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Fast Track Article

Decapods (Crustacea: Brachyura) from the Jurassic of Germany and Lithuania, with descriptions of new species of *Planoprosopon* and *Tanidromites*

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With 9 figures

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Abstract: A Callovian erratic boulder from Pleistocene glacial drift deposits of NE Germany yielded a 'prosopid' crab, which is described here as a new species of the genus *Planoprosopon* Schweitzer Feldmann & Lažar, *Planoprosopon quadratum.* It represents the first unequivocal record of *Planoprosopon* from the Middle Jurassic and thus one of the stratigraphically oldest records of the genus. Another new species, *Planoprosopon thiedeae*, is described from the Kimmeridgian of SW Germany. *Tanidromites lithuanicus* n. sp., a member of Tanidromitidae, is recorded from the Callovian of Lithuania. It is compared with new well-preserved material of other representatives of this genus. *Tanidromites richardsoni* (Woodward) is recorded for the first time from the Bajocian of SW Germany. *Tanidromites insignis* (v. Meyer), *Tanidromites sculpta* (Quenstedt), and *Tanidromites scheffnerae* n. sp., all coming from the Kimmeridgian of SW Germany, are briefly described. *Prosopon aequilatum* v. Meyer is excluded from *Tanidromites* and now assigned to *Eodromites* Patrulius, and a neotype is designated for this species. Possibly, the early diversification of crabs took place during the Middle Jurassic in more temperate, Subboreal shallow water areas lacking reefal habitats and accelerated when reefs occupied these areas in the Late Jurassic.

Key words: Brachyura, longodromitids, tanidromitids, goniodromitids, diversification, palaeoecology, taxonomy, Geschiebe, Middle Jurassic, Late Jurassic, Germany, Lithuania.

1. Introduction

Prosopids and allied crabs represent the most primitive brachyurans, recorded from the late Early Jurassic to the Palaeocene (Wehner 1988; Müller et al. 2000). Their taxonomic relationship and systematic placement is just under revision in an ongoing research programme, especially by R. Feldmann and C. Schweitzer (Kent State University, Ohio, U.S.A.). In the Late Jurassic, these tiny decapods strongly diversified, possibly favoured by the development of numerous cryptic habitats within sponge-microbial mounds and coral reefs on the northern margin of the Tethys Ocean (Collins & Wierzbowski 1985; Wehner 1988; Müller et al. 2000; Feldmann et al. 2006; Schweitzer et al. 2007; Schweitzer & Feldmann 2008a, b, 2009a-c; Franţescu 2010). In contrast, their Early and Middle Jurassic ancestors are still poorly known (e.g., Förster 1979, 1985, 1986; Schweigert 2006; Krobicki et al. 2007; Krobicki & Zatón 2008; Schweitzer & Feldmann 2011). The reasons for this limitation are unknown. Possibly the Liassic and Middle Jurassic crabs had not entered reefal environments, or they were overlooked due to the scarcity of favourable lithologies or other collecting biases.

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Fig. 1. Provenances of the specimens of this study. 1: Lithuania (Middle Jurassic, autochthonous), 2: West Pomerania (Middle Jurassic, allochthonous), 3: Swabia (Upper Jurassic, autochthonous). 4: Franconia (Middle and Upper Jurassic, autochthonous).

Fig. 2. *Planoprosopon quadratum* n. sp.; Middle Callovian Geschiebe from Pleistocene glacial deposits, Demmin, West Pomerania, NE Germany; no. GG-350-1.

Krobicki & Zatón (2008) provided a comprehensive overview on all previously known records of Early and Middle Jurassic prosopids and allied crabs, together with comments on the palaeoenvironments of their occurrences. Most recently, Crônier & Boursicot (2009) reported three new taxa from the Callovian of NW France. Subsequently, interesting new material appeared from various other regions (Fig. 1), as a result of previous publications becoming known to amateur fossil collectors and colleagues working on other Middle Jurassic fossils. This material allows presenting some additional data on the brachyuran genus *Planoprosopon* Schweitzer et al., 2007 and a brief re-evaluation of some Middle and Late Jurassic representatives of the recently erected brachyuran family Tanidromitidae Schweitzer & Feldmann, 2008a.

Institutional abbreviations: The herein newly described specimens from Lithuania, NE and SW Germany are housed in the collections of the Institute of Geography und Geology, University of Greifswald, Germany and of the Staatliches Museum für Naturkunde Stuttgart, Germany. BSP = Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; GG = Geology Collection, Greifswald,
Germany; IFGT = Institut für Geowissenschaften der Universität Tübingen, Germany; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany.

2. Systematic palaeontology

Remark: Concerning the higher systematic placement of the herein studied brachyuran genera we follow the latest revisions by Schweitzer & Feldmann (2008a, b, 2009a, b, c).

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Subsection Dromiacea De Haan, 1833
Superfamily Glaessneropsoidea Patrulius, 1959
Family Longodromitidae Schweitzer & Feldmann, 2009a

Genus *Planoprosopon* Schweitzer, Feldmann & Lažar, 2007

Type species: *Prosopon heydeni* v. Meyer, 1860.

Included species: *Foersteria cornuta* Wehner, 1988, *Foersteria dumosa* Wehner, 1988, *Prosopon heydeni* v. Meyer, 1860, *Planoprosopon hystricosus* Schweitzer &

Feldmann, 2009c, ?*Prosopon major* Hee, 1924, *Planoprosopon quadratum* n. sp. (herein), *Planoprosopon rhathamingus* Schweitzer & Feldmann, 2009c, *Planoprosopon schweigerti* Schweitzer & Feldmann, 2009b, *Planoprosopon thiedeae* n. sp. (herein).

Planoprosopon quadratum n. sp.
Fig. 2

Holotype: Specimen illustrated on Fig. 2, housed in the collection of the University of Greifswald (formerly deposited in the 'Pommersche Geologische Landessammlung'), now in the holotype collection of the Institut für Geologie und Geographie, Greifswald, no. GG-350-1.

Etymology: Named after the (sub-)quadratic outline of the carapace.

Type locality: Abandoned gravel pit at Demmin, NE Germany (Western Pomerania).

Type horizon: The holotype comes from an erratic boulder ("Geschiebe") within the Pleistocene glacial drift deposits. Other fossils occurring in the same lithofacies are especially ammonites and bivalves. These ammonites (e.g., *Kosmoceras jason*) are of middle Callovian age and thus allow a precise dating of the deposits which are mostly eroded today by the Pleistocene glaciers or hidden in the subsurface of the Baltic area and further to the south. The source area providing such Geschiebe from the middle Callovian is a tectonic high structure (Pomeranian-Kuiavian Swell of the Mid-Polish Trough, see Krzywiec 2006) located in the subsurface of the estuary mouth of the River Oder (NW Poland).

Studied material: Holotype only.

Occurrence: At present only known from the type locality.

Diagnosis: Species of *Planoprosopon* with very narrow hepatic region of carapace, thus leading to subquadratic outline, disregarding rostrum.

Description: The holotype is preserved as an internal cast (steinkern) lacking its shell. The smooth surface of the steinkern gives no hints for an ornamentation of the shell. The counterpart of the specimen and the anterior part of the rostrum are missing. The total length of the carapace including the preserved parts of the rostrum is 9 mm, its maximum width is 7.5 mm. Its height is not measurable, but it is very flat, typical of the genus. The lateral sides run parallel and are not bordered.

The epigastric region grades into the rostrum. The hepatic region is short and broad-oval, indistinctly separated from a small protogastric area. The urogastric region is very narrow in the midline, posteriorly grading into the cardiac region. Epibranchial lobes are well-developed. The cervical groove is very deep and broad, and the areas between mesobranchial lobe and lateral margins are deepest and broadest. The postcervical groove is deep and well-developed. The branchiocardiac groove runs almost parallel to the cervical groove and is marked by deep incisions at the lateral margin. The cardiac region is elongate-triangular and lacks any knobs. The posterior margin is slightly concave. The appendages are not preserved.

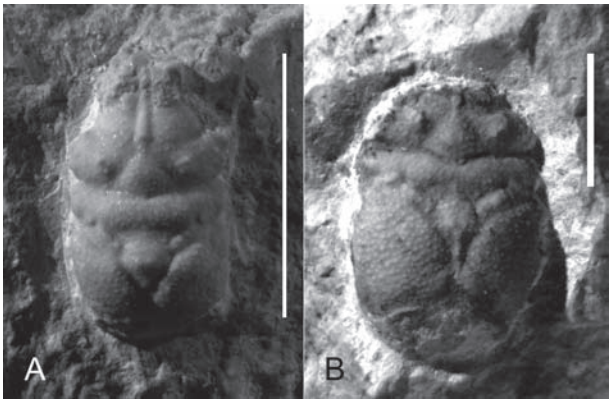

Fig. 3. A – *Planoprosopon thiedeae* n. sp.; Geisingen an der Donau, quarry "Am Saufang", Swabia, SW Germany; lowermost Untere Felsenkalke Formation, upper Kimmeridgian, Acanthicum Zone, SMNS 67518. **B** – *Planoprosopon* cf. *thiedeae* n. sp.; Storzingen near Sigmaringen; Obere Felsenkalke Formation, upper Kimmeridgian, Beckeri Zone, SMNS 67680 (coll. A. Scherzinger). – Scale equals 5 mm.

Comparisons: *Planoprosopon quadratum* n. sp. differs from the type species *P. heydeni* and all other species included in this genus in having a much shorter, narrow hepatic area, resulting in the typical subquadratic outline of the carapace. There is some resemblance of *P. quadratum* n. sp. with unnamed *Planoprosopon* specimens described as '*Nodoprosopon* sp.' from the Upper Jurassic of Japan (Karasawa & Kato 2007); however, the latter differs in showing a much longer hepatic region.

Remarks: 'Prosopids' from Middle Jurassic erratic boulders in NE Germany have been briefly mentioned by Hucke (1917, 1967) and Richter (1986), but none of these specimens was illustrated. Therefore the present specimen is the first record of this group to be studied in detail.

Planoprosopon quadratum n. sp. represents the stratigraphically oldest unequivocal record of the genus. Schweitzer & Feldmann (2009b) tentatively included *Prosopon major* Hée, 1924 from the Bajocian of France in *Planoprosopon*. This record would be in fact older than *P. quadratum* n. sp., but the affiliation of *Prosopon major* to *Planoprosopon* is not confirmed, because the holotype could not be traced in collections, and the description of the species was only accompanied by an interpretative line drawing.

Interestingly, the Late Jurassic type species of *Planoprosopon, P. heydeni*, is not only known from sponge-microbial

reefs of the northern Tethys shelf (Schweitzer et al. 2007), but also by a single specimen from a Late Jurassic 'Geschiebe' from the gravel pit Basedow near Parchim in NE Germany (Thiede & Schweigert, 2010). This interesting find may indicate that the genus have originated in the Baltic area and survived there for a long time. Another specimen referred to *P. heydeni* from a 'Geschiebe' of presumed Kimmeridgian age from Marienfelde near Berlin in Germany (Wehner 1988: 42), however, was misidentified; the latter seems to represent a probably new species of the recently introduced genus *Abyssophthalmus* Schweitzer & Feldmann, 2009a.

Planoprosopon thiedeae n. sp.
Fig. 3A

Holotype: Specimen illustrated on Fig. 3A, housed in the collection of the SMNS, no. 67518.

Etymology: Named after Karina Thiede (Parchim) who kindly donated the unique specimen for description.

Type locality: Quarry 'Am Saufang' near Geisingen an der Donau, SW Swabian Alb (SW Germany). Recently, van Bakel et al. (2008) studied other Late Jurassic crustaceans coming from this quarry.

Type horizon: According to the lithology of the rock matrix, the specimen comes from biodetritic beds in the lowermost part of the Untere Felsenkalke Formation (Upper Jurassic, upper Kimmeridgian, Acanthicum Zone) which are exposed in the topmost part of the quarry. This part of the section is unpublished.

Studied material: Holotype, and one cf.-specimen (SMNS 67680; Fig. 3B) from the Obere Felsenkalke Formation (Beckeri Zone) of Storzingen near Sigmaringen, SW Germany.

Occurrence: At present only known from the Swabian Alb, SW Germany.

Diagnosis: Species of *Planoprosopon* with rectangular outline of carapace, spiny knobs developed on mesogastric and hepatic regions, and well-developed cardiac region.

Description: The holotype is preserved with its shell. The anteriormost part of the carapace bearing the rostrum is partly broken off before the burial of the specimen. The surface of the carapace is almost equally ornamented with small pustules. The anterior lobe of the mesogastric region bears a spiny knob. Hepatic region is subdivided by a hepatical furrow. The posteriolateral parts of the hepatic region also bear a pair of spiny knobs. A few pustules close to the margin of the hepatic region are pronounced. An anterolateral spine is well-developed. The total length of the carapace including the preserved parts of the rostrum is 4.3 mm; its maximum width is 3.1 mm, and height is c. 1 mm. Lateral sides run almost parallel and are not bordered. The urogastric region is long and forms a pair of distinct hemisphaerical elevations. The pronounced pustule or weak spine is present on interior borders of epibranchial regions. Epibranchial lobes are well-developed, and separated by a weak incision. The cervical and postcervical grooves are deep, whereas the branchiocardiac groove fades out rapidly towards the cardiac region. The cardiac region is triangular, well separated from branchial reagions, and lacks distinct knobs. The posterior margin is slightly concave. Appendages are not preserved.

An incomplete specimen (Fig. 3B; SMNS 67680) from a younger bed than the type horizon, but still late Kimmeridgian in age, is tentatively assigned to this species. It is much larger than the holotype (width 7 mm). The branchial regions appear to be broader than in the holotype, which is probably caused by a stronger compaction, and the cardiac region is much less elevated. However, the frontal part and anterior parts of the hepatic region are not preserved due to pre-burial damage. Therefore a specific identity cannot be confirmed with certainty.

Comparisons: *Planoprosopon thiedeae* n. sp. differs from all other species of the genus in its characteristic ornamentation of the carapace. The morphologically closest species seems to be *P. schweigerti* Schweitzer & Feldmann, 2009b from the Tithonian of Austria. *Planoprosopon thiedeae* n. sp. differs from *P. schweigerti* mainly in having a more pronounced cardiac region and lacking lateral spines in the epibranchial region. Possibly, the compared specimen from the Beckeri Zone of Swabia represents a transitional form between the two taxa.

Superfamily Homolodromioidea Alcock, 1899
Family Tanidromitidae Schweitzer & Feldmann, 2008a
Genus *Tanidromites* Schweitzer & Feldmann, 2008a

Type species: *Prosopon insigne* v. Meyer, 1857.

Included species: *Prosopon insigne* v. Meyer, 1857; *Prosopon sculptum* Quenstedt, 1857; *Prosopon richardsoni* Woodward, 1907; *Tanidromites lithuanicus* n. sp. (herein); *Tanidromites montreuilensis* Crônier & Boursicot, 2009; *Tanidromites scheffnerae* n. sp. (herein).

Tanidromites lithuanicus n. sp.
Fig. 4

Holotype: Specimen illustrated on Fig. 4, housed in the collection of the University of Greifswald no. GG-350-2 (leg. J. Koppka).

Etymology: After Lithuania, the country from which the holotype was collected.

Type locality: Papartinė near Papilė (Popilani), Lithuania.

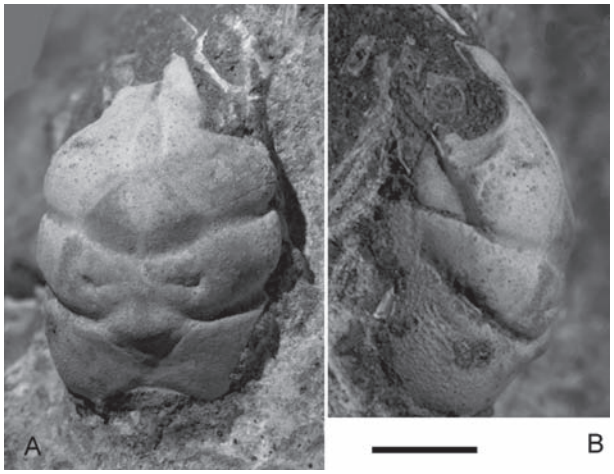

Fig. 4. A, B – *Tanidromites lithuanicus* n. sp.; Papartinė near Papilė (Popilani), Lithuania; Papartinė Formation, middle Callovian, Coronatum Zone, Grossouvrei Subzone; no. GG-350-2 (leg. J. Koppka). – Scale equals 5 mm.

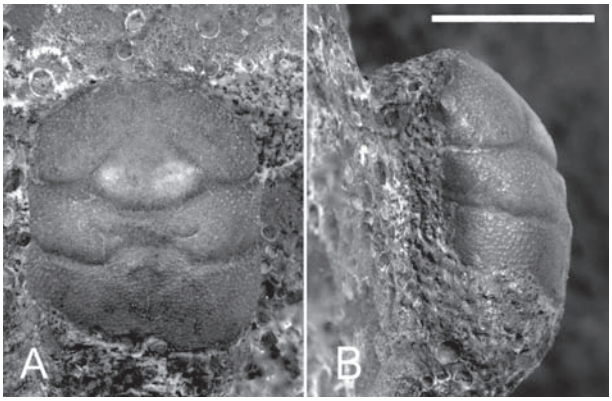

Fig. 5. A, B – *Tanidromites richardsoni* (Woodward, 1907); Göllersreuth near Thalmässing, Bavaria, S Germany, Sengenthal Formation, Parkinsonien-Oolith Member, Parkinsoni Zone, Truellei Subzone, SMNS 67339 (coll. V. Dietze, Riesbürg). – Scale equals 5 mm.

Type horizon: The holotype comes from a 95-120 cm thick, weakly cemented red-brown sandstone bed ('horizon n' in Grigelis 1985) with intercalated iron-oolithic calcareous sandstone concretions in the upper part (were the specimen was found) within the Middle Jurassic Papartinė Formation (for regional lithological subdivision see Grigelis 1985). The age of this bed is the middle Callovian Coronatum Zone, Grossouvrei Subzone, dated after co-occurring finds of ammonites (*Kosmoceras castor, Kosmoceras* cf. *grossouvrei, Kosmoceras pollux, Erymnoceras* sp.) collected by the second author.

Studied material: Holotype only.

Occurrence: At present only known from the type locality.

Diagnosis: Species of *Tanidromites* with weak pustulate ornamentation, well-developed anterolateral spine, and broad epigastric area.

Description: Apart from small parts of the rostrum and the right part of the frontal margin in the subhepatic area, the holotype is three-dimensionally preserved, still with its shell. The carapace has a total length of 13 mm and a height of c. 4.0 mm. Broadest part of the carapace with a maximum width of 9 mm are located in the epibranchial area. The surface of shell is very finely punctate and partly covered with widely scattered small pustules, especially in the anterior and lateral parts of the carapace. In the medium parts of urogastric and branchial regions pustules are absent.

The augenrest, a structure lateral to the orbits as recently defined by Schweitzer & Feldmann (2009a) is crescent-shaped, shallow, and bordered by a dense row of small, equally sized tubercles. The anterolateral edge bears a prominent spine, and separated from the hepatic region by a shallow groove. The mesogastric region is well-defined, with only few scattered pustules, otherwise smooth, bearing a pair of pores in its posterior end. The mesogastric region anteriorly grades into a deep median furrow pointing to the top of a triangular rostrum. The hepatic region exhibits a strong and broad depression related to the eye muscle.

The cervical groove is deep and well-developed in all parts of the carapace; the deep branchiocardiac groove fades out towards the ventral margin of the carapace. The postcervical groove is restricted to deep depressions lateral from the cardiac region and not connected with the branchiocardiac groove.

The lateral margins are high, rounded, but lack a defined crest, except of the subhepatical region. The cardiac area is rhombic, and posteriorly bordered by distinct furrows, anteriorly grading into the urogastric region. The urogastric region has deep, triangular grooves not connected with the postcervical groove. The posterior end of the carapace is slightly incised. Appendages are not preserved.

Comparisons: *Tanidromites richardsoni* exhibits a much stronger pustulate ornamentation of the shell than *T. lithuanicus* n. sp., and shows a well-developed spine in the anterolateral corner. Moreover, the epibranchial area bordered by the cervical and branchiocardiac grooves is relatively wider than that of *T. lithuanicus* n. sp. The other species of *Tanidromites* differ significantly in their length/width ratios of the carapace, the relative length of the urogastric region, and their ornamentation.

Tanidromites richardsoni (Woodward, 1907)
Fig. 5

*1907 *Prosopon Richardsoni.* – Woodward, p. 80, text-figs. 1-2.

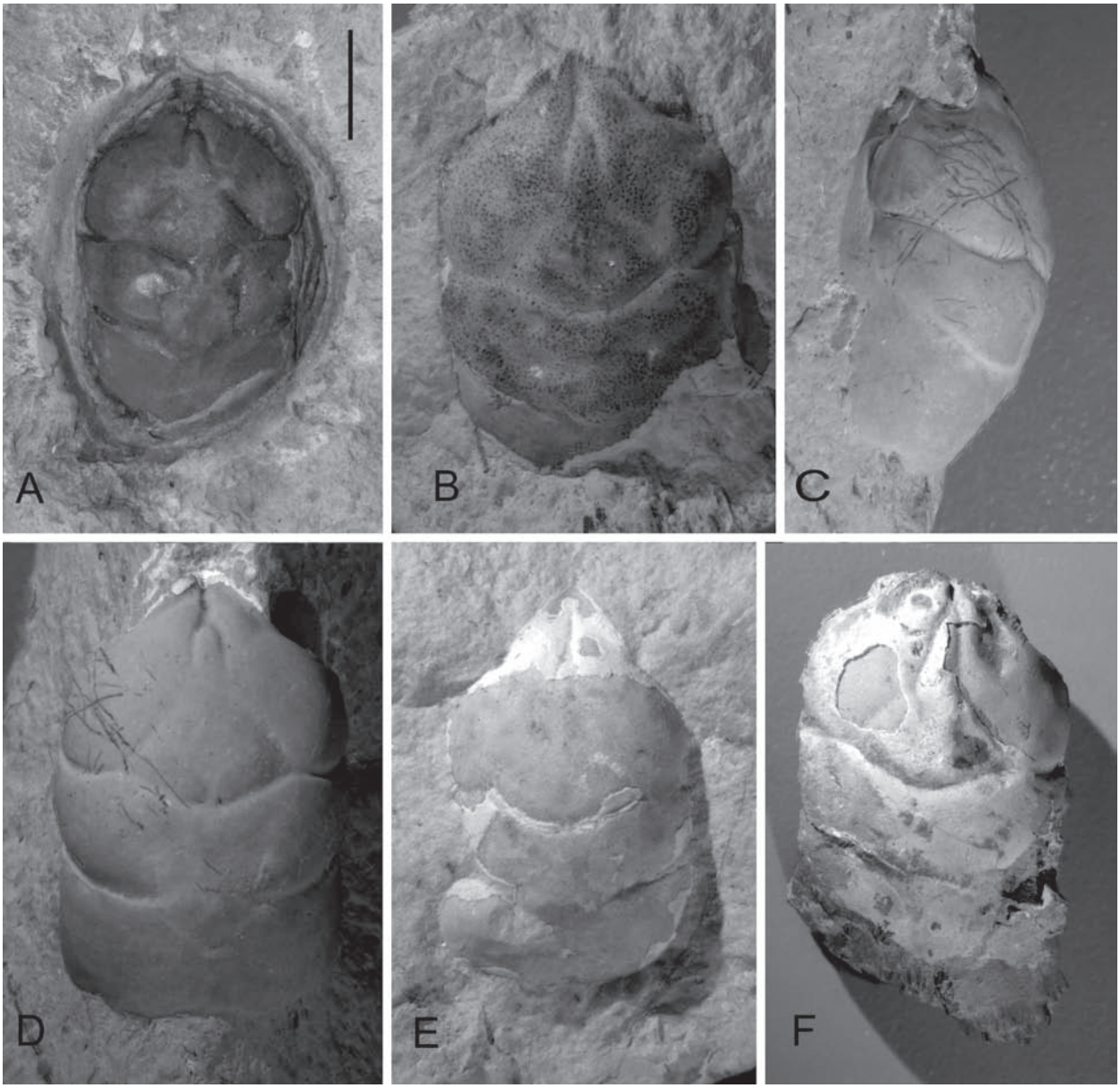

Fig. 6. *Tanidromites insignis* (v. Meyer, 1857); **A** – holotype (= v. Meyer 1860, pl. 23, fig. 4) Fürsitz/Braunenberg near Aalen-Wasseralfingen, SW Germany, lower Kimmeridgian, Platynota Zone, SMNS 61641. **B** – Topotype, Fürsitz/Braunenberg near Aalen-Wasseralfingen, SW Germany, lower Kimmeridgian, Platynota Zone, SMNS 67337 (coll. A. Weinschenk). **C** – Specimen figured by Wehner (1988, pl. 5, fig. 3), Sauserbrunnen near Laufen/Eyach, SW Germany, lower Kimmeridgian (= upper Oxfordian sensu gallico), Planula Zone, SMNS 61640 (coll. A. Hagenlocher). **D** – Specimen from Engen, SW Germany, upper Kimmeridgian, Beckeri Zone, Ulmense Subzone, SMNS 66655 (coll. A. Scherzinger, Immendingen-Hattingen). **E** – Specimen with partly preserved shell, Plettenberg quarry near Schömberg, SW Germany, upper Oxfordian, Bimammatum Zone, SMNS 67355 (coll. A. Matzke). – Scale equals 5 mm.

1925 *Prosopon richardsoni* H. Woodward sp., 1907. – Van Straelen, p. 361.
1933 *Pithonoton* ? *richardsoni* Wood. – Glaessner, p. 181.
1951 *Prosopon richardsoni* (H. Woodward). – Withers, p. 174, pl. 15, figs. 1-6, text-figs. 1-3.
1962 *Prosopon richardsoni* (H. Woodward). – Donovan, p. 195.
1980 *Pithonoton richardsoni* (Woodward). – Morris, p. 14.
1988 *Pithonoton richardsoni* (Woodward). – Wehner, p. 69, fig. 19.

2007 *Tanidromites richardsoni* (Woodward, 1907). – Schweitzer & Feldmann, p. 141, pl. 6, fig. K.
2010 *Tanidromites richardsoni* (Woodward, 1907). – Schweitzer et al., p. 61.

Studied material: Cast of holotype (BSP collection), 1 carapace from the upper Bajocian part of the Sengenthal Formation of Franconia (Southern Germany) described herein.

Occurrence: Bajocian of Great Britain and SW Germany.

Description: The new specimen form the Bajocian of Franconia is lacking its rostrum but otherwise perfectly preserved, even with its shell. The rostrum must have been broken before the fragile carapace was finally buried in a highly energetic, iron-oolitic environment. The preserved length of the specimen is 8 mm, its total width is 7.3 mm, and the preserved height is c. 3.5 mm.

Comparisons: See above (*Tanidromites lithuanicus* n. sp.).

Discussion: Recently, *Prosopon richardsoni* Woodward was included in *Tanidromites* (Schweitzer & Feldmann 2008a). The clearly discernible triangular rostrum, the development of the orbits with the lateral eye grooves, the rectangular outline of the carapace and the groove pattern leave no doubt about this systematic affiliation.

The holotype of *Prosopon richardsoni* comes from the upper Bajocian "Clypeus Grit" of the Inferior Oolite Group (for more details see Mudge 1995) in the Cotteswold region of Southern England. Additional specimens were recovered from the upper Bajocian of Dundry in Somerset and described by Withers (1951). Thus, the present specimen from Franconia is the first record of this species outside of England. The specimen is preserved in an iron-oolitic lithology. Probably this lithology points to a rather shallow environment for this species.

Similar forms which were tentatively assigned to this species occur in the Upper Jurassic of Romania (Franţescu 2011).

Tanidromites insignis (v. Meyer, 1857)
Fig. 6

*1857 *Prosopon insigne*. – v. Meyer, p. 556.
1858 *Prosopon insigne*. – v. Meyer, p. 61.
1860 *Prosopon insigne*. – v. Meyer, p. 193, pl. 23, fig. 4.
1925 *Avihomola insignis* von Meyer sp., 1857. – Van Straelen, p. 344.
1925 *Prosopon insigne* H. v. M. – Beurlen, p. 468.
1929 *Pithonoton insigne* v. Meyer, 1860. – Glaessner, 1929, p. 320.
1933 *Pithonoton insigne* (von Mey.). – Glaessner, p. 181.
1928 *Pithonoton insigne* H. v. M. – Beurlen, p. 149.
1985 *Coelopus etalloni* Collins, sp. n. – Collins & Wierzbowski, p. 81, pl. 2, fig. 1.
1985 *Pithonoton insigne* (von Meyer, 1860). – Collins & Wierzbowski, p. 83, pl. 3, figs.1 (non pl. 2, figs. 3-4 = *Eodromites aequilatus*).
1988 *Pithonoton insigne* (von Meyer, 1960). – Wehner, p. 71, pl. 5, figs. 1-3.
2000 *Pithonoton insigne* (von Meyer). – Müller et al., fig. 17K, L.
2008a *Tanidromites insignis* (von Meyer, 1857). – Schweitzer & Feldmann, p. 138, pl. 6, figs. A-F.
2008a *Tanidromites etalloni* (Collins in Collins & Wierzbowski, 1985). – Schweitzer & Feldmann, p. 140, pl. 6, figs. G-H.
2008 *Pithonoton insigne* (von Meyer). – Krobicki & Zatoń, p. 38.
2010 *Tanidromites insignis* (von Meyer, 1857). – Schweitzer et al., p. 61.

Holotype: Specimen figured by v. Meyer (1860, pl. 23, fig. 4) and Schweitzer & Feldmann (2008a, pl. 6, fig. A); today housed in the SMNS collection, number 61641.

Type locality: According to the original label, the holotype comes from the "Weißer Jura γ" [or δ?] of "Fürsitz", a location at the Braunenberg hill, near Aalen-Wasseralfingen (SW Germany).

Type horizon: Upper Jurassic, after the lithology of the matrix of the piece of rock containing the holotype it comes from slightly spongiolithic limestones. Limestones of this lithology occur from the lower Kimmeridgian Planula Zone to the Acanthicum Zone (formerly Weißer Jura β-δ). Closest to the locality "Fürsitz", spongiolithic beds of the Lower Kimmeridgian Platynota Zone (Weißer Jura γ) crop out which recently proliferated a topotype.

Studied material: Holotype (Fig. 6A), topotype (Fig. 6B), and 3 further specimens (Figs. 6C-E).

Occurrence: Upper Jurassic of SW Germany and Poland. The stratigraphically oldest record is from the Middle Oxfordian (Transversarium Zone) of extra-alpine Switzerland (Wehner 1988: 74). The hitherto youngest stratigraphical record is a newly recovered specimen from the uppermost Kimmeridgian (Beckeri Zone, Ulmense Subzone) of SW Germany (Fig. 6D).

Description: See Wehner (1988) and Schweitzer & Feldmann (2008a). A recently recovered very large specimen – width of carapace is 18 mm – from the late Oxfordian (Bimammatum Zone) of the Plettenberg quarry near Schömberg (Swabian Alb, SW Germany) is preserved with most of its shell (Fig. 6E). The surface of the cuticle is almost smooth. Only towards the lateral margins of the hepatic and epibranchial areas some few tiny, forwardly directed pustules are discernible.

Comparisons: *Tanidromites insignis* (v. Meyer) differs from co-occurring *Eodromites aequilatus* (v. Meyer) (see below) in having a relatively longer carapace with a slightly shorter epibranchial region. The lateral margins of the epibranchial and hepatical regions are rounded in *T. insigne*, but bear a ventrally declining edge in *E. aequilatus*. In the latter the anterolateral edge is marked by a spine (which may, however, easily break off). Moreover, the augenrest is

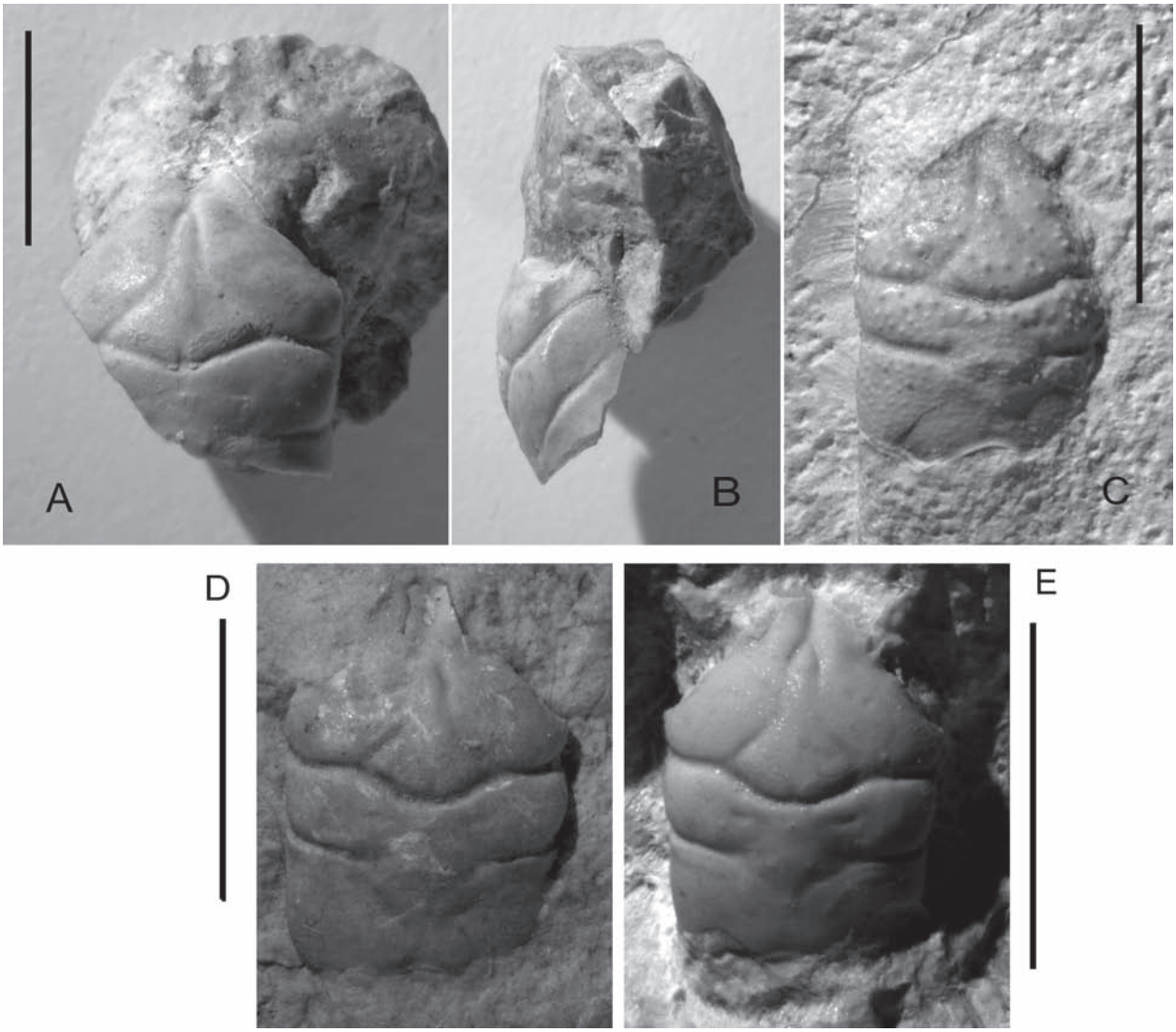

Fig. 7. *Tanidromites sculpta* (Quenstedt, 1857); **A, B** – holotype (= Quenstedt 1857, pl. 95, fig. 48) in dorsal and dorsolateral view, Nollhof near Sigmaringen, SW Germany, upper Kimmeridgian, Beckeri Zone, Ulmense Subzone, IFGT, without no. (Quenstedt collection); **C** – specimen with nicely preserved shell, Braunenberg near Aalen-Wasseralfingen, SW Germany, lower Kimmeridgian (= upper Oxfordian sensu gallico), Planula Zone, Galar Subzone, SMNS 67338 (coll. A. Weinschenk). **D** – Specimen figured as holotype of *Prosopon wuergauensis* (Kuhn, 1939, pl. 15, fig. 41), Würgau, Franconia, upper Oxfordian, Bimammatum Zone, SMNS 60244 (Schattenberg collection). **E** – Specimen figured by Wehner (1988: pl. 6, fig. 7), Biburg, Bavaria, lower Kimmeridgian (= upper Oxfordian sensu gallico), Planula Zone, BSP 1980 XXX 889. – Scale equals 5 mm.

extremely shallow and not as deeply incised as in *Eodromites aequilatus* (v. Meyer) (see below), and the depression of the eye muscle visible on the hepatical region is small and punctuate in *Eodromites*, but much more expanded in *Tanidromites*.

Discussion: Schweitzer & Feldmann (2009b) recently included *Coelopus etalloni* from the Planula Zone in their newly erected genus *Tanidromites* and considered this taxon to be very close to *T. insignis*. These authors, however, kept this taxon distinct from *T. insigne* because of a less prominent cardiac region and some minor differences in the morphology of the epigastric region. In our view, the epigastric region with their distinct epigastric lobes matches perfectly with that of *T. insigne*, and the cardiac region is very poorly preserved and most likely abraded in the holotype and sole specimen of *T. etalloni*, so that we concur with Wehner (1988) and consider *T. etalloni* as a junior subjective synonym of *T. insignis*.

Tanidromites sculpta (QUENSTEDT, 1857)
Fig. 7

*1857 *Prosopon sculptum*. – QUENSTEDT, p. 778, pl. 95, fig. 48.
?1857 *Prosopon elongatum*. – v. MEYER, p. 556.
1858 *Prosopon lingulatum*. – v. MEYER, p. 61.
1860 *Prosopon lingulatum* von MEYER. – v. MEYER, p. 205, pl. 23, fig. 17.
1925 *Prosopon lingulatum* von MEYER. – BEURLEN, p. 476.
1929 *Pithonoton lingulatum* (von MEYER). – GLAESSNER, p. 322.
1933 *Prosopon lingulatum* von MEYER. – GLAESSNER, p. 180.
1939 *Prosopon würgauensis* n. sp. – KUHN, p. 492, pl. 15, fig. 41.
1988 *Pithonoton lingulatum* (von MEYER, 1960) *sic.* – WEHNER, p. 77, pl. 5, figs. 6-7.
2008a *Tanidromites lingulata* (von MEYER, 1858). – SCHWEITZER & FELDMANN, p. 140, pl. 6, figs. I-J.
2010 *Tanidromites sculpta* (QUENSTEDT, 1857). – SCHWEITZER et al., p. 61.

Holotype: Specimen figured by QUENSTEDT (1857, pl. 95, fig. 48), re-figured here in Fig. 7A, B; housed in the collection of Tübingen University, without number ('QUENSTEDT-collection').

Type locality: Vicinity of "Nollhaus" (modern spelling: "Nollhof"), an inn and former farmhouse located c. 2.5 km N of the town of Sigmaringen, southern border of Swabian Alb, SW Germany.

Type horizon: Upper Jurassic bioclastic beds of the so-called "Nollhof-Fazies" of ROLL (1931), which are latest Kimmeridgian (Beckeri Zone, Ulmense Subzone) in age. The oldest records of this species come from the late Planula Zone (early Kimmeridgian).

Studied material: Holotype (Fig. 7A, B), 4 further illustrated specimens (Fig. 7C-E), and 4 un-figured specimens.

Occurrence: The species is only known from the Upper Jurassic of Swabia and Franconia.

Description: See SCHWEITZER & FELDMANN (2008a), for *Tanidromites lingulata*. The holotype of *T. sculpta* (QUENSTEDT) is incomplete in the posterior part of the carapace but three-dimensionally preserved. It is preserved as a steinkern lacking any remains of the shell. The surface of the steinkern indicates no ornamentation (but see below!). The right lateral margin and the frontal part of the carapace with the long, triangular rostrum, the orbits and the augenrest are well-preserved. The distance between the anterolateral edge and the cervical groove is very short; this feature is of special significance for the species. Outline of the carapace long-rectangular in dorsal view, with lateral margins running almost parallel, only slightly diverging towards the anterolateral edge, where the carapace reaches its maximum width. Mesogastric region with strongly developed muscle scars along its posterior margin. Depressions of eye muscles in the posterior part of the hepatical areas poorly discernible. Cervical groove deep and well developed, branchiocardiac groove slightly weaker. Postcervical groove restricted to shallow depressions lateral from the cardiac region. Epibranchial area remarkably long. Shallow cardiac area bears a small, fine knob at its anterior end and two ones (only one of which, the right one, is preserved in the holotype) in its centre. Hepatical and urogastrical areas somewhat bordered by an indistinct shoulder, whereas the carapace is curved in the branchial parts. Appendages are not preserved.

Discussion: WEHNER (1988) considered that *Prosopon lingulatum* was the senior synonym of *Prosopon elongatum*. Most strangely, she did not realize that in this case *P. elongatum* would be the proper name for this species because it was validly published slightly earlier in a short note by v. MEYER (1857). Unfortunately, the type specimens of both taxa were lost during World War II so that it is in fact impossible to prove this assumption. However, SCHWEITZER & FELDMANN (2008a), when discussing both taxa, based their opinion on the expanded descriptions of v. MEYER (1860) and his illustrations, assuming that both taxa are valid and well-defined. In the case of *P. lingulatum* they restudied the new material figured by WEHNER (1988) and concluded that this material indeed belongs to the species of v. MEYER, whereas no further specimens for *P. elongatum* were traced. However, *Prosopon sculptum*, which was established in [October] 1857, not in 1858 as often cited (see W. QUENSTEDT 1963: 32), is undoubtedly conspecific with *P. lingulatum*. Also both type localities have the same stratigraphical age. Hence, *Tanidromites sculpta* is considered as a senior subjective synonym of *T. lingulata* and thus a good basis for this species, because the holotype of QUENSTEDT's species is still available and illustrated herein (Fig. 7A, B). *Prosopon elongatum* is tentatively included in the synonymy of *T. sculpta.*

Recently, SCHWEITZER & FELDMANN (2008a) provided a revised description of *Tanidromites sculpta*, based on the original drawing of v. MEYER (1860) and the material previously studied and illustrated by WEHNER (1988). All this material is preserved as steinkerns, lacking the original surface of the carapace. In contrast, a newly recovered specimen (Fig. 7C) from the late Planula Zone (early Kimmeridgian) of Aalen-Wasseralfingen is the sole one preserved mostly with its shell. Surprisingly, its tuberculate ornamentation is much stronger than thought from the absolutely smooth steinkerns of this species, and covers the whole surface of the shell. The posterior margin of the carapace is strongly incised and bordered by a smooth rim. Despite the presence of a prominent anterolateral edge in the steinkerns, there is no equivalent spine developed on the shell.

The holotype of *Prosopon wuergauensis* from the upper Oxfordian of Würgau in northern Franconia (S Germany) was considered as untraceable and thus its precise taxonomic affiliation remained unclear (WEHNER 1988: 101). However, this specimen is stored in the collection of the SMNS and photographically illustrated here for the first time (Fig. 7D). The outline and groove pattern as well as

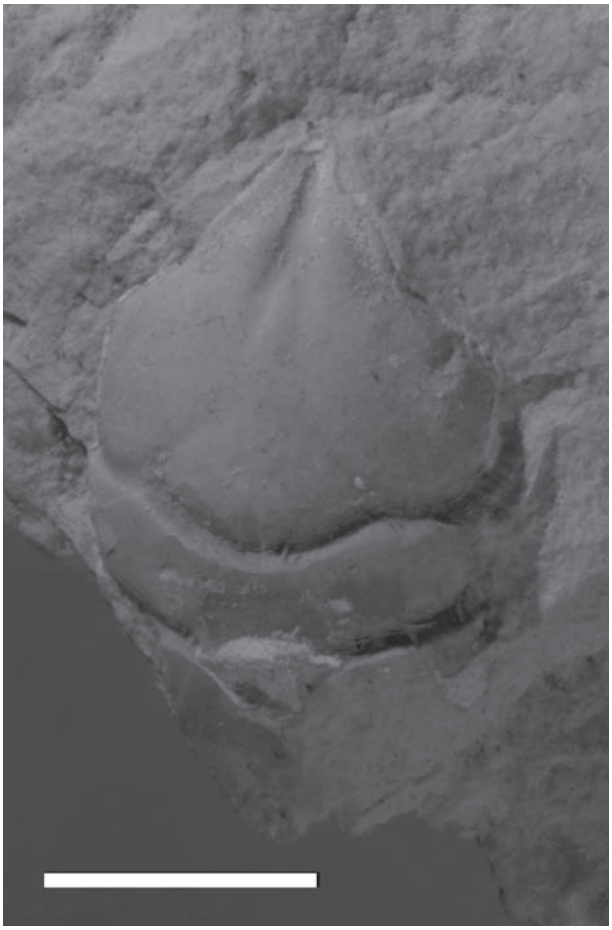

Fig. 8. *Tanidromites scheffnerae* n. sp., holotype. Gundelsheim SW Treuchtlingen, Bavaria, Treuchtlingen Formation, upper Kimmeridgian, Pseudomutabilis Zone, SMNS 67145 (coll. M. Scheffner). – Scale equals 5 mm.

the frontal area clearly match with those in *Tanidromites sculpta*. The elongate, blunt shape of the rostrum is a preparation artefact; in reality, its outline is triangular and pointed as usual in this genus. Taking into account all the studied material, *T. sculpta* seems to be considerably smaller than the other known species of the genus.

Tanidromites scheffnerae n. sp.
Fig. 8

Holotype: Specimen illustrated on Fig. 8, housed in the collection of the SMNS, no. 67145.

Etymology: Named after Mrs. Margot Scheffner, Walldorf, who kindly donated the unique specimen for description.

Type locality: Gundelsheim near Treuchtlingen, Franconian Alb, Bavaria, Southern Germany.

Type horizon: The holotype comes from the Treuchtlingen Formation (= 'Treuchtlingen Marble', 'Malm δ'). In the quarry of Gundelsheim thick spongiolithic limestone beds of the upper Kimmeridgian Pseudomutabilis Zone are exposed, covered by allochthoneous deposits of the Miocene Ries Crater impact.

Studied material: Holotype only.

Occurrence: At present only known from the type locality.

Diagnosis: Medium-sized species of *Tanidromites* with depressed, long-rectangular carapace.

Description: The rectangular, strongly compressed carapace is preserved as an inner cast lacking its shell, apart from a few chalky remains. These shell relics indicate that its surface was finely punctuate, like in other species of the genus, and an additional tubercular ornamentation was mostly restricted to the hepatical regions. In the frontal area, a long, forwardly pointed triangular rostrum is developed. The lateral margins of the carapace run parallel. The epigastric lobe well-developed. The hepatical region is large with a rounded anterolateral edge. The supraorbital margin is also rounded. The cervical and branchiocardiac grooves are very deep and pronounced, and posteriorly bordered by angular shoulders. The cardiac region forms a small triangle which is not ornamented with any knobs. The urogastric region exhibits a postcervical groove, which is restricted to small, shallow depressions on both sides of the carapace and thus hardly discernible. This postcervical groove is not connected with the branchiocardiac groove. The branchial regions and the posterior part are damaged and partly lost. Appendages are not preserved.

Comparisons: In contrast to *Tanidromites sculpta*, the hepatical regions are much longer and larger than those in *T. scheffnerae* n. sp., especially concerning the much longer distance between the anterolateral edge and the cervical groove. *T. scheffnerae* n. sp. differs from *T. insigne* in showing a relatively longer and taller carapace, a less inflated hepatical region and especially a much shorter epibranchial region. Moreover, the supraorbital margins are rounded and lack an angle. As in *T. insignis* the lateral margins also lack edges. *Eodromites aequilatus* (v. Meyer) differs by having a much broader carapace and the presence of supraorbital and laterohepatical edges dipping ventrally.

Family Goniodromitidae Beurlen, 1932
Genus *Eodromites* Patrulius, 1959

Type species: *Prosopon grande* v. Meyer, 1860.

Included species: *Prosopon depressum* v. Meyer, 1857; *Prosopon grande* v. Meyer, 1860; *Prosopon nitidus* Milne Edwards, 1865; *Pithonoton polyphemi* Gemmellaro, 1870; *Prosopon rostratum* v. Meyer, 1840 (see Schweitzer & Feldmann 2008a), and *Prosopon aequilatum* v. Meyer, 1857 (herein).

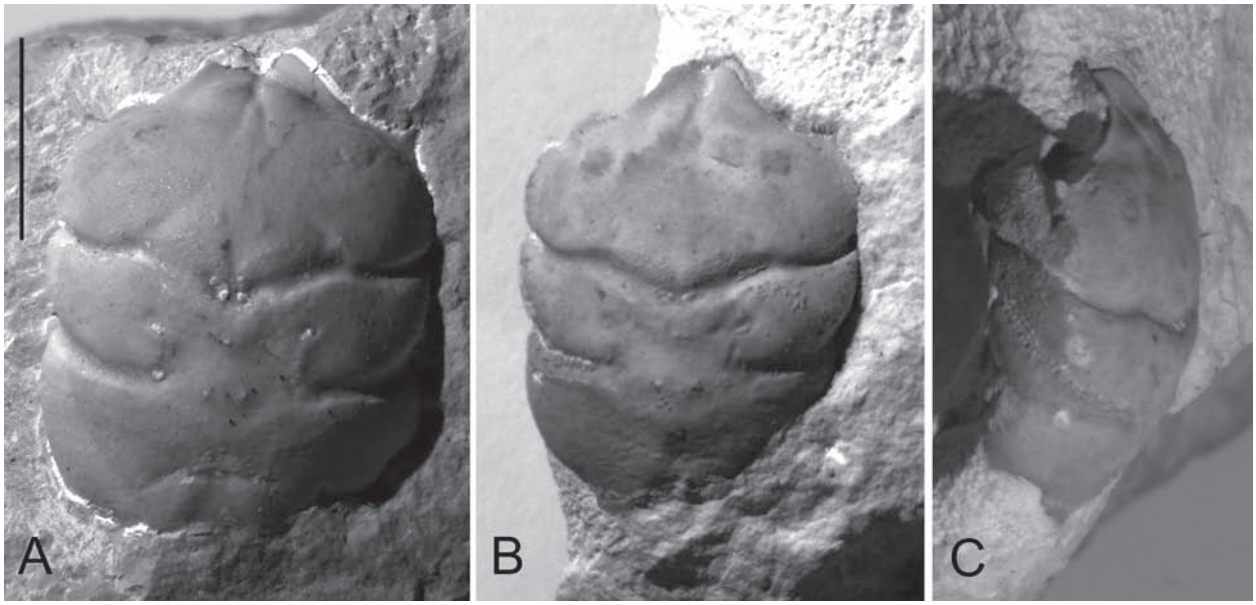

Fig. 9. *Eodromites aequilatus* (v. Meyer, 1857); **A** – neotype, Braunenberg near Aalen-Wasseralfingen, SW Germany, lower Kimmeridgian (= upper Oxfordian sensu gallico), Planula Zone, Galar Subzone, SMNS 67336/1 (coll. A. Weinschenk). **B** – Further topotype, SMNS 67336/2 (coll. A. Weinschenk). – Scale equals 5 mm.

Eodromites aequilatus (v. Meyer, 1857)
Fig. 9

1842 *Prosopon rostratum*. – v. Meyer, p.74, pl. 15, figs. 5-6 (non fig. 4 = holotype of *Prosopon rostratum* v. Meyer).
*1857 *Prosopon aequilatum*. – v. Meyer, p. 556.
1860 *Prosopon aequilatum*. – v. Meyer, p. 194, pl. 23, fig. 5.
1929 *Pithonoton aequilatum* (v. Meyer), 1860. – Glaessner, p. 318.
1985 *Pithonoton aequilatum* (v. Meyer, 1860). – Collins & Wierzbowski, p. 82, pl. 2, fig. 2.
1985 *Pithonoton insigne* (v. Meyer, 1860). – Collins & Wierzbowski, p. 82, pl. 2, figs. 3-4 (non pl. 3, fig. 1 = *T. insignis*).
1988 *Pithonoton aequilatum* (v. Meyer, 1860). – Wehner, p. 74, pl. 5, figs. 4-5.
2008a *Pithonoton aequilatum* (von Meyer, 1860). – Schweitzer & Feldmann, p. 130, pl. 3, figs. E-F.
2010 *Pithonoton aequilatum* (von Meyer, 1860) s.l. – Schweitzer et al., p. 60.

Lectotype and neotype: Originally, *Prosopon aequilatum* was based on two specimens coming from the Upper Jurassic in the vicinity of Aalen (SW Germany). The larger specimen illustrated by v. Meyer (1842, pl. 15, fig. 5) and re-figured by v. Meyer (1860, pl. 23, fig. 5) was obviously destroyed during World War II in Munich. The same happened with the smaller specimen (v. Meyer 1842, pl. 15, fig. 6) which Wehner (1988: 79) later interpreted as *Pithonoton marginatum*. She erroneously mentioned the larger specimen being the "holotype" (together with a "paratype", which is the smaller specimen of the two syntypes), but did not designate the neotype for this taxon, because there were no topotypes available at that time. Formally, we here designate the larger specimen illustrated by v. Meyer (1842, pl. 15, fig. 5) as the lectotype. Meanwhile, we have got access to well-preserved newly collected material from the type locality and horizon, and thus we use this opportunity to designate here the specimen illustrated in Fig. 8A as the neotype. It is housed in the collection of the SMNS, no. 67336/1.

Type locality: Vicinity of Aalen (SW Germany). Most likely from the quarry area of the Braunenberg near Aalen-Wasseralfingen.

Type horizon: In his original description v. Meyer (1842) mentioned that he got his material from the "yellow Jurassic limestones" in the vicinity of Aalen. He mentioned that the specimens of his newly erected taxa *Prosopon spinosum* (= *Abyssophthalmus spinosus*), *Prosopon* "*rostratum*" (= *Eodromites aequilatus*) and *Prosopon marginatum* (= *Pithonoton marginatum*) come from the same beds. After that, v. Meyer (1860) surprisingly spoke of the "upper White Jurassic", what is highly misleading. The higher part of the Upper Jurassic in the vicinity of Aalen consists either of dolomites and dedolomites or of pure, silica-rich limestones, which almost lack any macrofossils. From the com-

position of his original sample it is clear that it must come from the beds exposed in the quarry area of the Braunenberg near Aalen-Wasseralfingen, which covers the higher part of the Planula Zone and the lowermost part of the Platynota Zone of the lower Kimmeridgian. The neotype and a topotype were collected from the highest part of the Planula Zone (Galar Subzone). Additional 40 specimens of about the same age were collected from Biburg in Franconia (Wehner 1988). The species occurs also in the Oxfordian (or possibly early Kimmeridgian) of the Polish Holy Cross Mountains (Collins & Wierzbowski 1985).

Studied material: Neotype, one topotype (Fig. 9B) and more than 40 further specimens.

Occurrence: Upper Jurassic of SW Germany and Poland.

Emended description: See Wehner (1988). The neotype described herein is preserved as an internal cast (steinkern) with very poor remains of its chalky shell at the tip of the rostrum and along the lateroventral margins of the carapace. The surface of the steinkern indicates that a weak postulate ornamentation was developed mainly along the lateral margins of the hepatical and epibranchial margins. The total length of the carapace including the rostrum is 14.5 mm; its maximum width is 10.8 mm. Its height is c. 5 mm. The lateral sides run parallel and are not bordered.

The triangular rostrum is curved ventrally. Along its basis, in the epigastric region, blunt lobes occur. The orbital margin is sharply bordered, lacking any ornamentation. Both the orbits and adjacent augenrest are deep and tall. Both are hardly separated from each other. The epigastric region is only weakly separated from the hepatic regions. In the posterior part of the epigastric region strong muscle scars are developed. In the hepatic regions relatively large depressions of the eye muscles occur. The augenrest is laterally bordered by an anterolateral spine. Ventrally from this spine, a crescent area is formed by the curved cervical groove. The dorsal margin of the carapace is laterally bordered by a weak crest both in the hepatical and epibranchial areas. This morphological development of the subhepatical region is typical for the genus *Eodromites*, together with the deep orbits and the narrow, very deeply incised augenrests.

The cervical and branchiocardiac grooves are deep and slightly curved; both run almost parallel in their lateral parts. The branchiocardiac groove fades out towards the ventral margin of the carapace. The urogastric region grades into the shallow cardiac region, which bears two small knobs. The cardiac region is triangular, lacking any knobs. The postcervical groove is reduced to deep punctual depressions and poorly connected with the branchiocardiac groove. Anterior to these depressions there are transversal chains of muscle scars. The posterior margin of the carapace is slightly concave, bordered by a small rim. Between the posterior end of the cardiac area and the posterior margin an unnamed transversal groove structure is developed which runs parallel to the posterior margin. Appendages are not preserved.

Comparisons: In dorsal view *Eodromites aequilatus* superficially resembles *Tanidromites insignis* (v. Meyer), but it differs from the latter in its shorter epibranchial region and especially in its inflated subhepatical region. Moreover, the frontal margin in the hepatic area bears a well-developed crest in *E. aequilatus*, and the augenrest is very narrow and deeply incised in the latter species. In *Eodromites grandis* the posterolateral margins significantly converge towards the posterior margin whereas they run almost parallel in *E. aequilatus*. *Tanidromites montreuilensis* Crônier & Boursicot, 2009 is another species which is morphologically very close to *Eodromites aequilatus* in respect of the groove pattern and the general outline, but it lacks a transversal groove posterior to the cardiac area. Although the exact shape of the augenrest is unknown in *T. montreuilensis*, the latter may represent a transitional form between *Tanidromites* and *Eodromites*. The strong similarities between *Eodromites* and *Tanidromites* point to a very close phyletic relationship between Tanidromitidae and Goniodromitidae.

3. Palaeoecology

Most of the presently known records of Jurassic homolodromioid crabs appear to have lived in rather shallow environments (Krobicki et al. 2007; Krobicki & Zatón 2008). Especially reefal habitats like shallow coral bioherms or the somewhat deeper sponge-microbial mounds widespread in the Late Jurassic deposits of the northern Tethyan shelf were favourably settled by these crabs. This is the case in the above described species of *Eodromites* and *Tanidromites* except *T. lithuanicus* n. sp. and *T. richardsoni*, the only Middle Jurassic representatives of the genus. Even the recently described records of primitive crabs from the Upper Jurassic of Japan which are said to come from "shales" (Karasawa & Kato 2007) are in fact marly deposits closely associated with massive coralliferous reef limestones (pers. comm. H. Karasawa). However, contrary to the statement of Krobicki & Zatón (2008), the oldest known homolodromioid, the unique *Eoprosopon klugi* Förster, 1986 from the late Pliensbachian (see Schweitzer & Feldmann 2010), does not come from peri-reefal habitats but from dark clays rich in ammonites and belemnites but without any indicators of a shallow environment. The ammonite fauna of the finding horizon consists almost exclusively of Subboreal amaltheids, and therefore suggests, together with its lithology devoid of carbonates, relatively cool seawater provided by currents from the north.

The matrix of the herein described holotype of *Planoprosopon quadratum* n. sp. is a fine-grained calcareous grit which is typical of the Middle Callovian in the subsurface of NW Poland. Hermatypic corals or other shallow-water reef constructors do not occur in deposits of this age in that area, but the densely packed, winnowed sediment as well as the rich, co-occurring benthic macrofauna within these boulders (e. g., KOPPKA 2004) suggest a rather shallow environment. Similarly, *Tanidromites richardson* and *T. lithuanicus* n. sp. both occur in high-energetic ironoolitic or bioclastic deposits lacking reefal habitats. Since the latter two, together with *Planoprosopon quadratum* n. sp., the Bajocian *Abyssophthalmus hebes* (v. MEYER, 1840), the Bathonian *Prosopon mammillatum* WOODWARD, 1886, several poorly defined taxa described by VAN STRAELEN (1925) from the French Middle Jurassic, and some new, still undescribed material studied by KROBICKI et al. (2007) and KROBICKI & ZATÓN (2008), are among the stratigraphically oldest representatives, so that the question arises if diversification of crabs started generally outside reefal habitats, possibly in the more temperate Subboreal or Submediterranean provinces of the Jurassic. When sponge-microbial reefs entered more northern areas during the Late Jurassic, the brachyurans had the chance to diversify from this stock and occupy various ecological niches. On the other hand, early representatives of Tanidromitidae occur in the Bajocian of Tanzania, suggesting a Tethyan origin of that group (SCHWEITZER & FELDMANN 2008a).

In any case, studies of reefal deposits of late Early or Middle Jurassic ages are much less in number compared with Late Jurassic examples, and the small crabs could have been easily overlooked or diagenetically destroyed.

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