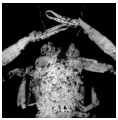


Morphological diversity of extant polychelidan lobsters does not reach former heights despite the evolution of morphological differentiation during development

CHARLOTTE KÖNIG, CAROLIN HAUG, JOACHIM T. HAUG & FLORIAN BRAIG



Deep-sea blind lobsters, representatives of the group Polychelida, are nowadays only found in the deep sea. The fossil record of the group reaches back to the Triassic (230 mya) with the majority of species occurring during the Triassic and Jurassic in a large geographical range. Since the Late Jurassic, the group has lost most of its species diversity. We investigated whether the loss of species diversity within the group is correlated with a loss of morphological diversity. We used outline analysis to approximate the shape of the shield and chela (propodus and dactylus separately) of polychelidan lobsters as a proxy for their morphological diversity. Our results indicate that morphological diversity had reached higher peaks in the past, and that some morphologies are lost today. These morphologies were likely better adapted to shallow waters. Furthermore, a distinct difference in larval versus adult morphology can be recognised in modern forms. There was no such pronounced difference in the fossil record, indicating a more expressed differentiation of ecological functions in the modern fauna, coupled to the giant “eryoneicus-type” larvae. • Key words: biodiversity, blind lobsters, geometric morphometrics, quantitative morphology, ontogeny, Polychelidae.

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Polychelida is an ingroup of Decapoda, its representatives are commonly known as deep-sea blind lobsters. The group is characterized by chelae on at least the 4th to 7th thoracopods (= pereopods 1–4) in adults (Fig. 1). Their vernacular name stems from the reduced eyes and deep-sea lifestyle of extant representatives (Galil 2000). Fossil representatives of the group were not exclusive to the deep-sea, with representatives also known from shallow waters (Beurlen 1931; Audo *et al.* 2014a, 2018, 2021; Gašparič *et al.* 2020). The group Polychelida dates back to the Triassic (*ca.* 230 mya), and showed a large area of distribution during the Jurassic (Karasawa *et al.* 2003, Audo *et al.* 2020, Gašparič *et al.* 2020). The group also showed a large species diversity during this time (Ahyong 2009). Today, there are more fossil species known than extant ones, which may be part of the reason why fossil representatives of the group were discovered before any extant representatives had been found (Galil 2000).

Modern representatives of the group Polychelida have some morphological characters in common, that differ from most fossil representatives. A reduction of the eyes, a narrowing of the cephalothoracic shield (in many fossils it was rather broad; the cephalothoracic shield is often called “carapace”, an ambiguous term), or the major chelipeds becoming more elongated and more slender in shape (Ahyong 2009).

The inner phylogeny and taxonomy of Polychelida is still not resolved in a stable manner (Audo *et al.* 2021). Several studies have investigated these issues on extant and fossil representatives of the group (Galil 2000, Ahyong 2009, Audo *et al.* 2021, Chang *et al.* 2024). Additionally, new species and species groups are still being described regularly (*e.g.* Karasawa *et al.* 2013, Audo *et al.* 2017a, Gašparič *et al.* 2020).

The post-embryonic development in Polychelida includes several morphologically distinct phases: the pre-zoea,

the eryoneicus zoea, and the eryoneicus megalopa. Hereby, individuals go through numerous zoea stages before moulting into the megalopa phase (exact number of megalopa stages unknown), from which they moult into juveniles already largely resembling the adult (Martin 2014, Torres *et al.* 2014, Fig. 2). The pre-zoea cannot swim yet, as it has poorly developed pleopods and uropods. The zoea phase is characterised by natatory exopods on the thorax (Williamson 1969). This differs from the following megalopa phase, where the larva can swim via their well-developed pleopods. These megalopa stages are the ones that stand out through their distinct shape and large size with balloon-like shields (Martin 2014, Eiler *et al.* 2016). These morphological features led authors in the late 19th and early 20th century to believe that these specimens were adults and identified them to a separate genus “*Eryoneicus*”, a group of lobsters (Martin 2014). Some authors already in the early 20th century believed the specimens to be larval stages, however only in 1964 the genus name was suppressed (ICZN 1964, Martin 2014). The uncertainty regarding the specimens had of course caused phylogenetic uncertainties. Larvae of Polychelida have not always been as distinct from their adults though. Fossil specimens still showed a more gradual developmental pattern (Haug *et al.* 2015, Eiler & Haug 2016).

Here, we investigate the morphological diversity of the group Polychelida and compare fossil and extant specimens, using two morphological features as proxies. We focus on the cephalothoracic shield (“carapace”) and the chela of the fourth thoracopod (“1st pereopod”). The shield provides protection, plays a role in hydrodynamics and burying, and provides a robust attachment site for the musculature of the appendages (Olesen 2013). The chela fulfils several functions, such as feeding, sensory reception, and aggressive interactions (Mariappan *et al.* 2000). We test whether these structures show a loss in morphological diversity, reflecting the loss in species diversity of the group. We furthermore investigate whether the specialization of larval and adult morphology to the respective habitats balanced out this loss.

Material and methods

Material

Material originated from literature, museum collections and private collections. Furthermore, GBIF was used to find suitable material (GBIF: The Global Biodiversity Information Facility 2022). Material from literature in-

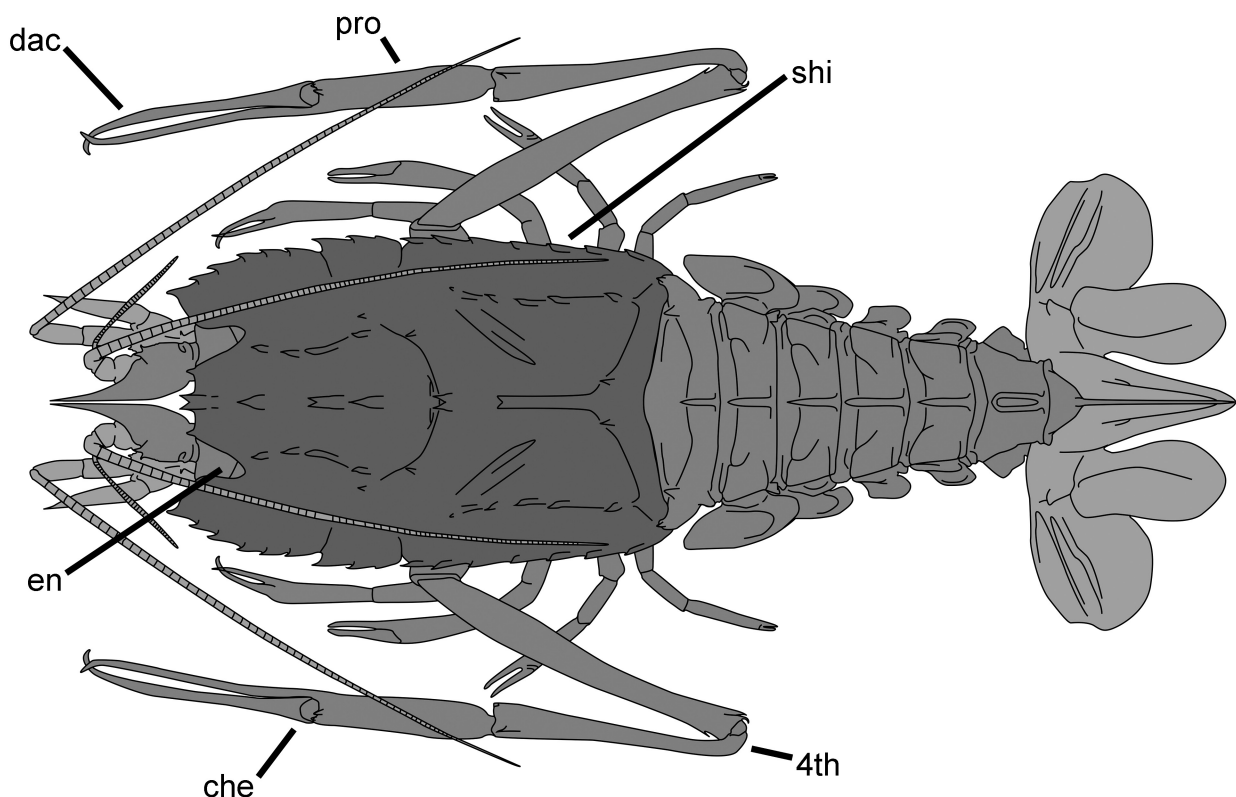


Figure 1. Schematic reconstruction of an extant adult representative of the group Polychelida, after Galil (2000). Abbreviations: che – chelae; dac – dactylus; en – eye notch; pro – propodus; shi – shield; 4th – fourth thoracopod (1st pereopod).

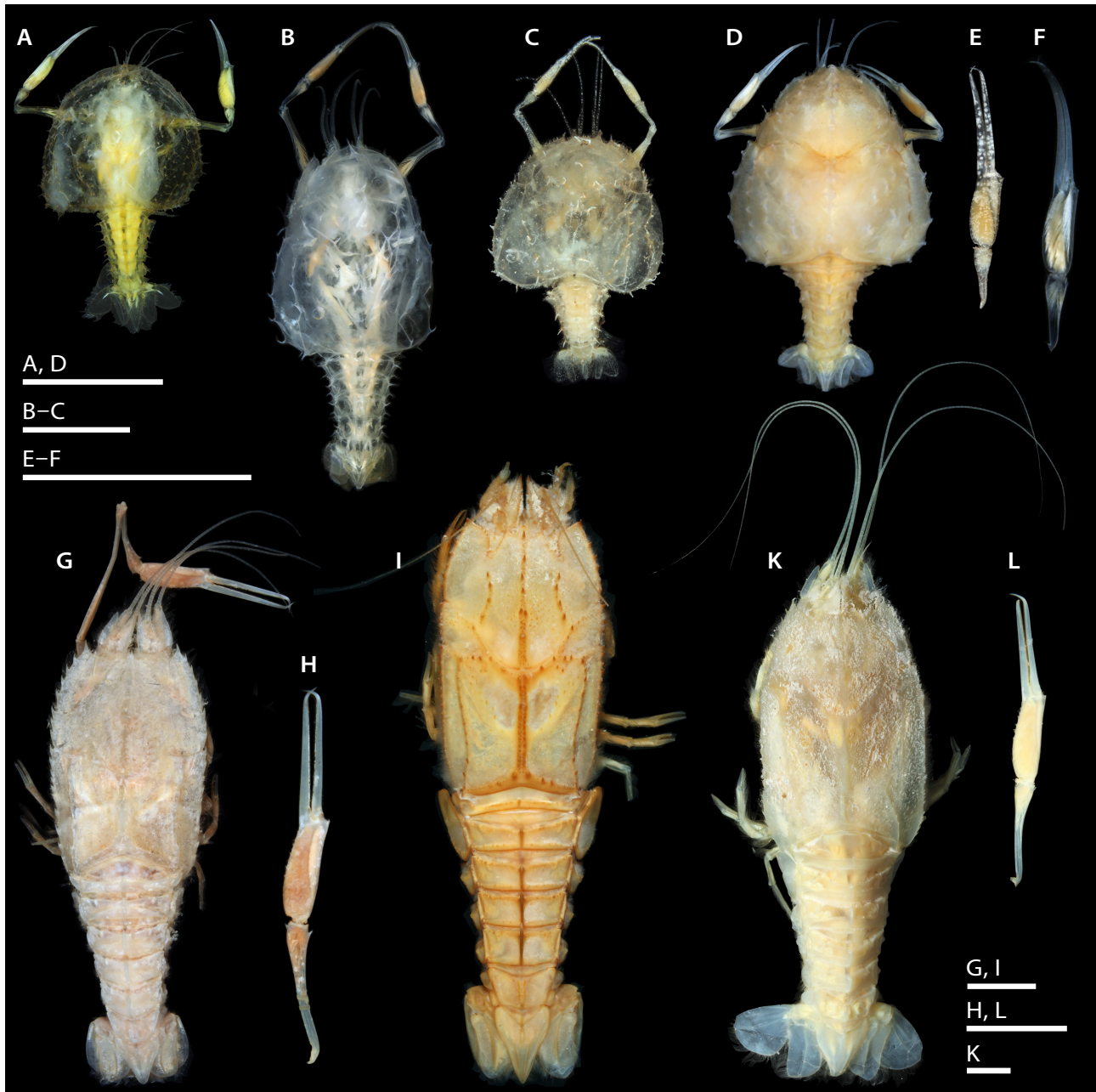


Figure 2. Cross-polarized light images of larval and adult representatives of Polychelidae. • A – “*Eryoneicus*” *puritanii* Lo Bianco, 1903 (ZSM 1504/2), larva, dorsal view. • B, E – “*Eryoneicus*” *spinoculatus* Bouvier, 1905 (ZSM A_20100241); B – larva, dorsal view; E – larva, detail of chela. • C, F – “*Eryoneicus*” *atlanticus* Lenz & Strunk, 1914 (ZSM 1452/3); C – larva, dorsal view; F – larva, detail of chela. • D – *Stereomastis suhmi* Bate, 1878 (ZSM 1488/3), larva, dorsal view. • G – *Stereomastis sculpta* Smith, 1880 (ZSM 1492/2_A), adult; G – dorsal view; L – detail of chela. • H – *Polycheltes typhlops typhlops* Heller, 1862 (ZSM 1493/1_B), adult, dorsal view. • I – *Willemoesia leptodactyla* Thomson, 1873 (ZSM 1579/3), adult, dorsal view. • K – *Polycheltes typhlops typhlops* Heller, 1862 (ZSM 1493/6), adult, detail of chela. All scale bars 10 mm.

cluded drawings and images that were reconstructed (Quintana & Retamal 1984; Teruzzi 1990; Guerao & Abelló 1996; Galil 2000; Ah Yong & Brown 2002; Karasawa *et al.* 2003; Garassino & Schweigert 2004; Ah Yong & Galil 2006; Garassino & Gironi 2006; Boyko 2006; Ah Yong & Chan 2008; Haug *et al.* 2011a; Galil 2013; Artüz *et al.* 2014; Audo 2014; Audo *et al.* 2014a, 2017a,

b, 2021; Audo & Furrer 2020; Martin 2014; Torres *et al.* 2014; Eiler & Haug 2016; Konishi *et al.* 2021; Schweitzer & Feldmann 2023). Material from museum collections included fossils as well as specimens preserved in alcohol (AM – Australian Museum, Sydney; ZSM – Bavarian State Collection of Zoology, Munich; MNHN – Muséum nationale d’histoire naturelle, Paris; NHM –

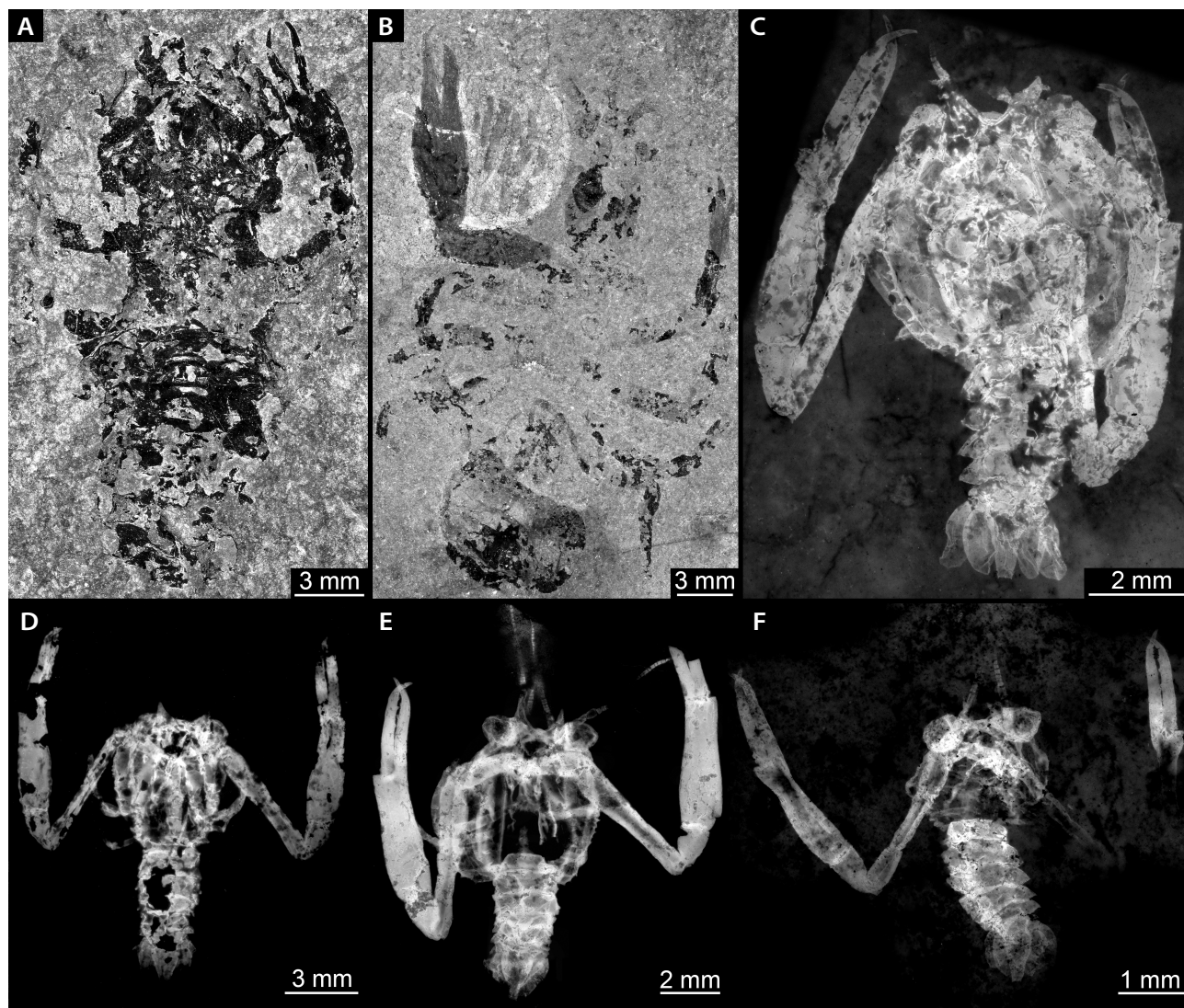


Figure 3. High-resolution images of Triassic (A, B) and Jurassic (C–F) fossil representatives of the group Polychelida. • A – cross-polarized light image of *Tetrachela raiblana* Bronn, 1858. (BMNH_In_41876). • B – cross-polarized light image of *Tetrachela* sp. (BMNH_In_44953). • C – autofluorescence image of *Palaeopentacheles roettenbacheri* Münster, 1839 (169_MG_2013). • D–F – autofluorescence image of *Palaeopentacheles* sp.; D – (197_MG_2014); E – (SMNS_67903); F – (NE_RF_2016_05).

Natural History Museum, London; Figs 2–4). Material from private collectors included only fossil material (Manfred Ehrlich; Michael Fecke; Roger Frattigiani; Markus Gebert; Udo Resch; Figs 3–5; for a detailed list of data origin see App. 1).

A total of 105 shields of extant individuals were reconstructed for the analysis (73 adults, 32 larvae), and 72 shields of fossil individuals (68 adults, 4 larvae of *Palaeopentacheles roettenbacheri*, see Eiler & Haug 2016). Hereby, all extant individuals are representatives of the group Polychelidae, an ingroup of Polychelida. Furthermore, the chelae of 37 extant individuals (21 adults, 16 larvae) and 39 fossil individuals (38 adults, 1 larvae) were reconstructed for the analysis (for a detailed list of data origin see App. 1).

Documentation process

Extant material was documented using a Canon EOS 650 D camera with a Canon EF-S 18–55 mm lens. For detailed shots or small objects, either a 13 mm or 21 mm macro extension tube was added to the lens. Two Yongnuo Speedlight YN565EX II flashes or one Yongnuo Speedlight YN24EX flash were used to illuminate the objects. A polarizing filter was used on both the lens and the flashes to eliminate specular reflexions. The specimens were placed in a black tub and covered in 75% ethanol. Smaller specimens were fixed between several microscope slides and cover slips and documented in one or two parts. Larger individuals were too large to be fixed entirely. Therefore, they were alternatively fixed and documented

in two to three parts. A bench out of microscope slides was built to fixate part of the body which was then documented, usually anterior and posterior of the animal or sometimes, anterior, middle, and posterior. The documented but not fixated part of the specimen was then cut from the image, merging the leftover individual parts to a full panorama of the whole specimen. With an adjustable mount, images were recorded at 3 mm intervals from the lowest focal plane to the highest focal plane (Haug & Haug 2014, Eiler et al. 2016).

Previously undocumented fossil specimens were documented with a Keyence BZ-9000 inverse epifluorescence microscope, with DAPI (360 nm excitation wavelength) and GFP (470 nm excitation wavelength) filters with a lens magnification of 2×, 4× or 10× (resulting in 20×, 40× and 100× magnification). This imaging technique is possible due to the autofluorescence properties of the specimens (e.g. Haug et al. 2011b). Again, multiple images in different focus layers were recorded.

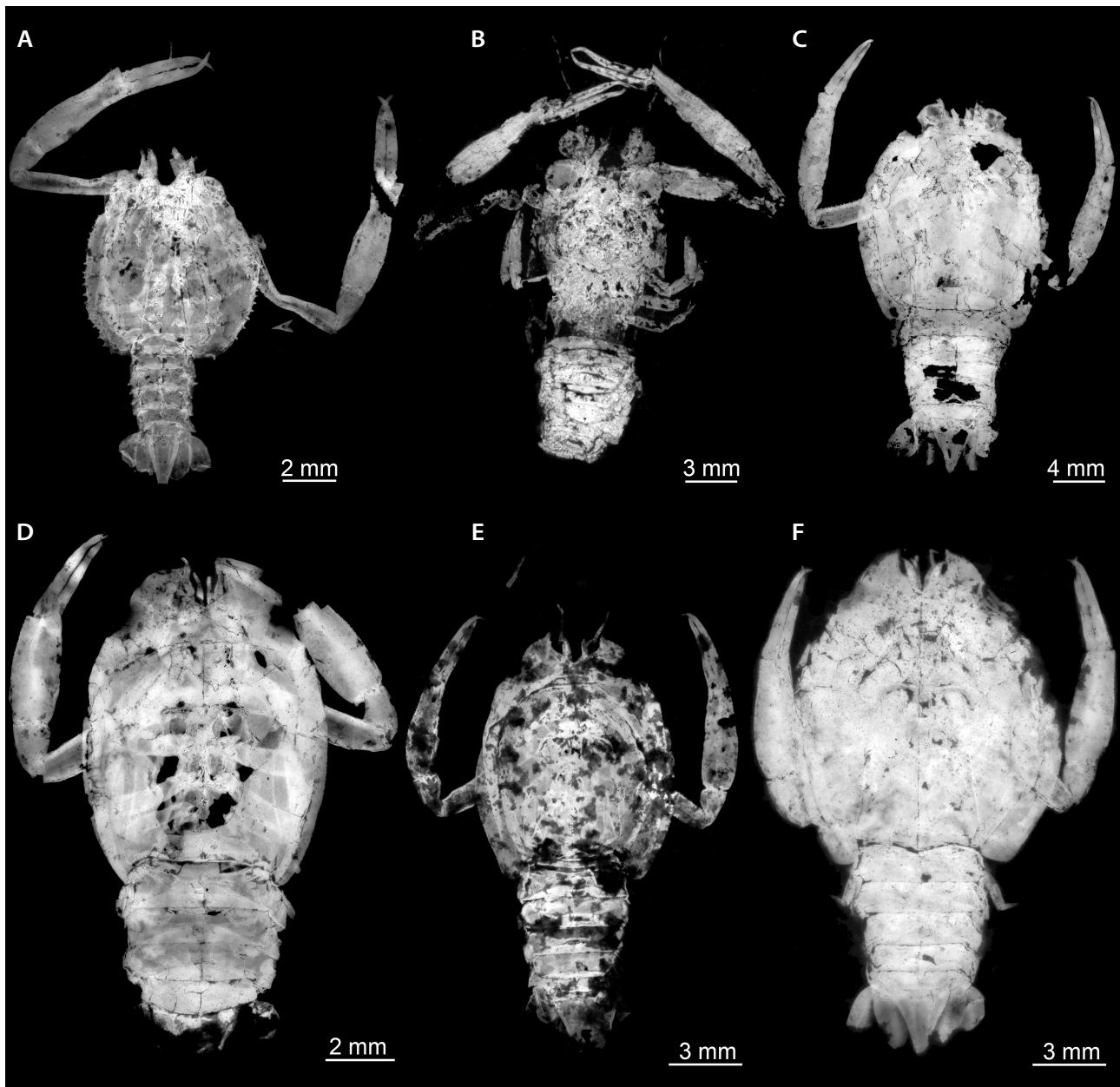


Figure 4. Autofluorescence images of Jurassic fossil representatives of the group Polychelida. • A, B – *Palaeopentacheles roettenbacheri* Münster, 1839; A – (MF_JO14_A6); B – (D_2014). • C–F – *Knebelia schuberti* von Meyer, 1836; C – (SMNS_67806); D – (JMS_085); E – (263); F – (MG_JO14_A1).

Image processing

Using the software CombineZP (Hadley 2010), images of larvae recorded at different focal planes were combined into one entirely focused image. For adults, the image with the best focus was chosen from each adult stack and used in the next step.

The selected or stacked images were merged in Photoshop CS3 and corrected for brightness, cut out and properly aligned (Haug & Haug 2014). The documented and collected images were then individually uploaded into Inkscape where their outlines were traced and filled in to produce vector graphics. For the chelae, the dactylus and the propodus were traced individually and saved separately to ensure the angle of opening does not affect the following outline analysis. For the shield, only one better preserved half was drawn, then duplicated, mirrored and fused to create a full shield outline. In cases where material was damaged or otherwise not fully accessible, we conducted minor extrapolations. For example, when a small piece of dirt was covering the outline of a feature, the course of the outline was extrapolated. Material where large parts of the outline were obstructed was discarded.

Data analysis

The outlines of the dactylus were analyzed using the software package SHAPE (Iwata & Ukai 2002). Hereby, all vector graphics are transformed into chain-codes, which then are turned into normalized elliptical Fourier descriptors (NEFDs), which can be compared (Braig *et al.* 2023). The number of harmonics was set to 10, aligned along the 1st harmonic of each shape. A principal component analysis (PCA) was used to analyze variation within the data.

The shield and propodus were analysed with the package Momocs (ver. 1.4.1, Bonhomme *et al.* 2014) in the R-statistics-environment (R Core Team 2024). The principle of the elliptic Fourier transformation is the same, but the Momocs package provides more functionality regarding calibration of harmonics, but struggles sometimes with aligning complex elongated shapes as the dactylus. We used 21 harmonics for the shield and 10 for the propodus, following a calibration function to determine the number of harmonics to describe 99% of variation.

Further steps were conducted solely in the R-statistics environment (R Core Team 2024). The data was plotted

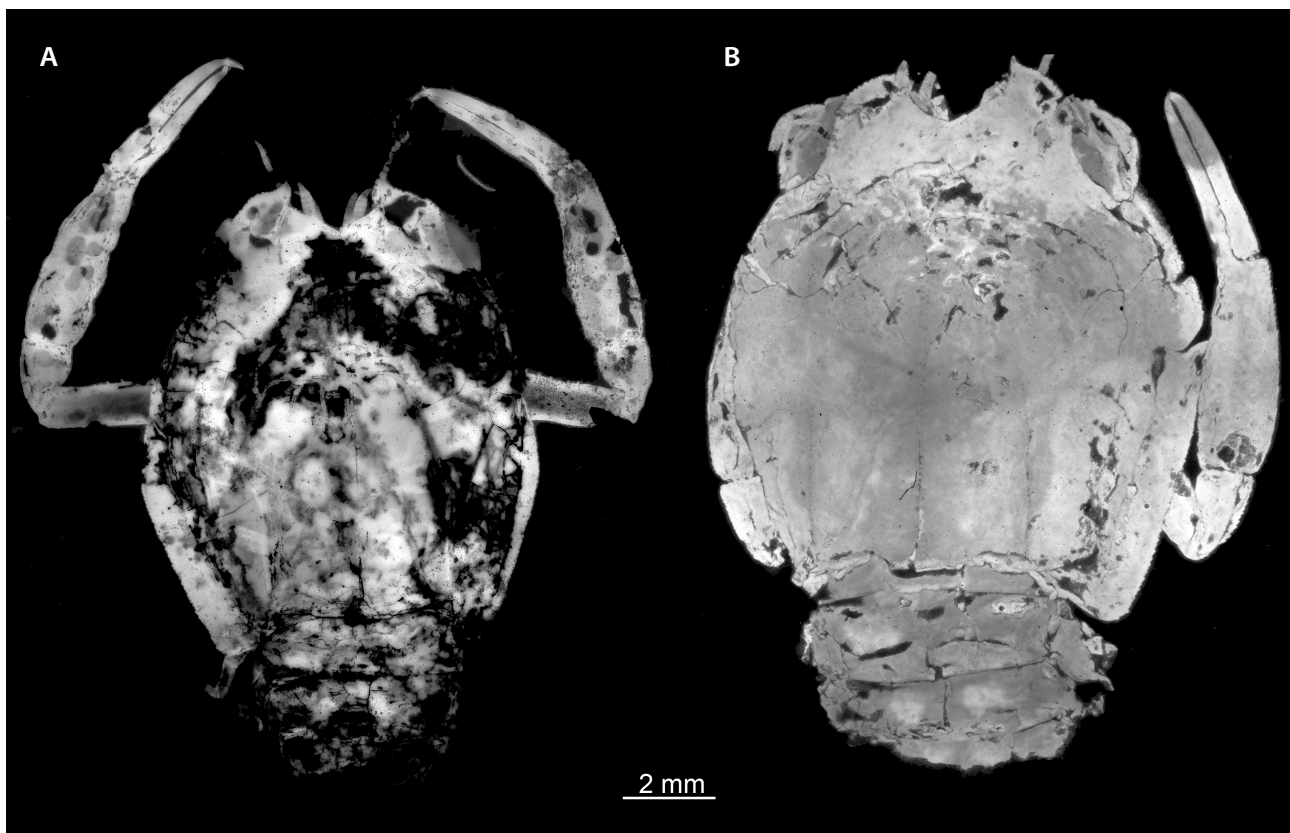


Figure 5. Autofluorescence images of Jurassic fossil representatives of the group Polychelida. • A, B – *Knebelia schuberti* von Meyer, 1836; A – (MF_JO14_A4); B – (MF_JO14_A3).

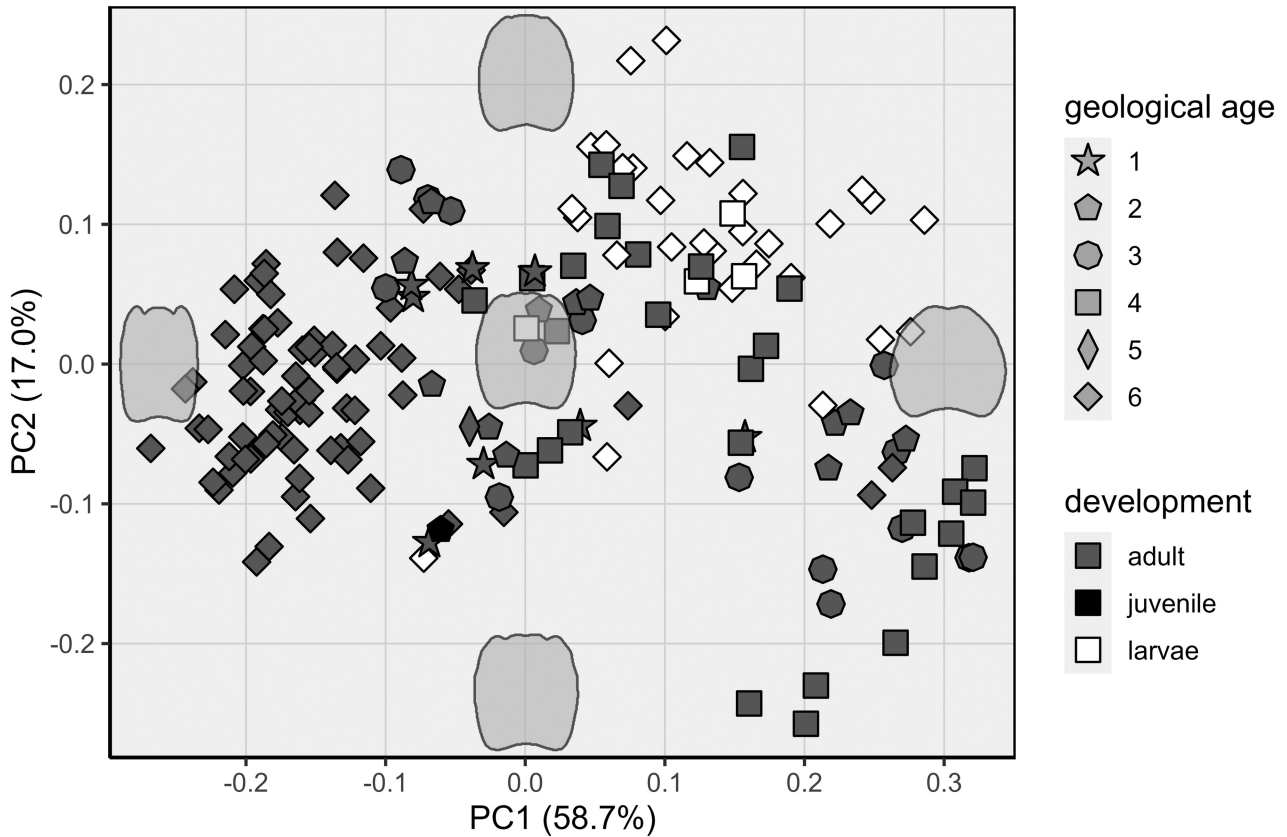


Figure 6. Scatter plot of the first two principal components resulting from the PCA on the outline analysis of shields of Polychelida. Grey shapes represent mean and ± 2 S.D. variation of the respective component. Geological age: 1 – Upper Triassic; 2 – Lower Jurassic; 3 – Middle Jurassic; 4 – Upper Jurassic; 5 – Lower Cretaceous; 6 – extant.

using the package *ggplot2* (ver. 3.3.6, Wickham 2016) for an initial visualization of morphospaces. To quantify these morphospaces, we tested morphospace occupation and position within the morphospace, using the package *disprity* (ver. 1.9, Guillerme 2018). We grouped individuals based on geologic age and developmental status, we omitted groups with less than 3 representatives from quantitative comparisons due to bootstrapping constraints. Data was then bootstrapped ($n = 1499$, Davidson & MacKinnon 2000) and rarefied to the group with the smallest sample size to account for outliers and differences in sample size. This approach is also efficient at mitigating the Lagerstätten-effect, in this case oversampling of certain time slices. We used the sum of variances across dimensions as a measure for morphospace occupation of a group. We used the median of centroid distances of a group members and the centre of the morphospace as a measure for position within the morphospace. To see if differences in space occupation and position were statistically significant between groups, data was bootstrapped and corrected for sample size, then tested with a Welch Two Sample t-test, Benjamini-Hochberg corrected for multiple testing. The code used is included in the appendix (App. 2).

Results

Morphospace of the shield

For each structure, the two most relevant principal components (PCs), *i.e.* PC1 and PC2, were plotted against each other to visualize the morphospace. The two axes represent different morphological variations of the structure, which were visualized through graphical component loadings (App. 3 for principal component scores of individuals, App. 4 for graphical component loadings of the axis demonstrating the variation each axis represents).

The PCA of the shield data set resulted in a total of 22 PCs, representing over 99% of variation in the shield. PC1 (58.7% of variation) is dominated by the width of the shield, positive values showing wider shields with shallow eye notches, negative values showing slimmer shields with deep eye notches. PC2 (17.0% of variation) is dominated by the general shape of the shield, positive values showing anteriorly more tapering shields, negative values showing more square shaped shields (Fig. 6).

Although there is some overlap between fossil and extant specimens, the clusters differ in their occupation of the morphospace markedly. The extant individuals plot

more towards the left side of the morphospace, indicating slimmer and longer shields with more pronounced incisions in the frontal margin (Fig. 6). Fossil individuals show more variation regarding PC2. They stretch towards the right and bottom of the morphospace, representing the unusually broad and short shields found only in the fossil record.

Adult and larval individuals of extant species differ along PC1 and PC2 (Fig. 6). The shields of extant larvae have a more bulbous or balloon-like form, with a concave posterior margin. Extant adults have a straight posterior margin, with more distinct incisions on the anterior margin. Two recognisable fossil larvae plot to the top right of the centre of the morphospace, in the middle of the group of fossil adults and extant larvae.

Morphospace of the propodus of the 4th thoracopod (1st pereiopod)

The PCA of the propodus data set resulted in a total of 16 PCs, representing over 99% of the variation in propodus shape (App. 5 for principal component scores of individuals, App. 4 for graphical component loadings of the axis demonstrating the variation each axis represents). PC1 (36.0% of variation) is dominated by the width of the propodus and the length of the fixed finger relative to the rest of the propodus, positive values showing wide propodi with short fixed fingers, negative values showing

slim propodi and elongated fixed fingers (Fig. 7). PC2 (22.2% of variation) is dominated by the curvature of the propodus, positive values showing concave propodi with outward curved tips, negative values showing straight propodi with inward curved tips.

Extant and fossil individuals are mostly separated within the morphospace, with fossil individuals plotting on the top half of the morphospace representing outwardly curved propodi and extant individuals plotting mainly in the bottom left, representing slim straight propodi. Most of the overlap is caused by individuals from the early Jurassic overlapping with extant larvae (Fig. 7).

Within the extant individuals, adults and larvae plot loosely following PC1 (Fig. 7). Extant larvae plot more on the left side of the morphospace, representing slim propodi, while extant adults plot also on the right side, representing broad propodi. Within fossil individuals, one larva plotted again between fossil adults, extant adults, and extant larvae, in the centre of the morphospace. Its position indicates an intermediate propodus shape with a slightly curved tip of the fixed finger.

Morphospace of the dactylus of the 4th thoracopod (1st pereiopod)

The PCA of the dactylus data set resulted in a total of 15 PCs, representing over 99% of the variation in dactylus

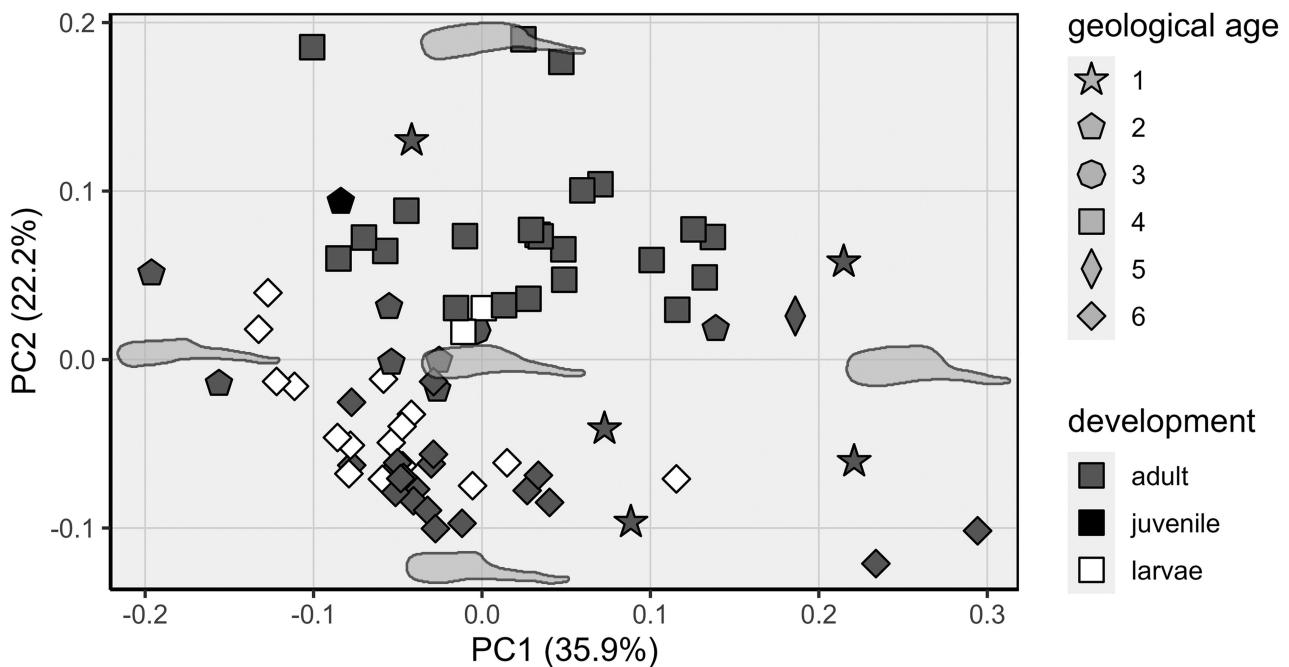


Figure 7. Scatter plot of the first two principal components resulting from the PCA on the outline analysis of propodi of Polychelida. Grey shapes represent mean and ± 1 S.D. variation of the respective component. Geological age: 1 – Upper Triassic; 2 – Lower Jurassic; 3 – Middle Jurassic; 4 – Upper Jurassic; 5 – Lower Cretaceous; 6 – extant.

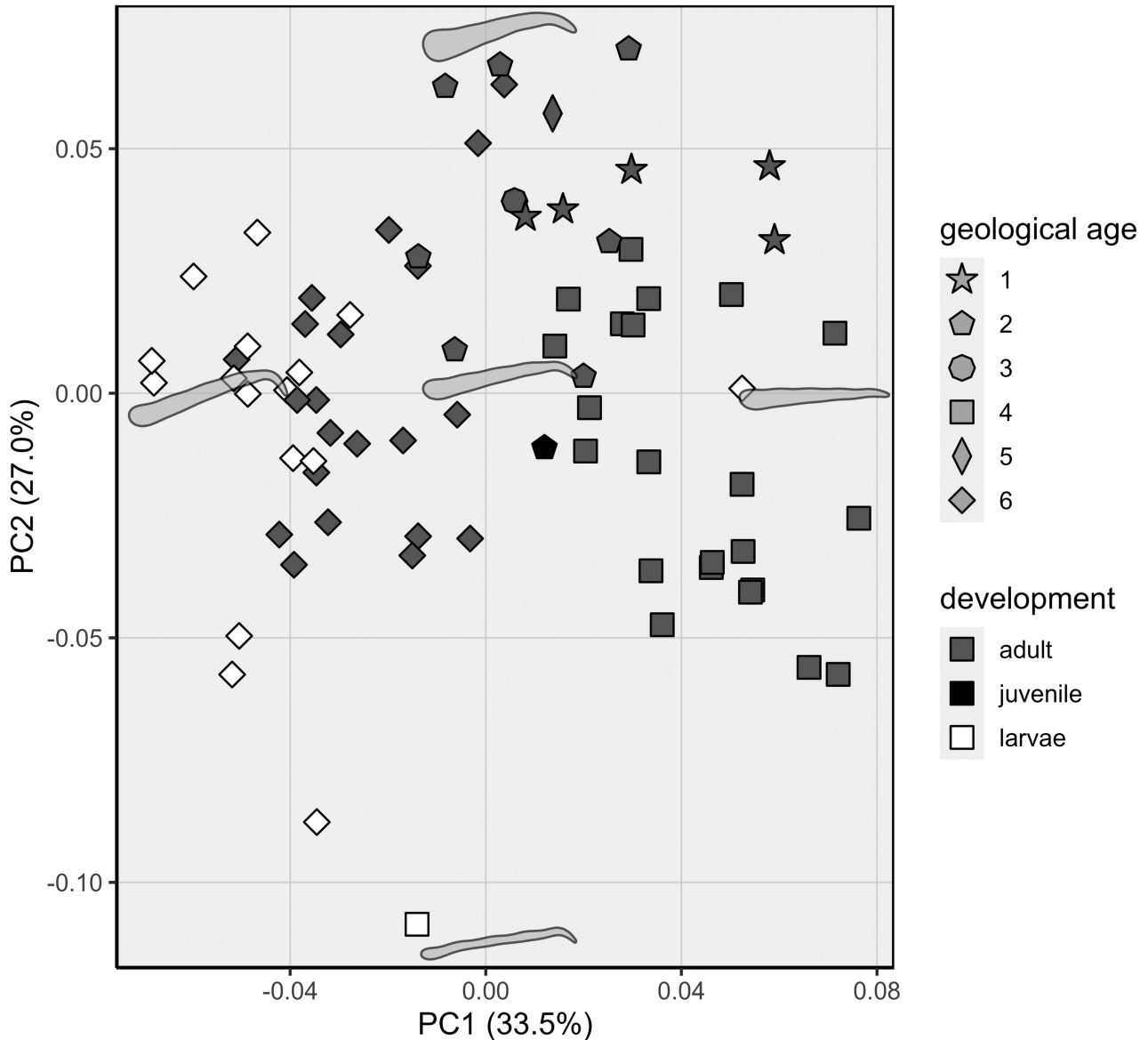


Figure 8. Scatter plot of the first two principal components resulting from the PCA on the outline analysis of dactyli of Polychelida. Grey shapes represent mean and ± 2 S.D. variation of the respective component. Geological age: 1 – Upper Triassic; 2 – Lower Jurassic; 3 – Middle Jurassic; 4 – Upper Jurassic; 5 – Lower Cretaceous; 6 – extant.

shape (App. 6 for principal component scores of individuals, App. 4 for graphical component loadings of the axis demonstrating the variation each axis represents). PC1 (33.5% of variation) is dominated by the width of the dactylus, positive values describing thick dactyli, negative values describing thinner dactyli with serration. PC2 (27.0% of variation) is dominated by the tip curvature of the dactylus, positive values showing a straight tip, negative values showing a strongly inward curved tip (Fig. 8).

Fossil specimens plot more on the right side of the morphospace, indicating thicker dactyli, while extant specimens plot more on the left side, indicating thinner dactyli (Fig. 8). However, there is one fossil outlier at the

bottom of the morphospace that has prominent spines on the inner margin of its dactylus.

Regarding developmental status, extant larvae plot rather on the bottom left side of the morphospace and show more variation than the extant adults (Fig. 8). The strongly curved dactylus shape is more prominent in the extant adults, whereas the straight dactylus is specific to extant larvae.

Disparity analysis

To quantify the differences in morphological diversity, we performed disparity analyses, comparing size occupation

of the morphospace as well as position within the morphospace of the fossil versus extant individuals. We found significant differences in both size and position for most comparisons for the shields, propodi and dactyli between extant and fossil individuals (Welch's Two-sample t-test, Benjamini-Hochberg corrected, $p < 0.001$). Exceptions were seen in the propodus morphological diversity between the Upper Jurassic and extant individuals, and the dactylus morphological diversity between the Lower Jurassic and extant individuals (Welch's Two-sample t-test, Benjamini-Hochberg corrected, $p > 0.001$).

Discussion

Limitations of the analysis

Deformations in extant larval material due to their softness, and partially preserved fossil material were causes for smaller sample sizes. To counteract this issue, in some instances of only minor damage to the material, extrapolations about the outline were made by the authors.

A lack of fossil larvae caused issues when comparing developmental patterns between fossil and extant polychelidans. There is so far only a handful of specimens interpreted as larval stages in the fossil record. Most of these were not well enough preserved to be used for this analysis.

In the fossil context, some specimens may have been exuviae. We do not think that these would strongly influence our analysis, as we discarded broken or badly preserved specimens and reconstructed only half shields. Furthermore, exuviae should not affect the shape of the appendage strongly, similarly in the shield. They might add some increased variation, but we do not estimate it to significantly affect the analysis. Additionally, in fossils it is often challenging to determine if a specimen is an exuvia or a carcass that has decayed for some time; only in cases where distinct open moult sutures are apparent an interpretation as an exuvia is likely.

Another aspect to be considered is the Lagerstätte effect, specifically caused by the large amount of fossil material. We binned the fossil material, comparing several time slices, as well as performing rarefaction, to counter potential bias caused by the Lagerstätte effect. Despite these limitations, the analyses show a strong signal. This signal indicates that the results are still informative.

Morphological diversity of the shield

Our results show that the morphological diversity of the shield in the group Polychelida varied over time and is

smaller in extant specimens than in specimens from the Middle Jurassic, despite the lack of larval specimens for the fossil time slice (App. 7). When comparing fossil and extant morphospace occupation, extreme morphologies, such as the wide and circular shields seen in the fossil record, are no longer present (Fig. 6). The reduction of the eyes, and consequently narrower eye notches, and the narrowing of the shield were among the morphological changes interpreted as adaptations to the deep-sea habitat (Ahyong 2009). Eyes as well as a wide shield protecting from predation and intra-specific competition are less needed in a dark and vast habitat, especially since a burrowing lifestyle has been suggested for extant representatives of Polychelidae (Firth & Pequegnat 1971, Gore 1984, Ahyong 2009, Audo *et al.* 2021). The slimmer rectangular shield shape, usually better suited for burrowing in soft substrate, therefore could provide a better adaptation to the deep sea. This morphology is rarely found in the fossil record (Audo & Furrer 2020). Although, there are fossil individuals described that already inhabited the deep sea, or at least deeper waters (Audo *et al.* 2018, Audo & Furrer 2020).

The extreme balloon-like shields did not yet exist in the few fossil larvae that are so far described, supporting earlier studies (Fig. 6; Haug *et al.* 2015). The bulbous, “eryoneicus”-type appearance (Fig. 2) is likely well suited for a planktic lifestyle (Martin 2014, Eiler & Haug 2016). This shield shape provides protection from predators and potentially reduces sinking rates, by reducing the relative density of the larva, as well as allowing for longer distance dispersal. The lack of this morphology in the fossil record suggests that fossil larval representatives of Polychelida were not yet specialised to a long life in the plankton and settled to the ground at smaller sizes (Haug *et al.* 2015, Eiler & Haug 2016). The few fossil specimens interpreted as larvae in our analysis (see discussion in Eiler & Haug 2016) plot in an intermediate position between fossil adults, extant adults, and extant larvae, reinforcing this assumption. One could argue that the intermediate position of the two fossil larvae of *P. roettenbacheri* indicate a plesiomorphic morphology. However, the sample size of fossil larvae is still too small to draw any such conclusions.

Morphological diversity of the chelae

Our results show that the morphological diversity of the chelae decreased over time as well, especially in the propodus. In the dactylus an increase, followed by a slight decrease can be seen (App. 7). Certain fossil morphologies of the chelae are also no longer present today (Figs 7, 8). In both cases, shield and chelae, the structures of the fossils are shorter and wider than in

extant individuals. There are some wide and short chelae still found in extant representatives, but only in adults. The slender and elongated morphology of the extant individuals is interpreted to be better adapted for a life in the deep sea, well suited for an ambush predator lifestyle as assumed for extant individuals (Firth & Pequegnat 1971, Gore 1984, Ah Yong 2009, Audo *et al.* 2021). Most fossil representatives presumably pursued a more active predation strategy (Ah Yong 2009).

Furthermore, the tips of the propodi and dactyli of extant individuals often strongly curve inwards, whereas fossils possess more straight tips. This pattern could be an ecological signal pointing towards different grasping strategies. It has been suggested though that it is rather caused by preparation of specimens; the tips tapering into the sediment; and therefore, not being a true signal (D. Audo, pers. comms. 2025). One fossil representative does not show straight dactyli, but instead has prominent spines along the inner margin of the dactylus (Fig. 8). The specimen in question is interpreted to be an immature of *Palaeopentacheles roettenbacheri* Münster, 1839, a Jurassic species (Eiler & Haug 2016). Other specimens of this species have spines as well, yet they are often so small that they do not significantly affect the simplified outline created by the harmonics. These spines have been described as sexual dimorphism before (Audo *et al.* 2014b). The individual may thus be a female.

Within the extant species, a difference in adult and larval morphology is also observable when looking at the chelae. While larvae show straight tips for the chelae, adults show tips of both the finger of the propodus and the dactylus that strongly curve inward. This suggests that larvae do not need their chelae for piercing objects or prey, but rather for grasping. A similar pattern can be observed, *e.g.* in squilloidean mantis shrimps. Here, larvae show straight spineless claws, while adults do have claws with spines (*e.g.* Hamano & Matsuura 1987).

Deep or shallow water origins of the group

The origins of Polychelida, shallow or deep-sea environments, have been a topic of discussion. A shallow water origin had been suggested early for the group, based on mostly Jurassic representatives (Beurlen 1931, Ah Yong 2009). This hypothesis was later questioned with the description of new fossil species from deep-sea environments (Audo & Furrer 2020; Audo *et al.* 2018, 2020, 2021). The evolutionary trajectory thus shifted to a scenario of an early colonization of the deep-sea and a later extinction of shallow-water species (Audo *et al.* 2021). Recently, Chang *et al.* (2024) concluded that the diversification of extant deep-sea lobsters started during

the Late Jurassic, based on a phylogenetic analysis of the group (Chang *et al.* 2024). Fossil representatives of Polychelida were therefore already present in deep-sea environments, although probably not as deep as the deepest extant representatives (Chang *et al.* 2024).

In our data, we see an overlap of fossils and extant specimens for the shield, especially for shield shapes with medium width and shallow ocular incisions. Hereby, mostly adults from the Early and Middle Jurassic seem to overlap with extant adults. In the propodus, we see an overlap for shapes with long and straight fixed fingers. In the dactylus we see almost no overlap, except for some Early Jurassic individuals with straight dactyli, overlapping with extant ones. These results seem to reinforce the pattern, that representatives of Polychelida have already inhabited deep-sea environments during the Jurassic (the exact timing still remains unclear) but further diversified and conquered larger depths, while those living in shallow waters went extinct (Audo *et al.* 2021, Chang *et al.* 2024). Furthermore, the wide and bulky chelae and wide shields in fossils may have facilitated an epibenthic omnivorous lifestyle, also seen, *e.g.* in many fossil and extant crabs. Competition for ecological roles could therefore have been a driver of the extinction of shallow water species (Beurlen 1931).

Increase of ecological diversity over time

Especially in the shape of the shield, a distinct differentiation of the larvae and adults is apparent in the modern fauna. Such a differentiation is absent in the Mesozoic forms, it must have evolved after the Late Jurassic (likely in a stepwise manner, Haug *et al.* 2015, Eiler & Haug 2016). The area occupied by the extant larvae even seems slightly larger than that of the extant adults. Given that it is unlikely that we have a full taxonomic coverage on the larval side, the true morphological diversity of extant larvae is likely to be even larger.

A strong selective pressure leading to such a differentiation has been recognised for several different crustacean lineages (Haug & Haug 2013; Haug *et al.* 2013, 2016; Haug 2020; Chang *et al.* 2024), yet mostly on qualitative characters. The here presented quantitative data emphasise the general observation of a stronger morphological and ecological differentiation between immatures and adults in many independent lineages.

Conclusion

The morphological diversity of the group Polychelida varied during its evolutionary history and was generally larger during the Jurassic than it is today. Some morph-

ologies are lost while an increased morphological differentiation between extant larvae and extant adults provides new diversity. The ecological roles facilitated by these morphologies match adaptations to different habitats. We find some support for an early adaptation to deep-sea habitats in some representatives of Polychelida.

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References

- AHYONG, S.T. 2009. The polychelidan lobsters: phylogeny and systematics (Polychelida: Polychelidae). *Decapod Crustacean Phylogenetics, Crustacean Issues* 18, 369–396. DOI 10.1201/9781420092592-c19
- AHYONG, S.T. & BROWN, D.E. 2002. New species and new records of Polychelidae from Australia (Crustacea: Decapoda). *Raffles Bulletin of Zoology* 50(1), 53–80.
- AHYONG, S.T. & CHAN, T.Y. 2008. Polychelidae from the Bohol and Sulu seas collected by PANGLAO 2005 (Crustacea: Decapoda: Polychelidae). *Raffles Bulletin of Zoology* 19, 63–70.
- AHYONG, S.T. & GALIL, B.S. 2006. Polychelidae from the southern and western Pacific (Decapoda, Polychelida). *Zoosystema* 28(3), 757–767.
- ARTÜZ, M.L., KUBANÇ, C. & KUBANÇ, S.N. 2014. *Stereomastis artuzi* sp. nov., a new species of Polychelidae (Decapoda, Polychelida) described from the Sea of Marmara, Turkey. *Crustaceana* 87(10), 1243–1257. DOI 10.1163/15685403-00003353
- AUDO, D. 2014. *Les Polychelida, un groupe de crustacés énigmatiques. Systématique, histoire évolutive, paléoécologie et paléoenvironnements*. 548 pp. Ph.D. thesis, Museum National d'Histoire Naturelle – Ecole Doctorale Sciences de la Nature et de l'Homme, Paris.
- AUDO, D. & FURRER, H. 2020. A new polychelidan lobster from the Alpine Lower Jurassic of southeastern Switzerland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 296(1–2), 29–40. DOI 10.1127/njgpa/2020/0900
- AUDO, D., CHARBONNIER, S., SCHWEIGERT, G. & MARTIN, J.P.S. 2014a. New eryonid crustaceans from the Late Jurassic Lagerstätten of Cerin (France), Canjuers (France), Wattendorf (Germany) and Zandt (Germany). *Journal of Systematic Palaeontology* 12(4), 459–479. DOI 10.1080/14772019.2013.777809
- AUDO, D., SCHWEIGERT, G., HAUG, J.T., HAUG, C., SAINT MARTIN, J.-P. & CHARBONNIER, S. 2014b. Diversity and palaeoecology of the enigmatic genus *Knebelia* (Eucrustacea, Decapoda, Eryonidae) from Upper Jurassic plattenkalks in southern Germany. *Palaeontology* 57(2), 397–416. DOI 10.1111/pala.12071
- AUDO, D., WILLIAMS, M., CHARBONNIER, S. & SCHWEIGERT, G. 2017a. *Gabaleryon*, a new genus of widespread early Toarcian polychelidan lobsters. *Journal of Systematic Palaeontology* 15(3), 205–222. DOI 10.1080/14772019.2016.1167786
- AUDO, D., SCHWEIGERT, G., CHARBONNIER, S. & HAUG, J.T. 2017b. Systematic revision and palaeobiology of *Rosenfeldia triasica* and *Rogeryon oppeli* gen. et comb. nov. (Eucrustacea, Polychelida). *European Journal of Taxonomy* 367, 1–23. DOI 10.5852/ejt.2017.367
- AUDO, D., CHARBONNIER, S. & KROBICKI, M. 2018. Rare fossil polychelid lobsters in turbiditic palaeoenvironments. *Journal of Systematic Palaeontology* 16(12), 1017–1036. DOI 10.1080/14772019.2017.1359690
- AUDO, D., SCHWEIGERT, G. & CHARBONNIER, S. 2020. *Proeryon*, a geographically and stratigraphically widespread genus of polychelidan lobsters. *Annales de Paléontologie* 106(2), 102376. DOI 10.1016/j.annpal.2019.102376
- AUDO, D., BARRIEL, V. & CHARBONNIER, S. 2021. Phylogeny and evolutionary history of polychelidan lobsters. *Journal of Systematic Palaeontology* 19(6), 417–439. DOI 10.1080/14772019.2021.1918773
- BATE, C.S. 1878. XXXII. On the *Willemoesia* Group of Crustacea. *The Annals and Magazine of Natural History* 5(2), 273–283, pl. 13. DOI 10.1080/00222937808682426
- BEURLIN, K. 1931. Die Besiedlung der Tiefsee. *Natur und Museum* 61, 269–278.
- BONHOMME, V., PICQ, S., GAUCHEREL, C. & CLAUDE, J. 2014. Momocs: Outline Analysis Using R. *Journal of Statistical Software* 56(13), 1–24. <http://www.jstatsoft.org/v56/i13/> DOI 10.18637/jss.v056.i13
- BOUVIER, E.-L. 1905. *Palinurides* et *Eryonides* recueillis dans l'Atlantique oriental pendant les campagnes de d'Hirondelle et de la Princesse-Alice. *Bulletin de Musée Océanographique de Monaco* 28, 1–7.
- BOYKO, C.B. 2006. New and historical records of polychelid lobsters (Crustacea: Decapoda: Polychelidae) from the

- Yale Peabody Museum collections. *Bulletin of the Peabody Museum of Natural History* 47(1), 37–46.
DOI 10.3374/0079-032X(2006)47[37:NAHROP]2.0.CO;2
- BRAIG, F., HAUG, C. & HAUG, J.T. 2023. Phenotypic variability in the shield morphology of wild- vs. lab-reared eumalacostracan larvae. *Nauplius* 31, e2023004.
DOI 10.1590/2358-2936e2023004
- BRONN, H.G. 1858. Beiträge zur Triasischen Fauna und Flora der bituminösen schiefer von Raibl, nebst anhang über die kurr'sche sippe *Chropteris* aus dem Lettenkohlen-Sandsteine. *Jarhbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1–32.
- CHANG, S.-C., AHYONG, S.T. & TSANG, L.-M. 2024. Molecular phylogeny of deep-sea blind lobsters of the family Polychelidae (Decapoda: Polychelida), with implications for the origin and evolution of these “living fossils”. *Molecular Phylogenetics and Evolution* 192, 107998.
DOI 10.1016/j.ympev.2023.107998
- DAVIDSON, R. & MACKINNON, J.G. 2000. Bootstrap tests: How many bootstraps? *Econometric Reviews* 19(1), 55–68.
DOI 10.1080/07474930008800459
- EILER, S.M. & HAUG, J.T. 2016. Larval development of fossil polychelidan crustaceans, exemplified by the 150 million years old species *Palaeopentacheles roettenbacheri*. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 279, 295–310. DOI 10.1127/njgpa/2016/0557
- EILER, S.M., HAUG, C. & HAUG, J.T. 2016. Detailed description of a giant polychelidan Eryoneicus-type larva with modern imaging techniques. *Spixiana* 39(1), 39–60.
- FIRTH, R.M. & PEQUEGNAT, W.E. 1971. *Deep-sea lobsters of the families Polychelidae and Nephropidae (Crustacea, Decapoda) in the Gulf of Mexico and Caribbean Sea*. 106 pp. Texas A & M University, Department of Oceanography.
- GALIL, B. 2000. Crustacea Decapoda: Review of the genera and species of the family Polychelidae Wood-Mason, 1874. In CROSNIER, A. (ed.) *Résultats des Campagnes MUSORSTOM, 21, Mémoires du Muséum national d'Histoire naturelle* 184, 285–387.
- GALIL, B.S. 2013. On a collection of Polychelidae from Papua New Guinea (Crustacea, Decapoda, Polychelida). *Zoosystema* 35(4), 495–502. DOI 10.5252/z2013n4a4
- GARASSINO, A. & GIRONI, B. 2006. *Coleia boboi* n. sp. (Crustacea, Decapoda, Eryonoidea) from the Late Triassic (Rhaetian) of Monte Verzegnis (Udine, NE Italy). *Atti della Società italiana di scienze naturali e del museo civico di storia naturale di Milano* 147(1), 93–102.
- GARASSINO, A. & SCHWEIGERT, G. 2004. *Cycleryon wulfi* n. sp. (Crustacea: Decapoda: Eryonidae) from the Upper Jurassic of Eichstätt (Bavaria, S Germany). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 145(2), 243–250.
- GAŠPARIČ, R., AUDO, D., HITIJ, T., JURKOVŠEK, B. & KOLAR-JURKOVŠEK, T. 2020. One of the oldest polychelidan lobsters from Upper Triassic (Carnian) beds at Kozja dnina in the Julian Alps, Slovenia, 107–117. In JAGT, J.W.M., FRAAIJE, R.H.B., VAN BAKEL, B.W.M., DONOVAN, S.K. & MELLISH, C. (eds) *A lifetime amongst fossil crustaceans: a tribute to Joseph S. H. Collins (1927–2019)*. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 296(1–2).
DOI 10.1127/njgpa/2020/0899
- GBIF: THE GLOBAL BIODIVERSITY INFORMATION FACILITY 2022. What is GBIF? Available from <https://www.gbif.org/what-is-gbif> [13 August 2022].
- GORE, R.H. 1984. Abyssal lobsters, genus *Willemoesia* (Palinura, Polychelidae), from the Venezuela Basin, Caribbean Sea. *Proceedings of the Academy of Natural Sciences of Philadelphia* 135, 1–11.
- GUERARO, G. & ABELLÓ, P. 1996. Description of the first larval stage of *Polycheles typhlops* (Decapoda: Eryonidea: Polychelidae). *Journal of Natural History* 30(8), 1179–1184.
DOI 10.1080/00222939600770631
- GULLIERME, T. 2018. dispRity: a modular R package for measuring disparity. *Methods in Ecology and Evolution* 9(7), 1755–1763. DOI 10.1111/2041-210X.13022
- HADLEY, A. 2010. CombineZP. <http://www.hadleyweb.pwp.blueyonder.co.uk/>
- HAMANO, T. & MATSUURA, S. 1987. Egg size, duration of incubation, and larval development of the Japanese mantis shrimp in the laboratory. *Nippon Suisan Gakkaishi* 53(1), 23–39. DOI 10.2331/suisan.53.23
- HAUG, C. & HAUG, J.T. 2014. Defensive enrolment in mantis shrimp larvae (Malacostraca: Stomatopoda). *Contributions to Zoology* 83(3), 185–194. DOI 10.1163/18759866-08303003
- HAUG, J.T. 2020. Metamorphosis in crustaceans, 254–283. In ANGER, K., HARZSCH, S. & THIEL, M. (eds) *Vol. 7. Developmental Biology and Larval Ecology. The Natural History of the Crustacea*. Oxford University Press, Oxford.
- HAUG, J.T. & HAUG, C. 2013. An unusual fossil larva, the ontogeny of achelatan lobsters, and the evolution of metamorphosis. *Bulletin of Geosciences* 88, 195–206.
DOI 10.3140/bull.geosci.1374
- HAUG, J.T., HAUG, C., WALOSZEK, D. & SCHWEIGERT, G. 2011a. The importance of lithographic limestones for revealing ontogenies in fossil crustaceans. *Swiss Journal of Geosciences* 104(Supp. 1), 85–98. DOI 10.1007/s00015-010-0033-1
- HAUG, J.T., HAUG, C., KUTSCHERA, V., MAYER, G., MAAS, A., LIEBAU, S., CASTELLANI, C., WOLFRAM, U., CLARKSON, E.N.K. & WALOSZEK, D. 2011b. Autofluorescence imaging, an excellent tool for comparative morphology. *Journal of Microscopy* 244, 259–272.
DOI 10.1111/j.1365-2818.2011.03534.x
- HAUG, J.T., AUDO, D., CHARBONNIER, S. & HAUG, C. 2013. Diversity of developmental patterns in achelate lobsters—today and in the Mesozoic. *Development Genes and Evolution* 223, 363–373. DOI 10.1007/s00427-013-0452-x
- HAUG, J.T., AUDO, D., HAUG, C., ABI SAAD, P., PETIT, G. & CHARBONNIER, S. 2015. Unique occurrence of polychelidan lobster larvae in the fossil record and its evolutionary implications. *Gondwana Research* 28, 869–874.
DOI 10.1016/j.gr.2014.05.004
- HAUG, J.T., HAUG, C. & GARWOOD, R. 2016. Evolution of insect wings and development – new details from Palaeozoic nymphs. *Biological Reviews* 91, 53–69.
DOI 10.1111/brev.12159

- HELLER, C. 1862. Beiträge zur näheren Kenntnis der Macrouren. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien*, 389–426.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (IZCN) 1964. Opinion 702: *Stereomastis* Bate, 1888 (Crustacea, Decapoda); validated under the plenary powers. *Bulletin of Zoological Nomenclature* 21, 111–112.
- IWATA, H. & UKAI, Y. 2002. SHAPE: a computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. *Journal of Heredity* 93(5), 384–385. DOI 10.1093/jhered/93.5.384
- KARASAWA, H., TAKAHASHI, F., DOI, E. & ISHIDA, H. 2003. First notice of the family Coleiidae Van Straelen (Crustacea: Decapoda: Eryonoidea) from the upper Triassic of Japan. *Paleontological Research* 7(4), 357–362. DOI 10.2517/prpsj.7.357
- KARASAWA, H., SCHWEITZER, C.E. & FELDMANN, R.M. 2013. Phylogeny and systematics of extant and extinct lobsters. *Journal of Crustacean Biology* 33(1), 78–123. DOI 10.1163/1937240X-00002111
- KONISHI, K., TAKAMI, M. & YANAGIMOTO, T. 2021. Morphological description of *Pentalcheles [sic] laevis* postlarva collected from Suruga Bay, Japan (Crustacea, Decapoda, Polychelidae). *Crustacean Research* 50, 1–7. DOI 10.18353/crustacea.50.0_1
- LENZ, H. & STRUNCK, K. 1914. Die Dekapoden der Deutschen Südpolar-Expedition 1901–1903. I. Brachyuren und Macruren mit Ausschluss der Sergestiden, 257–345. In DRYGALSKI, E. VON (ed.) *Deutsche Südpolar Expedition 1901–1903 im Auftrage des Reichsamtes des inner herausgegeben von Erich von Drygalski, Leiter der Expedition. Zoologie* 15(7). Georg Reimer, Berlin. DOI 10.5962/bhl.title.10415
- LO BIANCO, S. 1903. Le pesche abissali eseguite da F.A. Krupp col Yacht Puritan nelle adiacenze di Capri ed in altre località del Mediterraneo. *Mittheilungen aus der Zoologischen Station zu Neapel* 16, 109–278.
- MARIAPPAN, P., BALASUNDARAM, C. & SCHMITZ, B. 2000. Decapod crustacean chelipeds: an overview. *Journal of Biosciences* 25(3), 301–313. DOI 10.1007/BF02703939
- MARTIN, J.W. 2014. Polychelida, 279–282. In MARTIN, J.W., OLESEN, J. & HØEG, J.T. (eds) *Atlas of Crustacean Larvae*. JHU Press. DOI 10.1353/book.31448
- MEYER, H. VON 1835. Beiträge zu *Eryon*, einem Geschlechte fossiler langschwänziger Krebse. *Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum* 18, 261–283. DOI 10.5962/bhl.title.13859
- MÜNSTER, G.G. 1839. Abbildung und Beschreibung der fossilen langschwänzigen Krebse in den Kalkschiefern von Bayern. *Beiträge zur Petrefakten-Kunde* 2, 1–88.
- OLESEN, J. 2013. The crustacean carapace—morphology, function, development, and phylogenetic history, 103–139. In WATLING, L. & THIEL, M. (eds) *Functional Morphology and Diversity (Natural History of the Crustacea)*. Oxford University Press. DOI 10.1093/acprof:osobl/9780195398038.003.0004
- QUINTANA, R. & RETAMAL, M.A. 1984. Two pelagic stages of *Stereomastis pacifica* (Faxon) collected in the Chile-Peru trench (Polychelidae: Macrura). *Researches on Crustacea* 13, 133–142. DOI 10.18353/rcrustacea.13.14.0_133
- R CORE TEAM 2024. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. <https://www.R-project.org/>
- SCHWEITZER, C.E. & FELDMANN, R.M. 2023. Part R, Revised, Volume 1, Systematic descriptions: Additions to Infraorder Polychelida. *Treatise Online* 177(1), 1–7. DOI 10.17161/to.vi.21571
- SMITH, S.I. 1880. Notice of a new species of the “*Willemoesia* Group of Crustacea”, recent Eryontidae. *Proceedings of the United States National Museum* 2, 345–353. DOI 10.5479/si.00963801.2-99.345
- TERUZZI, G. 1990. The genus *Coleia* Broderip, 1835 (Crustacea, Decapoda) in the Sinemurian of Osteno Lombardy. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 131(4), 85–104.
- THOMSON, W. 1873. Notes from the “Challenger”. *Nature* 8, 400–403. DOI 10.1038/008400a0
- TORRES, A.P., PALERO, F., DOS SANTOS, A., ABELLÓ, P., BLANCO, E., BONÉ, A. & GUERAO, G. 2014. Larval stages of the deep-sea lobster *Polycheltes typhlops* (Decapoda, Polychelida) identified by DNA analysis: morphology, systematic, distribution and ecology. *Helgoland Marine Research* 68(3), 379–397. DOI 10.1007/s10152-014-0397-0
- WICKHAM, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, <https://ggplot2.tidyverse.org>
- WILLIAMSON, D.I. 1969. Names of larvae in the Decapoda and Euphausiacea. *Crustaceana* 16(2), 210–213. DOI 10.1163/156854069X00510

Electronic appendices

Appendix 1. Detailed list of material used in this study.

Appendix 2. R-Code used in the analysis including annotation.

Appendix 3. Principal component scores of the principal component analysis of the elliptic Fourier analysis on the shield of fossil and extant polychelidans.

Appendix 4. Graphical component loadings of the first five principal components resulting from the principal component analysis of the elliptic Fourier analysis on the shield, propodus and dactylus of fossil and extant polychelidans.

Appendix 5. Principal component scores of the principal component analysis of the elliptic Fourier analysis on the propodus of fossil and extant polychelidans.

Appendix 6. Principal component scores of the principal component analysis of the elliptic Fourier analysis on the dactylus of fossil and extant polychelidans.

Appendix 7. Boxplots depicting the values for the shield, propodus and dactylus, respectively for the size metric (sum of variances) and position metric (median of centroid distances) by geological age group. Values obtained after bootstrapping ($n = 1499$) and rarefaction (to the smallest group in each comparison) of the groups. Abbreviations: age1: Upper Triassic; age2: Lower Jurassic; age3: Middle Jurassic; age4: Upper Jurassic; age5: Lower Cretaceous; age6: extant.