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First report of Jurassic Anomura (Galatheoidea) and Brachyura (Dromiacea, Goniodromitidae) in Russia

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Articles

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Abstract

This is the first report of Jurassic brachyurans and anomurans from the territory of Russia. These findings come from the Upper Jurassic (Oxfordian) reef limestones of the North Caucasus. The anomuran *Gastrosacus wetzleri* von Meyer, 1851 was collected from the locality near the Urup River and is the first find of this species outside of western Europe. The dromiacean crab, *Goniodromites aliquantulus* Schweitzer, Feldmann, and Lazăr, 2007, was discovered from another locality near the Kamennomostsky village. This species was first described from the Oxfordian of Romania. Findings of fossil remains of *Goniodromites aliquantulus* and *Gastrosacus wetzleri* from the Oxfordian of the North Caucasus indicate an interconnected paleobiogeographical community of decapod faunas in the Late Jurassic in the Tethys basins.

Non-technical Summary

This is the first report of Jurassic crabs and their relatives, the squat lobsters, from the territory of Russia. These findings come from the Upper Jurassic (Oxfordian) reef limestones of the North Caucasus. The squat lobster *Gastrosacus wetzleri* von Meyer, 1851, collected from the locality near the Urup River, is the first find of this species outside of western Europe. The crab *Goniodromites aliquantulus* Schweitzer, Feldmann, and Lazăr, 2007 was discovered from another locality near the Kamennomostsky village. This species was first described from the Oxfordian of Romania. These fossil remains from the Oxfordian of the North Caucasus indicate an interconnected marine community of crabs and squat lobsters in the Late Jurassic in the Tethys basins.

Introduction

Few localities of Mesozoic fossils of Anomura and Brachyura from the vast territory of Russia have been described (Table 1). Species of Brachyura known from the Cretaceous of the Moscow Oblast (region of Central Russia including the Albian [Gavrilkovo Formation]), *Homolopsis glabra* Wright and Collins, 1972 and *Personadorippe kalashnikovi* Van Bakel et al., 2021, and *Necrocarcinus gorbenkoi* Mychko et al., 2023 described from Cenomanian rocks (Lyamino Formation) (Ilyin, 2005; Van Bakel et al., 2021; Mychko et al., 2023). The only record of Anomura from this region comes from Jurassic deposits (Volgian [= Tithonian]), by the remains of a hermit crab (Paguroidea gen. indet. sp. indet.) of poor preservation in an ammonite shell (Mironenko, 2020). A unique hermit crab, *Mutotylaspis tripudium* Fraaije et al., 2024, was recently described from a neighboring region, the Vladimir Oblast. It was discovered from an almost complete carapace and appendages found in a concretion in Lower Cretaceous (Albian) rocks (Fraaije et al., 2024). The assemblage of Lower Cretaceous crabs from Dagestan is quite interesting and includes *Levashidromites cornutus* Van Bakel et al., 2021, *Personadorippe levashiensis* Van Bakel et al., 2021, and *Vectis collinsi* Van Bakel et al., 2021, fossil remains of which were discovered in Aptian deposits (Van Bakel et al., 2021). The Cretaceous of Crimea contains a relatively high number of crab remains, which were found in various geological formations. The oldest species is *Abyssophthalmus* (?) *dzhafarberdensis* (Ilyin, 2005), described from deposits of the Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Lower Berriasian) boundary (Ilyin, 2005; Klompmaker et al., 2020). Albian crabs are represented by *Necrocarcinus bodrakensis* Levitskiy, 1974, *Necrocarcinus tauricus* Ilyin and Alekseev, 1998, and *Macroacaena yanini* (Ilyin and Alekseev, 1998) (Levitskiy, 1974; Ilyin and Alekseev, 1998; Ilyin, 2005; Van Bakel et al., 2021). Cenomanian crabs are represented only by

Table 1. Mesozoic brachyuran and anomuran occurrences from Russia. For other generic occurrence references, consult Schweitzer et al. (2012, 2023)

Family	Species	Stage and Formation/ Zone	Region	Reference	Other generic occurrences
ANOMURA					
Munidopsidae	*Gastrosacus wetzleri* von Meyer, 1851	Oxfordian	Krasnodar Krai	herein	Eastern Europe
Paguroidea	Paguroidea gen. indet. sp. indet.	Volgian (= Tithonian), *Kachpurites fulgens* biozone	Moscow	Mironenko, 2020	N/A
Paguridae	*Palaeopagurus couloni* (de Tribolet, 1874)	Upper Valanginian–Hauterivian	Crimea	Levitskiy, 1974; Ilyin, 2005	Europe; eastern USA
	Palaeopagurus? sp. indet.	Lower Hauterivian	Crimea	Ul'shin et al., 2020	Europe; eastern USA
	Orhomalus tombecki (de Tribolet, 1874)	Lower Hauterivian	Crimea	Levitskiy, 1974; Ilyin, 2005	Europe
Probeebeidae	*Mutotylaspis tripudium* Fraaije et al., 2024	Lower Albian, *Arcthoplites jachromensis* biozone	Vladimir Oblast	Fraaije et al., 2024	N/A
Brachyura					
Goniodromitidae	*Goniodromites aliquantulus* Schweitzer, Feldmann, and Lazăr, 2007	Oxfordian	Adygea Republic	herein	Europe; Japan
Longodromitidae	*Abyssophthalmus* (?) *dzhafarberdensis* (Ilyin, 2005)	Upper Tithonian– Lower Berriasian	Crimea	Ilyin, 2005; Klompmaker et al., 2020	Europe
	Levashidromites cornutus Bakel et al., 2021	Middle Aptian, Kubina Formation	Dagestan Republic	Van Bakel et al., 2021	N/A
Viaiidae	*Vectis collinsi* Bakel et al., 2021	Middle Aptian, Kubina Formation	Dagestan Republic	Van Bakel et al., 2021	Spain; UK
Telamonocarcinidae	*Personadorippe levashiensis* Bakel et al., 2021	Middle Aptian, Kubina Formation	Dagestan Republic	Van Bakel et al., 2021	N/A
	Personadorippe kalashnikovi Bakel et al., 2021	Cenomanian, Lyamino Formation	Moscow Oblast	Van Bakel et al., 2021	N/A
Homolidae	*Homolopsis glabra* Wright and Collins, 1972	Albian, Gavrilkovo Formation	Moscow Oblast	Ilyin, 2005	cosmopolitan
Necrocarcinidae	*Necrocarcinus bodrakensis* Levitskiy, 1974	Upper Albian, Mangush Formation	Crimea	Levitskiy, 1974; Ilyin, 2005; Mychko et al., 2023	Europe; Japan; Texas and New Jersey, USA N/A N/A
	Necrocarcinus tauricus Ilyin and Alekseev, 1998	Upper Albian, Mangush Formation	Crimea	Ilyin and Alekseev, 1998; Ilyin, 2005; Mychko et al., 2023	
	Necrocarcinus gorbenkoi Mychko et al., 2023	Cenomanian, Lyamino Formation	Moscow Oblast	Mychko et al., 2023	
Lyreididae	*Macroaceana yanini* (Ilyin and Alekseev, 1998)	Upper Albian, *Mortoniceras inflatum* biozone	Crimea	Ilyin and Alekseev, 1998; Ilyin, 2005	Northern Hemisphere
Palaeocorystidae	*Notopocorystes normani* (Bell, 1863)	Middle Cenomanian	Crimea	Ilyin, 2005	UK; Madagsacar
Orithopsidae	*Silvacarcinus cisuralicus* Mychko et al., 2024	Campanian	Orenburg Oblast	Mychko et al., 2024	Belgium

Notopocorystes normani (Bell, 1863) (Ilyin, 2005). Anomurans of Crimea are found in the Lower Cretaceous (Valanginian–Hauterivian) and are represented by the remains of *Orhomalus tombecki* (de Tribolet, 1875), *Palaeopagurus couloni* (de Tribolet, 1874), and *Palaeopagurus*? sp. indet. (Levitskiy, 1974; Ilyin, 2005; Ul'shin et al., 2020). Recently, the authors of this paper described a new brachyuran species, *Silvacarcinus cisuralicus* Mychko et al., 2024, from the Upper Cretaceous (Campanian) in the Orenburg Oblast (Mychko et al., 2024).

This is the first scientific publication on Jurassic brachyurans and anomurans from Russia. Geographically, the closest region to Russia with Jurassic (Callovian) crabs was Lithuania, from which the species *Tanidromites lithuanicus* Schweigert and Koppka, 2011 was described.

Jurassic brachyurans and anomurans are abundant and diverse from European localities and have received considerable attention in recent years. Jurassic brachyuran and anomuran localities in southern Germany include localities of the

Pliensbachian (Förster, 1986; Schweigert et al., 2013), Middle Callovian (Pleistocene glacial boulder; Schweigert and Koppka, 2011), Kimmeridgian (Dietl and Schweigert, 2001; Garassino et al., 2005; Van Bakel et al., 2008; Feldmann and Schweitzer, 2009; Schweigert and Koppka, 2011; Lang et al., 2017; Schweigert, 2021), and Tithonian (Paulsen, 1964; Garassino et al., 2005). Jurassic crabs from France are represented by several localities from the Middle and Upper Jurassic. A detailed list of these taxa and their localities in this region has been provided in several recent following works (Krobicki and Zatoń, 2008; Van Bakel and Guinot, 2023). Anomurans and brachyurans have been described from the Bajocian of northern Switzerland (Förster, 1985). Oxfordian and Kimmeridgian brachyurans from Switzerland were also reported (Étallon, 1859, 1861). In northeastern Italy, the remains of crabs have been discovered and are confined to the Oxfordian–Kimmeridgian limestones of the Fonzaso Formation (De Angeli and Garassino, 2006). Dromiacean crabs are reported from Lower Callovian deposits in Austria (Krobicki and Zatoń, 2008, 2016; Stolley, 1914). A high diversity of Anomura and Brachyura has been found in the Tithonian (Ernstbrunn Limestone) in Austria, documented in several works (Bachmayer, 1947; Schweitzer and Feldmann, 2009; Schweitzer et al., 2012, 2023; Robins et al., 2013). Pliensbachian, Aalenian, and Bathonian brachyurans and anomurans have been reported from England (Woodward, 1868, 1907; Withers, 1932; Krobicki and Zatoń; 2008).

From eastern Europe, there are a number of localities of Jurassic anomurans and brachyurans in southern Poland. These localities are represented by Bajocian and Bathonian (Krobicki and Zatoń, 2008), Callovian (Krobicki and Zatoń, 2008), Oxfordian (Collins and Wierzbowski, 1985; Trammer, 1989; Garassino and Krobicki, 2002; Van Bakel et al., 2008; Starzyk et al., 2012), and Tithonian rocks (Patrulius, 1966; Schweitzer et al., 2012, 2023). From Slovakia, brachyurans and anomurans were described from Middle Oxfordian limestones (Hyžný et al., 2011); anomurans were also described from the Kimmeridgian–Tithonian of Slovenia (Gašparič et al., 2020). Several Tithonian anomuran and brachyuran localities are known from the Czech Republic, notably from the Štramberk Limestones (Moericke, 1889; Blaschke, 1911; Kummel, 1956; Bachmayer, 1959; Schweitzer and Feldmann, 2009; Schweitzer et al., 2012, 2023). A large number of localities and taxa of Jurassic decapods (Anomura and Brachyura) come from Romania, including Oxfordian (Feldmann et al., 2006; Schweitzer et al., 2007; Franțescu, 2011), Oxfordian–Kimmeridgian (Schweitzer et al., 2017), and Tithonian deposits (Patrulius, 1959; Muțiu and Bădăluță, 1971; Schweitzer et al., 2012, 2023; Robins et al., 2016).

The easternmost findings of Jurassic crabs are confined to China and Japan. From China, crabs are known from Tibet (Zhamunaqu Formation; Smith and Xu, 1988). Dromiacean crabs have been found in the Upper Kimmeridgian–Lower Tithonian sandstones of the Nakanosawa Formation in Japan (Kato et al., 2010) and several Upper Jurassic species of prosopid crabs are known from Torinosu Group (Karasawa and Kato, 2007).

The southernmost Jurassic brachyurans were discovered in the Bajocian Lugoba Formation in Tanzania and are represented by a number of taxa, including *Prosopon* sp. indet., *Gabriella lugobaensis* (Förster, 1985), and others (Förster, 1985; Krobicki and Zatoń, 2008).

This brief overview of Jurassic decapod anomuran and brachyuran occurrences demonstrates that although they are known from most areas of Europe, occurrences in Russia have until now been absent. This report fills this gap in knowledge of these organisms and establishes that the Russian fauna has close affinities with those of southeastern Europe.

Locality and geological setting

The decapod fossils described in this paper were found in two localities located in the Adygea Republic and Krasnodar Krai (Fig. 1). These localities are both confined to outcrops of Oxfordian limestone, which is common in the region.

Dachovskaya–Kamennomostsky (Fig. 1.4). In the Belaya River Valley, between the Guzeripl' village and the Kamennomostsky village, rich fossil remains of Callovian and Oxfordian deposits have been found. There, south of the Kamennomostsky village, near the recreation center 'Chalet Dakh' (Fig. 1.4; 44°16'08.2"N, 40°13'22.4"E, WGS84), in crushed limestone, amateur paleontologist Ksenia Belikova from 24–26 July 2023 discovered fossils of various invertebrates (Fig. 2.5, 2.6) including crab carapaces. The crushed stone was extracted from limestones exposed in the Belaya River Valley and mined in a quarry south of the Kamennomostsky village.

Coral limestones were first discovered and described there by Nikshich in 1915. In that work, he indicated the presence of three 'zones' with fauna: (1) light-colored coralline limestone with various bivalves, brachiopods, and corals; (2) layered yellow limestone almost devoid of fossils; (3) limestone with flint nodules and remains of sponges, brachiopods, crinoids, and sea urchins, as well as ammonites (Nikshich, 1915, p. 517).

The most recent and complete description of these deposits near the Kamennomostsky village was made by Lominadze in 1982. He identified six layers (Lominadze, 1982, fig. 64), of which there are four Callovian terrigenous layers and two early Oxfordian limestone layers. Lominadze (1982) noted a large number of ammonite shells in the deposits under discussion.

Later authors (Kiselev et al., 2013) noted that ammonites from these deposits have never been depicted. Kiselev (2022) provided a brief description of the Callovian-Oxfordian boundary section studied in several outcrops along the road running west of the Belaya River from the Kamennomostsky village and the Dakhovskaya village to the Lago-Naki Plateau. In that work, it was noted that Layer 3, represented by light-colored limestone with abundant remains of sponges, solitary corals, serpulids, terebratulides, and sea urchins, contains remains of the ammonite *Cardioceras* (*Scarburgiceras*) *scarburgense* (Young and Bird, 1828). According to this ammonite species, Layer 3 can be attributed to the lowest biostraton of the Oxfordian stage—the *scarburgense* biohorizon. Above Layer 3 there is a multimeter layer of rhythmically alternating sponge-algal limestones and silts, in which no ammonites were found (Kiselev, 2022, p. 336).

Urup River (Fig. 1.5). In the area of the Gusarovskoye village (44° 34'56.194"N, 41°24'57.485"E, WGS84) on the Urup River, in crushed limestone (as in the first locality), amateur paleontologist Maxim Sukhot'ko discovered fossil remains of Jurassic invertebrates in 2020, including the anomuran carapace described in this paper, as well as, later, the brachyuran *Goniodromites aliquantulus* Schweitzer, Feldmann, and Lazăr, 2007, the same species as from the previous locality (Dachovskaya–Kamennomostsky) on the Belaya River. The place of extraction of this crushed stone is located near the Bolshoi Zelenchuk River.

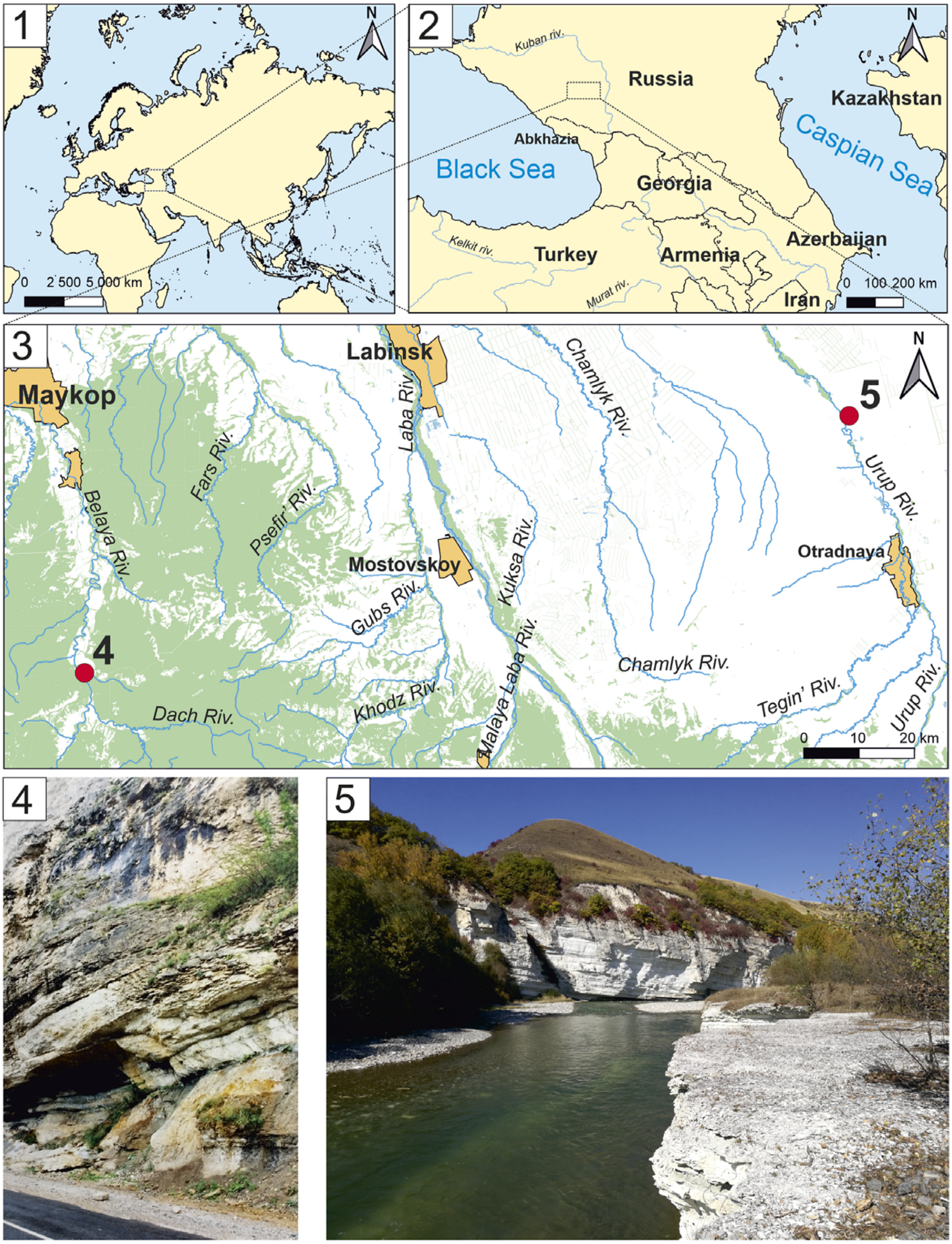

Figure 1. Localities of described decapods of North Caucasus: (**1**) schematic map of the Eastern Hemisphere; (**2**) schematic map of the Caucasus and Transcaucasia; (**3**) terrain map of the North Caucasus with localities (**4**) and (**5**) (Republic of Adygea and Krasnodar Krai, Russia); (**4**) Dachovskaya–Kamennomostsky, Oxfordian limestone near the Kamennomostsky village (photo by D. Kiselev); (**5**) Urup River, Oxfordian limestone on Bolshoi Zelenchuk River (photo by M. Sukhot'ko).

Upper Callovian–Oxfordian bioherms are widely developed in this region. They are separated by beds of layered limestone, often alternating with marls, and due to their massive composition, they are clearly distinguished in relief (Loginova, 1964). According to Rostovtsev et al. (1992), these deposits are included in the Herpegem Formation. At the base of the Herpegem Formation lies a basal horizon of limestone conglomerates and brecciated limestones, which to the east of the watershed of the Bolshaya Laba and Urup rivers is mixed with sandstones and gravelites. Above it is a layer of limestone, underlain by interlayers of marls, and in the middle part there are massive dolomitized limestones, which in places contain large reef bioherms mentioned by Loginova (1964). These reef bodies often contain corals, brachiopods, ammonites, and other fossil fauna (Figs. 2.1–4).

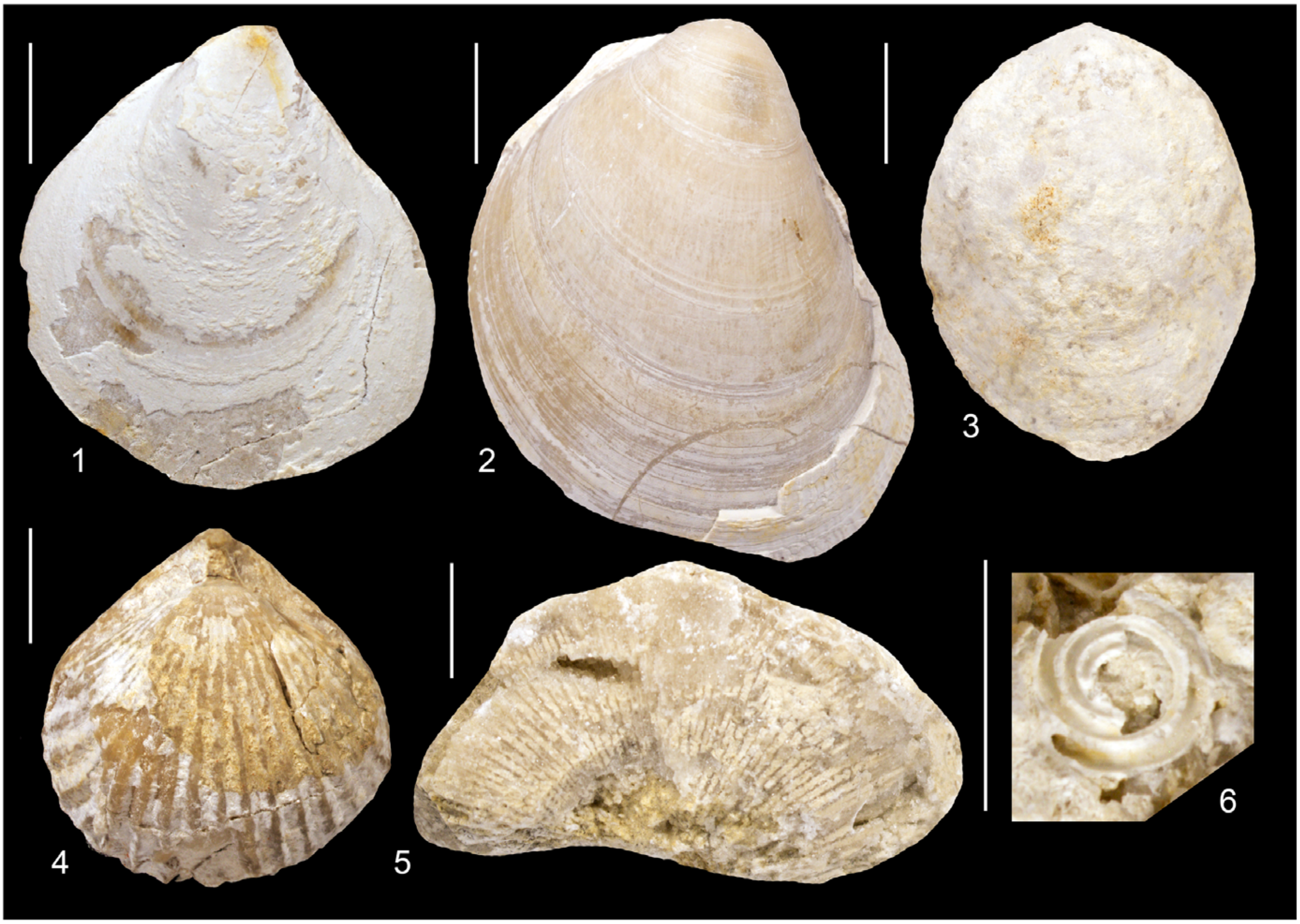

Figure 2. Fossil remains from deposits with described decapods of North Caucasus: (**1–4**) collected from locality near Urup River: (**1, 2**) bivalves, MWO 1 no. 12877, 12878; (**3**) terebratulid brachiopod, MWO 1 no. 12874; (**4**), rhynchonellid brachiopod, MWO 1 no. 12880; (**5, 6**) collected from locality near the Kamennomostsky village: (**5**) fragment of hexacoral, MWO 1 no. 12873; (**6**) serpulid annelid worm, MWO 1 no. 12879. Scale bars = 1 cm.

Materials and methods

Abbreviations. CaW = width of cardiac region; CL = maximum carapace length; CW = maximum carapace width; GH = length of gastric region; GW = width of the gastric region; L = length of carapace excluding rostrum; LR = total length of carapace including rostrum; MW = maximum mesogastric width; OW = orbital width; PW = posterior width; R = length of rostrum; RW = rostral width; TW = total width of anterior margin; UW = width of urogastric region; W = maximum width.

Repositories and institutional abbreviations. MWO = Museum of the World Ocean, Kaliningrad, Russia; LPBIIIart = Laboratory of Paleontology, Department of Geology and Paleontology, University of Bucharest, Romania; SNSB-BSPG = Bayerische Staatssammlung für Paläontologie und Historische Geologie, München (Munich), Germany.

Systematic paleontology

We follow the classification published in Treatise Online for Dromiacea and Galatheoidea (Schweitzer et al., 2012, 2023, respectively).

Order **Decapoda** Latreille, 1802
Infraorder **Anomura** MacLeay, 1838
Superfamily **Galatheoidea** Samouelle, 1819
Family **Munidopsidae** Ortmann, 1898
Genus ***Gastrosacus*** von Meyer, 1851

Type species. *Gastrosacus wetzleri* von Meyer, 1851.

Other species. *Gastrosacus aequabus* Robins et al., 2013; *Gastrosacus carteri* Van Straelen, 1925; *Gastrosacus eminens* (Blaschke, 1911), originally as *Galathea* Fabricius, 1793; *Gastrosacus ernstbrunnensis* Bachmayer, 1947; *Gastrosacus*? *latirostris* (Beurlen, 1929), originally as *Gastrosacus*; *Gastrosacus levocardiacus* Robins et al., 2013; *Gastrosacus limacurvus* Robins et al., 2013; *Gastrosacus meyeri* (Moericke, 1889), originally as *Galathea*; *Gastrosacus pisinnus* Robins et al., 2013; *Gastrosacus raboeufi* Fraaije et al., 2019; *Gastrosacus robineaui* (de Tribolet, 1874); *Gastrosacus straeleni* (Ruiz de Gaona, 1943); *Gastrosacus torosus* Robins et al., 2013; *Gastrosacus tuberosiformis* (Lörenthey in Lörenthey and Beurlen, 1929), originally as *Galatheites* Balss, 1913; *Gastrosacus tuberosus* (Remeš, 1895), originally as *Galathea*; and *Gastrosacus ubaghsi* (Pelseneer, 1886), originally as *Galathea*.

Diagnosis. As by Robins et al. (2013, p. 181).

Gastrosacus wetzleri von Meyer, 1851
Figure 3

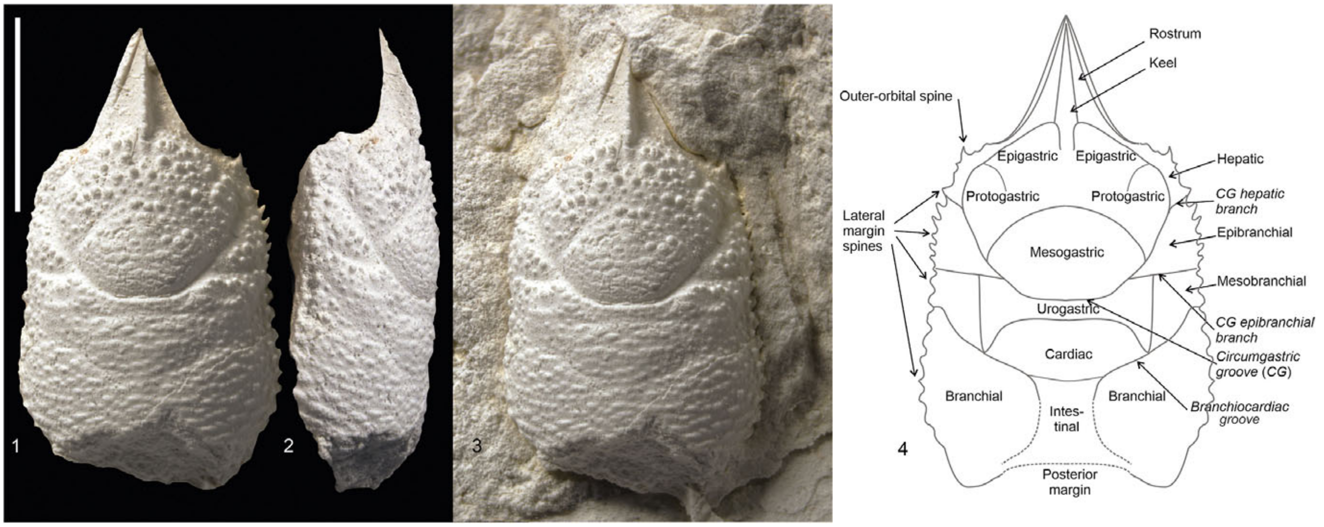

Figure 3. *Gastrosacus wetzleri* von Meyer, 1851, almost complete carapace, MWO 1 no. 12876, from crushed limestone near the Urup River, district of the Gusarovskoye village, Krasnodar Krai, Russia; Oxfordian, Upper Jurassic: (**1**) dorsal view; (**2**) left lateral view; (**3**) the specimen in the rock; (**4**) schematic of carapace morphology. Scale bars = 5 mm (**1, 2**).

1851 *Gastrosacus wetzleri* von Meyer, p. 677.
1854 *Gastrosacus wetzleri*; von Meyer, p. 51, pl. 10, figs. 3, 4.
1857 *Prosopon aculeatum* von Meyer, 1857; Quenstedt, p. 779, pl. 95, figs. 46–47.
1860 *Gastrosacus wetzleri*; von Meyer, p. 219, 220, pl. 23, fig. 34.
1868 *Prosopon aculeatum*; Quenstedt, p. 315, pl. 26, fig. 14.
1898 *Gastrosacus wetzleri*; Carter, p. 18, pl. i, fig. 3a, b.
1925 *Gastrosacus Carteri* 'von Meyer, 1851'; Van Straelen, p. 299, 300, fig. 135.
1925 *Gastrosacus Wetzleri*; Van Straelen, p. 300.
2011 *Gastrosacus wetzleri*; Klompmaker et al., p. 228.
2013 *Gastrosacus wetzleri*; Robins et al., p. 167, 168, 179, 181, 182, 184, 188, 226, 242, 243, pls. 6.11, 7.1.
2013 *Gastrosacus carteri* Van Straelen, 1925; Robins et al., p. 184, fig. 7.9.
2014 *Gastrosacus wetzleri*; Fraaije, p. 123, fig. 3A–C.
2015 *Gastrosacus wetzleri*; Robins et al., p. 87–89, figs. 2, 3.
2023 *Gastrosacus wetzleri*; Schweitzer et al., p. 14, fig. 8.5

Neotype. An almost complete carapace, SNSB-BSPG IX 683; uppermost Kimmeridgian, Upper Jurassic; Oerlinger Tal near Ulm, Germany; designated by Robins et al. (2015, p. 89).

Diagnosis. As by Robins et al. (2015, p. 87).

Occurrence. Upper Kimmeridgian (see Robins et al., 2015) of Germany–Oxfordian of England (see Carter, 1898; Robins et al., 2015) and Russia (crushed limestone near the Urup River, near the Gusarovskoye village, Krasnodar Krai; the limestone was extracted near the Bol'shoy Zelenchuk River in the Krasnodar Krai).

Description. Carapace longitudinally subrectangular, tapering very slightly from posterior to anterior, weakly convex longitudinally and transversely, CL/TW 1.7, CL/MW 1.29. Rostrum relatively wide, long in proportion to carapace, slightly deflected downward; keel of rostrum high, visible; lateral margins of rostrum angling slightly toward each other, converging to a point; lateral edges limited by groove and swelling. Orbital margin rimmed. Carapace bearing triangular outer orbital spine, small, curved toward rostrum. Several small spines on orbital margin. Lateral margin straight with at least 16 very small spines; these sharp, curved toward anterior carapace. Circumgastric groove pronounced, deep, separating urogastric from mesogastric region. Groove horizontal in central part, but curving forward at epibranchial furrow. There, circumgastric groove dividing into hepatic branch posteriorly and epibranchial branch anteriorly. Hepatic branch continuation of circumgastric groove, more obvious and deeper than epibranchial branch. Tubercles round and large in anterior mesogastric region, flattened in posterior mesogastric region, turning into wrinkled texture. Epigastric and protogastric regions small, steep, separated by barely noticeable groove not reaching middle regions. Hepatic region very small, flattened. Epibranchial region behind it much larger, wedge-shaped.

Surface of carapace on epibranchial, hepatic, epigastric, and protogastric regions covered with large tubercles. Largest tubercles located toward lateral margin and closer to rostrum. Urogastric region very narrow, widening slightly laterally, separated from cardiac region by faint groove; surface covered with small transversely oblong tubercles, more reminiscent of wrinkles. Mesobranchial regions subrectangular, small. Cardiac region flattened, subcrescent shaped, larger than urogastric. Branchial regions very large, covered with oblong tubercles. Posterior margin possibly rimmed with concave inflection. Ventral surface and appendages not preserved.

Material examined. An almost complete carapace, MWO 1 no. 12876.

Measurements (in mm). LR 11.5; L 8.8; R 2.7; GH 4.1; RW 2.7; OW 4.8; TW 5.3; GW 5.6; UW 3.9; CaW 4; W 6.8; L/W 1.29; L/TW 1.7.

Remarks. This specimen is very similar to various specimens of *Gastrosacus wetzleri* from the Upper Jurassic of Germany, including the neotype, in its carapace ornamentation and the shape of the rostrum.

Infraorder **Brachyura** Linnaeus, 1758
Section **Dromiacea** De Haan, 1833
Superfamily **Homolodromioidea** Alcock, 1900
Family **Goniodromitidae** Beurlen, 1932
Genus ***Goniodromites*** Reuss, 1858

Type species. Goniodromites bidentatus Reuss, 1858, by subsequent designation (Glaessner, 1929).

Other species. Goniodromites aliquantulus Schweitzer, Feldmann, and Lazăr, 2007; *Goniodromites complanatus* Reuss, 1858; *Goniodromites cenomanensis* (Wright and Collins, 1972); *Goniodromites dacica* (von Mücke, 1915); *Goniodromites dentatus* Lörenthey in Lörenthey and Beurlen, 1929; *Goniodromites hirotai* Karasawa and Kato, 2007; *Goniodromites kubai* Starzyk et al., 2012; *Goniodromites laevis* (Van Straelen, 1940); *Goniodromites narinosus* Franțescu, 2011; *Goniodromites polyodon* Reuss, 1858; *Goniodromites sakawense* Karasawa and Kato, 2007; *Goniodromites transsylvanicus* (Lörenthey in Lörenthey and Beurlen, 1929).

Diagnosis. As by Schweitzer et al. (2012, p. 4).

Goniodromites aliquantulus Schweitzer, Feldmann,
and Lazăr, 2007
Figure 4

2007 *Goniodromites aliquantulus* Schweitzer, Feldmann, and Lazăr, p. 107, fig. 4.1.
2007b *Goniodromites aliquantulus*; Schweitzer and Feldmann, p. 126, fig. 2G.
2009 *Goniodromites aliquantulus*; Schweitzer et al., p. 6.
2010 *Goniodromites aliquantulus*; Schweitzer et al., p. 59.
2012 *Goniodromites aliquantulus*; Starzyk et al., p. 145.
2015 *Goniodromites aliquantulus*; Hyžný et al., p. 639.

Holotype. An almost complete carapace, LPBIIIart 0150; Oxfordian, Upper Jurassic; WP123, Gura Dobrogei, Romania; by original designation.

Diagnosis. As by Schweitzer et al. (2007, p. 107, 108).

Occurrence. Oxfordian, Upper Jurassic; crushed limestone near the Kamennomostsky village, Maikop district, Republic of Adygea, Russia, as well as Gura Dobrogea (Schweitzer et al., 2007).

Description. Carapace hexagonal, elongated, narrowing anteriorly and posteriorly. Greatest width of carapace occuring in epibranchial regions. Cephalic region, measured from anterior to cervical groove along midline, constituting half of total carapace length. Rostrum bilobed, wide; frontal margins continuous with orbital margin. Outer-orbital angle as well-developed spine. Outer orbital edge with row of small spines. Second large spine posterior to outer-orbital spine. Margins of epibranchial regions each containing four small spines. Margins of branchial regions in anterior part with small spines, at least six but total number unknown. Cervical groove strongly developed, deep, wide, continuous across axis; lateral segment at angle of 80° to axis. Postcervical groove clear, deep, corresponding in width to mesogastric region. Greatest depth of postcervical groove located closer to margins of carapace; in central part barely noticeable. Branchiocardiac groove strongly developed laterally, less strongly developed in axial direction, continuous across axis. Lateral segments of branchiocardiac groove merging posteriorly with cardiac region, continuing to intersect with posterior margin. Segments of branchiocardiac groove barely noticeable in cardiac region. Epigastric regions spherical, small, located near rostrum, with apices directed toward each other. Mesogastric region clearly visible in both posterior and anterior parts; posterior part subtriangular, slightly swollen, bounded by pair of small grooves disappearing at approximate midlength of protogastric region; anterior part located between epigastric regions, elongated along axis of carapace. Protogastric and hepatic regions confluent, slightly swollen, separated from mesogastric region in anterior and posterior parts. Epibranchial regions slightly swollen, laterally elongated, bounded by branchiocardiac and cervical grooves; postcervical groove extending through epibranchial region. Cardiac region subtriangular, slightly swollen, merging posteriorly with flattened large branchial regions. Remainder of branchial regions broad, poorly ornamented, undifferentiated. Height of carapace highest in cardiac region. Posterior margin of carapace wide, entire, curved toward anterior part. Dorsal carapace ornamented with small, rough rows of tubercles over entire surface; largest tubercles closer to margins of carapace.

Material examined. Two almost complete carapaces, MWO 1 nos. 12875-1, 12875-2.

Measurements. Measurements (in mm) taken on specimens of *Goniodromites aliquantulus* are presented in Table 2.

Remarks. The new specimens are referred to *Goniodromites aliquantulus* based upon their longer-than-wide carapace, weak dorsal ornamentation, and short metagastric region. Other species are more equal in terms of length and width (*Goniodromites bidentatus*, *Goniodromites cenomanensis*, *Goniodromites laevis*, *Goniodromites polyodon*) and all other referred species have larger granules or scabrous ridges on the dorsal carapace, which *Goniodromites aliquantulus* lacks. The holotype of *Goniodromites aliquantulus*, described by Schweitzer et al. (2007, fig. 4.1), has no front part of the carapace. The material that we describe expands the understanding of the morphology of this species, and in particular, we can now say that the rostrum of *Goniodromites aliquantulus* is bilobed and wide. We also note that the new specimens of this species are significantly larger than the holotype from Romania. However, the ratios of measurement parameters between Caucasian specimens and the holotype are approximately the same (Table 2). These measurements also show small variability in the ratios of the parameters. For example, the ratio of length of carapace to maximum carapace width in two Caucasian specimens is 1.08 in the large specimen and 1.22 in the small one. This value roughly corresponds to the ratio of these parameters in the holotype (Table 2). We consider these variations as intraspecific variability.

Discussion

As previously noted, many researchers (Krobicki and Zatoń, 2008; Fraaije et al., 2013; Schweigert, 2021; Van Bakel and Guinot, 2023) have shown that brachyuran fossils in the Middle Jurassic are quite rare. The same is observed in the geological record of Anomura, in particular for Paguroidea, which has similarly high diversity but is recorded only in the Tithonian (Fraaije et al., 2022).

However, in the Late Jurassic, coral and sponge-microbial reefs began to spread widely, especially confined to the edge of the warm waters of the Tethys Ocean. Therefore, in deposits of this

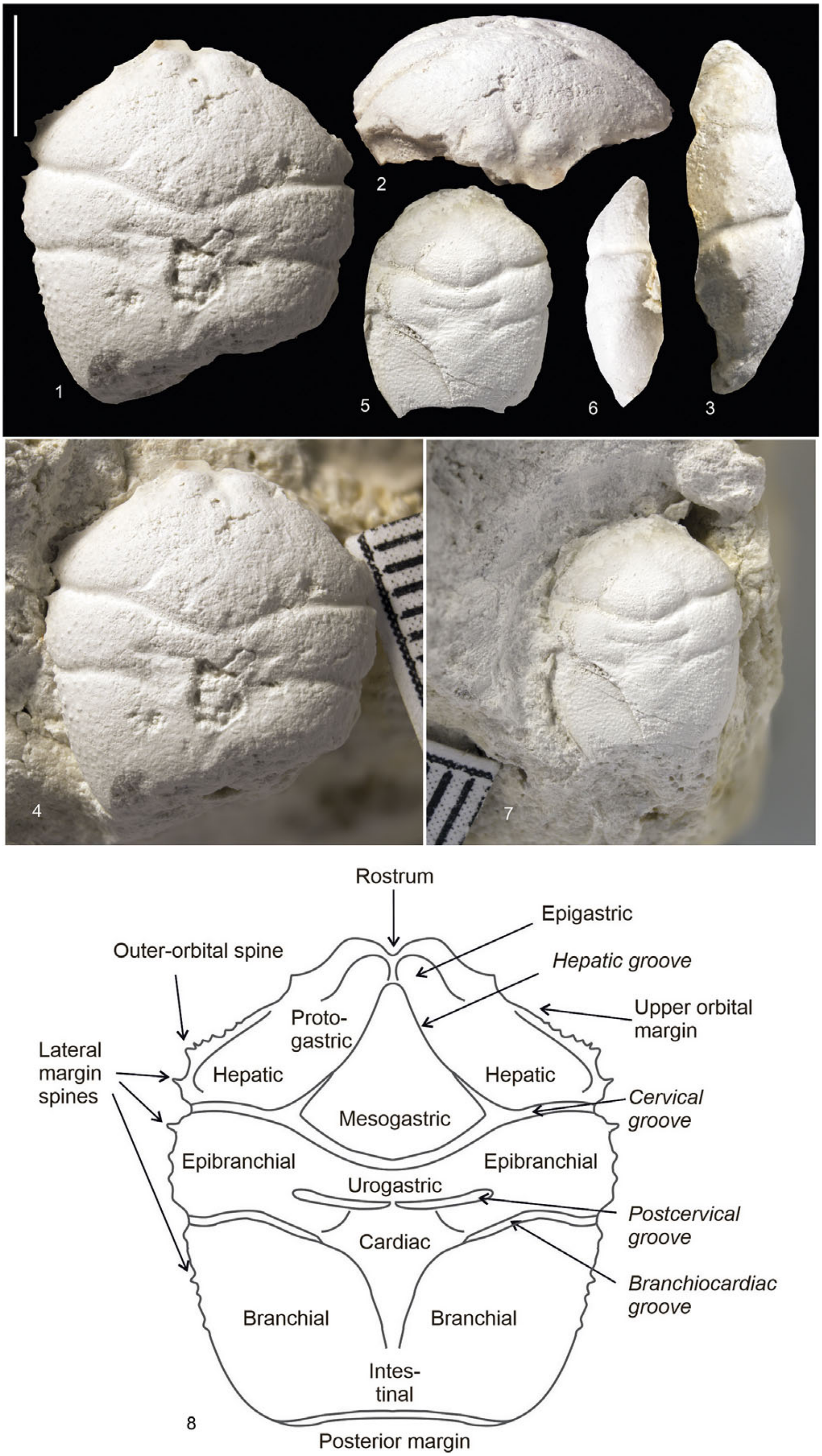

Figure 4. *Goniodromites aliquantulus* Schweitzer, Feldmann, and Lazăr, 2007, collected from crushed limestone near the Kamennomostsky village, Maikop district, Republic of Adygea, Russia; Oxfordian, Upper Jurassic: (**1–4**) MWO 1 no. 12875-1: (**1**) dorsal view; (**2**) anterior view; (**3**) left lateral view; (**4**) the specimen in the rock; (**5–7**) MWO 1 no. 12875-2: (**5**) dorsal view; (**6**) right lateral view; (**7**) the specimen in the rock; (**8**) schematic of carapace morphology. Scale bar = 5 mm.

Table 2. Measurements (in mm) of specimens of *Goniodromites aliquantulus* Schweitzer, Feldmann, and Lazăr, 2007

Specimen	CL	CW	MW	PW	RW	CL/CW	CW/MW	CW/RW
Holotype, LPBIIIart 0150	> 4.6	4.1	1.8	2.1	< 1.4 (?)	1.12	2.27	~3
MWO 12875–1	> 15	13.9	5.7	~9.5	4.6	1.08	2.43	3.02
MWO 12875–2	9.6	7.9	3.3	6	2.6	1.22	2.39	3.04

geological age, especially in southern Europe, siliceous sponge-microbial and coral facies are widespread. Many researchers (Klompmaker et al., 2013, 2020; Schweigert, 2021) have linked the diversification of crabs in these paleobiogeographic areas to the presence of reefs.

Findings of *Goniodromites aliquantulus*, as well as other species of *Goniodromites*, are often confined to carbonate prereef and reef facies. Various species of *Goniodromites* from the Jurassic and Cretaceous of Europe and Asia (Japan) demonstrate that the intervening deposits are not limited to a single type. For example, Klompmaker et al. (2012, table 1) noted a wide diversity of ecological settings for this genus: sponge microbial limestones, coral reefal limestones, sponge limestones, limestones (without specification), and sands/marls/chalks and shale. Thus, *Goniodromites* was apparently a eurytypic crab and lived in a wide variety of environments. For example in Romania, Schweitzer et al. (2017) noted that the depositional conditions of the rocks in which *Goniodromites* species occur are variable and can be represented by sponge limestone, coral limestone, algal limestone, and even siliciclastic facies. However, it is interesting that the Romanian *Goniodromites aliquantulus*, like the Caucasian occurrence, comes from sponge limestone of Oxfordian age. Thus, *Goniodromites* is a widespread, commonly occurring genus in Jurassic rocks of Europe, and it has been recovered from coral, sponge-algal, and nonreefal limestones as well as lithographic limestones (Schweitzer and Feldmann, 2007a; Feldmann et al., 2016).

The discovery of *Gastrosacus wetzleri* expands the geographic distribution of this species, previously found only in the Kimmeridgian of Germany and the Oxfordian of England (Robins et al., 2015). This suggests that both *Goniodromites* and *Gastrosacus* were eurytypic genera and survived in many types of environments. This could explain why both genera are so speciose and widespread in the Jurassic and Cretaceous of Europe. Findings of fossil remains of the brachyuran *Goniodromites aliquantulus* and the anomuran *Gastrosacus wetzleri* from the Oxfordian in the North Caucasus indicate an interconnected paleobiogeographical decapod fauna in the Late Jurassic in the Tethys basins.

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