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New species of Longodromitidae Schweitzer and Feldmann, 2009, from the Ernstbrunn Formation, Late Jurassic (Tithonian), Austria

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(With 4 figures and 2 tables)

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Abstract

Three new species from the Upper Jurassic (Tithonian) Ernstbrunn Limestone, *Abyssophthalmus schultzi*, *Planoprosopon hystricosus*, and *P. rhathamingus*, demonstrate the variability and diversity of the Longodromitidae Schweitzer & Feldmann, 2009. More importantly, the speciose nature of genera within the Longodromitidae and other families in Late Jurassic (Tithonian) rocks suggests that niche-partitioning may have been an important evolutionary driver early in the history of the Brachyura.

Keywords: Brachyura, Longodromitidae, Jurassic, Austria, New taxa

Introduction

The Longodromitidae Schweitzer & Feldmann, 2009 was diverse and well-represented during the late Tithonian in what is now the area of the Ernstbrunn quarries north of Vienna, Austria (fig. 1). Herein we describe three new species, in two genera, within this family, bringing the total number of longodromitid species found within the formation to eight, arrayed within three genera. This relatively high level of species diversity within genera has not been recognized until recently for Jurassic genera (Schweitzer & Feldmann 2008 [imprint 2007]), and the pattern deserves careful study. Investigation of the pattern is ongoing; this paper is one of a series in which new taxa are named and described so that the full diversity of the fauna can be evaluated.

Collecting Localities

Ernstbrunn Limestone

The majority of the specimens discussed here were collected by Friedrich Bachmayer and amateur paleontologists from various quarry localities in the Ernstbrunn Limestone near Dörfles and Ernstbrunn, Austria (fig. 1). The rocks are considered to be late Titho-

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nian (latest Jurassic) based upon ammonites (Zeiss 2001). Numerous brachyurans have previously been reported from the formation (Bachmayer 1947, 1948; Schweitzer & Feldmann 2008 [imprint 2007], 2009).

Štramberk Limestone

The Štramberk Limestone is also of Tithonian age (Houša, 1975; Eliášová, 1981). The decapod-rich outcrops of this unit occur in eastern Czech Republic (fig. 1). Reports of decapods have been published beginning in the 19th century (Moericke, 1889, 1997; Remeš, 1895) and study of them continues (Schweitzer & Feldmann, 2009).

Systematic Paleontology

Infraorder Brachyura Latreille, 1802

Section Podotremata Guinot, 1977

Superfamily Glaessneropsoidea Patrulius, 1959

Family Longodromitidae Schweitzer & Feldmann, 2009

Genus *Abyssophthalmus* Schweitzer & Feldmann, 2009

T y p e s p e c i e s : *Prosopon spinosum* von Meyer, 1842, by original designation.

I n c l u d e d s p e c i e s : *Abyssophthalmus schultzi* nov. spec.; *A. mirus* (Moericke, 1889), as *Prosopon*; *A. spinosus*; *A. stotzingensis* (von Meyer, 1856), as *Prosopon*.

D i a g n o s i s : Rostrum long, sulcate, lateral margins flared, tip markedly downturned; orbits deep, usually directed forward but may be directed anterolaterally, bounded by outer-orbital, suborbital, and usually intra-orbital spines; outer-orbital spine prominent, directed forward or anterolaterally; cervical and branchiocardiac grooves deep; post-cervical groove composed of two distinct segments; lateral margins approximately parallel sided, may be granular or with spines; subhepatic region well-developed; dorsal carapace ornamentation granular or with larger tubercles and spines interspersed; carapace generally vaulted transversely and longitudinally.

R e m a r k s : Schweitzer & Feldmann (2009) published complete synonymies for the above species other than the new species, at least for publications that were confirmed by them. We will not repeat the synonymies herein. At the time they erected the genus, only one species was known from multiple, well-preserved specimens, *Abyssophthalmus spinosus*. Herein, we expand that to three and therefore expand the range of variation known within the genus as well.

Several of the new specimens from the Ernstbrunn Formation are referable to *Abyssophthalmus mirus*, based upon their oblique orbits, very narrow area between the cervical and branchiocardiac grooves, and broad rostrum. These specimens permit expanding the description for that species, which was previously based upon the fragmental type specimen of Moericke (1889), BSP AS III 315 (fig. 2.1) (BSP = Bayerische Staatsammlung für Paläontologie und historische Geologie München [Munich], Germany). The new

Fig. 1. Map showing the location of Ernstbrunn, Austria, and Štramberk, Czech Republic, where specimens for the present study were collected.

specimens demonstrate that the orbits are in fact directed anterolaterally, which expands the diagnosis for the genus. In addition, the species possesses tiny spines along the entire length of the lateral margins (fig. 2.6), differentiating it from other species of the genus. However, the overall carapace shape, regional development, orbital ornamentation, and development of grooves are very similar to other members of the genus; thus we retain it in *Abyssophthalmus* at this time.

Most of the known specimens of the various species of *Abyssophthalmus* had been known from localities in Germany, including all of the known specimens of *Abyssophthalmus spinosus* (SCHWEITZER & FELDMANN 2009). The type specimen of *Abyssophthalmus mirus* was described from the Štramberk locality in what is now the Czech Republic (MOERICKE 1889, 1897). Thus, the specimens referred to *A. mirus* and the new species described below expand the known occurrences of the genus to the Ernstbrunn Formation in Austria. However, it remains that the genus seems to be restricted to the Late Jurassic of northern and central Europe.

Abyssophthalmus mirus (MOERICKE, 1889)
(fig. 2)

M a t e r i a l e x a m i n e d : BSP AS III 315, original specimen of MOERICKE (1889), interpreted to be the holotype (BSP = Bayerische Staatsammlung für Paläontologie und historische Geologie München [Munich], Germany); NHMW (Naturhistorisches Museum Wien [Vienna], Austria) 1990/0041/787, NHMW 1990/0041/2316, NHMW 1990/0041/3361, NHMW 1990/0041/3482, and NHMW 1990/0041/5124.

O c c u r r e n c e : All of the material was collected from the Ernstbrunn, Austria, localities, except the holotype, collected from the Štramberk locality (MOERICKE 1889, 1897).

E m e n d e d d i a g n o s i s : Carapace longer than wide or about as long as wide, maximum width about 90 to 100 percent maximum length; carapace moderately vaulted transversely and longitudinally; regions densely granular overall; rostrum wide; orbits directed obliquely anterolaterally; lateral margins with tiny spines along entire length.

M e a s u r e m e n t s : Measurements (in mm) taken on the dorsal carapace of *Abyssophthalmus mirus* are presented in Table 1.

E m e n d e d d e s c r i p t i o n : Carapace longer than wide or nearly as long as wide, maximum width between 90 and 100 percent maximum carapace length, widest at hepatic region or epibranchial region, about 40 to 65 percent the distance posteriorly on carapace; carapace moderately vaulted both transversely and longitudinally; regions well-defined by grooves and granular ornamentation.

Rostrum wide, width measured at base about half maximum carapace width; axially sulcate, tip concave axially, downturned; lateral edges gently rounded but not flared or ridged as in other species. Orbits deep, directed anterolaterally; inner orbital angle formed by rostrum; intra-orbital spine broad, projected well-beyond orbital margin, directed anterolaterally, separated from outer-orbital spine by notch; outer-orbital spine short, directed forward; suborbital margin ornamented with bulbous inner suborbital spine, separated from small outer suborbital spine by very broad gap; fronto-orbital width about 90 percent maximum carapace width.

Lateral margins parallel to one another, ornamented with tiny spines on projecting flange on segments anterior to cervical groove and between cervical and branchiocardiac grooves (fig. 2.6); segment posterior to branchiocardiac groove with tiny spines (fig. 2.6). Posterior margin concave, rimmed.

Epigastric regions inflated, spherical, situated at base of rostrum. Protogastric regions strongly inflated, granular, with one large tubercle posteriorly; hepatic regions moderately inflated, with several large inflations. Mesogastric region triangular posteriorly, with long anterior process, process terminating at base of rostrum but a beaded keel extending from it into axis of rostrum. Metagastric region much wider than mesogastric, constricted axially, bounded posteriorly by postcervical groove. Urogastric region developed only as widened groove, depressed below level of metagastric region. Cardiac region pentagonal in shape, inflated, extending nearly to posterior margin of carapace, with two tubercles situated next to one another at about midlength.

Cervical groove deep, slightly sinuous but overall path separates carapace in half; postcervical groove nearly continuous across entire carapace, interrupted about one-third the distance to lateral margins by swelling, converging with and then paralleling branchiocardiac groove at lateral margin; branchiocardiac groove weakly oblique posteriorly toward cardiac region.

Epibranchial region with complex ornamentation along branchiocardiac groove, composed of various nodes and swellings, ovate swelling situated near cardiac region. Remainder of branchial regions undifferentiated, densely granular overall.

Subhepatic swelling small, elongate parallel to long axis of carapace, situated below orbit, bounded ventrally by deep antennar groove and posteriorly by ventral extension of

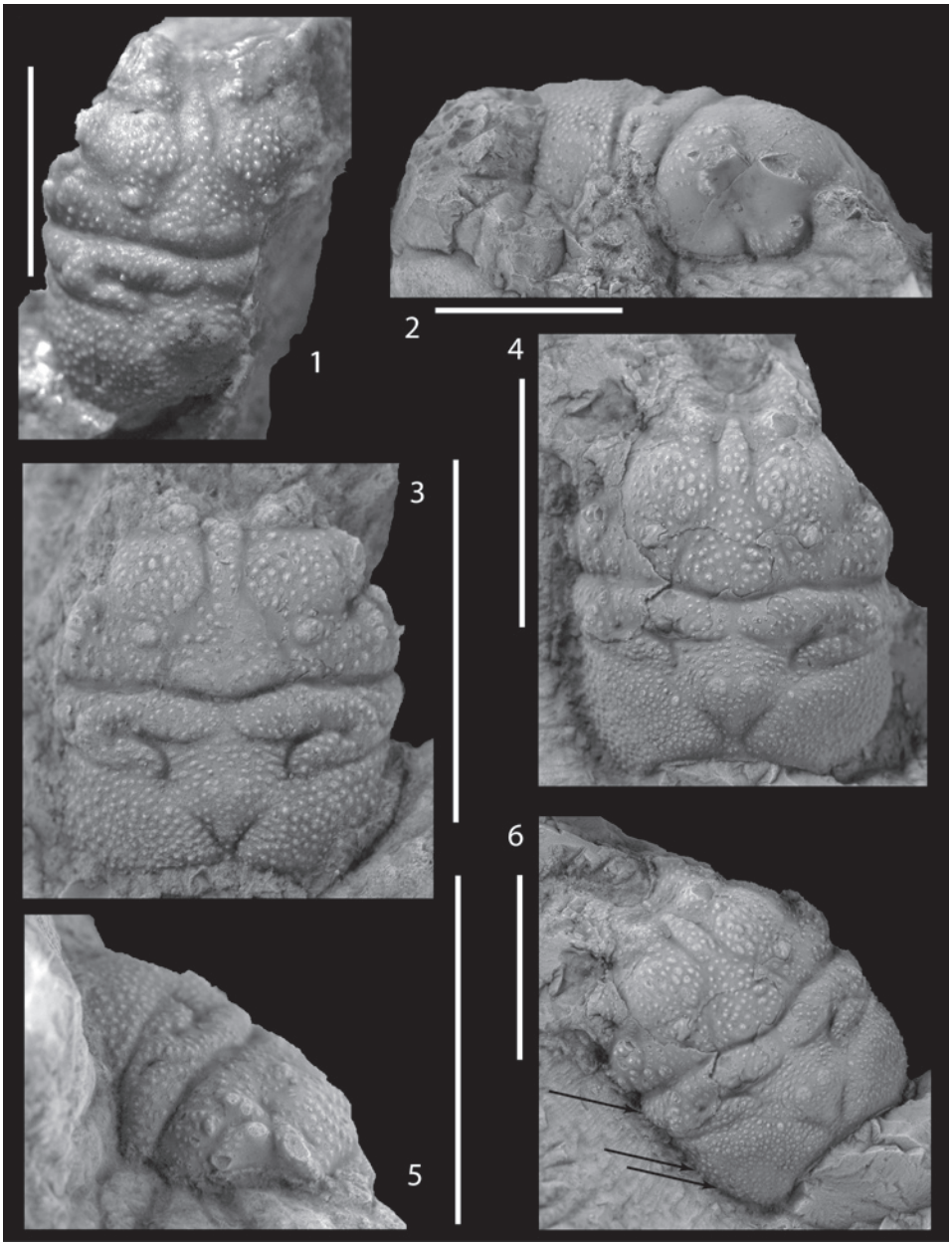

Fig. 2. *Abyssophthalmus mirus* (MOERICKE, 1889). All specimens from near Dörfles, Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic) except (1). 1, BSP AS III 315, holotype, unwhitened, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 2, NHMW 1990/0041/5124, right lateral view showing orbit; 3, NHMW 1990/0041/2316, dorsal carapace; 4, NHMW 1990/0041/3361, dorsal carapace; 5, NHMW 1990/0041/2316, oblique right lateral view showing orbit; 6, NHMW 1990/0041/3361, oblique left lateral view, arrows indicate lateral spines. Scale bars equal 1 cm.

cervical groove. Branchiocardiac and postcervical grooves extending onto lateral sides; forming two short, wide subdorsal regions.

Remainder of carapace and appendages unknown.

R e m a r k s : As discussed above, the new specimens expand the definition for the species and for the genus. The Ernstbrunn specimens are much more complete than the type specimen of MOERICKE (1889). Thus, an emended diagnosis and description are provided.

There are some notable differences between *Abyssophthalmus mirus* and the type species for the genus, *A. spinosus*. *Abyssophthalmus spinosus*, and the new species described below, have deep, forward directed orbits. In *A. mirus* the orbits are deep but directed anterolaterally. In other regards, the orbits are similar to those of the type species, notably in possessing intraorbital spines, outerorbital spines, and suborbital spines. *Abyssophthalmus mirus* has tiny spines all along the lateral margins of the carapace; it is unknown as to whether *A. spinosus* possessed such ornamentation because the known specimens lack cuticle. *Abyssophthalmus mirus* has a broader rostrum than does *A. spinosus*, but otherwise, the rostra are similar. Both species have similar carapace regions and groove development; thus, we maintain *Abyssophthalmus mirus* in the genus at this time.

***Abyssophthalmus schultzi* nov. spec.**
(fig. 3)

T y p e s : The holotype is NHMW (Naturhistorisches Museum Wien [Vienna], Austria) 2007z0149/0011, and paratypes are NHMW 1990/0041/39, NHMW 1990/0041/3362, NHMW 1990/0041/4382, NHMW 1990/0041/4897, NHMW 1990/0041/4904, NHMW 1990/0041/5123, NHMW 2007z0149/0012, and NHMW 2007z0149/0013.

L o c u s T y p i c u s : All of the material was collected from the Ernstbrunn localities in Austria.

S t r a t u m T y p i c u m : Ernstbrunn Limestone, Tithonian, Upper Jurassic.

E t y m o l o g y : The species name honors Dr. Ortwin SCHULTZ, now retired from NHMW and who assisted us greatly in locating and borrowing BACHMAYER'S Ernstbrunn specimens, which form the basis of this, previous, and future papers.

D i a g n o s i s : Carapace longer than wide, width about three-quarters maximum carapace length; rostrum long, triangular, tip downturned and oriented at nearly 90 degree angle to dorsal carapace; orbits deep, directed forward; bounded on inner orbital angle by rostrum; bounded on outer orbital angle by long, anterolaterally directed outer-orbital spine, suborbital spine broad, separated from outer orbital spine by broad notch and from inner orbital angle by notch.

M e a s u r e m e n t s : Measurements (in mm) taken on specimens of *Abyssophthalmus schultzi* are presented in Table 1.

D e s c r i p t i o n : Carapace longer than wide, width about 75 percent maximum length, widest at position of mid-branchial region about 75 percent the distance pos-

teriorly on carapace; carapace flattened transversely and longitudinally but with steep lateral sides and downturned rostrum; carapace regions well-marked by grooves and granular ornamentation.

Rostrum long, triangular, axially sulcate, margins thickened, tip downturned and oriented at nearly 90 degree angle to dorsal carapace, rostral width measured at base about 40 percent maximum width. Orbits deep, directed forward; bounded on inner orbital angle by rostrum; bounded on outer orbital angle by long, anterolaterally directed outer-orbital spine, spine granular on upper surface; suborbital spine broad, separated from outer orbital spine by broad notch and from inner orbital angle by notch; fronto-orbital width about 80 percent maximum carapace width.

Epigastric region very weak, essentially marking base of rostrum. Protogastric and hepatic regions confluent, inflated, especially anteriorly; ornamented with several large tubercles and numerous granules. Mesogastric region triangular posteriorly, with long anterior process extending to base of rostrum, terminating at base of rostrum, with a large tubercle about half the distance along anterior process.

Table 1. Measurements (in mm) taken on the dorsal carapace of *Abyssophthalmus* spp.

Specimen Number	Length Excluding Rostrum	Maximum Carapace Width	Width at Base of Rostrum	Length to position of Maximum Width	Fronto-Orbital Width
Abyssophthalmus schultzi nov. spec.					
NHMW 2007z0149/0011 (Holotype)	13.6	9.5	3.5	10.2	8.0
NHMW 1990/0041/3362	15.5	11.2	4.2	12.4	9.5
NHMW 1990/0041/4382	13.0	11.1	4.9	10.8	9.2
NHMW 1990/0041/4897	12.0	9.3	-	10.2	7.8
NHMW 1990/0041/5123	20.9	15.6	6.3	15.1	12.3
NHMW 2007z0149/0013	12.8	10.2	3.9	10.6	7.1
NHMW 2007z0149/0012	13.2	10.2	3.6	10.5	7.6
Abyssophthalmus mirus (MOERICKE, 1889)					
NHMW 1990/0041/2316	10.2	9.3	-	6.6	-
NHMW 1990/0041/3361	16.7	14.8	8.2	7.6	14.2
NHMW 1990/0041/3482	14.3	14.2	-	11.2	5.9

Cervical groove nearly straight overall, deep, originating on lateral margin about one-third the distance posteriorly. Postcervical groove nearly continuous across entire carapace, interrupted about one-third the distance to lateral margins by swelling, converging with and then paralleling branchiocardiac groove at lateral margin. Branchiocardiac groove weak, directed obliquely posteriorly toward cardiac region, originating about two-thirds the distance posteriorly on carapace. Postcervical groove present, separating metagastric and urogastric regions.

Metagastric region wider than long, weakly constricted axially, slightly wider than widest part of mesogastric region. Urogastric region very short, about as wide as mesogastric region, and depressed below level of mesogastric region. Cardiac region pentagonal, inflated; intestinal region small, triangular, apex directed toward cardiac region, depressed below level of cardiac region.

Epibranchial region smooth or with scattered, fine granules anteriorly; posteriorly, ornamented with a series of scalloped ridges along anterior edge of branchiocardiac groove. Remainder of branchial region undifferentiated, moderately inflated, granular overall.

Subhepatic region inflated, positioned posterior to orbit, bounded posteriorly by ventral extension of cervical groove and ventrally by antennar groove. Branchiocardiac and postcervical grooves extending onto lateral sides; forming two short, wide subdorsal regions.

Remainder of carapace and appendages unknown.

R e m a r k s : *Abyssophthalmus schultzi* is unique among species of the genus in possessing forward-directed orbits with anterolaterally directed outer-orbital spines and lacking intra-orbital spines. None of the other species possesses this combination of characters. In addition, the rostrum is triangular overall, whereas in the other species, it is rectangular. Thus, the new species possesses a unique combination of characters.

Genus *Planoprosopon* Schweitzer, Feldmann, & Lazăr, 2007

T y p e s p e c i e s : *Prosopon heydeni* von Meyer, 1857, by original designation.

I n c l u d e d s p e c i e s : *Planoprosopon aequus* (von Meyer, 1857), as *Prosopon*; *P. heydeni*; *P. hystricosus* nov. spec.; *P. rhathamingus* nov. spec.

E m e n d e d d i a g n o s i s : Carapace longer than wide, widest at position of epibranchial or hepatic region; highly dorso-ventrally compressed; rostrum axially sulcate, extending well beyond orbits; orbital concavity shallow, directed forward or anterolaterally; with limited orbital ornamentation that may include a small intraorbital spine, a small suborbital spine, a suborbital granular rim, or none of the above; outer orbital spine projecting anterolaterally. Protogastric and hepatic regions moderately defined, may be ornamented by spines, large tubercles, or granules; region between cervical and branchiocardiac grooves narrow. Cervical groove deep; branchiocardiac groove moderately deep; post-cervical groove discontinuous; subhepatic swelling weak; ventral extension of cervical and branchiocardiac grooves meeting to form triangular subepibranchial swelling (modified after Schweitzer & Feldmann 2009).

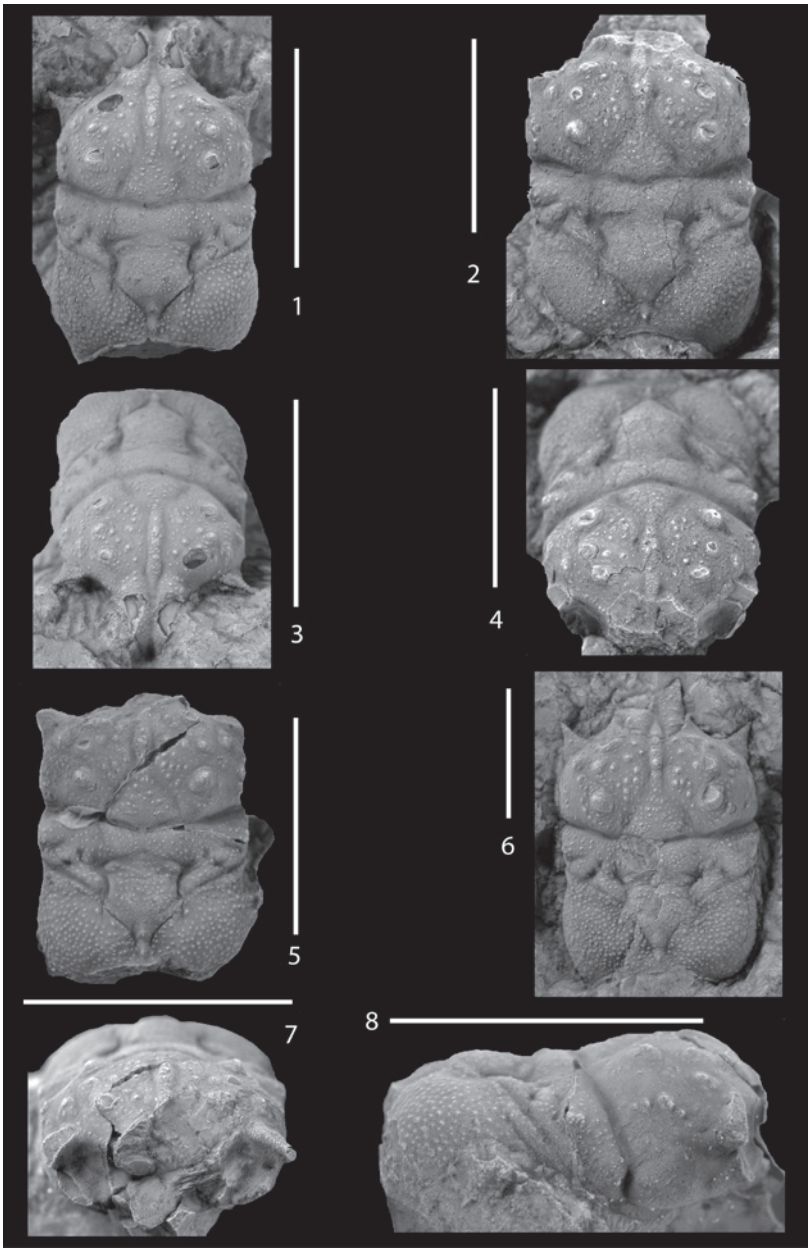

Fig. 3. *Abyssophthalmus schultzi* nov. spec. All specimens from near Dörfles, Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic). 1, NHMW 2007z0149/0011, holotype, dorsal carapace; 2, NHMW 1990/0041/3362, paratype, dorsal carapace; 3, NHMW 2007z0149/0011, holotype, oblique anterior view showing orbits and outer orbital spines; 4, NHMW 1990/0041/3362, paratype, oblique anterior view showing orbits; 5, NHMW 1990/0041/4897, paratype, dorsal carapace; 6, NHMW 1990/0041/5123, paratype, dorsal carapace view; 7, NHMW 1990/0041/4897, paratype, anterior view showing orbits; 8, NHMW 1990/0041/1897, paratype, right lateral view showing orbit and lateral side. Scale bars equal 1 cm.

R e m a r k s : The new specimens permit the refining of the generic diagnosis for *Planoprosopon*. The orbital ornamentation until now has been poorly known, based upon poorly preserved specimens. The specimens described herein demonstrate that the orbits are indeed poorly ornamented in *Planoprosopon* but can have weak spines and rims. The dorsal carapace ornamentation can range from spinose to granular. These are each the types of variations seen among species of a genus and thus do not represent major revisions to the generic diagnosis. Indeed, the range of variation in *Planoprosopon* spp. is similar to that seen in *Longodromites*, which is known from several species. Thus, the new species help to demonstrate the range of variation that can be expected within genera of the Longodromitidae.

Planoprosopon heydeni (von Meyer, 1857)
(figs 4.1, 4.2)

M a t e r i a l e x a m i n e d : Wehner (1988) designated a neotype for the species, Museum Tübingen, Quenstedt 1856-57, pl. 95, fig. 36. Other material examined here includes NHMW (Naturhistorisches Museum Wien [Vienna], Austria) 1990/0041/1125, NHMW 1990/0041/4590.

O c c u r r e n c e : The type locality is the Oerlinger Thals, of Late Jurassic age, in Germany (von Meyer, 1860). The newly referred specimens were collected from the Ernstbrunn localities in Austria.

E m e n d e d d i a g n o s i s : Carapace longer than wide, reaching maximum width at about one-quarter the distance posteriorly, maintaining that width until about three-quarters the distance posteriorly where carapace narrows; carapace very compressed dorsoventrally; rostrum projected well-beyond orbits, axially sulcate, with strongly flared lateral edges; orbit ornamented with anterolaterally projected intra-orbital spine situated at base of rostrum, outer-orbital spine directed anterolaterally; regions well-differentiated; hepatic region especially inflated; intestinal region wide, much wider than cardiac region.

R e m a r k s : The species has been recently discussed and a lengthy synonymy provided for it (Schweitzer et al. 2007; Schweitzer & Feldmann 2009). The two new specimens from the Ernstbrunn Formation are referable to it based upon the extreme dorsoventral compression of the carapace, the sulcate rostrum, and the narrow, long, dorsal carapace. The new specimens show that the intraorbital spine is distinct and well-developed; that spine is visible on the neotype but is quite worn due to erosion.

Planoprosopon rhathamingus nov. spec.
(fig. 4.3)

T y p e : Holotype, NHMW (Naturhistorisches Museum Wien [Vienna], Austria) 1990/0041/3015a.

L o c u s T y p i c u s : The specimen was collected from the Ernstbrunn localities in Austria.

Fig. 4. *Planoprosopon* spp. All specimens from near Dörfles, Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic). 1, *P. heydeni* (VON MEYER, 1857), NHMW 1990/0041/4590, dorsal carapace, showing orbit and orbital ornamentation; 2, *P. heydeni*, NHMW 1990/0041/1125, partial dorsal carapace showing extended rostrum; 3, *P. rhathamingus* nov. spec., NHMW 1990/0041/3015a, holotype; 4, *P. hystricosus* nov. spec., NHMW 1990/0041/1416, paratype; 5, *P. hystricosus*, NHMW 1990/0041/0056, paratype; 6, *P. hystricosus*, NHMW 1990/0041/4917, holotype. Scale bars equal 1 mm.

S t r a t u m T y p i c u m : Ernstbrunn Limestone, Tithonian, Upper Jurassic.

E t y m o l o g y : The species name is derived from the Greek word *rhathaminx*, meaning grain or drop, in reference to the granular ornamentation on the dorsal carapace of this species.

D i a g n o s i s : Carapace with dense granular ornamentation overall; position of maximum width about 15 percent the distance posteriorly at hepatic region; orbits essentially unornamented except for outer-orbital spine and beaded suborbital rim; grooves defining anterior regions becoming shallower posteriorly.

M e a s u r e m e n t s : Measurements (in mm) taken on the sole specimen of *Planoprosopon rhathamingus* are presented in Table 2.

D e s c r i p t i o n : Carapace rectangular, longer than wide, maximum width about 80 percent maximum carapace length excluding rostrum, widest at hepatic region, about 15 percent the distance posteriorly excluding rostrum; regions well marked by grooves and dense, granular ornamentation; carapace flattened longitudinally, moderately vaulted transversely.

Rostrum projecting well-beyond orbits, axially sulcate. Orbits shallow; inner orbital angle formed by rostrum; intraorbital ornamentation consisting of weak protuberance; outer orbital spine round in cross-section, projected anterolaterally; suborbital margin with a weak, beaded rim.

Lateral margins overall nearly straight, parallel; segment anterior to cervical groove convex, granular; segment between cervical and branchiocardiac grooves weakly convex, granular; segment posterior to branchiocardiac groove convex, granular. Posterior margin concave centrally, rimmed.

Protogastric region quadrate, granular; grooves defining axial and lateral margin deepest anteriorly, becoming shallower or disappearing posteriorly. Hepatic region triangular,

Table 2. Measurements (in mm) taken on the dorsal carapace of specimens of *Planoprosopon* spp.

Specimen Number	Length Excluding Rostrum	Maximum Carapace Width	Width at Base of Rostrum	Length to position of Maximum Width	Fronto-Orbital Width
Planoprosopon hystricosus nov. spec.					
NHMW 1990/0041/4917 (Holotype)	11.8	9.4	3.9	3.0	8.7
NHMW 1990/0041/0056	3.7	3.3	1.7	1.8	3.0
NHMW 1990/0041/1416	2.8	2.6	1.2	1.6	2.3
Planoprosopon rhathamingus nov. spec.					
NHMW 1990/0041/3015a (Holotype)	3.9	3.2	1.6	0.6	3.0

apex directed toward mesogastric region, with broad swelling; region granular overall. Mesogastric region broadly triangular posteriorly, with long, parallel-sided, anterior process, process appearing to have extended onto rostrum; grooves defining process deepest anteriorly and weakening posteriorly. Metagastric region broad, wider than base of mesogastric region. Urogastric region narrow, short, depressed slightly below level of metagastric and cardiac regions. Cardiac region triangular, apex directed posteriorly, with two tubercles situated aside one another anteriorly and third situated at apex. Intestinal region short, poorly defined. Cervical groove deep, composed of three arcs, lateral two arcs convex forward, bounding posterior margins of hepatic regions, axial arc weakly convex forward, bounding posterior margin of mesogastric region; overall path of cervical groove nearly straight. Postcervical groove deep, discontinuous axially. Branchiocardiac groove directed obliquely posteriorly, deepest laterally.

Epibranchial region with weak inflation along lateral margin, followed by ovate, transverse inflation situated anterior to branchiocardiac groove; followed by much larger ovate, obliquely directed inflation. Remainder of branchial regions undifferentiated, granular overall.

Subhepatic region small, situated post-orbitally, bounded posteriorly by ventral extension of cervical groove and ventrally by antennar groove. Cervical and branchiocardiac grooves extending ventrally to define triangular subepibranchial region. Subbranchial region high, higher than in other species of genus.

Remainder of carapace and appendages unknown.

R e m a r k s : *Planoprosopon rhathamingus* nov. spec. differs from other species of *Planoprosopon* in possessing fine, densely granular ornamentation on the entire dorsal carapace. Other species of the genus are densely ornamented, but the ornamentation is neither as fine nor as densely spaced as in *P. rhathamingus*. In addition, the orbits of *P. rhathamingus* are essentially unornamented except for a beaded suborbital rim and its position of maximum width is positioned quite far anteriorly compared to other species of the genus. *Planoprosopon rhathamingus* is not as dorsoventrally compressed as is *P. heydeni*, to which it is most similar. *Planoprosopon heydeni* is markedly compressed dorsoventrally, so that the lateral sides are only a few millimeters high. Thus, although *P. rhathamingus* is relatively small in size, its features are sufficiently distinct to suggest strongly that it is not a juvenile of another species.

***Planoprosopon hystricosus* nov. spec.**
(figs 4.4-4.6)

T y p e s : Holotype, NHMW (Naturhistorisches Museum Wien [Vienna], Austria) 1990/0041/4917; paratypes NHMW 1990/0041/0056, NHMW 1990/0041/1416; NHMW 2007z0149/0014.

L o c u s T y p i c u s : The specimens were collected from the Ernstbrunn localities in Austria.

S t r a t u m T y p i c u m : Ernstbrunn Limestone, Tithonian, Upper Jurassic.

E t y m o l o g y : The species name is the Latin word *hystricosus*, meaning spiny, in reference to the large lateral and dorsal carapace spines in this species.

D i a g n o s i s : Carapace about 80-90 percent as wide as long; regions well ornamented by spines in large specimens; outer orbital spine long; lateral margin with large spine anterior to cervical groove; intra-orbital margin with broad spine; entire cervical groove concave anteriorly, more so than in other species.

M e a s u r e m e n t s : Measurements (in mm) taken on the dorsal carapace of *Planoprosopon hystricosus* nov. spec. are presented in Table 2.

D e s c r i p t i o n : Carapace longer than wide, maximum width about 80 percent maximum length, narrowing slightly posteriorly; position of maximum width at hepatic region about 25 percent the distance posteriorly on carapace in large specimens and at epibranchial region about half the distance posteriorly in smaller specimens; carapace very weakly vaulted transversely and longitudinally; regions moderately well-marked by grooves and granular ornamentation.

Rostrum broken, about 40 percent maximum carapace width measured at base. Orbits shallow, directed forward; inner orbital angle formed by rostrum; intraorbital spine small, broadly triangular, granular; outer orbital spine triangular, directed anterolaterally, preceded by granular rim; suborbital area with weak granular rim.

Lateral margins rather sinuous, converging weakly posteriorly overall. Segment anterior to cervical groove with one prominent spine excluding outer orbital spine, spine triangular, directed laterally. Segment between cervical and branchiocardiac grooves convex, with blunt spine centrally which is situated almost dorsally. Segment posterior to branchiocardiac groove weakly convex, granular. Posterior margin concave, rimmed.

Protogastric region quadrate, with large tubercles along lateral margin bordering hepatic region, remainder with evenly spaced granules. Hepatic region triangular, apex directed toward axis, large tubercle situated at axis, two smaller tubercles situated close to lateral margin. Mesogastric region rhomboid posteriorly, with long anterior process which appears to have extended onto rostrum. Metagastric region markedly bilobed, constricted axially, most inflated of all axial regions. Urogastric region short, narrow, depressed below level of metagastric and cardiac regions. Cardiac region small, pentagonal, apex directed posteriorly. Intestinal region poorly defined.

Cervical groove deep, composed of three sinuous arcs, lateral arcs weakly concave forward, axial arc strongly concave forward; entire cervical groove converging axially and posteriorly slightly. Branchiocardiac groove less deep than cervical groove, converging posteriorly, deepest laterally, weakening axially. Post-cervical groove deep, composed of two segments on either side of axis which arc posteriorly and connect with branchiocardiac groove.

Epibranchial region composed of several swellings, lateral-most swelling contains lateral spine; followed by weak central, posterior swelling; followed by oblong ovate swelling, directed at cardiac region. Branchial region moderately inflated, granular overall.

Subhepatic swelling very small, situated under orbit, bounded posteriorly by ventral extension of cervical groove and ventrally by antennar groove. Epibranchial region ex-

tending onto lateral side, bounded by cervical and branchiocardiac grooves. Remainder of lateral side very short, as if it may not have been well-calcified ventrally.

Remainder of carapace and appendages unknown.

R e m a r k s : *Planoprosopon hystricosus* nov. spec. differs from all other species of *Planoprosopon* in possessing large, spinose ornamentation on the anterior carapace regions and a well-developed lateral spine positioned posterior to the outer-orbital spine. Even the smallest specimens of the new species exhibit this lateral spine. In addition, the carapace is longer than wide in *P. hystricosus*, but the width can reach nearly 90 percent of the maximum length in the smaller specimens. In other species, the length tends to be much longer as compared to the width.

The smaller specimens exhibit subdued ornamentation as compared to the much larger specimen. In addition, some of the overall carapace proportions differ in the smaller specimens as compared to the larger specimen. For example, the width occupies a somewhat higher percentage of the length measured excluding the rostrum, about 90 percent in the smaller specimens and 80 percent in the large specimen. The width of the base of the rostrum occupies about 40 percent the maximum width of the carapace in the larger specimen and 45-50 percent in the smaller specimens. The most notable difference is the position of maximum width, which is about one quarter the distance posteriorly in the large specimen and about half the distance posteriorly in the smaller specimens. We interpret these differences to be due to allometric growth and differential development of cuticle ornamentation between juvenile and adult specimens. It has been well-demonstrated that allometric growth occurs in brachyurans (WRIGHT & COLLINS 1972; SCHWEITZER & FELDMANN 2000) and that ornamentation may change with growth (GUINOT 1989). The main features of the carapace, such as the ornamentation of the orbits; the orientation of the cervical and branchiocardiac grooves; and the relative proportions of the carapace regions to one another are the same in the small and large specimens. Thus, we attribute the specimens to the same species and not to two different species.

WEHNER (1988) illustrated several specimens that she attributed to *Nodoprosopon heydeni*, now referred to *Planoprosopon* (pl. 2, figs 5-8). The specimens in her figures 6 and 7 bear some resemblance to those herein referred to *P. hystricosus* in possessing a carapace not much longer than wide; large granules on the protogastric and hepatic regions; and a large lateral spine posterior to the outer-orbital spine. However, formal referral of these specimens to the species should await examination of the actual specimens rather than photographs. It is also notable that the specimen in fig. 8 (WEHNER 1988, pl. 2) does not appear to belong to any of the named species of *Planoprosopon*. Formal evaluation of this specimen must await examination of the material.

Discussion

Like other Jurassic brachyuran genera, *Abyssophthalmus* and *Planoprosopon* are highly speciose within a small geographic area (i.e., the same formation and same localities). Thus far, three species of *Planoprosopon* are known from the Ernstbrunn Formation and a fourth is known from the Jurassic of Germany. Two species of *Abyssophthalmus* are reported from the Ernstbrunn Formation, and four are known from east-central Europe.

All of these species are known from coral reef environments, and at least one species of *Planoprosopon* is also known from sponge-algal biostromes (Schweitzer et al. 2007). Thus, it is suspected that niche partitioning within these early brachyuran lineages may have played a role in high speciation levels within genera. Other genera with similarly high or higher numbers of species within a relatively small geographic area and short time interval include *Longodromites* Patrulius, 1959; *Glaessneropsis* Patrulius, 1959; and *Goniodromites* Reuss, 1858 (Schweitzer & Feldmann 2008 [imprint 2007]; 2009). Investigation of this phenomenon is ongoing.

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