CYCLOPOID COPEPODS OF THE GENUS *TUCCA* (TUCCIDAE), PARASITIC ON DIODONTID AND TETRAODONTID FISHES

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ABSTRACT

The female of *Tucca impressus* Krøyer is redescribed, on the basis of specimens taken from *Chilomycterus schoepfi* (Walbaum) in the Gulf of Mexico. Both genus *Tucca* Krøyer and family Tuccidae Vervoort are redefined, and the genus is treated as monotypic. A restudy of the specimens in the U.S. National Museum revealed that *T. corpulentus* Wilson should be synonymized with *T. impressus* and that the males of *T. impressus* described by Wilson (1911) are actually some immature adult females of the same species before complete metamorphosis.

Metamorphosis occurs only in the cephalothorax and the last two segments of the metasome; the second pedigerous segment and the urosome remain unchanged. The metamorphosis is widening rather than lengthening in the head, but more lengthening than widening in the trunk.

Some geographical variation in size and shape is observed in the metamorphosed parts of the body. The three recognized geographical types are: Atlantic type (with slightly bilobed lateral wings of head and less prominent posterior lobes in trunk), Gulf type (with unlobed lateral wings of head and less prominent posterior lobes in trunk), and Caribbean type (with prominent bilobed lateral wings of head and posterior lobes in trunk). This variation is not strictly expressed, however, by every individual in a given geographical range.

This study was developed from the identification of two specimens of immature adult females of *Tucca impressus* Krøyer, which were collected from the caudal fin of a spiny boxfish, *Chilomycterus schoepfi* (Walbaum), at Alligator Harbor, Fla. The specimens were collected by Jack Rudloe and sent to William A. Newman, Museum of Comparative Zoology, Harvard University, for identification, and subsequently were passed to me through Arthur G. Humes, Department of Biology, Boston University, in May 1965. Because my observations on these two parasites were so different from the description by Wilson (1911), five more collections were obtained and studied. In addition, I reexamined the specimens in the USNM (U. S. National Museum) which were studied by Wilson. This reexamination revealed that Wilson (1911) had introduced errors into our knowledge of the species of the genus *Tucca* Krøyer. The later establishment of a subfamily (by Vervoort, 1962) and family (by Yamaguti, 1963) to contain *Tucca* is based on the information supplied by Wilson.

A redescription of the species and redefinition of the genus and the family are given here. Observations on metamorphosis and geographical variation in morphology are also included.

The redescription of the female of *T. impressus* given below is mainly based on specimens collected off Cape San Blas, in the Gulf of Mexico, because this collection is the largest of my collections, contains numerous females in various stages of growth, and indicates a certain pattern of metamorphosis. The data given in tables 2, 3, and 4 were prepared from this collection to aid in the explanation of metamorphosis.

After the discovery of a certain degree of geographical variation of *T. impressus*, tables 5 and 6 were prepared from the two largest collections in the USNM, one from North Carolina and the other from Jamaica. Table 4 gives data on the specimens taken from the Gulf of Mexico, which also helps to explain geographical variation.

The specimens were dissected and examined in lactic acid, and the figures were drawn with the aid of a camera lucida.

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SYSTEMATIC ACCOUNT

FAMILY TUCCIDAE VERVOORT, 1962

Diagnosis

Female. — Metamorphosed cyclopoid. Body composed of head, neck, trunk, and "tail." Head formed by fusion of cephalosome and first pedigerous segment, globular dorsally, flattened and hollowed ventrally, and winged laterally. Cephalic appendages and first leg housed in ventral concavity. Neck short, wider than long, formed by second pedigerous segment, distinctly separated from trunk posteriorly. Trunk composed of fused third and fourth pedigerous segments, inflated, much wider than head and neck. "Tail" composed of transformed urosome with all segments completely fused, flattened, wider than long, attached posteroventrally to trunk. Caudal rami small. Eggs multiserate; egg sacs elongate, cylindrical.

First antenna 5- or 6-segmented, with numerous setae. Second antenna 3-segmented; terminal segment armed, in addition to claws and setae, with pectinate, lamelliform process at tip and several rows of teeth or scales over posterior surface. Labrum with marginal teeth; labium weakly developed. Mandible elongate, with two denticulated spines. Paragnath present. First maxilla a small, rounded protrusion, bearing four setae. Second maxilla 2-segmented, tipped with three denticulated spines. Maxilliped indistinctly 3-segmented, terminal segment strongly bent and pointed. Four pairs of biramous legs; rami with reduced segments. Leg five, 1-segmented, segment very small, tipped with three setae. Leg 6 absent.

Male.—Unknown.

Remarks

This family contains but a single genus, *Tucca* Krøyer, 1837. The genus *Tuccopsis* Pearse, 1952, which was included in the family by Yamaguti (1963), is synonymous with *Blias* Krøyer, 1864, of the family Chondracanthidae. This synonymy was first pointed out by Causey (1955: 7) and followed by Vervoort (1962: 93).

When Vervoort (1962) reviewed the family Bomolochidae, he included the genus *Tucca*, following Wilson's (1911) opinion, but he set the genus in a new subfamily Tuccinae. Since Vervoort did not himself examine specimens of the genus *Tucca*, his accounts on the Tuccinae Vervoort, *Tucca* Krøyer, *T. impressus* Krøyer, *T. corpulentus* Wilson, and *T. verrucosus* Wilson were wholly based on Wilson's inaccurate observations (see Remarks in the following two sections). Yamaguti's (1963) account was also based entirely on Wilson's descriptions. Therefore, neither the diagnosis of the family Tuccidae given by Yamaguti (1963: 42) nor the diagnosis of the subfamily Tuccinae given by Vervoort (1962: 92) can be adopted here. The status of the family is then: a redefined family Tuccidae Yamaguti, 1963, embracing within it the redefined and promoted subfamily Tuccinae Vervoort, 1962.

Wilson (1911: 353) pointed out that the copepods of the genus *Tucca* are closely related to the bomolochid copepods, a relationship especially suggested by the mouth parts and other cephalic appendages. I consider the following characteristics of the female of the genus *Tucca*, however, so different from those of the bomolochids that *Tucca* should be placed in a different family:

1. The female undergoes metamorphosis after the last copepodid stage. All known bomolochids (this means all the copepods attributed to the subfamily Bomolochinae by Vervoort in 1962) have no metamorphosis, and all have a cyclopoid form of body. In the tuccids, however, a metamorphosed adult female has its body distinctly separated into head, neck, and "tail;" the appearance is not at all cyclopoid.

2. The urosome of the female is rudimentary, its length less than one tenth of the body. The urosome of the bomolochids is always at least one third as long as the body and distinctly 5-segmented; it comprises a fifth pedigerous segment, a genital segment, and three postgenital segments. Tuccids have a rudimentary fifth pedigerous segment, a genital segment, and a single postgenital segment, all fused into one unit and unsegmented.

3. The fifth leg is very rudimentary, merely a small, single segment armed with three setae. The fifth leg of a typical bomolochid is 2-segmented and consists of a small intermediate

segment and a large spatulate, terminal segment; even in those with a 1-segmented fifth leg, such as the species of *Pseudoeucanthus* Brian and *Orbitacolax* Shen, the free segment is still well developed and spatulate. The terminal, spatulate segment of the bomolochids is usually armed with one spine on the outer surface and two spines and one seta at the distal end.

GENUS *TUCCA* KRØYER, 1837

Diagnosis

Type species is *Tucca impressus* Krøyer, 1837.

Female.—Body form and mouth parts as defined for the family. Eggs multiserate; egg sacs cylindrical, longer than body. First antenna 5- or indistinctly 6-segmented, basal segment armed with a strong hook on ventral surface. Second antenna 3-segmented, bearing terminally five weak claws, three setae, and one pectinate, lamelliform process; distal segment covered with teeth posteriorly. Leg 1 biramous, flattened, and 3-segmented, located on posterior wall of ventral concavity in head. Leg 2 biramous, 2-segmented. Leg 3 and leg 4 with 2-segmented exopod and 1-segmented endopod; intercoxal plate missing. Leg 5 very small, a single segment tipped with three setae. Leg 6 absent.

Male.—Unknown.

Remarks

When Krøyer (1837) established this genus, he gave almost no account of the appendages, and neither did Nordmann (1864) in his description of West African specimens that he called *T. impressus*. Consequently, lacking such information, these authors were inconsistent in the familial attribution of the genus *Tucca*. Krøyer placed it in the family Dichelestiidae and Nordmann in the famliy Chondracanthidae. Both Milne-Edwards (1840) and Bassett-Smith (1899) followed Krøyer's opinion.

The nature of the mouth parts of *Tucca* was not known until 1911, when Wilson studied the specimens of *Tucca* in the collections of the U.S. National Museum. According to his observations, he placed the genus in the subfamily Bomolochinae of the family Ergasilidae, but later, in 1932, he promoted the subfamily to the familial level.

Wilson's additional information on the morphology of the species of *Tucca* was, however, correct only in the gross anatomy of the mouth parts and not entirely right in the fine structures of the mouth parts and other appendages. I discovered these errors after restudying the specimens of *Tucca* that had been studied by Wilson in 1911 (the collections from Woods Hole, Mass., and Beaufort, N.C.), in 1913 (the collections from Montego Bay, Jamaica), and in 1932 (the collections from Woods Hole, Mass.). The new species, *Tucca corpulentus*, described by him, is only a deformed specimen of *T. impressus;* and some immature adult females of *T. impressus* were mistaken by him for adult males. As Vervoort (1962: 93–96) and Yamaguti (1963: 43–44) were misled by Wilson's inaccurate observations, their accounts of the species of the genus *Tucca* should be used with reservations. This problem is discussed in more detail in a later section.

The specimens described by Nordmann (1864: 491–494, pl. VI, figs. 7–10) as *T. impressus* were claimed by Wilson (1911: 359–360) to be a new species, to which he gave the name *T. verrucosus*. I refrain from making any decision on the validity of *T. verrucosus* without consulting either the original material studied by Nordmann or other specimens collected from the same locality (west coast of Africa) and the same host (*Diodon* sp.). If Wilson's assumption is correct, then *T. verrucosus* would naturally be the second species of the genus; however, I now prefer to treat the genus as monotypic.

A doubtful form, *Tucca* sp., was introduced to the genus by Pearse (1952: 12, figs. 23–27). This species, however, has been questioned by Causey (1955: 11) as being probably a mutilated specimen of *Blias prionoti* Krøyer, 1864. The mandible of Pearse's *Tucca* sp. is very convincing evidence that it is not a tuccid. Its form of a "slightly curved hook" indicates a chondracanthid type of mandible rather than a tuccid type.

TUCCA IMPRESSUS KRØYER, 1837

Tucca impressus Krøyer, 1837, pp. 479–482, pl. V, fig. 2(a–h). Milne-Edwards, 1840, p. 496. Bassett-Smith, 1899, p, 469. Wilson, 1908, p.

625; 1911, pp. 354–387, pl. 48, figs. 102–108, pl. 49, figs. 109–115, 118–120; 1913, p. 200; 1932, pp. 379–380, fig. 243(a,b). Bere, 1936, p. 582. Heegaard, 1947, pl. 25, fig. 195. Sewell, 1949, p. 157. Carvalho, 1951, p. 136. Pearse, 1952, p. 191. Causey, 1955, p. 3. Vervoort, 1962, pp. 93–95. Yamaguti, 1963, p. 43, pl. 47, figs. 1(a–k).

Tucca corpulentus Wilson, 1911, pp. 358–359, pl. 49, figs. 116, 117, pl. 50, figs. 121–127; 1932, pp. 380–381, fig. 235 (a,b). Heegaard, 1947, pl. 25, fig. 194. Sewell, 1949, p. 157. Veervoort, 1962, pp. 95–96. Yamaguti, 1963, p. 43, pl. 46, fig. 1(a–g).

Material Examined

Two immature adult females from caudal fins of 2 *Chilomycterus schoepfi*, caught in mullet seine, at Alligator Harbor, Fla., March 1965; 7 ovigerous females, 3 immature adult females, and 1 copepodid from fins of three *C. schoepfi*, caught in gill net, at Panacea, Fla., May 14, 1965; 44 ovigerous females, 9 immature adult females, and 2 copepodids taken from 14 *C. schoepfi*, caught in shrimp trawl, off Cape San Blas, Fla., May 16, 1965; 6 ovigerous females on dorsal and pectoral fins of 2 *C. schoepfi*, caught in shrimp trawl, off Carrabelle, Fla., July 18, 1965; 9 ovigerous females from fins and body surface of *C. schoepfi*, caught in shrimp trawl by R/V *Oregon*, off St. Simons Island, Ga., November 17, 1965.

In addition to the above collections, I examined the following 16 collections in the USNM (the host names for USNM 38619, 38628, 47748, and 74375 are here changed from *C. geometricus to C. schoepfi*):

6090—3 adult females "from exterior surface of rough swellfish, P. Stewart's pound," Woods Hole, Mass., July 26, 1882.

38369—3 adult females and 3 immature adult females from fins of *C. schoepfi*, collected in Louisiana by M. H. Spaulding, August 10, 1907.

38625—8 adult females and 3 immature adult females from fins of *C. schoepfi*, collected at Beaufort, N.C., in 1904.

38627—8 adult females from pectoral fins of *C. schoepfi*, collected at Beaufort, N.C., in 1905.

38628—11 adult females from pectoral fins of *C. schoepfi*, collected at Beaufort, N.C., in 1902.

42251—7 adult females from fins of *C. antennatus* (Cuvier), collected at Montego Bay, Jamaica, June 22, 1910.

42264—5 adult females from pectoral fins of *Diodon hystrix* Linnaeus, collected at Montego Bay, Jamaica, June 22, 1910.

42265—2 immature adult females from pectoral fins of *Spheroides marmoratus* (Ranzani), collected at Montego Bay, Jamaica, June 20, 1910.

42269—1 deformed immature female on fin of *S. marmoratus*, collected at Montego Bay, Jamaica, September 15, 1910.

42273—57 adult females, 1 immature adult female, and 1 copepodid from fins of *C. antennatus*, collected at Montego Bay, Jamaica, June 15, 1910.

47748—19 adult females from *C. schoepfi*, collected at Morehead City, N.C., April 7, 1891.

53525—5 adult females from Beaufort, N.C. (no host or date given).

74375—7 adult females on fins of *C. schoepfi*, collected at Beaufort, N.C., August 1905.

79089—2 adult females under pectoral fin of *C. spinosus* (Linnaeus), collected at Lemon Bay, Fla., in 1934–35.

The following two collections from USNM are labeled as *Tucca corpulentus:*

38619—"Type," 2 adult females (1 decapitated) from fins of *C. schoepfi*, collected at Woods Hole, Mass., in 1887 (see Remarks).

79595—3 adult females on gill of *S. maculatus* (Bloch and Schneider), collected at Woods Hole, Mass., by G. A. Maccallum (no date given; see Remarks).

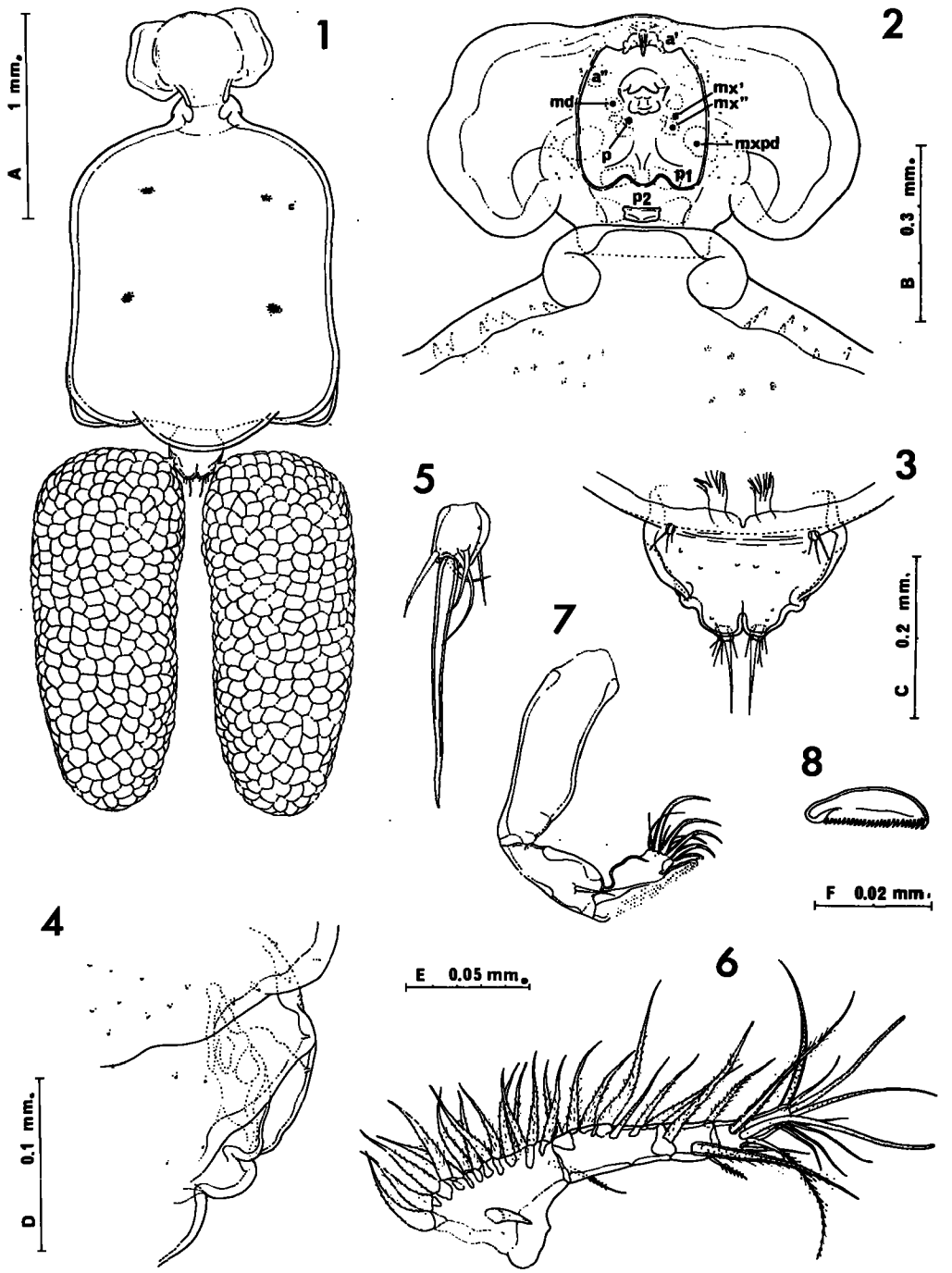
Distribution

See table 1.

TABLE 1.—*Hosts and distribution of* Tucca impressus [1]

Host	Locality	Collection of	Authority
Family Tetraodontidae			
Spheroides maculatus.	Woods Hole, Mass.	USNM 6090	Wilson (?)
S. marmoratus.	Montego Bay, Jamaica.	USNM 42265	Do. (1913)
		USNM 42269	Do. (1913)
Family Diodontidae			
Diodon hystrix	Danish West Indies	?	Krøyer (1837)
	Montego Bay, Jamaica.	USNM 42264	Wilson (1913)
Chilomycterus antennatus.	Montego Bay, Jamaica.	USNM 42251	Do. (1913)
		USNM 42273	Do. (1913)
C. schoepfi	Woods Hole, Mass.	USNM 38619	Do. (1911)
	Beaufort, N.C.	USNM 38625	Do. (1911)
		USNM 38627	Do. (1911)
		USNM 38628	Do. (1911)
	Louisiana	USNM 38369	Do. (?)
	Morehead City, N.C.	USNM 47748	Do. (?)
	Beaufort, N.C.	USNM 74375	Do. (?)
	Sao Paulo, Brazil	?	Carvalho (1951)
	Alligator Harbor, Fla.	?	Pearse (1952)
	Pascagoula, Miss.	Author	Causey (1955)
	Panacea, Fla.	do	Present paper
	Cape San Blas, Fla.	do	Do. paper
	Carrabelle, Fla.	do	Do. paper
	St. Simons Island, Ga.	do	Do. paper
C. spinosus	Lemon Bay, Fla.	USNM 79089	Bere (1936)

[1] Nordmann's record of *Tucca impressus* from the west coast of Africa is excluded, because of its uncertain identification. USNM 53525 is also not included because the host was not identified.



FIGURES 1–8. *Tucca impressus*, female, from *Chilomycterus schoepfi* taken off Cape San Blas, Fla., in the Gulf of Mexico. The letter in the parentheses after the explanation of each figure refers to the scale at which the figure was drawn. 1. Entire, dorsal (A). 2. Head, neck, and anterior end of trunk, showing relative position of various cephalic appendages, ventral (B). 3. "Tail" (= urosome), ventral (C). 4. Genital segment, showing egg sac attachment area, dorsal (D). 5. Caudal ramus, ventral (E). 6. First antenna, exterior (E). 7. Second antenna, exterior (E). 8. Lamelliform process at tip of second antenna, interior (F). (a'.=first antenna; a".=second antenna; md.=mandible; mx'.=first maxilla; mx".=second maxilla; mxpd.=maxilliped; p.=paragnath; p_1.=leg 1; p_2.=leg 2).

Description of Stages

Three stages are described below: mature ovigerous female, immature adult female, and female copepodid.

Mature ovigerous female: — Body (fig. 1) noncyclopoid, 1.51 to 2.92 mm. long, composed of head, neck, trunk, and "tail." Head (fig. 2) small, 0.46 by 0.71 mm., representing a fusion of cephalosome and first pedigerous segment; inflated dorsally, flattened ventrally (fig. 25), and with two wide lobed wings laterally, which in a fully grown adult female protrude beyond anterior margin of cephalosome. Ventral surface of head deeply invaginated at center, forming a hollow disk (fig. 2) which is reinforced anteriorly by rostrum and bases on first antennae and posteriorly by flattened leg 1. Second antennae, mouth parts, and maxillipeds found on bottom of this disk. Rostrum (fig. 2) well developed, bearing some refractile points, two sclerotic protrusions, and one fairly strong hook pointing posteroventrally.

Head jointed to trunk by a short neck (fig. 2) which is formed by second pedigerous segment; this segment completely fused with head anteriorly. This portion of body highly variable in length in different individuals, fully extended in some specimens and completely contracted in others, leaving practically no space between head and trunk. Trunk (fig. 1) made up of third and fourth pedigerous segments, 1.54 by 1.31 mm., nearly square, with rounded corners. Posterior corners slightly produced on each side into one dorsal and one ventral lobe (fig. 25), and a third lobe produced from posteromedial end of trunk between two dorsal lobes. Four depressions (fig. 1) on dorsal surface of trunk. "Tail" (fig. 3) flattened, 0.17 by 0.26 mm., attached to trunk posteroventrally (fig. 25), totally or partially concealed by dorsal posteromedial lobe. No appreciable segmentation seen in "tail," which apparently represents a fusion of the narrow fifth pedigerous segment, the circular genital segment, and one small postgenital segment. Egg sac attachment area (fig. 4) well developed, occupying about two-thirds of lateral surface of "tail." Caudal ramus (fig. 5) small, 23 by 20 μ, armed with five short setules and one long seta 114 μ long. Egg sac elongate, cylindrical; fully grown sac longer than body, containing numerous small eggs with a diameter of 90 μ. Many micropits on surfaces of head and trunk, as shown in detail in figs. 2 and 4, penetrating deeply into sclerotic covering of body.

First antenna (fig. 6) distinctly 5-segmented, but second segment suggesting a division into two segments. Armature on these five segments, from proximal to distal: 15 + 1 hook (on ventral surface), 8, 3, 3, + 1 aesthete, and 7 + 1 aesthete.

Second antenna (fig. 7) 3-segmented; basal segment longest, naked; second segment bearing one seta. Terminal segment having subterminally a rod-shaped process and one pectinate, lamelliform process (fig. 8), and carrying terminally three setae and five weak claws; several rows of teeth on posterior surface.

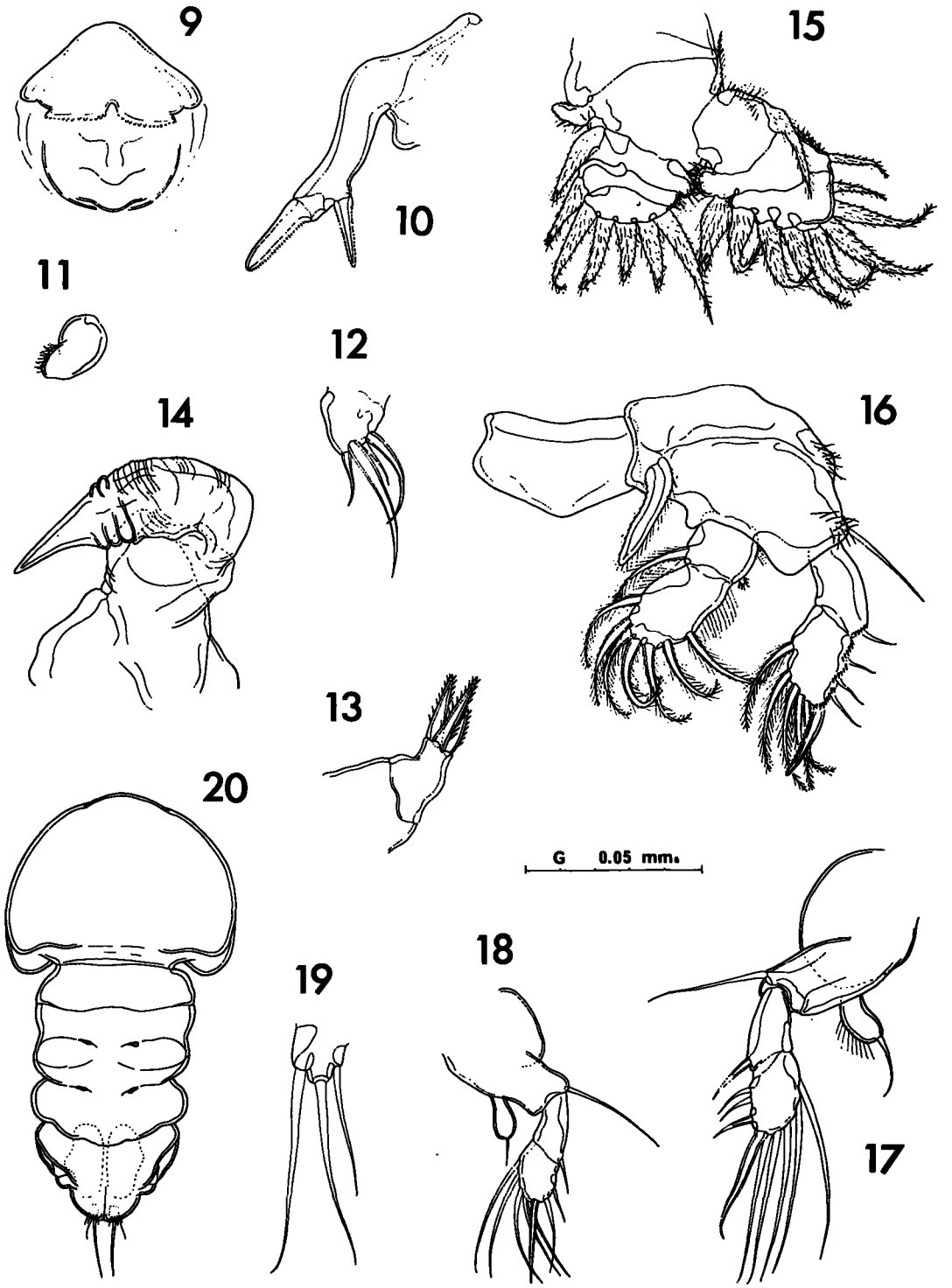
Labrum (fig. 9) well developed, with fine teeth on posterior free margin; labium weak. Mandible (fig. 10) composed of a large plate produced into long process, armed with one terminal masticatory process and one subterminal, bilaterally denticulated spine. Paragnath (fig. 11) bearing setules, located posteromedially to mandible. First maxilla (fig. 12) a small rounded protrusion, located laterally to paragnath, bearing four setae, one of which is fairly long. Second maxilla (fig. 13) 2-segmented, terminal segment armed with three bilaterally denticulated spines.

Maxilliped (fig. 14) powerfully developed, indistinctly 3-segmented; terminal segment strongly bent inward and almost perpendicular to first two segments. Last segment sharply pointed, with well-developed sclerites cutting into ventral and posterior surfaces, thus making these surfaces corrugated. In many specimens, the terminal, pointed process, broken when the parasite was removed from the host, appeared as a blunt process.

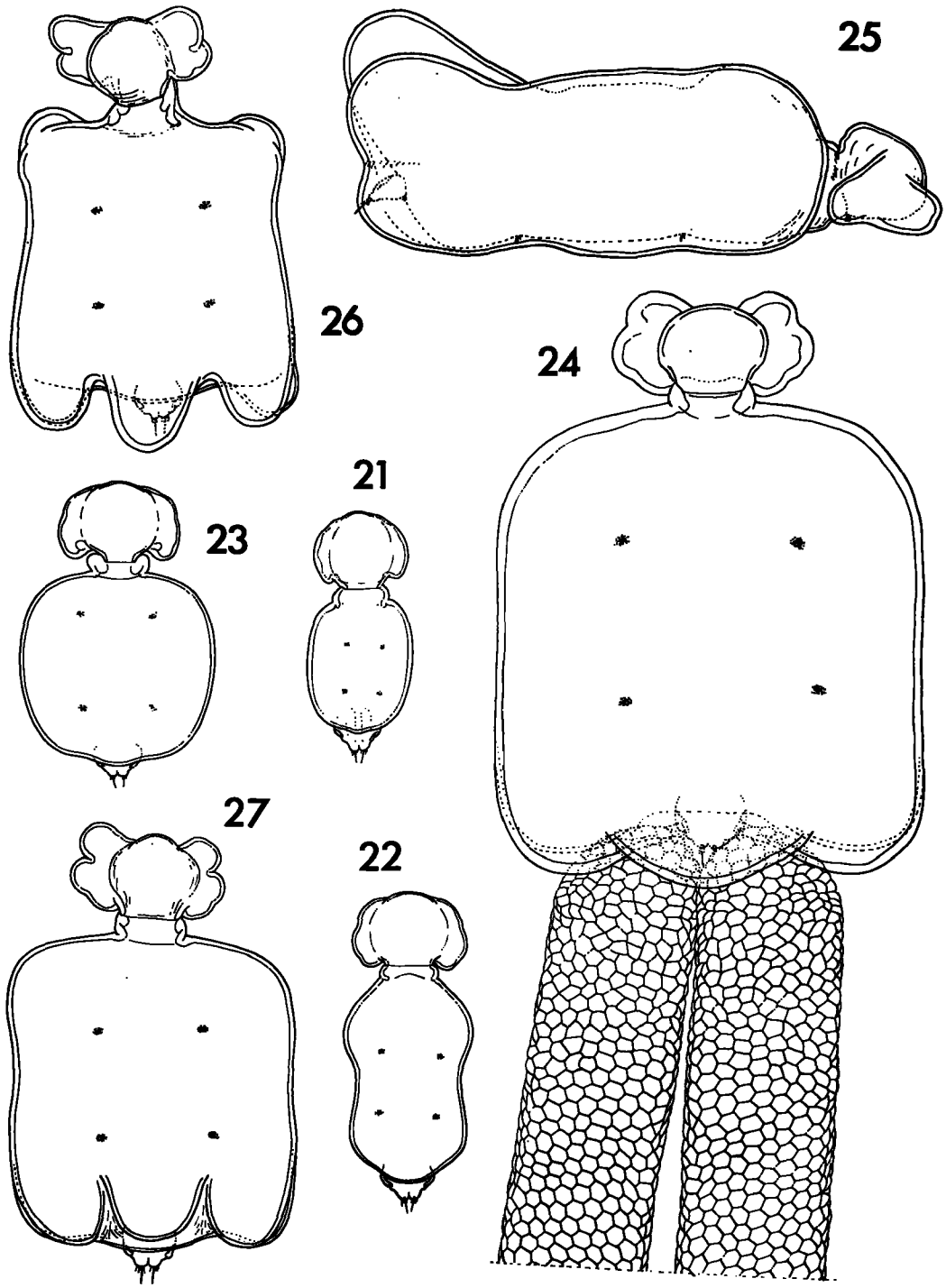
Formula of spines and setae on first four pairs of legs as follows (Arabic numerals represent setae and Roman numerals spines):

	Protopod	Exopod	Endopod
Leg 1	0-0 1-0	1-0 1-1 7	0-1 0-1 5
Leg 2	0-0 1-I	1-0 III-I-5	0-1 7
Leg 3	0-0 1-0	I-0 III-I-5	1
Leg 4	0-0 1-0	I-0 II-I-5	1

Leg 1 (fig. 15) strongly flattened, its setae



FIGURES 9–20.—*Tucca impressus*, female, from *Chilomycterus schoepfi* taken off Cape San Blas, Fla. in the Gulf of Mexico. 9. Labrum and labium, ventral (G). 10. Mandible, posterior (G). 11. Paragnath, ventral (G). 12. First maxilla, anterior (G). 13. Second maxilla, anterior (G). 14. Maxilliped, posteroventral (D). 15. Leg 1, anterior (D). 16. Leg 2 and intercoxal plate, anterior (E). 17. Leg 3, anterior (G). 18. Leg 4, anterior (G). 19. Leg 5, ventral (F). 20. Copepodid, dorsal (B).



FIGURES 21-27.—*Tucca impressus*, female. Figures 21-23, from *Chilomycterus schoepfi* taken off Cape San Blas, in the Gulf of Mexico; 24-25, from *C. schoepfi* taken off St. Simons Island, Ga.; 26-27, from *C. antennatus* at Montego Bay, Jamaica. 21. Immature adult with short trunk, dorsal (A). 22. Immature adult with guitar-shaped trunk, dorsal (A). 23. Immature adult with circular trunk, dorsal (A). 24. Entire, dorsal (A). 25. Same, lateral (egg sacs omitted) (A). 26. Entire, dorsal (egg sacs omitted) (A). 27. Entire, showing absence of anterior lobes in trunk (egg sacs omitted) (A).

densely haired. Medial surface of basis produced into blunt process, covered with hairs; marginal surfaces of every segment in each ramus also covered with hairs. Spines on outer surfaces of exopods of leg 2 (fig. 16), leg 3 (fig. 17), and leg 4 (fig. 18) weakly developed, setiform, and naked. Intercoxal plate absent in leg 1, leg 3, and leg 4; coxa and basis not completely separated in leg 3 and leg 4. Leg 5 (fig. 19) uniramous, very rudimentary, 10 by 9 μ; located at junction of "tail" and trunk and armed with three long setae. Leg 6 absent.

Immature adult female.—Body (figs. 21-23) noncyclopid, shaped differently in different stages of metamorphosis; proportions of various body regions also different in different stages (see table 2).

TABLE 2.—*Measurements of immature adult females taken from* Chilomycterus schoepfi *off Cape San Blas, Fla., in the Gulf of Mexico.*

Specimen number	Head	Neck	Trunk	"Tail"	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.28 by 0.44	0.08	0.47 by 0.47	0.17 by 0.24	0.96
2	.36 by 0.49	.09	.45 by 0.49	.17 by 0.23	1.07
3	.34 by 0.49	.10	.51 by 0.57	.17 by 0.27	1.12
4	.31 by 0.49	.10	.74 by 0.56	.17 by 0.25	1.13
5	.33 by 0.52	.10	.70 by 0.54	.18 by 0.24	1.23
6	.30 by 0.47	.11	.82 by 0.60	.17 by 0.23	1.31
7	.34 by 0.55	.10	.73 by 0.56	.18 by 0.23	1.33
8	.34 by 0.57	.09	.75 by 0.60	.17 by 0.26	1.35
9	.31 by 0.56	.11	.85 by 0.86	.16 by 0.25	1.43
Average	0.32 by 0.51	0.10	0.67 by 0.64	0.17 by 0.25	1.21

Structure of appendages similar to mature ovigerous female. Details of these immature adult females are given in following section in discussion of metamorphosis.

Female copepodid.—Body (fig. 20) cyclopoid, 0.70 by 0.37 mm. (excluding setae on caudal rami); no segmentation on cephalothorax and urosome, but with clear distinction between each two adjoining regions of four body regions. Cephalothorax semicircular anteriorly and rather truncated posteriorly; posterior surface roughly separated into dorsal and ventral portions. Second pedigerous segment (= neck of adult), 0.08 by 0.26 mm., attached to center of posterior surface of cephalothorax, carrying leg 2 ventrally at anterior margin. Third pedigerous segment, 0.13 by 0.26 mm., slightly invaginated on both sides and incompletely separated from fourth pedigerous segment on dorsal surface. Fourth pedigerous segment, 0.12 by 0.26 mm., with posterior margin protruding over about one-third of urosome. Urosome (= "tail" of adult) 0.17 by 0.23 mm., carrying inside a pair of seminal receptacles (or cement glands ?). Egg sac attachment area similar to that in adult.

Caudal ramus attached to posteroventral surface of urosome, its armature as in adult. Two sclerites on dorsal surface of third and fourth pedigerous segment. Micropits present on body surface (omitted in fig. 20).

All appendages similar to those in adult ovigerous female and immature adult female.

Remarks

In the vial labeled Cat. No. 38619 in the collection of USNM are two specimens (one decapitated) designated by Wilson (1911) as the type specimens of *Tucca corpulentus*. The trunk of the headless specimen appears like the one shown in fig. 24, namely, squarish and distinctly 3-lobed on its posterodorsal surface. The head of this specimen was supposedly dissected by Wilson for study of the mouth parts and other cephalic appendages, and probably was the source of his figs. 122–125. The other specimen (with head) is, doubtlessly, the source of his fig. 121. I have examined the latter specimen with great care in lactic acid. Nevertheless, I was not able to find any appendages that are significantly different from those described above. In addition, the posterodorsal surface of the trunk is also 3-lobed, not as smooth as illustrated by Wilson in his fig. 121. The circular appearance of this specimen is possibly due to the fact that the parasite was somewhat pressed (by the fin, on which the parasite was attached, pressing against the body surface) before preservation, because its trunk appears unusually thin. The absence of pits or impressions on body surface, one of the characters cited by Wilson for establishing the new species, is conceivably also due to mechanical deformation prior to preservation.

Consequently, as far as these two type specimens are concerned, *T. corpulentus* does not differ from *T. impressus* and should be synonymized with it. There are some inconsistencies

between the label of Cat. No. 38619 in the USNM and the statement of Wilson (1911: 359): "There is but a single lot of this species, which was taken from the northern swell-toad, *Spheroides maculatus*, at Woods Hole, Massachusetts, and is numbered 38619, U.S.N.M. It includes three females, two of which bear egg-strings." The label of Cat. No. 38619 clearly says, however, that there are only "2 ♀ specimens," the host is *"Chilomycterus geometricus,"* and no egg strings were found in the vial. Another USNM collection of *T. corpulentus* is Cat. No. 79595. The label of this collection fits better with Wilson's statement. It says that there are "3 specimens" and the host is "Gills, *Spheroides maculatus,*" but the three specimens of this collection are *Pseudochondracanthus diceraus* Wilson. They are mature adult females and all carry a pygmy male on their poster-oventral surface. This collection was not mentioned by Wilson in any of his reports, not even in his reports of *P. diceraus* (1908: 436; 1932: 496), but the label says "Identified by C. B. Wilson." I have taken the two specimens kept in the vial of Cat. No. 38619 as Wilson's type specimens of *T. corpulentus* and synonymized the species with *T. impressus*.

One of the three immature adult females in the vial of Cat. No. 38625 was obviously mistaken by Wilson for an adult male. The rather small size, the different shape and proportion of various body regions, and the two bean-shaped reproductive organs inside the urosome might suggest incorrectly a male, if the process of metamorphosis in the female is unknown. The pair of stout hooks described by Wilson on the ventral surface at the posterior corners of the genital segment of this "male" specimen are merely two sclerotic protrusions (see fig. 3).

NOTES ON METAMORPHOSIS

The absence of the male parasites on the diodontid and tetraodontid fishes perhaps occurs because males do not grow beyond the copepodid stage. They probably die after copulation as do the males in the families Lernaeidae, Lernaeoceridae, and Pennellidae, in which only the female copepodid (after copulation) attaches to the fish host and metamorphoses into an adult.

The two youngest females recovered from the diodontid fish caught off Cape San Blas, Fla., still show a cyclopoid form of body; they are particularly reminiscent of bomolochid and taeniacanthid copepods (see fig. 20). The cephalothorax is the widest part of the body, and the metasomal segments are still distinguishable (see table 3 for measurements). These features, in comparison with the metamorphosed adult female, indicate that they are either still in the last copepodid stage or, at most, just on the way to metamorphosis. The somewhat older females that I have in the same collection are the nine copepods that show no segmentation in the metasomal region, have swollen trunks as wide as the head or a little wider, and carry no egg sacs (see figs. 21, 22).

TABLE 3.—*Measurements of female copepodid from three collections.*

Record and body part measured	Specimen 1	Specimen 2	Specimen 3	Specimen 4
Host	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus antennatus*
Locality	Panacea, Fla.	Cape San Blas, Fla.	Cape San Blas, Fla.	Montego Bay, Jamaica
Date	May 14, 1965	May 16, 1965	May 16, 1965	June 15, 1910
Cephalothorax (head)	0.27 by 0.37	0.31 by 0.41	0.30 by 0.42	0.31 by 0.47
Thorax (neck +trunk)	.30 by 0.26	.34 by 0.32	.36 by 0.31	.41 by 0.37
Urosome ("tail")	.17 by 0.23	.16 by 0.23	.17 by 0.21	.15 by 0.23
Total length	.70	.81	.83	.86

These females I have considered as the immature adults inasmuch as they have attained sexual maturity and have copulated but have not yet produced egg sacs.

Metamorphosis occurs only in the cephalothorax and the last two segments of the metasome. As far as the size and shape are concerned, the second pedigerous segment and the urosome in the copepodid are not significantly different from the neck and the "tail" in the immature adult female, nor in the ovigerous female. The second thoracic segment, urosome, and all appendages are not transformed during metamorphosis, but the cephalothorax and the third and fourth pedigerous segment are tremendously changed.

The size of the head of an immature adult

female (0.32 by 0.51 mm.) is not much different from that of the cephalothorax in the copepodid (0.31 by 0.42 mm.); the shape, however, is markedly different. The expansion is seen mostly in anterior corners, posterior subcorners, and the dorsal surface of the head. The head of an ovigerous female (0.33 by 0.59 mm.) differs from that of the immature adult female chiefly in the more globular appearance of the middorsal surface; it is not lengthened but definitely widened. The metamorphosis in the head involves changes in form from semicircular to rectangular (in dorsal view) and from slightly convex to globular (in lateral view of the dorsal surface). The amount of increase in proportions of the head is about 10 percent in the length and 45 percent in the width; this widening rather then lengthening during metamorphosis is due to the formation of the lateral wings.

The second and third pedigerous segments are completely fused into a unit at the onset of metamorphosis (fig. 21). This fused trunk is then enlarged in three dimensions, the shape (in dorsal view) changes from oval (as in fig. 21) to guitar-shaped (as in fig. 22) or nearly circular (as in fig. 23) and then to squarish (as in fig. 1). The posterior lobes, three on the dorsal and two on the ventral surface, are not formed in the immature adult female. The four chitinized platelets on the dorsal surface of the thorax of the copepodid are retained throughout metamorphosis. As these platelets are the points of attachment of trunk muscles on the tergum of the second and third pedigerous segment, they have not been elevated by the enlarging action in the course of metamorphosis. Thus, the four platelets form the bottom of the "four pits" on the dorsal surface of the ovigerous female. The amount of increase in proportions of the trunk is about 270 percent in the length and 120 percent in the width. The metamorphosis of the trunk, contrary to that of the head, involves more lengthening than widening.

Specimens 4, 5, 6, 7, and 8 of table 2 have trunks distinctly longer than wide; they look like that in fig. 22. The remaining four specimens (1, 2, 3, and 9) of the immature adult females in the same collection have trunks nearly as long as wide and resemble fig. 23. In the present state of knowledge, we can say only that immature adult females have two forms. Which form comes first in the process of metamorphosis is unknown.

A comparison between table 2 and table 4 shows that the maturity of the females can be judged by the size of the trunk, in addition to the presence or absence of egg sacs. The trunk is definitely longer and wider in ovigerous females than in immature adults, although the size of the head overlaps broadly in the two stages.

The first ovigerous female in table 4 has smaller body length, but a definitely larger trunk, than the largest immature adult female in table 2. As noted in the previous section, the neck of this ovigerous female is unusually shrunken; therefore, body length alone is not a good measure for determining the maturity of a female.

GEOGRAPHICAL VARIATION

According to our present knowledge of parasitic copepods of fishes, *Tucca impressus* is parasitic exclusively on two families of fishes, Tetraodontidae and Diodontidae—especially the fishes of the latter family (porcupine fish or boxfish). Our past records show that it is most abundant on the fishes of the genus *Chilomycterus* (Diodontidae) and always found either on the fins or on the body surface.

A certain degree of variation is observed in the head and the trunk of the ovigerous females collected from three different areas, namely the west coast of North Atlantic Ocean, the Gulf of

TABLE 4.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus schoepfi *off Cape San Blas, Fla., in the Gulf of Mexico*

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.29 by 0.50	0.06	1.30 by 0.95	0.17 by 0.24	0.84	1.38
2	.30 by 0.61	.11	1.10 by 1.22	.16 by 0.23	1.29	1.51
3	.33 by 0.55	.09	1.12 by 0.93	.17 by 0.25	.75	1.54
4	.31 by 0.56	.09	1.19 by 1.02	.18 by 0.23	1.10	1.59
5	.31 by 0.64	.09	1.14 by 0.87	.19 by 0.26	broken	1.68
6	.30 by 0.60	.08	1.33 by 1.12	.18 by 0.26	broken	1.71
7	.35 by 0.56	.10	1.30 by 1.40	.18 by 0.25	1.34	1.75
8	.36 by 0.65	.09	1.31 by 1.31	.18 by 0.24	1.84	1.77
9	.38 by 0.59	.11	1.28 by 1.48	.16 by 0.25	broken	1.78
10	.33 by 0.65	.10	1.59 by 1.14	.18 by 0.26	1.41	2.02
Average	0.33 by 0.59	0.09	1.24 by 1.17	0.17 by 0.25		1.67

TABLE 5.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus schoepfi *at Morehead City, North Carolina (from USNM 47748)*[1]

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.38 by 0.67	0.10	1.76 by 1.65	0.18 by 0.24	(2.79)	2.24
2	.30 by 0.78	.09	2.02 by 1.60	.17 by 0.23	-------	2.47
3	.35 by 0.96	.08	2.15 by 2.06	.19 by 0.24	-------	2.63
4	.37 by 0.91	.12	2.30 by 1.79	.16 by 0.25	-------	2.79
5	.31 by 0.84	.13	2.29 by 1.89	.16 by 0.26	-------	2.80
6	.34 by 0.88	.11	2.50 by 1.98	.16 by 0.24	-------	2.90
7	.36 by 0.85	.12	2.39 by 1.95	.17 by 0.27	-------	2.97
8	.37 by 0.91	.09	2.51 by 1.86	.18 by 0.26	-------	2.98
9	.38 by 0.94	.11	2.49 by 2.42	.19 by 0.27	-------	3.09
10	.40 by 0.89	.12	2.46 by 1.95	.17 by 0.25	(4.61)	3.16
Average	0.36 by 0.86	0.11	2.39 by 1.92	0.17 by 0.25	-------	2.80

[1] The egg sacs were found free in the vial. Since there is no way to identify each sac with its female, only the shortest and the longest sacs were measured.

TABLE 6.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus antennatus *at Montego Bay, Jamaica (from USNM 42273)*

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.31 by 0.48	0.11	0.93 by 0.83	0.17 by 0.26	0.68	1.42
2	.32 by 0.54	.09	.96 by 0.78	.19 by 0.27	broken	1.46
3	.33 by 0.60	.09	1.15 by 1.13	.18 by 0.25	1.02	1.59
4	.35 by 0.56	.10	1.29 by 1.10	.16 by 0.27	1.77	1.75
5	.34 by 0.58	.08	1.42 by 1.22	.18 by 0.26	broken	1.78
6	.35 by 0.59	.11	1.35 by 1.29	.16 by 0.23	1.59	1.81
7	.34 by 0.56	.12	1.41 by 1.26	.15 by 0.24	2.05	1.83
8	.33 by 0.66	.09	1.47 by 1.27	.18 by 0.26	2.14	1.95
9	.36 by 0.66	.10	1.46 by 1.36	.18 by 0.25	broken	2.00
10	.34 by 0.68	.11	1.67 by 1.41	.17 by 0.26	broken	2.14
Average	0.34 by 0.59	0.10	1.31 by 1.17	0.17 by 0.26	-------	1.77

Mexico, and the Caribbean Sea. This variation occurs only in the metamorphosed parts of the body, and is in the size and the shape. A comparison of fig. 1 (a representative from the Gulf of Mexico), fig. 24 (a representative from the west coast of North Atlantic Ocean), and fig. 26 (a representative from the Caribbean Sea) together with reference to tables 4, 5, and 6 shows this picture of geographical variation. In the following discussion, for the sake of convenience, the specimens from Georgia, North Carolina, and Massachusetts are termed as the Atlantic type; the specimens from Florida (west coast), Mississippi, and Louisiana, the Gulf type; and the specimens from Jamaica, the Caribbean type.

The bilobed condition of the lateral wings of the head is generally most pronounced in the Caribbean type (figs. 26, 27), but the wings are almost unlobed in the Gulf type (fig. 1). The lateral wing of the Atlantic type (fig. 24) is only slightly bilobed; the posterior lobe is larger than the anterior lobe and is wider than those in the other two geographical types.

In both Gulf type and Atlantic type, the posterior lobes in the trunk are usually less pronounced, and there are no anterior lobes. These anterior and posterior lobes are, however, present and well formed in the Caribbean type. A fully grown ovigerous female of an Atlantic type is much larger than those of the Gulf type and the Caribbean type. The following data were derived by considering all collections from a general geographical region as a whole to show the size ranges (in millimeters) of the ovigerous females of the three different geographical types:

	Caribbean type	Gulf type	Atlantic type
	Mm.	*Mm.*	*Mm.*
Smallest	1.36 (in USNM 42251)	1.51 (off Cape San Blas, Fla.)	1.59 (in USNM 38625)
Largest	2.14 (in USNM 42273)	2.51 (Carrabelle, Fla.)	3.16 (in USNM 47748)
Longest egg sac	2.78	4.09	4.61

Thus, the shape of the trunk indicates that the Gulf type is closer to the Atlantic type than to the Caribbean type, but the size of the trunk indicates that the Gulf type is, on the contrary, closer to the Caribbean type than to the Atlantic type. In other words, comparisons of the trunk show that the Gulf type is intermediate between the Atlantic type and the Caribbean type. The variation of the head, in the Atlantic type, instead of the Gulf type, shows the intermediate character in the bilobed condition of the lateral wings.

I have found specimens in USNM collections (Cat. No. 38625 and 74375), from Beaufort, N.C., which, instead of having the Atlantic type trunk, have the posterior lobes of the trunk fairly well defined as in the Caribbean type. Moreover, in the collections from Jamaica, some individuals lack the anterior lobes in the trunk, as shown in fig. 27. It appears, therefore, that the variation in the head and the trunk is not absolute, or, in other words, that this variation is merely a general tendency of modification that exists in a certain geographical area but is not strictly expressed by every individual of

this species found in a given geographical range. As the hosts of this parasitic copepod are mostly inshore fishes and not powerful swimmers, considerable distant movement probably is accomplished only by drifting with the current. At present, however, it is impossible to determine whether the Gulf Stream has influenced this picture of geographical variation.

The single specimen of *T. impressus* described by Krøyer (1837) is a female taken from the inner surface of the pectoral fin of a *Diodon hystrix* in the Danish West Indies. It definitely belongs to the Caribbean type, since in Krøyer's fig. 2a (dorsal view) and fig. 2b (lateral view) the posterior lobes, anterior lobes, and the bilobed condition in the head are of that type. According to Krøyer's description (p. 479) this Danish West Indian specimen measures 2 lines, of which the egg sac is about half. In other words, the length of the parasite's body is about 2.11 mm., which falls within the range of the Caribbean type (see table 6).

The 37 specimens of *T. impressus* described by Carvalho (1951) from Brazilian *C. schoepfi* measure from 1.52 to 1.80 mm., and so fall within the range of the Caribbean type.

In his discussion of the validity of Nordmann's *T. impressus,* Wilson (1911: 359) expressed his doubt upon the variation of the specimens of *T. impressus:* "either Nordmann's species or that of the present author is new to science. They can not both be identical with Krøyer's *T. impressus.*" This implies that Wilson's specimens are different from Krøyer's *T. impressus* to a certain degree, but this difference is not as significant as the discrepancy between Krøyer's *T. impressus* and Nordmann's *T. impressus.* Consequently, Wilson identified his specimens collected in Beaufort, N.C., as *T. impressus,* and created *T. verrucosus* for Nordmann's *T. impressus.*

The total length (1.67 mm.) given by Wilson (1911: 356) for the species of *T. impressus* is too small for the Atlantic type. I have measured all 30 specimens that were identified by Wilson as *T. impressus* in USNM collections. The collections, number of specimens, and maximum sizes are:

Catalogue number	Number of specimens	Smallest (*mm.*)	Largest (*mm.*)
USNM 38625..	11 (3 immature)	1.13	1.69
USNM 38627..	8	2.04	2.23
USNM 38628..	11	1.86	2.49

It is obvious, therefore, that Wilson took into consideration only the specimens in USNM 38625. This collection unfortunately contains no fully grown ovigerous females (judged by the length of the egg sac). One of the three immature adult females in this collection was described by Wilson as a male, and the measurements given for it are (Wilson, 1911: 357):

Total length, 1.27 mm.; cephalothorax, 0.3 by 0.5 mm.; trunk 0.75 by 0.51 mm.; and width of genital segment, 0.25 mm.

These figures lie within the range of the immature adult female with a longer (guitar-shaped) trunk given in table 2.

The 10 specimens of *T. impressus* reported by Nordmann (1864) were taken from a "fleckigen Diodon–Art." According to Nordmann's description on p. 491, these parasites measure about 5 mm. long including the egg sac. Judging from his illustration of a complete parasite in pl. VI, fig. 7, the body is about 3.15 mm. long and the egg sac, 1.85 mm.; therefore, the size is about that of the Atlantic type of the *T. impressus.* According to what Nordmann described (pp. 491–494) and illustrated (pl. VI, figs. 7–10), however, this West African species of *Tucca* is definitely different from all three types of *T. impressus* in the North and South American waters.

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