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Crushing and Cutting: Shape Variation and Morphological Integration Between the Claws of Two Swimming Crab Species (Brachyura: Portunidae)

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ABSTRACT

This study investigated shape variations and morphological integration between the components of crusher and cutter claws in two species of swimming crabs, *Callinectes danae* and *Callinectes ornatus*. The propodi and dactyli of the claws were analysed in males and females of both species, using geometric morphometric techniques to identify subtle shape differences and analyse the integration between the components. The analysis of morphological integration assesses the coadaptation between two correlated traits, whose modifications may result in improvements in functional performance. The crusher claws, associated with agonistic interactions and breaking prey with hard tissues, showed greater robustness than the cutter claws, which are specialised in cutting tasks and agile capture. Despite these functional differences, a high degree of morphological integration was found between the propodus and dactylus in both types of claws, regardless of sex or species. Statistical analyses confirmed significant differences in the shape of the structures between crusher and cutter claws, highlighting variations in robustness and proportions of the components. These findings indicate that, even though each type of claw is frequently used to acquire different resources, they do not differ in terms of morphological integration, as they are coadapted to perform different functions with high efficiency.

1 | Introduction

Appendages in arthropods exhibit a diverse array of specialised morphologies and functions, which have contributed to their success during adaptive radiation (Browne and Patel 2000; Jockusch 2017). This diversification arises from selective pressures acting on each body plan, through the interaction of ecological demands, behavioural adaptations and genetic factors (Williams and Nagy 1996). In spiders, morphological disparity can be linked to niche specialisation, including behavioural traits, web architecture and microhabitat use, which influence locomotion strategies for prey capture

(Wolff et al. 2022). Similarly, in lepidopteran larvae, ontogenetic changes in mandible morphology, transitioning from a toothed cutting edge to a smooth edge, correlate with feeding behaviour, from grazing on grass to consuming leaves (Hochuli 2001).

Variation in symmetry within an organism can often be observed in body parts with multiple functions, as in the forceps of earwigs, which exhibit asymmetry and are used by males both in aggressive interactions and courtship (Moore and Wilson 1993; Munoz and Zink 2012). In insects, asymmetric mandibles primarily function in food processing but can also be linked to copulation and social niche specialisation, as documented in ants (Casadei-Ferreira et al. 2021). Beetles that exhibit aggressive behaviour may display mandibular laterality, where one mandible is larger than the other, correlating with side preference and differential use within a population (Okada et al. 2008; Vendl et al. 2018).

A chela is a claw-shaped structure that often exhibits multifunctionality. It can be observed in the chelicerae or pedipalps of some arachnid species, such as the asymmetric chelate appendages found in pseudoscorpions and harvestmen (Taylor 2009; van der Meijden et al. 2012). Additionally, crustaceans represent the most well-documented example of heterochely with morphologically distinct claws adapted to different functions, such as feeding or intraspecific competition (Mariappan et al. 2000).

In Decapoda, chelae are highly specialised structures capable of generating and transmitting substantial forces, conferring advantages in food acquisition and predator defence (Smith and Hines 1991; Bildstein et al. 1989). These claws exhibit wide diversity and are often associated with defence, predation, resource competition and agonistic interactions, shaped by local ecological characteristics (Emberts et al. 2021; Silva et al. 2017; Palaoro et al. 2017). Swimming crabs of the genus *Callinectes* Stimpson 1860, including *Callinectes danae* Smith 1869, and *Callinectes ornatus* Ordway 1863, both widely distributed along the Brazilian coast (Melo 1996), are notable for their aggressive behaviour and complex agonistic interactions, in which their chelipeds play a central role (Reichmuth et al. 2011; Jachowski 1974).

Different selective pressures act on these structures, influencing traits such as size, shape, dentition pattern, muscle composition and the morphological integration between the segments comprising the claw (propodus and dactylus) (Hamilton et al. 1976; Nogueira et al. 2022; Spani et al. 2020). Previous studies have shown that both parts of the claw are morphologically integrated regardless of developmental stage or behavioural context, such as fighting (da Silva and Nogueira 2023; Nogueira et al. 2022). Although selective pressures act on this structure, the claws, like other crustacean appendages, have their development regulated by a shared set of genes (Pavlopoulos and Wolff 2020). Therefore, it is plausible that the observed morphological integration may not solely reflect functional adaptation, but could also be a by-product of the underlying genomic architecture that regulates appendage development, as the propodus and dactylus grow along the same morphological trajectory, forming an integrated unit.

In the literature, these claws are classified as crusher (primary) and cutter (secondary). Crusher claws feature molariform teeth and a robust manus, whereas cutter claws have pointed teeth and a slender manus (Seed and Hughes 1995). Previous studies have analysed these structures across different species, exploring aspects such as mechanical force, muscle histology (Govind and Blundon 1985; Schenk and Wainwright 2001), ontogenetic development (Lane-Medeiros et al. 2021) and linear and geometric morphometrics (da Silva and Nogueira 2023; João et al. 2024; Tsuchida and Fujikura 2000).

Geometric morphometrics is an analytical tool on the basis of landmark coordinates, allowing for the identification of subtle shape differences in structures across groups (Mitteroecker and Gunz 2009). This method uses landmarks, which represent biologically homologous points and semilandmarks, distributed along structural curves (Bookstein 1997; Mitteroecker and Gunz 2009). These techniques reveal subtle morphological differences between species, demographic groups or populations, highlighting evolutionary processes and patterns of integrated morphological development (Klingenberg 2014; Nogueira et al. 2023; Rosenberg 2001).

Previous studies on crabs of the genus *Callinectes* have addressed aspects such as claw-generated force and linear morphometric differences (Blundon and Kennedy 1982; Seed and Hughes 1997). Although crusher and cutter claws exhibit distinct specialisations, size differences are often restricted to manus height, which is directly correlated with the muscle volume within this structure (Schenk and Wainwright 2001). In this context, the present study aims to investigate whether significant shape differences exist between the crusher and cutter claws of *C. danae* and *C. ornatus*, details that remain unexplored in the literature. Additionally, we will analyse the morphological integration between the dactylus and propodus of each claw type. It is expected that crusher claws, because of their role in agonistic interactions, will exhibit greater robustness than cutter claws.

2 | Materials and Methods

Crab sampling was conducted in Ubatuba Bay (23°26′S, 45°01′W), located on the northern coast of São Paulo State, Brazil. Specimens of *C. danae* and *C. ornatus* were collected over the course of 1 year (July 2021–June 2022) using a shrimp trawler equipped with double-rig trawl nets. Only adult individuals were included in the analyses, classified as such on the basis of the absence of pleon adhesion to the sternum and the presence of gonopods (males) or well-developed pleopods (females). Captured crabs were stored in plastic bags on ice, placed in boxes and transported to the laboratory, where they were preserved in 70% ethanol.

Species identification followed Melo (1996), and sex determination was based on pleon morphology: females have a semicircular pleon adapted for oviposition, whereas males possess an inverted "T"-shaped pleon. Crusher and cutter claws were identified on the basis of the morphology of the denticles on the cutting edges of the fixed finger of the propodus and the movable finger (dactylus) (Govind and Blundon 1985) (Figure 1).

Individuals with anomalies, such as the absence of one claw type, the presence of claws of the same type, regenerating claws or structural damage, were excluded from the analyses.

The claws were photographed using a Canon EOS Rebel T100 camera equipped with a 100 mm macro lens and mounted on a tripod. Photographs were taken at maximum resolution, with a fixed distance of 30 cm between the lens and the structure. During the procedure, the claws were positioned dorsally, with the movable finger fully extended.

In crabs of the genus *Callinectes*, there is no defined pattern of laterality in adults, and thus crusher and cutter claws can occur on either side of the body (Hamilton et al. 1976; Haefner 1990). To standardise the analysis, all images were mirrored, ensuring the same anatomical orientation for all individuals (Klingenberg et al. 2002). The photographs were compiled into a single dataset for the digitisation of landmarks and semilandmarks on the propodus and dactylus of both claw types. Six landmarks and eight semilandmarks were defined for the propodus, whereas four landmarks and ten semilandmarks were defined for the dactylus, using the software tpsUtil v1.78 and tpsDig2 v2.31 (Rohlf 2018, 2019) (Figure 2). The inserted landmarks are classified as Type I (Bookstein 1997), that is, points with clear anatomical correspondence across all specimens, placed at specific anatomical locations on the propodus or dactylus (Figure 2). The semilandmarks, in turn, are classified as Type III (Bookstein 1997), as they are positioned along the surface of the structure to capture shape variation between fixed landmarks (Type I). These points were distributed equidistantly along the surface of the structure.

The data analysis focused on comparing the shape of the propodus and dactylus between the two claw types for each sex and species. The landmark coordinates were subjected to Generalised Procrustes Analysis (GPA) to remove variation related to translation, rotation and scale, thereby standardising specimens based solely on shape. This procedure superimposes landmark configurations by minimising the sum of squared distances between homologous points (Rohlf and Slice 1990). The resulting aligned coordinates were used in subsequent analyses, representing only shape variation among individuals. Using the matrix generated by the GPA, a principal component analysis was performed to assess the patterns of data distribution; Hotelling's T^2 tests and discriminant analyses were conducted to identify significant differences in the shape of the claw components (i.e., propodus and dactylus) among groups. PCA was

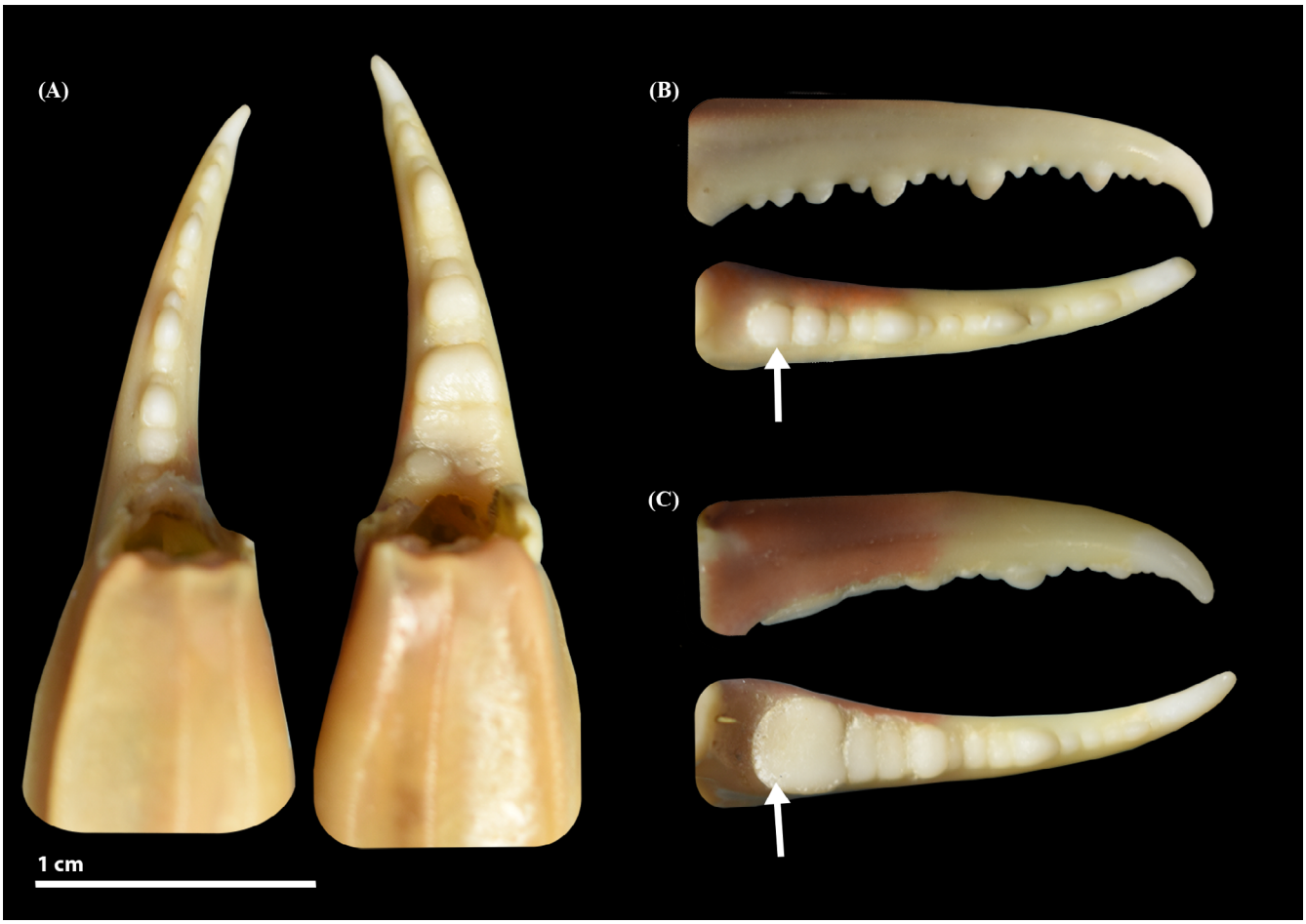

FIGURE 1 | Cutting edge of the fixed and movable fingers of the claws of *Callinectes ornatus*. (A) Ventral view of the posterior region of the manus and the cutting edge of the fixed fingers of the cutter (left) and crusher (right) claws. (B) Lateral and ventral views of the movable finger (dactylus) of the cutter claw. The white arrow indicates the pointed teeth located at the base of this structure. (C) Lateral and ventral views of the movable finger (dactylus) of the crusher claw. The white arrow indicates the molariform teeth located at the base of this structure. [Colour figure can be viewed at wileyonlinelibrary.com]

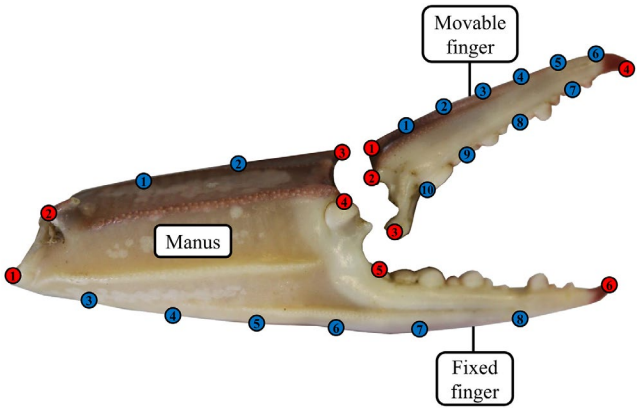

FIGURE 2 | Location of landmarks (red circles) and semilandmarks (blue circles) digitised on the propodus and dactylus to characterise the shape of these structures. The same anatomical points were consistently applied to both articles, regardless of whether they belonged to cutter or crusher claws. [Colour figure can be viewed at wileyonlinelibrary.com]

employed as a preliminary exploratory analysis to visually assess whether the analysed groups occupy distinct regions within the morphospace (Mitteroecker and Gunz 2009). Hotelling's T^2 test was used to evaluate statistically significant differences in shape between the different claw types (Mitteroecker and Gunz 2009). Discriminant analysis was subsequently applied to quantify the degree of morphological separation among the claws and to identify the shape variables that contributed most to group discrimination. Classification accuracy was estimated through the correct reclassification rate, validated using random permutation tests (Bookstein 1997; Klingenberg et al. 2002).

Morphological integration is related to the pattern of covariation among anatomical structures within an organism, reflecting functional and evolutionary connections between them (Klingenberg 2008; Olson and Miller 1958). When two structures are integrated, any change in one is expected to be accompanied by corresponding changes in the other, thereby preserving the functionality of the system (Wagner et al. 2007). In this context, the analysis of morphological integration helps to understand how morphological modules, that is, sets of correlated structures, are formed and maintained throughout evolution (Klingenberg 2009). Morphological integration was assessed to measure the degree of association between the propodus and dactylus of each claw type, subsequently comparing crusher and cutter claws across both sexes and species. A two-block partial least squares (PLS) analysis was performed to calculate the degree of integration between the components of each claw type (Rohlf and Corti 2000). The results were compared between claw types using the effect size obtained from the PLS analysis (Adams and Collyer 2016). All statistical analyses were conducted in the R software environment, using the geomorph package (R Core Team 2021).

3 | Results

A total of 86 specimens of *C. danae* were analysed, comprising 53 females and 33 males, along with 90 individuals of *C. ornatus*, of which 44 were females and 46 were males. Although the PCA plots showed a clear visual separation between the two claw types, with minimal overlap of points, the first two principal components (PC1 and PC2) did not account for a large proportion of the shape variation observed in the propodus and dactylus (Figure 3). For the propodus, the highest explanatory values of variation were observed in females of *C. danae*, with PC1 and PC2 combined accounting for 60.99% of the shape variation. For the dactylus, the highest explanatory values were found in males of *C. danae*, with PC1 and PC2 together explaining 75.25% of the shape variation (Figure 3).

The results of Hotelling's T^2 test revealed significant differences ($p < 0.001$) between the propodus and dactylus of crusher and cutter claws in both sexual groups of *C. danae* and *C. ornatus* (Table 1). Discriminant analysis demonstrated high accuracy in separating the propodus types, with over 95.5% correct classification for each type across all analysed groups. For the dactylus, the accuracy exceeded 87.21% in distinguishing the types within each group (Table 1; Figure 4).

The main differences between the propodus of crusher and cutter claws across all analysed groups are related to the shape of the manus, robustness, and the length of the fixed finger (Figure 5). In the propodus of the crusher claw, the manus is visibly more robust, both dorsally and ventrally, compared to the manus of the cutter claw. The fixed finger is also more robust at its base but shorter in length than the fixed finger of the cutter claw (Figure 5). For the dactylus, the primary differences between crusher and cutter types are concentrated at the base and apex of the structure (Figure 4). In all crusher-type dactyli, the base is more robust than in cutter-type dactyli. The apex of the crusher dactylus exhibits a characteristic curvature, being slightly more robust and shorter compared to the apex of the cutter dactylus (Figure 5).

Regarding the morphological integration of each claw type, the results of the PLS analysis showed a high degree of integration between the components (propodus and dactylus), regardless of the sex group or species ($p < 0.01$; Table 2). In comparison, no significant differences were found in the degree of integration between the propodus and dactylus of crusher and cutter claws in any of the comparisons ($p > 0.05$; Table 2).

4 | Discussion

The results of this study demonstrated that the components of crusher and cutter claws, that is, the propodus and dactylus, exhibited distinct shapes, regardless of the species or sex group analysed, directly reflecting the functions performed by these structures. Crusher claws are more robust in both sex groups of both species investigated, whereas cutter claws display a thinner and more elongated shape, supporting our predictions. Despite the functional differences between these claw types, a high degree of morphological integration was found between their components, with no significant variations in the comparisons made. These findings are novel and contribute to the understanding of important characteristics of this group of swimming crabs, such as their behaviour and aggressiveness.

The analyses showed that the manus and fixed finger of the propodus are significantly more robust in the crusher claw. As

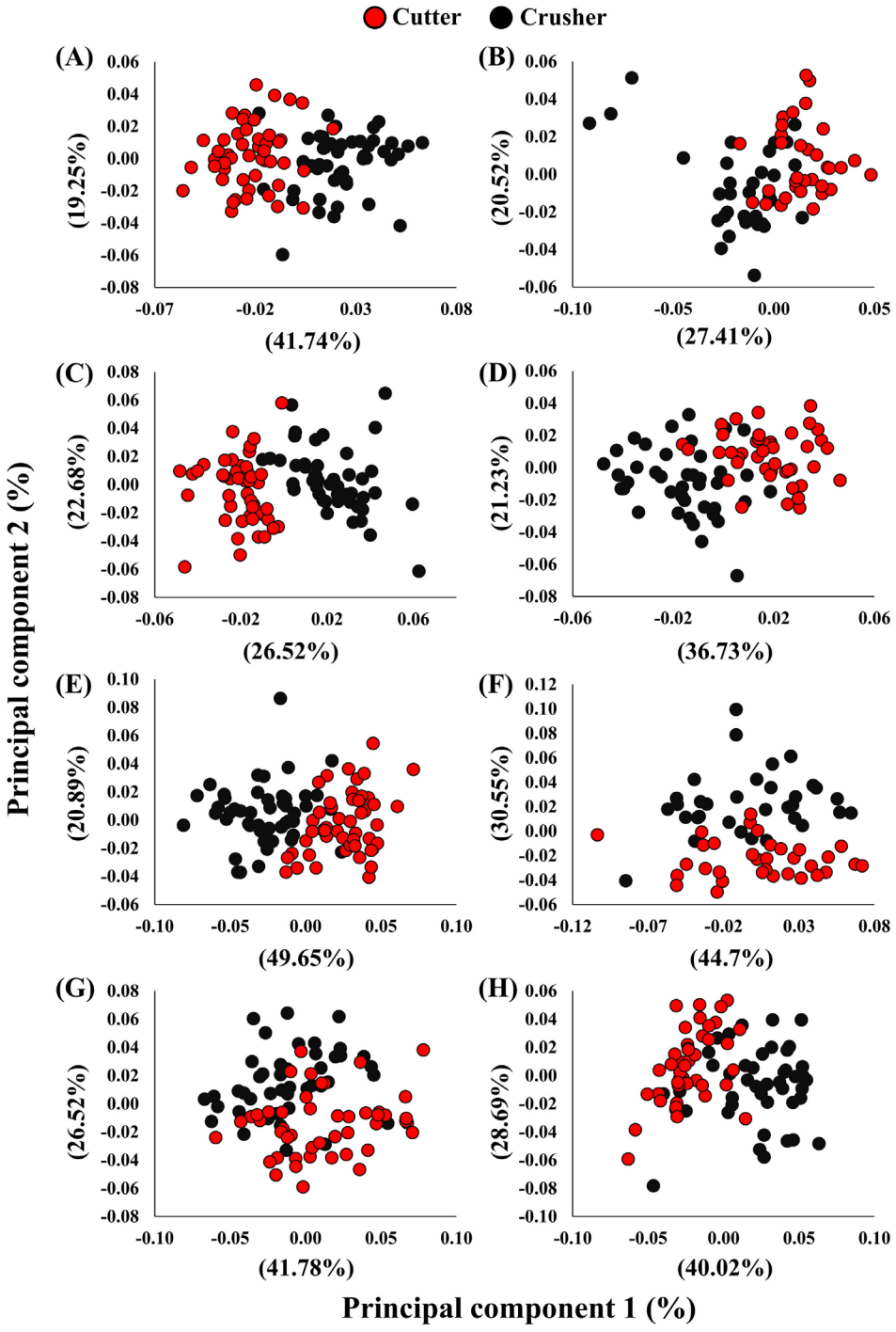

FIGURE 3 | Results of the principal component analyses. Explanatory values of the first and second principal components for all analysed structures. (A–D) shape variation of the propodus in females and males of *Callinectes danae* (A and B) and *Callinectes ornatus* (C and D), respectively. (E–H) shape variation of the dactylus in females and males of *Callinectes danae* (E and F) and *Callinectes ornatus* (G and H), respectively. Red points represent cutter-type segments (propodus or dactylus), whereas black points represent crusher-type segments. [Colour figure can be viewed at wileyonlinelibrary.com]

mentioned earlier, the greater the robustness of the claw, the greater the muscle volume and, consequently, the force generated (Schenk and Wainwright 2001). This force is transmitted by the movable finger (dactylus) through the "lever system" formed by these structures (Levinton et al. 1995). The dactylus displayed morphological characteristics compatible with its function of force transfer, including a robust base with molariform teeth and a reduced length, which minimises rotation in the lever movement (Warner and Jones 1976). Swimming crabs are widely recognised for their ability to prey on organisms with hard tissues, such as mussels and snails (Wilcox and Rochette 2015; Yamada and Boulding 1998). In addition to playing an essential role in agonistic conflicts (Mariappan et al. 2000), the crusher claw is crucial for obtaining these food resources. Such prey, with hard bodies, tend to be more abundant in the environment because of the reduced number of predators capable of exploiting

TABLE 1 | Results of the Hotelling's T^2 test and percentage of correct classification obtained from the discriminant analysis for the propodi and dactyli of crusher and cutter claws of *Callinectes danae* and *Callinectes ornatus*, in both sexual groups.

Species	Article	Sex	T^2	F	p	%
Callinectes danae	Propodus	Female	414	13.2	<0.001	97
		Male	202.58	5.4	<0.001	97
	Dactylus	Female	237.85	7.58	<0.001	96
		Male	161.31	4.3	<0.001	95.45
Callinectes ornatus	Propodus	Female	457.9	14.3	<0.001	98.94
		Male	244.9	7.1	<0.001	95.35
	Dactylus	Female	202.28	6.32	<0.001	94.68
		Male	187.88	5.68	<0.001	87.21

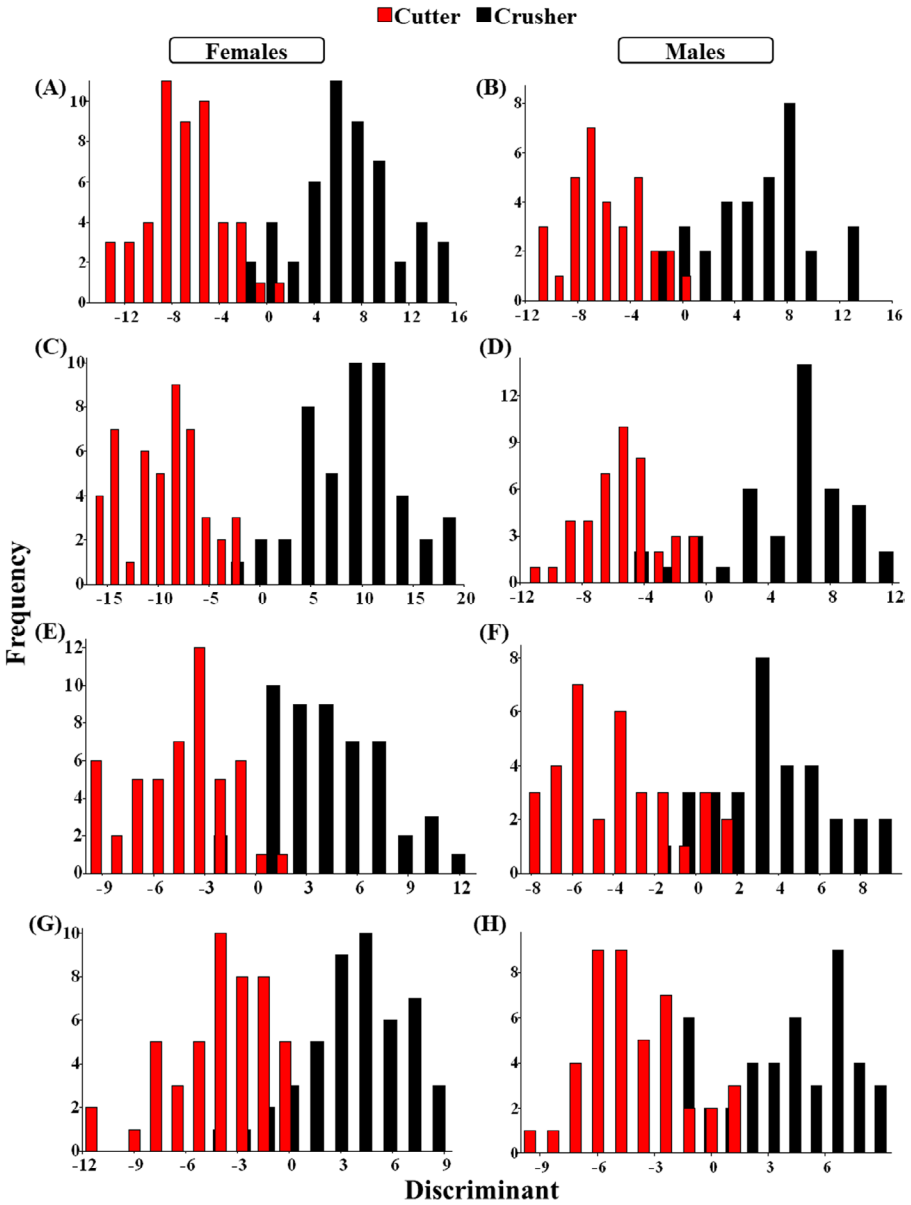

FIGURE 4 | Results of the discriminant analyses. (A–D) propodus of females and males of *Callinectes danae* (A and B) and *Callinectes ornatus* (C and D), respectively. (E–H) shape variation of the dactylus in females and males of *Callinectes danae* (E and F) and *Callinectes ornatus* (G and H), respectively. Red bars represent cutter-type segments (propodus or dactylus), whereas black bars represent crusher-type segments. [Colour figure can be viewed at wileyonlinelibrary.com]

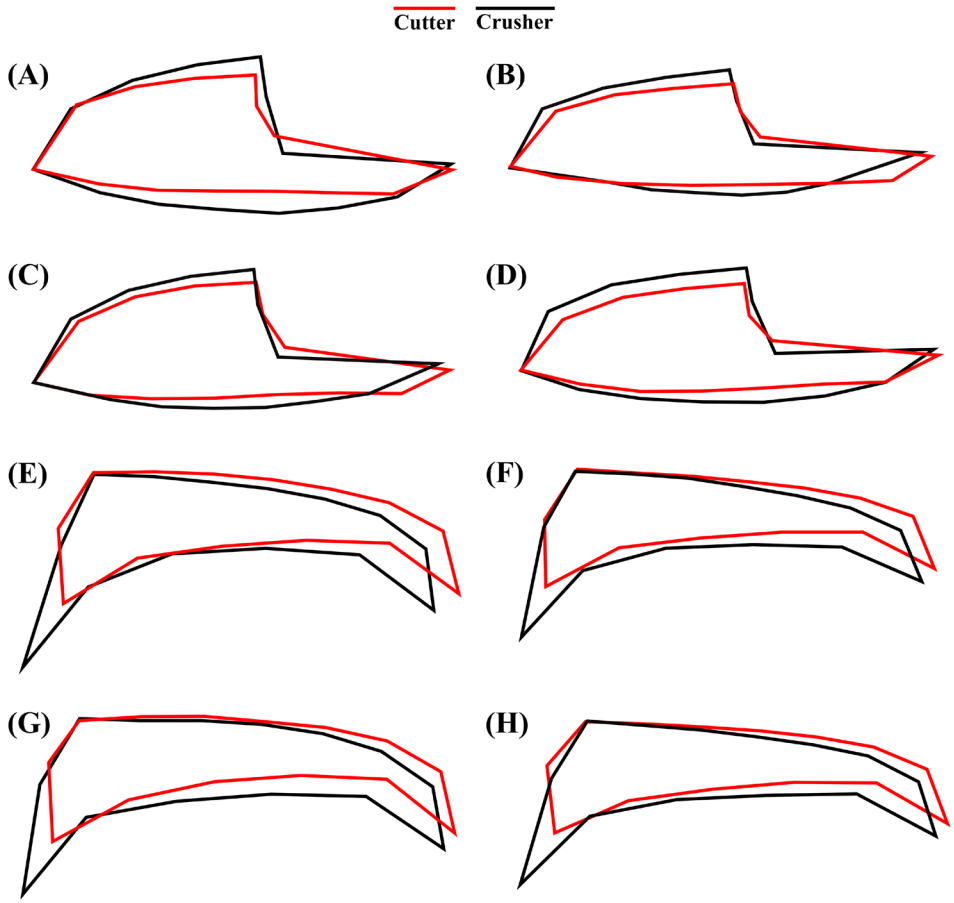

FIGURE 5 | Shape comparison between crusher and cutter claws for each sexual group of *Callinectes danae* and *Callinectes ornatus*. (A–D) propodus of females and males of *Callinectes danae* (A and B) and *Callinectes ornatus* (C and D), respectively. (E–H) dactylus of females and males of *Callinectes danae* (E and F) and *Callinectes ornatus* (G and H), respectively. Differences were observed in all comparisons. Black lines represent the components (propodus or dactylus) of crusher claws, whereas red lines represent the components of cutter claws. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 | Results of the integration analysis (Two-block PLS) and comparisons of the degree of morphological integration between the crusher and cutter claws for each sexual group of *Callinectes danae* and *Callinectes ornatus*.

		Crusher claw			Cutter claw			Crusher vs. cutter	
Species	**Sex**	**r-PLS**	**Effect size**	***p***	**r-PLS**	**Effect size**	***p***	**Effect size**	***p***
Callinectes danae	F	0.687	2.96	0.003	0.846	5.04	0.001	0.84	0.2
	M	0.676	2.51	0.007	0.765	3.39	0.001	0.94	0.17
Callinectes ornatus	F	0.619	2.56	0.007	0.623	2.81	0.004	0.87	0.19
	M	0.783	4.27	0.001	0.873	4.76	0.001	0.31	0.38

them, as this requires morphological specialisation to overcome their defences.

According to behavioural observations made in brachyuran crabs, the cutter claw is a highly agile structure, particularly effective in tasks involving drilling and cutting targets (Schenk and Wainwright 2001; Warner and Jones 1976). In this functional context, in addition to having numerous sharp teeth, the manus, fixed finger, and movable finger of this claw are thin and elongated, which likely provides greater mobility, allowing the capture of highly agile live prey (da Silva and Kassuga 2024; Warner and Jones 1976). The presence of dimorphic claws in shape may offer a significant advantage to these animals, allowing access to different types of food resources: from hard-bodied prey to those with soft tissue but high mobility (da Silva and Kassuga 2024). This functional versatility may be one of the factors contributing to the radiative success of these organisms (Braig et al. 2023; Tsang et al. 2014; Wolfe et al. 2024), enabling their populations to reach high densities and colonise a wide variety of environments.

The integration between the components of the claws was high, yet no significant differences were found between the types of claws, regardless of sex (male or female) or species (*C. danae* or *C. ornatus*). This integration ensures that the organism possesses functionally efficient structures. The claws of decapods are composed of two main components: the propodus and the dactylus, which work together to perform various tasks. This pattern of high morphological integration has already been reported for other decapods (da Silva and Nogueira 2023; Nogueira et al. 2022). However, the absence of differences between demographic groups has been tested only in species that use their claws as weapons. To deepen the understanding of the selective and evolutionary pressures involved, future studies could investigate morphological integration in crustaceans whose claws are primarily used for signalling, as seen in fiddler crabs from the subfamilies Gelasiminae and Ocypodinae (Detto 2007; McCullough and O'Brien 2022; Shih et al. 2016). Although the claws of crustaceans perform basic functions, such as gripping and pushing targets, they are key structures for a wide range of tasks. In some species, these structures exhibit exaggerated traits, either in size (Dinh 2022; Levinton and Weissburg 2021) or robustness (Hughes and Elner 1989). These extreme traits, related to size and shape, are often associated with the functional spectrum of claws, both for weaponry and signalling (Mariappan et al. 2000; McCullough and O'Brien 2022).

This study provides significant contributions to the understanding of the shape and integration of claws in two species of swimming crabs (*C. danae* and *C. ornatus*) that possess both cutter and crusher-type claws. The patterns observed are consistent with those reported for other decapod species that use their claws in fights. Additionally, we emphasise that future investigations into the integration and functionality of claws in crustaceans that primarily use them for signalling are essential to fully elucidate a broader perspective of the selective pressures involved in the development of these structures.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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