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Gross Morphology of the Brain of Pilargid Polychaetes: Taxonomic and Systematic Implications

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ABSTRACT

The gross morphology of the brains of representative species of the pilargid genera *Ancistrosyllis*, *Cabira*, *Litocorsa*, *Parandalia*, *Pilargis*, *Sigambra*, and *Synelmis* is described and compared. Results suggest brain morphology may provide useful taxonomic and systematic characters within the Pilargidae. Results of a cladistic analysis are

presented for selected genera and species groups based on traditional morphological characters and gross brain morphology. Sister-group relationships are discussed from these results, as well as implications for the definitions of *Sigambra*, *Synelmis*, and *Litocorsa*, and the status of the subfamilies Sigambrinae and Synelminae.

INTRODUCTION

Depending upon interpretation, 10 to 13 genera currently comprise the Pilargidae Saint-Joseph (see below). Generic distinctions are, for the most part, well defined (e.g., Hartman, 1947; Pettibone, 1966; Emerson and Fauchald, 1971; Wolf, 1984). One curious feature, however, "a large glandular organ," was first mentioned by Pearson (1970: 72) in his description of *Litocorsa stremma*.

Wolf (1984) stated that this structure also occurred in other pilargid genera, albeit variously developed, and that it may be of some systematic importance. This unknown organ is actually the brain (fide Wolf, 1986) and is similar to that described for some syllids (Perkins, 1980).

There have been numerous studies describing the brains of polychaetes (e.g., Raw,

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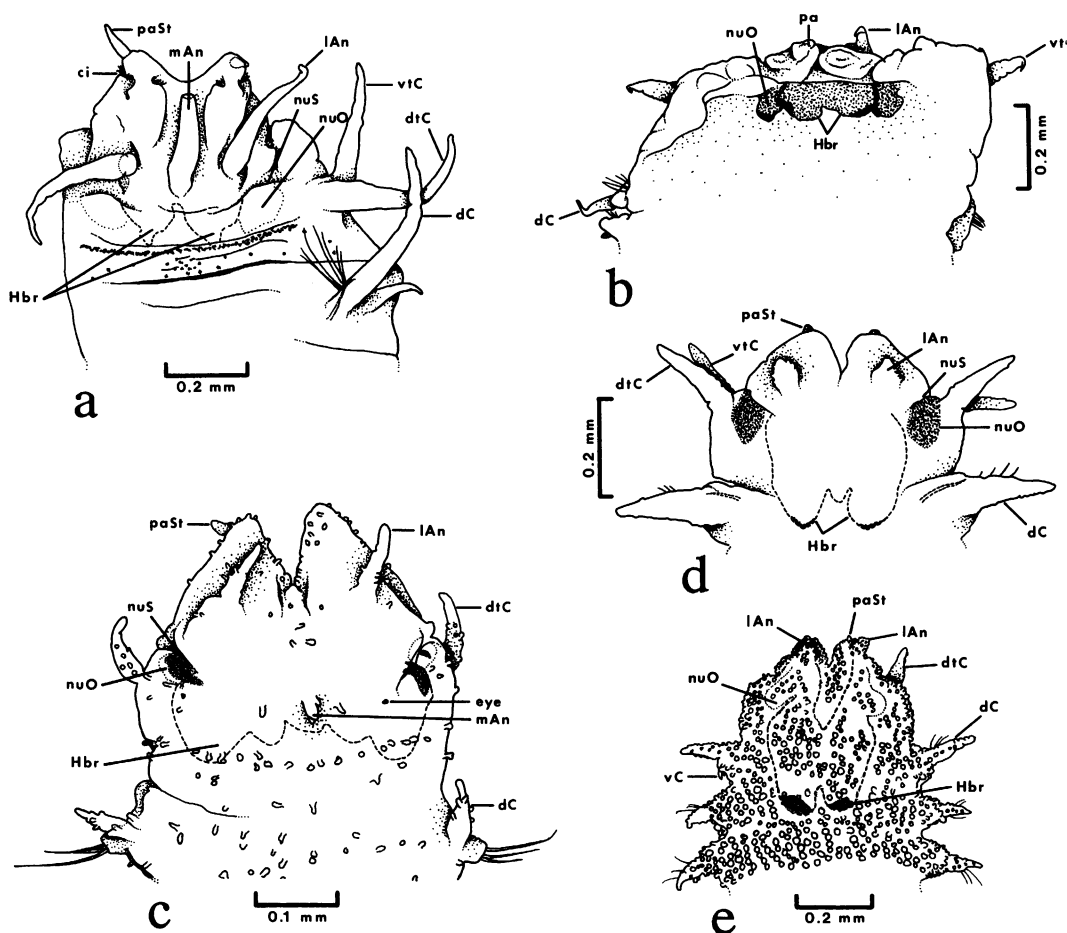


Fig. 1. Anterior ends of specimens of selected pilargid genera (all drawn after removal of pharynx): a, *Sigambra tentaculata*, dorsal view; b, *Sigambra wassi*, ventral view (body wall spread to view brain); c, *Ancistrosyllis jonesi*, dorsal view; d, *Pilargis* sp., dorsal view; e, *Pilargis berkeleyae*, dorsal view. [Figure 1e after Wolf, 1984: fig. 29-24a]

1949; Bullock and Horridge, 1965; Orrhage, 1966, 1978; Strelzov, 1973), but these studies, as well as others, have bypassed gross morphology of the brain in favor of minute detail of the nervous system. While a histological approach is certainly most valuable, it is often neither available to nor practical for polychaete taxonomists.

In many families, gross morphology of the brain will be of little systematic value because of the difficulty in obtaining accurate observations. In some families, however, the brain can be more easily observed. For example, Perkins (1980: 1114) described and figured the brain of several species of the syllid genus *Sphaerosyllis* Claparède and commented on

its possible taxonomic importance. In the Pilargidae, the brain is sometimes large enough to be seen through the integument, but when dissection is necessary, only simple techniques are needed (see below). It thus seems that the brain may provide an additional diagnostic character for the Pilargidae, and, therefore, an assessment of its usefulness is presented in this study.

The purpose of this study is to (1) describe the intrafamilial gross morphology of the pilargid brain, (2) show how this gross morphology may be an important taxonomic character at the generic and specific level, and (3) use brain morphology, along with more traditional morphological characters, to de-

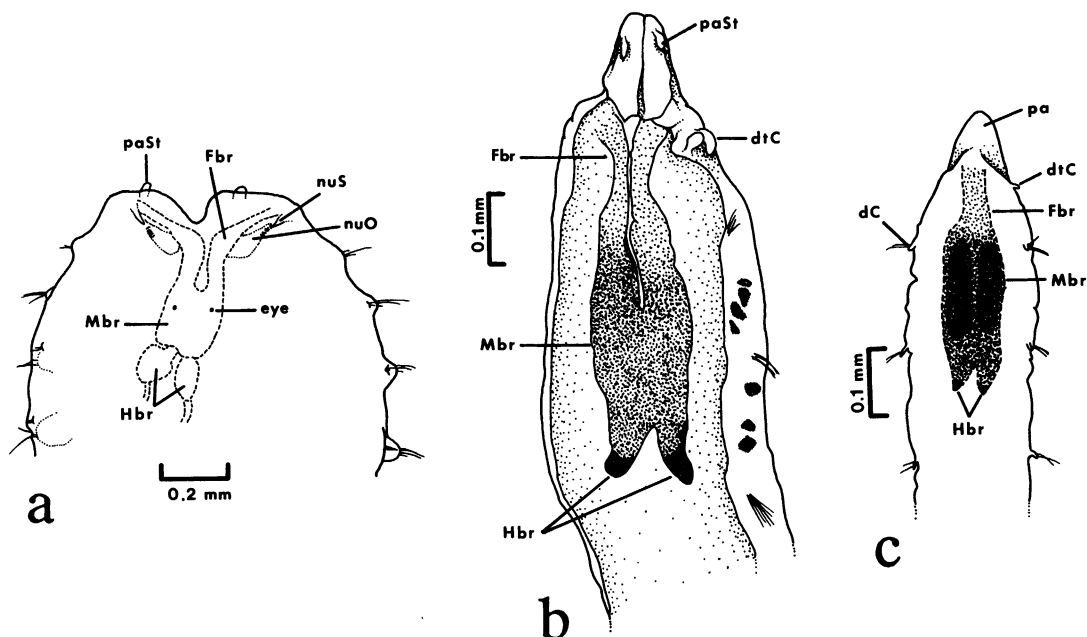


Fig. 2. Anterior ends of specimens of selected pilargid genera (all drawn after removal of pharynx): a, *Parandalia* sp., ventral view; b, *Synelmis ewingi*, ventral view (body wall spread to view brain); c, *Litocorsa antennata*, dorsal view. [Figure 2c after Wolf, 1986: fig. 1i]

termine hypotheses of sister-group relationships for selected genera and species.

FIGURE ABBREVIATIONS

ci	cilia
dC	dorsal cirrus
dtC	dorsal tentacular cirrus
Fbr	forebrain
Hbr	hindbrain
lAn	lateral antenna
mAn	median antenna
Mbr	midbrain
nuO	nuchal organ
nuS	nuchal slit
pa	palp
paSt	palpostyle
vC	ventral cirrus
vtC	ventral tentacular cirrus

AN OVERVIEW OF THE PILARGID BRAIN

The pilargid brain is relatively large when compared to the brain of other polychaete families and is here divided into three regions: forebrain, midbrain, and hindbrain. The exact boundaries of each region are only defined from a gross morphological standpoint, not

according to histological differentiation. Indeed, detailed histological studies of brains in species of other polychaete families fail to identify any such regional boundaries (e.g., Bullock and Horridge, 1965; Orrhage, 1978).

The forebrain is located in the posterior portion of the prostomium, though its exact anterior boundary cannot be determined using the methods employed here. The forebrain probably contains, as it does in other polychaete taxa, palpal and stomodeal centers, and the anterior roots of the circumesophageal connectives (Bullock and Horridge, 1965). In the Pilargidae, the forebrain grades almost indistinguishably into the midbrain. In *Synelmis* and *Parandalia*, however, the forebrain is easily recognized because it is long and bifurcate (fig. 2a, b).

The midbrain generally includes antennal and optic centers as well as the posterior roots of the circumesophageal connectives (Bullock and Horridge, 1965). Within the Pilargidae, the midbrain is best seen in the genus *Parandalia* (fig. 2a), in which eyespots are present, and in *Synelmis* and *Litocorsa* where the midbrain is rather dense and barrel-shaped (fig. 2b, c).

Histologically, the hindbrain is defined as that portion which contains the nuchal centers (Bullock and Horridge, 1965). In this study, definition of the hindbrain is more restrictive, being that region which bears the posterior lobes. In the pilargids, there are 2–5 posterior lobes. In those genera with more than two lobes (e.g., *Ancistrostylis* and *Pilargis*) the median lobe is smaller than the outer lobes (fig. 1c, d). In pilargids with only two lobes, the lobes may be slightly dissimilar in size (e.g., *Synelmis*, *Parandalia*, and *Litocorsa*; fig. 2a–c) or equal in size (e.g., *Sigambra*; fig. 1a). The posterior lobes, exclusive of the median lobe, are almost always pigmented distally and sometimes laterally (figs. 1d, e; 2b, c).

In the pilargid genera studied, except *Litocorsa* and most species of *Synelmis*, a pair of organs is located lateral to the brain in the area of the tentacular cirri (e.g., figs. 1b, c; 2a). These organs are only narrowly connected to the brain and are located directly below nuchal slits. They were never found to be everted in preserved material and we could not find associated cilia in dissected specimens. Whether or not these structures are actually nuchal organs has not yet been determined, but here they are considered homologous to the nuchal organs found in other families because they are associated with what appear to be nuchal slits.

MATERIALS AND METHODS

BRAIN MORPHOLOGY

The material studied during this research was taken from the laboratory museum of Barry A. Vittor & Associates, Inc., Mobile, Alabama, and the National Museum of Natural History, Smithsonian Institution, and was collected from various areas in the Gulf of Mexico and east coast of Florida. Species examined belong to the following genera: *Ancistrostylis* McIntosh, 1879, *Cabira* Webster, 1879, *Litocorsa* Pearson, 1970, *Parandalia* Emerson and Fauchald, 1971, *Pilargis* Saint-Joseph, 1899, *Sigambra* F. Müller, 1858, and *Synelmis* Chamberlin, 1919.

All material examined had been fixed in a seawater-formalin solution, stained with Rose

Bengal, then transferred to 70 percent ethyl or isopropyl alcohol. To examine the brain, a midventral, longitudinal slit was made beginning at the lower lip of the mouth. The pharynx, upper and lower lips of the mouth, and connecting muscles were removed, exposing the brain. In order to clear the integument, small specimens were mounted in Hoyer's mounting medium on a slide and then examined using a compound microscope. Large specimens were examined in a petri dish using a stereo dissecting microscope. In most cases, the brain was observed in both ventral and dorsal views. Drawings of external morphology were made with the aid of a camera lucida or drawing tube on a microscope.

CLADISTIC ANALYSIS

The following genera and species were used in the cladistic analysis: *Ancistrostylis*, *Cabira*, *Litocorsa antennata* Wolf, 1986, *L. stremma* Pearson, 1970, *Loandalia* Monro, 1936, *Paracabira* Britaev and Saprova, 1981, *Parandalia*, *Pilargis*, *Sigambra*, *Synelmis klatti* (Friedrich, 1950), *Synelmis* complex A, and *Synelmis* complex B. The two presently recognized species of *Litocorsa* were considered separately in the analysis because of the presence of antennae in *L. antennata* and their absence in *L. stremma*.

Gross morphology of the brain was examined for selected species in all the above genera except *Loandalia* and *Paracabira*. In the cladistic analysis it was assumed (and is predicted) that the brain morphology of *Loandalia* is the same as that of *Parandalia*, and for *Paracabira* the same as *Cabira*. *Synelmis* was treated as three separate groups: *S. klatti*, *Synelmis* complex A, and *Synelmis* complex B. As discussed below, certain morphological characters appear to suggest *S. klatti* might belong in a separate genus. Based on the other species examined, *Synelmis* can be further separated into two complexes. *Synelmis* complex A contains those species [e.g., *S. albin* (Langerhans, 1881), *S. rigida* (Fauvel, 1919), and an undescribed species] which have neuropodial furcate setae, but lack acicular spines in the same fascicles. *Synelmis* complex B comprises species (e.g., *S. acu-*

minata Wolf, 1986, and *S. ewingi* Wolf, 1986) with straight neuropodial acicular spines and no furcate setae. Our reasons for making these distinctions stem from the fact that monophyly of this genus has never been established (see Discussion).

The genus *Otopsis* Ditlevsen, 1917, was not included in the analysis because specimens were not examined. Predictions concerning brain morphology would be difficult and nuchal organs have not been described for this genus. *Talehsapia* Fauvel, 1932, has been recognized as a pilargid by Mesnil and Fauvel (1939), Hartman (1947), Pettibone (1966), Pearson (1970), and Salazar-Vallejo (1986), whereas Fauvel (1932), Emerson and Fauchald (1971), and Fauchald (1977) considered it incertae sedis, and Fauvel (1953) placed it in the Hesionidae. We did not examine specimens of *Talehsapia* and leave open the possibility that it could be a pilargid.

Salazar-Vallejo (1986) removed *Antonbruunia* Hartman and Boss, 1965, from the Antonbruunidae Fauchald, 1977, placing it in the Pilargidae on the basis of general parapodial structure as well as by the presence of bifid neurosetae. The bifid neurosetae in *Antonbruunia* are thick and acicular, not at all resembling the thin, more delicate, bifid setae seen in pilargids and syllids (see below). That these setal forms are said to be bifid is, we consider, more a limitation of terminology than an indication of relationship. Salazar-Vallejo apparently regarded as simple palps the ventrolateral "antennae" described by Hartman and Boss (1965). No reasons were given for this distinction. Until more extensive taxonomic revisions are attempted, there is no firm evidence to support Salazar-Vallejo's recognition of *Antonbruunia* as a pilargid and that genus is not considered in this study.

The distinction between *Ancistrostylis* and *Ancistargis* Jones, 1961, has usually been based on the presence of three antennae in the former genus and two in the latter. There has, however, been no agreement as to the separation of species into these two genera (e.g., Jones, 1961; Emerson and Fauchald, 1971; Fauchald, 1972, 1977; Salazar-Vallejo, 1986) as opposed to placement of all species in *Ancistrostylis* (e.g., Pettibone, 1966; Gar-

diner, 1976; Wolf, 1984). We did not recognize *Ancistargis* in the present study because of the need for a complete systematic examination of genera with a papillated integument. Including *Ancistargis* in the analysis would simply bring into question the monophyly of this genus in relation to *Ancistrostylis*, *Cabira*, and *Paracabira*.

Fifteen morphological characters were used in the analysis (Appendix I), with the assumption that brain character states are invariant at the specific level. However, one of those characters requires clarification. With respect to species commonly placed in the genus *Loandalia*, or later *Parandalia*, several workers (e.g., Hartman, 1947; Pettibone, 1966; Wolf, 1984) have implicitly or explicitly stated that the thick, emergent notopodial spines are homologous to notoacacula. Several of these same workers (e.g., Pettibone, 1966; Wolf, 1984, 1986) have referred to similar spines as notosetal in origin in other genera, e.g., *Synelmis* and *Litocorsa*. These interpretations apparently follow from the view that presence of a spine in conjunction with a typical, embedded, slender notoaciculum (as in *Synelmis* and *Litocorsa*) implies that the spine is a notoseta. When, however, only spines are present, as in *Parandalia* (or most species of *Loandalia* prior to 1971), it has been called an emergent notoaciculum. Emerson and Fauchald (1971) noted that notoacacula, as well as thick spines, are absent in the type species of *Loandalia*, *L. aberrans* Monro, 1936. While Emerson and Fauchald described the notopodial spines in their new genus, *Parandalia*, they did not discuss the differentiation between notosetae and notoacacula. As stated by Wolf (1984), for example, "spines" in anterior setigers of *Parandalia* are completely embedded, characteristic of acicula, becoming emergent in median and posterior setigers as what appear to be stout notosetal spines. Based on such a regional transition, these "spines" do appear to be emergent acicula in *Parandalia*. For the sake of clarity, we have restricted use of the term "notopodial spines" or "neuropodial spines" to those structures that are homologous to other setal forms, and not acicula per se.

General character state polarities were de-

terminated by outgroup comparison (e.g., Eldredge and Cracraft, 1980; Maddison et al., 1984; Watrous and Wheeler, 1981; Wiley, 1981). A general outgroup was initially recognized, comprising the Syllidae-Hesionidae-Nereididae complex, which is part of the suborder Nereidiformia, and to which the Antonbruunidae and Pilargidae are members (Fauchald, 1977). At this time, we conform to Fauchald's (1977) classification of these families within the Nereidiformia, implying that all are sister taxa, forming an exclusive, monophyletic group. There are, however, no synapomorphies presently recognized that will define this suborder. As a result, we tentatively assume a monophyletic sister-group relationship at this level, and consider the Syllidae-Hesionidae-Nereididae complex as a potential source for outgroups.

Subsequently, a more specific outgroup was restricted to the Syllidae. A potential synapomorphy denoting a Syllidae/Pilargidae sister-group relationship is the presence of simple neurosetae with bifid distal ends. For the present analysis, the Syllidae were regarded as four different outgroup types, taking into consideration degree of antennal development and fusion of palps. Thus, the possible combinations of outgroup conditions are: (1) palps separate, antennae well developed, (2) palps separate, antennae reduced, (3) palps completely fused, antennae well developed, or (4) palps completely fused, antennae reduced.

CLASSIFICATORY METHODS

Cladograms were constructed with the data matrix (Appendix II) using the *ie** command in the cladistic computer package **Hennig86**, version 1.5, developed by J. S. Farris (1988). This command generates cladograms by the exhaustive search strategy, "implicit enumeration," producing all possible minimum-length cladograms. All apomorphic states of multistate characters were treated as non-additive. Computer runs were made on a Toshiba T1200 computer. Resulting transformation series and consistency indices (c.i.) for each character were determined using the **xsteps** command with the **h** and **c** options, respectively.

RESULTS

GROSS MORPHOLOGY OF THE BRAINS OF SELECTED PILARGID GENERA AND SPECIES

Sigambra F. Müller

Specimens of *Sigambra tentaculata* (Treadwell, 1941; fig. 1a), *S. bassi* (Hartman, 1945), and *S. wassi* Pettibone, 1966 (fig. 1b), were examined. The brains are similar in all three species, i.e., wider than long and not extending posteriorly beyond the tentacular segment. The fore- and midbrain areas are fused and indistinctly delineated. The hindbrain is bilobed, each lobe tapering posteriorly (fig. 1a) or broadly rounded (fig. 1b). In some specimens the hindbrain lobes are distinctly pigmented while in others the pigment seems to have faded. In *S. wassi* additional pigment is present at the junction of the brain and nuchal organs (fig. 1b). Nuchal organs are large, conspicuous, and sometimes pigmented (fig. 1a, b). They are narrowly attached laterally on either side of the brain and do not appear to be eversible but each lies below a transverse nuchal slit located dorsally on the prostomium just posterior to the lateral antennae. Cilia were not seen within nuchal slits nor on the nuchal organs. *Sigambra tentaculata* and *S. bassi* do have two paired groups of cilia located dorsally on the prostomium on either side of raised areas at the base of the palpophores (fig. 1a) but we could not find slits associated with these ciliated areas.

Ancistrosyllis McIntosh

Ancistrosyllis jonesi Pettibone, 1966 (fig. 1c), *A. carolinensis* Gardiner, 1976, *A. hartmanae* Pettibone, 1966, and three undescribed species were examined. In each species the brain is wider than long and does not extend beyond the tentacular segment except in *A. hartmanae*, in which it extends to the posterior margin of setiger 1. The fore- and midbrain areas are fused and indistinctly delineated. The hindbrain is composed of five lobes including a median lobe and two pairs of larger lateral lobes. The two outermost lobes are sometimes faintly pigmented posteriorly. In some specimens the midbrain is pigmented laterally at the junction with the nuchal organs. A pair of very small eyespots

is located dorsolaterally on the midbrain(?) of some specimens. The nuchal organs are small but conspicuous when pigmented, attached laterally on either side of the brain near the tentacular cirri. Nuchal organs were not observed to be eversible but each lies below an oblique nuchal slit located dorsolaterally on the prostomium. Cilia were not seen on either the nuchal organs or within nuchal slits.

Pilargis Saint-Joseph

Pilargis berkeleyae Monro, 1933 (fig. 1e), and two undescribed species (fig. 1d) were examined. The brain is slightly longer than wide and extends into setiger 1 (fig. 1d) or 2 (fig. 1e). The fore- and midbrain areas are fused and indistinctly delineated. The forebrain of *P. berkeleyae* appears to be bifurcate (fig. 1e), unlike that of other species examined in which it is entire (not shown in fig. 1d). The hindbrain of all three species is trilobed with the median lobe being much smaller than lateral lobes (fig. 1d; median lobe not shown in fig. 1e). The lateral lobes are usually pigmented posteriorly. Nuchal organs are rather large, conspicuous, and usually pigmented. They appear to be narrowly attached laterally to either side of the forebrain. They do not appear to be eversible but each lies below a transverse nuchal slit located on the prostomium dorsolateral to the tentacular cirri (fig. 1d). Cilia were not seen within the nuchal slits nor on the nuchal organs.

Cabira Webster

Specimens of *Cabira incerta* Webster, 1879, were examined. The brain is quite similar to that of *Pilargis* in being trilobed posteriorly. The hindbrain lobes, however, do not extend beyond the posterior margin of the tentacular segment. Pigmented nuchal organs are located lateral to what appears to be the forebrain and these are associated with transverse nuchal slits on the prostomium. One specimen has cilia within the nuchal slits but cilia could not be found in other specimens.

Parandalia Emerson and Fauchald

One undescribed species of *Parandalia* (fig. 2a) was examined. The brain is longer than

wide and extends to the posterior margin of setiger 3. The forebrain is distinctly bifurcate with the anterior portions strongly divergent. The midbrain is barrel shaped and bears a pair of small, dorsal eyespots. The hindbrain is composed of a pair of slightly dissimilar lobes that are unpigmented in all specimens examined. The nuchal organs are rather large, club-shaped, and pigmented distally. Each appears to be attached laterally to the forebrain. The nuchal organs do not appear to be eversible but each is located below a small, V-shaped nuchal slit present dorsolaterally on the prostomium (fig. 2a). Cilia were not seen on the nuchal organs or within nuchal slits.

Synelmis Chamberlin

Synelmis ewingi Wolf, 1986 (fig. 2b), *S. acuminata* Wolf, 1986, *S. klatti* (Friedrich, 1950), and one undescribed species were examined. In these species, except *S. klatti*, described later, the brain is quite similar (fig. 2b). It is much longer than wide and extends into setigers 2 and 3 depending on the species. The forebrain is bifurcate, with the anterior ends only slightly divergent (fig. 2b). The midbrain appears more dense than the forebrain, is not bifurcate, and does not bear eyespots. The hindbrain has two slightly dissimilar lobes which are usually pigmented posteriorly. Nuchal organs and nuchal slits are apparently absent in all specimens examined.

Synelmis klatti has a brain similar to that of *Sigambra*, i.e., wider than long, extending no farther than the tentacular segment, with fore- and midbrain areas fused and indistinctly delineated, and with the hindbrain bilobed. This casts doubt as to its generic placement (see cladistic results and discussion below).

Litocorsa Pearson

Litocorsa stremma Pearson, 1970, and *L. antennata* Wolf, 1986 (fig. 2c), were examined. In both species the brain appears identical. It is much longer than wide and extends into setiger 2. The forebrain is long but not bifurcate. The midbrain is barrel shaped, about twice the width of, and more dense than, the forebrain. The hindbrain is com-

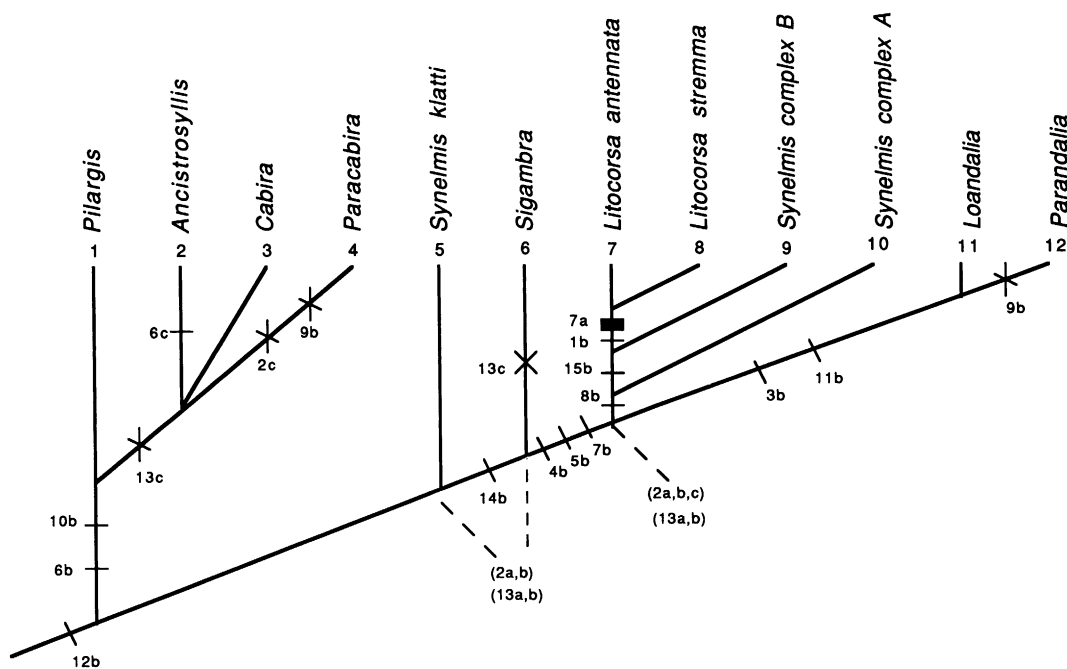


Fig. 3. Minimum-length cladogram for selected pilargid taxa using outgroup A (reduced antennae plesiomorphic). Taxa are numbered and referred to by these numbers in figures 4–7. Unambiguous state changes are shown on stems: slash = synapomorphy, \times = homoplasy, dark rectangle = reversal. Ambiguous state assignments are indicated in parentheses at the node(s) in question.

posed of a pair of unequal-size lobes that are pigmented posteriorly. Nuchal organs and nuchal slits could not be found, although this may be due to the small size of the specimens.

CLADISTIC RESULTS

The shortest-length cladograms produced were those using outgroups in which palps are separate for at least part of their length and with either well-developed or reduced antennae. Seven cladograms were produced when the reduced antennal condition was considered plesiomorphic (referred to hereafter as outgroup A), and six cladograms when the well-developed state was plesiomorphic (outgroup B). Each of these cladograms has a length of 25 steps and a c.i. of 0.72. The two other outgroups considered (see above) produced cladograms with lengths of 26 steps each. Topologies obtained with these latter outgroups do not differ from those of cladograms which are one step shorter. Only results obtained using the two former outgroups will be presented and discussed.

Cladograms produced using outgroup A are presented in figures 3–5. Differences in these cladograms are due to several possible placements of *Synelmis klatti* and *Sigambra* relative to one another and other genera, and slight movements of *Pilargis* and *Ancistrostylis*. Only two cladograms generated using outgroup B (well-developed antennae as plesiomorphic) have the same topology as any of the cladograms produced using outgroup A (compare fig. 6a, b with figs. 3, 5b). These latter cladograms differ mainly as a result of changing transformation series of character 2 for the plesiomorphic condition of the outgroup. All other cladograms generated using outgroup B differ from other cladograms in the placement of *S. klatti* and *Sigambra* relative to other genera (figs. 6c, 7a–c).

In all cladograms using both outgroups, two clades can be identified which remain stable. The larger of the two contains *Synelmis* complex A and B, *Litocorsa*, *Parandalia*, and *Loandalia* (e.g., fig. 3), defined at least by presence of a brain which is longer than wide (state 4b), brain divisions well divided (state

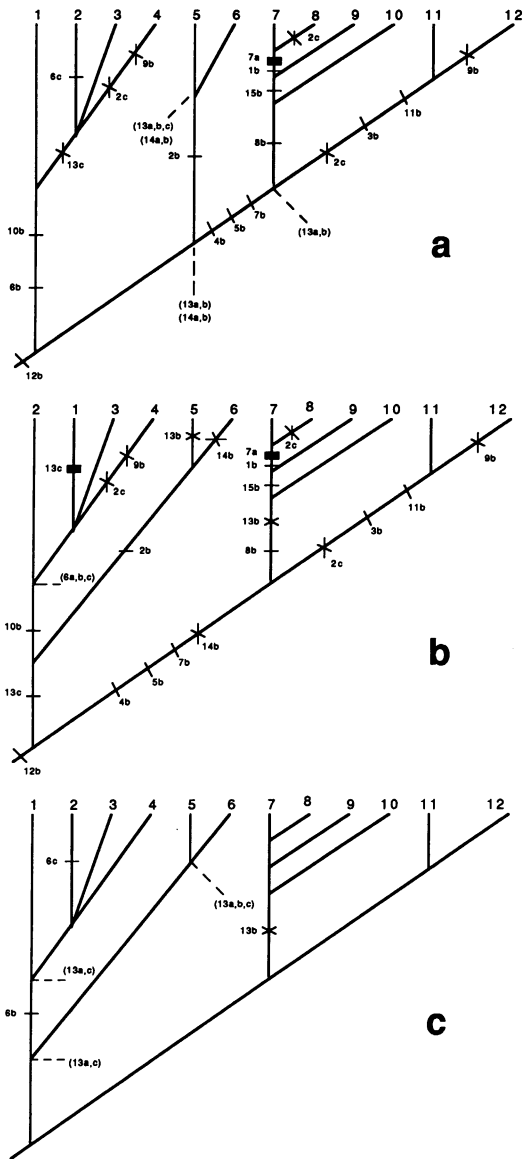


Fig. 4. Minimum-length cladograms for selected pilargid taxa using outgroup A (reduced antennae plesiomorphic). Taxa numbered as in fig. 3; see fig. 3 for explanation of state changes. All state changes are shown in fig. 4a, b; changes in fig. 4c are the same as in fig. 4b except where indicated.

5b), and a bifurcate forebrain (state 7b). *Synelmis* complex A and B, and *Litocorsa* form a monophyletic group by the absence of nuchal organs (state 8b). *Synelmis* complex B is the sister taxon to *Litocorsa*, while *Synel-*

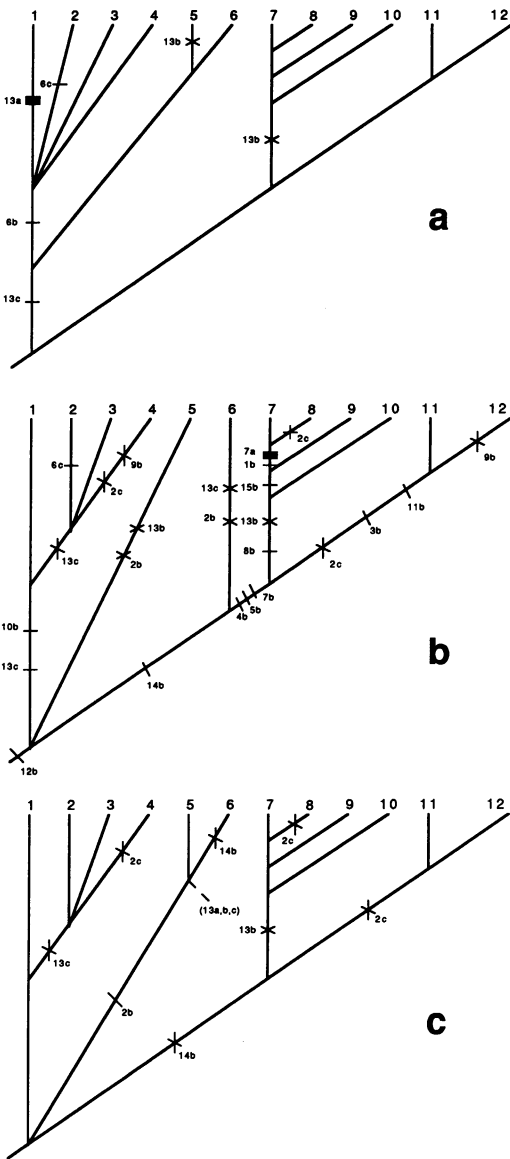


Fig. 5. Minimum-length cladograms for selected pilargid taxa using outgroup A (reduced antennae plesiomorphic). Taxa numbered as in fig. 3; see fig. 3 for explanation of state changes. State changes in fig. 5a are the same as in fig. 4b; changes in fig. 5c are the same as in fig. 5b except where indicated.

mis complex A is plesiomorphic to this grouping. *Parandalia* and *Loandalia* form a clade which is a sister group to the clade comprising *Synelmis* complex A and B, and *Litocorsa*.

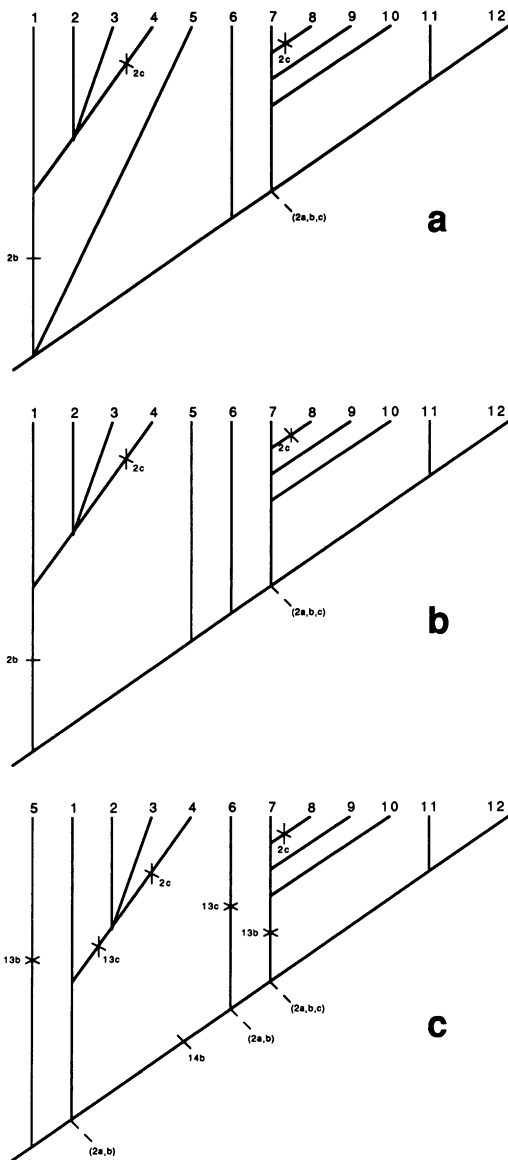


Fig. 6. Minimum-length cladograms for selected pilargid taxa using outgroup B (well-developed antennae plesiomorphic). Taxa numbered as in fig. 3; see fig. 3 for explanation of state changes. State changes in fig. 6a are the same as in fig. 5b; changes in fig. 6b, c are the same as in fig. 3 except where indicated.

The other principal clade contains those genera with a papillated integument (state 10b). In most cladograms (figs. 3; 4a, c; 5b, c; 6, 7), the clade includes *Ancistrostylis*, *Cabira*, and *Paracabira* as a trichotomy defined

by the presence of curved notopodial spines (state 13c), a state also found in *Sigambra*. *Pilargis* is the sister taxon to this trichotomy. The two exceptions to this topology are where (1) *Ancistrostylis* is a sister taxon to a trichotomy between *Pilargis*, *Cabira*, and *Paracabira* (fig. 4b), and (2) all four genera form a polytomy (fig. 5a). As noted above, all other differences in topologies are the result of movements of *Synelmis klatti* and *Sigambra*.

Three multistate characters were included in the analysis: antennal size (character 2), number of hindbrain lobes (character 6), and shape of notopodial spines (character 13). In one of the cladograms using outgroup A (fig. 3) and three of the cladograms produced with outgroup B (fig. 6), antennal size displays several equally parsimonious transformation series. All other cladograms generated using outgroups A and B (figs. 4, 5, 7, respectively) show independent loss of antennae occurring three times, in *Paracabira*, *Litocorsa stremma*, and the *Parandalia-Loandalia* clade. Derivation of the well-developed antennal state (2b) in *Synelmis klatti* and *Sigambra* when using outgroup A shows several possible transformation series (e.g., figs. 3, 4a, 5b). Similarly, when outgroup B is used the reduced state is derived several different ways (e.g., fig. 6a, c).

The transformation series for number of hindbrain lobes (character 6) has several possibilities. In all cladograms except one (fig. 4b), the plesiomorphic bilobed state (state 6a) gives rise to the three-lobe condition (state 6b) as a synapomorphy for the clade comprising *Pilargis*, *Ancistrostylis*, *Cabira*, and *Paracabira*. Derivation of the five-lobe state (6c) in *Ancistrostylis* is from this former condition. The exception to this transformation series is seen in figure 4b, where several possible transformations are possible as a result of movement of *Pilargis* and *Ancistrostylis*.

Because of the different placements of *Synelmis klatti* and *Sigambra*, transformation series for notopodial spines (character 13) may show several patterns (figs. 3–7). As a result, it is possible to hypothesize multiple origins of straight (state 13b) and curved (state 13c) spines in different transformation series. With regard to *Pilargis* and the *Parandalia-Loandalia* clade, absence of spines may be a ple-

siomorphic condition (e.g., figs. 3, 5b) or a loss (reversal; e.g., figs. 3, 4b).

Of the binary characters, character 7 (fore-brain entire or bifurcate) displays a single reversal in all cladograms, which is a synapomorphy for *Litocorsa*. The apomorphic state of character 9 (absence of dorsal cirri) is homoplasious, being derived in *Paracabira* and *Parandalia*.

DISCUSSION

BRAIN MORPHOLOGY AT THE GENERIC LEVEL

Based on the material examined, it appears that gross morphology of the pilargid brain can provide useful diagnostic characters. At least three different brain morphologies appear within the Pilargidae: (1) the *Sigambra-Ancistrostylis* type, which is wider than long with a small, entire (nonbifurcate) forebrain and 2–5 lobes on the hindbrain; (2) the *Parandalia-Synelmis* type, which is much longer than wide and has a long, well-developed, bifurcate forebrain and two well-developed lobes on the hindbrain; and (3) the *Litocorsa* type, which is similar to the *Parandalia-Synelmis* type except that the forebrain is entire. The brain of *Pilargis* most closely resembles that of the *Sigambra-Ancistrostylis* type. Consistency, however, of the bifurcate versus entire forebrain in *Pilargis* needs to be assessed further.

Another possible diagnostic character is the form of the nuchal slits of some genera (putatively absent in *Synelmis* and *Litocorsa*) examined during this study. The nuchal slits are well developed and transverse to oblique in *Sigambra*, *Ancistrostylis*, *Cabira*, and *Pilargis* (e.g., fig. 1a, c, d), but are small, oblique, and V-shaped in *Parandalia* (fig. 2a).

The brain of *Synelmis klatti* is not at all like that of other species of *Synelmis* we have examined. Rather, it is like that of *Sigambra*, which contains nuchal organs. *Synelmis klatti* is, presumably, placed within this genus because it has notopodial spines (e.g., Pettibone, 1966; Wolf, 1984). *Synelmis klatti* should probably be removed from this genus, though present results suggest against placement in *Sigambra*. While cladistic results support this view on the basis of brain and

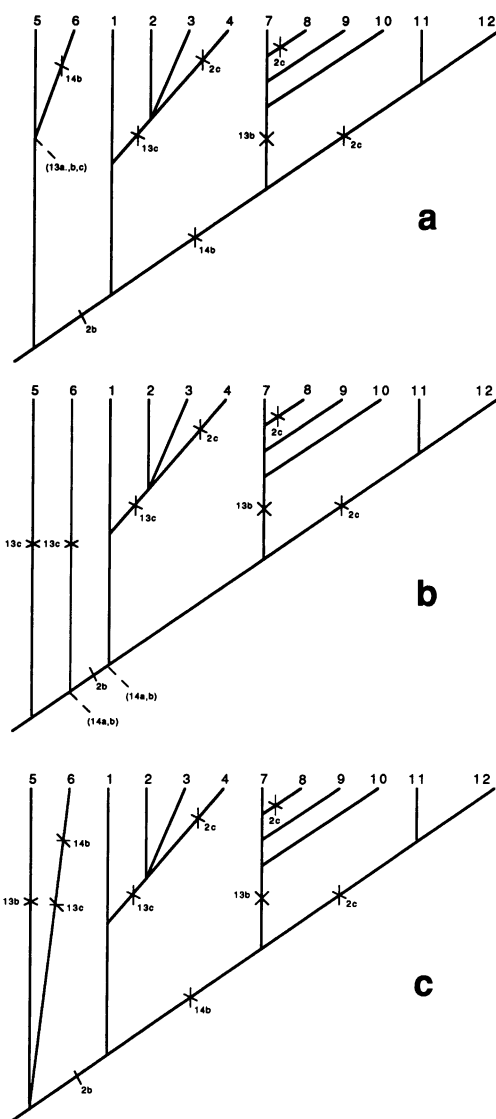


Fig. 7. Minimum-length cladograms for selected pilargid taxa using outgroup B (well-developed antennae plesiomorphic). Taxa numbered as in fig. 3; see fig. 3 for explanation of state changes. States are the same as in fig. 3 except where indicated.

external morphological features, there is also the questionable monophyletic status of *Sigambra* (see below). Conceivably, *S. klatti* could be placed back into *Glyphohesione* Friedrich, 1950, its nominal genus. Such a revision awaits further studies to determine consistency of brain shape within *Synelmis*.

SISTER-GROUP RELATIONSHIPS WITHIN THE PILARGIDAE

Though relationships of the Pilargidae to other polychaete families have been discussed, or implied, by some workers (e.g., Dales, 1962; Fauchald, 1977; Britaev and Saprionova, 1981; Pettibone, 1982), no definitive statements have been made concerning sister-group relationships of taxa within the family. In referring to the then known genera, Hartman (1947: 484–485) did state that the “affinities of each of these genera to the others remain obscure but it now seems possible that the pilargids as known today are distinctly divisible into 2 branches. . . . In one group including *Pilargis* and *Ancistrostylis* . . . ; in the other including *Loandalia* and *Talehsapia*. . . .” Hartman also suggested that the Pilargidae is quite old, which could explain the great degree of divergence seen between genera.

In many respects, Hartman’s use of the terms “affinities” and “branches” tends to connote a view concerning phylogenetic divergence within the family. Pearson (1970: 74) cited Hartman’s (1947) idea of two major branches within the Pilargidae, but suggested that *Litocorsa stremma* “falls midway between the two groups” because the latter has tentacular cirri but lacks antennae. Pearson’s statements are vague and it is unclear if he was referring to systematic relationships or simply general appearances.

The distinctions made by Hartman (1947) and Pearson (1970) were reflected in the two subfamilies, Sigambrinae and Synelminae, erected by Salazar-Vallejo (1986). The Sigambrinae contains *Ancistargis*, *Ancistrostylis*, *Antonbruunia*, *Cabira*, *Otopsis*, *Paracabira*, *Pilargis*, and *Sigambra*, while the Synelminae comprises *Litocorsa*, *Loandalia*, *Parandalia*, *Synelmis*, and *Talehsapia*. Salazar-Vallejo’s subfamily diagnoses do not, however, recognize any features which would support either as being monophyletic.

Our analysis found two stable monophyletic groups. One group, with *Litocorsa*, *Synelmis* complex A-B, *Loandalia*, and *Parandalia*, is defined by brain characters (states 4b, 5b, and 7b). The other group, containing *Ancistrostylis*, *Cabira*, *Paracabira*, and *Pilargis*, is defined by papillation of the integu-

ment (state 10b). These groupings are similar to the subfamilies of Salazar-Vallejo, as well as the groups recognized by Hartman (1947) and Pearson (1970).

Based on present results there is no firm evidence to support the Sigambrinae and Synelminae. The most problematic area concerns the relationship of *Synelmis klatti* and *Sigambra* to other genera. Whether this ambiguity is due simply to a lack of data and/or the questionable status of *Sigambra* as a monophyletic group (see below) is not yet known.

Of the cladograms generated using out-group A, there are three topologies (figs. 4b, c; 5a) which agree with Salazar-Vallejo’s subfamilies. In these instances, the Sigambrinae is defined by presence of curved notopodial spines (state 13c), with subsequent loss in *Pilargis* and modification to the straight spine state (13b) in *Synelmis klatti*. The Synelminae is defined by several brain states (4b, 5b, 7b) and modification of the distal ends of neurosetae to a tapered point (state 14b). Note, however, that *Otopsis*, *Talehsapia*, and *Antonbruunia* were not considered in our analysis. We doubt inclusion of these latter genera will reduce or greatly alter the present problems of defining subfamilies.

Based on the material examined, *Synelmis* is not a monophyletic group. *Synelmis klatti* not only differs with respect to brain morphology from other examined species of *Synelmis*, but also has elongate antennae, nuchal organs, and brain characteristics which are more similar to those seen in *Sigambra*. Past placement of this species within *Synelmis* has been based only on the presence of straight notopodial spines in conjunction with the presence of antennae and tentacular cirri (e.g., Pettibone, 1966; Pearson, 1970). None of the recent diagnoses of *Synelmis* (e.g., Pettibone, 1966; Wolf, 1984, 1986) have given any indication that the genus is monophyletic. If the present situation for *Synelmis* is substantiated by a complete examination of species within this genus, it appears likely that *S. klatti* should be placed back into its nominal genus, *Glyphohesione* Friedrich, 1950, as noted above.

Relationships between *Litocorsa* and *Synelmis* complex A and B raise doubts about the status of both genera. Monophyly of *Sy-*

nelmis complex A appears to be established by the presence of bifurcate neurosetae. *Synnelmis* complex B, which contains *S. acuminata* and *S. ewingi*, has no characters that would suggest it is monophyletic. If necessary, both *Litocorsa* species could be grouped into a single genus with *Synnelmis* complex B species, with monophyly being based on the presence of straight neuropodial spines. This would modify the definition of *Litocorsa* only to the extent that completely fused palps would no longer be a synapomorphy.

The cladistic patterns among *Synnelmis* complex A-B and *Litocorsa* are further substantiated by general body shapes. For example, species in *Synnelmis* complex A have a broadly rounded prostomium that is wider than long, and with short, rounded palps (e.g., Hartman, 1947: plate 62, fig. 1 for *S. rigida*; Wolf, 1984: figs. 29–32a, b and 29–34a, b for *S. cf. albin* and *Synnelmis* sp. A, respectively). The prostomium and palps of species in *Synnelmis* complex B are more elongate, very similar to what is seen in *Litocorsa* (e.g., Wolf, 1986: figs. 2a, b and 3a, b for *S. acuminata* and *S. ewingi*, respectively). With respect to these features, and those used in the present analysis, *Synnelmis* complex A appears to represent a transitional form, displaying the more common pilargid prostomial and palpal shapes, but with brain characteristics seen in *Litocorsa* and *Synnelmis* complex B.

As for *Synnelmis*, monophyly of *Sigambra* is at this time undecided. Past definitions of *Sigambra* have distinguished the genus by the combination of long antennae, long tentacular cirri, and curved notopodial spines. A number of the present cladograms (e.g., fig. 3) suggest that curved notopodial spines are homoplasious, defining the clade comprising *Ancistrostylis*, *Cabira*, and *Paracabira*, as well as being a synapomorphy for *Sigambra*. There is, however, the other possibility of curved spines being derived once (e.g., fig. 4b), leaving open the question of *Sigambra* being monophyletic.

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APPENDIX I

Characters and States Used in the Present Study
State *a* is plesiomorphic with subsequent states apomorphic. Polarity was determined by use of the Syllidae as outgroup. Outgroups A and B differ only in the plesiomorphic condition for antennal size. Possible transformation series for multistate characters are discussed in the text.

Character	Character states
1. Palps	a. separate, at least in part; b. fused completely
2. Antennal size	Outgroup A: a. reduced; b. well developed; c. absent Outgroup B: a. well developed; b. reduced; c. absent.
3. Tentacular cirri	a. present; b. absent
4. Brain	a. about as wide as long; b. much longer than wide
5. Brain divisions	a. poorly divided; b. well divided
6. Hindbrain lobes	a. 2; b. 3; c. 5
7. Forebrain	a. entire; b. bifurcate
8. Nuchal organs	a. present; b. absent
9. Dorsal cirri	a. present; b. absent
10. Integument	a. smooth; b. papillated
11. Anal plaque	a. absent; b. present
12. Setae	a. some compound; b. all simple
13. Notopodial spines	a. absent; b. present, straight; c. present, curved
14. Distal ends of neurosetae	a. bifid; b. tapered
15. Neuropodial spines	a. absent; b. present

APPENDIX II

Data Matrix of Taxa and Character States (see Appendix I) Used in the Present Study
States for character 2 are separated into 2a and 2b according to use of outgroups A and B, respectively.

Taxon	Character and state															
	1	2a	2b	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Ancistrosyllis</i>	a	a	b	a	a	a	c	a	a	a	b	a	b	c	a	a
<i>Cabira</i>	a	a	b	a	a	a	b	a	a	a	b	a	b	c	a	a
<i>Litocorsa stremma</i>	b	c	c	a	b	b	a	a	b	a	a	a	b	b	b	b
<i>Litocorsa antennata</i>	b	a	b	a	b	b	a	a	b	a	a	a	b	b	b	b
<i>Loandalia</i>	a	c	c	b	b	b	a	b	a	a	a	b	b	a	b	a
<i>Paracabira</i>	a	c	c	a	a	a	b	a	a	b	b	a	b	c	a	a
<i>Parandalia</i>	a	c	c	b	b	b	a	b	a	b	a	b	b	a	b	a
<i>Pilargis</i>	a	a	b	a	b	a	b	a	a	a	b	a	b	a	a	a
<i>Sigambra</i>	a	b	a	a	a	a	a	a	a	a	a	a	b	c	b	a
<i>Synelmis klatti</i>	a	b	a	a	a	a	a	a	a	a	a	a	b	b	a	a
<i>Synelmis</i> complex A	a	a	a	a	b	b	a	b	b	a	a	a	b	b	b	a
<i>Synelmis</i> complex B	a	a	a	a	b	b	a	b	b	a	a	a	b	b	b	b