

The phylogenetic position of the Pilargidae with a cladistic analysis of the taxon – facts and ideas

Frank LICHER & Wilfried WESTHEIDE

Universität Osnabrück, Fachbereich Biologie/Chemie, Spezielle Zoologie
D-49069 Osnabrück, Germany

ABSTRACT

The taxon Pilargidae is considered to be a group of derived hesionid species. This view is supported by the fact that apparent pilargid-specific features also occur in a few hesionid taxa. The idea is also based on the hypothesis that the pilargid stem species evolved by early maturation ("progenetically") of a juvenile stage of a large-bodied hesionid species. Making use of all characters available and using a hesionid taxon as outgroup, a cladogram of all pilargid genera was constructed with the program HENNIG 86, vers. 1.5. It shows well developed prostomial appendages and separate biarticulated palps to be the plesiomorphic character states. The genera *Synelmis* and *Litocorsa* are newly defined. For phylogenetic systematic implications the pilargid taxa should be included in the Hesionidae.

RÉSUMÉ

Position phylogénétique des Pilargidae avec analyse cladistique du taxon - faits et idées.

Le taxon des Pilargidae est considéré comme étant dérivé d'un groupe d'Hesionidae. Ce point de vue est conforté par le fait que des caractères typiques des Pilargidae se rencontrent également chez quelques Hesionidae. L'idée est basée sur l'hypothèse que l'espèce souche des Pilargidae a évolué à partir du stade juvénile d'un hésionide de grande taille qui aurait acquis une maturité sexuelle précoce (progenèse). En se fondant sur tous les caractères disponibles et en prenant un hésionide comme groupe extérieur, un cladogramme de tous les genres de Pilargidae a été construit à l'aide du programme HENNIG 86, version 1.5. Cela révèle que des appendices prostomiaux bien développés et les palpes biarticulés représentent l'état plésiomorphe. Les genres *Synelmis* et *Litocorsa* sont redéfinis. Dans une optique de systématique phylogénétique, les Pilargidae devraient être inclus dans les Hesionidae.

INTRODUCTION

When he described *Pilargis verrucosa*, SAINT-JOSEPH (1899) erected the Pilargidae to contain it, starting a long-lasting discussion on the systematic validity of this polychaete taxon. The first descriptions of pilargid species were actually much earlier, but the authors considered the worms to be orbiniids (*Sigambra grubii* Müller,

1858, as Amytidea; and *Parandalia tricuspis* Müller, 1858, as Ariciaea) or syllids (*Ancistrostylis groenlandica* McIntosh, 1879; *Cabira incerta* Webster, 1879; *Pilargis tardigrada* (Webster, 1879), as *Phronia*; *Synelmis albini* (Langerhans, 1881), as *Ancistrostylis*. EHLERS (1908) was the first to consider these species to be hesionids. For most polychaete taxonomists, however, these species appeared to be too different from "typical" hesionids to be included in this family. For instance, HESSLE (1925) argued that *Ancistrostylis* was neither a syllid nor a hesionid - an opinion which has persisted to the present.

One of us (W. WESTHEIDE) became extremely interested in pilargids when first seeing living *Sigambra* individuals at the northern coast of China in 1987. The form of these specimens, under a low power dissecting microscope, and their locomotion seemed so similar to those features of the interstitial hesionid species *Hesionides maxima* Westheide, 1967 and *Hesionides pettiboneae* Westheide, 1987 (WESTHEIDE, 1967, 1987a) that the later identification of the fixed specimens as a pilargid taxon was rather astonishing. We asked ourselves whether our many years of experience in recognizing live meiofauna-taxa just by their appearance and locomotory characters had failed in this case or whether this apparent mistake might be due to a very close systematic relationship between interstitial hesionids and pilargids.

This prompted an investigation of the phylogenetic systematics within the Pilargidae to see if there was any support for this hypothesized relationship. Our findings resulted in reinvestigations of several pilargid taxa and a review of the entire pilargid literature, especially JONES (1961), EMERSON & FAUCHALD (1971), BRITAEV & SAPHRONOVA (1981), FITZHUGH & WOLF (1990) and SALAZAR-VALLEJO & SOLÍS-WEISS (1992). A comprehensive analysis of the taxon suffers from the fact that no true anatomical or any ultrastructural details are available. FITZHUGH & WOLF (1990) in their cladogram especially used brain gross morphology as a taxonomic and systematic character. Although it is based only on the outlines of various brains taken from whole mounted specimens their cladistic analysis has been of considerable help. However, we do not agree with their phylogenetic interpretation in all points. Our phylogenetic analysis differs from their results because we make use of a different outgroup.

CLADISTIC ANALYSIS

DIAGNOSTIC FEATURES OF THE PILARGIDAE. — The pilargid body is cylindrical or dorsoventrally flattened, and anterior segments can be inflated. The integument may be smooth or papillated. The prostomium bears antennae (three, two, or none at all) and biarticulated palps, consisting of large palpophores and palpostyles of different length and shape. Small pigmented eyes may be present. The pharynx is eversible and usually has a circlet of distal papillae; jaws may be present.

The achaetous peristomium is usually equipped with two pairs of tentacular cirri, which may be absent. The parapodia are usually well developed and biramous. In most of the species the notopodia possess a single stout spine or hook, and a notoacicula; additional capillary chaetae may occur. The neuropodia are equipped with an acicula and several simple chaetae, which may be capillary, slightly unidentate, serrated, smooth, spinous or furcate. Dorsal and ventral cirri are usually present, and they may be of different lengths. Gills exist in one genus. The pygidium has two or three anal cirri.

The following characters are considered to be autapomorphic, defining the monophyly of the Pilargidae: (1) possession of a simple specific stout emergent notochaeta, to be reduced in some genera, (2) possession of exclusively simple, neuropodial mainly capillary chaetae, and (3) possession of fleshy biarticulated palps.

LIST OF PILARGID GENERA. — The assumed autapomorphies of the pilargid taxa are briefly mentioned; the material examined during this study is listed in brackets.

Sigambra Müller, 1858: this first described genus and most species-rich taxon of the family was recognized as a pilargid not earlier than in the middle of this century (HARTMAN, 1959; PETTIBONE, 1966). Since the notopodial hooks are considered by the authors to be plesiomorphic within the Pilargidae the taxon possesses primitive features only, but see FITZHUGH & WOLF (1990) (*Sigambra bassi* USNM 86966; *S. grubii* USNM 103016; *S. tentaculata*, USNM 86975; *S. wassi*, USNM 30987; specimens from Thailand and China).

Ancistrostylis McIntosh, 1879: the monophyly of the taxon may be based on its five-lobed brain (FITZHUGH & WOLF, 1990). *Ancistargis* Jones, 1961, is tentatively included (PETTIBONE, 1966; GARDINER, 1976; WOLF, 1984), although the species of this genus are clearly separated from *Ancistrostylis* in possessing two antennae only. If *Ancistargis* were accepted as a separate taxon, no synapomorphic character for *Ancistrostylis*-species with three antennae would be available (*Ancistrostylis breviceps* LACMNH AHF POLY 0143, LACMNH Velero st. 7498-

61; *A. carolinensis* USNM 86909; *A. hartmanae* USNM 30989; *A. papillosa* USNM 86923, and specimens from other sources).

Cabira Webster, 1879: the monophyly of this taxon is clearly shown by the possession of jaws (BRITAEV & SAPHRONOVA, 1981) (*Cabira incerta* USNM 30985).

Pilargis Saint-Joseph, 1899: since the papillated integument is considered to be a synapomorphy, this taxon should be closely related to *Ancistrostylis-Ancistargis*, *Cabira* and *Paracabira*. A notopodial spine or hook is absent. As notopodia in all pilargid taxa - except *Otopsis* - are equipped with spines or hooks the absence of a chaetae of this kind in *Pilargis* is considered to be a derived character (*Pilargis berkeleyae* USNM 86959).

Otopsis Ditlevsen, 1917: the genus resembles *Synelmis*, but lacks notopodial spines or hooks, which is interpreted as a loss (see also *Pilargis*).

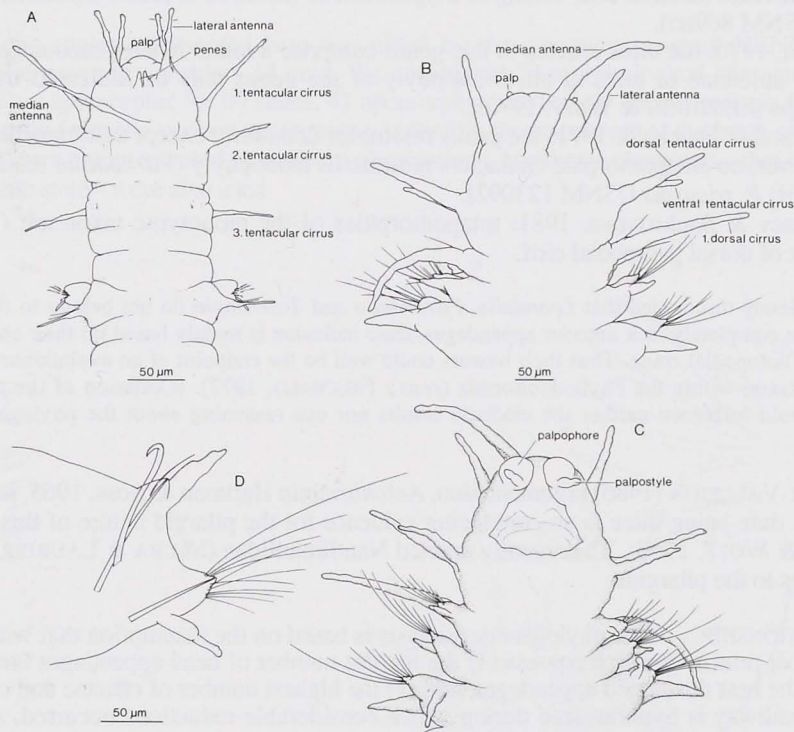


FIG. 1. — *Hesionides gohari* Hartmann-Schröder, 1960 and *Sigambra* sp. from Yellow Sea, near Qingdao: a, *Hesionides gohari*, anterior end, dorsal view. — b, *Sigambra* sp., anterior end, dorsal view. — c, anterior end, ventral view. — d, parapodium, mid-body region.

Synelmis Chamberlin, 1919: we adopt the view of FITZHUGH & WOLF (1990) and partition *Synelmis* species between "complex A" (species with furcate neuropodial spines) and "complex B" (species with non-furcate neuropodial spines). The non-furcate, less complex chaetal type is considered to be the apomorphic character state. For the monophyly of the two *Synelmis* complexes see "Discussion" (*Synelmis albini*, collection of the senior author; *S. simplex*, USNM 19480).

Talehsapia Fauvel, 1932: this monotypic, poorly known taxon is included in the analysis although its assignment to the Pilargidae has been repeatedly questioned (e.g., PETTIBONE, 1966, EMERSON & FAUCHALD, 1971), mainly because of the possession of jaw-like structures. The shape of the body, especially of the anterior region, the absence of prostomial and tentacular appendages, the presence of an emergent notopodial spine, the absence of notoaciaculae and dorsal cirri, and the possession of only simple chaetae suggest a close relationship

with the *Loandalia-Parandalia* complex. The possession of jaws is the autapomorphic character of this taxon; they differ distinctly from those in *Cabira*.

Loandalia Monro, 1936: this is the only pilargid genus with branchiae, clearly indicating its monophyletic status.

Glyphohesione Friedrich, 1950: the opinion that this monotypic taxon should be included in *Ancistrostylis* (ELIASON, 1962) or *Synelmis* (PETTIBONE, 1966) is rejected (see also FITZHUGH & WOLF, 1990, LICHER, in press) and the genus *Glyphohesione* should be retained. Specimens identified as *Synelmis klatti* (Friedrich, 1950) (six in the collection of the Zoologisk Museum Copenhagen (ZMUC) and one in the collection of the Senckenberg Museum Frankfurt (SMF)) differ from all pilargid taxa in possessing elongate, non-papilliform palpostyles and lateral antennae which are located near the anterior margin of the prostomium. They also do not possess emergent neuropodial spines which are characteristic for *Synelmis*. This is also true for two specimens from Florida in the collection of the U.S. National Museum Washington, although they differ slightly in other characters. The European and the American material both belong to *Glyphohesione* (LICHER, in press) (*Synelmis klatti* SMF 4432; ZMUC-POL-178; USNM 86986).

Litocorsa Pearson, 1970: the three species in this genus comprise a rather heterogeneous group in possessing three antennae, two antennae or none at all. Monophyly of the genus may be indicated by the presence of completely fused palps (FITZHUGH & WOLF, 1990).

Parandalia Emerson & Fauchald, 1971: the genus resembles *Loandalia* except that branchiae are absent. For the time being, however, no autapomorphic characters indicate its monophyly (*Parandalia ocularis*, collection of L. HARRIS, LACMNH; *P. tricuspis* USNM 123092).

Paracabira Britaev & Saphronova, 1981: tutapomorphies of the monotypic taxon are (1) lack of lateral antennae and (2) lack of dorsal parapodial cirri.

It cannot be completely discounted that *Loandalia*, *Parandalia* and *Talehsapia* do not belong to the Pilargidae at all. Because they almost or completely lack anterior appendages, their inclusion is mainly based on their comparatively simple parapodia with a stout notopodial spine. Thus their bearers could well be the endpoint of an evolutionary reductional series starting from another taxon within the Phyllocociformia (*sensu* FAUCHALD, 1977). (Omission of the three taxa from the analysis, however, would influence neither the cladistic results nor our reasoning about the phylogenetic origin of the Pilargidae.)

Despite SALAZAR-VALLEJO's (1986) argumentation, *Antonbruunia* Hartman & Boss, 1965, is not considered in our analysis. For the time being there is no convincing evidence for the pilargid nature of this monotypic taxon (see also FITZHUGH & WOLF, 1990). The recently erected Nautiliniellidae (MIURA & LAUBIER, 1989) have only superficial similarities to the pilargids.

OUTGROUP RELATIONSHIP. — Our phylogenetic analysis is based on the assumption that within the Pilargidae those taxa are the most primitive which possess (1) the highest number of head appendages (antennae, palps and tentacular cirri), (2) the best developed appendages, and (3) the highest number of chaetae and chaetal types. That is, an evolutionary pathway is hypothesized during which considerable reductions occurred, starting from taxa with three filiform antennae, two pairs of filiform tentacular cirri, biarticulated palps, and filiform dorsal parapodial cirri and leading to forms without any prostomial, tentacular and notopodial appendages (but see above). The general basis for this hypothesis is the idea that the stem species of the Phyllocociformia was richly equipped with head and body appendages which became differently and independently reduced within various taxa, especially in species with a totally endoparasitic way of life.

By this line of argument *Sigambra* and *Glyphohesione* should be the most primitive pilargid taxa (LICHER, in press). Indeed, they show strong similarities with those small hesionid species which possess only a small number of body appendages. Similarities in number and arrangement of head appendages are obvious (Fig. 1). All the appendages in, e.g., a species of the genus *Hesionides* Friedrich, 1937 can be found in a *Sigambra* with the exception of the third tentacular cirri, which are still notopodial cirri of the first chaetigerous segment in *Sigambra*. The anterior-most ventral filiform appendages in *Hesionides* have a cirrus-like appearance. Investigations of their innervation, however, could prove them to be palps and therefore most likely homologous to the more fleshy and biarticulated palps in the pilargids [ultrastructural and immunohistochemical investigations by one of us (F. LICHER)].

For these interstitial hesionids a progenetic evolution has been considered (LAUBIER, 1967; WESTHEIDE, 1987b; WESTHEIDE & RIEGER, 1987); that is, it has been assumed that their speciation has taken place by genetically fixed maturation of juvenile stages of macrofaunal hesionid taxa. Now, we hypothesize that the pilargid stem species also evolved by progenesis of a larger hesionid's juvenile stage. The juvenile development of

non-interstitial hesionid species is characterized among other things by (1) a gradual increase in number of achaetous head segments, (2) an increase in the number of tentacular cirri, and (3) an expansion of articulation in the body appendages (HAALAND & SCHRAM, 1982, 1983) (Fig. 2). Adult hesionids belonging to different taxa especially differ in having different numbers of tentacular cirri - from three to eight pairs. Their youngest stage, e.g., an 8-chaetiger benthic stage of *Ophiodromus flexuosus* (Delle Chiaje, 1825) (corresponding to the earliest stage in the developmental series of Fig. 2) possesses the entire set of five prostomial appendages, but only one achaetous tentacular segment with two pairs of almost smooth cirri (HAALAND & SCHRAM, 1983). Thus its head morphology corresponds well with that of some pilargid taxa.

The idea that the pilargid stem species might have evolved by progenesis of a hesionid taxon caused us to use one of the hesionid taxa as the outgroup taxon for the data matrix of our cladogram (Table 2).

METHODS

The phylogenetic analysis presented here was aided by the computer program HENNIG 86, version 1.5 (FARRIS, 1988). The program considers 14 taxa. We considered 28 morphological characters and 68 character states of which 40 are apomorphic (or 69 states, 41 apomorphic, see below) for the analysis (Table 1). Characters were compiled mainly from the various descriptions, including the characters of the brain study by FITZHUGH & WOLF (1990), and were complemented by our own observations. Multistate characters - that is, characters of more than one apomorphic state - were also used.

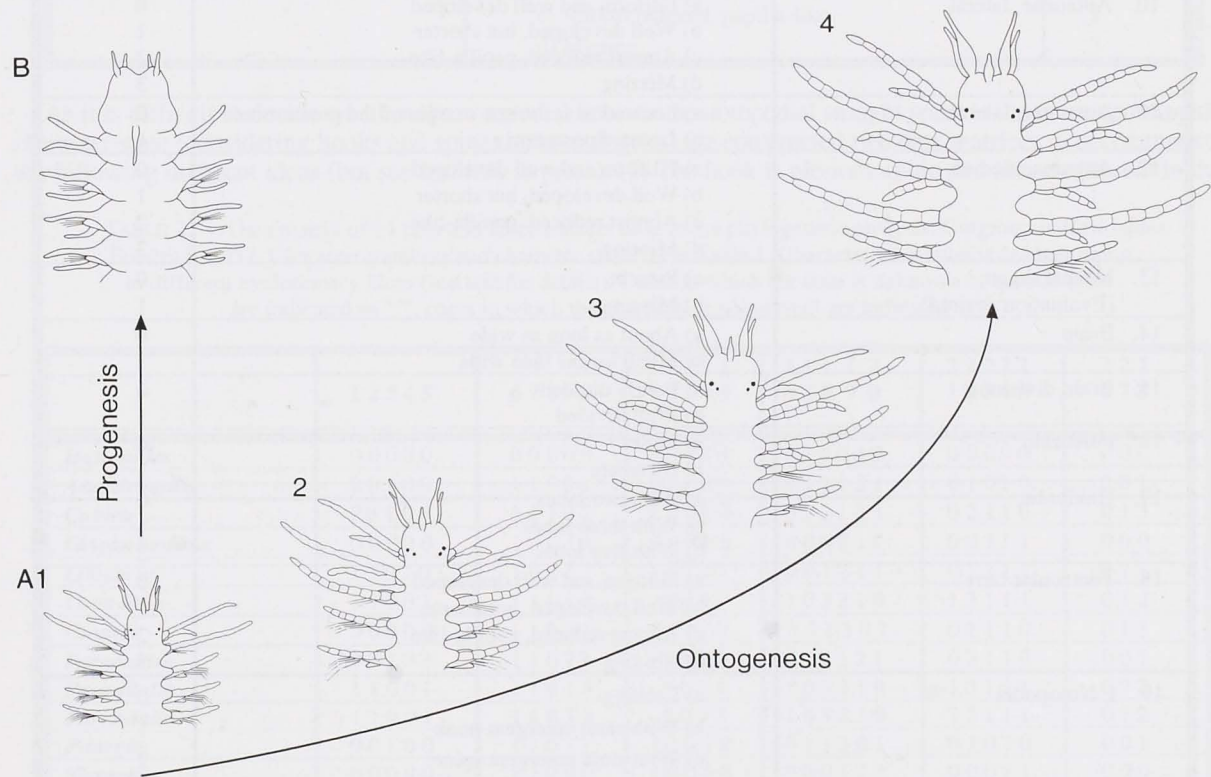


FIG. 2. — Schematic representation of progenesis of a primitive pilargid species from a hesionid juvenile stage: a, 1-4. Hesionid developmental series of a non-interstitial species, with (1) gradual increase in number of achaetous head segments, (2) a gradual increase in the number of tentacular cirri, and (3) an expansion of articulation in the cirral appendages, (see HAALAND & SCHRAM, 1983). — b, anterior end of a primitive pilargid taxon.

TABLE 1. — Characters and character states used in the phylogenetic analysis to set up the cladogram. Characters 10, 12, 17, 18, 22, 26 and 28 are multistate characters. Character 19 is coded twice belonging to different evolutionary ideas (see text for details). State "a" is plesiomorphic, subsequent states are apomorphic.

Features	Character states	Coding
1. Body-shape	a) Depressed b) Cylindrical	0 1
2. Integument	a) Without papillae b) With papillae	0 1
3. Anterior body region	a) Not inflated b) Inflated	0 1
4. Prostomium	a) Wider than long or half rounded b) Longer than wide	0 1
5. Prostomium	a) Clearly discernable b) Largely reduced	0 1
6. Palps	a) Filiform, apparently not articulated b) Fleshy, well developed and biarticulated	0 1
7. Palpostyles	a) Elongate b) Papillae-like	0 1
8. Pharynx	a) Without jaws b) Jaws present	0 1
9. Pharynx	a) Ring of papillae around the opening b) Without ring of papillae around the opening	0 1
10. Antennae, lateral	a) Filiform and well developed b) Well developed, but shorter c) Almost reduced, papilla-like d) Missing	0 1 2 3
11. Antennae, lateral	a) Located near the ant. margin of the prostomium b) Located posteriorly	0 1
12. Antenna, median	a) Filiform and well developed b) Well developed, but shorter c) Almost reduced, papilla-like d) Missing	0 1 2 3
13. Nuchal organ (Evaluation desired)	a) Present b) Missing	0 1
14. Brain	a) About as long as wide b) Much longer than wide	0 1
15. Brain divisions	a) Poorly divided b) Well divided	0 1
16. Forebrain	a) Entire b) Bifurcate	0 1
17. Hindbrain	a) With two lobes b) With three lobes c) With five lobes	0 1 2
18. Tentacular cirri	a) Filiform and well developed b) Well developed, but shorter c) Almost reduced, papilla-like d) Missing	0 1 2 3
19. I. Notopodia	a) Lacking b) With stout emergent hook c) With stout emergent spine d) Missing	0 1 2 3
19. II. Notopodia	a) Lacking b) With stout emergent spine c) With stout emergent hook	0 1 2
20. Notopodia	a) With capillary notochaetae besides spine or hook b) Further notochaetae missing	0 1

Features	Character states	Coding
21. Notopodial aciculae	a) Present b) Missing	0 1
22. Dorsal cirri	a) Filiform and well developed b) Well developed, but shorter c) Almost reduced, papilla-like d) Missing	0 1 2 3
23. Dorsal cirri 1	a) Longer than following ones b) Not longer than following ones	0 1
24. Neuropodia	a) With compound chaetae b) Simple chaetae only	0 1
25. Neuropodia	a) Distal ends of neurochaetae bifid b) Distal ends of neurochaetae pointed	0 1
26. Neuropodia	a) Without emergent spines b) With two emergent spines, distally bifurcated c) With two emergent spines, distally pointed	0 1 2
27. Ventral cirri 1	a) Present b) Missing	0 1
28. Anal cirri, lateral	a) Filiform and well developed b) Well developed, but shorter c) Almost reduced, papilla-like d) Missing	0 1 2 3

As it is difficult to decide whether the notopodial hook or the notopodial straight spine is the more apomorphic character state (considering hooks and spines as homologous) we constructed two data matrices to accommodate the following different ideas (but see LICHER, in press): (1) The hook is plesiomorphic and already present in the

TABLE 2. — Data matrix of 14 taxa and 28 characters used in the phylogenetic analysis. Outgroup is *Hesionides* Friedrich, 1937. Character numbers and character states as in Table 1. Character 19 is subdivided belonging to different evolutionary ideas (see text for details). Cases in which the state is unknown or questionable are indicated as "?", cases in which the character is not present are indicated as "-".

	1 2 3 4 5	1 6 7 8 9 0	1 1 1 1 1 1 2 3 4 5 I II	1 1 1 1 2 6 7 8 9 0	2 2 2 2 2 1 2 3 4 5	2 2 2 6 7 8
<i>Hesionides</i>	0 0 0 0 0	0 0 0 0 0	0 0 ? 0 0	0 ? 0 0 0 0	0 0 0 0 0	0 0 0
<i>Ancistrosyllis</i>	0 0 1 0 0	1 1 0 0 1	? 1 0 0 0	0 2 1 1 2 1	0 1 0 1 0	0 0 1
<i>Cabira</i>	? 0 1 0 0	1 1 1 0 2	1 3 0 0 0	0 1 2 1 2 1	0 2 1 1 0	0 1 3
<i>Glyphohesione</i>	0 0 0 0 0	1 0 0 ? 0	0 0 0 0 0	0 0 0 2 1 1	0 0 1 1 1	0 0 0
<i>Litocorsa</i>	1 ? 0 1 0	1 0 1 1	? 1 1 1 1	0 0 1 2 1 1	0 1 1 1 1	2 ? 1
<i>Loandalia</i>	1 1 0 0 1	1 1 0 1 3	- 3 0 1 1	1 0 3 2 1 0	1 3 1 1 1	0 1 2
<i>Otopsis</i>	0 0 0 0 0	1 1 0 0 1	1 1 ? ? ?	? ? 1 3 0 ?	0 1 1 1 0	0 1 ?
<i>Paracabira</i>	? 0 1 0 ?	1 1 0 ? 3	- 3 ? 0 0	0 1 2 1 2 1	0 3 1 1 0	0 0 ?
<i>Parandalia</i>	1 1 0 0 1	1 1 0 1 3	- 3 0 1 1	1 0 3 2 1 0	1 3 1 1 1	0 ? 2
<i>Parandalia</i>	1 1 0 0 1	1 1 0 1 3	- 3 0 1 1	1 0 3 2 1 0	1 3 1 1 1	0 ? 2
<i>Pilargis</i>	0 0 1 0 0	1 1 0 ? 1	1 3 0 1 0	0 1 1 3 0 1	0 1 0 1 0	0 0 1
<i>Sigambra</i>	0 0 0 0 0	1 1 0 0 0	1 0 0 0 0	0 0 0 1 2 ?	0 0 0 1 1	0 0 0
<i>Synelmis</i> complex A	1 0 0 0 0	1 1 0 1 1	1 1 1 1 1	1 0 1 2 1 1	0 1 1 1 1	1 0 1
<i>Synelmis</i> complex B	1 0 0 1 0	1 1 0 ? 1	? 1 1 1 1	1 0 1 2 1 1	0 1 1 1 1	2 0 1
<i>Talehsapia</i>	1 1 0 0 1	- - 1 ? 3	- 3 ? ? ?	? ? 3 2 1 1	1 3 1 1 ?	0 0 2

stem species of the Pilargidae; the spine is apomorphic and derived from a hook by simplification; the absence of hooks and spines is secondary, possibly reduced several times. (2) Lack of hooks or spines is plesiomorphic; a spine is apomorphic and evolved from a simple notochaeta within the Pilargidae; a hook is more apomorphic and derived from a spine, possibly derived several times (see FITZHUGH & WOLF 1990). Both ideas are reflected in our data matrix (Table 2): character 19 (I) corresponds to the first idea, character 19 (II) to the second one.

The cladogram was constructed from the data matrix using the *ie** command. This command generates cladograms by implicit enumeration, producing all possible minimum-length cladograms. Successive character weighting was carried out using the *xs - w* command. Computer runs were made on an IBM-compatible 486 DX, 33 MHz computer.

RESULTS

Considering the notopodial hook to be the plesiomorphic character state (coding I for character 19) only a single cladogram is produced (Fig. 3a). The length is 63 steps, consistency index (c.i.) is 0.66, retention index (r.i.) is 0.79. An analysis that considers the notopodial hook to be the most apomorphic state (coding II for character 19) yielded two cladograms, one of which is the same as in coding I (Figs 3a-b). The lengths of the two cladograms are 63 steps (c.i. 0.65, r.i. 0.78). Successive character weighting yielded one minimum-length tree (Fig. 3b).

The results of both codings are nearly the same: *Glyphohesione* is the adelphotaxon of all other pilargids, of which *Sigambra* is the sister-group of the remaining 11 taxa. The latter genera are arranged in two groups and *Otopsis*: (1) *Ancistrostylis*, *Pilargis*, *Cabira* and *Paracabira*, and (2) the two *Synelmis*-complexes, *Litocorsa*, *Talehsapia*, *Parandalia* and *Loandalia*. In both cladograms the relationships are identical with the exception of *Otopsis* (see Figs 3a-b).

The two cladograms show *Glyphohesione* to be the pilargid with the highest number of plesiomorphic characters (e.g., elongate palpostyles, lateral antennae located at the anterior margin of the prostomium). All other pilargids bear papilla-like palpostyles (state 7b, Table 1 and Fig. 4) and lateral antennae located posteriorly (11b). *Glyphohesione* is characterized by three autapomorphies (19c, 23b, 25b, using coding I) or by two autapomorphies (19c, 23b, using coding II). The monophyly of *Sigambra* is questionable when the notopodial hook is considered to be plesiomorphic (coding I).

The *Ancistrostylis*-group, *Otopsis* and the *Synelmis*-group possess prostomial, tentacular, parapodial and anal appendages (10b, 12b, 18b, 22b, 28b), which are shorter than in *Glyphohesione* and *Sigambra*. The *Ancistrostylis*-group is clearly characterized by the possession of a papillated integument (2b) and a three-lobed hindbrain (17b). Using coding II the possession of a dorsal hook would be an additional synapomorphy. *Ancistrostylis* may be characterized by its five-lobed hindbrain (17c), whereas the stem-species of *Pilargis*, *Cabira* and *Paracabira* lost the median antenna (12d). Autapomorphies of *Pilargis* are the loss of notopodial hooks (19d - reversion) and the possession of a brain which is much longer than wide (14b). In the stem-species of *Cabira* and *Paracabira* further reductions occurred (10c, 18c, 22c, 23b). *Cabira* bears jaws (8b) and lacks ventral cirri on chaetiger 1 as well as anal cirri (27b, 28d). *Paracabira* lacks lateral antennae and dorsal cirri (10d, 22d).

Otopsis and the *Synelmis*-group are equipped with dorsal cirri on chaetigerous segment 1, which are not longer than the following ones (23b). *Otopsis* is characterized by two reductions (19d, 27b). The *Synelmis*-group possesses a series of synapomorphic features: a cylindrical body (1b), a pharynx without distal papillae (9b), only simple capillary neurochaetae (25b), and several characters of brain gross morphology considered to be characteristic for them by FITZHUGH & WOLF (1990) (14b, 15b, 16b). Possession of a notopodial spine (19c) is an additional synapomorphy of this taxon when the hook is considered to be the plesiomorphic character state.

The two *Synelmis* complexes and *Litocorsa* possess two emergent neuropodial spines (26b) and lack nuchal organs (13b) according to FITZHUGH & WOLF (1990). The *Synelmis*-species (= *Synelmis* complex A plus *Synelmis* complex B) can be shown to form a paraphyletic group. Synapomorphies for *Synelmis* complex B and *Litocorsa* are the possession of pointed neuropodial spines (26c) and possession of a prostomium which is somewhat longer than wide (4b). Autapomorphies for *Litocorsa* are an "entire" forebrain (16a - reversion) and fused palps. Presence of prostomial pigmented eyes may be the autapomorphy of *Synelmis* complex A. For the time being no autapomorphies exist for *Synelmis* complex B.

Talehsapia, *Parandalia* and *Loandalia* show several synapomorphies: an inflated anterior body region (3b), a largely reduced prostomium (5b), loss of lateral and median antennae, tentacular cirri and dorsal cirri (10d, 12d, 18d, 22d), loss of notopodial aciculae (21b), loss of ventral cirri on chaetiger 1 (27b), and possession of papilla-

like anal cirri (28c). *Talehsapia* is characterized by the possession of jaws (8b). The notopodia of *Loandalia* and *Parandalia* are equipped with simple capillary notochaetae accompanying the stout spine (20a - reversion). *Loandalia* is unique in possessing branchiae and has lost the ventral cirri in chaetiger 1 (27b). Monophyly of *Parandalia* is questionable.

DISCUSSION

OUTGROUP RELATIONSHIP. — FITZHUGH & WOLF (1990) recognized either the Syllidae-Hesionidae-Nereididae complex or the Syllidae alone as possible outgroups of the Pilargidae. Whereas the relationship of the Pilargidae to the Nereidiformia is evident, a syllid-pilargid sister-group relationship based only on the presence of simple neurochaetae with bifid distal ends, however, appears to us less probable.

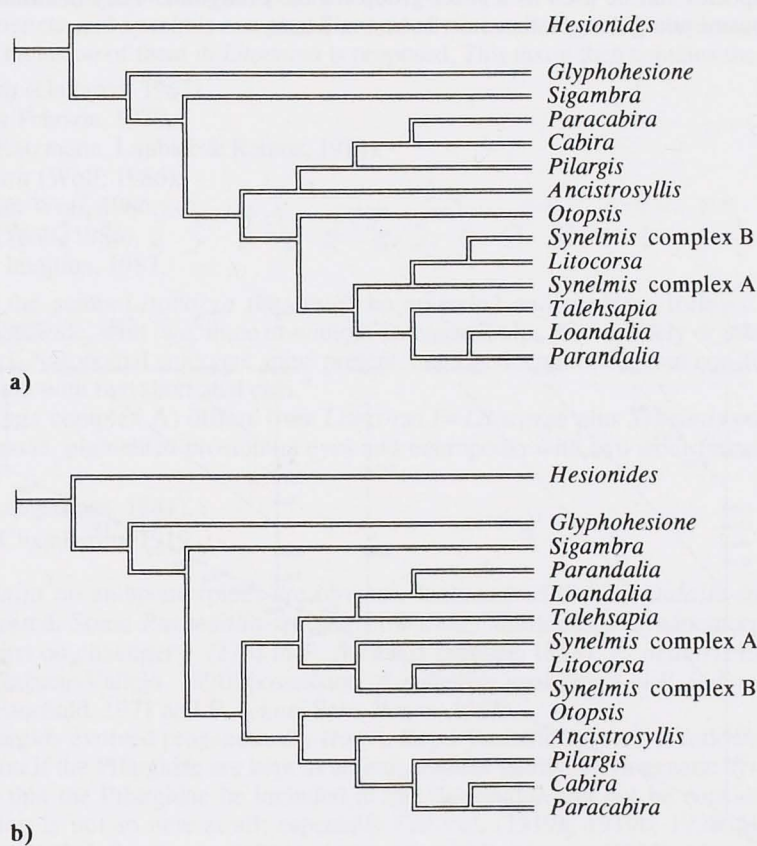


FIG. 3. — Cladograms of pilargid genera using different codings for character 19: a, the only cladogram produced using coding I. — b, the retained cladogram after successive character weighting using coding II (see text for details).

A possible nereidid-pilargid relationship was mentioned, e.g., by GLASBY (1990). A pilargid progenetic evolution of nereidid macroforms appears also conceivable, since nereidids possess a juvenile stage with two pairs of tentacular cirri (HAUENSCHILD & FISCHER, 1969, Fig. 8) which resembles primitive pilargid taxa (e.g., *Sigambra*). The nereidid juveniles, however, possess jaws, and lack a median antenna.

We, therefore, strongly support the Hesionidae as closest relatives of the Pilargidae. There is not only the high similarity between juvenile hesionids and primitive pilargid taxa; both taxa also generally coincide in the

morphology of head, parapodia and pharynx. The genus *Hesionides* is only slightly less reduced than primitive pilargids in possessing two tentacular segments and three tentacular cirri (see Fig. 1). However, the probability of an independent progenetic evolution of both *Hesionides* and the pilargid stem species cannot be excluded.

The largest differences between Hesionidae and Pilargidae were hitherto seen in their chaetation: pilargids with their acicula-like stout notopodial hooks or spines and exclusively simple neurochaetae versus hesionids with mostly capillary notochoetae and a neuropodial chaetation which always includes compound chaetae. Chaetation in the two taxa, however, may be less different than formerly supposed: (1) Spines and hooks are not homologous to aciculae, but derived notochoetae, which in some cases occur together with a true acicula (as FITZHUGH & WOLF, 1990 pointed out). (2) Just recently two hesionid species have been found with apparent pilargid chaetal features. *Microphthalmus simplicichaetosus* Westheide & Purschke, 1992, has exclusively simple bidentate neurochaetae. An undescribed *Microphthalmus* (WESTHEIDE, in prep.) is equipped with typical notopodial hooks. HARTMANN-SCHRÖDER (1962) described a *Microphthalmus ancistrostylisiformis* [sic!] because of its conspicuous notopodial spines. A strong notopodial spine is also present in *Hesiospina* Imajima & Hartman, 1964. Without doubt none of these species can be used as a sister-group for the Pilargidae. They demonstrate, however, that potential tendencies toward pilargid chaetation exist in hesionid taxa.

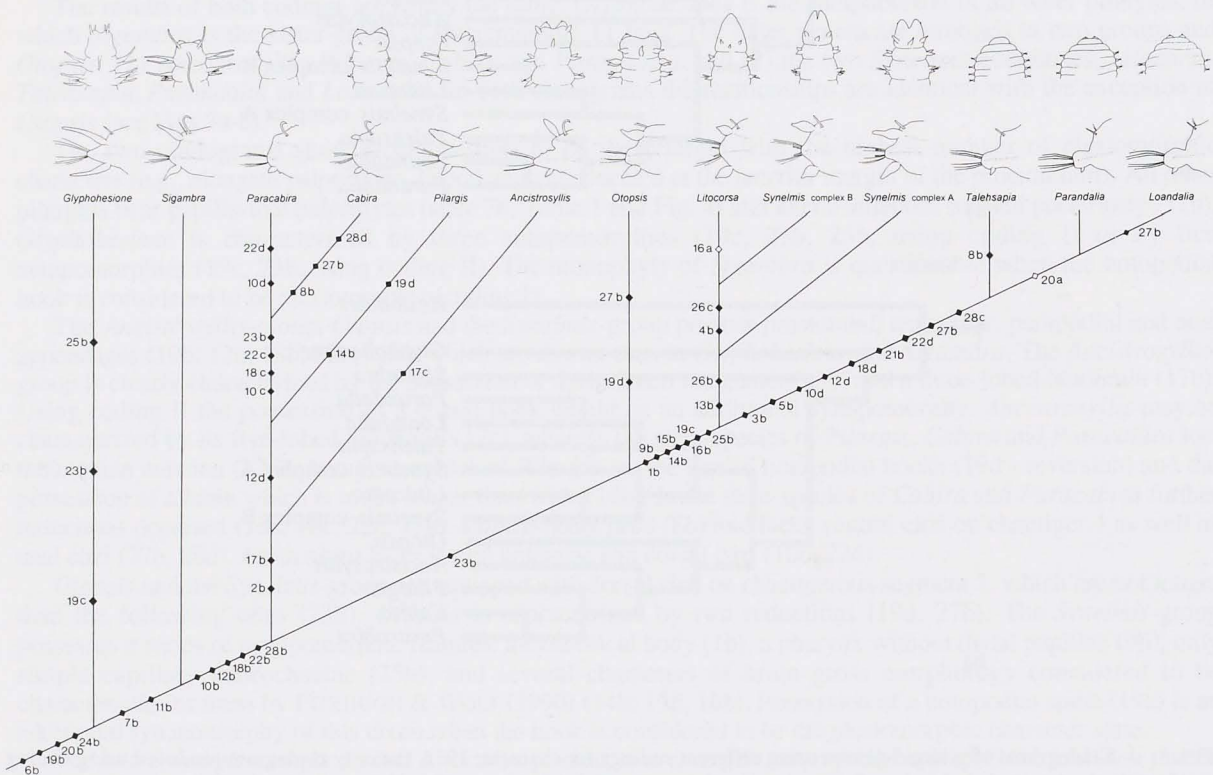


FIG. 4. — Cladogram of pilargid genera together with the outlines of anterior ends and parapodia. The outgroup is *Hesionides* Friedrich, 1937. Solid rhombs represent apomorphies, open rhombs symbolize character reversals. Numbers refer to characters in Table 1.

Unfortunately, most of the hesionid-pilargid similarities may be considered to be plesiomorphic characters going back to the stem species of the Nereidiformia. The autapomorphic character for the Hesionidae with the

strongest probability may be a large number of tentacular cirri (eight pairs), which, however, is not present in the hesionid juvenile stages (see above). Thus, even species assumed to be evolved from hesionid juveniles - the pilargid stem species in our opinion - cannot possess this character. This renders it extremely difficult to demonstrate a synapomorphy for Hesionidae and Pilargidae.

RELATIONSHIPS WITHIN THE PILARGIDAE. — There is no evidence that a division of the Pilargidae into Synelminae and "Sigambrinae" (SALAZAR-VALLEJO, 1986, 1990, SALAZAR-VALLEJO & SOLÍS-WEISS, 1992), or Synelminae and "Pilarginae" (SALAZAR-VALLEJO & ORENSANZ, 1991) is justified (see also FITZHUGH & WOLF, 1990). The "Sigambrinae" (= "Pilarginae") consisting of *Sigambra*, *Ancistrostylis*, *Ancistargis*, *Pilargis*, *Cabira* and *Paracabira* are not based on any apomorphic feature.

Considering the absence of a notopodial hook in *Pilargis* and *Otopsis* to be a loss is more probable than to be the plesiomorphic state. In the latter case one must assume that a notopodial hook was independently evolved three times: in *Sigambra*, in *Ancistrostylis*, and in the stem-species of *Cabira* and *Paracabira*. Therefore, *Otopsis* is likely the adelphotaxon of the *Synelmis*-group (Fig. 4).

The species of *Litocorsa* and *Synelmis* complex B are closely related (Fig. 4). Since no autapomorphies for the latter could be found, inclusion of them in *Litocorsa* is proposed. This taxon then contains the following species:

- Litocorsa annamita* (Gallardo, 1967),
- Litocorsa strenna* Pearson, 1970,
- Litocorsa dineti* (Katzmann, Laubier & Ramos, 1974),
- Litocorsa acuminata* (Wolf, 1986),
- Litocorsa antennata* Wolf, 1986,
- Litocorsa ewingi* (Wolf, 1986),
- Litocorsa dentata* Imajima, 1987.

The diagnosis of the genus *Litocorsa* thus must be emended and reads as follows: "Body cylindrical. Prostomium longer than wide, with two, three or without antennae. Palps incompletely or totally fused. Two pairs of short tentacular cirri. Notopodial emergent spine present, neuropodia with two stout non-furcate spines besides capillary ones. Pygidium with two short anal cirri."

Synelmis (= *Synelmis* complex A) differs from *Litocorsa* (= *Litocorsa* plus *Synelmis* complex B) in always possessing three antennae, pigmented prostomial eyes and neuropodia with two stout furcate spines; it includes the following species:

- Synelmis albini* (Langerhans, 1881),
- Synelmis simplex* Chamberlin, 1919.

Also for *Parandalia* no autapomorphies are obvious. Inclusion of the *Parandalia*-species in *Loandalia*, however, is not suggested. Some *Parandalia*-species show closer similarities (synapomorphies?) to *Loandalia* (absence of ventral cirri on chaetiger 1 (27b) in *P. tricuspis* (Müller, 1858), *P. ocularis* Emerson & Fauchald, 1971, *P. vivianneae* Salazar-Vallejo, 1990; possession of a median anal cirrus in *P. indica* (Thomas, 1963), *P. ocularis* Emerson & Fauchald, 1971 and *P. bennei* Solís-Weiss, 1983).

Given that the pilargids evolved progenetically from a larger hesionid species, it follows that the Hesionidae are a paraphyletic taxon if the Pilargidae are kept as an independent family. Phylogenetic systematic implications consequently require that the Pilargidae be included in the Hesionidae and not be considered an independent family. This suggestion is not so new at all; especially FAUVEL (1919a, 1919b, 1920, 1923, 1932), but also EHLERS (1908), HORST (1921), SOUTHERN (1921), AUGENER (1927), MONRO (1933), MESNIL & FAUVEL (1939), BERKELEY & BERKELEY (1941) and TREADWELL (1941) positioned pilargid species in the taxon Hesionidae. The phylogenetic systematical partitioning within such an enlarged family Hesionidae to create, e.g., subfamilies must be reserved till a comprehensive revision has been made of the "true" hesionid taxa.

ACKNOWLEDGEMENTS

We are indebted to Prof. Dr. K. FAUCHALD, Smithsonian Institution Washington (USNM), Dr. M.E. PETERSEN, Zoological Museum, University of Copenhagen (ZMUC), L.H. HARRIS, Los Angeles County Museum of Natural History (LACMNH), Dr. D. FIEGE, Senckenberg Museum Frankfurt (SMF), and A. NATEEWATHANA, Phuket Marine Biological Center, Thailand for the friendly loan of pilargid species. Special thanks are due to Dr.

D. EIBYE-JACOBSEN, (ZMUC) for his helpful advice in using HENNIG 86. Many ideas and comments he provided have been of considerable help in setting up our cladograms.

REFERENCES

- AUGENER, H., 1927. — Polychaeten von Südost- und Süd-Australien. *Vidensk. Meddr dansk naturh. Foren*, **83** : 71-275.
- BERKELEY, E. & BERKELEY, C., 1941. — On a collection of Polychaeta from Southern California. *Bull. South. Calif. Acad. Sci.*, **40** : 16-60.
- BRITAEV, T.A. & SAPHRONOVA, M.A., 1981. — New species of the family Pilargidae (Polychaeta) from the Sea of Japan and revision of the genus *Cabira*. *Zool. Zhur.*, **60** : 1314-1324. [In Russian, English summary]
- EHLERS, E., 1908. — Die bodensässigen Anneliden aus den Sammlungen der Deutschen Tiefsee-Expedition. *Wiss. Ergeb. Deutschen Tiefsee-Exped. 1897-1899*, **16** : 1-168.
- ELIASON, A., 1962. — Undersökningar över Öresund, 41: Weitere Untersuchungen über die Polychaetenfauna des Öresunds. *Lunds Univ. Arsskr.*, n.f., **58** : 1-97.
- EMERSON, R.R. & FAUCHALD, K., 1971. — A revision of the genus *Loandalia* Monro with description of a new genus and species of pilargiid polychaete. *Bull. South. Calif. Acad. Sci.*, **70** : 18-22.
- FARRIS, J.S., 1988. — *Hennig 86 reference, version 1.5*. New York, 41 Admiral Street, Port Jefferson Station 11776, 17 pp.
- FAUCHALD, K., 1977. — *The polychaete worms. Definitions and keys to the orders, families and genera*. Nat. Hist. Mus. Los Angeles County, California, **28** : 1-190.
- FAUVEL, P., 1919a. — Annélides Polychètes des îles Gambier et Touamotou. *Bull. Mus. natl Hist. nat., Paris*, **25** : 336-343.
- FAUVEL, P., 1919b. — Annélides Polychètes de Madagascar, de Djibouti et du Golfe Persique. *Zool. Exp. Gén., Paris*, **58** : 315-473.
- FAUVEL, P., 1920. — Les genres *Ancistrostylis* et *Pilargis* (Hesionidae). *Bull. Soc. Zool. Fr.*, **45** : 205-213.
- FAUVEL, P., 1923. — Polychètes Érrantes. *Faune Fr.*, **5** : 1-488.
- FAUVEL, P., 1932. — Annelida Polychaeta of the Indian Museum, Calcutta. *Mem. Indian Mus., Calcutta*, **12** : 1-262.
- FITZHUGH, K. & WOLF, P.S., 1990. — Gross morphology of the brain of pilargid polychaetes: Taxonomic and systematic implications. *Amer. Mus. Nov.*, **10024** (2992) : 1-16.
- FRIEDRICH, H., 1937. — Polychaetenstudien I - III. *Kieler Meeresforsch.*, **1** : 343-345.
- GARDINER, S.L., 1976. — Errant polychaete annelids from North Carolina. *J. Elisha Mitchell Sci. Soc.*, **91** : 77-220.
- GLASBY, C.J., 1990. — Phylogenetic relationships in the Nereididae (Annelida: Polychaeta), chiefly in the subfamily Gymnonereidinae, and the monophyly of the Namanereidinae. *Bull. Mar. Sci.*, **48** : 559-573.
- HAALAND, B. & SCHRAM, T.A., 1982. — Larval development and metamorphosis of *Gyptis rosea* (Hesionidae, Polychaeta). *Sarsia*, **67** : 107-118.
- HAALAND, B. & SCHRAM, T.A., 1983. — Larval development and metamorphosis of *Ophidromus flexuosus* (Delle Chiaje) (Hesionidae, Polychaeta). *Sarsia, Bergen*, **68** : 85-96.
- HARTMAN, O., 1959. — Catalogue of the polychaetous annelids of the world. Part 1, 2. *Allan Hancock Found. Publ. Occ. Pap.*, **23** : 1-628.
- HARTMANN-SCHRÖDER, G., 1962. — Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der argentinischen Küste Südpatagoniens unter besonderer Berücksichtigung der Polychaeten und Ostracoden. II. Die Polychaeten des Eulitorals. *Mitt. Hamb. Zool. Mus. Inst.*, Ergänzungsband zu **60** : 57-167.
- HAUENSCHILD, C. & FISCHER, A., 1969. — *Platynereis dumerilii*. *Mikroskopische Anatomie, Fortpflanzung, Entwicklung*. Großes Zoologisches Praktikum, Fischer, Stuttgart, Heft **9b** : 1-55.
- HESSLE, C., 1925. — Einiges über die Hesioniden und die Stellung der Gattung *Ancistrostylis*. *Ark. Zool. Stockholm*, **17a** : 1-36.
- HORST, R., 1921. — A review of the family of Hesionidae with a description of two new species. *Zool. Meded., Leyden*, **6** : 73-83.

- IMAJIMA, M. & HARTMAN, O., 1964. — The polychaetous annelids of Japan, pt. 1. *Allan Hancock Found. Publ. Occ. Pap.*, **26** : 1-237.
- JONES, M.L., 1961. — Two new polychaetes of the families Pilargidae and Capitellidae from the Gulf of Mexico. *Amer. Mus. Nov.*, **2049** : 1-18.
- LAUBIER, L., 1967. — Adaptations chez les Annélides Polychètes interstitielles. *Ann. Biol.*, **6** : 1-16.
- MESNIL, F. & FAUVEL, P., 1939. — Polychètes sédentaires de l'expédition du Siboga: Maldanidae, Cirratulidae, Capitellidae, Sabellidae et Serpulidae. *Siboga-Expedition*, **24** : 1-42.
- MIURA, T. & LAUBIER, L., 1989. — *Nautilina calyptogenicola*, a new genus and species of parasitic polychaete on a vesicomid bivalve from the Japan Trench, representative of a new family Nautiliniellidae. *Zool. Sci., Japan*, **6** : 387-390.
- MONRO, C.C.A., 1933. — On a new species of Polychaeta of the genus *Pilargis* from Friday Harbour, Washington. *Ann. Mag. Nat. Hist.*, **10** (11) : 673-675.
- PETTIBONE, M.H., 1966. — Revision of the Pilargidae (Annelida: Polychaeta), including descriptions of new species, and redescriptions of the pelagic *Podarmus ploa* Chamberlin (Polynoidae). *Proc. U.S. Nat. Mus.*, **118** (3525) : 155-208.
- SAINT-JOSEPH, A. de, 1899. — Note sur une nouvelle famille d'Annélides Polychètes (Pilargidiens). *Bull. Mus. Hist. nat., Paris*, **5** : 41-42.
- SALAZAR-VALLEJO, S.I., 1986. — Pilargidae (Annelida: Polychaeta) de Mexico: Lista de especies, nueva especie y biografía. *Cah. Biol. mar.*, **27** : 193-209.
- SALAZAR-VALLEJO, S.I., 1990. — Redescriptions of *Sigambra grubii* Müller, 1858 and *Hermundura tricuspis* Müller, 1858 from Brazil and designation of neotypes (Polychaeta: Pilargidae). *J. Nat. Hist.*, **24** : 507-517.
- SALAZAR-VALLEJO, S.I. & ORENSANZ, J.M., 1991. — Pilárgidos (Annelida: Polychaeta) de Uruguay y Argentina. *Cah. Biol. mar.*, **32** : 267-279.
- SALAZAR-VALLEJO, S.I. & SOLÍS-WEISS, V., 1992. — Biogeography of the pilargid polychaetes (Polychaeta Pilargidae) of the subfamily Synelminae. In: S.P. DARWIN & A.L. WELDEN (eds.), Biogeography of Mesoamerica. Proceedings of a Symposium, Mérida, México, Oct. 1984. *Tulane Stud. Zool. Bot.*, Suppl. Publ. 1.
- SOUTHERN, R., 1921. — Fauna of the Chilka Lake. Polychaeta of the Chilka Lake and also of fresh and brackish waters in other parts of India. *Mem. Ind. Mus.*, **5** : 565-660.
- TREADWELL, A.L., 1941. — Polychaetous annelids from the New England region, Porto Rico and Brazil. *Amer. Mus. Nov.*, **1138** : 1-4.
- WESTHEIDE, W., 1967. — Monographie der Gattungen *Hesionides* Friedrich und *Microphthalmus* Mecznirow (Polychaeta, Hesionidae). II. Zoologisches Institut und Museum der Universität Göttingen. *Z. Morph. Tiere*, **61** : 1-159.
- WESTHEIDE, W., 1987a. — The interstitial polychaete *Hesionides pettiboneae* n.sp. (Hesionidae) from U.S. east coast and its transatlantic relationship. *Bull. Biol. Soc., Wash.*, **7** : 131-139.
- WESTHEIDE, W., 1987b. — Progenesis as a principle in meiofauna evolution. *J. Nat. Hist.*, **21** : 843-854.
- WESTHEIDE, W. & PURSCHKE, G., 1992. — *Microphthalmus simplichaetosus* (Annelida: Polychaeta), a new hesionid from the Northwestern American Pacific Coast with exclusively simple chaetae. *Proc. Biol. Soc., Wash.*, **105** (1) : 132-135.
- WESTHEIDE, W. & RIEGER, R.M., 1987. — Systematics of the amphiatlantic *Microphthalmus-listensis* species-group (Polychaeta: Hesionidae): facts and concepts for reconstruction of phylogeny and speciation. *Z. zool. Syst. Evolutionsforsch.*, **25** : 12-39.
- WOLF, P.S., 1984. — Family Pilargidae Saint-Joseph, 1899. In: J.M. UEBELACKER & P.G. JOHNSON (eds), *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico*, **7** (4). Barry A. VITTOR & Ass., Mobile, **29** : 1-41.