

PROTEOCEPHALIDEAN CESTODES FROM VENEZUELAN SILURIFORM FISHES, WITH A REVISED CLASSIFICATION OF THE MONTICELLIIDAE

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Abstract.—Specimens of proteocephalidean cestodes collected in siluriform fishes from the delta of the Orinoco River represent five species: *Proteocephalus* cf. *kyukyu*, *Nomimoscolex kaparari*, *Goezeella siluri*, *Amphoteromorphus praeputialis*, and *Choanoscolex abscissus*. The last species is reported in new collections for the first time since its description in 1896; it possesses cortical gonads and is thus a monticelliid. The delta of the Orinoco is a new locality for all five species. *Megalodoras irwini* is a new host for *P. kyukyu*, *Brachyplatystoma vaillanti* is a new host for *N. kaparari*, *Pseudoplatystoma fasciatum* is a new host for *C. abscissus*, and *Pseudocetopsis othonops* is a new host for *G. siluri* and *A. praeputialis*. Examination of these specimens allowed character analysis for a suite of morphological characters leading to a phylogenetic hypothesis for the monticelliids which is superior to the one proposed earlier by the first author.

Classification of the cestode order Proteocephalidea has been hampered by a lack of critical character analysis and by incomplete information regarding many taxa. Brooks (1978) summarized published data used to classify proteocephalideans based on a phylogenetic systematic analysis. In that study, the relationships of the genera comprising the family Monticelliidae LaRue, 1911, were marked by extensive parallel evolution. Postulates of parallel evolution stemming from phylogenetic analyses at the supra-specific level may be the result of (1) real parallel evolution, (2) para- and polyphyletic groupings or (3) inadequate character analysis.

Phylogenetic trees produced by cladistic analysis, and the classifications derived from them, are explicit hypotheses predicting certain distributions of characteristics among species. They can be tested by finding new characters and determining their distributions. If the new data are incongruent with previous observations, they may force a modification of the original phylogenetic hypothesis. This study represents the first test of Brooks' (1978) hypothesis of monticelliid relationships. Collection of proteocephalidean material from the delta of the Orinoco River during the winter of 1978 has permitted re-evaluation of some characters. This, coupled with extension of the analysis to the species level to test the monophyly of the generic groupings, has reduced the apparent parallel evolution shown by the monticelliids.

Materials and Methods

Hosts were collected by hook and line or trawl and examined immediately for parasites. Cestodes were removed from hosts, studied alive, then relaxed in river water, fixed in steaming AFA and stored in 70% ethanol. Whole mounts were

prepared by hydrating specimens, staining them with Mayer's hematoxylin, dehydrating them, clearing them with methyl benzoate, and mounting them in Canada balsam. Some specimens were embedded in paraffin, serially cross sectioned at 8 μm , and stained with hematoxylin-eosin for study. Figures were drawn with the aid of a drawing tube.

Results

Proteocephalus cf. *kyukyu* Woodland, 1935

Host.—*Megalodoras irwini* Eigenmann (Siluriformes: Doradidae), new host.

Locality.—Vicinity of Isla Tres Caños, delta of the Orinoco River, Venezuela, new locality.

Site of Infection.—Anterior third of intestine.

Deposition of Specimens.—University of Nebraska State Museum, No. 22455; James R. Adams Parasitology Collection, University of British Columbia.

Woodland (1935) described *Proteocephalus kyukyu* from immature specimens found in the gut of *Pseudodoras niger* and *P. brunneascens*. His specimens exhibited simple scolices, a very long unsegmented portion of strobila, and a few segments at the posterior end. Even the posteriormost segments lacked formed reproductive organs although anlagen of ovaries and cirrus sacs were present. Freze (1965) considered this a species inquirenda.

We found over 100 specimens in the intestine of one *Megalodoras irwini*, all of which agreed with Woodland's (1935) description. The immaturity of the strobilae in specimens collected from the Amazon (Woodland) and Orinoco (present study) suggests that this might be a normal aspect of the biology of this species. The implication of such a thought is that *P. kyukyu* might be hyperapolytic, with maturity and reproduction occurring after the proglottids have left the strobila. However, we found no such detached proglottids in the infected host. Until more is known we concur with Freze and consider this a species inquirenda.

Nomimoscolex kaparari Woodland, 1935

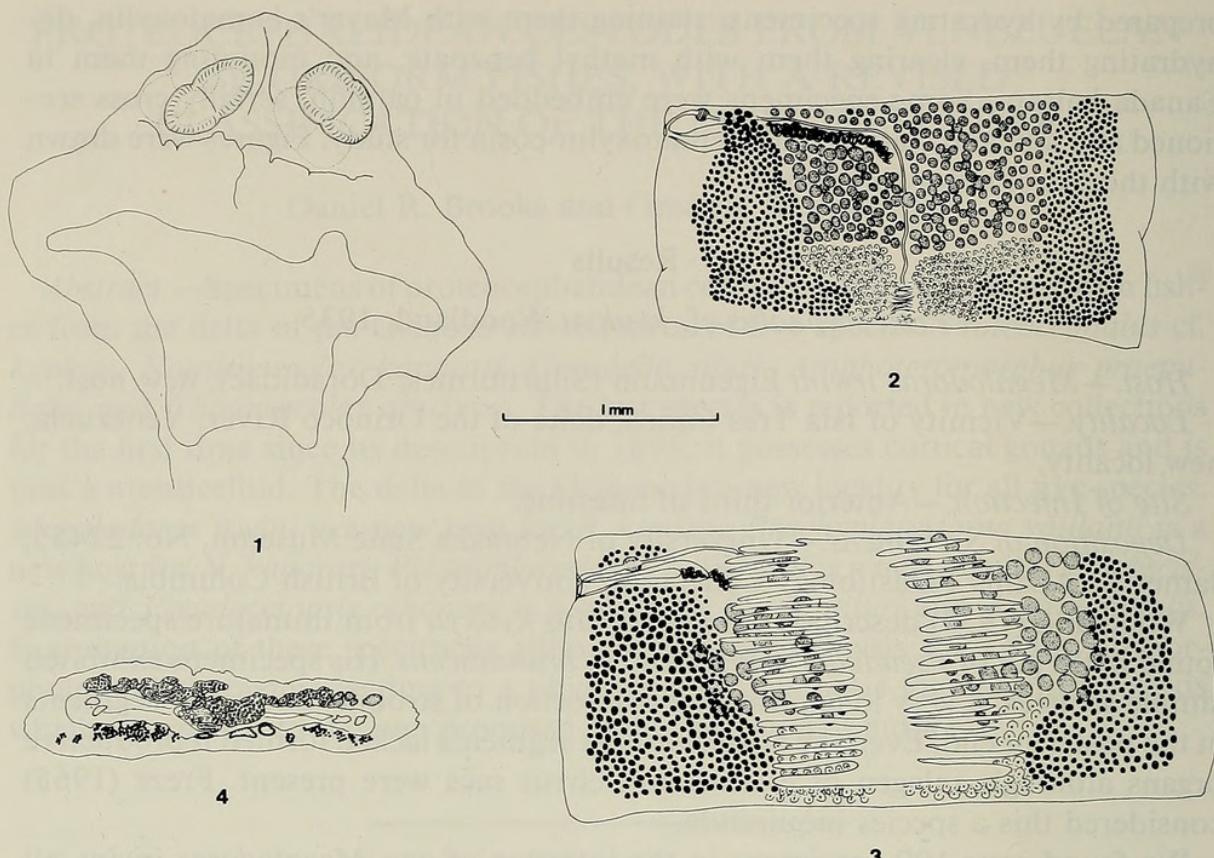
Host.—*Brachyplatystoma vaillanti* (Cuvier and Valenciennes) (Siluriformes: Pimelodidae), new host.

Locality.—Vicinity of Isla Tres Caños, delta of the Orinoco River, Venezuela, new locality.

Site of Infection.—Anterior third of intestine.

Deposition of Specimens.—University of Nebraska State Museum No. 22451.

We collected three immature proteocephalideans exhibiting scolices with four simple suckers with two muscular papillae, one on each side of the anterior margin. Woodland (1935) reported that *N. kaparari* possessed eight "unguiculate protrusions," two on each sucker. They appear to be the same as structures found on the suckers of *N. alovarius* Brooks and Deardorff, 1980, a parasite of *Pimelodus clarias* in the Magdalena River of Colombia (see Brooks and Deardorff 1980). The papillae of *N. alovarius* are positioned on the anterior portion of the suckers rather than on the margins of the anterior portions. *Nomimoscolex kaparari* has previously been reported in *Brachyplatystoma filamentosum* and *Pseudoplatystoma tigrinum* in the Amazon River.



Figs. 1-4. *Goezeella siluri*. 1, Scolex; 2, Mature proglottid; 3, Gravid proglottid; 4, Cross section of young gravid proglottid. Scale in millimeters.

Goezeella siluri Fuhrmann, 1916

Figs. 1-4

Host.—*Pseudocetopsis othonops* (Eigenmann) (Siluriformes: Cetopsidae), new host; immature specimens in *Brachyplatystoma vaillanti*.

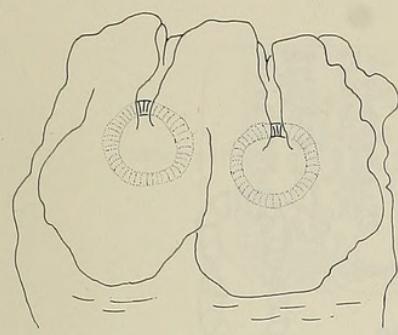
Locality.—Vicinity of Los Castillos, of Isla Tres Caños, and of La Portuguesa, delta of the Orinoco River, Venezuela, new localities.

Site of Infection.—Posterior fifth of intestine.

Deposition of Specimens.—University of Nebraska State Museum, No. 22452, 22454; James R. Adams Parasitology Collection, University of British Columbia.

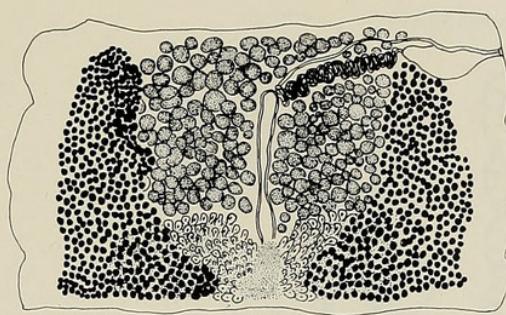
Collection of a number of *G. siluri* permitted examination of living worms and of sectioned material. By observing live specimens, we were able to confirm that the metascolex is formed by an expansion of the neck tissue posterior to the scolex. Contracted specimens do not show this clearly (e.g., see Brooks and Deardorff 1980). A vaginal sphincter was found in all proglottids, and the vagina was found to pass anterior or posterior to the cirrus sac. The single specimen reported by Brooks and Deardorff (1980) from *Ageneiosus caucanus* in Colombia had all vaginae passing anterior to the cirrus sac.

Cross sections of *G. siluri* show cortical testes, ovaries, vitellaria, and uteri. The vitelline follicles converge towards the ventral midline of the proglottid, and the uterine wall is very thin (Fig. 4).



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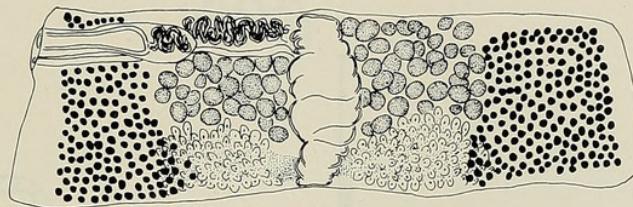
500 μm



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8



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Figs. 5–8. *Amphoteromorphus praeputialis*. 5, Scolex; 6, Mature proglottid; 7, Gravid proglottid; 8, Cross section of young gravid proglottid. Scale in micrometers.

Amphoteromorphus praeputialis Rego, Dos Santos and Silva, 1974
Figs. 5–8

Host.—*Pseudocetopsis othonops*, new host.

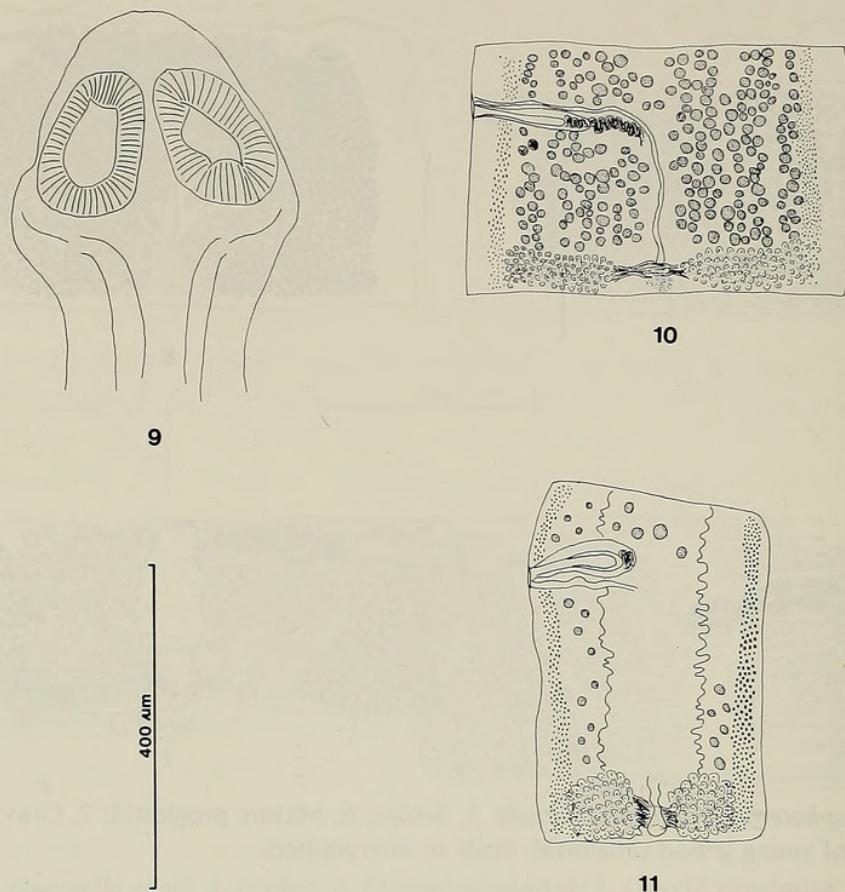
Site of Infection.—Anterior fifth of intestine.

Locality.—Vicinity of Los Castillos, of Isla Tres Caños, and of La Portuguesa, delta of the Orinoco River, Venezuela, new localities.

Specimens Deposited.—University of Nebraska State Museum, No. 22449, 22453, 22457, 22458; James R. Adams Parasitology Collection, University of British Columbia.

Our specimens agree well with the original description of this species in *Cetopsis caecutiens* (Licht.) from the Amazon River near Maicuru, Brazil. There appears to have been some confusion in labelling some of the diagrams in the original description (see Rego *et al.* 1974). Their figures 23–24, labelled as scolices of *Monticellia siluris* (=*G. siluri*), show contracted specimens with uniloculate suckers; *G. siluri* has biloculate suckers (see Fig. 1). Figure 25 by Rego *et al.* is an unclear photomicrograph of a specimen called *M. siluris*, but the nature of the sucker faces cannot be determined. Finally, their figures 26–27 are labelled photomicrographs of *M. siluris*, but judging from the shape of the uterus, they are specimens of *A. praeputialis* (see Figs. 6–7).

The metascolex of *A. praeputialis* is formed by a proliferation of tissue around each sucker rather than by the expansion of the neck seen in *G. siluri* (compare Figs. 1 and 5). In addition, all gonads except the vitellaria are medullary in *A. praeputialis*, and the uterus is very narrow (Figs. 6–7) and thick-walled (Fig. 6).



Figs. 9–11. *Choanoscolex abscissus*. 9, Scolex; 10, Mature proglottid; 11, Gravid proglottid. Scale in micrometers.

We examined 18 *Pseudocepsis othonops* from four different localities during this study. Both *A. praeputialis* and *G. siluri* were found in all four localities. Fifteen of the 18 fish (83%) were infected with at least one species of cestode. Nine of those 15 (60%) carried *A. praeputialis* and 12 of 15 (80%) carried *G. siluri*; 6 of 15 (40%) carried both species. *Amphoteromorphus praeputialis* always occurred in the anterior fifth of the intestine whereas *G. siluri* always occurred in the posterior fifth of the intestine, regardless of the presence of other species. We found no other helminths in *P. othonops*. Based on our phylogenetic analysis (presented later), *G. siluri* appears to be a colonizer of *P. othonops*, while *A. praeputialis* exhibits an apparent coevolutionary relationship with its cetopsid hosts. Thus, it is surprising that *G. siluri* occurred more often in *P. othonops* than did *A. praeputialis*. The small sample size precludes any stringent conclusions from being drawn, but this does illustrate the point that degree of coevolution cannot necessarily be drawn from host specificity or incidence data (see also Brooks 1979).

Choanoscolex abscissus (Riggenbach, 1896) LaRue, 1911
Figs. 9–11

Host.—*Pseudoplatystoma fasciatum* (Linnaeus) (Siluriformes: Pimelodidae), new host.

Locality.—Vicinity of Isla Tres Caños, delta of the Orinoco River, Venezuela, new locality.

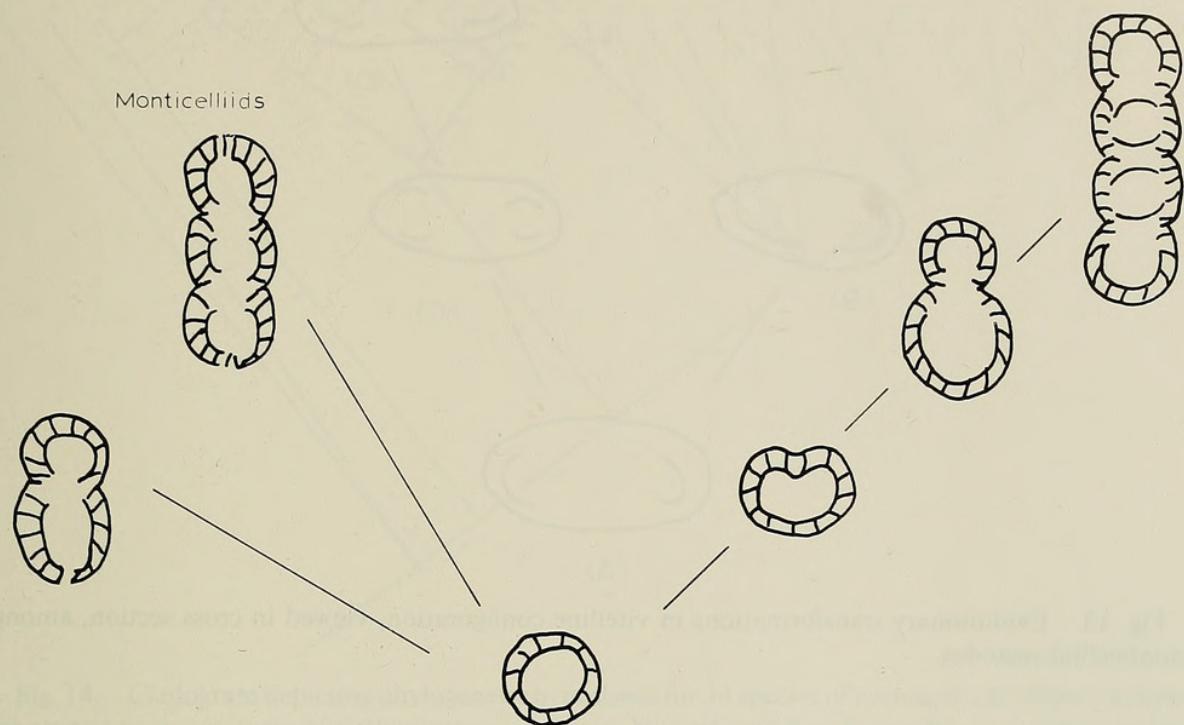


Fig. 12. Evolutionary transformations in scolex suckers among proteocephalideans.

Site of Infection.—Anterior third of intestine.

Deposition of Specimens.—University of Nebraska State Museum, No. 22456.

This species was described by Rigganbach (1896) from specimens collected in "Silurus sp." (probably a pimelodid) from the Paraguay River. To our knowledge, it has never been reported in new collections until now. Unfortunately, our specimens are only of marginal quality, so we will not attempt a redescription at this time. However, we have been able to make a number of observations which help us place this species in a more suitable taxonomic context. Rigganbach reported (1) approximately 100 testes per proglottid, and our specimens have 130–173 testes, (2) a large number of uterine diverticula, and our specimens show 70–80 total diverticula, (3) a flat but folliculate ovary, which our material confirms, (4) a genital pore in the anterior fourth of the proglottid, in general agreement with our measurements, which show the genital pore in the anterior 16–25% of mature proglottids and 23–25% of gravid proglottids, and (5) a metascolex, which our observations of living and relaxed fixed material show to be formed by an expansion of the neck region, similar to that of *G. siluri*. In addition, we were able to provide a few cross sections which provided very little detail beyond the recognition that the gonads are cortical. This necessitates removal of *C. abscissus* from the Proteocephalidae and placement of it in the Monticelliidae.

Discussion

The new data supplied by study of the present specimens permit re-interpretation of some of the characters listed by Brooks (1978), and the use of some new characters.

1. Metascolex (Brooks' character 5). This study demonstrates that the monticelliids exhibit at least two different types of metascolex. One type is exhibited

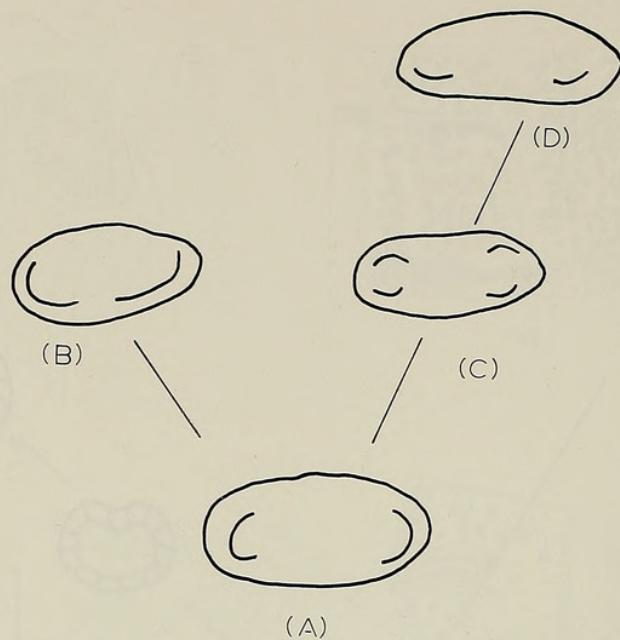


Fig. 13. Evolutionary transformations in vitelline configuration, viewed in cross section, among monticelliid cestodes.

by *Goezeella siluri* and *Choanoscolex abscissus*, in which the metascolex is formed by an expansion of the neck. The other type is exhibited by *Amphoteromorphus praeputialis* and its relatives. In the latter species, the metascolex is formed by proliferation of tissue around each sucker on the scolex. Within the Proteocephalidae, metascolices of the Corallobothriinae are formed by a general proliferation of scolex tissue around the base of the suckers. Thus, at least three different structures have all been called "the proteocephalidean metascolex." Re-coding of this character eliminates three cases of parallel evolution from the cladogram depicted by Brooks (1978).

2. Uterine structure. *Amphoteromorphus praeputialis* possesses thick-walled, narrow uteri, which differ from those of most other proteocephalideans. Illustrations of *Zygodothrium megacephalum* and the other species of *Amphoteromorphus* suggest that this structure is representative of this small group of monticelliids.

3. Scolex papillae. Three species, *Nomimoscolex kaparari*, *N. alovarius*, and *Myzophorus woodlandi*, are known to possess papillae on the suckers or sucker margins of the scolex. For *N. kaparari*, there are two papillae on the margins of each sucker; *N. alovarius* also has two papillae per sucker, but they are situated on the suckers themselves; and *M. woodlandi* has four papillae on the margin of each sucker.

4. Ovarian structure. Most monticelliids possess highly follicular ovaries (see Figs. 2, 6), which differ from those of other proteocephalideans. This includes those of the members of the Acanthotaeniinae, which have compact ovaries with digitiform lobes, and of the Corallobothriinae, whose compact ovaries may be lobulated.

5. Sucker structure. The primitive state for proteocephalidean scolex suckers is the uniloculate condition. In one proteocephalid lineage and in the monticelliids, bi-, tri- and tetraloculate suckers have arisen. The transformation series for these changes is shown in Fig. 12.

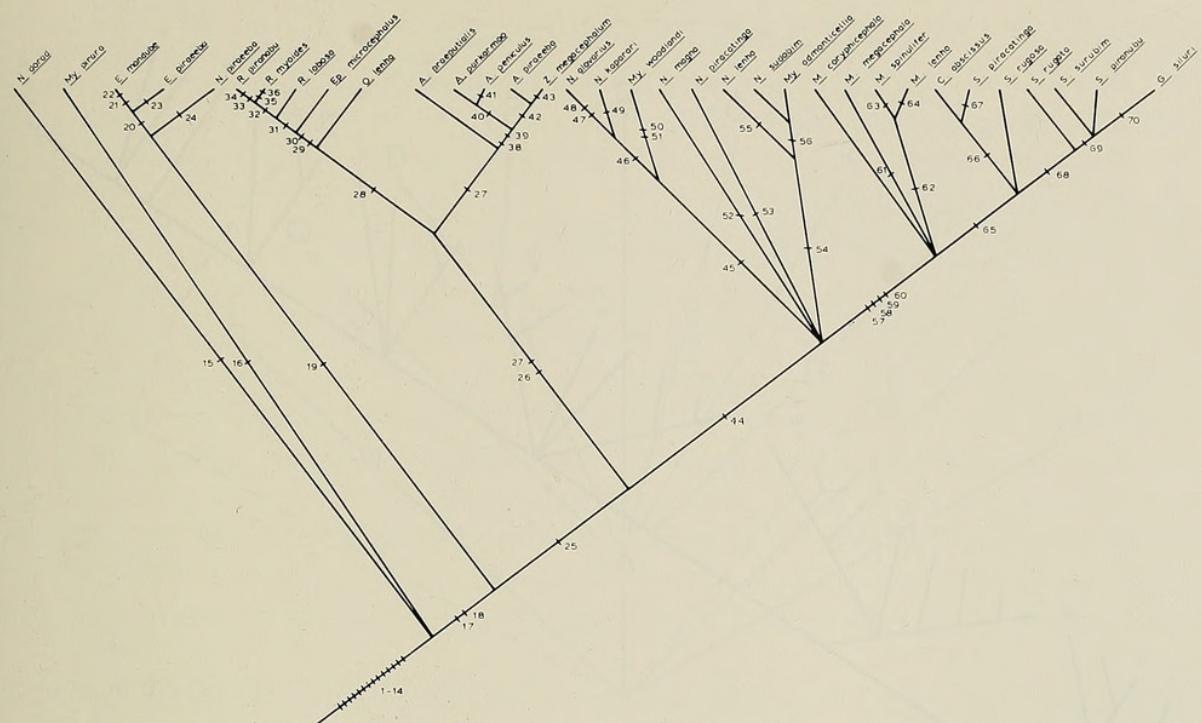


Fig. 14. Cladogram depicting phylogenetic hypothesis for 34 species of monticelliids. Abbreviations for generic names include: N = *Nomimoscolex*; My = *Myzophorus*; E = *Endorchis*; O = *Othinoscolex*; Ep = *Ephedocephalus*; R = *Rudolphiella*; A = *Amphoteronomorphus*; Z = *Zygobothrium*; M = *Monticellia*; S = *Spatulifer*; C = *Choanoscolex*; G = *Goezeella*. Numbers accompanying slash marks on branches refer to derived traits (synapomorphies) listed in Appendix.

6. Embryonation of eggs. None of the monticelliids which we examined have any evidence of embryonated eggs in utero. This is a condition found in at least some tetraphyllidean, trypanorhynch and lecanicephalan cestodes. The presence of embryonated eggs in utero may be of use in distinguishing some groups of cestodes. At present, not enough is known to draw conclusions, but we include the character for future reference.

7. Ovarian position in cross section (Brooks' character 2). Primitively, the ovary is medullary. In some monticelliids, the ovary is partially cortical, and in others it is almost entirely cortical.

8. Vitelline configuration in cross section. There are four different basic configurations found in monticelliids. The plesiomorphic condition is derived from outgroup comparisons. These are shown in Fig. 13.

9. Testes number. The primitive state for monticelliids appears to be between 100 and 150 testes per proglottid based on both outgroup comparisons with other proteocephalideans and on functional outgroup analysis. Other states include: (1) 80–120, with a mean of 100; (2) 40–60; (3) 150–200; and (4) 200–400.

10. Position of vaginal opening relative to cirrus sac. The primitive condition among proteocephalideans is the presence of vaginal openings irregularly alternating between anterior and posterior to the cirrus sac. In some monticelliids, the vagina is reported to pass either only anterior or only posterior to the cirrus sac.

The cladogram corresponding to the most parsimonious representation of the above data, and data previously recorded by Brooks (1978), for 34 species of monticelliids is shown in Fig. 14. The high rate of parallel evolution found by

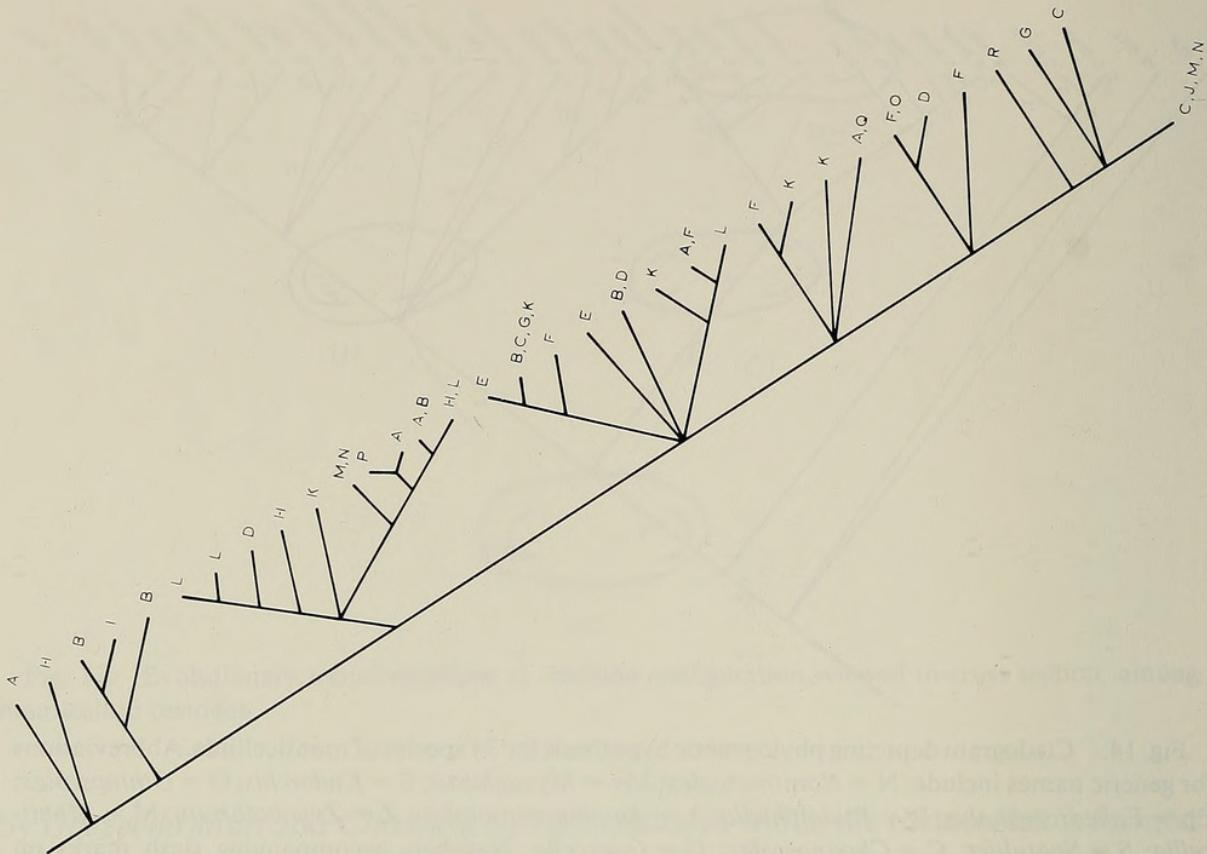


Fig. 15. Cladogram from Fig. 14 with letter codes indicating host identity superimposed. Refer to text for host names.

Brooks (1978) can be seen to have been due to the para- and polyphyletic nature of some of the generic groupings, in particular *Nomimoscolex*, *Myzophorus*, *Amphoteromorphus*, and *Monticellia*. An indicator of the degree to which characters showing parallel evolution have been used to construct a phylogeny is the consistency index (CI) (Kluge and Farris 1969; Farris 1970). The higher the CI (1.0 is maximal), the lower the parallel evolution. For Fig. 14, the CI is 0.57, which is average for phylogenetic analyses of various kinds of organisms (see Mickevich 1982). However, virtually all of the parallel evolution can be attributed to two characters, vaginal position and testes number. If we remove those characters, the CI for the tree is 0.83, indicating very little parallel evolution in the majority of other characters.

If the results of this study are corroborated by future work, it will be necessary to revise the taxonomy of the monticelliids considerably to make it consistent with their phylogeny. However, until we have made a thorough examination of available material, we refrain from making such nomenclatural changes.

Host-Parasite Relationships

The search for monticelliids in neotropical siluriforms cannot be termed extensive. On the other hand, recent collections in Brazil (Rego, Dos Santos, and Silva 1974), Colombia (Brooks and Deardorff 1980) and Venezuela (present report) have produced only two new species in *Nomimoscolex*, one of *Spatulifer* and one of *Amphoteromorphus*. This suggests that although monticelliids are

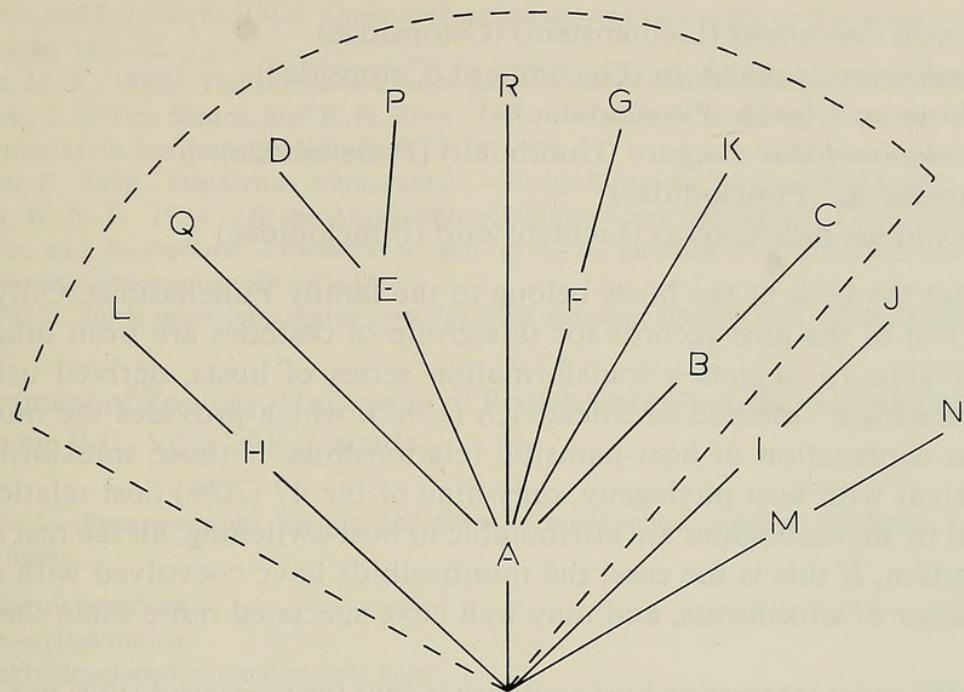


Fig. 16. Transformation series for best-fitting hypothesis of host-parasite relationships. Species enclosed in dotted circle belong in the family Pimelodidae.

highly divergent morphologically, they may not be particularly speciose. In addition to the monticelliids, only nine species of proteocephalids are known from South America, one of *Corallotaenia* (see Brooks and Deardorff 1980), one of *Megathylacus* and seven of *Proteocephalus*, including four in siluriform fishes (*P. fossatus*, *P. jandia*, *P. kyukyu*, *P. platystomi*). Thus, proteocephalidean diversity in South America may not be striking. The six species reported in this study appear to have relatively broad distributions in South America.

The cladogram in Fig. 15 represents the phylogenetic relationships of the monticelliids considered in this study with letters superimposed at the ends of branches indicating the identity of piscine hosts used by each cestode species. The letters refer to the following hosts (families listed in parentheses):

- A. *Brachyplatystoma flavicans* (Castelnau) (=*B. rousseauxii*) (Pimelodidae)
- B. *Brachyplatystoma filamentosum* (Lichtenstein) (Pimelodidae)
- C. *Brachyplatystoma vaillanti* (Cuvier and Valenciennes) (Pimelodidae)
- D. *Luciopimelodus pati* (Cuvier and Valenciennes) (=*Pimelodus pati*) (Pimelodidae)
- E. *Pimelodus clarus* (Bloch) (Pimelodidae)
- F. *Pseudoplatystoma fasciatum* (Linnaeus) (Pimelodidae)
- G. *Pseudoplatystoma tigrinum* (Cuvier and Valenciennes) (Pimelodidae)
- H. *Phractocephalus hemiliopterus* (Schneider) (Pimelodidae)
- I. *Ageneiosus brevifilis* Cuvier and Valenciennes (=*Pseudogeneiosus brevifilis*, *P. zungaro*) (Ageneiosidae)
- J. *Ageneiosus caucanus* Steindachner (Ageneiosidae)
- K. *Platystomatichthys sturio* (Kner) (Pimelodidae)
- L. *Pinirampus pirinambu* (Cuvier and Valenciennes) (=*Pirara bicolor*) (Pimelodidae)

- M. *Cetopsis caecutiens* (Lichtenstein) (Cetopsidae)
- N. *Pseudocetopsis othonops* (Eigenmann) (Cetopsidae)
- O. "Silurus sp." (prob. Pimelodidae)
- P. *Pseudopimelodus zungaro* (Humboldt) (Pimelodidae)
- Q. *Rhamdia* sp. (Pimelodidae)
- R. *Calophysus macropterus* (Lichtenstein) (Pimelodidae)

Note that the bulk of the hosts belong to the family Pimelodidae. Only six of the 47 (13%) of the host records for this group of cestodes are from other siluriforms. Figure 16 depicts a transformation series of hosts, derived using the "nearest-neighbor" method of Mickevich (1982), which provides the most parsimonious explanation of host-parasitic relationships. If those transformations are consistent with host phylogeny, only nine of the 47 (20%) host relationships postulated by the cladogram are attributable to host-switching; all the rest are due to coevolution. If this is the case, the monticelliids have coevolved with a fairly small number of siluriforms, and may well have speciated more often than their hosts.

One of the most interesting host switches is that for *Goezeella siluri* in *Cetopsis caecutiens* and *Pseudocetopsis othonops* (family Cetopsidae). When *G. siluri* is found in other hosts (pimelodids and ageneiosids), it occurs in the anterior third of the intestine. We found immature specimens of *G. siluri* in the anterior third of the intestine of *Brachyplatystoma vaillanti*. But when it inhabits cetopsids, it is found in the posterior third of the intestine. This does not appear to be a function of competitive exclusion by *Amphoteromorphus praeputialis*, which inhabits the anterior third of the intestine of cetopsids, because *G. siluri* lives in the posterior third of the gut even if *A. praeputialis* is absent. We suggest that the site selection by *G. siluri* in cetopsids is a function of the location in the gut of a host cue (either physical or physiological) to which *G. siluri* responds and is not a function of the presence of other helminths.

Summary

The previous phylogenetic hypothesis for monticelliids (Brooks 1978) overestimated the amount of parallel evolution exhibited by the group. This was due to faulty character analysis and the use of non-monophyletic generic groupings. The present study, while far from a complete analysis, nonetheless presents a more stable phylogenetic hypothesis. At present, monticelliid cestodes appear to be a distinctive group of cestodes which has coevolved primarily with pimelodid catfish.

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Appendix 1.—Synapomorphy list for cladogram of monticelliid cestodes inhabiting neotropical siluiform fishes.

1. Uniloculate suckers
2. Thin-walled uterus
3. Weakly-developed internal muscle layer
4. Compact ovary
5. Vagina alternating between anterior and posterior to cirrus sac
6. Apical organ present
7. Vitellaria partially cortical
8. 100–150 testes per proglottid
9. Vitelline bands arranged like two parentheses on either side of the proglottid
10. Ovary medullary
11. Testes medullary
12. Uterus medullary
13. No metascolex
14. No papillae on suckers
15. Vagina posterior to cirrus sac only
16. 50–60 testes
17. Ovary follicular
18. Vitellaria totally cortical
19. Internal muscle layer strongly developed
20. Vagina anterior to cirrus sac only
21. Triloculate suckers
22. No apical organ
23. Vitellaria in four quadrants, two dorsal and two ventral, along lateral margins
24. Vagina posterior to cirrus sac only
25. No apical organ
26. Metascolex I (*Amphoteromorphus* type)
27. Vitellaria in four quadrants, two dorsal and two ventral, along lateral margins
28. Partly cortical ovary
29. Vitellaria in two ventral bands on either side of proglottid
30. 150–200 testes
31. Elongate eggs
32. 100 testes
33. Vagina anterior to cirrus sac only
34. Short, thin egg filaments
35. Long, thick egg filaments
36. Vagina posterior to cirrus sac only
37. Uterus thick-walled, tubular
38. Biloculate suckers
39. Spinose scolex
40. 40 testes
41. Vitelline bands arranged like two parentheses on either side of the proglottid

42. 150–200 testes
43. Tissue growth around suckers so pronounced that only an anterior and posterior opening remain
44. Ovary partially cortical
45. Two papillae on margin of each sucker
46. 40–60 testes per proglottid
47. Alate ovarian lobes
48. Two papillae on tops of each sucker
49. Vagina posterior to cirrus sac only
50. Vagina anterior to cirrus sac only
51. Four papillae on margins of each sucker
52. Vagina anterior to cirrus sac only
53. Vagina posterior to cirrus sac only
54. 200–250 testes per proglottid
55. Vagina posterior to cirrus sac only
56. Vagina anterior to cirrus sac only
57. Ovary cortical
58. Testes cortical
59. Uterus cortical
60. Vitelline bands converging towards midline ventrally
61. 200 testes per proglottid
62. Spinose suckers
63. 60 testes per proglottid
64. 200 testes per proglottid
65. Metascolex II (*Goezeella* type)
66. 100 testes per proglottid
67. 40–50 testes per proglottid
68. 150–200 testes per proglottid
69. 200–400 testes per proglottid
70. Bilobulate suckers



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Brooks, D. R. and Rasmussen, G. 1984. "Proteocephalidean Cestodes From Venezuelan Siluriform Fishes, With A Revised Classification Of The Monticelliidae." *Proceedings of the Biological Society of Washington* 97, 748-760.

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