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Phenotypic variability in the shield morphology of wild- vs. lab-reared eumalacostracan larvae

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ABSTRACT

Morphological identification of planktic crustacean larvae is required in many scientific contexts, such as ecology or taxonomy. Due to a still low availability of genetic sequences for many ingroups of Eumalacostraca, this task is still more feasible by morphological methods. Our understanding of eumalacostracan larval morphology is challenged by phenotypic variability. We investigated four eumalacostracan ingroups: Galatheidae, Hippoidea, Raninidae and Stomatopoda. Representatives of all four groups develop through spine-bearing planktic larval stages. Incorporating dorsal and lateral shield outlines into three-dimensional shape analysis of the shields, we compare specimens from the wild with laboratory-reared specimens. Using graphical and statistical analysis methods, we find that at least the lateral morphology of the shields of Hippoidea and Raninidae seems to be too strongly dependent on phylogeny to show phenotypic variability with our current sample size, but Hippoidea do show phenotypic variability in their dorsal shield morphology. In Galatheidae and Stomatopoda, a clear difference in shield morphology can be found between wild-caught and laboratory-reared specimens. This difference likely represents phenotypic variability. The exact environmental signals causing this phenotypic variability are still unknown, but some candidates are discussed.

KEYWORDS

Galatheidae, Hippoidea, morphological diversity, Raninidae, Stomatopoda.

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INTRODUCTION

Identifying crustacean larvae is frequently required in many ecological contexts, such as diversity studies or diet analyses, as they make up a large part of the zooplankton (e.g., Lindley, 1998; Sharma et al., 2017; Sorell et al., 2017; MacLeod et al., 2018; Bar-On and Milo, 2019; da Silva et al., 2019). Despite the advances of genomic methods for species identification in the past years, morphological methods are still easier to apply and cheaper in these contexts (Brown et al., 2015; Bucklin et al., 2016). Furthermore, for some crustacean larvae, widespread genetic identification is still hampered due to incomplete reference libraries (e.g., Heimeier et al., 2010; Tang et al., 2010; Brandão et al., 2016). Therefore, it is still important to have a fundamental understanding of the morphology and development of crustacean larvae to correctly identify species from wild samples. This information is often provided by laboratory-rearing studies supplying information on the developmental series of different species (e.g., Provenzano and Mannig, 1978; Konishi, 1987; Christiansen and Anger, 1990). However, larvae can exhibit differences when reared in the laboratory compared to growing up in the wild (e.g., Knight, 1967; Criales and Anger, 1986; Morgan and Provenzano, 1979; Braig et al., 2021). Environmental conditions impact the life-history, survival rates and development (among others) of crustacean larvae, but studies on the impact on their morphology are scarce (e.g., Anger 2001; 2006; Spitzner et al., 2019). Braig et al. (2021) found that shield configuration and spine length of some decapodan larvae can be influenced by the environment, by applying methods of quantitative morphology. Other authors have mentioned similar observations before (e.g., Knight, 1968; Furigo and Anger, pers. comm.) on a qualitative level.

Here, we investigate the morphological differences of selected eumalacostracan larvae from the laboratory and the wild. We focus on four different groups: Galatheidae (squat lobsters), Hippoidea (sand crabs), Raninidae (frog crabs), and Stomatopoda (mantis shrimps). The first three groups pass through a zoea phase during their development. The plesiomorphic (ancestral) condition for the zoea larva appears to have a shield without prominent spines as seen in most zoea larvae of Caridea (true shrimps) and many clawed lobsters (e.g., Hayashi and Hamano, 1984; Magalhães and Walker, 1988; Thatje et al., 2001; Rötzer and Haug, 2015). However, the three groups considered here all have developed zoea-type larvae with rather large spines (Fig. 1). The larval phase of mantis shrimps (Stomatopoda) is different from that of the other three (all ingroups of Decapoda) due to a more distant relationship, but includes larvae that are at least distantly comparable to zoea stage larvae (see discussion in Gurney, 1942). Mantis shrimp larvae again have spiny shields, like those of the other three groups.

Especially in these spines, we expect to find phenotypic variability (Braig et al., 2021). Therefore, we investigate the morphological diversity (related to "disparity"; Hopkins and Gerber, 2017) and potential phenotypic variability of the shield in dorsal and lateral view of these four eumalacostracan groups using quantitative morphology. We compare these aspects for planktic larvae caught in the wild and larvae reared in laboratory. The obtained results and implications are discussed in an ecological context.

MATERIAL AND METHODS

Material

Material for this study originated in parts from published literature, which provided images and reconstruction drawings of specimens. Additionally, specimens caught in the wild and stored in museum collections were directly investigated.

Literature sources include: Lebour, 1930; 1931; Johnson and Lewis, 1942; Manning and Provenzano, 1963; Knight, 1967; 1968; Fagetti and Campodonico, 1971; Sakai, 1971; Michel and Manning, 1972; Shanbhogue, 1975; Rice and Ingle, 1977; Provenzano and Manning, 1978; Gamô, 1979; Morgan and Provenzano, 1979; Greenwood and Williams, 1984; Stuck and Truesdale, 1986; Morgan and Goy, 1987; Seridji, 1988; Christiansen and Anger, 1990; Minagawa, 1990; Manning, 1991; Diaz, 1998; Konishi and Saito, 2000; Fujita et al., 2001; Fujita and Shokita, 2005; Siddiqi and Ghory, 2006; Fujita, 2007; Fonghoy, 2015; Rudolf et al., 2016; Mujica et al., 2019; Braig et al., 2021. Further material was provided by museums and collections: 'Museum für Naturkunde' Berlin,



Figure 1. Comparison of unidentified larvae of the four groups of Eumalacostraca, museum specimens under cross-polarized light. A–C: Representative of Galatheidae, specimen MNHN-IU-2014-5513B. A. Ventral view. B. Lateral view. C. Dorsal view. D–F: Representative of Hippoidea, specimen MNHN-IU-2014-5468 (after Rudolf et al., 2016). D. Anterior view. E. Ventral view. F. Posterior view. G–H: Representative of Hippoidea, specimen NMHD-86486 (Old number: ZMUC-CRU-8682; after Rudolf et al., 2016). G. Dorsal view. H. Ventral view. I: Representative of Raninidae, specimen MNHN-IU-2014-5467, lateral view. J: Representative of Raninidae, specimen MNHN-IU-2014-5360, lateral view. K–L: Representative of Stomatopoda, specimen NHMD-916095 (Old number: Stat-3955-II-A). K. Ventral view. L. Dorsal view. M–O: Representative of Stomatopoda, specimen ZMUC-CRU-8660 (after Haug et al., 2016). M. Ventral view. N. Dorsal view. O. Lateral view.

'Natural History Museum of Denmark' Copenhagen, 'Senckenberg Naturmuseum' Frankfurt, 'Muséum national d'Historie naturelle' Paris and 'Centrum für Naturkunde' Hamburg.

In total, 266 larval specimens were documented in dorsal and/or lateral view: 62 specimens of Galatheidae, 49 specimens of Hippoidea, 18 specimens of Raninidae and 137 specimens of Stomatopoda. The composition of the groups considering sample origin (i.e., wild-caught or lab-reared) are given in Tab. 1. For a detailed list of all material used in this study, see App. 1. If an individual was caught in the

	Wild-caught	Laboratory	Identified sp.	Accepted sp.	Taxonomic coverage (%)
Galatheidae	27	35	15	215	7
Hippoidea	25	24	7	87	8
Raninidae	3	15	2	39	5
Stomatopoda	103	34	31	489	6

Table 1. Group composition (wild-caught and laboratory specimens given in numbers) as well as number of species identified in the data set. Current number of accepted species of the group (WoRMS Editorial Board, 2021) and the resulting taxonomic coverage of the group by our data in percent.

wild (e.g., plankton sampling) and preserved and then documented either by us or by an author in the literature, it would be classified as "wild-caught". Specimens that originated from lab-rearing, i.e., when a gravid female was caught in the wild and its eggs were reared in the laboratory, and the consecutive stages were documented in the literature, they were classified as "lab-reared".

The four groups of crustaceans here were chosen firstly because data on specimens of these groups from the wild was available in high quality from multiple collections by our own documentation. This meant that we could ensure multiple images in different orientations of the same specimen, as well as a wider geographic coverage of specimens, which was a necessity for the study. Furthermore, we only chose groups with planktic and spiny larvae, as this was the trait we assumed to show variation from previous studies. Including more groups in the analysis would be desirable, but due to the state of documentation in the literature it is currently not possible. Larvae are rarely depicted in more than one orientation so that creating a sufficient sample size was hardly possible for more than the four groups presented here.

Data generation

For the documentation of specimens provided by museum collections, a macro-photography set-up was used. The specimens were photographed using a Canon Rebel T3i digital camera with a MP-E 65 mm macro lens. To reduce light-reflection induced artefacts, cross-polarized light was used, provided by a Canon Macro Twin Flash MT-24 or a Meike FC 100 LED ring light equipped with polarization filters and a cross-polarized filter in front of the camera lens (for a detailed description see Haug and Haug, 2014; Eiler et al., 2016). The specific components of this setup varied, but the principles and methodology remained the same throughout the documentation process. In such high-resolution set-ups, specimens were recorded as stacks of images with changing in-focus layers. For larger specimens, multiple images were taken per specimen to cover the entire organism. To create sharp images from the focus stacks, we used the free software CombineZP (Alan Hadley, GNU), which combines the sharp (in-focus) regions of each image of a focus stack into one sharp image (Haug et al., 2008). In cases in which the specimen was documented via multiple stacks, the sharp images resulting from these stacks were then stitched together to full images, using the Photomerge function of Photoshop CS4 or CS6 (Haug et al., 2008).

We used Adobe Illustrator CS2 to manually reconstruct the outline of shields in dorsal and lateral view (see App. 1 for availability of dorsal and lateral outlines per specimen; Fig. 2). The only exception to this was the group Raninidae, for which no dorsal data was available. To eliminate the influence of leftright asymmetry on the data set in dorsal view, we only reconstructed the left or right half of the shield, depending on which one was preserved better, and then duplicated and mirrored it in anterior-posterior axis and stitched it together to form a whole symmetric shield.

Morphometric conversion

To analyse the outlines of the specimens, an elliptic Fourier transformation was performed on the scaled reconstruction drawings (Fig. 2). Following Iwata and Ukai (2002) and Braig et al. (2019) we used the SHAPE software (© National Agricultural Research Organization of Japan) to first transform the outlines into vectorised objects, called chain codes. These chain codes consist of numeric values representing the vectorised shape and are then transformed into normalised elliptic Fourier descriptors (EFDs). This step is based on the Fourier transformation of functions, though not applied to functions, but to shapes of natural objects (Iwata and Ukai 2002;



Figure 2. Schematic figure of data generation process. **s1:** Reconstructing one half of the shield of a specimen; **s2:** duplicating, mirroring, and removing background; **s3:** chain coding the shield; **s4:** checking of graphical interpretation of chain code for accuracy; **s5:** transforming chain code into elliptic Fourier descriptor; **s6:** principal component analysis of elliptic Fourier descriptors of all specimens.

Braig et al., 2019). This step includes alignment, normalization, and scaling, which is important to decrease the influence of size difference in specimens on the analysis.

We decided on the outline-based approach in favor of landmarks, as high-quality landmarks were hard to select for shields apart from spine tips. Furthermore, outline approaches have been found to be equally efficient as landmark approaches (Dujardin et al., 2014).

Statistical analysis

The EFDs representing the specimens were then analysed with a principal component analysis (PCA; e.g., Hotelling, 1933; as featured in the SHAPE software package). Component loadings of the PCA are not given numerically using this method, but graphically to understand the change in shield shape. The mean shield shape as well as +/- 2 standard deviations of the mean shield shape in one or the other direction for each principal component are depicted. This imbalance can sometimes create positive/negative shapes which are impossible in nature. Such over-exaggerated shapes occur when some extreme forms are expressed in one direction, but not in the other. Then the extreme form is extrapolated for the other side of the respective component. Therefore, some shapes depicted by the component loadings do not actually exist in the data set, these are always marked as such in the figures. All further investigation of the data set was conducted in the R-statistics environment (ver. 4.1.0; R Core Team, 2021) using the interface R-Studio. Packages used were *dispRity* (ver. 1.6.0; Guillerme, 2018), *ggplot2* (ver. 3.3.5; Wickham, 2016), *RColorBrewer* (ver. 1.1-2; Neuwirth, 2014), *readxl* (ver. 1.3.1; Wickham and Bryan, 2019), and *vegan* (ver.2.5-7; Oksanen et al., 2020). Part of the R-code is after Guillerme et al. (2020), full R-code is provided in App. 2.

The individual component scores for the different PCAs were visualised using their origin (i.e., wildcaught or lab-reared) for color coding and in the cases of Hippoidea and Raninidae using their phylogeny for symbol coding. To enable interpretation of the morphology beyond only one orientation, the first principal component of the dorsal data set was plotted against the first principal component of the lateral data set. This allowed us to graphically interpret a more complete morphological variation of the animals, not just looking at variation of one orientation (i.e., dorsal or lateral) akin to a 3D representation. All resulting plots are used as proxies for the respective morphospaces. Morphospaces are multi-dimensional spaces that describe the morphology and phenotypic configuration of organisms (Ricklefs and Travis, 1980; Gould, 1991; Mitteroecker and Huttegger, 2009). For visual inspection they are reduced to two dimensions, that being the first two principal components. For quantification, all effective components are used. "Effective" in this case means that the proportion of total variation described by each of these principal components had a value larger than 1/(number of total analyzed components), in this case 1/99.

Quantification of morphological diversity between groups in the morphospace was achieved by calculating "average displacement" of groups as outlined by Guillerme et al. (2020). Hereby, the ratio between the position of an observation in relation to the centroid of the observations' group and the centre of the morphospace is calculated as displacement. This measure is then averaged for all observations of a group. The significance of the grouping variable (i.e. lab vs. wild) was tested using PERMANOVA (multivariate analysis of variance; Anderson, 2001). Advantageous of this approach is that all dimensions or principal components of a data set can be considered simultaneously.

RESULTS

Results of the morphological analysis of Galatheidae

The analysis of Galatheidae resulted in two PCAs, one of the dorsal and one of the lateral data set, with thirteen and twelve effective principal components, respectively, showing the morphological diversity of shield shapes apparent in the data sets. For visual inspection of morphological diversity, we only looked at the first two principal components of every data set due to limitations of graphical representation and the fact that the first two principal components covered most of the variation for all data sets (Galatheidae: dorsal PC1+2 = 80 %, lateral PC1+2 = 75 %; Hippoidea: dorsal PC1+2 = 85 %, lateral PC1+2 = 83 %; Raninidae: lateral PC1+2 = 84 %; Stomatopoda: dorsal PC1+2 = 70 %, lateral PC1+2 = 60 %). Therefore, a precise description is given on the first two components for every data set. The remaining principal components of the data sets will not be explained in detail, but graphical component loadings are given in the appendix (App. 3).

For the morphospace of the dorsal data set, PC1 described the width of the shield and length of spines. Positive values represented rather slim shields with a long rostrum and deep posterior notch, while negative values described wide shields with short rostrum and shallow posterior notch. PC2 described the prominence of the eye notch and posterior spines. Positive values described a wide rostrum base and a deep posterior notch, while negative values described a slim rostrum base and shallow posterior notch, with deep eye notches (Fig. 3A). Specimens from the plankton seemed to plot into the top right of the morphospace, indicating slimmer shields with relatively longer spines. Specimens from laboratory-rearings plotted into the bottom left of the morphospace, indicating bulkier shields with relatively short spines (Fig. 3A).

For the morphospace of the lateral data set, PC1 described the height of the shield, length of spines and prominence of the eye notch. Positive values represented a high shield with a short rostrum and a prominent, strongly inclined, eye notch, while negative values described slim shields with a long rostrum and more pronounced posterior spines and a shallow eye notch that almost appears missing. PC2 described the dorsal outline of the shield. Positive values described a weaker eye notch and posterior dorso-ventrally widened shield (dorsally convex outline), while negative values described a larger and pronounced eye notch and posteriorly slimmer shields (dorsally straighter outline; Fig. 3B). Specimens from the wild plotted on the left side of the morphospace, indicating slimmer shields with longer spines. Specimens from laboratory-rearings plotted on the right side of the morphospace, indicating bulkier shields with relatively short spines but more pronounced eye notches (Fig. 3B).

When incorporating both orientations by plotting PC1 of the dorsal data set against PC1 of the lateral data set, this separation became more apparent (Fig. 4A). Wild-caught specimens plotted on the center to bottom right of the morphospace, indicating slim, flat, and spiny shields. Lab-reared specimens plotted on the top left of the morphospace, indicating bulky and less spiny shields.



Figure 3. Plot of principal components from the PCA on the SHAPE analysis of shield outlines of Galatheidae. **A**: PC1 plotted against PC2, both from the dorsal analysis. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. **B**: PC1 plotted against PC2, both from the lateral analysis.



Figure 4. Plot of principal components from the PCA on the SHAPE analysis of shield outlines of Galatheidae and Hippoidea. **A:** PC1 of the dorsal analysis plotted against PC1 of the lateral analysis of Galatheidae. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. Color coding: dark grey: shapes of PC1 from the dorsal analysis; light grey: shapes of PC1 of the lateral analysis. **B**: PC1 of the dorsal analysis plotted against PC1 of the lateral analysis of Galatheidae. Shapes included are from graphical component loadings and depict the mean shape. Color coding: dark grey: shapes of PC1 of the lateral analysis of Hippoidea. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. Color coding: dark grey: shapes of PC1 from the dorsal analysis; light grey: shapes of the mean shape. Color coding: dark grey: shapes of PC1 from the dorsal analysis; light red: impossible shapes of PC1 of the lateral analysis; light red: impossible shapes of PC1 of the lateral analysis.

The morphological diversity analysis of the shields supported the graphical interpretation. Both the dorsal and lateral data set showed a significant influence of the sample origin on the position of the group within the morphospace (Tab. 2).

Results of the morphological analysis of Hippoidea

The analysis of Hippoidea resulted in two PCAs, one of the dorsal and one of the lateral data set, with eight and ten effective principal components respectively (for component loadings see App. 4).

For the morphospace of the dorsal data set, PC1 described the width of the shield and direction of

posterior spines. Positive values described a wide shield in triangular shape with more laterally protruding posterior spines, while negative values described a slim shield with posteriorly protruding posterior spines. PC2 described the presence of posterior spines. Positive values describe an overly thin shield with triangular shape and steep protruding posterior spines, while negative values described a wider elliptic shield with no posterior spines (Fig. 5A). Specimens from the wild seemed to plot rather on the top right of the morphospace, indicating shields with relatively longer spines which also protrude in steeper angles. Specimens from laboratory-rearings plotted rather on

Table 2. Results of permutational multivariate analysis of variance (PERMANOVA) on "average displacement" scores of wild-caught vs. laboratory specimens. Significant p-values are marked in bold. Abb.: F: pseudo F-statistic; R²: proportion of explained variation.

Taxonomic group	View	F	R ²	<i>p</i> -value
Galatheidae	dorsal	4.90	0.077	0.004
Galatheidae	lateral	16803.00	0.352	0.001
Hippoidea	dorsal	3.82	0.085	0.020
Hippoidea	lateral	0.57	0.021	0.620
Raninidae	lateral	0.63	0.038	0.619
Stomatopoda	dorsal	3.46	0.027	0.023
Stomatopoda	lateral	7.22	0.106	0.001



Figure 5. Plot of principal components from the PCA on the SHAPE analysis of shield outlines of Hippoidea. **A:** PC1 and PC2 of the dorsal analysis plotted against each other. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. Color coding: dark grey: possible shapes of dorsal analysis; red: impossible shapes of dorsal analysis. **B:** PC1 and PC2 of the lateral analysis plotted against each other. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. Color coding: light grey: possible shapes of lateral analysis; light red: impossible shapes of lateral analysis.

the left and bottom of the morphospace, indicating slimmer shields with relatively short spines, especially considering posterior spines (Fig. 5A).

For the morphospace of the lateral data set, PC1 described the overall configuration of the spines. Positive values described a slim shield with a long rostrum and posteriorly protruding posterior spines. Negative values described a higher shield with ventrally protruding posterior spines. PC2 described the dorsal outline of the shield and the rostrum. Positive values described a higher shield (dorsally strongly convex) with shorter rostrum, while negative values described a slimmer shield shape without ventral spines and a longer rostrum (Fig. 5B). Here, no separation between lab-reared and wild-caught specimens was visible. Instead, a separation into the major ingroups of Hippoidea became apparent. Hippidae plotted on the left side of the morphospace, Blepharipodidae in the middle and Albuneidae on the right (Fig. 5B).

When incorporating both orientations, this phylogenetic separation of the three ingroups of Hippoidea was again visible. Larvae of Albuneidae plotted on the top left of the morphospace, larvae of Hippidae on the bottom right and larvae of Blepharipodidae in between (Fig. 4B).

The morphological diversity analysis of the shields showed that only in the dorsal data set, sample origin had a significant influence on the position of the groups within the morphospace (Tab. 2).

Results of the morphological analysis of Raninidae

Due to a lack of dorsal data for specimens, the analysis of Raninidae resulted only in a PCA of the lateral data set with ten effective principal components (for component loadings see App. 5).

PC1 of the lateral data set described the height of the shield. Positive values represented a flat shield with long rostrum and posterior spine, while negative values described a high shield with a ventrally prominent eye notch. PC2 described the bending of the shield. Positive values described a smaller shield with convex spines, while negative values described a larger shield with concave spines (Fig. 6). Here, no separation due to sample origin could be seen. Instead, a clear separation between the two species in the data set could be seen (Fig. 6). Representatives of *Ranina ranina* (Linnaeus, 1758) and *Raninoides benedicti* Rathbun, 1935 plotted in two discrete clusters. The former plotted on the right of the morphospace due to its smaller shield and longer spines. The latter plotted on the left of the morphospace due to its larger shield and shorter spines.

The morphological diversity analysis of the shields showed no significant influence of the sample origin on the position of the groups within the morphospace (Tab. 2).

Results of the morphological analysis of Stomatopoda

The analysis of Stomatopoda resulted in two PCAs, one of the dorsal and one of the lateral data set, with thirteen and fifteen effective principal components, respectively (for component loadings see App. 6).

For the morphospace of the dorsal data set, PC1 described the width of the shield. Positive values described a slim shield with a long rostrum and deep posterior notch, while negative values described a wide shield with short rostrum and short posterior spines. PC2 described the prominence of spines. Positive values described a rectangular shield shape with short spines, while negative values described a more triangular shape with longer spines (Fig. 7A). Wild-caught specimens extend to the bottom-left and top-left corners of the morphospace, indicating wide shields with steep protruding spines and wide shields with additional anterior spines, respectively. Lab-reared specimens mostly plot in the center of the morphospace, indicating medium sized shields with relatively small spines (Fig. 7A).

For the morphospace of the lateral data set, PC1 described the presence of dorsal and posterior spines. Positive values described a shield with a dorsal spine but lack of posterior spines, while negative values described a shield without a dorsal spine but posterior spines present. PC2 described how flat the shield was. Positive values described a slim shield with long and straight rostrum and posterior spines, while negative values described a higher shield with a convex rostrum and prominent eye notch (Fig. 7B). Here, an imbalance of the sample sizes for wild vs. lab specimens of three to one becomes apparent (Fig. 7B). Lab-reared specimens plot mostly in the center of the morphospace and in the bottom left, indicating flatter shields, with smaller rostrum and dorsal spine to bulky shields with extended posterior spines. Wild-caught specimens



Figure 6. Plot of principal components from the PCA on the SHAPE analysis of shield outlines of Raninidae. PC1 and PC2 of the lateral analysis plotted against each other. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. Color coding: dark grey: possible shapes of the lateral analysis; red: impossible shapes of the lateral analysis.

plot in the top two quarters of the morphospace and the bottom right, indicating shields with extended posterior and dorsal spines to flat shields with smaller dorsal spines and long rostrums (Fig. 7B).

When incorporating both orientations, sample sizes were more balanced. The group of wild-caught larvae plotted diagonally across the morphospace from the top left of the morphospace to the bottom right (Fig. 8). This indicated wide shields and dorsal spines on the top left and slim shields with long spines on the bottom right. The lab-reared larvae plotted on the bottom right of the morphospace also indicating slim shields with long spines. Some outliers made an exception for the lab-reared specimens, plotting on the bottom middle of the morphospace (Fig. 8).

The morphological diversity analysis of the shields showed a significant influence of the sample origin on the position of the groups within the morphospace, both for the dorsal and lateral data set (Tab. 2).

DISCUSSION

Limitations of the approach

Gathering data for this analysis posed a challenge, as high-quality depictions of larvae in more than one orientation in literature were scarce. Often, only one orientation was available, reconstruction drawings in the literature were of low quality (e.g., Seridji, 1995), or scales were missing, rendering potential material useless for this study. This affected the total sample size of Raninidae the most. The group Stomatopoda was affected, as well. Due to our previous work with the group (e.g., Haug et al., 2016; 2018), we had a large sample size for wild-caught specimens from our own documentation efforts, but a comparatively small sample size for laboratory specimens. A result of not every specimen having a depiction of both orientations, was that the dorsal or lateral data sets included more specimens than the combined one.



Figure 7. Plot of principal components (PCs) from the principal component analysis (PCA) on the SHAPE analysis of shield outlines of Stomatopoda. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. **A:** PC1 plotted against PC2 from the dorsal analysis. **B**: PC1 plotted against PC2 from the lateral analysis. Color coding: dark grey: possible shapes of the dorsal analysis; red: impossible shapes of the dorsal analysis; light grey: possible shapes of lateral analysis; light red: impossible shapes of lateral analysis.

Another issue was low taxonomic coverage. Across groups, the taxonomic coverage ranges between 5 to 10 percent, mostly because specimens from museum collections (mostly wild-caught material) could not be identified to species level. Therefore, the number of actual taxonomic diversity covered is likely higher for each group than stated here. In the data set of Stomatopoda, many specimens are wildcaught, originating from museum collections and could not be identified to species level. The inability to associate larvae with adults is a general problem for mantis shrimps (Tang et al., 2010). This taxonomic uncertainty led to a correlation of phylogeny and sample origin for mantis shrimps in our analysis.

Phylogenetic diversity also influenced the data, especially for Hippoidea. To reduce the effect, a smaller ingroup could be chosen, e.g., Hippidae instead of Hippoidea. However, the current availability of



Figure 8. Plot of principal components from the PCA on the SHAPE analysis of shield outlines of Stomatopoda. PC1 of the dorsal analysis plotted against PC1 of the lateral analysis. Shapes included are from graphical component loadings and depict the mean shape of the principal component and +/-2 standard deviations of the mean shape. Color coding: dark grey: shapes of PC1 from the dorsal analysis; light grey: shapes of PC1 of the lateral analysis; dark red: impossible shapes of PC1 from the dorsal analysis; light red: impossible shapes of PC1 of the lateral analysis.

data in the literature makes this approach not feasible (e.g., only 13 specimens of Hippidae were available in dorsal and lateral view).

Expressed morphological diversity of larvae

The graphical analysis of the dorsal and lateral data set of Galatheidae showed separation between specimens from the wild and the lab. Wild-caught larvae show slimmer shields with longer rostrums and longer posterior spines (Figs. 3, 4). Laboratoryreared larvae show shorter rostrums and shorter poster spines with wider shields and less variation in morphology (Figs. 3, 4). This expressed phenotypic variability of the group Galatheidae agrees with our expectation. The statistical analysis, incorporating all principal components of a data set into one analysis, also showed that sample origin had a significant effect on the position of groups within the respective morphospaces (Tab. 2).

The graphical analysis of the dorsal and lateral data set of Hippoidea did not show a strong separation between lab-reared and wild-caught larvae. Wildcaught larvae show shields with laterally protruding spines, lab-reared specimens show more posteriorly protruding spines and especially forms with no posterior visible spines in dorsal view (Fig. 5). This difference in morphology of the groups is in line with an earlier observation of Braig et al. (2021). A stronger separation in the data sets is actually caused by the shield configuration of the three ingroups, which becomes apparent when coding for phylogenetic ingroups of Hippoidea (Fig. 4B). Larvae of Albuneidae have two posterior dorsal spines reaching posteriorly, while those of Hippidae have posterior ventral spines reaching ventrally (Knight, 1967; Stuck and Truesdale, 1986). Larvae of Blepharipodidae lastly have no posterior spines (Johnson and Lewis, 1942; Fig. 4B). The statistical analysis showed a significant effect of sample origin on the group position within the morphospace of the dorsal data set, but not the lateral data set.

The graphical analysis of the Raninidae data set did not reveal any phenotypic variability. A lack of dorsal data was added to the fact that only two identified species made up the data set, *Ranina ranina* and *Raninoides benedicti*. The morphological differences between those two species were discerned by the analysis of the lateral data set when adding phylogenetic coding (Fig. 6). Representatives of *R*. *benedicti* showed prominent shields and short spines, while representatives of *R*. *ranina* showed slimmer shields and longer spines. The statistical analysis showed no significant effect of sample origin (Tab. 2).

The graphical analysis of the dorsal and the lateral data set of Stomatopoda showed, respectively, a larger morphological diversity expressed by wild-caught larvae compared to laboratory-reared larvae (Figs. 7, 8). While wild-caught specimens expressed dorsal spines and wider shields as well as slimmer shields and longer spines, lab-reared specimens mostly showed slim shields with small dorsal spines. Therefore, the difference between groups mostly lies within the dorsal and lateral spines that wild-caught larvae express more dominantly than lab-reared ones. The statistical analysis showed a significant effect of sample origin on the group position within the morphospace of the dorsal and lateral data sets (Tab. 2).

Observations from literature

In the literature, phenotypic variability of Galatheidae has been mentioned considering larval development, which has been described to be variable and can lead to a different number of larval stages (e.g., Christiansen and Anger, 1990).

The developmental cycle in Hippoidea has been generally described as variable (Knight, 1967). Especially concerning comparison between wildcaught and lab-reared larvae, the former having been described to be further developed compared to the latter, when looking at equivalent larval stages (Knight, 1967). Yet, this increased maturity of wild-caught larvae concerned the setation on some appendages and general body growth, not the shield specifically.

For Raninidae, phenotypic variability has been reported in the literature. Knight (1968) mentioned that representatives of *R. benedicti* from the wild have longer spines on the shield than those reared in the laboratory. This observation coincides with our expectation of phenotypic variability between wild-caught and lab-reared larvae. However, we could not replicate this observation quantitatively in our analysis. Laboratory specimens of Raninidae have also been reported to be smaller than wild-caught larvae of the same larval stage (Knight, 1968).

Phenotypic variability in eumalacostracan larvae

The phenotypic variability found in five of the seven data sets does mostly match with our expectations. For Galatheidae, specimens from the wild express longer spines than laboratory-caught specimens. For Hippoidea, at least dorsally, wild-caught specimens show longer, more laterally protruding posterior spines. For Stomatopoda, wild-caught specimens show wider shields with dorsal spines. Therefore, the overall pattern of the groups seems to be indeed a more prominently spiny appearance for plankton specimens.

The driver behind this phenotypic variability is still unclear. It however seems to be the case that larvae become larger in the wild than in the lab (Knight, 1967; 1968). A larger body size makes it easier for visual predators, such as juvenile fishes, to spot the larvae (O'Brien, 1987; Anger, 2001; Kiørboe, 2011). Therefore, larger spines could be a defensive mechanism against predation. Using spines as a defensive mechanism was already described in some crab zoeas (Morgan, 1990). On the other hand, reaching a certain size threshold can protect from predation by different predators (O'Brien, 1979; Leonie, 2017). These size thresholds can be reached faster by increasing relative spine length.

A larger body size also has the effect of increasing body weight and therefore faster sinking rates of the larvae. To counteract this, the larva would either have to spend more energy on locomotion to maintain its position in the water column or increase its hydrostatic updrift. The latter could be achieved by larger spines as well (Anger, 2001). Lastly, the larger spines could be a general side effect of larger body size. However, it was also mentioned that spines in some groups were relatively longer as well, not just absolutely (Knight, 1968). Here, a connection could be seen to the relative development of the larvae. Authors before have observed that larvae from the wild would be further developed than larvae from the lab (Knight, 1967; Christiansen and Anger, 1990). Relatively longer spines could be one expression of this maturity.

A discrepancy in observed morphological differences is that while larvae of Galatheidae from the wild show slim shields rather than wide ones (Fig. 4A), larvae of Stomatopoda from the wild do also show wide shield forms. These wide shields often belong to "extreme types" of mantis shrimp larvae ("balloon shaped" or "flying saucer shaped"; Haug et al., 2016; 2018), of which there are not as many in the lab-reared data set. Such extreme shapes have not been described in Galatheidae so far. We cannot exclude that these "extreme types" of mantis shrimp larvae are representatives of species only found in the wild-caught sample, making it a phylogenetic signal rather than due to sample origin. But the lab-reared data set covers all larger ingroups of Stomatopoda and has larvae from both 'spearer' and 'smasher'-type mantis shrimps (two types of mantis shrimps are usually differentiated due to the morphology of the adult major raptorial appendages; Patek et al., 2004; Patek and Caldwell, 2005). Therefore, this seems insufficient to be the sole explanation of the observed morphological diversity.

CONCLUSION

Some of the investigated eumalacostracan larvae show phenotypic variability in their shield morphology. This variability especially concerns shield spines, which are more prominent in wild-caught larvae than in lab-reared larvae. Possible reasons could be decreasing predation pressure or increasing hydrostatic updrift, but further studies are needed to evaluate these possibilities. In the groups where we could not find such patterns, strong phylogenetic signals could be identified as a reason. Larger sample sizes of smaller phylogenetic groups are needed in these cases to investigate phenotypic variability. However, this approach is so far not possible due to a lack of material in the literature. This unavailability of morphological data is somewhat puzzling, since crustacean larvae make up a large part of the zooplankton and are important components in food webs. Yet, morphological data on its larger representatives is not widely available. We therefore hope that this study emphasizes the importance of careful documentation and consideration of larval material and stimulates the accumulation of more quantifiable data.

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ADDITIONAL INFORMATION AND DECLARATIONS

Author Contributions

Conceptualization and Design: JTH, FB. Performed research: FB.

Acquisition of data: FB, JTH, CH. Analysis and interpretation of data: FB, JTH.

Preparation of figures/tables/maps: FB, JTH, CH. Writing – original draft: FB, JTH, CH. Writing – critical review & editing: CH, FB, JTH.

Consent for publication

All authors declare that they have reviewed the content of the manuscript and gave their consent to submit the document.

Competing interests

The authors declare no competing interest.

Data availability

All study data are included in the article and/or supplementary material.

Funding and grant disclosures

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Study association

This study is a follow-up on Braig et al. (2021).

Study permits

Not applicable.

APPENDIX

Appendix 1. Material used in this study. Where major group affiliation of a specimen was left as "unidentified", the criterium was not used in the analysis.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
gal_001	unknown	unknown	unknown	wild	~	~		MNHN- IU-2014-5463	MNHN Paris		Hors campagne INVMAR, stat. 15A	yes	yes
gal_002	unknown	unknown	unknown	wild	~	~		MNHN-IU- 2014-5473A	MNHN Paris			yes	yes
gal_003	unknown	unknown	unknown	wild	1	~		MNHN-IU- 2014-5473B	MNHN Paris			yes	yes
gal_004	unknown	unknown	unknown	wild	~	~		MNHN-IU- 2014-5513A	MNHN Paris		Hors campagne INVMAR, stat. 309	yes	yes
gal_005	unknown	unknown	unknown	wild	~	~		MNHN-IU- 2014-5513B	MNHN Paris		Hors campagne INVMAR, stat. 309	yes	yes
gal_006	unknown	unknown	unknown	wild	~	~		MNHN- IU-2014-5515	MNHN Paris		Hors campagne INVMAR, stat. 311	yes	yes
gal_007	unknown	unknown	unknown	wild	~	~		MNHN-IU- 2014-5516A	MNHN Paris		Hors campagne INVMAR, stat. 309	yes	yes
gal_009	unknown	unknown	unknown	wild	/	/		MNHN- IU-2014-5520	MNHN Paris			yes	yes
gal_010	unidentified	Galathea	intermedia	lab	Christiansen and Anger	1990	fig. 1A					yes	yes
gal_011	unidentified	Galathea	intermedia	lab	Christiansen and Anger	1990	fig. 1B					yes	yes
gal_012	unidentified	Galathea	intermedia	lab	Christiansen and Anger	1990	fig. 1C					yes	yes
gal_013	unidentified	Galathea	intermedia	lab	Christiansen and Anger	1990	fig. 1D					yes	yes
$\operatorname{gal}_{-}014$	unidentified	Pleuroncodes	пороиот	lab	Fagetti and Campodonico	1971	fig. 1.1					yes	ou
gal_015	unidentified	Pleuroncodes	нороиот	lab	Fagetti and Campodonico	1971	fig. 1.2					yes	ou
gal_016	unidentified	Pleuroncodes	noponom	lab	Fagetti and Campodonico	1971	fig.1.3					yes	ou

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Appendix 1. Cont.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
gal_017	unidentified	Pleuroncodes	пороиот	lab	Fagetti and Campodonico	1971	fig. 1.4					yes	ou
gal_018	unidentified	Pleuroncodes	пороиот	lab	Fagetti and Campodonico	1971	fig. 3.39					yes	ou
gal_019	unidentified	Galathea	inflata	lab	Fujita et al.	2001	fig. 1A					yes	yes
gal_020	unidentified	Galathea	inflata	lab	Fujita et al.	2001	fig. 3A					yes	yes
gal_021	unidentified	Galathea	inflata	lab	Fujita et al.	2001	fig. 5A					yes	yes
gal_022	unidentified	Galathea	inflata	lab	Fujita et al.	2001	fig. 7A					yes	yes
gal_023	unidentified	Galathea	inflata	lab	Fujita et al.	2001	fig. 9A					yes	yes
gal_024	unidentified	Galathea	amboinensis	lab	Fujita et al.	2003	fig. 3A					yes	yes
gal_025	unidentified	Galathea	amboinensis	lab	Fujita et al.	2003	fig. 3B					yes	yes
gal_026	unidentified	Galathea	amboinensis	lab	Fujita et al.	2003	fig. 3D					yes	yes
gal_027	unidentified	Galathea	amboinensis	lab	Fujita et al.	2003	fig. 3E					yes	yes
gal_028	unidentified	Munida	rugosa	lab	Lebour	1930	Plate I A, B					yes	yes
gal_029	unidentified	Munida	rugosa	wild	Lebour	1930	Plate I C					yes	ou
gal_030	unidentified	Galathea	strigosa	lab	Lebour	1930	Plate II A, B					yes	yes
gal_031	unidentified	Galathea	strigosa	wild	Lebour	1930	Plate II C					yes	ou
gal_032	unidentified	Galathea	strigosa	wild	Lebour	1930	Plate II D					yes	ou
gal_033	unidentified	Galathea	strigosa	wild	Lebour	1930	Plate II E					yes	ou
gal_034	unidentified	Galathea	dispersa	lab	Lebour	1930	Plate III A					yes	ou
gal_035	unidentified	Galathea	dispersa	wild	Lebour	1930	Plate III B					yes	ou
gal_036	unidentified	Galathea	dispersa	wild	Lebour	1930	Plate III C					yes	ou
gal_037	unidentified	Galathea	dispersa	wild	Lebour	1930	Plate III D					yes	ou
gal_038	unidentified	Galathea	dispersa	wild	Lebour	1930	Plate III E					yes	ou
gal_039	unidentified	Sadayoshia	edwardsii	lab	Fujita and Shokita	2005	fig. 2A					yes	yes
gal_040	unidentified	Sadayoshia	edwardsii	lab	Fujita and Shokita	2005	fig. 2C					yes	yes
gal_041	unidentified	Sadayoshia	edwardsii	lab	Fujita and Shokita	2005	fig. 2E					yes	yes
gal_042	unidentified	Sadayoshia	edwardsii	lab	Fujita and Shokita	2005	fig. 2F					yes	yes
gal_043	unidentified	Lauriea	gardineri	lab	Fujita	2007	fig. 1B					yes	yes
$\mathrm{gal}_{-}044$	unidentified	Phylladiorhynchus	integrirostris	lab	Fujita	2007	fig. 3B					yes	yes
gal_045	unidentified	Allogalathea	elegans	lab	Fujita	2010	fig. 2A					yes	yes
$\mathrm{gal}_{-}046$	unidentified	Allogalathea	elegans	lab	Fujita	2010	fig. 2B					yes	yes
gal_047	unidentified	Allogalathea	elegans	lab	Fujita	2010	fig. 2C					yes	yes
gal_048	unidentified	Allogalathea	elegans	lab	Fujita	2010	fig. 2D					yes	yes

Appendix 1. Cont.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
gal_049	unidentified	Agononida	incerta	lab	Konishi and Saito	2000	fig. 1A					yes	ou
gal_050	unidentified	Munida	striola	lab	Konishi and Saito	2000	fig. 3A					yes	ou
gal_051	unidentified	Phylladiorhynchus	pusillus	wild	Mujica et al.	2019	fig. 1					yes	ou
gal_052	unidentified	Phylladiorhynchus	pusillus	wild	Mujica et al.	2019	fig. 1					yes	ou
gal_053	unidentified	Phylladiorhynchus	pusillus	wild	Mujica et al.	2019	fig. 1					yes	ou
gal_054	unidentified	Phylladiorhynchus	pusillus	wild	Mujica et al.	2019	fig. 1					yes	ou
gal_055	unidentified	Phylladiorhynchus	pusillus	wild	Mujica et al.	2019	fig. 1					yes	ou
gal_056	unidentified	Galathea	squamifera	lab	Lebour	1931	Plate 1A					yes	ou
gal_057	unidentified	Galathea	squamifera	wild	Lebour	1931	Plate 1B					yes	ou
gal_058	unidentified	Galathea	squamifera	wild	Lebour	1931	Plate 1C					yes	ou
gal_059	unidentified	Galathea	squamifera	wild	Lebour	1931	Plate 1D					yes	ou
gal_060	unidentified	Galathea	intermedia	lab	Lebour	1931	Plate 1F					yes	ou
gal_061	unidentified	Galathea	intermedia	wild	Lebour	1931	Plate 1G					yes	ou
gal_062	unidentified	Galathea	intermedia	wild	Lebour	1931	Plate 1H					yes	ou
hip_001	Hippidae	Emerita	analoga	lab	Johnson and Lewis	1942	Plate I 3					yes	ou
hip_002	Hippidae	Emerita	analoga	wild	Johnson and Lewis	1942	Plate I 5					ou	yes
hip_003	Blepharipodidae	Blepharipoda	occidentalis	lab	Johnson and Lewis	1942	Plate III					yes	yes
hip_004	Blepharipodidae	Blepharipoda	occidentalis	wild	Johnson and Lewis	1942	Plate IV					yes	yes
hip_{005}	Albuneidae	Lepidopa	sdoƙu	lab	Johnson and Lewis	1942	Plate V					yes	yes
hip_006	Hippidae	Emerita	holthuisi	lab	Siddiqi and Ghory	2006	fig. la					yes	ou
hip_007	Hippidae	Emerita	holthuisi	lab	Siddiqi and Ghory	2006	fig. 2a					yes	ou
hip_008	Hippidae	Emerita	holthuisi	lab	Siddiqi and Ghory	2006	fig. 3a					yes	ou
hip_009	Hippidae	Emerita	holthuisi	lab	Siddiqi and Ghory	2006	fig. 4a					yes	ou
hip_010	Hippidae	Emerita	holthuisi	lab	Siddiqi and Ghory	2006	fig. 5a					yes	ou
hip_011	Hippidae	Emerita	holthuisi	lab	Siddiqi and Ghory	2006	fig. 6a					yes	ou
hip_012	Hippidae	Emerita	sp.	lab	Fonghoy	2015	fig. 25					yes	yes
hip_013	Hippidae	Emerita	sp.	lab	Fonghoy	2015	fig. 27					yes	yes
hip_014	Hippidae	Emerita	sp.	lab	Fonghoy	2015	fig. 29					yes	yes
hip_015	Hippidae	Emerita	sp.	lab	Fonghoy	2015	fig. 31					yes	yes
hip_016	Hippidae	Emerita	sp.	lab	Fonghoy	2015	fig. 33					yes	yes
hip_017	Hippidae	Emerita	sp.	lab	Fonghoy	2015	fig. 35					yes	yes
hip_018	Hippidae	unknown	unknown	wild	Braig et al.	2021	fig. 4A-B	MNHN-IU- 2014-5475A	MNHN Paris	3°38'S 9°22'E, west of Gabun	Ombango 1960, c. 12, station 301	yes	ou

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Shield differences of wild- vs. lab-reared larvae

Appendix 1. Cont.

Lateral	ou	yes	yes	yes	yes	yes	yes	yes	yes	yes	ou	ou	оп	оп	оц
Dorsal	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Cruise	Ombango 1960, c. 12, station 301	I	I	Calypso 1961-62, station 108	Calypso 1961-62, station 108	Calypso 1961-62, station 139	I	Calypso 1961-62, station 26	Calypso 1961-62, station 139	Calypso 1961-62, station 153					
Geographic information	3°38'S 9°22'E, west of Gabun	20°S 73°W, west of Chile	20°S 73°W, west of Chile	23°07'S - 43°11'W, south of Brazil	23°07'S - 43°11'W, south of Brazil	24°03'S - 46°22'W, south of Brazil	Sansibar	08°25'S - 34°48'W, east of Brazil	24°03'S - 46°22'W, south of Brazil	I					
Museum	MNHN Paris	CeNak Hamburg	CeNak Hamburg	MNHN Paris	MNHN Paris	MNHN Paris	CeNak Hamburg	MNHN Paris	MNHN Paris	MNHN Paris	MNHN Paris	CeNak Hamburg	NHMD Copenhagen	NHMD Copenhagen	NHMD Copenhagen
Accession number	MNHN-IU- 2014-5475B	ZMH- K07448B	ZMH- K07448A	MNHN-IU- 2014-5524A	MNHN-IU- 2014-5524B	MNHN- IU-2014-5526	ZMH-K16356	MNHN- IU-2014-5523	MNHN- IU-2014-5527	MNHN- IU-2014-5518	MNHN- IU-2014-5468	SMF-Mu_267	NHMD-86483 (Old number: ZMUC- CRU-8679)	NHMD-86484 (Old number: ZMUC- CRU-8680)	NHMD-86486 (Old number: ZMUC- CRU-8682)
Figure	fig. 4C–D	fig.4E-H	fig. 3A–D	fig. 3E–F	fig. 3G-I	fig. 3J-L	fig. 1	fig. 2A–C	fig. 2D–F	fig. 2G-H	fig. 5	fig. 5	fig. S	fig. S	fig. S
Year	2021	2021	2021	2021	2021	2021	2021	2021	2021	2021	2016	2016	2016	2016	2016
Author	Braig et al.	Braig et al.	Braig et al.	Braig et al.	Braig et al.	Braig et al.	Braig et al.	Braig et al.	Braig et al.	Braig et al.	Rudolf et al.	Rudolf et al.	Rudolf et al.	Rudolf et al.	Rudolf et al.
Origin	wild	wild	wild	wild	wild	wild	wild	wild	wild	own wild own wild own wild own wild own wild		wild	wild		
Species	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown unknown unknown		unknown	unknown		
Species group	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown
Major group	Hippidae	Hippidae	Hippidae	Hippidae	Hippidae	Hippidae	Hippidae	Albuneidae	Albuneidae	Albuneidae	Hippidae	Hippidae	Hippidae	Hippidae	Hippidae
No	hip_019	hip_020	hip_021	hip_022	hip_023	hip_024	hip_025	hip_026	hip_027	hip_028	hip_029	hip_030	hip_031	hip_032	hip_033

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Shield differences of wild- vs. lab-reared larvae

Appendix 1. Cont.

No Maj hip_034 H													
hip_034 H	ior group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
	ippidae	unknown	unknown	wild	Rudolf et al.	2016	fig. 5	NHMD-86487 (Old number: ZMUC- CRU-8683)	NHMD Copenhagen			yes	yes
hip_035 H	ippidae	unknown	unknown	wild	Rudolf et al.	2016	fig. 5	NHMD-86488 (Old number: ZMUC- CRU-8684)	NHMD Copenhagen			yes	ou
hip_036 All	ouneidae	Albunea	carabus	wild	Seridji	1988	fig. 1a					yes	ou
hip_037 All	ouneidae	Albunea	carabus	wild	Seridji	1988	fig. 2a					yes	ou
hip_038 All	ouneidae	Albunea	carabus	wild	Seridji	1988	fig. 3a					yes	ou
hip_039 All	ouneidae	Lepidopa	benedicti	lab	Stuck & Truesdale	1986	fig. 1					yes	yes
hip_040 All	ouneidae	Lepidopa	benedicti	lab	Stuck & Truesdale	1986	fig. 2					yes	ou
hip_041 All	ouneidae	Lepidopa	benedicti	lab	Stuck & Truesdale	1986	fig. 3					yes	ou
hip_042 All	ouneidae	Lepidopa	benedicti	lab	Stuck & Truesdale	1986	fig. 4					yes	yes
hip_043 H	ippidae	Emerita	rathbunae	lab	Knight	1967	fig. 1					ou	yes
hip_044 H	ippidae	Emerita	rathbunae	lab	Knight	1967	fig. 2					ou	yes
hip_045 H	ippidae	Emerita	rathbunae	lab	Knight	1967	fig. 3					ou	yes
hip_046 H	ippidae	Emerita	rathbunae	wild	Knight	1967	fig. 4, 7, 9					yes	yes
hip_047 H	ippidae	Emerita	rathbunae	wild	Knight	1967	fig. 5					ou	yes
hip_048 H	ippidae	Emerita	rathbunae	lab	Knight	1967	fig. 6					yes	ou
ran_001 ur	ıknown	unknown	unknown	wild	This paper		Fig. 1 I	MNHN- IU-2014-5467	MNHN Paris			ou	yes
ran_002 ur	nwonat	unknown	unknown	wild	This paper		Fig. 1 J	MNHN- IU-2014-5360	MNHN Paris	23° 20' 30.0012'' S ; 168° S' 6.0252'' E	SMIB 5, stat. DW101	оп	yes
ran_003 Ra	uninidae	Raninoides	benedicti	lab	Knight	1968	figs. 1, 5, 6					yes	yes
ran_004 Ra	uninidae	Raninoides	benedicti	lab	Knight	1968	figs. 2, 7, 8					yes	yes
ran_005 Ra	uninidae	Raninoides	benedicti	lab	Knight	1968	figs. 3, 9, 10					yes	yes
ran_006 Ra	uninidae	Raninoides	benedicti	lab	Knight	1968	figs. 4, 11, 12					yes	yes
ran_007 Ra	uninidae	Ranina	ranina	lab	Minagawa	1990	fig. 1					ou	yes
ran_008 Ra	uninidae	Ranina	ranina	lab	Minagawa	1990	fig. 2					ou	yes
ran_009 Ra	uninidae	Ranina	ranina	lab	Minagawa	1990	fig. 3					ou	yes
ran_010 Ra	aninidae	Ranina	ranina	lab	Minagawa	1990	fig. 4					ou	yes
ran_011 Ra	aninidae	Ranina	ranina	lab	Minagawa	1990	fig. 5					ou	yes
ran_012 Ro	aninidae	Ranina	ranina	lab	Minagawa	1990	fig. 6					ou	yes

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Appendix 1. Cont.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
ran_013	Raninidae	Ranina	ranina	lab	Minagawa	1990	fig. 7					ou	yes
ran_014	Raninidae	Ranina	ranina	lab	Minagawa	1990	fig. 8					ou	yes
ran_015	Raninidae	Ranina	ranina	wild	Rice and Ingle	1977	fig. 1					ou	yes
ran_016	Raninidae	Ranina	ranina	lab	Sakai	1971	fig. 1					ou	yes
ran_017	Raninidae	Ranina	ranina	lab	Sakai	1971	fig. 2					ou	yes
ran_018	Raninidae	Ranina	ranina	lab	Sakai	1971	fig. 3					ou	yes
sto_001	unidentified	Squilla	sp.	wild	Diaz	1998	fig. 2					yes	ou
sto_002	unidentified	Squilla	sp.	wild	Diaz	1998	fig. 4					yes	ou
sto_003	unidentified	Squilla	sp.	wild	Diaz	1998	fig. 6					yes	ou
sto_004	unidentified	Squilla	sp.	wild	Diaz	1998	fig. 8					yes	ou
sto_005	unidentified	Squilla	sp.	wild	Diaz	1998	fig. 10					yes	ou
sto_006	unidentified	Squilla	sp.	wild	Diaz	1998	fig. 12					yes	ou
sto_007	unidentified	Squilla	sp.	wild	Diaz	1998	fig. 14					yes	ou
sto_008	unidentified	Lysiosquilla	sp.	wild	Gamô	1979	fig. 1	KH79-1-5-1		5°38.8'N, 130°20.2'E - 5°28.0'N,	KH-79-1	yes	ou
										130°19.9'E			
sto_012	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig. 4					yes	yes
sto_013	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig. 5					yes	yes
sto_014	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig. 6					yes	yes
sto_015	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig. 7					yes	yes
sto_016	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig. 8					yes	yes
sto_017	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 1A					yes	ou
sto_018	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 1B					yes	ou
sto_019	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 1C					yes	ou
sto_020	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 12					yes	ou
sto_021	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 15					yes	ou
sto_022	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 17A					yes	ou
sto_023	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 17B					yes	ou
sto_024	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 19					yes	ou

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Appendix 1. Cont.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
sto_025	unidentified	Squilla	empusa	wild	Morgan and Provenzano	1979	fig. 21					yes	ou
sto_026	unidentified	Gonodactylus	oerstedii	lab	Provenzano and Manning	1978	fig. 2					yes	yes
sto_027	unidentified	Gonodactylus	oerstedii	lab	Provenzano and Manning	1978	fig. 3					yes	yes
sto_028	unidentified	Gonodactylus	oerstedii	lab	Provenzano and Manning	1978	fig. 4					yes	yes
sto_029	unidentified	Gonodactylus	chiragra	wild	Shanbhogue	1975	fig. 1A					yes	ou
sto_030	unidentified	Gonodactylus	sp.	wild	Shanbhogue	1975	fig. 1C					yes	ou
sto_031	unidentified	Gonodactylus	sp.	wild	Shanbhogue	1975	fig. 1E					yes	ou
sto_032	unidentified	Gonodactylus	sp.	wild	Shanbhogue	1975	fig. 1G					yes	ou
sto_033	unidentified	Gonodactylus	sp.	wild	Shanbhogue	1975	fig. 1J					yes	ou
sto_034	unidentified	Pseudosquilla	ciliata	wild	Shanbhogue	1975	fig. 2A					yes	ou
sto_035	unidentified	Pseudosquilla	sp.	wild	Shanbhogue	1975	fig. 2C					yes	ou
sto_036	unidentified	Acanthosquilla	multifasciata	wild	Shanbhogue	1975	fig. 2G					yes	ou
sto_037	unidentified	Lysiosquilla	duvaucelli?	wild	Shanbhogue	1975	fig. 3A					yes	ou
sto_038	unidentified	Lysiosquilla	sp.	wild	Shanbhogue	1975	fig. 3E					yes	ou
sto_039	unidentified	Alima	hieroglyphica	wild	Shanbhogue	1975	fig. 4A					yes	ou
sto_040	unidentified	Alima	sp.	wild	Shanbhogue	1975	fig. 4C					yes	ou
sto_041	unidentified	Harpiosquilla	harpax	wild	Shanbhogue	1975	fig. 5A					yes	ou
sto_042	unidentified	Harpiosquilla	sp.	wild	Shanbhogue	1975	fig. SC					yes	ou
sto_043	unidentified	Harpiosquilla	sp.	wild	Shanbhogue	1975	fig. SE					yes	ou
sto_044	unidentified	Miyakella	nepa	wild	Shanbhogue	1975	fig. SH					yes	ou
sto_045	unidentified	Oratosquilla	gonypetes	wild	Shanbhogue	1975	fig. 6A					yes	ou
sto_046	unidentified	Oratosquilla	woodmansoni	wild	Shanbhogue	1975	fig. 6B					yes	ou
sto_047	unidentified	Oratosquilla	sp.	wild	Shanbhogue	1975	fig. 6C					yes	ou
sto_048	unidentified	Oratosquilla	sp.	wild	Shanbhogue	1975	fig. 7C					yes	ou
sto_252	unidentified	unknown	unknown	wild	/	/		23_09_1903_ X01E	MfN Berlin			yes	ou
sto_253	unidentified	unknown	unknown	wild	/	/		20500	MfN Berlin			yes	ou
sto_257	unidentified	unknown	unknown	wild	Haug et al.	2016	fig. 1	NHMD-86459 (Old number: ZMUC- CRU-8655)	NHMD Copenhagen			yes	оп
sto_258	unidentified	unknown	unknown	wild	_	~		NHMD- 232158	NHMD Copenhagen			yes	yes

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Appendix 1. Cont.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
sto_259	unidentified	unknown	unknown	wild	/	~		NHMD- 916092	NHMD Copenhagen			yes	ou
sto_260	unidentified	unknown	unknown	wild	~	~		NHMD- 273050	NHMD Copenhagen			yes	ou
sto_261	unidentified	unknown	unknown	wild	/	~		1192_VII_A	NHMD Copenhagen			yes	ou
sto_262	unidentified	unknown	unknown	wild	/	~		NHMD- 916093	NHMD Copenhagen			yes	ou
sto_264	unidentified	unknown	unknown	wild	~	~		NHMD- 232168	NHMD Copenhagen			yes	yes
sto_265	unidentified	unknown	unknown	wild	Haug et al.	2018	fig. 1	NHMD- 232175	NHMD Copenhagen			yes	yes
sto_267	unidentified	unknown	unknown	wild	_	~		NHMD- 916094	NHMD Copenhagen			yes	yes
sto_268	unidentified	unknown	unknown	wild	~	~		NHMD- 232176	NHMD Copenhagen			yes	yes
sto_269	unidentified	unknown	unknown	wild	Haug et al.	2016	fig. 8	NHMD-86472 (Old number: ZMUC- CRU-8668)	NHMD Copenhagen			yes	ou
sto_270	unidentified	unknown	unknown	wild	This Paper		Fig. 1 K-L	NHDM- 916095 (Old number: Stat- 3955-II-A)	NHMD Copenhagen			yes	ou
sto_271	unidentified	unknown	unknown	wild				NHMD- 232173 (Old number: Stat- 3955-II-B)	NHMD Copenhagen			yes	yes
sto_272	unidentified	unknown	unknown	wild	~	~		016096 DI6096	NHMD Copenhagen			yes	ou
sto_274	unidentified	unknown	unknown	wild	~	~		NHMD- 232181	NHMD Copenhagen			yes	yes
sto_276	unidentified	unknown	unknown	wild	~	~		016097 916097	NHMD Copenhagen			yes	ou
sto_277	unidentified	unknown	unknown	wild	/	~		NHMD- 232161	NHMD Copenhagen			yes	yes
sto_278	unidentified	unknown	unknown	wild	Haug et al.	2018	fig. 5	NHMD- 232162	NHMD Copenhagen			yes	yes
sto_279	unidentified	unknown	unknown	wild	/	~		NHMD-86475	NHMD Copenhagen			yes	ou
sto_280	unidentified	unknown	unknown	wild	~	~		NHMD- 232163	NHMD Copenhagen			yes	yes

Nauplius, 31: e2023004

Appendix 1. Cont.

al Lateral	ou	yes	yes	yes	ои	yes	yes	yes	yes	yes	yes	yes	ou	yes	yes	yes	
Dorsa	yes	yes	yes	yes	yes	ou	yes	yes	yes	yes	yes	yes	yes	ر), yes و	yes	yes	
Cruise														MD32 (REUNION stat. CP146			
Geographic information														20° 32' 42'' S; 55° 40' 53.9976'' E			
Museum	NHMD Copenhagen	NHMD Copenhagen	NHMD Copenhagen	NHMD Copenhagen	NHMD Copenhagen	NHMD Copenhagen	NHMD Copenhagen	MNHN Paris	MNHN Paris	MNHN Paris	MNHN Paris	MNHN Paris	MNHN Paris	MNHN Paris	MNHN Paris	MNHN Paris	
Accession number	916098	NHMD- 232165	NHMD-86470 (Old number: ZMUC- CRU-8666)	NHMD-86471 (Old number: ZMUC- CRU-8667)	NHMD-86468 (Old number: ZMUC- CRU-8664)	NHMD- 232171	NHMD- 232160	MNHN-IU- 2014-5493C	MNHN- IU-2014-5495	MNHN- IU-2014-5498	MNHN- IU-2014-5499	MNHN-IU- 2014-5493B	MNHN- IU-2014-5509	MNHN- IU-2014-5474	MNHN- IU-2014-5476	MNHN- IU-2014-5477	
Figure			fig. S	fig. 8	fig. 8												
Year	~	~	2016	2016	2016	~	~	~	~	~	~	~	~	~	~	~	
Author	~	~	Haug et al.	Haug et al.	Haug et al.	/	~	/	~	~	~	~	/	~	~	/	
Origin	wild	wild	wild	wild	wild	wild	wild	wild	wild	wild	wild	wild	wild	wild	wild	wild	
Species	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	
Species group	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	unknown	
Major group	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	unidentified	
No	sto_281	sto_282	sto_284	sto_285	sto_287	sto_289	sto_290	sto_296	sto_297	sto_298	sto_299	sto_300	sto_301	sto_302	sto_303	sto_304	

Appendix 1. Cont.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
sto_306	unidentified	unknown	unknown	wild	/	~		MNHN- IU-2014-5489	MNHN Paris			yes	yes
sto_307	unidentified	unknown	unknown	wild	/	~		MNHN-IU- 2014-5493A	MNHN Paris			yes	yes
sto_308	unidentified	unknown	unknown	wild	/	~		MNHN- IU-2014-5494	MNHN Paris			yes	yes
sto_309	unidentified	unknown	unknown	wild	/	~		MNHN- IU-2014-5500	MNHN Paris			yes	yes
sto_311	unidentified	unknown	unknown	wild	_	~		MNHN- IU-2014-5507	MNHN Paris			yes	yes
sto_312	unidentified	unknown	unknown	wild		~		MNHN- IU-2014-5511	MNHN Paris			yes	yes
sto_313	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 4					yes	yes
sto_314	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 5					yes	yes
sto_315	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 6					yes	yes
sto_316	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 7					yes	yes
sto_317	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 8					yes	yes
sto_318	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 9					yes	yes
sto_319	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 10					yes	yes
sto_320	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 11					yes	yes
sto_321	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 12					yes	yes
sto_322	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 13					yes	yes
sto_338	unidentified	Squilla	hieroglyphica	wild	Alikunhi	1944	fig. 1					yes	ou
sto_339	unidentified	Heterosquilla	tricarinata	lab	Greenwood and Williams	1984	fig. 1					yes	ou
sto_340	unidentified	Heterosquilla	tricarinata	lab	Greenwood and Williams	1984	fig. 1					yes	ou
sto_341	unidentified	Heterosquilla	tricarinata	lab	Greenwood and Williams	1984	fig. 1					yes	ou
sto_342	unidentified	Gonodactylus	oerstedii	lab	Manning and Provenzano	1963	fig. 1					yes	yes
sto_343	unidentified	Gonodactylus	oerstedii	lab	Manning and Provenzano	1963	fig. 3					yes	yes
sto_344	unidentified	Gonodactylus	oerstedii	lab	Manning and Provenzano	1963	fig. 5					yes	yes
sto_345	unidentified	Gonodactylus	oerstedii	lab	Manning and Provenzano	1963	fig. 7					yes	yes
sto_346	unidentified	Chorisquilla	tuberculata	wild	Michel and Manning	1972	fig. 1					yes	yes

Appendix 1. Cont.

No	Major group	Species group	Species	Origin	Author	Year	Figure	Accession number	Museum	Geographic information	Cruise	Dorsal	Lateral
sto_347	unidentified	Chorisquilla	tuberculata	wild	Michel and Manning	1972	fig.3					yes	yes
sto_348	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig. 1					yes	yes
sto_349	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig. 2					yes	yes
sto_350	unidentified	Gonodactylus	bredini	lab	Morgan and Goy	1987	fig.3					yes	yes
sto_351	unidentified	Acanthosquilla	sp.	wild	Shanbhogue	1975	fig. 2E					yes	ou
sto_352	unidentified	Coroniderichthus	sp.	wild	Shanbhogue	1975	fig. 3H					yes	ou
sto_353	unidentified	Coroniderichthus	sp.	wild	Shanbhogue	1975	fig. 3J					yes	ou
sto_354	unidentified	Clorida	laterilli	wild	Shanbhogue	1975	fig. 4E					yes	ou
sto_355	unidentified	Squilla	sp.	wild	Townsley	1953	fig. 22A					yes	ou
sto_356	unidentified	Squilla	sp.	wild	Townsley	1953	fig. 22B					yes	ou
sto_357	unidentified	Squilla	sp.	wild	Townsley	1953	fig. 22C					yes	ou
sto_358	unidentified	Squilla	sp.	wild	Townsley	1953	fig. 22D					yes	ou
sto_359	unidentified	Pseudosquilla	ciliata	wild	Townsley	1953	fig. 23A					yes	ou
sto_360	unidentified	Pseudosquilla	ciliata	wild	Townsley	1953	fig. 23B					yes	yes
sto_361	unidentified	Pseudosquilla	ciliata	wild	Townsley	1953	fig. 23D					ou	yes
sto_362	unidentified	Lysiosquilla	sp.	wild	Townsley	1953	fig. 25B					ou	yes
sto_363	unidentified	Coronida	sp.	wild	Townsley	1953	fig. 26A					ou	yes
sto_364	unidentified	Coronida	sp.	wild	Townsley	1953	fig. 27A					yes	ou
sto_365	unidentified	Odontodactylus	sp.	wild	Townsley	1953	fig. 28A					ou	yes
sto_366	unidentified	Odontodactylus	sp.	wild	Townsley	1954	fig. 28B					ou	yes
sto_367	unidentified	Oratosquilla	oratoria	lab	Hamano	1986	fig. 3					yes	yes
sto_368	unidentified	unknown	unknown	wild	1	~		MNHN- IU-2014-5481	MNHN Paris			yes	yes
sto_369	unidentified	unknown	unknown	wild	1	~		MNHN-IU- 2014-5483B	MNHN Paris			yes	ou
sto_370	unidentified	unknown	unknown	wild	1	~		MNHN- IU-2014-5487	MNHN Paris			yes	yes
sto_371	unidentified	unknown	unknown	wild	/	~		MNHN- IU-2014-5502	MNHN Paris			yes	ou
sto_372	unidentified	unknown	unknown	wild	/	~		MNHN- IU-2014-5510	MNHN Paris			yes	yes
sto_373	unidentified	unknown	unknown	wild	Haug and Haug	2014	fig. 4	NHMD-88528 (Old number: ZMUC- CRU-20243)	NHMD Copenhagen			yes	yes

Appendix 2. R-code used in this study. # R-Code of Braig, F., Haug, C. & Haug, J. T. # Geometric morphometrics uncover phenotypic variability in the shields of wild-*#* vs. lab-reared eumalacostracan larvae # START WORKFLOW -----library(ggplot2) library(MASS) library(car) library(vegan) library(tidyverse) library(RColorBrewer) library(dispRity) set.seed(1234) # DATA SETS ------# gal dor <- Dorsal data set of Galatheidae # gal lat <- Lateral data set of Galatheidae # gal dorlat <- Dorsal and Lateral data set of Galatheidae combined # hip dor <- Dorsal data set of Hippoidea # hip lat <- Lateral data set of Hippoidea # hip dorlat <- Dorsal and Lateral data set of Hippoidea combined # ran lat <- Lateral data set of Raninidae # sto dor <- Dorsal data set of Stomatopoda # sto lat <- Lateral data set of Stomatopoda # sto dorlat <- Dorsal and Lateral data set of Stomatopoda combined # PLOTS -----#Plot 2 PC's as basic as possible ggplot(gal dor, aes(x=PC1, y=PC2, color=origin)) +geom point() #Plot 2 PC's accoridng to origin with labels and ellipses ggplot(gal lat, aes(x = PC1, y = PC2, color = origin, label = no)) +geom point() + scale color manual(values=c("purple", "orange")) + geom text(aes(label=no), hjust = 0, vjust = 1, show.legend = FALSE) + stat ellipse(geom = 'polygon', alpha = .1, aes(fill = origin)) + scale_fill_manual(values = c("purple", "orange")) + coord fixed (ratio = 1, xlim = NULL, ylim = NULL, expand = TRUE) + theme gray() # MORPHOLOGICAL DIVERSITY ANALYSIS-----data <- data.frame(gal dor[, 6:18]) #Only numerical data rownames(data) <- 1:nrow(data) galdor subsets <- custom.subsets(data, group = list("lab" = c(1:35), "wild" = c(36:61)))galdor bootstrapped <- boot.matrix(data = galdor subsets, bootstraps = 10000) disparity.metric <- function(matrix) mean(dispRity::displacements(matrix)) galdor disparity <- dispRity(data = galdor bootstrapped, metric = disparity.metric) summary(galdor disparity) plot(galdor disparity) plot(galdor disparity, type = "preview") test.dispRity(galdor disparity, test = adonis.dispRity) #Passing on to # ANOVA function from package package vegan test.dispRity(galdor disparity, test = t.test, correction = "bonferroni")

Α	-2 S.D.	mean	+2 S.D.	В	-2 S.D.	mean	+2 S.D.
PC1 (44.3%)				PC1 (61.6%)			
PC2 (33.6%)				PC2 (13.3%)			
PC3 (7.6%)				PC3 (9.1%)			
PC4 (3.9%)				PC4 (6.3%)			
PC5 (2.7%)				PC5 (2.7%)			
PC6 (1.5%)				PC6 (1.4%)			
PC7 (1.2%)				PC7 (1.0%)			
PC8 (0.9%)				PC8 (0.9%)			
PC9 (0.8%)				PC9 (0.7%)			
PC10 (0.6%)				PC10 (0.6%)			
PC11 (0.5%)				PC11 (0.5%)			
PC12 (0.3%)				PC12 (0.3%)			
PC13 (0.2%)							

Appendix 3. Principal components of Galatheidae from principal component analysis on the shield outline and percentage of total variation in the data set explained by each principal component. **A:** Dorsal data set. **B:** Lateral data set.

	Α	-2 S.D.	mean	+2 S.D.	В	-2 S.D.	mean	+2 S.D.
PC1 (59.5%	.)	>			PC1 (59.5%)			
PC2 (24.4%	b)				PC2 (22.8%)			
PC3 (8.8%)					PC3 (8.3%)			
PC4 (3.7%)					PC4 (3.9%)			
PC5 (1.2%)					PC5 (1.4%)			
PC6 (0.7%)					PC6 (1.0%)			
PC7 (0.4%)					PC7 (0.9%)			
PC8 (0.3%)					PC8 (0.5%)			
				•	PC9 (0.4%)			
					PC10 (0.3%)			

Appendix 4. Principal components of Hippoidea from principal component analysis on the shield outline and percentage of total variation in the data set explained by each principal component. **A:** Dorsal data set. **B:** Lateral data set.

	-2 S.D.	mean	+2 S.D.
PC1 (53.3%)			
PC2 (29.5%)			
PC3 (6.7%)			
PC4 (5.0%)			
PC5 (2.0%)			
PC6 (1,4%)			
PC7 (0.7%)			
PC8 (0.4%)			
PC9 (0.3%)			
PC10 (0.3%)			

Appendix 5. Principal components of Raninidae from principal component analysis on the lateral shield outline and percentage of total variation in the data set explained by each principal component.

Α	-2 S.D.	mean	+2 S.D.	В	-2 S.D.	mean	+2 S.D.
PC1 (48.6%)				PC1 (36.0%)			
PC2 (23.2%)				PC2 (25.,%)			
PC3 (9.8%)				PC3 (12.4%)			
PC4 (5.4%)				PC4 (8.6%)			
PC5 (3.9%)				PC5 (5.7%)			
PC6 (2.8%)				PC6 (3.0%)			
PC7 (1.3%)				PC7 (2.7%)			
PC8 (1.1%)				PC8 (1.1%)			
PC9 (0.6%)				PC9 (1.0%)			
PC10 (0.6%)				PC10 (0.7%)			
PC11 (0.5%)				PC11 (0.5%)			
PC12 (0.3%)				PC12 (0.4%)			
PC13 (0.3%)				PC13 (0.3%)			
				PC14 (0.3%)			
				PC15 (0.3%)			

Appendix 6. Principal components of Stomatopoda from principal component analysis on the shield outline and percentage of total variation in the data set explained by each principal component. **A:** Dorsal data set. **B:** Lateral data set.