

Description of the first fossil species of *Bathynectes* (Brachyura, Polybiidae) in the Badenian (middle Miocene) of the Medobory Hills (Ukraine, Central Paratethys), with remarks on its habitat ecology

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Resum

OSSÓ, À. i STALENNUY, O. Descripció de la primera espècie fòssil del gènere *Bathynectes* (Brachyura, Polybiidae) en el Badenian (Miocè mig) dels Turons Medobory (Ucraïna, Paratethys central), amb notes sobre l'ecologia del seu habitat. El descobriment d'una nova espècie del gènere *Bathynectes* Stimpson, 1871 (*B. muelleri* n. sp.) en els complexos d'esculls del Badenian (Miocè mig) de la pedrera de Maksymivka (Conca d'avantpaís dels Càrpats septentrionals), en els denominats Turons Medobory, prop de Ternopil (Ucraïna), representa el primer registre fòssil d'aquest gènere. La majoria de les espècies actuals d'aquest gènere, són d'aigües profundes. Es descriu *Bathynectes muelleri* n. sp. i s'argumenta el possible origen del gènere i els seus canvis d'hàbitat al llarg del temps. També s'analitza l'abundor de restes de decàpodes al complex d'esculls de Maksymivka i es presenta una hipòtesi per explicar la seva presència.

Paraules clau: *Bathynectes*, Polybiidae, Badenian, Paratethys central, Maksymivka, Ucraïna.

Резюме

ОССО, А., СТАЛЕННИЙ, О. Опис першого викопного виду роду *Bathynectes* (*B. muelleri* n. sp. Brachyura, Polybiidae) баденіанських часів (середній міоцен) з Медоборських пагорбів (Україна, Центральний Паратетіс) з коментарями екології середовища проживання. Відкриття нових видів роду *Bathynectes* Stimpson, 1871 (*B. muelleri* n. sp.) у баденіанських (середній міоцен) коралових структурах Максимівського кар'єру (північ Карпатського крайового прогину) у так званих Медоборських пагорбах поблизу Тернополя (Україна) представляє перше визнання скам'янілості цього роду. Усі представники цього роду, які існують сьогодні, є головним чином глибоководними крабами. У цій публікації описано род *Bathynectes muelleri* n. sp., надані коментарі можливого походження роду та різних місцеперебувань протягом різних періодів. Також проаналізовано поширеність решток декаподів у цьому кораловому середовищі та представлено гіпотезу їх присутності.

Ключові слова: *Bathynectes*, Polybiidae, Badenian, Центральний Паратетіс, Максимівка.

Abstract

The discovery of a new species of the genus *Bathynectes* Stimpson, 1871 (*B. muelleri* n. sp.) in the Badenian (middle Miocene) coralline frameworks of the Maksymivka quarry (northern Carpathian Foredeep Basin), in the so-called Medobory Hills, near Ternopil (Ukraine), represents the first recognition as fossil of this genus. All extant species of this genus are mainly living in deep water habitats. *Bathynectes muelleri* n. sp. is described herein with comments on both the possible origin of the genus and the habitat changes through time. The abundance of decapod remains in this coralline environment is also analysed and a hypothesis for their presence presented.

Key words: *Bathynectes*, Polybiidae, Badenian, Central Paratethys, Maksymivka, Ukraine.

INTRODUCTION

A preliminary account of the crustacean decapod species and palaeobiology from the Maksymivka quarry (Ternopil, Ukraine; Figs. 1 and 2) has previously been reported by Radwański *et al.* (2006).

In addition to *Bathynectes muelleri* n. sp., *Galathea weinfurteri* Bachmayer, 1950 (Galatheididae Samouelle, 1819), *Petrolisthes magnus* Müller, 1984 (Porcellanidae

Haworth, 1825), *Dromia neogenica* Müller, 1979 (Dromiidae De Haan, 1833), *Daira speciosa* Reuss, 1871 (Dairiidae Serène, 1965), *Pilumnus mediterraneus* Lörenthey, 1897 (Pilumnidae Samouelle, 1819), *Cancer* cf. *C. styriacus* Bittner, 1884 (Cancriidae Latreille, 1802), *Rakosia carupoides* Müller, 1984 (Portunidae Rafinesque, 1815), *Panopeus* cf. *P. wronai* Müller, 1984 (Panopeidae Ortmann, 1893), *Chorodiella juglans* Müller, 1984, *Xantho moldavicus* Janakevich, 1977 (Xanthidae MacLeay, 1838) and an unidentified majid represented by several pieces of carapace, have been recognised. This decapod assemblage (Fig. 3) is also characteristic other Central Paratethyan coral reefs (Müller, 1996).

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We herein report the occurrence of a new crab species, belonging to the genus *Bathynectes*, as well as provide additional information on accompanying species and on the ecology of the habitat.

MATERIALS AND METHODS

Geological setting. Middle Miocene (Badenian) corallgal reefs are well exposed in the Carpathian Foredeep Basin usually preserved nowadays as hills; the Roztocze Hills in southeast Poland and the Medobory Hills in Ukraine and Moldova are good representatives of these ancient corallgal reefs. In western Ukraine, the middle Miocene reefs between Pidkamin (NNW of Ternopil) and Nahoriany (SE of Kaminanest Podilsky), form a narrow belt clearly visible over the almost flat landscape (Radwański *et al.*, 2006; Studencka & Jasionowski, 2011).

At Maksymivka quarry (Fig. 4), the corallgal buildups are composed of red-algae (lithothamnian) colonies interfingering with crusts of supposedly blue-green algae origin that are associated with scattered hermatypic corals, with *Porites vindoboniarium prima* Kühn, 1927 and *Tarbellastrea reussiana* Milne-Edwards & Haime, 1850 as the dominant species. Amongst the buildups, the intraframeworks base composed of algal thalli and coarse bioclastic sediment is profusely burrowed, possibly by thalassinoid or alpheid shrimps. Burrows and crevices are filled with large bioclastic material like remains of mollusc shells, crabs and echinoids (Figs. 5 and 6).

The Maksymivka quarry sequence suggests extremely shallow-marine conditions influenced by high-energy water dynamics, as shown by the structure of the corallgal buildups and by the presence of bivalve borings (Radwański *et al.*, 2006).

Samples. Decapod specimens used in this paper were collected by one of us (O. S.) at the Maksymivka quarry, in the intraframework crevices and burrows, filled by bioclastic sediment and found as very well preserved

disarticulated carapaces and isolated chelae, without signs of predation. Type specimens of *Bathynectes mueleri* n. sp. are housed in the Regional Museum of Ternopil (Ukraine) under acronym TKMP and Museu de Geologia de Barcelona-Museu de Ciències Naturals de Barcelona under acronym MGB. Photographic material of extant *Bathynectes* species for comparison comes from the Museu Balear de Ciències Naturals of Sóller (Majorca, Balearic Islands) under acronym MBCN, Xavier Castellà (Badalona, Catalonia) private collection (XC), Pere Abelló (Barcelona) private collection (PA) and Antonio de Angeli (Verona, Italy) private collection (DA). Other specimens figured herein under acronym AO, belong to the collection of one of the present authors (A. O.).



Fig. 1. Location map on eastern Europe. Source: <http://mapsof.net>
Fig. 1. Mapa de situació de la localitat en l'est d'Europa. Font: <http://mapsof.net>

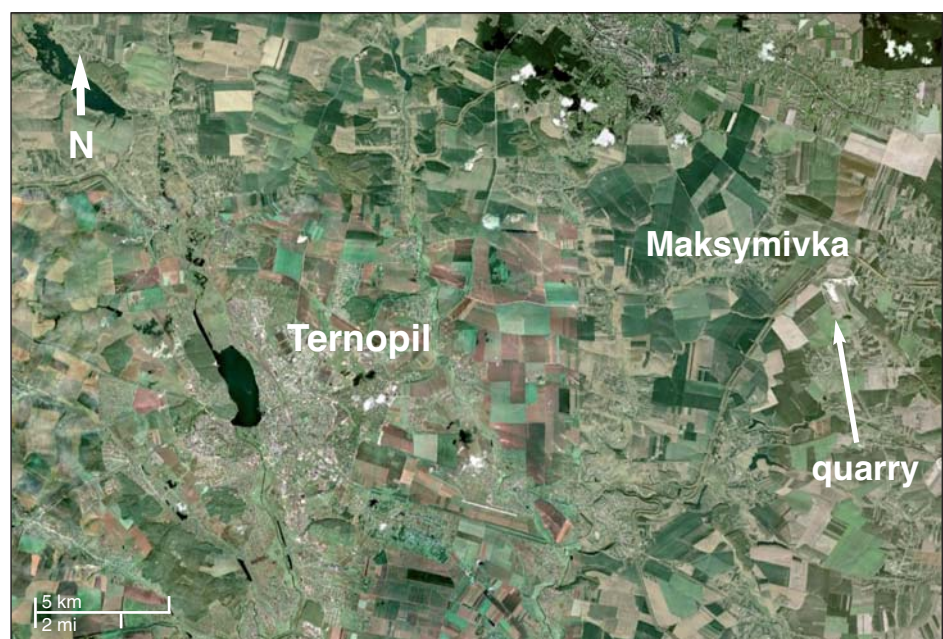


Fig. 2. Location map of fossil locality (arrow) near Ternopil (western Ukraine). Source: Google maps.

Fig. 2. Mapa de situació del jaciment a prop de Ternopil (Ucraïna occidental). Font: Google maps.

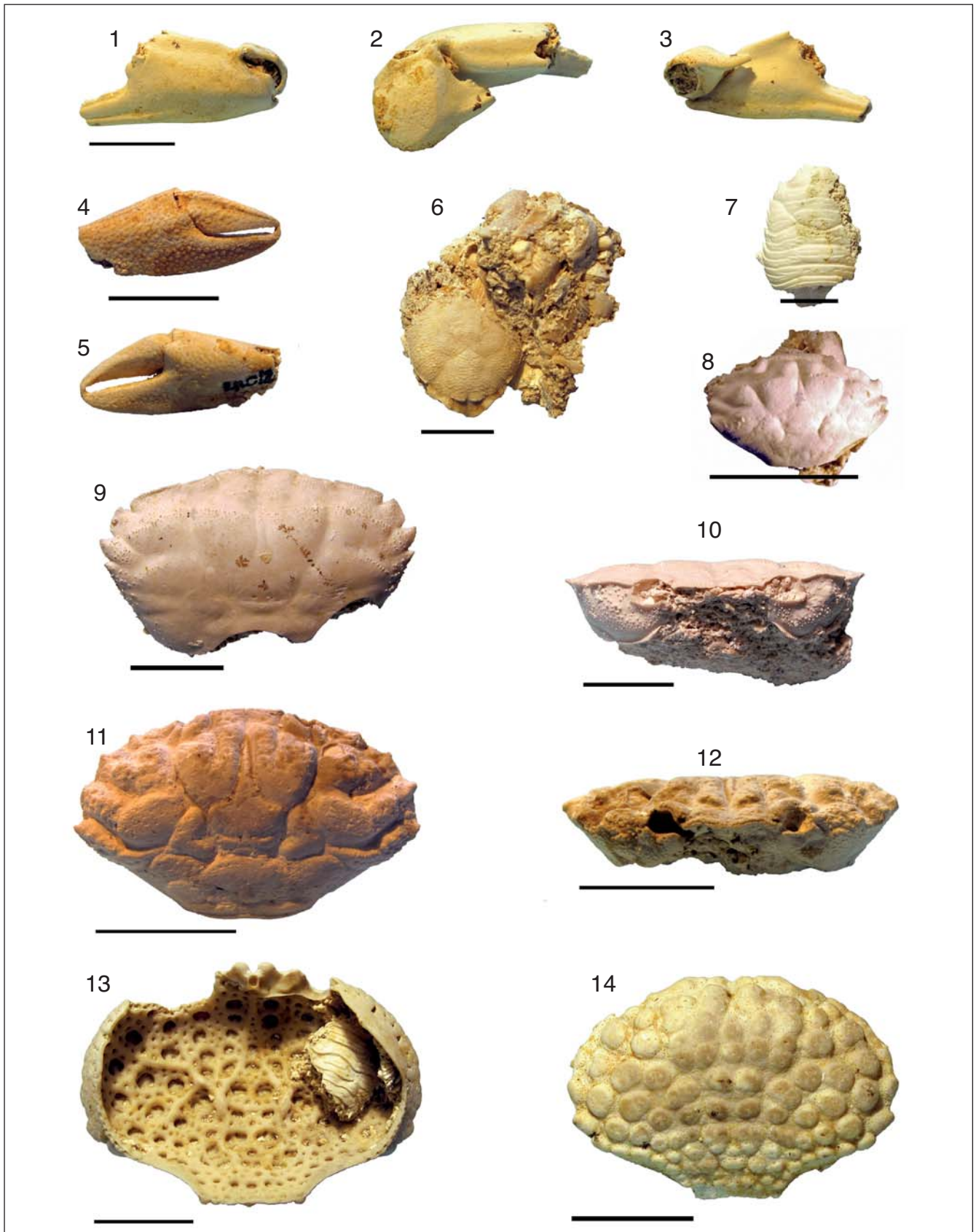


Fig. 3. 1, 2, 3: Polybiid claw attributed to *Bathynectes muelleri* n. sp. MGB 59605; 4, 5: *Petrolisthes magnus* Müller, 1984 AO C410-2; 6: *Petrolisthes magnus* Müller, 1984 AO C410-6; 7: *Galathea weinfurteri* Bachmayer, 1950 AO C418-3; 8: *Chorodiella juglans* Müller, 1984 AO C410-6; 9, 10: *Panopeus wronai* Müller, 1984 AO C412.2; 11, 12: *Xantho moldavicus* Janakevich, 1977 AO C049.3.1; 13: *Daira speciosa* Reuss, 1871 AO C418.4; 14: *Daira speciosa* Reuss, 1871 AO C085.4. Scale bar 1 cm.

Fig. 3. 1, 2, 3: Pinça de polibiid atribuída a *Bathynectes muelleri* n. sp. MGB 59605; 4, 5: *Petrolisthes magnus* Müller, 1984 AO C410-2; 6: *Petrolisthes magnus* Müller, 1984 AO C410-6; 7: *Galathea weinfurteri* Bachmayer, 1950 AO C418-3; 8: *Chorodiella juglans* Müller, 1984 AO C410-6; 9, 10: *Panopeus wronai* Müller, 1984 AO C412.2; 11, 12: *Xantho moldavicus* Janakevich, 1977 AO C049.3.1; 13: *Daira speciosa* Reuss, 1871 AO C418.4; 14: *Daira speciosa* Reuss, 1871 AO C085.4. Escala 1 cm.

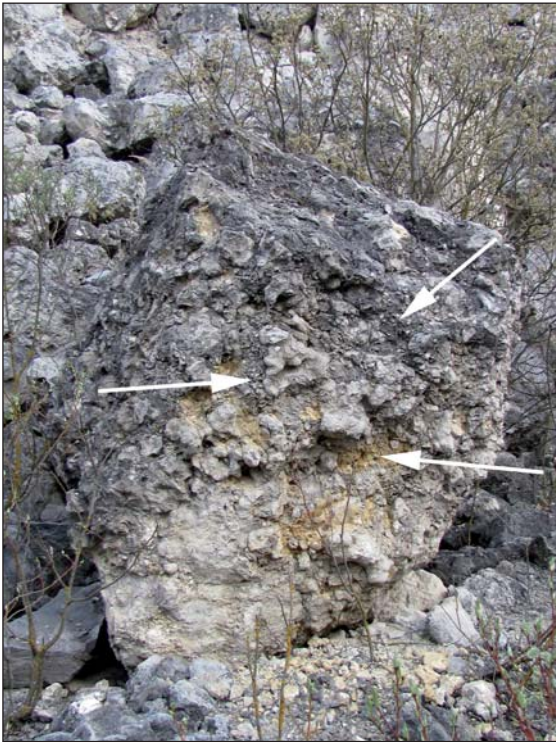


Fig. 4. View of Maksymivka quarry with the coralgal limestones; the underlying calcarenites are exploited.

Fig. 4. Vista de la pedrera de Maksymivka amb les calcàries coralgals; les calcarenites infrajaccents són objecte d'explotació industrial.

◀ Fig. 5. Spread blocs showing the typical aspect of bioclast material infilling voids of frameworks (see arrows).

Fig. 5. Blocs escampats mostrant l'aspecte del material bioclàstic que rebleix els espais de les estructures coral·lines (fletxes)



Fig. 6. Close-up of bioclasts (crab remains, molluscs, echinoid and coarse shell-grit) infilling holes, crevices and burrows. 1, 2: *Daira speciosa* Reuss, 1871; 3: *Rakosia carupoides* Müller, 1984; 4: *Daira speciosa* Reuss, 1871 and *Brissus unicolor* Leske, 1778.

Fig. 6. Primer pla dels bioclats (fragments de crancs, mol·luscs, eriçons) reblint forats, esquerdes i galeries. 1, 2: *Daira speciosa* Reuss, 1871; 3: *Rakosia carupoides* Müller, 1984; 4: *Daira speciosa* Reuss, 1871 i *Brissus unicolor* Leske, 1778.

SYSTEMATIC PALAEOLOGY

Order DECAPODA Latreille, 1802
 Infraorder BRACHYURA Latreille, 1802
 Superfamily PORTUNOIDEA Rafinesque, 1815
 Family POLYBIIDAE Ortmann, 1893

***Bathynectes* Stimpson, 1871**

= *Thranites* Bovallius, 1876

Type species: *Bathynectes longispina* Stimpson, 1871, by subsequent designation by Fowler, 1912, not Rathbun, 1930, p. 27 (Ng *et al.* 2008, p. 155).

Other species: *Bathynectes longipes* (Risso, 1816); *Bathynectes maravigna* (Prestandrea, 1839) = *Thranites velox* Bovallius, 1876 = *Portunus superbus* Costa, in Costa & Costa, 1853; *Bathynectes piperitus* Manning & Holtuiss, 1981. *Bathynectes brevispina* Stimpson, 1871 is not considered here (Ng *et al.* 2008, p. 155).

***Bathynectes muelleri* n. sp.**

Fig. 7, 1-6

Materials and dimensions (in mm). Three specimens (carapaces) in dorsal view and a left chela (carpus and propodus). Holotype TKMP 1701 95840: carapace length = 24; width* = 31; orbito-frontal width = 10; posterior margin width = 11. Paratype TKMP 1702 10638: carapace length = 19; width* = 23; orbito-frontal width = 8; posterior margin width = 10. Paratype MGB 59600 (right margin incomplete): carapace length = 26; width* = 32; orbito-frontal width = 9; posterior margin width = 12. Left chela MGB 59605. *width from the base of the epibranchial tooth (last anterolateral tooth).

Etymology: dedicated to Prof. Pál Müller, author of important studies on Paratehtyan Tertiary decapod faunas, of which this paper is indebted.

Type locality: Maksymivka quarry, ENE of Ternopil, Ukraine.

Geological age: Badenian (middle Miocene).

Diagnosis. Carapace subhexagonal, slightly wider than long; convex longitudinally, more at anterior third, relatively less convex in transverse section; maximum width at mid-length of carapace; regions weakly defined; dorsal surface almost smooth. Dorsal regions weakly defined, epigastric and hepatic regions slightly swollen; protogastric, metagastric, epibranchial, and cardiac regions inflated. Branchial lobes inflated, laterally forming a low transverse ridge that connects epibranchial teeth across metagastric region. Front weakly four-lobed, outer lobes larger than inner lobes. Orbits small with two closed fissures on supraorbital margin; infraorbital margin visible in dorsal view. Anterolateral margin convex, with four teeth, excluding outer orbital tooth, first and second ones triangular, third and fourth teeth spiniform. Posterolateral margin slightly concave, smooth, converging posteriorly, with reentrant of fifth pereopod well marked and almost parallel mesobranchial keel. Posterior carapace margin straight, rimmed.

Description. Carapace small, subhexagonal in outline, somewhat broader than long, maximum width at level of epibranchial (last anterolateral) tooth; dorsal surface slightly convex longitudinally, strongly vaulted at anterior third, slightly convex at medial transverse section, surface smooth but finely granular at anterior portion of protogastric lobes, epibranchial lobes and at posterolateral margins. Front relatively large, about one-third maximum width of carapace, weakly four-lobed, outer lobes twice width of inner lobes. Orbits relatively small, deep, complete, supraorbital margin rimmed, finely serrated, prominent inner supraorbital lobe, two closed fissures, one median and second close to outer orbital tooth; infraorbital margin visible dorsally, with prominent blunt triangular inner tooth and with open fissure at outer corner beneath outer orbital tooth. Anterolateral margin convex and with four teeth excluding outer orbital tooth; first and second teeth blunt, triangular, anteriorly directed; third and fourth teeth progressively sharper and spiniform, curved, directed laterally, fourth (last anterolateral tooth) most prominent. Posterolateral margins slightly concave, converging posteriorly, well marked reentrant of the fifth pereopod about one-third of total length of posterolateral margin; fine keel present on mesobranchial region almost parallel to posterolateral margin. Posterior margin, straight, rimmed, somewhat broader than fronto-orbital margin. Dorsal regions weakly defined, cervical and gastro-hepatic grooves not well defined; two small epigastric swellings present at the base of the front, protogastric lobes large, swollen, with two small transversal rows of granules, mesogastric region not well marked; hepatic region slightly swollen; metagastric region inflated, urogastric region depressed, and metagastric and urogastric regions separated by a pair of submedian gastric pits; branchial lobes inflated, laterally forming complete transversal ridge with the metagastric lobe; mesobranchial region depressed. Cardiac region large, very swollen, forming short cardiac ridge. Intestinal region flat.

Comparison. Considering its coralline habitat, *Bathynectes muelleri* n. sp. was originally compared to extant coral-inhabiting portunid crabs from subfamilies Carupinae Paulson, 1875, Portuninae Rafinesque, 1815 and Thalamitinae Paulson, 1875 (Spiridonov & Neumann, 2008). *Bathynectes muelleri* differs from all these groups by the shape and number of anterolateral teeth, the maximum width located in a different place of the carapace, a front with distinct orbito-frontal ratio or a different number of frontal teeth.

Bathynectes muelleri n. sp. was also compared with the representative genera of family Polybiidae Ortmann, 1893 (*sensu* Schubart & Reuschel, 2009) considering only the dorsal characters which we are dealing with, and the only one that could clearly accommodate the new species was *Bathynectes* Stimpson, 1871. Genera *Liocarcinus* Stimpson, 1871, *Macropipus* Prestandrea, 1833 and *Ovalipes* Rathbun, 1898 have a front with three lobes or teeth, whereas *Bathynectes muelleri* n. sp. has four; in addition, their carapace shape, ornamentation and number and form of anterolateral teeth are different than in

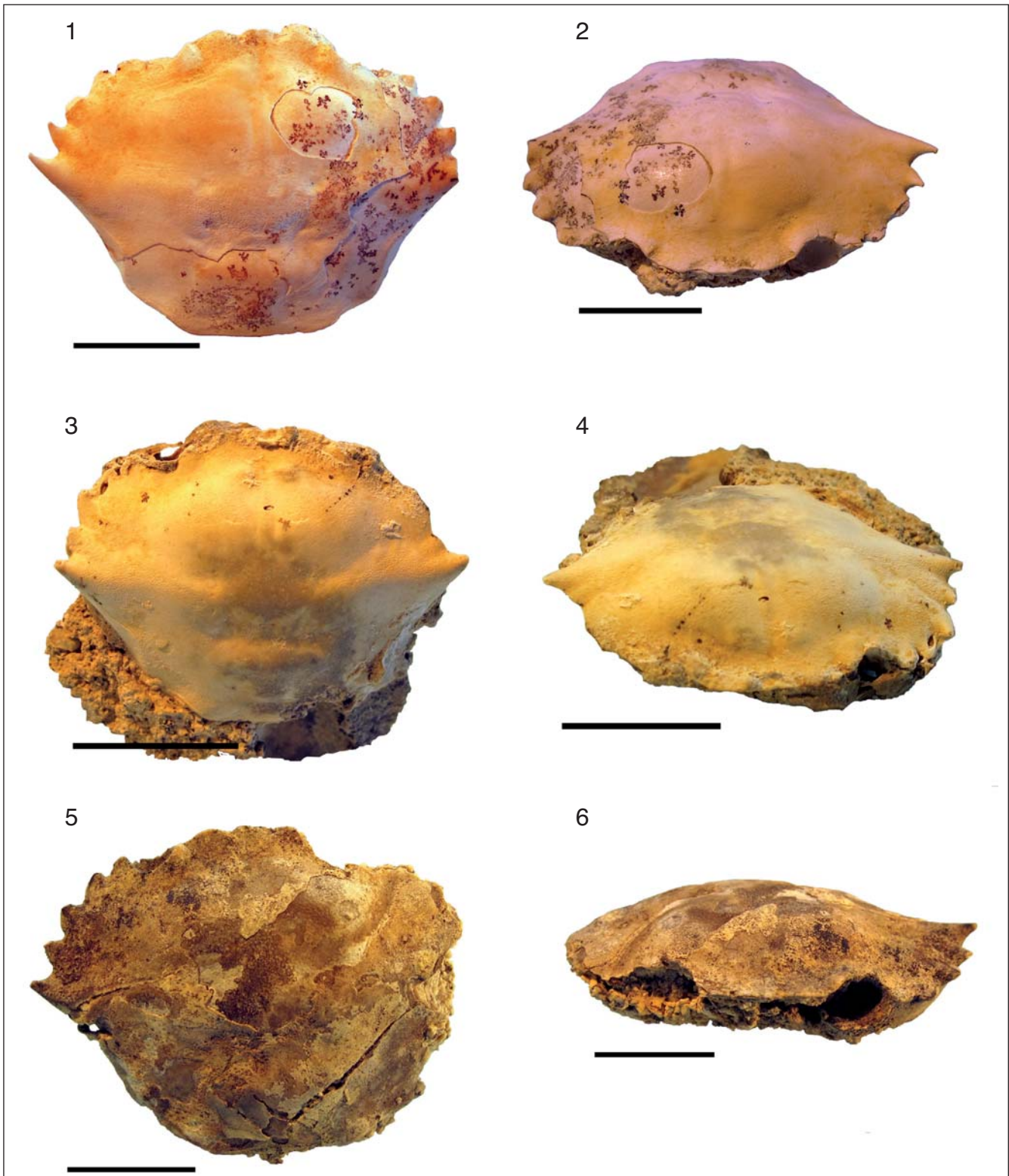


Fig. 7. *Bathynectes muelleri* new species. Holotype TKMP 1701 95840, 1: dorsal view; 2: frontal view. Paratype TKMP 1702 10638, 3: dorsal view; 4: frontal view. Paratype MGB 59600, 5: dorsal view; 6: frontal view. Scale bar 1 cm.

Fig. 7. *Bathynectes muelleri* nova espècie. Holotip TKMP 1701 95840, 1: vista dorsal; 2: vista frontal. Paratip TKMP 1702 10638, 3: vista dorsal; 4: vista frontal. Paratip MGB 59600, 5: vista dorsal; 6: vista frontal. Escala 1 cm.

the new species. The species of *Necora* Holthuis, 1987 show eight to ten frontal lobes and five equal anterolateral teeth thus differing from *B. muelleri*. Genus *Polybius* Leach, 1820 differs from *B. muelleri* by its flattened carapace without epibranchial ridges and the small and equal anterolateral teeth.

Genus *Bathynectes* Stimpson, 1871 can accommodate the new fossil species considering its similarities with the extant ones: four anterolateral teeth (excluding the outer orbital tooth), a four-lobed front, a more or less marked transversal ridge connecting the long epibranchial teeth, a subtle oblique ridge that extends from the third

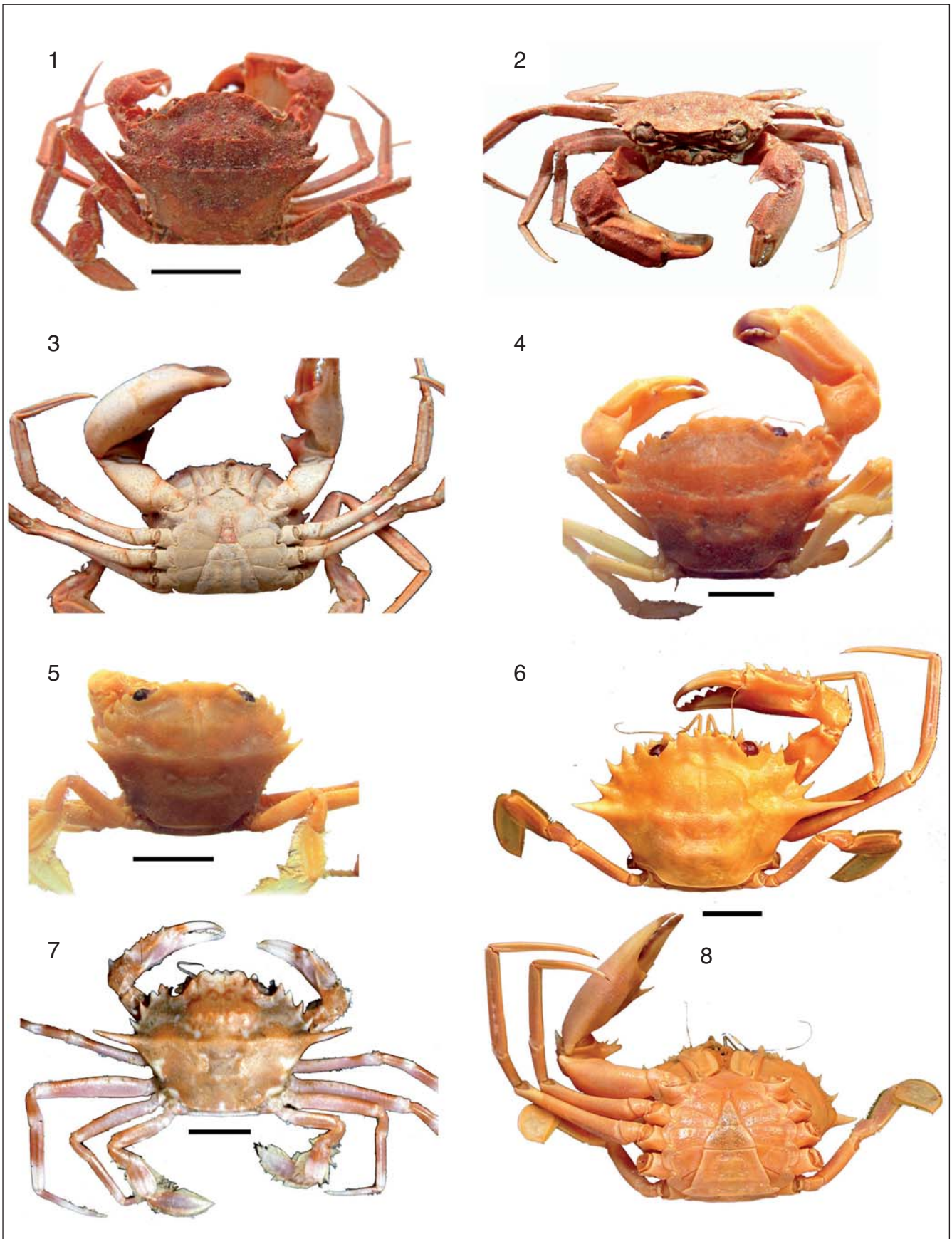


Fig. 8. *Bathynectes longipes* (Risso, 1816), 1: XC 193, dorsal view; 2: same specimen, frontal view; 3: same specimen, ventral view; 4: MBCN 3528, dorsal view; 5: MBCN 3640, dorsal view. *Bathynectes maravigna* (Prestandrea, 1839), 6: DA unnumbered, dorsal view; 8: same specimen, ventral view. *Bathynectes piperitus* Manning & Holthuis, 1981, 7: PA unnumbered, dorsal view. Scale bar 1 cm.

Fig. 8. *Bathynectes longipes* (Risso, 1816), 1: XC 193, vista dorsal; 2: mateix exemplar, vista frontal; 3: mateix exemplar, vista ventral; 4: MBCN 3528, vista dorsal; 5: MBCN 3640, vista dorsal. *Bathynectes maravigna* (Prestandrea, 1839), 6: DA sense número, vista dorsal; 8: mateix exemplar, vista ventral. *Bathynectes piperitus* Manning & Holthuis, 1981, 7: PA sense número, vista dorsal. Escala 1 cm.

anterolateral teeth and reaches the epibranchial ridge, and a short cardiac ridge as explained below in the discussion chapter.

Bathynectes muelleri n. sp. can be easily distinguished from the four extant species of the genus. *Bathynectes longispina* Stimpson, 1871 has four frontal teeth that are more prominent and acute; a more prominent transversal ridge connecting the epibranchial teeth; two short transverse ridges present on both protogastric lobes; and an anterolateral margin armed with four widely spaced, sharp spiniform teeth, with the epibranchial tooth relatively more acute and proportionally longer than in *B. muelleri* n. sp. (cf. Stimpson, 1871, p. 146). *Bathynectes maravigna* (Prestandrea, 1839) (Fig. 8: 6, 8) differs from *B. muelleri* n. sp. in having a more prominent and acute frontal teeth; a more prominent transverse blunt ridge that connects the teeth at the lateral angle; and anterolateral teeth relatively longer and sharper, with the last anterolateral tooth (epibranchial) extremely long and directed almost horizontally (cf. Rathbun, 1930, p. 28; Manning & Holtuis, 1981, p. 76). *Bathynectes piperitus* Manning & Holthuis, 1981 (Fig. 8: 7) has four blunt frontal teeth; however these teeth are relatively longer and more prominent than in *B. muelleri* n. sp.; the well marked four transverse ridges (mainly the gastric ones) and the complete, sinuous and tuberculate ridge connecting the epibranchial teeth also differentiates *B. piperitus* from *B. muelleri* (cf. Manning & Holtuis, 1981, p. 77). The fourth species of the genus, *Bathynectes longipes* (Risso, 1816), (Fig. 8: 1, 2, 3, 4, 5), is most similar to *B. muelleri* n. sp. in the relatively low four-lobed front and structure of the anterolateral margin. *Bathynectes longipes* differs from *B. muelleri* in having a very well-marked, complete and acute (mainly in young specimens) ridge that connects the two epibranchial teeth whereas in *B. muelleri* the swollen transverse ridge is less developed and is interrupted at the metagastric level. *Bathynectes longipes* also has an open medial supraorbital fissure which is closed in *B. muelleri*, perhaps because of the fossilization process. In addition, the two transverse ridges present on both protogastric lobes of *B. longipes* are absent in the new species (Risso, 1816, p. 50, pl. 1, fig. 5; Bell, 1844-1853, p. 361).

Discussion. Dorsal features of *Bathynectes muelleri* n. sp. match well with the diagnostic characters of the genus *Bathynectes* used by Stimpson (1871, p. 146) when describing *B. longispina*, and also with the useful generic diagnosis and specific keys provided by both Zariquiey (1968, pp. 380-383, figs. 127 c, f, g) for *B. longipes* and *B. superbus* (= *B. maravigna*) and Manning & Holthuis (1983, pp. 76-83) for *B. piperitus* and *B. maravigna*.

When working on fossil crabs, the available characters that can be used in a diagnosis will clearly be less than with extant crabs. It depends a great deal on the degree of preservation of the fossils. While it has been shown that sternal and abdominal characters are important, reef associated fossil decapods frequently only have their carapaces and/or isolated chelae preserved.

Other than isolated chelae that could be assigned to *B. muelleri*, which closely resembles that of *B. longipes* chelae (Fig. 3: 1, 2, 3) we have had no choice but to limit

the comparison between the two species to the dorsal carapace characters. Nevertheless, we think that the stated differences are sufficient to separate them. The stratigraphic record also suggests that *B. muelleri* may be an ancestor of *B. longipes*.

To discuss the familial placement of *Bathynectes* is beyond the purpose of this work; however, it deserves a short discussion. Karasawa *et al.* (2008) moved *Bathynectes* from Polybiinae Ortmann, 1893 (*sensu* Ng *et al.*, 2008) to Macropipidae Stephenson & Campbell, 1960 according to the results of a phylogenetic analysis based upon adult morphological characters of extant and fossil portunoid taxa. Besides *Bathynectes*, a heterogeneous group of fossil and extant portunoid genera was placed within the Macropipidae such as the late Cretaceous genus *Ophthalmoplax* Rathbun, 1935 or the extant genus *Necora* Holthuis, 1987, amongst other. The genera placed within the Macropipidae display different characters across them; for example: the male abdominal somites range from 3-5 fused to all free, or the diverse conformation of the fifth pereopod (Karasawa *et al.*, 2008, pp. 100-103). Thus, assignment of some of these genera within this family should be re-examined.

Schubart & Reuschel (2009) propose a new taxonomic system derived from two concordant phylogenetic hypotheses after the results of two molecular phylogenies based on both mtDNA and nDNA. Their results concluded that *Bathynectes* belongs to Polybiidae Ortmann, 1893, together with other European representative genera, and recognized Polybiidae as a full family (Schubart & Reuschel, 2009, pp. 544-545). Consequently, as proposed by Schubart and Reuschel (2009, table 4), we place *Bathynectes* within the family Polybiidae Ortmann, 1893.

The occurrence of *B. muelleri* amongst other middle Miocene reef associated fauna represents the oldest record of this genus ever described, thus suggesting that its origins may be in reefs and/or shallow water environment and species later migrated to deeper waters, perhaps by the end of the middle Miocene (Badenian/Sarmatian). This is when the first intermittent and, later definitive closure of the connection between Central Paratethys and the Mediterranean Sea caused dramatic changes in the Carpathian Foredeep area (Rögl, 1999).

Living *Bathynectes* species usually inhabit soft deep bottoms of the Mediterranean basin (including adjacent seas) and of the Atlantic Ocean. The present distribution of *B. longipes* comprises the whole Mediterranean Sea, Marmara Sea and the eastern Atlantic from the British Islands to south Portugal and Madeira, and is considered to be much less abundant than the rest of *Bathynectes* species. It inhabits rocky bottoms on the continental shelf, in much shallower waters than the rest of *Bathynectes* species (Abelló *et al.*, 2001), therefore recalling the middle Miocene habitat where the genus might have appeared. This fact suggests that *B. longipes* could represent, both from the morphological and the ecological points of view, an intermediate step between *B. muelleri* and the other living species of *Bathynectes*.

It is noteworthy that most of the genera or species identified at Maksymivka quarry also appear in the upper

Miocene (Messinian) coralline build-ups of the Mediterranean Sea. Nevertheless, none of the portunoid genera recorded in the middle Miocene coralline facies of the Paratethys (Müller, 1984, p. 103, table 2 and 1996) is present in the upper Miocene coralline structures scattered across the Mediterranean area, with the sole exception of a chela attributed to *Xaiva bachmayeri* Müller, 1984 (Gatt & de Angeli, 2010). As seems to have happened with *Bathynectes*, these portunoid crabs might have chosen different habitats during the upper Miocene.

ANALYSIS OF THE ABUNDANCE OF DECAPOD REMAINS

The Maksymivka quarry is interpreted as a shallow water environment with high energy dynamics (Radwański *et al.*, 2006); thus, the presence of the polybiid decapod brachyuran *Bathynectes* points to a possible shallow /coralline environment origin of the genus, before its eventual migration to the Mediterranean realm deep waters after the definitive closure of its connection with the Central Paratethys Sea (Rögl, 1999; Studencka & Jasionowski, 2011).

The diversity of decapod remains in Maksymivka quarry is relatively low compared to other coeval Paratethyan localities; this may be due to the “collecting factor” (Müller, 2004). Indeed, the collection of the studied specimens has emphasised larger and well preserved samples, with work taking place almost exclusively on the bioclasts that filled the voids of the coralline rocks. As many broken parts and small pieces have been discarded, this rather biased sam-

pling may hide the true richness of this outcrop. A more thorough collection in this quarry would provide more data, especially concerning samples of the smallest species.

Mass accumulations of crab remains in Maksymivka outcrop, with *Daira speciosa* Reuss, 1877 as the dominant species, were previously regarded as discarded carapaces during moulting in a sheltered site, for instance on buildup crevices, burrows and other cavities (Radwański *et al.*, 2006). However, most of the crab remains found in Maksymivka are in fact very well preserved and do not show signs of decalcification or deformations that are typical of many fossil crab moults. Furthermore, in many cases fossil crab moults are usually complete or at least, with some appendages in connection with the carapace, which is not the case for the Maksymivka quarry specimens, where all the collected crab remains correspond to disarticulated carapaces or chelae, with no remains of ambulatory legs. In addition, only a few fragments of sternum were found. Also plausible is the hypothesis (Radwański *et al.*, 2006; Gatt & de Angeli, 2010) that such accumulations could correspond to “kitchen-middens” or left-over remains of an “unknown predator”.

The coralline frameworks are a perfect habitat for some types of predators, like octopuses, and it is known that depending on availability, crabs are their preferential food resource (Ambrose, 1984; Villanueva, 1993). The strategy and ability of predators such as octopus species are able to consume the tissues and soft parts of crabs without destroying their exoskeletons or leaving signals like bites or perforations on them, and discarding the strong chelae



Fig. 9. Chelae with open fingers attributed to: *Xantho moldavicus* Janakevich, 1977, 1: AO C049-5; 2: AO C049-6. *Pilumnus mediterraneus* Lörenthey, 1897, 3: AO C204-7. *Daira speciosa* Reus, 1871, 4: AO C085-5. Scale bar 1 cm.

Fig. 9. Pinces amb els dits oberts atribuïdes a: *Xantho moldavicus* Janakevich, 1977, 1: AO C049-5; 2: AO C049-6. *Pilumnus mediterraneus* Lörenthey, 1897, 3: AO C204-7. *Daira speciosa* Reus, 1871, 4: AO C085-5. Escala 1 cm.

as food, is well known and documented (Ibáñez *et al.*, 2009). Many of the chelae of Maksymivka were found with the movable finger open, in what could look like a defensive reflex, but this fact may be simply due to a mechanical effect of waters energy on the hollow chelae while they were buried (Fig. 9). Many remains of molluscs as *Haliotis* sp., common in the diet of octopuses, reinforce the hypothesis that the “unknown predator” may well be octopuses. According to Müller (1993, 2004) and Radwański *et al.* (2006), these disarticulated crab parts were washed together and swept with echinoid skeletons and abundant shell-grit by high-energy agents, filling the buildup holes, crevices or burrows of the reef structure. However, several of the remains collected in the Maksymivka quarry might well be crab moults since their examined caparaces are extremely thin (Müller, 2004).

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