

Larval development of fossil polychelidan crustaceans, exemplified by the 150 million years old species *Palaeopentacheles roettenbacheri*

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With 8 figures and 2 tables

Abstract: Here we present new ontogenetic data on a fossil polychelidan crustacean. Polychelida are benthic decapods known nowadays only from deep-sea habitats. Fossil representatives of Polychelida are known to inhabit shallower depths than the modern deep-sea inhabiting forms (= Polychelidae). Therefore, fossil polychelidans still retain certain ancestral traits such as compound eyes that are reduced in the modern forms. Such differences and the evolutionary changes are important to understand the evolutionary history of Polychelida. Furthermore, as Polychelida is the sister group to all other reptantian lobsters, Polychelida are crucial for a better understanding of the evolution of reptantian lobsters as a whole. In this study, we present an analysis of morphological development during the ontogeny of Palaeopentacheles roettenbacheri, a fossil representative of Polychelida from the 150 million years old (Upper Jurassic) Solnhofen Lithographic Limestones of southern Germany. The investigated specimens have exceptionally preserved tiniest details, which can be well visualised with autofluorescence microscopy. We discuss the morphological changes of the different developmental stages of *P. roettenbacheri* and how these changes point to a change in the life style: the shift from a pelagic mode of life to a benthic one. Furthermore, the potential evolutionary transformations of morphological traits are discussed by comparing morphological structures of modern polychelidan larvae to those of fossil ones. Based on these data, an evolutionary reconstruction is presented for the change of the larval development in Polychelida, ultimately leading to the highly specialised giant larvae known from modern forms.

Key words: Solnhofen Lithographic Limestones, megalopa, palaeo-evo-devo, heterochrony, metamorphosis.

1. Introduction

Polychelida is a group of decapod lobsters in an important phylogenetic position between the shrimp-like Caridea and/or Stenopodida and Eureptantia, as they are the sister group to the latter and representatives of Reptantia (SCHOLTZ & RICHTER 1995; DIXON et al. 2003; BRACKEN-GRISSOM et al. 2014). As an in-group of Reptantia they have derived traits such as a dorso-ventrally compressed pleon. Yet, they also retain more ancestral traits. For example, they share a triangular telson with Caridea and Stenopodida (e.g., SCHOLTZ & RICHTER 1995). Due to their phylogenetic position and retention of many plesiomorphic traits, their morphology is key to reconstructing the ground pattern of Reptantia.

The extant representatives of the group (= Polychelidae) have many traits they share with their fossil relatives, but also traits they do not share with the latter. Extant forms exhibit numerous adaptations to their specific habitat, the deep sea, while the fossil forms appear to lack these adaptations, retaining more ancestral traits.

One example are the eyes, which are (still) present in the fossil representatives while the eyes of the extant species have become reduced probably in response to their deep-sea habitat, so that in most cases only eye

Specimen	Labelling	Collections/Collectors		
A	SMNS 67903	Staatliches Museum für Naturkunde Stuttgart		
В	169	Markus Gebert		
С	197	Markus Gebert		
D	211	Markus Gebert		
E	167	Michael Fecke		
F	363	Michael Fecke		
G	170	Markus Gebert		
Н	SMNS 70295/1	Staatliches Museum für Naturkunde Stuttgart		
I	SMNS 70295/3	Staatliches Museum für Naturkunde Stuttgart		
J	SMNS 70295/2	Staatliches Museum für Naturkunde Stuttgart		
K	217	Markus Gebert		
L	SMNS 70295/4	Staatliches Museum für Naturkunde Stuttgart		
Μ	MB.A 4229	Museum für Naturkunde Berlin		
Ν	202	Manfred Ehrlich		
0	BSPG AS I 1972	Bayerische Staatssammlung für Paläontologie und Geologie München		
Р	BSPG AS I 993	Bayerische Staatssammlung für Paläontologie und Geologie München		
Q	MB.A 1118	Museum für Naturkunde Berlin		

Table 1. Labelling, origin and species of investigated specimens.

stalks are retained (GALIL 2000; AHYONG 2009). Fossil species still possess well-developed compound eyes. Most of these species appear to have been living in comparably shallow waters (AHYONG 2009).

By comparing the morphological traits of the fossil polychelidans with those of the extant species, evolutionary changes such as the reduction of eyes can be recognised leading to a better understanding of the evolutionary history of the group. This knowledge of this specifc groups is then again informative for understanding the evolution of reptantian lobsters.

One of the evolutionary novelties shown by the modern representatives of Polychelida is their ontogeny: most modern polychelidans develop through highly specialized larval forms, the so-called eryoneicus larvae; it is a form of giant larva reaching several centimetres in size (e.g., TORRES et al. 2014; HAUG et al. 2015; EILER et al. accepted). These are characterized by a strongly inflated shield (SCHOLTZ & RICHTER 1995; WILLIAMSON 1983; HAUG et al. 2015) which bears numerous setae and spines, strongly spinose pleonal tergites and strongly setose thoracic appendages (GALIL 2000; TORRES et al. 2014). Probably, these characters are specializations to a prolonged life in a pelagic habitat (HAUG et al. 2015).

Recently, also fossil specimens of eryoneicus-like larvae have been found in 90 million year old (Cretaceous) deposits of Lebanon (HAUG et al. 2015). These larvae show several adaptations of the modern "Eryoneicus" larvae, e.g. large body size, strongly setose and spinose shield, and strong spines along the midline of the pleon. However, other specializations of modern polychelidan larvae were still missing, especially the inflated shield. These specimens were interpreted by HAUG et al. (2015) as representing a species closer related to modern polychelidans than other previously discovered fossil representatives of Polychelida (e.g., GARASSINO et al. 2012; AUDO et al. 2014a, b; BRAVI et al. 2014). The new specimens demonstrate a step-wise acquisition of the larval specializations finally leading to the highly specialized modern forms.

Other fossil polychelidans appear to lack a giant larva; when reaching a size in the centimetre range they already strongly resemble their corresponding adults (e.g., BRAVI et al. 2014; HAUG et al. 2015). There should be some older forms present in the fossil record before the 90-million-year-old eryoneicus-like larvae that possess the one or other character of the latter. With this, it would be possible to break down their set of specializations further into a stepwise acquisition series.



Fig. 1. Scatter plots of measured lengths and widths plotted against shield lengths. A - Drawing of *P. roettenbacheri* marked with measured traits. B - Major cheliped propodus length versus shield length. C - Shield width versus shield length. D - Pleon length versus shield length. dl: dactylus length; pl: pleon length; ppl: propodus length; pw: pleon width; sl: shield length; sw: shield width.

Until now, few ontogenetic series of fossil polychelidans have been reconstructed and hence only few possible late larval specimens have been investigated (e.g., HAUG et al. 2011; AUDO et al. 2014; BRAVI et al. 2014). In this study, we provide new insights into the ontogenetic changes of the morphology of the 150 million years old (Jurassic) species *Palaeopentacheles roettenbacheri*. According to the phylogenetic analysis of AHYONG (2009), this species is relatively closely related to the modern representatives of Polychelida and hence has the potential to already show some of the larval adaptations of modern-type "*Eryoneicus*" larvae.

2. Material and methods

2.1. Material

All specimens included in this study are representatives of *Palaeopentacheles roettenbacheri*. Examined specimens came from various museum collections as well as from private collectors (see Table 1 for details). All specimens originate from the lithographic limestones of Southern Germany and are hence of Jurassic age. High resolution images (acting as "virtual specimens") are deposited in the online data base MorphDBase (Supplementary file 1), to allow future studies on these.



Fig. 2. Scatter plots of measured lengths and widths plotted against shield and propodus length. A - Dactylus length versus shield length. B - Shield width versus propodus length. C - Pleon length versus propodus length. D - Dactylus length versus propodus length. dl: dactylus length; pl: pleon length; ppl: propodus length; sl: shield lenght; sw: shield width.

2.2. Documentation

Fossils were documented either with a fluorescence compound microscope (mostly Keyence BZ-9000) by composite autofluorescence imaging (e.g., HAUG et al. 2008, 2011a; KERP & BOMFLEUR 2011) or with the macro-fluorescence method described by HAUG et al. (2011a) by using a Canon Rebel T3i digital camera and a MP-E 65 mm macro lens. This way of documentation was enabled by the autofluorescence capacities of the fossils. Objectives used at the Keyence microscope were 2×, 4× and 10× resulting in 20×, 40× and 100× magnification. Wave lengths used were 520 nm and 447 nm.

Images made with the compound microscope were recorded as stacks and were fused with Combine ZP afterwards. Additionally several details of the images had to be taken because of the size of the fossils and the exceptional preservations of some structures. Images taken with the Keyence microscope and with the digital camera were then stitched to a single panorama using Microsoft Image Composite Editor or the photomerge function of Adobe Photoshop CS3.

2.3. Measurements and scatter plots

To enable an exact differentiation of the succeeding ontogenetic stages of *Palaeopentacheles roettenbacheri* several important and obvious traits were measured (Fig. 1; complete list see Table 2).

Subsequently several scatter plots (Figs. 1-3) were produced with OpenOffice. Growth stages were identified based on apparent clusters. Then morphological differences between such clusters were identified. Besides plotting direct dimensions, ratios were plotted as well to see possible changes of these ratios throughout the ontogeny.

Shield lengths and pleon lengths were summed for each specimen to get their total sizes. Then for each growth stage

	Shield length [mm]	Shield width [mm]	Major cheliped propodus length [mm]	Major cheliped dactylus length [mm]	Pleon length [mm]	Pleon width [mm]	Shield length/ width	Shield width/ pleon width
A	5.25	5.5	7.25	3	4.75	2.25	0.95	2.44
B	6	6.25	6.75	3	4.25	2.5	0.96	2.5
С	5	4.75	6.75	2.5	5.5	2.5	1.053	1.9
D	5.75	4.75	7.75	3.75	6	3	1.21	1.58
E	7	7	7.25	3.25	5	2.75	1	2.54
F	7	7.25	7	3.25	5.25	2.5	0.97	2.9
G	7.25	5.75	8.5	3.75	5.25	2.5	1.26	2.3
Н	7.25	8.5	7.5	3.25	5	2.75	0.85	3.09
I	7.5	7.75	7.25	3.5	5.25	3	0.97	2.58
J	7.5	8.25	8.75	3.5	5.5	2.75	0.91	3
K	-	-	8	4	5.25	2.75	-	-
L	-	-	7.5	3.75	-	-	-	-
Μ	8.5	8	-	-	6.75	4	1.06	2
N	8	9.25	10.5	6.25	6.75	3.75	0.86	2.47
0	8.75	8.75	11.5	5.75	7.5	4	1	2.1875
P	20	19.5	22.5	11.75	18	11.25	1.023	1.73
Q	32.5	29	34.25	17.5	22.31	14.75	1.12	1.97

Table 2. Measurements of different traits of examined Palaeopentacheles roettenbacheri.



Fig. 3. Scatter plots of measured relations plotted against shield length. A – Shield width to pleon width versus shield length. B – Shield length to shield width versus shield length, pw: pleon width; sl: shield length; sw: shield width.

the average of the total sizes were calculated. Based on this also the growth rates were calculated by dividing the average total size of the smaller stage by the average total size of the larger stage.

2.4. Digital drawings

To emphasise morphological changes and differences during the ontogenetic development of *Palaeopentacheles roettenbacheri* line drawings of the obviously different ontogenetic



Fig. 4. Overview of investigated specimens (for details see Table 1). Stages are sorted in alphabetical order. Stage 1 (A-D), stage 2 (E-L), stage 3 (M-O), stage 4 (P), stage 5 in the background (in tables referred to as Q).

stages were made. We followed the principles laid out by COLEMAN (2003) and used Adobe Illustrator CS3-5. Slight shading was applied in Adobe Photoshop CS3-5 (COLEMAN 2003)

3. Results

3.1. Ontogenetic stages

All specimens described here are interpreted as conspecific. There are recognisable differences between them, yet these appear to be directly correlated to size.



Fig. 5. Schematic line drawings of the shields from stage 1 to stage 4.

Hence, such differences are more likely caused by ontogenetic differentiation than by different species.

According to the dimensions of the shield we can identify five different clusters in the investigated material of *Palaeopentacheles roettenbacheri* (Fig. 1). These clusters are interpreted as different ontogenetic stages. Stage 1 is represented by 4 specimens (Fig. 4A-D), stage 2 is represented by 6 specimens (Fig. 4E-J), stage 3 is represented by 3 specimens (Fig. 4M-O), stage 4 is represented by only 1 specimen (Fig. 4P) and stage 5 is represented by only 1 specimen either (Fig. 4Q). Two specimens (Fig. 4K, L) are not included in this analysis because of their absent shields. Yet a size comparison of the measured specimens allows a rough attribution to a stage.

The first three stages are most likely subsequent stages as the size increase is within the usual range for crustaceans of between ca. 10% to 30% size increase from one developmental stage to the next one (see e.g. KUTSCHERA et al. 2012 and references therein). Size



Fig. 6. Schematic line drawings of two stages of *Palaeopentacheles roettenbacheri* with the most strikingly morphological changes. A - Stage 2. B - Stage 3.

increase from stage 1 to stage 2 is about 14.7%, size increase from stage 2 to stage 3 is about 19.2%. Growth stages 4 and 5 however, are each much larger than the previous stages, with an increase of about 59.4% from stage 3 to stage 4 and 30.7% from stage 4 to stage 5. Therefore, there were probably additional stages present but which are not represented in the investigated material.

Only 4 different clusters are apparent when plotting the lengths of the major cheliped (fourth thoracopod). In this case cluster 1 is represented by 12 specimens (Fig. 4A-L), cluster 2 is represented by 2 specimens (Fig. 4N-O), cluster 3 is represented by only 1 specimen (Fig. 4P) and stage 4 is also represented by only 1 specimen (Fig. 4Q). Specimen M is not included in this analysis because of its absent propodus of the cheliped.

It seems most likely that cluster 1 combines the first two ontogenetic stages, indicated by the analysis of growth of the shield. Furthermore, it is apparent that the size gain for the cheliped exceeds the usual range for crustaceans of between 10% to 30% size increase from one developmental stage to the next one (Fig. 2). Size increase of propodus length from stage 1 to stage 2 is about 31.6%, from stage 2 to stage 3 is about 51.1% and between stages 3 and 4 it is about 34.3%.

The shield width decreases in relation to the pleon width between the different growth stages of the investigated material of *Palaeopentacheles roettenbacheri*. However, the analysis also shows that shield length is slightly increasing in relation to the shield width between the different developmental stages. Therefore, as can also be seen in Fig. 5, the shield is getting narrower and more elongate from stage to stage.

3.2. Description of the morphology

A detailed description is given in the descriptive matrix as a supplementary file 2.

3.3. Summarising the morphological changes through ontogeny

The succeeding growth stages of *Palaeopentacheles roettenbacheri* exhibit numerous morphological differences. The degree of morphological change during the ontogeny varies between the different moults. For example from stage 1 to stage 2, it seems that the main change is an increase in size. The morphological changes between stages 3 and 4 as well as between stages 4 and 5 are quite gradual. Most striking are the changes between stage 2 and stage 3. Here we can see the strongest morphological changes (Fig. 6).

The shield is becoming relatively narrower from stage 2 to stage 3 and develops spines on the dorsal side. Furthermore the shield of stage 3 has numerous tubercles, which are still absent in stage 2. As an additional structure, the cervical groove is not well apparent before stage 3.

An obvious change can be seen at the chelae of the fourth thoracopod. The chelae of stage 2 have very few and comparably stout spines on the inner sides (Fig. 7B). In stage 3 the chelae possess many new, and now more massive spines (Fig. 7C), which change only little further in later stages (Fig. 7D, E). In addition, the relative length of the fixed finger and the dactylus of stage 3 is increasing in relation to their width compared to stage 2. In stage 2, the ratio of length to width of dactylus is about 6.1 and in stage 3 it is about 9.2.

Furthermore, each visible element of the thoracopods of stage 3 has tubercles; merus and carpus still have just a few tubercles but the propodus is entirely covered with them, just like the shield. In stage 2, only carpus and propodus have a few tubercles. Such tubercles are also present on every pleomere in stage 3 but are lacking in stage 2. In relation to the size of the shield, the pleon is increasing from stage 2 to stage 3 so that the body is disproportionally increasing in its overall length.

The general morphology of the telson appears roughly similar in all stages. In all stages the telson is elongate, tapers distally, hence has a roughly triangular outline, but with a blunt tip. Posteriorly it has a spine on each lateral side.

Differences become apparent only under higher magnifications. The posterior edge between the lateral spines can appear straight but is convex in the wellpreserved specimens (Fig. 7G, I), at least in the smaller stages. In such specimens, additionally small insertions are apparent, indicating former setation (Fig. 7J). In stage 4, the telson is not too well-preserved. In stage 5, we see further changes. The sides are now armed with spines. The posterior edge appears to lack the setae but bears an additional spine medially (Fig. 7K).

4. Discussion

4.1. Identifying stages

Based on the shield length there are five different growth stages in the investigated specimens. This result seems to be reasonable; the shield appears to be a



Fig. 7. Morphological differences of telson and chela of the thoracopod 4 between the different growth stages. A - Chela of specimen 169 (stage 1). B - Chela of specimen SMNS 70295/2 (stage 2). C - Chela of specimen BSPG AS I 1972 (stage 3). D - Chela of specimen BSPG AS I 993 (stage 4). E - Chela of specimen MB.A 1118 (stage 5). F - Telson of specimen 169 (stage 1). G - Telson of specimen 167 (stage 2). H - Telson of specimen SMNS 70295/3 (stage 2). I - Telson of specimen BSPG AS I 1972 (stage 3). J - Detailed view of insertion points of telson of specimen 167 (stage 2). K - Telson of specimen MB.A 1118 (stage 5).

reliable representative value or proxy to the total size of the body.

Relative lengths of the propodus result in only four different clusters, indicating only four growth stages. It seems that the propodus length is not pronouncedly increasing during the development of the first two growth stages that were indicated by shield dimensions. It appears most likely that the five growth stages that are indicated by the shield dimensions are more reasonable than the four growth stages that are indicated by the propodus relations. The size increases are between 15% and 20% during development of the first three stages, in the five stages scenario. Brook's Law (FowLer 1909) predicts that growth factors during early development should approximately be constant (see discussion in KUTSCHERA et al. 2012). The directly succeeding stages appear to be missing in the material. With a size increase of about 60% from stage 3 to stage 4 we can estimate that probably 3 to 4 stages are not represented by actual specimens. With a size increase of about 30% from stage 4 to stage 5 there are probably one or two stages missing.

There is another indication that the propodus length is not a representative value to the total size of the body: The size increase from (factual) stage 2 to stage 3 (which appear as clusters 1 and 2 in the plot) of more than 30% of the propodus is not within the usual range for growth gain in crustaceans.

Hence, we conclude that *Palaeopentacheles roettenbacheri* is represented by five different growth stages instead of four in our material. We also conclude that the three first stages are consecutive without missing stages in between.

4.2. Morphological development of structures

Shield: The general body proportions of *Palaeopentacheles roettenbacheri* are changing during ontogenetic development (Figs. 5, 6). The shield width is decreasing in relation to the pleon width, whereby the shield length is increasing in relation to the shield width. Hence, *P. roettenbacheri* became more slender, i.e. longer and narrower from stage to stage.

In the first two stages of *P. roettenbacheri* the preservation of the shield is very different compared to later ones. In some specimens parts of the thoracopods can be seen through the shield, in others the shield is poorly preserved or entirely lacking. This implies that the shield was only weakly sclerotised in the first two stages. This interpretation is supported by the fact that in stage three also further surface details become apparent, such as the tuberculation and the cervical groove.

A less sclerotized shield should lead to reduced mass. This would have led to a more neutral buoyancy of the earlier stages and could well indicate that these were not yet benthic, but probably still pelagic.

Major cheliped: The chelae (just like the shield, see above) undergo a drastic change in morphology from stage 2 to stage 3 as they get much more elongate (Fig. 6). In the first two stages, the chelae look very similar. Also in stages 4 and 5 the chelae look very much like in stage 3.

The drastic change in morphology from stage 2 to stage 3 would be in concordance with a marked shift

in life habits, as mentioned above. The different morphologies of the chela from stage 2 to stage 3 could indicate that the earlier stages have been using a different food source than the later stages. It seems unlikely that, in this early stage, the change in chela morphology is related to a maturation process.

In other early polychelids the chelae become longer in relation to body size and also thinner due to allometric growth (BRAVI et al. 2014). Usually this occurs in a gradual manner; here we find a pronounced differentiation in one moult.

Telson: The telson also undergoes morphological changes during ontogeny. In the first three stages, the telson has a more or less convex posterior edge that bears insertions where probably setae arose. The telson of the stage 4 specimen cannot be examined as it is not preserved, but the telson of the stage 5 specimen has developed a small median spine, spines along the edges and apparently no setae. The shift from the one morphology to the other appears here not between stages 2 and 3, but later.

Probably the narrower telson of stage 5 specimen and its absent setation is also coupled to a developmental specialization to a benthic life. The larval stages need the setae on the telson probably for surface enlargement and for improving the swimming ability in their pelagic habitat by the flap of their tail fan, due to the lower Reynolds numbers coupled to their size. Yet here we find no pronounced transition from stage 2 to 3. Most likely stage 3 individuals could still (as younger ones) use the more pronounced armature for a tail flip escape reaction.

4.3. Ontogenetic status of the early stages

The early stages, 1 and 2, possess a quite different morphology of the shield and the chelae of the major cheliped. The changes in both structures possibly indicate a marked transition of the life habits of *P. roettenbacheri* from stage 2 to 3. In stage 2, the animal possibly has still been pelagic and using a different food source than in stage 3 where the animal possibly has been fully benthic.

In other reptantian decapods, the megalopa (sensu WILLIAMSON 1969) is the stage that makes the transition from the pelagic to the benthic phase. This specific transitory stage is alternatively termed decapodid (KÄSTNER 1970) or also "post-larva" (GURNEY 1942; FELDER et al 1985; Martin et al. 2014; see discussion in ANGER 2001).



Fig. 8. Evolutionary scenario of morphological development of polychelid crustacean larvae.

We think it is plausible to assume that the stages 1 and 2 represent megalopa-stage larvae of *P. roettenbacheri*. In Eureptantia there is generally only one megalopa stage, yet in modern polychelids (MARTIN 2014) and carideans there can be several such stages (e.g., WILLIAMSON 1982). Recent investigations (TORRES et al. 2014) have demonstrated that the zoea phase is rather short in modern polychelids. The giant eryoneicus forms are therefore only possible when there are numerous megalopa stages.

Hence the moult from stage 2 to 3 is interpreted to represent the transition from the larval to the "postlarval" phase (for an opposing view see FELDER et al. 1985, for problems with the term 'post-larval' see AN-GER 2001). The moult is therefore (most likely) coupled to the second most drastic changes in post-embryonic ontogeny and can be addressed to as a metamorphic moult (the most drastic one being the moult from zoea to megalopa; see also further below).

4.4. Comparison to modern larvae

According to the phylogenetic analysis of AHYONG (2009), *Palaeopentacheles roettenbacheri* is relatively closely related to the modern representatives of Polychelida and hence has the potential to already show some of the larval adaptations of modern-type "*Eryoneicus*" larvae. Comparing the megalopa larvae of *P. roettenbacheri* to extant eryoneicus-megalopa larvae actually several similar morphological structures can be seen:

Both have a wide shield, not strongly sclerotised that enhances buoyancy. Yet, there is no inflated balloonlike shield as seen in the extant larvae in *P. roetten*- *bacheri.* One could argue that the absence of such a shield is only preservational, i.e. that the large spherical shield became compressed along the dorso-ventral axis. In such a case, we would expect to see wrinkle lines or similar deformation signs, which is not the case.

Modern eryoneicus larvae bear numerous spines and setae, most likely providing additional buoyancy (cf. GURNEY 1942). These structures are absent in the adults (e.g., AHYONG & CHAN 2004).

The telson of younger stages of *P. roettenbacheri* is also setose. In addition, the extant eryoneicus larvae have numerous setae around the telson (e.g., TORRES et al. 2014; EILER et al. accepted). This also might be due to a specialization to a life in pelagic water as the setae are enlarging the surface of the telson that probably improves the larvae's swimming ability. As these structures do not become lost at the moult to the juvenile in *P. rottenbacheri* the smaller juveniles might still have had an advantage by this armature during the tail flip escape reaction.

Furthermore, in all stages of *P. roettenbacher* i the pleon has strong spines along the dorsal midline and lateral spines at each pleomere but the last one (e.g., GARASSINO & SCHWEIGERT 2006). In modern forms only larvae possess these spines in corresponding positions while they seem to be absent or at least reduced in most modern adults (e.g., GURNEY 1942; AHYONG & CHAN 2004). Such spines are not known in other fossil adult polchelidans such as eryonids (e.g., GARASSINO & SCHWEIGERT 2006; BRAVI et al. 2014).

4.5. Evolutionary scenario of larval development in Polychelida

In the following, the reconstruction of the evolution towards modern polychelidan larvae is attempted. This includes the evolution from shallow water conditions that are known from *Palaeopentacheles roettenbacheri* to a life in deep sea that is known from modern polychelidan larvae. Although *Palaeopentacheles roettenbacheri* is already relatively closely related to the modern polychelidans (AHYONG et al. 2009) larval stages of 90 million year old polychelidans are most likely even closer related to the modern forms (HAUG et al. 2015).

We will compare early polychelidans (e.g., eryonids), *P. rottenbacheri*, the 90 million year old larvae and the modern eryoneicus (megalopa) larvae for aspects of larval adaptations. This will reveal a more finely graded order in which the different adaptations of the modern forms evolved (Fig. 8). **Giant larval size:** Modern eryoneicus larvae of many species grow to astonishing sizes, at least for a larva (comparable or even larger sizes of larvae are only reached in Achelata and Stomatopoda; e.g., AHYONG et al. 2014; PALERO et al. 2014). It seems plausible that the evolutionary appearance of such super-sized larvae evolved in a step-wise manner. Although not all modern polychelid species exhibit a giant larva we can expect that among fossil polychelids we find representatives with already slightly enlarged ones. Indeed we also find that the 90 million years old eryoneicus-like larvae are quite large already (HAUG et al. 2015), although not as large as some modern forms.

The megalopa larvae of *P. roettenbacheri* can also be recognised as comparably large. The presumable last megalopa stage is about 14 mm large. This is significantly smaller than in the 90 million years old eryoneicus-like larvae, yet quite large compared to earlier polychelidans. Early juveniles of *Knebelia* (Audo et al. 2014) and *Cycleryon* (HAUG et al. 2011) are about the same size as the last megalopa of *P. rottenbacheri*, hence their megalopa larvae must have been smaller, although the exact size remains unclear for these. For *Tethyseryon campanicus* juveniles are known down to 6 mm overall body length. Hence, the megalopa larvae was most likely not more than 5 mm in size.

The larvae of *P. roettenbacheri* may not be giant larvae (but compare GAMô 1979 for a stomatopod larva of a comparably size which was classified as 'giant'), but are already moderately large. The 90 million year old eryoneicus-like larvae are larger than those of *P. roettenbacheri*, but still possibly slightly smaller than in the modern forms. Hence, we can see a step-wise evolution towards a larger size of the megalopa larvae from the small ones in eryonids, to moderately sized ones in *P. roettenbacheri* and over the bigger ones in the 90 million years old eryoneicus-like larvae (HAUG et al. 2015) towards the modern giant polychelidan larvae.

Yet, within Polychelidae not all species appear to have super-sized larvae (AHYONG pers. comm. 2015). Our knowledge of modern polychelid larvae is still very scarce and we do not know the larval stages for most species. Thus, it is currently unclear how large the larvae were in the ground pattern of Polychelidae. The situation is most likely more complicated. The length of the pelagic phase may also be more flexible depending on environmental conditions. In addition, even if the larva of the stem species of Polychelidae was large this does not exclude that ingroups again have smaller larvae. In conclusion, we see a certain increase in size in the lineage towards modern polychelids, but we lack resolution in the early branches of Polychelidae.

Inflated balloon-like shield: Modern polychelidan larvae are highly specialized for a life in pelagic water, while reaching enormous sizes. Due to their relatively large size, they need special structures for providing additional buoyancy. Their more or less balloon-shaped shield most likely acts as such a flotation structure.

The early stages of *Palaeopentacheles roettenbacheri* also have a relatively larger shield. Yet, it was not inflated as it is in modern polychelidan larvae. In addition, the 90 million years old polychelidan larvae do not yet possess an inflated balloon-like shield.

The large inflated balloon-like shield was probably advantageous for additional buoyancy due to the evolution of giant larvae. Jurassic polychelidans appear to have lacked giant larvae; hence, they did not yet have the necessity for additional structures for providing more buoyancy.

Representatives of *P. roettenbacheri* on the other hand inhabited shallower waters so that the more or less flattened but wide shield is sufficient in shallower depths. The shield width was probably enough to generate a sufficient buoyancy for their pelagic life style, as they entered the benthic realm at a smaller size.

The balloon-like shield appears to have evolved in the stem-species of the modern forms as it is also absent in the 90 million year old larvae. As these were presumably not deep-water forms, a coupling to the habitat change is at least plausible.

Rostrum: The rostrum proves difficult to interpret. Most modern eryoneicus-larvae, as modern polychelid adults have a rather short rostrum that could be described as roughly tri-forked. In contrast, in P. roettenbacheri we see only two spine-like horns, which quite likely correspond to the two lateral thorns of the outer orbital spines of the modern forms. In the 90 million years old larvae there is a single elongate rostrum, most likely corresponding to the zoea-larva rostrum in other decapods (e.g., PROVENZANO 1962; BOUSQUETTE 1980; HARVEY 1992; DE ALMEIDA RODRIGUES 1994; GUERAO & ABELLÓ 1996; STRASSER & FELDER 1999). This would therefore also correspond to the rostral spine/spines of the modern forms. The rostrum in P. roettenbacheri is similar in megalopa and juveniles and resembles the rostrum in early polychelidans such as eryonids (e.g., BERNARD 1953; GALIL 2000). Hence, the situation in P. roettenbacheri is most likely the plesiomorphic (adult and juvenile) condition. Still with this pattern

the different rostrum forms do not provide a step-wise transformation series and the exact pattern of character evolution remains partly unclear.

Spination of the shield: *Palaeopentacheles roettenbacheri* has only small spines on the shield, but not before the juvenile phase. The 90 million years old eryoneicus-like larvae have prominent spines that are grouped into about eleven rows on the shield (HAUG et al. 2015). In modern eryoneicus larvae the spine pattern is variable, yet often the shield has also numerous spines but slightly fewer. With this pattern it remains unclear if the spines in the juvenile *P. roettenbacheri* correspond to the spines on the shield in the 90 million years old eryoneicus-like larvae and the modern eryoneicus larvae.

Spination of the pleon: The spines (along the midline and laterally) on the pleon of the 90 million years old eryoneicus-like larvae and modern eryoneicus larvae are very apparent. They are absent in modern adults and in earlier polychelidans such as eryonids. Hence they have been interpreted as larval adaptations (HAUG et al. 2015), most likely providing additional buoyancy. In the larvae of *P. roettenbacheri* we see spines in the corresponding positions hence these are most likely homologous. We could therefore conclude that the pleon spination evolved in the stem species of the monophyletic group including *P. roettenbacheri*, the 90 million year old eryoneicus-like larvae and the modern forms (Polychelidae).

Yet, the spines are also present in non-larval individuals of *P. roettenbacheri*, hence in this species they do not represent a true larval feature. As neither eryonids nor most modern forms possess such spines in juveniles or adults we see it at most likely that the presence of these spines after the larval phase is an autapomorphy of *P. roettenbacheri*, that might be convergently found in some modern forms (AHYONG et al. 2009). The evolutionary process explaining this would be relatively simple, retaining larval features into the adult phase. This is most likely representing a case of paedomorphosis. The exact sub-type is unclear.

To summarise, the megalopa larvae of *P. roetten*bacheri show already some larval adaptations seen in modern forms, among them the moderately large size of the megalopa and the spination for the pleon. Other features such as the even larger size or the spination of the shield as seen in the 90 million years old eryoneicus larvae are still missing as well as the characters of the modern forms such as the inflated ballon-like shield. With this *P. roettenbacheri* provides additional insights into the step-wise character acquisition of the aberrant eryoneicus larvae.

4.6. The metamorphosis (?) of Palaeopentacheles roettenbacheri

The transition from the megalopa to the first juvenile has been referred to as a metamorphosis (e.g., HARVEY 1996; HARZSCH & DAWIRS 1996; ANGER 2001). Yet usually the transition from the last zoea to the megalopa is more drastic. As HAUG & HAUG (2013) have pointed out there can be no absolute criterion for distinguishing a metamorphic from a non-metamorphic moult. Hence, we could only compare it to corresponding moults in other species. Yet, for many possible comparisons, we simply lack information about this transition. We still lack megalopa larvae of eryonids, although these may be present among the available fossil material (see discussion in HAUG et al. 2011). We lack the non-larval stages of the 90 million years old eryoneicus-like larvae. Hence, we can only compare it to modern forms. As modern larvae show more larval adaptations than P. roettenbacheri the transition to the first juvenile is more drastic in the modern forms. In addition, as P. roettenbacheri retains the larval feature 'pleon spination' the transition appears even less drastic. Hence, we must state that P. roettenbacheri has a less metamorphic development than modern polychelidans.

It may have a more pronounced metamorphosis than eryonids, as it already possesses some larval adaptations. Yet our knowledge is still too incomplete to come to a clear conclusion here. As a last comment: due to the fact that, although the juveniles are paedomorphic we can still recognise the transition from larva to juvenile, the term metamorphosis could well be used if one wants to emphasise this transition. In addition, the likely change in life habits from pelagic to benthic supports the use of metamorphosis in this case to stress the possible ecological transition.

5. Conclusion and outlook

We summarise here our new findings about the ontogeny of the 150 million years old polychelid lobster *Palaeopetacheles roettenbacheri*:

There is allometric change of body proportions as already observed in other early polychelidans.

The earliest available stages differ markedly from the later ones by:

a) A shield, which is weakly sclerotized;

b) A lack of tuberculation;

c) A chela, which is quite short and has significantly smaller spines.

Hence, these early stages are interpreted as late larvae, megalopa, which are still pelagic.

The larvae possess some larval adaptations seen in modern forms and hence provide evidence for a stepwise character acquisition towards modern forms.

Juvenile and adult *P. roettenbacheri* appear to be paedomorphic, retaining some larval traits.

This investigation demonstrates again that polychelidans are an interesting candidate group for studying evolution of developmental sequences within decapods. We should aim at reconstructing more ontogenetic sequences of this group and also attempt to fill the gaps in the ontogenetic sequence of *P. roettenbacheri*.

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The pdf-version of this paper includes an electronic supplement:

Table of contents – Electronic Supplementary Material (ESM)

Supplementary file 1. Numbers of the images of the specimens in the online data base MorphDBase (https://www. morphdbase.de/#).

Supplementary file 2. Detailed description of the developmental stages of *Palaeopentacheles roettenbacheri* provided as descriptive matrix.

Please download the electronic supplement and rename the file extension to .zip (for security reasons Adobe does not allow to embed .exe, .zip, .rar etc. files).