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Virginia León-Règagnon, Gerardo Pérez-Ponce de León, Daniel R. Brooks

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Virginia León-Règagnon
Universidad Nacional Autónoma de México

Gerardo Pérez Ponce de León
Universidad Nacional Autónoma de México, ppdleon@servidor.unam.mx

Daniel R. Brooks
University of Toronto, dnlbrooks@gmail.com

León-Règagnon, Virginia; Pérez Ponce de León, Gerardo; and Brooks, Daniel R., "Phylogenetic Analysis of the Bunocotylinae Dollfus, 1950 (Digenea: Hemiuridae)" (1988). *Faculty Publications from the Harold W. Manter Laboratory of Parasitology*. 288.
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PHYLOGENETIC ANALYSIS OF THE BUNOCOTYLINAE DOLLFUS, 1950 (DIGENEA: HEMIURIDAE)

Virginia León-Règagnon, Gerardo Pérez-Ponce de León*, and Daniel R. Brooks

Center for Historical Ecology and Biodiversity, Department of Zoology, University of Toronto, 25 Harbord St. Toronto, Ontario, Canada M5S 3G5

ABSTRACT: The phylogenetic analysis of the 16 recognized genera in the Bunocotylinae, based upon 30 morphological transformation series, produced 2 most parsimonious trees, each with a consistency index of 0.62. The monophyly of the group is supported by 6 synapomorphies. *Ahemiurus, Aphanuroides, Aphanurus, Myosaccium,* and *Indoderogenes* separate independently in the basal part of the tree. *Saturnius* and *Bunocotyle* separate next, forming a clade. *Machidatrema, Duosphincter, Theletrum,* and *Monolecithotrema* separate independently; and in the most derived part of the tree *Opisthadena* + *Neopisthadena* + *Mitrostoma, Genolinea,* and *Neotheletrum* grouped together form a clade. Optimization of hosts and geographic distribution onto the 2 most parsimonious trees suggests that the bunocotylines originated from an ancestor that was host specific to fishes of the Clupeidae and was distributed in the Tethys Sea.

Digeneans of the order Hemiuriformes (sensu Brooks et al., 1985) are 1 of the most common and diverse groups parasitizing marine fish. One of the the most diverse and widely distributed hemiuriform taxa is the Buonocotylinae, generally considered a member of the Hemiuridae. Like that of most digeneans, the classification of the bunocotylines has been unstable historically. Yamaguti (1971) included 4 genera in the subfamily: *Bunocotyle* Odhner, 1928, *Saturnius* Manter, 1969, *Theletrum* Linton, 1910, and *Pseudobunocotyla* Yamaguti, 1935. Gibson and Bray (1979) established the Bunocotylidae and subdivided it into 4 subfamilies: Bunocotylinae, comprising *Bunocotyle* Odhner, 1928 and *Saturnius* Manter, 1969; Aphanurinae, comprising *Aphanurus* Looss, 1907, *Ahemiurus* Chauhan, 1954, *Aphanuroides* Nagaty and Abdel-Aal, 1962, *Duosphincter* Manter and Pritchard, 1960, and *Myosaccium* Montgomery, 1957; Opisthadeninae, comprising *Opisthadena* Linton, 1910, *Genolinea* Manter, 1925, *Mitrostoma* Manter, 1954, *Neotheletrum* Gibson and Bray, 1979; and Theletrinae, comprising *Theletrum* Linton, 1910, *Indoderogenes* Srivastava, 1937 and *Monolecithotrema* Yamaguti, 1970. In their evolutionary scenario, Gibson and Bray (1979) depicted the Bunocotylidae as the sister group of the Hemiuridae. Brooks et al. (1985) provided the first phylogenetic systematic analysis of the group , using the taxa and characters listed by Gibson and Bray (1979). The phylogenetic study indicated that Gibson and Bray's conception of the Hemiuridae was paraphyletic if the Bunocotylidae were excluded from it; hence, Brooks et al. (1985) returned the Bunocotylidae sensu Gibson and Bray to subfamilial status within a monophyletic Hemiuridae. The phylogenetic analysis of the Bunocotylinae, however, failed to provide any synapomorphies supporting the monophyly of that particular group. Since Gibson and Bray's (1979) study, 3 additional genera belonging to this group have been established: (1) *Neopisthadena* Machida, 1980; (2) *Neoaphanurus* Tang, Shi, Cao, Guan and Pan, 1983; and (3) *Machidatrema* León-Règagnon, 1997.

In this study, the monophyly of the Bunocotylinae is assessed and a phylogenetic hypothesis for the genera included in the group is proposed.

MATERIALS AND METHODS

Specimens examined

All available literature as well as the following museum specimens were examined for comparison (accession numbers in parentheses): Colección Nacional de Helmintos, Instituto de Biología, UNAM, México (CNHE): *Genolinea laticauda* (807); *Myosaccium ecaude* (2791–2797); *Neotheletrum gravidum* (999); *Neotheletrum lissosomum* (1517); *Opisthadena dimidia* (899, 2631, 2632, 898, 1379, 1483); *Parahemiurus merus* (2633–2641). United States National Parasite Collection (USNPC): *Duosphincter zancli* (39167); *Genolinea dactylopargi* (49151); *Genolinea anura* (49177); *Genolinea montereyensis* (36952); *Genolinea noblei* (60290); *Machidatrema frontilatum* (63328); *Machidatrema kyphosi* (63748); *Mitrostoma nothoteniae* (49150); *Myosaccium ecaude* (38185); *Myosaccium opisthonemae* (39393); *Neotheletrum gravidum* (9369), *N. lissosomum* (9368), *Neotheletrum magnasaccum* (39500), *Neotheletrum pomacentri* (60292); *O. dimidia* (8489); *Opisthadena bodegensis* (37338); *Opisthadena kyphosi* (63790); *Saturnius segmentatus* (71219); *Saturnius maurepasi* (73270); *Saturnius mugilis* (63747); *Saturnius belizensis* (74167); *Saturnius papernai* (73271); *Theletrum fustiforme* (8500, 39392). Harold W. Manter Laboratory (HWML): *N. lissosomum* (120, 121); *N. gravidum* (122, 123, 124, 125); *M. frontilatum* (631); *T. fustiforme* (473, 124642). Meguro Parasitological Museum (MPM): *Aphanurus harengulae* (22700); *Aphanurus caesionis* (22703); *Aphanurus dorosomatis* (22702); *M. kyphosi* (15184); *Monolecithotrema kala* (15187); *O. kyphosi* (15245); *S. mugilis* (15180). National Science Museum, Tokyo, Japan (NSMT): *M. kyphosi* (Pl3161a, Pl2292a); *Machidatrema chilostoma* (Pl2292b, Pl2234a); *Machidatrema akeh* (Pl3184); *M. kala* (Pl2140, Pl3177, Pl3794); *Neopisthadena habei* (Pl2293); *O. dimidia* (Pl2234b). It was impossible for us to examine specimens from *Aphanuroides, Indoderogenes, Ahemiurus,* and *Bunocotyle,* because these are monotypic and in the original descriptions it is not indicated if types were deposited in a collection; in these cases, available literature was consulted.

Phylogenetic analyses

Phylogenetic analyses were performed using the methods of phylogenetic systematics (Hennig, 1966; Wiley et al., 1991). Results were confirmed quantitatively using the PAUP (phylogenetic analysis using parsimony) computer program version 3.1.1. (Swofford, 1993), run on a Macintosh Power Mac 8500. The following options were specified: (1) characters 19 and 25 ordered; (2) out groups: plesiomorphic conditions determined using the out-group method (Watrous and Wheeler, 1981; Maddison et al., 1984) by the states observed in the genera *Hemiurus, Parahemiurus,* and *Anahemiurus* (Hemiurini), recognized as the sister group of bunocotylids (Gibson and Bray, 1979; Brooks et al., 1985); (3) optimization: acctran, deltran; and (4) tree-building algorithms: branch and bound.

Character argumentation

We used the following characters and their states in phylogenetic analysis. Characters are listed in order of their appearance in Table I. 0 = plesiomorphy; 1, 2 = apomorphies.

TABLE I. Data matrix for phylogenetic analysis of Bunocotylinae genera.*

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
O.G.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Buno	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	2	1	0	1	0	0	2	1	1	?	0	1	1	1
Satu	1	1	1	1	1	1	0	0	0	0	1	0	0	1	1	0	2	1	0	1	0	0	2	1	1	?	0	0	1	2
Apha	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	?	0	0	0	1
Ahem	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	1	0	0	0	1	0	0	0	1	?
Ades	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	1	1	0	1	1	?
Duos	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	2	1	1	1	0	0	0	0	1	2	0	0	0	2
Myos	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	2	0	0	0	0	1	1	0	0	0	1
Opis	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	2	0	2	0	1	1	1	0	1	0	0	0	0	2
Neop	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	2	0	1	0	1	1	1	0	1	0	0	0	0	2
Geno	1	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	2	0	0	0	1
Mitr	1	1	0	0	0	0	1	0	1	1	1	0	0	1	1	0	2	0	1	0	0	1	1	0	1	1	0	0	0	1
Neot	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	2	1	1	1	0	1	1	0	2	2	0	0	0	1
Thel	1	1	0	0	0	0	1	1	0	0	1	0	0	1	1	0	2	1	1	1	0	0	0	0	1	2	0	0	1	2
Indo	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	?	0	1	0	0	0	0	1	1	0	1	0	?
Mono	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	1	1	1	0	0	0	1	1	?	0	0	0	1
Mach	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	2	1	1	2	0	0	0	0	1	1	1	0	0	2

* Characters are numbered as in the text; for description of characters and polarity arguments, see text. 0 = plesiomorphic condition; 1,2 = apomorphic conditions; ? = unknown. O.G. (out group) = Hemiurini (Hemiurus, Parahemiurus, Anahemiurus); Buno = Bunocotyle; Satu = Saturnius; Apha = Aphanurus; Ahem = Ahemiurus; Ades = Aphanuroides; Duos = Duosphincter; Myos = Myosaccium; Opis = Opisthadena; Neop = Neopisthadena; Geno = Genolinea; Mitr = Mitrostoma; Neot = Neotheletrum; Thel = Theletrum; Indo = Indoderogenes; Mono = Monolecithotrema; Mach = Machidatrema.

(1) Ecsoma. The absence of an ecsoma is plesiomorphic for all digeneans. An ecsoma is present in all members of the Hemiuridae except Bunocotylinae and is unique among digeneans in that family. In order to include the Bunocotylinae in the Hemiuridae, some authors have described vestigial ecsomas, but our examination of specimens and illustrations from the literature leads us to believe that at times the large excretory pore typical of the bunocotylines has been confused with a small invaginated ecsoma. Phylogenetic analysis of the hemiuriforms indicates that its absence is apomorphic within the Hemiuridae; we therefore code this apparent secondary loss as apomorphic in this analysis. 0 = present; 1 = absent.

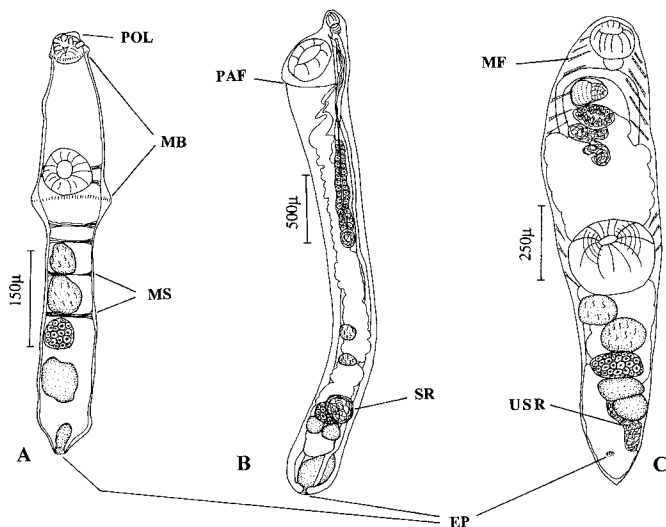(2) Cuticular plications. The absence of cuticular plications is plesiomorphic for all digeneans. Phylogenetic analysis of the hemiuriforms indicates that its absence is apomorphic within the Hemiuridae; we therefore code this apparent secondary loss as apomorphic in this analysis. 0 = present; 1 = absent.

(3) Muscular belt surrounding body at level of acetabulum (Fig. 1). 0 = absent; 1 = present. This structure, present in Bunocotyle and Saturnius, differs from the postacetabular fold described in Opisthadena, Neopisthadena, Theletrum, and Mitrostoma, even though the same term, "postacetabular ridges," has been applied to both conditions.

(4) Muscular belt surrounding body at level of oral sucker (Fig. 1). 0 = absent; 1 = present.

(5) Internal muscular septa (Fig. 1). 0 = absent; 1 = present.

(6) Muscular papillae on oral sucker. 0 = absent; 1 = present.

(7) Postacetabular fold (Fig. 1). 0 = absent; 1 = present.

(8) Cuticular papillae. 0 = absent; 1 = present.

(9) Muscular sphincter in acetabulum. 0 = absent; 1 = present.

(10) Preacetabular pit. 0 = absent; 1 = present.

(11) Preoral lobe. 0 = absent; 1 = present.

(12) Strong muscle fibers in forebody (Fig. 1). 0 = absent; 1 = present.

(13) Excretory pore position (Fig. 1). 0 = terminal or subterminal; 1 = far from the posterior end, ventral.

(14) Excretory pore size. 0 = inconspicuous; 1 = large.

(15) Excretory vesicle. 0 = elongate; 1 = bulbous.

(16) Intestinal ceca. 0 = ending separated; 1 = united.

(17) Testes position. 0 = symmetric; 1 = oblique; 2 = tandem.

(18) Seminal vesicle position. 0 = postacetabular; 1 = preacetabular.

(19) Seminal vesicle shape. 0 = subspherical; 1 = elongate; 2 = elongate, coiled, enclosed in a seminal sac.

(20) Pars prostatica. 0 = long; 1 = short; 2 = prostatic vesicle.

(21) Ejaculatory duct. 0 = absent; 1 = present.

(22) Uterine seminal receptacle (Fig. 1). 0 = present; 1 = absent. The seminal fluid storage structures have been used as important taxonomic characters in this group. In most of the hemiuriforms, the proximal end of the uterus functions as a seminal receptacle (uterine seminal receptacle). In some genera of bunocotylines a specialized structure has developed to fulfill that function.

(23) Structures derived from Laurer's canal (Fig. 1). 0 = Juel's organ; 1 = seminal receptacle; 2 = Laurer's canal derivatives lacking. Laurer's canal is present in some groups of hemiuriforms, including the Azygi-

FIGURE 1.   Selected structures of bunocotylines. A. Saturnius sp. B. Opisthadena sp. C. Machidatrema sp. EP = excretory pore; MB = muscular belt; MF = muscle fibers; MS = muscular septa; PAF = postacetabular fold; POL = preoral lobe; SR = seminal receptacle; USR = uterine seminal receptacle.

idae, Accacoeliidae, and Hirudinellidae. In others, such as the Hemiuridae, this structure has modified into a Juel's organ, which is glandular, has a central vesicle where it has been proposed that excess seminal and vitelline material is stored, degraded, and reabsorbed, and which has no connection to the exterior. In some Bunotocylinae, the Juel's organ has been modified further, losing its glandular nature and becoming a seminal receptacle that replaces the uterine seminal receptacle. *Bunocotyle* and *Saturnius* lack Juel's organ or seminal receptacle.

(24) Number of vitelline masses. 0 = 2; 1 = 1. In some species of bunocotylids 3 vitelline masses have been described, but when examining the specimens and drawings, we noticed that the anterior mass was strongly bilobed, which was misinterpreted as the existence of 3 masses.

(25) Shape of vitelline masses. 0 = 2 slightly lobed masses, with 3 and 4 lobes respectively; 1 = 2 entire masses. In 2 *Machidatrema* species vitelline masses may present slightly irregular margins; 2 = bilobed anterior mass.

(26) Vitelline mass position. 0 = symmetric; 1 = oblique; 2 = tandem.

(27) Hermaphroditic duct. 0 = not divided; 1 = divided in 2 regions. In members of *Machidatrema*, the distal region of the hermaphroditic duct is strongly muscular and may be extruded as a temporary sinus organ. This differs from the genital atrium described by Gibson and Bray (1979), for several species of hemiurids.

(28) Sinus sac. 0 = present; 1 = absent.

(29) Sinus organ. 0 = presence of a temporary sinus organ; 1 = absent.

(30) Genital pore location. 0 = at level of oral sucker; 1 = at level of pharynx; 2 = posterior to pharynx.

RESULTS

In this analysis, all 14 genera in the Bunocotylinae sensu Brooks et al. (1985, 1989) and the Bunocotylidae sensu Gibson and Bray (1979), as well as *Neopisthadena* and *Machidatrema* were considered valid. In the original diagnosis of the *Neoaphanurus*, Tang et al. (1983) reported a seminal vesicle occupying the posterior region of the body and a seminal receptacle. Examination of original description and drawings showed that most of the traits of these specimens match with those of *Aphanurus*, with the exception of the 2 aspects mentioned above. Within the Hemiuridae, the seminal vesicle is always pretesticular; for this reason we consider that the structure described as a seminal vesicle to be actually a coiled uterine seminal receptacle (both structures look similar when filled with sperm). A uterine seminal receptacle is normally associated with a Juel's organ and not with a seminal receptacle, and these 2 structures may easily be confused with each other. We believe this species belongs to the genus *Aphanurus*, but as the specimens were not available, we consider this taxon as a species inquirendae and did not include it in the analysis.

The phylogenetic analyses of the 16 taxa we considered valid produced 2 equally parsimonious trees, with a consistency index of 0.62 (58 transformations to 36 possible apomorphies), excluding character 29 from the analysis (Fig. 2). This character (the presence or the absence of a sinus organ) was originally included in the analysis, producing 10 equally parsimonious trees, each with a consistency index of 0.597. Two of those trees correspond with the 2 trees shown in Figure 2. The other 8 differed in the position of the 5 basal genera (*Ahemiurus, Aphanuroides, Aphanurus, Myosaccium,* and *Indoderogenes*). In 6 of the trees, *Ahemiurus* and *Aphanuroides* formed a clade as the sister group of the rest of the taxa, supported only by the lack of a sinus organ. The sinus organ is a very difficult structure to be observed when retracted. We were unable to

examine specimens of the relevant genera, and original descriptions are very poor, so we excluded this character from the analysis because it is possible that the sinus organ was present but was not observed in those genera where it has been described as absent. When this character was excluded, the relationships of those 5 basal taxa were highly stable, and the 2 resulting trees differed only in the position of the *Genolinea* in relation to the clade *Opisthadena* + *Neopisthadena* + *Mitrostoma* and *Neotheletrum*. This suggests to us that *Genolinea*, as presently constituted, may not be monophyletic (see Pérez-Ponce de León and Brooks [1995] for a similar situation involving *Pleurogonius* within the Pronocephalidae).

DISCUSSION

The monophyly of the Bunocotylinae is supported by the following synapomorphies: 1 (lack of ecsoma), 14 (large excretory pore), 15 (bulbous excretory vesicle), 17 (testes in tandem), 25 (entire vitelline masses), and 30 (genital pore at the level of pharynx or posterior to it). The consistency index (0.621) is lower than those obtained for other groups of digeneans (0.71 for the general Digenea data matrix; Brooks and McLennan, 1993a, 1993b) and particular groups of bunocotylids (León-Règagnon et al., 1996; León-Règagnon, 1997). A high proportion of the homoplasy in the group is concentrated in the clade *Mitrostoma* + *Neopisthadena* + *Opisthadena*. When this group is removed from the analysis, the consistency index rises to 0.74, but whether or not these taxa are included, the relationships among all other members of the subfamily remained consistent. This suggests that the clade *Mitrostoma* + *Neopisthadena* + *Opisthadena* exhibits an unusual amount of homoplasy at the generic level. At the specific level, however, this pattern is not repeated (see León-Règagnon et al., 1996). The proportion of evolutionary losses observed in our analyses (15.5%) is comparable to those reported by Brooks and McLennan (1993a, 1993b) (12%), supporting their conclusion that parasites do not show high levels of evolutionary simplification.

The polytomy formed by the groups *Neotheletrum, Genolinea,* and *Opisthadena* + *Neopisthadena* + *Mitrostoma* is probably due to extreme interspecific morphological variability among members of *Genolinea*, which is the bunocotyline genus with the largest number of nominal species, many of which have been poorly described. A phylogenetic analysis of the species of this genus would help to solve this polytomy. Comparing the generic grouping in our analysis with those proposed by Gibson and Bray (1979) (Fig. 3), we note that the groups formed by *Bunocotyle* + *Saturnius* (Bunocotylinae sensu Gibson and Bray, 1979) and *Opisthadena* + *Mitrostoma* + *Genolinea* + *Neotheletrum* (Opisthadeninae sensu Gibson and Bray, 1979) were maintained. *Monolecithotrema,* and *Theletrum* (members of the Theletrinae sensu Gibson and Bray, 1979) are paraphyletic to the clade formed by *Opisthadena* + *Neopisthadena* + *Mitrostoma* + *Genolinea* + *Neotheletrum.* *Duosphincter* was grouped in the Aphanurinae, which, according to their analysis is paraphyletic at the base of the tree, but our analysis places it as the sister group of the clade *Opisthadena* + *Neopisthadena* + *Mitrostoma* + *Genolinea* + *Neotheletrum,* *Monolecithotrema* and *Theletrum,* which are nonbasal members of the subfamily. The clade *Bunocotyle* + *Saturnius* is the sister group of those taxa plus *Machidatrema,* instead of being the
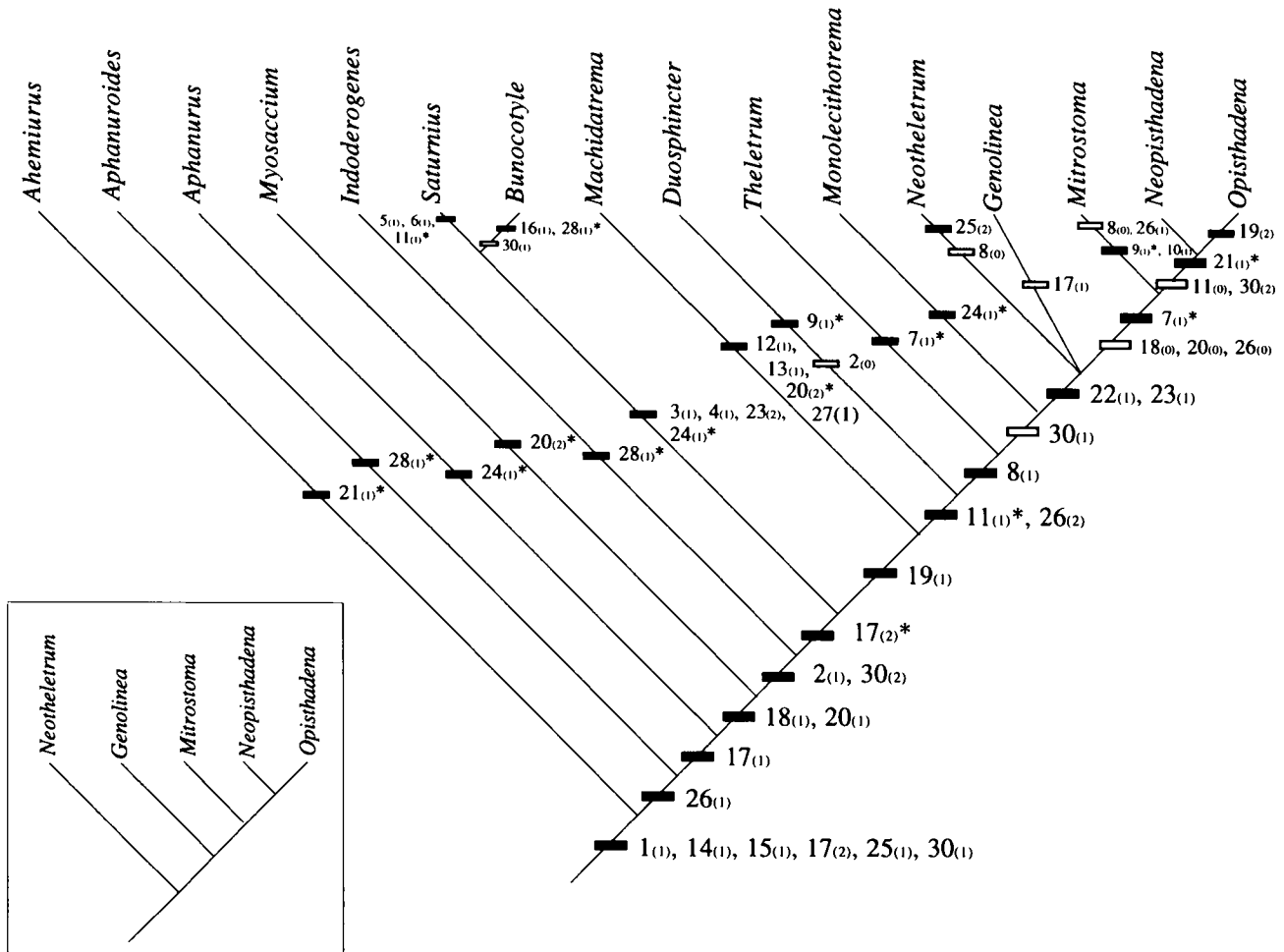
FIGURE 2. Phylogenetic trees for genera in the subfamily Bunocotylinae. Large tree is the consensus tree and also 1 of the 2 equally parsimonious trees. Insert is alternative equally parsimonious tree. Numbers accompanying slash marks on tree indicate apomorphic traits supporting each branch (character number followed by character state in parentheses; empty slashes indicate reversals; * = homoplasy). For character identity refer to text. Characters 20 and 26 are ambiguous and can be optimized in more than 1 way without changing the topology of the tree.
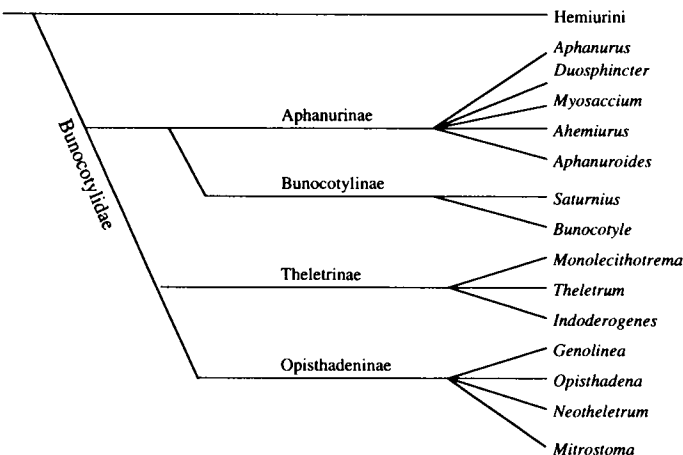
FIGURE 3. Evolutionary scheme of bunocotylines proposed by Gibson and Bray (1979).

sister group of the Aphanurinae (sensu Gibson and Bray, 1979). Our analysis supports the polarization of the Laurer's canal derivatives proposed by Gibson and Bray (1979) (Juel's organ may have given rise to a seminal receptacle or may have been lost).

On the contrary, it does not support the idea that there is a linear tendency toward reduction in body size, and this was the primary reason some of the groups proposed by Gibson and Bray were not maintained. This is not surprising, because the concept of linear macroevolutionary trends is a legacy of the orthogenetic, rather than Darwinian, evolutionary ideas that pervaded parasitological systematics during the period 1890–1940, and which continue to be expressed today (see Brooks and McLennan, 1993a). The phylogenetic hypothesis for the Hemiuridae proposed by Brooks et al. (1985, 1989) was based upon the same characters used by Gibson and Bray (1979) in their diagnoses. The difference in results is due to the use of phylogenetic methods by Brooks et al. (1985) and of intuition by Gibson and Bray (1979). We have noticed that the monophyly of some of the taxa are supported by characters that are greatly variable within them. It is necessary to perform a phy-
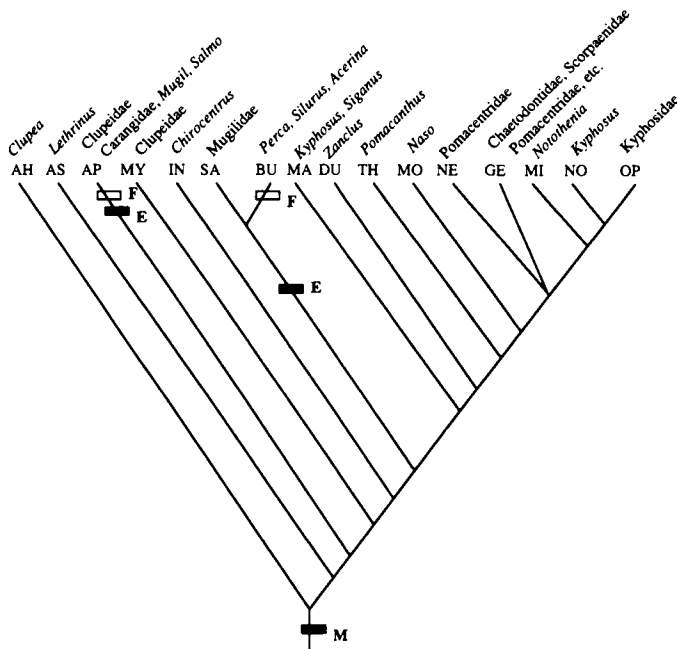
FIGURE 4. Definitive host group and primary habitat (M = marine; E = estuarine; F = freshwater) optimized onto phylogenetic tree for bunocotyline genera. The tree supports 2 separate invasions to estuarine and then freshwater habitats. AH = *Ahemiurus*; AS = *Aphanuroides*; AP = *Aphanurus*; MY = *Myosaccium*; IN = *Indoderogenes*; SA = *Saturnius*; BU = *Bunocotyle*; MA = *Machidatrema*; DU = *Duosphincter*; TH = *Theletrum*; MO = *Monolecithotrema*; NE = *Neotheletrum*; GE = *Genolinea*; MI = *Mitrostoma*; NO = *Neopisthadena*; OP = *Opisthadena*.
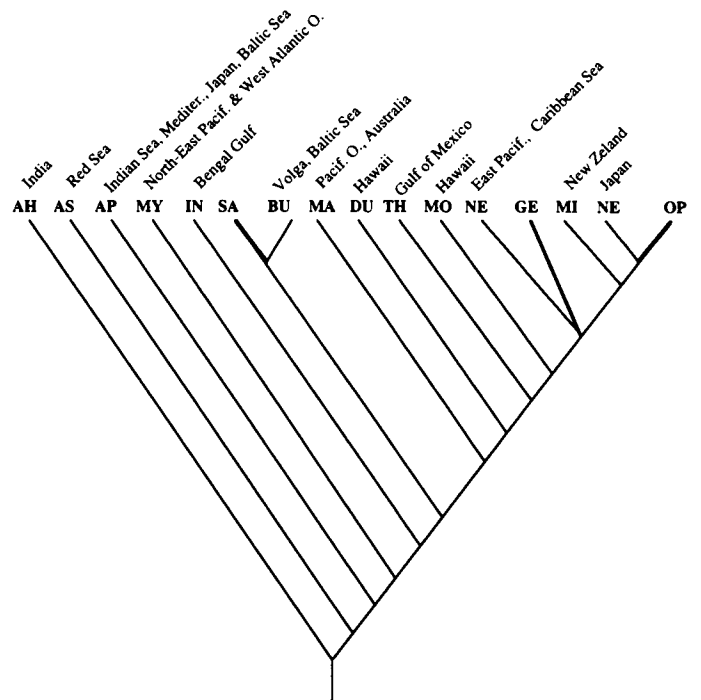

FIGURE 5. Optimization of geographical distribution onto phylogenetic tree of genera of Bunocotylinae. Bold lines indicate widely distributed taxa (Pacific Ocean, Australia, Indian Ocean, Mediterranean, and Gulf of México). AH = *Ahemiurus*; AS = *Aphanuroides*; AP = *Aphanurus*; MY = *Myosaccium*; IN = *Indoderogenes*; SA = *Saturnius*; BU = *Bunocotyle*; MA = *Machidatrema*; DU = *Duosphincter*; TH = *Theletrum*; MO = *Monolecithotrema*; NE = *Neotheletrum*; GE = *Genolinea*; MI = *Mitrostoma*; NO = *Neopisthadena*; OP = *Opisthadena*.

logenetic study of particular genera and species to obtain a classification scheme that reflects the genealogy of the taxa of this controversial group of digeneans.

Optimizing the definitive host taxa and habitat (marine, estuarine, or freshwater) onto the consensus tree (doing the same onto the alternative tree does not make any difference in the interpretation of results) (Fig. 4), we notice that the group is predominantly and primitively marine, and that most of the basal genera (*Ahemiurus, Aphanurus, Myosaccium*) inhabit mostly fishes of the family Clupeidae, the same as the outgroups. Species of *Aphanurus* have occasionally been recorded parasitizing euryhaline fish in *Mugil* and *Salmo*, possibly indicating some host-switching events coupled with habitat change. *Machidatrema* and its sister group parasitize a wide variety of perciform fishes. Only *Opisthadena* and *Neopisthadena* show pronounced host specificity, parasitizing only fishes of the Kyphosidae (León-Règagnon et al., 1996, 1997). The tree indicates that the clade *Bunocotyle* + *Saturnius* separated from its sister group as the result of a host-switching event associated with a change in habitat, from marine to estuarine or freshwater, in a manner similar to that observed in *Aphanurus*. The species of *Saturnius* are specific to the euryhaline *Mugil*, whereas species of *Bunocotyle* apparently colonized freshwater fishes.

Optimizing geographic distributions on the phylogenetic tree (Fig. 5) demonstrates that all basal groups, except *Myosaccium* and *Bunocotyle*, are restricted to Arabian Sea, Arabian Gulf, and Mediterranean Sea. *Saturnius* has a wide geographic distribution, corresponding to that of its fish hosts (*Mugil* spp.).

Machidatrema and its sister group also have a wide geographic distribution (east and west Pacific, New Zealand, Australia, the Gulf of México, Caribbean Sea, and Arabian Sea). The distribution of basal groups in the vicinity of the Arabian Sea, Arabian Gulf, and Mediterranean Sea is consistent with an hypothesis of origin in the Tethys Sea. Evolutionary radiation into the Pacific Ocean may have begun with the ancestor of *Bunocotyle* + *Saturnius* and of *Machidatrema* and its sister group. The colonization of the Gulf of México and Caribbean Sea by some taxa may have taken place before the appearance of Panama Isthmus as a barrier between Pacific and Atlantic Oceans, approximately 4 million yr ago (Lessios, 1979). This radiation may have been associated with host switching from clupeids into the most diverse and widely distributed order of fish, the Perciformes. The capability of colonizing hosts other than clupeids may have permitted the bunocotylines to increase their geographic distribution.

The biogeographic history of the Bunocotylinae is complex, as would be expected from parasites of marine organisms, whose vagility can produce complex biogeographic patterns (Pérez-Ponce de León et al., 1996). That is the case of Pronocephalidae, primitive and primarily parasites of marine turtles; Pérez-Ponce de León and Brooks (1995) discovered a biogeographic distribution pattern suggesting a combination of vicariance and dispersion during a long period of time. Hoberg (1995) found that the role of intermediate hosts (zooplanktonic Crustacea) in the isolation or maintenance of gene flow (and consequently speciation) of tetrabothriid cestode populations in-

habiting phocids in the Subarctic is insignificant, in contrast with that played by paratenic or definitive hosts (fish and phocids, respectively) with more restricted distribution, focused feeding habits, and established migratory patterns. Little is known about the life cycles of bunocotylines; presumably their intermediate hosts are copepods or chaetognaths as in other hemiurid groups (Køie, 1979; Køie and Lester, 1985). Only with the study of the biology of these worms and their intermediate and definitive hosts, in conjunction with species-level analyses of the various genera within the Bunocotylinae, will we be able to elucidate further the evolutionary history of this fascinating group.

ACKNOWLEDGMENTS

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