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The shape of sucker ring teeth in the hectocotylized part of kisslip cuttlefish (*Sepia lycidas*)

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ABSTRACT: Decapodiform cephalopods have ‘sucker ring teeth’ in the suckers of their arms and tentacles. The sucker ring teeth are hard structures, and their shape is related to their function; for example, the sucker ring teeth on the arm are long and sharp, aiding in prey capture.
Among decapodiform cephalopods, cuttlefish have small suckers on their hectocotylus, in addition to their arms and tentacles. The hectocotylus, a modified (hectocotylized) arm present in male cephalopods, is specifically morphologically adapted for grasping and transferring a batch of spermatophores to females during mating. Therefore, understanding the shape of the hectocotylus is crucial for comprehending the mating behavior and reproductive strategy of cephalopods. However, the morphology of the sucker ring teeth on the hectocotylus in cuttlefish remains unknown.
Here, we report the morphological features of the sucker ring teeth on the hectocotylized part of *Sepia lycidas*. We examined and quantified the teeth of the sucker ring using field emission scanning electron microscopy (FE-SEM) and compared the shape of the sucker teeth on the hectocotylus with those on the regular arm. The teeth on the hectocotylized part were shorter and more obtuse compared to those on the arm, and there were little differences in teeth shape by position on the ring circumference. In contrast, the teeth on the arm were longer and sharper, and their length and sharpness varied between the oral and aboral sides. Possible causes for the morphological features of hectocotylized suckers in mating behavior are discussed; we suggest that the shorter and more obtuse sucker teeth around the circumference of hectocotylized part would be optimized to avoid damaging the spermatophores and to efficiently transfer them to the female. This result contributes to understanding the basic morphology of the hectocotylus and mating strategy of cuttlefish.
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KEY WORDS: cuttlefish, Decapodiforms, hectocotylus, Mollusca, sucker, sucker ring teeth.

Форма зубцов присосок гектокотилизированных рук у каракатицы *Sepia lycidas*

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РЕЗЮМЕ: У десятируких головоногих моллюсков на роговых кольцах присосок рук имеются зубцы. Зубцы на присосках — твердые структуры, форма которых связана с их функцией; например, зубцы на присоске руки длинные и острые, что помогает захватывать добычу. У каракатиц, относящихся к десятируким головоногим моллюскам, имеются небольшие присоски не только на руках и щупальцах, но и на гектокотиле. Гектокотиль — присущая самцам головоногих модифицированная (гектокотилизированная) рука — морфологически приспособлен для захвата и передачи сперматофора самке во время спаривания. Поэтому изучение формы гектокотиля имеет решающее значение для понимания брачного поведения и репродуктивной стратегии головоногих моллюсков. Однако морфология зубцов кольца присоски на гектокотиле у каракатиц до сих пор не выяснена.
В данной работе мы рассматриваем морфологические особенности зубцов присоски на гектокотиле *Sepia lycidas*. Мы изучили и количественно оценили зубцы присоски с помощью эмиссионной сканирующей электронной микроскопии (FE-SEM) и сравнили форму зубцов присоски на гектокотиле с зубцами на обычной руке. Зубцы присосок гектокотиля оказались короче и тупее по сравнению с зубцами на руке, а различия в форме зубцов в зависимости от положения по окружности кольца незначительными. Напротив, зубцы на руке оказались длиннее и острее, причем их длина и острота различались на оральной и аборальной сторонах. Обсуждаются возможные причины влияния морфологических особенностей гектокотилизированных присосок на брачное поведение. Мы предполагаем, что более короткие и тупые зубцы по окружности присоски гектокотилизированной руки специализированы для того, чтобы не повреждать сперматофоры и эффективно передавать их самке. Эти данные вносят вклад в понимание базовой морфологии гектокотиля и стратегии спаривания каракатиц.
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КЛЮЧЕВЫЕ СЛОВА: каракатицы, Decapodiforms, гектокотиль, Mollusca, присоски, зубцы присоски.

Introduction

Cephalopod mating behavior is very unique as it is carried out using a modified arm. Most male cephalopods have a modified arm called the hectocotylus, which is used for transferring a batch of spermatophores to females (Drew, 1911; Squires *et al*., 2013; Hanlon, Messenger, 2018; Ibáñez *et al*., 2019). The hectocotylus was first described in Aristotle's work. The name hectocotylus was given by George Cuvier, who initially considered it a parasitic worm and gave it a generic name by combining 'hundred' and 'hollow thing' in 1829 (Tompson, 1913).

The shape of the hectocotylus (the modified part is called the hectocotylized part) is specific and unique to the males of each species (Nixon, Yonge, 2003; Okutani, 2010). For example, the hectocotylus in males of *Euprymna morsei* (Verrill, 1881) is greatly modified, with fleshy papillae formed from enlarged and elongated swollen sucker pedicels (Raid *et al*., 2005), and the hectocotylus of *Loligo forbesii* (Steenstrup, 1857) males has its sucker pedicel modified into long papillae, which gradually decrease in size distally (Raid *et al*., 2005). These modified shapes are considered effective for grasping a batch of spermatophores and transferring them to the female (Okutani, 2010). Therefore, knowledge of the hectocotylus's morphology is important to understand their mating strategy.

In most members of the family Sepiidae (cuttlefish), the hectocotylized part has been described as having 'smaller' or 'reduced' suckers compared to the other arms (Raid *et al*., 2005; Nateewathana, 2008). However, the

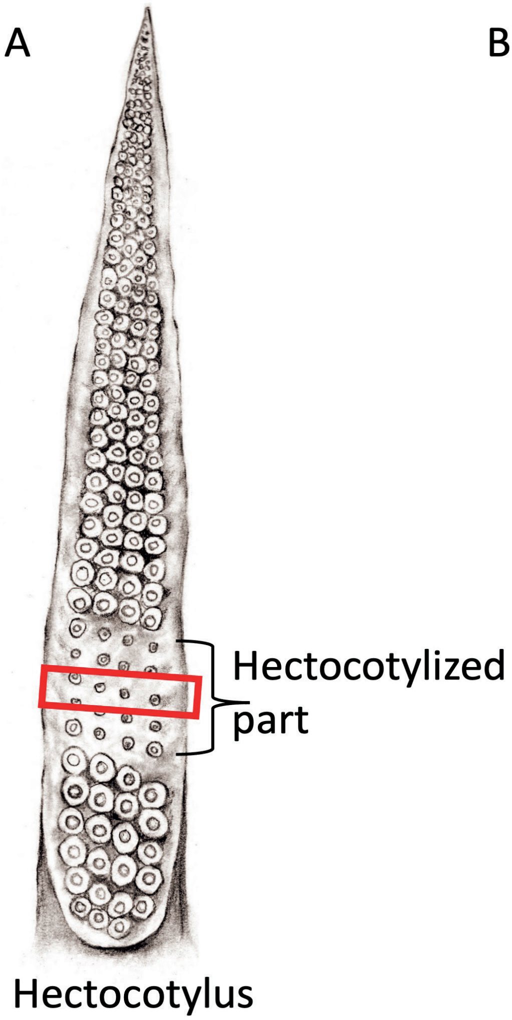

Fig. 1. Diagram of the hectocotylus (left arm) and the arm (right arm) of *Sepia lycidas* (modified from Sasaki, 1929). A — hectocotylus; B — arm. The red square shows four suckers that were observed with the scanning electron microscope. The hectocotylus has a hectocotylized part at its base. There are small suckers on the hectocotylized part.
Рис. 1. Схема гектокотиля (левой руки) и руки (правой руки) *Sepia lycidas* (по Sasaki, 1929, с изменениями). A — гектокотиль; B — рука. Красным прямоугольником показаны четыре присоски, которые были исследованы с помощью сканирующего электронного микроскопа. В основании гектокотиля имеется гектокотилизированная часть. На гектокотилизированной части имеются небольшие присоски.

more detailed morphology of the sucker on the hectocotylized part (hectocotylized sucker) of Sepiidae is not well understood.

In particular, the shape of the sucker ring teeth is important for understanding its function. In general, a decapodiformes' sucker has sucker ring teeth (Nixon, Dilly, 1977; Santi, Graziadei, 1975; Tsuchiya, 2013), which are hard structures assembled from a protein family called 'suckerins' (Hiew, Miserez, 2017). A sucker ring has many sucker teeth on its circumference. The shapes of the sucker teeth on both the arm and

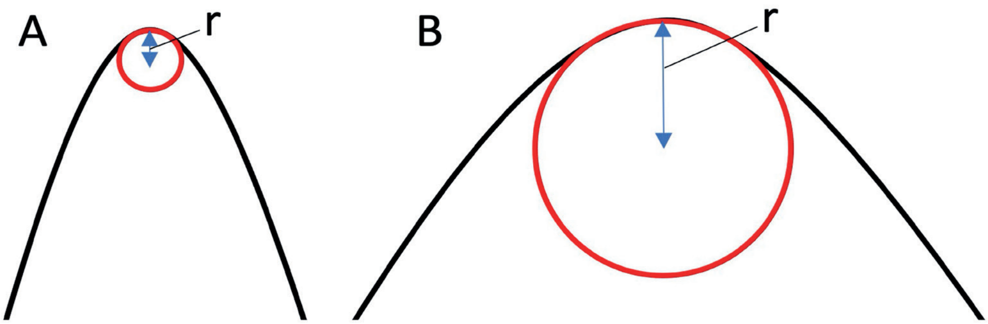

Fig. 2. The curvature radius of a sucker tooth used for quantifying the sucker tooth sharpness. It corresponds to the radius of a circle with the same curve as the arc. A — a steeper curve (sharper tooth) that shows a smaller curvature radius; B — a gentler curve (more obtuse tooth) that shows a larger curvature radius.
Abbreviation: r — curvature radius.

Рис. 2. Радиус кривизны зубца присоски, используемый для количественной оценки остроты зубца присоски. Он соответствует радиусу окружности с той же кривизной, что и дуга. A — более крутая кривая (более острый зуб), которой соответствует меньший радиус кривизны; B — более пологая кривая (более тупой зуб), которой соответствует больший радиус кривизны.
Обозначения: r — радиус кривизны.

tentacle are related to their hunting function: the sucker ring teeth on the arm, which are mainly used to hold prey and transfer it to the mouth during eating, are sharper than the teeth rings on the tentacle, whose main purpose is to catch and retract prey during hunting (Nixon, Dilly, 1977; Nixon, Yong, 2003). However, to the best of our knowledge, the shape of the sucker ring teeth on the hectocotylized part (hectocotylized sucker) of Sepiidae remains unrevealed.

Here, we report the morphological features of the sucker ring teeth of the hectocotylized sucker in Sepiidae. We compared the length and sharpness of the sucker teeth on the hectocotylized sucker with those on the corresponding arm.

Material and methods

SPECIMENS. We used adult males of kisslip cuttlefish (*Sepia lycidas* Gray, 1849) (n = 4, Mantle length were 21.5, 22.5, 23.4, 28.1 cm, respectively). Fresh fisheries specimens were purchased at Washizu Port (Shizuoka, Japan) at their breeding in May 2017, which is their breeding season (April to July in Japan; Natsukari, Tashiro (1991)). Since male Sepiidae develop their hectocotylus for mating behavior ontogenetically, we used specimens during this season to observe the morphology actually utilized in mating behavior.

The hectocotylized part of the left arm IV and the corresponding site on the right arm were amputated and pre-fixed overnight in 2% glutaraldehyde (TAAB, Berkshire, UK) in DPBS (Dulbecco's phosphate buffer saline; Sigma-Aldrich, MO, USA) at 4C. The specimens were then rinsed several times in DPBS, post-fixed for 2 h in 1% osmium tetroxide (Nisshin EM, Tokyo, Japan) in the same buffer at room temperature, dehydrated though a graded series of ethanol solutions, after substitution of ethanol with t-butyl alcohol and immersed in 100% t-butyl alcohol three times at 37C. Then the specimens were freeze-dried (JFD300; JEOL, Tokyo, Japan) for overnight at 2C. Dried specimens were coated with osmium using an osmium plasma coater (HPC-1SW; VACUUM DEVICE, Mito, Japan).

We have analyzed four suckers on the middle of hectocotylized part (left arm IV) (Fig. 1A) and the corresponding site on the right arm IV (Fig. 1B) for each individual (i.e., a total eight of suckers for each individual) for observation and quantification as below.

OBSERVATION OF THE SUCKER RING TEETH. To understand for observing surface fine structure at high resolution of the hectocotylized suckers, we compared the structures of hectocotylus and arm suckers by Field Emission Scanning Electron Microscopy (FE-SEM) at Hamamatsu University of School of Medicine (Shizuoka, Japan). Hitachi S-4800 Field Emission Scanning Electron Microscope (Hitachi, Tokyo, Japan) was used to perform FE-SEM observations and operated at an acceleration voltage of 5.0 kV. The vaccum level of the observation chamber was 10^{-3} to 10^{-7} Pa. The detector for secondary electrons was a mixture of signals from upper and lower

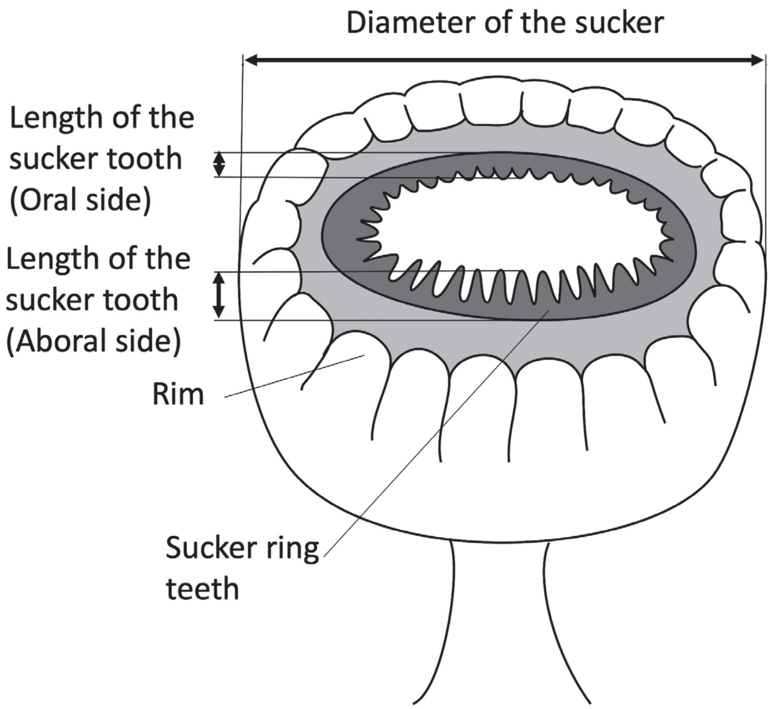

Fig. 3. Diagram of the sucker. The sucker consists of the sucker ring teeth (hard part) surrounded by the rim (soft part). Sucker tooth length is the distance between the base of the sucker tooth and the tip of the sucker tooth.
Рис. 3. Схема присоски. Присоска состоит из зубчатого кольца (твердая часть), окруженного ободком (мягкая часть). Длина зубца присоски — это расстояние между основанием и вершиной зубца.

detectors. The following experimental parameters were used: working distance, 30 mm; aperture size, 100 mm; and scan speed, 10 to 15 frames/s. These whole processes were done at Hamamatsu University of School of Medicine (Shizuoka, Japan).

MORPHOLOGICAL QUANTIFICATION OF THE SUCKER AND SUCKER RING TEETH. To examine the morphological features of the suckers on the hectocotylized part, we quantitatively compared the suckers on the hectocotylus and the arm. We used four suckers on the middle of hectocotylized part (left arm IV) (Fig. 1A) and the corresponding site on the right arm IV (Fig. 1B) for each individual (i.e., a total eight of suckers for each individual). We quantified five sucker teeth on each side.

First, we quantified the length of the sucker tooth and the sharpness of the sucker tooth on both the oral and aboral sides. The length of the sucker tooth was measured from acquired SEM images using Adobe Photoshop CS5 software. Here, we defined the length of the sucker tooth as the distance between the base of the sucker tooth and the tip of the sucker tooth (Fig. 2). The length of the sucker tooth was standardized against the length of the dorsal mantle. We measured the curvature radius of the tooth tips as the sharpness of the sucker teeth (Fig. 3). Since the tips of the sucker tooth are not exactly pointed, we used the curvature radius instead of the angle to quantify the sharpness of the sucker tooth. The curvature radius corresponds to the radius of a circle with the same curve as the arc. A steeper curve (sharper teeth) shows a smaller curvature radius (Fig. 3A), while a gentler curve (more obtuse teeth) shows a larger curvature radius (Fig. 3B). We considered the base-to-base distance between teeth as a curve and measured its curvature radius on SEM images using Adobe Illustrator CC 2019 software.

Additionally, we measured the diameter of the suckers from SEM images (Fig. 2) using Adobe Photoshop CS5 software.

The significance of the differences was statistically compared using Welch's t-test with the statistical computing software R.

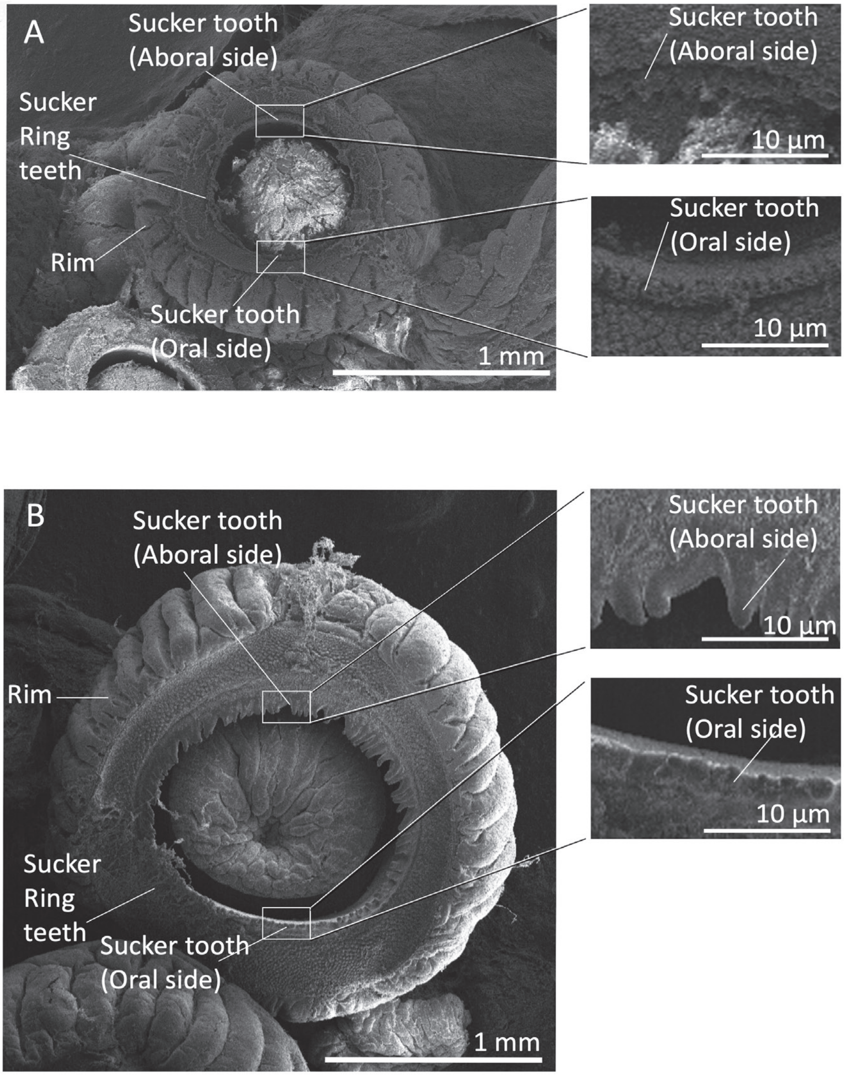

Fig. 4. Scanning electron microscope images of suckers of *Sepia lycidas*. A — the sucker of the hectocotylized part; B — the sucker of the corresponding arm (right arm). The left images show the suckers, and the right images show magnified images of the sucker ring teeth. The upper side is the aboral side, and the lower side is the oral side.

Рис. 4. Присоски *Sepia lycidas*, сканирующая электронная микроскопия (СЕМ). A — присоска гектокотилизированной части; B — присоска соответствующей руки (правая рука). На левых изображениях показаны присоски, а на правых — увеличенные изображения зубцов присоски. Верхняя сторона — аборальная, нижняя — оральная.

Results

The shape of the sucker teeth differed between the hectocotylus and the arm. The sucker teeth of the hectocotylus were observed to be shorter and more obtuse in comparison to those found on the arm (Fig. 4). The length and sharpness of the sucker teeth on the hectocotylus did not noticeably differ over the entire circumference (Fig. 4A). Moreover, no statistically significant differences were detected in the length and sharpness of the sucker teeth between the

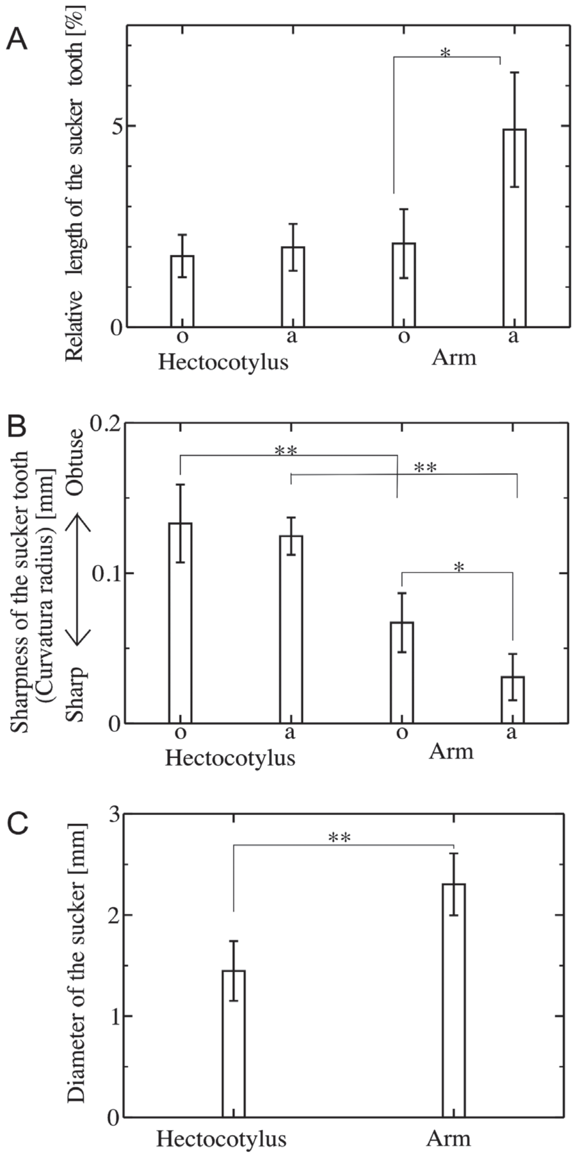

Fig. 5. Morphological quantification of the sucker and sucker ring teeth. A — average length of the sucker tooth on the oral and aboral sides of the hectocotylus and the arm; B — average sharpness (curvature radius) of the sucker tooth on the oral and aboral sides of the hectocotylus and the arm; C — average diameter of the sucker of the hectocotylus and the arm. The error bar represents the standard deviation. Single asterisk indicates $p < 0.05$, and double asterisk indicates $p < 0.01$.
Abbreviations: o — oral side; a — aboral side.

Рис. 5. Морфологическая количественная оценка присосок и зубцов присосок. А — средняя длина зуба присоски на оральной и аборальной сторонах гектокотиля и руки; B — средняя острота (радиус кривизны) зуба присоски на оральной и аборальной сторонах гектокотиля и руки; C — средний диаметр присоски гектокотиля и руки. Диапазон погрешностей показывает стандартное отклонение. Одиночная звездочка обозначает $p < 0,05$, двойная звездочка — $p < 0,01$.
Обозначения: o — оральная сторона; a — аборальная сторона.

oral and aboral sides of the hectocotylus (Fig. 5A, B).

In contrast, the sucker teeth of the arm were longer and sharper compared to those of the hectocotylus (Fig. 4). Specifically, the arm's oral side exhibited shorter and more obtuse teeth, whereas the aboral side displayed longer and sharper teeth (Fig. 4B). These differences were statistically significant (Fig. 5A; average length of the sucker tooth; oral side: 2.01 ± 0.85 [range] (average ± standard error [range]) vs. aboral side: 4.90 ± 1.42 [range]; t-test, p < 0.05, Fig. 5B; average sharpness of the sucker tooth; oral side: 0.06 ± 0.02 [range] (average ± standard error [range]) vs. aboral side: 0.03 ± 0.02 [range]; t-test, $p < 0.05$).

Furthermore, the diameter of the hectocotylus suckers was noticeably smaller in comparison to those of the arm (Fig. 4), a difference that proved to be statistically significant (Fig. 5C; hectocotylus: 1.45 ± 0.29 [range] (average ± standard error [range]) vs. arm: 2.30 ± 0.36 [range]; t-test, $p < 0.01$)."

Discussion

In this study, we first report that the shape of sucker ring teeth of the hectocotylized part of *S. lycidas* differs from that of the arm sucker. The overall structure was typical of Sepiidae's suckers; it had a soft rim encircling the infundibulum, within which was a ring with sucker teeth (Nixon, Young, 2003). As the shape of sucker ring teeth is known to have a relation to its function (Nixon, Dilly, 1977; Okutani, 2010; Tsuchiya, 2013; Omura, Ikeda, 2022), the morphological features of the sucker ring teeth of the hectocotylus would be useful for mating behavior. Possible adaptation strategies are discussed below.

Firstly, the short and obtuse features of the sucker teeth around the entire circumference of the hectocotylized part would be suitable for grasping spermatophores without hooking and scratching and for smoothly transferring them to a female. Generally, the sucker teeth of decapodiforms (including cuttlefish) are used to catch prey by hooking (Nixon, Dilly, 1977; Okutani, 2010; Tsuchiya, 2013; Omura, Ikeda, 2022) and can damage prey or an enemy (Cerullo, Roper, 2012). As for this hooking usage, the sucker teeth of the control (non-hectocotylized) arm were longer and sharper than those of the hectocotylized part, and the teeth on the aboral side are longer and sharper than those on the oral side (Figs 4, 5) for holding prey and transferring it to the mouth (Okutani, 2010). Comparing to the longer and sharper sucker teeth, shorter and more obtuse sucker teeth would not be suitable for hooking. The hectocotylus is used for grasping spermatophores and pressing them against the female during mating (Hanlon *et al.,* 1999; Wada *et al.*, 2010). For this usage, the sucker teeth of the hectocotylus need to avoid hooking and scratching in any direction when the hectocotylus grasps the batch of spermatophores. Therefore, the shorter and more obtuse features of the sucker teeth around the entire circumference of the hectocotylized part would be beneficial for grasping spermatophores without damaging them and for smoothly transferring them to a female.

Secondly, small-diameter suckers without sharp hooking would enhance the hectocotylus' ability to grasp spermatophores. In general, small suckers without sharp hooking act as a non-slip structure on a surface, enabling them to strongly grasp and manipulate the batch of spermatophores effectively; such a structure appears in a non-slip glove (David, 2002). Similarly, small suckers on the hectocotylized part of *S. lycidas* may aid in enhancing the control of grasping and manipulating spermatophores. The existence of small suckers on the hectocotylized part of Sepiidae is consistent with the earlier report about the macroanatomy of *S. lycidas* (Sasaki, 1929) and other species of cuttlefish (Raid *et al.,* 2005; Nateewathana, 2008).

We analyzed the morphology of the sucker ring teeth of the hectocotylus of *S. lycidas* and discussed hypotheses for morphological adaptations for mating behavior. Further investigations of the mating behavior of *S. lycidas* might support our conclusions. First, whether the structure of the hectocotylized sucker can grip spermatophores without scratching them should be studied. The firmness of spermatophores and gripping force of the hectocotylus should be measured. Second, verifying whether the hectocotylized sucker functions effectively as an anti-slip device when gripping spermatophores is needed. Observing the surface structure of spermatophores and measuring the friction and adhesion forces of the hectocotylized sucker through experimental studies should be conducted. This study contributes to our understanding of the basic morphology and mating strategies of cuttlefish.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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