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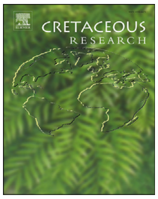

New Cretaceous crabs (Crustacea, Brachyura) from Moscow Oblast and Dagestan (Russia): patterns in phylogeny and morphospace of the oldest eubrachyurans (Dorippoidea)☆

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ABSTRACT

Four new brachyuran species, assigned to two new genera and one existing genus, are recorded from Lower and Upper Cretaceous strata of Moscow Oblast (Moskovskaya Oblast) and Dagestan, Russia. Three new taxa, *Personadorippe levashiensis* gen. et sp. nov., *Levashidromites cornutus* gen. et sp. nov. and *Vectis collinsi* sp. nov., were recovered from Aptian strata in Dagestan; these constitute the first formal description of Cretaceous crabs from the northern Caucasus. Of these, *Personadorippe levashiensis* gen. et sp. nov. represents one of the oldest eubrachyuran crabs known to date, being of middle Aptian age and thus predating the late Aptian *Telamonocarcinus antiquus* Luque, 2014 (see Luque, 2014a) from Colombia. A single carapace of *Personadorippe kalashnikovi* gen. et sp. nov. constitutes the first ever record of crabs from Upper Cretaceous deposits of the Moscow region. *Vectis collinsi* sp. nov. represents only the third species of the genus, and the first outside the United Kingdom. The genus *Vectis* is reassessed and here reassigned to the Viaiidae, which now comprises three genera. *Rathbunopon*? *atherfieldense* Wright, 1997 is also transferred to *Vectis*. The family Longodromitidae is here restricted to six genera, inclusive of *Levashidromites* gen. nov., and a new diagnosis is supplied. *Navarrara*, previously assigned to the Longodromitidae, is reassigned to the Telamonocarcinidae. *Withersella* is also transferred to the Telamonocarcinidae; the genus constitutes the oldest dorippoid (and hence, currently assigned eubrachyuran) crab. *Personadorippe* gen. nov., here described on the basis of two new species, follows shortly after. *Eodorippe connori* Nyborg, Garassino, Vega and Kovalchuck, 2019 is here reassigned to *Personadorippe* gen. nov. Carapace tripartition and branchial condensation, i.e., the ratio between the median carapace portion and the relative distance of the branchial groove to the cervical groove, are here used as important proxy characters for reconsidering the taxonomic placement of primitive crabs. Phylogenetic analyses and assessment of phylomorphospace have revealed that the new genera described herein are part of a Jurassic–Cretaceous radiation of primitive crabs. This radiation proceeded via a high-magnitude morphological shift away from the morphology typical of *Tanidromites*, with subsequent expansion in all directions of morphospaces occupied.

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1. Introduction

Despite the large areal extent of the Russia Federation, only a few Mesozoic crabs have been recorded to date (Table 1). So far, there are only a few published records of decapod crustaceans from Cretaceous strata in the Moscow area (Moscow Oblast). However, in recent years, crabs have been collected at several localities in this region; these are here formally named, described and illustrated.

Ilyin (2005, p. 186, pl. 9, fig. 1) assigned a crab carapace, collected by Dr Evgenij Yu. Baraboshkin near the village of Gavrilkovo (Moscow Oblast, Dmitrovsky District, River Volgusha), to *Homolopsis glabra* Wright and Collins, 1972. Located near that village is a well-studied section of Lower Cretaceous sands that are referred to the Gavrilkovo Formation (Fig. 1). These levels have yielded the middle Albian zonal ammonite species *Hoplites dentatus* (J. Sowerby, 1821) (see Olferev, 1986). From the same strata, Dr Aleksandr S. Alekseev collected fragments of thoracic segments of decapod crustaceans in 1989, but these could not be identified in detail (Ilyin, 2005). As far as we are aware, these are the only references in the literature to Cretaceous crabs in the Moscow region. However, the website of Russian fans of palaeontology (www.ammonit.ru) includes photographs of fragmentary appendages, such as propodi and meri, of decapod crustaceans from the locality of Varavino, originating from the Cenomanian Lyaminsk Formation (Fig. 1).

Despite the vast territory of the northern Caucasus and significant outcrops of Cretaceous rocks in that area, decapod crustaceans have only rarely been recorded in the literature. Aliev and Aliev (1980) described and illustrated two new species of ghost shrimp, *Protocallianassa caucasica* and *P. sarysuensis*, from Upper Cretaceous (Coniacian) sandstones of the Lesser Caucasus, i.e., different regions of Azerbaijan and Armenia. Other records from Cretaceous levels of the Caucasus pertain to references without descriptions and/or illustrations, such as a paper by Mordvilko (1960), who noted small bivalves, conchostracans and teeth of pycnodont fishes from a particular level within Lower Cretaceous (Valanginian) limestones near Kislovodsk. In the same paper, reference is made to common finds of crab carapaces in Aptian and Albian strata of the Caucasus, but their taxonomic affiliation is not indicated. In short, the present record is the first formal description of Cretaceous crabs from the northern Caucasus.

A certain variety of Cretaceous crabs are known from Crimea. For instance, the oldest species known, *Nodoprosopon dzhafarberdensis*, was described by Ilyin (2005, p. 171) from Upper Jurassic levels in the Simferopol district. Early Cretaceous crabs are more diverse, being represented by *Necrocarcinus bodrakensis* Levitskiy, 1974, *Necrocarcinus tauricus* Ilyin and Alekseev, 1998 and *Raninella yanini* (Ilyin and Alekseev, 1998), all from the upper Albian of the Bakhchisaray district (Levitskiy, 1974; Ilyin and Alekseev, 1998), as well as *Notopocorystes* (*Notopocorystes*) *normani* (Bell, 1863) from the middle Cenomanian of the same area (Ilyin, 2005, p. 217).

2. Localities

2.1. Nikolskoye

A single carapace, here referred to *Personadorippe kalashnikovi* gen. et sp. nov., was collected near the village of Nikolskoye (Dmitrovsky district, Moscow Oblast) in 2011. Around 500 m to the west of Nikolskoye, there used to be a sand pit (Fig. 1C–D); excavation at this site came to a halt in 2005.Today, this pit is completely filled up and lost. Strata formerly exposed here had a complex facies structure: interspersed with sands and clays of

Table 1
List of all Mesozoic brachyurans from Russia described to date.

Species	Locality	Horizon	References
Nodoprosopon dzhafarberdensis Ilyin (2005)	Crimea, Simferopol district, close to village of Druzhnoe	Upper Jurassic to Lower Cretaceous: upper Tithonian to lower Berriasian; Yailino Series	Ilyin (2005, p. 171)
Levashidromites cornutus gen. et sp. nov.	Dagestan, Levashinsky district, village of Levashi	Lower Cretaceous: middle Aptian, *Parahoplites melchioris* ammonite Zone; Kubina Formation	Herein
Personadorippe levashiensis gen. et sp. nov.	Dagestan, Levashinsky district, village of Levashi	Lower Cretaceous: middle Aptian, *Parahoplites melchioris* ammonite Zone; Kubina Formation	Herein
Vectis collinsi sp. nov.	Dagestan, Levashinsky district, village of Levashi	Lower Cretaceous: middle Aptian, *Parahoplites melchioris* ammonite Zone; Kubina Formation	Herein
Homolopsis glabra Wright and Collins, 1972	Moscow Oblast, Dmitrovsky district, village of Gavrilkovo	Lower Cretaceous: middle Albian, below *Hoplites dentatus* ammonite Zone; Gavrilkovo Formation	Ilyin (2005, p. 189)
Necrocarcinus bodrakensis Levitskiy, 1974 (= *N. labeschii* (Eudes Deslongchamps, 1835; see; Ilyin, 2005, p. 198, p. 198)	Crimea, Bakhchisaray district, village of Prohladnoe (Mangushsky ravine)	Lower Cretaceous: upper Albian, *Hysteroceras varicosum* ammonite Zone; Mangush Formation	Levitskiy (1974, p. 115)
Necrocarcinus tauricus Ilyin and Alekseev, 1998	Crimea, Bakhchisaray district, village of Prohladnoe (Mangushsky ravine)	Lower Cretaceous: upper Albian, *Hysteroceras varicosum* ammonite Zone; Mangush Formation	Ilyin and Alekseev (1998, p. 46)
Raninella yanini (Ilyin and Alekseev, 1998)	Crimea, Bakhchisaray district, village of Prohladnoe (Selbuhra and Vysoky Bugor mountains)	Lower Cretaceous: upper Albian, *Mortoniceras inflatum* ammonite Zone; Vysokobugorsk Formation	Ilyin and Alekseev (1998, p. 48)
Personadorippe kalashnikovi gen. et sp. nov.	Moscow Oblast, Dmitrovsky district, village of Nikolskoye	Upper Cretaceous: lower Cenomanian, *Schloenbachia varians* ammonite Zone; Lyaminsk Formation	Herein
Notopocorystes (*Notopocorystes*) *normani* (Bell, 1863)	Crimea, Bakhchisaray district, village of Prohladnoe (Selbuhra Mountain)	Upper Cretaceous: middle Cenomanian; Member IV-2	Ilyin (2005, p. 217)

glacial origin (till) were sands of Cretaceous age (Fig. 1D–E) and clayey levels of Late Jurassic age. Most likely, these Mesozoic deposits were glacially transported masses during the Pleistocene, in particular at the time of the Moscow glaciation (Astakhov, 2004). The border of the Moscow glaciation passed from the southwest to the northeast of the Moscow region, approximately halfway. The period of the Moscow glaciation coincides with glaciation of the Alps, where it is called Riess II.

In the vicinity of this locality are widely distributed deposits of a Late Cretaceous date that are included in the Lyaminsk Formation (Olferev, 1986). According to more recent stratigraphical data (Stratigraficheskaya …, 2004), the Lyaminsk Formation can be assigned to the Polpino Horizon, or lower Cenomanian. The section formerly exposed at this site attained a thickness of about 40 cm. The bottom part consisted of a condensed layer of sand with concretions and gravel, overlain by a solid sandstone level and sand in the uppermost layer of the section.

The sands of the Lyaminsk Formation are rich in a range of macrofossils (Fig. 2A–P), with the largest concentration being found in the condensed sandstone layers. The commonest fossils are shark teeth, while remains of bony fish, reptiles, decapod crustaceans and ammonites are rarer. The find of the ammonite *Schloenbachiavarians* (J. Sowerby, 1817) confirms the early Cenomanian age of these deposits (compare Wilmsen and Mosavinia 2010; Kennedy 2013).

2.2. Levashi

Other brachyuran carapaces (*Personadorippe levashiensis* gen. et sp. nov., *Levashidromites cornutus* gen. et sp. nov. and *Vectis collinsi* sp. nov.) have been recovered from Aptian deposits near the village of Levashi (Levashinsky district, northern Caucasus, Dagestan). Lower Cretaceous deposits in this region have been relatively well studied and a number of formations identified.

In the vicinity of Levashi various Aptian strata crop out, namely the lower and upper levels of a sandy-argillaceous nature, the intermediate one being essentially sandy. In the middle and upper units of this formation spherical sandy-calcareous concretions are found (Fig. 1G–K); these measure up to 2 m in diameter (Snezhko et al., 2011). It is in these concretions that decapod crustacean material is often found, including the crab carapaces here described. The collector, O. Khapisov, has informed us that these carapaces were found associated with the ammonite *Parahoplites melchioris* Anthula, 1899, which is a zonal species and confirms the middle Aptian age of these concretions. On this evidence, this part of the section can be correlated with the Kubina Formation (Sostoyanie … 2008).

The associated fossil fauna at Levashi is very diverse (Fig. 2R–W), including numerous ammonites, various benthic forms (bivalves, gastropods, crayfish and sometimes starfish) and rare remains of vertebrates such as fishes and marine reptiles.

3. Systematic palaeontology

Here we adopt the classification scheme proposed by Guinot et al. (2013) and Jagt et al. (2015).

Institutional abbreviations: IGM, Colombian Geological Survey (Bogotá, Colombia); MAB, Oertijdmuseum (Boxtel, the Netherlands); MGSB, Museo Geológico del Seminario de Barcelona (Spain); MSNM, Muséum national d'Histoire naturelle (Paris, France); MWO, Museum of the World Ocean (Kaliningrad, Russia); NHMUK, The Natural History Museum (London, United Kingdom); NZGS, New Zealand Geological Survey (Lower Hutt, New Zealand). Other abbreviations include: CL, carapace length; CW, carapace width.

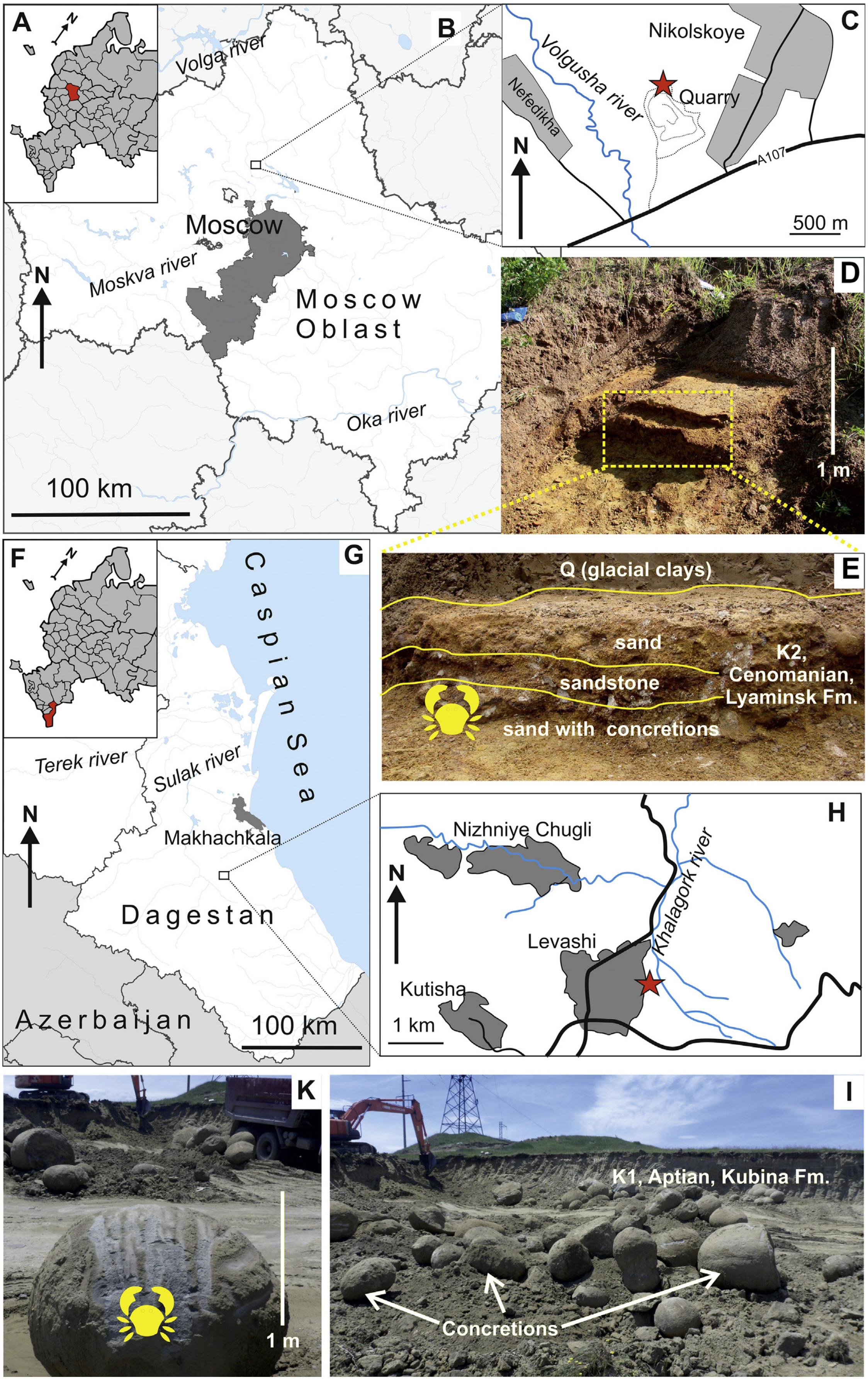
Infraorder Brachyura Linnaeus, 1758
Section Podotremata Guinot, 1977
Subsection Dynomeniformia Guinot, Tavares and Castro, 2013
Superfamily Dromioidea De Haan, 1833
Family Longodromitidae Schweitzer and Feldmann, 2009a

Genera included. *Abyssophthalmus* Schweitzer and Feldmann, 2009a, *Longodromites* Patrulius, 1959, *Pilidromia* Schweitzer, Feldmann, Lazăr, Schweigert and Franţescu, 2018, *Levashidromites* gen. nov., *Planoprosopon* Schweitzer et al., 2007b and *Rosadromites* Schweitzer, Feldmann, Rader and Franţescu, 2016.

Diagnosis. Carapace elongated subrectangular, longer than wide, lateral margins subparallel, slightly narrowing towards posterior margin; weakly convex transversely, nearly flat longitudinally; rostrum produced, projected, widely triangular or subtrapezoidal, anterior margin concave; fronto-orbital width equalling maximum carapace width; orbital fossae very large, appearing as well-delineated, deeply concave sockets at anterior carapace; orbits anteriorly and weakly anterolaterally directed; outer orbital spine directed anterolaterally, subtle or robust. Lateral margin subvertical, sinuous, blunt in cross section, without spines, restricted where branchial and cervical grooves notch lateral margins. Carapace areolation normally weak; deep and well-defined cervical and branchial grooves; carapace tripartite, cervical and branchial grooves well separated, branchial condensation weak; cervical groove low V-shaped to subhorizontal, notching lateral carapace margin; branchial groove well defined, subparallel to cervical groove, notching lateral carapace margin. Posterior margin wide, strongly concave. Protogastric, mesogastric, epibranchial and cardiac regions well delineated and inflated, anterior mesogastric process narrow, elongate; posterior branchial region large. Dorsal carapace surface densely granular, anterior regions usually with few tubercles. Elements other than carapace unknown (in genera here assigned to Longodromitidae).

Remarks. A new diagnosis of the Longodromitidae is given above, because previous diagnoses were based on an unfortunate mix of genera. When the family Longodromitidae was erected, it contained three genera (Schweitzer and Feldmann, 2009a, p. 100), namely *Longodromites*, *Abyssophthalmus* and *Planoprosopon*. Here we maintain these three genera, and accept three more: *Levashidromites* gen. nov., *Pilidromia* and *Rosadromites*. Previous authors have included various other genera (see Table 2), with a wide variety of morphologies, rendering any diagnosis useless. In many discussions, the ‘Augenrest’ was used as a proxy character, or even an apomorphy. However, this feature was insufficiently diagnosed and not studied in detail and is thus in need of a thorough revision. The orbital structures of primitive crabs (Dynomeniformia) are highly variable and convergent and no apomorphy can be assigned at the present stage. The other genera assigned to the Longodromitidae by Schweitzer et al. (2017, p. 216) and Schweitzer et al. (2018, p. 320) need to be transferred to other families.The taxonomic heterogeneity of the assemblage previously described by those authors is illustrated well by the genus *Navarrara* Klompmaker, 2013, which is here placed in the Telamonocarcinidae (Eubrachyura; see below). Work on *Glaessnerella* is underway (Van Bakel and others).

Longodromitids were originally included in the superfamily Glaessneropsoidea Patrulius, 1959 (Schweitzer and Feldmann, 2009a, p. 82; see also; Schweitzer and Feldmann, 2009b); as far as we are aware it has never been included into other higher taxonomic groups. The orbital structures are well developed and well defined, with large, deep fossae to accommodate the (apparently large) eyes. The lateral margins are developed, not gently rounded as in the Homolodromiidae or Glaessneropsidae, but at least the anterolateral margin is defined, often sharp and


A
N
B
Volga river
Moscow
Moskva river
N
Moscow Oblast
Oka river
100 km
C
Nikolskoye
Volgusha river
Quarry
Nefedikha
N
A107
500 m
D
1 m
E
Q (glacial clays)
sand
K2, Cenomanian, Lyaminsk Fm.
sandstone
sand with concretions
F
N
G
Caspian Sea
Terek river
Sulak river
Makhachkala
N
Dagestan
Azerbaijan
100 km
H
Nizhniye Chugli
Khalagork river
N
Levashi
Kutisha
1 km
K
1 m
I
K1, Aptian, Kubina Fm.
Concretions

ornamented or reinforced with teeth and rims. The family Longodromitidae cannot be accommodated in the Homolodromiidae because the former have a well-developed front and orbital fossae, unlike the disposition in the latter. Moreover, longodromitids have a more condensed medium carapace portion. Here we refer the Longodromitidae to the Dromioidea, on the basis of the nature of the orbitofrontal margin and lateral carapace margins.

The superfamily Glaessneropsoidea has been maintained by other authors, as based on assumed characters, in particular of the orbitofrontal margin. A review is needed to determine whether or not this superfamily is indeed valid, or that families included in it are in need of reassessment (see also Guinot, 2019).

*Genus **Levashidromites*** nov.
urn:lsid:zoobank.org:act:10324979-D8E5-44CD-A2DC-6DFE215DDB75.
Type species: *Levashidromites cornutus* sp. nov., the sole species known to date.

Etymology. From Levashi, the town near which the material was discovered, and -*dromites*, referring to many other dromioid crabs.

Diagnosis. Carapace elongated subrectangular, longer than wide, widest at hepatic spine and posterior part of mesobranchial region, weakly convex transversely and longitudinally; rostrum produced, projected, widely triangular; fronto-orbital width corresponding to maximum carapace width; small inner orbital spine; outer orbital spine directed anterolaterally; orbits very large, appearing as concave open sockets at anterior carapace, outer orbital spines robust, pointed; lateral margin sinuous, blunt in cross section, without spines; carapace surface granular, anterior regions with few tubercles; areolation weak; deep cervical and branchial grooves, cervical groove well defined, widely U-shaped, notching lateral carapace margin; branchial groove well defined, arched, notching lateral carapace margin. Posterior margin wide, axially strongly concave; dorsal surface densely granulated; protogastric, mesogastric, epibranchial and cardiac regions well delineated and inflated; branchial region developed, wide.

Remarks. *Levashidromites* gen. nov. is assigned to the Longodromitidae on account of having subparallel, weakly arched to subhorizontal cervical and branchial grooves; a slightly condensed epibranchial region; pronounced and well-developed, outwardly directed outer orbital spines; orbital margins with notches and teeth; large orbital fossae that occupy the entire anterior margin; a well-defined mesogastric region with wide triangular basal portion and a narrow, acute anterior mesogastric process, as well as enlarged granules/tubercles on the proto- and mesogastric regions.

Levashidromites gen.nov. differs from *Abyssophthalmus* in having stronger, outwardly directed outer orbital teeth, a proportionally larger and wider posterior carapace as well as a waisted (hourglass-shaped) overall carapace outline.The new genus can be differentiated from *Longodromites* in having stronger, outwardly directed outer orbital teeth, a widened posterior carapace (*vs* posterolateral margins converging towards posterior margin in *Longodromites*) and a short, acute and oblique groove on the epibranchial region.

Levashidromites gen. nov.differs from *Pilidromia* in having stronger, outwardly directed outer orbital teeth, a conspicuously low urogastric region (*vs* well-developed, proportionally large and bilobed in *Pilidromia*) and a short, acute and oblique groove on the epibranchial region.

From *Planoprosopon* the new genus can be distinguished by possessing a proportionally wider carapace, also posteriorly, and stronger, outwardly directed outer orbital teeth.

Finally, *Levashidromites* gen. nov. differs from *Rosadromites* in having a more strongly widened posterior branchial region and a conspicuously low urogastric region and in lacking a groove that separates the protogastric from the hepatic region. In both *Levashidromites* gen. nov. and *Rosadromites* a short, acute and oblique groove on the epibranchial region is present. Unfortunately, the entire anterior carapace margin of *Rosadromites* is missing from the unique type specimen, precluding comparison of the outer orbital spines or orbital construction. However, it would seem that *Levashidromites* gen. nov. is morphologically quite closely comparable to *Rosadromites*.

Levashidromites gen. nov. (Aptian of Dagestan, Russia) and *Rosadromites* (Albian of Texas, USA) are the youngest members of the Longodromitidae which, by the mid-Cretaceous, was widely distributed geographically. Species of *Planoprosopon* and *Abyssophthalmus* appear closely similar morphologically; in fact, characters among species of both genera may overlap. Thus, a comprehensive reassessment of these two genera is needed in order to validate their status.

Levashidromites cornutus sp. nov.
urn:lsid:zoobank.org:act:6B7981B0-41FD-4761-A06D-61C9B46148E5.
Figs. 4A–D, 7D

Material. The holotype is the sole specimen known to date (Museum of the World Ocean, Kaliningrad, Russia), number MWO 1 9977.

Etymology. Latin *cornutus*, meaning ‘horned’, in reference to the strong outer orbital spines that render a horned appearance to the crab.

Diagnosis. As for genus.

Type locality and stratigraphical level. Near the village of Levashi, Levashinsky district (Dagestan, Russia); Kubina Formation (Lower Cretaceous, middle Aptian; *Parahoplites melchioris* ammonite Zone).

Description. Carapace subpentagonal, longer than wide, widest at hepatic spine and posterior part of mesobranchial region, weakly vaulted transversely and longitudinally; fronto-orbital width equalling maximum carapace width; orbits wide, shallow, directed forwards, small inner orbital spine, outer orbital spine directed anterolaterally; triangular mesogastric region with axial depression, long, well-delineated, mesogastric process bordered by row of three hepatic tubercles; protogastric region bulbous with one large, central spine; deep sinuous cervical groove continuing to lateral incision; epibranchial region bulbous, covered with granules and small lateral spine; broad, well-delineated urogastric region; deep branchial groove curving anteriorly from cardiac towards epibranchial; bulbous and triangular cardiac region extending almost to posterior margin; large globular mesobranchial region regularly covered with granules; lateral margin sinuous; posterior margin wide, axially strongly concave; ventral aspects and appendages unknown.

Remarks. For differences with allied forms, see the remarks above (under *Levashidromites* gen. nov.).

Superfamily *incertae sedis*.
Family Viaiidae Artal, Van Bakel, Fraaije, Jagt and Klompmaker, 2012

Fig. 1. Localities Nikolskoye (A–E) and Levashi (G–K). A, F. European part of Russia with administrative division; B. Moscow Oblast and adjacent regions; C. neighbourhood of the locality Nikolskoye; D. photograph of the cleared section Nikolskoye in 2012; E. photograph of the section Nikolskoye and its structure; G. Dagestan and adjacent regions; H. neighbourhood of the locality of Levashi; I. photograph of cleared section Levashi in 2016; K. concretions from Aptian deposits in Levashi.

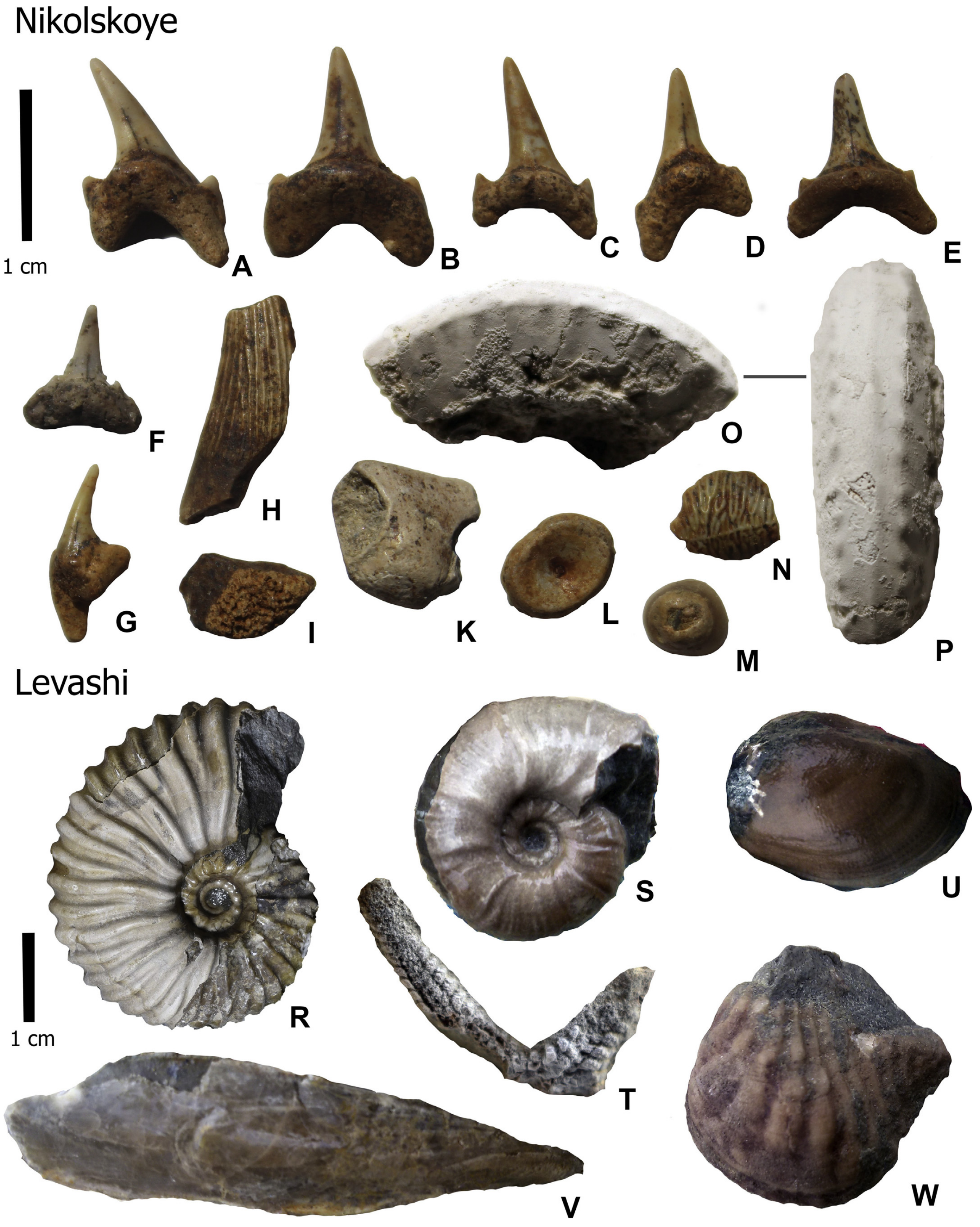


Fig. 2. Typical faunal elements from the localities of Nikolskoye (A–P) and Levashi (R–W).A–G. Shark teeth: A, B, D. *Archaeolamna* sp.; C, E. *Eostriatolamia subulata* (Agassiz, 1844); F.*Synechodus* sp.; G. *Leptostyrax* sp.; H. plesiosaur tooth; I. fragment of chimaerid dental plate; K. fragment of palm of crab; L. chondrichthyan vertebra; M. bony fish tooth; N. tooth of *Acrodus* sp. (Hybodontiformes); O, P. fragment of ammonite *Schloenbachia varians*; R. ammonite *Parahoplites melchioris*; S. ammonite *Zuercherella* sp. juv.; T. indeterminate asteroid fragment; U. indeterminate bivalve; V. bivalve *Gervillia* cf.*solenoidea* Defrance, 1820; W. bivalve *Linotrigonia* cf. *fittoni* (Deshayes *in* Leymerie, 1842).

Table 2
Composition of the family Longodromitidae according to authors.

Schweitzer and Feldmann, 2009a, p. 100)	*Longodromites* Patrulius, 1959
	Abyssophthalmus Schweitzer and Feldmann, 2009
	Planoprosopon Schweitzer, Feldmann and Lazăr, 2007
Karasawa et al. (2011, p. 536)	*Abyssophthalmus* Schweitzer and Feldmann, 2009
	Antarctiprosopon Schweitzer and Feldmann, 2011
	Coelopus Étallon, 1861
	Dioratiopus Woods, 1953
	Glaessnerella Wright and Collins, 1975
	Longodromites Patrulius, 1959
	Planoprosopon Schweitzer, Feldmann and Lazăr, 2007
	Vespridromites Schweitzer and Feldmann, 2011
Schweitzer et al. (2017, p. 216)	*Abyssophthalmus* Schweitzer and Feldmann, 2009
	Antarctiprosopon Schweitzer and Feldmann, 2011
	Coelopus Étallon, 1861
	Dioratiopus Woods, 1953
	Glaessnerella Wright and Collins, 1975
	Longodromites Patrulius, 1959
	Navarrara Klompmaker, 2013
	Planoprosopon Schweitzer, Feldmann and Lazăr, 2007
	Rosadromites Schweitzer, Feldmann, Rader and Franţescu, 2016
	Vespridromites Schweitzer and Feldmann, 2011
Schweitzer et al. (2018, p. 320)	*Abyssophthalmus* Schweitzer and Feldmann, 2009
	Antarctiprosopon Schweitzer and Feldmann, 2011
	Coelopus Étallon, 1861
	Dioratiopus Woods, 1953
	Glaessnerella Wright and Collins, 1975
	Longodromites Patrulius, 1959
	Navarrara Klompmaker, 2013
	Pilidromia Schweitzer, Feldmann, Lazăr, Schweigert and Franţescu, 2018
	Planoprosopon Schweitzer, Feldmann and Lazăr, 2007
	Vespridromites Schweitzer and Feldmann, 2011
	[NOTE: *Rosadromites* is not included here; *Pilidromia* was added]
Present paper	*Abyssophthalmus* Schweitzer and Feldmann, 2009
	Longodromites Patrulius, 1959
	Pilidromia Schweitzer, Feldmann, Lazăr, Schweigert and Franţescu, 2018
	Levashidromites gen.nov.
	Planoprosopon Schweitzer, Feldmann and Lazăr, 2007
	Rosadromites Schweitzer, Feldmann, Rader and Franţescu, 2016

Fig. 11

Genera included. *Heeia* Wright and Collins, 1972, *Vectis* Withers, 1946 and *Viaia* Artal, Van Bakel, Fraaije, Jagt and Klompmaker, 2012.

Diagnosis (modified after Artal et al., 2012; modifications underlined). Carapace small (*Heeia*, *Vectis*) to medium (*Viaia*) in size, subtriangular in outline, much longer than wide; maximum width in posterior half of carapace; front triangular, weakly (*Vectis*), moderately (*Viaia*) to widely projected (*Heeia*); ventral side of front inclined (*Viaia*); orbits relatively large, deep, oblique, directed forwards and outwards; anterolateral margins of carapace short, posterolateral margins longer and convex; posterior margin short, nearly straight, bounded laterally by small concavities; dorsal regions in anterior portion of carapace moderately differentiated, small mesogastric region, defined only by short basal grooves; urogastric region crescent shaped; epibranchial regions arched, inclined; posterior branchial regions large, swollen; cardiac region narrow (*Heeia*, *Viaia*) to normal (*Vectis*); intestinal region small, subtriangular; cervical groove well marked, complete from side to side; branchiocardiac grooves sinuous, long, reaching anterior portions of cardiac region; posterior branchial grooves well marked, arched from lateral margins of carapace towards axis, bounding posterior lateral portions of cardiac region; lateral sides of carapace with deep cavity at level of cervical groove, bounded by strong spines or nodes; epistome triangular, smooth, with strong spine ventral of front (*Viaia*, others unknown); dorsal surface of carapace densely granulated.

Remarks. *Vectis* was originally included in the Prosopidae (Homolodromioidea), but transferred to the Glaessneropsidae Patrulius, 1959 (Glaessneropsoidea) by Karasawa et al. (2011, p. 538) and Schweitzer et al. (2012, p. 22). The orbits of *Glaessneropsis* Patrulius, 1959 are large, well defined with well-developed, subhorizontal, notched orbital margins and distinct outer orbital spines; a completely different disposition from that seen in *Vectis*. The Glaessneropsidae was elevated to superfamily status, Glaessneropsoidea, by Schweitzer and Feldmann (2009a, table 1). The status and validity of this supposed superfamily are far from certain, the diagnosis given by Schweitzer and Feldmann (2009a, p. 82) having been based on plesiomorphies, and lack of an 'Augenrest', a structure *sensu* Schweitzer and Feldmann (2009a, p.61) which must be discussed in detail and is possibly equal to the orbit (or orbital fossa), 'false orbit' *sensu* Wright and Collins (1972, p. 43), 'plage orbitaire' *sensu* Guinot and Richer de Forges (1995, p. 303) or 'unprotected eye' *sensu* Breton (2009, fig. 9). *Vectis* and Viaiidae do not appear to be closely related to the Glaessneropsidae, and we leave the superfamily status open as *incertae sedis*.

Addition of *Vectis* to the Viaiidae is not directly obvious, but morphological comparisons have now revealed *Vectis* to be a basal, not distinctly modified, member of that family. *Vectis* shows an elongate carapace outline with a wide posterior branchial region, converging lateral margins that taper anteriorly, a single, projected and widely triangular front, oblique orbits that do not occupy the entire carapace width and do not have distinct outer orbital corners and it lacks well-defined carapace margins. The cervical groove is widely U-shaped; a distinct branchial groove notches the lateral carapace margin; there is a weak branchial condensation (branchial and cervical grooves well divided) as well as an oblique groove that subdivides the protogastric region and an oblique groove that separates the proto- and epigastric regions. In addition, the branchial groove reaches the cardiac region halfway and merges with the anterolateral cardiac region into a recurved

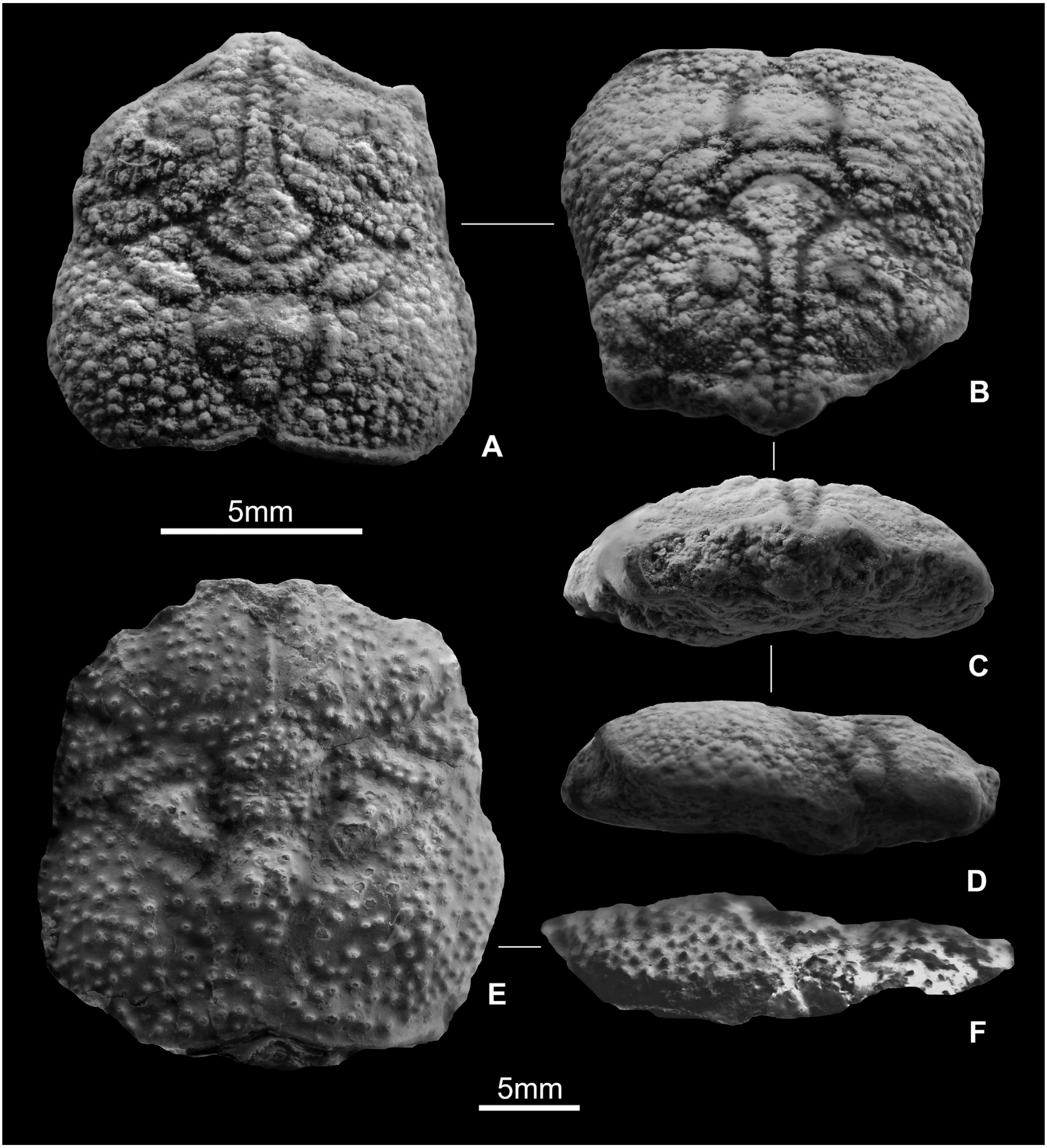
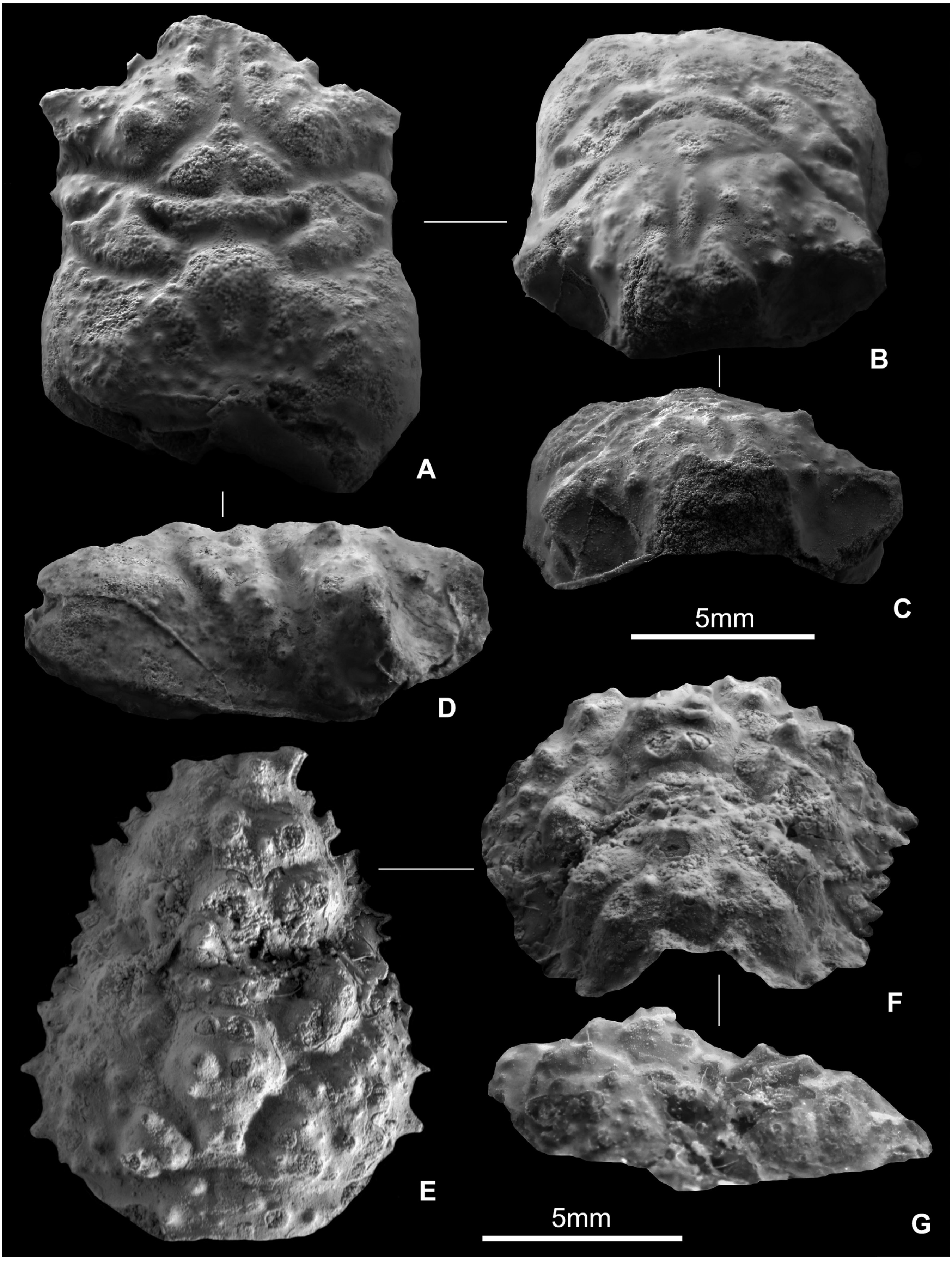


Fig. 3. A–D. *Personadorippe kalashnikovi* gen. et sp. nov., holotype (MWO 1 9298), complete carapace; Moscow Oblast, Dmitrovsky district, near the village of Nikolskoye; Upper Cretaceous, lower Cenomanian, Polpino Horizon, Lyaminsk Formation. Dorsal (A), oblique frontal (B), frontal (C) and right lateral (D) views. E–F. *Personadorippe levashiensis* gen. et sp. nov., holotype (MWO 1 9381), complete carapace; Dagestan, Levashinsky district, village of Levashi; Kubina Formation; Lower Cretaceous, middle Aptian, *Parahoplites melchioris* ammonite Zone. Dorsal (E) and right lateral (F) views.

epibranchial groove. These characters of *Vectis* are remniscentof *Heeia* and *Viaia* (compare Fig. 11) and differ from the carapace ‘Bauplan’ of the Glaessneropsidae and also of e.g., the Nodoprosopidae Schweitzer and Feldmann, 2009a (Schweitzer and Feldmann, 2009a).

Guinot (2019, p. 764) hypothesised that, “… it [*Vectis*] might not be a podotreme crab at all”, and that it could belong to the Eubrachyura. One of the features on which this hypothesis was based is the nature of the posterior carapace margin, termed ‘biconvex’ or ‘flanged’ (Guinot, 2019, p. 781).


A
B
C
D
5mm
E
F
G
5mm

The well-defined, deep branchial groove, which notches the lateral carapace margin, is well separated from and semi-parallel to the cervical groove; together, these two grooves divide the carapace into three parts with a non-condensed anterior (epi)branchial region. The presence of a large and wide posterior branchial region and the lack of well-defined carapace margins (which are completely rounded) do not favour placement in the Eubrachyura. Some majoids are reminiscent of *Vectis* and of the Viaiidae, in particular some taxa contained in the family Inachoididae Dana, 1851. Worthy of note is the overall resemblance to *Esopus* A. Milne-Edwards, 1875; this unusual majoid has recently been discussed in detail by Guinot and Van Bakel (2020).

Heeia is known from the Cenomanian of France and the United Kingdom, while *Viaia* has been recorded from the upper Albian–lower Cenomanian of northern Spain. *Vectis* is the stratigraphically oldest member of the family Viaiidae, known from Aptian deposits in southern England and Dagestan (Russia).

Genus ***Vectis*** Withers, 1946.

Type species: *Vectis wrighti* Withers, 1946, by original designation.

Species included. In addition to the type species, *Vectis atherfieldensis* (Wright, 1997) (as *Rathbunopon*? *atherfieldense*), *V. caseyi* Wright and Collins, 1972, *V. collinsi* sp. nov. and *V. echinorum* Wright and Collins, 1972.

Diagnosis (adapted from Schweitzer et al., 2012, p. 238). “Carapace tiny, longer than wide, width about three quarters length, widest in branchial region about three-quarters the distance posteriorly; granular ornamentation overall; rostrum downturned, axially sulcate; orbits elongate, directed anterolaterally, upper-orbital margin with thick rim, outer-orbital spine present, fronto-orbital width about 84 percent maximum carapace width; cervical, postcervical, and branchiocardiac grooves well defined, cervical and branchiocardiac grooves extending onto flanks; flanks defined on branchial regions by row of small spines; regions well defined; mesobranchial region separated into two subregions; cardiac region well defined, separated from posterior margin by moderately long intestinal region.”

Remarks. Wright (1997) described *Rathbunopon*? *atherfieldense* from the Aptian of the Isle of Wight (southern England); this is here transferred to *Vectis*. The validity of this species must await re-examination of all type material of species of *Vectis* from the United Kingdom, as these co-occur in Aptian and Albian strata of the Isle of Wight with several species described from unique, partially preserved material.

Vectis collinsi sp. nov.
urn:lsid:zoobank.org:act:BF4B5181-672D-4D5E-A9A3-04298F76E09E.
Figs. 4E, F, 7C

Material. A single carapace, lacking cuticle, is the holotype (Museum of the World Ocean, Kaliningrad, Russia), number MWO 1 9382.

Etymology. The trivial name honours the late Joe S.H. Collins, who added enormously to our knowledge of Cretaceous crabs.

Diagnosis. *Vectis* with strongly inflated regions, coarse granulation, distinct and deep cervical and branchial grooves and a subtle protogastric tubercle. Carapace pyriform, well delineated, with inflated and coarsely tuberculated regions, moderately arched longitudinally, strongly convex transversely; distinctly wide posterior branchial region; downturned rostrum; posterolateral margins with coarse spines; anterolateral margins with (paired) spines and notches; deep cervical and branchial grooves; swollen epigastric regions; posterior part of mesogastric region with central furrow, mesogastric process covered with row of two large tubercles; hepatic region swollen; inflated epibranchial region; distinct, tumid pentagonal cardiac region; large intestinal region; strongly tuberculated metabranchial region. No appendages and/or ventral elements preserved.

Type locality and stratigraphical level. Near the village of Levashi, Levashinsky district (Dagestan Russia); Kubina Formation (Lower Cretaceous, middle Aptian; *Parahoplites melchioris* ammonite Zone).

Description. Pyriform carapace, well delineated with inflated and coarsely tuberculated regions, widest at middle of metabranchial region, moderately arched longitudinally, strongly convex transversely; wide, downturned rostrum with median sulcus; orbits or orbital spines not completely preserved (no description possible); substraight anterolateral margin and convex posterolateral margin; posterolateral margins with 4–5 robust spines; anterolateral margins with (paired) spines and notches; slightly concave posterior margin approximately half of maximum carapace width; deep cervical and branchial grooves running almost parallel from cardiac region to lateral notches; tumid epigastric regions covered with large central tubercle; posterior part of mesogastric region with central furrow, mesogastric process covered by two large tubercles; tumid hepatic region with at least one large tubercle; reniform, inflated epibranchial region; prominent tumid pentagonal cardiac region surrounded by broad and deep branchiocardiac groove; wide and high intestinal region covered with few variably sized tubercles separated from large inflated, strongly tuberculated metabranchial region by broad and deep groove starting from cardiac region and ending in posterolateral notch. No appendages and/or ventral elements preserved.

Remarks. *Vectis collinsi* sp. nov. differs from the type species,*V. wrighti*, in a much coarser surface granulation, a narrower posterior cardiac apex with concave lateral grooves and lateral carapace margins that have strong conical spines. In addition, it has small tubercles on the proto- and mesogastric regions and carapace grooves are wider. *Vectis collinsi* sp. nov. shows better-developed spines and notches on the lateral carapace margin, but this may be a preservational difference since both species are known from unique type specimens only.

Of *Vectis caseyi*, represented by a single specimen from the lower Albian of Surrey, United Kingdom, only the posterior part of the carapace is preserved. The grooves are thin and acute, and the carapace surface finely granular; these features readily differentiate it from *Vectis collinsi* sp. nov.

Vectis echinorum from the upper Aptian of the Isle of Wight, United Kingdom, is represented by partially or poorly preserved specimens. *Vectis collinsi* sp. nov. differs from *V. echinorum* in having a coarsely granular intestinal region, a more vaulted and coarsely granular cardiac region and carapace margins with conical spines.

Section Eubrachyura de Saint Laurent, 1980
Superfamily Dorippoidea MacLeay, 1838
Family Telamonocarcinidae Larghi, 2004

Type genus: *Telamonocarcinus* Larghi, 2004

Other genera included. *Eodorippe* Glaessner, 1980, *Navarrara* Klompmaker, 2013, *Personadorippe* gen.nov. and *Withersella* Wright and Collins, 1972.

Fig. 4. New crabs from the locality of Levashi (Levashinsky district, Dagestan); Kubina Formation, Lower Cretaceous, middle Aptian, *Parahoplites melchioris* ammonite Zone. **A–D.***Levashidromites cornutus* gen. et sp. nov., holotype (MWO 1 9977), dorsal (A), oblique frontal (B), frontal (C) and right lateral (D) views. **E–G.***Vectis collinsi* sp. nov., holotype (MWO 1 9382), dorsal (E), oblique frontal (F) and right lateral (G) views.

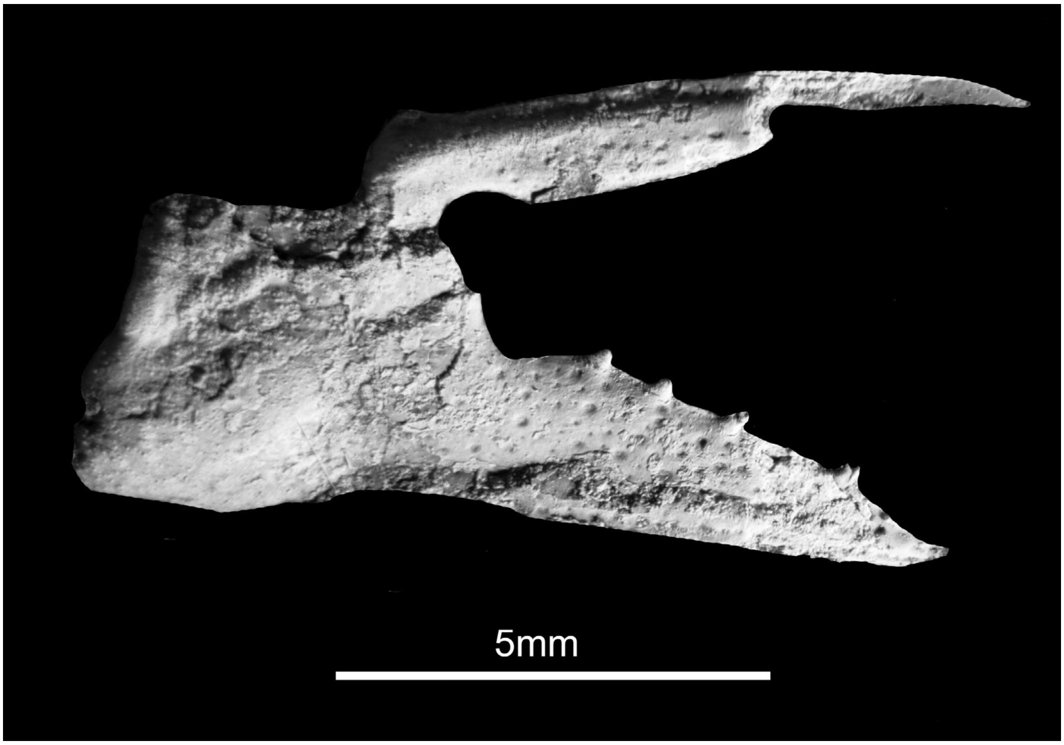


Fig. 5. Claw of *Personadorippe levashiensis* gen. et sp. nov., MWO 1 9381; Dagestan, Levashinsky district, village of Levashi; Kubina Formation; Lower Cretaceous, middle Aptian, *Parahoplites melchioris* ammonite Zone.

Diagnosis. See Luque (2014a).

Remarks. *Navarrara*, *Withersella* and *Personadorippe* gen.nov. are here included in the Telamonocarcinidae (see Fig. 6) for the first time, adding significant geological and stratigraphical data on that Early and mid-Cretaceous family of dorippoid crabs (Figure 10). Luque (2014a) included only *Eodorippe* and *Telamonocarcinus*. The Telamonocarcinidae belong “to the oldest heterotreme representatives” (Guinot, 2019, p. 288).

Navarrara was originally assigned to the Longodromitidae (included in the Glaessneropsoidea) by Klompmaker (2013, p. 154). This was done, “because it matches the diagnosis given in Schweitzer and Feldmann (2009a, p. 100) quite well”. However, the diagnosis of the Longodromitidae given by those authors is so general and based on a non-monophyletic lot of genera that many Jurassic and Cretaceous crabs, now assigned to a range of families and superfamilies, could be included in that family. In order to be able to accommodate *Navarrara*, the diagnosis of the Longodromitidae was emended by Klompmaker (2013, p. 154). From Appendix B (see below), it is clear that *Navarrara* and *Longodromites*, the generic type of the family, have quite different character sets (no fewer than 15 out of 19 characters are rated differently). This results in a completely different position in all possible trees (see Figs. 8 and 9). This observation calls for a thorough re-consideration of the family diagnoses within the superfamily Homolodromioidea and in what is now called the Glaessneropsoidea. The validity of the latter needs to be tested.

Withersella was earlier assigned to the family Torynommidae Glaessner, 1980 by Van Bakel et al. (2003), Schweitzer et al. (2007a, p. 19; 2010, p. 78), Karasawa et al. (2011), Schweitzer and Feldmann (2011) and Klompmaker (2013, p. 173) or to the Carcineretidae (Collins et al., 1995; Fraaye, 1996; Wright, 1997; Collins, 2003). Nyborg et al. (2019, p. 134) noted that *Eodorippe connori* was most closely similar in shape to *Withersella*.

Withersella differs from *Torynomma* in six (out of 19) characters, as rated in Appendix B. The most prominent differences include the condensation of the anterior branchial region between the branchial and cervical grooves in *Withersella* and the subequal length of the anterior mesogastric process to the posterior mesogastric triangle (anterior mesogastric process elongate in *Withersella*). *Torynomma* is a podotreme crab, with the groove system subdividing the carapace into three parts. In all aspects, *Withersella* is different from the derived portunoid *Carcineretes*, some obvious differences including overall carapace shape (converging carapace margins in *Withersella* (*vs* diverging in *Carcineretes*), an orbital margin with several teeth and notches in *Carcineretes* and a substraight posterior carapace margin in *Carcineretes* (*vs* concave in *Withersella*).

Withersella can be placed in the Telamonocarcinidae with confidence; our cladistic analysis supports this (see Figs. 8 and 9). It appears morphologically closest to *Personadorippe* gen. nov. (see below).

The Telamonocarcinidae was erected, as a subfamily, by Larghi (2004), on the basis of abundant, well-preserved and complete material from the Cenomanian of Lebanon, so the dorippoid affinities of this family was proved by dorsal and ventral morphology, as well as completely preserved appendages. Guinot et al. (2013) noted that the Telamonocarcinidae showed a combination of dorippid and ethusid features, that it might not be monophyletic and probably contained the oldest known dorippoids. A cladistic analysis (see Appendices A and B) has been performed for the present paper in order to study the homology of composition and characters of the group. The condensation between the branchial and cervical grooves, subdivided anterior branchial region, long and narrow mesogastric process, subsquare carapace with widened branchial regions and wide and oblique orbitofrontal margins without distinct orbital notches form a consistent character set. The oldest records of the family are recorded herein with *Withersella crepitans* from the lower Aptian *Deshayesites forbesi* ammonite Zone

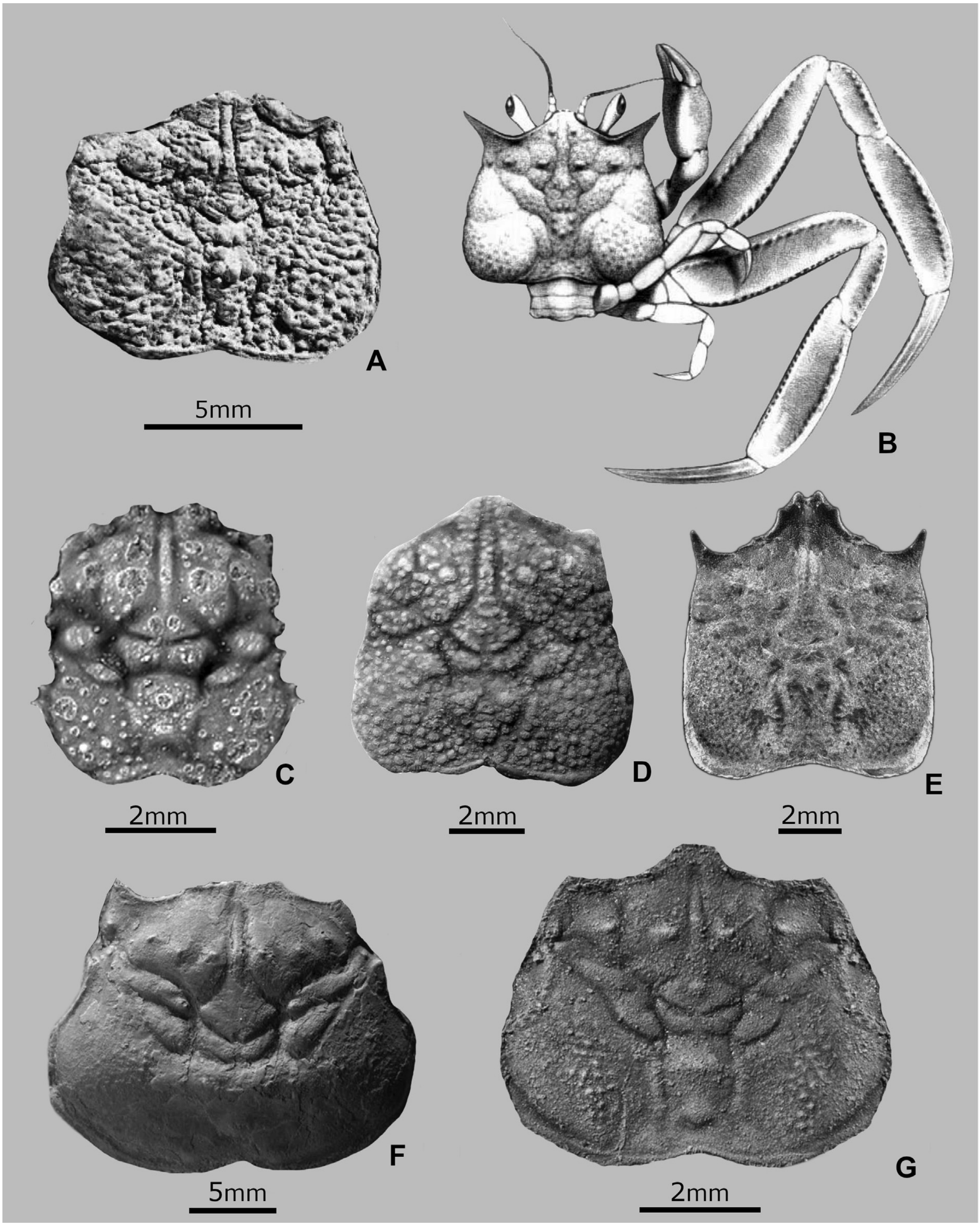


Fig. 6. Telamonocarcinid crabs (Eubrachyura, Dorippoidea) known to date. **A, B.** *Telamonocarcinus gambalatus* Larghi, 2004, from Cenomanian–Turonian strata in central-western Lebanon, Hgula and Haqil: **A**. holotype (MSNMi26033; see Larghi, 2004, fig. 4). **B**. reconstruction of appearance in life (see Larghi, 2004, fig. 5). **C**. *Navarrara betsieae* Klompmaker, 2013, from upper Albian Aldoirar patch reef (Albeniz Unit, Eguino Formation) of Koskobilo, northern Spain: compilation photograph based on MGSB77705 and MAB k.3004 (see Klompmaker, 2013, fig. 4g). **D**. *Personadorippe kalashnikovi* gen. et sp. nov., holotype (MWO 1 9298), from the lower Cenomanian (Lyaminsk Formation, *Schloenbachia varians* ammonite Zone), Moscow Oblast, Dmitrovsky district, village of Nikolskoye. **E**. *Withersella crepitans* Wright and Collins, 1972 (NHMUK IC15; see Schweitzer and Feldmann, 2011, fig. 7) from the Aptian, Isle of Wight, United Kingdom. **F**. *Eodorippe spedeni* Glaessner, 1980, holotype (NZGSAR 675; see Luque, 2014a, fig. 2e), Campanian–Maastrichtian, New Zealand, Te Hoc River. **G**. *Telamonocarcinus antiquus* Luque, 2014a, 2014b, holotype (IGM p881012; see Luque, 2014a, fig. 2a) from lower Albian (Tablazo Formation) of Colombia, department of Santander, near the town of La Fuente.

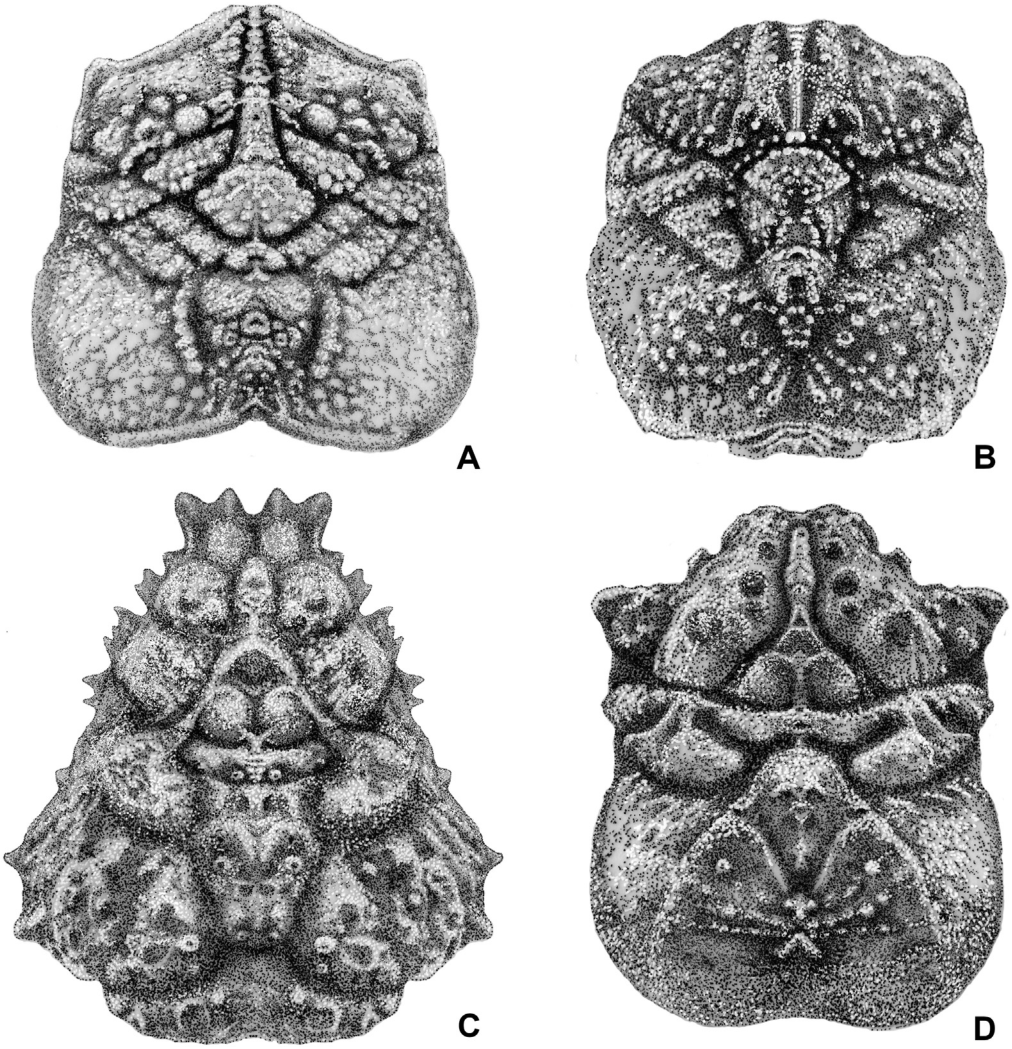


Fig. 7. Drawings (not to scale) of carapaces of the new crab taxa erected herein. **A**. *Personadorippe kalashnikovi* gen. et sp. nov. **B**. *Personadorippe levashiensis* gen. et sp. nov. **C**. *Vectis collinsi* sp. nov. **D**. *Levashidromites cornutus* gen. et sp. nov.

of the Isle of Wight, United Kingdom, followed by *Personadorippe levashiensis* nov. gen., nov. sp. from the middle Aptian *Parahoplites melchioris* ammonite Zone from Dagestan, Russia. Albian records are from Spain (*Navarrara betsiae* Klompmaker, 2013) and Colombia (*Telamonocarcinus antiquus* Luque, 2014a), Cenomanian records from Russia (Moscow area) (*Personadorippe kalashnikovi* nov. gen., nov.sp.), Lebanon (*Telamonocarcinus gambalatus* Larghi, 2004) and Japan, and the youngest record is from New Zealand (see Luque, 2014a, table 1). Thus, this family was geographically widely distributed and represented by several genera (i.e., a wide variation), suggesting a long evolutionary history, dating back to the Jurassic.

In a subsequent study, the carapace morphology of the Telamonocarcinidae should be compared in detail with that of the older (Early Jurassic—Early Cretaceous) Lecythocaridae Schweitzer and Feldmann, 2009a, a possibly basal family of dorippoids (see also Guinot et al., 2019).

The Lecythocaridae Schweitzer and Feldmann, 2009a may well be eubrachyuran in nature and ancestral to the Telamonocarcinidae. The range of the Lecythocaridae is Upper Jurassic (Kimmeridgian) (Schweigert, 2018, p. 3) to Lower Cretaceous (Berriasian) (BWMvB and RHBF, pers. obs., work underway); species have been recorded from Germany, Austria, Romania and the Czech Republic (Schweigert and Robins, 2016).

An important proxy character and evolutionary polarity in brachyuran macro-evolution is ‘branchial condensation’, occurring at intrafamilial level. The epibranchial region, i.e., the median carapace portion between the cervical and branchial grooves, is large (long) in basal forms, while it is reduced in size, or absent/evanesced in more derived, stratigraphically younger forms. Over geological time the branchial groove shifted gradually towards the cervical groove and finally the two grooves morphed into a single groove, the cervical groove.

For example: in the early Kimmeridgian *Prolecythocaris hauckei* Schweigert and Robins, 2016, the epibranchial condensation is less well developed than in the late Kimmeridgian *Lecythocaris paradoxa* (von Meyer, 1858) (compare Schweigert and Robins, 2016, fig. 2A, B with C, D) and the coeval *Prolecythocaris rieberi* (compare Schweigert, 2018, fig. 2).

This change in external morphological character state raises questions about the arrangement and function of the internal brachyuran body. The branchial groove is linked to the position,

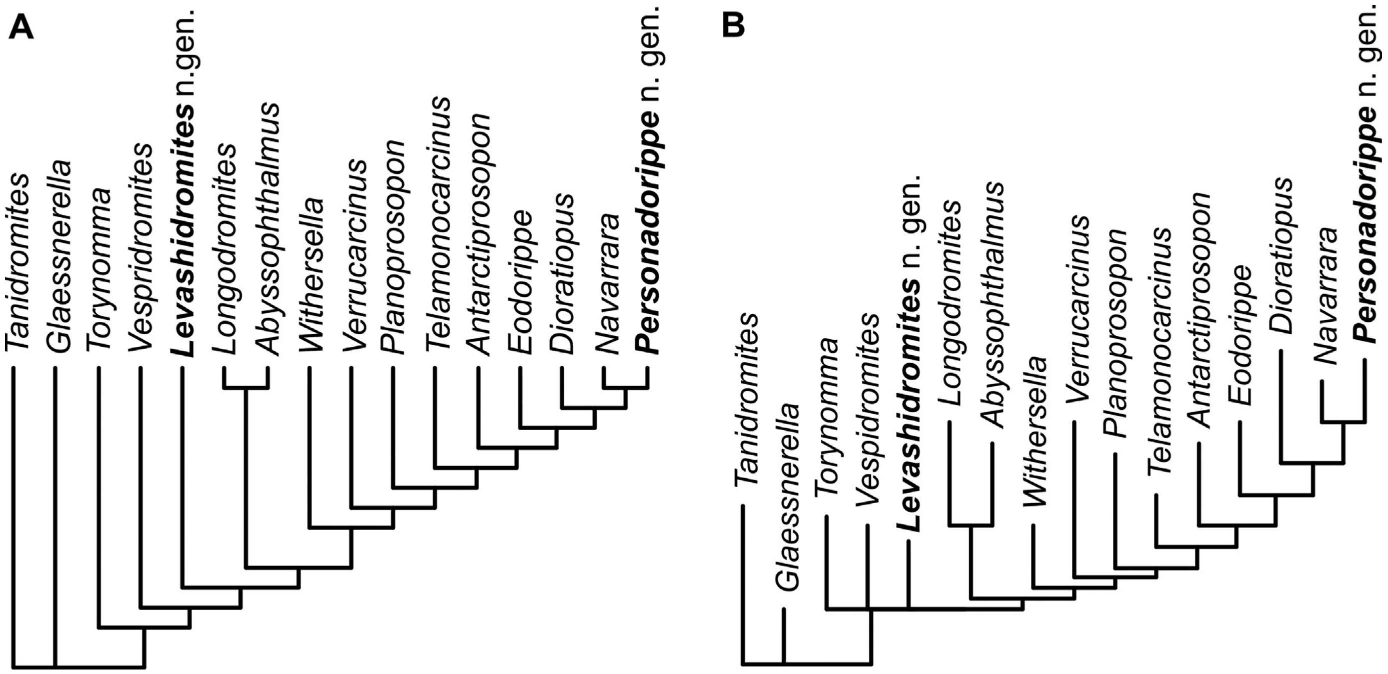


Fig. 8. A. Most parsimonious tree found using the ratchet parsimony method. **B.** ACCTRAN phylogram.

architecture and anatomy of the respiratory system in the branchial chamber, the area between the body and carapace enclosing the gills/branchiae.The pleura, or body wall separating the gills from the body, are connected to the ventral internal ridge that is visible externally as the branchial groove. Whenever the carapace between the cervical and branchial grooves is shortened, the gill chamber is expanded proportionately.

The mechanism behind this phenomenon may be a metabolic rate increase with would have meant more oxygen extraction from sea water. Griffen and Sipos (2018) concluded that metabolic rates in brachyurans strongly increased with temperature and that their metabolism was correlated with their ecological niche, varying with both diet strategy and habitat.

Branchial condensation through time can be recognised in a wide array of extinct crabs. The Palaeocorystoidea, in particular the basal group of the Necrocarcinidae and its subfamily Paranecrocarcininae (compare Van Bakel et al., 2012), have well-defined branchial grooves that are subparallel to the cervical groove, with a well-developed median portion of the carapace (epibranchial region), e.g., in *Bellcarcinus aptiensis* Luque, 2014 (Luque, 2014b, pl. 1). In the vast majority of younger forms of the Palaeocorystoidea, the branchial groove is very weak to indiscernible; if it can be traced at all, it lies close to the cervical groove.

In summary, branchial condensation appears to be a good proxy character for determining the relationship of crabs and their taxonomic position, in particular whether these are podotreme or not, or occupy a basal position in their clade. Good examples are the genera *Binkhorstia* Noetling, 1881 and *Torynomma* Woods, 1953, which were included in the Torynommidae Glaessner, 1980 by several authors (Glaessner, 1980; Van Bakel et al., 2003; De Grave et al., 2009, p. 29; Schweitzer et al., 2010, p. 78). *Torynomma* shows a subequal division of the carapace into three portions by the branchial and cervical grooves (compare Schweitzer and Feldmann, 2011, fig. 6), a basal condition typical of basal podotreme crabs. This is a completely different condition than the one seen in *Binkhorstia* (see Van Bakel et al., 2003, fig. 1), which shows a near-complete branchial condensation: the branchial and cervical grooves are subparallel and nearly merged. The epibranchial region in *Binkhorstia* is condensed, leaving only a narrow strip. These conditions demonstrate that *Torynomma* is a basal podotreme that occupies a completelydifferent taxonomic position from the eubrachyuran *Binkhorstia.* The taxonomic position of *Binkhorstia* will be clarified by Van Bakel et al. (in prep.).

In other groups of decapod crustaceans, branchial condensation can be observed as well. Fraaije et al. (2012, fig. 4) hypothesised a transition in Triassic to Late Jurassic anomurans in which the branchial groove shifted forwards and led to a single cervical groove on the dorsal carapace in diogenid paguroids from the Upper Jurassic onwards.A similar branchial condensation occurs in other group of paguroids as well (compare Fraaije, 2014, figs. 5–6). Fraaije et al. (2018) described how a huge increase in phyto- and zooplankton during the Jurassic led to a worldwide increase in meiofaunal diversity directly and indirectly triggered a radiation of many benthic groups. Increased metabolic rates in brachyurans could well have been caused by this macroevolutionary polarity and have triggered ecological specialisation such as burying, swimming and carrying foreign objects.

A wide posterior branchial chamber, together with condensation (shortening) of the median portion of the carapace, can be observed in diverse basal eubrachyuran clades in the Cretaceous. Ancient eubrachyurans such as the Telamonocarcinidae (oldest occurrence: Aptian), Archaeopidae Karasawa, Kishimoto, Ohara and Ando, 2019 (oldest occurrence: Turonian) and Archaeochiapasidae Guinot, Carbot-Chanona and Vega, 2019 (occurrence: Cenomanian) have a wide posterior carapace and various gradations of branchial condensation. The geological record of majoids is particularly incomplete in the Cretaceous, but majoids are considered, next to the Dorippoidea, to represent the most ancient and most basal eubrachyuran crabs (see e.g., Guinot et al., 2019, p. 782; Guinot and Van Bakel, 2020). The carapace outline of majoids is usually pyriform, with a wide posterior carapace, which is comparable with the outline in the Dorippoidea.

Genus ***Personadorippe*** nov.
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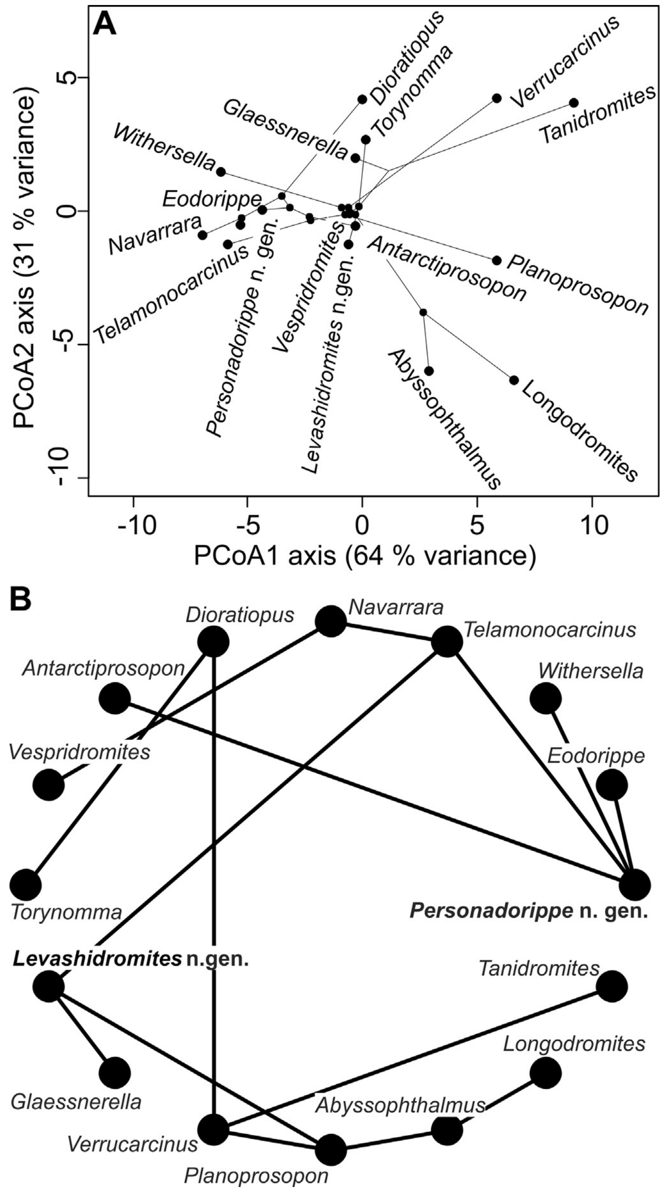

Fig. 9. A. Phylomorphospace of early crabs with projected phylogram and estimated morphologies of ancestors (internal branching points). **B.** Minimum spanning tree of early crabs.

Type species: *Personadorippe kalashnikovi* sp. nov., by current designation.

Other species included. *Eodorippe connori* Nyborg, Garassino, Vega and Kovalchuck, 2019 and *P. levashiensis* sp. nov.
Etymology. Latin '*persona*', meaning mask, with reference to the appearance of the dorsal carapace.
Diagnosis. Carapace subrectangular in outline, length slightly exceeding width; gently curved in longitudinal and transverse cross sections; regions weakly vaulted; front axially sulcate; orbitofrontal margin occupying most of carapace width; orbital margin oblique, without notches; outer orbital spine short, triangular; lateral margins sinuous, blunt, without spines; carapace surface granular; cardiac region narrow, cervical groove widely V-shaped, reaching lateral carapace margin; branchial groove well defined near cardiac region. Posterior carapace margin rimmed, concave. Cheliped palm compact, fingers long, with sharp, toothed cutting margin.

Remarks. *Personadorippe* gen. nov. shows a character set which places it unambiguously in the Telamonocarcinidae, i.e., condensation between branchial and cervical grooves, a subdivided anterior branchial region, a long and narrow mesogastric process, a subsquare carapace shape with widened branchial regions and wide and oblique orbitofrontal margins without distinct orbital notches. The results of our cladistic analysis (see appendices A, B; Figs. 8–9) confirm the close relationship with other included genera. We consider that these genera form a distinct, basal family within the Dorippoidea. *Personadorippe* gen. nov. is morphologically most closely similar to *Navarrara* and *Withersella* in its squarish carapace shape, overall granular carapace dorsal surface, a rather straight, oblique orbital margin with a single notch and curvature of the branchial region. The new genus differs from *Navarrara* in having less inflated regions, an undefined intestinal region, a lack of lateral teeth and spines and of central cardiac and paired mesogastric tubercles. *Personadorippe* gen. nov.differs from *Withersella* in having a wider cardiac region, wider posterior branchial regions (i.e., a wider posterior carapace), tubercles on anterior regions, a wider cardiac region and a straight orbital margin (*vs* curved in *Withersella*). Carapaces of *Telamonocarcinus* and *Eodorippe* are wider than long, have more oblique, converging lateral margins and a narrower cardiac region, in comparison with *Personadorippe* gen.nov.
Eodorippe connori Nyborg, Garassino, Vega and Kovalchuck, 2019, from the Albian of Oregon, USA, appears better assigned to *Personadorippe* gen. nov. It differs from *E. spedeni* Glaessner, 1980 in having a more subsquarish carapace shape and different carapace ratios, a narrower and W-shaped posterior carapace margin, a subdivided epibranchial region and granular carapace microstructure. It was originally assigned to *Eodorippe* (Nyborg et al., 2019, p. 134) but described as, "It is most similar in shape to *Withersella* Wright & Collins, 1972 …". *Eodorippe binodosa* Collins, Kanie and Karasawa, 1993 is here left in *Eodorippe*; this species' posterior margin is shaped more like the type species, *E. spedeni*, and the carapace surface is less granular than in members of *Personadorippe* gen. nov.

Personadorippe kalashnikovi sp. nov.
urn:lsid:zoobank.org:act:6E1D22F9-9D53-4974-B675-80ED4246FC95.
Figs. 3A–D, 6D, 7A

Material. A single specimen, the holotype, MWO 1 9298.
Etymology. Named in honour of Alexei Kalashnikov (Moscow, Russia), who donated this unique specimen.
Diagnosis. *Personadorippe* gen. nov. with flattened granules, a single large central protogastric tubercle, a relatively wide urogastic and cardiac region and the mesogastric region that equals over half the total carapace length.
Type locality and stratigraphical level. An abandoned sand pit in the village of Nikolskoye, Dmitrovsky district, Moscow Oblast; Lyaminsk Formation (Upper Cretaceous, lower Cenomanian, *Schloenbachia varians* ammonite Zone).
Description. Carapace small (CL = 11 mm), subsquare in outline, length subequal to width, widest at 20 per cent of maximum carapace length from posterior, in branchial region; regions weakly inflated; carapace gently curved in longitudinal and transverse sections. Rostrum incompletely preserved, slightly projected, slightly downturned, axially sulcate. Orbital margin oblique, without notches; outer orbital spine short, triangular. Lateral margin converging anteriorly, slightly broadening at mesobranchial region, posteriorly constricted. Posterolateral margin longer, convex, in particular posteriorly. Posterior margin concave, inverted V-shaped, with smooth rim.

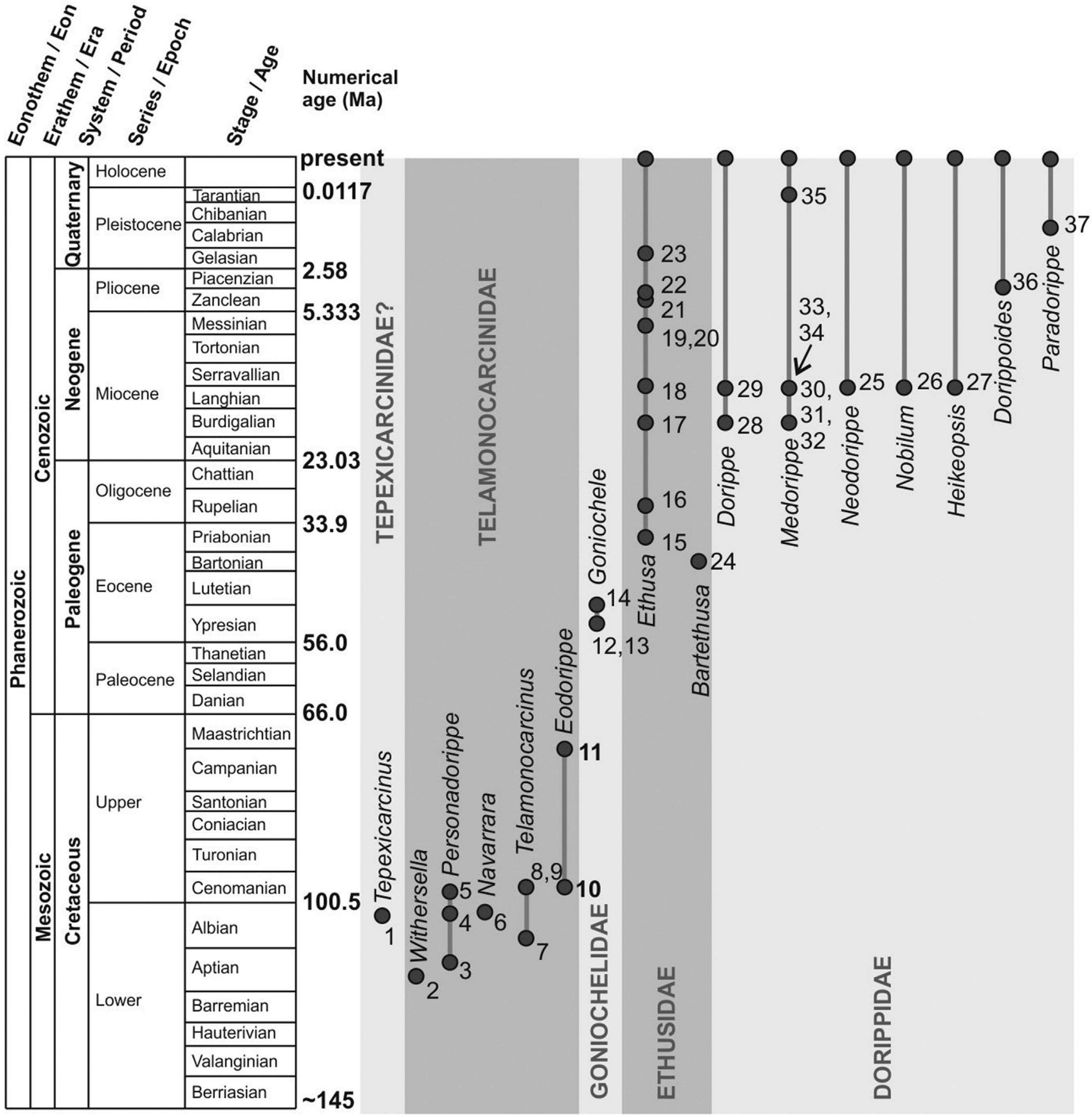

Fig. 10. Stratigraphical distribution of dorippoid genera. **1**. *Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate and Bishop, 1998. **2.** *Withersella crepitans* Wright and Collins, 1972. **3**. *Personadorippe levashiensis* gen. et sp. nov. **4**. *Personadorippe connori* (Nyborg, Garassino, Vega and Kovalchuk, 2019) comb. nov. **5**. *Personadorippe kalashnikovi* gen. et sp. nov. **6**. *Navarrara betsieae* Klompmaker, 2013. **7**. *Telamonocarcinus antiquus* Luque, 2014a, 2014b (*sensu* Luque, 2014a). **8**. *Telamonocarcinus* sp. (*sensu* Luque, 2014a). **9**. *Telamonocarcinus gambalatus* Larghi, 2004. **10.** *Eodorippe binodosus* Collins, Kanie and Karasawa, 1993. **11.** *Eodorippe spedeni* Glaessner, 1980. **12**. *Goniochele angulata* Bell, 1858. **13.** *Goniochele* cf. *angulata* Bell, 1858 (*sensu* Van Straelen, 1921 and Van Bakel et al., 2006). **14**. *Goniochele madseni* Collins and Jakobsen, 2004. **15.** *Ethusa evae* Müller and Collins, 1991; **16**. *Ethusa berica* De Angeli and Beschin, 2008. **17**. *Ethusa* sp. *sensu* Artal and Gilles, 2007. **18**. *Ethusa octospinosa* Müller, 2006. **19**. *Ethusa* cf. *mascarone* (Herbst, 1785) *sensu* Müller, 1984. **20**. *Ethusa popognensis* De Angeli, Garassino and Pasini, 2009. **21**. *Ethusa chibai* Karasawa, 1993.**22.** *Ethusa* sp. *sensu* Pasini and Garassino, 2016. **23.** *Ethusa* cf. *mascarone* (Herbst, 1785) *sensu* Baldanza et al., 2017. **24**. *Bartethusa hepatica* Quayle and Collins, 1981. **25.** *Neodorippe carpathica* (Förster, 1979). **26**. *Nobilum wenchii* Hu and Tao, 1996. **27**. *Heikeopsis tuberculata* (Morris and Collins, 1991). **28.** *Dorippe fankhauseri* Studer, 1892. **29.** *Dorippe ornatissima* Müller, 2006. **30.** *Medorippe* sp. *sensu* Artal and Gilles, 2007. **31.** *Medorippe tanabei* Karasawa, 2000. **32**. *Medorippe* aff. *lanata* Linnaeus, 1767. **33**. *Medorippe ampla* Garassino, De Angeli, Gallo and Pasini, 2004. **34**. *Medorippe margaretha* (Lőrenthey, *in* Lőrenthey and Beurlen, 1929). **35**. *Medorippe lanata* (Linnaeus, 1767). **36**. *Dorippoides facchino* (Herbst, 1785) *sensu* Van Straelen, 1938. **37**. *Paradorippe granulata* (De Haan, 1841).

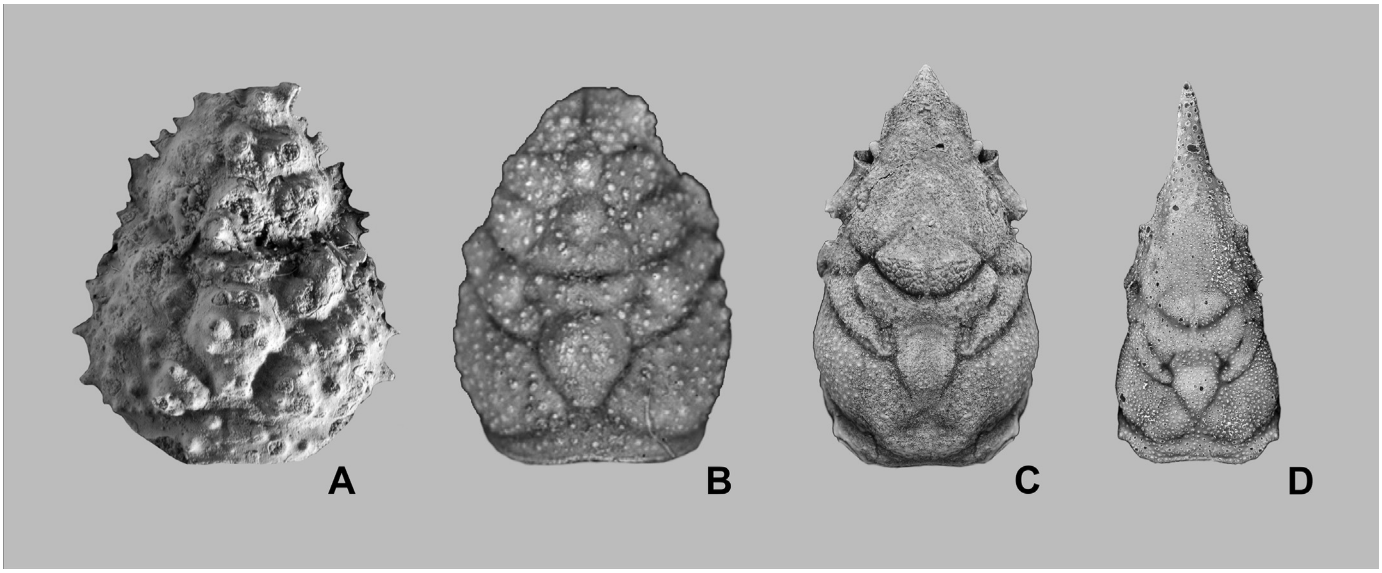

Fig. 11. A. *Vectis collinsi* sp. nov., holotype (MWO 1 9382), Levashi (Levashinsky district, Dagestan); Kubina Formation, Lower Cretaceous, middle Aptian. **B**. *Vectis wrighti* Withers, 1946, holotype (NHM In.60908), Atherfield (Isle of Wight, UK); Atherfield Clay Formation, Lower Cretaceous, lower Aptian (see Collins et al., 2020, fig. 3c). **C**. *Viaia robusta* Artal, Van Bakel, Fraaije, Jagt and Klompmaker, 2012, paratype (compilation photograph based on MGSB28146), Monte Orobe (Olazagutía, Navarra, Spain); Albian–Cenomanian reefal limestones (see Artal et al., 2012, fig. 1.1). **D**. *Heeia villersensis* (Hée, 1924) (compilation photograph based on JSHC2035 [now in NHMUK collections]), Wilmington (Devon, southern England); Cenomanian sands (see Artal et al., 2012, fig. 2.1).

Mesogastric region elongate, covering anterior half of carapace length, pinched in between epigastric elevations, with long, narrow mesogastric process, with subvertical lateral margins; posterior portion broadly subrhombic with convex posterior margin. Protogastric region suboval, bearing central tubercle; weakly differentiated from small, subrectangular hepatic region. Urogastric region slightly wider than base of mesogastric region, low, consisting of two transversely lined lobes, divided by axial depression. Epibranchial region conspicuously small, pointed triangular, positioned laterally; mesobranchial region consisting of two lobes; anterior one larger, elongated transversely, eye shaped; posterior one smaller, more axially placed, weakly delimited posteriorly. Cardiac region subpentagonal, apex pointed downwards, region bearing two anterior tubercles and a single smaller posterior tubercle. Intestinal region undefined. Metabranchial region large, rather plain, with convex lateral margin.

Cervical groove narrow, acute, broadly V-shaped, best defined axially. Branchiocardiac groove short, anteriorly well defined. Branchial groove shallow, not clearly defined. Grooves enclosing mesogastric region, urogastric region and epibranchial region well developed.

Carapace surface covered with granules and tubercles, cuticle not preserved. Ventral surface and appendages not preserved.

Remarks. Having been collected from Cenomanian strata at Nikolskoye, this is the youngest of the two species of *Personadorippe* gen.nov. described herein, and it represents the most northerly occurrence of the Telamonocarcinidae to date. The areolation with the appearance of a face and the wide posterior branchial region, are typical features of this species.

Personadorippe levashiensis sp. nov.
urn:lsid:zoobank.org:act:6607214E-5768-4080-B4AA-F3D35571EF33.
Figs. 3E–F, 5, 7B

Material. A unique specimen, the holotype, MWO 1 9381.

Etymology. The trivial name is based on the village of Levashi (Levashinsky district, Dagestan, northern Caucasus), where the type material was recovered.

Diagnosis. Species of *Personadorippe* gen. nov. with spaced, acute granules; no tubercle on protogastric region, narrow urogastric and cardiac regions and mesogastric region stretching clearly less than half total carapace length.

Type locality and stratigraphical level. Near the village of Levashi (Levashinsky district, Dagestan, northern Caucasus); Lower Cretaceous, middle Aptian strata of the Kubina Formation (*Parahoplites melchioris* ammonite Zone).

Description. Carapace rather small (CL = 22 mm), subsquare in outline, length and width subequal, widest at 20 per cent of maximum carapace length from posterior in branchial region; regions weakly inflated; carapace nearly flat in longitudinal and transverse sections. Rostrum not preserved; base of rostrum axially sulcate. Orbital margin subhorizontal, without notches, outer orbital spine broken at base, apparently well developed. Anterolateral margins subvertical, parallel; posterolateral margin subequal in length, convex all along branchial region. Posterior margin concave, inverted V-shaped, divided into two curved portions, with acute rim.

Mesogastric region rather small, covering anterior half of carapace length, with acute, narrow mesogastric process, lateral margins subvertical; posterior portion broadly triangular with convex posterior margin. Protogastric region large, subrectangular, clearly separated from rather large subrectangular hepatic region. Urogastric region subequal in width than mesogastric region, widely rectangular, divided by weak axial groove. Epibranchial region small, triangular, positioned laterally; mesobranchial region consisting of two lobes; anterior one oblique; posterior one more axially placed, subtriangular. Cardiac region pentagonal, apex pointed downwards, region acutely delineated posteriorly. Intestinal region undefined. Metabranchial region large, weakly vaulted, with convex lateral margin.

Cervical groove broadly V-shaped, axially bluntly curved. Branchiocardiac groove short, anteriorly and posteriorly well defined. Branchial groove as well defined as cervical groove, angle slightly steeper, weakly curved. Grooves subdividing anterior branchial region oblique, acute, well developed.

Carapace surface covered with granules, decalcified portions of cuticle preserved. Ventral surface not preserved. Right-hand cheliped preserved; palm compact, rounded, margin of carpal articulation oblique, lower margin bluntly rounded, fingers long, pollex relatively large, triangular, flat, with sharp, toothed cutting margin; dactylus slender, straight, with dorsal ridge and sharp cutting margin.

Remarks. This species represents one of the oldest dorippoids, i.e., one of the earliest eubrachyurans, currently known. Only *Withersella crepitans* from the lower Aptian (*Deshayesites forbesi* ammonite Zone) of the Isle of Wight, United Kingdom, is older.

Personadorippe levashiensis gen. et sp. nov. differs from *P. kalashnikovi* gen. et sp. nov. (see above) in having a relatively shorter anterior mesogastric process in comparison to the posterior mesogastric triangle; in having a narrower cardiac region, with its posterior apex further away from the posterior carapace margin; in having a narrower urogastric region; in lacking the prominent central tubercles on the protogastric region; and in having a different groove system and subdivision in the anterior branchial region (between branchial and cervical grooves). The claw is directly associated with the carapace, placed under the carapace *insitu*, and can be assigned to this species with confidence. It shows a distinct morphology; fingers are longer than the palm, the flat, high fixed finger with sharply toothed cutting edge and slender untoothed dactylus. It can be compared within the Telamonocarcinidae only with *Telamonocarcinus gambalatus*, of which also claws are known (see Larghi, 2004, figs. 5, 6.7, 6.8). The claws of *T. gambalatus* have fingers that are shorter than the palm, and the claws appear more robust overall. The claw of *Personadorippe levashiensis* gen. et sp. nov. resembles that of extant dorippoids.

4. Phylogenetic reconstruction, phylomorphospace and minimum spanning tree analysis

For the purpose of phylogenetic framing and quantitative morphological characterisation of the two new crab genera described herein, a set of analyses were performed. The phylogenetic analysis was performed on the matrix of 16 primitive crab genera and 19 morphological characters that describe these (character data in Appendix). The phylogenetic analysis was performed in the R computational environment (R Development Core Team, 2015), using packages ‘ape 5.0’ (Paradis and Schliep, 2018) and ‘phangorn’ (Schliep, 2010). The following matrix of contrasts was used in the parsimony analysis:

Character states	0	1	2
0	0	0	0
1	0	1	0
2	0	0	1
?	0	0	0

The first approximate tree was found by using a random addition parsimony search. Later on, this tree was used as an input for a more effective parsimony ratchet tree search (Nixon, 1999). Finally, accelerated transformation (ACCTRAN), which assumes that most changes occurred down the tree (Felsenstein, 2004) (i.e., the expected result of an adaptive evolutionary radiation), was performed on the most parsimonious tree, yielding the most parsimonious phylogram.

Phylomorphospace analysis was performed through the following steps: *i*) the discrete character matrix was transformed into a distance matrix calculating Manhattan distance using R package ‘vegan’; *ii*) principal co-ordinate analysis (PCoA) was performed on the given matrix in order to minimise the dimensionality of the data; *iii*) the first two PCoA co-ordinates (which explained 64 per cent and 31 per cent of variance in character data) were used for plotting the taxa; *iv*) finally, aphylomorphospace graph was drawn using the most parsimonious tree and projecting it onto this two-dimensional PCoAmorphospace using the package ‘phytools’ (Revell, 2012). Although uncertain/missing values in the taxon/character matrix could have biasing effects in the determination of morphospace occupancy (Lehmann et al., 2019), in the current data set such entries were uncommon (11 out of 304 or just 3.6 per cent), and thus should have yielded a very low bias.

Complementary to the phylomorphospace approach, the so-called minimum spanning tree method was used. This allows a better understanding of the pattern of morphological/phenetic similarities between previously known and newly described genera. First, taxa were seriated according to their pattern of distribution of character states (see palaeoecological applications in Ryan et al., 1999), thus forming the gradient from most “primitive” to most “advanced”, and later on these were connected by minimum spanning tree calculated from the primary distance matrix (step (*i*) in phylomorphospace analysis), using function *mst* of the ‘vegan’ package (Oksanen et al., 2015).

5. Discussion: trends in phylogeny and morphospaces

The cladogram and phylogram that resulted from maximum parsimony analysis reveal the placement of the newly described crab genera as well as the broader context of early crab evolution (Fig. 8A, B). The genera *Tanidromites* and *Glaessnerella* assume basal positions in both diagrams, while *Torynomma*, *Vespridromites* and *Levashidromites* gen. nov. appear as a polytomy, sister to more advanced clades that contain *Personadorippe* gen. nov., which is sister to *Navararra*. Both phylogram and cladogram show that these two new genera belong to two distinct derived clades: *Personadorippe* gen. nov. is closely related to *Withersella*, *Abysssophthalmus*, *Verrucarcinus* and *Navararra*, whereas *Levashidromites* gen. nov. assumes a more basal, intermediate position between *Vespridromites* and *Longodromites*.

Due to the relatively low number of characters in relation to the available number of crab taxa analysed for the presented analysis, the fine subdivision and exact relationships of separate genera should be seen as preliminary. The possible use of stratigraphical distribution of taxa, in the case of a limited number of morphological characters, could be a helpful option in deciphering bifurcation paths of crab phylogeny through the use of stratocladistics (Fisher, 2008). To date, the known fossil record of the group analysed is very patchy, and many taxa are known from single localities only, which makes use of their temporal distribution rather difficult and most probably strongly affected by sampling artefacts. Therefore, significant sampling over a wide of stratigraphical intervals, geographical regions and palaeoenvironments is needed to ensure sufficient information density of the temporal distribution patterns of crab taxa, which is a pre-requisite for the use of stratocladistic methods.

The distribution of early crab taxa in the phylomorphospace (Fig. 9A) reveals distinct trends in the macroevolution of this group. *Tanidromites*, the most primitive taxon analysed, is clearly separated from the remainder of the taxa, and the transition to the advanced groups proceeded through a high-magnitude directional shift in morphospace (to the left side of the graph), where most of the subsequent Jurassic–Cretaceous diversification occurred. This pattern indicates directional shift in morphospace occupancy and morphological diversification through time (Adams and Collyer, 2019). Interestingly, it appears that, after initial diversification in the "advanced" portion of the morphospace, there was a centrifugal diversification in many directions where the genera *Planoprosopon*?, *Longodromites* and *Abyssophthalmus* assumed novel morphologies, and *Verrucarcinus* secondarily evolved a more primitive condition. The new genera, *Personadorippe* and *Levashidromites*, are located in the tight morphological cluster of derived crab taxa. However, it can be seen that *Personadorippe* gen. nov.sits further to the left, in a more "advanced" portion of the phylomorphospace.

The seriated positions of taxa on the circle are approximately proportional to their phylogenetic relationships, as revealed by the present analyses. However, a very uneven character of morphological similarities is exhibited by the minimum spanning tree of primitive crabs (Fig. 9B), which indicates a non-linear progression of crab morphology during macroevolution. Phenetically, *Tanidromites* is placed in proximity to *Verrucarcinus* by morphospace analysis because both taxa exhibit plenty of primitive character states. In other words, both taxa are found to be phenetically close to each other by the absence of joint derived characters. *Verrucarcinus* is also closely similar to *Dioratiopus* and *Planoprosopon*. This observation concurs with the distribution of taxa in the phylomorphospace, and the conclusion that during crab macroevolution there was repeated convergence and reversal in morphology to more primitive states. In the phenetic network discussed, *Levashidromites* gen. nov. exhibits the closest links to the relatively primitive *Glaessnerella*, the more advanced *Planoprosopon* and the more closely related, yet more derived *Telamonocarcinus* clade. Morphologically, the new genus *Personadorippe* is most closely linked to its sister taxon, the more advanced *Eodorippe*, and to more primitive members of the same advanced clade of *Telamonocarcinus* and *Withersella* (Fig. 9B). The overall pattern of morphospace occupation matches interpretations of opportunistic phylogenetic diffusion well, with multiple innovations and acquisitions of convergent morphologies in ecological expansion of crabs during the Mesozoic marine revolution (e.g.,Vermeij, 1977; Klompmaker et al., 2015) in concert with dynamics of their main habitat: biogenic reefs (Klompmaker, 2013), which are the most diverse and complex marine environments that promote macroevolution (Kiessling et al., 2010).

6. Concluding remarks

The new taxa described herein from Lower and Upper Cretaceous strata of Moscow Oblast and Dagestan, Russia, are part of the Jurassic–Cretaceous radiation of both primitive and derived crabs. The Dorippoidea appears to be more diverse and widespread in Lower Cretaceous strata than hitherto described, and can be recognised on carapace morphology. Carapace tripartition and branchial condensation, are important proxy characters for reconsidering the taxonomic placement of primitive crabs. The families Viaiidae and Longodromitidae are revised on the basis of proxy characters; several other Mesozoic families are in urgent need of reconsideration. The phylomorphospace analysis applied here shows distinct early macroevolutionary trends and there is great potential for future exploration early brachyuran evolution.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2020.104675.