

New findings of Decapoda (Crustacea) in the Callovian of the Ryazan region (Central European Russia)

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Non-technical Summary.—There are very few articles dedicated to the study of crustacean remains in the marine sediments of the Mesozoic despite the widespread distribution of such remains in Central European Russia. This research is the first general study on decapods of the Ryazan region of Central European Russia and is focused on the Callovian of that area. The Ryazan region is renowned for its large number of outcrops and high concentration of well-preserved marine decapod fossils. Two genera and five species of crustaceans are identified for the first time from Central European Russia. In addition, diagnostic signs of previously noted taxa are factually discussed.

Abstract.—The decapod crustaceans of Central European Russia have been the subject of studies since the nineteenth century, and the only species, *Eryma quadriverrucatum* Trautschold, 1866 (Erymidae), has been found in the Callovian to the Oxfordian of that region. The present paper discusses the new exceptional findings of Solenoceridae, Glypheidae, and Mecochiridae from the upper Callovian sites of the Ryazan Region. The previously reported presence of *Archeosolenocera* sp. is confirmed in detail; *Glypheopsis* aff. *G. etalloni* (Oppel, 1861) and *Eumorphia* sp. are noticed for the first time for this area. Modern identification of erymids is reported: *Eryma* aff. *E. ventrosum* (von Meyer, 1835), *E. ornatum* (Quenstedt, 1858), and *Stenodactylina insignis* (Oppel, 1862) are noted in addition to *E. quadriverrucatum*. These findings address the gaps in the fragmented knowledge about the decapod fauna of Central European Russia and exhibit a differentiation of the local Russian decapod assemblage from those of Western Europe. The decapod community of the Ryazan region is considered to be associated with soft substrates of upper sublittoral zone.

Introduction

European decapods from the Middle Jurassic are a highly diverse and abundant group of invertebrates (Schweitzer and Feldmann, 2014). The excellent preservation of representative samples of the rich decapod fauna is well known for Dendrobranchiata Bate, 1888, Erymida Van Straelen, 1925, Glypheoidea von Zittel, 1885, and other groups from the La Voulte Lagerstätte (Callovian of Central France) (Etter, 2002; Charbonnier et al., 2010; Chény et al., 2023). Crônier and Courville (2004) have described the local Bajocian-Oxfordian decapod fauna of erymids and pagurids from Etrochey, Northern France. Several recent studies were dedicated to crustaceans from the Kimmeridgian and Tithonian of Solnhofen, Germany, where the richest crustacean assemblage was discovered (Schweigert and Garassino, 2003, 2004; Garassino and Schweigert, 2006). Active investigations of erymid and glypheid lobsters significantly enriched the available evidence of crustacean diversity (Charbonnier et al., 2013, 2014a; Schweigert, 2013; Devillez and Charbonnier, 2017, 2019).

Whereas the crustacean assemblages of Western Europe were thoroughly studied, those of European Russia got little

attention, despite the high abundance of the crustaceans discovered in the Middle and Late Jurassic in the region. There are only a few reliable publications (Trautschold, 1866; Lahusen, 1894; Gerasimov, 1955; Gerasimov et al., 1995, 1996) describing four species of Erymidae and Glypheidae. According to Gerasimov's (1955) work, the only species, Eryma quadriverrucatum Trautschold, 1866, is found in the middle–upper Callovian and Oxfordian of Central European Russia; the two species of Eryma (E. mosquensis Lahusen, 1894 and E. gracilimanum Lahusen, 1894), and the single glypheid taxon were spotted in the Tithonian (regional stage is the Volgian; Rogov, 2014). However, by the latest revision of the erymids (Devillez and Charbonnier, 2021), Eryma mosquensis Lahusen, 1894 is considered to be a junior synonym for E. quadriverrucatum. Another Tithonian species, E. gracilimanum Lahusen, 1894, is included in E. lerasi (Étallon, 1861). Finally, Glypheopsis vosinskyi Lahusen, 1894 (Glypheidae), which is the third species mentioned by Gerasimov (1955), was recently attributed to Erymidae (Charbonnier et al., 2013; Devillez and Charbonnier, 2021). In addition, several specimens of erymids and two unidentified species of Prosopidae were found in the late Tithonian of Moscow and the Moscow Region and described by Gerasimov (1955). However, the present authors have doubts concerning the accuracy of the determination of those damaged remains. In general, the poor and incomplete preservation of

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crustaceans made it challenging to account for the accurate specifications of these samples. Since 1996, a few additional papers were published. Tesakova (2008) reported the presence of *Mecochirus* sp. in the Callovian of the Dubki locality (Saratov Region, Russia). In addition, *Archeosoleonocera straeleni* Carriol and Riou, 1991 was reported from Mikhailovtsement (Ryazan region, Russia) by Shmakov (2016). Unfortunately, both publications contained no pictures of the specimens; the specimen of *Archeosolenocera* from Shmakov (2016) is included in the present work. Later, Mironenko (2020) reported the occurrence of a hermit crab buried in an ammonite shell (Tithonian of Moscow). The present paper provides new and detailed information on several recently discovered samples of crustaceans that have never been previously reported for the area.

Geological setting

The material described herein was found in the Gorenka, Spartak, and Mikhailovtsement quarries (Mikhailov District, Ryazan Region) and Nikitino Lagerstätte (Spassk District, Ryazan region) (Fig. 1). The Jurassic deposits in all the sections include the Callovian and lower and middle Oxfordian. The reddish and brown sandstones and silts of the lower Callovian (Koenigii zone) contain mostly bivalves, belemnites, and rarer nuclei of ammonites, which are more abundant in Gorenka (Figs. 1, 2) and Spartak (Figs. 1, 3) locations. The marine deposits of Mikhailovtsement (Figs. 1, 4) were previously described (Kiselev and Rogov, 2018). The only report of *Eryma* is from the Mikhailovtsement. The middle Callovian (Jason zone) is composed of brown sands and red-brown ferruginous sandstones with carbonate concretions including a few ammonites. The Coronatum zone of the middle Callovian includes brown sands, light brownish-gray siltstone, and dark-brown clay. The upper Callovian (Phaeinum and Proniae subzones of the Athleta zone) is similar to the middle Callovian and consists of brownish-gray clay with a rich assemblage of invertebrate fossils that were frequently preserved as pyrite molds. These layers have a thickness of up to 8 m. Small ferruginous oolites are observed at the top of the Proniae subzone. The dense brownishgray clay of the Lamberti zone contains small ferruginous oolites and larger yellowish-gray marlstone concretions with an assemblage of cephalopods, gastropods, bivalves, polychaetes, and rarer crinoids or marine reptiles. The layer of phosphatized marlstone oolites is found at the top of this zone with multiple decapod fossils and pyrite inclusions. The concretions are usually less than 10 cm in diameter, with a pale gray surface and black dense kernel. The crustaceans are preserved on the surface of oolites, partially submerged in the marlstone or inside it. The fossils are three-dimensional, occasionally deformed, black or rarely pale-colored, and often pyritized. The isolated pereopod and antennae segments are the most abundant, whereas the carapaces and chelae occur rarer, mostly as disarticulated remains.

The deposits of Nikitino (Figs. 1, 5) represent the Jurassic (Callovian and lower Oxfordian) and Lower Cretaceous. The shale marlstones of the Koenigi zone of the lower Callovian are reddish yellow with oolites. The Calloviense zone consists of various very argillaceous siltstones from reddish to gray in color. Both subzones are rich in invertebrates such as ammonites, bivalves, and gastropods, as well as remains of marine



Figure 1. Distribution of the studied localities. 1 = Gorenka quarry (54.238392, 38.848255); 2 = Spartak quarry (54.232961, 38.866298); 3 = Mikhailovtsement quarry (54.211668, 38.955771); 4 = Nikitino Lagerstätte (54.353765, 40.407202). The red stars mark the proper locations of the studied deposits.



Figure 2. The Callovian section of Gorenka quarry. The red star marks the layer where the crustacean remains were found.



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Figure 3. The Callovian section of Spartak quarry. The red star marks the layer where the crustacean remains were found.

reptiles. The single occurrence of decapods from Nikitino is attributed to the Enodatum subzone. The Jason zone of the middle Callovian is composed of gray clays with large concretions at the base. The Coronatum zone consists of very argillaceous dark-brown siltstone with numerous tiny oolites and reddishgray marlstone with a brownish-red surface. In the upper part of the section, beds of the upper Callovian dark-gray clays are exposed (Gulyaev, 2001).

Materials and methods

Twenty-one specimens from the regional collections of the Paleontological Institute of Russian Academy of Science (PIN) and the Museum of Natural History at Moscow Children and Youth Centre for Ecology, Local History and Tourism (MCYCELHT) were used for the present research (Table 1). The crustacean remains were prepared using a pneumatic engraver. All the specimens were photographed with a gradual shift of focus by a digital camera Nikon D800; focusing was accomplished manually. The resulting series of photos were uploaded to the Helicon Focus Pro 6.0.18 software, and the processing of images was completed by the Adobe Photoshop CS2. The glaring specimens were sprayed with a powder of dry ammonium chloride to reduce surface gloss and to reveal their structure before taking pictures. All of the pictures and line drawings were made by I.A. Dadykin.

The following abbreviations are used in the figures and text body: a = branchiocardiac groove; ar = antennal ridge; b = antennal groove; b₁ = hepatic groove; bas = basipodite of uropod; c = postcervical groove; cd = cardiac groove; cp = carpus of P1; d = gastro-orbital groove; dac = dactylus of P1 chela; db = dactylar bulge; di = diaeresis; e₁e = cervical groove; en = endopod of uropod; ex = exopod of uropod; i = inferior groove; ic = intercervical groove; in = index of P1 chela; ip = intercalated plate; or = orbital ridge; p = pereopods; P1 = pereopod 1; P5 = pereopod 5; pl = pleopods; pn = pleon; PoA = postorbital area of the cephalic region; pr = propodus of P1; r = rostrum; s = pleonal somite; sc = scaphocerite; ts = telson; u = uropods; χ = attachment site of the testis muscle; ω = attachment site of the mandibular muscle (for the explanatory diagrams, see Charbonnier et al., 2013; Devillez and Charbonnier, 2019, 2021).

Substage	ZONE	Lithol. column	
	LAMBERTI		
Upper Callovian	ATHLETA	0-0-0-0	*
M iddle allovian	CORONATUM		
-0	JASON		

Figure 4. The Callovian section of Mikhailovtsement quarry. The red star marks the layer where the crustacean remains were found.

Substage	ZONE	Subzone	Lithol. column	
Upper Callovian				
Callovian	CORONATUM			
Middle	JASON		0.0	
Callovian	CALLOVIENSE	Enodatum		*
Lower	KOENIO	Calloviense		
	KUENIGI		- - - - -	

Figure 5. The Callovian section of Nikitino Lagerstätte. The red star marks the layer where the crustacean remains were found.

Repositories and institutional abbreviations.—MCYCELHT = Museum of Natural History at Moscow Children and Youth Centre for Ecology, Local History and Tourism, Moscow, Russia; MNHN = Muséum national d'Histoire naturelle, Paris, France; NHMUK = Natural History Museum, London, UK; OSUG UJF-ID = Observatoire des Sciences de l'Univers de Grenoble, Institut Dolomieu, Grenoble, France; PIN = Paleontological Institute of Russian Academy of Science, Moscow, Russia; SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany.

Systematic paleontology

Order Decapoda Latreille, 1802 Infraorder Dendrobranchiata Bate, 1888 Superfamily Penaeoidea Rafinesque, 1815 Penaeoidea gen. indet. sp. indet. Figure 6.1–6.3

Description.—The specimen PIN 5477/3771 exposes the isolated pleon with preserved P5 coxae. The pleonal somites are not carinate; each somite overlaps the next one; the pleurae are smooth and rounded. The coxae of P5 are globose. The pleopods are poorly preserved, biflagellate; flagellae are multiarticulate. The uropods are poorly preserved as well, ornamented by minute tubercles.

Material.—PIN 5477/3771 from the upper Callovian of Mikhailovtsement.

Remarks.—The specimen PIN 5477/3771 is insufficiently preserved and cannot be attributed to any family with confidence. However, we attribute this specimen to Penaeoidea since it has the first pleonal somite overlapping the second one and biflagellate pleopods with multiarticulate flagellae (Garassino et al., 2013). Another specimen (PIN 5477/2933) might be attributed to family Solenoceridae Wood-Mason in Wood-Mason and Alcock, 1891 on the basis of the cervical groove not reaching the dorsal margin, the antennal groove widening anteriorly, the subhorizontal hepatic groove, and the inferior groove directed frontward (Jauvion et al., 2017). Unfortunately, the anterior part of the carapace is strongly damaged; thus, the presence of suprarostral spines characteristic of Solenoceridae (Jauvion et al., 2017; Alencar et al., 2018) could not be confirmed.

Family Solenoceridae Wood-Mason in Wood-Mason and Alcock, 1891 Genus Archeosolenocera Carriol and Riou, 1991

Type species.—Archeosolenocera straeleni Carriol and Riou, 1991 by monotypy.

Archeosolenocera sp. Figure 6.4–6.7

Description.—The specimen PIN 5477/2933 includes a carapace and four pleonal segments. The carapace is elongate

Та	ble	1.	List	of	the	studied	Ca	llovi	ian	decapods	s of	the	Rya	azan	regio	n.
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Taxon	Specimen number	Locality	Age	Comments	
Archeosolenocera sp.	PIN 5477/2933	Mikhailovtsement	Upper Callovian	Carapace + abdomen	Fig. 6.1, 6.2, 6.3, 6.4
Penaeoidea indet.	PIN 5477/3771	Mikhailovtsement	Upper Callovian	Abdomen	Fig. 6.5, 6.6, 6.7
Eumorphia sp.	PIN 5477/3787	Gorenka	Upper Callovian	Well preserved	Fig. 7.5, 7.6, 7.7, 7.8
Eumorphia sp.	PIN 5477/3788	Gorenka	Upper Callovian	Well preserved	Fig. 7.1, 7.2
Eumorphia sp.	PIN 5477/3789	Gorenka	Upper Callovian	Well preserved	Fig. 8.1, 8.2, 8.3
Eumorphia sp.	PIN 5477/4547	Gorenka	Upper Callovian	Well preserved	Fig. 7.3, 7.4
Eumorphia sp.	PIN 5477/4548	Gorenka	Upper Callovian	Well preserved	Fig. 8.7, 8.8
Eumorphia sp.	PIN 5477/4549	Gorenka	Upper Callovian	Well preserved	Fig. 8.4, 8.5, 8.6
Glypheopsis cf. G. etalloni (Oppel, 1861)	PIN 5477/4536	Gorenka	Upper Callovian	Carapace	Fig. 9.3, 9.4
Glypheopsis sp.	PIN 5477/3786	Mikhailovtsement	Upper Callovian	Posterior part of the carapace	Fig. 9.6
Glypheopsis sp.	PIN 5477/4542	Mikhailovtsement	Upper Callovian	Posterior part of the carapace	Fig. 9.5
Glypheidae indet.	PIN 5477/3724	Nikitino	Lower Callovian	Posterior part of the carapace	Fig. 9.1, 9.2
<i>Eryma</i> aff. <i>E. ventrosum</i> (von Meyer, 1835)	PIN 5477/0925	Mikhailovtsement	Upper Callovian	Carapace + pereiopods	Fig. 10.1, 10.2
Eryma aff. E. ventrosum (von Meyer, 1835)	PIN 5477/4535	Gorenka	Upper Callovian	Carapace	Fig. 10.3
Eryma ornatum (Quenstedt, 1858)	PIN 5477/3765	Spartak	Lower Callovian	P1 chela	Fig. 10.4
<i>Eryma quadriverrucatum</i> Trautschold, 1866	MCYCELHT 2/226	Mikhailovtsement	Upper Callovian	Carapace + abdomen	Fig. 11.1
Eryma quadriverrucatum Trautschold, 1866	PIN 5477/3784	Mikhailovtsement	Upper Callovian	Carapace	Fig. 11.3, 11.4
Eryma quadriverrucatum Trautschold, 1866	PIN 5477/4537	Gorenka	Upper Callovian	Carapace	Fig. 11.2
<i>Eryma</i> sp.	PIN 5477/4538	Gorenka	Upper Callovian	P1 chela	Fig. 12.6
Eryma sp.	PIN 5477/4539	Gorenka	Upper Callovian	P1 chela	Fig. 12.4, 12.5
Eryma sp.	PIN 5477/4953	Gorenka	Upper Callovian	P1 chela	Fig. 12.1, 12.2, 12.3
Stenodactylina insignis (Oppel, 1862)	PIN 5477/4540	Mikhailovtsement	Upper Callovian	P1 chela	Fig. 12.8, 12.9
Stenodactylina sp.	PIN 5477/4541	Gorenka	Upper Callovian	P1 finger	Fig. 12.7

(74 mm long), laterally compressed, almost smooth. Its dorsal margin is straight; ventral margin is slightly convex. The rostrum is poorly preserved, wide. Cervical groove is deep and short, inclined, joined ventrally to straight antennal groove; antennal groove short, widening anteriorly; hepatic groove is elongate, subhorizontal, slightly inclined posteriorly, joined anteriorly to cervical and antennal grooves, forming an angle of 100° with the cervical groove; no spine at junction of the cervical and the hepatic grooves; inferior groove wide, inclined, joined to hepatic groove anteriorly to its junction to cervical groove. The pleon is laterally compressed; the pleonal segments are smooth, and the pleura are rounded.

Material.—PIN 5477/2933 from the upper Callovian of Mikhailovtsement.

Remarks.-Family Solenoceridae comprises three extinct monotypic genera (Alencar et al., 2018): Archeosolenocera Carriol and Riou, 1991 (Middle Jurassic, France), Eogordonella Garassino et al., 2014 (Eocene, Iran), and Priorhyncha Alencar et al., 2018 (Early Cretaceous, Brazil). Priorhyncha differs from our specimen in having a cervical groove only. Eogordonella has a serrate dorsal margin of the cephalic region and the hepatic, branchiocardiac, and submarginal carinae, which are absent in specimen PIN 5477/ 2933. We may attribute this specimen to Archeosolenocera due to its specific groove pattern: antennal, cervical, hepatic, and inferior grooves present; cervical groove well developed and not reaching the dorsal margin of the carapace; hepatic and antennal grooves represented; inferior groove slightly incurved and subparallel to the dorsal margin. However, the specimen PIN 5477/2933 differs from the diagnosis of Jauvion et al. (2017) in the absence of a hepatic spine and junction of inferior groove to hepatic groove at the level of the antennal groove, anteriorly to the junction of the cervical groove. Thus, PIN 5477/2933 probably does not belong to the single known species of the genus, A. straeleni Carriol and Riou, 1991 from the Callovian of France. Unfortunately, the preservation of our material is not quite good enough to clarify the taxonomy of the specimen. Therefore, we attribute the specimen PIN 5477/2933 to *Archeosolenocera* sp.

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Infraorder Pleocyemata Burkenroad, 1963 Superfamily Glypheoidea von Zittel, 1885 Family Mecochiridae Van Straelen, 1925 Genus *Eumorphia* von Meyer, 1847

Type species.—Eumorphia socialis (von Meyer, 1841) (*=Mecochirus socialis* (von Meyer, 1841)), by monotypy, from the upper Callovian of St. Ives, Huntingdonshire, Great Britain.

Eumorphia sp. Figures 7, 8

Description.—All the specimens share similar morphological features and expose the carapaces with partially preserved thoracic appendages and pleon.

Carapace.—The carapace is ovoid in the lateral view; it is laterally compressed (carapace length is $\sim 10-15$ mm; carapace height is \sim 7 mm). The rostrum is short, pointed, smooth, with medial dorsal longitudinal depression. The antennal-pterygostomial margin is slightly convex. The cervical groove is long, deep, oblique, joining to the dorsal margin at an angle of \sim 37°, delimiting the short cephalic region. The cephalic region is almost smooth, bearing a single orbital ridge. The postcervical and branchiocardiac grooves are subparallel, shallow, reaching the posterior margin of the carapace, forming an angle of $\sim 18^{\circ}$ with the dorsal margin. The narrow lobe between the postcervical and the branchiocardiac grooves is represented. The postcervical groove is narrow and incurved anteriorly, slightly curved medially, joined dorsally to the cardiac groove; the branchiocardiac groove is narrow and straight, joined ventrally to the hepatic groove. The cardiac groove is elongate, straight or slightly incurved backward, inclined forward, and reaching the



Figure 6. (1-3) Penaeoidea gen. indet. sp. indet. from Mikhailovtsement, upper Callovian (PIN 5477/3771): (1, 2) right lateral view; (3) uropods, ventral view. (4–7) *Archeosolenocera* sp. from Mikhailovtsement, upper Callovian (PIN 5477/2933): (4, 5) left lateral view; (6, 7) dorsal view. b = antennal groove; b₁ = hepatic groove; di = diaeresis; e₁e = cervical groove; en = endopod of uropod; ex = exopod of uropod; i = inferior groove; P5 = pereopod 5; pl = pleopods; pn = pleon; ts = telson; u = uropods. Scale bars = 10 mm.

dorsal margin at an angle of $\sim 60^{\circ}$; the cardiac grooves do not join at the midline of the carapace. The hepatic groove is shallow and deepening posteriorly. Its posterior end is turning forward, forming a circular slightly convex hepatic lobe. The cephalic, the hepatic, the pterygostomial, and the cardiac regions are almost smooth, ornamented only by a few minute tubercles. The branchial region is densely tuberculate, with the largest tubercules situated at the center of the region.

Pleon.—The pleon is about twice as long as the carapace. The pleomeres are bearing longitudinal carina laterally, with rounded dorsal margin almost smooth. The pleurae are rounded and tuberculate, bearing short transverse grooves anteriorly and posteriorly. The s1 is short; s2 is the longest one; s3–5 are of similar length; s6 is short and subtriangular. The telson is subrectangular, flattened, smooth, and posteriorly rounded.

Thoracic appendages.—The P1–5 are strongly damaged; subchelate P1, slender, 1.5 times longer than the carapace; P1 carpus flattened laterally, with a row of tubercles at posterior edge; P1 propodus elongate, subtriangular in section, densely tuberculated; P2–5 thin, slightly flattened laterally, almost smooth.



Figure 7. *Eumorphia* sp. (Mecochiridae) from Gorenka (upper Callovian), dusted with ammonium chloride: (1, 2) complete shrimp (PIN 5477/3788), left lateral view; (3, 4) complete shrimp (PIN 5477/4547), left lateral view; (5–8) complete shrimp (PIN 5477/3787): (5, 6) left lateral view; (7, 8) pleon, dorsal view. a = branchiocardiac groove; b_1 = hepatic groove; $c = postcervical groove; cd = cardiac groove; cp = carpus of P1; <math>e_1e = cervical groove; en = endopod of uropod; ex = exopod of uropod; or = orbital ridge; p = pereopods; P1 = pereopod 1; pn = pleon; pr = propodus of P1; ts = telson. Scale bar = 10 mm.$

Pleonal appendages.—The pleopods are not preserved. The uropods are biramous; the basipodite is smooth and globose; the exopod and the endopod are of similar shape, ovoid, with a wide longitudinal carina narrowing distally, ornamented by sparse tubercles; the exopod lacks diaeresis; outer margin of exopod is smooth. *Material.*—PIN 5477/3787, PIN 5477/3788, PIN 5477/3789, PIN 5477/4547, PIN 5477/4548, and PIN 5477/4549 from the upper Callovian of Gorenka.

Remarks.—All specimens discussed in the preceding (Figs. 7, 8) are assigned to Mecochiridae on the basis of the following



Figure 8. *Eumorphia* sp. (Mecochiridae) from Gorenka (upper Callovian), dusted with ammonium chloride: (1–3) complete shrimp (PIN 5477/3789): (1) left lateral view, (2, 3) carapace, dorsal view; (4–6) complete shrimp (PIN 5477/4549): (4, 5) right lateral view, (6) left lateral view; (7, 8) complete shrimp (PIN 5477/4549): (7) left lateral view, (8) right lateral view, a = branchiocardiac groove; b₁ = hepatic groove; bas = basipodite of uropod; c = postcervical groove; c = cardiac groove; e₁ = cervical groove; e = endopod of uropod; e = exopod of uropod; or = orbital ridge; p = pereopods; pn = pleon; r = rostrum; ts = telson. Scale bar = 10 mm.

characteristic features (after Karasawa et al., 2013): the presence of the cervical, postcervical, and branchiocardiac grooves; the low angles of the cervical and the branchiocardiac grooves to dorsal surface; the closely spaced and subparallel postcervical and branchiocardiac grooves; the absence of an inferior groove; the elongated pereopod 1; and the presence of cephalic ridges (Karasawa et al., 2013).

Family Mecochiridae remains unrevised, and its systematics is still in progress (S. Charbonnier, personal communication, 2023). To date, mecochirids include four valid genera: *Atherfieldastacus* Robin et al., 2016, *Huhatanka* Feldmann and West, 1978, *Meyeria* M'Coy, 1849, and *Mecochirus* Germar, 1827. Two more genera are considered to be invalid: *Jabaloya* Garassino, Artal, and Pasini, 2009 is a junior synonym for *Meyeria*, and *Meyerella* Simpson and Middleton, 1985 is recently replaced by *Atherfieldastacus* (Robin et al., 2016). A relation of *Pehuenchia* Rusconi, 1948 and *Zapalianassa* Schweitzer, Feldmann, and Casadio, 2022 (Late Jurassic, Argentina) to Mecochiridae was recently argued (Schweitzer et al., 2022). Family Mecochiridae includes both Jurassic and Cretaceous species (Glaessner, 1969; Simpson and Middleton, 1985; De Grave et al., 2009; Garassino et al., 2009; Astrop, 2011; Karasawa et al., 2013; Robin et al., 2016; Schweitzer et al., 2022).

The diagnostic features of studied specimens are as follows: a single cephalic ridge; subparallel postcervical and branchiocardiac grooves reaching the posterior margin of the carapace; the cardiac groove represented; the inferior groove absent; the hepatic groove strongly incurved, forming a hepatic lobe; the hepatic ridge absent; no diaeresis on the exopod of uropods, the latter one with smooth outer margin (Figs. 7, 8). On the basis of these characteristics, discussed specimens do not belong to Meyeria (three cephalic carinae and the inferior groove is represented), Mecochirus (three cephalic carinae, the cardiac groove is absent, the exopod with a diaeresis), or Atherfieldastacus (three cephalic carinae, the exopod with a diaeresis and serrate outer margin) (Garassino et al., 2009; Robin et al., 2016; Charbonnier et al., 2021). S. Charbonnier suggested that the name Eumorphia von Meyer, 1847 continue to be considered a junior synonym of Mecochirus for individuals without the diaeresis and with the cardiac groove represented (S. Charbonnier, personal communication, 2023). Thus, we propose the name Eumorphia sp. for all of the studied material in this section. The record of Mecochirus sp. by Tesakova (2008) from the upper Callovian of Dubki quarry, Saratov region, probably relates to that taxon. (For more information on Eumorphia socialis (von Meyer, 1841), see Carter, 1886; Woods, 1928; Glaessner, 1969).

> Family Glypheidae Winkler, 1882 Glypheidae gen. indet. sp. indet. Figure 9.1, 9.2

Description.—The specimen PIN 5477/3724 exposes the isolated posterior part of the carapace. The carapace is elliptical in dorsal view (length of preserved part is ~ 20 mm); the postcervical, branchiocardiac, and cardiac grooves are represented; the postcervical and branchiocardiac grooves converge dorsally, forming an elongate lobe; the postcervical groove is shallow; the branchiocardiac groove is deep and wide, reaching the dorsal margin of the carapace at an angle of $\sim 20^{\circ}$; the branchiocardiac grooves are connected dorsally; the cardiac groove is shallow and short, inclined forward; the carapace is ornamented by large pits.

Material.—PIN 5477/3724 from the early Callovian of Nikitino.

Remarks.—The family has numerous paleontological records for the Mesozoic and Cenozoic (Charbonnier et al., 2013, 2014a). To date, eight extinct and two extant genera of Glypheidae are known (Charbonnier et al., 2014a). We attribute the specimen PIN 5477/3724 to the family Glypheidae because of the following taxonomically important features: the postcervical and branchiocardiac grooves are subparallel and converging dorsally, forming an elongate lobe. The presence of the cardiac groove, a single lobe between the postcervical and branchiocardiac for both *Glypheopsis* Beurlen, 1928 and *Trachysoma* Bell, 1858. Unfortunately, the condition of the discussed specimen does not allow further determination.

Genus Glypheopsis Beurlen, 1928

Type species.—Orphnea ornata Quenstedt, 1857 by the subsequent designation of Glaessner (1929) from the Callovian of Pfullingen, Baden-Württemberg, Germany.

Glypheopsis sp. Figure 9.3, 9.4

Description.—The specimens PIN 5477/3786 and PIN 5477/ 4536 expose the posterior parts of carapaces. The cervical groove is deep, forming an angle of \sim 70° with the dorsal margin, joining ventrally to the antennal groove, with delimiting elongate cephalic region (it is absent on specimen PIN 5477/3786). The cardiac groove is shallow and almost straight, inclined anteriorly, and forming an angle of \sim 47° with the dorsal margin. The hepatic groove is deep and bilobed, joined to the cervical groove; the adductor muscle area is not inflated. The intercervical groove is weak, slightly incurved upward, delimiting small hepatic lobe. The branchial, pterygostomial, and hepatic regions are densely ornamented by tubercles; those of the branchial region decrease in size ventrally; the cardiac region with scarce and largest tubercles.

Material.—PIN 5477/3786 and PIN 5477/4542 from the upper Callovian of Mikhailovtsement.

Remarks.—The discussed specimens might be attributed to *Glypheopsis* Beurlen, 1928 on the basis of the postcervical and branchiocardiac grooves forming a single elongate lobe; the cardiac groove represented; the laterocardiac groove absent; the hepatic groove bilobed; the intercervical groove represented; the gastro-orbital groove absent (Charbonnier et al., 2014a). To date, the 26 species of *Glypheopsis* are reported from the Early Jurassic to the Eocene (Garassino et al., 2019; Becker et al., 2021). Among them, the seven species occur in the Callovian and Oxfordian of Europe (Charbonnier et al., 2013).

The ornamentation pattern of specimens PIN 5477/3786 and PIN 5477/4542 is characteristic for *Glypheopsis etalloni* (Oppel, 1861) and *G. pseudomuensteri* (Martin, 1961) (both from the Oxfordian of France) or *G. calloviensis* (Woods, 1927) (late Callovian of the United Kingdom) (Charbonnier et al., 2013). Here we identify the specimens PIN 5477/3786 and PIN 5477/4542 only at the generic level.

Glypheopsis aff. G. etalloni (Oppel, 1861) Figure 9.5, 9.6

Type material.—Lectotype MNHN.F.A29575, collection of Étallon, Muséum national d'Histoire naturelle, Paris, France (Charbonnier et al., 2013, p. 122, fig. 237).

Description.—The specimen PIN 5477/4536 is a well-preserved carapace with fragments of P1. The cervical groove is deep. The carapace is elongate in the lateral view (length of carapace is \sim 34 mm; height of carapace is \sim 15 mm). The rostrum is not preserved. The cervical groove is deep, forming an angle of \sim 70° with the dorsal margin, joining ventrally to the antennal groove, with delimiting elongate cephalic region. The cephalic region bears four longitudinal spiny carinae, which do not



Figure 9. Glypheidae from Middle Jurassic of Ryazan region: (1, 2) Glypheidae gen. indet. sp. indet. from Nikitino, middle Callovian (PIN 5477/3724): (1) dorsal view, (2) right lateral view; (3, 4) *Glypheopsis* sp. from Mikhailovtsement, upper Callovian: (3) carapace (PIN 5477/3786), left lateral view; (4) carapace (PIN 5477/4542, dusted with ammonium chloride), left lateral view; (5, 6) *Glypheopsis* aff. *G. etalloni* (Oppel, 1861): carapace from Gorenka, upper Callovian (PIN 5477/4536, dusted with ammonium chloride), right lateral view; a = branchiocardiac groove; b = antennal groove; b₁ = hepatic groove; c = postcervical groove; cd = cardiac groove; e₁e = cervical groove; i = inferior groove, ic = intercervical groove. Scale bars = 10 mm.

reach the cervical groove: the orbital, the gastro-orbital, the antennal, and the supra-antennal carinae. The intercarinal spaces are smooth; the antennal region is ornamented by dense tubercles. The antennal groove is narrow, deep, strongly incurved posteriorly, and slightly incurved upward at its middle part. The postcervical and branchiocardiac grooves converge ventrally and dorsally and form a single elongate lobe; the postcervical groove is slightly tortuous, converging with the hepatic groove ventrally, connected to the intercervical and cardiac grooves. The branchiocardiac groove is almost straight, bending up posteriorly and reaching the dorsal margin of the carapace at an angle of \sim 75°. The P1 propodus (partially preserved) is ornamented by longitudinal rows of spines.

Material.—PIN 5477/4536 from the upper Callovian of Gorenka.

Remarks.—The specimen PIN 5477/4536 (Fig. 9.5, 9.6) shares the diagnostic features of Glypheopsis etalloni: four longitudinal spiny carinae on the cephalic region; weakly inflated adductor muscle area; the ornamentation by tubercles decreasing in size ventrally in the branchial region (Charbonnier et al., 2013, figs. 237-246). However, the specimen PIN 5477/4536 is distinguished from G. etalloni by the presence of the bilobed hepatic groove (sinuous in G. etalloni) and the flat adductor muscle area (inflated in G. etalloni); in addition, the space between the antennal and supra-antennal carinae is smooth in specimen PIN 5477/4536 (it bears a row of tubercles in G. etalloni). G. pseudomuensteri (Martin, 1961) from the Oxfordian of France is a very similar species to G. etalloni and may be its junior synonym (Charbonnier et al., 2013). The specimen PIN 5477/4536 differs from this species by having four cephalic carinae (three for G. pseudomuensteri), tuberculate pterygostomial region (smooth for *G*. pseudomuensteri), and flat adductor muscle insertion area (Charbonnier et al., 2013, figs. 283, 284). The specimen PIN 5477/4536 is distinct from other same-aged Glypheopsis species by having four cephalic carinae (five for G. calloviensis (Woods, 1927), three for G. ornata (Quenstedt, 1858), G. bronnii (Roemer, 1839), G. trouvillensis Charbonnier et al., 2013, and G. voultensis Charbonnier et al., 2013), the ornamentation of the carapace by tubercles decreasing in size ventrally (uniform tubercles for G. ornata, pits for G. bronnii and G. trouvillensis, and almost absent for G. voultensis), and flat adductor muscle insertion area (inflated for G. ornata, G. calloviensis, G. bronnii, and G. voultensis). A biconvex hepatic groove is observed in many Cretaceous and Cenozoic Glypheopsis species (Charbonnier et al., 2013). However, no such taxa have been reported from the Callovian to Oxfordian. Hence, we propose a preliminary combination Glypheopsis aff. G. etalloni for the specimen PIN 5477/4536.

> Infraorder Astacidea Latreille, 1802 Superfamily Erymoidea Van Straelen, 1925 Family Erymidae Van Straelen, 1925 Genus *Eryma* von Meyer, 1840b

Type species.—Macrourites modestiformis von Schlotheim, 1822 by subsequent designation of Glaessner, 1929, from the Kimmeridgian–Tithonian of Eichstätt, Bavaria, Germany.

Material.—PIN 5477/0925, PIN 5477/3784, and MCYCELHT 2/226 from the upper Callovian of Mikhailovtsement; PIN 5477/3765 from the lower Callovian of Spartak; PIN 5477/4535, PIN 5477/4537, PIN 5477/4538, PIN 5477/4539, and PIN 5477/4953 from the upper Callovian of Gorenka.

Eryma aff. *E. ventrosum* (von Meyer, 1835) Figure 10.1–10.3

Type material.—Probably lost, cast MNHN.F.B12484 (Devillez and Charbonnier, 2021, fig. 11A, B).

Description.—Carapace.—The carapace of PIN 5477/0925 is ovoid in the lateral view (carapace length is ~56 mm; carapace height is ~ 26 mm). The rostrum is short, pointed; the dorsal margin of the rostrum is serrate. The postorbital area is represented. The cervical groove is strongly inclined dorsally and slightly inclined ventrally, joined to the antennal groove ventrally, delimiting short cephalic region. Two cephalic carinae, converging toward the posterior, reach the middle part of the cephalic region; both carinae bear spines. The orbital spine is represented. The gastro-orbital groove is very short. The antennal groove is wide, shallow, slightly convex posteriorly. The postcervical groove is deep, wide, joining to the branchiocardiac groove at the carapace mid-height; the branchiocardiac groove is deep, shallower, slightly incurved at the junction with the postcervical groove, joins ventrally to the hepatic and inferior grooves.

The length of the carapace PIN5477/4535 is ~49 mm; the height is ~23 mm. The specimen shares features of PIN 5477/ 0925, despite the surface of the pterygostomial, hepatic, cardiac, and branchial regions being strongly damaged. The hepatic groove is concavo-convex, joining anteriorly to the cervical groove; the χ and ω areas are strongly damaged. The inferior groove is represented on the specimen PIN 5477/4535, deep and wide, incurved forward.

Carapace ornamentation.—The cephalic region bears two to three large spines between the orbital and antennal rows; the middle part of the cephalic region is approximately smooth, with circular depressions only. The gastric, cardiac, and branchial regions of PIN 5477/0295 are ornamented by sparse tubercles interspersed with circular depressions; the antennal region is ornamented by large tubercles without depressions.

Cephalic appendages.—Antennae are partially preserved in PIN 5477/0925. The scaphocerite is ~ 8 mm long, trapezoidal, with an elongated and slightly narrowing dorsal expansion equal in length to the basal part of the segment; the scaphocerite is smooth. Flagellum is strongly damaged.

Thoracic appendages.—The appendages are represented on the specimen PIN 5477/0925. The propodus is \sim 18 mm long, compressed dorsoventrally, ornamented by multiple tubercles; the pereopods are smooth.

Material.—PIN 5477/0925 from the upper Callovian of Mikhailovtsement; PIN 5477/4535 from the upper Callovian of Gorenka.

Remarks.—The specimens PIN 5477/0925 and PIN 5477/4535 belong to Erymidae on the basis of the cervical, postcervical, hepatic, and inferior grooves present; the short and shallow gastro-orbital groove; and the delimited postorbital area. I addition, the P1 propodus is preserved on PIN 5477/0925 (Fig. 10.1, 10.2). For a diagnosis of the family, see Devillez et al. (2018).

Both specimens share features of *Eryma* von Meyer, 1840 (von Meyer, 1840a): the postcervical groove ventrally joins to the branchiocardiac groove; the branchiocardiac groove ventrally joins to the hepatic groove; the hepatic groove is concavoconvex, forming χ and ω areas; the orbital spine of the orbital

Figure 10. (1–3) *Eryma* aff. *E. ventrosum* (von Meyer, 1835): (1, 2) carapace from Mikhailovtsement, upper Callovian (PIN 5477/0925), left lateral view (dusted with ammonium chloride), (3) carapace from Gorenka, upper Callovian (PIN 5477/4535, dusted with ammonium chloride), left lateral view; (4) *Eryma ornatum* (Quenstedt, 1858), P1 chela from Spartak, lower Callovian (PIN 5477/3765), dorsal view. a = branchiocardiac groove; ar = antennal ridge; b = antennal groove; b₁ = hepatic groove; c = postcervical groove; cp = carpus of P1; d = gastro-orbital groove; dac = dactylus of P1 chela; e₁e = cervical groove; i = inferior groove; in = index of P1 chela; or = orbital ridge; p = pereopods; POA = postorbital area of the cephalic region; pr = propodus of P1; r = rostrum; sc = scaphocerite. Scale bars = 10 mm.

row is represented. (For a diagnosis of *Eryma*, see Devillez et al., 2018; Devillez and Charbonnier, 2021).

The specimens are similar to *E. ventrosum* (von Meyer, 1835) from the Late Jurassic of Europe in having the junction of the postcervical and branchiocardiac grooves at the midheight of the carapace, as well as having the same cervical, hepatic, gastro-orbital, and inferior groove patterns. However, the studied material differs from typical *E. ventrosum* (Devillez and Charbonnier, 2021, figs. 4, 5) by the presence of a few large spines at the space between the cephalic rows (absent for *E. ventrosum*); serrate rostrum (smooth for *E. ventrosum*); ornamentation by tubercles interspersed with circular depressions or without pits (tubercles with crescent-shaped depressions for *E. ventrosum*). Thus, we propose a preliminary name *Eryma* aff. *E. ventrosum* (von Meyer, 1835) for the studied specimens.

Eryma ornatum (Quenstedt, 1858) Figure 10.4

Type material.—GPIT/CU/00349, collection of Fachbereichs Geowissenschafte, Eberhard Karls Universität, Tübingen, Germany (Devillez and Charbonnier, 2019, fig. 8A).

Description.—Isolated P1 chela. The propodus is short (propodus length without index ~13 mm; width ~9 mm), trapezoidal, laterally compressed; the inner and outer margins are narrow; the ventral surface of the propodus with a longitudinal inflexion. The dactylar bulge is narrow, delimited by a deep groove. The fingers are thin (length ~25 mm), slightly incurved, progressively narrowing, and equal in length; index is wide at its base, with a steep incurvation and a wide shallow longitudinal groove on ventral surface. The occlusal margins have small, closely spaced teeth. The ornamentation of the chela is represented by small, dense tubercles with crescent-shaped depressions.

Material.—PIN 5477/3765 from the lower Callovian of Spartak.

Remarks.—The specimen PIN 5477/3765 is attributed to family Erymidae and genus *Eryma* on the basis of the following: P1 is chelate; P1 propodus is laterally compressed, with narrow inner and outer margins; the dactylar bulge is narrow, delimited by a groove; the P1 fingers are equal in length and thin; they are longer than the propodus; index wider than the dactylus.

The specimen PIN 5477/3765 can be attributed to *E. ornatum* (Quenstedt, 1858) from the Middle Jurassic of Europe because the propodus is trapezoidal, the fingers are slightly incurved, the index base does not form an angle with its distal part, and the ornamentation of P1 is represented by tubercles with crescent-shaped depressions.

The closely related species Eryma compressum (Eudes-Deslongchamps, 1842) differs from *E. ornatum* by having a wider base of the index forming a slight angle between proximal and distal parts of the index (J. Devillez, personal communication, 2021; Devillez and Charbonnier, 2019, fig. 5D, F). The specimen PIN 5477/3765 lacks this feature; no curvature is observed in a proximal part of the index (Fig. 10.4). The specimen differs from E. mandelslohi (von Meyer, 1840b) (Callovian, Europe) by having a trapezoidal propodus and slightly incurved dactylus (Devillez and Charbonnier, 2019, fig. 7E, F); from E. ventrosum (Callovian to Kimmeridgian, Europe) and Eryma lerasi (Étallon, 1861) (Late Jurassic, Europe and European Russia) by possessing a trapezoidal propodus (Devillez and Charbonnier, 2019, 2021); from Eryma georgeii Carter, 1886, (Oxfordian, United Kingdom) by fine ornamentation of chela (Devillez and Charbonnier, 2019). Therefore, we suggest attributing the specimen PIN 5477/3765 to E. ornatum.

Eryma quadriverrucatum Trautschold, 1866 Figure 11

Type material.—NHMUK 22917, collection of the Natural History Museum, London, UK (Devillez and Charbonnier, 2019, p. 10, fig. 5A, B).

Description.—MCYCELHT 2/226 exposes a well-preserved carapace with joined pleon and thoracic appendages (Fig. 11.1); PIN 5477/4537 (Fig. 11.2) and PIN 5477/3784 (Fig. 11.3, 11.4) expose the isolated carapaces.

Carapace.-The carapace is elongate in the lateral view and subcylindrical in the cross section (length of specimen MCY-CELHT 2/226 ~38 mm; height ~18 mm). The rostrum of specimen PIN 5477/3784 (Fig. 11.3, 11.4) is short and spineless. The postorbital area is narrow; the intercalated plate is fusiform (represented on specimen PIN 5477/3784). The cervical groove is strongly inclined dorsally, slightly inclined ventrally, joins to antennal groove ventrally, delimiting short cephalic region. Two cephalic carinae are represented, converging toward the middle part of the cephalic region; the orbital spine is represented. The antennal groove is deep and short, slightly convex posteriorly. The gastro-orbital groove is very short. The postcervical and branchiocardiac grooves are deep and subparallel, not reaching the dorsal margin of the carapace; the postcervical groove is inclined, slightly incurved, joins to the branchiocardiac groove at the carapace mid-height, bears a short ventral extension; the branchiocardiac groove is inclined, strongly incurved at its junction to the postcervical groove, joining ventrally to the hepatic groove. The hepatic groove is shallow and concavo-convex, joining anteriorly to the cervical groove; the χ and ω areas are both inflated. The inferior groove is wide and shallow, joining

Figure 11. *Eryma quadriverrucatum* Trautschold, 1866: (1) well-preserved specimen from Mikhailovtsement, upper Callovian (MCYCELHT 2/226, dusted with ammonium chloride), left lateral view; (2) carapace from Gorenka, upper Callovian (PIN 5477/4537, dusted with ammonium chloride), right lateral view; (3, 4) carapace from Mikhailovtsement, upper Callovian, left lateral view (PIN 5477/3784). a = branchiocardiac groove; b = antennal groove; b = hepatic groove; c = postcervical groove; d = gastro-orbital groove; e₁ = cervical groove; i = inferior groove; i = intercalated plate; or = orbital ridge; pn = pleon; PoA = postorbital area of the cephalic region; r = rostrum; χ = attachment site of the testis muscle; ω = attachment site of the mandibular muscle. Scale bars = 10 mm.

anteriorly to the hepatic groove. The carapace is densely ornamented by tubercles interspersed with irregular pits.

Pleon.—The pleonal segments are represented on specimen MCYCELHT 2/226 (Fig. 11.1); the tergites are subrectangular; the pleurae are subtriangular, directed backward, and bear a lateral bulge basally; s1 is short; s2 and s3 are of equal length; s4–6 are poorly preserved. The pleurae are ornamented by dense tubercles.

Thoracic appendages.—The P1 is partially preserved. The carpus of P1 is subcylindrical and laterally compressed, ornamented by dense tubercles. The propodus and dactylus are not preserved.

Material.—PIN 5477/3784 and MCYCELHT 2/226 from the upper Callovian of Mikhailovtsement; PIN 5477/4537 from the upper Callovian of Gorenka.

Remarks.—The specimens MCYCELHT 2/226 (Fig. 11.1), PIN 5477/3784 (Fig. 11.3, 11.4), and PIN 5477/4537 (Fig. 11.2) share characteristics of Erymidae as follows: the cervical,

postcervical, hepatic, and inferior grooves are represented; short and shallow gastro-orbital groove beginning from the medial inflexion of the cervical groove; the postorbital area is delimited (not preserved on specimen PIN 5477/4537); the intercalated area is represented (specimen PIN 5477/3784, Fig. 11.3). (For a diagnosis of the family, see Devillez et al., 2018).

The studied material can be attributed to *Eryma* von Meyer, 1840 (von Meyer, 1840a) because the postcervical groove ventrally joins to the branchiocardiac groove; the branchiocardiac groove is concavo-convex, forming the χ and ω areas; the orbital spine of the orbital row is represented. (For a diagnosis of *Eryma*, see Devillez et al., 2018; Devillez and Charbonnier, 2021).

The studied specimens demonstrate peculiarities of *E. quadriverrucatum* as follows: the cervical groove is wide and strongly inclined; the gastro-orbital groove is short and deep; the postcervical and branchiocardiac grooves are deeply

Figure 12. (1–6) *Eryma* sp.: (1–3) P1 chela from Gorenka, upper Callovian (PIN 5477/4953, dusted with ammonium chloride): (1) right ventral view, (2) right dorsal view, (3) basal view; (4, 5) P1 chela from Gorenka, upper Callovian (PIN 5477/4539, dusted with ammonium chloride): (4) left ventral view, (5) left dorsal view; (6) P1 chela from Gorenka, upper Callovian (PIN 5477/4538, dusted with ammonium chloride), left dorsal view. *Stenodactylina* sp.: (7) P1 finger from Gorenka, upper Callovian (PIN 5477/4541, dusted with ammonium chloride), left dorsal view. *Stenodactylina* sp.: (7) P1 finger from Gorenka, upper Callovian (PIN 5477/4541, dusted with ammonium chloride), lateral view. (8, 9) *Stenodactylina insignis* (Oppel, 1862), P1 chela from Mikhailovtsement, upper Callovian (PIN 5477/4540): (8) left dorsal view, (9) left ventral view. dac = dactylus of P1 chela; db = dactylar bulge; in = index of P1 chela; pr = propodus of P1. Scale bars = 10 mm.

inclined; both χ and ω areas are inflated; the inferior groove is deep and wide; the ornamentation is represented by dense small tubercles surrounded with irregular depressions; the

morphology of the pleonal somites is typical for the species (Devillez and Charbonnier, 2021). It is important to note that the junction of the postcervical and branchiocardiac grooves

of the studied specimens is situated at the mid-height of the carapace (Fig. 11.2-11.4). However, E. quadriverrucatum sensu Devillez and Charbonnier, 2021 is characterized by a junction of the postcervical and branchiocardiac grooves situated very low on the carapace. Unfortunately, Devillez and Charbonnier did not study the type series but only original pictures of Trautschold (Devillez and Charbonnier, 2021, fig. 11A, C). Thus, this feature of E. quadriverrucatum could be a misinterpretation of Trautschold's original work (Trautschold, 1866) as the specimens depicted by Gerasimov were damaged but had crossing of the postcervical and branchiocardial grooves at the midheight of the carapace (Gerasimov, 1955, pl. 8, figs. 1, 3; Devillez and Charbonnier, 2021, fig. 11C, D). According to Devillez and Charbonnier (2021), the type age of E. quadriverrucatum is Tithonian; however, the age of the specimens could have been misinterpreted by Trautschold. Thus, we propose here the emended diagnosis for E. quadriverrucatum from the upper Callovian of Ryazan region.

The studied material differs from other Eryma species from the Middle and Late Jurassic by the following features: both χ and ω areas are inflated while only one or neither is inflated for E. compressum (Eudes-Deslongchamps, 1842), E. georgeii Carter, 1886, E. jungostrix Feldmann and Titus, 2006, E. lerasi (Étallon, 1861), E. mandelslohi (von Meyer, 1840b), and E. ventrosum (von Meyer, 1835); the carapace is ornamented by tubercles with irregular depressions while there are depressions only for E. mandelslohi and E. punctatum Oppel, 1861, tubercles with crescent-shaped depressions for E. compressum (Eudes-Deslongchamps, 1842), E. lerasi, and E. ventrosum, and tubercles only for E. jungostrix, E. osciensis Garassino et al., 2014, and E. westphali Schweigert et al., 2000. E. quadriverrucatum differs from E. ornatum (Quenstedt, 1858) and E. punctatum in that the postcervical and branchiocardiac grooves are crossing at the level of the gastro-orbital groove (crossing lower for E. ornatum and E. punctatum), and the postcervical groove has a ventral extension (absent for E. ornatum and E. punctatum). E. quadriverrucatum also differs from E. westphali by the spineless rostrum and from *E. modestiforme* (von Schlotheim, 1822) by the rougher ornamentation of the carapace (despite the fine ornamentation for E. modestiforme).

Eryma sp. Figure 12.1–12.6

Description.—The specimens PIN 5477/4539 (Fig. 12.4, 12.5) and PIN 5477/4953 (Fig. 12.1–12.3) expose the isolated P1 chelae. The propodus is slightly laterally compressed (propodus length without index is \sim 12 mm; width is \sim 8 mm); the dorsal and ventral margins are narrow and carinate; the outer surface is slightly globose. The dactylar bulge is narrow and delimited by a deep groove. The fingers are elongate and equal in length; the index is strongly incurved at its basal part; the dactylus is almost straight and triangular in cross section. The ornamentation is represented by tubercles preceded with crescent-shaped depressions.

The specimen PIN 5477/4538 (Fig. 12.6) exposes the isolated P1 chela as well as other specimens. The propodus is subrectangular and laterally compressed, with narrow inner and outer margins. The dactylar bulge is narrow and delimited by a deep groove. The P1 fingers are thin, poorly preserved; the dactylus is subtriangular in cross section; the occlusal margin of the dactylus bears large closely spaced teeth. The ornamentation is represented by tubercles without depressions.

Material.—PIN 5477/4538, PIN 5477/4539, and PIN 5477/4953 from the upper Callovian of Gorenka.

Remarks.—The studied material can be attributed to family Erymidae and genus *Eryma* on the basis of the subrectangular propodus laterally compressed, bearing a narrow dactylar bulge; thin fingers; uniform ornamentation (Devillez and Charbonnier, 2021). However, these features are not sufficient to identify the specimens on the species level with confidence.

The general shape of specimens PIN 5477/4539 (Fig. 12.4, 12.5) and 5477/4953 (Fig. 12.1–12.3) is similar to those of E. mandelslohi (Devillez and Charbonnier, 2019, fig. 7E, F) and E. lerasi (Devillez and Charbonnier, 2021, fig. 6B). However, E. mandelslohi is considered to possess a bulge near the index base, which is not observed on the discussed specimens (Devillez and Charbonnier, 2019). In the case of E. lerasi, the chelae attributed to this species by Devillez and Charbonnier (2021) strongly vary. The specimens depicted in their fig. 6F-I well correspond to the species diagnosis, whereas the specimens in their fig. 6A, B have a shorter propodus, which is less compressed in fig. 6B and more rounded in fig. 6A compared with the other depicted chelae (Devillez and Charbonnier, 2021). The holotype of E. gracilimanum Lahusen, 1894 (Devillez and Charbonnier, 2021, fig. 6B) is considered to originate from the Tithonian, which could be the author's misinterpretation (Lahusen, 1894).

Genus Stenodactylina Beurlen, 1928

Type species.—Stenodactylina liasina Beurlen, 1928 by original designation from Toarcian, Holzmaden, Baden-Württemberg, Germany.

Stenodactylina insignis (Oppel, 1862) Figure 12.8, 12.9

Type material.—Cast of the holotype MNHN.F.A24613, collection of Muséum national d'Histoire naturelle, Paris, France (Devillez and Charbonnier, 2021, fig. 16A)

Description.—The specimen PIN 5477/4540 exposes the isolated P1 chela. The propodus is subrectangular and strongly elongate (length \sim 30 mm; width \sim 15 mm), globose in cross section, with outer margin more convex than inner one; the dactylar bulge is wide, delimited by a groove; the fingers are thin, very long, equal in width and length (preserved part \sim 30 mm); the index is wide basally, narrow at its middle and distal parts, having a strong inflexion at its basal third and sinuous distally; the dactylus is slightly incurved at its middle part; the occlusal margin has short conical teeth closely situated; the ornamentation of propodus is represented by small tubercles.

Material.—PIN 5477/4540 from the upper Callovian of Mikhailovtsement.

Remarks.—The specimen PIN 5477/4540 exposes the isolated chela (Fig. 12.8, 12.9) and is attributed to family Erymidae and genus *Stenodactylina* because the propodus is globose in cross section, the dactylar bulge is wide, the finger is slender, and the index is wide at its base and immediately narrowing distally.

Stenodactylina species are erected mostly on isolated chelae or carapaces (Feldmann et al., 2020). The few species are known from the Callovian to the Oxfordian (Feldmann et al., 2020; Devillez and Charbonnier, 2019, 2021): *S. walkerae* (Feldmann and Haggart, 2007) (Bajocian-Callovian, Canada), *S. burgundiaca* (Crônier and Courville, 2004) (Callovian, France), *S. insignis* (Oppel, 1862) (Oxfordian, France), and S. shotoverigiganti Devillez and Charbonnier, 2021 (Oxfordian, UK). The specimen PIN 5477/4540 (Fig. 12.8, 12.9) is similar to *S. insignis* in the following: subrectangular propodus; index wide basally, with strong medial inflexion; short conical teeth on the occlusal margin; the ornamentation represented by small tubercles (Devillez and Charbonnier, 2021, fig. 16A, C).

The specimen PIN 5477/4540 differs from *S. burgundiaca* in that the ornamentation is represented by small tubercles only (tubercles with crescent-shaped depressions for *S. burgundiaca*). Comparisons with *S. walkerae* and *S. shotoverigiganti* are quite difficult as those species are known only by isolated carapaces (Devillez and Charbonnier, 2019).

Stenodactylina sp. Figure 12.7

Description.—The specimen PIN 5477/4541 exposes the isolated finger of P1 chela. The finger is large (preserved part is \sim 20 mm long), slender, slightly inflected basally, rounded in cross section, ornamented by small tubercles; the occlusal margin bears short, close, conical teeth.

Material.—PIN 5477/4541 from the upper Callovian of Gorenka.

Remarks.—We attribute the specimen PIN 5477/4541 to *Stenodactylina* because of its size, form, and ornamentation, which well correspond to those of the specimen PIN 5477/4540 fingers, whereas all the *Eryma* remains from the studied deposits are far smaller. Due to the lack of diagnostic features, we propose the combination *Stenodactylina* sp. for the specimen PIN 5477/4541.

Discussion

Although only three species of decapods, *Archeosolenocera* sp., *Eryma quadriverrucatum* Trautschold, 1866, and *Mecochirus* sp., have been reported from the Callovian to the Oxfordian of European Russia, our study revealed a diverse assemblage of the crustaceans in the Ryazan region, which includes at least seven species from the four families (Solenoceridae, Mecochiridae, Glypheidae, and Erymidae). Among them, five taxa—*Eumorphia* sp., *Glypheopsis* aff. *G. etalloni* (Oppel, 1861), *Eryma* aff. *E. ventrosum* (von Meyer, 1835), *E. ornatum* (Quenstedt, 1858), and *Stenodactylina insignis* (Oppel, 1862)—have

never been previously acknowledged within the locations in European Russia.

Erymids of the Russian Middle Jurassic were traditionally attributed to *E. quadriverrucatum* Trautschold, 1866 (Gerasimov, 1955; Gerasimov et al., 1996), the presence of which in the studied deposits is here confirmed. The two other *Eryma* species, *E.* aff. *E. ventrosum* (von Meyer, 1835) and *E. ornatum* (Quenstedt, 1858), are much less abundant, and the latter is a single decapod species observed in the Koenigii zone of the lower Callovian. We also report about an occurrence of *Stenodactylina insignis* (Oppel, 1862) in the deposits of Mikhailovtsement and Gorenka quarries. *S. insignis* is usual in the Callovian of France, but it has never been reported from European Russia. The new records of *E. ornatum* and *S. insignis* extend their area to the east and outline a faunistic exchange between decapod fauna of European Russia and those of Western Europe in the Callovian and the lower Oxfordian.

Mecochiridae are the second-most abundant family after Erymidae, previously noted in the Saratov region (Tesakova, 2008). However, in the Moscow depression, they were overlooked by collectors and scientists for a long time, probably due to their small size. Most mecochirids are considered to be either epibenthic or half-burrowing animals (Simpson and Middleton, 1985; Robin et al., 2016), although in some works they are considered to be endobenthic (Förster, 1971; Etter, 2004). In Mikhailovtsement, Eumorphia sp. fossils are the most numerous in thin clay layers with phosphatized oolites. The same preservation is typical for Cretaceous Atherfieldastacus and Meyeria (Simpson and Middleton, 1985; Robin et al., 2016), which were associated with muddy substrates of the sublittoral zone. This condition is also specific for several localities in France containing Callovian crustacean remains (Crônier and Courville, 2004).

In contrast with Erymidae and Mecochiridae, glypheids are rare in the Jurassic of Moscow depression. Here we report first occurrences of glypheids in the middle and upper Callovian of European Russia. The lifestyle of extinct glypheids is considered to be similar to that of their living relatives (Boisselier-Dubayle et al., 2010; Charbonnier et al., 2012, 2014a), *Neoglyphea inopinata* Forest and de Saint Laurent, 1975 and *Laurentaeglyphea neocaledonica* (Richer de Forges, 2006). Modern glypheids are either epi- or endobenthic and occur mostly on the muddy substrates or in burrows at depths of 180–260 and 360–530 m, respectively (Forest, 2006; Charbonnier et al., 2012).

The single occurrence of solenocerid Archeosolenocera sp., previously reported by Shmakov (2016) as Archeosolenocera straeleni Carriol and Riou, 1991 in the Mikhailovtsement quarry, Ryazan region, is quite surprising. Solenoceridae have become quite an abundant group recently, yet they were represented, until now, by three samples of extant genera (Alencar et al., 2018) in the fossil record. Among them, only *Pryorhyncha feitosai* Alencar et al., 2018 from the Cretaceous of Brazil was found in shallow-water deposits (Alencar et al., 2018). The other two species, *Archeosolenocera straeleni* and *Eogordonella iranianiensis* Garassino et al., 2014, are considered to inhabit the soft surfaces in deep water (Charbonnier et al., 2009; Garassino et al., 2014; Jauvion et al., 2017). Moreover, *A. straeleni* is endemic to La Voulte, the deposits

		Locality						
Geological age	Group	Mikhailovcement	Gorenka	Spartak	Nikitino			
Upper Callovian	Erymidae	<i>Eryma quadriverrucatum</i> Trautschold, 1866 <i>Eryma</i> aff. <i>E. ventrosum</i> (von Meyer, 1835) <i>Eryma</i> sp.						
		Stenodactylina insignis (Oppel, 1862)	Stenodactylina (?) sp.					
	Glypheidae	Glypheopsis sp.	<i>Glypheopsis</i> cf. <i>G. etalloni</i> (Oppel, 1861)					
	Mecochiridae	Eumorphia sp.						
	Dendrobranchiata	Archeosolenocera sp. Penaeoidea indet.						
Lower Callovian	Erymidae			<i>Eryma ornatum</i> (Quenstedt, 1858)				
	Glypheidae			,	Glypheidae indet.			

Table 2. List of the revealed taxonomic assemblages for the studied localities.

of which originate from the hydrothermal vent (Charbonnier et al., 2009; 2014b). Such specific habitat does not correspond to typical conditions in the Middle Russian Sea (Sahagian et al., 1996; Tesakova et al., 2017) and might reflect the lower specificity of the genus *Archeosolenocera* to a particular depth. Among recent decapods, eurybathic distribution of a particular genus or even species is not exceptional (Fortibuoni et al., 2010; Linse et al., 2019; Rodriguez-Flores et al., 2022).

Whereas occurrences of crustaceans in the lower and middle Callovian of the region are still occasional, the upper Callovian and lower Oxfordian deposits contain abundant and relatively rich decapod assemblage (Table 2). An increase in the number of crustacean remains is more probably connected with good preservation conditions during this time rather than with real diversity changes. The modern stratigraphic data (Sahagian et al., 1996; Tesakova and Shurupova, 2018) indicate the average depth of the sea in European Russia was 40 m or less by the end of the Callovian. The oolites with the crustacean remains were formed during a regression phase by slow sedimentation (Stepanov et al., 2019) and were the most abundant in the upper sublittoral zone (Sahagian et al., 1996). Therefore, the Callovian decapod assemblage of the Mikhailovtsement and Gorenka quarries (Table 2) was composed mostly of epibenthic species and existed in the sublittoral zone on soft substrate. This assumption is confirmed by a specific ostracod composition (Tesakova, 2008; Tesakova et al., 2017; Tesakova and Shurupova, 2018) and the presence of a rich assemblage of burrowing bivalves, such as Pholadomya Sowerby, 1823, Gresslya Agassiz, 1843, Pleuromya Agassiz, 1842, and Trigonia Bruguière, 1789, in the same localities. The decapod community of the Ryazan region is quite similar to the West European Callovian-Oxfordian faunas on the generic level. However, at least three observed species are specific for the region. The most abundant decapod observed only in European Russia, Eryma quadriverrucatum, is probably endemic for the area. Eryma aff. E. ventrosum and Glypheopsis aff. G. etalloni demonstrate significant differences from the European populations of those species. However, their statuses, together with those of Archeosolenocera sp. and Eumorphia sp., need further clarification. The relatively poor taxonomical composition of studied localities compared with the European Jurassic Lagerstätten (Van Straelen, 1925; Etter, 2002; Garassino and Schweigert, 2006; Charbonnier et al., 2009; Odin et al., 2019) might be due to the limited number of studies and the problems with preservation of large crustaceans. Most of the remains are extremely damaged or fragmented and preserved only in the small nodules; thus, the specific geological conditions created a bias to the lesser forms, lacking such groups as Aegeridae Burkenroad, 1963, Coleiidae van Straelen, 1925, and Polychelidae Wood-Mason, 1874. The biodiversity of decapods in the studied area is still incomparable with those of Solnhofen (~70 crustacean species) and La Voulte (60 species) Lagerstätten (Garassino and Schweigert, 2006; Charbonnier et al., 2009; Jauvion et al., 2017). However, the occurrence of some other groups there, e.g., Prosopidae von Meyer, 1860 and Tanidromitidae crabs (Crônier and Boursicot, 2009) mentioned by Gerasimov, 1955, is expected. Future efforts will shed more light on the decapod diversity of the Middle Russian Sea during the Callovian.

Conclusions

Seven species of Decapoda belonging to four families are observed in the localities of the Ryazan region, Central European Russia. Among them, four taxa (Glypheopsis aff. G. etalloni, Eryma ornatum, E. aff. E. ventrosum, and Stenodactylina insignis) are newly recorded in the Jurassic of the Ryazan region. For E. quadriverrucatum, the emended diagnosis is offered. In addition, the morphology and status of Archeosolenocera sp., recorded as A. straeleni by Shmakov (2016), and Eumorphia sp., recorded as Mecochirus sp. by Tesakova (2008), are discussed. The crustacean assemblage is composed mostly of small decapods that inhabited the shallow sublittoral zone with a soft substrate. The late Callovian-early Oxfordian faunistic complex of Gorenka and Mikhailovtsement includes several specific taxa absent in Western Europe. The hidden decapod diversity reflects a poor knowledge about the regional fauna, which probably includes some more groups overlooked by researchers.

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Declaration of competing interests

The authors declare no competing interests.

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