



Additions to the morphology of Munidopsidae (Decapoda: Anomura) and Goniidromitidae (Decapoda: Brachyura) from the Jurassic Solnhofen-type lagerstätten, Germany

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With 7 figures

Abstract: Recognition of remains of sterna, pleons, and pereopods of *Aulavescus paintenensis* n. sp. (Munidopsidae) and *Goniidromites serratus* BEURLEN, 1929, from the Late Jurassic Solnhofen-type lagerstätten in Bavaria, Germany, provides the first description of these structures in Jurassic Munidopsidae and Goniidromitidae. Addition of these morphological characters to Goniidromitidae and cladistic analysis secured the position of the family within Homolodromioidea and Dromiacea.

Key words: Decapoda, *Aulavescus*, Munidopsidae, *Goniidromites*, Goniidromitidae, morphology, Germany.

1. Introduction

The Late Jurassic Solnhofen-type lagerstätten in southern Germany are world-famous for the exquisite preservation of invertebrate and vertebrate fossils. Among them, decapod crustaceans are well represented by numerous species of shrimp and lobsters. Only rarely are fossil crabs or anomurans encountered. Recently, collections of tiny crabs and anomurans exhibiting a nearly complete array of body parts and appendages from three localities have been assembled. These specimens are extremely important because they permit not only description of anatomical parts not previously known but they also make it possible to further test the phylogenetic position of ancient crabs previously known only from dorsal carapace morphology. The purpose of this work is to describe and illustrate previously unknown elements of the sternum, pleon, pereopods, and eyes of a goniidromitid brachyuran and the pleon and pereopods of a galatheoid anomuran.

2. Geological setting

The completely preserved anomuran and brachyuran decapods described herein come from three localities of Late Jurassic (latest Kimmeridgian to earliest Tithonian) age in Solnhofen-type lagerstätten of Southern Germany (Fig. 1). A few previously recorded specimens of badly preserved brachyurans came from coeval 'plattenkalks' of the Pfalzpaint and Zandt localities (FRICKHINGER 1994; GARASSINO et al. 2005; SCHWEIGERT 2011), whereas such fossils are almost unknown from the Solnhofen Lithographic Limestones s. str., summarized now as the Altmühltal Formation (NIEBUHR & PÜRNER 2013). Additionally, J. HAUG et al. (2015) described a crab larva from Solnhofen rocks near Blumenberg, Germany.

The stratigraphically oldest locality providing material is known as the Oechselberg quarry. The quarry is located on a hill (Öchselberg) near the small village of Breitenhill (ca. 30 km E from Eichstätt, Bavaria, S

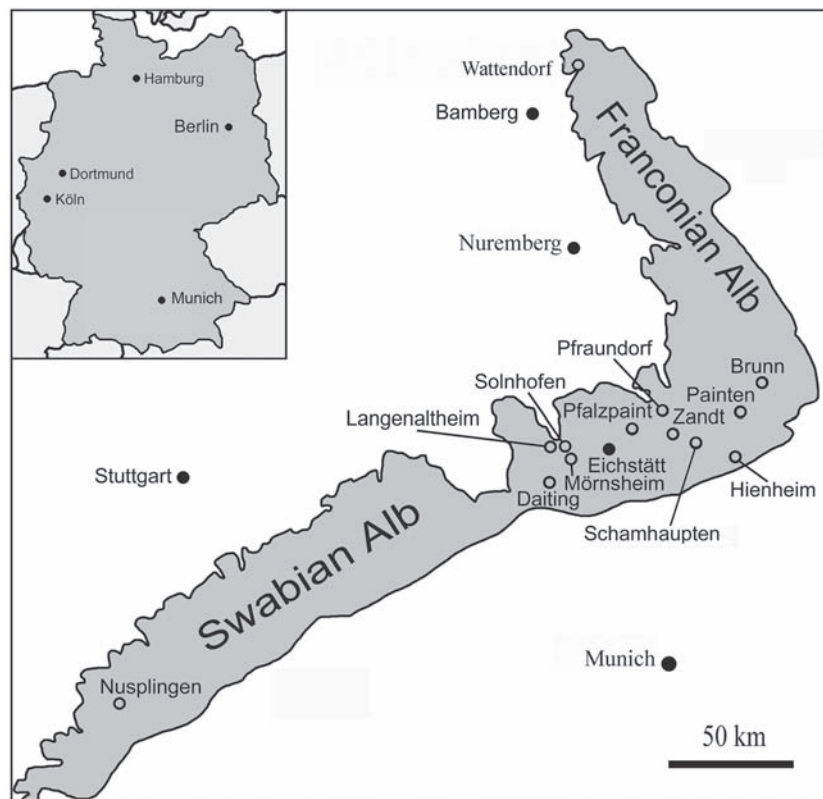


Fig. 1. Map showing various localities with lithographic limestones in southern Germany showing localities from which the specimens reported herein were collected. Modified from FÜRSICH et al. (2007).

Germany). The laminated limestones ('plattenkalks') exploited in this quarry belong to the lower part of the Zandt Member of the Painten Formation (lithostratigraphic terminology recently updated by NIEBUHR & PÜRNER 2013). According to some age-diagnostic ammonites such as *Sutneria bracheri*, the plattenkalks of the Oechselberg quarry are latest Kimmeridgian in age (Beckeri Zone, *rebouletianum* biohorizon). The Zandt Member is better known from earliest Tithonian lithographic limestones with marly intercalations higher up in the section, which are well-known for their rich decapod fauna associated with benthic organisms such as brittlestars and echinoids (AUDO et al. 2014; SCHWEIGERT 2015b). These limestones are quarried closer to the name-bearing village of Zandt. The Zandt lagoon ('Zandter Wanne') – with the Zandt and Oechselberg quarries – is separated from a nearby lagoon to the east, the Schamhaupten lagoon ('Schamhauptener Wanne') by a dolomitized ridge originally representing areas with sponge-microbial and coral reefs.

The second locality is a small limestone quarry opened for amateur collectors, located NW from Schamhaupten, a village only ca. 4 kilometres east from Breitenhill. The lamination of the lagoonal deposits results from oxygen-depletion within and above the seafloor that prevented the settling of epi- and endobenthic animals. The laminated limestones of Schamhaupten belong to two Upper Jurassic formations. The lower one (Torleite Formation, Arnstorf Member) comprises silicified laminates and occasional calciturbidite layers. The Torleite Formation of Schamhaupten has become famous for the unique find of a small well-preserved theropod dinosaur, *Juravenator starki* (GÖHLICH & CHIAPPE 2006, 2010). Many other taxa of exceptionally preserved fossils of vertebrates (fish, turtles, marine crocodiles) and invertebrates (ammonites, squids, crustaceans, echinoids) as well as terrestrial plants were recovered during several years of scientific excavations governed by the Jura-Museum Eichstätt (VIOHL & ZAPP 2006, 2007; VIOHL 2015). These outstanding

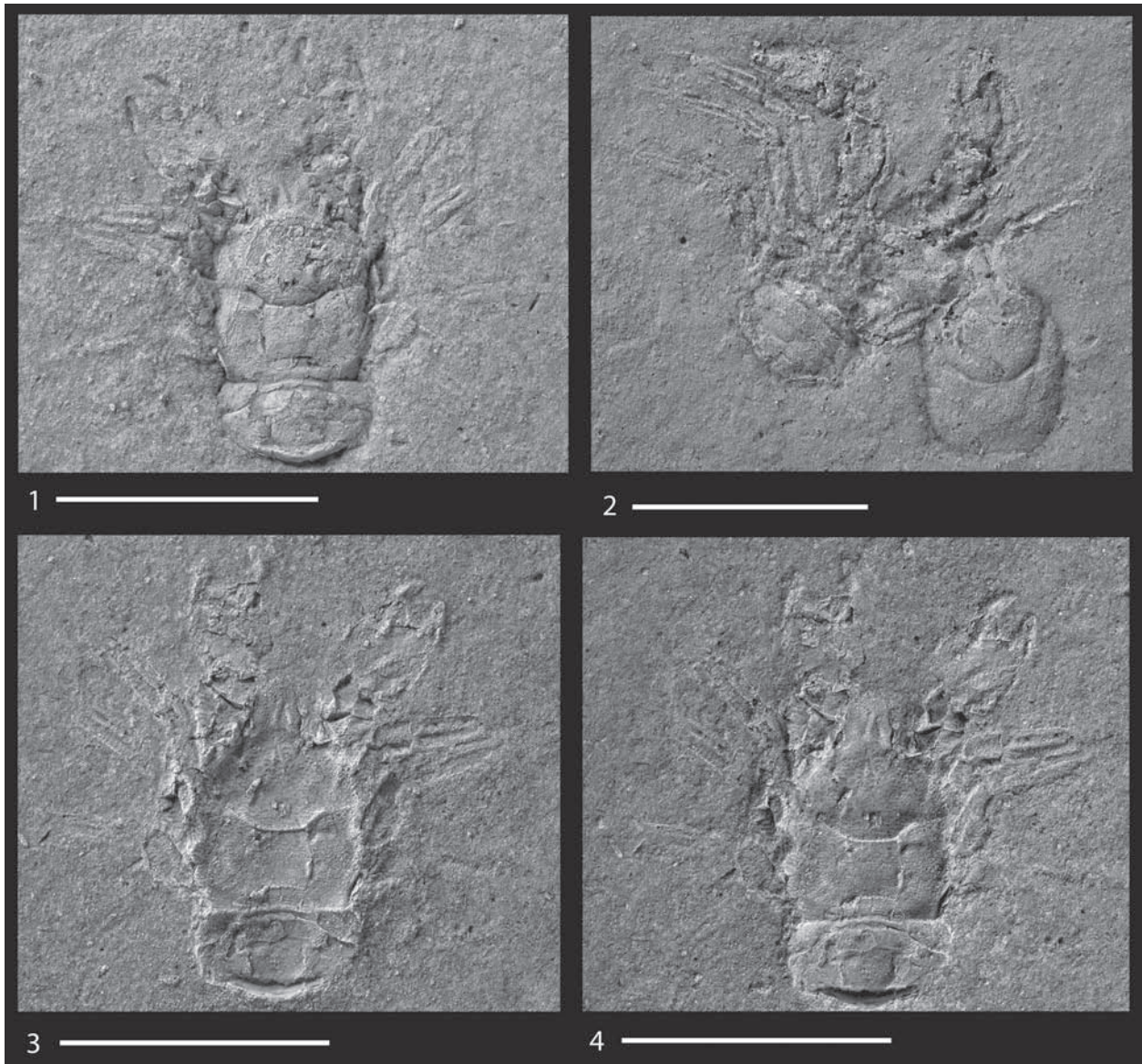


Fig. 2. *Aulavescus paintenensis* n. sp. **1** – SMNS 70306a, Paratype, female. **2** – SMNS 70000, Holotype, female. **3** – SMNS 70306b, counterpart of SMNS 70306a. **4** – SMNS 70306b, reverse imaging with illumination from the lower right. Specimens tinted with Dr. Ph. Martin's Synchronatic Transparent Water Color and whitened with ammonium chloride. Scale bars = 1 cm.

fossiliferous beds represent a conservation fossilagerstätte (*sensu* SEILACHER et al. 1985) and are latest Kimmeridgian in age (SCHWEIGERT 2007, 2015a). The silicified beds of the Torleite Formation are conformably overlain by the lithographic limestones of the Painten Formation, which are exposed in the above-mentioned small quarry. In contrast to the underlying beds, little is known of the fossil content of these limestones, except for a few ammonites (e.g., *Lithacoceras eigeltingense*) indicating an earliest Tithonian age (Hybonotum Zone,

eigeltingense biohorizon) and the spectacular find of a still undescribed *Archaeopteryx* specimen, which is kept in a private collection. Although these beds appear to be much poorer in fossils than the underlying Torleite Formation, they quite frequently yield 'ghosts' of poorly sclerotized crustaceans such as brachyurans and anomurans (SCHWEIGERT 2015b).

The third locality which has provided material for this study is the vicinity of the town of Eichstätt, where the classical Solnhofen 'plattenkalks' are exploited



Fig. 3. *Aulavescus paintenensis* n. sp. **1** – SMNS 70040, Paratype, male, reverse imaging with illumination from the lower right. **2** – SMNS 70040, Paratype, moldic preservation with illumination from upper left. Specimens tinted with Dr. Ph. Martin's Synchronatic Transparent Water Color and whitened with ammonium chloride. Scale bars = 1 cm.

in numerous quarries. The bulk of the fossils known as “Solnhofen” fossils come from these quarries. The early Tithonian ‘plattenkalks’ near Eichstätt represent the Eichstätt Member of the Altmühltal Formation. The laminated limestones which are used for roof and ground tiles are world-famous for their well-preserved vertebrates (e.g., *Archaeopteryx*) and numerous invertebrates, especially insects. Decapod crustaceans in general are very diverse there as well (SCHWEIGERT 2011, 2015b), but among them, anomurans and brachyurans occur only sporadically, probably because of the com-

paratively long distance of shallower areas from the hostile environment at the place of burial. However, we must take into account that the quarrymen and amateur collectors may easily overlook such delicate fossils, especially when the fossils are covered and hidden by microbial mats.

It seems that special diagenetic conditions during the deposition of the Painten Formation in the area of Schamhaupten and Breitenhill are responsible for the exceptional preservation of both brachyurans and anomurans. Brachyurans and anomurans are hypothesized



Fig. 4. *Munidopsis crassa* SMITH, 1885. Unnumbered extant specimen from the spirit collections of the U. S. National Museum of Natural History showing sternal form and array of pereopods. Scale bar = 1 cm.

to have originally lived in shallower areas within the sponge-microbial bioherms and coral reefs surrounding the deeper lagoons and were passively transported to their places of burial as exuviae. The same happened during the time of deposition of the underlying Torleite Formation, where such decapods (e.g., *Gastrosacus wetzleri*) occur in the turbidite layers (VIOHL & ZAPP 2006, 2007). The probable original habitats in the surroundings of the Schamhaupten and Zandt lagoons cannot be directly reconstructed due to the dolomitization processes during which all fossil remains within these rocks were destroyed.

3. Systematic palaeontology

Institutional abbreviations: BSP, Bayerische Staatssammlung für Paläontologie und Geologie, München (Munich), Germany; LF, Lauer Foundation for Paleontology, Science & Education NFP, Wheaton, Illinois, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Order Decapoda LATREILLE, 1802
 Infraorder Anomura H. MILNE-EDWARDS, 1832
 Superfamily Galattheoidea SAMOUELLE, 1819
 Family Munidopsidae ORTMANN, 1898

Genus *Aulavescus* ROBINS, FELDMANN & SCHWEITZER, 2013.

Type species: *Aulavescus exutus* ROBINS et al., 2013, by original designation.

Other included species: *Aulavescus paintenensis* n. sp., *A. tectus* ROBINS et al., 2013.

Diagnosis: See ROBINS et al. (2013).

Discussion: Prior to this study, the only galatheid recorded from the Solnhofen-type limestones (Schamhaupten and Nusplingen) was *Gastrosacus wetzleri* v. MEYER, 1851. This species is characterized by a triangular, sharply crested rostrum; a well developed branchiocardiac groove; and coarse, granular ornamentation that becomes stronger in the metabranchial region (see ROBINS et al. 2015). By contrast, species of *Aulavescus* bear a more rounded rostrum with a weak keel, a branchiocardiac groove that is weak or absent, and nearly obscure carapace ornamentation. The new material is characterized by the latter. Thus, the description of *Aulavescus paintenensis* n. sp. herein documents just the second genus of galatheid from the Solnhofen limestones, both within the Munidopsidae.

Aulavescus paintenensis n. sp.
 Figs. 2, 3

2015b *Gastrosacus wetzleri* MEYER. – SCHWEIGERT, p. 280, fig. 562.

Etymology: The trivial name refers to the Painten Formation, from which the species was collected.

Types: The holotype is SMNS 70000, and paratypes are SMNS 70306a & b, and SMNS 70040.

Occurrence: The holotype and one paratype (SMNS 70040) were collected from the Schamhaupten quarry; Painten Formation, Late Jurassic, latest Kimmeridgian; near Schamhaupten, Bavaria, Germany. The second paratype (SMNS 70306a & b) was collected from the Oechselberg quarry;

Zandt Member of Painten Formation; Late Jurassic, latest Kimmeridgian; near Breitenhill, 30 km E from Eichstätt, Bavaria, Germany.

Diagnosis: Rostrum broadly triangular with rounded, truncated termination and weak axial keel that does not reach termination. Circumgastric groove moderately well developed; branchiocardiac groove reduced to subtle groove defining margins of urogastric and cardiac regions; hepatic region curves anteriorly and axially but does not terminate in a postorbital spine. Carapace surface uniformly granular.

Description: Carapace quadrate, longer than wide; length excluding rostrum 1.1 times maximum width measured at level of base of circumgastric groove. Rostrum broad, 43% maximum carapace width, long, 28% total length of carapace including rostrum. Carapace weakly arched transversely, flattened longitudinally.

Rostrum straight-sided, widening posteriorly with smoothly rounded tip, depressed below frontal region. Margins of rostrum rimmed, beaded. Axis of rostrum sulcate, bounded by subtle, lanceolate, beaded rim. Orbital margin inclined anterolaterally at 54° angle to midline; extends from base of rostrum to anterior termination of smoothly parabolic circumgastric groove. Lateral margin straight; posterolateral corner smoothly rounded; posterior margin concave posteriorly.

Frontal lobes wider than long, inclined at about 60° angle to long axis, inflated. Anterior process of mesogastric region elongate, triangular. Remainder of gastric and hepatic regions undifferentiated, coarsely granular, bounded by circumgastric groove. Epibranchial region triangular, bounded by circumgastric groove and posterior cervical groove (groove terminology of KLOMPMAKER et al. (2012). Remainder of branchial regions undifferentiated, bearing granules ranging from circular anteriorly to transversely elongate posteriorly. Cardiac region large, circular, slightly inflated, with fine transverse ridges.

Terminal three pleonites and telson of female and two pleonites and telson of male preserved. Pleonites wider than long in both, but proportionately wider in female. Lateral margins gently rounded. Telson of female short, rounded posteriorly. Telson of male short, triangular.

Sternum poorly preserved, triangular, with distinct sternites, and apparently bearing axial and lateral pits.

Pereiopods short. Cheliped with broad merus, about twice as long as wide, flattened. Carpus poorly preserved, short. Propodi apparently isochelous, hand inflated, fingers short, pointed. Occlusal surfaces not well exposed. P2-P4 similar in form, becoming shorter and more delicate posteriorly. Meri broad, smooth. Carpi and propodi narrower, with two longitudinal ridges. Dactyli short, sharply pointed.

Discussion: *Aulavescus paintenensis* n. sp. conforms closely to the description of the genus. The specimens have a subtriangular rostrum with a blunt termination and a weak axial keel that does not extend to the termination of the rostrum. The circumgastric groove is well developed, and the branchiocardiac groove is poorly expressed. Axial regions are moderately well defined, and lateral regions are less well differentiated. The metagastric region is slightly elevated above the remainder of the gastric region and the urogastric and cardiac regions are not readily distinguished. The latter two are bounded laterally by the weak vestige of the branchiocardiac groove. The margins of the hepatic region converge anteriorly. The carapace surface is covered by transversely elongate granules. Thus, placement within *Aulavescus* is secure.

The specimens referred to *Aulavescus paintenensis* share significant morphological features, including the sulcate, spatulate rostrum, development of the circumgastric groove, lack of branchial definition, claw form, and length and shape of the walking legs. Primary differences in superficial appearance of the specimens can be attributed to preservational style and vagaries of lighting. Excellent preservation of the outer surface of cuticle is exhibited on the paratype SMNS 70040, whereas the surfaces exposed on the holotype SMNS 70000 and paratype SMNS 70306a and b have experienced exfoliation of the cuticle. Further, the specimens have been variously compressed and incompletely preserved which renders the specimens somewhat different from one another in appearance.

Interpretation of sex of the specimens is approached with caution. The broad pleon with rounded margins, as wide or slightly wider than the carapace on the holotype and paratype SMNS 70306a and b are interpreted to be adult female characters. By contrast, the pleon of paratype SMNS 70040 is narrower than the carapace and is apparently straight sided, suggestive of its being a male specimen.

The genus has been known previously from only two specimens representing two species. *Aulavescus paintenensis* differs from the type species, *A. tectus*, as the latter has a broader, sulcate rostrum with a blunt, trifold termination. The circumgastric groove is better developed, and the granulation on the metagastric region is more coarse than on other parts of the carapace on *A. tectus*. *Aulovescus exutus* can be distinguished from *A. paintensis* because the former bears a slightly narrower, and less sulcate, rostrum; the anterior margins of the hepatic region are more clearly defined and are drawn into small outer orbital spines on *A. exutus*. The overall carapace surface of *A. exutus* is more finely granular.

The two previously described species are known only by partially preserved dorsal carapaces, so that the discovery of elements of the pleon, sternum, and appendages provide valuable new information for the genus as well as the Mesozoic

Fig. 5. *Goniodromites serratus* BEURLEN, 1929. **1** – SMNS 70003a, positive image of partial carapace, sternum and fragments of pereiopods of molted individual. **2** – SMNS 70003b, counterpart of 70003a illuminated from upper left. **3** – SMNS 70003b, reversed imaging with illumination from lower right. **4** – SMNS 70039a, positive image of nearly complete carapace and pereiopods. **5** – SMNS 70039b, counterpart of 70039a illuminated from upper left. **6** – SMNS 70039b, reversed imaging with illumination from lower right. Specimens tinted with Dr. Ph. Martin's Synchronatic Transparent Water Color and whitened with ammonium chloride. Scale bars = 5 mm.

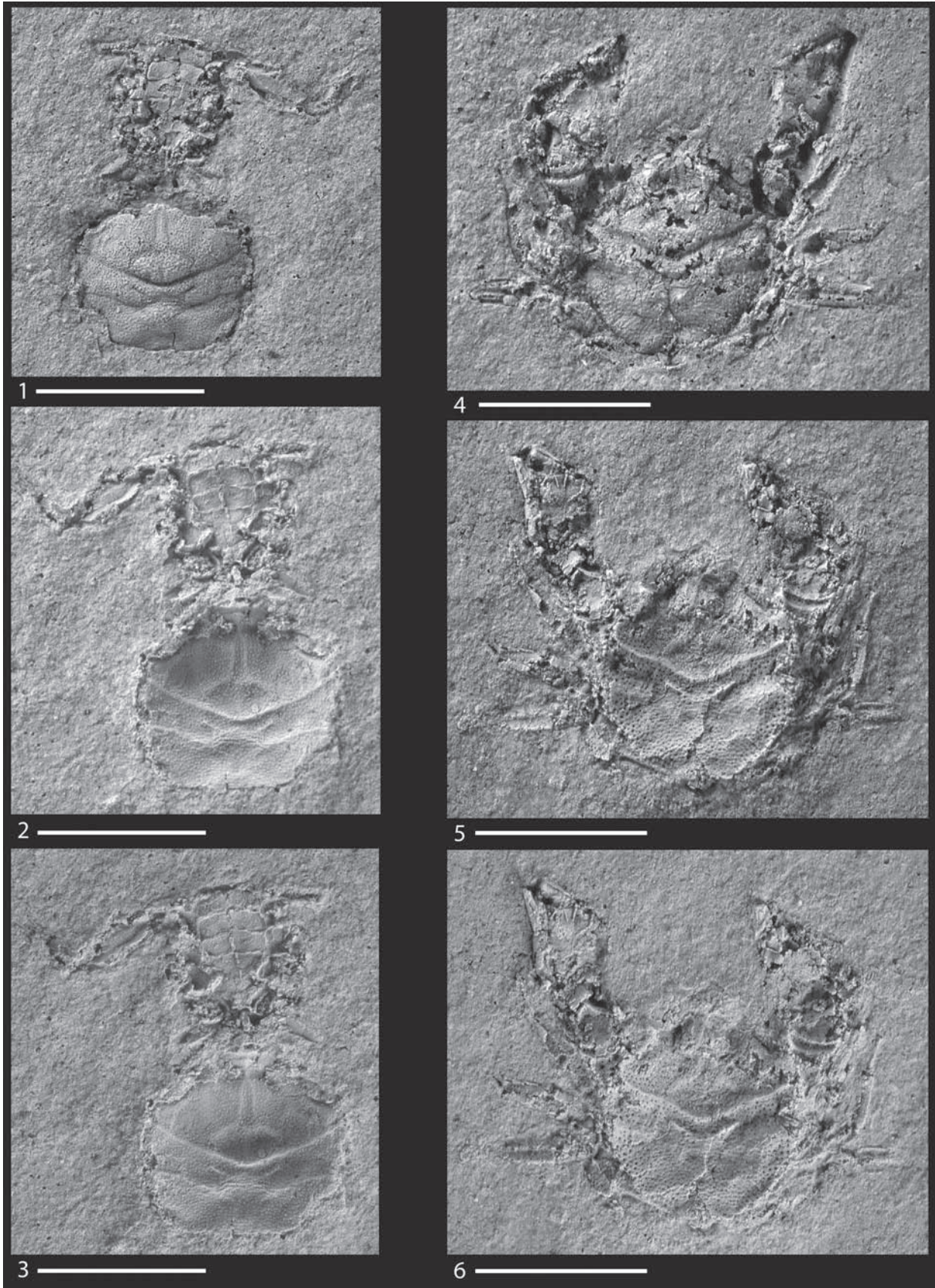


Fig. 5.

munidopsids. Morphology of the sternum helps to secure placement within Munidopsidae as illustrated by *Munidopsis crassa* SMITH, 1885 (Fig. 4). The sternum of both the extant form and *Aulavescus paintenensis* are triangular, widening posteriorly, with well defined sternites and axis. Further, the length of the cheliped (P1) is shorter than the length of the first walking leg (P2) which is typical of extant munidopsids (MACPHERSON, personal commun., 2015).

One of the specimens, SMNS 70000, represents a molt. The carapace has been separated from the sternum, pleon, and appendages that have remained largely intact and rotated dorsally so that the ventral surface of the sternum, pleon, and appendages lies in the same plane as the dorsal surface of the carapace. This attitude suggests that there was little current agitation in the environment in which the animal cast off its exoskeleton. Little, if any, disarticulation is evident.

Infraorder Brachyura LINNAEUS, 1758
Section Dromiacea DE HAAN, 1833
Superfamily Homolodromioidea ALCOCK, 1900
Family Goniiodromitidae BEURLEN, 1932

Genus *Goniiodromites* REUSS, 1858

Type species: *Goniiodromites bidentatus* REUSS, 1858, by subsequent designation of GLAESSNER (1929: 327).

Other included species: *Goniiodromites aliquantulus* SCHWEITZER, FELDMANN & LAZÁR, 2007; *G. complanatus* REUSS, 1858 [imprint 1857]; *G. cenomanensis* (WRIGHT & COLLINS, 1972); *G. dacica* (v. MÜCKE, 1915); *G. dentatus* LÖRENTHEY in LÖRENTHEY & BEURLEN, 1929; *G. hirotai* KARASAWA & KATO, 2007; *G. kubai* STARZYK, KRZEMIŃSKA & KRZEMIŃSKI, 2012; *G. laevis* (VAN STAELLEN, 1940b); *G. narinus* FRANTĚSCU, 2011; *G. polyodon* REUSS, 1858 [imprint 1857]; *G. sakawense* KARASAWA & KATO, 2007; *G. serratus* BEURLEN, 1929; *G. transsylvanicus* LÖRENTHEY in LÖRENTHEY & BEURLEN, 1929.

Diagnosis: See SCHWEITZER et al. (2012).

Discussion: Previous records of Goniiodromitidae from Solnhofen limestones include *Goniiodromites serratus* BEURLEN, 1929, *Pithonoton marginatum* (v. MEYER, 1842), and *Pithonoton* sp. (fide GARASSINO et al. 2005). *Pithonoton* sp. conforms to the outline of *Goniiodromites* spp. and appears to have a truncate rostral region with an axial reentrant. The specimen is notable because, although poorly preserved, it bears pereopods (GARASSINO et al. 2005, fig. 6). *Pithonoton marginatum*, as well as the genus in general, is characterized by a carapace that is much longer than wide, a prominent rostrum, and a branchiocardiac groove that is nearly as strong as the cervical groove. The branchiocardiac groove is developed not only on the adaxial region but also curves posteriorly to sharply define the margins of the cardiac region (SCHWEITZER et al. 2012). These features readily distinguish the specimens discussed herein from species of *Pithonoton* v. MEYER, 1842. The specimens herein are only slightly longer

than wide, have a branchiocardiac groove that is prominent laterally but is not well expressed around the cardiac region, and appear to have a short rostral region, although it is not well preserved. The specimens bear close resemblance to specimens previously assigned to *Goniiodromites serratus*. The type description of *G. serratus* was recently translated from German into English (FELDMANN et al. 2006), and it is the type description that permits confident placement of the specimens from the Solnhofen rocks within this species. WEHNER (1988, pl. 6, figs. 2, 3) illustrated two specimens she referred to *G. serratus*; however, neither specimen bears a postcervical groove and neither has a cardiac groove bearing the three nodes described by BEURLEN (1929). Thus, her material cannot be assigned to *G. serratus*, and the specimens must be re-examined to assure proper placement.

Goniiodromites serratus BEURLEN, 1929
Figs. 5–7

Referred specimens: Seven specimens, SMNS 70001a & b, 70003a & b, 70039a & b, LF 1673, 1677, 1823, and 2154, are referred to *Goniiodromites serratus* herein.

Occurrence: SMNS 70001, 70003, and 70039 were collected from the Schamhaupten quarry; Painten Formation, Late Jurassic, latest Kimmeridgian; near Schamhaupten, Bavaria, Germany. LF 1673, 1677, and 1823 were collected from the Oechselberg quarry; Zandt Member of Painten Formation; Late Jurassic, earliest Tithonian; near Zandt, Bavaria, Germany. LF 2154 was collected from Eichstätt Member of the Altmühl Formation; Late Jurassic, early Tithonian; Schernfeld near Eichstätt, Bavaria, Germany.

Description of material: Carapace as wide as long, outline subquadrate, weakly vaulted, carapace regions clearly delineated by narrow, shallow grooves. Surface uniformly and finely granular.

Front poorly preserved, appears to be weakly axially sulcate, missing rostrum, about 42% maximum width measured at midlength of carapace; augenrests long, directed anterolaterally, inclined at 42° angle to midline, weakly rimmed. Lateral margins weakly convex. Posterolateral corner smoothly rounded into weakly concave posterior margin.

Epigastric regions bilobed, small, flanking sulcate front. Mesogastric region with long, narrow, lanceolate anterior process and broad, wider than long, ovate, swollen posterior region, about 36% maximum carapace width. Mold of the interior of mesogastric region with small nodes near lateral corners of broad region. Protogastric and hepatic regions weakly arched and separated by very weak groove. Metagastric region short, concave forward in outline, bounded anteriorly by chevron-shaped cervical groove and posteriorly by concave forward postcervical groove extending anterolaterally, spanning about 33% maximum carapace width. Urogastric region poorly defined, wider than long, depressed. Cardiac region poorly defined, broader than long, ovoid, with two transversely positioned subtle nodes. Intestinal region short, depressed. Epibranchial region bounded anteriorly by cervical groove and posteriorly by shallow branchiocardiac

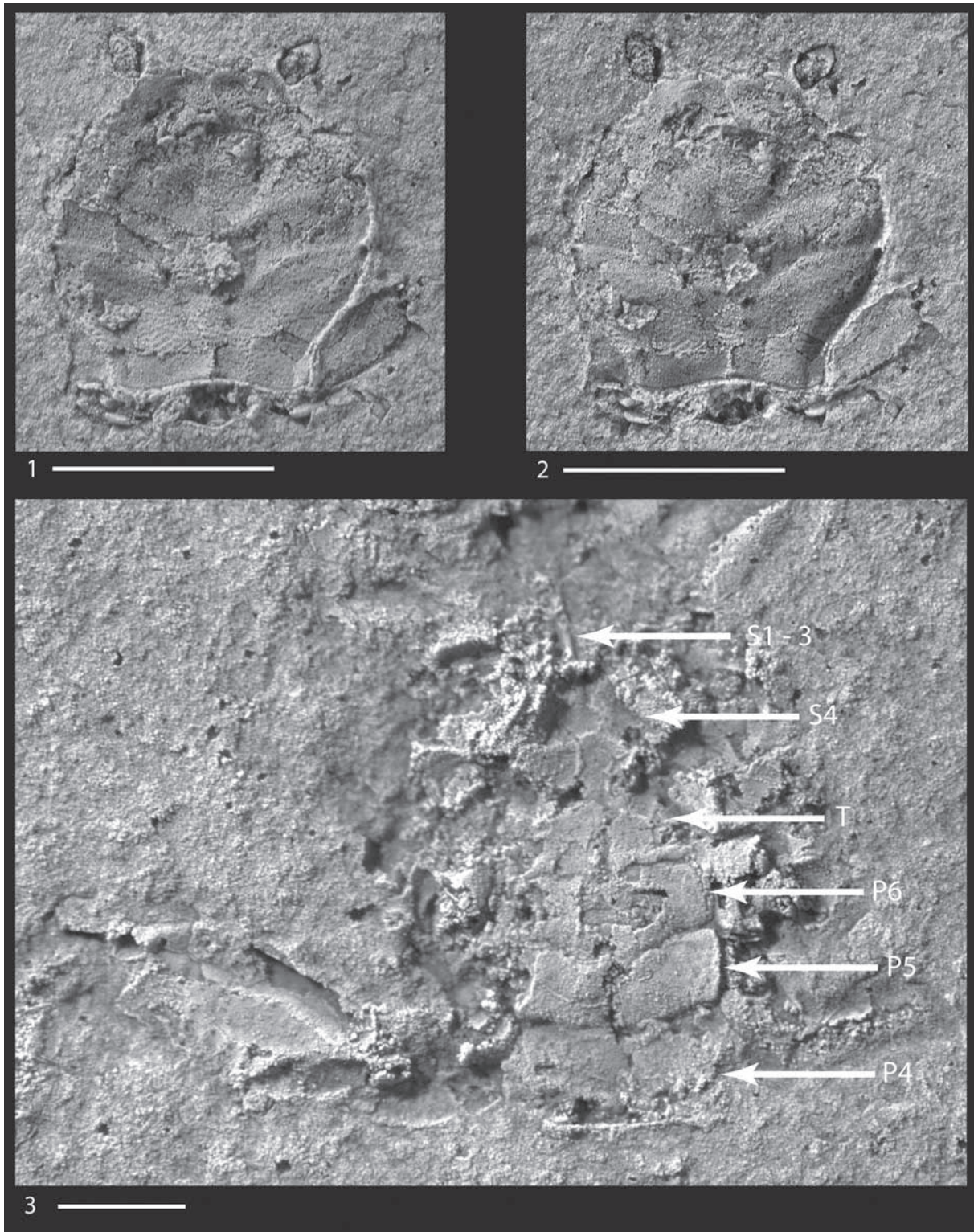


Fig. 6. *Goniidromites serratus* BEURLIN, 1920. **1** – SMNS 70001a, mold of the exterior of a nearly complete carapace with preserved eyes. **2** – SMNS 70001a, reversed imaging with illumination from lower right. **3** – SMNS 70003a, enlargement of sternum and pleon. S1-S3 = sternites 1-3, or anterior process of sternite 4. S4 = sternite 4. P4-P6 = pleonites 4-6. T = telson. Specimens tinted with Dr. Ph. Martin's Synchronic Transparent Water Color and whitened with ammonium chloride. Scale bars = 1 cm.

groove paralleling cervical groove and extending axially to terminate at widest point of cardiac region. Remaining branchial regions undifferentiated.

Anteriormost preserved region of sternum that may represent sternites 1-3 or the anterior extension of sternite 4 with triangular projection 1.5 times as long as wide, with axial ridge. Sternite four broadens posteriorly in axially concave arc to apparent sharp episternal projection (Fig. 6.3). Remainder of sternum not visible.

Pleonite 1 narrow, short, poorly exposed (Fig. 7.4). Pleonite 2 as long as pleonites 3-6 (Fig. 7.3); broadens to about 2/3 maximum pleon width. Pleonite 3 broadens posteriorly to attain maximum pleon width; tergum weakly arched, pleuron tapers laterally to rounded termination. Pleonites 4-6 similar in form with weakly arched terga, quadrate pleura (Fig. 7.1-7.4). Sutures between pleonites transverse with no evidence of articulating rings. Telson rounded triangular (Figs. 6.3, 7.2), wider than long, surface apparently smooth.

Pereiopods short, stout. Total exposed length of P1 shorter than carapace length and proximal segments shorter than robust, apparently isochelous propodi (Fig. 7.6). Propodi rotated into horizontal position with fixed finger placed laterally and dactylus positioned axially. Hands slightly longer than wide, broadens distally; upper and lower surfaces convex, weakly crenulated. Outer surface transversely ridged and bearing fine granulations. Fixed finger slightly downturned, short, tapering to blunt termination; occlusal surface not well preserved. Dactylus short, stout, occludes with fixed finger at steep angle; occlusal surface not well preserved. Remaining pereiopods short, slender, P2 and P3 similar in length and somewhat longer than P4. P5 poorly preserved, subdorsal (Fig. 7.6, arrow).

Eyes large, elongate ovoid, directed anterolaterally, with short eyestalks. Ocular surface not preserved (Fig. 6.1, 6.2).

Discussion: *Goniodromites serratus* has variously been assigned to *Goniodromites* (BEURLEN 1929; FELDMANN et al. 2006; SCHWEITZER & FELDMANN 2007; STARZYK et al. 2012; SCHWEITZER et al. 2012) and *Pithonoton* (COLLINS & WIERZBOWSKI 1985; WEHNER 1988; MÜLLER et al. 2000; GARASSINO et al. 2005). As discussed above, the material studied herein conforms to the concept of *Goniodromites*.

Several aspects of the morphology of *Goniodromites serratus* that are preserved on the specimens in question have not been described previously, and many have been unknown until the present collection was brought together. Appendages of specimens that are poorly preserved, but which can be assigned to *Goniodromites*, were illustrated by FRICKHINGER (1994, fig. 229, as “unnamed crab”), GARASSINO et al. (2005, fig. 6, as *Pithonoton* sp.), and SCHWEIGERT (2011, fig. 3, as “poorly preserved brachyuran”); however, none described their morphology.

Sternal and pleonal morphology has never been recognized in goniodromitids to our knowledge. Although only the anterior part of the sternum is exposed, it provides useful characters that can be coded for cladistic analysis. Similarly, the morphology of the pleon and the nature of the pereiopods provides additional characters for analysis. Taken together, they represent valuable information for testing the placement of this extinct family within the Homolodromioidea. KARASAWA et al. (2011) performed a cladistic analysis of extinct and extant representatives of the so-called podotrematous crabs, and the Goniodromitidae nested within the Homolodromioidea; however, the analysis at that time considered only dorsal carapace characters of Goniodromitidae. With the additional information on pereiopods, sternum, and pleon of the specimens at hand, additional characters were coded for *G. serratus* and the analysis was rerun. The rate of missing data of Goniodromitidae was reduced from 56.8% to 35.1%. The phylogenetic analysis was again based upon KARASAWA et al. (2011: 523-529). The analysis yielded 15 most-parsimonious trees, whereas the original analysis yielded 39 most-parsimonious trees. The new tree length was 225 steps as compared to 224 steps long in the previous tree with a consistency index (CI) of 0.5911 (new) as compared to 0.5938 (previous), a retention index (RI) of 0.8017 as compared to 0.8030, and a rescaled consistency index (RC) of 0.4747 as compared to 0.4768 (previous). The additional scoring for Goniodromitidae reinforces its homolodromioid affinities, being recovered in the same unresolved polytomy with Homolodromiidae, Bucculentidae, and Prosopidae, as initially recovered by KARASAWA et al. (2011).

4. Discussion and conclusions

Recognition of *Aulavescus paintensis* n. sp. in the Painten Formation provides only the second occurrence of Munidopsidae within Solnhofen-type lagerstätten. The preservation of structures other than the dorsal carapace is remarkable, given that Jurassic galatheoids were previously known only from dorsal carapaces. For that matter, the only other member of the Galatheoidea to exhibit preserved pereiopods is *Mulleristhes africana* GARASSINO, DE ANGELI & PASINI, 2008, from the Late Cretaceous of Morocco (GARASSINO et al. 2014). The same is generally true for previous notices of Goniodromitidae in which only anecdotal records of appendages went undescribed. Throughout Europe, a large number of species of these groups have been described and well documented as inhabitants of sponge

Fig. 7. *Goniodromites serratus* BEURLEN, 1929. **1** – LF 1673, mold of the exterior of carapace, pleon, and pereiopods. **2** – LF 1673, reversed imaging with illumination from lower right. **3** – LF 2154, mold of the exterior of carapace, pleon, and partial first pereiopod. **4** – LF 2154, reversed imaging with illumination from lower right. **5** – LF 1823, dorsal view of carapace and pereiopods. Pereiopod 5 (arrow) is subdorsal. **6** – LF 1823, Long wave ultraviolet illumination reveals detail of the surface of chelipeds and pereiopods 2-4. Specimens not tinted or whitened. Scale bars = 1 cm.

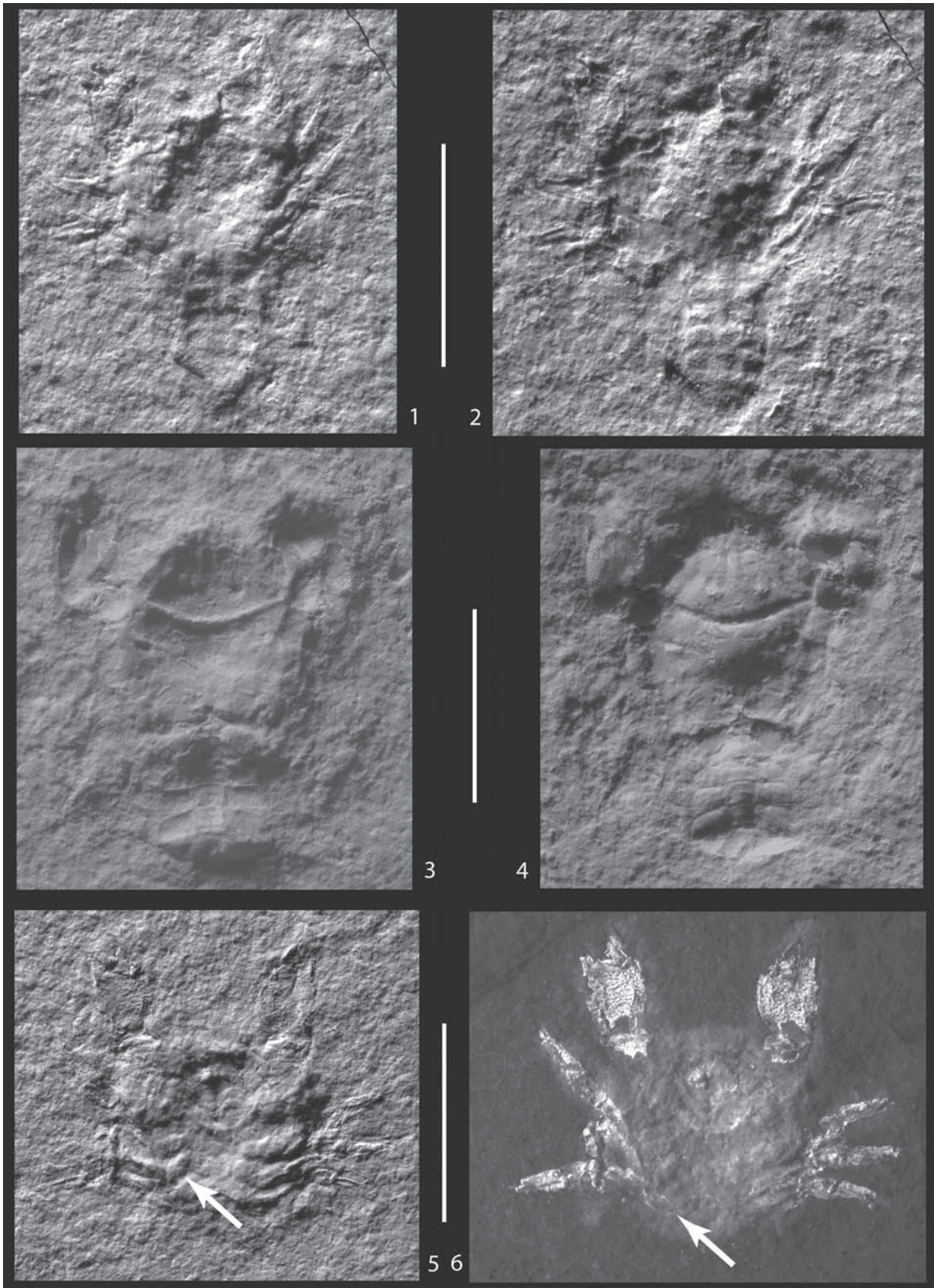


Fig. 7.

and coral reef habitats (see summaries in SCHWEITZER & FELDMANN 2007, KARASAWA et al. 2012 and ROBINS et al. 2013). Those workers and others generally attributed the absence of ventral, pleonal, and appendage elements to the fragile nature of the cuticle of these parts. Some isolated chelipeds have been described; however, because they were not intimately associated with carapace material it was not possible to attribute the claws to a specific taxon.

Although the remains of sterna and pleons described herein are incomplete, they are extremely important in confirming placement of the specimens within higher taxa. Comparison of those structures as well as the pereopods with extant munidopsids shows a strong similarity. For example, examination of the sternum of *Munidopsis crassa* SMITH, 1885, a widespread Atlantic species (GORE 1983) in the collections of the Smithsonian Institution reveals (Fig. 4) the same outline. The sternum of both species is triangular, increasing to attain maximum width at sternite 6 on *M. crassa*; although difficult to discern all the sternites on *A. paintenensis*, the overall outline is also triangular. Episternal projections are either greatly reduced or absent on both species. Development of transverse sternal sutures clearly differentiate sternites on *M. crassa* as do those in *Aulavescus paintenensis*. Comparison of claw morphology and general conformation of the pereopods of the Jurassic species with representative extant forms (AMBLER 1979; POORE et al. 2011) documents the conservative nature of these features. Claws in both *M. crassa* and *A. paintenensis* tend to be relatively short and the other pereopods, although longer than the first pereopod, are not extremely long. The form of the chelipeds is similar in both species in that they are carried in the general plane of the body and with the dactylus positioned axially. Thus, the new material firmly places *Aulavescus* with Munidopsidae.

Because Goniidromitidae are extinct, comparisons can only be made at higher taxonomic levels. Description of the anterior sternites, the pleon, and the appendages of *Goniidromites serratus* herein provide a sufficient number of characters for coding that the position of the genus could be retested in the phylogenetic analysis previously performed by KARASAWA et al. (2011). The results reconfirmed placement within Homolodromioidea. This outcome is important because considerable emphasis for systematic assignment is placed on these characters. In particular, it is notable that discrete large uropodal plates are not visible in the pleon, differentiating Goniidromitidae from Dynomeinidae and Dromiidae.

Although anomurans and brachyurans are much more rare than shrimp and lobsters in the Solnhofen-type lagerstätten in Germany, the discovery of the specimens forming the basis for this work are of special importance. Despite the tiny size and marginal preservation, the specimens have made it possible to assign the forms with much more confidence than previously.

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