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Chapter 23

Review of the Taxonomy, Diversity, Ecology, and Other Biological Aspects of Order Tanaidacea from Japan and Surrounding Waters

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Abstract The order Tanaidacea is a group of benthic crustaceans, most of which are small, up to a few millimeters long. Tanaidaceans are distributed worldwide, with more than 1,200 described species. Following the first taxonomic paper on a Japanese tanaidacean in 1936, many researchers have studied their taxonomy, morphology, reproductive biology, or ecology in the waters around Japan. This chapter presents a brief introduction to tanaidaceans and then reviews what is known of their systematics (taxonomy and phylogeny), biology (including feeding habits, phenology, morphology, reproductive modes, parasites, predators), and ecology in Japan. The chapter ends with a summary and prospects for future research. The general conclusion is that tanaidaceans have been under-studied, both globally and within Japan; the 104 nominal species reported from around Japan and the 1,200 species reported globally likely represent a fraction of the actual diversity. The phylogeny of tanaidaceans is largely unresolved at all taxonomic levels. Recent, significant new discoveries dealing with herbivory, selfing, skin-digging activity in holothuroid hosts, possible sound production, and tube building suggest that much remains to be learned about their general biology.

Keywords Crustacea • Peracarida • Tanaidacea • Taxonomy • Biology • Ecology • Japan

23.1 Introduction

The order Tanaidacea is a group of aquatic crustaceans in the superorder Peracarida, which includes Isopoda, Amphipoda, Cumacea, and some other groups. More than 1,200 living tanaidacean species have been described worldwide, comprising 33 families, with several dozens of species regarded as family *incertae sedis* (Anderson 2013); this is likely only a small fraction of the actual species diversity (cf.

Błażewicz-Paszkowycz 2014). Tanaidacea also includes a few extinct species; 16 fossil taxa have been recorded from the Lower Carboniferous to the Middle Cretaceous (see

Sánchez-García et al. 2015). Tanaidaceans differ from other crustaceans in the following combination of characters: 1) a cephalon and the two most anterior thoracic somites form a cephalothorax, resulting in a pereon consisting of six pereonites; 2) the cephalothorax is covered with a carapace; 3) the cephalothorax has a branchial chamber posterolaterally on each side, each containing an epignath (an organ related to respiration); 4) the appendage on the second thoracic somite (seventh segment in the cephalothorax) is a cheliped (it is subchelate in a few groups; cf. Kakui and Angsupanich 2012); and 5) there is one pair of narrow, biramous or uniramous uropods.

Tanaidaceans are typically a few millimeters long, though the largest reported is 75 mm long (Gamo 1984). While several groups inhabit non-marine environments such as brackish lakes, freshwater systems, and anchialine caves (Kakui et al. 2010; Chapman et al. 2011; Guțu and Iliffe 2011; Błazewicz-Paszkowycz et al. 2012), most species are marine. Marine species have been reported worldwide, ranging in depth from the intertidal zone to bathyal depths at around 9,000 m. Aside from a few parasitic or symbiotic species such as *Exspina typica* Lang, 1968 and *Terebellatanais floridanus* Suárez-Morales et al., 2011 (Alvaro et al. 2011; Suárez-Morales et al. 2011), tanaidaceans are free living (cf. Błazewicz-Paszkowycz 2014). They show diverse modes of life (Fig. 23.1); for example, most apseudomorph tanaidaceans are burrowers; some species in the family Pagurapseudidae utilize empty gastropod shells as a mobile shelter, like hermit crabs; and many species use threads to construct tube-like nests in the sea bottom, or on the surfaces of seaweeds, seagrasses, other animals, or abiotic substrata (Hassack and Holdich 1987; Kakui and Hiruta 2014; hereafter, ‘tube-dwellers’). Tanaidaceans are typical peracaridans, in that they lack a planktonic larval stage and brood their young, and release benthic offspring directly (so-called ‘direct development’), a feature that might be responsible for the occasionally extremely high local densities reported, e.g., 146,000 individuals/m² in *Allotanais hirsutus* (Beddard, 1886) and 140,000 individuals/m² in *Mesokalliapseudes crassus* (Menzies, 1953) (Barnard 1970; Delille et al. 1985).

The earliest report of tanaidaceans from the waters surrounding Japan was Stephensen (1936), dealing with a tanaidid species collected in the Kurile Islands. There have been many subsequent studies, continuing to the present, that deal with taxonomy, phylogeny, biology, and ecology. In this chapter, I review previous studies on the systematics, biology, and ecology of tanaidaceans around Japan.

23.2 Systematics

Tanaidacean systematics (including taxonomy) remains active, with recent discoveries

of taxa even at the family level (e.g., Larsen 2012). In this section, I review tanaidacean systematics around Japan.

23.2.1 *Taxonomic and Phylogenetic Studies of Tanaidaceans Around Japan*

Knud Hensch Stephensen, a Danish zoologist, published the first report specifically dealing with a tanaidacean from Japanese waters. This study (Stephensen 1936), based on specimens collected by Denzaburo Miyadi from a lake on Kunashiri Island, Kurile Islands, reported and redescribed *Sinelobus stanfordi* (Richardson, 1901).

The first Japanese specialist on tanaidacean taxonomy was Sueo Shiino, who also actively studied other crustaceans, including isopods, copepods, and rhizocephalans. His publications include five papers on the Japanese tanaidacean fauna (Shiino 1937, 1951a, b, 1952, 1966), with descriptions of seven new species, as well as five papers on tanaidaceans outside Japan (e.g., Shiino 1963).

Another relevant specialist was the Soviet researcher Rosalia Konstantinovna Kudinova-Pasternak, who studied deep-sea tanaidaceans collected from the Sea of Japan, the Kurile–Kamchatka Trench, the Japan Trench, the Izu–Ogasawara Trench, and the Pacific abyssal plane, and described more than 25 new species from these areas (Kudinova-Pasternak 1966a, b, 1970, 1976, 1978, 1984). Other researchers were active around the same time. Kussakin and Tzareva (1972) described several tanaidomorphs from the Kurile Islands. Sieg (1980) described two new tanaidids, *Zeuxo coralensis* Sieg, 1980 and *Z. maledivensis* Sieg, 1980; although the type locality of these species is the Maldivian Islands, Sieg included Japanese specimens in the material examined for the original descriptions. Ishimaru (1985) described two leptocheliids, one of which was new to science.

After a hiatus of nearly two decades in Japanese tanaidacean studies, Nunomura (2005) described a new brackish apseudomorph from Okinawa. A further boost to tanaidacean taxonomy came in 2007, when the Danish researcher Kim Richard Larsen came to Japan for a 2-year stay. He and his host, Michitaka Shimomura, studied both shallow-water and deep-sea tanaidaceans, described 12 new species in four papers, and edited a monograph (with the participation of four other researchers) that included descriptions of 15 new species (Larsen and Shimomura 2006, 2007a, b, 2008, 2009; Bamber 2007; Bird 2007a, b; Błażewicz-Paszkowycz 2007; Larsen 2007; McLelland 2007). Around the same time, colleagues and I began studies that resulted in eight new species described from Japan, with several redescrptions (Kakui et al. 2007, 2010, 2012; Kakui and Kajihara 2011; Kakui and Yamasaki 2013; Kakui and Kohtsuka 2015; Kakui and Naruse 2015). Another currently active specialist is the Polish researcher

Magdalena Błażewicz-Paszkowycz, who has published descriptions of nine new species collected by two joint Russian–German expeditions, SoJaBio (Sea of Japan) and KuramBio (Kurile–Kamchatka Trench) (Błażewicz-Paszkowycz et al. 2013, 2015a, b).

The known tanaidacean fauna around Japan currently stands at 104 species (Table 23.1; Fig. 23.2), although some of these records may be in error due to misidentification (cf. Błażewicz-Paszkowycz et al. 2013). Some papers have only presented new distributional records or partial descriptions (e.g., Nunomura 1985; Ariyama and Ohtani 1990; Saito 1996; Kakui et al. 2014).

Since the pioneering work by Drumm (2010), three molecular phylogenetic studies on tanaidaceans have been published, all of which have included representative species collected around Japan. Kakui et al. (2011) focused on the relationships among families or higher taxa and obtained the first sequence data from neotanaisids; based on the results, these authors proposed a two-suborder, four-superfamily classification for Recent tanaidaceans. Kakui et al. (2012) and Błażewicz-Paszkowycz et al. (2015b) studied the phylogenetic position of *Arctotanais* and *Protanais*, respectively, within Tanaidomorpha.

23.2.2 *Some Remarks on the Tanaidacean Fauna Around Japan*

Japan extends across several climatic zones and is affected by two warm and two cold currents, and thus the tanaidacean fauna in coastal area shows some regionality (Kakui unpubl. data from several years of sampling, including by snorkeling and SCUBA). At the family level, for example, Kalliapseudidae, Parapseudidae, Apseudidae, and Pagurapseudidae have been detected only from Honshu to the Nansei Islands, but not around Hokkaido. Metapseudidae from coastal regions includes species in genera previously reported (*Apseudomorpha* and *Synapseudes*; Shiino 1951b) as well as representatives of other genera such as *Curtipleon* (Kakui unpubl. data), with differences in distributional ranges among genera. To date, *Apseudomorpha* has been collected from Hokkaido to the Ryukyu Islands; *Synapseudes* from central Honshu to the Ryukyu Islands; and *Curtipleon* only in the vicinity of the Ogasawara and Ryukyu Islands (Kakui unpubl. data). Nototanaidae is presently known from only around the Ryukyu Islands (Kakui and Yamasaki 2013). These distributional differences may result from differences in habitat preference (e.g., brown alga bed, mudflat, coral reef, etc.) as well as differences in tolerance across a wide range of water temperature related to latitude and ocean currents. In addition, mangrove forests extend farther north in Japan than anywhere else in the world except Bermuda (Giri et al. 2011), contributing to tanaidacean diversity—as evidenced, for example, by the nototanaisid *Nesotanais*

ryukyuensis Kakui et al., 2010, so far known only from brackish waters around islands with mangroves (Kakui and Yamasaki 2013). Likewise, the parapseudid *Longiflagrum nasutus* (Nunomura, 2005) is known only from the Manko mangrove wetland on Okinawa Island. It is presently unknown whether these species simply inhabit tropical/subtropical brackish waters, or are specifically associated with mangrove environments. Interestingly, both species appear to be distributional outliers, with the nearest neighboring congener thousands of kilometers away: for *Nesotanais*, *N. macLaughlinae* Guțu and Iliffe, 1989 from Palau; for *Longiflagrum*, *L. koyonense* Angsupanich, 2004 from Thailand (Guțu and Iliffe 1989; Angsupanich 2004).

Tanaididae is one of two families commonly occurring in nearshore and brackish environments in Japan. *Zeuxo*, the most species-rich genus in this family, is distributed from Hokkaido to the Ryukyu Islands, with high population abundances from Hokkaido to Kyushu, and can be collected from many microhabitats such as laminarian holdfasts, as epibionts on seagrasses or algae (Fig. 23.1c), or sandy bottoms. Pairs of sympatric species are known, from several areas (e.g., around the Misaki Marine Biological Station), that show different pigmentation patterns (Fig. 23.3) and different frequencies of occurrence among various microhabitats, which implies habitat segregation. Many different pigmentation patterns are evident in *Zeuxo* specimens collected in Japan, each likely corresponding to an independent species (Kakui unpubl. data). To date, three species have been reported in Japan (Table 23.1), though their type localities are far away: Addu Atoll (Maldives) for *Z. coralensis*; Fadiffolu Atoll (Maldives) for *Z. maledivensis*; Monterey Bay (USA) for *Z. normani* (Richardson, 1905) (Sieg 1980). The validity of the previous identifications of *Zeuxo* species in Japan are thus suspect and need to be checked.

The confamilial genus *Tanais* is also distributed throughout Japan, with high population abundances in southern Japan (in contrast to *Zeuxo*). Species in *Tanais* are positively phototactic and can be collected at night with a light trap (Naoto Jimi pers. comm.). *Sinelobus* is distributed in brackish lower river regions and estuaries from northern to southern Japan. Japanese material currently treated as *Sinelobus stanfordi* actually contains at least two species, one in northern and the other in southern Japan, but they are sympatric at least in Kochi Bay, Shikoku (Kakui unpubl. data).

The other common family in coastal regions is Leptocheliidae, species of which occur abundantly intertidally in coral-rubble beds, and throughout Japan on sandy or muddy bottoms, and are also common subtidally in the shelf zone. Despite their abundance, leptocheliids have been poorly studied in Japan (Kussakin and Tzareva 1972; Ishimaru 1985; Larsen and Shimomura 2007a), with only one subtidal record

(Larsen and Shimomura 2007a), and many species likely remain to be discovered.

Tanaidacean samples from the deep sea around Japan contain numerous paratanaoid species; among 15 paratanaoid families with deep-sea records (cf. Suárez-Morales et al. 2011; Bird 2012; Blazewicz-Paszkowycz et al. 2012), only Mirandotanaidae has not been reported. One neotanaoid and three apseudoid families (Neotanaidae; Apseudidae, Parapseudidae, and Sphyrapodidae) are also represented. In addition, the tanaidoid *Protanais birsteini* (Kudinova-Pasternak, 1970) has been reported from hadal depths along the Kurile–Kamchatka Trench (Kudinova-Pasternak 1970; Błazewicz-Paszkowycz et al. 2015b). Sphyrapodidae is especially well represented; to date, two genera and four species have been reported from the deep sea around Japan [excluding doubtful records of *Pseudosphyrapus serratus* (G. O. Sars, 1882)] (Table 23.1). Sphyrapodids have been detected all around Japan, except off the Pacific coast from eastern Hokkaido to central Honshu (Fig. 23.4) (Kakui unpubl. data). However, the distributions of the four species are more limited, as indicated in Fig. 23.4. Unidentified specimens in *Pseudosphyrapus* (*P.* sp. in Fig. 23.4) that are closely related to or possibly conspecific with *P. quintolongus* occur off the coasts of Shikoku and Honshu. The congener *P. anomalus* (G. O. Sars, 1969), with a circumpolar Arctic distribution, occurs to the north of Japan, but no other congeners have been reported from Pacific except for those around Japan. A phylogeographic study would shed light on this interesting distributional pattern.

23.3 Biology and Ecology

The biology of tanaidaceans has long interested biologists; Darwin (1872), for example, referred to their male dimorphism in “The Origin of Species”. In addition, their high abundance in bottom habitats suggests tanaidaceans might play an important role in ecosystems (Larsen et al. 2015). However, there have been relatively few studies in tanaidacean biology and ecology, perhaps due to the small size of individuals and the difficulty of identification, which relies on microscopic characters. In this section, I review knowledge on several aspects of tanaidacean biology and ecology derived from studies in Japan.

23.3.1 Morphology

Tanaidacean morphology has been studied for well over a century, as the following examples illustrate. Blanc (1884) made detailed observations on the thoracic glands associated with thread production in a tube dweller, *Heterotanaais oerstedii* (Krøyer, 1842). Dennell (1937) illustrated feeding and respiratory structures in *Apseudes talpa*

(Montagu, 1808). Johnson and Attramadal (1982a) studied morphological structures and behavior related to tube dwelling in *Tanais dulongii* (Audouin, 1826). Drumm (2005) examined feeding, respiratory, and cleaning behaviors and their related morphology in two kalliapseudid species, and Wirkner and Richter (2008) studied the morphology of the haemolymph vascular system among three superfamilies [*T. dulongii*, *Paradoxapseudes bermudeus* (Băcescu, 1980), and *Neotanais* sp.].

Several studies in Japan have also dealt with morphology. In a study of the ultrastructure of the branchial chamber and epignath in *Sinelobus stanfordi*, Kikuchi and Matsumasa (1993) showed that the epithelia of both the epignath and the inner wall of the carapace (branchiostegite) are the ion-transporting type but differ in structure; the authors suggested that the latter epithelium plays a major role in osmoregulation and respiratory gas exchange. Kakui et al. (2010) observed opposing serial ridges on the inner surface of the left and right chelipeds in two *Nesotanais* species. Through behavioral observations and a comparison with similar structures in sesarimid crabs used to produce sound, that study suggested that the paired ridges in *Nesotanais* might likewise function to produce sound. In the tanaidid *Arctotanais alascensis* (Richardson, 1899), Kakui et al. (2012) discovered a unique semicircular ischium on all pereopods and speculated that this character might represent a transitional stage between the circular-shaped ischium present in most tanaidaceans and complete loss of that article in tanaidids other than *A. alascensis*. Finally, in a study of the thread-producing system in the kalliapseudid apseudomorph *Phoxokalliapseudes tomiokaensis* (Shiino, 1966), Kakui and Hiruta (2014) reported four distinct types of secretory system in the pereopods, with the type in pereopod 1 possibly involving secretory setae.

23.3.2 Reproductive Modes

Tanaidaceans are highly diverse in reproductive mode. Most species are gonochoristic, like humans, with males and females engaging in sexual reproduction. However, simultaneous hermaphroditism also occurs, first reported in a species in *Apseudes* (Lang 1953). Only recently, Kakui and Hiruta (2013) showed that the simultaneously hermaphroditic *Apseudes* sp., collected from a public aquarium in Japan, can self-fertilize, the first example of self-fertilization in the crustacean class Malacostraca. The same showed that *Apseudes* sp. becomes simultaneously hermaphroditic via a male-like phase in which only the testes are mature, which means that this species is a protandric simultaneous hermaphrodite. Specimens bearing both male and female external reproductive features have been reported in several species in genera other than *Apseudes* (cf. Rumbold et al. 2015), and some of these may likewise be functional

simultaneous hermaphrodites.

Some tanaidaceans are sequential hermaphrodites. Bückle Ramírez (1965) demonstrated that *Heterotanais oerstedii* is diandrous, producing both primary males (developing directly from juveniles) and secondary males (developing by sex change from females). *Nototanais* and subsequently several other tanaidomorphs have proven similarly to be protogynous sequential hermaphrodites, changing in sex from female to male during the life cycle (cf. Rumbold et al. 2015). Although protandric sequential hermaphrodites (changing sex from male to female) have also been suspected among tanaidaceans (Wolff 1956), no case has been confirmed. Błażewicz-Paszkowycz et al. (2014) demonstrated that a single species (*Agathotanais ingolfi* Hansen, 1913) can produce two different male morphs (a sedentary form and a swimming form) (see also Bird and Holdich 1988), indicating there is much left to learn about tanaidacean life cycles; future studies of their reproductive systems will help elucidate the evolution of reproduction in Tanaidacea, and even in Malacostraca.

23.3.3 Phenology

Tanaidacean phenology has not been well studied, though there are a few reports dealing with several families (e.g., Aboul-Dahab et al. 2001; Fonseca and D’Incao 2003; Pennafirme and Soares-Gomes 2009). Several species appear to have an annual breeding period (Johnson and Attramadal 1982b; Fonseca and D’Incao 2003), whereas others reproduce year-around (Aboul-Dahab et al. 2001). Pennafirme and Soares-Gomes (2009) showed that the life cycle can vary (e.g., presence or absence of a distinct breeding period) between tropical and subtropical populations of a single species.

Several papers have described seasonal changes in tanaidacean density in Japan. Mukai (1971) and Kito (1975) documented seasonal fluctuations associated with brown macroalgae in the genus *Sargassum*. While the former study just identified tanaidaceans to the ordinal level (Tanaidacea), the population involved probably belonged to Tanaididae; the latter study identified the populations studied as “*Anatanais normani* (Richardson).” Both studies detected an acute annual density peak of tanaidaceans during the withering season for *Sargassum* seaweeds, i.e., around 2–4 months after the peak of the mean wet weight of the seaweeds. These results suggest that the tanaidaceans studied have a breeding period, and that this period partly overlaps the season of maximum growth and biomass accumulation of the seaweed. In a study on the distribution patterns of five peracaridans in relation to environmental factors in a shallow, brackish lagoon, Matsumasa and Kurihara (1988) included phenological data

from April 1984 to May 1985 for the tanaidid *Sinelobus stanfordi*, which inhabited the concrete wall of the lagoon embankment. The tanaidid density was quite low from April to June, increased in July, remained relatively constant until January, and then gradually decreased from February to May. As above, these data may indicate a breeding period for the *Sinelobus* population in the study area, possibly from June to November or December. Nakaoka et al. (2001) studied seasonal and between-substrate variation in the mobile epibiont community (including *Zeuxo* sp., discussed under 'Feeding habits' below) in a multi-species seagrass bed. Although the density of *Zeuxo* sp. was close to zero most months, an acute peak occurred in July (on *Zostera marina* L.) or August (on *Zostera caulescens* Miki), presumably associated with spathe use by the tanaidid. That study also found that *Zeuxo* sp. utilizes the spathes of both *Zostera* seagrass species from June to August, but detected juveniles only in August. These data indicate seasonal breeding, but the duration remains unknown.

23.3.4 Feeding Habits

Tanaidaceans show diverse feeding modes and include detritivores, scavengers, browsers, raptorial carnivores, opportunists, and filter-feeders (see Larsen et al. 2015). Nakaoka (2002) discovered an interesting mode in a *Zeuxo* species in Japan. Nakaoka (2002) first found *Zeuxo* sp. inside spathes of the seagrasses *Zostera marina* and *Z. caulescens*, and observed bored seeds. Through laboratory experiments and a monthly field survey, he showed that *Zeuxo* sp. consumes seagrass seeds by boring, constructs dwelling tubes in the spathes, and utilizes the spathes as the site of reproduction and as a nursery. However, *Zeuxo* sp. only seasonally utilizes the spathes, because flowering and fruiting by the seagrasses are restricted to a few summer months; during the remainder of the year, this tanaidid is nearly absent from the plants (Nakaoka et al. 2001).

Species in *Protanais* are one of the main indicators of successional stages in deep-sea wood-fall communities (McClain and Barry 2014), and are suspected of preying on *Xylophaga* wood-boring bivalves (another of the main indicators), their fecal pellets, or associated fecal bacteria (Larsen 2006; McClain and Barry 2014). Błażewicz-Paszkowycz et al. (2015b), however, found wood tissue and bacterial cells in the tanaidacean digestive tract, and nematodes and protists on the mouthparts, but no residues from bivalves. This suggests that, as with the hadal amphipod *Hirondellea gigas* (Birstein and Vinogradov, 1955) (Kobayashi et al. 2012), *Protanais birsteini* may be xylophagous and contain wood-digesting enzymes.

23.3.5 Parasites

Despite high local abundances of tanaidaceans, there are only a few reports of associated parasites or commensal animals. Peritrich ciliates, foraminiferans, lasaeid bivalves, tantulocarideans, and nicothoid copepods have been reported as ecto- or mesoparasites on tanaidaceans (Warén and Carrozza 1994; Fernandez-Leborans and Sorbe 2003; Larsen 2005; Oliver et al. 2010; Błażewicz-Paszkowycz 2014), and mites, harpacticoid copepods, and ostracods have been reported as commensals in their burrows or tubes (Johnson and Attramadal 1982b; Drumm 2005). A few ecto- and mesoparasites are known from Japanese waters. Kakui and Kohtsuka (2015: fig. 8) presented an image of unidentified peritrich ciliates parasitic on *Agathotanais misakiensis* Kakui and Kohtsuka, 2015 and Błażewicz-Paszkowycz et al. (2015b) reported fibrous filamentous bacteria attached to appendages of *Protanais birsteini*. In addition, Kakui (2015b) reported copepods parasitic on the tanaidaceans *Fageapseudes* sp. and *Leptochelia* sp. collected from the East China Sea and Pacific Ocean. The copepods proved to represent two undescribed species in the nicothoid genus *Rhizorhina*—the first report of copepods parasitic on tanaidaceans from the North Pacific, and only the third worldwide.

Until recently, only nematodes and acanthocephalan larvae had been reported as endoparasites of tanaidaceans (cf. Larsen 2005). Kakui (2014) added trematodes to this list, after discovering the encysted metacercariae of a trematode inside the body cavity of the parapseudid *Longiflagrum nasutus*. Morphology and DNA sequence data placed the trematode in the family Microphallidae, species of which chiefly utilize birds as the definitive host. The true diversity of animals parasitic on tanaidaceans may be greatly underestimated.

23.3.6 Predators

Tanaidaceans have been reported in stomach contents from diverse animal groups, including crustaceans, polychaetes, sea anemones, wading birds, and fishes (Shaffer 1979; Oliver et al. 1982; Larsen 2005). In Japan, Sano et al. (1984) found that 14 species of coral-reef fishes in 10 families consume tanaidaceans. Other studies (Nakagami et al. 2000; Nakamura et al. 2003; Inoue et al. 2005; Abe 2007) have found tanaidacean prey in shallow-water fishes. Tsubaki et al. (2012) reported tanaidacean as a rare prey component in stomach contents of the deep-sea fish *Caelorinchus anatirostris* Jordan and Gilbert, 1904 (Macrouridae). Kakui (2015a) reported *Zeuxo* sp. from the stomach of an intertidal goby (*Chaenogobius annularis* Gill, 1859) and compared the sex ratio and size-distribution of this tanaidacean in the stomach with those in an environmental substratum sample. The sex ratio in the tanaidacean prey was

significantly male biased, and males in the stomach were significantly larger than those in the environmental sample. Kakui (2015a) concluded that the observed sex and size bias of the prey was likely related to a prey-size preference by the fish, and perhaps to behavioral differences between male and female *Zeuxo* sp., as Johnson and Attramadal (1982b) had previously suggested for a confamilial species.

23.3.7 Ecological Surveys

Tanaidaceans are sometimes reported in ecological surveys documenting faunal assemblages. In Japan, a few such surveys have included this crustacean, including the four studies (Mukai 1971; Kito 1975; Matsumasa and Kurihara 1988; Nakaoka et al. 2001) mentioned above under ‘Phenology’; studies on temporal and spatial variation in community structure and the effects of environmental factors in a seagrass ecosystem (Yamada et al. 2007, 2014); studies of differences in the faunal assemblage among habitats (seagrass bed–coral surface–sandy bottom) or along a depth gradient (Nakamura and Sano 2005; Nakamura et al. 2012; Takada et al. 2012); and a study comparing tanaidacean diversity and abundance among deep-sea sampling sites (Błażewicz-Paszkowycz et al. 2015a). By using experimental substrata in a brackish lagoon, Matsumasa (1994) examined the effects of secondary substratum type on small crustacean assemblages, focusing on three amphipods and a tanaidid, *Sinelobus stanfordi*, and found that the type of secondary substratum directly determined the dominant species. Larsen and Shimomura (2008) investigated the recolonization ability of tanaidaceans on a shallow sandy bottom, and found that a burrower (*Parapseudes arenamans* Larsen and Shimomura, 2008) had greater recolonizing ability than a tube dweller (*Paranesotanais longicephala* Larsen and Shimomura, 2008).

23.4 Summary and Future Perspectives

As mentioned, the numbers of tanaidacean species hitherto reported both globally and from around Japan are likely a small fraction of the actual diversities. This is true even among putatively common shallow-water species; for example, even well-surveyed faunas in the vicinity of marine biological stations harbor many species new to Japan or previously undetected (Fig. 23.5) (Kakui and Kohtsuka 2015; Kakui and Naruse 2015; Nakano et al. 2015). Deep-sea tanaidaceans are even more poorly known.

Błażewicz-Paszkowycz et al. (2015a) detected at least 48 species in the KuramBio collection, none of which has yet been identified to the species level, and which likely include many undescribed species. Likewise, collections made during recent cruises by research/training vessels (e.g., *Nagasaki-maru*, *Seisui-maru*, *Soyo-maru*, *Tansei-maru*,

Toyoshio-maru) around Japan include many deep-sea and some shallow-water tanaidaceans (Fig. 23.5), with a high proportion of species new to Japan or undescribed (Kakui unpubl. data). Tanaidacean systematics is also in its infancy. Further molecular studies are badly needed at all taxonomic levels; even the monophyly of and relationships among the four “superfamilies” sensu Kakui et al. (2011) remain open to question.

Observations of living animals have recently elucidated various new aspects of tanaidacean biology, including a novel feeding mode (seed consumption; Nakaoka 2002), selfing (Kakui and Hiruta 2013), “skin-digging” activity in the holothuroid host by *Exspina typica* (Alvaro et al. 2011), the possibility of producing sound (Kakui et al. 2010), and thread production in apseudomorphs (Drumm 2005; Kakui and Hiruta 2014). This high rate of recent discoveries suggests that many other important discoveries remain to be made, especially with the application of approaches (e.g., breeding experiments) or techniques (e.g., bioimaging, microCT, volume electron microscopy, next-generation sequencing, micromanipulation, genome editing) not previously applied to tanaidaceans. New discoveries will not only broaden our knowledge of tanaidaceans, but will also better place this minor but attractive group in the broader contexts of crustacean biology and general biology.

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Figure legends

Fig. 23.1 Examples of modes of life among tanaidaceans. **a** A sphyrapodid in its burrow, **b** a pagurapseudid inhabiting an empty gastropod shell, **c** a tanaidid in its self-woven, tube-like nest (*arrow*) on a seagrass leaf (tube-dweller)

Fig. 23.2 Map showing records of tanaidaceans from around Japan (only those identified to the species level). The bathymetric contour interval is 1000 m. The map, plots, and bathymetric contour lines were generated with GMT5 software (Wessel et al. 2013) using the ETOPO1 dataset (Amante and Eakins 2009). The source of all records is given in Appendix

Fig. 23.3 Two sympatric species in *Zeuxo* found around the Misaki Marine Biological Station; ethanol fixed specimens. **a** *Zeuxo* sp. 1, with the carapace having small white marks on a dark background, and a dark antennular article 3; this species is abundant on seagrass leaves and sandy bottoms, but rare in holdfasts, **b** *Zeuxo* sp. 2, with the carapace having large white marks and a thick white transverse line on a dark background, and a white antennular article 3; this species is common in holdfasts but rare on seagrass and sandy bottoms

Fig. 23.4 Map showing records of sphyrapodids from around Japan. The five bathymetric contour lines indicate 200, 400, 600, 800, and 1000 m. The map, plots, and bathymetric contour lines were generated with GMT5 software (Wessel et al. 2013) using the ETOPO1 dataset (Amante and Eakins 2009). Based on data from Kakui et al. (2007); Kakui and Kajihara (2011); Błażewicz-Paszkowycz et al. (2013); and Kakui (unpubl. data)

Fig. 23.5 Apseudomorphs new to Japan and/or undescribed, collected from waters in the vicinity of marine biological stations (**a–c**) or during research cruises (**d–f**); fresh specimens. **a d e** Apseudids, **b f** parapseudids, **c** a pagurapseudid in gastropod shell

Table 23.1 Tanaidacean species recorded around Japan

Species/classification	reference ^a	Species/classification	reference ^a
APSEUDOMORPHA			
Apseudidae			
<i>Apseudes nipponicus</i>	Shiino 1937	<i>Akanthophoreus imputatus</i>	LS 2007b
<i>Carpoapseudes spinigena</i>	LS 2007b	<i>Akanthophoreus lispopygmos</i>	BP 2013
<i>Carpoapseudes varindex</i>	LS 2007b	<i>Akanthophoreus longiremis</i> ^b	KP 1978
<i>Fageapseudes brachyomos</i>	LS 2007b	<i>Akanthophoreus undulatus</i>	LS 2007b
<i>Paradoxapseudes littoralis</i>	Shiino 1952	<i>Akanthophoreus verutus</i>	BP 2013
Kalliapseudidae			
<i>Phoxokalliapseudes tomiokaensis</i>	Shiino 1966	<i>Chauliopleona armata</i> ^b	KP 1984
Metapseudidae			
<i>Apseudomorpha albida</i>	Shiino 1951b	<i>Chauliopleona hansknechti</i>	LS 2007a
<i>Hoplomachus toyoshious</i>	LS 2006	<i>Chauliopleona sinusa</i>	LS 2009
<i>Synapseudes setoensis</i>	Shiino 1951b	Anarthruridae	
Pagurapseudidae			
<i>Indoapseudes bamberi</i>	KaN 2015	<i>Anarthruopsis langi</i>	KP 1976
Parapseudidae			
<i>Longiflagrum nasutus</i>	Nunomura 2005	<i>Anarthruopsis longa</i>	KP 1984
<i>Longipedis fragilis</i>	LS 2006	<i>Keska sei</i>	BP 2013
<i>Parapseudes algicola</i>	Shiino 1952	<i>Siphonolabrum tenebrosus</i>	LS 2007b
<i>Parapseudes arenamans</i>	LS 2008	Colletteidae	
Sphyrapodidae			
<i>Kudinopasternakia balanorostrata</i>	KaK 2011	<i>Collettea cylindrata</i> ^b	KP 1970
<i>Pseudosphyrapus cuspidiger</i>	KaK 2011	<i>Collettea minima</i>	KP 1978
<i>Pseudosphyrapus malyutiniae</i>	BP 2013	<i>Leptognathiopsis langi</i>	LS 2007b
<i>Pseudosphyrapus quintolongus</i>	Ka et al. 2007	<i>Nippognathiopsis petila</i>	BP 2013
<i>Pseudosphyrapus serratus</i> ^b	KP 1984	<i>Tumidochelia knighti</i>	LS 2007a
Cryptocopidae			
Heterotanoididae			
Leptocheliidae			
Cryptocopoides			
		<i>Cryptocopoides arcticus</i> ^b	KP 1978
		<i>Cryptocopoides pacificus</i>	LS 2007b
Heterotanoididae			
		<i>Heterotanoides ornatus</i>	KP 1976
Leptocheliidae			
		<i>Leptochelia itoi</i>	Ishimaru 1985
		<i>Leptochelia savignyi</i>	Shiino 1951a
		<i>Makassaritanais modestus</i>	KT 1972
		<i>Mesotanais birdi</i>	LS 2007a
Leptognathiidae			
		<i>Biarticulata greveae</i>	KP 1976
		<i>Biarticulata parelegans</i>	KP 1970
		<i>Forcipatia rotundicauda</i>	LS 2007b
		<i>Leptognathia aneristus</i>	LS 2007b
		<i>Leptognathia bamberi</i>	LS 2007a
Nototanaidae			
		<i>Nesotanais ryukyuensis</i>	Ka et al. 2010
		<i>Nototanoides ohtsukai</i>	KaY 2013
		<i>Paranesotanais longicephalus</i>	LS 2008
Paratanaidae			
		<i>Paratanais impressus</i>	KT 1972
Pseudotanaidae			
		<i>Pseudotanais abathagastor</i>	BP 2013
		<i>Pseudotanais affinis</i> ^b	KP 1984
		<i>Pseudotanais intortus</i>	BP 2013
		<i>Pseudotanais nipponicus</i>	LS 2007b
		<i>Pseudotanais nordenskioldi</i>	KP 1978
TANAIDOMORPHA			
NEOTANAOIDEA			
Neotanaidae			
<i>Neotanais americanus</i>	KP 1978		
<i>Neotanais kuroshio</i>	LS 2007b		
<i>Neotanais oyashio</i>	LS 2007b		
<i>Neotanais tuberculatus</i>	KP 1970		
<i>Neotanais wolffi</i>	KP 1966b		
PARATANAOIDEA			
Agathotanaidae			
<i>Agathotanais hadalis</i>	LS 2007b		
<i>Agathotanais ingolft</i> ^b	KP 1970		
<i>Agathotanais misakiensis</i>	KaKo 2015		
<i>Agathotanais toyoshioae</i>	KaKo 2015		
<i>Paragathotanais abyssorum</i>	LS 2007b		
<i>Paranarthrura vitjazi</i>	LS 2007b		
Akanthophoreidae			
<i>Akanthophoreus crassicauda</i>	LS 2007b		
<i>Akanthophoreus gracilis</i> ^b	KP 1984		

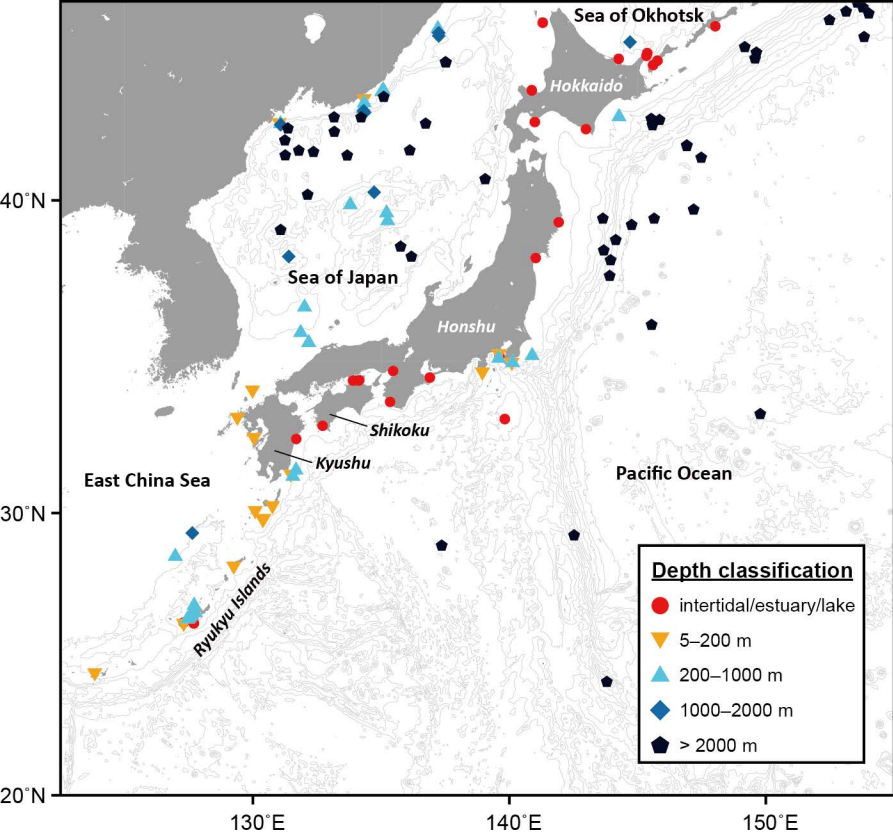
Table 23.1 (continued)

Species/classification	reference ^a	Species/classification	reference ^a
<i>Pseudotanaeis soja</i>	BP 2013	<i>Typhlotanaeis magdalensis</i>	LS 2007a
<i>Pseudotanaeis vitjazi</i>	KP 1970	<i>Typhlotanaeis ohtsukae</i>	LS 2007a
Tanaellidae		<i>Typhlotanaeis rectus</i>	KP 1978
<i>Arthrura andriashevi</i>	KP 1966a	<i>Typhlotanaeis simplex</i>	BP 2013
<i>Arthrura longicephala</i>	KP 1978	Family incertae sedis	
<i>Tanaella forcifera</i> ^b	KP 1984	<i>Leptognathia microcephala</i>	LS 2007b
<i>Tanaella kommitzia</i>	LS 2007a	<i>Leptognathia vinogradovae</i>	KP 1970
Tanaopsididae		<i>Metatanaeis cylindricus</i>	Shiino 1952
<i>Tanaopsis curta</i>	KP 1984	<i>Robustochelia robusta</i>	KP 1978
<i>Tanaopsis rugaris</i>	BP 2013		
Typhlotanaidae		TANAIDOIDEA	
<i>Larsenotanaeis kamchatikus</i>	LS 2007b	Tanaididae	
<i>Paratyphlotanaeis japonicus</i>	BP 2013	<i>Arctotanaeis alascensis</i>	Ka et al. 2012
<i>Peraeospinosus magnificus</i>	LS 2007b	<i>Protanaeis birsteini</i>	BP 2015b
<i>Torquella angularis</i>	LS 2007b	<i>Sinelobus stanfordi</i>	AO 1990
<i>Torquella elegans</i>	KP 1978	<i>Tanaeis tinhauae</i>	Ka et al. 2011
<i>Torquella grandis</i>	KP 1970	<i>Tanaeis vanis</i> ^b	Sieg 1980
<i>Typhlamia mucronata</i>	KP 1970	<i>Zeuxo coralensis</i>	Sieg 1980
<i>Typhlotanaeis compactus</i>	LS 2007b	<i>Zeuxo maledivensis</i>	Sieg 1980
<i>Typhlotanaeis kussakini</i>	KP 1970	<i>Zeuxo normani</i>	Shiino 1951a
<i>Typhlotanaeis longicephala</i>	KP 1970		

AO, Ariyama and Ohtani; BP, Błażewicz-Paszkowycz et al.; Ka, Kakui; KaK, Kakui and Kajihara; KaKo, Kakui and Kohtsuka; KaN, Kakui and Naruse; KaY, Kakui and Yamasaki; KP, Kudinova-Pasternak; KT, Kussakin and Tzareva; LS, Larsen and Shimomura

^a only a selected source is presented, ^b the distribution around Japan is questionable



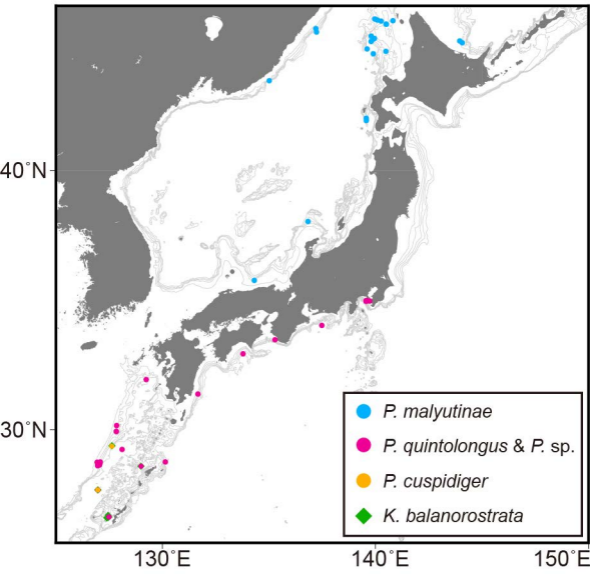


a



b





a**b****c****d****e****f**

Appendix: List of literatures for Fig. 23.2

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