



Revision of *Jaxea kuemeli* BACHMAYER, 1954 (Decapoda: Gebiidea: Laomediidae) from the Miocene of Europe, with remarks on the palaeobiogeography of the genus *Jaxea* NARDO, 1847

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With 7 figures and 2 tables

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Abstract: The present contribution reevaluates the fossil record of the genus *Jaxea* (Decapoda: Gebiidea: Laomediidae) and gives an emended diagnosis and an updated description of *Jaxea kuemeli* based on well preserved material from the lower and middle Miocene strata of Austria, Slovakia and Hungary. The species is distinguished from the extant *J. nocturna* on the basis of the tooth formula of the chelipeds. The geographic distribution and the palaeobiogeography of the genus is discussed and migration from the Tethys eastward towards the present-day Indo-Pacific Ocean during the Miocene time is proposed. The fossil record of the family Laomediidae is shortly reviewed. The monotypical genus *Reschia* from the Tithonian of southern Germany once tentatively assigned to Laomediidae is excluded from the family.

Key words: Decapoda, Laomediidae, *Jaxea*, Miocene, palaeobiogeography.

1. Introduction

A recent study of the type material of *Jaxea kuemeli* BACHMAYER, 1954 from the middle Miocene of the Vienna Basin, plus additional specimens from several localities in Austria, Slovakia and Hungary (Fig. 1) permits a refinement of the original description and an emendation of the diagnosis of the species. Up to now, the only material assigned to *J. kuemeli* were the rather poorly preserved types (Fig. 2), which explains why doubts were occasionally expressed as to the validity of this taxon (MÜLLER 1993, 1998). According to BACHMAYER (1954), *J. kuemeli* is extremely close to *J. nocturna* NARDO, 1847, the differences involving the smaller size of the former, the slightly more slender shape of the carapace and the more posteriorly

oriented cervical groove. However, a re-examination of the type material has now revealed that what was described as a complete dorsal carapace is only a fragment lacking the posterior portion. As a consequence, the position of the cervical groove only appeared to be more posterior from the midpoint of the carapace (exclusive of rostrum). However, it actually is more or less identical with that of the two extant species *J. nocturna* and *J. novaezealandiae* WEAR & YALDWIN, 1966. *Jaxea kuemeli* is here considered as a distinct species distinguishable from its congeners on the basis of the tooth formula of the chelipeds.

All Miocene occurrences of *Jaxea* have been re-examined and screened by the author.

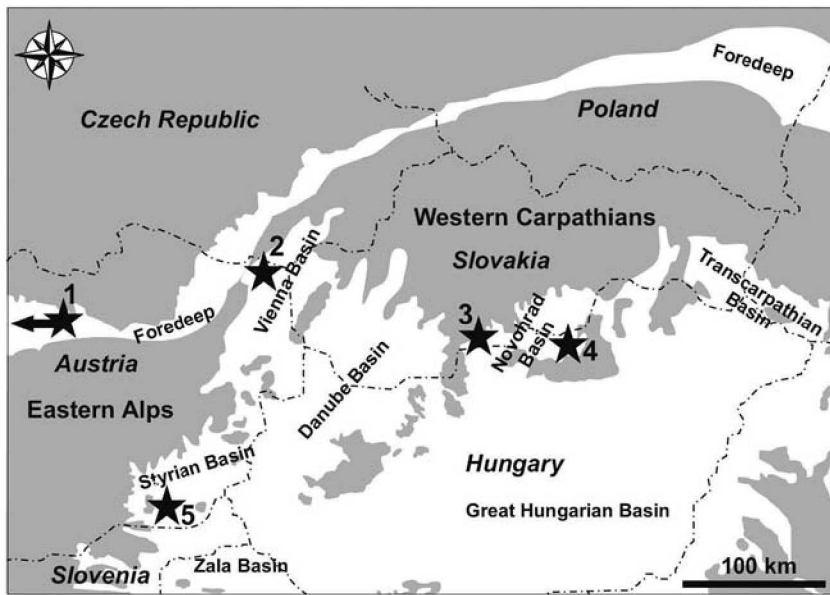


Fig. 1. Studied area of the Carpathian-Pannonian Basin complex of the Central Paratethys (modified from HARZHAUSER et al. 2003). Pre-Neogene sediments and basement are shaded in grey. Studied localities: 1 – Pramhof and Ottwang (“Ottngian”), 2 – borehole Hohenruppersdorf 23 near Martinsdorf (middle-late “Badenian”), 3 – Plášťovce (lower “Badenian”), 4 – boreholes Alsószuha 1 and Mátraalmás T-4 (“Karpatian”), 5 – Retznei (lower “Badenian”).

2. The family Laomediidae Borradaile, 1903 in the fossil record

This family currently comprises five genera (DE GRAVE et al. 2009), namely *Espeleonaushonia* JUARRERO & MARTÍNEZ-IGLESIAS in JUARRERO et al., 1997; *Jaxea* NARDO, 1847; *Laomedia* DE HAAN, 1847; *Laurentiella* LE LOEUFF & INTÈS, 1974 and *Naushonia* KINGSLEY, 1897. The fossil record of the family is very patchy and up to now only three, exclusively fossil, species have been confidently assigned to the family. These are *Jaxea kuemeli*, *Laomedia praeastacina* KA-

RASAWA, 1989 and *Laurentiella imaizumii* KARASAWA, 1993, all known from Miocene strata (Table 1).

The genus *Axianassa* SCHMITT, 1924, once considered to be a laomediid, has recently been removed from the family and accommodated in a family of its own, the Axianassidae SCHMITT, 1924 (DE GRAVE et al. 2009).

Lately, another monotypical genus, *Reschia* SCHWEIGERT, 2009, was described from the lower Tithonian Solnhofen Lithographic Limestones in southern Germany, on the basis of a single, rather poorly preserved specimen, tentatively assigned to the Laomediidae (SCHWEIGERT 2009). However, in that genus at least the first two pairs of pereopods are chelate, which conflicts with the diagnosis of the family Laomediidae, whose members never possess a chelate second pair of pereopods (WEAR & YALDWYN 1966: 3; YALDWYN & WEAR 1972: 127; POORE 1994: 103). Moreover, a *linea thalassinica* is not visible (SCHWEIGERT pers. comm., June 2010) in the type of *Reschia barbarae* SCHWEIGERT, 2009 and the shape of the reconstructed cervical groove (SCHWEIGERT 2009: fig. 7b) is unlike that of any known laomediid. Thus, *Reschia* is herein excluded from the family Laomediidae.

Table 1. Occurrences of the family Laomediidae in the fossil record:

<i>Jaxea nocturna</i>	early Pliocene	Italy, Spain
<i>Jaxea kuemeli</i>	early-middle Miocene	Austria, Slovakia, Hungary
<i>Laomedia praeastacina</i>	early-middle Miocene	Japan
<i>Laurentiella imaizumii</i>	early-middle Miocene	Japan

Note. – NGOC-HO (2003) considered the material of *Jaxea* cf. *nocturna* described by DELLE CAVE (1988) and MÜLLER (1993) to be conspecific with extant *Jaxea nocturna*. I concur.

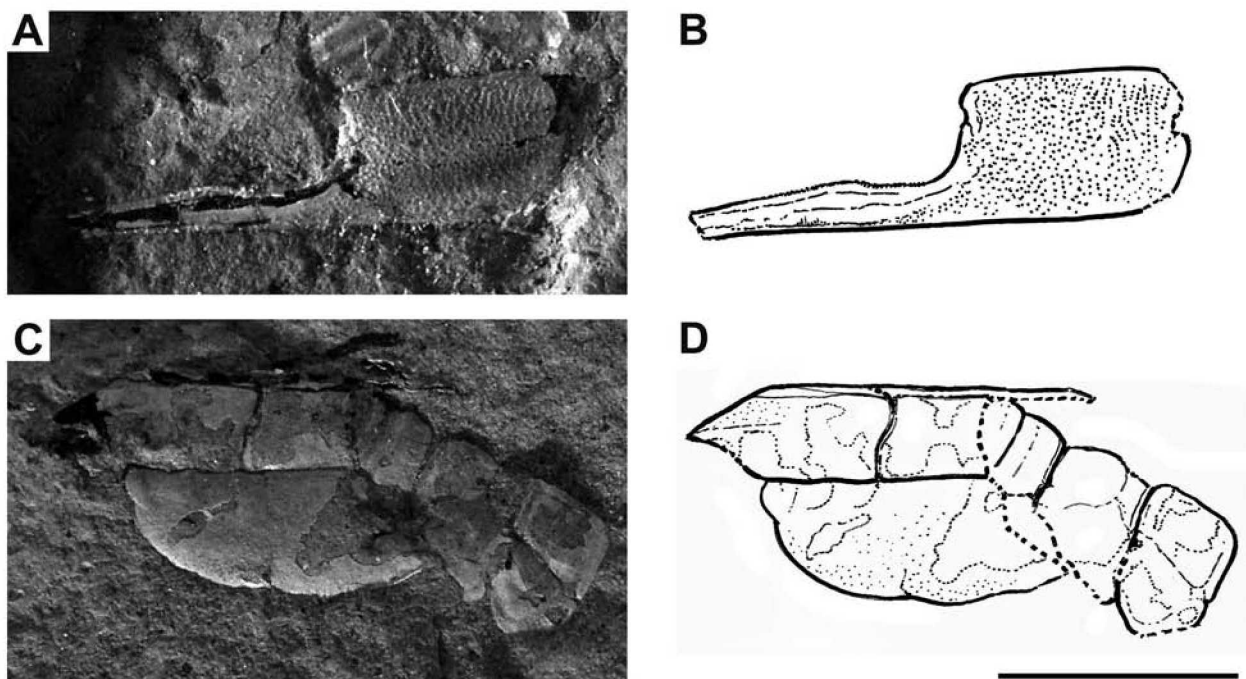


Fig. 2. Type material of *Jaxea kuemeli* BACHMAYER, 1954. **A, B** – Isolated left propodus (paratype – NHMW 2006z0422/0002) and its interpretive drawing. **C, D** – Broken cephalothorax with three abdominal segments (holotype – NHMW 2006z0422/0001) and its interpretive drawing. Scale bar for all figures = 5 mm.

3. The genus *Jaxea* in the fossil record

For recognition of *Jaxea* in the fossil record the typical cheliped shape usually suffices.

The only known exclusively fossil species of *Jaxea* was described as *J. kuemeli* by BACHMAYER (1954), on the basis of two specimens (Fig. 2). This material originates from borehole Hohenrappersdorf 23 in Lower Austria and represents the only fossil remains of *Jaxea* from the Vienna Basin.

Other published occurrences of fossil *Jaxea* include reports from the Miocene of Spain (MÜLLER 1993) and northern Hungary (MÜLLER 1993: 5), and the Pliocene of Spain (MAYORAL et al. 1998; GARASSINO et al. 2009) and Italy (DELLE CAVE 1988). For a short review of these occurrences, reference is made to GARASSINO et al. (2009).

DELLE CAVE (1988) reported thirty fragmented adult specimens from the lower Pliocene of Tuscany (Italy) referred to as *Jaxea* cf. *nocturna* and pointed out it was not possible to differentiate them from extant *J. nocturna*. Later, NGOC-HO (2003) considered that material to be conspecific with that species. I concur with this opinion. According to MÜLLER (1993), the same

could be said of *J. kuemeli*. SCHWEITZER et al. (2010) listed *Jaxea kuemeli* as a separate species.

The present contribution adds several occurrences of *J. kuemeli* from the Miocene of Austria and Slovakia and introduces in detail for the first time fossil material from Hungary, which was until now only briefly mentioned in the literature (MÜLLER 1993: 5; GARASSINO et al. 2009: 74).

4. Systematic palaeontology

Institutional abbreviations: The repositories of specimens illustrated or referred to below are as follows: NHMW – Naturhistorisches Museum, Wien (Austria); SNM-Z – Prírodovedné múzeum SNM, Bratislava (Slovakia); M – Hungarian Natural History Museum, Budapest (Hungary); GW – Gerhard Wanzenböck Collection, Bad Vöslau (Austria).

Infraorder Gebiidea DE SAINT LAURENT, 1979
Family Laomedidiidae BORRADAILE, 1903

Genus *Jaxea* NARDO, 1847

Type species: *Jaxea nocturna* NARDO, 1847, by original designation.

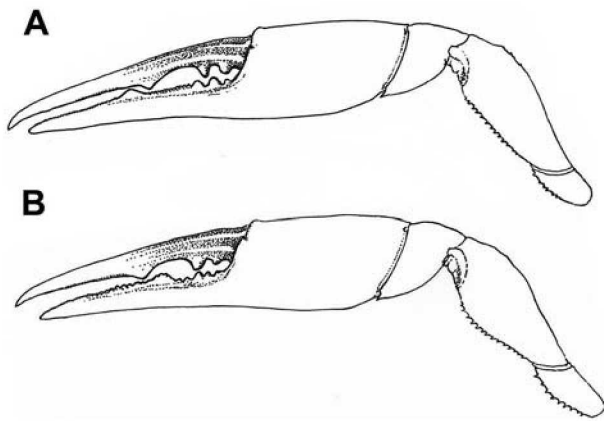


Fig. 3. Chelipeds of *Jaxea nocturna* NARDO, 1847 and *Jaxea kuemeli* BACHMAYER, 1954. **A** – *J. nocturna*. **B** – *J. kuemeli*. Note the position of large median tooth on pollex.

Diagnosis: See NGOC-HO (2003: 501).

Remarks: Currently, the genus *Jaxea* is represented by just two species, *J. nocturna* and *J. novaezealandiae*. However, there are several reports of specifically distinct, yet unnamed species of the same genus known only as larvae. DAKIN & COLEFAX (1940) and WEAR & YALDWYN (1966) recorded four types of such larvae from New Zealand and Australian coastal waters. KURIAN (1956) and THIRIOT (1976) reported on another larva which was specifically distinct from *J. nocturna* from Banyuls, southern France and the Adriatic.

Morphology of chelipeds: Chelae are usually quite variable in many decapod crustaceans. However, it seems that in members of the Laomedidae cheliped shape is relatively constant. On the basis of results presented here, this is particularly true for the genus *Jaxea* and its species. *Jaxea nocturna* is a well-known species and a superficial scan of figures in the literature (RAWLINSON 1938: pl. 2, fig. 1; BOUVIER 1940: fig. 66C; ZARIQUIEY ALVAREZ 1968: fig. 94b; PERVESLER & DWORSCHAK 1985: pl. 1, fig. 1; NGOC-HO 2003: fig. 22D) shows a markedly constant tooth formula and general cheliped shape. This conclusion is also supported by a comparison with an extant male specimen of *J. nocturna* from Rovinj (NHMW 298). The cutting edge of the pollex has three or four large, rounded teeth positioned proximally followed by several smaller teeth, a large triangular median tooth and small round teeth in the distal half (Fig. 3A). The same pattern is seen in fossil specimens of *Jaxea* which are attributable to the extant *J. nocturna* (DELLE CAVE 1988: pl. 2, figs. 1, 2a; GARASSINO et al. 2009: figs. 3, 5-6; MAYORAL et al. 1998: fig. 2.2).

On the other hand *J. kuemeli* exhibits a slightly different tooth formula (Fig. 3B; see below). To support the notion of species distinction within the genus *Jaxea* on the basis of

chelipeds it should be noted that the other extant species, *J. novaezealandiae*, can be distinguished from *J. nocturna* on various features of the third maxilliped, dorsal carapace as well as the chelipeds (for more details see WEAR & YALDWYN 1966: 4). The tooth formula of *J. novaezealandiae* differs markedly from that of *J. nocturna* (compare WEAR & YALDWYN 1966: fig. 1; holotype photograph of *J. novaezealandiae* available at the Museum of New Zealand web-site <http://collections.tepapa.govt.nz/objectdetails.aspx?oid=512945>).

Jaxea kuemeli BACHMAYER, 1954

Figs. 2A-D, 3B, 5A-C, 6A-C, 7A-D

- v*1954 *Jaxea kumeli* BACHMAYER, 1954, p. 64, pl. 1, figs 1-2.
 1966 *Jaxea kuemeli* BACHMAYER. – WEAR & YALDWYN, p. 4.
 1969 *Jaxea kuemeli* BACHMAYER. – GLAESSNER, p. R477, fig. 284.4a, b.
 1984 *Jaxea kuemeli* BACHMAYER. – MÜLLER, p. 49.
 1985 *Jaxea kuemeli* BACHMAYER. – PERVESLER & DWORSCHAK, table 3.
 1988 *Jaxea kuemeli* BACHMAYER. – DELLE CAVE, p. 4.
 1993 *Jaxea kuemeli* BACHMAYER. – MÜLLER, p. 5.
 v 1993 some, yet not described, chelae. – MÜLLER, p. 5.
 1998 *Jaxea kumeli* BACHMAYER. – MAYORAL et al., p. 508.
 1998 *Jaxea kuemeli* BACHMAYER. – MÜLLER, p. 9.
 2009 *Jaxea kumeli* BACHMAYER. – GARASSINO et al., p. 74.
 v 2009 „indeterminated chelae“ – GARASSINO et al., p. 74.
 2010 *Jaxea kuemeli* BACHMAYER. – SCHWEITZER et al., p. 41.

Material examined: In total, 17 specimens of *Jaxea kuemeli* have been examined: type material from borehole Hohenruppersdorf 23 consisting of a broken cephalothorax with three abdominal segments (holotype – NHMW 2006z0422/0001) and an isolated left propodus with broken pollex (paratype – NHMW 2006z0422/0002); one cheliped (M 2010.339.1) from borehole Mátraalmás T-4; two chelipeds of the same specimen (M 2010.340.1) and a cheliped with scattered remains of dorsal carapace, branchiostegites and telson (M 2010.341.1) from borehole Alsószuha 1; seven specimens (GW RET92-002, GW RET92-003, GW RET95-004, GW RET92-005 – RET92-008) from Retznei quarry, some of which are nearly complete; two near-complete specimens (NHMW 2009z0150/0001 and NHMW 2010/0090/0001) from Ottngang, the stratotype locality of the “Ottngangian” regional stage; two chelipeds of the same specimen (NHMW 2009z0160/0001) from Pramhof; one near-complete specimen (SNM-Z 36891) and one preserving cephalothorax and chelipeds (SNM-Z 36892) from Plášťovce.

For comparative purposes, a male specimen of extant *Jaxea nocturna* (NHMW 298) was examined.

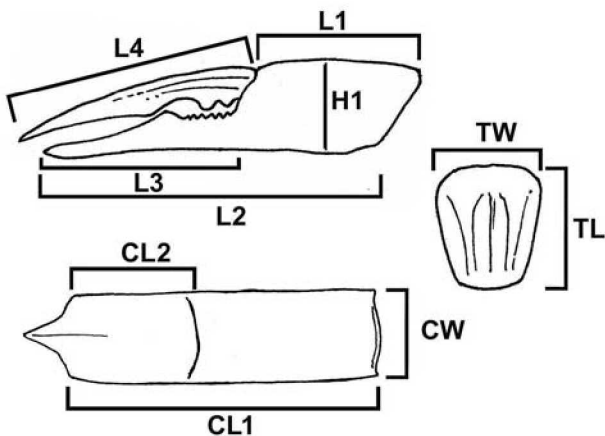
Measurements: See Table 2.

Emended diagnosis: Cylindrical carapace with triangular rostrum with denticulate lateral margins; *linea thalassinica* and cervical groove well defined, not crossing each other. Telson slightly longer than wide with median longitudinal

Table 2. Measurements (in mm) of specimens of *Jaxea kuemeli* BACHMAYER, 1954. For explanation of measured parameters see Fig. 4.

specimen	right chela					left chela					carapace			telson	
	RL1	RH1	RL2	RL3	RL4	LL1	LH1	LL2	LL3	LL4	CL1	CL2	CW	TL	TW
NHMW 2006z0422/0001	-	-	-	-	-	-	-	-	-	-	10.5*	4.7*	-	-	-
NHMW 2006z0422/0002	4.5	4.0	>10.3	>5.8	-	-	-	-	-	-	-	-	-	-	-
NHMW 2009z0150/0001	3.8	2.4	8.5	4.6	5.1	3.9	2.5	8.0	4.6	5.0	6.8	2.5	-	-	-
NHMW 2009z0160/0001	5.5	3.4	10.3	6.0	6.9	-	-	-	-	-	-	-	-	-	-
NHMW 2010/0090/0001	7.6	>3.5	>15.6	8.9	-	7.6	>3.5	>14.6	>8.5	>9.5	-	-	-	-	-
M 2010.339.1	6.4	3.7	15.6	9.0	10.5	-	-	-	-	-	-	-	-	-	-
M 2010.340.1	-	-	-	-	-	5.5	>3.0	>11.5	>6.5	7.0	-	-	-	-	-
M 2010.341.1	4.2	3.2	10.5	5.7	>6.0	-	-	-	-	-	8.2	3.6	3.0	2.8	2.5
SNM-Z-36891	-	-	-	-	-	5.3	3.4	>11.3	>6.6	8.0	8.8	3.0	3.2	3.5	2.8
SNM-Z-36892	4.6	2.4	>9.6	>5.2	6.4	4.0	3.0	9.6	5.3	>5.3	7.6	3.1	>2.3	-	-
GW RET92-002	5.5	3.6	>10.7	6.3	7.1	5.3	3.9	10.4	6.4	6.8	>6.3	3.6	2.7	>3.2	2.1
GW RET92-003	>4.8	>4.0	13.9	7.4	8.7	>5.6	5.0	>12.6	>6.7	>5.4	11.3	4.6	4.4	-	-
GW RET95-004	6.2	5.7	12.7	7.0	7.6	6.2	5.0	13.0	7.3	8.2	-	-	-	-	-
GW RET92-005	-	>2.1	10.0	6.5	7.1	-	-	-	-	-	-	-	-	-	-
GW RET92-006	6.4	5.0	>11.0	>6.3	>7.2	-	-	-	-	-	-	-	-	-	-
GW RET92-007	5.2	3.7	>9.6	>4.5	7.2	4.5	2.7	11.4	6.6	7.5					
GW RET92-008	2.8	2.3	7.3	4.1	4.5	3.0	2.1	7.6	4.4	5.2	6.5	2.7	-	>2.0	1.8

* - reconstructed value

**Fig. 4.** Measured parameters of *Jaxea kuemeli* BACHMAYER, 1954; chela (propodus + dactylus): L1 – length of manus, H1 – maximum height of manus, L2 – length of propodus with pollex, L3 – length of pollex, L4 – length of dactylus; dorsal carapace: CL1 – length of carapace (exclusive of rostrum), CL2 – length of the anterior portion of carapace (exclusive of rostrum), CW – width of carapace; and telson: TW – width of telson, TL – length of telson. For measurements see Table 2.

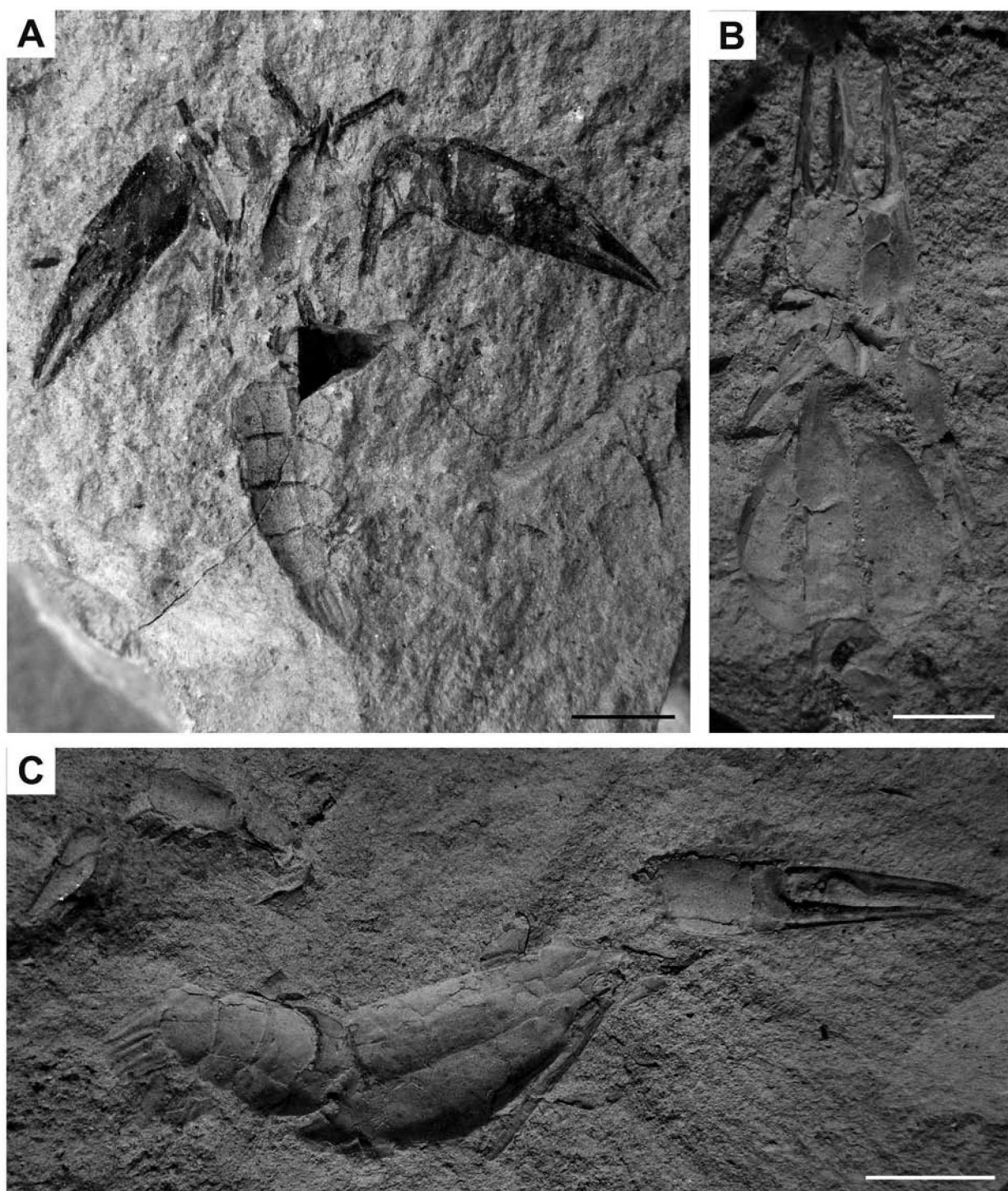


Fig. 5. *Jaxea kuemeli* BACHMAYER, 1954. **A** – Near-complete specimen, Retznei, lower „Badenian“ (GW RET92-002). **B** – Cephalothorax and chelipeds, Plášťovce, lower “Badenian” (SNM-Z 36892). **C** – Counterpart of near-complete specimen, Plášťovce, lower “Badenian” (SNM-Z 36891), whitened with ammonium chloride. Scale bar in all figures = 5 mm.

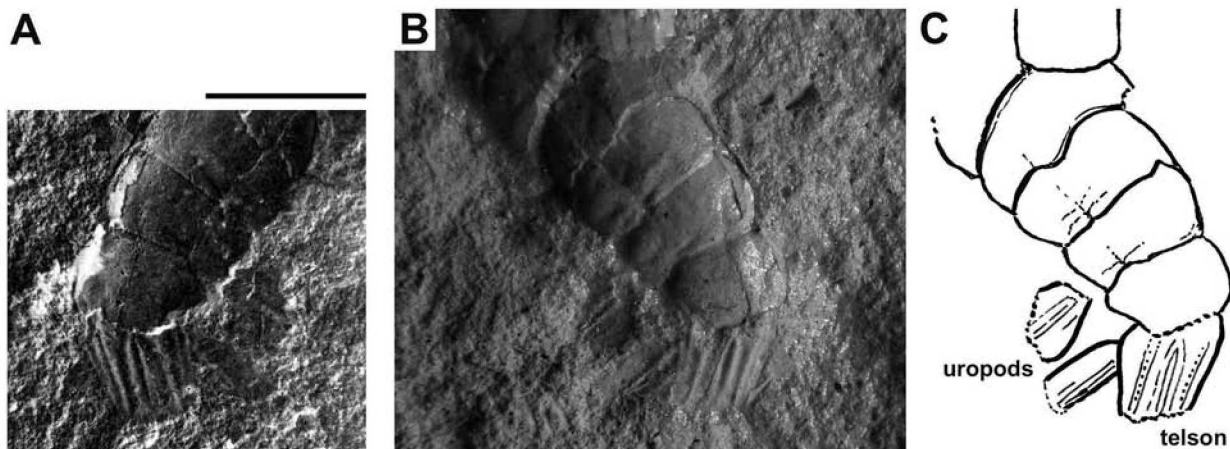


Fig. 6. *Jaxea kuemeli* BACHMAYER, 1954. A-C – Last four abdominal segments with telson and fragments of uropods, Plášťovce, lower “Badenian” (SNM-Z 36891); A: counterpart of the specimen, inverted to enhance contrast; B: part under normal light; C: interpretive drawing of B. Scale bar for all figures = 5 mm.

groove and two pairs of longitudinal ridges. First pereopods chelate, equal or subequal, well developed, approximately as long as the cephalothorax; ischium and merus with spinules on entire lower margin; carpus with small lower distal spine; propodus granulate. Pollex with three or four larger round teeth positioned proximally followed with several smaller teeth, or with several round same sized teeth; large median triangular tooth positioned more proximally, usually composed from several smaller teeth; distal half of the cutting edge with numerous small round teeth. Dactylus with two or three larger round teeth positioned proximally followed with a broad notch and large median tooth. Second to fifth pereopods simple.

Emended description: Nearly entire body covered with granules: chelipeds strongly granulated (Fig. 2A, B); dorsal carapace almost smooth, rostrum slightly granulated; branchiostegites slightly granulated, more granules on the lower half.

Carapace cylindrical (Fig. 5), terminating in a triangular rostrum, shorter than the abdomen; lateral margins of rostrum denticulate, dorsal surface of rostrum with indistinct longitudinal median groove. *Linea thalassinica* well defined, straight anteroposteriorly; cervical groove present, situated dorsally, positioned relatively anteriorly to midpoint of carapace, exclusive of rostrum.

Abdomen well developed (Fig. 6), abdominal pleurae broadly rounded with weakly concave posterolateral margins. Telson quadrate, longer than wide, posterior margin convex, dorsal surface with median longitudinal groove and two pairs of longitudinal ridges, outer bearing row of several spinules.

Antennal and antennular peduncle with elongate articles 3 and 4.

First pereopods chelate, equal or subequal (Fig. 7; one

chela usually slightly longer and more slender – see Table 2), well developed, slender and elongate, as long as carapace inclusive of rostrum, dactylus longer than pollex. Cutting edge of both fingers with teeth. Pollex with three or four larger, rounded teeth positioned proximally followed by several smaller teeth (Figs. 3B, 7B), or by several rounded, equal-sized teeth (Fig. 7A, D); large median triangular tooth positioned more proximally, usually composed of several smaller teeth (Figs. 3B, 7B); distal half of cutting edge with numerous small, rounded teeth. Dactylus with two or three larger round teeth positioned proximally followed by a broad notch and a large median tooth, the latter sometimes accompanied by a smaller one positioned in a notch distally. Manus rectangular, slightly longer than high. Carpus with lower distal hook. Merus and ischium with spinules on entire lower margin (Fig. 7C). Upper margin of merus distinctly convex distally, lower margin strongly convex.

Second to fifth pereopods simple.

Occurrence: The species has been identified in lower and middle Miocene (upper Burdigalian to Langhian) strata at several localities (Fig. 1):

1. North Alpine Foreland Basin – The localities of Pramhof and Ottmang (Upper Austria). Both expose strata of “Ottmangian” (late Burdigalian) age. For details see GRUNERT et al. (2010) and references cited therein.
2. Vienna Basin – Borehole Hohenruppersdorf 23 (depth: 160–172 m) located close to Martinsdorf near Hohenruppersdorf in Lower Austria (Vienna Basin). The age is middle to late “Badenian” (Langhian) (KROH pers. comm., July 2010).
3. Novohrad Basin (Slovak part) – The locality of Plášťovce (southern part of Slovakia). The age is early “Badenian” (Langhian). For details see SUKATCHEVA et al. (2006).
4. Novohrad Basin (Hungarian part) – Boreholes Alsószuha

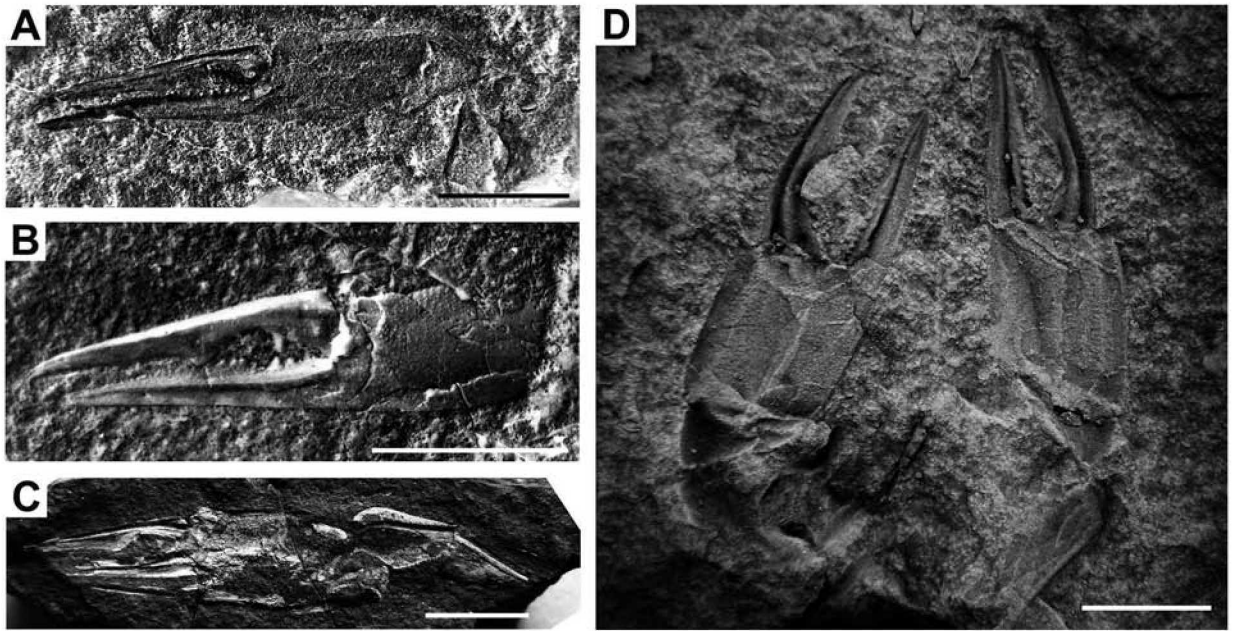


Fig. 7. Chelipeds of *Jaxeia kuemeli* BACHMAYER, 1954. **A** – Isolated cheliped, Mátraalmás T-4, “Karpatian” (M 2010.339.1), whitened with ammonium chloride and inverted to enhance contrast. **B** – Cheliped of a near-complete specimen, Plášťovce, lower “Badenian” (SNM-Z 36891), inverted to enhance contrast. **C** – Isolated chelipeds, Alsószuha 1, “Karpatian” (M 2010.340.1). **D** – Chelipeds of fragmented specimen, Retznei, lower “Badenian” (GW RET95-004), whitened with ammonium chloride. Scale bar in all figures = 5 mm.

1 (depth: 128 m – *Hinia-Turritella* Zone; 555.9–562.9 m – lower *Amussium* Zone) and Mátraalmás T-4 (depth: 20.9 m) in northern Hungary. Both penetrate strata of “Karpatian” (latest Burdigalian) age. For details see BALDI & RADÓCZ (1971).

5. Styrian Basin – Retznei quarry (Steiermark, Austria). The age is early “Badenian” (Langhian). For details see FRIEBE (1990) and GROSS et al. (2007).

At the time of deposition, all these localities were part of the Central Paratethys.

Discussion: In his description of the type material of *Jaxeia kuemeli*, BACHMAYER (1954) did not recognise that the preserved cephalothorax was incomplete (Fig. 2C, D), which led him to state that the cervical groove was oriented more posteriorly (BACHMAYER 1954: 64). This observation was repeated by WEAR & YALDWYN (1966), who noted that *J. kuemeli* was clearly different from both extant species in possessing a more posteriorly positioned cervical groove (WEAR & YALDWYN 1966: 4). This is simply not true, because, as mentioned above, the dorsal carapace of the holotype is broken. Moreover, the more complete material presented here (Fig. 5) clearly shows that the position of the cervical groove in *J. kuemeli* is more or less identical with that of both modern species. Interestingly, MÜLLER (1984, 1993, 1998) and MAYORAL et al. (1998) considered *J. kuemeli* to be possibly conspecific with *J. nocturna*, although these authors did not study the type material of the former.

It should also be stressed that the type material of *J. kuemeli* has never been re-examined since its first description.

The most obvious distinctive character (see diagnosis above) is the position of the large median tooth on the cutting edge of the pollex. In *J. kuemeli* this is located posteriorly relative to the position of the median tooth on the dactylus (Fig. 3B), while it is positioned anteriorly in *J. nocturna* (Fig. 3A). Moreover, in *J. kuemeli* it is less pronounced than in *J. nocturna*, which explains why it is sometimes not easily seen in the fossil state (Fig. 7A, D). The different morphology of the chelipeds points to the specific distinction of both species; in fact, they were already identified as such in SCHWEITZER et al. (2010). The tooth formula of *J. novaezealandiae* is easily distinguished from that of both other species. Fingers of *J. kuemeli* are generally shorter than those of *J. nocturna*; however, this character is rather variable and one specimen in the present suite of *J. kuemeli* (M 2010.339.1) exhibits particularly long fingers (Fig. 7A).

BACHMAYER (1954) also stated that the abdominal segments of *J. kuemeli* were wider than in *J. nocturna*. However, no clear difference in shape and arrangement of abdominal segments is observable in the material presented here as compared to *J. nocturna*. I interpret the BACHMAYER’s statement to be mainly an erroneous assumption of the completeness of the preserved carapace of the holotype of *J. kuemeli*, which made the animal more “bulky” and distinctly shorter than *J. nocturna*. After reconstruction the main proportions appear to be roughly the same as in *J. nocturna*.

5. Palaeoecological and palaeobiogeographical implications

Palaeoecology: AS DELLE CAVE (1988) pointed out, data for extant *Jaxea nocturna* are useful for interpreting and reconstructing the biotope of extinct members of the genus. All fossil specimens mentioned here were found in fine siliciclastic (Ottang, Pramhof, Martinsdorf, Retznei, Mátraalmás, Alsószuha) or volcanoclastic (Plášťovce) strata documenting rather muddy or fine sandy substrate which is typically inhabited by extant members of the genus (WEAR & YALDWYN 1966; NGOC-HO 2003: 505).

To date, *Jaxea* is known mainly from rather shallow-marine settings (up to 100 m depth; WEAR & YALDWYN 1966; NGOC-HO 2003), although it has been recorded from depth exceeding 400 m (DIEZ et al. 1994). In general, most specimens were collected from the depths less than 100 m.

Jaxea is a burrower. Burrow morphology of extant *J. nocturna* was described and discussed by PERVESLER & DWORSCHAK (1985), NICKELL & ATKINSON (1995) and PERVESLER & HOHENNEGER (2006). Interestingly, at Plášťovce, fossil burrow structures were observed in close proximity of remains of *J. kuemeli* fossils (pers. obs.). However, these burrows have not yet been examined in detail, and interpretation of this species as tracemaker is preliminary and rather speculative.

From several localities with *J. kuemeli* the associations of other decapod species are known. At Plášťovce (lower Badenian) the decapod association is composed of three species – *J. kuemeli*, *Tasadia carniolica* (BITTNER, 1884) and *Retropluma borealis* FRAAIJE, HANSEN & HANSEN, 2005. At the same locality, although from different horizon, wings of caddis flies were reported (SUKATCHEVA et al. 2006). During the deposition the area with the locality represented a sea shore between shoreface and offshore zones (KOVÁČ et al. 1999). The association of *T. carniolica* and *R. borealis* is known also from the upper Miocene clays of Gram, Denmark (FRAAIJE et al. 2005).

From Retznei (lower Badenian) rather different association is known – *J. kuemeli* was found in the same stratum together with *Styrioplax exiguus* (GLAESSNER, 1928). The same association is known also from Alsószuha borehole (Karpatian). Interestingly, *S. exiguus* was recently reported from rather deep-water sediments of Karpatian age (early Miocene) of the Vienna Basin (HYŽNÝ & SCHLÖGL in press).

Palaeobiogeography: DELLE CAVE (1988: 8) already pointed out that it was difficult to explain the recent

geographic distribution of the genus *Jaxea*, i.e. the Mediterranean, the eastern Atlantic and New Zealand. She hypothesised that larvae of *Jaxea* had migrated from the Pacific Ocean through the East Indies, based on views expressed by NATIONS (1975) for the crab genus *Cancer* LINNAEUS, 1758. Concerning the genus *Jaxea*, this hypothesis does not find any support in the fossil record. In fact, extinct *Jaxea* is restricted to the Miocene and Pliocene of Europe as discussed above, although the absence of material may in part be attributed to collection failure.

Recent studies on the distribution of several groups of molluscs (gastropods and bivalves) and echinoderms (ophiuroids) (HARZHAUSER et al. 2007, 2008) have suggested migratory routes of Cenozoic Tethyan marine faunas to have been eastward towards the present-day Indo-Pacific Ocean. The same has already been postulated for certain decapod groups during the Cenozoic, mainly the Miocene. FELDMANN & SCHWEITZER (2006: 93) stated that several decapod genera known either from the fossil record or from recent seas of New Zealand have their rootstock in the Tethys. Interestingly, similarities between the Miocene record of decapods of the Central Paratethys and the modern Indo-Pacific assemblages have led some authors to consider the European palaeodecapod faunas to be of Indo-Pacific origin (e.g. MÜLLER 1979, 1984). As mentioned above, the opposite appears more plausible. In this way, the distribution of the genus *Jaxea* can also be explained.

When considering morphological similarities between fossil and modern species of *Jaxea*, it may be assumed that *J. kuemeli* is very closely related to *J. nocturna*. On the other hand, the rather different tooth formula of *J. novaezealandiae* would speak for an earlier divergence from the Tethyan stock, when the common ancestor gave rise to at least two lineages: one represented by *J. kuemeli* and *J. nocturna*, the other one of only *J. novaezealandiae* only. However, as studies of larval stages (DAKIN & COLEFAX 1940; KURIAN 1956; THIRIOT 1976) suggest, there should be several more extant species of *Jaxea* in both lineages. More data on this issue might help resolve the evolutionary history of the genus, at least in part.

A time estimate for the divergence *Jaxea* lineages is difficult. However, most probably it occurred prior to the early Miocene, which would be in accordance with the results gained from studies of molluscs and echinoderms (HARZHAUSER et al. 2007, 2008).

Jaxea kuemeli and *J. nocturna* seem to represent sister taxa to each other. The most parsimonious scenario speaks for the divergence via allopatric origin of

the species after the closure of the seaway between the Mediterranean and the Paratethys during the Sarmatian (latest Serravallian) (PILLER et al. 2007). Whether the place of origin of the older species, presumably *J. kuemeli*, was Paratethys or Mediterranean is difficult to judge right now. More data from the fossil record are needed to draw further conclusions.

6. Conclusions

Jaxea kuemeli is restricted to the Miocene strata of Europe. It is closely related to the extant *J. nocturna* from which it can be distinguished on the basis of the tooth formula of the chelipeds. Modern representatives of the genus *Jaxea* are rather shallow-water burrowers in muddy or sandy substrates and the fossil record confirms the preference of such bottoms also in *J. kuemeli*. The present geographic distribution of the genus, i.e. the Mediterranean, the eastern Atlantic and New Zealand, can be explained with the migration of the genus from Tethys towards the present-day Indo-Pacific Ocean during the late Cenozoic, presumably the Miocene time.

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