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Revision of *Cycloprosopon* and additional notes on *Eodromites* (Brachyura: Homolodromioidea: Goniodromitidae)

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(With 5 figures and 3 tables)

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Abstract

Cycloprosopon Lőrenthey *in* Lőrenthey & Beurlen, 1929, is redefined and referred to the Goniodromitidae Beurlen, 1932. Four new species, *Cycloprosopon conspicuum*, *C. devexum*, *C. octonarium*, *C. stenofrons*, as well as two new combinations, *Goniodromites transsylvanicus* (Lőrenthey *in* Lőrenthey & Beurlen, 1929) and *Eodromites dobrogea* (Feldman, Lazăr & Schweitzer, 2006), resulted from the revision. Representatives of *Eodromites* often retain well-calcified elements of the appendages and lateral portions of the carapace, unusual among Jurassic brachyurans.
Keywords: Brachyura, Jurassic, Homolodromioidea, Dromiacea, new taxa, Austria.

Introduction

Previous work on the Goniodromitidae Beurlen, 1932, and *Cyclothyreus* Remeš, 1895 (Schweitzer & Feldmann 2008 [imprint 2007]; Schweitzer & Feldmann 2009b) has refined those groups to the point where a significant outlier remains, *Cycloprosopon* Lőrenthey *in* Lőrenthey & Beurlen, 1929. It is the purpose of the present work to diagnose and revise *Cycloprosopon* as well as to record new taxa as a result of an ongoing study of the Bachmayer Collection housed at the Naturhistorisches Museum Wien, of Jurassic material contained in other museums throughout Europe, and of material collected by ourselves at various localities. The Goniodromitidae now embraces five genera.

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Study Areas

Ernstbrunn Limestone

The Ernstbrunn Limestone of middle to late Tithonian (latest Jurassic) age (Zeiss 2001) is exposed in various quarries near the villages of Dörfles and Ernstbrunn, north of Vienna, Austria. Quarry Dörfles V is at lat. 48˚33'3.5"N, long. 16˚20'48.0"E, and is one of the localities from which Bachmayer's material originates. All of the Ernstbrunn quarries from which decapods were collected lie within a few kilometers of this quarry.

Štramberk Limestone

The Štramberk Limestone of Tithonian (latest Jurassic) age (Houša 1975; Eliášová 1981) is well-known to contain decapod crustaceans (Moericke 1889, 1897; Remeš 1895; Schweitzer & Feldmann 2009a, b). Some specimens from this unit were collected from the Kotouč Quarry, just outside the village of Štramberk, Czech Republic, at lat. 49˚35'01.2"N, long. 18˚07'1.2" E. Others are from historic collections, and the exact localities are not known but may be exposures located under the ruins of the castle in Štramberk village.

Purcăreni, Romania

The limestone olistolith from which decapod specimens were collected is Tithonian in age based upon calpionellids (Patrulius 1959; 1966; Patrulius et al. 1967). The locality is about 15 km east of Brašov, outside the village of Purcăreni, Romania, at lat. 45˚38'14.5"N, long. 25˚48'14.7"E.

Abbreviations

BSP	Bayerische Staatsammlung für Paläontologie und Geologie München (Munich), Germany
JU	Jagiellonian University, Institute of Geological Sciences, Muzeum Geologiczne, Kraków, Poland
LPB	Laboratory of Paleontology, Department of Geology and Paleontology, University of Bucharest, Romania
NHMW	Naturhistorisches Museum Wien (Natural History Museum Vienna), Austria
NM	Národní Muzeum, Prague, Czech Republic
PC	Collection of VSB-Technical University, Ostrava-Poruba, Czech Republic
PL	paleontological collection of the Muzeum Novojičínska in Nový Jičín, Czech Republic
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany; SMO, Slezské museum v Opavě, coll. palaeontologica, Opava, Czech Republic

Systematic Paleontology

Order Decapoda Latreille, 1802

Infraorder Brachyura Linnaeus, 1758

Section Podotremata Guinot, 1977

Superfamily Homolodromioidea Alcock, 1900

Family Goniodromitidae Beurlen, 1932

Included genera: *Cycloprosopon* Lőrenthey *in* Lőrenthey & Beurlen, 1929; *Eodromites* Patrulius, 1959; *Goniodromites* Reuss, 1858 [imprint 1857]; *Pithonoton* von Meyer, 1842; *Sabellidromites* Schweitzer & Feldmann, 2008 [imprint 2007].

Genus *Cycloprosopon* Lőrenthey *in* Lőrenthey & Beurlen, 1929

Type species: *Pithonoton* (*Cycloprosopon*) *typicum* Lőrenthey *in* Lőrenthey & Beurlen, 1929, by original designation.

Other species: *Cycloprosopon complanatiforme* (Moericke, 1889), as *Prosopon*; *Cycloprosopon conspicuum* nov. spec.; *Cycloprosopon devexum* nov. spec.; *C. etalloni* (Gemmellaro, 1869), as *Prosopon*; *Cycloprosopon octonarium* nov. spec.; *C. stenofrons* nov. spec.

Table 1. Key to the species of *Cycloprosopon*. Features for *C. typicum* and *C. etalloni* based upon illustrations.

1. Front bilobed	2
1'. Front triangular	5
2. Outer orbital spines present	3
2'. Outer orbital spines absent	*C. typicum*
3. Front broad, bilobed but nearly straight, weakly downturned; outer augenrest spine directed anterolaterally	*C. conspicuum*
3'. Front narrow, distinctly bilobed, moderately downturned; outer augenrest spine directed forward	4
4. Lateral margins convex, postcervical groove poorly defined	*C. complanatiforme*
4'. Lateral margins sinuous; postcervical groove well-defined	*C. etalloni*
5. Front narrow, triangular, downturned nearly at right angles to carapace surface	*C. devexum*
5'. Front broad, triangular, only slightly downturned	6
6. Front merges smoothly with upper augenrest margin	*C. octonarium*
6'. Frontal margin separated from upper augenrest margin by pronounced inflection	*C. stenofrons*

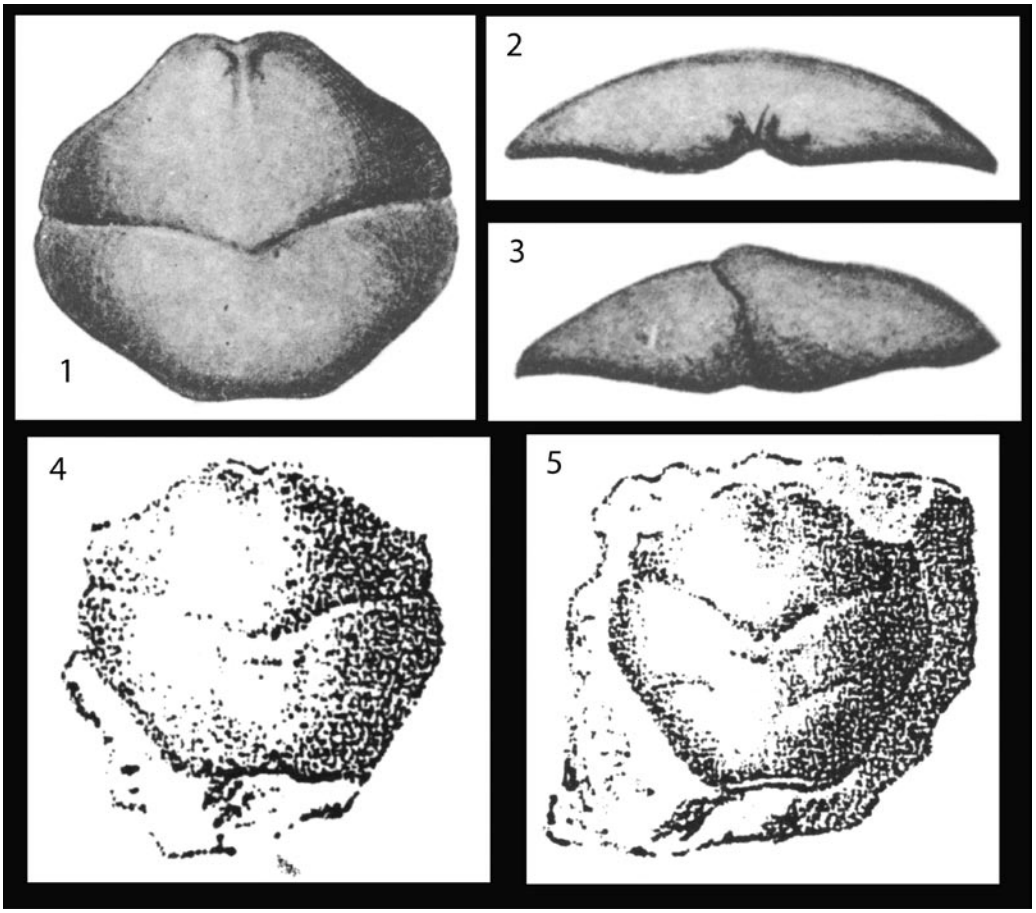


Fig. 1. *Cycloprosopon* spp. 1-3, *Cycloprosopon latum* Lőrenthey *in* Lőrenthey & Beurlen, 1929, digital images from Lőrenthey & Beurlen (1929: pl. 3, figs. 12a-c); 4-5, *Cycloprosopon etalloni* (Gemmellaro, 1869), digital images from Gemmellaro (1869: pl. 2, figs. 50, 51).

Diagnosis: Carapace wider than long, octagonal in shape, maximum width at or posterior to position of intersection of cervical groove with anterolateral margin; carapace moderately vaulted longitudinally and transversely; variously described as smooth or with fine granules or punctae.

Rostrum broad, bilobed, weakly concave or axially notched, may be downturned; augenrest moderately deep, directed weakly anterolaterally, weakly rimmed; anterolateral margin short, sometimes with spines; posterolateral margin longer; posterior margin narrow, concave. Mesogastric region poorly defined, best defined at anterior tip and posteriorly; epigastric regions developed as weak swellings or not at all; cardiac and urogastric regions sometimes weakly marked; otherwise, regions not defined. Cervical groove always better developed than branchiocardiac groove; postcervical groove weakly or well-de-

Table 2. Measurements (in mm) taken on *Cycloprosopon* spp. L1 = maximum carapace length; L2 = length from front to position of maximum width of carapace; W1 = maximum width of carapace; W2 = fronto-orbital, including augenrests.

Specimen Number	L1	W1	W2	L2
Cycloprosopon complanatiforme (Moericke, 1889)				
BSP AS III 312 (Holotype)	10.3	11.7	9.4	-
JU 127P 3/1	14.5	16.2	12.6	8.8
NHMW 1990/0041/5154	15.8	16.6	15.4	8.0
NHMW 2007z0162/0004	15.2	17.0	14.9	7.2
LPBIIIart-077	9.1	11.1	9.9	4.9
LPBIIIart-079	6.2	7.6	7.4	3.7
LPBIIIart-080	10.3	11.5	11.2	4.5
LPBIIIart-084	6.6	7.3	6.9	3.2
Cycloprosopon conspicuum nov. spec.				
PL 2012	9.6	11.6	10.6	4.1
PL 2013	6.2	7.2	7.2	3.9
Cycloprosopon devexum nov. spec.				
NHMW 1990/0041/1072 (holotype)	6.3	7.3	6.5	3.3
PL 995	9.4	10.9	10.0	5.4
NM T3314	11.3	12.4	-	-
Cycloprosopon octonarium nov. spec.				
NHMW 2007z0149/0047 (holotype)	10.5	11.5	9.9	5.7
NHMW 1990/0041/5114	-	10.8	9.2	-
NHMW 1990/0041/4013	5.2	5.4	5.0	1.6
Cycloprosopon stenofrons nov. spec.				
NHMW 2007z0149/0050	8.6	9.7	8.3	3.6
NHMW 2007z0149/0051 (holotype)	11.8	13.6	12.3	5.8
NHMW 1990/0041/3812	11.9	14.0	11.8	4.4

fined, interrupted axially; branchiocardiac groove often incomplete or entirely missing; lateral flanks angled under carapace, subhepatic region weakly or uninflated.

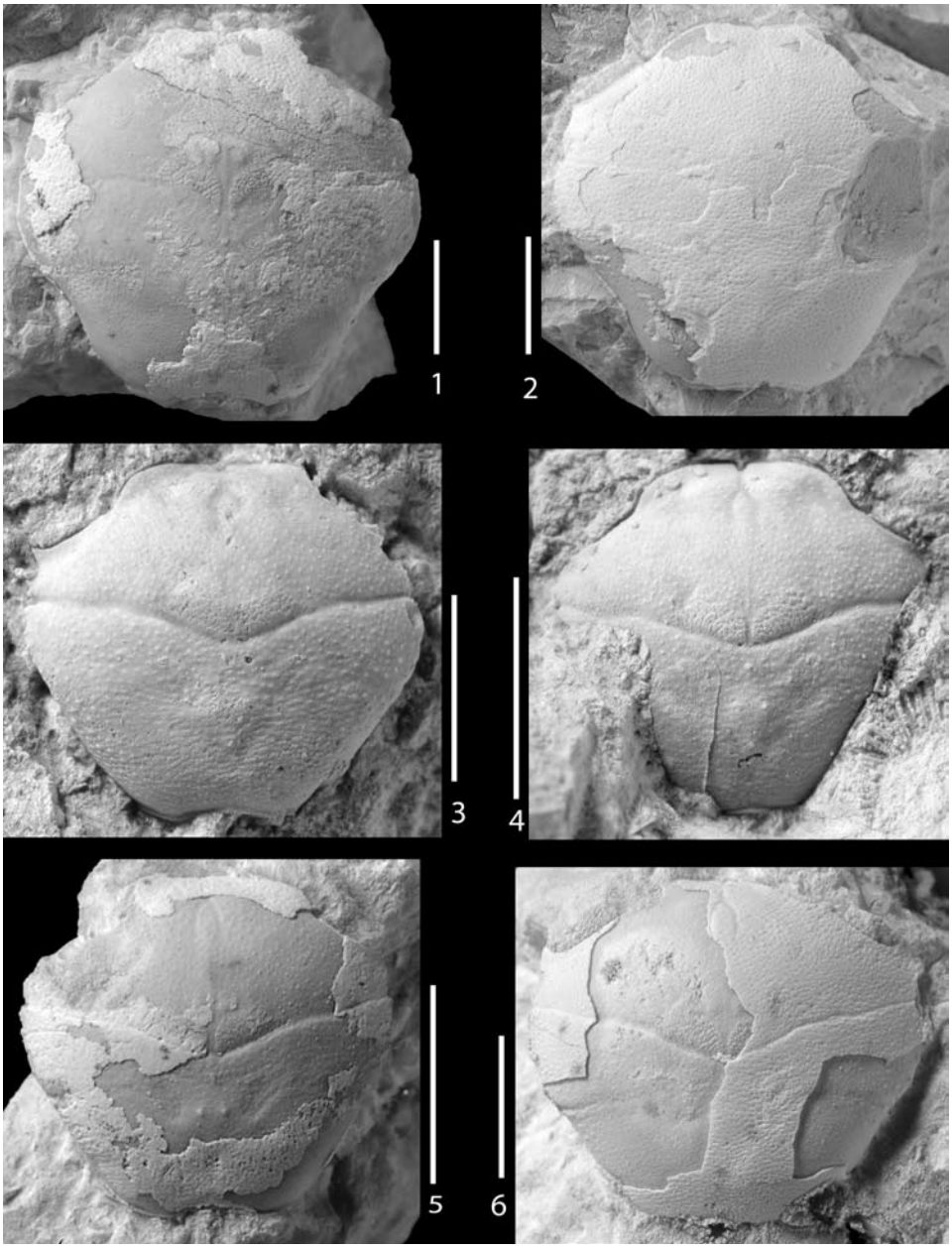
Nomenclature: Because they used the species name *typicum*, it is apparent that Lőrenthey *in* Lőrenthey & Beurlen (1929) intended for *Cycloprosopon* to be a name with neuter gender. "-um" is a neuter ending in Latin, and the word "prosopon" is neuter in Greek.

Discussion: Schweitzer et al. (2007) removed *Cycloprosopon* from the Prosopidae and assigned it to the Dynomenidae based upon its possession of a rounded carapace, better development of the cervical groove as compared to the branchiocardiac groove; and oblique orbits, all of which are typical of the Dynomenidae Ortmann, 1892, *sensu lato* and as defined broadly in the fossil record.

Examination of the original description and illustrations of the type species, *Cycloprosopon typicum*, a cast of the holotype of *C. complanatiforme*, and several specimens which are clearly conspecific with the holotype of *C. complanatiforme*, many with well-preserved orbits, augenrests, and suborbital regions, indicates that *Cycloprosopon sensu stricto* is more appropriately referred to the Goniodromitidae (Schweitzer & Feldmann 2008 [imprint 2007]). Herein, we restrict *Cycloprosopon* to those species with an angular, flattened, octagonal carapace, oblique orbits with a long augenrest; smooth carapace with weak to absent branchiocardiac groove and poorly or undefined carapace regions; and a broad front. These features distinguish *Cycloprosopon* from the closely related *Goniodromites*, which has very well-defined axial regions and cervical and branchiocardiac grooves, and from *Pithonoton*, which has a strongly inflated carapace transversely and longitudinally. Thus, *Cycloprosopon* occupies a distinct morphology within the Goniodromitidae.

Gemmellaro (1869) described *Prosopon etalloni* from Tithonian rocks of Sicily. It was subsequently referred to *Goniodromites* (Glaessner 1929; 1933), and later, Schweitzer & Feldmann (2008 [imprint 2007]) suggested it might belong to a new genus. Examination of Gemmellaro's original description and illustrations suggests that it is probably best accommodated in *Cycloprosopon* as herein restricted, based upon its octagonal cara-

Fig. 2. *Cycloprosopon* spp. 1, *Cycloprosopon complanatiforme* (Moericke, 1889), NHMW 1990/0041/5154, dorsal carapace, near Dörfles, Lower Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 2, *Cycloprosopon complanatiforme*, dorsal carapace, NMHW 2007z0162/0004, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 3, *Cycloprosopon conspicuum* nov. spec., PL 2012, holotype, dorsal carapace, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 4, *Cycloprosopon conspicuum* nov. spec., PL 2013, paratype, dorsal carapace with complete front, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 5, *Cycloprosopon stenofrons* nov. spec., NHMW 2007z0149/0050, dorsal carapace, holotype, near Dörfles, Lower Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 6, *Cycloprosopon stenofrons* nov. spec., NHMW 2007z0149/0049, paratype, dorsal carapace, near Dörfles, Lower Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic). Scale bars equals 5 mm. ►



pace, poorly defined regions, small outer-orbital spine, lobate front, and well-developed cervical groove and poorly developed branchiocardiac groove. All of these features are typical of *Cycloprosopon*. The current location of Gemmellaro's material is unknown (A. Garassino, personal communication).

Schweitzer & Feldmann (2009b) have already removed several species from *Cycloprosopon sensu stricto* that are better placed within *Cyclothyreus* Remeš, 1895. Feldmann et al. (2006) referred a new species to *Cycloprosopon*, *C. dobrogea*. Examination of that species, comparison of it to the original description for *Cycloprosopon typicum*, and recovery of new material referable to *C. dobrogea* suggests that it is better placed within *Eodromites*, based upon its possession of a strongly inflated subhepatic region; deep cervical and branchiocardiac grooves; steep, perpendicular flanks of the carapace; deep augenrests with a subaugenrest margin that extends beyond the upper augenrest margin; and lateral margins composed of arcuate segments that are drawn into a thin edge laterally. All of these features are diagnostic for *Eodromites* and are not seen in *Cycloprosopon*. Thus, *Cycloprosopon dobrogea* is redescribed below and reassigned to *Eodromites*. *Cycloprosopon* now comprises three previously described species and four new species described below (Table 1).

Cycloprosopon typicum Lőrenthey *in* Lőrenthey & Beurlen, 1929

Fig. 1.1.-1.3

1929	*Cycloprosopon typicum* Lőrenthey *in* Lőrenthey & Beurlen, 1929, p. 90-91, pl. 3, figs 12a-c.
1929	*Pithonoton* (*Cycloprosopon*) *typicum* (Lőrenthey, 1929). – Glaessner, p. 326.
1933	*Goniodromites typicum* (Lör. et Beurlen). – Glaessner, p. 181.
1969	*Pithonoton* (*Cycloprosopon*) *typicum* Lőrenthey, 1928 [sic]. – Glaessner, p. R485, fig. 293.5.
2006	*Cycloprosopon typicum* Lőrenthey *in* Lőrenthey & Beurlen, 1929. – Feldmann et al., p. 15.
2007	*Cycloprosopon typicum* Lőrenthey *in* Lőrenthey & Beurlen, 1929. – Schweitzer et al., p. 109.

Type: Unfortunately, the type appears to be lost (P. Müller, personal communication, November, 2008).

Diagnosis: Carapace octagonal; front broad, bilobed; regions not defined, cervical groove deep; branchiocardiac groove absent.

Description (translated from Lőrenthey in Lőrenthey & Beurlen 1929: 90-91): "The steinkern of the single, small cephalothorax is wider than long, weakly vaulted in longitudinal as well as in transverse orientation, strongly in the posterior part of the gastric region. The maximum width of the cephalothorax is approximately in the middle, slightly behind the cervical groove. The margins are smooth and inarticulate. The somewhat projected and downward-directed frontal margin is divided by an axial furrow. The antero-

lateral margin proceeds from the axis of the front margin in a weak concave-forward arc and then arcs weakly into the straight posterolateral margin. The front margin is approximately equal in length to the posterior margin which is weakly sinuous in the middle.

The surface of the carapace is almost completely smooth and inarticulate, and it is divided into two halves by the cervical groove. This rather distinct groove is strongly arched toward the posterior axially. The margins are interrupted where this groove intersects them. Only the foremost part of the gastric region, with a beaklike extension near the front lobe, is to some extent indicated. On both sides of the anterior end of the mesogastric region are the epigastric regions which are protruding weak inflations. As for the rest of the regions, they are scarcely indicated."

Occurrence: The type and sole specimen was collected from Tithonian rocks of Hungary (Lőrenthey & Beurlen, 1929).

Discussion: The illustration in Lőrenthey & Beurlen (1929), as well as their description, clearly indicates a taxon with an angular, octagonal carapace; a bilobed front; and a deep cervical groove and poorly developed branchocardiac groove. Regions are not developed. *Cycloprosopon complanatiforme*, the type of which still exists, is quite similar to *C. typicum* although it has a better developed, albeit still weak, branchiocardiac groove. Thus, we maintain the two as separate.

Cycloprosopon complanatiforme (Moericke, 1889)

Fig. 2.1, 2.2

1889	*Prosopon complanatiforme* Moericke, p. 66, pl. 6, fig. 19.
1897	*Prosopon complanatiforme* Moericke, p. 66, pl. 6, fig. 19.
1905	*Prosopon complanatiforme* Moericke. – Remeš, p. 36.
1924	*Cyclothyreus complanatiformis* (Moericke). – Van Straelen, p. 374. [imprint 1925]
1929	*Pithonoton* (*Cycloprosopon*) *complanatiforme* (Moericke). – Glaessner, p. 325.
1933	*Goniodromites complanatiforme* (Moer). – Glaessner, p. 181.
1988	*Pithonoton bidentatum* (Reuss). – Wehner, pl. 6, fig. 5.
2006	*Cycloprosopon complanatiforme* (Moericke). – Feldmann et al., p. 15.
2007	*Cycloprosopon complanatiforme* (Moericke). – Schweitzer et al., p. 109.

Material examined: *Prosopon complanatiforme*, original specimen of Moericke (1889) and interpreted as the holotype because he did not designate it as such but it is the sole specimen, BSP AS III 312; JU127P 3/1, originally referred to *Pithonoton etalloni*; newly referred material NHMW 1990/0041/5154; NHMW 2007z0162/0004; LPBIIIart-077, 079, 080, 082-086.

Diagnosis: Carapace octagonal, flattened; front broad, weakly concave; augenrest long, shallow; cervical groove continuous; branchiocardiac groove developed only as small groove at lateral margin of carapace; regions undifferentiated.

Original description (translated from Moericke 1889: 66): "The cephalothorax which is widest in the middle constricts anteriorly and posteriorly. The curved rostrum is remarkably wide, and becomes divided into two rounded lobes through a small median furrow. Of the gastric region, only the anterior, narrow end is distinct. The anterior clear transverse groove [cervical] forms a small arc exactly in the center of the carapace, laterally it goes then on each side in a longer, somewhat more arcuate furrow. The posterior transverse groove [branchiocardiac] is only incised on the sides of the cephalothorax, in the middle it becomes in comparison entirely invisible. The cardiac region takes the form of a relatively very large pentagon, however the outer delimiting furrows are exceptionally weakly developed. The posterior margin of the carapace has in the middle a small, sharp incision, edged by a narrow, smooth groove. The shell is uniformly decorated with a quantity of small, round pits. The lateral margins each have two projecting flaps in the upper half of the carapace."

Description of original specimen: Carapace octagonal, wider than long, L/W = 0.88, widest at position of anterolateral corner, just less than half the distance posteriorly on carapace; moderately vaulted transversely and longitudinally, ornamented with small punctae, especially posteriorly.

Rostrum wide, about 38% maximum carapace width, blunt, weakly concave; augenrests shallow, directed weakly anterolaterally, weakly rimmed, fronto-orbital width about 80% maximum carapace width; anterolateral margins short, apparently with small teeth; posterolateral margin initially weakly concave, then becoming straight; posterior margin narrow, about one-third maximum carapace width, concave, rimmed.

Epigastric regions small, weakly inflated; mesogastric region barely delimited, best defined at anterior tip and posteriorly; urogastric and cardiac region very weakly defined; other carapace regions not delimited. Cervical groove weakly incised, straight at lateral margins, then curving strongly axially around posterior end of mesogastric region; branchiocardiac groove only weakly incised at lateral margins, then disappearing completely.

Description of additional material: Carapace wider than long, length about 90% maximum carapace width, positioned about half the distance posteriorly on carapace and posterior to intersection of cervical groove with lateral margin; carapace moderately vaulted longitudinally and transversely; ornamented with small punctae overall, which are possibly setal pits.

Front broadly bilobed, axially notched, merging into augenrest margin. Orbits under rostrum, augenrests large, moderately deep, oriented anterolaterally, ending in small, forward-directed spine; fronto-orbital width (including augenrest) about 90% maximum carapace width.

Anterolateral margin nearly straight, diverging posteriorly from axis, notched where intersected by cervical groove. Posterolateral margin sinuous, concave centrally, much longer than anterolateral margin. Posterior margin concave, rounded, rimmed.

Epigastric regions very weakly inflated. Mesogastric region very weakly delineated at anterior and posterior end. Cervical groove extending in weakly concave forward arcs to mesogastric region, concave forward around posterior margin of mesogastric region; entire cervical groove taken together nearly straight. Cardiac region very weakly inflated. Postcervical and branchiocardiac grooves barely visible.

Lateral sides angled below dorsal carapace; cervical groove extending onto lateral side, initially straight, then curving in a concave-forward arc, bounding subhepatic region which is not inflated; posteriorly, lateral sides not well-calcified, becoming shorter.

Measurements: Measurements (in mm) taken on specimens of *Cycloprosopon complanatiforme* are presented in Table 2.

Occurrence: The type specimen was collected from the Štramberk locality in what is now the Czech Republic. Additional referred specimens were collected from the Ernstbrunn localities (NHMW 1990/0041/5154); Purcăreni (LPBIIIart-077, 079, 080, 082-086), from the Štramberk Limestone (NHMW 2007z0162/0004), and from the Tithonian of the western Polish Carpathians (JU127P 3/1) (Patrulius 1966).

Discussion: Herein we refer several specimens to the species which help to demonstrate placement of *Cycloprosopon* in the Goniodromitidae, most notably, in their possession of well-developed augenrests. *Cycloprosopon complanatiforme* differs from all other species of the genus in having a carapace that is about as long as wide; barely developed postcervical and branchiocardiac grooves; a bilobed front; and subhepatic regions that are defined but not inflated. Because the type specimen of this species still exists, the concept of *Cycloprosopon* will largely be based on this species.

Specimens herein assigned to *Cycloprosopon complanatiforme* are variable in size and in length/width ratios, with smaller specimens being somewhat more equant. We attribute this to allometric growth. All specimens referred to the species have the diagnostic characters as listed above, and it seems imprudent at this time to erect a new species for smaller specimens that otherwise share the diagnostic features of the species. *Cycloprosopon complanatiforme* was widespread during the Tithonian, having been collected from localities in Poland, the Czech Republic, Austria, and Romania.

Cycloprosopon etalloni (Gemmellaro, 1869)

Fig. 1.4, 1.5

1869 *Prosopon etalloni* Gemmellaro, p. 12, pl. 2, figs 50, 51.
1924 *Prosopon etalloni* Gemmellaro. – Van Straelen, p. 355. [imprint 1925]
1925 *Prosopon grande* von Meyer. – Beurlen, p. 469, 501.
1929 *Pithonoton* (*Goniodromites*) *etalloni* (Gemmellaro, 1869). – Glaessner, p. 327.
1933 *Goniodromites etalloni* (Gemm.). – Glaessner, p. 181.
2008 *Goniodromites etalloni* (Gemmellaro). – Schweitzer & Feldmann, p. 124. [imprint 2007]

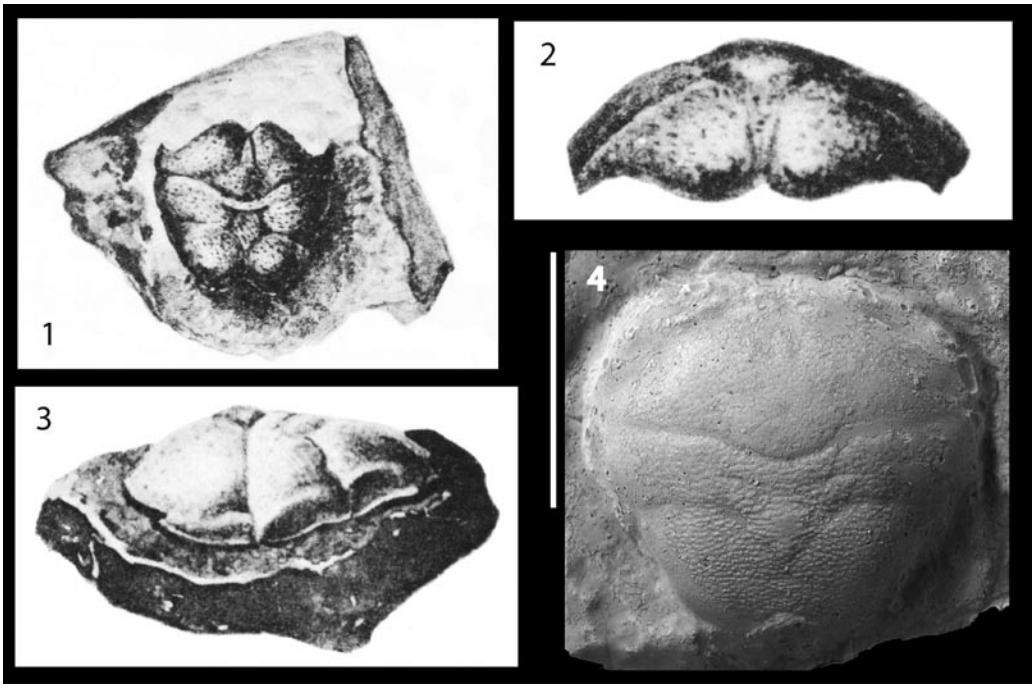


Fig. 3. *Goniodromites transsylvanicus* (Lőrenthey *in* Lőrenthey & Beurlen, 1929). 1-3, digital images from Lőrenthey & Beurlen (1929: pl. 3, figs. 9a-c); 4, cast of apparent holotype.

Type: The type material for the brachyuran specimens of Gemmellaro (1869) has not been located in museums in Italy (A. Garassino, personal communication).

Original description (translated from Gemmellaro 1869: 12): "Maximum length of carapace:15 mm, maximum width of the carapace at the center of the middle first segment: 17 mm, maximum length of the first segment anterior to the dorsal line, 8 mm, length of the first segment middle to side: 4 mm, length of the principal segment posterior to side: 5.5 mm.

The cephalothorax of this species is irregularly octagonal. Its principal anterior segment in the peripheral posterior part presents a weak sinuosity which terminates in a spine, is narrowing, formed in front an obtuse angle, rotund and incised with a median line. In this is distinguished the anterior part of the gastric region, which consists of a granular body circumscribed on the edges with a weak groove, which stops at a distance of 2 mm from the front margin. In the rest is the not very prominent hepatic region, which is not circumscribed and distinct. The hepatic region is regularly convex and presents, to each side of the anterior apex of the gastric region, a small and weak protuberance [epigastric region]. The anterior transverse groove [cervical] is distinct, and its dorsal sinuosity, which outlines the gastric region, bears a pair of pores. The genital region forms in the posterior a weak and straight transverse groove (postcervical groove). The transverse

posterior groove (branchiocardiac) is much less distinct than the anterior groove and limited behind the cardiac region which is pentagonal, however indistinct. The branchial region is not divided into two lateral parts. It [apparently the carapace] narrows in back and the posterior margin is weakly incised along all of its length and bordered by a weak groove.

The entire surface of the carapace is provided with small granules, equal and rather similar. In the posterior part of the branchial region, however, this granulation is less protruding, less similar, and arranged in an ordered transverse series with the aspect of wrinkled skin.

The species is near to the form of *P. depressum*, H. Mey. and to *Prosopon bidentatum*, Reuss sp. The first of these two species, however, is less advanced forward anteriorly, and has the branchial regions shorter in the front than that of *P. etalloni* Gemm. The second of these has a hexagonal form and is supplied with punctured granulations, which are not found in *Prosopon* under examination."

Occurrence: *Cycloprosopon etalloni* was described from Tithonian rocks of Sicily, Italy.

Discussion: As already mentioned, the best placement for this species appears to be *Cycloprosopon* until types or additional material from the type locality are recovered. Gemmellaro's (1869) illustrations show that the branchiocardiac groove can be variably developed, and indeed, that seems to be a defining feature for this species. The branchiocardiac groove is better developed in this species than in others of the genus. Based upon Gemmellaro's illustration, the species bears some resemblance to *C. complanatiforme* in the shape of the front, development of the outer augenrest spine, and conformation of the cervical groove. Because Gemmellaro's material appears to be lost, we maintain the two species as separate for now.

Lőrenthey *in* Lőrenthey & Beurlen (1929) erected a variety of *Prosopon etalloni*, *Prosopon etalloni* var. *transsylvanica* (Fig. 3). What appears to be the type of that form is the property of Magyar Állami Földtani Intezet and was examined by us at the NHMW during the summer of 2008. It has been transferred back to MAFI, and a cast is being kept at NHMW under the number NHMW 2009z0174/0001 (A. Kroh, personal communication, Nov., 2009). At least two additional specimens are referable to this taxon, NHMW 2007z0162/0021 and SMNS 61665. Because *Prosopon etalloni* var. *transsylvanica* has well-defined axial regions, deep cervical and branchiocardiac grooves, augenrests, and a somewhat longer than wide carapace, we afford it full specific status and place it within *Goniodromites*, resulting in *Goniodromites transsylvanicus* new combination. The well-defined regions and deep grooves preclude it from being placed within *Cycloprosopon*.

***Cycloprosopon conspicuum* nov. spec.**
Fig. 2.3, 2.4

Types: The holotype is PL 2012, and paratypes include PL 2013-2020.

Locus typicus: The specimens were collected from the Kotouč Quarry locality.

Stratum typicum: Štramberk Limestone.

Etymology: The trivial came is derived from the Latin *conspicuus*, meaning visible, prominent, in reference to the very clear, bilobed, broad front on this species.

Diagnosis: Front very broadly bilobed, marked inflection where it meets augenrest margin, outer-augenrest spine short, triangular, directed anterolaterally; cervical groove straight initially, then concave forward around posterior margin of mesogastric region; post-cervical groove weak to absent.

Description: Carapace wider than long, length about 84% maximum width, widest posterior to intersection of cervical groove with lateral margin, about half the distance posteriorly on carapace; carapace moderately vaulted longitudinally and transversely.

Front very broad, bilobed, each lobe sloping posteriorly, forming marked inflection at intersection with upper augenrest margin, inflection at about 60 degree angle; axially sulcate, flared upward at edges, weakly downturned. Augenrest margin weakly concave, directed anterolaterally; outer-augenrest spine short, triangular, directed anterolaterally.

Anterolateral margins straight, parallel to one another, with several tiny spines, notched at intersection of cervical groove; posterolateral margins converging posteriorly, nearly straight; posterior margin concave centrally, rimmed.

Epigastric regions weakly inflated, quadrate; mesogastric region moderately well marked along entire shape, with short longitudinal groove in posterior portion; cardiac region triangular, apex directed posteriorly; urogastric and metagastric regions united, weakly defined.

Cervical groove initially straight from lateral margins, oriented obliquely posteriorly, then arcing concave forward around posterior margin of mesogastric region. Postcervical groove very weak to absent; composed of two short, oblique segments. Branchiocardiac groove better developed than on most other species, deepest laterally, much weaker than cervical groove.

Measurements: Measurements (in mm) taken on two complete specimens of *Cycloprosopon conspicuum* nov. spec. are presented in Table 2.

Discussion: The new species differs from all congeners in having a very large, bilobed front that intersects the upper augenrest margin at a relatively high angle and an outer-augenrest spine that is directed anterolaterally. No other species has such a broad, lobate front. As is not uncommon for crabs from this locality, one specimen has two encrusting foraminifera on the dorsal carapace.

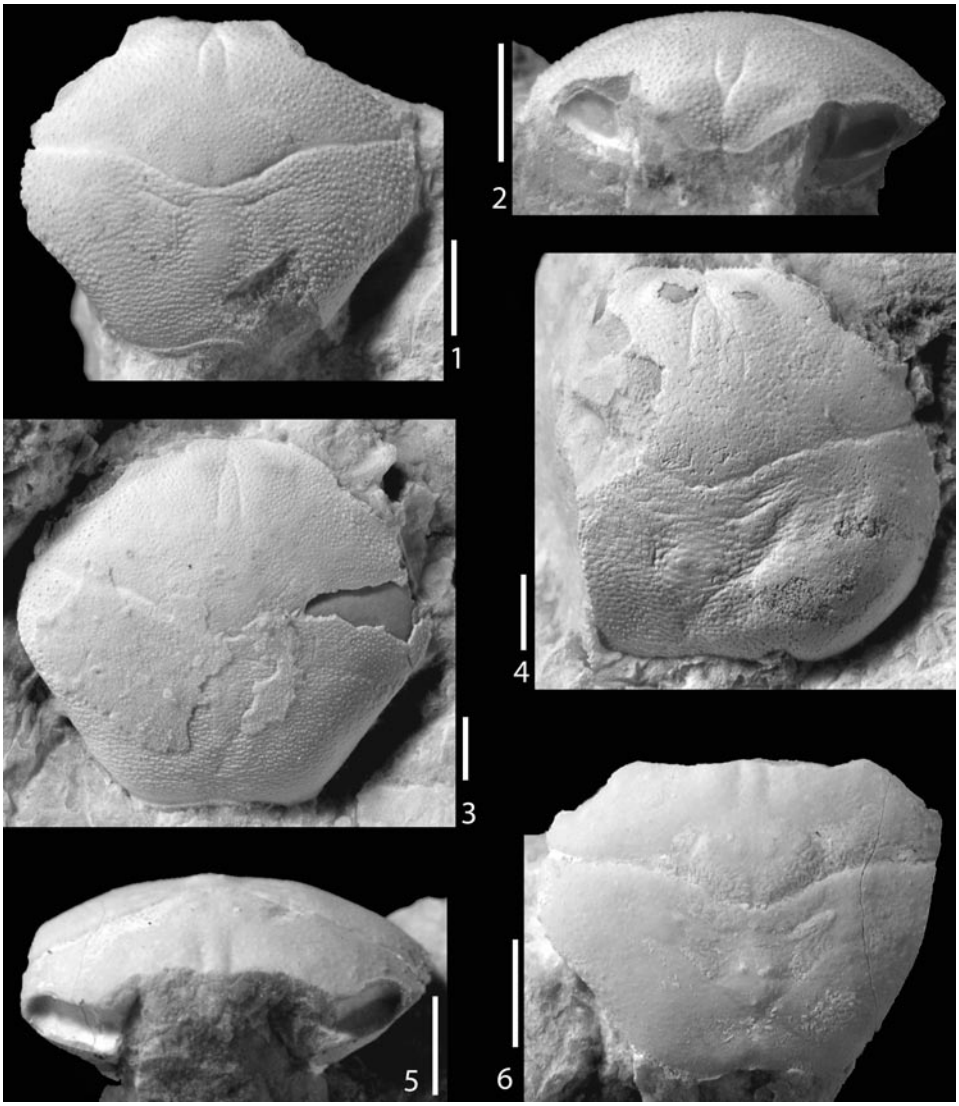


Fig. 4. *Cycloprosopon* spp. 1-2, *Cycloprosopon devexum* nov. spec., NHMW 1990/0041/1072, holotype, dorsal carapace (1) and anterior view showing strongly deflexed front (2); 3, *Cycloprosopon octonarium* nov. spec., NHMW 2007z0149/0047, holotype, dorsal carapace; 4, *Cycloprosopon octonarium* nov. spec., NHMW 2007z0149/0049, paratype, dorsal carapace with large bopyrid swelling in right branchial chamber; 5-6, *Cycloprosopon octonarium* nov. spec., NHMW 1990/0041/5114, paratype, anterior view showing augenrests (5) and dorsal carapace (6). All specimens from near Dörfles, Lower Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic). Scale bars equals 2 mm.

***Cycloprosopon devexum* nov. spec.**
Fig. 4.1, 4.2

Types: The holotype is NHMW 1990/0041/1072, and paratypes are NHMW 2007z0149/0046, PL 995, and NM T3314.

Locus Typicus: The holotype and paratype NHMW 2007z0149/0046 were collected from the Ernstbrunn localities, and PL 995 and NM T3314 were collected from the Štramberk Limestone.

Stratum Typicum: Ernstbrunn Limestone.

Etymology: The trivial name is derived from the Latin *devexus*, meaning inclined, sloping, in reference to the strongly downturned front in this species.

Diagnosis: Front strongly downturned so as to be at 90 degree angle with dorsal carapace; augenrest with beaded rim on upper and lower margins; cervical groove sinuous; subhepatic region weakly inflated.

Description: Carapace octagonal, wider than long, length about 82% maximum carapace width positioned posterior to cervical groove, about half the distance posteriorly on carapace; carapace moderately vaulted longitudinally and transversely; ornamentation granular anteriorly, composed of scabrous ridges of granules posteriorly.

Front blunt triangular, weakly axially notched, rimmed; edged with small beads; tip very strongly downturned so as to be at right angle to dorsal carapace. Front merging with upper augenrest margin, which is rimmed and beaded; augenrest moderately deep; lower augenrest margin beaded; outer-augenrest spine small, directed forward.

Anterolateral margin weakly convex, with a few spines; posterolateral margin sinuous, initially beaded, then becoming weakly concave centrally, then arcing convexly to posterolateral corner. Posterior margin axially concave, rimmed.

Epigastric regions broadly inflated, quadrate; mesogastric region moderately well defined anteriorly, weakly defined posteriorly, with short longitudinal groove in posterior portion. Metagastric region very short, wide, defined by deep oblique segments of postcervical groove. Urogastric and cardiac regions united, weak, elongate-oval.

Cervical groove sinuous, weakly concave-forward, then strongly concave-forward around posterior of mesogastric region. Branchiocardiac groove very weak or undefined, visible laterally on mold of interior.

Flanks angled below dorsal carapace; cervical groove extending onto flank, initially straight, then curving in a concave-forward arc, bounding subhepatic region which is weakly inflated.

Measurements: Measurements (in mm) taken on the dorsal carapace of specimens of *Cycloprosopon devexum* nov. spec. are presented in Table 2.

Discussion: *Cycloprosopon devexum* is distinctive in possessing a front that is downturned at a ninety degree angle to the dorsal carapace. No other species exhibits a front that is nearly as strongly deflexed. The specimens from the Ernstbrunn Limestone are very well preserved and exhibit scabrous and granular ornamentation that is common within the Goniodromitidae. Like many brachyuran species in the Tithonian, *Cycloprosopon devexum* nov. spec. is known from both the Ernstbrunn and Štramberk limestones.

***Cycloprosopon octonarium* nov. spec.**

Fig. 4.3-4.5

Types: The holotype is NHMW 2007z0149/0047, and paratypes include NHMW 1990/0041/4013, 1990/0041/5114, 2007z0149/0048, and 2007z0149/0049.

Locus Typicus: All of the specimens were collected from the Ernstbrunn quarry localities.

Stratum Typicum: Ernstbrunn Limestone.

Etymology: The trivial name is derived from the Latin *octonarius*, meaning eight, in reference to the obviously octagonal nature of the carapace of this species.

Diagnosis: Front broadly triangular; anterolateral margins converging markedly anteriorly, with spines and granules; epigastric regions spherical, moderately inflated.

Description: Carapace not much wider than long, maximum length about 90% maximum carapace width, widest just over half the distance posteriorly and posterior to intersection of cervical groove with lateral margin; regions poorly differentiated, granular; moderately vaulted transversely and longitudinally.

Front broadly and bluntly triangular, margin beaded, weakly rimmed; marked inflection between front and rim of augenrest. Rim of augenrest granular, weakly rimmed, frontoorbital width (including augenrest) about 85% maximum carapace width. Augenrest directed anterolaterally, long, moderately deep, separated from orbit by weak ridge; outer-augenrest spine directed forward.

Anterolateral margins converging anteriorly, with one spine not including outer-augenrest spine anterior to and several granules posterior to intersection of cervical groove with lateral margin; posterolateral margins converging posteriorly, with granules anteriorly, nearly straight. Posterior margin concave axially, rimmed.

Epigastric regions small, spherical, weakly inflated. Mesogastric region defined at anterior tip and posterior end. Cardiac region long, narrow on cuticular surface; with two distinct nodes anteriorly and one posteriorly on mold of interior. Regions better defined on mold of interior. Ornamentation on cuticular surface granular anteriorly and composed of short, scabrous ridges posteriorly.

Cervical groove sinuous, extending in concave-forward arc from lateral margin, then markedly concave-forward around posterior margin of mesogastric region; entire groove with concave-forward path. Postcervical groove very weak on cuticular surface, stronger on mold of interior, composed of two short segments, directed obliquely toward lateral margin, parallel to cervical groove. Branchiocardiac groove very weak, composed of weak, convex-forward arc from posterolateral margin to cardiac region, barely visible on cuticular surface, even weaker on mold of interior.

Flanks angled below dorsal carapace; cervical groove extending onto flank, initially straight, then curving in a concave-forward arc, bounding subhepatic region which is not inflated; branchiocardiac groove extending onto lateral flanks in a oblique, straight line, directed forward; flanks not well-calcified, becoming shorter.

Measurements: Measurements (in mm) taken on specimens of *Cycloprosopon octonarium* nov. spec. are presented in Table 2.

Discussion: *Cycloprosopon octonarium* nov. spec. differs from all congeners in possessing anterolateral margins that are not parallel to one another or convex but rather converge markedly anteriorly. In addition, the species has an outer-augenrest spine that is directed forward and a granular rim on the front and augenrest, not typically seen. One specimen exhibits a large bopyrid swelling (Fig. 4.4) in the right branchial chamber, not uncommon for members of the family but the only specimen of *Cycloprosopon* of those mentioned herein to display such a swelling.

***Cycloprosopon stenofrons* nov. spec.**

Fig. 2.5, 2.6

Types: The holotype is NHMW 2007z0149/0050, and paratypes include NHMW 1990/0041/3812 and 2007z0149/0051.

Occurrence: All of the specimens were collected from the Ernstbrunn quarry localities.

Etymology: The trivial name is derived from the Greek *stenos* meaning narrow and the Latin *frons*, meaning front, referring to the short distance between the tip of the front and the point of maximum width.

Diagnosis: Carapace wider than long, widest 42% the distance posteriorly, weakly vaulted; subhepatic region not inflated.

Description: Carapace wider than long, length about 87% maximum carapace width, widest about 42% the distance posteriorly, just posterior to intersection of cervical groove with lateral margin; carapace weakly vaulted transversely and longitudinally; regions poorly defined.

Front broadly and bluntly triangular; marked inflection perpendicular to axis with augenrest margin about half the distance distally to lateral margin of carapace. Augenrest mar-

gin directed very weakly anterolaterally; outer-augenrest spine small, directed forward, augenrest long, moderately deep.

Anterolateral margin weakly convex, granular anterior and posterior to intersection of cervical groove. Posterolateral margin weakly sinuous, concave following anterolateral margin and then convex approaching posterior margin. Posterior margin concave axially.

Epigastric regions not differentiated. Mesogastric region weakly defined at anterior tip and posterior base. Cardiac region weakly defined. Remainder of regions undifferentiated.

Cervical groove very deep; initially weakly sinuous from lateral margin, then arcing concavely around base of mesogastric region. Postcervical groove very weak, two segments parallel to cervical groove. Branchiocardiac groove best seen on mold of interior, arcing convex-forward toward cardiac region, deepest laterally, not visible on cuticular surface.

Flanks angled below dorsal carapace; cervical groove extending onto flank, initially straight, then curving in a concave-forward arc, bounding subhepatic region which is not inflated.

Measurements: Measurements (in mm) taken on the dorsal carapace of *Cycloprosopon stenofrons* nov. spec. are presented in Table 2.

Discussion: Like *Cycloprosopon octonarium* nov. spec., all of the specimens of *Cycloprosopon stenofrons* nov. spec.were collected from the Ernstbrunn Limestone. It is a distinctive species in having a short distance to the point of maximum width of the carapace, less than half the carapace length, and a short distance from the front to the outer-augenrest spine. In addition, the augenrests are directed very weakly anterolaterally, almost directed forward, a different configuration than seen in other species.

Genus *Eodromites* Patrulius, 1959

Type species: *Prosopon grande* von Meyer, 1857, by original designation.

Included species: *Eodromites depressus* (von Meyer, 1860), as *Prosopon*; *E. dobrogea* (Feldmann, lazăr & schweitzer, 2006), as *Cycloprosopon*; *E. grandis*; *E. nitidus* (A. Milne-Edwards, 1865), as *Ogydromites*; *E. polyphemi* (Gemmellaro, 1869), as *Prosopon*; *E. rostratus* (von Meyer, 1840), as *Prosopon*.

Range: Oxfordian – Neocomian.

Diagnosis: As in Schweitzer & Feldmann, 2008 [imprint 2007].

Additional material examined: NHMW 1990/0041/0006, 1990/0041/3303, 1990/0041/3381, 1990/0041/3385, 1990/0041/5139, 1990/0041/5147, 2007z0149/0052, 2007z0149/0053, all *Eodromites grandis*; and Museum Tübingen specimen Quenstedt 1883: pl. 31, fig. 13, *Eodromites rostratus*, possibly an original specimen of Quenstedt.

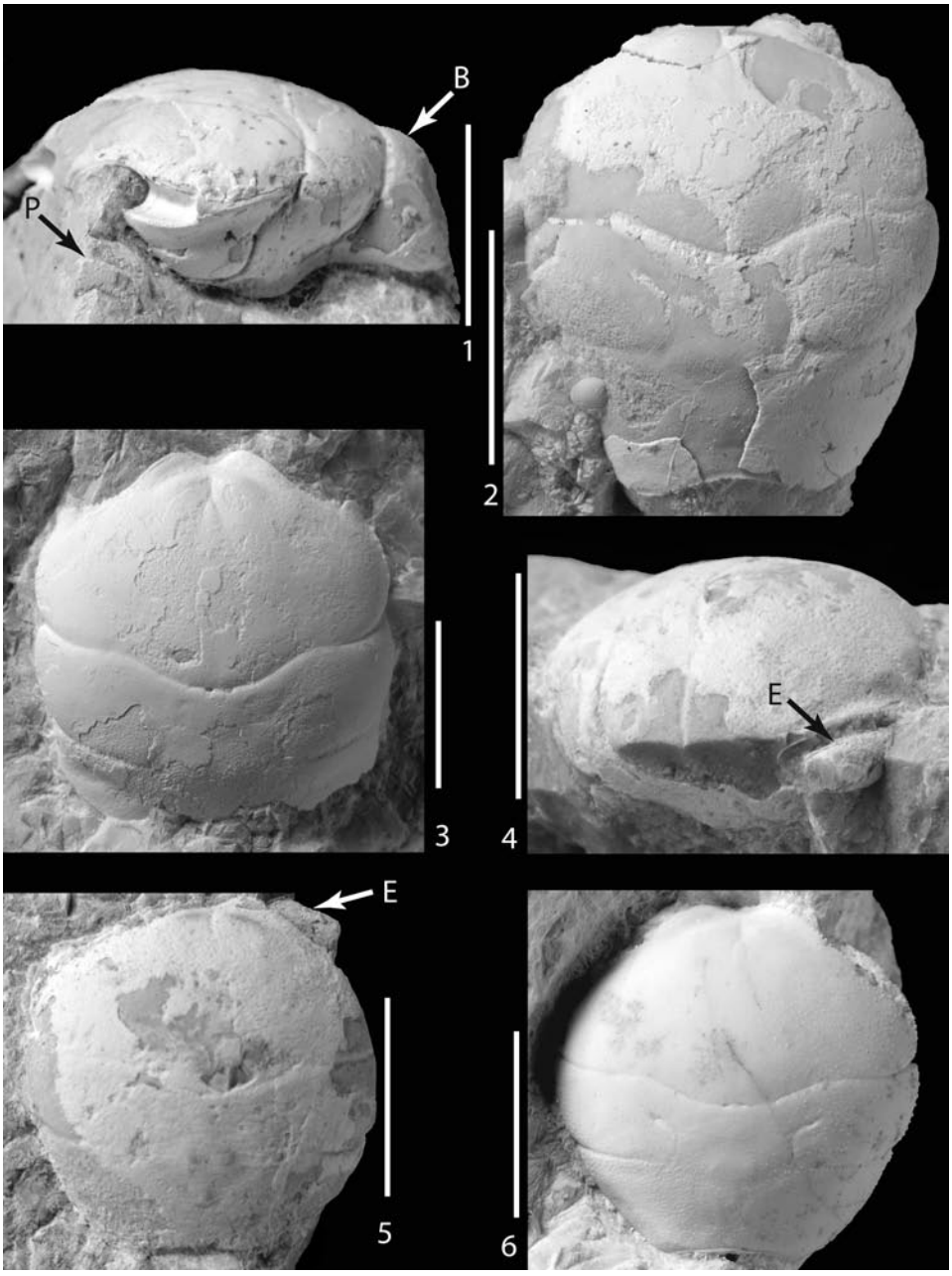
Discussion: Schweitzer & Feldmann (2008 [imprint 2007]) have already diagnosed and revised *Eodromites*. Herein we refer *Cycloprosopon dobrogea* to *Eodromites* based upon its possession of diagnostic features of the genus. Assignment of that species to *Eodromites* does not change the diagnosis for it, because the generic diagnosis of Schweitzer & Feldmann (2008 [imprint 2007]) already could accommodate specimens that were about as wide as long.

In examining several specimens of *Eodromites grandis* and one herein referred to *E. dobrogea* we have noted that at least three are preserved with appendages in what appear to be articulated position. This is extremely unusual for Jurassic brachyurans; in fact, only *Pithonoton elongatum* (von Meyer, 1860) has ever been collected with appendages in place (von Meyer, 1860, pl. 23, fig. 16; reproduced in Schweitzer & Feldmann, 2008 [imprint 2007], pl. 3J). Specimen NHMW 2007/0149/0001b possesses an element of the left first pereiopod in articulated position, anterior to the carapace (Fig. 5.1). NHMW 2007z0149/0053 has a fragment of the right first pereiopod in the same position. Most spectacularly, SMO 11958 retains the right eyestalk lying within the augenrest (Figs 5.4, 5.5), confirming the hypothesis of Schweitzer & Feldmann (2009a) that the augenrest structure accommodated the eye and protected it.

In addition to the preservation of appendages, *Eodromites* is notable in having well-preserved flanks and pterygostomial areas, better than any other members of the family and other Jurassic brachyurans. NHMW 1990/0041/5139 and NHMW 2007z0149/0052 have extremely well-preserved augenrests, sub-augenrest areas, subhepatic regions (Figs 5.1-5.4), and lateral sides such that the three-dimensional shape of the crab can be seen, which is not typical for Jurassic crabs.

We suggest that *Eodromites* may have had a more strongly calcified carapace than other members of the family, and other Jurassic brachyurans. This could explain the well-preserved dorsal carapace that exposes lateral surfaces as well as dorsal, as well as the retention of delicate structures such as eyestalks which have not been reported previously. We are unsure why this taxon would be preferentially calcified, although size may have played a role, as *Eodromites* is in general one of the larger of the Jurassic crabs (Fig. 5, note scale). Size may have required sequestration of more calcite into the cuticle, making it more durable. In addition, the larger size may have made the animals more visible to

Fig. 5. *Eodromites* spp. 1, *Eodromites grandis* (von Meyer, 1857), NHMW 2007z0149/0001, oblique view of dorsal carapace showing well-defined lateral margins, bopyrid swelling (B), and element of first pereiopod (P) in living position; 2, *Eodromites grandis*, NHMW 2007z0149/0052, dorsal carapace; 3, *Eodromites grandis*, NHMW 1990/0041/3303, dorsal carapace; 4-5, *Eodromites dobrogea* (Feldmann, Lazăr, & Schweitzer, 2006), SMO 11958, oblique anterior view showing preserved eyestalk in augenrest (4) and dorsal carapace showing eyestalk (5), Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 6, *Eodromites dobrogea*, NHMW 1990/0041/0002, dorsal carapace. All except 4 and 5 from near Dörfles, Lower Austria, Ernstbrunn Limestone, Tithonian (Upper Jurassic). Scale bars equals 1 cm. ►



predators, requiring a more durable cuticle. In spite of the stronger calcification, we have yet to find sterna or abdomina associated with dorsal carapaces of *Eodromites*.

Like other genera within the family, *Eodromites* extends from the Late Jurassic into the Early Cretaceous. Most of the species are of Late Jurassic age (Schweitzer & Feldmann, 2008 [imprint 2007]), but *E. nitidus* was recorded from the earliest Cretaceous of France (A. Milne-Edwards, 1865).

Eodromites dobrogea (Feldmann, Lazăr, & Schweitzer, 2006) nov. comb.

Fig. 5.4-5.6

2006 *Cycloprosopon dobrogea* Feldmann, Lazăr, & Schweitzer, 2006, p. 16, fig. 3.10.
2007 *Cycloprosopon dobrogea* Feldmann, Lazăr, & Schweitzer. – Schweitzer et al., p. 109.
2009 *Cycloprosopon dobrogea* Feldmann, Lazăr, & Schweitzer. – Schweitzer et al., p. 7.

Material examined: SMO 11958; NHMW 1990/0041/0002, 1990/0041/0095, 1990/0041/4744, 2007z0149/0054, 2007z0149/0055, 2007z0149/0056, 2007z0149/0057; PL 1003, PC44.

Emendation to diagnosis: Carapace ovate, length to width about equal; front broadly triangular.

Emended description: Carapace ovate, about as long as wide, length about 95 to 100% maximum carapace width, widest about half the distance posteriorly on carapace,

Table 3. Measurements (in mm) taken on specimens of *Eodromites dobrogea* (Feldmann, Lazăr & Schweitzer, 2006). L1 = maximum carapace length; L2 = length from front to position of maximum width of carapace; W1 = maximum width of carapace; W2 = fronto-orbital, including augenrests.

Specimen Number	W1	L1	W2	L2
PC44	25.1	24.2	20.0	11.9
SMO 11958	18.0	16.9	17.6	7.2
NHMW 1990/0041/4744	12.5	12.6	10.8	5.6
NHMW 2007z0149/0054	4.9	5.0	-	2.8
NHMW 1990/0041/0002	18.8	18.1	17.0	10.2
NHMW 1990/0041/0095	10.0	8.3	8.2	4.2

just posterior to intersection of cervical groove with lateral margin; strongly vaulted longitudinally and transversely; carapace weakly ornamented with broadly spaced, tiny tubercles which can appear as pits if some layers of cuticle are missing.

Front broadly, bluntly triangular, edges flared dorsally, merging into upper augenrest margin; augenrest deep; augenrest margin granular or with tiny spines, directed anterolaterally, weakly concave, lower augenrest margin extending further anteriorly than upper augenrest margin so as to be visible dorsally; fronto-orbital width (including augenrest) about 80-90% maximum carapace width; eyestalk stout, circular in cross-section, lying in augenrest.

Lateral margins composed of convex arcs, markedly notched at intersections of cervical and branchiocardiac grooves; arcs anterior to cervical groove granular; arcs between cervical and branchiocardiac grooves with tiny spines. Posterolateral margins converging toward posterior margin, nearly straight; posterior margin short, weakly convex, narrowly rimmed.

Epigastric region broadly inflated, mesogastric region very weakly marked, most-markedly anteriorly, with large, ovate muscle scars posteriorly; cardiac region a weak triangular swelling with apex directed posteriorly.

Cervical groove deep, sinuous, composed of concave-forward arcs laterally, then arcing concave forward around posterior margin of mesogastric region, with two pits axially. Postcervical groove composed of two very short segments. Branchiocardiac groove deep laterally, composed of nearly straight segments extending from lateral margin toward axis, then becoming shallower axially.

Flanks steep, lateral margins produced into thin ridge on edge; cervical groove extending onto flank anteriorly, then arcing around strongly inflated subhepatic region. Branchiocardiac groove extending obliquely anteriorly. Flanks becoming less high posteriorly.

Measurements: Measurements (in mm) taken on specimens of *Eodromites dobrogea* nov. comb. are presented in Table 3.

Occurrence: SMO 11958 and the PL + PC specimens were collected from the Štramberk Limestone, and the NHMW specimens were collected from the Ernstbrunn localities. *Eodromites dobrogea* was previously known from the Oxfordian of Romania (Feldmann et al. 2006).

Discussion: The new material herein referred to *Eodromites dobrogea* agrees well with the original description. We provide an emended description because the new material is so much more complete, including a better-preserved front, orbits, and flanks.

The oldest occurrence of *Eodromites dobrogea* is from Oxfordian rocks of Romania, and it also occurs in Tithonian rocks of Austria and the Czech Republic.

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