SPECIES DIFFERENTIATION IN SYNIDOTEA (ISOPODA: IDOTEIDAE) AND RECOGNITION OF INTRODUCED MARINE SPECIES: A REPLY TO CHAPMAN AND CARLTON

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ABSTRACT

Nominal species of the idoteid isopod genus Synidotea from Japan (S. laevidorsalis), western U.S.A. (S. laticauda), South Africa (S. hirtipes), and Australia (S. keablei and S. grisea) are shown to be morphologically distinct. Others probably are also. Contrary to the views of Chapman and Carlton (1991, 1994), the Japanese species has not been widely distributed by shipping. The Australian species fail several of Chapman and Carlton's attributes of introduced species: their recent discovery and restricted distribution are anticipated in a poorly explored fauna, there is no evidence of postintroduction range extension, no known human mechanisms of introduction exist, they are not associated with known introductions, nor with altered environments, and exotic evolutionary origin cannot be assessed while the phylogeny of the genus is not known. The species in the western U.S.A. is ecologically as well as morphologically distinct, being estuarine rather than marine. A record of S. laevidorsalis from the Gironde estuary, France, is, in fact, of S. laticauda and therefore an introduction from the U.S.A. rather than from Japan.

This study demonstrates the importance of careful taxonomic analysis before it is concluded that marine species are introduced.

Introductions of marine organisms from one coast to another have been long known. In Australia, the occurrence of the European crab Carcinus maenas (L.) in Port Phillip Bay, Victoria, was first recorded in 1900 (Fulton and Grant, 1900), and, since then, a diverse range of introduced animals and plants has been noted in harbors of this remote continent (Pollard and Hutchings, 1990a, b; Jones, 1991). Chapman and Carlton (1991, 1994) used the supposed synonymy of several species of the idoteid isopod genus Synidotea to argue that a Japanese species, S. laevidorsalis (Miers, 1881), has been widely spread by shipping to many coasts, including Australia, over the last century. They deduced on this basis that introductions may contribute a significant fraction of species to otherwise endemic biotas.

Synidotea is a cosmopolitan genus of 56 nominal species (Appendix 1). Most have narrow distributions in shallow waters of the North Pacific, extending into the Arctic Sea, and as far south as China (30°N), Japan, and Korea in the west, and the tropical Gulf of California, Mexico, in the east. Species occur in the western Atlantic from

are reported from the Indo-West Pacific region, from the central Pacific, southern Australia, the Indian Ocean, and South Africa. Local populations are similar to each other in overall appearance, but differences between them are well documented and, in terms of the morphological criteria accepted by crustacean taxonomists, are recognized as species.

The Synidotea hirtipes group (Monod, 1931; Menzies and Miller, 1972) is said to be a group of similar species characterized by a smooth body, entire or slightly excavate front of the head, and excavate pleotelson apex. It was suggested that this included species from the Indian Ocean, but their taxonomic and phylogenetic unity has not been established. This description applies to many species from many localities.

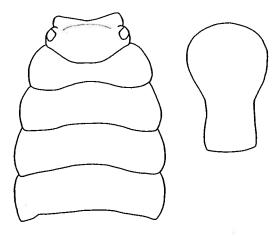
This study demonstrates that five species of *Synidotea* from widely separate localities in the Pacific and Indian Oceans are morphologically very different and are therefore not a single species introduced throughout this area by shipping. Species chosen for detailed analysis are *S. hirtipes* and those synonymized by Chapman and Carlton (1991, 1994) with *S. laevidorsalis* from Japan. Others figured in the literature

FURTHER COMMENT

Since publication of my paper "Species differentiation in Synidotea (Isopoda: Idoteidae) and recognition of introduced marine species: a reply to Chapman and Carlton. Journal of Crustacean Biology 16(2): 384–394, 1996" more specimens of Synidotea grisea Poore & Lew Ton, 1993 have become available. These are all from Bass Strait in eastern Victoria and include one adult male (Museum of Victoria J42641).

The male characters confirm differences between this species and the others with which it was compared. The single specimen is 14.7 mm long. Lateral margins of pereonite 1 lack the subtle angle seen in S. laticauda and S. keablei. The head is more similar to these species than to S. laevidorsalis (see figure below). The length: width ratio of the pleotelson is 0.97. The penial plate is narrow basally and much more discoid than in any other species (see figure below). All pereopods of the male have dense mats of long setae.

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MATERIAL

Material Examined Includes.—Synidotea laevidorsalis (Miers, 1881). Jatiyama Bay, Japan. Natural History Museum, London, 1878.11, 2 syntypes of Edotia hirtipes laevidorsalis, δδ, 21.2–28.7 mm.—Hamakurosaki, Toyama City, Toyama Prefecture, Japan. Collected by N. Nunomura, 6 August 1974. Toyama Science Museum, 1 juvenile, 9.6 mm; 1 ovigerous ♀, 12.3 mm; 8 δδ, 12.3–16.8 mm.—Nagatejima, Shibagaki, Hakui City, Ishikawa Prefecture, Japan. Collected by N. Nunomura, 15 July 1973. Toyama Science Museum, 9 juveniles, 4.6–12.1 mm; 1 δ, 25.7 mm.—Inlet of Ama, Japan. Collected by Prof. Hozawa, 18 August 1927. Museum of Victoria J22335, 1 δ, 29.2 mm.

S. laticauda Benedict, 1897. Sonoma Boat Harbor at mouth of Sonoma River, San Francisco Bay, California, U.S.A., from floats. Collected by J. Chapman, 13 January 1992. Museum of Victoria J27677, 5 juveniles, 7.3-13.9 mm; 1 ovigerous ♀, 11.3 mm; 1 ♂, 17.3 mm.—Port Sonoma, Sonoma County, California, U.S.A., from float. Collected by J. Chapman et al., 3 October 1993 (material reported by Chapman and Carlton, 1994). United States National Museum, 2 juveniles, 4.0-5.5 mm; 2 & &, 22.5-23.2 mm; 2 ovigerous ♀♀, 12.7-15.8 mm.—Willapa Bay, South Bent, Washington, U.S.A., Fisheries Inc. float, on dense hydroids and Molgula. Collected by J. Chapman, 11 October 1987 (material reported by Chapman and Carlton, 1994). United States National Museum, 12 juveniles, to 12.0 mm; 2 & &, 10.8-15.1 mm; 4 ovigerous ♀♀, to 13.4 mm.—Gironde estuary, France (material reported by Mees and Fockedey, 1993, and Chapman and Carlton, 1994). United States National Museum, 9 juveniles, 6.7-13.3 mm; 2 & &, 13.0-16.5 mm; 3 ovigerous ♀♀, 13.5-17.7 mm.

S. hirtipes (Milne Edwards, 1840). Dassen Island, South Africa, from piece of kelp. Collected by T. Mortensen, 1929–30, Zoological Museum, Copenhagen CRU-1042, 5 juveniles, 11.7-18.6 mm; 6 ovigerous \$\foat2\$, 12.1-17.7 mm.—Cape St. Blaize. Collected by Dr. Gilchrist. Natural History Museum, London, 1928.12.1.1329.38, 1 juvenile, 8.6 mm; 5 ovigerous \$\foat2\$, \$\foat8\$, \$\foat6-11.5\$ mm; 3 \$\foat6\$, \$\foat11.8\$-15.1 mm.

S. keablei Poore and Lew Ton, 1993. Type material from New South Wales, Australia, 3 juveniles, 6.3–9.3 mm; 1 ovigerous \Re , 5.8 mm; 3 \Im \Im , 12.0–16.9 mm.

S. grisea Poore and Lew Ton, 1993. Type material from New South Wales and Victoria, Australia, plus 1 specimen from off Woodside Beach, Victoria, 2 juveniles, 3.4 and 4.5 mm; 1 ovigerous 9, 7.5 mm.

MORPHOLOGICAL COMPARISONS

The five species differ in numerous morphological characters (Figs. 1, 2; Table 1). The characters chosen are those of adult specimens and were checked for all available specimens. Since very small specimens tend to be similar across all species, measurements and comments apply only to males with penial plates or ovigerous fe-

Chapman and Carlton (1991, 1994) to be distributed by shipping.

The adult male of S. laticauda is much smaller than S. laevidorsalis. It has a different pattern of chromatophores visible even in preserved specimens. The male pereiopod 1 of S. laticauda is not as grossly modified and the lower surfaces of all the pereiopods are covered with an extremely dense mat of long setae, much more pronounced than in S. laevidorsalis. The eye is more pronounced in S. laticauda, the head is relatively narrower, and there are consistent differences in the shapes of the pleotelson, head, pereionite margins, fused penial plates, and uropodal exopod. Chapman and Carlton (1991) found no consistent differences in the "spination patterns and setation" between the pereiopods of the two species. They failed to notice the real differences between this pair of species. Females and juveniles of S. laticauda have longer setae splayed at right angles to the axis of the limb (Fig. 2c, d). All of these differences are seen over a wide size range and are of specific value.

Synidotea hirtipes also differs from S. laevidorsalis in overall shape, especially of the pereionite margins, head, and pleotelson. This species is the only one with two oblique ridges on the face of the uropodal peduncle.

Synidotea keablei has a characteristic pigmentation pattern similar to that seen in some specimens of S. laticauda. It differs from all four species in overall shape, especially in the head of the adult male, which is strongly domed, has deep sutures laterally next to the bulbous eyes, and has an excavate front. The fused penial plate is broad and uniquely apically notched. Chapman and Carlton (1994) believed that the morphology of male S. keablei (Fig. 1c; Poore and Lew Ton, 1993: figs. 47, 48) "closely matches" that of male S. laticauda (see Menzies and Miller, 1972: figs. 4, 5). This is not so. The pleotelson notch, head, and pereiopods 1 and 7 clearly differ. Figure 1c shows that the head of the Australian species is strongly grooved, has prominent eyes, and a concave front, while that of the Californian species is weakly grooved, has moderate ever and a straight front

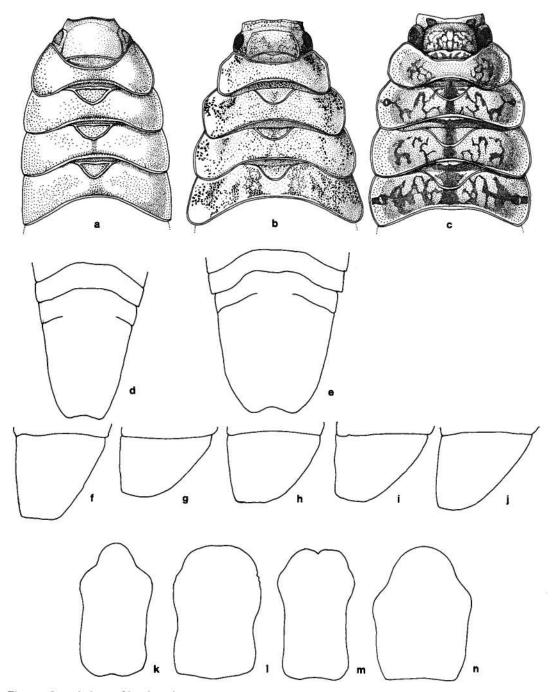


Fig. 1. Dorsal views of heads and pereionites 1-4 of adult males drawn to same size: a, Synidotea laevidorsalis from Hakui; b, S. laticauda from Sonoma River; c, S. keablei holotype from Twofold Bay.—Dorsal views of pereionite 7 and pleon of ovigerous females drawn to same size: d, Synidotea laevidorsalis from Toyama; e, S. laticauda from Sonoma River.—Uropodal exopods of ovigerous females drawn to same size: f, Synidotea laevidorsalis from Toyama; g, S. hirtipes from Dassen I.; h, S. laticauda from Sonoma River; i, S. keablei paratype from Belmont Beach; j, S. grisea holotype from Twofold Bay.—Fused penial plates drawn to same size: k, Synidotea laevidorsalis from Hakui; l, S. laticauda from Sonoma River; m, S. keablei holotype from Twofold Bay.—S. hirtipes from Cane St. Blaize

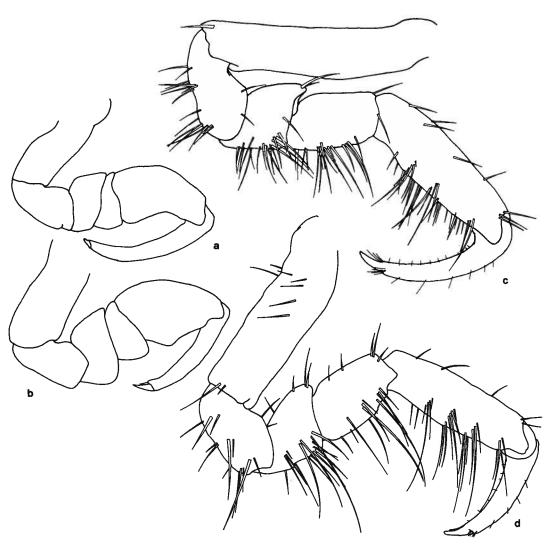


Fig. 2. Outlines of pereiopods 1 of adult males drawn to same size: a, Synidotea laevidorsalis from Hakui; b, S. laticauda from Sonoma River.—Pereiopods 2 of adult females drawn to same size: c, Synidotea laevidorsalis from Toyama; d, S. laticauda from Sonoma River.

cies, but differs in color and shape of the pereionite margin and pleotelson.

The five species illustrated here and by Poore and Lew Ton (1993) demonstrate some of the characters useful in diagnosing species of *Synidotea*. Importantly, these were consistent within species, but differed between them. The value of the shape of the fused penial plate as a taxonomic character was doubted by Chapman and Carlton (1994). As Fig. 1k-n shows, at least for four species, there are real differences. The structure was consistent in males of all sizes

da. The three males of S. keablei possessed the characteristic apical notch. Real differences are seen in the shape of the uropodal exopods of the five species illustrated (Fig. 1f-j). These figures are all of ovigerous females and therefore truly comparable. Finally, maximum size is a real specific character. There is abundant material of S. laevidorsalis, S. laticauda, and S. hirtipes; their maximum recorded sizes of males and females differ (Table 1). In the course of comparing these five, more subtle differences in the proportions of articles of the

The same characters can be used to distinguish species described from other places and suggested by Chapman and Carlton (1991, 1994) to be also identical to S. laevidorsalis. Adults of S. marplatensis are considerably smaller (Moreira, 1972). S. variegata has a more triangular uropodal exopod and obscure pleotelsonic notch (Collinge, 1917). The pleotelson of S. brunnea is almost parallel-sided (Pires and Moreira, 1975). Similarly, the five species from India and the Arabian Sea (S. fecunda, S. fluviatilis, S. indica, S. hunumantharoei, and S. worlinensis) differ from each other and from S. laevidorsalis (see Joshi and Bal, 1959; Pillai, 1963; Kumari and Shyamasundari, 1984; Javed and Yasmeen, 1994).

This is clearly a very different conclusion from that of Chapman and Carlton, who based their synonymies largely on a detailed analysis of regressions of width: length, pleotelson length:body length, and pleotelson length: width of animals of all sizes. All species of Synidotea have similar proportions and this test is not sufficiently sensitive to detect specific differences when used in this way. Juveniles of all species tend to be more similar than adults. Specific differences, obvious in adults, may not be apparent in juveniles, which, because they are so common, swamp the regressions. It is possible to demonstrate that pleotelson length:width ratios of adult males alone are different between S. laevidorsalis and S. laticauda. The data given in Table 1 for males of these two species are the means of 12 and 7 individuals, respectively, and are significantly different from each other (arcsine square-root transformation, P = 0.004).

CONFORMITY WITH ATTRIBUTES OF INTRODUCED SPECIES

Chapman and Carlton (1991) introduced 10 (later 9) attributes which, assuming taxonomic accuracy, could be used to recognize introduced marine species. Their (1994) conclusions about how well the Australian species conformed with some of these attributes are suspect.

Attribute 1: Previously Unknown in Local Region.—The fact that the earliest known

dating from 1886 in the collections of the Museum of Victoria as S. keablei (see Poore and Lew Ton, 1993) was wrong. The specimens, of uncertain provenance, probably belong to S. hirtipes from South Africa.) Most of the peracarid crustaceans in museums in Australia have been collected since the late 1960s and comprise many undescribed species. This is a very different situation from that in Europe and North America. For example, recent surveys of benthic infauna in eastern Bass Strait (11-51-m depth) have captured 417 species of peracarids of which 203 (49%) cannot be identified as a described species (Poore, unpublished results). Many that are named were described in the last two decades. The attribute is, therefore, of little value in the populated southeastern coast of Australia and of no value for the rest of the coast.

Attribute 2: Postintroduction Range Extension.—The numbers of individuals collected over the last 35 years are three for S. grisea and seven for S. keablei. There is no evidence of range extension and inquiries have not turned up more material.

Attribute 3: Human Mechanisms of Introduction.—Both Australian species were collected from sandy shelf sediments at depths of 7.6–18 m along with numerous other infaunal species and seem not to be associated with macroalgae or fouling epifauna. This largely offshore habitat does not preclude artificial transport, but is not typical of introduced species. With the exception of Twofold Bay, none of the sites where Australian species of Synidotea have been taken are ports, and even this locality is an open marine bay with shelf sediments.

Attribute 4: Association with Known Introductions.—Both S. grisea and S. keablei were found in Twofold Bay where other introductions occur. However, their habitat at 7.6–10-m depth on sediment is different from that of the introduced species in the port area. Furthermore, both occur elsewhere along the New South Wales and Victorian open coast on sediment down to 15 m. Neither species occurs in Sydney Harbor, contrary to Chapman and Carlton's assertion. A. A. Racek's record "off Sydney" is taken in Australia to mean on the shelf

ined all museum collections from marine bays in New South Wales and Victoria, Hawkesbury River, Port Jackson, Jervis Bay, Western Port, and Port Phillip Bay, and estuaries of southern New South Wales, all places where extensive surveys have been undertaken and where introductions might be expected. No specimens of *Synidotea* were found.

Attribute 5: Association with Artificial or Altered Environments.—The Australian records are not from altered environments. All are offshore, not in harbors, and, for S. grisea, from sediment off Woodside Beach, at a locality hundreds of km remote from any harbor. Both Australian species inhabit only fully marine environments.

Attribute 6: Discontinuous or Restricted Distribution.—The paucity of observations in Australia reflects the paucity of systematic collecting and is not real.

Attribute 7: Disjunct Global Distribution.—Demonstration of a disjunct distribution is possible if the taxonomic identity of remote populations is unquestionable. This is not the case for Synidotea.

Attribute 9: Exotic Evolutionary Origin.— The hirtipes group of species to which S. laevidorsalis and others are said to belong is loosely defined and its evolutionary unity is not tested. Until the phylogeny of the genus is analyzed, the evolutionary relationships of its numerous species are unknown. Poore and Lew Ton (1993) thought S. grisea most similar to two northeastern Pacific species, not usually thought of as members of the hirtipes group, but did not suggest any evolutionary relationships.

Chapman and Carlton (1994) considered the occurrence of Synidotea in the southern hemisphere as an "enigma" and that most southern species are members of the "hirtipes group." The southern hemisphere is not a biogeographic region and the distribution of the genus is not unusual in biogeographic terms. There is a strong cluster of species in the North Pacific and several species scattered throughout the Indian Ocean region and western Atlantic (Appendix 1). The three species in southern Australia are not necessarily closely related and

all idoteid genera and the only one to have radiated successfully in the northern hemisphere. It is this, its success in boreal environments, that is atypical for the family.

In their synonymy of S. laticauda from California with the Japanese species, Chapman and Carlton (1991) failed to take into account their different ecological preferences. Synidotea laevidorsalis occurs subtidally down to about 10-m-depth in marine macroalgal and sea-grass communities (e.g., Phyllospadix japonicus Makino, Sargassum spp.) and not in estuarine situations (Kang and Yun, 1988; N. Nunomura, personal communication). Synidotea laticauda prefers the warmer parts of San Francisco Bay, where salinity is reduced (Menzies and Miller, 1972: fig. 2). Introduction of a marine species into an estuarine environment seems improbable. On this basis, one would predict that the recent record of a Synidotea from the Gironde estuary, France, to be of an estuarine rather than a marine species. This is, in fact, the case. Mees and Fockedey (1993) and Chapman and Carlton (1994) reported a species from this locality as S. laevidorsalis from Japan, but the specimens seen by me belong to the American estuarine species S. laticauda, agreeing in all the characters listed in Table 1. Mees and Fockedey (1993) made their identification by comparison with figures of the American species; their error was in assuming the synonymy was correct. On ecological grounds alone, the marine Australian species could be predicted to be not S. laevidorsalis.

It could be argued on similar ecological grounds that the record of *S. laevidorsalis* from the estuary of the Changjiang River, China (Huang *et al.*, 1981) is also a misidentification. Nunomura (personal communication) believes that the species is most common in the Sea of Japan (see also, Kwon, 1986; Kang and Yun, 1988) and does not occur this far south in Japan.

CONCLUSIONS

On the basis of this analysis, I refute the synonymies proposed by Chapman and Carlton and show that *Synidotea* is a widespread genus with numerous species, each with limited geographic range. This treat-

1.

1. Comparison of five species of Synidotea from Indo-Pacific coasts. Data from own observations except some maximum lengths taken from literature.

	S. laevidorsalis	S. laticauda	S. hirtipes	S. keablei	S. grisea
um length of ovi- us female	12.3 mm	13 mm	17.7 mm	(5.8 mm)	7.5 mm
t male	35 mm	22.5 mm	25 mm	16.9 mm	I
in alcohol	even brownish tan	blue grey with middorsal stripe and dark chro- matophores	even yellowish tan	blue grey; head and pleotelson especially pigmented; transverse stripes on coxae 2 and	grey
son length (coxa apex): width in s (number of imens)	1.22 (12)	1.07 (7)	I	4 and pleotelson 0.98 (2)	I
ı margin	pereionite 1 with subtle curved angle, 2-7 making continuous margin	pereionite 1 evenly curved and oblique, 2 and 3 convex, 4-7 straight	pereionite 1 evenly curved, 2–7 convex, not making continuous margin	pereionites 1-7 markedly convex, not making continuous margin	pereionite 1 especially convex, 2-7 convex, not making continuous
of head; dorsal pture	straight; weak transverse depression in front of eyes	straight; clear transverse depression in front of eyes	straight with produced anterolateral angles; no transverse depression in front of evee	concave; strong transverse groove in front of eyes and deep grooves medi-	concave; strong transverse grove in front of eyes and deep grooves medi-
vidth:pereionite 4 h	0.56	0.49	0.58	0.54	al of eyes 0.54
ood 1 of male	palm of propodus deeply concave; dactylus reaching middle of me- rus	palm of merus, carpus, and propodus lobed; dactylus reaching me- rus-carpus suture	palm of merus and carpus weakly lobed, propodus with shallow concavity; dactylus reaching mens-carpus suture	palm of propodus con- cave, dactylus reaching merus-carpus suture	I
n of ischium- odus of pereio- of female	short setae along lower margins	long splayed setae along lower margins	short setae along lower margins	short setae along lower margins	short setae along lower margins
n of ischium- odus of pereio- od male	sparse mats of short setae	dense mats of long setae	dense mats of long setae	dense mats of long setae	I
penial plate	waisted; tapered beyond prominent shoulders near apex	waisted; apically rounded	broadest near midpoint; broadly rounded in dis- tal third	waisted; with obscure shoulders, apically notched	I
lal peduncle	1 oblique ridge	1 oblique ridge	2 oblique ridges	1 oblique ridge	no oblique ridge

	S. laevidorsalis	S. laticauda	S. hirtipes	S. keablei	S. grisea
dal exopod; h: width	clear corner between lateral margin and truncate apex; 0.98	r between laterourve between lateral in and truncate margin and truncate apex; 0.77	apex rounded, angled only tapering to convex apex; medially, 0.66 0.72	tapering to convex apex; 0.72	tapering to rounded ape 0.90

vestigate morphological differences between populations. To deny that species based on traditional morphological criteria are realities is to question the basis of much ecological thought. Above all else, it questions the basis on which introduced species are recognized.

Chapman and Carlton (1994) concluded that their synonymy of 5-8 species of Synidotea questioned the assumption that most isolated populations of shallow-water marine organisms are the result of natural processes. Southern Australia has a largely endemic marine invertebrate fauna with about 90-95% of known species endemic to this region (Wilson and Allen, 1987) and the rest shared with other parts of Australia or New Zealand. This makes the recognition of introduced species in well-studied taxa relatively easy, for example, in the case of molluscs and crabs. This is not so for lesserknown groups. The family Idoteidae to which Synidotea belongs is one of the easiest to collect in this region and is relatively well represented in museum collections, but the recent revision (Poore and Lew Ton, 1993) almost doubled the number of known species to 23. Taxonomic studies of other families of isopods and amphipods in the last 20 years have often increased the number of species 10-fold. Detecting introduced species in this environment is very difficult and can only be assured after thorough comparison with material from the suspected source.

Two other groups of peracarids are worth investigating. The tanaidacean Tanais dulongii (Audouin) has been reported from South Australia (Jones, 1991), but tanaidaceans superficially similar to this are widespread in Victorian coastal waters remote from ports and may well be an endemic undescribed species. European and North American species of the amphipod genus Corophium have been identified from Australian estuaries, but detailed morphological comparisons have not been published. These observations do not deny that introductions occur and are a problem for local biotas, but emphasize that, unless correct taxonomic decisions are made, the scale of the problem is unknown.

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Appendix 1. Species of *Synidotea* Harger with general remarks on distribution and synonyms. Menzies and Miller (1972), Kussakin (1982), and Rafi and Laubitz (1990) listed many species, but other recent references are given for others.

Species	Distribution and synonyms
acuta Richardson, 1909	Bering Sea.
angulata Benedict, 1897	British Columbia to California.
bathyalis Gurjanova, 1955	northwestern Pacific Ocean.
berolzheimeri Menzies and Miller, 1972	western U.S.A.
bicuspida (Owen, 1839)	western North America. Junior synonyms: <i>Idotea pul-chra</i> Lockington, 1877, <i>I. rugulosa</i> Buchholz, 1874, <i>Synidotea incisa</i> Sars, 1880.
birsteini Kussakin, 1971	northwestern Pacific Ocean.
bogorovi Gurjanova, 1955	northwestern Pacific Ocean.
braznikovi Gurjanova, 1933	Sea of Japan.
brunnea Pires and Moreira, 1975	Brazil.
calcarea Schultz, 1966	southern California.
cinerea Gurjanova, 1933	Sea of Okhotsk.
consolidata (Stimpson, 1856)	Alaska to California (Rafi and Laubitz, 1990). Junior synonym: S. macginitiei Maloney, 1933.
cornuta Rafi and Laubitz, 1990	British Columbia.
epimerata Richardson, 1909	Sea of Japan.
erosa Benedict, 1897	Bering Sea.
esoensis Nunomura, 1991	Japan.
fecunda Javed and Yasmeen, 1994	Pakistan.
fluviatilis Pillai, 1954	southern India (Pillai, 1963).
francesae Brusca, 1983	western Mexico.
grisea Poore and Lew Ton, 1993	Victoria, Australia.
hanumantharaoi Kumari and Shyamasundari, 1984	India.
harfordi Benedict, 1897	western North America.
hikigawaensis Nunomura, 1974	Japan; Korea (Kwon, 1986).
hirtipes (Milne Edwards, 1840)	South Africa (Kensley, 1978).
indica Javed and Yasmeen, 1994	Pakistan.
ishimarui Nunomura, 1991	Japan.
keablei Poore and Lew Ton, 1993	New South Wales, Australia.
laevidorsalis (Miers, 1881) laevis Benedict, 1897	northwestern Pacific Ocean (Kwon, 1986). Bering Sea. Possible junior synonym of <i>S. nodosa</i> (Rai 1985).
lata Gurjanova, 1933	northwestern Pacific Ocean. Junior synonym: S. excava ta Gurjanova, 1933.
laticauda Benedict, 1897	northern California and Washington, U.S.A.
littoralis Pires and Moreira, 1975	southeastern Brazil.
longicirra Gurjanova, 1933	Sea of Okhotsk.
magnifica Menzies and Barnard, 1959	California.
marmorata (Packard, 1867)	Atlantic Ocean; Bering Sea.
marplatensis Giambiagi, 1922	southern Brazil (Moreira, 1972).
media Iverson, 1972	California.
minuta Rafi and Laubitz, 1990	British Columbia.
muricata (Harford, 1877)	Sea of Okhotsk; Greenland. Junior synonyms: Synidote spinosa Gurjanova, 1933, S. spinosa anadyrensis Gurjanova, 1955.
nebulosa Benedict, 1897	Bering Sea.
neglecta Birstein, 1963	northwestern Pacific Ocean.
nipponensis Nunomura, 1985	Toyama Bay.
nodulosa (Krøyer, 1846)	northeastern Pacific Ocean; circumarctic. Junior synonym: S. picta Benedict, 1897 (Rafi, 1985).
otsuchiensis Nunomura, 1985	northern Japan (replacement name for S. acuta Nunomura, 1984, junior homonym of S. acuta Richardson 1909).
	Tuamotou Islands.
pacifica Nobili, 1906	
<i>pacifica</i> Nobili, 1906 <i>pallida</i> Benedict, 1897 <i>pettiboneae</i> Hatch, 1947	Bering Sea; northwestern Pacific Ocean. British Columbia and Washington.

Appendix 1. Continued.

Species	Distribution and synonyms
S. ritteri Richardson, 1904	western North America.
S. sculpta Gurjanova, 1955	northwestern Pacific Ocean.
S. setifer Barnard, 1914	South Africa (Kensley, 1978).
S. subarmorata Kussakin and Mezhov, 1979	northwestern Pacific Ocean.
S. tuberculata Richardson, 1909	Sea of Okhotsk. Junior synonym: S. pavlovskii Gurjanova 1955.
S. variegata Collinge, 1917	Gulf of Mannar (Pillai, 1963; Kensley, 1978).
S. watsonae Poore and Lew Ton, 1993	western Australia.
S. worliensis Joshi and Bal, 1959	India,