

## TWO NEW LAMIPPID COPEPODS PARASITIC ON GORGONIANS FROM HAWAII AND THE BAHAMAS

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**Abstract.**—Descriptions are presented of *Linaresia magna*, new species, and *Sphaerippe caligicola*, new genus and species, gorgonian-inhabiting lamippid copepods parasitic within galls on a Hawaiian *Placogorgia* and a Bahaman *Callogorgia* respectively. *L. magna* is the first lamippid described from the Pacific. It differs from the two previously known species of *Linaresia* in its greater size, in the shape of the lateral arms and lack of ventromedial knobs in the female, and in details of setation. It lives in galls formed from individual host polyps, with a density of 0.42 individuals per centimeter of host skeleton. The sex ratio is nearly even; spermatophores are attached in pairs to the females and eggs are found in loose bundles within the galls. Some specimens are associated with the ascothoracican cirriped *Gorgonolaureus*. The new genus *Sphaerippe* is distinguished by a globular female, bands of papillae on the male, no maxillipeds, broad, weakly segmented second antennae, a short furca with spines, and multidigitate thoracic limbs with acicules. *S. caligicola* lives as a male-female pair within a boot-shaped gall. Several egg masses containing about 40 eggs each are found within the gall.

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The Lamippidae are a small family of poecilostome copepods parasitic within various Octocorallia. Those found in the vicinity of Banyuls-sur-Mer, France, are the best known, having been studied by de Zulueta (1908, 1910, 1911), Bouligand & Delamare-Deboutteville (1959a, b), and Bouligand (1960a, b, 1961, 1965). The most extensive recent review is that of Bouligand (1966). Here he recognized two genera, *Lamippe* (subgenera *Lamippe*, *Lamippula*, *Lamippina*, *Lamippella*, *Enalcyonium*, and *Isidicola*) and *Linaresia*. Except for *Lamippula*, which was newly defined, the subgenera of *Lamippe* were previously of generic rank. Stock (1973) reestablished all these taxa as genera and presented a key for distinguishing them. A representative of a new genus, *Magnippe*, has recently been described by Stock (1978).

The two new lamippids described in this paper were discovered fortuitously while I was examining gorgonians for gallicolous ascothoracican cirripeds. Ms. Katherine Muzik of the Museum of Comparative Zoology at Harvard University sent me dried branches of a new *Placogorgia* (n. sp. A) from off Makapuu Point, Oahu, Hawaii, where they had been collected



by Boh Bartko in the *Star II* submersible at 366 meters. This dried material was reconstituted overnight in a trisodium phosphate solution. Some ascothoracicans (*Gorgonolaureus* sp.) were present in a few large galls, but much more numerous smaller galls contained peculiar stellate animals that could be assigned to the lamippid genus *Linaresia*. The two species of this genus previously known are *L. mammillifera* de Zulueta (1908) and *L. bouligandi* Stock (1979) from the Mediterranean coast of Spain and the west coast of Florida, respectively. This is the first lamippid known from Hawaii, and, aside from undescribed species present at La Jolla, California (Taylor, unpublished) and at Corona del Mar, California (Illg, personal communication), it is the first from anywhere in the Pacific.

Dr. Frederick Bayer of the Smithsonian Institution sent a collection of gorgonian-associated ascothoracican material including a stalk of *Callogorgia* (USNM Acc. no. 295887) from off Grand Bahama Island with a small, boot-shaped growth on it. This gall contained a pair (male and female) of lamippid copepods, rather than ascothoracicans; these specimens are described herein as representatives of a new genus, *Sphaerippe*. A number of lamippids are already known from the West Atlantic and the Caribbean (Patton, 1963; Dudley, 1973; Stock, 1973, 1978, 1979).

All figures were drawn by the author with the aid of a camera lucida from whole specimens mounted and cleared in lactic acid, or in some cases for *Linaresia*, dissected specimens mounted in glycerol or Turtox CMC-10 with acid fuchsin.

### *Linaresia* de Zulueta

#### *Linaresia magna*, new species

##### Fig. 1

*Material*.—Holotype, ♀, at U.S. National Museum of Natural History, USNM 173711; Paratypes: 15 ♀♀, 15 ♂♂, and a *Placogorgia* branch with unopened galls, USNM (for the lot) 173712; 15 ♀♀, 15 ♂♂, at Museum of Comparative Zoology, Harvard University; numerous ♀♀ and ♂♂ and unopened galls retained at Scripps Institution of Oceanography.

*Type-locality*.—About 10 kilometers east of Makapuu Point, Oahu, Hawaii (21°19'N, 157°34'W), at 366 meters depth. Taken by Boh Bartko in *Star II* submersible in 1979.

*Distribution*.—Known only from type-locality.

*Host*.—Endoparasitic in *Placogorgia* sp.

*Etymology*.—From Latin *magnum* (=large), referring to the animal's size relative to its congeners.

*Description*.—Female (Fig. 1a–g): Length varying due to uneven shrinkage in dried state, 1.4–2.3 mm, averaging 1.9 mm (n = 30) not including furca or lateral processes. Body (Fig. 1a) yellow to amber in color, outline



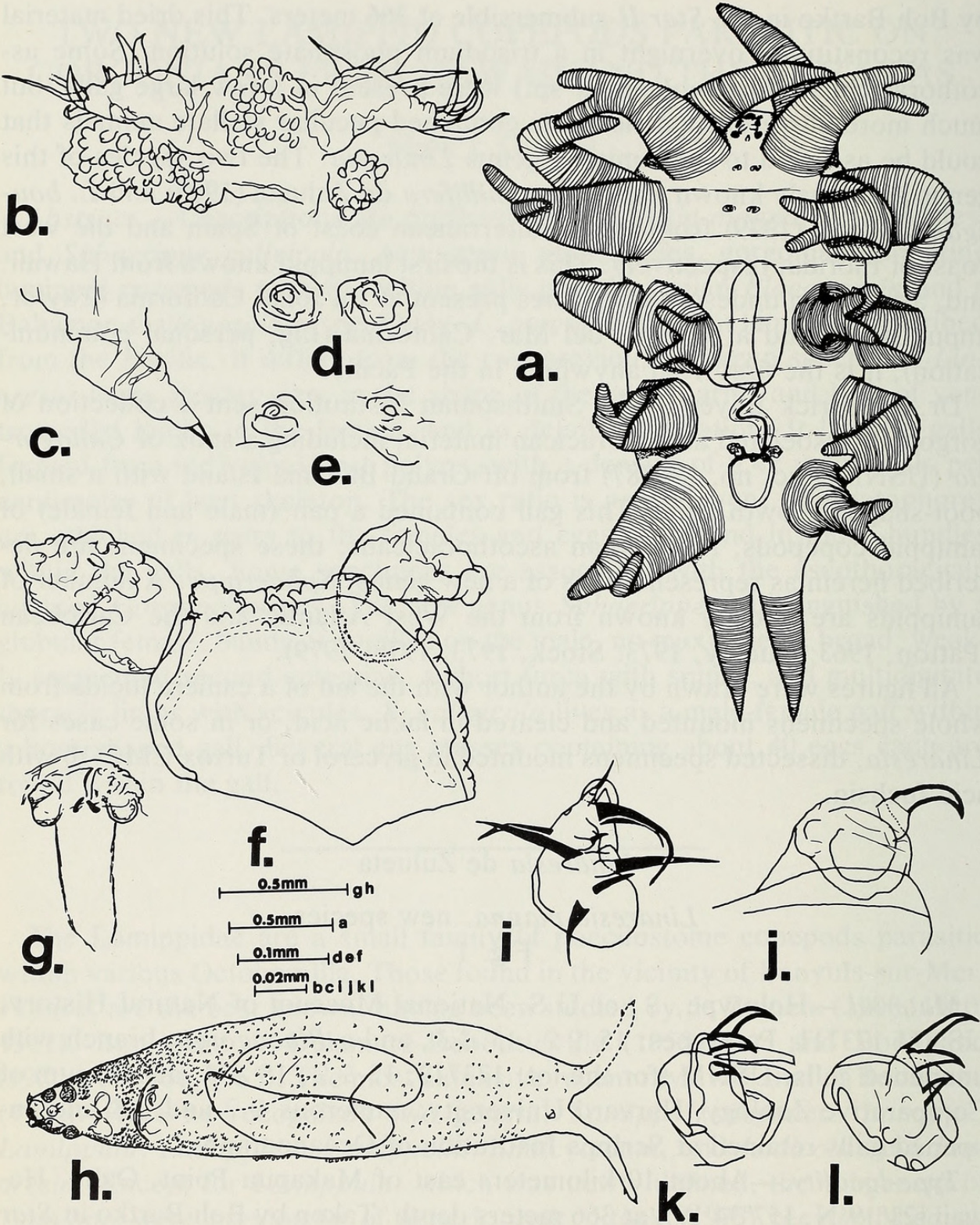


Fig. 1. *Linaresia magna*: a-g, Female; h-l, Male: a, Ventral aspect of female, reconstruction, anterior end uppermost, showing pair of spermatophores with duct leading to genital apparatus; b, First antennae, ventral aspect, including the 3 most anterior papillate tubercles; c, Second antenna, ventromedial aspect; d, First pair of thoracopods, ventral aspect; e, Second pair of thoracopods, ventral aspect; f, Female genital apparatus (genital plate and vulvae), ventral aspect, genital plate displaced somewhat to left during mounting; g, Same as f with genital plate removed to show clavate projections between vulvae and depression which accomodates convex upper surface of plate; h, Ventral aspect of male, anterior end at left, showing spermatophores within body and terminal swelling at base of furca; i, First antenna, median aspect; j, Second antenna, median aspect; k, First thoracic limb, lateral aspect; l, Second thoracic limb, lateral aspect.



variable, but typically roughly rectangular, twice as long as wide, tapering slightly posteriorly to a furca. Each furcal ramus about 1 mm long with annulate ridges, tapering to a spine. Sixteen lateral processes (arms) along sides of body arranged into 5 sets along each side; all arms about 1 mm long, cylindrical with annulate ridges, tapering to blunt ends. First 3 pairs each with biramous ventral and uniramous dorsal element. Posterior tip of biramous arm slightly narrower and longer than anterior, bifurcation occurring in distal quarter of arm. Last 2 pairs with only biramous ventral element, last pair wider than the others. Arms produced laterally, but usually bent ventrally. Other external features including 2 pairs of antennae, oral cone, 2 pairs of thoracic limbs, and genital plate ("terminal swelling" of Bouligand, 1966) with associated structures. Ventral surface with several transverse folds or ridges, which, together with intervening cuticle, bear minute slits and depressions, triangular in side view, and more common anteriorly. Antennae and oral cone between first pair of arms; first antennae on anteriormost end of animal. Five papillae-laden tubercles anteriorly, 1 dorsal of first antennae, 2 lateral between pairs of antennae, and 2 lateral posterior to second antennae. First thoracic limbs equidistant between oral cone and second thoracic limbs, latter between second pair of arms. First antennae (Fig. 1b) 0.05 mm long, directed laterally. Five setae on anterior border and 5 more terminal, short but not spinelike. Segmentation obscure, possibly 2 segments. Second antennae (Fig. 1c) slightly larger and conical, segmentation obscure, single hooked claw at tip. Oral cone a very small projection antero-posteriorly elongate. Thoracic limbs (Fig. 1d–e) reduced to nipplelike structures lacking setae. Genital apparatus (Fig. 1f) just anterior to last pair of arms. Plate roughly pentagonal, 0.3 mm wide and slightly longer, with convoluted anterior edge. Plate prehensile, with rear edge anchored and upper side convex. Vulvae at anterior corners of plate, bulbous part of each partly overlain by plate; tapered lateral part of each free. A pair of narrow, clavate projections pointing posteriorly from beneath anterior edge of plate (Fig. 1g).

Male (Fig. 1h–i): Length 0.9–1.6 mm, averaging 1.3 mm ( $n = 27$ ) not including furca. Body (Fig. 1h) yellow to amber in color, fusiform, tapering more anteriorly than posteriorly; widest point (0.5–0.6 mm) at midlength. A posterior furca, each ramus stout and tapering, with a terminal and external subterminal spine. Furcal rami 20–25% as long as rest of body. Other appendages including 2 pairs of antennae and 2 pairs of thoracic limbs anteriorly; also spherical ventral protrusion (terminal swelling) just anterior to furca. Transverse genital slit ventrally, just posterior of widest point of body, bowed slightly forward in middle. Papillae covering integument, but sparse posteriorly and on ventral surface near thoracic and cephalic appendages. Five papillae-covered tubercles at anterior end arranged as in female. First antennae (Fig. 1i) 0.06 mm long, with no apparent segmentation, conical with 1 baso-medial seta, 2 long and 2 short setae in center of



medial side, 1 seta on middle of anterior side or on medial face, and 2 long and 1 short terminal setae. All setae stout and tapering to a point. Second antennae (Fig. 1j) of same dimensions as first, with indistinct basal segment, spherical segment with sclerites, and slightly bulbous distal segment bearing stout, hooked claw. Mouth posterior to second antennae, reduced to minute indented oval. Mandibles, maxillae, and maxillipeds absent. First and second thoracic limbs (Fig. 1k-l) about same size as antennae. Protopodites with sclerites. Exopodites with 3 claws, 2 terminal and smaller one between and proximal to these on posterior side. Endopodites absent. Interpodal plate connecting each pair of limbs across midline.

*Remarks.*—The 5 papillate cephalic tubercles, the simple tapering furcal rami, and the pronounced development and precise arrangement of the female lateral processes (arms) are diagnostic of the genus *Linaresia* de Zulueta (1908). Two other species are known, *L. mammillifera* de Zulueta (1908), the type-species of the genus, and *L. bouligandi* Stock (1979).

The female of *L. mammillifera* is more rotund than that of *L. magna*. Its length is only 1.1 mm, 40% shorter than the new species. The arms of *L. mammillifera* are capitate, unlike *L. magna*, where they taper gradually. On bifurcate arms, the posterior branch is clearly subordinate in *L. mammillifera*, being acapitate and set off at a right angle. In *L. magna* there is a slight asymmetry, but no obvious subordination between the bifurcate tips. The first antennae of the female *L. mammillifera* lack a subterminal seta found in *L. magna*, and the thoracic limbs are slightly less degenerate in the former species. Three enigmatic structures are arranged serially on the ventral side of the *L. mammillifera* female posterior to the thoracopods. The anterior 2 are round knobs situated medially, while the posterior one may also be on the midline, or be manifested in other individuals as a paired structure. Stock (1978) considers these to be rudimentary limbs. These structures are absent in *L. magna*. The furcal rami of the male *L. mammillifera* are proportionately longer than those of *L. magna*, and its main body is only half as long as the present species. There are 2 extra setae on the medial side of the first antennae in *L. magna* males. No mention is made of a terminal swelling in the males of *L. mammillifera*.

Only the female is known of *L. bouligandi*. Its main body is 0.5–0.6 mm long, much smaller than *L. magna*. The body outline is also more rotund. The arms are proportionately longer and narrower than in *L. magna*, and have wider annulations. The bifurcations of the ventral arms are very long compared to *L. magna*. The first antennae are more reduced in *L. bouligandi*, with only 0–3 setae, compared to 10 in *L. magna*. The claw on the second antenna is bifid in *L. bouligandi*, but simple in *L. magna*. Two medial swellings on the ventral surface, similar to those in *L. mammillifera*, are found in *L. bouligandi*, but not in *L. magna*. According to Stock (1979), *L. bouligandi* has 2 arcuate sclerites connected by a straight, transverse



sclerite some distance anterior of the genital plate ("terminal swelling"). He tentatively labelled this structure the vulva, citing Bouligand & Delamare-Deboutteville (1959a). The structure on *L. mammillifera* referred to by Stock was in later papers by Bouligand redescribed as the third (single or paired) ventral knob, discussed above. Bouligand (1960a) showed that the oviducts open at the true vulvae, the structures at the anterior corners of the genital plate. Stock's "vulva" is probably homologous to the third ventral knob in *L. mammillifera*, and is probably not a reproductive structure. The structure is lacking in *L. magna*. The genital plate is situated at the extreme posterior end of the body in *L. bouligandi*, rather than farther forward as in the other 2 species. In all 3 species the position of the genital plate is fairly constant relative to the last pair of arms. There is apparently no armanent of the furcal rami in *L. bouligandi*.

*Life cycle*.—Many males have a pair of spermatophores developing within chambers that are one-third the length of the animal (0.8 mm). The spermatophores must exit through the ventral transverse slit. They are attached in pairs by a cord to the female. Attachment may be at various places on the underside, but usually just in front of the genital plate. This cord is over 1 mm long and is twisted; it contains the ducts leading from each spermatophore. These may join distally, or they may remain separate for most of the length of the cord. The duct narrows greatly at the point of attachment. No sperm were seen. Spermatophores attached to the female (Fig. 1a) are 0.6 mm long and reniform.

Most females are associated with eggs, either loosely attached within the gall or confined in thin membranous sacs on the underside of the female. Egg sacs are not reported from either of the other species of *Linaresia*. The eggs are about 0.14 mm in diameter. One was seen with a developing nauplius inside. It was impossible to see much detail, but the larva did have 3 pairs of appendages with 3–5 terminal setae per ramus. Stages intermediate between the male and female are known for *L. mammillifera* (Bouligand, 1960a), but not in *L. magna* or *L. bouligandi*. It is possible, though, that all 3 species are protandric hermaphrodites.

*Ecological notes*.—Each gall corresponds to a single polyp. *L. magna* apparently does not live within the polyp, for a membrane separates the gastro-vascular cavity of the polyp from the space within which the copepod is living. The dorsal side of the female is appressed to the gorgonian's axis, with the body lined up longitudinally, producing a lenticular swelling of the gorgonian's bark. Unlike *L. mammillifera*, there are no cases of the arms of the parasite being exposed and possibly simulating a missing polyp.

Each gall contains a female and, usually, a male (rarely 2 or 3) and eggs. Solitary males were found, but not within galls. Often there were one or more females associated with galls formed by an ascothoracican cirriped (*Gorgonolaureus* sp.). Here there were no enlarged polyps; the parasitic



copepod lived between the valves of the ascothoracican and the gorgonian tissue covering it. In order to estimate the degree of infestation, branches of the gorgonian totalling 139 mm in skeletal length were thoroughly searched for copepods; 59 individuals were found, corresponding to a density of 0.42 copepods per centimeter of host. Thirty-one of these were females and 28 males, suggesting a 1:1 sex ratio.

The host of *L. mammillifera* is *Paramuricea clavata* of the family Paramuriceidae (potentially confusing name change of this gorgonian explained in Stock, 1979). Both *L. bouligandi* and *L. magna* are found in *Placogorgia* species, also in the Paramuriceidae. It is too soon to tell, however, whether *Linaresia* is confined to this one family of gorgonians. Both *L. mammillifera* (subtidal) and *L. bouligandi* (76 m) are from shallow waters, while *L. magna* (366 m) is from bathyl depths. The 3 species of *Linaresia* currently encompass the Mediterranean, Western Atlantic, and Indo-West Pacific biogeographical provinces. This may be construed as a Tethyan distribution, in which case it is reasonable to expect that more species will be discovered at similar latitudes in the future.

### *Sphaerippe*, new genus

*Diagnosis*.—Lamippid copepods endoparasitic within a gall on a gorgonian (*Callogorgia* sp.). Sexually dimorphic, female much larger than male and with slightly different armament on appendages. Female globose, with slight anterior appendage-bearing protrusion; male less rotund, with more prominent appendage-bearing protrusion and 5 bands of papillae around trunk. Both sexes with biarticulate first antennae (single spine on basal segment, many on terminal segment); broad, weakly biarticulate (possibly triarticulate in female) second antennae terminating in hooked claw; 2 pairs of thoracopods with uniarticulate protopodites, exopodites, and endopodites; and separated furcal rami, conical, with a subterminal and 4 terminal spines. Maxillipeds absent. Thoracic endopodites of both sexes well-developed with palmately arranged digitations, each terminating in an acicule. Exopodites similar to endopodites, but with more digitations. Sometimes inexact symmetry of numbers of digitations on left and right sides of animal, and males possessing more digitations than females.

*Remarks*.—*Sphaerippe* differs from *Linaresia* and *Magnippe* Stock (1978) in not having the lateral arms that give the females of these two genera stellate appearances. *Lamippe* Bruzelius (1859) and *Isidicola* Gravier (1914) have well-developed maxillipeds, which are lacking in *Sphaerippe*. *Lamippina* Bouligand (1960) has well-developed thoracic endopodites like *Sphaerippe*, but also has rudimentary maxillipeds, furcal acicules, and a clearly articulated second antenna with 3 segments in both sexes, conditions found wanting in *Sphaerippe*. *Lamippula* Bouligand (1966) lacks maxillipeds but has furcal acicules and long, clearly segmented first and second



antennae, contrary to the condition found in *Sphaerippe*. *Enalcyonium* Olson (1869) is similar to *Lamippula*, though lacking furcal acicules, but otherwise distinguishable from *Sphaerippe* by the same criteria as *Lamippula*. *Lamippella* Bouligand & Delamare-Deboutteville (1959) is the closest of the known genera to *Sphaerippe* in lacking maxillipeds and furcal acicules and in having circular rows of papillae and poorly segmented antennae, but it has reduced, unarmed endopodites on its thoracic limbs, contrasting with the well-armed endopodites of *Sphaerippe*. *Sphaerippe* is much more rotund than any other genus, and, aside from *Isidicola*, is the only relatively unmodified lamippid to live in a gall (Gravier, 1914). Pronounced sexual dimorphism has previously been known only in *Linaresia* and *Lamippina*, through there is a size difference between the sexes in *Lamippe* (Bouligand, 1966).

*Etymology*.—From Latin *sphaera* (=sphere) and the ending of *Lamippe*, the type-genus of the family Lamippidae, referring to the globular shape of the female. Gender feminine.

*Type-species*.—*Sphaerippe caligicola*, new species.

*Sphaerippe caligicola*, new species

Fig. 2

*Material*.—Holotype, ♂, USNM 173709; Paratype, 1 ♀ with eggs, USNM 173710.

*Type-locality*.—Off Southwest Point, Grand Bahama Island (26°31'N, 98°51'W). Taken at 366 meters on 14 February 1965; *Gerda* Station 503.

*Distribution*.—Known only from type-locality.

*Host*.—Endoparasitic within a gall on *Callogorgia* sp.

*Etymology*.—From Latin *caliga* (=boot) and Latin *-icola* (=an inhabitant), referring to the boot-shaped gall within which the copepod lives.

*Description*.—*Male* (Fig. 2a–d): Body (Fig. 2a) ellipsoidal, 0.62 mm long and 0.32 mm wide, with anterior end protruding. Color white. Cuticle smooth except for 5 bands of hemispherical papillae encircling trunk. Two pairs of antennae, oral cone, and 2 pairs of thoracic limbs near anterior end, ventral transverse genital slit just anterior to fourth band of papillae, and pair of short furcal rami also present. First antennae (Fig. 2b) 0.05 mm long, biarticulate. Basal segment with 1 short, median seta, terminal segment with 8 short setae. Second antennae (Fig. 2b) 0.06 mm long, with bulbous base and short, conical second segment terminating in strong, hooked claw. Oral cone round, covered by labrum with straight posterior edge. From posterior opening, oral cavity leading forward to center of cone, then straight into body; this cavity distally a transverse slit, but proximally, bifurcation at each end of slit may reveal pair of mouthparts not protruding past posterior edge of labrum. Maxillipeds absent. First thoracic legs (Fig. 2c) biramous,



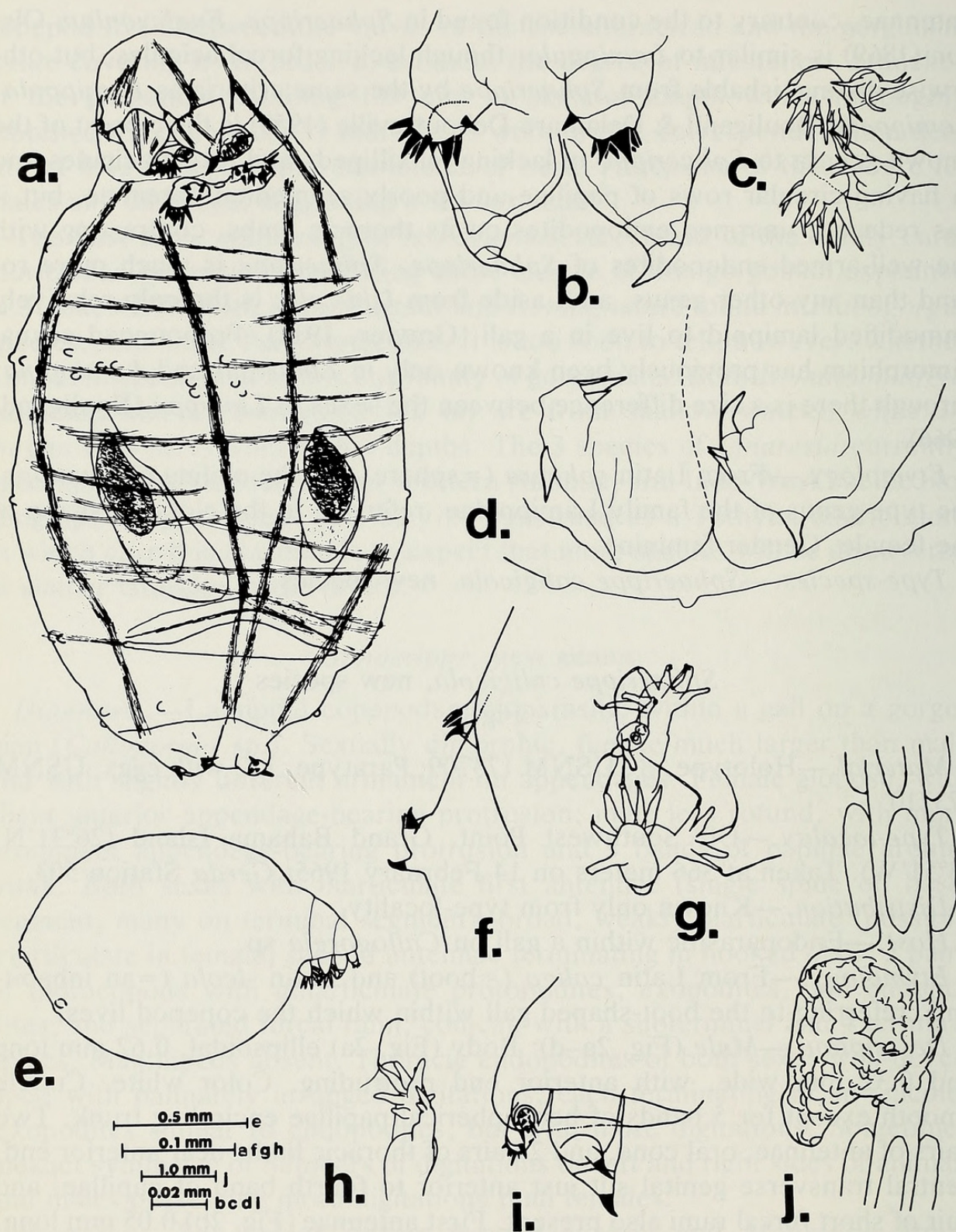


Fig. 2. *Sphaerippe caligicola*: a–d, Male; e–i, Female: **a**, Ventral aspect of male (Holotype) showing developing spermatophores and bands of papillae (more papillae present than shown here); **b**, First (above) and second (below) antennae, antero-lateral aspect; **c**, Right first (above) and second (below) thoracopods, ventral aspect; **d**, Furca, ventro-posterior aspect; **e**, Lateral aspect of female (Paratype), showing vulvae below and anterior to furca; **f**, Furca, ventro-lateral aspect; **g**, Right (above) and left (below) second thoracopods, ventro-lateral aspect, with exopodites oriented vertically, showing extended acicules; **h**, Right first thoracopod, medial aspect, showing acicules; **i**, First (left) and second (right) antennae on anterior end of body; **j**, Gall in place of *Callogorgia*, ovals representing stylized polyps.



with uniarticulate protopodites, exopodites, and endopodites. Interpodal plate connecting this pair across midline. Endopodite and exopodite terminating in digitations (integral parts of segment, not spines or setae) that are slightly bulbous basally, presumably with a retracted acicule at tip of each. Right endopodite of first pair of legs with 4 digitations, right exopodite with 11, left endopodite with 4, and left exopodite with 12. On second pair (Fig. 2c) components similar to those in first, except interpodal plate more pronounced. Right endopodite with 5 digitations, right exopodite with 10, left endopodite with 5, and left exopodite with 9. Digitations arranged palmately on all limbs, 2 rows on exopodites. Genital slit bowed slightly forward in middle. Furcal rami (Fig. 2d) separated on buttockslike lobes, each ramus a flabby cone with 1 large and 2 small terminal spines and 1 subterminal lateral spine as large as largest terminal one.

Internal structure including 4 longitudinal muscle bands, many circular muscles, and pair of developing spermatophores anterior to genital slit. Muscles present in antennae and limbs. Each row of papillae on slight annulus probably representing a segment, but perhaps only reflecting a state of arrested peristalsis.

*Female* (Fig. 2e–i): Body (Fig. 2e) globose, 1.24 mm long with anterior end protruding slightly. Surface smooth. Other features arranged as in male except for genital apparatus. First antennae (Fig. 2i) 0.05 mm long, cylindrical with median seta on first segment and many very short setae on second. Second antennae (Fig. 2i) twice as long as first, apparently biarticulate (suture around cylindrical basal segment perhaps indicating that 3 segments are present), with hooked claw at tip. Oral cone and mouthparts not observed due to difficulty of obtaining ventral view. Thoracic limbs similar to males except for number of digitations and presence of an extended acicule on many of them. Distribution of digitations as follows: on first pair (Fig. 2h), exopodites with 7 and endopodites with 2; on second pair (Fig. 2g), exopodites with 6 and endopodites with 5. Furca (Fig. 2f) as in male. Vulvae anterior to furca, but still on posterior side of sphere, hemispherical knobs on each side of midline with 2 arcuate sclerites surrounding opening on each.

*Remarks.*—*Sphaerippe caligicola* is distinguished from other lamippids because of its rotundity (other lamippids are sausage-shaped to vermiform), and the acicule-bearing digitations of the thoracic limbs are quite unusual. *Lamippina aciculifera*, as its name implies, bears many acicules, including some on digitations of its thoracic limbs (Bouligand, 1961), but there are also normal setae and claws on its limbs, as well as additional acicules on the furca. Many other lamippids bear acicules, either on the furca (for examples, see de Zulueta, 1908) or over the body surface (*Enalcyonium chattoni*), but on these, the endopodite is reduced and naked, or, at most, armed with a few normal setae. The combination of acicule-laden thoracic limbs



and furcal rami armed only with spines is unique to this new species of lamippid.

The asymmetry in the number of digitations, at least in the male, may limit the value of this character in distinguishing *S. caligicola* from any undiscovered species in the genus *Sphaerippe*.

*Effect on host.*—The axis of the *Callogorgia* host has polyps arranged in rings of 4, the rings spaced 2 mm apart. The gall containing the pair of copepods took the place of one of these rings. The gall (Fig. 2j) was boot-shaped, with the “sole” distal and parallel to the axis. It extended 1.3 mm away from the axis, was 3 mm long, and was covered with spicules like the rest of the gorgonian. No external opening was present. The inside of the gall was lined with a membrane with a 6-fold symmetry in cross-section at the “toe.” It is not known whether this membrane was secreted by the host or the parasite.

*Life cycle.*—Five egg clusters totalling 198 eggs were found within the gall distal to the axis along the “sole” and within the “toe” of the boot. Dimensions of the eggs averaged  $110 \times 80 \mu\text{m}$ . The female had a large number of oocytes within its ovaries, and a pair of spermatophores was being produced by the male. No empty spermatophores were found; nor were any larvae, developing or hatched. It may be that this species of lamippid mates for life, since the male and female are enclosed in a common gall. Alternatively, the male's small size and more formidable armament may allow it to break out of the gall and reinvade the same or another gorgonian as a female. Such a system of protandric hermaphroditism has so far been demonstrated only in *Linaresia mammillifera* (Bouligand & Delamare-Deboutteville, 1959a; Bouligand, 1960a). Presumably the gall must rupture at some time to release newly hatched larvae, though a small hole bored by one would also allow the others egress.

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