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Article

A new crab species from the Oxfordian of Poland (Decapoda: Brachyura: Goniodromitidae)

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With 10 figures

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Abstract: Representatives of *Goniodromites* are the most common brachyurans in Jurassic localities of southern Poland. Analysis of *Goniodromites* from four Oxfordian localities of southern Poland yielded three species: *G. serratus*, *G. narinosus* and a new species, *G. kubai*. The differences between these species are based upon features of the rostral region and the augenrest, and also are mirrored in the morphometric analysis. Numerous specimens of *G. narinosus* enabled us to supplement the original description.

Key words: *Goniodromites*, Homolodromioidea, Brachyura, Decapoda, Jurassic, Oxfordian.

1. Introduction

The family Goniodromitidae belongs to one of the oldest Brachyuran superfamilies – Homolodromioidea which comprises the most primitive crab families: Goniodromitidae, Tanidromitidae, Bucculentidae, Prosopidae, Longodromitidae, and Homolodromitidae (Karasawa et al. 2011).

The family Goniodromitidae comprises ten genera: *Cycloprosopon* Lörenthey, in Lörenthey & Beurlen, 1929; *Cyclothyreus* Remeš, 1895; *Distefania* Checchia-Rispoli, 1917; *Eodromites* Patrulius, 1959; *Goniodromites* Reuss, 1858; *Palaeodromites* A. Milne-Edwards, 1865; *Pithonoton* von Meyer, 1860; *Plagiophthalmus* Bell, 1863; *Sabellidromites* Schweitzer & Feldmann, 2008, and *Trachynotocarcinus* Wright & Collins, 1972 (De Grave et al. 2009). Seven genera were represented in the Jurassic or at the Jurassic/Cretaceous boundary: *Cycloprosopon*, *Cyclothyreus*, *Distefania*, *Eodromites*, *Goniodromites*, *Palaeodromites*, *Pithonoton*, and *Sabellidromites*. The present generic composition of the family has resulted from several earlier revisions of particular genera. *Cycloprosopon* and *Cyclothyreus* were revised by Schweitzer & Feldmann (2009, 2010b). *Palaeodromites*, *Distefania*, and *Cyclothyreus* which historically belonged in Dynomenidae were re-evaluated and transferred to Goniodromitidae by Schweitzer & Feldmann (2010a). These authors described also *Sabellidromites* and added new species to *Eodromites*, *Goniodromites* and *Pithonoton* (Schweitzer & Feldmann 2008).

Goniodromites has been known in Europe for a century and a half (Reuss 1859). The genus has been considered a subgenus of *Pithonoton* (Glaessner 1929) or a synonym of *Pithonoton* (Collins & Wierzbowski 1985; Wehner 1988; Müller et al. 2000). Beurlen (1932) and Glaessner (1933) separated *Goniodromites* and *Pithonoton* into a new subfamily Goniodromitinae within the Prosopidae, based upon the former having a strong cervical groove and a weaker branchiocardiac groove, weakly projected rostrum, development of lateral flanks and ornamentation of the carapace that is weaker than in other prosopids. The subfamily was raised to family status by Schweitzer et al. (2007).

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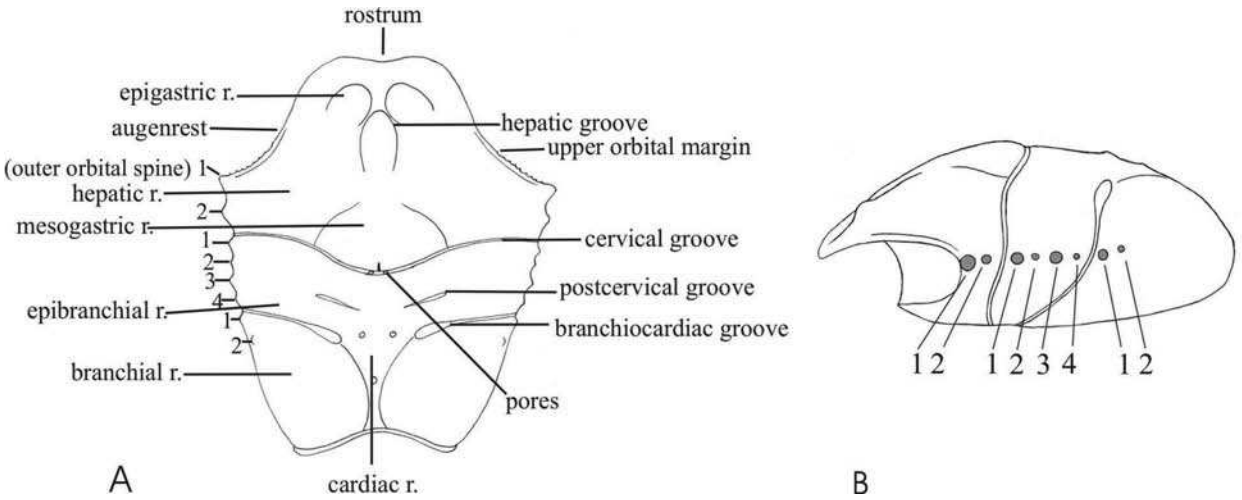


Fig. 1. A – Groundplan of the morphological structures in the three species of *Goniodromites* (*G. narinosus*, *G. serratus*, *G. kubai* n. sp.). **B** – Arrangement of main lateral spines. Numbers refer to spines within the regions; further explanation in text.

Representatives of *Goniodromites* are known from the Late Jurassic (Oxfordian) to Late Cretaceous (Cenomanian). It is the genus of longest range within the Mesozoic Homolodromioidea.

Goniodromitids are known from the territory of Europe and Japan. A widely spread European species, *G. serratus*, was first described from the Oxfordian of France (Beurlen 1929; Schweitzer & Feldmann 2008) and is known also from the Oxfordian localities of Poland: in the Holy Cross Mountains, the Polish Jura, the Kujawy region (Collins & Wierzbowski 1985) and Kraków – Zakrzówek quarry (Müller at al. 2000), and was recently recorded also from Dobrogea, Romania (Feldmann et al. 2006). From the latter locality, *G. aliquantulus* is recorded (Schweitzer et al. 2007) as well as a recently described species, *G. narinosus* (Late Oxfordian – Early Kimmeridgian; Franţescu 2010).

From the Tithonian of Europe five species are known. *Goniodromites polyodon* has been known for a long time from the Czech Republic (Reuss 1858). *Goniodromites dentatus* and *G. transylvanicus* were recorded from Hungary (Lörenthey in Lörenthey & Beurlen, 1929). *Goniodromites bidentatus* is known from the Polish Carpathians (Woźniki) (Patrulius 1966), Austria (Ernstbrunn) and Czech Republic (Schweitzer & Feldmann 2008).

Two Late Jurassic species from Japan, *G. hirotai* and *G. sakawense*, were described by Karasawa & Kato (2007).

Next in age come the Late Cretaceous species (Cenomanian). *Goniodromites laevis* and *G. cenomanensis* are known from Britain (Wright & Collins 1972), and *G. laevis* has been reported from Spain (Schweitzer & Feldmann 2008).

In this paper a new species of *Goniodromites* is described from four localities of the Polish Jura Chain. The species is accompanied in all localities by two other congeners, *G. serratus* and *G. narinosus*. The three species are apparently closely related based upon several characters of the carapace.

The specimens belong to a large, newly acquired collection of c. 7000 Late Jurassic crabs from the Polish Jura Chain, housed in the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences; ul. Sławkowska 17; 31-016 Kraków, Poland (ISEA). The collection comprises also *Bucculentum bucculentum* (Starzyk et al. 2011) and several species of Anomura (Pylochelidae and Diogenidae; three papers of Fraaije et al., in press).

2. Material and methods

Specimens examined here were collected from four localities in southern Poland (Kraków-Wieluń Upland; Oxfordian) – Bzów, Grabowa, Niegowonice and Ogrodzieniec. Each species occurs in all four localities. All crabs were collected by a family of amateur collectors: Iwona, Robert and Karolina Borek. In total, there are about 1100 specimens of the three species determined thus far. For this study we choose 103 of the best preserved specimens (25 – *G. serratus*, 26 –

G. narinosus, 52 – *G. kubai* n. sp.).

Terminology of the carapace structures is explained in Fig. 1A. The length and width of each specimen was measured and some other measurements were taken from 55 specimens (13 – *G. serratus*, 13 – *G. narinosus*, 29 – *G. kubai*). At earlier stages of this work various combinations of measurements were tried and their number has been eventually reduced to nine, according to the preliminary results of Principal Components Analysis. The Discriminant Analysis was based on these nine measurements taken in horizontal position of carapace (Fig. 10A): L- maximum length of carapace, MtF – distance from posterior end of mesogastric region to anterior border of the rostrum, MtC – distance from posterior end of mesogastric to a tubercle marking the posterior end of cardiac region, CtE – distance between this tubercle and distalmost end of carapace, CtBC – distance from the cervical to branchiocardiac groove laterally, BCtE - distance from branchiocardiac groove to distalmost end of carapace laterally, LPM – length of posterior (broad) part of mesogastric region, WM – maximum width of mesogastric region, WR – width of rostrum at the point of mesogastric anterior end, W – maximum width of carapace. A statistical package Statistica 6.1 was used.

3. Age of localities

Ogrodzieniec – On ammonite evidence, the section exposed at Ogrodzieniec Quarry can be dated as early to middle Oxfordian. With the exception of the discontinuous Mariae Zone, all zones and subzones from the Cordatum to the Transversarium have been documented (Głowniak, 2006; Starzyk et al. 2011).

Bzów – This pit, the northerly portion of which is in the village of Bzów, represents a prolongation of the large quarry at Ogrodzieniec. Ammonites indicate the middle Oxfordian Transversarium Zone. A single specimen in this lot might represent *Cardioceras tenuiserratum*, which would indicate the upper Plicatilis Zone (Matyja & Wierzbowski 1994).

Niegowonice – The sequence exposed at this quarry ranges from the upper Elisabethae Subzone to the upper Wartae Subzone; middle and late Oxfordian age (Głowniak 2006; Starzyk et al. 2011).

Grabowa – The quarry is east of the quarry of Negowonice and very close to it. The age of these sediments was until now not known from the literature. One accompanying ammonite was recently determined by E. Głowniak and A. Wierzbowski as *Taramelliceras externnodosum*, which correlates with the Upper Oxfordian zone of the uppermost Bifurcatus to the lowermost Bimammatum (subzone: Hypselum) (according to Głowniak & Wierzbowski 2007, fig. 2).

4. Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Dromiacea De Haan, 1833
Superfamily Homolodromioidea Alcock, 1900
Family Goniodromitidae Beurlen, 1932 (= Pithonotinae Glaessner, 1933)

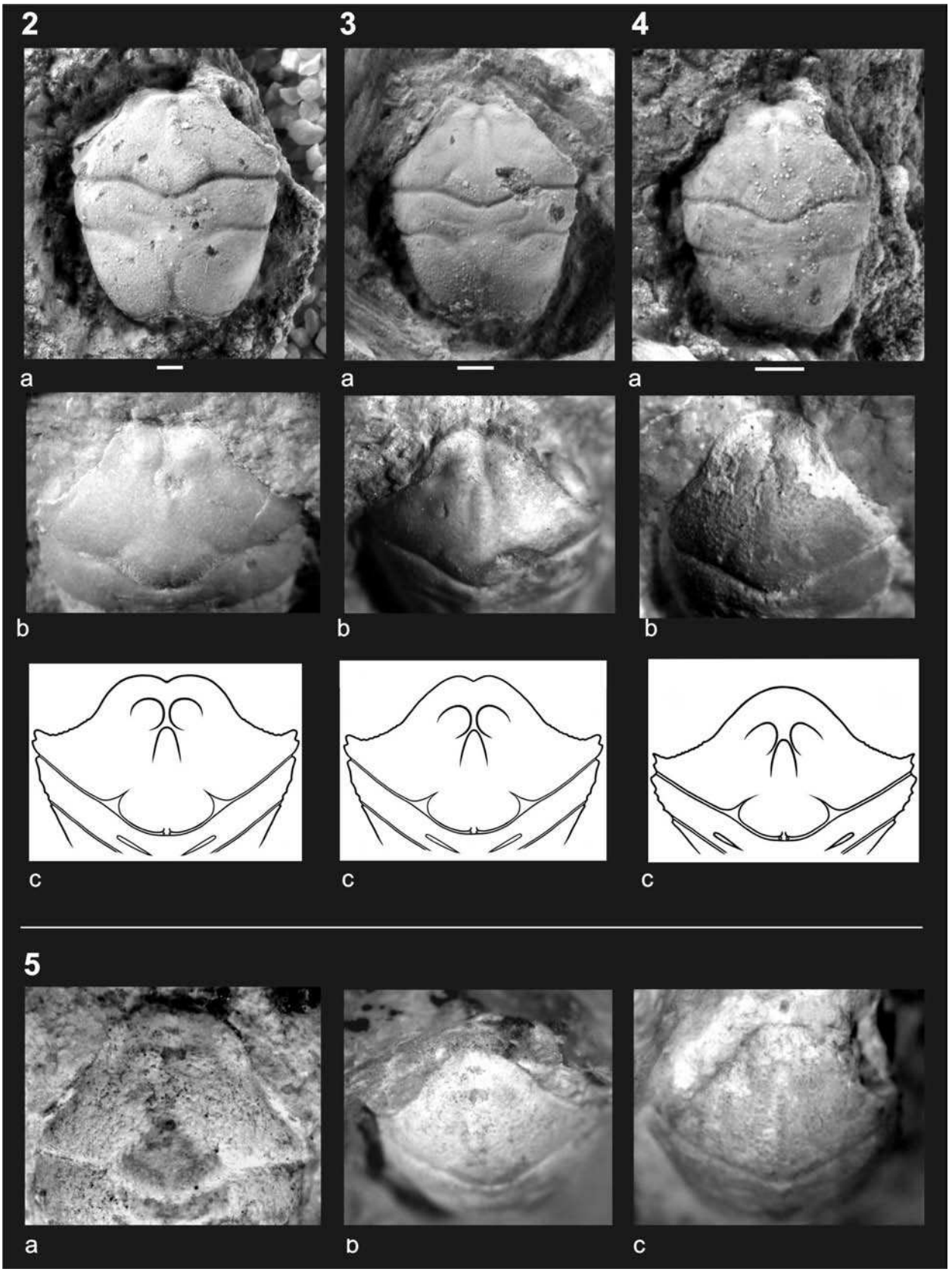
Genus *Goniodromites* Reuss, 1858

Type species: *Goniodromites bidentatus* Reuss, 1858, by original designation.

Other species included: *G. aliquantulus* Schweitzer, Feldmann & Lazăr, 2007; *G. cenomanensis* (Wright & Collins, 1972) as *Pithonoton*; *G. dentatus* Lörenthey in Lörenthey & Beurlen, 1929; *G. laevis* (Van Straelen, 1940) as *Iberihomola*; *G. narinosus* Franţescu, 2011; *G. polyodon* Reuss, 1858; *G. serratus* Beurlen, 1929; *G. hirotai* Karasawa & Kato, 2007; *G. sakawense* Karasawa & Kato, 2007; *G. transylvanicus* Lörenthey in Lörenthey & Beurlen, 1929, and *G. kubai* n. sp., described herein. All members, including some disputable species, are overviewed by Schweitzer et al. (2007).

Comments: The present study shows that three of the Oxfordian or older species: *G. serratus*, *G. narinosus* and *G. kubai* n. sp. form a group of species distinguished by shared characters of the augenrest and lateral border of carapace. Both margins of the augenrest, upper and lower, are finely serrated. The lateral border of the carapace is set with coarse spines present in a constant position (groundplan Fig. 1A, B): two along the hepatic region (the first one, large and sharp, known as the outer orbital spine), four spines (1, 3 – larger, 2, 4 – smaller) between the cervical and branchiocardiac grooves, and two small spines behind the branchiocardiac groove; the last one shifted slightly to the dorsal side. This arrangement of lateral spines was till now known to be characteristic only to *G. serratus* (Beurlen 1929; translation of original description by Feldmann et al. 2006).The interspecific differences concern the shape of the rostrum, augenrest, overall proportions of the carapace, and, to a lesser extent, also the body size.

At present it is not clear whether or which other species of the genus *Goniodromites* shares the above groundplan. The distribution of lateral spines is discussed by Schweitzer et al. (2007) and in Schweitzer & Feldmann (2008) in the discussion on *G. serratus*. Judging from the description of *G. aliquantulus* Schweitzer, Feldmann & Lazăr, 2007, this species is distinctive by outer-orbital spines being small and blunt, but may share similar arrangement of remaining lateral spines. The same may be true for *G. polyodon* (see also discussion of *G. serratus*, this paper). On the other



Figs. 2-5

hand, *G. dentatus* can be excluded in having only two large spines between cervical and branchocardiac grooves on lateral margin (basing on Schweitzer & Feldmann 2008, pl. 2E). Presence and arrangement of these spines in other congeners should be confirmed in future.

Goniodromites narinosus Franţescu, 2011
Figs. 2, 6, 9B

2011 *Goniodromites narinosus* n. sp. – Franţescu, p. 280, fig. 8.

Amended diagnosis: Carapace slightly longer than wide, strongly convex; shape rounded. Rostrum broad and short, directed downward, incised in the middle, divided through the median groove into two rounded lobes. There is an inflection at the point where the posterior margin of the rostrum and upper orbital margin meet. The augenrest is relatively narrow, almost twice as long as wide. Upper and suborbital margins of the augenrest are finely serrated; the suborbital margin protrudes distinctly in advance of the upper margin. Epigastric regions lie close to each other in front of mesogastric region. Mesogastric region pyriform, with narrow anterior and broad posterior portions equal in length (axially). On the lateral border of carapace there are six spines (including outer orbital spine), arranged as in Fig. 1.

This species reached a carapace size up to 9 mm, i. e., larger than *G. serratus* and *G. kubai* n. sp.

Material: Specimens from Bzów: I-F/MP/**1250**/1508/08, I-F/MP/**1748**/1517/08. Specimens from Niegowonice: I-F/MP/**1015**/1502/08, I-F/MP/**3008**/1532/08, I-F/MP/**3012**/1532/08, I-F/MP/**3032**/1532/08, I-F/MP/**3102**/1532/08, I-F/MP/**3106**/1532/08, I-F/MP/**3241**/1532/08, I-F/MP/**3297**/1532/08, I-F/MP/**3346**/1532/08, I-F/MP/**3401**/1532/08, I-F/MP/**4520**/1534/08, I-F/MP/**4581**/1534/08, I-F/MP/**4584**/1534/08, I-F/MP/**4727**/1534/08, I-F/MP/**4731**/1534/08, I-F/MP/**5415**/1543/09, I-F/MP/**5455**/1543/09, I-F/MP/**5476**/1543/09, I-F/MP/**5537**/1543/09, I-F/MP/**5583**/1543/09, I-F/MP/**6213**/1588/11 and I-F/MP/**6214**/1588/11. Specimens from Ogrodzieniec: I-F/MP/**163**/1489/08 and IF/MP/**6212**/1588/11. (Subsequently only the numbers in bold will be referred to).

Dimensions: The carapace length ranges from 5.69-9.06 mm (Fig. 9B).

Description of material: Carapace is slightly longer than wide, rounded (Fig. 2a), strongly longitudinally and transversely convex. Posterior border of carapace is long and distinctly concave. The angle between lateral and posterior border is rounded.

Rostrum is broad and very short (estimating from the border of rostrum to anterior border of epigastric regions), directed downward, divided by flattened median groove into two rounded lobes. Anterior margin of rostrum is incised medially; the character visible also when the rostrum is bent to anterior side (compare Fig. 2a-c).

There is an inflection at the point where the posterior margin of the rostrum and upper orbital margin meet. Upper and lower margins of the augenrest are covered with small serrations (especially well preserved in specimens 6212, 6213 and 6214). Characteristic is a very long augenrest, 1.9x longer than wide (Fig. 6; this character is visible also in Franţescu 2011, fig. 8.) The suborbital margin of the augenrest is strongly projected in advance of the upper margin and slightly flanged to outside (well visible in specimens 163, 1015, 4581, 6212, 6213 and 6214). The orbital margin is rimmed in the outer half, which disappears toward the rostrum.

Epigastric regions are swollen, rounded and positioned close to each other in front of the mesogastric region (Fig. 2b, c). Mesogastric region is pyriform, composed of a narrow anterior and a very wide posterior portion of same length (axially). The region is clearly visible, as the anterior part is defined by hepatic grooves, and a posterior part, by the cervical groove. There is a small incision directed axially in middle of the posterior part of mesogastric region.

The outer orbital spine is sharp, behind it there is another one before the cervical groove. Between the cervical and branchiocardiac grooves, on lateral border, there are further four spines (1, 3 – bigger, 2, 4 – smaller), and two spines behind the branchiocardiac groove (groundplan: Fig. 1A, B). The last one is shifted slightly to the dorsal side, and thus is less visible from above, when the specimen is laid in a horizontal position.

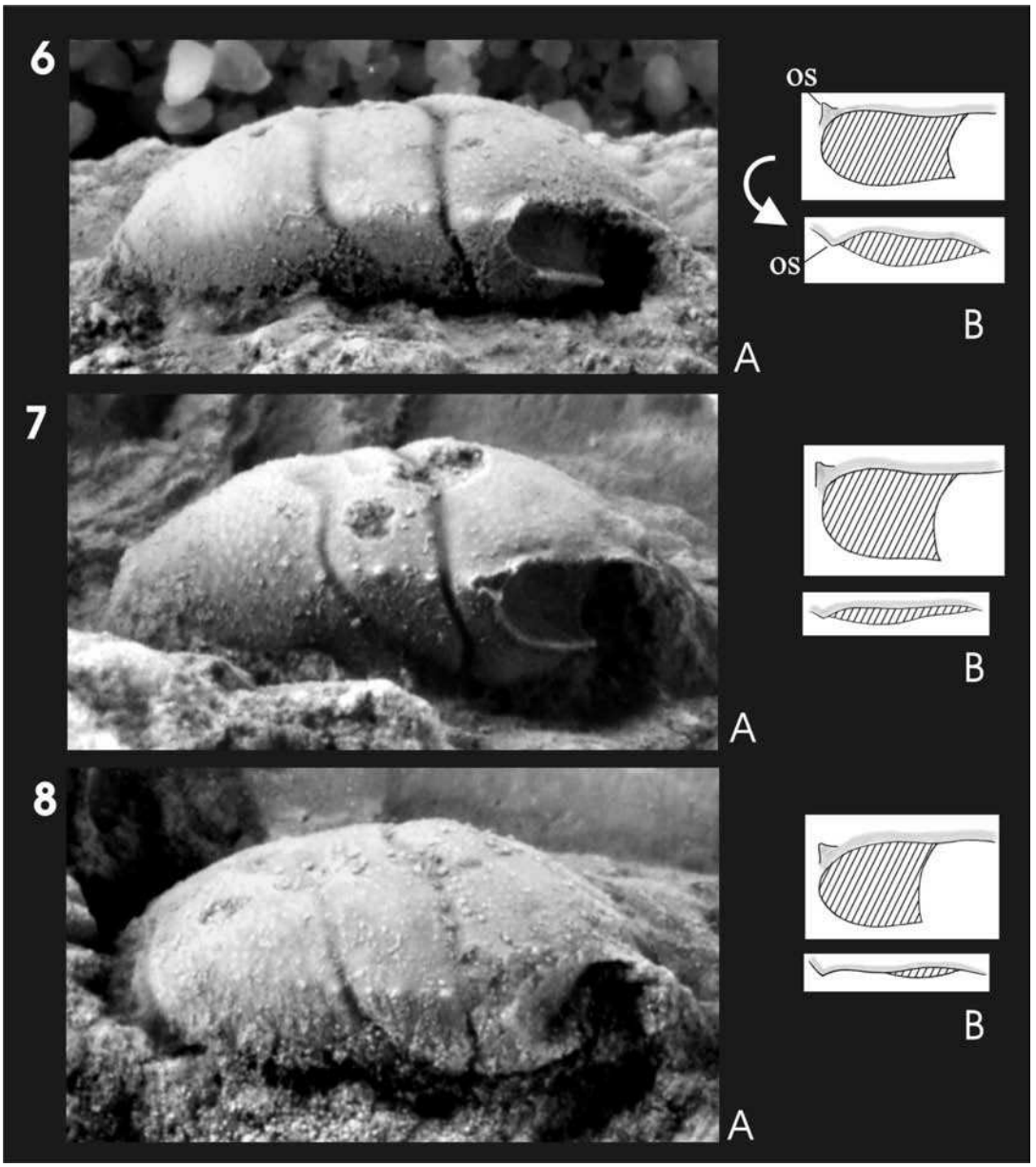
Cervical groove is strongly concave forward; there is a pair of pores lying in the middle. They are more visible than those in *G. serratus*. Postcervical groove is not always interrupted in the middle, but sometimes is only a little weaker (ex., specimens 3012 and 5415).

Branchiocardiac groove is parallel to cervical groove and weaker in lateral sections than in *G. serratus*. In the cardiac region these lateral parts end in wide, flat depressions. The continuation of the branchiocardiac groove defines posterior part of cardiac region. It is a flat, wide, weak median groove extending to the posterior margin of the carapace and dividing the branchial region into halves.

The cardiac region is triangular, with one spine on the posterior part and two nodes in front of it.

Remarks: The identity of this species is based on comparison with excellent photographs in original

Figs. 2-5. Three species of the genus *Goniodromites*. **2** – *G. narinosus*: (No. 6213, Niegowonice). **3** – *G. serratus*: (No. 1075, Niegowonice). **4** – *G. kubai* n. sp.: holotype (No. 3003, Niegowonice). **a** – specimen, **b** – rostral area in the same specimens inclined to anterior side; **c** – reconstruction of rostral area inclined as in **b**. Scale bar 1 mm. **5** – *Goniodromites*. *kubai* n. sp., further examples of rostral area inclined anteriorly; **a**, **b** – specimen 149 at two different angles; **c** – specimen 6251.



Figs. 6-8. Lateral view of carapace (A) and scheme of augenrest (B) in lateral (top) and apical view (below). **5** – *G. narinosus* (No. 6213), **6** – *G. serratus* (No. 1075, Niegowonice), **7** – *G. kubai* n. sp., holotype (No. 3003). Area of augenrest striated; upper orbital margin shaded, os – outer orbital spine.

description (Franţescu 2011, fig. 8). Although, according to this description, the lateral margins of specimens from Dobrogea are not well preserved, the traces of four lateral spines between cervical and branchiocardiac grooves are visible on the left side of the holotype (Franţescu 2011, fig. 8A). All further characters listed in original description are concordant with our specimens.

Goniodromites serratus Beurlen, 1929
Figs. 3, 7, 9A

1929 *Goniodromites serratus*. – Beurlen, p. 130, fig. 4.
1985 *Pithonoton serratum* (Beurlen). – Collins & Wierzbowski, p. 84, pl. 3, figs. 2-4, pl. 4, figs. 1-2.
2000 *Pithonoton serratum* (Beurlen). – Müller et al., fig. 18C.
2006 *Goniodromites serratus* (Beurlen). – Feldmann et al., p. 10.
2008 *Goniodromites serratus* (Beurlen). – Schweitzer & Feldmann, p. 128, pl. 2, fig. F.

Diagnosis: Carapace roughly pentagonal, longer than wide. Rostrum relatively narrow, directed downward, incised in the middle, divided by a median groove into two rounded lobes. There is an inflection at the point where the posterior margin of the rostrum meets the upper orbital margin. The augenrest is c. 1.3x as long as wide, with upper and lower orbital margins finely serrated; the lower margin expands anteriorly slightly in advance of the upper margin. Mesogastric region pyriform, with narrow anterior portion slightly longer (axially) than broad posterior portion. Epigastric regions are close to each other; the anteriormost portion of mesogastric region just protrudes between their bases.

On the lateral border of carapace there are six spines (including outer orbital spine), arranged as in Fig. 1.

Material: Specimens from Bzów: I-F/MP/**1530**/1509/08, I-F/MP/**1572**/1509/08, I-F/MP/**1611**/1509/08, I-F/MP/**1870**/1517/08, I-F/MP/**1899**/1517/08, I-F/MP/**2676**/1530/08. Specimen from Grabowa I-F/MP/**5397**/1543/09. Specimens from Niegowonice: I-F/MP/**1075**/1508/08, I-F/MP/**1095**/1508/08, I-F/MP/**3048**/1532/08, I-F/MP/**3332**/1532/08, I-F/MP/**3407**/1532/08, I-F/MP/**4591**/1534/08, I-F/MP/**4595**/1534/08, I-F/MP/**4944**/1543/09, I-F/MP/**5249**/1543/09, I-F/MP/**5262**/1543/09, I-F/MP/**5428**/1543/09, I-F/MP/**5499**/1543/09, I-F/MP/**5566**/1543/09. Specimens from Ogrodzieniec: I-F/MP/**13**/1489/08, I-F/MP/**177**/1489/08, I-F/MP/**572**/1502/08, I-F/MP/**577**/1502/08, I-F/MP/**616**/1502/08, I-F/MP/**629**/1502/08.

Dimensions: The largest measured specimen is 6.4 mm long, and the smallest – 4.29 mm long (Fig. 9A).

Additional description: Carapace is distinctly longer than wide, pentagonal, convex (Fig. 3a). Rostrum is moderately broad, directed downward, incised in the middle, divided by the median groove into two rounded lobes. The distance from the border of the rostrum to epigastric regions is longer than in *G. narinosus*, but not as long as in *G. kubai* n. sp. (Fig. 3b; compare Figs. 2b and 4b).

The augenrest is comparatively broad and short, c. 1.3x as long as wide, parallel-sided (Fig. 7). The lower orbital margin projects slightly beyond the upper margin (Fig. 7B) and hence it is visible in apical view when the carapace is laid flat in horizontal position. The upper orbital margin is curved inward in the place where the posterior margin of the rostrum and upper orbital margin meet. Both lower and upper margins of the augenrest are finely serrated. This character is visible only in the best preserved specimens (Nos. 13, 1075, 2676, 3332 and 5249). The outer half of the orbital margin is rimmed, which disappears toward the rostrum.

Carapace is moderately convex. Epigastric regions are swollen and slightly elongated (Fig. 3b, c). Mesogastric region is pyriform, with the anterior narrow part a little longer than posterior broad part. The anteriormost portion protrudes between bases of epigastric regions. The region is well defined anteriorly by hepatic grooves, and in posterior part, by the cervical groove. There is a small axial incision in the middle of posterior portion.

Posterior border of carapace is long and convex forward. The cervical groove is strongly concave forward, with a pair of pores in the middle, less visible than in *G. narinosus*. Postcervical groove is interrupted in the middle. The branchiocardiac groove extends parallel to the cervical groove in lateral sections which are deep and well marked. More medially these sections diffuse into two wide, flat, roundish depressions, from which the very shallow grooves turn posteriorly and are fused behind the cardiac region into one groove dividing the branchial regions into two halves and reaching the posterior border of the carapace.

The cardiac region is triangular. There is one spine on the posterior angle of the triangle and two nodes in both anterior angles. Carapace posteriorly narrowed; lateral borders of branchial regions are almost straight. The angle between lateral and posterior border is less rounded than in *G. narinosus*.

Remarks: *Goniodromites serratus* is known to be abundant in Oxfordian localities of Poland (Collins & Wierzbowski 1985). The diagnostic features applied by these authors for classification were based upon characters listed by Beurlen (1929; translation of original description by Feldmann et al. 2006). Among them, important were the five spines along lateral margin (apart from the outer orbital spine), which are partially visible on some photographs (Collins & Wierzbowski 1985, pl. 3, fig. 3B, pl. 4, fig. 1B). Noteworthy is also the augenrest of shape as described herein, and anterior mesogastric region protruding between bases of epigastric regions, which are slightly oval.

The identity of *G. serratus* was checked by us against *Goniodromites polyodon* Reuss, 1858 which seems to have a very similar shape when viewing a cast of the co-type in Schweitzer & Feldmann 2008, pl. 2C, and especially Franţescu 2011, fig. 6. It is now not certain whether the cited difference in the number and distribution of spines on the lateral border of carapace really exists, since we found multiple spines also in two other related species, described herein. Schweitzer & Feldmann (2008) emphasize for *G. polyodon* a characteristically long cardiac region which leaves only a small section of fused branchiocardiac groove terminating in the posterior border. When measured from the photograph of the co-type cast, the fused section is only 0.28 x the distance from the branchiocardiac groove to posterior border (ratio: CtE/BCtE in Fig. 10A). Our specimens of *G. serratus* have a shorter cardiac region, and accordingly the fused section of branchocardiac groove is longer. The calculated mean of ratio: CtE/BCtE equals 0.42 (range: 0.366-0.503), which is rather beyond the value estimated for *G. polyodon*. Therefore in our opinion the two species should remain separate until a larger sample of *G. polyodon* is examined.

Goniodromites kubai n. sp.
Figs. 4, 5, 8, 9C

Diagnosis: Carapace longer than wide, roughly pentagonal, with posterior portions rounded. The anterior part of carapace, in front of cervical groove, is longer than in *G. serratus* and *G. narinosus*. Rostrum long, directed downward, narrowing in anterior part and similar to that

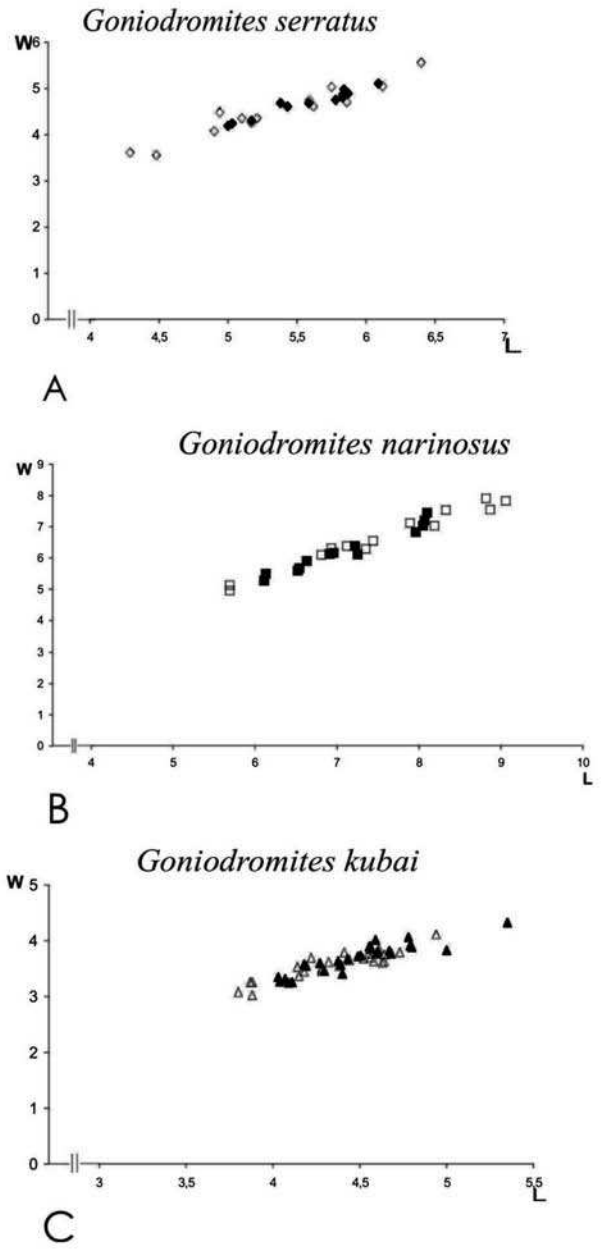


Fig. 9. Ontogenetic variation in carapace length (L) and with (W) in three species of the genus *Goniodromites*: **A** – *G. narinosus*, **B** – *G. serratus*, **C** – *G. kubai* n. sp.

of *G. dentatus*, but differing by the absence of incision in the middle of anterior border of rostrum (the character is visible in specimen bent to anterior side). The augenrest is broad and very short, only a little (1.1x) longer than wide; upper and suborbital margins are finely serrated. Epigastric regions are positioned at both sides of mesogastric region. Anterior (narrow) part of mesogastric region is distinctly longer than posterior (broad), while in *G. serratus* and *G. narinosus* these parts are almost of same length.

The spines along the lateral border of the carapace are distributed as in *G. serratus* and *G. narinosus*.

Type material: Holotype: I-F/MP/**3003**/1532/08; type locality: Niegowonice; age: middle Oxfordian (ISEA). Paratypes: I-F/MP/**123**/1489/08, I-F/MP/**622**/1502/08 from Niegowonice; I-F/MP/**1737**/1517/08, I-F/MP/**1911**/1517/08 from Bzów; I-F/MP/**149**/1489/08 and MP/6251/1588/11 from Ogrodzieniec (ISEA). Age as for holotype.

Additional material: Specimens from Bzów: I-F/MP/**1548**/1509/08,I-F/MP/**1552**/1509/08,I-F/MP/**1564**/1509/08, I-F/MP/**1600**/1509/08, I-F/MP/**1696**/1517/08, I-F/MP/**1741**/1517/08, I-F/MP/**1773**/1517/08, I-F/MP/**1818**/1517/08, I-F/MP/**1901**/1517/08, I-F/MP/**2040**/1517/08, I-F/MP/**2059**/1517/08, I-F/MP/**4639**/1534/08. From Grabowa: I-F/MP/**5378**/1543/09, I-F/MP/**5390**/1543/09. From Niegowonice: I-F/MP/**962**/1502/08, I-F/MP/**2806**/1530/08, I-F/MP/**2808**/1530/08, I-F/MP/**3028**/1532/08, I-F/MP/**3052**/1532/08, I-F/MP/**3079**/1532/08, I-F/MP/**3082**/1532/08, I-F/MP/**3089**/1532/08, I-F/MP/**3162**/1532/08, I-F/MP/**3163**/1532/08, I-F/MP/**3280**/1532/08, I-F/MP/**4514**/1534/08, I-F/MP/**4944**/1543/09, I-F/MP/**5065**/1543/09, I-F/MP/**5212**/1543/09, I-F/MP/**5240**/1543/09, I-F/MP/**5308**/1543/09, I-F/MP/**5323**/1543/09. From Ogrodzieniec: I-F/MP/**87**/1489/08, I-F/MP/**94**/1489/08, I-F/MP/**103**/1489/08, I-F/MP/**110**/1489/08, I-F/MP/**120**/1489/08,I-F/MP/**139**/1489/08,I-F/MP/**145**/1489/08, I-F/MP/**155**/1489/08, I-F/MP/**167**/1489/08, I-F/MP/**174**/1489/08, I-F/MP/**624**/1502/08, I-F/MP/**651**/1502/08, I-F/MP/**739**/1502/08, I-F/MP/**755**/1502/08 (all ISEA).

Dimensions: The largest measured specimen was 5.35 mm long, and the smallest – 3.8 mm long (Fig. 9C).

Description of material: Carapace is pentagonal and longer than wide (Fig. 4a), convex. Maximum width of carapace is across the anterior part of epibranchial regions.

Rostrum is directed downward, narrowing anteriorly and characteristically long. When the specimen is inclined anteriorly, the rostrum shows no trace of incision (Figs. 4b-c, 5) and differs in that character from *G. serratus* and *G. narinosus,* which have the rostrum distincly incised (compare Figs. 2b-c, 3b-c). Entire anterior portion of carapace from the border of rostrum to epigastric regions is longer than in *G. serratus* and *G. narinosus*, comparable only to that in *G. dentatus* (Schweitzer & Feldmann 2008, pl. 2E). It is divided by the median groove into two lobes.

The incision at the point where the posterior part of rostrum and upper orbital margin meet is less visible than in *G. serratus* and *G. narinosus* (Fig. 4c) – this character is especially distinct in the rostrum bent to anterior side (Figs. 2b, 3b, 4b). Upper and suborbital margins of the augenrest are covered with small serrations. Augenrest is short, only 1.1x longer than wide (Fig. 8B). Suborbital margin barely projects beyond upper orbital margin and is not bent outward as in *G. serratus* and *G. narinosus*, a feature clearly visible on the holotype and in best preserved specimens (ex., 755 and 1911). In the outer half the orbital margin is rimmed, which disappears toward the rostrum.

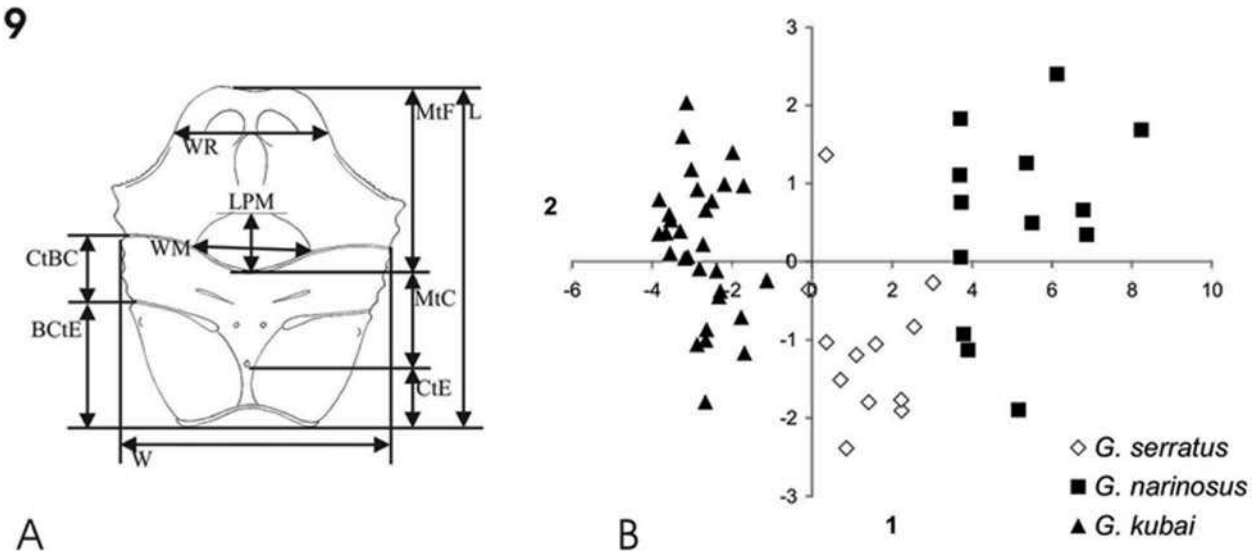


Fig. 10. Discriminant Analysis of 55 specimens of *G. serratus*, *G. narinosus*, *G. kubai* n. sp. **A** – Measurements taken for the Discriminant Analysis; **B** – plot of canonical scores (roots 1 and 2.

Epigastric regions are swollen, elongate and lie at the distance from each other on both sides of the mesogastric region which protrudes up to between them (Fig. 4c). Mesogastric region is pyriform; anterior (narrow) part is distinctly longer than posterior (broad) part. The region is clearly visible anteriorly, defined by hepatic grooves, and posteriorly by the cervical groove. A small axial incision in middle of posterior part of the mesogastric region is poorly visible.

The distibution and relative size of lateral spines on lateral border of carapace is as in both previously described species (Fig. 1B).

The cervical groove is concave forward, with a pair of pores in the middle. Cervical and branchiocardiac grooves are deep and parallel to each other laterally. Postcervical groove is not always interrupted axially, but sometimes only a little weaker (ex., specimens 167 and 4639).

Branchiocardiac groove defines posterior part of cardiac region. At the cardiac region the lateral portions of the branchiocardiac groove end in wide, flat, round depressions. The posterior continuation of the branchiocardiac groove is a flat, wide, weak median groove extending to the posterior margin of the carapace, so that the branchial region is separated into halves.

The cardiac region is triangular. There is one spine on posterior part and two nodes in front of it. Branchial regions are broad and rounded posteriorly, relatively shorter than in *G. narinosus* and, the more so, in *G. serratus.*

5. Discussion

5.1. Comparison between *Goniodromites narinosus, G. serratus* and *G. kubai* n. sp.

The differences between the three species are expressed in proportions of the carapace and of particular regions. *G. narinosus* is only a litle longer than wide, while *G. kubai* n. sp. and *G. serratus* are proportionally longer. Rostra of *G. narinosus* and *G. serratus* are distinctly incised medially, while the anterior outline of the rostrum of *G. kubai* is regularly rounded, without trace of incision. The proportions of the mesogastric region are similar in *G. serratus* and *G. kubai* in the narrow anterior portion being longer than the posterior broad one; in *G. kubai* this difference is more strongly expressed. In *G. narinosus* both portions of this region are almost equally long. Epigastric regions differ in shape and position. In *G. narinosus* the regions are in the shape of rounded swellings close to each other and positioned anteriorly to the mesogastric region. In *G. serratus* the epigastric regions are slightly elongated and partially separated by the anterior portion of the mesogastric region protruding between their bases. In *G. kubai* the epigastric regions are distinctly elongated and even more broadly separated, lying at sides of the mesogastric region.

Especially interesting are differences in the augenrest (Figs. 6-8) which conveys the length of eyestalks and eyes. The stalks and eyes combined were longest in *G. narinosus*. Such eyes may have required more support in the resting position, hence, in this species the lower margins of the augenrest protrude much more in advance of the upper margins. In *G. serratus* the augenrests are distinctly shorter, and are even shorter in *G. kubai*. Accordingly, the lower rims of the augenrests did not protrude so much, as if the reduced weight of eyes did not demand so much support from beneath.

5.2. Morphometric analyses of the three species

Width/length diagrams for carapaces of the three species treated here are presented in Fig. 9. *G. narinosus* is the largest species (length ranges 5.69-9.06 mm) and *G. kubai* – the smallest (length range: 3.8-5.35 mm). *G. serratus* is of intermediate size and its length range (4.29-6.4 mm) overlaps those of two other species. Remarkably, specimens of *G. kubai* form a small and compact group when compared to more dispersed clouds of remaining species. This is despite the fact that the number of specimens of *G. kubai* taken for analysis (49) almost twice exceeds those of *G. serratus* and *G. narinosus* (each 26 specimens).

Most complete specimens of these species were subject to the Discriminant Analysis (Fig. 10B; specimens taken to DA are marked black in Fig. 9). Three measurements appeared to have a greatest discriminant power: MtF, MtC and LPM, of which two reflect the observed differences in length of anterior portion with rostrum (MtF) and length of wider portion of the mesogastric region (LPM); MtC conveys a more or less elongated medial part of the carapace.

Again, a cloud of points representing the specimens of *G. kubai* is much smaller and more compact than in the case of *G. serratus* and *G. narinosus*.

5.3. Co-occurrence of three species of *Goniodromites*

The co-occurrence of three similar, obviously closely related species of goniodromitid crabs at several localities might seem surprising. At the first glance it might even be suspected that all these specimens may represent the same species at different ontogenic stages, regarding the overlap in size ranges (Fig. 9). This hypothesis can be safely rejected in view of pronounced differences in shape of rostral area and of the augenrest. There are no transition series in these features between the three species; our specimens fall clearly within three groups without intermediate stages.

According to known facts of biology and speciation, the presence of several related species in the same localities should be rather expected. In recent fauna usually there are more than one related species (congeners) living in same habitat. These species differ generally in genital organs, but also in some other specializations. Among the most frequent are the feeding habits which may be reflected by the shape of mouthparts and other structures used in the feeding process. Our three species differing in the shape of rostrum and the eyes probably exemplified this phenomenon.

The co-occurrence of other congeneric species of fossil brachyuran crabs is known from other localities, as the following examples document (from: Schweitzer & Feldmann 2009; Feldmann et al. 2006; Franţescu 2011). In an Oxfordian locality Dobrogea (Roumania) lived four species of *Goniodromites*: *G. serratus*, *G. bidentatus*, *G. polyodon* and *G. narinosus*. From the famous Tithonian locality Ernstbrunn (Austria) there are two species of *Abyssophthalmus* known: *A. mirus* and *A. schultzi*, two species of *Planoprosopon* (*P. heydeni*, *P. rhathamingus*), and two species of *Laeviprosopon* (*L. laculatum*, *L. grandicentrum*). In Oerlinger Tal near Ulm (Kimmeridgian; Germany) the latter genus is represented by two species, *L. laeve* and *L. sublaeve*. In Stramberk (Tithonian; Czech Republic) three species of *Cyclothyreus* co-existed: *C. strambergensis*, *C. latus* and *C. transitorius*.

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