

Phylogenetic Taxonomy, a Farewell to Species, and a Revision of *Heteropodarke* (*Hesionidae*, *Polychaeta*, *Annelida*)

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Abstract.—Cladistic relationships between 7 parts of the hesionid polychaete group *Heteropodarke* are assessed in a parsimony analysis based on 34 morphological characters. Taxon names are defined by apomorphy-based phylogenetic definitions, without reference to Linnean ranks or types. Species entities are omitted and denied any role in taxonomy; taxon names refer to monophyletic groups only. Linnean binomial species names are not employed, and all taxa are assigned uninomials. Previously known parts of *Heteropodarke* (*Africana* Hartmann-Schröder, 1974; *Formalis*, Perkins, 1984; *Heteromorpha* Hartmann-Schröder, 1962; *Lyonsi* Perkins, 1984; *Xiamenensis* Ding, Wu, and Westheide, 1997) are reexamined, and *Bidentata*, new taxon, and “*Zmyrina*” (informal name) are described from Papua New Guinea and Belize, respectively. The new taxon *Crassichaetae* is named for a subgroup of *Heteropodarke*, which is diagnosed by enlarged, anteriorly situated falcigers, and includes *Africana*, *Heteromorpha*, *Lyonsi*, and *Xiamenensis*. Within this group *Africana* and *Heteromorpha* are treated as *taxa inquirendae*. {Apomorphy-based definitions; Linnean nomenclature; phylogenetic taxonomy; polychaetes; ranks; species concepts; species names; types.}

The Linnean nomenclatural system was formulated when views on systematics differed radically from today (even though resulting classifications for various reasons sometimes have remained unchanged). Trees as models for depicting cladistic/phylogenetic relationships appear at least from the middle of the 19th century literature (e.g., Darwin, 1859:117; see also drawing from Darwin's notebook, Young, 1989:60), but it was not until Hennig (e.g., 1950, 1966) and early followers in the 1960–1980s (e.g., Brundin, 1966; Farris, 1970; Nelson, 1972; Rosen, 1978) that explicit tree-thinking (O'Hara, 1988) entered a larger part of the systematic community. Still, the Linnean system of nomenclature is utilized to transform tree information into written classifications (or systematizations; Griffiths, 1974; de Queiroz, 1988), and, as outlined below, this is problematic both in relation to the use of types (holotype, type species, etc.) and the use of ranks (genus, family, etc.). Suggestions to abandon ranks appear already in Hennig (1969) and Griffiths (1974, 1976), but a more integrated system with tree-based definitions of taxon names without Linnean types and ranks was not available prior to de Queiroz and Gauthier's (1990, 1992, 1994) proposal of phylogenetic taxonomy.

The merits of this system are currently under debate (e.g., Lidén and Oxelman, 1996; Lee, 1996; de Queiroz, 1997; Dominguez and Wheeler, 1997; Lidén et al., 1997; Härlin and Sundberg, 1998; Moore, 1998). In my view, phylogenetic taxonomy has three important advantages: (1) It adapts our nomenclature to tree-thinking, (2) it permits us to redefine current taxon names such that we abandon an outdated system without dismissing 250 years of taxonomy, and (3) it provides unequivocal definitions of taxon names. A series of more conceptual and general papers have been written on these issues (e.g., de Queiroz and Gauthier, 1990, 1992, 1994; de Queiroz, 1992, 1994, 1995, 1996; Bryant, 1994, 1996; Sundberg and Pleijel, 1994; Ghiselin, 1995; Schander and Thollesson, 1995; Lee, 1996; Härlin and Sundberg, 1998), joined by more applied studies (e.g., de Queiroz, 1987; Reisz et al., 1992; Cannatella and Hillis, 1993; Flynn et al., 1995; Bryant, 1996; Wyss and Meng, 1996; Cantino et al., 1997; Pleijel, 1998), but no consistent applications have been published in association with revisionary studies. For further evaluation of practical as well as conceptual consequences, this study represents an experiment in which phylogenetic taxonomy for the first time is consistently applied in a primary revision.

The debate on what species are and how they can/may/should be defined seems to be never-ending (see, e.g., Ereshefsky, 1992, and references within). Rather than entering into this discussion or forwarding yet another concept, I apply a view where species simply are denied any role in taxonomy and where only monophyletic groups are recognized by formal Latin names. For this reason I also apply uninomials for all names, because this treatment does not recognize any species entities and applies the same nomenclature for all taxa (see also Cain, 1959; Michener, 1963, 1964; de Queiroz and Gauthier 1992; Schander and Thollesson, 1995).

The present study thus combines de Queiroz and Gauthier's system with a view that species entities should not be recognized as taxa, and applies these ideas in a revision of a small group of hesionid polychaetes, *Heteropodarke* Hartmann-Schröder, 1962. These animals occur on marine shallow sand bottoms in tropical and subtropical areas, with five taxa previously described: *Heteromorpha* Hartmann-Schröder, 1962; *Africana* Hartmann-Schröder, 1974; *Formalis* Perkins, 1984; *Lyonsi* Perkins, 1984; and *Xiamenensis* Ding, Wu, and Westheide, 1997. To these I add two new parts from Papua New Guinea and Belize.

The study also forms part of a series of hesionid revisions, where the position of *Hesionidae* Grube, 1850 (for reasons explained below all taxon names are italicized), was analyzed in Pleijel and Dahlgren (1998), and the more inclusive interrelationships within *Hesionidae* were addressed in Pleijel (1998). Although the latter study actually included phylogenetic definitions of taxon names (paralleling Linnean ones), this represented a starting point for further evaluations and was, for several reasons, not possible to carry through in a fully consistent way; in the current paper these ideas are fully applied. As for the delineation and systematic position of *Heteropodarke*, it is currently the best confirmed hesionid group (Pleijel, 1998) and belongs in *Ophiodrominae* Grube, 1850, as seen from the pattern of dorsal cirri alternation (group IIIa1 as presented in Pleijel, 1998), and in *Ophiodromini* Grube, 1850, as seen from, e.g., a frontally inserted median antenna

and median antennal furrows. Although more uncertain, present evidence (Pleijel, 1998) indicates that *Parasyllidea* (Pettibone, 1961) is the sister group to *Heteropodarke* (Pleijel, 1998), with *Ophiodromus* as sister to *Parasyllidea* and *Heteropodarke*.

MATERIAL AND METHODS

Specimens

Newly collected specimens (*Bidentata*, new taxon, *Formalis*, *Lyonsi*, and "*Zmyrina*" {informal newly introduced name}) were relaxed in 7% magnesium chloride in fresh water, studied alive, preserved in 10% formaldehyde (i.e., 25% formalin) in seawater for one or a few days, rinsed in distilled water, and transferred to 70–80% ethanol (in some cases animals were preserved without prior relaxation, which usually evokes eversion of the proboscis). Specimens for light microscopy were mounted in Gurr Aquamount, either unpreserved (which makes tissues transparent and eases examination of details of chaetae and aciculae) or after formalin preservation. For scanning electron microscopy (SEM), specimens were similarly relaxed, preserved for a few hours in 1–2% osmium tetroxide in filtered seawater (except for SEM studies of "*Zmyrina*," which are based on formalin-preserved specimens), rinsed and stored in distilled water, transferred to alcohol, dried to the critical point, and sputter-coated with carbon, gold, or both. Drawings were prepared with a camera lucida attached to a compound microscope.

Museums are indicated by the following abbreviations: HZM (Universität Hamburg, Zoologisches Institut und Museum), LACM-AHF (Allan Hancock Foundation Collection of the Los Angeles County Museum of Natural History), MNHN (Muséum National d'Histoire Naturelle, Paris), SAM (South African Museum, Cape Town), SMF (Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main), SMNH (Swedish Museum of Natural History, Stockholm), USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.), and ZMUC (Zoological Museum, University of Copenhagen). Material labeled FP is currently in my own col-

lection but will eventually be deposited at SMNH.

Phylogenetic Methodology

All five nominal *Heteropodarke* taxa were employed as terminals, plus the two previously undescribed ones, *Bidentata* and "*Zmyrina*." Evidence for monophyly of each ingroup terminal is provided as autapomorphies in the cladistic analysis; obviously additional (homoplastic) autapomorphies may appear after the analysis. The specimens listed in the material-examined sections for each taxon form the basis for character scoring and descriptions, plus specimens for outgroup assessment (previously listed by Pleijel, 1998). It was not possible to obtain information relating to all characters from all examined specimens. Some were incomplete, and others were prepared for special purposes. For example, the extension of the pregut region cannot be examined in SEM-prepared specimens, and characters such as presence of the minute aciculae in the anterior-most segments could be observed only from live mounted specimens or from mounted specimens without prior preservation. Terminals, for this reason, represent combinations of observations. However, the terminals are based solely on specimens I could refer unequivocally.

Based on the results from the analysis in Pleijel (1998), trees were rooted with *Flexuosus* (*Ophiodromus*) delle Chiaje, 1825; *Pugetensis* (O.) Johnson, 1901; and *Humesi* (*Parasyllidea*) Pettibone, 1961, as outgroups (e.g., Watrous and Wheeler, 1981; Farris, 1982). The monophyly of *Heteropodarke* is evidenced by, e.g., the extended pregut region and the presence of nobbed neuroaciculae (Pleijel, 1998).

Absence/presence coding (Pleijel, 1995; Pleijel and Dahlgren, 1998) was employed to transform character observations into a matrix. The matrix was edited and trees were analyzed in MacClade 3.01 (Maddison and Maddison, 1992); tree searches were performed in PAUP 3.1.1 (Swofford, 1993), with the branch and bound search algorithm and "collapse 0-length branches" activated. Clade stability was assessed by branch support (Farris et al., 1982; Bremer,

1988, 1994; Donoghue et al., 1992) with PAUP (same settings as above).

PHYLOGENETIC TAXONOMY

The Linnean system, as utilized by cladists, is employed to communicate tree information. However, whereas I regard the study of tree topologies and recognition of monophyletic groups as a search for historical entities, the Linnean nomenclature with its typifications and rank allocations is poorly suited for the communication of the hierarchical relationships.

Within this system, taxa are referred to ranks such as species, genera, and families, a procedure that lacks any empirical justification: Monophyletic groups are recognized by apomorphies, but no such markers, of course, exist that may serve as rank identifiers. Further, ranks invite users of taxonomies to unwarranted horizontal comparisons in trees, such as one "genus" versus another "genus", although the represented information only relates to nested groups and sister groups (see also, e.g., Gauthier et al., 1988; Doyle and Donoghue, 1993).

Taxon names are defined by types: in the case of a family group, a type genus name, in turn defined by a type species name, in turn defined by a type specimen (cf. the Codes of Botanical and Zoological Nomenclature [ICZN]; International Commission on Zoological Nomenclature, 1985; Greuter et al., 1994). This typification is problematic because of the weak association between the definitions of the names and the relevant groups, just as if a name of an individual multicellular organism were defined by reference to one of its single cells only.

The use of ranks and types in conjunction leads to a series of problems (e.g., de Queiroz and Gauthier, 1994). The implication is that taxa referred to the same ranks are nonoverlapping and that the taxa always include their types. This, however, may be less informative than what is immediately apparent. First, not only these taxa have the nonoverlapping properties, but so do a vast number of other taxa; in other words, the statement that two taxa are nonoverlapping is simply not very specific. Second, the information that the same rank

taxa are nonoverlapping is virtually completely tree-dependent. Assume two family-level taxa: All that is known in the absence of tree topologies is that each of these two families is provided with their type genera, type species, and in the end, type specimens. The communicated information is then reduced to two nonoverlapping deposited specimens.

This low degree of precision gives rise to situations in which taxonomists may have full agreement on tree topologies and nomenclatural principles but still provide different applications of taxon names (see also, e.g., Griffiths, 1976; de Queiroz, 1996). None of the taxonomists makes an error; they simply disagree on what constitutes, for instance, a family-level group associated with a type and therefore come up with the same names for different groups or different names for the same groups. Although this "degree of freedom" or "flexibility" of taxon names has been described as a strength (Lidén and Oxelman, 1996), I believe communication in natural sciences requires clarity, and this is not a property of taxon names under the Linnean system.

Phylogenetic taxonomy differs from the Linnean system in two main respects: Taxa are named without rank allocations, and taxon names are defined by reference to tree topologies. Because ranks are of little relevance in the description of nested systems, I find their omission straightforward and unequivocal, and the new taxa below are introduced exactly as such, i.e., "new taxon" rather than "new genus," "new family," etc. As to the definition of taxon names, de Queiroz and Gauthier (e.g., 1990, 1992) suggested three kinds of phylogenetic name definitions: node-based ("the least inclusive clade including X and Y"), stem-based ("the most inclusive clade including X but not Y"), and apomorphy-based ("the monophyletic group diagnosed by apomorphy α ") (for formulations of these definitions, see also Schander and Thollesson, 1995; Lee, 1998). For several reasons I favor the apomorphy-based approach. Node-based definitions require reference either to less-inclusive monophyletic groups or to less-inclusive entities such as populations or individual organisms (de Queiroz, 1992). In the first case, they are not applicable for

names of the least inclusive taxa, which lack internal nested structure; in the second case, they introduce a difference between the name definitions of the least inclusive taxa and other taxa. This can be problematic because necessary information about internal structure often is wanting, and we may erroneously use populations or individual organisms to define names of groups that actually could be further divided into different monophyletic groups. Stem-based definitions require reference to sister groups, which I regard as a weakness because I do not identify groups on the basis of their sister relationships. A large number of unique characters may provide strong evidence for a taxon, but we may still have ambiguous or no information regarding its nearest neighbors.

Apomorphy-based definitions connect taxon names to the actual empirical evidence for the group recognition and can be applied similarly to all monophyletic groups, whether lacking internal nested structure or not. Apomorphy-based definitions have been rarely used (but see Envall, 1996; Crane and Kenrick, 1997; and, in a modified version, Polly, 1996) and are criticized because they may become ambiguous in the presence of newly discovered, post-definition homoplasy (Bryant, 1994; Schander and Thollesson, 1995; Holtz, 1996; Cantino et al., 1997). However, this may be avoided if the apomorphy is identified in agreement with a single specimen in the group (K. de Queiroz, pers. comm., is gratefully acknowledged for this suggestion); e.g., "*Hesionidae* is the monophyletic group diagnosed by the apomorphy enlarged ventral cirri on segment 3 homologous with those in *Hesione* Lamarck, 1818" (note that this definition also ties the name *Hesionidae* to the name *Hesione*). This feature in *Hesione*, in turn, may be diagnosed by an even less-inclusive group and, in the end, by a deposited specimen. Of course, the statement that a name "refers to the group diagnosed by α " does not imply that this feature has to be observable in all parts of the group (Platnick, 1979; de Queiroz and Gauthier, 1990); it may be altered (including reduced), in which case other characters identify group affinity. The apomorphy " α " merely helps us specify a particular monophyletic group.

As seen above, I prefer using the term "monophyletic group" instead of "clade" in the name definitions. "Clade" implies a branching event, whereas "monophyletic" (defined as an ancestral individual organism or population and all its descendants) makes no statement about the presence or absence of an internal nested structure. Phrased this way, the definition does not require references to entities such as "species" (see below).

In the choice of how much tree information to transform into taxon names, I see no need for naming each group. The selection is dictated by the amount of evidence present and by the actual need for a name (i.e., even a poorly confirmed group could be named if considered important for communication).

Species entities within phylogenetic taxonomy may, or may not, be accorded a special position. Reviews of species concepts are provided elsewhere (e.g., Otte and Endler, 1989; Ereshefsky, 1992; Claridge et al., 1997). Currently employed species can be divided into those based (directly or indirectly) on some notion of gene flow and reproduction, such as the biological species concept (e.g., Mayr, 1940), and into a heterogeneous assembly sometimes labeled phylogenetic species concepts. I consider different reproduction-based concepts inappropriate in taxonomy because, as shown by Bremer and Wanntorp (1979) and Rosen (1979), they are incompatible with tree-thinking and monophyly. Among the phylogenetic concepts are those that are character based (e.g., Rosen, 1979; Nelson and Platnick, 1981; Nixon and Wheeler, 1990), others based on history or tree topologies (cf. Wiley, 1978; Mishler and Donoghue, 1982 {in part}; Baum and Donoghue, 1995 {in part}; de Queiroz and Donoghue, 1988 {in part}), and others again made up of combinations of both (e.g., Cracraft, 1983; McKittrick and Zink, 1988) or represent more pluralistic approaches to the levels in relation to reticulation and branching in tree models where species names may be applied (Mishler and Donoghue, 1982; de Queiroz and Donoghue, 1988; Sluys, 1991; Graybeal, 1995). All of these concepts differentiate recognition of species entities from other taxa,

either by treating them as a special class separate from other taxa, or in some sense by pinpointing them as borderline groups.

For three reasons I regard current views on species as problematic: lack of consensus, lack of empirical connotations, and confusion of nomenclatural systems. Although we are free to define our concepts in any way we choose, agreements in use are desirable, and too many species concepts have been propagated too many times for the concept to be useful and consensual (see Mayden, 1997, for a review of 22 concepts in current use). I regard the term as corrupted by previous use and without any prospects for a future consensus.

Most species descriptions provide either one (or more) unique characters or unique combinations of plesiomorphic characters. In the first case, they refer to a monophyletic group—which then should be recognized as such; in the second case, they identify a heterogeneous assembly ("metaspecies" as used by Donoghue, 1985; and references within), which may consist of either an actual monophyletic group (but with undetected apomorphies) or a paraphyletic group, the status of which can be established only by an absence of evidence (i.e., no apomorphies). Applying species names, and thereby making statements about gene flow, lineages, or monophyly of these groups, is inappropriate and has no observational basis.

As an alternative, I here advocate that species entities should be disregarded and not used in taxonomy. There is a zone I recognize as fundamental, which separates hierarchical from reticulate relationships (cf. The tree model in O'Hara, 1993:Fig. 6) and in which these two distinct patterns dictate different research approaches. On one side of the zone, we can identify monophyletic groups, which then may be named as taxa; on the other side, we instead are dealing with tokogenetic relationships and apply a different kind of terminology relating to organisms, demes, and populations. (The situation that borders may be difficult to recognize except in retrospect represents a practical rather than a conceptual problem.) In this tree model I see no need for any species concepts. Taxon names are accord-

ingly restricted to monophyletic groups and the word species loses its meaning; In the presence of apomorphies we describe taxa, in the absence of apomorphies we don't.

A practical outcome of this view is that many currently named species ("meta-species") will not be recognized as taxa. I do not regard this as a disadvantage: They constitute a composite of different kinds, and clarity will not be achieved by uniting them into a single class and labeling them "species." Whenever necessary, we can, of course, specify informally that we refer to a certain population of a taxon.

The names of species are traditionally given in the form of binomials, in which the first name denotes generic affinity. Naturally, the reference to generic affinity is inappropriate within a rank-free taxonomy (see also Cain, 1959; Michener, 1963, 1964). Griffiths (1976), de Queiroz and Gauthier (1992), and Sundberg and Pleijel (1994) discussed the possibility of keeping the first name as a "praenomen" without any generic implications. This represents an option also in a species-free taxonomy; former binomials could then become united single taxon names, where the first part loses the connotation of higher group affinity. However, this option has several drawbacks: Confusion may arise when praenomina sometimes do, but sometimes do not, take the same name as more-inclusive groups, and transferred binomials may also erroneously be interpreted as distinguishing some entities as being less inclusive than the original uninomials. Schander and Thollesson (1995) instead suggested a solution wherein all taxon names take the same uninomial form. Former species names referring to monophyletic groups would then consist of the second (now capitalized) part of the binomen; e.g., *Ophiodromus flexuosus* would become simply *Flexuosus*. Confusion resulting from homonyms can be avoided by specification of authors, or of more-inclusive taxa, or both (a unique identification number could also form part of the name). There are several possibilities, and I have opted here to write names at first mention with the least inclusive taxon first, followed by more-inclusive ones within brackets, and ending with author and year of the

taxon, such as *Flexuosus* (*Ophiodromus*, *Hesionidae*) Sars, 1862. At subsequent mentions I use only the single name, e.g., *Flexuosus*, or follow the single name with an abbreviation of a more-inclusive taxon, e.g., *Flexuosus* (O.)—whatever is considered necessary for clarity.

Consider *Bidentata*, new taxon, as an example of newly introduced name in a species-free taxonomy. It is a single name without any generic or other rank connotation and will be left unchanged even if evidence at some later point indicates that it belongs to a different, nonoverlapping taxon, e.g., *Ophiodromus* instead of *Heteropodarke*. Further, should additional evidence show that *Bidentata* actually may be subdivided into several less-inclusive monophyletic groups, then these subdivisions will have no bearing on the name. The newly detected groups will be given their own names, and they will constitute subgroups within *Bidentata*. Similarly, to the overwhelming majority of all new species descriptions, I have no observations or analyses whatsoever on gene flow, or internal relationships, etc., within the named group. I recognize the affinity of *Bidentata* by the characters shared with *Heteropodarke* and recognize it as new because of its unique characters. This is all the available information; there is no evidence for further statements.

This is not to state that each new taxon description necessarily needs to be accompanied by new phylogenetic analyses (but see Bryant [1996] for an opposing view). If, in the presence of unique characters, we have reason to assume that a group constitutes a monophyletic group, then this may be sufficient evidence for a description. On the other hand, if the potential new taxon can only be recognized not by a single unique character but by character combinations of which none is unique per se, then further analysis is required to sort out the individuality of the group. For example, in the present study the evidence for monophyly of "*Zmyrina*" is weak and its identity is in need of further research; I therefore provide only an informal name within quotation marks.

My view on the dismissal of species entities is related to the "species-as-genera"

concept in Mishler and Donoghue (1982: 499): “they {species} are assemblages of populations united by descent just as genera are assemblages of species united by descent, etc.”), where species were regarded just as other taxa, i.e., as monophyletic groups (see also Lidén and Oxelman, 1989). But my proposal differs in that rank allocations are absent; neither species nor genera are recognized, and taxa are simply described as taxa. Donoghue (1985) and de Queiroz and Donoghue (1988) also outlined a “disjunctive species concept” based on tree topologies but deviating from my present suggestion by retaining the species term and viewing species as either populations or monophyletic groups. Løvtrup’s (1987) suggestion to view species as terminal taxa in the phylogenetic hierarchy likewise differs, both in recognizing species and in assigning them a special place (further, he did not specify whether they should be monophyletic or not). Nelson (1989:60) apparently approached the current opinion in the statement: “Among taxa there are some that arbitrarily are termed families, there are others termed genera, and there are others termed species.” Mishler (in press) suggests that species simply can be conceived as the least inclusive taxa within a rank-free taxonomy, a view that, to a high degree, conforms with the one presented here and combines phylogenetic taxonomy with “species-as-just-another-taxon.” Our approaches differ in that I, because of all different meanings of the word, would avoid any species term and, further, prefer not to assert that some taxa lack internal nested structures.

Even though the views I present on phylogenetic definitions and “a farewell to species” provide an integrated system, they are not necessarily interdependent. Disallowing species a special role is possible also within the Linnean system, where it then transforms into a “species-as-genera” concept (Mishler and Donoghue, 1982). Likewise, the phylogenetic system may, of course, be combined with a view on species as special entities.

Naming of groups designated as “new taxon” (i.e., without rank specification) has earlier been applied by paleontologists (e.g., Benton and Clark, 1988; Altangerel et

al., 1993; Holtz, 1994) but then has been restricted to more-inclusive groups that fall outside the scope of nomenclatural codes. Perhaps the only previous applications for a less-inclusive group were by Norell and de Queiroz (1991) in the introduction of a new iguanine lizard (which differed from the current study in having the name defined by a holotype rather than via a tree reference) and by Cantino et al. (1997) in a classification of Lamiaceae.

The newly introduced taxon names in this study may, or may not, be regarded as *nomina nuda* in the sense of the ICZN. If regarded as names belonging to the family, genus, or species groups, then indeed they do not fulfill the mandatory requirements, but in the absence of ranks they may equally well be viewed as suprafamiliar categories, which then fall outside the scope of the ICZN. Another formal issue is the current habit to italicize names of genus and species in texts; in this study, I instead have chosen to set all taxon names in italics.

PHYLOGENY OF *HETEROPODARKE*

Two analyses were performed on the basis of the character matrix in Table 1: one including *Africana*, which yielded four equally parsimonious trees (44 steps; strict consensus illustrated in Fig. 1a), and one excluding this taxon, which resulted in a single shortest tree (also 44 steps).

Africana is problematic in that all available specimens are in extremely poor condition, and observations for many characters are lacking. It unequivocally belongs to the new taxon *Crassichaetae*, which includes also *Heteromorpha*, *Lyonsi*, and *Xiamenensis* (Fig. 1a), but the position within this group is uncertain; *Africana* is treated as *taxon inquirenda* within *Crassichaetae*, because there currently is no evidence for monophyly of the taxon. Instead, I base the further discussions on the restricted tree in Figure 1b.

Numerals above the branches in Figure 1b refer to the apomorphies; numerals below branches are branch support. The latter indicate two well-supported clades on the tree: the whole ingroup *Heteropodarke*, and the *Crassichaetae*.

That the *Heteropodarke* group is well corroborated is in agreement with the hesionid

TABLE 1. Character matrix for parsimony analysis. Character numbers correspond to those in *Appendix*. *Flexuosus* (*Ophiodromus*), *Pugettensis* (*Ophiodromus*), and *Humesi* (*Parasyllidea*) were designated as outgroups. "?" indicates lack of information.

| Taxon | Characters | | | | | | |
|-----------------------------------|------------|-------|-------|-------|-------|-------|------|
| | 12345 | 1 | 11111 | 11112 | 22222 | 22223 | 3333 |
| | | 67890 | 12345 | 67890 | 12345 | 67890 | 1234 |
| <i>Flexuosus</i> (<i>O.</i>) | 01?00 | 10000 | 11101 | ?0110 | 01110 | 00000 | 0000 |
| <i>Pugettensis</i> (<i>O.</i>) | 01?00 | 10000 | 11101 | 00110 | 01100 | 00000 | 0000 |
| <i>Humesi</i> (<i>P.</i>) | 0??00 | ?0000 | 00101 | 000?? | 00000 | 00000 | 0000 |
| <i>Africana</i> (<i>H.</i>) | 1?111 | ?10?1 | ????1 | 11000 | 10001 | 11110 | 000? |
| <i>Bidentata</i> (<i>H.</i>) | 10001 | 11111 | 11110 | 010?? | ?0001 | 00111 | 101? |
| <i>Formalis</i> (<i>H.</i>) | 10001 | 11111 | 00101 | ?1001 | 01011 | 01111 | 1000 |
| <i>Heteromorpha</i> (<i>H.</i>) | 1?111 | ?10?1 | 10001 | 1100? | 10001 | 11110 | 0000 |
| <i>Lyonsi</i> (<i>H.</i>) | 10111 | 01011 | 10001 | 11000 | 10001 | 11110 | 100? |
| <i>Xiamenensis</i> (<i>H.</i>) | 1??11 | 11011 | 10101 | 1100? | 10001 | 11110 | 010? |
| " <i>Zmyrina</i> " (<i>H.</i>) | 10001 | 11111 | 10101 | ?1011 | 01101 | 00000 | 0001 |

analysis in Pleijel (1998), even though that was based on a more restricted set of *Heteropodarke* taxa. "*Zmyrina*," sister to all other *Heteropodarke*, retains several plesiomorphic features shared with, e.g., *Ophiodromus*, such as furcate notochaetae, slender falcigers, and smooth ventral cirri, although its *Heteropodarke* affinity is clearly indicated by, e.g., the presence of a thin, threadlike body shape, short and wide nuchal organs, knobbed neuroaciculae, and elongated and differentiated pregut. The monophyly of "*Zmyrina*," however, is considered weak and is evidenced by only two homoplastic characters (which are present also in closely related taxa) plus the neuropodial capillaries in posterior neuropodia, which have an uncertain distribution outside *Heteropodarke* (see below). For these reasons, the name is not formally introduced.

Within *Crassichaetae*, the relation between *Heteromorpha* and *Lyonsi* is problematic, given the absence of *Heteromorpha* autapomorphies, a situation that leaves several options: (1) The name *Heteromorpha* (or *Lyonsi*) could be applied to the group in Figure 1b, which currently encompasses both *Heteromorpha* and *Lyonsi*, or (2) *Lyonsi* could be recognized as a monophyletic group, with *Heteromorpha* being treated as *taxon inquirenda*. In the absence of apomorphies for *Heteromorpha*, the topology presented may indicate that *Lyonsi* actually is nested within *Heteromorpha*, with the latter then becoming paraphyletic at recognition of the former; in this case, I would opt for alterna-

tive 1. On the other hand, the quality of the examined *Lyonsi*-specimens was much better than for *Heteromorpha*, and the problem may actually be easily solved whenever new specimens from Peru become available. In the absence of good study material, I therefore chose alternative 2, which emphasizes the current lack of reliable character observations. The definition of *Crassichaetae* connects the name to the first ancestor with enlarged falcigers as these occur in *Lyonsi*, rather than in *Xiamenensis* or the two other parts; I made this choice simply because I had access to better study material of *Lyonsi* than of the other groups. In any case, I consider future detection of homoplasy in this character unlikely, and the measure is therefore probably of no practical importance. The presence of spinigers in posterior neuropodia represents evidence of monophyly for *Lyonsi* (although this occurs independently also in the {*Bidentata*, *Formalis*} group), and the presence of non-enlarged falcigers with round-tipped blades is evidence for *Xiamenensis*.

The identity of the *Bidentata-Formalis* group is weak and evidenced only by the presence of single spinigers already from the first chaetiger, plus the presence of these spinigers also in posterior segments (as noted above, also appearing independently in *Lyonsi*). Evidence for monophyly of *Bidentata* is represented by enlarged dorsal and ventral cirri on segment 4, appearance of neuropodia and neurochaetae first from segment 5, and bidentate falcigers;

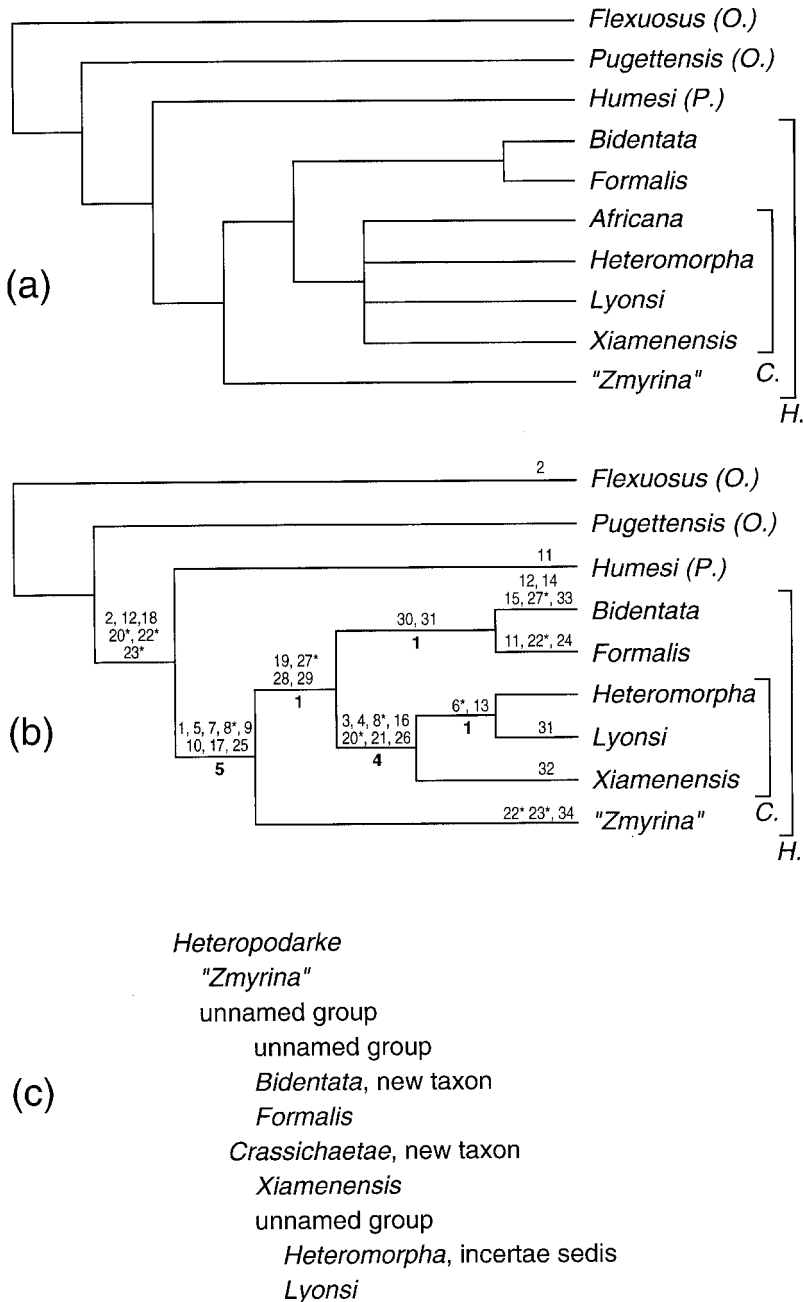


FIGURE 1. *Heteropodarke* cladograms and systematization. (a) Strict consensus of four primary trees from analysis with *Africana* included. (b) Single most-parsimonious tree from analysis with *Africana* excluded. O., *Ophiodromus*; P., *Parasyllidea*; C., *Crassichaetae*; H., *Heteropodarke*. (c) Systematization of the tree in (b). Note that "Zmyrina" and *Heteromorpha* may have less-inclusive positions than indicated on tree and in systematization (see text). Numerals above lines in (b) represent character transformations (optimized with ACCTRAN; equivocal transformations indicated by *); numerals below lines are branch support.

monophyly in *Formalis* is supported by the lack of prolonged dorsal cirri on segment 2 and the presence of single capillary notochaetae.

DIAGNOSES, DESCRIPTIONS,
AND TAXON NAME DEFINITIONS

Descriptions of taxa below are based only on primary observations unless specified by explicit reference to earlier descriptions. "Descriptions" constitute the observations that form the basis of the tree estimates (plus additional observations that were not possible to delineate in a meaningful way for character scoring); "diagnoses," on the other hand, represent tree-dependent homology hypotheses. That is, descriptions and diagnoses correspond to primary versus secondary homology statements as used by de Pinna (1991). No description is provided for *Heteropodarke*; because this is a primary revision, I consider it important to communicate character information for each of the least inclusive taxa, thereby stating explicitly when actual observations are missing or present.

As an alternative to an identification key, useful characters for the determination of *Heteropodarke* parts are provided in Table 2.

Heteropodarke Hartmann-Schröder, 1962

Heteropodarke (Hartmann-Schröder, 1962: 117–118)

Apomorphy-based name definition.—Although the present study addresses relationships within *Heteropodarke* rather than the actual monophyly of this group, I consider the taxon sufficiently well corroborated to provide a name definition: *Heteropodarke* is the group diagnosed by the apomorphy nobbed neuroaciculae homologous with those in *Heteromorpha* (specimen HZMP-14155).

Diagnosis.—*Ophiodromini* with thin, threadlike body shape, short palpophores, small eyes, short and wide nuchal organs, 10 terminal proboscis papillae, elongated pregut, articulated ventral cirri, and nobbed neuroaciculae.

Distribution.—Circumtropical and subtropical: Peru, California, Belize, Gulf of Mexico, Florida, North Carolina, South

Africa, Gulf of Aqaba, Yellow Sea, Papua New Guinea, New Caledonia.

Remarks.—For earlier treatments of *Heteropodarke*, see Hartmann-Schröder (1962: 117–118), Fauchald (1977:76), Dorsey (1978: 82), Hilbig (1994:254–256), and Pleijel (1998: 136). Hartmann-Schröder (1962, 1974) noted variability in the number of tentacular cirri (or, rather, appearance of first chaetiger, which apparently represented the actual observations; see below regarding terminology) for *Heteromorpha* and *Africana*, and Perkins (1984) noted this for *Lyonsi*. As seen in Blake (1975), Haaland and Schram (1982, 1983), Schram and Haaland (1984), and Pleijel (1998), the anterior cirri during the ontogeny of hesionids become enlarged, the parapodial lobes and chaetae become reduced, and the appearance of "normal", segmental parapodia is successively transferred backwards—a process that continues until the adult stage is reached. The descriptions by earlier authors of polymorphic populations of *Heteromorpha*, *Africana*, and *Lyonsi* are based on mixtures of different ontogenetic stages. In all other observed hesionids, the adult expression of these characters is present already in small specimens (~25 segments), but in some *Heteropodarke* the final condition is reached at a later stage: I have observed specimens as large as ~35 segments that were provided with parapodia on more anterior segments than is found in adult stages. The character list for the analysis (Appendix) includes only what I determine as characters of adult stages (usually evidenced by presence of sexual products). This includes neuropodia with neurochaetae appearing from segment 4—as in *Africana*, *Formalis*, *Heteromorpha*, *Lyonsi*, and "*Zmyrina*"—versus from segment 5 as in *Bidentata*.

The term "tentacular cirri" is avoided in accordance with Pleijel (1998) and is replaced by specific references to segmental position and morphology of anterior cirri and absences of chaetae and chaetigerous lobes from anterior segments.

"*Zmyrina*", Informal Name (Fig. 2)

Material examined.—Belize, Carrie Bow Cay (CBC), 16°48.2'N, 88°04.5'W; SCUBA, coll. FP: SMNH 5189a, 1 specimen, W CBC,

TABLE 2. Useful characters for identification of *Heteropodarka* parts. Note that separation of *Africana* and *Heteromorphia* is currently problematic (see text).

| Characters | Taxa | | | | | | | |
|--|-----------------|---------------------|-----------------|----------------------|---------------|--------------------|----------------------|--|
| | <i>Africana</i> | <i>Bidentata</i> | <i>Formalis</i> | <i>Heteromorphia</i> | <i>Lyonsi</i> | " <i>Zmyrina</i> " | <i>Ximeneris</i> | |
| Anterior and posterior eyes | Separate | Close | Close | Separate | Separate | Close | Separate | |
| Palp insertion | Ventral | Distal | Distal | Ventral | Ventral | Distal | Ventral | |
| Prostomial shape | Elongated | Quadrangular | Quadrangular | Quadrangular | Elongated | Elongated | ? | |
| Chaetae from segment no. | 4 | 5 | 4 | 4 | 4 | 4 | 4 | |
| Anterior dorsal cirri | Long | Long | Short | Long | Long | Long | Long | |
| Notochaetae | Absent | Absent | Present | Absent | Absent | Present | Absent | |
| Spinigers | Present | Present | Present | Present | Present | Absent | Present ^a | |
| Spinigers first chaetigers | Absent | Present | Present | Absent | Absent | Absent | Absent | |
| Spinigers median ^b and posterior segms. | Absent | Present | Present | Uncertain | Present | Absent | Absent | |
| Enlarged anterior falcigers ^c | Present | Absent | Absent | Present | Present | Absent | Present | |
| No. anterior falcigers ^d | ~5 | >5 | >5 | ~5 | ~5 | >5 | ~5 | |
| Falcigers median and posterior segms. | Unidentate | Bidentate | Unidentate | Unidentate | Unidentate | Unidentate | Rounded | |
| Posterior hooked notoaciculæ | Present | Absent ^d | Absent | Present | Present | Absent | Present | |

^a Possibly apillaries (see taxon description).^b Posterior to pregut region.^c Except first 2–3 chaetigers.^d Posterior-most segments not observed.

sand among *Thalassia*, depth 1 m, 18 Sep 1997; SMNH 5189b, 1 specimen (mounted), E CBC, coarse sand with *Halimeda*-remains among corals, depth 30 m, 21 Sep 1997; SMNH 5189c, 18 specimens (3 anterior and 1 posterior end mounted, 13 in ethanol, 2 mounted for SEM), E CBC, coarse sand with *Halimeda*-remains among corals, depth 26 m, 23 Sep 1997; SMNH 5189d, 13 specimens (1 mounted, 7 in ethanol, 5 mounted for SEM), E CBC, coarse sand with *Halimeda*-remains among corals, depth 12 m, 23 Sep 1997.

Diagnosis.—*Heteropodarke* with posterior neuropodial capillaries and possibly (equivocal optimization) furcate notochaetae.

Description.—Relationship between segment number and length illustrated in Figure 3a. Body thin, threadlike, rather short, of uniform width, last segments tapering, cylindrical with flattened venter in cross-section. Eyes red, other pigmentation absent, opaquely transparent. Preserved specimens whitish. Prostomium with transverse ciliated band, medially interrupted. Each segment dorsally with two transverse bands: one midsegmental reaching dorsal cirrophores, and one at boundary between segments. Prostomium quadrangular, posteriorly rounded (Fig. 2a). Paired antennae and palpostyles similar in size, proximally slightly inflated with tapering distal parts; palpostyles usually slightly shorter. Palpophores short, anteriorly inserted (Fig. 2b). Median antenna similar in shape to paired antennae but $\frac{2}{3}$ to $\frac{3}{4}$ as long, inserted on elevation on anterior margin, dorsally to paired antennae (Fig. 2a). Eyes small, of similar size or anterior pair slightly larger; anterior and posterior pair situated close together or coalescing; anterior pair varying from rounded to kidney-shaped. Nuchal organs short, wide lateral bands of cilia, middorsally well separated (Fig. 2a, 2c). Facial tubercle indistinct, possibly weakly developed. Proboscis smooth, separated in proximal and distal ring; distal ring with ten pointed, triangular terminal papilla, ciliated on inferior side (Fig. 2d). Dorsal cirri on segment 1 highly variable in length, reaching segments 5–7 with 8–14 articles; dorsal cirri of segment 2 reaching segments 7–8 with 16–19 articles; dorsal cirri of segment 3 reaching segments 6–7

with 9–13 articles. Dorsal cirri on segments 1–3 distinctly longer and stouter than on following segments. Ventral cirri of segment 1 reaching segments 3–4 with 7–8 articles; ventral cirri on segment 2 reaching segment 4 with 6–8 articles; ventral cirri on segment 3 reaching segments 4–5 with 5–7 articles. Ventral cirri on segments 1–3 all of similar length, stouter and longer than on following segments and situated on large distinct cirrophores. Single aciculae in all cirrophores on segments 1–3. Muscular pregut reaching segments 8–11, length size-dependent (Fig. 3b). Segment 4 with dorsal cirri, chaetae, chaetigerous lobes, and ventral cirri similar to following segments. Small, rounded prechaetigerous lobes on all chaetigers. Dorsal cirri of chaetigerous segments several times longer than ventral, annulated with 7–10 articles, cirrophores distinct. Elevated and prolonged dorsal cirri on segments 5, 8, 10, 12, 15, 17, 19, 21, 23, 26, 27, 29, and 31; shorter and horizontally directed on other segments. Notoaciculae single, fine. Single (rarely double) furcate notochaetae from segments 6–7, emerging near end of notoacacula (Fig. 2e, 2f); prongs straight, fine, pointed, subequal in length; no visible serrated areas. Stout, distally curved posterior notoaciculae absent. Neuroaciculae single, fine, knobbed with subdistal constriction. Enlarged falcigers and spinigers absent. Segment 4 with 5–6 falcigers, segment 5 with 6–7, other anterior segments with 8–9, posterior segments with 6–7. Falcigers longer and finer than in other *Heteropodarke*, similar to outgroups and most other *Hesionidae*; blades straight or slightly bent, highly variable in length within each fascicle. All blades unidentate. Posterior-most 2–3 segments with few capillary chaetae, presumably transitory. Chaetal shafts internally both chambered and with weak internal striation. Ventral cirri (Fig. 2g) similar to dorsal, but much shorter, not reaching as far as chaetae, and without distinct annulation; cirrophores small, indistinct. Pygidial cirri long, annulated. Median pygidial papilla absent (Fig. 2h).

Etymology.—The name “*Zmyrina*” is obtained from graffiti in Pompeii; it also occurs in the poem “Graffito” by Ekelöf (1959).

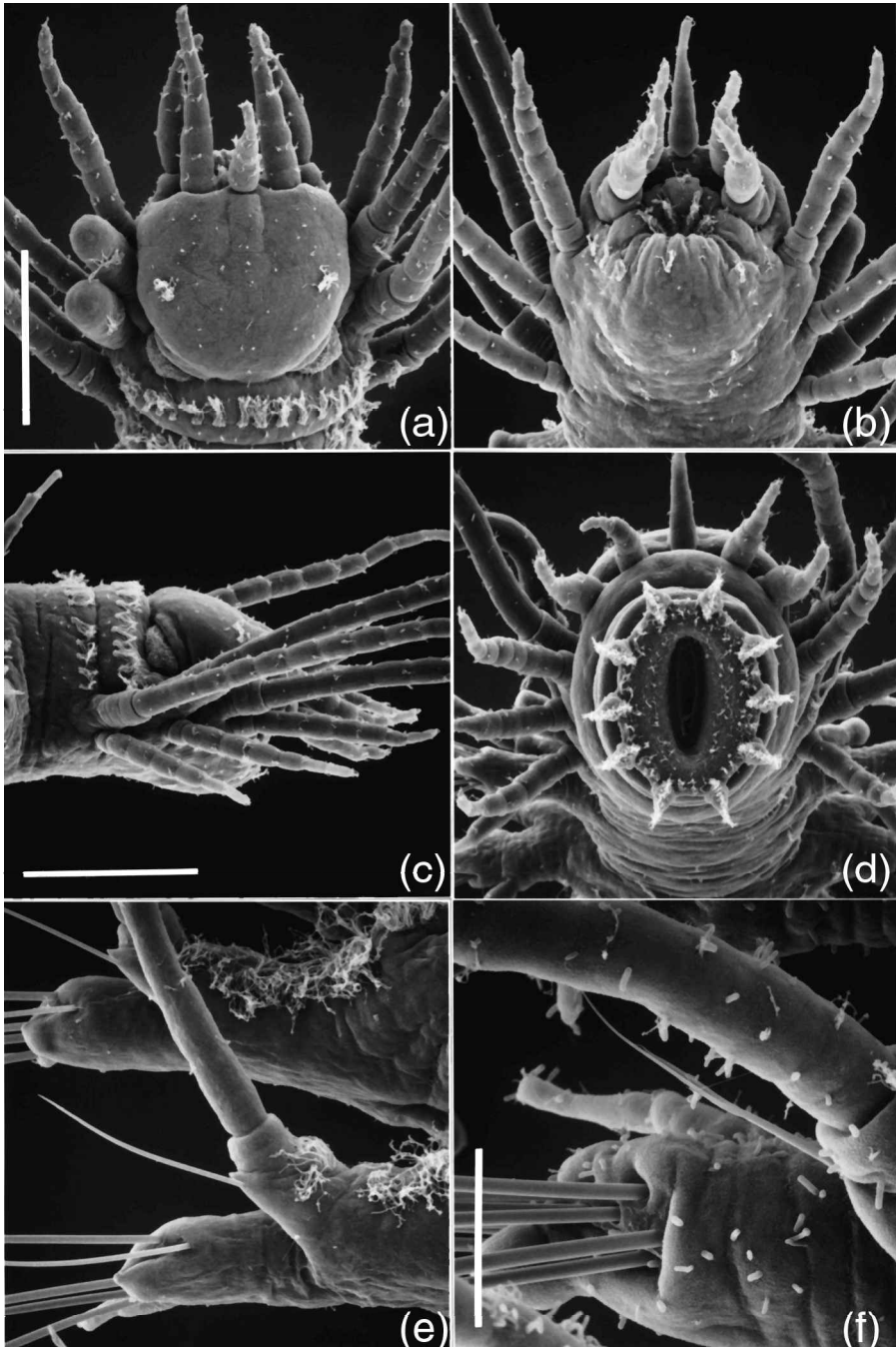


FIGURE 2. "*Zmyrina*", informal name. SEM photographs of specimens from Belize. (a) Anterior end, dorsal view. Bar = 75 μm . (b) Anterior end, ventral view. Same scale as (a). (c) Anterior end, lateral view. Bar = 86 μm . (d) Proboscis, anterior view. Same scale as (c). (e) Postero-median parapodium, right side, antero-dorsal view. Bar = 43 μm . (f) Parapodium segment 9, right side, antero-dorsal view. Bar = 25 μm . (Continued on next page).

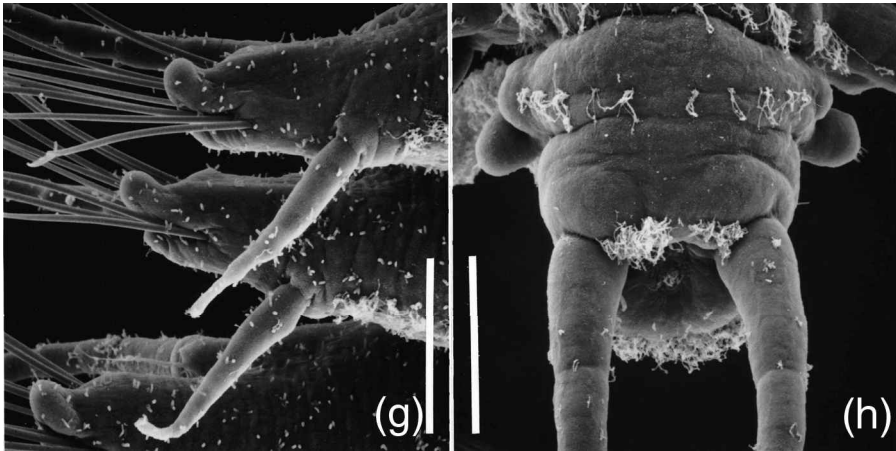


FIGURE 2. (Continued). (g) Median parapodium, right side, antero-ventral view. Bar = 60 μ m. (h) Posterior end, ventral view. Same scale as (e).

Distribution.—Known only from Belize.

Remarks.—Examined specimens include both males and females with sexual products; eggs very small, ~40 μ m in diameter. I have chosen not to introduce “*Zmyrina*” as a formal taxon name in this study. In Figure 1A and 1B it is the sister group to the remaining *Heteropodarke*, the affinity to this group being clearly indicated by the presence of nobbed neuroaciculae and elongated pregut. It obviously possesses a unique combination of features, but the only currently known apomorphy that can be unequivocally optimized is the very fine capillary neurochaetae present in the posterior-most segments. Lacking observations on the more specific distribution of this character among taxa outside *Heteropodarke*, the evidence for monophyly is weak. There is a risk that the presence of these chaetae is actually more widely distributed than currently known, which could point to a much larger group than originally intended if used in the definition of the name. The informal “*Zmyrina*” plus the absence of a name definition acknowledges the uncertainty about its delineation and status.

Bidentata, New Taxon (Figs. 4–5)

Material examined.—Papua New Guinea, Madang Lagoon, Tab Anchorage, W Tab Island, 05°10.3'S, 145°50.6'E, sandy slope with *Halimeda* residuals, SCUBA, coll. FP: SMNH 5190a, 1 specimen, depth 11 m, 18

Dec 1994; SMNH 5190b, 1 specimen, (including 3 mounted slides with parapodia mountings), depth 6 m, 20 Dec 1994; SMNH 5190c, 1 specimen, depth 11 m, 23 Dec 1994; SMNH 5190d, 1 specimen (including 15 median segments cut off and mounted on slide; SMNH 5190e), depth 10 m, 1 Jan 1995.

Apomorphy-based name definition.—*Bidentata* is the group diagnosed by the apomorphy bidentate falcigers homologous with those in SMNH 5190b.

Diagnosis.—*Heteropodarke* with enlarged dorsal and ventral cirri on segment 4, neuropodia appearing first from segment 5, and bidentate falcigers present.

Description.—Relationship between segment number and length unknown (no entire specimens have been observed). Body thin, threadlike, of uniform width, cylindrical with flattened venter in cross-section; posterior end unknown. Eyes red-orange, other pigmentation absent, opaquely transparent. Preserved specimens white. Prostomial or segmental ciliation not observed. Prostomium quadrangular with rounded corners (Fig. 4a). Paired antennae and palpostyles similar in size and shape, proximally slightly inflated with elongated distal parts (Fig. 4a). Palpophores short, anteriorly inserted. Median antenna similar in shape to paired antennae but slightly to distinctly shorter, inserted on elevation on anterior margin, dorsally to paired antennae. Antennae and palpostyles weakly annulated. Eyes small, of similar size or anterior

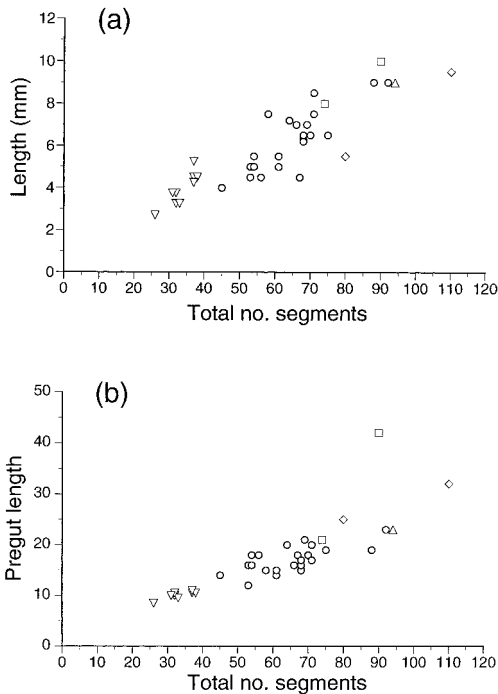


FIGURE 3. Relationships between (a) the length in millimeters and the total number of segments, and (b) the segment number at which the pregut ends and the total number of segments, in "*Zmyrina*," *Formalis*, *Lyonsi*, *Xiamenensis*, and *Heteromorpha*. Only entire specimens without any indications of regeneration were included. ∇ "*Zmyrina*" (specimens from Belize); \circ *Formalis* (specimens from Belize and Florida); \square *Lyonsi* (specimens from Florida); \diamond *Xiamenensis* (specimens from East China Sea); \triangle *Heteromorpha* (specimen from California).

pair slightly larger; anterior and posterior pair situated close but separated from each other (Fig. 4a); anterior pair rounded to slightly kidney-shaped, posterior pair rounded. Nuchal organs short, wide lateral bands of cilia, middorsally well separated. Facial tubercle not observed. Proboscis smooth, short, separated in proximal and distal ring; distal ring with ten pointed, triangular terminal papillae, ciliated on inferior side. Dorsal cirri on segment 1 reaching segments 5–8 with 13–16 articles; dorsal cirri on segment 2 reaching segments 8–10 with 20–22 articles; dorsal cirri on segment 3 reaching segments 6–8 with 12–16 articles; dorsal cirri on segment 4 reaching segments 7–9 with 14–17 articles. Dorsal cirri on segments 1–4 distinctly longer than on following segments; cirrophores enlarged. Ventral

cirri on segment 1 reaching segments 4–5 with 6–8 articles; ventral cirri on segment 2 reaching segments 5–6 with 7–8 articles; ventral cirri on segment 3 reaching segments 6–7 with 8–9 articles; ventral cirri on segment 4 reaching segments 7–8 with 7–8 articles. Ventral cirri on segments 1–4 of approximately same length, longer than on following segments, and situated on distinct cirrophores. Aciculae in anterior achaetigerous segments in cirrophores of dorsal cirri of segments 1–3 and in cirrophores of ventral cirri of segments 1 and 4; remaining ones unknown. Muscular pregut reaching segments 23–26, length probably size-dependent. Segment 5 with dorsal cirri, chaetae, chaetigerous lobes, and ventral cirri similar to following segments. Small preacicular and larger postacicular lobes present; distinct finger-shaped prechaetal lobes absent. Anterior neuropodial lobes rectangular in anterior or posterior view, gradually becoming more pointed from about segments 15–20. Dorsal cirri of chaetigerous lobes >2 times as long as ventral, annulated with 10–18 articles, cirrophores distinct (Fig. 4b). Dorsal cirri alternation difficult to observe on available specimens, but elevated, prolonged cirri probably present on segments 5, 8, 10, 12, 15, 17, 19, 21, 23, 25, 27, and 29; shorter and horizontally directed on other segments. Notoaciculae single, fine. Capillary notochoetae absent. Stout, distally curved posterior notoaciculae not observed. Neuroaciculae single or double, stout, knobbed with subdistal constriction; tips finely fringed (Fig. 4g). Enlarged falcigers absent although chaetae of pregut region have slightly stouter appearance. First chaetigers with 6–8 falcigers (Fig. 4c) and 1 spiniger (Fig. 4d), increasing to ~10–12 falcigers and 1–2 spinigers (Fig. 5a, 5b); from segments 14–20 with ~5–6 falcigers and usually single spinigers (Fig. 4b, 4f). Single or double spinigers present on all chaetigers (observed till segment 60). Anterior falcigers all unidentate (Fig. 4c); bidentate falcigers (Figs. 4e, 5c) appear posterior to segments 14–20. Shafts of spinigers and falcigers distally bilobed. Internal longitudinal chaetal striation weakly developed (Fig. 5c). Ventral cirri similar to dorsal but less distinctly annulated, with ~5–6 articles, reaching slightly beyond parapodium; small

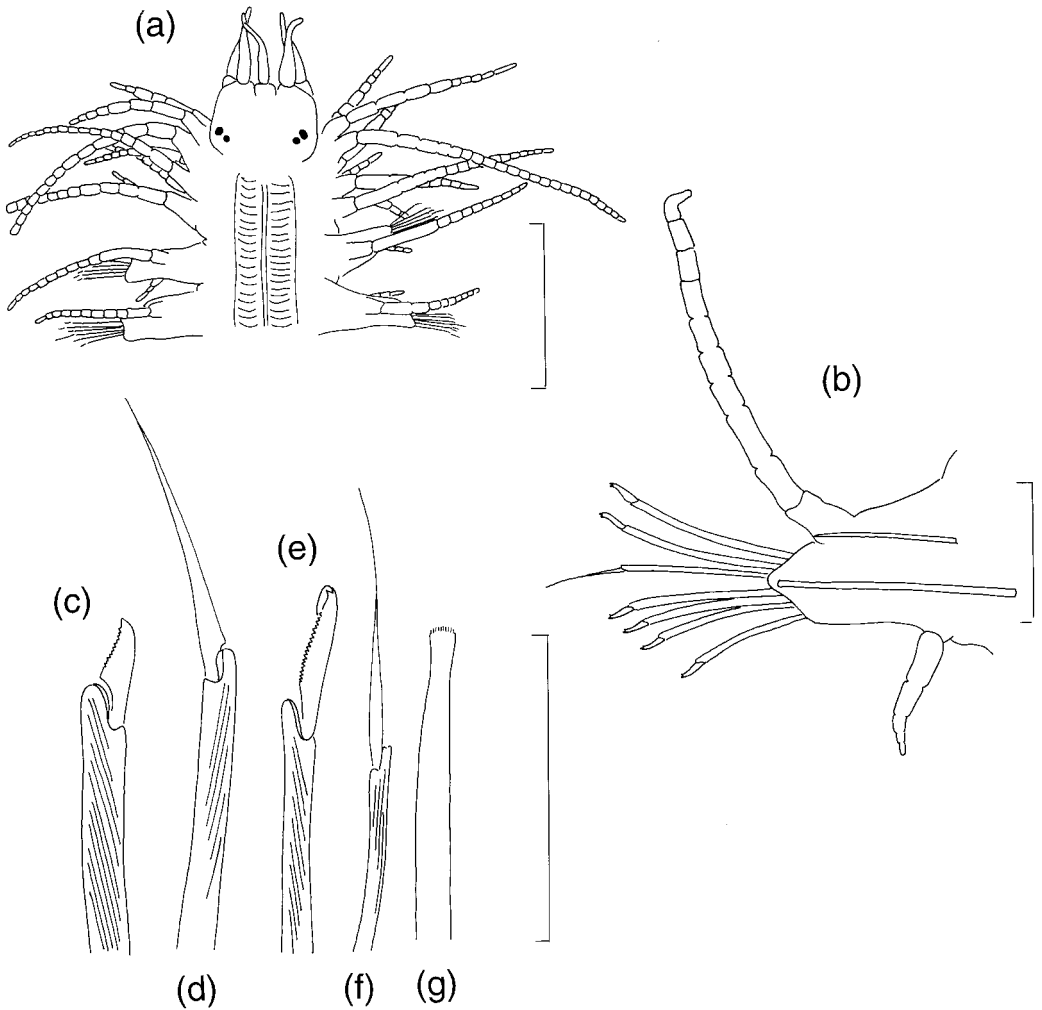


FIGURE 4. *Bidentata*, new taxon. Drawings from specimen SMNH 5190b. (a) Anterior end, dorsal view. Bar = 0.25 mm. (b) Parapodium segment 35, anterior view. Bar = 100 μ m. (c, d) Falciger and spiniger from segment 12. (e-g) Falciger, spiniger, and neuroacicula from segment 35. Bar (c-g) = 25 μ m.

cirrophores possibly present. Posterior end and pygidium unknown.

Etymology.—From Latin “bidentata,” “with two teeth,” referring to (within *Heteropodarke* and related groups) the unique bidentate median falcigers.

Distribution.—Known only from Madang Lagoon, Papua New Guinea.

Remarks.—This is the same taxon referred to as “*Heteropodarke A*” in Pleijel (1998). One male was present among the examined specimens, indicating that the description above relates to adult stages. The absence of chaetigerous lobes and the presence of enlarged dorsal and ventral cirri on segments

1–4 represent the highest known degree of cephalization observed within *Heteropodarke* and related taxa (Pleijel, 1998). These also represent evidence that more homoplasy is present in the distribution of the anterior, prolonged cirri and the start of chaetigerous lobes than earlier acknowledged.

Formalis Perkins, 1984 (Figs. 6, 7)

Heteropodarke formalis (Perkins, 1984: 569–572, Fig. 7)

Material examined.—Off U.S. Georgia: USNM 61747 (as *Heteropodarke* sp.), 2 specimens, 31°03'N, 80°26'W, 34 m, 16 May 1977.

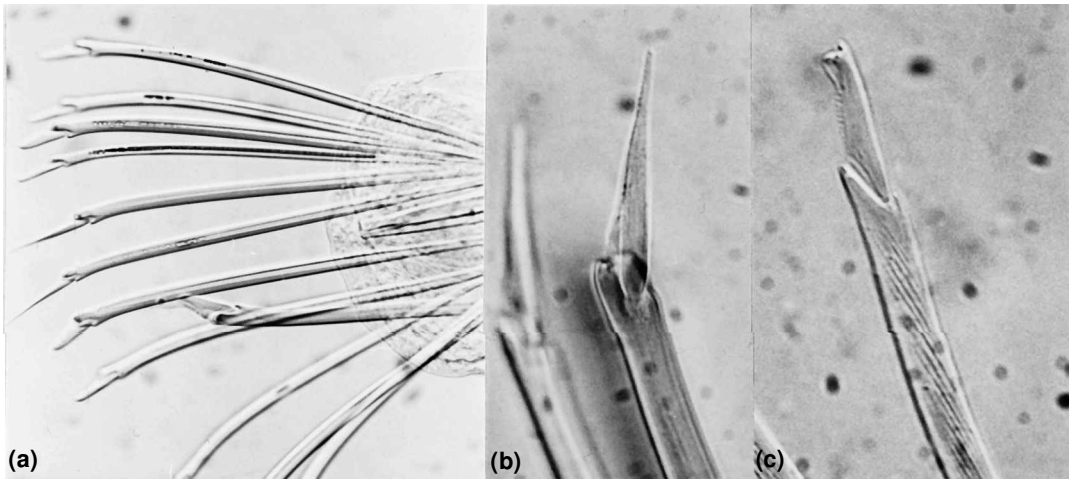


FIGURE 5. *Bidentata*, new taxon. Light microscopy photographs. (a) Specimen SMNH 5190a, parapodium segment 10. (b) Specimen SMNH 5190b, spinigers segment 12. (c) Specimen SMNH 5190d, falciger from median segment.

E Florida: USNM 80533, holotype, 27°21.6'N, 80°13.2'W, 11 m, coarse calcareous sand, May 1972; LACM-AHF Poly 1396, 14 paratypes, 27°21.6'N, 80°13.2'W, 11 m, coarse calcareous sand, Sep 1972; ZMUC, 5 paratypes, 27°20.7'N, 80°12.8'W, 11 m, coarse calcareous sand, May 1973; USNM 80536, 15 paratypes, 27°21.6'N, 80°13.2'W, 11 m, coarse calcareous sand, Jul 1973; ZMUC, 1 paratype, 27°21.6'N, 80°13.2'W, 11 m, coarse calcareous sand, Jul 1973; USNM 61461 (as *Heteropodarke* sp.), 1 specimen, 29°31'N, 80°40'W, 18 m, 20 May 1977; FP, ~50 specimens (~20 mounted for SEM, including SMNH 5192), 27°21.6'N, 80°13.2'W, 11 m, coarse calcareous sand, 21 Apr 1997; LACM-AHF Poly 1397, many paratypes, 27°20.7'N, 80°12.8'W, 11 m, coarse calcareous sand, no date.

W Florida: USNM 129301 (as *Heteropodarke* sp.), 7 specimens, 26°32.1'N, 82°24.3'W, 16 m, 4 Dec 1982; USNM 129442 (as *Heteropodarke* sp.), ~10 specimens, 26°17.0'N, 82°25.2'W, 17 m, 4 Dec 1982; USNM 129512 (as *Heteropodarke* sp.), 4 specimens, 26°17.2'N, 82°18.5'W, 16 m, 15 Dec 1982; USNM 129345 (as *Heteropodarke* sp.), 5 specimens, 26°32.1'N, 82°24.3'W, 16 m, 30 May 1983; USNM 112265, 4 specimens, 26°17.1'N, 82°19.5'W, 16 m, 5 May 1984; USNM 90630 (as *Heteropodarke* sp. A), 4 specimens, 29°18.02'N, 84°19.59'W, 29 m, Aug 1987.

Belize: FP, ~40 specimens (~10 mounted for SEM), W Carrie Bow Cay, 16°48.2'N 88°04.5'W, patches of medium sand among *Thalassia* beds, 1 m, SCUBA, 30 Apr–4 May 1993; 8 specimens, same locale, Sep 1997.

Apomorphy-based name definition.—*Formalis* is the group diagnosed by the apomorphy capillary notochaetae homologous with those in SMNH 5192.

Diagnosis.—*Heteropodarke* with capillary notochaetae and without distinctly prolonged dorsal cirri on segment 2.

Description.—Relationship between segment number and length illustrated in Fig. 3a. Body thin, threadlike, of uniform width, posteriorly tapered, cylindrical with flattened venter in cross-section. Eyes red-orange, other pigmentation absent, opaquely transparent. Preserved specimens brownish-white to yellowish. Prostomium with dorsal transverse ciliated band, medially interrupted (Fig. 6a, 6c). Each segment dorsally and ventrally with 2 transverse bands: 1 midsegmental reaching dorsal cirrophores, and 1 at boundary between segments (Fig. 6a). Prostomium quadrangular with rounded posterior corners (Figs. 6c, 7a) (wider than long on poorly relaxed preserved specimens with everted proboscis). Paired antennae and palpostyles similar in size and shape, proximally slightly inflated with elongated distal parts (Fig. 6a). Palpophores short, anteriorly inserted (Fig.

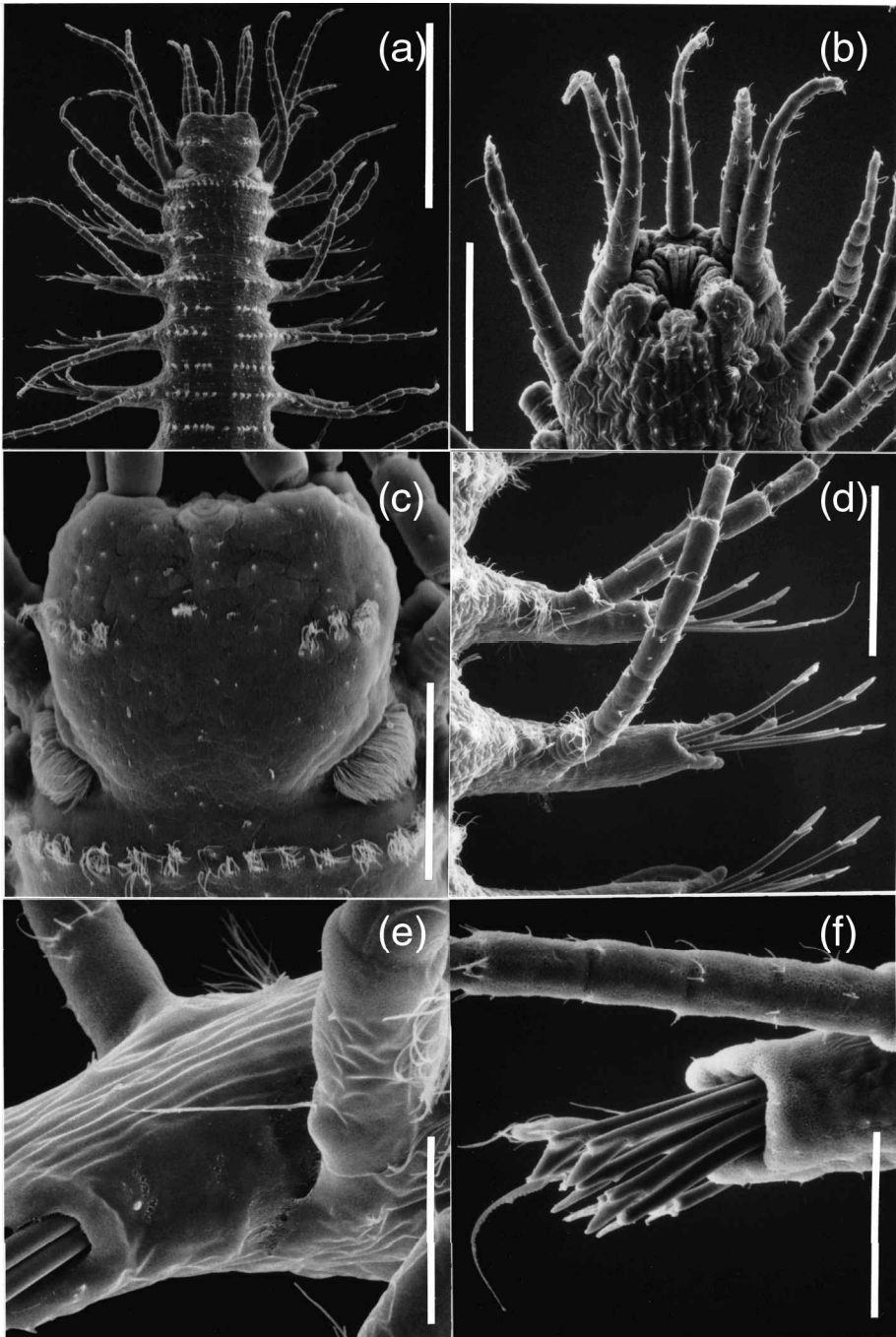


FIGURE 6. *Formalis*. SEM photographs of specimens from Belize (c) and Florida (a, b, d–j). (a) Anterior end, dorsal view. Bar = 231 μm . (b) Anterior end, ventral view. Bar = 100 μm . (c) Prostomium, dorsal view. Bar = 50 μm . (d) Parapodia segments 4 and 5, right side, dorsal view. (e) Notochaeta, median segment, dorsal view. (f) Parapodium segment 12, right side, dorsal view. (Continued on next page).

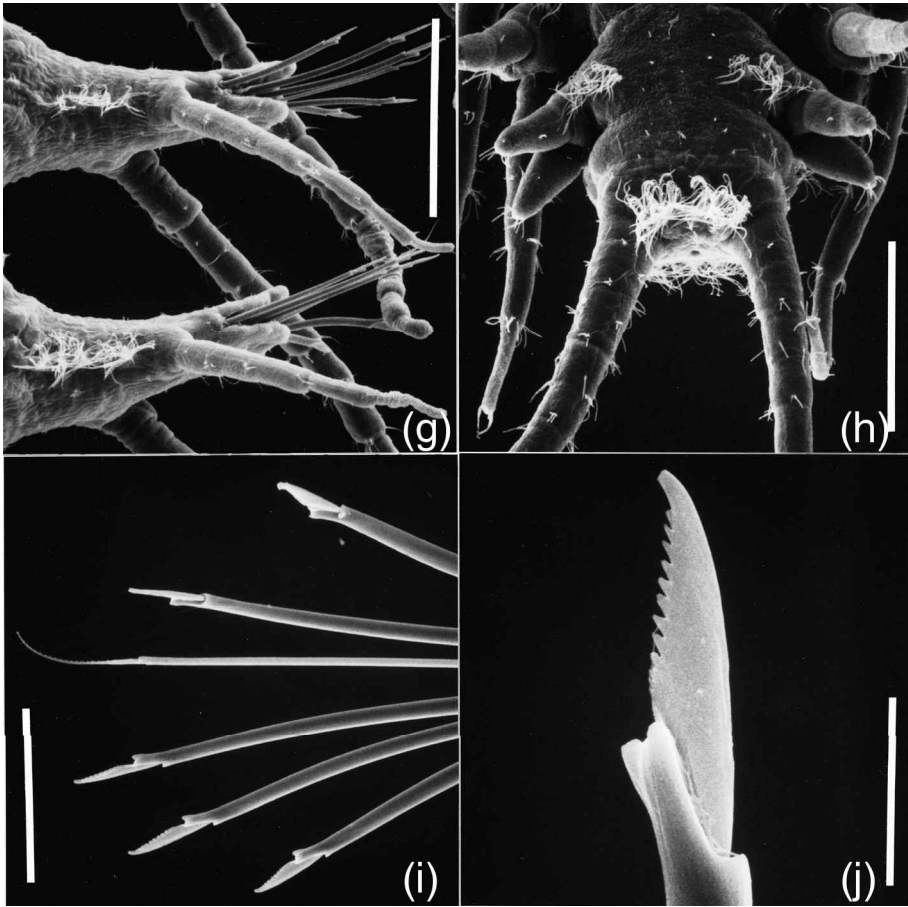


FIGURE 6. (Continued). (g) Median parapodium, left side, ventral view. (h) Posterior end, ventral view. Bar = 50 μm . (i) Neurochaetae, median parapodium. Bar = 30 μm . (j) Median neurochaeta. Bar = 6 μm .

6b). Median antenna similar in shape to paired antennae but $\frac{1}{2}$ to $\frac{2}{3}$ as long, inserted on elevation on anterior margin, dorsally to paired antennae (Fig. 6b). Antennae and palpostyles weakly annulated. Eyes small, of similar size or anterior pair slightly larger; anterior and posterior pair situated close together, approaching curved transverse line across posterior half of prostomium (Fig. 7a); anterior pair varying from rounded to kidney-shaped, posterior pair rounded. Nuchal organs short, wide lateral bands of cilia, middorsally well separated (Fig. 6c). Facial tubercle indistinct, possibly weakly developed. Proboscis smooth, short, separated in proximal and distal ring; distal ring ending with pointed, triangular papillae, varying in number between 10 and 11, ciliated on inferior side. Dorsal cirri on segment 1 reaching seg-

ments 5–7 with 12–14 articles; dorsal cirri of segment 2 reaching segments 5–7 with 10–14 articles; dorsal cirri of segment 3 reaching segments 6–8 with 9–12 articles. Dorsal cirri on segments 1–3 only slightly stouter than on following segments and indistinctly differentiated; cirrophores similar or slightly larger than on following segments. Ventral cirri on segment 1 reaching segments 4–5 with 7–8 articles; ventral cirri on segment 2 reaching segments 5–6 with 7–9 articles; ventral cirri of segment 3 reaching segments 6–7 with 8–9 articles. Ventral cirri on segments 1–3 all of same length, stouter and longer than on following segments, and situated on distinct cirrophores (Fig. 7b). Single aciculae in all cirrophores on segments 1–3. Muscular pregut reaching segments 13–23, length size-dependent (Fig. 3b). Segment 4 with dorsal cirri,

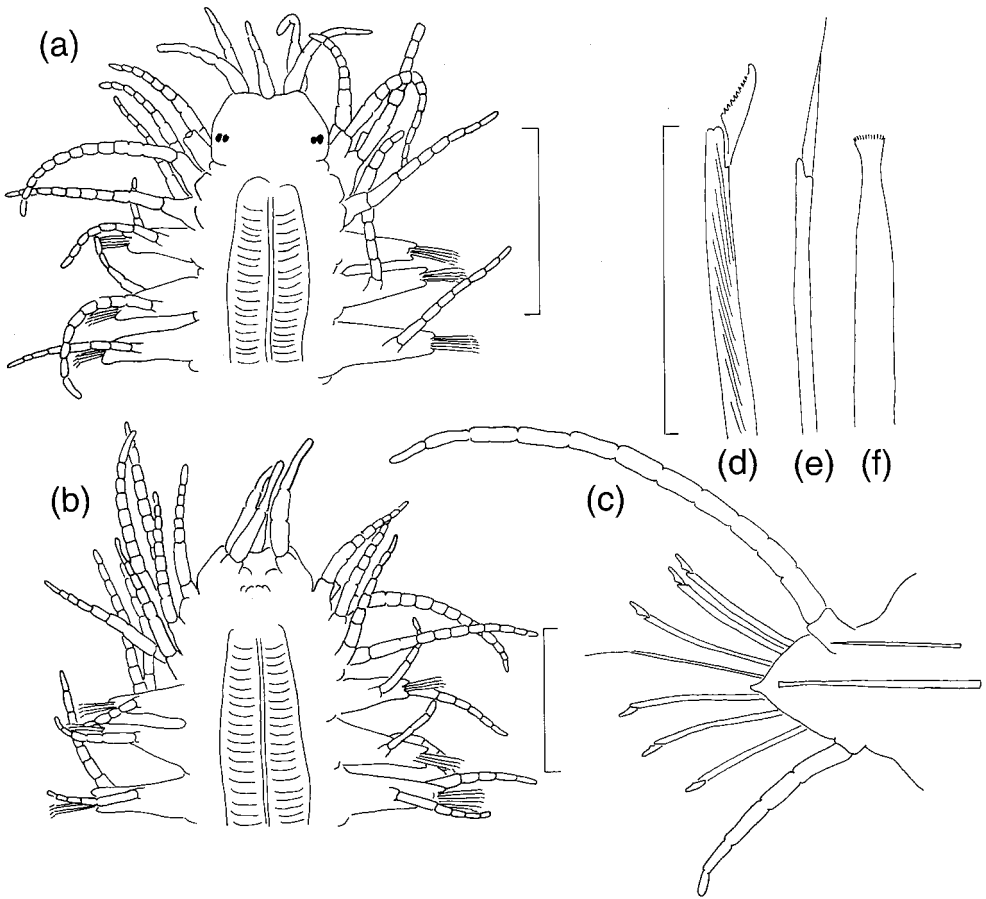


FIGURE 7. *Formalis*. Drawings from specimens from Belize. (a) Anterior end, dorsal view. Bar = 0.25 mm. (b) Anterior end, ventral view. Bar not shown; drawing same scale as (a). (c) Parapodium segment 36, anterior view. Bar = 100 μ m. (d–f) Falciger, spiniger, and neuroacicula, respectively, from segment 36. Bar = 25 μ m.

chaetae, chaetigerous lobes, and ventral cirri similar to following segments (Fig. 6d). Small, indistinct prechaetigerous lobes on first chaetigers, best developed on chaetiger 1. Dorsal cirri of chaetigerous segments \sim 2 times as long as ventral, annulated with 10–12 articles, cirrophores distinct (Fig. 7c). Slightly elevated dorsal cirri on segments 5, 8, 10, 12, 15, 17, 17, 19, 21, 23, 25, 27, 29, 31, and 33; shorter and horizontally directed on other segments. Notoaciculae single, fine. Single, very fine capillary chaetae emerging at end of notoacicula (Fig. 6e); difficult to detect and distribution uncertain (may possibly fall off easily; observed at least from segment 15, apparently absent from posterior segments). Stout, distally curved posterior notoaciculae absent. Neu-

roaciculae single, stout, knobbed, with subdistal constriction; tips finely fringed (Fig. 7f); neurochaeta in anterior chaetigers lacking subdistal constriction. Enlarged falcigers absent although chaetae of pregut region slightly stouter in appearance. First 2 chaetigers and those after pregut region usually with 5–6 falcigers with short, broad blades, and 1, occasionally 2, spinigers ventral-most in superior chaetal bundle (Fig. 6d, 6i); pregut region with 7–8 falcigers (Fig. 6f). Spinigers (Fig. 7e) in all chaetigers. All blades unidentate (Fig. 6j, 8d). Shafts of falcigers distally bilobed, indistinct in spinigers. Capillary chaetae absent in posterior-most 2–3 segments. Falcigers internally striated; indistinct in spinigers. Ventral cirri similar to dorsal, but shorter, with

~6 articles, reaching about as far as chaetae; cirrophores small (Fig. 6h). Pygidial cirri long, annulated. Median pygidial papilla absent.

Distribution.—North Carolina, Georgia, east and west coasts of Florida, Alabama, Belize. Reexamination of voucher specimens of *Heteropodarke* sp. A of Uebelacker (1984:28.17, his Figs. 28.14a–e) from the northeastern Gulf of Mexico shows them to belong to *Formalis*. San Martín and Gómez Esteban's (1992) record of *Formalis* from Cuba is not included in the distribution because I have not had the opportunity to examine the specimens.

Remarks.—Chaetal shafts were in the original description described as having uniform internal structure, but close examination of both type specimens and newly collected specimens shows internal striation present. Presence of very fine capillary notochaetae was overlooked in the original as well as in subsequent descriptions (Uebelacker, 1984; Pleijel, 1998). All observed specimens were provided with enlarged dorsal and ventral cirri on segments 1–3 and with chaetae and chaetigerous lobes from segment 4. The smallest examined entire specimen had 45 segments, indicating that the adult condition for these characters is reached before this size.

Crassichaetae, *New Taxon*

Apomorphy-based name definition.—*Cras-sichaetae* is the group diagnosed by the apomorphy enlarged anterior falcigers homologous with those in *Lyonsi* (USNM 80525).

Diagnosis.—*Heteropodarke* with narrow prostomium (uncertain in *Xiamenensis*), ventrally inserted palps, finger-shaped lobes on anterior chaetigers (uncertain in closest neighboring terminals), enlarged anterior falcigers, and hooked notoacaculae in posterior segments.

Distribution.—Peru, California, Gulf of Mexico, Florida, North Carolina, Natal, South Africa, Gulf of Aqaba, East China Sea, Yellow Sea, New Caledonia.

Africana Hartmann-Schröder, 1974,
Taxon Inquirenda

Heteropodarke heteromorpha africana (Hartmann-Schröder, 1974:40–42, His Figs. 6–11)

Material examined.—South Africa, Natal, Umkomaas, fine sand, 20 m depth, 1966: HZM P-14157, holotype; HZM-P14158, 4? paratypes (4 anterior ends and 2 median pieces); SAM A-21019, 4? paratypes (4 anterior ends and 4 other pieces).

Description.—Relationship between segment number and length unknown (no entire specimens examined). Body thin, threadlike, of uniform width, posteriorly tapered; cylindrical with flattened venter in cross-section. Preserved specimens brownish-yellow to white; eyes brownish. Ciliation not observed. Prostomium rounded elliptical, longer than wide. Paired antennae and palpostyles similar in size and shape, proximally slightly inflated with elongated distal parts. Palpophores short, ventrolaterally inserted. Median antenna not observed. Paired antennae and palpostyles annulated. Eyes small; anterior pair slightly larger; anterior pair and posterior pair well separated. Nuchal organs and facial tubercle not observed. Proboscis with 10 pointed triangular terminal papillae. Dorsal cirri of segment 1 not observed; dorsal cirri of segment 2 reaching about segment 11 with 21 articles; dorsal cirri of segment 3 reaching segments 5–7 with 7–9 articles. Cirrophores well developed, larger than on chaetigerous segments. Comparison between dorsal cirri on segments 1–3 and on following segments uncertain because of poor condition of specimens. Ventral cirri of segment 1 reaching segments 3–5 with 6 articles; ventral cirri of segment 2 reaching segments 4–5 with 5–6 articles; ventral cirri of segment 3 reaching segments 5–6 with 7 articles. Cirrophores distinct. Comparison between ventral cirri on segments 1–3 and on following segments uncertain because of poor condition of specimens. Aciculae in anterior achaetigerous segment not observed. Muscular pregut reaching segments 19–33, length probably size-dependent. Segment 4 with dorsal cirri, chaetae, chaetigerous lobes, and ventral cirri similar to following segments. Small finger-shaped prechaetigerous lobes on segments 4–6, largest on segment 4 and then decreasing in size; not visible on segment 7 or thereafter on segments with distinctly enlarged falcigers; reappearing abruptly on segment after region with enlarged falcigers. Dorsal

cirri on chaetigerous segments annulated with 7–11 articles; cirrophores distinct. Dorsal cirri alternation not observed. Notoaciaculae pointed; stout and distally curved in posterior segments. Neuroaciaculae single, stout, nobbed with subdistal constriction; tips finely fringed. Enlarged falcigers from segments 6–7 to 16–31 (ending probably size-dependent); five per parapodium; blades rounded. Falcigers on first chaetigers approaching enlarged ones in shape but thinner and with longer blades, dissimilar to falcigers in region after enlarged ones. Blades of falcigers on posterior segments strongly curved; usually six per parapodium. Single spinigers from segments 6–7, absent from segments after region with enlarged falcigers. All blades unidentate. Shafts of spinigers and falcigers distally bilobed. Falcigers internally striated. Ventral cirri similar to dorsal, but shorter, with 4–6 articles; distinct cirrophores absent. Pygidium unknown.

Distribution.—Natal, South Africa.

Remarks.—One mature female was observed with eggs, diameter ~80–90 μm . Available specimens are all in poor condition, and description of many characters are incomplete from the original and only present description. Although *Africana* obviously belongs to *Crassichaetae*, more information is needed, and at present it cannot be stated whether *Africana* is nested within *Heteromorpha*, *Lyonsi*, or *Xiamenensis* or constitutes a separate monophyletic group from each of these taxa. No name definition or diagnosis is provided until further specimens become available; it is currently considered *taxon inquirenda* within *Crassichaetae*. The original description states that ventral cirri are absent from “1. parapodium” (i.e., segment 4 in mature specimens, but may also refer to segment 3 in immature specimens), and that one of the paratypes is provided with eight pairs of tentacular cirri (presumably indicating that parapodia appear first on segment 5). However, a reexamination indicates that all anterior ventral cirri are present and that the first parapodia appear on segment 3 or 4 (immature versus mature specimens) rather than segment 5. Possibly the enumeration of the anterior segments was confused. Further, the proboscis was described as having nine terminal papillae,

but 10 are present in the only two specimens with visible proboscises. The statement that the very fine chaetae accompanying the falcigers are simple rather than compound could be neither confirmed nor rejected from available material. I have not had the opportunity to examine the specimens from the Yellow Sea reported and described by Wu and Zhao (1992); however, they appear to be juveniles, judging from parapodia appearing already from segment 2. The specimens obviously belong to *Heteropodarke* and *Crassichaetae*, as seen from the distinctly enlarged falcigers on the anterior part of the body, but any further assignment would require examination of adult specimens.

Xiamenensis Ding, Wu, and Westheide,
1997 (Fig. 8)

Heteropodarke xiamenensis (Ding et al., 1997:319–325, Their Figs. 1–3)

Material examined.—China, East China Sea, Xiamen: SMF 6092, holotype, 24°27'N, 118°04'E, Huangchu Beach, intertidal, 25 Sep 1994; SMF 6093–94, 2 paratypes, 24°27'N, 118°04'E, Huangchu, subtidal, 30 Sep 1994; SMF 6095, paratype, 24°27'N, 118°04'E, Jiyu Island, subtidal, 6 Oct 1994.

Apomorphy-based name definition.—*Xiamenensis* is the group diagnosed by the apomorphy round-tipped blades of the non-enlarged falcigers homologous with those in SMF 6092.

Diagnosis.—*Crassichaetae* with round-tipped blades of the nonenlarged falcigers.

Description.—Relationship between segment number and length illustrated in Fig. 3a. Body thin, threadlike, of uniform width, posteriorly tapered, cylindrical with flattened venter in cross-section. Posterior half with distinct intersegmental constrictions. Live specimens not observed; preserved specimens brownish-yellow to white, eyes red. Prostomial or segmental ciliation not observed. Details of prostomial shape uncertain. Paired antennae and palpostyles similar in size and shape (Fig. 8a), tapering. Palpophores short, ventrolaterally inserted (Fig. 8b). Median antenna similar in shape to paired antennae but $\sim\frac{3}{4}$ as long, inserted on elevation on anterior margin, dorsally to paired antennae. Antennae and palpostyles distinctly annulated. Eyes small, anterior

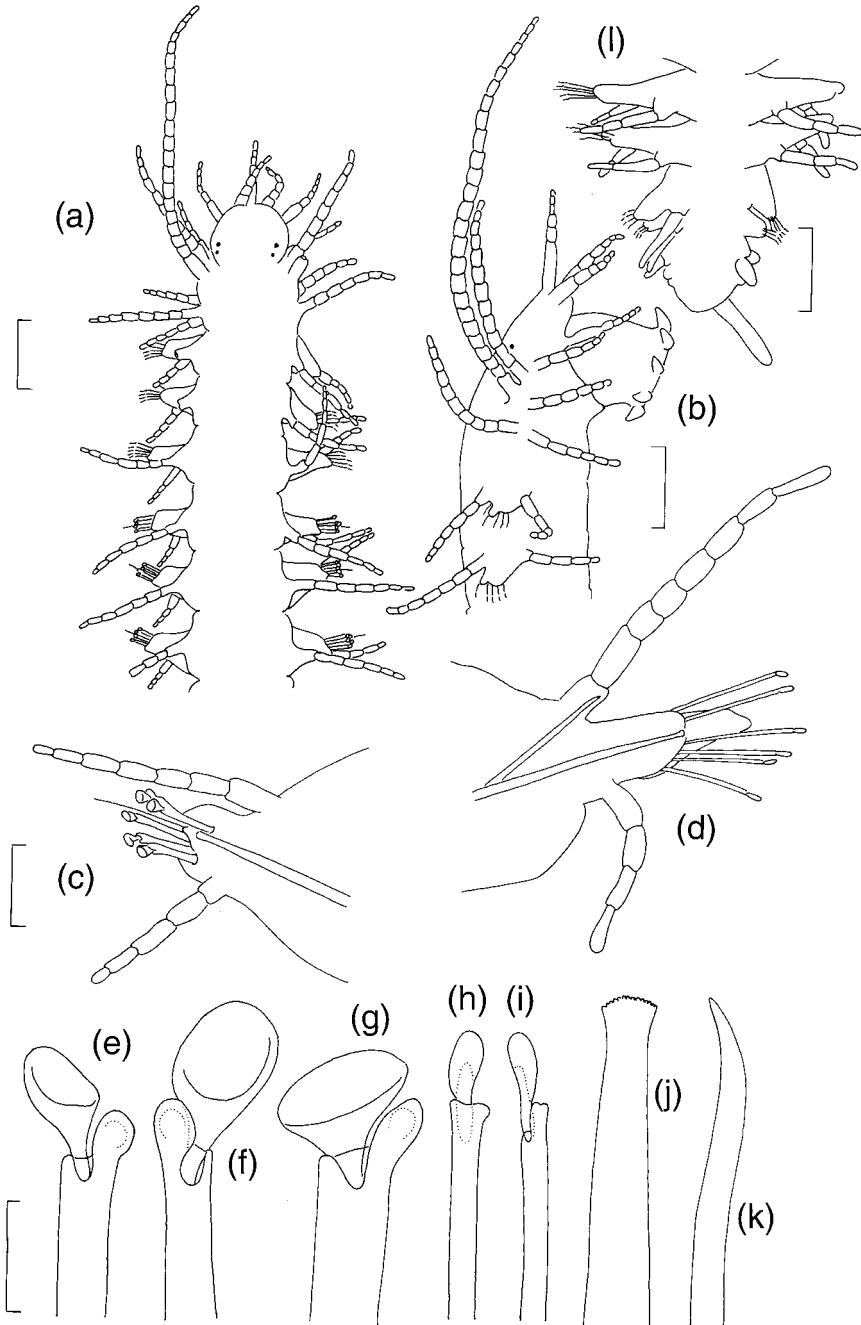


FIGURE 8. *Xiamenensis*. Drawings modified from Ding et al. (1997). (a) Anterior end, dorsal view. Bar = 100 μ m. (b) Anterior end, lateral view. Bar = 100 μ m. (c) Parapodium segment 16, right side, anterior view. Bar = 100 μ m. (d) Parapodium segment 47, left side, anterior view. Bar = 50 μ m. (e) Enlarged falciger, segment 7. (f, g) Enlarged falciger, segment 14. (h) Falciger, segment 6. (i) Falciger, segment 39. (j) Neuroaciacula, segment 14. (k) Notoaciacula, segment 39. Bar (e–k) = 10 μ m. (l) posterior end, dorsal view. Bar = 50 μ m.

pair slightly larger; anterior and posterior pair well separated; anterior pair varying from rounded to kidney-shaped, posterior pair rounded. Nuchal organs short, wide lateral bands of cilia, middorsally well separated. Facial tubercle not observed. Proboscis smooth, with 10 pointed, triangular terminal papillae, ciliated on inferior side. Dorsal cirri on segment 1 reaching segments 5–7 with 10–11 articles; dorsal cirri on segment 2 reaching segments 8–9 with 18–21 articles; dorsal cirri on segment 3 reaching segment 6 with 8–10 articles. Dorsal cirri on segments 1–3 stouter and longer than on following segments; cirrophores slightly enlarged. Ventral cirri on segment 1 reaching segments 4–5 with 5–6 articles; ventral cirri on segment 2 reaching segments 4–6 with 5–6 articles; ventral cirri on segment 3 reaching segments 5–6 with 5–7 articles. Ventral cirri on segments 1–3 all of same length, similar to following ventral cirri except for well-developed cirrophores. Single or double aciculae in cirrophores of all anterior cirri. Muscular pregut reaching segment 25–33, length probably size-dependent (Fig. 3b). Segment 4 with dorsal cirri, chaetae, chaetigerous lobes, and ventral cirri similar to following segments. Small finger-shaped prechaetigerous lobes on segments 4–6, not visible on segment 7 or thereafter on segments with enlarged falcigers, but reappearing abruptly and of larger size on first segment after region with enlarged falcigers (Fig. 8d). Dorsal cirri on chaetigerous segments <2 times as long as ventral, annulated with 9–10 articles, cirrophores distinct. Dorsal cirri alternation not observed. Notoaciculae on anterior chaetigers not observed; stout and distally curved in segments posterior to muscular pregut (Fig. 8k). Emerging notochaetae absent. Neuroaciculae single, stout, knobbed with subdistal constriction; tips finely fringed (Fig. 8j); enlarged in region with enlarged falcigers. Enlarged falcigers from segment 7 to 24–31 (ending probably size-dependent); 4–6 (usually 5) per parapodium (Fig. 8c); blades rounded, spoon-shaped (Fig. 8f, 8h). Falcigers on segments 4–7 and after segments 24–31 thinner with elongated, round-tipped blades (Fig. 8h, 8i); usually 5–6 per parapodium. Single, rarely double, spinigers or capillaries (inde-

cise observations; see *Remarks*) from segment 7, ending on same segment as enlarged falcigers. All blades unidentate. Details of shafts of chaetae not observed. Capillary chaetae in posterior-most 2–3 segments unknown. Falcigers internally striated. Ventral cirri similar to dorsal, but shorter, with ~4–6 articles, reaching about as far as chaetae; cirrophores not observed. No entire pygidial cirri observed. Median pygidial papilla absent (Fig. 8l).

Distribution.—Known only from East China Sea.

Remarks.—Unfortunately all available specimens are whole-mounted in an uncompressed state and without any parapodia mountings, thus making observations of, e.g., chaetal details difficult. For this reason it was not possible to determine whether the very fine chaetae accompanying the falcigers on anterior segments are simple capillaries or spinigers (or both) or to examine details of prostomial shape; my observations are inconclusive.

Heteromorpha Hartmann-Schröder, 1962, Taxon Inquirenda (Figs. 9, 10)

Heteropodarke heteromorpha (Hartmann-Schröder, 1962:118–120, Figs. 30–34)

Material examined.—Peru: HZM, P-15401, 3? paratypes (2 anterior ends, 1 median part and 1 posterior end), and P-14156 16? paratypes (9 anterior ends plus pieces), Isla Santa, 24 Apr 1956, coll. Noodt; HZM, P-14155, holotype, Callao, 29 May 1956, coll. Noodt.

California: LACM-AHF, 1 specimen, Los Angeles County, Santa Monica Bay, 33°55'10"N, 118°26'56"W, 7 fathoms, light-colored beach, coll. AHF R/V *Velero IV*, cruise 218, 15 Sep 1955; ~25 specimens NPWPCP, st. 29.2, 12 Aug 1974 (further locality details unknown); 1–2 specimens (anterior end and median part), Los Angeles County, Los Angeles Harbor, st. 27a, muddy sand, depth unknown, Aug 1975, id. J. Dorsey; 3 specimens, Ventura County, Ormond Beach, st. C3a, 30 feet, sand, June 1976, coll. MBC, id. J. Dorsey; 1 specimen, Huntington Beach, st. 1-D, ~20 feet, sand, id. J. Dorsey; 1–2 specimens (anterior end and median part), Los Angeles County, San Pedro, inner Cabrillo Beach, st. 3M3, Feb

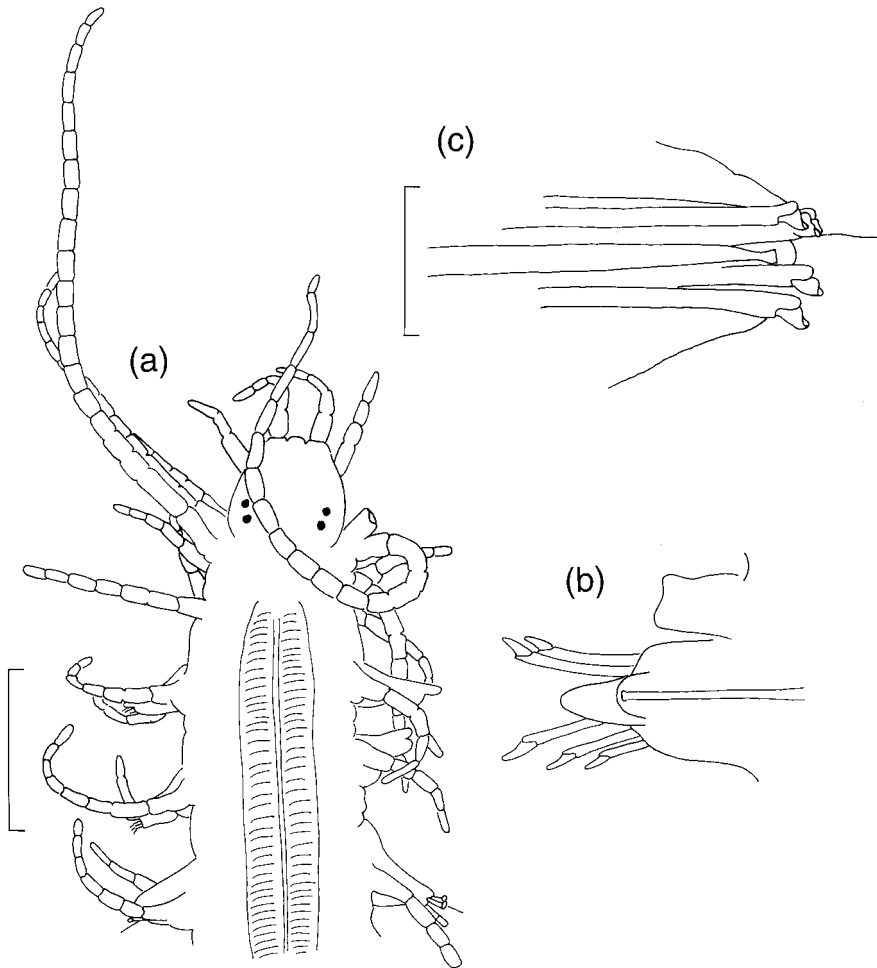


FIGURE 9. *Heteromorpha*. Drawings from specimens from California. (a) Anterior end, dorsal view. Bar = 100 μm . (b) Parapodium segment 4. Bar = 50 μm . (c) Parapodium segment 20. Same scale as (b).

1979; 1 male, BLM st. 81509 BF1, id. S. Williams (further locality details unknown).

Description.—Relationship between segment number and length illustrated in Fig. 3a. Body thin, threadlike, of uniform width, posteriorly tapered, cylindrical with flattened venter in cross-section. Posterior half with distinct intersegmental constrictions. Live specimens not observed, preserved specimens brownish-yellow to white, eyes brownish-red. Prostomial or segmental ciliation not observed. Prostomium rounded elliptical, longer than wide. Paired antennae and palpostyles similar in size and shape, proximally slightly inflated with elongated distal parts. Palpophores short,

ventrolaterally inserted. Median antenna similar in shape to paired ones but slightly shorter, inserted on elevation on anterior margin, dorsally to paired antennae. Antennae and palpostyles weakly annulated. Eyes small, approximately of equal size; anterior and posterior pair well separated; both pairs rounded (Fig. 9a). Nuchal organs not clearly observable on available specimens. Prostomium middorsally poorly delineated from following segment. Facial tubercle not observed. Proboscis smooth, with 10 pointed, triangular terminal papillae. Dorsal cirri on segment 1 reaching about segment 5 with 11–13 articles; dorsal cirri on segment 2 reaching segments 7–8

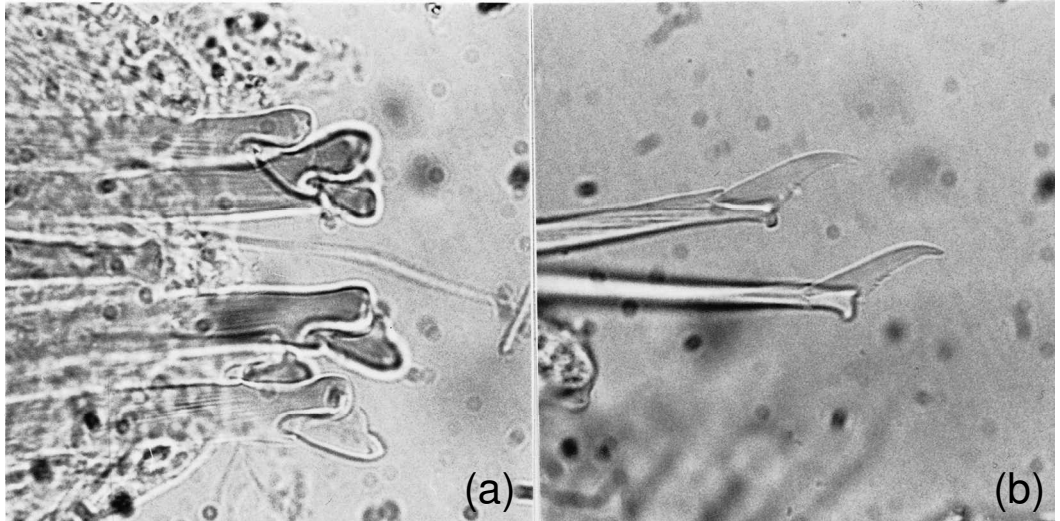


FIGURE 10. *Heteromorpha*. Light microscopy photographs of specimens from California. (a) Enlarged falcigers segment 7. (b) Falcigers from posterior segments.

with 16–21 articles; dorsal cirri on segment 3 reaching segment 6 with 9 articles. Dorsal cirri on segments 1–3 stouter and longer than on following segments; cirrophores slightly enlarged. Ventral cirri on segment 1 reaching segments 3–4 with 5–6 articles; ventral cirri on segment 2 reaching segment 4 with 5–6 articles; ventral cirri on segment 3 reaching segments 4–5 with 5–6 articles. Ventral cirri on segments 1–3 all of same length, similar to following ventral cirri except for well-developed cirrophores. Aciculae in cirrophores of anterior cirri not observed. Muscular pregut reaching segments 14–23, length probably size-dependent (Fig. 3b). Segment 4 with dorsal cirri, chaetae, chaetigerous lobes, and ventral cirri similar to following segments. Small finger-shaped prechaetigerous lobes on segments 4–5 or 4–6 (Fig. 9b), not visible on segment 7 or thereafter on segments with enlarged falcigers; reappearing in vicinity of end of enlarged falcigers. Dorsal cirri on chaetigerous segments <2 times as long as ventral cirri, annulated with 7–10 articles, cirrophores distinct. Dorsal cirri alternation not observed. Notoaciculae on anterior and median chaetigers fine, pointed; stout and distally curved in posterior-most segments, sometimes protruding. Emerging noto-chaetae absent. Neuroaciculae single, stout, knobbed with subdistal constriction; tips

finely fringed; enlarged in region with enlarged falcigers. Enlarged falcigers (Figs. 9c, 10a) from segment 6 to 12–21 (ending probably size-dependent); five per parapodium; blades short with rounded tips. Falcigers on segments 4 and 5 with shorter blades than on median and posterior segments. Falcigers after segments 12–21 abruptly thinner with curved blades (Fig. 10b), usually five per parapodium. Single spinigers from segments 6–7, often ending a few segments after enlarged falcigers, but occasionally present in more posterior segments. All blades unidentate. Details of shafts of chaetae not observed. Capillary chaetae in posterior-most 2–3 segments absent. Falcigers internally striated. Ventral cirri similar to dorsal, but shorter, with 4–6 articles, reaching as far as chaetae or slightly further; cirrophores not observed. Pygidial cirri 3–4 times as long as dorsal cirri, proximally smooth but distally segmented. Median pygidial papilla absent.

Distribution.—Peru, California.

Remarks.—No name definition or diagnosis is given in the absence of evidence for monophyly of *Heteromorpha*. Hartmann-Schröder in the original description noted covariation between size and number of anteriorly enlarged cirri and first appearance of chaetigerous lobes and observed that the adult condition in *Heteromorpha* is reached

later than in other hesionids. Most examined specimens are represented by anterior ends only, but one specimen of 36 segments, plus another posteriorly incomplete of 37 segments, were both provided with chaetae from segment 3, corroborating Hartmann-Schröder's observation. That the adult stage actually is reached when chaetiger 1 equals segment 4 is evidenced by a highly mature male of 94 segments (California, LACM-AHF Poly BLM st. 81509 BF1), which exhibits this condition (assuming that no further reductions take place after maturity). Laubier (1967), while expressing some doubts regarding identity, recorded *Heteromorpha* from New Caledonia. One of the commented differences from the original description related to the morphology of chaetae on anterior most segments. According to Hartmann-Schröder (1962:118), these chaetae are similar to those present in the region following the enlarged falcigers, whereas Laubier (1967:95, his Fig. 1E) instead described them as more similar to the enlarged falcigers. Reexamination of *Heteromorpha* types as well as of several Californian specimens confirms Hartmann-Schröder's description, and the New Caledonian specimens may represent an undescribed part of *Crassichaetae*. Unfortunately, Laubier's specimens seem to be lost (not present at MNHN or Laboratoire Arago, Banyuls); and description of a possibly new taxon will have to await recollection of specimens. Amoureux (1983:730–731, his Fig. 3) recorded *Heteromorpha* from the Red Sea (by mistake as "*H. heteropoda*") and reported nine terminal proboscis papillae and the presence of a single anterior proboscis tooth. However, because none of the 16 specimens (MNHN A895) had the proboscis everted, this could not be confirmed by reexamination. As seen from the enlarged falcigers, his specimens clearly belong to *Crassichaetae*, but more specific identity is currently considered uncertain. Dorsey (1978:82–87, his Fig. 1) and Hilbig (1994:256–258, his Fig. 9.6) extended the distribution to California. Part of Dorsey's specimens were reexamined and agree well with the original specimens from Peru. Perkins (1984:569) stated that *Lyonsi* differs from *Heteromorpha* in having posteriorly situated enlarged, emergent notoaciaculae. As

noted by Hilbig (1994:256), and as seen from the description above, these are present also in *Heteromorpha*. Their emergence in both *Heteromorpha* and *Lyonsi*, however, may be a fixation artifact from contraction.

Lyonsi Perkins, 1984 (Figs. 11, 12)

Heteropodarke lyonsi (Perkins, 1984:565–569, Figs. 5, 6)

Material examined.—North Carolina: USNM 59195 (as *H. heteromorpha*), 3 specimens, 33°20'N, 77°46'W, 25 m, 10 May 1977.

Georgia: USNM 59193 (as *H. heteromorpha*), 3 specimens, 30°59'N, 80°08'W, 46 m, 30 Aug 1977; USNM 59200 (as *H. heteromorpha*), 2 specimens, 31°05'N, 80°35'W, 25 m, 30 Aug 1977.

E Florida: USNM 80532, 1–2 specimens, 27°21.36'N, 80°13.12'W, 3 Jan 1972; USNM 80525, holotype, 27°21.6'N, 80°13.2'W, 11 m, calcareous sand, 15 Jul 1972; USNM 56634 (as *H. heteromorpha*), 1 specimen, 31°40'N, 80°16'W, Feb 1977; USNM 59199 (as *H. heteromorpha*), 2 specimens, 29°31'N, 80°40'W, 18 m, 20 May 1977; USNM 59196 (as *H. heteromorpha*), 3 specimens, 31°08'N, 80°50'W, 14 m, 31 Aug 1977; USNM 59198 (as *H. heteromorpha*), 1 specimen, 30°23'N, 81°20'W, 17 m, 31 Aug 1977; SMNH 5191, 1 specimen (mounted for SEM), 27°21.6'N, 80°13.2'W, 11 m, calcareous sand, 21 Apr 1997.

W Florida: LACM-AHF Poly 1399, 1 paratype, 29°51'N, 86°06.5'W, 41 m, coarse calcareous sand-rubble, 14 Nov 1971; USNM 129300 (as *H. cf heteromorpha*), 2 specimens, 26°32.13'N, 82°24.30'W, 16 m, 4 Dec 1982; USNM 129409 (as *H. cf heteromorpha*), 3 specimens, 26°01.01'N, 82°07.53'W, 18 m, 7 Dec 1982; USNM 129547 (as *H. cf heteromorpha*), 1 specimen, 26°17.24'N, 82°18.53'W, 16 m, 30 May 1983; USNM 129998 (as *H. cf heteromorpha*), 2 specimens, 25°20.30'N, 81°51.30'W, 16 m, 3 Jun 1983; USNM 112266, 4 specimens, 26°17.16'N, 82°19.56'W, 16 m, 5 May 1984.

Alabama: USNM 75479 (as *H. cf heteromorpha*), 1 specimen, 30°05.59'N, 87°55.17'W, 15 m, 1 Nov 1980.

Louisiana: USNM 80528, 1 paratype, 29°48'N, 89°09.5'W, 45 m, coarse sand, Feb 1976.

Apomorphy-based name definition.—*Lyonsi* is the group diagnosed by the apomorphy presence of spinigers in posterior neuro-

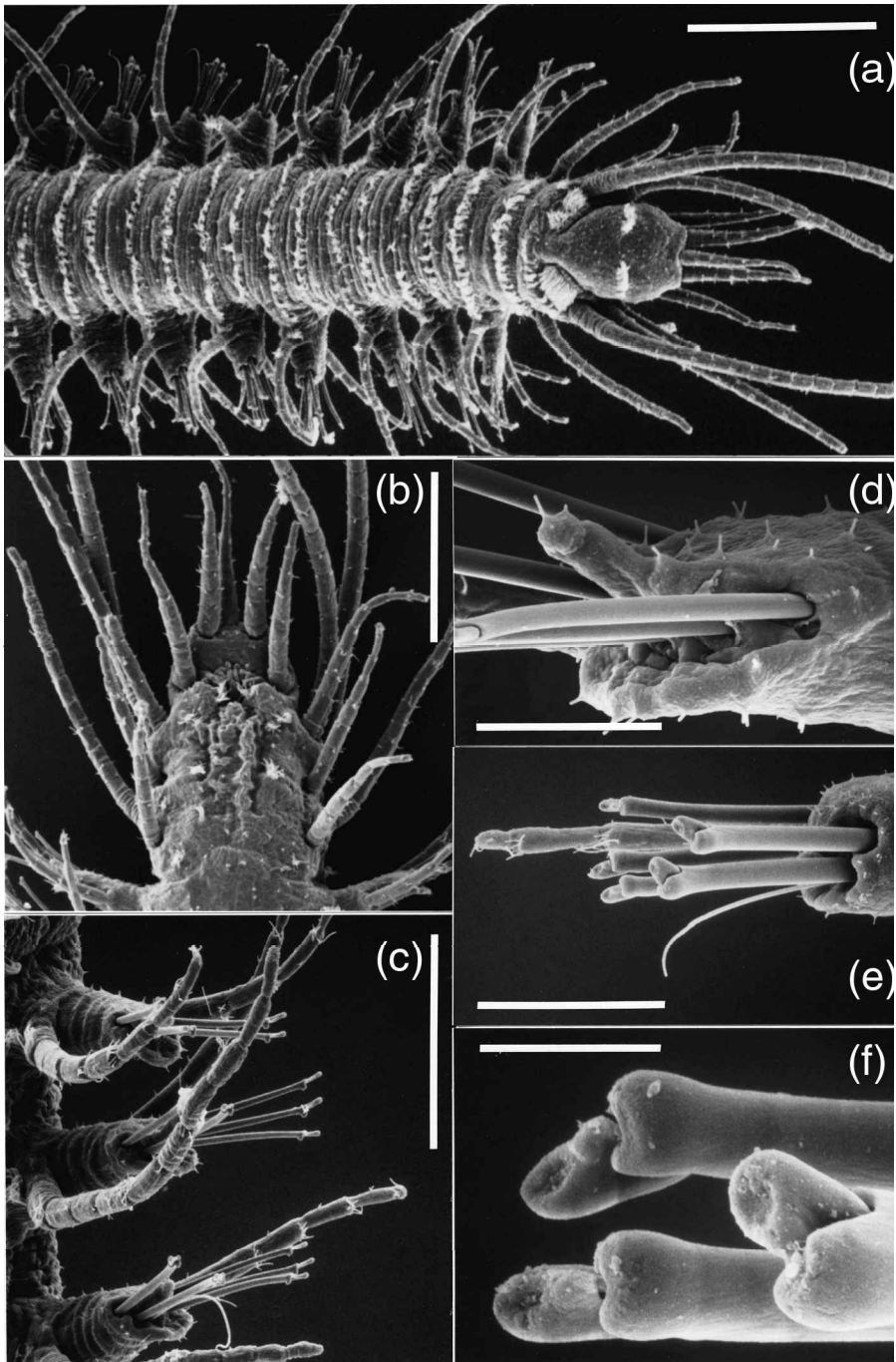


FIGURE 11. *Lyonsi*. SEM photographs of specimens from Florida. (a) Anterior end, dorsal view. Bar = 190 μm . (b) Anterior end, ventral view. Bar = 125 μm . (c) Segments 4-6, right side, dorsal view. Bar = 86 μm . (d) Segment 5, right side, ventral view. Bar = 23 μm . (e) Segment 18, left side, dorsal view. Bar = 50 μm . (f) Chaetae segment 16. Bar = 10 μm .

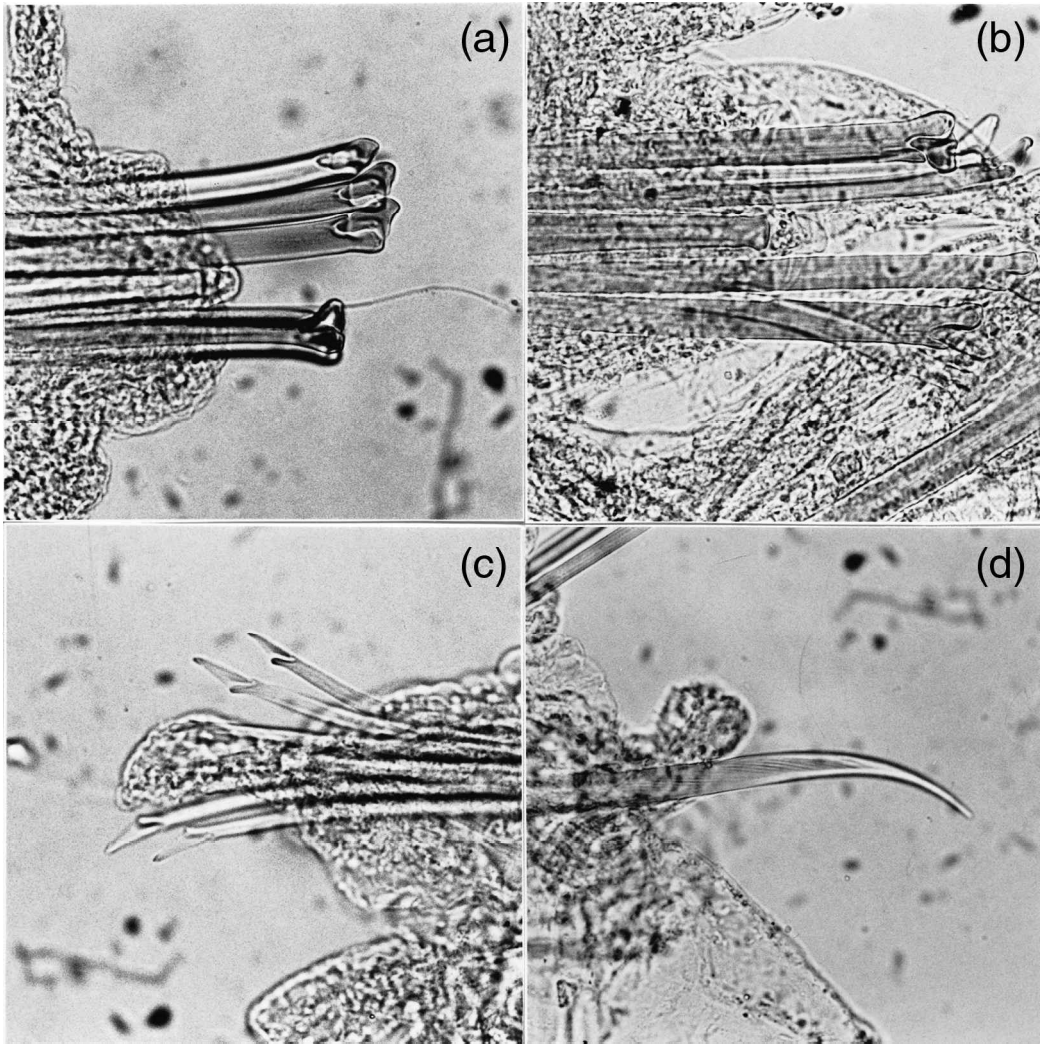


FIGURE 12. *Lyonsi*. Light microscopy photographs of specimens from Florida. (a) Enlarged falcigers segment 16. (b) Enlarged falcigers and nobbed neuroacicula, segment 35. (c) Neuropodium, segment 50. (d) notoacicula, segment 90.

podia homologous with those in USNM 80528.

Diagnosis.—*Heteropodarke* with spinigers in median and posterior neuropodia; possibly also by median antenna that approaches in length or is similar to the paired antennae (uncertain for the closely related *Heteromorpha* and *Xiamenensis*).

Description.—Relationship between segment number and length illustrated in Fig. 3a. Body thin, threadlike, of uniform width, posteriorly tapered, cylindrical with flattened venter in cross-section. Posterior half with distinct intersegmental constrictions.

Eyes red-orange, other pigmentation absent, body opaquely transparent. Preserved specimens white to yellowish. Prostomium with dorsal transverse ciliated band, medially interrupted (Fig. 11a). Each segment dorsally and ventrally with 2 transverse bands: 1 midsegmental reaching dorsal cirrophores, and 1 at boundary between segments (Fig. 11a). Prostomium rounded, elliptical, longer than wide (Fig. 11a). Paired antennae and palpostyles similar in size and shape, with narrowing distal parts (Fig. 11a, 11b). Palpophores short, ventrolaterally inserted (Fig. 11b). Median an-

tenna similar in shape to paired ones, of equal length or slightly shorter, inserted on elevation on anterior margin, dorsally to paired antennae. Antennae and palpostyles weakly annulated. Eyes small, anterior pair slightly larger; anterior and posterior pair well separated; both pairs rounded. Nuchal organs short, wide lateral bands of cilia, middorsally well separated (Fig. 11a). Facial tubercle not distinctly developed. Proboscis smooth, with 10 pointed, triangular terminal papillae, ciliated on inferior side. Dorsal cirri of segment 1 reaching segments 5–7, with 11–13 articles; dorsal cirri of segment 2 very long, reaching segments 8–10, with 17–21 articles; dorsal cirri of segment 3 reaching segments 6–8, with 8–11 articles. Dorsal cirri of segments 1–2 stouter and longer than on following segments; cirrophores enlarged. Ventral cirri of segment 1 reaching segment 4, with 7–8 articles; ventral cirri of segment 2 reaching segments 4–6 with 6–7 articles; ventral cirri of segment 3 reaching segments 4–6 with ~6 articles. Ventral cirri of segment 1 slightly longer than following ones, on segments 2–3 being successively shorter and thinner; ventral cirri on segments 2–3 weakly differentiated from following segments but situated on distinct cirrophores. Aciculae at least in dorsal and ventral cirri of segments 2 and 3; uncertain observations for segment 1. Muscular pregut reaching segments 21–42, length probably size-dependent (Fig. 3b). Segment 4 with dorsal cirri, chaetae, chaetigerous lobes, and ventral cirri similar to following segments (Fig. 11c). Small finger-shaped prechaetigerous lobes on segments 4–6 (Fig. 11d), largest on segment 4, and then decreasing in size; not visible on segment 7 or thereafter on segments with enlarged falcigers; reappearing abruptly on first segment after region with enlarged falcigers. Dorsal cirri of chaetigerous segments ~2 times as long as ventral cirri, annulated with 8–13 articles; cirrophores elongated, distinct. Dorsal cirri alternation with elevated and prolonged cirri on segments 5, 8, 10, 12, 15, 17, 19, 21, 23, 26, and 27; shorter and horizontally directed on other segments. Notoaciculae usually single, sometimes double; on anterior segments fine, pointed; stout and distally curved in posterior segments, sometimes

protruding. Emerging notochaetae absent. Neuroaciculae single, stout, knobbed with subdistal constriction; enlarged in region with enlarged falcigers. Enlarged falcigers (Fig. 11e, 11f) from segments 6–7 to 18–37 (ending probably size-dependent); 5 per parapodium; blades rounded, weakly spoon-shaped. Falcigers on segments 4–5 approaching enlarged ones in shape but thinner and with longer blades, dissimilar to falcigers in region after enlarged ones. Falcigers on posterior segments strongly curved, 5–6 per parapodium. Single, rarely double, spinigers (Fig. 11e) from segment 6 in all chaetigers, very fine and sometimes absent from posterior-most segments. All blades unidentate. Shafts of falcigers and spinigers distally bilobed. Capillary chaetae in posterior-most 2–3 segments unknown. Falcigers internally striated. Ventral cirri similar to dorsal, but shorter, with 6–9 articles; without distinct cirrophores. Pygidial cirri not observed. Median pygidial papilla probably absent (uncertain observation).

Distribution.—East coast of U.S. from North Carolina to northern parts of Gulf of Mexico.

Remarks.—On the basis of examined specimens, I include *Heteropodarke* cf. *heteromorpha* in Uebelacker (1984:28.15–28.16, his Figs. 28.12a–g) as parts of *Lyonsi*. The above description disagrees with Perkin's original description in a few details. Thus, palps are inserted ventrally on the prostomium rather than distally, chaetal shafts are longitudinally striated rather than uniform, and, instead of being present up to about segment 80, spinigers in some specimens occur also after this segment till the end of body.

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APPENDIX. CHARACTERS AND CHARACTER DISTRIBUTIONS

Character numbers correspond to matrix in Table 1. All characters are binary and scored as present/absent.

1. *Body shape thin and threadlike*. Characteristic for all *Heteropodarke*; absent from other hesionids except *Sinohesione* Westheide, Purschke, and Mangerich, 1994, where it occurs as a homoplasy (Pleijel, 1998).
2. *Uniform brown pigmentation*. Present in *Flexuosus* (O.) and *Pugettensis* (O.). The pigmentation disappears in ethanol but is absent from all other hesionids that have been examined alive (Pleijel, 1998); it was scored with question marks for those taxa that have been observed in preserved condition only.
3. *Narrow elongated prostomial shape*. Present in *Africana*, *Heteromorpha*, and *Lyonsi* (e.g., Fig. 11a), wider and more rectangular prostomium in other *Heteropodarke* and outgroups (e.g., Fig. 6a, 6c). Shape uncertain for *Xiamenensis* (owing to possible fixation artifacts and difficulty of observing from mounted specimens), so scored with a question mark.

4. *Ventral palp insertion*. Present in *Africana*, *Heteromorpha*, *Lyonsi*, and *Xiamenensis* (e.g., Fig. 11a, 11b); distally inserted in other *Heteropodarke* and outgroups (e.g., Fig. 6a, 6b).
5. *Short palpophores*. Present in all *Heteropodarke* (e.g., Fig. 6b); distinctly longer in outgroups.
6. *Median antenna shorter than paired antennae*. Present in all taxa (e.g., Fig. 2a) except *Lyonsi*, where median antenna length approaches or is similar to paired antennae (Fig. 11a, 11b); uncertain for *Africana* and *Heteromorpha*.
7. *Small eyes*. Present in all *Heteropodarke* (e.g., Figs. 4a, 7a); distinctly larger in outgroups (e.g., Pleijel, 1998).
8. *Anterior and posterior pair of eyes closely situated*. Present in *Bidentata*, *Formalis*, and "*Zmyrina*" (Figs. 4a, 7a), such that all four eyes appear almost on single, curved line; well separated in other *Heteropodarke* and outgroups (Figs. 8a, 9a).
9. *Short, wide nuchal organs*. Present in all *Heteropodarke* (but uncertain observations for *Africana* and *Heteromorpha*) (e.g., Figs. 6c, 11a); much narrower in outgroups.
10. *Ten terminal proboscis papillae*. Present in all *Heteropodarke* (e.g., Fig. 2d); absent in outgroups. Ontogenetic evidence for various hesionids indicate that 10 papillae may be the plesiomorphic state for *Hesionidae*, but in *Heteropodarke* this appears as a homoplasy (Pleijel, 1998). Although not scored, also the triangular, pointed shape of the papillae and the ciliated inferior side may be characteristic for *Heteropodarke*.
11. *Prolonged dorsal cirri segment 2*. Present in all ingroup and outgroup taxa except *Formalis* and *Humesi* (P.); in *Formalis* (Figs. 6a, 7b) and *Humesi* (P.) (see Pleijel, 1998), these cirri could not be distinguished from other "normal" dorsal cirri.
12. *Prolonged dorsal cirri segment 4*. Present in *Bidentata* (Fig. 4a), *Flexuosus* (O.), and *Pugettensis* (O.) (see Pleijel, 1998); absent from other ingroup and outgroup taxa. This feature is probably in some sense correlated to appearance of neuropodia and chaetae, although not in a simple way; in *Bidentata* the enlarged dorsal cirri occur only on anterior segments lacking chaetae, whereas in *Flexuosus* (O.) and *Pugettensis* (O.) they are present also on the first chaetigerous segment.
13. *Enlarged anterior ventral cirri*. Present in ingroups and outgroups, except in *Heteromorpha* and *Lyonsi* (uncertain observations for *Africana*), where they are similar to the following cirri (Fig. 11a, 11b). In all ingroups and outgroups the anterior cirri deviate from other ventral cirri in being provided with (comparatively) large cirrophores, but this character was excluded because it is uninformative.
14. *Enlarged ventral cirri segment 4*. Unique for *Bidentata* among *Heteropodarke* and outgroups.
15. *Neuropodia segment 4*. Present in all taxa except *Bidentata* (Fig. 4a). There is some confusion in earlier literature regarding on which segment in *Heteropodarke* the neuropodia actually start. As noted in the *Remarks* sections in the descriptions of the taxa, this is the result of mixtures between adult and subadult stages.
16. *Finger-shaped preacicular lobes on anterior neuropodia*. Present in *Africana*, *Heteromorpha*, *Lyonsi*, and *Xiamenensis* (e.g., Fig. 11d), usually most distinct on segment 4, and then decreasing in size; uncertain for *Formalis* and "*Zmyrina*"; absent from *Bidentata* and outgroups. In *Heteropodarke* with enlarged falcigers, the lobes reappear in modified shape after this region, but this feature was not included because of delineation problems towards the preacicular extensions, such as occur, for example, in *Flexuosus* (O.).
17. *Extended, differentiated pregut*. Present in all *Heteropodarke* (Fig. 7a, 7b) and unique for the group. Pregut length is obviously size-related and reaches segments 10–40 in observed specimens (Fig. 3b). It appears to be muscularized but does not form part of the eversible part of the proboscis, which is very short in *Heteropodarke*. The pregut can be observed through the body wall with use of a dissecting microscope but is most easily seen in mounted specimens.
18. *Distally inserted ventral cirri*. Present in *Flexuosus* (O.) and *Pugettensis* (O.) (Pleijel, 1998); absent from all *Heteropodarke* and *Humesi* (P.), which have ventral cirri subdistally inserted on the neuropodium (e.g., Fig. 2g).
19. *Smooth, unarticulated ventral cirri*. Present in *Flexuosus*, *Pugettensis* (Pleijel, 1998), and "*Zmyrina*," which has (at least distally) articulated ventral cirri (Fig. 2g); uncertain for *Humesi* (P.); absent in other *Heteropodarke* (e.g., Fig. 6g).
20. *Cirrophores of ventral cirri*. Present (but small) in *Formalis* and "*Zmyrina*" at insertion of ventral cirri (Figs. 2g, 6g); uncertain in *Bidentata*, *Heteromorpha*, *Xiamenensis*, and *Humesi* (P.); absent in *Africana*, *Lyonsi*, *Flexuosus* (O.), and *Pugettensis* (O.).
21. *Stout, hooked, posterior (sometimes median) notochaetae*. Present in *Africana* (Fig. 12d), *Heteromorpha*, *Lyonsi*, and *Xiamenensis* (Fig. 8l); uncertain in *Bidentata* (no specimen with entire posterior end has been examined); absent in remaining taxa.
22. *Notochaetae*. Present (except in anterior-most chaetigers) in *Formalis* (Fig. 6e), "*Zmyrina*" (Fig. 2e, 2f), *Flexuosus* (O.), and *Pugettensis* (O.) (Pleijel, 1998) but absent in remaining taxa. Notochaetae in *Formalis* are very small and have been overlooked in earlier descriptions (including Pleijel, 1998).
23. *Furcate notochaetae*. Present in "*Zmyrina*" (Fig. 2f), *Flexuosus* (O.), and *Pugettensis* (O.) (Pleijel, 1998); absent from remaining taxa.
24. *Capillary notochaetae*. Present in *Formalis*, *Flexuosus* (O.), and *Pugettensis* (O.) (Fig. 6e; Pleijel, 1998); absent from remaining taxa.
25. *Nobbed neuroaciculae with subdistal constriction*. Present in all *Heteropodarke* (e.g., Figs. 4g, 12b); absent from outgroups. Tip of aciculae appears fringed when observed in high magnification in compound microscope. Outside analyzed taxa, this character has a homoplastic occurrence also within some *Syllidae* (e.g., Ding and Westheide, 1994).
26. *Enlarged, stumped falcigers*. Present on anterior segments (co-occurring with pregut region) in *Africana*, *Heteromorpha*, *Lyonsi*, and *Xiamenensis* (Figs. 8f, 8h, 10a, 11f, 12a); absent from remaining taxa.
27. *About 5 falcigers in anterior chaetigers*. Present in all *Heteropodarke* except *Formalis* and "*Zmyrina*"; re-

- maining taxa have larger and more variable number of falcigers within each taxon.
28. *About 5 falcigers in median chaetigers.* Same distribution among taxa as character 27, except present also in *Bidentata* and *Formalis*.
 29. *Fine single or double neuropodial spinigers.* Present in all *Heteropodarke*; absent from outgroups. In *Xiamenensis* these "spinigers" are extremely fine and were originally described as capillaries. On the basis of available specimens, it was not possible to observe whether these spinigers are composite or not. In both cases, however, I would regard them as homologous to spinigers of other *Heteropodarke*.
 30. *Fine spinigers on first chaetigers.* Present in *Bidentata* and *Formalis* (Fig. 6d); absent from first chaetigers in remaining taxa provided with spinigers.
 31. *Fine spinigers on posterior segments.* Present in *Bidentata*, *Formalis*, and *Lyonsi*; confined to antero-median segments in other taxa with spinigers.
 32. *Rounded tips of nonenlarged falcigers.* Unique for *Xiamenensis* (Fig. 8i, 8j).
 33. *Bidentate falcigers.* Unique for *Bidentata* (Figs. 4e, 5c). Bidentate falcigers are present as homoplasies among various other polychaetes and occur within other *Hesionidae* also in *Hesionini* and *Psamathe* (Pleijel, 1998).
 34. *Posteriorly situated neuropodial capillaries.* Unique for "*Zmyrina*"; uncertain for *Africana*, *Bidentata*, *Lyonsi*, and *Xiamenensis*.