# Burrow morphology of two callianassid shrimps, *Callianassa japonica* Ortmann, 1891 and *Callianassa* sp. (= *C. japonica*: de Man, 1928)(Decapoda: Thalassinidea)

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***Abstract.*** — Polyester resin casts of burrows of the thalassinidean shrimps, *Callianassa japonica* Ortmann, 1891 and *Callianassa* sp. (= *C. japonica*: de Man, 1928), were collected on intertidal sandflats in western Kyushu, Japan. The difference in basic architecture of the burrows of these two species was obvious: the burrow of *C. japonica* had alternating shafts and chambers, with a single surface opening, while that of *Callianassa* sp. was basically Y-shaped, with two surface openings. The average dimensions of individual components of the burrows are given for each species and possible functions of these components, especially with regard to the shrimps' trophic modes, are discussed.

## Introduction

Thalassinidean shrimps are one of the commonest mega-invertebrates in marine intertidal and subtidal sediments. These organisms reside in a variety of burrows for shelter, reproduction, and feeding. In recent years, the functional morphology of thalassinidean burrows, especially in relation to trophic modes, has been intensively investigated (e.g., see reviews in Dworschak, 1983; Griffis & Suchanek, 1991; Nickell & Atkinson, 1995). The burrow architectures of thalassinideans, and callianassids in particular, have attracted a great deal of attention. Of Japanese callianassids, the burrow morphology was described only for *Callianassa japonica* Ortmann (Miyazaki, 1937; Ohshima,

1967; Utashiro et al., 1972; Tamaki et al., 1992). However, there are some inconsistencies in their descriptions of the burrow structures.

In his revision of Japanese callianassids, Sakai (1969) concluded that several reported species of the genus *Callianassa* should be grouped into two species, *C. petalura* Stimpson, 1860 and *C. japonica* Ortmann, 1891. The synonyms of *C. japonica* Ortmann included *C. harmandi* Bouvier, 1901, *C. californiensis* var. *japonica* Bouvier, 1901, and *C. californiensis* var. *bouvieri* Makarov, 1938. However, careful examination of specimens collected from a number of intertidal sandflats along the estuary - open sea gradient in western Kyushu, Japan [from Ariake Sound (estuary), via Tachibana Bay, to East China Sea (open sea) (Fig. 1)] has disclosed that the definition of *C. japonica* made by Sakai is misleading. The material examined apparently fits his definition of *C. japonica*, but, in fact, it includes two species: one is the true *C. japonica* and the other can be differentiated from that species and referred to as *C. japonica*: de Man, 1928 which Sakai merged with the former species (Manning & Tamaki, in preparation; hereafter in the present paper, the latter species will be referred to as *Callianassa* sp.). This will help resolve the ambiguity of earlier information about the burrows of *C. japonica* Ortmann, which may have been caused by not only taxonomic confusion but also by intraspecific variation in the burrow architecture. The previous papers

on the burrows of *C. japonica* Ortmann need to be assessed in terms of both species identity and their burrow architecture, based on our belief that burrow morphology is species-specific.

The purpose of the present paper is to establish the burrow morphology of the two species on the basis of resin casts of burrows collected from their habitats in western Kyushu. The possible functions of individual components of the two types of burrows will be discussed from a comparative viewpoint.

## Materials and Methods

*Distribution of* Callianassa *sp. and* C. japonica *in the study area*

The presence of *Callianassa* sp. and *C. japonica* in their respective habitats is easily detected by their numerous burrow openings and sediment mounds/funnel-shaped craters around the openings on the sandflat surface. For our study area (Fig. 1), Manning & Tamaki (in preparation) have revealed that the major habitat of *Callianassa* sp. is basically characterized by the relatively small-sized sandflats and sandy beaches of medium - fine sands located in 'the open-sea regime' ( = East China Sea + Tachibana Bay + the outermost 1/3 part of Ariake Sound), while *C. japonica* occurs almost exclusively on the extensive sandflats of medium - fine sands located in the middle 1/3 part of Ariake Sound. Table 1 of Sakai (1969), which lists the localities of the specimens examined from the Japanese waters, includes various habitat types ranging from estuaries to the open sea. These localities include the Arao sandflat situated in the innermost portion of the middle part of Ariake Sound and Higashihama beach situated in Tachibana Bay (Fig. 1). For a long time, the present first author (A. T.) and his co-workers have investigated various ecological aspects of the species misidentified as *C. japonica* Ortmann
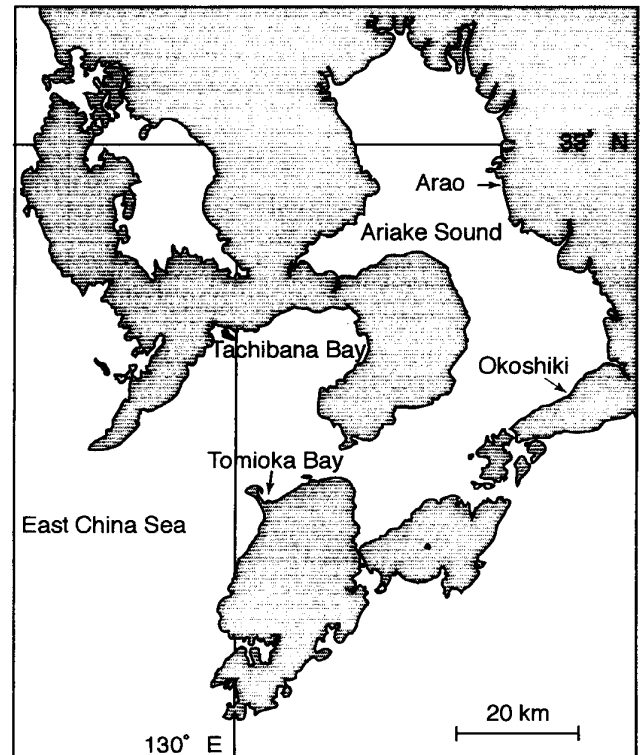


Fig. 1. Location of the study area in western Kyushu, Japan. Higashihama beach in Sakai (1969) is identical to the Tomioka Bay sandflat in Tamaki *et al.* (1992), Tamaki *et al.* (1997), and in the present study.

inhabiting an intertidal sandflat (called the Tomioka Bay sandflat) in Tachibana Bay, which is identical to the above-mentioned Higashihama beach [Tomioka Bay is a branch bay of Tachibana Bay, located just offshore of the sandflat (Fig. 1)] (e.g., Tamaki *et al.*, 1992; Tamaki *et al.*, 1997). At present all the specimens from the Tomioka Bay sandflat have been identified as *Callianassa* sp. Since, in the present study area, *Callianassa* sp. and *C. japonica* have been designated as 'open-sea species' and 'estuarine species', respectively, the salinity values of the waters in which they are distributed will provide a cue to the species identification occurring in the other Japanese waters; according to Manning & Tamaki (in preparation), *Callianassa* sp. is found in the salinity range of 34.0–30.5‰ in July (10-year-averaged values measured at a

depth of 5 m from the sea surface), while *C. japonica* occurs in the range of 30.5–28.5‰ (as above). Moreover, the difference in the breeding season (as determined by the occurrence of ovigerous females) will be another cue: from June to October for *Callianassa* sp. (Tamaki et al., 1997) and from late February to September for *C. japonica* (Tamaki, unpublished).

*Collection of burrow casts and laboratory treatments*

The burrow casts of *Callianassa* sp. and *C. japonica* were collected on the Tomioka Bay sandflat during 23 to 24 April 1989 and on the Okoshiki sandflat (located in Ariake Sound) during 6 to 7 April 1997, respectively (Fig. 1). Following Hamano (1990), a polyester-resin liquid mixture (the volumetric ratio of polyester resin: wax: catalyst = 1000: 20: 4–6) was poured into a polypropylene collar enclosing a few burrow openings on the sandflat surface. About 24 h later the burrow casts were recovered. The success of each casting was evaluated by the depth of the lowermost position of the cast relative to the thickness of the sand layer; the thickness on the Tomioka Bay sandflat varied from about 30 to 40 cm (Tamaki et al., 1997), below which lay an accumulation of gastropod and bivalve shell remains; and that on the Okoshiki sandflat varied from 66 to 88 cm, as judged from the reach of a 100 cm long coring tube (Tamaki, unpublished), but what existed below the sand layer could not be confirmed. Later in the laboratory each burrow cast was photographed. After identification of the individual components constituting the burrow (shown in Fig. 3), their numbers per burrow were recorded. Furthermore, a variety of dimensions (lengths and angles) for the components were measured using either a vernier caliper to the nearest 0.1 mm or a graduator to the nearest 0.1°. Based on the averaged value for each component from all burrow casts, a representative burrow configuration was synthesized for each *Callianassa* species for comparison.

## Results

*Major difference in the burrows of the two species*

A total of eight and six burrow casts were collected for *Callianassa* sp. and *C. japonica*, respectively. Of these only one burrow cast for each species was reasonably complete (Fig. 2a, right & Fig. 2b, left), possessing every component and occupying almost the entire sand column at each collection site (ca. 30 cm and ca. 65 cm). For *Callianassa* sp., four other burrow casts would also have reached the bottom of the sand layer, suggesting the use of the entire sand column by the shrimp, but some components were not successfully cast along the way. The other three burrow casts lacked the lower parts. For *C. japonica*, the other five burrow casts could not have reached the bottom of the sand layer. The difference in the basic architecture of the burrows of the two species is obvious. The burrow of *Callianassa* sp. is basically Y-shaped with two openings on the sandflat surface, while that of *C. japonica* has a single surface opening. Sometimes shrimps of both species had been entrapped in burrow casts. Including our other observations for both species, only a single 'adult-sized' (the definitions are given below) individual has been found to inhabit each burrow.

*Terminology and definition of dimensions*

Before going further, the definition of terms is given to designate the basic components of the burrows (Figs. 2a, b & 3a, b). We avoid the addition of any qualifiers to the terms, so as not to invoke any functions associated with the components. a) Components common to both species: 1) 'chambers'=swollen parts distributed at intervals along the burrow axis; 2) 'shafts' and 'tunnels'=According to Frey (1973), a 'shaft' means a dominantly vertical bur-
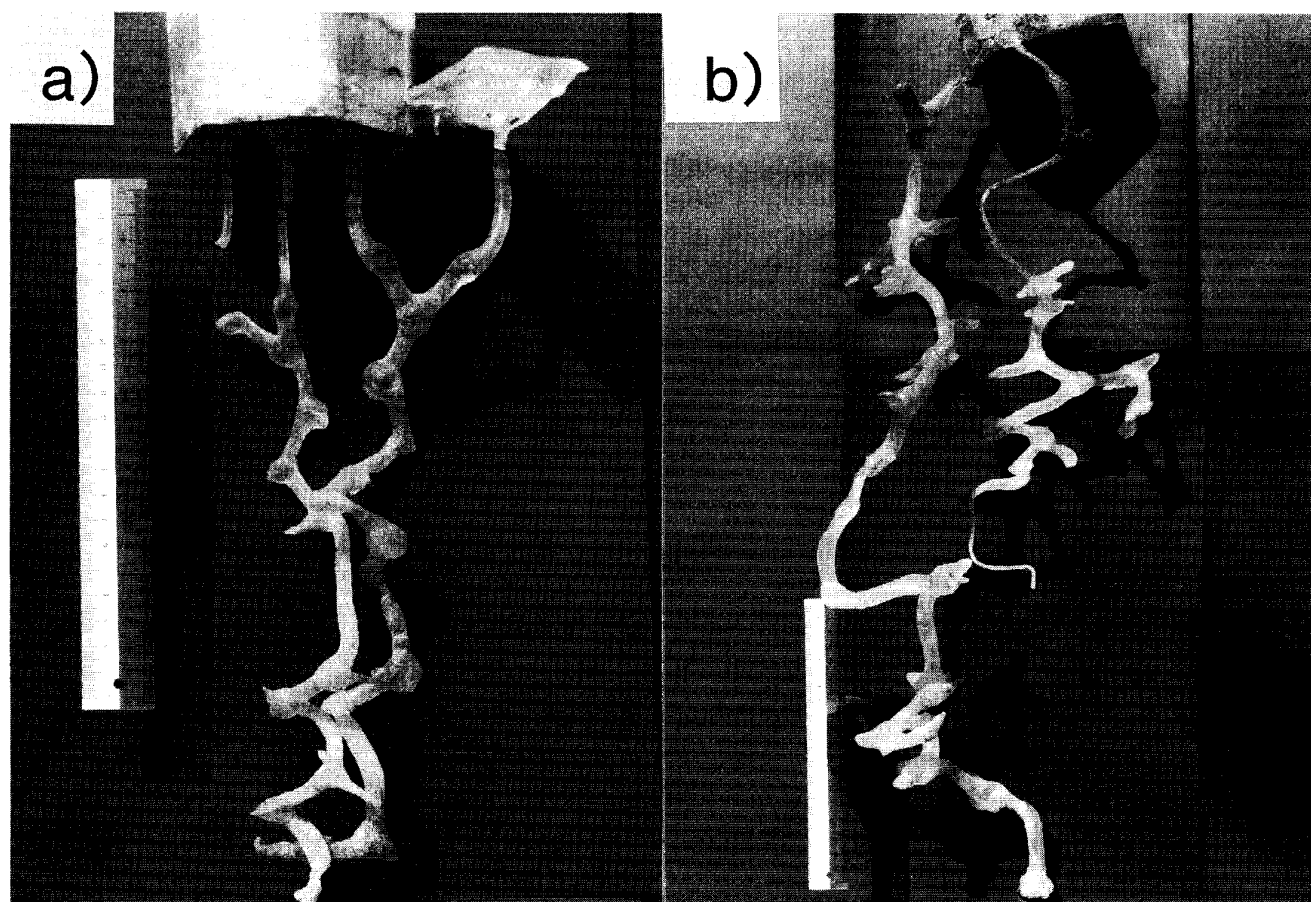
Fig. 2. a) Two burrow casts of *Callianassa* sp. collected on the Tomioka Bay sandflat. The right cast was the most complete of all eight casts obtained (see text). For the left cast, the left vertical shaft of the upper Y (see Fig. 3a) was incomplete. b) Two burrow casts of *C. japonica* Ortmann collected on the Okoshiki sandflat. The left cast was the most complete of all six casts obtained (see text). For the right cast, the central axis of the burrow from the sandflat surface divides into two in the lower part (see text). For both a) and b), the full range of the scale is 20 cm.

row, or a dominantly vertical component of a burrow system having prominent vertical and horizontal parts, while a 'tunnel' (≡'gallery') is a dominantly horizontal burrow, or a dominantly horizontal component of a burrow system. In the present burrows, although some interconnections between chambers are obliquely or horizontally oriented, apparently each species burrow as a whole may well be regarded basically a shaft system. Thus we designate every interconnection between two adjacent chambers as a 'shaft' irrespective of its actual orientation; and 3) 'branches'≡lateral projections (if any) from chambers, of which lengths are

mostly shorter than those of the nearby shafts, some tapering ('tapered branch') and others terminating in a single chamber ('chambered branch') (Figs. 2a, b & 3a, b). b) Components peculiar to *Callianassa* sp.: 1) 'the Y'≡the burrow as a whole; 2) 'the central chamber'≡the chamber at the node in the Y; and 3) 'the upper Y' and 'the lower Y'≡the portion of the Y above the central chamber (excluding the chamber) and that portion below (including the chamber), respectively. Secondly, to describe a synthesized burrow architecture for each species, the dimension of each component is given as a mean ± SD value ($n$ = number of measurements). The value

of $n$ varied for each component, depending on its availability from all burrow casts. To obtain the diameter values of a shaft, whose cross section approximated a circle, the data from three equidistant points along the shaft axis were normally taken, with one-three additional measurements made for the longer or winding shafts.

### Burrow of Callianassa sp.

Fig. 3a shows a representative burrow architecture of *Callianassa* sp., which is described as follows: 1) there were no laterally creeping, tunnels from any part of the burrow; 2) in the chambered branches there was no evidence for any stored material; 3) the maximum depth and the maximum horizontal extension of the burrow is $363.6 \pm 58.6$ mm ($n = 5$) and $88.0 \pm 27.7$ mm ($n = 4$); 4) the depth of the lowermost point of the upper Y ( = top of the central chamber) is $96.3 \pm 22.3$ mm ($n = 8$), occupying ca. 26% of the entire burrow depth; 5) the shape of the upper Y is almost symmetrical, composed of the two parallel 'vertical shafts' and the lower, two 'oblique shafts' joining at the central chamber. The mean %-difference in the diameters of the two vertical shafts from each of the burrow casts ($n = 5$) is only 8.7 %; the diameter of the vertical shaft is $5.9 \pm 1.0$ mm ($n = 39$). The mean %-difference in the diameters of the two oblique shafts from each of the burrow casts ($n = 6$) is smaller (3.4 %); the diameter of the oblique shaft is $7.8 \pm 0.8$ mm ($n = 42$), which is larger than in the vertical shaft. The narrower, vertical shafts may not be usually passed through by the shrimp. Each oblique shaft has one chamber ('oblique-shaft chamber') just below the junction with the vertical shaft. The chamber is ellipsoid in shape, with the $13.2 \pm 1.9$ mm major axis ($n = 14$) and the $10.8 \pm 1.0$ mm minor axis ($n = 14$). The horizontal distance between the two vertical shafts at their centers is $47.9 \pm 7.6$ mm ($n = 5$). The length of the vertical shaft is $82.0 \pm 26.4$ mm ($n = 8$). The interior angle between the two oblique shafts (at the central chamber) is $54.3 \pm 14.0°$ ($n = 7$); and 6) the lower Y, starting from the central chamber, is a repetition of shafts and chambers with lateral branches in places. The number of the chambers per burrow that would have reached the bottom of the sand layer is $8.6 \pm 2.3$ ($n = 5$). The chambers are more spherical than the oblique-shaft chambers of the upper Y. For the lower Y, therefore, the representative diameter of a chamber as a 'sphere' was calculated as a mean of three orthogonal diameters. Based on each mean value, the diameter of the central chamber and that of the other chambers are $15.2 \pm 2.0$ mm ($n = 8$) and $13.8 \pm 2.1$ mm ($n = 41$), respectively [overall, $14.1 \pm 2.1$ mm ($n = 49$)]. The interior angle between the uppermost shaft of the lower Y and one ('right') oblique shaft of the upper Y (at the central chamber) is $151.4 \pm 19.5°$ ($n = 7$), giving the mean interior angle of $154.3°$ against the other ('left') oblique shaft. This indicates the almost vertical (to the sandflat surface) orientation of the uppermost shaft of the lower Y. The length of the shaft is $33.3 \pm 23.5$ mm ($n = 44$). The diameter of the shaft is $6.5 \pm 1.7$ mm ($n = 128$), about half that of the chamber and slightly smaller than that of the oblique shaft of the upper Y. The shaft diameter gives an estimate for the size of the shrimp present in the burrow. Tamaki *et al.* (1992) have presented a linear regression equation of the total length (TL, mm) of Callianassa sp. on carapace width (CW, mm), as follows: $TL = 4.38CW + 2.67$ ($n = 36$; $R^2 = 0.74$; $p < 0.001$). If it is assumed that the shaft diameter approximates the CW of shrimps, an estimated TL of $31.1 \pm 10.1$ mm is obtained. The shrimps of these sizes are 'adult' members of the population, ranging from the 1-year-old to 2-year-old (the maximum life span) cohorts (Tamaki *et al.*, 1997). This mean TL is close to the

a)

upper Y

lower Y

vertical shaft

oblique-shaft chamber

oblique shaft

central chamber

shafts

chambers

chambered branch

tapered branch

50 mm

b)

shafts

chambered branch
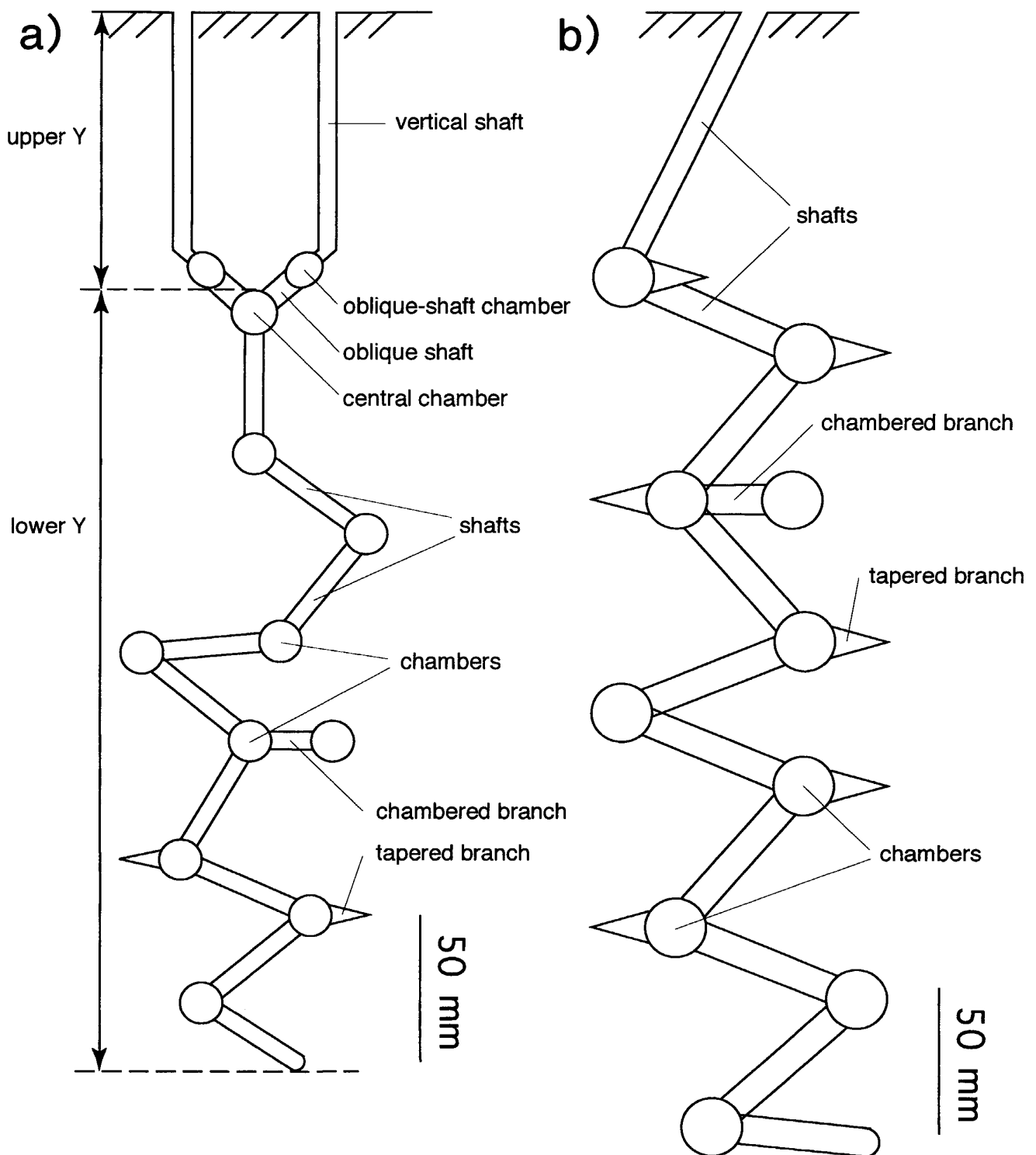
tapered branch

chambers

50 mm

Fig. 3. The representative burrows of a) *Callianassa* sp. and b) *C. japonica* Ortmann. For the definition of individual components, see text. The length dimension of each component is based on the averaged value from multiple burrow casts (see text). The angle dimension given in the text is not precisely reproduced due to the limitation of the projection from 3D to 2D.

mean shaft length. The arrangement of two adjacent shafts varies from nearly straight to spiral, overall giving the adjacent interior angle of $102.0 \pm 40.1°$ ($n = 40$). The number of branches per burrow is $2.8 \pm 1.5$ ($n = 6$), protruding from 33% of the chambers along the lower-Y axis. The ratio of the numbers of tapered and chambered branches is about 2:1. The length of the branch is $12.9 \pm 5.3$ mm ($n = 17$), 38% of the shaft length.

*Burrow of* C. japonica

Fig. 3b shows a representative burrow architecture of *C. japonica*, which is described as follows: 1) there were no laterally creeping, tunnels from any part of the burrow; 2) in one burrow cast, there was an exception to the normal branching pattern (the lower part in Fig. 2b, right), in which the 'branch' did not terminate in a chamber but had further two sets of a shaft and a chamber (the dimensions about these shafts and chambers are incorporated into the calculation of the overall mean ± SD); 3) in the chambered branches there was no evidence for any stored material; 4) the shaft cross section was roughly circular but seemed more irregular than in the shaft for *Callianassa* sp.; 5) the maximum depth of the burrow varies from 237.0 to 645.0 mm, with $392.0 \pm 138.8$ mm mean ± SD ($n = 6$). The maximum horizontal extension varies from 12.4 to 182.0 mm, with $97.8 \pm 72.7$ mm mean ± SD ($n = 4$); 6) the number of chambers along the central axis of the burrow varies from 4 to 16, with the mean ± SD of $8.5 \pm 5.0$ ($n = 6$). The chamber diameter is $20.3 \pm 3.6$ mm ($n = 51$); 7) the uppermost shaft is vertical or oblique to the sandflat surface, the interior angle being $66.7 \pm 22.5°$ ($n = 6$). The arrangement of two adjacent shafts varies from nearly straight to spiral, overall giving the adjacent interior angle of $113.5 \pm 33.5°$ ($n = 51$); 8) the depth and length of the uppermost shaft (from the opening on the sandflat surface to the top of the upper-

most chamber) is $81.4 \pm 33.7$ mm and $90.3 \pm 28.1$ mm ($n = 6$), respectively. The length for the subsequent shafts is $45.3$-$\pm 32.9$ mm ($n = 49$), and the overall value, including the uppermost-shaft length, is $50.2 \pm 35.2$ mm ($n = 55$). The diameter of the uppermost shaft is $7.7 \pm 2.8$ mm ($n = 25$), being smaller than that for the subsequent, lower shafts [$10.2 \pm 2.3$ mm ($n = 169$)] and overall giving the value of $9.9 \pm 2.5$ mm ($n = 194$). This value is about half the chamber diameter. The TL of an individual of *C. japonica* that resides in the burrow can be estimated as for *Callianassa* sp. [6] in the preceding section] by using the equation, $TL = 4.19CW + 19.01$ [$n = 34$; $R^2 = 0.66$; $p < 0.001$ (Tamaki, unpublished)], which gives an estimated TL of $61.7 \pm 28.6$ mm. Since the study on the whole population structure of *C. japonica* is still in progress, precise judgment could not be made for the assignment of the present shrimps to cohorts. Fortunately, recourse can be made to Fig. 2 of Utashiro *et al.* (1972) (for the species identification, see Discussion), in which the TL-frequency distribution is shown, so that the present specimens may be regarded as members of the two largest size-classes of the population. This mean TL is a little greater than the mean shaft length; 9) the number of branches per burrow is $7.2 \pm 5.3$ ($n = 6$). The length of the branch is $17.8 \pm 9.4$ mm ($n = 43$), 36% of the shaft length. Along the central burrow axis, the proportion of the chambers that have branches varies from 40 to 100%, with a mean of 80% ($n = 6$). Of these branches the number of tapered branches is far greater than that of chambered branches (about 10:1).

## Discussion

Now that the burrow morphologies of *Callianassa* sp. and *C. japonica* have been described, comparisons can be made with those already reported by Miyazaki (1937), Ohshima (1967), Utashiro *et al.*

(1972), and Tamaki *et al.* (1992). They all collected specimens from intertidal sandflats with medium to fine sands and identified them as *C. japonica* Ortmann. The basic common components of the burrows in these four papers are alternating shafts and chambers, which were regarded as the places for passage and turn-round by the shrimp, respectively.

In the first place, the specimens examined by Tamaki *et al.* (1992) were derived from the present study area for *Callianassa* sp.

Although Miyazaki (1937) gave no detailed accounts of the morphological characters for his specimens, two lines of evidence suggest that his species would be *C. japonica*: 1) the reproductive season was described as from mid-March to around the end of August at his study site located in the middle of Tokyo Bay, central Honshu and 2) a long-term averaged salinity value in August there is ca. 29‰ (Coastal Oceanography Research Committee, The Oceanographical Society of Japan, 1985). The burrow cast made with plaster of Paris, attaining a depth of up to 30 cm, basically composed of alternating (vertically to obliquely oriented) shafts and chambers, with a single surface opening. All these features accord with those of *C. japonica* given in the present study.

The study site of Ohshima (1967) was located in Usu Bay, Hokkaido, northern Japan. He gave neither morphological accounts of the species nor its life-history information. The salinity range of the bay in July, 26.6–32.8‰ [converted from chlorinity values given in Ohshima (1963)], cannot be a clue toward the species identification because the range covers the potential habitats of both species. His description of the burrow morphology based on the plaster of Paris casts conforms well with that of *Callianassa* sp. in the present study (Fig. 3a). Fig. 4 shows the schematic burrow architectures after Fig. 1 of Ohshima (1967), which is sum-
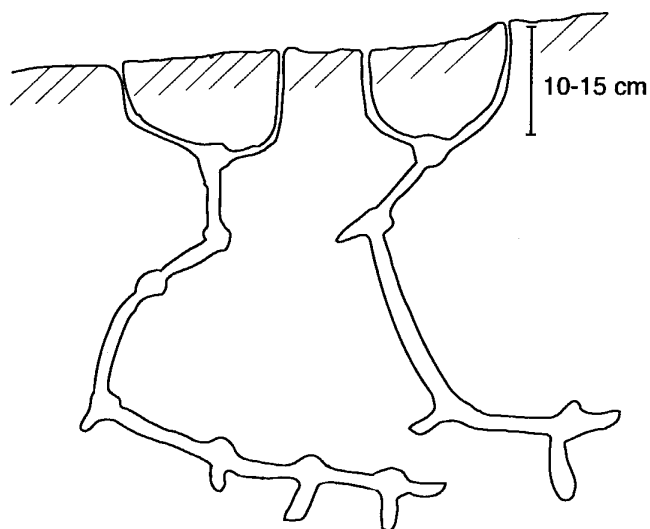


Fig. 4. Schematic burrow architecture of *C. japonica* Ortmann adapted from those given in Fig. 1 of Ohshima (1967). The shape is similar to that of *Callianassa* sp. in the present study (Fig. 3a).

marized as follows (we translate his terminology into that used in the present study): 1) the burrow is largely composed of three parts, and the overall form is basically Y-shaped with two surface openings; 2) the first part of the burrow is the upper Y, occupying a 10–15 cm depth, with the diameter of the vertical shafts (5–7 mm) smaller than in the lower parts. He noted that the shrimp inside the burrow could not pass through these shafts; 3) the central chamber is the place both toward which the shrimp transports sediments produced as a result of excavation of the lower parts for burrow extension/deposit feeding and from which the shrimp extrudes, with the use of currents generated by pleopods, these sediments through one burrow opening; 4) the second part of the burrow is the lower Y, reaching a depth of 30 cm below the substratum surface and being composed of both slightly oblique shafts with unequal lengths and chambers with a fewer number of branches than in the lowest, third part; 5) the third part of the burrow, occupying a depth range between 30 and 50 cm, is rather horizontally
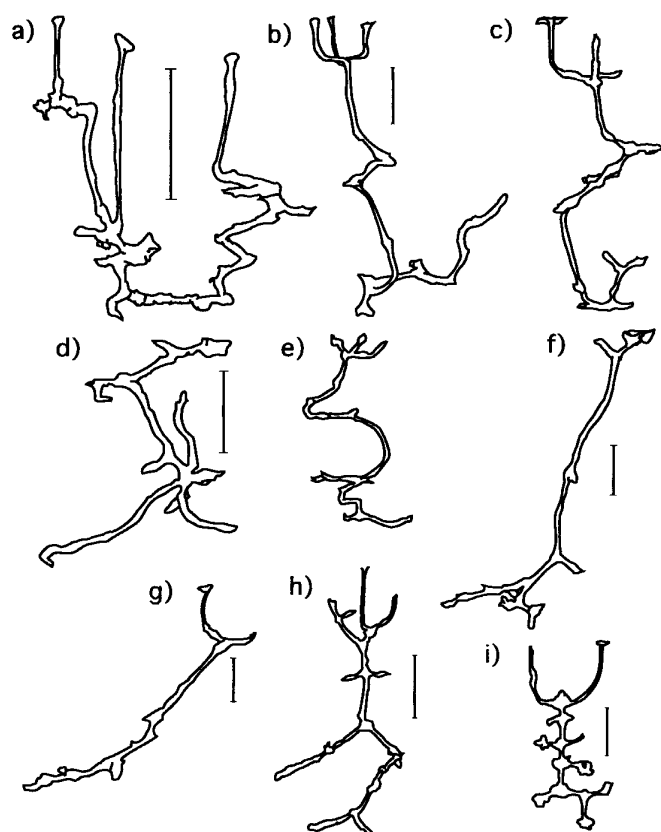
Fig. 5. Nine typical burrow casts of *C. japonica* Ortmann adapted from those drawn in Plates II – IV of Utashiro *et al.* (1972). The scale bar = 10 cm [not given for c) and e) in the original plates]. From the photograph of the shrimps in Fig. 1 of Utashiro *et al.* (1972), the species is confirmed as *C. japonica* Ortmann as defined in the present study.

oriented like a tunnel (*sensu* Frey, 1973); this part was not observed in the present study – the length of each shaft is nearly the same; and 6) the cross sections of the shafts are circular with a diameter of 1.5–2 cm, lined with silt-clay.

Utashiro *et al.* (1972) have given the most detailed account of the morphology of the burrow of *C. japonica* Ortmann, based on 21 plaster of Paris burrow casts collected at Matsukawaura Cove, northeastern Honshu. Judging from the clear photograph of the shrimps in their Fig. 1, the species can be confirmed as *C. japonica*. The salinity range of the water of their study site in July indicated in their Table 5, ca. 21.0–30.0‰ (converted from chlorinity values), further supports the correctness

of the identification of the species. Fig. 5a–i shows the nine typical burrow casts after Plates II–IV in Utashiro *et al.* (1972). The basic architecture is similar to that of *C. japonica* in the present study, but there are some differences. The features of the burrows in Utashiro *et al.* (1972) that are different from or similar to (but with different dimensions) those in the present study are summarized as follows. Firstly, the different points-a) in some burrows (e.g., Fig. 5a, b, d), there are laterally creeping, tunnels (*sensu* Frey, 1973) at the lowest sand layers; and b) of the collected burrow casts, the half have a single surface opening (e.g., Fig. 5c, d, f, g, h), but two or three surface openings are detected for the other half (e.g., Fig. 5a, b, e, i). In the latter case, the multiple uppermost shafts leading to either a common uppermost chamber (Fig. 5b, e, i) or different chambers at different depths (Fig. 5a) are asymmetrical with each other. This is strikingly different from the symmetrical architecture of the upper Y of the *Callianassa* sp. burrow in the present study (Fig. 3a). Apparently, Utashiro *et al.* (1972) misidentified their burrow casts as the same type as those of Ohshima (1967) (Fig. 4). Likewise, Tamaki *et al.* (1992) made an erroneous comment that the shape of their burrow casts was similar to that in Utashiro *et al.* (1972). Secondly, the common points-a) the maximum depth of the burrows varies from 18 to 85 cm, with a mean of 55 cm (no SD values are given). The maximum horizontal extension varies from 18 to 70 cm, with a mean of 38.3 cm; b) the number of chambers per burrow varies from 5 to 18, with a mean of 10; c) the number of branching points along the (multiple) central burrow-axes per burrow varies from 2 to 20, with a mean of 8 [note that in the usage of terms in Utashiro *et al.* (1972), all these points are not regarded as chambers, different from that in the present study]; d) the uppermost shaft, with a mean length of 9 cm, is almost vertical to

the substratum surface; the diameter of the shaft varies from 0.3 to 0.8 cm, with a mean of 0.5–0.6 cm, through which the shrimp would not be able to pass due to the narrowness; e) the diameter of the lower shafts is wider, varying from 0.25 to 2.0 cm, with a mean of 1.21–1.23 cm and being about half that of the chambers; and f) the arrangement of two adjacent shafts varies from nearly straight to spiral, with the latter predominant (i.e., the acute interior angles between the shafts).

The difference in the basic burrow architectures of *Callianassa* sp. and *C. japonica* revealed in the present study would be a good indicator in paleo-environmental reconstructions of ancient tidal flats by using these trace fossils (e.g., either open-sea or estuarine shores). However, as Griffis & Suchanek (1991) pointed out, there would be intraspecific variations in thalassinidean burrow morphology in response to changes in habitat parameters such as tidal heights, thicknesses of sediment layers, and grain-size composition. In fact, some burrow components that were not cast in the present study had appeared in other studies [e.g., laterally creeping tunnels for both species (Figs. 4 & 5); multiple surface openings for *C. japonica* (Fig. 5)]. The population densities of shrimps could be another factor in determining burrow dimensions. For example, in the present *Callianassa* sp. population on the Tomioka Bay sandflat, if it is assumed that a circle with a diameter equivalent to the horizontal distance between the two vertical shafts (i.e., 47.9 mm) equals the exclusive two-dimensional area of an individual shrimp's burrow extension, a carrying capacity of 555 shrimps $m^{-2}$ on the sandflat would be expected. This figure accords very well with the actual density recorded at the highest tidal station in Tamaki *et al.* (1997). But the above dimension could vary depending on population density. Thus caution must be used in conducting such kinds of ichnological studies.

The function of the whole architecture or individual components of the burrows of *Callianassa* sp. and *C. japonica* could be partly deduced by consulting several reviews (e.g., Dworschak, 1983; Griffis & Suchanek, 1991; Nickell & Atkinson, 1995) and by our observations on behaviour of shrimps in a laboratory aquarium containing fine sand (A. T. & H. U., pers. obs: at present a limited number of records are available only for *Callianassa* sp.). Griffis & Suchanek (1991) classified the thalassinidean burrows into six types based on morphological and ecological characteristics. Of these, their Type-2 burrow is the commonest form, described as relatively simple, twisting shafts with bulbous chambers and branches that extend vertically from a Y-shaped connection to the substratum surface. This type of burrow was mostly cast from callianassids, apparently including the present *Callianassa* sp. (Figs. 2a & 3a). Griffis & Suchanek (1991) designated the trophic mode of these shrimps as exclusively deposit feeding, in which materials derived from surface/subsurface/burrow-wall sediments are utilized and the 'surplus' sediment is expelled from a surface opening to form a mound. There is another Y-shaped burrow (their Type 5), described as a simple Y with no chambers and branches in the lower portion of the Y and without surface mounds; all these burrows belong to species of *Upogebia* and their trophic mode is regarded as exclusively filter/suspension feeding. Most recently, Nickell & Atkinson (1995) have proposed a new approach to thalassinidean trophic classification based on individual components of burrow morphology rather than the complete burrow; the U or upper-Y feature is indicative of current generation for feeding, irrigation of the burrow, and removal of fine waste/occluding material. Thus there would be no reason for beforehand excluding the possibility of suspension/filter-feeding mode for the Type-2 members in Griffis &

Suchanek (1991). So far, however, we have detected only deposit-feeding behaviour for *Callianassa* sp., gleaning for sediment inside the burrow. To determine the shrimp's feeding modes, future observations under varying speeds and directions of water flow over the substratum will be needed. For burrows of some thalassinideans which have two (or more) uppermost shafts, the differentiation into wider inhalant and narrower exhalant shafts is recorded, also being indicative of current generation (Nickell & Atkinson, 1995). By contrast, the two uppermost shafts of *Callianassa* sp. are symmetrical (Figs. 2a & 3a), which is also commonly found in thalassinidean burrows (Griffis & Suchanek, 1991). This may be a response to oscillatory currents in the waters overlying intertidal flats. The oblique-shaft chambers in the burrow of *Callianassa* sp. (Figs. 2a & 3a) would be used as 'blowout chambers', from which sediments are expelled through the uppermost vertical shafts by means of currents generated by the shrimp's pleopods (cf., Ohshima, 1967; Nickell & Atkinson, 1995; Ziebis *et al.*, 1996). In the branches along the central axis of the burrow casts of *Callianassa* sp., no stored material was found. But we observed that in the aquarium, shrimps discarded coarser material encountered during burrow excavation, such as 2–4 mm shell fragments, into the outermost part of the branches; later this part was often filled with finer sediments either by the shrimp (active fill) or by the natural collapse of the burrow wall (passive fill).

The burrow of *C. japonica* (Figs. 2b & 3b) does not belong to any of the six types in Griffis & Suchanek (1991), although Dworschak (1983: Fig. 13) had already listed this type of burrow with a single surface opening as one typical burrow of callianassid shrimps. In such a burrow, water stagnation could easily occur, and hence it is anticipated that *C. japonica* should suffer from oxygen deficiency more than *Callianassa* sp. Some burrows of *C. japonica* with two or three surface openings obtained by Utashiro *et al.* (1972) (Fig. 5) were different from the symmetrical Y-shaped burrow of *Callianassa* sp. (Figs. 2a & 3a). In those burrows of Utashiro *et al.* (1972), the two or three uppermost shafts leading to the respective surface openings, especially originating from the different chambers, would rather function as the multiple routes to surface access for removal of waste/occluding material or for introducing oxygen/surface food-material (cf., Nickell & Atkinson, 1995). If we follow the scheme in Fig. 3 of Nickell & Atkinson (1995), the possibility of suspension feeding for *C. japonica* would be less; it would be either a deposit feeder or an omnivorous scavenger. If so, it will be interesting to investigate the shrimp's nutritional source and the functions of tunnels and many branches protruding from the central axis of the burrow (Fig. 5).

The present study has revealed that the basic architectures of the burrows of *Callianassa* sp. and *C. japonica* were quite different. To elucidate the function of individual components of the burrows for each shrimp's activities, it is necessary to collect further data on behaviours of the shrimps and intraspecific variations in the burrow morphologies under various environmental conditions.

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[Addendum]
After submission of the present paper, the taxonomic status of *Callianassa japonica* Ortmann, *Callianassa* sp., and *C. petalura* Stimpson has been revised [see Manning, R. B., & Tamaki, A., 1998. Proceedings of the Biological Society of Washington, 111 (4): 889–892].