

Problems of classification of South American Proteocephalids (Cestoda). On a new classification for the group

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ABSTRACT. The taxonomy of the Order Proteocephalidea, parasites of freshwater fishes, amphibia and reptilia, is being reapraised. The taxa of proteocephalids parasitizing fishes from South American rivers are evaluated on utilizing morphological characters, with the help of phylogenetic systematics. The Woodland's classification divides the South American proteocephalids into two groups, Proteocephalidae and Monticellidae, depending on the position of vitellaria and gonads in medullar or cortical parenchyma of proglottids. With the intention to propose modifications in the classification, we discuss the trees that resulted from phylogenetic analysis. The conclusions are that the actual taxonomy of the group, based on the papers of Woodland (1933-1935), can not be supported by these analyses; consequently, it is suggested the suppression of Monticellidae and its subfamilies. It is accepted only one family, Proteocephalidae, with five subfamilies: Proteocephalinae Mola, 1929, Corallobothriinae Freze, 1965, Sandonelliinae Khalil, 1960, Gangesiinae Mola, 1929 and Acanthotaeniinae Freze, 1963. The monticellid species were transferred to Corallobothriinae or Proteocephalinae, depending on the presence or not of a metascolex.

Key words: Cestoda, Proteocephalidea, taxonomy, phylogenetic systematic.

RESUMO. Problemas na classificação dos Proteocefalídeos (Cestoda) da América do Sul. Uma nova classificação para o grupo. É discutida a classificação da Ordem Proteocephalidea, Cestóides, cujas espécies são parasitas de peixes de água doce, anfíbios e répteis. Os proteocefalídeos que parasitam os peixes da América do Sul são reavaliados por meio de análises filogenéticas, utilizando caracteres morfológicos. A classificação de Woodland divide a Ordem Proteocephalidea em dois grupos, Proteocephalidae e Monticellidae, se houver os vitelinos e ou as gônadas na medula ou no córtex do parênquima dos proglótides. Foram obtidas algumas árvores de gêneros e espécies e os resultados não validam a classificação baseada em Woodland (1933-1935); em consequência, é proposta a supressão da família Monticelliidae e suas subfamílias. É aceito apenas uma família Proteocephalidae Mola, 1929, com cinco subfamílias: Proteocephalinae Mola, 1929, Corallobothriinae Freze, 1965, Sandonelliinae Khalil, 1960, Gangesiinae Mola, 1929 and Acanthotaeniinae Freze, 1963. Os gêneros de monticelídeos são transferidos para Corallobothriinae ou Proteocephalinae, se estes possuírem ou não um metascolex.

Palavras-chave: Cestoda, Proteocephalidea, taxonomia, sistemática filogenética.

Introduction

Cestodes of the order Proteocephalidea (Mola, 1928) inhabit freshwater fishes but also parasitize, but in less degree, Amphibia and Reptilia. Recently, a species parasite of the Mammalian *Didelphis marsupialis* was described from Mexico (Cañeda-Guzman *et al.*, 1999), an amazing finding because proteocephalids were not yet recovered from homeotherms.

The primary hosts of proteocephalids are siluriform fishes, whose species are found in every Continent, except in Australia.

The life-cycles of South American proteocephalids are unknown except for some references to the finding of cysticercoid-like larvae in the peritoneum and liver of freshwater fishes, and hyperparasitism of these cysticercoids in proteocephalids strobilae (Rego and Gibson, 1989). The recent finding of proteocephalid larvae in freshwater copepods in the *Paraná* river, Brazil (data not published), points to these invertebrates as the first intermediate hosts; fishes are the second intermediate hosts that hosts the plerocercoid, but with a form of a cysticercoid-like, a innovation in the types of larvae in proteocephalids; the

proteocephalids from Amphibia for instance have procercoids and pelrocercoids, similar to the Tetraphyllidea.

Paratenic hosts also have an important role in the life-cycles of proteocephalideans.

Morphologically, the proteocephalids are characterized by the scolex with acetabula, the same kind of suckers found in terrestrial Cyclophyllidea, but differing from them by the reproductive organs, but especially the vitellaria lateral, that is more closely related to the Tetraphyllidea and other marine Orders. Differently from the Palearctic forms, whose species are more uniform (ex. *Proteocephalus*), the South American proteocephalids are very polymorphic, the forms of scolex and the disposition of gonads in cortex and medulla vary greatly.

The first tentative of re-organizing the Order, utilizing phylogenetic analyses, was conducted by Brooks (1978), and in subsequent papers, Brooks and Deardorff (1980), Brooks and Rasmussen (1984) and Brooks (1995). Unfortunately, the interpretations presented by Brooks and co-workers were limited by a shortage of reliable and complete data for many South American genera, with the results that many taxa were not resolved in the cladogram presented.

Zehnder and Mariaux (1999) utilized two ribosomal DNA sequences to infer phylogenetic relationships among the Proteocephalidea; as a result, they stated: "The monophyly of the Order Proteocephalidea is supported; however, neither of the two families as currently conceived, the Proteocephalidae and Monticellidae appears as a natural group, both are paraphyletic. Moreover, the monophyly of most subfamilies (of Monticellidae) is not supported in our analysis".

Material and methods

Relationships among proteocephalideans genera/species were analyzed using phylogenetic systematics. Morphological characters were analyzed with the program "Phylogenetic Analysis Using Parsimony", Version 3.05 (PAUP).

The analysis was based on critical observations of features in most proteocephalidean species studied by Rego, Rego *et al.*, Pavanelli *et al.*, and Chambrier *et al.*, (see references). Results of the studies of extensive material of proteocephalids from Amazon and Paraguay. In addition, some voucher specimens, specially species from other Continents have been examined.

Characters used in the analysis were derived mainly from comparative morphological and

taxonomix studies of the present author. In some groups, we relied on morphological data derived from the extensive literature.

Results and discussion

Excepting the papers of Diesing (1850, 1854) Monticelli (1892) and La Rue (1911, 1914), the bulk of papers on this group, specialty of South American fauna, were published by Woodland (1925, 1933 a, b, c-1935 a, b, c). Recently, the proteocephalids are being largely scrutinized by Rego (1984, 1987, 1989, 1990, 1991, 1992, 1994, 1995), Rego *et al.* (1995, 1998, 1989, 2001, 1985, 1987, 1990, 1992a, 1992b, 1999), Pavanelli and Rego (1989, 1991, 1992), Pavanelli and Santos (1992), Pavanelli and Takemoto (1991), Pavanelli *et al.* (1994), Chambrier and Rego (1994, 1995).

However, the knowledge of the South American proteocephalids resulted incomplete, as less than one hundred proteocephalid species were described from about seventy fish host species. There are a presumible fauna of two thousand fishes species in South American rivers; there are many proteocephalids taxa to be described and consequently it exists gaps in the knowledge of the group. To note however, that many of the old species were incompletely described, resulting that some species are not distinguished from each other in the basis of the known characters.

As mentioned earlier, in recent years (loc.cit.) a quantity of papers have appeared describing new forms of proteocephalids from South America; it resulted that to the anteriorly described monotypic genera were added new species.

Until Woodland (decade of 30') less than 50 proteocephalid species were known from South America, and it is not surprising the great quantity of monotypic genera he described. In fact, there are many genera with few species. It differs from the Palearctic and Nearctic forms, with few genera with many species (ex. *Proteocephalus*).

The classification of South American proteocephalids is now controversial. Many authors prefer to maintain the classifications of Woodland (1933-1935) and Freze (1965), this last author accepted two families, Proteocephalidea and Monticelliidae in the Order Proteocephalidea. These families differing on the disposition of vitellaria and reproductives organs, ovary, testes and uterus, disposed in the medullar parenchyma (Proteocephalidae) or in the cortex, total ou partly (Monticelliidae), this one with the subfamilies: Zygobothriinae, Rudolphiellinae, Ephedrocephalinae, Othinoscolecinae and Monticelliinae (Figures 1-8).

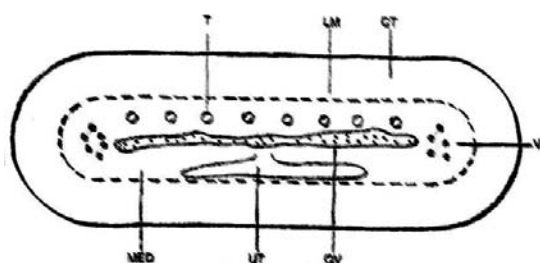


Figure 1. *Proteocephalus* (section, schematic): T = testes; LM = longitudinal muscles; CT = cortical parenchyma; V = vitellaria; MED = medulla; UT = uterus; OV = ovary

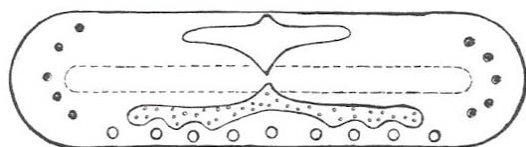


Figure 2. *Monticellia*: vitellaria and reproductive organs entirely cortical

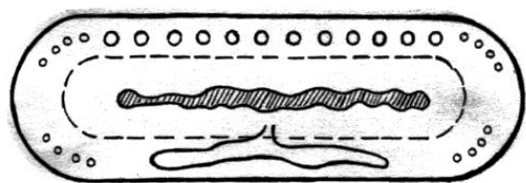


Figure 3. *Othinoscolex*: only ovary medullar

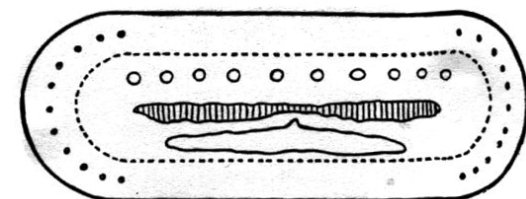


Figure 4. *Nomimoscolex*: vitellaria cortical; reproductive organs medullar

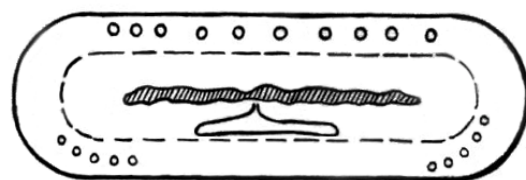


Figure 5. *Ephedrocephalus*: ovary and uterus medullar; testes and vitellaria cortical

Rego (1995) criticized the classification of the South American proteocephalids; he stated that: "The scheme of Woodland was useful for decades,

but with the discovery of new forms, with intermediate characters between the proteocephalids and monticelliids, it reduced the value of the arrangement of vitellaria and gonads in the cortical parenchyma, as characteristically distinctive". An example of the difficulty to utilize this classification could be the problem of *Nupelia portoricensis* Pavanelli and Rego, 1991, in this species, the reproductive organs and vitelline follicles are situated partly in the medulla and partly in the cortex (Figure 7), making it impossible to establish the subfamily (sensu Woodland) to the species they belong to.

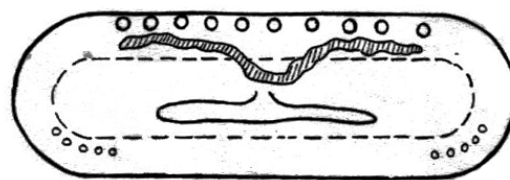


Figure 6. *Rudolphiella*: uterus medullary; ovary partly medullar; testes cortical; vitellaria in ventral cortex

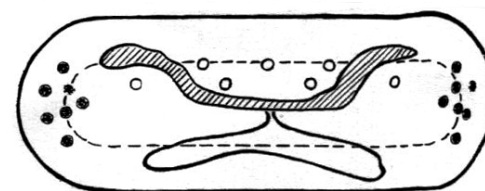


Figure 7. *Nupelia*: vitellaria and reproductive organs partly cortical partly medullar (vitellaria paramuscular).

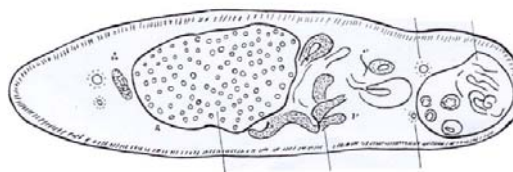


Figure 8. *Travassia*: Longitudinal musculature inconspicua; impossible to define the position cortical or medullar of gonadas and vitellaria.

Rego *et al.*, (1998) as a result of the 2nd Workshop of Tapeworms in Nebraska, published a cladistic analysis based on comparative morphology to examine the subfamily relationships within the Order Proteocephalidea. Unfortunately, the analysis started from the pre-existing families and it is not surprising that the results confirmed the "status quo", i. é, the conservative scheme of Woodland-Freze (loc.cit.).

Characters:

1. Position of viteline follicles. Three states: 0 = medullary; 1 = cortical; 2 = paramuscular.
2. Distribution of vitelline follicles (cross-section). Three states: 0 = lateral bands, or crescent-shaped; 1 = only ventral bands; 2 = in two bands, dorsal and ventral.
3. Distribution of vitelline follicles. Three states: 0 = equally distributed along lateral fields; 1 = distributed along lateral fields, but not anteriorly to the level of genital pore. 2 = along lateral fields, but more concentrated towards ovary (L-shaped).
4. Position of vitellaria relatively to longitudinal osmoregulatory canals. Three states: 0 = externally; 1 = internal; 2 = both (some follicles internal, some external).
5. Position of ovary. 4 states: 0 = medullary; 1 = origin in medulla, but developing to cortex; 2 = cortical; 3 = origin in cortex, but developing to medulla.
6. Form of ovary. Two states: 0 = biwinged, with delicate follicles; 1 = bilobate, more or less massive.
7. Position of testes. Three states: 0 = medullary; 1 = cortical; 2 = paramuscular.
8. Distribution of testes. Three states: 0 = in a single field, continuous; 1 = in two fields, connected anteriorly; 2 = in two separate fields.
9. Position of uterus. Four states: 0 = medullary; 1 = cortical; 2 = originated in medulla, but outgrowths penetrating the cortex; 3 = originated in cortex, but outgrowths penetrating the medulla.
10. Shape of uterus. Three states: 0 = tubular, with few development of diverticula; 1 = tubular, with numerous diverticula; 2 = tubular, with diverticula, but later split in egg sacs.
11. Appearance of uterus (anlagen). Two states: 0 = in mature segments; 1 = in immature segments (preformed).
12. Uterine wall. Two states: 0 = thin wall; 1 = thick wall.
13. Eggs morphology. Two states: 0 = eggs with filaments, or with polar structures; 1 = eggs round or oval without filaments or polar structures.
14. Embryonation of eggs when laid. Two states: 0 = embryonated, with visible hooks; 1 = unembryonated, hooks not visible.
15. Genital pore. Two states: 0 = alternating regularly or irregularly; 1 = tendency to be unilateral.
16. Opening of vagina relatively to cirrus pouch. Three states: 0 = anterior; 1 = posterior; 2 = anterior or posterior in the same strobila.
17. Vaginal sphincter. Two states: 0 = inconspicuous or absent; 1 = conspicuous.
18. Shape of mature proglottids. Three states: 0 = longer than wide; 1 = more or less square/quadrangle; 2 = wider than long.
19. Tegumental wrinkles on strobila. Two states: 0 = absent; 1 = present.
20. Velum or laciniae. Two states: 0 = present (craspedote); 1 = absent (acraspedote).
21. Disposition of longitudinal musculature of parenchyma. Two states: 0 = isolated fibres/diffuse fibres; 1 = bundles of fibres.
22. Development of longitudinal musculature of parenchyma. Two states: 0 = well developed, with bundles of fibres; 1 = weakly developed/inconspicuous.
23. Neck. Two states: 0 = conspicuous; 1 = inconspicuous/very small.
24. Metascolex. Two states: 0 = absent; 1 = present.
25. Development of metascolex. Two states: 0 = well developed, numerous folds, "collar-like"; 1 = other forms, not "collar-like".
26. Apical muscular sucker. Two states: 0 = absent; 1 = present.
27. Frontal apical glands on scolex. Two states: 0 = absent; 1 = present.
28. Suckers shape. Two states: 0 = more or less spherical; 1 = other forms.
29. Sucker cavities. Five states: 0 = one cavity, simple; 1 = one cavity, but notched, heart-shaped; 2 = one cavity, two openings; 3 = two cavities, biloculate; 4 = three cavities, trilobulate.
30. Suckers disposition. Two states: 0 = external, visible/ not sessile; 1 = internal, sac-like, appearing as holes.
31. Spination of suckers (microtriches). Two states: 0 = absent; 1 = present.
32. Auriculae or other projections of suckers. Two states: 0 = absent; 1 = present.
33. Distal sphincter on suckers. Two states: 0 = absent; 1 = present.
34. Types of hosts. Three states: 0 = fish; 1 = Amphibian; 2 = Reptilia.

Table 1. Character matrix

	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	31	32	33	34	
Ophiotaenia bonariensis	0	0	0	0	0	1	0	2	0	1	0	0	1	0	0	2	1	0	0	0	1	0	1	0	0	-	0	1	0	0	0	0	0	1	
Tejodotaenia appendiculata	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	2	1	0	0	1	1	0	1	0	-	0	0	1	0	0	0	0	0	2	
Proteocephalus regoi	0	0	0	2	0	1	0	1	0	1	1	0	1	0	0	1	0	2	0	1	1	0	0	0	-	0	1	0	0	0	0	0	0	0	
Crepidobothrium garsoni	0	0	0	0	0	1	0	2	0	1	1	0	1	0	0	2	0	0	0	1	1	0	0	0	-	0	1	0	1	0	0	0	0	2	
Ceirasi	2	0	1	0	0	0	0	0	0	1	1	0	1	0	0	2	0	1	0	0	1	1	0	0	-	0	0	0	1	0	0	0	0	0	
Travassella avitellina	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	2	0	1	0	1	0	0	-	0	0	0	0	0	0	0	0	0	
Euzetiella tetraphylliformes	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	-	0	1	1	0	0	0	0	0	0	
Brayella karuatayi	0	0	0	0	0	0	0	2	0	0	0	0	1	1	1	0	0	0	2	0	1	1	0	0	0	-	0	0	0	3	0	0	0	0	
Gibsonella mandube	2	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	1	1	1	1	0	0	0	-	0	0	0	4	0	0	0	0	0	
Monticella belavistensis	1	0	0	0	2	1	1	0	1	1	0	0	1	0	0	0	1	1	0	1	1	0	0	0	-	0	0	0	0	0	0	0	0	0	
Nomimoscolex Piracaba	2	0	0	0	1	1	0	0	3	1	1	0	1	0	0	2	1	2	0	1	1	0	0	0	-	0	1	0	0	0	1	0	0	0	
Myzophorus admonticella	1	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	-	0	1	0	0	0	0	0	0	
Agenciella brevifilis	1	0	2	0	3	1	1	0	3	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	-	0	0	1	3	0	0	0	0	
Endorchis aucheniipetri	1	2	0	0	1	1	0	0	3	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	1	0	3	0	0	0	0	
Vaucheriella bicheni	1	1	1	0	0	0	0	2	0	0	1	0	1	0	0	1	1	0	0	1	0	1	0	0	-	0	1	0	0	0	0	0	0	2	
Zygobothrium megacephalum	1	2	2	0	0	0	0	0	0	1	0	0	1	1	0	2	1	2	1	0	1	0	1	0	-	0	0	0	2	0	0	0	1	0	
Hussayella sudobim	2	0	0	0	0	0	0	2	0	1	0	0	1	0	0	0	2	0	1	1	0	0	0	-	0	0	0	0	0	0	0	1	0	0	
Harriscolex kaparari	2	2	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	-	0	0	0	0	0	0	0	1	0	
Nupella portoniensis	2	0	0	0	1	1	2	0	3	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	-	0	0	0	0	0	0	0	0	0	
Cangarella arandasi	2	1	0	1	0	1	0	1	2	1	0	0	0	0	0	2	0	0	1	1	1	0	0	0	-	0	0	0	0	0	0	0	0	0	
Megathylacus	0	0	2	0	0	1	0	2	0	1	0	0	0	1	0	0	0	2	0	1	1	0	0	1	1	0	0	0	0	1	0	0	1	0	
Spatulifer maringaensis	1	1	0	0	2	1	1	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	
Goezeella situri	1	1	2	2	1	0	1	0	1	1	0	0	0	1	0	0	1	2	1	1	1	0	1	1	0	0	0	1	3	0	0	0	0	0	
Paramonticella itaipuensis	1	0	2	0	3	1	1	0	1	1	0	0	1	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	
Mariauxiella pimelodi	1	0	0	0	1	1	1	0	3	1	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0
Choanoscolex absconditus	1	0	0	0	2	1	1	0	1	1	0	0	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	
Amphoteromorphus	1	2	2	2	0	1	0	0	0	1	0	1	0	0	0/1	0	1	2	1	1	1	0	1	1	0	0	0	1	3	0	0	0	0	0	
Pelidocotyle rugosa	1	2	?	0	0	1	1	0	1	1	0	0	1	1	0	0	1	2	1	1	1	0	1	1	0	0	0	1	3	0	0	0	0	0	
Othinoscolex (syn. Woodlandiella)	1	2	0	2	0	1	1	0	1	0	0	0	1	1	0	0	1	2	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	
Jaella glandicephalus	1	2	0	0	0	1	1	0	2	1	0	0	1	1	0	0	2	0	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	
Ephedrocephalus microcephalus	1	1	0	2	0	1	1	0	0	1	0	0	0	1	0	?	0	2	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	
Sciadocephalus megalodiscus	0	0	0	0	0	1	0	2	0	2	1	0	1	1	0	2	0	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	
Rudolphiella	1	1	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	
Marsypocephalus rectangulus (African)	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	2	0	2	1	1	1	0	1	0	-	0	0	0	0	0	0	0	0	1	0
Tetraphyllidea (OUTGROUP)	0	0	0	0	0	0/1	0	0/1	0/1	0	0	0	0/2	0	0	0	0/1	0	0	0	0/1	0/1	0/1	0	0/1	?	0	0	1	0/4	0	0	0	0	0

Cladistic analysis

Thirty-four characters were identified in the thirty-five taxa included in the analysis, represented by Thirty-three South American species and two species from other Continents, *Paraproteocephalus parasiluri* and *Marsypocephalus rectangulus*. One of the resulting trees (Figure 9) with 176 steps and level of consistence, CI = 0,34, demonstrated the existence of homoplasies to several characters and groups of taxa. This preliminary analysis produced a large number of equally parsimonious trees, a strict consensus of which failed to support the current classification.

We think that the difficulties in resolving relationships exists as expected, since the proteocephalids of South America have undergone a high degree of morphological diversification. The diversification has resulted in a large number of taxa characterized by what appears to be autapomorphies

that cannot be linked evolutionarily. As well, as in many cestode groups, the parallelism associated with many other characters adds difficulty to the task of uncovering relationships in an objective manner.

The results of the phylogenetic analyses of the group does not validate the actual classification of the Proteocephalids. There is no justification to isolate a Monticellidae family, to place the genera that exhibit migration of vitellaria and, or gonads to the cortex. However, these characters are considered very important at the level of genera". Consequently, he accepted only one family, Proteocephalidae, and suggested the elimination of Monticellidae and its subfamilies. The genera of Monticellidae were transferred to Corallobothriinae or Proteocephalinae, depending on the presence or not of a metascolex. The subfamilies Sandonelliinae, Gangesiinae and Acanthotaeniina are maintained, because they have sufficient characteristics to

distinguish them from the other taxa. The Marsypocephalinae Woodland, 1933 is suppressed for unnecessary and the genus *Marsypocephalus* Wedl, 1861 is transferred to Proteocephalinae.

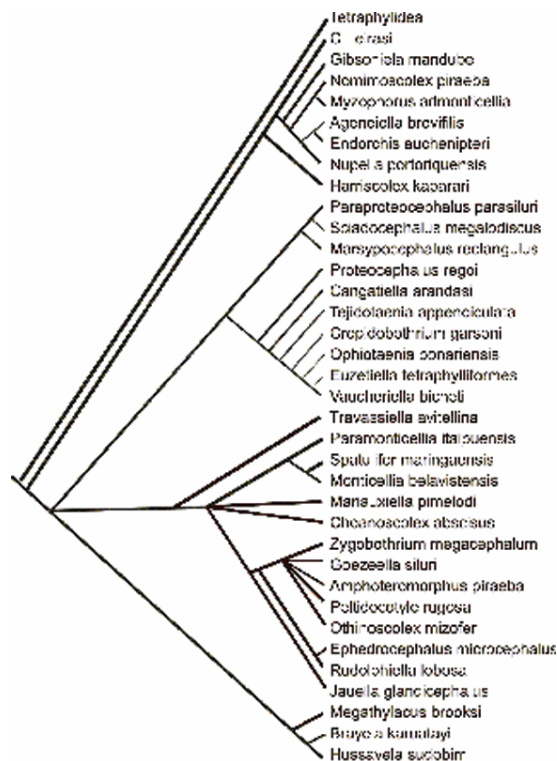


Figure 9. Cladogram showing phylogenetic relationships among South American proteocephalid genera. Most of the taxa are not resolved

As stated by Rego (1999): "Morphological characteristics of metascolex and scolex, that include frontal (apical) glands, apical sucker, appendices of suckers and spines or microtriches, could provide more precise data in order to separate genera and subfamilies rank in the Order Proteocephalidea"

The classification is a provisional one, it is possible that in the future, discoveries of new forms of proteocephalids, and a better knowledge of the life-cycle of South American and African species could carry out modification in this scheme.

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