Publ. Seto Mar. Biol. Lab., 46: 42–54, 2021 (published online, 20 Sept. 2021)

Differences in the spatial distribution and shell morphology of *Thylacodes adamsii* (Gastropoda: Vermetidae) distributed in the Pacific and the Sea of Japan coastal areas of Japan

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Abstract. *Thylacodes adamsii* is a sessile gastropod and common inhabitant of rocky shores along the warm temperate coastal regions of Japan. We investigated the spatial distribution of this species in Shirahama facing to the Pacific Ocean, and in Maizuru facing to the Sea of Japan. Results showed that this species inhabits the middle intertidal zone in low densities in Shirahama, whereas it lives in high densities on oyster shells in the subtidal zone in Maizuru. Additionally, distinct shell morphology was found in the populations between the two localities. Observations of radular morphology suggest that they are most probably conspecific. Distinct shell morphology may be a result of adaptation to the different habitats.

Keywords: *Thylacodes daidai*, *Thylacodes medusa*, radular morphology, intraspecific variation

1. Introduction

Vermetid worm snails are common inhabitants of coral reefs and rocky shores found throughout tropic to warm temperate shores (e.g., Schiaparelli et al., 2006; Calvo et al., 2009; Hasegawa, 2017). They present tube-like shells without the regular shell coiling, that are usually embedded within coral or cemented to hard substrata.

Due to their sessile life, a large number of studies on feeding, reproduction and early development are available on this group from the Mediterranean Sea (Calvo et al., 1998; Calvo and Templado, 2004; Schiaparelli et al., 2006), the Red Sea (Hughes, 1974; Kappner et al., 2000), French Polynesia (Philipps and Shima, 2009), Hawaii (Hadfield et al., 1972; Hadfield and Hopper, 1980) and Africa (Keen and Morton, 1960). However, only a few biological studies have been conducted on Japanese species (e.g. Ino, 1942; Habe, 1953; Nishiwaki, 1969; Scheuwimmer, 1979).

There have been few taxonomic studies for Vermetidae due to their irregular shell shapes. Scheuwimmer and Nishiwaki (1982) conducted comparative studies on three Japanese species of *Thylacodes—Thylacodes adamsii, Thylacodes daidai and Thylacodes medusa*—and observed that they are clearly distinct from each other based on several diagnostic characteristics, including growth ridges on the shell surface, protoconch shape, body color, maturation season and shape of the central cusp of the rachidian tooth.

Thylacodes adamsii is one of the most common vermetid species distributed in Japan (Hasegawa, 2017). Although it is common in the intertidal zone in Shirahama facing the Pacific Ocean (Ohgaki and Takenouchi, 1986, 1987), Ishida (2003) reported its presence also in the subtidal zone in Fukui, facing the Sea of Japan. We investigated the spatial distribution of *T. adamsii* in Shirahama and Maizuru. Surprisingly, the Shirahama and Maizuru populations presented a completely different vertical distribution and shell morphology. Therefore, we conducted detailed comparisons of shell morphology, body color, and radula shapes for *T. adamsii* between the two localities.

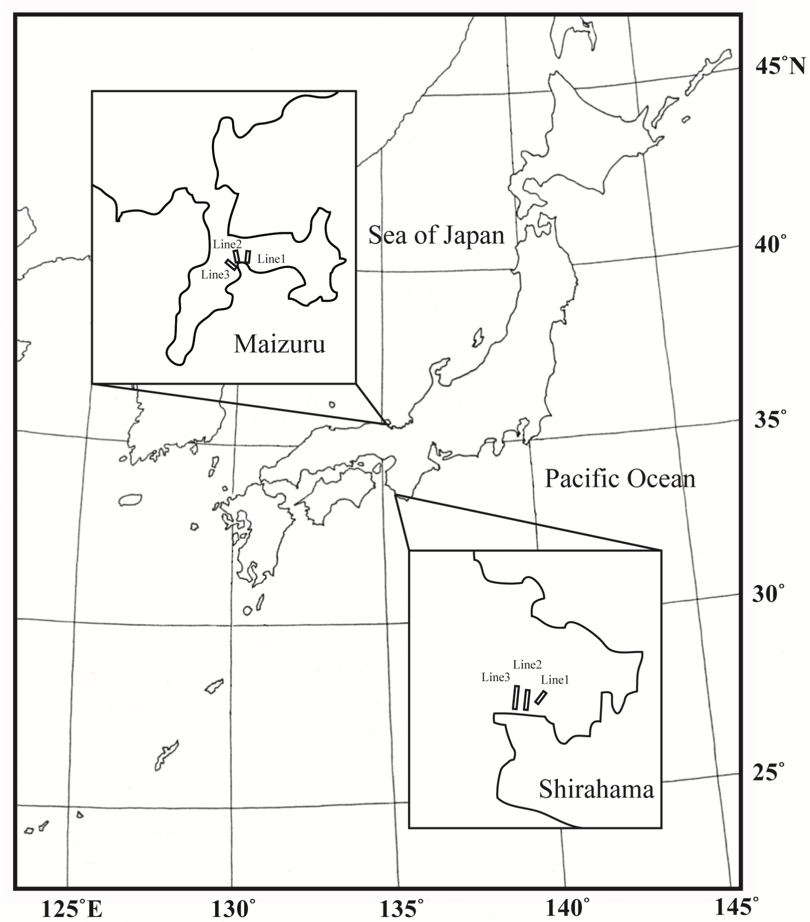

Figure 1. Geographical setting of the two study sites. (A) Shirahama; the north side of Bansho–zaki (B) Maizuru; beach in front of the Maizuru Fisheries Research Station. The approximate position of the line transects in each site are shown.

2. Materials and Methods

2.1. Geographical setting of two study sites

The surveys of the spatial distribution of *T. adamsii* were carried out in the intertidal zone on the north side of Bansho–zaki in Shirahama (33.69°N, 135.33°E) and in the intertidal zone to subtidal zones of the beach in front of the Fisheries Research Station in Maizuru (35.49°N, 135.37°E) (Fig.1). The survey site in Shirahama was located at the entrance of Tanabe Bay. The bottom here is characterized by wide rocky reef coverage and the tide level difference is about 220 cm (The Maritime Safety Agency of Japan, 2019). The survey site in Maizuru was located in the inner part of Maizuru Bay. The bottom here consists of mud, covered by fragments of oyster shells and pebbles derived from the beach and scattered approximately 10 m apart from each other. In addition, the area is covered by masses of live oysters distributed about 10–20 m apart from each other. The tidal level difference is about 30 cm (The Maritime Safety Agency of Japan, 2019).

2.2. Spatial distribution of Thylacodes adamsii

In Shirahama, the survey was carried out on September 19 and 20, 2017. During low tide, three line transects were placed on the rocky reef, perpendicular to the shore line. The lengths of the lines were 17, 30, 40 m, and the distance between lines was about 15 m. Along each line, 17, 30 and 40 quadrats (100 cm × 100 cm) were arranged every meter, respectively.

The elevation from the reference plane to the center of each quadrat was measured using a transparent tube filled with water. The reference plane was defined as the 0 cm plane in the tide table of Tanabe Port published by the Maritime Safety Agency of Japan. Additionally, attempts were to find *T. adamsii* three times in the subtidal zone above a depth of 5 m.

In Maizuru, the survey was carried out on November 29 and 30, 2018. Three line transects were placed, perpendicular to the shore line. The lengths of the lines were 16, 20, 22 m and the distance between lines was about 5 m. Along each line, 8, 10 and 11 quadrats (50 cm × 50 cm) were arranged every 2 m, respectively.

The elevation from the reference plane to the center of each quadrat was measured using a dive computer and a ruler. The reference plane was defined as the 0 cm plane in the tide table of Maizuru Port published by the Maritime Safety Agency of Japan.

All the *Thylacodes adamsii* individuals present in each quadrat were recorded. In order to compare the spatial distribution data between Shirahama and Maizuru, the following analyses were carried out for each site: calculation of the average for density of *T. adamsii* (/m2), average, maximum, minimum and mode of elevation of the quadrat in each quardut containing living individuals (cm). Furthermore, an ANOVA was performed in order to examine the variation between localities.

2.3. Observation of shell morphology and color of animals

Thylacodes adamsii specimens were collected in Shirahama from rocky surfaces using a scraper and a hammer. In Maizuru, individuals were collected with their substrata of living oysters, because all specimens were cemented to oyster shells. The color of animals was observed from the aperture in living *T. adamsii*.

2.4. Radula morphology

The radulae were removed from the individuals collected in Shirahama and Maizuru. Extracted radulae were placed in proteinase K at 55°C for 1 hour, and were then rinsed in distilled water. Radula morphologies were observed using a scanning electron microscope (SEM). The radulae of three individuals from Shirahama and of two individuals from Maizuru were observed.

3. Results

3.1. Cross section and features of the transect lines

Cross sections of six lines, three from Shirahama and three from Maizuru, are shown in Figs. 2 and 3. In Shirahama, the studies area was a rocky substrate. The rocky reef was located on the wave-cut platform extending in width over 20–40 m, and descending in a gradual slope toward the subtidal zone. Along line 1, large stones with a diameter of 1–2 m were present between 6 and 14 m (Fig. 2). In Maizuru, the studied area was a muddy bottom, and each transect line area was covered by fragments of oyster shells and pebbles between –13 and –0 m. Also, the transects examined were covered by masses of live oysters with a diameter of 20–50 cm between –19 and –12 m (Fig. 3; elevation: from –350 to –100 cm), which were identical to those present in the precipitous slope zone.

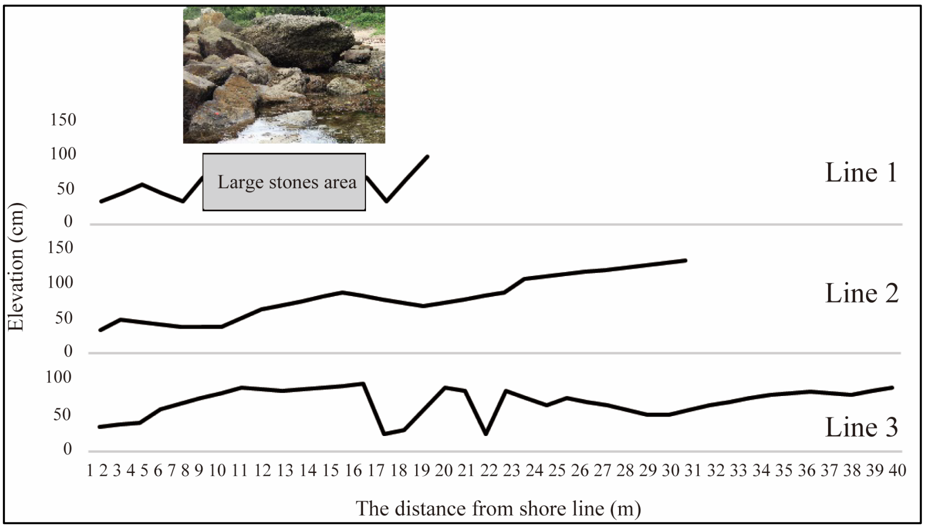

Figure 2. Sectional view along the three line transects in Shirahama. In the area presenting large stones, the elevation could not be measured.

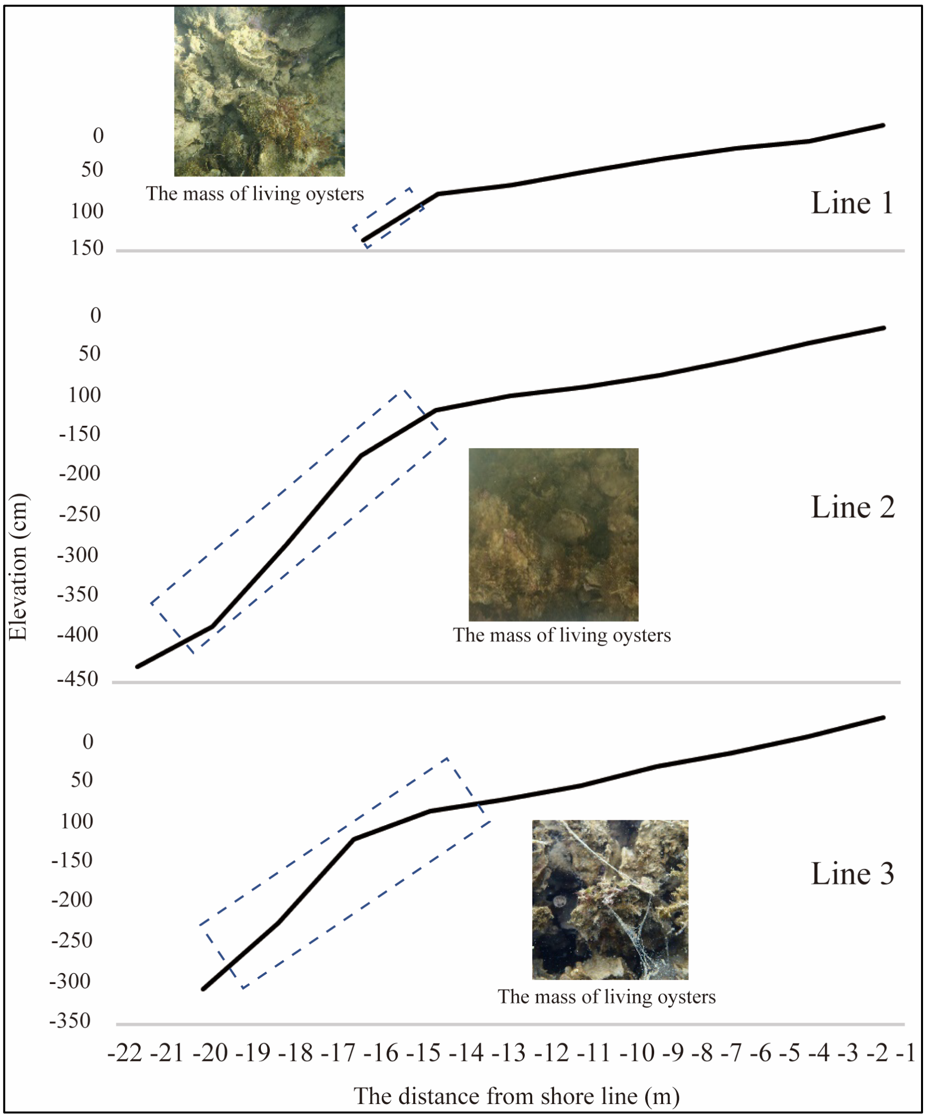

Figure 3. Sectional view along the three line transects in Maizuru. The square with the broken line corresponds to an area characterized of numerous masses of living oysters.

3.2. Spatial distribution of Thylacodes adamsii

The density of *T. adamsii* at each elevation is shown in Fig. 4. In Shirahama, the spatial distribution of the species was characterized by the following values: average density, 2.5 snails per square meter; average elevation, 62.5 cm; maximum elevation, 110 cm; minimum elevation, 30 cm; mode of elevation 75 cm. The species was never found in the subtidal zone (elevation: –400 to 30 cm) (Fig. 4A).

In Maizuru, the spatial distribution of the species was characterized by following values: average density, 22.1 snails per square meter; average elevation, –160.5 cm; maximum elevation, –40 cm; minimum elevation,–427 cm; mode of elevation, –124 cm.

Individuals were mainly observed from 30 to 100 cm in Shirahama and from –400 to 50 cm in Maizuru. In these layers, there were quadrats where individuals were absent in Shirahama; in contrast there were only a few quadrats without any individual in Maizuru (Fig. 4B). In order to analyze the difference in spatial distribution between Shirahama and Maizuru, an ANOVA was carried out, which confirmed the existence of a significant difference between the two locations ($F_{(1, 857)} = 1622$, $p < 0.01$).

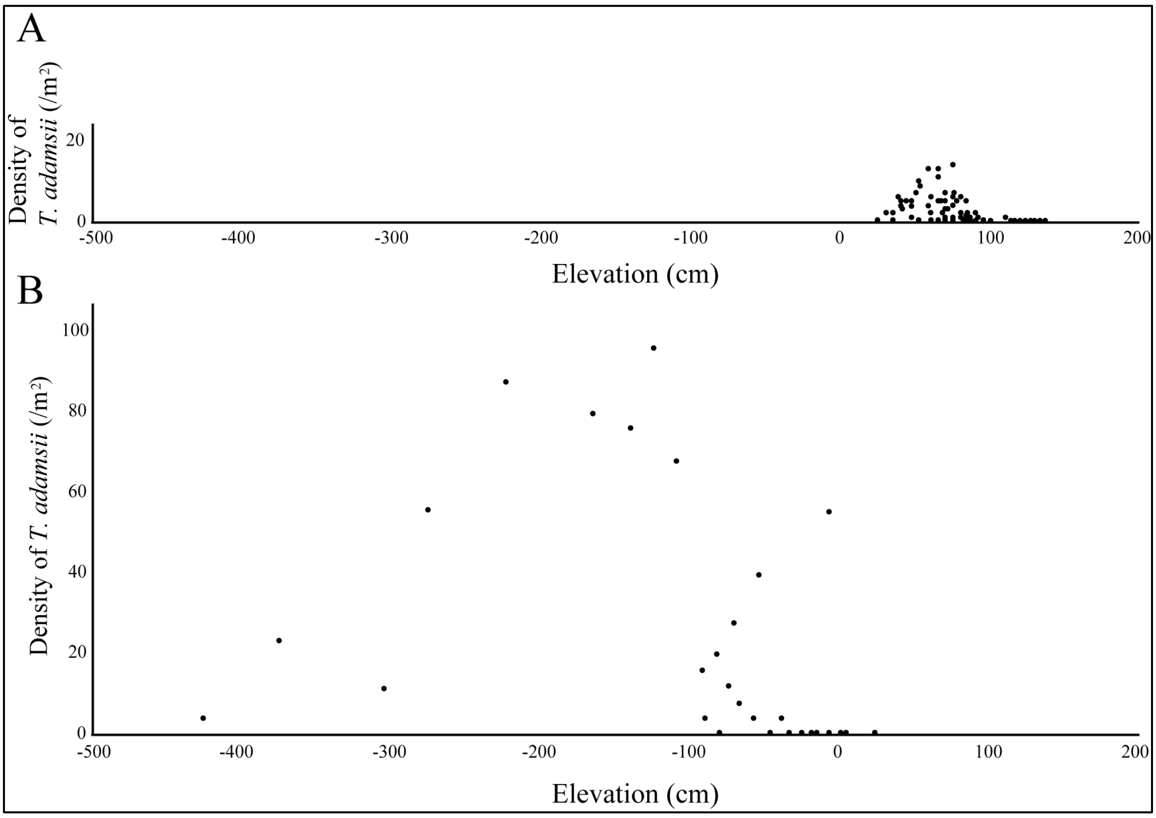

Figure 4. Spatial distribution and density of *Thylacodes adamsii*. (A) Shirahama, (B) Maizuru.

3.3. Shell morphology

The typical shell morphologies of individuals from Shirahama and Maizuru are shown in Plates 1–3, respectively. In Shirahama, individuals were attached to rocky surfaces or stones. On rocky reefs, most of them developed isostrophic or hyperstrophic sinistral (ultradextral) shells (Plate 1A, B); in contrast, some individuals on stones developed irregular shells (Plate 1C, D). Furthermore, an individual presenting a chimney-like shell (Plate 2A) was found on a rocky reef near a mud flat (Torinosu coast).

In Maizuru, all individuals were attached to masses of oysters. Although most of them were attached to living oysters, some individuals were attached to dead oyster shells as well. Both living and dead oysters were located on bottom, like boulders, not attached. Most of the individuals presented irregular shells, including chimney-like types (Plate 2B-E) and most of those living on the masses of oysters extended their shells toward the sea surface (Plate 3). The shells collected from Maizuru were characterized by a reddish color shell.

3.4. Body color

In Shirahama, only the individuals with a gray-brown body color were found (Fig. 5A, B). In Maizuru, most of the individuals also presented the same body color (Fig. 5C); however, some had an orange body (Fig. 5D). The ratio of orange one to gray-brown one was about 1 to 10.

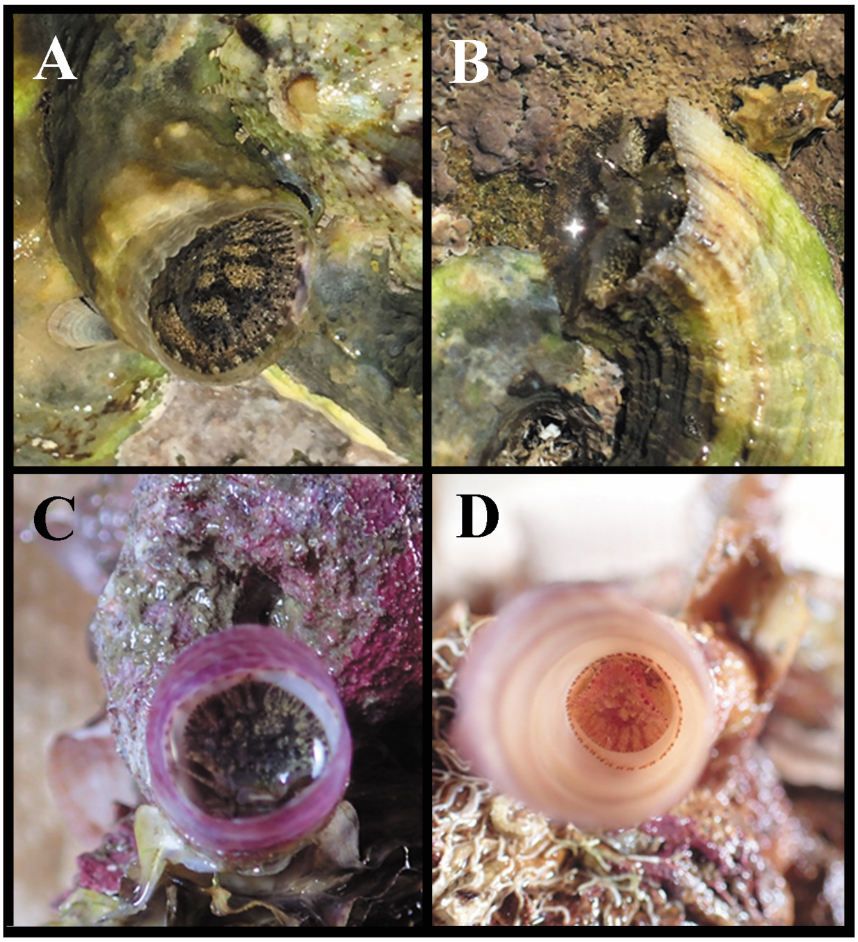

Figure 5. Body color variations of *Thylacodes adamsii*. (A), (B) Gray-brown individual collected from Shirahama. (C) Gray-brown individual collected from Maizuru. (D) Orange body individual collected from Maizuru.

3.5. Radula morphology

The radulae of individuals from Shirahama and Maizuru, presenting the two color types, are shown in Fig. 6. Three samples from Shirahama, and two samples from Maizuru— one gray-brown and one orange—were selected. In the Shirahama samples, each radula had 28, 25, and 24 rows of teeth (Fig. 6A), while in the Maizuru samples, the gray-brown individual had 29 rows of teeth (Fig. 6B), and the orange individual had 24 rows of teeth (Fig. 6C). Each transverse row of teeth consisted of a single median rachidian tooth, a pair of lateral teeth and two pairs of marginal teeth, so the radula formula is 2.1.1.1.2. The central cusp of each rachidian tooth was shaped as an isosceles triangle with acute apex (Fig. 6C-F). The degree of frictional wear did not depend on position.

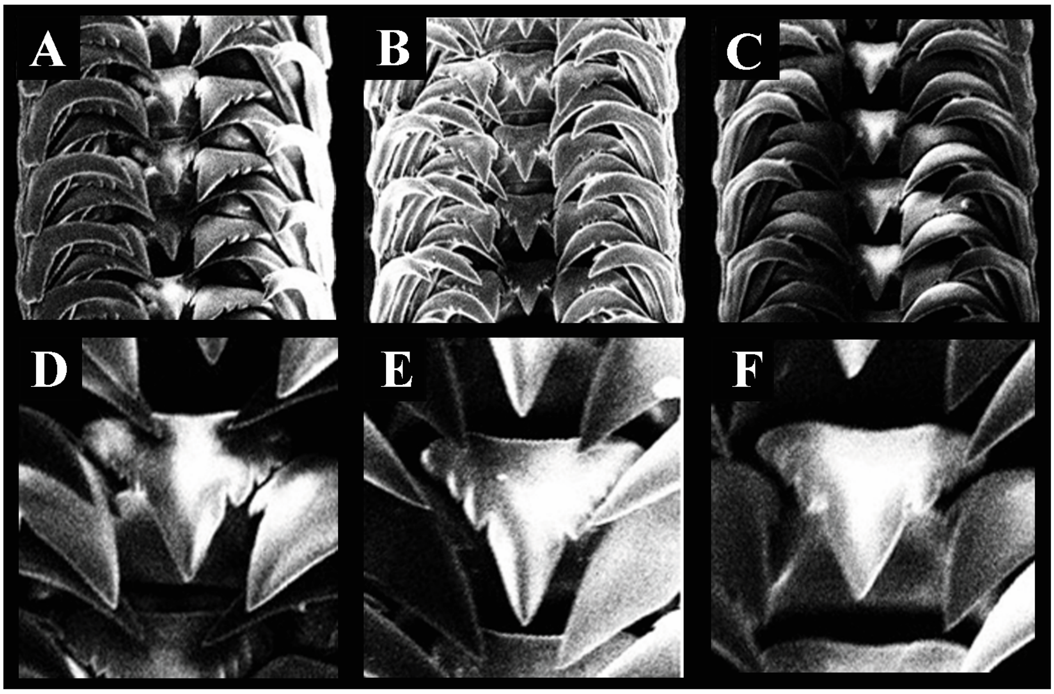

Figure 6. *Thylacodes adamsii*. Radula morphology and central cusp of the rachidian tooth captured in detail by SEM. (A), (D) Gray-brown individual from Shirahama. (B), (E) Gray-brown individual from Maizuru. (C), (F) Orange individual from Maizuru.

4. Discussion

4.1. Effects of the environment on spatial distribution

Ceraesignum maximum has been shown to be considerably less abundant in gullies or hollows, preferring the flatter areas of reef rock (Hughes and Lewis, 1974). In this survey, *T. adamsii* showed a similar tendency. Near the bottom, water currents occur less frequently than near the surface (Mann and Lazier, 1996). Being a suspension feeder, this species may prefer open space in order to feed efficiently.

In Shirahama, *T. adamsii* individuals were observed within a narrow range and in low densities; in contrast, in Maizuru, they were present within a wide range and in high densities. The cause of the high density in Maizuru may be the limited hard substrates available, as almost all substrates in this area were covered with mud except for the spots where oysters were present. *Thylacodes adamsii* could only attach to oyster masses, resulting in the high density of individuals here observed.

In contrast, the cause of low density in Shirahama may be presence of grazers that remove younger *T. adamsii* from the substrate during feeding. Barnacles are sessile animals with a pelagic larval stage. It has been suggested that one of the causes of mortality of the intertidal barnacle *Chthamalus challengeri* is the grazing activity by chitons and limpets (Mori, 1986). The same cause may apply to *T. adamsii*. In fact, a large number of chitons, such as *Liolophura japonica* and *Acanthopleura loochooana*, and limpets, such as *Cellana toreuma* and *Patelloida lanx*, were observed in Shirahama, but, in contrast, these grazers were hardly present on the mud flats in Maizuru.

From 2005 to 2018, *T. adamsii* individuals have been frequently observed in Tanabe Bay, where several long-term monitoring surveys have been conducted. Specifically, they were observed frequently in the intertidal zone of Hatakejima Island in 2008 (Ohgaki, 2012), 2013, 2018 (Nakano, unpublished data), and on Motoshima Island in 2005 and 2010 (Ohgaki et al., 2007; Ohgaki, 2011). This species was also frequently reported in the intertidal zone on Hatakejima Island in 1969 (Ohgaki and Tanase, 1984). However, the density of *T. adamsii* from 1983 to 2003 was low on this island (Ohgaki, 2001; 2002; 2003; Ohgaki et al., 1985). On Motoshima Island, individuals were not observed from 1999 to 2001, and here the density of the species in 2002 was low (Ohgaki et al., 2006). Based on these studies, it is suggested that a large number of *T. adamsii* individuals may have settled immediately on Hatakejima Island during five years from 2003 to 2008, and on Motoshima Island during two years from 2001 to 2003.

In Maizuru, a number of younger individuals with a shell diameter of 2–6 mm was observed, but only one or two younger individuals were observed in Shirahama during the whole survey. Almost all the individuals in Shirahama had a shell diameter larger than 7 mm, indicating that they may have settled a few years before. The density of grazer species, such as *Acanthopleura loochooana*, *Cellana toreuma*, *Patelloida lanx*, was low in 2001 on Motoshima Island (Ohgaki et al., 2006). It is possible that the ratio of *T. adamsii* settlement depends on the density of grazers, and a lot of larvae could settle when the predation pressure of grazers is low.

4.2. Effects of the environment on shell morphology

Thylacodes adamsii individuals thriving on steady substrate, like rocky reef, tended develop a regular shell morphology, whereas, individuals on unstable substrates, such as stones or oyster masses, developed an irregular shell morphology in both Shirahama and Maizuru.

Individuals attached to boulders can be turned upside down due to the strong wave action typically affecting rocky shores. Schiaparelli et al. (1999) reported that *Vermetus triquetrus* changed shell orientation when obstacles were placed in front of the shell aperture. Vermetid gastropods need a clear space in front of the aperture to spread their mucous net during feeding. The elongated shell shape observed in *T. adamsii* may be a result of modifications in direction of the shell for effective feeding on unstable substrates.

Chimney-like shell morphology is frequently observed in muddy environments, where individuals may extend their shell tube toward the sea surface in order to avoid being buried. This type of shell morphology is also observed in T. medusa, a species living on other shells or rocks at depths between 40 and 100 m (Kuroda et al., 1971).

4.3. Body color and radula morphology

Thylacodes adamsii and *T. daidai* are conchologically very similar to each other. However, the former has a gray-brown body, while the latter has an orange body (Scheuwimmer and Nishiwaki, 1982). Additionally, the deep water species *T. medusa*, is considered a deep-sea form of *T. adamsii* (Kuroda et al., 1971). The radula morphology is a primary characteristic common to these species, and its detailed observation is particularly useful for the identification of vermetid gastropods (Scheuwimmer and Nishiwaki, 1982).

In our observations, the radula morphology did not differ in the two study sites nor in body color types, so the all the individuals in Shirahama and Maizuru are most probably conspecific. The central cusp of the rachidian tooth of *T. adamsii* is shaped as an isosceles triangle with acute apex, while in *T. daidai* it is shaped as an equilateral triangle (Scheuwimmer and Nishiwaki, 1982). In the present study, the structure of the central cusp of all individuals was identical to that of *T. adamsii*. Therefore, the individuals with orange body in Maizuru are not *T. daidai* but *T. adamsii*.

Molecular phylogenetic analyses have not been conducted for *T. adamsii*, *T. daidai* and *T. medusa* to date, but they would be recommended in order to further confirm the species identification of these three species.

Acknowledgements.

We gratefully thank Prof. Reiji Masuda, Maizuru Fisheries Research Station, Kyoto University, for his help in carrying out the field survey and advice throughout this study. We are also indebted to the members of SMBL for advising throughout this study, especially Mr. Ryo Nakayama and Dr. Mariko Kawamura.

Literature cited

Calvo, M and Templado, J. 2004. Reproduction and development in a vermetid gastropod, *Vermetus triquetrus*. Invertebrate Biology, 123, 289–303.

Calvo, M., Templado, J. and Penchaszadeh, P.E. 1998. Reproductive biology of the gregarious Mediterranean vermetid gastropod *Dendropoma petraeum*. Journal of Marine Biological Associations, U.K., 78, 525–549.

Calvo, M., Templado, J., Oliverio, M. and Machordom, A. 2009. Hidden Mediterranean biodiversity: molecular evidence for a cryptic species complex within the reef building vermetid gastropod *Dendropoma petraeum* (Mollusca: Caenogastropoda). Biological Journal of the Linnean Society, 96, 898–912.

Habe, T. 1953. Studies on the eggs and larvae of the Japanese gastropods (4). Publications of Seto Marine Biological Laboratory, 3, 161–167.

Hadfield, M.G. and Hopper, C.N. 1980. Ecological and evolutionary significance of pelagic spermatophores of vermetid gastropods. Marine Biology, 57, 315–325.

Hadfield, M.G., Kay, E.A., Gillette, M.U., and Lloyd, M.C. 1972. The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. Marine Biology, 12, 81–98.

Hasegawa, K. 2017. Family Vermetidae. In: Okutani, T. (ed). Marine Mollusks in Japan: Second Edition. Tokai University Press, Kanagawa.

Hughes, R.N. and Lewis, A.H. 1974. On the spatial distribution, feeding and reproduction of the vermetid gastropod *Dendropoma maximum*. Journal of Zoology, 172, 531–547.

Ino, T. 1942. Feeding-habit of the worm-shell, *Lemintina imbricata* (Dunker). Zoologisches Magazin, 54, 285–286.

Ishida, S. 2003. Kleptoparasitism of polychaetes against *Serpulorbis imbricatus* (Gastropoda: Vermetidae) by ingesting its mucus net. Bulletin of the City Museum of Natural History, 50, 41–43.

Kappner, I., Al-Moghrabi, S.M. and Richter, C. (2000). Mucus-net feeding by the vermetid gastropod *Dendropoma maxima* in coral reefs. Marine Ecology Progress Series, 204, 309–313.

Keen, A.M. and Morton, J.E. 1960. Some new African species of *Dendropoma* (Vermetidae: Mesogastropoda). Proceedings of Malacological Society of London, 34, 36–51.

Kuroda, T., Habe, T. and Oyama, K. 1971. The Sea Shells of Sagami Bay. 741 + 489 + 51 pp., 121 pls, Maruzen, Tokyo.

Mann, K.H. and Lazier, J.R.N. 1996. Dynamics of Marine Ecosystems, Second Edition, 18–20.

Mori, K. 1986. Life history and its variation of an intertidal barnacle, *Chthamalus challengeri* Hoek (preliminary report). Japanese Journal of Benthology, 29, 50–57.

Nishiwaki, S. 1969. Seasonal size variations of the pallial slit in the female *Serpulorbis imbricatus* (Prosobranchia, Vermetidae). Science Reports of the Tokyo Kyoiku Daigaku, Series B, 14, 69–78.

Ohgaki, S. 2001. Distribution of intertidal macrobenthos around Hatakejima Island, 1993. Argonauta, 5, 32–47.

Ohgaki, S. 2002. Distribution of intertidal macrobenthos around Hatakejima Island, 1998. Argonauta, 6, 15–31.

Ohgaki, S. 2003. Distribution of intertidal macrobenthos around Hatakejima Island, 2003. Argonauta, 9, 21–34.

Ohgaki, S. 2011. Distribution of intertidal molluscan species around Motoshima Island, 2010. Argonauta, 19, 34–43.

Ohgaki, S. 2012. Distribution of intertidal molluscan species around Motoshima Island, 2010. Argonauta, 20, 23–36.

Ohgaki, S. and Takenouchi, K. 1986. The malacofauna of Bansho Cape, Shirahama, Wakayama, 1985 and 1986, part 1. The Nanki Seibutsu, 28, 135–141 (in Japanese).

Ohgaki, S. and Takenouchi, K. 1987. The malacofauna of Bansho Cape, Shirahama, Wakayama, 1985 and 1986, part 2. The Nanki Seibutsu, 29, 37–41 (in Japanese).

Ohgaki, S. and Tanase, H. 1984. Intertidal animals found on Hatakejima Island, 1949–1983, part 2. The Nanki Seibutu, 26, 105–111.

Ohgaki, S., Komemoto, K. and Funayama, N. 2006. Species composition of a molluscan species around Motoshima Island, 2005. Argonauta, 13, 26–38.

Ohgaki, S., Abe, N., Takegami, T. and Wada, K. 1985. Spatial occurrence of 91 intertidal animal species on Hatakejima Island, 1983. Publications of Seto Marine Biological Laboratory, 30, 325–332.

Phillips, N.E. and Shima, J.S. 2010. Reproduction of the vermetid gastropod *Dendropoma maximum* (Sowerby, 1825) in Moorea, French Polynesia. Journal of Molluscan Studies, 76, 133–137.

Schiaparelli, S., Albertelli, G. and Cattaneo-Vietti, R. 2006. Phenotypic plasticity of Vermetidae suspension feeding: a potential bias in their use as biological sea-level indicators. Marine Ecology, 27, 44–53.

Scheuwimmer, A. 1979. Sperm transfer in the sessile gastropod *Serpulorbis* (Prosobranchia: Vermetidae). Marine Ecology Progress Series, 1, 65–70.

Scheuwimmer, A. and Nishiwaki, S. 1982. Comparative studies on three Japanese species of *Serpulorbis* (Prosobranchia: Vermetidae) with description of a new species. Venus, 41, 85–101.

The Maritime Safety Agency of Japan. (2019). The table of mean seawater level, highest high-seawater level, lowest low-seawater level in Japan. (referring 2019-1-10). http://www1.kaiho.mlit.go.jp/KANKYO/TIDE /enkan/Suijun_hyo/Pub.No741 /index.pdf

Received: 20 June 2021.

Accepted: 3 Sept. 2021.

Published online: 20 Sept 2021.

Plate 1. Shell morphology of *Thylacodes adamsii*.
(A), (B) Individuals on rocky surfaces with coiled shells in Shirahama.
(C), (D) Individuals on boulders with partly uncoiled shells in Shirahama.
Scale bar = 10 mm.

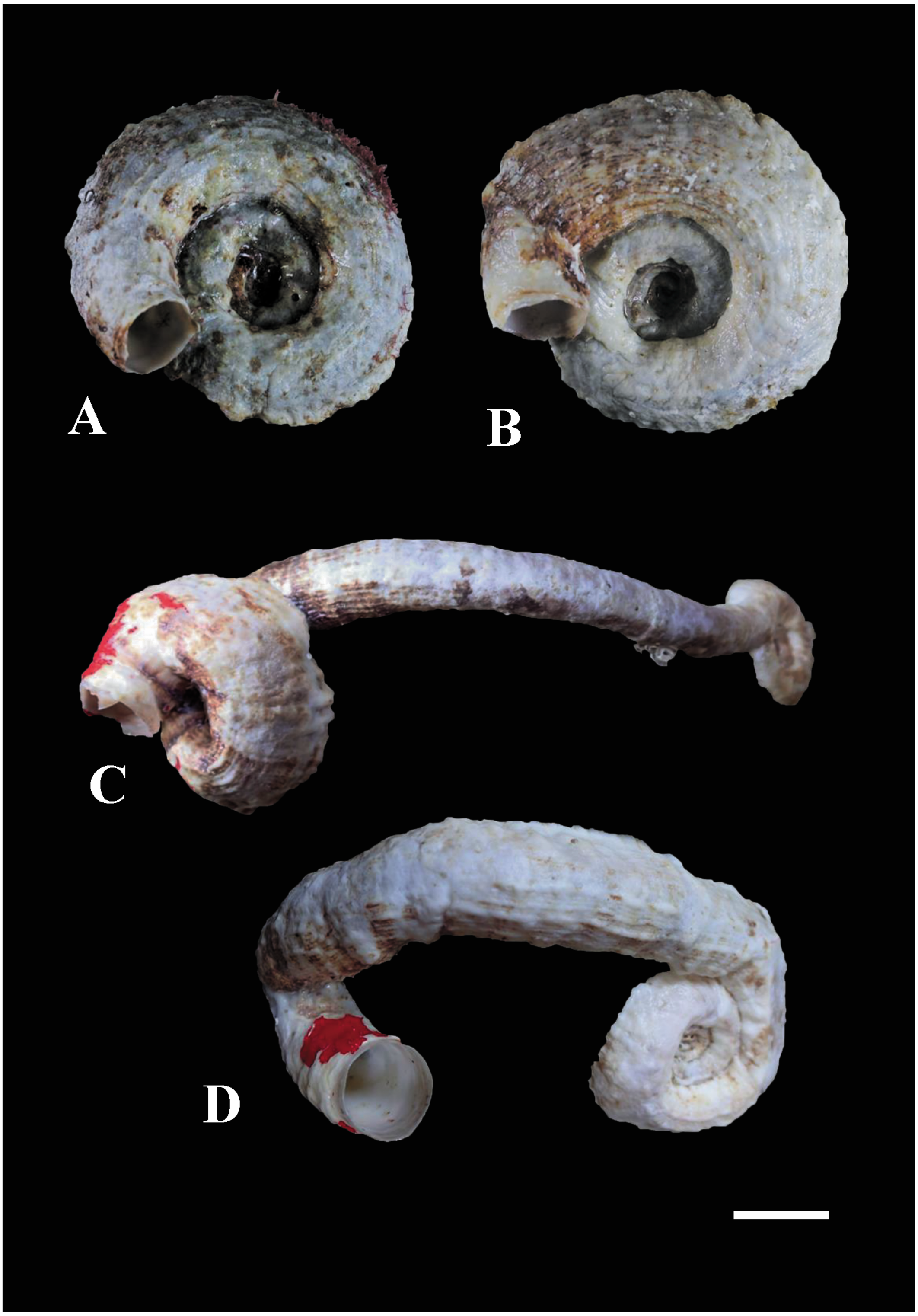

Plate 2. Shell morphology of *Thylacodes adamsii*.
(A) A chimney-like shell buried in mud in Shirahama.
(B), (C), (D), (E) Chimney-like shells on the mass of living oysters.
Scale bar = 10 mm.

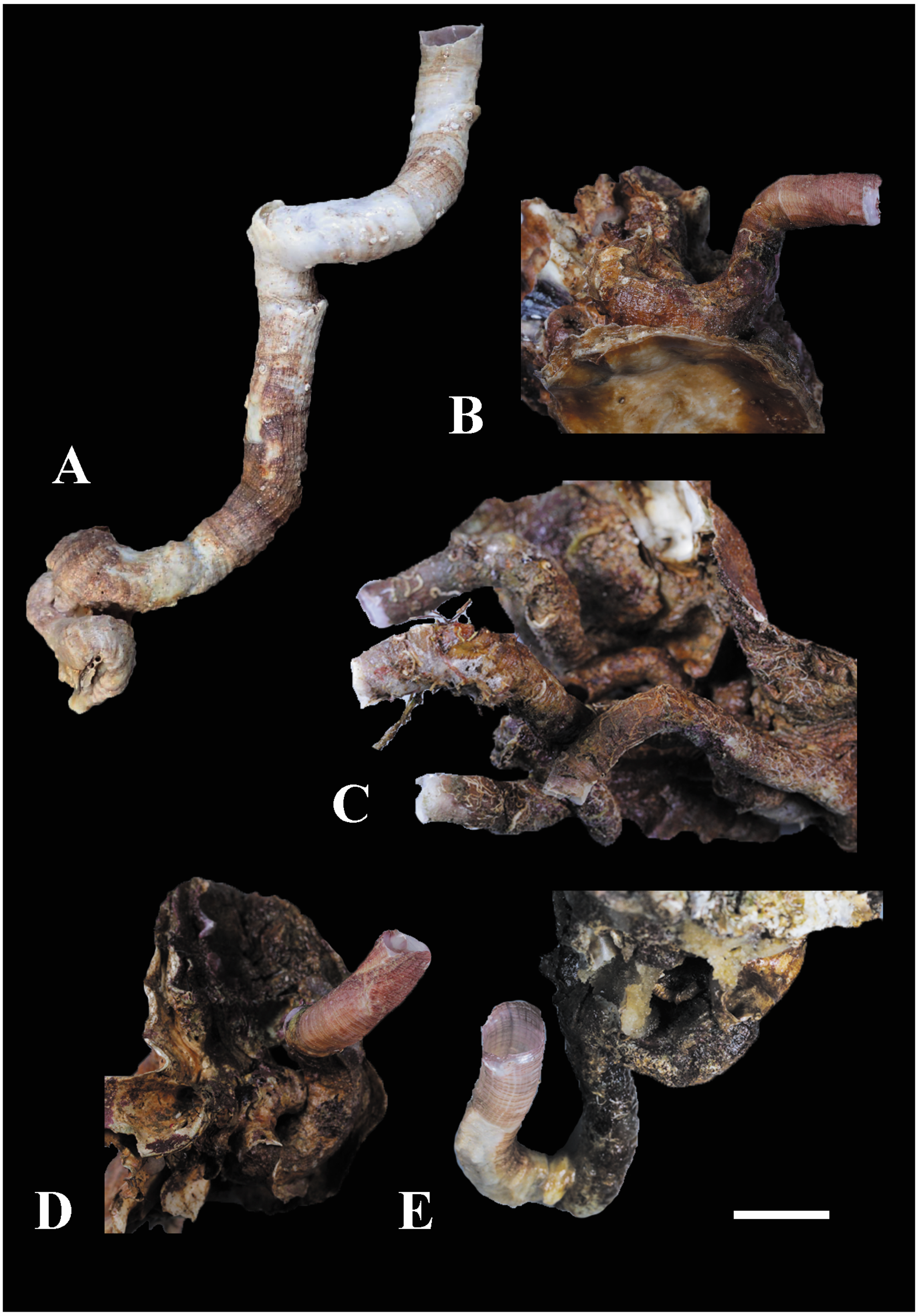

Plate 3. *Thylacodes adamsii* on a mass of living oysters.
White arrows indicate the aperture of each individual.
Scale bar = 10 mm.