ROBERT J. MENZIES
and MILTON A. MILLER

Systematics and Zoogeography of the Genus Synidotea (Crustacea: Isopoda) with an Account of Californian Species

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY NUMBER 102

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ABSTRACT

Menzies, R. J., and M. A. Miller. Systematics and Zoogeography of the Genus *Synidotea* (Crustacea: Isopoda) with an Account of Californian Species. *Smithsonian Contributions to Zoology,* number 102, 33 pages, 1972.—A general survey of the systematics and distribution of the 36 species comprising the idoteid genus *Synidotea* is presented, followed by a more detailed account of the eight species represented in California. The characteristics of the Idoteinae are briefly reviewed, and the relationship of *Synidotea* to the other genera in this subfamily is indicated. Generic characters are discussed and the status of dubious species is clarified. The geographic, thermal, and bathymetric distributions of the included species are given. Most species of *Synidotea* occur in the Northern Hemisphere, predominantly in the Arctic–Boreal regions of the North Pacific. Distributional data, combined with paleoclimatic considerations, suggest the hypothesis that the North Pacific was its center of origin and radiation. It is thought that the genus originated in the late Mesozoic or early Cenozoic, when northern waters were much warmer than now, and that ancestral populations emigrated and speciated rapidly during the glacial Pleistocene. Lines of dispersal are postulated southward along both sides of the Bering arc, and northward into the Arctic through the Bering Strait. *S. laticauda* of San Francisco Bay is regarded as a relict descendant of an ancestral warm-water species, which also gave rise to the morphologically similar *S. harfordi* of southern California and the Sea of Japan. An association between size, latitude, and depth is indicated, with larger species occurring at higher (colder) latitudes and greater depths. Keys, descriptions, and ecological notes are given for the eight Californian species, including a new one from the central California coast, *S. berolzheimeri.*

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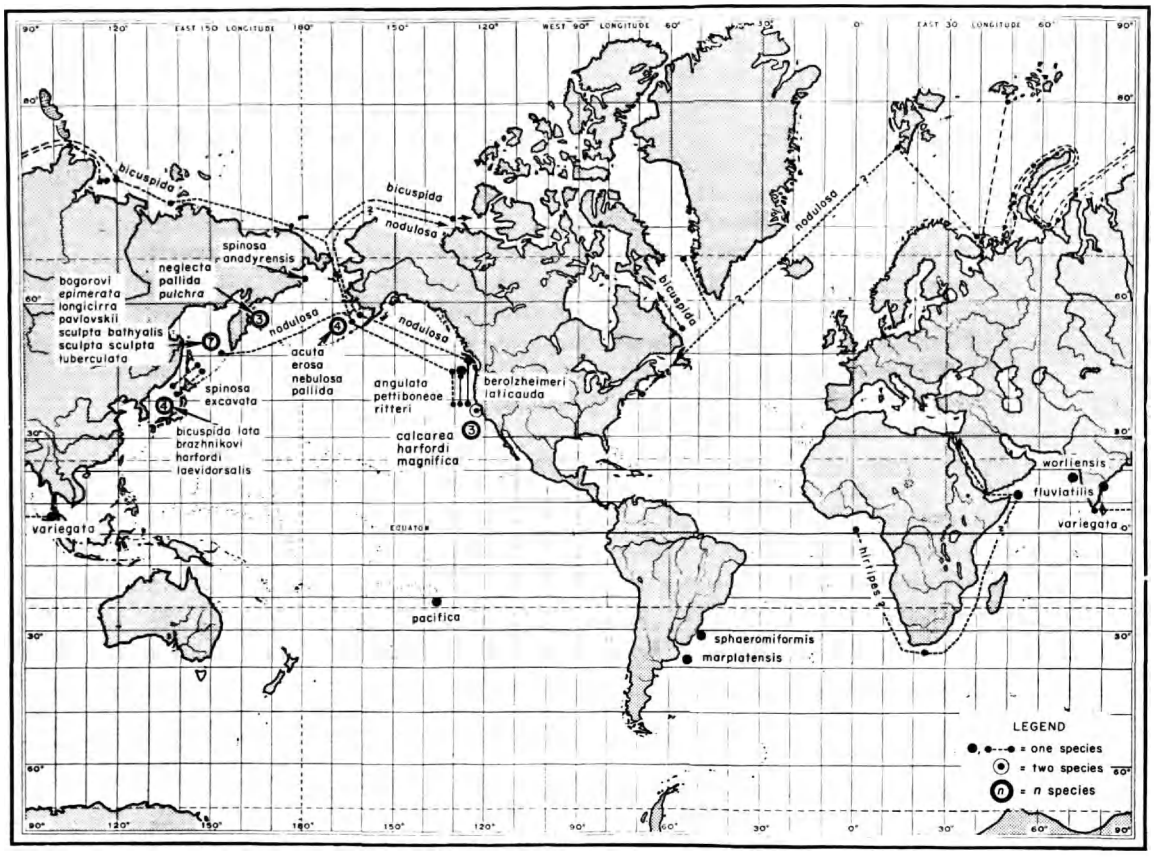

FIGURE 1.—Distribution of *Synidotea*. Note preponderance of species in Northern Hemisphere, especially in the North Pacific.

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Introduction

The present paper deals in general with the systematics and distribution of the 36 species and subspecies now comprising the isopod genus *Synidotea* Harger, and in particular with the eight species (including a new one herein described) that occur along the coast of California.

A biosystematic review of this genus is needed. The last previous attempt was made by Benedict (1897) who published a revision of *Synidotea* comprising at that time 15 species. The genus has also been treated, of course, in Miers' (1881) revision of the family Idoteidae, to which it belongs, and in regional monographs and checklists (notably, Richardson 1905, Hatch 1947; Gurjanova 1936, and Schultz 1969).

The distributional picture is doubtless distorted as a consequence of unequal collecting and reporting of these isopods from all geographic areas. Nevertheless, a synthesis of the scattered information on the included species should lead to a better understanding of their relationships and of factors governing their distribution and evolution. Also, in view of the need for up-to-date monographic accounts of most invertebrate groups on the Pacific coast, the authors deem it desirable to include in this article a key to and descriptions of the Californian species of *Synidotea* along with ecological notes.

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Systematic Account

Family IDOTEIDAE Dana, Miers, 1881

Subfamily IDOTEINAE Dana, 1852

The Idoteinae, to which *Synidotea* and the great majority of idoteid genera belong, differ from the other idoteid subfamilies in that the uropods are uniramous (except in *Cleantis*), the first three pairs of pereopods are not subchelate (prehensile), and the head is not laterally produced. The single ramus (apical or terminal plate) of the idoteine uropod doubtlessly corresponds to the larger or ventral plate of the biramous uropod of other valviferans, but authorities differ as to whether this represents the archetypal endopod or exopod. Calman (1909) and Racovitza and Sevastos (1910) interpret it as the

TABLE 1.—*Generic characters in Idoteinae.*

Genera	*Pleonal sutures complete + partial*	*Pereonites with dorsally visible epimeral sutures*	*Articles in flagellum of antenna 2*	*Articles in maxillipedal palp*
Zenobiana Stebbing	3+1	(1–2)–7	1–3	5
Cleantis Dana	(2–3)+1	2–7	1–3	4–5
Idotea (Idotea) Fabricius	2+1	2–7	many	4
I. (Pentidotea Richardson) Menzies	2+1	2–7	many	5
Cleantiella Richardson	1+2	2–7	1	5
Engidotea Barnard	1+2	2–7	many	5
Paridotea Stebbing	1+2	5–7	many	5
Barnardidotea Menzies and Miller	1+0	0	many	3
Glyptidotea Stebbing	0+3	2–7	many	5
Pentias Richardson	0+3	2–7	many	5
Euidotea Collinge	0+3	2–7	many	4
Crabyzos Spence Bate	0+3	0	many	5
Synischia Hale	0+3	0	many	5
Synisoma Collinge (*Stenosoma* Auct.)	0+(2–3)	2–7	few	4
Colidotea Richardson	0+1	5–7	few	4
Synidotea Harger	0+1	0*	many	3
Eusymmerus Richardson	0+1	6–7	1	4
Edotea Guérin-Méneville	0+1	0*	1	3
Ronalea Menzies and Bowman	0+1	5–7**	1	4
Erichsonella Benedict	0+0	(1–2)–7***	1	4

*Epimera distinct only beneath pleural expansions of pereonites 2–4; none visible dorsally.
**Epimera distinct on all but pereonite 1; visible dorsally only on last three pereonites.
***Anterolateral expansions of pleura on peronite 1 have sometimes been mistaken for epimera.

endopod, Tait (1917) thinks it is the exopod, whereas Nordenstam (1933) believes both explanations are possible. Until further evidence (especially from embryology and paleontology) can establish the homologies, it would be better not to use the terms "endopod" and "exopod" in referring to the branches of the valviferan uropod.

The principal characteristics used in distinguishing the 19 idoteine genera and the relationship of *Synidotea* to these are indicated in Table 1. It is evident that fusion of parts—pleonites, epimera, antennal flagellum, and maxillipedal palp—has played a prominent role in idoteid evolution. There seems to be some linkage between pleonal and epimeral fusions and reductions in various other parts, but there are many instances in which the correlation breaks down.

The fact that idoteine genera can be arranged in linear series on the basis of the degree of fusion in one or more structures suggests the hypothesis that they represent stages in evolution from an ancestral idoteid which showed little or no fusion or reduction of parts. The prototype was probably not unlike the Oligocene fossil, *Proidotea haugi* Racovitza and Sevastos (1910). According to this concept, *Synidotea* represents a fairly advanced stage, as it has a completely consolidated pleotelson (except for a pair of lateral incisions), completely coalesced epimera, and maxillipedal palp reduced to three articles. The flagellum of the second antenna, however, still shows the generalized multiarticulate condition.

Genus *Synidotea* Harger, 1878

The genus *Synidotea* was established by Oscar Harger (1874:374) for *Idotea nodulosa* Krøyer, a circumpolar species, with the following description (in it, he later placed *I. bicuspida* Owen): "Antennae with an articulated flagellum. Epimeral sutures not evident from above. Pleon apparently composed of two segments, united above but separated at the sides by short incisions. Operculum with a single apical plate. Palpus of maxillipeds three-jointed."

Miers (1881) relegated *Synidotea* (along with three other genera) to the synonymy of *Edotea* with

the statement, "The only distinction that can be cited to separate the species of *Synidotea* from *Edotea,* viz., the long antennae with the more numerous articulated flagellum, is, I think, scarcely of generic importance, since the length of the flagellum is subject to considerable variation, even in different individuals of a single species." He divided *Edotea* into three sections, however, one containing the two species that Harger placed in *Synidotea* plus *E. hirtipes* (Milne-Edwards). He also described a new variety of the latter from Japan *(E. hirtipes laevidorsalis),* which Benedict (1897) elevated to full species status in the restored genus *Synidotea.*

Benedict (1897) divided the genus *Synidotea,* as then constituted, into two new sections on the basis of whether the pleotelson is emarginate or pointed at the distal end. It is more or less emarginate in all but seven species: It is pointed in *S. nodulosa* (Krøyer), *S. spinosa spinosa* Gurjanova, and *S. s. anadyrensis* Gurjanova; broadly rounded in *S. magnifica* Menzies and Barnard and *S. calcarea* Schultz; and truncate in *S. pulchra* Birstein and *S. neglecta* Birstein. (In the latter two species, lateral teeth bordering the truncate apical margin make it appear somewhat excavate.) The pleotelson tapers narrowly in *S. sculpta* Gurjanova and *S. s. bathyalis* Gurjanova, but the author's figures indicate a slight terminal emargination in both. The pleotelson of *S. bogorovi* Gurjanova is spatulate (somewhat as in *S. magnifica* and *S. calcarea*), but again her illustrations show a slight emargination of the apex. Two observations support the view that an entire, pointed apex is the primitive condition. (1) The pleotelson of the fossil *Proidotea haugi* Racovitza and Sevastos (1910) terminates thus. (2) In species having an emarginate pleotelson, the apical excavation may be absent or inconspicuous in small, immature specimens, suggesting that ontogeny recapitulates phylogeny.

There has been some confusion regarding epimeral fusion in *Synidotea.* In his revision of the genus, Benedict (1897) emended the second sentence of Harger's original diagnosis to read, "Epimeral sutures not evident above on the first four segments; on the last three the lines of demarcation are more or less distinct." Richardson (1905) states that the epimera of all the thoracic segments in *Synidotea* are ". . . perfectly and firmly united with the segments . . ." but she also mentions the occasional presence on the last three pereonites of ". . . a faint depression marking the place of coalescence." The epimeral condition in *Synidotea* was clarified by Sheppard (1957) who observed that the so-called epimera of the first four somites in this genus are actually pleural expansions of the terga, whereas those of the posterior three are coxal in origin. She found that the coxal joints of the first four pereopods are clearly defined and that the outer, ringlike margin of all but the first is marked off from the overhanging ventral surface of the pleuron by a suture not visible in dorsal view. The epimera of the first and posterior three pereonal somites, however, are completely fused to their tergites. Hence, it may be stated that, in *Synidotea,* no epimeral sutures are visible in dorsal view, but can be seen from below on pereonites 2–4.

Another emendation was added by Menzies and Miller (1956) who noted that, in *Synidotea,* the genital apophyses on the midventral line of the seventh pereonal segment of the male are fused to form a single penis. As Sheppard (1957) shows, fusion of the paired penial processes is uncommon, but not unique, in the Idoteidae, since it also occurs in the closely related genus *Edotea.* She also points out that a single penis is characteristic of the Astacillidae, Pseudidotheidae, and Amesopodidae.

Thirty-six valid species have been described to date (Table 2). Compilation of the list was difficult because of the lack of a recent critical revision, the scattered literature, and the many inadequate and poorly illustrated descriptions. The task was somewhat easier for western American species, as specimens were available in our collections which helped resolve several taxonomic tangles.

Fairly complete synonymies for the eight species represented in California are given in the last section which gives an account of these species. Additional taxonomic considerations regarding several non-Californian species are given below.

Synidotea setifer Barnard, 1914, an African species, has been transferred to another genus, *Barnardidotea* Menzies and Miller, 1956, as it has one complete pleonal suture, rather than the single incompletely fused suture characteristic of *Synidotea.*

Synidotea epimerata Richardson, 1909, reported from the Sea of Okhotsk, has been regarded as a dubious member of the genus for two reasons. (1) Richardson's figure of this species indicates a complete, rather than a partial, pleonal suture. This is explained, however, by her text statement, "The abdomen is composed of a single segment with a suture line distinct at the sides, but less distinct in the mid-

TABLE 2.—*Geographic, biogeographic (thermal) and bathymetric distribution of* Synidotea.

Species	*Geographic Distribution*	*Biogeographic Region**	*Depth*	*Length***
			meters	mm
S. acuta Richardson, 1909	N. Pacific (Bering Sea)	Arctic (Subarctic)–Boreal (Beringian).	86	12
S. angulata Benedict, 1897	N. Pacific (Washington)	Boreal (N.W. American Temperate).	56–79	8.5–11.5
S. berolzheimeri, n. sp.	N. Pacific (central California)	Boreal (N.W. American Temperate).	Intertidal	11.8
S. bicuspida (Owen, 1839)	N. Pacific (Alaska, Bering Sea, Washington, central California); Arctic; N. Atlantic (Labrador).	Arctci-Boreal (Beringian–N.W. American Temperate).	29–88	25, 32
S. b. lata Gurjanova, 1933	N. Pacific (Sea of Japan)	Boreal (E. Asiatic Temperate)	5–20	20
S. bogorovi Gurjanova, 1955	N. Pacific (Sea of Okhotsk)	Arctic (Subarctic)	2,300	29
S. brazhnikovi Gurjanova, 1933	N. Pacific (Sea of Japan)	Boreal (E. Asiatic Temperate)	5–25	20
S. calcarea Schultz, 1966	N. Pacific (southern California).	N. Warm Temperate (W. American Transition).	813	6
S. epimerata Richardson, 1909	N. Pacific (Sea of Okhotsk)	Arctic (Subarctic)	20–80	13
S. erosa Benedict, 1897	N. Pacific (Alaska, Bering Sea)	Arctic (Subarctic)–Boreal (Beringian).	869	21
S. excavata Gurjanova, 1933	N. Pacific (Sea of Okhotsk, Sea of Japan).	Arctic (Subarctic)–Boreal (E. Asiatic Temperate).	?	12
S. fluviatilis Pillai, 1954	Indian (Chilka Lake, Quilon, Cochin).	Tropical (E. Indian)	?	12.3
S. harfordi Benedict, 1897	N. Pacific (Sea of Japan; Morro Bay, Southern California; Baja California).	Boreal (E. Asiatic and W. American Temperate)–N. Warm–Temperate (W. American Transition).	0–10	18
S. hirtipes (Milne-Edwards, 1840).	Red Sea (Suez); S. Atlantic (Cameroons, Saldhana Bay).	Tropical–S. Warm–Temperate	?	4, 9, 10
S. laevidorsalis (Miers, 1881)	N. Pacific (Sea of Japan)	Boreal (E. Asiatic Temperate)	9.5	19, 25, 28
S. laticauda Benedict, 1897	N. Pacific (San Francisco Bay, California).	Boreal (W. American Temperate).	1–9	17.5
S. longicirra Gurjanova, 1933	N. Pacific (Sea of Okhotsk)	Arctic (Subarctic)	30–141	26
S. magnifica Menzies and Barnard, 1959.	N. Pacific (southern California).	N. Warm Temperate (W. American Transition).	55–92	6
S. marplatensis Giambiagi, 1922	S. Atlantic (Argentina)	Antiboreal	Littoral	12.5
S. nebulosa Benedict, 1897	N. Pacific (Alaska, Bering Sea, Washington).	Arctic (Subarctic)–Boreal (Beringian).	10–60	19, 21
S. neglecta Birstein, 1963	N. Pacific (Northwest region)	Arctic-Boreal	1,693	9.3
S. nodulosa (Krøyer, 1848)	N. Pacific (British Columbia, Alaska, Sea of Okhotsk); Arctic; N. Atlantic (George's Banks, Halifax, Greenland, Spitzbergen).	Arctic-Boreal	10–198	14, 26
S. pacifica Nobili, 1906	S. Pacific (Tuamotus, Mangareva?).	Tropical (S.E. Polynesian)	?	3
S. pallida Benedict, 1897	N. Pacific (Alaska, Bering Sea, NW, Pacific).	Arctic-Boreal	1,380; 1,641	22, 8.5
S. pavlovskii Gurjanova, 1955	N. Pacific (Sea of Okhotsk)	Arctic (Subarctic)	135	12
S. pettiboneae Hatch, 1947	N. Pacific (Washington, central California).	Boreal (N.W. American Temperate).	Intertidal	7.5–10.5
S. pulchra Birstein, 1963	N. Pacific (northwest region)	Arctic-Boreal	2,887–2,917	15
S. ritteri Richardson, 1904	N. Pacific (Vancouver Island, B.C.; central California).	Boreal (N.W. American Temperate).	Intertidal	12.5

TABLE 2.—*Geographic, biogeographic (thermal) and bathymetric distribution of* Synidotea—Continued.

Species	*Geographic Distribution*	*Biogeographic Region**	*Depth*	*Length***
S. sculpta Gurjanova, 1955	N. Pacific (Sea of Okhotsk)	Arctic (Subarctic)	124–240	20
S. s. bathyalis Gurjanova, 1955	N. Pacific (Sea of Okhotsk)	Arctic (Subarctic)	400	16
S. sphaeromiformis Mañé-Garzón, 1946.	S. Atlantic (Uruguay, Puerto de la Paloma).	Antiboreal	4.5	8
S. spinosa Gurjanova, 1933	N. Pacific (Sea of Okhotsk, Sea of Japan).	Arctic (Subarctic)–Boreal (E. Asiatic Temperate).	80–90	16
S. s. anadyrensis Gurjanova, 1955.	N. Pacific (Bering Sea)	Arctic (Subarctic)	40–80	18
S. tuberculata Richardson, 1909	N. Pacific (Sea of Okhotsk)	Arctic (Subarctic)	120–135	16.5
S. variegata Collinge, 1917	Indian (Gulf of Manaar, Indochina).	Tropical (E. Indian, Indochinese).	?	7.5, 8.0
S. worliensis Joshi and Bal, 1959	Indian (Bombay)	Tropical (E. Indian)	Littoral	10

*Biogeographic regions adapted from Hedgpeth (1957), Sverdrup et al. (1942), and Thorne (1963).

**Measurements separated by commas are of specimens from different localities; those hyphenated indicate ranges in one locality.

TABLE 3.—*Distribution of* Synidotea

A. Geographic Distribution			*B. Latitudinal (Thermal) Distribution*				*C. Bathymetric Distribution*			
Oceans	*No. of species*		*Regions*	*No. of species*	*Length*		*Depth*	*No. of species*	*Length*	
	Total	*Endemic*			*Mean ±S.E.* (*mm*)	*Range* (*mm*)	(*m*)		*Mean ±S.E.* (*mm*)	*Range* (*mm*)
Arctic	2	0	Arctic	8	18.8±2.6	12–29	0–10	9	13.8±2.0	8–24
N. Pacific	29	27	Arctic–Boreal	10	17.0±3.0	9–32	10–100	10	16.9±2.4	6–32
S. Pacific	1	1	Boreal	9	16.0±1.9	9–24	100–1,000	8	17.4±2.8	6–26
N. Atlantic	2	0	N. Warm-Temperate	3	10.0	6–18	1,000–2,000	1	15.3	8.5–22
S. Atlantic	3	2	Tropical	5	8.0±2.2	3–12	2,000–3,000	2	22	15–29
Indian	3	3	S. Warm-Temperate	1	8.0	.....				
Antarctic	0	....	Antiboreal	2	10.0	8–12				
			Cold-Water	29	16.7±1.1	8–32				
			Warm-Water	9	9.0±1.4	3–18				

dle, indicating another partly coalesced segment at the base." (2) The figure also shows distinct epimera on the first pereonite, and the accompanying text states that they ". . . arise from the lateral margin and project anteriorly beyond the place where they are visible in dorsal view." This question has been resolved, however, by one of our reviewers who states that examination of specimens in the collections of the National Museum of Natural History would show Richardson to be in error on this point.

Synidotea excavata Gurjanova, 1933, is included on this list of valid species, but with some hestitation as it may be conspecific with *S. epimerata*. Both occur in the Sea of Okhotsk and seem quite similar from their descriptions, assuming the above interpretations of the pleonal and epimeral conditions in *S. epimerata* are correct. Gurjanova apparently regards them as distinct, but she may have been mislead by Richardson's figures which she reproduces in her 1936 paper. The figures, however, indicate other differences which might warrant specific separation, if constant. For example, *S. excavata* seems to lack certain tubercles on the head shown by *S. epimerata*, and it has only three middorsal tubercles on the

pereon (pereonites 2–4), whereas *S. epimerata* has a longitudinal row of seven (one middorsally on each pereonite). Critical morphological and ecological comparisons of the two forms are indicated.

Synidotea laevis Benedict, 1897, and *S. muricata* Benedict, 1897, we regard as junior synonyms of the widely distributed *S. nodulosa* Krøyer, 1848. Hence, these two species are not listed and their distributions are incorporated with data for the senior species in the next section.

Synidotea marplatensis Giambiagi, 1922, a South American species, we now consider correctly placed. In our 1956 paper, we had suggested that it perhaps should be put in a separate genus on the basis of Mañé-Garzón's (1946) figures of this species. These show a completely consolidated telson with *no* lateral incisions and a maxillipedal palp of two, rather than three, articles. Since Mañé-Garzón states in the text, however, that there is a pleonal suture line and that the maxillipedal palp is triarticulate (as in Giambiagi's original descriptions and figures), judgment was suspended pending clarification. We can now confirm that Mañé-Garzón's text statements are correct, but his figures are in error on both counts. Through the courtesy of Plínio Soares Moreira of the Oceanographic Institute of the University of São Paulo, we received specimens of *S. marplatensis* which he collected at Praia Grande, south coast of Brazil, at a depth of 16 meters. Although these isopods were taken considerably north of the previously known range of this species (previously recorded from Mar del Plata, Buenos Aires [type-locality] and Rocha, Uruguay), they conform nicely to the descriptions and confirm its generic assignment.

Zoogeography

Geographic Distribution

The 36 species of the genus *Synidotea* are widely, but unevenly distributed around the world (Figure 1, Tables 2 and 3A). Of these, 33 species occur in the Northern Hemisphere. One of these, *S. hirtipes*, occurs also in the Southern Hemisphere, being found on both sides of the equator in the Ethiopian region (Red Sea, Cameroons, and Saldhana Bay). About three-fourths of the known species of the genus occur in the Northern Pacific, predominantly in the Bering, Okhotsk, and Japanese seas. Most of these have been described, relatively recently, by Gurjanova (1933, 1935). By contrast, only two species (*S. nodulosa* and *S. bicuspida*) are represented in the North Atlantic. Both of these are also found in the North Pacific and Arctic oceans. They are probably circumpolar with southward extensions into cold-temperate waters of both the Atlantic and Pacific.

In the Southern Hemisphere, only four species have been reported—one in the central Pacific (*S. pacifica*), two along the temperate east coast of South America (*S. marplatensis* and *S. sphaeromiformis*), and one in South Africa (*S. hirtipes*), mentioned above as the only bipolar species.

The preponderance of Arctic–Boreal species and the paucity of species in the antipodal Antarctic–Antiboreal and tropical regions are most striking. Although additional collecting will doubtless reveal additional species, it seems unlikely that future discoveries will essentially alter the present imbalance. The poor representation in warm waters is not too surprising since valviferans in general are scarce in tropical and subtropical regions (Miller, 1968).

In both hemispheres, major gaps disrupt the circumglobal distribution of the genus. No species have been reported from the presumably well-surveyed European Atlantic and Mediterranean coasts. The genus is not listed in the South Australian fauna (Hale 1929), nor in the New Zealand area (Hurley 1961), nor among Chilean marine isopods (Menzies 1962).

Within the genus, one finds an interesting diversity of distributional patterns. The records indicate a high degree of endemicity, but some of this may be more apparent than real, due to inadequate collections and perhaps to incorrect determinations. Nevertheless, it does appear that there are just a few wide-ranging species and that the rest are relatively restricted.

The most widely distributed species are *Synidotea nodulosa* and *S. bicuspida* whose ranges widely overlap along the western coast of Canada and Alaska and probably along the Arctic coast of North America (Figure 1). It should be mentioned, parenthetically, that the distributions of these two species herein given incorporate the localities of their synonyms. Moreover, it is assumed that their distributions are essentially continuous between reported localities. Another far-ranging species is *S. hirtipes* found along the coasts of western, southern, and northern Africa, again assuming continuous distribution between reported lo-

calities. It is the only species of *Synidotea* known from that entire continent.

A species with restricted distribution is *Synidotea laticauda* which is confined to the less saline (mesohaline and oligohaline) and warmer reaches of the San Francisco Bay system and its freshwater tributaries (Petaluma River and near the Suisun Bay delta of the Sacramento–San Joaquin rivers (Figure 2). Two other estuarine or freshwater species, *S. fluviatilis* of India and *S. marplatensis* of South America, also have limited distributions. There are, of course, several marine species known from single localities, such as *S. pacifica* which, when more collections are made, probably will be found to have wider distribution than the records indicate.

An intriguing case of disjunct distribution is the occurrence of *Synidotea harfordi* on both sides of the North Pacific. Along the eastern coast, it ranges from temperate Morro Bay, California, to warm-temperate Baja California with long gaps between the few known localities (Morro Bay and San Diego area, California, and Magdalena Bay, Baja California). On the west side of the Pacific, Gurjanova (1933) reports it from the temperate littoral waters of the Sea of Japan. The widely distributed *S. bicuspida* and *S. nodulosa* also occur on both sides of the Pacific, in the Arctic, and in the Atlantic with long gaps between reported localities. Discontinuities, of course, may sometimes be attributed to inadequate collecting. Hypotheses to account for the distribution of these and other species will be presented next.

The distributional data indicate a North Pacific center of origin and radiation of the genus *Synidotea*, as Gurjanova (1935) has already stated. Assuming its probable establishment there in the warm environment of the Cretaceous or early Cenozoic, we might imagine a veritable explosive evolution and dispersal associated with paleoclimatic changes, notably the cooling of northern waters culminating in the Pleistocene (Durham 1950, Ericson et al. 1956, Ewing and Donn 1956, Briggs 1970). Durham presents evidence that during the Paleocene, the 20°C. marine isotherm along the Pacific coast, at least, was probably north of 49° north latitude, and in the Eocene it certainly was. Since then, he finds, it has been shifting southward, possibly with minor oscillations, until the Pliocene when it reached its present position at about 24° north latitude. During the Pleistocene, the marine isotherms apparently shifted intermittently northward and southward, corresponding to glacial and interglacial epochs.

The original species in the North Pacific probably responded to these climatic changes in various ways, either adapting or migrating or a combination of both. The major lines of dispersal from the North Pacific center of origin are visualized as follows.

1. Emigrants along the west side of the Pacific basin gave rise to present day forms in the Sea of Okhotsk and the Sea of Japan.

2. Some ancestral populations presumably continued southward into the Indian Ocean giving rise to the existing Indian and African species. The two South American species may have derived from this line. This hypothesis is supported by the similarity of many species along the postulated migratory route from the North Pacific center of origin southward along the Asiatic coast, around the Malayan Peninsula to India, then westward to Africa, and around the Cape of Good Hope to west Africa and South America. In order of occurrence, the similar species along this line are *S. laevidorsalis* and *S. harfordi* (Sea of Japan), *S. variegata* (Indochina, Ceylon, Chilka Lake), *S. hirtipes* (Africa), and *S. marplatensis* (South America). All of these are more or less smooth bodied, all have the frontal margin of the head entire (or with only a slight median excavation), and all show an emarginate pleotelson. They are so similar that Monod (1931) has suggested that these forms comprise "un groupe '*hirtipes*'." The other South American species, *S. sphaeromiformis* Mañé-Garzón (1946), is somewhat similar to Monod's *hirtipes*-group, being smooth bodied with an entire frontal margin and an emarginate (slightly) pleotelson, but its broadly ovate, depressed form sets it apart. This distinction does not preclude the possibility that it could have evolved from the same line. Also, Monod's inclusion of *S. laticauda* of San Francisco Bay, California, in his hirtipes group is not inconsistent with our hypothesis, as will become apparent under point 5.

3. Emigrants along the east side of the Pacific basin gave rise to the present-day species of *Synidotea* occurring along the western coast of North America from Alaska to Baja California.

4. A few species, represented today by *Synidotea bicuspida* and *S. nodulosa*, dispersed northward through the Bering Strait (open since late Pliocene) and spread both eastward and westward along the Arctic coasts of North America and Eurasia to the far North Atlantic and to the Barents Sea, respectively.

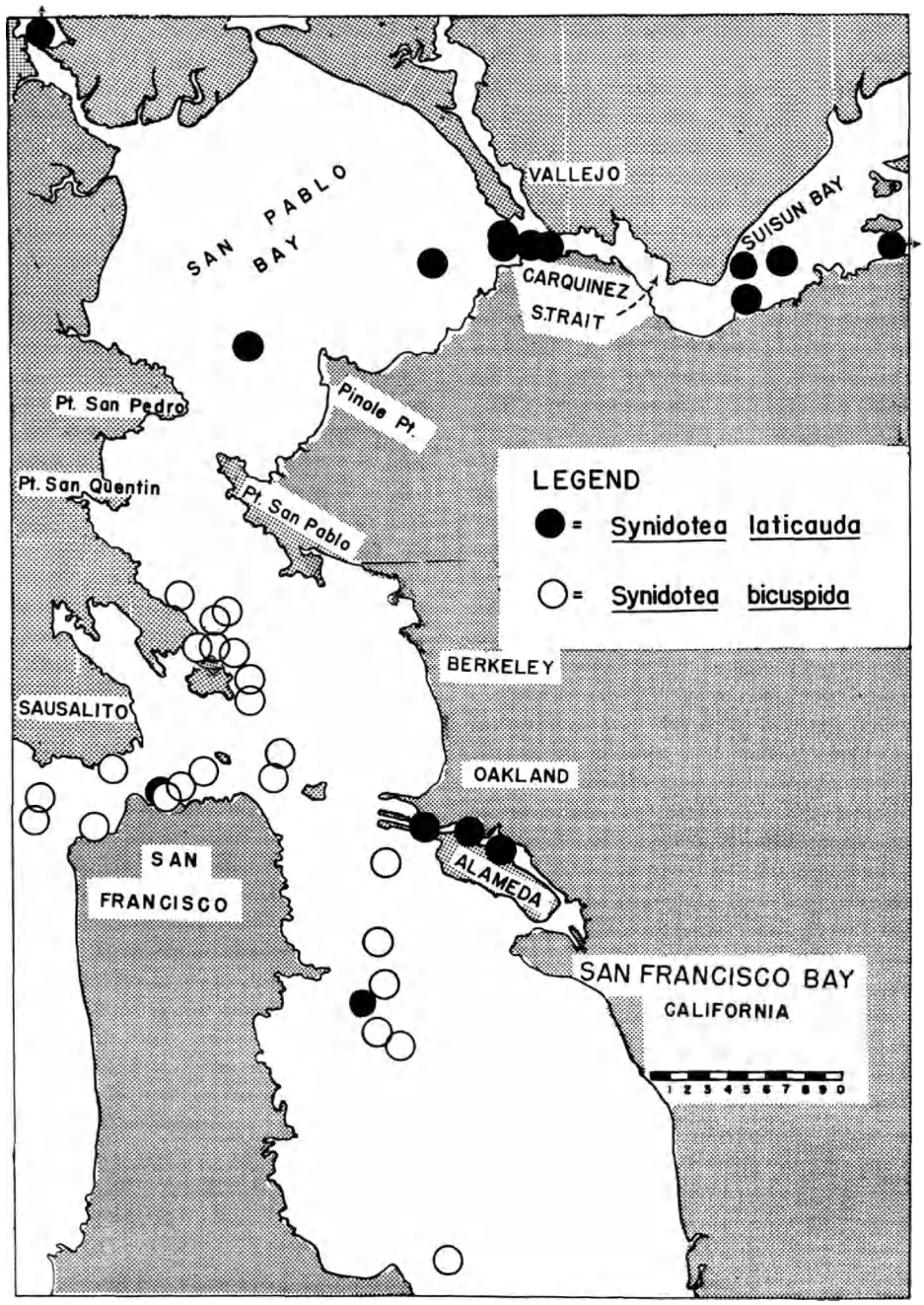

FIGURE 2.—Distribution of *Synidotea laticauda* and *S. bicuspida* in San Francisco Bay. Note that *S. laticauda* occurs mainly in the warmer, less saline parts of the bay system, probably as a relict species (see text, page 10). *S. bicuspida* occupies the mouth and southern arm of the bay, and extends northward along the Pacific coast to Alaska and circumpolar regions.

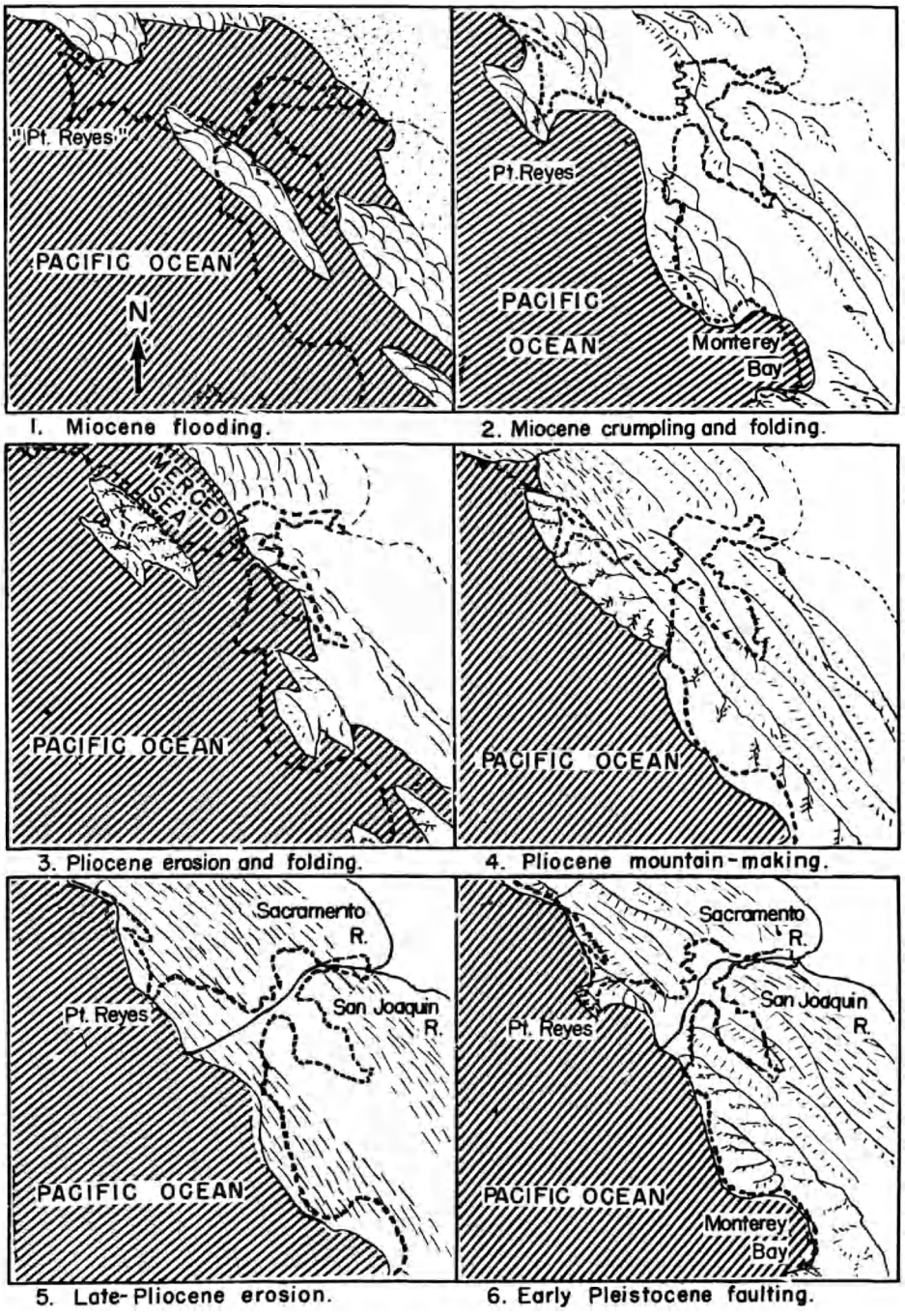

FIGURE 3.—Evolution of the central California landscape during the Cenozoic. The present shoreline of the coast and San Francisco Bay is indicated by dashed lines (see also Figure 2). (Adapted from Howard 1962.)

Apparently, however, they did not quite reach the western European coast from either direction (Gurjanova, 1933b). The migration of species from the North Pacific to the North Atlantic apparently followed the predominantly eastward trend noted by Durham and MacNeil (1967) for other invertebrates, notably mollusks. They attribute this largely unidirectional migration to the prevailing eastward current pattern in the Arctic. They also suggest that the marked dominance of Pacific emigrants may be a function of the richer biotas of the Pacific than those of the Atlantic. Briggs (1970) also comments on the relatively depauperate contemporary shore faunas of the North Atlantic and further suggests that this ocean ". . . has provided its marine fauna a more rigorous environment than the North Pacific," primarily, more severe temperature alterations during the Pleistocene. The distributional data for *Synidotea* supports the assumptions of these authors.

5. Some ancestral species emigrated southward along both sides of the Bering arc, as indicated by the occurrence of three contemporary species on both sides of the Pacific, namely, *Synidotea harfordi, S. bicuspida,* and *S. nodulosa.* As mentioned above, the precursors of the latter two also dispersed northward through the Bering Strait, thus radiating in several directions from their presumed center of origin in the North Pacific.

Present distributions indicate that *Synidotea bicuspida* and *S. nodulosa* are cold-water species, whereas *S. harfordi* is warm-temperate. In line with our previously stated hypothesis of a North Pacific center of origin of the genus followed by radiation and dispersal associated with paleoclimatic changes, we suggest that the ancestral *S. harfordi* originated when North Pacific waters were warm and, being relatively stenothermal, it later retreated southward along both sides of the Bering arc before the advancing cold water from the north. The precursors of *S. bicuspida* and *S. nodulosa,* however, either adapted to, or originated in, the cooling North Pacific waters, and then moved southward with the advancing cold water. They thus followed and replaced the earlier warm-water emigrants in northern latitudes.

On the Asiatic side, the southward emigrating populations of *Synidotea harfordi* reached the now temperate Sea of Japan where their descendants exist today. On the opposite side of the Pacific, they eventually reached as far south as Baja California, leaving detachments along the California coast now represented by populations at Morro Bay and in the San Diego region.

On the west Pacific coast, the ancestral *Synidotea bicuspida* apparently reached the Sea of Japan and evolved the subspecies *S. b. lata*—the only form known and the only locality recorded for this species along the entire Asiatic coast. On the eastern side, it is known from several widely separated localities from Alaska to central California.

The ancestor of *Synidotea nodulosa* seemingly did not migrate as far south on either side of the Pacific as the ancestral *S. bicuspida.* On the Asiatic side, *S. nodulosa* is found in the Sea of Okhotsk; on the North American side, this species is not known south of British Columbia.

The close morphological resemblance between *Synidotea harfordi* and *S. laticauda* and their distinctness from other Californian species clearly indicates a common ancestry despite their present geographical separation. The wide gap between their known ranges (Table 2) can readily be explained by extension of the preceding hypothesis regarding *S. harfordi.* Let us assume that the ancestral, warm-water precursor of this species, retreating slowly southward along the western American coast, arrived in central California before San Francisco Bay was formed. Populations became established in the area and flourished in the warm coastal waters during the successive periods of subsidence, elevation, folding, erosion, and faulting that preceded the ultimate formation of the San Francisco Bay system in the late Pleistocene (Figure 3). They were thus in an advantageous position to move into it as the outside waters became colder, and cold-water species, such as *S. bicuspida,* arrived in the area. There they adapted to the lower salinities and favorable ambient bay temperatures and eventually evolved as *S. laticauda.* If speciation occurred after San Francisco Bay was formed, which seems likely, the origin of *S. laticauda* may be dated as not earlier than the late Pleistocene when local subsidence, coupled with postglacial rises in sea level, inundated the common mouth of the Sacramento and San Joaquin rivers to form it (Howard 1962).

Meanwhile, other populations of the ancestral *Synidotea harfordi* moved down to southern and Baja California, leaving *S. laticauda* as a relict descendant in San Francisco Bay. Outside, they were completely replaced by *S. bicuspida* and other colder water species now living in the area (Figures 1 and 2).

S. bicuspida occurs today along the outer coast and in the central and southern parts of San Francisco Bay where it overlaps slightly with *S. laticauda*. Because of the tidal influx through the narrow Golden Gate and relatively minor freshwater dilution in those parts of the bay occupied by *S. bicuspida,* salinities are higher and temperatures lower than in the regions where *S. laticauda* is abundant (Table 5).

Dispersal and Establishment

The above-postulated dispersals doubtless occurred slowly over long periods of geologic time. Being benthic and lacking larvae, these isopods must depend on transport either by natural rafts or currents or both for dispersal over long distances. Such mechanisms leave much to chance. Founding populations would have to be preadapted or able to adapt to conditions of existence in the new locality which might be quite different. Not only would the immigrants have to survive, but they would also have to produce viable offspring in sufficient numbers to establish and maintain the population. The presence among the new arrivals of many females with young in the brood pouch would favor establishment. The availability of open ecological niches, absence or paucity of predators, and reinforcements would also favor colonization.

Several questions regarding the geographical distribution of *Synidotea* remain unanswerable in the present state of our knowledge. How did the genus cross the tropical barrier and reach its present loci in the Southern Hemisphere? Some speculations as to the origin of the two South American species and the lone African species have been presented. But it is difficult to conceive how the genus reached the Tuamotus in the central Pacific where *S. pacifica* occurs as the only member of the genus in the whole South Pacific—separated by thousands of miles of ocean from any other species of *Synidotea*. Future collections, especially in the western Pacific, may help close the gap, but until then the origin of this isolated species must remain a mystery.

Another question is, why is it absent from the seemingly ecologically suitable Australian, Chilean, and European regions? Partial answers may be distance from the supposed North Pacific center of origin and prior occupation of ecological niches in these areas by dominant competitors and predators.

Thermal Distribution

On the point of thermal distribution, the great majority are cold-water forms (Table 3B). Most are rather stenothermal with 23 species found in only one province. Twelve species occupy two provinces, but none more than two.

Although *Synidotea* and valviferans generally do not conform to the rule of tropical diversity, as exemplified by many invertebrates including other isopods, they do fit the generalization that tropical forms tend to be smaller than their cold-water relatives. Sive in valviferans increases poleward (analgous to Bergmann's rule for homoiotherms), and some frigid-zone species are remarkably large (e.g., *Glyptonotus* in the Antarctic and *Saduria* in the Arctic region).

In *Synidotea,* a positive association between size and latitude is clearly indicated, at least in the northern hemisphere (Table 3B). Mean lengths increase progressively poleward from 8.0 $\pm$ 2.2 mm in the five tropical species to 18.8 $\pm$ 2.6 mm in the eight Arctic species, a highly significant difference ($P < 0.01$). The smallest species (*S. pacifica,* 3 mm) is tropical; the largest (*S. bicuspida,* up to 32 mm) is Arctic–Boreal. In the higher latitudes (Boreal to Arctic), the differences in mean length of species in contiguous regions are small and not statistically significant, although consistently in the expected direction. Pooled data show that cold-water species average significantly larger than warm-water species.

In the foregoing analysis of size in relation to latitude, depth was disregarded. It would be desirable, of course, to compare sizes of isopods in the major latitudinal regions at the same depth intervals, as well as sizes within each region at various depths. Unfortunately, the data are too meager for such critical comparisons. For example, no Arctic or Arctic–Boreal species is recorded from shallow water (<10 meters), and there are no depth data for four of the five tropical species. The relationships of size to depth, disregarding latitude, will be analyzed in the following section, and the role of temperature will be discussed.

Bathymetric Distribution

Synidotea ranges from intertidal to depths of nearly 3,000 meters (Table 3C). Nineteen of 30 species for which depths are recorded occur at depths of less

than 100 meters; only three have been found below 1,000 meters.

There is some indication of a relationship between size and depth per se, but this can not be demonstrated statistically from available data. Shallow-water species (<10 meters) average smaller than those of deeper waters (Table 3C), but the difference between means of these two categories (13.7 ± 2.0 mm and 18.1 ± 1.3 mm, respectively) is not quite statistically significant (P = 0.08). Statistical significance could be established, however, if the four small tropical species for which no depth data are available should prove to be shallow-water forms—a strong possibility. Inclusion of their measurements with the known shallow-water species would lower the mean for this group to 12.2 ± 1.8 mm, which is significantly lower than that for the deeper water species (P<0.02). The largest species, *S. bicuspida,* is recorded from 10 to 100 meters.

The reason for increased size in *Synidotea* with latitude and possibly with depth is not readily apparent, but ambient temperature is probably involved. In both cases, larger mean sizes are associated with colder temperatures. Lowered temperatures, of course, reduce metabolic rate in poikilotherms. As Sverdrup et al. (1942) suggest, however, this is counterbalanced by the fact that lowered metabolism lengthens the time required for such animals to reach sexual maturity, thus permitting a longer growing period with resultant larger size. They also state that warm-water animals are relatively smaller, because of more rapid attainment of sexual maturity and more rapid turnover of generations. Other suggestions to account for larger size of cold-water forms include more food and dissolved oxygen, and less competition and predation.

The foregoing analyses of the relationship of size to latitude, depth, and temperatures are somewhat crude. The original data are taken mainly from the literature which usually gives measurements of type-specimens or others which may or may not be representative, and little or no information on size variation, especially upper limits. Depth and temperature data are frequently lacking. The distribution of most species is imperfectly known, some being recorded only from the type-locality. Analyses are based on mean sizes of species, grouped rather broadly because of paucity of data. It would be highly interesting to compare sizes within a single wide-ranging species such as *S. bicuspida* to determine whether a cline in this character can be demonstrated in relation to latitude and depth parameters. Finally, more studies are needed to establish causes for the observed relationships.

Systematics and Ecology of Californian Species

Eight species of *Synidotea* are represented in the coastal waters of California: *S. bicuspida* (Owen), *S. harfordi* Benedict, *S. laticauda* Benedict, *S. magnifica* Menzies and Barnard, *S. calcarea* Schultz, *S. pettiboneae* Hatch, *S. ritteri* Richardson, and a new one herein described. As indicated in the key given below, these species can readily be distinguished by the nature of the sculpturing (if any) on the dorsal surface. Supplementary key characteristics include the emargination (or lack of it) of the frontal margin of the head and apex of the telson. Additional characteristics are given in the detailed descriptions which follow the key. As noted below, some of these are more useful than others.

The appendixes masculinae are of taxonomic value since they show distinct differences among the species examined as well as some similarities which help establish relationships. For example, these stylets are quite similar in *Synidotea laticauda* of San Francisco Bay and *S. harfordi* of southern California (see Figures 4*e* and 6*g*). These two species also closely resemble each other and differ from the remaining six Californian species in lacking tubercles, carinae or other sculpturing on the dorsal body surface, and in the absence of a median notch on the frontal margin of the head. It will be recalled that a special hypothesis was advanced in the zoogeographical section of this paper to account for the close morphological resemblance of these now geographically isolated species. Again, the appendixes masculinae of *S. pettiboneae* and of our new species are rather similar (see Figures 11*d* and 12*d*) and differ from those described in other species. This similarity correlates with the similarity of sculpturing, especially of the head, in these two species, thus confirming their close relationship. Unfortunately, the structure of the appendix masculina is unknown in two closely related species, *S. magnifica* and *S. calcarea,* from southern California; their descriptions are based on female holotypes.

Among the less useful characteristics are mouthparts and the epistomal region which have been valuable in distinguishing Californian species of other

idoteid genera, notably *Idotea*. For instance, the maxillipeds in all Californian *Synidotea* have a single coupling hook, except *S. calcarea* in which it is presumed to be absent as it is neither mentioned nor figured in the description. Also, the frons in all species examined lacks a protruding frontal process; it is completely hidden in dorsal view under the prominent postfrontal ridge or shelf, even in forms with a median frontal notch. In the latter, however, the protruding upper lamina of the clypeus, but not the frons, is visible in dorsal view through the notch.

Certain other relationships may be noted. *Synidotea bicuspida* is intermediate between the smooth and the heavily sculptured forms. All Californian species have emarginate pleons except *S. magnifica* and *S. calcarea* of southern California in which the telson is apically rounded. These resemble *S. bogorovi* of the Sea of Okhotsk in the shape of the telson.

Key to Californian Species of *Synidotea*

1. Body smooth. Head without preocular horns or other projections 2
   Body with tuberculations, carinae or bumps. Head with preocular horns and other processes of various size and shape 3
2. Pleotelson much less than 1/3 longer than broad (pleotelson length measured along middorsal line, width at broadest part near its anterior end). Frontal margin of head transverse or slightly concave with a slight median excavation ..... **1. *S. laticauda***
   Pleotelson at least 1/3 longer than broad. Frontal margin of head transverse or slightly convex with no median emargination ..... **2. *S. harfordi***
3. Apex of pleotelson broadly rounded 4
   Apex of pleotelson broadly emarginate 5
4. Dorsum of head between eyes bearing 2 large, conical tubercles (larger than preocular tubercles). Margins of head and pereon minutely serrated; posterolateral margins of pleotelson denticulate. Eyes lightly pigmented, with few ocelli ..... **3. *S. calcarea***
   Dorsum of head bearing 2 small interocular tubercles (smaller than preocular tubercles). Margins of head, pereon and pleon smooth, not serrate or denticulate. Eyes darkly pigmented, with many ocelli ..... **4. *S. magnifica***
5. Dorsal surface of body with transverse carinae on each pereonal somite, but without tuberculations or bumps. Preocular horns not reaching frontal border of head ..... **5. *S. bicuspida***
   Dorsal surface of body with tubercles. Preocular horns large, extending to or beyond frontal border of head 6
6. Middorsal line of pereon generally lacking tubercles. Preocular horns project forward. **6. *S. ritteri***
   Middorsal line of pereon with at least 1 tubercle on each somite. Preocular horns project laterally 7
7. Lateral borders of first 4 pereonites acute. Each pereonal somite with a transverse row of 3 pointed tubercles ..... **7. *S. pettiboneae***
   Lateral borders of second, third, and fourth pereonites blunt. Pereonal somites beset with small tubercles ..... 8. ***S. berolzheimeri***

1. *Synidotea laticauda* Benedict, 1897

FIGURES 4 and 5

Synidotea laticauda Benedict, 1897, pp. 393–394, fig. 4.—Richardson 1899, p. 849; 1900, p. 228; 1905, pp. 386–387, figs. 425–426.—Filice 1958, p. 186.—Miller 1968, pp. 21–22, fig. 3.—Schultz 1969, p. 67, fig. 75.

DIAGNOSIS.—Cephalon. Preocular horns absent; frontal margin concave or transverse and with slight median excavation; eyes bulge outward, forming part of lateral cephalic margin; tubercles or rugosities lacking.

Pereon. Dorsal surface and lateral margins smooth, lacking rugae, tubercles, or scales; first three pereonites with lateral margins evenly rounded, not sharply angulate; borders of other pereonites fairly straight. Median semilunar or crescentic patterns set off on anterior part of tergum of pereonites 2–4, becoming markedly narrower on posterior pereonites.

Pleon. Apex with medial terminal excavation. Appendix masculina straight, apex bluntly pointed, lateral margin covered with scales. Pleotelson only slightly longer than wide.

GEOGRAPHICAL RANGE.—This species is known only from the San Francisco Bay system, predominantly its northern section, including Oakland Estuary, San Pablo Bay, Carquinez Strait, Suisun Bay, and the mouths of the Petaluma and San Joaquin rivers.

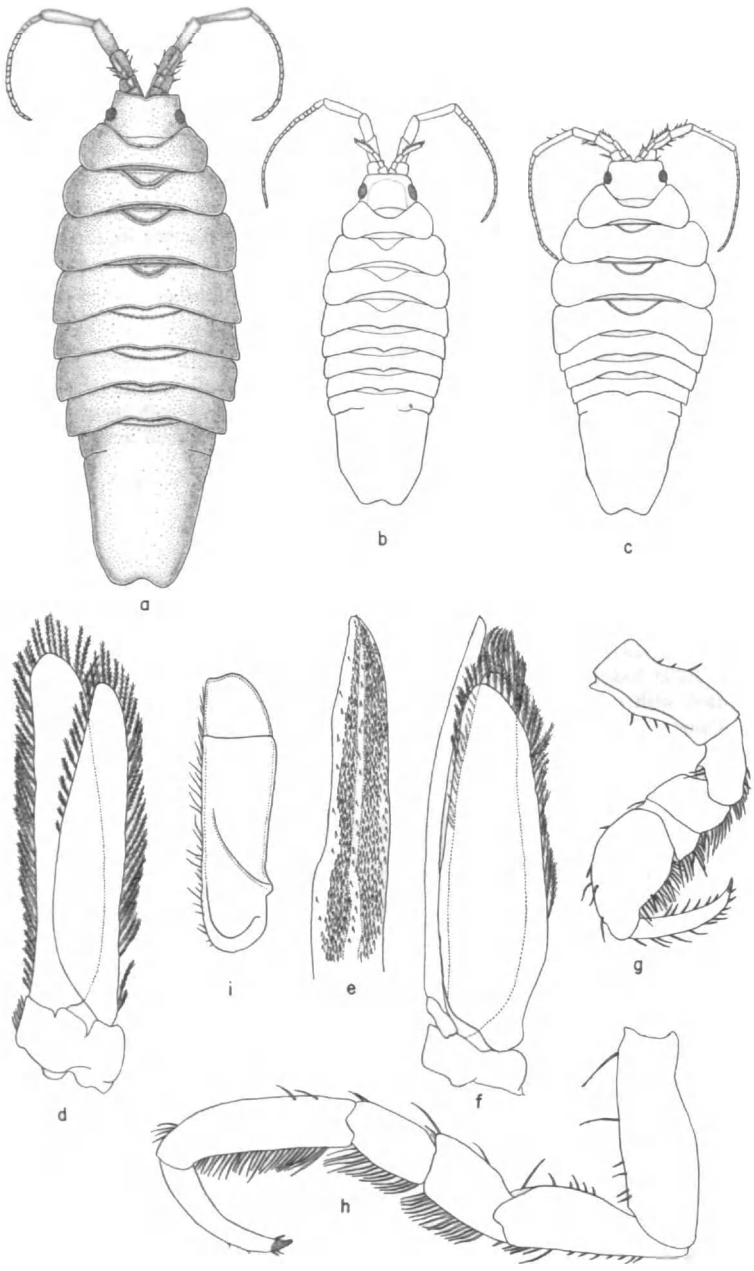

FIGURE 4.—*Synidotea laticauda*: *a*, dorsal view of male; *b*, female; *c*, ovigerous female; *d*, pleopod 1 of male; *e*, tip of appendix masculina; *f*, pleopod 2 of male; *g*, pereopod 1 of male; *h*, pereopod 7 of male; *i*, uropod.

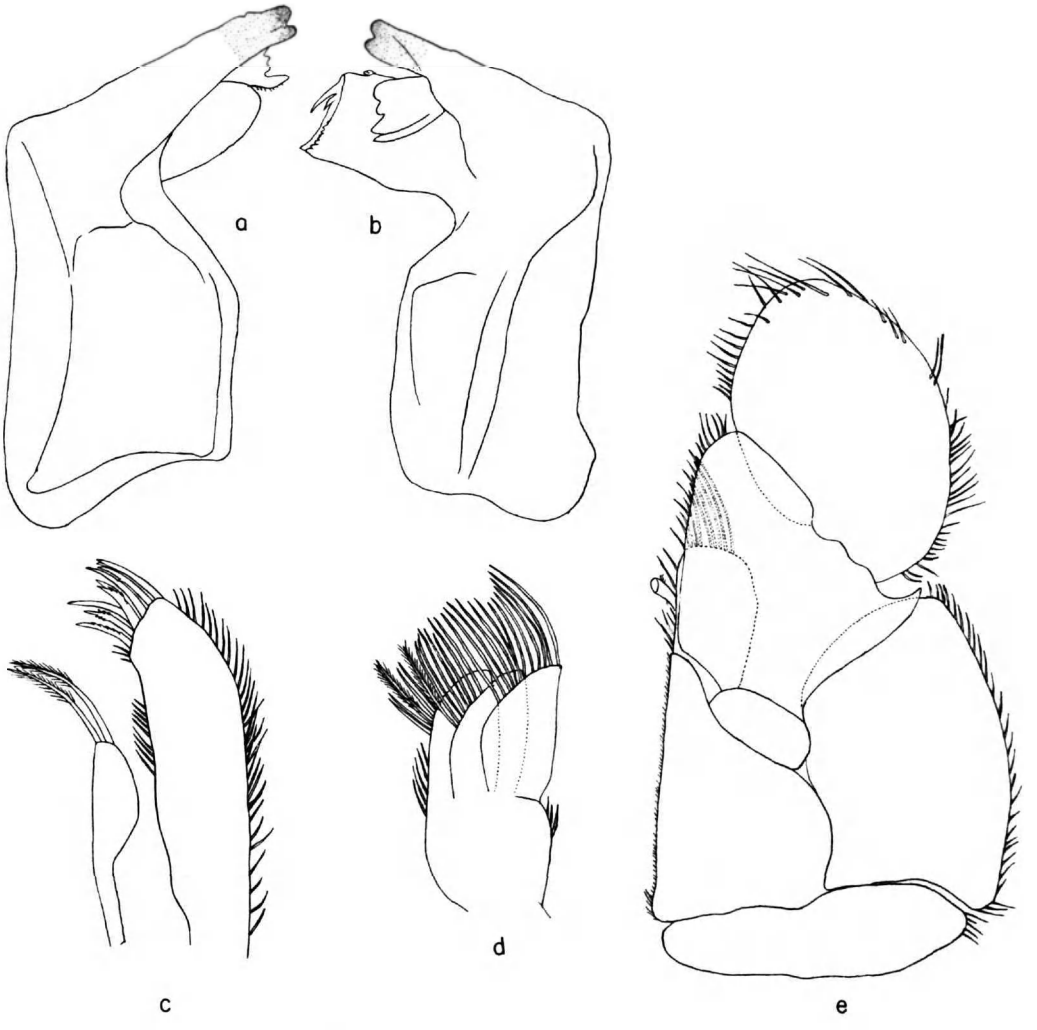

FIGURE 5.—Mouthparts of *Synidotea laticauda*, male: *a* and *b*, right and left mandibles, respectively; *c*, maxilla 1; *d*, maxilla 2; *e*, maxilliped.

LOCALITIES.—*California.*

San Francisco Bay System. "Albatross" dredge stations (Schmitt, 1921, Appendix IIA: 323–379. See also Fig. 2): #5720, 20 February 1912; #5721, 20 February 1912; #5766a, 8 April 1912; #5760, 23 April 1912; #5793, 7 October 1912; #5816, 3 December 1912; #5817, 3 December 1912; #5819, 10 December 1912. South San Francisco Bay: San Francisco Buoy #1, 29 July 1943, M. A. Miller. Central San Francisco Bay: Crissey Field Seaplane Station Buoy CF, 5 August 1943, M. A. Miller; Oakland Estuary, May, June, July, and September 1941, H. W. Graham; Berkeley Yacht Harbor, 2 August 1949, E. Swan.

San Pablo Bay. San Pablo Lighted Buoy #10, 20 July 1943, M. A. Miller. Carquinez Strait: Point Edith Buoy, 26 July 1943, M. A. Miller; Carquinez Strait Restricted Area Buoy, 4 August 1943, M. A. Miller. Suisun Bay: near Seal Island, 29 November 1951, F. Filice. San Joaquin River: near Pittsburg,

July 1961, A. F. Heart. Petaluma River: about 6 miles from mouth, August 1967, A. Kuris and J. Born; 2–3 miles from mouth, 6 February 1968, W. M. Hamner and G. Davies.

REMARKS.—The restricted distribution of this species doubtless accounts for its slight mention in the literature and its simple synonymy.

The most distinctive features of *Synidotea laticauda* are its relatively wide pleon, smooth body, and the absence of preocular horns. In the latter two respects, it closely resembles *S. harfordi*. Only its relatively wide pleon, and the concave and medially excavated frontal margin of its head, distinguish it from *S. harfordi*. Because of the great morphological similarity between these two geographically isolated species, it has been suggested (page 10) that *S. laticauda* is a relict descendant of a once widespread *S. harfordi* or of a common ancestral species similar to it.

As usual with quantitative characters, there is considerable variation in relative lengths of the pleotelson and some overlapping between *Synidotea harfordi* and *S. laticauda* with respect to this character (Table 4). Intraspecific variations are due to age and sex with ovigerous females in general having wider pleotelsons than males and non-ovigerous females. Mean values for pleotelson indices (median length/greatest width) in each of these three categories differ greatly between the two species, however, and the differences are highly significant, both statistically and systematically. It should be easy to distinguish at least between adults of *Synidotea laticauda* and *S. harfordi* on the basis of pleotelson indexes alone, although an occasional specimen with an intermediate pleotelson might be difficult to identify.

2. Synidotea harfordi Benedict, 1897

FIGURE 6

Idotaea marmorata Harford, 1877, p. 117.

Synidotea harfordi Benedict, 1897, p. 402, fig. 13.—Richardson 1899, p. 849; 1905, pp. 387–388, figs. 427, 428.—Gurjanova 1936, pp. 163–164, 266, fig. 100.—Schultz 1969, p. 67, fig. 76.

DIAGNOSIS.—Cephalon. Preocular horns absent; frontal margin transverse or slightly convex, with no median emargination; eyes bulge outward, forming part of contour of lateral margin; tubercles or rugae lacking.

Pereon. Dorsal surface and lateral margins smooth, lacking rugae, tubercles, or scales; first three pereonites with lateral margins evenly rounded, not sharply angulate; borders of other pereonites straight. Median dorsal pattern on pereonites 2–4 triangulate, rather than rounded posteriorly as in *Synidotea laticauda*.

Pleon. Posterior border with a median excavation. Appendix masculina straight, apex bluntly pointed, lateral margin scaly. Pleotelson about one-fourth longer than its greatest width, appearing much longer than wide.

GEOGRAPHIC RANGE.—Morro Bay, California, to Magdalena Bay, Baja California, Mexico; Sea of Japan.

LOCALITIES.—

California. Morro Bay, 23 January 1959, M. O. Brown. La Jolla: 18 August 1946, gravid female from *Phyllospadix* roots, R. J. Menzies and R. J. Berman; June, 1949, 3 females among seaweed cast up into tide pool, T. Bowman. Pacific Beach, 1 February 1943, R. J. Menzies.

TABLE 4.—*Pleotelson indices (PI = length/width) in two closely related species of* Synidotea

Species	*Females*		*Males*	*All*
	Ovigerous	*Non-ovigerous*		
S. laticauda				
No. examined	66	120	43	229
Mean PI ± S.E.	1.13 ± 0.01	1.24 ± 0.01	1.20 ± 0.01	1.20 ± 0.007
Range PI	1.00–1.38	1.05–1.43	1.00–1.38	1.00–1.43
S. harfordi				
No. examined	3	1	2	6
Mean PI ± S.E.	1.46 ± 0.03	2.08	1.47	1.57 ± 0.11
Range PI	1.42–1.52	.....	1.38–1.55	1.38–2.08

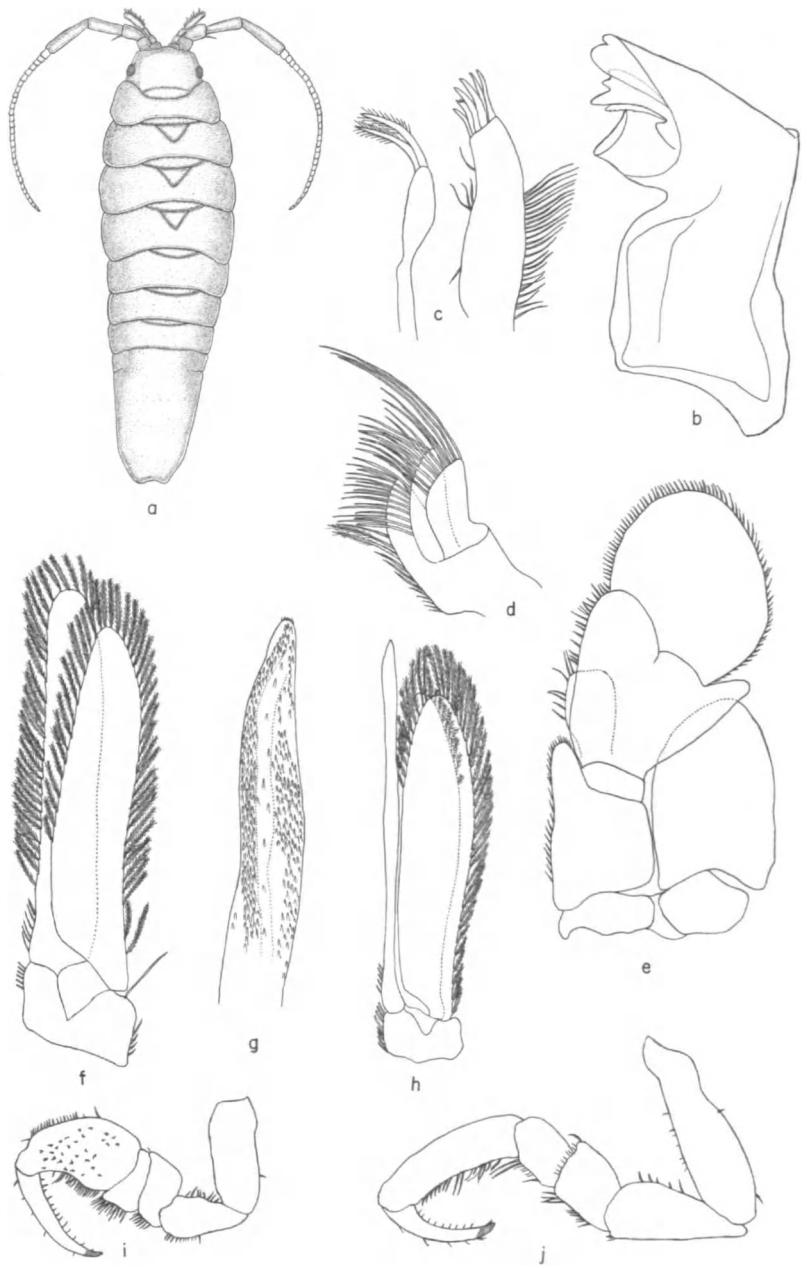

FIGURE 6.—*Synidotea harfordi*, male: *a*, dorsal view; *b*, left mandible; *c*, maxilla 1; *d*, maxilla 2; *e*, maxilliped; *f*, pleopod 1; *g*, tip of appendix masculina; *h*, pleopod 2; *i*, pereopod 1; *j*, pereopod 7.

Mexico. Cedros Island, 11 July 1953, male, intertidal, L. Berner.

REMARKS.—Harford's original description of this species, under the name of *Synidotea marmorata*, contains mainly generic characters. It is considered applicable, however, because it is the only intertidal species of the three species of the genus occurring in southern California and Baja California, and the only one of them with an incised telson. Benedict (1897) gave the species its present name upon discovering that Harford's name was preoccupied by *S. marmorata* Packard, a name now considered a junior synonym of *S. bicuspida* (Owen).

Marjorie Brown's discovery (unpublished) of *Synidotea harfordi* in Morro Bay, California, extends the previously known northern limit of this species in the eastern Pacific (formerly the San Diego Bay region) some 300 miles northwesterly along the California coast. Her find also reduces by half the former 600-mile gap between it and its closest relative, *S. laticauda* of San Francisco Bay. More significantly, this extends the thermal distribution of *S. harfordi* from the warm–temperate waters (Western American Transition) of southern and Baja California with their distinctive fauna (Garth 1955) into the colder waters (West American Temperate) north of Point Conception (34½° north latitude, 13°C. isocryme). This major thermal breakpoint between these two provinces lies about 70 miles south of Morro Bay. The discovery of *S. harfordi* in temperate waters of California was not too surprising in view of Gurjanova's (1933) report of this species from equivalent waters of the Japanese Sea (East Asiatic Temperate).

The disjunct and spotty distribution of *Synidotea harfordi* on both sides of the Pacific and the long gap between it and the closely related *S. laticauda* of San Francisco Bay are explained by a hypothesis presented in the zoogeographical section of this paper (page 10).

3. *Synidotea calcarea* Schultz, 1966

FIGURE 7

Synidotea calcarea Schultz, 1966, p. 21, pl. 15; 1969, p. 68, fig. 78.

DIAGNOSIS.—Body. Covered with fine short hairs. Margins of head and pereonal segments minutely serrate.

Cephalon. Preocular and anteromedial tubercles submarginal; dorsum bearing 2 large conical tubercles between eyes. Eyes lightly pigmented, with few ocelli.

Antenna 1 with 4 joints; antennae 2 with 5 peduncular and 6 flagellar articles. Mandible with toothed incisor; lacinia mobilis with setal row; molar process toothed. Endopod of maxilla 1 with 2 sensory projections. Maxillipedal palp much wider than endite; endite with several sensory setae.

Pereon. Pereonites bear 2 or 3 dorsolateral longitudinal rugae with 2 large mediolateral tubercles. Pereopod 1 with long unguis; dactylus and propodus somewhat chelate. No pereopods bearing projecting flanges on basis.

Pleon. Bluntly rounded, spatulate, with several small teeth on posterolateral margins. Pleotelson crossed by 3 suture lines, indicating former presence of 4 segments; first pleonal suture continuous with grooves in lateral margins of pleotelson. Uropods with 2 sensory dorsolateral setal spines.

GEOGRAPHICAL RANGE AND LOCALITIES.—Known only from type locality, Tanner Canyon, a submarine canyon off southern California, 32°37′54″ north latitude, 118°58′40″ west longitude. Depth 813 m; green mud and sand substrate.

REMARKS.—The apically rounded, spatulate pleotelson of *Synidotea calcarea* and *S. magnifica* distinguishes them from all other Californian species of the genus which have excavated telsons. Both closely resemble *S. bogorovi* Gurjanova (1955) of the Okhotsk Sea in body shape and pattern of sculpturing. These three species show progressive reduction in pereonal rugae with depth, possibly also with ambient temperature; *S. magnifica* (55–92 meters) is much more rugose than *S. calcarea* (813 meters) which is more sculptured than *S. bogorovi* (2,300 meters). In the Okhotsk species, the flagellum of the second antenna has more articles (15) than that of the Californian species (8 in *S. magnifica*, 6 in *S. calcarea*), and its telson is more truncate than theirs. The two Californian species can be distinguished from each other by the characteristics given in the key and in the above remarks.

4. *Synidotea magnifica* Menzies and Barnard, 1959

FIGURE 8

Synidotea magnifica Menzies and Barnard, 1959, pp. 26–27, figs. 20, 21.—Schultz 1969, p. 69, fig. 79.

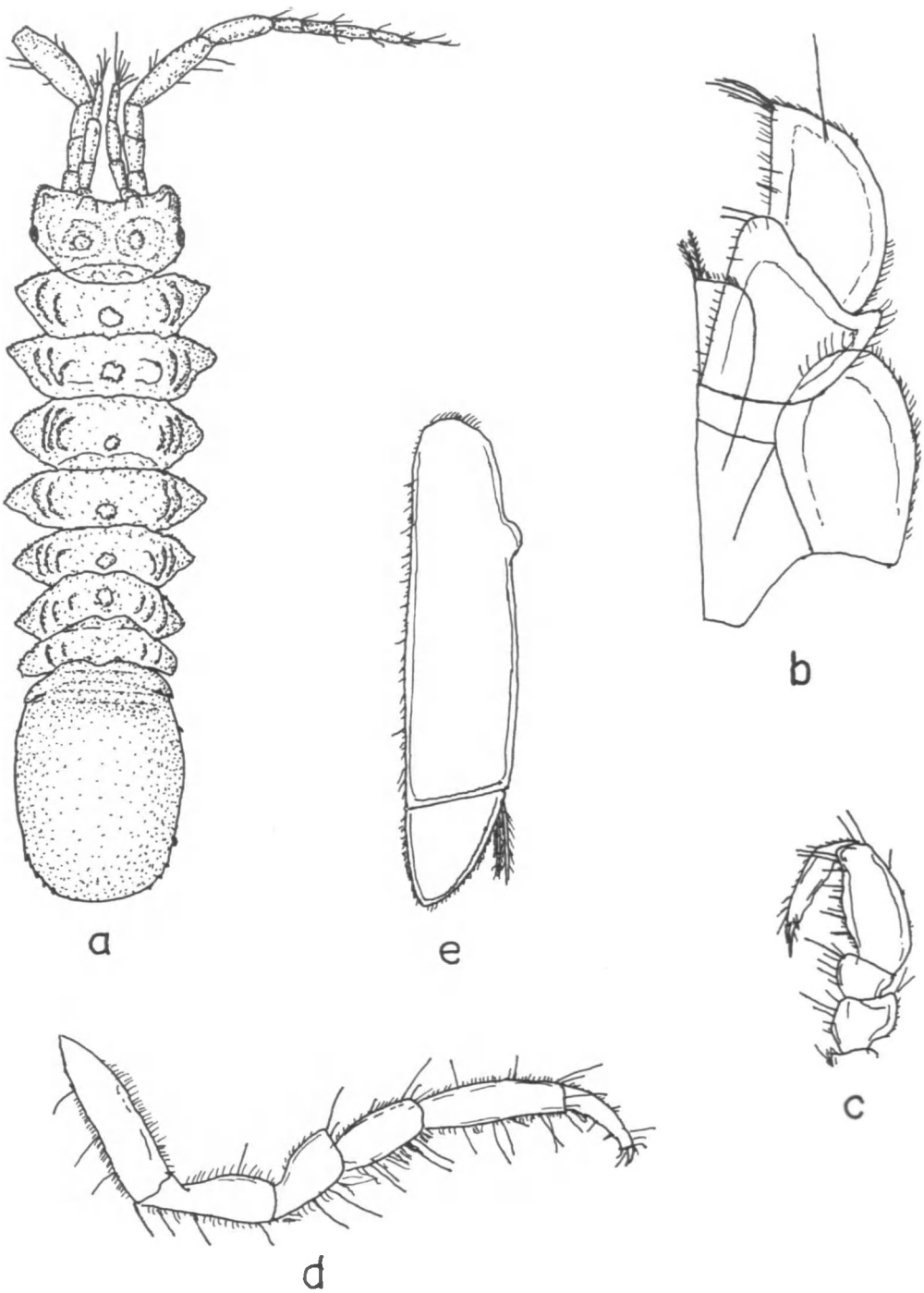

FIGURE 7.—*Synidotea calcarea*, female: *a*, dorsal view; *b*, maxilliped; *c*, pereopod 1; *d*, pereopod 7; *e*, uropod. (After Schultz, 1966)

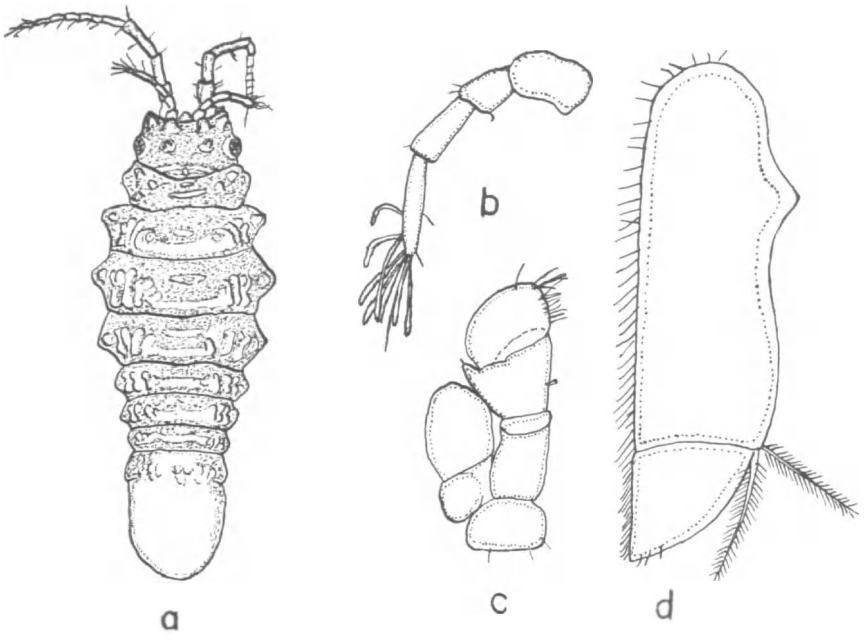

FIGURE 8.—*Synidotea magnifica*, female: *a*, dorsal view; *b*, first antenna; *c*, maxilliped; *d*, uropod. (After Menzies and Barnard 1959)

DIAGNOSIS.—Cephalon. Tubercle in front of eye and anteromedial tubercles submarginal; dorsum of head bearing a pair of smaller tubercles between eyes; anterolateral preocular processes of head not hornlike.

Pereon. Body segments bearing 3–4 dorsolateral longitudinal rugae; anterior segments tuberculate. Pereopods 2–6 bear flange on upper third of article 2.

Pleon. Apex bluntly rounded, spatulate.

GEOGRAPHICAL RANGE.—Southern California coastal shelves: Point Conception to Oceanside.

LOCALITIES.—Menzies and Barnard (1959) report this species from 12 stations with a depth range of 30–50 fathoms (55–91 meters).

REMARKS.—As mentioned for the preceding species, the affinities of *Synidotea magnifica* are with another southern Californian species, *S. calcarea*, and a deep-water form from the Sea of Okhotsk, *S. bogorovi*. All have spatulate pleotelsons.

5. *Synidotea bicuspida* (Owen 1839)

FIGURE 9

Idotea biscuspida Owen 1839, p. 92, pl. 27, fig. 6.—Streets and Kingsley 1877, p. 108.

Idotaea consolidata Stimpson 1856, p. 97; 1857, p. 502.

Idotaea marmorata Packard 1867, pp. 296–297, pl. 8, fig. 6.—Whiteaves 1875, p. 262.

Idothea rugulosa Buchholz 1874, p. 285.

Idotaea pulchra Lockington 1877, p. 45.

Synidotea bicuspida.—Harger 1879, p. 160.—Sars 1885, p. 116, pl. 10, figs. 24–26.—Benedict 1897, pp. 391–392, fig. 1.—Richardson 1899, p. 228; 1905, pp. 385–386, fig. 424; 1909, p. 110.—Hatch 1947, p. 219 [*"biscuspida* Owen"].—Schultz 1969, p. 63, fig. 67.

Synidotea incisa Sars 1880, p. 433.

Edotea bicuspida.—Miers 1881, p. 66.

Synidotea marmorata.—Benedict 1897, pp. 392–393, fig. 2.—Richardson 1901, p. 542; 1905, p. 384, fig. 422.—Ortman 1901, p. 153.—Gurjanova 1936, pp. 154–155, 267, fig. 90.—Schultz 1969, p. 64, fig. 68.

Synidotea macginitieii Maloney 1933, pp. 144–146, fig. 1.

Synidothea bicuspida.—Gurjanova 1936, pp. 152–153, 267, fig. 88.

Synidothea bicuspida var. *lata* Gurjanova 1836, pp. 153–154, 267, fig. 89.

DIAGNOSIS.—Cephalon. Prefrontal lobes small, close to frontal margin; frontal margin usually slightly concave, with slight median excavation; eyes swollen, but may or may not extend beyond lateral margin; 2 minute tubercles located toward front of head near midline.

Pereon. Covered with minute scales, particularly evident along margins; each pereonite with a slight

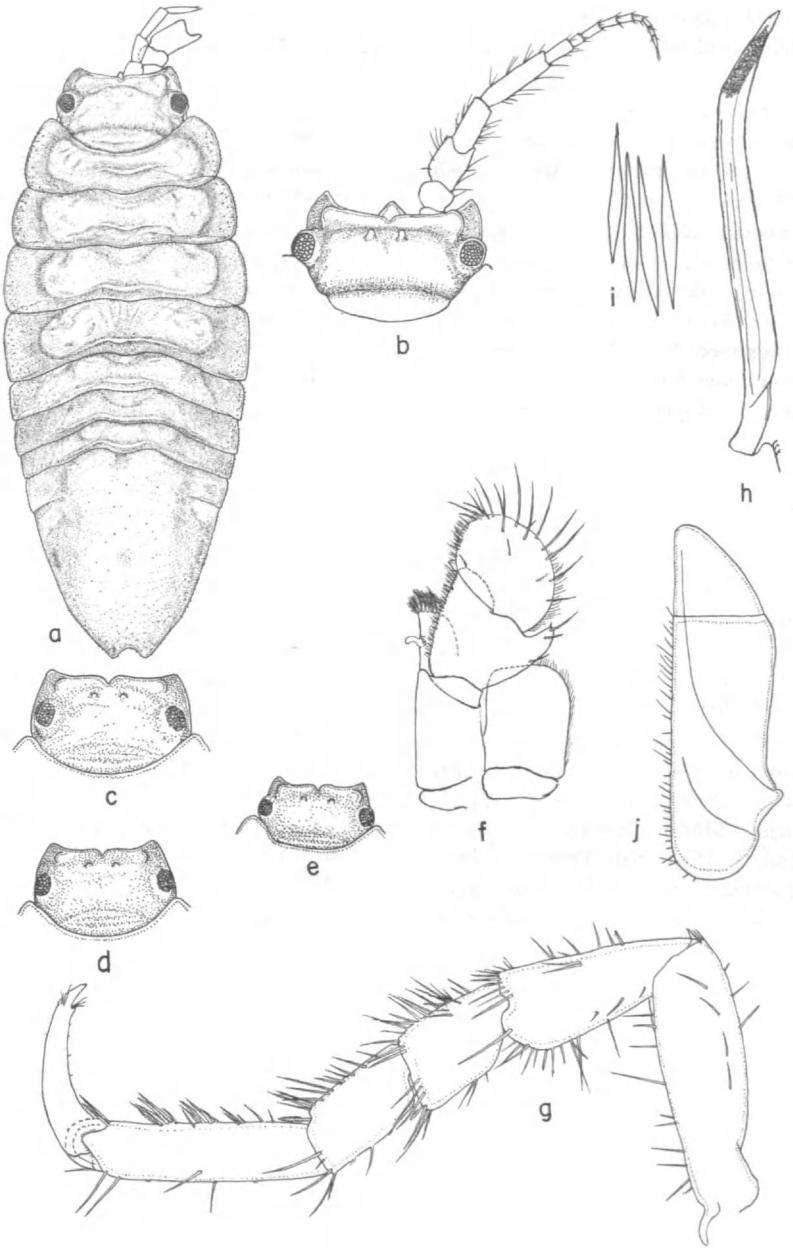

FIGURE 9.—*Synidotea bicuspida: a*, dorsal view of young male; *b*, head of female; *c*, head of adult male; *d*, head of young male; *e*, head of small ovigerous female; *f*, maxilliped; *g*, pereopod 7; *h*, appendix masculina; *i*, scales at apex of appendix masculina; *j*, uropod. Drawings are of topotypes and homeotypes of *S. macginitiei* Maloney taken 14 December, 1912 from mud in San Francisco Bay at *Albatross* Station D5821 USNM 53165) which had been determined by Pearl H. Boone as *S. laticauda*. Maloney's species is herein assigned to the synonymy of *S. bicuspida* (see page 20).

transverse ride near its posterior border; first two pereonites with lateral margins evenly rounded, not sharply angulate; borders of other pereonites generally straight.

Pleon. Posterior border with median excavation. Appendix masculina curved medially near apex which is pointed; ventrolateral margin near apex densely covered with spines.

GEOGRAPHICAL RANGE.—*Synidotea bicuspida* is a circumpolar Arctic–Boreal–Temperate species, which is known on the Pacific coast as far south as central California, and on the Atlantic coast as far south as Labrador. Gurjanova's records (1933, 1936) indicate that it is a prominent member of the isopod fauna of the Arctic Ocean. A subspecies, *S. bicuspida lata,* occurs in the Sea of Japan.

LOCALITIES.—

Washington. San Juan Islands and vicinity: San Juan Channel, Puget Sound, 16 July 1928, 20 meters, K. L. Hubbs; Shoal Bay, Mud Bay, Lopez Sound, 23 July 1952, Beam Trawl, L. B. Holthuis; Friday Harbor, 16, 31 August and 2 September 1949, J. L. Mohr; Whidby Island, Partridge Bay, 13 meters, M. Pettibone. Clallam County, Lapush, intertidal, 29 August 1969, M. A. Miller.

California. Sonoma County: Bodega Rock, 21 meters, summer 1968, R. Sikora; Bodega Bay, near entrance, 9–10 meters, August 1946, July, August 1947, R. J. Menzies. Marin County: off Estero Americano, 23 January 1948. San Francisco Bay: "Albatross" dredge stations (Schmitt 1921, Appendix IIA: 323–379. See also fig. 2): #5704, 1, 2 February 1912; #5705, 6 February 1912; #5711, 16 February 1912; #5712, 16 February 1912; #5724, 6 March 1912; #5727, 8 March 1912; #5731, 11 March 1912; #5732, 11 March 1912; #5733, 11 March 1912; #5738, 13 March 1912; #5739, 13 March 1912; #5741, 18 March 1912; #5742, 18 March 1912; #5745, 18 March 1912; #5767(a), 9 April, 1912; #5776(b), 17 April 1912; #5779(a), 8 May 1912; #5799, 29 October 1912; #5805, 30 October 1912; #5821, 17 December 1912; #5828, 30 January 1913; #5830, 21 March 1913.

REMARKS.—The synonymy of *Synidotea bicuspida* (Owen) indicates more than the usual nomenclatural confusion so often associated with an early described, widely distributed, variable species. Much of the tangled taxonomy resulted from the failure of Benedict (1897) and subsequent American authors, notably Richardson (1905), to follow completely Miers' (1881) synonymy of this species. Miers erred only in placing it in the genus *Edotea,* from which it was correctly removed and transferred to *Synidotea* by Benedict. With this amendment and some additions, we accept Miers' synonymy in full. In the following discussion, we shall analyze several difficult cases and give the bases for our decisions.

Miers (1881) referred *Idotaea consolidata* Stimpson to the synonymy of Owen's *bicuspida,* but Benedict and his followers did not concur and compounded the error by applying the name *consolidata* to a strikingly different species of *Synidotea.* Menzies and Miller (1954) assigned Benedict's misidentified form to *S. pettiboneae* Hatch, 1947 (see later discussion of that species). In our opinion, Miers was correct in his interpretation of Stimpson's *consolidata* for the following reasons:

1. Stimpson (1857: 503) described in his specimens, "a sharp, slightly elevated transverse ridge across the thorax on each segment near its posterior margin." These ridges are characteristic of *S. bicuspida,* which otherwise has an unsculptured pereon.

2. Stimpson did not mention the transverse row of three prominent tubercles on each pereonal tergite which Benedict, Richardson, and others describe in their version of *consolidata* and which are characteristic of *S. pettiboneae.* Stimpson surely would have noted these conspicuous tubercles had they been present on his specimens.

3. Distributional and locality data, though not conclusive alone, reinforce the morphological evidence that the *consolidata* of Stimpson and that of Benedict and his followers are distinct species, now recognized as *S. bicuspida* and *S. pettiboneae,* respectively. Stimpson's description was based on specimens taken from sandy bottom at 10 fathoms (about 18 meters) near the entrance of San Francisco Bay, where *S. bicuspida* has often been found (Figure 2). The specimens presumed by Benedict to belong to Stimpson's species were taken about 100 miles southward at Pacific Grove, bottom and depth unspecified. There is no record of *S. pettiboneae* in San Francisco Bay or its entrance, although it does occur both north and south of that area, usually on outer coastal reefs.

Benedict (1897) and his followers, including Richardson (1905), also did not recognize Miers' referral of *Idotea marmorata* Packard to Owen's

bicuspida, but maintained it as a distinct species of *Synidotea.* Descriptions and figures given by Benedict (1897: 391–392), however, indicate that the distinction is based on body proportions, *marmorata* being smaller and slightly narrower with thinner epimera than *bicuspida* and having relatively longer and more slender antennal joints. Such differences among isopods are suspect as criteria for distinguishing species; size and shape often vary with age, sex, and breeding condition (ovigerous females are usually wider than non-gravid females and males). Small or unrepresentative samples may lead to erroneous conclusions. Unless found statistically significant or clearly correlated with other characters, slight differences in bodily proportions or size should not be used for taxonomic distinctions. Since *marmorata* is only found in the North Atlantic whereas *bicuspida* occurs in the Pacific and Arctic oceans, it might be argued that the above-mentioned differences are associated with their distribution. In support of this argument is the fact that Gurjanova's (1936) variety or subspecies, *S. bicuspida lata,* is broader than the species proper and that it is isolated from the latter in the Sea of Japan. In this instance, however, there are also other morphological differences so that some taxonomic distinction is warranted, whereas no other differences are indicated in the case of *marmorata.* Hence, we accept Miers' disposition of *marmorata* as a synonym of *bicuspida.*

Maloney (1933) distinguished his *Synidotea macginitiei* from *S. bicuspida* (Owen) on variable characteristics, especially the number of apical setae on the maxillae. This character shows considerable developmental variation. Examination of specimens identified by Maloney indicates that they are probably identical with *S. bicuspida.* If so, Monterey Bay, where Maloney's specimens were taken, is the only record of *S. bicuspida* south of San Francisco Bay and its southern limit.

6. *Synidotea ritteri* Richardson, 1904

FIGURE 10

Synidotea ritteri Richardson, 1904, pp. 219–220, figs. 99a, 100, 101a; 1905, pp. 377–378, figs. 409–410.—Hatch 1947, p. 220, pl. 8, fig. 98.—Menzies and Miller 1954, pp. 144, 154.—Schultz 1969, p. 64, fig. 69.

DIAGNOSIS.—Cephalon. Preocular horns large, projecting well beyond frontal margin; frontal border markedly excavate medially; eyes bulging, forming part of lateral contour; a pair of large spiniform tubercles anterior and medial to eyes; behind these is another pair of swollen tubercles.

Pereon. Dorsolateral surfaces of each somite with 2–4 rugosities in a transverse row; first two pereonites with lateral borders evenly rounded, not sharply angulate; borders of others straight.

Pleon. Posterior border with median excavation. Appendix masculina straight and pointed near apex which bears 2 setae, spines or scales lacking. Pleotelson slightly wider than long.

GEOGRAPHICAL RANGE.—Cox Bay, Vancouver Island, British Columbia, to Lands End, San Francisco, California.

LOCALITIES.—

British Columbia. Vancouver Island, Cox Bay, 15, 16 October 1970, M. A. Miller.

Oregon. Coos County, Coos Head, intertidal, 1940, G. M. Shearer.

California. Sonoma County: Goat Rock, 23 September 1968, J. Bodle; Shell Beach, intertidal, 10 July 1967, M. A. Miller; Schoolhouse Beach, intertidal, 24 September 1968, J. and J. Bodle; Bodega Head, 8 August 1967, J. Brill. Marin County: Dillon Beach, January 1935, O. Hartman; 15 May 1947, M. Barr; on algae, bryozoans, and hydroids (especially *Aglaophenia*), 1946–1947, R. J. Menzies; 26 October 1954, M. A. Miller and J. Downey.

REMARKS.—Richardson's (1904) original description of *Synidotea ritteri* was sufficiently lucid to permit its subsequent recognition, and no taxonomic complications have been encountered. Its most distinctive features are the highly developed, forward and upward projecting preocular horns and the dorsolateral pereonal rugosities. Generally, middorsal tubercles are lacking on the pereon, but some specimens show a low tubercle on the middorsal line, particularly on the anterior four pleonites. Richardson does not mention any sculpturing on the pereon. The apex of the appendix masculina is exceptionally simple, unlike that of the other Californian species.

This species resembles *Synidotea pettiboneae* and *S. berolzheimeri,* especially in the sculpturing on the head.

7. *Synidotea pettiboneae* Hatch, 1947

FIGURE 11

Synidotea consolidata.—Benedict, 1897, p. 393, fig. 3.—Richardson 1899, p. 848; 1900, p. 227; 1905, pp. 383–

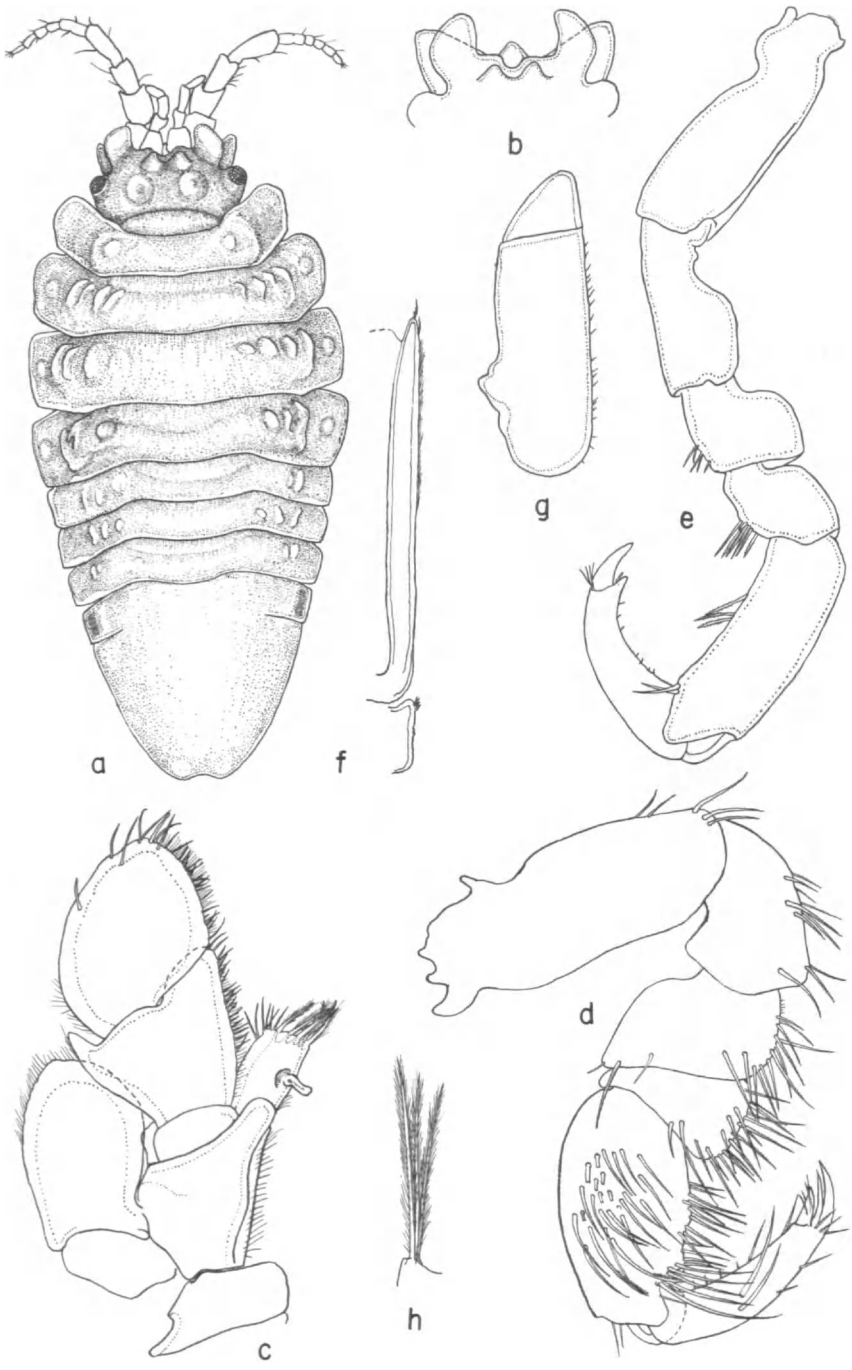

FIGURE 10.—*Synidotea ritteri*, male: *a*, dorsal view; *b*, anterior part of head; *c*, maxilliped; *d*, pereopod 1; *e*, pereopod 7; *f*, appendix masculina; *g*, uropod; *h*, setae at apex of uropodal sympod.

384, figs. 420, 421.—Hatch 1947, p. 219.—Menzies and Miller 1954, pp. 144, 154.—Schultz 1969, pp. 65–66, fig. 72.

Synidotea pettiboneae Hatch, 1947, p. 221, pl. 14, figs. 168, 169.—Menzies and Miller 1954, p. 154.—Schultz 1969, p. 65, fig. 70.

DIAGNOSIS.—Cephalon. Preocular horns large but directed laterally, rather than frontally (as in *S. ritteri*), and accordingly extend only slightly beyond frontal margin; frontal border slightly excavate between preocular horns; eyes bulging and extending outward as part of lateral contour; 2 large spiniform tubercles in front of, and medial to, eyes; behind these is another pair of more swollen tubercles.

Pereon. Dorsolateral surface of each pereonite with a transverse row of 3 sharp tubercles; pereonites 1–3 with lateral margins sharply angulate; borders of others become progressively less angulate posteriorly.

Pleon. Posterior border with median excavation. Appendix masculina flattened and expanded near apex, with lateral and medial borders near expanded areas serrated, apex pointed. Pleotelson slightly wider than long.

GEOGRAPHICAL RANGE.—Neah Bay, Washington to Pillar Point, San Mateo County, California.

LOCALITIES.—

Washington. Clallam County: Neah Bay, 27–55 meters, 6 July 1940, M. Pettibone (University of Washington collections of M. Hatch); Lapush, intertidal, 29 August 1969, M. A. Miller.

California. Sonoma County, Shell Beach, 14 August 1968, J. Bodle. Marin County: Dillon Beach, intertidal with hydroids and bryozoans, October 1947, R. J. Menzies; 0.5–1.0 mile west of Dillon Beach, 9–10 meters, 11 July 1947, R. J. Menzies; intertidal on *Aglaophenia* (with our later described new species), 12 June 1941, G. M. Schreiber. San Mateo County, Pillar Point, intertidal, 4 June 1939, W. M. Marshal. Monterey County, Pacific Grove (Benedict 1897).

REMARKS.—It seems apparent from the original description of *S. consolidata* that Stimpson (1856, 1857) was referring to the species *Synidotea bicuspida* (Owen) and not to the species which Benedict and Richardson called his *S. consolidata*. This left Benedict's and Richardson's *S. consolidata* without a name. Hatch (1947) described *S. pettiboneae* as a new species which he thought was related to the *S. consolidata* (of Richardson 1905, not Stimpson), and examination of his specimens shows them indeed to be identical with that species. Accordingly, Hatch's name for the species becomes available. In view of Stimpson's original description, it is difficult to comprehend Benedict's and Richardson's assignment of their *S. consolidata* to Stimpson's *S. consolidata* because these two species now known as *S. pettiboneae* and *S. bicuspida,* respectively, are strikingly different species. Curiously, Miers (1881: 66) equated Stimpson's *S. consolidata* with *S. bicuspida* (Owen) but his work was not followed, although it was cited, by both Benedict and Richardson.

The pointed bumps on the body and head of *Synidotea pettiboneae* consitute its most diagnostic feature. In the strong development of preocular horns, this species is like *S. ritteri* except that those of the latter curve inward, whereas those of *S. pettiboneae* project outward.

8. *Synidotea berolzheimeri,* new species

FIGURE 12

DIAGNOSIS.—Cephalon. Preocular horns large, directed laterally and extending only slightly beyond frontal margin; frontal border slightly excavate between preocular horns; eyes bulging and forming part of lateral contour; a pair of small tubercles just behind frontal notch, a pair of minute tubercles between eyes, and a transverse row of three minute tubercles behind occipital groove.

Pereon. First pereonite with angulate lateral borders; sides of following somites slightly convex or straight, with little or no intersegmental incisions. Each tergite bears a low median tubercle and several minute lateral tubercles.

Pleon. Telson with median terminal excavation. Anterior end bears a few inconspicuous median and lateral tubercles. Appendix masculina (Figure 12*d*) with expanded, flattened shoulder; outer, but not inner, border spinulate at shoulder; distal third beyond shoulder narrow, medially bent and apically pointed. Pleotelson slightly wider than long.

Measurements. Holotype male: length 11.8 mm., width (at third pereonal somite) 4.5 mm. Allotype ovigerous female: length 7.6 mm., width 3.5 mm.

GEOGRAPHICAL RANGE.—Central California from Morro Bay, San Luis Obispo County, to Shell Beach, Sonoma County.

LOCALITIES.—*California.* Marin County—Dillon

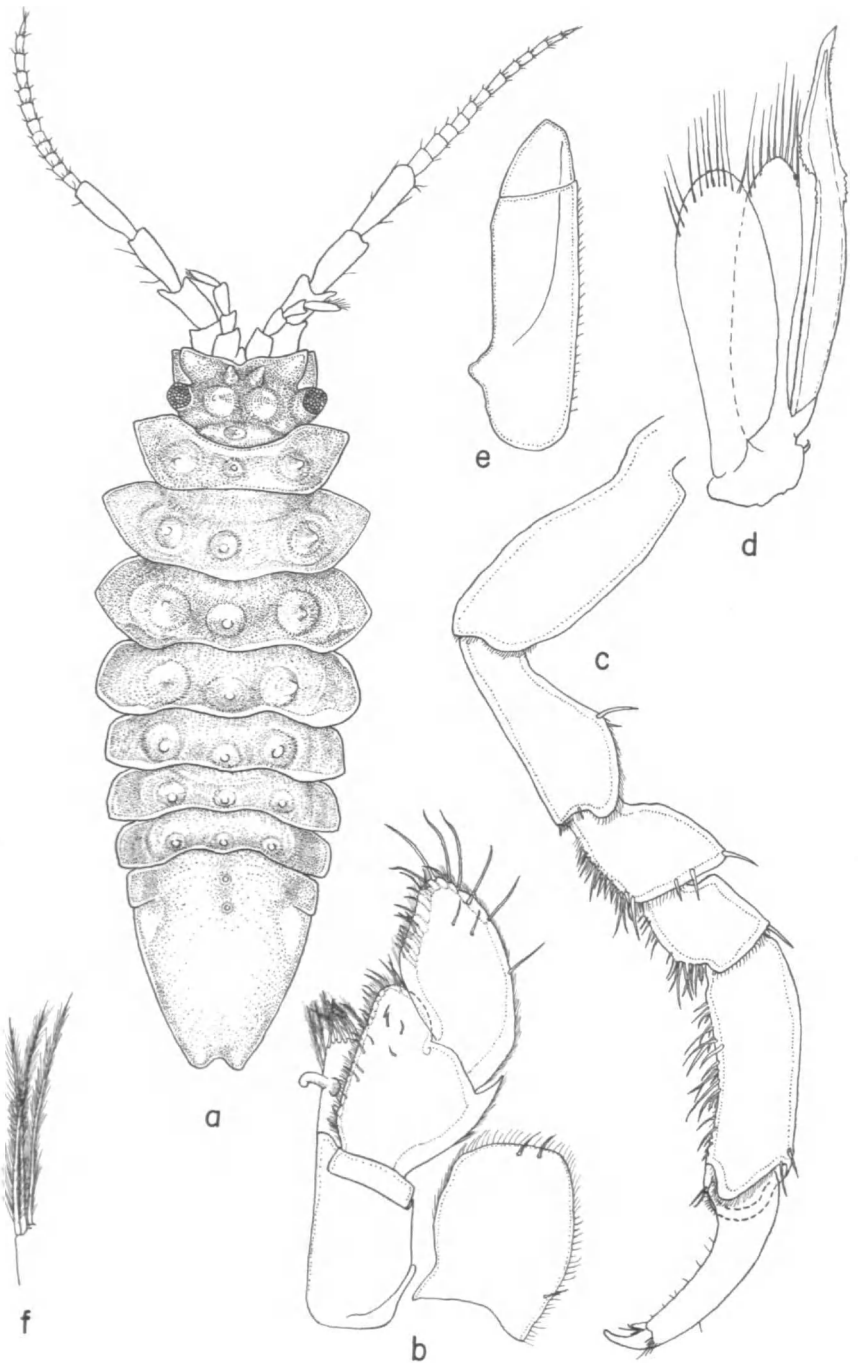

FIGURE 11.—*Synidotea pettiboneae*, male: *a*, dorsal view; *b*, maxilliped; *c*, pereopod 7; *d*, pleopod 2; *e*, uropod; *f*, setae at apex of uropodal sympod.

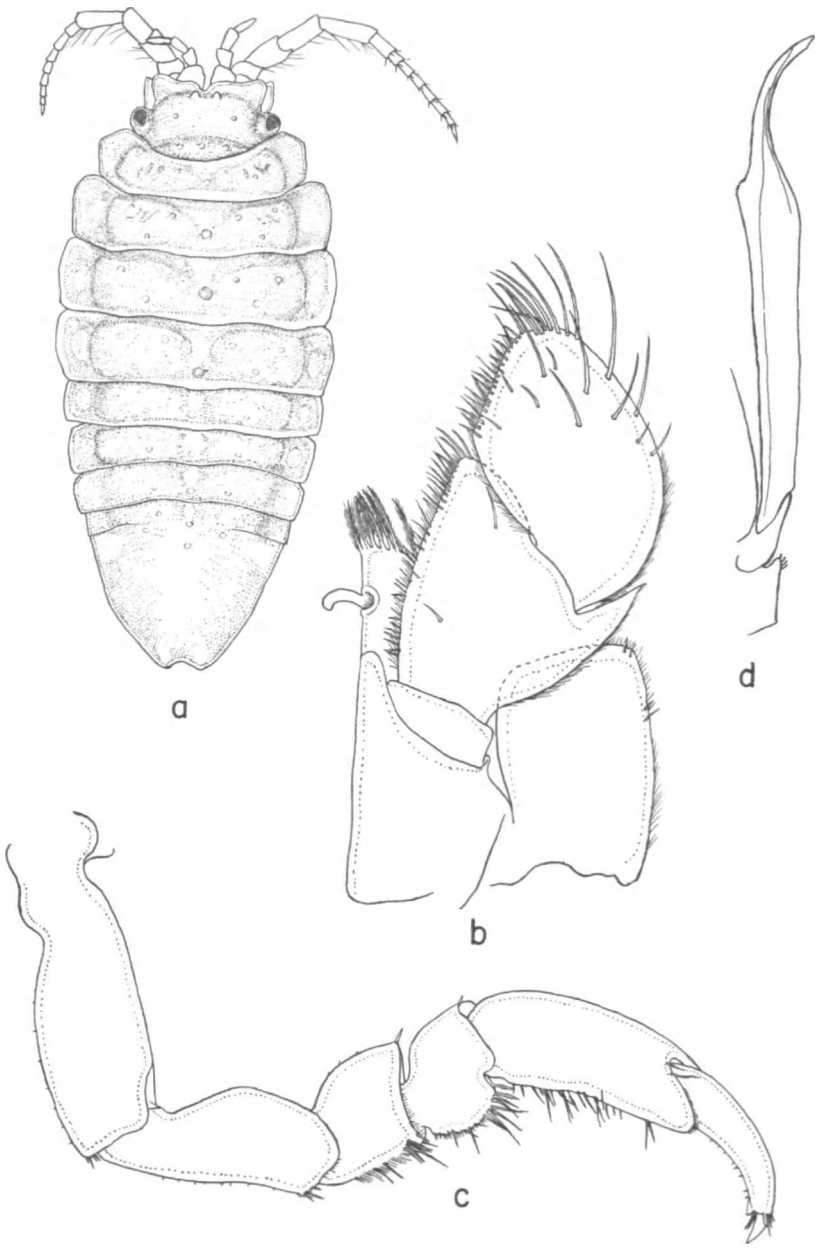

FIGURE 12.—*Synidotea berolzheimeri*, new species, male: *a*, dorsal view; *b*, maxilliped; *c*, pereopod 7; *d*, appendix masculina.

Beach (type-locality): On hydroid *Aglaophenia,* 21 February 1948, R. J. Menzies; on *Aglaophenia,* July 1935, O. Hartman; on *Aglaophenia,* 12 June 1941, G. M. Schreiber; 20 July 1948, V. Schomberg; 31 October 1958, M. A. Miller; July 1960, B. Neal.—Tomales Point, on *Aglaophenia,* June 1941, R. J. Menzies.—Off Estero Americano, 23 January 1948, R. J. Menzies. Sonoma County, Shell Beach, 14 August 1968, J. Bodle. San Luis Obispo County, Morro Bay, 23 January 1958, M. O. Brown.

DISPOSITION OF MATERIAL.—Types are deposited in the United States National Museum, catalog numbers: holotype ♂ 134489, allotype ♀ 134490, paratypes 134491. Other material is in the authors' collections.

REMARKS.—This species is named for Mr. Charles P. Berolzheimer of Stockton, California, in appreciation of his enthusiasm in the development of the Pacific Marine Station of the University of the Pacific at Dillon Beach, Marin County, California, near which this species was first collected, and of his interest in this study.

Synidotea berolzheimeri more closely resembles *S. pettiboneae* than any other Californian species. Both are tuberculate dorsally with a median row of tubercles, but those of the former are minute compared to the spine-like tubercles of the latter, and the lateral ones are differently arranged.

The constant association of our new species with *Aglaophenia* indicates that it preys on that hydroid.

The rather long gap between the southern limit of *Synidotea berolzheimeri* at Morro Bay, California, and the next known locality to the north (Tomales Point, Marin County) will probably be filled in by future collections along the intervening coast.

Ecology of Californian Species

The following ecological notes summarize what little is known concerning the relationships of Californian species of *Synidotea* to their environment. Most of our knowledge is perforce inferred from rather scanty collection data. Clearly, many aspects of their ecology remain to be investigated.

Distributional data indicate that temperature plays an important role in the ecology of most species of *Synidotea.* Of the eight Californian species, five occur north of Point Conception (34½° north latitude) and two south of it, and one (*S. harfordi*) on both sides of it. Point Conception is a major thermal breakpoint which separates the warm-temperate waters off the southern California coast from the colder temperate waters of the central and northern part of the state. The southern group comprises *S. harfordi, S. magnifica* and *S. calcarea*; the northern contingent includes *S. pettiboneae, S. ritteri, S. berolzheimeri, S. bicuspida,* and *S. laticauda. S. harfordi* might also be included in the northern group, but it is predominantly a southern California species.

All species are benthic. Four of them, *Synidotea harfordi, S. berolzheimeri, S. pettiboneae* and *S. ritteri* typically inhabit the lower intertidal zone of wave-swept rocky coasts. Specimens of the latter two, however, have also been taken subtidally at depths of a few fathoms, and it is likely that the other intertidal species may also extend into subtidal regions. In southern California, *S. magnifica* lives on the subtidal shelf, whereas its close relative, *S. calcarea,* inhabits submarine canyons. The typically subtidal species of northern California are the wide ranging *S. bicuspida* and the restricted *S. laticauda.*

Both *Synidotea bicuspida* and *S. laticauda* occur in the San Francisco Bay system, but are geographically and ecologically segregated there, as well as morphologically distinct. *S. bicuspida* is widely distributed along the coast of North America from Monterey Bay, California, to Point Barrow, Alaska, and elsewhere in Arctic–Boreal areas. In San Francisco Bay, it occurs only in the colder, more saline sections around the mouth and in the central and southern sections. It is replaced in the warmer, less saline northern part of the bay system by *S. laticauda* which also ranges into oligohaline Suisun Bay, the Petaluma River, and near the delta of the Sacramento–San Joaquin rivers. There is apparently some overlap in the distribution of these species as *S. laticauda* has recently been reported in both the southern and central sections of the bay (Miller 1968).

It is difficult to say which factor or combination of factors is responsible for the segregation of *Synidotea bicuspida* and *S. laticauda* in San Francisco Bay. Salinities to which the latter are exposed are lower and more variable than those encountered by the former. For bay localities where *S. bicuspida* has been found, they range between 30–31 ‰ (near the Golden Gate) to 27–29 ‰ in the middle and southern division. For *S. laticauda,* they scale down from these values to 25 ‰ (south San Pablo Bay), 10–16 ‰ (Carquinez Strait), and 0.3–1.0 ‰ (near the Sacramento–San Joaquin delta) (Miller et al., 1928;

TABLE 5.—*Physical factors in the environment of two species of Synidotea occurring in San Francisco Bay and vicinity. (Data based on* Albatross *investigations in 1912.)*

Species	*Annual Mean*				*Bottom*	*Depth (meters)*
	Salinity (‰)		*Temperature (°C.)*			
	Average	*Range*	*Average*	*Range*		
S. laticauda	18.57	15.24–29.14	12.99	12.44–13.29	soft-mud-gravel	1.8–110
S. bicuspida	30.34	26.97–34.00	12.12	10.00–13.53	soft mud-hard, clean, gray sand	3.8–26

Filice 1954. See also Table 5). The lower salinities in the upper reaches of the bay, where *S. laticauda* abounds, are due to dilution by fresh water from the large Sacramento and San Joaquin rivers and lesser Napa and Petaluma rivers which empty into the northern arm of the bay system. Bay salinities fluctuate diurnally with the tides, and seasonally with the annual rainfall cycle which features a rainy winter and early spring and a prolonged dry season during the summer and fall when runoff is greatly reduced. Fluctuations are less in the southern arm of the bay system which has no large freshwater tributaries. Within recent years, several large dams have been built across the major tributaries to the California central valley drainage and more are planned to control floods and equalize runoff. This should greatly decrease the amplitude of seasonal salinity fluctuations, at least in the upper reaches of the bay. What effect these changes will have on the bay biota and particularly on populations of *S. laticauda* remains to be seen.

Temperatures are lower outside and at the mouth of San Francisco Bay, where *Synidotea bicuspida* occurs, than in the inner parts to which *S. laticauda* is adapted. Miller et al. (1928) report that the lowest average temperature in 1923 was 14.1°C. at Fort Point near the entrance to the bay, with increases to 17.8°C. at the middle of the bay (Oakland), to 20.6°C. at Dumbarton Bridge in the southern part, and to 19.1°C. at Carquinez Strait at the northern end (see also Table 5).

Other factors that may be involved in the segregation of *Synidotea bicuspida* and *S. laticauda* are turbidity, dissolved oxygen, and substrate. Turbidity is relatively high at the two ends of the bay, especially at the northern end owing to silt from the large rivers. Toward its mouth, the water becomes clearer with negligible turbidity at the Golden Gate. Oxygen content is higher in the colder, less polluted water at the bay entrance than in the upper reaches where it is almost invariably below saturation. The bottom inhabited by both species was not greatly different though *S. laticauda* was found most often where the bottom was muddy, whereas *S. bicuspida* was more frequently taken from a sandy bottom (Table 5). The latter species was taken from a mud bottom often enough (22 percent of the stations), however, to rule out the possibility that bottom texture alone exerts a strong influence on its distribution.

From the foregoing comparison of distribution and habitat of the two species of *Synidotea* occurring in the San Francisco Bay system, we conclude that *S. laticauda* is better able to tolerate low salinities and salinity fluctuations, higher temperatures, turbidity, and other estuarine conditions than *S. bicuspida*. The latter is confined to those parts of the bay which are more oceanic with respect to the factors mentioned. It appears to be a predominantly cold-water, open coast form which may have been carried into the bay by strong tidal currents and has established populations in the more oceanic parts of it. *S. laticauda*, on the other hand, is regarded as an estuarine species, with greatest abundance in the upper, meso- and oligohaline reaches of the bay. Strong currents, especially at ebb tide, could transport it seaward and thus account for its occurrence near the mouth of the bay, the seaward limit of its distribution. The overlap of *S. laticauda* and *S. bicuspida* in the central and

southern parts of the bay indicates that conditions there represent limits of tolerance for both and thus constitute a physiological barrier to the distribution of each. Whether the limiting factors operate on survival of adults or young, reproduction, or indirectly through food supply is a question that might be resolved by experiment.

The food, predators, and other biotic relationships of the Californian species of *Synidotea* have not been adequately studied. The frequent association of *S. pettiboneae* and *S. berolzheimeri* with the hydroid *Aglaophenia* indicates that they feed on it. *S. laticauda* doubtless feeds upon the gymnoblastic hydroid, *Bimeria franciscana* Torrey in San Francisco Bay (Miller 1968). The association of many species with bryozoans also leads one to suspect that these are a common source of food.

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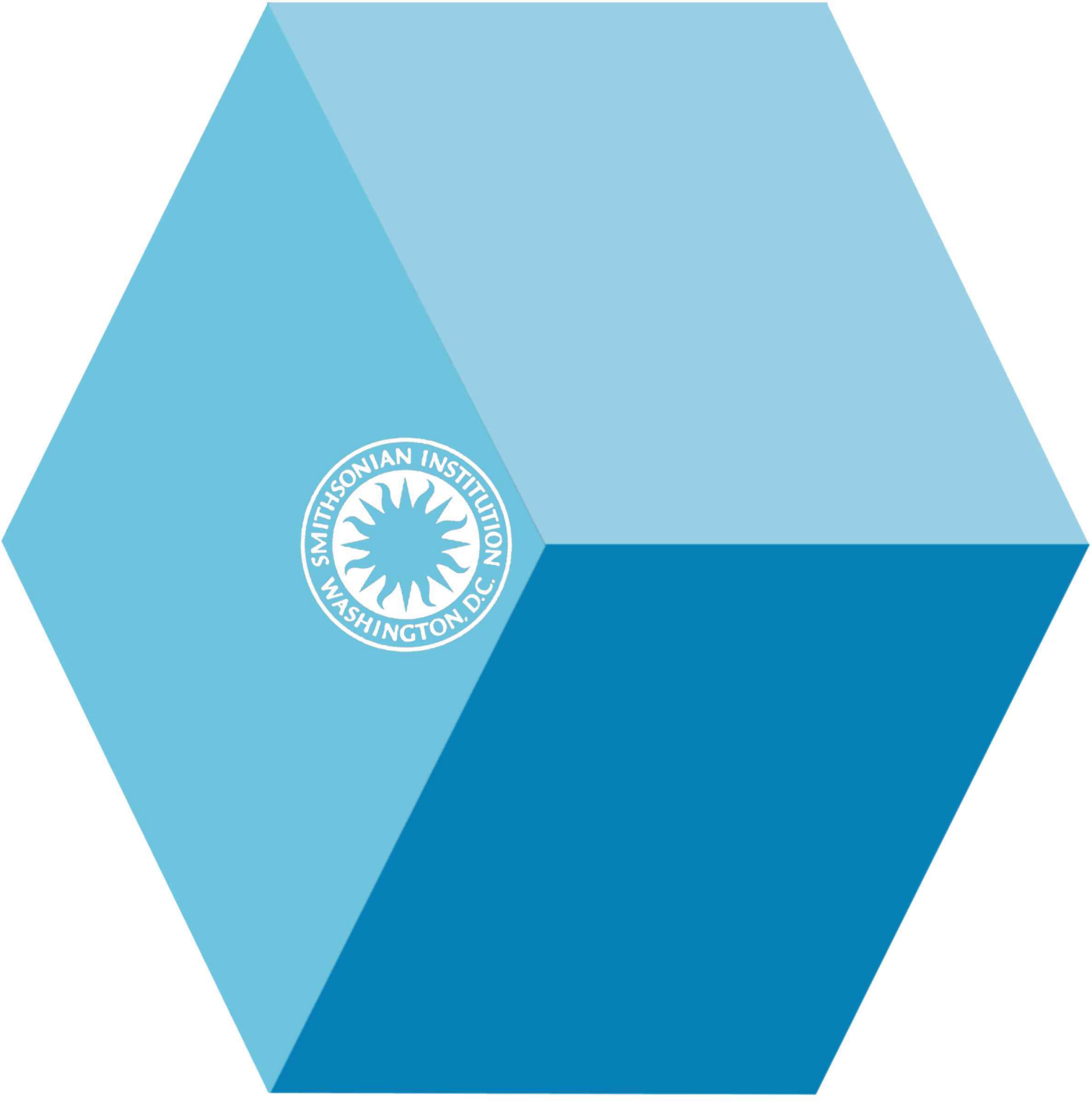
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