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Revisiting brachyuran crabs (Malacostraca: Decapoda) from Oligocene and Miocene fish beds of Europe

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Abstract: The fossil records of decapod crustaceans (Malacostraca) from Oligocene and Miocene fish beds (i.e. laminated deposits with exceptional fish preservation and high organic content) of Europe have lacked a uniform taxonomic approach, prohibiting assessments of their diversity and distribution. Therefore, we revisited the systematics of brachyuran crabs from these deposits preserved in the Great Caucasian Basin, the Outer Carpathian Basin, and the Pannonian Basin. The revised material originates from the Lower Oligocene of Hungary (Tard Clay Formation), Poland (Menilite Formation), Romania (Dysodilic Shale Formation), and Ukraine (Menilite Formation); Upper Oligocene of Poland (Menilite Formation); and the Lower Miocene of Azerbaijan (Maikopian Series), the Czech Republic (Ždánice–Hustopeče Formation), and Russia (Maikopian Series). Previously unreported material includes decapod specimens from the Lower Oligocene of Abadzekhskaya, Russia. In total, three crab species were distinguished, including *Platymaia lethaea* (Smirnov, 1929), *Liocarcinus oligocenicus* (Paucă, 1929), and *Necronectes* sp. Among them, *L. oligocenicus* occurs at all studied localities and is the most widespread taxon. Although earlier records of this species were often recognized as separate taxa, we propose that *Portunus musceli* Paucă, 1929; *Portunus lancetidactylus* Smirnov, 1929; *Portunus arcuatus* var. *priscus* Smirnov, 1929; *Nautilograpsus prior* Smirnov, 1929; and *Portunus atropatanus* Aslanova & Dzhafarova, 1975, are junior subjective synonyms of *Liocarcinus oligocenicus*. Although decapod specimens preserved in Oligocene and Miocene fish beds are often represented by complete or near-complete articulated bodies, their extreme flattening distorts the outline of exoskeleton elements and obscures diagnostic characters on the dorsal carapaces, such as the development of grooves, regions, and cuticular ornamentation, posing a major problem in taxonomic evaluation of these decapods. Other traits commonly not preserved in the fossil record, such as eyes, antennae, and even gonopods can be observed, although their comparison with modern counterparts is limited.

Keywords: Decapod crustaceans, crabs, Oligocene, Miocene, taxonomy, fossil preservation

Introduction

Malacostraca-bearing Lagerstätten are primarily known from the Mesozoic (Klompmaker et al. 2019) and include, among others, the Lower Jurassic Posidonia shales in Germany (Beurlen 1930; Förster 1967; Schweigert et al. 2003; Audo 2016), Upper Jurassic Solnhofen-type plattenkalks in Germany (Garassino & Schweigert 2006; Schweigert 2011; Schweigert et al. 2016), and Cretaceous Lagerstätten of Hakel, Hadjoula, and Sahel Alma in Lebanon (Charbonnier et al. 2017).

In contrast, Cenozoic Lagerstätten with Malacostraca are generally less explored and less common. The best-known Cenozoic Lagerstätten are represented by the Eocene deposits at "Pesciara" (Bolca) and Monte Postale (Altissimo) in Italy (Secretan 1975; Pasini et al. 2019, in press). Remains of Oligocene decapods preserved in laminated shales were reported from Romania (Paucă 1929, 1933; Jerzmańska 1967), Hungary (Weiler 1933; Tasnádi-Kubacska 1936), Ukraine (Gorbach 1956), Poland (Jerzmańska 1967; Bieńkowska-Wasiluk 2010), Switzerland (Fröhlicher 1951), and Germany (Weiler 1966), whereas those from the Miocene were reported from Russia (Smirnov 1929; Garassino & Teruzzi 1996; Garassino & Novati 2001), the Czech Republic (Jaroš 1937, 1939), and Azerbaijan (Aslanova & Dzhafarova 1975).

Oligocene and Miocene malacostracan occurrences are related to the palaeogeographic evolution of the circum-Mediterranean region that led to the formation of semi-enclosed basins with high primary productivity and reduced ventilation of bottom waters. Only a handful of studies of Oligocene and

Miocene fish beds (i.e. laminated shales with high organic content and yielding exceptionally preserved articulated fish skeletons and other animal remains deposited under anoxic conditions) include systematic analysis of the decapod fauna. Most publications focus on fishes and mention crabs or other malacostracan crustaceans as an admixture in fish assemblages only (e.g. Bieńkowska-Wasiluk 2010; Schindler et al. 2011).

Here we provide an overview of all malacostracan taxa reported to date from Oligocene and Miocene fish beds of Europe as well as the results of thorough taxonomic revision of the brachyuran crabs (including the specimens from new localities) recorded in these deposits.

Malacostracan crustaceans in Oligocene and Miocene fish beds: previous research

Although decapods do not represent a major component of fossil assemblages in fish beds, they are conspicuous enough to be noted and at least briefly described. Their first systematic description dates back to 1929, when two contributions appeared simultaneously, reporting decapod associations from the North Caucasus, Russia (Smirnov 1929) and from Romania (Paucă 1929). Except for the revision by Garassino & Novati (2001), no special attention has been paid to the taxonomy of decapods described in these publications.

Smirnov (1929) described the decapod fauna from the Oligocene fish beds of the North Caucasus, consisting of several new taxa such as *Palaemon mortuus*, *Pasiphaea mortua*, *Portunus lancetidactylus*, *P. arcuatus* var. *priscus*; *Inachus lethaeus*, *Macropodia* (=*Stenorhynchus*) *lethaeus*, and *Nautilograpsus prior*. Paucă (1929) described two species, *Portunus oligocenicus* and *P. musceli*, from Oligocene deposits of Suslăneşti-Muscel and Bezdead-Dâmbovița in Romania. Paucă (1933) considered both taxa conspecific (*P. musceli* being a synonym of *P. oligocenicus*) and mentioned the occurrence of the species in Brzezówka (modern Poland). Based on F. Legányi's collection, Weiler (1933) reported the occurrence of crabs in the Oligocene of Eger, Hungary. Later, Tasnádi-Kubacska (1936) attributed these crabs to *Portunus oligocenicus*. Fröhlicher (1951) reported and figured two crab specimens attributed to Portunidae from the Lower Oligocene (Rupelian) fish beds of Luzern (Switzerland) – cf. *Portunus* sp. and cf. *Polybius* sp. Their taxonomic identification was carried out by Victor Van Straelen. Gorbach (1956) reported the occurrence of *P. oligocenicus* in Menilite shales in the territory of modern Ukraine. Aslanova & Dzhafarova (1975) documented a diverse crab assemblage from Azerbaijan, similar to the one described by Smirnov (1929).

Glaessner (1965) presented a synopsis of fossil decapods found in fish beds. He had studied Smirnov's original material then deposited in the Palaeontological Institute of the Academy of Sciences of USSR in Moscow. Glaessner (1965) also presented a new record of *Parribacus* sp. from the Oligocene of Galicia (southern Poland). Weiler (1966) mentioned crab specimens from Oligocene deposits in the surroundings of Heidelberg, Germany. Jerzmańska (1967) reported *P. oligocenicus* from Oligocene fish beds of Jamna Dolna and Rudawka Birczańska in Poland, and Bugiile de Sus in Romania. Jerzmańska & Kotlarczyk (1968) and Kotlarczyk (1991) reported the presence of crab fossils in the territory of Poland.

Garassino & Novati (2001) revised the crabs originally described by Smirnov (1929), although the revision was based on newly collected specimens from the Lower Miocene strata of the Apsheronsk Region, Russia, whereas the type locality, according to Smirnov (1929), was located in Vladikavkaz and was of Oligocene age. Garassino & Novati (2001) assigned *Portunus lancetidactylus* to *Liocarcinus* and placed *Inachus lethaeus* into the genus *Platymaia*.

Schweitzer et al. (2009: fig. 6) illustrated *Portunus oligocenicus* deposited in the University of Bucharest, Romania. Bieńkowska-Wasiluk (2010) reported crabs without closer identification from the Oligocene fish beds of Poland.

All above-mentioned records are characterized by a common mode of preservation: the crab specimens are flattened but are almost complete and often articulated. There are several decapod records having a different mode of preservation. From the Miocene of Moldova, Macarovici (1970) reported three-dimensionally preserved cheliped fingers. Although the material is represented by fragments, a new species, *Portunus thalae* Macarovici, 1970, was erected. Nevertheless, isolated fingers as depicted by Macarovici (1970, pl. 1, figs. 1–3) do not correspond to portunids but show traits of cancrids (Schram & Ng 2012; Hyžný & Dulai 2021).

From the Oligocene Kiscell Clay Formation of Hungary, overlying the Tard Clay Formation with highly flattened decapod specimens (Weiler 1933; Tasnádi-Kubacska 1936), a decapod assemblage formed by three-dimensionally preserved specimens was reported by Beurlen (1939) and revised by Hyžný & Dulai (2014) and Hyžný et al. (2020). The latter work (Hyžný et al. 2020) also included coeval material from Slovenia.

In addition to decapods, other malacostracan groups were reported from Oligocene fish beds as well. Racovitza & Sevastos (1910) described a new isopod genus and species *Proidotea haugi* from the Oligocene of Romania (figured also by Schweitzer et al. 2009: fig. 8). Van Straelen (1928) described *Proidotea carpathica* from the Menilite Series of Poland; later it was also reported by Kotlarczyk (1979). These isopod species have not been revised since their first description. Amphipods were reported from the Oligocene and Lower Miocene of Poland by Jerzmańska et al. (2001) and Bieńkowska-Wasiluk (2010). Amphipods depicted by Bieńkowska-Wasiluk (2010: text-fig. 43C–F) probably represent pleons of decapod shrimps.

Geological and stratigraphic settings

Finely laminated, organic-rich beds of Oligocene and Miocene age characterized by well-preserved fish assemblages yielding the decapod material considered in this study are exposed in the territory of modern Azerbaijan, the Czech Republic, Hungary, Poland, Romania, Russia, and Ukraine (Table 1, Fig. 1). Most of them were deposited within the former Outer Carpathian Basin, while the localities in Azerbaijan and Russia are confined to the Greater Caucasian Basin.

Greater Caucasian Basin (Azerbaijan) – Maikopian Series. Aslanova & Dzhafarova (1975) documented the presence of decapod fossils in diatomaceous laminated clays of the Apsheronsk Peninsula and Shemakhinsky district, where they were found in a number of localities (Atashkia, Binagady, Engekharan, Perekeshkul, Qayiblar, and Shaiblar). The information about the lithology and age of these deposits is rather limited. Aslanova & Dzhafarova (1975: 42) suggested that they are "identical to those of Chernaya Rechka" in Russia (see below). Therefore, these specimens could be tentatively assigned to the Lower Miocene.

Outer Carpathian Basin (Czech Republic) – Ždánice–Hustopeče Formation. Jaroš (1937, 1939) described an ichthyofauna together with crab specimens of *Portunus oligocenicus* in grey marly shales exposed in Vážany nad Litavou (formerly Linhartské Vážany). The locality is situated 4 km south-west of Slavkov (Austerlitz) in the Czech Republic. The fish fauna consisting of at least nine taxa was presented by Jaroš (1937), Kalabis (1968), and Reichenbacher et al. (2018). Remains of marine algae and continental flora were also recorded (Hably pers. comm. in Reichenbacher et al. 2018). The Ždánice–Hustopeče Formation is considered to be of Early Miocene (Aquitanian–Burdigalian) age (Stráník et al. 2007).

Pannonian Basin (Hungary) – Tard Clay Formation. Crab fossils were reported from Eger-Kiseged in Hungary (Weiler 1933; Tasnádi-Kubacska 1936). This locality is situated in the north-east of the country, ca. 130 km north-east of Budapest. Strata of the Tard Clay Formation exposed here yield specimen-rich fossil flora (Andreánszky 1964; Kvaček & Hably 1998; Hably & Erdei 2015) and fauna (Weiler 1933, 1938; Tasnádi-Kubacska 1936; Báldi 1973; Báldi et al. 1983; Monostori 1986, 1987; Erdei et al. 2011). The Tard Clay Formation is composed of brownish grey argillaceous siltstones with a high silica content (Erdei et al. 2011) and of laminated shales (Nagymarosy 1983, 1986) strongly resembling those of the coeval Menilite or Dysodilic shales in the flysch zone of the Carpathians (Báldi 1983; Erdei et al. 2011). Their sedimentation had taken place under anoxic conditions as suggested by Bechtel et al. (2012). The age of the fossiliferous layers at Eger-Kiseged was estimated as Early Oligocene, Rupelian (Andreánszky 1964; Báldi 1983; Nagymarosy & Báldi-Beke 1988). Crab fossils occurring together with plant remains are confined to the upper part of the Tard Clay Formation, which is assigned to the NP 23 Zone (Nagymarosy & Báldi-Beke 1988; Kvaček and Hably 1998; Vakarcs et al. 1998).

Outer Carpathian Basin (Poland) – Menilite Formation. Decapod crustaceans were collected together with fish fossils from a number of Oligocene localities in the territory of Poland (Paucă 1933; Glaessner 1965; Jerzmańska 1967; Kotlarczyk & Jerzmańska 1988; Kotlarczyk 1991; Bieńkowska-Wasiluk 2010; Přikryl et al. 2016). Here, in the Skole, Subsilesian, and Silesian tectonic units of the Outer Western Carpathians, pelitic sediments (e.g. grey siliceous-clayey or calcareous shales and micritic limestones) of the Menilite Formation are exposed (Kotlarczyk et al. 2006). The beds with crab fossils belong to the Rudawka Tractionite, Błażowa, Korzeniówka, and Šitbořice members (Kotlarczyk et al. 2006).

Table 1: Generalized data on the studied record localities yielding the remains of Oligocene and Miocene brachyuran crabs.

Country	Locality	Coordinates	Age		Reference
			relative	absolute	
Azerbaijan	Perekeshkul	40.5047, 49.6060	Early Miocene, Burdigalian	–	Aslanova & Dzhafarova 1975
Czech Republic	Vážany nad Litavou	49.1313, 16.8557	Early Miocene, Burdigalian	20.4–19.1 Ma	Reichenbacher et al. 2018
Hungary	Eger-Kiseged	47.9000, 20.5000	Early Oligocene, Rupelian	–	Tasnádi-Kubacska 1936
Poland	Błażowa (B-1)	49.8812, 22.1021	Late Oligocene, Chattian	ca. 25.5 Ma	Bieńkowska-Wasiluk 2010
Poland	Brzezówka	49.9370, 22.1357	Early Oligocene, Rupelian	ca. 31.5 Ma	Paucă 1934
Poland	Iwonicz near Krosno	49.6078, 21.8044	Early Oligocene, Rupelian	ca. 32.5 Ma	Glaessner 1965
Poland	Jamna Dolna	49.6401, 22.5596	Early Oligocene, Rupelian	ca. 31.5 Ma	Jerzmańska 1967
Poland	Rudawka Birczańska	49.7083, 22.4240	Early Oligocene, Rupelian	ca. 31.5 Ma	Jerzmańska 1967
Poland	Krępak	49.7009, 22.5269	Late Oligocene, Chattian	25.5 Ma	Bieńkowska-Wasiluk 2010
Romania	Bezdead-Dâmbovița	45.1822, 25.4955	Early Oligocene, Rupelian	ca. 31.0 Ma	Paucă 1929
Romania	Buciumeni	45.1641, 25.4601	Early Oligocene, Rupelian	ca. 31.0 Ma	Schweitzer et al. 2009
Romania	Bugiile de Sus (=Bughea de Sus)	45.2893, 25.0217	Early Oligocene, Rupelian	ca. 31.0 Ma	Jerzmańska 1967
Romania	Fieni near Campulung	45.1468, 25.4195	Early Oligocene, Rupelian	ca. 31.0 Ma	Schweitzer et al. 2009
Romania	Suslănești-Muscel	45.2410, 25.1258	Early Oligocene, Rupelian	ca. 31.0 Ma	Paucă 1933–1934
Romania	Târgoviște	44.9164, 25.5058	Early Oligocene, Rupelian	ca. 31.0 Ma	Schweitzer et al. 2009
Russia	Chernaya Rechka	43.5933, 43.8372	Early Miocene, Burdigalian	–	Smirnov 1929
Russia	Apsheronsk	–	Early Miocene, Burdigalian	–	Garassino & Novati 2001
Russia	Abadzekhskaya	44.4173, 40.2038	Early Oligocene, Rupelian	ca. 33–32 Ma	herein
Ukraine	Liubizhnia	48.5167, 24.6167	Early Oligocene, Rupelian	ca. 32-31 Ma	Gorbach 1956
Ukraine	Verkhnie Syniovydne	49.0833, 23.5833	Early Oligocene, Rupelian	ca. 32-31 Ma	Gorbach 1956

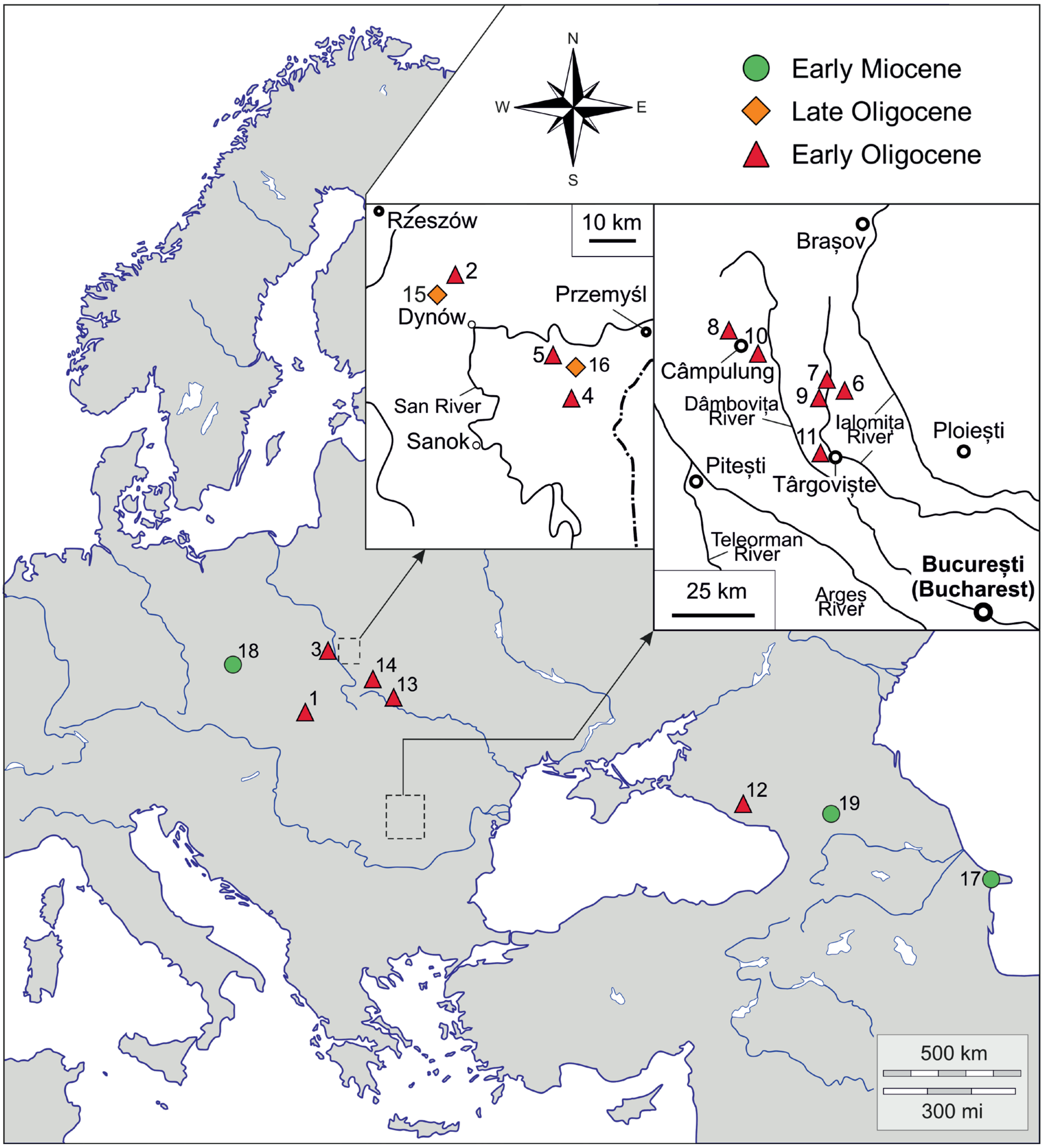

Fig. 1. Studied localities with Oligocene and Miocene fish beds (laminated shales) yielding decapod crustaceans. 1 – Eger-Kiseged, Hungary; 2 – Brzezówka, Poland; 3 – Iwonicz near Krosno, Poland; 4 – Jamna Dolna, Poland; 5 – Rudawka Birczańska, Poland; 6 – Bezdead-Dâmbovița, Romania; 7 – Buciumeni, Romania; 8 – Bugiile de Sus, Romania; 9 – Fieni near Câmpulung, Romania; 10 – Suslănești-Muscel, Romania; 11 – Târgoviște, Romania; 12 – Abadzekhskaya, Russia; 13 – Liubizhnia, Ukraine; 14 – Verkhnie Syniovydne, Ukraine; 15 – Błażowa, Poland; 16 – Krępak, Poland; 17 – Perekeshkul, Azerbaijan; 18 – Vážany nad Litavou, the Czech Republic; 19 – Chernaya Rechka, Russia; 20 – Apsheronsk, Russia.

The depositional setting of these localities was interpreted as either neritic-sublittoral or bathyal based on differences in the species composition of fish and accompanying fauna (Kotlarczyk et al. 2006; Bieńkowska-Wasiluk 2010). Although the studied sites are located rather close to each other, the age of collected fossil remains covers almost the entire Oligocene. The studied crab fossils are confined to several ichthyofaunal zones: IPM 1 (ca. 32.5 Ma), IPM 2 (ca. 31.5 Ma), and IPM 4A (ca. 29.5 Ma) within the Rupelian, as well as IPM 6 (26.0–25.5 Ma), and IPM 7 (ca. 24.5 Ma) within the Chattian (Kotlarczyk et al. 2006; Bieńkowska-Wasiluk 2010).

Outer Carpathian Basin (Romania) – Dysodilic Shale Formation. Suslănești-Muscel is one of the most important localities yielding fish fossils within the area of the former

Paratethys (Paucă 1933; Constantin 1999). It is located in the Câmpulung Muscel Depression in the south-eastern region of the Southern Carpathians (Băcăuanu et al. 1992). The studied crab fossils were collected from beds of the Dysodilic Shale Formation. Based on the study of fish fossils, Paucă (1933) considered the age of the Lower Dysodilic Shales as Early Oligocene. The Rupelian age of these deposits was confirmed later by studies of calcareous nannofossils based on the presence of *Reticulofenestra circus* (FO in NP22, LO in NP23) and *Reticulofenestra umbilicus* (LO in NP23 at 32.02 Ma) (Melinte, unpublished data). Crab fossils collected from Bugiile de Sus (Jerzmańska 1967; Constantin 1999), Bezdead-Dâmbovița (Paucă 1929), Buciumeni (Schweitzer et al. 2009), Fieni near Câmpulung, and Târgoviște (Schweitzer et al. 2009) are also confined to the Dysodilic Shale Formation, NP 23 Zone, as evidenced by the presence of *Transversopontis fibula* and *Reticulofenestra ornata* (Melinte-Dobrinescu & Brustur 2008).

Greater Caucasian Basin (Russia) – Maikopian Series (lower part). The decapod-bearing locality of Abadzekhskaya is situated on the bank of the Belaya River, near the eponymous village in Maikopskyi District, Republic of Adygea, Russia. Decapod remains were recovered from the Pshekha Horizon, assigned to the lower (Khadumian) substage of the Maikopian Series (Daniltshenko 1960; Bannikov & Parin 1997; Bannikov 2010). It corresponds to the lower part of the Rupelian, Lower Oligocene (Popov et al. 2009; Sachsenhofer et al. 2017).

Greater Caucasian Basin (Russia) – Maikopian Series (upper part). A diverse decapod assemblage together with fish imprints was collected by V. P. Smirnov in clayey shales of the Chernaya Rechka locality (Russia) in the 1920s (Garassino & Teruzzi 1996; Kovalchuk et al. 2020). Smirnov (1929) erroneously assigned the upper Maikopian layers with fossils to the Oligocene. Daniltshenko (1960, 1980) corrected their age as Lower Miocene (Bannikov et al. 2009) and correlated it with the Sakaraulian (equivalent to Eggenburgian, lower Burdigalian).

Outer Carpathian Basin (Ukraine) – Menilite Formation. Gorbach (1956) reported the finding of two well-preserved crab specimens from Lower Oligocene deposits of western Ukraine. The first specimen comes from dark grey clayey shales of the stream Liubizhnia near the village of Deliatyn, Ivano–Frankivsk Oblast. The second one (associated with fish fossils, namely of *Palaeogadus*) comes from the flint series (black sillicites and laminated shales) exposed near the village of Verkhnie Syniovydne (former Siniewodsko Wyżne), Lviv Oblast. According to Gorbach (1956), these fossils are older than the ones described by Smirnov (1929) from the North Caucasus. Their age was estimated as Early Oligocene (Rupelian), being equal to the Khadumian substage of the Maikopian Series of the Caucasus (Gorbach 1956). Crab-bearing strata were deposited later than those belonging to the Rybnitsa Member (L 7-8 at the scheme in Přikryl et al. 2017); therefore, they could be tentatively dated to 32–31 Ma.

Material and methods

Most fossil crabs presented here were studied first-hand (Table 2); that is, much effort has been made to re-examine all of the previously published records. The original crab material from the Oligocene of Romania presented by Paucă (1933) was studied via photos. Additionally, in the collections of NHMW, a single specimen of *Liocarcinus oligocenicus*, collected and donated by M. Paucă, was examined together with newly collected material from the type locality of this species. Part of the original material collected by Smirnov (1929) in the North Caucasus was found in NHMUK (by MH). In addition, specimens from Smirnov's personal collection (Berezovsky et al. 2021) were also studied. All crab specimens from the Oligocene of Poland and Romania presented by Jerzmańska (1967) and stored in ZPALWr. were re-examined as well (by OK and EŚ).

Crab specimens from Eger, Hungary, identified by Pál Müller and deposited in MBFSZ come from the same locality as those described by Weiler (1933) and Tasnádi-Kubacska (1936) and, in fact, may represent the same collection. A single specimen of *Portunus oligocenicus* from Vážany nad Litavou, Czech Republic was studied too (by MH); the specimen was collected and identified by Jaroš himself (see Jaroš 1937, 1939). Finally, part of the material reported in Garassino & Novati (2001) and coming from the Miocene of the North Caucasus was also re-examined. The repository of specimens described by Gorbach (1956) is unknown. Nevertheless, we examined a crab specimen collected later at the same locality and recently deposited in the NMNHU-P. The specimens described by Aslanova & Dzhafarova (1975) were studied only on the basis of published figures. Previously unpublished material presented here includes the specimens collected by Kiselev in 1978 from the Lower Oligocene deposits of the Abadzekhskaya locality. The material was documented photographically under various light settings, including angled light because of the low relief of the specimens. Some specimens were immersed in alcohol prior to photographing. Details of gonopods in the material of Smirnov (1929) were documented using a Stereo Zoom Microscope ZEISS Axio Zoom.V16 with AxioCam HRC and a Canon EOS 750D camera with EF 50 mm f/2.5 Compact Macro Lens.

Repositories: KNU – Department of Geology and Applied Mineralogy, Kryvyi Rih National University, Kryvyi Rih, Ukraine; MBFSZ – Mining and Geological Survey of Hungary, Budapest, Hungary; MNSPN-PC – Paleontological Collection of the Natural Sciences Museum Piatra-Neamţ, Romania; NGMR – National Geology Museum, Bucharest, Romania; NHMUK – Natural History Museum, London, UK; NHMW – Natural History Museum Vienna, Austria; NMNHU-P – Department of Palaeontology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv, Ukraine (collection IN); PIN – Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; ZPALWr. – Department of Palaeozoology, University of Wrocław, Poland.

Table 2: Studied specimens of brachyuran crabs. Y = Yes; N = No.

Repository	Number	Country	Locality	Taxon (current status)	Taxon (as published)	Reference to published figure	personally examined
		Azerbaijan	Perekeshkul	*Liocarcinus oligocenicus*	*Portunus atropatanus*	Aslanova & Dzhafarova 1975: pl. 1, fig. 1	N
		Azerbaijan	Perekeshkul	*Liocarcinus oligocenicus*	*Portunus atropatanus*	Aslanova & Dzhafarova 1975: pl. 1, fig. 2	N
		Azerbaijan	Perekeshkul	*Liocarcinus oligocenicus*	*Portunus* cf. *lancetodactylus*	Aslanova & Dzhafarova 1975: pl. 1, fig. 3	N
		Azerbaijan	Perekeshkul	*Liocarcinus oligocenicus*	*Portunus* cf. *lancetodactylus*	Aslanova & Dzhafarova 1975: pl. 1, fig. 4	N
		Azerbaijan	Perekeshkul	*Liocarcinus oligocenicus*	*Inachus* sp.	Aslanova & Dzhafarova 1975: pl. 2, fig. A	N
		Azerbaijan	Perekeshkul	*Platymaia lethaea*	*Inachus* sp.	Aslanova & Dzhafarova 1975: pl. 2, fig. B	N
		Azerbaijan	Perekeshkul	*Platymaia lethaea*	*Inachus* sp.	Aslanova & Dzhafarova 1975: pl. 2, fig. C	N
MZM	Ge25029	Czech Republic	Vážany nad Litavou	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
		Czech Republic	Vážany nad Litavou	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jaroš 1939: fig. 2	N
MBFSZ	O.1334	Hungary	Eger-Kiseged	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MBFSZ	O.1334	Hungary	Eger-Kiseged	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MBFSZ	O.1334	Hungary	Eger-Kiseged	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MBFSZ	O.1334	Hungary	Eger-Kiseged	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MBFSZ	O.1334	Hungary	Eger-Kiseged	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MBFSZ	O.1334	Hungary	Eger-Kiseged	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MBFSZ	O.1334	Hungary	Eger-Kiseged	*Platymaia lethaeus*	*Portunus oligocenicus*		Y
		Poland	Jamna Dolna	*Liocarcinus oligocenicus*	"crab"	Bieńkowska-Wasiluk 2010: text-fig. 43A	N
ZPALWr.	A/224	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/225	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: fig. 2b	Y
ZPALWr.	A/226	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/227	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/228	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/229	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/230	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: fig. 2a; Jerzmańska & Kotlarczyk 1968: fig. 4.	Y
ZPALWr.	A/231	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/232	Poland	Jamna Dolna	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	Kr/4	Poland	Krępak	*Necronectes* sp.			Y
ZPALWr.	Kr/5	Poland	Krępak	*Necronectes* sp.			Y
ZPALWr.	Kr/6	Poland	Krępak	*Necronectes* sp.			Y
		Poland	Krępak	*Necronectes* sp.	"crab"	Bieńkowska-Wasiluk 2010: text-fig. 43B	N
ZPALWr.	A/233	Poland	Rudawka Birczańska	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: fig. 1	Y
ZPALWr.	A/234	Romania	Bugiile de Sus	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/235	Romania	Bugiile de Sus	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
ZPALWr.	A/236	Romania	Bugiile de Sus	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Jerzmańska 1967: material	Y
MNSPN	PC No. 925	Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MNSPN	PC No. 926	Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MNSPN	PC No. 927	Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MNSPN	PC No. 928	Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MNSPN	PC No. 929	Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
MNSPN	PC No. 930	Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
		Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus musceli*	Paucă 1933: pl. 5, fig. 6	N
NHMW	1930/0004/0001	Romania	Suslănești-Muscel	*Liocarcinus oligocenicus*	*Portunus oligocenicus*		Y
LPB	IIIart017	Romania	Fieni	*Liocarcinus oligocenicus*	*Liocarcinus oligocenicus*	Schweitzer et al. 2009: fig. 6	N
NMNHU-P	IN 1	Russia	Abadzekhskaya	*Liocarcinus oligocenicus*			Y
NMNHU-P	IN 2	Russia	Abadzekhskaya	*Liocarcinus oligocenicus*			Y
NMNHU-P	IN 3	Russia	Abadzekhskaya	*Liocarcinus oligocenicus*			Y
NMNHU-P	IN 4	Russia	Abadzekhskaya	*Liocarcinus oligocenicus*			Y
NMNHU-P	IN 5	Russia	Abadzekhskaya	*Platymaia lethaea*			Y
NMNHU-P	IN 6	Russia	Abadzekhskaya	*Platymaia lethaea*			Y

Table 2 (continued)

Repository	Number	Country	Locality	Taxon (current status)	Taxon (as published)	Reference to published figure	personally examined
NMNHU-P	IN 7	Russia	Abadzekhskaya	*Platymaia lethaea*			Y
NMNHU-P	IN 8	Russia	Abadzekhskaya	*Platymaia lethaea*			Y
MSNM	i22863	Russia	Apsheronsk	*Liocarcinus oligocenicus*	*Liocarcinus lancetidactylus*	Garassino & Novati 2001: fig. 5	Y
MSNM	i22864	Russia	Apsheronsk	*Liocarcinus oligocenicus*	*Liocarcinus lancetidactylus*	Garassino & Novati 2001: fig. 4	Y
PIN	4504-6	Russia	Apsheronsk	*Liocarcinus oligocenicus*	*Liocarcinus lancetidactylus*	Garassino & Novati 2001: fig. 3	N
PIN	4504-9	Russia	Apsheronsk	*Platymaia lethaea*	*Platymaia lethaeus*	Garassino & Novati 2001: fig. 6	N
MSNM	i13531	Russia	Apsheronsk	*Platymaia lethaea*	*Platymaia lethaeus*	Garassino & Novati 2001: fig. 7	N
MSNM	i22860	Russia	Apsheronsk	*Platymaia lethaea*	*Platymaia lethaeus*	Garassino & Novati 2001: fig. 8	N
NHMUK	In36651	Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Portunus lancetidactylus*	Smirnov 1929: pls, fig. 3	Y
NHMUK	In36650	Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus lancetidactylus*	Smirnov 1929: material	Y
NHMUK	In36652	Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus arcuatus priscus*	Smirnov 1929: material	Y
NHMUK	In36653	Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus arcuatus priscus*	Smirnov 1929: material	Y
KNU	4	Russia	Chernaya Rechka	*Platymaia lethaea*	*Platymaia lethaeus*	Berezovsky et al. 2021: fig. 4	Y
KNU	3	Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus prior*	Berezovsky et al. 2021: figs. 1a, 3	Y
KNU	5	Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Platymaia lethaeus*	Berezovsky et al. 2021: fig. 5	Y
KNU	2	Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus prisca*	Berezovsky et al. 2021: fig. 2	Y
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Portunus lancetidactylus*	Smirnov 1929: pls, figs. 1, 2	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Portunus lancetidactylus*	Smirnov 1929: pls, fig. 4	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Portunus lancetidactylus*	Smirnov 1929: pls, fig. 5	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Portunus lancetidactylus*	Smirnov 1929: pls, fig. 6	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Portunus lancetidactylus*	Smirnov 1929: pls, fig. 7	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus arcuatus priscus*	Smirnov 1929: pls, fig. 17	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus arcuatus priscus*	Smirnov 1929: pls, fig. 18	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus arcuatus priscus*	Smirnov 1929: pls, fig. 19	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus arcuatus priscus*	Smirnov 1929: pls, fig. 20	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Liocarcinus arcuatus priscus*	Smirnov 1929: pls, fig. 21	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Nautilograpsus prior*	Smirnov 1929: pls, fig. 22	N
		Russia	Chernaya Rechka	*Liocarcinus oligocenicus*	*Nautilograpsus prior*	Smirnov 1929: pls, fig. 23	N
		Russia	Chernaya Rechka	*Platymaia lethaea*	*Inachus lethaeus*	Smirnov 1929: pls, figs. 27, 29	N
		Russia	Chernaya Rechka	*Platymaia lethaea*	*Inachus lethaeus*	Smirnov 1929: pls, figs. 28, 30	N
		Russia	Chernaya Rechka	*Platymaia lethaea*	*Macropodia* sp.	Smirnov 1929: pls, fig. 31	N
		Russia	Chernaya Rechka	*Platymaia lethaea*	*Inachus lethaeus*	Smirnov 1929: pls, fig. 32	N
NMNHU-P	IN 9	Ukraine	Liubizhnia	*Liocarcinus oligocenicus*			Y
		Ukraine	Liubizhnia	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Gorbach 1956: fig. 1a	N
		Ukraine	Liubizhnia	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Gorbach 1956: fig. 1b	N
		Ukraine	Liubizhnia	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Gorbach 1956: fig. 1c	N
		Ukraine	Liubizhnia	*Liocarcinus oligocenicus*	*Portunus oligocenicus*	Gorbach 1956: fig. 2	N

Systematic palaeontology

Decapoda
Brachyura
Majoidea
Inachidae
Platymaia Miers in Tizard, Moseley, Buchanan & Murray, 1885

Type species: *Platymaia wyvillethomsoni* Miers in Tizard, Moseley, Buchanan & Murray, 1885, by monotypy.

Platymaia lethaea (Smirnov, 1929)
Figure 2A–F

1929 *Inachus lethaeus* – Smirnov, p. 28, text-fig. 10, text-fig. 11 (left), pls. 11–14 (figs. 27–30, 32, 39–50).
1929 *Macropodia* (*Stenorhynchus*) *lethaeus* – Smirnov, p. 30, text-fig. 11 (right), pls. 12–14 (figs. 31, 51–54).
1975 *Inachus* sp. – Aslanova & Dzhafarova, p. 44, pl. 2, figs. b–c. [fig. a = *Liocarcinus oligocenicus*]
2001 *Platymaia lethaeus* (Smirnov) – Garassino & Novati, p. 273, figs. 2, 6–8.

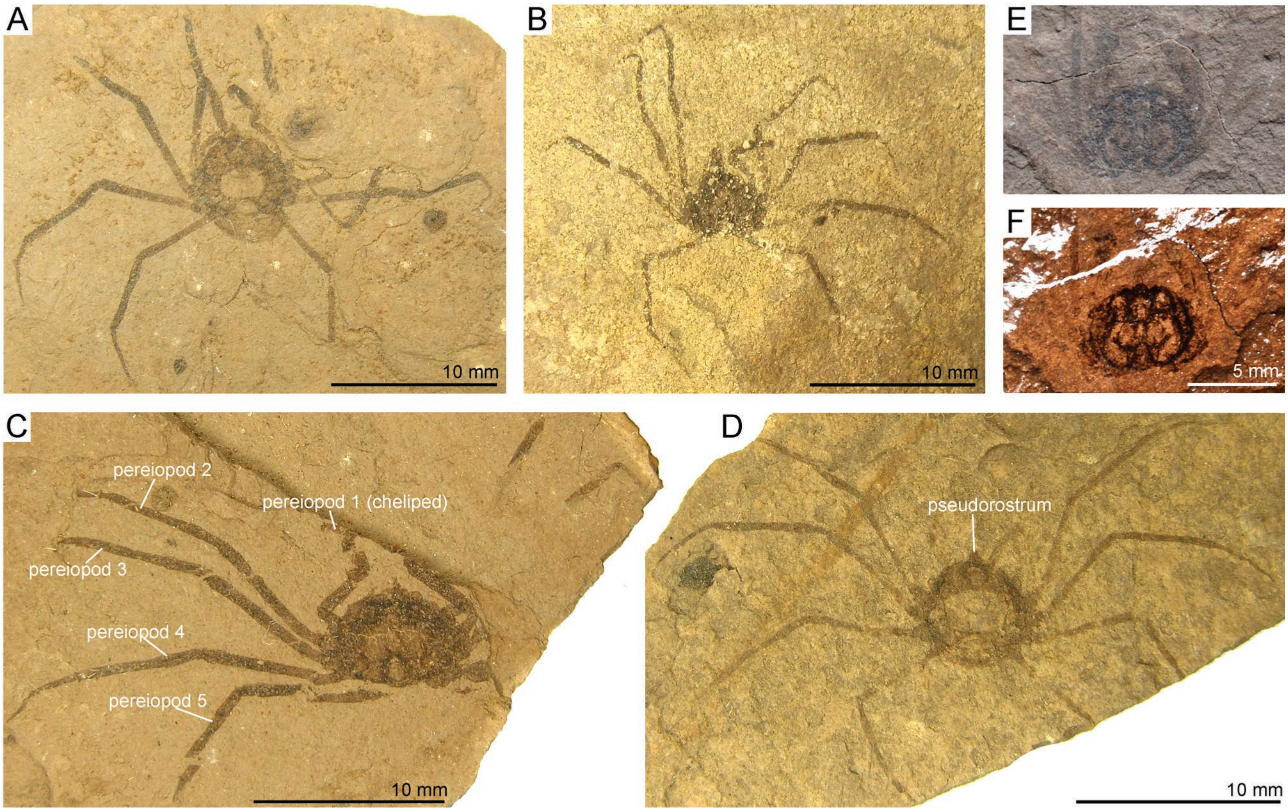

Fig. 2. *Platymaia lethaea* (Smirnov, 1929). **A** — Near-complete female (NMNHU-P IN 6). **B** — Near-complete individual of indeterminate sex (NMNHU-P IN 5). **C** — Near-complete male (NMNHU-P IN 8). **D** — Near-complete female (NMNHU-P IN 7). **E** — Near-complete individual of indeterminate sex (KNU 4). **F** — The same as in E, photographed under alcohol to enhance contrast. Localities: Abadzekhskaya, Russia (A–D), Chernaya Rechka, Russia (E, F).

2010 *Stenorhynchus lethaeus* (Smirnov) – Schweitzer et al., p. 94.
2010 *Inachus lethaeus* (Smirnov) – Schweitzer et al., p. 94.
2021 *Platymaia lethaeus* (Smirnov) – Berezovsky et al., p. 21, fig. 4. [fig. 5 = *Liocarcinus oligocenicus*]

Studied material: Four near-complete specimens from Abadzekhskaya, Russia (NMNHU-P IN 5–8); one near-complete specimen from Chernaya Rechka, Russia (KNU 4); one incomplete specimen from Eger-Kiseged, Hungary (MBFSZ O.1334).

Emended diagnosis: Carapace pyriform to subcircular, approximately as wide as long (without pseudorostral spines), lateral margins without apparent spination; orbits with postorbital spines; cardiac region presumably wider than gastric region; pereiopods 1 (chelipeds) distinctly shorter and slightly stouter than pereiopods 2–5; pereiopods without apparent spination except one distal spine on pereiopod 1 merus and three distal spines on pereiopod 1 carpus.

Description: Carapace pyriform to subcircular/subovoid in outline (depending on nature of secondary flattening), approximately as wide as long except for medium pseudorostral spine accompanied by one smaller spine on each side; lateral margins without spines. Orbits with well-developed postorbital spines. Carapace regions poorly discernible; branchial regions large, cardiac region appearing wider than gastric region. Eyestalks short, eyes very large. Pereiopods 1 (chelipeds) distinctly shorter and slightly stouter than pereiopods 2–5. Pereiopod 1 merus with distal spine, carpus with three spines at joint with propodus, fingers as long as or slightly longer than manus. Pereiopods 2–5 of equal length, approximately twice as long as pereiopod 1, all elements slender, dactyli with acute distal tips. Sternum subcircular, details not discernible. Female pleon as wide as sternum.

Remarks: Smirnov (1929) assigned the crab specimens from fish beds of the North Caucasus having a small pear-shaped carapace and long legs to two genera, *Inachus* and *Macropodia*, both being representatives of Inachidae. Unfortunately, the specimens were rather small and do not offer many taxonomically important details, such as the number and arrangement of tubercles on the dorsal carapace. Therefore, the assignment to respective genera was based on the size of the rostrum, position of the eyes, and the shape of "orbits." Nevertheless, Smirnov (1929: p. 30) admitted that both forms were very similar to one another. Later, Garassino & Novati (2001) noted that there were no morphological differences between the specimens attributed by Smirnov (1929) to *Inachus* and *Macropodia*. They considered that both taxa represent *Inachus lethaeus*, and assigned it to the genus *Platymaia* Miers in Tizard, Moseley, Buchanan & Murray, 1885 (as revised by Guinot & Richer de Forges 1986).

Schweitzer et al. (2010) listed both species as distinct taxa, *Platymaia lethaea* and *Stenorhynchus lethaeus*. We concur with Garassino & Novati (2001) and consider the observable differences between *I. lethaeus* and *S. lethaeus* as a taphonomical artifact. Morphological details of the flattened specimens are often obscured, and the outline of the carapace and appendages preserved in this manner may not correspond to its original state. Based on the recommendation of ICZN, we modified herein the original species name *lethaeus* to reflect the feminine gender of the genus name *Platymaia*.

The assignment of Smirnov's material to the genus *Platymaia* is considered here as preliminary. Although we concur with Garassino & Novati (2001: 274) that "the subovoidal carapace with well-developed branchial regions, the short rostrum [sic!] with one small tooth on the base of lateral margins, pereiopod I shorter than the others (…) and the pereiopods II–V of the same length, are typical morphological features of the living genus *Platymaia*," other important details discussed by Guinot & Richer de Forges (1986) are unavailable, either because of their absence or insufficient preservation. The apparent absence of multiple spines on the carapace and pereiopods of *P. lethaea* is a distinctive character that discriminates this species from its extant congeners (Rathbun 1916; Macpherson 1984; Guinot & Richer de Forges 1986). It may also imply the distinctiveness of the fossil species, especially in the light of its occurrence far from the geographic distribution of modern species in the Indo-Pacific (Guinot & Richer de Forges 1986). In addition, the cardiac region in the sketch of *Inachus lethaeus* as depicted by Smirnov (1929, pl. 13, fig. 39) appears to be distinctly wider than the gastric region, which is not the case in modern representatives of *Platymaia* (Guinot & Richer de Forges 1986). The preservation of the available material does not allow the carapace regions of *P. lethaea* to be reconstructed with confidence. Nevertheless, for the time being, we keep the respective species classified within *Platymaia*. No other fossil species attributable to *Platymaia* is known.

Unfortunately, the majority of original material of Smirnov that was assigned to *Platymaia lethaea* is considered lost. The only specimen of this species demonstrably coming from Smirnov's collection was re-examined by Berezovsky et al. (2021) and is refigured herein (Fig. 2E, F). Garassino & Novati (2001) selected a neotype of *P. lethaea*, being a specimen (PIN 4504-9) of a near-complete individual collected from the Apsheronsk Region.

Based on the examination of the photographs of *Inachus* sp. from the Lower Miocene of Azerbaijan (Aslanova & Dzhafarova 1975), that record is also assigned to *Platymaia lethaea*. One of the specimens assigned to *P. lethaeus* by Berezovsky et al. (2021: fig. 5), in fact, represents *Liocarcinus oligocenicus*.

Occurrence: Lower Oligocene of Hungary (herein) and Russia (herein); Lower Miocene of Russia (Smirnov 1929; Garassino & Novati 2001; Berezovsky et al. 2021) and Azerbaijan (Aslanova & Dzhafarova 1975).

Portunoidea

Polybiidae

Liocarcinus Stimpson, 1871

Type species: *Portunus holsatus* Fabricius, 1798, by original designation.

***Liocarcinus oligocenicus* (Paucă, 1929)**

Figures 3A–F, 4A–F, 5A–G, 6A–C

1929 *Portunus oligocenicus* – Paucă, p. 15, fig. 1.
1929 *Portunus musceli* – Paucă, p. 16, fig. 2.
1929 *Portunus lancetidactylus* – Smirnov, p. 13, text-figs. 4–7, pls. 3–8 (figs. 1–16).
1929 *Portunus arcuatus* var. *priscus* – Smirnov, p. 23, pls. 9–10 (figs. 17–21).
1929 *Nautilograpsoides* (varietas dubia) – Smirnov, p. 24, text-fig. 9, pls. 10–11 (figs. 22–26, as *Nautilograpsus prior*).
1933 *Portunus oligocenicus* Paucă – Paucă, p. 75, text-fig. 30, pl. 5, fig. 6.
1936 *Portunus oligocenicus* Paucă – Tasnádi-Kubacska, p. 116.
1956 *Portunus oligocenicus* Paucă – Gorbach, p. 308, figs. 1–2.
1965 *Macropipus oligocaenicus* [sic!] (Paucă) – Glaessner, p. 114, fig. 10.
1967 *Portunus oligocenicus* Paucă – Jerzmańska, p. 541, figs. 1–2.
1975 *Inachus* sp. – Aslanova & Dzhafarova, p. 44, pl. 2, fig. a.
1975 *Poptunus* [sic!] *atropatanus* – Aslanova & Dzhafarova, p. 42, pl. 1, fig. a–b.
(?) 1975 *Portunus* cf. *lancetodactylus* [sic!] Smirnov – Aslanova & Dzhafarova, p. 42, pl. 1, figs. c–d.
2001 *Liocarcinus lancetidactylus* (Smirnov) – Garassino & Novati, p. 271, figs. 1, 3–5.
2009 *"Portunus" oligocenicus* (Paucă) – Schweitzer et al., p. 9, fig. 6.
2010 Crab – Bieńkowska-Wasiluk, text-fig. 43A.
2010 *Liocarcinus oligocaenicus* [sic!] (Paucă) – Schweitzer et al., p. 106.
2010 *Liocarcinus lancetidactylus* (Smirnov) – Schweitzer et al., p. 105.
2010 *Planes prior* (Smirnov) – Schweitzer et al., p. 142.
2021 *Nautilograpsus prior* (Smirnov) – Berezovsky et al., fig. 1a.
2021 *Liocarcinus prisca* (Smirnov) – Berezovsky et al., fig. 2.
2021 *Liocarcinus prior* (Smirnov) – Berezovsky et al., fig. 3.
2021 *Platymaia lethaeus* Smirnov – Berezovsky et al., fig. 5.

Studied type material: Lectotype of *Portunus oligocenicus* Paucă (NGMR 1107); lectotype of *Portunus lancetidactylus* Smirnov (NHMUK In36651).

Other studied material: One incomplete specimen from Vážany and Litavou, the Czech Republic (MZM Ge25029); six near-complete specimens from Eger-Kiseged, Hungary (MBFSZ O.1334); nine near-complete specimens from Jamna Dolna, Poland (ZPALWr. A/224–A/232); one incomplete specimen from Rudawka Birczańska, Poland (ZPALWr. A/233); three incomplete specimens from Bugiile de Sus, Romania (ZPALWr. A/234–A/236); seven near-complete specimens from Suslăneşti-Muscel, Romania (MNSPN PC No. 925–930; NHMW 1930/0004/0001); four incomplete specimens from Abadzekhskaya, Russia (NMNHU-P IN 1–4); two specimens from Apsheronsk, Russia (MSNM i22863, i22864); seven near-complete specimens from Chernaya Rechka, Russia (NHMUK In36650, In36652, In36653;

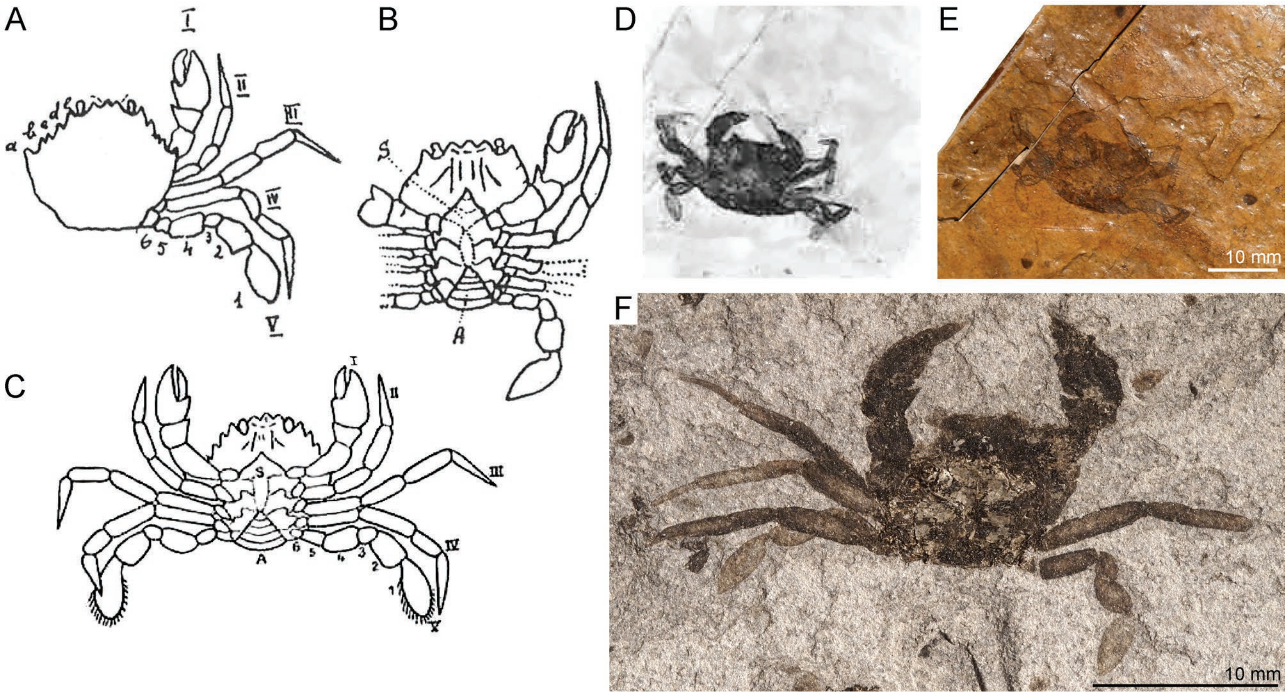

Fig. 3. *Liocarcinus oligocenicus* (Paucă, 1929). **A** — Digital copy of "*Portunus oligocenicus*" from Paucă (1929: pl., fig. 1). **B** — Digital copy of "*Portunus musceli*" from Paucă (1929: pl., fig. 2). **C** — Digital copy of "*Portunus musceli*" from Paucă (1933: fig. 30). **D** — Near-complete individual of "*Portunus musceli*" from Paucă (1933: pl. 5, fig. 6). **E** — Lectotype of *Portunus oligocenicus* (NGMR 1107). **F** — Near-complete female (MNSPN PC No. 930). Specimens in D–F are from Suslănești-Muscel, Romania.

KNU 2, KNU 3, KNU 5); one incomplete specimen from Liubizhnia, Ukraine (NMNHU-P IN 9).

Emended diagnosis: Carapace subhexagonal, frontal margin weakly trilobed, anterolateral margins with four teeth (excluding outer orbital tooth), first and third tooth smaller than others; outer lateral margin of pereiopod 1 carpus with two distinct spines, carpal process long and acute; pereiopod 2–5 merus elongate, pereiopod 5 merus reaching half-length of pereiopod 2–4 merus, pereiopod 5 propodus as long as pereiopod 5 merus, pereiopod 5 dactylus lanceolate in outline.

Description: Carapace subhexagonal. Frontal margin faintly trilobed, in larger specimens almost straight (entire) and with faint median lobe. Orbits large; supraorbital margin with two fissures (incisions). Inner orbital tooth inconspicuous, outer orbital tooth large, pointing anteriorly. Anterolateral margins with four teeth (excluding outer orbital tooth), first and third tooth smaller than others. Posterolateral margins concave anteriorly and convex posteriorly. Posterior margin straight, wider than front. Regions not discernible (due to preservation). All pleonal somites free in females, pleonal somites 3–5 fused in males. Telson triangular in outline. Eyestalks short. Basal antennal article long, antennal flagellum insufficiently preserved. Pereiopods 1 (chelipeds) slightly unequal and stout, shorter than pereiopods 2–5. Outer lateral margin of pereiopod 1 carpus with two distinct spines, carpal process long and acute; propodus with several longitudinal carinae, upper margin with distinct outer proximal spine. Pereiopod 2–5 merus elongate; pereiopod 5 merus reaching half-length of pereiopod 2–4 merus. Pereiopod 5 propodus as long as pereiopod 5 merus. Pereiopod 5 dactylus longer than pereiopod 5 merus, with sharp tip, broadly elongate (lanceolate) in outline. Gonopods 1 broad on its base, distal tips narrow and curved laterally.

Remarks: Paucă (1929) described two species of *Portunus* from Oligocene fish beds of Romania with only two schematic drawings (Fig. 3A, B) and no photos accompanying the descriptions. Paucă (1933) recognized both taxa as representing a single species and synonymized *Portunus musceli* with *Portunus oligocenicus*. Paucă (1933) also presented a single photograph of *P. oligocenicus* (Fig. 3D), the specimen of which is selected here as the lectotype (Fig. 3E). Smirnov (1929) described two species of *Portunus* from upper Maikopian (Lower Miocene) fish beds of Vladikavkaz, North Caucasus. The larger species, *P. lancetidactylus* (Fig. 4D, E), was documented in detail, including the anterior portion of the carapace, sternum, pereiopods, pleon, and (male) gonopods. The other species was attributed to a new variety of the extant species *P. arcuatus* Leach, 1814 – *P. arcuatus* var. *priscus* (Fig. 4A–C). Berezovsky et al. (2021) considered it a distinct species (*Liocarcinus priscus*). Garassino & Novati (2001) presented a revision of *Portunus lancetidactylus* based on a new sample of crab fossils (Fig. 5A, B) collected by A.F. Bannikov in the 1990s from Lower Miocene strata of the Apsheronsk Region, ca. 450 km north-west from Vladikavkaz. The original material of Smirnov (1929) was claimed to be lost, and therefore Garassino & Novati (2001) have designated a neotype for *P. lancetidactylus*. However, the revision of the fossil crab material deposited in the Natural History Museum in London (by MH) revealed the presence of the counterpart of one syntype of *P. lancetidactylus* (Smirnov 1929: fig. 3; Fig. 4D) given to the museum personally by V. P. Smirnov in October 1937. Thus, the neotype selected by Garassino & Novati (2001) is not valid and the only remaining syntype in the NHM London should be considered a lectotype. Among the specimens deposited in the NHM London, there are two identified as *P. arcuatus* from the same strata (Fig. 4A, B). The importance of these specimens cannot be

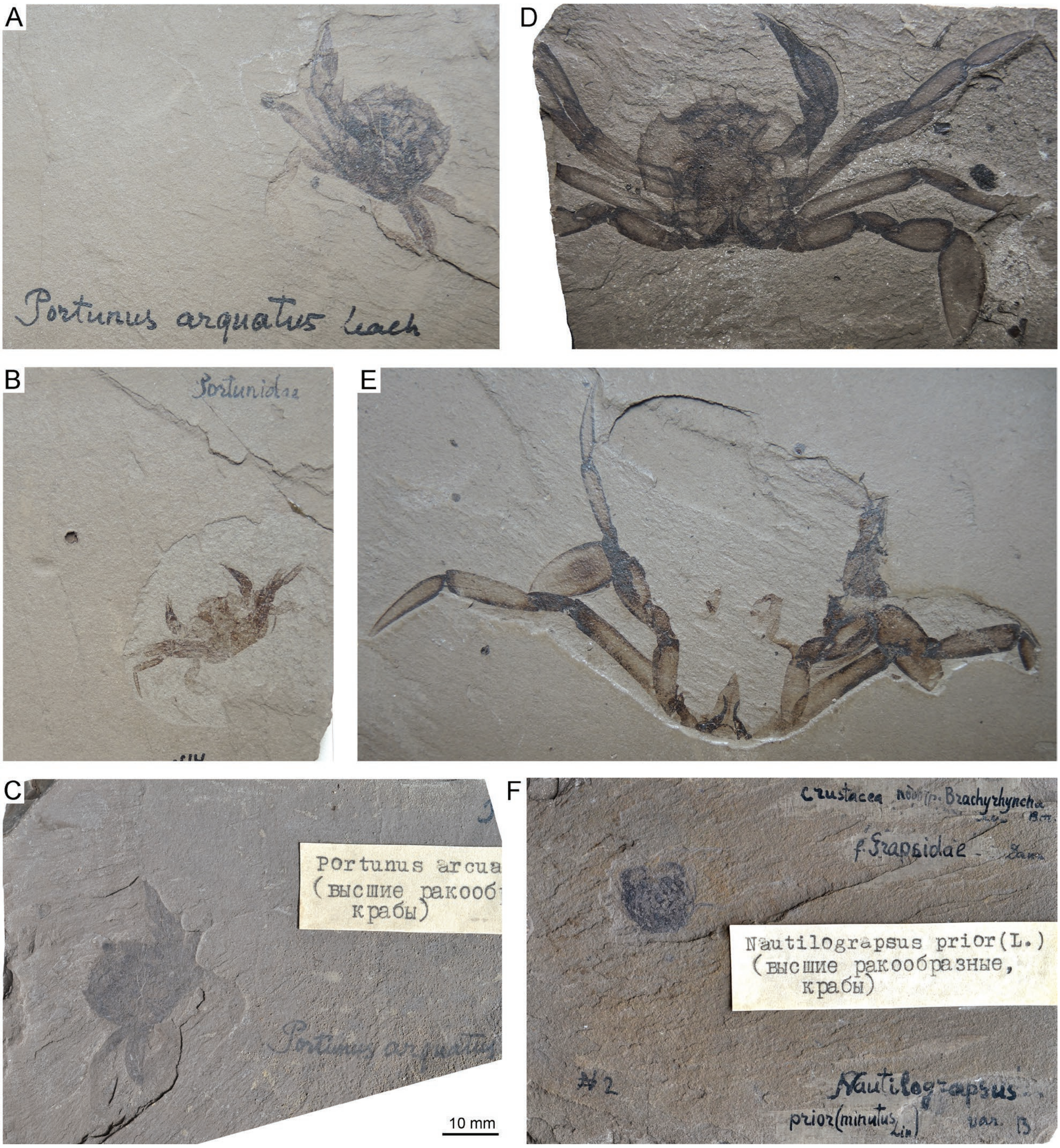

Fig. 4. *Liocarcinus oligocenicus* (Paucă, 1929). Original material of Smirnov (1929), collected from Chernaya Rechka, Russia. **A** — Near-complete male of *Portunus arcuatus priscus* Smirnov, 1929 (NHMUK In36653). **B** — Complete female of *P. arcuatus priscus* (NHMUK In36652). **C** — Near-complete male of *P. arcuatus priscus* (KNU 2). **D** — Lectotype of *Portunus lancetidactylus* Smirnov, 1929 (NHMUK In36651). **E** — Incomplete male of *P. lancetidactylus* (NHMUK In36650). **F** — Near-complete individual of indeterminate sex of *Nautilograpsus prior* Smirnov, 1929 (KNU 3). All specimens are to the same scale.

overestimated, as the type material of *P. arcuatus* var. *priscus* is considered lost. Since they were identified by V.P. Smirnov himself, they represent the concept of *P. arcuatus* var. *priscus* sensu Smirnov (1929). Based on the close examination of the specimens of *Portunus arcuatus* var. *priscus* and comparison with specimens of *P. lancetidactylus*, we argue that both taxa represent the same species. Garassino & Novati (2001, p. 272) have already noted that "on the basis of Smirnov's iconographical material, it seems to us that there are no morphological differences between *P. lancetidactylus* Smirnov, 1929 and *P. arcuatus* Leach, 1814...". The subsequent statement claiming the distinctness of these species should be considered erroneous (A. Garassino, pers. comm., May 2021).

Unfortunately, the revision of *Portunus lancetidactylus* presented by Garassino & Novati (2001) suffers from several flaws. The reconstruction presented in their fig. 1 does not correspond to the actual material (Fig. 5A, B), as it was observed by one of the authors (MH) during the re-examination of crabs from the Apsheronsk Region. The line drawing (Garassino & Novati 2001: fig. 1) depicts three (including outer orbital tooth) anterolateral teeth instead of five (including outer orbital tooth); incorrect shape of cheliped carpus with a single prominent spine instead of three; and pereiopod five with all its elements not matching the fossil specimens. Most notably, the characteristic shape of the pereiopod five dactylus (lanceolate with acute point) and pereiopod five merus (elongate, approximately three times longer than high) are not represented correctly in the figure. Similarly, the diagnosis of *Liocarcinus lancetidactylus* incorrectly mentions "three teeth on the antero-lateral margins" and "a single strong tooth on the inner margin of the carpus of pereiopod I" (Garassino & Novati 2001: p. 271). The description of the material states that "the chelae are short and stout with smooth inner and outer margins, without teeth along dactylus and index" (Garassino & Novati 2001: p. 271). However, the propodus clearly possesses longitudinal carinae and fingers have developed dentition, although details are obscured due to the preservation (flattening) and subsequent preparation having fine structures partly removed along the edges of the fossil(s).

Paucă (1933, p. 76), when revising his crab species from the Oligocene of Romania, stated that *P. oligocenicus* is very close ("eine sehr enge Verwandtschaft") to *P. arcuatus* var. *priscus* described by Smirnov (1929). Examination of the specimens from Eger, Hungary (Fig. 5F), identified by Paucă (1933) as *P. oligocenicus* and comparison with newly collected material from the type locality of *P. oligocenicus* (Fig. 3E, F) shows that all four crab species reported from Oligocene fish beds of several countries represent the same animal. All four taxa share the diagnostically important characters on the carapace (front, anterolateral margins), chelipeds (carpus), and pereiopod 5 (merus, carpus, dactylus), as illustrated herein (Figs. 3–5).

Interestingly, Glaessner (1965, p. 116) mentioned "*Macropipus oligocaenicus*" from the Oligocene of the Caucasus and Romania, although, at that time, the records from the respective countries were not considered conspecific, that is, they were formally not recognized as a single species. *Portunus oligocenicus* Paucă, 1929 is selected here as the senior subjective synonym of all taxa presented above. This name was already preferred by Paucă (1933) when synonymizing his two species, *P. oligocenicus* and *P. musceli*. The works by Paucă (1929) and Smirnov (1929) introducing all four taxa were published in the same year creating a difficulty in adopting the priority rule. The work by Paucă (1929) was demonstrably published in June 1929, whereas the precise time of publication of Smirnov's work (Smirnov 1929) remains unknown. Therefore, we adopt the ICZN Article 21.3.2, which states that if the day of publication is not specified in a work, the date to be adopted is the last day of the year when only the year is demonstrated.

Paucă (1929) did not select holotypes of his two "*Portunus*" species but only mentioned the repository as Collections of Geological Survey in Bucharest. Therefore, after studying his material we selected the specimen (Fig. 3E) matching the only published photo of the species (Fig. 3D) as the lectotype.

In addition to the two species of *Portunus* mentioned above, Smirnov (1929) reported five distinctly smaller crab specimens which he questionably assigned to *Nautilograpsus* H. Milne Edwards, 1837 (=*Planes* Bowdich, 1825) as "*Nautilograpsoides* (varietas dubia)" and "*Nautilograpsus prior*." Garassino & Novati (2001, p. 272) expressed doubts about the taxonomic identity of the material noting that "the specimens look like those belonging to *Portunus* Weber, 1795, but since their state of preservation is bad it was difficult to observe their main morphological features." Berezovsky et al. (2021) examined some specimens from Smirnov's collection, including the material assigned to *Nautilograpsus prior*; they stated that "the specimen of *Nautilograpsus prior* Smirnov should be assigned to *Liocarcinus prior* Smirnov." This particular specimen is documented herein (Fig. 6). The material of Smirnov (1929) assigned to *Nautilograpsus* differs significantly from representatives of *Planes*, which have more robust legs and differently shaped sternum (compare Rathbun 1914, pl. 3). Long and slender pereiopods of the material studied by Smirnov (1929) suggest the attribution of these specimens to *Portunus lancetidactylus* (=*L. oligocenicus* as revised herein). Additionally, the carapace outline of *Nautilograpsus prior*, as far as it can be deduced from the rather poorly preserved specimens, fits the proportions and the nearly square outline of the carapace of *Liocarcinus* juveniles (Guerao & Abelló 2011: fig. 1), which are up to 3 cm in length. Close examination of one of the specimens of *N. prior* demonstrates a presence of a trilobed rostrum (Fig. 6C), which is characteristic for representatives of *Liocarcinus*. Therefore, *Nautilograpsus prior* sensu Smirnov (1929) is considered herein a juvenile representative of *Liocarcinus oligocenicus*, and, as such, it should be synonymized with the latter species.

Representatives of *Liocarcinus* are slightly heterochelous, the right chela usually being the crusher, and the left one the cutter (Palmer 1927; Abelló et al. 1990). Concerning the material from the Caucasus, Smirnov (1929: p. 18) already stated that "the claws on both sides are almost equal in size." Close inspection of the available specimens allows confirming that there is a slight heterochely present in *L. oligocenicus*, although it can not be observed in all specimens, largely due to the extreme flattening of the material.

Liocarcinus oligocenicus differs from its extant congeners by a combination of characters, including the size of anterolateral teeth (the first and third being smaller than the second

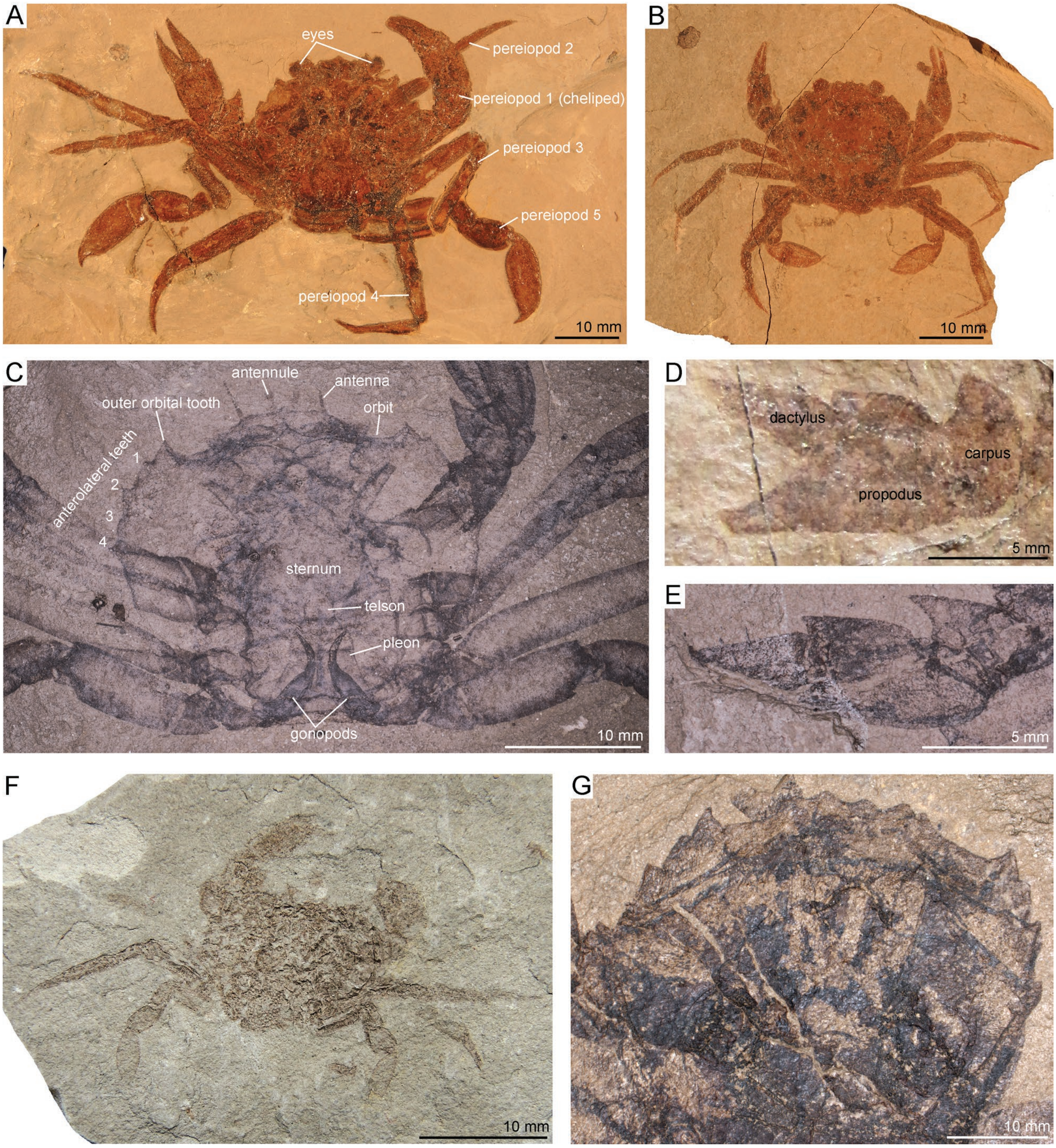

Fig. 5. *Liocarcinus oligocenicus* (Paucă, 1929). **A** — Complete female (MSNM i.22863). **B** — Complete individual of indeterminate sex (MSNM i.22864). **C** — Near-complete male (NHMUK In36651). **D** — Right claw in lateral view (ZPALWr. A/228). **E** — Right claw in dorsal view (NHMUK In36653). **F** — Near-complete individual of indeterminate sex (MBFSZ O.1334). **G** — Near-complete individual of indeterminate sex (NHMUK In36653). Localities: Apsheronsk, Russia (A, B), Chernaya Rechka, Russia (C, E, G), Jamna Dolna, Poland (D), Eger-Kiseged, Hungary (F).

Fig. 6. *Liocarcinus oligocenicus* (Paucă, 1929). A specimen from Smirnov's collection identified as *Nautilograpsus prior* (KNU 3). **A** — Dry. **B** — Immersed in alcohol. **C** — Interpretive drawing. The specimen comes from Chernaya Rechka, Russia.

and fourth), the armature of pereiopod 1 carpus and development of pereiopod 5 elements. Especially, the rather blunt outline of the first and the third anterolateral teeth can be used for differentiation of *L. oligocenicus* from extant congeners (cf. Palmer 1927; Ingle 1980), although anterolateral margins are not always preserved in their entirety in the fossil specimens. In many crab individuals from fish beds, pereiopods 5 are preserved and these are morphologically identical in all studied specimens. Other Miocene representatives of *Liocarcinus* are known mainly from isolated carapaces and cheliped fingers (Hyžný & Dulai 2021). They can be differentiated from *L. oligocenicus* by differently shaped rostrum and anterolateral teeth. So far, *L. oligocenicus* has been reported only from the fish beds deposits as discussed herein.

Occurrence: Oligocene of Hungary (Weiler 1933; Tasnádi-Kubacska 1936), Poland (Jerzmańska 1967; Bieńkowska-Wasiluk 2010), Romania (Paucă 1929, 1933), Ukraine (Gorbach 1956), and Russia (herein); Lower Miocene of Russia (Smirnov 1929; Garassino & Novati 2001; Berezovsky et al. 2021) and Azerbaijan (Aslanova & Dzhafarova 1975).

Portunidae
Necronectinae
Necronectes A. Milne-Edwards, 1881

Type species: *Necronectes vidalianus* A. Milne-Edwards, 1881, by original designation.

***Necronectes* sp.**
Figure 7A–C

2010 Crab – Bieńkowska-Wasiluk, text-fig. 43B.

Studied material: Three incomplete specimens form Krępak, Poland (ZPALWr. Kr/4–Kr/6).

Description: Carapace transversely subhexagonal, slightly wider than long, widest at last anterolateral tooth. Front narrow, with four well-separated teeth. Orbits subcircular, supraorbital margin with two fissures with tooth in between. Anterolateral margins arcuate, with seven broadly triangular, evenly sized teeth pointing forward and one slender lateral tooth directed outward. Posterolateral margins straight, converging posteriorly. Posterior margin slightly narrower than orbitofrontal margin. Carapace regions and grooves not discernible. Chelipeds (pereiopods 1) robust, carpus with at least one carpal spine, fingers insufficiently preserved.

Remarks: Although many details of the carapace and cheliped cannot be observed in the studied specimens (Fig. 7A–C), the preserved outlines of the respective body parts are sufficient to assign the material to *Necronectes* A. Milne-Edwards, 1881. Important taxonomic characters include the frontal margin with four well-developed teeth (excluding inner orbital teeth), the anterolateral margin with seven teeth (excluding outer orbital tooth), and the transversely (sub)hexagonal carapace (Schweitzer et al. 2006; Karasawa et al. 2008). *Necronectes* differs from the closely related genus *Scylla* De Haan, 1833 [in De Haan, 1833–1850] by the number of anterolateral teeth: representatives of *Scylla* have eight anterolateral teeth (excluding outer orbital tooth), whereas *Necronectes* have only seven (Schweitzer et al. 2006; Karasawa et al. 2008).

Necronectes is a well-known genus from a number of occurrences across the Oligocene and Miocene strata of Europe, including the basins of the former Paratethys Sea. *Necronectes schafferi* Glaessner, 1928 has been reported from the Upper Oligocene of Germany and the Miocene of Austria, Hungary, Poland, Ukraine, Italy, France, and Malta (Hyžný & Dulai 2021 and references therein). Given the stratigraphic span and geographic distribution of *N. schafferi*, it is possible that also the here reported occurrence from the Krępak locality belongs to that species. Nevertheless, we refrain to assign it to *N. schafferi* because of insufficient preservation of diagnostic features in the Krępak specimen.

Occurrence: Upper Oligocene of Poland (Bieńkowska-Wasiluk 2010).

Discussion

A major obstacle of taxonomic analyses of decapod remains from fish beds is their extreme flattening that distorts the outlines of exoskeleton elements and hinders the evaluation of

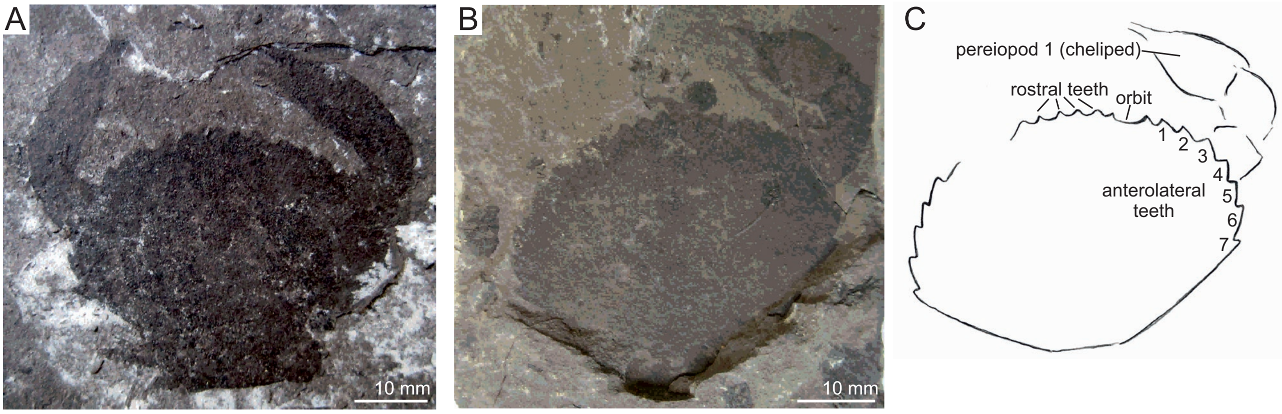

Fig. 7. *Necronectes* sp. **A** — Carapace with articulated chelipeds (ZPALWr. Kr/5). **B** — Carapace with articulated cheliped (ZPALWr. Kr/4). **C** — Interpretive drawing of B. Specimens come from Krępak, Poland.

morphological details of the cuticular surfaces. In brachyuran crabs, numerous carapace features such as grooves, development of regions, and ornamentation thus often cannot be observed. On one hand, these characters are considered of major importance for palaeontological studies (Glaessner 1969; Schweitzer 2003). On the other hand, the preservation of decapods in dysoxic environments not affected by scavenging or bioturbation allows the preservation of features that are frequently not preserved at all. Eyes, antennae, and even gonopods can be observed (Fig. 5), which is especially important since the latter are extremely rare in the fossil record.

Smirnov (1929) described both male and female specimens of his species *Portunus lancetidactylus*. The sex identification was based not only on the morphology of the pleon, which differs significantly between the respective sexes (McLay & Becker 2015), but also on male pleopods (i.e., gonopods) as also depicted by Smirnov (1929). Nevertheless, due to the supposed re-mineralization of the structures and the coarseness of the substrate, the taxonomically important details are not discernible, hindering the comparison with extant species of *Liocarcinus*. Brachyuran gonopods are only lightly sclerotized and do not preserve readily in the sedimentological record. Thus, their preservation in the studied fish beds is noteworthy as besides that of Smirnov (1929) there are only few reports of fossilized brachyuran gonopods (Secretan 1975; Karasawa & Kato 2001, 2019; Feldmann et al. 2011; Luque et al. 2018, 2019).

Brachyuran crabs preserved in Oligocene and Miocene fish beds often represent complete or near-complete articulated bodies, allowed by calm depositional conditions and a quick burial without subsequent physical disturbance or biotic reworking (Plotnick et al. 1988; Stempien 2005; Mutel et al. 2008; Krause et al. 2011; Klompmaker et al. 2017). The carapace is sometimes missing, whereas the sternum is still present together with articulated pereiopods (suggesting a mix of crab corpses and exuviae in the studied material). Such mode of preservation has led to misidentification of some crab specimens. When the specimen of *Liocarcinus oligocenicus* is missing its carapace but retains an intact sternum with pereiopods, the overall body outline is similar to the species *Platymaia lethaea* having slender walking legs and a relatively smaller carapace. In such cases, the sternum of *L. oligocenicus* is misinterpreted as the carapace of *P. lethaea*. Careful examination of the specimens in question can reveal this error, usually due to the presence of comparatively much larger chelipeds and more robust walking legs in *L. oligocenicus* than in *P. lethaea*. Misidentification of these otherwise very distinct taxa can be explained by the flattening of fossils obscuring fine details and the limited knowledge of crab taphonomy resulting in this specific mode of preservation. Specifics of the taphonomy of crabs in fish beds is the subject of a separate study (Kovalchuk et al. 2022).

Liocarcinus and *Necronectes* are well-documented genera from the Oligocene and/or Miocene strata of Europe, including the basins of the former Paratethys. Nevertheless, *Liocarcinus oligocenicus* presents a set of characters not observable in its roughly coeval congeners from other geological settings and as such it represents a faunal element, unique to laminated deposits with exceptional fish preservation and high organic content, with a wide geographic distribution. In this respect, the occurrence of *Necronectes* sp. from Krępak, Poland does not seem to be a typical element of these settings as it does not occur at any other studied locality with exposed fish beds, whereas other species of *Necronectes* have been reported from many localities preserving reef-associated faunas (Hyžný & Dulai 2021). Besides *Platymaia lethaea*, there is no other fossil occurrence of the respective genus. As such, it occurs only at limited number of fish beds localities. Thus, *L. oligocenicus* is a unifying decapod faunal element of all studied Oligocene and Miocene fish beds so far.

Conclusions

All previously published records of malacostracan crustaceans from the Oligocene and Miocene fish beds of Europe are reviewed herein. Newly collected specimens include those from the Oligocene of the Abadzekhskaya locality, North

Caucasus, Russia. Based on the revision of brachyuran crabs from respective strata, three species are recognized, including *Platymaia lethaea* (Smirnov, 1929); *Liocarcinus oligocenicus* (Paucă, 1929); and *Necronectes* sp. The most widespread taxon is represented by *L. oligocenicus*. This species occurs in all of the studied strata, i.e. the Maikopian Series of Azerbaijan and the North Caucasus, the Ždánice-Hustopeče Formation of the Czech Republic, the Tard Clay Formation of Hungary, the Dysodilic Shale Formation of Romania, and the Menilite Formation of Poland and Ukraine. Several formerly recognized distinct taxa represent junior subjective synonyms of *L. oligocenicus*, including *Portunus musceli* Paucă, 1929; *Portunus lancetidactylus* Smirnov, 1929; *Portunus arcuatus* var. *priscus* Smirnov, 1929; *Nautilograpsus prior* Smirnov, 1929; and *Portunus atropatanus* Aslanova & Dzhafarova, 1975. A major obstacle in taxonomic evaluation of brachyuran crabs from Oligocene and Miocene fish beds is the extreme flattening of exoskeleton elements. Other features commonly not preserved in the fossil record, such as eyes, antennae, and even gonopods can be observed, although they are of limited use in direct comparison with modern counterparts.

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