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**Diverse Pereopodal Secretory Systems Implicated in Thread Production in an
Apseudomorph Tanaidacean Crustacean**

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20 **ABSTRACT** Among arthropods, various insects, spiders, and crustaceans produce
21 thread. The crustacean order Tanaidacea includes species that use thread mainly to
22 construct dwelling tubes. While thread production was previously known only in the
23 superfamilies Tanaoidea and Paratanaoidea, it was recently discovered in two species
24 in the family Kalliapseudidae (superfamily Apseudoidea), although information on the
25 morphology of the thread-producing system was lacking. Using histology, and light
26 and scanning electron microscopy, we found that the kalliapseudid *Phoxokalliapseudes*
27 *tomiokaensis* **comb. nov.** lacks the sort of glandular structures associated with thread
28 production in the pereonites, but has these structures in pereopods 1–6. We observed
29 four types of glandular systems defined by the types and distribution of glands they
30 contain: Type A (pereopod 1), Type B (pereopods 2 and 3), Type C (pereopods 4 and 5),
31 and Type D (pereopod 6). All types have small rosette glands and lobed glands; Type A
32 additionally has large rosette glands. The inferred thread-producing apparatus in *P.*
33 *tomiokaensis* is very different from that in the superfamilies Tanaoidea and
34 Paratanaoidea, suggesting that kalliapseudids evolved thread production independently
35 from the latter two groups.

36

KEY WORDS: Tanaidacea; Apseudoidea; Kalliapseudidae; thread production;
tegumental glands

INTRODUCTION

Among Arthropoda, the ability to produce and in many cases spin thread has been well studied in hexapods (e.g., silkworms; Sutherland et al., 2010) and arachnids (e.g., spiders; Craig, 2003). In crustaceans, thread-producing species are widely distributed among the Ostracoda, Decapoda, Amphipoda, and Tanaidacea, although the secretory system involved varies across taxa. In ostracods, a spinneret gland is located in the forehead, with the duct from the gland passing through the antenna and opening at the tip of the antennal exopod (Athersuch et al., 1989), which is sometimes called the “spinneret seta” (e.g., Meisch, 2000). Some amphipods have two different types of thread glands in pereopods 3 and 4, with a duct opening at the tip of each dactylus (Kronenberger et al., 2012b). Callianassid decapods have thread glands in several segments of maxilliped 3 and pereopods 2 and 3, with the opening located on the surface of the segment (Dworschak, 1998). Crustaceans use threads to construct a dwelling tube or space (Cerdeira et al., 2010), to stabilize the burrow wall (Dworschak, 1998), to attach themselves to the substrate or the mother’s body (Wouters and de

Grave, 1992; Vogt, 2008), or to make a cocoon in which they molt (Horne and Chivas, 2002).

The crustacean order Tanaidacea includes four extant superfamilies classified into two extant suborders (superfamily [SF] Apseudoidea in suborder [SO] Apseudomorpha; SFs Tanaoidea, Paratanaoidea, and Neotanaoidea in SO Tanaidomorpha) (Kakui et al., 2011). Before 2005, thread production was known only in the superfamilies Tanaoidea and Paratanaoidea (Larsen, 2005), species of which use the thread as an anchoring line, or to construct tubes in sediment or on substrata such as algae and animals (Johnson and Attramadal, 1982; Morales-Vela et al., 2008).

Blanc (1884) studied in detail the morphology of structures used to produce thread in the paratanaoid *Heterotanaïs oerstedii* (Krøyer, 1842). He described three pairs of secretory glands (“*glandes thoracique*”, or thoracic glands), one on each of pereonites 1–3, with each gland consisting of several glandular elements bearing a canal, and a common collecting duct opening at the tip of the unguis comprising the distal end of the pereopod (Fig. 1). Each glandular element is a cell having two nuclei and one canal (Blanc, 1884: fig. 19), suggesting that the glands are a type of lobed gland. Siewing (1953) was the first and only study to observe the histology of the thoracic glands in paratanaoids, in the species *H. oerstedii* and *Tanaissus lilljeborgi*

(Stebbing, 1891).

Species in the family Kalliapseudidae (Apseudoidea) typically inhabit estuarine or shallow marine environments, burrowing in the bottom (Drumm and Heard, 2011). Drumm (2005a, b) reported that two kalliapseudids, *Mesokalliapseudes macsweenyi* (Drumm, 2003) and *Psammokalliapseudes granulosus* Brum, 1973, that use their anterior pereopods to construct organic tubes within the sediment, which suggested that thread production might occur in a superfamily other than Tanaoidea or Paratanaoidea. Molecular phylogenetic studies (Drumm, 2010; Kakui et al., 2011) have indicated Kalliapseudidae to be basal to other apseudoids, although some of the analyses by Kakui et al. (2011) placed this family as the sister clade to a tanaidomorph clade, which includes the superfamilies having thread-producing species. The molecular phylogenies are thus inconclusive as to whether this ability evolved once, or more than once, in tanaidaceans. To address this question from another direction, we examined the morphology of the thread-producing system in a kalliapseudid species; similarity to tanaidomorph systems would suggest a single origin, whereas fundamental differences might suggest independent origins.

In a population of a kalliapseudid species in the Iorigawa River, Miyazaki, Japan (Miura et al., 2012), we discovered that individuals made dwelling tubes,

suggesting that they might be able to produce thread. In this study, we used light and scanning electron microscopy (LM and SEM, respectively) and histological techniques to examine the relevant secretion system(s) and the structure of the tube walls. We compare our results with the conditions in the superfamilies Tanaoidea and Paratanaoidea, and discuss the evolution of thread-producing ability in the order Tanaidacea.

MATERIAL AND METHODS

Kalliapseudids were collected from the estuary of the Iorigawa River, Miyazaki, Japan (32°28'46.91"N 131°40'44.65"E; retrieved from Google Earth) in August 2009 and April 2013. For observations of behavior and dwelling tubes, live individuals were kept for a week in a small aquarium, the bottom of which was covered with ca. 1.5 cm of sediment from the collecting site.

Animals and one dwelling tube were fixed in 70% ethanol, dehydrated in an ethanol series, and dissected with chemically sharpened tungsten needles. Two tanaidaceans were observed by LM (Olympus BX51) for species identification. For SEM, five animals and one tube were dried by hexamethyldisilazane treatment, sputter coated with gold, and observed at 15 or 30 kV accelerating voltage with a Hitachi

109 S-3000N instrument.

110 Fourteen specimens were fixed in Bouin's fluid. Paraffin sections 5 μ m thick
111 were prepared and stained with Mayer's hematoxylin and eosin (HE) using standard
112 techniques, and observed by LM (Olympus BX51).

113 For whole-mount observation of appendages, specimens were fixed in 4%
114 paraformaldehyde in phosphate-buffered saline (PBS, pH 7.4) and preserved in PBS.
115 The appendages from four specimens were dehydrated in an ethanol series, mounted in
116 glycerin, and observed by LM (Olympus BX51). The appendages from three other
117 individuals were treated with Proteinase K in ATL buffer (Qiagen) for 10–18 hours at
118 56°C to digest soft tissues, mounted in glycerin, and observed under a fluorescence
119 microscope (FM; Olympus BX50) through U-MWU (excitation 330–385 nm; emission
120 420 nm) or U-MWBV (excitation 400–440 nm; emission 475 nm) band pass filters. To
121 visualize protein distribution, the appendages from two individuals were transferred into
122 75% ethanol and subsequently stained with 0.2 μ g/ml Coomassie Brilliant Blue R-250
123 (CBB; Nacalai Tesque) in acetic ethanol, washed in acetic ethanol, dehydrated in an
124 ethanol series, mounted in glycerin, and observed by LM (Olympus BX51).

125 To examine living animals in situ, a digital movie was recorded with a Pentax
126 WG-III camera through a Nikon SMZ-10 stereomicroscope and edited with

MediaImpression 3.6.2 LE (ArcSoft). Digital images of appendages were taken with a Nikon DS-5Mc or DS-Fi1 camera system attached to an Olympus BX50 or BX51 microscope, and were processed with Adobe Photoshop/Illustrator CS6. A series of images taken at different focal planes was assembled by using CombineZM (Hadley, 2008).

The terminology used herein for orientation and morphology follows the usage of Larsen (2003); the terminology for tegumental glands follows the usage of Talbot and Demers (1993). Without knowing the exact functions of secretions from the pereopodal glandular systems we describe, we avoid referring to these systems as ‘thread-producing systems,’ acknowledging that some of the secretions from the pereopods may be in a form other than threads. We also avoid the term ‘spinning,’ which Craig (1997: p. 246) defines as “a process in which the protein is stressed at secretion, forcing the molecules to shear and orient into the parallel-beta conformation”; spinning usually involves a specialized behavior and is distinct from processes of simple secretion, deposition, or ejection.

We initially identified the species we treated as *Kalliapseudes tomiokaensis* Shiino, 1966. Drumm and Heard (2011) suspected that *K. tomiokaensis* actually belongs in the genus *Phoxokalliapseudes*, but Shiino’s (1966) original description

lacked information on two critical diagnostic characters. Unable to locate Shiino's (1966) type material, we observed a topotype specimen collected from Tomioka Bay in 1993, now deposited in the collections of the Amakusa Marine Biological Laboratory under catalog number 6-A-1-100. This specimen is conspecific with our material and shows the two critical diagnostic characters for *Phoxokalliapseudes* not included in the original description: four spines on the clypeus ['labrum' in Drumm and Heard (2011: p. 36)] and ventrodistal spiniform setae on antennule article 1 (Fig. 2A, B). Accordingly, we identify the kalliapseudid species we collected from Iorigawa River (Fig. 2C) as *Phoxokalliapseudes tomiokaensis* (Shiino, 1966) **comb. nov.**

RESULTS

Tube wall structure

All animals put into the aquarium immediately dug into the muddy-sand bottom and remained there throughout the observation period. A few holes that may have been burrow entrances were evident on the surface of the bottom. A week after the animals were placed in the aquarium, the sand was removed and some flexible tubes were found, one of which was occupied by an ovigerous female individual (Fig. 3A and Supporting Information Video S1). The tubes were coherent enough to be

picked up with forceps and were covered with adhering particles and sand grains. SEM observation showed that the inner tube walls (Fig. 3B) contained threads (Fig. 3b1) and amorphous secretory material (Fig. 3b2).

Pereopodal glandular systems

Horizontal sectioning of the whole body revealed that this species lacks thoracic glands in all pereonites, but instead bears secretory glands in pereopods 1–6 in both sexes. We classified the glandular systems in the pereopods into four types (Figs. 4–8): Type A, in pereopod 1; Type B, in pereopods 2 and 3; Type C, in pereopods 4 and 5; and Type D, in pereopod 6. All types contained small rosette glands and lobed glands; Type A additionally contained large rosette glands.

In Type A (Figs. 4 and 5), large rosette glands (Figs. 4b1, c1, 5B arrow) were located in the outer part of the merus and carpus (blue in Fig. 4A). Small rosette glands (Fig. 4b2, c2) were widely scattered throughout all pereopodal segments, which was also the case for Types B–D. The large and small rosette glands each had an independent duct opening on the segmental surface (Fig. 4C, arrowheads), with the larger size of gland having a larger opening diameter (cf. Fig. 4c1, c2). The rosette glands stained strongly with CBB (Fig. 4b1, b2), and stained red-violet with HE (Fig.

5B, arrow). Lobed glands (Fig. 5A, B) were present in the ischium, merus, and carpus (violet in Fig. 4A); these did not stain strongly with CBB (Fig. 4b1, asterisk), as was also the case with Types B–D. The lobed glands stained violet with HE (arrowheads in Figs. 5B, 6C, 7C, 7D, 8C). Ducts arising from the lobed glands were not evident in untreated whole-mount specimens, as was also the case for Types B–D. In samples treated with Proteinase K, however, around five duct-like structures were evident (Fig. 5D, d1: arrowheads); these connected to the root of the setal tuft on the dactylus (Fig. 5d1, asterisk). Around five of the setae in the tuft were thicker than the rest (red in Fig. 5E; white arrowhead in Fig. 5C), with each bearing a short, hollow tube at the base (Fig. 5C, black arrowhead) and a large pore at the distal end (Fig. 5e1, arrowhead).

In Type B (Fig. 6), lobed glands were present in the basis, ischium, merus, and carpus (violet in Fig. 6A). In specimens treated with Proteinase K, a fascicle of several duct-like structures was seen to pass through each segment (Fig. 6D, arrowheads), and seven pores opened at the tip of the dactylus (Fig. 6E, e1, F).

In Type C (Fig. 7), lobed glands were present in the carpus and propodus (violet in Fig. 7A). Two duct-like structures were evident in samples treated with Proteinase K (Fig. 7E: arrowheads), and a single pore was evident in the inner subdistal region of the dactylus (Fig. 7F, f1, f2).

In Type D (Fig. 8), a lobed gland occupied the proximal part of the carpus and distal part of the merus (violet in Fig. 8A). In samples treated with Proteinase K, one duct-like structure was evident (Fig. 8D, arrowheads), and single pore opened at the tip of the dactylus (Fig. 8E, e1).

DISCUSSION

Although we failed to trace gland-duct-pore connections for the lobed glands, the positions of the duct-like structures in Types A–D (arrowheads in Figs. 5D, d1, 6D, 7E, 8D) suggest that these are ducts arising from the glands, and if so they might also connect to the observed pores. Assuming gland-duct-pore connections, we concluded that *Phoxokalliapseudes tomiokaensis* bears secretory systems in all pereopods. We have no direct evidence that these systems are actually involved in secreting material for dwelling tubes, but the following observations suggest that the glandular systems in at least pereopods 1–3 are used for this purpose. First, a large volume of glandular tissue occupied each of pereopods 1–3, and pereopodal glandular tissue is known to be involved in thread production in other crustaceans, such as some amphipods and callianassid decapods. In addition, in specimens dried for SEM, we observed a solidified secretion in the openings to large rosette glands on pereopod 1 (Fig. 4c1).

Furthermore, the dactylus of pereopods 2 and 3 is long and acute (Fig. 6E, e1), and strikingly similar to pereopod 1 in species in superfamilies Tanaoidea and Paratanaoidea in which this pereopod is known to secrete threads for tube construction (Johnson and Attramadal, 1982; Krasnow and Taghon, 1997). Finally, the inner wall of the tube appears to contain amorphous secretions as well as threads (Fig. 3b1, b2), which is consistent with the hypothesis that different glands in at least the Type A and Type B secretory systems in pereopods 1 and 2–3, respectively, contribute different kinds of secretions in tube construction.

The CBB staining suggested that the composition of the secretions differs between the rosette glands and lobed glands, with the rosette glands secreting protein-rich material. The staining pattern for the lobed glands was similar to that for lobed glands in amphipods, which secrete mucopolysaccharides (Kronenberger et al., 2012a, b), although we did not use a stain specific for mucopolysaccharides.

We detected two types of setae in the setal tuft on the dactylus of pereopod 1; most setae were thin, but a few thicker ones were present (Fig. 5E). Though previous workers have regarded all setae in such tufts as aesthetascs, or chemoreceptors (see Drumm and Heard, 2011), we interpret the thicker setae as functioning to release secretions from the lobed glands, for the following reasons. First, the thinner setae

have a tiny terminal pore characteristic of aesthetascs, whereas the pore on the thicker setae is two orders of magnitude larger, is elongate, and extends subterminally (both types of openings are shown in Fig. 5e1). Second, although we could not trace one-to-one correspondence, the number of ducts connecting to the root of the setal tuft corresponds roughly to the number of thicker setae. Finally, we observed conspicuous droplets in the thicker setae (Fig. 9), compatible with a secretory function, but none in the thinner setae. If our interpretation is correct, this species is unique among crustaceans in having secretory setae located within a tuft of aesthetascs. The function of these putative secretory setae is unclear, but since the setal tuft faces outward, they might function to deposit secretions onto the inner wall of the tube.

From parsimony and other analyses of morphological characters, various authors (e.g., Gardiner, 1975; Sieg, 1983; Larsen and Wilson, 2002) have concluded that a system of thread-producing thoracic glands is a synapomorphy for a clade grouping superfamilies Tanaoidea and Paratanaoidea (Fig. 10A); according to this phylogenetic hypothesis, this system was present in the common ancestor of Tanaoidea + Paratanaoidea. However, relationships indicated in molecular phylogenies (Fig. 10B, B') (Kakui et al., 2011) suggest two equally parsimonious alternatives: one gain and one loss (white arrowheads in Fig. 10B, B') of a thread-producing system, or two gains

(black arrowheads in Fig. 10B, B'). Surprisingly, our study did not shed light on the origin of the tanaoidean/paratanaoidean (T/P) system, but instead detected what appears to be a quite different thread-producing system in a kalliapseudid (K) (Fig. 11). The two types of systems differ in the location of the glands (pereonites in T/P; pereopods in K); the number of pereopods associated with secretory function (three in T/P; six in K); and the occurrence of large rosette glands (lacking in T/P; present in K). These marked differences suggest that the thread-producing system in kalliapseudids evolved independently of that in the tanaoid/paratanaoid lineage.

Siewing (1953) found several differences in the thread-producing system between two paratanaoids (for example, in the position of the thoracic glands in the pereonites), which raised a question about homology. Our results indicating the convergent evolution of these systems means that homology cannot be assumed a priori even for all the thread-producing systems in tanaoideans and paratanaoideans, but must be tested by mapping the distribution of systems or even their morphological components onto a robust molecular phylogeny.

The pereopodal secretory apparatus in *P. tomiokaensis* appear to show high morphological diversity relative to comparable systems in other crustaceans; the lobed glands, for example, exhibit several types of ejectors (secretory setae and variously

placed dactylar openings), and the system of large rosette glands is restricted to only one pereopod. Most thread-producing species, including many insects, use a small number of systems or devices, and apply thread for only one or two functions (cf. Sutherland et al., 2010). Spiders, which have diverse spinning systems, use secretions from different glands for different functions (Vollrath and Knight, 2001). In *P. tomiokaensis*, it is unclear whether some pereopods produce secretions for specific functions other than tube building, or whether all pereopods contribute to different aspects of tube building. Our study raises many interesting questions for future research, such as the animals' behavior in tube building, the functional morphology of the glandular systems, the chemical composition of secretions from different glands and different pereopods, and the phylogenetic distribution of tube builders in Apseudoidea.

AUTHOR CONTRIBUTIONS

KK collected the animals, identified the species, observed living animals, and made the whole-mount and SEM observations. CH prepared stained sections and observed internal morphology. KK and CH wrote the paper.

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FIGURE LEGENDS

Fig. 1. Thread-producing system in *Heterotanaïs oerstedii*. The arrowheads indicate secretory glands, each consisting of a cluster of glandular elements. Modified from Blanc (1884).

Fig. 2. *Phoxokalliapseudes tomiokaensis* (Shiino, 1966) **comb. nov.** **A, B**, male topotype specimen (No. 6-A-1-100); **C**, individuals from Iorigawa River. **A**, two (left side) of four spines (arrowheads) on clypeus; **B**, two distal spiniform setae (both broken; arrowheads) on ventral side of article 1 of left antennule, LM image; **C**, living female (left) and male (right). Scale bars: A, B = 100 μm ; C = 1 mm.

Fig. 3. Dwelling tube and tube-wall structure in *P. tomiokaensis*. **A**, living animal inside a dwelling tube; arrow, left cheliped; **B**, SEM image of inner surface of tube cut open along long axis (yellow and blue squares indicate positions of enlargements in b1 and b2, respectively); **b1**, threads in wall, two of which are indicated by arrowheads; **b2**, amorphous secretion (arrowhead) in wall. Scale bars: B = 1 mm; b1, b2 = 50 μm .

Fig. 4. Type A glandular system in pereopod 1 of *P. tomiokaensis*. **A**, distribution of

glands, LM image, colored by using Photoshop CS6; blue, large rosette glands; violet, lobed glands; **B**, ischium to dactylus stained with CBB, outer view, LM image; **b1**, higher magnification view of a large rosette gland and its opening (arrowhead), and a lobed gland (asterisk); **b2**, higher magnification view of a small rosette gland and its opening (arrowhead); **C**, distribution of openings (arrowheads) of large and small rosette glands from ischium to carpus, outer view, SEM image; **c1**, higher magnification view showing opening of large rosette gland; **c2**, higher magnification view showing opening of small rosette gland. Scale bars: A, B, C = 100 μm ; b1, b2 = 50 μm ; c1, c2 = 1 μm .

Fig. 5. Type A glandular system in pereopod 1 of *P. tomiokaensis*. **A**, lobed glands in ischium and merus, outer view, LM image; **B**, cross section of merus, HE stained, LM image; arrowhead, large rosette gland; arrow, lobed gland; *d*, dorsal; *o*, outer; **C**, setal tuft on dactylus, Proteinase K treated, outer view, LM image; white arrowhead, thicker seta; black arrowhead, short hollow tube; **D**, distribution of ducts from ischium to propodus, Proteinase K treated, outer view, FM image through U-MWU filter; arrowheads, ducts; **d1**, enlargement from D, FM image through U-MWBV filter; arrowheads, ducts; asterisk, setal tuft prepared for next intermolt; **E**, setal tuft on

dactylus, outer view, SEM image, colored by using Photoshop CS6; red, thicker setae; **e1**, enlargement of tip of one thicker and three thinner setae; arrowhead, subterminal pore on thicker seta; arrows, terminal pores on thinner setae. Scale bars: A–C, d1, E = 50 μm ; D = 100 μm ; e1 = 5 μm .

Fig. 6. Type B glandular system in pereopods 2 and 3 of *P. tomiokaensis*. **A**, distribution of glands, LM image, colored by using Photoshop CS6; violet, lobed glands; **B**, lobed gland in carpus, outer view, LM image; **C**, cross section of carpus, HE stained, LM image; arrowhead, lobed gland; *d*, dorsal; *o*, outer; **D**, distribution of ducts (arrowheads) from basis to propodus, Proteinase K treated, outer view, FM image through U-MWU filter; **E**, dactylus and distal half of propodus, outer view, SEM image; **e1**, higher magnification view showing openings (arrowheads) on tip of dactylus; **F**, diagram indicating positions of seven openings evident in e1. Scale bars: A, D, E = 100 μm ; B, C = 50 μm ; e1 = 1 μm .

Fig. 7. Type C glandular system in pereopods 4 and 5 of *P. tomiokaensis*. **A**, distribution of glands, LM image, colored by using Photoshop CS6; violet, lobed glands; **B**, lobed glands in the carpus and propodus, outer view, LM image; arrowheads,

lobed glands; **C**, **D**, cross sections of carpus and propodus, respectively, HE stained, LM images; arrowheads, lobed glands; *d*, dorsal; *o*, outer; **E**, distribution of ducts in propodus, Proteinase K treated, outer view, FM image through U-MWU filter; arrowheads, ducts; **F**, opening (arrowhead) on dactylus, inner view, SEM image; **f1**, enlargement from **F**; **f2**, further enlargement from **F**. Scale bars: A = 100 μm ; B–E = 50 μm ; F, f1 = 10 μm ; f2 = 1 μm .

Fig. 8. Type D glandular system in pereopod 6 of *P. tomiokaensis*. **A**, position of gland, LM image, colored by using Photoshop CS6; violet, lobed gland; **B**, lobed gland in carpus, outer view, LM image; arrowhead, lobed gland; **C**, cross section of carpus, HE stained, LM image; arrowhead, lobed gland; *d*, dorsal; *o*, outer; **D**, duct (arrowheads) running from merus to propodus, Proteinase K treated, inner view, FM image through U-MWU filter; **E**, dactylus and distal half of propodus, ventral view, SEM image; **e1**, enlargement from **E** showing distal tip of dactylus. Scale bars: A, E = 100 μm ; B–D = 50 μm ; e1 = 1 μm .

Fig. 9. Setal tuft on dactylus of pereopod 1 in *P. tomiokaensis*. The thicker setae (arrowheads) contain droplets. Scale bar: 50 μm .

Fig. 10. Hypotheses of phylogenetic relationships within Tanaidacea. **A**, tree based on morphological characters (after Larsen and Wilson, 2002); relationships within Apseudoidea are according to Sieg (1983); **B**, **B'**, maximum likelihood (B) and maximum parsimony (B') trees based on 18S rRNA gene sequences (modified from Kakui et al., 2011). A, Apseudoidea; N, Neotanaoidea; T, Tanaoidea; P, Paratanaoidea; k, Kalliapseudidae; g, gain of thread-producing ability; l, loss of thread-producing ability; black arrowheads, two-gain evolutionary scenario; white arrowheads, one-gain and one-loss evolutionary scenario; blue branches, superfamilies Tanaoidea and Paratanaoidea; red branch, Kalliapseudidae.

Fig. 11. Diagrams of pereopod-associated glandular systems in Tanaidacea. **A**, glandular systems in *P. tomiokaensis* (Kalliapseudidae); **B**, thread-producing glandular systems in *H. oerstedii* (representative of thread-producing systems in Tanaoidea and Paratanaoidea), after Blanc (1884); P1–6, pereonites 1–6; blue, large rosette glands; violet, lobed glands and ducts.

SUPPORTING INFORMATION

Video S1. Living kalliapseudid in dwelling tube.





















