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Aeger crassipes Bronn, 1858 (Crustacea, Decapoda, Penaeidae) from the Carnian of Austria and Italy revisited: implications for taxonomy of fossil penaeoid shrimps

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(with 4 figures)

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Abstract

Aeger crassipes, a penaeid shrimp from the Late Triassic (Carnian) of Cave del Predil (Raibl), Italy and Polzberg, Austria is revisited. Based on the restudied original material of Bronn and Glaessner, the species is considered poorly defined. Moreover, because of lack of important taxonomic characters on the preserved fossils the species cannot be assigned confidently on the genus level. We therefore treat it in open nomenclature and simultaneously refuse to suggest possible relationship with a particular genus. The resulting binomen is "Genus? *crassipes*". Such treatment may be used for fossil penaeoid shrimps of uncertain affinities rather than classifying them in the "catch-all" or "waste-basket" genera.

Key words: Malacostraca, Triassic, taxonomy, Konservat-Lagerstätte, fish beds.

Introduction

The so-called fish beds ("Fisch-Schiefer") often include – among other fossil fauna – well-preserved decapod crustaceans. Among the best-known Mesozoic examples are Middle Triassic Lagerstätte of Luoping in China (Hu *et al.* 2011; Feldmann *et al.* 2012; Schweitzer *et al.* 2014), Late Triassic Lagerstätten of Raibl (Cave del Predil)

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and Polzberg in Italy and Austria, respectively (Glaessner 1930, 1931; Audo *et al.* 2018), Late Triassic Lagerstätten of Calcare di Zorzino (Bergamo), Argilliti di Riva di Solto (Bergamo) and Dolomia di Forni (Udine), all in Italy (Pinna 1974; Garassino & Teruzzi 1993; Garassino *et al.* 1996), Early Jurassic Lagerstätten with the famous Posidonia Shales in the surroundings of Holzmaden in Germany (Beurlen 1930; Förster 1967; Schweigert *et al.* 2003; Audo 2016) and the Lagerstätte of Osteno in Italy (Garassino 1990), Middle Jurassic Plattenkalk of Monte Fallano in Italy (Bravi *et al.* 2014), Late Jurassic Solnhofen-type Plattenkalk in Germany (*e.g.*, Garassino & Schweigert 2006; Schweigert 2011; Charbonnier & Garassino 2012; Schweigert *et al.* 2016), and Late Cretaceous Lebanese Lagerstätten of Hakel, Hadjoula and Sahel Alma (Charbonnier *et al.* 2017). The occurrences of decapod crustaceans in the fish beds known to date, although differing greatly from the taxonomic and taphonomic point of view, were briefly reviewed by Glaessner (1965). Since the early descriptions of these decapod faunas, a number of taxa have been revised recently (Garassino & Schweigert 2006; Schweigert *et al.* 2016; Charbonnier *et al.* 2017; Audo *et al.* 2018), some of them, however, still need attention, such as the natant shrimp *Aeger crassipes* Bronn, 1858, treated for a long time as a representative of *Antrimpos* Münster, 1839 (Schweitzer *et al.* 2010). Although this species has been considered the most common shrimp from the Raibl Beds (Förster 1967: p. 172), it has not been revised since Glaessner (1930). The present contribution aims for re-evaluation of *A. crassipes* based on re-study of museum collections, including the original material of Bronn (1858) and Glaessner (1930, 1931). Additionally, we discuss the implications for taxonomic treatment of fossil penaeoid shrimps.

Geological settings

Aeger crassipes has so far been identified at two localities, Raibl (Cave del Predil) in nowadays Italy (Friuli-Venezia Giulia) and Polzberg from Austria (Lower Austria). The sediments of both Lagerstätten were deposited during the Carnian (Late Triassic) Pluvial Event (Hornung *et al.* 2007), a biological crisis reflected in a demise of rimmed carbonate platforms (Keim *et al.* 2001) and a switch to carbonate or mixed ramps (Bosellini *et al.* 2003).

At Raibl, oil shales of the Raibl Beds divided in several series (Jerz 1966; Tollmann 1976) are exposed. According to Rettori *et al.* (1998) and De Zanche *et al.* (2000) they were probably deposited in deep water of a basinal environment. A subtidal lagoon environment of an inner shelf was interpreted for these strata by Hornung *et al.* (2007) and Krainer *et al.* (2011).

The first report on fossils from the locality is that by Boué (1835); the assemblage was later described by Bronn (1858) and revised by Glaessner (1930). Raibl Beds as mentioned by Bronn (1858) and Glaessner (1930) probably corresponds to the Fish-beds *sensu* Suess (1867). A deep-water evidence for the Carnian Pluvial Event was documented also in the Lagonegro Basin in Italy (Rigo *et al.* 2007).

At Polzberg, shales of the Reingraben Beds are exposed, which were deposited in a low energy environment without bottom currents (Forchielli & Pervesler 2013). A diverse, predominantly nektonic fauna of arthropods, ammonoids, and fishes has been documented from the locality (Glaessner 1931; Griffith 1977). The deposits were interpreted as deriving from a deeper marine environment (Hornung & Brandner 2005; Hornung *et al.* 2007). Occasionally low oxygen levels were present as documented by the accumulation of juvenile specimens of the bivalve *Halobia* (McRoberts 2001; Hopkin & McRoberts 2005). Dysoxic to anoxic bottom conditions of the Reingraben Shales are supported also by the presence of pyrite crystals, the absence of sessile organisms and the lack of bioturbation (Forchielli & Pervesler 2013). Anoxia do not significantly inhibit decay (Allison 1988; Butler *et al.* 2015), but may increase the possibility of soft part preservation and apparently promoted also preservation of shrimps.

Unfortunately, there is often an overlap and a mixture of information between the Lunz and Polzberg Lagerstätten in the collections and older scientific works, including that of Glaessner (1931), although there is no connection between the two Lagerstätten: age, environment, and also taphonomic pathways differed significantly from one another (Forchielli & Pervesler 2013). When reporting a decapod crustacean fauna from the Polzberg Lagerstätte, Glaessner (1931) caused confusion by assigning the Reingraben Shales erroneously to the Lunz Beds.

Material and methods

The studied specimens represent old acquisitions deposited in the University of Heidelberg (Fig. 1), the Geological Survey, Vienna (Figs 2–3) and Natural History Museum, Vienna (Fig. 4). No further preparation was performed. Use of angled side-light is crucial in documenting morphological details of decapod specimens from the Raibl and Reingraben beds, because the specimens are highly compressed and flattened. Moreover, due to the dark colour of the shales, the specimens are often not well discernible. Therefore, some specimens were coated with ammonium chloride prior to photography to enhance the contrast (Cooper 1935; Teichert 1948). Alternately, the specimens were immersed in ethanol. We also attempted to use polarized light to reveal details not discernible by using conventional illumination (see Pott *et al.* 2007) – unfortunately, without much success.

Abbreviations

a1 – antenna

a2 – antennula

Mxp3 – maxilliped 3

P1–P5 – pereiopods 1–5

Plp1–Plp5 – pleopods 1–5

s1–s6 – pleonal somites 1–6

Institutional abbreviations

GBA – Geological Survey, Vienna, Austria

NHMW – Department of Geology & Palaeontology, Natural History Museum, Vienna, Austria

Systematic Palaeontology

Order Decapoda Latreille, 1802

Suborder Dendrobranchiata Bate, 1888

Superfamily Penaeoidea Rafinesque, 1815

Family Penaeidae Rafinesque, 1815

Discussion: The fossil record of penaeid shrimps is poor due to the comparatively low fossilization potential of natant shrimps in general (Plotnick 1986; Klompmaker *et al.* 2017). Nearly all known fossil occurrences of supposed Penaeidae come from Lagerstätten with finely laminated shales or lithographic limestones (*e.g.*, Münster 1839; Oppel 1862; Glaessner 1930, 1931; Schweigert 2001a; Schweigert *et al.* 2016; Charbonnier *et al.* 2017). Nearly all fossil taxa are attributed to extinct genera; from 25 penaeid genera with fossil representative(s), only one genus, *Penaeus* Fabricius, 1798, is represented today (Schweitzer *et al.* 2010; Garassino *et al.* 2013). Apparently, the attribution of the fossil material to extant genera is difficult, largely because of the low fossilization potential of taxonomically important characters; in this respect the fossil species of *Penaeus* are pending a revision taking into account advances in the systematics and taxonomy of Dendrobranchiata (Ma *et al.* 2009; Tavares *et al.* 2009; Tavares & Martin 2010; De Grave & Fransen 2011). Also the rate of evolution within shrimps surely has been rapid enough to generate major differences between taxa from different time periods; thus, it is not surprising that Mesozoic shrimps often are attributed to higher taxa on their own. This may, however, lead to the usage of collective genera. Such a collective genus is also *Antrimpos* Münster, 1839, currently consisting of nearly 20 species (Schweitzer *et al.* 2010; Brandt & Schulz 2013; Garassino *et al.* 2014). As already noted by Glaessner (1969, p. R477), *Antrimpos* is a genus *"in which many fossil species not showing diagnostic characters of Recent Penaeidae have been placed"*. In fact, no reliable diagnosis of *Antrimpos* is at hand. According to Schweigert *et al.* (2016) *Antrimpos speciosus* Münster, 1839, the type species of the genus, has an elongate rostrum with nine dorsal teeth and one ventral tooth positioned distally, epigastric tooth (spine), short and smooth Mxp3, and uropodal exopods with a subrounded diaeresis. Importantly, the characters on rostrum, which are considered taxonomically important also in extant taxa (Pérez Farfante & Kensley 1997; Tavares & Martin 2010), are highly variable among species attributed to *Antrimpos*, although in the type species this character is constant. Thus, the genus as used throughout the literature (*e.g.*, Glaessner 1929, 1930, 1931; Pinna 1974; Etter 1994; Schweigert 2001a; Schweitzer *et al.* 2010; Brand & Schulz 2013) is in a need of careful revision.

Genus undetermined

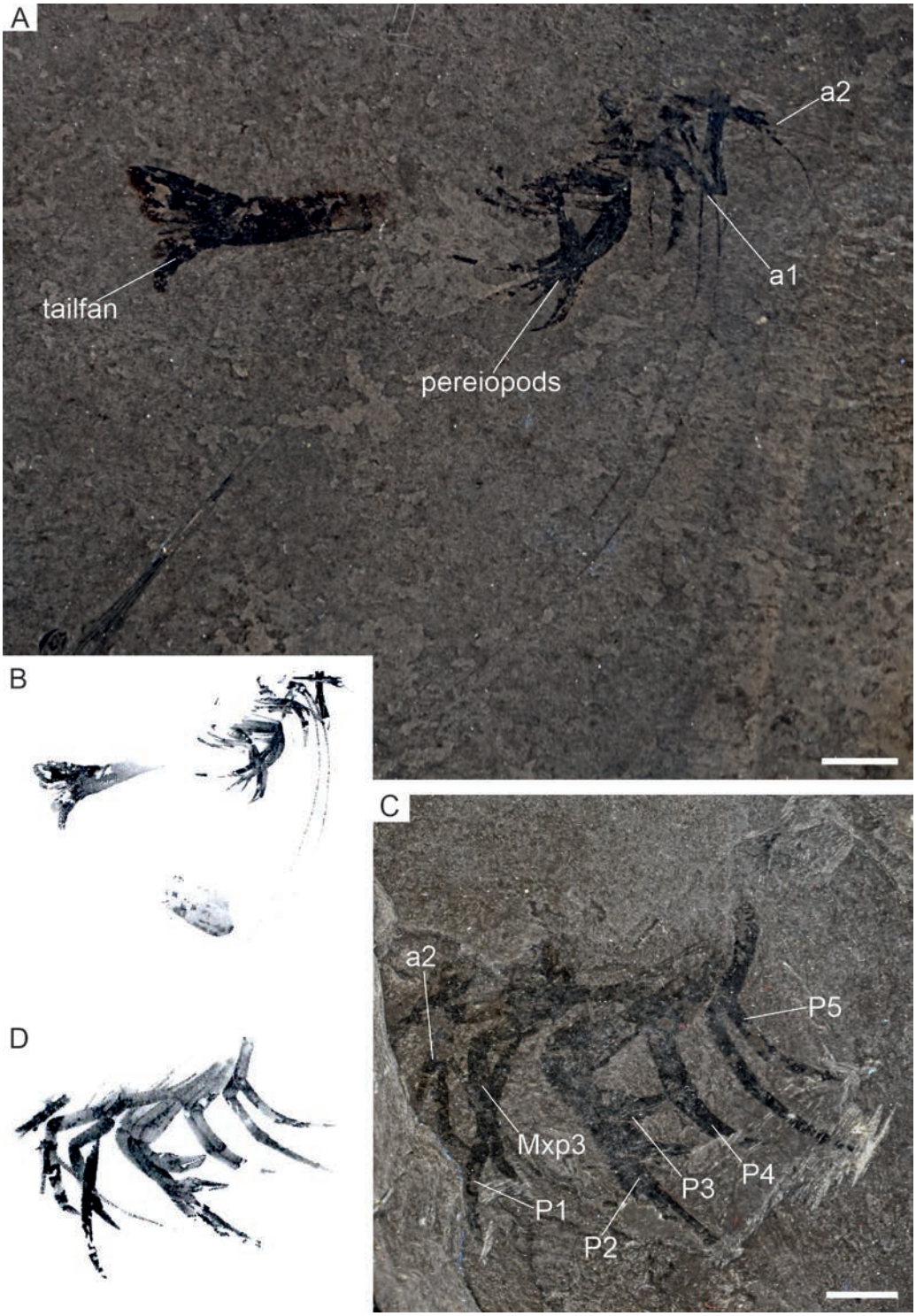
Genus? *crassipes* BRONN, 1858
(Figures 1–4)

1858 *Aeger crassipes* BRONN, p. 26, pl. 5, figs 1, 2 [non pl. 4, fig. 5].
1893 *Aeger crassipes* BRONN, 1858 – WÖHRMANN, p. 689.
1922 *Aeger crassipes* BRONN, 1858 – BALSS, p. 128.
1929 *Antrimpos crassipes* (BRONN, 1858) – GLAESSNER, p. 54.
1930 *Antrimpos crassipes* (BRONN, 1858) – GLAESSNER, p. 139, pl. 6, fig. 1, pl. 10, fig. 4 [erroneously indicated as *Aeger Straeleni*].
1931 *Antrimpos crassipes* (BRONN, 1858) – GLAESSNER, p. 473.
1965 *Antrimpos crassipes* (BRONN, 1858) – GLAESSNER, p. 112, fig. 1.
1967 *Antrimpos crassipes* (BRONN, 1858) – FÖRSTER, p. 172.
1994 *Antrimpos crassipes* (BRONN, 1858) – ETTER, p. 227.
1998 *Antrimpos crassipes* (BRONN, 1858) – MÜLLER, p. 7.
2013 *Antrimpos crassipes* (BRONN, 1858) – BRANDT & SCHULZ, p. 78.
2014 *Antrimpos crassipes* (BRONN, 1858) – GARASSINO *et al.*, p. 17.
2016 *Antrimpos crassipes* (BRONN, 1858) – HYŽNÝ & ZORN, p. 137, pl. 14, figs 1a–c.
2018 *Antrimpos crassipes* (BRONN, 1858) – AUDO *et al.*, p. 42.

Material examined: Herein designated lectotype is a specimen without collection number from the "Originaliensammlung" collection, Institute of Geosciences, University of Heidelberg, as depicted in Fig. 1A. Other material consists of a number of specimens in various states of preservation; the assignment of poorly preserved specimens of fragmentary nature to the respective species is considered problematic. For the sake of completeness, however, we list here all the material identified as "*Aeger crassipes*" by former authorities (*e.g.*, Martin F. GLAESSNER): a near-entire individual in lateral aspect from Raibl (GBA 1930/002/0001), a near-entire individual in lateral aspect from Raibl (NHMW 1866/0040/0453), an incomplete pleon from Schindelberggraben (Polzberg) near Lunz (NHMW 1910/0015/0019), a lump of pereiopods from Raibl (NHMW 1887/0009/0110), fragmentary remains of pereiopods from Rinngraben, Raibl (NHMW 1887/0009/0116), a lump of pereiopods from Raibl (NHMW 1864/0052/0035), isolated pereiopods and tailfan from Rinngraben, Raibl (NHMW 1887/0009/0106), fragmentary remains from Schindelberggraben (Polzberg) near Lunz (NHMW 1910/0015/0020), fragmentary remains from Schindelberggraben (Polzberg) near Lunz (NHMW 1910/0015/0021), and fragmentary remains from Schindelberggraben (Polzberg) near Lunz (NHMW 1910/0015/0030).

Occurrence: The type locality is Cave del Predil (Raibl), Friuli-Venezia Giulia, Italy; Upper Triassic (Carnian), Raibl Formation (Raibler Schichten). Besides the type locality, the species is known also from Polzberg, Lower Austria, Austria; Upper Triassic (Carnina), Reingraben Formation.

Emended description: Carapace: Subrectangular carapace slightly restricted anteriorly due to weak curvature of the ventral margin; straight dorsal margin; posterior


A
a2
a1
tailfan
pereiopods
B
D
C
a2
P5
Mxp3
P3
P4
P1
P2

margin dorsally concave with marginal ridge; rostrum not preserved, anterior margin with large antennal notch.

Ornamentation of carapace: Carapace largely smooth, lower half of branchiostegites adorned with tiny evenly spaced tubercles. *Pleon* – Subrectangular somites; s1 shorter than the others; s3 larger than s4–s5; s1–s6 with smooth terga and pleura; rounded s1–s5 pleura; s4–s6 with discontinuous dorsomedian carina; s6 with distinct cicatrix and dorsolateral sulcus; s4 and s5 with posterior margin showing median articulation between s4–s5 and s5–s6 respectively; long and subrectangular s6; triangular telson; telson shorter than uropods.

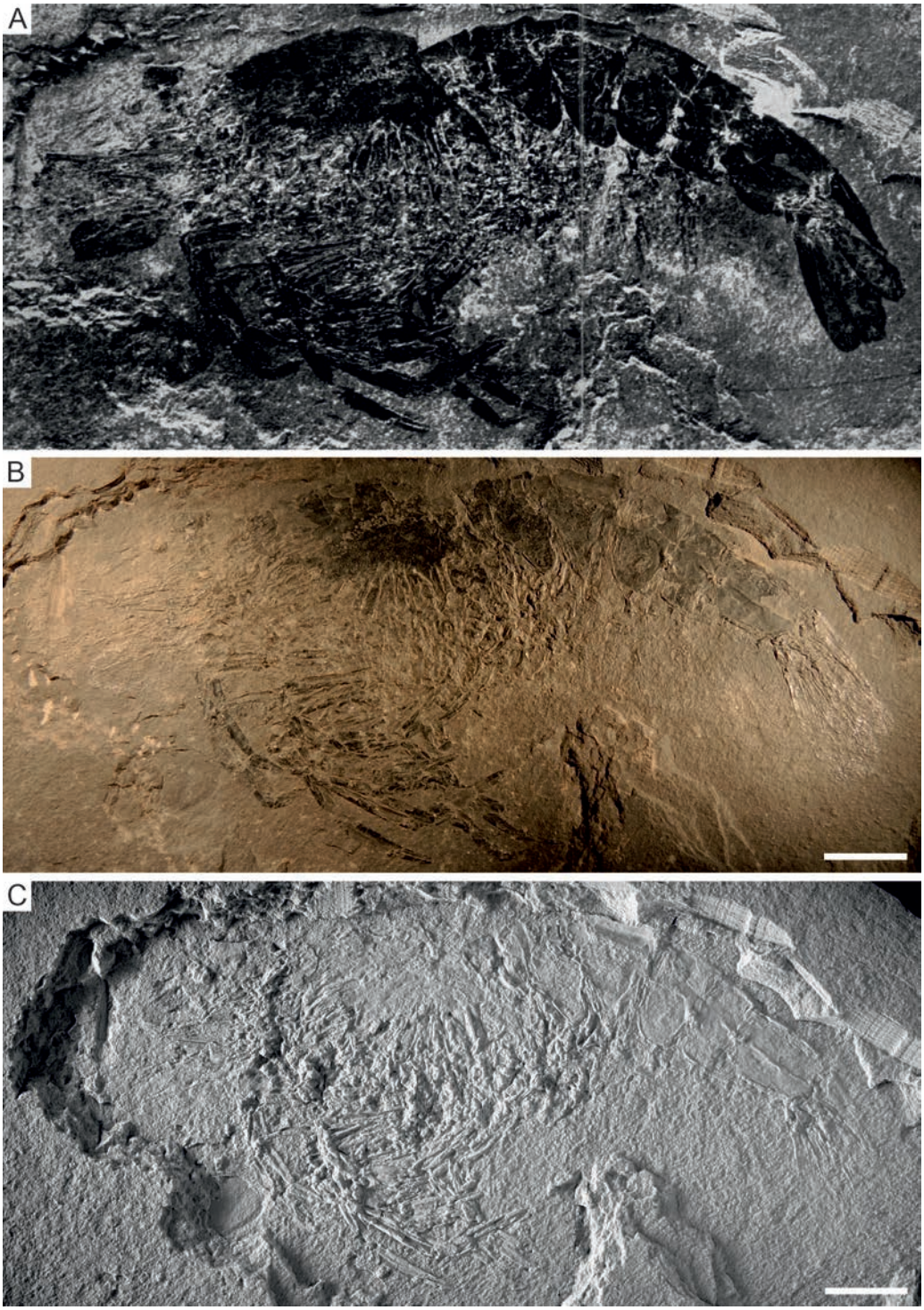
Cephalic appendages: Poorly preserved; flagellae of antennae (in some specimens) very long; lamellar scaphocerite; flagellae of antennulae much shorter.

Thoracic appendages: Mxp3 long and leg-like, with triangular-shaped distal segment; chelate and slender P1–P3; P3 longer than P1 and P2; P1–P3 chelae relatively long and slender with smooth occlusal margins, manus longer than fingers; achelate and slender P4 and P5.

Pleonal appendages: Pleopods poorly preserved; uropods one fourth longer than telson, uropodal endopod with longitudinal median carina; uropodal exopod with longitudinal median carina and rounded diaeresis.

Discussion: The species was described by Bronn (1858) and, based on additional material from the type locality, it was revised by Glaessner (1930). Later, the species was recognized also in the Polzberg fauna (Glaessner 1931). The original description of Bronn (1858) was based on four incomplete specimens (two of them are deposited in the University of Heidelberg, Germany and are figured herein as Fig. 1), none of them possessed the cephalothorax. Glaessner (1930) mentioned 23 specimens from Raibl, six of them with carapace and pleon preserved; most of them consisting only of pereiopods and uropods (tailfan). From Polzberg, Glaessner (1931) mentioned four specimens, two of them with carapace and pleon preserved. These specimens were deposited in the NHMW (Fig. 4). Glaessner (1931) also mentioned four additional specimens from Polzberg, which could belong to *A. crassipes*, but which were insufficiently preserved. It is important to note, that none of specimens examined by Glaessner (1930, 1931) preserve a rostrum, which is explicitly mentioned in the text of his studies. Re-examination of the material confirmed this observation: in all specimens with preserved cephalothorax the rostrum is missing or was not developed at all.

◀ Fig. 1. *Aeger crassipes* Bronn, 1858. Two specimens originally reported by Bronn (1858) from Cave del Predil (Raibl) and currently deposited without collection number in the "Originaliensammlung" collection, Institute of Geosciences, University of Heidelberg, Germany. **A**: Herein designated lectotype of *Aeger crassipes*. **B**: Scanned copy of the original figure of Bronn (1858: pl. 5, fig. 1). **C**: Herein designated paralectotype of *Aeger crassipes*. **D**: Scanned copy of the original figure of Bronn (1858: pl. 5, fig. 2). Scale bars equal 10 mm.


A
B
C

Bronn (1858) described the species as a representative of *Aeger* Münster, 1839. Later, Glaessner (1930) wondered why Bronn (1858) treated the species under this taxon and not as *Antrimpos*, and re-assigned the species into the latter genus. Indeed, the species named as *Aeger crassipes* by Bronn (1858) does not possess hypertrofied Mxp3 with movable spines and branch-like dactylus, so typical of *Aeger* (Schweigert 2001b; Schweigert *et al.* 2016; Charbonnier *et al.* 2017). However, Glaessner (1930) admitted that it was not possible to discuss the relationship between *Antrimpos crassipes* and its (supposed) congeners, apparently because of poor preservation of *A. crassipes*, and thus, the attribution to *Antrimpos* is also questionable. Moreover, *A. crassipes* possesses elongate Mxp3 (Fig. 3C), quite unlike any other species of *Antrimpos* described thus far (for a full list see Schweitzer *et al.* 2010). Elongate Mxp3, however, cannot be considered of major taxonomic importance, as numerous extant penaeoid shrimps possess it, including (among others) representatives of Aristeidae, Benthesicymidae and Penaeidae (Pérez Farfante & Kensley 1997).

Remarks on taxonomy

If the main taxonomic characters are missing one may attempt to choose some relevant proxy characters (*cf.* Schweitzer 2003). Selection of proxy characters must be done carefully with reasonable argumentation. In our case, however, we are convinced that this is not possible. First of all, the genus *Antrimpos* is pending revision and as such it is used deliberately as a catch-all (or even waste-basket) taxon. We opine that such treatment makes taxonomy of fossil shrimps unnecessarily confusing. We consider the placement of *A. crassipes* to either, *Aeger* and *Antrimpos*, as untenable, but simultaneously we do not find sufficient taxonomic characters in the studied material to classify it within any known (fossil or extant) genus.

We refrain from keeping the species in the open nomenclature, both in "*Aeger*" or "*Antrimpos*", because we are concerned that such an approach would remove the systematic uncertainty from the formal taxonomic nomenclature. This has been done previously, when Müller (1984) treated a number of fossil decapod crustacean taxa in open nomenclature; nevertheless, these taxa appeared as valid representatives of respective genera in various lists without further explanation (Schweitzer *et al.* 2010; Hyžný *et al.* 2014). Therefore, we treat the species of Bronn (1858) as a representative of an undetermined genus (Genus?)

Förster (1967: p. 172) noted the extraordinary length of antennulae in *A. crassipes* as compared with Jurassic representatives of *Antrimpos*. However, at least the material studied herein contradicts this observation, as the antennulae are rather short, whereas long

◀ Fig. 2. *Aeger crassipes* Bronn, 1858. A near complete individual from Cave del Predil (Raibl) deposited as GBA 1930/002/0001. **A**: Scanned copy of the original figure of Glaessner (1930: pl. 6, fig. 1). **B**: Unwhitened specimen under angled light. **C**: Specimen whitened with ammonium chloride sublimate. Scale bars equal 10 mm.

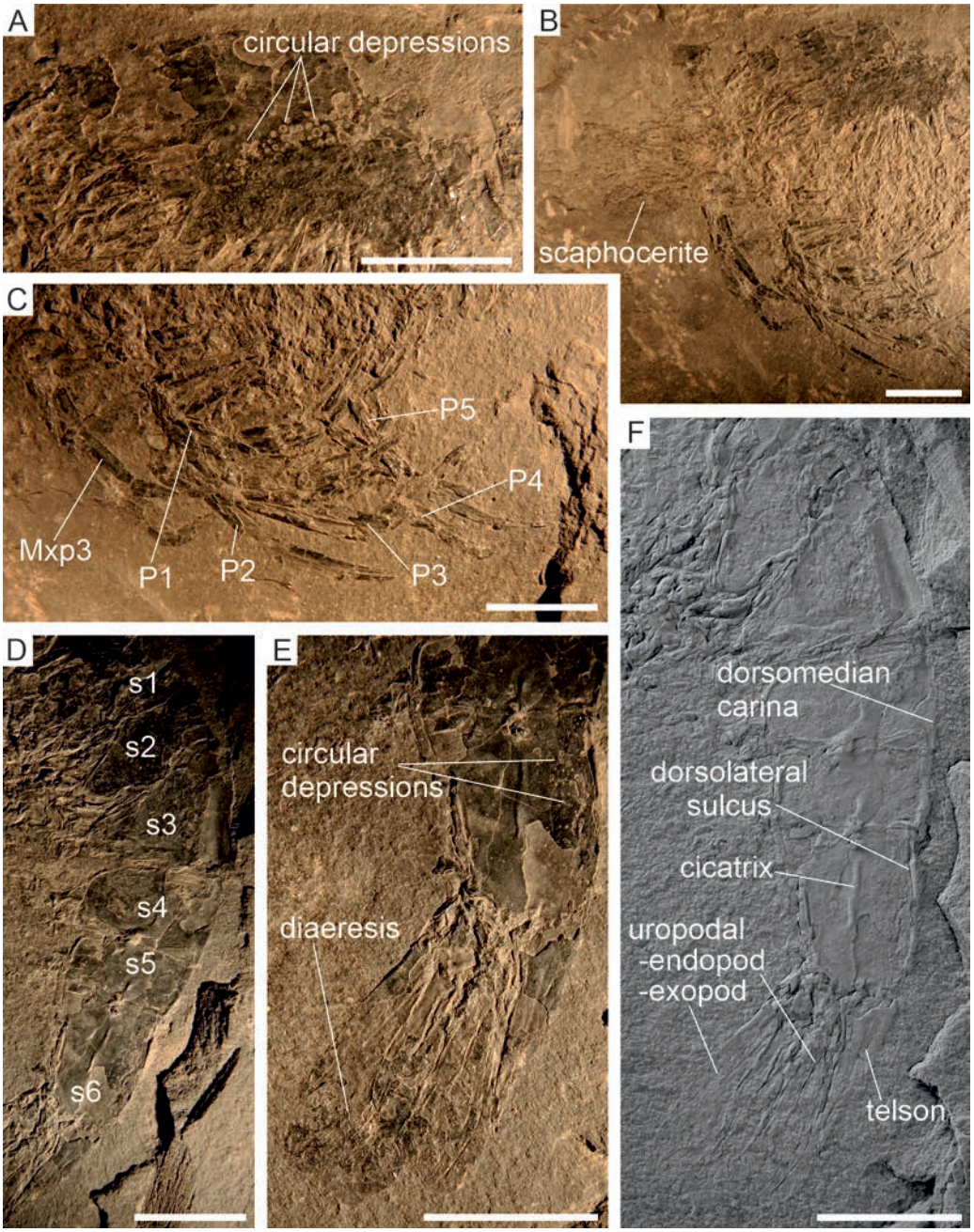


Fig. 3. *Aeger crassipes* Bronn, 1858. Detailed views on respective parts of a near complete individual from Cave del Predil (Raibl) deposited as GBA 1930/002/0001. **A**: Carapace with circular depressions. **B**: Scaphocerite. **C**: Thoracopods. **D**: Pleonal somites. **E**: Last pleonal segment and telson with uropods. **F**: Pleon with tailfan (whitened with ammonium chloride sublimate). Scale bars equal 10 mm.

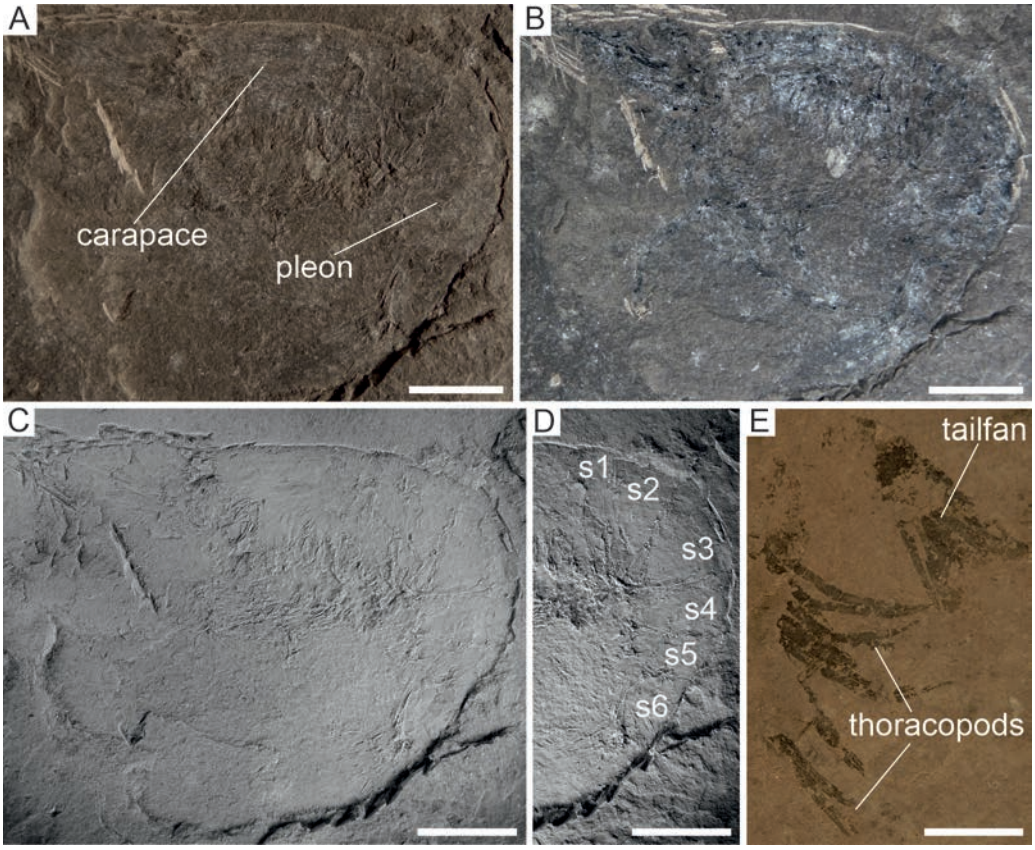


Fig. 4. *Aeger crassipes* Bronn, 1858. **A–D**: Near-entire individual in lateral aspect from Raibl (NHMW 1866/0040/0453), unwhitened under normal light (**A**), under polarized light (**B**) and whitened with ammonium chloride sublimate (**C, D**). **E**: Individual without carapace and pleon from Raibl (NHMW 1887/0009/0106). Scale bars equal 10 mm.

flagella are present in antennae. Long antennulae are in general suggestive of juvenile stages; these, however, are not always present in the studied material and the role of heterochrony cannot be completely ruled out (*e. g.*, Haug & Haug 2013, 2016). Together with apparently adult specimens of Genus? *crassipes* (Figs 2–4), also much smaller shrimps were found. These were described as *Bombur aonis* by Bronn (1858) and Förster (1967: p. 172) suggested they actually represent the juveniles of *A. crassipes*. Future research should include a detailed revision of all the shrimps from the respective localities with *A. crassipes* and *B. aonis* taking into account potential ontogenetic changes.

Remarks on taphonomy

In numerous, mostly comparatively small, individuals of Genus? *crassipes* (Figs 1A, 1C, 4E), the carapace and pleon is not preserved, whereas only a lump of pereiopods is visible on the bedding plane. This type of preservation is suggestive of being remains of

(fish?) predation or eating exuviae. A similar preservation was reported, for example in *Antrimpos undenarius* Schweigert, 2001 and *Blaculla nikoides* Münster, 1839 from the Kimmeridgian of Nusplingen (Schweigert 2001a: p. 9, text-fig. 4) and the lower Tithonian of Eichstätt (Schweigert *et al.* 2016: pl. 13, fig. 6), respectively.

Glaessner (1930) noted that the "lateral surfaces" (branchiostegites) of the carapace of *A. crassipes* are covered with fine pinhole-like depressions (Fig. 3A). Similar circular depressions were reported and figured by Schweigert (2001a: p. 9, pl. 8, fig. 3) in fragmentary remains of *Antrimpos* sp. from the Nusplingen Lithographic Limestone. Schweigert (2001a) interpreted them as being caused by nematodes or digestion in the guts of fish or reptiles. In the Raibl material, however, the circular depressions are present on the carapace and pleon of a large, near-complete individual (Figs 3A, 3E); hence, this particular specimen does not represent remains of the digestive process of any animal. More comparative material is needed for further speculation on the nature of the circular depressions. At present it can only be stated that they are unlike any known holes caused by predation on decapods reported thus far (Klompmaker *et al.* 2013).

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References

Allison, P.A. (1988): The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. – Paleobiology, **14**: 139–154.

Audo, D. (2016): *Tonneleryon*, a new gregarious polychelidan lobster from the early Toarcian Posidonia Shale of Holzmaden (Germany). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **280**: 285–298.

Audo, D., Hyžný, M. & Charbonnier, S. (2018): The early polychelidan lobster *Tetrachela raiblana* and its impact on the homology of carapace grooves in decapod crustaceans. – Contributions to Zoology, **87**: 41–57.

Balss, H. (1922): Studien an fossilen Decapoden. I. – Paläontologische Zeitschrift, **5**: 123–147.

Bate, C.S. (1888): Report on the Crustacea Macrura collected by the H.M.S. Challenger during the years 1873–76. – Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, **24**: 1–942.

Beurlen, K. (1930): Nachträge zur Decapodenfauna des schwäbischen Jura. I. Neue Decapodenfunde aus dem Posidonienschiefer von Holzmaden. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände, **B64**: 219–234.

Bosellini, A., Gianolla, P. & Stefani, M. (2003): The Triassic platforms of the Dolomites (Northern Italy): their evolution and stratigraphic framework. – Memorie di Scienze Geologiche, **54**: 111–114.

Boué, A. (1835): Aperçu sur la constitution géologique des provinces Illyriennes. – Mémoires de la Société Géologique de France, **2**: 43–89.

Brandt, S. & Schulz, M. (2013): Zwei neue natante Dekapoden aus dem Oberen Muschelkalk (Mittel-Trias, Ladin) des Germanischen Beckens – *Antrimpos germanicus* n. sp. und *Parapalaemonetes thuringiacus* n. gen., n. sp. – Vernate, **32**: 67–95.

Bravi, S., Garassino, A., Bartiromo, A., Audo, D., Charbonnier, S., Schweigert, G., Thévenard, F. & Longobardi, C. (2014): Middle Jurassic Monte Fallano Plattenkalk (Campania, sourthern Italy): first report on terrestrial plants, decapod crustaceans and fishes. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **272**: 79–107.

Bronn, H.G. (1858): Beiträge zur triasischen Fauna und Flora der bituminösen Schiefer von Raibl. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefacten-Kunde, **1858**: 1–32.

Butler, A.D., Cunningham, J.A., Budd, G.E. & Donoghue, P.C.J. (2015): Experimental taphonomy of *Artemia* reveals the role of endogenous microbes in mediating decay and fossilization. – Proceedings of the Royal Society B, **282**: 20150476.

Charbonnier, S. & Garassino, A. (2012): The marine arthropods from the Solnhofen Lithographic Limestones (Late Jurassic) in the collections of the Muséum national d'Histoire naturelle, Paris. – Geodiversitas, **34**: 857–871.

Charbonnier, S., Audo, D., Garassino, A. & Hyžný, M. (2017): Fossil Crustacea of Lebanon. – Mémoires du Muséum national d'Histoire naturelle, **210**: 1–252.

Cooper, C.L. (1935): Ammonium chloride sublimate apparatus. – Journal of Paleontology, **9**: 357–359.

De Grave, S. & Fransen, C.H.J.M. (2011): Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). – Zoologische Mededelingen, Leiden, **89**/5: 195–589.

De Zanche, V., Gianolla, P. & Roghi, G. (2000): Carnian stratigraphy in the Raibl/Cave del Predil area (Julian Alps, Italy). – Eclogae geologicae Helvetiae, **93**: 331–347.

Etter, W. (1994): A new penaeid shrimp (*Antrimpos mirigiolensis* n.sp., Crustacea, Decapoda) from the Middle Triassic of the Monte San Giorgio (Ticino, Switzerland). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1994**/4: 223–230.

Fabricius, J.C. (1798): Supplementum Entomologiae Systematicae. – 572 pp., Hafniae (Proft et Storch).

Feldmann, R.M., Schweitzer, C.E., Hu, S., Zhang, Q., Zhou, Ch., Xie, T., Huang, J. & Wen, W. (2012): Macrurous Decapoda from the Luoping biota (Middle Triassic) of China. – Journal of Paleontology, **86**: 425–441.

Forchielli, A. & Pervesler, P. (2013): Phosphatic cuticle in thylacocephalans: a taphonomic case study of *Austriocaris* (Arthropoda, Thylacocephala) from the Fossil-Lagerstätte Polzberg (Reingraben shales, Carnian, Upper Triassic, Lower Austria). – Austrian Journal of Earth Sciences, **106**: 46–61.

Förster, R. (1967): Zur Kenntnis natanter Jura-Dekapoden. – Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie, **7**: 157–174.

Garassino, A. (1990): The genus *Aeger* Münster, 1839 in the Sinemurian of Osteno in Lombardy (Crustacea, Decapoda). – Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano, **131**/5: 105–136.

Garassino, A. & Schweigert, G. (2006): The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions. Part I. Infraorders Astacidea, Thalassinidea, and Palinura. – Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano, **34**/1: 1–64.

Garassino, A. & Teruzzi, G. (1993): A new decapod crustacean assemblage from the Upper Triassic of Lombardy (Italy). – Paleontologia Lombarda, nuova serie, **1**: 3–27.

Garassino, A., Schweigert, G. & Muscio, G. (2014): *Acanthochirana triasica* n. sp. and *Antrimpos colettoi* n. sp. (Decapoda: Aegeridae, Penaeidae) from the Upper Triassic (Norian) of northern Carnic Pre-Alps (Udine, northeastern Italy). – Gortania, **35**: 11–18.

Garassino, A., Teruzzi, G. & Dalla Vecchia, F.M. (1996): The macruran decapod crustaceans of Dolomia di Forni (Norian, Upper Triassic) of Carnia (Udine, N. Italy). – Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano, **136**/1: 15–60.

Garassino, A., Vega, F.J., Calvillo-Canadell, L., Cevallos-Ferriz, S.R.S. & Coutiño, M.A. (2013): New decapod crustacean assemblage from the Upper Cretaceous (Cenomanian) of Chiapas, Mexico. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **269**: 261–270.

Glaessner, M.F. (1929): Crustacea Decapoda. – In: Pompeckj, F.J. (ed.): Fossilium catalogus, 1: Animalium, 41. – 464 pp., Berlin (W. Junk).

Glaessner, M.F. (1930): Dekapodenstudien. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, **63**: 137–173.

Glaessner, M.F. (1931): Eine Crustaceenfauna aus den Lunzer Schichten Niederösterreichs. – Jahrbuch der k. k. Geologischen Bundesanstalt Wien, **81**: 467–486.

Glaessner, M.F. (1965): Vorkommen fossiler Dekapoden (Crustacea) in Fisch-Schiefern. – Senckenbergiana Lethaea, **46a**: 111–122.

Glaessner, M.F. (1969): Decapoda. – In: Moore, R.C. (ed.): Treatise on invertebrate paleontology, Part R. Arthropoda 4 (2). – R399–R533, Lawrence (Geological Society of America, Boulder, and University of Kansas Press).

Griffith J. (1977): The Upper Triassic fishes from Polzberg bei Lunz, Austria. – Zoological Journal of the Linnean Society, **60**: 1–93.

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.

Haug, J.T. & Haug, C. (2016): "Intermetamorphic" developmental stages in 150 million-year-old achelatan lobsters – The case of the species *tenera* Oppel, 1862. – Arthropod Structure & Development, **45**: 108–121.

Hopkin, E.K. & McRoberts, C.A. (2005): A new Middle Triassic flat clam (Pterioida: Halobiidae) from the middle Anisian of North-Central Nevada, USA. – Journal of Paleontology, **79**: 796–800.

Hornung, T. & Brandner, R. (2005): Biochronostratigraphy of the Reingraben Turnover (Hallstatt facies belt): Local black shale events controlled by regional tectonism, climatic change and plate tectonics. – Facies, **51**: 460–479.

Hornung, T., Brandner, R., Krystyn, L., Joachimski, M.M. & Keim, L. (2007): Multistratigraphic constraints on the NW Tethyan 'Carnian Crisis'. – In: Lucas, S.G. & Spielmann, J.A. (eds): The Global Triassic. – New Mexico Museum of Natural History Bulletin, **41**: 59–67.

Hu, S., Zhang, Q., Chen, Z.-Q., Zhou, C., Lü, T., Xie, T., Wen, W., Huang, J. & Bengtson, M.J. (2011): The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. – Proceedings of the Royal Society B, **278**: 2274–2282.

Hyžný, M. & Zorn, I. (2016): A Catalogue of the Type and figured Fossil Decapod Crustaceans in the Collections of the Geological Survey of Austria in Vienna. – Jahrbuch der Geologischen Bundesanstalt, **156**: 127–177.

Hyžný, M., Van Bakel, B.W.M. & Guinot, D. (2014): *Etisus evamuellerae*, a new xanthid crab (Decapoda, Brachyura) from the Middle Miocene of Austria and Hungary. – In: Fraaije, R.H.B., Hyžný, M., Jagt, J.W.M., Krobicki, M. & Van Bakel, B.W.M. (eds): Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. – Scripta Geologica, **147**: 221–231.

Jerz, H. (1966): Untersuchungen über Stoffbestand, Bildungsbedingungen und Paläogeographie der Raibler Schichten zwischen Lech und Inn (Nördliche Kalkalpen). – Geologica Bavaria, **56**: 3–102.

Keim, L., Brander, R., Krystyn, L. & Mette, W. (2001): Termination of carbonate slope progradation: an example from the Carnian of the Dolomites, Northern Italy. – Sedimentary Geology, **143**: 303–323.

Klompmaker, A.A., Karasawa, H., Portell, R.W., Fraaije, R.H.B. & Ando, Y. (2013): An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. – Palaios, **28**: 599–613.

Klompmaker, A.A., Portell, R.W. & Frick, M.G. (2017): Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. – Palaeontology, **60**: 773–794.

Krainer, K., Lucas, S.G. & Strasser, M. (2011): Vertebrate Fossils from the Northalpine Raibl Beds, western Northern Calcareous Alps, Tyrol (Austria). – Austrian Journal of Earth Sciences, **104**: 97–106.

Latreille, P.A. (1802): Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite aux Œuvres de leclerc de Buffon, et partie du Cours complet d'Histoire naturelle rédigé par C.S. Sonnini, membre de plusieurs Sociétés savantes. Paris, Dufart, **5**: 1–407, **6**: 1–391.

Ma, K.Y., Chan, T.-Y. & Chu, K.H. (2009): Phylogeny of penaeoid shrimps (Decapoda: Penaeoidea) inferred from nuclear protein-coding genes. – Molecular Phylogenetics and Evolution, **53**: 45–55.

McRoberts, C.A. (2001): Paleobiology of the Triassic "Flat Clam" *Halobia* in oxygen-deficient marine facies. – Geological Society of America, Abstracts with Programs, **33**/2: A-8.

Müller, P. (1984): Decapod Crustacea of the Badenian. – Geologica Hungarica, Series Palaeontologica, **42**: 3–317.

Müller, P. (1998): Crustacea Decapoda. – In: Flügel, H.W. (ed.): Catalogus Fossilium Austriae. – 48 pp., Wien (Verlag der Österreichischen Akademie der Wissenschaften).

Münster, G. von (1839): Decapoda Macroura. Abbildung und Beschreibung der fossilen langschwänzigen Krebse in den Kalkschiefern von Bayern. – Beiträge zur Petrefaktenkunde, **2**: 1–88.

Oppel, A. (1862): Ueber jurassische Crustaceen. – Palaeontologische Mittheilungen aus dem Museum des koeniglich Bayerischen Staates, **1**: 1–120.

Pérez Farfante, I. & Kensley, B.F. (1997): Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera. – Mémoires du Muséum national d'Histoire naturelle, **175**: 1–233.

Pinna, G. (1974): I crostacei della fauna triassica di Cene in Val Seriana (Bergamo). – Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano, **21**/1: 5–34.

Plotnick, R.E. (1986): Taphonomy of a modern shrimp: Implications for the arthropod fossil record. – Palaios, **1**: 286–293.

Pott, C., Kerp, H. & Krings, M. (2007): *Pseudoctenis cornelii* nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria. – Annalen des Naturhistorischen Museums in Wien, Serie A, **109**: 1–17.

Rafinesque, C.S. (1915): Analyse de la nature ou tableau de l'univers et des corps organisés. – 224 p., Palermo (C.S. Rafinesque).

Rettori, R., Loriga, C. & Neri, C. (1998): Lower Carnian foraminifers from the type locality of the Calcare del Predill (Raibl group, northeastern Italy). – Rivista Italiana di Paleontologia e Stratigrafia, **104**: 369–380.

Rigo, M., Preto, N., Roghi, G., Tateo, F. & Mietto, P. (2007): A rise in the Carbonate Compensation Depth of western Tethys in the Carnian (Late Triassic): Deep-water evidence for the Carnian Pluvial Event. – Palaeogeography, Palaeoclimatology, Palaeoecology, **246**: 188–205.

Schweigert, G. (2001a): Eine neue Art der Gattung *Antrimpos* Münster (Crustacea, Decapoda, Penaeidae) aus dem Oberjura Süddeutschlands. – Stuttgarter Beiträge zur Naturkunde, Serie B, **307**: 1–33.

Schweigert, G. (2001b): The late Jurassic decapod species *Aeger tipularius* (Schlotheim, 1822) (Crustacea: Decapoda: Aegeridae). – Stuttgarter Beiträge zur Naturkunde, Serie B, **309**: 1–10.

Schweigert, G. (2011): The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: A historical review and some recent discoveries. – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **260**: 131–140.

Schweigert, G., Garassino, A., Hall, R.L., Hauff, R.B. & Karasawa, H. (2003): The lobster genus *Uncina* Quenstedt, 1851 (Crustacea: Decapoda: Astacidea: Uncinidae) from the Lower Jurassic. – Stuttgarter Beiträge zur Naturkunde, Serie B, **332**: 1–43.

Schweigert, G., Garassino, A. & Pasini, G. (2016): The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions. Part II. Superfamily Penaeoidea and Infraorder Caridea. – Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano, **41**: 1–40.

Schweitzer, C.E. (2003): Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura). – Journal of Paleontology, **77**: 1107–1128.

Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H. & Schweigert, G. (2010): Systematic list of fossil decapod crustacean species. – Crustaceana Monographs, **10**: 1–222.

Schweitzer, C.E., Feldmann, R.M., Hu, S., Huang, J., Zhou, Ch., Zhang, Q., Wen, W. & Xie, T. (2014): Penaeoid Decapoda (Debdrobranchiata) from the Luoping biota (Middle Triassic) of China: systematics and taphonomic framework. – Journal of Paleontology, **88**: 457–474.

SUESS, E. (1867): Raibl. – In: SUESS, E. & MOJSISOVICS, E. (eds): Studien über die Gliederung der Trias- und Jurabildungen in den östlichen Alpen. – Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt, **17**: 554–574.

TAVARES, C. & MARTIN, J.W. (2010): Suborder Dendrobranchiata Bate, 1888. – In: SCHRAM, F.R., VAUPEL KLEIN, J.C. VON, CHARMANTIER-DAURES, M. & FOREST, J. (eds): Treatise on Zoology – Anatomy, Taxonomy, Biology. (The Crustacea, Decapoda, Vol. 9A). – pp. 109–219, Leiden (Brill).

TAVARES, C., SEREJO, C. & MARTIN, J.W. (2009): A preliminary phylogenetic analysis of the Dendrobranchiata based on morphological characters. – In: MARTIN, J.W., CRANDALL, K.A. & FELDER, D.L. (eds): Decapod Crustacean Phylogenetics. – pp. 261–279, Boca Raton, London, New York (CRC Press, Taylor & Francis Group).

TEICHERT, C. (1948): A simple device for coating fossils with ammonium chloride. – Journal of Paleontology, **22**: 102–104.

TOLLMANN, A. (1976): Analyse des klassischen nordalpinen Mesozoikums. Stratigraphie, Fauna und Fazies der Nördlichen Kalkalpen. – 580 pp., Wien (Franz Deuticke).

WÖHRMANN, S. (1893): Die Raiblerschichten nebst kritischer Zusammenstellung ihrer Fauna. – Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt, **1893**: 617–768.