

SYSTEMATICS AND DISTRIBUTION OF THE FOUR SIBLING SPECIES COMPRISING THE GENUS *PONTELLINA* DANA (COPEPODA, CALANOIDA)

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ABSTRACT

A global-scale study on systematics and distribution of the epipelagic copepod genus *Pontellina* (Family Pontellidae) was carried out on materials sorted from about 2,000 zooplankton samples collected at stations scattered throughout the circumglobal warm-water belt. Four distinctive species were found and described, three being new to science.

Each species was examined for evidence of conspicuous polytypy and geographical variation. Morphology and geographical distribution were utilized comparatively to perceive relationships that would shed light on the nature of selection pressures operating on external morphology. Morphology and distribution were also considered to determine phylogenetic relationships within the genus.

The geographic distribution of the four species was considered relative to major near-surface hydrographic features characterizing tropical and subtropical latitudes and especially the occurrence of eutrophic and oligotrophic areas in each ocean.

Sets of similarly collected, quantitative samples were used to determine the relative abundance of each species, and co-occurrences among the species were tested by recurrent group analysis. The trophic role of each species was considered and conclusions tested by a limited series of observations on stomach contents.

Geographical perspective, too often absent from studies on marine plankton, is a powerful tool for dealing with sibling species. Evidence of reproductively isolated populations that are morphologically similar in planktonic calanoids and other zooplankton as well has been presented in a number of studies combining geographical distribution and morphology (e.g., Schmaus, 1917; Johnson, 1935; Bowman, 1955, 1967; Brodsky, 1959; Foxtan, 1961; Jones, 1966; Fontaine, 1967; Fleminger, 1967b; Frost and Fleminger, 1968; Mullin, 1969; Jaschnov, 1970). Our resolution of the sibling species comprising the genus *Pontellina* Dana is offered as an additional example.

In contrast to the 22 nominal species by our count comprising *Pontellopsis* Brady, the pontellid genus most similar in morphology, *Pontellina* has been universally regarded as monotypic since Giesbrecht's (1892) monumental review of planktonic marine copepods. Mori (1937) presented evidence of polytypy in *Pontellina*

with his description of a unique male distinguished by an unusual chela. Apparently influenced by Sewell's views on copepod ontogeny (1929, 1932), Mori ascribed the specimen taken off Japan to *plumata*, suggesting that it represented the fully mature state and that previous descriptions of the *plumata* male were based on incompletely mature specimens. Our study was prompted by the appearance of other seemingly minor morphological features distinguishing adult individuals of both sexes that correlated with indications of distinctive geographical distributions among the observed forms.

In this paper we redefine the genus and describe its four species. The distribution of each species is considered in the context of our geographical records. Distribution is also discussed with respect to morphological similarities among the species and relationships to general oceanic circulation. Detailed considerations and views regarding environmental conditions that shape these distributions and the circumstances yielding the contemporary *Pontellina* speciation pattern will be presented separately elsewhere.

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MATERIALS AND METHODS

Materials

Plankton samples examined for the genus *Pontellina* in the course of this study were obtained from three major sources: the zooplankton collections of Scripps Institution of Oceanography, R. Scheltema's collection of Atlantic zooplankton maintained at the Woods Hole Oceanographic Institution, and quantitative sortings of *Pontellina* from the International Indian Ocean Expedition plankton collections, processed and furnished by the Indian Ocean Biological Centre, Cochin, India. Additional collections or specimens were obtained with the kind cooperation of the National Marine Fisheries Service; the U.S. Naval Oceanographic Office; T. K. S. Björnberg, University of São Paulo, Brazil; A. DeDecker, Division of Sea Fisheries, Cape Town, Republic of South Africa; B. Kimor, Israel Oceanographic and Limnological Research Ltd., Haifa, Israel; J. E. H. Legaré, Instituto Oceanográfico, Cumaná, Venezuela; D. J. Tranter, CSIRO, Cronulla, Australia.

Geographical distribution of the samples is shown in Figure 1a, and the localities yielding *Pontellina* are listed by species in Table 1. These collections broadly outline most major sectors of the Pacific, Indian, and Atlantic Oceans, the South Atlantic being the notable omission. Most of the samples were taken with open conical plankton nets $\frac{1}{2}$ to 1 m in diameter at the mouth. Nets were towed obliquely, vertically, or horizontally between the surface and 200 m of depth. Stations were occupied irrespective of time of day or cloud cover.

Sample Analysis

Plankton samples were examined in rectangular plastic trays ($5 \times 7.5 \times 1$ cm) at $16 \times$ magnification with the aid of a stereomicroscope. The entire sample was scanned if the settling volume did not exceed 20 cc. Otherwise volumetric subsamples were drawn, generally with the aid of a 10-cc piston pipette, after standardizing the total volume and stirring vigorously. Usually more than 2% of the total sample was examined, the actual percentage varying inversely with the size of the original sample.

Estimates of abundance and frequency of

occurrence were obtained from particular sets of quantitative samples (Figure 1b) selected for homogeneity of sampling. In the case of Pacific zooplankton samples collecting procedures followed standard CalCOFI (California Cooperative Oceanic Fisheries Investigations) sampling practices (cf. Smith, 1971). The Indian Ocean samples (Figure 1b) are a composite of quantitative Indian Ocean Standard Net tows (Currie, 1963) obtained by various participants in the International Indian Ocean Expedition. Preliminary quantitative processing of these samples was carried out by the Indian Ocean Biological Centre, Cochin, India (Tranter, 1969). The Centre provided us with specimens of *Pontellina* sorted from known fractions of the original samples. Standard quantitative sampling from the Atlantic Ocean was unavailable to us.

Specimen Analysis

For routine examinations specimens were mounted loosely in a drop of glycerol. To enhance examination of fine denticles and spines, soft tissue was removed by warming specimens in a 10% aqueous solution of KOH at about 90°C for 1 to 2 h. After a brief rinse in distilled water the cuticle was transferred to 35% ethanol, then to 70% ethanol for 1 min and then stained in a solution of 1% Chlorazol Black E dissolved in 70% ethanol. Intensive staining usually requires not more than $\frac{1}{2}$ min and should be followed immediately by a 1-min rinse in distilled water.

Examinations and dissections were carried out under stereomicroscopes at $12 \times$ to $100 \times$ magnification and under compound microscopes at various magnifications up to $600 \times$. All drawings were made with the aid of a compound microscope equipped with a drawing attachment.

Several females and males of each species were studied under a scanning electron microscope after preparation by the critical point drying method (Cohen, Marlow, and Garner, 1968).

Measurements

For each species intact specimens with a reasonably straight urosome were chosen at random from localities scattered over the entire

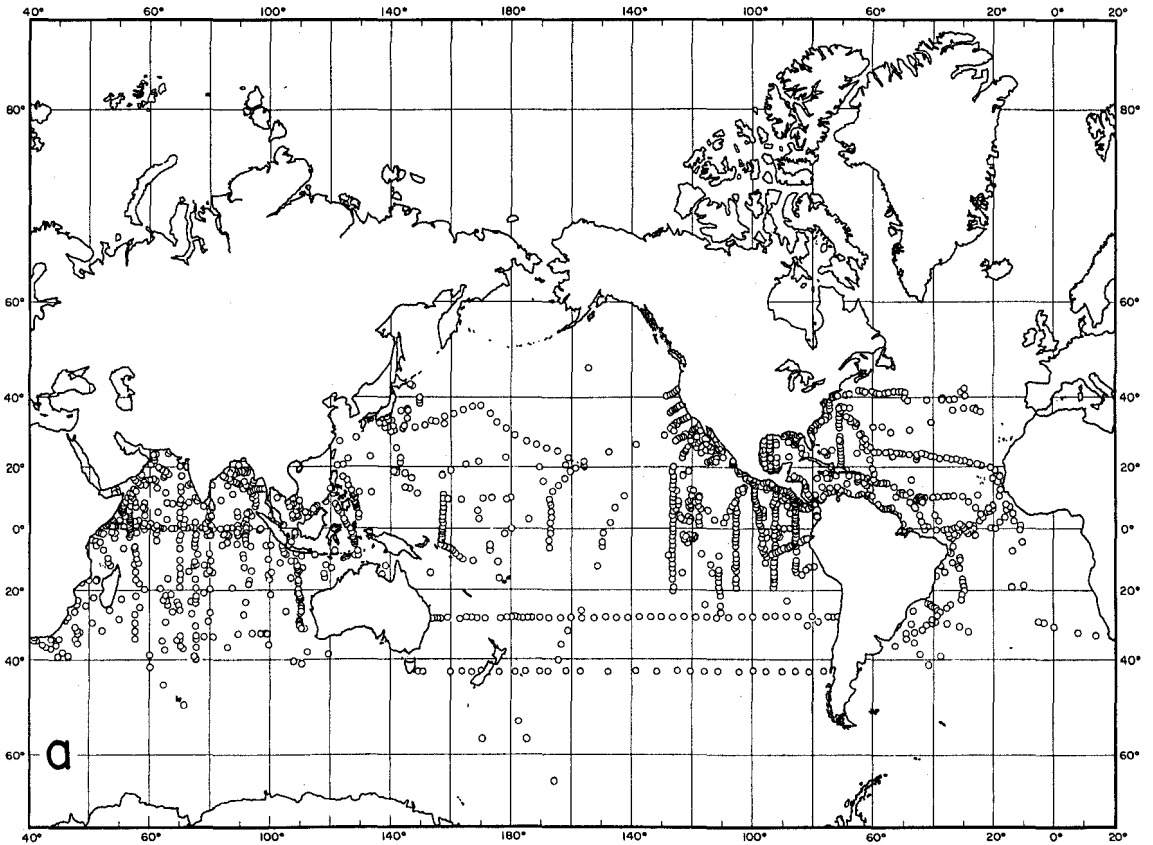


FIGURE 1a.—Geographical distribution of sampling stations. Each open circle represents one or more samples. Overlapping stations and replicate sampling are omitted for the purpose of clarity. Areas intensively surveyed are shown symbolically as evenly spaced grid.

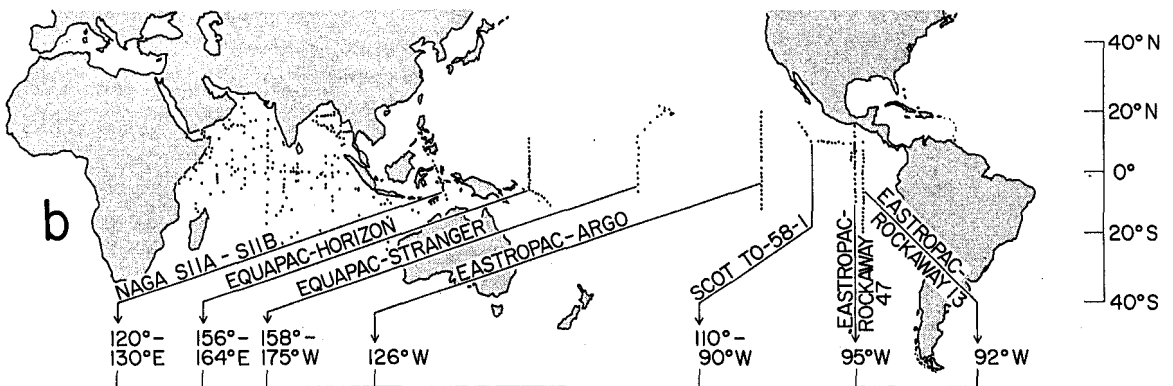


FIGURE 1b.—Distribution and identification of sets of quantitative zooplankton samples used to estimate the frequency of *Pontellina* in the Pacific Ocean. Sets were selected for similarity of sampling; i.e., each set obtained by the same procedures and stations occupied in a closely ordered sequence during the same cruise. Dots indicate the sampling localities. Indian Ocean localities represent Indian Ocean Standard Net samples collected during the International Indian Ocean Expedition that were examined quantitatively for *Pontellina* in the course of this study. See Table 14 for summary of sampling data and Materials and Methods for analytical details.

TABLE 1.—Continued

Location and station	Source of collecting data ¹	Location and station	Source of collecting data ¹
Circe II Exp.: RV <i>David Starr Jordan</i>	9, 11, 12, 14. B	<i>Jordan</i> 12: RV <i>Rockaway</i> 13: El Golfo II Exp.: Harpoon Exp.: La Creuse Exp.:	033, 037, 041, 059, 063, 077, 100. 048, 056, 060, 064, 071, 075, 083. XVIII B1-D1, B2-D1, A6-D1, B1-N1. 13 (16°00'N 95°12'W). 15, 16, 17, 18, 21, OT-1, OT-6, OT-12, B
57:	002 (13°42'N 120°13'W), 012 (13°16'N 119°23'W), 025 (10°30'N 119°43.5'W), 064 (04°00'N 120°43'W), 076 (03°20'N 119°42'W), 108 (06°32'N 119°50'W), 132 (09°45'N 120°12'W).	Muddauber Exp.: Piquero V Exp.: Shellback Exp.: RV <i>Townsend Cromwell</i>	125-4, 126-1, TDS-86. 40D, 43D, 44. 47, 51, 63, 67, 185. 51:
60:	056 (03°22'S 119°30'W), 067 (01°36'N 117°22'W), 071 (02°00'N 117°17'W), 122 (04°00'N 116°41'W), 132 (06°34'N 116°22.3'W), 134 (07°05'N 116°58'W), 148 (09°27.7'N 117°49'W), 156 (10°36'N 117°17'W).	051 (03°15'S 118°23'W), 061 (02°30'S 119°47'W), 064 (03°30'S 120°45'W), 076 (02°28'S 121°42'W), 079 (02°42'N 121°49'W).	B B A
65: Dragon Exp.:	N-1. B	TO-58-1 Cruise (Scot):	16, 17, 27, 29, 31, 32, 33, 35, 36, 37, B 38, 42, 45, 46, 48, 56.
EASTROPAC Exp.:		TO-58-2 Cruise:	9, 16. B
RV <i>Argo</i> 11: RV <i>David Starr</i>	234, 291, 299. D		

¹ A Snyder and Fleminger, 1965

B Snyder and Fleminger, 1972

C Anonymous, 1969

D Love, 1972

E Fleminger, 1967a

F Scheltema, 1971 (only chart)

G Anderson, Gehringer, and Cohen, 1956; Anderson and Gehringer, 1958, 1959a, 1959b

H Collier, Drummond and Austin, 1958

area of its geographical distribution. Total length (TL), prosome, i.e., cephalosome and thorax combined (P), and urosome (U) were measured with an ocular micrometer at 50× magnification under a stereoscopic microscope; smaller structures were measured under a compound microscope at 100× to 400× magnification. The morphological terms and abbreviations in general follow those of Fleminger (1967b).

Measurements, drawings, and descriptions refer to the right side or to appendages from the right side unless stated otherwise. TL and the length of U were measured (Figure 2a) to the distal end of the right furcal ramus, without allowance for any telescoping of segments. The length and width of the furcal rami were measured in dorsal view. In the adult female, the right ramus is fused to the anal segment; the length was obtained from the distance between the medial notch indicating the place of fusion with the anal segment and the insertion of the second innermost furcal seta (Figure 2d). The length of the left furcal ramus was also measured from the medial junction with the anal segment to the insertion of the second innermost furcal seta from the median. In both males and immature females the lengths of the right and left furcal rami were measured from the lateral margin at the proximal end to the insertion of the second innermost seta at the distal end

(Figure 2c). For all stages the right furcal ramus was measured across its maximum width (Figure 2c).

The segments of the fifth legs (P5) of the female were measured from the anterior side (Figure 2f). The length of the exopod (Re) was taken as extending from the junction with the second basal segment (B2) to the base of the longest distal seta; the endopod (Ri) was measured from the junction with B2 to the tip of the medial spine. The length of the point on the fifth thoracic segment (ThV) is taken in lateral view as the distance between its tip and its base where the point is delineated by a distinct step or turn to the posterior (Figure 2g). The length of the spermatophore sac was measured as the distance from the distal end to the outer margin of the proximal convolution taking care to position the spermatophore to avoid diminution by an oblique angle of view (Figure 2b). Measurements of segments 13-17 and the succeeding three free segments of the male right antennule (A1) were taken from intact specimens positioned in lateral view (Figure 2e). P5 of the male was measured from the posterior side: the length of the second free segment of the left leg extends from the junction with B2 to the distal margin near the seta (Figure 2h); the length and width of the proximal segment of the chela are, respectively, the shortest distance

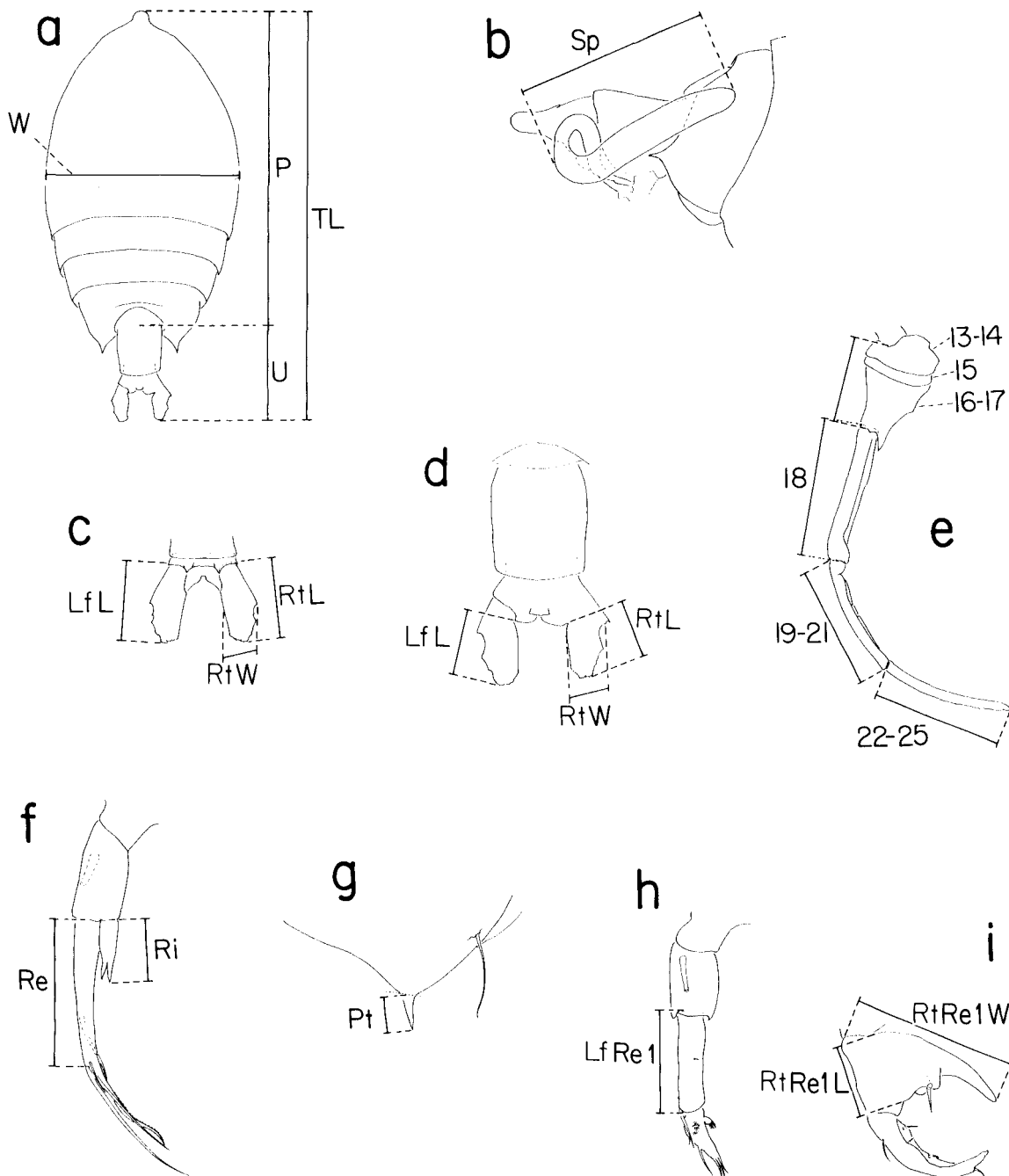


FIGURE 2.—Measurements taken from *Pontellina* specimens. a. dorsal view, female; b. abdomen with spermatophore, ThIV-V, lateral view, female; c. anal segment and furcal rami, dorsal view, male; d. urosome, dorsal view, female; e. right A1, segments 13-25 male; f. right P5, anterior view, female; g. spine on right ThIV-V, lateral view, female; h. left P5, posterior view, male; i. chela of right P5, posterior view, male. L = length; Lf = left; P = prosome length; Pt = spine; Re = exopod; Re1 = first exopodal segment; Ri = endopod; Rt = right; Sp = spermatophore; TL = total length; U = urosome length; W = prosome width.

between the shallow swelling in the proximal lateral corner and the distal margin, and the distance between the proximal medial corner and the tip of the large lateral prong (Figure 2i).

Types and reference specimens have been deposited with the Smithsonian Institution, U.S. National Museum, Washington, D.C.

GENUS *PONTELLINA* DANA

Pontella Dana, 1846 (in part), p. 184, type not designated; Dana, 1849, p. 26, type not designated.

Pontellina Dana, 1853 (in part), p. 1135, type not designated; Giesbrecht, 1889, p. 29, type by monotypy, *Pontellina plumata* (Dana); Giesbrecht, 1892, p. 73, 497; Giesbrecht and Schmeil, 1898, p. 149.

Calanops Claus, 1863, p. 211, type by monotypy, *Calanops messiuensis* Claus = *Pontellina plumata* (Dana), Giesbrecht, 1889, p. 29.

Pseudopontia Claus, 1892, p. 861, 864, type by monotypy, *Pseudopontia plumata* (Dana) = *Pseudopontella plumata* (Dana), Claus, 1893, p. 278.

Pseudopontella Claus, 1893, p. 278, type by monotypy, *Pseudopontella plumata* (Dana) = *Pontellina plumata* (Dana), Giesbrecht and Schmeil, 1898, p. 149.

Not *Pontellina* Claus, 1892, p. 851; 1893, p. 272.

Diagnosis

Relatively small pontellids, less than 2 mm in TL. Prosome in dorsal view broadly oval, less than twice as long as maximum width; forehead lacking headhooks; ThIV-V corners symmetrical; rostrum proximally protuberant, bifurcate at base, and extending ventrad as slender, elongate, flexible filaments; in lateral view, filaments more than 10 times longer than wide at maximum width; ventral eye present but inconspicuous, scarcely produced, and lacking a distinctive lens. In A1 (except sexually modified right A1 of male) segments 13, 14, and 15 separate and about equal in length. A2 with Re about as long as Ri1, length of Ri1 less than 4 times maximum width.

Female lacking distinctive dorsal lenses in forehead. Furcal rami weakly asymmetrical, right ramus fused to anal segment. P5 with monomeric Re bearing 1 lateral and 3 terminal setae, in addition to one medial setiform process fused to Re and serrated along medial margin;

Ri monomeric and terminating in one or two apical spines. A2 and mandible (Mnd) with elongate setae reaching beyond thorax when extended posteriad.

Male with one pair of dorsal lenses in forehead.

Additional Description

Both sexes with cephalic groove and agreeing in meristic features of all appendages except for those modified by sexual maturation. Nonsexually modified appendages agree with those of *Pontellina plumata* as shown by Giesbrecht (1892, pl. 25, fig. 1, 6, 7, 9, 12-14, 18, 20, 21, 23-25). Segmentation, setation, and spination of nonsexually influenced appendages are virtually identical among the four species and, except for A1, closely resemble those of *Pontellopsis*. They are as follows:

- A1: 17 free segments; segments 2-5, 6-8, 24-25 fused, 9-11 partly fused.
- A2: 2 basal segments; Re: 3 segments with 1, 4, 3 setae, respectively; Ri: 2 segments; Le: 6, Li: 6 + 2 setae.
- Mnd: palpus 1 seta; Re: 5 segments with a total of 6 setae; Ri: 2 segments with 4 and 6 setae, respectively.
- Mx1: Li1: 14 spines; Li2: 3 spinelike setae; Li3: small, 3 setae; B2: 3 + 2 setae; Ri: 4 + 1 setae; Re: 8 setae; Le: 1 + 8 setae.
- Mx2: lobe 1: 3 + 1 setae; lobes 2-5: 2 + 1 setae each; Ri: 6 + 1 setae.
- Mxp: 5-segmented, fingered lobe on B1 with 2, 2, 3 setae.
- P1: trimerous Re: 1, 1, 4 Si; 1 St; 1, 1, 2 Se; trimerous Ri: 1, 2, 4 Se; 1 St; 0, 0, 1 Se.
- P2 and P3: trimerous Re: 1, 1, 5 Si; 1 St; 1, 1, 3 Se; bimerous Ri: 3, 5, Si; 1 St; 0, 2 Se.
- P4: trimerous Re: 1, 1, 5 Si; 1 St; 1, 1, 3 Se; bimerous Ri: 3, 4 Si; 1 St; 0, 2 Se.
- Se of P1 smooth; Se of Re1 and Re2 of P2 with toothed medial margin; Se of Re3 with toothed medial and lateral margins; in Se of P3 and P4 also both margins toothed.
- St of Re 3 of P1 to 4 with toothed lateral margin.
- B1 of P1 to 4 with 1 Si; B2 usually without setae.

Right A1 in male with segments 13-17 swollen, 13-14 and 16-17 fused; length of swollen section varies considerably due to either telescoping of segments or expansion of articulations. Distal three free segments slender and consisting of segment 18 followed by a compound segment formed by fusion of segments 19-21, and ending in a compound segment fusing segments 22-25.

Mandibular blade (Giesbrecht 1892, pl. 25, fig. 14) bearing a one-pointed apical (ventral) tooth, a two-pointed subapical tooth, two deeply cut two-pointed medial teeth, and three basal (dorsal) teeth; basal seta lacking; dorsal accessory bristles exceed teeth in length; patches of spinules appear on anterior side of blade.

P5 segmentation in both sexes typically pontellid; B2 of male bearing a large plumose seta on posterior surface, Ri lacking, Re bimerous; right leg with elongate B1, cheliform Re; left leg with reduced B1 fused to precoxa, distal segment of Re armed with four short setiform processes.

Spermatophore with relatively long neck bearing one full counterclockwise turn relative to proximal end, helix occurring between spermatophore sac and place of attachment located in a cement mass overlying genital pore of female. Elongate spermatophore neck may also be connected secondarily to right side of genital segment proximal to helix, thereby orienting sac dorsad or anterodorsad with helix and sac flanking right side of genital segment. When secondary lateral cementation absent, neck, helix, and sac hang free from ventral side of genital segment.

PONTELLINA PLUMATA (DANA)

(Figures 3 and 4)

Pontella plumata Dana, 1849, p. 27 (type locality not designated); Brady (in part), 1883, p. 92, pl. 37, fig. 1-10 only.

Pontella turgida Dana, 1849, p. 28 (type locality not designated).

Pontellina plumata: Dana, 1853, p. 1135; Dana, 1855, pl. 79, fig. 10; Giesbrecht, 1889, p. 29; Giesbrecht, 1892, p. 497, pl. 4, fig. 1, pl. 25, fig. 1, 4, 6, 7, 9, 12-14, 18, 20, 21, 23-26, 36, pl. 40, fig. 49-53; Mori (in part), 1937, p. 99, pl. 47, fig. 7-11 only; Grice, 1962, p. 240, pl. 34, fig. 11-15; Brodsky, 1962, p.

147, fig. 47; Park, 1968, p. 569, pl. 13, fig. 15-16.

Pontellina turgida: Dana, 1853, p. 1136; Dana, 1855, pl. 79, fig. 11, 12.

Calanops messinensis Claus, 1863, p. 212, pl. 2, fig. 11, pl. 36, fig. 13-16, pl. 37, fig. 10 (Messina).

Pontellopsis speciosus Brady, 1915, p. 138, pl. 10, fig. 1-8 (Durban Bay). NEW SYNONYMY.

Pontellopsis aequalis Mori, 1932, p. 172, 175, pl. 4, fig. 7-13 (25°20'50"N, 124°7'30"E). not *Pontella plumata*: Brady (in part), 1883, p. 93, pl. 37, fig. 11 only.

not *Pontellina navalium* Oliveira, 1947, p. 472, fig. 12; Vervoort, 1965, p. 191.

Specimens seen: 1,259 adult females, 917 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean (\bar{x})	Range	Standard error $s_{\bar{x}}$	Speci- mens
Female	1.69	1.44-1.94	0.0126	75
Male	1.51	1.34-1.92	0.0130	67

Prosome-urosoma length ratio (PUR):

	Median	Range	Specimens
Female	3.28:1	2.92-3.72:1	75
Male	3.07:1	2.84-3.93:1	52

Diagnosis

Female

Posterior corner of ThIV-V in lateral view produced into conspicuous spiniform process of characteristic shape (Figure 3 a, b, d-g). Ventral margin of spine more or less continuous with ventral margin of ThIV-V, transition with dorsal margin abrupt and stepped; junction of distal end of spine and thicker basal portion usually set off by weak shoulder, spine extending posteriad, sometimes tilted weakly ventrad or dorsad. In dorsal view spine more or less continuous with posterior tapering of corner, shoulder or constriction sometimes present; spine usually directed posteriad and slightly laterad, sometimes straight or turned slightly mediad.

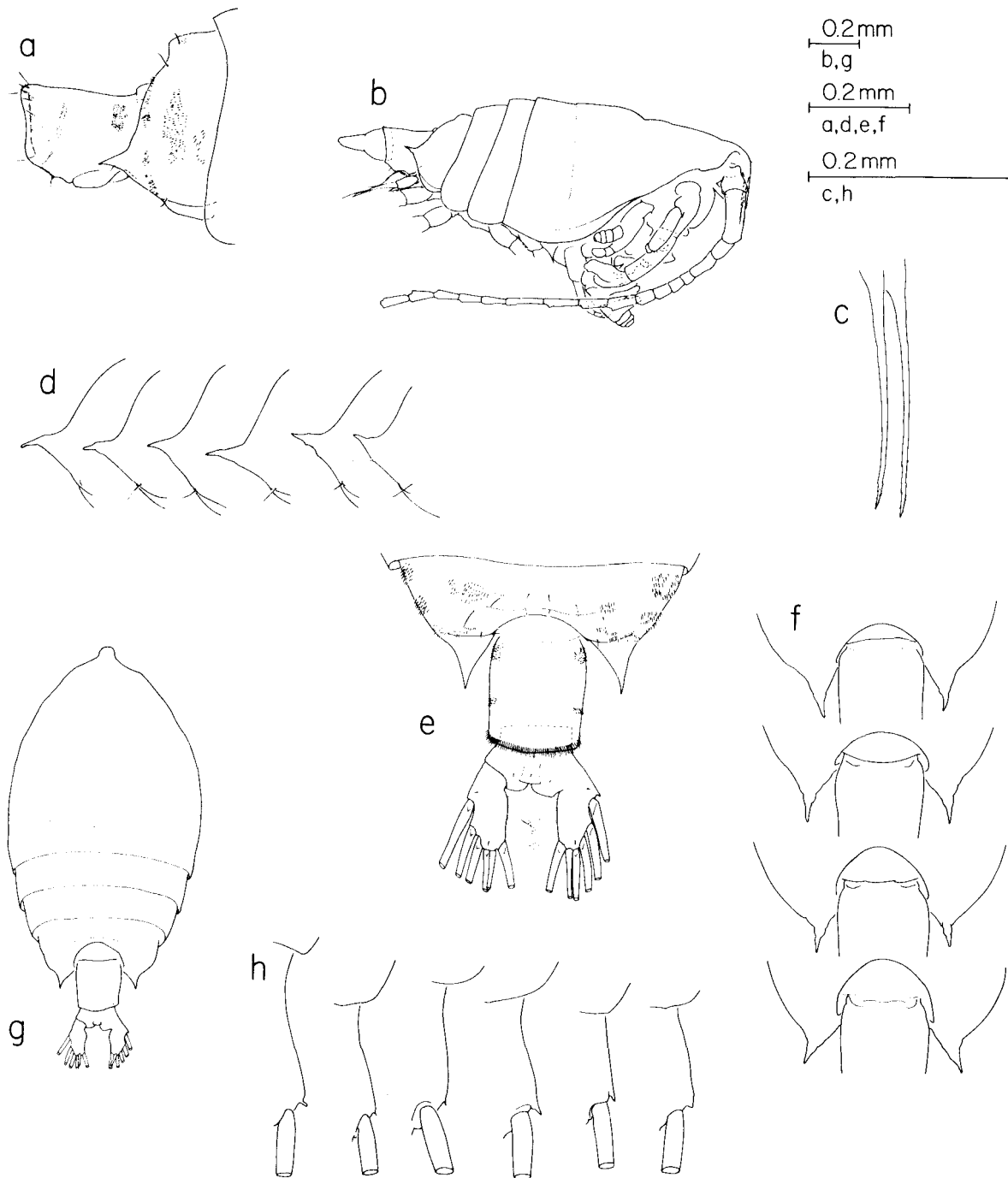


FIGURE 3.—*Pontellina plumata* s.str., adult female: **a**. ThIV-V, genital segment, lateral view (TRANSPAC 96A); **b**. habitus, lateral view, swimming legs incomplete (same station as **a**, different specimen); **c**. rostral filaments, lateral view (*Atlantis II-31-2*); **d**. range of variation observed in ThIV-V, lateral view (left to right: *Lusiad VI-8*; *Chain 49-11*; *Lusiad II-66*; *Chain 49-11*, different specimen; *Atlantis II-31-73*; same station, different specimen); **e**. ThIV-V, urosome, dorsal view (same specimen as **a**); **f**. range of variation observed in ThIV-V, dorsal view (top to bottom: *Scorpio II-118*; *Chain 49-11*; same station, different animal; *Chain 49-20*); **g**. habitus, dorsal view (same specimen as **b**); **h**. lateral margin of right furcal ramus of various specimens, dorsal view (left to right: *Atlantis II-31-2*; *Troll 28A*; *Atlantis II-20-22*; *Dodo VI-65*; *Troll 25*; *Scorpio II-182*).

Genital segment bearing anterolateral and posterolateral clusters of hairs on both sides of segment (Figure 3 a, e); anterior cluster larger, best seen in dorsal view. Posterior cluster less prominent, of similar or coarser hairs. A row of relatively long, fine hairs encircling segment near distal margin.

Male

In lateral view posterior corner of ThIV-V somewhat angular, apex usually bearing one minute denticle (Figure 4e-h). Chela of right P5 with proximal segment extending distolaterad as a relatively slender digitiform process opposing apex of distal falcate segment (Figure 4i); base of distolateral digitiform process flanked by small anterior process, triangular in lateral view, and small angular posterior process bearing a sensoriiform seta (Figure 4j); in lateral view posterior basal process and digitiform process with relatively straight margins intersecting at an angle greater than 70° (Figure 4j); in posterior view two basal processes overlapping, both extending toward center of lumen of chela; additional sensoriiform setae on proximal segment of chela: one anteromedial near articulation with distal segment; on distal segment: one proximo-medial, one mediosubapical, and three lateral. Left P5 (Figure 4i) with proximal segment of Re (Re1) short relative to other three species below. Length of right furcal ramus exceeds left Re1 by 1.55-1.85 times, 46 specimens (see Figure 30).

Additional Description

Female

Right furcal ramus fused to anal segment, varying directly with prosome length, relatively longer than that in Indian and Pacific congeners described below (Figure 25); ratio of length to width highest in genus, usually 1.5 times longer than wide (median 1.56:1, range 1.28-1.74:1, 134 specimens), showing apparent overlap only with the equatorial Atlantic congener (see Figure 27); lateral margin of right furcal ramus with small pointed projection somewhat variable in shape and size just anterior to base of outermost seta (Figure 3e, h). Glandlike tissue within right furcal ramus with associated duct-like structure extending toward lateral point.

Left furcal ramus not fused and appreciably longer than right ramus (see Figure 19).

P5 (Figure 4a, c, d) with inner margin of Re lacking hair, Ri polymorphic with one or two apical spines fused to segment, spines on left and right Ri may differ in number in same specimen (Figure 4b, Table 7); Re 2 to 3 times longer than Ri, median 2.37:1, range 1.97-3.08:1, 59 specimens, differing strongly from Indian and Pacific congeners (see Figure 29).

Attached spermatophore observed on four specimens (see Figure 33 a, b; Table 5), hanging free from single place of attachment in vicinity of genital pore, neck with small helical turn near place of attachment and larger helical turn at origin of sac.

Male

Right furcal ramus not fused to anal segment, about equal in length to left ramus (see Figure 19), varying directly with prosome length (see Figure 26); ratio of length to width relatively high (median 2.30:1, range 2.0-2.53:1, 44 specimens), but showing more overlap with congeners than found among females (see Figure 28).

Types

Unknown, presumed to be lost. Reference specimens from the Atlantic, Pacific, and Indian Oceans have been deposited in the U.S. National Museum, Smithsonian Institution.

Reference Specimens

- 4 ♂, 4 ♀, *Atlantis II*-31-5, lat. 39°13.0'N, long. 63°26.5'W, 14 Jan. 1967, ¾-m net, oblique tow, maximum cable out 200 m.
 2 ♂, 2 ♀, Capricorn 31, lat. 06°31'N, long. 124°41'W, 13 Feb. 1953, 1-m net, oblique tow, maximum cable out 200 m.
 2 ♂, 2 ♀, TRANSPAC 134A, lat. 23°26.3'N, long. 161°49.6'W, 17 Nov. 1953, 1-m net, oblique tow between surface and 129 m est.
 2 ♂, 4 ♀, Lusiad V-76, lat. 02°01'S, long. 91°58'E, 24 Apr. 1963, 1-m net, oblique tow, maximum cable out 280 m.
 2 ♂ Lusiad V-104, lat. 03°01'S, long. 52°58'E, 10 May 1963, 1-m net, oblique tow, maximum cable out 280 m.

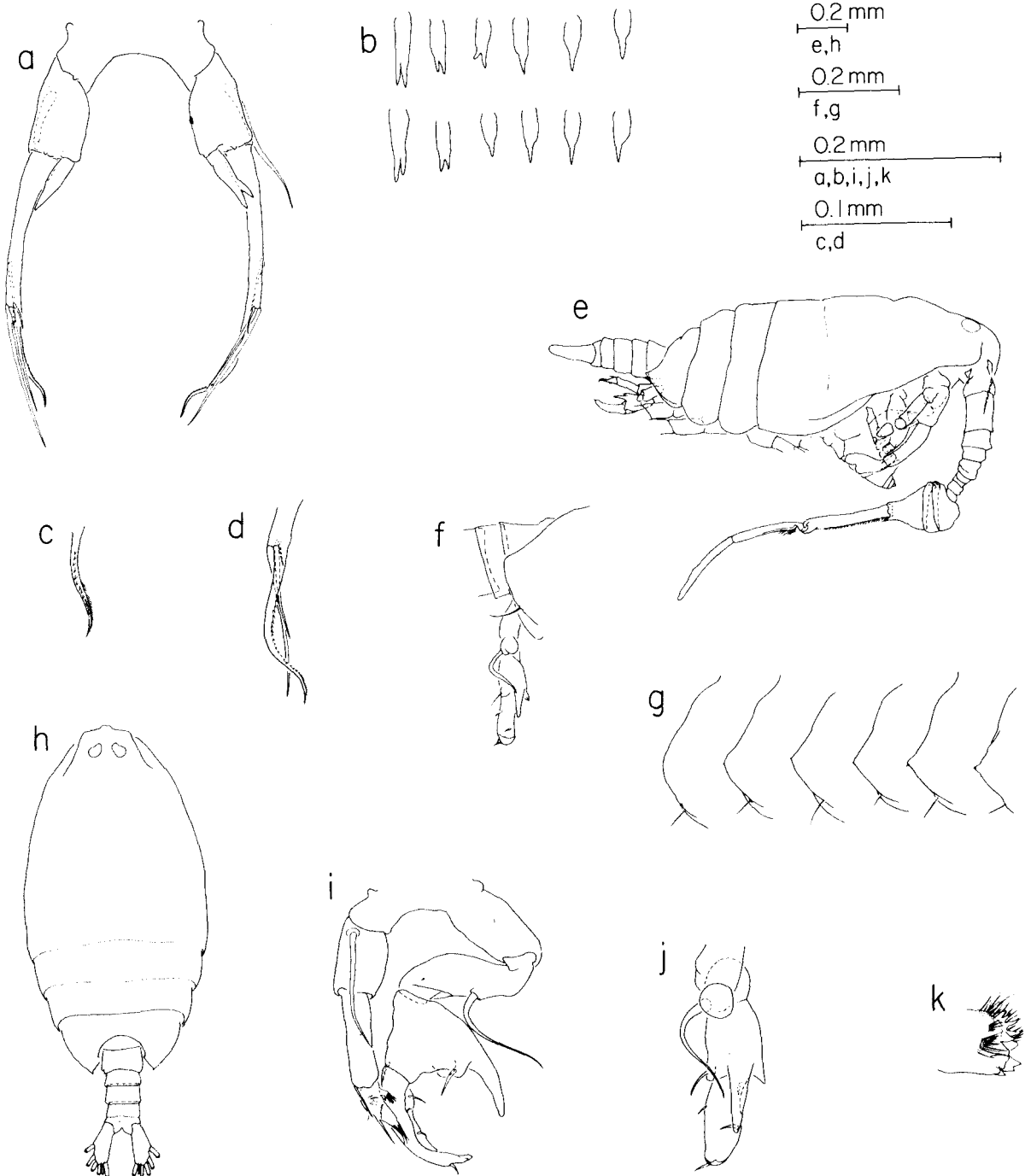


FIGURE 4.—*Pontellina plumata*, s.str. Adult female: a. P5 anterior view (TRANSPAC 96A); b. P5 Ri of other specimens, right side above, left side below (left to right: Scorpio II-146; Lusiad II-66; La Creuse 3; same station, different specimen; *Atlantis* II-31-6; Lusiad V-45); c. enlargement of P5 apex; d. enlargement of P5 Re distal process (TRANSPAC 96A). Adult male: e. habitus, lateral view (*Atlantis* II-31-28); f. ThIV-V, part of urosome, P5, lateral view (TRANSPAC 92B); g. variation observed in ThIV-V, lateral view (left to right: Dodo VI-70; Gill 8-9; La Creuse 7; *Gascoyne* G1/5/63; Circe NT-38; Monsoon 18). h. habitus, dorsal view (same as e); i. P5, posterior view (same as f); j. P5 chela, lateral view (same as f); k. mandible, gnathobase, lateral view.

Remarks on Synonymy and Variability

Dana (1849, 1853, 1855) described the male and female of *P. plumata* as separate species based on specimens obtained from several equatorial localities (in the Atlantic Ocean: lat. 08°30'N to 00°, long. 23° to 18°W; 00°15'N, 31°00'W; 01°00' to 04°30'S, 17°30' to 21°30'W; 04°30'S, 25°00'W). Our efforts to use his descriptions and illustrations to separate the two species in our Atlantic collections were fruitless. Moreover, Dana's specimens of *Pontellina* are apparently lost (T. E. Bowman, in litt.).

The present concept of *P. plumata* originates from Giesbrecht's (1892) redescription and synonymy which have been generally accepted. Hence we regard his description of the species as the basis for the type species of the genus.

Several authors have noted morphological variation in *plumata*, observations that may indicate that they had examined specimens of two or more of the four species we recognize in the genus. Thus, Dana (1853) reported that the furcal rami were relatively longer in males from the Cape of Good Hope region than in males from the Pacific Ocean. Giesbrecht (1892) found that the posterolateral corners of ThIV-V were longer in males from the Pacific than in those from waters off Naples. Tanaka (1964) mentions differences in the posterolateral corners of ThIV-V in both sexes of *plumata*. Mori (1937) believed the differences he encountered in specimens of *Pontellina* were a function of ontogeny. On the other hand, a number of authors have published illustrations which appear to be based solely on *plumata* specimens (e.g., Giesbrecht, 1892; Brodsky, 1962; Grice, 1962; Park, 1968).

Distribution

P. plumata exhibits a warm-water circum-global distribution bounded in the north and south roughly by the subtropical convergence zones of each hemisphere (Figure 5). Adults were frequent in occurrence but relatively low in abundance. For example, in 131 zooplankton samples containing the species from the Indian and Pacific Oceans (Indian Ocean Standard Net and CalCOFI Standard Net zooplankton samples; tows through the epipelagic layer) abun-

dance estimates ranged from 0.002 to 0.4 adults per m³ water strained, the median being 0.02. In the sets of samples selected for quantitative analysis (Figure 1b) the species appeared infrequently and in minimal numbers in the eastern tropical Pacific. In the remainder of the equatorial Pacific and in the Indian Ocean *plumata* was found in about half of the samples examined.

Values of mean abundance in temporally and geographically related sets of samples usually exceeded 0.02 per m³ of water strained (see Figure 35, Table 14). With regard to the Atlantic Ocean our impressions from the available nonquantitative collections is that the abundance of *plumata* is not appreciably different from that in the Indian and Pacific Oceans.

The widespread co-occurrence of three sibling species (described below) imposes serious reservations on the use of previously published records of *plumata*. It would be best to consider earlier records primarily as evidence of the occurrence of the genus, a useful attribute considering the virtual absence of the genus at latitudes above 40°.

PONTELLINA PLATYCHELA SP.N.

(Figures 6 and 7)

Specimens seen: 168 adult females, 466 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean (\bar{x})	Range	Standard error $\frac{s}{\sqrt{N}}$	Speci- mens
Female	1.70	1.54-1.96	0.0173	30
Male	1.56	1.41-1.74	0.0089	57

Prosome-urosome length ratio (PUR):

	Median	Range	Specimens
Female	3.44:1	3.19-3.89:1	30
Male	3.22:1	2.86-3.55:1	49

Diagnosis

Female

Posterolateral corner of ThIV-V ending in a relatively minute dentiform process extending posteriad or weakly medioposteriad (Figure

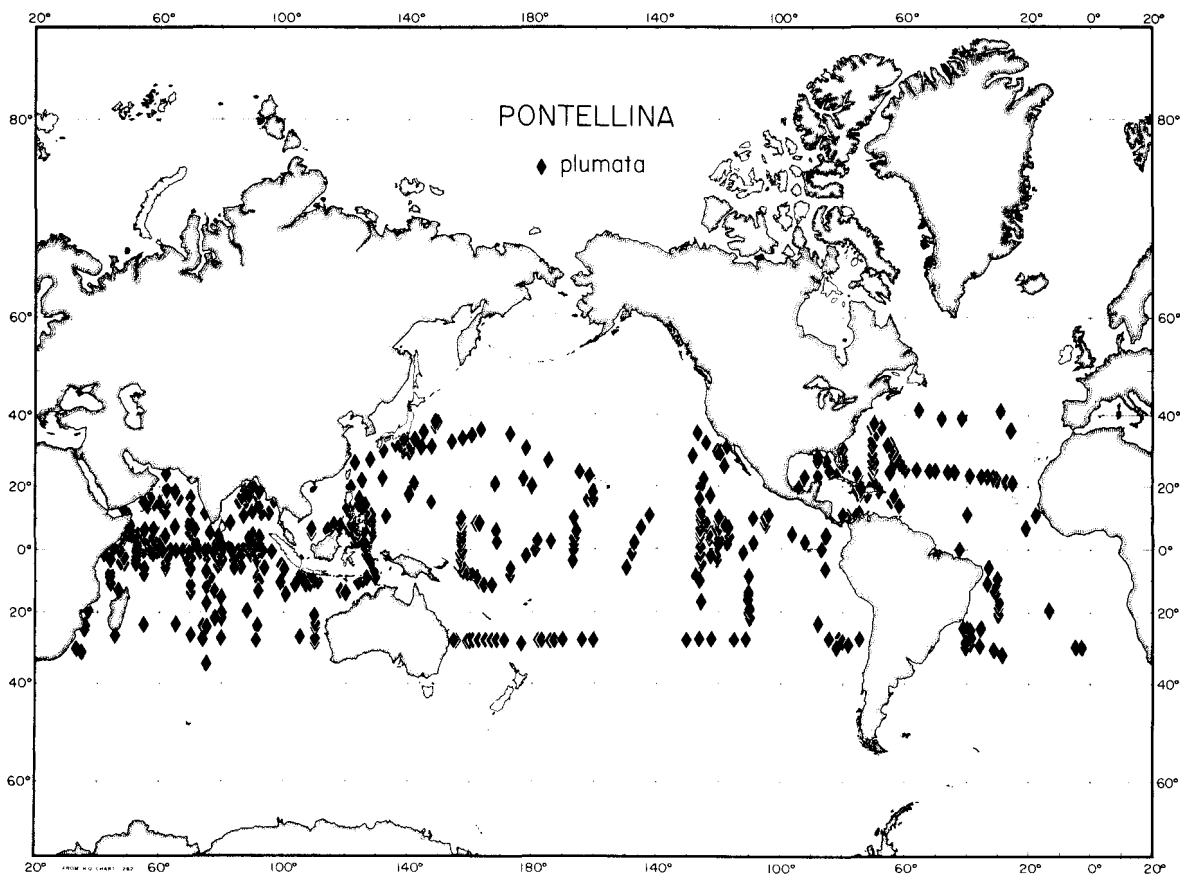


FIGURE 5.—*Pontellina plumata* s.str. Geographical distribution of captures recorded during the present study.

6a-c, f-h); in dorsal view denticle not sharply set off from tapering lateral margin of ThIV-V. Genital segment (Figure 6f, g) with several isolated lateral sensory hairs and line of slender hairs along distal margin, lacking lateral clusters of coarse hairs.

Male

Posterolateral corners of ThIV-V in lateral view tending to be rounded and lacking denticle (Figure 7c, d). Chela of P5 differing markedly from that in *plumata* due to strong antero-posterior expansion of both segments (Figure 7a, b); distal segment spatulate; in proximal segment base of laterodistal digitiform process greatly expanded; in posterior view posterior basal process barely differentiated but sensoriform seta present, anterior basal process relatively small, and extending toward center of lumen of chela. Left P5 (Figure 7a) with proxi-

mal segment of Re (Re1) somewhat longer than that in *plumata*, length of right furcal ramus exceeds Re1 by 1.3-1.5 times, 21 specimens (see Figure 30).

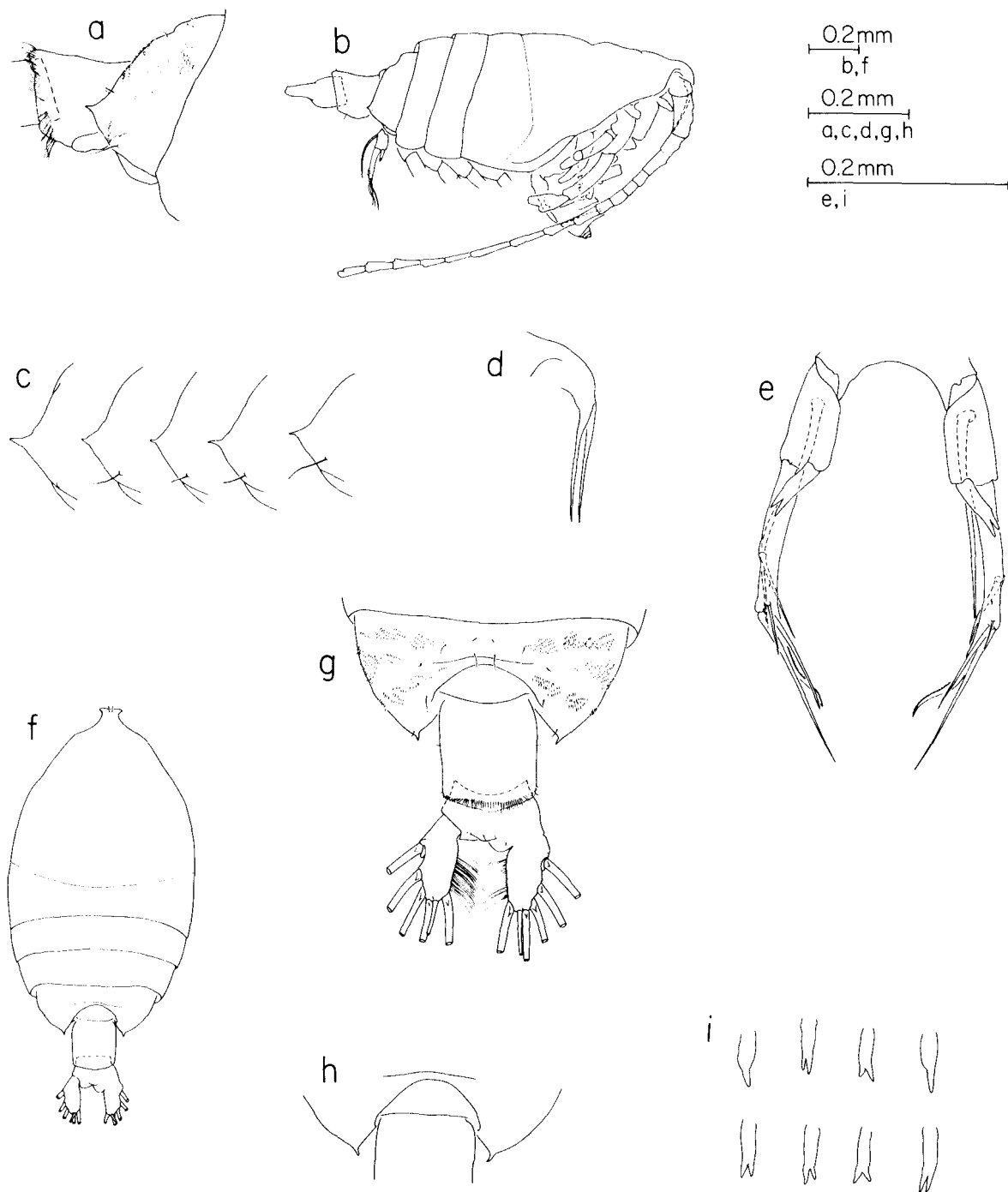
Etymology

The name *platychela* is derived from the Greek words *platys* (= broad) and *chela* (= crab's claw) and refers to the relatively large chela of the adult male.

Types

Holotype: Adult male, TL 1.52 mm, PUR 3.22:1; sorted from plankton sample taken at *Atlantis II*-31 stn. 48, lat. 00°56'N, long. 25°20'W, 12 Feb. 1967, ¾-m net, oblique tow, maximum cable out 200 m. USNM No. 141613.

Allotype: Adult female, TL 1.72 mm, PUR



0.2mm
b,f
0.2mm
a,c,d,g,h
0.2mm
e,i

FIGURE 6.—*Pontellina platychela*, sp.n., adult female: **a**. ThIV-V, genital segment, lateral view (*Atlantis II-20-28*); **b**. habitus, lateral view (*Atlantis II-20-2*); **c**. range of variation in ThIV-V, lateral view (left to right: *Lusiad VII-81 H13*; *Atlantis II-31-40*; *Lusiad VII-81 H13*, different specimen; *Atlantis II-20-31*; same station, different specimen); **d**. rostrum, lateral view (same as **a**); **e**. P5, anterior view (same as **a**); **f**. habitus, dorsal view (same as **b**); **g**. ThIV-V, urosome, dorsal view (same as **a**); **h**. ThIV-V, dorsal view, another specimen (*Atlantis II-20-31*); **i**. P5 Ri of other specimens, right side above, left side below (all four specimens *Lusiad VII-69 H4*).

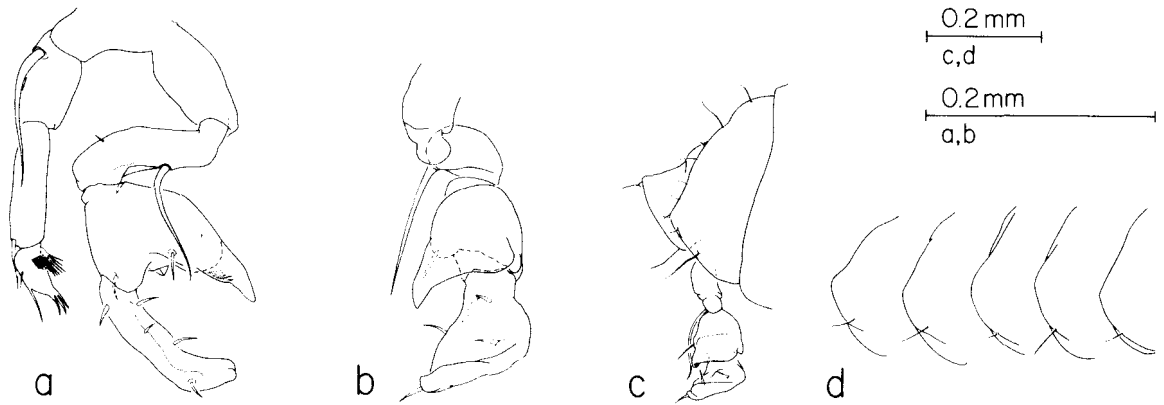


FIGURE 7.—*Pontellina platychela* sp.n., adult male: **a.** P5, posterior view (*Atlantis* II-20-24); **b.** P5 chela, lateral view (same as **a.**); **c.** ThIV-V and P5, lateral view (*Atlantis* II-20-27); **d.** range of variation in ThIV-V (left to right: 3 specimens Amazon 17; La Creuse 7; *Oregon* 1293).

3.52:1; right furcal ramus length 0.110 mm, width 0.075 mm; from same sample as male. USNM No. 141614.

Paratypes: 3♂, 3♀ from same sample. USNM No. 141615.

Reference specimens: 5♂, 5♀, *Oregon* stn. 1293, lat. 19°55'N, long. 74°10'W, 23 Apr. 1955, G III net towed between surface and 2m. USNM No. 141616.

Distribution

P. platychela was found only in epipelagic tows taken in equatorial latitudes of the Atlantic Ocean (Figure 8). The species appeared regularly in samples collected between lat. 10°S and 10°N. The more extensive sampling available to us from north of the equator indicates that few *platychela* extend as far as lat. 21° or 22°N and that the species disappears abruptly at higher latitudes. We anticipate that in the vicinity of the Gulf Stream its northward occurrence may be extended somewhat by examination of additional samples, paralleling occurrences to the south in the Brazil Current.

Additional Description

Female

Right furcal ramus somewhat shorter than in *plumata* (see Figure 27), typically 1.4 times

longer than wide (median 1.44:1, range 1.28-1.55:1, 35 specimens), lateral process anterior to proximal seta lacking, but interior of ramus with glandlike tissue and ductlike structure leading to lateral margin as in *plumata*.

P5 (Figure 6e) essentially as in *plumata* including proportional length relationship of Re and Ri, median 2.27:1, range 1.69-2.91:1, 49 specimens (see Figure 29); Ri polymorphic with one or two apical spines fused to segment, in same specimen spines on left and right Ri may differ in number as in *plumata* (Figure 6i, Table 7).

Attached spermatophore observed in one specimen (see Figure 33c-e, Table 5); neck cemented to ventral side of genital segment in vicinity of genital pore and buried within large irregular mound of cement extending across entire length of genital segment and right ventral side of anal segment, neck extending to right anterolateral side of anal segment along with continuation of cement fixing it to anal segment, large helical counterclockwise turn following emergence of neck from cement orienting succeeding sac anterodorsad.

Male

Right furcal ramus as in *plumata* (see Figures 19, 26), but relatively wider (see Figure 28), ratio of length to width typically 2:1 (median 2.06:1, range 1.91-2.34:1, 37 specimens).

Our impression from the available Atlantic

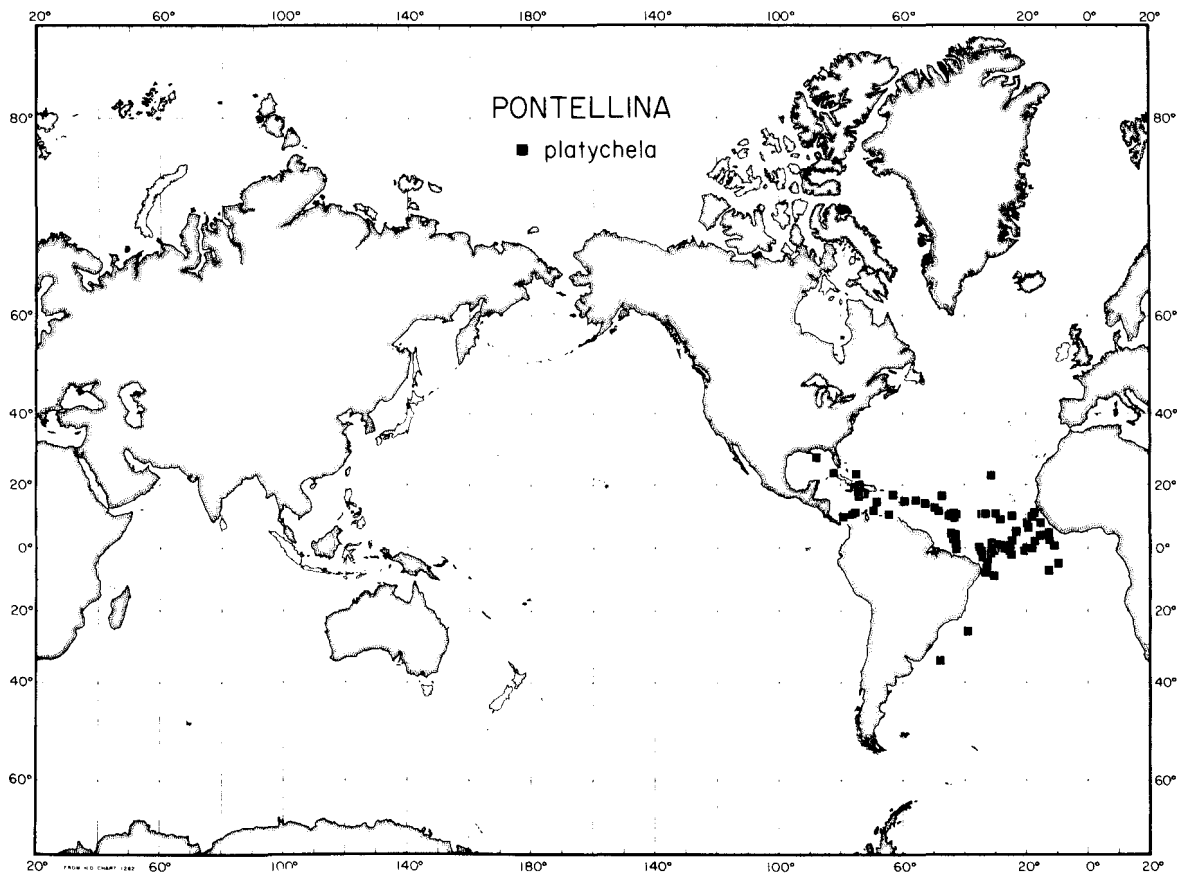


FIGURE 8.—*Pontellina platychela* sp.n. Geographical distribution of captures recorded during the present study.

collections is that the abundance of *platychela* is generally similar to the numbers of *Pontellina* in the Indian and Pacific Oceans (cf. Tables 14, 18), i.e., typically less than 0.2 adults per m³ of water strained.

***PONTELLINA MORII* SP.N.**

(Figures 9 and 11)

Pontellina plumata: Mori (in part), 1937, p. 99, pl. 48, fig. 1-12 only; Dakin and Colefax, 1940, p. 99, fig. 139. NEW SYNONYMY. Specimens seen: 433 adult females, 284 adult males.

Standard measurements: specimens randomly selected from localities spanning the observed geographical area of distribution.

Total length (TL), mm:

	Mean (\bar{x})	Range	Standard error $s_{\bar{x}}$	Speci- mens
Female	1.61	1.38-1.88	0.0145	54
Male	1.44	1.26-1.68	0.0100	58

Prosome-urosoma length ratio (PUR):

	Median	Range	Specimens
Female	3.64:1	3.39-4.10:1	35
Male	3.34:1	2.87-3.73:1	50

Diagnosis

Female

Posterolateral corner of ThIV-V ending in a short spiniform process extending posteriad or somewhat medioposteriad; in contrast to *plumata* junction of spine and ThIV-V corner relatively

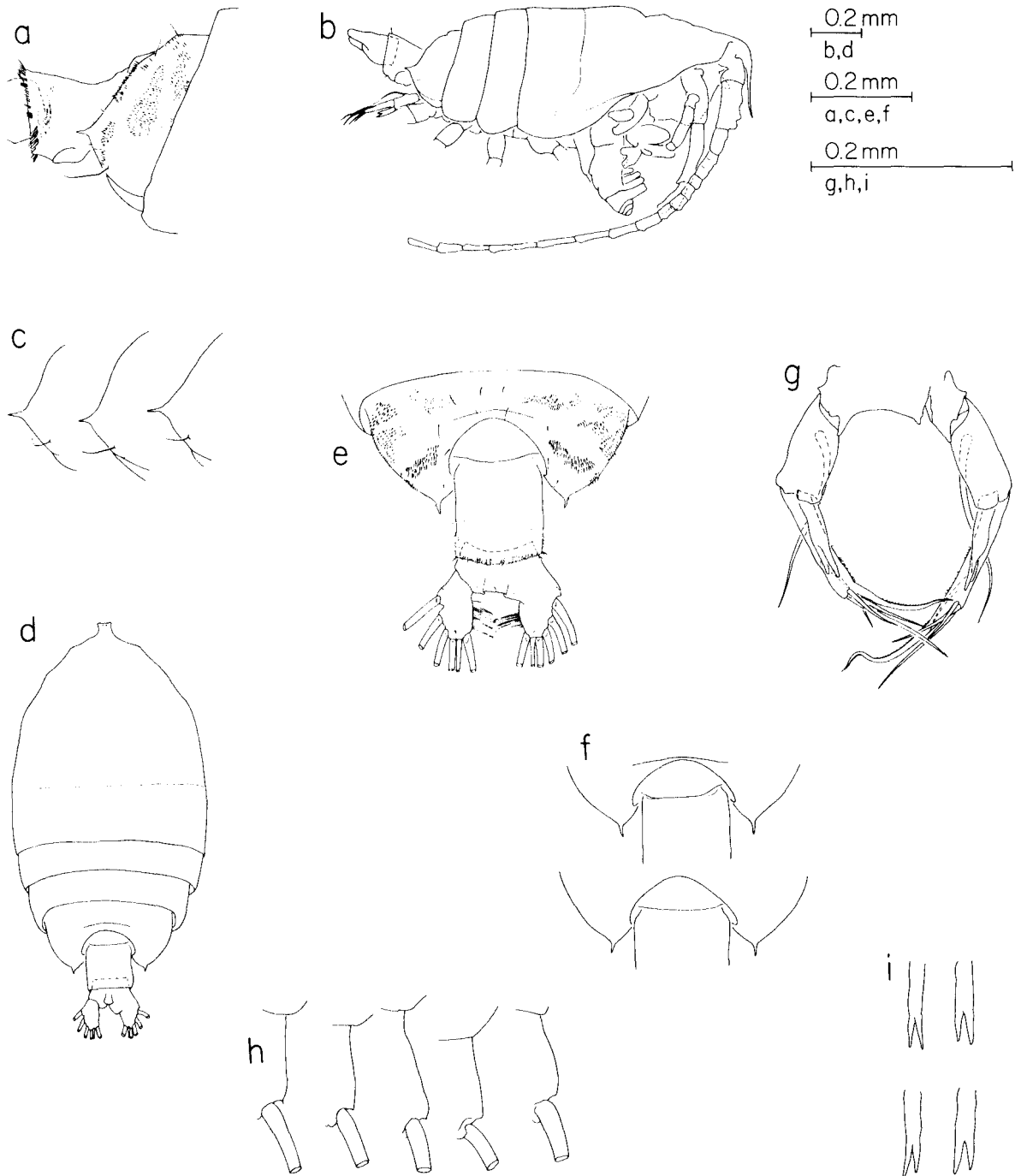


FIGURE 9.—*Pontellina morii* sp.n., adult female: **a**. ThIV-V and genital segment, lateral view (Lusiad V-66); **b**. habitus, lateral view (Circe III NT-27); **c**. variation in ThIV-V, lateral view (left to right: Troll 31A, 2 specimens Lusiad II-66); **d**. habitus, dorsal view (Circe III NT-26); **e**. ThIV-V and urosome, dorsal view (same as **a**); **f**. variation in ThIV-V, dorsal view (top: Troll 31A; bottom: Lusiad II-66); **g**. P5, anterior view (Lusiad V-66); **h**. variation observed in lateral margin of right furcal ramus, dorsal view [left to right: Scan IV-3; TO-58-1 (Scott) 14; Lusiad II-13; Lusiad II-10; Lusiad V-45]; **i**. P5 Ri in other specimens, right side above, left side below (left: Troll 30; right: Silas Bent 1-12).

abrupt in both dorsal and lateral views (Figure 9a-f), right and left sides symmetrical (Table 2), spine small, not exceeding 0.035 mm irrespective of TL (Figure 10), spine roughly one-half as long as that in its congener from the eastern equatorial Pacific described below. Genital segment with posterolateral cluster of coarse hairs on both sides, lacking anterolateral cluster found in *plumata* although several fine hairs may occur at this site (Figure 9a, e): posterior margin of segment bordered by fine, long hairs as in *plumata*.

Male

ThIV-V typically ending posteriorly in a small spiniform process (Figure 11b, c) similar to female. P5 with chela of *plumata*-type but both segments showing distinctive features; distal segment short, not reaching opposing disto-lateral digitiform process on proximal segment (Figure 11d), apex of distal segment with prominent triangular spur on posterior side (Figure 11d-f); proximal segment in lateral view with basal process posterior to digitiform process acuminate, intersection of posterior basal process and digitiform process usually in form of a deep angular notch; in posterior view proximal segment with axis of posterior basal process extending somewhat parallel to digitiform process and not overlapping anterior basal process, latter angled toward articulation between proximal and distal segments. Left P5 with Re1 longer than that in *plumata* (see Figure 30).

Additional Description

Female

Right furcal ramus considerably shorter than in *plumata* relative to prosome (see Figure 25), right furcal ramus with median ratio of

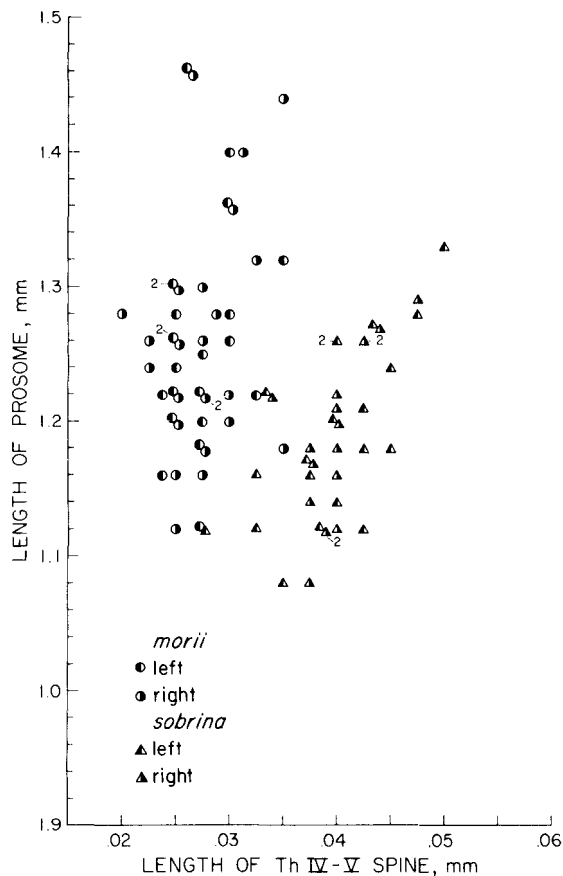


FIGURE 10.—Length of prosome (ordinate) plotted against length of ThIV-V spine (abscissa) for females of *Pontellina morii* and *P. sobrina*.

length to width 1.25:1, range 1.12-1.44:1, 46 specimens; lateral edge of right ramus with small point variable in shape just anterior to base of outermost seta (Figure 9e, h), glandular tissue within ramus as in *plumata*.

P5 with Re bearing hairs along median margin (Figure 9g); Ri relatively longer than that

TABLE 2.—Length of posterior spine on thoracic segment IV-V in adult females of *Pontellina morii* and *P. sobrina*.

Species		\bar{x} (mm)	Range (mm)	s	N
<i>P. morii</i>	left side	0.0263	0.018-0.035	0.0010	38
	right side	0.0275	0.020-0.035	0.0032	40
	combined	0.0269	0.018-0.035	0.0037	78
<i>P. sobrina</i>	left side	0.0409	0.033-0.050	0.0032	33
	right side	0.0404	0.028-0.049	0.0032	32
	combined	0.0407	0.028-0.050	0.0045	65

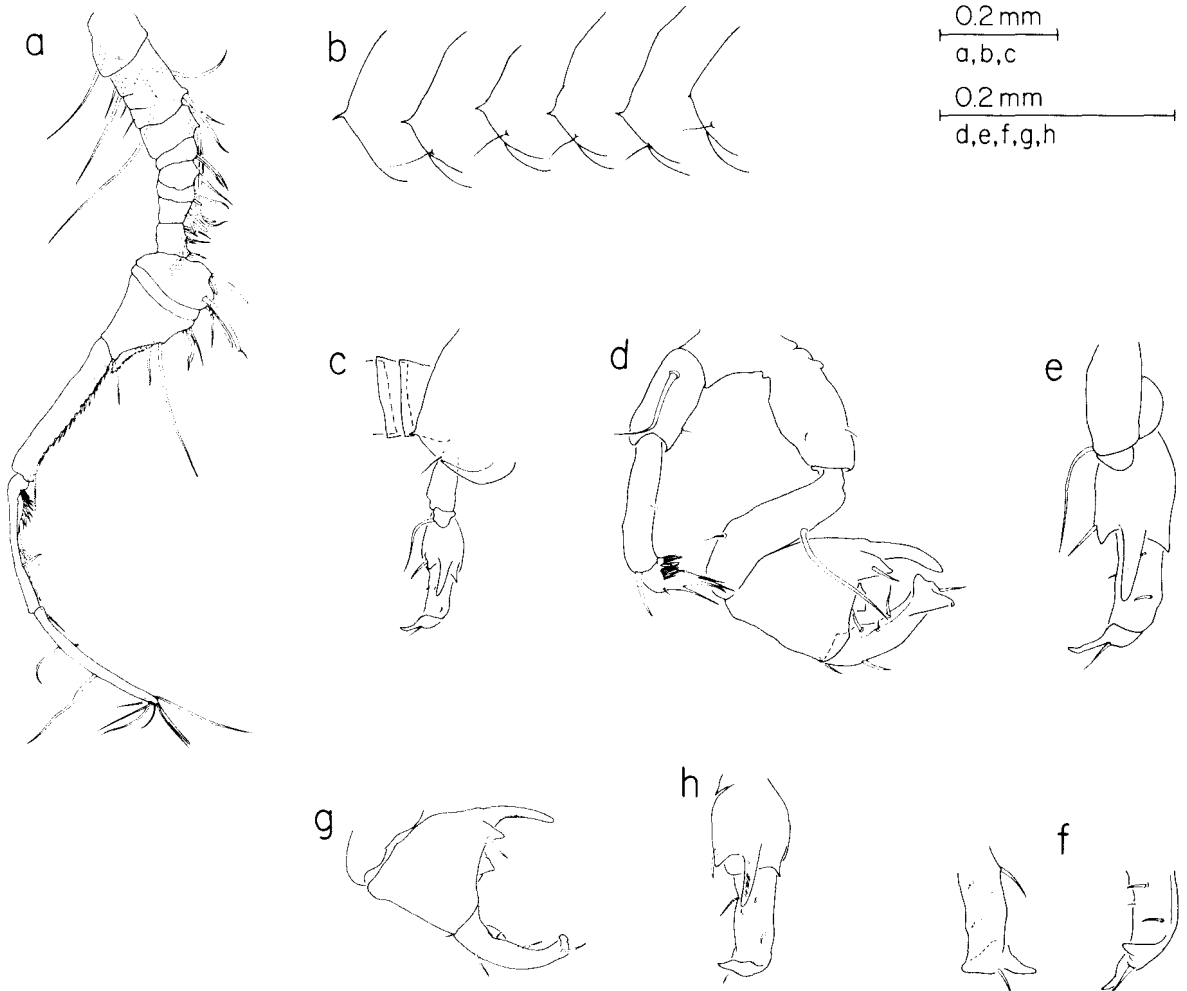


FIGURE 11.—*Pontellina morii* sp.n., adult male: **a**, right A1, dorsal view (Lusiad II-66); **b**, variation in ThIV-V spine, lateral view (left to right: Shellback 105; Troll 25; Lusiad II-55; Troll 32A; 2 specimens Monsoon 6); **c**, ThIV-V, P5 and first two segments of urosome, lateral view (Lusiad V-78); **d**, P5, posterior view (same as **a**); **e**, P5 chela, lateral view (same as **c**); **f**, apex of distal segment of P5 enlarged (same as **c**); **g**, aberrant chela showing a weakened subapical spur on distal segment, posterior view (*Anton Brunn* I-58); **h**, aberrant chela, lateral view (same as **g**).

in *plumata*, Re being less than 1.8 times longer than Ri, median 1.45:1, range 1.22-1.76:1, 55 specimens (see Figure 29); Ri typically with two relatively equal apical spines (Figure 9g, i; Table 7).

Attached spermatophore observed in four specimens (see Figure 33f-h, Table 5), appearance and orientation similar to that in *platychela* except for less cement on ventral side of urosome, especially on anal segment.

Male

Right furcal ramus differing from that in

plumata in having a relatively shorter length (see Figure 26), median length-to-width ratio 1.93:1, range 1.80-2.07:1, 39 specimens, but overlapping extensively with its congener from the eastern equatorial Pacific (described below). Left P5 with Re1 considerably longer than that in *plumata*: in *morii* length of left P5 Re1 to length of right furcal ramus ranges from 1.08 to 1.26:1, 20 specimens (see Figure 30).

Etymology

This patronym commemorates the late

Takamochi Mori who first called attention to the distinctiveness of this species and for his pioneering contributions to our knowledge of Pacific Calanoida.

Types

Holotype: Adult male, TL 1.36 mm, PUR 3.25:1; sorted from plankton sample taken at Lusiad II stn. 66, lat. $01^{\circ}54'N$, long. $79^{\circ}01'E$, 30 Aug. 1962, 1-m net, oblique tow, maximum cable out 280 m, USNM No. 141621.

Allotype: Adult female, TL 1.56 mm, PUR 3.87:1, right furcal ramus length 0.090 mm, width 0.080 mm, from same sample as male. USNM NO. 141622.

Paratypes: 5♂, 5♀ from same sample. USNM No. 141623.

Reference specimens: 2♂, 2♀, Lusiad V stn. 76, lat. $02^{\circ}01'S$, long. $91^{\circ}58'E$, 24 Apr. 1963, 1-m net, oblique tow, maximum cable out 280 m. USNM No. 141625. 2♂, 2♀, Capricorn stn. 2, lat. $02^{\circ}54'N$, long. $168^{\circ}40'E$, 28 Nov. 1952, 1-m net, oblique tow, maximum cable out 200 m. USNM No. 141624.

Distribution

P. morii was found primarily at Indian and Pacific Ocean localities distributed in a zonal band lying roughly between lat. $20^{\circ}N$ and $20^{\circ}S$ (Figure 12). Occurrences at higher latitudes are few and mostly in the vicinity of western boundary currents; e.g., in the Kuroshio Current region just east of Japan and east of southern Africa in the region of the Mozambique and Agulhas Currents. In the eastern

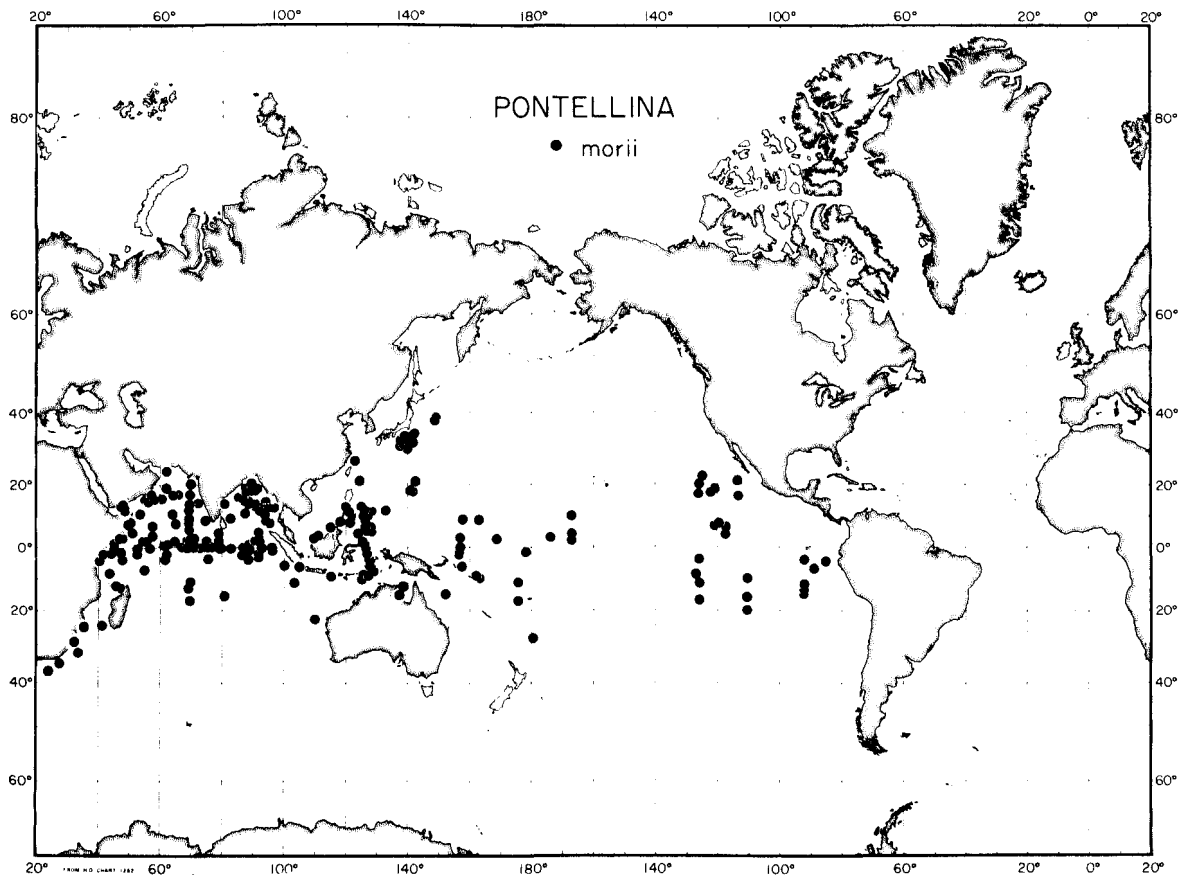


FIGURE 12.—*Pontellina morii* sp.n. Geographical distribution of captures recorded during the present study.

Pacific *morii* approached the Americas in the vicinity of Baja California and also at the latitudes of the Gulf of Guayaquil.

Among the 72 quantitatively analyzed samples containing *morii* estimates of abundance ranged from 0.003 to 0.5 individuals per m³, the median being 0.01. In the sets of samples selected for quantitative analysis (Figure 1b) mean abundance in the Indian Ocean exceeded 0.04 individuals per m³, 5 or more times higher than that found in sets of samples from the Pacific Ocean (Figure 35, Table 14); frequency of occurrence in the Indian Ocean (~30%) was also higher than in the Pacific Ocean (≤20%).

PONTELLINA SOBRINA SP.N.

(Figures 13 and 14)

Specimens seen: 421 adult females, 364 adult males.

Standard measurements: specimens randomly selected from locations spanning the observed geographical distribution.

Total length (TL), mm:

	Mean (\bar{x})	Range	Standard error $s_{\bar{x}}$	Speci- mens
Female	1.57	1.42-1.78	0.0134	50
Male	1.41	1.18-1.64	0.0118	56

Prosoma-urosome length ratio (PUR):

	Median	Range	Specimens
Female	3.73:1	3.17-4.16:1	33
Male	3.43:1	3.06-3.75:1	51

Diagnosis

Female

Most similar in appearance to *morii*. Spini-form process strongly demarcated from ThIV-V corner and typically symmetrical as in *morii*, but spine almost twice as long (Figure 10, Table 2); in dorsal view weakly curved spines extending posterolaterad (Figure 13g). Genital segment with two lateral clusters of hairs on both sides, anterior cluster consisting of fine hairs, posterior cluster consisting of coarse hairs (Figure 13 a, g); posterior margin of segment with border of long fine hairs as in all preceding species.

Male

ThIV-V (Figure 14a, b) as in female. P5 (Figure 14c, d) most similar to that in *morii* with notable differences present in chela. Distal segment of chela relatively long, apex extending beyond apex of laterodistal digitiform process of proximal segment. Moreover, distal segment lacking subapical spur (Figure 14c, d); in lateral view posterior basal process and digitiform process of proximal segment separated by rounded notch (Figure 14d); proximal segment in posterior view as in *morii*. Left P5 with Re1 longer than that in *plumata* (see Figure 30).

Additional Description

Female

Right furcal ramus somewhat shorter relative to its width as well as to length of prosoma (see Figures 25, 27), median ratio of right furcal ramus length to width 1.12:1, range 1.02-1.31:1, 66 specimens; lateral edge of right ramus usually with broad point immediately anterior to base of outermost seta (Figure 13h), glandular tissue within ramus as in *plumata*.

P5 (Figure 13i) similar to that in *morii* except that ratio of lengths of exopod to endopod tends to be smaller, median 1.29:1, range 1.07-1.50:1, 52 specimens (see Figure 29); Ri typically with two relatively equal apical spines (see Table 7).

Attached spermatophore observed in 27 specimens (see Table 5), not differing appreciably in general features from those observed in *morii*.

Male

Right furcal ramus similar to that in *morii* in both relative length (see Figure 26) and in proportion of length to width, median 1.88:1, range 1.71-2.07:1, 40 specimens (see Figure 28); Re1 of left P5, compared to length of right furcal ramus, relatively longer than that in *morii* (see Figure 30), this ratio in *sobrına* ranging from 0.96-1.17:1, 21 specimens.

Etymology

The name *sobrına*, Latin for cousin, was chosen to acknowledge the close morphological relationship to *morii*.

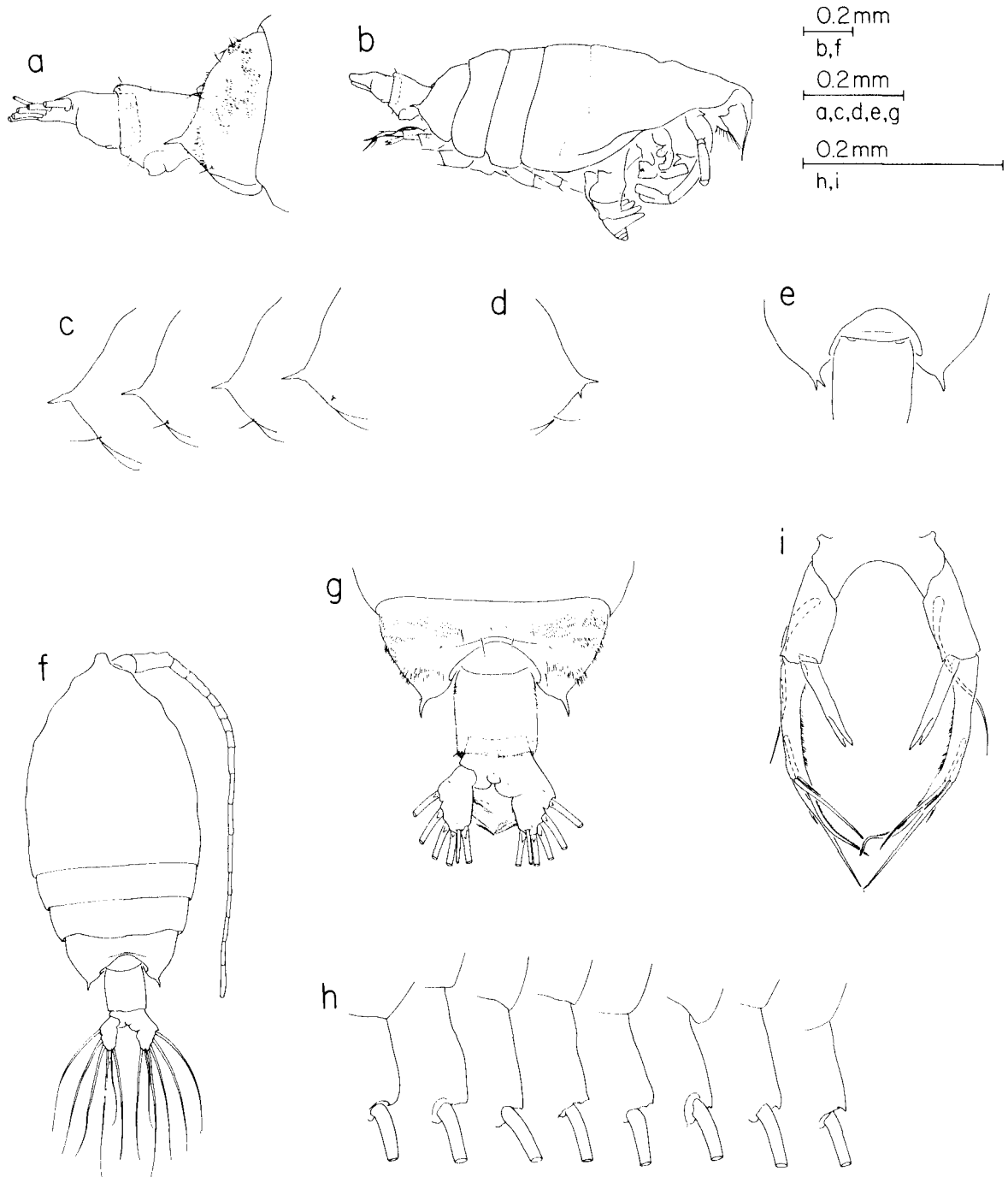


FIGURE 13.—*Pontellina sobrina* sp.n., adult female: **a**. ThIV-V, urosome, lateral view (Bonacca 35); **b**. habitus, lateral view (same as **a**); **c**. variation in ThIV-V spine, lateral view (left to right: EASTROPAC Jordan 037; 2 specimens Bonacca 31, Shellback 51); **d**. variation in left ThIV-V, lateral view, specimen with two spines (Bonacca 50); **e**. variation in left ThIV-V, dorsal view (La Creuse OT-6); **f**. habitus, dorsal view (same as **a**); **g**. ThIV-V and urosome, dorsal view (same as **a**); **h**. variation in lateral margin of right furcal ramus, dorsal view (left to right: La Creuse OT-6; La Creuse 18; La Creuse OT-14; La Creuse 17; La Creuse OT-14, different specimen; 2 specimens La Creuse 18; Bonacca 33); **i**. P5, anterior view (same as **a**).

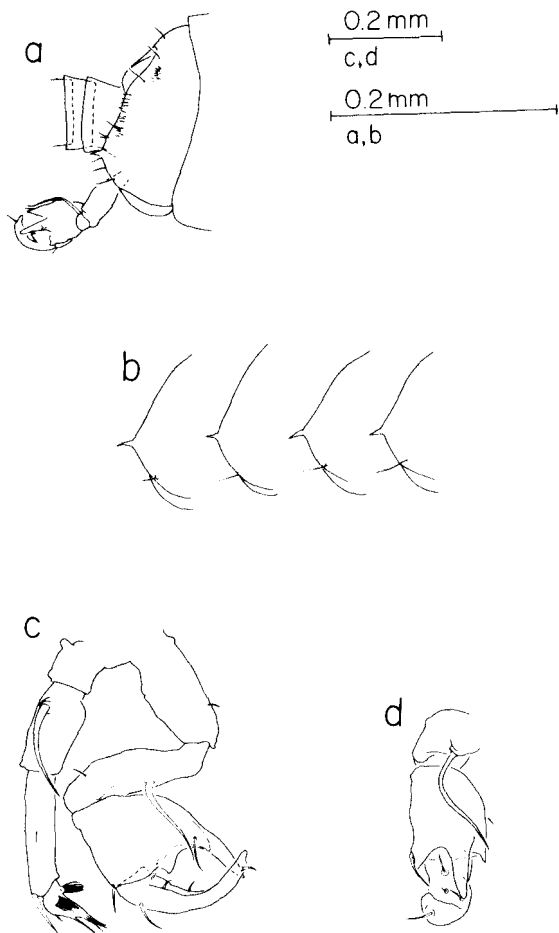


FIGURE 14.—*Pontellina sobrina* sp.n., adult male: **a**. ThIV-V, part of urosome and P5, lateral view [TO-58-1 (Scot) 33]; **b**. variation observed in ThIV-V spine, lateral view (left to right: Bonacca 55; Bonacca 43; 2 specimens Bonacca 51); **c**. P5, posterior view (La Creuse 21); **d**. chela P5, lateral view (Shellback 51).

Types

Holotype: Adult male, TL 1.42 mm, PUR 3.44:1, sorted from plankton sample taken at Bonacca stn. 51, lat. 13°44'N, long. 90°51'W, 19 Aug. 1963, ½-m net, oblique tow, maximum cable out 200 m. USNM No. 141617.

Allotype: Adult female, TL 1.52 mm, PUR 3.75:1, right furcal ramus length 0.080 mm, width 0.075 mm, from same sample as male. USNM No. 141618.

Paratypes: 5♂, 5♀ from same sample. USNM No. 141619.

Reference specimens: 5♂, 5♀, La Creuse stn. 15, lat. 08°41.2'N, long. 79°31.2'W, 4 May 1962, GV net towed between 0 and 4 m. USNM No. 141620.

Distribution

P. sobrina is obviously indigenous to the eastern tropical Pacific Ocean (Figure 15). The species was found only at Pacific stations east of long. 130°W. Occurrences at latitudes higher than 20° were restricted to a few samples taken near the mouth of the Gulf of California. Thus, the apparent boundaries coincide in general with the North and South Equatorial Currents, and its westernmost limits lie in the path of the Equatorial Countercurrent.

In 31 quantitative samples containing *sobrina* abundance varied from 0.01 to 0.66 individuals per m³, the median being 0.04. In the sets of samples selected for quantitative analysis (Figure 1b) *sobrina* showed mean abundance values (ranging from 0.02 to 0.09 individuals per m³) similar to those of *mori* in the Indian Ocean and to *plumata* outside of the eastern tropical Pacific (see Figure 35, Table 18).

DEVELOPMENTAL STAGES AND BREEDING

Immature specimens of *Pontellina* were sorted routinely together with adults. They were neither as abundant nor as frequent as the adults, a difference that is at least partially attributable to escapement of younger stages through the relatively coarse mesh (~0.5 mm) of most of the nets used to obtain our samples. General *Pontellina* habitus characteristics such as appearance of the prosome in dorsal view, rostrum, strong Mx2, and relatively long setae on A2 and Mnd served to distinguish the specimens. The number of swimming legs and body segments as well as total body length were used to determine their ontogenetic stage. Identification to species was reasonably certain only for stage V copepodids; details are presented below. Specimens of stages III and IV were tentatively assigned to species on the basis of their geographical origin. The following

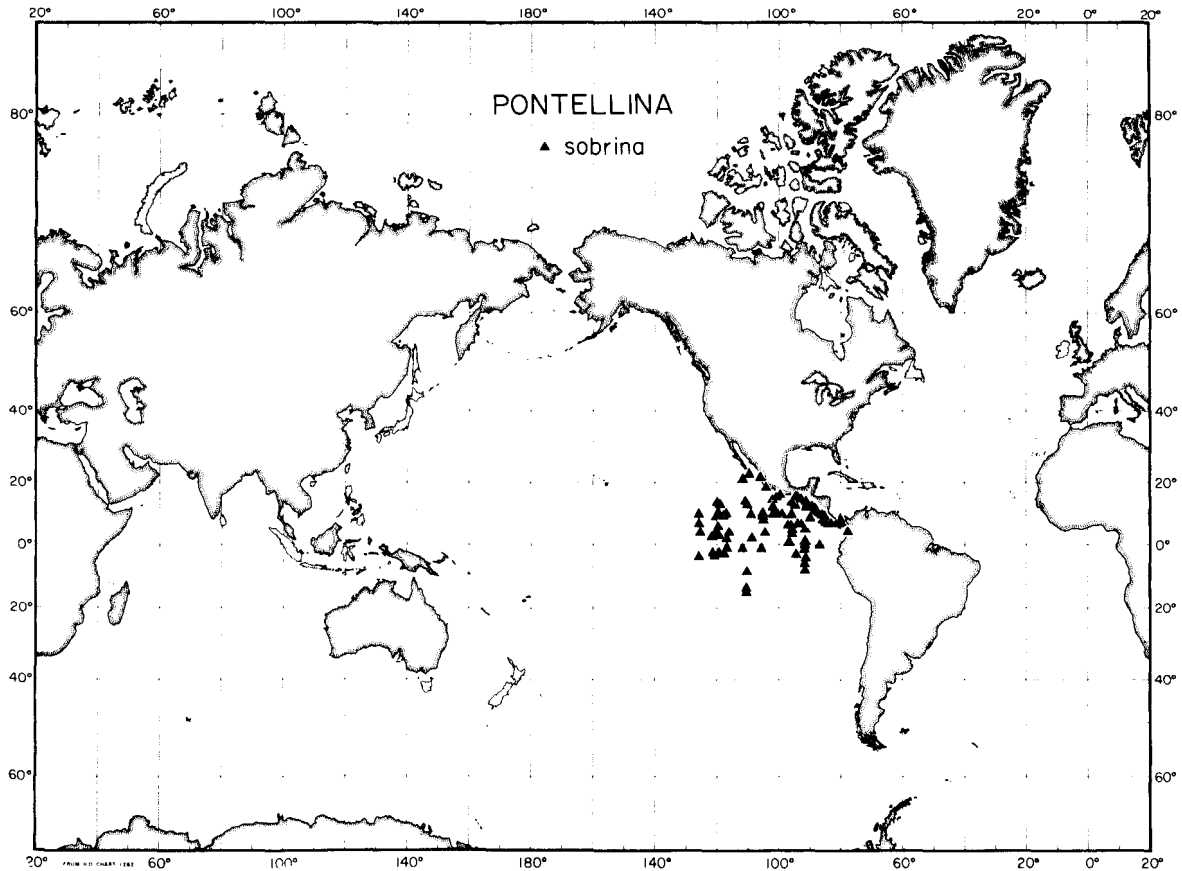


FIGURE 15.—*Pontellina sobrina* sp.n. Geographical distribution of captures recorded during the present study.

notes and Table 3 summarize ontogenetic characteristics of stages II through V prevailing in the genus.

Stage II

TL 0.72-0.76 mm (5 specimens). Rostral filaments and dorsal ocelli-like structures present; prosome with 4 free segments, urosome with 2 segments. Re of P1 and P2 bimerous, Ri of P1 and P2 and both rami of P3 unimerous, P4 consisting of a pad with folds, short setae and an incipient Ri; P5 lacking.

Stage III

(Figure 16c)

TL 0.82-0.88 mm (20 specimens). Neither sexes nor species distinguishable. Prosome with

5 segments, urosome with 2 segments. Re of P3 bimerous, Ri of P3 as well as both rami of P4 unimerous. P5 lobiform, bearing one apical seta.

Stage IV Female

(Figure 16a)

TL 0.90-1.10 mm (22 specimens, probably including all four species). Urosome with 3 segments. Re of P3 and P4 bimerous, Ri unimerous. Re of P5 unimerous; right Re and elongate seta on mediobasal corner of Re slightly larger than those of left P5; Ri lobiform, incompletely separated from B2.

Stage IV Male

(Figure 16b)

TL 0.95-1.10 mm (22 specimens, probably including all four species). Male resembles

TABLE 3.—Ontogenetic development in copepodite stages of *Pontellina*.

	II	III	IV♂	IV♀	V♂	V♀
Thoracic segments	4	5	5	5	5	5
Free abdominal segments	2	2	3	3	4	3
Rostral filaments	present	present	present	present	present	present
Dorsal ocelli	present	present	present	present	present	present
Right A1					segments 13-16 swollen	
P1 Re segments	2	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P2 Re segments	2	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P3 Re segments	1	2	2	2	3	3
Ri segments	1	1	1	1	2	2
P4 Re segments	lobe, 1 seta	1	2	2	3	3
Ri segments	lobe, 1 seta	1	1	1	2	2
P5 Re segments	absent	lobe, 1 seta	1 right leg slightly larger than left	1 right leg slightly larger than left	2 right leg larger than left	1 right leg with 5 setae, left leg with 6 setae
Ri segments	absent	absent	rudimentary	1	absent	1

corresponding stage of female, but P5 with Ri absent or appearing as a small distal swelling on B2. Right Re also slightly larger than left.

Stage V Female

(Figure 17a-l)

TL 1.18-1.48 mm (40 specimens, all species represented). ThIV and V almost completely separated. Urosome with 3 segments, genital segment largest and with weak ventral swelling. Furcal rami incompletely separated from anal segment. Lateral margin of right furcal ramus proximal to first seta lacking protrusion. Left and right A1 symmetrical. Re of P3 and P4 trimerous, Ri bimerous. P5 with proportions of Re and Ri showing similarity to those of adult. Re unimerous with 5 setae on right leg, 6 setae on left leg; proximal Si of left side notable for its size and curved shape, an asymmetry lacking in the adult.

Stage V Male

(Figure 18a-q)

TL 1.20-1.44 mm (40 specimens, all species represented). ThIV and V almost completely separated. Urosome with 4 segments. Furcal rami incompletely separated from anal segment.

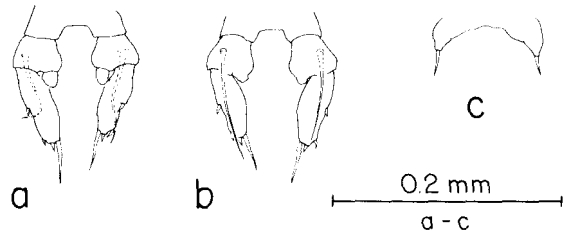


FIGURE 16.—*Pontellina* sp. copepodite stages: a, stage IV female, P5, anterior view; b, stage IV male, P5, posterior view; c, stage III copepodid, P5.

Right A1 with segments 13-16 slightly swollen, segments distal to swelling partly fused. P5 trimerous, slightly curved medially; right leg longer than left leg, Ri not developed.

In other genera of Pontellidae, as well as in a number of other heterarthrandrid families (Diaptomidae, Temoridae, Centropagidae, Pseudodiaptomidae) we note that fusion of urosomal segments I and II in the female first appears in the stage V copepodid (Gurney, 1931; Johnson, 1935; Crisafi, 1960; Lawson and Grice, 1970; Grice, 1971). Morphological features of the genital plate, antrum, and internal structures such as the seminal receptacles (Fahrenbach, 1962; Frost and Fleminger, 1968) are lacking in the stage V female. We also note that in most amphiscandrid families (e.g., Calanidae, Para-

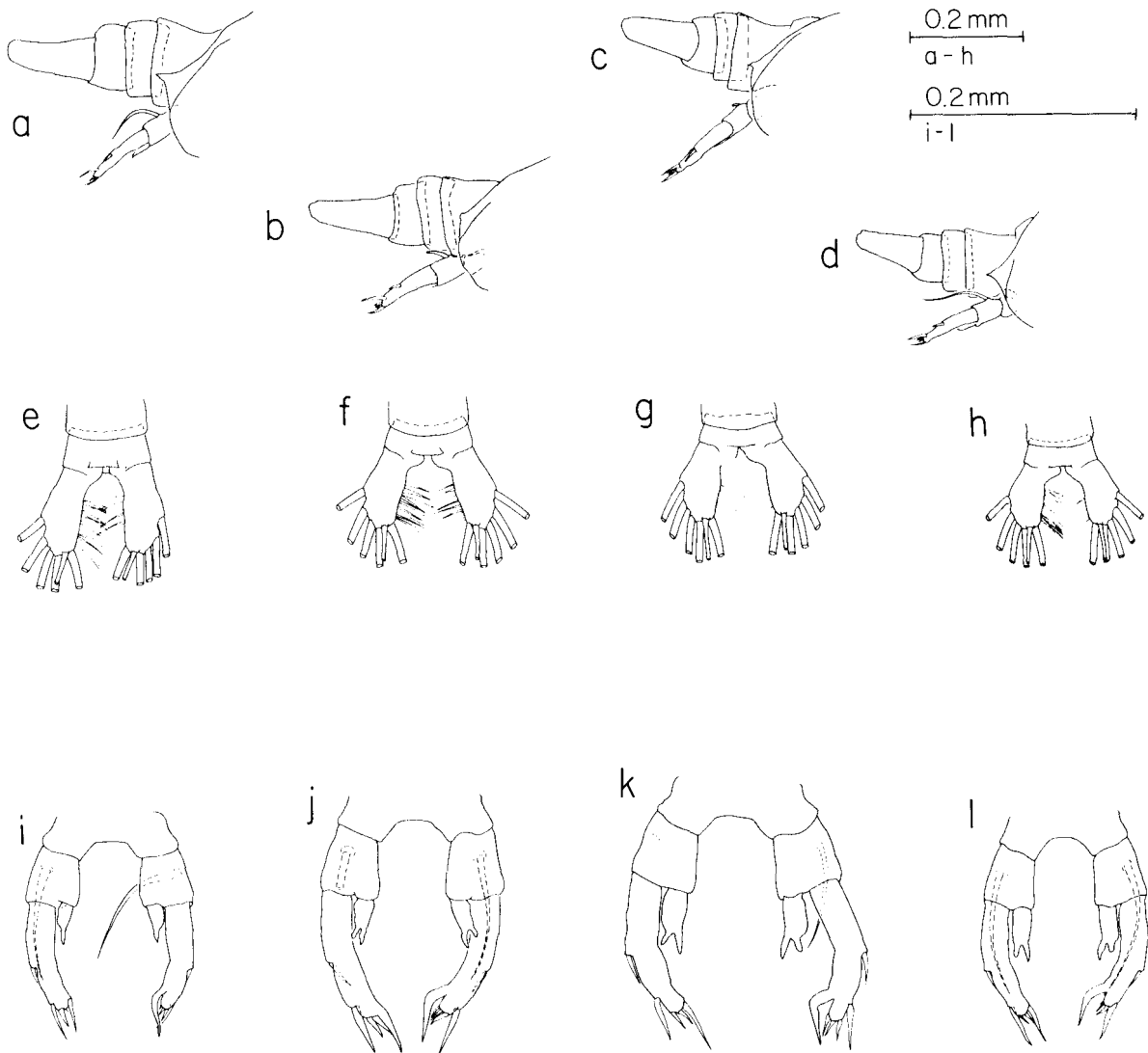


FIGURE 17.—Copepodite stage V, females: **a-d**. ThIV-V, right P5 and urosome, lateral view; **e-h**. anal segment, furcal rami, dorsal view; **i-l**. P5, anterior view. *Pontellina plumata*: **a, e** (*Atlantis II-31-1*); **i** (*Lusiad V-60*). *P. platychela*: **b, f, j** (*Atlantis II-20-42*). *P. morii*: **c, g, k** (*Dodo VI*, near Mombasa Harbor). *P. sobrina*: **d, h, l** [*TO-58-1* (Scot) 56].

calanidae, Pseudocalanidae, Aetideidae, Euchaetidae, Phaennidae, Scolecithricidae) but not in Eucalanidae (Johnson, 1937; Sewell, 1929; Björnberg, 1967; and our unpublished observations of all species) fusion of urosomal segments I and II seems to be delayed until the appearance of the sexually mature female. This pattern has been documented by a number of ontogenetic studies on individual species (With, 1915; Nicholls, 1934; Campbell, 1934; Marshall and Orr, 1955; Matthews, 1964; and our unpublished observations).

Notes on Individual Species

Pontellina plumata

(Figures 17a, e, i; 18a, e, i, m, p)

Copepodite stage V female: TL \bar{x} 1.38 mm, range 1.26-1.48 mm, 10 specimens. Posterolateral corner of ThV (Figure 17a) produced into a strong point similar to the adult. Furcal rami symmetrical (Figures 17e, 19), length of right ramus relative to width greater than that in *morii* (Figure 20). P5 Ri shorter than in *morii* (Figure 20).

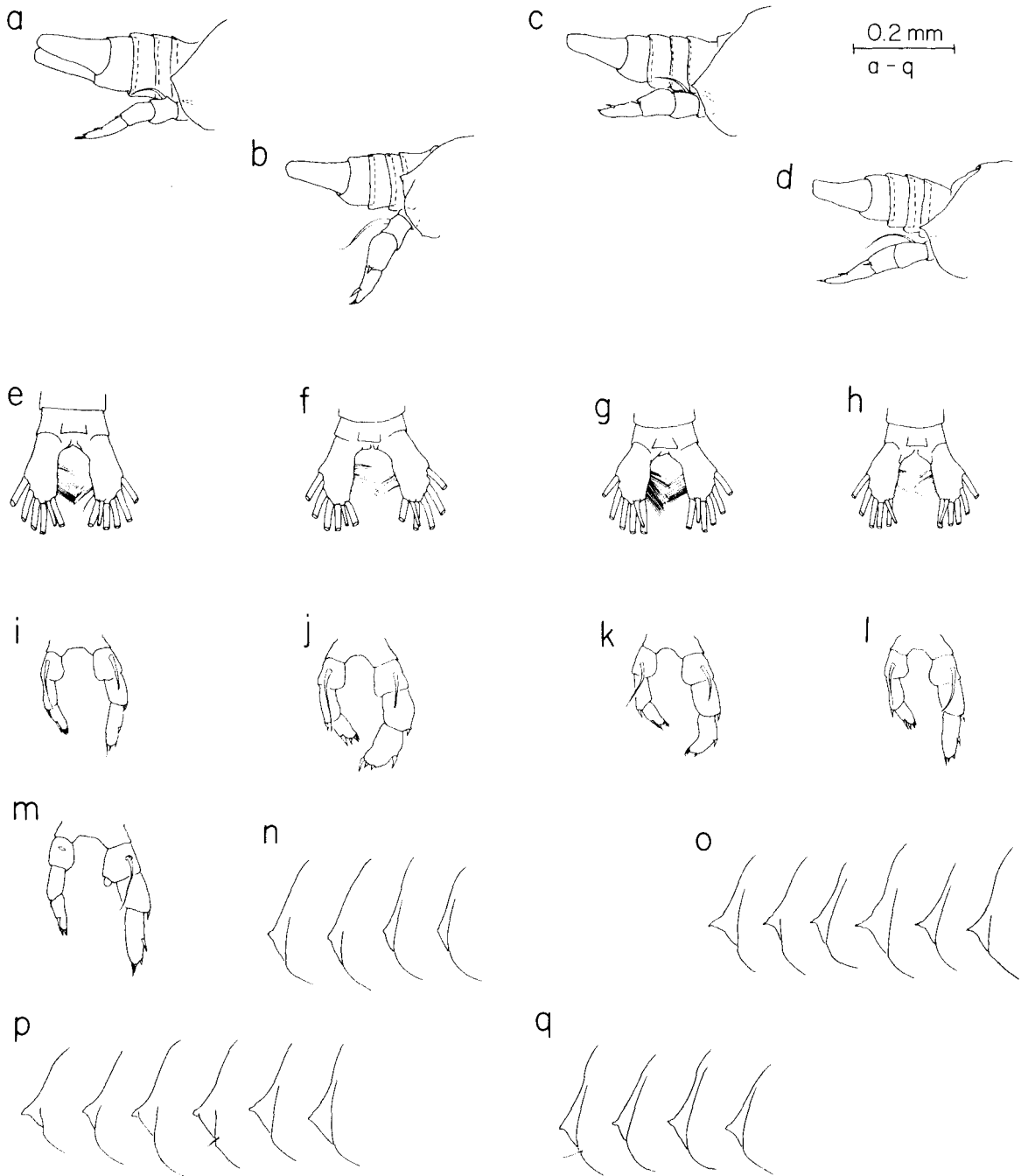


FIGURE 18.—Copepodite stage V, males: **a-d**. ThIV-V, right P5 and urosome, lateral view; **e-h**. anal segment, furcal rami, dorsal view; **i-m**. P5, posterior view; **n-q**. range of variation in ThIV-V, lateral view. *Pontellina plumata*: **a, e, i** (Lusiad V-43); **m** (Monsoon 2, atypical P5 with Ri); **p** (left to right: *Atlantis II-31-74*; *Atlantis II-31-7*; *Atlantis II-31-28*; *Atlantis II-31-23*; *Gascoyne G1/32/63*; Troll 25A). *P. platychela*: **b** (*Atlantis II-31-60*); **f, j** (*Atlantis II-31-15*); **n** (left to right: *Oregon 1289*; *Atlantis II-31-50*; *Atlantis II-20-42*; *Atlantis II-31-57*). *P. morii*: **c, g, k** (Lusiad V-43); **q** (left to right: *EQUAPAC Horizon 31*; *Lusiad V-68*; *Anton Bruun II-58*; *Anton Bruun I-60*). *P. sobrina*: **d, h, l** (La Creuse 18); **o** [left to right: *EASTROPAC Rockaway 064*; *TO-58-1 (Scot) 29*; *TO-58-1 (Scot) 38*; *EASTROPAC Rockaway 071*; *TO-58-1 (Scot) 36*; *EASTROPAC Rockaway 056*].

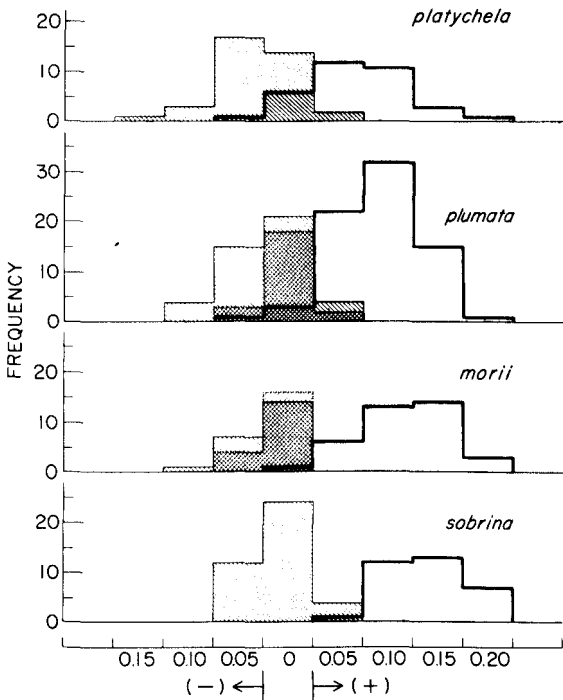


FIGURE 19.—Frequency distribution of differences in length of left furcal ramus and right furcal ramus for the four species of *Pontellina*. Gray with heavy outline = adult females; left-diagonal hatch with light outline = adult males; right-diagonal hatch with dotted outline = stage V females.

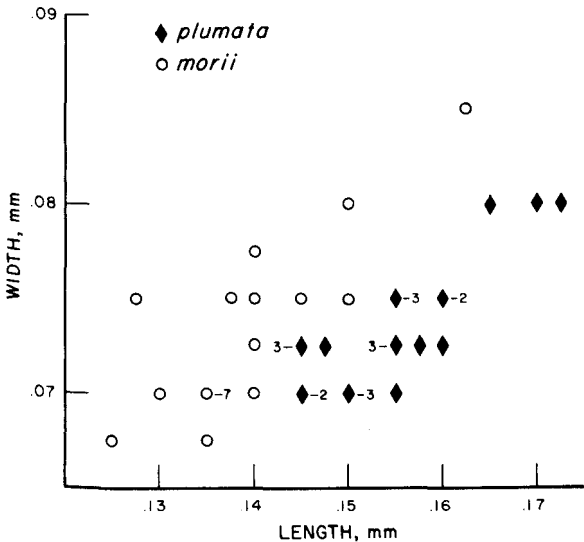


FIGURE 20.—Width of right furca (ordinate) plotted against length (abscissa) for female stage V copepodids of *Pontellina plumata* and *P. morii*.

relative to length of right furcal ramus (Figure 21). Re to Ri length ratio, median 3.0:1, range 2.3-3.5:1, 19 specimens (Figure 22); left P5 with medialmost seta on Re small and gently curved (Figure 17i) relative to that in *morii* (Figure 17k).

Copepodite stage V male: TL \bar{x} 1.30 mm, range 1.20-1.44 mm, 10 specimens. Posterolateral corner of ThV ending in a broad point (Figure 18a, p). Terminal segment of right P5 about 3.1 times longer than wide (Figure 18i), endopod rarely present (Figure 18m). Furcal rami (Figure 18e) similar in relative length and width to those of female.

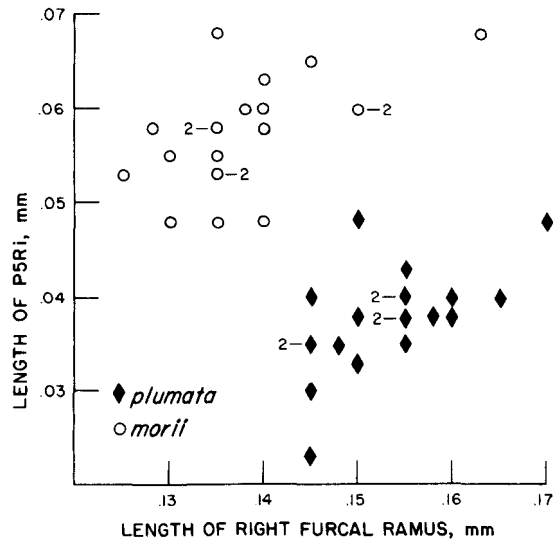


FIGURE 21.—Length of P5 Ri (ordinate) plotted against length of right furcal ramus (abscissa) for female stage V copepodids of *Pontellina plumata* and *P. morii*.

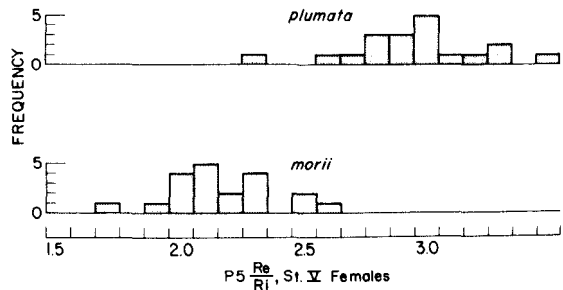


FIGURE 22.—Frequency distribution of P5 Re:Ri ratio for female stage V copepodids of *Pontellina plumata* and *P. morii*.

Pontellina platychela

(Figures 17b, f, j; 18b, f, j, n)

Copepodite stage V female: TL \bar{x} 1.37 mm, range 1.18-1.46 mm, 10 specimens. ThV posterolateral corners rounded and ending in a small denticle (Figure 17b) as in adult. Furcal rami (Figure 17f) and P5 (Figure 17j) resembling those of *plumata*.

Copepodite stage V male: TL \bar{x} 1.30 mm, range 1.24-1.36 mm, 10 specimens. Margin of posterolateral corner of ThV with weak denticle (Figure 18b, n). P5 with distinctive right leg (Figure 18j), Re considerably broader than in the other three species, about 1.6 times as long as wide. Furcal rami (Figure 18f) as in *plumata*.

Pontellina morii

(Figures 17c, g, k; 18c, g, k, q)

(Notes based on specimens from localities in the Indian Ocean.)

Copepodite stage V female: TL \bar{x} 1.28 mm, range 1.18-1.36 mm, 10 specimens. ThV corner typically with a small spiniform point (Figure 17c) resembling that in the adult. Ri of P5 (Figure 17k) longer than in *plumata* (Figure 21), typically with 2 spines; Re:Ri length ratio considerably less (median 2.1:1, range 1.7-2.6:1, 20 specimens) than in *plumata* (Figure 22). Furcal rami symmetrical (Figure 19), shorter than those in *plumata* (Figure 20), as in sexually mature stages. Medial setalike process of Re of left P5 (Figure 17k) more abruptly bent ($\sim 90^\circ$) than that of the other three species (Figure 17i).

Copepodite stage V male: TL \bar{x} 1.21 mm, range 1.12-1.32 mm, 10 specimens. Posterolateral corner of ThV ending in a relatively short spiniform point (Figure 18c, q) about one-half the length of that in *sobrīna* (Figure 18d, o) and much less robust than that in *plumata* (Figure 18a, p). Distal segment of right P5 distinctly bent mediad (Figure 18k). Furcal rami (Figure 18g) similar in relative length and width to those in female.

Pontellina sobrīna

(Figures 17d, h, l; 18d, h, l, o)

(Notes based on juvenile specimens from easternmost Pacific localities which were accompanied by large numbers of adults; the localities are relatively distant from those yielding *morii*.)

Copepodite stage V female: TL \bar{x} 1.25 mm, range 1.18-1.34 mm, 10 specimens. Differences between sexually immature *sobrīna* and *morii* females are relatively weak, e.g., greater length of the ThV point (Figure 17d) and the weaker bend of the medial setalike process on the left Re of P5 (Figure 17l), appear to be useful, but lack confirmation by measurements from a geographically representative series of specimens.

Copepodite stage V male: TL \bar{x} 1.25 mm, range 1.12-1.38 mm, 10 specimens. Posterolateral corner of ThV produced into a relatively long slender point (Figure 18d, o). Right P5 with straight distal segment resembling that in *plumata*, but all segments in P5 of *sobrīna* appear slightly wider.

Sex Ratios

In laboratory-reared populations sex ratios among adult copepods of several families have been found to vary widely (for recent comments see Heinle, 1970; Katona, 1970; Paffenhöfer, 1970). In natural populations, however, late immature copepodids have been found to produce males and females in about equal numbers (Marshall, 1949). Among randomly sorted, sexually mature adults of the four species of *Pontellina* females consistently outnumbered males by roughly 1.3:1 (Table 4).

Assuming that the sexes are genetically one to one, the observed male-to-female ratios in *Pontellina* could be readily accounted for if females live longer than males, a likelihood suggested by many authors for various amphiscandrid copepod genera. In a small series of rearing experiments on *Labidocera trispinosa*, A. Barnett (pers. comm., 1972) has found that following the adult moult females live 2 to 3 wk and males about 1 wk.

TABLE 4.—Frequency of sexually mature individuals and sex ratios in *Pontellina*.

Species	♀		♂		sex ratio	No. samples
	N	%	N	%		
<i>platychela</i>	1159	54	1137	46	1.16	72
<i>plumata</i>	1,259	58	917	42	1.37	531
<i>morii</i>	433	60	284	40	1.52	240
<i>sobrīna</i>	421	54	364	46	1.16	113

¹ One sample, i.e., *Atlantis II* 20-42, was omitted because it provided the extremely disproportionate capture of 327 males and 10 females.

REMARKS ON SEASONAL OCCURRENCE AND BREEDING

Capture records alone do not necessarily disclose the distribution of the optimal habitat of a planktonic species (Fleminger, 1972), i.e., the region in which reproduction is usual, typically successful, and from which the progeny is likely to become entrained in a circulation system that ultimately provides new breeding stocks with suitable conditions for their offspring. Our sampling of *Pontellina* is incomplete for critical assessment of the impact of seasonal change on occurrence, geographical distribution, or reproduction. Moreover, as a consequence of the relatively large mesh sizes of the nets (see Table 15) sampling of most juvenile stages was not representative. Thus spermatophore occurrence on females is the only source of breeding information available to us.

In *Calanus*, spermatophores constitute evidence of mating within the past 48 h (Marshall and Orr, 1955). In other copepods, spermatophores are lost or shed soon after attachment; in *Labidocera trispinosa* discarding of the spermatophore has been observed to occur just prior to egg laying (G. Theilacker, pers. comm., 1970).

Few spermatophores were observed in *Pontellina* (Table 5) suggesting that as in *Calanus* they are not retained for an appreciable time after attachment. The 27 records of *sobrina* females bearing a spermatophore afford a glimpse of breeding patterns in that species. Spermatophore-bearing females appeared in February, May, and August samples. The localities span most of the latitudinal extent of *sobrina* captures on record, but all lie to the east of long. 98°W, and most are relatively close to the mid-American coast. In contrast, the few records of *morii* and *plumata* bearing spermatophores are widespread, suggesting that both species breed over a more extensive range in accordance with their more extensive geographical distributions.

PHYLOGENETIC RELATIONSHIPS AMONG THE *PONTELLINA* SIBLINGS

Dobzhansky (1972) stressed the heuristic value of sibling species when he pointed out

“ . . . sibling species permit the dissection of the process of speciation into studiable components.” *Pontellina* appears especially well suited to explore the question of speciation in the planktonic biotope. Restriction to shallow tropical and subtropical oceanic waters apparently limits opportunities for complex diversity in planktonic calanoids (Fleminger and Hulsemann, 1973). The four species of *Pontellina* satisfy the number of suitable ranges that appear to be available within these biogeographical limits.

Three of these ranges reflect the geographically limited and relatively shallow lenses of Tropical Surface Water (Wyrтки, 1966, 1967) described from the eastern equatorial Pacific but also known on the basis of similar general features to prevail in the equatorial Atlantic Ocean (Muromtsev, 1963) and in the equatorial Indian Ocean (Wyrтки, 1971). The fourth range consists of the series of deeper lenses of warm water beyond Tropical Surface Waters and lying between the subtropical convergences in the Atlantic, Indian, and Pacific Oceans.

Pontellina's position as a distinctive genus is unchallenged, being strongly separated from its closest relative, *Pontellopsis*, in both morphology and habitat. Compelling evidence favoring consideration of the four populations of *Pontellina* as separate species is furnished by the morphological distinctions of each, their independent geographical distributions, and the morphological integrity of their diagnostic features. That is, despite widespread regions of geographical overlap where two or three of the species may be captured in the same net tow, no evidence of intergradation or hybridization has been observed.

Evidence of strongly regionalized habitat adaptation may be inferred from the apparent failure of each species to colonize areas occupied by its adjacent congener. Failure to colonize must be regarded as significant. All four species occur in surface layers (Wilson, 1942; Heinrich, 1961; Vinogradov and Voronina, 1964; Fleminger and Hulsemann, unpublished data) where air-sea interactions provide opportunity for dispersal and advection with neighboring circulation systems, but the distribution of each species overlaps at most only a portion of the range of its neighboring congeners.

TABLE 5.—Adult female specimens of *Pontellina* bearing a spermatophore.

Species	Sampling date	Latitude	Longitude	Station	Total length (mm)	Sac length (mm)
<i>P. platychela</i>	III-8-66	00°08'S	18°31'W	Atlantis II-20-42	1.66	0.490
<i>P. plumata</i>	VI-15-69	33°49'N	139°10'E	Scan IV-1	1.66 1.76	0.460 0.460
	VI-6-52	01°00'S	112°24'W	Shellback 47	1.50	0.425
	III-30-69	21°54'S	110°02'W	Piquero V-49	1.56	0.365
<i>P. morii</i>	IV-19-68	05°11'N	123°58'E	Circe II-NT 11	1.58	0.420
	VII-2-52	05°18'S	85°04'W	Shellback 105	1.86	0.440
<i>P. sobrina</i>	II-12-67	00°28'N	92°02'W	EASTROPAC Rockaway 060	1.68	0.390
	V-12-58	07°22'N	92°47'W	Scot 46	1.56 1.70	0.360 0.395
	V-4-62	08°41'N	79°31'W	La Creuse 15	1.40 1.44 1.46 1.42	0.340 0.385 0.370 0.355
	V-7-58	09°45'N	96°04'W	Scot 35	1.62	0.410
	VIII-16-63	09°51'N	85°43'W	Bonacca 42	1.48 1.46	0.385 0.320
	V-17-62	13°07'N	91°34'W	La Creuse OT-6	1.48 1.50	0.330 0.355
	VIII-18-63	13°29'N	90°09'W	Bonacca 50	1.50 1.62 1.52 1.48	0.320 0.360 0.340 0.340
	VIII-19-63	13°44'N	90°51'W	Bonacca 51	1.50 1.52	0.390 0.340
	VIII-20-63	13°57'N	92°02'W	Bonacca 58*	1.54 1.56 1.48 1.56 1.50 1.50 1.52 1.50	0.390 0.415 0.355 0.365 0.375 0.380 0.395 0.385

* One additional specimen was observed in this sample with a damaged spermatophore.

Morphology and distribution also support our conclusion that the four species are phylogenetically close and, in fact, comprise a monophyletic unit—or holophyletic in Ashlock's (1971) terminology—appearing to have been recently derived from a single tropical-subtropical epiplanktonic precursor (in preparation).

Our objective in this section is to examine the degree of similarity among the siblings as a basis for determining phylogenetic relationships. In the absence of a fossil record, inferences drawn from comparative morphology, geograph-

ical distribution, and essential habitat adaptation may provide a relative historical perspective for judging phylogeny within a taxon.

Phylogenetic relationships within *Pontellina* were judged both intuitively and objectively on the basis of characters that showed a cohesive pattern of similarity or dissimilarity. We concur with the rebuttals of Throckmorton (1965, 1968) and Voris (1971) to the views of orthodox numerical taxonomy in defense of the weighting of taxonomic characters: i.e., characters differ in their taxonomic usefulness, and the adaptive significance of these differences is not beyond logic and comprehension.

Throckmorton and Voris show empirically that characters are decidedly not equal in their content of phylogenetic information. Their operational method for character selection rests upon the direct and assumption-free advantages of *a posteriori* weighting of correlated sets of derived characters.

Judging from the numerous articles in Systematic Zoology, numerical taxonomic phylogenies derived from large numbers of unweighted characters do not vary from phylogenies implicitly or explicitly arranged by experienced workers employing sets of correlated adaptive characters.

Body Dimensions and Proportions

Total Length (TL)

Intraspecific sexual differences in TL are greater than interspecific differences; males are about 10% shorter than females (Table 6, Figure 23). In both sexes *morii* and *sobrına* are smaller than *platychela* and *plumata*. The difference between the mean TL of males or females of species belonging to the same pair is not significant. However, the difference between the mean TL of either species of one pair with that of either species in the other pair is highly significant in both sexes (Student's *t*-test). The overall difference is produced largely by the distance between the rostrum and the cephalic groove and the length of the furca (see below).

Prosome-Urosome Length Ratio (PUR)

In both sexes *morii* and *sobrına* occur at the high end of the PUR distribution (Table 6, Figure 24). In males, *morii* and *sobrına* have similar distributions at the high end of the

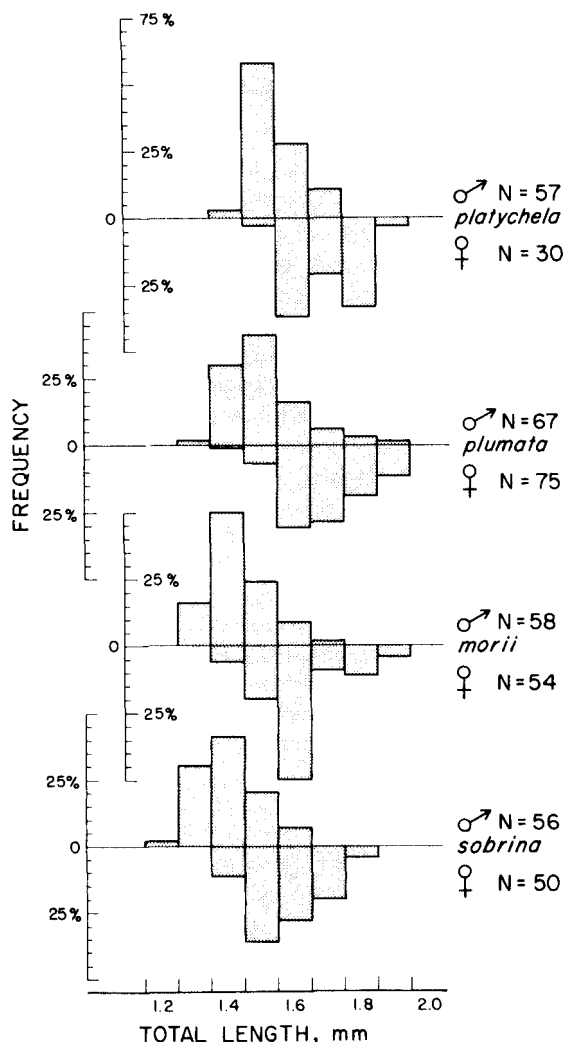


FIGURE 23.—Frequency distribution of total length for both sexes of the four species of *Pontellina*.

TABLE 6.—Total length (TL) and prosome-urosome length ratio (PUR) of *Pontellina* spp. adults; data from various geographical localities combined.

Species	TL (mm)				PUR			
	\bar{x}	Range	$s^2 \bar{x}$	N	\bar{x}	Range	$s^2 \bar{x}$	N
Males:								
<i>P. platychela</i>	1.699	1.54-1.96	0.0173	30	3.438:1	3.19-3.89:1	0.0362	30
<i>P. plumata</i>	1.692	1.44-1.94	0.0126	75	3.282:1	2.92-3.72:1	0.0179	75
<i>P. morii</i>	1.608	1.38-1.88	0.0145	54	3.643:1	3.39-4.10:1	0.0360	35
<i>P. sobrına</i>	1.570	1.42-1.78	0.0134	50	3.732:1	3.17-4.16:1	0.0417	33
Females:								
<i>P. platychela</i>	1.556	1.41-1.74	0.0089	57	3.223:1	2.86-3.55:1	0.0228	49
<i>P. plumata</i>	1.511	1.34-1.92	0.0130	67	3.066:1	2.84-3.93:1	0.0243	52
<i>P. morii</i>	1.435	1.26-1.68	0.0100	58	3.339:1	2.87-3.73:1	0.0245	50
<i>P. sobrına</i>	1.406	1.18-1.64	0.0118	56	3.426:1	3.06-3.75:1	0.0235	51

range, *platychela* being intermediate and *plumata* occupying the low end. Females follow the same general pattern, but *morii* and *sobrigna* show considerably less overlap.

Length of Furcal Rami

The length of both rami is directly related to prosome length as well as TL. Shortening and fusion of the right ramus in adult females introduces asymmetry but the change does not alter the essential relationship to body length. In the female sex (Figure 25) *morii* and *sobrigna* occupy one side of the overall distribution of length of the right ramus, *platychela* and *plumata* the other with virtually no overlap between the two pairs of species. Males show more scatter (Figure 26) and apparent differences in allometry; *sobrigna* and *morii* tend to diverge with respect to furcal length while *plumata* and *platychela* tend to diverge with respect to prosome length.

Examination of furcal length relative to furcal width increases separation of the three equatorial species. It also enhances separation of *platychela* and the Atlantic samples of *pluma-*

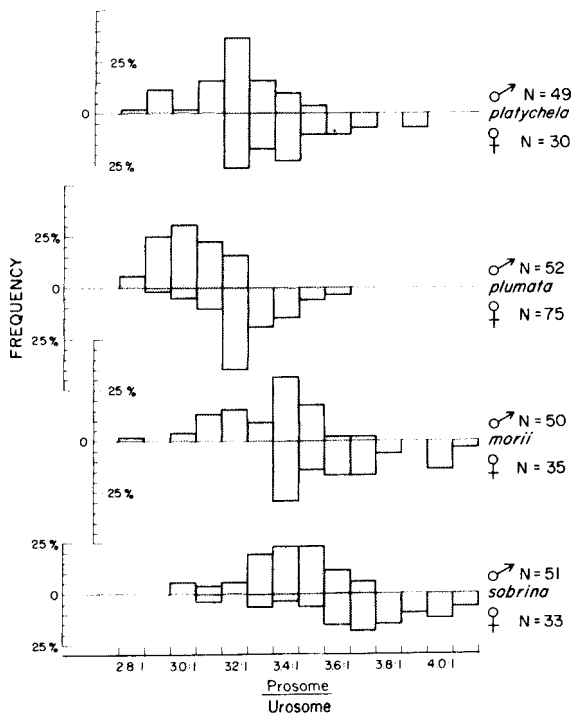


FIGURE 24.—Frequency distribution of P:U ratio for both sexes of the four species of *Pontellina*.

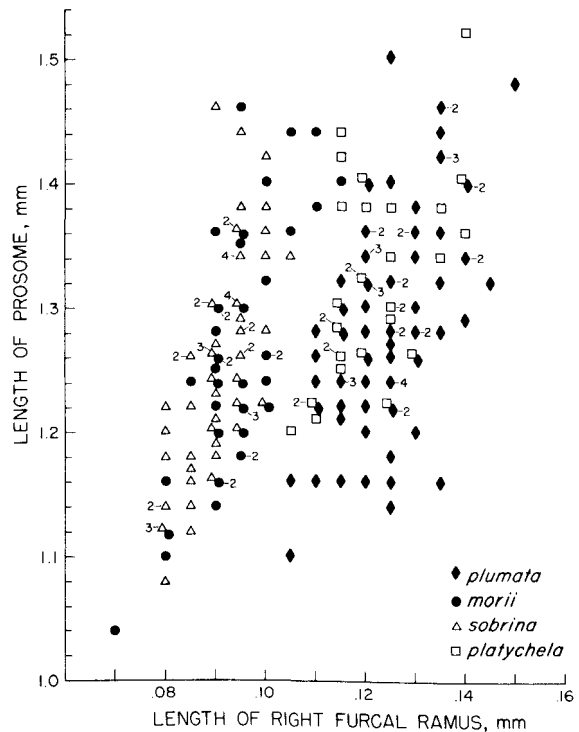


FIGURE 25.—Length of P (ordinate) plotted against length of right furcal ramus (abscissa) for females of the four species of *Pontellina*.

ta as well as separation of *morii* and the Indo-Pacific samples of *plumata* (Figure 27). A generally similar pattern is seen in the males (Figure 28) except that *morii* and *sobrigna* overlap freely with respect to the furcal length: width ratio.

ThIV-V Posterior Spine

Strong sexual dimorphism appears in adults. Among the females, *plumata* is unique; the base of the posteriorly directed spine rises roughly at the level of the proximal margin of the genital segment, the spine is robust and broadly triangular in both dorsal and lateral views (Figure 3a, d-f). The spines in the three equatorial species are similar to each other in being diminutive and needlelike or dentiform. They differ primarily with respect to relative length of the spine (Figures 6a, c, g, h; 9a, c, e, f; 11; 13a, c, g).

The ThIV-V spine in males appears in three states: *plumata* exhibits a minute denticle that

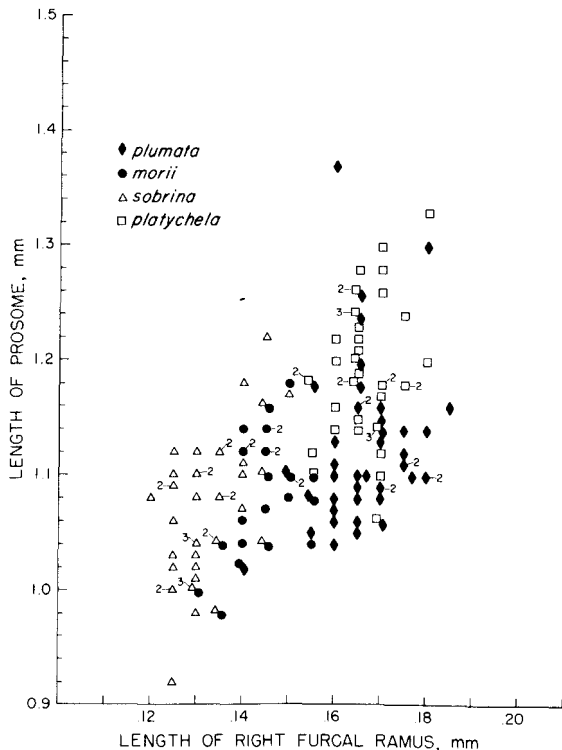


FIGURE 26.—Length of P (ordinate) plotted against length of right furcal ramus (abscissa) for males of the four species of *Pontellina*.

may be borne on a weakly produced boss; *morii* and *sobrina* bear a small spine resembling that found in the female of the species; *platychela* has no outgrowth whatsoever.

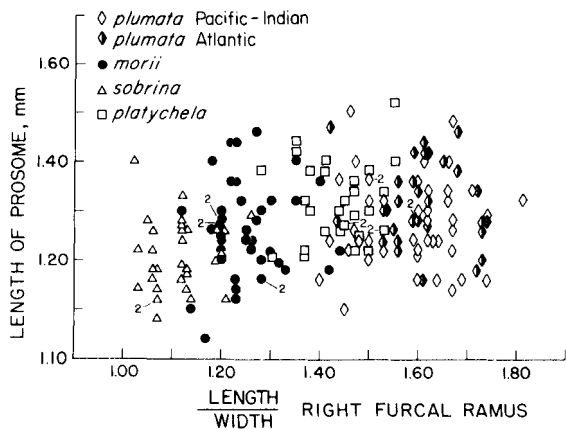


FIGURE 27.—Length of P (ordinate) plotted against length:width ratio of right furcal ramus (abscissa) for females of the four species of *Pontellina*.

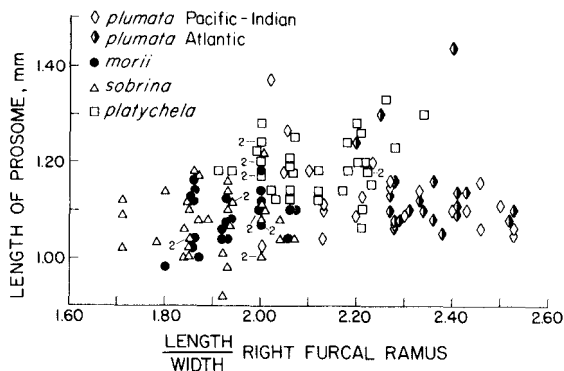


FIGURE 28.—Length of P (ordinate) plotted against length:width ratio of right furcal ramus (abscissa) for males of the four species of *Pontellina*.

Female Genital Segment

The distribution of lateral clusters of spinules provides the basis for distinguishing the different character states. Two species, *sobrina* and *plumata*, are similar in having two clusters on each side; *morii* has one cluster and *platychela* has none. There is preliminary evidence from examination with the scanning electron microscope (SEM), however, that the similarity of *plumata* with *sobrina* may in fact be superficial. Cluster size and spinule size differ even under the light microscope, and the SEM indicates the presence of fine sensoriiform filaments in *sobrina* and *morii*, but not in *plumata* or *platychela*. The SEM also revealed a second cluster consisting of minute denticles in *morii* anterior to the one visible with the aid of a light microscope (in preparation).

Female Fifth Pair of Swimming Legs

The two characters found in P5 that provide diagnostic information, i.e., the Re:Ri length ratio (Figure 29) and the distribution of spines on the endopod (Table 7) agree in showing strong similarity between *morii* and *sobrina* on the one hand and between *platychela* and *plumata* (all geographical sectors combined) on the other. It should be noted, however, that the similarity between *platychela* and *plumata* is weakened when the comparison is restricted to Atlantic Ocean samples of *plumata* (in preparation).

The distribution of the spines on the endopod is also noteworthy by virtue of the compelling

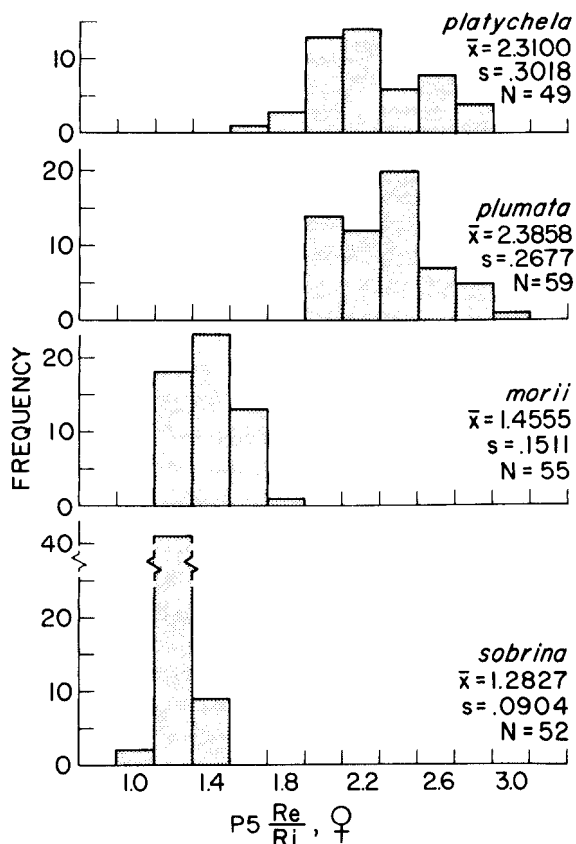


FIGURE 29.—Frequency distribution of P5 Re:Ri ratio for females of the four species of *Pontellina*.

evidence it provides in support of our judgment that the four siblings are valid species recently derived from the same parent species. The frequencies and widespread geographical occurrence of phenotypes are evidence of simple Mendelian inheritance and indicative of balanced polymorphism. Another pontellid, *Labidocera diandra*, has also been shown to be polymorphic (Fleminger, 1967b). In both *Pontellina* and *Labidocera* the apparent polymorphism affects a sexually modified appendage before the onset

of maturity, the phenotypes being distinguishable in copepodite stage V. However, within its species group, only *L. diandra* displays the polymorphism which is visible in the male sex.

Male Fifth Legs and Right First Antenna

Segment lengths of sexually modified appendages that we examined tend to vary directly with prosome length. We chose the length of the right furcal ramus (Figure 25) instead of the prosome as our standard body length reference for comparing morphometry of sexual appendages because the furcal ramus length yielded graphic presentations with considerably less scatter within each sample.

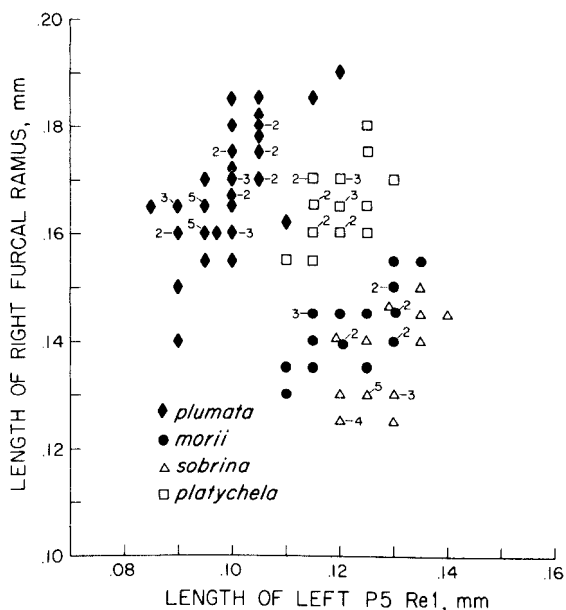


FIGURE 30.—Length of right furcal ramus (ordinate) plotted against length of left P5 Re1 (abscissa) for males of the four species of *Pontellina*.

TABLE 7.—Frequencies (%) of phenotypes varying in the number of spines on the endopod of the fifth pair of swimming legs in *Pontellina* spp. females.

Species (N)	Left leg:	1 spine	1 spine	2 spines	2 spines
	Right leg:	1 spine	2 spines	1 spine	2 spines
<i>platychela</i> (100)		34	16	12	38
<i>plumata</i> (300)		37	12	16	34
<i>morii</i> (200)		1	2	1	96
<i>sobrina</i> (100)		0	1	0	99

TABLE 8.—Dimensions of selected segments of sexually modified appendages of *Pontellina* spp. adult males.

Segments and species	\bar{x} (mm)	s	N	Range (mm)
Left P5 Re1 length:				
<i>platychela</i>	0.1193	0.0048	21	0.110-0.130
<i>plumata</i>	0.0988	0.0067	48	0.085-0.120
<i>morii</i>	0.1221	0.0079	19	0.110-0.130
<i>sobrina</i>	0.1269	0.0060	21	0.120-0.140
Right P5 Re1 width:				
<i>platychela</i>	0.1895	0.0109	20	0.170-0.210
<i>plumata</i>	0.1647	0.0112	47	0.140-0.195
<i>morii</i>	0.1960	0.0091	20	0.180-0.215
<i>sobrina</i>	0.1814	0.0098	21	0.165-0.200
A1 segment 18 length:				
<i>platychela</i>	0.3417	0.0152	26	0.300-0.365
<i>plumata</i>	0.3364	0.0220	32	0.285-0.400
<i>morii</i>	0.3063	0.0159	31	0.280-0.340
<i>sobrina</i>	0.3014	0.0137	29	0.280-0.335

Length of Left First Exopodal Segment

This segment is much shorter in *plumata* than in the other three species (Figure 30, Table 8). Small differences appear among the three equatorial species but they are inconspicuous in comparison to their distribution as a group relative to that of *plumata*.

Width of Right First Exopodal Segment

As in the section above on the left, Re1, the

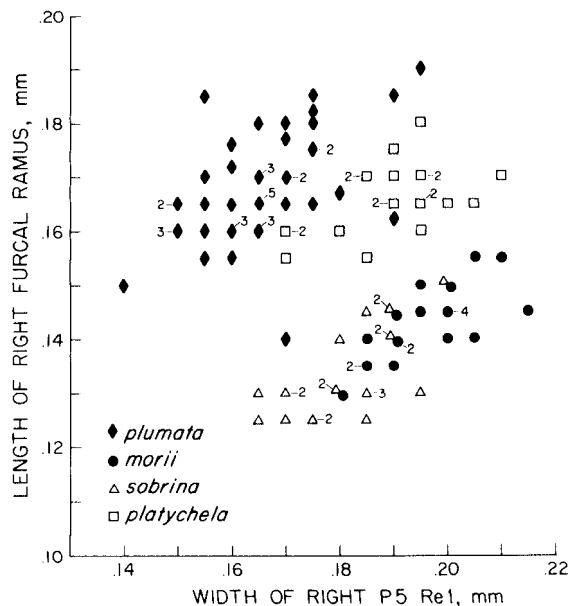


FIGURE 31.—Length of right furcal ramus (ordinate) plotted against width of right P5 Re1 (abscissa) for males of the four species of *Pontellina*.

distributions of the three equatorial species broadly overlap, but *plumata* tends to be appreciably smaller (Figure 31, Table 8).

Morphology of Right First Exopodal Segment

The proximal segment of the chela appears in three essential states: the swollen condition of *platychela* (Figure 7a, b), the slender condition of *plumata* (Figure 4i, j) and the slender condition characterized by a more distal position of the posterolateral outgrowth shared by *morii* and *sobrina* (Figures 11d, e; 14c, d).

Morphology of Right Second and Third Exopodal Segments

The distal segment of the chela appears in three states: the swollen condition of *platychela* (Figure 7b), the shortened, spurred condition of *morii* (Figure 11d, f) and the simple attenuated condition shared by *plumata* and *sobrina* (Figures 4j, 14d).

Length of Segment 18, Right First Antenna

Two siblings, *plumata* and *platychela*, broadly overlap and occupy the upper half of the overall distribution; the other two, *morii* and *sobrina*, broadly overlap in the lower half of the distribution (Figure 32, Table 8).

Spermatophore Attachment

(Figures 33, 34)

The three equatorial species agree in having

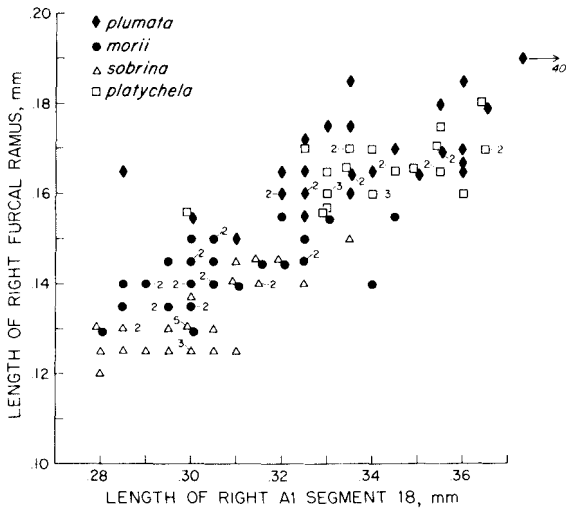


FIGURE 32.—Length of right furcal ramus (ordinate) plotted against length of segment 18 of right A1 (abscissa) for males of the four species of *Pontellina*.

the proximal end of the sac cemented to the right side of the genital segment, *morii* and *sobrina* in a virtually identical fashion, differing somewhat from the condition found in *platychela*. In *plumata*, however, attachment is restricted to the proximal end of the neck, the remainder of the neck and the entire sac hanging free from the body but showing helical convolutions similar to those present in the other congeners.

Geographical Occurrence

Three of the species, *morii*, *sobrina*, and *platychela*, were found primarily in low latitudes between 20°N and 20°S (Figures 8, 12, 15). The three species are essentially allopatric to one another, each predominating in a geographically different segment of equatorial circulation in the world's oceans (see Table 20). Relatively high frequencies of abundance or occurrence coincided with eutrophic equatorial regions characterized by a shallow O₂ minimum layer (≤ 1 ml/liter) lying at or near the permanent thermocline. The three species tend to concentrate in the uppermost 20 to 30 m of depth and virtually disappear below 50 m (in preparation).

The fourth sibling, *plumata*, is widespread in subtropical latitudes (Figure 5) and may be locally abundant in tropical regions downstream from areas of persistent upwelling. It is the

only species of the genus with a circumglobal range but tends to be infrequent to absent in tropical areas dominated by its equatorial cognates (see Table 20). Its vertical distribution appears to encompass the surface to 200-m depth in subtropical latitudes, the lower limit shoaling to about 100 m in tropical latitudes (in preparation).

Summation of Phylogenetic Similarities

Thus within the framework of the 17 characters considered above, *morii* and *sobrina* show the highest frequency of similar character states. In practice their overall morphological similarity is sufficient to require routinely close inspection at appreciable magnifications for reliable separation. Though the next most frequently linked pairing, *plumata* and *platychela*, show similarity in about 60% of the features in Table 9, at low magnifications under a stereomicroscope they are almost as distinct from one another as each is from *morii* or *sobrina*.

As noted in the calanoid genera, *Labidocera* and *Clausocalanus* (Fleminger 1967b; Frost and Fleminger, 1968), the distinguishing features of the sibling species in *Pontellina* are limited to sexually modified characters, i.e., the fifth legs, the genital segment, the posterior corner of ThIV-V, the male right A1, and the caudal furca.

There is reason to regard *plumata* as retaining the strongest similarity to the *Pontellina* ancestral stock. This view rests upon two features: the slightly stronger resemblance of sexually modified structures in *plumata*, especially the ThIV-V spine in the female, to those of *Pontellopsis* and of the more eurytopic circumglobal distribution of *plumata* in comparison to the restricted distributions of its equatorial congeners.

To examine the statistical significance of the phylogenetic relationships inferred from the characters given in Table 9 we have utilized a computer program that detects significant levels of co-occurrence among sets of overlapping functions. The program has been informative in the detection of communities as well as in systematic classifications of flexibacteria (Fager, 1969).

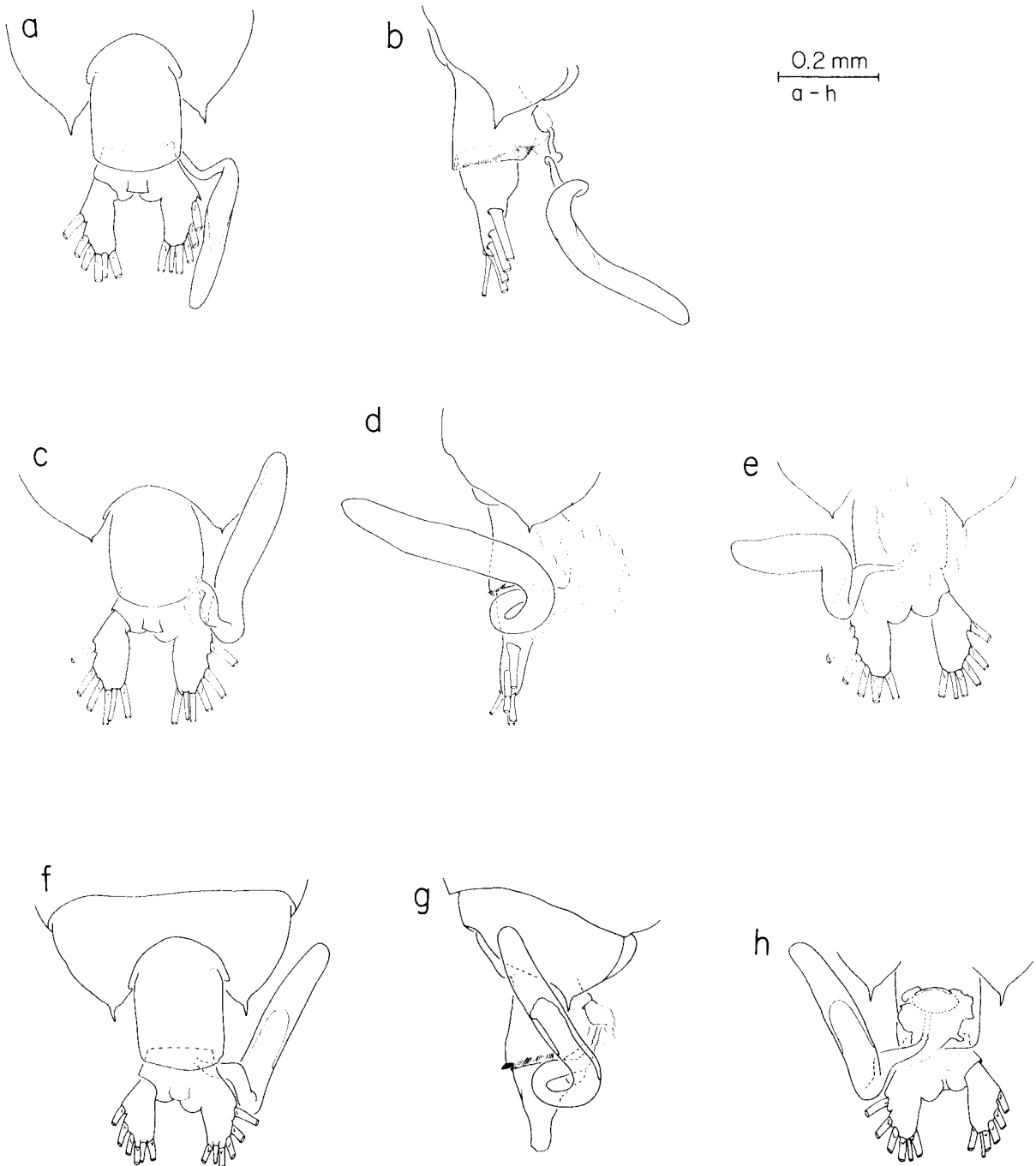


FIGURE 33.—ThIV-V and urosome of female with attached spermatophore. **a, b.** *Pontellina plumata*. **c-e.** *P. platychela*. **f-h.** *P. morii*. **a, c, f** dorsal view; **b, d, g** lateral view; **e, h** ventral view.

TABLE 9.—Shared character states among species of *Pontellina*.

Character	No. of states	Species sharing same state	Species with unique character state	Remarks
1. $\bar{x}TL$ ♀	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		Significant differences produced by furcal ramus length
♂	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
2. PUR ♀	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		Significant differences produced by furcal ramus length
♂	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
3. Furcal ramus length ♀	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
♂	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
4. Furcal ramus length:width ratio ♀	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
♂	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
5. Th IV-V ♀	2	<i>morii</i> , <i>sobrina</i> , and <i>platychela</i>	<i>plumata</i>	
6. Th IV-V ♂	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		Minor differences between <i>plumata</i> and <i>platychela</i> ignored
7. Genital segment ♀	3	<i>plumata</i> and <i>sobrina</i>	<i>platychela</i> ; <i>morii</i>	SEM results ignored
8. P5 ♀, Re:Ri ratio	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
9. P5 ♀, Ri spines	4	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
10. P5♂, left Re1 length	2	<i>morii</i> , <i>sobrina</i> , and <i>platychela</i>	<i>plumata</i>	
11. P5♂, right Re1 width	2	<i>morii</i> , <i>sobrina</i> , and <i>platychela</i>	<i>plumata</i>	
12. P5♂, right Re1 morphology	3	<i>morii</i> and <i>sobrina</i>	<i>plumata</i> ; <i>platychela</i>	
13. P5♂, right Re 2-3 morphology	3	<i>plumata</i> and <i>sobrina</i>	<i>morii</i> ; <i>platychela</i>	
14. A1 ♂ right seg. 18 length	2	<i>morii</i> and <i>sobrina</i> ; <i>plumata</i> and <i>platychela</i>		
15. Spermatophore attachment	3	<i>morii</i> and <i>sobrina</i>	<i>plumata</i> ; <i>platychela</i>	
16. Geographical distribution	4		<i>plumata</i> ; <i>platychela</i> ; <i>morii</i> ; <i>sobrina</i>	
17. Latitude and depth distribution	2	<i>morii</i> , <i>sobrina</i> , and <i>platychela</i>	<i>plumata</i>	

Frequency of similarities in 17 characters:

morii and *sobrina* linked in 15 instances or 82%.
platychela linked with *morii* and *sobrina* in 4 instances or 24%.
plumata and *platychela* linked in 10 instances or 59%.
plumata and *sobrina* linked in 1 instance or 6%.
plumata unique in 7 instances or 41%.
platychela unique in 5 instances or 29%.
morii unique in 3 instances or 18%.
sobrina unique in 1 instance or 6%.

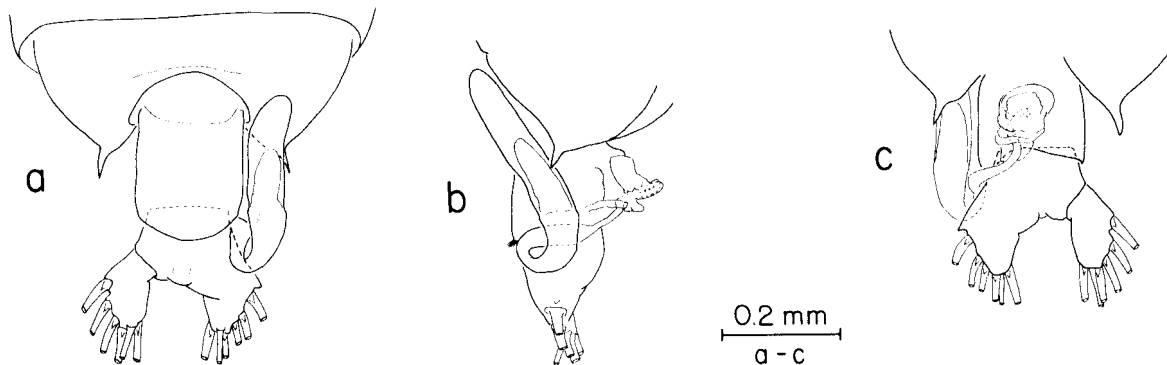


FIGURE 34.—ThIV-V and urosome of female *Pontellina sobrina* with attached spermatophore: a. dorsal view; b. lateral view; c. ventral view.

The program calculates an index of affinity for all possible pairs of species as the geometric mean of the proportion of common character states corrected for the number of characters used in the analysis: i.e., $J/\sqrt{A \times B} - \frac{1}{2}\sqrt{B}$, where A and B are the total number of characters recorded for the two species, $B \geq A$, and J is the number of shared character states. Values of the index above 0.5 have been found empirically to provide objective repeatable groupings of related sets of values.

A number of characters listed in Table 9 were omitted from the recurrent group analysis to avoid biasing the computations with redundant information. Characters 1, 2, and 4 were not scored since their morphometric states are determined largely by the value of character 3. Characters 11 and 14 were deleted since they parallel character 10 in showing a direct relationship to TL and to furcal length. In the absence of a fossil record the distributional characters 16 and 17 were not scored on the intuitive grounds that they are complex derivatives of both 1) overall genetic adaptation and 2) fortuitous abiotic historical events that might obscure essential phylogenetic patterns. All of the scored characters were weighted equally and disregard the preliminary results from SEM observations.

The recurrent group analysis reveals only one grouping with an index higher than 0.5, that of *morii* and *sobrina* (Table 10). Similarity between *plumata* and *platychela* falls well below the acceptable level of significance. The other possible pairings are dissimilar in most to virtually all of the 10 characters used in the

analysis. Assuming equal rates of evolution the results indicate that the divergence of *plumata*, *platychela*, and the *morii-sobrina* lineage are likely to be divisions of greater age than that of *morii* and *sobrina*.

GEOGRAPHICAL VARIATION AND SYMPATRY

In the course of this study two conspicuous and parallel instances of geographical variation were encountered in the fifth legs of *plumata* females. This variation was expressed in the number of spines at the distal end of the endopod and the length of the exopod relative to that of the endopod.

As noted above the number of spines on the endopod of the female's fifth leg is polymorphic throughout *Pontellina*. The bilateral two-spined morph is overwhelmingly dominant in *morii* and *sobrina*. However, four morphs are common in *platychela* and *plumata*. Comparison of randomly selected samples of Atlantic specimens of *plumata* with specimens from the Indian and Pacific Oceans indicate significant differences

TABLE 10.—Values of the recurrent group affinity index (Fager, 1969) and the probability of obtaining this or higher values by chance for all possible pairs of *Pontellina* spp. Further discussion in text.

Species pair	Affinity index	p
<i>morii</i> and <i>sobrina</i>	0.642	<0.001
<i>platychela</i> and <i>plumata</i>	0.242	>.4
<i>platychela</i> and <i>morii</i>	0.042	>.8
<i>platychela</i> and <i>sobrina</i>	0.042	>.8
<i>plumata</i> and <i>sobrina</i>	0.042	>.8
<i>plumata</i> and <i>morii</i>	0	---

in the frequency of the four morphs (Table 11). The bilateral one-spined morph is much more frequent than the bilateral two-spined morph in the Atlantic Ocean whereas in the Indian and Pacific Oceans the frequencies of the two morphs are more alike and the differences are not significant.

Notably, the frequencies of the morphs in *platychela* differ significantly from those of the *plumata* sample from the Atlantic but not from those of the Indian and Pacific samples of *plumata*. Of the pairs of species sharing common boundaries only *morii* and *sobrini* do not appear to have appreciably different morph frequencies (Table 11).

In the ratio exopod to endopod length for the fifth legs in females, the distribution of the Atlantic sample of *plumata* differed significantly from those of the Indian and Pacific Oceans (Table 12). As in the case of the endopodal spines, pairs of species with common boundaries showed significantly different distributions of the exopod-endopod ratios.

Extrapolating from the similarity of Indian and Pacific Ocean samples, differences between Atlantic and Indian-Pacific populations of *plumata* appear to be geographically abrupt. Thus they may be viewed as reflecting 1) local

pressures on *plumata* within each geographical population, 2) restricted gene flow between the Indian and Atlantic Ocean populations, 3) or both. *P. plumata* showed the highest frequency of unique character states in *Pontellina* (Table 9). Furthermore it tends to occupy a conspicuously peripheral position relative to the other three species in its dimensions of sexually modified appendages in both sexes (e.g., Figures 27, 28, 30, 31). It is also the only species of the genus sharing common boundaries with the other three species of *Pontellina*. Therefore, the geographical differences between Atlantic and Indian-Pacific populations of *plumata* parallel the extensive character divergence (Mayr, 1970: 51-53) otherwise distinguishing the species. Considering the fact that all morphological structures involved are sexually modified it would appear that we are witnessing reinforcement of pre-mating barriers (Dobzhansky, 1970:376-382).

Similar disjunct morphological differences distinguishing Atlantic from Indian and Pacific populations of epipelagic calanoids have been reviewed (Fleminger and Hulsemann, 1973) and the number of examples increased (Fleminger and Hulsemann, 1973; Fleminger, 1973). Similar patterns in the strength of divergence in secondary sexual characters relative to

TABLE 11.— χ^2 test of homogeneity in the distribution of spines on the endopod of the fifth legs in adult females.

Population	Number of spines on endopod (left leg-right leg):				Total
	2-2	1-2	2-1	1-1	
<i>platychela</i> , Atlantic Ocean	38	16	12	34	100
<i>plumata</i> , Atlantic Ocean	22	11	16	51	100
<i>plumata</i> , Pacific Ocean	39	14	15	32	100
<i>plumata</i> , Indian Ocean	41	11	18	30	100
<i>morii</i> , Indian Ocean	94	2	1	3	100
<i>morii</i> , Pacific Ocean	98	0	2	0	100
<i>sobrini</i> , eastern tropical Pacific Ocean	99	1	0	0	100
	χ^2	d.f.	<i>p</i>		
<i>plumata</i> Atl. vs. <i>plumata</i> Pac.	9.48	3	<0.025 <i>p</i> >0.01		
<i>plumata</i> Atl. vs. <i>plumata</i> Ind.	11.3	3	0.01		
<i>plumata</i> Pac. vs. <i>plumata</i> Ind.	0.76	3	<0.9 <i>p</i> >0.75		
<i>platychela</i> vs. <i>plumata</i> Atl.	9.14	3	<0.05 <i>p</i> >0.025		
<i>platychela</i> vs. <i>plumata</i> Pac.	3.61	3	<0.5 <i>p</i> >0.25		
<i>platychela</i> vs. <i>plumata</i> Ind.	2.5	3	<0.75 <i>p</i> >0.5		
<i>morii</i> Pac. vs. <i>sobrini</i>	3.01	3	<0.5 <i>p</i> >0.25		
<i>morii</i> Ind. and Pac. vs. <i>plumata</i> Ind. and Pac.	146.84	3	<0.001		
<i>sobrini</i> vs. <i>plumata</i> Pac.	84.34	3	<0.001		

buildup of anaerobic conditions. Division of tank bottoms into sundry tunnels and levels was created by specific placement of bricks and clay drain tiles.

AERATION STUDY

Aeration provided by jetting streams of filtered seawater into respective tanks was compared to aeration supplied by bubbling air through airstones into tanks in which water was continuously added with no agitation of the water column for an 8-week period. Two airstones were placed in each tank and valve-regulated air lines controlled the pressure at approximately 4 psi. Oxygen levels were monitored periodically and used along with survival rates as a basis for evaluation of replicate groups aerated by each method.

STOCKING DENSITY STUDY

Survival data were compared among triplicate tanks stocked at 10, 20, and 40 shrimp per m² for an 8-week period. These densities of approximately 40, 80, and 160 g/m² were chosen on the basis of data provided in pond and laboratory culture of penaeid shrimp (Broom, 1969; Subrahmanyam and Oppenheimer, 1969).

PRELIMINARY NUTRITIONAL STUDY

Triplicate groups of ten 4 g brown shrimp (*P. aztecus*) were fed a series of pelleted diets. Growth data (biomass increase) was used as a means of evaluation. Diets examined consisted of those patterned after Japanese purified diets (i.e., diets containing only chemical ingredients) (Table 1, Group I) (Diet 1 was conducted for 5 weeks and Diets 2, 3, and 4 for 11 weeks each); a second group of semipurified diets (i.e., containing defined chemical ingredients but containing one or more natural products) providing four combinations of levels of protein, fat, shrimp, and fish meal (Group II) (conducted for 11 weeks); and a third group designed to compare the nutritional value of casein, yeast, and soy hydrolysates (Group III) (conducted for 6 weeks). All of these groups were fed at 5%

TABLE 2.—Percent of pellet dissolved over time and at three concentrations of binder. (Values are means and standard deviation on two replicates with Diet 1.)

Percent binder (collagen) added	Hours		
	6	12	24
1			
3	13 ± 1.2	14 ± 0.9	18 ± 1.7
5	11 ± 0.8	10 ± 0.6	10 ± 0.6
10	10 ± 0.6	10 ± 1.1	10 ± 1.0

of their respective biomass daily. In addition, Diet 6 was fed at 5, 10, and 15% of biomass (Group IV) (conducted for 6 weeks).

Combined environmental factors which produced best survival in each of the environmental experiments (i.e., culture conditions consisting of bare fiber glass tank bottoms, supplied aeration, and a stocking density of approximately 40 g/m²) were used in all nutritional studies. This combination offered a maximum potential for an increase in biomass and therefore allowed accurate evaluation of differences among diets tested. Although survival in bare fiber glass tanks was not significantly different from sand substrates, the fact that bare tanks were simpler to maintain dictated that they be used for the nutritional studies.

Prior to starting nutritional studies, the physical properties of pelleted diets were evaluated for acceptability as shrimp food. Pellet consistency was determined according to its ability to resist dissolution over a given period of time, and texture and size were chosen according to animal performance when presented several choices. Collagen⁴ proved to be a suitable binding agent. Using an experimental design with time and collagen levels as variables, a pellet with 5% collagen added as a binder was found to offer optimum consistency over a 24-hr immersion in salt water (Table 2). Percent dissolution was measured by taking dry weights after 6, 12, and 24 hr of immersion (no shattering of pellets was observed, and all loss of weight was therefore assumed to be from dissolution). Animals were observed to feed most readily on

⁴ Supplied on an experimental basis by the Hides and Leather Division of the U.S. Department of Agriculture Eastern Utilization Laboratory in Philadelphia, Pa.

pellets 0.3 cm in diameter by approximately 1.5 cm in length and which sink in water, and hence, pellets having these characteristics were used in both environmental and nutritional experiments.

RESULTS AND DISCUSSION

SUBSTRATE STUDY

A survival rate of 80% was obtained after 5 weeks in tanks without substrate, 80 to 90% survival was maintained over much of the duration of the experiment among both treatments having sand-shell substrates, and less than 60% survival occurred among tanks having brick subdivisions (Figure 1). Although *P. setiferus* is reported to burrow less than either *P. duorarum* or *P. aztecus* (Anderson, 1966; Pérez Farfante, 1969), it apparently was able to avoid predation, especially during the highly vulnerable moulting period, quite successfully with or without a sand substrate, since 5-week survival data among the two sand-shell treatments and the bare tank bottom treatment were not significantly different ($P < 0.05$) (Duncan, 1955). If the type of shelter is a factor in increased survival for penaeids maintained under culture conditions, the brick subdivisions should have enhanced survival. However, the markedly high mortality

rate among this group, significantly different from the other three treatments ($P < 0.05$), may have resulted from either failure of the shrimp to behaviorally segregate and thus fully utilize this protection or from physical abrasion against the sharp and coarse brick surface. Although there may have been toxic substances in the brick materials, the bricks were carefully washed and assumed to be otherwise inert in any chemical effect they may have had on the animals. Although differences in volume of water caused by placing various substrates in their respective treatments was not controlled for, it was felt that these differences in a running water system were not critical to the survival of shrimp. Differences in bottom area among the treatments caused by placement of different types of substrate were neither controlled for nor measured but were also thought to be negligible compared to differences found among treatment groups. The high degree of cannibalism noted by Subrahmanyam and Oppenheimer (1969) in tanks without substrate was not observed in any groups.

AERATION STUDY

The group having oxygen supplied by injecting air through airstones had significantly higher survival rates ($P < 0.05$) when compared with a treatment aerated by agitation of the water column (Figure 2). Although the average oxygen levels were similar between the two treatments (3.4-6.8 ppm), such levels in tanks aerated by high-pressure nozzles often dropped for short intervals due to clogging of the nozzles with silt and biological debris. Electrical power failures which affected water flow but not the compressed air supply (equipped with stand-by DC power) also caused intermittent drops in oxygen levels. Such short-term irregularities may have been more critical to shrimp tolerances than is indicated from reference to average oxygen level values, per se. Also, at the relatively high temperatures maintained throughout the study, short drops in oxygen levels could have been very critical. Decreased survival in tanks with agitation of the 0.75-m water column may also have resulted from physical agitation of the animals.

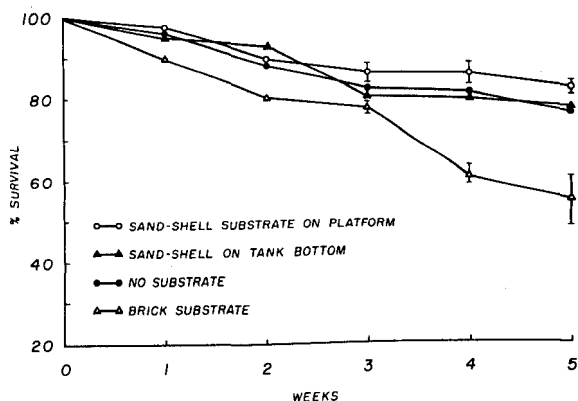


FIGURE 1.—Mean and standard error for percentage of animals surviving after 5 weeks of growth on four different substrates.

TABLE 14.—Mean abundance (No./m³) and frequency of occurrence of adult *Pontellina* in sets of samples forming meridional transects crossing the Equator.
*Vertical tows with Indian Ocean Standard Net (~200-0 M). ** Oblique tows with CalCOFI Standard Net (~200-0 m or less).

Region	Longitude	Latitude	No. of Samples	Sampling dates	<i>plumata</i>		<i>morii</i>		<i>sobrina</i>		<i>platychela</i>	
					\bar{x} No./m ³	Percentage occurrence	\bar{x} No./m ³	Percentage occurrence	\bar{x} No./m ³	Percentage occurrence	\bar{x} No./m ³	Percentage occurrence
Indian Ocean	40°E-80°E	35°S-25°N	233*	Jan.-Dec. 1962-65	0.0741 ± .028	33	0.0678 ± .019	29	0	0	0	0
	80°E-110°E	27°S-18°N	107*	Jan.-Dec. 1962-64	0.0438 ± .034	48	0.0425 ± .020	37	0	0	0	0
Austral-Asian Seas Pacific Ocean	120°E-130°E	12°S-12°N	23**	Mar.-May 1961	0.0395 ± .015	83	0.0200 ± .010	65	0	0	0	0
	156°E-164°E	12°S-12°N	23**	Aug.-Sep. 1956	0.0182 ± .008	83	0.0045 ± .004	22	0	0	0	0
	174°W-160°W	06°S-21°N	15**	Aug.-Sep. 1956	0.0313 ± .030	40	0.0033 ± .005	20	0	0	0	0
	126°W	12°S-20°N	22**	Feb.-Mar. 1967	0.0710 ± .037	77	0.0034 ± .003	18	0	0	0	0
	124°W-112°W	14°S-17°N	13**	Feb. 1953	0.0938 ± .090	46	0	0	0	0	0	0
	113°W-86°W	05°N-16°N	23**	Apr.-May 1958	0.0008 ± .0001	4	0.0004 ± .0001	4	0.0243 ± .021	43	0	0
	95°W	10°S-15°N	19**	Sep. 1967	0.0058 ± .006	21	0.0031 ± .005	11	0.0863 ± .072	79	0	0
92°W	20°S-10°N	22**	Feb.-Mar. 1967	0.0077 ± .007	18	0.0095 ± .013	23	0.0186 ± .014	36	0	0	

TABLE 15.—Above: Maximum linear dimensions of *Pontellina* cephalothorax. Dorso-ventral height taken in lateral view includes Mx2 with setal fan closed, width across trunk taken in dorsal view (mm).
Below: Mesh width of nets listed in Table 14.

Copepodite stage	II		III		IV		V		Adult	
	—		—		—		♂	♀	♂	♀
Typical specimen	0.30 × 0.28		0.38 × 0.34		0.48 × 0.44		0.61 × 0.56	0.62 × 0.60	0.70 × 0.66	0.90 × 0.75
Small specimen	0.28 × 0.26		0.36 × 0.34		0.46 × 0.42		0.58 × 0.54	0.56 × 0.56	0.62 × 0.60	0.75 × 0.64
Nets ¹	Juday net		IOSN		CalCOFI SN		POFI SN			
Mesh widths (mm)	0.18		0.33		0.55/0.25 (silk) 0.505/0.28 (nylon)		0.66/0.31			

¹ IOSN = Indian Ocean Standard Net
CalCOFI SN = California Cooperative Oceanic Fisheries Investigations Standard Net.
POFI SN = Pacific Oceanic Fisheries Investigation Standard Net.

TABLE 16.—Comparison by Student-*t* test of mean abundance in day (0601 to 1800 h local time) and night (1801 to 0600 h local time) collections. Samples of each set selected for similarity of geographical origin, collecting procedures and the presence of the species, i.e., samples negative for the species omitted. Samples derived primarily from those listed in Table 14.

Species	Source of samples	Day			Night			<i>t</i>	<i>p</i>
		mean/m ³	<i>s</i> ²	<i>N</i>	mean/m ³	<i>s</i> ²	<i>N</i>		
<i>plumata</i>	Indian Ocean	0.0945	2.7318	70	0.1048	1.7640	48	0.0370	>0.9
	Austral-Asian Seas	0.0483	0.1488	12	0.0413	0.0784	7	0.6000	>0.9
	Pacific Ocean	0.0770	1.2224	43	0.0405	0.1720	41	0.1986	>0.8
	Atlantic Ocean	0.0857	2.7429	7	0.0133	0.0033	3	1.0251	>0.3
<i>morii</i>	Indian Ocean	0.1504	3.7540	56	0.1550	5.1996	41	0.0107	>0.9
	Austral-Asian Seas	0.0300	0.0400	12	0.0400	0.1040	6	0.0081	>0.9
	Pacific Ocean	0.0332	0.0804	22	0.0462	0.4721	24	0.0881	>0.9
<i>sobrina</i>	Pacific Ocean	0.0307	0.0858	16	0.0914	2.8169	35	0.1423	>0.8

TABLE 17.—Occurrence of *Pontellina* spp. in day (0601 to 1800 h local time) and night (1801 to 0600 h local time) samples. + present, - absent.

	Day		Night		χ^2	<i>p</i>
	+	-	+	-		
Atlantic Ocean:						
<i>plumata</i>	25	16	13	22	3.389	0.1 > <i>p</i> > 0.05
<i>platychela</i>	23	18	23	12	0.383	0.75 > <i>p</i> > 0.5
Eastern Pacific Ocean:						
<i>plumata</i>	15	19	13	49	4.360	0.05 > <i>p</i> > 0.025
<i>morii</i>	6	28	13	49	0.015	0.9 > <i>p</i> > 0.75
<i>sobrina</i>	9	25	26	36	1.648	0.25 > <i>p</i> > 0.1
Indian-Western Pacific Ocean:						
<i>plumata</i>	108	30	87	31	0.491	0.5 > <i>p</i> > 0.25
<i>morii</i>	80	58	66	52	0.040	0.9 > <i>p</i> > 0.75

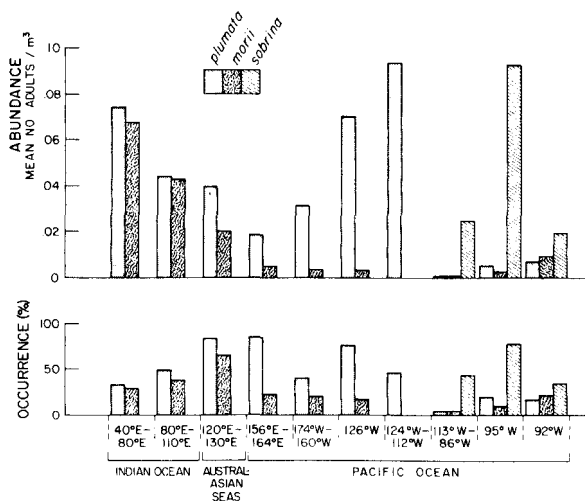


FIGURE 35.—Mean abundance (No. adults/m³) and percentage frequency of occurrence in sets of samples shown in Figures 1b and 38 and listed in Table 14. Confidence limits of the means shown in Table 14. Further discussion in text.

The appearance of *sobrina* is restricted to the eastern tropical Pacific where its abundance and occurrence resemble the values for *morii* and *plumata* in their regions of dominance, respectively.

Quantitative data on *Pontellina* in the Atlantic Ocean are few. In six quantitative samples from the western Atlantic *plumata* abundance ranged from 0.01 to 0.46 adults per m³. Two samples containing *platychela* provided estimates of 0.001 and 0.08 adults per m³.

Extremely high values of *plumata* s.l., however, have been reported from the Atlantic. Judging from their geographical origin, the northeastern Gulf of Guinea, these abundance estimates (Mahnken, Jossi, and McCabe, 1968) are probably referable to *platychela*. Mahnken and his co-workers record the species at 18 of 63 sampled localities scattered offshore from the Bight of Benin west to Cape Palmas. They indicate areal abundance of the species by contouring selected class intervals of number per 1,000 m³ water strained. In lieu of the actual estimates per sample we used midpoints of each contoured interval to calculate the mean abundance. The yield is a surprisingly high mean of 1.01 individuals per m³, an order of magnitude higher than our highest mean values from the Pacific and Indian Oceans. Aside from possible bias introduced by our extrapolations

several factors may be responsible for these unusually high values: e.g., count of immature as well as adult specimens, use of nets with smaller mesh width (0.281 mm), use of surface tows in a region relatively rich in zooplankton presumably concentrated in the very shallow layer of tropical surface water above the permanent thermocline, etc.

Summing our mean values of *plumata*, *morii*, and *sobrina* in each meridional set of samples, we find remarkably good agreement between our abundance estimates and those derived by previous studies of *plumata* s.l. in the Pacific Ocean (Table 18). We normalized the published data to conform to the units employed in the present study. Normalization was simplified by the following assumptions:

- we assumed 100% filtration efficiency;
- we assumed that *Pontellina* occurs only above 200 m and, in calculating volume of water strained by the net, omitted segments extending below 200 m;
- in sets of vertically stratified tows we considered the overall estimate of abundance as if it were from a continuous tow sampling between 200 m and the surface;
- we assumed that previous studies on *Pontellina* failed to discriminate among the different species; the published values were regarded as representing a combined estimate of the abundance of all species of the genus found in the region.

Estimates obtained from Heinrich (1968) and Vinogradov and Voronina (1963) are about one order of magnitude higher than other middle and west Pacific estimates. These higher values may be accounted for by two factors, namely that the counts include immature copepodids and that the samples were taken with nets of 0.18-mm mesh, small enough to retain *Pontellina* copepodids of stage II and possibly of stage I as well (Table 15). Sherman's (1963, 1964) counts appear to have been derived from adult specimens, partly by inference from his text and partly from the relatively wide mesh comprising most of the filtering cone in the POFI (Pacific Oceanic Fisheries Investigation) Standard Net (0.66 mm).

TABLE 18.—Mean abundance (No./m³) of *Pontellina* spp. in meridional transects crossing the Equator.

Region	Longitude	Latitude	Source of data	\bar{x} no. adults	\bar{x} no. adults and juveniles	Number of samples	Sampling months	Depth, tow, net
Indian Ocean (west)	40°E-80°E	35°S-25°N	present study	0.1419	—	233	Jan.-Dec. (1962-65)	200-0 m, vert., IOSN ¹
Indian Ocean (east)	80°E-110°E	27°S-18°N	present study	0.0863	—	107	Jan.-Dec. (1962-64)	200-0 m, vert., IOSN ¹
Austral-Asian Seas	125°E-135°E	12°S-12°N	present study	0.0596	—	23	Mar.-May (1961)	150-0 m, obl., CalCOFI SN ² (silk)
Pacific Ocean	156°E-164°E	12°S-12°N	present study	0.0230	—	23	Aug.-Sept. (1956)	150-0 m, obl., CalCOFI SN ² (silk)
	160°E	04°S-16°30'N	Vinogradov and Voronina, 1963	—	0.1023	17	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	176°W	14°S-13°N	Vinogradov and Voronina, 1963	—	0.3790	21	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	120°E-175°W	04°S-30°N	Heinrich, 1968	—	0.1910	91	W of 160°E Jul.-Aug. (1957)	500-0 m, vert., Juday 80 cm
							E of 160°E Nov.-Feb. (1957-58)	
	168°E-155°W	20°S-20°N	Sherman, 1964	0.1379	—	59	Jan.-Apr. (1962)	Surface, POFI SN ³
	174°W-160°W	06°S-21°N	present study	0.0346	—	15	Aug.-Sep. (1956)	150-0 m, obl., CalCOFI SN ² (silk)
	158°W	07°S-21°N	Sherman, 1963	0.0438	—	13	June-July (1961)	Surface, POFI SN ³
	154°W	13°S-13°N	Vinogradov and Voronina, 1963	—	0.1172	18	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	140°W	18°S-17°30'N	Vinogradov and Voronina, 1963	—	0.1600	29	Sep.-Dec. (1961)	500-0 m, vert., Juday 80 cm
	126°W	12°S-20°N	present study	0.0744	—	22	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN ² (nylon)
	95°W	10°S-15°N	present study	0.0952	—	19	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN ² (nylon)
	92°W	20°S-10°N	present study	0.0358	—	22	Feb.-Mar. (1967)	150-0 m, obl., CalCOFI SN ² (nylon)

¹ IOSN = Indian Ocean Standard Net.

² CalCOFI SN = California Cooperative Oceanic Fisheries Investigations Standard Net.

³ POFI SN = Pacific Oceanic Fisheries Investigation Standard Net.

Disregarding collecting and sample enumerating procedures as well as differences among the individual species, estimates of mean abundance of *Pontellina* across the Pacific (Table 18) vary from 0.023 to 0.379 with a median of 0.1 individuals per m³. For epipelagic copepods this appears to be a rather low and remarkably uniform set of values that varies within the unusually narrow range of one order of magnitude. Summing the abundance of the three species produces a notable lack of any pro-

nounced geographical trend though the mean abundance shows moderate, irregular undulations along the equatorial belt crossing the Indian and Pacific Oceans.

Low abundance and relatively uniform dispersion throughout the geographical region occupied by each species suggests that the species of *Pontellina* are high-order predators. This impression is supported for adults at least by the exclusive presence of animal remains in their stomach and the predominance of copepod

fragments (Table 19). Though all of the species appear to be similarly predaceous within their respective epiplanktonic communities, we must conclude that appreciable differences in the abundance and occurrence of the sibling species are indicative of real changes in habitat conditions and real differences in the adaptive optima for each species.

Remarks on Geographical Distribution

This discussion hinges upon inferences drawn from the evidence presented in the preceding sections. Chief among them are the validity of the four sibling species of *Pontellina* as separate noninterbreeding populations. Based on morphological homogeneity each population appears to be closely adapted genetically to prevailing environmental conditions in the geographically limited hydrographic systems comprising its particular habitat. Except for differences between Atlantic and Indian-Pacific populations of *plumata* morphological indications are that panmixis prevails in each species.

The three tropical species, *morii*, *sobrina*, and *platychela*, occupy eutrophic waters characterized by equatorial upwelling and a

shallow, steeply graded, permanent thermocline. The mixed layer overlying the thermocline is relatively homogeneous in temperature and has been referred to as Tropical Surface Waters (Wyrтки, 1966, 1967). In our use of this term, Tropical Surface Waters are restricted to the surface layer in regions where the permanent thermocline has a temperature gradient of $\geq 0.1^{\circ}\text{C}$ per m and encompasses an overall decrease in temperature from about $24^{\circ} \pm 1^{\circ}\text{C}$ at the top to about $15^{\circ} \pm 1^{\circ}\text{C}$ at the bottom. These pools of warm water are subjected to seasonally repetitive changes in the strength of the equatorial Trade Winds (Wyrтки, 1966, 1967; Taft, 1971). The seasonal changes produce monsoonlike reverses in the circulation of the equatorial segment inhabited by each species. This phenomenon apparently provides a sufficiently closed hydrographic circulation to maintain breeding stocks in proximity to suitable nursery grounds and thus ensures continual success of each species.

The equatorial distributions of the tropical species of *Pontellina* are not without precedence. The tropical Atlantic has previously been characterized in faunistic terms, for example, by a number of mesopelagic fishes (Backus et al., 1970) as well as by a sergestid shrimp

TABLE 19.—List of identified particles from microscopic analysis of stomach contents in adult female *Pontellina*.

Species	Specimen number	Copepod parts	"Oncaea" parts	"Paracalanus" parts	Crustacean parts	Algal parts	Source of specimen:		
							Ocean	Station	
<i>plumata</i>	1	x	x				Atlantic	La Creuse 5	
	2	x					Indian	Dodo VI-81	
	3	x	x				Pacific	Scorpio II-146	
	4	x	x				Indian	Lusiad V-45	
	5	x	x				Pacific	Jordan 57-076	
Percentage no. with ingested particles in midgut:							71%		
<i>platychela</i>	1	x		x			Atlantic	<i>Atlantis II</i> 20-28	
	2	x	x				Atlantic	La Creuse 5	
	3	x					Atlantic	<i>Atlantis II</i> 31-40	
	4				x		Atlantic	<i>Atlantis II</i> 31-54	
	5		x				Atlantic	Oregon 1289	
Percentage no. with ingested particles in midgut:							63%		
<i>morii</i>	1	x	x				Pacific	Troll 30	
	2	x					Pacific	TRANSPAC 98B	
	3	x	x				Pacific	EQUAPAC H-31	
	4	x					Indian	Lusiad V-45	
	5	x					Indian	Lusiad II-14	
Percentage no. with ingested particles in midgut:							63%		
<i>sobrina</i>	1	x	x				Pacific	Bonacca 35	
	2	x					Pacific	CalCOFI 5801: 153.50	
	3	x	x				Pacific	Scot 45	
	4	x	x				Pacific	Jordan 60-056	
	5	x	x				Pacific	Bonacca 31	
Percentage no. with ingested particles in midgut:							83%		

(Judkins, 1972). Among the Atlantic Foraminifera listed by Bé and Tolderlund (1971) as tropical species only *Candeina nitida* shows a geographical distribution similar to that of *P. platychela*.

In general species characterizing the eastern tropical Pacific, unlike *sobrina*, tend to follow the coastline of the Americas from about lat. 30°N to 20°S and extend westward to long. 160° to 180°W: e.g., *Euphausia distinguenda*, (Johnson and Brinton, 1963), *Eucalanus inermis*, (Lang, 1967), *Melamphaes spinifer*, (Ebeling, 1962), *Stomias colubrinus*, (Gibbs, 1969).

These distributions are meridionally and zonally more extensive than the limited dispersion observed in *P. sobrina* and others like *Pontella danae*, *P. agassizi*, and *Pontellopsis lubbockii* (Heinrich, 1964; Fleminger, 1967b; and unpublished records). The dissimilarities probably relate to differences in depth range, the more widespread forms having access to subsurface currents flowing northward (Wooster and Jones, 1970) and southward (Wooster and Gilmartin, 1961) under the eastern boundary currents as well as westward in the tongue of low oxygen water accompanying the North Equatorial Current which is traceable to the Philippines (Reid, 1965; Wyrтки, 1966; Tsuchiya, 1968).

Distributions of epipelagic species in the equatorial Indian and Pacific Oceans resembling that of *morii* include a number of other copepods, e.g., several species of *Eucalanus*, (Fleminger and Hulsemann, 1973; Fleminger, 1973); *Clausocalanus minor*, (Frost and Fleminger, 1968); several euphausiids such as *Euphausia diomediae*, *E. paragibba*, and *Stylocheiron microphthalmum*, (Brinton, 1962); and fishes such as *Scopelogadus unispinus*, (Ebeling and Weed, 1963) and *Stomias affinis*, (Gibbs, 1969) though the lattermost is also considered to inhabit the tropical Atlantic.

Although the ubiquitous *plumata* overlaps geographically with each of the tropical species, *plumata*'s overall range lies mostly in the enormous basin of oligotrophic waters spreading across the tropics and subtropics of each ocean, waters markedly different in vertical thermal structure from those of its tropical congeners. The almost mutually exclusive distributions of *plumata* and its more localized congeners, *platychela* in the equatorial Atlantic and *sobrina*

in the eastern tropical Pacific, are evidence of relatively intensive environmental gradients and the adaptive response to appreciably different environmental optima, which separate the distributions of these pairs of species.

For example, *morii* has been found at the edge of the south Atlantic as well as the edge of the eastern tropical Pacific; concomitantly *sobrina* occurs in the North Equatorial Current, but successfully extends only a few degrees of longitude to the west of its habitat; *platychela* is adjacent to but fails to establish itself in the Sargasso Sea; finally *plumata*, despite apparent circumglobal distribution, does not appear in large numbers where its equatorial congeners abound. Thus, the optimum habitats appear to be regionally distributed and those that are contiguous are sufficiently different to prevent colonization by expatriated congeners transported to the margin of the habitat. The possibility of interference among the species is open but in the light of available knowledge of calanoids it seems intuitively to be most unlikely.

Thus, the two classes of epipelagic warm-water distributions found in *Pontellina* suggest a fundamental dichotomy in the circumglobal warm-water belt. The three tropical species correlate with geographically separated shallow lenses of eutrophic water. Each lens is known to overlie regions of intense temperature and oxygen gradients and to be partially bounded by the similarly intense tropical convergences (Neumann and Pierson, 1966).

P. plumata, however, correlates with the circumglobal warm-water pool that is largely oligotrophic. The oligotrophic pool tends to be deep, the permanent thermocline often exceeding 200 m in depth. Temperature gradients in the thermocline and along its margins at the subtropical convergence are relatively weak, and oxygen is generally at or near saturation (Neumann and Pierson, 1966). Evidence that the Atlantic pool may be at least partially isolated with respect to *Pontellina* whereas the Indian and Pacific pools are confluent is suggested by morphological differences in the *plumata* populations reported above.

The circulation systems and physical conditions known to maintain these lenses of eutrophic tropical water and the pools of oligotrophic tropical-subtropical waters are the obvious mechanisms sustaining the geographical dis-

tribution of the four species of *Pontellina*. This is apparent in the relationship between the distribution of each species and the location of prevailing near-surface isotherms that locate the hydrographic limits of these bodies of water. The localities for the tropical species are largely enveloped by the mean winter season position of the 24°C isotherm at 10 m (Figure 36), the lower thermal limit of Tropical Surface Water. The 10-m depth was chosen to reduce the influence of diurnal fluctuations. The localities for *plumata*, however, vary broadly between the position of the 20° and 15°C mean winter season isotherms (Figure 37). Factors confining the distributions to the observed limits, however, are not obvious; more data on depth range, vertical migratory behavior, and depth of food organisms would probably be enlightening.

Notably, more than three-quarters of the samples (77.5%) containing *Pontellina* yielded

specimens of only one species. To examine joint occurrences of *Pontellina* congeners more closely, all capture records of a species were tallied by ocean and grouped with respect to the presence or absence of other congeners in the same sample (Table 20). Comparison of singular and joint occurrences for all possible pairings indicates that the latter are relatively infrequent. In no case of joint occurrences did the index of affinity (Fager and McGowan, 1963) reach a positive value. No two species within the genus would appear to occupy the same spatial habitat or, in other words, be members of the same community. Thus, the extensive overlapping of *morii* and *plumata* in the equatorial Indian and Pacific Oceans may be viewed as a function of intermingling due to the spatial proximity of the two habitats and perhaps also due to a greater number of similarities shared by these two habitats than between those of the other possible pairings within the genus.

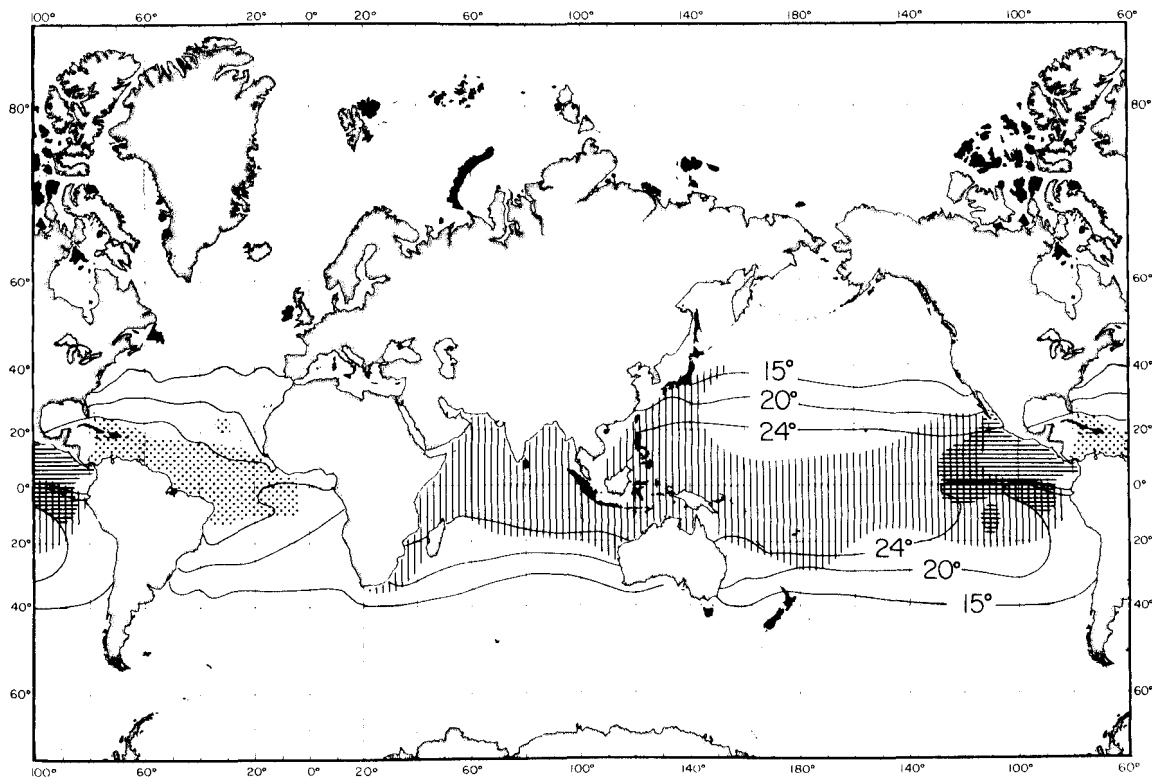


FIGURE 36.— Comparison of geographical area enveloping all capture records of tropical species of *Pontellina* with selected mean isotherms at 10 m for winter season of each hemisphere. Data from Muromtsev (1958, 1963) and Wyrki (1971). Dotted shading outlines capture records of *P. platychela* shown in Figure 8; horizontal shading outlines capture records of *P. sobrina* shown in Figure 15; vertical shading encloses the capture records of *P. morii* shown in Figure 12.

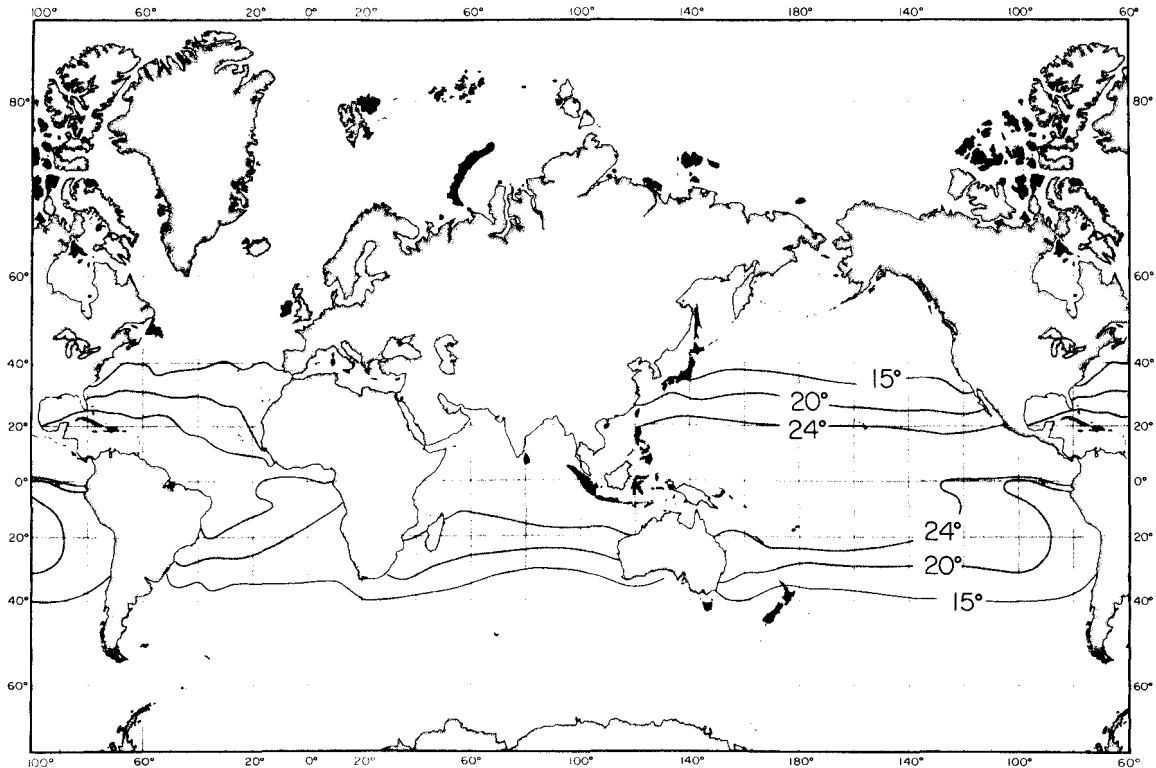


FIGURE 37.—Comparison of shaded area enveloping all capture records of *Pontellina plumata*, shown in Figure 5 with selected mean isotherms at 10 m for winter season of each hemisphere. Data from Muromtsev (1958, 1963) and Wyrтки (1971). Further discussion in text.

TABLE 20.—Separate and joint occurrences among species of *Pontellina*. Values in parentheses are the index of affinity; a value greater than 0.5 suggests joint membership in the same communal assemblage of species.

	<i>plumata</i>	<i>morii</i>	<i>sobrına</i>	<i>platychela</i>	Total
Indian Ocean and Australasian Seas:					
<i>plumata</i>	129	96 (-7.01)	0	0	225
<i>morii</i>		78	0	0	78
<i>sobrına</i>			0	0	0
<i>platychela</i>				0	0
Total	129	174	0	0	303
Pacific Ocean:					
<i>plumata</i>	136	46 (-3.77)	23 (-5.20)	0	205
<i>morii</i>		23	6 (-2.69)	0	29
<i>sobrına</i>			85	0	85
<i>platychela</i>				0	0
Total	136	69	114	0	319
Atlantic Ocean:					
<i>plumata</i>	80	0	0	14 (-3.93)	94
<i>morii</i>		0	0	0	0
<i>sobrına</i>			0	0	0
<i>platychela</i>				58	58
Total	80	0	0	72	152
All records combined:					
<i>plumata</i>	345	137	18	4	514
<i>morii</i>		101	1	0	102
<i>sobrına</i>			85	0	85
<i>platychela</i>				58	58
Totals	345	238	104	72	759

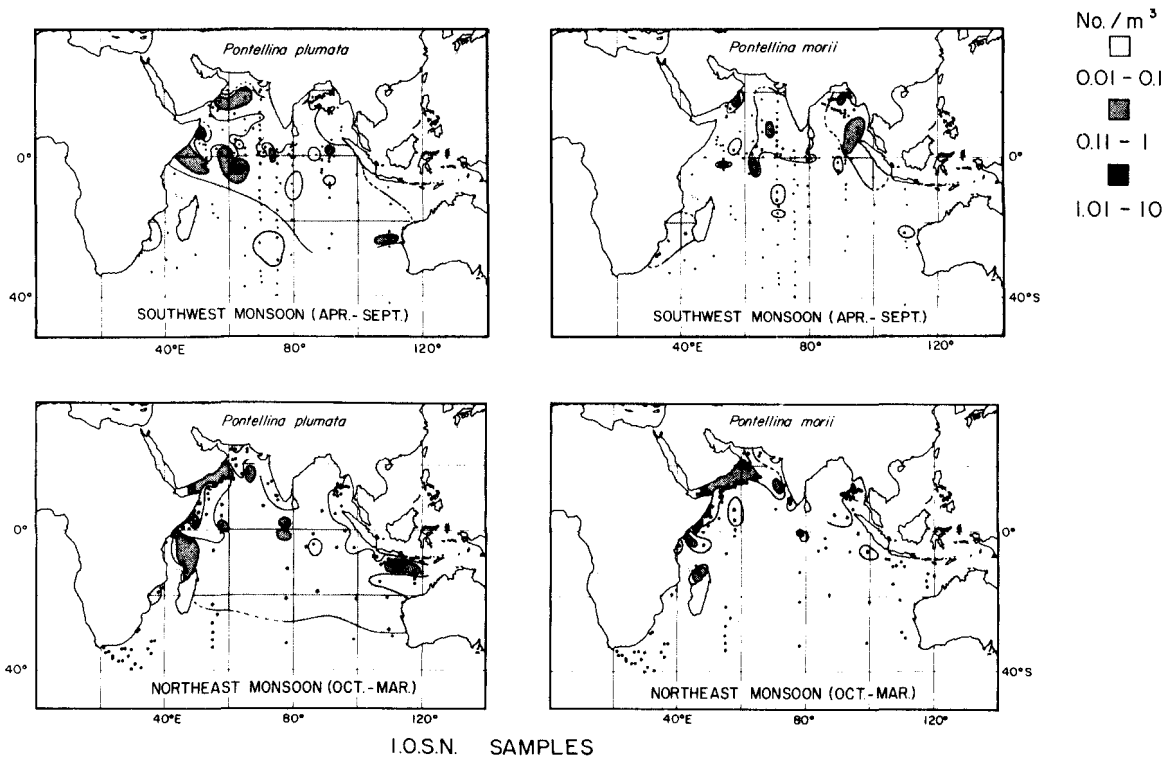


FIGURE 38.—Abundance of *Pontellina morii* and *P. plumata* in Indian Ocean Standard Net (IOSN) collections. Samples collected during southwest and northeast monsoon seasons. Dots represent localities sampled. Abundance values are estimated number of adults per m³ water strained.

P. morii and *plumata* exhibit distinctive distributions in both monsoon seasons (Figure 38) as well as general zonal separation (Figure 39), differences that are blurred in charts prepared without regard for seasonal variation (e.g., Figures 5, 12). During the southwest monsoon, *plumata* appeared in large numbers off the Somali coast and near the Seychelles whereas *morii* was much more frequent in the eastern Arabian Sea and the eastern Bay of Bengal. In the northeast monsoon both species were abundant in the Somali Current. However, only *morii* appeared to be common in and about the Andaman Sea whereas an indication of large numbers of *plumata* appeared just south of Java.

Morphological relationships analyzed above indicate the species have common ancestry that produced three main lines of descent represented respectively by *plumata*, *platychela*, and the Indian-Pacific tropical pair of siblings, *morii* and *sobrigna*. Ample evidence of co-occurrence

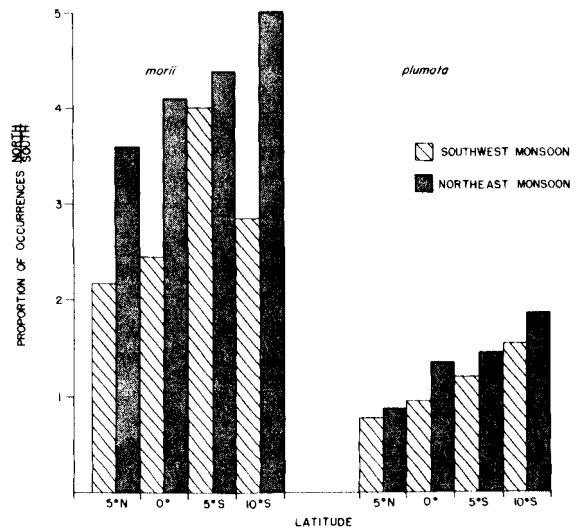


FIGURE 39.—Frequency of occurrence of *Pontellina plumata* and *P. morii* in the Indian Ocean north of selected latitudes compared to that south of the same latitudes.

without intergradation between *morii* and *sobrīna* support the conclusion that both are valid species that have evolved relatively recently.

Morphological-geographical patterns provide inferential evidence that sympatry among subsets of the four species have led to modifications of secondary sexual features, presumably in the course of developing pre-mating barriers to hybridization. Obvious examples of this emerge from comparison of pairs of species which have extensive contiguous boundaries: e.g., *plumata* and *platychela* in the Atlantic and *plumata* and *morii* in the Indian and Pacific Oceans. In each pair of species the chela on the male fifth leg in the tropical congener is broadened in contrast to the slender chela found in *plumata*. In the females of each pair the hair patches on the genital segment are either missing or reduced to one pair in the tropical species while *plumata* maintains two prominent pairs. Another source of evidence lies in the geographical variations in the female fifth legs of *plumata* which follows a pattern indicative of character displacement.

CONCLUSIONS

1. The genus *Pontellina* represented by four species is epipelagic and occupies oceanic sectors of the circumglobal warm-water belt.

2. Three of the species occur chiefly in eutrophic sectors of equatorial latitudes where the layer above the thermocline is relatively homogeneous; the distinctiveness of this layer was noted by Wyrтки who refers to it as Tropical Surface Water. One species, *platychela*, occupies the tropical Atlantic; *sobrīna* is in the eastern tropical Pacific; and *morii* is found in the tropical Indian and tropical Pacific Oceans.

3. The fourth species, *plumata* s.str., occurs most frequently in oceanic, oligotrophic regions in tropical and subtropical latitudes.

4. Morphological differences among the species are subtle and restricted to secondary sexual structures.

5. The four species comprise a monophyletic complex showing three basic derivatives, *plumata*, *platychela*, and a third that underwent a subsequent episode of speciation to produce *morii* and *sobrīna*.

6. The female fifth leg is polymorphic and represented by four phenotypes or morphs.

Geographical variation in the frequency of morphs in *plumata* distinguishes Atlantic from Indian and Pacific populations; relationships with *platychela* in the Atlantic and *morii* and *sobrīna* elsewhere suggest the variation is the result of character displacement. Three of the four morphs in *morii* and *sobrīna* appear to be extremely rare.

7. Each species exhibits a distinctive geographic range independent of the other three. Absence of conspicuous geographical variation indicates sufficient transport and advection to maintain panmixis within each species except the Atlantic and Indian-Pacific populations of *plumata*.

8. Abundance of all four species is low despite relatively frequent occurrence within the limits of the distribution. These indications of high-order predation are supported by examination of gut contents in sexually mature adults in which the remains consisted primarily of particles from small copepods.

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