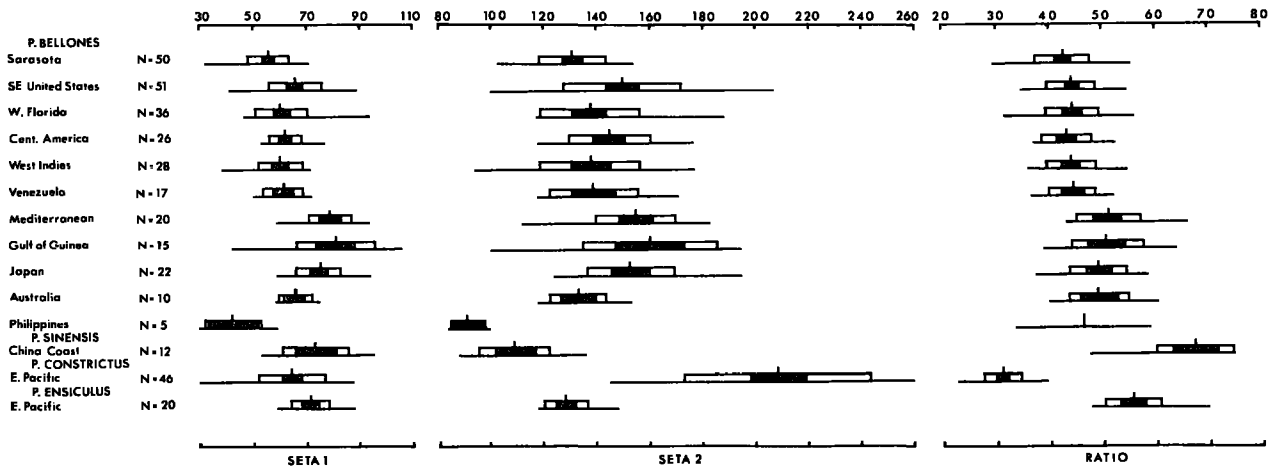


FIGURE 188.—Lengths of two setae on leg 5 of four species of *Parabomolochus* by geographic area. Symbols as in figure 187. The first line represents a single sample from *Strongylura timucu* from Sarasota, Fla.

influence or the ecology of the host. And in *Lernanthropus belones* and *Parabomolochus bellones*, intraspecific variation is clearly geographic.

Relative Rates of Evolution

An often cited axiom of modern parasitology asserts that because parasites evolve more slowly than their hosts, information on the parasites will assist in understanding the evolution of the hosts. In other words, hosts that harbor closely related parasites may themselves be closely related. This axiom is related to the question of host specificity. Four worldwide species of copepods (*Caligodes laciniatus*, *Lernanthropus belones*, *L. tylosuri*, and *Colobomatus goodingi*) show little geographic variation except in total length. The four worldwide species of needlefishes show varying amounts of geographic variation (Collette and Parin, 1970). This variation is weakest in *Ablennes hians*. *Tylosurus crocodilus* has at least two subspecies, one restricted to the eastern Pacific. *T. acus* has five subspecies: western Atlantic, Mediterranean, Gulf of Guinea, Indo-West Pacific, and eastern Pacific. *Platybelone argalus* has seven subspecies: western Atlantic, Annobon-Fernando Póo, Ascension-St. Helena, Cape Verdes, Red Sea, Indo-West Pacific, and eastern Pacific. Thus, the four worldwide species of needlefishes appear to be more highly differentiated than are the four worldwide species of copepods. It must be remembered, though, that studies of geographic variation have not been carried out in copepods with the same degree of thoroughness as in fishes.

Another widespread copepod, *Parabomolochus bellones*, has differentiated to the specific level (*P. constrictus*) after isolation in the eastern Pacific. In comparison, three of the four worldwide hosts have differentiated to only the subspecific level. Here, evolution may have proceeded faster in the copepod than in its host. The apparent "loose" specificity to their hosts of the cyclopoid copepods discussed here may explain the unsettled nature of their relationship.

Effect of Host Size

Another parasitological axiom states that older (=larger) host individuals have a greater parasite fauna because they have been exposed longer. To examine this axiom, data were examined on the mean body lengths of the commonest 16 species of marine needlefishes infested with the commonest 8 species of copepods. The copepods were divided into two major categories: specialized (*Lernanthropus*, *Caligodes*, *Colobomatus*) and generalized (*Parabomolochus* and *Nothobomolochus*). By specialized we mean possessing adaptations used as holdfasts (and exhibiting a higher degree of host specificity); by generalized we mean those copepods (Bomolochidae) that are free to wander about (and show less host specificity). Because the species of needlefishes vary widely in length, a ranking comparison was used to substitute relative

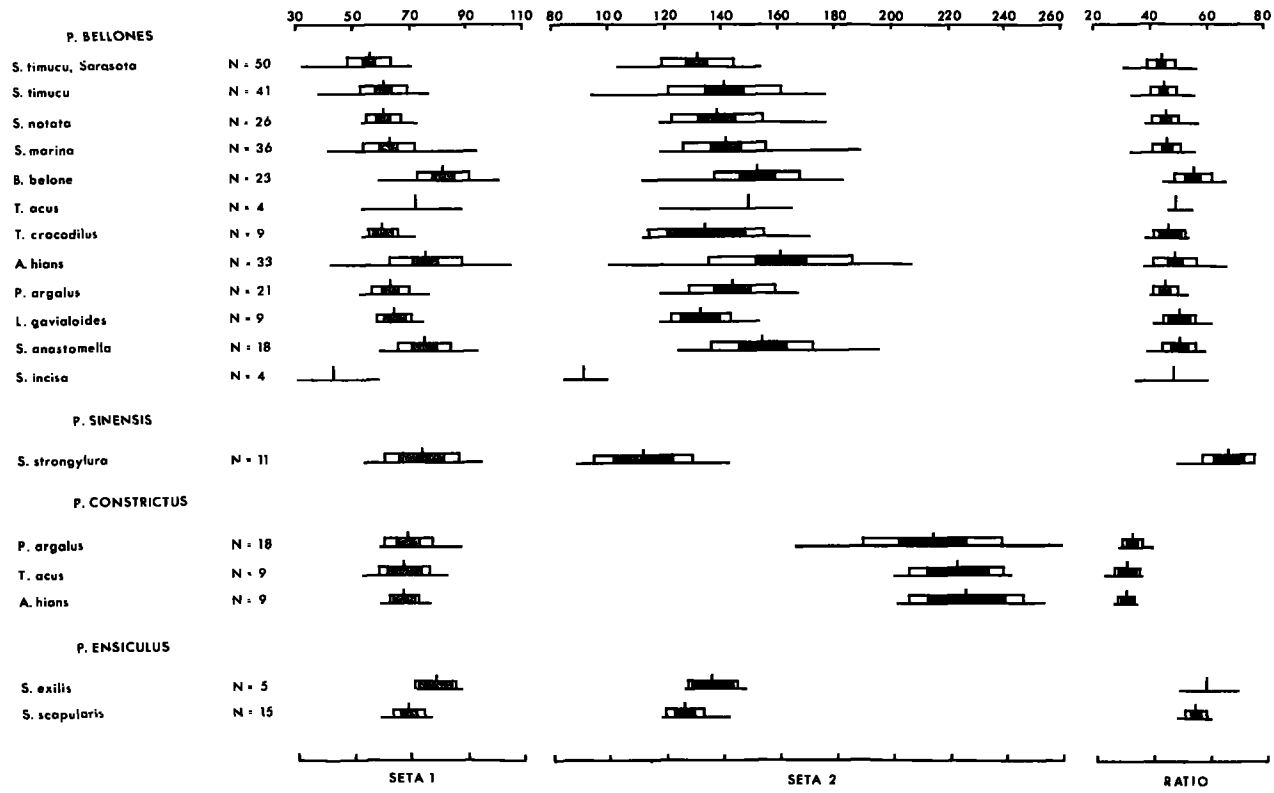


FIGURE 189.—Lengths of two setae on leg 5 of the species of *Parabomolochus* by hosts. Symbols as in figure 187.

length for absolute length. For each species of needlefish infested with a given species of copepod, three mean body lengths were compared: mean body length of all specimens examined, mean body length of all specimens that lacked copepods, and mean body length of all specimens infested with the particular copepod. The least mean body length was ranked 1, the next 2, and the greatest 3.

The specialized copepods (table 6) show consistent results. Without exception, the needlefishes without a specific copepod had the smallest mean body length (1) and the needlefishes with a particular species of specialized copepod had the largest mean body length (3). The mean body length of the total specimens examined was intermediate (2). We interpret this sequence to mean that these four specialized species of copepods are attached to needlefishes of larger than average size because of needing sufficient space and time to become attached.

The generalized copepods show a different picture. As with the specialized copepods, three species (*Parabomolochus constrictus*, *P. ensiculus*, and *Nothobomolochus gibber*) are usually found on needlefishes with greater mean body lengths than the needlefishes with no copepods. Summing the ranks for each of these three species of copepods, however, shows that the mean body lengths of needlefish infested with one of these copepods is about equal to the mean body lengths of the total number of needlefishes examined. Thus, the distribution of these three copepods is unrelated to the size of the needlefishes.

Unlike the situation with the seven species of copepods previously discussed, the mean body length of specimens infested with *Parabomolochus bellones* is equal to or less than the mean body lengths of all specimens examined. This fact seems to indicate that *P. bellones* selects smaller specimens of needlefishes to infest.

The above analysis confirms the subjective impressions that Collette gained while collecting copepods from preserved needlefishes: bomolochids more frequently infest smaller needlefishes than do the specialized copepods. Also, the chance of finding an individual needlefish infested with one

TABLE 6.—*Ranking comparisons of mean body lengths of all specimens of needlefish species examined with mean body lengths of specimens with no copepods and specimens with a particular copepod (1=smallest mean body length; 3=largest mean body length)*

Needlefishes with generalized copepods				Needlefishes with specialized copepods			
Needlefish species	All specimens	No copepods	*Parabomolochus bellones*	Needlefish species	All specimens	No copepods	*Lernanthropus belones*
Ablennes hians	3	1	2	*Strongylura exilis*	2	1	3
Belone belone	2	3	1	*Strongylura marina*	2	1	3
Platybelone argalus	3	2	1	*Strongylura notata*	2	1	3
Lhotskia gavialoides	2	3	1	*Strongylura scapularis*	2	1	3
Strongylura anastomella	2	1	3	*Strongylura strongylura*	2	1	3
Strongylura marina	3	2	1	*Strongylura timucu*	2	1	3
Strongylura notata	3	1	2	Total	12	6	18
Strongylura timucu	2	1	3				
Tylosurus acus	3	2	1				*Lernanthropus tylosuri*
Tylosurus crocodilus	3	2	1	*Ablennes hians*	2	1	3
Total	26	18	16	*Strongylura anastomella*	2	1	3
			Parabomolochus constrictus	*Strongylura leiura*	2	1	3
Ablennes hians	3	1	2	*Strongylura strongylura*	2	1	3
Platybelone argalus	2	1	3	*Tylosurus acus*	2	1	3
Strongylura exilis	2	1	3	*Tylosurus crocodilus*	2	1	3
Strongylura scapularis	3	1	2	Total	12	6	18
Tylosurus acus	3	1	2				
Tylosurus crocodilus	2	3	1				*Caligodes laciniatus*
Total	15	8	13	*Ablennes hians*	2	1	3
			Parabomolochus ensiculus	*Lhotskia gavialoides*	2	1	3
Strongylura exilis	3	1	2	*Tylosurus acus*	2	1	3
Strongylura scapularis	2	1	3	*Tylosurus crocodilus*	2	1	3
Total	5	2	5	Total	8	4	12
			Nothobomolochus gibber				*Colobomatus goodingi*
Ablennes hians	3	1	2	*Ablennes hians*	2	1	3
Platybelone argalus	1.5	1.5	3	*Strongylura marina*	2	1	3
Tylosurus crocodilus	3	2	1	*Strongylura notata*	2	1	3
Total	7.5	4.5	6	*Strongylura timucu*	2	1	3
				Tylosurus acus	2	1	3
				Tylosurus crocodilus	2	1	3
				Total	12	6	18

of the four specialized copepods increases greatly with the size of the needlefish.

Competition Between Copepods

Another question that we ask is: Does the presence of one species of copepod interfere with and thereby reduce the likelihood of infestation with a second species of copepod? We examined the relative numbers of individual needlefishes infested by more than one species of copepod (table 7) and then considered the combinations of copepod species (table 8) in the multiple-species infestations. Some individuals of half the species of needlefishes had two or more species of copepods. Most of these are either large species of needlefishes or species of which large numbers of specimens were examined. As shown in the previous section, the likelihood of infestation of a host by a specialized species of copepod increases with the size of the host. And obviously, the more specimens we examined, the more likely we were to find some individuals with more than one species of copepod.

The commonest combination of copepods (table 8) is *Parabomolochus bellones* and *Lernanthropus belones* (65 of 308 records). These combinations all come from the three western Atlantic species of *Strongylura*, *timucu* (33), *marina* (21), and *notata* (11), although both species of copepods occur from the western Atlantic through the western Pacific. The reason for the absence of this combination elsewhere is due to the lack of *L. belones* in the eastern Atlantic and western Indian Oceans which is caused by the scarcity of *Strongylura* hosts in these areas. Also, *P. bellones* is rarer in the Indian and Pacific Oceans where it is frequently replaced by *P. sinensis* and the two species of *Nothobomolochus*.

The next commonest combinations of copepods involve *Parabomolochus bellones*, *Colobomatus goodingi*, *Caligodes laciniatus*, and *Lernanthropus tylosuri*: *P. bellones* and *Colobomatus* (37 rec-

TABLE 7.—*Needlefish infestation by different numbers of copepod species as related to number of specimens examined and maximum host size (in mm. body length)*

Species	Species of copepods	Maximum BL	Total examined	Infested with copepods	With 2 species of copepods	With 3 to 5 species of copepods
	Number	*Mm.*	*Number*	*Percent*	*Percent*	*Percent*
Ablennes hians	8	725	251	57.0	10.8	3.2
Belone belone	3	537	77	44.2	0	0
Belone svetovidovi	2	320	15	26.7	0	0
Lhotskia gavialoides	2	665	24	54.2	8.3	0
Platybelone argalus	7	300	487	33.7	.2	0
Potamorrhaphis guianensis	1	157	63	9.5	0	0
Pseudotylosurus angusticeps	1	255	25	8.0	0	0
Strongylura anastomella	4	580	33	63.6	30.3	0
S. exilis	6	490	97	37.1	6.2	0
S. fluviatilis	1	321	33	12.1	0	0
S. incisa	5	450	75	17.3	0	0
S. krefftii	1	388	44	13.6	0	0
S. leiura	4	501	49	22.4	0	2.0
S. marina	7	418	316	32.0	7.0	0
S. notata	4	245	200	62.0	7.0	1.5
S. scapularis	4	245	38	84.2	15.8	0
S. senegalensis	2	263	27	81.5	0	0
S. strongylura	5	233	69	53.6	4.3	1.4
S. timucu	5	275	281	46.3	16.0	1.4
S. urvillii	4	228	21	19.0	0	0
Tylosurus acus	8	950	147	46.3	12.2	2.0
T. choram	3	415	18	33.3	0	0
T. crocodilus	8	860	212	56.6	18.9	3.8
T. punctulatus	3	385	31	22.6	0	0
Xenentodon cancila	2	169	65	15.4	0	0

ords); *Caligodes* and *L. tylosuri* (36); *P. bellones* and *L. tylosuri* (26); *L. tylosuri* and *Colobomatus* (25); and *Caligodes* and *Colobomatus* (22). The three species of needlefishes most involved in these combinations are the three large worldwide species: *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus*. They account for almost all the *Caligodes–L. tylosuri*, *Caligodes–Colobomatus*, and *L. tylosuri–Colobomatus* combinations (76 of 83 records). *T. crocodilus* and *Ablennes* are also important in the *P. bellones–Colobomatus* and *P. bellones–L. tylosuri* combinations (27 records) but three species of *Strongylura* are also involved: *S. timucu* (16 records) and *S. notata* (6) in the former combination and *S. anastomella* (10) in the latter.

All the common combinations mentioned above (212 of 308 records) involve copepods living in different ecological niches on their host needlefishes: *Caligodes* under the oral valves, *Colobomatus* in the cephalic lateral line canals, *Lernanthropus* attached to the gill filaments, and *Parabomolochus bellones* moving about under the opercles and in the mouth, especially under the oral valves. No hosts had both *L. belones* and *L. tylosuri*, which occupy the same niche, although some host species may have both species of *Lernanthropus* on different individuals (see Host Specificity). The habitat of *P. bellones* includes the oral valves to which *Caligodes* is restricted. We found 12 *P. bellones-Caligodes* combinations on four species of needlefishes, mostly on *Ablennes* (8 records). Four of these *Ablennes* were large Gulf of Guinea specimens (418–530 mm. BL) with four or five species of copepods.

The absence or rarity of some copepod combinations is due partly to the influence of host specificity (or host ecology). Thus, there are no *Caligodes laciniatus-Lernanthropus belones* combinations because *Caligodes* is restricted to *Ablennes*, *Tylosurus*, and a few species of *Strongylura*, whereas *L. belones* is found primarily on a different group of *Strongylura*.

The absence of some other combinations is purely geographic: the eastern Pacific *Parabomolochus constrictus* and *P. ensiculus* cannot be

TABLE 8.—*Infestation of needlefishes by more than one species of marine copepod. Upper right half of table gives total number of individual needlefishes with a particular combination of copepods. Lower left half of table gives number of species of needlefish with the particular combination of copepods*

Species	*Parabomolochus*				*Nothobomolochus*		*Caligodes laciniatus*	*Lernanthropus*		*Colobomatus goodingi*	*Caligus* spp.
	belones	*sinensis*	*constrictus*	*ensiculus*	*gibber*	*digitatus*		*tylosuri*	*belones*		
	Number										
Parabomolochus bellones							12	26	65	37	6
P. sinensis						1		1			
P. constrictus				3			6	6	2	5	1
P. ensiculus			1						6		
Nothobomolochus gibber								1		4	1
N. digitatus	1	1					1	4	2		1
Caligodes laciniatus	4		3			1		36		22	6
Lernanthropus tylosuri	4	1	3		1	3	4			25	9
L. belones	3		1	2		1				13	
Colobomatus goodingi	5		3		2		3	3	2		6
Caligus spp.	3		1		1	1	2	4		3	
Total number of species of copepods found with each species.	6	2	6	2	3	5	6	8	5	7	7

373-320 O—70——11

found with *P. bellones*, *P. sinensis*, *Nothobomolochus gibber*, or *N. digitatus*, which are found only outside the eastern Pacific.

The rarity of some combinations may be related to competition between species of copepods. For example, we found no records of *Parabomolochus bellones* with *Nothobomolochus gibber*, only one record of *P. bellones* with *N. digitatus*, and none of *N. gibber* with *N. digitatus*. The geographical distributions of these three species overlap broadly, and they live in similar ecological niches on needlefish. On the basis of this lack of co-occurrence and on the greater abundance of *Nothobomolochus* from the eastern Indian Ocean to the central Pacific, we believe *Nothobomolochus* (and *P. sinensis*) may have evolved more recently and may be in the process of replacing *P. bellones* in the above areas.

Evidence also exists of competition between the two eastern Pacific species of *Parabomolochus*. *P. ensiculus* is usually found in the mouth, under the oral valves; *P. constrictus* is usually found under the opercles. There are only three records of co-occurrence on a specimen of needlefish. In at least one of these, two *P. constrictus* were under the opercles and one *P. ensiculus* was under the oral valves.

In this study, no two species of ergasilid copepods were taken from the same host individual although two ergasilids, *Ergasilus spatulus* and *Acusicola tenax*, were taken from what is now considered one species of needlefish, *Strongylura marina*, at different localities. Ergasilids are generally fresh-water copepods and other needlefish copepods are marine; it would be surprising, then, to find an ergasilid on the same host individual with a marine copepod. We found two such records, however, *E. inflatipes* and *Parabomolochus bellones* on a specimen of *S. senegalensis* from Ebzie Lagoon, Ivory Coast, and *E. coleus* and *Nothobomolochus digitatus* from *S. strongylura* from Sandakan Bay, Borneo.

We have shown that larger needlefishes are more likely to have specialized copepods than smaller needlefishes. Do they also have more species of copepods? Seven species of needlefishes had more than two species of copepods on the same individual host (table 7). A total of only nine specimens represented the four species of *Strongylura* with individuals having more than two species of copepods (three each): one *S. leiura* with *Caligodes*, *L. tylosuri*, and *N. digitatus;* three *S. notata* and four *S. timucu* with *Colobomatus*, *L. belones*, and *P. bellones;* and one *S. strongylura* with *P. sinensis*, *N. digitatus*, and *L. tylosuri*. The other cases of more than two species of copepod on the same host individual are indeed in the three large worldwide species: *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus*. One specimen of *T. acus* had three species of copepods, two specimens had four; eight specimens of *T. crocodilus* had three species; three specimens of *Ablennes* had three species, three had four species, and two specimens had five. Seven species of copepods were involved in the 19 multiple combinations: *L. tylosuri* (17); *Colobomatus* (15); *Caligodes* (13); *Caligus* spp. (8); *P. bellones* (6); *P. constrictus* (4); and *N. digitatus* (1).

The two specimens of *Ablennes* with five species of copepods were both from the Gulf of Guinea: a 418-mm. BL specimen with 2 female *Caligodes*, 2 female *L. tylosuri*, 6 female *P. bellones*, 3 female *Caligus* sp. A, and 1 female *Colobomatus;* and a 530-mm. BL specimen with 25 female *Caligodes*, 1 male *L. tylosuri*, 3 female *P. bellones*, 1 male and 1 female *Caligus* sp. A, and 3 female *Colobomatus*.

The three *T. acus* specimens were 316, 374, and 535 mm. BL; the eight *T. crocodilus* 203, 227, 236, 261, 268, 300, 320, and 388 mm. BL; and the eight *Ablennes* 418, 455, 462, 483, 490, 508, 530, and 540 mm. BL. The species means (408, 275, 486) are greater than the mean body lengths of uninfested specimens, of all specimens examined (347, 250, 306), and of specimens infested by any particular species of copepod except the mean body length of *T. crocodilus* infested with *Caligodes*—303 mm. Thus, although the multiple-infested needlefishes are not the largest specimens of their species, they are larger than other groupings of their species.

Variation in Infestation With Time and Space

We have relatively few data on changes with time in infestation in a given population of needlefish. The best data come from the infestation by *Colobomatus goodingi* of three Bahamian samples of *Strongylura notata* taken in 1927, 1935, and 1963 (table 9). Four of six specimens from Crooked Island taken in 1927 were infested. Ten of 12 specimens collected at Bimini in 1935 were

TABLE 9.—*Sites of occurrence of* Colobomatus goodingi *in the cephalic lateral line canals of* Strongylura notata *from the Bahama Islands*

Locality and date	Specimens	Length range (BL)	Lower jaw		Interorbital		Upper jaw		Preorbital		Total
			R	L	R	L	R	L	R	L	
	Number	*Mm.*	*Number of specimens*								
Crooked Island:											
March 26, 1927	6	87–123	2	4	0	0	0	0	0	0	6
Bimini:											
Sept. 18–25, 1935	12	127–173	8	6	2	1	1	0	0	0	18
August 26, 1963	14	108–137	10	13	3	3	0	2	1	0	32
Total			20	23	5	4	1	2	1	0	56

infested, and all 14 specimens over 108 mm. BL were infested in 1963. Two specimens (76–80 mm. BL) from Crooked Island and five (58–65 mm. BL) from Bimini were uninfested in the 1963 collection. The average number of *Colobomatus* sites per fish (over 80 mm. BL) was 1.0 in 1927, 1.5 in 1935, and 2.6 in 1963. Thus, in this small sample, relative infestation seemed to be increasing over this time span.

Information is more plentiful on geographic variation in infestation. For example, the incidence of infestation by *Parabomolochus bellones* generally decreases from the Atlantic to the western Pacific (tables 4 and 5), probably because of competition with *P. sinensis* and the two species of *Nothobomolochus*.

The infestation of *Platybelone argalus* with juvenile stages of *Caligus* sp. varies widely from area to area. In the eastern Atlantic 42 percent of the *P. argalus* were so infested (table 4); this figure reaches nearly 100 percent if the uninfested populations at some island groups (Azores, Cape Verdes, Ascension, and St. Helena) are eliminated. Of 46 *P. a. annobonensis* taken at Annobon Island in 1964 and 1965, all but 3 had juvenile *Caligus* attached to the fins, and as many as 13 copepods were picked off a single needlefish. However, none of 11 *P. a. annobonensis* taken at the nearby island of Fernando Poó had any copepods.

Another clear example of geographic differences in infestation was found in *Tylosurus acus*. All populations were infested with *Caligodes*, *L. tylosuri*, and *Colobomatus* except for the Mediterranean *T. acus imperialis*, on which no copepods were found. This gross difference in infestation of the Mediterranean population of *T. acus* from the western Atlantic *T. a. acus* and the Gulf of Guinea *T. a. rafale* lends support to the taxonomic distinctness of the Mediterranean population.

Rather large amounts of interarea variation appear in the infestation of *Ablennes hians*, *Tylosurus acus*, and *T. crocodilus* by *Caligodes laciniatus*, *Lernanthropus tylosuri*, and *Colobomatus goodingi*. Some of this variation is no doubt due to differences in sizes of the hosts, larger hosts being more likely to be infested; some is definitely correlated with geography. For example, *Colobomatus* was found on only two large western Atlantic *Ablennes* and on no Indian Ocean specimens, yet it was very common in the Gulf of Guinea (41 percent). Interestingly, a similarly low rate of infestation by *Lernanthropus tylosuri* was found in the western Atlantic and the Indian Oceans.

At present, we can offer no explanation for these differences in infestation. The geographic differences are important in indicating restricted amount of interchange between populations of needlefishes and so serve to point out those populations that may be taxonomically distinct.

Nature of the Symbiotic Relationship

It is difficult to assess accurately the true nature of the relationship that exists between most species of "parasitic" copepods and their hosts. In the absence of measurable or observable damage to host tissue, it is open to question whether or not an organism is parasitic in the strict sense or if the relationship is commensalistic or mutualistic. For purposes of this discussion parasitism is defined as a relationship in which the host suffers tissue damage or is impeded in efficiency because of the presence of "parasites." Commensalism is that relationship whereby the host provides shelter (protection) or food to the "commensal" and neither suffers hardship nor benefits. Mutualism is defined as that relationship whereby both organisms benefit. Unless exhaustive life history observations are made,

all of these situations are difficult to assess except where damage or reduced efficiency to the host can be demonstrated.

Colobomatus goodingi is clearly parasitic. The host reaction is evidence that this copepod is causing some damage to the needlefish. The capsules formed on the jaw of the host must cause hydrodynamic interference with swimming and hence with the food-getting process.

Caligodes laciniatus must reduce the efficiency of the oral valves. We have examined specimens in which the oral valves were literally bulging with this parasite. As in all other caligid copepods, its mandibles are adapted for cutting and rasping and it undoubtedly feeds on the hosts' tissues. Usually tissue damage was not observed, and it is probable that caligid copepods inflict serious physical damage to their hosts only when present in great numbers.

No damage to the host tissue was apparent from adult *Caligus*, but they have to be considered parasitic because their mouth parts are adapted to feed on tissue. The fins of *Platybelone argalus* from Annobon Island that were infested with chalimus stages of this genus were deformed (Collette and Parin, 1970). The damage probably would reduce the efficiency of the fins.

No observable injury was caused by the presence of *Lernanthropus* on the gill filaments. Because the mouth parts are adapted for cutting and rasping, however, they must inflict some tissue damage. As with many other species of parasitic copepods, small numbers of these may be tolerated by the hosts with little damage or discomfort.

We cannot demonstrate that ergasilids were causing injury to the gill filaments to which they were attached but reports (Dogiel, Petrushevski, and Polyanski, 1961, p. 315; Rogers, 1969, p. 445), cite severe damage to host tissue when the parasites are present in large numbers. Because of this capability they must be considered parasitic.

The only group of needlefish copepods which we do not consider parasitic are the bomolochids. It seems likely to us that this relationship is commensal or even mutualistic. Bomolochid copepods are not highly modified in comparison with the other copepods considered here. They are able to move about freely within their preferred habitats (oral or gill chamber) and may actually clean these areas of detritus, accumulated mucus, or other undesirable matter. Because they do not attach to the host securely (unlike most of the other species considered here) they probably do not feed on host tissue. To do so would require the ability to maintain one position for a long period of time, and, in view of their weakly developed mouth parts, they are probably not able to do this.

Until we know more of the feeding and interference effects of copepods found on fishes the question of relationship to the host of most of them cannot be answered definitively.

ADDENDUM

Subsequent to the completion and submission of this manuscript the junior author examined additional material in several Australian museums. The additional new records are as follows (none of these are included in the maps, tables, or any portion of the main body of this paper):

Neoergasilus sp. (probably new) from *X. cancila*, Madras, India.

Ergasilus coleus from *S. strongylura*, Arnhem Land, Australia.

Ergasilus semicoleus from *S. krefftii* from Flinders River, Queensland, Australia.

Parabomolochus bellones from *Lhotskia gavialoides* (2 collections), New South Wales: *S. strongylura*, Gulf of Carpentaria and Onslow, Australia: *S. leiura*, Gulf of Carpentaria: *A. hians*, Port Stevens, New South Wales, Australia.

Nothobomolochus digitatus from *S. strongylura*, Onslow, Gulf of Carpentaria, Northern Territory (all Australia); Bombay, India.

Caligodes laciniatus from *L. gavialoides* (2 collections), New South Wales: *S. leiura*, Gulf of Carpentaria: *T. crocodilus* (5 collections), Percy Is. and Hayman Is., Queensland; Murray Is., Torres Strait; Gulf of Carpentaria; Tonga Is.

Lernanthropus tylosuri from *S. leiura*, Gulf of Carpentaria (2 collections) and Queensland; *S. strongylura*, Bombay, India; *T. crocodilus*, Tonga Is.

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