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REVISION OF THE FAMILY LYSARETIDAE, AND
RECOGNITION OF THE FAMILY
OENONIDAE KINBERG, 1865
(EUNICIDA: POLYCHAETA)

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Abstract. — As recognized by previous authors, the family Lysaretidae Kinberg, 1865 includes genera with dissimilar jaw morphology and composition. Lysaretidae is restricted here to include only *Lysarete* Kinberg, characterized by jaws mineralized with calcite and relatively short carriers with transverse musculature. *Oenone* Savigny, *Halla* Costa and *Tainokia* Knox & Green are removed into the family Oenonidae Kinberg, 1865. These genera are characterized by heavily sclerotized jaws which are not mineralized, and by long carriers with oblique-longitudinal musculature.

Hartman (1944) published a family-level revision of the eunicoid polychaetes which was widely accepted. Drawing on the work of Kinberg (1865) and Ehlers (1868), she placed heavy emphasis on the configuration of the jaws as a taxonomic character.

Hartman recognized three basic maxillary jaw patterns within the superfamily Eunicia: the labidognath pattern ascribed to the Eunicidae, Onuphidae, and Lumbrineridae; the prionognath pattern in the Arabellidae and Lysaretidae; and a third pattern (later named ctenognath by Kielan-Jaworowska 1966) found only in the Dorvilleidae. Labidognath jaws are characterized by having two relatively short, broad carriers, in contrast to the two long, slender carriers with a ventral median ligament (or "third carrier") which characterize prionognath jaw apparatuses. In the ctenognath condition the maxillae consist of two to four rows of numerous separate denticles.

During a study of the composition and fossilization potential of polychaete jaws, I divided eunicoid jaws into three groups based on their composition (Colbath 1986). Labidognath jaws are mineralized with calcium carbonate in the form of aragonite in the Onuphidae and Eunicidae, and calcite in the Lumbrineridae. Labidognath jaws are

also weakly sclerotized, and the outer protein wall is readily leached in 2% KOH (Hartmann-Schröder 1967, Colbath 1986). In contrast, prionognath and ctenognath jaws are amorphous to x-rays, do not react with HCl, and are relatively resistant to leaching in KOH (Colbath 1986).

The jaws of species of *Lysarete* Kinberg, 1865 are mineralized with calcite (Colbath 1986), and exhibit other labidognath morphological characters. Other genera previously included within the Lysaretidae have jaws of the prionognath type, prompting a revision of the family, and recognition of the family Oenonidae Kinberg, 1865.

History of Study

Early classifications of the eunicoid polychaetes were based exclusively on features of the external anatomy, and produced arbitrary groupings of genera which are dissimilar internally (Hartman 1944:1). First to emphasize the importance of jaw parts in classification was Kinberg (1865). Kinberg recognized ten families which he divided into four major groups (labeled informally as A-D). He defined group C by the presence of mandibles with separated right and left halves (an ontogenetically variable feature), and included only *La-*

randa Kinberg, 1865, which was considered unrecognizable by Hartman (1944:10, 1948:98). Kinberg's other groups correspond to the labidognath (A), prionognath (B), and ctenognath (D) jaw types presently recognized. Kinberg considered the *Lysaretae* (sic) and *Oenonidea* (sic) distinct, including the former in group A and the latter in group B.

Ehlers (1868:280–282) also emphasized the importance of jaw configuration in classifying these polychaetes, but did not formalize the distinctions. Instead, he recognized a single family *Eunicea* (sic), which he informally divided into the *Eunicea labidognatha* and *Eunicea prionognatha*. Ehlers (1868) did not stress the morphology of maxillary carriers as strongly as did Kinberg, but rather subdivided the eunicoids according to whether the anterior maxillae are arranged in a semicircle (*labidognatha*) or in parallel rows (*prionognatha*).

In contrast to Kinberg, Ehlers (1868) placed the genus *Lysarete* close to *Aglaurides* Ehlers (= *Oenone* Savigny) in the prionognath subdivision. He later (Ehlers 1887:107–108) acknowledged the close similarity between the jaws of *Lysarete* and those of *Lumbriconereis* Grube (= *Lumbrineris* Blainville), but did not emend his earlier taxonomic treatment.

Hartman (1944:2) essentially formalized the 1868 scheme of Ehlers using the family-level nomenclature of Kinberg. She retained six of the ten families recognized by Kinberg, placing the *Oenonidae* into synonymy with the *Lysaretidae*.

Fauchald (1970:118) removed *Iphitime* Marenzeller from the *Lysaretidae*, and erected the family *Iphitimidae*. He later (Fauchald 1977) erected the order *Eunicida* to include the seven families within the superfamily *Eunicea*, plus two additional families (*Histriobdellidae*, *Ichthyotomidae*) which were not assigned to a superfamily.

Materials and Methods

All lysaretids in the collection of the U.S. Museum of Natural History (USNM) were

examined for the present study, and selected specimens were dissected for examination of the jaws. Additional specimens of *Lysarete* were obtained on loan from the Florida Department of Natural Resources (FSBC). The holotype of *L. brasiliensis* Kinberg, 1865 was obtained from the Swedish National Museum, Stockholm.

One specimen of *Lysarete brasiliensis* with jaws in excellent condition (USNM 55884) was used for the chemical and mineralogical analyses, and for scanning electron microscopy. The maxillary apparatus was removed, dehydrated in an alcohol series, and prepared for SEM by critical point drying. The specimen was initially coated with carbon only, and chemically analyzed using x-ray dispersion. The specimen was then coated with gold palladium for routine scanning electron microscopy. The mandibles were removed, photographed with a Wild 400 wide-field optical microscope, and analyzed with the Gandalfi x-ray spectrometer in the Department of Mineralogy, Smithsonian Institution.

Taxonomic Characters

Jaw morphology and composition.—X-ray dispersion analysis of the maxillae of *Lysarete brasiliensis* indicates the presence of abundant calcium carbonate. The mandibles are mineralized with calcite, as are jaws in the lumbrinerids (Colbath 1986). Calcification is also evident in *L. australiensis* Benham, 1915, in that the blades of the mandibles are white, and the maxillae are dark brown rather than black. The presence of calcite is inferred by comparison with *L. brasiliensis*.

In contrast to *Lysarete*, jaws in species of *Oenone* Savigny, *Halla* Costa and *Tainokia* Knox & Green (commonly included in the *Lysaretidae*) are not mineralized, but rather are composed almost exclusively of scleroprotein. As a consequence, both maxillae and mandibles are jet black in color. The distinction between heavily sclerotized and calcified jaws is apparent upon inspection,

and was described by Benham (1915:233, 236–237). Benham made no comment about the utility of this distinction above the species level, however.

Other aspects of jaw morphology are correlated with the difference in mineralization. In *Lysarete* the maxillary carriers are relatively short (approximately equal to the length of the maxillae) and broad (Fig. 1b), with no ventral ligament (=“third carrier”). A thick band of transverse muscles joins the carriers dorsally (Fig. 2f), allowing them to be pulled closed in the “trap” motion described by Wolf (1980) for other labidognath jaws. The MI (maxilla I) elements in the maxillary apparatus are the same length (Fig. 2c), which allows the anterior tips to come together in a pincer-like fashion as part of the trap motion. The posterior dorsal surfaces of the MIs exhibit an interlocking ridge and furrow system (Fig. 2e), which may help to lock the apparatus in a closed position (Wolf 1980).

In species of *Oenone*, *Halla* and *Tainokia* the carriers are narrow and much longer than the combined length of the maxillae, and are not equipped with a transverse muscle band. Instead, a series of long, oblique-longitudinal muscles are attached along the length of the carriers. A ventral ligament is present. The right and left MI elements may be of different lengths (Crossland 1924; Hartman 1944; Kielan-Jaworowska 1966), and no basal ridge and furrow system is present to lock the jaws in a closed position. Such jaws are presumably incapable of performing a trap motion, as Wolf (1980) also concluded for the arabellids.

Soft-part morphology.—The genera traditionally included within the Lysaretidae share an elongated post-setal lobe and prominent dorsal cirrus on posterior parapodia. The morphology of the head, however, is distinctly different in each of the four genera under discussion. Although the difference between *Lysarete* and the other genera may not merit consideration as a family-level character, the anterior mor-

phology is none-the-less a useful key character.

In *Lysarete*, three antennae emerge from the posterior margin of the prostomium, and may lie flat in a V-shaped notch (Fig. 1a). In adult specimens the notch extends posteriorly across the peristomial rings, and in some cases across the first one or two setigers. *Halla* has three antennae which may lie back in a semicircular notch in the two peristomial rings (Fig. 1e). *Tainokia* has a single antennae, and a slight invagination which extends posteriorly only partially across the first of two peristomial rings (Knox & Green 1972, fig. 1). In *Oenone*, three antennae are tucked into a nuchal fold (Fig. 1d), no notch is present, and dorsally the peristomium has only one distinct ring.

Setae and acicula.—All of the worms considered here have simple geniculate setae. In addition, bifid hooks have been reported in *Oenone* and *Halla*. In *Lysarete*, *Oenone*, and *Tainokia* the geniculate setae are smooth (Knox & Green 1972, figs. 6, 7; pers. observ.). In *Halla*, however, the dorsal setae are denticulate, and the ventral setae are marked by distinctive oblique striae (Fig. 2a, b; Fauvel 1923:427, fig. 169 g, h).

Both described species of *Lysarete* have black acicula. In *Oenone fulgida* (Savigny, 1818) and *Halla parthenopeia* (Chiaje, 1828) the acicula are amber, while Knox & Green (1972:433) described the acicula in *Tainokia iridescens* as colorless. Black acicula are thus useful for distinguishing *Lysarete* from the other three genera, supporting the family-level distinction based on jaw morphology.

Systematics

Order Eunicida Fauchald, 1977

Family Lysaretidae Kinberg, 1865

Emended diagnosis.—Eunicoid polychaetes with jaws mineralized with calcite. Mandibles flat with semicircular growth rings anteriorly (Fig. 2d). Maxillary carriers no longer than combined length of maxillae,

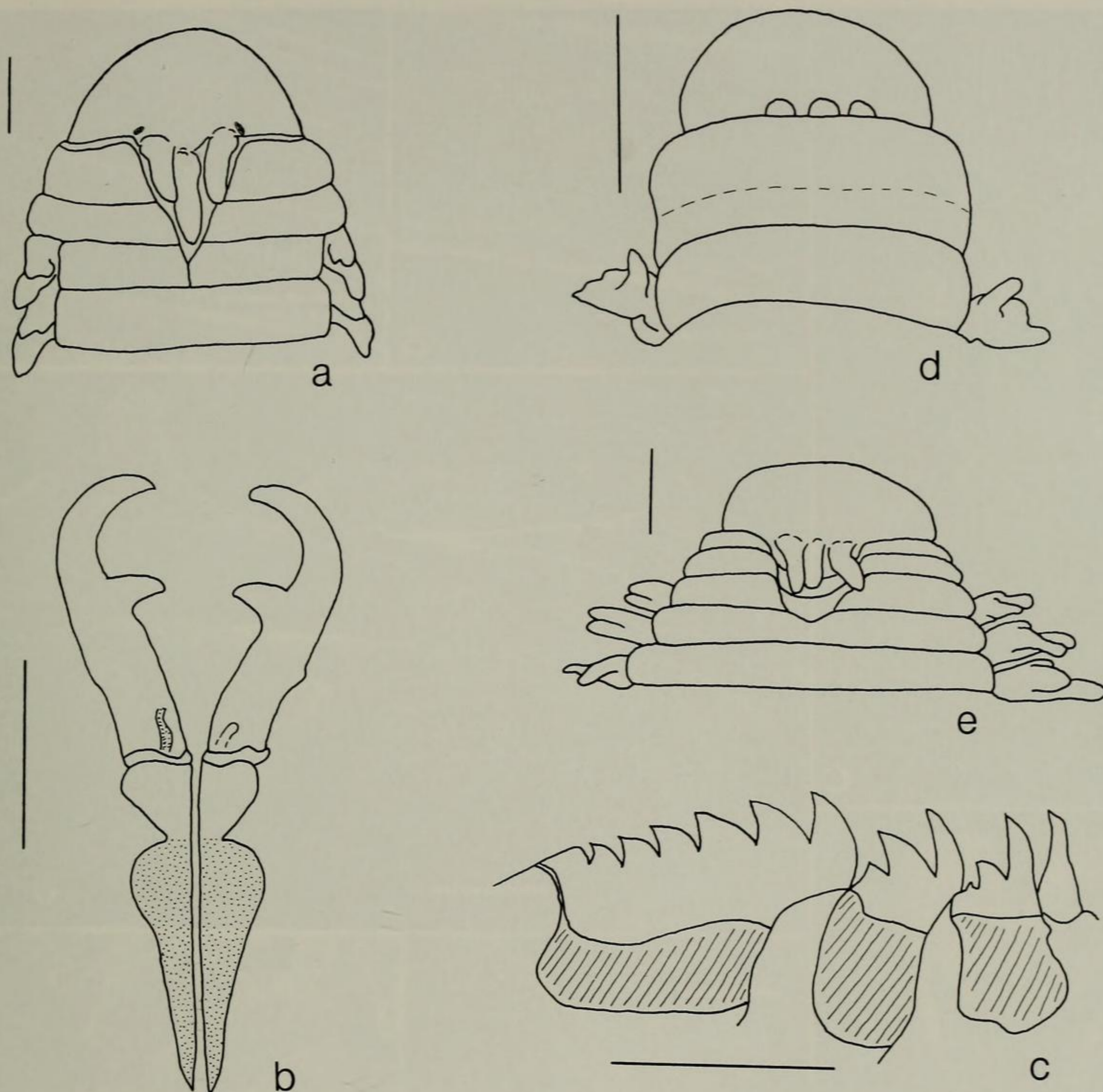


Fig. 1. a–c, *Lysarete brasiliensis*, holotype, Brazil; a, Dorsal view, anterior end, illustrating V-shaped notch in peristomium; b, Dorsal view, MI elements and carriers, muscle attachment stippled; c, Labial view, MIIL-MVL. d, *Oenone fulgida*, USNM 17729, Dry Tortugas, dorsal view, anterior end, note tips of antennae protruding from nuchal fold. e, *Halla parthenopeia*, USNM 5147, Bay of Naples, dorsal view, anterior end, note semicircular notch in peristomium. All scale bars = 1 mm.

articulated by prominent transverse muscular bundle, no ventral ligament. Maxillary jaws symmetrical. MI elements of identical length, distally falcate with prominent secondary fang, additional small denticles may be present at base. Three short antennae arise from base of prostomium. Elongate post-setal lobe and flattened dorsal cirrus (or notopodium) developed in posterior parapodia. Simple geniculate setae present, bifid hooks absent.

Comparison.—The Lysaretidae are distinguished from the Oeononidae based on

jaw morphology and mineralogy. *Lysarete*, the only genus presently recognized within the family, is further distinguished from the Oeononidae in having black acicula, and a V-shaped notch in the dorsal surface of the peristomium.

The Lysaretidae are similar to the Lumbrineridae in having: 1) jaws mineralized with calcite; 2) flat mandibles with a semicircular blade; 3) symmetrical maxillary jaws; 4) transverse musculature on the carriers. The Lysaretidae are distinguished from the Lumbrineridae by: 1) well-developed

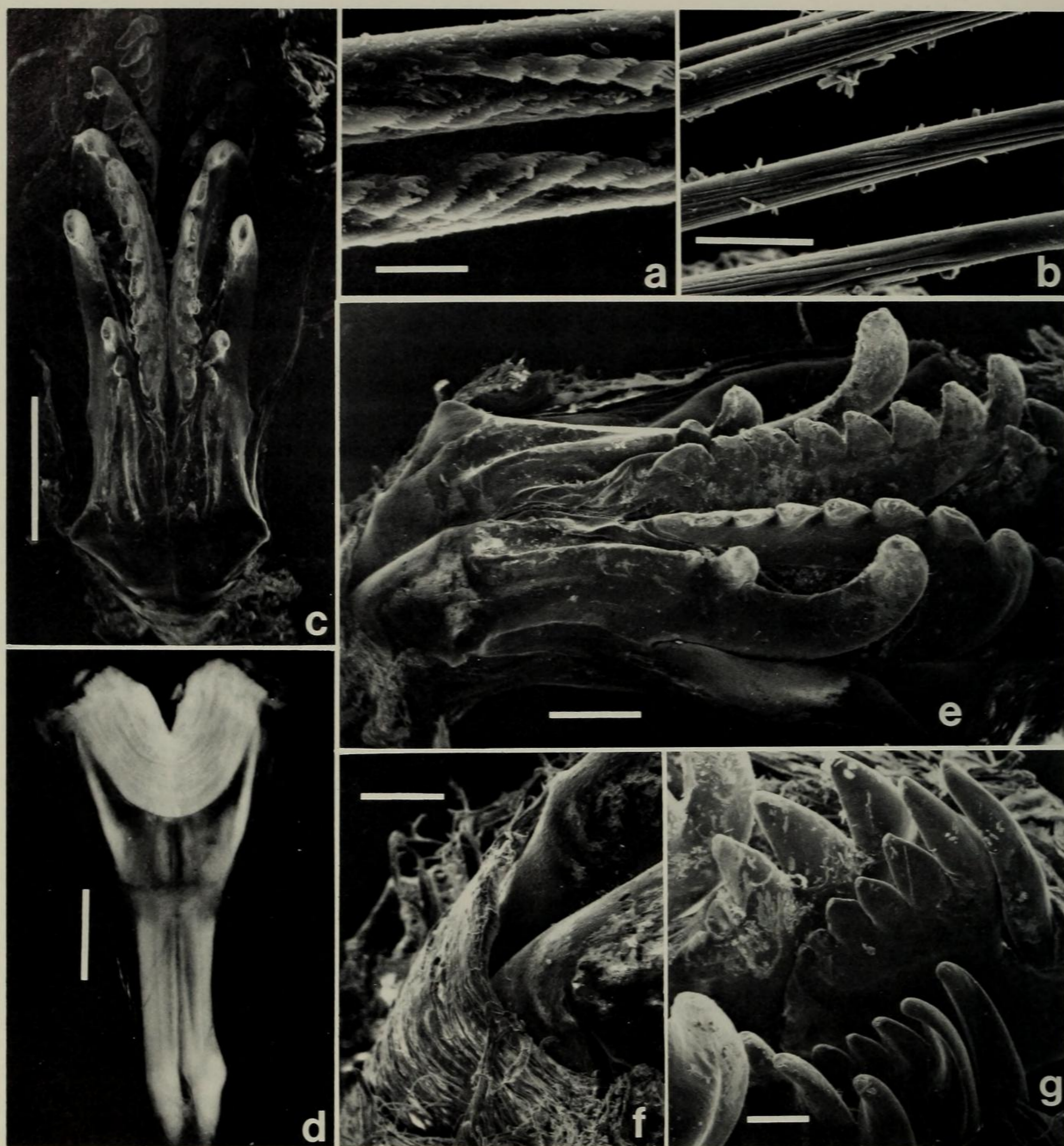


Fig. 2. a, b, *Halla parthenopeia*, USNM 5147, Bay of Naples; a, SEM dentate setae from dorsal bundle, posterior parapodium, scale bar = 10 μ m; b, SEM striate setae from ventral bundle, scale bar = 50 μ m. c–g, *Lysarete brasiliensis*, USNM 55884, Gulf of Mexico; c, SEM maxillary apparatus, dorsal view, scale bar = 1 mm; d, Light photomicrograph mandibles, ventral view, scale bar = 1 mm; e, SEM MI elements, oblique-lateral view, note ridges and grooves on bases of MIs, scale bar = 0.5 mm; f, SEM carriers, oblique-lateral view, carriers canted at an angle to MIs, note transverse muscle band, scale bar = 0.2 mm; g, SEM anterior maxillary jaws, oblique-lateral view, scale bar = 0.2 mm.

dorsal cirri; 2) a prominent secondary fang on the MI elements of the maxillae; 3) the absence of hooded hooks. *Kuwaita* Mohammad, 1973 is intermediate between the Lysaretidae and Lumbrineridae in having an-

tennae on the prostomium, but clearly belongs in the Lumbrineridae based on the 3 criteria above (Mohammad 1973:34, 36, figs. 6, 7).

Distribution.—*Lysarete* includes one

species recorded from the east coast of North and South America in low latitudes, and a second species from a single locality east of Australia. *Larymna* Kinberg, 1865 may also belong in the Lysaretidae based on jaw morphology (Hartman 1948:99). The type and only specimen (from Mozambique) is so poorly preserved that, according to Hartman, attribution cannot be made below the family level, and *Larymna* should be regarded as unrecognizable.

Genus *Lysarete* Kinberg, 1865

Type species.—*L. brasiliensis* Kinberg, 1865:570.

Lysarete brasiliensis Kinberg, 1865 Figs. 1a–c, 2c–g

Lysarete brasiliensis Kinberg 1865:570; 1910:49, pl. 17, fig. 30.—Ehlers 1887:107–108, pl. 33, figs. 1–8.—Rioja 1944:130–131, figs. 47–50.—Hartman 1951:65, pl. 14, figs. 7, 8.—Orensanz 1975:106–108, fig. 8.—Gardiner 1976:213, figs. 29b–e.—Gilbert 1984:43-6–43-7, figs. 43-3, 43-4.
?Oenone brevimaxillata.—Treadwell 1931: 1–3, figs. 4–8.

Remarks.—In her re-appraisal of Kinberg's type material, Hartman (1948:8) did not consider the holotype of *Lysarete brasiliensis*, but instead referred to an earlier revision by Ehlers (1887:107–108, pl. 33). Ehlers did not figure the Brazilian type of *L. brasiliensis*, but rather figured a specimen collected from Florida. The posthumous publication of Kinberg's plates (Kinberg 1910) did not include illustrations of the jaws of the holotype. The maxillae are therefore illustrated here (Fig. 1b, c).

On the holotype, maxillary jaws III and IV each have a prominent anterior denticle, with two progressively smaller denticles posteriorly. The jaws in a specimen from Argentina (Rioja 1944, fig. 50) are similar, except that the MIII elements have four denticles instead of three.

Most specimens examined from the east

coast of the United States have five to six denticles on the MIII and four to seven denticles on the MIV elements (Fig. 2g). The anterior three denticles on the MIII element are sub-equal in length, unlike those of the type.

One specimen from Florida (FSBC I 31008) has MIII jaws like the type, however, and a specimen from Argentina illustrated by Orensanz (1975, fig. 8-3) has MIIIs and IVs indistinguishable from most of the North American specimens. There is thus some overlap in jaw morphology between the North and South American populations. The number and shape of denticles on anterior jaws is variable in eunicoid polychaetes, and the two populations are tentatively considered conspecific in spite of their disjunct geographic ranges.

The type and only specimen of *Oenone brevimaxillata* Treadwell, 1931 was never deposited (H. S. Feinberg, AMNH, pers. comm. 1985), and is presumed lost. Treadwell's (1931, fig. 8) illustration of the maxillae is schematic, and insufficient for detailed comparison.

Family Oenonidae Kinberg, 1865

Emended diagnosis.—Jaws jet black, composed primarily of scleroprotein, no crystalline mineral phases present. Mandibles H-shaped. Maxillary carriers much longer than anterior jaws, attached to bundles of oblique-longitudinal muscles, ventral ligament present. Maxillae commonly asymmetrical, MIs differ slightly to markedly in length. One or three antennae arise from base of prostomium. Elongate post-setal lobe and prominent dorsal cirri developed on posterior parapodia. Geniculate setae present, bifid hooks present or absent.

Key to the genera of Oenonidae

- 1a. One or 3 antennae recline in notch in peristomium, 2 peristomial rings dorsally, bifid hooks present or absent 2
1b. Three antennae tucked into nuchal

- fold, 1 peristomial ring dorsally, bifid hooks present *Oenone*
- 2a. One antenna, peristomial notch weakly developed, bifid hooks absent, setae smooth *Tainokia*
- 2b. Three antennae, distinct semicircular peristomial notch, bifid hooks present (small individuals only), dorsal setae dentate, ventral setae striated *Halla*

Genus *Halla* A. Costa, 1844

Type species.—*Halla parthenopeia* (Chiaje) Costa, 1844:63.—*Lysidice parthenopeia* Chiaje, 1828:175.

Remarks.—Fauvel (1923:427, fig. 169f) described *Halla parthenopeia* as having bifid hooks, in addition to the setae figured here (Fig. 2a, b). Hooks are absent in parapodia from the large specimen of *H. parthenopeia* examined here (USNM 5147), nor were hooks recorded from the large specimen figured by Ehlers (1868:28, figs. 27, 28). The type of *Halla okudai* Imajima (1967:437) is also a large worm, and lacks hooks (Imajima & Hartman 1964:267–268). Individuals of *Halla* which attain large size may lose their bifid hooks. A similar condition prevails in several large species within the Eunicidae (K. Fauchald, pers. comm. 1985).

Distribution.—All western hemisphere specimens deposited in the USNM collection as *Halla* proved to be misidentified members of *Oenone* or *Lysarete*. *Halla* may be restricted to the Old World, with documented reports from the Mediterranean (Fauvel 1923) and Japan (Imajima 1967).

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