

**A new approach to the systematics of
Laeviprosopon (Brachyura: Homolidae),
with remarks on the molting process of early brachyurans**

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ABSTRACT

Our understanding of the molting process in the Jurassic brachyurans is very scarce because useful material is rare. New specimens from Poland and Germany, in addition to previously known specimens, let us further investigate the molting process. Specimens of *Laeviprosopon laeve* reveal characters not known before. On the dorsal carapace, molting lines are confirmed in three species of *Laeviprosopon*: the type species *L. laeve*, *L. laculatum* and *L. fraasi*. This brought questions about the systematic position of *Laeviprosopon*, which we here reassign to Homolidae within Homoloidea. Furthermore, two specimens ascribed previously to *L. sublaeve* are transferred to *L. fraasi*, and one specimen ascribed previously to *Navarrahomola hispanica* is transferred to *Laeviprosopon hispanicum*. Three new species of *Laeviprosopon* (*L. joecollinsi* n. sp. and *L. lanceatum* n. sp. from the Oxfordian of Poland, and *L. ewakrzeminskae* n. sp. from the Tithonian of Austria) are erected. Finally, we deliberate on *Laeviprosopon* as a possible phyletic link between homolodromioids and homoloids in the light of new data on the evolution of molting line.

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INTRODUCTION

The systematic position of *Laeviprosopon* Glaessner, 1933, has changed several times due to the interpreted presence or absence of a molting line, often referred to as a *linea homolica* for crabs ascribed to Homoloidea. Glaessner (1933) initially placed this genus in the family Prosopidae von Meyer, 1860 (superfamily Homolodromioidea Alcock, 1900), but Patruilius (1966) transferred it to the superfamily Homoloidea due to the inferred presence of a *linea homolica*. His reassignment was followed by Collins and Wierzbowski (1985), Wright and Collins (1972) and Wehner (1988) (as also summarized in Klompmaker et al., 2013).

However, according to Schweitzer and Feldmann (2008), species of *Laeviprosopon* lack a true *linea homolica* and its presumed presence, noticed by Patruilius and others, might be a preservational

artifact. Therefore, *Laeviprosopon* was placed in the Prosopidae again by them, followed by others subsequently (e.g., Franțescu, 2011; Klompmaker, 2013; Klompmaker et al., 2020; Starzyk, 2020).

Six Late Jurassic species (Figure 1) from the Bachmayer collection housed in the Natural History Museum in Vienna were revised and described by Schweitzer and Feldmann (2008), including two new species: *L. laeve* (von Meyer, 1860), *L. sublaeve* (von Meyer, 1860), *L. punctatum* (von Meyer, 1860), *L. fraasi* (Moericke, 1889), *L. laculatum* Schweitzer and Feldmann, 2008, and *L. grandicentrum* Schweitzer and Feldmann, 2008. These authors also mentioned the Cretaceous species *L. icaunensis* (Van Straelen, 1936), which they treated as being specifically distinct from *L. fraasi* (opposite to Wehner, 1988). The arguments for that view were the geographic and age differences between *L. icaunensis* (Hauterivian of France –

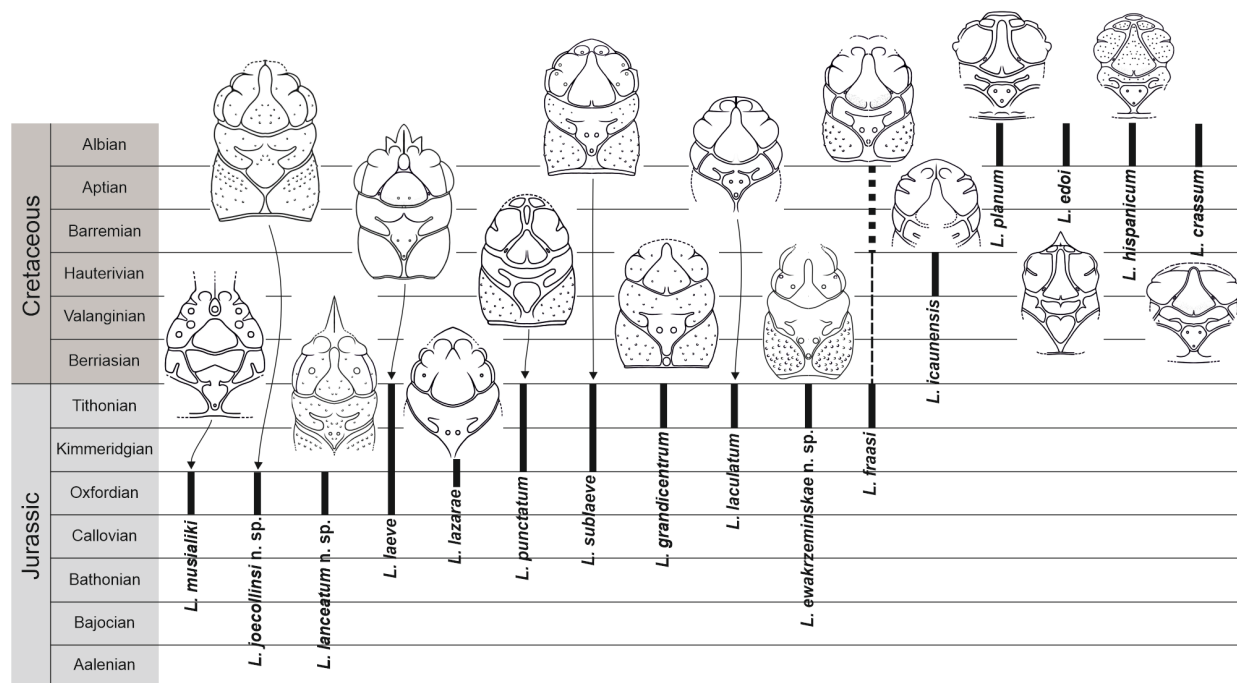


FIGURE 1. Stratigraphic range of the species herein considered within *Laeviprosopon* with schematic drawings of all the species.

Van Straelen, 1936) and *L. fraasi* (Tithonian of Poland [Moericke, 1889] and Romania [Patrulius, 1966]). As Klompmaker (2013: table 2) noted, *L. fraasi* was also mentioned by Patrulius (1966) from the Urgonian (Barremian–Aptian) of Romania, but that specimen was not illustrated. Since there is a time gap of at least 15 Ma between the type specimen of *L. fraasi* and the specimen mentioned by Patrulius (1966), it is likely that the latter represents a different species.

New specimens of *Laeviprosopon punctatum* were mentioned recently (Schweigert et al., 2016; Schweigert, 2019) from the late Kimmeridgian of Geislingen an der Steige (= Bad Überkingen-Oberböhringen) and Saal an der Donau, southern Germany, and one other specimen was illustrated by Klompmaker et al. (2020) from the Tithonian of Ernstbrunn in Austria.

In 2011, Franțescu described another species, *L. lazarae* Franțescu, 2011, from the Late Jurassic (late Oxfordian to early Kimmeridgian) of Romania (Figure 1).

Subsequently, Klompmaker (2013) described four new species: *L. planum* Klompmaker, 2013; *L. hispanicum* Klompmaker, 2013; *L. edoi* Klompmaker, 2013; and *L. crassum* Klompmaker, 2013. They originate from the mid-Cretaceous (late Albian) of Spain and are the stratigraphically youngest species of the genus (Figure 1). In 2020, Starzyk described the oldest species of *Laeviprosopon*: *L. musialiki* Starzyk, 2020, from the Late Jurassic (early Oxfordian) of Poland.

Schweitzer and Feldmann (2008) modified the diagnosis of *Laeviprosopon* created by Glaessner (1933), based on seven Jurassic and Cretaceous species: *L. laeve*, *L. fraasi*, *L. grandicentrum*, *L. icaunensis*, *L. laculatum*, *L. punctatum* and *L. sublaeve*. As four Cretaceous species described by Klompmaker (2013) differ from the diagnosis of *Laeviprosopon* by Schweitzer and Feldmann (2008), he expanded it to include also species with a wider carapace (Klompmaker, 2013). He also discussed the issue of the presence of a *linea homolica* in the Cretaceous representatives of the genus. All four species described by him have a symmetrical breakage on both sides of the carapace, which corresponds to the expected position of a *linea homolica* (Klompmaker, 2013). This observation leads to the question whether a *linea homolica* has evolved only once, within Homoloidea, or that similar structures evolved independently in different brachyuran groups.

The goals of this paper are to study the systematics and diversity of Jurassic and Cretaceous

Prosopidae and Homolidae with a focus on *Laeviprosopon*, and also to study and hypothesize about modes of molting in basal crabs in the Mesozoic.

LOCALITIES AND STRATIGRAPHY

The new material described herein originates from five Oxfordian localities in the southern Polish Uplands, north-west of Kraków (Bzów - 50°28'04"N 19°31'12"E, Ogradzieniec - 50°27'54"N 19°31'23"E, Niegowonice - 50°24'10"N 19°24'35"E, Szklary - 50°16'16"N 19°70'08"E, Żarki - 50°37'42"N 19°22'03"E) and a Kimmeridgian locality in Bad Überkingen-Oberböhringen, Germany (48°37'15"N 9°47'58"E) (Figure 2). The first three localities and their stratigraphy have been reported in Fraaije et al. (2012a, b), Krzemińska et al. (2015), Starzyk et al. (2012) and Starzyk (2015a, b).

The locality in Szklary is dated as middle Oxfordian (Müller et al., 2000; Garassino and Krobicki, 2002). The age of the sediments in Żarki is dated as early Oxfordian *costicardia* Subzone of the *cordatum* Zone (Głowniak, 2012). The age of the natural outcrop in Oberböhringen, is dated as early late Kimmeridgian *acanthicum* Zone based on the ammonite fauna (Schweigert et al., 2016). The age of the Štramberk Limestone at Kotouč Quarry in the Czech Republic is dated as Tithonian to early Berriasian (Vašíček et al., 2018).

The crab-bearing Oxfordian localities of Poland and the Kimmeridgian locality in Germany are situated in deep-water environments character-



FIGURE 2. Studied areas: 1 – five Oxfordian localities in southern Polish Uplands (Poland); 2 – late Kimmeridgian locality of Oberböhringen (Germany); 3 – Tithonian locality of Ernstbrunn (Austria); 4 – Tithonian - early Berriasian locality of Štramberk (Czech Republic).

ized by exhaustive siliceous sponge-microbial buildups, which occurred in a belt along the northern Tethys shelf and span from the subsurface of present-day Atlantic to extra-Carpathian Romania (e.g., Leinfelder et al., 1994, 1996; Leinfelder and Keupp, 1995; Matyja and Wierzbowski, 1996). In the Oxfordian Polish localities, namely that of Szklary near Kraków, the crabs occur autochthonously within the reef mounds (Fraaije et al., 2022), whereas in the Germany locality of Kimmeridgian age the rock matrix is a thick-bedded biodetritic spongiolitic limestone pointing to episodic mudflows from adjacent reefs (G.S., pers. observation).

The Tithonian to Berriasian Štramberk Limestone in the Czech Republic has formed on an isolated carbonate platform of the Tethys similar to the coeval Ernstbrunn Limestone of Austria. Both are characterized by scleractinian coral patch reefs and predominantly associated biodetritic rudstones and grainstones. Microfacies as well as dasycladalean algae and typical microencrusters at both occurrences are indicative of shallow-water environments within the photic zone (e.g., Schneider et al., 2013, Hoffmann et al., 2017).

MATERIAL AND METHODS

The specimens studied herein come from collections of the following museums: Geological Museum of Warsaw University, Poland (IGPUW); Natural History Museum of Vienna, Austria (NHMW); Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany (BSP, AS); Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS); Oertijdmuseum, Boxtel, The Netherlands (MAB); Museum of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków, Poland (ISEA PAS, museal prefix - I-F/MP); Florida Museum of Natural History (Division of Invertebrate Paleontology), University of Florida, Gainesville, Florida, USA (UF).

In total, there are 19 specimens described herein in the collection of ISEA PAS. Abundant material of fossil crabs from this collection has been described previously (Brachyura: Starzyk et al., 2011, 2012; Starzyk, 2013, 2015a, 2015b, 2016, 2020; Klompmaker et al., 2020; and Anomura: Fraaije et al., 2012a, 2012b, 2014; Krzemińska et al., 2015). Specimens from the collection of the Museum of ISEA PAS were collected by a family of amateur collectors: Iwona, Robert and Karolina Borek; two paratypes of *L. joecollinsi* n. sp. were collected by Adiël Klompmaker; 12

specimens of *L. laeve* described herein were collected by Horst Kuschel.

The length of the mesogastric region, width of the carapace at the hepatic region and the length of the carapace without the rostrum were measured (Figure 3). The total length was not measured because the rostrum in most of the carapaces is poorly preserved or broken.

SYSTEMATIC PALAEOLOGY

Order DECAPODA Latreille, 1802
 Infraorder BRACHYURA Linnaeus, 1758
 Superfamily HOMOLOIDEA de Haan, 1839
 Family HOMOLIDAE de Haan, 1839
 Genus *LAEVIPROSOPON* Glaessner, 1933

Type species. *Prosopon laeve* von Meyer, 1860, by original designation.

Other species included. *Laeviprosopon crassum* Klompmaker, 2013; *L. edoi* Klompmaker, 2013; *L. ewakrzeminskae* n. sp.; *L. fraasi* (Moericke, 1889) as *Prosopon*; *L. grandicentrum* Schweitzer and Feldmann, 2008; *L. hispanicum* Klompmaker, 2013; *L. icaunensis* (Van Straelen, 1936) as *Prosopon*; *L. joecollinsi* n. sp.; *L. laculatum* Schweitzer and Feldmann, 2008; *L. lazarae* Frantescu, 2011; *L. lanceatum* n. sp.; *L. musialiki* Starzyk, 2020; *L. planum* Klompmaker, 2013; *L. punctatum* (von Meyer, 1860) as *Prosopon*; *L. sublaeve* (von Meyer, 1860) as *Prosopon*.

Diagnosis. As in Klompmaker (2013). “Carapace rectangular, typically longer than wide, often narrowing slightly anteriorly; regions well-defined by deep grooves; rostrum variable, projected well beyond orbits; orbits shallow, rimmed, directed forward, located at base of rostrum; augenrest poorly formed to nearly absent; subhepatic region

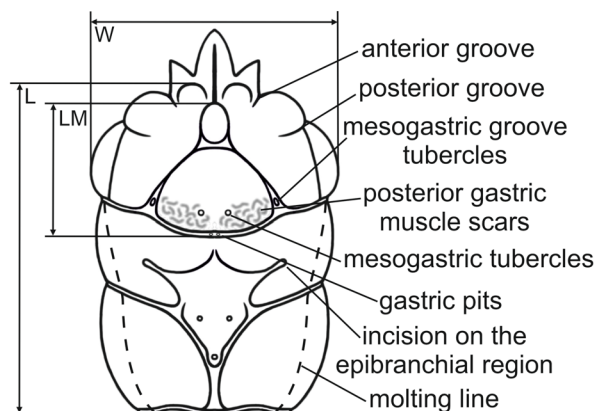


FIGURE 3. Carapace with morphological structures in *Laeviprosopon* using the type species, *L. laeve*.

inflated, sometimes greatly; epigastric region separated from protogastric and hepatic regions by transverse groove; hepatic and protogastric regions confluent or partly divided by groove on lateralmost part of dorsal carapace; cervical groove deep, strongly concave forward to sinuous; branchiocardiac groove usually shallower than cervical groove; post-cervical groove usually short; posterolateral portions of carapace often broken as if less calcified than other portions of carapace."

Remarks. As was mentioned in the introduction, the systematic position of *Laeviprosopon* has changed several times. Authors that did not confirm the presence of *linea homolica* placed it in the family Prosopidae (superfamily: Homolodromioidea), while authors that confirmed the presence of this structure in *L. laeve* placed the genus in the family Homolidae (superfamily: Homoloidea). In this paper, we show unequivocal evidence of the presence of *linea homolica* in three Late Jurassic representatives of *Laeviprosopon*. Eleven new specimens of *L. laeve* represent molds with clearly visible molting lines similar to a *linea homolica*, which is also present on the carapaces of *L. fraasi* and *L. laculatum*. Specimens of four Cretaceous species of *Laeviprosopon* (*L. hispanicum*, *L. planum*, *L. edoi* and *L. crassum*) are also molds presenting the same type of molting line. These observations are sufficient to reassign *Laeviprosopon* to the family Homolidae as it includes the oldest known brachyurans with a *linea homolica* (see chapter Discussion for more details).

Laeviprosopon laeve (von Meyer, 1860)
Figures 1, 3, 4, 5

- 1857 *Prosopon laeve* von Meyer, p. 556.
1860 *Prosopon laeve* von Meyer, 1857. – von Meyer, p. 209, pl. 23, figure 21.
1895 *Prosopon laeve* von Meyer, 1857. – Remeš, p. 202, pl. 12, figure 14.
1966 *Laeviprosopon laeve* (von Meyer, 1857). – Patrušius, p. 506, figure 2a, 4, pl. 30, figure 7.
1985 *Laeviprosopon laeve* (von Meyer, 1857). – Collins in Collins and Wierzbowski, p. 86, pl. 4, figure 3-3.
2008 *Laeviprosopon laeve* (von Meyer, 1857). – Schweitzer and Feldmann, p. 277, figure 1.1-1.5.
2018 *Laeviprosopon sublaeve* (von Meyer, 1857). – Schweigert and Kuschel, p. 19, figure 8.

Diagnosis. (After Schweitzer and Feldmann, 2008, emended). Species reaching relatively large

size (length of mesogastric region of largest specimen is 16.1 mm). Carapace longer than wide, rectangular, strongly vaulted transversally and moderately vaulted longitudinally; cuticle smooth or covered with small granules. Rostrum trifid. Orbit flattened, short, distinctly bordered, with a suborbital spine. Mesogastric region with two gastric spines and posterior gastric muscle scars posterior to these spines. Mesogastric groove tubercles present. Anterior part of carapace and epibranchial region convex, branchial region flatter. Molting lines similar to *linea homolica* present.

Type material. *Laeviprosopon laeve* was described by von Meyer in 1860 based on two specimens which are both lost (Schweitzer and Feldmann, 2008). They have been collected from the Kimmeridgian locality Oerlinger Tal in Germany. Herein we describe new material from the upper Kimmeridgian locality Bad Überkingen-Oberböhringen, which is stratigraphically close to the Oerlinger Tal locality. Therefore, we assign a neotype: specimen SMNS 70527/1.

Material Examined

Austria. Ernstbrunn (Tithonian of Waschberg Zone): NHMW 1990/0041/3309; NHMW 1990/0041/3834; NHMW 1990/0041/4915; NHMW 2007z0149/0020; NHMW 2007z0149/0021; NHMW 2007z0149/0022.

Poland. Rudniki (lower Kimmeridgian, *planula* Zone): IGPUW/C/1/128, Niwiska Dolne (lower Kimmeridgian, *planula* Zone): IGPUW/C/1/129.

Germany. Bad Überkingen-Oberböhringen (upper Kimmeridgian): SMNS 70527/1 - neotype, SMNS 70527/2, SMNS 70527/3, SMNS 70527/4, SMNS 70527/5, SMNS 70527/6, SMNS 70527/7, SMNS 70527/8, SMNS 70527/9, SMNS 70527/10, SMNS 70527/11.

Poland. Bzów (middle Oxfordian): I-F/MP/3663/1533/08; I-F/MP/3914/1533/08; I-F/MP/4627/1534/08.

Niegowonice (middle – upper Oxfordian): I-F/MP/915/1507/08; I-F/MP/3245/1532/08; I-F/MP/3295/1532/08; I-F/MP/4810/1534/08; I-F/MP/5467/1543/09; I-F/MP/6275/1599/12.

Ogrodzieniec (lower – middle Oxfordian): I-F/MP/172/1489/08.

Dimensions. The state of preservation of the material from the ISEA collection is not good enough to take measurements of all specimens. The length of the mesogastric region of the smallest specimen is 3.6 mm and that of the largest one 8.8 mm. The length of the mesogastric region of specimen SMNS 70527/1 is 5.4 mm, 4.0 mm for

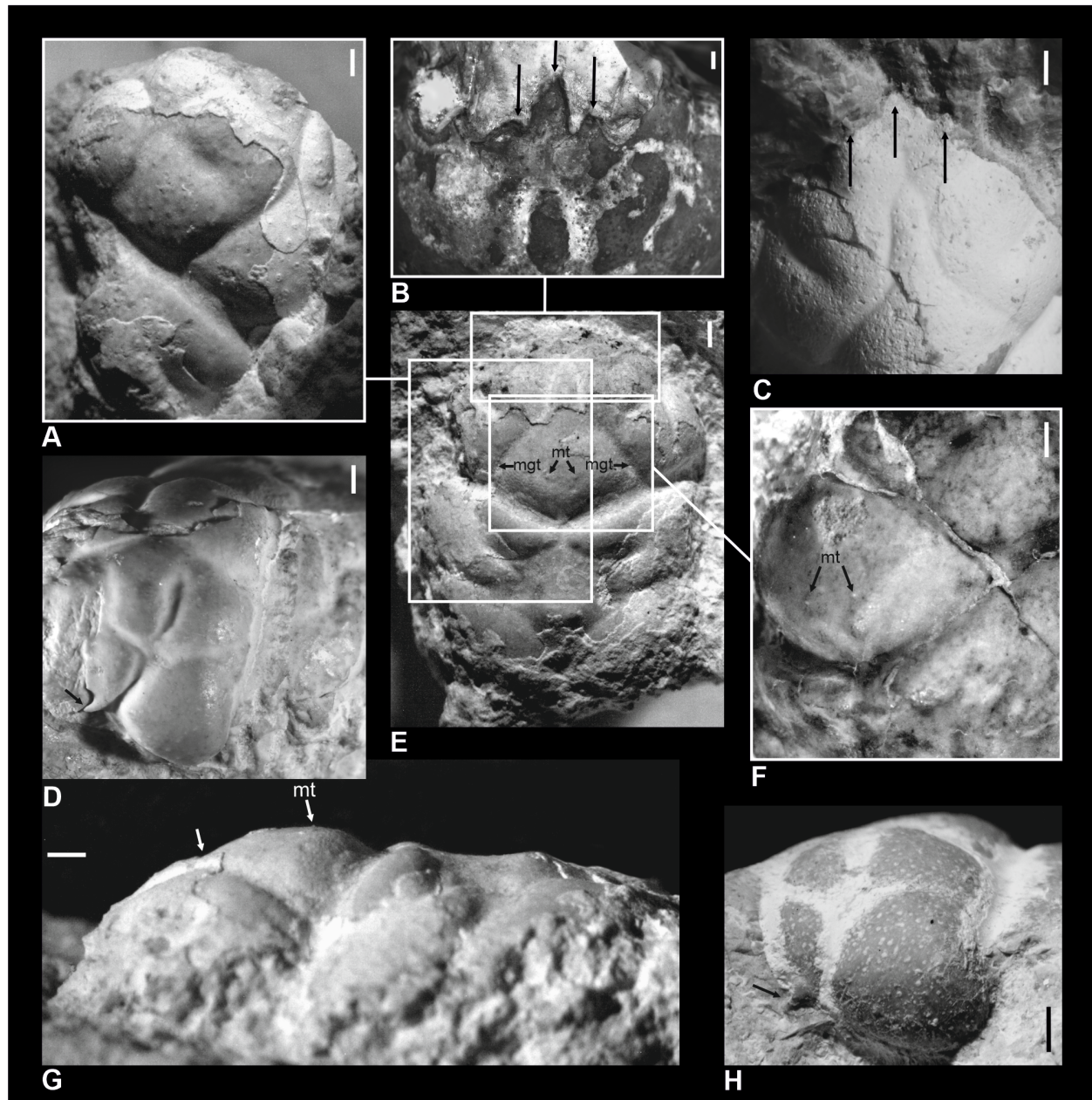


FIGURE 4. *Laeviprosopon laeve*. A - anterior left part of the carapace with granules visible (I-F/MP/3663/1533/08, Bzów); B - rostrum, bases of the spines marked with black arrows (NHMW 2007z0149/0022, Ernstbrunn); C - rostrum, bases of the spines marked with black arrows (SMNS 70527/8, Oberböhringen); D - suborbital spine (IGPUW C/1/128, Rudniki); E - carapace (I-F/MP/3914/1533/08, Bzów); F - mesogastric region with symmetric tubercles visible (I-F/MP/6275/1599/12, Niegowonice); G - left lateral view (I-F/MP/3914/1533/08); H - suborbital spine marked with black arrow (SMNS 70527/5, Oberböhringen). mt – mesogastric tubercles, mgt – mesogastric groove tubercles. Scale bars equal 1.0 mm.

SMNS 70527/4, and 4.45 mm for SMNS 70527/2. Total length without rostrum is 12.0 mm in the specimen SMNS 70527/1, 9.1 in the specimen SMNS 70527/4 and 10.3 mm in the specimen SMNS 70627/2. The width at the hepatic region is 9.2 mm in the specimen SMNS 70527/1.

Emended description. As a large number of new specimens show characters not known before, a redescription is needed.

The carapace is longer than wide, strongly vaulted transversally and moderately vaulted longitudinally, widest in the hepatic region. The rostrum

is well preserved only for 2007z0149/0022, showing three spines, of which the middle one is the longest and directed downwards. There is only a forked base of the rostrum visible in SMNS 70527/8 (Figure 4C marked with black arrows). There are distinct spines situated laterally from the rostrum (Figure 4D, H).

The anterior groove is visible in the intersection of the rostrum and the upper orbital margin. The epigastric regions are rounded. The mesogastric region is distinctly bordered by mesogastric grooves; the length of its anterior (narrow) part is about 0.59 of the posterior (wide) part; the separation between these parts is marked by an incision. The posterior gastric muscle scars are present on the posterior mesogastric region, and in front of them there are two tubercles (Figure 4E-G). Mesogastric groove tubercles are present (Figure 4E).

The gastric pits are rounded. The urogastric region is vaulted, with an incision in the center dividing it into two parts (Figure 4E). A tubercle on the urogastric region is very small. Lateral parts of the postcervical groove are connected with the branchiocardiac groove. These grooves bound narrow surfaces anterior to the cardiac region (Figures 4E; 5A, D-E).

The cardiac region is distinctly delimited by the branchiocardiac groove. There are two tubercles in the anterior part of this region and one in the posterior part (Figure 5A-B, D-E).

The anterior part of the carapace and the epibranchial region are convex, and the branchial region is more flattened. The highest point of the carapace lies in the posterior part of the mesogastric region (Figure 5G-H). The grooves are deep and wide, and the cervical groove is the widest. The branchiocardiac groove reaches the posterior margin of the carapace. Few of the specimens from ISEA (I-F/MP/915/1507/08, I-F/MP/54671543/09) have almost smooth carapaces with only few tubercles on the steinkern; the cuticle is not preserved. Others from ISEA (I-F/MP/3663/1533/08, I-F/MP/3914/1533/08 and I-F/MP/6275/1599/12) have carapaces covered with tubercles (Figure 4A). Specimens from Oberböhringen and Ernstbrunn are also covered with tubercles. The cuticle of these specimens is relatively thick, and its surface is covered with tiny pits, each of which corresponds to a tubercle on the steinkern. Pits on the cuticle and corresponding tubercles on the steinkern are also visible on specimen I-F/MP/3663/1533/08 (Figure 4A). The posterior margin of

the carapace is preserved only partially or not at all.

Most specimens from the Polish localities are damaged in the posterior part, but specimens I-F/MP/39141533/08, I-F/MP/6275/1599/12 (Figure 5C), IGPUW/C/1/128 and IGPUW/C/1/129 are showing a loss of lateral parts of the branchial regions. Most specimens from the German locality Oberböhringen are also molts with a molting line similar to a *linea homolica* (Figure 5A-B, D-G). Only one specimen shows an entire, unbroken carapace and the molting line is not visible on it (Figure 5H). Molting lines are laying on the dorsal surface of the branchial and epibranchial regions and crossing on the ventrolateral side of the hepatic region (Figure 5B).

Discussion. The new specimens of the type species from the German locality Oberböhringen are crucial for reassessing the systematic placement of *Laeviprosopon*. These specimens are ascribed to the type species due to their characters which correspond to the original illustration of *L. laeve*. The overall shape and convexity of the carapace and each region and groove, the presence of gastric muscle scars and the mesogastric groove tubercles are consistent with *L. laeve*.

There is intraspecific variation visible in the ornamentation of the carapace of specimens from different localities, apparently not related to preservation. There are specimens with and without tubercles on the steinkern in the collection of ISEA PAS. Specimens from Oberböhringen and Ernstbrunn are also covered with tubercles on the steinkern. These tubercles correspond with pits on the cuticle where preserved.

These pits in the cuticle and corresponding tubercles on the steinkern are also present on specimen I-F/MP/3663/1533/08. Because all other characters correspond well with *Laeviprosopon laeve*, the presence of tubercles is considered to represent intraspecific variation.

Laeviprosopon sublaeve (von Meyer, 1860)

Figure 1

- 1857 *Prosopon sublaeve* von Meyer, p. 556.
 1860 *Prosopon sublaeve* von Meyer. – von Meyer, p. 209, pl. 23, figure 23.
 1925 *Prosopon sublaeve* von Meyer. – Beurlen, p. 484, 485.
 1929 *Prosopon laeve* var. *sublaevis* von Meyer. – Glaessner, p. 344.
 1933 *Laeviprosopon laeve* var. *sublaevis* (von Meyer). – Glaessner, p. 180.

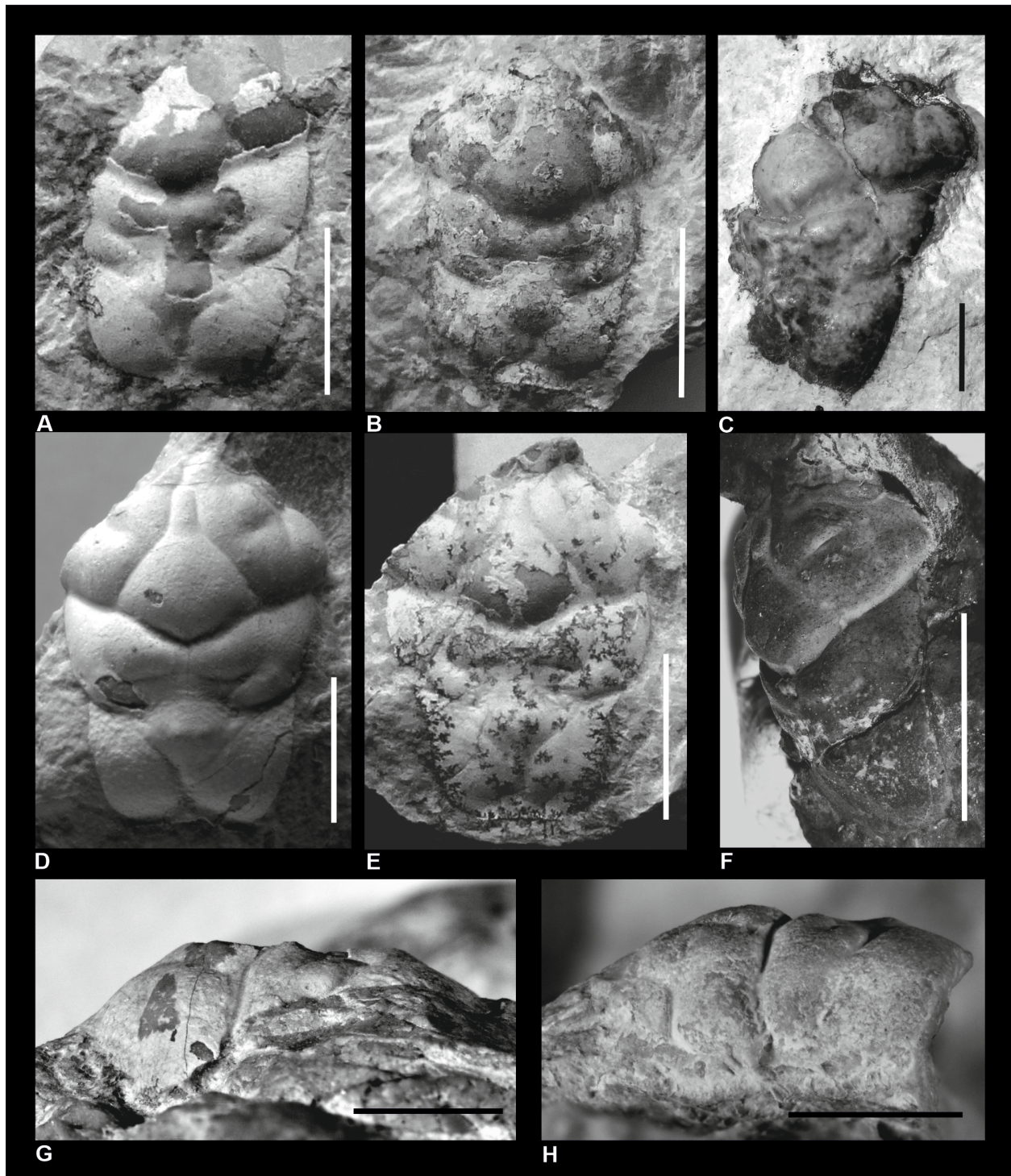


FIGURE 5. *Laeviprosopon laeve*, specimens interpreted as molts with molting lines similar to *linea homolica* A - SMNS 70527/3 (Oberböhringen); B - SMNS 70527/4 (Oberböhringen); C - I-F/MP/6275/1599/12 (Niegowonice); D - SMNS 70527/1 (Oberböhringen); E - SMNS 70527/2; F - right lateral view, NHMW 1990/0041/4915 (Ernstbrunn); G - left lateral view, SMNS 70527/6 (Oberböhringen); H - left lateral view, SMNS 70527/11 (Oberböhringen) lateral sides of the carapace with no signs of the molting lines. Scale bars equal 5.0 mm.

1988 *Laeviprosopon sublaeve* (von Meyer). – Wehner, p. 119, text-figure 32, pl. 8, figure 3.

Diagnosis. (After Schweitzer and Feldmann 2008, emended). Carapace longer than wide, rectangular; front broadly convex; orbits well-developed for genus; regions ornamented with tubercles and larger nodes, especially posteriorly, five tubercles on each side of mesogastric region.

Discussion and type designation. *Laeviprosopon sublaeve* was described by von Meyer (1860), who illustrated a drawing of a specimen from Oerlinger Thal near Ulm (late Kimmeridgian). He drew transverse grooves dividing areas laying on both sides of the mesogastric region on epigastric, protogastric, hepatic and subhepatic regions and five tubercles laying on each side of the mesogastric region. Both on the drawing and in the description (translated in Schweitzer and Feldmann, 2008), the transverse grooves are present. Unfortunately, all of the six syntypes of von Meyer are lost, so that there is no possibility left to select a lectotype.

Wehner (1988) illustrated a specimen (GPIT-PV-51741) of *Laeviprosopon sublaeve* from Oerlinger Thal housed in the Museum of the University in Tübingen. Wehner cited the label with the wrong information: the mentioned specimen is not one of the specimens illustrated by Quenstedt (1857, pl. 95) and probably not illustrated in later books of Quenstedt (see Quenstedt 1885, pl. 31, fig. 21). As this information was erroneous, we cannot be sure if the locality described as Oerlinger Thal is right. However, as all six syntypes are lost, we here designate the specimen described by Wehner as a neotype. Its current number in the paleontological collection of Tübingen University is GPIT-PV-51741.

The specimen has all the diagnostic characters described and drawn by von Meyer. On the photo published by Wehner, two tubercles seem to be visible on each side of the mesogastric region, while the drawing made by Wehner (who studied the actual specimen) shows only one tubercle on each side (Wehner, 1988, figure 32B, C; pl. 8, figure 3).

The specimens assigned to *L. sublaeve* by Schweitzer and Feldmann (2008, figure 1.10 and 1.11, herein Figure 6) differ. Both specimens have transverse grooves between the cervical and branchial groove, which are absent in the specimens described by von Meyer (1860) and Wehner (1988). From the neotype specimen we consider it is barely possible that both von Meyer and Wehner could have overlooked the presence of these

grooves on their drawings and descriptions. As specimens NHMW 1990/0041/4051 and NHMW 1990/0041/3295 described by Schweitzer and Feldmann (2008) are most similar to *Laeviprosopon fraasi*, we consider them to represent this species (see text below and Figure 6).

Laeviprosopon fraasi (Moericke, 1889)
Figures 1, 6

- 1889 *Prosopon fraasi* Moericke, p. 63, pl. 6, figure 17.
1897 *Prosopon fraasi* Moericke, p. 63, pl. 6, figure 17.
1895 *Prosopon fraasi* Moericke. – Remeš, p. 203, pl. 3, figure 15.
1905 *Prosopon fraasi* Moericke. – Remeš, p. 35.
1925 *Avihomola fraasi* (Moericke). – Van Straelen, p. 347.
1929 *Nodoprosopon fraasi* (Moericke). – Glaesner, p. 271.
1933 *Laeviprosopon fraasi* (Moericke). – Glaesner, p. 180.
1966 *Laeviprosopon fraasi* (Moericke). – Patruilius, p. 507.
1988 *Laeviprosopon fraasi* (Moericke). – Wehner, p. 119, text-figure 32, pl. 8, figure 4a, 4b.
2008 *Laeviprosopon fraasi* (Moericke). – Schweitzer and Feldmann, p. 281, pl. 1.6.
2008 *Laeviprosopon sublaeve* (von Meyer). – Schweitzer and Feldmann, p. 278–280, pl. 1.10, 1.11.

Diagnosis. (After Schweitzer and Feldmann, 2008, emended.) Carapace longer than wide, regions well defined, smooth on anterior part, with tubercles on posterior part. Grooves deep; carapace flattened longitudinally and moderately vaulted transversely. Orbits flattened, short, distinctly bordered, narrowing posteriorly. Mesogastric region with posterior gastric muscle scars. Mesogastric groove tubercles present. Molting lines similar to *linea homolica* present.

Material Examined

Czech Republic. Štramberk (Tithonian): holotype BSP AS III 309.

Austria. Ernstbrunn (Tithonian of Waschberg Zone): NHMW 1990/0041/3295; NHMW 1990/0041/4051.

Dimensions. Dimensions of specimens are given in Schweitzer and Feldmann (2008, p. 279, table 1).

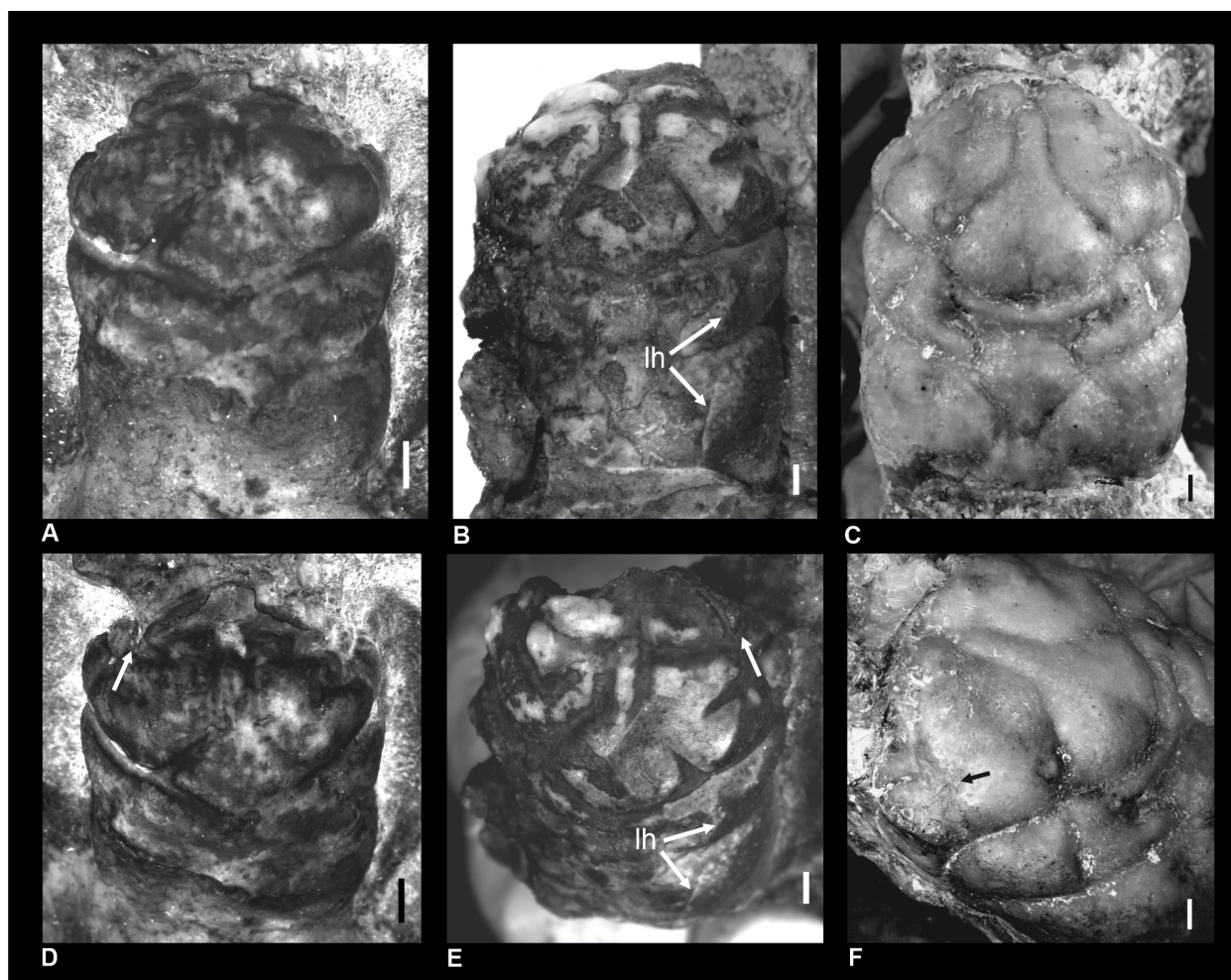


FIGURE 6. *Laeviprosopon fraasi* A - NHMW 1990/0041/3295, Ernstbrunn; B - NHMW 1990/0041/4051, Ernstbrunn; C - holotype, BSP AS III 309, Štramberk; D - NHMW 1990/0041/3295; E - NHM W1990/0041/4051; F - holotype, BSP AS III 309. Orbital margin marked with an arrow. lh – *linea homolica*. Scale bars equal 1.0 mm.

Discussion. Schweitzer and Feldmann (2008) assigned two specimens from Ernstbrunn to *L. sublaeve*, although their characters distinctly differ from the holotype. Specimens NHMW 1990/0041/4051 and NHMW 1990/0041/3295 (Figure 6; Schweitzer and Feldmann, 2008, figure 1.10, 1.11) are very similar to *L. fraasi* because their groove pattern on both sides of the mesogastric region and transverse grooves between the cervical and branchiocardiac grooves are alike. They have a short rostrum, shortened epigastric regions, and the ornamentation on the posterior part of the carapace is similar.

There is a difference between the holotype of *L. fraasi* (Figure 6C, F) and one of the specimens from Ernstbrunn; specimen NHMW 1990/0041/3295 (Figure 6A, D) has a smaller posterior part of

the mesogastric region, opposite to specimen NHMW 1990/0041/4051 (Figure 6B, E), but given all other matching characters we consider both specimens to represent *L. fraasi*.

There is a molting line similar to a *linea homolica* visible on specimen NHMW 1990/0041/4051 (Figure 6B, E). This specimen presents a complete carapace and the molting line is shaped similar as in *L. laeve*; on the dorsal part of the branchial and epibranchial regions, it is not reaching the anterior margin, but it is directed to the ventral surface of the carapace on the level of the cervical groove. Patrušius (1966) also mentioned the presence of a *linea homolica* on the specimens of *L. laeve* and *L. fraasi*. This view was supported by Wright and Collins (1972) and Collins and Wierzbowski (1985).

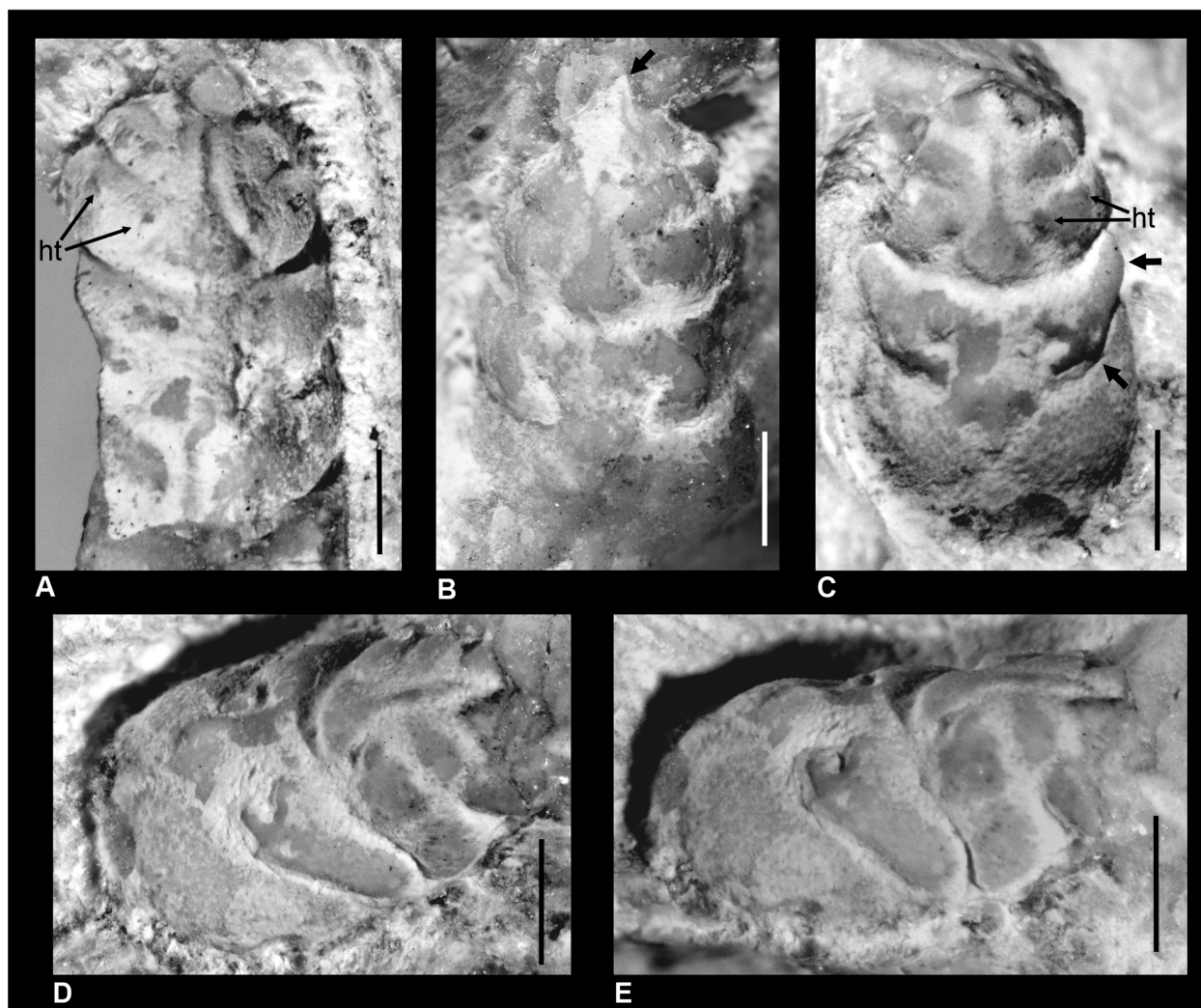


FIGURE 7. *Laeviprosopon ewakrzeminskae* n. sp. A - carapace (NHMW 1990/0041/5179, paratype, Ernstbrunn); B - carapace, rostrum marked by an arrow (NHMW 2014/0194/0978, paratype, Ernstbrunn); C - carapace, spines on the epibranchial region marked by an arrow (NHMW 1990/0041/2744a, holotype, Ernstbrunn); D - lateral right view (NHMW 1990/0041/2744a); E - lateral right view (NHMW 1990/0041/2744a). ht – hepatic tubercle. Scale bars equal 1.0 mm.

Laeviprosopon ewakrzeminskae n. sp.

Figures 1, 7

zoobank.org/004C6A33-3FC4-45B7-8C5A-D3002EC6B540

Diagnosis. Carapace very elongate, narrowing anteriorly, strongly vaulted transversally and moderately vaulted longitudinally. Orbits not differentiated. Very long and narrow mesogastric region. Two tubercles on each side of mesogastric region present. Branchial region ornamented with very small tubercles.

Etymology. The species name is dedicated to Ewa Krzemińska (ISEA PAS), with a deep gratitude for being an advisor and a mentor of Natalia Starzyk. Ewa is a renowned specialist of recent

and fossil Diptera, also working on fossil Brachyura and Anomura.

Comparisons. Specimens of *Laeviprosopon ewakrzeminskae* n. sp. are narrowing anteriorly as in *L. joecollinsi*, *L. lazarae* and *L. grandicentrum*. The carapace is elongated unlike in *L. planum* and *L. crassum*. It has a long and narrow mesogastric region unlike in *L. joecollinsi*, *L. musialiki*, *L. lanceatum*, *L. laeve*, *L. punctatum*, *L. sublaeve*, *L. laculatum*, *L. fraasi*, *L. icaunensis*, *L. hispanicum* and *L. crassum*. Symmetric tubercles on the mesogastric region present in *L. laeve* are absent in *L. ewakrzeminskae* n. sp., but there are two tubercles on each side of the mesogastric region which are absent in *L. joecollinsi*, *L. laeve*, *L. punc-*

tatum, *L. laculatum*, *L. fraasi*, *L. icaunensis*, *L. edoi*, *L. planum*, *L. hispanicum* and *L. crassum*. Epigastric, protogastric and hepatic regions are separated by transverse grooves as in *L. laeve*.

Material Examined

Type material. Holotype: NHMW 1990/0041/2744a; type locality: Ernstbrunn; age: Tithonian.

Paratypes. NHMW 1990/0041/5179, NHMW 2014/0194/0978; locality: Ernstbrunn; age: Tithonian.

Additional material. NHMW 1990/0041/3959b; locality: Ernstbrunn; age: Tithonian.

Dimensions. The state of preservation of the material from the NHMW collection is not good enough to take measurements of all specimens. The length of the mesogastric region of the holotype is 1.4 mm, and that of the paratypes are 1.7 and 1.4 mm, respectively. The width at the hepatic region of the holotype is 2.4 mm. The width of the branchial region of the holotype is 2.3 mm. As the posterior margin is not preserved on any of the specimens, it is not possible to measure the length of the carapace.

Description. The carapace is longer than wide, widest on the branchial region, strongly vaulted transversally and moderately vaulted longitudinally (Figure 7).

Only the base of the rostrum is preserved in specimen NHMW 2014/0194/0978 (Figure 7B). The anterior groove is deep, visible at the intersection of the rostrum and the upper orbital margin (Figure 7). The epigastric regions are rounded. The mesogastric region is very long, flattened with a very narrow anterior part. There is no separation between the anterior and posterior part of this region (Figure 7). The posterior gastric muscle scars are absent.

Gastric pits and mesogastric groove tubercles are absent. There are two hepatic tubercles on each side of the mesogastric region (Figure 7A, C). The epigastric, protogastric and hepatic regions are separated by transverse grooves (Figure 7B, D-E).

The urogastric region is undivided (Figure 7C). The cardiac region is distinctly bordered by the branchiocardiac groove, narrowing posteriorly, with two tubercles in the anterior part and a tubercle in the posterior part (Figure 7C).

The carapace is covered with granules only in its posterior part. They are visible on the internal mold and in places with the cuticle preserved. The grooves are wide and deep. The lateral parts of the postcervical groove are connected with the branchial groove. The branchiocardiac groove reaches

the posterior margin of the carapace. The posterior margin of the carapace is not preserved in any of the specimens.

All of the specimens are almost complete carapaces not showing any traces of molting lines.

Laeviprosopon lanceatum n. sp.

Figures 1, 8

zoobank.org/4A54E1D0-43A6-4786-A202-005D820F9D4D

Diagnosis. Carapace longer than wide. Rostrum with a very long central spine. Orbital margin round, surface posterior to orbits convex. Epigastric regions strongly vaulted. Large tubercle on each hepatic region. Epigastric, protogastric and hepatic regions separated by transverse grooves.

Etymology. The name *lanceatum* derives from the Latin word “lancea” – spear. It refers to the prominent rostrum.

Comparisons. The holotype of *Laeviprosopon lanceatum* n. sp. is much smaller than specimens of *L. laeve*, but there is not enough material to ascertain whether the small size is a true character of this species or the specimens are just juveniles. Its carapace is widest on the hepatic region, as in most species of the genus except *L. joecollinsi* n. sp., *L. musialiki*, *L. lazarae* and *L. ewakrzeminskae* n. sp. The carapace is elongated unlike in *L. planum*, *L. crassum* and *L. hispanicum*. The anterior and posterior part of the mesogastric region of *L. lanceatum* n. sp. is more or less the same length unlike in *L. musialiki*, *L. laeve*, *L. lazarae*, *L. sublaeve*, *L. grandicentrum*, *L. laculatum*, *L. fraasi*, *L. planum*, *L. hispanicum* and *L. crassum*. Symmetrical tubercles on the mesogastric region present in *L. laeve* are absent in *L. lanceatum* n. sp. A single large tubercle on each side of the posterior part of the mesogastric region present in *L. lanceatum* n. sp. is also present only in *L. lazarae* and *L. grandicentrum*. Epigastric, protogastric and hepatic regions are separated by transverse grooves as in *L. laeve*, *L. joecollinsi*, *L. lazarae*, *L. sublaeve*, *L. ewakrzeminskae* n. sp. and *L. fraasi*. Epigastric regions are rounded in *L. lanceatum* n. sp., not short and wide as in *L. lazarae* and *L. sublaeve*. *Laeviprosopon lanceatum* n. sp. has a rostrum with a very long central spine not noticed in any other species of the genus.

Material Examined

Type material. Holotype: I-F/MP/736/1502/08; type locality: Ogodzieniec; age: early–middle Oxfordian.

Paratype. I-F/MP/342/1497/08; locality: Niegowonice; age: middle – late Oxfordian (upper *elizabethae* Subzone – upper *wartae* Subzone).

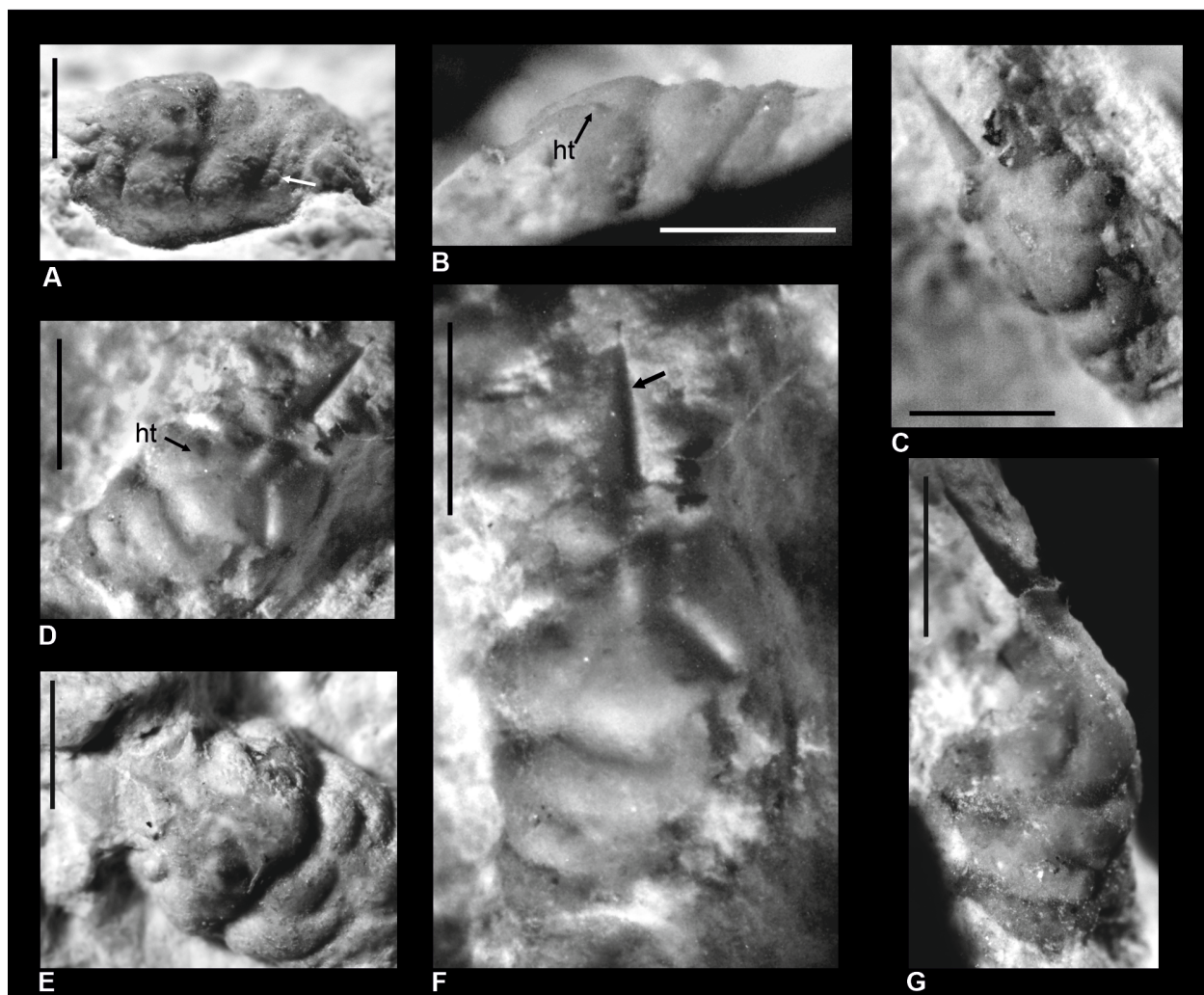


FIGURE 8. *Laeviprosopon lanceatum* n. sp. A, B - left lateral view (A) I-F/MP/342/1497/08, paratype, Niegowonice; (B) I-F/MP/736/1502/08, holotype, Ogrodzieniec); C - carapace with the orbital margin visible (I-F/MP/736/1502/08); D - carapace (I-F/MP/736/1502/08); E - carapace with the orbital margin visible (I-F/MP/342/1497/08); F - carapace (I-F/MP/736/1502/08); G - oblique view (I-F/MP/736/1502/08). Scale bars equal 1.0 mm.

Dimensions. Specimens are not well preserved, and thus most measurements cannot be taken accurately. Length of the mesogastric region of the holotype is 0.9 mm, of the paratype 1.4 mm. Carapace width at the level of the hepatic region is 1.4 mm for the holotype and 1.6 mm for the paratype.

Description. The carapace is longer than wide, widest on the hepatic region, strongly vaulted transversally and moderately vaulted longitudinally (Figure 8A-B, F). The anterior part of the carapace in front of the cervical groove is relatively long.

The rostrum is only preserved as an impression with a very long central spine preserved in both specimens. The base of rostrum is very wide, and the central spine is located between damaged

bases of the lateral parts of rostrum (Figure 8C, D, E, F). The orbital margin is rounded. There is a groove separating the base of the rostrum and the orbital margin. The surface behind the orbits is slightly convex (Figure 8A, C, E).

The epigastric regions are rounded, strongly vaulted, partially preserved on both specimens. The mesogastric region is distinctly bounded by grooves. The anterior (narrow) and posterior (wide) part of this region are more or less the same length. The posterior part is the highest point of the carapace. There is no incision between the anterior and posterior part of this region (Figure 8).

A pair of small, rounded gastric pits is present in the cervical groove. There is a pair of large hepatic tubercles on both sides of the posterior part

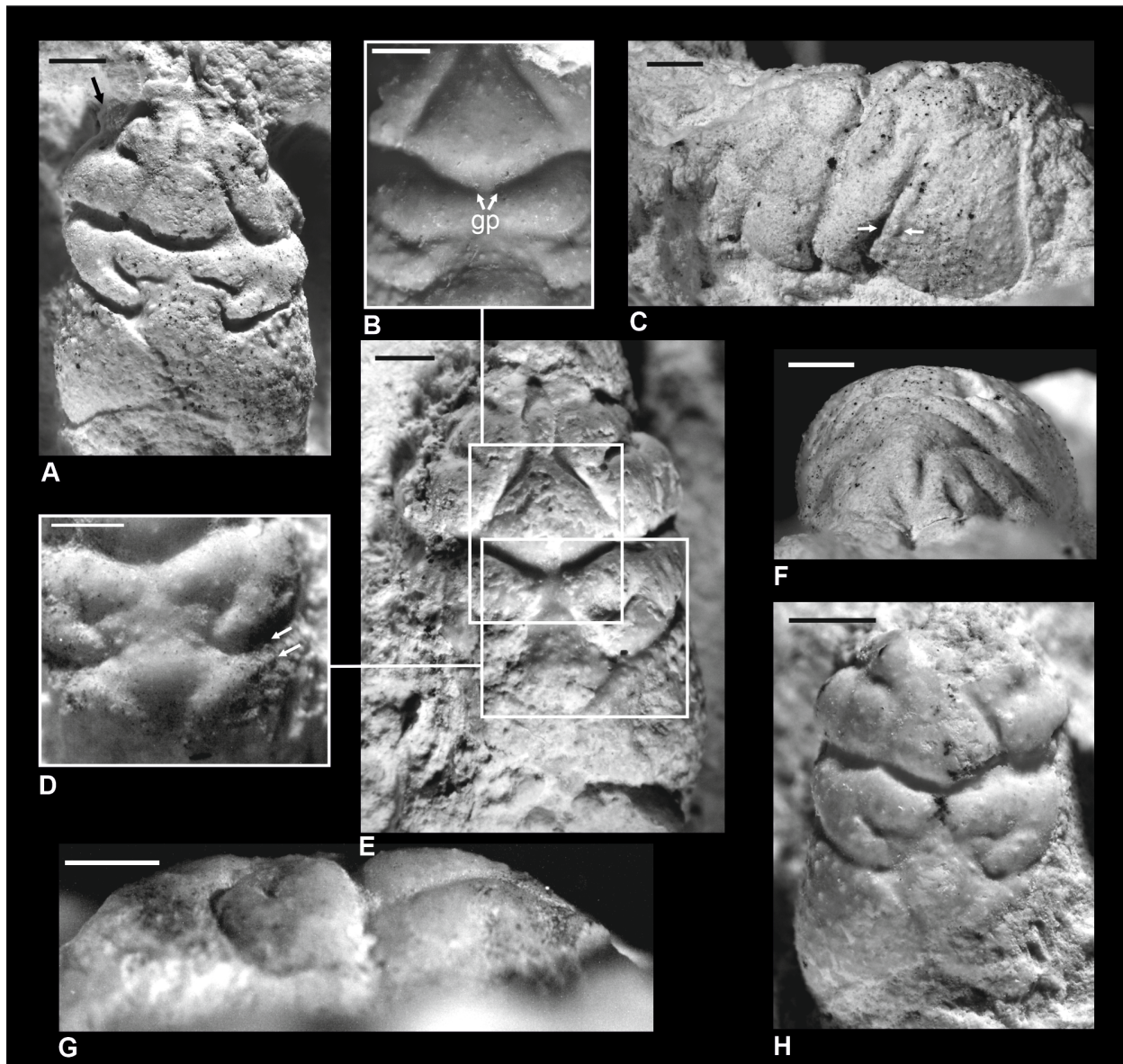


FIGURE 9. *Laeviprosopon joecollinsi* n. sp. A - carapace (paratype, UF272115, Szklary); B - carapace (I-F/MP/30381532/08, Niegowonice) gp – gastric pits; C - lateral left view (paratype, UF272115) groove parallel to the branchio-cardiac groove; D - carapace (I-F/MP/741/1502/08, paratype, Ogródzieniec) groove parallel to the branchio-cardiac groove; E - carapace (I-F/MP/6264/1599/12, holotype, Niegowonice); F - anterior view (paratype, UF272115); G - lateral right view (I-F/MP/741/1502/08); H - carapace (paratype, UF272119, Szklary). Scale bars equal 1.0 mm.

of the mesogastric region (one on each side) (Figure 8A-B, D, G). The epigastric, protogastric and hepatic regions are separated by transverse grooves (Figure 8A).

The urogastric region is convex and relatively broad, delimited by the postcervical groove. There are very narrow grooves laying parallel to the lateral parts of the branchiocardiac groove (Figure 8A). The cardiac region is not distinctly bordered, narrowing posteriorly, with two tubercles in the posterior part.

The grooves are very wide and deep. The cervical groove is the deepest. The internal mold of the carapace is covered with small tubercles. The cuticle is not preserved.

Laeviprosopon joecollinsi n. sp.
Figures 1, 9

zoobank.org/C569B457-C53E-4130-88E9-2DD874756F88

Diagnosis. Carapace longer than wide, widest on branchial region (length of holotype from epigastric region to posterior margin: 6.7 mm), strongly

vaulted transversally and moderately vaulted longitudinally. Epigastric, protogastric and hepatic regions separated by transverse grooves. Internal mold of carapace densely covered with granules posteriorly, sparsely so in anterior part; granules also visible on cuticle. Shallow grooves laying parallel to branchial groove.

Etymology. The name *joecollinsi* is dedicated to Joseph (Joe) S.H. Collins (1927–2019), a specialist of fossil crustaceans, especially decapods.

Comparisons. The carapaces of *L. laeve* are less convex. *Laeviprosopon joecollinsi* n. sp. also differs from *L. laeve* in the absence of the symmetrical tubercles on the mesogastric region and in having a narrower posterior part of this region. The mesogastric region of *L. joecollinsi* n. sp. is not divided in the middle as in *L. punctatum*, *L. laeve* and *L. musialiki*. It has a distinct narrow anterior and broad posterior part more or less the same length unlike in *L. lazarae*, *L. sublaeve*, *L. grandicentrum*, *L. laculatum*, *L. edoi*, *L. hispanicum*, *L. planum* and *L. crassum*. The species has round epigastric regions, not short and wide as in *L. sublaeve*, *L. fraasi*, *L. edoi*, *L. planum* and *L. hispanicum*. The species does not have a transverse groove from the cervical to the branchio-cardiac groove as in *L. sublaeve*, *L. fraasi*, *L. musialiki* and *L. icaunensis*. The species does not have any large tubercles on the carapace as in *L. musialiki*, *L. lanceatum* n. sp. and *L. lazarae*. The epigastric, protogastric and hepatic regions are separated by transverse grooves as in *L. laeve*, *L. lazarae*, *L. sublaeve*, *L. fraasi*, *L. ewakrzeminskae* n. sp. and *L. lanceatum* n. sp.

Material Examined

Type material. Holotype: I-F/MP/6264/1599/12; type locality: Niegowonice; age: middle – late Oxfordian (upper Elizabethae Subzone – upper Wartae Subzone).

Paratypes. I-F/MP/5061/1543/09; type locality: Niegowonice; age: middle – late Oxfordian; I-F/MP/741/1502/08; type locality: Ogrodzieniec; age: early–middle Oxfordian; UF272115, UF272119; type locality: Szklary; age: middle Oxfordian.

Additional material. Niegowonice: I-F/MP/3037/1532/08; I-F/MP/3038/1532/08; I-F/MP/3873/1533/08; I-F/MP/4623/1534/08.

Dimensions. The state of preservation of the material is not good enough to take most of the measurements. The length of the holotype from the epigastric region to the posterior margin is 6.7 mm, 9.5 mm for paratype UF272115. The maximum width of paratype 5061 in the epibranchial region is

5.3 mm. The length of the mesogastric region of paratypes 5061 and 741 is 3.4 mm and 2.7 mm, respectively.

Description. The carapace is longer than wide, widest in the branchial region, strongly vaulted transversally and moderately vaulted longitudinally (Figure 9A, E, G-H).

The rostrum is not preserved on any specimen. The orbital margin is rounded, with a flattened suborbital spine (Figure 9A, marked with a black arrow). The anterior groove is distinct.

The epigastric regions are rounded and lay in front of the mesogastric region, which is distinctly bordered by grooves. The length of the anterior (narrow) part of this region is about 0.6x the posterior (wide) part, and the posterior part is the highest point of the carapace. There is no incision in the posterior border of this region. It is covered with many granules on the internal mold and the cuticle; gastric spines are absent. Epigastric, protogastric and hepatic regions are separated by transverse grooves (Figure 9C, E). A pair of small, elongated gastric pits is present in the cervical groove (Figure 9B).

The urogastric region is convex and divided into two parts by an incision, which connects to the postcervical groove (Figure 9A, D-E, H). Incisions laying on the epibranchial region, with the postcervical and branchial groove, bound surfaces directed to the cardiac region. The cardiac region is not distinctly bordered, widening anteriorly.

The grooves are very deep and wide. The cervical groove is the deepest. The branchiocardiac groove reaches the posterior margin of the carapace.

The posterior border of the carapace is rimmed and concave in the middle (Figure 9A, C). The whole surface of the carapace is covered with granules, which occur both on the internal mold and on the cuticle. In the anterior part, they are sparsely present, but they are denser in the posterior part. On the branchial region, they are positioned in lines parallel to the branchial groove (Figure 9C-D).

Genus *Navarrahomola* Artal, Van Bakel, Fraaije, Jagt, Klompmaker, 2012

Type species. *Navarrahomola hispanica* Artal, Van Bakel, Fraaije, Jagt, Klompmaker, 2012

Diagnosis. As in Artal et al. (2012: p. 405).

Navarrahomola hispanica Artal, Van Bakel, Fraaije, Jagt, Klompmaker, 2012

2012 *Navarrahomola hispanica* Artal et al., p. 405, figure 3.1, 3.3 (non 3.2).

2013 *Navarrahomola hispanica* Artal et al. – Klompmaker, p. 171, figure 12.

Diagnosis. As for the genus.

Remarks. *Navarrahomola hispanica* was described from the upper Albian reefal limestones of Spain (Monte Orobe and Koskobilo quarries). One of the paratypes (MGSB28141) is not conspecific to the holotype and the other paratype because the lateral borders of the mesogastric region are more continuously curved and the anterior carapace contains fewer large tubercles compared to *N. hispanica* (Artal et al., 2012: pl. 3.1, 3.3; Klompmaker, 2013: figure 12). Instead, MGSB28141 likely represents the largest known specimen of *Laeviprosopon hispanicum*, a species also reported from Koskobilo (Klompmaker, 2013). This specimen compares best to the specimen figured in Klompmaker (2013: figure 6H), which also shows evenly spaced granules, unlike on smaller specimens in which no clear granules are visible. Thus, we ascribe MGSB28141 to *Laeviprosopon hispanicum* for now. Apparently, granules become only visible on the internal mold in larger specimens for this species.

DISCUSSION

Reassignment of *Laeviprosopon* to Homolidae

The overall shape of the carapace, regions and grooves show similarities between *Laeviprosopon* and Homolidae. For example, the Cretaceous species of *Laeviprosopon* from Spain, namely *L. edoi*, is similar to *Homolopsis glabra* Wright and Collins, 1972, in the shape of the mesogastric, hepatic and cardiac regions, the shape of grooves and the overall shape of the carapace. This species of *Laeviprosopon* has a relatively smooth carapace, while this *Homolopsis* is covered with small tubercles. This difference applies to other taxa as well. Representatives of *Laeviprosopon* have relatively smooth carapaces with some species exhibiting small and sparse tubercles, mostly in the posterior part, whereas most of the homolid genera and species have numerous large tubercles on their carapaces, which might be an argument against transferring *Laeviprosopon* to Homolidae. However, the ornamentation of the carapace is a variable character and might differ between genera of one family or even within species of one genus (*Prosopon abbreviatum* Schweitzer and Feldmann, 2009, and *Prosopon mammillatum* Woodward, 1868, *Prosopon* and *Protuberosa* in Schweitzer and Feldmann, 2009; *Planoprosopon* and *Dioratiopus* in Schweitzer and Feldmann, 2011). Among

Homolidae, most of the genera have strong tubercles, but some species of *Homolopsis* have a smooth carapace (Bishop and Brannen, 1992, figure 1; Collins, 1997, figure 3). Moreover, many other characters match as mentioned above. Based on these data, herein we transfer the genus *Laeviprosopon* to the superfamily Homoloidea and family Homolidae. As specimens of *Laeviprosopon* show the oldest unequivocal molting lines on most of the dorsal carapace, we speculate that they may have given rise to other homoloids with molting lines entirely visible on the dorsal carapace in the Late Jurassic or Early Cretaceous.

Molting Lines in Jurassic and Cretaceous Homolodromioidea and Homoloidea – Homology or Homoplasy?

Homolodromioidea. The molting process in Homolodromioidea is insufficiently known. In the Jurassic and in modern homolodromioids, no molting lines are present on the dorsal carapace, along which it could break. There are only large, poorly calcified areas on the latero-ventral sides in modern representatives – the branchiostegites (Ng et al., 2008). The molting lines in these regions are clearly visible on the flanks or in ventral view in fossils ascribed to Homolodromioidea (e.g., Schweitzer and Feldmann, 2008; Klompmaker et al., 2011, 2012, 2016, 2020; Starzyk, 2013, 2015a), but they are rarely illustrated.

Regarding *Laeviprosopon*, insufficient preservation is often an issue when trying to determine the position of the molting line. As Frăntescu (2011) wrote, the posterolateral sides of the carapace in *Laeviprosopon lazarae* are not preserved most likely due to their weak calcification or post-mortem damages, therefore it is not possible to ascertain the presence or absence of molting lines in that species. The carapace of *Laeviprosopon punctatum* is preserved with its lateral sides and shows no clear molting lines (Figure 10A-B, Schweitzer and Feldmann, 2008, figure 1.7; Klompmaker et al., 2020, figure 13B). *Laeviprosopon musialiki* has only small parts of the lateral flanks damaged, and there are also no remnants of molting lines visible (Starzyk, 2020, figure 3).

However, the molting line on the dorsal carapace of *L. laculatum* is present; specimen NHMW 1990/0041/4221 is a molt. The margin of this molt is partially destroyed on the left side, but the right side is similar to the one in *L. laeve* (Figure 10C; Schweitzer and Feldmann, 2008, figure 1.9). Most of the specimens of *L. fraasi* have the posterolateral borders preserved. The molting line is pre-

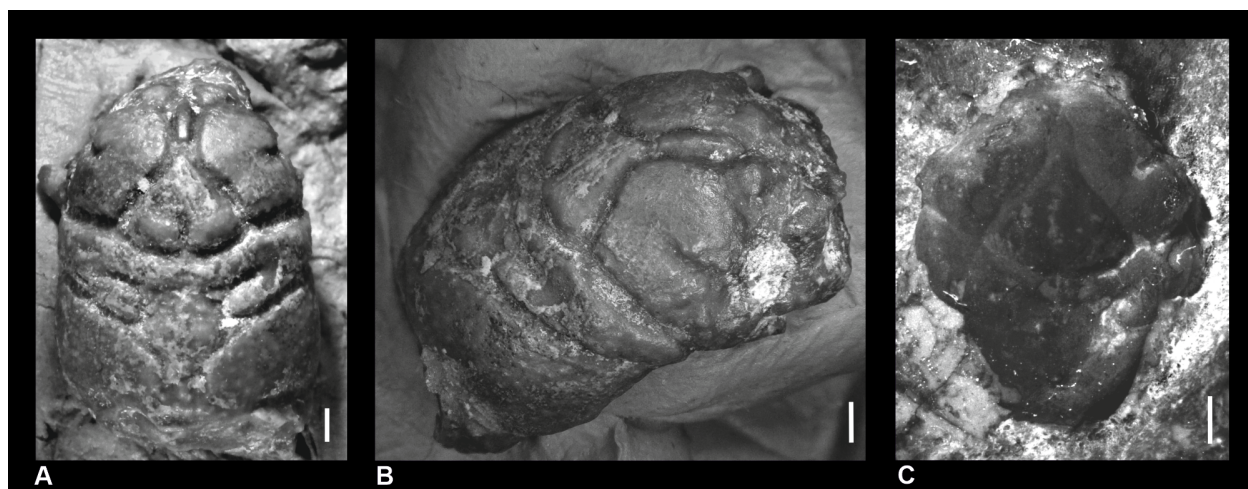


FIGURE 10. A - *Laeviprosopon punctatum*, carapace (holotype, BSP AS III 307); B - *Laeviprosopon punctatum*, oblique lateral view (holotype, BSP AS III 307); C - *Laeviprosopon laculatum* (holotype, NHMW 1990/0041/4221). Scale bars equal 1.0 mm.

served on the specimen NHMW 1990/0041/4051 (Figure 6B, E) and is also visible in the reconstruction of Wehner (1988, figure 32A), but there are no signs of such a line on the holotype. Patruilius (1966), Wright and Collins (1972) and Collins and Wierzbowski (1985) also mentioned the presence of *linea homolica* on specimens of *L. fraasi*. Prosopidae, to which *Laeviprosopon* was assigned repeatedly, do not bear molting lines on their dorsal carapaces, just as with other representatives of Homolodromioidea. Molting lines are probably laying on the ventral side of the carapace as in *Tanidromites montreuillensis* Crônier and Boursicot, 2009 (Figure 11A) and in other homolodromioids (see Karasawa et al., 2006, figures 1, 2; Klomp-maker, 2013, figure 5; Klomp-maker et al., 2011, figures 3, 5, 6; Klomp-maker et al., 2020, figures 10, 11, 14, 15). Unfortunately, only the dorsal aspects are available or illustrated for many other homolodromioid taxa.

Homoloidea. As mentioned before, *Laeviprosopon laeve* has been transferred several times between the families Prosopidae (Homolodromioidea) and Homolidae (Homoloidea), giving rise to doubts about the presence or absence of the *linea homolica*. New specimens reported herein showing undoubted molting lines indicate that *Laeviprosopon laeve* is hitherto the oldest known species with a *linea homolica*. Specimens of *L. fraasi* from Tithonian also show *linea homolica*. For these reasons, *Laeviprosopon* is confirmed as a member of Homoloidea.

Until this paper, there was only one member of the family Homolidae known from the Jurassic,

Doerflesia ornata Feldmann and Schweitzer, 2009, (Figure 12A) and four species of the family Tithonohomolidae (Figure 12B, C) from Štramberk and Ernstbrunn. They all have a confirmed *linea homolica* (Feldmann and Schweitzer, 2009, figures 2, 4, 5). The molting line in these species extends parallel to the anterolateral and posterolateral margins of the carapace, reaching the anterior margin (Figure 11).

On the carapaces of the post-Jurassic representatives of Homolidae, the *linea homolica* extends in a different way than the representatives of *Laeviprosopon* (compare Figure 11B-C): it is visible on the dorsal side of the carapace along its entire length from the orbits to the posterior margin, for example in the genera *Homolopsis* (Figure 11C; Collins, 1997, figure 3.1, 3.3), *Ariecornibus* (Frățescu, 2014, figure 7), *Peedeehomola* (Garassino et al., 2015, figure 5), *Zygastrocarcinus* (Collins, 1997, figure 6.1), *Latheticocarcinus* (Feldmann and Schweitzer, 2015, figure 2.1; Schweitzer et al., 2004, figure 2), *Cretalamoha* (Nyborg and Garassino, 2017, figures 1, 2), *Paromola* (Nyborg and Garassino, 2017, figure 3, 4) *Nogarhomola* (De Angeli and Alberti, 2012, figure 2, pl. 1) and *Paromolopsis* (Schweitzer et al., 2004, figure 4). *Linea homolicae* extends this way also in recent Homolidae such as *Homola* (Guinot and Richer de Forges, 1995, figure 8B-D, 14B, 14D, 14F), *Paromola* (Guinot and Richer de Forges, 1995, figure 21, 23), *Latreillopsis* (Guinot and Richer de Forges, 1995, figure 29A, B, F, G), *Hypsophrys* (Guinot and Richer de Forges, 1995, figure 59B, D, F) and

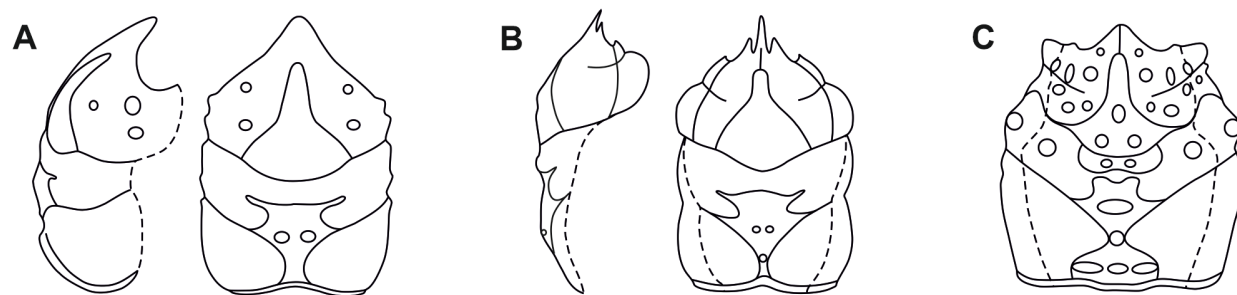


FIGURE 11. A - probable molting line (dashed line) of Jurassic Homolodromioidea exemplified by *Tanidromites montreuilensis*; B - molting lines of the Jurassic homoloid *Laeviprosopon laeve*; C - molting lines in Cretaceous Homoloidea exemplified by *Homolopsis edwardsii* (Bell, 1863).

Homolomania (Guinot and Richer de Forges, 1995, figure 63B-D, F).

Molting Process Conclusions. *Laeviprosopon laeve*, *L. laculatum* and *L. fraasi* are the only Jurassic species of *Laeviprosopon* in which it is possible to ascertain the presence of a molting line (Figure 6B, E; 10C). This line extends partially through the dorsal side of the carapace. There are no carapaces of *L. laeve* with lateral parts preserved in the collection of the ISEA PAS or the NHMW collection. There is only one specimen (SMNS 70527/11), which is a complete carapace, that does not have any remains of molting line (Figure 5H).

In the reconstruction of *L. fraasi* presented by Wehner (1988, figure 32A), there is a molting line extending in a similar way as in *L. laeve*, but there are no traces of such a line on the holotype. In contrast, the molting line is visible on specimen NHMW 1990/0041/4051 (Figure 6B, E). It is located on the right side, where the posterolateral border is preserved.

The specimens of *L. laeve*, *L. fraasi* and *L. laculatum* that show a molting line raise the question whether specimens of the same species developed molting lines only in some periods of their lifetime because not all specimens show a clear molting line. The mentioned specimen of *L. fraasi* might show a premolting stage, when the carapace was about to break at the molting line. In that case, there is a possibility that other Jurassic specimens of *Laeviprosopon*, with the posterolateral carapaces preserved and no signs of molting lines, molted in the same way. Their carapaces could break through lines similar to *L. laeve*, where molting lines are laying on the dorsal surface of the branchial and epibranchial regions and crossing on the latero-ventral side of the hepatic region, not reaching the orbits (Figure 5, 11B).

Other Jurassic and Cretaceous species of *Laeviprosopon* do not show any dorsal molting lines when complete carapaces are preserved (Figures 7-10; Wehner, 1988, pl. 8, figures 3, 4; Schweitzer and Feldmann, 2008, figure 1). In other cases, the lateral sides are not shown or studied. They might have molted in a way similar to *L. laeve*, but our state of knowledge is insufficient to confirm this. However, other morphological characters in the Jurassic and Cretaceous *Laeviprosopon* species provide convincing arguments for a close relationship between *L. laeve* and other species of *Laeviprosopon* that have not revealed their molting lines so far.

Among the Jurassic Homolidae and Tithonohomolidae, there are only molds broken along the *linea homolica*; therefore, it is uncertain whether the *linea* was developed on the carapace between molts (Figure 12; Feldmann and Schweitzer, 2009, figures 2, 4, 5).

Specimens of Homolidae from the Aptian, Albian and geologically younger stages described and documented in many papers (Figure 12C; Wright and Collins, 1972, pls. 6, 7, 8, figure 1; Bishop, 1986, figures 2.2, 3.1, 4.1, 4.2, 4.4; Bishop and Brannen, 1992, figure 1; Collins, 1997, figures 3.1, 3.2, 3.3, 9; Crawford, 2008, figures 2, 3; Feldmann et al., 2013, figure 7) show clear *linea homolica* also when the carapace is not broken along it. It might mean it was visible during the time interval between molts for at least some Cretaceous species.

Contrary, the *linea homolica* does not seem to be visible on some of the carapaces of the Cretaceous homoloid species: *Ariecornibus schweitzeriae* Frantescu, 2014 (Frantescu, 2014, figure 7C) and *Zygastrocarninus richardsoni* (Woodward, 1896) (Bishop, 1986). Both of these specimens have lateral sides of the carapace pre-

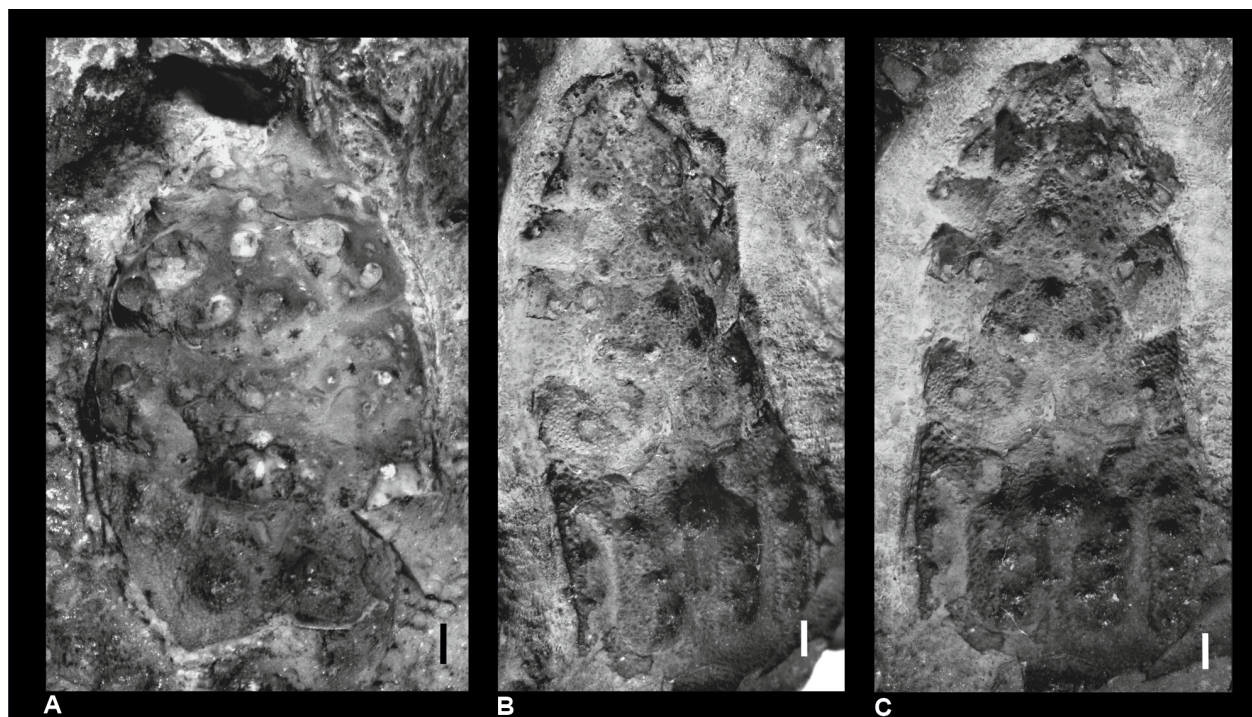


FIGURE 12. A - *Doerflesia ornata* Feldmann and Schweitzer, 2009, carapace (NHMW 2007z0149/0015); B - *Tenuihomola ortwini* Feldmann and Schweitzer, 2009, lateral view (NHMW 2007z0149/0017); C - *Tenuihomola ortwini*, carapace (NHMW 2007z0149/0017). Scale bars equal 1.0 mm.

served at least partially. There are also appendages visible on the specimen of *A. schweitzerae*, which suggests they are carcasses rather than molts. Similar to *L. fraasi*, molting lines in these specimens may have become visible only before molting. This observation in other Mesozoic homoloids supports placement of *Laeviprosopon* in Homoloidea. In contrast, molting lines are consistently visible during the time interval between molts in recent homoloids (Guinot and Richer de Forges, 1995, figures 8, 14, 29, 59, 63; Richer de Forges and Ng, 2007, figures 2, 3, 6, 7).

Because of the preservation of Jurassic homoloid crabs, it is hard to evaluate whether their molting pattern is homologous to that of the Cretaceous and younger ones. Other characters such as the thoracic sternum are usually not preserved in Jurassic crabs either; therefore, it is not possible to rely on them (Guinot, 2019). However, our research sheds some light on this process in the oldest brachyurans. In most Jurassic *Laeviprosopon* species (except *L. fraasi*), there are no confirmed molting lines developed between molting episodes (opposite to most Homoloidea, see paragraph above). This might be a matter of different preservational conditions in different localities and geological ages or, more likely, a genuine pattern

fairly common in Jurassic homoloids, less common in Cretaceous specimens, and absent in modern homoloids.

The genus *Laeviprosopon* may be a possible phyletic link between Homolodromioidea and Homoloidea. Based on the current state of knowledge, it seems to be the first group with molting lines on the dorsal surface of the carapace, at least partially (Figure 11B). A possible scenario of molting line evolution is that the posterior part of the molting line shifted from the ventral to the dorsal surface of the carapace faster than the anterior part. In *Laeviprosopon*, its posterior part lies on the dorsal surface, but it is still present on the ventral side when reaching the cervical groove. This type of molting line lasted at least to the Albian and is present on the carapaces of *L. crassum*, *L. edoi*, *L. hispanicum* and *L. planum*. Subsequently, the molting line of homoloids was present solely on the dorsal carapace.

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