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# New erymid lobsters from the Nusplingen and Usseltal formations (Upper Jurassic) of southwest Germany

## Novi jastogi iz družine Erymidae iz formacij Nusplingen in Usseltal (zgornja jura) iz jugozahodne Nemčije

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*Ključne besede:* dekapodni raki, Erymidae, kimmeridgij, tithonij, litografski apnenec, tafonomija

**Abstract**

Two new species of Late Jurassic erymid lobsters, *Stenodactylina devillezi* sp. nov. and *Stenodactylina geigerae* sp. nov., are described on the basis of isolated, but well-preserved chelipeds from the upper Kimmeridgian of Swabia and the lower Tithonian of Bavaria, respectively. The incomplete nature of the material indicates that these lobsters were not autochthonous elements of the Plattenkalk lagoons, but resulted from predation in nearby shallow-water settings.

**Izvleček**

V prispevku predstavljamo dve novi vrsti zgornjejurskih jastogov iz družine Erymidae, to sta *Stenodactylina devillezi* sp. nov. in *Stenodactylina geigerae* sp. nov. Novi vrsti sta opisani na podlagi izoliranih, vendar dobro ohranjenih škarnikov iz zgornjega kimmeridgija Švabske in spodnjega tithonija Bavarske. Slabša ohranjenost primerkov kaže, da tovrstni jastogi niso bili avtohtoni prebivalci zgornje jurskih lagun, ampak so verjetno poseljevali bližnja plitvovodna okolja.

## Introduction

The Upper Jurassic Solnhofen-type lithographic limestones ("plattenkalks") of southwest Germany are renowned for their exceptionally preserved fossils, making them one of the classic examples of conservation Fossillagerstätten (Seilacher et al., 1985). In addition to iconic vertebrate fossils such as the ancient bird *Archaeo-pteryx* von Meyer, 1861, hundreds of taxa have been recorded over the centuries (e.g., Leich, 1968; Barthel et al., 1990; Frickhinger, 1994, 1999; Arratia et al., 2015). However, it should be noted that fossils labelled "Solnhofen" come from various deposits of different lithology and age (Schweigert, 2007, 2015a). Decapod crustaceans from these lithographic limestones, and erymid lobsters in particular, have been described from the early 19th century onwards (e.g., Desmarest, 1817, 1822; von Schlotheim, 1822; zu Münster, 1839; Oppel, 1861, 1862). More recently, Beurlen (1928) and Förster (1966) studied Jurassic erymids. However, some of their systematic assignments remained questionable. Taxa based on material from shallow-water deposits consist either of carapace remains or of isolated chelae. More complete specimens, with the carapace and corresponding chelae preserved, are only found when conditions were favourable or within concretions (e.g., Hyžný et al., 2015). At generic level, erymid lobsters are distinguished mainly by their characteristic carapace groove pattern (Devillez & Charbonnier, 2017, 2019, 2020; Devillez et al., 2018), while chela shape is less characteristic, at least in *Eryma* s. str. In the latter, there is one clade that has chelae with relatively short fingers; this group is distinguished

from another with strikingly longer, straight fingers, although the groove pattern of the carapace is the same. As a result, some species of *Eryma* of the second clade, previously included in a distinct genus, *Erymastacus* Beurlen, 1928 (see Hyžný et al., 2015), have later been considered to belong to *Eryma* s. str. (Devillez & Charbonnier, 2017, 2019, 2020). However, there are further taxa that have long and curved fingers, but a different groove pattern on their carapace. These are now included in the genus *Stenodactylina* Beurlen, 1928. Remains of *Stenodactylina* are easily recognised on the basis of their chelae even if such occur isolated (Devillez & Charbonnier, 2019a, 2019b). Most Late Jurassic remains of *Stenodactylina* represent chelae or chelipeds from coral-bearing limestones or other shallow-water lithologies (e.g., Étallon, 1859, 1861; Krause, 1891; Bachmayer, 1959). Here we describe the first examples of *Stenodactylina* from Upper Jurassic lithographic limestones.

## Geological settings

Two of the specimens of *Stenodactylina* described here come from the upper Kimmeridgian Nusplingen Plattenkalk, also known as Nusplingen Lithographic Limestone. The site of provenance is located in the western part of the Swabian Alb (Fig. 1). The Nusplingen Plattenkalk was deposited in a *c.* 80-100 metres deep lagoon surrounded by shallower areas and small islands (Stevens et al., 2014). Known since the mid-19th century, it has meanwhile provided more than 400 fossil taxa, among them pterosaurs, marine crocodiles, sharks and numerous other fishes, but also squid-like teuthoids and decapod crustaceans (Dietl & Schweigert, 2011). Ammonites have allowed to date it as late *Beckeri* Zone, *Ulmense* Subzone, *hoelderi* Biohorizon (Schweigert, 2007, 2015a). Especially common are large-sized penaeid prawns (Schweigert, 2001b, 2017; Odin et al., 2019), but polychelid, glypheid and erymid lobsters have been recorded as well (Fraas, 1855; Oppel, 1861, 1862; Schweigert & Dietl, 1999; Schweigert et al., 2000; Schweigert, 2001a; Charbonnier et al., 2013; Audo et al., 2014). Erymid material from Nusplingen is often incomplete due to predation or decay; however, several valid taxa have been described on the basis of such incomplete specimens (Oppel, 1861, 1862; Schweigert et al., 2000). Recently, this material has been restudied within the context of a comprehensive review of all Late Jurassic erymid lobsters (Devillez & Charbonnier, 2020).

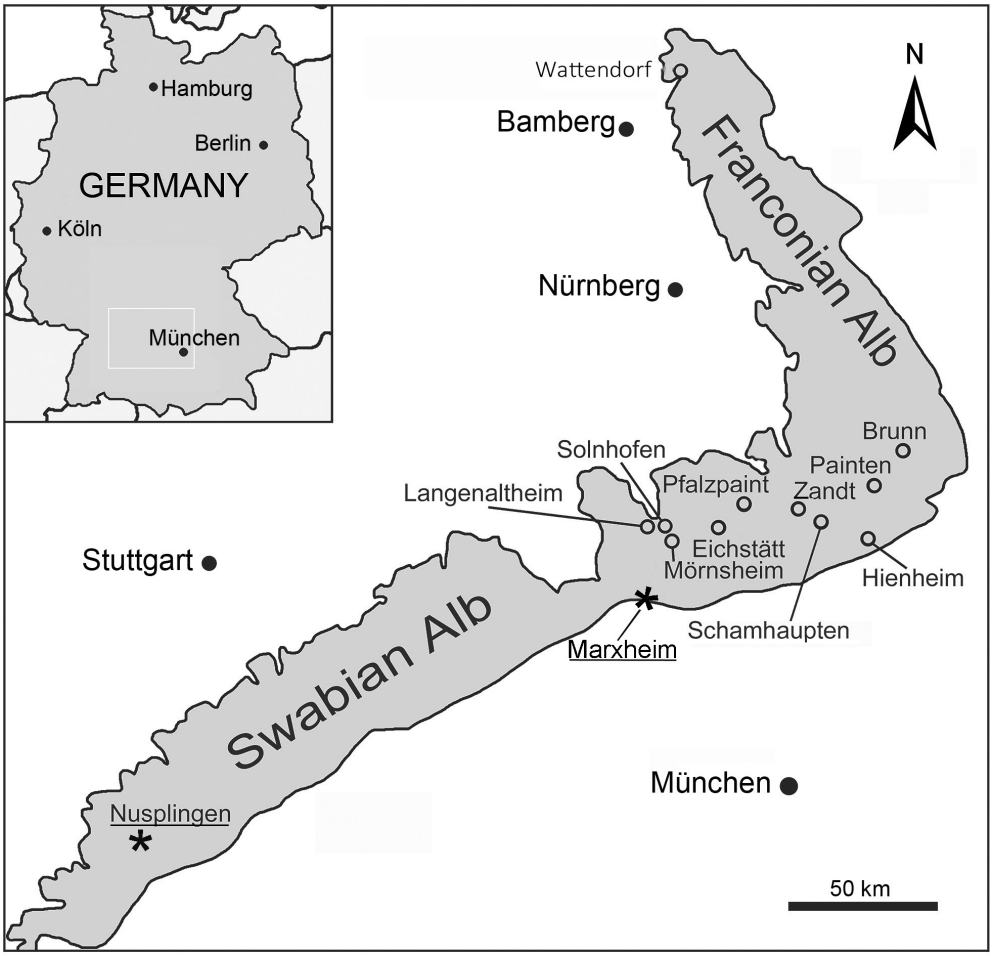


Fig. 1. Localities that yielded the material of *Stenodactylina* (asterisks) and additional Upper Jurassic Plattenkalk localities in southwest Germany (modified from Fürsich et al., 2007).

A third specimen of *Stenodactylina* comes from Upper Jurassic plattenkalks exposed at the northern hillside of the River Danube, southwest of the village of Marxheim (Fig. 1). These plattenkalks had not been studied previously for their fossil content. Fesefeldt (1962) mapped the area around Marxheim and described several sections and outcrops. From his descriptions the plattenkalks in question match the so-called "Spindeltal-Schiefer", an informal lithological unit which is included in the lower Tithonian Usseltal Formation (Zeiss, 1977; Niebuhr & Pürner, 2014). For a determination of the age of these plattenkalks, several ammonite remains were sampled from the scree; these include *Subplanitoides spindelense* Zeiss, 1968 (Fig. 2), *Subplanitoides* sp., "*Torquatisphinctes*" *regularis* Zeiss, 1968 and *Usseliceras* sp. This association clearly indicates the *franconicum* Biohorizon of the lower Tithonian *Mucronatum* Zone (see Schweigert, 2015a). The Submediterranean *Mucronatum* Zone corresponds approximately to the Tethyan *Darwini* Zone (Scherzinger & Schweigert, 2003). Assuming the duration of a biohorizon to have been around 165 ka (Schweigert, 2006), the Tithonian type horizon of the specimen from Marxheim is around 1.15 myr younger than the Kimmeridgian Nusplingen site.

## Methods

The specimens studied were carefully prepared mechanically with needles and scalpels using a binocular with 50 × magnification. Photographs were taken with digital cameras under normal or ultraviolet illumination. Ultraviolet illumination is often used to enhance the contrast between phosphatic fossils and the surrounding rock matrix (e.g., Haug et al., 2009; Tischlinger, 2015). The photographs were finally mounted as illustrations using Adobe Photoshop version CS5.1.

## Systematic palaeontology

Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Superfamily Erymoidea Van Straelen, 1925
Family Erymidae Van Straelen, 1925
Genus *Stenodactylina* Beurlen, 1928

**Included species:** *Stenodactylina armata* (Secretan, 1964), *S. australis* (Secretan, 1964), *S. burgundiaca* (Crônier & Courville, 2004), *S. delphinensis* (Moret, 1946), *S. devillezi* sp. nov. (herein), *S. falsani* (Dumortier, 1867), *S. geigerae* sp. nov. (herein), *S. guisei* (Wright, 1881), *S. insignis* (Oppel, 1862), *S. lagardettei* (Hyžný, Schlögl, Charbonnier, Schweigert, Rulleau & Gouttenoire, 2015), *S. liasina* Beurlen, 1928 (type species), *S. rogerfurzei* Schweigert, 2013, *S. spinosa* (Étallon, 1861), *S. strambergensis* (Bachmayer, 1959), *S. triglypta* (Stenzel, 1945) and *S. walkerae* (Feldmann & Haggart, 2007).

### ***Stenodactylina devillezi*** sp. nov.

2003 *Erymastacus* sp. nov. – Schweigert & Garassino, fig. 2B.
2020 [fragmentary] *Stenodactylina*. – Devillez & Charbonnier, in press.

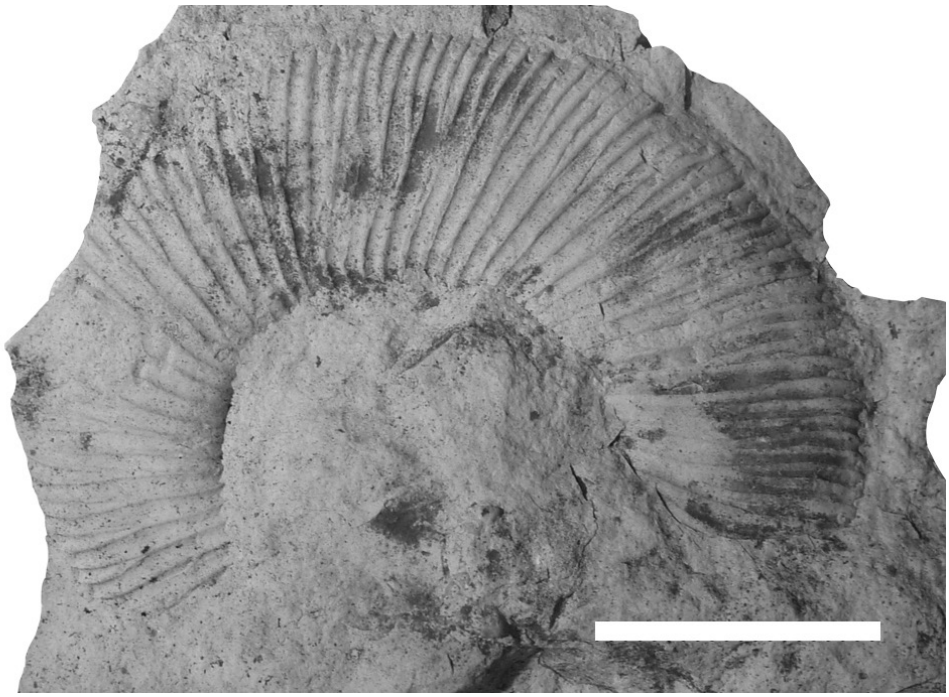

Fig. 2. The ammonite *Subplanitoides spindelense* Zeiss, 1968 from the lower Tithonian, *Mucronatum* Zone (= *Darwini* Zone), 'Spindeltalschiefer' of Usseltal Formation, Marxheim (leg. K. Geiger). Photograph: K. Geiger. Scale bar equals 20 mm.


Fig. 3. *Stenodactylina devillezi* sp. nov., A, holotype, SMNS 64872; B, paratype, SMNS 70506. Upper Kimmeridgian, *Beckeri* Zone, *Ulmense* Subzone, Nusplingen Formation, Nusplingen Quarry, Westerberg hill west of Nusplingen, southwest Germany. Photographs: G. Schweigert. Scale bars equal 10 mm.

**Holotype**: SMNS 64872, from the Nusplingen Formation (upper Kimmeridgian, *Beckeri* Zone) of Nusplingen, Baden-Württemberg, southwest Germany (Fig. 1).

**Paratype:** SMNS 70506, from same locality and biohorizon as the holotype.

**Etymology:** Named after Julien Devillez (Paris), who revised all previously described erymid taxa from the Jurassic and Cretaceous.

**Type locality and horizon:** Nusplingen Quarry, west of Nusplingen, southwest Swabian Alb (Fig. 1); Nusplingen Formation (upper Kimmeridgian, *Beckeri* Zone, *Ulmense* Subzone; see Schweigert, 2007).

**Diagnosis:** Species of *Stenodactylina* with a P1 chela that is characterised by a slender subrectangular manus, a completely toothless dactylus and an index with seven teeth in the proximal half and a sinuosity in the distal part.

**Description:** The holotype is a relatively large left cheliped consisting of a well-preserved chela with manus and remains of the carpus. Manus subrectangular, length 33 mm, width 17 mm. Manus and carpus covered with fine, randomly scattered pustules; fingers lacking pustules, only with a few setal pits. Dactylus length 34 mm; index and dactylus terminally curved inwards. Occlusal surface of dactylus toothless; index bearing seven teeth in its proximal part, the strongest one is the third as counted from the distal side, with a longer distance between the first and the second. Distal half of index with a sinuosity.

The paratype is a right cheliped consisting of a manus with chela, the carpus and merus. Manus

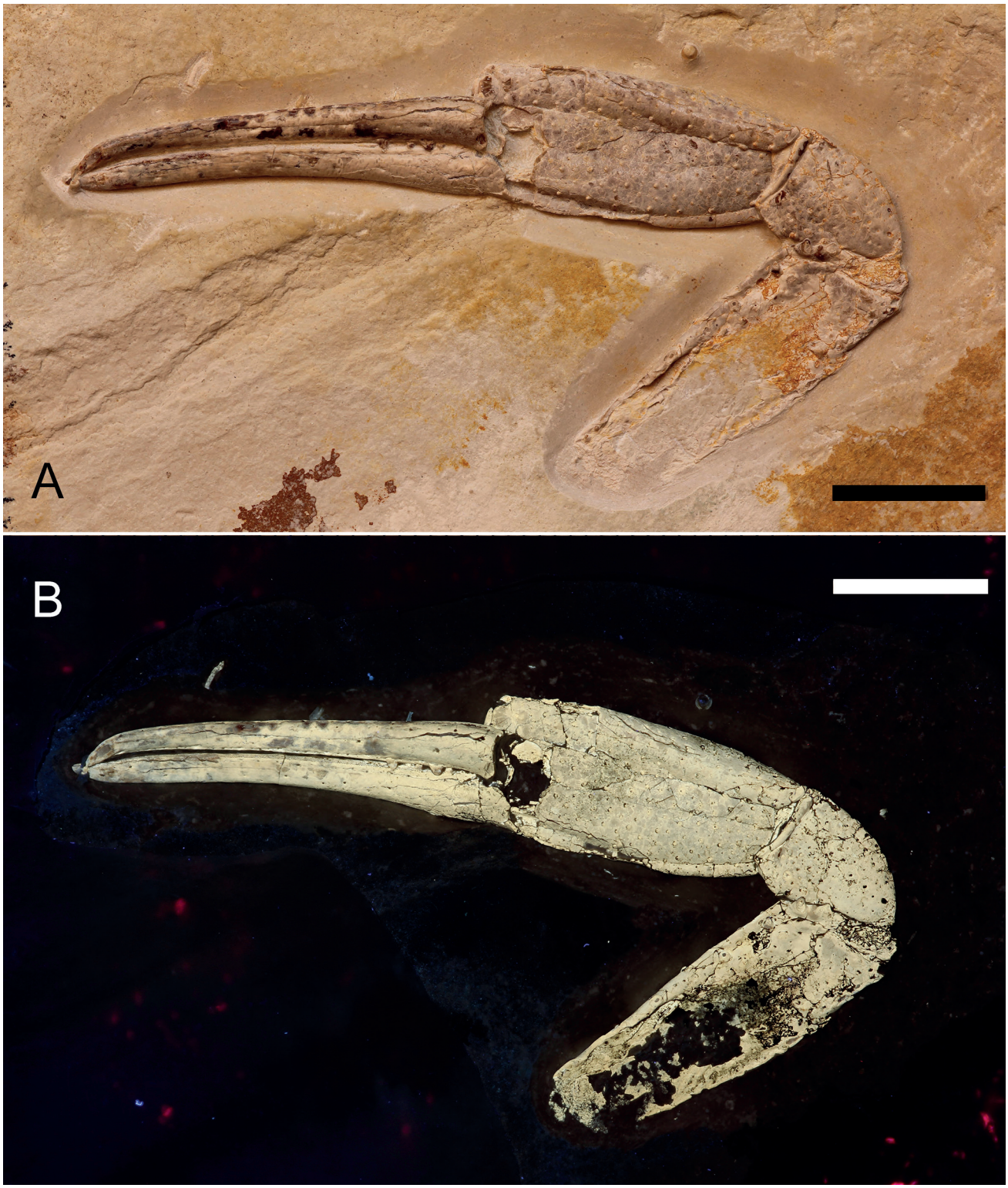


Fig. 4. *Stenodactylina geigerae* sp. nov., holotype, SMNS 70507. A: photographed under normal illumination; B, photographed under ultraviolet illumination. Lower Tithonian, *Mucronatum* Zone (= *Darwini* Zone), 'Spindeltalschiefer' of Usseltal Formation, Marxheim, southwest Germany. Photographs: J. Härer. Scale bars equal 10 mm.

subrectangular, length 22 mm, width 10.5 mm. Carpus 10.5 mm long; merus poorly preserved, 26 mm long. Ornamentation of manus and carpus identical to that in the holotype. Dactylus length 26 mm, with some setal pits, otherwise smooth, distally curved, slightly dislocated during burial. Index mostly covered by dactylus, distal half broken off.

**Remarks:** The slight differences in the fingers/manus length ratio between the left and right cheliped (although observed in different individuals) point to heterochely in *S. devillezi* sp. nov., which is well known in other species of *Stenodactylina* (see Hyžný et al., 2015). A very fragmentary chela from Nusplingen that shows long and slender fingers with strong and widely spaced teeth,

originally recorded in open nomenclature (Schweigert et al., 2000: pl. 5, fig. 4, as "Erymidae gen. et. sp. indet."), possibly belongs to *Enoploclytia* M'Coy, 1849, another erymid genus recently recorded from the Upper Jurassic (Devillez et al., 2018). The rather atypical, slender appearance of the propodus is caused by incomplete preservation. No further specimen has been found so far.

***Stenodactylina geigerae*** sp. nov.

**Holotype:** SMNS 70507, from the Usseltal Formation (lower Tithonian, *Mucronatum* Zone) of Marxheim, Bavaria, southwest Germany (Fig. 1).

**Etymology:** Named after Katharina Geiger (Munich), who found and kindly donated the specimen.

**Type locality and horizon:** Northern hillside of the River Danube, southwest of Marxheim, Bavaria, Germany (Fig. 1), Usseltal Formation, lower Tithonian, *Mucronatum* Zone (= Submediterranean equivalent of Tethyan *Darwini* Zone).

**Diagnosis:** Species of *Stenodactylina* with a P1 chela that is characterised by only two teeth in the proximal third of the dactylus and index.

**Description:** The holotype is a left cheliped with the manus, carpus and merus preserved. Several fine cracks are detectable resulting from compaction of the hollow fossil. Manus subrectangular, 19 mm long, 9.5 mm wide. Merus, carpus and manus covered with randomly scattered small pustules; coarser tubercles occur only along the inner margins of the merus and carpus. Merus length 23 mm, with a few spiny tubercles along the articulation towards the carpus. Carpus length 12 mm, distally bordered by a smooth seam. Fingers *c*. 28 mm long, lacking any pustules, only bearing a few tiny setal pits. Occlusal surfaces of dactylus and index each with two prominent teeth in the most proximal parts, otherwise smooth. Strongest tooth is the first one, counted from the proximal side of each finger.

## Discussion

The preservation of isolated chelipeds of *Stenodactylina* in lithographic limestones probably results from predation activity in nearby shallower environments. The lobsters themselves usually did not inhabit the hostile sea floor of the lagoons. The most common way for erymid lobsters and most other decapod crustaceans to become fossilised complete in Solnhofen-type plattenkalks is via exuviae (Schweigert & Garassino, 2003). The bulk of exuviae, however, represent juvenile specimens, whereas larval stages are rare as well due to their poor sclerotization (Haug et al., 2011). Juvenile stages of erymid lobsters are not easy to differentiate and much more material is needed to reconstruct their ontogenies.

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