Pelagic Amphipods of the Genus Hyperia and Closely Related Genera (Hyperiidea: Hyperiidae)

THOMAS E. BOWMAN

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ABSTRACT

Bowman, Thomas E. Pelagic Amphipods of the Genus *Hyperia* and Closely Related Genera (Hyperiidea: Hyperiidae). *Smithsonian Contributions to Zoology,* number 136, 76 pages, 1973.—The genus *Hyperia* is restricted to large species with no fusion of pereonites, mandibular palp present in both sexes, and coxae not fused with pereonites. Eight species are recognized, of which two are new, and one, *Hyperia macronyx,* is transferred to *Hyperiella.* The small species of *Hyperia,* with some pereonites fused, mandibular palp absent in female, and coxae fused to pereonites, are assigned to *Hyperioides* (1 species); *Lestrigonus* Milne Edwards, restored from synonymy (6 species, 1 new); *Hyperietta,* new genus (5 species, 3 new); *Themistella* (1 species); and *Hyperionyx,* new genus (1 species). Keys are given to the species of each genus. Available information on distribution is summarized for each species.

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Thomas E. Bowman

Introduction

A comprehensive taxonomic treatment of the amphipod family Hyperiidae has not appeared since the 1889 monograph of Bovallius. Important contributions to the taxonomy of this family have been made by Vosseler (1901), Stephensen (1924), Barnard (1930, 1932), and Yang (1960), but the need for an up-to-date revisionary study remains unsatisfied. In my studies of the Hyperiidae collected during the California Cooperative Oceanographic Fisheries Investigations (CalCOFI), I encountered several undescribed species as well as taxonomic problems that I felt unable to resolve without making comparative studies of hyperiids from other parts of the world. I therefore published only the results of my investigations of the genus *Parathemisto* (Bowman, 1960) and have delayed until now the presentation of a revision of *Hyperia* and closely related genera.

The present work considers the genus *Hyperia* and the species now assigned to it. Some of these species are transferred herein to currently recognized genera (*Hyperiella, Hyperioides*), to genera now considered synonyms of *Hyperia* (*Lestrigonus, Themistella*), and to new genera (*Hyperietta, Hyperionyx*); all these genera are reviewed in this paper. The other genera of Hyperiidae include three monotypic genera (*Bougisia, Pegohyperia, Phronimopsis*), *Iulopis* with two species, and *Hyperoche*. Of these only *Hyperoche* presents obvious taxonomic problems, and a monographic treatment of it will be offered later.

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MATERIAL.—For this investigation I have had available the amphipod collections of the Division of Crustacea, Smithsonian Institution, obtained from many sources. Their careful curation and arrangement for maximum convenience by the late Clarence R. Shoemaker has facilitated my work considerably. Several recent major collections of hyperiids used extensively in this study and now deposited in the Division of Crustacea are from the following:

CalCOFI Cruises 1, 5, 9, 20, off the Pacific coast of the United States from the latitude of the Columbia River to that of Punta Eugenia in middle Baja California, made available to me by Dr. Martin W. Johnson, Scripps Institution of Oceanography.

Cruises of the University of Washington R/V *Brown Bear* in the northeastern Pacific, sent to me by Dr. William I. Aron.

Cruises 12, 13, 14 of R/V *Ombango* in the Gulf of Guinea, sent to me by Dr. Alain Crosnier, Office de le Recherche Scientifique et Technique Outre Mer (ORSTOM) Republique du Congo.

Collections of Hyperiidae by ships participating in the International Indian Ocean Expedition, 1962–65 (IIOE), sorted from plankton samples and sent to me by Mr. Chandrasekharan Nair, Indian Ocean Biological Centre.

I am most grateful to the persons listed above, as well as to the following, who have made it possible for me to examine specimens from their museums: Drs. R. W. Ingle and Roger Lincoln, British Museum (Natural History); Dr. H.-E. Gruner, Zoologisches Museum, Berlin; Dr. Charlotte Holmquist, Naturhistoriska Riksmuseet, Stockholm; Dr. Torben Wolff, Universitets Zoologiske Museum, Copenhagen.

ZOOGEOGRAPHY.—The above collections have enabled me to extend the known distribution of a number of species and to give some idea of the overall pattern of distribution of other species. The principal aim of this study, however, has been to improve our understanding of the taxonomy of the Hyperiidae, and the comments on species distribution will perhaps be of most service in indicating the gross inadequacy of our current knowledge of the distribution of pelagic amphipods. For some of the species occurring in the CalCOFI area, I have tentatively extrapolated from distributions there to overall Pacific distribution patterns found by Brinton (1962) to be characteristic of species of euphausiids.

TAXONOMICALLY USEFUL CHARACTERS.—To assist the reader, a diagram of a typical ♂ hyperiid, with the parts labeled, is given in Figure 1.

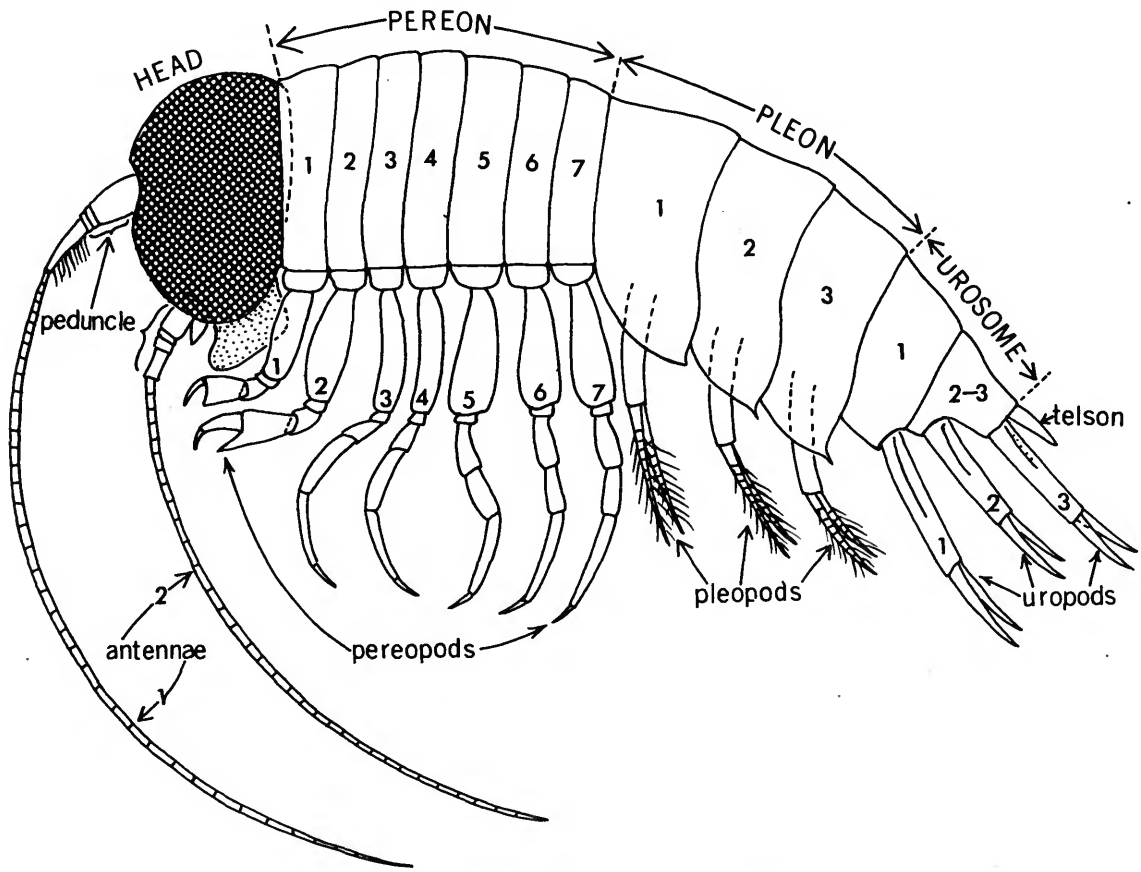


FIGURE 1.—Diagram of a ♂ hyperiid amphipod.

The following abbreviations are used throughout this paper:

A1, A2 = antenna 1 and 2
Md = mandible
Mx1, Mx2 = maxilla 1 and 2
Mxp = maxilliped
P1–P7 = pereopods 1–7
s1–s7 = segments 1 (coxa) to 7 (dactyl) of pereopods
Up1–Up3 = uropods 1–3

In arranging the species of *Hyperia*, Bovallius (1889) separated them initially according to the degree of fusion of the pereonites. His scheme, which was followed by subsequent workers, remains basically valid and is used herein. Bovallius believed that the amount of pereonite fusion in a species did not vary with sex or age. He reached this conclusion after examining young specimens of *Hyperia faberi* (=*Hyperietta vosseleri* in this paper), one of several species comprising the new genus *Hyperietta*, in which pereonites 1–2 are fused in both sexes and in all growth stages. As shown by Yang (1960) and Laval (1968), the amount of fusion varies with age and sex in certain other species (those included here in *Lestrigonus*). This variation will be discussed in the accounts of the individual species, but the following summary may be helpful:

TABLE 1.—*Fusion of Pereonites in the Family Hyperiidae*

None	♀ ♂ 1–2	♀ ♂ 1–3	♀ ♂ 1–5	♀ 1–3, ♂ 1–2	♀ 1–4, ♂ 1–2	♀ 1–5, ♂ 1–4
Hyperia	Bougisia	Hyperionyx	Themistella	Lestrigonus crucipes	L. latissima	L. bengalensis
Hyperiella	Hyperietta			L. schizogeneios	L. macrophthalma	
Hyperoche	Hyperioides				L. shoemakeri	
Iulopis	Phronimopsis					
Parathemisto						
Pegohyperia						

Other characters emphasized by previous workers are the form of the head, the armature of the pereopods and uropods, the size and shape of the telson, and to a limited extent the mouthparts, especially the presence or absence of the Md palp in the ♀. The ventral process of the head has received some attention, but it has not been emphasized that this process is actually the gland cone bearing the orifice of the antennal gland. In gammaridean amphipods it can be easily seen that the gland cone opens on the second of the 5 free peduncular segments of A2. In the Hyperiidae the gland cone and the segment on which it opens are fused to the surface of the head. In ♀ *Hyperia* and *Hyperiella* the gland cone segment is followed by 2 short free peduncular segments and a longer 1-merous flagellum (Figures 8*a*, 18*c*, 20*c*, 22*b*). In *Hyperioides* there is only 1 free peduncular segment (Figure 24*d*), and in *Lestrigonus, Hyperietta, Themistella,* and *Hyperionyx* the entire A2 is reduced to a single rudimentary free segment. Evidently the first 2 antennal segments are always fused with the head in ♀ Hyperiidae, but the pattern of fusion among the other segments is not known.

The size and shape of the gland cone are helpful taxonomic characters, especially in the genus *Lestrigonus*. The extent to which it overlaps or is separated by a gap from the buccal mass, when viewed laterally, is also useful.

Among the mouthparts I have found the Mxp to be especially valuable taxonomically. The outer lobes are separate and elongate in *Hyperia, Hyperiella,* and *Lestrigonus*; fused medially and rather broad in *Hyperietta*; separate and obovate in *Hyperionyx*. The inner lobe is greatly reduced in *Hyperietta* and *Themistella*. The most convincing evidence that *Lestrigonus fabrei* Milne Edwards is not the same species as that called *H. fabrei* by subsequent authors (=*H. vosseleri* Stebbing) lies in the entirely different form of the Mxp of the two species (compare Figures 27*c* and 41*f*). Curiously, this difference has not been pointed out previously, not even by Stebbing, who established *H. vosseleri* because he thought it too small to fit into Milne Edwards' species.

The armature of the dactyls and distal margin of the propus of P5–7 offer characters of generic significance. The propal margin may be produced into a spine (*Lestrigonus;* Figures 29*e*; 33*k,l*; 35*p*,

r; 36*k*) or a spinulose lobe (*Hyperietta*; Figures 44*h*; 47*d*, *e*) that overlaps the dactyl medially; in *Lestrigonus crucipes* (Figure 31*a*) the dentate spine immediately identifies the species. The presence or absence of spinules on the proximal part of the occluding margin of the dactyl is also a dependable character.

Family HYPERIIDAE Dana, 1852

Head usually globular; eyes almost always occupying most of lateral surface of head. A1–2 short in ♀, with 1–segmented flagellum; long in ♂, with slender, multisegmented flagellum. Md palp present in ♂, often absent in ♀. Outer lobes of Mxp free (most genera), or fused medially (*Hyperietta*). P1 simple, subchelate, or chelate; P2 chelate. P3–4 similar, sometimes prehensile. P5–7 similar, sometimes elongate, usually not prehensile. Gills on pereonites 2–6. Urosomites 2–3 fused. Up 1–3 with 2 rami. Type genus: *Hyperia* Latreille.

Sexual dimorphism is marked in the Hyperiidae, and at one time males of the genus *Hyperia* were placed in a separate genus, *Lestrigonus* Milne Edwards. In addition to the differences in A1–2, the female has a shorter and plumper body. The male body is more elongate, owing to the greater development of the pleon and pleopods, and the male is obviously the more active sex. Although nothing is known about reproductive behavior in these amphipods, the greater development of sensory and locomotor structures in the male indicates that he actively seeks out the female. The great preponderance of males in collections made under a light at night supports this proposition.

Key to Genera of the Family Hyperiidae

1. Pereonites all separate. Coxae separated from pereonites by sutures 2
   At least pereonites 1–2 fused. Coxae fused with pereonites (except in *Bougisia*) 7
2. Eyes without facets. Head produced anteriorly into acute process between A1 and A2 ..... ***Pegohyperia*** Barnard
   Eyes normal, with facets. Head not produced between A1 and A2 3
3. Anterior pereonites raised into transverse folds. Body covered with fine pubescence ..... ***Iulopis*** Bovallius
   Pereonites not raised into folds. Body not covered with fine pubescence 4
4. P1–2, carpal process laterally compressed, knife-shaped, without spines ***Hyperoche*** Bovallius
   P1–2, carpal process spoon-shaped, with somewhat concave center and raised margins armed with spines 5
5. P3–4 prehensile, dilated s5 closing against s6. ..... ***Parathemisto*** Boeck
   P3–4, s5 not dilated 6
6. P5 or P5–6 longer than P3–4 ..... II. ***Hyperiella*** Bovallius
   P3–4 longer than P5–6 ..... I. ***Hyperia*** Latreille
7. Eye small. Head produced anteriorly into acute process between A1 and A2. Coxae distinct ..... ***Bougisia*** Laval
   Eye covering most of head surface. Head not produced between A1 and A2. Coxae fused with pereonites 8
8. First 2 pereonites fused in adult ♂ and ♀ 11
   First 3, 4, or 5 pereonites fused in adult ♀; first 2, 3, or 4 pereonites fused in adult ♂ 9
9. P5–7 subequal; P6 only slightly longer than P5 and P7. Telson of moderate size ..... IV. ***Lestrigonus*** Milne Edwards
   P5 much shorter or distinctly longer than P6–7. Telson very short 10
10. Pereonites 1–3 fused. P5 much shorter than P6–7. ..... VII. ***Hyperionyx,*** new genus
    Pereonites 1–5 fused. P5 much longer than P6–7 ..... VI. ***Themistella*** Bovallius
11. P2 chelate; s7 closing against process of robust s6; P3–7 prehensile ..... ***Phronimopsis*** Claus
    P2 chelate, s6 closing against process of s5. P3–7 nonprehensile 12
12. ♀ A2 moderately long, shape sinuous in profile. Md incisor with serrate apex. Mxp with well-developed inner lobe. Exopods of Up1–3 with notched lateral margins ..... III. ***Hyperioides*** Chevreux
    ♀ A2 rudimentary. Md incisor with smooth apex. Mxp with rudimentary inner lobe. Exopods of Up1–3 without notches ..... V. ***Hyperietta,*** new genus

I. *Hyperia* Latreille, in Desmarest, 1823

DIAGNOSIS.—Large species, 10–30 mm in length. Head deeper than long. Pereon more or less dilated in ♀; all pereonites free. Coxae not fused to pereonites. A1 peduncle 3-merous; ♀ flagellum 1-merous. A2 peduncle 3-merous; 1st segment fused with gland cone. Md with serrate molar; palp present in both sexes. Mxl, outer lobe with 5 apical spines; palp with robust spine at mediodistal corner. Inner lobe of Mxp well developed, usually with 2 terminal spines. P1 subchelate or barely chelate, carpal process only slightly developed. P2 chelate; carpal process spoon-shaped, bearing spines along edges of spoon. S5–6 of P1–2 with many spines. P5–7 shorter than P3–4. Inner ramus of ♂ Up3 broad.

DERIVATION OF NAME.—From Hyperia, a fountain at Pherae in Thessaly. Gender feminine.

TYPE-SPECIES.—By objective synonymy, *Cancer medusarum* O. F. Müller, 1776. In his original diagnosis of *Hyperia,* Latreille (1823) included a single species, *H. sueurii* Latreille, n. sp., based on his figures of *Phronima* published a few years earlier (Latreille, 1818; pl. 328: figs. 17–18). These figures were copies of much earlier illustrations by Størm (1762, pl. 1: figs. 12–13) of his nonbinominal species "Pulex cancriformis antennis brevissimus, corpore latiore." Since Müller's *Cancer medusarum* is also based entirely on Størm's animal, it is a senior objective synonym of *Hyperia sueurii* and must be cited as the type-species of *Hyperia.*

Species of *Hyperia* spend at least part of their lives in association with scyphomedusans (Holloway, 1947; Dahl, 1959a, 1959b; Bowman, Meyers, and Hicks 1963; Metz, 1967). They inhabit cool water, living either at high latitudes or at depths where cool water occurs in low latitudes.

The status of several of the nominal species of *Hyperia* (as restricted above) has remained unsettled right up to the present. There has been general agreement that *H. latreillei* Milne Edwards and *H. hystrix* Bovallius are junior synonyms of *H. galba* Montagu and *H. medusarum* (Müller) respectively, but beyond this opinions have varied widely. *H. gaudichaudii* Milne Edwards has been considered a junior synonym of *H. galba* by some authors (Walker, 1904, 1907; Stephensen, 1924; Barnard, 1930, 1932; Vinogradov, 1956); others have recognized it as a distinct species (Stebbing, 1888; Bovallius, 1889; Walker, 1903; Chilton, 1912; Barnard, 1916). *H. spinigera* has been synonymized with *H. galba* (Stephensen, 1924; Reid, 1955; Hurley, 1960a), and *H. antarctica* with *H. galba* (Vinogradov, 1956) and *H. spinigera* (Barnard, 1932). Both are recognizable species, in my opinion.

Key to the Species of *Hyperia*

1. Posterior margin of s5–6 of P3–4 completely unarmed, even when viewed with high magnification ..... 5. ***H. antarctica***
   Posterior margin of s5–6 of P3–4 armed with setae which may be very short or as long as width of segment and which may be very closely shaped or widely scattered 2
2. Setae on posterior margins of s5–6 of P3–4 uniformly short and closely spaced. Posterior margin of pleonite 3 very convex ..... 6. ***H. spinigera***
   Setae on posterior margins of s5–6 of P3–4 longer and not uniform in length, less numerous and more scattered, sometimes missing from s6 3
3. Up3 protopod less than half as wide as long ..... 7. ***H. leptura***
   Up3 protopod half or more than half as wide as long 4
4. Coxa of P4 pointed and projecting laterad in adult. Limited to Antarctic (including South Georgia) ..... 4. ***H. macrocephala***
   Coxa of P4 not pointed or projecting laterad in adult. Not limited to Antarctic 5
5. Up3 endopod distinctly more than half as wide as long ..... 8. ***H. crassa***
   Up3 endopod half or less than half as wide as long 6
6. Posterior margin of s6 of P1–2 not overlapped by spines ..... 2. ***H. galba***
   Posterior margin of s6 of P1–2 overlapped by spines 7
7. Spines on distal part of s6 of P1–2 reaching or extending beyond apex of s7 ..... 1. ***H. medusarum, medusarum*** form
   These spines not reaching apex of s7 8
8. Length 10–15 mm. North Pacific ..... 1. ***H. medusarum, hystrix*** form
   Length more than 20 mm. South Atlantic and Pacific ..... 3. ***H. gaudichaudii***

1. *Hyperia medusarum* (O.F. Müller)

FIGURES 2–6

Cancer medusarum O. F. Müller, 1776:196.

Hyperia medusarum (O. F. Müller).—Murdock, 1885:143.—Bovallius, 1887b:16; 1889:147–159, pl. 9: figs. 1–21 [literature, synonymy].—Holmes, 1908:490.—Stephenson, 1923:15–17, chart 2 [synonymy, distribution]; 1924:80–81.—Dunbar, 1942:37; 1954:782–783; 1963:3 [distribution].—Bousfield, 1951;138–139; 1956:144.—Shoemaker, 1955:71–72.—Vinogradov, 1956:210–211.—Oldevig, 1959:125.

Hyperia latreillei H. Milne Edwards, 1830:388, pl. 11: figs. 1–7.—Bovallius, 1889:164–175, pl. 9: figs. 31–43, pl. 10: figs. 1–17.

Hyperia hystrix Bovallius, 1889:159–163, pl. 9: figs. 22–30.

Hyperia galba (Montagu).—Brusca, 1967a:388; 1967b:542–543 [misidentification].

DERIVATION OF NAME.—Not specifically stated, but presumably refers to association of species with scyphomedusae reported by Strøm (1762).

TYPE-LOCALITY.—Søndmør, Norway.

DIAGNOSIS.—Head length (lateral view) subequal to length of pereonites 1–2 combined. Interantennal lobe prominent (*medusarum* form) to moderate (*hystrix* form). Female A1 flagellum falcate; A2 flagellum very slender. Relative length of segments of Md palp, 1:1.7:2.1; segment 2 gently arched; segment 3 nearly straight. Outer lobe of Mxp much longer than inner lobe; seta on anterior surface of inner lobe long, numerous, and dense. S6 of P1 and P2 with many spines on medial and lateral surfaces, more numerous and longer in older and larger specimens. In *medusarum* form (Figures 4*c,d,f,g*) some spines reach beyond apex of s7; in *hystrix* form (Figures 4*a,b,e*) spines are shorter and dactyl is relatively longer. Posterior margins of s6 and s7 serrate; serrations present in *medusarum* form but obscured by spines and twisting of segment, hence not readily apparent and margin appears notched. S4–s5 of P3–P4 with series of long and short spines on anterior margin, long spines about equal in length to width of segment; spines more numerous in *medusarum* form (Figure 3*a*), less numerous in ♂, where they may be limited to s5. S6 minutely serrate, anterior margin usually unarmed, but may bear a few spines. P5–P7 subequal in length in ♀; in ♂ P5>P6=P7, usually unarmed except for cluster of spines at anterodistal corner of s2 of P7. Additional setae occasionally present, especially in young of *medusarum* form; variation in setation shown in Figure 3. Posterolateral corners of pleonal epimera ending in points, most pronounced in pleonite 3.

VARIATIONS.—This species, the most common along the Pacific coast of North America, is rather variable. Specimens from Pt. Barrow, Alaska, are about 20 mm in length and closely resemble USNM specimens from Frenchman's Bay, Maine. This is the typical *H. medusarum* described by Bovallius and Sars which occurs along the east coast of North America as far south as Connecticut and which is commonly found on scyphomedusae in Alaskan and Canadian Pacific waters. (Bowman, Meyers, and Hicks, 1963). Adults collected at Friday Harbor, Washington, in may cases from medusae, resemble those from Pt. Barrow, but are smaller and may have shorter spines on the gnathopods.

Specimens taken in plankton nets and midwater trawls between the latitudes of Vancouver Island and San Diego are smaller (9–15 mm), although fully mature, and the setal armature of the pereopods is less well developed. These specimens may belong to the form given specific status (*Hyperia hystrix*) by Bovallius (1889) and reduced to a synonym of *H. medusarum* by Stephensen (1924) after examining Bovallius' syntypes. After studying carefully the material in the Smithsonian Institution I am inclined to accept Stephensen's position, at least for the present. Although the majority of North Pacific specimens can be assigned with reasonable confidence to either *H. medusarum* (sensu stricto) or *H. hystrix*, the presence of seemingly intermediate specimens at Friday Harbor suggests the possibility of intergradation between the two forms. A definitive study based on more material than is available to me now is needed to resolve the question.

DISTRIBUTION.—The *hystrix* form was taken in limited numbers on the CalCOFI cruises, and Figure 6 shows its combined occurrences on Cruises 1, 5, and 9. Most of the positive stations were north of Point Conception, reflecting an affinity for cooler water. The *medusarum* form was not found in the CalCOFI samples, perhaps because of its closer association with scyphomedusae in coastal waters, or because it is limited to cooler water than that in the area of the CalCOFI cruises.

The distribution of *H. medusarum* in the Atlantic Ocean will be considered with the discussion of the distribution of *H. galba*.

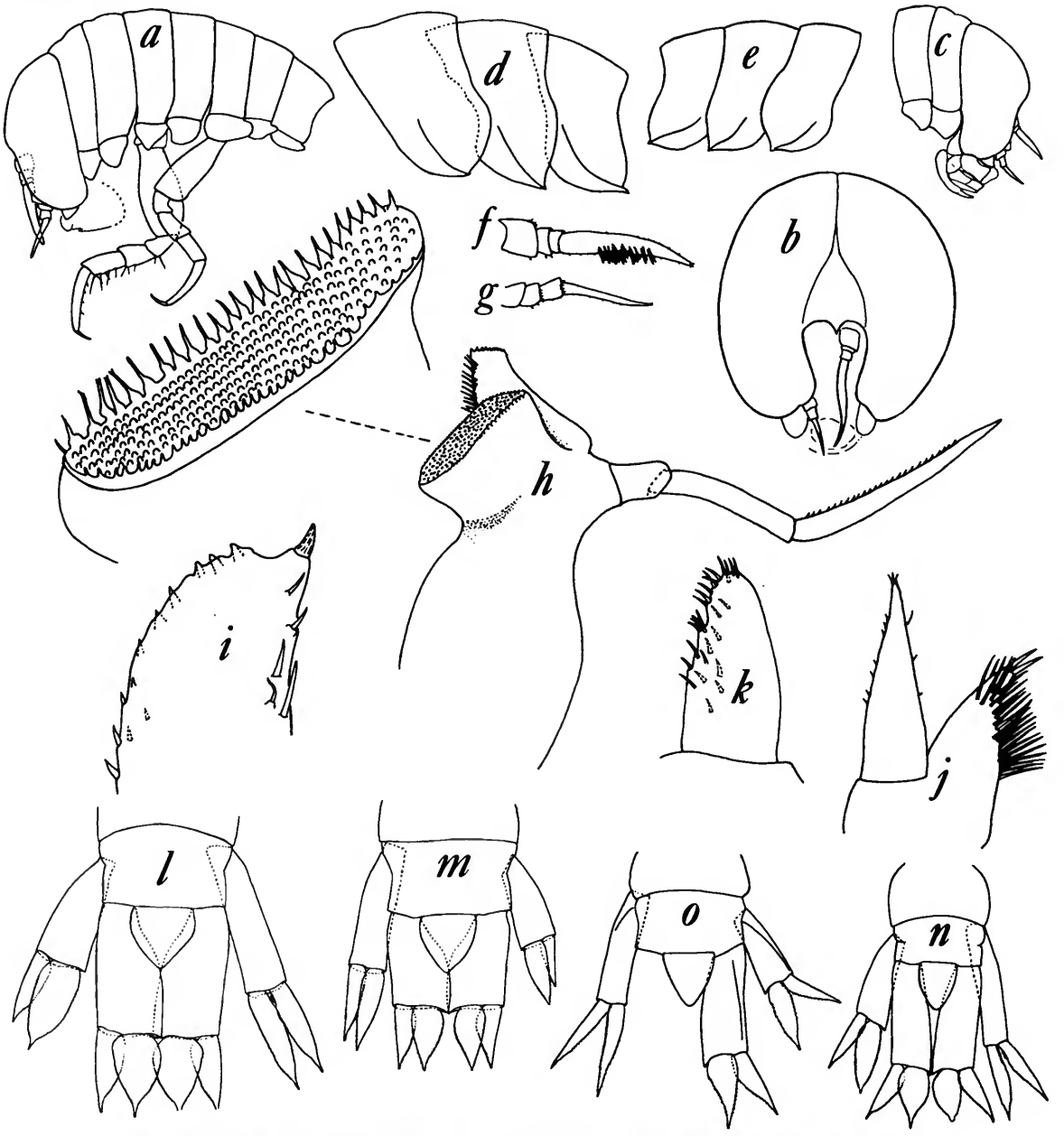


FIGURE 2.—*Hyperia medusarum* (a-g, ♀): *a*, *hystrix* form, Puget Sound, Washington; *b*, head, anterior, *hystrix* form, North Pacific (40°34'N, 147°55'W); *c*, head, *medusarum* form, Pt. Barrow, Alaska; *d*, pleon, *hystrix* form, off San Francisco; *e*, pleon, *medusarum* form, Pt. Barrow; *f-g*, A1–2, *hystrix* form, off San Francisco; *h*, Md, ♂ *hystrix* form, off San Francisco; *i*, Mx2 outer lobe, ♀ *hystrix* form, off San Francisco; *j*, Mxp, lateral, ♀ *medusarum* form, Pt. Barrow; *k*, outer lobe of same, posterior surface; *l–m*, urosomes of ♂ and ♀, Pt. Barrow; *n-o*, urosomes of ♂ and ♀, off San Francisco.

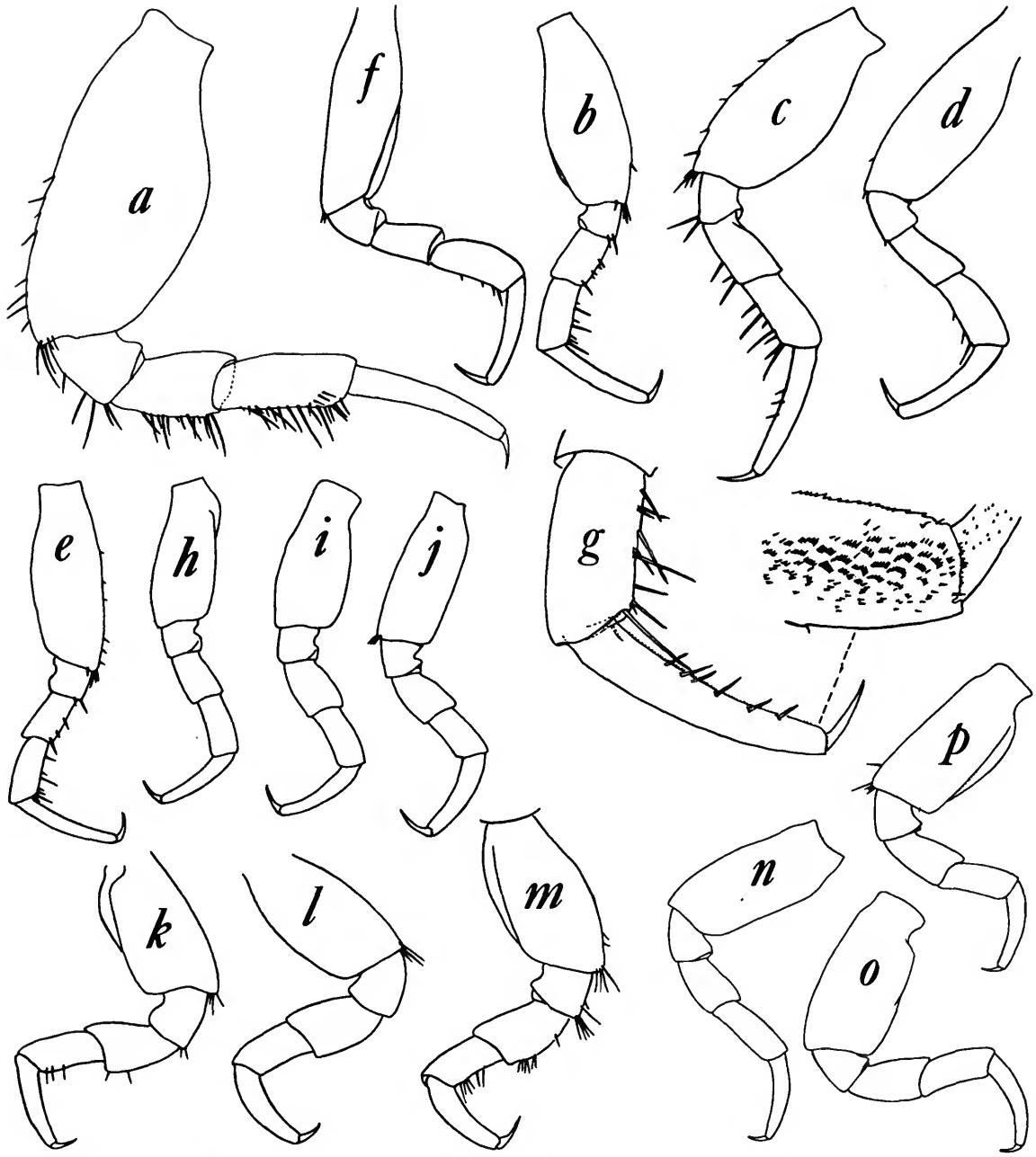


FIGURE 3.—*Hyperia medusarum*: *a*, P3, *medusarum* form ♀, Pt. Barrow, Alaska; *b*, P3, hystrix form ♀, off San Francisco; *c*, P3, *medusarum* form ♀, Puget Sound, Washington; *d*, P3, *medusarum* form ♂, Friday Harbor, Washington; *e*, P4, *hystrix form* ♀, off San Francisco; *f*, P4, *medusarum* form ♂, Friday Harbor; *g*, P4, medial surface, *medusarum* form ♀, Kuleet Bay, Vancouver Island; *h-j*, P5–7, *hystrix* form ♀, off San Francisco; *k-m*, P5–7, *hystrix* form ♀, Monterey Bay, California; *n-p*, P5–7, *medusarum* form, ♀, Pt. Barrow.

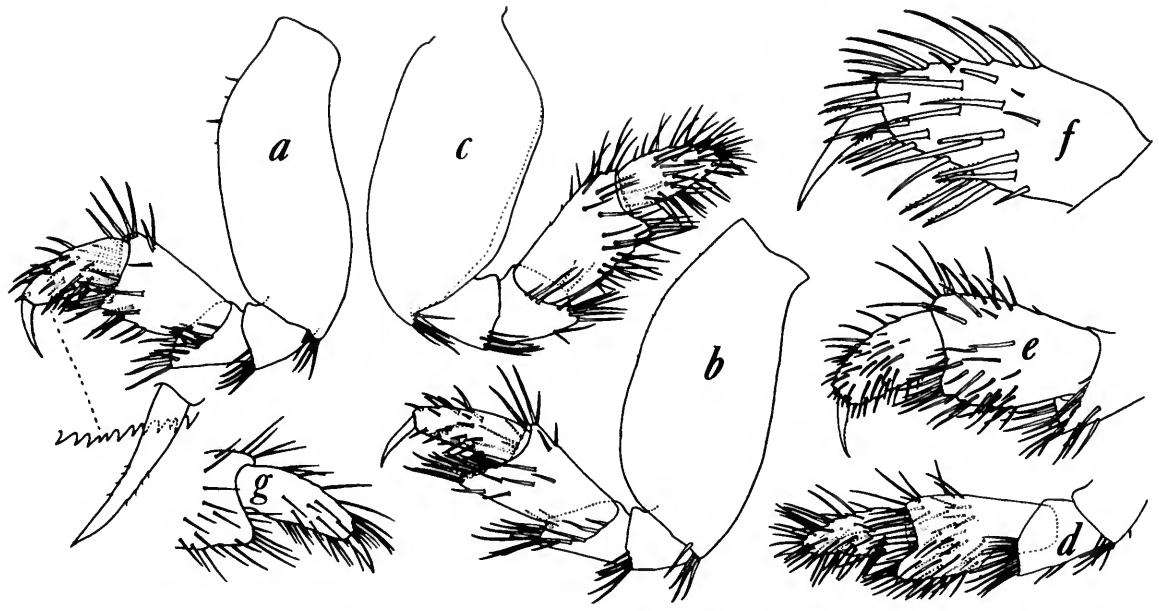


FIGURE 4.—*Hyperia medusarum* ♀: *a-b*, P1-2, *hystrix* form, off San Francisco; *c-d*, P1-2 *medusarum* form, Pt. Barrow, Alaska; *e*, P1, *hystrix* form, Monterey Bay, California; *f*, P1, *medusarum* form, Friday Harbor, Washington; *g*, P1, *medusarum* form, Frenchman's Bay, Maine.

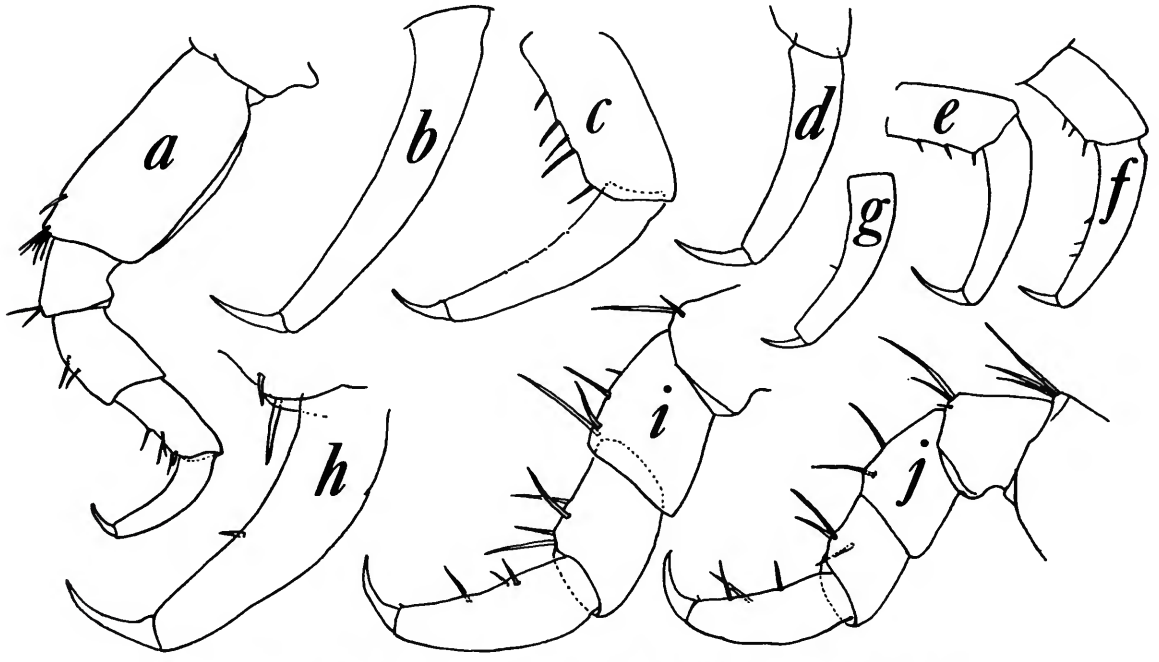


FIGURE 5.—*Hyperia medusarum*, P7: *a*, ♀, 16.5 mm, Monterey Bay, California; *b*, ♀, 21 mm, Bering Sea; *c*, juvenile, locality unknown; (*d-j*, from Auke Bay, Alaska) *d*, ♂ 14 mm; *e*, ♂ 10.5 mm; *f*, ♂ 9.5 mm; *g*, ♀ 10.0 mm; *h*, ♀ 7.5 mm; *i*, ♀ 5.0 mm; *j*, ♀ 3.7 mm.

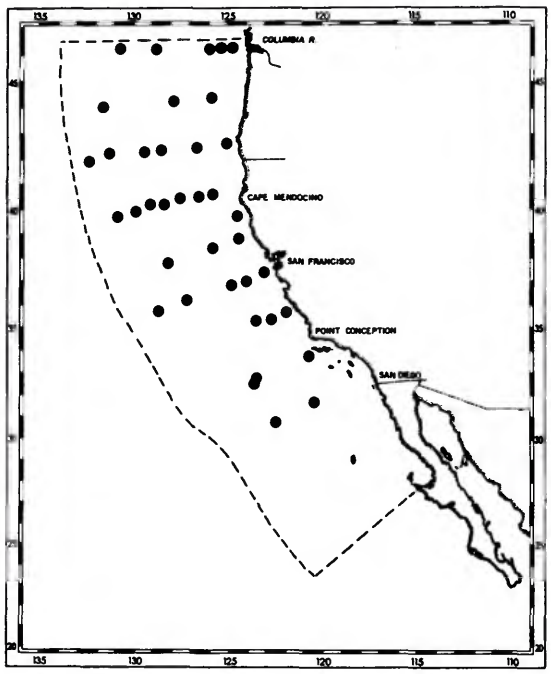


FIGURE 6.—Distribution of *Hyperia medusarum, hystrix* form, CalCOFI Cruises 1, 5, and 9 combined. Dashed line shows approximate limits of area sampled during cruises.

2. *Hyperia galba* (Montagu)

FIGURES 7, 15p

Cancer gammarus galba Montagu, 1813:4, pl. 2; fig. 2.

Hyperia galba (Montagu).—Guerin, 1825:771.—Bovallius, 1889:180–188, pl. 10: figs. 25–32 [literature, synonymy].—Stephensen, 1923:17–19, chart 3 [distribution]; 1924:81–83, chart 11; 1944:9.—Shoemaker, 1920:24E; 1926:3; 1955:71.—Chevreux and Fage, 1925:401–402, fig. 401.—Behning, 1939: 354.—Dunbar, 1942:37; 1954:783 [distribution]; 1963:3 [distribution].—Schellenberg, 1942:241–242, fig. 202.—Hollowday, 1946:passim [association with medusae].—Bousfield, 1951:138; 1956:144.—Certain, 1953 [chromosomes]; 1960 [chromosomes].—Alvarado, 1955:219–220.—el Maghraby and Perkins, 1956:494.—Vinogradov, 1956:210.—Dahl, 1959a; 1959b [evidence for ectoparasitism].—Oldevig, 1959:125.—Bowman, Meyers, and Hicks, 1963:140–146, figs. 1, 2e-h.—Bulycheva, 1964:317–318.—Metz, 1967 [association with medusae].

DERIVATION OF NAME.—Presumably from the Latin "galbus" [=yellow], referring to color of the animal.

TYPE-LOCALITY.—South coast of Devonshire, England.

DIAGNOSIS.—Head shorter than pereonites 1–2 combined; gland cone rather pointed. Posterolateral corner of pleonal epimeron 3 ending in small point; posterior margin moderately convex. Outer lobe of Mxp with a few short setae along inner margin; inner lobe about ¾ as long as outer lobe. Surfaces of s6 and s7 of P1–P2 with relatively few setae, those of s6 not extending past serrate posterior margin of base of dactyl. S5 of P3–P4 with a few short setae; posterior margin of s6 finely serrate, without setae. S2 of P5–P7 rather narrow; P5 without setae, P6–P7 with cluster of setae at distal corner of s2. Length of adult ♂ and ♀, 10–24 mm.

DISTRIBUTION.—As Bulycheva (1964) has pointed out, *Hyperia galba* is limited to the Arctic and the cooler regions of the northern Atlantic and Pacific Oceans. It has been reported from the South Atlantic, Antarctic, and Indian Oceans, but none of these records is supported by illustrations or descriptions. Some have resulted from the authors considering *H. spinigera,* a valid and distinct species, to be a junior synonym of *H. galba.* I list below the published records of *Hyperia galba* that I consider unacceptable. Bulycheva (1964) also considers the Antarctic and Indian Ocean records of *H. galba* to be erroneous.

Doubtful and Erroneous Records of *Hyperia galba*

Author	*Locality*
Calman, 1898	Puget Sound
Walker, 1904	Gulf of Manaar, Ceylon
Stewart, 1913	off Madeira
Spandl, 1924	northern Red Sea
Spandl, 1927	north of Cape Verde Is.
Barnard, 1930	west of Falkland Is.
	Melbourne Habor, Australia
Barnard, 1932	west of Falkland Is.
	South Africa
Ruffo, 1949	Chile?, Argentine?, Antarctic (locality uncertain)
Reid, 1955	Gulf of Guinea
Hurley, 1960a	Indian sector of Antarctic
Siegfried, 1963	Atlantic coast of southern Africa
Brusca, 1967a,b	southern California
White and Bone, 1972	South Orkney Is.

H. galba has a circumpolar distribution in the Arctic Ocean (Bulycheva, 1964). In the western Atlantic it extends south to Chesapeake Bay (Bowman, Myers, and Hicks, 1963), and in the eastern Atlantic it reaches the coasts of England, France,

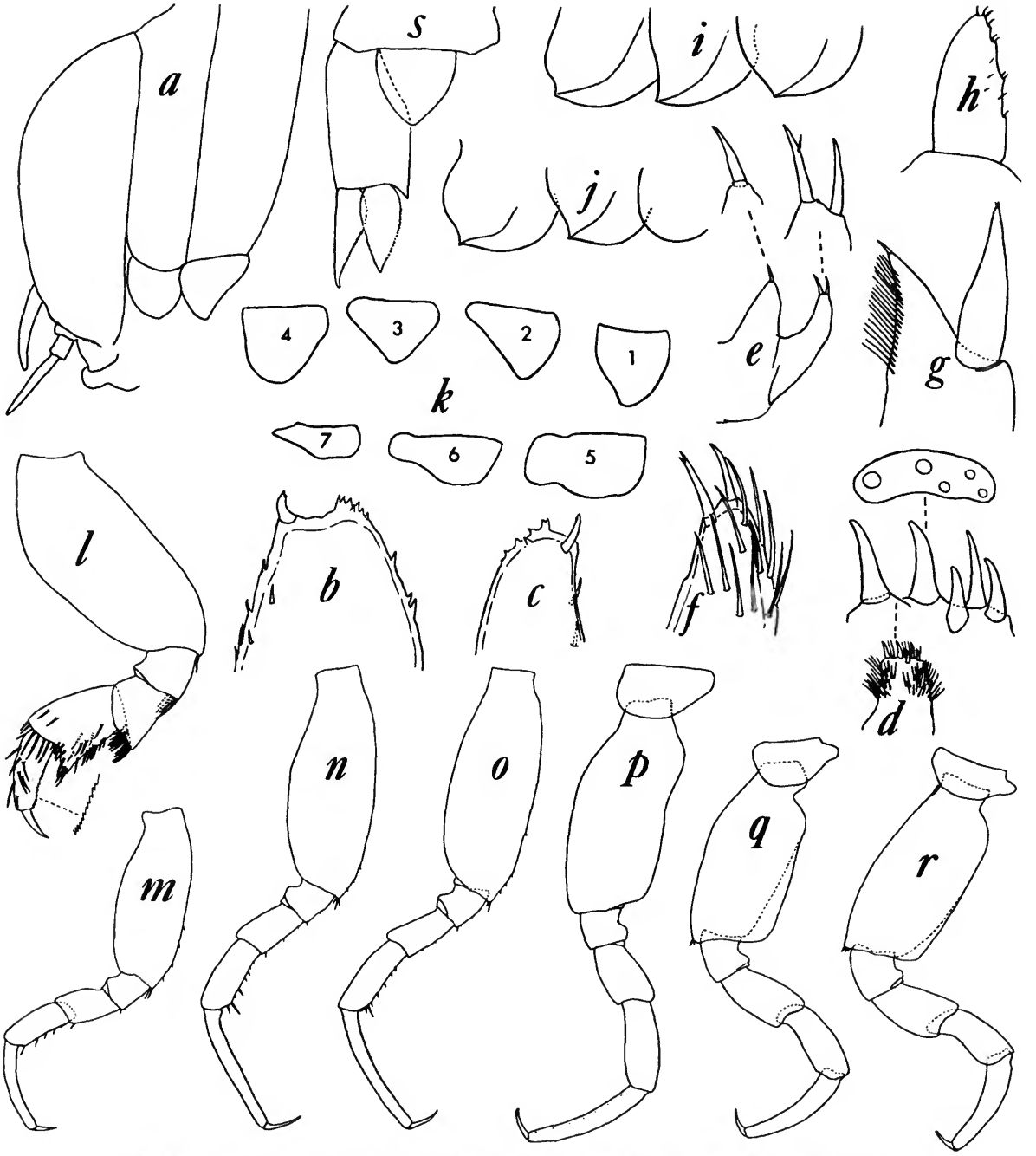


FIGURE 7.—*Hyperia galba* (*a-h*, ♀ from Newfoundland): *a*, anterior end, lateral; *b-c*, Mx1 outer lobe of adult and 4.9 mm juvenile; *d*, Mx1 inner lobe; *e*, Mx2, adult, setae omitted; *f*, Mx2 outer lobe, juvenile; *g*, Mxp lateral; *h*, Mxp outer lobe, posterior; (*i-j*, pleonal epimera) *i*, ♀ from Nova Scotia; *j*, ♂ from Long Island Sound; (*k-s*, from Ireland) *k*, coxae 1–7, ♀; *l*, ♀ P1, medial; *m*, ♀ P3; *n-r*, ♂ P3–7; *s*, telson and Up3.

and Spain (Stephensen, 1923, 1924; Alvarado, 1955). It is said to have been collected from numerous localities in the areas surrounding the Azores by Prince Albert Ier of Monaco (Chevreux, 1900, 1935; Pirlot, 1939); these identifications require confirmation, since they are at or beyond the southern boundary for this species. It is the only hyperiid occurring in the Baltic. It is apparently absent from the Mediterranean (Stephensen, 1924), although some authors (e.g., Chevreux and Fage, 1925; Spandl, 1927; Pirlot, 1929) include the Mediterranean within its range.

Records of *H. galba* from the Pacific are much fewer than those from the Atlantic. Derjavin (1927) recorded it from Avachinska Inlet (at Petropavlovsk) on the Kamchatka Peninsula. Behning (1939) reported it from the Bering, Okhotsk, and Japan Seas, without giving specific localities. Buycheva (1964) considers the Japan Sea record erroneous. Vinogradov (1956) found it in the western Bering Sea, the Gulf of Anadir, the Kamchatka region, and the waters of the Kurile-Kamchatka Trench. Yoo (1971) found it off Japan north of 37°50'N. None of these western Pacific records is supported by descriptions or illustrations.

In the eastern Pacific *H. galba* was reported from Puget Sound by Calman (1898), and from southern California by Brusca (1967a, 1967b), but it is likely that these authors actually had the *hystrix* form of *H. medusarum*. The USNM has specimens of *H. galba* from four localities near the Alaska Peninsula: Kodiak; Unalaska; St. George I., Pribilof Is.; and in the Bering Sea east of the Pribilof Is. (*Albatross* sta. 3540, 56°27'N, 166°08'W). I have not seen specimens of *H. galba* from elsewhere in the Pacific in spite of examing numerous specimens of *Hyperia* collected by towing nets and trawls and by removing them from medusae. Apparently it does not occur off the Pacific coast of Canada or the contiguous United States.

Compared with *H. medusarum, H. galba* is abundant in the Atlantic and scarce in the Pacific. The distribution of the two species in the Atlantic is considered below.

Comparison of Atlantic Distribution of *Hyperia medusarum* and *H. galba*

Both *H. galba* and *H. medusarum* are Arctic-Subarctic-Boreal species associated with scyphomedusae. Is there competition between the two species or is this avoided by niche differentiation? So little is known of the habits and ecological requirements of the two species that I can only summarize what I have gleaned from published works.

H. galba seems to be by far the more abundant species in the Atlantic. Stephensen (1924) reports that the *Thor* obtained 615 specimens of *H. galba* from 40 stations, mostly southwest of Ireland, and only 2 specimens of *H. medusarum* from 2 stations. The *Ingolf* (Stephensen, 1923) collected about 20 specimens of *H. galba* from 6 stations, mostly north of 60°N, but failed to collect *H. medusarum*. From plankton collections in Ungava Bay, Dunbar (1954) reported 12 specimens of *H. galba* from 4 stations and 2 specimens of *H. medusarum* from 2 stations. Collections in Belle Isle Strait, reported on by Bousfield (1951), yielded 13 specimens of *H. galba* from 4 stations and only 1 specimen of *H. medusarum*. Collecting from *Cyanea capillata,* Hicks obtained 120 *H. galba* and 1 *H. medusarum* in Narragansett Bay, and 57 *H. galba* and 3 *H. medusarum* in the Niantic River, Connecticut (Bowman, Meyers, and Hicks, 1963).

The host preferences of the two species are not known. Both have been found associated with *Aurelia, Chrysaora, Cyanea,* and *Rhizostoma*. In addition, *H. medusarum* has been taken from *Thaumantias* (Stephensen, 1923), and young individuals of *H. galba* may be found on the hydromedusan *Melicertidium octocostatum* (Schellenberg, 1942). Occasionally *H. galba* may be found on the ctenophore, *Beroe* (Stephensen, 1923; Schellenberg, 1942). Dales (1966) states that *H. medusarum* is associated with *Rhizostoma pulmo,* whereas *H. galba* occurs with *Rhizostoma octopus* and *Chrysaora hyoscella*. Dales does not document this statement nor say whether it is his own observation. Experimental studies of host preference might aid us to understand the differences between these two species of *Hyperia*.

Comparing the occurrence of the two species off the west coast of Ireland, Tattersall (1906) suggested that *H. medusarum* was a more distinctly oceanic form than *H. galba*. According to Schellenberg, *H. galba* penetrates farther into the Baltic, reaching Warnemünd, whereas *H. medusarum* only reaches the Great Belt (Store Baelt). Metz (1967) reports that *H. galba* is abundant in the Isefjord

Area of Denmark (S 17.6–21.8‰), but does not mention *H. medusarum*.

H. galba extends farther south in the Atlantic than *H. medusarum*, reaching at least to the latitude of the coast of Spain (Alvarado, 1955). According to Schellenberg (1942) *H. medusarum* does not penetrate the inner North Sea, and its absence from Chevreux and Fage's (1925) volume on the amphipods in the Faune de France series indicates that it does not occur on the Atlantic coast of France. In the eastern Atlantic the presence of *H. galba* and the absence of *H. medusarum* from Cheasapeake Bay (Bowman, Meyers, and Hicks, 1963) also suggests a tolerance for higher temperature in *H. galba*.

3. *Hyperia gaudichaudii* H. Milne Edwards

FIGURES 8–10

Hyperia gaudichaudii H. Milne Edwards, 1840:77.—Nicolet, 1849:245.—Bovallius, 1887b:16; 1889:175–179; pl. 10: figs. 18–24.—Stebbing, 1888:1394–1398, pl. 169; 1914:374.—Walker, 1903:40; 1907:7.—Chilton, 1912:513.—Barnard, 1916:25–286.—Dick, 1970:55–56.

Lestrigonus gaudichaudii.—Bate, 1862:289, pl. 48: fig. 3.

Hyperia galba (Montagu).—Barnard, 1930:411–412; 1932: 273.—Siegfried, 1963:8.—Hurley, 1969:33.

DERIVATION OF NAME.—Presumably after the French botanist Charles Gaudichaud-Beaupré, 1789–1854, who made important collections during his voyages on the *Uranis*, *L'Herminie*, and *La Bonite*.

DIAGNOSIS.—Very similar to *H. medusarum, hystrix* form, but generally larger (10-14 mm). Confined to the southern hemisphere in antiboreal and perhaps Antarctic zones.

RELATIONSHIPS.—Illustrations are given here of specimens from the west coast of southern Africa reported as *H. galba* by Siegfried (1963), sent to me by R. I. Dick, University of Cape Town. A few figures are also given of a female and a male from *Challenger* station 312 in the Straits of Magellan, loaned to me by R. W. Ingle, British Museum (Natural History). The similarity to the *hysterix* form of *H. medusarum* is obvious, and maintaining *H. gaudichaudii* as a separate species is not easily defended. My reasons for doing so are largely zoogeographical. Whereas *hystrix* has a boreal distribution, that of *gaudichaudii* is antiboreal, and there is no possibility of gene flow between them. Biantitropical species among epiplanktonic Crustacea are rare and are becoming rarer as their taxonomy is examined more closely. Of the few biantitropical hyperiids the best known example is *Parathemisto gaudichaudii*, whose distribution is reviewed in detail by Kane (1966). The vast majority of coldwater hyperiids, however, are confined to one hemisphere; consequently I prefer to give full specific status to *Hyperia gaudichaudii* rather than to maintain that *H. medusarum* is a biantitropical species.

DISTRIBUTION.—*H. gaudichaudii* is known to occur along the southern coasts of Africa, Australia, and South America (Figure 10). Walker's two records from the Ross Sea (1903, 1907) seem questionable since they are the only reported occurrences south of the Antarctic Convergence. I suspect that Walker's specimen's were immature *Hyperia macrocephala* in which the coxae of P4 had not yet developed the pointed and splayed form so characteristic of the adult of that species. Chilton's (1912) record from *Scotia* station 541 (37°41′N, 29°25′W) is also unacceptable; it lies well outside the range of *H. gaudichaudii* but within that of *H. galba* and may well refer to the latter species.

4. *Hyperia macrocephala* (Dana)

FIGURES 11, 12

Tauria macrocephala Dana, 1853:988–989.—Bovallius, 1885: 16–17; 1887b:19; 1889:81–82, figs. 1–4 [from Dana].—Chevreux, 1913:86 [in list].—Shoemaker, 1914:76.—Spandl, 1927: 156–158, fig. 3a-g.

Taura macrocephala.—Dana, 1855; pl. 68: fig. 2 [typographical error].

Hyperia macrocephala (Dana).—Bate, 1862:296, pl. 49: fig. 2 [from Dana].—Shoemaker, 1945a:291–293, fig. 2A-B.—Emison, 1968:202, fig. 11.

Hyperia galba (Montagu).—White and Bone, 1972: passim.

DERIVATION OF NAME.—From the Latin, meaning "large head."

TYPE-LOCALITY.—Antarctic Ocean, off Oates Coast (ca. 66°S, 157°E).

DIAGNOSIS.—Head about as long as pereonites 1–2 combined; gland cone rather short. Coxa of P4 of large mature specimens pointed, projecting laterally. Outer lobe of Mxp armed with short setae only; inner lobe shorter than outer, with dense covering of setae on anterior surface and 2 terminal spines. P1–2 with very spinose distal segments. P3–4 with numerous short setae on s5–6;

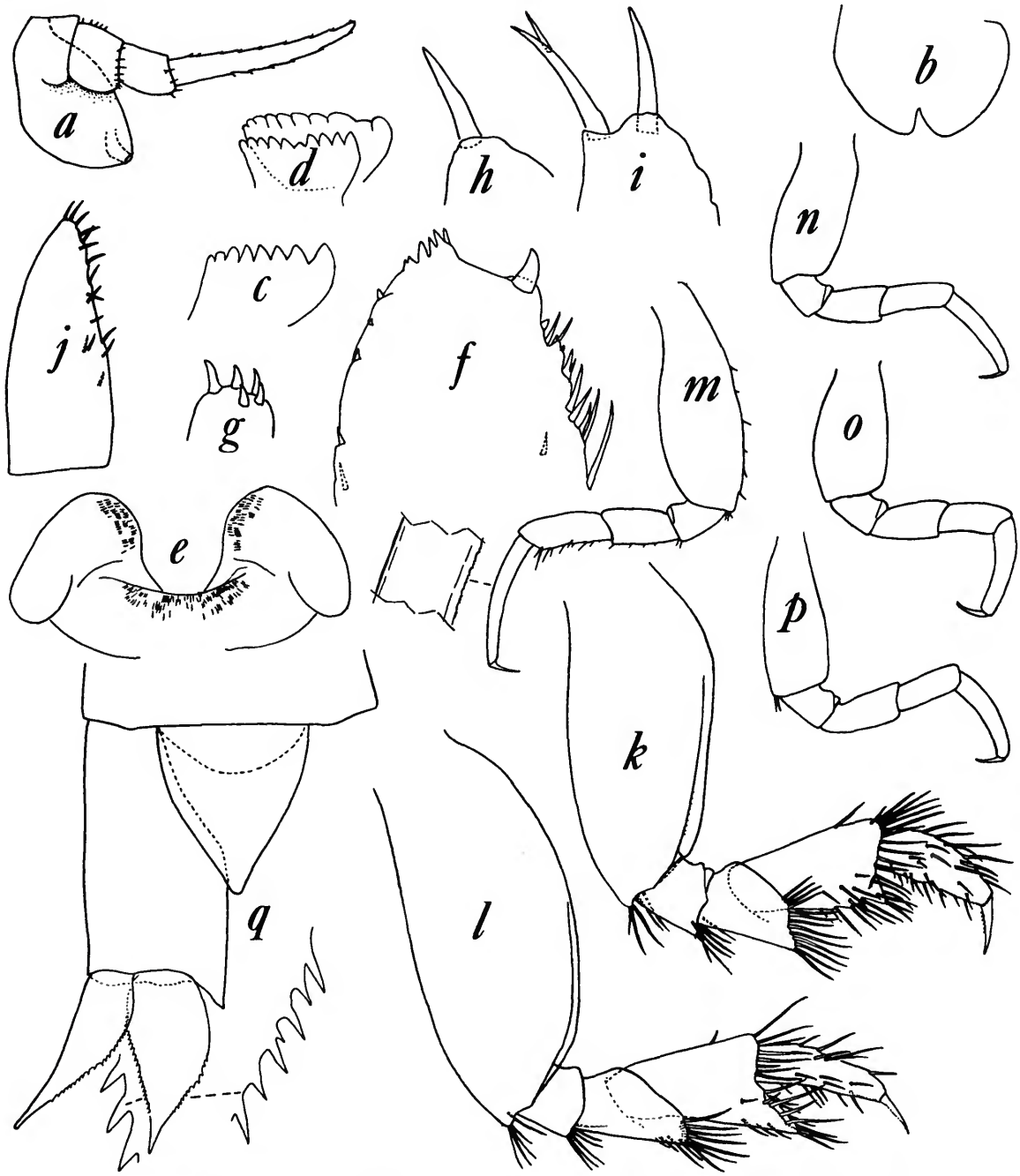


FIGURE 8.—*Hyperia gaudichaudii*, ♀ from west coast of southern Africa: *a*, A2, lateral; *b*, labrum; *c*, incisor of right Md; *d*, incisor and lacinia of left Md; *e*, labium; *f*, Mx1 outer lobe; *g*, Mx1 inner lobe; *h*, Mx2 inner lobe; *i*, Mx2 outer lobe; *j*, Mxp outer lobe; *k*, P1 medial; *l*, P2 medial; *m*, P3; *n-p*, P5–7; *q*, telson and Up3.

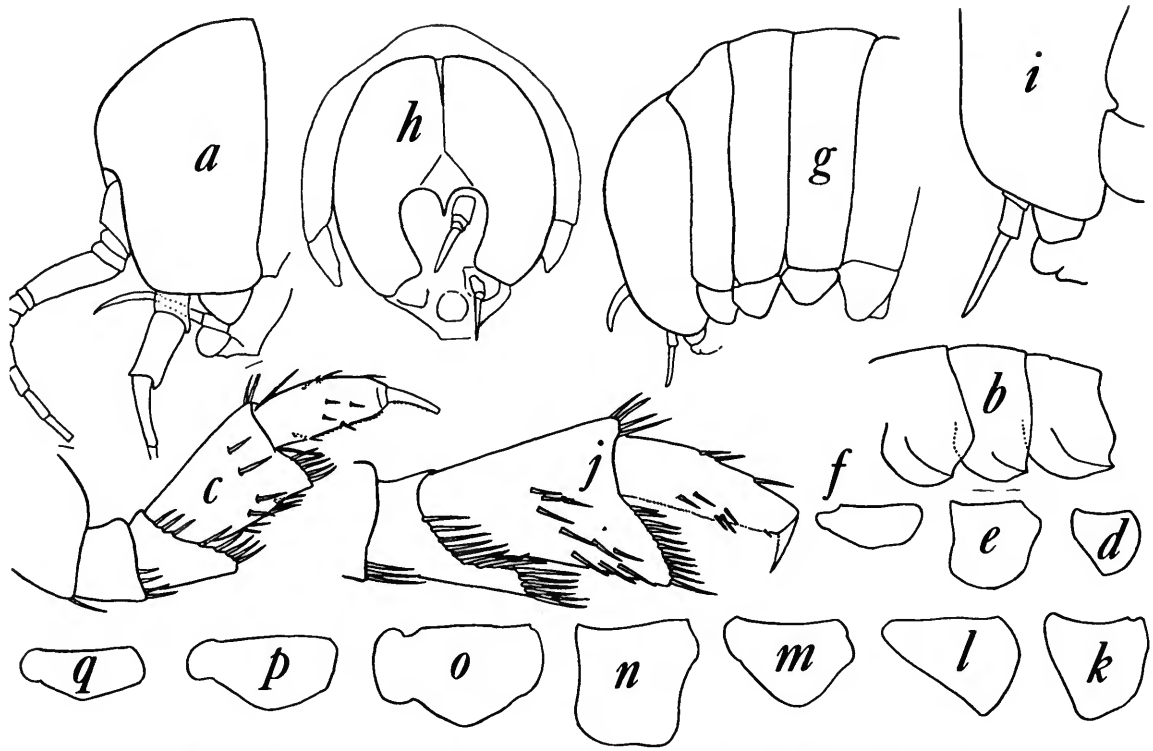
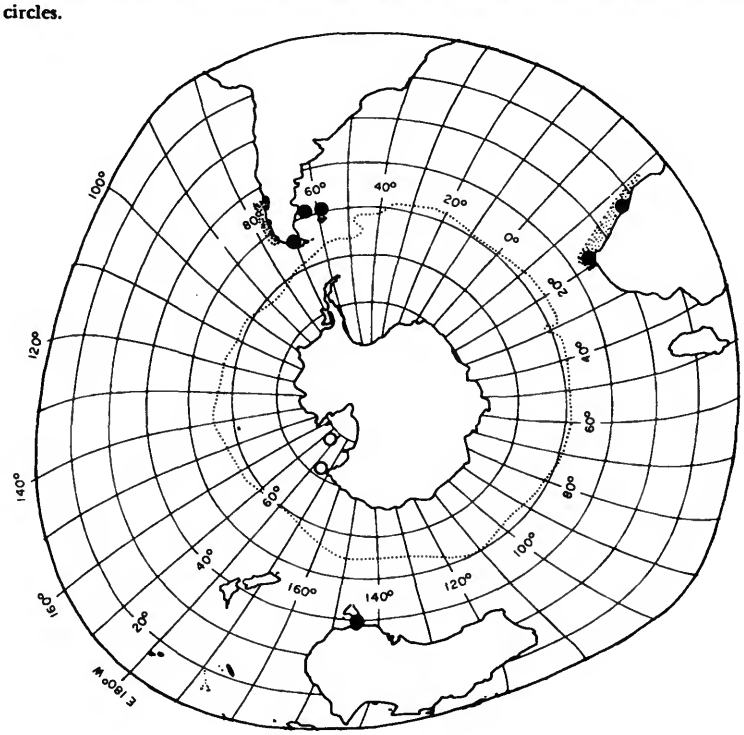


FIGURE 9.—*Hyperia gaudichaudii*, from *Challenger* station 312, Straits of Magellan (*a-f*, ♂): *a*, head, lateral; *b*, pleon, lateral; *c*, P1, lateral; *d*, P1 coxa; *e*, P4 coxa; *f*, P7 coxa; (*g-q*, ♀) *g*, anterior end, lateral; *h*, head, anterior; *i*, ventral part of head, lateral; *j*, P2, lateral; *k-q*, coxae of P1–7.

FIGURE 10.—Distribution records for *Hyperia gaudichaudii*. Stippling indicates areas where exact localities were not given. Walker's Ross Sea records, considered questionable, are indicated by open circles.



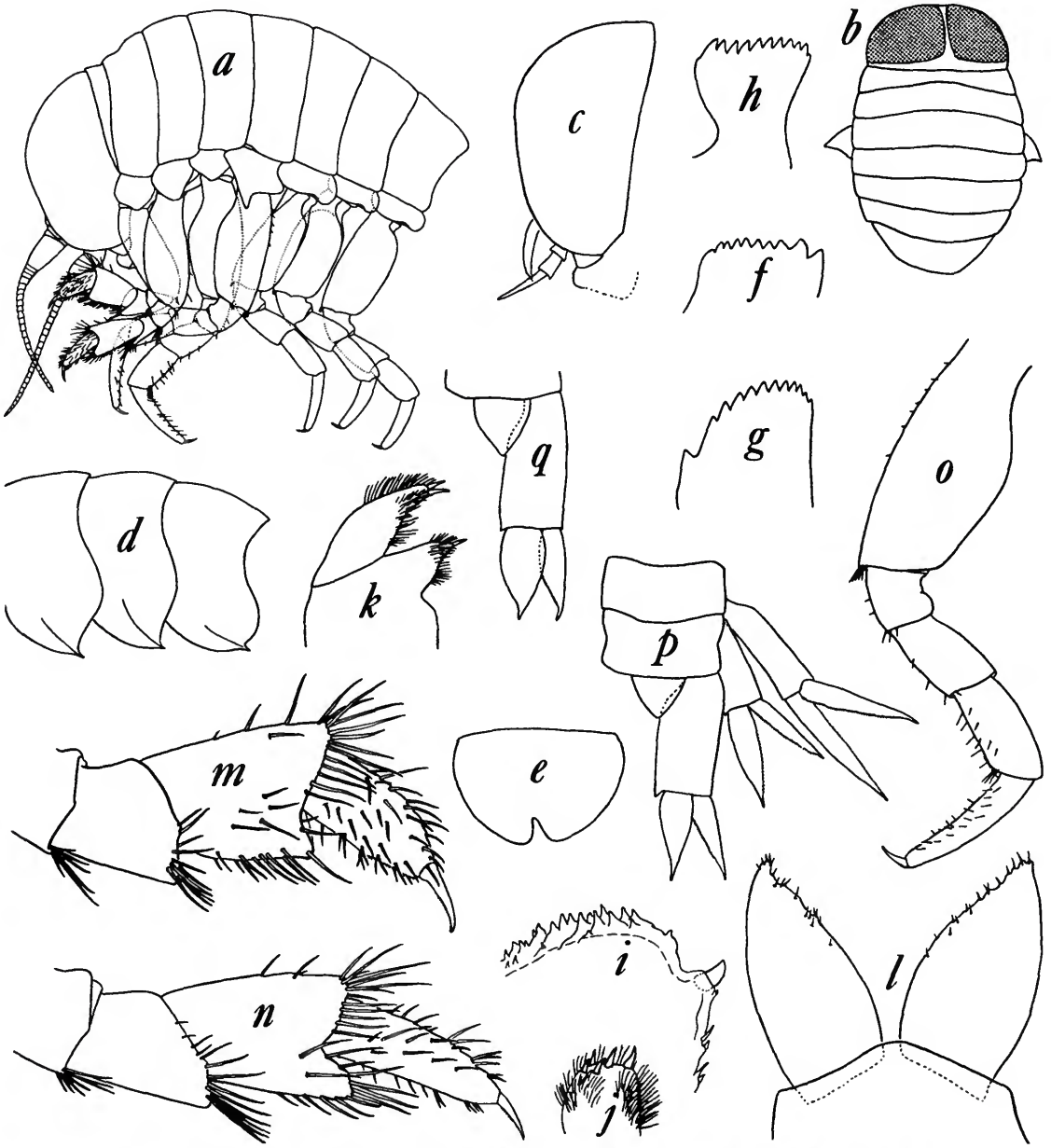


FIGURE 11.—*Hyperia macrocephala: a,* head and pereon, lateral, young ♂ (drawing by C. R. Shoemaker, 1945b, fig. 2A); *b,* ♀ head and pereon, dorsal; *c,* ♀ head; *d,* ♀ pleon; *e,* ♀ labrum; *f,* incisor of ♀ right Md; *g,* incisor of ♀ left Md; *h,* ♀ lacinia mobilis; *i,* ♀ Mxl outer lobe; *j,* ♀ Mxl inner lobe; *k,* ♀ Mx2; *l,* ♀ Mxp outer lobes; *m,* P1 medial, young ♂; *n,* P2 medial, young ♂; *o,* P3 medial, young ♂; *p,* ♀ urosome; *q,* ♂ telson and Up3.

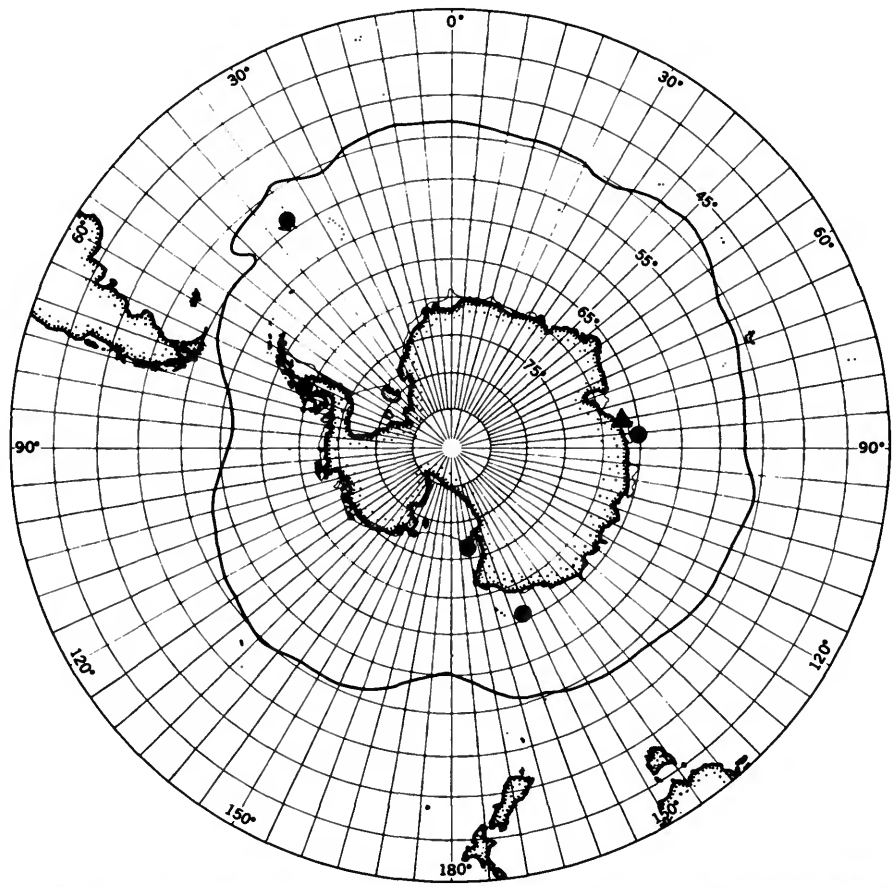


FIGURE 12.—*Hyperia macrocephala*, distribution records (circles). *Hyperia antarctica* Spandl, type-locality (triangle).

anterior margin of s6 and distal part of anterior margin of s5 minutely serrate. P5–7 naked except for cluster of setae at anterodistal corner of s2 of P6–7. Pleonites with sharply pointed posterolateral corners; posterior margin of epimera of pleonite 3 rather strongly convex. Uropods rather slender. Telson as long as width at base (♂) or slightly shorter (♀), about 0.4 as long as peduncle of Up3. Length up to 29 mm.

RELATIONSHIPS.—Mature individuals of this distinctive species, the largest of the genus, are easily recognized by the winglike coxa 4. Immature specimens have normal coxae. Thus far only 8 specimens have been reported, 7 from 3 localities adjacent to Antarctica and 1 from South Georgia. With the exception of Spandl's (1927) specimen, from the stomach of an Adélie penquin, all were collected from medusae.

DISTRIBUTION.—As a result of the increased biological investigations in the Antarctic in recent years, additional specimens of *H. macrocephala* have come to the Smithsonian Institution, all from the McMurdo Sound area of the Ross Sea. William Emison contributed 12 specimens collected from the stomachs of Adélie penguins (Emison, 1968). Carleton Ray donated two large collections from medusae, one containing 59 females and 42 males, the other consisting of 28 females and 21 males. The first collection also contained a female *Hyperiella dilatate* Stebbing.

The known distribution of *H. macrocephala* (Figure 12) shows that it occurs around the entire

Antarctic continent. Thus far the only record outside of Antarctic coastal waters is one from South Georgia (Shoemaker, 1914). From the large number, 101, found on a single medusa by Ray, it appears that *H. macrocephala* may be rather abundant in Antarctic waters. Curiously, it is not included by Hurley (1969) in his distribution maps of Antarctic hyperiids, although it, rather than *H. antarctica,* despite the latter's specific name, appears to be the most common species of *Hyperia* in Antarctic waters. *H. antarctica* lives at greater depths and unlike *H. macrocephala* is not restricted to the Antarctic but has a nearly worldwide distribution.

In my opinion, Antarctic records of species of *Hyperia* other than *H. macrocephala* and *H. antarctica* are highly questionable.

5. *Hyperia antarctica* Spandl

FIGURES 12–14

Hyperia antarctica Spandl, 1927:153–155, fig. 2a-g.—Hurley, 1969:33.

Hyperia spinigera Bovallius.—Shoemaker, 1945:238 [females only; misidentification].

DERIVATION OF NAME.—Not stated, but obviously refers to type-locality.

TYPE-LOCALITY.—Antarctic Ocean, off Leopold and Astrid Coast (68°18′S, 80°27′E).

DIAGNOSIS.—Female. General appearance of body more narrow and elongate than in ♀ of other species of *Hyperia,* and more nearly resembles ♂ of these species. Pereonites relatively long. Posterior corners of pleonite 1 rounded, of pleonites 2–3 with small points. A1 flagellum digitiform, in contrast with usual slender shape in *Hyperia,* with cluster of apical setae and moderate number of esthetes on concave medial surface. Md with shorter marginal setae on molar than in *H. medusarum;* teeth of incisor limited to molar half; segments of palp subequal, distal segment markedly falcate. Inner margin of outer lobe of Mxp with a number of short setae and a long seta inserted at about ⅓ the distance from base; inner lobe longer than outer lobe, strongly recurved, with 2 robust spines at apex. Posterior parts of distal margins of s2–4 of P1–2 with long setae; distal margin of s6 of P1 rounded, not produced into carpal process, with very long setae, some nearly as long as s6; posterior margin of s6 with long setae, notched where setae are inserted, but not serrate. S5 of P2 with very short setose carpal process, medial setae very long; posterior margin of S6 notched but not serrate, with long setae. P3–4 similar, unarmed except P3 has cluster of setae at posterior distal corner of s2 and 1–2 setae at posterior distal corner of s3. P5–7 robust; unarmed except for cluster of setae at anterior distal corner of s2 in P7; in length P7>P6=P5. Uropods very similar to those of *H. medusarum.* Telson slightly longer than width at base, slightly more than half as long as peduncle of Up3. Length of adult 12–28 mm.

MALE.—The male of *H. antarctica* has not been reported previously. The immature male from off Vancouver Island is very similar to the female. Except for A1 and A2 there is no obvious difference in the male at this stage of maturity.

RELATIONSHIPS.—K. Barnard (1932) considered *H. antarctica* to be identical with *H. spinigera,* but there are many significant differences between the two species: e.g., the proportions of the Md palp segments, the length of the Mxp inner lobe, the armature of P1–4, and the relative width of the Up3 inner ramus.

Because of the incompleteness of Spandl's account (he described and illustrated only the pereopods) I was at first uncertain of the correctness of my identification of *H. antarctica.* Fortunately I was able to compare my specimens with the holotype, borrowed from the Zoologisches Museum der Humboldt Universität, Berlin, through the kindness of Dr. H.-E. Gruner, and to confirm their identity. Spandl gave the length of the holotype as about 10 mm, but this measurement was apparently only approximate and made with the pleon bent under the pereon. With the pleon unfolded and held in a naturally curved position the holotype measures about 24 mm. It is a fully mature ♀ with well-developed oostegites.

Of the specimens recorded as *Hyperia spinigera* from the Bermuda area by Shoemaker (1945b), three are in the Smithsonian Institution. One of these, a 14.5 mm ♀ with fully developed oostegites, collected in a net towed at 1463 m, is a typical specimen of *H. antarctica.*

DISTRIBUTION.—The only published record for *H. antarctica* is the original one of Spandl (1927) from a 200 m vertical tow in the Indian Ocean sector of the Antarctic (68°18′S, 80°27′E; see Figure

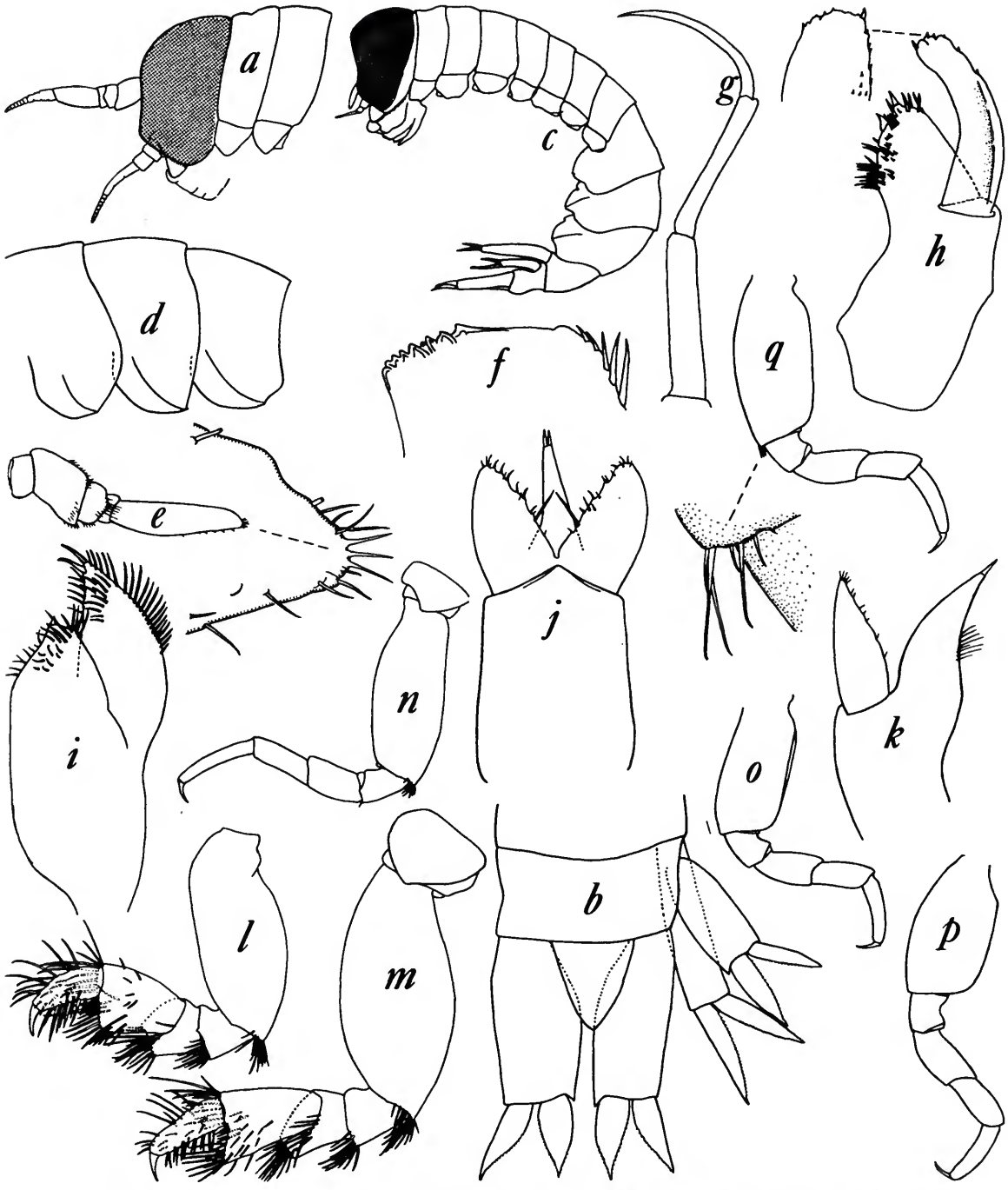


FIGURE 13.—*Hyperia antarctica* (*a-b*, ♂): *a*, anterior end, lateral; *b*, urosome; (*c-q*, ♀) *c*, lateral view; *d*, pleon lateral; *e*, A1 lateral; *f*, incisor of right Md; *g*, Md palp; *h*, Mxl; *i*, Mx2; *j*, Mxp, posterior; *k*, Mxp, lateral; *l*, P1; *m*, P2; *n*, P3; *o*, P5; *p*, P6; *q*, P7.

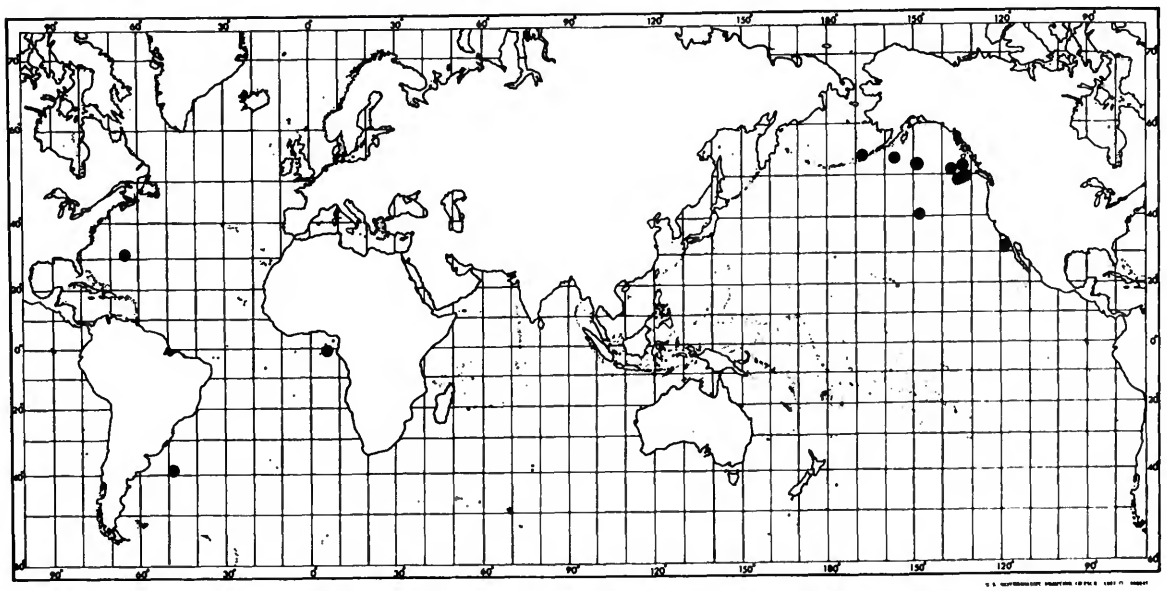


FIGURE 14.—*Hyperia antarctica*, distribution records. The type-locality is shown on Figure 12.

12). I have found it in samples from 14 additional widely scattered localities shown in Figure 14. The depths of sampling ranged from 200 m to about 2000 m with most of the tows being made at 400–600 m. Even from such limited data it is evident that *H. antarctica* has a very wide distribution at mesopelagic depths. Presumably it is associated with medusae, like other species of *Hyperia*, but there is no hint at present as to what medusae may be involved.

6. *Hyperia spinigera* Bovallius

FIGURES 15–16

Hyperia spinigera Bovallius, 1889:191–194, pl. 10: figs. 33–39.—Vosseler, 1901:58.—Tattersall, 1906:22.—Barnard, 1932: 273–274, fig. 160.—Thorsteinson, 1941:87–88, pl. 8: figs. 79–82.—Dunbar, 1942:37 [*spingera!*]; 1963:3.—Shoemaker, 1945a:238, text-fig. 35A-D[♂ specimens only].—Hurley, 1955:140–143, figs. 83–95; [?] 1965:15.—Oldevig, 1959:125.—Brusca, 1967a:388; 1967b:452.

Hyperia galba (Montagu).—Norman, 1900:128 [partim].—Stephensen, 1924:81–83 [partim].—Barnard, 1930:412.—Hurley, 1960a:111–112; 1969:33.

DERIVATION OF NAME.—Not given, presumably refers to the armature of the gnathopods.

TYPE-LOCALITY.—Spitzbergen; off northern coast of Norway; off south coast of England.

DIAGNOSIS.—Body moderately robust, length up to 21 mm. Posterior margin of pleonal epimeron 3 strongly convex. Segments of Md palp subequal; incisor with about 15 teeth. Outer lobe of Mxp longer than inner lobe; setae on inner and outer lobes shorter and sparser than in *H. medusarum*. Setae of P1 and P2 short compared with those of other species of *Hyperia*. P3–4, posterior margins of s4, s5, and s6 densely covered with short slender spinules. S2 of P5–7 broad, with group of spines at anterodistal corner in P7; anterior margins of s4–5 with dense covering of short spinules in P5, bare in P6–7. Inner ramus of Up2 and Up3 broad.

RELATIONSHIPS.—The collections of the Copenhagen Museum contain 6 vials labeled *"Hyperia spinosa"* by Bovallius and stated by Stephensen (1924) to be syntypes of *H. spinigera*. Stephensen considered these syntypes to be aged specimens of *H. galba*, and therefore placed *H. spinigera* in synonymy with *H. galba*.

These same 6 vials were kindly loaned to me by Dr. Torben Wolff. The 17 mm male from the north side of Iceland labeled "Borch ded. 1859" is a

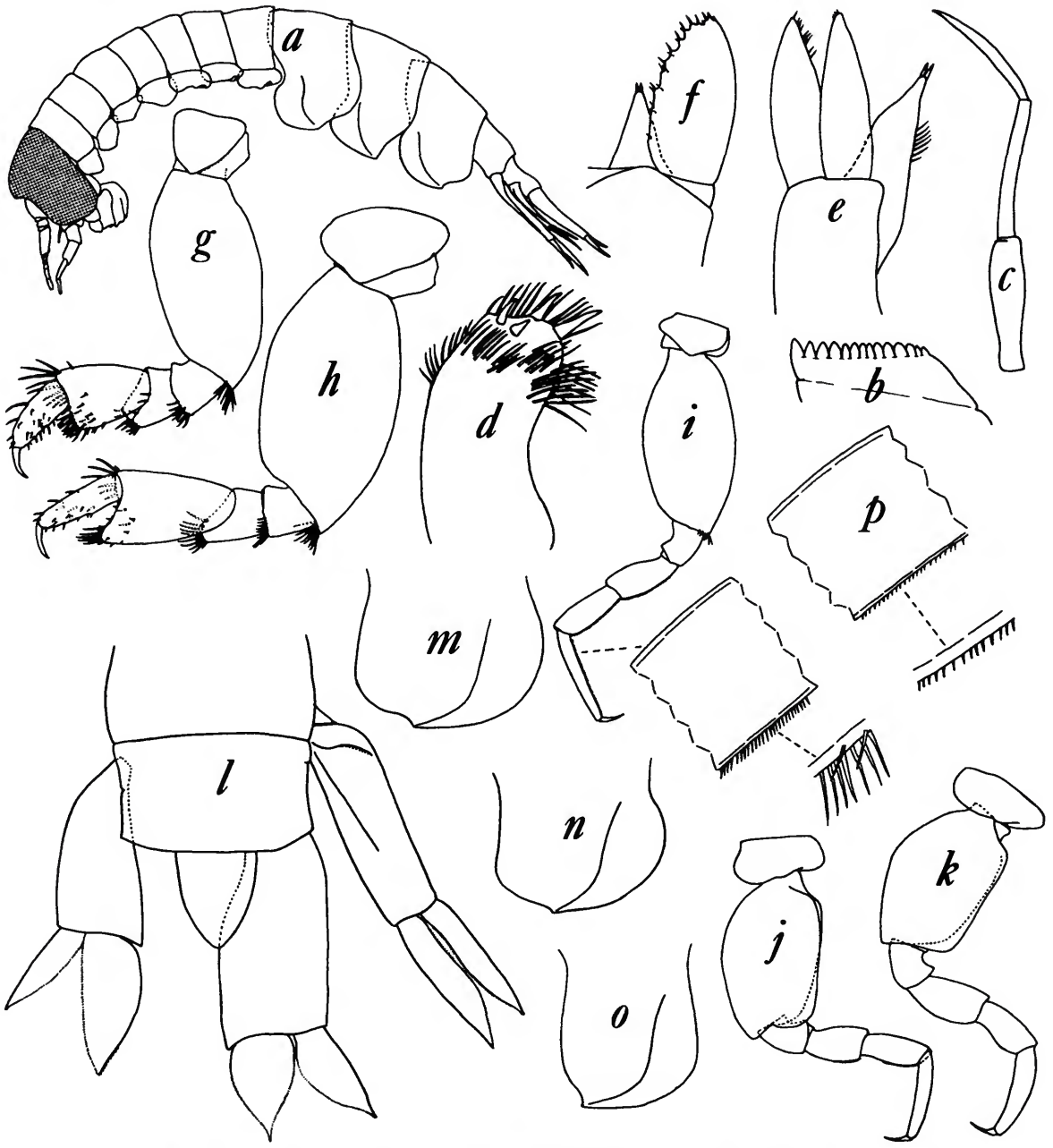


FIGURE 15.—*Hyperia spinigera*, ♂: *a*, lateral view; *b*, incisor of right Md; *c*, Md palp; *d*, Mxl, inner lobe; *e*, Mxp, oblique view; *f*, Mxp, posterior; *g*, P1; *h*, P2; *i*, P3; *j*, P5; *k*, P6; *l*, urosome; (*m-o*, pleonal epimera of specimens in Copenhagen Museum labeled "Hyperia spinosa" by Bovallius) *m*, "61°N, 20°W, Olrich ded. 1867"; *n*, "18°S, 2°W, Andréa ded. 1864"; *o*, "North side of Iceland, Borch ded. 1859" [=*H. medusarum*, *hystrix* form]. *Hyperia galba*, ♂: *p*, s6 of P3.

specimen of *Hyperia medusarum, hystrix* form; the other specimens are clearly distinct from *H. galba,* and as pointed out by Stephensen must constitute at least part of the type-series of *H. spinigera,* although, curiously, none are from localities listed by Bovallius in his original account of the species.

The specimens of the type-series, as well as the other specimens that I have examined, exhibit very little variation. Characters useful in distinguishing them from *H. galba* are the following:

1. Some of the spines on s6 of P1 and P2 extend across the posterior margin in *H. spinigera;* this margin is devoid of spines in *H. galba.*

2. The posterior margins of s5 and s6 of P3 and P4 have longer spinules in *H. spinigera* (compare Figures 15*i* and 15*p*). S5 usually has several spines in *H. galba,* none in *H. spinigera.*

3. The epimera of pleonite 3 are more strongly produced posteriorly in *H. spinigera* than in *H. galba* (compare Figures 15*a,m,n* and 7*i,j*). Although Tattersall (1906) stated that the posterolateral corners of pleonite 3 are sharply pointed in *H. galba* and rounded in *H. spinigera,* Shoemaker (1945b) showed clearly that the corners are pointed in *H. spinigera.* The difference between the epimera of the two species is not in the development of the points but in the more strongly convex posterior margin in *H. spinigera,* shown by Shoemaker (1945b, fig. 35c) and Hurley (1955, fig. 94).

The female of *H. spinigera* has not been described. Several authors (Norman, 1900; Barnard, 1932; Shoemaker, 1945b; Hurley, 1956) have recorded females, unsupported by descriptions or illustrations, except for Barnard's figure of the urosome. None of these records can be confirmed.

Norman (1900) considered *H. spinigera* a synonym of *H. galba,* but stated, "Should other authors disagree with my views in this matter, the [2] female specimens of *H. galba* taken by me at Birturbuy Bay and the one taken off Valentia [both localities off Ireland] by the 'Porcupine' are, from the character of the gnathopods, to be referred to *H. spinigera.*" I have examined Norman's 3 females, loaned to me by the British Museum (Natural History) through the courtesy of R. W. Ingle; in my opinion they are typical *H. galba.*

Barnard's female from *Discovery* station 298 in the North Atlantic (13°01′N, 21°34′W) was also loaned to me by the British Museum (Natural History). It is identical with specimens from the Gulf of Guinea assigned in this paper to a new species, *Hyperia crassa.* My reasons for proposing

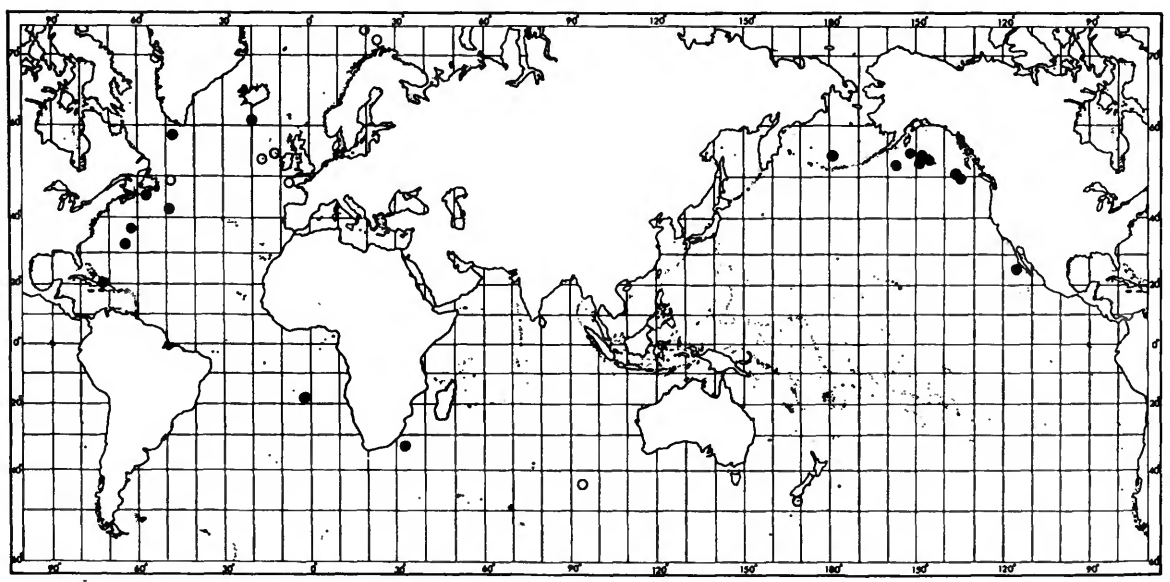


FIGURE 16.—*Hyperia spinigera,* distribution records.
● records verified by examination of specimens ○ unverified records from the literature

a new species for these specimens rather than placing them in *H. spinigera* are discussed under *H. crassa*.

I have examined Shoemaker's female specimens from Bermuda, which are deposited in the Smithsonian Institution; they are typical specimens of *H. antarctica*.

DISTRIBUTION.—Figure 16 shows the occurrences that I have compiled from the literature and from specimens in the Smithsonian Institution. *H. spinigera* is obviously a widespread species and the present compilation gives only a fragmentary picture of its distribution. Most of the collections were made at considerable depths.

7. *Hyperia leptura*, new species

FIGURE 17

DERIVATION OF NAME.—From the Greek "leptos" [=slender] + "oura" [=tail], referring to the slender uropods.

TYPE.—Holotype and only specimen, ♀ with embryos in marsupium, USNM 111244, from CalCOFI Cruise 20, station 130.35, off Bahía Ballenas, Baja California (26°19.5′N, 113°49′W), in 140–0 m net tow, 14 November 1950.

DIAGNOSIS.—Head longer than pereonites 1–2 combined; gland cone rounded. Outer lobe of Mxp with several long setae near inner margin; inner lobe about half as long as outer lobe, anterior surface heavily setose, apex with single strong spine. S2 of P1–2 relatively narrow, about 2.5 times as long as wide, with a number of short setae on proximal part of anterior margin; s5–6 long and narrow, armed with numerous long spines. P3–4 long; posterior margins of s3–6 spinose; posterior margin of s6 finely serrate. Setae on P5–7 limited to a few on anterior margins of s2 and s5 (Figure 17*j–k*). Epimera of pleonite 3 not produced posteriorly. Up1–3 long and slender; rami lanceolate, those of Up1 especially long. Telson slightly shorter than width at base.

RELATIONSHIPS.—Only one specimen of this species has been discovered, but its characters are so distinctive that I have no hesitation in establishing a new species for it. It appears to be closest to *H. macrocephala*, but in addition to its much smaller size, it differs in the form of coxa 4, pleonal epimera 3, the Mxp, and the narrower peduncle of Up3.

8. *Hyperia crassa*, new species

FIGURES 18–19

Hyperia spinigera Bovallius.—Barnard, 1932:273–4 [♀ only], fig. 160b.

DERIVATION OF NAME.—The specific name, from the Latin "crassus" [=thick, fat], refers to the broad protopods and endopods of the uropods.

TYPES.—All from *Ombango* Cruise 12 in the Gulf of Guinea. Holotype ♀, USNM 137502, station 298 (Grand Schmidt 2), 3°01′S, 9°25′E, 300 meters of wire, 1 May 1960, 1040 hrs. Allotype ♂, USNM 137503, station 302 (Grand Schmidt 19), 4°47′S, 10°42′E, 1100 meters of wire, 4 May 1960, 0450 hrs. Paratypes, 3 ♀, USNM 137504, station 300 (Grand Schmidt 11), 3°48′S, 19°08′E, 200 meters of wire, 2 May 1960, 1800 hrs.

DIAGNOSIS.—Body rather compact and heavyset, length 12–15 mm. Head unusually large, longer than pereonites 1–3 combined, in lateral view much longer dorsally than ventrally. Pereonites with distinctive dorsal profile shown in Figure 18*a*; pereonite 2 highest, pereonite 7 concave anteriorly, convex posteriorly; pereonites 2, 3, and 4 with transverse folds. Pleonal epimera with pointed posteroventral corners; posterolateral margin of pleonite 3 only weakly convex. Proximal segment of Md palp much shorter than distal segments; incisor with 9 or 10 teeth. Mxp inner lobe long, with long apical spines. Segments of P1–2 with well-developed spines; s2 of P1 with very convex anterior margin. P3–4 with very few spines on posterior margins of s4–5. P5–7 unarmed, with rather narrow s2. Up2–3 with very broad protopods and endopods.

RELATIONSHIPS.—Barnard (1932) called attention to the very broad uropods of a female *Hyperia* which he identified as *H. spinigera*. In his discussion he gave the impression that he had some reservations about this identification, and these reservations have proved to be entirely justified. This female, loaned to me by the British Museum (Natural History), closely resembles the *Ombango* females of *H. crassa*, as can be seen by comparing Figures 18 and 19. The long head and broad uropods on both *Ombango* and *Discovery* females,

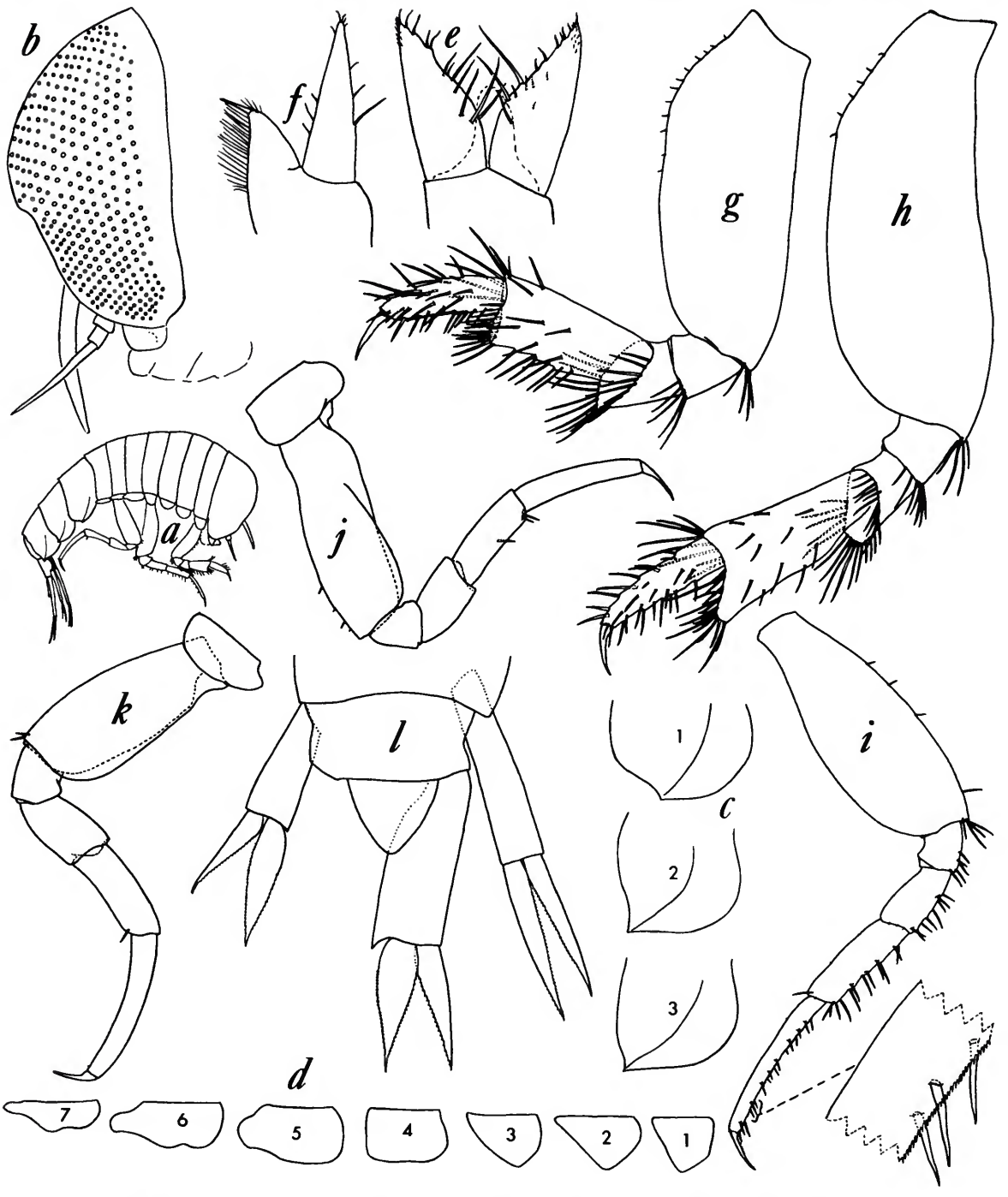


FIGURE 17.—*Hyperia leptura*, new species, ♀ holotype: *a*, lateral view; *b*, head, *c*, pleonal epimera; *d*, coxae; *e*, Mxp, posterior; *f*, Mxp, lateral; *g*, P1; *h*, P2; *i*, P3; *j*, P5; *k*, P6; *l*, urosome, dorsal.

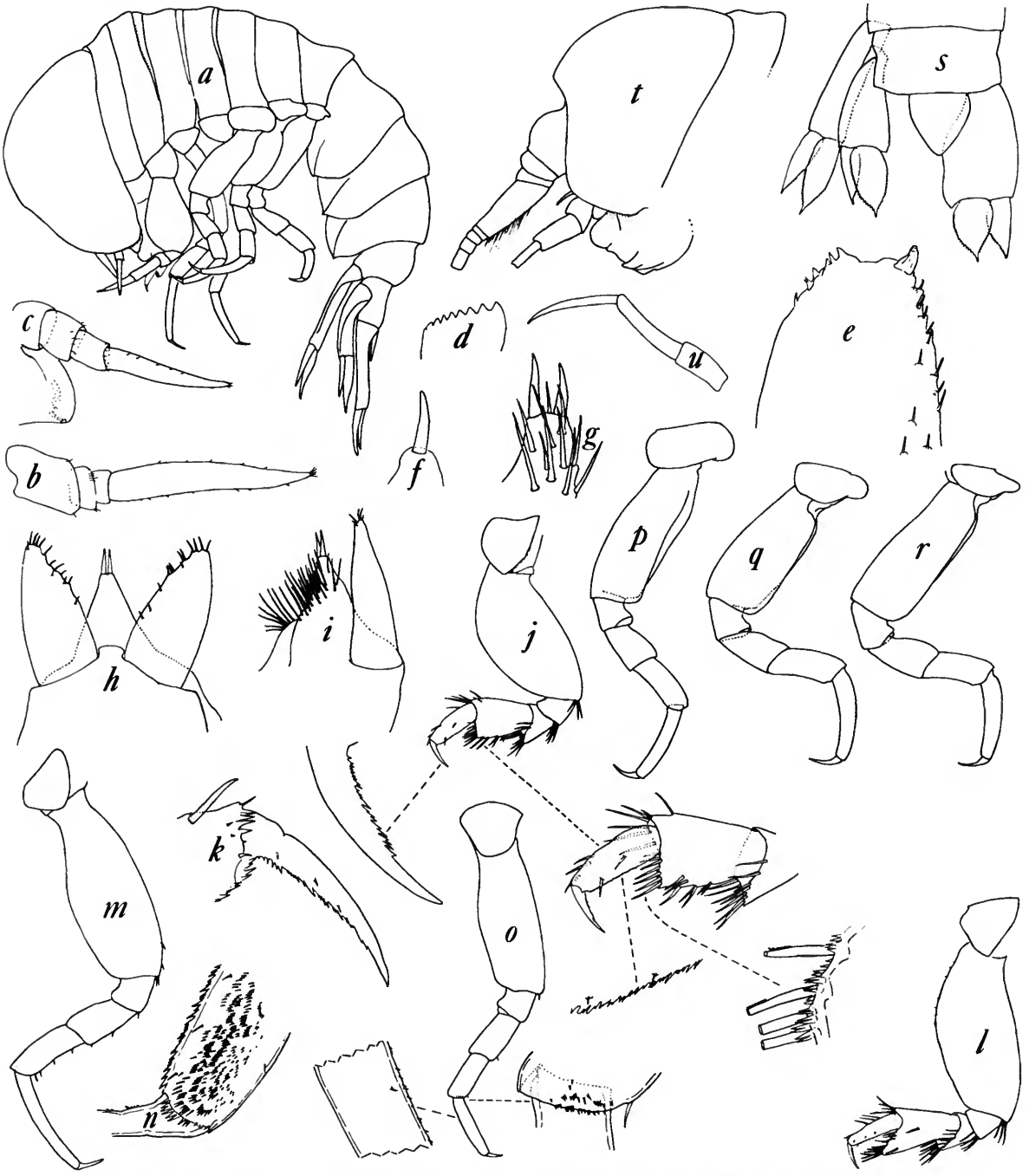


FIGURE 18.—*Hyperia crassa*, new species (*a-s*, ♀): *a*, lateral view; *b*, A1; *c*, A2; *d*, incisor of right Md; *e*, Mx1 inner lobe; *f*, Mx2 inner lobe; *g*, Mx2 outer lobe; *h*, Mxp posterior; *i*, Mxp lateral; *j*, P1; *k*, P1 dactyl, medial; *l*, P2; *m*, P3; *n*, P3, part of s6 and s7, medial; *o*, P4; *p*, P5; *q*, P6, *r*, P7; *s*, urosome; t, ♂ head, lateral; *u*, ♂ Md palp.

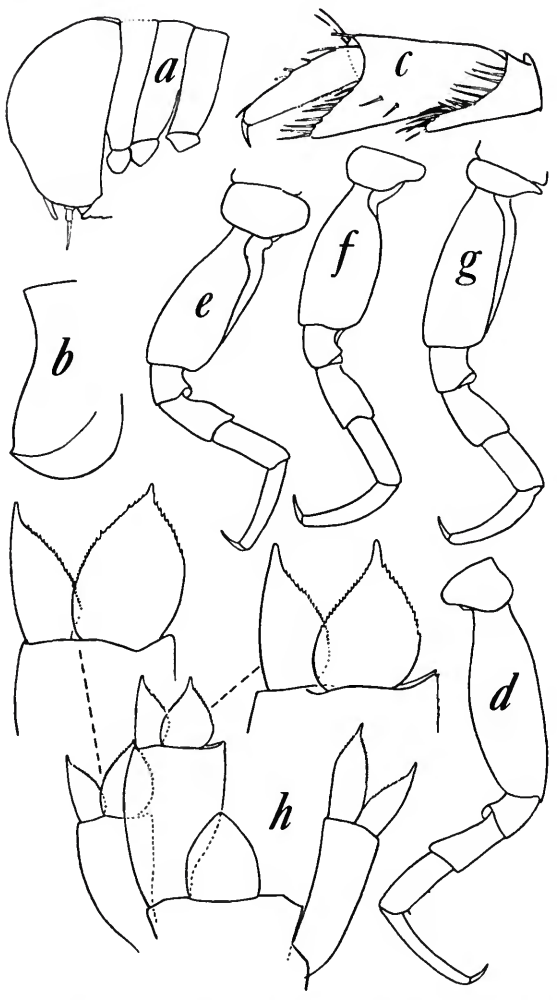


FIGURE 19.—*Hyperia crassa*, new species, ♀ from *Discovery* station 298: *a*, head and pereonites 1–3, lateral; *b*, pleonite 3, lateral; *c*, P2, distal segments; *d*, P4; *e*, P5; *f*, P6; *g*, P7; *h*, urosome, dorsal.

unique features of *H. crassa*, clearly establish their specific identity.

DISTRIBUTION.—West coast of Africa, 3–5°S (*Ombango* stations). SE of Cape Verde Islands, 13°01'N, 21°34'W, *Discovery* station 298 (Barnard, 1932).

II. *Hyperiella* Bovallius, 1887b

DIAGNOSIS.—Body small to moderate sized; pereon rather plump; pereonites all separate. ♀ A1 and A2 4-merous. Md palp present in ♀; incisor serrate. Mx1, inner lobe with 5 terminal spines. Mx2 with 1 terminal spine on inner lobe, 2–3 on outer lobe. Mxp, inner lobe well developed, ending in 2 spines; outer lobes separate. P1 subchelate; P2 chelate; posterior margin of s6 serrate in both P1 and P2. P3–4, posterior margins of s5 and s6 serrulate, that of s5 bearing a few slender spines. P5 (or P5–6) much longer than P3–4; P7 (or P6–7) subequal to P3–4. S7 of at least P3–5 very long. Up3 elongate, except in *H. macronyx*.

DERIVATION OF NAME.—Not given, presumably diminutive of *Hyperia*. Gender feminine.

TYPE-SPECIES.—Designated by Bovallius, 1889, *Hyperiella antarctica* Bovallius, 1887b.

REMARKS.—The foregoing diagnosis is modified from the original by Bovallius in order to accommodate *Hyperia macronyx* Walker (1906). *H. macronyx* differs from the two other members of the genus in that both P5 and P6 are elongate and Up3 is shorter, but in other respects it is more similar to *Hyperiella antarctica* and *H. dilatata* than to any of the species of *Hyperia* as restricted herein. The alternative to transferring *H. macronyx* to *Hyperiella* would be to propose a monotypic genus for Walker's species. The latter course seems less desirable, since it would not call attention to the similarity of *H. macronyx* to *H. antarctica* and *H. dilatata*.

Hyperiella is close to *Hyperia*, but is smaller than any species of *Hyperia*, and P5 (or P5–6) are relatively longer. In some respects it resembles *Parathemisto;* P3–4 approach the prehensile condition of these legs in *Parathemisto*, and elongate uropods and characteristic of *Parathemisto*.

Key to the Species of *Hyperiella*

1. P5–6 subequal, longer than other pereopods. Up3 peduncle about twice as long as telson ..... 11. ***H. macronyx***
   P5 much longer than P6. Up3 peduncle distinctly more than twice as long as telson 2
2. Anterodistal corners of P6–7 produced into sharp triangular processes. Up3 ♂, exopod 2/3 or more as wide as endopod ..... 10. ***H. dilatata***
   Anterodistal corners of P6–7 produced into blunt processes. Up3 ♂, exopod less than 2/3 as wide as endopod ..... 9. ***H. antarctica***

9. *Hyperiella antarctica* Bovallius

FIGURES 20*n*, 21*g-i*

Hyperiella antarctica Bovallius, 1887a:20; 1887b:566, pl. 45: figs. 72–80; 1889:242–246, text-fig. p. 242, pl. 11: figs. 42–51.—Stewart, 1913:256.—Barnard, 1930:414; 1932:275, fig. 161 [distribution].—Kane, 1962:301–302.—Vinogradov, 1962:25.—Hurley, 1969:32, map 5 [distribution].

DERIVATION OF NAME.—Not given; presumably geographical.

TYPE-LOCALITY.—Drake Passage, 58°43′S, 76°W.

DIAGNOSIS.—Length 6–8 mm. Posteroventral corners of pleonal epimera blunter and less prominent than in *H. dilatata*. P5–7, anterodistal corners of s2–4 produced into more or less pointed processes, but processes weaker and blunter than in *H. dilatata*. Up3 ♂, exopod less than ⅔ as wide as endopod.

RELATIONSHIPS.—See discussion under *H. dilatata*.

DISTRIBUTION.—According to Hurley (1969), *H. antarctica* inhabits the region between the Subtropical Convergence and the edge of the pack ice.

10. *Hyperiella dilatata* Stebbing

FIGURES 20*a–m*, 21*a–f*

Hyperiella dilatata Stebbing, 1888:1403–1404, pl. 171.—Bovallius, 1889:247.—Walker, 1907:8.—Spandl, 1927:162–164, fig. 5a-h.—Barnard, 1930:413–414; 1932:274–275, fig. 161 [distribution]; 1937:4.—Stephenson, 1947:76.—Hurley, 1961: 600; 1969:33, sheet 2, map 5[distribution].—Vinogradov, 1962:25.—Emison, 1968:passim [food of Adélie penguin].

DERIVATION OF NAME.—Refers to the inflated pereon.

TYPE-LOCALITY.—Indian sector of Antarctic, 63° 30′S, 88°57′E.

DIAGNOSIS.—Length 6–8 mm. Posteroventral corners of pleonal epimera sharper and more prominent than in *H. antarctica*. P5–7, anterodistal corners of s2–4 produced into conspicuous triangular processes. Up3 ♂, exopod ⅔ or more as wide as endopod.

RELATIONSHIPS.—The differences that previous workers have used to distinguish between *H. antarctica* and *H. dilatata* are not altogether convincing, but the material at my disposal has not allowed me to shed much light on the problem. My specimens of *H. dilatata*, collected from the stomachs of Adélie penguins by William B. Emison, are somewhat deformed and partly digested, but were sufficiently intact to permit illustration of most of the significant details. With regard to *H. antarctica*, I have examined only 3 males from the collections of the Copenhagen Museum, identified by Bovallius and believed to be syntypes. The original label for these specimens is lost, and a label in K. Stephensen's handwriting reads (translated from the Danish by Torben Wolff), "Amongst the 'Icebergs' of the South Polar Sea. Wessell." In his original description Bovallius (1887b) gave the locality as "Antarctic Seas, around Cape Horn." In 1889 Bovallius cited the type-locality more precisely: "The American Antarctic region: Lat. 58°43′; Long. 76°W." This locality lies in the western part of the Drake passage, south of the northern limit of drift ice, hence is compatible with the syntype label.

Accepting the 3 males as syntypes leaves unresolved the question of whether *H. antarctica* and *H. dilatata* are distinct species, since the condition of the specimens is only fair. A brief history of the taxonomy of the two species may help to show the nature of the problem.

The original description of each species was based on only one sex, the male for *H. antarctica* and the female for *H. dilatata*. Bovallius (1889) gave a key to the two species that distinguished them by 3 characters: (1) The pleonal epimera, with posterolateral corners rounded in *H. antarctica* and pointed in *H. dilatata*. (2) The anterodistal corners of s2–4 of P5–7, rectangular in *H. antarctica* and acutely produced in *H. dilatata*. (3) The endopod of Up3, "ovate" in *H. antarctica*, "narrowly elongate and sharp-pointed" in *H. dilatata*.

The usefulness of the first character became doubtful when Stewart (1913) noted pointed pleonal epimera on a ♂ *H. antarctica*. This finding was verified by Barnard (1930, 1932), although he stated that the points were not as well developed as in *H. dilatata*. In the specimens seen by me the points are somewhat stronger in *H. dilatata* (compare Figures 20*m* and 20*n*), but it is risky to rely on such a purely quantitative character when nothing is known about its variability. Moreover, the appearance of the points may be affected by the action of the preservative; inflation of the epimera, obscuring the nature of the margins, is frequently seen in preserved hyperiids.

That Bovallius' second difference is also a matter of degree was noted by Barnard (1930, 1932), who

FIGURE 20.—*Hyperiella dilatata* (*a-k*, ♀): *a*, A1; *b*, A2; *c-d*, incisor and palp of right Md; *e-f*, outer and inner lobes of Mx1; *g*, Mx2 (setae omitted); *h-i*, posterior and oblique views of Mxp; *j*, Mxp, inner lobe (setae omitted); *k*, P1; *l*, P1 dactyl; *m*, pleonal epimera ♂. *Hyperiella antarctica* ♂: *n*, pleon, lateral.

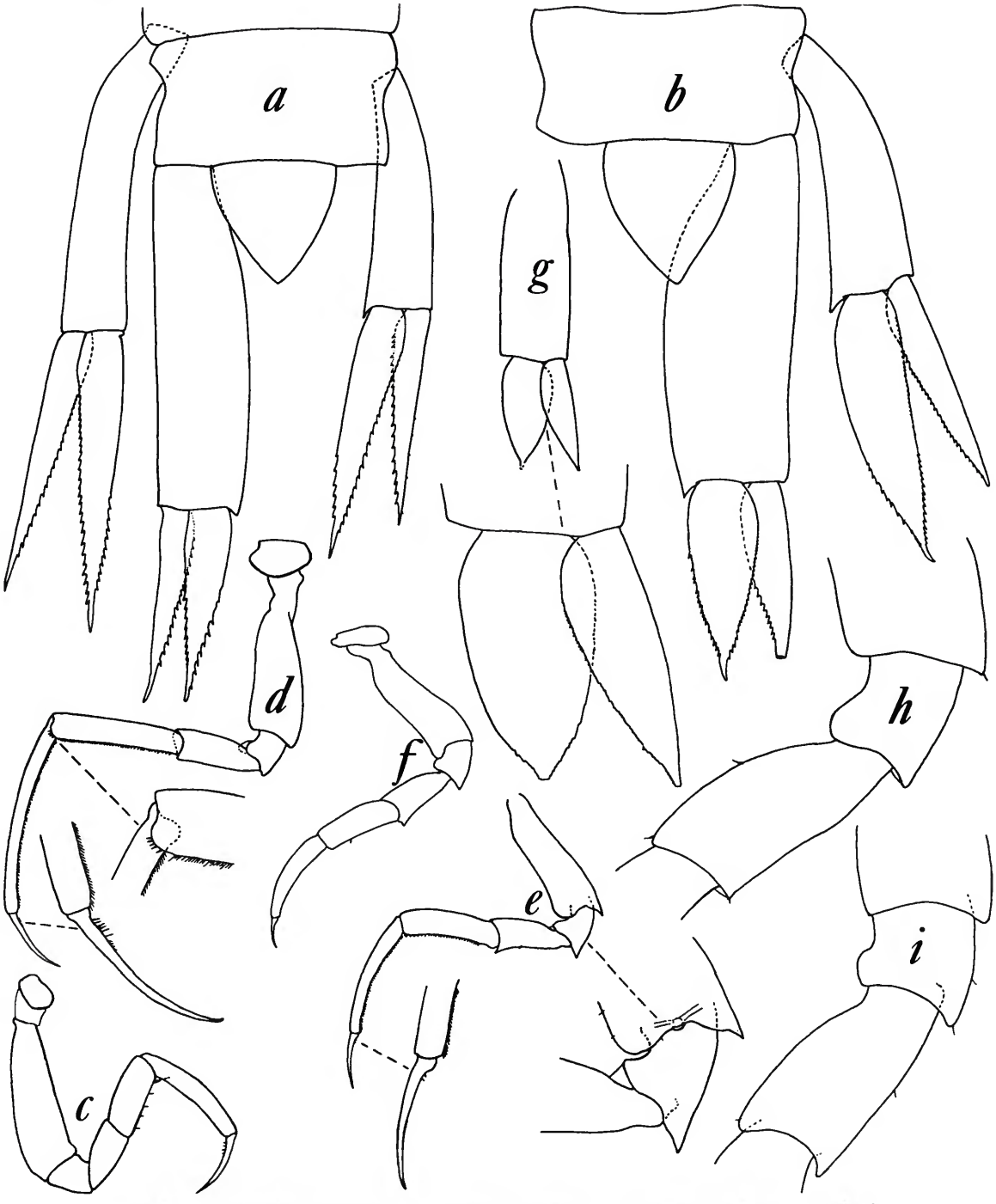


FIGURE 21.—*Hyperiella dilatata*: *a*, ♀ urosome, dorsal; *b*, ♂ urosome, dorsal; *c*, ♀ P3, *d*, ♀ P5; *e*, ♂ P6; *f*, ♂ P7. *Hyperiella antarctica*: *g*, Up3; *h*, P6; *i*, P7.

found pointed anterodistal corners on s2–4 of P5–7 in *H. antarctica* less prominent than those on *H. dilatata*. In specimens seen by me the points are distinctly more prominent in *H. dilatata*, but I cannot rule out the possibility that the points have been abraded in the *H. antarctica* syntypes.

The third difference in Bovallius' key concerned a sexually dimorphic character. The broader "ovate" endopod of Up3 of *H. antarctica* was that of a male *Hyperiella*, and the "narrowly elongate" endopod of *H. dilatata* was an attribute of a female *Hyperiella* (compare Figures 21*a* and 21*b* of the ♂ and ♀ uropods of my specimens of *H. dilatata*). As Barnard (1930) observed, Spandl (1927) added to the problem by describing the uropods of an immature male of *H. dilatata*; uropods of young males are narrow, like those of females. But Barnard himself compounded the confusion by stating that the endopods of Up2–3 of the male *H. antarctica* are lanceolate and slightly narrower than those of the female *H. antarctica*. My drawing of the uropods of the ♂ *H. dilatata* (the first for this species) shows the endopod of Up3 ovate and only slightly narrower than that of the male *H. antarctica*. Figures of the uropods of the female *H. antarctica* have not yet been published, and I am unable to evaluate Barnard's statement concerning them.

In summary, none of the characters said to be useful in distinguishing between *H. antarctica* and *H. dilatata* are of proven reliability. Both species (if they are not conspecific) are in need of detailed redescriptions, including studies of their variability.

DISTRIBUTION.—From the Antarctic Convergence to the Antarctic continent (Hurley, 1969).

11. *Hyperiella macronyx* (Walker), new combination

FIGURES 22–23

Hyperia macronyx Walker, 1906:452; 1907:7–8, pl. 1: fig. 1.—Barnard, 1930:412–413.—Emison, 1968:203–206 [food of Adélie penguin].—Hurley, 1969:33, map 5 [distribution].

DERIVATION OF NAME.—Not given; presumably from the Greek "macro" [=large] + "onyx" [=claw], referring to the long dactyls on P3–7.

TYPE-LOCALITY.—Two locations in the Ross Sea, Antarctica: (1) Coulman Island; (2) *Discovery* winter quarters, on tip of Cape Armitage, south side of Ross Island, McMurdo Sound.

DIAGNOSIS.—Length, up to 13 mm. Pereon not so plump as in other species of *Hyperiella*. Pleonite 3 with point on posterolateral margin. Mx2 with 3 spines at apex of outer lobe. Mxp without row of spines on distal margin of basal plate. P6 slightly longer than P5, both considerably longer than P7, which is subequal to P3–4. S7 of P3–7 elongate. Telson slightly longer than wide, about half as long as peduncle of Up3.

RELATIONSHIPS.—Easily distinguished from its congeners by the characters given in the key.

DISTRIBUTION.—Known only from the Ross Sea.

III. *Hyperioides* Chevreux

Hyperioides Chevreux, 1900:143.
Parahyperia Vosseler, 1901:56 [conditional name].

DIAGNOSIS.—Small species with body rather compressed laterally. Head globular, produced anteriorly above insertion of A1; eyes occupying most of its surface or limited entirely to dorsal surface. Pereonites 1–2 fused in both sexes. Coxae fused with pereonites. Posterior elevation of ♂ pleonite 1 pronounced. Telson rather short. ♀ A1 2–3-merous. ♀ A2 1-merous, moderately long, with characteristic sinuous shape in lateral view; gland cone rounded below. Md with dentate incisor; palp absent in ♀. Mx 1 outer lobe with 3 large terminal spines and a smaller subterminal spine. Mx 2 outer lobe with 1 terminal and 1 subterminal spine; inner lobe with 1 terminal spine. Mxp inner lobe well developed, with 2 terminal spines. P1–2 chelate, with spoon-shaped carpal process bearing marginal spines. P5–6 distinctly longer than P3–4 and P7; dactyls of P5–7 long, with comb of fine setules on proximal 3rd of anterior margin. Outer rami of uropods notched.

DERIVATION OF NAME.—Not given; presumably from Hyperia + the Greek "oides" [=resembling].

TYPE-SPECIES.—By monotypy, *Hyperioides longipes* Chevreux, 1900. Gender feminine.

REMARKS.—The above diagnosis modifies that of Chevreux (1900) to include characters which this study has convinced me are significant at the generic level. Until now *Hyperioides* has been monotypic, but I am transferring to it a second species,

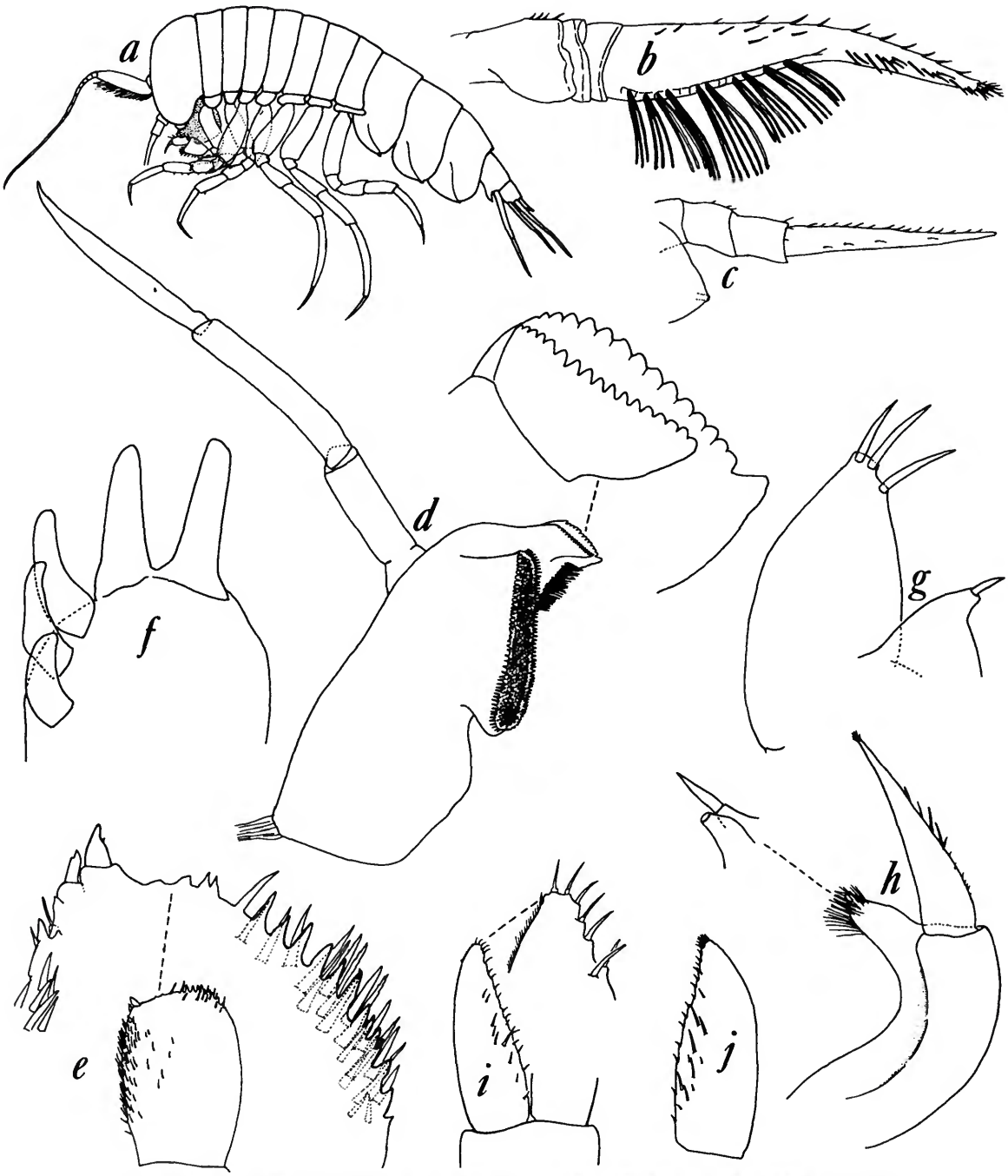


FIGURE 22.—*Hyperiella macronyx*: *a*, ♂ lateral; *b*, ♀ A1, medial; *c*, ♀ A2, lateral; *d*, left ♂ Md; *e*, Mx1, outer lobe; *f*, Mx1, inner lobe, apex, setae omitted; *g*, ♂ Mx2, setae omitted; *h*, Mxp, lateral; *i*, ♂ Mxp, outer lobe, posterior; *j*, ♀ Mxp, outer lobe, posterior.

FIGURE 23.—*Hyperiella macronyx*: *a*, ♀ P1, medial; *b*, ♀ P2, medial; *c*, ♀ P3, lateral; *d*, ♀ P3, juncture of s6–7, medial, *e*, ♂ P6, lateral; *f*, ♂ P7, lateral; *g*, ♀ urosome.

Hyperia sibaginis Stebbing (1888). This action was foreshadowed by Vosseler's (1901) misidentification of *H. longipes* as *H. sibaginis*; Vosseler was of course unaware of Chevreux's description of *H. longipes*. Chevreux's diagnosis of *Hyperioides* accommodates *H. sibaginis* except for his statement that the eyes are limited to the upper part of the head.

Key to the Species of *Hyperioides*

Eyes limited to upper part of head ..... 12. ***H. longipes***
Eyes occupying most of head surface ..... 13. ***H. sibaginis***

12. *Hyperioides longipes* Chevreux

FIGURES 24, 25

Hyperioides longipes Chevreux, 1900:143–145, pl. 17: fig. 2; 1913:6; 1935:189–191.—Lo Bianco, 1902:422, 447; 1904:43, pl. 22: fig. 66.—Walker, 1903:229–230, pl. 19: figs. 7–13.—Stebbing, 1904:34–36.—Fowler, 1904:49, 53 [table].—Tattersall, 1906:23.—Stewart, 1913:256.—Stephensen, 1924:93–94.—Chevreux and Fage, 1925:407–408, fig. 405.—Spandl, 1927: 164.—Pirlot, 1929:124–126; 1930:19–20; 1939:37.—Schellenberg, 1927:637, fig. 42.—Barnard, 1930:414–415; 1932:276; 1937:184.—Ruffo, 1938:148.—Shoemaker, 1945b:238.—Bulycheva, 1955:1048 [in table].—Hure, 1955:48.—Hurley, 1956: 15; 1960b:280; 1969:33.—Trégouboff and Rose, 1957:460, pl. 132.—Kane, 1962:302.—Vinogradov, 1962:25.—Siegfried, 1963:8.—Hure, 1965:48.—Pillai, 1966:211–212, fig. 5.—Vives, 1966:96, table 19; 1968:460, table 1.—Dick, 1970:57.—Hure, Scotto di Carlo, and Basile, 1971:passim.—Yoo, 1971:57.

Hyperia sibaginis ? Stebb.—Vosseler, 1901:60–64, pl. 7: fig. 6–20 [misidentification].

Hyperia sibaginis var. *longipes* Vosseler, 1901:63 [conditional name].

Hyperia longipes Vosseler, 1901:63 [conditional name].

Hyperia longipes Chevreux.—Reid, 1955:18 [lapsus].

DERIVATION OF NAME.—Not given; presumably refers to length of P5–6.

TYPE-LOCALITY.—Eastern Atlantic, 4 *Hirondelle* stations west of Bay of Biscay, 44°42′–48°25′N, 9°16′–22°14′W.

DIAGNOSIS.—See below, under *H. sibaginis*.

DISTRIBUTION.—*H. longipes* has been recorded from warm parts of all the world oceans, but little is known of the details of its distribution. Charts of its occurrence on 4 CalCOFI cruises show its consistent presence offshore from San Francisco south, closer to the coast in the southern part of the area. This pattern fits in general the eastern limits of Brinton's (1962) pattern for his "central" euphausiid species, which occupy ocean gyrals of midlatitudes 15°–40° in both hemispheres in the Pacific, but with such limited data I can only suggest this possibility.

13. *Hyperioides sibaginis* (Stebbing), new combination

FIGURE 26

Hyperia sibaginis Stebbing, 1888:1379–1382, pl. 165.—Bovallius, 1889:201–203.—Barnard, 1931:127–128.—Chiba, Tsurutu, and Maeda, 1955:194, 196, 200.

Hyperia sibaginis ? Stebbing.—Pirlot, 1930:18–19, fig. 6.

[not] *Hyperia sibaginis* ? Stebb.—Vosseler, 1901 [= *H. longipes* Chevreux].

DERIVATION OF NAME.—Not expressly stated, but presumably for Sibago Island, Philippines.

TYPE-LOCALITY.—*Challenger* station 200, northeast of Sibago Island, east of Zamboango Peninsula, Philippines: 6°47′N, 122°28′E.

DIAGNOSIS.—Both species of *Hyperioides* have been well described and illustrated, and in view of the ease with which this genus may be identified, diagnoses of its two species may be presented conveniently by the following tabular comparison.

Hyperioides longipes	*Hyperioides sibaginis*
Dorsal profile of head nearly straight	Dorsal profile of head rounded
Eye facets limited to dorsal part of head	Eye facets cover both dorsal and lateral parts of head
A1 3-merous	A1 2-merous
A2 slightly> 1/2 A1	A2 nearly = A1
Epistome distinctly posterior to gland cone	Epistome nearly reaches anterior margin of gland cone
Carpal process of P2 reaches midlength of s6	Carpal process of P2 reaches about 1.25 length of s6
Up3 protopod about 2 times as long as wide; only slightly longer than exopod	Up3 protopod about 2.8 times as long as wide, about 1.5 times longer than exopod

IV. *Lestrigonus* Milne Edwards

Lestrigonus Milne Edwards, 1830:392; 1840:81–82.

DIAGNOSIS.—Small species, with rather plump pereon. Head globular; eyes occupying most of its

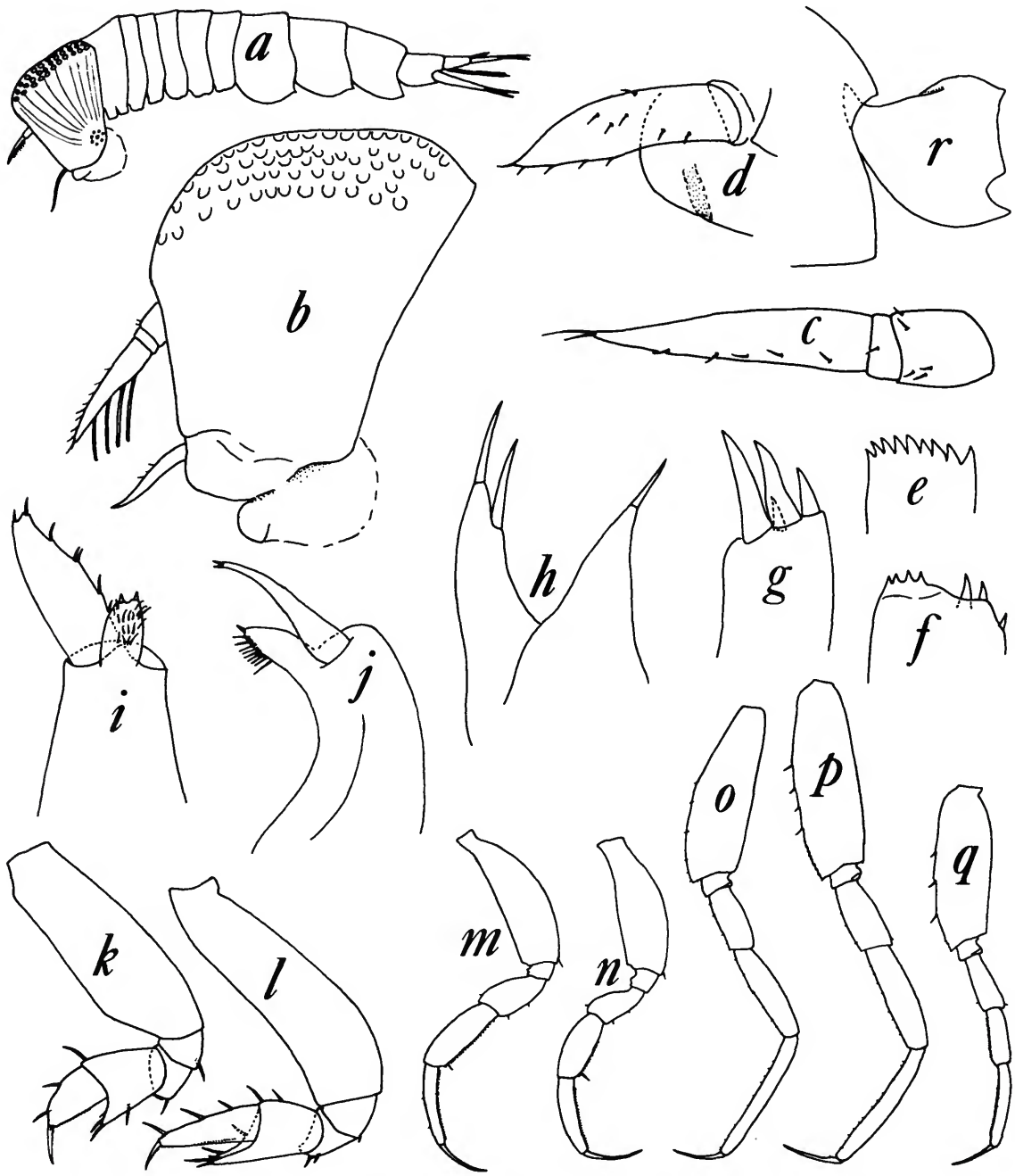


FIGURE 24.—*Hyperioides longipes*, off California (*a-q*, ♀): *a*, lateral view; *b*, head, lateral; *c*, A1, dorsal; *d*, A2, dorsal; *e*, incisor of right Md; *f*, Mx1, apex of palp; *g*, Mx1 outer lobe; *h*, Mx2 (setae omitted); *i*, Mxp, anterior; *j*, Mxp, lateral; *k*, P1; *l*, P2; *m*, P4; *n*, P3; *o*, P5; *p*, P6; *q*, P7; *r*, ♂ urosomite 1, lateral.

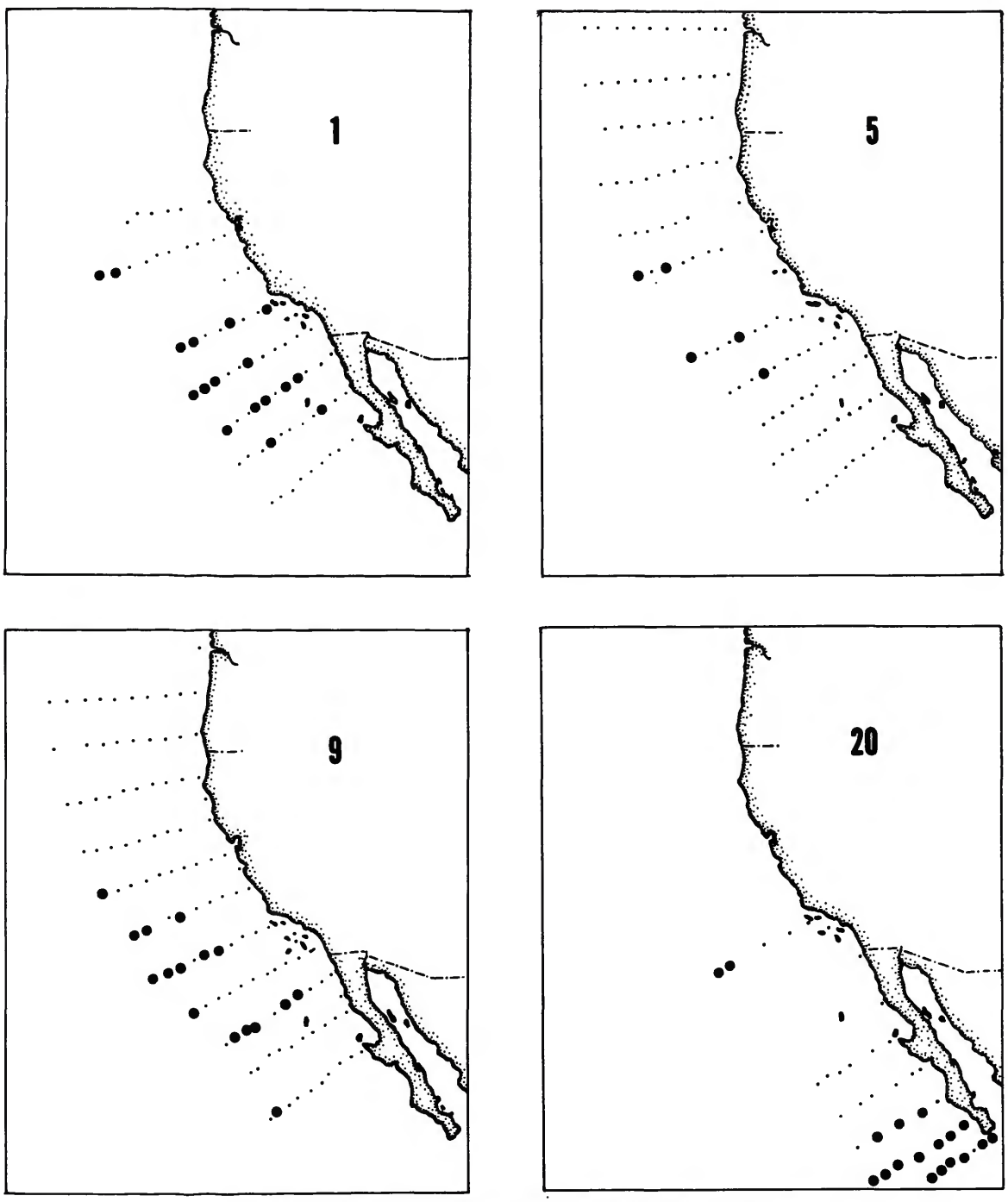


FIGURE 25.—Distribution of *Hyperioides longipes* on 4 CalCOFI cruises.

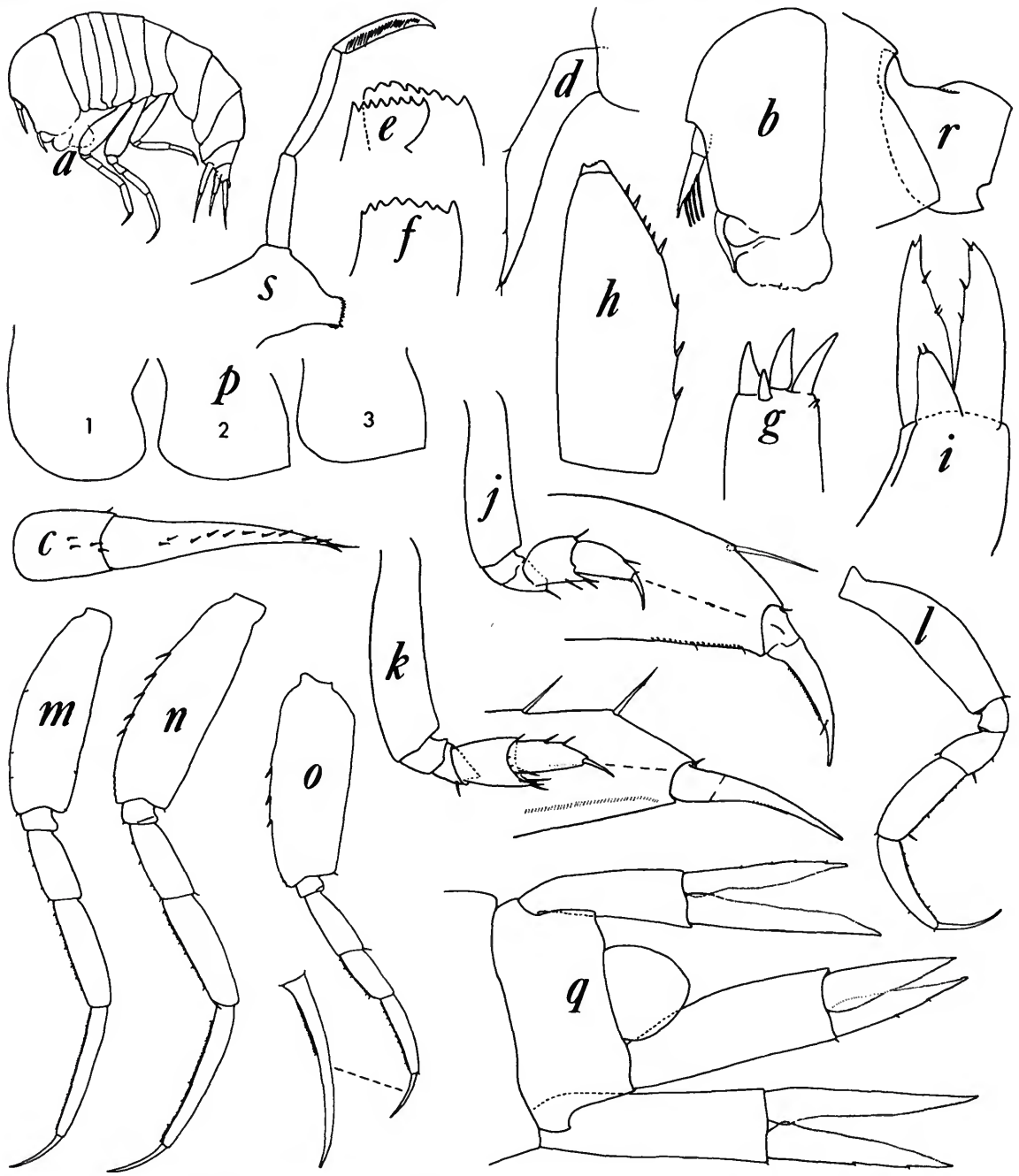


FIGURE 26.—*Hyperioides sibaginis*, Golfo Elena, Panama (*a-q*, ♀): *a*, lateral view; *b*, head, lateral; *c*, A1; *d*, A2; *e*, left Md, incisor and lacinia mobilis; *f*, right Md, incisor; *g*, Mx1, outer lobe; *h*, Mx1, palp; *i*, Mxp, anterior surface; *j*, P1; *k*, P2; *l*, P4; *m*, P5; *n*, P6; *o*, P7; *p*, pleonal epimera; *q*, urosome; *r*, ♂ urosomite 1, lateral; *s*, ♂ right Md.

surface. Some of anterior pereonites fused (2?), 3–5 in ♀, 2–4 in ♂, always more in ♀. Coxae fused with pereonites. Telson of moderate size. ♀ A1 2–merous. ♀ A2 1–merous, usually very small; gland cone conspicuous, with pointed or rounded apex. Epistome prominent, strongly convex anteriorly. Md with dentate incisor; palp absent in ♀. Mx1 outer lobe with 3 large terminal spines and usually a smaller subterminal spine. Mxp outer lobes separate, tapering distally; inner lobe usually well developed. P1 subchelate or barely chelate. P2 distinctly chelate; carpal process spoon-shaped, with spines along margin of spoon. P5–7 usually longer than P3–4; P5 and P7 subequal, slightly shorter than P6.

DERIVATION OF NAME.—"Seemingly from Λαιστρυγόνες, an ancient savage tribe of Italy and Sicily" (Stebbing, 1888). Gender, masculine.

TYPE-SPECIES.—By monotypy, *Lestrigonus fabrei* H. Milne Edwards, 1830.

REMARKS.—Next to *Hyperia, Lestrigonus* is the oldest available generic name for this group of species. Since *Hyperia* is restricted herein to a different group of species, *Lestrigonus* becomes the valid name of the genus, and *L. fabrei* is automatically the type-species. This is not an ideal situation, since the true identity of *L. fabrei* is uncertain. The species called *Hyperia fabrei* by most authors is an entirely different species, *H. vosseleri* Stebbing, which I am transferring herein to the new genus *Hyperietta*. The true *Lestrigonus fabrei* has not been recorded since the original accounts by Milne Edwards (1830, 1838, 1840), which were limited to the male. Milne Edwards unfortunately gives little information concerning the characters that I have found most useful for distinguishing genera and species of *Hyperia* s.l. His illustrations (1840) include a lateral view of the male and drawings of the Md and Mxp; copies of these drawings are given in Figure 27. I am unable to add any details because the type-specimen appears to have been lost. Dr. J. Forest, Muséum National d'Histoire Naturelle, Paris, has kindly informed me that a vial containing a label reading *"Lestrigonus fabrei.* Mer des Indes. Raynaud coll." contains a second label in the handwriting of Bouvier stating that the vial was returned empty by Bovallius. For the time being *L. fabrei* remains a nomem dubium.

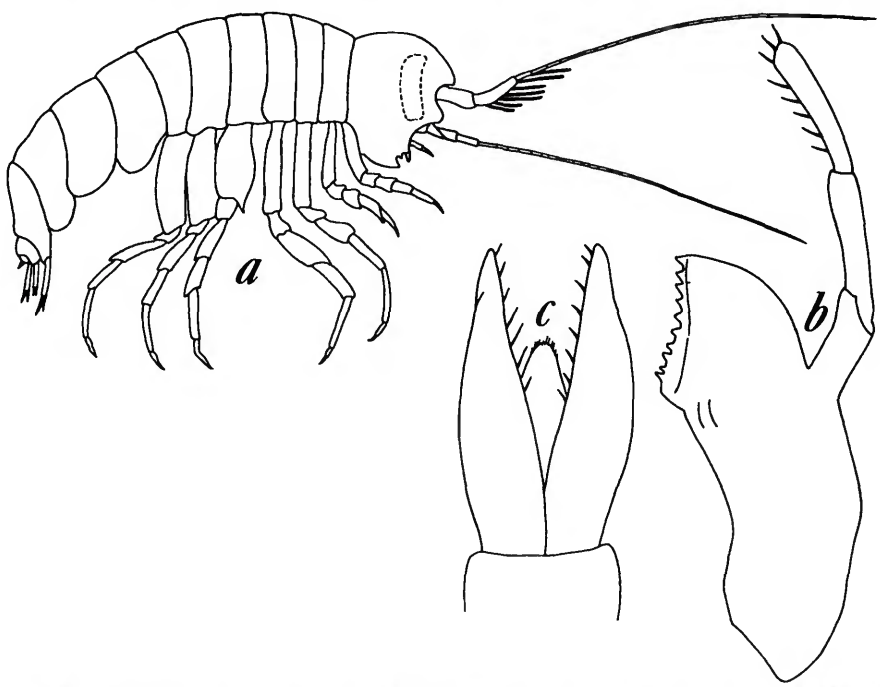


FIGURE 27.—*Lestrigonus fabrei*: *a*, ♂ lateral; *b*, Md; *c*, Mxp. Redrawn from Milne Edwards, 1840, pl. 30.

Milne Edwards' species can be excluded without difficulty from the genera of Hyperiidae other than *Lestrigonus* considered herein. Following each genus in the list below, I give the characters of *L. fabrei* that exclude it from that genus.

Hyperia and *Hyperiella*: Pereonites 1–2 fused; coxae fused with pereonites.

Hyperioides: P5–7 subequal.

Themistella: Pereonites 1–2 fused; P5–7 subequal; Mxp with well-developed inner lobe.

Hyperietta: Mxp with long narrow outer lobes and well-developed inner lobe; no long spines on s4–5 of P3–4.

Hyperionyx: Mxp with long narrow outer lobes; P5–7 subequal.

Only the rediscovery of *Lestrigonus fabrei* will enable us to know with certainty whether it agrees with the details in my emended diagnosis of *Lestrigonus*. There is nothing seriously incompatible with this diagnosis in Milne Edwards' description and illustrations except possibly the body length cited by him, "long d'environ cinq lignes." This length is about 11 mm, much longer than the species herein assigned to *Lestrigonus*, which rarely exceeds 4 mm. I suspect, but cannot prove, that Milne Edwards' measurement was inaccurate.

Attempting to sort out the valid species of *Lestrigonus* and their synonyms from published descriptions and illustrations has been very frustrating. In some instances previous authors assigned males and females or adults and juveniles of one species to different species or even different genera. Much of the confusion can be attributed to the fact that these authors, following Bovallius, used the number of fused pereonites as a primary character for separating species, but failed to realize that in any species the fusion is greater in females than in males and greater in juveniles than in adults. One can scarcely blame Pirlot (1939)

Key to the Species of *Lestrigonus* [1]

Females

1. Pereonites 1–3 fused 2
   Pereonites 1–4 fused 3
   Pereonites 1–5 fused ..... 19. ***L. bengalensis***
2. Gland cone pointed, extending ventrally beyond buccal mass. Spine on distal margin of s6 of P6–7 slender, simple ..... 14. ***L. schizogeneios***
   Gland cone rounded, not reaching ventral border of buccal mass. Spine on distal margin of s6 of P6–7 robust, with 1–2 teeth on anterior margin ..... 15. ***L. crucipes***
3. Head more than half as long as high, as long as fused pereonites 1–4. Gland cone reaching or exceeding ventral border of buccal mass. Telson about half as long as Up3 protopod ..... 17. ***L. macrophthalmus***
   Head about half or less than half as long as high. Gland cone not reaching ventral border of buccal mass. Telson about 3/5 as long as protopod of Up3 4
4. Fused pereonites with partial sutures dorsally. S6 of P1–2 with 1 spine on anterior margin ..... 16. ***L. shoemakeri***
   Fused pereonites 1–4 without partial sutures. S6 of P1–2 with 1–2 spines on anterior margin ..... 18. ***L. latissimus***

Males

1. Pereonites 1–2 fused 2
   Pereonites 1–4 fused ..... 19. ***L. bengalensis***
2. P5–7, distal margin of s6 produced into recurved dentate hook ..... 15. ***L. crucipes***
   Distal margin of s6 not produced in P5, in P6–7 produced into smooth spine 3
3. Gland cone bluntly rounded, clearly not reaching ventral margin of buccal mass 4
   Gland cone rather pointed, reaching or nearly reaching ventral margin of buccal mass ..... 14. ***L. schizogeneios***
4. Head more than half as long as high ..... 17. ***L. macrophthalmus***
   Head less than half as long as high 5
5. From Pacific Ocean ..... 16. ***L. shoemakeri***
   From Atlantic Ocean or Mediterranean ..... 18. ***L. latissimus***

[1] *L. fabrei* is omitted because its characters are largely unknown.

for retreating from the resultant problem by reducing most of the species herein assigned to *Lestrigonus* to synonyms of *Hyperia bengalensis*. Pirlot's action only added to the confusion, and unfortunately a number of subsequent workers have preferred to take refuge in his synonymy rather than to attempt the formidable task of sorting out the valid synonyms without the aid of adequate collections.

A definitive taxonomic treatment of the species of *Lestrigonus* is not possible with the material now available to me, but I hope that the arrangement of species proposed herein will decrease somewhat the chaos that now confronts us.

14. *Lestrigonus schizogeneios* (Stebbing)

FIGURES 28–30

Hyperia schizogeneios Stebbing, 1888:1391–1394, pl. 168.—Bovallius, 1889:221–224.—Chevreux, 1892:233–237, figs. 1–3; 1900:139–143, pl. 17: fig. la-m; 1935:188–189.—Vosseler, 1901:66–67.—Lo Bianco, 1902:446 [identification by Vosseler]; 1903:table facing p. 278 [identification by Vosseler].—Stewart, 1913:255–256.—Stephensen, 1924:86–90, Chart 13.—Spandl, 1924b:265.—Chevreux & Fage, 1925:402–404, fig. 402.—Pirlot, 1929:120–122; 1930:16–18.—Candeias, 1934:4.—Irie, 1948:36 [in table]; 1957a:351, fig. 12; 1957b:passim; 1958:107 [in table]; 1959:passim.—Alvarado, 1955:219.—Hure, 1955:47–48, fig. 57a-b; 1961:33.—Bulycheva, 1955:1048 [in list].—Trégouboff & Rose, 1957:456, pl. 132.—Yang, 1960:15–19, figs. 1–3.—Laval, 1965:6197–6198; 1968:passim; 1972:passim.—Vives, 1966:96, table 19; 1968:460, table 1.—Dick, 1971:56–57.—Hure, Scotto di Carlo, & Basile, 1971: passim.—Yoo, 1971:56, fig. 14.

Hyperia promontorii Stebbing, 1888:1385–1387, pl. 166B; 1910:475–476.—Bovallius, 1889:214–218, pl. 11: figs. 3–13.—Vosseler, 1901:64.—Lo Bianco, 1901:446 [identification by Vosseler]; 1903:table facing p. 278 [identification by Vosseler].—Barnard, 1930:411; 1937:183–184.—Dakin & Colefax, 1940:121, fig. 207.—Siegfried, 1963:8.

Hyperia bengalensis (Giles).—Pirlot, 1939:35–36.—Hurley, 1955:137–140, figs. 70–82; 1956:14–15; 1960b:279; 1969:19.—Reid, 1955:17, fig. 4.—Kane, 1962:299–300.—Vinogradov, 1962:24–25.—Brusca, 1967a:388; 1967b:452.

Hyperia zebui Stebbing, 1888:1394.

DERIVATION OF NAME.—From the Greek οχίζω =I cleave] + γένειον [=a chin], referring to the emarginate lower border of the head.

TYPE-LOCALITY.—Off St. Vincent, Cape Verde Is., 16°49′N, 25°14′W.

DIAGNOSIS.—Length of ♀ 2.2–3.5 mm, of ♂ 3.5–4.5 mm. Head about twice as high as long, about half as long as pereon. Pereonites 1–3 fused in ♀, 1–2 in ♂. Gland cone in ♀ conspicuous, rather sharply pointed, extending beyond buccal mass; in ♂ blunter, not quite or barely reaching ventral border of buccal mass. Md incisor with 8 teeth; lacinia with 6–8 teeth. Mx1 inner lobe with 3 long and 2 short terminal spines, 1 subterminal spine. Mx2 outer lobe with 1 subterminal and 2 terminal spines; inner lobe with a shorter terminal spine. Mxp outer lobes conical, about 3 times as long as wide, with 3–4 spines along inner margin. S2 of P1 with moderately convex anterior margin; s4 with 2–3 (rarely 4) posterodistal spines; carpal process with 5–6 spines; s6 with 2 (Atlantic specimens) or 3 (Pacific specimens) spines near anterior margin. P2 with carpal process about half as long as s6; s6 with 1–2 spines on anterior margin. P3–4, posterior margin of s5–6 with comb of spinules; s5 also with 2 spines on posterior margin. P5–7 with moderately broad s2 armed with a few spines on anterior margin; anterior margins of s5–6 with comb of spinules; s7 of P5 with a few anteroproximal spinules, s6 of P6–7 with spine on distal margin overlapping base of s7 medially. Telson triangular, in ♀ about half, in ♂ about 2/5 as long as protopod of Up3.

VARIATION.—Specimens from the Atlantic and Pacific are very similar, but have slight differences. I have not studied these differences in detail, but I have examined the armature of the anterior margin of s6 of P1, which was the most obvious difference to me, in my specimens from both oceans. Most of the adult Atlantic specimens had 2 spines on this segment, but occasionally there were 3. One female had 3 spines on the right and 2 on the left P1. Pacific specimens (from CalCOFI collections) usually had 2–3 spines in the adult female (stage 7 of Laval, 1968) and 3–4 in the adult male. The number of spines is less in younger individuals. Stage 5 and younger females have only 1 spine; in stage 6 there are 1–2 spines. Other groups of spines vary in the same way; the older the specimen the more spines in a group.

The number of fused pereonites also varies with maturity, as shown by Yang (1960) and Laval (1968). Laval found that young specimens from the marsupium, characterized by rudimentary pleopods and uropods and named by Laval "protopleon larvae" (stage 1), have all 7 pereonites

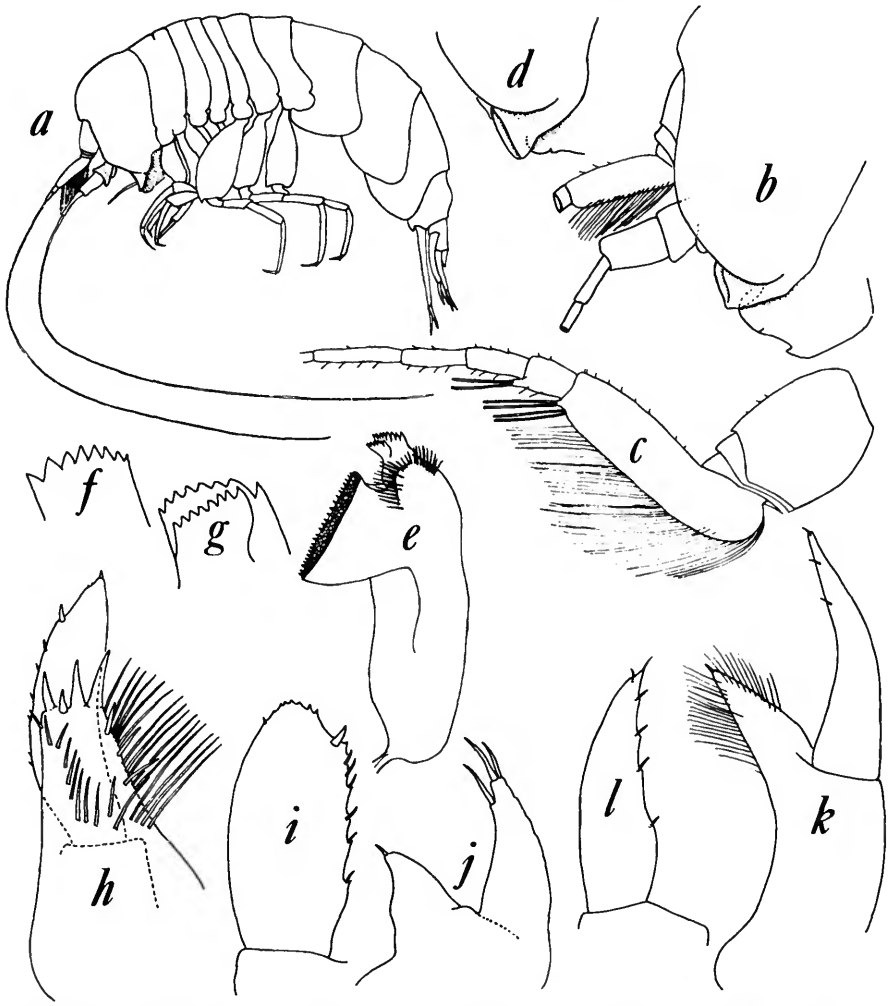


FIGURE 28.—*Lestrigonus schizogeneios*, (*a-c*, ♂) *a*, lateral view; *b*, ventral part of head, lateral; *c*, A1. (*d-l*, ♀) *d*, ventral part of head, lateral; *e*, left Md; *f-g*, incisors of right and left Md; *h*, Mx1; *i*, Mx1 palp, flattened; *j*, Mx2; *k*, Mxp, lateral; *l*, Mxp outer lobe, posterior surface. (California specimens, except d, from Sargasso Sea.)

free. CalCOFI specimens removed from the marsupium also have no fusion of pereonites. Laval observed that after the protopleon larvae leave the marsupium and settle on the host medusa, *Phialidium* sp., they molt into juveniles with pereonites 1–5 fused (stage 2). Three more instars, stages 3–5, follow in which pereonites 1–5 are fused. The female then enters the stage of prepuberty, stage 6, in which pereonites 1–4 are fused and rudimentary oostegites are present. Stage 7 is the adult, with pereonites 1–3 fused and fully developed oostegites. In the male the flagella of A1–2 remain short and unsegmented in stage 6 (pereonites 1–4 fused) and stage 7 (pereonites 1–3 fused). Stage 8 is the prepuberty stage, with pereonites 1–2 fused and the flagella of A1–2 segmented but only about

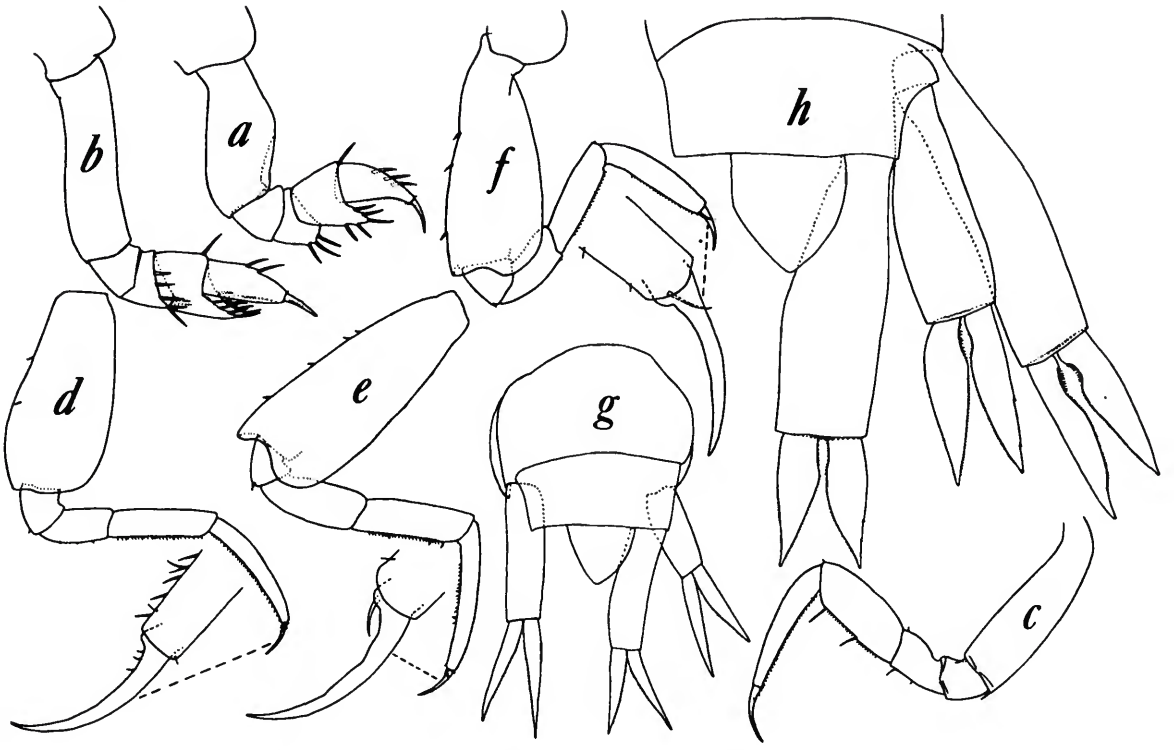


FIGURE 29.—*Lestrigonus schizogeneios* (*a-g*, ♀): *a*, P1; *b*, P2; *c*, P4; *d*, P5; *e*, P6; *f*, P7; *g*, urosome; *h*, ♂ urosome. California specimens.

as long as the pereon. The male does not become fully adult until stage 9, thus he requires 2 more molts than the female to attain maturity.

I have examined many specimens of *L. schizogeneios* from the CalCOFI collections and have found that the sequence of development agrees closely with that described by Laval.

It is generally agreed that *Hyperia schizogeneios* and *H. promontorii* are the female and male respectively of the same species. Both specific names have been used, but although *H. promontorii* has page precedence, the first revisor, Stephensen (1924), selected the name *schizogeneios*. Pirlot's (1939) indiscriminate lumping of 12 nominate species under *H. bengalensis* has made it difficult to know the real identity of specimens reported as *H. bengalensis* by subsequent authors. I have, for example, examined those reported by Shoemaker from Bermuda (1945) and Cuba (1948) and found them to be *Lestrigonus latissimus*, hence Shoemaker's references are not included in the synonymy given above for *L. schizogeneios*.

DISTRIBUTION.—Reported from warm waters around the world. In the CalCOFI area it is the second most abundant hyperiid, being exceeded only by *Parathemisto pacifica*. It extends farther south than the subarctic *P. pacifica*, but is replaced in the southernmost part of the CalCOFI area by the closely related *L. shoemakeri*. When its overall distribution in the Pacific becomes known it may prove to be an inhabitant of the transition zone (Brinton, 1962). Its abundance in the samples of the three 1949 CalCOFI cruises was least in March, greater in July, and highest in November, the average number per 1000 m^3 for the positive stations increasing from 17 to 64 to 102.

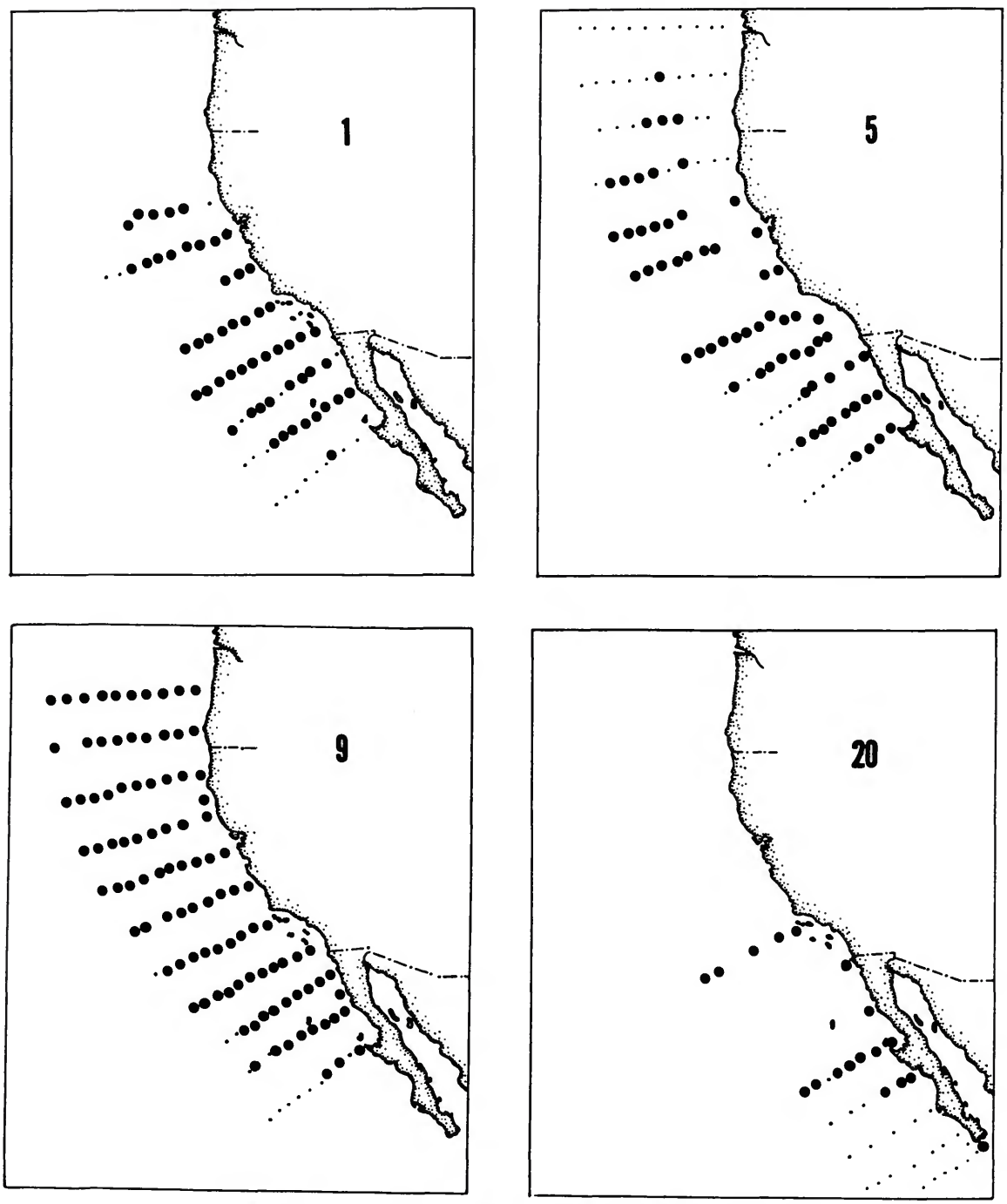


FIGURE 30.—Distribution of *Lestrigonus schizogeneios* on 4 CalCOFI cruises.

15. *Lestrigonus crucipes* (Bovallius)

FIGURE 31

Hyperia crucipes Bovallius, 1889:225–228, pl. 11: fig. 14–25.—Walker, 1904:236.—Stephensen, 1924:90.—Barnard, 1937: 184.—Pirlot, 1939:36.—Laval, 1968:64–65, fig. 12.—Dick, 1970:55.

DERIVATION OF NAME.—From the Latin "crucis" [=across] + "pes" [=foot], referring to spine overriding dactyl on P5–7.

TYPE-LOCALITY.—"The tropical region of the Atlantic: off Barbadoes."

DIAGNOSIS.—Length about 4 mm. Body rather plump and compact. Pereonites 1–2 fused in ♂, 1–3 in ♀. Pleonal epimera with rounded posterior corners. A1–2 of ♀ well developed for a *Lestrigonus;* gland cone obtuse, projecting obliquely anteriad. Md with broad molar; incisors with 8–9 teeth. Mx1 inner lobes with 5 apical spines. Mx2 with 2 and 1 spines on outer and inner lobes respectively. P1–2 with 3–4 spines on anterior margin of s6; carpal process of P2 reaching beyond midlength of s6; s7 of P1–2 with spinulose posterior margin. P3–4 longer than P5–7; s4–5 with 2–3 spines on posterior margin; s6 posterior margin armed with close-set spinules. P5–7 with broad s2 and rather robust s3–6; s6 produced distally into recurved hook with 1–2 spiniform teeth on convex margin; hook overlaps s7 medially. Up1–3 with slender peduncles and rami. Telson oval, slightly wider than long, about 0.4 the length of Up3 peduncle.

RELATIONSHIPS.—The specimens that I have examined, all from the Arabian Sea, differ from Bovallius' description so much that I was at first convinced that I was dealing with an undescribed species. But no specimens agreeing more nearly with Bovallius' account have come to hand, and the frustrations of trying to reconcile the species descriptions of Bovallius with the characters that can be seen on his species have led me to share the opinion of Bovallius' work expressed by Stephensen (1924), who wrote in evident exasperation, ". . . but in consideration of several positive misstatements in the work of Bovallius, there is hardly any reason to pay much attention to his remarks . . ." I am therefore assuming considerable error in Bovallius' account of *Hyperia crucipes.* The principal discrepancies between Bovallius' description and the specimens that I have examined are the following:

Bovallius' description	*IIOE specimens*
pereonites 1–3 fused in ♂	pereonites 1–2 fused in ♂
P5–7 subequal in length to P3–4	P5–7 distinctly shorter than P3–4
anterior margin s6 of P1–2 without spines	same with 3–4 spines
P5–6 with forked projection at base of s7, 1 branch of fork crossing s7 on each side (Fig. 31*r*)	P5–7 with toothed recurved hook projecting on medial side of s7 from distal margin of s6 (Fig. 31q)
P7 without projection at base of s7	P7 as in P5–6
telson half length of Up3 protopod	telson<half length of Up3 protopod

My disbelief in Bovallius' accuracy was reinforced by examination of a female amphipod in the collections of the Stockholm Museum from the Caribbean Sea east of Dominica (15°22′N, 62°41′W). This specimen, labeled *Hyperia crucipes* var, *macropis* by Bovallius (an unpublished varietal name), agrees closely with the IIOE specimens. I have also examined Stephensen's (1924) specimens from *Thor* stations 266, 377, and 399; they also closely resemble the IIOE specimens.

DISTRIBUTION.—Warm regions of the Atlantic (Bovallius, Pirlot, Laval, Stephensen) and Indian (Walker, Barnard) Oceans. The few specimens that I have examined were collected at three stations in the Arabian Sea during the International Indian Ocean Expeditions.

16. *Lestrigonus shoemakeri,* new species

FIGURES 32–34

DERIVATION OF NAME.—After the late Clarence R. Shoemaker, in recognition of his many contributions to amphipod taxonomy.

TYPES.—Holotype ♀, USNM 139096, allotype ♂, USNM 139097, CalCOFI Cruise 9, station 1106, 27°48′N, 119°14′W, west of Punta Eugenia, Baja California, 12 November 1949. 2 ♂ and 2 ♀ paratypes deposited at Scripps Institution of Oceanography.

DIAGNOSIS.—Length of ♀ 2.3–2.7 mm, of ♂ 3.5–4.0 mm. Head slightly more than twice as high as long, about ⅓ as long as pereon. Pereonites 1–4 fused in ♀, but sutures present dorsally, that between pereonites 1–2 shorter than others. Pereonites 1–2 fused in ♂; partial sutures usually absent in

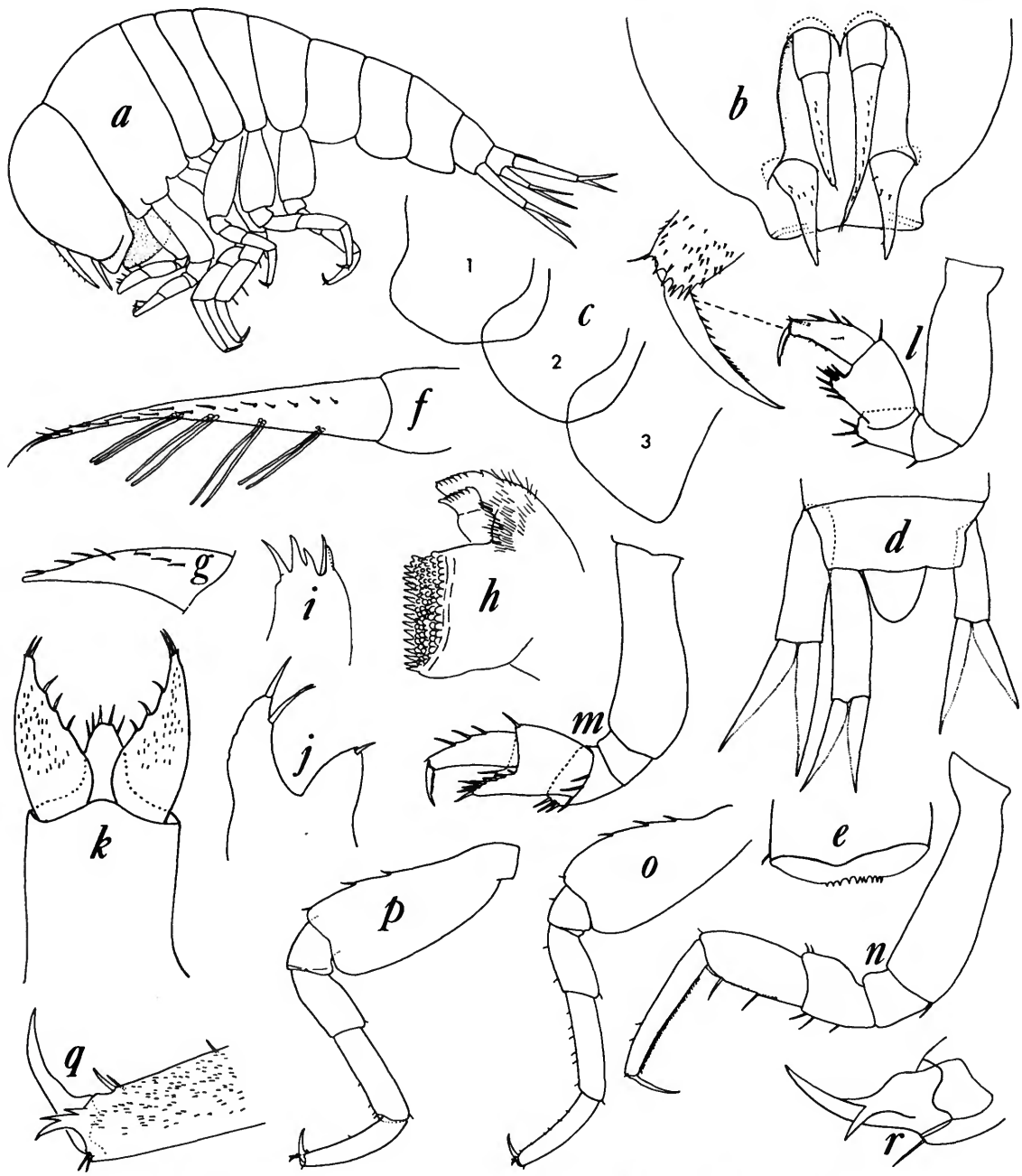


FIGURE 31.—*Lestrigonus crucipes*, ♀: *a*, lateral view; *b*, head, anterior view; *c*, pleonal epimera; *d*, telson and uropods, dorsal; *e*, protopod of Up3, showing distoventral serrations; *f*, A1; *g*, A2; *h*, left Md; *i*, Mx1, inner lobe; *j*, Mx2; *k*, Mxp; *l*, P1; *m*, P2; *n*, P3; *o*, P5; *p*, P7; *q*, P7, distal end, medial; *r*, P6, distal end (copied from Bovallius, 1889, pl. 11: fig. 23).

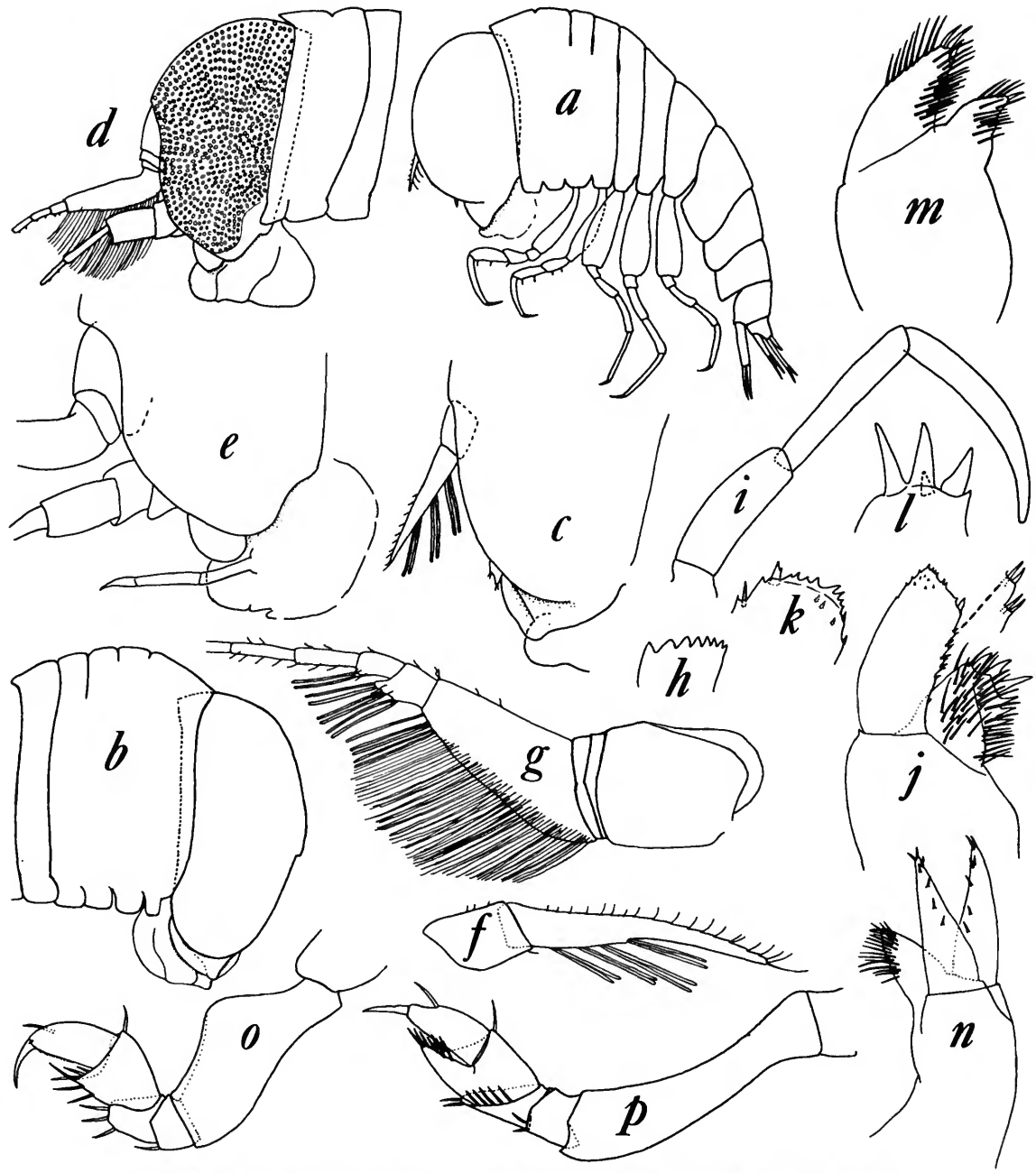


FIGURE 32.—*Lestrigonus shoemakeri*: *a*, ♀, lateral; *b*, ♀ head and pereonites 1–5, lateral; *c*, ventral part of ♀ head, lateral; *d*, ♂ head and pereonites 1–3, lateral; *e*, ventral part of ♂ head, lateral; *f*, ♀ A1; *g*, ♂ A1; *h*, incisor of ♀ right Md; *i*, palp of ♂ Md; *j*, ♀ Mx1; *k-l*, ♀ Mx1, apices of palp and outer lobe; *m*, ♀ Mx2; *n*, Mxp; *o*, ♀ P1; *p*, ♀ P2. (*b*, *d*, *f*, *g*, *i*, *j*, *m*, *n*, *o*, *p* from off Baja California; *a*, *c*, *e*, *h*, *k*, *l* from off Pacific coast of Nicaragua.)

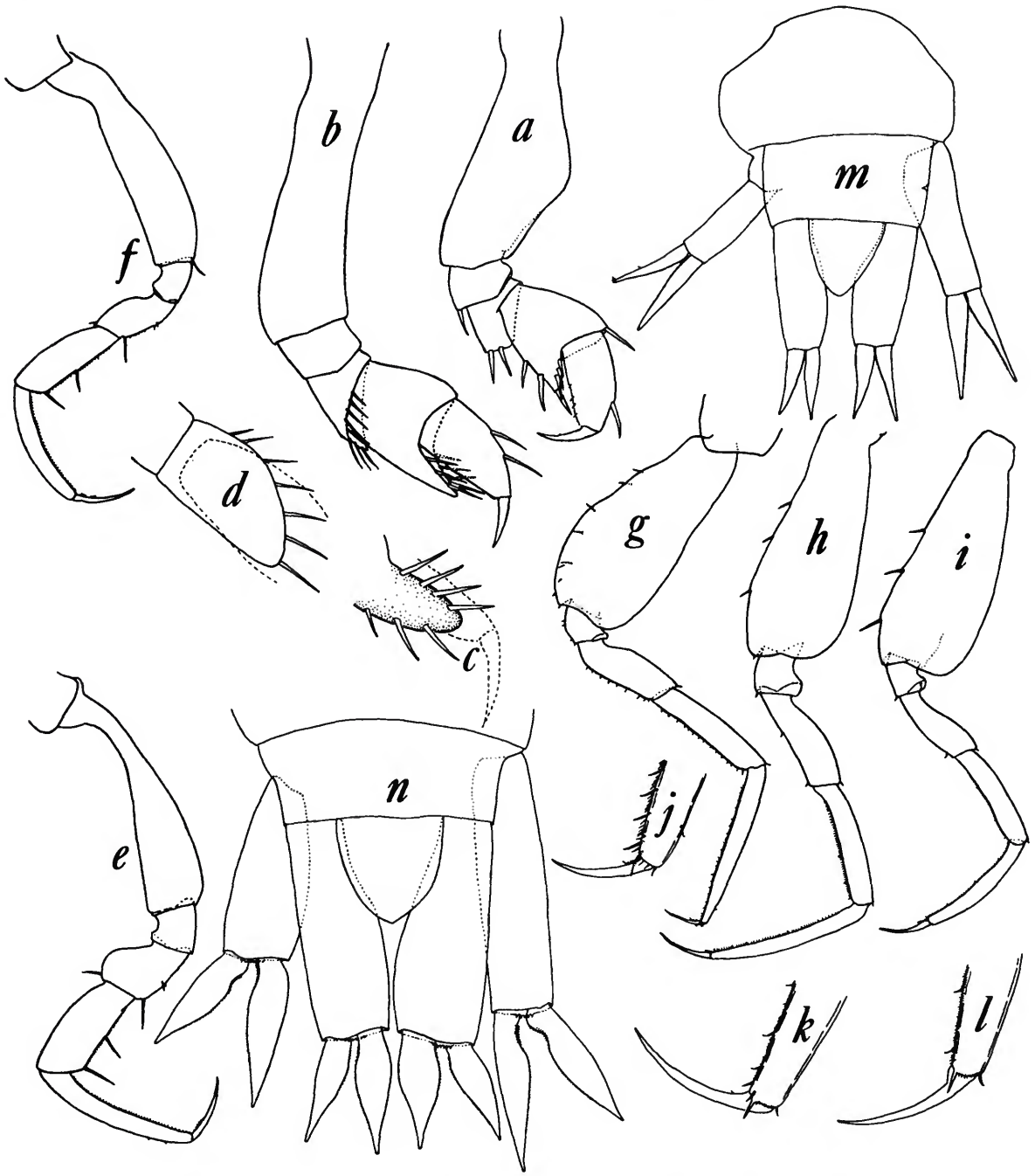


FIGURE 33.—*Lestrigonus shoemakeri* (*a-m*, ♀) *a*, P1; *b*, P2; *c*, carpal process of P2 from above; *d*, meral process of P2 from above; *e*, P3; *f*, P4; *g*, P5; *h*, P6; *i*, P7; *j-l*, dactyl and distal part of propus of P5–7, lateral; *m*, urosome. *n*. ♂ urosome. (*e-i*, *m,n* from off Baja California; *a-d*, *j-l* from off Pacific coast of Nicaragua.)

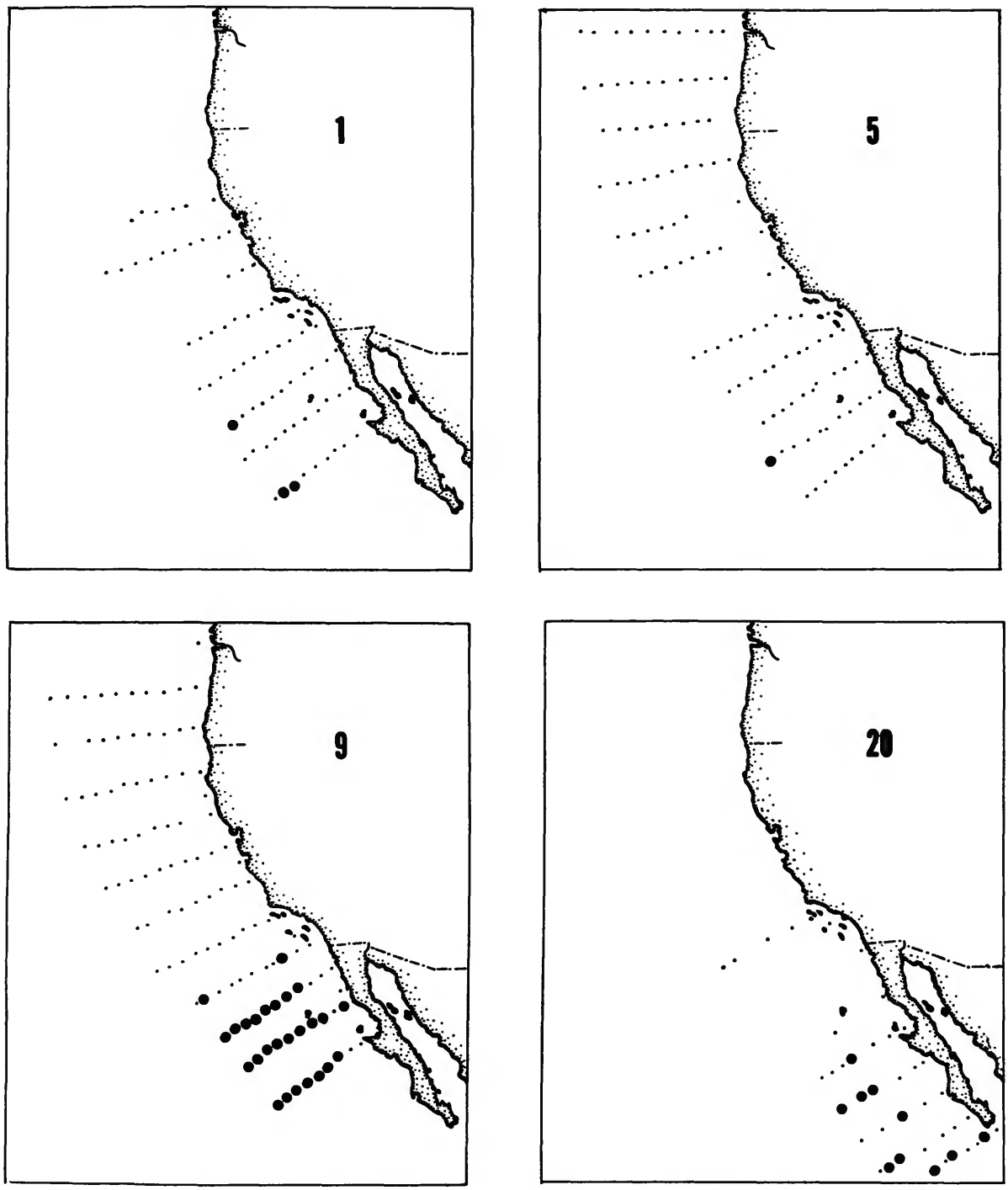


FIGURE 34.—Distribution of *Lestrigonus shoemakeri* on 4 CalCOFI cruises.

adult, present in immature specimens with more than 2 pereonites fused. Gland cone bluntly pointed, overlapping epistome, but not reaching ventral border of buccal mass. Md incisor with 8–9 teeth; lacinia with 7–8 teeth. Mx1 inner lobe with 3 long terminal spines and 1 shorter subterminal spine. Mx2 outer lobe with 1 subterminal and 2 terminal spines; inner lobe with shorter terminal spine. Mxp outer lobes conical, with about 5 spines along inner margin. S2 of P1 with strong bulge on anterior margin; s4 with 2–4 posterodistal spines; carpal process with 5–6 spines; s6 with single spine near anterior margin. P2 with carpal process more than half as long as s6; s6 with 1–2 spines on anterior margin. P3–4, posterior margins of s5–6 with comb of spinules; s5 with 2 spines, s4 with 1 spine on posterior margin. P5–7 with moderately broad s2 armed with a few spines on anterior margin; s5–6 with comb of spinules on anterior margin; s7 of P5 with a few anteroproximal spinules; s6 of P6–7 with spine on distal margin overlapping s7 medially. Telson of ♀ nearly ⅗, of ♂ about half as long as Up3 protopod.

VARIATION.—As in *Lestrigonus schizogeneios* more pereonites are fused in juveniles than in adults. The youngest free-living individuals have pereonites 1–5 fused. With increasing maturity the number of pereonites fused decreases until the adult condition is reached: pereonites 1–4 fused in the female, 1–2 fused in the male.

DISTRIBUTION.—Thus far I have identified *L. shoemakeri* only in samples from the warmest stations of the 4 CalCOFI cruises (Figure 34) and in a few samples in the eastern equatorial Pacific: (1) a few miles north of Clipperton Island; (2) west of Nicaragua, 12°35′N, 93°40′W; (3) west of Costa Rica, 10°03′N, 88°52′W; (4) west of Panama, 7°36′N, 85°09′W; (5) near the Galapagos Islands, 00°07′S, 86°55′W. These few records suggest that when better known the distribution of *L. shoemakeri* may be similar to that of *Euphausia eximia* and the other euphausiids that Brinton (1962) classifies as eastern Pacific equatorial species.

17. *Lestrigonus macrophthalmus* (Vosseler)

FIGURE 35

Hyperia macrophthalma Vosseler, 1901:70–72, pl. 6: fig. 16–25.—Yang, 1960:19–28, figs. 4–5.—Dick, 1970:56.

[?] *Hyperia hydrocephala* Vosseler.—Dakin & Colefax, 1940: 121, fig. 206a-c.

DERIVATION OF NAME.—Not given, presumably from the Greek μακρος [=long] + οφθαλμος [=eye]. Although Vosseler was technically incorrect grammatically in giving the noun thus formed a feminine ending and thereby treating it as an adjective (the correct adjective would have been *macrophthalmata*), I will continue the practice of other authors in considering the name an adjective.

TYPE-LOCALITY.—Six stations of the Plankton-Expedition in the tropical Atlantic.

DIAGNOSIS.—Length of ♀ 2–3.5 mm, of ♂ 3–4 mm. Head more globular than in other species, more than half as long as high, about as long as pereonites 1–4 combined. Pereonites 1–4 fused in ♀, 1–2 fused in ♂. Gland cone bluntly rounded below, in ♀ reaching or extending slightly beyond ventral border of buccal mass, in ♂ not reaching this border. Md incisor and lacinia with 7 teeth in immature ♀ dissected. Mx1 outer lobe with somewhat tapering apex extending well beyond distomedial spine. Mxp outer lobes slender, with 2 terminal setae and 2–3 setae on medial margin; inner lobe with 2 terminal spines. S2 of P1 with strong convexity on anterior margin; s4 with 2 posterodistal spines; s6 with 1 (♀) or 2 (♂) spines on anterior margin. P2 with carpal process about half as long as s6; s6 with 1 (♀) or 2 (♂) spines on anterior margin. S7 of P5 about ⅓–¼ length of s6, ¼ shorter than s7 of P6–7, armed with a few anteroproximal spinules; s6 of P6–7 with spine on distal margin overlapping base of s7 medially. Telson triangular, in ♀ about half, in ♂ less than half as long as protopod of Up3.

VARIATION.—As in other species of *Lestrigonus* the number of fused pereonites is greater in immature specimens, but never exceeds 5.

RELATIONSHIPS.—This species agrees with *L. latissimus* in having pereonites 1–4 fused in the female, but is distinguished by its smaller size and more globular head. In lateral view the gland cone overlaps the epistome less in *macrophthalmus* than in *latissimus*. Up protopod is more slender and longer in relation to the telson than in *L. latissimus*. S6 of P1–2 bears a single spine, whereas in *L. latissimus* s6 usually has 2 spines, but has 1 in immature specimens and in some adults. S7 of P5 is relatively shorter in *latissimus* than in *macrophthalmus*.

H. hydrocephala has been considered identical with *H. macrophthalma*, but I consider it to be an

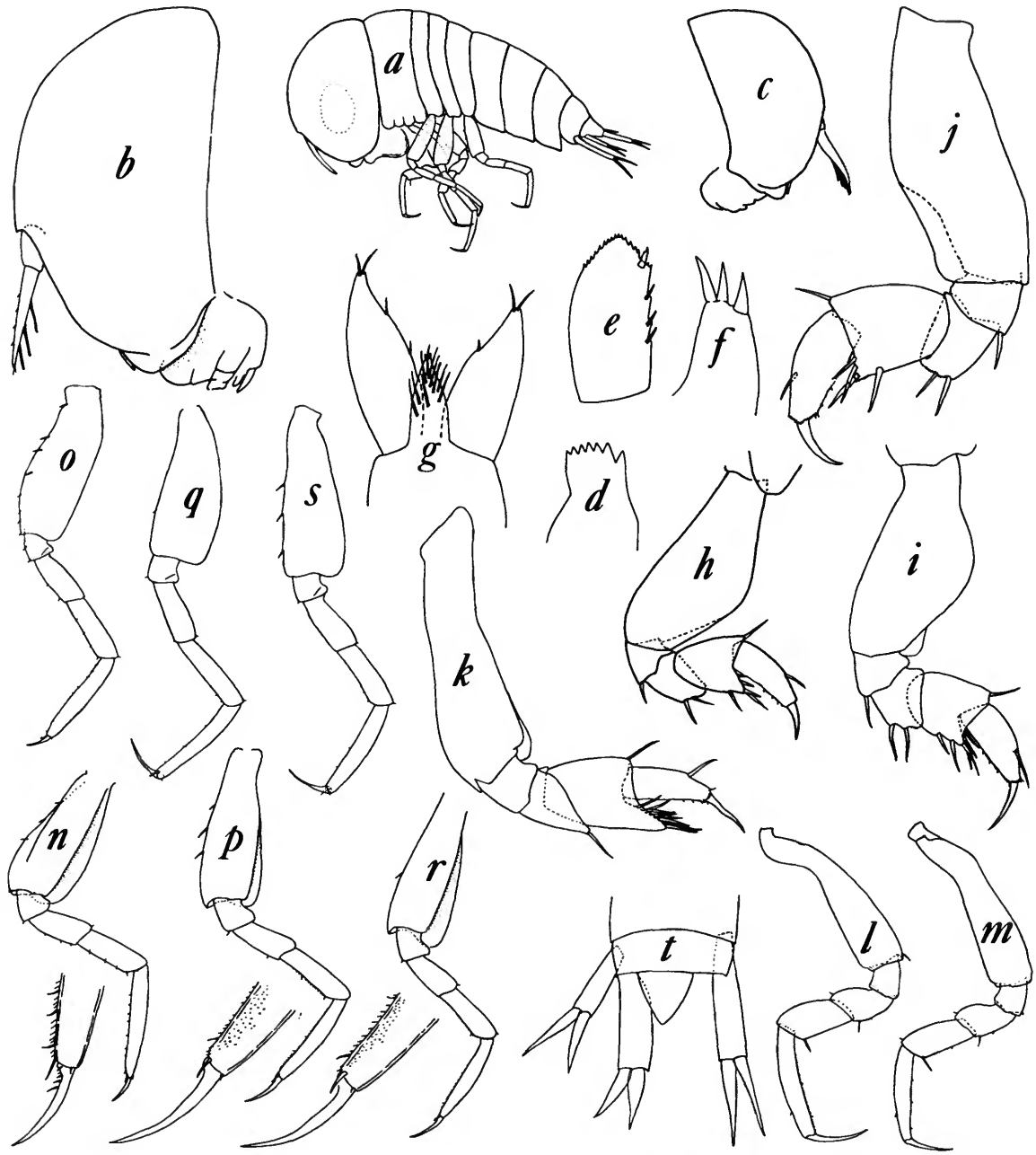


FIGURE 35.—*Lestrigonus macrophthalmus*, ♀: *a*, lateral view; *b-c*, head, lateral; d, incisor, right Md; *e-f*, outer lobe and palp of Mxl; *g*, Mxp; *h-j*, P1; *k*, P2; *l*, P3; *m*, P4; *n-o*, P5; *p-q*, P6; *r-s*, P7; *t*, urosome. (*a*, *i*, *k-m*, *o*, *q*, *s*, *t* from East China Sea [Albatross station 4909]; *b,j* from off South Carolina [T. N. *Gill* Cruise 3, station 59]; *d-g*, *n*, *p*, *r* from Sargasso Sea [Weather station "E"]; *c*, *h* from Gulf of Guinea [*Ombango* Cruise 14, station 329].)

immature *L. latissimus* (see discussion under the latter species). Dakin and Colefax's (1940) *H. hydrocephala* has the globular head of *L. macrophthalmus* and may be a young specimen in which pereonites 1–5 are fused.

DISTRIBUTION.—Tropical parts of the Atlantic, Pacific, and Indian Oceans. Not found in the CalCOFI area.

18. *Lestrigonus latissimus* (Bovallius)

FIGURE 36

Hyperia latissima Bovallius, 1889:229–232, pl. 11: figs. 26–36.—Vosseler, 1901:67.—Chevreux & Fage, 1925:404–405.—Stephensen, 1928:590.—Candeias, 1934:4, fig. 3.—Vives, 1966:96, table 19; 1968:460, table 1.

Hyperia hydrocephala Vosseler, 1901:74–76, pl. 6: figs. 26–28, pl. 7: figs. 1–5.—Steuer, 1911:677–679, pl. 2.—Stephensen, 1924:91–92, Chart 14.—Gamulin, 1948:21.

Hyperia sp. ? *hydrocephala* Vosseler.—Pesta, 1920:30–31, fig. 5a-c.

Hyperia bengalensis (Giles).—Shoemaker, 1945b:238; 1948: 12–13.

DERIVATION OF NAME.—Not given; presumably from the Latin "latus" [=broad], referring to the plump body.

TYPE-LOCALITY.—"The Southern temperate region of the Atlantic" (Bovallius, 1889).

DIAGNOSIS.—Length of ♀ 2–3 mm, of ♂ 3–4 mm. Head about 2.2 times as high as long, shorter than pereonites 1–4 combined. Pereonites 1–4 fused in ♀, 1–2 fused in ♂. Gland cone bluntly round below, not reaching ventral border of buccal mass. Md incisor and lacinia with 10 teeth. Mx1 outer lobe with truncate apex. Mxp outer lobes slender, with 3 apical setae and 2–4 setae on medial margin. P1 with pronounced bulge on anterior margin of s2; s4 with 4 posterodistal spines; s6 with 1 or 2 spines on anterior margin. P2 carpal process about half as long as s6; s6 with 2 spines on anterior margin. S7 of P5 about ¼-⅕ length of s6, ⅓ shorter than s7 of P6–7, armed with a few anterodistal spinules; s6 of P5–7 with spine on distal margin overlapping base of s7 medially. Telson triangular, in ♀ about ⅗, in ♂ about ½ as long as protopod of Up3.

RELATIONSHIPS.—*L. latissimus* is very similar to *L. shoemakeri,* but the two species appear to be allopatric, the former inhabiting the Atlantic, the latter the Pacific. The partial sutures on fused pereonites 1–4 of *L. shoemakeri* are absent in *L. latissimus. L. macrophthalmus* has a distinctly more globular head and is a smaller species.

I believe Vosseler's *H. hydrocephala* is an immature *L. latissimus* in which pereonites 1–5 are fused and not, as Stephensen (1924) maintained, conspecific with *L. macrophthalmus.* I have examined the specimens identified by Stephensen (1924) as *H. hydrocephala* from *Thor* station 224. The sample contains mature females with pereonites 1–4 fused and immature females with pereonites 1–5 fused. S6 of P1 has 1 spine on the anterior margin in immature specimens; mature specimens usually have 2 spines, but some have only 1. The *Thor* specimens agree with *L. latissimus* rather than with *L. macrophthalmus* in body size, gland cone-buccal mass relationship, and length of the telson in relation to Up3 protopod. Contrary to Stephenson's opinion, therefore, I consider *macrophthalma* to be distinct from *hydrocephala,* and believe the latter to be an immature *L. latissimus.*

DISTRIBUTION.—Reliably known only from the eastern Atlantic and the Mediterranean.

19. *Lestrigonus bengalensis* Giles

FIGURES 37–38

Lestrigonus bengalensis Giles, 1887:224–227, plates 6–7.

Hyperia bengalensis (Giles).—Bovallius, 1889:199–201, fig. [copied from Giles].—Walker, 1904:235; 1909:51.—Nayar, 1959:46–47, plate 16: figs. 1–5.

Hyperia dysschistus Stebbing, 1888:1388–1391, plate 167.—Bovallius, 1889:204–206, plate 11: figs. 1–2.—Spandl, 1924a: 23; 1924b:265.

Hyperia thoracica Bovallius, 1889:233–236, plate 11: figs. 37–41.—Vosseler, 1901:73–74, plate 6: figs. 1–4.—Stephensen, 1924:91.—Lewis and Fish, 1969:9.

Hyperia gilesi Bovallius, 1889:236–239.

Hyperia atlantica Vosseler, 1901:67–70, plate 6: figs. 5–15.—Yang, 1960:28–33, figs. 6–7.—Dick, 1970:55.

Hyperia latissima Bovallius.—Barnard, 1930:410–411 [misidentification].

Hyperia hydrocephala Vosseler.—Dakin and Colefax, 1940: 121, fig. 206 [misidentification].

DERIVATION OF NAME.—Not given, presumably geographical (Bay of Bengal).

TYPE-LOCALITY.—"About 100 miles from land in the Bay of Bengal, the depth of the water in the locality being 850 fathoms."

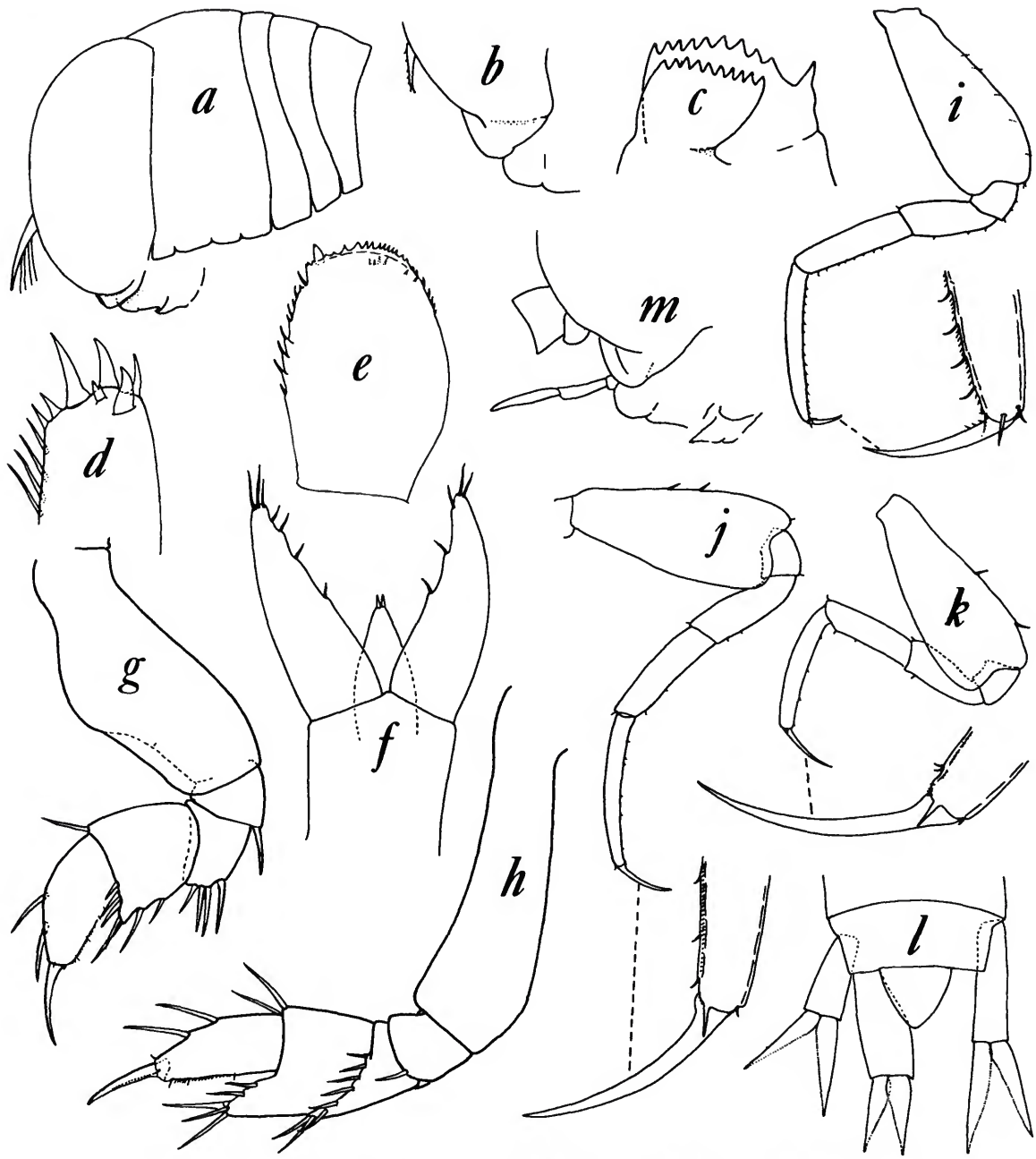


FIGURE 36.—*Lestrigonus latissimus* (*a-l*, ♀): *a*, head and pereon, lateral; *b*, ventral part of head, lateral; *c*, incisor of left Md; *d-e*, Mxl, outer lobe and palp; *f*, Mxp; *g*, P1; *h*, P2; *i*, P5; *j*, P6; *k*, P7; *l*, urosome; *m*, ventral part of ♂ head, lateral. (*a* from *Thor* station 224; *b-f*, *i-l* from *Ombango* Cruise 12, station 300; *g-h* from *Ombango* Cruise 14, station 329; *m* from *Ombango* Cruise 13, station 308.)

DIAGNOSIS.—Length of ♀ 2–2.5 mm, of ♂ 2.8–3.4 mm. Head of ♀ about twice, of ♂ about 1.6 times as high as long. Pereonites 1–5 fused in ♀, 1–4 fused in ♂. Gland cone of ♀ produced anteroventrally, overlapping and extending anterior to epistome; apex bluntly rounded; posterior margin subparallel to body axis. Gland cone of ♂ produced ventrally as rounded lobe, extending only slightly anterior to epistome. Md incisor with 8 teeth; lacinia with 7 teeth. Mx1 inner lobe with 3 long terminal spines and 1 shorter subterminal spine. Mx2 outer lobe with 1 subterminal and 2 slender terminal spines; inner lobe with 1 shorter terminal spine. S2 of P1 with strong bulge on anterior margin; s4 with 2 posterodistal spines; s5 with 1–2 spines on posterior margin and 3 on carpal process; s6 with single spine near posterior margin. S2 of P2 quite broad for a *Lestrigonus*; carpal process slightly less than half as long as s6, with 7 marginal spines. P3–4, posterior margins of s5–6 with comb of spinules; s4–5 with posterodistal spine. P5–7 with moderately broad s2 armed with 2–4 spines on anterior margin; s5–6 with comb of spinules on anterior margin; s7 of P5 7/8 as long as s7 of P6–7, armed with a few anteroproximal spinules; s7 of P6–7 sometimes with 1–2 anteroproximal spinules; s6 of P6–7 with spine on distal margin overlapping s7 medially. Telson of ♀ slightly more than 1/2, in ♂ about 3/8 as long as Up3 protopod.

VARIATION.—It is entirely possible that more than 1 species of *Lestrigonus* agrees with the above diagnosis. There is a noticeable variation in some characters in different populations included here under *L. bengalensis*, and illustrations are provided to show some of the variation in the armature of the distal segments of P5–7. Until sufficient collections for an adequate study of variations are available, I am including all *Lestrigonus* with 5 pereonites fused in the ♀ and 4 in the ♂ under *L. bengalensis*, realizing that this may be a gross oversimplification. There is some indication from available collections that *L. bengalensis* inhabits coastal waters, which would lead to populations becoming isolated and tending to differentiate from one another.

Stebbing's (1888) drawing of an immature male *H. dysschistus* in lateral view (plate 167) shows a complete suture between pereonites 1 and 2 and fusion of pereonites 2–5. This suture is not mentioned in Stebbing's description, which states that pereonites 1–5 are fused. I have examined the holotype of *H. dysschistus* and can confirm the complete fusion of pereonites 1–5. Nevertheless, Bovallius (1889) considered a free pereonite 1 to be the outstanding diagnostic character of *H. dysschistus* and stated that he had examined specimens which exhibited this peculiar segmentation. Spandl (1924a, 1924b) also claimed to have identified similar specimens of *H. dysschistus*.

Among the hundreds of specimens of *Lestrigonus* that I have examined, I have never found one with pereonite 1 free and succeeding pereonites fused, and I am convinced that such a condition does not exist in this genus. I suggest that Stebbing, Bovallius, and Spandl all mistook muscle bands or some other structure beneath the integument for a suture. Such a mistake can be expected in the study of small hyperiids, where sutures and other markings on the rather delicate and semitransparent cuticle are often less apparent than subcuticular structures. Such internal structures have frequently been mistaken for sutures between the coxae and their pereonites. In his lateral view of *Hyperia dysschistus* Stebbing shows free coxae, as he also does for *Hyperia schizogeneios* on plate 168. Bovallius (1889) shows distinct coxae on *Hyperia fabrei, H. promontorii, H. crucipes, H. latissima,* and *H. thoracica,* none of which have them. Other carcinologists who have portrayed species of *Lestrigonus* with what appear to be sutures between the coxae and their pereonites are Chevreux, Hurley, Irie, and Stephensen.

Giles (1887) described *Lestrigonus bengalensis* as having 7 free pereonites, but remarked on "the junction between the pleura and the coxal plates being hard to make out, as are also the junctions of the terga of the first 5 thoracic segments." In his illustrations the adult male has 7 free pereonites, but an immature male is shown with pereonites 1–5 fused and a female with pereonites 1–5 fused. Bovallius (1889) placed *H. bengalensis* among the species with 7 free pereonites, but it seems evident that Giles portrayed correctly the condition of the female and young male; *L. bengalensis* has pereonites 1–5 fused in the ♀ and 1–4 in the male.

The specimens that Barnard (1930) identified as *Hyperia latissima* are placed here under *L. bengalensis* because of Barnard's statement "The present

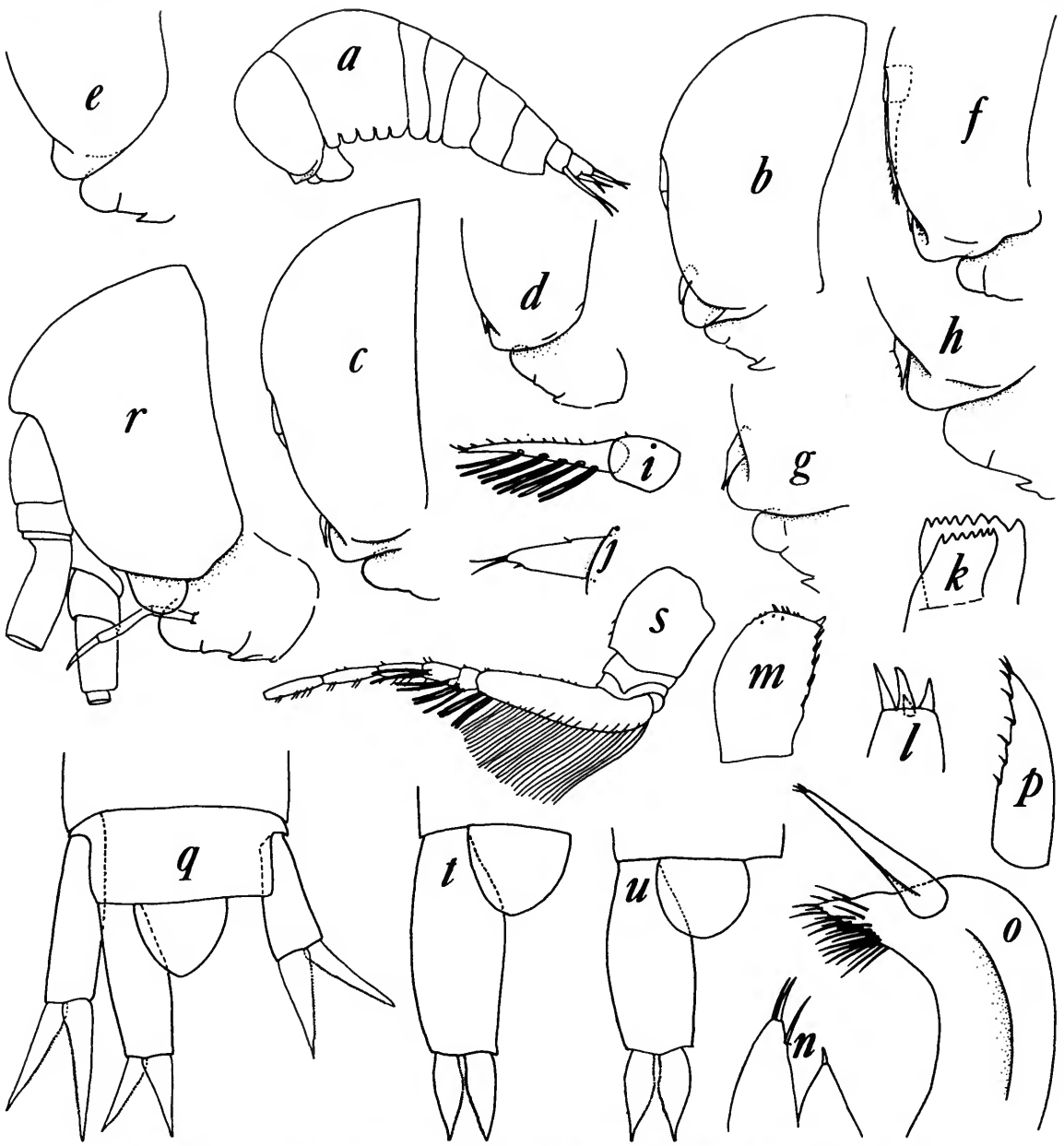


FIGURE 37.—*Lestrigonus bengalensis* (*a-q*, ♀): *a*, lateral view; *b-c*, head, lateral; *d-h*, ventral part of head, lateral; *i*, A1; *j*, A2; *k*, incisor and lacinia of left Md; *l-m*, outer lobe and palp of Mx1; *n*, Mx2; *o*, Mxp, lateral; *p*, outer lobe of Mxp, posterior; *q*, urosome; *r*, ♂ head, lateral; *s*, ♂ A1; *t-u*, ♂ telson and Up3. (*a*, *i*, *s*, *t* from off southern Baja California; *b*, *g* from Gulf of Camby, India; *c*, *h*, *j-q* from off Pacific coast of Central America; *d*, from off Savannah, Georgia; *e* from Gulf of Guinea; *f*, *r* from Bora Bora, Society Islands; *u* from Moorea, Society Islands.)

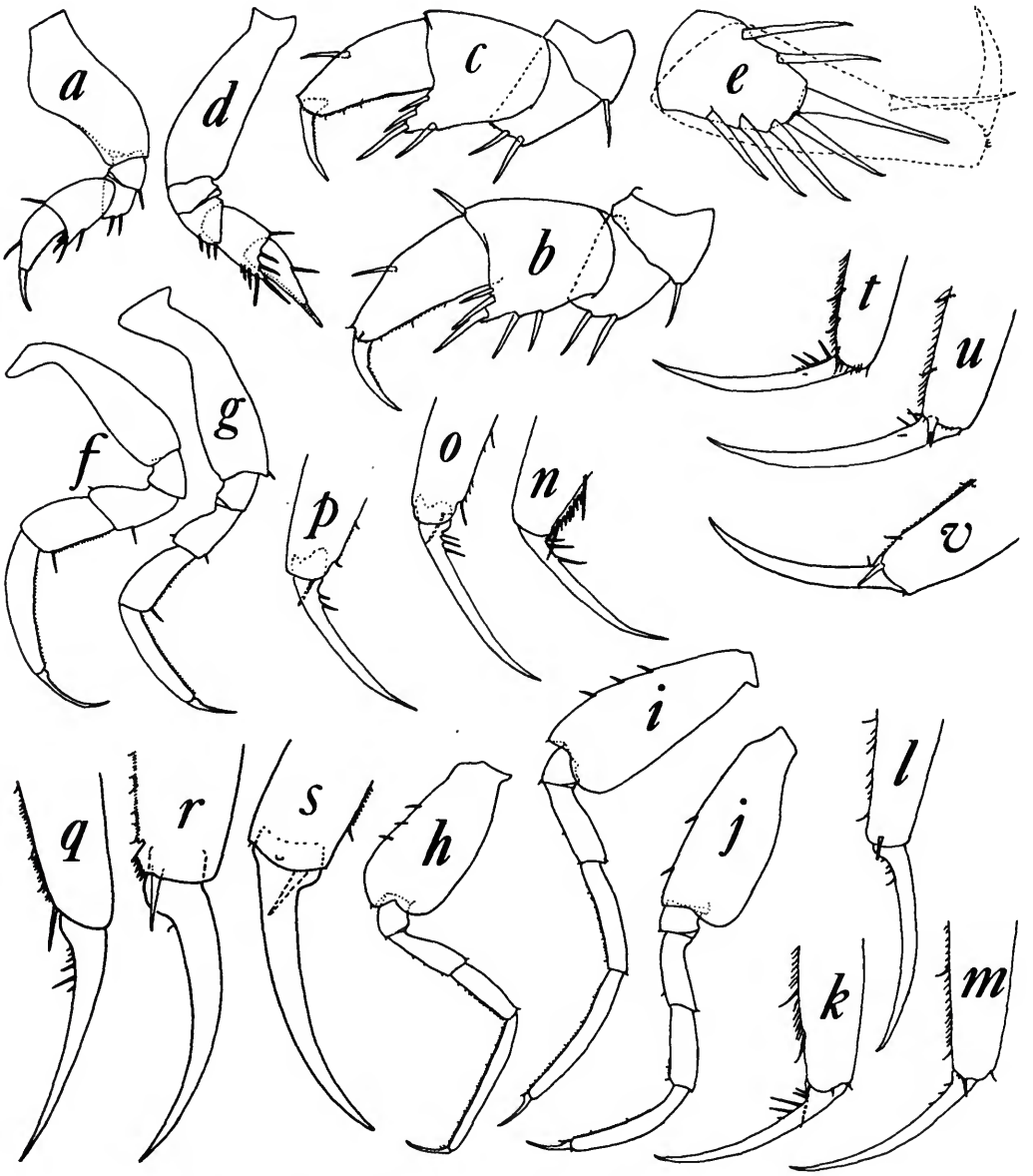


FIGURE 38.—*Lestrigonus bengalensis* (*a-s*, ♀): *a-c*, P1; *d*, P2; *e*, P2, carpal process from above; *f*, P3; *g*, P4; *h*, P5; *i*, P6; *j*, P7; *k-s*, dactyls of P5–7; *t-v*, dactyls of ♂ P5–7, from Moorea, Society Islands. (*a*, *d*, *f-j* from off Baja California; *b*, *e* from off Pacific Coast of Central America; *c* from Gulf of Cambay; *k-m* from off Savannah, Georgia; *n-p* from Gulf of Cambay, India; *q-s* from off Pacific coast of Nicaragua.)

specimens have segments 1–4 in ♂, 1–5 in ♀ coalesced."

DISTRIBUTION.—Worldwide in tropical waters, tending to occur in coastal waters.

V. *Hyperietta*, new genus

DIAGNOSIS.—Small species, with body rather compressed laterally. Head rather short anteroposteriorly; eyes occupying most of its surface. Pereonites 1–2 fused in both sexes. Coxae fused with pereonites. Telson inserted distinctly anterior to insertion of Up3 peduncle; ♀ telson at least half as long as Up3 protopod. Epistome small, inconspicuous. ♀ A1 2-merous. ♀ A2 1-merous, rudimentary; gland cones rather inconspicuous, in anterior view converging medially. Md with smooth incisor and dentate lacinia; molar narrow; palp absent in ♀. Mxl outer lobe with 3 terminal spines. Mxp outer lobes fused medially; inner lobe rudimentary. P1 simple, weakly subchelate, or barely chelate. P2 chelate, with spoon-shaped carpal process bearing marginal spines. ♀ P3–4 with 1 conspicuous spine on posterior margin of s4, 2 spines on posterior margin of s5; ♂ P3–4 with shorter spines in same positions. Distal margin of s6 of P6–7 and sometimes of P5 produced into spinose lobe medial to base of s7; s7 unarmed. Up 1–3 slender; margins of rami smooth or with extremely fine serrations.

DERIVATION OF NAME.—Diminutive of *Hyperia*, gender feminine.

TYPE-SPECIES.—By present designation, *Hyperia luzoni* Stebbing.

20. *Hyperietta luzoni* (Stebbing)

FIGURES 39–40

Hyperia luzoni Stebbing, 1888:1382–1384, pl. 166A.—Bovallius, 1889:212–214.—Lo Bianco, 1902:424, 425, 446 [identification by Vosseler]; 1903:table facing p. 278 [identification by Vosseler]; 1904:42.—Stewart, 1913:255.—Stephensen, 1924: 84–86, fig. 34, Chart 12.—Pirlot, 1929:122–123; 1939:35.—Barnard, 1930:410.—Hurley, 1960b:279; 1969:pl. 19 [map].—Kane, 1962:301.

[not] *Hyperia luzoni* Stebbing.—Vosseler, 1901:64–66, pl. 5: figs. 16–28.—Stebbing, 1904:33–34.

DERIVATION OF NAME.—Not given, presumably for the type-locality.

TYPE-LOCALITY.—South China Sea, west of Luzon Island, Philippines, 16°35′N, 117°47′E.

DIAGNOSIS.—Length of ♀ 2–3 mm, of ♂ 3–4 mm. Head slightly more than twice as high as long, about half as long as pereon. Gland cone just reaching or barely exceeding ventral margin of head, posteroventrally overlapping anterior part of buccal mass. Mxp outer lobes subpyriform, bearing a few setae on distal margin and on shelf. P1 simple; s2 sinuate, proximal part strongly bulging anteriorly, distal part much narrower; s5 twice as long as wide, with 1 spine at midlength and 2 at distal end of posterior margin; s6 with 1 spine at midlength of anterior margin. P2 very slender, chelate; s2 about 6 times as long as wide; carpal process ⅓ as long as s6; s6 with 2 spines on anterior margin. P3–4 very slender. P5–7 with moderately broad s2; other segments slender; s4–5 without long spines. Telson round-triangular, slightly longer than wide; in ♀ about ⅝, in ♂ ½ as long as protopod of Up3.

Key to the Species of *Hyperietta*

1. S5 of P5–7 with strong spine on anterodistal corner 3
   S5 of P5–7 without strong spine on anterodistal corner 2
2. P1, anterior margin of s2 evenly convex. P5, s2 about ¾ as wide as long ..... 21. ***H. vosseleri***
   P1, anterior margin of s2 with deeply concave distal part. P5, s2 about 2/3 as wide as long ..... 20. ***H. luzoni***
3. Anterior margin of head in lateral view flattened below insertion of A1. Pereon about 4 times as long as head ..... 24. ***H. parviceps***
   Anterior margin of head in lateral view evenly rounded. Pereon not more than 2–3 times as long as head 4
4. S5 of P1 with spine at midlength of posterior margin. S6 of P1–2 with 1 spine on anterior margin. Mxp with only a few spinules along inner margins of outer lobes 23. ***H. stephenseni***
   S5 of P1 without a spine at midlength of posterior margin. S6 of P1–2 with 2 spines on anterior margins. Outer lobes of Mxp with dense covering of fine setules at apex and few blunt spines on anterior surface ..... 22. ***H. stebbingi***

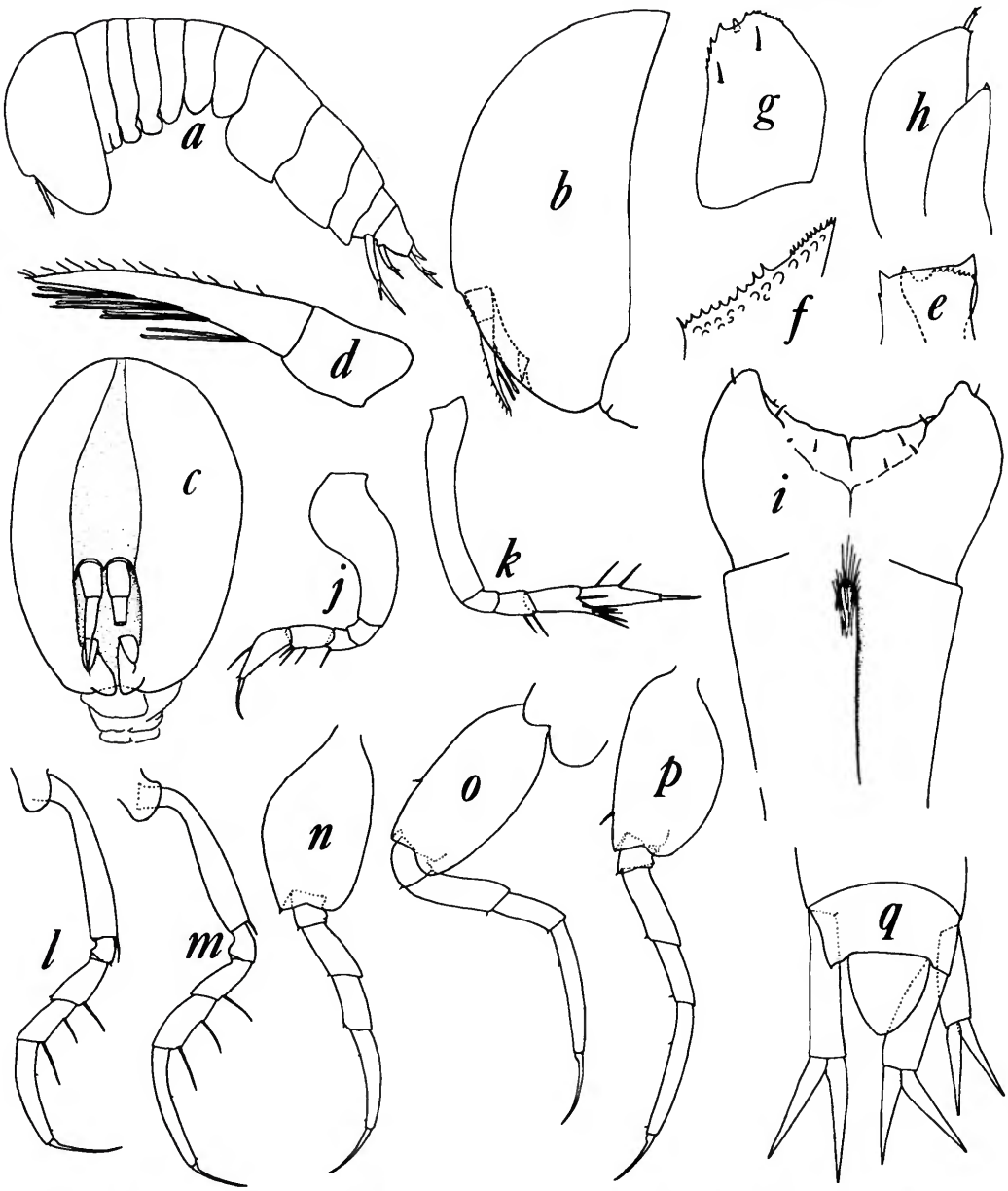


FIGURE 39.—*Hyperietta luzoni*, ♀ off southern California; *a*, lateral view; *b*, head, lateral; *c*, head, anterior; *d*, A1; *e*, left Md, incisor and lacinia; *f*, left Md molar; *g*, Mx1 palp, posterior; *h*, Mx2; *i*, Mxp, anterior *j*, P1; *k*, P2; *l*, P3; *m*, P4; *n*, P5; *o*, P6; *p*, P7; *q*, urosome.

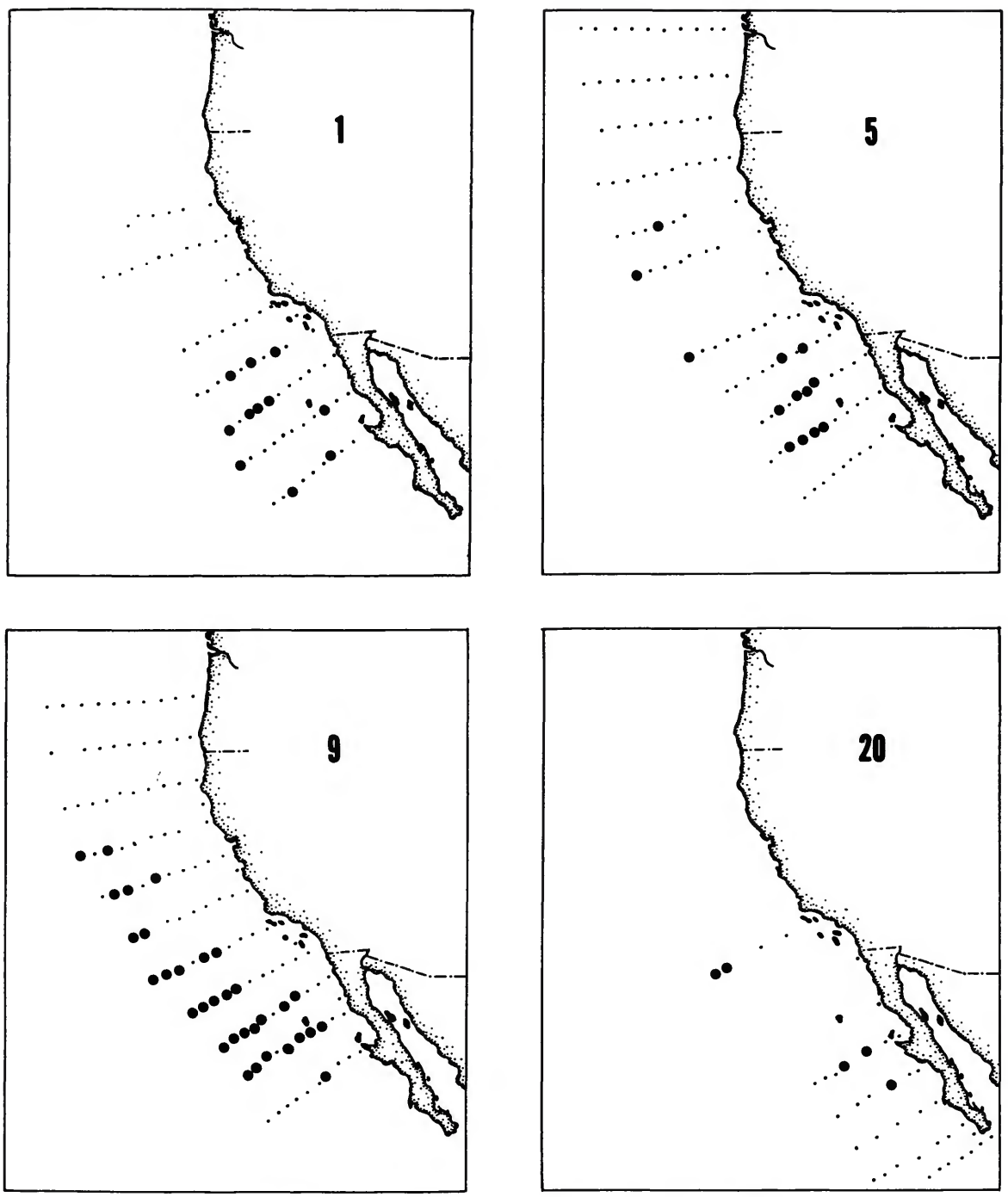


FIGURE 40.—Distribution of *Hyperietta luzoni* on 4 CalCOFI cruises.

RELATIONSHIPS.—The above synonymy includes all references to *H. luzoni* known to me, but only Stebbing's original account and that of Stephensen (1924) can be attributed to this species without question. Two new species described below are very similar to *H. luzoni,* and all three may be found in the same plankton sample. The absence of descriptions or illustrations of *H. luzoni* in the works of most authors who have recorded it makes it impossible to determine from their publications whether they in fact had *H. luzoni* or a similar but different species. Vosseler's (1901) *H. luzoni* is the new species described below as *Hyperietta stebbingi.* The species referred to as *Hyperia luzoni* by Stebbing in 1904 is not *H. luzoni* because of the presence of spines on s5 of P5–7, but might have been either of two new species proposed herein, *Hyperietta stebbingi* or *H. stephenseni.*

Stebbing's (1888) description and figures are of an immature male. Stephensen (1924) described and illustrated the adult male, but the female has not yet been described or figured.

DISTRIBUTION.—Reported by Stebbing (1888) from the Philippines (west of Luzon and Zebu Harbor) and the eastern South Pacific (38°6′S, 88°2′W). Stephensen (1924) listed it from a number of *Thor* Mediterranean and a few Atlantic stations, but it is possible that some of these records may be referable to one of the new species of *Hyperietta* described below.

In the CalCOFI collections it was present off the coasts of southern California and Baja California and farther offshore as far north as the latitude of San Francisco. Its pattern of distribution is consistent with that of *Euphausia brevis* and the other Pacific central euphausiid species (Brinton, 1962) which occupy oceanic gyrals of mid-latitudes 15°–40° in both hemispheres.

I have not found *H. luzoni* in any Atlantic plankton samples.

21. *Hyperietta vosseleri* (Stebbing)

FIGURES 41–42

Hyperia fabrei H. Milne Edwards.—Bovallius, 1889:206–211, pl. 10: figs. 40–55.—Vosseler, 1901:58–60, pl. 5: figs. 5–15.—Stephensen, 1924:83–84.—Spandl, 1924:22–23; 1927:153.—Barnard, 1930:410.—Pirlot, 1939:34.—Hurley, 1955:137.—Reid, 1955:15.—Yang, 1960:33–35, fig. 8.—Kane, 1962:301.—Dick, 1970:55.

Hyperia vosseleri Stebbing, 1904:33–34.—Stewart, 1913:255.—Chevreaux, 1935:189.

DERIVATION OF NAME.—Not given, but obviously after J. Vosseler, who described and illustrated this species in detail.

TYPE-LOCALITY.—Tropical Atlantic.

DIAGNOSIS.—Length of ♀ 2–3 mm, of ♂ 3–4 mm. Head slightly more than twice as high as long, in profile narrowing ventrally more than in other species of *Hyperietta.* ♀ A1 reaching well beyond ventral margin of head. Gland cone extending beyond margin of head; posterior margin slightly concave, separated by short gap from epistome. Left Md with lacinia nearly as wide as incisor, divided into 11–12 sharp teeth. Mxp outer lobes slightly more than 1.5 times as long as wide; apex narrow, bearing dense tuft of setae; distal margin rugose. P1 simple; s2 about twice as long as wide, with evenly convex anterior margin; s6 with single spine on inner surface near anterior margin. P2 chelate; carpal process nearly reaching midlength of s6. P5–7 with very broad s2, especially that of P5, which has very convex anterior margin. Telson about ⅔ as long as Up3 protopod in ♀, slightly less than half as long in ♂.

RELATIONSHIPS.—Stebbing (1904) believed that the species named *Lestrigonus fabrei* by Milne Edwards (1830) was much too large ("long d'environ cinq lignes"=about 11 mm) to be identical with the species called *Hyperia fabrei* by Bovallius (1889) and subsequent authors, which measured only 3–6 mm. Stebbing therefore proposed the name *Hyperia vosseleri* for the smaller species. Most authors have not accepted Stebbing's proposal, but it seems certain that he was correct. Not only is the size difference well beyond the limits of reasonable variation, but the maxilliped is entirely different in the two species. That of *H. vosseleri* has short, broad outer lobes and a rudimentary inner lobe. (Figure 41*f,s*), whereas Milne Edwards (1840, pl. 30: fig. 20) portrays the maxilliped of *L. fabrei* as having long slender outer lobes and a well developed inner lobe (Figure 27*c*). I consider the two species sufficiently distinct that I have placed them in different genera in this paper.

DISTRIBUTION.—Reported from the warm parts of the Atlantic, Pacific, and Indian Oceans. In the CalCOFI area its distribution was quite similar to that of *H. luzoni* (compare Figures 40 and 42), and

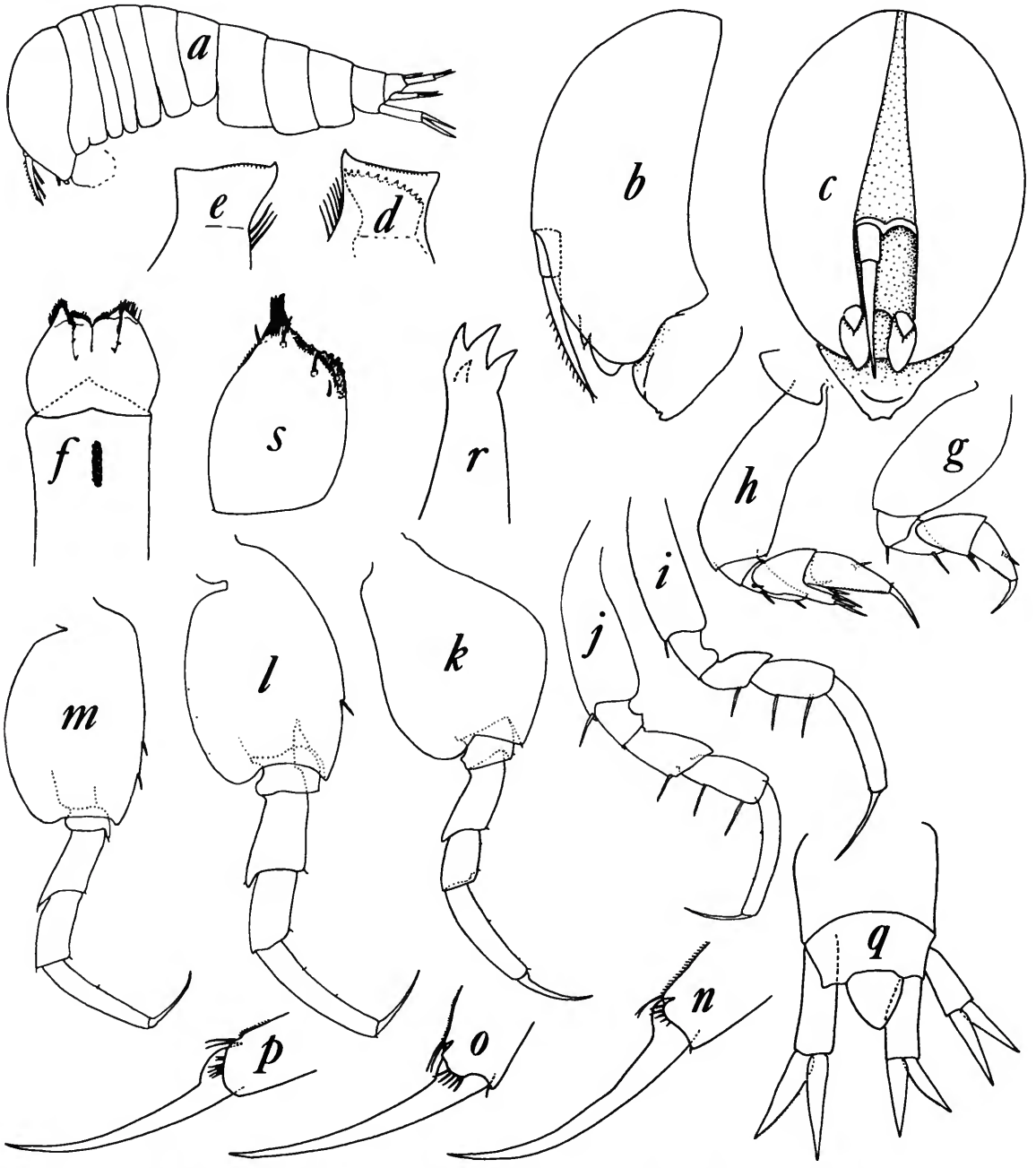


FIGURE 41.—*Hyperietta vosseleri* (*a-q*, ♀, off Baja California): *a*, lateral view; *b*, head, lateral; *c*, head, anterior; *d-e*, incisors of left and right Md; *f*, Mxp, anterior; *g*, P1; *h*, P2; *i*, P3; *j*, P4; *k*, P5; *l*, P6; *m*, P7; *n-p*, dactyls of P5–7, medial; *q*, urosome. (*r-s*, ♂, Gulf of Guinea) *r*, Mx1 inner lobe; *s*, Mxp outer lobe.

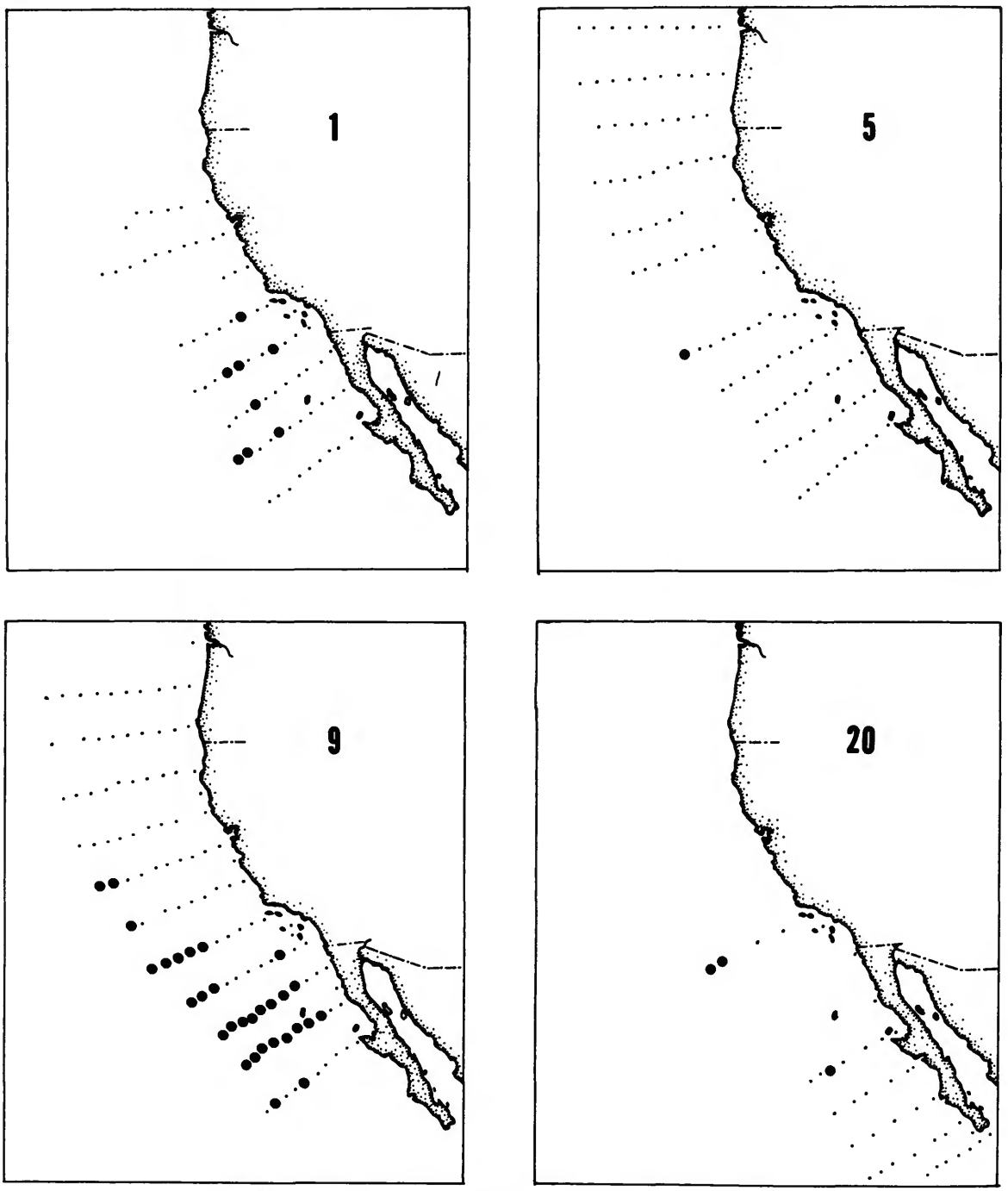


FIGURE 42.—Distribution of *Hyperietta vosseleri* on 4 CalCOFI cruises.

it may be also characterized as a Pacific central species.

22. *Hyperietta stebbingi*, new species

FIGURES 43–45

Hyperia luzoni Stebbing.—Vosseler, 1901:64–66, plate 5: figs. 16–28 [misidentification].

DERIVATION OF NAME.—The species is named for the distinguished English carcinologist, T. R. R. Stebbing.

TYPES.—All from CalCOFI Cruise 9, station 607, 12 November 1949, off central California, 35°58′N, 127°51′W, oblique tow from 66 m to surface. Holotype ♀ USNM 137510, allotype ♂, USNM 137511, 20 ♀ and 7 ♂ paratypes, USNM 137512; 2 ♀ and 2 ♂ paratypes deposited at Scripps Institution of Oceanography.

DIAGNOSIS.—Length of ♀ 2–3 mm, of ♂ 3–4 mm. Head about twice as high as long, evenly rounded ventrally. ♀ A1 reaching ventral margin of head. Gland cone barely reaching ventral margin of head, broadly rounded, separated from epistome by distinct gap in lateral view. Lacinia of left Md with about 8 teeth. Outer lobe of Mxp ⅓ longer than wide, bearing a series of spines on both surfaces near distal margin and scattered minute setules on distal part of anterior margin. S2 of P1 slightly more than twice as long as wide, both margins moderately convex; s5 with very small carpal process bearing 3–4 spines, posterior margin otherwise unarmed; s6 about twice as long as broad, with 2–3 spines on anterior margin. S6 of P2 bearing 2 spines on anterior margin. P6 only slightly longer than P5 and P7; s2 slightly wider in P5 than in P6–7, anterior margin convex and unarmed in P5, with 1 spine in P6, 2 spines in P7; s4 of ♀ with long spine at anterodistal corner, sometimes reduced or absent; s4 of ♂ with 2 shorter spines on anterior margin; s5 of ♀ always with long spine at anterodistal corner; s5 of ♂ with smaller spines at same position. Telson slightly shorter than width at base, in ♀ about ⅔, in ♂ slightly less than half of Up3 protopod.

DISTRIBUTION.—Warm parts of the Atlantic, Pacific, and Indian Oceans. In the CalCOFI area its distribution is similar to that of the much more abundant *Lestrigonus schizogeneios*, and it seems likely that *H. stebbingi* is also a transition zone species.

23. *Hyperietta stephenseni*, new species

FIGURES 46–48

DERIVATION OF NAME.—The species is named for the distinguished Danish carcinologist, Knut Stephensen.

TYPES.—All from CalCOFI Cruise 5, station 801, 13 July 1949, off southern California, 33°19′N, 120°45′W, oblique tow from 71 m to surface. Holotype, ♀, USNM 137507, allotype ♂, USNM 137508, 3 ♀ and 2 immature ♂ paratypes USNM 137509; 2 ♀ paratypes deposited at Scripps Institution of Oceanography.

DIAGNOSIS.—Length of ♀ about 2 mm, of ♂ 3–3.5 mm. Head about twice as high as long, evenly rounded ventrally. ♀ A1 reaching ventral margin of head. Gland cone barely reaching ventral margin of head, broadly rounded, separated from epistome by short gap in lateral view. Lacinia of left Md with about 7 teeth. Mxp like that of *H. luzoni;* outer lobe about ¼ longer than wide, bearing a few spinules on both surfaces near distal margin. S2 of P1 about 2.2 times as long as wide, anterior margin convex in proximal ⅔, concave in distal ⅓; s5 bearing a single spine at midlength of posterior margin and 3 at posterodistal corner; s6 about 3 times as long as wide, bearing a single spine on anterior margin in ♀, 1–2 spines in ♂. S6 of P2 with a single spine on anterior margin in ♀, 1–2 spines in ♂. P6 very slightly longer than P5 and P7; s2 slightly wider in P5 than in P6–7, anterior margin convex and unarmed in P5, nearly straight and bearing 1 spine in ♀, 2 spines in ♂ in P6–7; s4–5 of ♀ with long spines at anterodistal corners; s4–5 of ♂ with shorter anterodistal spine and additional short spines on anterior margins. Telson slightly shorter than width at base, slightly more than half length of Up3 protopod.

DISTRIBUTION.—Warmer parts of the Atlantic, Pacific, and Indian Oceans. In the CalCOFI area its distribution is similar to that of *H. stebbingi* and the much more abundant *Lestrigonus schizogeneios*. It seems likely that *H. stephenseni*, like the latter two species, inhabits the transition zone.

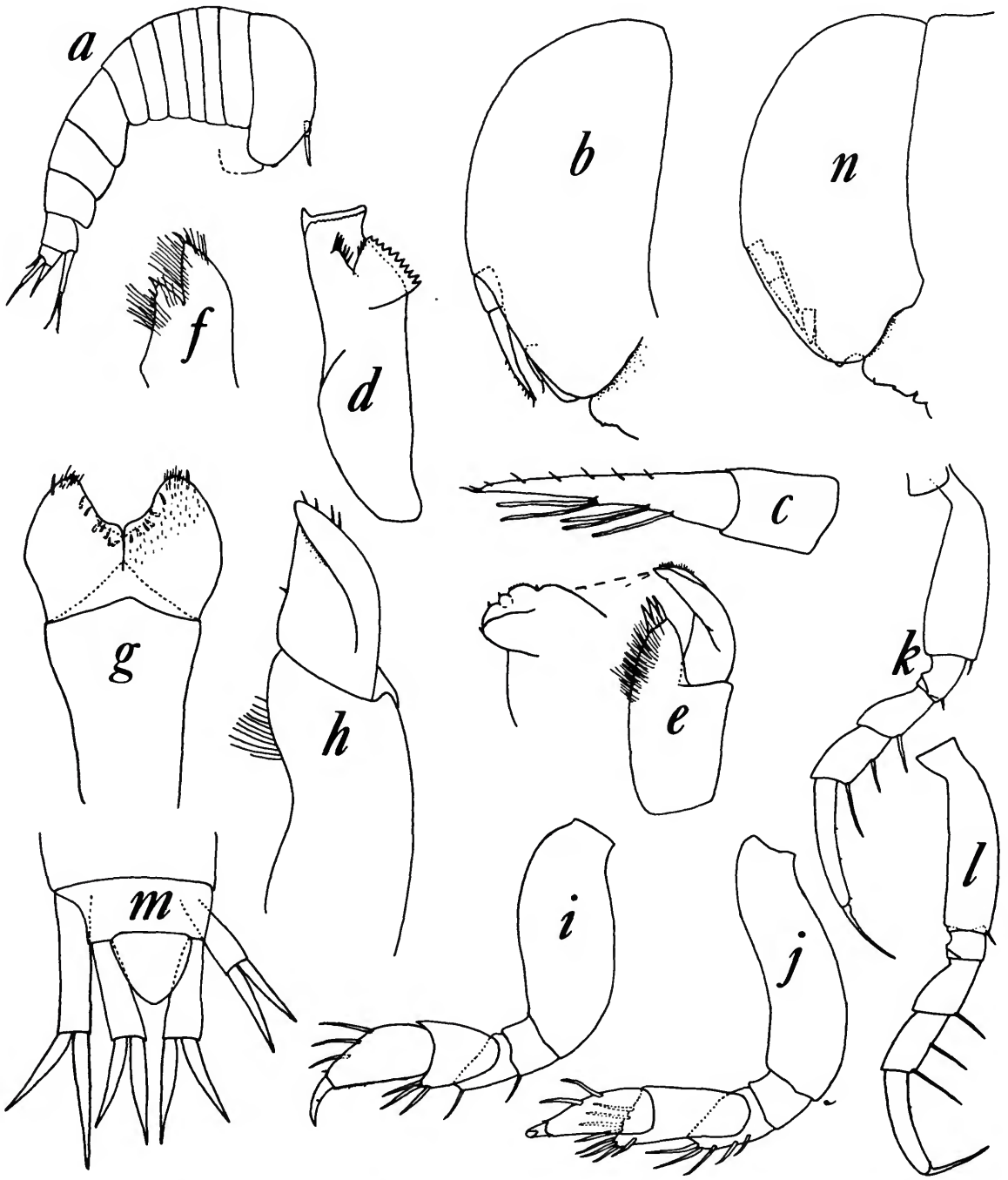


FIGURE 43.—*Hyperietta stebbingi*, ♀ (*a-m*, from off southern California): *a*, lateral view; *b*, head, lateral: *c*, A1; *d*, right Md: *e*, Mx1; *f*, Mx2; *g*, Mxp, posterior; *h*, Mxp, lateral; *i*, P1; *j*, P2; *k*, P3; *l*, P4; *m*, urosome; *n* (from Arabian Sea), head, lateral.

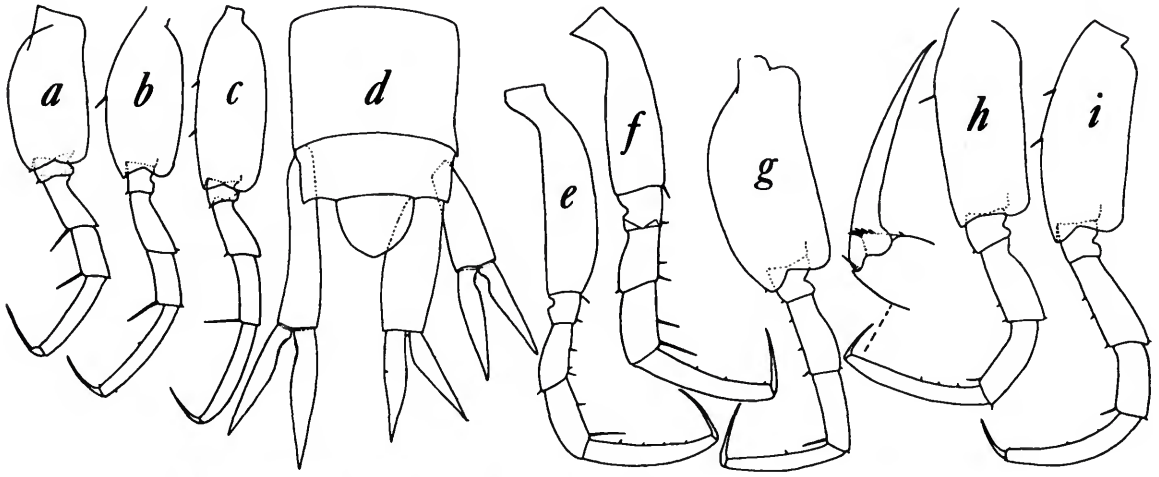


FIGURE 44.—*Hyperietta stebbingi*, from off southern California (*a-c*, ♀): *a*, P5; *b*, P6; *c*, P7; (*d-i*, ♂) *d*, urosome, *e*, P4; *f*, P3; *g*, P5; *h*, P6; *i*, P7.

24. *Hyperietta parviceps*, new species

FIGURES 49–50

DERIVATION OF NAME.—From the Latin "parvi-" [=small] + "-ceps" [=head], referring to the small head compared to other species of *Hyperietta*.

TYPES.—Holotype ♀, USNM 137505, allotype ♂, USNM 137506, both from CalCOFI Cruise 9, station 1011, west of Punta Eugenia, Baja California, 27°56'N, 122°59'W. 3 paratypes (2♀, 1♂) from the same sample have been deposited in the Scripps Institution of Oceanography.

DIAGNOSIS.—Length of ♀ 2–2.5 mm, of ♂ 3–3.5 mm. Head and pereon broader than in other species of *Hyperietta;* head about 1.6 times as broad as long, about twice as high as long, in profile rather flat below insertion of A1. Pereon quite convex dorsally, highest in pereonite 5. Gland cone bluntly rounded, clearly visible in lateral view, separated from epistome by distinct gap. Mxp outer lobe about 1.4 times as long as wide, with many fine setae on anterior surface and a few heavier setae on posterior surface; lateral margin with single long seta. P1 subchelate; s2 slightly more than twice as long as wide; s5 with small carpal process bearing 3 spines and 1 spine on posterior margin; s6 with long spine on anterior margin. P2 with carpal process about ¼ as long as s6, bearing about 6 spines on its margins. P3–7 with rather robust distal segments. P5–7 with strong spine on anterodistal corner of s4–5 of ♀ and s5 of ♂. Telson about as long as wide; in ♀ ⅘, in ♂ half as long as Up3 protopod.

DISTRIBUTION.—Thus far *H. parviceps* has been found only at two stations of CalCOFI Cruise 5 and five stations of CalCOFI Cruise 9, all well offshore in the southern part of the area (Figure 50).

VI. *Themistella* Bovallius, 1887b

DIAGNOSIS.—Small species with rather broad pereon. Head rather broad; eyes occupying most of its surface. Pereonites 1–5 fused in both sexes. Coxae fused with pereonites. Telson very short. ♀ A1 2–merous, rather long. ♀ A2 1–merous, rudimentary; gland cone small. Md with serrate incisor; palp absent in ♀. Mx1 outer lobe with 4 terminal spines plus 2 lateral and 1 medial subterminal spines. Mxp outer lobes narrow, tapering distally; inner lobe almost completely absent, apparently represented by slight unarmed bulge on basal segment. P1–7 with rather broad segments. P1–2 chelate; gauge-shaped carpal process bearing marginal spines. P5 much longer than P6–7. Dactyls of P6–7 with flexure slightly distal to midlength.

DERIVATION OF GENERIC NAME.—Diminutive of *Themisto* (a Greek nymph, daughter of Neptune and Doris); gender, feminine.

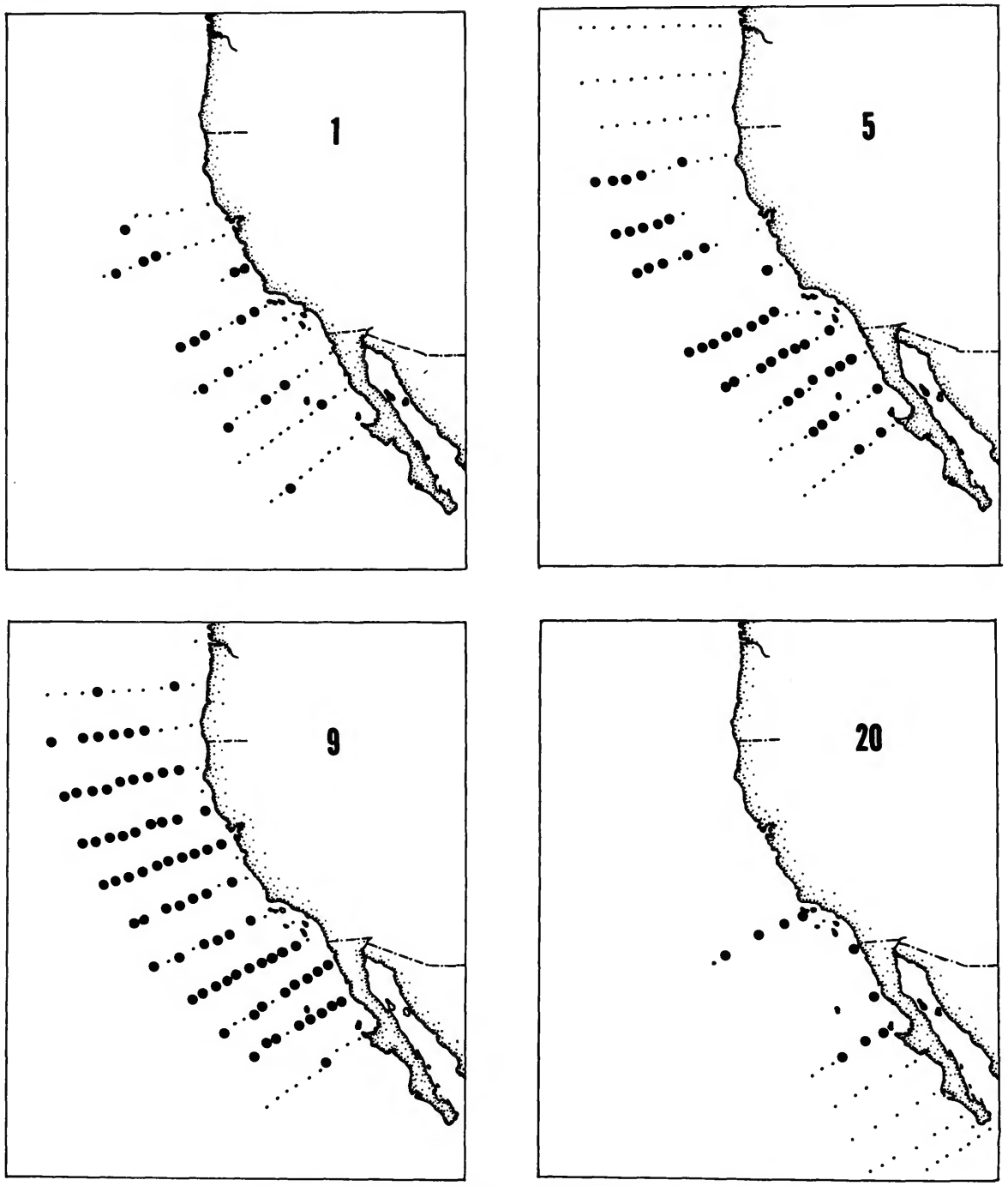


FIGURE 45.—Distribution of *Hyperietta stebbingi* on 4 CalCOFI cruises.

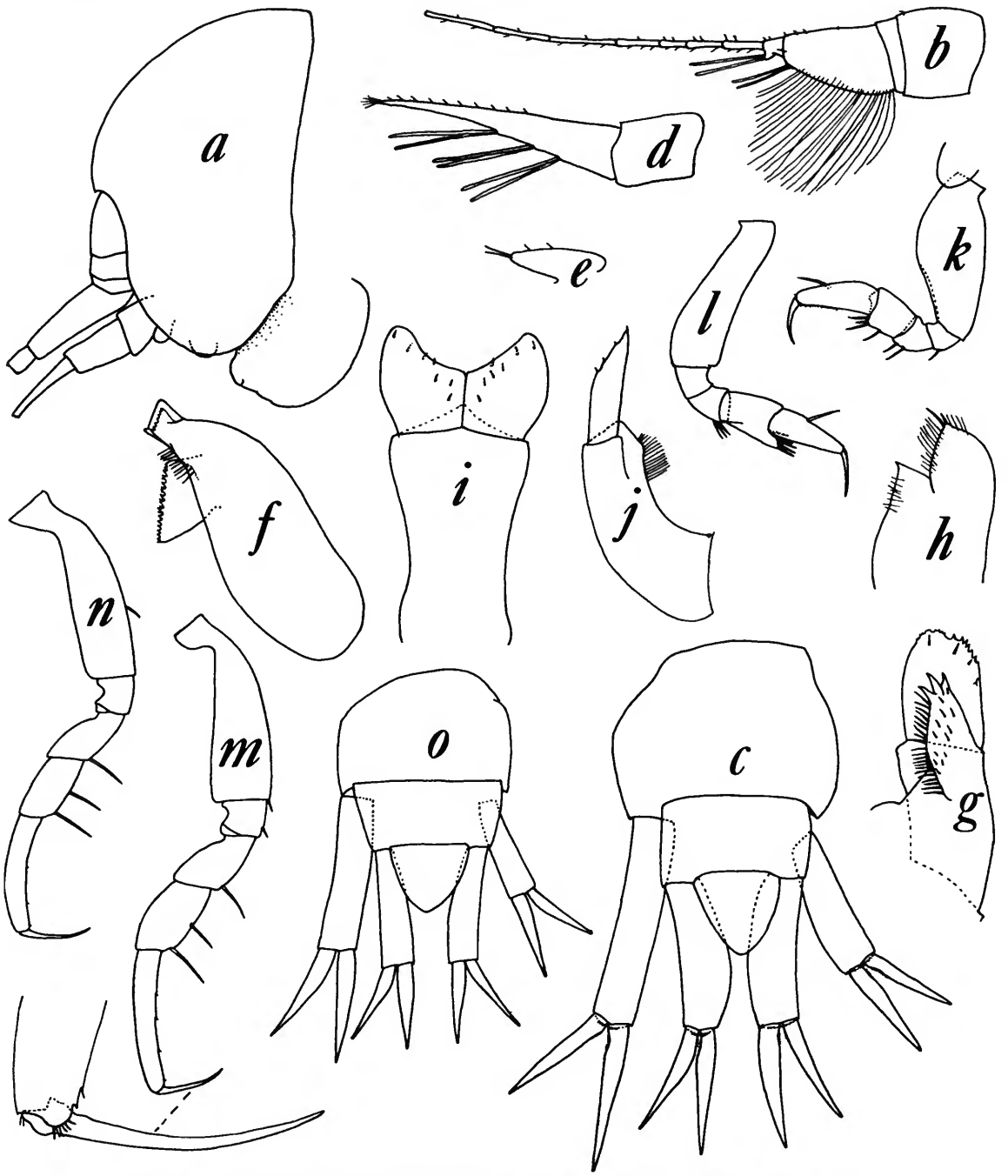


FIGURE 46.—*Hyperietta stephenseni*, from off California (*a-c*, ♂): *a*, head, lateral; *b*, A1; *c*, urosome; (*d-o*, ♀) *d*, A1; *e*, A2; *f*, left Md; *g*, Mx1; *h*, Mx2; *i*, Mxp, posterior; *j*, Mxp, lateral; *k-n*, P1–4; *o*, urosome.

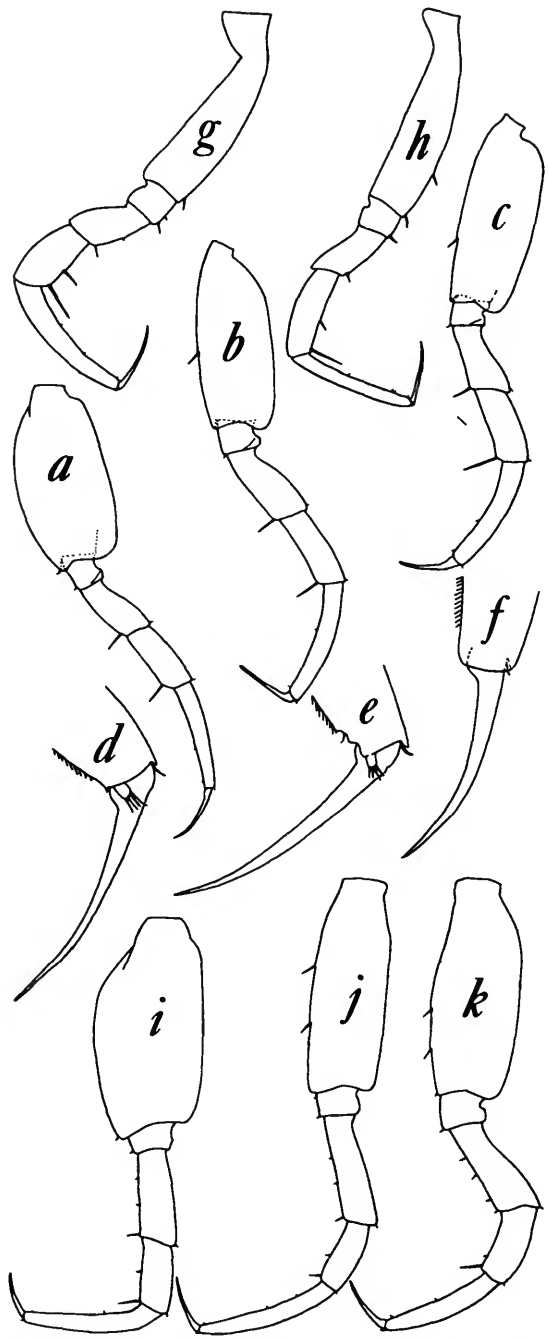


FIGURE 47.—*Hyperietta stephenseni*, from off California (*a-f*, ♀): *a-c*, P5–7; *d-f*, dactyls of P5–7, medial; *g-k*, ♂ P3–7.

TYPE-SPECIES.—By monotypy, *Themistella steenstrupi* Bovallius, 1887b.

REMARKS.—*Themistella* was originally a monotypic genus, but in 1889 Bovallius added to it *Lestrigonus fuscus* Dana (1853). The differences cited by Bovallius for considering the two species distinct are not convincing, since the descriptions and illustrations of both authors lack detail, and neither Dana nor Bovallius can be depended upon for a high degree of accuracy. Hence I am treating the two nominal species as synonyms.

In assigning the amphipod described below to *Themistella* I have assumed two major inaccuracies in the accounts of Dana and Bovallius. The first assumption concerns the number of fused anterior pereonites: for *L. fuscus* "thorax seven-jointed, first segment nearly concealed" (Dana, 1853); for *T. steenstrupi* "The first two peraeonal segments are coalesced, the following are free" (Bovallius, 1889). Bovallius' pl. 13: fig. 47, a lateral view of the male, shows faint sutures separating pereonites 2–5 from one another and heavier sutures on the margins of pereonites 6–7. I suggest that Bovallius misinterpreted muscle bands or other structures as the faint sutures and that his specimens actually had pereonites 1–5 fused.

My second assumption is that Dana and Bovallius did not notice the angular bend in the dactyls of P6–7. It is difficult to believe that this feature, so conspicuous to me, could have been overlooked, but a character that attracts the attention of one author may escape the notice of another.

If the above assumptions are accepted, there is no difficulty in equating the species described below as *T. fusca* with those proposed by Dana and Bovallius. The assumptions may appear overly bold and are to some degree intuitive, but they are based on considerable experience and much frustration in attempting to reconcile the accounts of hyperiid species by the above authors with the characters of specimens thought to belong to their nominal species.

25. *Themistella fusca* (Dana)

FIGURE 51

Lestrigonus fuscus Dana, 1853:983, pl. 67: figs. 8a–c.—Bate, 1862:291–292, pl. 48: fig. 8 [copied from Dana].
Hyperiella fusca (Dana).—Bovallius, 1887b:20.

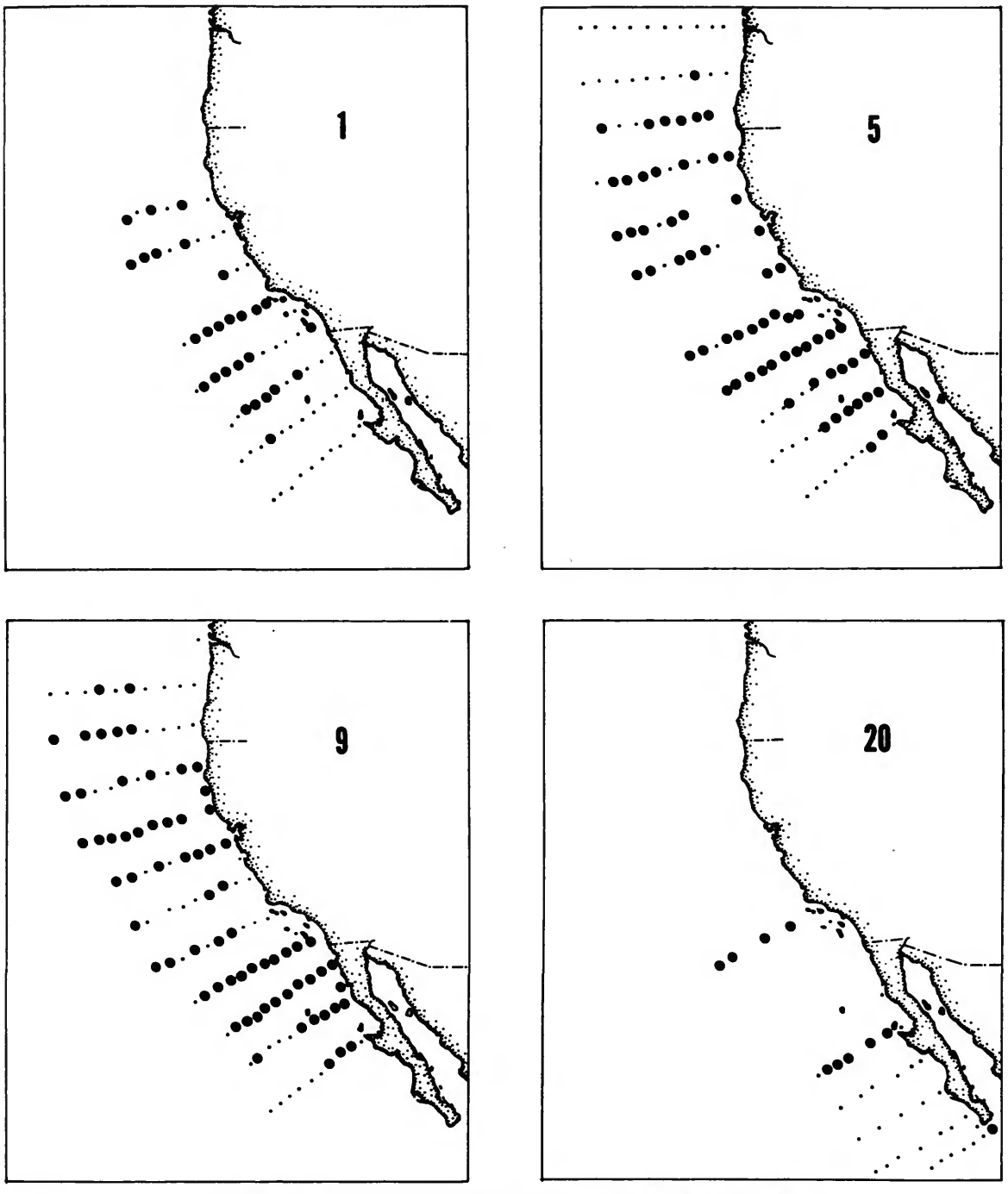


FIGURE 48.—Distribution of *Hyperietta stephenseni* on 4 CalCOFI cruises.

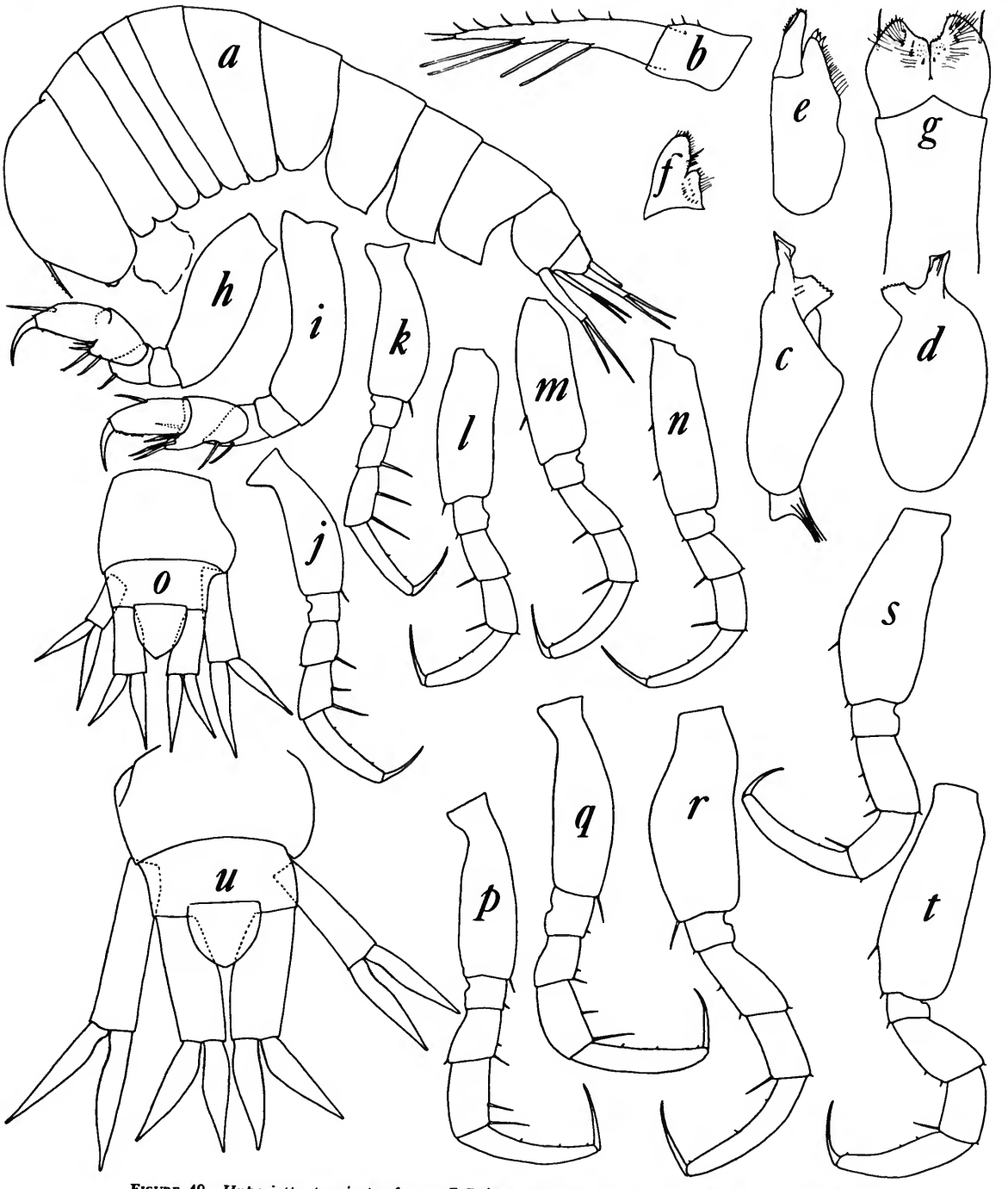


FIGURE 49.—*Hyperietta parviceps*, from off Baja California (*a-o*, ♀): *a*, lateral view; *b*, A1; *c*, right Md; *d*, left Md; *e*, Mx1; *f*, Mx2; *g*, Mxp; *h-n*, P1–7; *o*, urosome; *p-t*, ♂ P3–7; u, ♂ urosome.

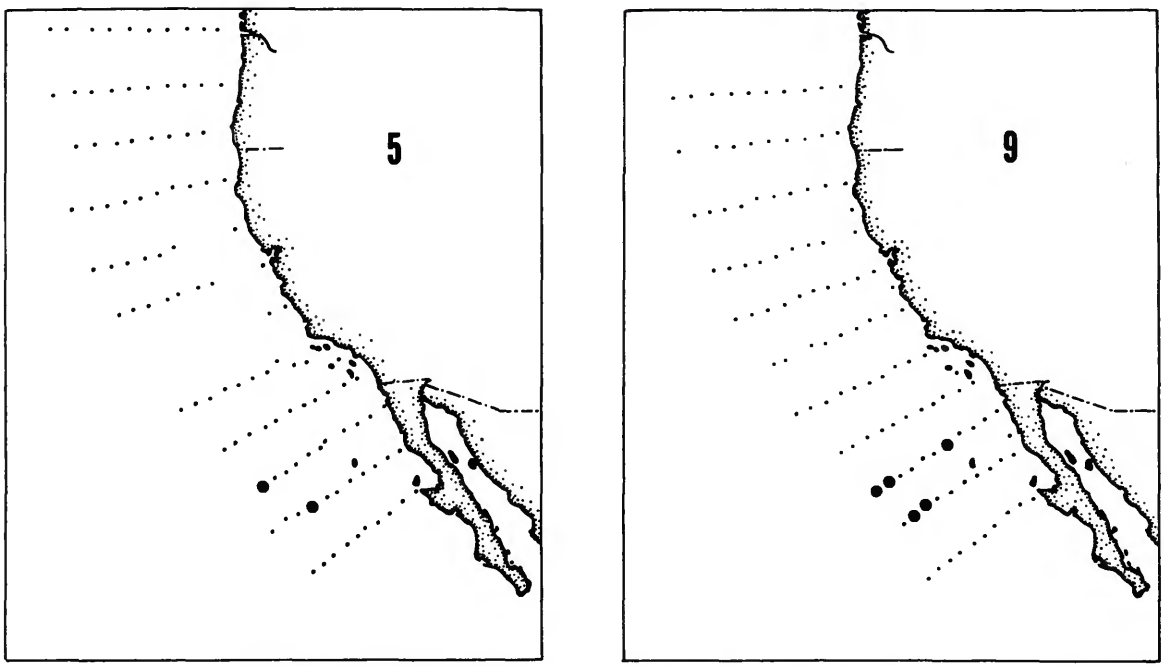


FIGURE 50.—Distribution of *Hyperietta parviceps* on 2 CalCOFI cruises.

Themistella steenstrupi Bovallius, 1887b:23; 1889:313–316, pl. 13: figs. 47–60.

Themistella fusca (Dana).—Bovallius, 1889:316–317, figs. 1–3 [copied from Dana].

Hyperia thoracica Bovallius.—Vosseler, 1901:73–74, pl. 6: figs. 1–4.—Stephensen, 1924:91.

DERIVATION OF NAME.—From the Latin "fuscus" [=dusky, dark], referring to the color of this species.

TYPE-LOCALITY.—Tropical Atlantic, 1°S, 17°–18°W.

DIAGNOSIS.—Since the genus is monotypic the generic diagnosis serves as a specific diagnosis also.

RELATIONSHIPS.—The short telson of Dana's *L. fusca* is characteristic of *Hyperioides* as well as of *Themistella,* and the possibility that Dana's *L. fuscus* was actually *Hyperioides sibaginis* must be considered. In Dana's fig. 8*a*, P7 is nearly as long as P6, whereas in *H. sibaginis* P7 is much shorter than P6. The uropods of *L. fuscus* in Dana's fig. 8*c* are slender as in *Themistella,* and the rami are much shorter than the protopods. In *H. sibaginis* the uropods are broader and the rami are much longer in proportion to the protopod lengths, especially in Up1–2.

The short telson and the structure of the uropods in Vosseler's (1901) pl. 6: fig. 4 are characteristic of *Themistella* and quite different from Bovallius' illustrations of these structures in *Hyperia thoracica,* hence I have listed Vosseler's reference to *H. thoracica* in the synonymy of *Themistella.* Stephensen (1924) also identified specimens of *Themistella* as *H. thoracica.* I have examined his specimen from the *Thor* Expeditions and found it to be a typical *Themistella.* The specimen in the Copenhagen Museum called *H. Reinhardi* by Bovallius (on the label) and *H. thoracica* by Stephensen (1924) is also a *Themistella.*

DISTRIBUTION.—I have examined specimens from the tropical Atlantic (off Barbados; Gulf of Guinea), the eastern Pacific (off the southern end of Baja California, Mexico; off Guatemala; off Nicaragua), and the Indian Ocean (Arabian Sea) and have found them all very similar. Previous records are from the tropical mid-Atlantic (Dana: 1°S, 17–18°W; Bovallius: 3°N, 25°W), North and South Atlantic (Vosseler), and near Madeira

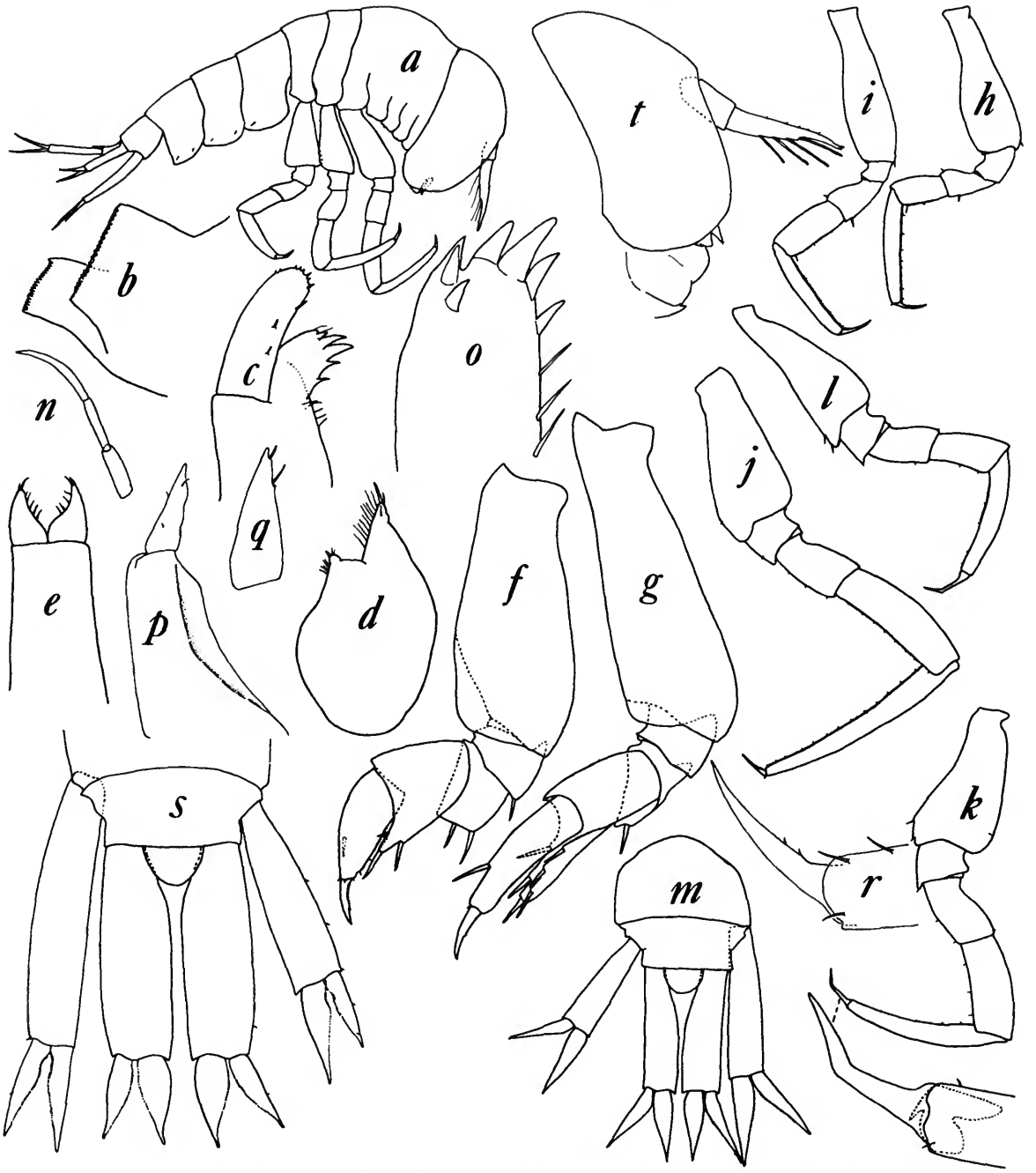


FIGURE 51.—*Themistella fusca* (*a-m*, ♀ from off Cape San Lucas, Baja California): *a*, lateral view; *b*, right Md; *c*, Mx1; *d*, Mx2; *e*, Mxp; *f-l*, P1–7; *m*, urosome. (*n-s*, ♂ from off Pacific coast of Central America) *n*, Md. palp; *o*, Mx1 palp; *p*, Mxp, lateral; *q*, Mxp, outer lobe, posterior; *r*, P5 dactyl, lateral; *s*, urosome; *t*, ♀ from Gulf of Guinea, head, lateral.

(Stephensen). The very limited records suggest a pantropical distribution for *T. fusca*.

VII. *Hyperionyx*, new genus

DIAGNOSIS.—Small species. Head globular, with eyes occupying most of its surface. Pereonites 1–3 fused in both sexes. Coxae fused with pereonites. Telson very short. ♀ A1 2-merous. ♀ A2 1-merous, slender, moderately long; gland cone small, triangular. Md reduced [?]; palp absent in ♀. Mx1 outer lobe with 1 terminal spine; palp with very few marginal setae. Mx2 with few setae; outer lobe with 2 terminal spines; inner lobe very short. Mxp with very few setae; inner lobe slender; outer lobes obovate. P1 subchelate. P2 chelate, with spinose spoon-shaped carpal process. P3–7 with strong, curved, unarmed dactyls; P3–4 and P6 subequal, P5 much shorter, P7 somewhat longer.

DERIVATION OF NAME.—*Hyperia* + the Greek "onyx" [= claw], referring to the strongly developed dactyls of P3–7; gender masculine.

TYPE-SPECIES.—*Hyperia macrodactyla* Stephensen, 1924.

REMARKS.—The distinctive characters of *H. macrodactyla* warrant the establishment of a new genus for it. The species is well described and illustrated by Stephensen (1924) and Yang (1960) except for the omission of descriptions of any of the mouthparts. The small size of *H. macrodactylus* (2–3 mm) together with the reduced mouthparts makes dissection of the latter difficult. After removing the posterior mouthparts it was apparent that I would not be able to remove the Md without excessively damaging the only Smithsonian specimen (1 of Yang's 2 ♀) and I did not attempt to do so. Even when the specimen was cleared I could not see the incisor or molar and I believe they are quite reduced.

Hyperionyx is the only genus of Hyperiidae in which pereonites 1–3 are fused in both sexes. It resembles *Themistella* in having a short telson and a small gland cone and shares with *Hyperioides* a well developed female A2, but in other respects it is quite distinct from the latter two genera.

26. *Hyperionyx macrodactylus* (Stephensen)

FIGURE 52

Hyperia macrodactyla Stephensen, 1924:90–91, fig. 35.—Hurley, 1960b:279.—Vives, 1968:460.—Dick, 1970:56.

Hyperia (Parahyperia) macrodactyla Stephensen.—Yang, 1960: 35–38, fig. 9.

DERIVATION OF NAME.—Not expressly stated; obviously refers to the long dactyls of P3–7.

TYPE-LOCALITY.—Mediterranean, from south of the Balearic Islands to the Sea of Marmora.

DIAGNOSIS.—With the characters of the genus.

RELATIONSHIPS.—This species, the sole representative of the genus, can be recognized immediately by the relatively short P5, illustrated clearly by Stephensen and by Yang. Supplementing their figures, illustrations are given here of the mouthparts, the head, showing the small pointed gland cone

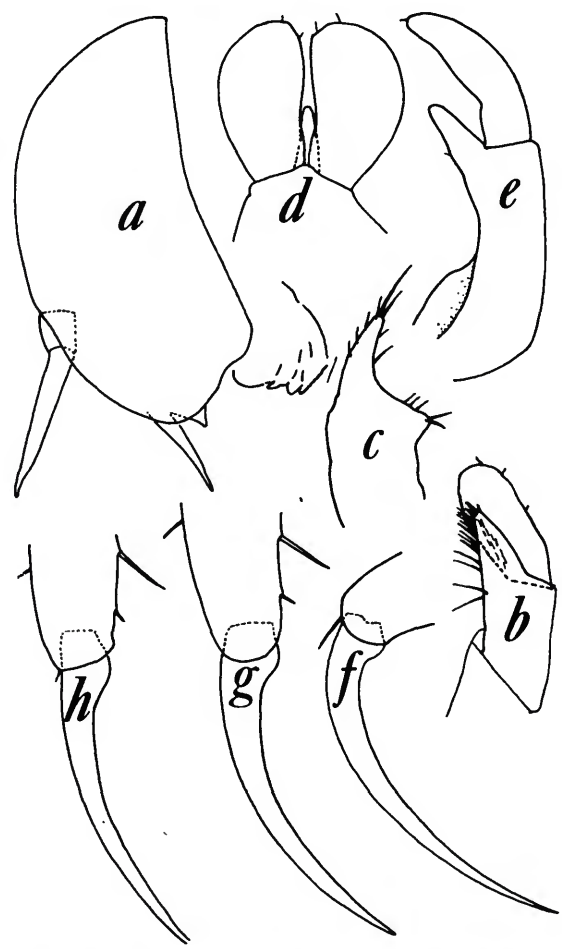


FIGURE 52.—*Hyperionyx macrodactylus*, ♀, from off Miami, Florida: *a*, head, lateral, *b*, Mx1; *c*, Mx2; *d*, Mxp, posterior; *e*, Mxp, lateral, *f-h*, dactyls of P5–7.

widely separate from the labrum, and the dactyls of P5–7. Yang shows a 2-merous A2, but I could not make out a suture in A2, possibly because I examined it only in situ.

DISTRIBUTION.—Mediterranean (Stephensen, 1924, 34 specimens from 4 stations; Vives, 1968); off Miami, Florida, in Florida Current (Yang, 1960, 2 ♀); South Atlantic, off South Africa (Dick, 1970); Fiji Islands (Hurley, 1960, 1 ♂). Presumably these records represent only a small part of its range.

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In *synonymy,* use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text,* use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

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In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

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