

Diversification events of the shield morphology in shore crabs and their relatives through development and time

Florian Braig, Carolin Haug, and Joachim T. Haug

ABSTRACT

The group of shore crabs and their relatives, Carcinidae, are first known from the Eocene (56–33.9 mya). Since the group's first appearance, its representatives have evolved a variety of lifestyles and morphologies. The exact evolutionary steps resulting in these morphologies are still a matter of debate. Here, we analyse the changes of morphology within Carcinidae over time. We also investigate the change of morphology through ontogeny to see how it relates to the evolutionary changes. We focus on the outline of the shield as a proxy for morphology, as it has a strong effect on the appearance of the crab and yields the largest sample size of all body parts. Using an elliptic Fourier transformation of the shield outline and a principal component analysis, we create a morphospace for the shields of Carcinidae. Using the morphospace as input data and a new phylogenetic tree based on a molecular and a morphological character matrix from literature, we reconstruct ancestral states for the shield. Combining data of fossil and extant specimens and reconstructed ancestral states, we analyse changes of the shield shape through time. From the morphospace, we find that the morphological diversity of the shield is strongly influenced by ontogeny, but not so much by ecology. Yet, the shields of the adults show a large diversity, corresponding to adaptations to different lifestyles. The reconstruction of ancestral states showed that the earliest representatives of Carcinidae had quasi-hexagonal shields, which could correspond to an epibenthic lifestyle. From these forms, different shapes evolved, significantly during the Oligocene (ca. 33 mya) and Pliocene (ca. 5 mya).

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INTRODUCTION

Carcinization describes an evolutionary process in crustaceans, by which representatives of different lineages of crustaceans evolve into a crab-like appearance (e.g., Borradaile, 1916; McLaughlin and Lemaitre, 1997; Keiler et al., 2017; Wolfe et al., 2021), with a rather broad body and the “shrimp tail” (pleon) being folded under the body (for more aspects of the process see Scholtz, 2014; Keiler et al., 2017). This crab morphology seems of evolutionary and ecological significance as crab-like animals are quite successful concerning number of species and range of conquered habitats.

The changes towards a crab-like body shape are mostly restricted to the juvenile and adult phases of development (Martin, 2014), while the larvae (see Haug, 2020a for ambiguities of the term) retain a more ancestral morphology (Haug, 2020b). Representatives of Brachyura (i.e., true crabs) usually first go through a planktic larval phase (zoea) after hatching, characterised by locomotory exopods on the thoracic appendages (Williamson, 1969). Zoea larvae are still far from crab-looking (Figure 1A). Their bodies are more laterally compressed with spiny shields and a pleon not yet folded underneath the body. The zoea phase is then followed by a transition phase (often a single stage), the megalopa larva, characterised as the first stage with functional pleopods (Williamson, 1969). The megalopa already appears more crab-like with the typical dorso-ventrally compressed body and wider shield (Figure 1B).

This pattern of development is, for example, well represented in species of Carcinidae sensu Spiridonov, 2020, the group of shore crabs. This ingroup of Portunoidea (relatives of swimming crabs; for competing taxonomic views, see Evans, 2018) has currently 48 formally described extant, exclusively marine species (Evans, 2018). Representatives of Carcinidae show a global distribution, not least due to the European shore crab *Carcinus maenas* (Linnaeus, 1758), which is a globally inva-

sive species (e.g., Roman and Palumbi, 2004; Young and Elliott, 2020). The group also shows a variety of adaptations to different lifestyles, such as burrowing or swimming (Spiridonov, 2020). The earliest fossil representatives of Carcinidae are known from the Eocene (56–39 mya; e.g., Rathbun, 1926).

Here, we analyse the changes in shield morphology in Carcinidae through time and ontogeny with the use of quantitative morphology. The shield is among the characters that is most often preserved in fossil representatives of Brachyura. It also dominates the general appearance of the body and provides adaptations to different lifestyles (Spiridonov, 2020). We investigate how the typical crab-like shield diversified in the group since their appearance in the early Eocene and what it may have looked like in the earliest representatives. We also analyse how the shield changes throughout ontogeny. We hypothesize that adult ecology is the major driver behind shield diversity and that it increased in the group over time. Furthermore, megalopa shield diversity is expected to be lower than adult shield diversity, as megalopae represent a transition phase, which likely possesses comparable constraints for all representatives of the group.

MATERIAL AND METHODS

Material

Material used for this study originated from published images and reconstruction drawings in literature (Appendix 1). Furthermore open databases (GBIF.org, 2022; WoRMS Editorial Board, 2022), collections and museums (Deutsches Zentrum für Marine Biodiversitätsforschung, DZMB; Florida Museum of Natural History, FM; Göteborg Natural History Museum, GNM; Instituto Español de Oceanografía Centro Oceanográfico de Cádiz, IEO; Institut de Ciències del Mar, ICM-CSIC; Muséum national d’Histoire naturelle Paris, MNHN; Natural History Museum of Denmark, NHMD;

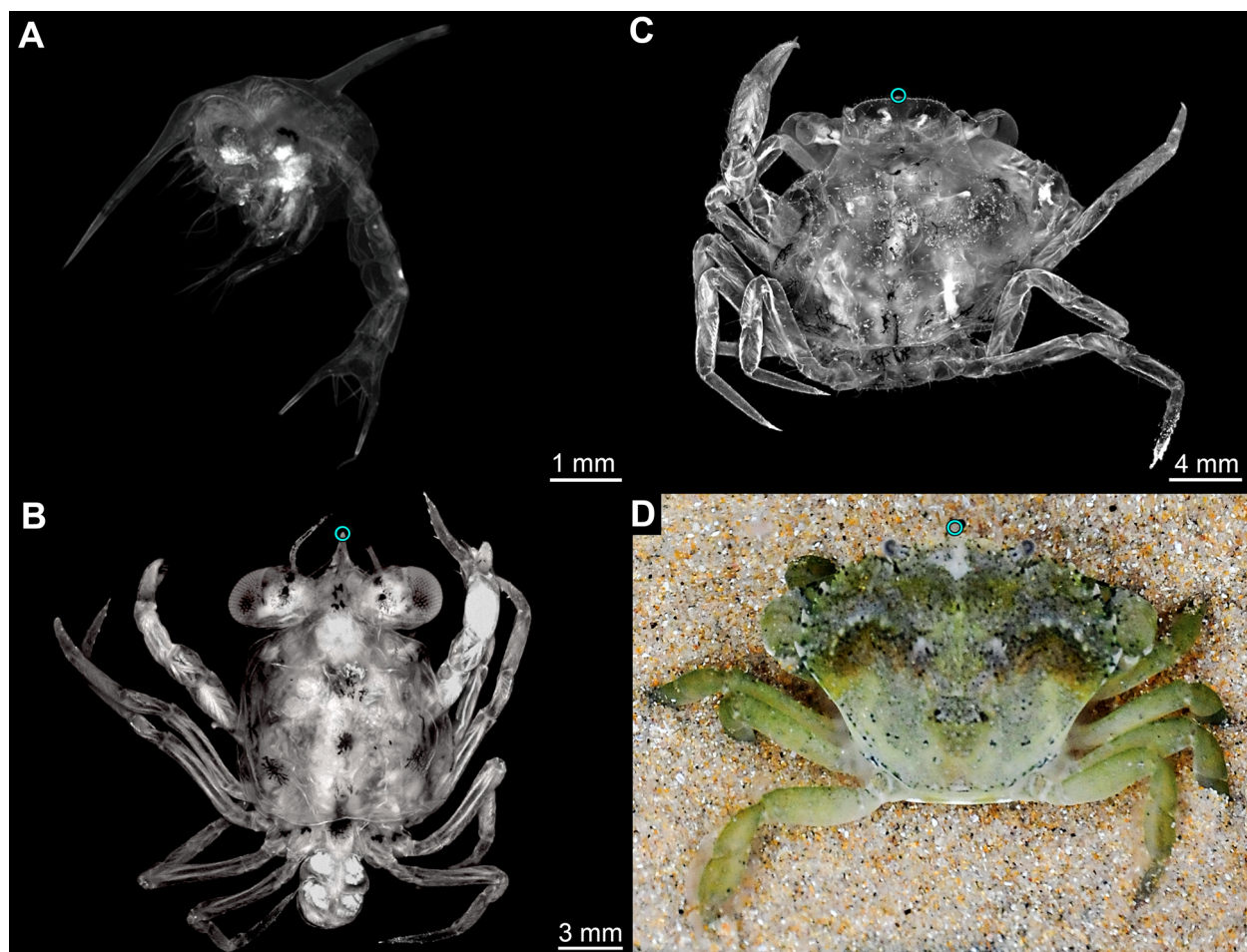


FIGURE 1. Different developmental stages of *Carcinus maenas* under fluorescent and natural light. Cyan-coloured circles mark position of first harmonic, used to align shapes. **A:** Lateral view of zoea under fluorescent light. **B:** Dorsal view of megalopa under fluorescent light (car_29G; Appendix 1). **C:** Dorsal view of juvenile under fluorescent light (car_2C; Appendix 1). **D:** Dorsal view of young adult under natural light (Oliver Mengedoht/Panzerwelten.de, Recklinghausen), source image did not contain a scale.

Senckenberg am Meer, SBaM; University Museum of Bergen, UiB) and a developmental series of *C. maenas* provided by the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Helgoland. Additional images were provided by Oliver Mengedoht/Panzerwelten.de, Recklinghausen. For a detailed overview on data origin, see Appendix 2. From these sources, the outline of the shield in dorsal view was reconstructed for each specimen (as in earlier studies; Braig et al., 2023).

In total, 127 adults, 16 juveniles (i.e., crab 1 and crab 2 stages), and 28 megalopae were reconstructed from extant material. We also reconstructed 19 fossil representatives, all of which were originally identified as adults (Table 1). We did not include zoea larvae in the ontogenetic comparison

for two reasons: 1) Zoea larvae appear drastically different in their shield morphology from megalopae, juveniles, and adults (e.g., Spitzner et al., 2018); 2) In the literature, zoea larvae of Carcinidae are often only depicted laterally, rendering a comparison with the dorsal depictions of megalopa and adult shields impossible (e.g., Paula, 1988).

We used vector graphic software, *Adobe Illustrator CS2* and the free and open software *Inkscape*, for the reconstruction of shield outlines. To prevent variation in the data due to left-right asymmetry, we only reconstructed the left or the right half of the shield and then duplicated and mirrored it in anterior-posterior axis and stitched it together to form an entire symmetric shield (Haug et al., 2020; Braig et al., 2023). Fluctuating asymmetry has been found in Carcinidae (Spani and Scalici,

TABLE 1. Table listing all species included in the analysis and respective numbers of included specimens per developmental stage.

| Species | Developmental phase | No. of specimens | Species | Developmental phase | No. of specimens |
|---|---------------------|------------------|--------------------------------------|---------------------|------------------|
| <i>Bathynectes longispina</i> | adult | 1 | <i>Megokkos</i> sp. | adult | 1 |
| <i>Bathynectes maravigna</i> | adult | 3 | <i>Minohellenus inexpressus</i> | adult | 1 |
| <i>Bathynectes muelleri</i> | adult | 1 | <i>Minohellenus macrocheilus</i> | adult | 1 |
| <i>Bathynectes piperitus</i> | adult | 1 | <i>Minohellenus traingulum</i> | adult | 1 |
| <i>Carcinides minor</i> | adult | 1 | <i>Miopipus pygmaeus</i> | adult | 1 |
| <i>Carcinus aestuarii</i> | adult | 6 | <i>Miopipus zavensis</i> | adult | 1 |
| <i>Carcinus aestuarii</i> | megalopa | 1 | <i>Miopipus zovensis</i> | adult | 1 |
| <i>Carcinus maenas</i> | adult | 25 | <i>Necora puber</i> | adult | 1 |
| <i>Carcinus maenas</i> | juvenile | 13 | <i>Olicarcinus trevisani</i> | adult | 2 |
| <i>Carcinus maenas</i> | megalopa | 19 | <i>Parathranites granosus</i> | adult | 2 |
| <i>Cicarnus fumiae</i> | adult | 1 | <i>Parathranites hexagonus</i> | adult | 3 |
| <i>Coelocarcinus</i> aff. <i>foliatus</i> | adult | 1 | <i>Parathranites intermedius</i> | adult | 1 |
| <i>Coelocarcinus foliatus</i> | adult | 2 | <i>Parathranites orientalis</i> | adult | 10 |
| <i>Coelocarcinus marindicus</i> | adult | 1 | <i>Parathranites ponens</i> | adult | 1 |
| <i>Liocarcinus corrugatus</i> | adult | 3 | <i>Parathranites tubero granosus</i> | adult | 2 |
| <i>Liocarcinus corrugatus</i> | megalopa | 1 | <i>Parathranites tuberosus</i> | adult | 3 |
| <i>Liocarcinus depurator</i> | adult | 2 | <i>Pirimela denticulata</i> | adult | 5 |
| <i>Liocarcinus depurator</i> | juvenile | 2 | <i>Pirimela denticulata</i> | megalopa | 2 |
| <i>Liocarcinus depurator</i> | megalopa | 1 | <i>Polybius henslowii</i> | adult | 1 |
| <i>Liocarcinus heintzi</i> | adult | 1 | <i>Portumnus latipes</i> | adult | 12 |
| <i>Liocarcinus holsatus</i> | adult | 1 | <i>Portumnus latipes</i> | early crab | 3 |
| <i>Liocarcinus holsatus</i> | juvenile | 1 | <i>Portumnus latipes</i> | megalopa | 4 |
| <i>Liocarcinus maculatus</i> | adult | 1 | <i>Portumnus lysianassa</i> | adult | 4 |
| <i>Liocarcinus marmoreus</i> | adult | 1 | <i>Portumnus tricarinatus</i> | adult | 1 |
| <i>Liocarcinus navigator</i> | adult | 1 | <i>Sirpus monodi</i> | adult | 1 |
| <i>Liocarcinus pusillus</i> | adult | 2 | <i>Sirpus ponticus</i> | adult | 2 |
| <i>Liocarcinus vernalis</i> | adult | 2 | <i>Sirpus zariquieyi</i> | adult | 6 |
| <i>Liocarcinus zariquieyi</i> | adult | 1 | <i>Thia scutella</i> | adult | 1 |
| <i>Macropipus australis</i> | adult | 1 | <i>Thia scutellata</i> | adult | 2 |
| <i>Macropipus tuberculatus</i> | adult | 2 | <i>Xaiva biguttata</i> | adult | 6 |
| <i>Maeandricampus starri</i> | adult | 1 | <i>Xaiva mcleayi</i> | adult | 3 |
| <i>Maeandricampus triangulum</i> | adult | 1 | <i>Xaiva mcleayi</i> | early crab | 1 |
| <i>Megokkos alaskensis</i> | adult | 2 | <i>Xaiva pulchella</i> | adult | 1 |

2018), but due to its random nature we disregarded it to reduce noise in the data. Furthermore, we used material from the Zoological State Collection Munich (ZSM) to investigate phylogenetic character states (referenced in Appendix 3).

Geometric Morphometrics

Quantitative comparison of shield outlines was achieved by outline analysis, creating a morphospace. We used elliptic Fourier analysis (EFA) of outlines to decompose the two-dimensional shield outline into a mathematical object. The shape is hereby decomposed into a harmonic sum

of trigonometric functions, weighted with harmonic coefficients describing the shape (Kuhl and Giardina, 1982; Bonhomme et al., 2014). The harmonic coefficients are aligned by the tip of the rostrum i.e., median point in the anterior rim of the shield (Figure 1; blue mark). The results of the outline analysis were then analysed with a principal component analysis (PCA) to extract the dimensions of largest variation (Bonhomme et al., 2014; Braig et al., 2019, 2023). The outline analysis was conducted with the *R-statistics environment* (ver. 4.1.0; R Core Team, 2021) using the package *Momocs* (ver. 1.3.2; Bonhomme et al., 2014). Shapes were registered with 2001 +/- 540 coordinates per shape. We used calibration functions of the *Momocs* package to calculate the optimal number of harmonics to use, resulting in 24 harmonics for the elliptic Fourier analysis. In this way, we created a morphospace of all specimens available to us.

Estimation of Ancestral States

To reconstruct the ancestral state (ASR) of the shield morphology in Carcinidae, we first had to obtain a phylogenetic tree for the group on which to base our analysis (Litsios and Salamin, 2012). We chose a total evidence approach based on two-character matrices, a morphological matrix from Karasawa et al. (2008) and a molecular matrix from Evans (2018; “163_taxa_concatenated_alignment”). Some species included in the molecular character matrix were not included in the morphological character matrix. For these specimens, we scored character states by investigating preserved material under dissection microscopes (updated character matrix in Appendix 3; character list and their states in Appendix 4).

We combined the two-character matrices in *Mesquite* (ver. 3.7; Maddison and Maddison, 2021), creating a matrix with one morphological and four molecular partitions (16s rRNA, CO1, H3, 28s rRNA), all characters being unweighted. Extant specimens had values for all partitions, fossil specimens had values only for the morphological partition. We then conducted a phylogenetic reconstruction in *MrBayes* (ver. 3.2.7a; Ronquist et al., 2012), following Aria and Caron (2017). We used a Bayesian MCMC method to create the tree (5,000,000 generations, four parallel chains, tree sample every 10,000 generations, 20% burn-in) with *Carpilius convexus* (Forskål, 1775) as outgroup. To account for the five fossil specimens in the tree not having molecular values we applied backbone constraint on the ingroups, following Aria and Caron (2017). We dated the tree with five fos-

sil specimens (one representative each of *Portunus tricarinatus* Lörenthey and Beurlen, 1929, *Bathynectes muelleri* Ossó and Stalennuy 2011, *Megokkos alaskensis* Rathbun, 1926, *Megokkos* sp., and *Liocarcinus heintzi* Schweitzer and Feldmann, 2010), following Zhang et al. (2016). These fossil specimens were included as individuals in the tree and assigned time ranges in the phylogenetic analysis, according to their occurrence data (Appendix 5). Clock rates were set to 0.0115 for mtDNA partitions and 0.00115 for nuclear DNA partitions as lognormal priors, following Liu et al. (2018). The code used is provided in Appendix 6 and the tree file in Appendix 7. We imported the resulting tree into the *R-statistics environment*, using *phytools* (ver. 0.7-90; Revell, 2012).

Although we created our own phylogenetic tree, we still could not include every species of our initial data set into said tree due to missing molecular data or inaccessibility of morphological characters for some specimens. To further progress with our analysis, we therefore had to create a subset of specimens, selecting one randomly chosen adult specimen for each species represented in our tree. This subset of our initial analysis, henceforth called “tree subset”, is representing the tip states for the ancestral state reconstruction. The tip states are a list of continuous characters for each tip in the tree, from which character states are then inferred for each node in the tree (Litsios and Salamin, 2012). To obtain a continuous character matrix for the tip states, we had to perform a second outline analysis (again 24 harmonics), repeating the methodology as for the complete data set (as detailed in the section “Geometric morphometrics”), but only including the specimens of the “tree subset”. This step was necessary because, as elliptic Fourier outline analysis has different results dependent on which specimens are included, a new outline analysis with only the specimens included in the tree contains less noise and variation. Using the continuous character matrix obtained from the PCA of this “tree subset” as tip data, we then computed the estimates for ancestral states of the shield morphology for every node in the tree. We hereby selected the first 10 principal components (PCs) of the continuous character matrix from the PCA as they represented over 95% of variation in the data, to reduce computational time and dimensionality. For these 10 dimensions, we computed the estimated values for every node in our tree. To do so, we fitted different models of character evolution to the data (i.e., matrix of first ten PCs from PCA of “tree subset” and the phylogenetic tree) using the

mvMORPH package (ver. 1.1.4; Clavel et al., 2015). We fitted univariate and multivariate “Brownian-motion” and “Ornstein-Uhlenbeck” models of character evolution to this data. We then compared Akaike information criterion values of these models, tested for significant differences between models, and tested if reliable solutions could be reached by each model. Based on these tests, we decided on a univariate Brownian-motion model.

The mathematical estimates for each node in the tree from the ASR-model were then used to reconstruct shield outlines within the morphospace provided by the PCA on the shield outline analysis of the “tree subset”. However, this could only be performed for two PCs at the same time, meaning that only the morphological variation explained by two PCs can be expressed graphically with this method. Therefore, the graphical representation (and only the graphical representation) comes with some uncertainty. The code used is provided in Appendix 8.

Statistical Analysis

Statistical analysis was conducted in the *R-statistics environment*, using the package *dispRity* (ver. 1.6.0; Guillerme, 2018).

For a quantitative comparison of groups, which were defined by phylogenetic relationship or by ontogenetic phase, we used different metrics for measuring morphological diversity (also called “disparity”; Guillerme et al., 2020). We calculated the sum of variances for all principal component coordinates for the groups, retrieved from the PCA on the whole data set. These measures were used as an estimation of the portion of morphospace occupied by each group. The median distance of each group to the centre of the morphospace was used as a measure of position within the morphospace (Guillerme et al., 2020).

Using the PCA of the “tree subset”, the estimates for ancestral character states, the phylogenetic results, as well as the occurrence data of the species (Appendix 5), we then calculated the change of morphospace occupation (sum of variance) through time, following Guillerme and Cooper (2018). We defined time bins according to geological periods (Cohen et al., 2023). The code used is provided in Appendix 8.

RESULTS

Morphospace of Carcinidae

The PCA performed on the outline analysis of the shields resulted in ten effective principal components, describing 95% of the morphological variation of shield shapes in the whole data set (PC1 = 66.7%; PC2 = 10.4%; PC3 = 6.2%; PC4 = 4.6%; PC5 = 1.8%; PC6 = 1.5%; PC7 = 1.3%; PC8 = 1.2%; PC9 = 0.8%; PC10 = 0.6%). Visual interpretation was performed by plotting the first two principal components of the PCA against each other, since they covered most variation in the data (77.1%). Graphical component loadings are given in the appendix (Appendix 9).

PC1 described the differences of slim and wide shields (Figure 2). Positive values described slim shields with prominent rostrums and posterior notches, while negative values described widened shields with antero-lateral extensions of the shield without a rostrum or posterior notch (Figure 2). PC2 described the differences between posteriorly wider and anteriorly wider shields (Figure 2). Positive values described shields that are anteriorly tapering with a wider posterior region, while negative values described anteriorly widened shields with extending antero-lateral regions and slimmer posterior regions.

Initial investigation of the morphospace showed that ontogenetic grouping best explained the patterns in the morphospace. Hereby, the cluster of megalopa larvae plotted on the right side of the morphospace in a tight spread, indicating their slim shields with prominent rostrums and posterior notches. In the centre of the morphospace, in a line along the PC1 axis, plotted the group of juveniles, showing rather oval shields with shallow rostrums. The adults plotted from the bottom of the morphospace, spreading out towards the upper left. This large spread indicated a range of body forms, from slimmer shields with tapering anterior ends to widened shields with strongly extending antero-lateral regions.

Considering the quantitative measurements, we found significant differences in the size of occupied morphospace between all groups (Welch Two Sample t-test; Bonferroni corrected; p-values < 0.001). Hereby, the size of the occupied area increased for each group with an increase in developmental stage, meaning that megalopae occupied the smallest area, while adults occupied the largest area (Table 2). Similarly, we found that all groups were significantly different in their position within

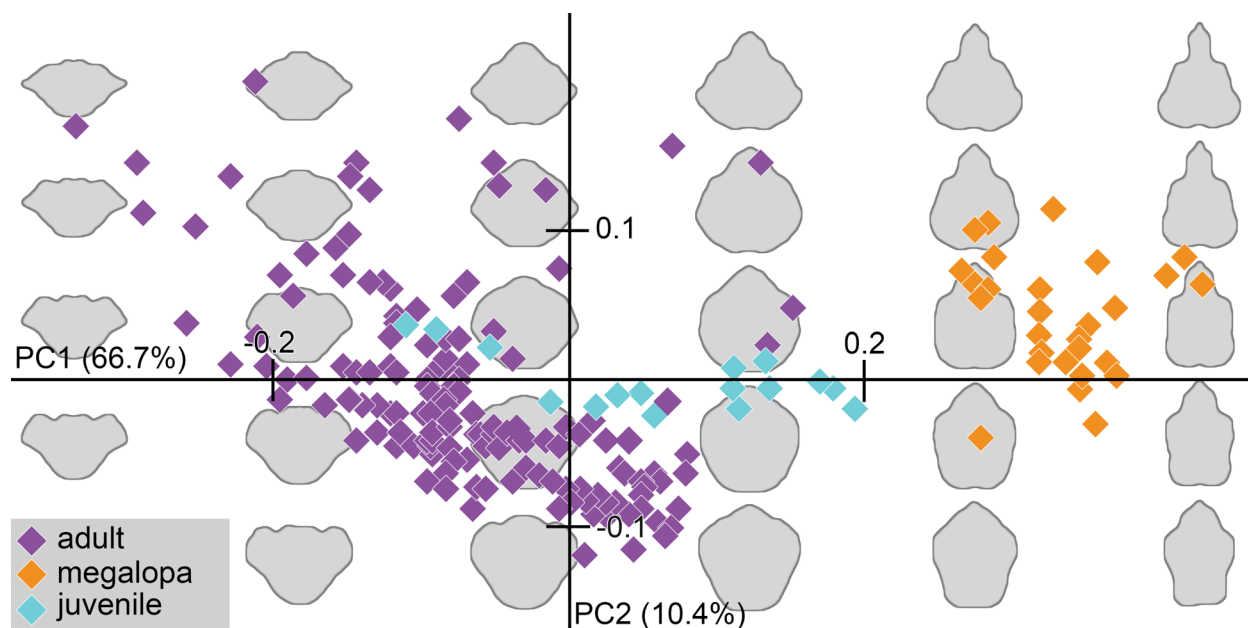


FIGURE 2. Scatter plot of the first two principal components from the PCA on the outline analysis of shields of Carcinidae. Grey outlines in the background describe shape variation across the morphospace.

the morphospace (Welch Two Sample t-test; Bonferroni corrected; p-values < 0.001; Table 2).

Reconstructed Ancestral States

The tree based on the total evidence approach largely agrees with the molecular tree from Evans (2018; Figure 3), except for the relationship between *Carcinus* (Leach, 1814), *Portumnus* (Leach, 1814) and *Xaiva* (MacLeay, 1838). Our tree resolves *Xaiva* and *Portumnus* as sister groups, and *Carcinus* as the sister group to *Xaiva* and *Portumnus*, whereas the tree by Evans (2018) resolves *Carcinus* and *Portumnus* as sister groups and does not include *Xaiva*. In this aspect, our tree agrees with Karasawa et al. (2008), which also resolves *Carcinus* as the sister group to *Portumnus* and *Xaiva*. However, Karasawa et al. (2008) suggest a more distant relationship between *Liocarcinus* (Stimpson, 1871) and *Polybius* (Leach, 1820);

TABLE 2. Table with obtained values for metrics used as measures of morphological diversity. For each group respectively is given the sample size corrected median of the metric.

| Group | Sum of variances corr. median | Median of centroid corr. median |
|----------|----------------------------------|------------------------------------|
| adult | 0.022 | 0.154 |
| juvenile | 0.012 | 0.180 |
| megalopa | 0.009 | 0.478 |

and *Bathynectes* (Stimpson, 1871) and *Necora* (Holthuis, 1987) than our tree.

The reconstruction of ancestral state estimates resulted in a reconstructed shield shape for every node in our tree (Figure 3). Based on the first three nodes of the tree, we could roughly assume the shape of the shield in the earliest representatives of Carcinidae. It seemed to be of quasi-hexagonal shape, with a rounded shallow rostrum, and anteriorly wider than posteriorly.

Diversity Through Time Analysis

Using the ancestral state estimates for phylogenetic correction, we grouped the species according to their first and last occurrence in the fossil record, to perform a diversity through time analysis (Figure 4). The sum of variance of the first 10 PCs of the outline analysis on the “tree subset” was plotted against the stratigraphic bins in our data set. It showed a strong and significant increase of morphological diversity between every time bin (Wilcoxon rank sum test; p < 0.001).

DISCUSSION

Limitations of the Approach

Due to a lack of suitable material in the literature, only a small number of fossils could be included into this data set. There are also no fossil megalopae included, as to date there is only one fossil crab megalopa (from the Jurassic) described

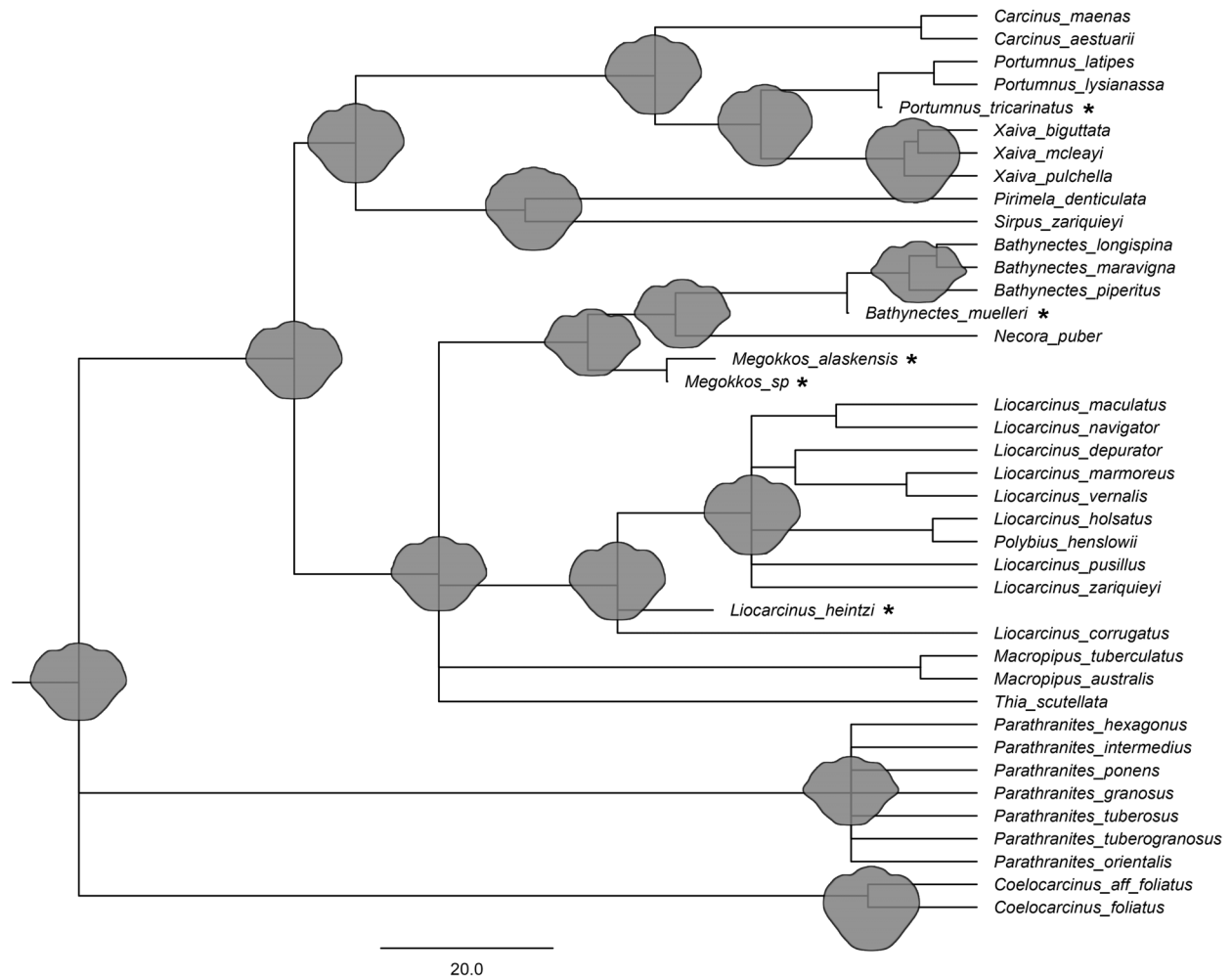


FIGURE 3. Phylogenetic tree of selected fossil and extant representatives of Carcinidae. Selected reconstructed shield outlines (based on PC1 and PC2 of outline analysis) based on ancestral state estimates are centered on the node they represent. Asterisks mark fossil species.

in the literature (Haug et al., 2015), which is somewhat puzzling. Therefore, we cannot analyse ontogenetic changes through time yet.

As the goal of this study was not to reconstruct the phylogeny of Carcinidae, the phylogenetic reconstruction herein provided is not based on all species, fossil and extant, of the group Carcinidae sensu Spiridonov, 2020. Instead, it contains most of the species used from the two published phylogenetic reconstructions, on which we based our total evidence approach (Karasawa et al., 2008, Evans, 2018). The reconstruction of ancestral states is therefore not based on all known representatives of the group Carcinidae sensu Spiridonov, 2020, but on a large fraction (46/122 extant and fossil species).

Prominence of the Ontogenetic Signal

Against our initial expectations, the diversity of adult morphologies is not dominating the variation within the morphospace (Figure 2). Instead, the ontogenetic signal is stronger in this regard, causing large differences and discrete clustering between megalopae and adult specimens. As to be expected, juveniles plot between the two groups, forming an ontogenetic trajectory within the morphospace. This positioning indicates that, although crabs undergo their last metamorphic moult by moulting from megalopa to crab 1 stage (Haug, 2020b), they still undergo significant morphological changes afterwards.

Furthermore, within the morphospace, megalopae form a tight cluster. In contrast, but in accordance with our expectations, adults show a large

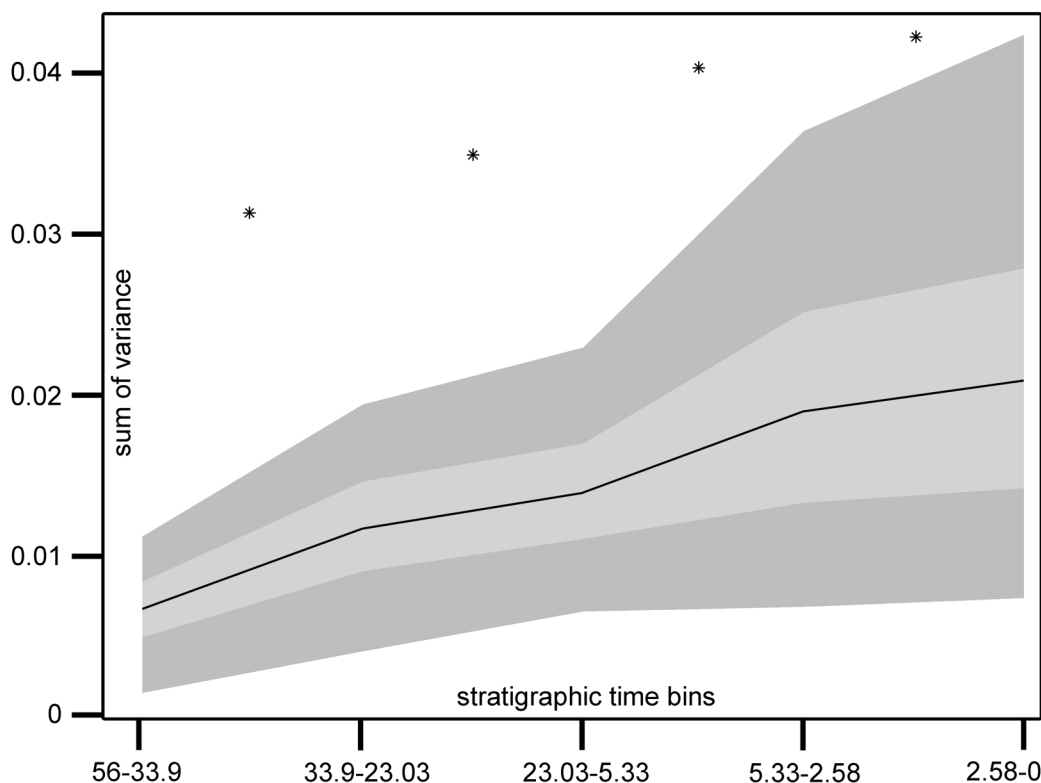


FIGURE 4. Analysis of morphological diversity changes through time. Black line represents mean, light grey and dark grey areas represent 50% and 95% confidence intervals, respectively. Sum of variances used as measure for morphological diversity on y-axis. Stratigraphic time bins in million years on x-axis, from left to right: Eocene, Oligocene, Miocene, Pliocene, Pleistocene including extant fauna. Ages following Cohen et al. (2023). Asterisks mark significant changes between time bins.

variation across the morphospace, indicating different shield forms adapted to swimming, epibenthic, or burrowing lifestyles. Megalopa shields do not show such large variation in their shield form. Their shields seem to be adapted to the transition between habitats, which seems to pose a similar selective pressure across all groups. An alternative interpretation would be that, due to a lack of strong selective pressures, the megalopa shield has retained a plesiomorphic state across Carcinidae. Yet, in the latter case we would expect genetic drift leading to a higher variation in shield shapes.

The Megalopa as a Transitory Stage and a Possible Phylotypic Stage

The lower variation of the megalopa in comparison to the adult is not an unusual pattern for a transitory stage. The previous life phase (in this case, zoea) is highly specialised for a planktic lifestyle, while the life phase afterwards, the juvenile-adult phase, is specialised for different lifestyles (often benthic). The megalopa mediates the transition from one habitat to the others, and from one

morphology to the others. It is likely that this transitory phase was ancestrally more gradual, as it is in many other lineages (e.g., Walossek, 1993; Haug & Haug, 2013, 2016; Haug et al., 2013, 2016, 2019; Haug, 2020b). However, there seems to be strong selective pressure that leads to a shortening of this phase down to a single stage, which in turn may leave fewer possibilities for variation in morphology.

In any case, a transitory stage with considerably less variation than former and later stages may be considered “phylotypic”, meaning a stage in which all representatives of a group show the largest amount of similarity (Slack et al., 1993), or the least amount of variation. Using this idea as a framework, we can draw an interesting comparison with the insectan group Holometabola, which is also characterised by a distinct transitory stage, the pupa. Like most megalopa larvae, the pupa is also a non-feeding stage. While many pupae are immobile, this is a derived condition, and in different lineages mobile pupae have been retained, making the ancestral pupa even more comparable

to a megalopa. The pupa may represent a phylotypic stage as well (Haug et al., 2023). Using quantitative morphology, it has been shown that the morphological variation in the pupa is significantly smaller than in the adult. This pattern is another similarity to the pattern observed here for the megalopa.

However, for further substantiating the assumption of both pupa and megalopa representing phylotypic stages, it will be necessary to include quantitative data of the prior stages because a phylotypic stage hypothesis requires the prior stage to be more diverse or variable. As pointed out, the challenge for such a comparison is that earlier stages are often depicted in a different orientation in crabs, but also in insectan larvae (Haug et al., 2023).

Ecological Function of Fossil Representatives of Carcinidae

Based on the graphical representation of the ancestral state reconstruction, we can assume that the earliest representatives of Carcinidae had similar shield forms to modern representatives of the *Liocarcinus* group, an ingroup of Carcinidae (Figure 3). These quasi-hexagonal shields are often found in species with epibenthic lifestyles; representatives of the *Liocarcinus* group are no different in this regard (e.g., Tutman et al., 2017; Spani and Scalici, 2018). Therefore, the earliest representatives of Carcinidae may have been epibenthic as well. Correlation analyses are needed to investigate this assumption (Ricklefs and Miles, 1994), but if true, it would indicate that all further adaptations expressed by the extant representatives of Carcinidae would have evolved secondarily from this body form. Such adaptations include round shields found in species expressing burrowing lifestyles such as the extant representatives of *Thia* or *Coelocarcinus* (Schäfer, 1954; Spiridonov, 2020), long lateral spines as in *Bathynectes*, or elongated shields deviating slightly from the typical crab-shape as in Pirimelinae.

This evolutionary reconstruction, however, would also mean that a burrowing lifestyle with a longer-than-wide shield evolved convergently twice within Carcinidae: once in *Coelocarcinus*, and once in the common ancestor lineage of the groups Carcininae, Platyonichinae and Pirimelinae (Figure 3). In this second branch, *Carcinus* and *Sirpus* would have secondarily lost the burrowing lifestyle again. Nevertheless, representatives in both lineages that express burrowing lifestyles also express round shields that are rather longer than wide. This shield

type therefore seems to have evolved convergently as an adaptation to the burrowing lifestyle.

Appendage morphologies specialized for burrowing lifestyles evolved convergently in many ingroups of Brachyura as well (Luque et al., 2019). Especially in Portunoidea, the swimming crabs, of which Carcinidae is an ingroup, since the adaptation to swimming often is preceded by an adaptation to burrowing (Luque et al., 2019). It is therefore not unlikely, that the shield form evolved convergently as well. Generally, burrowing lifestyles appeared during the Cenozoic also in other ingroups of Brachyura, alongside the diversification of some of those ingroups, potentially as an adaptation to increased competition (Hartzell et al., 2022).

The Rise of the Crabs

Our study indicates a strong increase of morphological diversity within the Carcinidae since the Eocene, indicated by the significant increases in diversity (Figure 4). New body forms arise in the fossil record, first longer-than-wide shields, then shields with long spines, first in *Megokkos* (Schweitzer and Feldmann, 2000) during the Eocene and Oligocene. Our phylogenetic reconstruction further suggests that during the Miocene and Pliocene, representatives of *Bathynectes* should already include forms with long spines as well. Yet *Bathynectes muelleri* (Ossó and Stalenny, 2011), the only fossil of the species group *Bathynectes* known so far, does not possess the long spines of extant relatives. During the Pliocene, round shields without spines as in *Thia* also appear in the fossil record, and more recently in *Coelocarcinus* (Edmondson, 1930).

This radiation into several lifestyles (indicated by different shield shapes) has been observed in other ingroups of Portunoidea as well as in Portunidae, for example, (Spiridonov, 2020). In general, an increase in diversity has been suggested during the Cenozoic for many sister groups of Portunoidea (Schweitzer and Feldmann, 2015; Hartzwell et al., 2022). The pattern of emergence of a group and consecutive increase in morphological diversity observed here is therefore not surprising. It may indicate the potential of the crab body form to be well-adaptable to a range of habitats and lifestyles.

Specific ecological factors driving this radiation have already been suggested. The development of, for example, reefs often correlates with an increase in taxonomic diversity of decapods (Ferratges et al., 2021). New reefs translate to a range

of new habitats that become available to be colonized by crabs. New morphologies and lifestyles may then be better adapted to these new habitats.

CONCLUSION AND OUTLOOK

The strongest factor for morphological diversity in the shield shape of Carcinidae is ontogeny. Phylogenetic variation is prominent though, especially within the adults, where it is the cause for a large amount of morphological diversity. The early history of the group was apparently less diverse. The graphical representation of ancestral states shows a quasi-hexagonal shield shape that was most likely connected to an epibenthic lifestyle for the earliest representatives of the group. The periods between Eocene and Oligocene, as well as between Miocene and Pliocene, show strong increases in the diversity of Carcinidae, with the emergence of new fossil morphologies as well as reconstructed ancestral states. Unfortunately, the lack of more fossil material, especially of larvae,

currently hinders more precise statements about the development of ontogeny through time in Carcinidae.

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APPENDICES

APPENDIX 1.

Reference list of material used in this study.

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APPENDIX 2.

Table of material used in the study with grouping variables and references. (Available for download at <https://palaeo-electronica.org/content/2023/4023-carcinidae-diversity>)

APPENDIX 3.

Updated morphological character matrix following Karasawa et al. (2008). (Available for download at <https://palaeo-electronica.org/content/2023/4023-carcinidae-diversity>)

APPENDIX 4.

Character list, indicating characters and their states as published by Karasawa et al. (2008).

[1] Carapace proportion: much wider than long (0), slightly wider than long or longer than wide (1)

[2] Front with median notch: present (0), absent (1)

[3] Front with median lobe: absent (0), present (1)

[4] Frontal teeth: present (0), absent (1)

[5] Front forming T-shape: absent (0), present (1)

[6] Lower orbital tooth: low (0), long, visible dorsally (1)

[7] Inner orbital angle defined as lobe or tooth: present (0), absent (1)

[8] Upper orbital fissures: present (0), absent (1)

[9] Epibranchial spine: short (0), long (1)

[10] Carapace dorsal ridge: absent (0), present (1)

[11] Carapace surface: smooth (0), with tubercles (1)

[12] Anterolateral teeth: 1-5 (0), 6-9 (1)

[13] Orbital length: normal (0), wide (1)

[14] Basal article of antenna reaching front: present (0), absent (1)

[15] Basal article of antenna: fixed (0), free (1)

[16] Laterodistal area of basal article of antenna: absent (0), spine or lobed (1)

[17] Laterodistal expansion of basal article of antenna: absent (0), present (1)

[18] Epistomial spine: absent (0), present (1)

- [19] Portunid lobe of maxilliped 1: absent (0), present (1)
- [20] Telson of male pleon reaching: posterior of sternite 4 (0), anterior of sternite 4 (1)
- [21] Telson of male pleon about as long as wide (0), much longer than wide (1)
- [22] Telson shape of male pleon: triangular (0), semicircular (1)
- [23] Male pleomere 6: wide (0), narrow (1)
- [24] Lateral margin of male pleomeres 4-5: nearly straight (0), sinuous or concave (1)
- [25] Male pleomere 3: narrow (0), wider than somite 4 (1), wide with rectangular corner (2)
- [26] Male pleomere 3 with keel: absent (0), present (1)
- [27] Sutures of male pleomeres: distinct (0), indistinct (1)
- [28] Sutures of male pleomeres, if present: movable (0), immovable (1)
- [29] Sternum width: distinctly narrow (0), relatively narrow (1), wide (2)
- [30] Sternum shape: narrowly ovate (0), ovate (1), rather rectangular posteriorly (2)
- [31] Sulcus delimiting sternites 3 and 4: well marked (0), indistinct (1)
- [32] Sulcus delimiting sternites 6 and 7: complete (0), interrupted medially (1)
- [33] Sulcus delimiting sternites 7 and 8: complete (0), interrupted medially (1)
- [34] Secondary sulcus delimiting sternites 6 and 7: absent (0), present (1)
- [35] Median transverse ridge between sternites 6/7: present (0), absent (1)
- [36] Median line on thoracic sternites: up to sternite 7 (0), up to sternite 6 (1)
- [37] Median groove on male thoracic sternite 3: present (0), absent (1)
- [38] Episternites 4-7: narrow (0), wide (1)
- [39] Posterolateral prolongation of male episternite 7: not marked (0), well developed (1)
- [40] Sternite 8: reduced (0), expanded laterally (1), well developed (2)
- [41] Penial groove on male sternite 8: absent (0), present (1)
- [42] Male sternite 8 visible posteriorly: indistinct (0), distinct (1)
- [43] Male sternite 8 visible ventrally: indistinct (0), distinct (1)

- [44] Cheliped fingers dark in color: present (0), absent (1)
- [45] Inner margin of cheliped merus with spines: absent (0), present (1)
- [46] Outer surface of cheliped palm: smooth (0), transversely ridged (1)
- [47] Cheliped length: longer than pereopods (0), shorter than pereopods (1)
- [48] Pereiopods 2-4 propodi: normal (0), foliaceous-like (1)
- [49] Dactyli 2-4 with corneous tip: present (0), absent (1)
- [50] Pereiopod 5 with foliaceous propodus: absent (0), present (1)
- [51] Pereiopod 5 dactyli: ensiform (0), narrow, lanceolate (1), lanceolate (2), ovate-elliptic (3)
- [52] Pereiopod 5 merus with postero-distal spine: absent (0), present (1)
- [53] Proximal insertion of pereiopod 5 propodus: absent (0), present (1)
- [54] Pereiopod 5 merus: equal or longer than propodus (0), shorter than propodus (1)
- [55] Gonopod 1 with subterminal spines: absent (0), present (1)

APPENDIX 5.

Table of occurrence dates, based on literature research for species included in the phylogeny. Abbreviations: FAD: first occurrence; LAD: last occurrence.

| Group | FAD | LAD |
|---|-------|-------|
| <i>Thia scutella</i> | 5.33 | 0 |
| <i>Liocarcinus corrugatus</i> | 5.33 | 0 |
| <i>Liocarcinus zariquieyi</i> | 2.58 | 0 |
| <i>Liocarcinus heintzi</i> | 33.9 | 27.82 |
| <i>Liocarcinus pusillus</i> | 2.58 | 0 |
| <i>Polybius henslowii</i> | 2.58 | 0 |
| <i>Liocarcinus holsatus</i> | 3.6 | 0 |
| <i>Liocarcinus vernalis</i> | 2.58 | 0 |
| <i>Liocarcinus marmoreus</i> | 2.58 | 0 |
| <i>Liocarcinus depurator</i> | 5.33 | 0 |
| <i>Liocarcinus navigator</i> | 2.58 | 0 |
| <i>Liocarcinus maculatus</i> | 0 | 0 |
| <i>Parathranites tubero granosus</i> | 2.58 | 0 |
| <i>Parathranites tuberosus</i> | 2.58 | 0 |
| <i>Parathranites ponens</i> | 2.58 | 0 |
| <i>Parathranites orientalis</i> | 2.58 | 0 |
| <i>Parathranites intermedius</i> | 2.58 | 0 |
| <i>Parathranites granosus</i> | 2.58 | 0 |
| <i>Parathranites hexagonus</i> | 2.58 | 0 |
| <i>Macropipus australis</i> | 2.58 | 0 |
| <i>Macropipus tuberculatus</i> | 2.58 | 0 |
| <i>Necora puber</i> | 5.33 | 0 |
| <i>Megokkos</i> sp. | 48.6 | 33.9 |
| <i>Megokkos alaskensis</i> | 33.9 | 23.03 |
| <i>Bathynectes piperitus</i> | 2.58 | 0 |
| <i>Bathynectes muelleri</i> | 15.97 | 13.82 |
| <i>Bathynectes maravigna</i> | 2.58 | 0 |
| <i>Baythnectes longispina</i> | 2.58 | 0 |
| <i>Coelocarcinus foliatus</i> | 0 | 0 |
| <i>Coelocarcinus</i> aff. <i>foliatus</i> | 0 | 0 |
| <i>Sirpus zariquieyi</i> | 0 | 0 |
| <i>Pirimela denticulata</i> | 2.58 | 0 |
| <i>Xaiva pulchella</i> | 2.58 | 0 |
| <i>Xaiva mcleayi</i> | 2.58 | 0 |
| <i>Xaiva biguttata</i> | 2.58 | 0 |
| <i>Portumnus tricarinatus</i> | 23.03 | 5.33 |
| <i>Portumnus lysianassa</i> | 2.58 | 0 |
| <i>Portumnus latipes</i> | 2.58 | 0 |
| <i>Carcinus aestuarii</i> | 2.58 | 0 |
| <i>Carcinus maenas</i> | 5.33 | 0 |

APPENDIX 6.

Code used for *MrBayes* analysis. (Available for download at <https://palaeo-electronica.org/content/2023/4023-carcinidae-diversity>)

APPENDIX 7.

Nexus format tree file. (Available for download at <https://palaeo-electronica.org/content/2023/4023-carcinidae-diversity>)

APPENDIX 8.

Code used for *R-statistics environment* analysis. (Available for download at <https://palaeo-electronica.org/content/2023/4023-carcinidae-diversity>)

APPENDIX 9.

Graphical component loadings of PCA on outline analysis of the whole data set.

