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About storage of tentacles in the pockets of cuttlefishes (Mollusca: Cephalopoda)

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ABSTRACT: Cuttlefishes store their tentacles in the pockets, which are open depressions in the anteroventral surface of the head between the bases of arms III and IV. When cuttlefishes hunt prey, they rapidly extend their tentacles from the pockets towards the prey, catch it using tentacular clubs, retract the tentacles to the pockets, and then hold it to their mouth using their arms. Tentacle storage in the pockets is important for hunting. However, the arrangement of the tentacles in the pockets remains unknown. In this study, I report the arrangement of tentacles in the pockets of pharaoh cuttlefish *Sepia pharaonis* (Ehrenberg, 1831) and golden cuttlefish *Sepia esculenta* (Hoyle, 1885) by morphological observation. Two patterns for keeping the tentacles in the pockets were observed. In the first pattern, tentacular clubs were located outside the tentacle pocket openings. The curling of tentacular stalks was less complex than that of the second pattern. In the second pattern, tentacular clubs were completely retained inside the pockets. The curling of the tentacular stalk was more complex than that of the first pattern. In both patterns, the tentacular stalks first turned from the origin towards the oral side and then curled with twisting from the oral side to the aboral side in the pockets. We observed that tentacular stalks did not tangle. This result contributes to understanding the basic morphology of tentacular storage in cuttlefish pockets. Possible causes for the differences between the two patterns are discussed.
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KEY WORDS: cuttlefish, storage pockets, tentacles, *Sepia pharaonis*, *Sepia esculenta*.

О размещении ловчих щупалец в карманах у каракатиц (Mollusca: Cephalopoda)

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РЕЗЮМЕ: Каракатицы прячут свои ловчие щупальца в специальных карманах, которые представляют собой открытые впячивания передне-вентральной поверхности головы и располагаются между основаниями рук III и IV. Когда каракатицы ловят добычу, они мгновенно выбрасывают ловчие щупальца из карманов и хватают жертву, используя дистальные булавовидные расширения ловчих щупалец. Затем щупальца вновь вворачиваются в карманы. Расположение ловчих щупалец в карманах чрезвычайно важно для успешной охоты каракатицы, однако, оно до сих пор остается не описанным. В настоящей работе изучено расположение ловчих щупалец в карманах у каракатиц двух видов: *Sepia pharaonis* Ehrenberg, 1831 и *Sepia esculenta* (Hoyle, 1885). В результате морфологических исследований выявлено два паттерна расположения ловчих щупалец в карманах. В первом случае булавовидные расши-

рения щупалец располагаются вне сторожевых карманов, а скручивание самой руки относительно не сложное по сравнению со вторым паттерном. Во тором случае булавовидные расширения полностью погружены в сторожевые карманы, а сама рука сложена в довольно сложную по форме спираль. В обоих случаях стебель каждой руки при складывании сначала поворачивается по направлению к оральной стороне, а затем сворачивается с поворотом к аборальной стороне сторожевого кармана. При этом рука никогда не запутывается. Эти результаты вносят вклад в понимание морфологии и функционирования ловчих щупалец каракатиц. В работе обсуждаются возможные причины существования двух паттернов расположения ловчих щупалец в сторожевых карманах.
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КЛЮЧЕВЫЕ СЛОВА: каракатица, сторожевые карманы, ловчие щупальца, *Sepia pharaonis*, *Sepia esculenta*.

Introduction

Some animals can keep their body parts inside and outside of their bodies. For example, crocodiles keep their erect penis inside the cloaca (Ziegler, Olbort, 2007), long-necked turtles snake their necks sideways under the carapace (Anquetin *et al*., 2017), and ladybugs tuck their large hindwings under harder wings in an origami-like style (Saito *et al*., 2017). The appropriate arrangement is important for these body parts to extend, retract, and perform their functions smoothly. It is also essential to understand how these animals live.

Cuttlefish store two long tentacles in their pockets, which are open depressions in the anteroventral surface of the head between the bases of arms III and IV (Jereb, Roper, 2005). Each tentacle consists of tentacular stalk and tentacular club (Fig. 1). They use these tentacles, which are specialized for prey capture via rapid elongation and retraction, in addition to eight arms for hunting (Boucher-Rodoni *et al*., 1987; Kier, 2016).

Concerning hunting behaviour, they use their tentacles and arms in the following ways: after detecting prey, they extend two tentacles from the pockets toward the prey (tentacular strike), catch the prey using tentacular clubs, retract the tentacles into the pockets, and then hold and transfer the prey to their mouths using the remaining eight arms (Boucher-Rodoni *et al*. 1987; Cole, Adamo, 2005; Hanlon, Messenger, 2018). Therefore, to understand the hunting behaviour of cuttlefish and their basic morphology, knowledge of the configuration in which the tentacles are placed in the pockets is important.

Although, there has not been enough research on how tentacles are stored in pockets, there are many studies on hunting behaviour, including behavioural observations (Boucher-Rodoni*, et al*. 1987; Cole, Adamo, 2005; Duval *et al*., 1984; Shinzato *et al*., 2018), tentacle and arm structure (Kier, 1992), and muscle fibre types (Kier, 1985). Many textbooks show only the diagram of a cuttlefish whose tentacles are outside the pockets of the diagram (Okutani, 1995; Nixon, Young, 2003; Jereb, Roper, 2005; Hanlon, Messenger, 2018). Though Sasaki (2008) described that cuttlefish ‘fold’ their tentacles in their pockets, no research shows actual tentacle storage.

The present study reports the arrangement of tentacles in the pockets of pharaoh cuttlefish (*Sepia pharaonis* Ehrenberg, 1831) by morphological observation. This species is widely distributed in the Indian Ocean and western Pacific, including the Red Sea and Arabian Sea south to Zanzibar and Madagascar, Andaman Sea to South China Sea, East China Sea, Taiwan Province of China, Japan (Kyushu and possibly southern Honshu), eastern Indonesia and northern Australia (Jereb, Roper, 2005), and its ecology and behaviour were well studied (e.g. Nabhitabhata, Nilaphat, 1999; Okamoto, 2017). However, the tentacles storage of this species remains largely unknown. Thus, the present study aimed to describe the arrangement of the tentacles in the pockets of pharaoh cuttlefish.

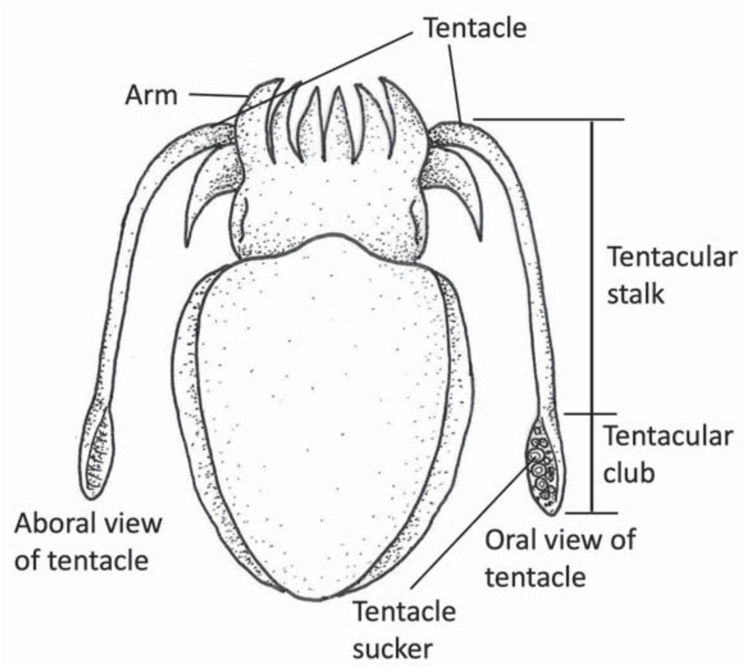

Fig. 1. Scheme of dorsal view of cuttlefish. The cuttlefish has two long tentacles. Each tentacle consists of tentacular stalk and tentacular club.
Рис. 1. Схема строения каракатицы со спинной стороны. Два длинных ловчих щупальца расположены с латеральных сторон и состоят из стебля и булавовидного расширения, несущего присоски.

Material and methods

SPECIMENS. Juvenile *Sepia pharaonis* (n = 40), which stores tentacles in pockets, was used in this study. The mantle lengths were within the range of 42.5 to 51.3 mm. We legally acquired the specimens from the National Museum of Nature and Science (Tsukuba, Japan), where they had been fixed in 10% seawater formalin and stored in 70% ethanol. The specimen number is NSMT-Mo79191.

To check whether there were the artifacts from fixing the specimens could cause some change of tentacle arrangement, we also observed raw cuttlefish specimens juvenile *Sepia esculenta* (Hoyle, 1885), (mantle length = 55.8 to 65.3 mm) (n = 6) which was bought Washizu fish market, Shizuoka, Japan.

OBSERVATIONS. The tentacle is ejected from a hole that is opened on the oral side of the pocket. In this study, I defined a hole as a “tentacle pocket opening” (Fig. 2). Firstly, tentacle pocket openings were observed on the oral side. Eight arms of the specimens were opened, and tentacle pocket openings were observed. Secondly, I observed how the tentacles were stored by dissecting the pockets from the ventral side using anatomical scissors. Thirdly, to quantify the complex curling of the tentacles, I counted the number of peaks in the upper and lower directions of the curling of tentacular stalks in the pockets (Fig. 3).

Images are recorded and viewed using a compact digital camera (Olympus TG-6, Tokyo, Japan).

Results

There are two patterns of tentacle storage in the pockets. Tentacular clubs are located near the tentacle pocket openings in the first pattern (n = 21). The tentacular clubs are emerged from the tentacle pocket openings to the outside of the pockets; therefore, tentacular clubs are observed from the oral side (Fig. 4A).

The frontal face (sucker-bearing face) of the tentacular clubs faces the inner side (Fig. 4A). The tentacular stalks first turn from the origin towards the oral side and then curl with twisting from the oral side to the aboral side in the pockets (Fig. 5A). There are four peaks in the upper and lower directions of the curling of the

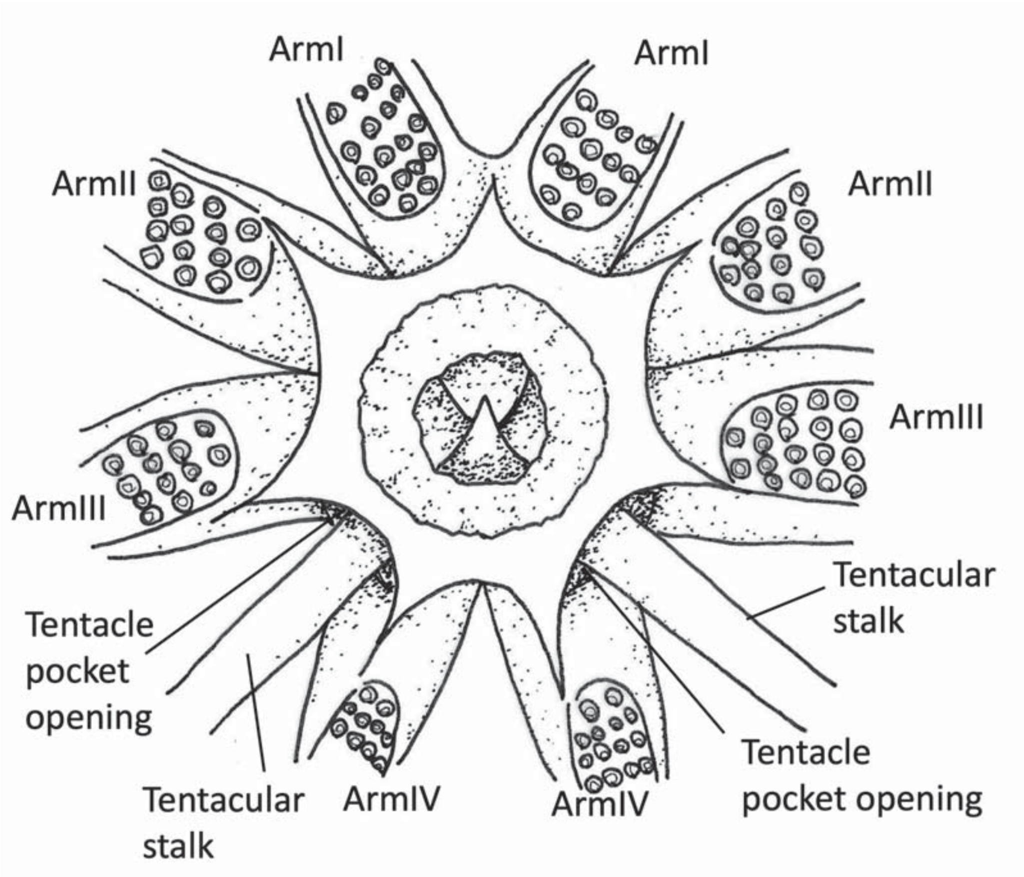

Fig. 2. Scheme of the positions of the tentacle pocket openings.
Рис. 2. Схема расположения рук, ловчих щупалец и сторожевых карманов: вид со стороны рта.

tentacular stalk in both the right and left pockets (Fig. 5A-3). I observed that tentacular stalks did not tangle. All the twenty-one fixed specimens and four raw specimens with the first pattern exhibited the same trends.

Tentacular clubs are completely stored in pockets in the second pattern (n = 19). Curled tentacular stalks are observed near tentacle pocket openings. Tentacular clubs are completely retained inside the pockets (Fig. 4B).

The tentacular stalks first turn from the origin towards the oral side and then curl with twisting from the oral side to the aboral side in the pockets (Fig. 5B). Curling is more complex than that of the first pattern; the number of peaks in the upper and lower directions of the curling is five in both the right and left pockets (Fig. 5B-3). I observed that tentacular stalks did not tangle. All nineteen fixed specimens and two raw specimens with the second pattern exhibit similar trends.

Discussion

The present study is the first report of the tentacle storage on cuttlefish. Though Okutani (1995) just described that cuttlefish fold their tentacles in the pockets, we observed *S. pharaonis* kept their tentacles curing with twisting from the oral side to the aboral side in the pockets, and there were two storage patterns. We also observed a similar tendency in the raw specimens of *Sepia esculenta*, the tentacle storage way observed in *S. pharaonis* would be shared among cuttlefish in that size.

The curling way of *S. pharaonis* would be advantageous for rapid retraction and extension. *S. pharaonis* kept their tentacles curing

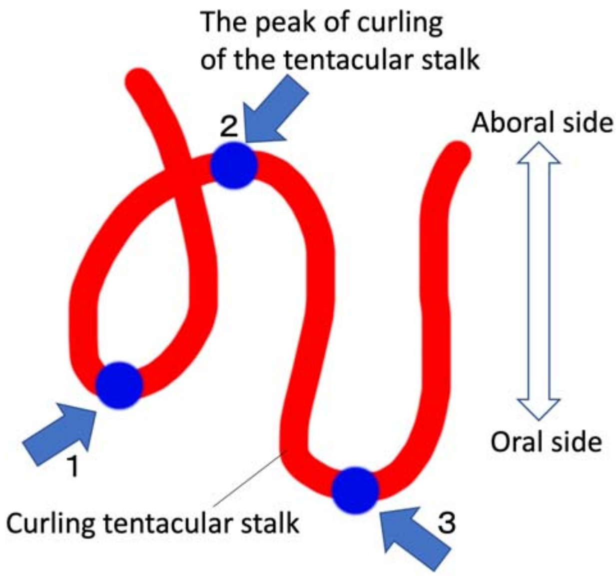

Fig. 3. Diagram of definition of peaks in the upper and lower directions of curling of the tentacular stalks in the pockets. Red line indicates the curling way of the tentacular stalk. Circle indicates the peak of curling of the tentacular stalk. In this diagram, there are three peaks.
Рис. 3. Диаграмма, показывающая максимальные верхние и нижние положения свернутых ловчих щупалец в карманах. Кружки обозначают пики свернутых рук; на этой диаграмме показано три пика.

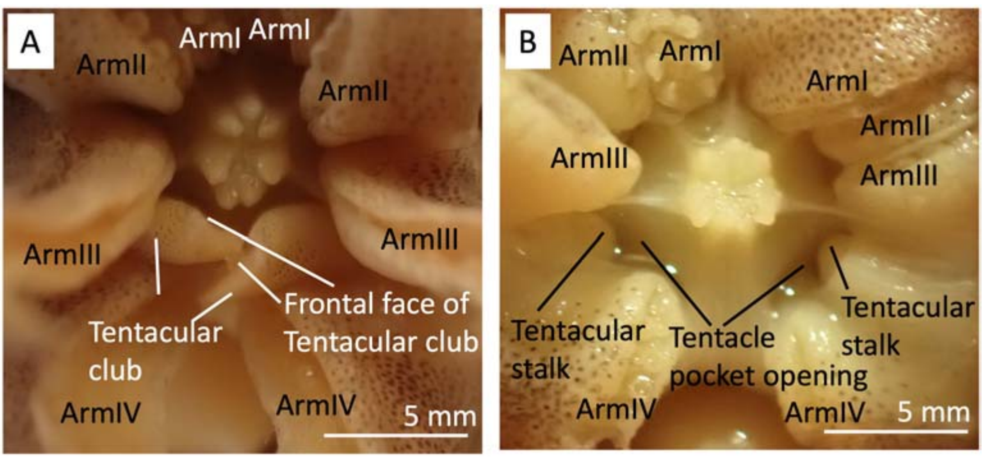

Fig. 4. Images of tentacle storage of *Sepia pharaonis* in the oral view. A — first pattern (n = 21). Tentacular clubs emerged from the tentacle pocket openings to the outside. The frontal face (sucker-bearing face) of the tentacular clubs faces the inner side; B — second pattern (n = 19). Tentacular clubs were completely inside the pockets. Curled tentacular stalks were observed near the tentacle pocket opening.
Рис. 4. Фотографии оральной стороны тела *Sepia pharaonis*. A — первый паттерн расположения ловчих щупалец в карманах (n = 21). Дистальные концы щупалец, несущие булавовидные расширения, расположены вне сторожевых карманов. Фронтальная сторона булавовидного расширения, несущая присоски, обращена к внутренней стороне; B — второй паттерн расположения ловчих щупалец в карманах (n = 19). Булавовидные расширения щупалец полностью спрятаны в сторожевых карманах. Скрученный стебель ловчего щупальца виден из отверстия сторожевого кармана.

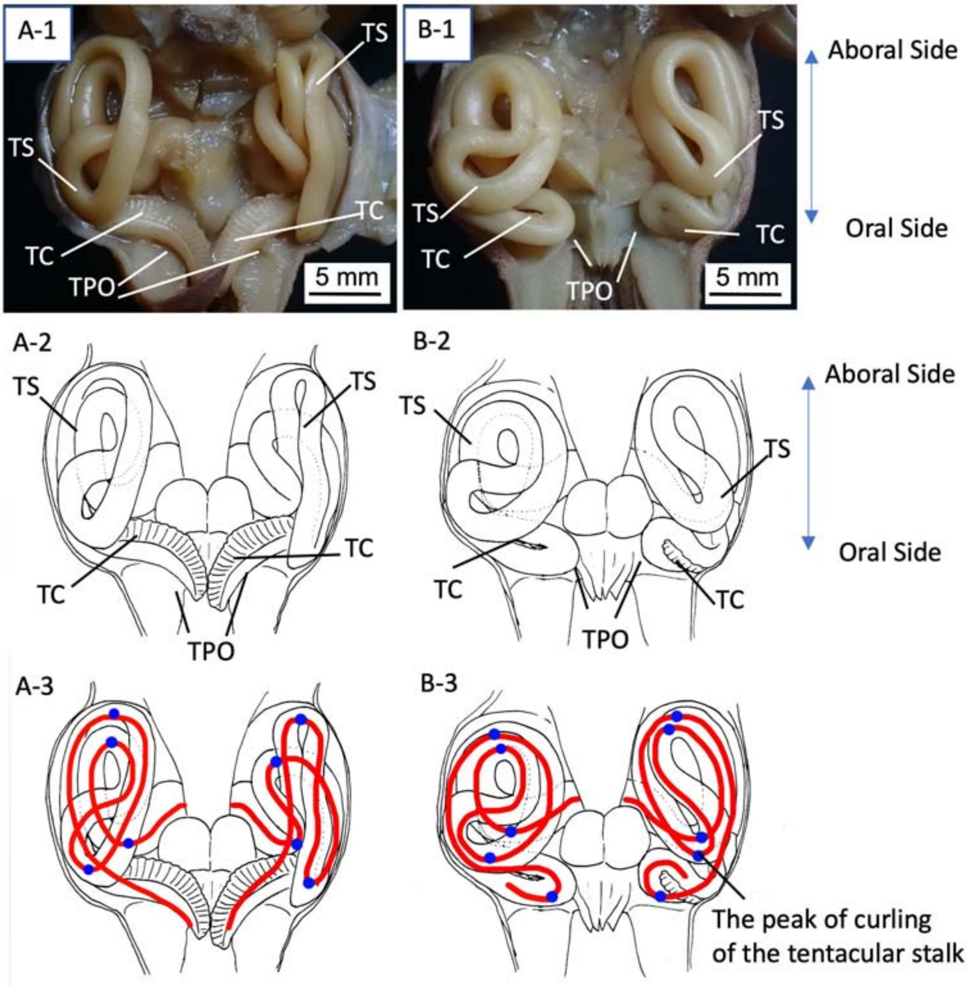

Fig. 5. Images and diagrams of tentacles in pockets of *Sepia pharaonis* from the ventral view. A — first pattern (n = 21); A-1,2 — the tentacular stalks first turned from the origin towards the oral side and then curled with twisting from the oral side to the aboral side in the pockets. Curling is less complex than the second pattern; A-3 — there were four peaks in the upper and lower directions of the curling in the pockets; B — second pattern (n = 19); B-1,2 — the tentacular stalks first turned from the origin towards the oral side and then curled with twisting from the oral side to the aboral side in the pockets. Curling is more complex than the first pattern; B-3 — there were five peaks in the upper and lower directions of the curling in the pockets. Abbreviations: TC — tentacular club; TS — tentacular stalk; TPO — tentacular pocket opening. Red line indicates the curling way of the tentacular stalk. Blue circle indicates the peak of curling of the tentacular stalk.

Рис. 5. Фотографии и схемы расположения ловчих щупалец в сторожевых карманах у *Sepia pharaonis*, вид с вентральной стороны. A — первый паттерн (n = 21); A-1,2 — стебель ловчего щупальца сначала повернут к оральной стороне, а затем скручивается, поворачиваясь к аборальной стороне сторожевого кармана; A-3 — имеется четыре пика верхнего и нижнего положения ловчих щупалец в сторожевых карманах; B — второй паттерн (n = 19); B-1,2 — стебель ловчего щупальца сначала повернут к оральной стороне, а затем скручивается, поворачиваясь к аборальной стороне сторожевого кармана; B-3 — имеется пять пиков нижнего и верхнего положения ловчих щупалец в сторожевых карманах.
Обозначения: TC — булавовидное расширение ловчего щупальца; TS — стебель ловчего щупальца; TPO — отверстие сторожевого кармана. Красной линией показано положение свернутых ловчих щупалец в карманах. Голубыми кружками показаны пики верхних и нижних положений свернутых ловчих щупалец.

with twisting from the oral side to the aboral side in the pockets (Fig. 5). The curling is similar to figure-eight-flake in ropework, a winding method in which the ropes are coiled in figure-eight coils that balance the left and right twists that are put into the rope during construction (Steve, 2012). The coiled rope in figure eight flake can be used quickly without tangling (Steve, 2012). As cuttlefish extend and retract their long tentacles quickly in their pockets during hunting (Boucher-Rodoni, Boucaud-Camou, 1987; Cole, Adamo, 2005; Hanlon, Messenger, 2018), the tentacles should not get tangled. Therefore, storing the tentacles with curling with twisting would be suitable for rapid retraction and extension.

Unfortunately, we could not see tentacular club's position from the outside in living specimens because tentacular clubs are covered by their arms in living situation. However, possible causes for the two storage patterns are discussed below.

The first coiling pattern may be for subsequent hunting. The tentacular clubs were outside of the tentacle pocket opening in the first pattern. There were four peaks in the upper and lower directions of the curling (Figs 4A, 5A). Cuttlefishes extend their tentacles to the oral side plane of the tentacular clubs inward and attach suckers to the tentacular clubs when catching prey, as recorded on some videos (ex. by Feord *et al.*, 2020; BBC Earth, 2021). Therefore, during hunting, they would set their tentacular clubs near the tentacular pocket opening with the oral side plane of the tentacular clubs inward. In general, the less complicated the coiling of a cord-like long object is, the smoother it can be extended without tangling (Pankow *et al.*, 2001; Primkulov *et al.*, 1985). Because the first pattern has less complex coiling (four peaks in the upper and lower directions of the curling) than the second pattern (five peaks in the upper and lower directions of the curling), the first pattern is better for extending the tentacles more smoothly.

In the second pattern, completely retained tentacular clubs inside the pockets (Figs 4B and 5B) might adopt when cuttlefish are not actively feeding at that time. Tentacular clubs outside the pockets would be disturbance when cuttlefish send a prey to their mouth by their arms because tentacle pocket openings are near the mouth. Cuttlefish extend the tentacles leading the tentacular clubs (Brauckhoff *et al.*, 2020). This curling way may retain the tentacles in the pockets by preventing the tentacular clubs leading the tentacular stalks from coming out. *Sepia latimanus* conducted tentacle stretching behaviour when it did not hunt prey (A.O., unpublished data based on three observations at Okinawa Churaumi Aquarium in 2022). This behaviour could support the hypothesis that cuttlefish arrange its tentacles from the second pattern to the first pattern in its pockets for the next hunting, though further research is needed.

Cuttlefish have pockets to store tentacles, whereas squids do not (Nixon, Young, 2003). Squid constantly swims, preys at a high frequency, and digests quickly (Boucaud-Camou, Boucher-Rodoni, 1983; Boucher-Rodoni *et al.*, 1987; Omura *et al.*, 2015). They always swim in preparation for their next predation (Boucaud-Camou, Boucher-Rodoni, 1983; Boucher-Rodoni *et al.*, 1987; Omura *et al.*, 2015). Therefore, they probably do not need to store their tentacles in pockets. However, cuttlefish are benthic and ambush predators (Sugimoto, Ikeda, 2013). They feed infrequently and digest slowly (Boucaud-Camou, Boucher-Rodoni, 1983; Boucher-Rodoni *et al.*, 1987; Omura *et al.*, 2015). They settle at the bottom (Nabhitabhata, Nilaphat 1999; Okamoto, 2017). Storing tentacles by adjusting the coiling method according to their situation may be suitable for the benthic lifestyle of cuttlefish.

The present study is relevant in demonstrating tentacle arrangements in the pockets. We could not observe tentacular club's position from the outside in living specimens, showing the tentacle storage can be the basis of understanding cuttlefish morphology. Further studies are needed to fully understand the tentacle arrangement in cuttlefish. Firstly, how and when they change the curling pattern of tentacles in the pocket should be studied. The inner structure of the pockets of living cuttlefish should be observed during hunting using computerized tomography (CT) to evaluate this. Secondly, the mechanism of tentacle curling should be elucidated through detailed histological observations. Thirdly, a comparison between the tentacles of cuttlefish and squid, which do not have pockets, should be conducted to clarify the tentacle storage strategy. This study contributes to our understanding of cuttlefish's basic morphology and hunting strategies.

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