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Inverse life positions of three species in the genus *Cadella* (Bivalvia: Tellinidae)

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Abstract

Bivalves have particular life orientations for each species. Species of Tellinidae and Semelidae burrow in sediment and are orientated with their commissure plane nearly horizontal and almost always rest on their left side. However, three species of the tellinid genus *Cadella*, which have the commissure plane nearly horizontal, lie on their right side. It is suggested that this reversed orientation in *Cadella* is an inversion of the normal left side orientation and appears to be the first example of behavioural inversion in bivalves.

Key words: Infaunal bivalves, *Cadella*, Tellinidae, burrowing behaviour

Introduction

Infaunal bivalves are known to position and orient themselves in the substrata in a way that is distinctive for each species, which is referred to as 'life position' or 'life orientation' (e.g. Stanley 1970; Fürsich 1980; Kondo 1987). The orientations in life of these bivalves can be divided into two types, one with their commissure plane nearly vertical, and the other with it inclined. Many burrowing bivalves adopt the former life position and most of them orient with the posterior end upwards. Inclined positions are observed in a few groups, the most significant being the Tellinoidea. In particular, many species of the Tellinidae and Semelidae orient their commissure plane nearly horizontal (Holme 1960; Stanley 1970).

It is also known that species in this group almost always rest on the left side (Holme 1960; Stanley 1970) (Table 1). The only exception is *Scissula similis* (Sowerby, 1806), which was reported without comment by Stanley (1970). The description was poor, and no data were provided about the number of observed individuals, so the credibility of this observation is debatable.

In the present report, three species of the genus *Cadella* (Dall, Bartsch & Rehder 1938) in Japan were observed to lie horizontally on their right side in the sediment as described in detail below.

Materials and Methods

Cadella (Type species *Tellina echriogramma* Melvill, 1893) is a genus-group taxon in the Tellinidae, which is sometimes regarded as a subgenus of *Tellina* (e.g., Keen 1969; Afshar 1969) or is treated as a genus (e.g., Habe 1977). It is characterized by having the beak located posteriorly, rounded posterior and anterior margins, and a rounded pallial sinus.

TABLE 1. Literature records of life orientations of the Tellinidae and Semelidae. *Eurytellina*, *Fabulina*, *Angulus*, *Scissula* and *Tellinella* are regarded as *Tellina* in Holme (1961) and Stanley (1970).

Species name	Resting side	References
Tellinidae		
Macominae		
Macoma tenta (Say, 1838)	Left	Stanley (1970)
Macoma incongrua (Martens, 1865)	Left	Kondo (1987)
Tellininae		
Tellina radiata Linnaeus, 1758	Left	Stanley (1970)
Tellina martinicensis D'Orbigny, 1842	Left	Stanley (1970)
Eurytellina alternata (Say, 1822)	Left	Stanley (1970)
Fabulina fabula (Gmelin, 1791)	Left	Holme(1961)
Angulus incarnata (Linnaeus, 1758)	Left	Holme (1961)
Angulus tenuis (da Costa, 1778)	Left	Holme (1961)
Angulus aglis (Stimpson, 1857)	Left	Stanley (1970)
Angulus tampaensis (Conrad, 1866)	Left	Stanley (1970)
Tellinella listeri (Röding, 1798)	Left	Stanley (1970)
Scissula similis (Sowerby, 1806)	Right	Stanley (1970)
Arcopagia crassa (Pennant, 1777)	Left	Holme(1961)
Arcopagia fausta (Pulteney, 1799)	Left	Stanley (1970)
Semelidae		
Semele proficua (Pulteney, 1799)	Left	Stanley (1970)

Individuals of three species, *Cadella narutoensis* Habe, 1960, *C. hoshiyamai* Kuroda, 1960 and *C. delta* Yokoyama,

1922, were collected in three localities of Japan (see Table 2) during May to November 2008. All localities had sandy substrata. Two species (*C. narutoensis* and *C. hoshiyamai*) were collected by dredge or scuba diving subtidally at 5–10 m and *C. delta* was collected on an intertidal flat. The specimens were placed in separate aquaria about 30 cm long, 20 cm wide and 25 cm deep filled with about 15 cm of sediment from the localities the specimens were collected from. Water overlying the sediment was aerated and was about 5 cm deep. About half of the individuals were laid on the surface of the sediment on their left side and half on their right.

About two hours after they had burrowed into the sediment, it was carefully excavated in order to observe their orientation. This is the same method used by Holme (1961), Rasmussen (1973) and Wikander (1980).

TABLE 2. List of the three *Cadella* species studied with the number of observed individuals and locality from which they were collected. N = Number of observed individuals

Species name	N	Locality
Cadella narutoensis Habe, 1960	13	Tsuyazaki (Northern Kyushu, Japan) N33°47’44’’, E130°27’34’’
Cadella hoshiyamai Kuroda, 1960	26	Motobu (Okinawa, Japan) N26°37’32’’, E127°53’3’’
Cadella delta (Yokoyama, 1922)	5	Awase (Okinawa, Japan) N26°18’41’’, E127°49’56’’

All of the specimens used in this study are housed in the Kyushu University Museum (KYUM-MO-010000, KYUM-MO-010001 and KYUM-MO-010002)

Results

Between five and 26 individuals were observed for each species and details about the localities and the number of individuals is given in Table 2. When burrowing, some individuals raised their shells into a vertical but others inclined their shells to the right and usually inclined their long axis about 60°–30° from vertical (Fig. 1).

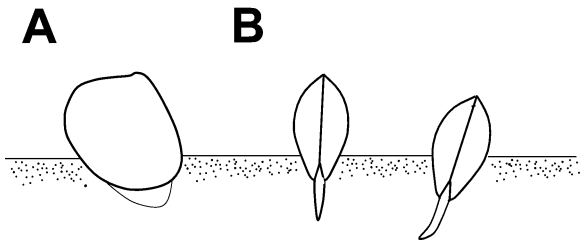

FIGURE 1. Burrowing position of the three *Cadella* speices. **A.** Right lateral view of typical burrowing position. **B.** Ventral view of erect individuals of *Cadella* in a burrowing position.

The burrowing motions of the three species are very rapid; most individuals finished burrowing within three seconds, and some rocking motions were observed. All individuals of the three species observed rest with their commissure plane nearly horizontal on the right side in the sediment as shown in Figure 2. All three species are very shallow burrowers, resting only 1–3 cm below the sediment surface.

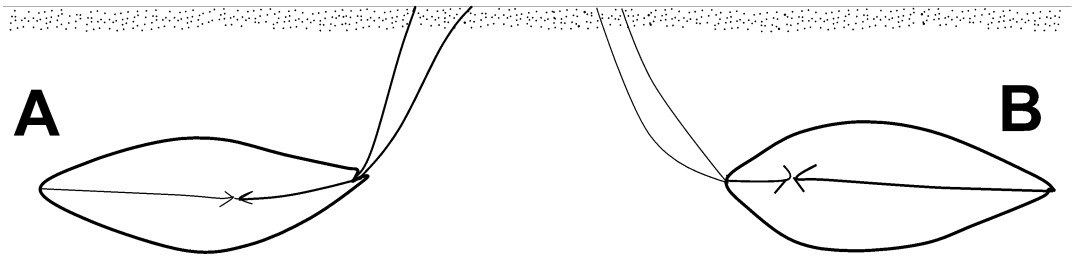

FIGURE 2. Two resting position in tellinids, **A**. Life orientation of typical tellinids. **B**. Life orientation of the three *Cadella* species. The condition of the siphons has not been confirmed.

Discussion

As noted in the introduction, most species of the Tellinidae and Semelidae rest on their left side. In the largest sample of a single species observed to date, Wikander (1980) observed 142 individual positions of *Abra longicallus*. 126 individuals rested horizontally on their left side, in 14 the commissure plane was nearly vertical and only two individuals rested on their right side. The consistency in the observed positions of the three *Cadella* species thus suggests a specialized behaviour and not an occasional aberration.

The left side down resting positions have been recorded in various taxa of the Tellinidae and Semelidae (Table 1). The Tellinidae is usually divided into two subfamilies, Macominae and Tellininae (e.g. Keen 1969) based on the presence of lateral teeth. The resting position on the left side

has been observed in both tellinid subfamilies (e.g. Stanley 1970) and in the Semelidae (Stanley 1970; Wikander 1980). *Cadella* is a typical Tellinine (Keen 1969) and is often regarded as a subgenus of *Tellina.* It is thus assumed to be closely related to other genera in the Tellinidae although the classification and phylogenetic relationships within this family remain controversial (Willan 1998). Given the generality of the left resting position in tellinids and semelids it is highly probable that the right side orientation in *Cadella* evolved from an ancestral left side position, suggesting a reversal of life orientation. Additionally, the prevalence of this position in three species suggests that it may be a feature of all species of *Cadella*.

Inversions often occur in morphology in some groups of Bivalvia as a part of inversion such as transposition of the hinges between the right and left valves (e.g., Popenoe and Findlay 1933; Eggleton and Davis 1962; Matsukuma 1996). A different type of inversion is seen in the Chamidae. The species in that family normally attach themselves to the substratum by the left valve but in the 'inverse' form, they are attached by the right valve. The shells of the left valve attached species are a mirror image of those attached by the right valve (e.g., Yonge 1967). Yonge (1967) suggested that one evolved from the other by inversion and that this inversion resulted from a change of the mantle with no inversion of other parts of the body. Inversion of internal organs has been detected in one genus of the Mytilidae, *Xenostrobus* (Wilson 1966). In this genus, the recurrent loop of mid gut lies on the right side instead of on the left as in the other mytilids.

The inversion in life positions of *Cadella* is different from those in other bivalves. All three species of *Cadella* have normal hinges, indicating that an inversion of the whole body has not occurred. Most tellinids that lie on their left sides have the posterior end twisted to the right (i.e., are right vented) facilitating the extension of the siphons (Holme 1961; Stanley 1970). In the three species of *Cadella*, this same relationship does not occur. It might be expected that these species would have 'left' vented posterior ends. *C. hoshiyamai* has a slightly vented posterior end (Fig. 3B) while *C. delta* and *C. narutoensis* vent the posterior end slightly right (Fig. 3A and C). Thus their shell morphology is similar to the left resting species and no inversion of the shell was detected suggesting that this inversion may be a very recent one. No anatomical study has been carried out yet so it is not known if the inversion is accompanied by any anatomical change. There remain two interesting questions—why is the life orientation in tellinids and semelids so uniform and what caused *Cadella* to change its behaviour? Whatever the reason, this 'behavioural inversion' appears to be a new example of inversion in Bivalvia.

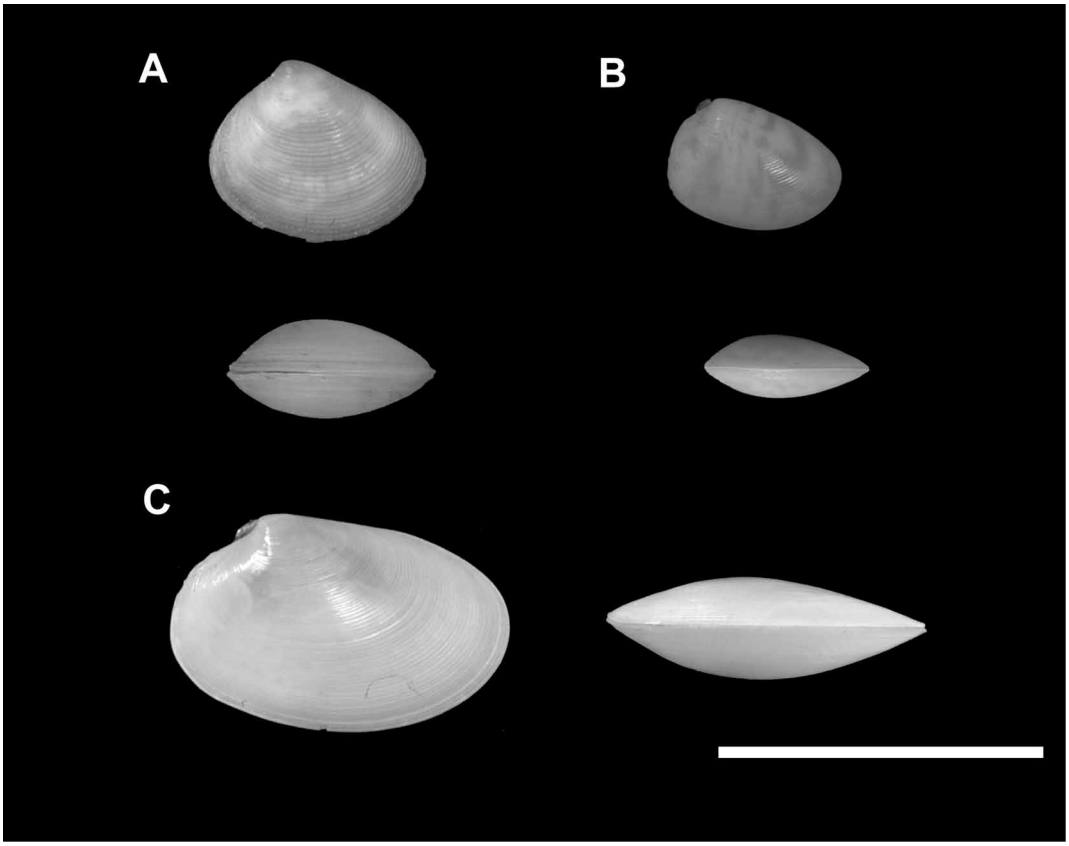

FIGURE 3. **A.** Right lateral and ventral view of *Cadella delta* (KYMU-MO-010000). **B.** Right lateral and ventral view of *Cadella hoshiyamai* (KYMU-MO-010001). **C.** Right lateral and ventral view of *Cadella narutoensis* (KYMU-MO-010002)
Scale bar =1 cm.

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