1 **Title:** Crabs Grab Strongly Depending on Mechanical Advantages of Pinching and
2 Disarticulation of Chela
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9 **Short title:** FUNCTIONAL MORPHOLOGY OF DECAPOD CHELA
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*ABSTRACT*   A small morphological variation of an organ can cause a great diversity of its function in animal evolution. A decapod chela has a great functional variation among taxa, between sex, and even within the individual, but also retains a simple mechanism of motion. Therefore, the decapod chela is one of the best structures to study the evolutionary process of functional diversifications, though the relationship between form and function is yet inadequately understood. We estimated the mechanical advantages of pinching and passive disarticulation resistance, and chela size relative to the carapace in 317 chelae of 168 decapod specimens, and compared these indices with the functions of each chela. Our study revealed that both mechanical advantages of pinching efficiency and passive disarticulation resistance were greatest in shell-crushing chelae, followed by gripping and pinching chelae, whereas the chela size relative to the carapace was not related to differences among these functions. We also found that the chelae are designed to retain the ratio between depth and width of the proximal dactylus. In the evolutionary process of decapods, the diversifications of chela functions were accompanied by the diversifications of the mechanical advantages, and played an essential role in their ecological diversification.

KEY WORDS: Brachyura; durophagous; moment arm; functional morphology.

**INTRODUCTION**

Chelae are pincer-like grasping organs derived from the distal two segments (the dactylus and the propodus) of the crustacean pereopod, and the pereopod bearing the chela is called the cheliped (Fig. 1A, B). Among the arthropods, grasping abilities, associated with the chelipeds, were independently acquired in several lineages of crustaceans, insecta, and cheliceratans (e.g., Boxshall, 2004; Regier et al., 2010; Weirauch et al., 2011; Meusemann et al., 2014). Decapods (Crustacea) are one of the most successful groups among these in terms of diversity. Decapod chelae are greatly diversified in their form and function. The forms vary not only among species (e.g., Hughes, 1989; Rosenberg, 2002), but also between sexes (e.g., Valiela et al., 1974), between right and left sides (e.g., Palmer, 2004), and between before and after the post-autotomy recovery (e.g., Pynn, 1998). There is also a great variety in pinching abilities of chelae (Taylor and Schram, 1999; Mariappan, et al., 2000). Many decapods have a pair of chela asymmetric in size, shape, and function (e.g., Warner, 1977; Palmer, 2004). Crushing and chipping abilities (C) are employed in some durophagous decapod major chela to crush/chip hard tissues of the prey (e.g., bivalve and crustacean shells: Table S1: Zipser and Vermeij, 1978; Lau, 1987; Hughes, 1989; Schweitzer and Feldmann, 2009). Gripping ability (G) is employed by many decapods to hold

struggling prey by using the teeth on the pinching surface of the chela (Table S1). Soft-pinching ability (P) is employed by detritus feeders to scoop particles or to pick up a tiny benthos using the distal-end of chela (Table S1). The major chela of the male fiddler crab (U: Ucinae, Ocypodidae) is known to be used for grasping the females or for grappling with the other males, as well as for waving to attract females, though the grasp does little damage to the other individuals (Table S1: Crane, 1966; Lau, 1987; Field, 1990; Levinton and Judge, 1993; Dennenmoser and Christy, 2013). Such diversification in decapod chelae function may have played an essential role in their diversification, especially in feeding behavior (Anker et al., 2006).

Though the forms and functions are diverse among decapods, their chelae employ a relatively simple structure and mechanism of motion. The lateral and medial facets on the distal articular surface of the propodus (the proximal segment of chela) occupy the lateral and medial fulcra on the articular surface of the proximal side of the dactylus (the distal segment), respectively (see points *b* and *c* in Figs. 1 and 2). The margins of the distal side of the propodus and the proximal side of the dactylus are connected to each other by an articular membrane (Fig. 1C, D). Due to the biarticular connections at the lateral and medial fulcra, the propodus-dactylus (P-D) joint forms a hinge joint (see axis *X* in Fig. 1B–D)—the structure of which can be comparable to the biarticular hinges in temporomandibular and costovertebral joints of vertebrates (e.g., Moore and Dalley, 2006), though the construction of the musculoskeletal system is different in decapods and vertebrates. The opening and closing motions of the chela at the P-D joint are controlled by the opener muscle, which insert to the dorsal margin of the proximal dactylus via the opener apodeme, and the closer muscle, which insert to the ventral margin of the proximal dactylus via the closer apodeme, respectively (Fig. 1B–D). These simple motion mechanisms of the joint are shared widespread among inter-segmental joints in malacostracan crustacean pereopods (Manton, 1968; Shultz, 1989), though non-biarticular joints are employed in some arthropods (e.g., screw joint in *Trigonopterus*, Coleoptera, Insecta [Van de Kamp et al., 2011]; and scissor-like joints in *Psalidopus*, Caridea, Decapoda [Chace and Holthuis, 1978]). Given their simple motion mechanism and their great diversity in forms and functions, the decapod (Malacostraca, Crustacea) chelae are one of the best examples to study the functional morphologies and the process of diversification within the group.

A number of studies have been conducted on the functional morphologies of crustacean and cheliceratan chelae—for example, the relationship between the pinching force and the height, width, cross-sectional area of the propodus, strength of chela, and volume, pennation angle, and sarcomere length of the closing muscle of chela have been studied in several taxa (e.g., Vermeij, 1977; Warner et al., 1982; Levinton and Judge,

89   1993; Backwell, 2000; Van der Meijden et al., 2010: Taylor et al., 2009; Van der
90   Meijden et al., 2012; Payne and Kraemer, 2013). Some of these studies used the
91   mechanical advantage of pinching efficiency (the ratio between the in-lever and
92   out-lever of the chela) as a morphological indicator of the pinching abilities of
93   arthropod chelae (Warner and Jones, 1976; Vermeij, 1977; Brown et al., 1979; Elner and
94   Campbel, 1981; Govind and Blundon, 1985; Levinton and Judge, 1993; Labadie and
95   Palmer, 1996; Yamada and Boulding, 1998; Palmer et al., 1999). However, the
96   mechanical advantage of pinching efficiency has been compared among a limited
97   number of taxa, up to six genera (Vermeij, 1977), because most of studies have focused
98   on the variation in pinching efficiency among a few genera, or among a population
99   within a single species whose chelae are referred to as sexually dimorphic or laterally
100  asymmetric (e.g., Labadie and Palmer, 1996). The relationship between form and
101  function would become clearer if data was obtained from a larger number of samples.

102      Strong pinching can be performed by having a joint with an adequate mechanical
103  strength, which is relatively difficult to disarticulate by the reaction force from the
104  object, in addition to having a relatively high mechanical advantage for pinching
105  efficiency. The relationship between form and function could be further elucidated with
106  data from multiple mechanical indices (e.g., moment arms of the extensor, flexor, and
107  adductor muscles in the tetrapod elbow joint for deducing their forelimb postures
108  [Fujiwara et al., 2011; Fujiwara and Hutchinson, 2012]). The additional mechanical
109  index for ability to resist disarticulation of the chela would be useful for a further
110  understanding of the relationship between the form and function of arthropod chela. If
111  these indices were directly reflected in chelae morphology, it would give new insight on
112  the basic design and the pinching ability of arthropod chela.

113      Here we combine indices measuring mechanical advantages of pinching and
114  resistance to mediolateral failure of the P-D joint to test the difference among the
115  decapod chelae with different functions (C, crushing/chipping; G, gripping; P, pinching;
116  U, grasping function employed by male ucine chela) by using a wide range of decapod
117  species.

118

**Mechanical Condition of Pinching**

120      Figure 2B shows a decapod chela pinching an object at the distal end. The closer
121  apodeme is pulled proximally by a certain contractive force ($F_{C1}$) of the closer muscle to
122  adduct the dactylus about the P-D joint axis (axis $X$) in Figure 2B. The distance from the
123  axis to the closer muscle contraction force vector is the moment arm of the force. The
124  moment arm is maximized at an angle where the force applied by the closing muscle
125  contraction ($F_{C1}$) and the line connecting the axis $X$ and the muscle insertion (point $d$)

126  are perpendicular with each other (Fig. 2B). Therefore, the distance between the axis $X$

127  and the point $d$ can be defined as a possible maximum moment arm of the closer muscle

128  ($C_1$). At the same time, the pinched object applies a reaction force ($F_{C2}$) to the distal end

129  of the chela to abduct the dactylus, and the moment arm of the force ($C_2$) is the distance

130  from the distal end of chela to the axis (Fig. 2B). We assumed that the chela is held in an

131  angle where the force vector of the closing muscle contraction ($F_{C1}$) is perpendicular to

132  the in-lever (the line segment connecting between axis $X$ and point $d$ in Fig. 2A, B). In

133  this joint angle, adduction ($F_{C1} \times C_1$) and abduction ($F_{C2} \times C_2$) torques of the dactylus

134  about the axis $X$ are balanced in following equation:

135  $$F_{C1} \times C_1 = F_{C2} \times C_2 \quad (1).$$

136  The equation can be developed as follows:

137  $$F_{C2} = (C_1/C_2) \times F_{C1} \quad (2),$$

138  where $C_1/C_2$ can be defined as a mechanical advantage of "pinching efficiency" (Waner

139  and Jones, 1976; Vermeij, 1977; Yamada and Boulding, 1998; Labadie and Palmer,

140  1996). Decapods with relatively high pinching efficiency ($C_1/C_2$) have advantages in

141  durophagous (shell-breaking) predation.

142

143  **Mechanical Condition of Passive Chela Disarticulation**

144       We also assumed a mechanical condition in which the distal end of the dactylus is

145  subjected to a lateral or medial out-force (Fig. 2C, D), such as the medio-lateral

146  component of the reaction force from an object pinched by the chela, or a medio-lateral

147  reaction force from the object when the crab is prying on the object (Fig. 2C). Such

148  lateral and medial out-forces function to rotate the dactylus about an axis through the

149  lateral and medial facets of P-D joint, respectively (see axes $Y$ and $Y'$ in Figs. 1 and 2).

150       The lateral-ward torque about the axis $Y$ in Figure 2C is defined as the product of

151  the lateral force ($F_{M2L}$) and the possible maximum moment arm ($M_{2L}$: the distance

152  between points $a$ and $b$ in Figs. 1 and 2). The disarticulation of the medial facet (point $c$)

153  is assumed to be prevented by the medial-ward torque generated by the product of

154  reaction force of the articular membrane ($F_{M1L}$ : Fig. 2C) and the possible maximum

155  moment arm about the axis $Y$ ($M_1$: the distance between points $b$ and $c$ in Figs. 1 and 2).

156  The condition of the rotational equilibrium about the axis $Y$ is described in following

157  equation:

158  $$F_{M1L} \times M_1 = F_{M2L} \times M_{2L} \quad (3).$$

159  The equation can be developed as follows:

160  $$F_{M1L} = F_{M2L} /( M_1/M_{2L}) \quad (4).$$

161  Likewise, the medial-ward torque about the axis $Y'$ in Figure 2E is defined as the

162  product of the medial reaction force ($F_{M2M}$) and the possible maximum moment arm

163   ($M_{2M}$: the distance between points *a* and *c* in Figs. 1 and 2). The disarticulation of the
164   lateral facet (point *b*) is prevented by the lateral-ward torque generated by the product of
165   reaction force of the articular membrane ($F_{M1M}$ : Fig. 2E) and the possible maximum
166   moment arm about the axis *Y'* ($M_1$). The condition of the rotational equilibrium about
167   the axis *Y'* is described in following equation:

$$F_{M1M} \times M_1 = F_{M2M} \times M_{2M} \quad (5).$$

169   The equation can be developed as follows:

$$F_{M1M} = F_{M2M} /(M_1/M_{2M}) \quad (6).$$

171   $F_{M1L}$ and $F_{M1M}$ are the tensile force on the medial and lateral articular membrane,
172   respectively. Therefore $M_1/M_{2L}$ and $M_1/M_{2M}$ can be defined as mechanical advantages
173   of "passive disarticulation resistance" against lateral- and medial reaction forces on the
174   distal end of the chela, respectively.

175   In this study, we defined $M_1/M_{2L}$ or $M_1/M_{2M}$ whichever is smaller ($M_1/M_2$) as an
176   index of the passive disarticulation resistance at the P-D joint. The passive
177   disarticulation resistance ($M_1/M_2$) can be used as a safety factor—the cabs with
178   relatively large $M_1/M_2$ have lower risks of the P-D joint disarticulation when they pinch
179   hard tissues or pry on bivalves. In addition to the reaction forces applied by the articular
180   membranes at the lateral and medial facets, respectively, forces applied proximally by
181   opener and closer muscles at the points *e* and *d*, respectively (Figs. 1 and 2), may also
182   contribute to actively provide resistant torques against the disarticulations. However, to
183   simplify the model, we focused on the passive disarticulation resistance provided by the
184   articular membrane for this study, but left considering the effect of the active
185   disarticulation resistance for the future studies.

186   Crushing chelae (C) are expected to provide a relatively high mechanical advantage
187   in both pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$).
188   $C_1/C_2$ and $M_1/M_2$ in gripping chelae (G) are expected to be lower than those in crushing
189   chelae, but larger than those in other chelae. The softly-pinching chelae (P), which are
190   used for feeding on detritus, are expected to require a relatively low mechanical
191   advantage in both $C_1/C_2$ and $M_1/M_2$. The male ucine (Ucinae) major chelae (U) are used
192   for pinching objects, but are not for gripping them strongly as in the cases of C and G
193   (e.g., Levinton and Judge, 1993), or for feeding on detritus like P (Crane, 1966).
194   Therefore, high mechanical advantages are not necessary in the male ucine major chelae
195   (U). In this study, we tested the following hypotheses; that the mechanical advantages of
196   both $C_1/C_2$ and $M_1/M_2$ are greater in C and G, but are lesser in P and U.

197   The moment arms $C_2$, $M_{2L}$, and $M_{2M}$ indirectly reflect the length of the dactylus
198   (Fig. 2A). Therefore, if the pinching efficiency ($C_1/C_2$) and the passive disarticulation
199   resistance ($M_1/M_2$) were correlated with each other, the aspect ratio between $M_1$ (the

200  width of the proximal dactylus) and $C_1$ (the depth of the proximal dactylus from the P-D
201  joint to the insertion of the closer muscle) may also be correlated with each other.
202
203  **MATERIALS AND METHODS**
204  **Materials and Functional Categorization of Chelae**
205      To test the above-mentioned hypotheses, we used 317 chelae of 168 brachyuran and
206  11 outgroup decapod (Anomura, Astacea, and Axiidea) specimens, for total of 34
207  families, 63 genera, and 92 species (Table S1). We followed Ng et al. (2008) for the
208  classification of the species. The study specimens are from the collections in the
209  Kanagawa Prefectural Museum of Natural History (Odawara, Japan), Toyohashi
210  Museum of Natural History (Toyohashi, Japan), National Museum of Nature and
211  Science (Tsukuba, Japan), and in the personal collections of the authors (Nagoya
212  University Museum, Nagoya, Japan). The personal collections were sampled by the
213  authors at Iriomote and Ishigaki islands (Okinawa, Japan), Fujimae Tidal Flat (Aichi,
214  Japan), and Yahagi River (Aichi, Japan); by S. Nawa (Tsuda Fishing Port, Tokushima,
215  Japan) at Seto Inland Sea (Japan); by Seike K. (The University of Tokyo, Kashiwa,
216  Japan) at Suncheon Tidal Flats (Suncheon, South Korea); and by Koizumi T. (Kyoto
217  University, Wakayama, Japan) at Kino River estuary (Wakayama, Japan). The study
218  specimens varied in taxa, body mass (0.930–3,070 g), and functions of their chelae
219  (Table S1).
220      The chela which is larger and smaller in size within a pair of chelipeds was
221  respectively defined as major and minor chelae. Both the major and minor chelae in the
222  studied taxa were categorized into four different functions in terms of pinching abilities
223  based on the available literature: C, crushing chelae; G, gripping chelae; P, pinching
224  chelae; U, male ucine major chelae; and X, the chelae whose abilities for pinching are
225  unknown (Table S1). Chelae, that are mainly used to pick up tiny particles at their tips,
226  were defined as P. In this way, the chelae of the studied taxa who rely on detritus were
227  included in this category. The major chelae of male fiddler crab (*Uca*) were defined as
228  U—their chelae are used for less destructive pinching, but are not used for feeding on
229  detritus like chelae categorized as "P" (e.g., Levinton and Judge, 1993). Chelae, that are
230  used to grab relatively large objects by using denticles on their chela, were categorized
231  as G. The major chelae of the studied taxa who crush or chip the molluscan shells were
232  categorized as C. The minor chelae of these taxa (the contralateral chela of C) were
233  categorized as group G if they were used to grip and hold relatively large objects, or
234  were categorized as P if they were mainly used to feed on detritus. The contralateral
235  chelae of C were not categorized as C in this study because it was uncertain from the
236  literature whether both chelae were used to crush molluscan shells. Functions of the

237   other chelae were categorized as unknown (X).

238

239   **Measurements**

240       Measurements were taken by a caliper (0.00–200.00 mm; Mitsutoyo Co., Ltd.) to

241   the nearest 0.01 mm and a Martin-type anthropometer (200–1950 mm; Takei Scientific

242   Instruments Co., Ltd.) to the nearest 1 mm for the length, and an electronic analytical

243   scale to the nearest 0.001 g (0.000–620.000 g; Shinko Denshi Co., Ltd.), a weighing

244   scale (620–2,000 g; Tanita Co., Ltd.) to the nearest 100 g, and a spring scale (2,000–

245   8,000 g; Sanko Seikohjo Co., Ltd.) to the nearest 100 g for the mass. We also referred

246   the body mass data, if available, which have been taken for the specimens in the

247   museum collections.

248       The size of the chela in relation to the size of the carapace was estimated for each

249   chela. To simplify the chelae and body sizes, we approximated the carapace, propodus,

250   and dactylus using rectangles and triangles. The product of the width and length (area of

251   the rectangle: Fig. 1A) was defined as carapace size (CS [mm$^2$]) (Fig. 1A, Table S1).

252   The propodus (PS [mm$^2$]) and dactylus (DS [mm$^2$]) sizes were defined as the area of

253   triangle formed by the distal end of the element and two fulcra at the proximal end,

254   respectively. PS is an area of triangle formed by points $f$, $g$, and $h$ in Figure 1; and DS is

255   an area of triangle formed by points $a$, $b$, and $c$ in Figure 1 (Table S1). Areas of the

256   triangles were calculated from lengths of the three sides by using following equation

257   (Heron's formula: see Dunham, 1990):

258   $$T = ((\alpha+\beta+\gamma)\times(-\alpha+\beta+\gamma)\times(\alpha-\beta+\gamma)\times(\alpha+\beta-\gamma))^{0.5}/4 \qquad (7)$$

259   where $T$ is an area, and $\alpha$, $\beta$, and $\gamma$ are the lengths of three sides of the triangle. The sum

260   of PS and DS was defined as the chela size. The relative size of the chela to the

261   carapace (RC), which can be calculated as "(PS+DS)/CS," was estimated for each chela

262   of the study specimens (Table S1).

263       We assumed that the pinching occurs at the distal-most point of the chela. The

264   mechanical advantage of pinching efficiency ($C_1/C_2$) is calculated as the ratio of

265   moment arms of the closer muscle ($C_1$) and the tip of the chela ($C_2$) (Fig. 2A, B). $C_1$ is

266   defined as the distance (line segment $d$-$d$' or $d$-$X$) between the insertion of the closing

267   muscle (point $d$) and an intersection (point $d$') between the P-D joint axis (line $X$) and a

268   perpendicular line to the line $X$ through the point $d$ (Fig. 2A, B). $C_2$ is defined as the

269   distance (line segment $a$-$a$' or $a$-$X$) between the distal end of the dactylus (point $a$) and a

270   foot on the P-D joint axis of a perpendicular line through the point $a$ (point $a$': Fig. 2A,

271   B). Thus, there are no landmarks of points $a$' and $d$' to take measurements on the

272   specimen (Fig. 2A). We therefore calculated the distance from the point $a$ (or $d$) to the

273   feet $a$' (or $d$') on the P-D joint axis ($X$) as a height of triangle formed by the vertices $a$

274    (or *d*), and medial and lateral fulcra of the P-D joint (points *b* and *c*: Fig. 2A). Areas of

275    triangles formed by vertices *a*, *b*, and *c*, and vertices *d*, *b*, and *c*, respectively, were

276    calculated by measurements on lengths of the three sides and Heron's formula. Finally,

277    the heights of these triangles (moment arms $C_1$ and $C_2$) were calculated by dividing the

278    length of the base (distance between points *b* and *c*) from twice the amount of the

279    triangle area.

280         The mechanical advantage of passive disarticulation resistance ($M_1/M_2$) is defined

281    as the ratio of $M_1$ and $M_{2L}$ or the ratio of $M_1$ and $M_{2M}$ whichever is smaller, where $M_1$,

282    $M_{2L}$, and $M_{2M}$ are moment arms of the closer muscle, the lateral and medial out-forces

283    applied at the distal-end of the chela, respectively (Fig. 2A, C–F). $M_1$ is defined as the

284    distance (line segment *c-b*) between the medial (point *c*) and the lateral (point *b*) fulcra

285    (Fig. 2A, C, D). $M_{2L}$ is defined as the distance (line segment *a-b*) between the distal end

286    of dactylus (point *a*) and the lateral fulcrum (point *b*: Fig. 2A, C, D). $M_{2M}$ is defined as

287    the distance (line segment *a-c*) between the distal end of dactylus (point *a*) and the

288    medial fulcrum (point *c*: Fig. 2A, E, F). $M_1$, $M_{2L}$, and $M_{2M}$ can be obtained using simple

289    measurements on the specimen.

290

291    **Comparison of Indices among Functional Categories**

292         We used statistical software R 3.1.0 (R Core Team, 2014) for our statistical analyses.

293    To test differences in distributions between pairs of three different indices among the

294    functional categories, we conducted a pair-wise non-parametric comparison

295    (Steel-Dwass test) for the mechanical advantages of pinching efficiency ($C_1/C_2$) and

296    passive disarticulation resistance ($M_1/M_2$), and relative size of chela (RC) among

297    functional categories (C, G, P, and U). This was done using a free source code released

298    for Steel-Dwass test (Aoki, 2004a) on R 3.1.0. The distributions of the two categories

299    are significantly different if the *p*-value did not exceed 0.05.

300         The relationships between $C_1/C_2$ and $M_1/M_2$, RC and $C_1/C_2$, and RC and $M_1/M_2$

301    were compared. Kernel density distributions of each functional category were drawn

302    using the package "ks" (Duong, 2007) in R 3.1.0. We also conducted Spearman's and

303    correlation tests for two-dimensional plots of whole chela, C, G, P, and U, to determine

304    whether the mechanical indices ($C_1/C_2$, $M_1/M_2$, and RC) were correlated with each other.

305    The null hypothesis was that there was no association between the two variables and it

306    is therefore rejected if the *p*-value did not exceed 0.05.

307         "$C_1/C_2$" and "$M_1/M_2$" could not be estimated in some chelae because their chelae

308    were too small to take measurements by caliper. "RC" could not be estimated in some

309    specimens that lacked a carapace. Therefore, we used 317 chelae in total (C, 34; G, 159;

310    P, 45; U, 21; X, 58) for the statistical analyses between the two mechanical advantages

311  ($C_1/C_2$ [%] and $M_1/M_2$ [%]), and 230 specimens (C, 24; G, 121; P, 33; U, 13; X, 39) for

312  the analyses between the relative size of chela (RC [%]) and the mechanical advantages

313  (See Table S1). The phylogenetic signals were estimated for these three indices to test

314  whether these indices are phylogenetically autocorrelated (Harvey and Pagel, 1991;

315  Abouheif, 1999; Blomberg and Garland, 2002; Münkemüller et al., 2012; Pavione and

316  Ricotta, 2012; Hallmann and Griebeler, 2015). We used six different phylogenetic trees

317  (Schubart et al., 2006; Ahyong et al., 2007; Tsang et al., 2008; Bracken et al., 2009;

318  Spiridonov et al., 2014; Tsang et al., 2014) for testing the phylogenetic signals (See

319  Appendix S1 for the detail).

320

321  **Basic Design of the Proximal Dactylus**

322       To test whether the proximal dactylus of decapods are designed to retain a definite

323  range of the aspect ratio between the depth ($C_1$) and the width ($M_1$) of the proximal

324  dactylus, Spearman's and correlation tests were used to determine the relationships

325  between the logarithmic values of $C_1$ and $M_1$ [mm] using R 3.1.3 (Fig. 2A). The tests

326  were conducted for all studied chelae ($n = 317$) and for those categorized as C ($n = 24$),

327  G ($n = 121$), P ($n = 33$), and U ($n = 39$).

328       To test the differences between the regression lines, we conducted a parallel line

329  analysis (PLA) and an analysis of covariance (ANCOVA) between pairs of regression

330  lines for each functional category (C, G, P, and U) using a free-source code released for

331  these statistical analyses (Aoki, 2004b) in R 3.1.0. PLA tests the null hypothesis that the

332  slopes of the regression lines between the categories are parallel. If the slopes were

333  found to be parallel to each other ($p \geq 0.05$), an ANCOVA was conducted to test the null

334  hypothesis that the adjusted means of the slopes were equal (Aoki, 2004b). Two

335  regression lines were considered to be equal if the null hypothesis in ACOVA was not

336  rejected ($p \geq 0.05$).

337

338  **RESULTS**

339  **Variations of three variables: $C_1/C_2$, $M_1/M_2$, and RC**

340       In the bivariate distribution of pinching efficiency ($C_1/C_2$) and passive

341  disarticulation resistance ($M_1/M_2$), the distributions of categories C, P, and U were

342  separated from each other (Fig. 3). By comparing median values among the functional

343  categories (C, G, P, and U), both the mechanical advantages of pinching efficiency

344  ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) were greatest in the crushing

345  chelae (C), followed by gripping (G), then other chelae (U, male ucine major chelae;

346  and P, pinching chelae). Notably, the difference between the medians of categories P and

347  U were not pronounced (box plots in Fig. 3 and Appendix S2). According to the

348    Steel-Dwass test, the similarity of distributions among each pair of functional categories
349    was rejected between every pair (C and G; C and P; C and U; G and P; G and U) except
350    for a single pair (P and U), regardless of the sample size (Table 1; Fig. 3; Appendix S2).
351        The major and the minor chelae varied in the mechanical advantages (Table S1; Fig.
352    4; Appendix S3). Both mechanical advantages tended to be greater in the major chelae
353    compared with the minor in some decapod clades (e.g., coenobitid anomurans, carpiliids,
354    calappids, parthenopines, dorippids, oziids, ocypodines [Appendix S3]). In contrast, the
355    differences of the mechanical advantages were not clear in astacoids, dromiaceans,
356    raninids, majoids, potamids, cancrids, leucosiids, xanthids, grapsoids, macrophthalmids,
357    and ucines (Appendix S3). In most of the decapod taxa whose major chelae have
358    crushing ability (C), the two mechanical advantages were greater in major chelae (C)
359    whereas those were lessor in the minor chelae (G) (Table S1). Among the crabs with
360    crushing on the major chelae (C), mechanical advantages in both major and minor
361    chelae were relatively large in cancrids, and there were little differences of mechanical
362    advantages between their major- and minor chelae (Appendix S3). In ucines, the
363    differences of mechanical advantages were not pronounced between major and minor
364    chelae (Appendix S3).
365        Among the functional categories of chelae (C, G, P, and U), median value of
366    relative chela size (RC) was by far the largest in U, followed by C, P, and G (boxplots in
367    Appendix S2). However, the difference of the median values among categories C, G,
368    and P were not pronounced. The Steel-Dwass test on RC among the four different
369    functional categories showed that the similarity of distributions between U and the other
370    functional categories (C, G, and P) were rejected ($p < 0.05$), whereas those among C, G,
371    and P were not rejected (Appendix S2).

372

**Correlation between Variables for Each Functional Category**

374        The ranges of two mechanical advantages ($C_1/C_2$ and $M_1/M_2$) were widespread in
375    several decapod lineages (Fig. 4; Appendix S3: Calappidae [$C_1/C_2$: 19–52%; $M_1/M_2$:
376    21–46%]; Parthenopidae [$C_1/C_2$: 23–55%; $M_1/M_2$: 30–44%]; Cancridae + Dorippidae +
377    Leucosiidae clade [$C_1/C_2$: 5–48%; $M_1/M_2$: 8–39%]; Portunoidea [$C_1/C_2$: 3–41%;
378    $M_1/M_2$: 4–39%]). The ranges of both mechanical advantages ($C_1/C_2$ and $M_1/M_2$) within
379    the group were especially pronounced in lithodids ($C_1/C_2$: 18–42%; $M_1/M_2$: 25–45%),
380    calappids, parthenopines ($C_1/C_2$: 23–46%; $M_1/M_2$: 30–41%), dorippids ($C_1/C_2$: 6–48%;
381    $M_1/M_2$: 17–39%), portunines ($C_1/C_2$: 3–41%; $M_1/M_2$: 4–39%), and ocypodines ($C_1/C_2$:
382    18–35%; $M_1/M_2$: 14–34%) (Fig. 4; Appendix S3). The functional categories of chelae
383    varied (more than two categories) within these clades as well (Table S1). The value RC
384    was extremely high in the major chelae (U) of fiddler crabs (Ucinae: Table S1; Fig. 4;

385    Appendix S2). In the other studied taxa, the RC were somewhat large (> 25%) in some
386    non-brachyuran taxa (e.g., major chelae in ghost shrimp [*Glypturus*], coconut crab
387    [*Birgus*]; and major and minor chelae in crayfish [*Pacifastacus*]), but were smaller than
388    25% in all the non-ucine brachyurans (Table S1; Appendix S2). Abouheif's test based
389    on a phylogenetic tree comprised of major lineages of brachyuran superfamilies
390    (Schubart et al., 2006; Ahyong et al., 2007; Spiridonov et al., 2014; Tsang et al., 014)
391    found that the pinching efficiency ($C_1/C_2$), passive disarticulation resistance ($M_1/M_2$),
392    and relative size of chela (RC), were not phylogenetically autocorrelated ($p \geq 0.05$) in
393    the major (L), minor (S), and the average of major and minor (L+S) chelae (Appendix
394    S1).

395         According to Spearman's test for two of three variables ($C_1/C_2$, $M_1/M_2$, and RC) in
396    all chelae used for this study, positive correlation was supported between $C_1/C_2$ and
397    $M_1/M_2$ (Table 2; Fig. 3: total), while the correlation was not supported between RC and
398    $C_1/C_2$ and between RC and $M_1/M_2$ (Appendix S2: total). The coefficient of
399    determination ($R^2$) was high (> 0.6) in relationship between $C_1/C_2$ and $M_1/M_2$ (Table 2:
400    total), whereas those were extremely low ($\simeq 0$) in relationships between RC and the
401    other two variables (Appendix S2: total).

402         According to the Spearman's and correlation tests used to find relationships
403    between $C_1/C_2$ and $M_1/M_2$, positive correlations were supported in all functional
404    categories, though the correlation coefficients were moderate ($0.4 < R^2 < 0.7$) (Table 2;
405    Fig. 3: C, G, P, U). In chelae belonging to categories C, G, and P, the regression lines
406    were close to each other (Fig. 3). However, in chelae belonging to category U, the
407    pinching efficiency ($C_1/C_2$) tended to be greater than passive disarticulation resistance
408    ($M_1/M_2$) compared with the other categories (Fig. 3).

409         Correlations between RC and $C_1/C_2$ and between RC and $M_1/M_2$ were not
410    supported in categories C and P (Appendix S2). Correlations between RC and $C_1/C_2$,
411    and between RC and $M_1/M_2$ were supported in category G; however, the coefficients of
412    determination were weak ($R^2 < 0.2$) in both cases (Appendix S2). Correlation between
413    RC and $M_1/M_2$ were supported in category U, and the correlation coefficient was
414    moderate ($\simeq 0.5$) (Appendix S2).

415

416    **Aspect Ratio at the Proximal Dactylus**
417         Significant correlations were found between the depth (log [$C_1$]) and width (log
418    [$M_1$]) of the proximal dactylus in all studied chela and every functional category (C, G,
419    P, and U: Fig. 5; Table 3). The coefficients of determination ($R^2$) were extremely high
420    ($0.85 < R^2$) in all functional categories and in all studied chelae (Table 3).
421         However, the aspect ratio between $C_1$ and $M_1$ ($M_1/C_1$) ranged from 0.636 to 2.91

422    (Fig. 5; Table S1). A relatively high aspect ratio indicates that the dactylus is flat in

423    depth ($C_1$), whereas a relatively low ratio indicates that the dactylus is narrow in width

424    ($M_1$). The aspect ratio ($M_1/C_1$) was highly concentrated at approximately 1.00; the

425    quartiles of the ratio in all studied chelae were as follows: first, 0.945; second (median),

426    1.061; third, 1.26 (Fig. 5).

427    The slopes of the regression lines were parallel between most pairs of functional

428    categories (pairs among C, G, and U, and between P and U: Table 4). However,

429    according to the covariance tests, none of the pairs were the same (Table 4). The aspect

430    ratio was relatively large in G and P, followed by C and U (in descending order, Fig. 5).

431    This result implies that the proximal dactyli in G and P were wider than deep ($M_1 > C_1$),

432    whereas those in U were deeper than wide ($C_1 > M_1$).

433

434    **DISCUSSION**

435    **Mechanical Advantages as Indices of Chela Function**

436    This study, to our knowledge, is the first study that compared mechanical

437    advantages of chela among a huge variety of decapod taxa (representing 63 genera:

438    Table S1). We also introduced a new indicator for passive disarticulation resistance

439    ($M_1/M_2$), in addition to an indicator for pinching efficiency ($C_1/C_2$) that has been used

440    by previous studies (e.g., Warner and Jones, 1976; Yamada and Boulding, 1998;

441    Labadie and Palmer, 1996; Schenk and Wainwright, 2001).

442    The most important outcome of our study is that mechanical advantages of both

443    pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) on decapod

444    chelae were elucidated to be good indices for estimating the function among

445    crushing/chipping (C), gripping (G), pinching (P), or male ucine major (U) chelae.

446    Specifically, the separation of the distribution of the two mechanical advantages

447    between the crushing/chipping (C) chelae and pinching (P) chelae were apparent—the

448    former are used to open hard shells, and the latter are dedicated for pinching small

449    particles, such as detritus, at the chela-tip (Fig. 3). The results were also consistent with

450    our hypotheses that crushing/chipping chelae (C) are relatively large in the mechanical

451    advantages, whereas pinching chelae (P) and male ucine major chelae (U) are relatively

452    small in the mechanical advantages. Neither mechanical advantage ($C_1/C_2$ or $M_1/M_2$)

453    was phylogenetically autocorrelated in tests based on the phylogenetic trees of decapods

454    with more than two studied taxa within most of the brachyuran superfamilies (Schubart

455    et al., 2006; Ahyong et al., 2007; Tsang et al., 2008; Bracken et al., 2009; Spiridonov et

456    al., 2014; Tsang et al., 2014: Appendix S1; Fig. 4). Therefore, diversifications of these

457    indices among decapods are interpreted to be independent from the phylogeny.

458    Preston et al. (1996) found that some durophagous brachyuran (portunid and

cancrid) taxa have major crushing chelae (C) with a relatively high pinching force and minor gripping chelae (G) with a relatively low pinching force. Most of the durophagous taxa we used had relatively high mechanical advantages for C and low mechanical advantages for G (Lithodidae, Carpiliidae, Tasmanian giant crab [*Pseudocarcinus*], Calappidae, Parthenopinae, Carcininae, mangrobe crab [*Scylla*], Oziidae, and Ocypodinae: Table S1; Fig. 4; Appendix S3); therefore, our results are consistent with results of Preston et al. (1996). However, reef crab (*Atergatis*: Xanthidae) was somewhat unique among the durophagous taxa we used. The mechanical advantages ($C_1/C_2$ and $M_1/M_2$) of both the major (C) and minor (G) chelae were high and similar (Table S1; Fig. 4; Appendix S3). The reef crab (*Atergatis*) chelae are described as isochelous (Schweitzer and Feldmann, 2010), so the minor chela may also have a crushing ability (C).

In an index of pinching efficiency ($C_1/C_2$), the numerator $C_1$ is the distance between the P-D joint axis and the insertion of the closer muscle, which may indirectly reflect a dorso-ventral depth of the proximal edges of the dactylus (Fig. 2A, B). In the same way, the dorso-ventral depth of the proximal dactylus reflects the dorso-ventral depth of the propodus (Fig. 2B). The relationship between pinching force and the dorso-ventral depth has been reported in several arthropod chelipeds (Van der Meijden et al., 2010; Taylor et al., 2009), and our results are consistent with these studies.

Dissimilarly, the passive disarticulation resistance ($M_1/M_2$), is directly proportional to the medio-lateral width ($M_1$) of the proximal dactylus (Fig. 2A, C). The mechanical advantage ($M_1/M_2$) is relatively simple to estimate because both the denomination ($M_2$) and the numerator ($M_1$) can be directly measured on the specimen, unlike the length of moment arms $C_1$ and $C_2$ in the estimation of pinching efficiency (Fig. 2A).

The relative size of the chela to the carapace size (RC) was relatively large only in ucine chelae (U); there was little difference in RC among the other categories of pinching abilities (C, G, and P) (Appendix S2). Moreover, all the chelae categorized as U in this study belonged to the major chelae of male fiddler crabs (*Uca*, Ucinae: Table S1), and it remains unclear whether the relatively high value of RC in U, estimated for a single genus (*Uca*), reflects the entire spectrum of ucine chelae among decapods. In conclusion, the relative size of the chela (RC) may not be a good indicator for determining the function of chelae at present.

The moment arms $C_1$ and $M_1$ showed a high correlation with each other, which suggests a high correlation between the dorso-ventral depth and the medio-lateral width of the proximal dactyli (Fig. 5). None of the dactylus in the studied chela were very small in width ($M_1/C_1 < 0.635$) nor in depth ($2.92 < M_1/C_1$: Table S1). These results indicate that the chelae are designed to retain the ratio between dorso-ventral depth and

medio-lateral width of the proximal dactylus. In other words, the pinching efficiency and the resistance against passive disarticulation are strongly correlated with each other in chelae with a pinching ability. This hypothesis can be validated if the mechanical advantages of several types of pereopods (e.g., chelate, carpochelate, semichelate, and the other non-chalate types) are comprehensively studied in the future (e.g., diversified pereopod morphology in reduviid hemipterans, [Weirauch et al., 2011]; chelate major- and semichelate minor chelae in callianassid axiideans [Hyžný and Gašparič, 2014]).

**Limitations**

There are some limitations in the methods used in this study. The first limitation is in the difficulty in determination of chela functions (Table S1). It is difficult to categorize the functions of chelae. There are numerous studies on diets of the studied taxa; however, there are few reports on how they use their chelae during feeding, mating, digging, or fighting. We simply assumed that the shell-crushing chelae (C) are expected to have large mechanical advantages ($C_1/C_2$ and $M_1/M_2$) over the other functional categories (G, P, and U). However, the strengths of molluscan shells vary by species and growth stages (e.g., Preston et al., 1996); therefore, the relatively large pinching force may not simply be correlated with the species' durophagy. Moreover, some non-durophagous decapods may have strong pinching abilities for other purposes. For example, among the non-durophagous taxa, coconut crabs (*Birgus*, Coenobitidae, Anomura) are known to have strong pinching force (Muraoka and Odawara, 1995). Mechanical advantages of their chelae were estimated as be as high as those for crushing chelae (C) (Table S1; Fig. S2). The functional categories should ideally be based on the differences of pinching force at the tip of chela ($F_{out}$: Fig. 2B, C); the functional categories based on difference in diets (C, G, P, and U) are not the most appropriate method to compare mechanical advantages. However, studies on pinching forces alone are still not sufficient to compare the mechanical advantages among various taxa (e.g., Elner, 1978; Govind and Blundon, 1985; Taylor et al., 2009; Van der Meijden, 2012). This limitation remains an issue for future study.

The second limitation concerns the potential role of the opener and closer muscles in resisting mediolateral disarticulations of the P-D joint. These muscles may function to rotate the dactylus about the axes $Y$ or $Y'$ for resisting against the P-D joint disarticulation (Fig. 1B). Therefore, the ratio between the moment arms of the dactylus ($M_2$) and these muscles (the mediolateral distance from points $d$ or $e$ to the axes $Y$ or $Y'$: Fig. 1B) may also be used as an additional index for the disarticulation resistance, and it is worth testing the validity of this index in the future studies.

The third limitation concerns the validity of the use of the triangular area (PS + DS)

533    for the proxy of chela size, because the value has not been widely used as the proxy in
534    previous studies. However, the correlation between the traditionally used proxy (the
535    propodus length) and our new proxy (PS + DS) was strongly supported (see Appendix
536    S4). Therefore, we consider that the use of the triangular area for the chela size is valid.
537        The fourth limitation concerns the points on the chelae that these taxa use to pinch
538    the object. Mechanical advantages employed in this study ($C_1/C_2$ and $M_1/M_2$) are based
539    on the assumption that the chelae pinch objects at the distal ends (Fig. 2B, C). However,
540    in many cases, objects are pinched at the teeth along the pinching surface of chela (Fig.
541    1C, D: e.g., Muraoka and Odawara, 1995). For example, many durophagous species are
542    known to have molariform or hooked teeth at the proximal portions of the pinching
543    surface on the chelae to crush or chip molluscan shells (Vermeij, 1977; Schweitzer and
544    Feldmann, 2010). Mechanical advantages of both pinching and passive disarticulation
545    resistance would be increased if the studied taxa pinched objects at these teeth, because
546    the distance between the rotational axis and the teeth is smaller than those between the
547    axis and the distal end of the dactylus (Fig. 2B, C). On the other hand, some detritus
548    feeders, such as mud crabs (*Macrophthalmus*: P) and fiddler crabs (*Uca*: P and U), have
549    few teeth, if any, at the distal portions of the pinching surfaces of the chelae (Table S1).
550    The mechanical advantages would not be increased dramatically if these studied taxa
551    pinched objects at these teeth. The concern on the points on the chelae to pinch the
552    object remains an issue for future study.
553
554    **Mechanical Advantages as Tools to Reconstruct Evolutionary Process of Chelae**
555    **Functions**
556        The mechanical advantages $C_1/C_2$ and $M_1/M_2$ can be calculated from simple
557    measurements on the chela. Therefore, these indices could be powerful tools to estimate
558    the functions of chelae in species whose ecologies are not well known (X, unidentified
559    chelae: Table S1). These indices could also be applied to estimate chelae function in
560    extinct species, whose functions have mainly been reconstructed by relying on the
561    morphological features of the chelae (e.g., Dietl and Vega, 2008; Schweitzer and
562    Feldmann, 2010). Further studies on the additional mechanical indices, such as the
563    cuticle strengths of the chela (Palmar et al., 1999; Van der Meijden et al., 2012) or the
564    ability of resistance against the torsion of the P-D joint, will provide us a deeper
565    knowledge on the relationship between the design and function of the chelae.
566        In the study specimens, the mechanical advantages of $C_1/C_2$ and $M_1/M_2$ were
567    diversified within the ranges of 0–60% in each lineage of decapods (Table S1; Fig. 4;
568    Appendix S3), and these indices were not phylogenetically autocorrelated at least in the
569    Abouheif's test based on the trees which comprise many taxa within each superfamily

570 (Appendix S1). These results indicate that the diversification of chela functions and
571 diets was accompanied by the diversifications of these mechanical advantages. Hence,
572 varying the mechanical advantages of pinching efficiency and passive disarticulation
573 resistance played significant role in ecological diversification of decapods, though these
574 variables were well correlated with each other.
575

576 **CONCLUSIONS**
577     In comparing the major and minor chelae of 93 decapod species of 63 genera, the
578 mechanical advantages of both pinching efficiency and passive disarticulation resistance
579 were demonstrated to be good indices for the evaluation of pinching abilities. Both
580 mechanical advantages were greater in the abilities of the shell-crushing/chipping chelae,
581 followed by the grasping, and the pinching/male ucine major chelae. On the other hand,
582 the relative size of the chelae to the carapace size was not related to differences among
583 the crushing/chipping, gripping, or pinching functions.
584

585 **AUTHOR CONTRIBUTIONS**
586     S.-i. Fujiwara: study conception, design, and shaping manuscript; H. Kawai:
587 sampling and measurements; S.-i. Fujiwara and H. Kawai: data analyses. The authors
588 declare that there are no conflicts of interest.
589

606

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# Tables

*TABLE 1*. Results of Steel-Dwass tests of three indices related to chela—pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$)—among four different functional categories (C, G, P, and U). The tests were conducted for all the study specimens ($n = 259$: C, 34; G, 159; P, 45; U, 21). Asterisk indicates that the variables among two categories were not significantly different ($p < 0.05$). See boxplots in Fig. 3.

|       | $C_1C_2$ | | $M_1/M_2$ | |
|-------|---------|-----------|---------|-----------|
|       | *t*-score | *p* | *t*-score | *p* |
| C:G   | 6.34    | 1.36e−09* | 5.64    | 1.01e−07* |
| C:P   | 7.11    | 7.03e−12* | 6.93    | 2.51e−11* |
| C:U   | 5.94    | 1.69e−08* | 6.18    | 3.73e−09* |
| G:P   | 3.94    | 4.67e−04* | 5.82    | 3.37e−08* |
| G:U   | 2.61    | 4.49e−02* | 7.08    | 7.73e−12* |
| P:U   | 0.0757  | 1.00      | 3.27    | 5.93e−03* |

*TABLE 2*. Spearman's correlation test between mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) ($n = 317$: C, 34; G, 159; P, 45; U, 21; X, 58). Spearman's $\rho$- and *p*-values, coefficient of determination ($R^2$), and regression line were indicated for each functional category (C, G, P, and U). See Fig. 3.

|       | *n* | $\rho$-value | *p* | $R^2$ | regression line |
|-------|-----|--------------|-----------|-------|-----------------|
| total | 317 | 0.789 | <2.2e−16* | 0.652 | $y = 0.583x + 11.0$ |
| C     | 34  | 0.744 | 1.10e−06* | 0.529 | $y = 0.474x + 15.7$ |
| G     | 159 | 0.662 | <2.2e−16* | 0.481 | $y = 0.441x + 15.9$ |
| P     | 45  | 0.879 | 2.46e−15* | 0.771 | $y = 0.609x + 9.23$ |
| U     | 21  | 0.584 | 1.68e−03* | 0.413 | $y = 0.527x + 5.60$ |

*Null-hypothesis that there is no association between the two variables was rejected ($p < 0.05$).

33 *TABLE 3*. Spearman's correlation test between moment arms of closing muscle contraction ($C_1$) and resistance force
34 of the articular membrane ($M_1$) ($n = 317$: C, 34; G, 159; P, 45; U, 21; X, 58). Spearman's $\rho$- and $p$-values, coefficient
35 of determination ($R^2$), and regression line were indicated for each functional category (C, G, P, and U). See Fig. 5.

| | $n$ | $\rho$-value | $p$ | $R^2$ | regression line |
|---|---|---|---|---|---|
| total | 317 | 0.933 | <2.2e−16* | 0.875 | $\log(M_1) = 0.908 \times \log(C_1) + 0.105$ |
| C | 34 | 0.971 | <2.2e−16* | 0.868 | $\log(M_1) = 1.02 \times \log(C_1) - 0.0482$ |
| G | 159 | 0.912 | <2.2e−16* | 0.866 | $\log(M_1) = 1.03 \times \log(C_1) + 0.0452$ |
| P | 45 | 0.905 | <2.2e−16* | 0.883 | $\log(M_1) = 0.858 \times \log(C_1) + 0.135$ |
| U | 21 | 0.932 | 2.87e−11* | 0.907 | $\log(M_1) = 1.12 \times \log(C_1) - 0.184$ |

43 *Null-hypothesis that there is no association between the two variables was rejected ($p < 0.05$).

47 *TABLE 4*. Results of pair-wise analysis of covariance (ANCOVA) between pairs of regression lines of closing muscle
48 contraction ($C_1$) and resistance force of the articular membrane ($M_1$) among the functional categories C ($n = 34$), G ($n$
49 $= 159$), P ($n = 45$), and U ($n = 21$). Parallel line analysis (PLA) tests the null hypothesis that the slopes of the
50 regression lines are parallel to each other. ANCOVA tests the null hypothesis that the adjusted means of the slopes are
51 equal. Similarity of the two slopse are supported if the $p$-values of the both tests exceed 0.05 ($p \geq 0.05$). See Table 3
52 and Fig. 5 for the regression lines.

| test | PLA | | ANCOVA | |
|---|---|---|---|---|
| | $F$-statistic | $p$-value | $F$-statistic | $p$-value |
| C : G | 0.116 | 0.733 | 1.93 | 1.89e−05 |
| C : P | 7.78 | 6.70e−03 | — | — |
| C : U | 0.439 | 0.510 | 16.2 | 1.82e−04 |
| G : P | 8.29 | 4.42e−03 | — | — |
| G : U | 0.333 | 0.565 | 6.58 | 8.07e−14 |
| P : U | 2.96 | 0.0905 | 3.87 | 4.47e−08 |
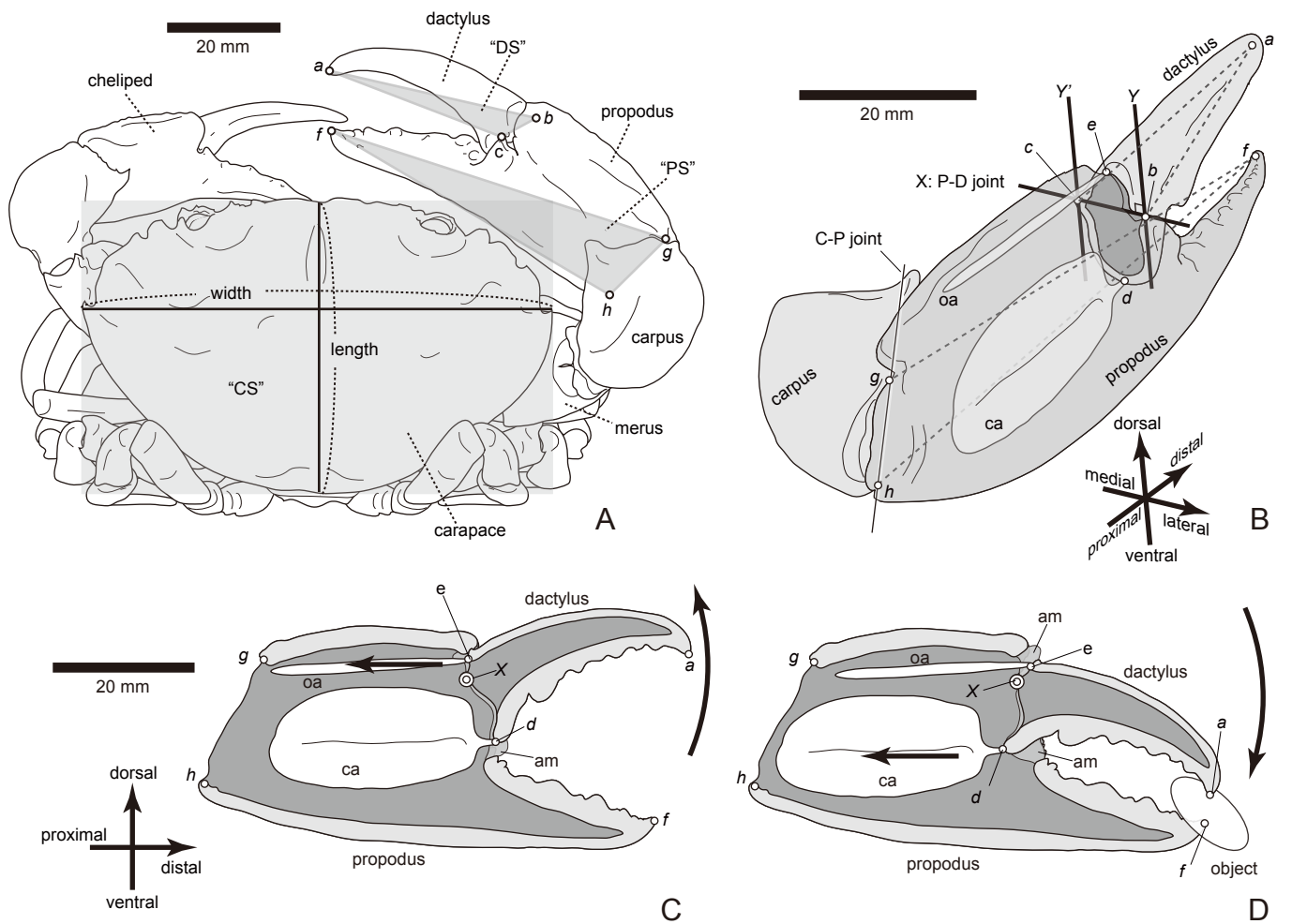
**Fig. 1**. Structures of decapod chela. (**A**) A scheme illustration of a decapod (*Baptozius vinosus*: KH66) with definition of carapace, dactylus, and propodus sizes in this study. (**B**) Connections of the distal three elements (carpus, propodus, and dactylus) of the right cheliped. These elements are connected via facet-fulcra articulations and articular membranes (am). (**C**) Opening and (**D**) closing phases of the propodus-dactylus (P-D) joint. Abbreviations: (*a*) distal-most point on the dactylus; (*b*) medial and (*c*) lateral fulcra of the P-D joint; (*d*) insertion of closer apodeme (ca), and (*e*) insertion of opener apodeme (oa) on the dactylus; (*f*) distal-most point on the propodus; (*g*) medial and (*h*) lateral fulcra of the carpus-propodus (C-P) joint. Axis *X* (a line through points *b* and *c*) correspond to the P-D joint. Axes *Y* and *Y'* are lines through points *b* and *c*, which are perpendicular to the plane formed by points *a–c*, respectively. The axes *X*, *Y*, and *Y'* are determined to calculate moment arms ($C_1$, $C_2$, $M_1$, $M_{2L}$, and $M_{2M}$: see Fig. 2). In (**A**), shaded area of rectangle represents the carapase size (CS), and shaded areas of triangles formed by points *a–c* and points *d–f*, respectively represent the propodus (PS) and dactylus (DS) sizes.
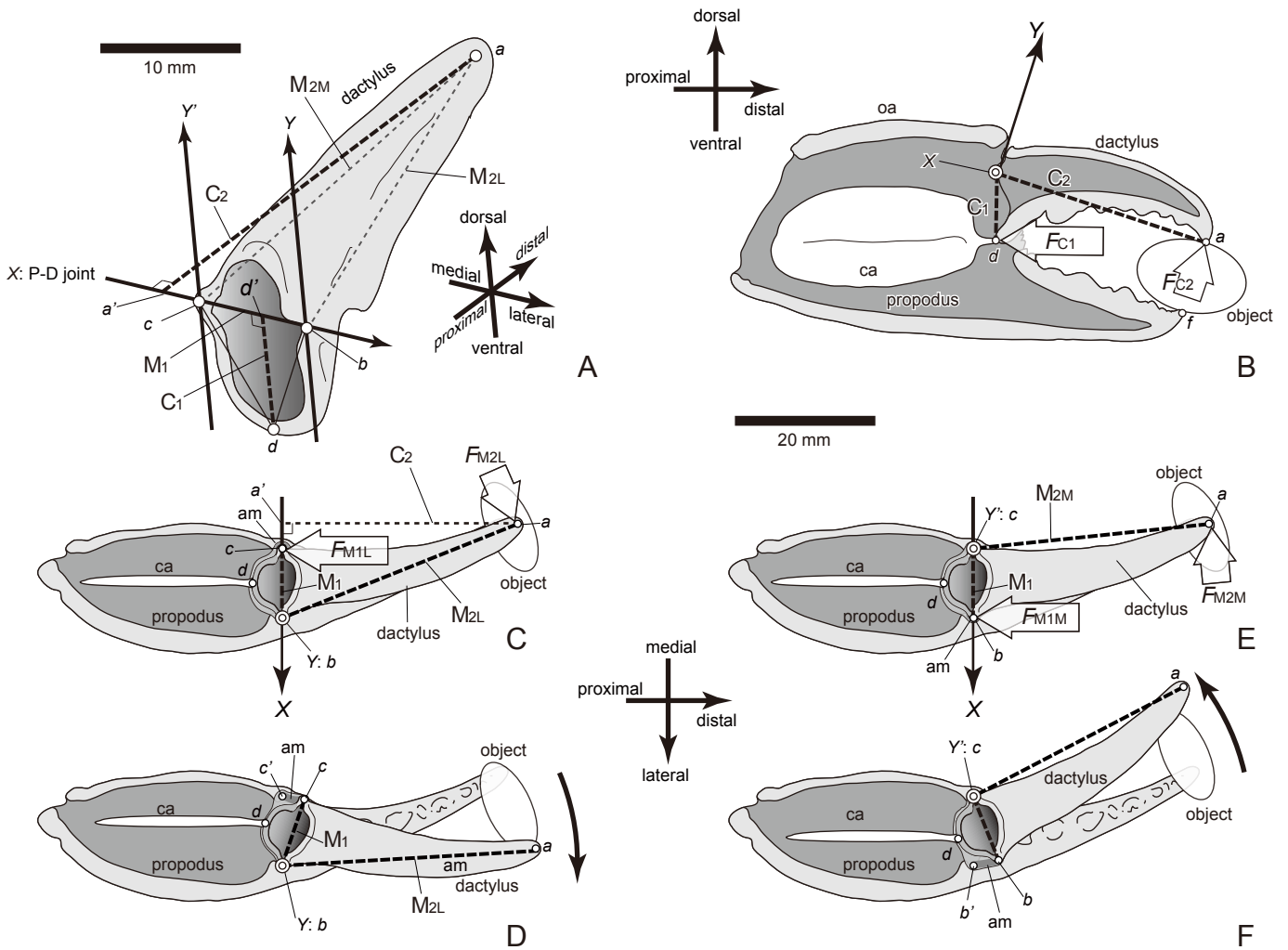
**Fig. 2**. (**A**) Measurement points on the dactylus, mechanical conditions of (**B**) pinching an object using the chela (in lateral view), and (**C**) and (**E**) resistance of the medial and lateral fulcra against lateral- and medial-ward thrusts on the chela tip that functions to dislocate the joint, respectively (in dorsal view). In (**B**), the dactylus rotate about axis $X$. A contractive force of closer muscle ($F_{C1}$) is applied to point $d$ during the pinching phase. A product of $F_{C1}$ and the in-lever moment arm $C_1$ is balanced by a product of a reaction force ($F_{C2}$) from the object to the tip of the dactylus (point $a$) and its moment arm $C_2$. In (**C**), the dactylus rotates about an axis $Y$. An external force ($F_{M2L}$) on the tip of the dactylus ($a$) rotates the dactylus laterally about the point $b$, whereas the articular membrane functions in resisting the torque at the medial fulcrum (point $c$) at a certain force ($F_{M1L}$). A product of $F_{M1L}$ and the in-lever moment arm $M_1$ is balanced by a product of the lateral force ($F_{M2L}$) from the object and its moment arm $M_{2L}$. (**D**) The medial fulcrum on the dactylus ($c$) is disarticulated with the medial facet on the propodus ($c'$) under the following conditions: $|F_{M1L} \times M_1| > |F_{M2L} \times M_{2L}|$. Likewise, in (**E**), the dactylus rotates medially about an axis $Y'$ by an external force ($F_{M2M}$) on the tip of the dactylus ($a$), while the articular membrane at the medial fulcrum (point $c$) produces resistant torque at a certain force ($F_{M1M}$): $|F_{M1M} \times M_1| = |F_{M2M} \times M_{2M}|$. (**D**) The lateral fulcrum on the dactylus ($b$) is disarticulated with the medial facet on the propodus ($b'$) under the following conditions: $|F_{M1M} \times M_1| > |F_{M2M} \times M_{2M}|$. Abbreviations: ($a$) distal-most point on the dactylus; ($a'$) a foot of perpendicular line through point $a$ on axis $X$; ($b$) medial and ($c$) lateral fulcra of the P-D joint; ($b'$) medial and ($c'$) lateral facets of the P-D joint; ($d$) insertion of closer apodeme (ca); ($d'$) a foot of perpendicular line through point $d$ on axis $X$; $X$, a line through points $b$ and $c$; $Y$ and $Y'$, lines through points $b$ and $c$, which are perpendicular to the plane formed by points $a$–$c$.
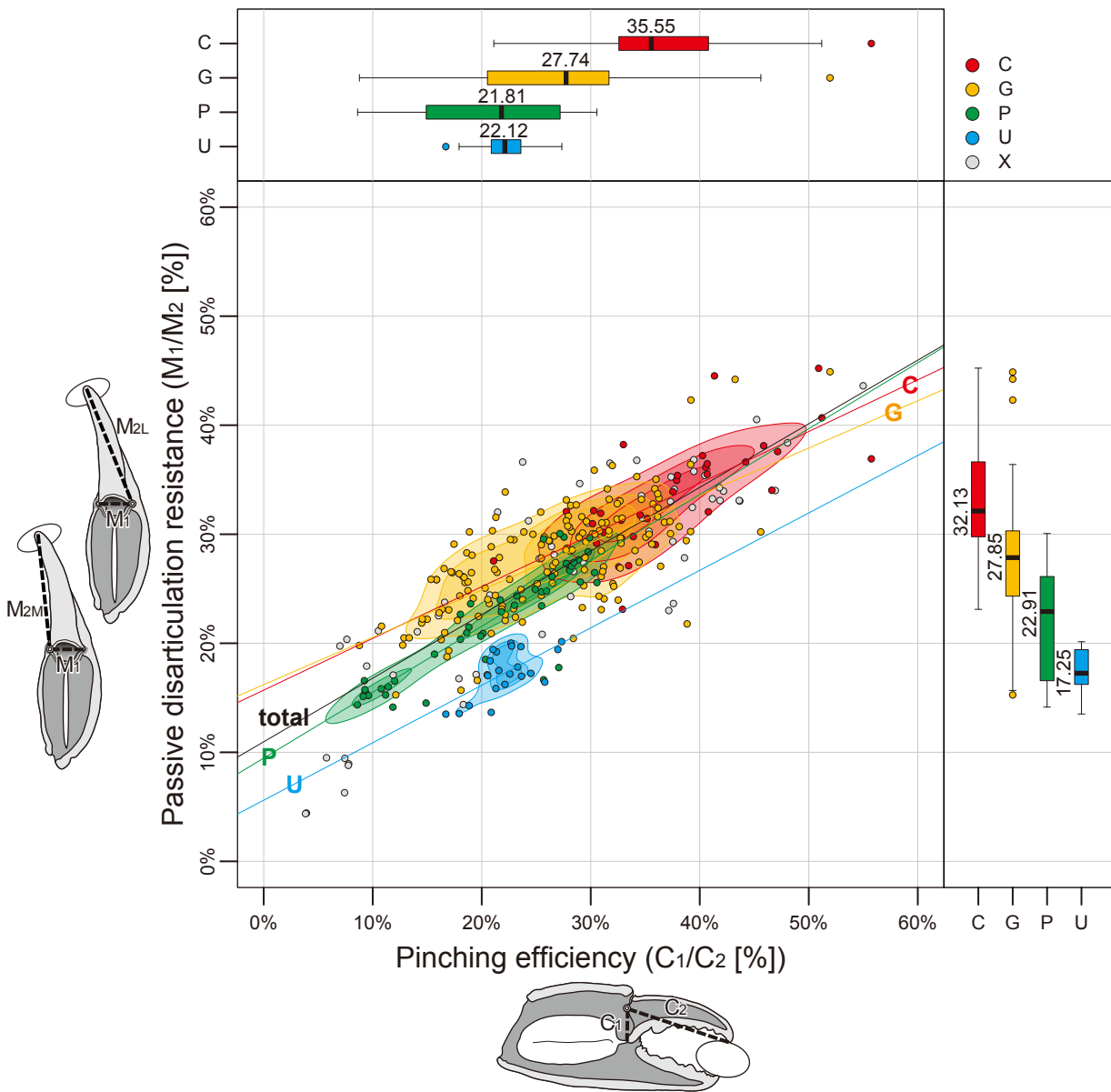
**Fig. 3**. Relationship between mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$). See main text for abbreviations. Each plot represents chela characteristics of the study specimens ($n = 317$ in total; C, crushing/chipping chela, $n = 34$; G, gripping chela, $n = 159$; P, pinching chela, $n = 45$; U, male ucine major chela, $n = 21$; X, uncategorized chela, $n = 58$). Bivariate kernel density distributions (densities: 25%, 50%, 75%) and box plots with median values are shown for each variable in the functional categories C, G, P, and U. See Table 1 for results of Steel-Dwass tests in the variables. Regression lines are drawn for total plots, in addition to the regression lines for plots of each functional category (C, G, P, and U). See Table 3 for slopes of the regression lines.
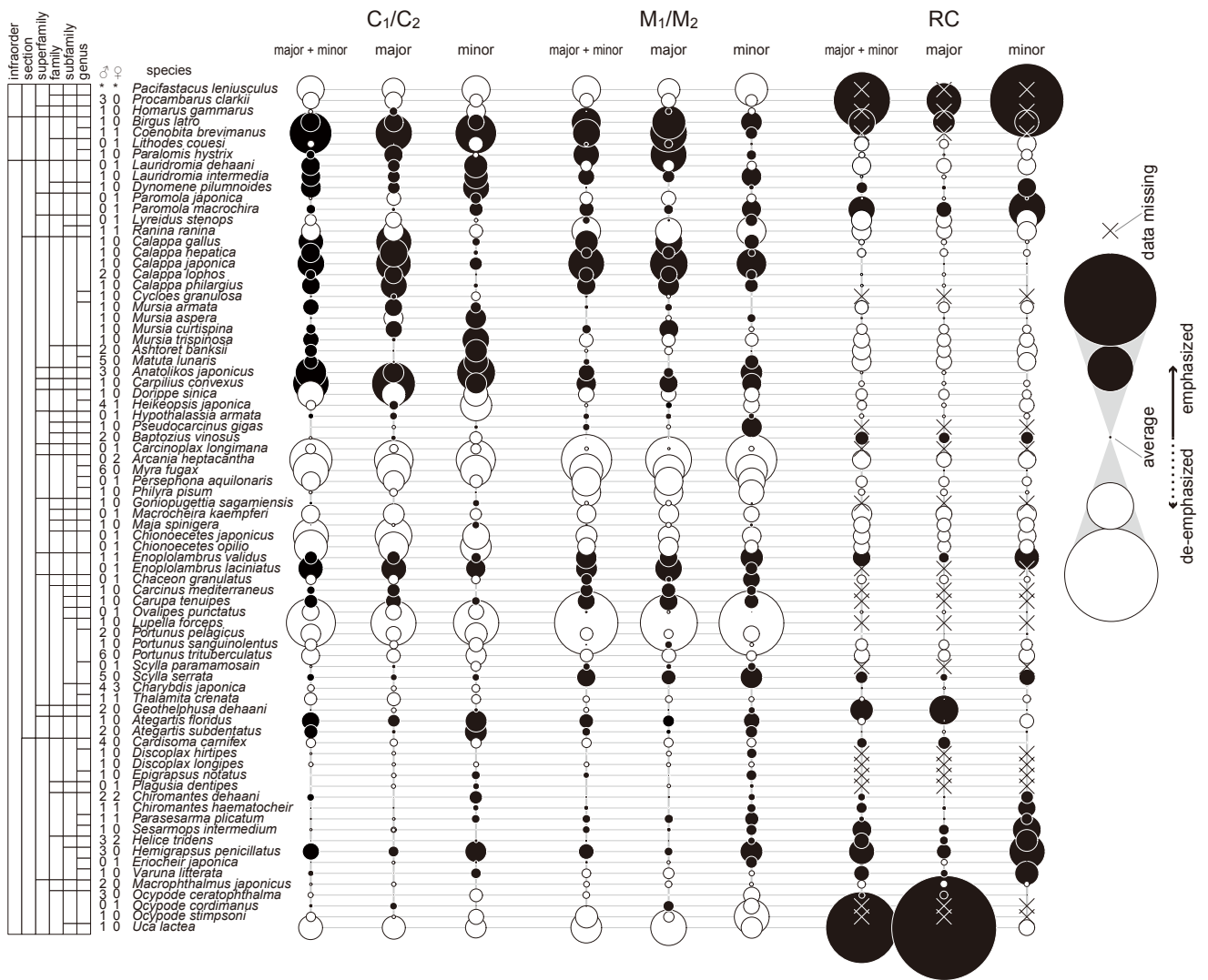
**Fig. 4**. Variations of three indices ($C_1/C_2$, $M_1/M_2$, and RC) among the studied species whose indices in both the major and minor chelae were available. The values of indices were estimated for the average of major and minor, major, and minor chelae. White and black symbols respectively correspond to values which are below and over the mean among the species. The values of indices were defined as the average of the studied chelae in the species. We followed Ng et al. (2008) for the ranks of classification (infraorder, section, superfamily, family, subfamily, and genus).
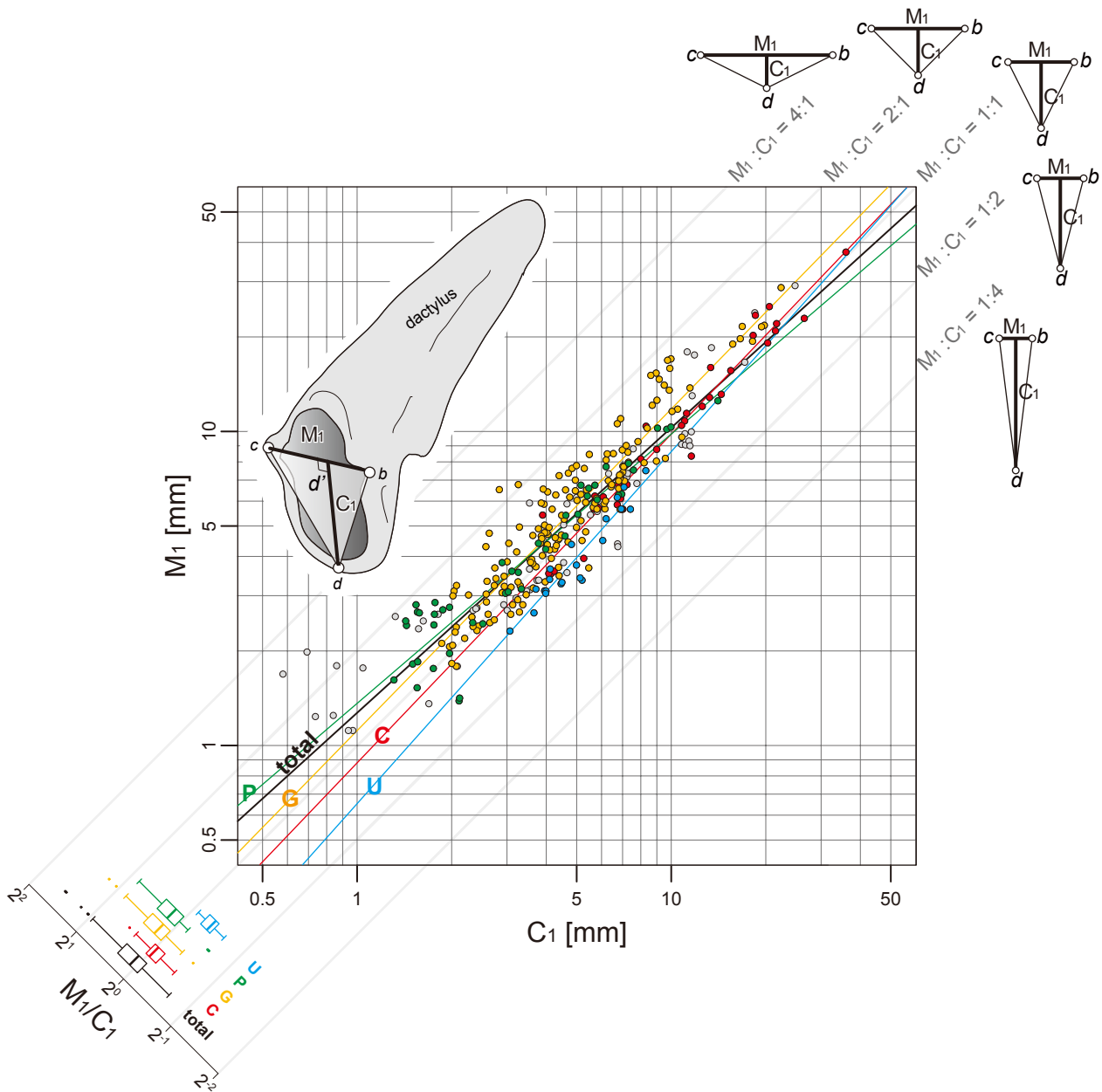
**Fig. 5**. Relationship between the moment arms of the closer muscle ($C_1$) and the articular membrane ($M_1$) of the proximal dactylus in the studied specimens. Regression lines are drawn for all the studied chelae (total) and each functional category (C, G, P, and U: see Table 3). The boxplots of the aspect ratio ($C_1/M_1$) are shown for the categories (total, C, G, P, and U) as well. See Figs. 1 and 2 for the abbreviations of the landmarks.

TABLE S1 . A table of the studied specimens and measurement data of the claws. Family; species; specimen number; sex ($\sigma$, male; $\varphi$, female); body mass (BM [g]); carapace size (CS [mm$^2$]); side of the chela (L, major; S, minor); function of the chela (Fn: C, crushing/wedging; G, gripping; P, pinching; U, ucine; X, unknown); the dactylus size (DS [mm$^2$]); the propodus size (PS [mm$^2$]); the relative size of the chela (RC: (DS+PS)/CS[%]); moment arms of the closer muscle ($C_1$ [mm]) and the distal end of the dactylus ($C_2$ [mm]) about the propodus-dactylus joint, and the pinching efficiency ($C_1/C_2$[%]); moment arms of the articular membrane ($M_1$ [mm]) and the distal ends of the dactylus ($M_{2L}$ and $M_{2M}$ [mm]) about the lateral and medial facets of the propodus-dactylus joint, and the passive disarticulation resistance ($M_1/M_2$[%]); the ratio between $C_1$ and $M_1$ ($M_1/C_1$[%]); and the references for the chelae functions are listed. See the bottom for the abbreviations of the references. Classification of the species is based on Ng et al. (2008).

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AXIIDEA | | | | | | | | | | | | | | | | | | | |
| Callianassidae | *Glypturus acanthochirus* | KH103 | $\sigma$ | — | 351 | L | G | 29.9 | 99.2 | 36.8 | 3.63 | 12.8 | 28.4 | 4.68 | 22.9 | 20.0 | 20.4 | 1.29 | D3; S3 |
| | | | | | | S | P | — | — | — | — | — | — | — | — | — | — | — | |
| ASTACIDEA | | | | | | | | | | | | | | | | | | | |
| ASTACOIDEA | | | | | | | | | | | | | | | | | | | |
| Astacidae | *Pacifastacus leniusculus* | KPM-NH106516 | — | 130 | 2,280 | L | G | 304 | — | — | 7.28 | 42.9 | 17.0 | 8.62 | 44.4 | 44.6 | 19.3 | 1.18 | G1, O1 |
| | | | | | | S | G | 159 | — | — | 3.96 | 32.6 | 12.1 | 5.04 | 32.6 | 33.0 | 15.3 | 1.27 | |
| Cambaridae | *Procambarus clarkii* | KPM-NH354 | $\sigma$ | 26.2 | 1,040 | L | G | 97 | 172 | 25.9 | 6.44 | 29.1 | 22.1 | 6.67 | 29.7 | 30.2 | 22.1 | 1.04 | O1, P2 |
| | | | | | | S | G | 100 | 165 | 25.7 | 6.30 | 28.8 | 21.9 | 6.98 | 29.2 | 29.8 | 23.4 | 1.11 | |
| | *P. clarkii* | KH99 | $\sigma$ | 10.5 | 569 | L | G | 21.4 | — | — | 2.74 | 13.2 | 20.7 | 3.24 | 13.4 | 13.7 | 23.6 | 1.18 | O1, P2 |
| | | | | | | S | G | 19.9 | — | — | 2.58 | 13.1 | 19.7 | 3.04 | 13.3 | 13.5 | 22.5 | 1.18 | |
| | *P. clarkii* | KH100 | $\sigma$ | 10.8 | 521 | L | G | 37.4 | — | — | 3.22 | 18.1 | 17.8 | 4.14 | 18.4 | 18.7 | 22.1 | 1.29 | O1, P2 |
| | | | | | | S | G | 35.4 | — | — | 3.00 | 18.4 | 16.3 | 3.85 | 18.6 | 18.9 | 20.3 | 1.28 | |
| NEPHOROIDEA | | | | | | | | | | | | | | | | | | | |
| Nephropidae | *Homarus gammarus* | KH102 | $\sigma$ | — | — | L | C | 627 | — | — | 20.3 | 57.7 | 35.2 | 19.2 | 58.5 | 61.0 | 31.4 | 0.945 | S2; Y1 |
| | | | | | | S | X | 553 | — | — | 11.8 | 71.4 | 16.6 | 17.6 | 72.0 | 73.8 | 23.8 | 1.48 | |
| ANOMURA | | | | | | | | | | | | | | | | | | | |
| Coenobitidae | *Birgus latro* | KH101 | $\sigma$ | 620 | 4,270 | L | G | 381 | 896 | 29.9 | 15.7 | 40.1 | 39.2 | 19 | 44.5 | 45.0 | 42.3 | 1.21 | R1; W1 |
| | | | | | | S | G | 181 | 623 | 18.8 | 10.5 | 30.6 | 34.2 | 11.8 | 32.9 | 33.4 | 35.3 | 1.13 | |
| | *B. latro* | KPM-NH141574 | $\varphi$ | 173 | 4,760 | L | G | 135 | 363 | 10.5 | 10.1 | 23.3 | 43.3 | 11.6 | 26.0 | 26.3 | 44.2 | 1.15 | R1; W1 |
| | | | | | | S | G | 80.3 | 306 | 8.11 | 7.02 | 21.6 | 32.4 | 7.42 | 23.7 | 23.6 | 31.4 | 1.06 | |
| | *Coenobita brevimanus* | NSMT-Cr.10289 | $\sigma$ | 29.3 | 602 | L | G | 43.2 | — | — | 6.80 | 13.1 | 51.9 | 6.59 | 13.7 | 14.7 | 44.9 | 0.969 | B1; H1 |
| | | | | | | S | G | 12.7 | — | — | 3.63 | 7.97 | 45.6 | 3.18 | 10.5 | 9.60 | 30.2 | 0.875 | |
| Lithodidae | *Lithodes couesi* | KPM-NH109042 | $\varphi$ | 506 | 21,000 | L | C | 354 | 942 | 6.18 | 13.4 | 44.1 | 30.3 | 16 | 49.8 | 48.9 | 32.2 | 1.20 | S2; V3 |
| | | | | | | S | G | 206 | 461 | 3.18 | 6.89 | 37.3 | 18.5 | 11 | 43.1 | 41.7 | 25.6 | 1.60 | |
| | *Paralomis hystrix* | KH105 | $\sigma$ | 705 | 21,200 | L | C | 622 | 1,350 | 9.31 | 20.5 | 49.7 | 41.3 | 25 | 55.9 | 56.2 | 44.5 | 1.22 | C3; S2 |
| | | | | | | S | G | 292 | 762 | 4.97 | 9.86 | 43.0 | 22.9 | 13.6 | 45.5 | 46.0 | 29.5 | 1.38 | |
| BRACHYURA | | | | | | | | | | | | | | | | | | | |
| PROTOTREMATA | | | | | | | | | | | | | | | | | | | |
| DROMIOIDEA | | | | | | | | | | | | | | | | | | | |
| Dromiidae | *Lauridromia dehaani* | KPM-NH101140 | $\varphi$ | 110 | 5,540 | L | X | 39.4 | 165 | 3.69 | 6.74 | 18.0 | 37.6 | 4.39 | 18.1 | 18.6 | 23.6 | 0.651 | — |
| | | | | | | S | X | 39.1 | 145 | 3.32 | 6.76 | 18.2 | 37.2 | 4.3 | 18.2 | 18.7 | 23.0 | 0.636 | |
| | *L. intermedia* | KPM-NH8 | $\sigma$ | 40.4 | 2,210 | L | X | 46.2 | 139 | 8.36 | 5.90 | 15.7 | 37.7 | 5.9 | 17.3 | 17.2 | 34.1 | 1.00 | — |
| | | | | | | S | X | 43.4 | 132 | 7.92 | 5.80 | 15.6 | 37.3 | 5.58 | 16.8 | 16.9 | 33.0 | 0.961 | |
| Dynomenidae | *Dynomene pilumnoides* | KPM-NH101091 | $\sigma$ | 2.65 | 572 | L | X | 23.2 | 47.4 | 12.3 | 4.54 | 12.1 | 37.5 | 3.83 | 13.0 | 13.1 | 29.3 | 0.843 | — |
| | | | | | | S | X | 21.5 | 48.9 | 12.3 | 4.66 | 12.1 | 38.6 | 3.56 | 12.5 | 12.8 | 27.8 | 0.764 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| HOMOLOIDEA | | | | | | | | | | | | | | | | | | | |
| Homolidae | | | | | | | | | | | | | | | | | | | |
| | *Paromola japonica* | KPM-NH0162161 | ♀ | — | 6,820 | L | G | 123 | 471 | 8.72 | 7.02 | 31.7 | 22.2 | 7.76 | 34.3 | 34.0 | 22.7 | 1.11 | C2; S2 |
| | | | | | | S | G | 106 | 468 | 8.42 | 8.21 | 26.5 | 31.0 | 7.96 | 34.5 | 32.1 | 23.1 | 0.97 | |
| | *P. macrochira* | NUM unnumbered | ♀ | 827 | 14,900 | L | G | 662 | 1,900 | 17.2 | 19.8 | 60.6 | 32.7 | 21.9 | 65.9 | 66.2 | 33.0 | 1.10 | C2; S2 |
| | | | | | | S | G | 646 | 1,850 | 16.7 | 19.4 | 59.8 | 32.4 | 21.6 | 65.9 | 65.6 | 32.8 | 1.11 | |
| RANINOIDEA | | | | | | | | | | | | | | | | | | | |
| Raninidae | | | | | | | | | | | | | | | | | | | |
| (Lyreidinae) | *Lyreidus stenops* | KPM-NH140088 | ♀ | 13.3 | 1,060 | L | G | 15.1 | 20.7 | 3.36 | 2.03 | 9.69 | 21.0 | 3.11 | 9.93 | 10.3 | 30.3 | 1.53 | S2 |
| | | | | | | S | G | 14.3 | 12.2 | 2.50 | 2.26 | 9.48 | 23.9 | 3.02 | 9.60 | 9.99 | 30.2 | 1.34 | |
| (Ranininae) | *Ranina ranina* | KPM-NH102036 | ♂ | 10.6 | 1,520 | L | G | 9.45 | 41.9 | 3.39 | 2.07 | 10.6 | 19.6 | 1.79 | 10.7 | 10.8 | 16.6 | 0.864 | B2; S2 |
| | | | | | | S | G | 8.93 | 37.3 | 3.04 | 2.00 | 9.76 | 20.5 | 1.83 | 10.7 | 10.5 | 17.1 | 0.915 | |
| | *R. ranina* | KPM-NH186 | ♀ | 188 | 7,750 | L | G | 71.4 | — | — | 4.56 | 27.1 | 16.8 | 5.27 | 27.9 | 28.1 | 18.8 | 1.16 | B2; S2 |
| | | | | | | S | G | 57.9 | — | — | 4.69 | 26.0 | 18.1 | 4.46 | 28.5 | 28.1 | 15.7 | 0.95 | |
| EUBRACHYURA | | | | | | | | | | | | | | | | | | | |
| HETEROTREMATA | | | | | | | | | | | | | | | | | | | |
| CALAPPOIDEA | | | | | | | | | | | | | | | | | | | |
| Calappidae | *Calappa gallus* | KPM-NH103158 | ♂ | 16.3 | 1,770 | L | C | 41.2 | 97.6 | 7.83 | 6.90 | 13.5 | 51.2 | 6.12 | 14.9 | 15.0 | 40.7 | 0.887 | S4 |
| | | | | | | S | G | 28.6 | 91.5 | 6.78 | 3.83 | 13.0 | 29.6 | 4.42 | 14.2 | 14.1 | 31.2 | 1.15 | |
| | *Ca. hepatica* | KPM-NH103245 | ♂ | 17.1 | 2,390 | L | C | 42.6 | 120 | 6.81 | 7.01 | 15.0 | 46.6 | 5.67 | 16.7 | 16.6 | 34.0 | 0.809 | S4 |
| | | | | | | S | G | 24.7 | 120 | 6.02 | 3.56 | 12.6 | 28.1 | 3.91 | 13.8 | 13.7 | 28.4 | 1.10 | |
| | *Ca. japonica* | KPM-NH103159 | ♂ | 52.3 | 4,570 | L | C | 126 | 318 | 9.71 | 11.2 | 22.0 | 50.9 | 11.4 | 25.3 | 25.1 | 45.2 | 1.02 | S4 |
| | | | | | | S | G | 95.7 | 290 | 8.43 | 6.98 | 21.8 | 32.0 | 8.76 | 24.1 | 24.1 | 36.3 | 1.25 | |
| | *Ca. lophos* | KH33 | ♂ | 209 | 9,830 | L | C | 209 | 587 | 8.10 | 13.2 | 32.6 | 40.7 | 12.9 | 36.2 | 36.0 | 35.5 | 0.97 | S4 |
| | | | | | | S | G | 169 | 572 | 7.54 | 8.38 | 32.9 | 25.5 | 10.3 | 35.2 | 35.4 | 29.0 | 1.23 | |
| | *Ca. lophos* | KH34 | ♂ | 126 | 6,220 | L | C | 147 | 431 | 9.30 | 11.0 | 27.2 | 40.6 | 10.8 | 29.7 | 29.9 | 36.1 | 0.98 | S4 |
| | | | | | | S | G | 113 | 391 | 8.09 | 6.54 | 26.5 | 24.7 | 8.52 | 28.0 | 28.4 | 30.0 | 1.30 | |
| | *Ca. lophos* | KPM-NH103068 | ♂ | — | 8,240 | X | X | 127 | 430 | 6.75 | 7.57 | 28.7 | 26.4 | 8.83 | 30.2 | 30.6 | 28.9 | 1.17 | S4 |
| | *Ca. philargius* | KPM-NH103611 | ♂ | 23.7 | 2,160 | L | C | 53.5 | 135 | 8.74 | 7.23 | 15.8 | 45.9 | 6.78 | 17.8 | 17.6 | 38.1 | 0.937 | S4 |
| | | | | | | S | G | 36.1 | 128 | 7.58 | 4.09 | 14.6 | 28.1 | 4.96 | 16.2 | 16.0 | 30.7 | 1.21 | |
| | *Cycloes granulosa* | KPM-NH130805 | ♂ | 114 | 1,130 | L | C | 20.2 | — | — | 4.15 | 12.4 | 33.5 | 3.54 | 12.8 | 13.1 | 27.1 | 0.852 | V2 |
| | | | | | | S | G | 22.0 | — | — | 2.59 | 12.1 | 21.4 | 3.34 | 12.2 | 12.6 | 26.5 | 1.29 | |
| | *Mursia armata* | KPM-NH103119 | ♂ | 9.32 | 1,310 | L | C | 18.7 | 51.8 | 5.40 | 4.24 | 10.4 | 40.8 | 3.6 | 11.1 | 11.2 | 32.1 | 0.849 | V2 |
| | | | | | | S | G | 14.2 | 45.1 | 4.54 | 3.13 | 10.1 | 30.9 | 2.81 | 10.7 | 10.8 | 26.1 | 0.898 | |
| | *M. aspera* | KPM-NH103460 | ♂ | 7.60 | 898 | L | G | 15.9 | 69.2 | 9.47 | 2.02 | 10.6 | 19.1 | 3 | 11.3 | 11.3 | 26.5 | 1.49 | V2 |
| | | | | | | S | C | 20.1 | 46.7 | 7.44 | 4.08 | 11.4 | 35.9 | 3.54 | 12.1 | 12.2 | 29.0 | 0.868 | |
| | *M. curtispina* | KPM-NH103320 | ♂ | 24.3 | 2,640 | L | C | 46.8 | 110 | 5.94 | 6.07 | 15.1 | 40.2 | 6.21 | 16.6 | 16.7 | 37.2 | 1.02 | V2 |
| | | | | | | S | G | 30.8 | 117 | 5.61 | 3.89 | 15.3 | 25.5 | 4.03 | 16.5 | 16.4 | 24.4 | 1.04 | |
| | *M. trispinosa* | KPM-NH103198 | ♂ | 32.4 | 2,980 | L | C | 31.6 | 93.3 | 4.18 | 5.26 | 16.0 | 32.9 | 3.95 | 17.1 | 17.1 | 23.1 | 0.751 | V2 |
| | | | | | | S | G | 25.9 | 96.1 | 4.09 | 5.46 | 14.1 | 38.8 | 3.68 | 16.9 | 16.1 | 21.8 | 0.674 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Matutidae | *Ashtoret banksii* | KPM-NH103094 | ♂ | 12.9 | 2,050 | L | G | 20.7 | 63.7 | 4.12 | 3.97 | 12.4 | 32.0 | 3.33 | 12.9 | 13.1 | 25.4 | 0.838 | S4 |
| | | | | | | S | G | 21.0 | 36.0 | 2.79 | 4.40 | 12.1 | 36.4 | 3.48 | 12.7 | 12.9 | 27.1 | 0.791 | |
| | *A. miersii* | NSMT-Cr.10062 | ♂ | 7.17 | 1,040 | L | G | 10.7 | — | — | 2.32 | 8.35 | 27.8 | 2.57 | 8.87 | 8.95 | 28.7 | 1.11 | P1 |
| | | | | | | S | G | 9.54 | — | — | 2.41 | 8.19 | 29.4 | 2.33 | 9.22 | 9.02 | 25.3 | 0.968 | |
| | *Matuta lunaris* | KH80 | ♂ | 7.63 | 1,020 | L | G | 9.48 | — | — | 2.44 | 7.87 | 31.0 | 2.41 | 8.43 | 8.46 | 28.5 | 0.989 | P1 |
| | | | | | | S | G | 6.18 | — | — | 2.20 | 5.62 | 39.2 | 2.2 | 5.67 | 6.04 | 36.4 | 1.00 | |
| | *M. lunaris* | KPM-NH103244 | ♂ | 4.20 | 1,200 | S | G | 10.0 | 29.2 | 3.26 | 2.65 | 8.10 | 32.7 | 2.47 | 9.18 | 8.96 | 26.9 | 0.932 | P1 |
| | | | | | | L | G | 11.1 | 28.9 | 3.32 | 2.73 | 8.77 | 31.2 | 2.52 | 9.22 | 9.33 | 27.0 | 0.922 | |
| | *M. lunaris* | KPM-NH130813 | ♂ | 53.0 | 3,900 | L | G | 49.6 | — | — | 5.64 | 17.2 | 32.7 | 5.75 | 19.4 | 19.0 | 29.7 | 1.02 | P1 |
| | | | | | | S | G | 45.1 | — | — | 6.15 | 15.9 | 38.7 | 5.68 | 19.3 | 18.3 | 29.4 | 0.923 | |
| | *M. lunaris* | NSMT-Cr.3045 | ♂ | 40.7 | 3,840 | L | G | 48.2 | — | — | 5.80 | 17.0 | 34.0 | 5.66 | 19.9 | 19.2 | 28.5 | 0.976 | P1 |
| | | | | | | S | G | 46.2 | — | — | 5.72 | 15.6 | 36.8 | 5.93 | 19.1 | 18.0 | 31.1 | 1.04 | |
| | *M. lunaris* | NSMT-Cr.3052 | ♂ | 15.5 | 1,750 | L | G | 27.7 | — | — | 4.02 | 12.8 | 31.4 | 4.33 | 13.9 | 13.9 | 31.1 | 1.08 | P1 |
| | | | | | | S | G | 23.0 | — | — | 4.25 | 10.9 | 39.2 | 4.23 | 14.0 | 12.9 | 30.2 | 0.994 | |
| CANCROIDEA | | | | | | | | | | | | | | | | | | | |
| Cancridae | *Anatolikos japonicus* | KPM-NH105093 | ♂ | 83.2 | 5,910 | L | X | 117 | 382 | 8.44 | 10.8 | 25.8 | 41.9 | 9.11 | 26.4 | 27.5 | 33.1 | 0.845 | — |
| | | | | | | S | X | 116 | 347 | 7.83 | 11.1 | 25.4 | 43.7 | 9.09 | 27.0 | 27.5 | 33.0 | 0.819 | |
| | *A. japonicus* | NSMT-Cr.7612 | ♂ | 132 | 6,920 | L | X | 141 | — | — | 11.6 | 28.2 | 41.1 | 10 | 28.8 | 30.1 | 33.3 | 0.863 | — |
| | | | | | | S | X | 129 | — | — | 11.1 | 26.2 | 42.2 | 9.86 | 29.0 | 28.9 | 34.0 | 0.892 | |
| | *A. japonicus* | NSMT-Cr.8239 | ♂ | 112 | 6,120 | L | X | 122 | — | — | 11.4 | 26.1 | 43.6 | 9.34 | 27.7 | 28.2 | 33.1 | 0.821 | — |
| | | | | | | S | X | 110 | — | — | 11.5 | 24.4 | 46.9 | 9.02 | 26.0 | 26.5 | 34.0 | 0.787 | |
| CARPILIOIDEA | | | | | | | | | | | | | | | | | | | |
| Carpiliidae | *Carpilius convexus* | KPM-NH107704 | ♂ | 112 | 4,410 | L | C | 86.9 | 285 | 8.45 | 11.6 | 20.8 | 55.7 | 8.36 | 21.8 | 22.6 | 36.9 | 0.721 | L1; V2 |
| | | | | | | S | G | 69.3 | 201 | 6.14 | 7.10 | 19.9 | 35.7 | 6.97 | 20.6 | 21.3 | 32.8 | 0.982 | |
| DORIPPOIDEA | | | | | | | | | | | | | | | | | | | |
| Dorippidae | *Dorippe sinica* | KPM-NH103562 | ♂ | 6.50 | 824 | L | X | 14.8 | 31.1 | 5.56 | 1.81 | 11.3 | 16.0 | 2.62 | 11.4 | 11.6 | 22.5 | 1.45 | — |
| | | | | | | S | X | 14.4 | 30.5 | 5.45 | 1.62 | 11.5 | 14.1 | 2.5 | 11.7 | 11.9 | 21.1 | 1.54 | |
| | *Heikeopsis japonica* | KH49 | ♂ | 10.3 | 596 | L | X | 16.2 | 40.7 | 9.56 | 3.79 | 9.63 | 39.3 | 3.37 | 10.2 | 10.4 | 32.5 | 0.89 | — |
| | | | | | | S | X | 9.01 | 17.5 | 4.45 | 0.69 | 9.06 | 7.65 | 1.99 | 9.77 | 9.69 | 20.4 | 2.87 | |
| | *H. japonica* | KH50 | ♂ | 9.34 | 615 | L | X | 11.6 | 33.4 | 7.31 | 3.55 | 7.39 | 48.0 | 3.14 | 8.09 | 8.18 | 38.4 | 0.885 | — |
| | | | | | | S | X | 5.83 | 13.7 | 3.17 | 1.04 | 6.58 | 15.8 | 1.77 | 6.66 | 6.85 | 25.8 | 1.70 | |
| | *H. japonica* | KH51 | ♂ | 9.80 | 600 | L | X | 12.9 | 39.6 | 8.75 | 3.47 | 8.30 | 41.8 | 3.11 | 8.99 | 9.07 | 34.3 | 0.896 | — |
| | | | | | | S | X | 7.35 | 12.7 | 3.34 | 0.86 | 8.16 | 10.5 | 1.8 | 8.43 | 8.51 | 21.2 | 2.09 | |
| | *H. japonica* | KH52 | ♂ | 10.9 | 610 | L | X | 13.0 | 31.4 | 7.28 | 3.33 | 8.23 | 40.5 | 3.15 | 8.58 | 8.90 | 35.4 | 0.946 | — |
| | | | | | | S | X | 7.02 | 19.3 | 4.32 | 0.58 | 8.30 | 6.99 | 1.69 | 8.44 | 8.55 | 19.8 | 2.91 | |
| | *H. japonica* | KH53 | ♀ | 23.4 | 1,240 | L | X | 18.1 | — | — | 1.33 | 14.1 | 9.43 | 2.58 | 14.2 | 14.4 | 17.9 | 1.95 | — |
| | | | | | | S | X | 15.6 | 48.3 | 5.15 | 1.57 | 13.2 | 11.9 | 2.36 | 13.8 | 13.8 | 17.1 | 1.50 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ERIPHIOIDEA | | | | | | | | | | | | | | | | | | | |
| Hypothalassiidae | *Hypothalassia armata* | KPM-NH106818 | ♀ | 568 | 14,400 | L | X | 410 | 876 | 8.94 | 17.1 | 49.3 | 34.7 | 16.6 | 51.7 | 52.9 | 31.5 | 0.971 | — |
| | | | | | | S | X | 285 | 615 | 6.26 | 11.7 | 43.7 | 26.7 | 13 | 45.5 | 46.3 | 28.1 | 1.12 | |
| Menippidae | *Pseudocarcinus gigas* | NSMT-Cr.15903 | ♂ | 3,070 | 45,800 | L | C | 2380 | — | — | 35.9 | 127 | 28.2 | 37.3 | 138 | 137 | 27.1 | 1.04 | C5 |
| | | | | | | S | G | 1160 | — | — | 22.3 | 80.5 | 27.7 | 28.8 | 85.0 | 86.9 | 33.1 | 1.29 | |
| Oziidae | *Baptozius vinosus* | KH66 | ♂ | 119 | 3,530 | L | C | 167 | 436 | 17.1 | 10.8 | 31.8 | 33.9 | 10.5 | 35.2 | 34.8 | 29.8 | 0.971 | V2 |
| | | | | | | S | G | 102 | 276 | 10.7 | 5.00 | 26.2 | 19.1 | 7.79 | 27.2 | 27.7 | 28.1 | 1.56 | |
| | *B. vinosus* | KH67 | ♂ | 150 | 4,070 | L | C | 231 | 317 | 13.5 | 12.6 | 38.3 | 32.8 | 12.1 | 39.8 | 40.7 | 29.6 | 0.959 | V2 |
| | | | | | | S | G | 124 | 317 | 10.8 | 6.20 | 30.5 | 20.3 | 8.12 | 32.2 | 32.4 | 25.1 | 1.31 | |
| GONEPLACOIDEA | | | | | | | | | | | | | | | | | | | |
| Goneplacidae | *Carcinoplax longimana* | TMNH unnumbered | ♀ | 68.0 | 2,530 | L | X | — | — | — | 6.32 | 25.0 | 25.3 | 7.35 | 26.0 | 26.5 | 27.8 | 1.16 | — |
| | | | | | | S | X | — | — | — | 5.00 | 24.1 | 20.7 | 6.17 | 24.9 | 25.3 | 24.4 | 1.23 | |
| LEUCOSIOIDEA | | | | | | | | | | | | | | | | | | | |
| Leucosiidae | *Arcania heptacantha* | KH59 | ♀ | 2.85 | 672 | L | X | 7.04 | 11.1 | 2.70 | 0.84 | 11.3 | 7.44 | 1.25 | 13.2 | 12.9 | 9.45 | 1.49 | — |
| | | | | | | S | X | 7.95 | 8.88 | 2.51 | 0.74 | 12.8 | 5.75 | 1.24 | 13.1 | 13.1 | 9.48 | 1.68 | |
| | *A. heptacantha* | KH60 | ♀ | 3.22 | 747 | L | X | 6.95 | 26.5 | 4.48 | 0.97 | 12.4 | 7.80 | 1.12 | 12.5 | 12.5 | 8.94 | 1.16 | — |
| | | | | | | S | X | 6.76 | 25.1 | 4.27 | 0.94 | 12.1 | 7.76 | 1.12 | 12.7 | 12.7 | 8.80 | 1.20 | |
| | *Myra fugax* | KH54 | ♂ | 12.6 | 1,150 | L | P | 19.1 | 94.9 | 9.92 | 1.76 | 15.7 | 11.2 | 2.43 | 15.7 | 15.9 | 15.3 | 1.38 | C4 |
| | | | | | | S | P | 18.6 | 91.7 | 9.61 | 1.43 | 15.4 | 9.31 | 2.42 | 15.4 | 15.6 | 15.5 | 1.69 | |
| | *M. fugax* | KH55 | ♂ | 16.0 | 1,280 | L | P | 26.3 | 114 | 10.9 | 1.77 | 18.4 | 9.61 | 2.86 | 18.7 | 18.8 | 15.2 | 1.62 | C4 |
| | | | | | | S | P | 24.1 | 111 | 10.5 | 1.56 | 18.1 | 8.61 | 2.67 | 18.6 | 18.6 | 14.3 | 1.72 | |
| | *M. fugax* | KH56 | ♂ | 13.7 | 1,110 | L | P | 22.9 | 97.5 | 10.8 | 1.58 | 17.3 | 9.11 | 2.65 | 17.3 | 17.5 | 15.1 | 1.68 | C4 |
| | | | | | | S | P | 19.2 | 47.5 | 5.99 | 1.43 | 15.4 | 9.29 | 2.5 | 15.8 | 15.9 | 15.7 | 1.75 | |
| | *M. fugax* | KH57 | ♂ | 7.18 | 811 | L | P | 11.5 | 43.2 | 6.75 | 1.50 | 12.7 | 11.9 | 1.82 | 12.8 | 12.9 | 14.1 | 1.21 | C4 |
| | | | | | | S | P | 7.96 | 33.7 | 5.14 | 1.55 | 10.4 | 14.9 | 1.53 | 10.5 | 10.5 | 14.5 | 0.986 | |
| | *M. fugax* | KH58 | ♂ | 15.9 | 1,290 | L | P | 23.5 | 113 | 10.5 | 1.54 | 16.7 | 9.22 | 2.81 | 16.7 | 17.0 | 16.6 | 1.82 | C4 |
| | | | | | | S | P | 21.4 | 110 | 10.2 | 1.77 | 16.3 | 10.8 | 2.62 | 16.4 | 16.6 | 15.8 | 1.48 | |
| | *M. fugax* | KPM-NH103565 | ♂ | 12.4 | 1,160 | L | P | 22.2 | 86.3 | 9.39 | 1.87 | 16.4 | 11.4 | 2.71 | 16.8 | 16.9 | 16.0 | 1.45 | C4 |
| | | | | | | S | P | 22.7 | 82.4 | 9.10 | 1.97 | 16.4 | 12.0 | 2.76 | 16.5 | 16.7 | 16.5 | 1.40 | |
| | *Persephona aquilonaris* | KPM-NH103254 | ♀ | 2.15 | 1,760 | L | X | 23.0 | 77.2 | 5.69 | 2.93 | 16.3 | 17.9 | 2.81 | 16.6 | 16.8 | 16.8 | 0.959 | — |
| | | | | | | S | X | 24.3 | 71.4 | 5.43 | 3.20 | 16.4 | 19.5 | 2.95 | 17.2 | 17.2 | 17.1 | 0.921 | |
| | *Philyra pisum* | KH21 | ♂ | 3.66 | 374 | L | P | 5.72 | 21.1 | 7.18 | 2.11 | 8.24 | 25.7 | 1.39 | 8.24 | 8.35 | 16.6 | 0.658 | K3 |
| | | | | | | S | P | 5.56 | 19.9 | 6.81 | 2.12 | 7.83 | 27.1 | 1.42 | 7.89 | 7.99 | 17.8 | 0.67 | |
| MAJOIDEA | | | | | | | | | | | | | | | | | | | |
| Epialtidae | *Goniopugettia sagamiensis* | TMNH unnumbered | ♂ | — | 2,820 | L | P | — | — | — | 6.95 | 22.9 | 30.3 | 6.34 | 23.3 | 23.9 | 26.5 | 0.912 | D2 |
| | | | | | | S | P | — | — | — | 6.80 | 23.4 | 29.1 | 6.27 | 23.9 | 24.5 | 25.6 | 0.922 | |
| Inachidae | *Macrocheira kaempferi* | KPM-NH104714 | ♀ | 182 | 12,600 | L | P | 69.2 | 317 | 3.05 | 4.61 | 25.6 | 18.1 | 5.42 | 26.4 | 26.6 | 20.4 | 1.18 | U1 |
| | | | | | | S | P | 68.4 | 309 | 2.98 | 5.04 | 25.0 | 20.1 | 5.46 | 25.9 | 26.1 | 20.9 | 1.08 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Majidae | *Maja spinigera* | KPM-NH104423 | ♂ | 94.9 | 8,900 | L | X | 91.0 | 269 | 4.04 | 7.21 | 25.4 | 28.4 | 7.17 | 26.7 | 27.0 | 26.6 | 0.994 | — |
| | | | | | | S | X | 91.3 | 267 | 4.03 | 7.27 | 24.8 | 29.3 | 7.37 | 26.9 | 26.8 | 27.4 | 1.01 | — |
| Oregoniidae | *Chionoecetes japonicus* | KPM-NH1024172 | ♀ | 231 | 8,560 | L | G | 106 | 290 | 4.62 | 2.83 | 32.3 | 8.78 | 6.55 | 32.5 | 33.1 | 19.8 | 2.31 | W2 |
| | | | | | | S | G | 102 | 185 | 3.36 | 4.04 | 31.7 | 12.8 | 6.44 | 32.0 | 32.5 | 19.8 | 1.59 | |
| | *C. opilio* | KH75 | — | — | — | X | G | 434 | — | — | 8.95 | 56.5 | 15.8 | 15.4 | 58.6 | 59.5 | 25.8 | 1.72 | W2 |
| | *C. opilio* | KH76 | — | — | — | X | G | 516 | — | — | 9.98 | 60.3 | 16.5 | 17.1 | 62.4 | 63.6 | 26.9 | 1.71 | W2 |
| | *C. opilio* | KH77 | — | — | — | X | G | 362 | — | — | 9.17 | 49.2 | 18.6 | 14.7 | 50.6 | 51.9 | 28.3 | 1.60 | W2 |
| | *C. opilio* | KH78 | — | — | — | X | G | 373 | 780 | — | 8.60 | 49.3 | 17.5 | 15.1 | 50.4 | 52.0 | 29.1 | 1.76 | W2 |
| | *C. opilio* | KH79 | — | — | — | X | G | 456 | — | — | 9.91 | 57.2 | 17.3 | 15.9 | 58.9 | 60.2 | 26.5 | 1.61 | W2 |
| | *C. opilio* | KPM-NH104454 | ♀ | 106 | 7,560 | L | G | 99.8 | 237 | 4.45 | 3.91 | 30.4 | 12.9 | 6.56 | 31.9 | 32.0 | 20.5 | 1.68 | W2 |
| | | | | | | S | G | 102 | 204 | 4.05 | 3.26 | 30.2 | 10.8 | 6.79 | 31.2 | 31.5 | 21.6 | 2.08 | |
| PARTHENOPOIDEA | | | | | | | | | | | | | | | | | | | |
| Parthenopidae | | | | | | | | | | | | | | | | | | | |
| (Daldolphinae) | *Daldorfia horrida* | KPM-NH104909 | ♂ | 340 | 11,600 | X | C | 646 | — | — | 26.5 | 56.3 | 47.2 | 23 | 58.0 | 61.1 | 37.6 | 0.866 | H3; V2 |
| | | | | | | X | G | — | — | — | — | — | — | — | — | — | — | — | |
| | *D. investigatoris* | KPM-NH104896 | ♂ | 5.63 | 1,210 | L | X | 48.4 | 123 | 14.2 | 7.77 | 14.1 | 55.0 | 6.85 | 14.3 | 15.7 | 43.6 | 0.881 | H3; V2 |
| (Parthenopinae) | *Enoplolambrus validus* | KH48 | ♂ | 22.7 | 1,130 | L | X | 43.3 | 138 | 16.1 | 4.66 | 14.7 | 31.7 | 5.89 | 15.9 | 16.1 | 36.5 | 1.26 | K4 |
| | | | | | | S | X | 44.2 | 135 | 15.9 | 3.54 | 14.9 | 23.7 | 5.92 | 15.5 | 16.2 | 36.6 | 1.67 | |
| | *E. validus* | KPM-NH104431 | ♀ | 89.6 | 4,690 | L | C | 215 | 430 | 13.7 | 14.4 | 32.6 | 44.2 | 13.2 | 35.6 | 35.9 | 36.6 | 0.913 | K4 |
| | | | | | | S | G | 139 | 410 | 11.7 | 10.8 | 29.0 | 37.3 | 9.62 | 29.9 | 30.9 | 31.2 | 0.89 | |
| | *E. laciniatus* | NSMT-Cr.13118 | ♀ | 9.75 | 732 | L | X | 33.3 | — | — | 5.54 | 12.2 | 45.2 | 5.44 | 12.4 | 13.4 | 40.5 | 0.982 | — |
| | | | | | | S | X | 17.8 | — | — | 3.74 | 10.6 | 35.3 | 3.36 | 10.6 | 11.1 | 30.2 | 0.899 | |
| PORTUNOIDEA | | | | | | | | | | | | | | | | | | | |
| Geryonidae | *Chaceon granulatus* | KPM-NH106820 | ♀ | 637 | 25,000 | L | X | 512 | 1,080 | 6.36 | 13.4 | 55.4 | 24.3 | 18.5 | 58.0 | 59.3 | 31.2 | 1.38 | — |
| | | | | | | S | X | 470 | 1,070 | 6.18 | 11.2 | 52.4 | 21.5 | 18 | 54.6 | 56.1 | 32.0 | 1.60 | |
| Portunidae | | | | | | | | | | | | | | | | | | | |
| (Carcininae) | *Carcinus aestuarii* | TMNH unnumbered | ♂ | 44.0 | 2,550 | L | C | — | — | — | 6.78 | 17.9 | 37.9 | 6.77 | 18.8 | 19.4 | 34.9 | 0.999 | E1; E2 |
| | | | | | | S | G | — | — | — | 4.48 | 17.1 | 26.2 | 5.41 | 18.3 | 18.4 | 29.4 | 1.21 | |
| (Carupinae) | *Carupa tenuipes* | NSMT-Cr.3405 | ♂ | 15.0 | 1,000 | L | X | 45.9 | — | — | 5.93 | 15.0 | 39.5 | 6.12 | 16.6 | 16.6 | 36.9 | 1.03 | — |
| | | | | | | S | X | 38.7 | — | — | 4.55 | 15.3 | 29.7 | 5.06 | 15.9 | 16.3 | 31.0 | 1.11 | |
| (Polybiinae) | *Ovalipes punctatus* | KPM-NH106360 | ♀ | 10.9 | 1,870 | L | C | 50.1 | 113 | 8.68 | 3.90 | 18.5 | 21.1 | 5.43 | 19.6 | 19.7 | 27.5 | 1.39 | L1; P3 |
| | | | | | | S | G | 44.7 | 94.7 | 7.44 | 3.29 | 18.0 | 18.3 | 4.97 | 18.8 | 19.0 | 26.1 | 1.51 | |
| (Portuninae) | *Lupella forceps* | NSMT-Cr.7144 | ♂ | 15.2 | 2,120 | L | X | 84.6 | — | — | 2.41 | 61.5 | 3.92 | 2.75 | 62.2 | 62.2 | 4.42 | 1.14 | — |
| | | | | | | S | X | 82.4 | — | — | 2.34 | 61.0 | 3.83 | 2.7 | 61.9 | 61.9 | 4.36 | 1.15 | |
| | *L. forceps* | NSMT-Cr.7641 | ♂ | 12.6 | 1,950 | X | X | 44.1 | — | — | 2.39 | 32.3 | 7.40 | 2.73 | 43.3 | 42.2 | 6.30 | 1.14 | — |
| | *Portunus (Portunus) pelagicus* | KH23 | ♂ | 22.5 | 4,240 | L | G | 101 | 236 | 7.94 | 6.91 | 27.6 | 25.1 | 7.31 | 28.0 | 28.7 | 25.5 | 1.06 | J1; W3 |
| | | | | | | S | G | 88.7 | 226 | 7.42 | 4.76 | 28.7 | 16.6 | 6.19 | 29.0 | 29.5 | 21.0 | 1.30 | |
| | *P. (P.) pelagicus* | KH24 | ♂ | 52.6 | 8,320 | L | G | 294 | 730 | 12.3 | 8.70 | 48.4 | 18.0 | 12.2 | 48.6 | 50.0 | 24.3 | 1.40 | J1; W3 |
| | | | | | | S | G | 268 | 527 | 9.56 | 6.74 | 50.5 | 13.4 | 10.6 | 50.8 | 51.8 | 20.5 | 1.57 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Portuninae [cont.]) | *Portunus (Portunus) pelagicus* | KH25 | ♀ | — | 4,700 | L | G | — | 218 | — | 5.17 | — | — | 6.41 | — | — | — | 1.24 | J1; W3 |
| | | | | | | S | G | 95.9 | 194 | 6.18 | 6.85 | 26.3 | 26.0 | 7.28 | 26.6 | 27.4 | 26.5 | 1.06 | |
| | *P. (P.) pelagicus* | KH26 | ♂ | — | 1,080 | X | G | 15.8 | — | — | 2.07 | 9.74 | 21.3 | 3.24 | 9.74 | 10.3 | 31.6 | 1.56 | J1; M1 |
| | *P. (P.) sanguinolentus* | KPM-NH106908 | ♀ | 62.1 | 6,590 | L | G | 105 | 278 | 5.81 | 6.26 | 24.6 | 25.4 | 8.51 | 26.1 | 26.6 | 32.0 | 1.36 | J1; M1 |
| | | | | | | S | G | 80.3 | 244 | 4.92 | 4.61 | 24.6 | 18.7 | 6.53 | 26.3 | 26.3 | 24.8 | 1.42 | |
| | *P. (P.) trituberculatus* | KH35 | ♂ | 62.8 | 5,570 | L | G | 76.0 | 196 | 4.88 | 6.12 | 25.8 | 23.7 | 5.9 | 26.6 | 26.9 | 21.9 | 0.965 | J1; M1 |
| | | | | | | S | G | 41.1 | 87.4 | 2.31 | 3.05 | 18.6 | 16.4 | 4.42 | 18.6 | 19.1 | 23.1 | 1.45 | |
| | *P. (P.) trituberculatus* | KH36 | ♂ | 56.9 | 4,910 | L | G | 77.6 | 200 | 5.65 | 5.79 | 25.3 | 22.9 | 6.14 | 26.3 | 26.5 | 23.2 | 1.06 | J1; M1 |
| | | | | | | S | G | 76.2 | 119 | 3.96 | 3.86 | 25.7 | 15.0 | 5.93 | 26.3 | 26.7 | 22.2 | 1.54 | |
| | *P. (P.) trituberculatus* | KH37 | ♂ | 62.6 | 5,310 | L | G | 92.1 | 193 | 5.37 | 6.45 | 27.2 | 23.7 | 6.78 | 27.7 | 28.3 | 24.0 | 1.05 | J1; M1 |
| | | | | | | S | G | 83.6 | 160 | 4.59 | 4.95 | 25.8 | 19.2 | 6.48 | 26.3 | 26.8 | 24.1 | 1.31 | |
| | *P. (P.) trituberculatus* | KH38 | ♂ | 102 | 7,100 | L | G | 113 | 275 | 5.48 | 6.80 | 32.6 | 20.9 | 6.97 | 32.7 | 33.4 | 20.9 | 1.02 | J1; M1 |
| | | | | | | S | G | 120 | 165 | 4.02 | 4.71 | 32.5 | 14.5 | 7.38 | 33.3 | 33.8 | 21.9 | 1.57 | |
| | *P. (P.) trituberculatus* | KH39 | ♂ | 84.4 | 7,740 | L | G | 125 | 171 | 3.83 | 7.06 | 32.3 | 21.9 | 7.75 | 32.9 | 33.5 | 23.1 | 1.10 | J1; M1 |
| | | | | | | S | G | 127 | 169 | 3.83 | 4.83 | 33.2 | 14.5 | 7.64 | 33.7 | 34.4 | 22.2 | 1.58 | |
| | *P. (P.) trituberculatus* | KH40 | ♂ | 765 | 6,720 | X | G | 102 | 229 | 4.93 | 4.96 | 29.2 | 17.0 | 7.01 | 29.9 | 30.4 | 23.1 | 1.41 | J1; M1 |
| | *P. (P.) trituberculatus* | KH41 | ♂ | 45.8 | 7,220 | X | G | 124 | 311 | 6.03 | 7.31 | 31.0 | 23.6 | 7.99 | 31.1 | 32.0 | 24.9 | 1.09 | J1; M1 |
| | *P. (P.) trituberculatus* | KH42 | ♂ | 65.1 | 6,090 | L | G | 85.4 | 195 | 4.60 | 5.38 | 26.2 | 20.6 | 6.53 | 26.6 | 27.2 | 24.0 | 1.21 | J1; M1 |
| | | | | | | S | G | 84.0 | 180 | 4.34 | 4.30 | 26.7 | 16.1 | 6.29 | 27.0 | 27.6 | 22.8 | 1.46 | |
| | *Scylla paramamosain* | NSMT-Cr.19947 | ♀ | 720 | 19,400 | L | C | 370 | — | — | 15.5 | 47.2 | 32.8 | 15.7 | 48.1 | 50.0 | 31.3 | 1.01 | L1 |
| | | | | | | S | G | 321 | — | — | 9.51 | 45.6 | 20.9 | 14.1 | 48.2 | 48.8 | 28.9 | 1.48 | L1 |
| | *S. serrata* | KH65 | ♂ | 184 | 7,700 | S | C | 156 | 386 | 7.04 | 8.31 | 30.0 | 27.7 | 10.4 | 32.1 | 32.4 | 32.1 | 1.25 | |
| | *S. serrata* | KH83 | ♂ | 1,900 | 22,200 | L | X | 760 | 2,400 | 14.3 | 18.4 | 63.5 | 29.0 | 23.9 | 67.5 | 69.0 | 34.7 | 1.30 | L1 |
| | | | | | | S | X | 1060 | 1,500 | 11.6 | 24.8 | 72.5 | 34.2 | 29.2 | 77.5 | 79.3 | 36.8 | 1.18 | |
| | *S. serrata* | KPM-NH107270 | ♂ | 581 | 16,600 | L | C | 631 | 1,500 | 12.9 | 21.7 | 57.1 | 37.9 | 22.1 | 61.5 | 62.4 | 35.4 | 1.02 | L1 |
| | | | | | | S | G | 567 | 1,370 | 11.7 | 18.1 | 58.5 | 31.0 | 19.4 | 61.1 | 62.5 | 31.0 | 1.07 | |
| | *S. serrata* | KPM-NH98 | ♂ | 573 | 15,400 | L | C | 613 | — | — | 18.2 | 60.5 | 30.2 | 20.3 | 65.0 | 65.4 | 31.0 | 1.11 | L1 |
| | | | | | | S | G | 435 | — | — | 9.73 | 51.6 | 18.9 | 16.9 | 55.8 | 55.9 | 30.2 | 1.74 | |
| | *S. serrata* | NSMT-Cr.14835 | ♂ | 593 | 15,500 | L | C | 660 | — | — | 18.5 | 56.2 | 33.0 | 23.5 | 59.4 | 61.5 | 38.2 | 1.27 | L1 |
| | | | | | | S | G | 600 | — | — | 16.8 | 55.5 | 30.3 | 21.6 | 58.5 | 60.3 | 35.9 | 1.29 | |
| | *S. serrata* | NSMT-Cr.16848 | ♂ | 650 | 16,000 | L | C | 553 | — | — | 21.5 | 52.8 | 40.7 | 20.9 | 55.3 | 57.4 | 36.5 | 0.973 | L1 |
| | | | | | | S | G | 520 | — | — | 16.6 | 52.6 | 31.5 | 19.8 | 57.8 | 57.8 | 34.2 | 1.19 | |
| (Thalamitinae) | *Charybdis japonica* | KH43 | ♂ | 79.3 | 3,760 | L | G | 115 | 262 | 10.0 | 7.18 | 25.5 | 28.2 | 9.05 | 27.5 | 27.7 | 32.6 | 1.26 | J1 |
| | | | | | | S | G | 108 | 238 | 9.20 | 5.28 | 28.2 | 18.7 | 7.65 | 29.6 | 29.9 | 25.6 | 1.45 | |
| | *Ch. japonica* | KH44 | ♂ | 74.1 | 4,130 | L | G | 130 | 119 | 6.01 | 5.48 | 30.6 | 17.9 | 8.48 | 31.5 | 32.2 | 26.4 | 1.55 | J1 |
| | | | | | | S | G | 92.8 | 101 | 4.68 | 4.40 | 25.6 | 17.2 | 7.25 | 27.1 | 27.3 | 26.6 | 1.65 | |
| | *Ch. japonica* | KH45 | ♀ | 33.2 | 2,170 | L | G | 47.7 | 101 | 6.86 | 5.16 | 18.3 | 28.2 | 5.21 | 18.4 | 19.1 | 27.3 | 1.01 | J1 |
| | | | | | | S | G | 40.8 | 95.7 | 6.28 | 2.63 | 17.2 | 15.3 | 4.75 | 18.3 | 18.4 | 25.9 | 1.8 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Thalamitinae [cont.]) *Charybdis japonica* | | KH46 | ♀ | 82.8 | 4,920 | X | G | 139 | 247 | 7.86 | 7.83 | 29.9 | 26.2 | 9.31 | 30.8 | 31.7 | 29.4 | 1.19 | J1 |
| | | | | | | X | G | 44.6 | — | — | — | — | — | — | — | — | — | — | |
| | *C. japonica* | KH47 | ♀ | 40.2 | — | X | G | 62.9 | 137 | — | 3.93 | 21.4 | 18.4 | 5.88 | 22.2 | 22.6 | 26.1 | 1.50 | J1 |
| | | | | | | X | G | — | — | — | — | — | — | — | — | — | — | — | |
| | *C. japonica* | KH61 | ♂ | 33.9 | 813 | L | G | 16.2 | 52.6 | 8.47 | 3.37 | 11.5 | 29.2 | 2.81 | 11.9 | 12.1 | 23.3 | 0.833 | J1 |
| | | | | | | S | G | 14.8 | 47.1 | 7.62 | 2.61 | 11.3 | 23.1 | 2.62 | 11.5 | 11.7 | 22.4 | 1.00 | |
| | *C. japonica* | KH62 | ♀ | 24.5 | 2,900 | X | G | 41.2 | 135 | 6.06 | 5.34 | 17.2 | 31.1 | 4.8 | 17.7 | 18.1 | 26.6 | 0.898 | J1 |
| | | | | | | X | G | — | — | — | — | — | — | — | — | — | — | — | |
| | *C. japonica* | KH63 | ♀ | 36.7 | 2,320 | L | G | 70.4 | 156 | 9.74 | 6.87 | 19.8 | 34.6 | 7.1 | 20.9 | 21.4 | 33.2 | 1.03 | J1 |
| | | | | | | S | G | 54.7 | 138 | 8.30 | 4.18 | 19.3 | 21.6 | 5.66 | 19.7 | 20.3 | 27.9 | 1.35 | |
| | *C. japonica* | KH64 | ♀ | 14.9 | 1,050 | L | G | 23.9 | 59.9 | 8.00 | 2.74 | 13.0 | 21.2 | 3.69 | 13.7 | 13.8 | 26.8 | 1.34 | J1 |
| | | | | | | S | G | 23.5 | 34.2 | 5.51 | 4.38 | 12.7 | 34.4 | 3.7 | 13.3 | 13.5 | 27.5 | 0.845 | |
| | *C. japonica* | KPM-NH107793 | ♂ | 13.5 | 5,140 | L | G | 250 | 496 | 14.5 | 11.5 | 36.2 | 31.7 | 13.8 | 41.5 | 40.5 | 33.2 | 1.20 | J1 |
| | | | | | | S | G | 250 | 481 | 14.2 | 9.00 | 39.8 | 22.6 | 12.6 | 42.3 | 42.7 | 29.5 | 1.40 | |
| | *Thalamita crenata* | KPM-NH539 | ♀ | 34.3 | 2,460 | L | G | 67.2 | 158 | 9.17 | 5.01 | 22.2 | 22.6 | 6.05 | 23.0 | 23.4 | 25.9 | 1.21 | C1 |
| | | | | | | S | G | 44.3 | 98.3 | 5.80 | 3.95 | 18.6 | 21.2 | 4.77 | 19.3 | 19.6 | 24.4 | 1.21 | |
| POTAMOIDEA | | | | | | | | | | | | | | | | | | | |
| Potamidae | *Geothelphusa dehaani* | KPM-NH106222 | ♂ | 5.61 | 503 | L | G | 33.8 | 83.9 | 23.4 | 4.05 | 14.3 | 28.3 | 4.72 | 15.6 | 15.6 | 30.3 | 1.16 | K2 |
| | | | | | | S | G | 12.8 | 29.3 | 8.35 | 2.58 | 8.90 | 29.0 | 2.87 | 9.61 | 9.63 | 29.8 | 1.11 | |
| | *G. dehaani* | TMNH unnumbered | ♂ | 7.00 | 540 | L | G | — | — | — | 4.02 | 15.1 | 26.6 | 4.78 | 15.6 | 16.0 | 29.8 | 1.19 | K2 |
| | | | | | | S | G | — | — | — | 2.07 | 7.80 | 26.5 | 2.39 | 8.82 | 8.62 | 27.1 | 1.15 | |
| XANTHOIDEA | | | | | | | | | | | | | | | | | | | |
| Xanthidae | *Atergatis floridus* | KPM-NH106520 | ♂ | 27.9 | 1,960 | L | C | 44.5 | 134 | 9.13 | 5.85 | 15.6 | 37.6 | 5.71 | 16.4 | 16.9 | 33.9 | 0.975 | M4 |
| | | | | | | S | G | 22.7 | 61.4 | 4.29 | 4.15 | 11.5 | 36.1 | 3.95 | 12.5 | 12.5 | 31.6 | 0.952 | |
| | *A. reticulatus* | KH28 | ♂ | — | 2,120 | X | X | 44.7 | 142 | 8.80 | 5.99 | 15.2 | 39.5 | 5.89 | 15.9 | 16.5 | 35.8 | 0.983 | M4 |
| | *A. reticulatus* | KH29 | ♀ | — | 2,540 | X | X | 47.5 | 143 | 7.48 | 5.90 | 15.8 | 37.4 | 6.03 | 16.6 | 17.1 | 35.3 | 1.02 | M4 |
| | *A. subdentatus* | KH31 | ♂ | 61.5 | 4,240 | L | C | 105 | 268 | 8.80 | 8.01 | 25.6 | 31.2 | 8.2 | 26.4 | 27.2 | 30.1 | 1.02 | M4 |
| | | | | | | S | G | 103 | 261 | 8.60 | 9.57 | 25.1 | 38.1 | 8.22 | 26.1 | 26.8 | 30.7 | 0.859 | |
| | *A. subdentatus* | KPM-NH106619 | ♂ | 56.6 | 4,220 | L | C | 114 | 258 | 8.83 | 8.99 | 26.0 | 34.6 | 8.78 | 26.6 | 27.7 | 31.8 | 0.977 | M4 |
| | | | | | | S | G | 103 | 254 | 8.47 | 8.96 | 25.6 | 35.1 | 8.07 | 26.5 | 27.2 | 29.7 | 0.901 | |
| THORACOTREMATA | | | | | | | | | | | | | | | | | | | |
| GRAPSOIDEA | | | | | | | | | | | | | | | | | | | |
| Gecarcinidae | *Cardisoma carnifex* | KH68 | ♂ | 163 | 4,170 | L | P | 198 | 497 | 16.7 | 9.68 | 38.9 | 24.9 | 10.2 | 40.1 | 40.8 | 24.9 | 1.05 | M2 |
| | | | | | | S | P | 91.8 | 210 | 7.23 | 5.16 | 27.2 | 19.0 | 6.76 | 28.4 | 28.6 | 23.6 | 1.31 | |
| | *C. carnifex* | KH69 | ♂ | 131 | 3,660 | L | P | 195 | 322 | 14.1 | 9.98 | 37.7 | 26.5 | 10.4 | 38.9 | 39.7 | 26.1 | 1.04 | M2 |
| | | | | | | S | P | 77.8 | 226 | 8.30 | 5.41 | 24.9 | 21.7 | 6.24 | 25.6 | 26.0 | 24.0 | 1.15 | |
| | *C. carnifex* | KPM-NH0161668 | ♂ | — | 5,260 | L | P | 289 | 565 | 16.2 | 14.1 | 46.0 | 30.6 | 12.6 | 49.0 | 49.1 | 25.6 | 0.892 | M2 |
| | | | | | | S | P | 137 | 335 | 8.96 | 7.31 | 31.8 | 23.0 | 7.94 | 33.8 | 33.8 | 23.5 | 1.09 | |
| | *C. carnifex* | KPM-NH106683 | ♂ | 116 | 4,360 | L | P | 213 | 508 | 16.5 | 9.04 | 41.4 | 21.8 | 10.3 | 44.8 | 44.5 | 22.9 | 1.14 | M2 |
| | | | | | | S | P | 95.9 | 246 | 7.85 | 5.46 | 29.0 | 18.8 | 6.61 | 30.8 | 30.8 | 21.5 | 1.21 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Gecarcinidae (cont.) | *Discoplax hirtipes* | NSMT-Cr.21715 | ♂ | 69.9 | 2,590 | L | P | 102 | — | — | 7.59 | 27.0 | 28.1 | 7.54 | 27.5 | 28.2 | 26.7 | 0.994 | N1 |
| | | | | | | S | P | 93.5 | — | — | 6.21 | 24.2 | 25.7 | 7.73 | 26.1 | 26.2 | 29.6 | 1.24 | |
| | *D. longipes* | NSMT-Cr.14238 | ♂ | 48.6 | 1,920 | L | P | 37.9 | — | — | 4.59 | 16.3 | 28.2 | 4.66 | 17.0 | 17.2 | 27.1 | 1.02 | N1 |
| | | | | | | S | P | 25.1 | — | — | 3.26 | 14.0 | 23.2 | 3.57 | 14.4 | 14.7 | 24.3 | 1.10 | |
| | *Epigrapsus notatus* | NSMT-Cr.13151 | ♂ | 9.98 | 648 | L | P | 30.2 | — | — | 3.78 | 13.7 | 27.6 | 4.41 | 14.8 | 14.8 | 29.7 | 1.17 | L2 |
| | | | | | | S | P | 28.2 | — | — | 3.99 | 13.3 | 29.9 | 4.23 | 14.0 | 14.2 | 29.7 | 1.06 | |
| Grapsidae | *Pachygrapsus crassipes* | KH27 | — | — | — | X | G | 56.7 | 162 | — | 6.18 | 18.8 | 32.8 | 6.02 | 20.6 | 20.5 | 29.2 | 0.974 | B3 |
| Plagusiidae | *Plagusia dentipes* | NSMT-Cr.14128 | ♀ | 39.9 | 1,900 | L | P | 16.4 | — | — | 2.97 | 10.7 | 27.8 | 3.06 | 10.9 | 11.2 | 27.3 | 1.03 | S1 |
| | | | | | | S | P | 16.2 | — | — | 3.03 | 10.5 | 28.9 | 3.09 | 11.1 | 11.2 | 27.6 | 1.02 | |
| Sesarmidae | *Chiromantes dehaani* | KH13 | ♂ | 6.41 | 386 | L | G | 15.0 | 34.2 | 12.8 | 3.09 | 9.40 | 32.9 | 3.2 | 10.1 | 10.2 | 31.5 | 1.04 | M3 |
| | | | | | | S | G | 14.7 | 32.0 | 12.1 | 3.45 | 9.70 | 35.6 | 3.03 | 10.3 | 10.4 | 29.1 | 0.878 | |
| | *C. dehaani* | KH14 | ♂ | 14.2 | 639 | L | G | 32.6 | 70.1 | 16.1 | 4.27 | 14.2 | 30.1 | 4.6 | 15.3 | 15.3 | 30.0 | 1.08 | M3 |
| | | | | | | S | G | 34.1 | 67.0 | 15.8 | 4.47 | 14.5 | 30.8 | 4.7 | 15.2 | 15.5 | 30.3 | 1.05 | |
| | *C. dehaani* | KH15 | ♀ | 19.0 | 923 | L | G | 23.4 | 65.5 | 9.63 | 3.71 | 12.6 | 29.5 | 3.72 | 13.1 | 13.4 | 27.9 | 1.00 | M3 |
| | | | | | | S | G | 23.4 | 55.4 | 8.54 | 3.62 | 12.3 | 29.5 | 3.81 | 12.7 | 13.0 | 29.3 | 1.05 | |
| | *C. dehaani* | KH16 | ♀ | 12.7 | 704 | L | G | 13.5 | 45.7 | 8.41 | 3.29 | 10.1 | 32.5 | 2.67 | 11.1 | 11.0 | 24.0 | 0.812 | M3 |
| | | | | | | S | G | 12.6 | 32.6 | 6.42 | 3.08 | 9.61 | 32.1 | 2.62 | 10.4 | 10.3 | 25.2 | 0.849 | |
| | *C. haematocheir* | KH11 | ♂ | 5.85 | 377 | L | G | 17.1 | 30.7 | 12.7 | 3.25 | 10.3 | 31.7 | 3.33 | 10.8 | 11.0 | 30.3 | 1.02 | M3 |
| | | | | | | S | G | 15.7 | 31.3 | 12.5 | 2.90 | 10.2 | 28.3 | 3.07 | 10.4 | 10.8 | 28.5 | 1.06 | |
| | *C. haematocheir* | KH12 | ♀ | 8.69 | 681 | L | G | 25.4 | 55.1 | 11.8 | 3.60 | 13.0 | 27.7 | 3.92 | 13.4 | 13.7 | 28.5 | 1.09 | M3 |
| | | | | | | S | G | 23.7 | 56.2 | 11.7 | 3.57 | 12.3 | 28.9 | 3.84 | 12.4 | 12.9 | 29.7 | 1.08 | |
| | *Parasesarma plicatum* | KH09 | ♂ | 13.2 | 625 | L | G | 32.3 | 59.7 | 14.7 | 3.77 | 13.2 | 28.7 | 4.91 | 15.0 | 14.7 | 32.7 | 1.30 | K5 |
| | | | | | | S | G | 30.4 | 59.4 | 14.4 | 3.87 | 13.3 | 29.2 | 4.57 | 14.5 | 14.5 | 31.6 | 1.18 | |
| | *Par. plicatum* | KH10 | ♀ | 5.83 | 410 | L | G | 7.74 | 19.8 | 6.70 | 1.86 | 7.30 | 25.5 | 2.12 | 7.36 | 7.62 | 27.8 | 1.14 | K5 |
| | | | | | | S | G | 7.78 | 18.7 | 6.45 | 2.05 | 6.76 | 30.4 | 2.3 | 7.67 | 7.50 | 30.0 | 1.12 | |
| | *Sesarmops intermedius* | KH20 | ♂ | 5.28 | 355 | L | G | 18.3 | 34.7 | 14.9 | 2.94 | 10.5 | 27.9 | 3.47 | 11.1 | 11.3 | 30.7 | 1.18 | M3 |
| | | | | | | S | G | 18.3 | 33.5 | 14.6 | 2.77 | 10.8 | 25.7 | 3.41 | 11.2 | 11.5 | 29.8 | 1.23 | |
| | *S. intermedius* | KH30 | ♂ | — | 816 | X | G | — | — | — | 2.57 | 11.6 | 22.1 | 4.3 | 12.6 | 12.7 | 33.9 | 1.67 | M3 |
| Varunidae (Cyclograpsinae) | *Helice tridens* | KH01 | ♂ | 26.0 | 861 | L | G | 54.4 | 147 | 23.4 | 5.34 | 18.3 | 29.3 | 5.96 | 19.8 | 19.8 | 30.1 | 1.12 | K5; T1 |
| | | | | | | S | G | 58.3 | 134 | 22.3 | 5.16 | 18.5 | 27.9 | 6.32 | 19.8 | 20.0 | 31.6 | 1.22 | |
| | *Hel. tridens* | KH02 | ♂ | 13.8 | 599 | L | G | 31.1 | 78.5 | 18.3 | 4.36 | 13.8 | 31.7 | 4.52 | 15.1 | 15.0 | 30.0 | 1.04 | K5; T1 |
| | | | | | | S | G | 32.4 | 65.4 | 16.3 | 3.86 | 13.9 | 27.8 | 4.66 | 14.6 | 14.9 | 31.2 | 1.21 | |
| | *Hel. tridens* | KH03 | ♂ | 5.76 | 343 | L | G | 13.4 | 32.1 | 13.3 | 3.25 | 9.19 | 35.3 | 2.92 | 9.46 | 9.74 | 30.0 | 0.899 | K5; T1 |
| | | | | | | S | G | 10.6 | 28.5 | 11.4 | 2.34 | 8.83 | 26.5 | 2.4 | 9.36 | 9.4 | 25.5 | 1.03 | |
| | *Hel. tridens* | KH04 | ♀ | 15.4 | 742 | L | G | 18.1 | 41.1 | 7.98 | 3.31 | 11.2 | 29.4 | 3.23 | 12.1 | 12.1 | 26.7 | 0.977 | K5; T1 |
| | | | | | | S | G | 17.7 | 35.4 | 7.16 | 2.94 | 11.0 | 26.8 | 3.22 | 11.7 | 11.7 | 27.4 | 1.09 | |
| | *Hel. tridens* | KH05 | ♀ | 4.73 | 323 | L | G | 7.63 | 16.3 | 7.41 | 1.97 | 7.37 | 26.7 | 2.07 | 7.77 | 7.84 | 26.4 | 1.05 | K5; T1 |
| | | | | | | S | G | 7.50 | 16.1 | 7.30 | 2.02 | 7.17 | 28.1 | 2.09 | 7.80 | 7.76 | 26.8 | 1.04 | |

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Varuninae) | *Eriocheir japonica* | KH22 | ♀ | 460 | 3,250 | L | P | 62.0 | 184 | 7.56 | 5.81 | 20.4 | 28.5 | 6.07 | 22.2 | 22.1 | 27.4 | 1.04 | K1 |
| | | | | | | S | P | 71.0 | 165 | 7.27 | 5.71 | 21.0 | 27.2 | 6.76 | 22.1 | 22.5 | 30.1 | 1.18 | |
| | *Hemigrapsus penicillatus* | KH17 | ♂ | 7.34 | 524 | L | G | 25.8 | 55.4 | 15.5 | 4.30 | 11.9 | 36.2 | 4.34 | 13.4 | 13.2 | 32.4 | 1.01 | M3 |
| | | | | | | S | G | 28.1 | 49.9 | 14.9 | 4.40 | 12.3 | 35.9 | 4.57 | 13.2 | 13.4 | 34.2 | 1.04 | |
| | *Hem. penicillatus* | KH18 | ♂ | 10.3 | 648 | L | G | 31.4 | 84.0 | 17.8 | 5.20 | 13.9 | 37.3 | 4.51 | 14.9 | 15.0 | 30.0 | 0.868 | M3 |
| | | | | | | S | G | 34.1 | 80.2 | 17.6 | 4.99 | 13.8 | 36.3 | 4.96 | 14.6 | 14.9 | 33.3 | 0.993 | |
| | *Hem. penicillatus* | KH19 | ♂ | 6.03 | 432 | L | G | 24.5 | 49.4 | 17.1 | 4.04 | 11.2 | 36.0 | 4.37 | 12.5 | 12.4 | 35.0 | 1.08 | M3 |
| | | | | | | S | G | 23.8 | 48.4 | 16.7 | 4.10 | 11.4 | 36.1 | 4.2 | 12.5 | 12.5 | 33.7 | 1.02 | |
| | *Varuna litterata* | KPM-NH140739 | ♂ | 27.8 | 1,740 | L | G | 63.1 | 174 | 13.6 | 6.97 | 22.3 | 31.2 | 5.66 | 23.3 | 23.5 | 24.1 | 0.813 | D1 |
| | | | | | | S | G | 63.3 | 173 | 13.5 | 6.87 | 22.4 | 30.7 | 5.66 | 22.8 | 23.3 | 24.3 | 0.824 | |
| OCYPODOIDEA | | | | | | | | | | | | | | | | | | | |
| Macrophthalmidae | *Macrophthalmus japonicus* | KH06 | ♂ | 3.88 | 321 | L | P | 4.47 | 11.7 | 5.05 | 1.97 | 6.63 | 29.8 | 1.97 | 6.69 | 6.94 | 28.4 | 0.999 | H2 |
| | | | | | | S | P | 5.31 | 10.3 | 4.87 | 1.75 | 6.85 | 25.5 | 1.76 | 6.94 | 7.12 | 24.7 | 1.01 | |
| | *M. japonicus* | KH07 | ♂ | 5.19 | 408 | L | P | 9.71 | 25.1 | 8.52 | 2.51 | 9.85 | 25.5 | 2.45 | 10.4 | 10.5 | 23.4 | 0.975 | H2 |
| | | | | | | S | P | 7.91 | 24.0 | 7.80 | 2.33 | 8.99 | 260 | 2.47 | 9.96 | 9.81 | 24.8 | 1.06 | |
| Ocypodidae | | | | | | | | | | | | | | | | | | | |
| (Ocypodinae) | *Ocypode ceratophthalma* | KPM-NH106326 | ♂ | 25.9 | 1,300 | L | C | 52.7 | 142 | 15.0 | 5.67 | 18.6 | 30.5 | 5.68 | 18.7 | 19.5 | 29.2 | 1.00 | R2; V2 |
| | | | | | | S | P | 28.1 | 71.6 | 7.66 | 3.11 | 15.6 | 19.9 | 3.6 | 17.4 | 17.1 | 20.6 | 1.16 | |
| | *O. ceratophthalmus* | KH81 | ♂ | — | 407 | X | P | 7.76 | — | — | 1.56 | 8.39 | 18.6 | 1.85 | 8.81 | 8.83 | 20.9 | 1.18 | R2; V2 |
| | | | | | | X | X | — | — | — | — | — | — | — | — | — | — | — | |
| | *O. ceratophthalmus* | KH82 | ♂ | 32.8 | 1,430 | L | C | 57.6 | 119 | 12.3 | 5.71 | 18.5 | 30.9 | 6.24 | 18.7 | 19.6 | 31.9 | 1.09 | R2; V2 |
| | | | | | | S | P | 30.7 | 79.3 | 7.66 | 2.89 | 16.0 | 18.1 | 3.83 | 16.8 | 16.9 | 22.7 | 1.32 | |
| | *O. ceratophthalmus* | NSMT-Cr.4578 | ♂ | 43.2 | 1,860 | L | C | 60.4 | — | — | 6.73 | 20.7 | 32.6 | 5.85 | 21.1 | 21.7 | 27.0 | 0.869 | R2; V2 |
| | | | | | | S | P | 25.9 | — | — | 3.33 | 16.4 | 20.4 | 3.16 | 17.0 | 17.1 | 18.5 | 0.948 | |
| | *O. cordimanus* | NSMT-Cr.10745 | ♀ | 7.38 | 451 | L | X | 18.7 | — | — | 3.54 | 10.2 | 34.6 | 3.65 | 10.3 | 10.9 | 33.5 | 1.03 | R2 |
| | | | | | | S | X | 7.30 | — | — | 2.08 | 8.16 | 25.5 | 1.79 | 8.60 | 8.61 | 20.8 | 0.859 | |
| | *O. stimpsoni* | KPM-NH106516 | ♂ | 5.50 | 441 | L | X | 14.4 | — | — | 3.01 | 10.7 | 28.2 | 2.7 | 10.9 | 11.1 | 24.3 | 0.898 | R2 |
| | | | | | | S | X | 6.28 | — | — | 1.69 | 9.24 | 18.3 | 1.36 | 9.41 | 9.46 | 14.4 | 0.804 | |
| (Ucinae) | *Uca (Austruca) lactea* | KPM-NH140616 | ♂ | 19.1 | 204 | L | U | 34.0 | 60.7 | 46.4 | 5.21 | 20.2 | 25.8 | 3.37 | 20.2 | 20.5 | 16.4 | 0.647 | V1 |
| | *U. (A.) lactea* | KH106 | ♂ | 14.9 | 680 | L | U | 118 | 267 | 56.6 | 6.93 | 41.5 | 16.7 | 5.68 | 41.7 | 42.0 | 13.5 | 0.820 | V1 |
| | | | | | | S | P | 6.78 | 19.0 | 3.79 | 1.31 | 8.36 | 15.7 | 1.62 | 8.39 | 8.53 | 19.0 | 1.24 | |
| | *U. (Gelasimus) vocans* | KH70 | ♂ | 2.5 | 224 | L | U | 28.5 | 42.0 | 31.5 | 3.71 | 18.1 | 20.5 | 3.15 | 18.3 | 18.5 | 17.0 | 0.849 | V1 |
| | *U. (G.) vocans* | KH71 | ♂ | 2.54 | 221 | L | U | 27.3 | 48.5 | 34.4 | 3.96 | 17.5 | 22.6 | 3.12 | 18.1 | 18.2 | 17.2 | 0.789 | V1 |
| | *U. (G.) vocans* | KH72 | ♂ | 2.29 | 196 | L | U | 30.9 | 51.1 | 41.9 | 4.46 | 18.8 | 23.7 | 3.28 | 19.1 | 19.3 | 17.0 | 0.735 | V1 |
| | *U. (G.) vocans* | KH73 | ♂ | 2.71 | 235 | L | U | 32.2 | 51.5 | 35.7 | 4.10 | 19.0 | 21.6 | 3.39 | 19.1 | 19.3 | 17.5 | 0.827 | V1 |
| | *U. (G.) vocans* | KH74 | ♂ | 2.33 | 223 | L | U | 26.7 | 39.8 | 29.8 | 3.99 | 17.1 | 23.3 | 3.11 | 17.2 | 17.5 | 17.8 | 0.779 | V1 |
| | *U. (G.) vocans* | KPM-NH106380 | ♂ | 1.65 | 244 | L | U | 19.8 | 35.5 | 22.7 | 3.66 | 14.9 | 24.5 | 2.65 | 15.2 | 15.4 | 17.3 | 0.724 | V1 |
| | *U. (G.) vocans* | KPM-NH140654 | ♂ | 2.55 | 309 | L | U | 42.0 | 70.2 | 36.3 | 5.13 | 24.6 | 20.9 | 3.42 | 24.9 | 25.0 | 13.7 | 0.667 | V1 |
| | *U. (Paraleptuca) chlorophthalmus* | KPM-NH106482 | ♂ | 0.930 | 141 | L | U | 16.7 | 33.0 | 35.3 | 3.07 | 14.4 | 21.3 | 2.32 | 14.5 | 14.6 | 15.9 | 0.756 | V1 |

*TABLE S1 (cont.)*

| family | species | specimen | sex | BM | CS | chela | Fn | DS | PS | RC | $C_1$ | $C_2$ | $C_1/C_2$ | $M_1$ | $M_{2L}$ | $M_{2M}$ | $M_1/M_2$ | $M_1/C_1$ | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Ucinae [cont.]) | *Uca (Tubuca) arcuata* | KPM-NH107735 | ♂ | 3.36 | 470 | L | U | 46.4 | 85.5 | 28.0 | 4.81 | 21.2 | 22.7 | 4.38 | 21.6 | 21.9 | 20.0 | 0.91 | V1 |
| | *U. (T.) arcuata* | NSMT-Cr.3205 | ♂ | 14.7 | 698 | L | U | 97.5 | — | — | 6.73 | 31.5 | 21.3 | 6.18 | 31.6 | 32.1 | 19.2 | 0.918 | V1 |
| | *U. (T.) arcuata* | NSMT-Cr.3905 | ♂ | 11.2 | 609 | L | U | 61.8 | — | — | 6.06 | 27.4 | 22.1 | 4.51 | 27.4 | 27.8 | 16.2 | 0.744 | V1 |
| | | | | | | S | P | — | — | — | — | — | — | — | — | — | — | — | |
| | *U. (T.) arcuata* | NSMT-Cr.7277 | ♂ | 14.5 | 706 | L | U | 112 | — | — | 7.08 | 33.6 | 21.0 | 6.66 | 33.7 | 34.3 | 19.4 | 0.941 | V1 |
| | | | | | | S | P | — | — | — | — | — | — | — | — | — | — | — | |
| | *U. (T.) arcuata* | NSMT-Cr.7577 | ♂ | 10.1 | 637 | L | U | 69.7 | — | — | 6.21 | 26.3 | 23.6 | 5.29 | 26.4 | 26.9 | 19.7 | 0.851 | V1 |
| | | | | | | S | P | — | — | — | — | — | — | — | — | — | — | — | |
| | *U. (T.) coarctata* | KPM-NH140347 | ♂ | 16.0 | — | L | U | 150 | 212 | — | 8.31 | 40.0 | 20.8 | 7.52 | 40.3 | 40.9 | 18.4 | 0.905 | V1 |
| | *U. (T.) dussumieri* | NSMT-Cr.1172 | ♂ | 4.20 | 334 | L | U | 34.3 | — | — | 5.00 | 18.3 | 27.3 | 3.76 | 18.3 | 18.7 | 20.1 | 0.752 | V1 |
| | | | | | | S | P | — | — | — | — | — | — | — | — | — | — | — | |
| | *U. (T.) arcuata* | NSMT-Cr.13131 | ♂ | 4.22 | 387 | L | U | 33.0 | — | — | 4.12 | 18.1 | 22.7 | 3.65 | 18.1 | 18.5 | 19.8 | 0.887 | V1 |
| | | | | | | S | P | — | — | — | — | — | — | — | — | — | — | — | |
| | *U. (Tubuca) forcipata* | NSMT-Cr.14131 | ♂ | 4.44 | 369 | L | U | 27.5 | — | — | 4.49 | 16.6 | 27.0 | 3.31 | 16.8 | 17.0 | 19.4 | 0.738 | V1 |
| | *U.* sp. | KH32 | ♂ | 15.3 | 791 | L | U | 117 | 265 | 48.2 | 7.41 | 41.4 | 17.9 | 5.66 | 41.4 | 41.7 | 13.6 | 0.763 | V1 |
| | *U.* sp. | KPM-NH140867 | ♂ | 1.53 | 188 | L | U | 32.4 | 62.7 | 50.6 | 3.99 | 21.2 | 18.8 | 3.06 | 21.2 | 21.4 | 14.3 | 0.768 | V1 |

Abbreviations of institution:

KH, personal collections of Hiroki Kawai, Nagoya University Museum, Nagoya, Japan; KPM, Kanagawa Prefectural Museum, Odawara, Japan; NSMT, National Museum of Nature and Science, Tokyo (formerly, National Science Museum, Tokyo), Japan; NUM, Nagoya University Museum, Nagoya, Japan; TMNH, Toyohashi Museum of Natural History, Toyohashi, Japan.

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V2:    Vermeij GJ. 1977. Patterns in crab claw size: the geography of crushing. Syst Zool 26:138–151.

V3:    Vinuesa JH, Varisco M, Balzi P. 2013. Feeding strategy of early juvenile stages of the southern king crab *Lithodes santolla* in the San Jorge Gulf, Argentina. Rev Biol Mar Oceanogr 48:353–353.

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W2:    Wieczorek SK, Hooper RG. 1995. Relationship between diet and food availabiligy in the snow crab *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. J Crustac Biol 15:236–247.

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Y1:    Yamada SB, Boulding EG. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. J Exp Mar Biol Ecol 220:191–211.

# Appendix S1: Phylogenetic signals of the indices used in this study

## INTRODUCTION

The relationship between a trait and its function cannot be strongly supported if a diversification of the traits were related to the phylogeny (Harvey and Pagel, 1991; Abouheif, 1999; Münkemüller et al., 2012; Pavione and Ricotta, 2012; Hallmann and Griebeler, 2015). Therefore, it is important to test whether a trait is autocorrelated with a phylogeny. Phylogenetic autocorrelation of a trait can be tested by determining a phylogenetic signal, which is defined by Blomberg and Garland (2002) as a tendency for related species to resemble each other more than they resemble species drawn at random evolution from the phylogenetic tree.

Three indices were used in this study, including mechanical advantages of pinching efficiency ($C_1/C_2$), passive disarticulation resistance ($M_1/M_2$), and relative size of chela (RC). We determined the phylogenetic signals for these indices to test whether they were autocorrelated with the phylogeny, though they seem to be diversified independently from the classification in Ng et al. (2008: Fig. 7).

## MATERIALS AND METHODS

Phylogenetic signals can be determined from the value of each index and the phylogenetic relationships among the studied taxa (Münkemüller et al., 2012). Phylogenetic signals were determined for three different indices in this study ($C_1/C_2$, $M_1/M_2$, and RC). Many decapods show a left-right asymmetry in their chela (Palmer, 2004), so the autocorrelation of the indices to the phylogenetic tree may vary between major and minor chelae. Therefore, we used specimens for which index values were estimated for both major and minor chelae (Table S1), and the major, minor, and average of the major and minor chelae were estimated for each index. Sexual dimorphism of chelae was not accounted for in this analysis because there was an inadequate number of samples to determine the phylogenetic signals for males and females.

Phylogenetic trees containing all studied species were not available in the literature. Furthermore, a consensus on the phylogenetic relationships among decapods has yet to be obtained (e.g., Ahyong et al., 2007; Tsang et al., 2008; Bracken et al., 2009; Tsang et al., 2014). Therefore, we used six phylogenetic trees from published literature that were comprised of more than seven species or genera of our studied taxa (Fig. S1: Schubart et al., 2006; Ahyong et al., 2007; Tsang et al., 2008; Bracken et al., 2009; Spiridonov et al., 2014; Tsang et al., 2014). We used species in these trees that corresponded with species used in our study (Table S1) for estimating the phylogenetic signals (see species in Fig. S1). By following the method of Batalha et al. (2011), the average value of each index for all specimens within a species was defined as the representing index value for the species. For a genus in a tree that corresponded to one used in our study, but with a different species, we first confirmed that the monophyly of the clade containing the genus was well-supported in the literature (maximum likelihood bootstrap [BP] ≥ 70; or Bayesian inference posterior probability [PP] ≥ 0.95). Then, we averaged the value of each index for all specimens of all the species within the genus and defined it as the representing index value of the genus (see genera with asterisks in Fig. S1). Synonymy of the taxonomic names among the literatures were checked carefully based on Ng et al. (2008).

The topologies of the phylogenetic trees are shown in Fig. S1. We followed the nodes which were well-supported (BP ≥ 70; or PP ≥ 0.95). If the phylogenetic relationships among the lineages within the node were not well-supported (BP < 70; or PP < 0.95), the node was dealt as plytomy. Members of the studied taxa in each tree depended on the taxa used in the original trees in the literature. The trees from Bracken et al. (2009) and Tsang et al. (2008) comprised species of astacideans, anomurans, and brachyurans: the former comprised 11 taxa (four species and seven other genera) and the latter comprised 11 taxa (eight species and three other genera). The tree from Tsang et al. (2014) and Ahyong et al. (2007) comprised species of anomurans and three sections (Prototremata, Heterotremata, and Thoracotremata) of brachyurans (30 taxa: 16 species and 14 other genera). The tree from Ahyong et al. (2007) comprised seven taxa (four species and three other genera) of the three sections of brachyurans. The tree in Spiridonov et al. (2014) comprised seven portunoid taxa and two other taxa (seven species and two other genera) of heterotremate brachyurans. The tree in Schubart et al. (2006) comprised 11 taxa (five species and six other genera) in ten thoracotremate and one heterotremate brachyurans. Although the topologies for the relationships among the studied taxa were available in these trees, the branch lengths were absent from the literature.

Among the several phylogenetic signals, we determined Abouheif's mean $C$-statistics (Abouheif, 1999) for each index, which was estimated using the topology of the phylogenetic tree, but was not related to branch length in the analysis (Münkemüller et al., 2012). Abouheif's mean $C$-statistics were used to determine the autocorrelation of values of neighboring taxa in the phylogenetic tree, and the null hypothesis (there is no phylogenetic autocorrelation) is rejected if the $p$-value does not exceed 0.05 (Abouheif, 1999).

We used packages "adephylo" and "ape" (Paradis et al., 2003; Jombart et al., 2010) in R 3.2.2 (R Core Team, 2015) for the Abouheif's tests—the package "ape" depends on R (≥ 3.0.0). We constructed phylogenetic trees among the taxonomic groups of studied taxa using package "ape" (Jombart and Dray, 2010). Abouheif's mean $C$-statistics were then estimated for each index using the function "abouheif.moran" of package "adephylo" in R (Jombart and Dray, 2010; Jombart et al., 2010).

# Appendix S1 (cont.)

**RESULT**

According to the Abouheif's test, the indices $C_1/C_2$, $M_1/M_2$, and RC were not phylogenetically autocorrelated ($p \geq 0.05$) in the major (L), minor (S), or the average of major and minor (L+S) chelae in most of the phylogenetic trees (Table S2). However, the $M_1/M_2$ of minor chelae (S) and the RC of chelae (L, S, and L+S) were phylogenetically autocorrelated in the trees of Bracken et al. (2009) and Tsang et al. (2008), which comprised only a single taxon within each brachyuran superfamily, or only a few taxa within each brachyuran section (Table S2; Fig. S1).

**DISCUSSION**

Overall, in Abouheif's test conducted on a tree comprised of major lineages of brachyuran superfamilies (e.g., the tree in Tsang et al. [2014]) or on relatively detailed trees of a brachyuran section/superfamily (e.g., the trees in Spiridonov et al. [2014] and Schubart et al. [2006]), the indices used in this study ($C_1/C_2$, $M_1/M_2$, and RC) were not autocorrelated with the phylogeny (Table S2). However, some indices were not phylogenetically independent on trees of decapod infraorders (e.g., Bracken et al.
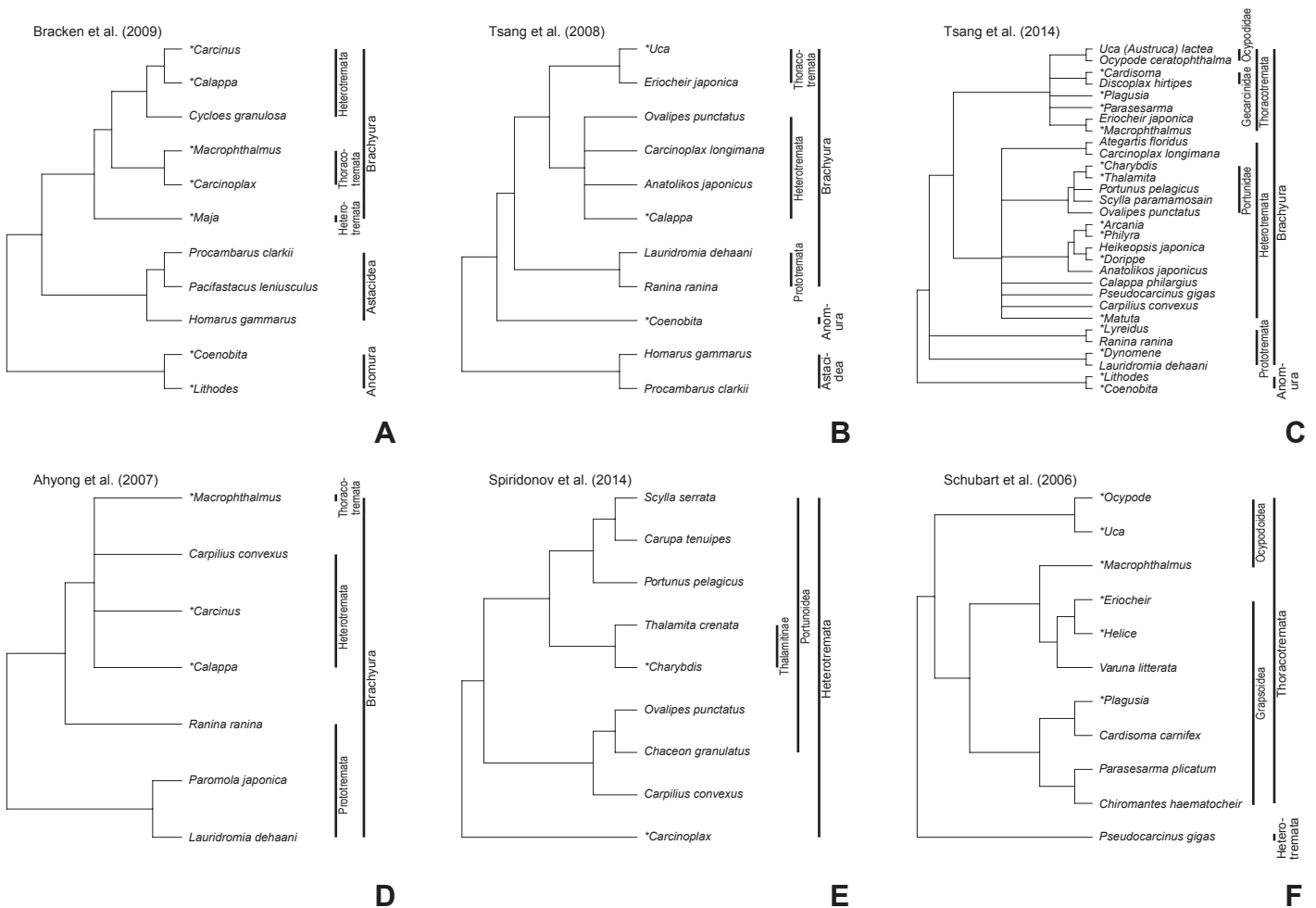


**Fig. S1.** Topologies of phylogenetic relationships among the studied taxa based on literatures supported by maximum likelihood boot strap values (>70) or by Bayesian inference posterior probabilities (>0.95): phylogenetic trees (A, B) among astacideans, anomurans, and brachyurans (A: Bracken et al., 2009; B: Tsang et al., 2008); (C) among anomurans and major lineages of brachyuran superfamilies (Tsang et al., 2014); (D) among prototremates, heterotremates, and thoracotremates (Ahyong et al., 2007); among portunoid brachyurans (Spiridonov et al., 2014); and among thoracotremate brachyurans (Schubart et al., 2006). Classification shown on the right side of each tree is based on Ng et al. (2008). The trees were constructed using species from this study that were also found in the available literature, and with studied taxa whose genera were the same, but whose species did not correspond with the one used in the literature. The names of genera whose species did not match the species in the literature are indicated with asterisks. Note that the branch lengths are not reflected in these topologies.

# Appendix S1 (cont.)

[2009] and Tsang et al. [2008]).

There are some limitations in the method utilized in this is study. The first limitation is that the phylogenetic relationships among decapods are yet to be fully understood. In particular, the debates on relationships among decapod infraorders, and among brachyuran superfamiles/families remain unresolved (e.g., Ahyong et al., 2007; Tsang et al., 2008; Bracken et al., 2009; Tsang et al., 2014). The tests on the phylogenetic signals delicately rely on the topologies of the trees, and therefore, as far as the consensus on phylogenetic relationships among decapods is unavailable, it is difficult to strongly argue that the indices used in this study are not phylogenetically autocorrelated. Note that the results in this appendix are case studies of Abouheif's test on six available decapod phylogenetic trees.

The second limitation concerns the use of phylogenetic tree whose species on the tip did not necessarily correspond to our study taxa for the estimation of phylogenetic significance (Fig. S1). Different topologies of phylogenetic trees could be proposed if a new phylogenetic analysis was conducted using all the taxa used in this study (Tables S1 and S2), which may affect the results of Abouheif's test. Additional analyses using a phylogenetic tree constructed from all the species included in our study may solve this problem.

The third limitation concerns the sexual differences of chelae within a species. The result of the phylogenetic autocorrelation of the indices would change if the phylogenetic signals were determined based solely on the either sex. Many brachyuran taxa, including *Uca* and *Hemigrapsus*, are known to show a pronounced sexual dimorphism in the size and shape of chelae (RC: e.g.,

*TABLE S2*. Results of Abouheif's tests for mechanical advantages of pinching efficiency ($C_1/C_2$), passive disarticulation resistance ($M_1/M_2$), and relative size of chela (RC), in the studied specimens whose indices in both the major and the minor chelae were available. The tests were conducted for major (L), minor (S), and the average of major and minor (L+S) chelae. The average of the indices within each taxon was used for the tests. See Fig. S1 for the phylogenetic tree and the taxa used to estimate Abouheif's mean *C*-statistics. The observed value of Abouheif's mean *C*-statistics (Obs), the standard deviation of Abouheif's mean *C*-statistics (Std.Obs.), and the *p*-value of the null hypothesis are listed.

| chela | $C_1/C_2$ Obs | Std.Obs | *p* | $M_1/M_2$ Obs | Std.Obs | *p* | RC Obs | Std.Obs | *p* |
|---|---|---|---|---|---|---|---|---|---|
| <Bracken et al. (2009)> | | | | | | | | | |
| L | 0.302 | 1.50 | 0.088 | 0.262 | 0.986 | 0.181 | 0.618 | 2.55 | 0.032* |
| S | 0.176 | 0.0669 | 0.382 | 0.368 | 2.51 | 0.017* | 0.603 | 2.50 | 0.054 |
| L+S | 0.259 | 0.871 | 0.196 | 0.311 | 1.59 | 0.093 | 0.611 | 2.41 | 0.042* |
| <Tsang et al. (2008)> | | | | | | | | | |
| L | 0.0601 | −1.49 | 0.988 | 0.0811 | −1.33 | 0.937 | 0.227 | −0.253 | 0.488 |
| S | 0.153 | −0.350 | 0.569 | 0.0936 | −1.08 | 0.873 | 0.411 | 5.13 | 0.001* |
| L+S | 0.0954 | −1.04 | 0.875 | 0.0841 | −1.25 | 0.926 | 0.293 | 0.774 | 0.226 |
| <Tsang et al. (2014)> L | | | | | | | | | |
| L | 0.132 | 1.86 | 0.053 | 0.122 | 1.47 | 0.076 | 0.0737 | −0.623 | 0.736 |
| S | 0.0490 | −0.897 | 0.835 | 0.106 | 0.887 | 0.179 | 0.0949 | −0.000265 | 0.431 |
| L+S | 0.859 | 0.322 | 0.307 | 0.123 | 1.46 | 0.09 | 0.0665 | −0.945 | 0.851 |
| <Ahyong et al. (2007)> | | | | | | | | | |
| L | 0.294 | −0.0834 | 0.338 | 0.426 | 0.866 | 0.267 | 0.222 | −0.519 | 0.642 |
| S | 0.394 | 0.786 | 0.187 | 0.372 | 0.539 | 0.303 | 0.180 | −0.754 | 0.778 |
| L+S | 0.237 | −0.538 | 0.538 | 0.404 | 0.739 | 0.296 | 0.199 | −0.617 | 0.75 |
| <Spiridonov et al. (2014)> | | | | | | | | | |
| L | 0.300 | 0.115 | 0.621 | 0.238 | 0.147 | 0.322 | 0.276 | 0.154 | 0.463 |
| S | 0.221 | −0.456 | 0.754 | 0.230 | 0.153 | 0.323 | 0.166 | −0.910 | 0.824 |
| L+S | 0.276 | 0.447 | 0.619 | 0.241 | 0.223 | 0.295 | 0.219 | −0.377 | 0.579 |
| <Schubart et al. (2006)> | | | | | | | | | |
| L | 0.126 | −0.774 | 0.752 | 0.158 | −0.230 | 0.519 | 0.419 | 2.08 | 0.07 |
| S | 0.332 | 1.88 | 0.065 | 0.321 | 1.82 | 0.069 | 0.239 | 0.00124 | 0.395 |
| L+S | 0.256 | 1.01 | 0.191 | 0.279 | 1.34 | 0.119 | 0.390 | 1.69 | 0.096 |

*Null-hypothesis that the index is not phylogenetically autocorrelated is rejected ($p < 0.05$).

# Appendix S1 (cont.)

Valiela et al., 1974; Ng et al., 2008; Miyajima et al., 2012). However, we could not determine whether there were differences in the mechanical indices of chela ($C_1/C_2$ and $M_1/M_2$) between sexes due to inadequate samples of both sexes (Table S1). In a case study of a shrimp crab (*Neotrypaea*), whose chelae are sexually dimorphic in size, the $C_1/C_2$ in master and minor chelae did not differ significantly between the sexes (Labadie and Palmer, 1996), though the taxa were not used in this study. It would be worthwile to test the differences of both mechanical indices of chelae ($C_1/C_2$ and $M_1/M_2$) for our studied species in the future.

## CONCLUSION

According to Abouheif's tests conducted on published decapod phylogenetic trees, comprised of the major lineages of brachyurans, the three indices ($C_1/C_2$, $M_1/M_2$, and RC) were not autocorrelated with the phylogeny.

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# Appendix S2: Relationships between relative size of chela (RC) and mechanical indices for pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$)

*TABLE S2*. Results of Steel-Dwass tests of three indices related to chela—pinching efficiency ($C_1/C_2$), passive disarticulation resistance ($M_1/M_2$), and relative size of chela (RC)—among four different functional categories (C, G, P, and U) (p. 1).

*TABLE S3*. Spearman's correlation test between relative size of chela (RC) and mechanical advantage of pinching efficiency ($C_1/C_2$) (p. 1).

*TABLE S4*. Spearman's correlation test between relative size of chela (RC) and mechanical advantage of passive disarticulation resistance ($M_1/M_2$) (p. 1).

**Fig. S2.** Relationship between relative size of chela (RC = (DS + PS)/CS) and mechanical advantage of pinching efficiency ($C_1/C_2$) (p. 2).

**Fig. S3.** Relationship between relative size of chela (RC = (DS + PS)/CS) and mechanical advantage of passive disarticulation resistance ($M_1/M_2$) (p. 3).

*TABLE S2*. Results of Steel-Dwass tests of three indices related to chela—pinching efficiency ($C_1/C_2$), passive disarticulation resistance ($M_1/M_2$), and relative size of chela (RC)—among four different functional categories (C, G, P, and U). The tests were conducted for the study specimens whose carapace sizes were able to be measured ($n = 191$: C, 24, G, 121; P, 33; U, 13). Asterisk indicates that the variables among two categories were not significantly different ($p < 0.05$). See boxplots in Figs. S2 and S3.

|         | $C_1/C_2$ |           | $M_1/M_2$ |           | RC        |           |
|---------|-----------|-----------|-----------|-----------|-----------|-----------|
|         | $t$- score | $p$      | $t$- score | $p$      | $t$- score | $p$      |
| C : G   | 5.54      | 1.78e–07* | 5.11      | 1.85e–06* | 0.883     | 8.14e–01  |
| C : P   | 6.09      | 6.63e–09* | 6.11      | 5.99e–09* | 0.760     | 8.73e–01  |
| C : U   | 4.71      | 1.48e–05* | 4.96      | 4.14e–06* | 4.96      | 4.14e–06* |
| G : P   | 4.82      | 8.57e–06* | 6.22      | 3.07e–09* | 0.112     | 9.99e–01  |
| G : U   | 2.78      | 2.80e–02* | 5.81      | 3.81e–08* | 5.80      | 3.98e–08* |
| P : U   | 0.915     | 7.97e–01  | 2.45      | 6.77e–02  | 5.23      | 9.98e–07* |

*TABLE S3*. Spearman's correlation test between relative size of chela (RC) and mechanical advantage of pinching efficiency ($C_1/C_2$) ($n = 230$: C, 24; G, 121; P, 33; U, 13; X, 39). Spearman's $\rho$- and $p$-values, coefficient of determination ($R^2$), and regression line were indicated for each functional category (C, G, P, and U). See Fig. S2.

|       | $n$ | $\rho$-value | $p$      | $R^2$    | regression line      |
|-------|-----|--------------|----------|----------|----------------------|
| total | 230 | 0.269        | 0.445    | 2.56e–03 | $y = 0.0565x + 25.9$ |
| C     | 24  | −0.0635      | 0.570    | 1.49e–02 | $y = −0.315x + 41.1$ |
| G     | 121 | 0.440        | 2.26e–05* | 1.41e–01 | $y = 0.437x + 22.4$ |
| P     | 33  | −0.182       | 0.835    | 1.43e–03 | $y = 0.0783x + 18.1$ |
| U     | 13  | −0.527       | 3.23e–02* | 0.353   | $y = −0.158x + 27.6$ |

*Null-hypothesis that there is no association between the two variables was rejected ($p < 0.05$).

*TABLE S4*. Spearman's correlation test between relative size of chela (RC) and mechanical advantage of passive disarticulation resistance ($M_1/M_2$) ($n = 230$: C, 24; G, 121; P, 33; U, 13; X, 39). Spearman's $\rho$- and $p$-values, coefficient of determination ($R^2$), and regression line were indicated for each functional category (C, G, P, and U). See Fig. S3.

|       | $n$ | $\rho$-value | $p$      | $R^2$    | regression line        |
|-------|-----|--------------|----------|----------|------------------------|
| total | 230 | 0.235        | 7.56e–02 | 1.38e–06 | $y = −0.0934x + 27.5$  |
| C     | 24  | 0.0183       | 0.991    | 6.53e–06 | $y = −0.00414x + 33.9$ |
| G     | 121 | 0.527        | 5.50e–06* | 0.160   | $y = 0.301x + 24.6$    |
| P     | 33  | −0.0491      | 0.648    | 6.81e–03 | $y = 0.112x + 19.5$    |
| U     | 13  | −0.830       | 4.66e–03* | 0.532   | $y = −0.146x + 21.8$   |

*Null-hypothesis that there is no association between the two variables was rejected ($p < 0.05$).
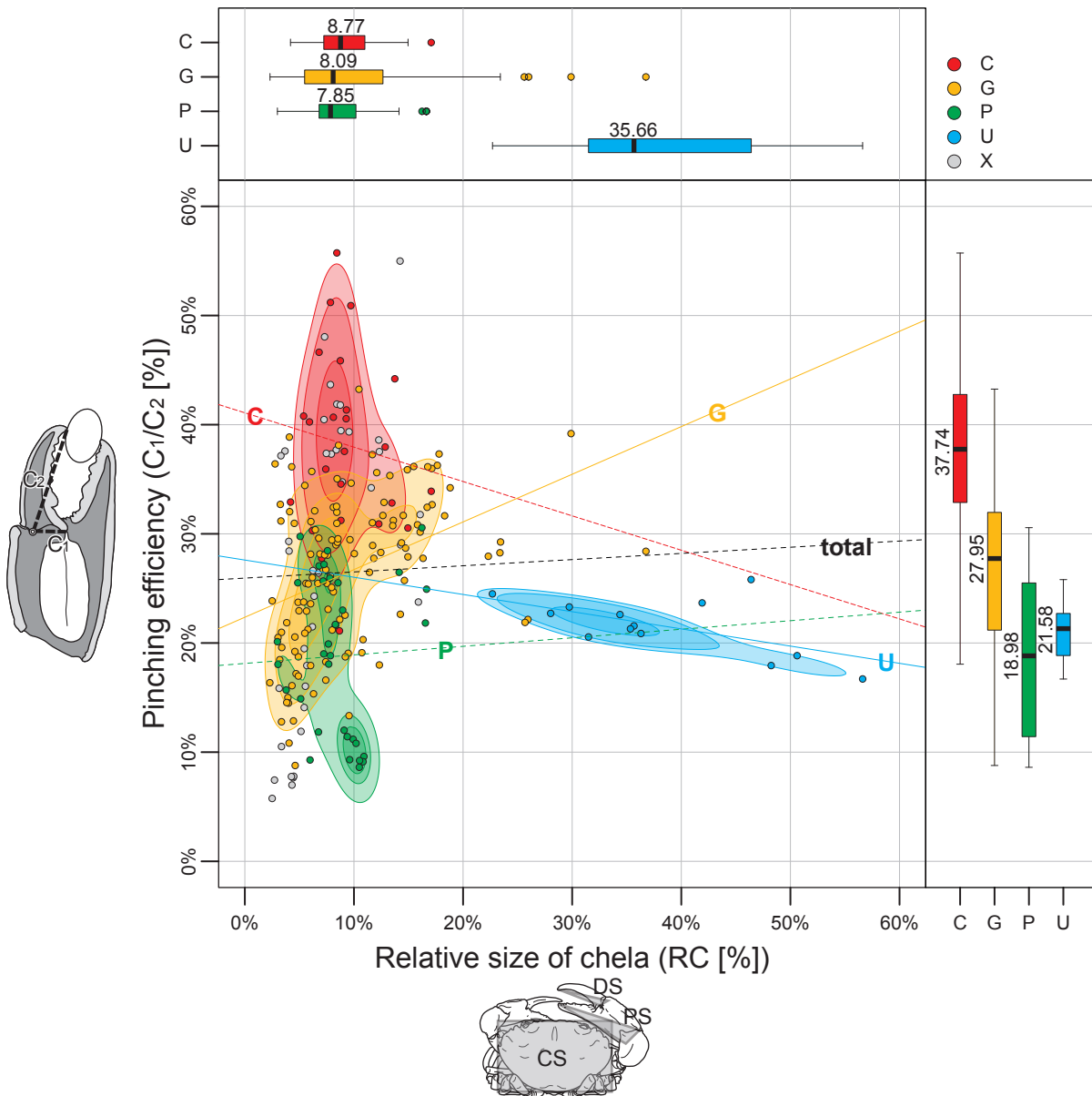
**Fig. S2.** Relationship between relative size of chela (RC = (DS + PS)/CS) and mechanical advantage of pinching efficiency ($C_1/C_2$). See main text for abbreviations. Each plot represents chela characteristics of the study specimens ($n = 230$ in total; C, crushing/chipping chela, $n = 24$; G, gripping chela, $n = 121$; P, pinching chela, $n = 33$; U, male ucine major chela, $n = 13$; X, uncategorized chela, $n = 39$). Bivariate kernel density distributions (densities: 25%, 50%, 75%) and box plots with median values are shown for each variable in the functional categories C, G, P, and U. See Table S2 for results of Steel-Dwass tests in the variables. Regression lines are drawn for total plots, in addition to the regression lines for plots of each functional category (C, G, P, and U). Absence of correlation between the variables is represented using dotted lines ($p < 0.05$: Table S3). See Table S3 for slopes of the regression lines.

**Fig. S3.** Relationship between relative size of chela (RC = (DS + PS)/CS) and mechanical advantage of passive disarticulation resistance ($M_1/M_2$). See main text for abbreviations. Each plot represents chela characteristics of the study specimens ($n$ = 230 in total; C, crushing/chipping chela, $n$ = 24; G, gripping chela, $n$ = 121; P, pinching chela, $n$ = 33; U, male ucine major chela, $n$ = 13; X, uncategorized chela, $n$ = 39). Bivariate kernel density distributions (densities: 25%, 50%, 75%) and box plots with median values are shown for each variable in the functional categories C, G, P, and U. See Table S2 for results of Steel-Dwass tests in the variables. Regression lines are drawn for total plots, in addition to the regression lines for plots of each functional category (C, G, P, and U). Absence of correlation between the variables is represented using dotted lines ($p$ < 0.05: Table S4). See Table S4 for slopes of the regression lines.

# Appendix S3: Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in chelae of the major group of the studied taxa
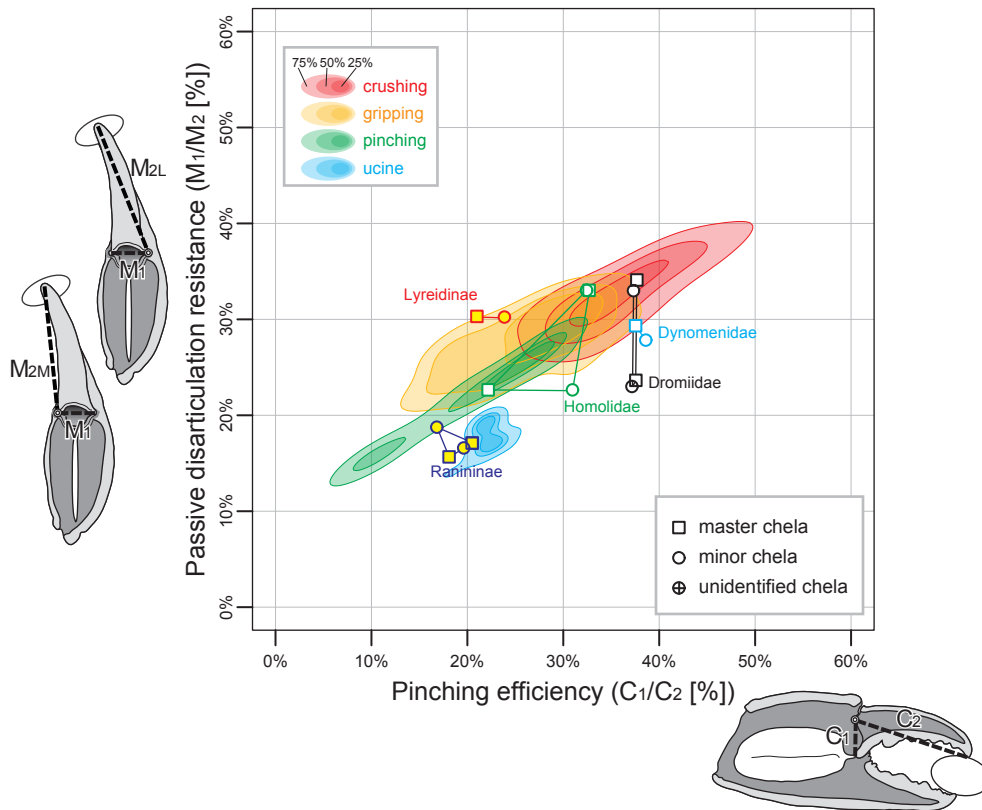
**Fig. S4.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major group of the studied specimens. Range of the plots of each group is shown in convex hull. (1) Astacidea (Fig. S5); (2) Anomura (Fig. S5); (3) Dromiidae + Dynomenidae + Homolidae (Fig. S6); (4) Raninidae (Fig. S6); (5) Epialtidae + Inachidae + Majidae + Oregoniidae (Fig. S7); (6) Calappidae (Fig. S8); (7) Parthenopidae (Fig. S8); (8) Cancridae + Dorippidae + Leucosiidae (Fig. S9); (9) Geryonidae + Portunidae (Fig. S10); (10) Hypothalassidae + Oziidae + Goneplacidae + Xanthidae (Fig. S11); (10) Thoracotremata (Figs. S12, S13). Monophylies of the groups (1)–(10) are well supported in Tsang et al. (2014). See Table S1 for the data.
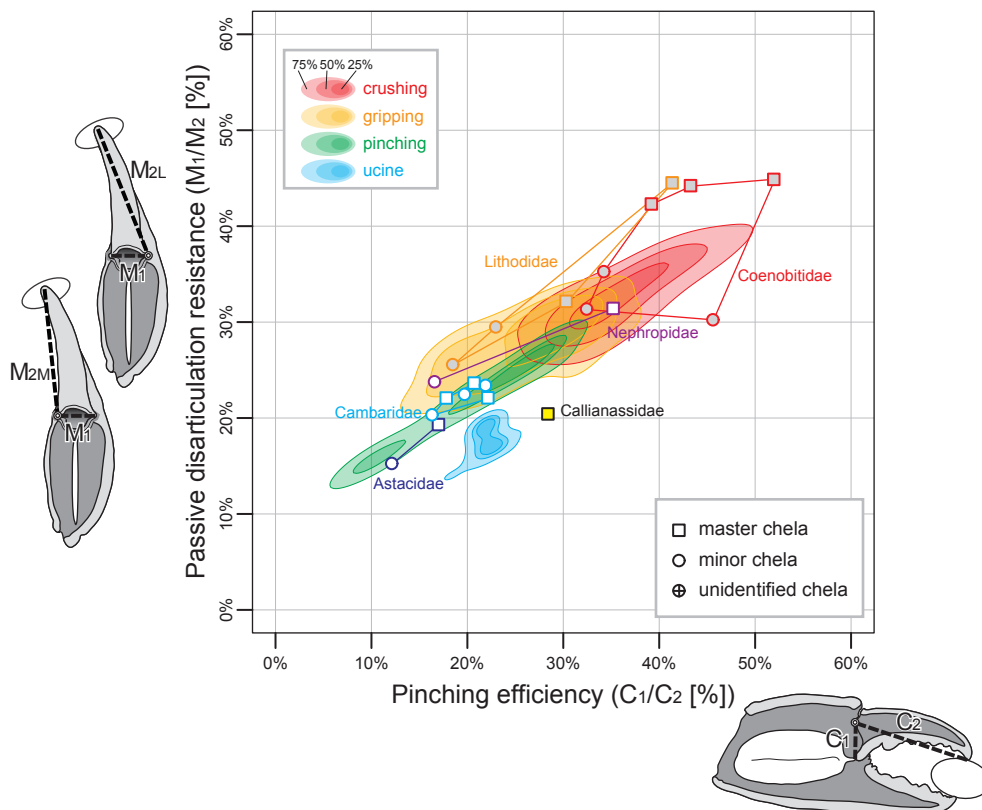


**Fig. S5.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of non-brachyuran decapods (Axiidea [Callianassidae], Astacidea [Astacidae, Cambaridae, and Nephropidae], and Anomura [Coenobitidae and Lithodidae]). Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.
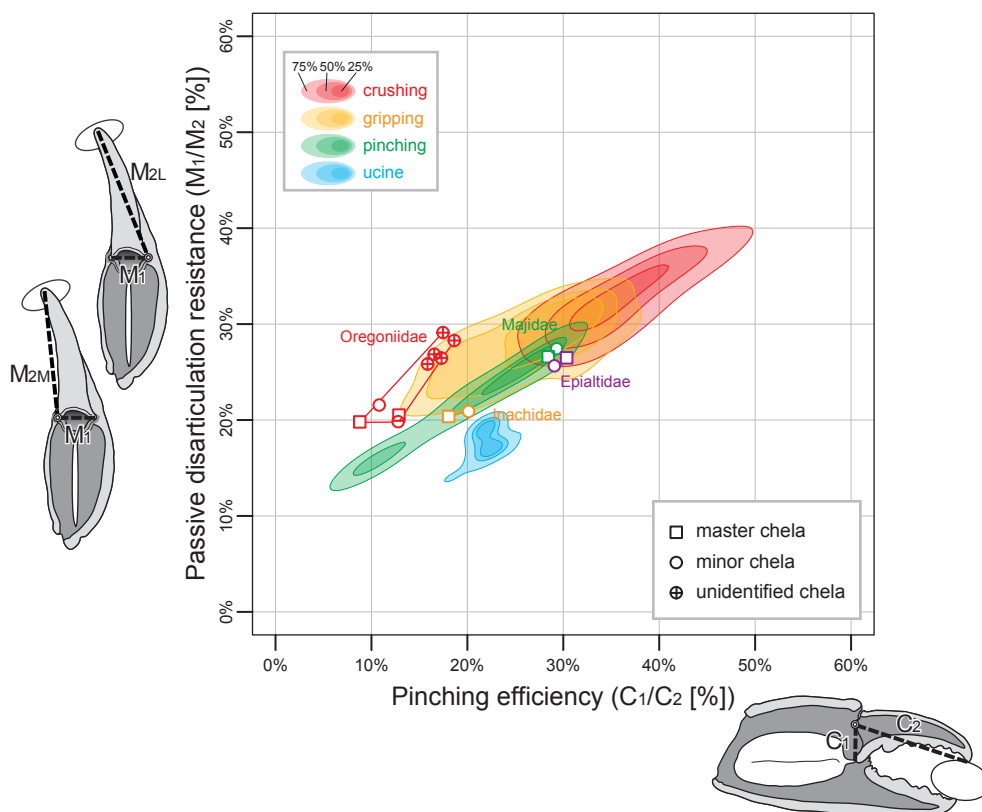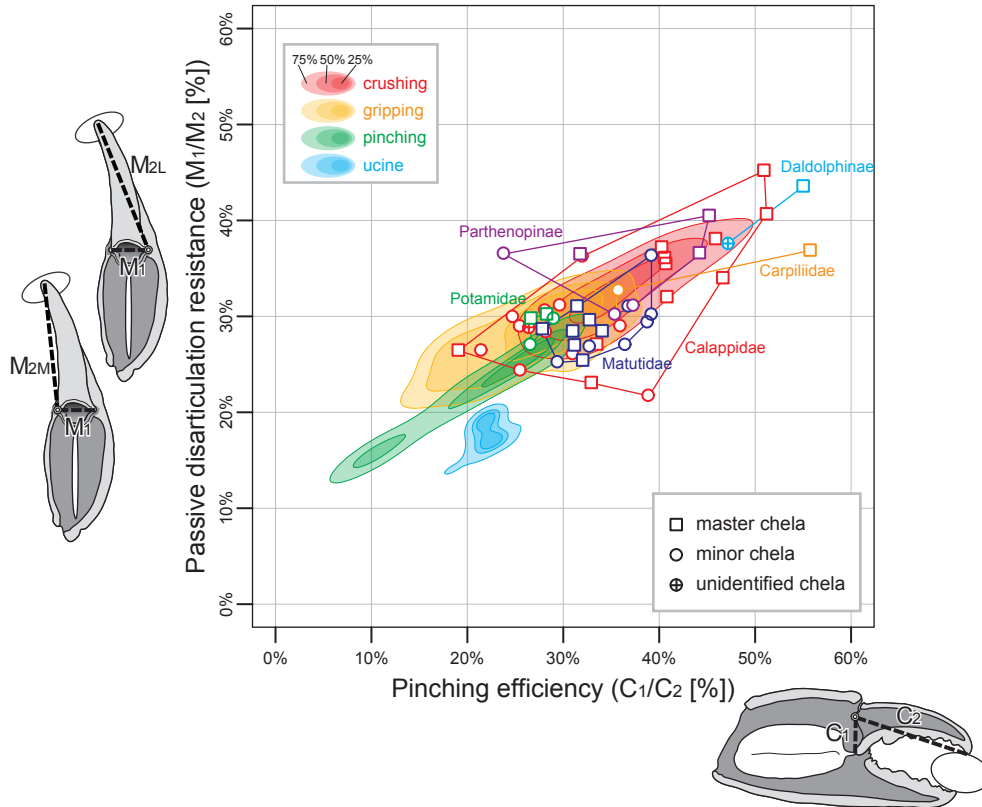
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**Fig. S6.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of "podotremate" brachyurans (Dromiacea [Dromiidae, Dynomenidae, and Homolidae] and Raninidae [Lyreidinae and Raninae]). Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.
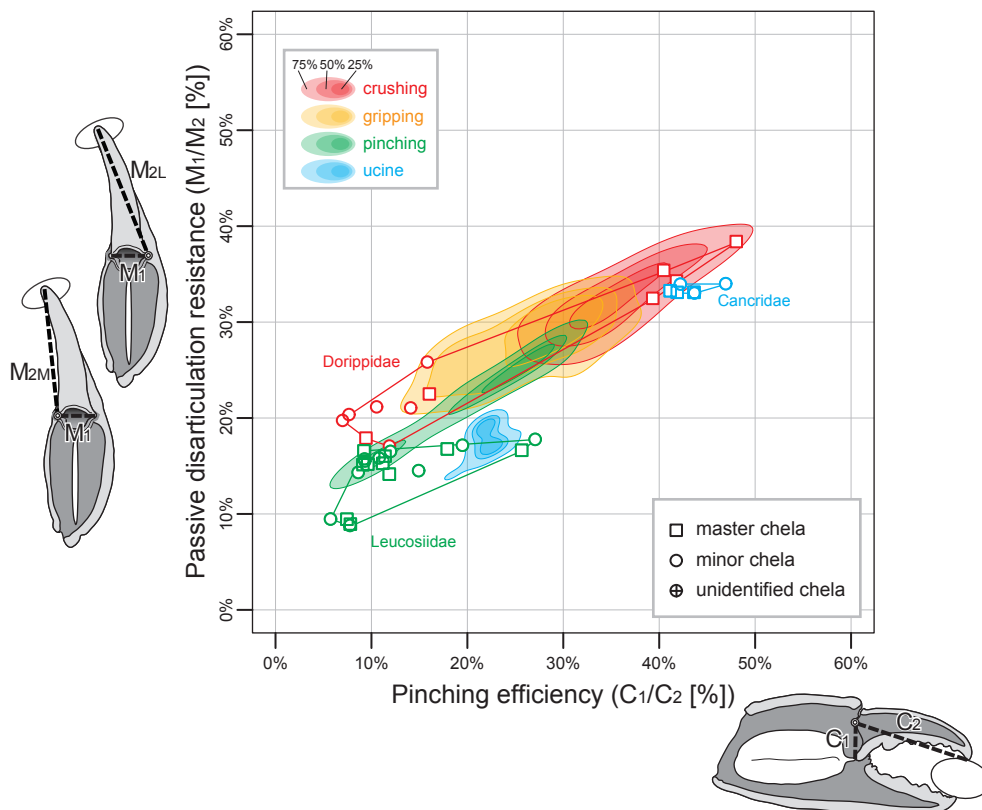


**Fig. S7.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of majoid brachyurans (Oregoniidae, Majidae, Inachidae, and Epialtidae). Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.
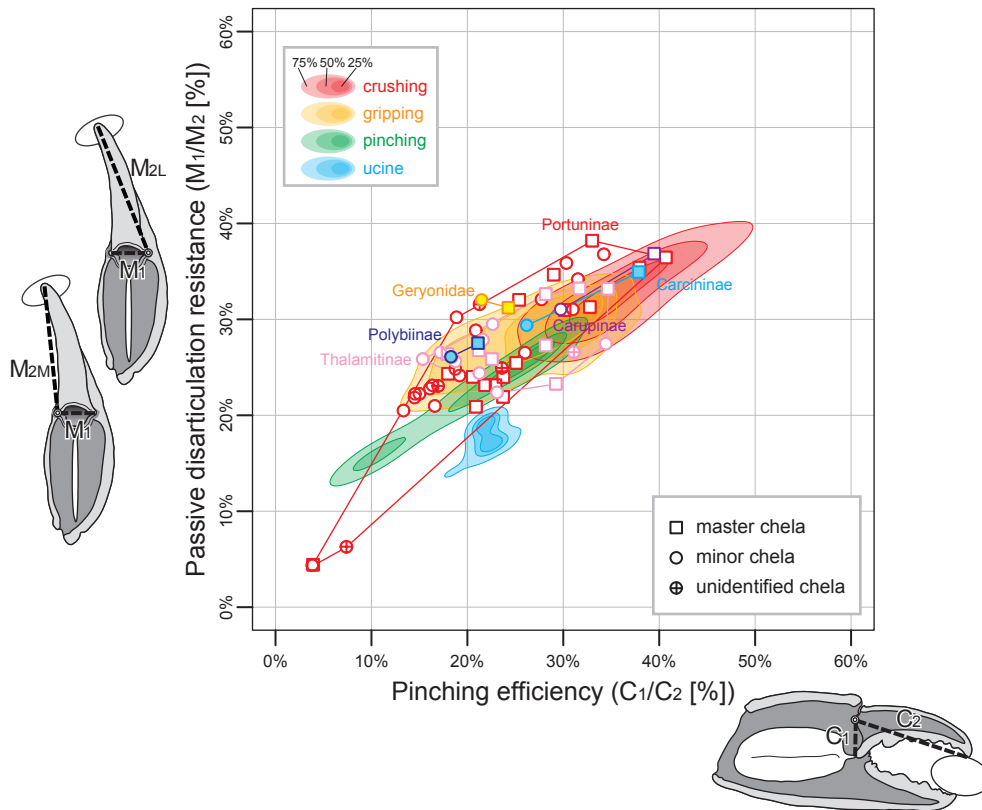
**Fig. S8.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of Calappidae, Matutidae, Potamidae, Carpiliidae, and Parthenopidae (Daldolphinae and Parthenopinae). Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.



**Fig. S9.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of a monophyletic brachyuran group which comprises Cancroidae, Dorippidae, and Leucosiidae. Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.
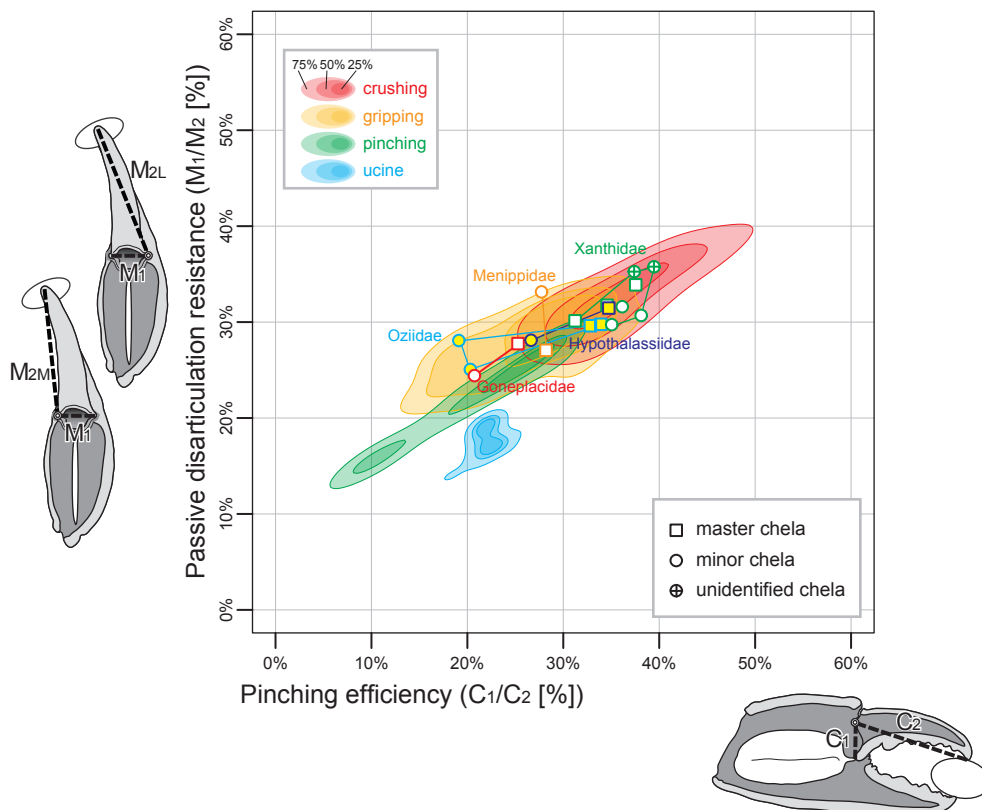
**Fig. S10.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of portunoids (Geryonidae and Portunidae [Carcininae, Polybiinae, Carupinae, Thalamitinae, and Portuninae]). Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.
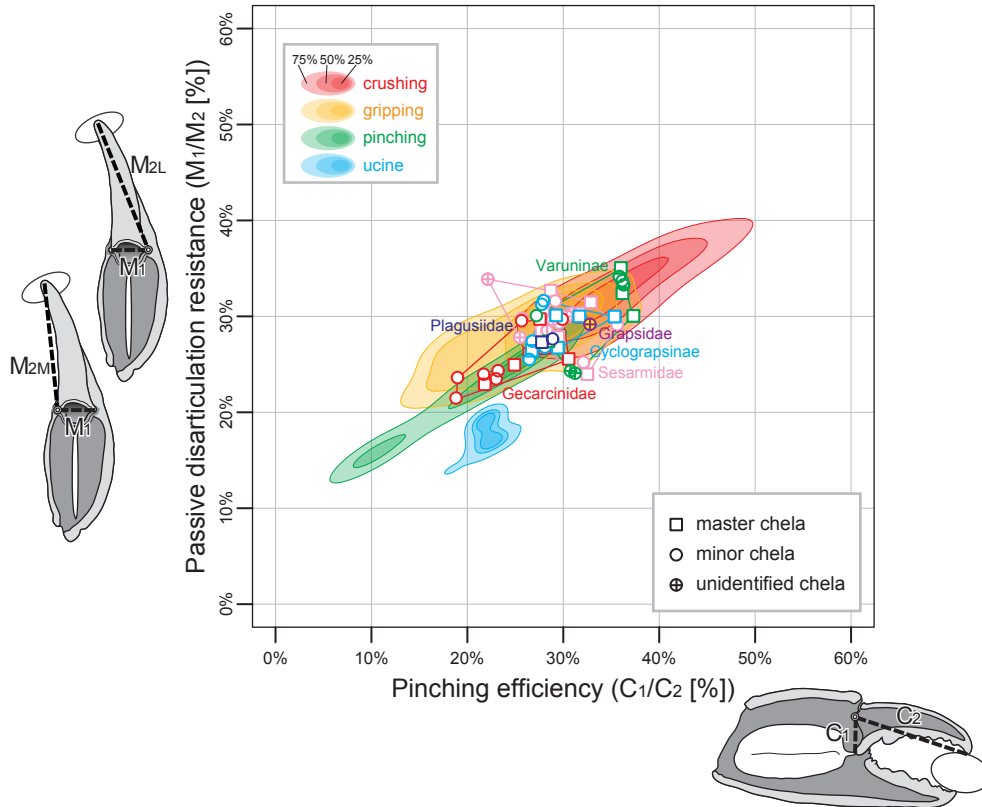


**Fig. S11.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of eriphioid (Hypothalassiidae, Menippidae, and Oziidae), goneplacoid (Goneplacidae), and xanthoid (Xanthidae) brachyurans. Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.
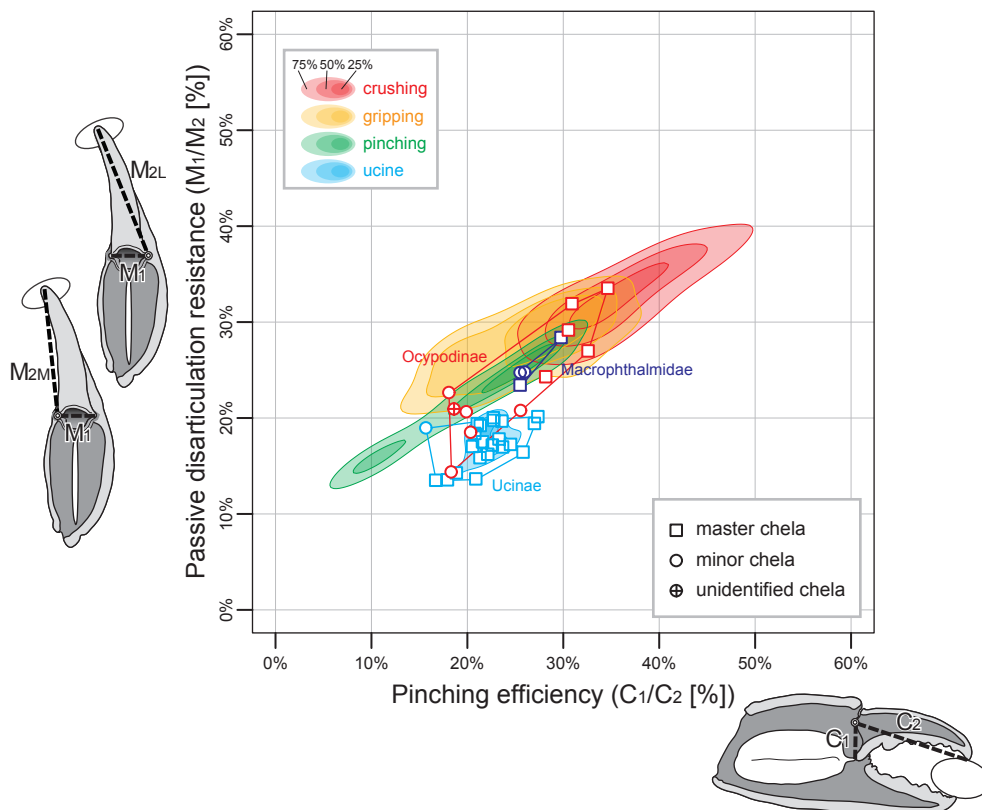
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**Fig. S12.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of grapsoid thorecotremates (Gecarcinidae, Grapsidae, Plagusiidae, Sesarmidae, and Varunidae [Cyclograpsinae and Varuninae]). Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.



**Fig. S13.** Mechanical advantages of pinching efficiency ($C_1/C_2$) and passive disarticulation resistance ($M_1/M_2$) in major and minor chelae of ocypodoid thoracotremates (Macrophthalmidae and Ocypodidae [Ocypodinae and Ucinae]). Colour gradations in the background are kernel densities (25%, 50%, and 75%) of chelae in the studied specimens for four different categories (crushing, gripping, pinching, and ucine). Range of the plots of each group is shown in convex hull. See Table S1 for the data.

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# Appendix S4: Use of triangle area as a proxy for the chela size

We assumed the chela as a triangle, and defined the area of the triangle as the size of the chela (see Fig. 1 and main text), while a distance from the proximal to the distal ends of the propodus has been used as a proxy for the chela size in many other studies (e.g., Savage and Sullivan, 1978; Abele et al., 1981; Brock and Smith, 1998). Therefore, the use of the triangular area (mm$^2$) as the proxy for the chela size need to be validated.

To answer the abovementioned concern, we tested the relationship between the chela sizes employed in previous studies (PL: propodus length which was defined as the distance between points *f* and *h* in Fig. 1 [mm]) and in this study (PS + CS: the triangle areas formed by points *a–c* and points *f–h* in Fig. 1) in the studied specimens (Table S1). Spearman's correlation test was conducted between "PL" and "PS + DS" by using a statistical software R 3.1.0 (R Foundation for Statistical Company). Null-hypothesis that there is no association between the two variables was rejected if *p*-value did not exceed 0.05.

According to the correlation test, "PL" and "PS + DS" were proved to be correlated ($p < 0.05$), and the coefficient of determination ($R^2$) was 0.875 (Fig. S14). Therefore, we consider that the use of "PS + DS" as a proxy of the chela size is valid.
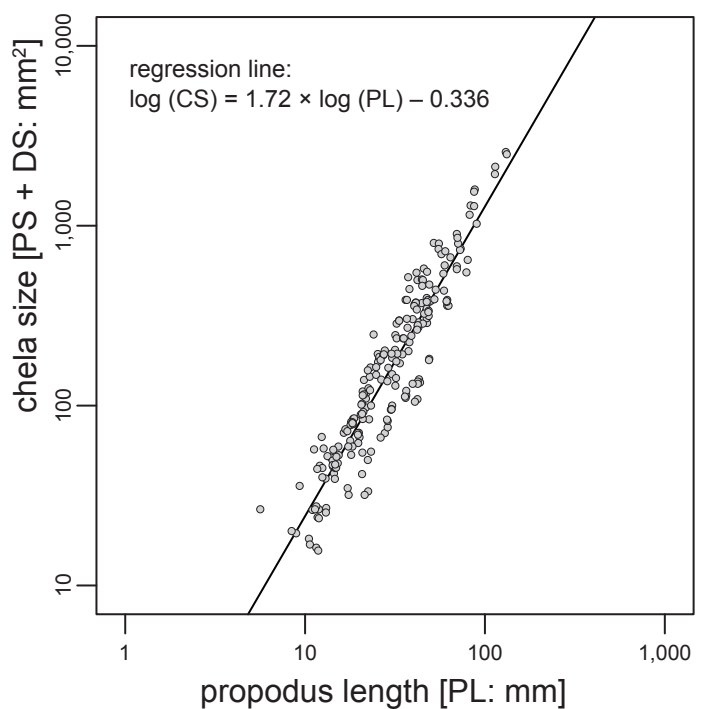


**Fig. S14.** Relationship between propodus length (PL: mm) and chela size (PS + DS: mm$^2$). An equation of the regression line is shown in the figure. Correlation between these two variables was supported by Spearman's correlation test: Spearman's $\rho$-value = 0.931; *p*-value < 2.2e–16; coefficient of determination ($R^2$) = 0.875.

**LITERATURE CITED**

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