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Research article

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Systematic revision and palaeobiology of *Rosenfeldia triasica* and *Rogeryon oppeli* gen. et comb. nov. (Eucrustacea, Polychelida)

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Abstract. Polychelidan lobsters (Decapoda: Polychelida) are crustaceans with extant species which are restricted to deep water environments. Fossil species, however, used to live in more varied palaeoenvironments, from shallow water to deep water, and were more diverse morphologically. We redescribe two species of polychelidan lobsters, the Late Triassic *Rosenfeldia triasica* Garassino, Teruzzi & Dalla Vecchia, 1996 and the Late Jurassic *Eryon oppeli* Woodward, 1866, recently assigned to the same genus, *Rosenfeldia*, based upon only a few characters. Our investigation of all available material of both species leads us to distinguish these two species and to erect *Rogeryon* gen. nov. to accommodate *Eryon oppeli*. The palaeobiology of both species is interpreted for the first time. *Rosenfeldia triasica* with its stout first pereopods and mandibles with both incisor and molar processes (documented for the first time in Polychelida) was benthic and probably fed either on slow-moving sedentary preys or was a scavenger. *Rogeryon oppeli* gen. et comb. nov. was benthic, visually adapted to shallow water palaeoenvironments, and possibly had a diet similar to that of slipper lobsters and horseshoe crabs. The redescription of these two species highlights the palaeobiological diversity of fossil polychelidans.

Keywords. Decapoda, palaeoecology, Solnhofen, Jurassic, Triassic.

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Introduction

Polychelidan lobsters are an unusual group of decapod crustaceans: they were first discovered fossilized in the famous Solnhofen-type outcrops of the Upper Jurassic of southern Germany (Desmarest 1817) long before being discovered in modern deep-sea environments (Heller 1862).

Polychelidans are easily recognizable by their four to five pairs of chelate pereopods (“walking limbs” = thoracopods 4–8, Galil 2000). They are also characterized by a complete reduction of the rostrum, replaced by a frontal margin, and by their dorsoventrally flattened carapace or cephalothorax shield (cylindrical or laterally flattened in most other decapods).

Compared to extant polychelidans, which are restricted to deep water (Galil 2000), fossil species seem to have inhabited more diverse palaeoenvironments, including shallow waters (that are environments in the euphotic zone; Ah Yong 2009; Audo *et al.* 2014a; Bravi *et al.* 2014) and deeper waters (that are dim-light palaeoenvironments; Charbonnier 2009; Audo *et al.* 2014c; Charbonnier *et al.* 2010, 2014). Fossil species are also more diverse morphologically (Audo *et al.* 2014c).

The present study aims at redescribing one of the most peculiar of fossil polychelidan lobsters: *Eryon oppeli* Woodward, 1866, from the famous Solnhofen-type lithographic limestones of southern Germany. This species was recently assigned to *Rosenfeldia* Garassino, Teruzzi & Dalla Vecchia, 1996 by Garassino & Schweigert (2006). However, a careful examination reveals that it actually bears little resemblance to the type species *Rosenfeldia triasica* Garassino, Teruzzi & Dalla Vecchia, 1996.

Our study will therefore first redescribe *Rosenfeldia triasica*, using up-to-date photographic methods to document specimens. These observations will provide comparative material to redescribe *Eryon oppeli* and to clarify its systematic position. Finally, morphological observations on both species will provide new insights on the palaeobiology of these species.

Material and methods

Fossil material

The redescription of *Rosenfeldia triasica* is based on 39 specimens housed at the Museo Friulano di Storia Naturale, Udine, Italy (acronym: MFSNgp). All specimens were imaged in cross-polarized light.

The study of *Eryon oppeli* is based on seven specimens housed at the Natural History Museum, London, United Kingdom (acronym: NHMUK), the Staatliches Museum für Naturkunde Stuttgart, Germany (acronym: SMNS) and in the private collections of U. Resch (Eichstätt, Germany) and K. and H. Schumacher (Dürrholz, Germany). These specimens were studied directly and based upon high-definition images mostly realized in natural light, except for the holotype NHMUK 44886, which was also documented in UV-light fluorescence. Specimens SMNS 66004 and SMNS 70102 were also imaged in green-orange fluorescence and in cross-polarized light, respectively.

Anatomical abbreviations

Mxp3 = third maxilliped
P1–P5 = pereopods 1 to 5
s1–s6 = pleonal somites 1 to 6

Imagery

The objective of cross-polarized and fluorescence macrophotography is to enhance the contrast between the fossil remains and the surrounding sediment, and to reveal small structures as a result of this greater contrast.

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Cross-polarized light images (see Bengtson 2000) are realized by illuminating the specimen with a polarized white-light source and filtering the light directly reflected on the specimen (same axis of polarization as light source) with a second polarizer on the camera lens. This way, reflections are cancelled and contrast is increased.

Green fluorescence (see Haug *et al.* 2009; Haug & Haug 2011) is obtained by illuminating the specimen with a green light (reduced spectrum compared to white “natural” light). In some outcrops, the minerals which replaced organic structures during the fossilisation process are fluorescent, and re-emit an orange fluorescence when exposed to green light. To observe this fluorescence, an orange/red filter is required to filter out the green light and mostly keep the orange fluorescence. Images are then colour equilibrated (often also desaturated) to simplify the visualisation of fluorescent parts.

UV fluorescence, more commonly used than green fluorescence, relies on a simple principle. Here, the incident light is a “dark light” (blue to UVA). This incident light is filtered by an orange filter (care was taken that this filter was not fluorescent under UV) to filter out blue, violet and UV light and keep the yellow/orange fluorescence. As for green-orange fluorescence, images are then colour equilibrated to simplify the visualization of fluorescent parts.

Results

Systematic Palaeontology

Malacostraca Latreille, 1802
Decapoda Latreille, 1802
Pleocyemata Burkenroad, 1963
Reptantia Boas, 1880
Polychelida Scholtz & Richter, 1995
Eryonoidea de Haan, 1841
Uncertain family

Genus *Rosenfeldia* Garassino, Teruzzi & Dalla Vecchia, 1996

Rosenfeldia Garassino, Teruzzi & Dalla Vecchia, 1996: 33–41, figs 6–10, 17–20.

Rosenfeldia – Garassino & Schweigert 2006: 30. — Ahyong 2009: 380. — De Grave *et al.* 2009: 23. — Schweitzer *et al.* 2010: 43. — Audo *et al.* 2014a: 464, fig. 2E; 2014c: 500; 2016: 13, figs 1h–k; 2017: 5, fig. 3M. — Feldmann *et al.* 2013: 3. — Audo 2016: 291, fig. 3M.

Type species

Rosenfeldia triasica Garassino, Teruzzi & Dalla Vecchia, 1996, by monotypy.

Included species

Rosenfeldia triasica.

Original diagnosis

Subround carapace, with longitudinal median carina originating from the posterior margin; two thin carinae run parallel to the median carina; two parallel rows of tubercles are located in the median portion of the cephalic region; chela of pereopod I with the dactylus longer than the index and bent at the distal extremity; subrectangular telson; exopodite without diaeresis.

Emended diagnosis

Subquadrate yet slightly rounded carapace (in dorsal view); inner angle of ocular incision blunt, not forming a spine; ocular incision fringed laterally by an expansion of carapace; cervical incision shallower than postcervical incision; posterolateral angle short, not projecting along pleonite 1; very rounded telson and strengthened by a media carina; third maxilliped ischium kidney-shaped; uropodal exopod not articulated (no diaeresis).

Remarks

Rosenfeldia was assigned to Eryonidae de Haan, 1841, because (1) it did not fit in other families then described (Coleiidae Van Straelen, 1925, Tetrachelidae Beurlen, 1930, Polychelidae Wood-Mason, 1874), and (2) based upon of its longitudinal median carina, two thin lateral carinae, elongate P1 propodus, subrectangular shape of pleonal somites and uropodal exopod without a diaeresis (Garassino *et al.* 1996). This opinion was followed by Ahyong (2009), De Grave *et al.* (2009), Schweitzer *et al.* (2010) and Feldmann *et al.* (2013), who did not discuss further the familial assignment. Our reinvestigation questions this familial assignment. Indeed, as noted by Garassino *et al.* (1996), the telson of *Rosenfeldia* is rounded in dorsal view, contrary to that of Eryonidae, which is triangular. Other important differences include: the scaphocerite is rounded with a median carina, a disposition well known in Coleiidae, but not in Eryonidae (fusiform, without median carina); the third maxilliped ischium is kidney-shaped, once again a character well known in Coleiidae, contrary to Eryonidae, in which it is subtriangular. Garassino *et al.* (1996) argued that the “lack of cervical and branchiocardiac grooves” was also typical of Eryonidae, however, the cervical and postcervical grooves at least are present, although poorly preserved. In fact, these grooves occur in all Polychelida (Fig. 2), but are often restricted to the median part of the carapace in Eryonidae. This is not the case in *Rosenfeldia*. Finally, the lack of diaeresis is a poor indicator since it is present in Coleiidae, Tetrachelidae and in *Hellerocaris* Van Straelen, 1925, which was considered as being close to Polychelidae (Audo *et al.* 2014c). A diaeresis is absent (= uropodal exopod in one part) in all other polychelidan lobsters. Taking into account these characters, the assignment of *Rosenfeldia* to Eryonidae is equivocal, and will be tested in a future work, the phylogenetic analysis of Polychelida.

Rosenfeldia triasica Garassino, Teruzzi & Dalla Vecchia, 1996
Figs 1, 2N, 3

Rosenfeldia triasica Garassino, Teruzzi & Dalla Vecchia, 1996: 33–41, figs 6–10, 17–20.

Rosenfeldia triasica – Garassino & Schweigert 2006: 30. — Schweitzer *et al.* 2010: 43. — Feldmann *et al.* 2013: 3. — Audo *et al.* 2014a: 464, fig. 2E; 2014c: 500; 2017: 5, fig. 3M. — Audo 2016: 291, fig. 3M.

Diagnosis

See genus.

Material examined

Holotype

ITALY: MFSNgp 16178 (Fig. 1A–B).

Paratypes

ITALY: 3 specimens (MFSNgp 16173, MFSNgp 16176, MFSNgp 16179).

Other material

ITALY: 35 specimens (MFSNgp 16110, MFSNgp 16122, MFSNgp 16139, MFSNgp 16151, MFSNgp 16152, MFSNgp 16155, MFSNgp 16171–16174, MFSNgp 16176–16179, MFSNgp 16181, MFSNgp 16183, MFSNgp 16185, MFSNgp 16186–16191, MFSNgp 16193–16194, MFSNgp 16198, MFSNgp 24712, MFSNgp 26783–26784, MFSNgp 27694, MFSNgp 27696, MFSNgp 32291, MFSNgp 34290, MFSNgp 34292, MFSNgp 40312) (Fig. 1C–D).

Type locality

ITALY: northern side of mount Auda (Succhieve, Udine, Italy).

Type age

Late Triassic, Norian (after Garassino *et al.* 1996).

Emendation to description

SHAPE OF CARAPACE. Dorsoventrally flattened carapace, subquadratic in outline in dorsal view; concave frontal margin; anterolateral angle blunt, pointing slightly outward; spiny lateral margin with ocular, cervical, and postcervical incisions; U-shaped, almost semi-circular ocular incision; anterolateral margin slightly rounded posteriorly, oblique compared to longitudinal axis, poorly preserved; cervical and postcervical incisions opening in anterior half of lateral margin; cervical incision subtriangular; mediolateral margin shorter than anterolateral margin, rounded posteriorly; postcervical incision subtriangular, slightly deeper than cervical incision; posterolateral margin, slightly rounded, fringed by small spines; posterolateral angle round, short, not fringing pleonite 1; posterior margin slightly concave, wider than frontal margin.

CARAPACE GROOVES AND CARINAE. Postrostral carina not visible; postcervical carina well-marked in posterior half of carapace; very thin branchial carina, with anterior branch possibly incorporating (merged with) postorbital carina and extending on $\frac{1}{3}$ of carapace length, posterior branch separated from anterior branch by cervical and postcervical grooves, extending to posterolateral angle; cervical groove poorly preserved, oblique, extending from cervical incision toward median line; postcervical groove poorly preserved, extending from postcervical incision toward median line, passing near cervical groove; branchiocardiac groove not visible; gastro-orbital groove thin, poorly preserved, extending obliquely from cervical groove toward median line.

PLEON AND TELSON. Pleon and telson slightly shorter than carapace; pleon narrower than carapace; pleonite 1 shorter and narrower than others; s2–s5 with subrectangular terga crossed by a pair of transverse grooves and an axial carina cutting the posterior transverse groove; s6 with subtrapezoidal tergum; s1 and s6 with narrow subtriangular tergopleura (also called “pleura” although it is structurally a part of terga); other tergopleura also subtriangular but wider than s1 and s6 tergopleura; telson rounded, strengthened by a pair of slightly oblique longitudinal carinae and with finely serrated margins.

EYE AND CEPHALIC APPENDAGES. Eye not protruding from ocular incision; antennula poorly preserved; antenna poorly preserved, with an ovoid scaphocerite strengthened by a median longitudinal carina; mandible with an asymmetric molar process (Fig. 1D) and an incisor process forming sharp irregular triangular teeth.

THORACIC APPENDAGES. Third maxilliped with kidney-shaped ischium carrying a few stocky podomeres; P1 slightly larger than others; P1 dactylus and pollex (= fixed finger) slightly curved; stocky P1 palm (portion of propodus excluding pollex), slightly longer than dactylus; P1 carpus short and subtriangular; P1 merus slightly longer than palm, with parallel margins; P2–P4 similar to P1, decreasing in size from the second to the fourth; P5 ending in a short dactylus, without claw in observed specimens.

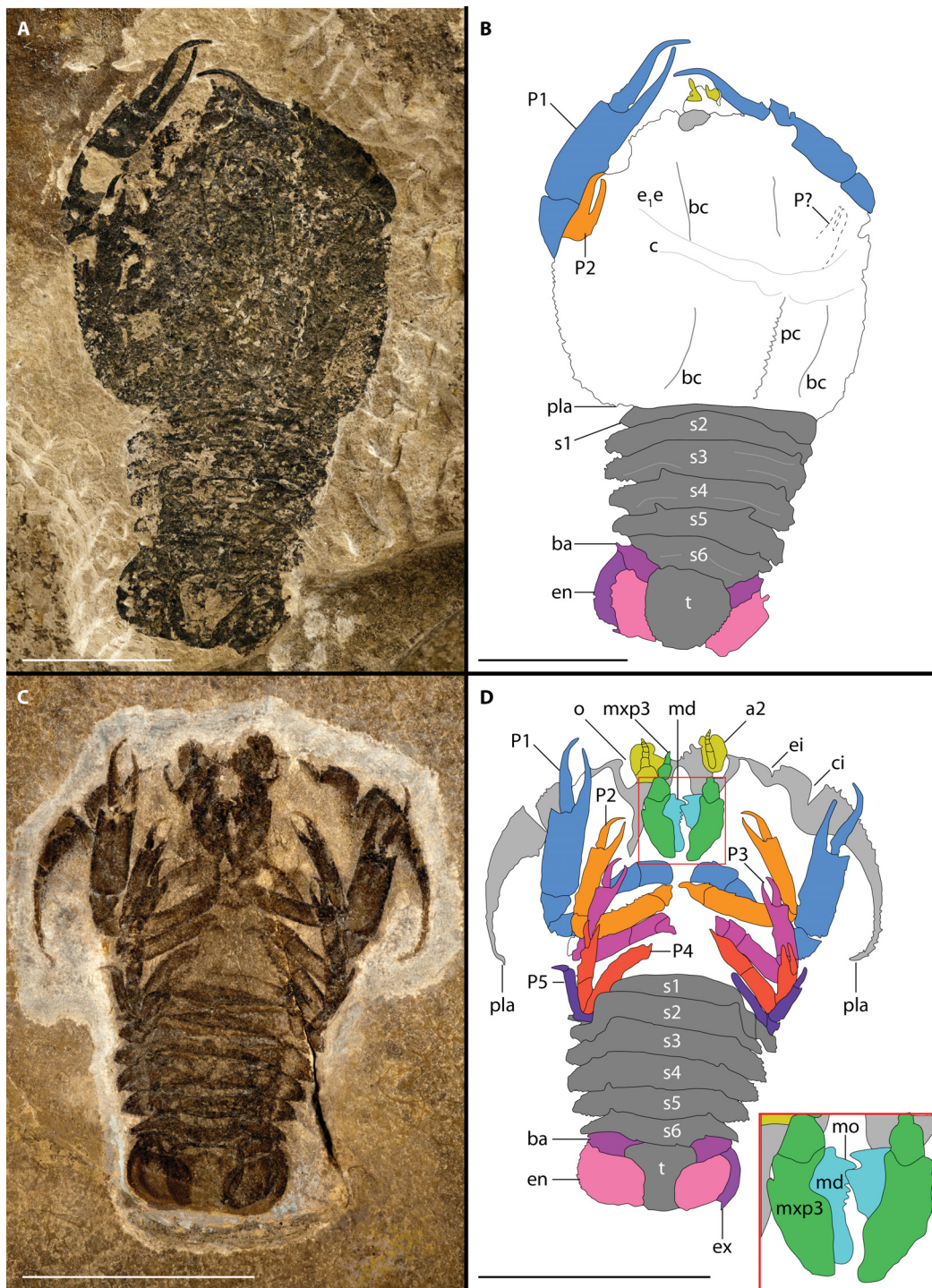


Fig. 1. *Rosenfeldia triasica* Garassino, Teruzzi & Dalla Vecchia, 1996 from the Upper Triassic (Norian) of Mount Auda, Italy. **A–B.** Holotype, MFSNgp 16178, dorsal view, cross-polarized light (A) and interpretative line-drawing (B). **C–D.** Specimen MFSNgp 40312, ventral view, cross-polarized view (C) and interpretative line-drawing (D). Abbreviations: a2 = antenna; ba = uropodal basipodite; bc = branchial carina; c = postcervical groove; ci = postcervical incision; e,e = cervical groove; en = uropodal endopod; ei = cervical incision; ex = uropodal exopod; md = mandible; mo = mandibular molar process; mxp3 = third maxilliped; o = ocular incision; P1–P5 = pereiopods 1 to 5; P? = indeterminate pereiopod; pc = postcervical carina; pla = posterolateral angle; s1–s6 = pleonites 1 to 6; t = telson. Scale bars: A–B = 10 mm; C–D = 20 mm. Photographs: D. Audo, © MFSNgp.

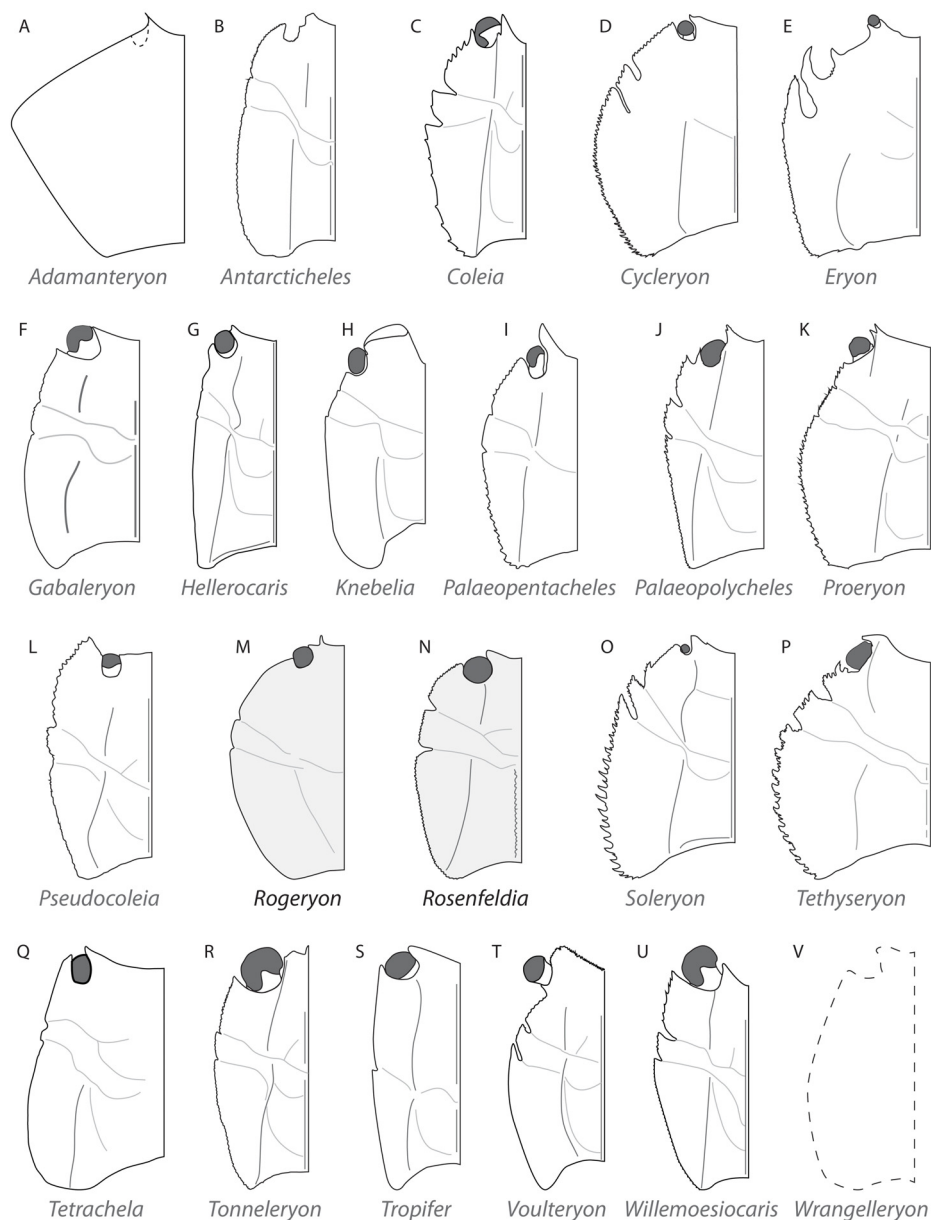


Fig. 2. Comparison of the general outline of carapaces (right sides omitted, adapted from Audo 2016 and Audo *et al.* 2017) of the type species of each genus of fossil Polychelida. **A.** *Adamanteryon fourneti* Audo, Schweigert, Saint Martin & Charbonnier, 2014. **B.** *Antarcticheles antarcticus* Aguirre-Urreta, Buatois, Chernoglasov & Medina 1990. **C.** *Coleia antiqua* Broderip, 1835. **D.** *Cycleryon propinquus* (Schlotheim, 1822). **E.** *Eryon cuvieri* Desmarest, 1817. **F.** *Gabaleryon coquelae* Audo, Williams, Charbonnier & Schweigert, 2017. **G.** *Hellerocaris falloti* (Van Straelen, 1923). **H.** *Knebelia bilobata* (Münster, 1839). **I.** *Palaeopentacheles roettenbacheri* (Münster, 1839). **J.** *Palaeopolycheles longipes* (Fraas, 1855). **K.** *Proeryon hartmanni* (Meyer, 1836). **L.** *Pseudocoleia mazzolenii* Garassino & Teruzzi, 1993. **M.** *Rogeryon oppeli* (Woodward, 1866) gen. et comb. nov. **N.** *Rosenfeldia triasica* Garassino, Teruzzi & Dalla Vecchia, 1996. **O.** *Soleryon amicalis* Audo, Charbonnier, Schweigert & Saint Martin, 2014. **P.** *Tethyseryon campanicus* Bravi, Garassino, Bartiromo, Audo, Charbonnier, Schweigert, Thévenard & Longobardi, 2014. **Q.** *Tetrachela raiblana* (Bronn, 1858). **R.** *Tonneleryon schweigerti* Audo, 2016. **S.** *Tropifer laevis* Gould, 1857. **T.** *Voulteryon parvulus* Audo, Schweigert, Saint Martin & Charbonnier, 2014. **U.** *Willemoesiocaris ovalis* (Van Straelen, 1923). **V.** *Wrangelleryon perates* Feldmann, Schweitzer & Haggart, 2013. Illustrations not to scale.

PLEONAL APPENDAGES. Pleopods 1–5 poorly preserved, with subrectangular basipod; uropods with a stocky basipod carrying very rounded endopod and exopod, both with thin serration of their margins; uropodal exopod with no visible diaeresis.

ORNAMENTATION. Carapace and pleonites and first pereiopod propodus covered with coarse tubercles.

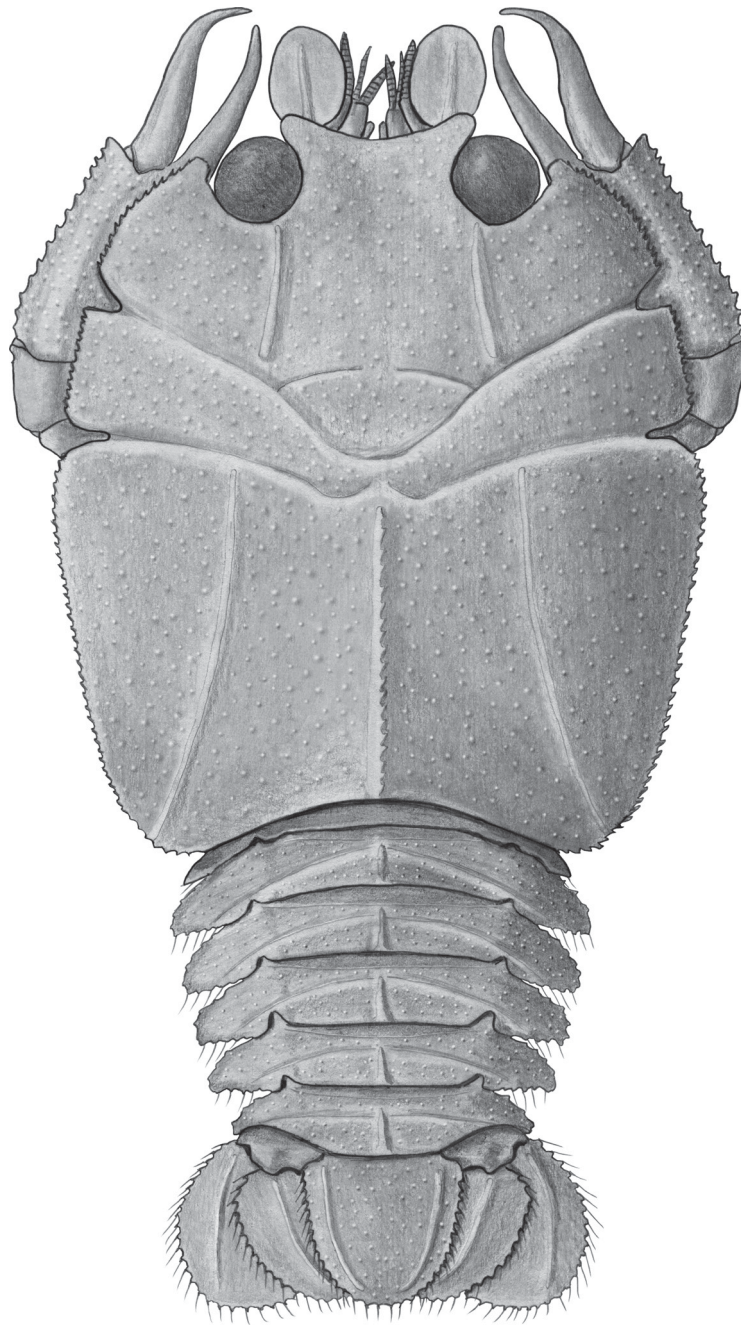


Fig. 3. Reconstruction of the dorsal aspect of *Rosenfeldia triasica* Garassino, Teruzzi & Dalla Vecchia, 1996. Please note that due to the preservation conditions of specimens, the precise outline of the carapace and shape of grooves are difficult to assess. Image hand-drawn by D. Audo.

Occurrence

Only known from the type locality. *Rosenfeldia triasica* is among the oldest polychelidan lobsters discovered, being preceded only by ?*Coleia uzume* Karasawa, Takahashi, Doi & Ishida, 2003 from the Carnian of Japan (Karasawa *et al.* 2003) and *Tetrachela raiblana* (Bronn, 1858) from the Carnian of Italy and Austria (Förster 1967).

Comments

Rosenfeldia triasica is known from 39 specimens. Most of these specimens are incompletely preserved, only appendages and pleon are often clearly visible. Among specimens which preserve the carapace, some appear to have a carapace that is longer than wide, such as in the holotype (Fig. 1A–B), others exhibit a very wide carapace, such as in specimen MFSN_{gp} 40312 (Fig. 1C–D). As a result, *R. triasica* was reconstructed as very wide by Garassino *et al.* (1996: figs 6, 8A–B). Indeed, Garassino *et al.* probably considered the more abundant wide specimens to be typical. Alternatively, Audio (2016: fig. 3M) and Audio *et al.* (2017: fig. 3M), based upon the holotype only, represented *R. triasica* as narrower. Our reinvestigation of all available material leads us to affirm these reconstructions. Indeed, the specimens with an apparently wide carapace are undoubtedly exuvia. Their carapaces are split open (Fig. 1C–D) and consequently seem superficially wider than they were (see also Audio 2016 for a short discussion of moulting in Polychelida). For this reason, we disagree with the reconstruction of *R. triasica* with a very wide carapace, proposed by Garassino *et al.* (1996). On the other hand, reconstructions by Audio (2016) and Audio *et al.* (2017) represent the carapace with indistinct cervical and postcervical incisions, which are, however, clearly represented by Garassino *et al.* (1996) and visible on some specimens (Fig. 1C–D). Clearly, these reconstructions, based only upon the holotype, which does not preserve the lateral margins well, are inaccurate. We therefore propose an emended catalogue of the carapaces of all genera of fossil Polychelida, each based on its type species (Fig. 2), and a new, complete reconstruction of *R. triasica* (Fig. 3), both based on most of the available specimens. However, it should be noted that grooves on a carapace are rarely preserved, so their shape on the reconstruction is based on available information and comparison with other polychelidans.

Genus *Rogeryon* Schweigert & Audio gen. nov.

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Eryon – Woodward 1866: 500 (*pro parte: E. oppeli*); 1881: 529 (*pro parte: E. oppeli*); 1911: 307 (*pro parte: E. oppeli*).— Glaessner 1929: 166 (*pro parte: E. oppeli*).

Rosenfeldia – Schweigert 2004a: 70 (*pro parte: R. oppeli*); 2004b: 329 (*pro parte: R. oppeli*); 2015: 273 (*pro parte: R. oppeli*). — Schweigert & Frattigiani 2005a: 198 (*pro parte: R. oppeli*); 2005b: 328 (*pro parte: R. oppeli*). — Garassino & Schweigert 2006: 30 (*pro parte: R. oppeli*). — Schweitzer *et al.* 2010: 43 (*pro parte: R. oppeli*). — Audio *et al.* 2016: 13, figs 1h–k (*pro parte: R. oppeli*).

Type species

Eryon oppeli Woodward, 1866.

Included species

Rogeryon oppeli gen. et comb. nov.

Diagnosis

Extremely thin exoskeleton; ovoid, slightly pear-shaped cephalothorax longer than wide, wider in its anterior half; very narrow frontal margin; small, shallow cervical and postcervical incisions; cervical groove strongly marked near cervical incision and near lateral margin, shallower between these two

areas; postcervical groove strongly marked from postcervical incision toward median line, longer than $\frac{1}{3}$ of carapace width; telson and uropods rounded; eyes with hexagonal ommatidia; median margin of third maxilliped ischium with a few proximal large teeth and numerous more distal small teeth (serrated aspect), first pereopods about as large as succeeding ones.

Etymology

Dedicated to Roger Frattigiani, an enthusiast amateur fossil collector who co-operates with researchers since several years. Gender of the genus is masculine.

Remarks

Rogeryon gen. nov. is represented by a single, very rare species: *Eryon oppeli* Woodward, 1866, from the Late Jurassic of Germany. The study of this species is complicated due to the preservation of many specimens: (1) the holotype does not preserve its carapace, but can fortunately be reliably associated with other specimens by the peculiar shape of tail fan and pereopods; (2) most known specimens have a very thin carapace that was variably deformed; (3) some specimens (SMNS 66004/2, SMNS 70102), whose carapaces are divided across median line, probably correspond to exuvia (see Audo 2016). We remark that the thinness of the carapace is unlikely directly linked to the preservation of exuviae in the case of some specimens. Exuviae occur abundantly in Solnhofen-type outcrops (Schweigert 2007a), but in polychelidans they do not present a particularly thin carapace, not as thin as that of *E. oppeli* or *Knebelia bilobata* (Münster, 1839) (see Audo *et al.* 2014b).

Since its first description, this species has never been studied in detail. Schweigert (2004a, 2004b), Schweigert & Frattigiani (2005a, 2005b) and finally Garassino & Schweigert (2006) questioned the original generic assignment to *Eryon* Desmarest, 1817 and proposed an assignment to *Rosenfeldia* based upon the denticulate margins of s4–s6, uropodal exopod and endopod and telson. Unfortunately, these characters cannot be considered as typical of *Rosenfeldia* since they occur in several other species of polychelidans. Indeed, a telson with spiny margins occurs in *Coleia boboi* Garassino & Gironi, 2006, *Proeryon hartmanni* (Meyer, 1836), *Coleia barrovensis* M'Coy, 1849, *Proeryon giganteus* (Van Straelen, 1923), *Palaeopentacheles roettenbacheri* (Münster, 1839) and *Tethyseryon campanicus* Bravi, Garassino, Bartiromo, Audo, Charbonnier, Schweigert, Thévenard & Longobardi, 2014. A spiny uropodal endopod occurs also in *Proeryon giganteus* (Van Straelen, 1923), *Proeryon hartmanni* and *Palaeopentacheles roettenbacheri*; a similar uropodal exopod occurs in *Proeryon hartmanni* (with a diaeresis in this latter case). Actually, all these margins are often fringed with small spines and setae in extant species; indeed, these structures increase the surface of the telson and uropods. We therefore consider these characters to be only marginally informative. *Rosenfeldia triasica* and *Eryon oppeli* also share a rounded telson, but this character, although rarer, also occurs in *Tetrachela raiblana* (Bronn, 1858). The rounded telson may therefore be a convergence between these three taxa.

Moreover, the redescription of *Eryon oppeli* allows the recognition of several characters almost unique to this species among other polychelidans: (1) an extremely thin exoskeleton, reminiscent of the thinness of the exoskeleton of *Knebelia bilobata*, *K. schuberti* (Meyer, 1836) and that of some extant species, but unlike that of other fossil species, which are distinctly thicker; (2) an ovoid, almost pear-shaped exoskeleton wider in its anterior half, distinct from other polychelidans (clearly ovoid, subcircular or pear-shaped, larger in posterior half in almost all other species); (3) a rounded telson, as in *Rosenfeldia*, rare in polychelidans (generally triangular); (4) a first pereopod about as large as succeeding ones, generally larger in other polychelidans, except in the poorly preserved *Wrangelleryon perrates* Feldmann, Schweitzer & Haggart, 2013; (5) finally, as indicated by Audo *et al.* (2016), *Eryon oppeli* possesses hexagonal ommatidia, contrary to all other polychelidans, for which preserved quadratic ommatidia were documented. Considering only these points, *E. oppeli* could resemble *W. perrates*, but these two species do not seem to be closely related as they differ in many aspects: *W. perrates* is narrower, has

AUDO D. *et al.*, *Rosenfeldia triasica* and *Rogeryon oppeli* gen. et comb. nov.

petaloid uropodal endopod and exopod, and its P5 is larger in proportion. Their resemblance is therefore superficial and possibly linked to similar constraints on the shape of their pereopods.

For these reasons, we consider that *Eryon oppeli* cannot be ascribed to any currently described genera of Polychelida and we propose the erection of *Rogeryon* to accommodate it.

The familial assignment of *Rogeryon* is not straightforward. Indeed, its morphology is very different from all other polychelidans. Its relatively wide carapace and the lack of a diaeresis on uropodal exopod could suggest an assignment to Eryonidae; however, both these characters occur regularly within polychelidans. Furthermore, its hemicircular Mxp3 is clearly different from the subtriangular one of Eryonidae (and narrow one of Polychelidae). *Rogeryon* bears some resemblance to the older *Adamanteryon* Audo, Schweigert, Saint Martin & Charbonnier, 2014 (uncertain Polychelida family): both have a very thin carapace marked by strong cervical and postcervical grooves, shallow cervical and postcervical incisions and a carapace wider in its anterior half. Nevertheless, *Adamanteryon* distinctly differs from *Rogeryon* by its slender P1 far longer than P2–P4 and a much broader, more angular carapace. In our current state of knowledge it is, therefore, impossible to assign *Rogeryon* to an existing family of Polychelida, and describing a new family would only complicate the systematics of polychelidan lobsters (which already comprise two monogeneric and monospecific families: the Tetrachelidae and the Palaeopentachelidae Ahyong, 2009).

Rogeryon oppeli (Woodward, 1866) gen. et comb. nov.

Figs 2M, 4–6

Eryon oppeli Woodward, 1866: 500, pl. 24, fig. 4.

Eryon oppeli – Woodward 1881: 529; 1911: 307. — Balss 1924: 175. — Glaessner 1929: 166.

Rosenfeldia oppeli – Schweigert 2004a: 70; 2004b: 329; 2015: 273. — Schweigert & Frattigiani 2005a: 198; 2005b: 328. — Garassino & Schweigert 2006: 30. — Schweitzer *et al.* 2010: 43. — Feldmann *et al.* 2013a: 3, fig. 2.4. — Audo *et al.* 2016: 13, figs 1h–k.

Material examined

Holotype

GERMANY: Häberlein coll., NHMUK 44886 (Fig. 4A–B).

Other material

GERMANY: 6 other known specimens: SMNS 70102 (U. Resch coll., Fig. 4D), SMNS 66004 (R. Frattigiani coll., Fig. 5A–C), SMNS 65545 (R. Frattigiani coll., Fig. 5D), SMNS 66004/2 (R. Frattigiani coll. Fig. 5E); one specimen from K. and H. Schumacher pers. coll., without number (Fig. 4D); one specimen from U. Resch pers. coll. JMS 118 (Fig. 4C).

Type locality

GERMANY: “Solnhofen”, Bavaria, Germany.

Type age

Late Jurassic, Early Tithonian, *Hybonotum* ammonite biozone (after Schweigert 2007b).

Diagnosis

See genus.

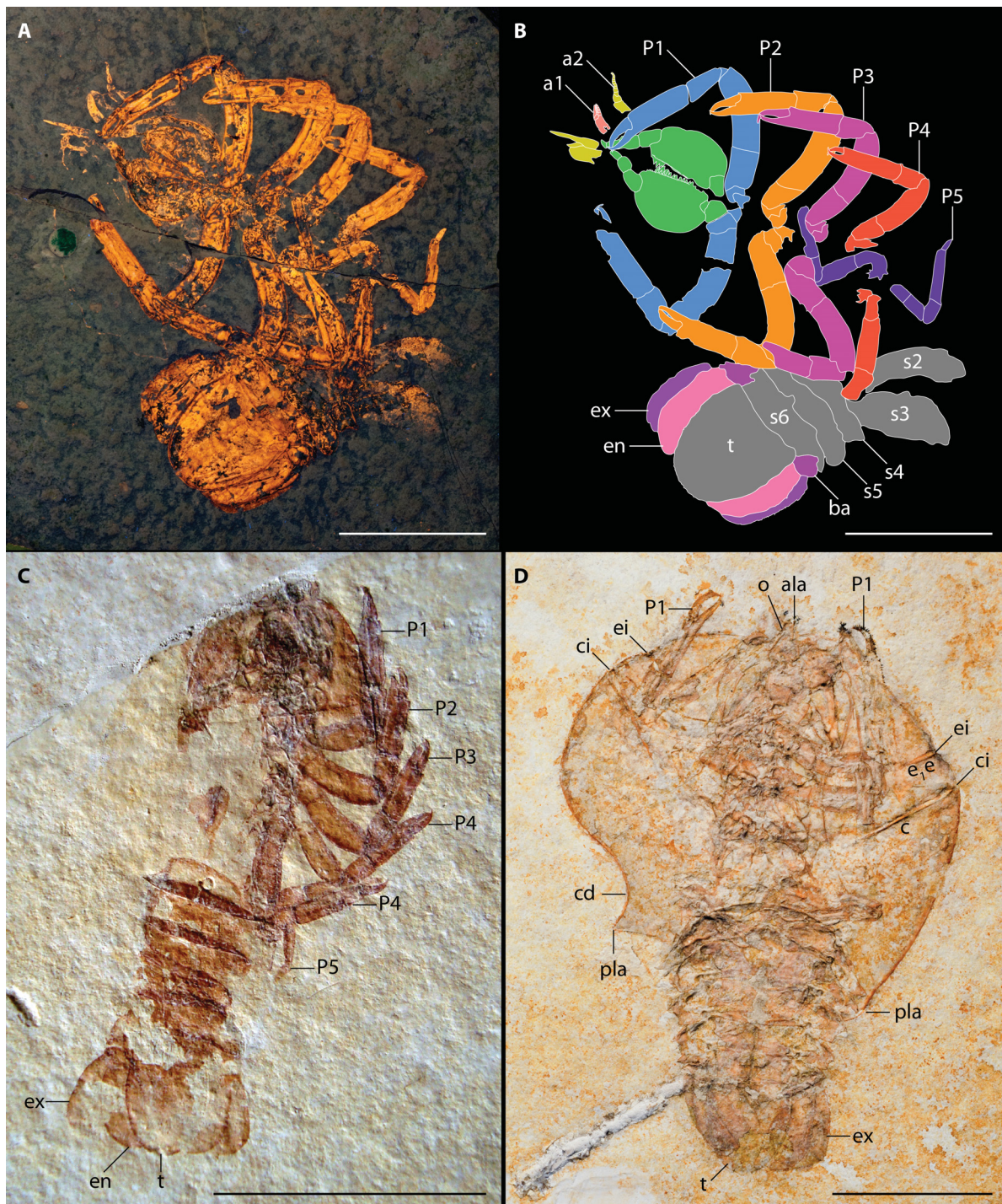


Fig. 4. *Rogeryon oppeli* (Woodward, 1866) gen. et comb. nov. from the Upper Jurassic (Tithonian) of Germany. **A–B.** Holotype NHMUK 44886 (Solnhofen area), dorsal view, UV-fluorescence (A) and interpretative line drawing (B). **C.** Specimen JMS 118 (Langenaltheim, Udo Resch coll.), dorsal view, natural light. **D.** Specimen SMNS 70102 (Solnhofen), dorsal view, cross-polarized light. Abbreviations: a1 = antennula; a2 = antenna; ala = anterolateral angle; ba = uropodal basipodite; c = postcervical groove; cd = carapace deformation; ci = postcervical incision; e₁e = cervical groove; en = uropodal endopod; ei = cervical incision; ex = uropodal exopod; o = ocular incision; P1–P5 = pereiopods 1 to 5; pla = posterolateral angle; s1–s6 = pleonites 1 to 6; t = telson. Scale bars: 20 mm. Photographs: D. Audo, © NHMUK (A) and G. Schweigert (C–D).

Description

SHAPE OF CARAPACE. Extremely thin exoskeleton; pear-shaped cephalothorax in outline in dorsal view, longer than wide, wider in its anterior half; very narrow and rather shallow frontal margin; side of frontal margin (anterolateral angle) forming a long spine; smooth lateral margin cut by ocular, cervical and postcervical incisions; deep ocular incision, hemicircular, opening laterally and closed ventrally; long

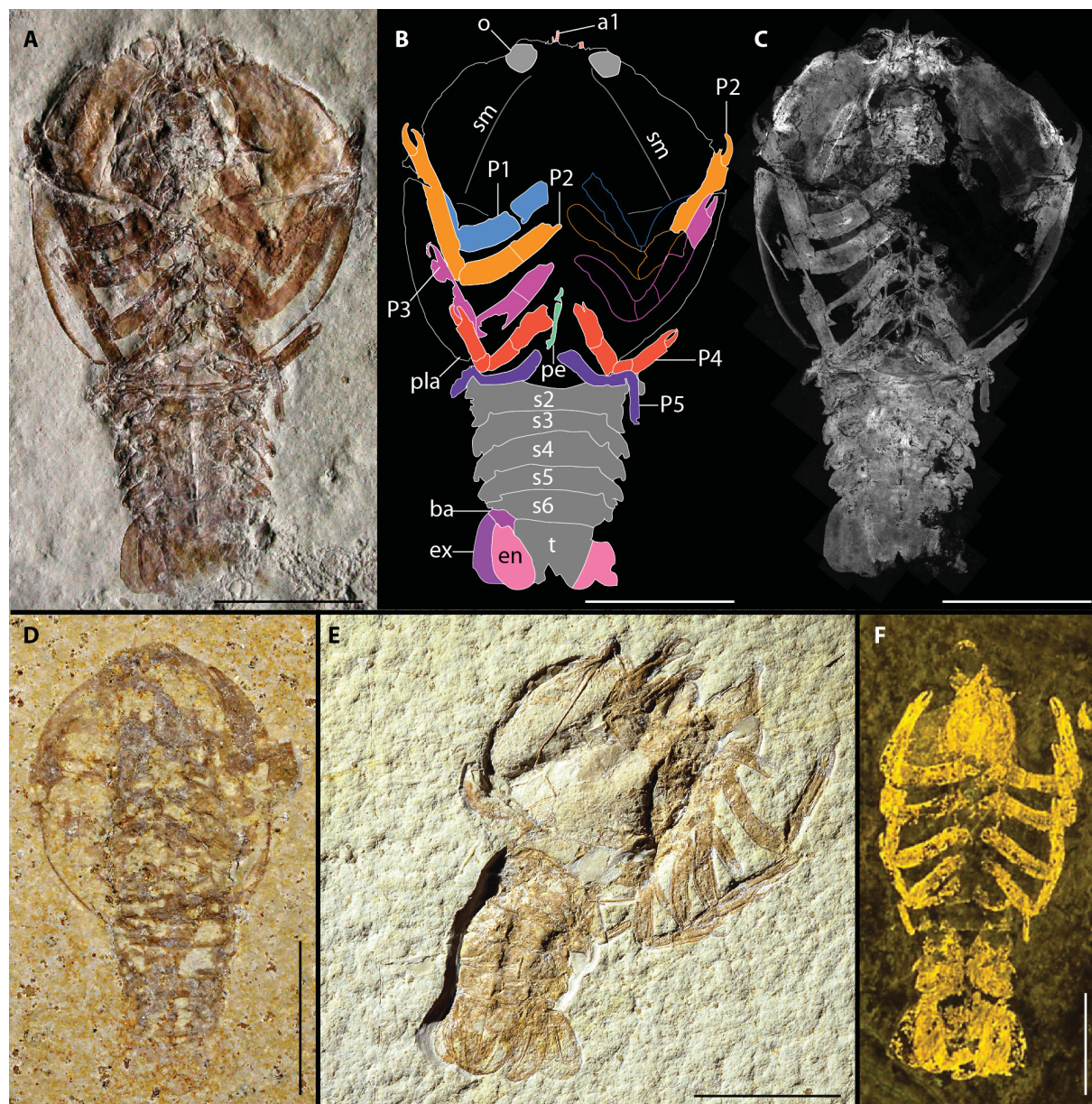


Fig. 5. *Rogeryon oppeli* (Woodward, 1866) gen. et comb. nov. from the Upper Jurassic (Tithonian) of Germany. **A–C.** Specimen SMNS 66004 (Sappenfeld), dorsal view, natural light (**A**), interpretative line-drawing (P1–P3 on one side were restored and are therefore drawn as outline (**B**) and green fluorescence (**C**). **D.** Specimen SMNS 65545 (Eichstätt), ventral view, natural light. **E.** Specimen SMNS 66004/2 (Langenaltheim), ventral view, natural light. **F.** Specimen without number (Mörsheim, K. and H. Schumacher coll.), ventral view, UV light. Abbreviations: a1 = antenna; ba = uropodal basipodite; en = uropodal endopod; ex = uropodal exopod; o = eye; pe = petasma; P1–P5 = pereopods 1 to 5; pla = posterolateral angle; s1–s6 = pleonites 1 to 6; sm = submarginal carina; t = telson. Scale bars: 20 mm. Photographs: G. Schweigert (**A**, **D**–**F**), J.T. Haug (**C**).

anterolateral margin, almost straight, oblique compared to longitudinal axis; small and shallow cervical and postcervical incisions, both opening in the anterior half of lateral margin; straight mediolateral margin, distinctly shorter than anterolateral margin; triangular posterolateral angle, projecting along s1; posterior margin concave, distinctly wider than anterior margin.

CARAPACE GROOVES AND CARINAE. Cervical groove extending from cervical incision, strongly marked medially and near lateral margin, probably cutting median line, and medially shallower between these two areas; postcervical groove longer than one third of carapace width, not connected to cervical groove, strongly marked from postcervical incision toward median line; shallow branchiocardiac groove extending obliquely in the posterior half of carapace; dorsal carinae (branchial, postorbital, median carinae) not visible; raised submarginal carina, extending ventrally parallel to lateral margin in the first half of carapace.

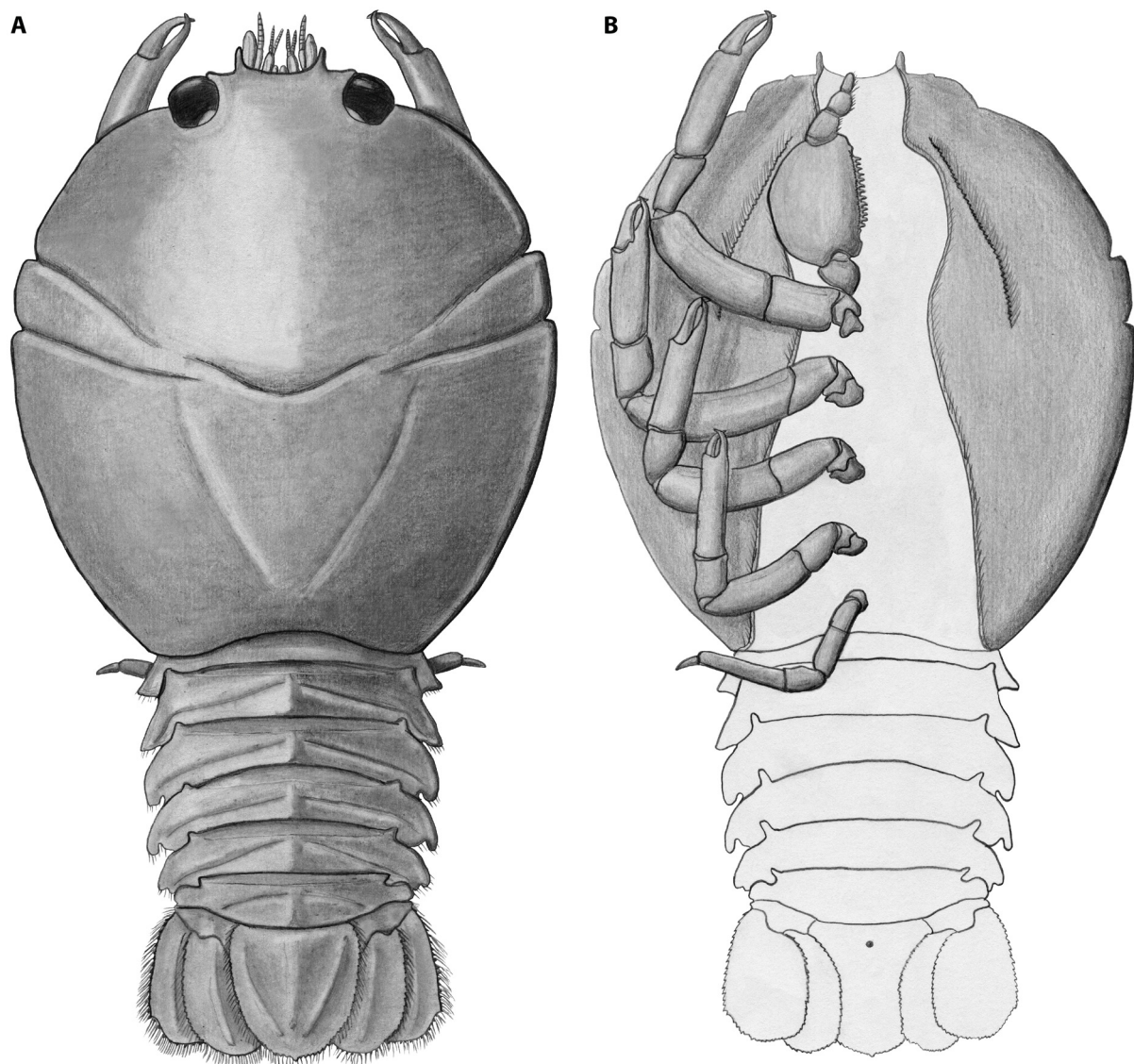


Fig. 6. Reconstruction of *Rogeryon oppeli* (Woodward, 1866). **A.** Dorsal aspect. **B.** Known parts of the ventral aspect, thoracic appendages omitted on the right side. Please note that due to the softness of the carapace, its precise outline is uncertain. Image hand-drawn by D. Audo.

PLEON AND TELSON. Pleon slightly shorter and one-half width of carapace; pleonite 1 poorly preserved, shorter than others; s2–s6 with terga crossed by two transverse grooves converging medially and by an axial carina placed posteriorly to anterior transverse groove and cutting posterior transversal groove to join with posterior margin; s3–s5 tergopleura with concave lateral margin, which appears hooked; s2–s5 tergopleura with a small anterior process articulating with a small notch in the preceding pleonite; sharp s6 tergopleuron; telson rounded distally, with finely serrated margins, a pair of serrated longitudinal carinae and, possibly, a median carina.

EYE AND CEPHALIC APPENDAGES. Large spherical eye with hexagonal ommatidia; mandible with a massive triangular coxal body and a subtriangular incisor process, the edge of which forms several teeth (poorly preserved); other cephalic appendages too poorly preserved to be described.

THORACIC APPENDAGES. Third maxilliped with a hemicircular ischium and short following podomeres; median margin of third maxilliped ischium inner margin serrated with numerous thin spines (*crista dentata*); stocky pereopods, decreasing in size from the first to the last, with slightly stocky and curved dactylus and pollex; P1 only slightly larger than P2.

PLEONAL APPENDAGES. Elongated petasma (modified pleopods 1 of male), poorly preserved; uropods with a short basipodite carrying a rounded endopod and a rounded exopod with a small spine on outer margin; uropodal endopod and exopod both strengthened by a longitudinal carina; uropodal exopod with no visible diaeresis.

ORNAMENTATION. Carapace covered with thin, rounded tubercles.

Occurrence

Early Tithonian of southern Germany.

Comments

All available specimens seem to differ from each other by the shape of their carapace. The shapes of both sides of the carapaces do not often match. These differences are undoubtedly due to the thinness of the carapace, which was deformed easily during fossilisation. In addition, due to its carapace which is probably divided across its median line, the specimen SMNS 70102 (Fig. 4D) is likely an exuvia; it shows a deformation possibly consistent with that interpretation. Due to these constraints, we base our reconstruction (Figs 2M, 6) of the outline of the carapace on specimens that seemed the less deformed such as SMNS 65545 (Fig. 4E) and SMNS 66004 (Fig. 5).

Discussion

Palaeobiology of *Rosenfeldia triasica*

Contrary to polychelidans which might have been more nektobenthic such as *Willemoesiocaris ovalis* (Van Straelen, 1923) (Audio *et al.* 2014c) or well-adapted to swim (Audio *et al.* 2014b), *Rosenfeldia triasica* seems to possess a rather thick carapace and stout pereopods. It was therefore undoubtedly mostly benthic.

Rosenfeldia triasica possesses rather stout P1. Contrary to many polychelidans with long slender claws, which are probably ambush predators, being able to deploy their first pereopods to catch preys (Ahyong 2009), *R. triasica* probably had to move close to its food or prey to catch it. It is therefore likely that *R. triasica* fed on slow moving and sedentary preys and / or was a scavenger.

The redescription of *R. triasica* permitted us to identify for the first time a mandible molar process in a fossil Polychelida (Fig. 1D). Extant Polychelidae do not possess this character and thus tend to swallow food items completely (Cartes & Abelló 1992). As a consequence, *R. triasica*, compared to extant Polychelidae, was probably more able to eat large or resistant food items. Schweitzer & Feldmann (2010) argued that polychelidans could feed on molluscs as palinurids do. Although we consider that polychelidans are probably not closely allied to palinurids and scyllarids (see Scholtz & Richter 1995; Bracken-Grissom *et al.* 2014 and references therein). It is possible that molluscs were part of the diet of *Rosenfeldia triasica*, perhaps more so than in the diet of other polychelidans, especially extant ones, whose mandibles seem to lack a molar process.

Palaeobiology of *Rogeryon oppeli* gen. et comb. nov.

Rogeryon oppeli gen. et comb. nov. possesses an unusual morphology among polychelidan lobsters: (1) a very thin, probably soft, carapace, (2) eyes with hexagonal ommatidia (probably apposition eyes: Audo *et al.* 2016), (3) P1 almost as large as P2–P4. Since none of these traits are common among polychelidan lobsters, most of them are likely autapomorphies (unique to *Rogeryon oppeli*) and unlikely to be ancestral characters retained in *Rogeryon oppeli*, but lost in most or all other polychelidans. As such, replacing *R. oppeli* in its palaeoenvironmental context and comparison of its traits to that of other polychelidans and arthropods might shed some light on its possible life-habits.

Palaeoenvironment

Rogeryon oppeli gen. et comb. nov. was discovered in the early Tithonian outcrops of southern Germany. These outcrops are considered to have been formed in relatively shallow water (20 to 60 m) in a subtropical, probably semi-arid zone (Barthel *et al.* 1990; Keupp *et al.* 2007). These outcrops preserve a diverse marine fauna and some terrestrial taxa, including tetrapods, insects and plants. In this fauna, *Rogeryon oppeli* is one of the rarest species: only 7 specimens are known to us, including specimens in private collections. Preservation of the specimens is generally excellent. Most specimens, except perhaps SMNS 65545 (Fig. 5D) and SMNS 66004 (Fig. 5A–C), seem to correspond to exuviae, the carapace either missing or partially disarticulated. It seems unlikely that these specimens were transported over a large distance. Indeed, the entire animal had a thin carapace and its exuviae were undoubtedly quite fragile, since they do not contain muscle and tissue limiting the disarticulation. Therefore, *R. oppeli* probably lived in a shallow water palaeoenvironment.

Vision

The eyes of *Rogeryon oppeli* gen. et comb. nov. exhibit hexagonal ommatidia. These hexagonal ommatidia suggest *R. oppeli* had apposition eyes (Audo *et al.* 2016). Apposition eyes provide a greater resolution but at the expense of poorer performance in dim-light conditions compared to superposition eyes (see Cronin & Porter 2008 for a full review of eye-types in crustaceans). Since most other polychelidans seem to have had superposition eyes (Audo *et al.* 2016), it is possible that the apposition eyes of *R. oppeli* correspond to an adaptation to a shallow water palaeoenvironment. This character seems congruent with the shallow water palaeoenvironments attributed to the Solnhofen-type outcrops. However, it should be noted that other polychelidans from Solnhofen-type outcrops with preserved ommatidia, had reflection superposition eyes (quadrate ommatidia: Audo *et al.* 2016). Therefore, the palaeoenvironment alone cannot explain the eye-type of *R. oppeli*. As a specialisation, or ecological differentiation, *R. oppeli* could have been diurnal, while other polychelidans were more active when light declined or during the night, as several extant subtidal species are (Moller & Naylor 1980; Kanciruk 1980; De Grave & Turner 1997). Unfortunately, due to the life-habits and reduced eyes of extant polychelidans, it might not be possible to draw stronger conclusion from this particularity of *R. oppeli*.

While so far we have considered the ultimate factors for the presence of hexagonal ommatidia in *R. oppeli* gen. et comb. nov., we can also address the proximate ones. Quadrate facets (and with this reflective superposition eyes) are widespread among adult decapods, larvae usually possess apposition eyes with hexagonal facets. It seems, therefore, likely that the presence of hexagonal facets and a supposed apposition eye is a simple retention of a larval condition into the adult phase, hence most likely a case of paedomorphic heterochrony (evolutionary shift in developmental timing). Unfortunately, our knowledge of the exact timing of this transition is rather limited in general and, due to the reduced eyes in modern forms, in polychelidans especially. The only case in which eyes are preserved in a fossil polychelidan larva is an eryoneicus type-larva with quadrate facets preserved (Haug *et al.* 2015). Yet, the apposition eye might more likely not be coupled to larval decapods in general, but to zoea-type larvae, and the later eryoneicus (and the eryoneicus-type) larvae are megalopa-type larvae.

Given the size of the eyes in relation to the body and number of ommatidia in *R. oppeli* gen. et comb. nov. we can furthermore suggest that the mode of paedomorphosis is neoteny. The other types of paedomorphosis (progenesis and post-displacement) would have led to comparably smaller eyes.

Also in other instances within Polychelida paedomorphosis has been suggested, e.g., for species of *Knebelia* Van Straelen, 1922 (Audo *et al.* 2014b). Yet, in *Knebelia* other structures were affected than in *R. oppeli* gen. et comb. nov., leading to quite different ecological adaptations (see also further below). This demonstrates that heterochrony played an important role in the diversification of Polychelida.

Relation to substrate

The thin exoskeleton of *R. oppeli* gen. et comb. nov. is reminiscent of that of *Knebelia bilobata*, which was possibly well-adapted for swimming (Audo *et al.* 2014b). In contrast to *K. bilobata*, *R. oppeli* does not seem to have had particularly developed uropods: the mean ratio between uropod length and carapace total length is only 0.21 (see method of measurement in Audo *et al.* 2014b: measurements on specimens SMNS 65545, SMNS 66004, SMNS 70102). Due to the small size of the sample, this comparison cannot be tested statistically. If *R. oppeli* did not actively swim, it may have floated. Extant eryoneicus larvae and juveniles of *Palaeopentacheles roettenbacheri* (Münster, 1839) seem to use their abundant spines to provide additional buoyancy (see Gurney 1942; Eiler *et al.* 2016). However, the exoskeleton of *R. oppeli* appears devoid of spines, except perhaps very small ones. Therefore, it seems unlikely that *R. oppeli* was well adapted to float in the water column. Besides, the structure of the pereopods in *R. oppeli* is more consistent with benthic life-habits: indeed, its pereopods seem more massive than those of *Knebelia bilobata*, *Willemoesiocaris ovalis* (Van Straelen, 1923) (Audo *et al.* 2014c) and even that of extant Polychelidae. Considering the relatively small uropods and massive pereopods, a thin carapace does not seem sufficient to propose a swimming life-habit for *Rogeryon oppeli*. The thinness of carapace could be: (1) an adaptation to its life-style, but not linked to improbable developed swimming capacities; (2) or be plesiomorphic (that is being primitive for *R. oppeli* and its closest relative), which is unlikely as within all polychelidans, only *Knebelia bilobata* and perhaps *Wrangelleryon perates* seem to have a thin carapace; (3) or, be linked to the evolution of other characters. This third possibility is in our opinion plausible. Indeed, we remark that the carapace thinness may be the result of *R. oppeli* having evolved through neoteny (see Audo *et al.* 2014b). This assertion would also be supported by the apposition eyes in *R. oppeli* (see Cronin & Porter 2008), and its relatively wide carapace compared to the pleon (see Bravi *et al.* 2014). Despite its thin carapace, *Rogeryon oppeli* seems, therefore, to have been a benthic animal.

As a benthic animal, *Rogeryon oppeli* gen. et comb. nov. does not seem to present adaptations to bury itself in sediments: (1) although antennulae and antennae are poorly preserved, the preserved parts do not seem to be enlarged to form a respiratory canal, unlike those known in polychelids (Ahyong 2009) and some eryonids (Audo *et al.* 2014a); (2) the carapace of *Rogeryon oppeli* also does not seem well-

suited for burrowing: it is very thin, possibly soft, wider than the pleon (see Ahyong 2009; note that this last character probably does not preclude burying, see Audo *et al.* 2014a); (3) the eyes of *Rogeryon oppeli* do not seem adapted to burying, indeed, they are neither surrounded by ocular incision as in many eryonids nor raised on stalks as in *Eryon*. Taking into account all these characters, it seems likely that *Rogeryon oppeli* was an epibenthic animal.

Diet

The first pereopods of *R. oppeli* gen. et comb. nov. are almost as large as the succeeding pereopods, contrary to other polychelidans, where the P1 is generally larger than the succeeding ones and generally held folded against the carapace sides so that they can strike prey from a buried position (Ahyong 2009). Contrary to the preceding characters, a short P1 does not seem to be linked to paedomorphosis since eryoneicus larvae (Bernard 1953; Eiler *et al.* 2016), and eryoneicus-like larvae (Haug *et al.* 2015) do have a larger P1. The size of pereopods is therefore likely closely linked to the palaeoecology of *Rogeryon* gen. nov. The P1 probably has a predatory role in both extinct (Garassino *et al.* 2012) and modern polychelidans (Gore 1984) as well as a defensive role (Santucci 1933). Gut content may yield information on the diet of fossil polychelidans. However, even in exceptionally well-preserved specimens, food items were not recognizable (Jauvion *et al.* 2016). Gut contents of modern polychelidans have shown they are either predators of small invertebrates or scavengers (Firth & Pequegnat 1971; Lagardère 1973; Gore 1984; Cartes & Abelló 1992). With its relatively short P1, *R. oppeli* was probably not able to catch preys at a distance by reaching out to them.

Such a disposition is in fact reminiscent of that of slipper lobsters which also have subequal pereopods, notably P1 (pers. obs. D.A.). Feeding habits of slipper lobsters are generally considered to consist mostly of epifaunal and endofaunal molluscs and worms, as well as scavenging (Suthers & Anderson 1981; Johnston & Alexander 1999; Johnston 2007). Slipper lobsters seem particularly suited to open bivalve shells (Johnston 2007). *Rogeryon oppeli* might have had a similar diet, especially since extant polychelidan lobsters prey on small invertebrates; it might have dug them up from a soft substrate. Slipper lobsters, however, are achelate and possess strong dactyli that can be used as wedges to open bivalve shells. The claws of *R. oppeli* were probably not as effective to open shells; however, it might have fed on other epifaunal and infaunal animals, including thin-shelled bivalves, as is the case for extant horseshoe crabs (xiphosuran chelicerates), which also have four chelate appendages. Horseshoe crabs also have chelicerae and gnathobases to reduce the food item they catch (Walls *et al.* 2002 and references therein), but the function of these parts is performed by mandibles, maxillulae, maxillae and three pairs of maxillipeds in decapod crustaceans.

It seems therefore likely that *R. oppeli* gen. et comb. nov. had a diet somewhat similar to that of slipper lobsters and horseshoe crabs. Besides, prey such as polychaete worms and bivalves were available in the environment, since fossilized specimens have been discovered in the Solnhofen-type outcrops (e.g., Frickhinger 1994, 1999). It could be noted that another species might have had a similar diet: *Wrangelleryon perrates*, which also possesses similar subequal pereopods.

Conclusion

Rogeryon oppeli gen. et comb. nov. is an unusual species of polychelidan lobster. Its inclusion in *Rosenfeldia* overlooked many of its unique characteristics. Although the reconstruction of its palaeobiology relies mostly on comparison with distant modern taxa, it is still obvious that it had life-habits unique among polychelidan lobsters.

During the Late Jurassic, the polychelidan diversity reached a peak (Audo *et al.* 2017). Although Solnhofen-type outcrops are clearly favourable to the preservation of crustacean remains, the occurrences of unusual polychelidan lobsters such as *Rogeryon* gen. nov. or *Knebelia* suggest that these settings also

represented an opportunity for crustaceans to diversify and exploit new environments and resources. The disappearance of these palaeoenvironments at the end of the Jurassic may be one of the factors leading to the decline of polychelidan lobsters immediately after this important diversification.

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