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Marine Leeches of the Eastern United States and the Gulf of Mexico with a Key to the Species

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Introduction

Unlike the Eurasian marine leeches (Johansson, 1896; Selensky, 1915; Herter, 1935; Vasileyev, 1939; Knight-Jones, 1961; Sawyer, 1970; Soós, 1965), those from North America comprise an unusually neglected group, due primarily to the bewildering taxonomy of the members. Most early descriptions were brief, ambiguous, and concerned only with superficial characters. Some of the nominal species reported from the eastern United States and Canada are unrecognizable today, thus perpetuating nomenclatural confusion.

We attempt to analyze critically the marine leeches from Newfoundland to Texas, with emphasis on those of the southern states from Virginia to Mississippi. An illustrated dichotomous key and a diagnosis for each species is presented. A synonymy, a list of hosts, the geographical distribution, and biological observations accompany the diagnoses. The poorly known Pacific marine leeches (Moore & Meyer, 1951; Moore, 1952a) will be deferred to another study.

We found 14 valid species in the Atlantic Ocean and in the Gulf of Mexico from Newfoundland to Texas. Fortunately, the internal anatomy of most is now well known: *Ozobranchus branchiatus* (Menzies, 1791); *O. margoi* (Apathy, 1890); *Stibarobdella macrothela* (Schmarda, 1861); *Branchellion torpedinis* Savigny, 1822; *Trachelobdella lubrica* (Grube, 1840); *Oxytonostoma typica* Malm, 1863; *Branchellion ravenelii* (Girard, 1850); *Trachelobdella rugosa* Moore, 1898; *Calliobdella vivida* (Verrill, 1872); *Platybdella buccalis* Nigrelli, 1946; *Malmiana nuda* Richardson, 1970; *Myzobdella lugubris* Leidy, 1851; *Austrobdella rapax* (Verrill, 1873); and a new species provisionally assigned to *Malmiana* Strand, 1942. The first six are also European or cosmopolitan species.

Trachelobdella lubrica, *Oxytonostoma typical*, and the undescribed species of *Malmiana* are new to the region under study. *Trachelobdella rugosa*, *Austrobdella rapax*, and *Platybdella buccalis* are reported for the first time since their original descriptions. In addition the following important synonyms are presented for the first time: *Calliobdella vivida* synonymous with *C. carolinensis* of Sawyer & Chamberlain (1972) and *C. nodulifera* of Threlfall (1969); *Myzobdella lugubris* synonymous with *Illinobdella alba*, *I. elongata*, *I. richardsoni*, and *I. moorei* of Meyer (1940), *Ichthyobdella rapax* of Wass (1972) and *Cystobranchus virginicus* of Paperna and Zwerner (1974); and the undescribed *Malmiana* species synonymous with *Piscicola funduli* of Causey (1953). *Piscicola zebra* Moore, 1898, is species inquirendae.

Materials and methods

This study utilizes collections from the US National Museum (USNM), British Museum (Natural History) (BMNH), Harvard Museum of Comparative Zoology (MCZ), Woods Hole Marine Biological Laboratory, Gulf Breeze Environmental Research Laboratory (GBERL), and Duke University Marine Biological Laboratory as well as specimens sent to the authors. Also, much firsthand information was gained by the authors through several years of collecting hundreds of leeches at the Virginia Institute of Marine Science (VIMS), the Grice Marine Biological Laboratory (GMBL), South Carolina, and the Gulf Coast Research Laboratory (GCRL), Mississippi.

Because material was collected by numerous individuals, specimens were relaxed, fixed, and stored using several different techniques. Relaxation, if any, was accomplished with heat, cold, chloretone, or coverslip pressure. Formalin, AFA, or 70% ethyl alcohol fixed the leeches before storage in 5 to 10% formalin or 70% alcohol with or without a small amount of glycerine. Sectioned material was stained with hematoxylin and eosin or by Masson's trichrome method.

The thousands of specimens represent hundreds of new records for hosts and specific geographical localities. Lacking space for all of these new records, we report the details of selected localities and hosts in each state involved with the remaining data summarized in the text. A complete list of locality and host records is filed in the reprint collection of the Division of Worms, US National Museum, under Hirudinea and under the authors' names. Names of fishes harboring leeches follow those cited in the American Fishery Society's list (Bailey, 1970), and order of presentation of the leeches follows that of the dichotomous key without any phylogenetic significance.

Key to the marine and estuarine leeches of the eastern United States and the Gulf of Mexico

1a. Body with conspicuous, laterally branching (digitiform), or foliaceous (phylliform projections (branchiae) 2
1b. Body without conspicuous branchiae 5
2a. Branchial projections branching, digitiform (fig. 1(C)); one pair of branchiae per segment; midbody segments biarmulate; on sea turtles; ***Ozobranchus*** 3
2b. Branchial projections nonbranching, phylliform (fig. 2(E)); three pairs of branchiae per segment; midbody segments triarmulate; on elasmobranchs; ***Branchellion*** 4

3a. With seven pairs of branchiae (fig. l(D)) . . ***Ozobranchus branchiatus*** (Menzies, 1791)
3b. With five pairs of branchiae . . . . . ***Ozobranchus margoi*** (Apathy, 1890)

4a. With 33 pairs of branchiae; in Europe and northeastern United States, ranging south to North Carolina . . . . . ***Branchellion torpedinis*** Savigny, 1822
4b. With 31 pairs of branchiae; in Gulf of Mexico and southeastern United States, ranging north to South Carolina (figs. 2(A)–(F)) . . . . . ***Branchellion ravenelii*** (Girard, 1850)

5a. Possessing 11–13 pairs of pulsatile vesicles along lateral margins of body (fig. 3(B)) . . 6
5b. No such pulsatile vesicles along lateral margins 8

6a. Caudal sucker relatively large, distinct from posterior end of body, about equal to maximum body width (fig. 3(F)); two distinct pairs of eyespots on oral sucker; vesicles relatively small (figs. 3(B); 4(A), (D)) . . . . . ***Calliobdella vivida*** (Verrill, 1872)
6b. Caudal sucker relatively small, not distinct from posterior end of body, terminal, one-half or less of maximum body width (fig. 1(A)); eyespots absent (or one diffusely pigmented pair); ***Trachelobdella*** 7

7a. Vesicles remarkably large and rounded; tegument smooth . . . . . ***Trachelobdella rugosa*** Moore, 1898
7b. Vesicles small and pointed; tegument rough . . . . . ***Trachelobdella lubrica*** (Grube, 1840)

8a. Tegument with large wartlike tubercles, rounded or pointed (fig. 3(A)); midbody segments triannulate; on elasmobranchs . . . . .***Stibarobdella macrothela*** (Schmarda, 1861)
8b. Tegument without large wartlike tubercles; annulation obscure, more than triannulate 9

9a. Caudal sucker small, terminal or subterminal, not distinct from posterior end of body, smaller than maximum body width (figs. 1(B); 5; 7(A), (C); 9) 10
9b. Caudal sucker large, discoidal, well demarcated from body, about equal to or larger than maximum body width 12

10a. Caudal sucker subterminal, slightly eccentric, shallow, not deeply cupped (fig. 7(C); 9(C)–(F)); metameric white regions along margins (if ideally preserved these regions clearly become part of a continuous lateral contractile lacuna); known from *Paralichthys dentatus* from New England region . . . . . ***Austrobdella rapax*** (Vorrilt, 1873)
10b. Caudal sucker terminal, without metameric white regions along margins 11

11a. Head distinct (fig. 9); tegument with minute, barely distinguishable tubercles, especially on dorsum; a small pair of nipple-like papillae in region of female gonopore; body not narrowing abruptly to form a trachelosome; known from skates from Massachusetts to the Bay of Fundy . . . . . ***Oxytonostoma typica*** Malta, 1863
11b. Head not distinct from anterior end of body (fig. 1(B)); tegument smooth (rarely with minute papillae on dorsum); body in anterior third narrowing somewhat abruptly to demarcate a faint neck region (trachelosome); primarily from brackish water teleosts from Chesapeake Bay southward . . . . . ***Myzobdella lugubris*** Leidy, 1851

12a. Oral sucker small, about same width as neck; body subcylindrical; caudal sucker larger than maximum body width (fig. 6); normally two pairs of eyespots on oral sucker (sometimes one additional pair on neck, or no eyespots evident if poorly preserved); caudal sucker folded longitudinally after preservation; conspicuous bursa,

commonly everted; 12 (possibly subdivided to 14) annulate; known from ***Macrozoarces*** and ***Anarrhichas*** from New England area . . . . ***Platybdella buccali*** Nigrelli, 1946

12b. Oral sucker large, wider than neck; body flattened; caudal sucker equal to or only slightly wider than maximum body width, not folded during preservation (fig. 7(D)–(F); 8) 13

13a. No eyespots on oral sucker (fig. 7(D)–(F); 8 (K)); juveniles rarely have two pairs of eyespots on sucker and one pair on neck); no functional male bursa; no epididymis; postcaeca unfused; no intestinal diverticula; known primarily from sculpins from tidal areas from Newfoundland to New England . . ***Malmiana nuda*** Richardson, 1970

13b. One pair of large eyespots on oral sucker (figs. 8 (A)–(J)); moderate sized male bursa; convoluted epididymis at ganglion XII; postcaeca fused, with fenestrae; five pairs of intestinal diverticula, first pair much larger than others; known from highly saline areas of Caribbean and the Gulf of Mexico . . . . . ***Malmiana philotherma***

Family ***OZOBRANCHIDAE*** Pinto, 1921 (emended Richardson, 1969)
Genus ***OZOBRANCHUS*** de Quatrefages, 1852
Ozobranchus branchiatus (Menzies, 1791)

Hirudo branchiata Menzies, 1791: 188, Pl. 17, fig. 3.
Ozobranchus branchiatus: MacCallum & MacCallum, 1918: 395, Pls. 33–38; Nigrelli, 1941: 15; Nigrelli, 1942: 539; Nigrelli & Smith, 1943: 107, Sanjeeva Raj & Penner, 1962: 364, Pls. 1–2; Soós, 1965: 444; Richardson, 1969, figs. 1(A)–(B), (D), 3(J).
Sanjeeva Raj & Penner (1962) provide a worldwide synonymy.

Selected locality records: FLORIDA. Tortugas, 29. vi. 1907, in mouth of *Chelonia mydas*, specimen had six or seven pairs of gills which got smaller posteriorly, USNM 39099; COSTA RICA. Limon Province, Tortuguére, on *Chelonia mydas*, USNM 39101.

Diagnosis: (fig. 1(C)–(D)) Gills digitiform, seven pairs (possibly variable) located along lateral margins of segments XIII–XIX; midbody segments consisting of two unequal annuli; body short (3.5–10.5 mm) and flattened; tegument smooth and unpigmented; oral sucker large, not distinct from neck; caudal sucker large, equal to or slightly wider than abdomen. External and internal anatomical accounts along with systematic discussions are presented by MacCallum & MacCallum (1918), Sanjeeva Raj & Penner (1962), and Richardson (1969).

Known hosts: In the United States, and throughout the world, the only reported host for this species is the green turtle, *Chelonia mydas* (see MacCallum & MacCallum, 1918; Sanjeeva Raj & Penner, 1962; Richardson, 1969).

Known distribution: Ozobranchus branchiatus is a rare warm-water species known from Japan, India, Sarawak, Australia, and Florida (Richardson, 1969). In the United States, it was previously known only from the Florida Keys (MacCallum & MacCallum, 1918; Sanjeeva Raj & Penner, 1962; Nigrelli & Smith, 1943). We found it in southern Florida and in Costa Rica, the first record for that region.

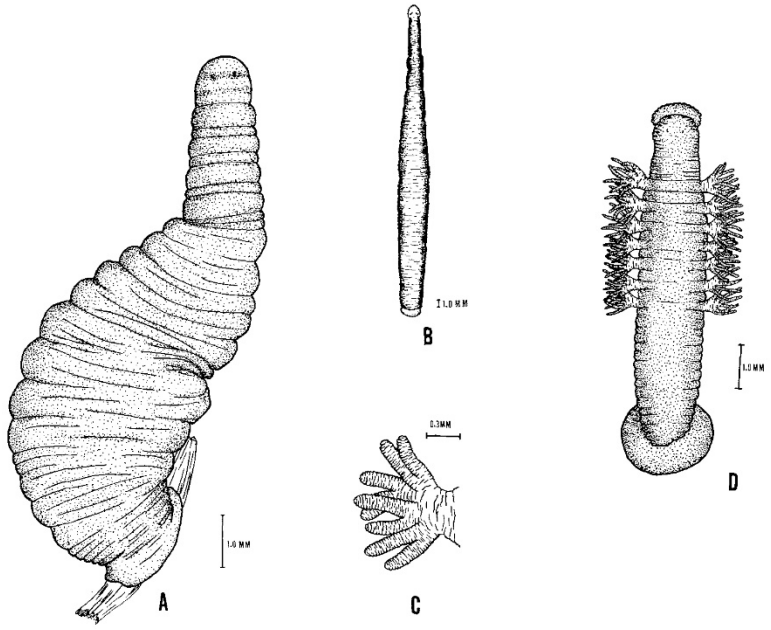

Figure 1. Some marine leeches from the eastern United States. (A), (B), (D), dorsal views; (C), frontal view. (A) *Trachelobdella rugosa* from Charleston, South Carolina, attached to gill arch of host; (B) *Myzobdella lugubris* from Beresford Creek, Charleston, South Carolina; (C) *Ozobranchus branchiatus*, frontal view of digitiform branchia; (D) *O. branchiatus* from southern Florida. Drawn by Ann F. Flowers; (C), (D) redrawn from Sanjeeva Raj & Penner (1962).

Ecology: Off the United States, *Ozobranchus branchiatus* has been found in the mouth, under the flippers, and on the neck. Unlike most leeches, this species appears to complete its life cycle on its turtle host. Its eggs are deposited in batches on the skin and covered with sclerous cementing material. Several authors suggested an association with this species and a fibropapilloma (Nigrelli, 1941, 1942; Sanjeeva Raj & Penner, 1962). As many as 50 leeches were cited per 1.3 cm square of tumor surface (Nigrelli & Smith, 1943). The leech appears to prefer high-salinity water; its occurrence in brackish water has never been documented.

Ozobranchus margoi (Apathy, 1890)

Pseudobranchellion margoi Apathy, 1890: 110.
Ozobranchus margoi: Blanchard, 1894: 10; Ringuelet, 1944: 194; Richardson, 1969: 67, fig. 1(C); Davies & Chapman, 1974: 104, figs. 1–3.
Richardson (1969) provided a complete summary of the systematics of this species.

Locality Records: FLORIDA. Tortugas, USNM 39106, in mouth of loggerhead turtle, with four pairs of large branching gills and one small posterior pair; Indian Pass, Gulf County, in mouth of *Caretta caretta*, five pairs of gills, USNM 39100 (J. P. Moore stated on label in vial,

"may be *Ozobranchus margoi*"); GEORGIA. Wassaw Island Beach, 7–23, vi. 1973, cloacal region and legs of *C. caretta*.

Diagnosis: Distinguished from *O. branchiatus* by five rather than seven pairs of digitiform branchiae. Of 44 specimens 4 to 22 mm in length examined from Georgia, all had five pairs of branchiae except one atypical specimen with three branchiae on one side. Typically the anterior-most pair is much larger than the rest, which become progressively smaller posteriorly. The anterior two or three pairs are usually bifurcated.

Known hosts: Until recently *O. margoi* was known only from the sea turtles *Thalassochelys corticata*, *Lepidochelys olivacea*, *Caretta caretta*, and *Chelonia mydas*, plus an unexpected record from the long-beaked dolphin, *Stenella longirostris* (= *Delphinus l.)* (see Apathy, 1890; Ringuelet, 1944; Richardson, 1969). It was recently reported by Davies & Chapman (1974) in the Wometco Miami Seaquarium on the sea turtles *Chelonia mydas mydas*, *Caretta caretta caretta*, *Eretomochelys imbricata imbricata*, and *Lepidochelys kempii*. Some of these hosts are probably unnatural due to the close conditions of captivity. In some cases up to 900 leeches were found on a turtle and lesions were associated with the sites of attachment. A similar epizootic outbreak of *O. margoi* under natural conditions on *C. mydas* and *C. caretta* was studied by F. J. Schwartz in North Carolina. We confirm his identification, and he will report the details of the outbreak later (Swartz, personal communication).

Known distribution: The type locality for *O. margoi* is the Gulf of Naples, Italy. In addition to the Mediterranean Sea, the leech is known from Japan and other areas in the Pacific and from Uruguay in the Atlantic (Ringuelet, 1944).

Ecology: Gerald K. Williamson (personal communication) of the Savannah Science Museum tagged 25 adult loggerhead turtles during the summer of 1973 on Wassaw Island, Georgia. Nearly all those turtles had infestations of *O. margoi*; some individuals were infested with over 100 specimens. The leech occurred primarily in the cloacal region but also in large numbers on the legs.

Family **PISCICOLIDAE** Johnston, 1865
Genus ***BRANCHELLION*** Savigny, 1822
Branchellion torpedinis Savigny, 1822

Branchellion torpedinis Savigny, 1822: 109, Sukatschoff, 1912: 397, Pls. 18–24; Meyer, 1941: 290; Pearse, 1948; 456; Soós, 1965: 431.
Branchellion ravenelii: Verrill, 1874: 624, Pl. XVIII, fig. 89.
Branchellion raveneli: Pratt, 1935: 365, fig. 497; new synonym.

Selected locality records: MASSACHUSETTS. Roger's Pond, Woods Hole, 10. vii. 1875, on tail of *Dasyatis centroura*, USNM 14187; CONNECTICUT. Noank, 28. viii. 1874, between eyes of *D. centroura*, MCZ 1743; NEW YORK. Gravesend Bay, southwest end of Long Island, USNM 43308; NORTH CAROLINA. No further details, USNM 36806 (see Pearse, 1948).

Diagnosis: Body elongate, somewhat flattened, divided by preputial ring into short trachelosome and much longer urosome; branchiae numbering 33 pairs, broadly flattened, foliaceous (phylliform), three pairs per midbody segment; pulsatile vesicles present, one at base of every third branchia; midbody segments triannulate; tegument smooth; oral

sucker large, distinct from neck; caudal sucker large, distinct from body, slightly wider than maximal body width (excluding branchiae); ventral surface of caudal sucker with many secondary suckers. Sukatschoff (1912) described the external and internal anatomy.

Known hosts: In the eastern Atlantic Ocean and the Mediterranean Sea, *Branchellion torpedinis* is recorded predominantly from rays and skates, being known from *Rhinobatus touin*?, *Raja clavata*, *Dasyatis pastinaca* (= *Trygon p.*), *Squatina squatina* (= *Rhina s.*), *Scophthalmus maximus* (= *Rhombus m.*), *Labrus* sp., and *Torpedo* sp. (see Herter, 1935). Off the United States it occurred on the skate *Myliobatis freminvillei* (= *Aetobatus f.*) (see Verrill, 1873) and *Gymnura micrura* (= *Pteroplatea m.*) (see Pearse, 1948). We found it on *Dasyatis centroura* and from unidentified hosts.

Known distribution: Branchellion torpedinis occurs in temperate waters of the Mediterranean Sea, the east coast of the Atlantic Ocean from Ireland and the North Sea to Senegal (Herter, 1935), and off the US from Massachusetts to North Carolina. Meyer (1941) accepted two species of *Branchellion* in the United States, rather than one, as suggested by Verrill (1874). All specimens of *Branchellion* examined in this study from the New England area, some of which were indicated as having been identified by Verrill as *B. ravenelii*, possessed the 33 pairs of branchiae characteristic of *B. torpedinis* and are considered by us as such. The reports by Verrill (1874) and Pearse (1948) were the only previous records from the United States. We encountered *B. torpedinis* in Massachusetts, New York, and North Carolina.

Ecology: Sites on hosts off the US include the tail and between the eyes.

Branchellion ravenelii (Girard, 1850)

Phyllobranchus ravenelii Girard, 1850: 124.
Branchellion ravenelii: Meyer, 1939: 22; Meyer, 1941: 289, figs. 1–3; Causey, 1953: 19, fig. 1; Hutton, 1964: 446; Soós, 1965: 431; Goldstein & Wells, 1966: 690; Rudloe, 1971: 211; Sawyer, 1972: 103.

Selected locality records: FLORIDA. Lemon Bay, 23. iii. 1939, on ventral surface of *Dasyatis americana* (= *D. hastata*), USNM 20538 (see Meyer, 1941); Mote Marine Laboratory, Sarasota, 13 February 1968, on *Gymnura micrura*, USNM 44390; Apalachicola, 28. vi. 1935, from ventral surface of sandshark, USNM 36849; MISSISSIPPI. off Horn Island, 5. vii. 1970, on ventral surface of *Narcine brasiliensis*, 2. vii. 1971 on *Dasyatis sayi*, and 21. xi. 1973 on *Raja eglanteria* (juvenile leech without branchiae).

Diagnosis: (fig. 2 (A)–(F)) *Branchellion ravenelii* closely resembles *B. torpedinis* but can be easily distinguished by having 31 pairs of branchiae, from segments XIIIa3 to XXIV, rather than 33. Meyer (1941) described the internal and external anatomy.

Known hosts: Branchellion ravenelii, which occurs almost exclusively on rays and skates, was previously known from *Dasyatis americana* (= *D. hastata*), *Dasyatis sabina* (= *Amphotistius sabinus*) (see Meyer, 1939, 1941), *Gymnura micrura* (see Goldstein & Wells, 1966; Rudloe, 1971), *Dasyatis sayi* (see Causey, 1953), and a "skate" (see Girard, 1850). We found it on *Aetobatus narinari*, *Narcine brasiliensis*, *Dasyatis americana*, *D. sabina*, *D. sayi*, *Gymnura micrura*, *Raja eglanteria*, and a "shark."

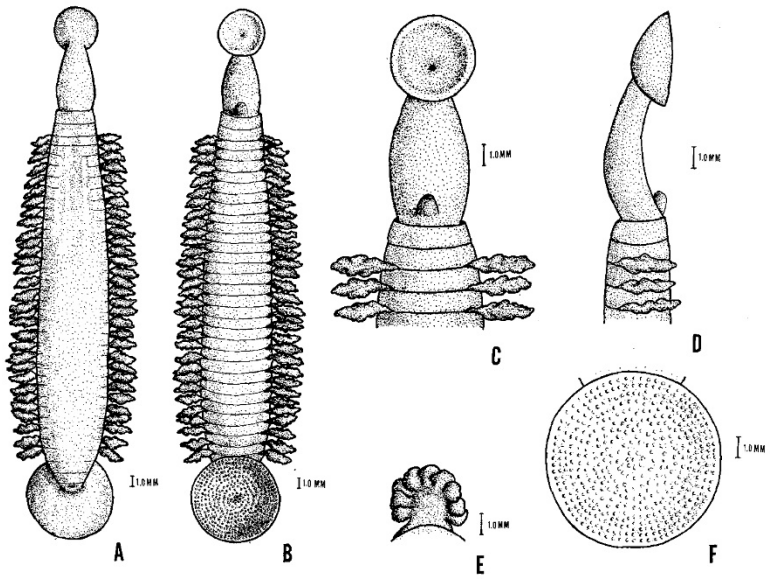

Figure 2. *Branchellion ravenelii* from *Aetobatus narinari,* 1. iv. 1962, Miami Seaquarium, Florida. (A) dorsal view; (B), (C) ventral views; (D) lateral view; (E) frontal view of phylliform branchia; (F) ventral view of caudal sucker. Drawn by Ann F. Flowers.

Known distribution: Unlike *B. torpedinis*, its northern counterpart, *B. ravenelii* is a warm-water species previously known from South Carolina (Girard, 1850), Florida (Meyer, 1939, 1941; Goldstein & Wells, 1966), and Mississippi (Causey , 1953). We found it to be common in Mississippi and along both coasts of Florida. It has never been found in South Carolina, in spite of repeated attempts, since the original description.

Ecology: Branchellion ravenelii has been encountered on seven different occasions, without exception, from the ventral surface of the host. Only one or two adults per host are normally encountered, and no substantiated reports record it unattached to a host. Occasionally in Mississippi numerous small individuals reside on a single ray and Rudloe (1971) reported as many as 50 specimens per *Gymnura micrura.* Goldstein & Wells (1966) collected 26 specimens on 31 *G. micrura* but failed to find it on 190 other fish representing 17 other species of fish off Florida in the Gulf of Mexico.

Branchellion ravenelii prefers high-salinity water. The few specimens collected from Mississippi were from water between 19° and 28°C.

Genus ***CALLIOBDELLA*** van Beneden & Hesse, 1863
Calliobdella vivida (Verrill, 1872) comb. nov.

Cystobranchus vividus Verrill, 1872: 126, fig. 1 (inadequate description; no type material known); Verrill, 1873: 458; Pratt, 1935: 365; Moore, 1952b: 3.
Trachelobdella vividus: Moore, 1898: 551, pl. XL, fig. 4 (The single specimen, USNM 242, basis for brief description of external anatomy, is lost; internal anatomy unknown; Wass, 1972: 120.
Calliobdella nodulifera: Threlfall, 1969: 807; new synonym.

Calliobdella carolinensis Sawyer & Chamberlain, 1972:470, figs. 1–3, USNM 45601; Sawyer, 1972: 103; Tucker, 1973: 108; Sawyer & Hammond, 1973: 373, new synonym.

Selected locality records: MASSACHUSETTS. Woods Hole, 6. ii. 1884, USNM 1041; CONNECTICUT. Stonington Harbor, 10. v. 1962, on *Pseudopleuronectes americanus*, USNM 30418; VIRGINIA. Gloucester Point, under York River bridge, 11. v. 1965, on ventral surface of *Opsanus tau*; NORTH CAROLINA. Morehead City, January 1951, from *O. tau*, USNM 36818; SOUTH CAROLINA. Beresford Creek, Charleston, 12. i. 1971, on *Brevoortia tyrannus*, USNM 45601; GEORGIA. two to three miles off Sapelo Island, on *B. tyrannus*; FLORIDA. Sabine Island, Santa Rosa Sound, 3. iii. 1964, on operculum and in mouth of *O. beta*, GBERL 1817; Apalachicola Bay; host unknown, USNM 3998; MISSISSIPPI. Davis Bayou, Ocean Springs, 9. i. 1970, on *Paralichthys lethostigma*; LOUISIANA. Madisonville, Lake Pontchartrain, 3. vii. 1928, from gill chamber of unidentified clam.

Diagnosis: (figs. 3 (B)–(F); 4) Body subcylindrical, not sharply divided into trachelosome and urosome; tegument smooth, without papillae or tubercles; suckers both distinct from body; caudal sucker slightly wider than maximal body width and about twice width of oral sucker; midbody segments 14 annulate; eyespots two pair on oral sucker; pigmentation in transverse metameric bands; pulsatile vesicles numbering 11 pairs on segments XIII through XXIII; anterior portion of vas deferens convoluted and extending to ganglion IX; seminal receptacle well developed, medial, muscular, confluent with bursa anteriorly and with ovaries posteriorly; testes numbering six pairs; postcaeca fused, with fenestrae.

Sawyer & Chamberlain (1972) described the internal and external anatomy of specimens from South Carolina. Dissections were made of adults from Mississippi (fig. 4 (A)–(C)); South Carolina (fig. 3 (B)–(F)), and Virginia (fig. 4 (D)–(F)). Those specimens clearly had the unpaired medial seminal receptacle characteristic of the genus. Those from Mississippi and South Carolina closely resembled the internal description in the size and degree of convolution of the vas deferens and the epididymis. Those from Virginia differed somewhat in having a smaller, less conspicuous portion of the vas deferens not necessarily extending as far anteriorly and a smaller, less convoluted epididymis. These differences could be of a geographic nature and do not support the establishment of a separate species.

Taxonomic note: Confusion over the specific name *vividus*, which has been cited but a few times in the last 75 years, stems from the vague and inadequate external descriptions of *Cystobranchus vividus* by Verrill (1872) and Moore (1898). No type material has been found, and, therefore, there is no way of determining the internal anatomy, which is the essential criterion for reliable taxonomy of the *Piscicola-Calliobdella-Cystobranchus* group of piscicolids. Since no encountered leeches other than *Calliobdella carolinensis* could be confused with the poorly described *Cystobranchus vividus*, and since we desire to preserve nomenclatural stability, we consider *Calliobdella carolinensis* a synonym of *Cystobranchus vividus*. We reassign the species to the genus *Calliobdella* as *Calliobdella vivida* (Verrill, 1872) comb. nov.

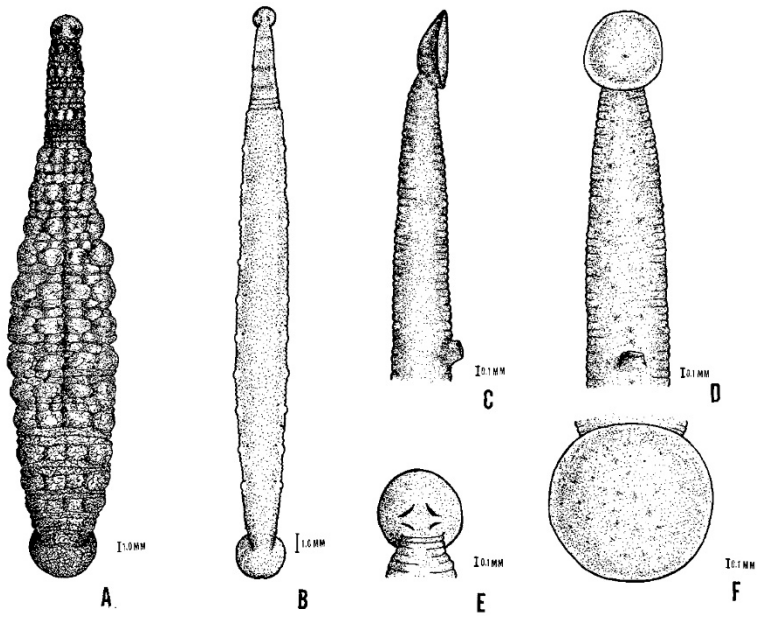

Figure 3. (A) *Stibarobdella macrothela*, dorsal view. Riviera Beach, off Ft. Worth Inlet, Florida; (B)–(F), *Calliobdella vivida*, Inlet Creek, Charleston, South Carolina; (B) dorsal view; (C) lateral view of anterior end showing partially protruded male bursa; (D) ventral view; (E) dorsal view of oral sucker; (F) ventral view of caudal sucker. Drawn by Ann F. Flowers.

Known hosts: Calliobdella vivida has been reported from *Fundulus heteroclitus* (= *F. piscuelentus*), *Opsanus tau*, *Brevoortia tyrannus*, *Alosa aestivalis*, *Raja eglanteria*, and *Paralichthys dentatus* (Verrill, 1872, 1873; Sawyer & Chamberlain, 1972; Wass, 1972; Sawyer & Hammond, 1973). It was commonly encountered on *B. tyrannus* in South Carolina estuaries, and less often on the following new hosts in other areas: *Opsanus beta*, *Paralichthys lethostigma*, *Pseudopleuronectes americanus*, *Micropogon undulatus*, *Sphoeroides maculatus*, *Strongylura marina*, *Squalus acanthias*, a "shark," *Callinectes sapidus*, a "clam," and unspecified hosts. A small collection from Sapelo Island, Georgia, included specimens from "flounders, *Fundulus* sp., toadfish, and Sapelo Beach."

Known distribution: Calliobdella vivida is an estuarine species previously known from South Carolina and Virginia (Sawyer & Chamberlain, 1972; Wass, 1972; Sawyer & Hammond, 1973). We encountered it numerous times in South Carolina estuaries and Chesapeake Bay, and less often in Massachusetts, Connecticut, North Carolina, Georgia, western Florida, Mississippi, and Louisiana (see also Strout, 1961).

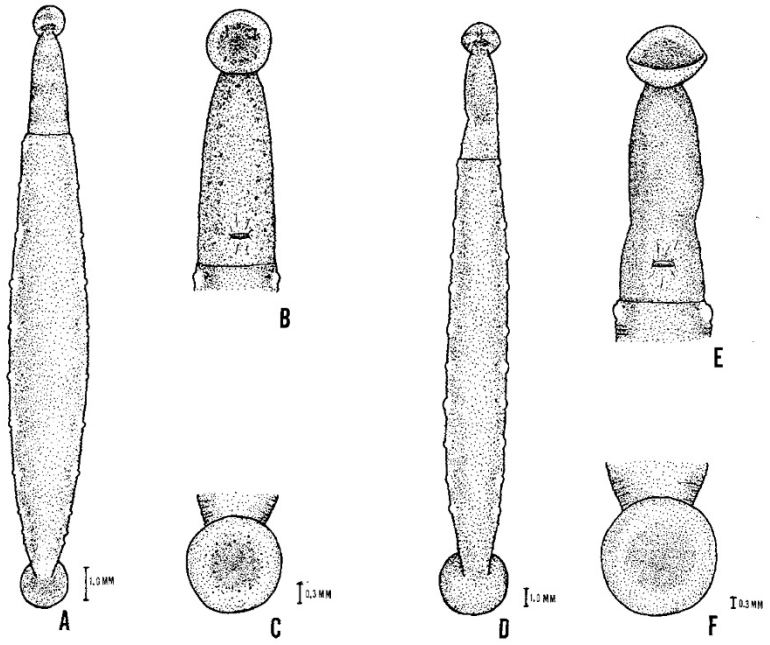

Figure 4. *Calliobdella vivida*. (A)–(C), from *Callinectes sapidus*, 17 i. 1971, Davis Bayou, Ocean Springs, Mississippi; (D)–(F), from *Opsanus tau*, 6. v. 1965, Gloucester Point, Virginia. (A), (D) dorsal views; (B), (E) ventral views of oral suckers; (C), (F) ventral views of caudal suckers. Drawn by Ann F. Flowers.

Ecology: Sawyer & Hammond (1973) reported the life history and behavior of *Calliobdella vivida* (= *C. carolinensis*) from South Carolina. Displaying a seasonal occurrence, it occurred more abundantly in late February and early March when the water was coldest (9° to 10°C). At that time, the leech bred and deposited at least 20 helmet-shaped cocoons. No adults were found from the end of April until the following mid-December.

Our study corroborates the seasonal appearance of the leech during winter and spring months. In fact, all collections of this species were from early December to the end of May, except for one collected 3. vii. 1928 in Louisiana from the gill chamber of an unidentified clam. In Virginia it was collected repeatedly on *Opsanus tau* and *Paralichthys dentatus* between 30 March and 25 May from 1964 to 1970 in water about 16° to 19°C.

Thirteen collections of *C. vivida* were from water 11° to 20°C and only two from 0° to 10°C. All occurred in water less than 22 ppt. Whereas specimens of *C. vivida* from *Brevoortia tyrannus* occurred exclusively in the mouth cavity, others, one to three in number and primarily from *O. tau* and *P. dentatus*, resided on the ventral surface. Others occurred on the caudal fin, the lower jaw, and in the mouth of the host. Specimens from *B. tyrannus* often occurred attached singly or clustered on the parasitic isopod *Olencira praegustator*. On 18. v. 1970 at VIMS, Virginia, one adult individual occupied the coelom of *O. tau* (275 mm TL), a rare site for a leech. Two specimens were recovered from the nostrils of *Micropogon undulatus* in Mississippi.

TRACHELOBDELLA Diesing, 1850
Trachelobdella rugosa Moore, 1898

Trachelobdella rugosa Moore, 1898: 553, Pl. XL, fig. 5; Soós, 1965: 453; Sawyer, 1972: 103.

The original description of this obscure species was based on six specimens taken off an unidentified "red snapper" from an unknown locality. Until now it had not been found since. Moore (1898) characterized it as follows: length 23 mm; body depressed with short traehelosome; tegument loose, in folds; pulsatile vesicles remarkably large, 12? in number, located along lateral margins; caudal sucker small, shallow, continuous with body, about one and one-half times the width of the oral sucker; maximal body width considerably greater than (about twice) the width of the caudal sucker; 12 annulate; eyespots lacking; internal anatomy unknown. The holotype (USNM 5035) and the five paratypes (USNM 36300) were examined. Each had a small, shallow terminal caudal sucker; 10 large and one small pair of conspicuous, hollow vesicles; a distinct preputial ring; a smooth trachelosome; and no nuchal constriction.

We encountered only one specimen resembling *T. rugosa* (USNM 51486) (fig. 1(A)). It was removed from the gills of a white grunt, *Haemulon plumieri*, collected on 1. x. 1970 about 78 km (32°2.8′N; 79°24.8′W) from the Charleston Light, South Carolina, depth 46–55 m. Its characters follow: body depressed, with short trachelosome; annulation obscure; pulsatile vesicles large, 12 in number, along lateral margins; tegument translucent; preputial ring present; caudal sucker small, terminal, considerably smaller than maximal body width; pigment spots in two transverse rows on oral sucker, reddish brown in color, resembling faint stripes; details of internal anatomy obscure, even upon clearing with xylene.

Trachelobdella lubrica (Grube, 1840)

Pontobdella lubrica Grube, 1840, p. 60. (see Soós, 1965, for a European synonymy).
Trachelobdella lubrica: Meyer, 1965: 242, fig. 1.
?*Trachelobdella* sp.: Hutton, 1964: 439.

This species has been known for a long time from the Mediterranean Sea, western Europe, and the east and west shores of tropical Africa. A brief anatomical account is given by Meyer (1965). The recent finding of this species in Puerto Rico by the senior author is the first record for the western hemisphere. On 13 iii. 1974 two individuals of *T. lubrica* were taken alive at La Parguera from the gill chamber of a Cubera snapper, *Lutjanus cyanopterus* (323 mm, SL), in 15–20 fathoms of water. One individual (USNM 51386) was engorged with blood to the extent of eclipsing the pulsatile vesicles. When undisturbed, leeches assumed the well-known S-shaped position characteristic of the species.

Trachelobdella lubrica is to be expected on snappers and grunts from shallow tropical waters of the Caribbean and the Gulf of Mexico. A commercial fisherman from Mississippi reported that red snappers in the Gulf of Mexico, at certain times, have as many as 100 leeches per fish from water about 180 m deep. Hutton (1964) reported a questionable record of *TrachelobdelIa* sp. from *Epinephelus itajara* (= *Promicrops i.*) in Tampa Bay.

Genus ***STIBAROBDELLA*** Leigh-Sharpe, 1925
Stibarobdella macrothela (Schmarda, 1861)

Pontobdella macrothela Sehmarda, 1861: 6, Pl. XVI, fig. 145; Caballero, 1955: 153, figs. 1–8; Hutton, 1964: 446; Sawyer, 1967: 36.
Pontobdella muricata: Moore, 1898: 557.
Pontobdella sp.: Causey, 1953: 19.
Pontobdellina macrothela: Soós, 1965: 450.
Stibarobdella macrothela: Llewellyn, 1966: 405, Sawyer, 1967: 37.
Llewellyn (1966) presented an incomplete synonymy from the world's literature.

Selected locality records: NORTH CAROLINA. 32 km SE of Beaufort Bar, 15. ix. 1973, on *Carcharhinus falciformis*; off Core Sound, Beaufort, 13. vi. 1968, on *Paralichthys dentatus* (= *Chaenopsetta ocellaris*), specimen in Duke University Marine Biological Laboratory collection; GEORGIA. Off coast, 1941, USNM accession number 21183; 31°25.5′N; 80°53.3′W in 21 m on 26. iv. 1966, from "old shells"; FLORIDA. Off Keyton Beach, Taylor County, unattached in shrimp-trawl; Conch Key, Florida Bay, 28. i. 1903, from crab; near Palm Beach, 26. v. 1968, on *Carcharhinus leucas*; TEXAS. near Rockport, Aransas Bay, 17. v. 1963, host unknown, USNM 30849; Gulf of Mexico. 26°05′N; 96°14′W, USNM 49658; PUERTO RICO. La Parguera, off SW Puerto Rico, 29. iii. 1972, on gill slit of *Ginglymostoma cirratum*; COLOMBIA. 11°02′N; 75°23′W in 137 m, on unidentified shark.

Diagnosis: (fig. 3(A)) Distinguishable from other members of Pontobdellinae by its triannulate segment in abdominal region; primary tubercles numbering 10 on middle (a2) annulus; midventral tubercle on a2 annulus lacking; oral sucker with "tentacles" (papillae) and one pair of eyespots, but no marginal fringe; caudal sucker relatively large, at least two to three times the diameter of the oral sucker. Llewellyn (1966) presented a full account of external and internal anatomy of the leech, along with its systematic position.

All of the specimens examined in this study agree basically with this diagnosis. There was, however, some variation in the shape and size of the tubercles, the number of smaller tubercles on annuli al and a3, and the size of the posterior sucker. Some specifics of the external anatomy of the individual from North Carolina are as follows: total length including suckers, 24 mm; caudal sucker 3.0 mm in diameter; tentacles three pairs on oral sucker, a dorsal, ventral, and dorso-lateral pair; marginal fringe lacking; one pair of conspicuous eyespots; a2 annulus of abdominal segment with 10 tubercles that become smaller ventrally; annuli a1 and a3 with 14 small tubercles each. The tubercles of this specimen were more pointed and the caudal sucker smaller than most of those from Florida, which had large rounded tubercles and a caudal sucker three or more times larger than the oral sucker.

This was the only member of the Pontobdellinae found; however, positive identification necessitated comparison with several closely related forms of *Stibarobdella* in Llewellyn's (1966) review of the group. Whereas Llewellyn retained the specific identity of several of these forms, Cordero (1937) believed, with some justification, that they were all synonymous with *Stibarobdella macrothela*.

Known hosts: Stibarobdella macrothela is found worldwide attached to the fins, mouth, claspers, and skin of a variety of elasmobranch hosts, especially certain sharks (Llewellyn,

1966). In the United States, it was previously known from the tongue of a shark (Moore, 1898), the dorsum of a guitarfish (Sawyer, 1967), and a crab (Causey, 1953). We examined specimens from *Carcharhinus falciformis*, *C. leucas*, *C. limbatus*, *C. obscurus*, *C. springeri*, *C. longimanus*, *Ginglymostoma cirratum*, *Sphyrna tudes*, several unidentified sharks, *Paralichthys dentatus*, an unidentified crab, and "old shells." It was occasionally found unattached to any host in trawls.

Known distribution: Stibarobdella macrothela is a relatively large, warm-water species known primarily from the tropical regions of the Atlantic, Pacific, and Indian Oceans (Soós, 1965; Llewellyn, 1966). In North and Central America, it was previously reported from Kingston, Jamaica, the type locality (Schmarda, 1861); the Florida Keys (Moore, 1898); Veracruz, Mexico (Caballero, 1955); and two undetermined locations in the Mississippi-Texas area (Causey, 1953; Sawyer, 1967). We found it on hosts off North Carolina, Georgia, western and southern Florida, Texas, British Guiana, Colombia, and well offshore in the Gulf of Mexico.

Ecology: In the United States, *Stibarobdella macrothela* has been found, usually one or two individuals per host, on the dorsal fin, the dorsal surface, the anal fin, the gill slits, and the tongue. The finding of this species unattached to hosts or on crabs suggests that it, like most piscicolids, leaves its fish host to deposit cocoons, possibly during winter months.

Stibarobdella macrothela, a high saline species, has never been documented from brackish water.

AUSTROBDELLA Badham, 1916
Austrobdella rapax (Verrill, 1873) comb. nov.

Pontobdella rapax Verrill, 1873: 625, fig. 91 (USNM 14250; 13974).
?*Pontobdella* sp.: Verrill, 1873: 625; Meyer and Barden, 1955: 297.
Piscicola rapax: Moore, 1898: 557; :Pratt, 1935: 364, fig. 496.

This species, provisionally assigned to the genus *Austrobdella* for the reasons given below, was reported by Verrill (1873) in his original account to be common on *Paralichthys dentatus* (= *Chaenopsetta ocellaris*) in Vineyard Sound. The syntypes (USNM 14250; 13974) labeled *Pontobdella rapax* from Vineyard Sound had the following characteristics (fig. 7 (A)–(C)): body clavo-fusiform, somewhat flattened; tegument without tubercles or foliaceous gills (branchiae); metameric white regions along margins (= barely discernible pulsatile vesicles); mid-body segments 12 to 14 annulate; oral sucker small but distinctly demarcated from neck region; neck attached to posterior third of oral sucker, so that there is only a short posterior lip to the sucker; caudal sucker subterminal, deeply cupped, attached to body slightly anterior to center of sucker so that the posterior lip of sucker is noticeably wider than anterior lip; the latter not directed posteriorly; caudal sucker smaller than maximum body width; posterior end of body not narrowing to meet caudal sucker which is about two times width of neck at point of attachment to oral sucker.

According to Verrill, in life the color is dark olive with a row of white spots along each side. Both suckers are tinged with green. The young are reddish brown.

Other specimens of *A. rapax* found in the US National Museum, from Massachusetts, were: Vineyard Sound (USNM 14188, viii. 1883, on flounder, fig. 9 (C)–(F)) and Woods Hole (USNM 14249, 6. ix. 1875, on ocellated flounder). Moore (1898) also reported *A. rapax* from Menemsha Bight, Vineyard Sound, 28. viii. 1883 on the exterior of *Paralichthys dentatus*.

This species clearly does not belong to the genus *Pontobdella* but rather appears to have its closest affinities with the genus *Austrobdella*, to which *Pontobdella rapax* is provisionally reassigned. The genus *Austrobdella* is characterized by having a contractile lacuna extending along the lateral margins of the urosome, rather than separate pulsatile vesicles. The type material does not clearly show these lacunae, but one specimen (USNM 14249) in another vial has, due to fortunate preservation, the strongly developed lacunae typical of *Austrobdella*. The other specimens and the syntypes have lateral whitish metameric regions which are in fact pulsatile lacunae (see fig. 9 (F)). Verrill (1873) clearly refers to this "row of square or oblong white spots along each side" in the original description. A detailed anatomical account of *A. rapax* based on fresh material is urgently needed. The relationship between *A. rapax* and *A. anoculatata* Moore, 1940, the only other species of *Austrobdella* known from the northern hemisphere, does not appear close. The description of the latter, which fails to mention the lateral lacunae may be based on immature specimens. The apparent relationship between *A. rapax* and the various species of *Johanssonia* Selensky, 1914, needs further examination.

OXYTONOSTOMA Malm, 1863 (emended Epshtein, 1968)
Oxytonostoma typiea Malm, 1863

(see Soós, 1965, for synonymy)

A species closely resembling, and probably identical with, *Oxytonostoma typica* Malm, 1863, was recently found by us in the US National Museum (fig. 9 (A)–(B)). It was apparently examined by A. E. Verrill but was never distinguished by him from *Austrobdella rapax*. The following brief description of this distinctive species sets it apart from other marine leeches in the New England area. A more detailed anatomical account must await better preserved material. One specimen (USNM 14251), labeled "Gulf of Maine, Sta. 54, 110 fms, 1874, A. E. Verrill," had the following characteristics; body cylindrical, not flattened, no trachelosome; no pulsatile vesicles; caudal sucker strongly terminal, deeply cupped; oral sucker relatively large, deeply cupped, folded along the longitudinal axis, attached to the neck slightly anterior to center of sucker so that there is a large region from the mid-ventral portion of neck (at point of attachment) to the posterior margin of sucker (unlike the situation in *Austrobdella rapax*, fig. 7 (B)); oral sucker distinct from neck; with a small teat-like papilla on either side of the female gonopore; male gonopore slit-like, in furrow, 3½ annuli anterior to female gonopore which is located on a ring; minute white metameric tubercles on most annuli, especially dorsally, about 6 or 7 on dorsal half; total length, inclusive of suckers, 18.0 mm; maximum body width 1.9 mm; caudal sucker, 1.4 mm; and oral sucker, 1.0 mm.

There were many other additional specimens of this species in the US National Museum, collected primarily off New England from 1871 to 1882, from which additional observations were made (including three dissections on very brittle material): oral sucker only slightly smaller than caudal sucker; body cylindrical to slightly flattened; midbody segments apparently 6(7)-annulate (annulation somewhat obscure); gonopore region slightly raised; fused posterior crop caeca with five fenestrae; loose epididymis at ganglion XII; a large muscular, cylindrical ejaculatory bulb extending from ganglion XII to XI, parallel to the atrial horns; a short ejaculatory duct curving posteriorly at ganglion XI to enter the large paired, bulbous atrial horns which remain independent almost their entire length (similar to that figured by Epshtein, 1968, fig. 4); bursa minute; no preatrial loop of the vas deferens extending to IX.

The small and teat-like papilla on either side of the female gonopore is a constant and distinguishing feature of the specimens from New England. The minute tubercles are not always easily discerned. Most individuals were about 15–20 mm, the largest being 36 mm. In general they closely resemble the *O. typica* illustrated by Epshtein (1968, fig. 1).

This is the first record of *O. typica* from the American side of the Atlantic. All the specimens in the Smithsonian collections were collected from off Massachusetts to the Bay of Fundy: off Martha's Vineyard (USNM 3955, on *Raja ocellata*, 4. x. 1882); off Woods Hole (USNM 3942, from "big skate," four individuals); off Cape Cod (USNM 13969, 1879; USNM 13994, USFC 1879, sta. 922); Vineyard Sound (USNM 13976, 1881); off Cape Ann (USNM 13954, 1878); Massachusetts Bay (USNM 13957, 1878; USNM 13953, 1878); off Gloucester (USNM 1528, 9. xi. 1896, from "common skate," eleven individuals); Gulf of Maine (USNM 14248; USNM 13988); off New England (USNM 13955, from skate *Raja*; USNM 4509, 21. ix. 1882, 40°02′N 70°41′W, USFC *Hawk*, on skate; USNM 13950, Jeffrey's Ledge, 51 fms); Bay of Fundy (USNM 14246, 1872). Where a host was specified, *O. typica* was always encountered on a skate, *Raja ocellata* being the only identified host.

The genus *Oxytonostoma* was recently emended by Epshtein (1961b, 1968) who reviewed the work of Malm (1863), Johansson (1898), and Moore (1921).

Genus ***MYZOBDELLA*** Leidy, 1851
Illinobdella Meyer, 1940; new synonym
Myzobdella lugubris Leidy, 1851

Myzobdella lugubris Leidy, 1851: 243 (type material unknown); Verrill, 1873: 625; Pearse, 1936: 181, Moore, 1946: 1, figs. 1–3 (USNM 38821-2); Meyer & Barden, 1955:302; Hutton & Sogandares-Bernal, 1959: 384, fig. 1 (USNM 38824); 1960: 287; Hutton, 1964: 446, Soós, 1965: 440; Richmond, 1968: 225; More, 1969: 1; Sawyer, 1967: 36; Sawyer, 1972: 103; Daniels, 1973: 109; Tucker, 1973: 108; Overstreet, 1973: 121; Daniels & Sawyer, in press (USNM 49962).

?*Ichthyobdellafunduli* Verrill, 1872: 126; Verrill, 1873: 624; Verrill, 1874: 686; Wass, 1972: 120; new synonym.

?*Piscicolafunduli:* Pratt, 1935: 365; not *P. funduli:* Causey, 1953: 21, fig. 2.

Illinobdella alba Meyer, 1940: 367, fig. 7; Meyer, 1946: 241, fig. 9; Hoffman, 1967: 298; new synonym.

Illinobdella elongata Meyer, 1940: 368, fig. 5; Meyer, 1946: 244, fig. 7; Hoffman, 1967: 298; new synonym.

Illinobdella richardsoni Meyer, 1940: 369, fig. 4; Meyer, 1946: 241, fig. 6; Hoffman, 1967: 298; new synonym.
Illinobdella moorei Meyer, 1940: 370, fig. 3; Meyer, 1946: 243, figs. 8, 10; Hoffman, 1967: 298, fig. 243; Daniels and Sawyer, 1973: 48; new synonym.
Myzobdella lubrigis: Pearse, 1948: 456.
Myzobdella funduli: Moore, 1952b: 4; Soós, 1965: 440.
Myzobdella moorei Meyer & Moore, 1954: 12; Soós, 1965: 441; new synonym.
Illinobdella sp.: Wurtz & Roback, 1955: 185.
"unidentified species": Wurtz & Roback, 1955: 185.
Ichthyobdella rapax: Wass, 1972: 120.
Cystobranchus virginicus: Paperna & Zwerner, 1974, figs. 1, 2 (specimens examined) (*nec C. virginicus* Hoffman, 1964).

Selected locality records: MASSACHUSETTS. (as *Piscicola funduli*), Great Pond, Falmouth, 21. viii. 1907, USNM 39997; NEW JERSEY. Creek behind Avalon, on *Callinectes sapidus*, (Moore, 1946); MARYLAND. Chesapeake Bay, Long Beach, Calvert County, 7. vii. 1972, host unknown; VIRGINIA. Fary Point, Sarah Creek, York River, 8. viii. 1963, on dorsal, caudal, and pectoral fins of most specimens of *Fundulus majalis*, (also common on *Ictalurus catus* and *C. sapidus*); NORTH CAROLINA. Mullet Pond, Beaufort, 26. vi. 1931, on *C. sapidus*, USNM 38821, (see Pearse, 1936); SOUTH CAROLINA. over 1 km above Middleton Plantation, Ashley River, Charleston, 31. x. 1971, on *I. catus* (see Daniels & Sawyer, in press), also common on *Mugil cephalus*, *C. sapidus*, and *Palaemonetes pugio*; GEORGIA. Ogchoee River, Ossabaw Sound, February 1973, on *I. catus* and Ossabaw Sound, winter 1972, *Ancylopsetta quadrocellata;* FLORIDA. Mulatto Bayou, Escambia Bay, common on *M. cephalus*, (also common on *C. sapidus*); ALABAMA. Lopka River, 4 km SW of Magnolia Springs, Baldwin County; MISSISSIPPI. Davis Bayou, Ocean Springs, 27. vii. 1970; Back Bay, Biloxi, 17. ii. 1971; and Griffen's Point, Escatawpa River, 2. xi. 1970 all on *Paralichthys lethostigma*, (also common on *M. cephalus*, *Fundulus similis*, *F. grandis*, *C. sapidus*, and P. *pugio*); LOUISIANA. Price Lake, Rockefeller Refuge, near Grand Chenier, 20. v. 1970, on *M. cephalus*, (also common on *C. sapidus*); TEXAS. Kerrville, 5. v. 1942, on unidentified catfish, USNM 37494.

Definition: (figs. 1(B); 5) Body elongate, clavo-fusiform, slightly flattened; tegument translucent, smooth, without conspicuous papillae, tubercles, ocelli, nor gills; body perceptibly divided into trachelosome and urosome regions, especially in adult or engorged individuals; oral sucker small, slightly wider than neck region and about three-fifths width of caudal sucker; eyespots one pair, on oral sucker; caudal sucker terminal, continuous with posterior end of the body and noticeably smaller than maximal body width; midbody segments with 12 to 14 annuli; esophageal diverticula paired; postcaeca fused, with hardly any trace of fenestrae; intestinal diverticula consisting only of one anterior pair, otherwise intestine without diverticula; coelomic system greatly reduced; testes five pair; male system simple; preatrial loop of vas deferens extending to ganglion IX lacking; epididymis convoluted in segments XI and XII; ejaculatory bulbs paired; atrium small, walls divided into paired atrial cornua; bursa small, capable of eversion and having atrium projecting as blunt cone with orifice at apex; freshwater and brackish water; parasitic on teleosts, or commensal on brackish water crustaceans. Meyer (1940, 1946) and Moore (1946) presented a full account of the external and internal anatomy.

Taxonomic note: The remarkably close anatomical features of the freshwater species *Myzobdella moorei* and the brackish water *M. lugubris* have been known for some time (Meyer, 1940, 1946; Moore, 1946). In the past these two forms had been distinguished on the basis of their habitats. The former was known to occur on many species of teleosts in fresh (and brackish) water throughout most of the United States and southern Canada. The latter was, until recently, thought to be a marine species restricted to the blue crab, *Callinectes sapidus*, and grass shrimp in the genus *Palaemonetes*. Recent ecological and physiological evidence presented below and elsewhere (Daniels & Sawyer, in press) showed that the ecological differences between the two forms were not so great as thought earlier. *Myzobdella lugubris* is a brackish water species and cannot tolerate even moderately high salinities for very long. It, however, can survive for several weeks, or even longer, in pond water. Also, it has been shown that, contrary to common belief, *M. lugubris* spends most of its life on certain brackish water teleosts, especially *Mugil cephalus*, *Ictalurus catus*, *Paralichthys* spp., and *Fundulus* spp. It gets on crustaceans only upon reaching maturity for cocoon deposition and dispersal. Conversely, the present physiological evidence shows that freshwater piscicolids, and presumably including *M. moorei*, have a relatively high degree of tolerance to increases of salinity. There is no longer any grounds for continuing the separation of *M. lugubris* from *M. moorei.* In fact, after examining specimens recognized by others as *I. alba*, *I. elongata*, *I. richardsoni*, and *M.* (= *I.*) *moorei*, we consider them all synonymous and recognize *M. lugubris* as the senior synonym of *I. alba*, the type-species of the genus *Illinobdella*. *Illinobdella* Meyer, 1940, thereby becomes a junior synonym of *Myzobdella* Leidy, 1851. The only remaining species in the genus is a Mexican species which we transfer to the genus *Myzobdella* as *M. patzcuarensis* (Caballero, 1940) comb. nov. It is similar to *M. lugubris* and requires additional study (Caballero, 1940).

Other examples of brackish water leeches with closely allied freshwater forms are known. In each studied case the brackish water form is more restricted in its host preference and geographic distribution than its evolutionarily more recent freshwater ally. The most notable example is *Piscicola geometra* (L.), which is found in brackish water regions of the upper Baltic Sea, as well as in many types of freshwater habitats throughout Eurasia. Johansson (1896), a careful worker, reported that the brackish form was distinguishable from the freshwater one only in the degree of pigmentation. A parallel eco-taxonomic problem also occurs with the brackish water species, *Caspiobdella caspiea* (see Selensky, 1915) and the freshwater "species" *C. fadejewi* (see Epshtein, 1961a). These ecologically distinct forms differ morphologically only in minor details, mainly pigmentation (Epshtein, 1961a). *Caspiobdella caspica* is found exclusively on the pipefish *Syngnathus nigrolineatus caspius* in brackish waters of the Caspian Sea, whereas *C. fadejewi* is found on a variety of fish in freshwater rivers flowing into the Black Sea and the Sea of Azov. Whether these represent one species or two ecologically distinct species remains unresolved.

Known hosts: In addition to its many brackish water hosts, *M. lugubris* is known to parasitize a variety of freshwater teleost hosts, especially catfishes, sunfishes, and perches (Meyer, 1940, 1946; Hoffman, 1967). In brackish water this common species was previously known from *Callinectes sapidus* (= *Lupa dicantha*, see Leidy, 1851; Moore, 1946; Wurtz & Roback, 1955; Meyer & Barden, 1955; Hutton & Sogandares-Bernal, 1959, 1960; Hutton, 1964; Richmond, 1968; More, 1969; Wass, 1972; Overstreet, 1973), *Palaemonetes* spp. (see

Meyer & Barden, 1955; Sawyer, 1967; Wass, 1972; Overstreet, 1973), *Penaeus setiferus* (see Overstreet, 1973), *Paralichthys dentatus* (= *Chaenopsetta ocellaris*), *Fundulus heteroclitus* (= *F. pisculentus*), *Neomysis americana* (= *Mysis americanus*) (see Verrill, 1872, 1873; Moore, 1898), *Lepomis gulosus* (= *Chaenobryttus coronarius*) (see Wurtz & Roback, 1955), *Mugil cephalus* (see Scott, 1972), and oysters (see Meyer & Barden, 1955). We found *M. lugubris* numerous times on *C. sapidus*, *Palaemonetes pugio*, *Ictalurus catus*, *M. cephalus*, *Paralichthys lethostigma*, *Fundulus majalis*, *F. similis*, and *F. grandis*. It also occurred on *Micropogon undulatus*, *Fundulus heteroclitus*, *Morone saxatilis*, *Brevoortia patronus*, *Gambusia affinis*, *Syngnathus floridae*, *Dormitator maculatus*, *Leiostomus xanthurus*, *Lepomis gulosus*, *Microgobius thalassinus*, *Mugil curema*, *Orthopristis chrysoptera*, *Ancylopsetta quadrocellata*, *Paralichthys dentatus*, *Trinectes maculatus*, *Lagodon rhomboides*, *Sciaenops ocellata*, a "catfish," *Palaemonetes* sp., *Penaeus aztecus*, *P. setiferus*, and unattached or on unspecified hosts.

Known distribution: Myzobdella lugubris, the most commonly encountered leech in the area of study, is a brackish and freshwater species, rather than marine. It was previously known from Massachusetts (Verrill, 1872, as *Ichthyobdella funduli*), New Jersey and Maryland (Moore, 1946), Virginia (Wass, 1972), North Carolina (Pearse, 1936; Moore, 1946, USNM 38821-3), South Carolina (Sawyer, 1972), Florida (Wurtz & Roback, 1955; Hutton & Sogandares-Bernal, 1959, USNM 38824, 1960; Hutton, 1964), Mississippi (Richmond, 1968; Overstreet, 1973), Louisiana (Meyer & Barden, 1955; Sawyer, 1967), and Texas (Wurtz & Roback, 1955; Meyer & Barden, 1955; More, 1969). Leeches in the US National Museum labeled *Piscicola funduli* (USNM 39997) from Great Pond, Falmouth, Massachusetts, also appear to be conspecific with *M. lugubris*. We encountered *M. lugubris* on dozens of occasions in Chesapeake Bay, South Carolina, Mississippi, and Louisiana, and at least once in North Carolina, Georgia, Florida, Alabama, and Texas.

Ecology: Locales with high densities of *M. lugubris* can be described as shallow, brackish regions usually with heavy vegetation. A brief ecological description of several especially noteworthy regions follows. Davis Bayou, Ocean Springs, Mississippi, has water of 1–28 ppt salt and 8°–33°C up to 2.5 m deep. The sand and mud substrata support the dominant vegetation, *Spartina alterniflora*, mainly intertidally. The non-ripe leech is found predominantly on flatfish, especially *Paralichthys lethostigma*, and on *Mugil cephalus* and species of *Fundulus*. Ripe individuals occur on *Callinectes sapidus* and *Palaemonetes pugio*. The latter directly associates with *Spartina alterniflora* whereas *P. vulgaris*, another common shrimp in Davis Bayou which has never been found infested with leeches, is not associated with *S. alterniflora*. In addition, *P. vulgaris* is usually found in higher salinity water with shell substrata. In Bayou Bernard, off Back Bay of Biloxi where the salinity is lower and *Juncus roemerianus* is the dominant vegetation, *M. lugubris* occurs more often and in greater numbers on blue crabs. Another area containing crabs with a high rate of infestation is the eastern portion of Lake Pontchartrain where the water of 1–15 ppt, is about 1.7 m deep and *Ruppia maritima* and *Vallisineria spiralis* abound. In the lower Ashley River, Charleston, South Carolina, the water is 0–14 ppt, 4–29°C, and 3 m deep. Sand and mud compose the bottom and *S. alterniflora* is abundant. In this area, *M. lugubris* is most abundant on *Ictalurus catus*, *M. cephalus*, and *Callinectes sapidus*. The shallows of the lower York River in Virginia are mostly less than 1.6 m deep with fine sand supporting extensive beds of eel grass, *Zostera marina*. Salinity ranges from 16.0–22.4 ppt, lowest in February, and temperature from 2.8–

28.3°C. There the leech primarily infests *Fundulus majalis*, *I. catus*, and *C. sapidus*. One *I. catus* 338 mm long had over 500 leeches, primarily around the mouth; lesions were associated with the points of attachment of the suckers (Paperna & Zwerner, 1974).

In February 1973, about 2000 *Ictalurus catus* were collected in Ogchoee River, Ossabaw Sound, Georgia. A total of 334 leeches (an average of 9.5 leeches per catfish) infested 34 of 35 catfish from a random sample 63–171 mm SL (averaging 109.8 ram). The average number of leeches removed from each region of the fish follows: pectoral fin, 2.9; first dorsal fin, 1.0; mouth, 0.9; pelvic fin, 0.8; barbel, 0.7; anal fin, 0.4; body surface, 0.2; caudal fin, 0.2; eye, 0.03; plus 93 leeches loose in container.

Under natural conditions, one leech or occasionally two infests a single *P. pugio* (fig. 5). In the laboratory, however, *M. lugubris* tends to congregate on shrimp already infested. For example, thirteen recently collected grass shrimp with one or two leeches each (for a total of 21 leeches) were maintained in a common container overnight. By the following day, two shrimp had eight leeches, one shrimp had three, ten shrimp had none, and two leeches were attached to the container. Similarly, five shrimp, each with one leech, were maintained in a common container and overnight all five leeches were on one shrimp. On several occasions it was noted that if a leech was added to a container with one infested and one uninfested shrimp, it attached to the infested one.

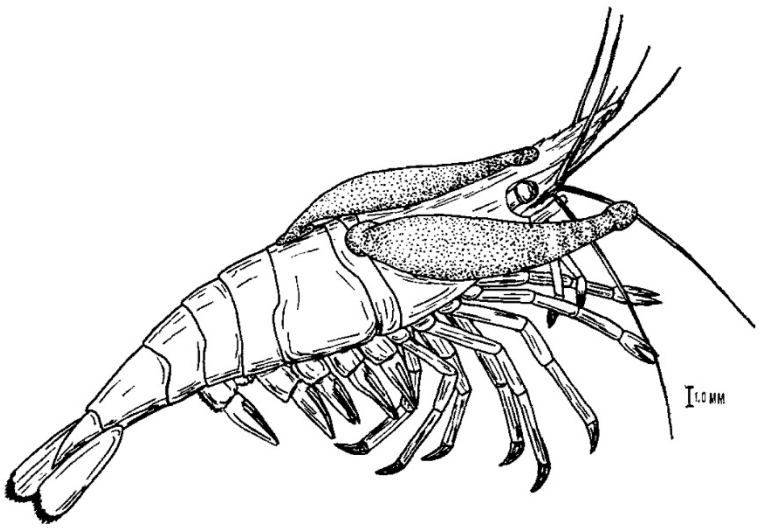

Figure 5. Two *Myzobdella lugubris* in typical position on carapace of *Palaemonetes pugio*. Drawn by Ann F. Flowers from a photograph by ARL and RMO.

The blue crab, *C. sapidus*, commonly harbored more than one leech. For example, at Back Bay, Biloxi, Mississippi (2 ppt), on 10. v. 1973, 24 leeches were taken from five individual blue crabs, and on 11. vi. 1973, 90 leeches were taken from 18 crabs. In the laboratory, both *C. sapidus* and *P. pugio* fed on the leech when able. The preference for specific crustacean hosts appears to be more than fortuitous. Leeches placed on four occasions to the carapace of the stone crab, *Menippe mercenaria*, detached themselves.

Myzobdella lugubris is a relatively warm-water species encountered most often at 21° to 30°C, occasionally at 16–20°C, and less often in colder water. In the laboratory it appears to be injured if suddenly cooled to 10–15°C. Also, to judge from our data, *M. lugubris* is a brackish to freshwater species encountered commonly in water 0 to 22 ppt. It was collected only one time each to 24 ppt (22°C) and 26 ppt (14°C). We are unaware of its presence in full-strength seawater; it is most common in water below 15 ppt.

To test further the degree of tolerance of *M. lugubris* to salt, two series of experiments were conducted by ARL. Adult leeches collected on *C. sapidus* and *P. pugio* from brackish water (1.1–1.7 ppt) were maintained in water from the collecting site for two and three days. All unable to attach to a substratum with their caudal suckers were discarded and each phase of the experiment was conducted at room temperature (23.0°–25.5°C) with salinities periodically determined throughout. Leeches were taken from the original *water* and plunged immediately into water of various salinities obtained by diluting seawater with distilled water. The containers, not aerated, were small stacking dishes 60 mm wide by 27 mm deep. In the first series of experiments, the dishes were uncovered for the first three days using the following salinities: 0.0 (distilled water), 0.0 (pond water), 1.1 (control from site of collection), 5.0, 11.1, 22.2, and 38.9 ppt. In the second series of experiments, the dishes were covered to reduce evaporation and a subsequent salinity change. The following salinities were used: 0.0 (pond water), 1.7 (control), 12.8, 27.8, and 38.9 ppt. Most dishes each had four leeches, but the lower salinities of the first experiment (11.1 ppt, and below) had three leeches each. Nonviability was determined by lack of response to touch.

In both experiments, the leeches reacted by immediate writhing and apparent death within 5–10 min at 38.9 ppt. The salinity recorded at the time of death for the last leech is listed below in parentheses after the initial salinity. In solutions of 27.8 (27.8) ppt, 22.2 (37.2) ppt, and distilled water they became stressed and nonviable within 45–65 min (dehydrated), 24–36 hours (dehydrated), and 21–25 hours (swollen), respectively. Beginning in solutions at 12.8 (15.0) ppt, and 11.1 (24.4) ppt, they lived for 10–16 days and 3–4 days, respectively. In water 5.0 (17.0), 1.7 (2.0), 1.1 (2.0) ppt, they lived for 16–31, 9–15, and 13–15 days, respectively. In pond water, all but one lived for 11–20 days.

These data corroborate our ecological observations that *M. lugubris* tolerates low salinities and fresh water. At 23.0–25.5°C, the maximal salinity tolerated under the abrupt changes in salinity was about 15 ppt.

During these experiments, the following observations on reproduction were made. Cocoons were deposited only in the dishes containing 12.8, 1.7, and 1.1 ppt salt and in the two dishes with pond water. In all, the 3–4 leeches in these dishes deposited 73, 25, 133, 114, and 126 cocoons, respectively. An average number of 43 cocoons per individual can be conservatively estimated based on the data of the first experiment; in the second experiment about 200 cocoons had already been deposited in the holding dish prior to trials. The daily cumulative total number of cocoons deposited by the three individuals in the 1.1 ppt dish was as follows: day 0 (0 cocoons in dish), day 4 (4), day 5 (23), day 6 (27), day 7 (38), day 8 (92), and day 16 (133). On day 34 after the first cocoons were laid, 27 cocoons were first noticed as hatched, and 9 and 2 cocoons hatched on days 35 and 36, respectively. Cocoons failed to develop in all other salinities. These leeches incubated 36 days or less at 23.0–

25.5°C. The minimal period could not be ascertained as the time of deposition of each cocoon was not determined.

Developing cocoons were dark brown; nondeveloping ones were light tan. Only one individual occupied a cocoon, and it emerged through the terminal pore. Young could swim somewhat, a weakly developed ability in adults. The 36 measured young averaged 1.38 mm in length (ranging between 1.01–1.78 mm), and closely resembled the adults in having an elongated, whitish body, small suckers, and one pair of eyespots.

The following additional observations were also previously made by one of us (ARL) with David E. Zwerner (at VIMS). Ten infested *Fundulus majalis*, collected on 3. viii. 1970 in York River, Virginia (water 30°C), were placed into a 0.04 m^3 plastic tank. On days 6 and 7 after collection, four engorged leeches which had fallen to the bottom of the tank were placed in a bottle in a 25°C incubator. Filtered York River water of undetermined salinity was changed daily. On day 14, the first cocoons were noticed, and on day 23, additional cocoons were found. On day 25, the first of several newly hatched young, 1.4–1.7 mm long, were observed, suggesting that hatching occurs in about 11 days at 25°C.

Three experimentally infested *P. pugio* from Mississippi with 4, 7, and 9 adult *M. lugubris* were placed into a large aerated finger bowl. After two days, the leeches had deposited about 90 cocoons on the glass container, air stone, and tubing, and only one cocoon on the carapace of a grass shrimp. Under natural conditions, cocoons were not observed on grass shrimp. They, however, were often seen on *C. sapidus*. Five leeches removed from shrimp and placed on the carapace of *C. sapidus* deposited thereon a total of 17 cocoons after 11 days.

An account of the relationships among *M. lugubris*; the white catfish, *Ictalurus catus*; and *C. sapidus* in South Carolina was presented by Daniels & Sawyer (in press).

Platybdella Malm, 1863

Platybdella buccalis Nigrelli, 1946: 215, Pl. VIII; Soós, 1965: 447.

Diagnosis: Tegument smooth, with no tubercles, papillae, nor gills; body cylindrical; no division of body into trachelosome and urosome; oral sucker a shallow cup, same width as neck; eyespots two pairs; sides of body parallel; distinct, discoidal caudal sucker, about twice maximum body width; midbody annulation obscure, about 12-annulate; bursa unusually large, commonly everted; testes five pairs; large ejaculatory bulbs separated by short ducts from elongate atrial cornua; median atrium small, opening at top of evertible bursa; intestine with five caeca; post-caeca unfused.

Taxonomic note: Nigrelli (1946) described this species from leeches taken from a single specimen of *Macrozoarces americanus*, presumably from the New England region. On 16. vi. 1961, five mature specimens (fig. 6) closely resembling the above description of *Platybdella buccalis* were taken at 37–55 m in Massachusetts Bay (42°15′N, 70°15′W) from the gills of *Anarrhichas* sp. (about 1 m TL). This is the first report of this species since the original account.

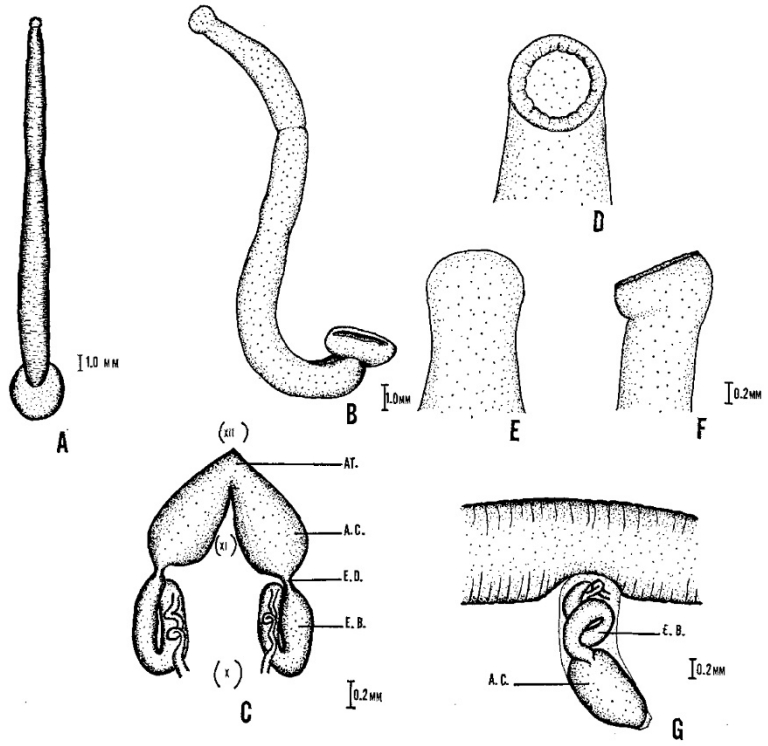

Figure 6. *Platybdella buccalis* from Massachusetts Bay. (B), (D)–(F), neotype (USNM 51431). (A) dorsal view of resting position, reconstructed from distorted preserved specimens; (13) dorsal view of neotype, somewhat distorted; (C), dorsal view of male reproductive system in region of ganglia X–XII, based on several dissections; (D) ventral view of oral sucker; (E) dorsal view of oral sucker; (F) lateral view of oral sucker; (G) lateral view of everted male bursa (anterior end of the animal is to the left); A.C., atrial cornua; AT., atrium; E.B., ejaculatory bulb; E.D., ejaculatory duct. Drawn by RTS.

The relationship of *P. buccalis* to other members of *Platybdella*, especially *P. anarrhichae*, must await a detailed account of the coelomic, reproductive, and digestive systems.

We believed it necessary to examine type material in order to properly establish characteristics of the species. Dr. R. F. Nigrelli, the original and only describer of *P. buccalis*, and Dr. Willard D. Hartman, Curator in Invertebrate Zoology, Peabody Museum of Natural History, reply that they cannot find the specimens nor any record in their catalogues that the types had ever been deposited either in the Bingham Oceanographic Lab, Yale University, nor the Peabody Museum of Natural History. They were not deposited in the US National Museum.

Neotype: Since the types are lost and there is a need to establish a new type, we designate as neotype the following specimen: USNM 51431 (fig. 6 (B), (D)–(F)). Body cylindrical, total length 17.0 mm, including suckers; pigmentation lacking; oral sucker with a shallow cup, same width as the neck, 1.0 mm wide; nuchal constriction lacking; sides of body parallel with widest portion 1.4 mm at posterior quarter of body; body narrowing abruptly to join

caudal sucker, latter well separated from body; caudal sucker attached to body only slightly anterior to center of sucker; sucker folded along longitudinal axis, 2.2 mm long, discoid, and about twice maximum body width; clitellum conspicuous, darker than rest of body, 3(6)-annulate; distinct constriction setting off posterior margin of clitellum, and similar, but fainter, constriction setting off anterior margin; male gonopore conspicuous, a large slit in furrow; female gonopore smaller and four annuli posterior to male pore; midbody annulation indistinct, basically 12-annulate.

Neoparatypes (USNM 51432): Four other individuals from same vial, total length 15, 15, 19, and 22 mm; anatomy closely resembles that of neotype. In clearing all specimens with xylene, dissecting two and sectioning one, the following internal characters were observed: testes five pairs; ovisacs with ripe ova (22 mm specimen); bursa unusually large, commonly everted (fig. 6(G)); male system (fig. 6(C)) consisting of enlarged ejaculatory bulbs (the "vesicula seminis" of Richardson, 1970) separated by short duct from elongate atrial cornua; median atrium small, opening at tip of everted bursa; ejaculatory bulbs enlarged, with connecting ducts somewhat convoluted, variable, extending to ganglion X (doubtful if ducts extend to ganglion IX); intestine with five caeca; postcaeca of two poorly preserved dissected specimens unfused along entire length; ventral coelom spacious and confluent with poorly defined laterals; dorsal coelom not clear, possibly absent; nature or presence of the epididymis and esophageal diverticula unknown. Additional specimens were recently found in the Smithsonian collections: "Massachusetts, off Gloucester, 1878, 25 fms, on *Zoarces'*, USNM 13959 (three pairs of eyes); and "Maine, Casco Bay, Sta. 715, July 1873, from wolffish," USNM 14956.

MALMIANA Strand, 1942
Malmiana nuda Richardson, 1970

?*Icthyobdella* sp., Verrill, 1875: 40.
Malmiana nuda Richardson, 1970: 841, figs. 1–6; Mace & Davis, 1972: 336.

Selected locality records: NEWFOUNDLAND. St. John's, on *Myoxocephalus scorpius*, USNM 42566; MASSACHUSETTS, Woods Hole, 16. xi. 1903, from unidentified sculpin, USNM 49574; Vineyard Sound, 4. viii. 1875, from mouth of unidentified sculpin, USNM 13952.

Diagnosis: Provisionally placed in the genus *Malmiana*, *M. nuda* presents some difficult taxonomic problems which are reviewed by Richardson (1970). The type (USNM 14250) was examined (fig. 7 (D)–(F)): body elongate and subcylindrical, lacking gills, tubercles, papillae, eyespots, and ocelli; annulation obscure, probably 6(12) annuli per segment; oral sucker relatively large with thin margins; nuchal constriction distinct; neck and abdomen continuous; abdomen narrowing abruptly to provide base for large caudal sucker; caudal sucker equal to or slightly larger than maximal body width. Richardson (1970) described the internal anatomy: male system simple, functional bursa and muscular organ lacking; testes five pairs; postcaeca independent; intestine without diverticula.

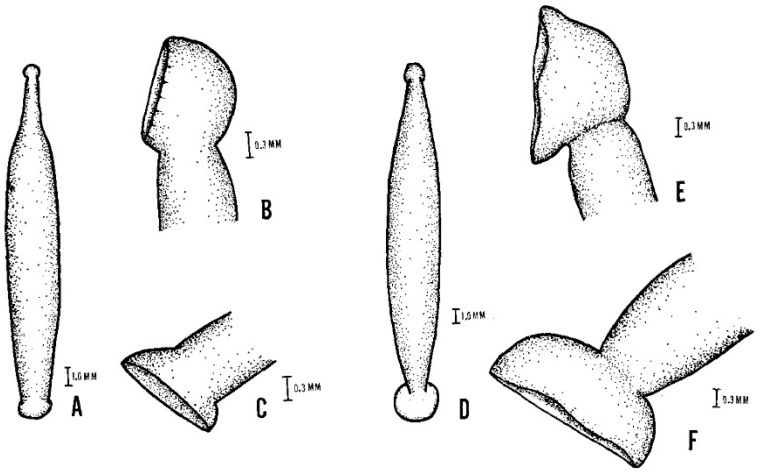

Figure 7. (A)–(C) holotype of *Austrobdella rapax*, Vineyard Sound, Massachusetts (USNM 14250); (D)–(F), holotype of *Malmiana nuda*, St. Johns, Newfoundland (USNM 42566); (A), (D) dorsal views; (B), (E) lateral views of oral suckers; (C), (F) lateral views of caudal suckers. Based on sketches made by RTS.

The external characters of many specimens from Woods Hole, Massachusetts, closely resemble this description (fig. 8(K)). Details of one individual from USNM 49574 are: total length, 20.0 mm; oral sucker width, 1.0 mm; maximal body width, 1.3 mm; caudal sucker width, 1.5 mm; five pairs of testes; intestine tortuous without diverticula; eyespots lacking. A dissection and one series of sections were made on two adults from Woods Hole. The reproductive system resembled that of the original description in having a pair of elongated seminal vesicles (= ejaculatory bulbs) connected to the atrial cornua by short ejaculatory duets. The postcaeca were clearly unfused, and there was a slight eversion of the bursa externally. The coelomic system consists of ventral and dorsal sinuses, both of which connect independently to the distinct lateral sinuses via tortuous transverse connectives.

Known distribution: Malmiana nuda was described from Newfoundland (Richardson, 1970), and the account by Verrill (1875) of "*Ichthyobdella*" sp. on a sculpin from Thimble Island, New England, is probably that of *M. nuda*. We found the leech off Newfoundland and Massachusetts.

Known hosts: Malmiana nuda was previously known from *Cottus* sp. (Verrill, 1875, as *Ichthyobdella* sp.) and *Myoxocephalus scorpius* (Richardson, 1970). We add to these an unidentified "sculpin," *Macrozoarces americanus*, and *Tautoga onitis*.

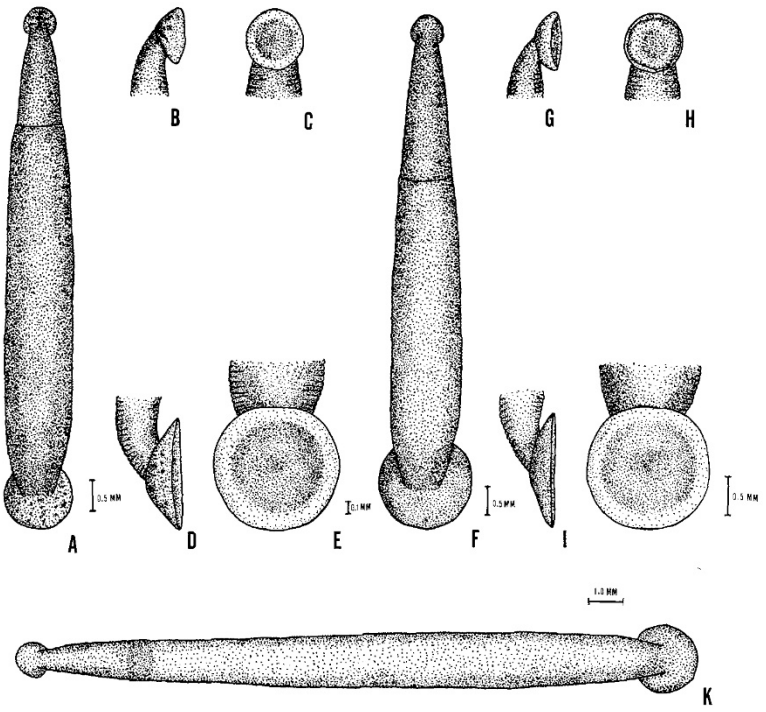

Figure 8. *Malmiana philotherma* (A)–(E), holotype from pelvic fin of *Trachinotus carolinus*, 15. vii. 1961, Dauphin Island, Alabama (USNM 51481); (F)–(J), from unknown host, 13. v. 1964, Buttonwood Canal, Everglades National Park, Florida (USNM 51484); (K) *Malmiana nuda*, Woods Hole, Massachusetts (USNM 49574); (A), (F), (K), dorsal views; (B), (G) lateral views of oral suckers; (C), (H) ventral views of oral suckers; (B), (F) lateral views of caudal suckers; (E), (J) ventral views of caudal suckers. Drawn by Ann F. Flowers.

Ecology: Mace & Davis (1972) investigated the energetics of the host-parasite relationship between *M. nuda* and *Myoxocephalus scorpius*. Oxygen demand by a 25 mg leech increased from about 3 μl O_2/hour at 3°C to about 8 μl O_2/hr at 10°C. They observed cocoons between May and July in their Newfoundland laboratory.

Dr. W. Threlfall kindly loaned us a large collection of marine leeches collected on sculpins from the east coast of Newfoundland, 32 km south of St. John's. All the leeches were *Malmiana nuda*, ranging in size from 6 to 36 mm. The vast majority were found on *Myoxocephalus scorpius*, with the others on *M. octodecemspinosus*. Most were found on the body, but a few, especially immature ones (below 12 mm), were found in the gill cavity. Some of the adult specimens had a conspicuously pigmented clitellum. Contrary to all the other specimens, two immature individuals (7 and 8 mm) had three pairs of faint but definite eyespots. Two pairs were located on the dorsal portion of the oral sucker, and the third pair was on the neck. The presence of eyespots had not been previously reported for *M. nuda*.

Extensive collections from Woods Hole, Massachusetts (USNM 49569–49579) suggest a seasonal occurrence for *Malmiana nuda*. Fourteen lots of leeches were taken between 1894 and 1915 from the sculpin (primarily from the head), with the exception of two lots, one

on 18. iv. 1911 from *M. americanus*, and the other on 26. iv. 1915 from *Tautoga onitis*. All were taken in different years between November 7–24 and April 18–May 9. That sampling occurred only at these times cannot be ruled out, but this apparent periodicity suggests a relationship between the leech and water temperature, as has been shown for *Calliobdella vivida* by Sawyer & Hammond (1973).

Another leech closely resembling *Malmiana nuda*, but differing in several important respects from it externally and in details of the digestive and reproductive systems, was found several times in Alabama, Mississippi, and southern Florida. It was first identified as *Piscicola funduli* in a popularized article by Causey (1953), who presented a photograph of a whole mount, clearly showing relative body dimensions, five pairs of testes, and other characteristics of the species. We believe the forms from Alabama-Mississippi and from southern Florida represent the same species, in spite of several differences described below.

Malmiana philotherma sp. nov.

Piscicola funduli: Causey, 1953: 19, fig. 2.

Holotype: (USNM 51481) (fig. 8 (A)–(E)) Body subcylindrical to flattened; maximal length, 9.0 mm; tegument translucent and smooth without gills, tubercles, or papillae; annulation obscure, basically 3(6) or 6 annulate with unequal subdivisions; oral sucker large, 0.55 mm in diameter; nuchal constriction 0.32 mm wide; clitellar constriction conspicuous anteriorly and fainter posteriorly; posterior end of body narrowing at point of attachment to 0.52 mm at caudal sucker; caudal sucker 1.15 mm wide, about equal to maximal body width of 1.1 mm; eyespots single pair on oral sucker; chromatophores large, black, and irregularly spaced dorsally on caudal sucker. Paratypes from Dauphin Island agree basically with this external description excepting some variation in size and annulation.

Internal anatomy: (based on cleared holotype, four cleared paratypes, and a series of sections of one paratype from Alabama): crop and small crop-caeca filled with nucleated blood; esophageal diverticula paired in region of ganglion X; postcaeca appearing fused, weak-walled, inconspicuous; intestine large, thick-walled, with five pairs of lateral diverticula, the first much larger than others; male system simple; testes five pairs; epididymis convoluted, located at ganglion XII; preatrial loop of vas deferens extending to ganglion IX lacking; vasa deferentia paired, enlarged at ganglion XI to form short ejaculatory ducts confluent with muscular paired atrial cornua; atrial cornua with anterior edges in regions of anterior clitellar constriction; medial atrium single, muscular, confluent with moderate-sized bursa; dorso-lateral muscles attaching to lateral margins of bursa; bursa opening between ganglia XI and XII; female system typical; coelom spacious, especially in region of ganglia.

Paratypes from Southern Florida: (USNM 51483–51484) (fig. 8 (F)–(J)) (specimens distorted from preservation). Typical specimen: body subcylindrical to flattened; body length 9.0 mm, narrowing to 0.95 mm wide at point of attachment to caudal sucker; tegument smooth, lacking pigment, gills, tubercles, papillae, eyespots, and ocelli; annulation obscure, about 6 (12–14); oral sucker relatively large, 0.9 mm wide; distinct nuchal constriction, 0.5 mm wide; clitellar constriction present; caudal sucker 1.5 mm wide, wider than maximal

body width of 1.25 mm. Internal anatomy (based on two whole specimens from Mississippi cleared with xylene and a sectioned one from Florida): crop and crop-caeca filled with nucleated blood; postcaeca large, fused, with fenestrae at ganglia; intestine with lateral diverticula and slightly convoluted walls; male system simple; five pairs of unusually small testes; epididymis convoluted, with spermatozoa; preatrial loop of vas deferens to ganglion IX lacking; ejaculatory ducts muscular; atrium single, medial; bursa moderate-sized; oviducts paired, with ova; body wall possibly delaminated midventrally in region of paired ovaries; coelom spacious, with lateral lacunae, with dorsal and ventral transverse lacunae in region of ganglia.

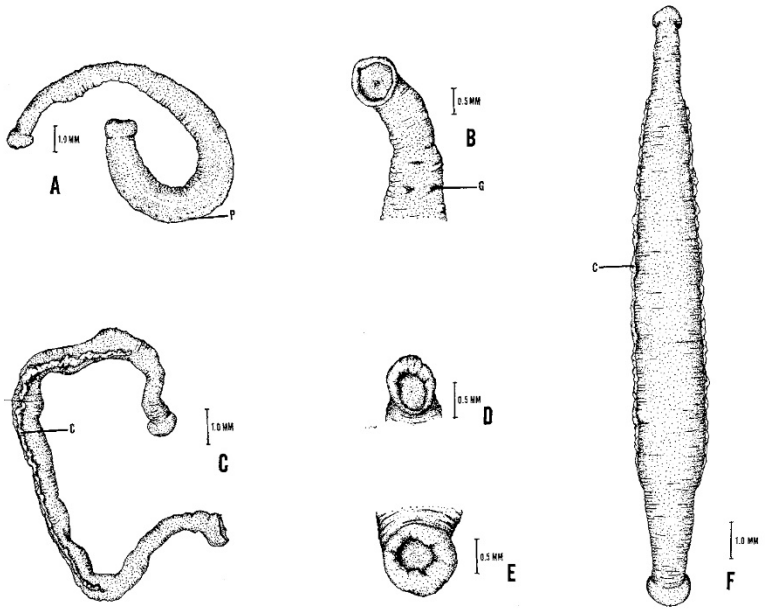

Figure 9. (A), (B) *Oxytonostoma typica*, from off Gloucester, Massachusetts, 9. xi. 1886, from "common skate" (USNM 1528). (A) lateral view; (B) ventral view of anterior end. (C)–(F), *Austrobdella rapax*, from Vineyard Sound, Massachusetts, August 1883, on "flounder" (USNM 14188). (C) poorly preserved specimen, drawn as found; (D) ventral view of oral sucker; (E) ventral view of caudal sucker; (F) artist's reconstruction of (C). c, lateral contractile lacuna; g, genital tubercle; p, papilla. Drawn by Ann F. Flowers.

Remarks: The Greek specific name *philotherma* means "warmth-loving" and refers to the predilection of the species for warmer environs compared with other members of the genus.

Type locality: Holotype from southwest end of Dauphin Island, Alabama, 15. vii. 1971, on pelvic fin of *Trachinotus carolinus* (38 mm SL), salinity about 40.0 ppt (USNM 51481). Paratypes from southwest end of Dauphin Island, Alabama, 15. vii. 1971, on gills and pelvic fins of two *T. carolinus* (49 and 51 mm SL); east end of Dauphin Island, Alabama, 27. vii. 1971, on anal fin of *T. carolinus*.

Other localities: MISSISSIPPI. Little Horseshoe, just north of Horn Island, 9. viii. 1972, on *Arius felis*, salinity 30.5 ppt; west end of Horn Island, 11. viii. 1974, one individual, 7 mm,

on underside of *Menticirrhus americanus*; ALABAMA. Mobile County, single immature specimen, host unknown (USNM 51387); FLORIDA. Buttonwood Canal, Everglades National Park, 11. iii, 13. v., and 2. vi. 1964, hosts, if any, unknown; salinity 33.7–40.0 ppt, and temperature 26.7°–29.4°C (USNM 51483–51484).

Ecology: In Mississippi, from one to seven specimens were found on three occasions in the mouth cavity of the host, twice on the pelvic fins, and once each from the body surface and the anal fin. It appears to prefer high saline (31–40 ppt) and warm water (26°–30°C).

Recently *M. philotherma* was discovered by Richard K. Wallace, Jr., of the Department of Marine Science, University of Puerto Rico, at Salinas near La Parguera, Puerto Rico. A full account of this find will be presented elsewhere, but briefly three individuals (22.0, 15.0, and 13.4 mm) were collected on 26. iii. 1974 immediately behind the pectoral fins of three Ballyhoo, *Hemiramphus brasiliensis*. The specimens (USNM 51485) are characterized by: elongate, flattened, smooth body; large caudal sucker (about equal to maximum body width); large, deeply cupped oral sucker, with one large pair of eyespots; a clitellar constriction; annulation 12(14); and uniformly green body pigment.

Four species of *Malmiana* have been described: *M. scorpii* (Malm, 1863), *M. brunnea* (Johansson, 1896), *M. stellata* (Moore, 1958) and *M. nuda* Richardson, 1970. Their relationships to one another and to members of related genera are unclear and a revision of this group of marine piscicolids is needed. *M. philotherma* differs from both *M. scorpii* and *M. brunnea* in not having six pairs of oral eyespots nor caudal ocelli. In addition *M. philotherma* (like *M. nuda*) has a transverse sinus connecting the ventral and lateral sinuses. *M. philotherma* differs from *M. nuda* in having one large pair of eyespots, a larger bursa, fused posterior crop caeca, and five pairs of intestinal diverticula. *M. philotherma* most closely resembles the poorly known *M. stellata* from Natal. It appears to differ from the latter species in having a more flattened body and a larger pair of eyespots. Unfortunately, nothing is known about the internal anatomy of this species and judgment must be reserved.

Species inquirendae

Piscicola zebra Moore, 1898: 555 (USNM 4818)

This species was taken in 1890 from the lips of *Petromyzon marinus* at Arichat, Cape Breton, Nova Scotia. According to Moore (1898), it has the general shape of species of *Piscicola*: caudal sucker nearly circular; midbody segments with 14 annuli; eyespots two pairs on oral sucker; ocelli about 14 in number on caudal sucker; pulsatile vesicles lacking. Type specimens (USNM 4818), poorly preserved and difficult to assess, had the following characters: body elongate, flattened; oral sucker small; nuchal constriction lacking; division of body into trachelosome and urosome lacking; midbody segments with 12 to 14 annuli; testes five pairs; caudal sucker about equal to maximal body width; paired whitish areas metamerically arranged along lateral margins; eyespots, on oral sucker, apparently one pair, other pigmentation lacking.

This species, unreported since the original description, was not encountered.

Discussion

Based upon the numerous new locality records presented in this study, the marine leeches from Newfoundland to the Gulf of Mexico display north-south geographic restrictions. Some species, *Ozobranchus branchiatus*, *O. margoi*, *Stibarobdella macrothela*, *Branchellion ravenelii*, *Trachelobdella lubrica*, and *Malmiana philotherma*, occur primarily or exclusively in the warm waters of the Gulf of Mexico and the extreme southeastern United States. The branchiae, tubercles, or small body size characterizing these species appear to be adaptations for increasing the ratio of surface area to volume, thereby increasing respiratory surfaces. A second group comprising *Myzobdella lugubris* and *Calliobdella vivida* occurs in the more temperate waters of the Gulf of Mexico, middle Atlantic coast, and New England; and similarly, *Branchellion torpedinis* occurs from the middle Atlantic coast to New England. A third group with *Malmiana nuda*, *Platybdella buccalis*, *Austrobdella rapax*, and *Oxytonostoma typica*, occurs primarily in the cold waters from Massachusetts and northward to at least Newfoundland. This group shows close affinity with the European leech fauna. The temperature optimum of *Trachelodella rugosa* remains unknown.

A similar trend emerges for the leeches with reference to ecological restrictions and tolerances to salinity. One group occurs exclusively in high-salinity water over 30 ppt: *Ozobranchus branchiatus*, *O. margoi*, *S. macrothela*, *B. ravenelii*, *T. lubrica*, *T. rugosa*, *P. buccalis*, *A. rapax*, *M. philotherma*, *O. typical*, and *M. nuda*. The euryhaline *C. vivida* and *M. lugubris* are both from brackish waters (0 to 25 ppt). *Calliobdella vivida*, but not *M. lugubris*, can survive indefinitely in full-strength sea water. On the other hand, *M. lugubris*, but not *C. vivida*, can survive indefinitely in freshwater.

One reason that marine leeches may have escaped much attention is the marked seasonality displayed by some species. For example, *C. vivida* is abundant from December through April and yet practically absent during the remainder of the year. This seasonality appears to relate with temperature and reproductive cycle. On the other hand, the common *M. lugubris* breeds primarily in the summer and early autumn but continues breeding at a low level throughout the year except mid-winter. In any case, our marine leeches, toward the end of their reproductive seasons, leave their host after a blood meal, deposit cocoons on a solid substratum, such as shells, rocks, or a crab, and then die. Two exceptions to this rule are *O. branchiatus* and *O. margoi* from sea turtles, which deposit cocoons upon their hosts.

In our study, *M. lugubris*, *S. macrothela*, and *C. vivida* were found on various crustacean hosts: *Callinectes sapidus*, *Palaemonetes pugio*, *Palaemonetes* sp., *Penaeus aztecus*, *P. setiferus*, *Neomysis americanus*, and unidentified crabs. With the exception of *C. sapidus*, on which *M. lugubris* deposits its cocoons, these crustacean hosts probably act primarily as a means of dispersal. There is no reason to believe the leeches ever feed on these crustaceans (see Meyer & Barden, 1955). Even though Hutton & Sogandares-Bernal (1959) reported *M. lugubris* associated with a pathological condition of blue crabs, we have examined thousands of infested crabs without seeing such a relationship. *Myzobdella lugubris* and *C. vivida* were also found among oysters.

While not normally suspected as planktonic, marine leeches occasionally occur in the plankton (Rest, 1963; Sawyer & Hammond, 1973). We also found *C. vivida* on the night of 27. ii. 1973 wriggling at the surface of Davis Bayou, Mississippi.

The probable role of piscicolid leeches as the chief, if not exclusive, transmitter of blood parasites to marine fish has received increasing attention in recent years (Becker, 1970; Khaibulaev, 1970). Recent qualitative and quantitative surveys of marine fish infected with various species of *Trypanosoma*, *Cryptobia*, and *Haemogregarina* from the Bahamas and Florida (Saunders, 1954, 1955, 1958a, 1958b, 1959a, 1959b, 1964), New England (Strout, 1965; Laird & Bullock, 1969), and Newfoundland (Khan, 1972; So, 1972) reveal that the hosts correspond remarkably well with those infested by leeches in the same areas. This correlation corroborates parasitological evidence that marine piscicolids are probably vectors of blood parasites. Although several of the above workers have implicated marine leeches as chief vectors, experimental proof is still lacking.

In the three major areas where the authors collected leeches, they also encountered haematozoa in fishes. In the York River, Virginia, *Sphoeroides maculatus* harbored a trypanosome as well as *Calliobdella vivida*. Several other Chesapeake Bay fishes were infected with blood parasites; however, they were not known to be associated with leeches.

In South Carolina, a haemogregarine, possibly *Haemogregarina brevoortiae* Saunders, 1964, occurred in the crop of *C. vivida*.

At least three species of haemoflagellates, including species of *Cryptobia* and *Trypanosoma* were encountered in Mississippi. *Paralichthys lethostigma*, *Micropogon undulatus*, *Mugil cephalus*, *Citharichthys spilopterus*, and *Trachinotus carolinus* were each infected by one of these. Also observed were at least three species of *Haemogregarina*, one of which infected *Raja eglanteria*, *M. cephalus*, *P. lethostigma*, *Trinectes maculatus*, *Achirus lineatus*, or *Symphurus plagiusa*. Notable is that all these hosts harboring blood parasites in Mississippi were hosts for leeches. Even though *C. spilopterus*, *A. lineatus*, and *S. plagiusa* were not listed in the text as hosts, all were observed to possess living leeches. Most of those leeches, either not saved or lost, were *M. lugubris*, but a few were *C. vivida*.

Reports on the haematozoa from the three regions will be published later.

Summary

(1) The marine leeches of the family Piscicolidae from Newfoundland to Texas are reviewed with emphasis on those of the southern United States from Virginia to Mississippi. In addition to an illustrated key and bibliography, a diagnosis, synonymy, references to known distribution, host-records, and other biological observations are included for each species.

(2) Fourteen valid species were encountered: *Ozobranchus branchiatus* (Menzies, 1791); *O. margoi* (Apathy, 1890); *Stibarobdella macrothela* (Schmarda, 1861); *Branchellion torpedinis* Savigny, 1822; *B. ravenelii* (Girard, 1850); *Trachelobdella lubrica* (Grube, 1840); *T. rugosa* Moore, 1898; *Calliobdella vivida* (Verrill, 1872); *Platybdella buccalis* Nigrelli, 1946; *Oxytonostoma typica* Malm, 1863; *Myzobdella lugubris* Leidy, 1851; *Austrobdella rapax* (Verrill, 1873); *Malmiana nuda* Richardson, 1970; and *Malmiana philotherma* sp. nov. *Trachelobdella rugosa*, *Austrobdella rapax*, and *Platybdella buccalis* are reported for the first time since their original descriptions. *T. lubrica* and *O. typica* are reported for the first time from the American side of the Atlantic.

(3) These marine leeches can be divided geographically into northern and southern species, and ecologically into brackish water and high-salinity species. They often display

marked seasonality associated with temperature and reproductive cycles. They occasionally occurred on crustaceans for dispersal and for cocoon deposition. Marine leeches probably serve as vectors for blood parasites of marine fish. Some hosts for haematozoa are presented.

(4) One new species, *Malmiana philotherma*, is described from Alabama, Mississippi, and southern Florida. It is similar to *M. nuda* and can be characterized by the following: body small and slightly flattened; tegument smooth without tubercles, papillae, or gills; midbody segments with 3(6) to 6 annuli; oral and caudal suckers large and distinct from body; oral sucker with one pair of eyespots; caudal sucker about equal to maximal body width; postcaeca fused; male system simple with five pairs of testes, convoluted epididymis, and moderate-sized bursa.

(5) The species *Oxytonostoma typica* is reported from off Massachusetts to the Bay of Fundy on the skate *Raja ocellata*. It is characterized by the following: body cylindrical to subcylindrical; no trachelosome nor pulsatile vesicles; minute white metameric tubercles on most annuli, especially dorsally; caudal sucker strongly terminal, deeply cupped; oral sucker only slightly smaller than caudal sucker; a small teat-like papilla on either side of the female gonopore.

(6) Three new combinations are made: *Calliobdella vivida*, formerly *Cystobranchus vividus* Verrill, 1872; *Myzobdella patzcuarensis*, formerly *Illinobdella patzcuarensis* Caballero, 1940; and *Austrobdella rapax*, formerly *Pontobdella rapax* Verrill, 1873. One genus is synonymized: *Illinobdella* Meyer, 1940, synonym of *Myzobdella* Leidy, 1851. Six species are synonymized: *Calliobdella carolinensis* Sawyer and Chamberlain, 1972, synonym of *Calliobdella vivida* (Verrill, 1872); *Ichthyobdella funduli* Verrill, 1872, *Illinobdella alba* Meyer, 1940, *I. elongata* Meyer, 1940, *I. richardsoni* Meyer, 1940, and *I. moorei* Meyer, 1940 are synonyms of *Myzobdella lugubris* Leidy, 1851. Other combinations of those species and misidentified specimens are also pointed out.

(7) *Myzobdella lugubris*, the most common and most widely distributed species encountered, is reported from brackish and fresh waters. Many original biological and taxonomic observations, including the role of temperature and salinity of the water in the deposition of cocoons, hatching of young, and presence of the adults, are presented.

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