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Article

Micro-Bulge Structure on Exoskeletons Surface of the Coconut Crab (*Birgus latro*)

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Abstract

This study investigated the surface morphology of the thoracic exoskeleton of the coconut crab (*Birgus latro*) from Okinawa using laser microscopy. While many aquatic crustaceans possess prominent raised surface structures to prevent the attachment of epibionts, the terrestrial coconut crab is thought to exhibit distinct characteristics adapted to its unique environment—one often dominated by limestone and characterized by relatively dry conditions. Three adult coconut crabs, varying in body weight (173 g, 437 g, 964 g), were analyzed. Quantitative surface analysis revealed a uniform micro-bulge structure across both black and yellow color zones of the exoskeleton. The diameter of these bulges consistently ranged from 10 to 17 µm with height between 1.3 and 2.2 µm, regardless of individual body size or coloration. This structural uniformity suggests evolutionary adaptation for durability, moisture retention, friction modulation, and resistance to abrasion and predators, in contrast to aquatic species where larger bulges assist in preventing marine organism attachment. The matte shell texture and micro-bulge arrangement further contribute to minimizing water loss—a crucial factor for terrestrial survival. The consistency of bulge size and distribution, independent of size and carapace pattern, highlights the functional conservation of these microstructures as a fundamental adaptation for terrestrial life.

Keywords: decapod crustacean; carapace; micro-bulge structure; laser microscopy; terrestrial adaptation; coconut crab

1. Introduction

Many organisms and plants are known to have surface morphological features closely associated with adaptation to diverse environments [1–6]. A classic example is the "self-cleaning" property of the lotus leaf—often termed the "lotus effect"—which arises from the synergy between surface microstructures and epicuticular wax-like deposits. Yet, in contrast to the vast body of biomimetic literature on plant surfaces, the surface morphology of crustacean carapaces has received far less attention. Nevertheless, preliminary findings indicate that crustacean shells, defended by their robust exoskeletons, feature fine, micro-scale bulge structures on their surfaces. In aquatic crab species such as the mud crab (*Scylla serrata*) [7], blue crab (*Callinectes sapidus*) [8], and brown crab (*Cancer pagurus*) [9], fine bulge structures have been reported on the exoskeleton surface. Furthermore, the exoskeleton surface of aquatic snapping shrimp also displays bulges with diameters ranging from 68 to 103 µm and heights up to 33 µm [10]. Detailed analysis using laser microscopy revealed that the surface morphology of the mud crab consists of a bimodal bulge structure, with large bulges of 265 µm and smaller bulges around 100 µm in diameter [11]. Interestingly, the size of these bulges does not depend on the body size or weight of the crab, which is

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consistent with the characteristic uniform density of placoid scales covering the surface of sharks, regardless of their body size [12,13]. The presence of such bulges is suggested to increase the overall surface area of the carapace while reducing the effective contact area with external surfaces, thereby preventing the attachment of fouling organisms and maintaining a clean exoskeleton [7,11]. Moreover, these bulges contribute to dispersing external forces, thereby enhancing the resistance of the exoskeleton to physical damage.

In contrast, the exoskeleton of terrestrial crustaceans such as the coconut crab (*Birgus latro*) lacks the gloss typically seen in aquatic species and instead exhibits a matte texture [14–18]. On the surfaces of the chelae and legs, small black protuberances, arranged in a regular pattern, are visible and thought to enhance grip and protect the surface during locomotion and escape [19]. These black protuberances are composed of flexible α-chitin, which differs greatly from the hard calcite-based tissue and structure of the main exoskeleton. Notably, such protuberances are not visible on the thoracic exoskeleton surface. Additionally, the thoracic exoskeleton surface exhibits color markings, with unique patterns present on each individual [20]. These patterns remain unchanged after repeated molting, allowing researchers to identify individuals without the use of passive integrated transponder tags [15].

There have been no previous reports analyzing the surface morphology of the coconut crab carapace. In this study, three coconut crabs of different body weights were examined with particular focus on the presence and size of bulges on the thoracic exoskeleton surface. The surface morphology of the exoskeleton was analyzed using laser microscopy, compared the results with those for aquatic crustaceans, and discussed the findings in the context of the ecology of these terrestrial crabs.

2. Materials and Methods

Three live coconut crabs (*Birgus latro*) in the intermolt stage—one male (964 g) and two females (173 g and 437 g)—were purchased from a local market in Naha, Okinawa, Japan, in July 2020 (male specimen) and July 2023 (female specimens). Because the coconut crab is an endangered species, the number of specimens was limited to three. The intermolt condition was assessed based on the hardness of the exoskeleton at the time of purchase. All specimens had sufficiently hardened exoskeletons and showed no signs of the immediate post-molt soft-shell condition. Previous studies [15,21,22] have reported seasonal molting patterns in coconut crabs, with larger individuals generally molting once annually during the winter dry season. However, molting frequency may vary depending on body size and developmental stage. After all crabs were euthanized via deep-freezing, the samples were frozen at −18 °C to prevent natural decay processes, and transported to our laboratory in Tsukuba. The test pieces were cut from the front cephalothorax (FC) and rear cephalothorax (RC) using a microgrinder, Minimo ONE SERIES ver.3 (MINITOR Co., LTD., Tokyo, Japan). For RC, each test piece was cut to a size sufficient for surface analysis while ensuring that the observed color spots were included. As shown in Figure 1, the RC surface can be classified into a yellow area and a black area by visual inspection. Next, the test piece was thawed in running water and thoroughly rinsed with water. The surface water droplets were then gently removed using a canned air duster, and the pieces were immediately mounted on the microscope stage with the observation surface facing upward to scan the morphology. To prevent any alteration in surface properties (particularly localized color variations) caused by dehydration, all surface observations were completed within 1 h after the water rinsing process. Since the presence of fine bulges was confirmed on exoskeleton surface, surface morphology was observed using a 3D laser scanning microscope, VK-X200 (Keyence Corporation, Japan). This instrument employs a pinhole confocal optical system equipped with a 408 nm violet laser (laser spot radius: 0.2 μm) to perform profile, roughness, and

thickness measurements with a Z-resolution of 0.5 nm. For the observation of micro-bulges, an ultra-long-working-distance 100× objective lens was utilized. The imaging parameters were set to a magnification of 100×, a numerical aperture (NA) of 0.73, an image resolution of 1024 × 768 pixels, a scan area of 144 × 110 µm, a Z-step size of 0.1 µm, and a gamma correction value of 0.45. During quantitative analysis, the observation application, VK-X1XV(v4.1.1.0) (Keyence Corporation, Japan) included with VK-X200 was employed to process the scanned images. Noise was removed using S- and L-filters in accordance with ISO 4287 [23]; tilt correction was applied via least-squares plane fitting, and the geometry of the micro-bulges was subsequently measured. The diameters of 10 bulges for each area were quantitatively measured using the observation application and they were recorded as (average values ± standard deviation).

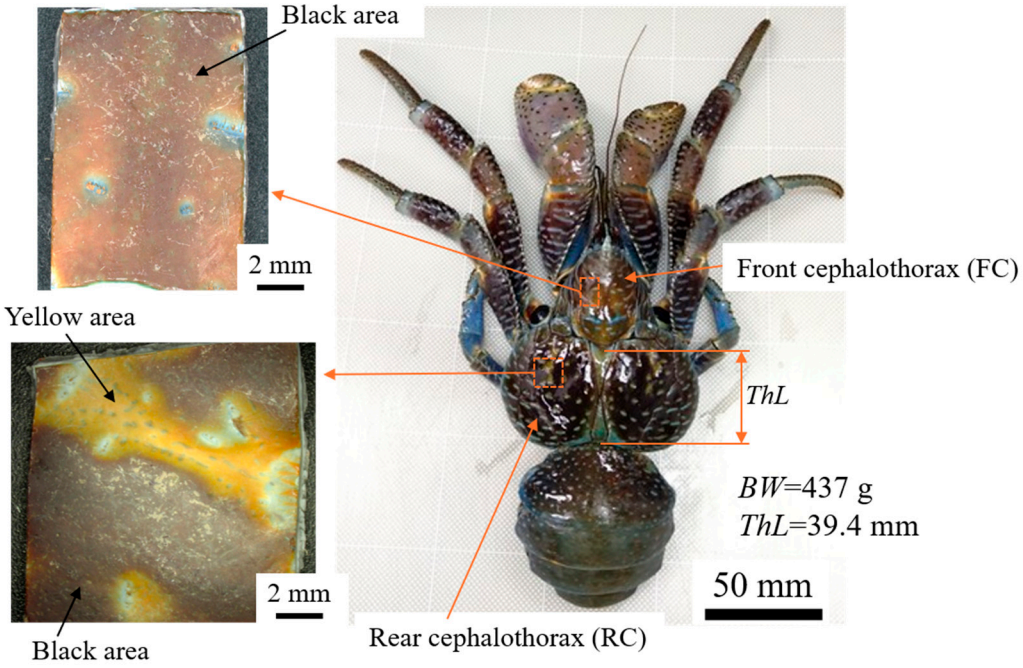


Figure 1. The coconut crab (*Birgus latro*) and enlarged views of the surface of the thoracic exoskeleton. *BW* denotes body weight and *ThL* denotes thoracic length.

3. Results

Figure 2 shows the result of surface analysis of the RC exoskeleton for a 437 g coconut crab, as shown in Figure 1. As a distinctive black-and-yellow pattern was observed on the surface of the RC exoskeleton, three sites (Ba, Bb, Bc) were selected from the black area and three sites (Ya, Yb, Yc) from the yellow area. A distinct bulge structure was observed at all sites, as shown in Figure 2b,d, and the 3D maps shown in Figure 2c,e clearly showed that there is unevenness on the exoskeleton surface. No significant differences were found in the diameter of the bulges (B_d), which ranged from 13.0 to 16.5 µm (see Figure S1a of the Supporting Materials for details). Here, some minor cracks and scratch-like depressions were occasionally observed on the carapace surface, as shown in Figure 2b and Figure S1a,b. Because the specimens were wild animals inhabiting rugged limestone environments, these features are considered to be natural wear and tear or minor physical damage sustained in their natural habitat or during capture. I confirmed that these surface markings were not artifacts of sample preparation, as the test pieces were carefully prepared without damaging the exceptionally hard and rigid exoskeleton. The bulge height (shown in Figure 3) is approximately 1.3–2.2 µm. It should be noted that the measured height of the micro-bulges is less accurate than their diameter. This is highly dependent on the

instrument's physical limitations and surface topography; specifically, due to the finite laser spot diameter of 0.4 μm, the laser beam may not fully reach the deepest valleys between adjacent micro-bulges [5]. Therefore, the height data presented in Figure 3 should be regarded as reference data. As a result, no notable difference in the size of the bulges was observed between the black and yellow areas. Figure 4 shows the RC surface results for two other crabs with different body weights (BW = 173 g and 964 g). Here, only the results for sites Bc and Yb are presented as representatives; data for the other sites are shown in Figure S1b and c of the Supporting Materials. Despite a more than fivefold difference in BW and a nearly twofold difference in a thoracic length (ThL), no significant difference was observed in the diameter of the bulge. Furthermore, as with the crab weighing 437 g shown in Figure 2, there was almost no difference in the bulge diameter between the black and yellow areas. Figure 5 shows the results of the surface analysis of the FC exoskeletons of all the coconut crabs, including quantitative analyses of the diameters of the bulges (see Figure S2 of the Supporting Materials for the bulge height). As shown in Figure 1, groove-like depressions were observed on the FC surface; however, since these were confined to the black areas, a single site within such an area was selected for measurement. There was no significant difference in the diameter of the bulges: Bd = 15.9 ± 1.20 μm for the 173 g crab, 15.8 ± 0.97 μm for the 437 g crab, and 16.0 ± 0.97 μm for the 964 g crab.

The relationship between BW and Bd is Figure 6. Although the Bd of the black area on the RC surface of a small coconut crab weighing 173 g is slightly smaller than that of larger crabs, it falls within the range of 10–17 μm, indicating that these diameters remain constant as BW increases.

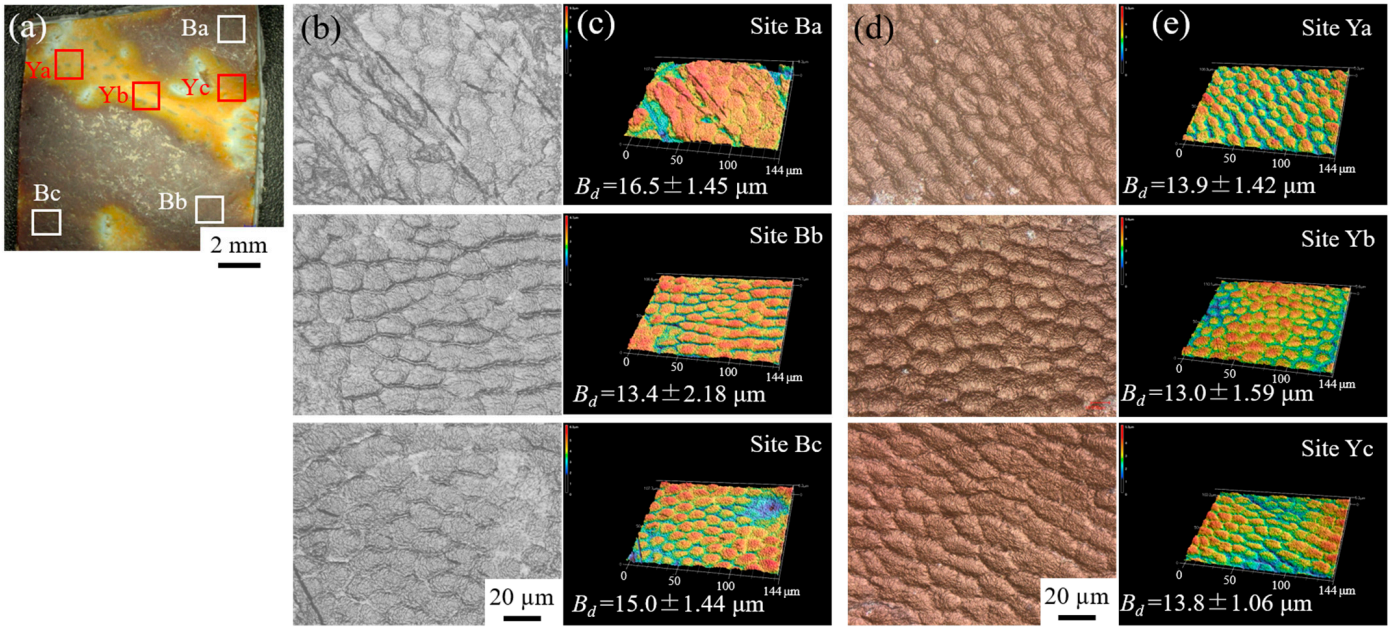


Figure 2. (**a**) Surface image of the RC exoskeleton of a coconut crab weighing 437 g. (**b**) Laser scanning microscope (LM) image, and (**c**) 3D color map corresponding to three sites (Ba, Bb, Bc) in the black area. (**d**) LM image, and (**e**) 3D color map corresponding to three sites (Ya, Yb, Yc) in the yellow area. Here, the diameters of the bulges (B_d) are presented as average values ± standard deviation. Here, in the color maps depicting the bulges, red indicates higher elevations, while blue indicates lower elevations.

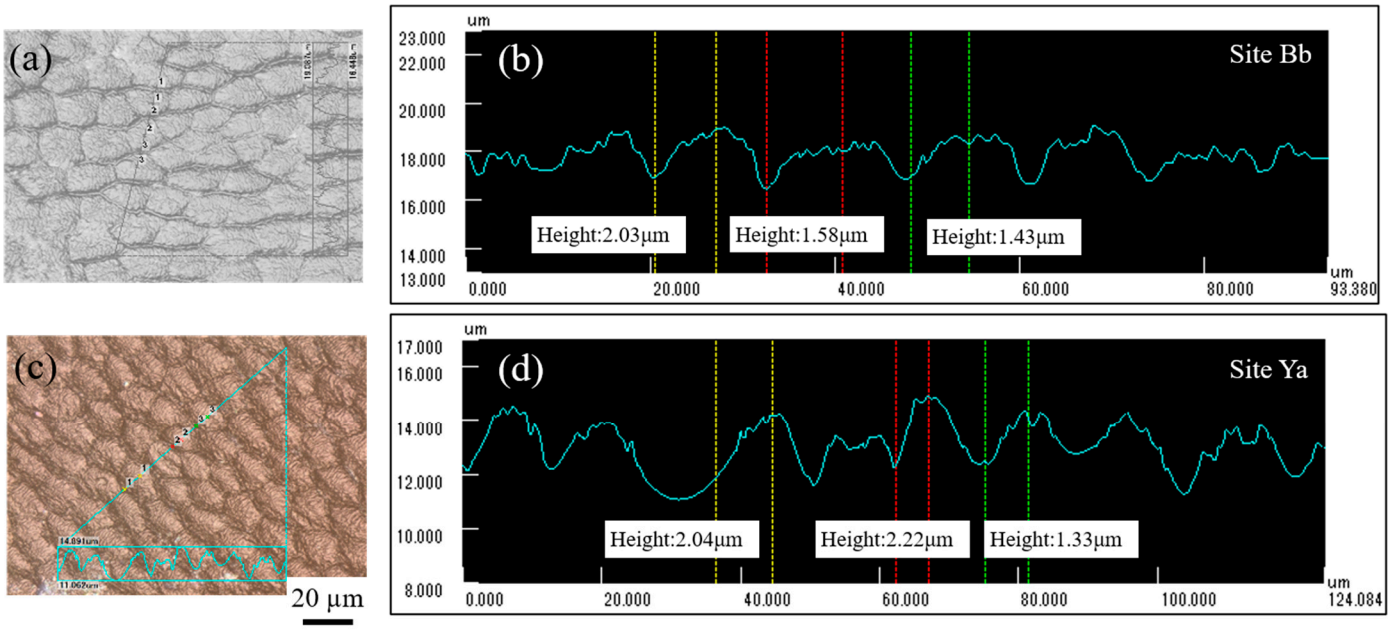


Figure 3. LM images of (**a**,**b**) site Bb and (**c**,**d**) site Ya in the RC exoskeleton of a coconut crab weighing 437 g. The line profiles in (**b**) and (**d**) show the cross sections along the lines in (**a**) and (**c**), respectively.

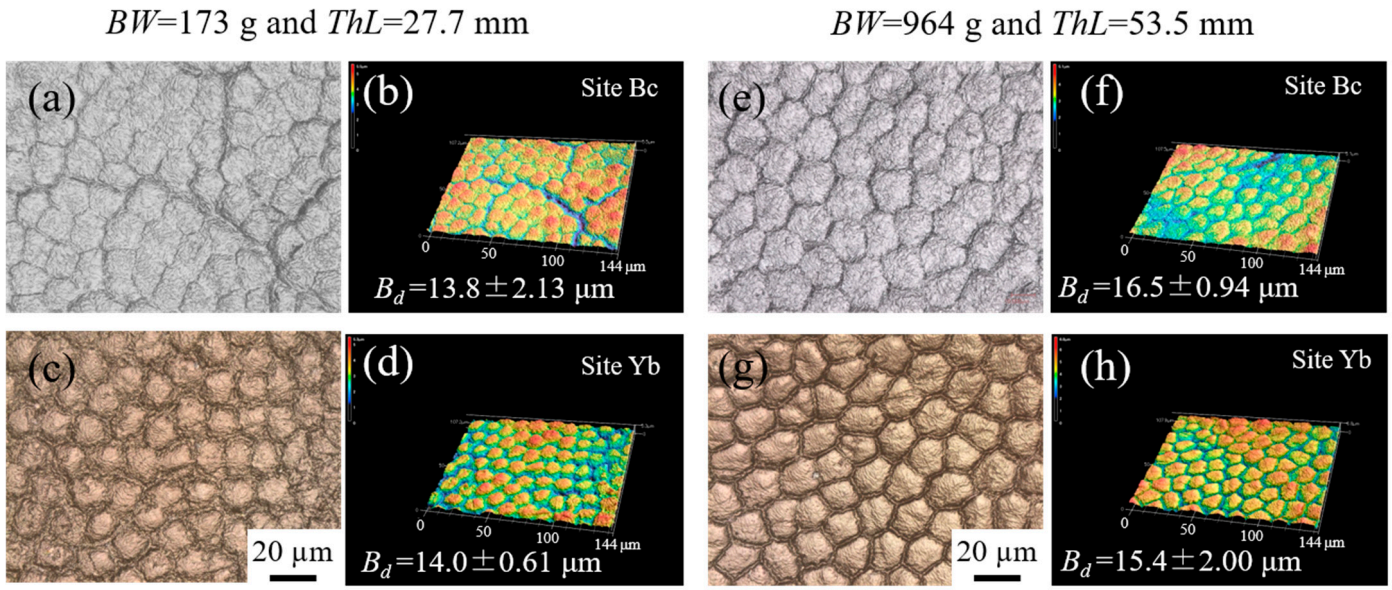
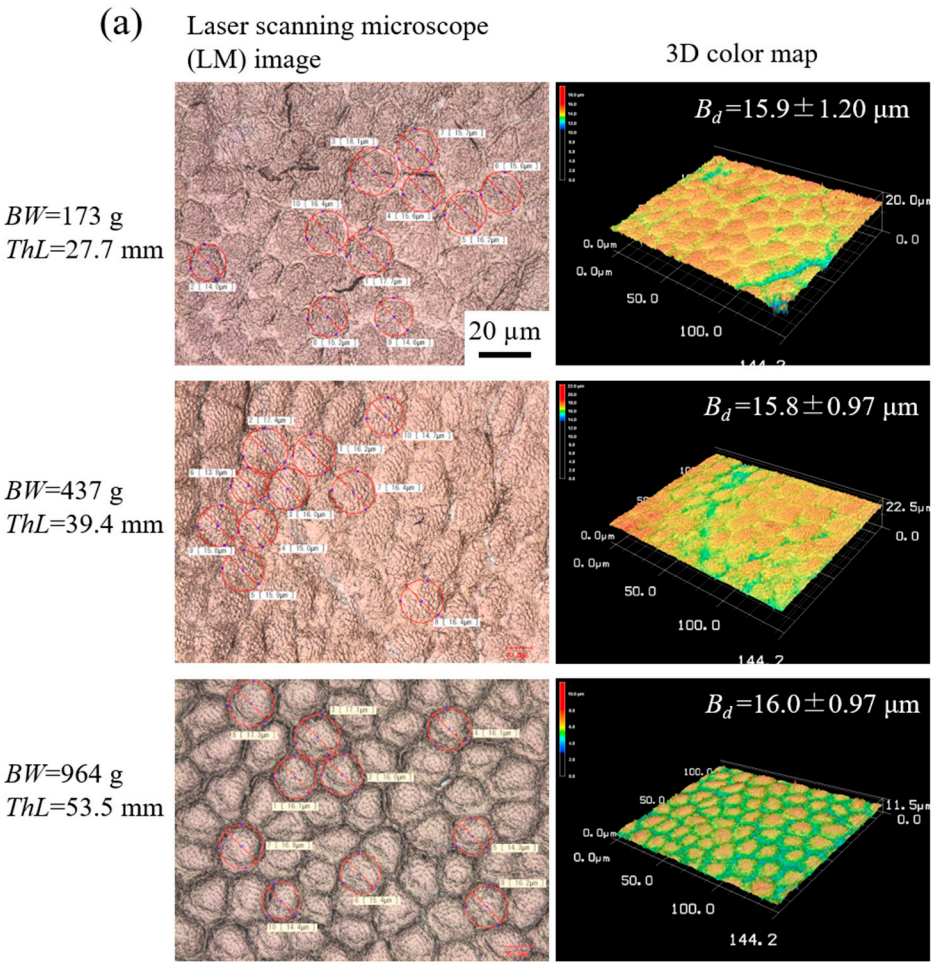


Figure 4. Surface morphology of the RC exoskeleton in coconut crabs with different body weights: (**a**,**b**,**e**,**f**) black areas and (**c**,**d**,**g**,**h**) yellow areas. (**a**,**c**,**e**,**g**) LM images and (**b**,**d**,**f**,**h**) 3D color maps showing bulges. Here, in the color maps depicting the bulges, red indicates higher elevations, while blue indicates lower elevations.

(a)



(b)

No	BW:173g	BW:437g	BW:964g
1	17.7	16.2	16.1
2	14.0	17.4	16.0
3	18.1	16.0	17.1
4	15.6	15.0	16.1
5	16.2	15.9	14.3
6	15.6	13.8	15.4
7	15.7	16.4	16.8
8	15.2	16.4	17.3
9	14.6	15.8	16.2
10	16.4	14.7	14.4
max.	18.1	17.4	17.3
min.	14.0	13.8	14.3
ave.	15.9	15.8	16.0
SD	1.20	0.97	0.97

SD : standard deviation, unit : μm

Figure 5. (**a**) LM image of the FC exoskeleton and 3D color map showing bulges, and (**b**) measured data. The diameter of 10 bulges for each sample was measured using the observation application included with the 3D laser scanning microscope. Here, in the color maps depicting the bulges, red indicates higher elevations, while blue indicates lower elevations.

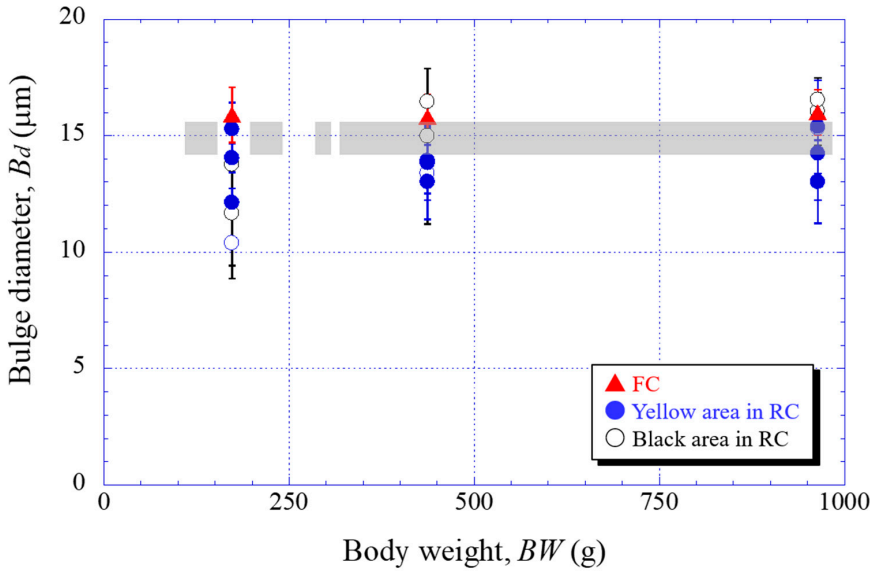


Figure 6. Relationship between *BW* and bulge diameter (B_d) in coconut crabs. Error bars indicate standard deviations.

4. Discussion

The coconut crab's carapace surface is characterized by uniformly distributed micro-bulge structures within the range of 10–17 μm in diameter, which remain consistent across individuals of varying body sizes and coloration. This unique morphology differs from the bimodal bulge structures seen in mud crabs (*Scylla serrata*) [11] and the scales of cartilaginous fish such as sharks and rays [12,13]. Furthermore, the coconut crab's bulges are significantly smaller than those reported in other decapod crustaceans.

Okinawa's limestone landscapes provide abrasive and rugged substrates, presenting significant terrestrial challenges for coconut crabs—particularly the risk of mechanical injury, abrasion, and rapid desiccation. Consequently, their exoskeleton is structurally adapted not only for predator defense, but also to maintain durability, moisture retention, and friction balance during movement across these harsh substrates. Unlike aquatic crustaceans, whose bulges largely serve to reduce fouling and enhance mechanical resistance, coconut crabs' micro-bulges likely play a critical role in dispersing external forces, preventing cracks, and modulating friction in both dry and wet conditions. These structures may also assist in suppressing excessive drying by increasing surface area, a vital adaptation supported by the presence of numerous pore canals connecting exoskeleton to soft tissue [17].

Furthermore, the fine bulges are distributed regardless of carapace color, indicating that their function is fundamental and conserved, independent of coloration or individual size. While aquatic crabs rely on surface bulges to deter attachment of fouling organisms, coconut crabs must primarily conserve moisture and resist abrasion—key requirements for survival in arid, limestone environments. The matte, non-glossy shell texture likely enhances micro-morphological complexity, further preventing water loss. Predator protection remains a crucial function for coconut crabs, whose micro-bulges reinforce the carapace and minimize direct contact points, potentially improving durability and defense against terrestrial predators.

5. Outlook

The study proposed that micro-bulges played roles in moisture retention, friction modulation for movement, wear resistance, and predator defense. However, it was currently based mainly on structural analogy (comparison with aquatic crabs) and theoretical inference, and direct evidence for these functions was still lacking. In addition, due to the small sample size ($n = 3$), this work should be regarded as a preliminary, exploratory investigation. The coconut crab (*Birgus latro*) is an endangered species under strict conservation, which severely limits the availability of specimens for research. Because coconut crabs undergo ecdysis (molting) inside deep limestone crevices or burrowed sand in the wild, and because successful molting under artificial rearing conditions remains extremely difficult to achieve, obtaining specimens at various stages of the molt cycle is exceptionally challenging. Consequently, whether and how the degree of exoskeletal hardening at different molt stages affects the micromorphology (such as micro-bulge height) remains unknown. All specimens in this study were in the stable intermolt stage, representing the fully hardened carapace. Future long-term studies with expanded sample sizes are essential to exclude potential variations associated with ontogenetic stages, specific molt cycles, or distinct geographic populations. In addition, future studies should address how these fine bulges affect real-world friction, moisture retention rates, and resistance to physical abrasion and predation, comparing terrestrial and aquatic crustaceans across varied environments [24,25]. In addition, it will be essential to include comparisons with coconut crabs inhabiting regions outside Okinawa, as differences in habitat may influence surface microstructure and its adaptive significance. Such analyses will deepen understanding of

crustacean exoskeleton evolution, especially regarding the role of surface microstructure in functional adaptation to terrestrial life.

6. Conclusions

This study investigated the surface morphology of the thoracic exoskeleton of Okinawan coconut crabs (*Birgus latro*) using laser microscopy. The analysis revealed that the exoskeleton surface is characterized by a uniform micro-bulge structure, with bulge diameters within the range of 10–17 µm, regardless of the crab's body weight (173–964 g) or distinctive carapace color patterns (black and yellow areas). Compared to aquatic crustaceans, which possess larger surface bulges for fouling resistance, coconut crab bulges are smaller and likely serve functions crucial for terrestrial adaptation—such as moisture retention, friction modulation for movement, resistance to abrasion, and predator defense. The consistency and functional significance of these microstructures highlight their role in enabling coconut crabs to thrive in the rugged, limestone-dominated environment of Okinawa, shedding light on crustacean surface evolution and ecological adaptation.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/jmse14212107/s1, Figure S1: Surface morphology of three sites (Ba, Bb, Bc) in the black area and three sites (Ya, Yb, Yc) in the yellow area on the RC of coconut crabs weighing (a) 437 g, (b) 173 g, and (c) 964 g by a 3D laser scanning microscope (VK-X200, Keyence Corporation, Osaka, Japan). The diameter of 10 bulges for each site was measured using the observation application (VK-X1XV, Keyence Corporation, Osaka, Japan) included with the VK-X200; Figure S2: LM images of the front cephalothorax exoskeleton for each crab and corresponding 3D maps. The line profiles represent the cross sections along the lines in each image, respectively. Here, in the color maps depicting the bulges, red indicates higher elevations, while blue indicates lower elevations.

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Informed Consent Statement: Not applicable.

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Conflicts of Interest: The authors declare no conflicts of interest.

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