



## A new genus and species of polychaete worm (Family Orbiniidae) from methane seeps in the Gulf of Mexico, with a review of the systematics and phylogenetic interrelationships of the genera of Orbiniidae

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**Abstract:** An abundant polychaete *Methanoaricia dendrobranchiata* gen. nov. et sp. nov., found in association with methane seeps (>500 m) in the Gulf of Mexico, has affiliations with the family Orbiniidae. These seepworms are large, up to 15 cm long, 7-9 mm wide anteriorly, with hundreds of crowded segments. Distinct body regions are absent. Branched branchiae extend over the entire body. The prostomium is narrow, elongate, directed ventrally, and bluntly rounded on the anterior margin. Eyes are absent; eversible nuchal papillae are present. The peristomium is reduced to a single, narrow achaetous ring. Parapodia bear long, laterally directed, cirriform noto- and neuropodial lamellae. Capillary chaetae have transverse rows of bristles. Narrow, pointed notopodial spines have a single subapical spur or secondary tooth. Neurochaetae of anterior chaetigers include a few threadlike capillaries, about 5 simple spines with weakly developed crenulations along their margins, and 3-4 emergent curved aciculae; spines are absent by the middle of the body. The pygidium has a terminal anus surrounded by several long, tapering cirri. The chaetal and branchial structure of these worms allies them most closely to the Orbiniidae despite the lack of distinct body regions. In order to understand the relationship of the seepworm with other orbiniid genera, a phylogenetic (cladistic) analysis was performed. The results of this analysis suggests that the current classification of orbiniid genera into subfamilies is not appropriate and a new classification is proposed that is based on increasing modification of body structure and chaetae. Two clades or subfamilies of Orbiniidae are proposed using these characters rather than the traditional peristomial ring structure. The seepworm appears to be a separate and distinct sister taxon.

**Résumé :** Description d'un nouveau genre et d'une nouvelle espèce d'Annélide Polychète (Famille des Orbiniidae) des suintements de méthane du Golfe du Mexique, et revue de la systématique et des relations phylogénétiques des genres d'Orbiniidae.

*Methanoaricia dendrobranchiata* gen. nov. et sp. nov., est une espèce abondante dans les suintements de méthane du Golfe du Mexique, à plus de 500 m de profondeur, qui présente des affinités avec la famille des Orbiniidae. Ces organismes sont de grande taille, jusqu'à 15 cm de long et 7-9 mm de large antérieurement, avec des centaines de segments serrés les uns contre les autres. Les branchies ramifiées sont présentes tout le long du corps. Le prostomium est étroit et long, orienté ventralement, arrondi antérieurement. Les yeux sont absents, mais il y a des organes nucaux. Le segment buccal est formé par un seul segment achète et étroit. Les parapodes portent des lamelles noto- et neuropodiales longues, cirriformes et orientées latéralement. Les soies capillaires présentent des rangées transversales d'épines. Les soies notopodiales en épines pointues et étroites présentent un seul éperon sous-apical ou dent secondaire. Les soies neuropodiales des sétigères antérieurs com-

prennent quelques soies capillaires fines, environ cinq épines simples bordées de denticulations peu développées et trois à quatre acicules recourbés et saillants. Les épines disparaissent à partir du milieu du corps. Le pygidium présente un anus terminal entouré de plusieurs cirres longs et fuselés. La morphologie des soies et des branchies de cette nouvelle espèce la rapproche des Orbiniidae, malgré l'absence de régions distinctes. Dans le but de comprendre les relations entre ce ver et les autres genres d'Orbiniidae, une analyse phylogénétique (cladistique) a été entreprise. Les résultats suggèrent que la classification actuelle des genres d'Orbiniidae dans les sous-familles n'est pas adéquate et une nouvelle classification est proposée sur la base d'une modification croissante de la morphologie du corps et des soies. Deux clades, ou sous-familles, se distinguent par ces caractères et non par la structure du segment buccal. La nouvelle espèce *Methanoaricia dendrobranchiata* se détache nettement et forme un taxon frère distinct.

*Keywords:* Polychaeta, Orbiniidae, Gulf of Mexico, seep communities, phylogeny, morphology.

## Introduction

Writhing masses consisting of literally thousands of specimens of a large polychaete have been found in association with hydrocarbon cold seeps in the Gulf of Mexico. First collected about ten years ago, this very abundant "seepworm" occurs with mussels that live in hydrocarbon enriched sediments surrounding brine seeps. The seep habitats and associated fauna are relatively long-lived and stable in contrast to hydrothermal vent habitats and faunas that change rapidly. These habitats have been described by MacDonald et al. (1990) and MacDonald (1998).

The seepworm exhibits unusual combinations of characters that pose problems in placing it into a known polychaete family, let alone a genus. A detailed morphological analysis of the seepworm has been conducted and the results suggest that it has more affinities to the Orbiniidae than to other polychaete families. In order to understand the systematic and phylogenetic relationships of the seepworm with other orbiniids, a review of orbiniid systematics is necessary.

The most important modern review of orbiniid systematics is by Hartman (1957), who redefined all of the genera and most of the common species. She was also the first to partition the family into two subfamilies, the Orbiniinae and Protoariciinae, based on the number of peristomial rings: Orbiniinae (one ring); and Protoariciinae (two rings). In developing her classification, Hartman relied heavily on the monograph of Eisig (1914), whose work she obviously admired. Other important contributions to orbiniid systematics have been made by Pettibone (1957), Day (1973, 1977), Mackie (1987), Solís-Weiss & Fauchald (1989), and Blake (1996). Other than clarifying the definitions of certain genera, especially the *Haploscoloplos* homonym problem (Day, 1977), none of these latter works substantially altered the classification system established by Hartman (1957). Many new species have been described (e.g., Mackie, 1987; Solís-Weiss & Fauchald, 1989) and many more are known (Blake, unpublished).

While reviewing the orbiniids from California and the Southern Ocean, I became aware of a taxonomic issue regarding descriptions of small species of Orbiniidae assigned to the subfamily Protoariciinae (Blake, 1996). Descriptions of genera and species of small orbiniids of the Protoariciinae have increased in recent years owing to the use of fine-mesh screens that retain smaller specimens of polychaetes. It is important to note that nearly all species of Protoariciinae are considerably smaller than species of Orbiniinae. Blake (1996) pointed out that some species described and assigned to genera of the Protoariciinae were actually juveniles of species of the larger species assigned to the Orbiniinae. Fauchald and Rouse (1997) provided definitions of each of the polychaete families and among other things indicated that the first achaetous ring in orbiniids was peristomial, whereas the second was considered an achaetous segment.

Studies of the larvae of nine species have demonstrated that the single achaetous peristomial ring is established early in the development of those genera such as *Leitoscoloplos* and *Scoloplos*, that have pointed prostomia. However, for the genus *Naineris*, available evidence suggests that two achaetous rings are established early in development with the transition to a single ring occurring later in development (Okuda, 1946; Blake, 1980; Giangrande & Petraroli, 1991). Pettibone (1963) illustrated an adult of *N. quadricuspida* (Fabricius, 1780) with two achaetous peristomial rings; the author has seen juveniles of both *N. dendritica* (Kinberg, 1866) and *N. quadricuspida* with two rings and adults with only one ring. These observations strongly suggest that both rings are peristomial and that the second is transitory in species of Orbiniinae. Because most of the described genera and species of Protoariciinae having two peristomial rings are small and have blunt-tipped prostomia characteristic of *Naineris*-like species, it is likely that many of the taxa currently assigned to this subfamily may actually be juveniles of species already described in the Orbiniinae (see Blake, 1996 for discussion and examples).

The discovery of the seepworm, newly described in this paper as *Methanoaricia dendrobranchiata* gen. nov. et sp. nov., prompted a review of orbiniid systematics in order to better understand its position among the orbiniid genera. Shared orbiniid characters include the vascular nature of the branchiae and the crenulated form and transverse arrangement of bristles along the capillary chaetae. However, other typical orbiniid characters such as distinct body regions, dorsally elevated posterior parapodia, and various types of modified chaetae including uncini, lyrate chaetae, and flail chaetae are not present.

In order to understand the relationship of *Methanoaricia* with other genera of the Orbiniidae and to test the validity of Hartman's classification of the family into two distinct subfamilies, a phylogenetic analysis was performed. This analysis also provided a means to test the classification system of the Orbiniidae proposed by Hartman (1957) and challenged by Blake (1996).

The present paper includes a detailed description of *Methanoaricia*, and the results of a phylogenetic analysis of *Methanoaricia* and 16 orbiniid genera. Based on these results, a revised classification of the Orbiniidae is proposed along with a discussion of possible morphological trends and phylogenetic interrelationships among the orbiniid genera.

## Methods

### Morphological examination of the seepworm

Specimens of the seepworm were collected by submersible on the continental slope off Louisiana and provided to me for study. In addition to traditional observations with light microscopy, several specimens were examined with the scanning electron microscope (SEM). Line drawings of critical morphology were prepared from observations using both types of microscopy. Type material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) and in the Los Angeles County Museum of Natural History, Los Angeles, California (LACM-AHF).

### Phylogenetic analysis

There are approximately 19 recognized genera currently referred to the Orbiniidae. For the purposes of the present investigation, *Pararicia* and *Pettibonella*, both problematic genera described by Solís-Weiss & Fauchald (1989), *Berkeleyia* Hartman, 1971 a probable synonym or at best subgenus of *Leitoscoloplos*, and *Uncorbinia* Hartmann-Schröder, 1979 a probable synonym of *Califia* Hartman, 1957 were excluded. Two species, *Orbiniella branchiata* Hartman, 1967 and *Naineris* sp. 1, that represent probable undescribed genera being considered as part of a

monograph on Southern Ocean orbiniids, are included in the analysis as provisional categories (Blake, unpublished).

Two primary data matrices were prepared for the analysis. Each matrix includes 17 orbiniid genera, *Methanoaricia*, and two outgroup genera, *Cirrophorus* and *Levinsenia*, both belonging to the orbiniid sister family Paraonidae (see Rouse & Fauchald, 1997). The two data matrices were treated differently. The first matrix (1) utilized a suite of characters that included the traditional peristomial ring morphology: one ring, two rings, or three rings (Tables 1, 2). In the second matrix (2), the peristomial morphology was deleted (Tables 3, 4) because larval studies have demonstrated that some genera with two rings as juveniles may have only one ring as an adult (see above and Blake, 1996). The first phylogenetic analysis therefore, dealt with orbiniid morphology in the traditional manner established by Hartman (1957), whereas the second followed chaetal, branchial, and prostomial morphology independent of superficial peristomial rings. Details of the cladistic analysis are as follows:

*Outgroup Taxa.* The Paraonidae is considered to be a sister family to the Orbiniidae (Rouse and Fauchald, 1997) and two typical genera, *Cirrophorus* and *Levinsenia*, based on their type species, *C. branchiatus* Ehlers, 1908 and *L. gracilis* (Tauber, 1879), were selected as outgroups.

*Ingroup Taxa.* The following genera were included: *Orbinia*, *Phylo*, *Leitoscoloplos*, *Scoloplos*, *Leodamas* (treated as a full genus after preliminary analysis), *Califia*, *Naineris* sp. 1 *Naineris*, *Falklandiella*, *Orbiniella*, *Microrbinia*, *Schroederella*, *Scoloplella*, *Proscoloplos*, *Protoaricia*, *Orbiniella branchiata*, *Protoariciella*, and *Methanoaricia*. Usually, the type species was used as the basis for the characters defining each of these genera. Non-type species (\*) were used in situations where the author lacked information or specimens of the type species or was otherwise unable to confirm the presence or absence of critical character states. The species used as the basis of the ingroup genera were as follows: \**Orbinia johnsoni* (Audouin and Milne Edwards, 1833), *Phylo felix* Kinberg, 1866, \**Leitoscoloplos pugettensis* (Pettibone, 1957), *Scoloplos armiger* (Müller, 1776), *Leodamas verax* Kinberg, 1866, *Califia calida* Hartman, 1957, *Naineris* sp. 1, *Naineris quadricuspida* (Fabricius, 1780), *Falklandiella annulata* Hartman, 1967, *Microrbinia linea* Hartman, 1965, *Schroederella pauliana* Laubier, 1962, *Scoloplella capensis* Day, 1963, *Proscoloplos confusus* Hartmann-Schröder, 1962, *Protoaricia oerstedii* (Claparède, 1864), *Orbiniella minuta* Day, 1954, \**Orbiniella branchiata* Hartman, 1967, *Protoariciella uncinata* Hartmann-Schröder, 1962, and *Methanoaricia dendrobranchiata* Blake, new genus, new species.

*Excluded taxa:* *Berkeleyia*, *Pararicia*, *Pettibonella*, and *Uncorbinia*.

**Table 1.** Orbiniid phylogenetic analysis: Characters and character states for analysis 1 with peristomial rings included and all character states as absence/presence (a/p).

**Tableau 1.** Analyse phylogénétique des Orbiniidae : caractères et états des caractères pour l'analyse 1 incluant les anneaux péristomiaux (caractère à plusieurs états) et les états des caractères codés en absence/présence (a/p).

0. Peri-/Prostomium separated, not fused: (0) Absent; (1) Present
1. Prostomium narrow, acutely pointed or sharply conical: (0) Absent; (1) Present
2. Prostomium bluntly conical: (0) Absent; (1) Present
3. Prostomium broadly rounded or truncate on anterior margin: (0) Absent; (1) Present
4. Prostomium elongate, narrow, rounded anteriorly: (0) Absent; (1) Present
5. Body Regions distinct: (0) Absent; (1) Present
6. One Peristomial Ring distinct from prostomium: (0) Absent; (1) Present
7. Two Peristomial rings distinct from prostomium: (0) Absent; (1) Present
8. Three Peristomial rings distinct from prostomium: (0) Absent; (1) Present
9. Branchiae: (0) Absent; (1) Present
10. Branchiae branched: (0) Absent; (1) Present
11. Posterior parapodia dorsally elevated: (0) Absent; (1) Present
12. Thoracic neuropodia elevated ridge: (0) Absent; (1) Present
13. Thoracic neuropodial postchaetal lamellae: (0) Absent; (1) Present
14. Neuropodial subpodial lobes: (0) Absent; (1) Present
15. Neuropodial stomach papillae: (0) Absent; (1) Present
16. Thoracic furcate notochaetae: (0) Absent; (1) Present
17. Thoracic capillary notochaetae crenulated: (0) Absent; (1) Present
18. Abdominal neuropodial aciculae: (0) Absent; (1) Present
19. Thoracic neuropodial uncini: (0) Absent; (1) Present
20. Thoracic neuropodial uncini small, inconspicuous among capillaries: (0) Absent; (1) Present
21. Thoracic neuropodial uncini large, conspicuous: (0) Absent; (1) Present
22. Thoracic neuropodia with narrow pointed spines (not uncini): (0) Absent; (1) Present
23. Thoracic neuropodial uncini limited to 1_few anterior thoracic chaetigers: (0) Absent; (1) Present
24. One to few Posteriormost thoracic neuropodia with modified spines: (0) Absent; (1) Present
25. Neuropodial swan hooks: (0) Absent; (1) Present

*Characters:* External morphological characters used for these analyses include structures normally used in taxonomic treatments of orbiniids, as defined by Hartman (1957) and as modified by Day (1973). The characters are listed in Tables 1 and 3.

*Character coding and scoring.* For the primary analyses of matrices 1 and 2, only binary characters (absence/presence or a/p) were used. Polymorphic states were not coded. In the event a species currently assigned to a genus had polymorphic characters, that species was not

**Table 2.** Character matrix used in cladistic analysis 1 with peristomial rings included and all character states as absence/presence (a/p).

**Tableau 2.** Matrice de codage des caractères utilisée dans l'analyse cladistique n° 1, incluant les anneaux péristomiaux et tous les caractères codés en absence/présence (a/p).

	0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2
Genus/ Character No.	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5
<i>Cirrophorus</i>	0 0 1 0 0 0 0 0 0 1 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0
<i>Levinsenia</i>	0 0 1 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
<i>Orbinia</i>	1 1 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 1 1 0 1 0 0 0 0
<i>Phylo</i>	1 1 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 1 1 0 1 0 0 1 0
<i>Leitoscoloplos</i>	1 1 0 0 0 1 1 0 0 1 0 1 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0
<i>Scoloplos</i>	1 1 0 0 0 1 1 0 0 1 0 1 1 1 0 0 1 1 1 1 1 0 0 0 0 0 0
<i>Leodamas</i>	1 1 0 0 0 1 1 0 0 1 0 1 1 1 0 0 1 1 1 1 0 1 0 0 0 0 0
<i>Califa</i>	1 1 0 0 0 1 1 0 0 1 0 1 0 1 0 0 1 1 1 1 0 1 0 1 0 1 0
<i>Naineris</i> sp. 1	1 0 0 1 0 1 1 0 0 1 0 1 1 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0
<i>Naineris</i>	1 0 0 1 0 1 1 0 0 1 0 1 1 1 0 0 1 1 1 1 0 1 0 0 0 0 0 0
<i>Falklandiella</i>	1 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0
<i>Orbiniella</i>	1 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0
<i>Microrbinia</i>	1 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0
<i>Schroederella</i>	1 1 0 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 1 ? 1 1 0 0 0 0 0 0
<i>Scoloplella</i>	1 0 0 1 0 1 0 1 0 1 0 1 0 0 0 1 0 0 0 1 ? 0 0 0 0 0 0 0 0
<i>Proscopolpos</i>	1 0 0 1 0 0 0 1 0 1 0 0 0 1 0 0 0 1 1 0 0 0 0 0 0 0 1
<i>Protoaricia</i>	1 0 0 1 0 1 0 1 0 1 0 1 0 1 0 0 1 1 1 1 1 0 0 0 0 0 0 0
<i>Orbiniella</i> <i>branchiata</i>	1 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0
<i>Protoariciella</i>	1 0 0 1 0 1 0 1 0 1 0 1 0 1 0 0 1 1 1 1 0 1 0 0 0 0 0 0
<i>Methanoaricia</i>	1 0 0 0 1 0 1 0 0 1 1 0 0 1 0 0 0 1 1 0 0 0 1 0 0 0 1 0 0 0

considered in the final generic definition. Unknown character states were coded as (?); inapplicable character states were coded as (-). In addition, a modified secondary analysis was carried out on matrix 1 (1B) where the peristomial shape and number of peristomial rings were coded as unordered multistate characters. No table for this analysis is presented. However, readers need only take characters and 1-4 and 6-8 from Table 1 and combine them into two characters with four and three states, respectively in order to reconstruct the multistate character list and corresponding matrix. For the most part, characters coded for each of the ingroup taxa are those that define the respective type species of the genus.

*Analysis:* Hennig86 Version 1.5 (Farris, 1988) was used for parsimony analysis. The data matrices and trees were edited in the Windows shell program, Tree Gardener

**Table 3.** Orbiniid phylogenetic analysis: characters and character states for analysis 2 with peristomial rings excluded and all character states as absence/presence (*a/p*).

**Tableau 3.** Analyse phylogénétique des Orbiniidae : caractères et états des caractères pour l'Analyse 2 excluant les anneaux péristomiaux, mais incorporant les autres caractères codés en absence/présence (*a/p*).

0. Peri-/Prostomium separated, not fused: (0) Absent; (1) Present
1. Prostomium narrow, acutely pointed or sharply conical: (0) Absent; (1) Present
2. Prostomium broadly conical, rounded anteriorly: (0) Absent; (1) Present
3. Prostomium broadly rounded or truncate on anterior margin: (0) Absent; (1) Present
4. Prostomium elongate, narrow, rounded anteriorly: (0) Absent; (1) Present
5. Distinct thorax and abdomen: (0) Absent; (1) Present
6. Branchiae: (0) Absent; (1) Present
7. Branchiae branched: (0) Absent; (1) Present
8. Posterior parapodia dorsally elevated: (0) Absent; (1) Present
9. Thoracic neuropodia with elevated ridge: (0) Absent; (1) Present
10. Thoracic neuropodial postchaetal lamellae: (0) Absent; (1) Present
11. Neuropodial subpodial lobes: (0) Absent; (1) Present
12. Neuropodial stomach papillae: (0) Absent; (1) Present
13. Thoracic furcate notochaetae: (0) Absent; (1) Present
14. Thoracic capillary notochaetae crenulated: (0) Absent; (1) Present
15. Abdominal neuropodial acicula: (0) Absent; (1) Present
16. Thoracic neuropodial uncini: (0) Absent; (1) Present
17. Thoracic neuropodial uncini small, inconspicuous among capillaries: (0) Absent; (1) Present
18. Thoracic neuropodial uncini large, conspicuous: (0) Absent; (1) Present
19. Thoracic neuropodia with narrow pointed spines (not uncini): (0) Absent; (1) Present
20. Thoracic neuropodial uncini limited to 1_few anterior thoracic chaetigers: (0) Absent; (1) Present
21. Posteriormost Thoracic neuropodia with modified spines: (0) Absent; (1) Present
22. Neuropodial swan hooks: (0) Absent; (1) Present

**Table 4.** Character matrix used in cladistic analysis 2 with peristomial rings excluded and all character states as absence/presence (*a/p*).

**Tableau 4.** Matrice de codage des caractères utilisée dans l'analyse cladistique n° 2, excluant les anneaux péristomiaux, mais incorporant les autres caractères codés en absence/présence (*a/p*).

	0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2
Genus/ Character No.	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2
<i>Cirrophorus</i>	0 0 1 0 0 0 1 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0
<i>Levensenia</i>	0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
<i>Orbinia</i>	1 1 0 0 0 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 0 0 0
<i>Phylo</i>	1 1 0 0 0 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 0 0 1 0
<i>Leitoscoloplos</i>	1 1 0 0 0 1 1 0 1 0 1 0 0 1 1 1 1 0 0 0 0 0 0 0
<i>Scoloplos</i>	1 1 0 0 0 1 1 0 1 1 1 0 0 1 1 1 1 1 0 0 0 0 0
<i>Leodamas</i>	1 1 0 0 0 1 1 0 1 1 1 0 0 1 1 1 1 1 0 1 0 0 0 0
<i>Califia</i>	1 1 0 0 0 1 1 0 1 0 1 0 0 0 1 1 1 0 1 0 1 0 1 0
<i>Naineris</i> sp. 1	1 0 0 1 0 1 1 0 1 1 1 1 0 0 1 1 1 0 0 0 0 0 0 0
<i>Naineris</i>	1 0 0 1 0 1 1 0 1 1 1 1 0 0 1 1 1 1 0 1 0 0 0 0
<i>Falklandiella</i>	1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0
<i>Orbiniella</i>	1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0
<i>Microrbinia</i>	1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0
<i>Schroederella</i>	1 1 0 0 0 1 1 0 0 0 0 0 0 0 0 1 ? 1 1 0 0 0 0 0 0
<i>Scoloplella</i>	1 0 0 1 0 1 1 0 0 0 1 0 0 0 1 ? 0 0 0 0 0 0 0 0
<i>Proscoloplos</i>	1 0 0 1 0 0 1 0 0 0 1 0 0 0 1 1 0 0 0 0 0 0 0 1
<i>Protoaricia</i>	1 0 0 1 0 1 1 0 1 0 1 0 0 1 1 1 1 1 1 0 0 0 0 0
<i>Orbiniella</i> <i>branchiata</i>	1 0 0 1 0 0 1 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0
<i>Protoariciella</i>	1 0 0 1 0 1 1 0 1 0 1 0 0 1 1 1 1 1 0 1 0 0 0 0
<i>Methanoaricia</i>	1 0 0 0 1 0 1 1 0 0 1 0 0 0 1 1 0 0 0 1 0 0 0 0

**Results**

**Systematic Account of the Seepworm**

FAMILY ORBINIIDAE

*Methanoaricia*, new genus

Type species

*Methanoaricia dendrobranchiata*, new species. Gender: feminine.

Diagnosis

Body large, robust, not divided into distinct regions; posterior parapodia lateral, not shifted dorsally. Prostomium narrow, elongate, rounded anteriorly; peristomium small, with single ring, separated from prostomium; nuchal organs present. Noto- and neuropodial postchaetal lamellae elongate, narrow; podia located close

Version 2.2 (Ramos, 1997). Two different Hennig86 commands intended to produce the most parsimonious trees were used: (1) mh\*(mhennig\*) + bb\* (branch swapping), and (2) ie\* (implicit enumeration, heuristic search). Output of each analysis was successively weighted (Farris, 1969; Carpenter, 1988). Nelson consensus was applied to trees resulting from equal and successively weighted trees. These commands were coded and executed from within Tree Gardener, from which the resulting trees and character state distributions were examined. Character states were mapped in Winclada Beta Version 0.9.95a (Nixon, 1999).

together; chaetal tori simple. Chaetae consisting of capillaries with transverse rows of spinelets (crenulated) and narrow pointed spines. Branchiae oval in cross-section, branched, with individual filaments bearing two blood vessels connected by numerous capillaries; distinct blood loop lacking; cilia present on two rows along length of branchia; branchiae present from anterior chaetigers continuing to posterior end. Pygidium with several long, tapering cirri.

#### Etymology

*Methano*, referring to the methane seep habitat of these worms and *Aricia*, Latin for nymph, the mythological wife of Hippolytes, and the generic name of the junior synonym of *Orbinia*.

#### Remarks

*Methanoaricia* differs strikingly from other large orbiniids in the nature of the prostomium, simple organization of the parapodia, lack of distinct body regions and corresponding absence of dorsally shifted posterior parapodia. Branched branchiae are rare in the Orbiniidae and are known only for one or two species of *Leodamas*. A few of the smaller orbiniids such as *Orbinella* and *Microrbinia* also lack distinct body regions and posteriorly shifted parapodia, but species of those genera lack branchiae and otherwise have typical appearing orbiniid parapodia.

#### *Methanoaricia dendrobranchiata*, new species

Figures 1-2

#### Type locality and type material

Gulf of Mexico, continental slope off Louisiana, Green Canyon, MMS Block 232, *Sea Link* Dive 2656, 10 Sep 1995, 27°43.327'N, 91°16.606'W, 650 m, in mussel beds adjacent to brine pool. Holotype (USNM 186776), 25 paratypes (USNM 186777); 25 paratypes (LACM-AHF Poly 1961).

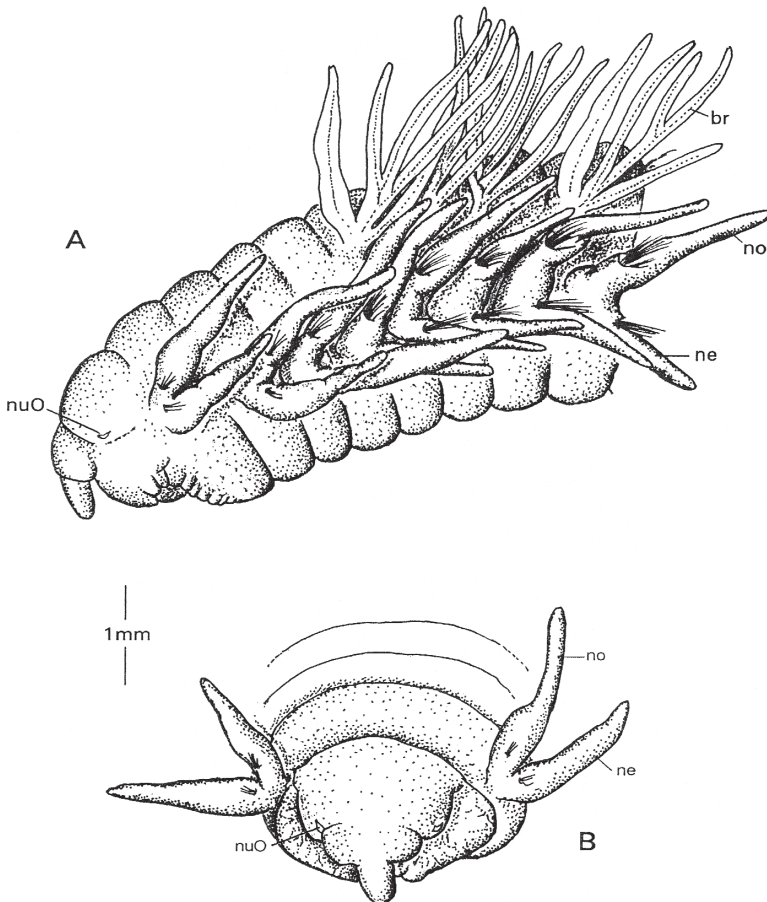
#### Description

Worms large, 10-15 cm long, 7-9 mm wide across the widest anterior segments, with hundreds of crowded segments; holotype 9.8 cm long, 8.5 mm wide across chaetiger 25, 4.0 mm wide across chaetiger 225, with 310 segments. Body widest anteriorly, gradually tapering posteriorly, distinct regions not apparent. Branchiae throughout body, but branched and most conspicuous in first one-fourth of body. Parapodia highly vascularized adjacent to branchiae, with numerous branching blood vessels.

Prostomium narrow, elongate, usually directed ventrally (Fig. 1A, B); bluntly rounded along anterior margin, with shape resembling that of capitellid; eyes absent; eversible nuchal organs present on anterior lateral margin of peristomium. Peristomium single, narrow, incomplete achaetous ring.

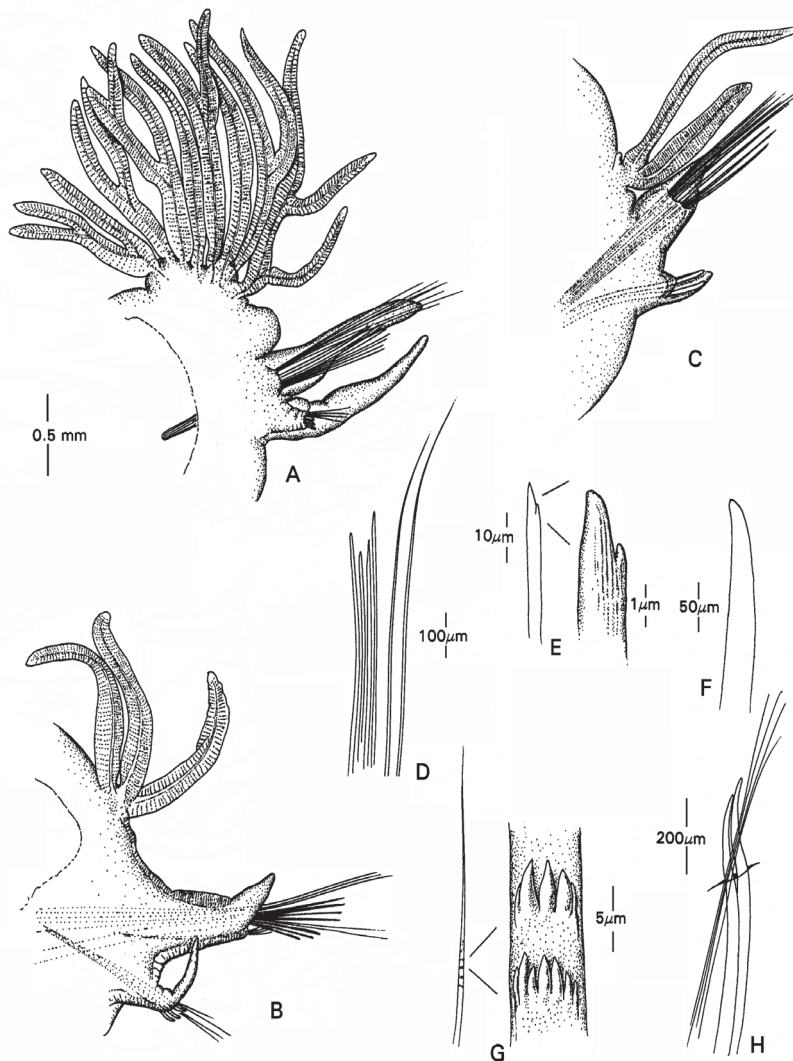
Chaetiger 1 and subsequent segments with long, cirriform noto- and neuropodial lamellae superficially resembling tentacular cirri (Fig. 1A, B); these close together, arising from single point of origin (Fig. 2A); after about 10-15 segments, podia separate, but never very far, continuing for length of body (Fig. 2B); posteriorly, both lamellae becoming shorter, with neuropodial lamella eventually reduced, short and pointed, about one-fourth length of dorsal one (Fig. 2C).

Chaetal fascicles of noto- and neuropodia arising very close to one another over first few chaetigers, then gradually separating, but never far. Notochaetae of anterior chaetigers longer, more numerous than



**Figure 1.** *Methanoaricia dendrobranchiata* gen. et sp. nov.. **A** anterior end, left lateral view; **B** anterior end, frontal view, showing prostomium. (*br*) branchiae; (*ne*) neuropodium; (*no*) notopodium, (*nuO*) nuchal organ.

**Figure 1.** *Methanoaricia dendrobranchiata* gen. et sp. nov.. **A** extrémité antérieure, vue latérale gauche ; **B** extrémité antérieure, vue frontale montrant le prostomium. (*br*) banchies ; (*ne*) neuropode ; (*no*) notopode ; (*nuO*) organe nuchal.



**Figure 2.** *Methanoaricia dendrobranchiata*. **A** chaetiger 6, anterior view; **B** middle body segment, posterior view; **C** posterior segment, anterior view; **D** notopodial spines and capillaries from anterior chaetiger; **E** details of anterior notopodial spines showing apical spur; **F** anterior neuropodial spine; **G** details of spinelets on capillaries; **H** posterior neuropodial acicular spines and capillaries. (Details of **E** and **G** taken from SEM).

**Figure 2.** *Methanoaricia dendrobranchiata*. **A** sétigère 6, vue antérieure ; **B** segment du milieu du corps, vue postérieure. **C** segment postérieur, vue antérieure ; **D** épines notopodiales et soies capillaires d'un sétigère antérieur ; **E** détail des épines notopodiales antérieures montrant la pointe apicale ; **F** épine neuropodiale antérieure vue antérieure ; **G** détail des denticulations sur les soies capillaires ; **H** épines aciculaires neuropodiales postérieures et soies capillaires. (Les détails en **E** et **G** proviennent d'observations au MEB).

neurochaetae, consisting of long, orbiniid-like capillaries bearing transverse rows of bristles (Fig. 2D, G) and 8-10 narrow spines with bluntly pointed tips, some with subapical spur or secondary tooth oriented forward along

shaft of spine (Fig. 2E); spines of middle and posterior chaetigers reduced to 4-6 per fascicle, without spur. Neurochaetae of anterior chaetigers with 3-4 elongate, thin spines with straight shaft and blunted tips accompanied by few threadlike capillaries; 3-4 short, protruding, curved aciculae or spines at base of fascicle (Fig. 2F); spines lost by middle body chaetigers, acicular spines reduced to two per neuropodium in posterior chaetigers (Fig. 2H); neuropodial spines and aciculae thicker than notopodial spines.

Branchiae from chaetiger 5, occurring dorsal to notopodium (Fig. 1A); branched branchiae in anterior segments with numerous dichotomies (Fig. 2A, B), reduced to single branched branchia posteriorly (Fig. 2C); all branchiae with central blood vessel connected to lateral blood vessel by numerous connecting capillaries; each branch with a paired row of cilia extending along length; branchiae superficially appearing striated due to elongate cells in integument.

Pygidium with terminal anus surrounded by several long, tapering cirri.

#### Etymology

*Dendro*, from the Greek *dendron* for tree, referring to the branched nature of the branchiae; *branchos*, Greek for gill.

#### Remarks

*Methanoaricia dendrobranchiata* is definitely allied to the Orbiniidae despite the narrow prostomium and lack of distinct body regions. Crenulated (sometimes called camerated) capillaries are known only from orbiniids, and the general distribution of spines along the body is also reminiscent of members of this family. The type of branchia with central and lateral blood vessels connected by blood capillaries is found in orbiniids and paraonids (Eisig, 1914; Strelsov, 1973). This type of branchia differs from those of spioniforms and cirratulids where the central blood vessel forms a loop, essentially bathing the interior of the branchia in blood. The cold-seep habitat where *M. dendrobranchiata* lives is characterized by low

dissolved oxygen and elevated sulphide levels (MacDonald et al., 1990). The numerous branched branchial filaments and highly vascularized parapodia suggest respiratory adaptations to such a hypoxic environment.

Distinct body regions, including the narrow posterior end with the ragged elevated appearance of parapodia so characteristic of large orbiniids, do not occur in the seepworm. Some recently described small orbiniids (e.g., genera *Orbiniella*, *Microrbinia*) also lack distinct body regions, but species of these genera are abranchiate. Branched branchiae are known for two species of *Leodamas* (Blake, unpublished data). The parapodial organization is decidedly not orbiniid-like. In most orbiniids the noto- and neuropodia are widely separated from one another. Additionally, the chaetal tori of orbiniids, especially in thoracic neuropodia, typically form distinct elevated cushions from which numerous neurochaetae arise in multiple rows. Even the small species of orbiniids have widely separated chaetal fascicles. In the seepworm, the podia are poorly developed, situated close to one another, and have a reduced number of chaetae confined to simple fascicles.

### Phylogenetic Analysis of the Orbiniid Genera

*Analysis (1)*. The results of Analysis (1) where the peristomial rings were included as a/p yielded the following results: the mh\*bb\* command sequence and equal weighting resulted in 602 trees and the ie\* command yielded 618 trees (L=47, CI=0.55, RI=0.75). Both sets of trees were successively weighted and yielded 6 most parsimonious trees (L=202, CI=0.87, RI=0.93). Tree No. 6 most closely approximates the consensus of these trees and is shown in Figure 3 where all characters are mapped.

In this analysis, two large clades are separated by the single- or multiple-ringed peristomium. This result follows the traditional classification of Hartman (1957) where those genera having a single peristomial ring are referred to the subfamily Orbiniinae and those with two or more such rings are referred to the subfamily Protoariciinae. The seepworm, *Methanoaricia*, appears at the base of the Orbiniinae suggesting that this type of orbiniid might be plesiomorphic to the other Orbiniinae genera; *Microrbinia* is included in the Orbiniinae in this result.

The results of the secondary analysis (1B), where the peristomial and prostomial characters were coded as unordered multistates yielded the following data. The mh\*bb\* commands yielded 2887 trees (L=43, CI=0.60, RI=0.75). After successive weighting, 26 most-parsimonious trees were produced (L=195, CI=0.84, RI=0.91). Three of the 26 trees and the consensus tree are shown in Figure 4. The most noticeable result is the breakup of the genera comprising the subfamily Protoariciinae. *Schroederella*, *Protoaricia* (the type genus), *Protoariciella*,

*Scoloplella*, and sometimes *Proscoloplos* are shifted to a closer relationship with the genera that normally comprise the Orbiniinae, leaving only *Orbiniella*, *Orbiniella branchiata*, and *Falklandiella*. *Microrbinia* is included with these three taxa and the four form a distinct clade, sometimes with *Methanoaricia* and *Proscoloplos*. *Methanoaricia* is not well resolved in this analysis, occurring both as a separate sister group and sometimes with *Orbiniella*, *Falklandiella*, and *Microrbinia*. These results are similar to the pattern seen in the next analysis when peristomial rings are omitted.

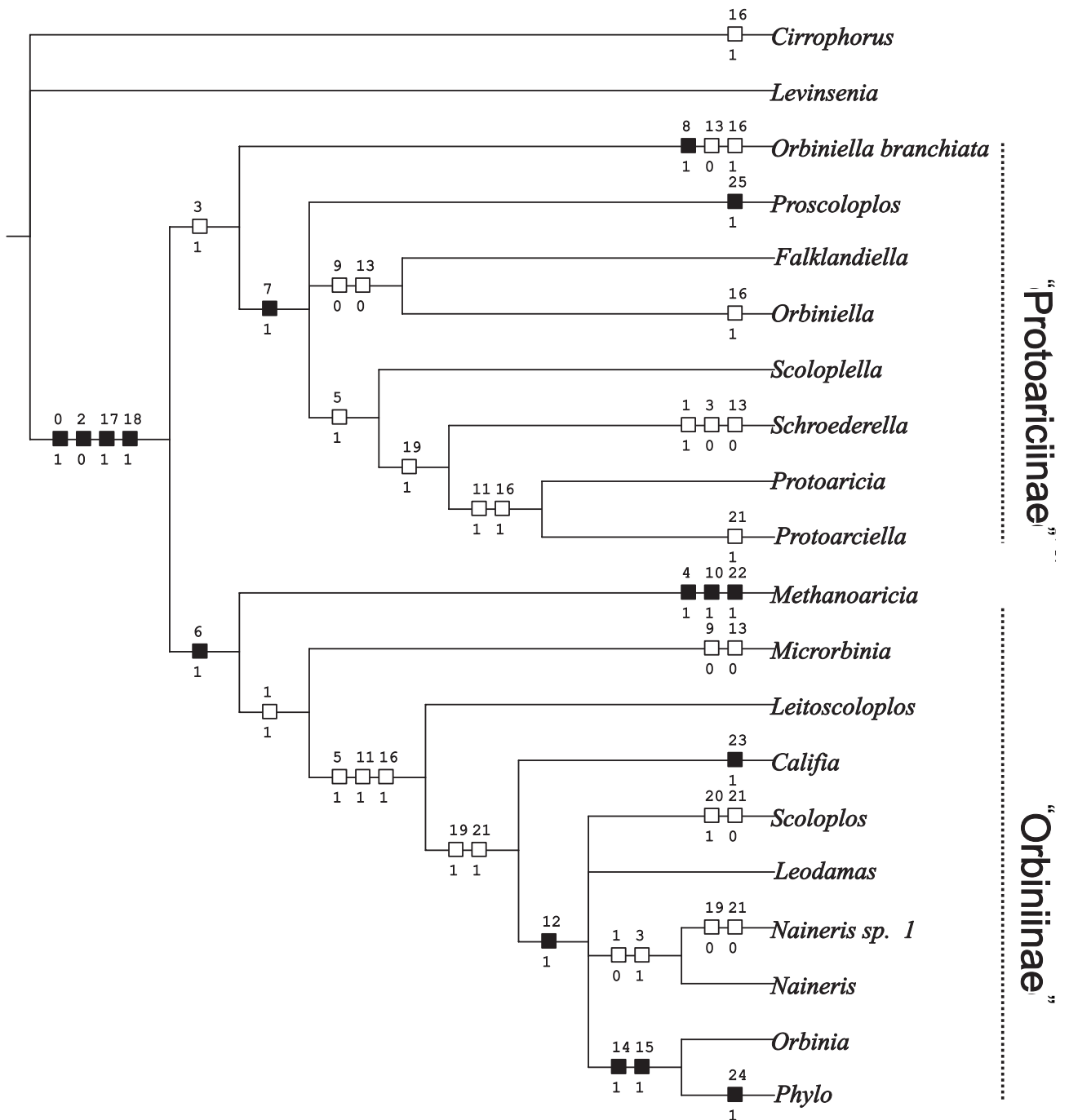
*Analysis (2)*. In this analysis the peristomial rings are excluded from the a/p character matrix. The mh\*bb\* command sequence and equal weighting resulted in 80 trees and the ie\* command yielded 81 trees (L=39, CI=0.58, RI=0.77). Both sets of trees were successively weighted and yielded the same 6 most parsimonious trees (L=190, CI=0.90, RI=0.95). Trees 1, 3, and 6 are shown in Figure 5, along with the consensus tree derived from these results. In this analysis, *Methanoaricia* is not part of a monophyletic sequence of orbiniid genera, but appears as a basal but separate sister taxon. The remaining orbiniid genera form two clades. The largest clade includes all of the usual Orbiniinae genera plus *Protoariciella*, *Protoaricia*, *Schroederella*, and *Scoloplella*, similar to analysis 1B (see above). Thus, this clade includes four genera normally assigned to the Protoariciinae, including its type-genus *Protoaricia*. The smaller clade includes *Proscoloplos*, *Falklandiella*, *Orbiniella*, *Orbiniella branchiata*, and *Microrbinia*. This clade consists of small orbiniids having poorly developed body regions and weakly developed parapodia; *Orbiniella* and *Microrbinia* lack branchiae. Within this smaller clade, *Proscoloplos* is not well resolved despite the autoapomorphic swan hooks.

## Discussion

### Traditional classification of the Orbiniidae

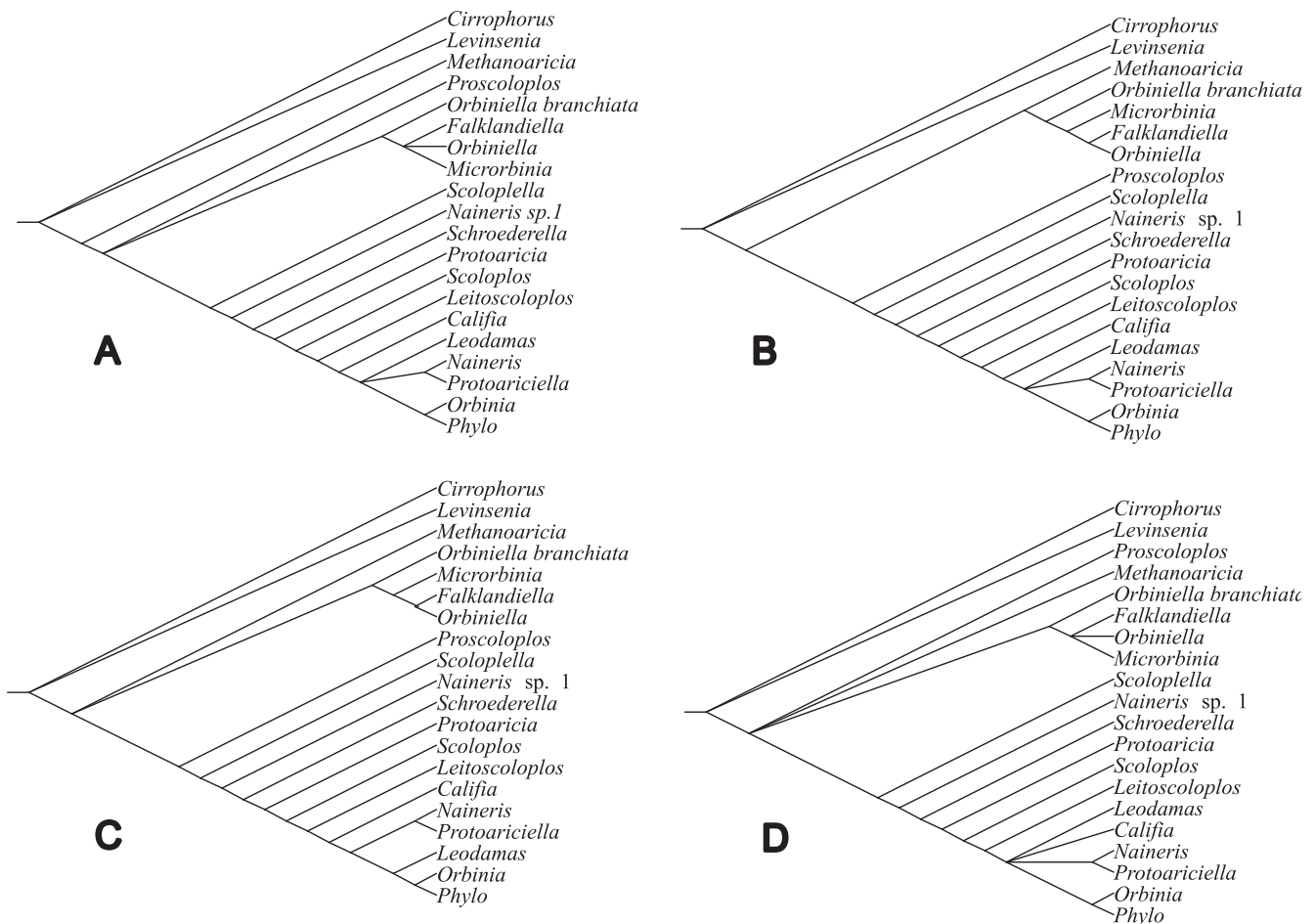
Orbiniids are traditionally classified by the arrangement seen in the results of Analysis (1) where there are two distinct groups of genera separated on the basis of the number of peristomial rings: Subfamily Orbiniinae (one ring) and Protoariciinae (two rings) (Figure 3). This arrangement was formalized by Hartman (1957) and has been used by most subsequent investigators. As noted in earlier remarks and by Blake (1996), this arrangement breaks down when developmental characteristics are taken into account. It has now been well documented for some species of Orbiniinae that the two peristomial rings present in late larvae and juveniles later coalesce into a single ring. These data plus the fact that nearly all described species of





**Figure 3.** Cladistic analysis of the orbiniid genera using absence/presence (*a/p*) of a traditional suite of characters including the number of peristomial rings. Cladogram represents a map of characters for tree no. 4 of 6 successively weighted most parsimonious trees that is most similar to the consensus tree. Solid blocks represent apomorphies; open blocks represent homoplasious characters. The two large clades represent the traditional subfamilies: Protoariciinae and Orbiniinae.

**Figure 3.** Analyse cladistique des genres d'Orbiniidae en absence/présence (*a/p*) de caractères morphologiques diagnostiques, incluant le nombre d'anneaux du péristomium. Le cladogramme représente la distribution des caractères sur l'arbre n° 4, obtenue par comparaison des six arbres les plus parcimonieux présentant la même topologie que l'arbre consensus. Les carrés noirs représentent les apomorphies ; les carrés blancs représentent les caractères homoplasiques. Les deux groupes principaux représentent les sous-familles traditionnelles : Protoariciinae et Orbiniinae.



**Figure 4.** Cladistic analysis of the orbiniiid genera using unordered multistate characters for peristomial rings and prostomia; binary absence/presence (*alp*) states are used for other characters. Cladogram shown in A-C represent trees 1, 12 and 17 of 26 successively weighted most parsimonious trees. Tree shown in D represents tree derived from Nelson consensus of all 26 trees.

**Figure 4.** Analyse cladistique des genres d'Orbiniidae utilisant des caractères polymorphes non ordonnés pour les anneaux du péristomium et les prostomiums. Les autres caractères sont codés en absence/présence (*alp*). Les cladogrammes A-C représentent les arbres 1, 12 et 17 des 26 arbres les plus courts et le cladogramme D correspond à l'arbre consensus de Nelson obtenu à partir de ces mêmes 26 arbres.

Protoariciinae are considerably smaller than Orbiniiinae intuitively suggests that some of those species might actually be juveniles of other orbiniiids. These facts suggest that the number of peristomial rings is not a reliable taxonomic character for defining either species or genera. Therefore, the results of Analysis (2) where peristomial ring characters are excluded need to be examined carefully. Mapped characters from Analysis 2 are shown in Figure 6.

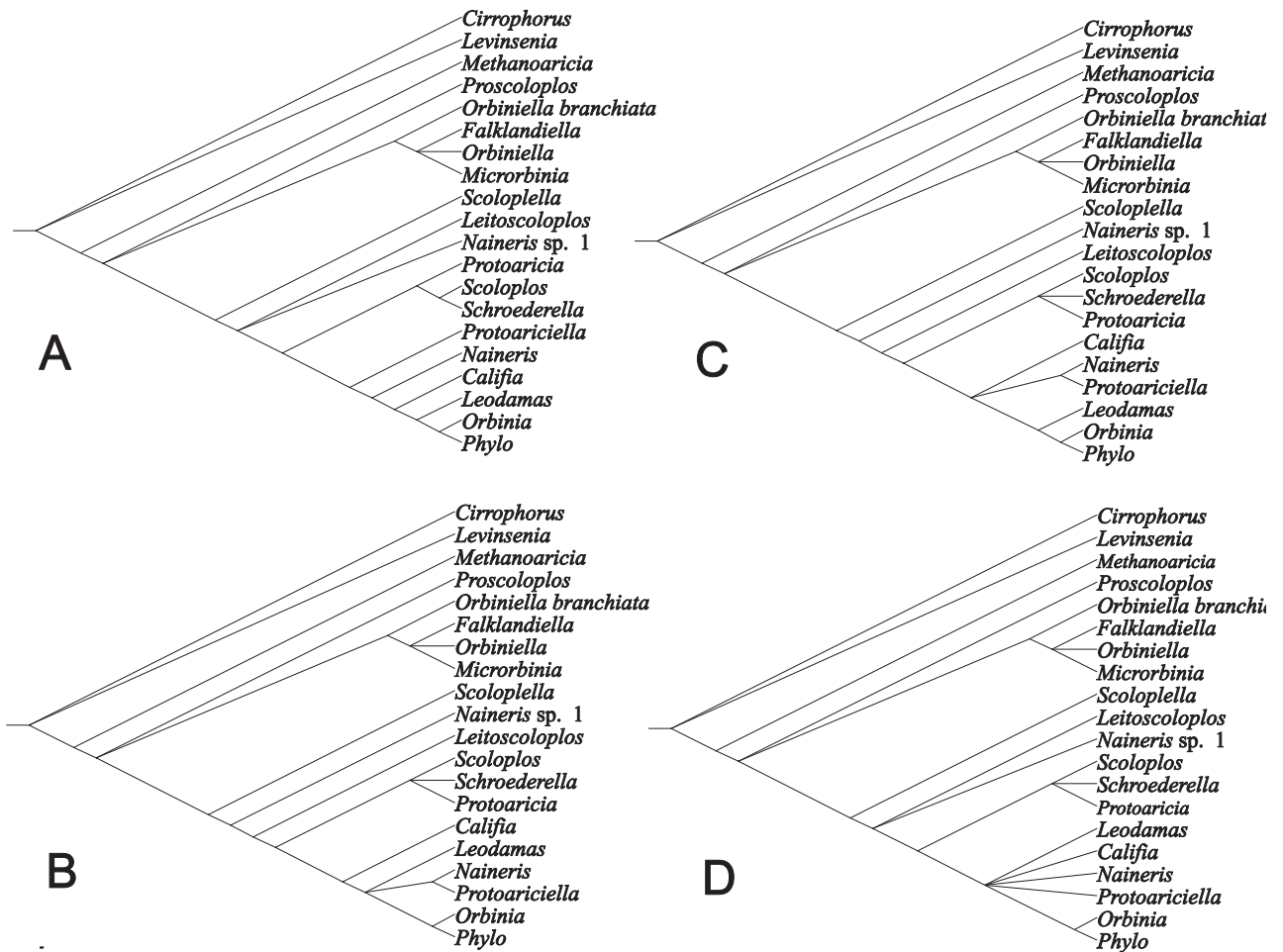
#### Homology of characters (Analysis 2)

##### *Differentiation of the body into regions.*

Differentiation of the body of orbiniiids into distinct thoracic and abdominal regions is derived and is reflected in the cladistic analysis as evidence of monophyly within the

family. The seepworm, *Methanoaricia*, and the smaller, mostly abranchiate orbiniiids such as *Orbiniella*, *Falklandiella*, and *Proscoplos* show no evidence of differentiation of the body into distinct regions. In contrast, all of the orbiniiids formerly and currently referred to the subfamily Orbiniiinae exhibit well-developed thoracic and abdominal regions.

*Prostomium.* The results of the cladistic analysis strongly suggest that prostomial shape, while important in defining genera and groups of species, is homoplastic and not an important character in defining monophyly of the genera. Several of the small abranchiate genera such as *Orbiniella*, *Falklandiella*, and *Proscoplos* have bluntly rounded prostomia and form a distinct clade in the analysis. The



**Figure 5.** Cladistic analysis of the orbiniid genera using absence/presence (*a/p*) of a traditional suite of characters that excludes the number of peristomial rings. Cladogram shown in A-C represent for trees 1, 3 and 6 of 6 successively weighted most parsimonious trees. Tree shown in D represents tree derived from Nelson consensus of all six trees.

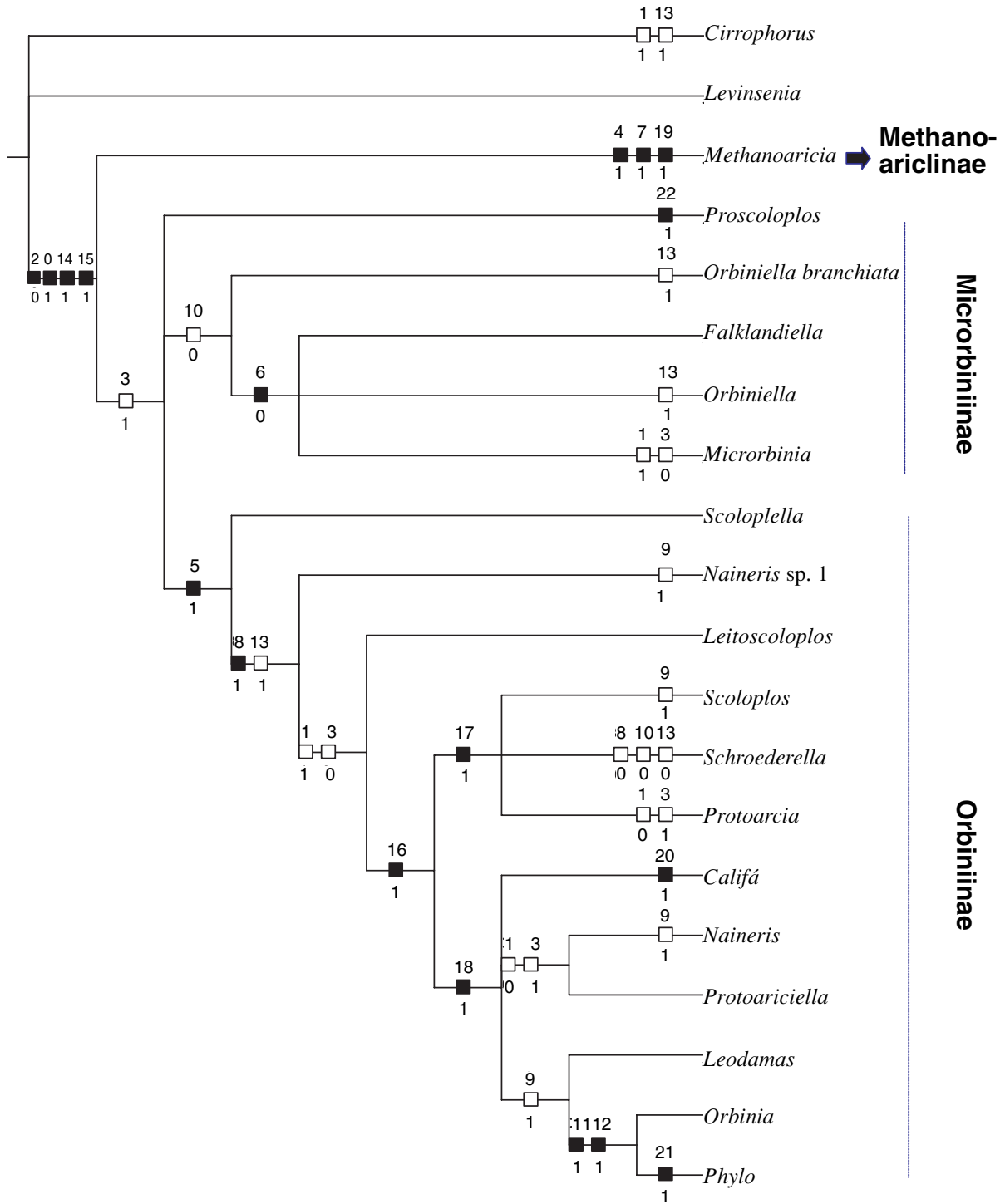
**Figure 5.** Analyse cladistique des genres d'Orbiniidae en absence/présence (*a/p*) d'une série traditionnelle de caractères, excluant le nombre d'anneaux du péristomium. Les cladogrammes A-C représentent les arbres 1, 3 et 6 des 6 arbres les plus courts et le cladogramme D correspond à l'arbre consensus de Nelson pour ces mêmes 6 arbres.

prostomial shape is very similar to species of other genera such as *Naineris*, *Protoaricia*, and *Scoloplella*.

**Parapodia.** Parapodial structure varies widely in orbiniids, but elaboration of the abdominal parapodia and their shift to a dorsal position is a derived characteristic for most of the larger orbiniids and a contributor to a monophyletic sequence within the large clade redefined here as Orbiniinae (see below). In the smaller abranchiate species and the seepworm *Methanoaricia*, the parapodia are simple and are not shifted to a dorsal position. This is the plesiomorphic state. *Scoloplella* also has simple abdominal parapodia and this taxon may be transitional between the two main clades of orbiniids. *Scoloplella* may represent a plesiomorphic genus in the subfamily Orbiniinae.

**Branchiae.** Branchiae of orbiniids are typically single and not branched. Therefore, the dendritically branched branchial development in *Methanoaricia* is highly autapomorphic. Multiple branchiae are known for two species of *Leodamas*, but these species have a palmately branched branchial arrangement (Blake, unpublished). The basic branchial structure of orbiniids and paraonids is similar in that a central and lateral blood vessel are connected by numerous thin capillaries (Eisig, 1914; Strelsov, 1973). This is in contrast to the blood loop arrangement found in branchiae of other families. The vascular nature of the branchiae of the seepworm, *Methanoaricia*, is similar to that of paraonids and orbiniids.

**Chaetae.** Chaetal development in orbiniids may be the



**Figure 6.** Cladistic analysis of the orbiniid genera using presence/absence (a/p) of a traditional suite of characters that excludes the number of peristomial rings. Cladogram represents a map of characters for tree no. 6 of 6 successively weighted most parsimonious trees. Solid blocks represent apomorphies; open blocks represent homoplasious characters. Three clades represent a revised arrangement of sub-families for the Orbinidae.

**Figure 6.** Analyse cladistique des genres d'Orbiniidae en présence/absence (a/p) d'une série traditionnelle de caractères, excluant le nombre d'anneaux du péristomium. Le cladogramme représente la distribution des caractères sur l'arbre n° 6, obtenue à partir d'une comparaison des six arbres les plus parcimonieux. Les carrés noirs représentent les apomorphies ; les carrés blancs représentent les caractères homoplasiques. Les trois clades représentent un nouvel arrangement des sous-familles des Orbiniidae.

most important aspect of eventually understanding the origin and evolution of orbiniids. The results of the cladistic analysis demonstrate clear monophyly among the genera with respect to the elaboration of chaetae on the thoracic neuropodia. Within the genera of Orbiniinae, there is a clear progression from those genera having all thoracic neuropodial capillaries (i.e., *Leitoscoloplos*), to the addition of smaller, inconspicuous spines (uncini) among the capillaries (i.e., *Scoloplos*), and to the development of large, heavy spines with few or no capillaries (i.e., *Leodamas*, *Naineris*, *Orbinia*, and *Phylo*).

#### Suggested classification of Orbiniidae

Based on the results of Analysis (2) where peristomial characters are excluded, a modified classification of Orbiniidae is suggested. Three clades include: (1) a clade consisting at this time only of the seepworm, *Methanoaricia*, which appears to possess traits that diverge from other orbiniids, (2) a small clade consisting of five genera: *Proscoloplos*, *Orbiniella branchiata*, *Falklandiella*, *Orbiniella*, and *Microrbinia*, of these, *Proscoloplos* is not well resolved, and (3) a large clade consisting of 12 genera including four formerly assigned to Hartman's subfamily Protoariciinae (including the type-genus *Protoaricia*) and eight that have traditionally been included in the Orbiniinae.

I suggest that these three clades be designated as subfamilies of Orbiniidae as follows: (1) Methanoariciinae, new subfamily, (2) Microrbiniinae, new subfamily, and (3) Orbiniinae Hartman, Emended. Figure 6 shows the arrangement of the genera within these taxa. Definitions of these clades (subfamilies) follow:

#### Methanoariciinae, new subfamily

Type-Genus: *Methanoaricia* Blake, new genus

##### Diagnosis

Body large, lacking distinct regions; parapodia lateral throughout, none shifted dorsally. Prostomium narrow, elongate, rounded anteriorly; nuchal organs present. Peristomium small, with single achaetous ring, separated from prostomium. Noto- and neuropodial postchaetal lamellae elongate, narrow; closely associated with podial lamellae. Bases of podia merged anteriorly, separated, but closely applied posteriorly. Chaetal tori simple; chaetal fascicles consisting of capillaries with transverse rows of bristles (crenulated) and narrow pointed spines; uncini, lyratae chaetae, swan hooks, and fail chaetae absent. Branchiae dendritically branched, oval in cross-section, with two rows of cilia along length; anterior branchiae with numerous branches; posterior branchiae with two branches; individual branchial branches each with two blood vessels connected by numerous capillaries; distinct blood loop lacking. Pygidium with several long, tapering cirri.

Inclusive genus: *Methanoaricia*.

#### Microrbiniinae, new subfamily

Type-Genus: *Microrbinia* Hartman, 1965

##### Diagnosis

Body small, lacking distinct regions; parapodia lateral throughout, none shifted dorsally. Prostomium broad, bluntly rounded or more elongate and conical; nuchal organs present. Peristomium with 1-3 achaetous rings, separated from prostomium. Noto- and neuropodial postchaetal lamellae reduced to short lobes. Bases of podia separated throughout; chaetal tori simple. Chaetae consisting of capillaries always present, blunt-tipped spines or uncini and swan hooks present or absent; lyratae chaetae absent. Branchiae typically absent, rarely present, if present, simple throughout, oval to flattened with two longitudinal rows of cilia. Pygidium with few cirri or cirri absent.

Inclusive genera: *Microrbinia*, *Orbiniella*, *Falklandiella*, and *Proscoloplos*. *Orbiniella branchiata* may represent a new genus, but further study is needed.

#### Subfamily Orbiniinae Hartman, 1957 Emended

Type genus: *Orbinia* Quatrefages, 1865

##### Diagnosis

Body large, with distinct regions; parapodia lateral in thoracic region, shifted dorsally in abdominal region. Prostomium bluntly rounded to acutely pointed; nuchal organs present; eyes present or absent. Peristomium with 1-2 achaetous rings, separated from prostomium. Noto- and neuropodial postchaetal lamellae single, simple lobe to multiple lobes, sometimes branched; subpodial lobes and stomach papillae present or absent; interramal cirri present or absent in abdominal region. Chaetae consisting of capillaries and lyratae chaetae; blunt-tipped spines (uncini), modified spear-like chaetae, and flail chaetae present or absent. Branchiae typically present, rarely absent; branchiae usually single, rarely palmately branched; oval to flattened, with two longitudinal rows of cilia and typical orbiniid structure with two blood vessels connected by numerous capillaries; branchiae of abdominal region thinner, more elongate than on thorax. Pygidium with several long filamentous anal cirri, or cirri absent.

Inclusive genera: *Califia*, *Leitoscoloplos*, *Leodamas*, *Naineris*, *Orbinia*, *Phylo*, *Protoaricia*, *Protoariciella*, *Schroederella*, *Scoloplella*, and *Scoloplos*. *Naineris* sp. 1 appears to represent a new genus.

Problematic genera: *Pararicia*, *Pettibonella*, *Berkeleyia*, and *Uncorbinia*.

### Phylogeny of the Orbiniidae

The results of the phylogenetic analysis suggest a pattern of increasing complexity, differentiation and specialization of body regions, chaetae, and parapodia. Nine of the 12 genera of the Orbiniinae have modified neuropodial spines (uncini) to some degree. The distribution and development of these spines is demonstrated to be more important than prostomial shape, a character that has traditionally been used to separate the genera from one another. The importance of chaetal structure and distribution is demonstrated in the topologies where *Naineris* sp. 1, an orbiniid having a blunted prostomium and that lacks modified neuropodial spines, is more closely related to other genera having pointed prostomia such as *Leitoscoloplos* and *Scoloplella* and also lacking neuropodial spines rather than to other *Naineris*. Typical *Naineris* species having modified neuropodial spines are related to *Califia*, *Protoariciella*, *Leodamas*, *Orbinia*, and *Phylo*. Prostomial shape is irrelevant in defining the relationships of those genera.

Another polytomy is that *Leodamas* species consistently group with *Naineris*, *Protoaricia*, *Orbinia*, and *Phylo*, all of which have heavy thoracic neuropodial spines, rather than with *Scoloplos* to which *Leodamas* is usually referred as a subgenus (Hartman, 1957). *Scoloplos* has narrow, less conspicuous spines among numerous capillaries. Given this result, *Leodamas* is here treated as a full genus rather than a subgenus.

The small orbiniids belonging to *Proscoloplos*, *Orbiniella*, *Falklandiella*, and *Microrbinia* are for the most part resolved on negative characters such as the absence of branchiae and poorly developed podial lobes and postchaetal lamellae. Given the small size of species referred to these genera, it is likely that some will eventually prove to be juveniles of larger orbiniids once reproductive and development data are analyzed more fully. However, *Microrbinia lineata* Hartman, 1965, although small, has been found to be sexually mature year-round at a 2000 m site off North Carolina (Blake, 1993). The unusual swan hooks that characterize *Proscoloplos* have not been found in other orbiniids and this genus appears to be unique within the Orbiniidae.

The unusual seepworm, *Methanoaricia*, consistently appears in a basal position in the cladograms. *M. dendrobranchiata* appears to represent a separate clade or branch of polychaetes that is related to orbiniids and paraonids. Its basal position may be an artifact of its unusual morphology and adaptation to a hypoxic environment rather than evidence that it possesses ancestral characteristics. The species is highly autapomorphic and in addition to what has been presented in this paper, the seepworm has an unusual sperm morphology that is unlike other polychaetes (K. Eckelbarger, unpublished). As data accumulates on the

seepworm and other orbiniids it should be possible to refine the phylogeny presented here.

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