Carpathocancer nov. nom. based on new findings of *Carpathocancer triangulatus* (MISIK, SOTAK & ZIEGLER, 1999) (type-species) nov. nom. in Triassic and Jurassic reefal carbonates of the Northern Calcareous Alps and their taxonomic re-interpretation as decapod crustacean appendages

By

FELIX SCHLAGINTWEIT, HANS-JÜRGEN GAWLICK & MATTHIAS AUER

with 6 figures, 1 table and 1 plate

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Address of the authors:
University of Leoben
Department of Applied Geosciences and Geophysics
Chair of Prospection and Applied Sedimentology
8700 Leoben
Austria

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Abstract

Carpathocancer is introduced as nomen novum for *Carpathiella* MISIK, SOTAK & ZIEGLER, 1999, with the type-species *Carpathocancer triangulatus* (MISIK, SOTAK & ZIEGLER, 1999) nov. nom. *Carpathiella triangulata* MISIK, SOTAK & ZIEGLER was defined as the type-species of the genus *Carpathiella*, interpreted in its original diagnosis as tubes of serpulid worms reported from Late Jurassic to Tertiary shallow water carbonates. The detection of so far unknown morphological (exceptional preservation of joint segments) and microstructural criteria (typical three-layered cuticle structure) allow the re-interpretation as being thoracic appendages (legs) of decapod crustaceans. As *Carpathocancer* nov. nom. represents only parts of an organism, it must be treated as a morpho-genus in the future, entailing also the emendation of the original diagnosis of the former *Carpathiella*. *Carpathocancer* nov. nom. is interpreted as a genus of tiny reef-associated crabs, which had their main evolutionary peak in Late Jurassic times. Findings of *Carpathocancer*-type crustacean remains are recorded for the first time from the Late Triassic Dachstein reefal limestone. Due to the long stratigraphic record of *Carpathocancer* nov. nom., it is assumed that different taxa of decapods, although different in their carapaxes features, may show equivalent thin-section appearances of their appendages (legs). Further remarks on the systematics and additional species of *Carpathocancer* nov. nom. are presented.

Zusammenfassung

Carpathocancer wird als Nomen Novum für *Carpathiella* MISIK, SOTAK & ZIEGLER, 1999, mit der Typusart *Carpathocancer triangulatus* (MISIK, SOTAK & ZIEGLER, 1999) nov. nom. eingeführt. *Carpathiella triangulata* MISIK, SOTAK & ZIEGLER, 1999 ist die Typusart der Gattung *Carpathiella*, die in ihrer Originalbeschreibung als Röhren von in oberjurassischen bis tertiären Flachwasserkarbonaten vorkommenden serpuliden Würmern interpretiert wurde. Der Nachweis von bislang nicht bekannten morphologischen (außergewöhnliche Erhaltung von verbundenen Segmenten) und mikrostrukturellen Merkmalen (typische 3-lagige Kutikel-Struktur) erlauben eine Neuinterpretatation als Thoraxanhänge (Beine) von decapoden Crustaceen. Da *Carpathocancer* nov. nom. nur Teile eines Organismus darstellt, muss sie zukünftig als Morphogattung behandelt werden. Gleichzeitig macht dies eine Emendierung der ursprünglichen Diagnose der früheren *Carpathiella* erforderlich. *Carpathocancer* nov. nom. wird als Reste von kleinen, riffbewohnenden Krebsen, die im späten Jura ein Maximum in ihrer Evolution aufwiesen, interpretiert. Erstmalig werden Crustaceen-Reste vom Typus *Carpathocancer* nov. nom. aus dem obertriassischen Dachsteinkalk in Rifffazies bekannt gemacht. Aufgrund der langen stratigraphischen Reichweite von *Carpathocancer* nov. nom., kann man annehmen, dass verschiedene Taxa der Decapoda, trotz unterschiedlicher Morphologie ihrer Carapaxe, in Dünnschliffen äquivalente Schnittbilder ihrer Anhänge (Beine) zeigen. Weitere Anmerkungen zur Systematik und zusätzlichen Arten von *Carpathocancer* nov. nom. werden gemacht.

1. Introduction

The genus *Carpathiella* with the type-species *Carpathiella triangulata* was established from Jurassic to Paleogene limestones of the Western Carpathians by MISIK et al. (1999) who interpreted *Carpathiella* as a serpulid worm tube. In the overview of different representatives of the genus *Carpathiella* coming from the Late Jurassic Plassen carbonate platform and the Late Cretaceous Lower Gosau Subgroup of the Northern Calcareous Alps SCHLAGINTWEIT et al. (2005) followed this interpretation. Due to the intense studies of Late Jurassic to Early Cretaceous shallow-water carbonates of the Northern Calcareous Alps during the last years, a lot of new material was collected and several thousand of thin-sections were analyzed. Findings of individual „tubes“ of *Carpathiella triangulata* joint together, a previously unknown morphological feature revealing a segmented bauplan incompatible with a serpulid nature, initiated this new study. The thin-section material included in the present paper comes from the Late Jurassic Plassen carbonate platform, especially Mount Rettenstein (see AUER et al. 2006, SCHLAGINTWEIT et al. 2006, for details) and the Early Cenomanian Branderfleck Formation of the Northern Calcareous Alps of Austria (see SCHLAGINTWEIT & WAGREICH 2005). Further material included stems from Neocomian shallow water limestones of Albania and the Late Triassic Dachstein reefal limestone of the Northern Calcareous Alps.

2. Palaeontology

When the genus name *Carpathiella* was introduced by

Misik et al. (1999), the authors apparently have overlooked, that this name was already occupied by a uniserial agglutinating foraminifer (Myatlyuk 1966). *Carpathiella* Myatlyuk was considered as a genus of uncertain status by Loeblich & Tappan (1988). In the state-of-the-art review of agglutinating foraminifera of Kaminski (2000: p. 186), the foraminiferal genus *Carpathiella* was discussed and treated as a synonym of *Caudammina* Montanaro-Gallitelli, 1955. *Caudamina*, on the other hand, was also included in the „genera of uncertain status" by Loeblich & Tappan (1988). According to article 52 of the International Code of Zoological Nomenclature (ICZN, 1999), *Carpathiella* Misik et al. (1999) thus represents a junior homonym of *Carpathiella* Myatlyuk, 1966 and has to be changed. According to our new findings and the complete reinterpretation from a worm tube to remnants of crustacean appendages, this problem can be solved in the following way: as new substitute name for *Carpathiella* Misik et al. (1999), *Carpathocancer* nomen novum is introduced in accordance with article 60.3 (junior homonym without synonym) of the ICZN. Following the newly proposed systematic position as crustacean appendages, *Carpathocancer* nov. nom. must be treated as morpho-genus as it represents only specific parts of an animal. The description of the wall structure is thus treated in terms of crustacean terminology (see discussion following the description for details). Other descriptive terms, e.g. concerning sculpture elements on the surface, are difficult in their usage since *Carpathocancer* nov. nom. is only known from random thin-sections not allowing a complete morphological interpretation of the organism. For example, the irregular corners or edges visible in transverse sections can either refer to longitudinal ridges or nodules/granules. It is assumed that the sharp corners in transverse sections belong to longitudinal elements on the surface (ridges, keels) whereas the rounded elements visible in transverse section refer to granules.

Morpho-Genus ***Carpathocancer*** nov. nom.

Derivatio nominis: The name is a geographical-systematic combination referring to the original description in the Western Carpathians and the new interpretation as crustacean remains (cancer = latin word for crab). The type-species *is Carpathocancer triangulatus* (Misik, Sotak & Ziegler, 1999) nov. nom. Original reference: Geologica Carpathica, **50**/4: 305-312, Bratislava. Holotype Pl. II, Fig. 3 in Misik et al. (1999) deposited with the thin-section number 6149 in the collection of Geology and Paleontology, Faculty of Sciences, J.A. Comenius University, Bratislawa, Slovakia.

Carpathocancer triangulatus (Misik, Sotak & Ziegler, 1999) nov. nom.

Text-Fig. 1, Pl. 1, fig. 1-12

1972 „section dans un appendice du crustacé" – Monleau & Philip: Pl. 3, fig. 2, Turonian of S-France.
1979 „sezione di piccola Rudista (*Eoradiolites* ? sp.)" – Luperto Sinni: Pl. 59, fig. 1, Senonian of S-Italy.
1993 Crustaceen-Rest – Darga: Pl. 2, fig. 2, Lower Priabonian of the Northern Calcareous Alps.
1995 „massive" section of crustacean propod – Masse: Pl. 5, Fig. 3, Albian of Congo/West-Africa.
1998 Accordi, G., Carbone, F. & Pignatti, J.: Pl. 8, c, not indicated (middle below), Upper Rupelian-Lower Aquitanian of Greece.
* 1999 *Carpathiella triangulata* n. sp. – Misik, Sotak & Ziegler: 309, pl. 2, fig. 3-9, Lower Cretaceous of Western Carpathians.
2003 *Carpathiella triangulata* Misik, Sotak & Ziegler – Schlagintweit et al.: Pl. 4, Fig. 4-12, Late Jurassic, Late Cretaceous of Northern Calcareous Alps.
2005 *Carpathiella triangulata* Misik, Sotak & Ziegler – Helm: 122, Pl. 38/1, Oxfordian of NW-Germany.

Description: Tubes made of yellowish to light-brownish radiaxial fibrous calcite, mostly triangle-shaped (diameter: 0.44-1.5 mm acc. to Schlagintweit et al. 2005, 0.45-1.12 mm acc. to Misik et al. 1999, up to 5.5 mm, this work, Fig. 1.1) often with two rounded corners and one more acute corner. In the latter, possibly represented by a longitudinal ridge or keel on the outer side, a thin dark line can be observed transecting the complete wall. The shape of the tube lumen more or less follows the outer shape varying from rounded to irregular triangular. In any case the inner side of the wall is always smooth, whereas at the outer surface rounded granules are often present (Fig. 1.1). Within the same specimen, these granules are either superimposed on the outer side without transecting inner cuticle layers or transecting/involving all cuticle layers (Fig. 1.4). The calcareous wall shows a three-layered composition: an inner laminated, comparable thick layer, interpreted as the endocuticle and an outer, more finely laminated layer of reduced thickness, interpreted as the exocuticle (Fig. 1.2, 1.6). Lamination (light and dark-brownish laminae) is always parallel to the surface. Both layers amount about 85 to 95 % of cuticle thickness. In some cases, between these two layers cannot be distinguished anymore as the cuticle shows an overall massive calcitic-fibrous appearance (e.g. Fig.1.1). More rarely, a third very thin layer lacking any signs of lamination is preserved covering also the granules, here interpreted as epicuticle (Fig. 1.3, 1.6). Depending on the article size, thicknesses of the epicuticle from 6.5 to 8 µm (maximum 80 µm) were observed. The thickness of the cuticle with respect to the total diameter is highly variable: the inner tube diameter can equal the wall thickness but can also be much larger than the latter. In both longitudinal (Pl. 1, Fig. 1) and transverse sections (Pl. 1, Fig. 5, 8) openings/interruptions in the wall can sometimes be observed. As the wall endings at the openings taper, these cannot be interpreted as broken specimens but must be regarded as article conjunctions. Also swollen-rounded segment endings, well illustrated by Misik et al. (1999) as „mouth of the tube" in „*Carpathiella* sp.", here regarded as presenting segments of *Carpathocancer triangulatus* (Misik et al. 1999) nov. nom., can be observed (Pl. 1, Fig. 8). The segmented character of *Carpathocancer triangulatus* (Misik et al. 1999) nov. nom. is clearly evidenced in rare cases where two adjoining articles are preserved (Pl. 1, Fig. 6, 9). Here also the tapering of the skeleton wall is clearly visible. Thus the specimens with „openings" can be referred

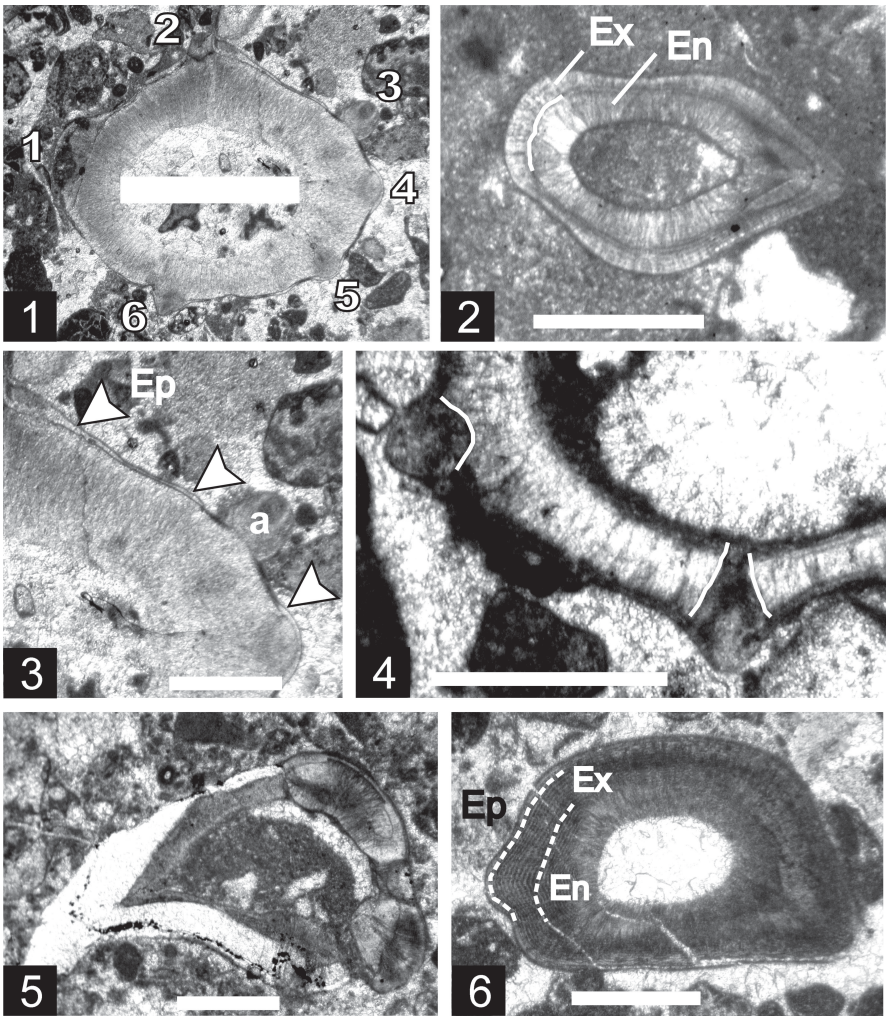

Fig. 1: *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. From the Late Jurassic and Paleocene of the Northern Calcareous Alps, and the Neocomian of Albania.
(1) Transverse section of a large tube showing the existence of six outer ridges or granules, either more sharp or more rounded in shape. Neocomian Munella platform of Albania, sample AL-2070. Scale bar = inner tube diameter = 3 mm. **(2)** Transverse section showing the wall structure composed of a thick inner endocuticle (En), making up about 70 % of the total cuticle thickness, and a finely laminated outer exocuticle (Ex). Paleocene Kambühel Limestones, Northern Calcareous Alps, Austria, sample KS-14-7, scale bar = 0.5 mm. **(3)** Detail from (1) showing the thin outer layer interpreted as epicuticle (Ep), thickness: 80 µm. Note the granule (diameter ~ 0.6 mm) superimposed on the outer side without transecting inner cuticle layers (a). Scale bar = 1 mm. **(4)** Detail from Plate 1, figure 3 showing granules within one specimen either transecting/involving all cuticle layers (below) or not (left). Note the darker outer epicuticle layer (thickness ~ 0.02 mm). Neocomian Munella platform of Albania, sample AL-2076, scale bar = 0.5 mm. **(5)** Different degrees of cuticle calcification or alteration phenomenon (? quartz replacement). Kimmeridgian Plassen carbonate platform of Mount Rettenstein/Northern Calcareous Alps, sample Rö-155, scale bar = 0.5 mm. **(6)** Specimen with preserved three cuticle layers: Endocuticle (En), exocuticle (Ex) and epicuticle (Ep, thickness: 6.5 - 8 µm). The approximate relationship of individual layers is 5 : 3 : 1 of total cuticle thickness. Late Jurassic of Mount Trisselwand/Northern Calcareous Alps, sample TK-21a, scale bar = 0.5 mm.

to sections cutting the plane of segment endings towards the next adjoining one.

Discussion: The species was so far interpreted as sections of small rudists, crustacean appendages and serpulid tubes in the generic diagnosis (see synonymy). Normally, the thoracic appendages of decapod crustaceans become disarticulated and fragmented post-mortem; the exceptional findings of two articles jointed together (Fig. 2), the absence of cemented specimens, the wall structure, and other observations, however, are not consistent with a serpulid nature but pointing to decapod crustaceans making a taxonomic reconsideration necessary. An attribution of sections of *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. to crustacean remains previous to the genus description by MISIK et al. (1999) was already provided by several authors, e.g. MONLEAU & PHILIP (1972), DARGA (1993) or MASSE (1995). The *„massive section of a crustacean propod" …"with a thick fibrous calcitic wall"* figured by MASSE (1995: Pl. 5, Fig. 3) from the Albian of West-Africa is identical to sections of *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. from the Late Jurassic of the Northern Calcareous Alps (e.g. SCHLAGINTWEIT et al. 2005: Pl. 4, Fig. 5, Late Kimmeridgian of Mount Krahstein). MASSE (1995: Pl. 5, Figs. 1-2) provided also longitudinal tube sections as „crustacean propod section" with comparable thin walls. Since it is uncertain whether these decapod remains belong to *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom., they are not included in the synonymy list. In conclusion, the following discussion focuses on the crustacean *versus* serpulid nature and mainly refers to the type-species *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom.

General morphological considerations

In most cases, the transverse sections of *Carpathocancer* nov. nom. show a pronounced asymmetry as one corner of the rounded triangles is elongated in one direction. Also in other specimens with more than three corners or ridges/ granules a plane of bilateral symmetry is not observable in

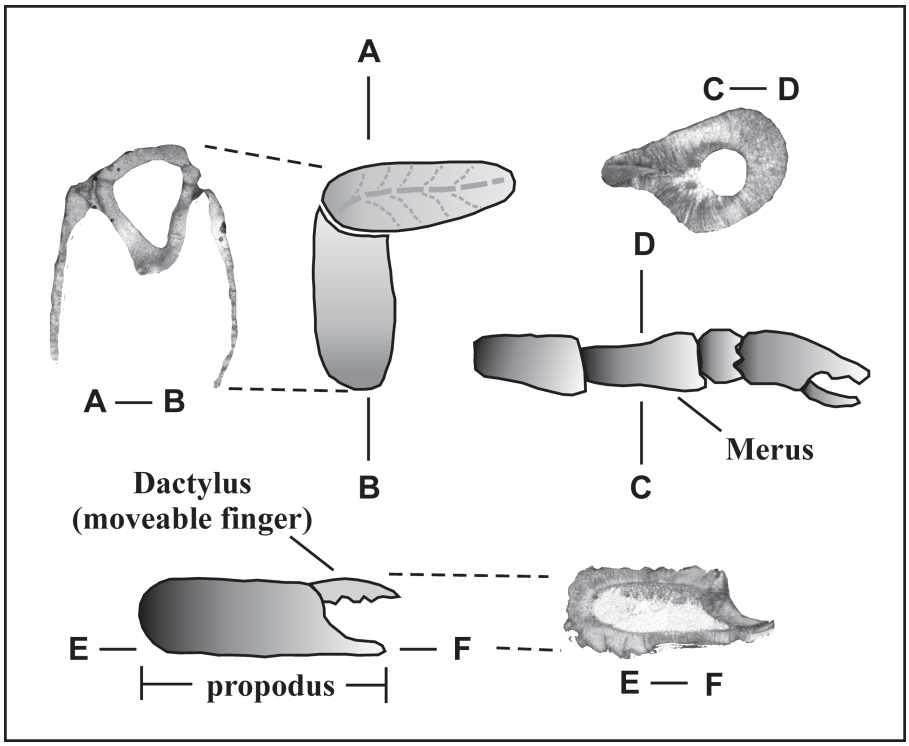

Fig. 2: Schematic drawing showing the re-interpretation of *Carpathocancer triangulatus* (Misik et al. 1999) nov. nom. as crustacean appendages (without scale). A-B: Section through two adjoining segments (hinge joint), the upper one transversly, the lower one longitudinally. C-D: Triangular transverse section of a segment, interpreted as merus, the fourth segment of the leg. E-F: Oblique longitudinal section of a propodus (stationary part of the claw); the movable finger-like dactyl became disarticulated at the propodus-dactyl junction (decapod terminology after Moore & McCormick 1969 and Martin 2006). Propodus length about 3.8 times length of the „fixed finger".

any case. In contrast, transverse sections of serpulids mostly show bilateral symmetric rounded to oval shapes. Even in the case of fixed serpulids, when the attached side is flattened, the sections show a bilateral symmetry. In *Carpathocancer* nov. nom., fixed specimens are missing. The specimen approached as „fixed on the alga *Pseudolithothamnium album*" figured by Misik et al. (1999: Pl. 2, Fig. 4) is here interpreted just the other way round: the fixation of the red algae on *Carpathocancer* nov. nom. This would be one exceptional case when epibionts are preserved since we never observed encrusting micro-organisms on *Carpathocancer* nov. nom.

The highly variable sizes of observed transverse sections can not only be explained by juvenile vs. adult specimens or sexual dimorphism but also in terms of crustacean appendages morphology. Thorough glossaries of terms of decapods were provided by Moore & McCormick (1969) and Martin (2006). Each thoracic appendage (five pairs of walking legs) is composed of individual elements (articles) joined by flexible articulations typically forming simple hinges (e.g. Lochhead 1961). At the joint of neighboring segments the exoskeleton remains uncalcified (so-called arthrodial membrane), remaining soft and flexible and thus allowing separate movements. In some crustaceans the articles are getting smaller from proximal to distal, but in clawed crustaceans like crabs or lobsters the last segment of the first pair with the claw is most often the largest and thickest one. Extremely rare sections of *Carpathocancer triangulatus* (Misik, Sotak & Ziegler, 1999) nov. nom. with parallel tube walls and one excentric acute ending are interpreted as legs bearing claws or chelae (so-called chelipeds) with the dactylus or dactyl (short first article, moveable „finger") and the propodus (longer second article, the fixed and stationary part of the claw) (Pl. 1, Fig. 7). In this example, the dactyl was lost and the propodus-dactyl junction is assumed nearly parallel. Typical triangular transverse sections, being the characteristic thin-section appearance of *Carpathocancer triangulatus* (Misik, Sotak & Ziegler, 1999) nov. nom., are variously reported from the meri of both fossil and extant crabs (e.g. Vega et al., Schubart et al. 1997, Huang & Hsueh 1998) and lobsters (e.g. Poupin 2003). The merus (plural = meri) or meropodite is the fourth article from the distal end of the leg; depending on genus and species, the merus can be the longest of the segments. In conclusion, it seems likely, that the triangular sections of *Carpathocancer triangulatus* (Misik, Sotak & Ziegler, 1999) nov. nom. represents the transverse sections of the meri of decapod crustaceans.

Microstructure

Especially marine crustaceans are known for their hard, in part massive exoskeleton or cuticle. It is generally divided in three layers called endocuticle, exocuticle and epicuticle (e.g. Neville & Berg 1971, Roer & Dillaman 1984, Feldmann & Gazdzicki 1998, Vega et al. 2005). Whilst the outer three layers are calcified, the innermost membranous hyperdermis is not. The epicuticle is the thinnest and outermost layer. In thin sections, the endocuticle and exocuticle exhibit a lamellar aspect parallel to the surface with calcite crystals interspersed within chitin-protein fibres (e.g. Roer & Dillaman 1984). Considering ultrastructural details, this two-dimensional structure may become three-dimensional as evidenced from modern lobsters for instance (e.g. Raabe et al. 2005). The integration of the cuticle microstructure has meanwhile become an important criterium in the classification of fossil decapods. In recent years, efforts were undertaken for a comparative analytical cuticle classification as a tool for taxonomic studies (Waugh 2002, Feldmann 2003, Waugh & Feldman 2003). Three different

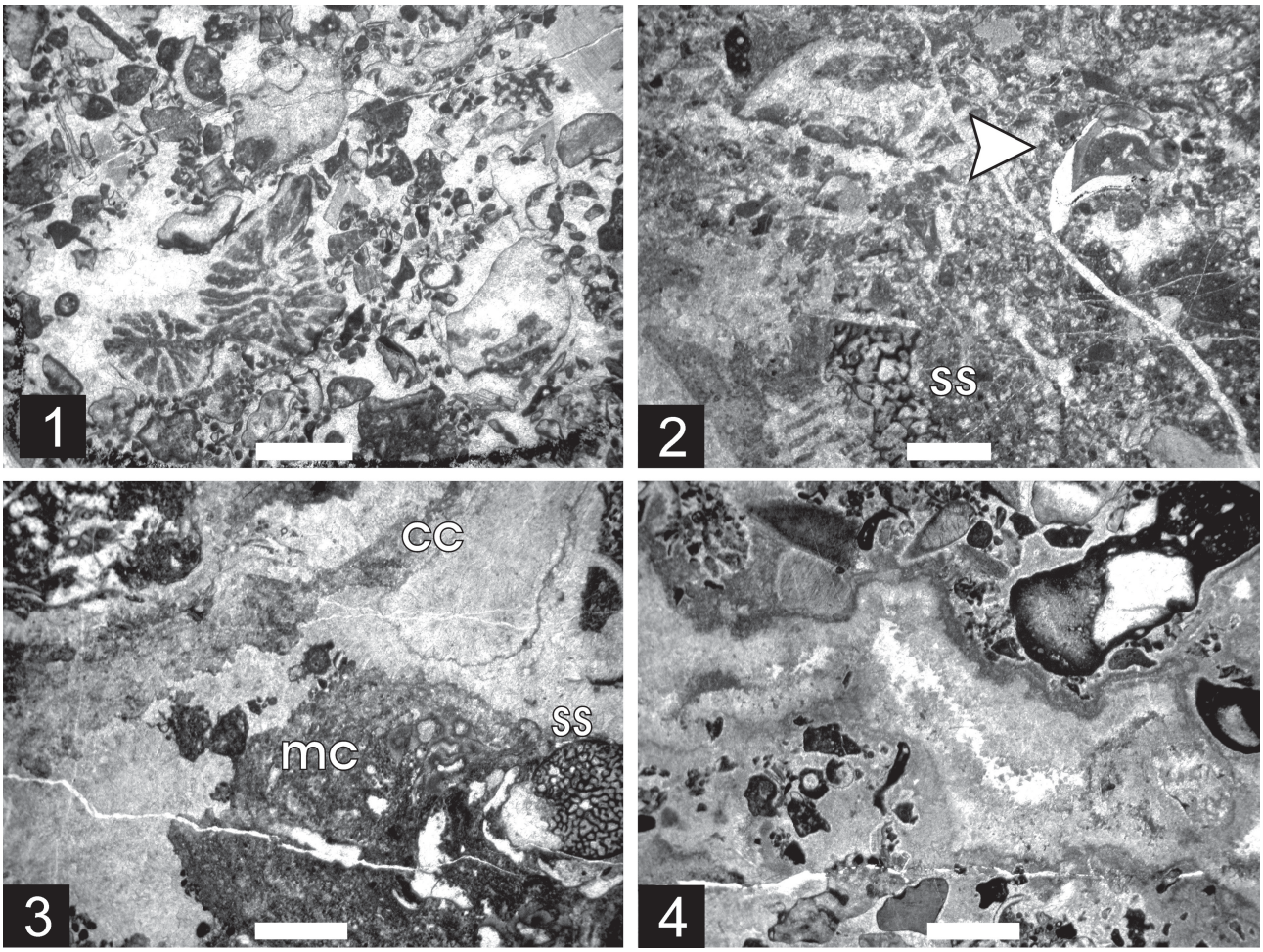

Fig. 3: Microfacies of Late Jurassic reefal margin deposits from Mount Rettenstein. *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. (white arrow in 2) was detected in all samples illustrated (1: Rö-18; 2: Rö-155; 3: Rö-166; 4: Rö-342): bioclastic packstones/rudstones with debris of corals, stromatoporoid sponges (ss), boundstones with microbial crusts (mc) and cement crusts (cc). Scale bar = 2 mm.

layers are also recognizable in *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. and are interpreted here in terms of decapod cuticle microstructure consequently as endocuticle, exocuticle and epicuticle (Fig. 1). The outermost cuticle is comparably thin, whereas the endocuticle is the most prominent layer reaching up to 2/3 of the total cuticle thickness. The yellowish to brownish appearance of *Carpathocancer* nov. nom. in thin-section can be due to the presence of carbonate-hydroxy-apatite or original tanning pigment (e.g. VEGA et al. 1994, RAABE et al. 2005: „nanocomposite material"). In contrast hereto, the microstructure of serpulids is diverse. Amongst the most characteristic is a double-layer wall with a thin inner layer with concentric laminae and a thicker outer layer with convex forward laminae, the so-called „Parabel-Schicht" (SCHMIDT 1955, REGENHARDT 1961) or „ordered chevron structure" (WEEDON 1994). More details to this main principal wall type were brought forward by SEM studies (WEEDON 1994 for details). The thick yellowish fibrous calcitic structure of *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. is unknown from serpulids.

As the crustacean animal grows, the exoskeleton made of protein chitin and calcium carbonate does not and must therefore periodically be removed and replaced by a larger one. The old shell splits along specific weak points. In this respect, the „dark line (suture)" within one triangle edge of *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. is interpreted to represent the weakening part of the crustaceans skeleton along which it splits off during the moulting process.

Palaeoenvironment

Also the palaeoenvironment wherein *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. dominates is in accordance with a crustacean origin. According to SCHLAGINTWEIT et al. (2003: Fig. 9), *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. is restricted to reefal platform margins with rocky substrates, an environment where also extant clawed crustaceans are prevailing. The carbonates containing *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. are bioclastic packstones to rudstones or boundstones with microbial and cement crusts (Fig. 3). Associated microbiota are benthic foraminifera, dasycladalean algae, echinoids, bryozoa and various microproblematica. Metazoan debris is represented by corals and „stromatoporoid sponges".

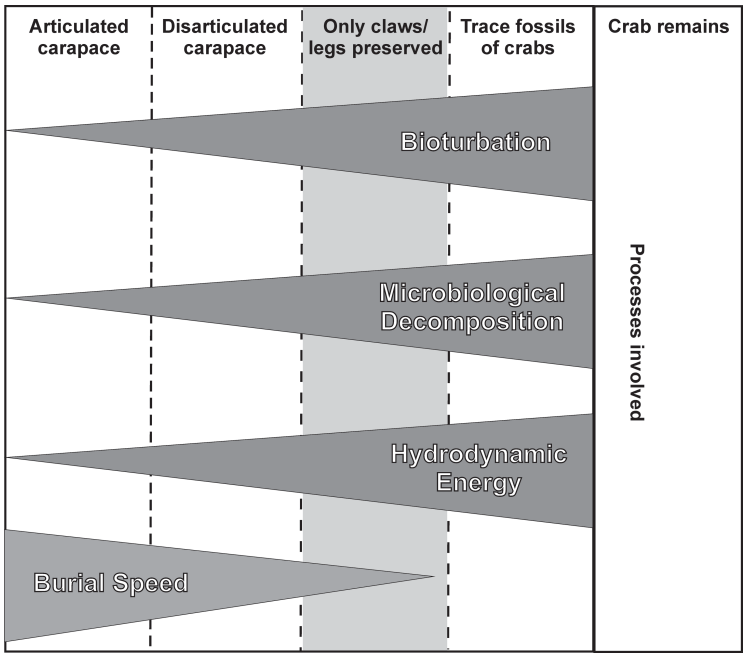

Fig. 4: Preservation of crabs according to taphonomical processes involved (after MÜLLER et al. 2000 and SHIRK 2006). The occurrences of *Carpathocancer triangulatus* (MISIK, SOTAK & ZIEGLER, 1999) nov. nom. and *Carpathocancer*? *perforatus* (MISIK, SOTAK & ZIEGLER, 1999) nov. nom. within the platform margin deposits of the Plassen carbonate platform are highlighted in light-gray. Note, that both taxa may become resedimented from the margin within less agitated slope environments.

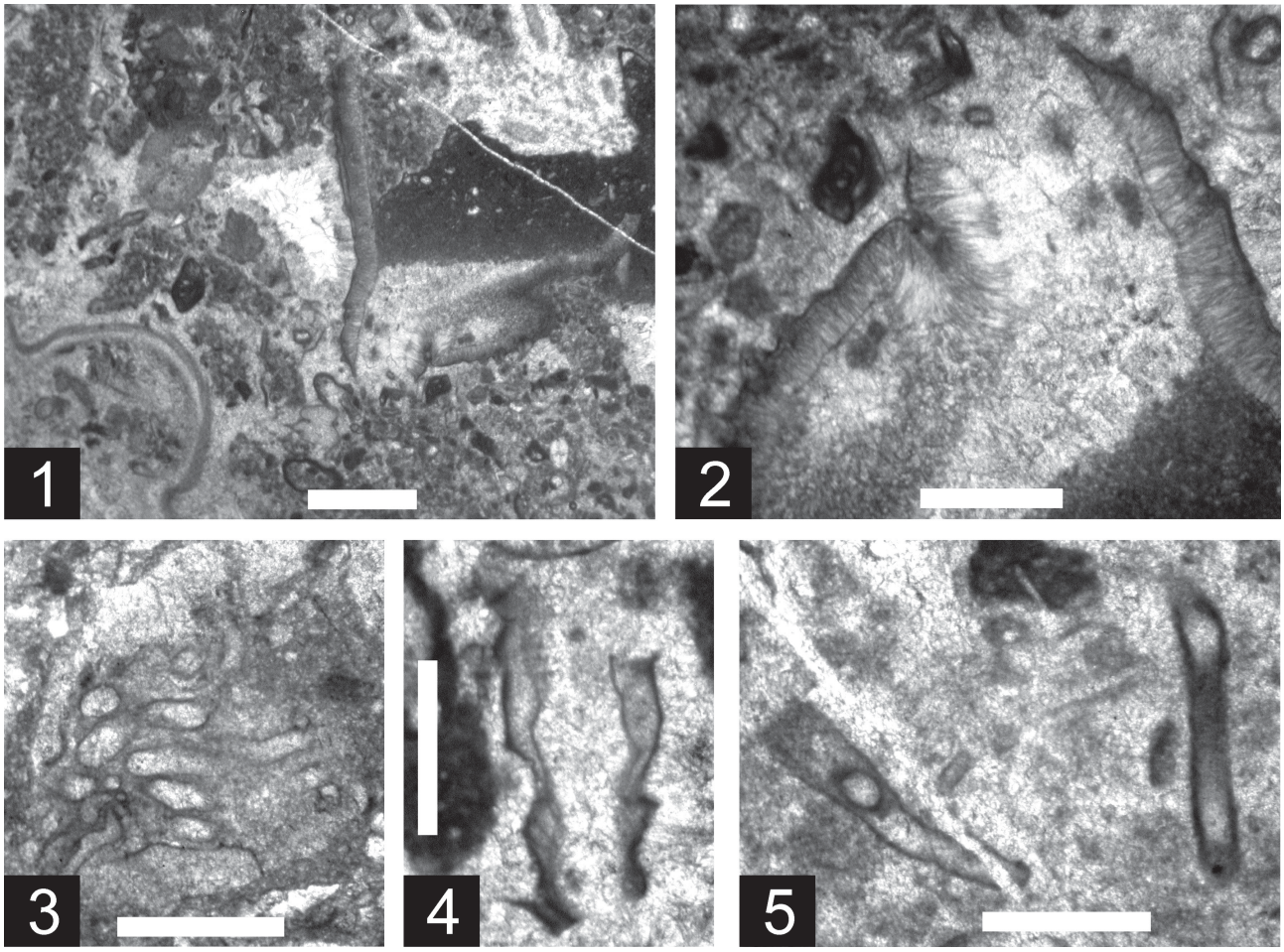

Fig. 5: Crustacean remains of *Carpathocancer* sp. from Late Triassic reefal Dachstein Limestone of the Northern Calcareous Alps. The occurrence of the benthic foraminifer *Alpinophragmium perforatum* FLÜGEL, 1967 together with the microproblematica *Actinotubella gusici* SENOWBARI-DARYAN, 1984 (3), *Lamellitubus cauticus* OTT, 1968 (in KRAUS & OTT 1968) (4) and *Paraeolisaccus endococcus* SENOWBARI-DARYAN & SCHÄFER, 1980 (5) indicate a Norian (?Rhaetian) age. (2) detail from (1). Locality Mount Elm, Austrian Salzkammergut, sample Elm-8 (1-2, 4), sample Elm-1 (3), sample Elm-9 (5). Scale bar 1 mm for (1), all others 0.5 mm.

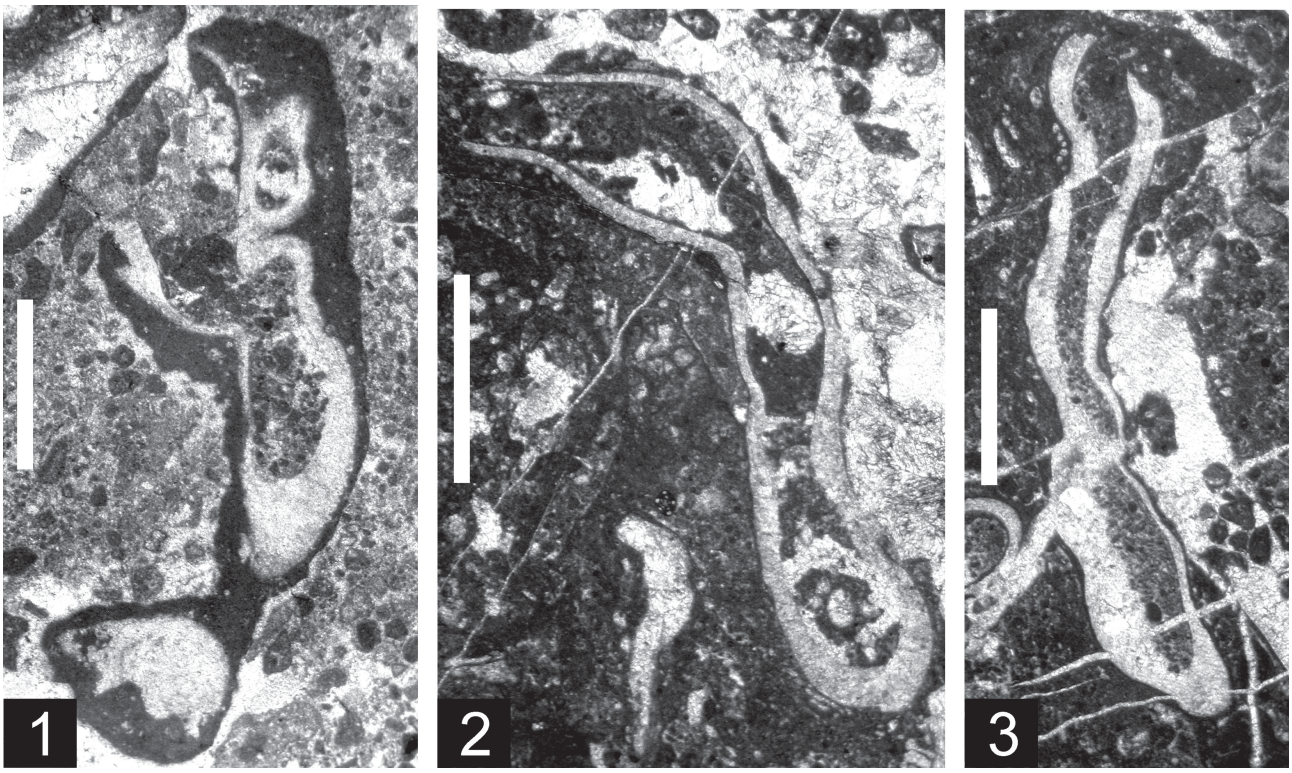

Fig. 6: Different longitudinal sections of *Carpathocancer*? *plassenensis* SCHLAGINTWEIT & GAWLICK 2002 nov. nom. showing irregular bending and a possible segmentation in (1). The maximum tube length is 7.9 mm in (3). Scale bars = 2 mm. 1: Mount Jainzen, sample A-3443, ?Kimmeridgian. 2-3: Mount Rettenstein, sample Rö-333, Kimmeridgian.

In this palaeoenvironment tiny crabs of the typus *Carpathocancer* nov. nom. obviously found both food and hiding places (e.g. caves) from predators. In that manner, the small size of (Late) Jurassic crabs was assumed to be controlled by predation pressure of the evolving reef fishes and especially cephalopods; therefore hiding in crevices was one main strategy in their evolution (FRAAIJE 2003). In Late Jurassic times, there was a main peak in the evolution of reef-associated decapod crustacean with the Prosopidae as one of the most important groups (MÜLLER et al. 2000, GARASSINO & KROBICKI 2002, FRAAIJE 2003: Fig. 1, SHIRK 2006). Noteworthy that *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. was never found in both open and closed lagoonal facies. From the closed lagoon of the Plassen carbonate platform at Mount Plassen, however, crustacean coprolites are reported with *Agantaxia biserialis* KRISTAN-TOLLMANN 1989 and *Favreina lahngangkogelensis* SCHLAGINTWEIT, GAWLICK & LEIN, 2005.
It is assumed, that water energy was the dominating process leading to the exclusive preservation of *Carpathocancer*-type appendages in the platform margin deposits of the Late Jurassic Plassen carbonate platform. The interplay of various taphonomic processes dominating the general preservation of crabs was discussed by MÜLLER et al. (2000) (see Text-Fig. 4).

Stratigraphic record: *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. has as yet been reported from Oxfordian to Oligocene (? Lower Miocene) strata (SCHLAGINTWEIT et al. 2005 for details). One section of crustacean debris of the type *Carpathocancer* nov. nom. was recently discovered in Late Triassic (Norian-Rhaetian) Dachstein reefal limestones, enlarging the known stratigraphic record significantly (Fig. 5). According to our knowledge, this is the first record of decapod crustacean remains from Late Triassic of the Northern Calcareous Alps. These findings are important since there is a general paucity of Permian and Triassic decapods (e.g. LISA et al. 2004). On the other hand, crustacean coprolites are well recorded from the Middle and Late Triassic (e.g. SEEGIS in SCHWEIGERT et al. 1997; SENOWBARI-DARYAN & BERNECKER 2000, 2005).

Emendation and systematic considerations: The original diagnosis of *Carpathiella* by MISIK et al. (1999: p.309) was provided as follows: „*Tubes relative thick (mostly 0.13-0.18 mm). The cross-sections tend to a triangular shape. The tube is formed by one layer; the calcite fibres are oriented radially in the cross-section.*“ The definition provided is incomplete with all characters observed by MISIK et al. (1999), as the recognition of specimens exhibiting „tube“ openings and swollen „tube“ was not integrated in the generic diagnosis. These forms were described separately as *Carpathiella* sp. by MISIK et al. (1999). It is here believed that these should be integrated in the variability of the type-species *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom.
The new morphological details observed and not included in the original diagnosis necessitate an emendation of the morpho-genus *Carpathocancer* nov. nom. The following emended diagnosis of *Carpathocancer* nov. nom. is

Species / Locality	*Carpathocancer triangulatus* (MISIK et al., 1999)	*Carpathocancer*? *perforatus* (MISIK et al., 1999)	*Carpathocancer*? *plassenensis* (SCHLAGINTWEIT et al., 2002)
Barmsteine	**X**		**X**
Bürgl	**X**		
Drei Brüder	**X**		
Falkenstein	**X**		**X**
Hochkranz			**X**
Jainzen	**X**	**?**	**X**
Knallalm			**X**
Krahstein	**X**	**X**	
Litzlkogel	**X**		**X**
Lugberg	**X**		
Plassen	**X**	**X**	
Rettenstein	**X**		**X**
Rötelstein*		**X**	
Sarstein	**X**		
Trisselwand	**X**		**X**
Untersberg*			**X**
Sillenköpfe Steinernes Meer	**X**		

Tab. 1: Occurrences of different species of *Carpathocancer* nov. nom. in the Late Jurassic Plassen carbonate platform (supplemented after SCHLAGINTWEIT et al. 2003) showing that both *Carpathocancer triangulatus* and *Carpathocancer*? *plassenensis* are widely distributed whereas *Carpathocancer*? *perforatus* is rare. Some data are provisionary, as further investigations of some localities (marked with asterisk) are currently in progress.

proposed here as follows: „*Segments composed of yellowish to light-brownish fibrous calcite arranged in three layers, interpreted as endocuticle, exocuticle and epicuticle. The former two composed of fine laminae amount to more than 3/4 of total cuticle thickness; epicuticle thin and not laminated. Thickness of wall variable. Cross-sections rounded, mostly triangular. One angular corner and/or several rounded outer granules may be present. Tubes are part of individual articles, rarely preserved jointed together. The cuticle may show distinct rounded swellings at the open segment endings*".

We assume a large intraspecific variability comprising tube diameter, wall thickness, and presence/absence of outer ridges/granules. Therefore, these criteria do not seem to be useful for an establishment of different species at the moment unless a larger number of well-preserved articles is available or, even better, complete organisms allowing detailed analyses. As the former *Carpathiella* was originally established as a serpulid worm tube, we can of course not exclude the possibility that with the new taxonomic interpretation a synonymy might exist with one of the various existing genera of fossil decapod crustaceans. On the other hand, also a mixing of different decapod taxa summarized as „*Carpathiella*" is possible also when considering the long stratigraphic range of these findings from Late Jurassic (?Late Triassic) to Tertiary. For example, the crab *Carcineretes planetarius* VEGA, FELDMANN, OCAMPO & POPE 1997 from the Maastrichtian of Belize and Chiapas/Mexico shows very similar thin-section appearance as *Carpathocancer* nov. nom. (e.g. Pl. 2, Fig. 13 in VEGA et al. 2005). The quiet water lagoonal environment assumed for the strata with *Carcineretes planetarius* (see also VEGA et al. 2001), however, is different from the well agitated perireefal environment in which *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. is found. Although Middle-Late Jurassic decapods are well recorded mainly with isolated carapaxes but also whole fossils (e.g. FÖRSTER & HILLEBRANDT, 1984; GARASSINO & KROBICKI 2002), only little is known about the morphology of their appendages in thin-sections. With a total propodus length of ~ 2.5 mm measured from the specimen figured in plate 1, figure 7, a size of 0.5 to 1.5 cm can roughly be estimated for the whole animal. Sizes of usually several millimetres up to 1.5 cm are typically for the disarticulated carapaxes of Late Jurassic reef-dwelling crabs (e.g. Prosopidae, Galatheinae, Pithonotidae) (e.g. SHIRK 2006). A direct correlation, however, is not possible at the moment. Last but not least, it is important to note, that decapod appendage morphology is prone to convergence resulting in a comparable low degree of taxonomic importance (TSHUDY & SORHANNUS 2000).

Taking into account these considerations, the emended diagnosis provided here is rather a diagnostic definition for the identification of *Carpathocancer* nov. nom. in random thin-sections than a true taxonomic diagnosis. Such systematic considerations and comparisons, that will become necessary because of the new interpretation, would represent an interesting topic for future research and is not further followed for the scope of the present paper. Anyway, the Late Jurassic crustacean remains of the type *Carpathocancer* nov. nom. are referred to tiny crabs, usually included in the infraorder Brachyura.

With respect to *Carpathocancer*? *perforatus* (MISIK, SOTAK & ZIEGLER, 1999) nov. nom., formerly *Carpathiella perforata* MISIK, SOTAK & ZIEGLER, 1999, an interpretation as parts of crustaceans can be envisaged as well. However, due to the lack of findings of joint articles such an interpretation can so far not be proven. For the U-shaped *Carpathocancer*? *plassenensis* (SCHLAGINTWEIT & GAWLICK, 2002) nov. comb., also some new observations can be presented. In our material we observed irregular bounded tubes of several millimetres length (maximum 7.9 mm) (Fig. 6). Some sections could be interpreted either as jointed articles or one strongly bent tube cut two times (Fig. 6.1). Strongly and irregular bent tubes are well known from certain serpulid taxa (for example Pl. 1 and 4 in JÄGER 1991). Thus, a final conclusion

on the systematic position is not possible at the moment. Therefore both species should be better treated with open nomenclature with respect to the generic status at the moment. *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. is the most widespread taxon in the Late Jurassic Plassen carbonate platform of the Northern Calcareous Alps, followed by *Carpathocancer*? *plassenensis* (SCHLAGINTWEIT & GAWLICK, 2002) nov. comb.; *Carpathocancer*? *perforatus* (MISIK, SOTAK & ZIEGLER, 1999) nov. nom. is very rare (Tab. 1).

3. Conclusions

The calcitic tube remains of *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom., formerly regarded as a serpulid worm tube, are comparably abundant in well agitated shallow water carbonates of Late Jurassic reefal margins of the Northern Calcareous Alps. The evidences of new microstructural and morphological features allow for an interpretation as decapod crustacean remains belonging to small crabs. Due to their tubiform shapes and the occurring adjoining articles, these can be attributed to decapod appendages. Since *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. is considered as only parts of an organism, it must be treated as morpho-genus. As the species is only known from thin-sections, it is at the moment impossible to explain the different morphologies of the tubes either as intra- or intraspecific variations. Furthermore, almost nothing is known about possible synonymies between *Carpathocancer* nom nov. and established genera of decapod crustaceans, respectively, as parts of the latter. Due to the long stratigraphic range, it seems improbable that all the thin-section records referred to *Carpathocancer triangulatus* (MISIK et al. 1999) nov. nom. belong to the same species or genera. It is assumed that different taxa, although being different in their carapaxes features and morphology, may show equivalent appearance of their appendages (legs!) in random thin-sections where their determination thus becomes extremely difficult if not impossible.

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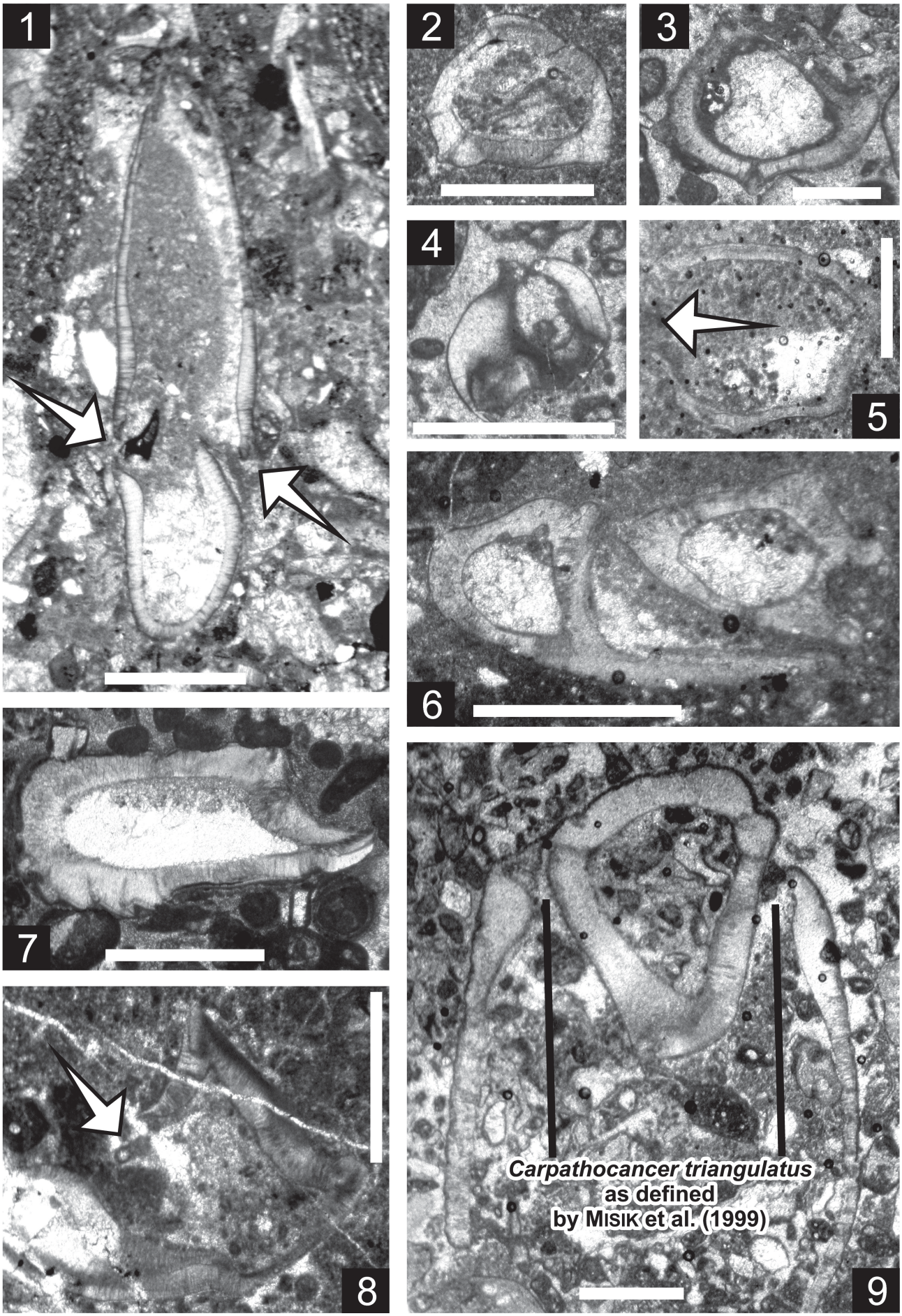
Plate 1

Carpathocancer triangulatus (MISIK et al. 1999) nov. nom. re-interpreted as decapod crustacean remains

Scale bars = 1 mm.
Fig. 1: Longitudinal section showing two articles. Note the thickening and the following tapering of the wall in the lower segment. Lower Cenomanian Branderfleck Formation of Northern Calcareous Alps (Northern Calcareous Alps), sample He-15.
Fig. 2: Transverse section. Kimmeridgian Plassen carbonate platform, Mount Rettenstein/Northern Calcareous Alps, sample Rö-55.
Fig. 3: Transverse section showing granules (detail see Text-Fig. 1.3). Kimmeridgian Plassen carbonate platform, Mount Sarstein/Northern Calcareous Alps, sample DD-88.
Fig. 4: Oblique transverse section. Kimmeridgian Plassen carbonate platform, Mount Rettenstein/Northern Calcareous Alps, sample Rö-17.
Fig. 5: Specimen showing an „opening“ in the wall (arrow). Kimmeridgian? Wolfgangsee carbonate platform, Mount Jainzen/Northern Calcareous Alps. Sample D-537.
Fig. 6: Two adjoining articles. Neocomian Munella platform, Albania. Sample AL-2002.
Fig. 7: Oblique longitudinal section interpreted as propodus of a leg bearing claws (see also Text-Figure 2). Kimmeridgian Sillenkopf Formation of Steinernes Meer/Northern Calcareous Alps. Sample SM-110.
Fig. 8: Transverse section opened to one side. Note rounded thickening of the wall at one side of the „opening“ („mouth of the tube“ sensu MISIK et al. 1999; arrow) and tapering on the opposite side. Kimmeridgian? Wolfgangsee carbonate platform, Mount Jainzen/Northern Calcareous Alps. Sample D-583.
Fig. 9: Two adjoining articles. Kimmeridgian Plassen carbonate platform, Mount Rettenstein/Northern Calcareous Alps, sample Rö-423a. The upper segment is cut transversly, the lower one longitudinally (see also Text-Figure 2).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Carpathocancer triangulatus
as defined
by MISIK et al. (1999)