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A NEW CORAL-ASSOCIATED DECAPOD ASSEMBLAGE FROM THE UPPER MIOCENE (MESSINIAN) UPPER CORALLINE LIMESTONE OF MALTA (CENTRAL MEDITERRANEAN)

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Abstract: A rich coral-associated decapod assemblage is recorded from the 'Depiru Beds' of the upper part of the Upper Coralline Limestone (Messinian, Upper Miocene), from the island of Malta. Nineteen species within 17 genera have been discovered, where 14 genera are new for Malta. Four new species are described, namely *Micippa annamariae* sp. nov., *Pilumnus scaber* sp. nov., *Panopeus muelleri* sp. nov. and *Herbstia melitense* sp. nov. *Herbstia melitense* sp. nov. constitutes the first record of the genus from the fossil record in the Mediterranean region. This discovery more than doubles the number of known fossil decapod species from Malta. The fossil bivalve *Jouannetia* (*J.*) *semicaudata* Des Moulins, 1830 and the extant decapod *Maja goltziana* D'Oliveira, 1888, are also recorded for the first time from Malta. Other Neogene coral-associated decapod assemblages are investigated and correlated with the new assemblage from Malta. The migration of taxa between the Mediterranean region and the Paratethys, particularly during the Lower Badenian (Langhian), is evidenced by the strong affinity of the Maltese decapod assemblage with that of the Middle Miocene Badenian assemblages from Hungary, Poland and Ukraine. Upper Miocene, Messinian assemblages from Spain, Algeria and Morocco are also similar to that from Malta.

Key words: Crustacea, coral-associated Decapoda, Taxonomy, Upper Miocene, Malta-Central Mediterranean.

DECAPODA from the Maltese Neogene are generally very poorly known and have been sparsely studied. Eleven species, all from different genera, have to date been identified in works by Woodward (1873), Glaessner (1933) and recently reviewed by one of the present authors (Gatt 2006). All have been confirmed in this latter work (Gatt 2006) as occurring in Maltese rocks with the exception of *Atergatis* sp. which was only recorded by Woodward (1873, p. 325).

The newly discovered coral-associated decapod assemblage described in the present work constitutes an important contribution to the study of fossil Decapoda species known from the Maltese Islands. The species discovered include *Callinassa munieri* Brocchi, 1883 (Callianassidae Dana, 1852); *Galathea weinfurteri* Bachmayer, 1950 and *Galathea* sp. (Galatheidae Samouelle, 1819); *Petrolisthes* cfr. *magnus* Müller, 1984 (Porcellanidae Haworth, 1825); ?*Pagurus turcus* Müller, 1984 (Paguridae Latreille, 1802); *Dardanus hungaricus* (Lőrenthey *in* Lőrenthey and Beurlen, 1929), *Paguristes cserhatensis* Müller, 1984, *Paguristes* sp. (Diogenidae Ortmann, 1892); *Dromia neogenica* Müller, 1979 (Dromiidae De Haan, 1833); *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen, 1929 (Calappidae De Haan, 1833); *Herbstia melitense* sp. nov. (Epialtidae Samouelle, 1819); *Maja biaensis* Lőrenthey *in* Lőrenthey and Beurlen, 1929, *Micippa annamariae* sp. nov. (Majidae Samouelle, 1819); *Daira speciosa* (Reuss, 1871) (Dairidae Serène, 1965); *Xaiva bachmayeri* Müller, 1984 (Carcinidae MacLeay, 1838); *Carpilius* sp. (Carpiliidae Ortmann, 1893); *Pilumnus scaber* sp. nov. (Pilumnidae Samouelle, 1819); *Panopeus muelleri* sp. nov. (Panopeidae Ortmann, 1893); and *Xantho moldavicus* (Yanakevich, 1977) (Xanthidae MacLeay, 1838).

Fourteen of the aforementioned coral-associated decapod genera are new for Malta, and only three, *Pagurus*, *Calappa* and *Maja*, have been recorded previously from Malta by Woodward (1873), Glaessner (1933) and Gatt (2006). *Pagurus* and *Petrochirus* are to date the only genera belonging to the Paguridae recorded from Maltese strata. *Pagurus* sp. and *Petrochirus priscus* have been found as occurring within grey, marly and fine-grained sediments associated with coralgal fragments at the base of the Upper Coralline Limestone (UCL), the former being infrequent while the latter is rare. *Petrochirus priscus*

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has been also recorded as very rare from the Greensand (Gatt 2006).

Remains of the species *Calappa heberti* from the Maltese Islands have been recorded from an unspecified division of the Globigerina Limestone (Glaessner 1933) and as very rare from the upper parts of the Upper Globigerina Limestone division, from the upper part of the Clay division in glauconitic clays, from the Greensand and as very rare in the basal parts of the Upper Coralline Limestone associated with coralline algae (Gatt 2006).

From the Majidae, remains of *Maja* sp. have been found as very rare throughout the Maltese strata where it has been recorded, i.e. from the lower parts of the Upper Coralline Limestone (UCL) associated with the coralgal bioherm; from the basal parts of the UCL, in coarse-grained greyish-green glauconitic sands, immediately above the Clay division where the Greensand is missing; from glauconitic clays in the upper parts of the Clay division; and from the Middle Globigerina Limestone (Gatt 2006).

There are no previous records from the Maltese Islands of Decapoda originating from the upper parts of the UCL associated with coral remains.

LOCALITIES, MATERIALS AND METHODS

Areas of exposed Upper Coralline Limestone (UCL) in the Maltese Islands form a topography that is generally composed of flat-topped garigue mesas with vertical-sided inland and coastal-bordering cliffs. The variable resistance to erosive elements of the strata forming this division, with durable and more resistant upper parts and softer underlying layers, results in undercutting in the lower parts. As a result of this undermining, overhanging blocks of the harder-resistant upper areas develop fissures and cracks that run horizontal to the cliff face and eventually detach onto the underlying clay slopes to form step-cliffs and screes composed of large blocks and other smaller debris. This process of erosion and rock-fall is especially accelerated during wet winter months when the very friable nature and impermeability of the clay layer beneath the UCL, serves as a lubricant.

The decapod material studied in this present work originates from the upper parts of the UCL at a stratigraphic level, which in most locations investigated in this study, is not readily and easily accessible. The process of step-cliff formation and screes, however, provides abundant material which can be studied with relatively more facility. As such, most of the material which forms the basis of this present work has been collected from detached cliff sections and scree material, primarily from a tract of coastline between Għajn Żnuber (or Snuber) and Golden Bay, the area that produced the most abundant and diversified material. Material originating from the upper parts of this formation could be readily distinguished from other material originating from the UCL on account of its very composition, durablity and colour.

Most of the specimens collected from Malta are preserved as carapace internal moulds, although much rarer specimens with their carapaces preserved have also been collected. Carapaces, especially those of *Daira*, form the bulk of the material retrieved in the field, together with more infrequent remains of palm and movable fingers; all of the other genera have been found to be quite infrequent to rare. Only a few specimens needed preparation and cleaning by means of a vibrating engraver, as most of the remains have been found either detached from surrounding matrix or preserved in small-sized portable blocks of UCL associated with a variety of other remains.

The associated fauna, besides Decapoda, has also been noted from the Maltese sites investigated in this study and compared with other records of coral-associated assemblages abroad.

The material which forms the basis of this study has been deposited at the National Museum of Natural History, Mdina, Malta.

Several sites in Malta (Text-fig. 1) where the UCL 'Depiru Beds' (Pedley 1978; Bosence and Pedley *in* Bosence 1991) are exposed have been investigated for decapod remains and other fauna.

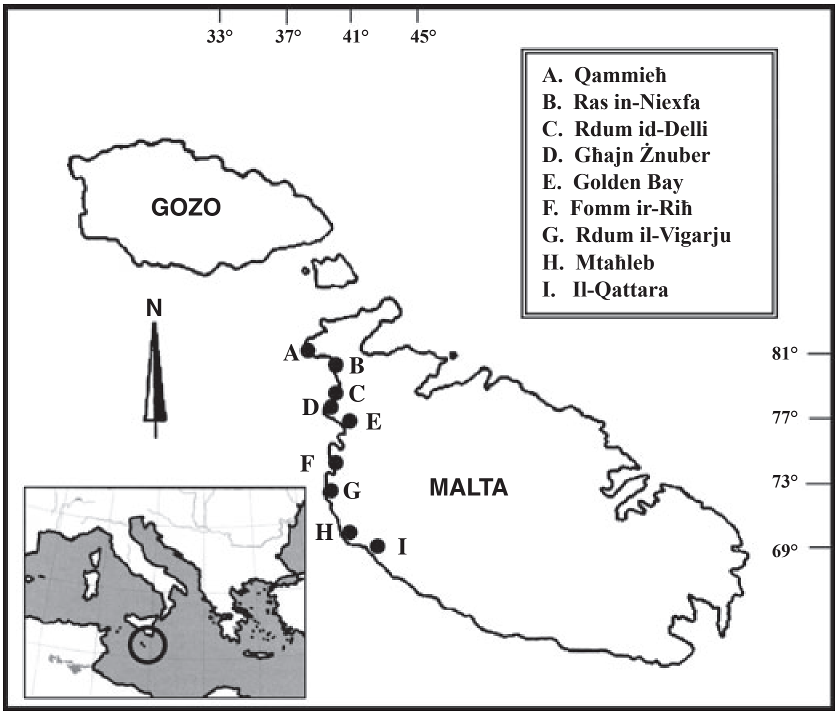
Grid references quoted refer to Geological Map of the Maltese Islands, Sheet 1, MALTA, Scale 1:25,000 published by the Oil Exploration Directorate, Office of the Prime Minister Valletta, Malta (Pedley 1993).

Qammieħ Point

Lower part of the upper division of the Upper Coralline Limestone (UCL) in this locality (389813) is composed of small patches of *Tarbellastraea* Alloiteau, 1850 corals and possibly *Porites* Link, 1807 occurring as undulose laminar fabrics associated with very coarse-grained and rubbly sediments. The fossil fauna is scant with very scarce *Haliotis* Linne, 1758, *Stylocidaris melitensis* (Wright, 1855), *Lima* Bruguière, 1797, and *Lithophaga* Röding, 1798. The only decapod material collected consists of one carapace internal mould of *Daira speciosa* found associated with coralgal remains. This constitutes, so far, the westernmost extremity in Malta where *Daira* remains have been found in this current work.

Ras in-Niexfa, limits of Anchor Bay

Only small patches of corals associated with coarse-grained, greyish-white sediments have been observed in



TEXT-FIG. 1. Sites investigated for coral-associated Decapoda in the Maltese Islands.

lower parts of the upper division of the UCL in this locality (403802). The fauna is similar to that observed in the area between Għajn Żnuber and Golden Bay; however, remains are much less abundant. *Tarbellastraea*, *Creusia* Leach, 1817, *Lithophaga*, *Haliotis*, *Fissurella* Bruguière, 1789, *Stylocidaris* Mortensen, 1909, *Brissus* Gray, 1825, and other as yet undetermined bivalve and gastropod internal moulds were collected. Only one detached, well-preserved carapace of *Xantho moldavicus* has been found in rubble accumulated at the base of a cliff exposure, associated with very coarse-grained sediments.

Rdum id-Delli

Only very rare, small patches of corals with scarce *Lithophaga* have been observed in the lower parts of the uppermost division of the UCL (407792), associated with coarse-grained and very sparsely fossiliferous sediments. No decapod material was observed.

Area between Għajn Żnuber and Golden Bay

Patch reefs composed mainly of *Tarbellastraea* occur in areas extensively bored by coral-encrusted *Lithophaga* and associated *Creusia*. The intraframework coarse-grained sediments are abundant in internal moulds of bivalves and gastropods, particularly of *Haliotis*. Undulose laminar patches of possibly *Porites* and other much rarer species of corals were also observed with *Tarbellastraea*. The echinoid *Stylocidaris melitensis* (Wright, 1855) represented by complete and partial tests, together with other cidaroid remains, *Brissus* sp., and regular echinoid tests were also recorded. *Daira speciosa* carapace internal moulds were found to be most frequent, associated with more infrequent and rarer remains of other decapods. This site (403783) (403774) produced the most abundant and diversified decapod fauna when compared to the other sites investigated in this study.

Fomm ir-Riħ

The coral-bearing stratum in the upper parts of the UCL could not be observed in the exposed cliff face at this location (403748). However, rare detached boulders composed primarily of *Tarbellastraea* corals have been discovered along a restricted area of the coastline, probably remnants of a patch-reef which no longer exists. One chela and seven carapaces of *Daira speciosa* together with one incomplete specimen of *Herbstia melitensis* sp. nov. and a very weathered specimen of a xanthid were collected. All material was found preserved within coarse-grained sediment infills between corals of *Tarbellastraea*. The associated fauna observed is very rare and includes *Haliotis*, test sections of a cidaroid, *Lithophaga*, and other bivalves.

Baħrija l/o. il-Blata steps and Rdum il-Vigarju

The upper part of the UCL is composed of indurated, compact, rubbly, coarse-grained sediments with some corals and sparse *Lithophaga* but no decapod remains. Access to under cliffs is limited by heavy undergrowth and human use (399734).

However, at Rdum il-Vigarju, in the immediate vicinity of Baħrija, one incomplete carapace of *Daira speciosa* was found, in a detached boulder of UCL perched at the very edge of these sea-bordering cliffs. Only *Tarbellastraea* corals and *Lithophaga* were recorded with this specimen.

Mtaħleb

Indurated, compact sediments with some *Tarbellastraea* corals and *Lithophaga* were recorded, but no decapod remains at this locality (417708).

Il-Qattara, l/o. Dingli

This recently excavated country passageway to agricultural land below cliffs presents another site (422698) where the *Daira* stratigraphic level is exposed and can be observed *in situ*. Here, the upper part of UCL consists of hard, compact, indurated, greyish-white micrites with a bed <1 m in thickness of rubbly material composed of coarse-grained sediments and coral fragments. Although no specimen of *Daira* was found directly embedded in this bed of rubbly material, it is most probable that the material collected from this site originated from this level. Several specimens of *Daira speciosa* carapace internal moulds were collected from spoil material together with frequent *Tarbellastraea* Alloiteau, 1850, coral remains and internal moulds of *Lithophaga* and *Haliotis*. One complete test and one fragment of *Stylocidaris melitensis* and one specimen of *Creusia costata* (Seguenza, 1871) were also collected. This site constitutes so far the southernmost range in Malta where *Daira speciosa* has been recorded.

PALAEOECOLOGY AND ASSOCIATED FAUNA OF THE MALTESE SITES

The upper part of the Upper Coralline Limestone division investigated in this study, termed as the 'Depiru Beds' – a subdivision of the 'Tal-Pitkal Member' (Pedley 1978; Bosence and Pedley, *in* Bosence 1991), is interpreted as an open framework of leeward ramp patch-reefs. The reefs are poorly linked into a framework, and coral structures make up <30 per cent of the total patch reefs with an associated 20–50 per cent intraframework of micrites. It is considered that the ramp patch-reefs, which stood not more than 1–3 m above the sea-floor, developed in a shallow-water, high-energy, sublittoral environment with depths ranging from 10 to 25 m and were influenced by an eastward directed current activity. The very undulose and sheet coral growth forms are also typical of ramp patch-reefs. A northeasterly palaeoslope upon which the ramp developed was created through incipient movement on the eastern margins of the Malta Graben (Pedley 1978; Bosence *et al.* 1981; Bosence and Pedley, *in* Bosence 1991; Pedley 1996).

Three sub-divisions constitute the upper parts of the UCL formation (Pl. 1), in the area between Għajn Żnuber and Golden Bay, which yielded the most abundant and diversified decapod material investigated in this study. The 'Depiru Beds' patch-reefs associated with intra-framework and fissure infill coarse-grained whitish sediments, form the lower division from which the new decapod material originated. Marine planation terminated the patch-reef development, and the resulting surface was then buried by oolithic grainstones (Pedley 1996).

Bed contact between the planar top of the 'Depiru Beds' and the overlying oolitic grainstones of the 'Tat Tomna Beds', a sub-division of the 'Ġebel Imbark Member', (Bosence and Pedley 1991) is sharp and marks a haitus between them. This hiatus was also reported from *Tat-Tomna Quarries* by Bosence and Pedley (1991). Fauna recorded from within these oolitic grainstones includes *Lima* sp., frequent cidaroid test fragments and sections, and very rare *Clypeaster* sp., which remains (high-domed

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EXPLANATION OF PLATE 1

Three sub-divisions constituting the upper parts of the UCL formation between Għajn Żnuber and Golden Bay.

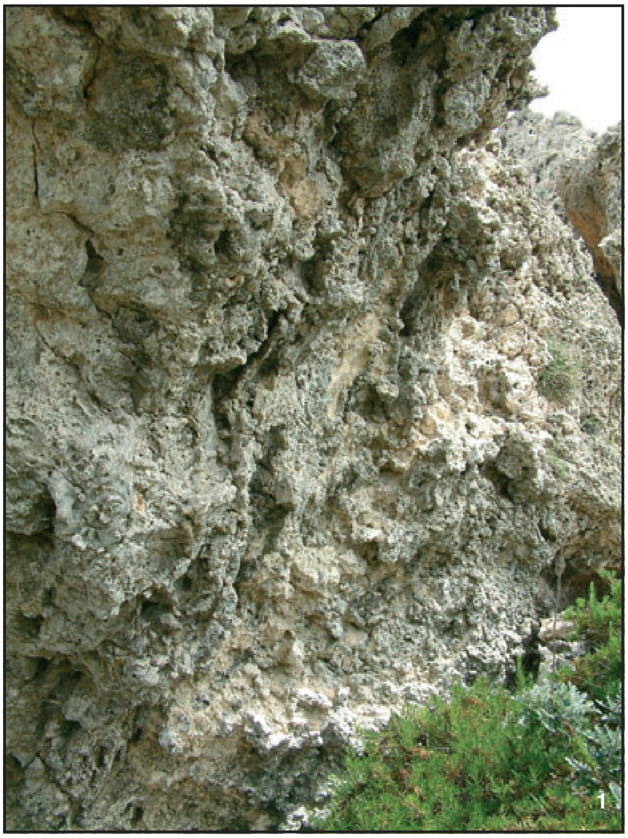
Fig. 1. Lower division 'Depiru Beds' patch-reefs.

Fig. 2. Detail of intra-framework and fissure infill coarse-grained whitish sediments, with test of echinoid *Stylocidaris melitensis* and *Xantho moldavicus* carapace.

Fig. 3. Middle division, oolitic grainstones of the 'Tat Tomna Beds', a sub-division of the 'Ġebel Imbark Member'.

Fig. 4. Uppermost division composed of laminates and cross-bedding, probably forming part of the 'Qammieħ Beds', also a sub-division of the 'Ġebel Imbark Member'.

PLATE 1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3


4

Clypeaster altus type) generally observed in cross section. One incomplete test of *Echinolampas* sp. was also collected. Rare but large agglomerations of gastropod internal moulds and of the bivalve *Glycymeris* sp. were also observed. The 'Tat Tomna Beds' are thought to have been deposited in a moderate energy, intertidal type of environment (Pedley *et al*. 1991).

The uppermost division overlying the 'Tat Tomna Beds' is composed of fine-grained pale grey, very indurated laminates forming horizontal beds associated with cross-bedding and ripple marks. A sheltered, possibly seaward margin, lagoon type of environment is envisaged with occasional stances of high-energy conditions, possibly caused by storm surges, accounting for the cross-bedding. Deposition in very shallow water ranging from shallow subtidal to possible intertidal and supratidal environments are also envisaged (Pedley *et al.* 1978*b*). The fossil fauna is very sparse, and only occasionally very rare bivalves have been observed. The bed contact between the 'Tat Tomna Beds' and the uppermost division is again sharp, suggesting a hiatus and the formation of a hardground. This uppermost division probably forms part of the 'Qammieħ Beds' (Pedley *et al*., 1991), also a sub-division of the 'Ġebel Imbark Member'.

The patch-reefs of the 'Depiru Beds' are composed of hermatypic corals, generally preserved only as moulds with lime mud, now micrite cement, infilling the trabecular cavities prior to the dissolution of aragonite, thus preserving the coral fabric in negative relief. The patch-reefs are dominated primarily by *Tarbellastraea reussiana* (H. Milne Edwards and Haime, 1850) and undulose laminar patches of *Porites*, associated to a much lesser extent with rare *Acanthastraea (Isophyllastraea) madeirensis* Chevalier, 1972 and *Siderastraea radians* (Pallas, 1766).

Because of high-energy, current-influenced conditions, very little fossil material is preserved on the patch-reef structure itself apart from the commonly occuring rock-boring bivalves *Lithophaga* (*L.*) *lithophaga* (Linnaeus, 1758) and *Lithophaga* (*L.*) *lithodomus* (Cuvier, 1817), frequent *Lima* sp. together with serpulid tubes and the barnacle *Creusia costata* (Seguenza, 1876). Infrequent internal moulds of the rock-boring bivalve *Jouannetia* (*J.*) *semicaudata* Des Moulins, 1830, have been collected from the area between Għajn Żnuber and Golden Bay and constitute the first record of this genus for Malta (Text-Fig. 7L, M). The abundance of bivalve borings in the reef may be indicative of a rapid lithification of the sediments (Pedley 1996).

No decapod remains have been observed directly preserved upon the coral buildups, but they have been collected from their immediate vicinity from coarse-grained sediment infills trapped and accumulated in crevices and between the same reef structures. Most of the material observed probably constitutes carapace moults that have been swept from the patch-reefs by high-energy agents. Remains of *Daira speciosa* carapaces were found to be the most abundant, preserved in close proximity to each other, occasionally even lying against each other, and also close to a variety of other faunal elements, most commonly *Tarbellastraea* sp. fragments, coral-encrusted *Lithophaga* bivalves, internal moulds of *Haliotis tuberculata* Linnaeus, 1758, and cidaroid tests and test segments. *Daira* was also found lying near other Decapoda including *Dromia*, *Panopeus*, *Xantho* and *Maja*.

The intraframework sediments contain a rich molluscan fauna. Bivalves recorded include *Arca* sp., *Anadara fichtelii* Deshayes, 1852, *Glycymeris* sp., *Lithophaga* (*L.*) *lithophaga* (Linnaeus, 1758), *Lithophaga* (*L.*) *lithodomus* (Cuvier, 1817), *Chlamys fasciculata* (Millet, 1866), *Spondylus* sp., *Lima squamosa* Lamarck, 1801, *Ostrea* sp., *Cardita* (*C.*) *calyculata* (Linnaeus, 1758), *Dosinia umbonaria* (Lamarck, 1819), *Pholadomya* sp., and *Clavagella* sp. Gastropoda include commonly occuring *Haliotis tuberculata* Linnaeus, 1758, *Fissurella* sp.?, *Cypraea fabagina* Lamarck, 1810, *Fusinus* sp., *Oliva* sp., and *Conus* sp. A species very similar to *Astraea italica* (Sacco, 1896) was also identified by means of internal casts produced from external imprints. Some mollusc specimens were found with borings of the sponge *Entobia*, also recorded by Pedley (1978) and Bosence *et al.* (1991). The presence of *Entobia* is, according to Pedley (1978, after Bromley, 1970), suggestive of shallow water conditions as it is commonest between low-water mark and depth of up to 25 m. Other fauna recorded include the echinoids *Brissus* sp. complete tests; very common test fragments and frequent entire tests of *Stylocidaris melitensis* (Wright, 1855) and other, as yet undetermined, cidaroid and regular echinoid remains. Rhodoliths of coralline algae and celleporiform bryozoan colonies are infrequent.

From a collective analysis of all the sites investigated in this study, it is evident that the fossil decapod-bearing beds in the upper part of the UCL are confined both geographically and stratigraphically to the patch-reefs. Decapod material has been observed to be best preserved in cavities and crevices within the coral structures themselves or in their immediate vicinity, suggesting that material had a better chance of preservation in sheltered areas and pockets. No material has been found directly preserved on the proper coral structures. The decapod material was also noted to become much rarer further away from the patch-reefs. The site between Għajn Żnuber and Golden Bay, where patch-reefs are most developed, in fact represents the best location and yielded the most abundant and diversified decapod material. Other sites investigated, including those of Qattara, Qammieħ Point, Ras in-Niexfa, and Fomm ir-Riħ, where only small coral patches and the occasional rare decapod have been observed, may represent a more exposed environment where debris flow from nearby patch-reefs had accumulated.

NEOGENE REEFAL DECAPOD ASSEMBLAGES – THEIR GEOGRAPHICAL AND CHRONOSTRATIGRAPHICAL DISTRIBUTION AND PALAEOECOLOGY

Miocene coral-associated decapod assemblages are widely distributed both chronologically and geographically and have been recorded from Japan (Karasawa 1993), Jamaica (Portell and Collins 2004), Poland (Müller 1996; Górka 2002), Ukraine (Radwański *et al.* 2006), Austria (Müller 1984*a*; Bachmayer and Tolmann 1953), Hungary (Müller 1984*a*), Spain (Müller 1984*b*), Algeria (Saint Martin and Müller 1988; Saint Martin 1990) Morocco (Saint Martin 1990) and now, Malta (Text-fig. 2). However, most of these sites do not constitute proper reefal buildups, and only the presence of coral remains suggest their proximity to a reef type of environment.

The most dominant and widespread of coral species from the European and African sites are within hermatypic coral genera *Porites* and *Tarbellastraea* together with other species which are in most cases much rarer.

Coral-associated decapod assemblages have also been reported from the Middle to Upper Pleistocene site of Coral Rock in Barbados (Collins and Morris 1976; Collins *et al.* 2009), together with another probable Pliocene (or Pleistocene) site from the Daito Limestone Formation of Japan (Karasawa 2000).

Miocene

At Olérdola and Casa Saja at San Pau d'Ordal, near Vilafranca del Penedés/Catalunya, Spain, from reef-lime-

	SPAIN			ALGERIA							MOROCCO		MALTA				
	Oran	Santa Pola	Majorca	Sebaa Chioukh	Souk el Khemis	Douar Ouled Sidi bou Azza	Murdjadjo	Tafaraoui	Algues & Coraux du Hammar Semmoumet	Ain Oumata	Oued Kell	Arham Amellal	Ras il-Qammieħ	Ras in-Niexfa	Ghajn Żnuber to Golden Bay	Fomm ir-Riħ	Qattara
?MIOCENE–MESSINIAN																	
Galathea squamifera		x															
Pisidia viai		x															
Anapagurus cf. *marginatus*		x															
Dromia neogenica	x																
Daira speciosa	x																
Actaea calzadai	x	x															
Xantho moldavicus		x															
Etisus nov. sp.	x	x															
Ethusa mascarone		x															
MIOCENE–MESSINIAN																	
Callianassa sp.											x						
Callianassa munieri															x		
Upogebia? sp.						x											
Galathea weinfurteri															x		
Galathea sp.															x		
Petrolisthes cfr. *magnus*															x		
cf. *Anapagurus*						x											
?*Pagurus turcus*															x		
Dardanus hungaricus															x		
Paguristes cserhatensis															x		
Paguristes sp.															x		
Dromia neogenica				x	x										x		
Calappa praelata															x		
Herbstia melitense sp. nov.															x	x	
Maja biaensis															x		
Micippa annamariae sp. nov.															x		
Daira speciosa			x		x					x	x	x	x		x	x	x
Xaiva bachmayeri															x		
Carpilius sp.															x		
Pilumnus scaber sp. nov.															x		
Panopeus muelleri sp. nov.															x		
Xantho moldavicus														x	x		
Actaea calzadai								x	x								
Lachnopodus murdjadjensis							x										

TEXT-FIG. 2. Messinian coral-associated decapod assemblages, species and their geographical distribution compared with the newly discovered reefal decapod assemblage from Malta.

stones, which may range from Langhian to Tortonian, the following species have been recorded:

Olérdola. *Callianassa*? *desmarestiana*, ?*Petrolisthes* sp., *Galathea*, *Dardanus hungaricus*, *Pilumnus mediterraneus*, *Chlorodiella mediterranea tetenyensis*, *Daira* cf. *speciosa*, *Xanthidae* sp. nov.?, and *Goneplacidae* sp. nov.?

Casa Saja at San Pau d'Ordal. ?*Ebalia* sp., *Xantho* cf. *moldavicus*, and *Xanthidae* nov. sp.? (Müller 1984*b*).

Lower Miocene

A coral-associated crab fauna unique to the Caribbean has been recorded from the central north coast of Trelawny, at Duncans Quarry, within exposures of the Lower Miocene Montpelier Formation, White Limestone Group of Jamaica. The decapod fauna has been retrieved from indurated bioclastic limestone composed primarily of coral rubble with interstitial echinoid tests and spines, mouldic molluscs and crabs. The bioclastic limestones are presumably derived from shallower water and deposited in a deeper-water environment by submarine mass flow processes. Sixteen species belonging to nine families have been recorded from this locality.

The dominant decapod species found was *Daira vulgaris* represented by various inner moulds of carapaces and some isolated chelae. Other species recorded include *Kromtitis spinulata*, *Dynomene variabilis*, *Duncania jamaicensis*, *Teleophrys acornis*, *Mithrax donovani*, *Mithrax unguis*, *Pseudoachelous schindleri*, *Lophopanopeus corallinus*, *Lophopanopeus toomeyorum*, *Micropanope pulcherrima*, *Panopeus nanus*, *Trapezia prisca*, *Actaeops frontalis*, *Chlorodiella occidentalis* and *Leptodius granulatus* (Portell and Collins, 2004).

Middle Miocene

Fifteen species of decapods were recorded mainly from detrital marls and marly limestones, containing predominantly red algae, of Middle Miocene, Badenian age, at Grobie, near Busko Zdrój, south of the Holy Cross Mountains, Poland. The marly limestones in this locality contain mounds of hermatypic corals, dominated by *Tarbellastraea reussiana* (H. Milne Edwards and Haime, 1850) and *Porites collegniana* (Michelotti, 1847), together with the subordinate *Stylophora reussiana* and *Montastrea* sp. These corals are embedded in poorly sorted, generally fine-grained matrix. Although the proper structure of the reef is not visible at Grobie, by analogy with similar sediments from Hungary and Austria, an environment including a patch reef with corals, at least partly buried in living position is envisaged (Müller 1996).

The coral patch reef at Grobie was studied in more detail by Górka (2002), who attributed to it a Lower Badenian age, corresponding to the Langhian Stage of the Mediterranean or the NN5 nannofossil zone. The development of this reefal buildup corresponds with a relatively short stillstand or slowing of the sea-level rise within a Lower Badenian transgressive sequence. A subsequent rapid rise in sea level associated with an increase in the supply of terrigenous sediment contributed to the burial and demise of the patch reef by detrital deposits.

Apart from the hermatypic coral species already identified by Müller (1996), Górka (2002) noted other associated fauna which included coralline-algae, foraminifers, bryozoans, echinoderms, brachiopods, molluscs and fishes. The bivalves *Chlamys* (*Aequipecten*) *scabrella* (Lamarck, 1819), and *Chlamys* cf. *multistriata* (Poli, 1795), were found to be numerous in the talus facies, while *Chlamys* (*Macrochlamis*) *latissima nodosiformis* (De Serres *in* Pusch, 1836) was recorded as common in the reef core facies. *Acanthocardia* (*A.*) *paucicostata* (Sowerby, 1834) and *Glycymeris* (*G.*) *deshayesi* (Mayer, 1868) were present in both types of deposits in association with the gastropod *Conus* sp. Associated with the corals, molluscs typical of a high-energy environment were also found as abundant. Most common were the sessile and boring species *Lithophaga* sp. and *Jouannetia* (*J.*) *semicaudata* Des Moulins, 1830. Other bivalve species recorded include *Barbatia barbata* (Linnaeus, 1758), *Spondylus crassicosta* Lamarck, 1819, *Anomia ephippum* Linnaeus, 1758, and the squatter *Sphenia* (*S.*) *anatina* (Basterot, 1825). From the back-reef talus deposits, the decapod species *Dardanus hungaricus* was recorded for the first time from the Miocene of Poland (Górka 2002).

Decapods recorded from the reef core at Grobie include: *Pylopagurus corallinus*, *Galathea weinfurteri*, *Petrolisthes haydni*, *Pisidia* aff. *P. viai*, *Kromtitis koberi*, *Dynomene emiliae*, *Rakosia rectifrons, Daira speciosa, Panopeus wronai*, *Eocarpilius antiquus*, *Chlorodiella mediterranea*, *Haydnella steiningeri*, *Pilodius*? sp. nov.?, *Maldivia plana*, and *Glabropilumnus fossatus*.

Decapods recorded from the back-reef talus deposits include *Calappa praelata*, *Liocarcinus* sp. and *Dardanus hungaricus* (Müller 1996; Górka 2002).

Seven species of decapods have been recorded from coralgal facies of Middle Miocene (Badenian) age from the northern shores of the Fore-Carpathian Basin, at Maksymivka in the Lviv-Ternopil region, Ukraine (Radwański *et al.* 2006). These coralgal buildups are composed of interfingering red-algal (lithothamnian) colonies and blue-green-algal crusts, associated locally with numerous hermatypic corals (*Tarbellastraea reussiana*, *Porites vindobonarum prima*), either isolated or overlapping each other.

The intraframework is filled with coarse bioclastic sediment (shell-grit), burrowed commonly by alpheid shrimps. These burrows served as taphonomic traps for decapods, both squat lobsters and crabs, the former represented by the species *Galathea weinfurteri* and the latter by the commonly occuring *Daira speciosa*, *Petrolisthes magnus*, *Xantho moldavicus*, and the much rarer *Petrolisthes* cf. *P. haydni*, *Chlorodiella* cf. *C. mediterranea tetenyensis* and *Pilumnus mediterraneus*. The most common crab species was *Daira speciosa* represented exclusively by carapaces that frequently occurred as accumulations of several specimens within shell-grit-filled crevices between algal thalli. These accumulations of *Daira* carapaces were interpreted as either left-overs of some unknown predator or as carapaces discarded after moulting in a sheltered site. The echinoid species *Eucidaris zeamays* and a brissid spatangoid very close or identical to *Brissus unicolor* were also recorded.

The environmental conditions under which the Maksymivka sequence formed were interpreted as extremely shallow-marine, often influenced by high-energy water dynamics. The ubiquitous presence of borings of the bivalves *Jouannetia* (*J.*) *semicaudata* Des Moulins, 1830, and *Lithophaga lithophaga* (Linnaeus, 1758) in the coralgal buildups and in particular in the coral colonies, as well as the reworking of some coral colonies, clearly indicate extremely shallow peritidal depths (Radwański *et al.* 2006).

One hundred and twenty species and subspecies of anomuran and brachyuran decapods have been recorded from the Middle Miocene, Central Paratethys, of Central and Eastern Europe, from a variety of habitats including rocky intertidal, reefal, shallower and deeper infralittoral and circalittoral. Twenty-five of the decapod species recorded have been found associated with coral reefs and tentatively correlated with three substages of the Badenian–Lower Badenian sites in the Börzsöny- and Pilis Mountains, Hungary; Middle Badenian sites at Gross-Höflein, 'Oberer Korallenkalk', Austria, and Upper Badenian in Budapest and Diósd, Hungary. Hermatypic corals recorded from the Lower Badenian sites include *Porites* sp., *Tarbellastraea* sp., *Acanthastraea* sp., *Stylophora subreticulata* and other forms. The four genera recorded from the Lower Badenian were also found in the Middle Badenian localities, whereas only the first two genera were recorded from the Upper Badenian sites. The decrease with time, in number of coral-genera, suggests perturbations in salinity in the upper parts of the Badenian (Müller 1984*a*).

A decapod assemblage of twenty species, which indicates a lagoon reef palaeoenvironment, has been also recorded from the Megami Formation of Japan. A Lower to Lower–Middle Miocene age is inferred for this formation. The assemblage is defined by the predominance of *Petrolisthes miocaenicus*, *Medaeops megamiensis*, and *Galathea keijii*, with *Paraxanthias fujiyamai*, *Palaeoxanthops minutus*, *Dynomene shinobui* and *Daira perlata* as the subdominant species. Other species recorded include *Lybia* sp., *Liomera* sp., *Carpilius* sp., *Leptodius crosnieri*, *Leptodius morrisi*, *Palaeoxanthops minutus*, *Palaeoxanthops okumurai*, *Megamia anaglypta*, *Pilodius parvus*, *Eriphia* sp., *Euryozius angustus*, *Euryozius bidentatus*, *Trapezia brevispinosa*, and *Trapezia* sp. (Karasawa 1993).

Upper Miocene

From Oran and its vicinity, and from Santa Pola, Spain, in *Porites* or *Tarbellastraea* reefs of probable Messinian age, the following species have been recorded:

Oran and its vicinity. *Dromia neogenica*, *Daira speciosa*, *Etisus*? sp., and *Actaea*? *calzadai*.

Santa Pola. *Pisidia viai*, *Galathea squamifera*, *Anapagurus* cf. *marginatus*, *Ethusa mascarone*, *Etisus*? sp., *Actaea*? *calzadai* and *Xantho moldavicus* (Müller 1984*b*).

From the Messinian coral reefs of Souk el Khemis and Aïn Oumata, Oranie (western Algeria), within intra-reef sediments and peripheral biodetrital sediments, three decapod species have been recorded i.e. *Daira speciosa*, *Dromia* cf. *D. neogenica* and *Xantho* cf. *X. moldavicus* (Saint Martin and Müller 1988).

Other decapods recorded in a later work by Saint Martin (1990) on the coral formations from the Upper Miocene of Algeria and Morocco include from Algeria, *Dromia neogenica* and other undetermined remains from Sebaa Chioukh, *Daira speciosa* and *Dromia neogenica* from Souk el Khemis, *Upogebia*? sp. and cf. *Anapagurus* from Douar Ouled Sidi bou Azza, *Lachnopodus murdjadjensis* from Murdjadjo, *Actaea calzadai* from Tafaraoui, *Actaea calzadai* from Algues and Coraux du Hammar Semmoumet and *Daira speciosa* from Ain Oumata. The primary reef-builder in the aforementioned localities is *Porites* associated with other coral species *Tarbellastraea*, *Palaeoplesiastraes*?, *Siderastraea*, *Acanthastrea* and *Balanophyllia*.

From Morocco, also in coral reef outcrops composed primarily of *Porites* but also of *Tarbellastraea*, *Favites* and *Siderastraea*, *Callianassa* sp. and *Daira speciosa* were recorded from Oued Kell while *Daira speciosa* was also found at Arham Amellal (Saint Martin 1990).

Carapaces and appendages of *Daira speciosa* have been recorded by Garcia Socias (1990) from reef deposits, interpreted as outer lagoon facies, in the Upper Miocene of Majorca Island (Balearics, Western Mediterranean).

Pliocene

Three species of decapods, all rare, have been recorded from the Pliocene–Pleistocene? coral limestone of the Daito Limestone Formation, Japan: *Neoliomera pubescens*, *Atergatis granulatus* and *Daira perlata*. A depositional environment within the reef flat and reef edge in coral reefs is envisaged (Karasawa 2000).

Pleistocene

Eleven species in seven genera are recorded from the Middle to Upper Pleistocene Coral Rock of Barbados. Fossils of living species of molluscs, corals and brachiopods have been found associated with the fossil species *Herbstia exserta* Collins and Morris, 1976, together with five extant species of majids, namely *Mithrax spinosissimus*, *M. hemphilli*, *M. verrucosus*, *M. hispidus*, *M. caribbaeus* and *M.* (*Mithraculus*) *ruber*, as well as *Portunus* (*P.*) *gibbesii*, *Portunus* (*P.*) *vocans*, *Actaea rufopunctata nodosa*, *Pilumnus* sp. and *Carpilius corallinus* (Collins and Morris 1976; Collins *et al.* 2009).

SYSTEMATIC PALAEONTOLOGY

Remarks. The systematic arrangement used in this paper follows the recent classification proposed by De Grave *et al.* (2009).

Repository. Catalogue numbers with prefix NMNH refer to the collections of the National Museum of Natural History, Malta; corresponding numbers denoted in brackets, with prefix Arth., and M. refer to one of the author's (MG) collection.

Order DECAPODA Latreille, 1802
Infraorder AXIIDEA de Saint Laurent, 1979
Infraorder THALASSINIDEA Latreille, 1831
Family CALLIANASSIDAE Dana, 1852

Genus CALLIANASSA Leach, 1814

Type species. Cancer (*Astacus*) *subterraneus* Montagu, 1808, by original designation.

Callianassa munieri Brocchi, 1883
Plate 2, figures 1–2

1883 *Callianassa Munieri* Brocchi, p. 5, pl. 5, figs 5–6.
1898 *Callianassa Munieri* Brocchi; Lőrenthey, p. 104.
1929 *Callianassa Munieri* Brocchi; Glaessner, p. 86.
1929 *Callianassa Munieri* Brocchi; Lőrenthey *in* Lőrenthey and Beurlen, p. 33, 62–64 (*pars*), pl. 2, figs 19–23 (*non* fig. 24).
1979*a* *Callianassa munieri* Brocchi; Müller, p. 274.
1984*a* '*Callianassa*' *munieri* Brocchi; Müller, p. 50, pl. 1, figs 1–7; pl. 2, figs 1–2.

Material. NMNH/C050 (Arth. 399) and NMNH/C051 (Arth. 475); from area between Għajn Żnuber and Golden Bay.

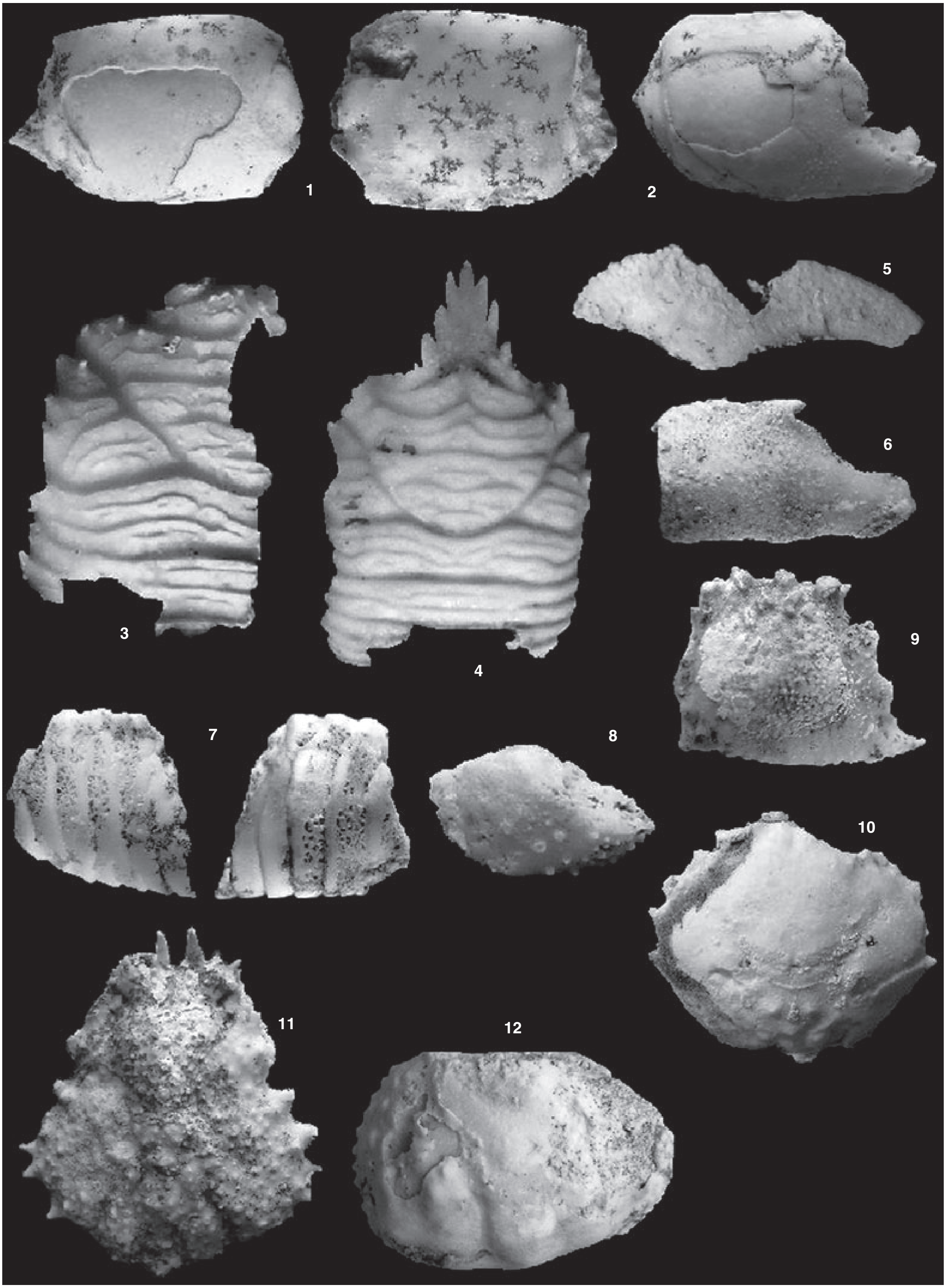
Description. The specimens examined have a subcylindrical propodus, which is longer than high. The inner margin is almost straight, with a serrated keel; the outer margin is slightly convex, with three small spines. The internal surface of the palm is slightly convex, with an ornament of numerous granulations on its medial area; the outer surface is more inflated, with a granulated ornament in the proximity of the fixed finger. There is a robust, round tooth on the occlusal margin of the fixed finger, and some pores are evident on the outer surface.

Remarks. Although little is preserved in the specimens examined, their general form and ornament of a few

EXPLANATION OF PLATE 2

Fig. 1. *Callianassa munieri* Brocchi. NMNH/C051 (Arth. 475); palm: mpw: 21.00 mm, mph: 15.50 mm; ×1.7.
Fig. 2. *Callianassa munieri* Brocchi. NMNH/C050 (Arth. 399); propodus: mprw: 23.90 mm, mprh: 15.00 mm; ×1.5.
Fig. 3. *Galathea* sp. NMNH/C056 (Arth. 401); carapace: mcw: 05.50 mm, mch: 08.90 mm (measurements of carapace fragment); ×5.4.
Fig. 4. *Galathea weinfurteri* Bachmayer. NMNH/C066 (Arth. 385); carapace: mcw: 06.10 mm, mch: 09.00 mm (incomplete); ×5.4.
Fig. 5. *Petrolistes* cfr. *magnus* Müller. NMNH/C057 (Arth. 485); dactylus: mw: 16 mm, mh: n/a.; ×2.7.
Fig. 6. *Pagurus turcus* Müller. NMNH/C058 (Arth. 468); propodus: mprw: 14.20 mm, mprh: 08.00 mm; ×2.2.
Fig. 7. *Dardanus hungaricus* Lőrenthey. NMNH/C060 (Arth. 471); propodus: mprw: 11.50 mm, 10.90 mm; ×2.1.
Fig. 8. *Paguristes cserhatensis* Müller. NMNH/C063 (Arth. 465); propodus: mprw: 06.10 mm, mprh: 04.00 mm; ×4.6.
Fig. 9. *Paguristes* sp. NMNH/C065 (Arth. 491); propodus: mprw: 11.10 mm, mprh: 08.20 mm; ×2.8.
Fig. 10. *Dromia neogenica* Müller. NMNH/C074 (Arth. 518); carapace: mcw: 21.9 mm, mch: 19.0 mm; ×1.6.
Fig. 11. *Maja biaensis* Lőrenthey. NMNH/C089 (Arth. 476); carapace: mcw: 47.90 mm, mch: 57.50 mm; ×0.8.
Fig. 12. *Calappa praelata* Lőrenthey. NMNH/C078 (Arth. 597); carapace: mcw: 34.90 mm, mch: 27.00 mm (specimen incomplete); ×1.1.
Abbreviations: mpw/mph, max. palm width/height; mprw/mprh, max. propodus width/height; mchw/mchh, max. chela width/height; mcw/mch, max. carapace width/height; mw/mh, max. width/height.

PLATE 2



GATT and DE ANGELLI, decapods from Malta small spines on the outer margin of the palm suggest a stong affinity with the *Callianassa munieri*, described from the upper Badenian of Hungary (Brocchi, 1883; Lőrenthey and Beurlen 1929; Müller 1979*a*, 1984*a*).

Infraorder ANOMURA MacLeay, 1838
Superfamily GALATHEOIDEA Samouelle, 1819
Family GALATHEIDAE Samouelle, 1819

Genus GALATHEA Fabricius, 1793

Type species. *Cancer strigosus* Linnaeus, 1761, by subsequent designation of Latreille, 1810.

Galathea weinfurteri Bachmayer, 1950
Plate 2, figure 4

1950	*Galathea weinfurteri* Bachmayer, p. 135, pl. 1, figs 2–4.
1953	*Galathea weinfurteri* Bachmayer; Bachmayer, p. 242, pl. 5, figs 3–4, 6.
1974*b*	*Galathea weinfurteri* Bachmayer; Müller, p. 276, pl. 1, fig. 4.
1976	*Galathea weinfurteri* Bachmayer; Müller, p. 516.
1979*a*	*Galathea weinfurteri* Bachmayer; Müller, p. 274.
1984*a*	*Galathea weinfurteri* Bachmayer; Müller, p. 60, pl. 21, figs 4–5; pl. 22, figs 1–5.
1996	*Galathea weinfurteri* Bachmayer; Müller, p. 8.
1998	*Galathea weinfurteri* Bachmayer; Müller, p. 14.
2002	*Galathea weinfurteri* Bachmayer; Górka, p. 528.

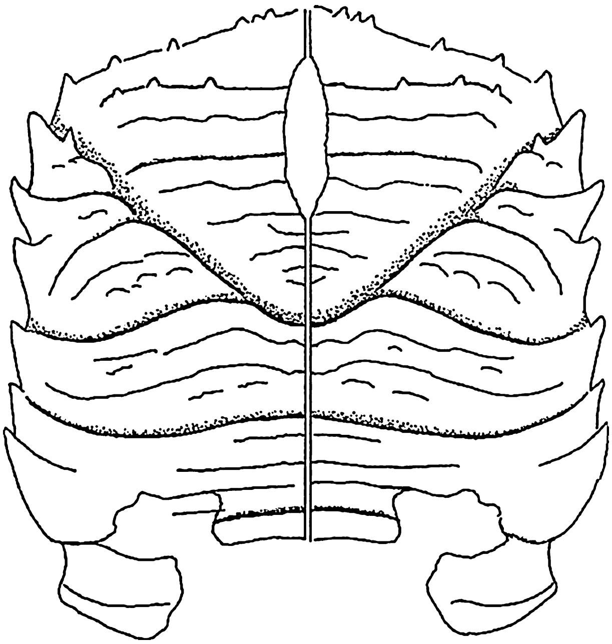
Material. NMNH/C052 (Arth. 385), NMNH/C053 (Arth. 386), NMNH/C054 (Arth. 463), NMNH/C055 (Arth. 519); incomplete carapaces from the area between Għajn Żnuber and Golden Bay.

Description. Specimens characterized by a longitudinally rectangular carapace, wider posteriorly and transversely convex. The rostrum is subtriangular in form, with a concave surface and ornament of four forward-pointing spines. The lateral margins are slightly convex and with an ornament of spines. Regions defined by cervical and branchio-cardiac grooves and ornamented with transversal ridges.

Remarks. Specimens examined correspond with the species *Galathea weinfurteri* from the Middle Miocene (Badenian) of Austria, Hungary and Poland (Bachmayer 1950, 1953; Müller 1984*a*, 1996; Górka 2002).

Galathea sp.
Plate 2, figure 3; Text-figure 3

Material. NMNH/C056 (Arth. 401); incomplete carapace from area between Għajn Żnuber and Golden Bay.



TEXT-FIG. 3. *Galathea* sp., reconstruction of carapace.

Description. Specimen consists of a carapace left portion, longitudinally rectangular in shape, widest posteriorly; lateral margins with spines and the dorsal surface with ornament of sinuous transversal ridges. The rostrum is missing; on the anterior part of the carapace is an epigastric granulated ridge; four continuous and almost straight ridges, interspersed by sinuous intermittent secondary ones, are present on the gastric and hepatic regions, which are poorly distinct from each other. Four spines present on the hepatic regions. Epibranchial regions subtriangular in shape and defined by cervical and branchiocardiac grooves, with three distinct ridges and a spine on the anterior part near to the cervical groove. Posterior branchial regions are wide and crossed by four transversal continuous ridges.

Remarks. The specimen exhibits characteristics typical of the genus *Galathea* and seemingly similar to the species *Galathea weinfurteri*; however, it has a larger number of sinuous secondary ridges interspersed with the primary ones and exhibits some spines on the hepatic and epibranchial regions. The specimen shows also some affinity with *G. valmaranensis* De Angeli and Garassino, 2002, from the Lower Oligocene of Mount Berici (Vicenza, Italy), which is characterized by an epibranchial spine, which is however positioned more posteriorly. *Galathea valmaranensis* is also distinguishable from this specimen by the absence of hepatic spines (De Angeli and Garassino 2002). Nonetheless, the attribution to a specific species of the Maltese specimen cannot be affirmed because of the fragmentary preservation of its carapace and the absence of the rostrum.

Family PORCELLANIDAE Haworth, 1825

Genus PETROLISTHES Stimpson, 1858

Type species. Porcellana violacea Guérin-Méneville *in* Duperry, 1829, by original designation.

Petrolisthes cf. *magnus* Müller, 1984

Plate 2, figure 5

Material. NMNH/C057 (Arth. 485); distal fragment of dactylus from the area between Għajn Żnuber and Golden Bay.

Description. Single dactylus still in matrix and with internal surface exposed. Movable finger elongate, upper margin laminate, very convex and serrated; external surface completely covered with small granulations.

Remarks. The examined movable finger, even though incomplete, exhibits characteristics which are typical of the genus *Petrolisthes* Stimpson, 1858. The shape and ornamentation of the external surface of dactylus is very similar to that of *P. magnus* Müller, 1984*a*, described from the Badenian (Middle Miocene) of Hungary.

Superfamily PAGUROIDEA Latreille, 1802

Family PAGURIDAE Latreille, 1802

Genus PAGURUS Fabricius, 1775

Type species. Cancer bernhardus Linneaus, 1758, by subsequent designation of Latreille, 1810.

?*Pagurus turcus* Müller, 1984

Plate 2, figure 6

1984*a* ?*Pagurus turcus* Müller, p. 56, pl. 12, fig. 6, pl. 13, figs 1–4.

Material. NMNH/C058 (Arth. 468); right palm from the area between Għajn Żnuber and Golden Bay.

Description. Specimen partially preserved with only outer surface exposed. Palm subcylindrical in shape, longer than high, outer margin of palm almost straight and with tubercles; inner margin slightly convex; outer surface of palm inflated and with an ornamentation of tubercles; fixed finger robust but distal part not preserved; inner margin of fixed finger curved and occlusal margin with small blunt teeth, inner surface of fixed finger decorated with conspicuous asymmetrical ornamentation resembling scales.

Remarks. The specimen from Malta is similar in both shape and ornamentation to two palms from the Lower Badenian (Middle Miocene) of Hungary, assigned by Müller (1984*a*) to ?*Pagurus turcus*.

Family DIOGENIDAE Ortmann, 1892

Genus DARDANUS Paul'son, 1875

Type species. Dardanus hellerii Paul'son, 1875, by original designation.

Dardanus hungaricus (Lőrenthey *in* Lőrenthey and Beurlen, 1929)

Plate 2, figure 7

1929 *Paguristes hungaricus* Lőrenthey *in* Lőrenthey and Beurlen, p. 34, pl. 3, fig. 4.
1976 *Paguristes*? *hungaricus* Lőrenthey; Müller, p. 508.
1979*a* *Dardanus hungaricus* (Lőrenthey); Müller, p. 274.
1984*a* *Dardanus hungaricus* (Lőrenthey); Müller, p. 58, pl. 18, figs 1–5.
1984*b* *Dardanus hungaricus* (Lőrenthey); Müller, p. 27, pl. 2, fig. 3.
1989 *Dardanus hungaricus* (Lőrenthey); Solé and Via Boada, p. 33.
1993 '*Dardanus hungaricus*' (Lőrenthey); Müller, p. 7, figs 3F–G.
2001 *Dardanus hungaricus* (Lőrenthey); Vega *et al*., p. 932.
2002 *Dardanus hungaricus* (Lőrenthey); Górka, p. 528, fig. 7.
2003 *Dardanus hungaricus* (Lőrenthey); van Bakel *et al*., p. 113.

Material. NMNH/C059 (Arth. 404), NMNH/C060 (Arth. 471), NMNH/C061 (Arth. 492) and NMNH/C062 (Arth. 600); palms from the area between Għajn Żnuber and Golden Bay.

Description. Specimens examined all incomplete; nonetheless, they exhibit characteristics typical of this species. Palm subcylindrical, with both internal and external surfaces well inflated and ornate with sinuous transversal ridges which are also found on the fixed finger.

Remarks. Vega *et al*. (2001) have stressed the need for a re-evaluation of certain species assigned to the genus *Dardanus*, amongst which are *D. hungaricus* and *D. arrosor*, due to their resemblance to *Ciliopagurus*. Van Bakel *et al*. (2003), however, argued that in the absence of stridulatory apparatus, and the fact that the ornamentation differs in both cheliped specimens from Hungary, these cannot be assigned to *Ciliopagurus*.

Dardanus hungaricus is well represented in the Middle Miocene of Hungary, Spain and Poland (Lőrenthey *in*

Lőrenthey and Beurlen 1929; Müller 1976, 1979*a*, 1984*a*, *b*, 1993; Górka 2002).

Genus PAGURISTES Dana, 1851

Type species. Paguristes hirtus Dana, 1851, by subsequent designation of Stimpson, 1858.

Paguristes cserhatensis Müller, 1984
Plate 2, figure 8

1984*a* *Paguristes cserhatensis* Müller, p. 59, pl. 19, figs 1–4.

Material. NMNH/C063 (Arth. 465); right palm from the area between Għajn Żnuber and Golden Bay.

Description. One small-sized specimen representing a right palm. The palm is very short, the outer surface inflated and densely ornate with large tubercles positioned in longitudinal files; the size of these tubercles decreases towards the outer margin. The fixed finger is short and robust with small teeth on its occlusal margin.

Remarks. The palm from Malta exhibits characteristics that are similar to *Paguristes cserhatensis* Müller, 1984, a species described from one specimen from the Lower Badenian (Middle Miocene) of Hungary.

Paguristes sp.
Plate 2, figure 9

Material. NMNH/C064 (Arth. 473) and NMNH/C065 (Arth. 491); right palm from the area between Għajn Żnuber and Golden Bay.

Description. Palm subcilindrical, as long as high; the outer margin of the palm is short and with four large tubercles; the inner margin convex and with a granulae ornament. The outer surface of the palm is inflated and has some large tubercles near the upper margin; the median area is depressed with an ornament of irregularly arranged small-sized tubercles. The fixed finger is triangular in shape, short, thin and pointed.

Remarks. The two Maltese specimens are incomplete and poorly preserved but exhibit similarities with *Paguristes cserhatensis* Müller, 1984 from the Lower Badenian of Hungary which is also characterized by a short palm; nonetheless, the presence of some large tubercles on the outer margin of the palm and the small-sized fixed finger clearly distinguish the two specimens from those of Hungary.

The two palms may thereby represent a new species; however, their incomplete preservation does not permit a more detailed description.

Infraorder BRACHYURA Linnaeus, 1758
Section DROMIACEA De Haan, 1833
Superfamily DROMIOIDEA De Haan, 1833
Family DROMIIDAE De Haan, 1833

Genus DROMIA Weber, 1795

Type species. Cancer personatus Linnaeus, 1758, subsequent designation by ICZN, 1964 (opinion 688).

Dromia neogenica Müller, 1979
Plate 2, figure 10

1979*a* *Dromia neogenica* Müller, p. 274, pl. 8, fig. 1.
1984*a* *Dromia neogenica* Müller; Müller, p. 63, pl. 29, figs 1–6.
1998 *Dromia neogenica* Müller; Müller, p. 18.

Material. NMNH/C066 (Arth. 385), NMNH/C067 (Arth. 406), NMNH/C068 (Arth. 429), NMNH/C069 (Arth. 467), NMNH/C070 (Arth. 469), NMNH/C071 (Arth. 490), NMNH/C072 (Arth. 494), NMNH/C073 (Arth. 517), NMNH/C074 (Arth. 518), NMNH/C075 (Arth. 576) (fragment), NMNH/C076 (Arth. 601) and NMNH/C077 (Arth. 634); carapaces from the area between Għajn Żnuber and Golden Bay.

Description. Specimens examined are of various sizes and mostly preserved complete. Carapace well convex; the frontal margin has three short teeth, with the middle one positioned at a lower level than those on the sides. The orbits are wide and terminate with an extraorbital spine. The anterolateral margin is convex and provided with three spines. The regions are poorly defined, and the branchiocardiac groove defines the urogastric and cardiac regions; there are three weak protuberances on the cardiac region; the postcervical groove is well defined; the dorsal surface is smooth.

Remarks. The species is represented in the Lower to Upper Badenian (Middle Miocene) of Hungary and Austria (Müller 1979*a*, 1984*a*, 1998), and probably also from the Messinian of Orania, Algeria (Saint Martin and Müller 1988).

Section EUBRACHYURA de Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Superfamily CALAPPOIDEA De Haan, 1833
Family CALAPPIDAE De Haan, 1833

Genus CALAPPA Weber, 1795

Type species. Cancer granulatus Linnaeus, 1758, subsequent designation by Latreille, 1810.

Calappa praelata Lőrenthey *in* Lőrenthey and Beurlen, 1929
Plate 2, figure 12

1929 *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen, p. 132, pl. 6, fig. 3.
1962 *Calappa* cf. *praelata* Lőrenthey; Bachmayer, p. 42.
1979*b* *Calappa* aff. *herberti* Brocchi; Förster, p. 255, pl. 1, figs 2, 4.
1984*a* *Calappa praelata* Lőrenthey; Müller, p. 66, pl. 35, figs 1–2, 7; pl. 36, fig. 6.
1984*b* *Calappa praelata* Lőrenthey; Müller, pl. 2, fig. 4.
1996 *Calappa praelata* Lőrenthey; Müller, p. 9, pl. 1, fig. 11.
1998 *Calappa praelata* Lőrenthey; Müller, p. 22.

Material. NMNH/C078 (Arth. 597); incomplete carapace from the area between Għajn Żnuber and Golden Bay.

Description. The frontal and posterior parts are not preserved; the lateral margin convex and ornate with lobes; the dorsal regions are well defined by deep branchiocardiac grooves; the branchial regions have numerous irregularly placed tubercles.

Remarks. Only the left part of the carapace is preserved in the specimen from Malta; however, this is sufficient to permit us to include this calappid species in the Miocene fauna of Malta.

Calappa praelata is recorded from the Middle Miocene (Badenian) of Hungary, southern Poland, Austria (Lőrenthey *in* Lőrenthey and Beurlen 1929; Bachmayer 1962; Förster 1979*b*; Müller 1996, 1998) and probably also from the Tortonian of the Iberian Peninsula (Veiga Ferreira 1954).

Superfamily MAJOIDEA Samouelle, 1819
Family EPIALTIDAE MacLeay, 1838
Subfamily PISINAE Dana, 1851

Genus HERBSTIA H. Milne Edwards, 1834

Type species. *Cancer condyliatus* Fabricius, 1787, by monotypy.

Known fossil species. *Herbstia exserta* Collins and Morris, 1976.

Herbstia melitense sp. nov.
Text-figures 4A–J, 5

Derivation of name. After the island of Malta – derived from the Phoenician word '*Maleth*' which means 'refuge', 'shelter', 'haven' or 'protected place' – probably referring to the natural harbours and bays which are found along the Maltese coastline. Following the Phoenicians, the Romans called the island '*Melita*', a name which could have been derived from '*Maleth*' or may also be ascribed to the Greek word '*Melita*', which means 'honey'.

Holotype. NMNH/C082 (Arth. 477) (Text-fig. 4B, H, J).

Paratypes. NMNH/C079 (Arth. 220), NMNH/C080 (Arth. 383), NMNH/C081 (Arth. 402) and NMNH/C085 (Arth. 613).

Type locality. Area between Għajn Żnuber and Golden Bay.

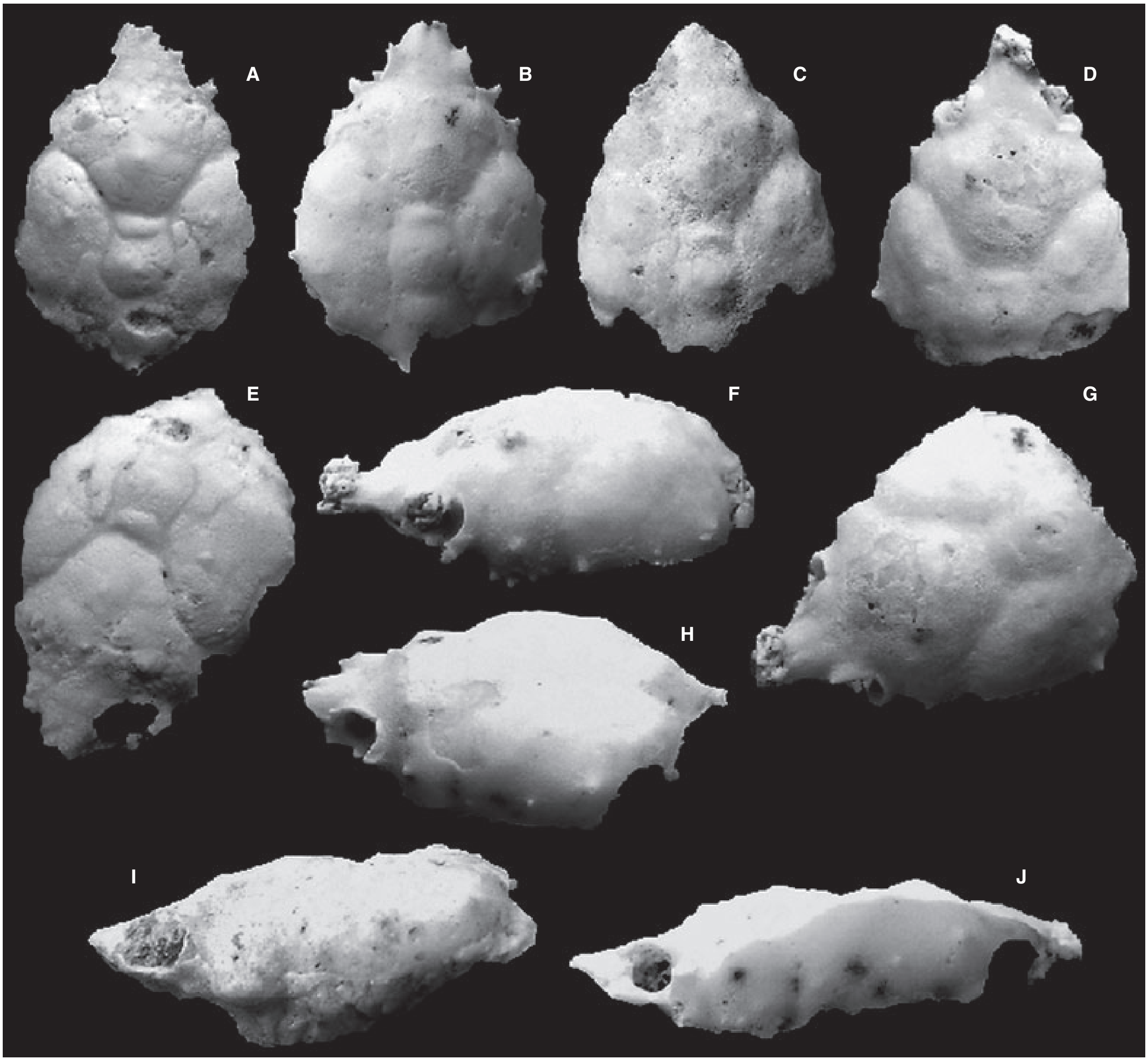
Material. NMNH/C079 (Arth. 220), NMNH/C080 (Arth. 383), NMNH/C081 (Arth. 402), NMNH/C082 (Arth. 477), NMNH/C083 (Arth. 493), NMNH/C084 (Arth. 568) (fragment), NMNH/C085 (Arth. 613), NMNH/C086 (Arth. 629) (fragment), NMNH/C087 (Arth. 634) (incomplete carapace); carapaces from the area between Għajn Żnuber and Golden Bay. NMNH/C088 (Arth. 564); carapace (fragment) from Fomm ir-Riħ.

Diagnosis. Carapace convex, suboval in outline, longer than wide; rostrum with two short flat spines; supraorbital margin with two shallow indentations, preorbital tooth long and pointing anterolaterally; extraorbital tooth well extended laterally; suborbital margin more extended than supraorbital and with an opening and spine; lateral margins convex and with three tubercles; posterior margin well convex medially and with a singular spine; regions poorly distinct and ornate with some tubercles.

Description. Carapace slightly convex, suboval in outline, longer than wide. The fronto-orbital margin occupies the entire anterior part of the carapace; the rostrum is composed of two short lamellar spines, separated by a median gap (the rostral spines are incomplete in the examined specimens and only the bases are preserved); the orbits are positioned obliquely; the supraorbital margin is concave and interrupted by two shallow indentations; the preorbital tooth is long, well distinct from the rostral spine; the extraorbital tooth has a convex margin and is extended laterally in the form of an acute spine. The suborbital margin is more extended than the supraorbital one, with an opening and one spine, extends beyond the preorbital tooth and exhibits a little spine on its anterior angle.

The margins are divergent and marked by an indentation produced by the cervical groove and exhibit a tubercle on the hepatic margin and two tubercles on the branchial margin. The posterolateral margin is short and converges at the posterior margin. The posterior margin is relatively wide and well convex medially where a single short protuberation may be observed.

The regions are only slightly defined with shallow grooves; the frontal region is depressed medially; the protogastric and mesogastric regions are slightly inflated and ornamented with a median tubercle. The metagastric region is rectangular in shape and well defined by grooves and ornamented with a single median tubercle. The cardiac region is well defined on the sides by branchiocardiac grooves, suboval in shape, slightly inflated and also ornamented with a single median tubercle. The intestinal region is well defined, extended posteriorly, and with a single pointed projection on its posterior part. The hepatic regions are



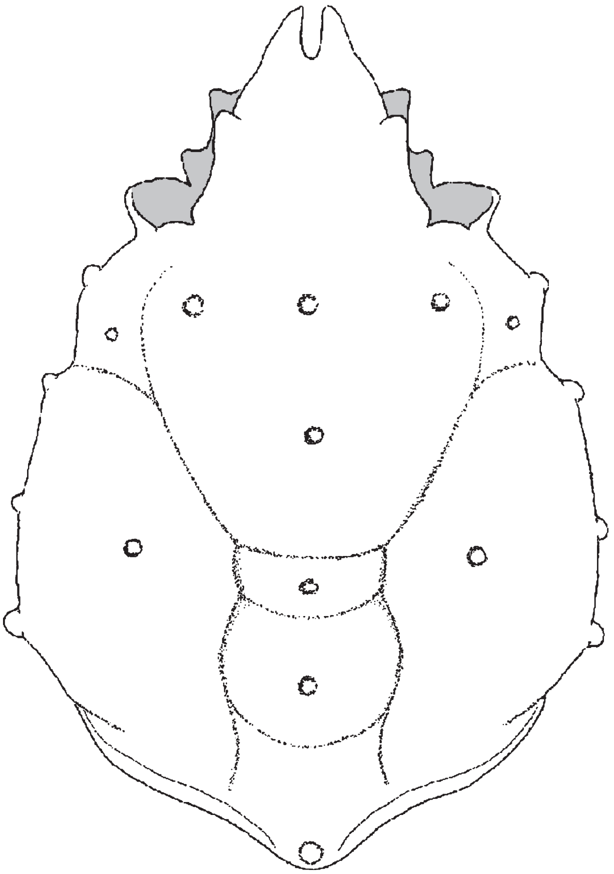
TEXT-FIG. 4. A, E, *Herbstia melitense* sp. nov. A, dorsal view. E, dorsal and lateral view of Paratype NMNH/C081 (Arth. 402); carapace: mcw: 10.50 mm, mch: 15.90 mm; ×2.5. B, H, J. *Herbstia melitense* sp. nov. B, dorsal view. H, dorsal and lateral view. J, lateral view of holotype NMNH/C082 (Arth. 477); carapace: mcw: 10.60 mm, mch: 15.10 mm; ×2.6. C, I, *Herbstia melitense* sp. nov. C, dorsal view. I, lateral view (internal mould) of paratype NMNH/C079 (Arth. 220): mcw: 11.90 mm, mch: 15.50 mm ×2.4. D, F, G, *Herbstia melitense* sp. nov. D, dorsal view. F, lateral view. G, dorsal and lateral view of paratype NMNH/C085 (Arth. 613); carapace: mcw: 11.80 mm, mch: 15.90 mm; ×2.4. Abbreviations: mcw/mch, max. carapace width/height.

subtriangular, well defined in the posterior portion by the cervical groove, convex dorsally and ornamented with a single small tubercle. Viewed laterally, three other subhepatic tubercles may be observed.

The branchial regions are elongated, inflated and ornamented with an epibranchial tubercle. The dorsal surface is finely granulated.

Remarks. The type is particularly well preserved and, besides the general characteristics of the carapace, it was also possible to observe the form of both supraorbital and suborbital marginal teeth, which conform to the morphological characteristics of the genus *Herbstia* H. Milne Edwards, 1834.

Herbstia melitense sp. nov. shows affinity with extant species of this taxon, which inhabit the Atlantic and Pacific coastal areas of America and West Africa (Rathbun 1925; Manning and Holthuis 1981), and particularly with *H. pyriformis* (Bell, 1835) which does not have tubercles



TEXT-FIG. 5. *Herbstia melitense* sp. nov., reconstruction of carapace.

on the gastric regions, and with *H. rubra* A. Milne Edwards, 1869, which has a larger number of spinose tubercles on its lateral margins.

Herbstia condyliata (Fabricius, 1787) is the only representative of this genus still extant in the Mediterranean. The latter species is also distributed from the southern part of the Bay of Biscay to tropical West Africa, the Azores, Madeira, the Canary Islands and the Sea of Marmara (Manning and Holthuis 1981; Falciai and Minervini 1995). It is included in the European Register of Marine Species. *Herbstia condyliata* has been recorded from Greek Aegean waters, the Evvoia marine region and Monenvasia; also from the Turkish Straits, Cyprus, and Rhodes Island (Corsini and Kondilatos 2006).

Herbstia condyliata may be distinguished from *H. melitense* sp. nov. by the presence of four spines on each branchial margin and from a trilobed projection on the posterior median margin of the carapace.

Herbstia melitense sp. nov. exhibits strict affinity with the fossil species *H. exserta* Collins and Morris, 1976, from the Pliocene of the Gibbons (Barbados). The gastric regions are, however, less elongated posterior, the cardiac region less defined by the branchiocardiac grooves, and the dorsal surface ornate with evident granulations, in the latter species.

Herbstia melitense sp. nov. constitutes the first fossil record attributed to this taxon from the Mediterranean region.

Family MAJIDAE Samouelle, 1819
Subfamily MAJINAE Samouelle, 1819

Genus MAJA Lamarck, 1801

Type species. Cancer squinado Herbst, 1788, subsequent designation by ICZN.

Maja biaensis Lőrenthey *in* Lőrenthey and Beurlen, 1929
Plate 2, figure 11

1873 *Maja* sp. Woodward, p. 325.
1929 *Maja biaensis* Lőrenthey *in* Lőrenthey and Beurlen, pp. 34, 148–150, pl. 7, fig. 1.
1929 *Maja biaensis* Lőrenthey; Glaessner, p. 247.
1976 *Maja biaensis* Lőrenthey; Müller, p. 510, pl. 3, fig. 2.
1979*a* *Maja biaensis* Lőrenthey; Müller, p. 274.
1984*a* *Maja biaensis* Lőrenthey; Müller, p. 71, pl. 48, figs 1–6; pl. 49, figs 1–3.
1996 *Maja biaensis* Lőrenthey; Müller, p. 9.

Material. NMNH/C089 (Arth. 476); complete carapace from the area between Għajn Żnuber and Golden Bay; NMNH/C090 (Arth. 432); incomplete carapace from the area between Għajn Żnuber and Golden Bay.

Remarks. The most complete and well-preserved specimen represents a carapace that is identical to the species *Maja biaensis* from the Middle Miocene (Upper Badenian) of Hungary and Poland, also figured by Müller (1984*a*, pl. 48, figs. 1–6).

Moissette and Müller (1990) discussed the three Miocene species: *Maja miocenica* Lőrenthey, 1907, from the Lower Miocene of Sardinia (Italy), *M. orbignyana* Millet, 1854, from the Lower Miocene of France, and *M. biaensis* Lőrenthey, 1929, from the Middle Miocene of Hungary, and concluded that there is very little to distinguish these species from one another.

Woodward (1873, p. 325) attributed to *Maja* sp. the remains of a carapace from the Miocene of Malta but failed to produce any figure of this specimen. Considering that the specimen originated from the Miocene rocks of Malta, we consider that Woodward's specimen could have belonged to *Maja biaensis*.

Subfamily MITHRACINAE MacLeay, 1838

Genus MICIPPA Leach, 1817

Type species. *Cancer cristatus* Linnaeus, 1758, by original designation.

Known fossil species. *Micippa antiqua* Beschin *et al*., 2001; *M. hungarica* (Lőrenthey *in* Lőrenthey and Beurlen, 1929) and *M. thalia* (Herbst, 1803) (fossil and Recent).

Micippa annamariae sp. nov.

Text-figures 6A, 7

Derivation of name. Dedicated to Anna Maria Gatt, wife of one of the authors (MG).

Holotype. NMNH/C091 (Arth. 456) (Text-fig. 6A).

Paratypes. NMNH/C092 (Arth. 400), NMNH/C093 (Arth. 511).

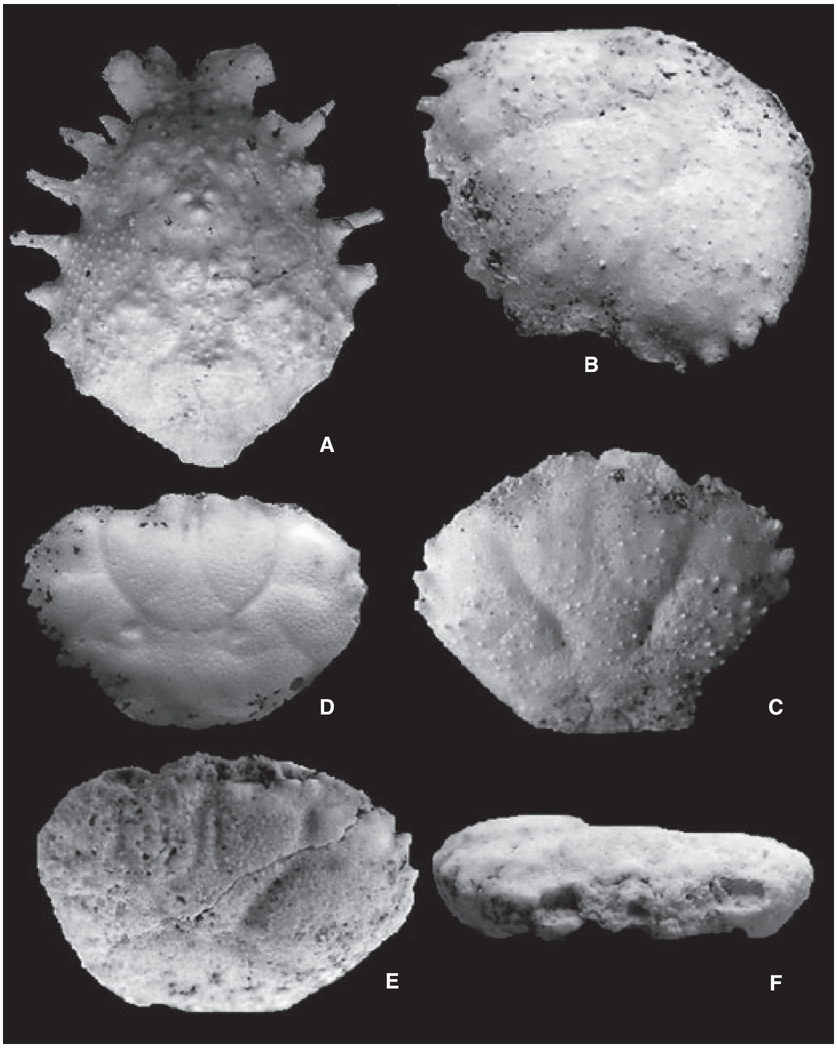
Type locality. Area between Għajn Żnuber and Golden Bay.

Material. NMNH/C091 (Arth. 456), carapace; NMNH/C092 (Arth. 400), NMNH/C093 (Arth. 511), incomplete carapace; all from the area between Għajn Żnuber and Golden Bay.

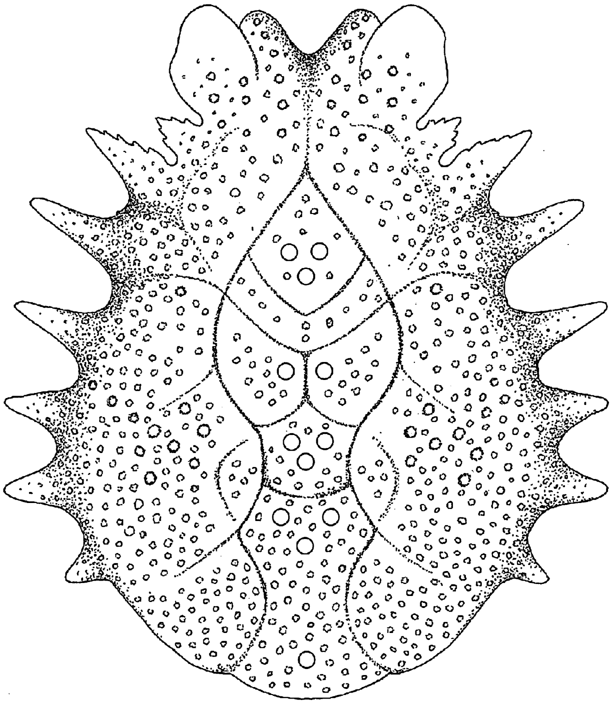
Diagnosis. Carapace convex, oval in outline, longer than wide; rostrum with two large lamellae curved downwards; supraorbital margins with two indentations and orbital teeth well developed and extended; lateral margins convex and with a long hepatic spine and four long branchial spines; regions well defined and ornate with tuberculation.

Description. Carapace oval in outline, surface convex, longer than wide, with maximum width corresponding with the second-third spine of the branchial margin.

The fronto-orbital margin occupies the entire anterior part of the carapace. Rostrum with two elongated lobes curved downwards, separated by a median gap; the orbits are wide and positioned obliquely; the supraorbital margin is interrupted by two



TEXT-FIG. 6 A, *Micippa annamariae* sp. nov.; dorsal view of Holotype NMNH/C089 (Arth. 476); carapace: mcw: 25.10 mm, mch: 37.00 mm; ×2.1. B, C, *Pilumnus scaber* sp. nov. B, dorsal and lateral view of holotype NMNH/C280 (Arth. 567); carapace: mcw: 13.20 mm, mch: 10.10 mm. C, dorsal view of holotype; ×4.2. D–F, *Panopeus muelleri* sp. nov. D, dorsal view of holotype NMNH/C283 (Arth. 470); carapace: mcw: 11.00 mm, mch: 08.00 mm; ×4.5. E, dorsal view of paratype NMNH/C298 (Arth. 459); internal mould: mcw: 14.20 mm, mch: 10.40 mm; ×3.5. F, frontal view of Paratype NMNH/C298 (Arth. 459). Abbreviations: mcw/mch, max. carapace width/height.



TEXT-FIG. 7. *Micippa annamariae* sp. nov., reconstruction of carapace.

deep indentations; the preorbital spine is large, and directed anterolaterally; the intraorbital tooth is subtriangular and with serrated margins; the extraorbital tooth is a long spine positioned obliquely anteriorly and with an dentate anterior margin. The lateral margins are convex and ornamented with long spines directed laterally. A large hepatic spine is found on the anterolateral margins, immediately behind the extraorbital spine. The divergent anterolateral margins which extend posteriorly, are ornamented with four other long branchial spines (the two posterior spines are incomplete and only their bases are preserved); the posterolateral margins converge rapidly at the posterior margin.

The dorsal regions are well defined; the frontal region is delineated by a longitudinal median depression; the protogastric regions are elevated and circular in outline; the mesogastric region is rhomboidal in shape and ornamented with three large tubercles; the anterior part of this region exhibits a narrow and elongated mesogastric process; the posterior part is, on the other hand, represented by two lobes positioned obliquely and ornamented with granulations. The metagastric region is well defined and with a convex posterior margin. The urogastric region is narrow and of pentagonal outline. The branchiocardiac grooves strongly narrow over the urogastric region. The cardiac region is wide and ornamented with two elevated tubercles. The hepatic regions are small and subtriangular; the branchial regions are well developed. The dorsal surface is ornate with small tubercles.

Remarks. The type specimen is very well preserved and exhibits charateristics that are typical of the genus *Micippa* Leach, 1817, represented by ten extant species (Ng *et al.* 2008).

The fossil species attributed to this taxon include *Micippa antiqua* Beschin, De Angeli and Checchi, 2001, from the Lower Oligocene of Vicenza (Italy), which may be distinguished from *M. annamariae* sp. nov. by means of the rostral spines that are much closer and positioned obliquely, the presence of a forked spine on the hepatic region, three spines on each branchial margin, and some spinose tubercles on the cardiac and branchial regions (Beschin *et al.* 2001; De Angeli and Beschin 2008). *Micippa hungarica* (Lőrenthey *in* Lőrenthey and Beurlen 1929) from the Middle Miocene of Hungary (Lőrenthey *in* Lőrenthey and Beurlen 1929; Müller 1984*a*) and Poland (Müller 1996), has a much wider carapace posteriorly, a cardiac region which is much narrower, and dorsal surface ornate with dense (Müller 1984*a*) when compared with *M. annamariae* sp. nov. The specimen from the Pleistocene of Japan, attributed to *M.* sp. cf. *M. thalia* is only represented by rostral spines (Kato and Karasawa 1998).

Müller (1984*a*) illustrated also a carapace, which originated from the Miocene outcrop of Rákos (Hungary), attributing it to a variety of *Micippa hungarica*. This specimen has a carapace similar to that from Malta; however, it may be distinguished from it by its much wider posterior part of the carapace, regions which are better defined, protogastric and frontal regions with two longitudinal rows of tubercles, and a narrower cardiac region.

Phrynolambrus weinfurteri Bachmayer, 1953 and *Maia austriaca* Bachmayer, 1953, both described from the Miocene of Austria, have been considered as synonyms of *Micippa hungarica* (Müller, 1984*a*).

Micippa is known from ten living species: *M. cristata* (Linnaeus, 1758), *M. curtispina* Haswell, 1870, *M. excavata* Lanchester, 1900, *M. margaritifera* Henderson, 1893, *M. parca* Alcock, 1895, *M. philyra* (Herbst, 1803), *M. platipes* Rüppell, 1830, *M. spinosa* Stimpson, 1857, *M. thalia* (Herbst, 1803), and *M. xishaensis* Chen, 1980 (Ng *et al.*, 2008). *Micippa annamariae* sp. nov. may be distinguished from extant species by means of its orbital margin teeth and lateral spines that are prominent and extended laterally and for its more convex posterior border.

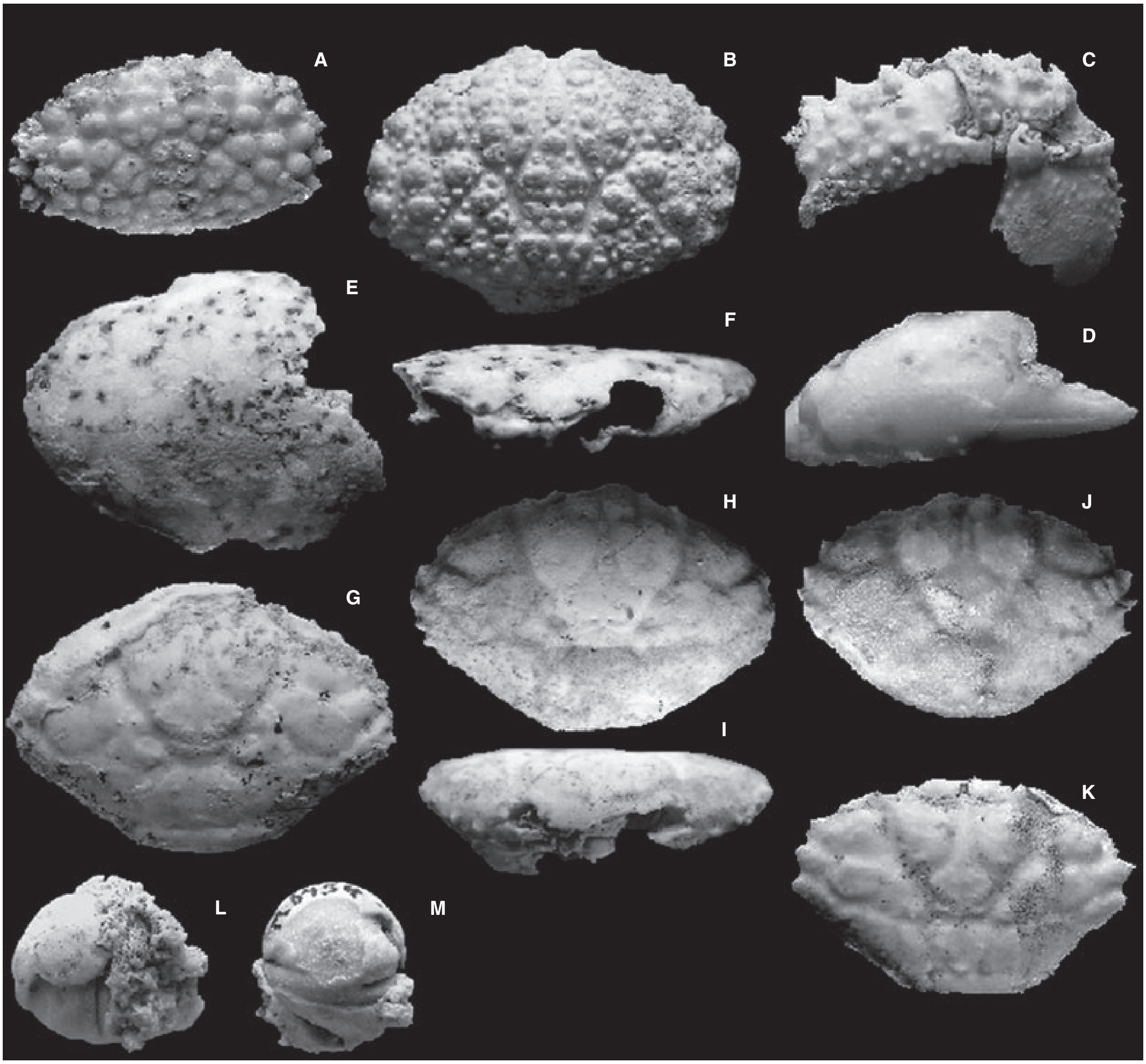
Superfamily DAIROIDEA Serène, 1965
Family DAIRIDAE Serène, 1965

Genus DAIRA De Haan, 1833

Type species. Cancer perlatus Herbst, 1790, subsequent designation by ICZN.

Daira speciosa (Reuss, 1871)
Text-figure 8A–C

1871 *Phymatocarcinus speciosus* Reuss, p. 326, figs 1–4.
1877 *Phymatocarcinus speciosus* Reuss; Bittner, p. 347, pl. 1.
1896 *Phlyctenodes irregularis* Ristori, p. 506, pl. 12, fig. 1.
1928 *Daira speciosa* (Reuss); Glaessner, p. 191.
1929 *Daira speciosa* (Reuss); Glaessner, p. 135.
1929 *Daira speciosa* (Reuss); Lőrenthey *in* Lőrenthey and Beurlen, p. 197, pl. 12, figs 10–11.
1949 *Daira speciosa* (Reuss); Schouppé, p. 139.
1953 *Daira speciosa* (Reuss); Bachmayer, p. 252.
1969 *Daira speciosa* (Reuss); Yanakevich, p. 25, pl. 1, figs 1–3.



TEXT-FIG. 8. A, *Daira speciosa* (Reuss), NMNH/C175 (Arth. 390); carapace: mcw: 16.10 mm, mch: 09.50 mm; ×2.2. B, *Daira speciosa* (Reuss), NMNH/C104 (Arth. 179); internal mould: mcw: 22.80 mm, mch: 15.50 mm; ×1.8. C, *Daira speciosa* (Reuss), NMNH/C255 (Arth. 398); cheliped. D, *Xaiva bachmayeri* Müller, NMNH/C278 (Arth. 466); cheliped: mchw: 25.50 mm; mchh: 09.90 mm; ×1.5. E–F, *Carpilius* sp. E, dorsal view. F, frontal view. NMNH/C279 (Arth. 380); internal mould: mcw: n/a., mch: 25.10 mm. G, *Xantho moldavicus* (Yanakevich). NMNH/C290 (Arth. 462); internal mould: mcw: 33.90 mm, mch: 23.90 mm; ×1.2. H, I, *Xantho moldavicus* (Yanakevich). H, dorsal view. I, frontal view. NMNH/C297 (Arth. 508); carapace: mcw: 37.00 mm, mch: 26.00 mm; ×1.1. J, *Xantho moldavicus* (Yanakevich), NMNH/C292 (Arth. 487); internal mould: mcw: 34.00 mm, mch: 22.90 mm; ×1.1. K, *Xantho moldavicus* (Yanakevich), NMNH/C286 (Arth. 356); internal mould: mcw: 22.60 mm, mch: 15.0 mm. L, M, *Jouannetia* (*J.*) *semicaudata* Des Moulins; M.6454; internal mould. Abbreviations: mchw/mchh, max. chela width/height; mcw/mch, max. carapace width/height.

1976 *Daira speciosa* (Reuss); Müller, p. 516.
1977 *Daira speciosa* (Reuss); Yanakevich, p. 79, pl. 10, figs 5–6.
1979*a* *Eriphia* sp. C Förster, p. 98, text-fig. 12, pl. 1, figs 5–6.
1979*a* *Daira speciosa* (Reuss); Müller, p. 275.
1984*a* *Daira speciosa* (Reuss); Müller, p. 90, pl. 79, figs 1–6, pl. 80, figs 1–2.
1984*b* *Daira* cf. *speciosa* (Reuss); Müller, p. 27, pl. 2, fig. 2.
1988 *Daira speciosa* (Reuss); Saint Martin and Müller, p. 253, pl. 1, fig. 7.
1989 *Daira* cfr. *speciosa* (Reuss); Solé and Via Boada, p. 33.
1996 *Daira speciosa* (Reuss); Müller, p. 11, pl. 2, fig. 5.
1998 *Daira speciosa* (Reuss); Müller, p. 27.
2002 *Daira speciosa* (Reuss); Górka, p. 528.
2006 *Daira speciosa* (Reuss); Radwański *et al.*, pl. 2, figs 3–4, pl. 3.

Material. NMNH/C094 (Arth. 242); carapace from Ras il-Qammieħ.

NMNH/C095 (Arth. 96), NMNH/C096 (Arth. 103), NMNH/C097 (Arth. 104), NMNH/C098 (Arth. 105), NMNH/C099 (Arth. 144), NMNH/C100 (Arth. 145), NMNH/C101 (Arth. 146), NMNH/C102 (Arth. 152), NMNH/C103 (Arth. 166), NMNH/C104 (Arth. 179), NMNH/C105 (Arth. 180), NMNH/C106 (Arth. 181), NMNH/C107 (Arth. 182), NMNH/C108 (Arth. 200), NMNH/C109 (Arth. 201), NMNH/C110 (Arth. 207), NMNH/C111 (Arth. 211), NMNH/C112 (Arth. 215), NMNH/C113 (Arth. 216), NMNH/C114 (Arth. 217), NMNH/C115 (Arth. 218), NMNH/C116 (Arth. 225), NMNH/C117 (Arth. 226), NMNH/C118 (Arth. 227), NMNH/C119 (Arth. 228), NMNH/C120 (Arth. 232), NMNH/C121 (Arth. 233), NMNH/C122 (Arth. 234), NMNH/C123 (Arth. 235), NMNH/C124 (Arth. 236), NMNH/C126 (Arth. 245), NMNH/C127 (Arth. 246), NMNH/C128 (Arth. 247), NMNH/C129 (Arth. 249), NMNH/C130 (Arth. 250), NMNH/C131 (Arth. 251), NMNH/C132 (Arth. 252), NMNH/C133 (Arth. 253), NMNH/C134 (Arth. 254), NMNH/C135 (Arth. 255), NMNH/C136 (Arth. 266), NMNH/C137 (Arth. 267), NMNH/C138 (Arth. 268), NMNH/C139 (Arth. 269), NMNH/C140 (Arth. 286), NMNH/C141 (Arth. 342), NMNH/C142 (Arth. 343), NMNH/C143 (Arth. 344), NMNH/C144 (Arth. 345), NMNH/C145 (Arth. 346), NMNH/C146 (Arth. 347), NMNH/C147 (Arth. 348), NMNH/C148 (Arth. 349), NMNH/C149 (Arth. 350), NMNH/C150 (Arth. 351), NMNH/C151 (Arth. 352), NMNH/C152 (Arth. 358), NMNH/C153 (Arth. 359), NMNH/C154 (Arth. 360), NMNH/C155 (Arth. 361), NMNH/C156 (Arth. 362), NMNH/C157 (Arth. 363), NMNH/C158 (Arth. 364), NMNH/C159 (Arth. 365), NMNH/C160 (Arth. 366), NMNH/C161 (Arth. 367), NMNH/C162 (Arth. 368), NMNH/C163 (Arth. 369), NMNH/C164 (Arth. 370), NMNH/C165 (Arth. 371), NMNH/C166 (Arth. 372), NMNH/C167 (Arth. 373), NMNH/C168 (Arth. 374), NMNH/C169 (Arth. 375), NMNH/C170 (Arth. 376), NMNH/C171 (Arth. 377), NMNH/C172 (Arth. 378), NMNH/C173 (Arth. 379), NMNH/C174 (Arth. 389), NMNH/C175 (Arth. 390), NMNH/C176 (Arth. 391), NMNH/C177 (Arth. 392), NMNH/C178 (Arth. 393), NMNH/C179 (Arth. 394), NMNH/C180 (Arth. 395), NMNH/C181 (Arth. 396), NMNH/C182 (Arth. 397), NMNH/C183 (Arth. 410), NMNH/C184 (Arth. 411), NMNH/C185 (Arth. 412), NMNH/C186 (Arth. 413), NMNH/C187 (Arth. 414), NMNH/C188 (Arth. 415), NMNH/C189 (Arth. 416), NMNH/C190 (Arth. 417), NMNH/C191 (Arth. 418), NMNH/C192 (Arth. 419), NMNH/C193 (Arth. 420), NMNH/C194 (Arth. 421), NMNH/C195 (Arth. 422), NMNH/C196 (Arth. 423), NMNH/C197 (Arth. 424), NMNH/C198 (Arth. 425), NMNH/C199 (Arth. 428), NMNH/C200 (Arth. 434), NMNH/C201 (Arth. 435), NMNH/C202 (Arth. 436), NMNH/C203 (Arth. 437), NMNH/C204 (Arth. 438), NMNH/C205 (Arth. 441), NMNH/C206 (Arth. 444), NMNH/C207 (Arth. 445), NMNH/C208 (Arth. 446), NMNH/C209 (Arth. 447), NMNH/C210 (Arth. 448), NMNH/C211 (Arth. 449), NMNH/C212 (Arth. 450), NMNH/C213 (Arth. 451), NMNH/C214 (Arth. 452), NMNH/C215 (Arth. 453), NMNH/C216 (Arth. 479), NMNH/C217 (Arth. 480), NMNH/C218 (Arth. 481), NMNH/C219 (Arth. 482), NMNH/C220 (Arth. 497), NMNH/C221 (Arth. 498), NMNH/C222 (Arth. 503), NMNH/C223 (Arth. 504), NMNH/C224 (Arth. 505), NMNH/C225 (Arth. 506), NMNH/C226 (Arth. 512), NMNH/C227 (Arth. 513), NMNH/C228 (Arth. 514), NMNH/C229 (Arth. 515), NMNH/C230 (Arth. 516), NMNH/C231 (Arth. 572), NMNH/C232 (Arth. 573), NMNH/C233 (Arth. 574), NMNH/C234 (Arth. 575), NMNH/C235 (Arth. 579), NMNH/C236 (Arth. 598), NMNH/C237 (Arth. 599), NMNH/C238 (Arth. 603), NMNH/C239 (Arth. 604), NMNH/C240 (Arth. 605), NMNH/C241 (Arth. 606), NMNH/C242 (Arth. 607), NMNH/C243 (Arth. 608), NMNH/C244 (Arth. 610), NMNH/C245 (Arth. 611), NMNH/C246 (Arth. 614), NMNH/C247 (Arth. 615), NMNH/C248 (Arth. 616), NMNH/C249 (Arth. 622), NMNH/C250 (Arth. 623), NMNH/C251 (Arth. 624), NMNH/C252 (Arth. 625), NMNH/C253 (Arth. 628) and NMNH/C254 (Arth. 639); carapaces from the area between Għajn Żnuber and Golden Bay. NMNH/C255 (Arth. 398) cheliped and NMNH/C256 (Arth. 488) propodus from the area between Għajn Żnuber and Golden Bay.

NMNH/C257 (Arth. 244), NMNH/C258 (Arth. 555), NMNH/C259 (Arth. 556), NMNH/C260 (Arth. 557), NMNH/C261 (Arth. 558), NMNH/C262 (Arth. 559), NMNH/C263 (Arth. 560), NMNH/C264 (Arth. 561) (2 fragments), NMNH/C265 (Arth. 562) (carpus and propodus); carapaces from Fomm ir-Riħ.

NMNH/C266 (Arth. 595) carapace from Rdum il-Vigarju, l/o. Baħrija.

NMNH/C267 (Arth. 259), NMNH/C268 (Arth. 260), NMNH/C269 (Arth. 261), NMNH/C270 (Arth. 262), NMNH/C271 (Arth. 263), NMNH/C272 (Arth. 264), NMNH/C273

(Arth. 294), NMNH/C274 (Arth. 295), NMNH/C275 (Arth. 296), NMNH/C276 (Arth. 297); carapaces from Il-Qattara, l/o. Dingli.

Remarks. *Daira speciosa* (Reuss, 1871) is the most frequently occuring decapod associated with corals from the Maltese assemblage. A large portion of the carapaces examined are preserved as internal moulds; nonetheless, some (e.g. NMNH/C257 (Arth. 244), NMNH/C175 (Arth. 390) have their original carapace material preserved, which is characterized by numerous large dorsal tubercles arranged in rows. One specimen NMNH/C255 (Arth. 398) represents a left cheliped with the external surface of the merus, carpus, and propodus exposed; the palm of the propodus is ornate with large rows of tubercles arranged longitudinally.

Daira speciosa has been recorded from the Lower? and Middle Miocene of Hungary (Reuss 1871; Bittner 1877; Lőrenthey and Beurlen 1929; Müller 1984*a*), Austria (Müller 1998), Spain (Müller 1984*b*; Solé and Via Boada 1989), Algeria (Saint Martin and Müller 1988), Balearics (Garcia Socias 1990), Poland (Förster 1979*a*; Müller 1996; Górka 2002) and Ukraine (Radwański *et al.* 2006).

Phlyctenodes irregularis Ristori, 1896, from the Middle Miocene of northern Italy, described from a single section of carapace, has been recently synonymized with *Daira speciosa* (De Angeli and Garassino, 2006).

The genus *Daira* is represented by *D. perlata* (Herbst, 1790), Recent Indo-West Pacific, and fossil from the Miocene of Japan and Pleistocene of Fiji Islands (Karasawa 1993; Rathbun 1945) and *D. americana* Stimpson, 1860, Recent of southern California to Ecuador (Rathbun 1930).

Other fossil species besides *Daira speciosa* are: *D. eocenica* (Lőrenthey, 1898) from the Upper Eocene of Hungary; *D. sicula* (Di Salvo, 1933) from the Lower and Upper Eocene of Veneto and Sicily regions (Italy); *D. salebrosa* Beschin *et al.*, 2002, and *D. coronata* Beschin *et al.*, 2005, from the Middle Eocene of Northeast Italy; *D. depressa* (A. Milne Edwards, 1865) from the Lower Oligocene of Northeast Italy, and *D. vulgaris* Portell and Collins, 2004 from the Lower Miocene of Jamaica (Lőrenthey 1898; Lőrenthey and Beurlen 1929; Airaghi 1905; Di Salvo 1933; Beschin *et al.* 2001, 2002, 2005; A. Milne Edwards 1865; Portell and Collins 2004).

Superfamily PORTUNOIDEA Rafinesque, 1815
Family CARCINIDAE MacLeay, 1838
Subfamily CARCININAE MacLeay, 1838

Genus XAIVA MacLeay, 1838

Type species. *Xaiva pulchella* MacLeay, 1838, by original designation, monotypy.

Xaiva bachmayeri Müller, 1984
Text-figure 8D

1984*a* ‘*Xaiva*’ *bachmayeri* Müller, p. 85, pl. 72, figs 5–7, ?fig. 8.
2008 *Xaiva bachmayeri* Müller; Karasawa *et al.*, pp. 99, 112, 125.

Material. NMNH/C277 (Arth. 357), NMNH/C278 (Arth. 466); right chelipedes from the area between Għajn Żnuber and Golden Bay.

Description. The merus is short and suboval, missing the cuticle on the outer margin; the propodus has a palm which is longer than high, with an inner margin which is almost straight; the outer margin is damaged; the external surface is inflated and smooth, with some weak punctuations; the fixed finger is long and subtriangular in shape, having a sulcus on the inner margin and four short teeth on the occlusal margin.

Remarks. Both chelae have an outer margin which is damaged; nonetheless, they exhibit strict affinity with the chela illustrated by Müller (1984*a*, pl. LXXII, fig. 8) from the Miocene of Hungary, attributed to *Xaiva bachmayeri* Müller, 1984.

Superfamily CARPILIOIDEA Ortmann, 1893
Family CARPILIIDAE Ortmann, 1893

Genus CARPILIUS Desmarest, 1823

Type species. *Cancer maculatus* Linnaeus, 1758, by original designation.

Carpilius sp.
Text-figure 8E, F

Material. NMNH/C279 (Arth. 380); incomplete carapace from the area between Għajn Żnuber and Golden Bay.

Description. Carapace convex, wider than long; frontal margin is not preserved; orbits small and roundish; anterolateral margin convex and smooth; posterolateral margin very convergent; regions nondefined; dorsal surface smooth.

Remarks. A complete description of the only specimen from Malta is not possible as the eroded carapace is missing the right and frontal part; nontheless, the outline and observed characteristics exhibit an affinity with representatives of *Carpilius* Leach, 1823, a genus represented by three extant species: *C. convexus* (Forskål, 1775), *C. corallinus* (Herbst, 1801) and *C. maculatus* (Linnaeus, 1758) and by three fossil species: *C. petreus* Beschin *et al.*, 2007 from the Ypresian of Italy (Vicenza), *C. lwangi* Hu & Tao, 2000 from the Pleistocene of Taiwan. *Carpilius antiquus* Glaessner, 1928, from the Badenian (Middle Miocene) of Hungary, Baden-Rauchstallbrunngraben (Niederösterreich, Austria), and from Grobie (Polond) (Müller 1984*a*, 1996, 1998), has been assigned to the genus *Eocarpilius* Blow and Manning, 1996 (Feldmann *et al.* 1998).

Superfamily PILUMNOIDEA Samouelle, 1819
Family PILUMNIDAE Samouelle, 1819

Genus PILUMNUS Leach, 1816

Type species. *Cancer hirtellus* Linnaeus, 1761, by original designation, monotypy.

Known fossil species. *Pilumnus cucaoensis* Feldmann *et al.*, 2005; *P. fookimensis* Collins *et al.*, 2003; *P. hirtellus* var. *villosa* Risso, 1826; *P. mediterraneus* (Lőrenthey, 1898); *P. olivellai* Müller, 1993; *P. subequus* Rathbun, 1919 (claws only); fossil and recent species: *P.* aff. *P. spinossimus* Rathbun, 1898; *P. villosissimus* found (Rafinesque, 1814); *P. hirtellus* (Linnaeus, 1761); *P. sayi* Rathbun, 1897; *P.* aff. *P. pannosus* Rathbun, 1898.

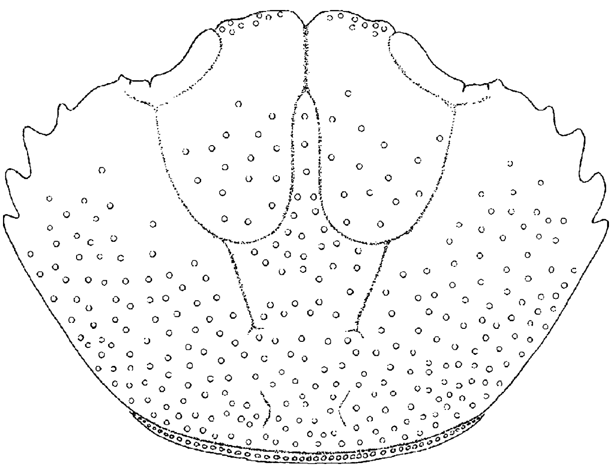
Pilumnus scaber sp. nov.
Text-figures 6B, C, 9

Derivation of name. *scaber –bra –brum* (Lat.) referring to the rough ornamentation of the dorsal surface.

Holotype. NMNH/C280 (Arth. 567) (Text-fig. 6B, C)

Type locality. Area between Għajn Żnuber and Golden Bay.

Material. NMNH/C280 (Arth. 567); carapace from the area between Għajn Żnuber and Golden Bay.



TEXT-FIG. 9. *Pilumnus scaber* sp. nov., reconstruction of carapace.

Diagnosis. Carapace subhexagonal, convex, wider than long, front sinuous, tetra-lobate, and with median incision; orbits separated from the inner orbital angle by notches, and with two short supraorbital fissures; anterolateral margin short and with four spines, long and conical 2–4 anterolateral spines; regions relatively well defined and adorned by spinose tubercles.

Description. Carapace subhexagonal, convex, wider than longer (ratio length/maximum width = 0.75). Orbito-frontal margin extends to about two-thirds of maximum width; entire frontal margin sinuous, tetra-lobate, the two inner ones are wide, the outers rudimentary, separated from the inner orbital angle by notches; frontal margin with granulations and a median incision; orbits ovoid; supraorbital margin with two short fissures, distinct from remaining frontal margin and slightly elevated; postorbital tooth slightly extended. Antero-lateral margins divergent and convex; margin immediately behind orbits is curved and smooth, followed by four spines (excluding the extraorbital spine), the first spines are small and the other three, larger and conical in form. The postero-lateral margins are convergent and longer than the preceeding. The posterior margin is relatively wide, slightly convex and with a granulated carina. The regions are not much defined; the frontal region is wide and curved downwards, with a median furrow; weak protuberances are noticeable on the epigastric lobes; the protogastric regions are wide and well defined; the meso-and metagastric regions form one lobe, pentagonal in shape. The anterior part of the mesogastric region is narrow and elongated between the protogastric regions. The cardiac region is relatively wide and is restricted posteriorly and is not defined by branchio-cardiac grooves. The hepatic region is not defined posteriorly by the cervical groove; the branchial regions are wide and with a slightly convex surface. The dorsal surface is ornate with numerous spinose tubercles directed anteriorally, most frequent on the median and posterior parts.

Remarks. The examined carapace from Malta has morphological characteristics attributable to both the Xanthidae and the Pilumnidae. Lack of the ventral surface and the poor preservation of the orbit-frontal margin, render difficult the precise identification of this crab. Nonetheless, the Maltese specimen shows strict affinity with *Pilumnus mediterraneus* (Lőrenthey, 1897) from the Middle Miocene (Badenian) of Hungary. This species has been figured by Müller (1984*a*) with four well-preserved carapaces originating from the type locality. *Pilumnus scaber* sp. nov. may be distinguished from *P. mediterraneus* from the spines present on the anterolateral margins which are smaller and from the more numerous spinose tubercles on the dorsal surface.

Other Miocene species attributed to *Pilumnus* are *P. olivellai* Müller, 1993 from the Langhian of Catalonia (Spain), which may be distinguished from the frontal lobes, which are more elongated and from the short anterolateral margin with three subequal teeth; and *Pilumnus* sp., described, but not figured, on the remains of a cheliped from the Helvetian–Tortonian of Austria (Glaessner 1928, 1929).

Superfamily XANTHOIDEA MacLeay, 1838
Family PANOPEIDAE Ortmann, 1893

Genus PANOPEUS H. Milne Edwards, 1834

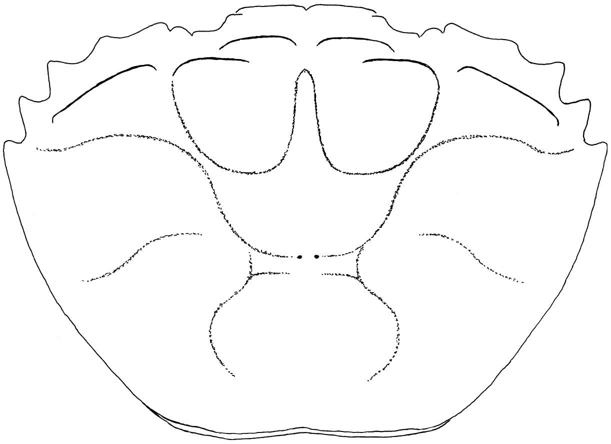
Type species. Panopeus herbstii H. Milne Edwards, 1834, subsequent designation by ICZN.

Known fossil species. Panopeus antepurpureus (Rathbun, 1918) (claw only); *P. baldwini* (Kooser and Orr, 1973); *P. bessmanni* Collins and Jakobsen, 2003; *P. bolcensis* Secretan, 1975; *P. capanemaensis* Martins Neto, 2001; *P. estellensis* Rathbun, 1935 (claw only); *P. granulineatus* Müller and Collins, 1991; *P. incisus* Beschin *et al*., 2007; *P. jerseyensis* Roberts, 1956 (claw only); *P. lauensis* Rathbun, 1945; *P. nanus* Portell and Collins, 2004; *P. olearis* (Rathbun, 1926); *P. piramidensis* Casadío *et al*., 2005; *P. prosakrolophos* Schweitzer, 2000; *P. soledadensis* (Rathbun, 1926); *P. torus* Schweitzer, 2000; *P. tridentatus* Rathbun, 1918 (claw only); *P. veintensis* Vega *et al*., 2008; *P. viai* Müller, 1993; *P. wronai* Müller, 1984; fossil and recent species: *P. herbstii* H. Milne Edwards, 1834 (claw only); and *P. rugosus* A. Milne Edwards, 1880 (claw only).

Panopeus muelleri sp. nov.
Text-figures 6D–F, 10

Derivation of name. Dedicated to Pál Müller for his important contribution to the study of European Tertiary decapod crustaceans.

Holotype. NMNH/C283 (Arth. 470) (Text-fig 6D).



TEXT-FIG. 10. *Panopeus muelleri* sp. nov., reconstruction of carapace.

Paratypes. NMNH/C281 (Arth. 270), NMNH/C298 (Arth. 459), NMNH/C284 (Arth. 566), NMNH/C285 (Arth. 578).

Type locality. Area between Għajn Żnuber and Golden Bay.

Material. NMNH/C281 (Arth. 270), NMNH/C298 (Arth. 459), NMNH/C283 (Arth. 470), NMNH/C284 (Arth. 566), NMNH/C285 (Arth. 578); carapaces from the area between Għajn Żnuber and Golden Bay.

Diagnosis. Carapace subhexagonal, slightly convex longitudinally, wider than long, front is straight, cut by a median incision; orbits small; supraorbital margin with two fissures; anterolateral margin short and with four spines; regions well defined by weak furrows and with a fine pitted ornamentation; epigastric, protogastric, hepatic and epibranchial regions with weak transversal ridges.

Description. Carapace moderately convex longitudinally, subhexagonal in outline, wider than long. The orbito-frontal margin occupies more than half the total width of the carapace, the front in line with anterolateral curvature of the carapace, is straight, cut by a median incision; the orbits are small; the supraorbital margin with two fissures; no spine is present at outer orbital angle. The anterolateral margin is convex and with four spines, equidistant from one another, the first spine is very short and the other three spines are more developed and triangular in form. The posterolateral margin is convergent and longer than the preceeding. The posterior margin is rather wide. The regions are well defined; the epigastric lobes are wide and exhibit two well-elevated transversal ridges; other transversal ridges are present on the protogastric, hepatic and epibranchial regions. The protogastric regions are wide and well defined; the mesogastric region is wide and well defined posteriorly by a curved furrow and with two small gastric depressions; the anterior mesogastric process is long and narrow and extends to the bases of the epigastric lobes; the metagastric region is wide and short and exhibits on the sides an epibranchial lobe; the cardiac region is not well defined by branchio-cardiac grooves and is very wide and slightly elevated. The hepatic regions are poorly defined; the branchial regions are wide; the epibranchial lobe is well defined. The dorsal surface is characterized by a dense and homogeneous ornamentation of small depressions that gives a pitted appearance to this species.

Remarks. Panopeus H. Milne Edwards, 1834 is represented by 17 extant species (Ng *et al.* 2008). The family Panopeidae and the species of the genus *Panopeus* were discussed by Schweitzer (2000).

The examined specimens exhibit strict affinity with *Panopeus wronai* Müller, 1984 from the Badenian (Middle Miocene) of Hungary, Poland and Austria (Müller 1984a, 1998, 1996) in having four pairs of transverse ridges and the presence of fine tubercles on the frontal parts of the epigastric, protogastric, hepatic and epibranchial regions.

Panopeus muelleri sp. nov. may be distinguished from the Hungarian species by the different arrangement of the spines on the anterolateral margins; by the absence of tubercles on the slightly elevated ridges and by means of the dorsal ornamentation that is characterized by a dense arrangement of punctulations which give this new species a rough appearance.

Panopeus viai Müller, 1993 from the Miocene (Langhian) of Catalonia (Spain) has a carapace, which is rectangular in outline, a very wide fronto-orbital margin and a mesogastric lobe that is delimited from the protogastric one by deep furrows.

Family XANTHIDAE MacLeay, 1838

Genus XANTHO Leach, 1814

Type species. Cancer incisus Leach, 1804, by original designation, monotypy.

Xantho moldavicus (Yanakevich, 1977)

Text-figure 8G–K

1928 *Titanocarcinus vulgaris* Glaessner, p. 185, 189, pl. 3, fig. 11 (*pars*).
1953 *Titanocarcinus vulgaris* Glaessner; Bachmayer, p. 254, pl. 4, figs 1–9, pl. 5, figs 1–2.
1974*a* *Xantho* cf. *incisus* Leach; Müller, p. 123, pl. 3, figs 1, 2.
1974*b* *Xantho* cf. *incisus* n. ssp? Müller, p. 280.
1975 *Xantho* cf. *incisus* Leach; Müller, p. 510.
1977 *Medaeus moldavicus* Yanakevich, p. 80, pl. 10, fig. 4.
1979*a* *Xantho* cf. *vulgaris* (Glaessner); Förster, p. 100, pl. 3, figs 1–3, pl. 4, figs 1–4.
1979*b* *Xantho* cf. *vulgaris* (Glaessner); Förster, p. 263, text-fig. 11, pl. 3, figs 1–3, pl. 4, figs 1–4.
1979*a* *Xantho* cf. *incisus* Leach; Müller, p. 274, pl. 20, figs 1–5.
1984*a* *Xantho moldavicus* (Yanakevich); Müller, p. 92, pl. 85, figs 5–8, pl. 86, figs 1–5, pl. 87, fig. 1.
1989 *Xantho moldavicus* (Yanakevich); Solé and Via Boada, p. 35.
1991 *Xantho moldavicus* (Yanakevich); Marras and Ventura, p. 110, pl. 2, fig. 2.
1996 *Xantho moldavicus* (Yanakevich); Müller, p. 11, pl. 2, fig. 6.
1998 *Xantho moldavicus* (Yanakevich); Müller, p. 34.
2006 *Xantho moldavicus* (Yanakevich); Radwański *et al.*, p. 96, pl. 2, figs 5–6.

Material. NMNH/C286 (Arth. 356), NMNH/C287 (Arth. 403), NMNH/C288 (Arth. 458), NMNH/C289 (Arth. 461), NMNH/C290 (Arth. 462), NMNH/C291 (Arth. 486), NMNH/C292 (Arth. 487), NMNH/C293 (Arth. 520), NMNH/C294 (Arth. 596), NMNH/C295 (Arth. 609), NMNH/C296 (Arth. 617); carapaces from the area between Għajn Żnuber and Golden Bay.

NMNH/C297 (Arth. 508); carapace from Ras in-Niexfa.

Remarks. The material examined exhibits strict affinity with *Xantho moldavicus* (Yanakevich) both in the elongated form of the carapace and also in the arrangement of the dorsal regions. This species has a wide distribution in the European Miocene and has been recorded from Hungary, Poland, Ukraine, Germany, Austria and Italy (Sardegnia). Some carapaces from the Miocene of Catalonia (Spain) have been attributed to *Xantho* aff. *moldavicus* (Müller, 1996) and a propodus and dactylus from the Miocene of Oran (Algeria) have been attributed to *Xantho* cf. *moldavicus* (Saint Martin and Müller 1988; Moissette and Müller 1990).

DISCUSSION

Biogeographical interchange

Interchange of oceanic water and hence of biota is evidenced in the newly discovered reef decapod assemblage of Malta, where as many as seven species which have been recorded associated with coral structures in the Central Paratethys (Müller 1984*a*, 1996; Górka 2002; Radwański *et al.* 2006), have also been found in Malta. A further three genera, *Carpilius*, *Pilumnus* and *Panopeus* have been found associated with corals, both in the Central Paratethys and Malta. Six genera: *Callianassa*, *Pagurus*, *Paguristes*, *Maja*, *Micippa*, and *Xaiva*, also recorded from the Badenian but not associated with corals, have been recorded with corals in Malta (Text-fig. 11).

Until the Upper Burdigalian, the Mediterranean Sea acted as an inter-connecting seaway between the Indo-Pacific and Atlantic Oceans, reaching a maximum connection with the Indian Ocean during the Upper Oligocene (Upper Chattian) and Lower Miocene (Lower Burdigalian) (Rögl 1998). Intermittent seaways and landbridges between the Paratethys and the Mediterranean have created a complex pattern of biogeographical affinities between both palaeobiogeographical regions (Harzhauser and Piller 2007).

Connections between the Mediterranean and the Paratethys, in the Miocene, have been proposed for the Aquitanian/upper Egerian (23.8–30.5 Ma, Rögl 1998), (25–21 Ma, Harzhauser and Piller 2007) and the Lower Burdigalian/Eggenburgian (20.5–18.8 Ma, Rögl 1998), (21–18 Ma, Harzhauser and Piller 2007), with a broard connection between the Indian Ocean and both the Mediterranean and Paratethys Seas. In the Middle Burdigalian/Ottnangian (18.8–17.3 Ma, Rögl 1998), a connection

MIDDLE MIOCENE	BADENIAN (LANGHIAN)					Messinian
	?	LOWER		MIDDLE	UPPER	
	UKRAINE	POLAND	HUNGARY	AUSTRIA	HUNGARY	
	Maksymivka	Grobie, Holy Cross Mountains	Börzsöny & Pilis Mountains	Gross-Höflein	Budapest & Diósd	MALTA
Galathea weinfurteri	x	x				x
Petrolisthes haydni	x	x	x	x		
Petrolisthes magnus	x				x	x
Pisidia aff. *viai*		x				
Pylopagurus corallinus		x				
Dardanus hungaricus		x	x		x	x
Dardanus arrosor			x			
Dardanus substriatiformis				x	x	
Dromia neogenica			x		x	x
Kromtitis koberi		x	x	x		
Dynomene emiliae		x	x	x		
Calappa praelata		x				x
Calappa heberti					x	
Daira speciosa	x	x	x	x	x	x
Charybdis mathiasi			x		x	
Liocarcinus sp.		x				
Rakosia rectifrons		x				
Rakosia carupoides				x	x	
Carupa cf. tenuipes			x			
Eocarpilius antiquus		x	x	?x	x	x *
Glabropilumnus fossatus		x				
Maldivia plana		x				
Trapezia glaessneri			x			
Actaea turcocampestris			x	?x		
Chlorodiella mediterranea		x	x	x	x	
Chlorodiella mediterranea tetenyensis			x	x	x	
Chlorodiella cf. mediterranea tetenyensis	x					
Chlorodiella juglans					x	
Haydnella steiningeri		x	x	x		
Panopeus wronai		x	x	x	x	
Pilodius ? sp. nov.?		x				
Pilodius vulgaris			x	x		
Xantho moldavicus	x		x	x	x	x
Pilumnus mediterraneus	x		x	?x	x	
Pilumnopeus paratethyensis					x	

x * = ?*Carpilius* sp.

TEXT-FIG. 11. Badenian (Langhian) decapod species recorded from the Paratethys associated with coral structures, compared with species found associated with the Messinian patch-reefs of Malta.

in the Central Paratethys, between the western Mediterranean via the Alpine Foredeep into the Rhône Basin, existed throughout most of the Ottnangian. By the Upper Ottnangian, biogeographical interchange between the Paratethys and the Mediterranea Sea ceased (Harzhauser and Piller 2007). In the upper Burdigalian/Karpatian (17.3–16.4 Ma, Rögl 1998), (17–16.3 Ma, Harzhauser and Piller 2007) and the Lower Badenian (16.4-*c.* 15 Ma), a seaway extending from the Venetian Basin along the 'Trans-Tethyan-Trench-Corridor', linked the Mediterranean with the Central Paratethys. Another possible connection with the Mediterranean may have also existed along western Anatolia, in a tectonically unstable zone with the Aegean plate. This broad connection with the Mediterranean via the Slovenian 'Trans-Tethyan-Trench-Corridor', coupled with a general warming trend, favoured a northward migration as evidenced by warm-water indicators such as *Globigerinoides* or *Globorotalia* together with a thermophilic mollusc fauna (Harzhauser and Piller 2007). The 'Trans-Tethyan-Trench-Corridor' connection was however closed by the Upper Badenian/Lower Serravallian times (14-*c.* 13 Ma) and a salinity decrease in the Paratethys, caused the extinction of euhaline elements and establishment of the highly endemic Sarmatian fauna (Rögl 1998).

Migration and exchange of shallow-water faunas in the Upper Oligocene and Lower Miocene followed a primarily westerly direction, with warm tropical waters reaching into the Paratethys through a broad marine seaway between the Indian Ocean and the Mediterranean Iranian and African-Arabian plates (Rögl 1998). Nevertheless, it cannot be excluded that some forms may have risen in the Mediterranean or the Paratethys and the direction of migration was an opposite one (Müller 1984*a*). This dispersal was largely controlled by prevailing tropical–subtropical climatic and ecological conditions, influenced by tectonic and eustatic factors.

A study assessing climatic changes in the Lower to Middle Miocene of the Central Paratethys, based on echinoderm diversity, shows that the overwhelming part of the Central Paratethys echinoid species were immigrants from the Mediterranean area. Migration of species occurred in three distinct waves – a large influx into the Paratethys during the Upper Eggenburgian, a minor one in the Karpatian and largest in the Lower Badenian. An analysis of echinoderm composition and diversity of the Central Paratethys indicates a shift from warm temperate conditions prevailing during the Upper Eggenburgian, to a tropical climate in the Badenian. The echinoid fauna of the Neogene Central Paratethys has also few endemic species and is essentially of Mediterranean origin because many species already occured in the Mediterranean before making their appearance in the Paratethys (Kroh 2007).

Another similar study focusing on gastropods and foraminifera of the Western Paratethys shows similar migration patterns. In the Eggenburgian, immigrations into the Paratethys brought elements of the Proto-Mediterranean-Atlantic Region, such as the pectinid *Flexopecten palmatus* (Lamarck) and the echinoid *Arbacia*. The Meditteranean element of Western Paratethys faunas became predominant during times of high immigration influxes of the Upper–Lower Miocene Karpation or the Lower-Middle Badenian. Karpatian gastropods exhibit about 70–75 per cent typical inhabitants of the Proto-Mediterranean-Atlantic region. Another huge influx of gastropod species occurred in the Lower Badenian (=Langhian), with about 500 new occurences, where 270 gastropod species recorded in the Karpatian, increase to more than 770 species in the Badenian. Similarly, but in less extensive numbers, foraminifers increase from 147 species in the Karpatian to 215 species in the Lower Badenian. An expansion of the Tropical zone during the Burdigalian/Langhian climatic optimum, coupled with a relative sea-level rise in the Langhian which caused considerable transgression also in the Paratethys, contributed to the takeover of Mediterranean taxa in the Paratethys (Harzhauser and Piller 2007).

Corals and reef structures

Reefs in the southern parts of the Lower Badenian Paratethys were fairly diverse, and in the Styrian Basin, *Montastrea*, *Tarbellastraea*, *Leptoseris* and *Porites* were recorded. However, a change in reef structure occured in the Upper Badenian, and complex reefs are no longer recorded. This is also evidenced in the Vienna and the Styrian Basins of the southern Paratethys. Instead, coral carpets that developed along detached islands are dominated by *Porites*, *Tarbellastraea*, *Caulastrea*, *Acanthastrea* and *Stylocora*. A climatic deterioration triggered by the global mid-Miocene Climate Transition is seemingly attributed to this shift in reef structures (Harzhauser and Piller 2007). The decrease in time in the number of coral genera represented in the Central Paratethys is also indicative of perturbations in oceanic salinity in the Upper Badenian (Müller 1984*a*).

However, conditions favouring the establishment of reef-building in the Upper Miocene prevailed in a period spanning from the Upper Tortonian to the Messinian and is manifest in all the Mediterranean region where reefal buildups have been recorded from Spain, the Balearic Isles, Italy, Sicily, Malta, Tunesia, Crete, Cyprus, Israel and Turkey. This exceptional activity of reef building was the result of a conjunction of several climatic, tectonic and eustatic factors which favoured the establishment of areas where shallow, warm seas encouraged flourishing and profusion of coral-reef construction. The Middle Miocene cooling phase that led to the onset of permanent glaciations in Antartica, coupled with biogeographical isolation and the gradual northern shift of the Mediterranean region outside the tropical belt, may be considered as the principal factors that ultimately led to the almost complete disappearance of zooxanthellate corals and coral reefs from the Mediterranean after the end of the Miocene (Bosellini 2006).

The hermatypic corals *Porites* and *Tarbellastraea* constituted an important element in the reef-building process of Neogene times and have been identified in most Badenian and Upper Miocene European and Northern African localities, sometimes with other less-represented coral species. These two coral genera must have been best adapted to prevailing environmental and ecological conditions, perhaps more tolerant of fluctuations in salinity, than other species of corals. This is also evidenced in the coral-reef sites of the Badenian where four genera are recorded from the Lower and Middle Badenian while only two, *Porites* and *Tarbellastraea*, are identified from the Upper Badenian (Müller 1984*a*). Extant faviids are also known, under severe competition, to maintain their position within pioneer modern reef communities by aggressive displacement through digestive dominance interactions. Such a strategy could have been equally effective in Miocene reefs (Pedley 1996).

The same is the case for Malta where the same two aforementioned coral genera are predominant, associated with other corals that are much rarer. The genera *Siderastraea* and *Acanthastraea* are also reported from the Upper Coralline Limestone Formation of Malta, while others including *Montastraea*, *Diploastraea*, *Acropora* and *Favites* constitute probable misidentifications. *Montastraea* is absent in the Mediterranean Miocene, and previous records from Malta (Pedley *et al.* 1976; Bosence and Pedley 1979, 1982) may be attributed to *Tarbellastraea*. Also, *Diploastraea* and *Acropora* do not occur in the coral fauna of other Tortonian–Messinian reefs of the Mediterranean region, and it cannot be excluded that certain forms attributed to *Favites* are most probably *Acanthastraea* (Saint Martin and Andre 1992). A recent review (Gatt 2006) of Maltese fossils including corals could not confirm the occurrence of *Favites, Montastraea* and *Diploastraea* from the Maltese Islands and features these genera as having been reported by Pedley *et al.* (1976). The presence in Malta of *Acanthastraea* and *Siderastraea* is confirmed in this present work.

Similarly, the neighbouring central Mediterranean Mid-Miocene reefs of Sicily are composed of generally small structures with sparse frameworks and low coral diversity dominated by *Porites* and *Tarbellastraea* (less than five species, occasionally only one), but with other biota that may be diverse (Pedley 1996). Tortonian coral structures from the eastern Mediterranean island of Gavdos (South Greece) exhibit similar characteristics, in the sense that *Porites* and *Tarbellastraea* are most predominant and from a total of eleven species recorded, four belong to the former genus, while two to the latter. *Favites*, *Heliastraea* and *Thegioastraea* (=*Acanthastraea*) were also recorded. Compared with the Central Mediterranean, the number of coral species from this eastern locality seems to be higher and as much as eight different species are recorded from one single locality – Korfe, also on Gavdos (Tsaparas and Marcopoulou-Diacantoni 2005).

The Badenian coral buildups from Poland (Górka 2002) and Ukraine (Radwański *et al.* 2006) exhibit a strong affinity with the newly discovered site from Malta. Most of the fauna, besides decapods, recorded from the coral buildups of these Polish and Ukranian sites have also been found within the patch-reefs of Malta. The rock-boring bivalves *Lithophaga* and *Jouannetia* thrived within the corals, associated with other molluscs including *Chlamys*, *Glycymeris*, *Spondylus* and *Conus*. Cidaroid and brissid echinoids are also represented from both Ukraine and Malta. The taphonomy, with decapod and other material accumulating within burrows and crevices between the patch-reefs, is again similar for both Maltese and Ukranian sites.

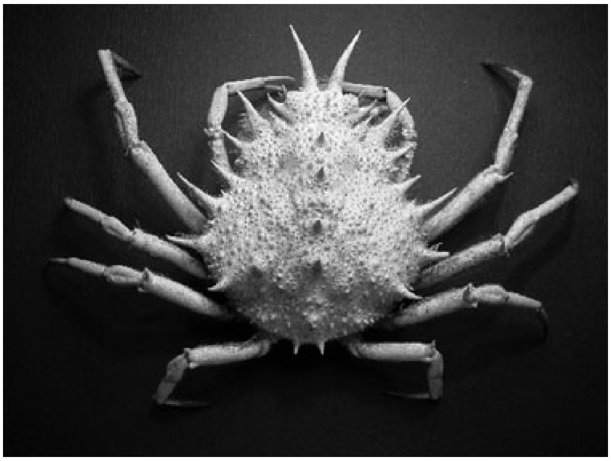
Decapoda – palaeoecology and extant ecology

A common element is the predominant decapod species *Daira speciosa*. Being reported from all Badenian and Upper Miocene sites, this species was probably the most successful and best adapted to life upon the coral reefs. *Daira speciosa* has been found to be the predominant species in Maksymivka, Ukraine, while *Daira vulgaris* has also been found as the most predominant and commonest of decapods recorded from the Lower Miocene Montpelier Formation, White Limestone Group of Jamaica. *Daira speciosa* was found to be the predominant species in Malta.

From an ecological point of view, the extant species *Daira perlata* confirms further the adaptability to life on coral reefs. This species has been recorded from French Polynesia as inhabiting the reef crest where it is able to withstand strong currents and wave surges because of its robust pereiopods that enable this decapod to anchor itself firmly to the reef's head. It seeks refuge in cavities within the reef where it lives (Poupin 1994). *Daira perlata* has also been recorded from the barrier-reef front of Tiahura, French Polynesia, where it is the dominant species along with *Eupilumnus globosus* and *Paraxanthias notatus* (Monteforte 1987).

The dorsal carapace ornamentation of *Daira speciosa* may have also served as an adaptation to life on coral reefs and may have afforded this species a kind of camouflage. A striking similarity has been observed in *Daira* carapace material collected in Malta, with fossilized corallites of *Tarbellastraea*.

Most of the genera recorded associated with corals from the Messinian (Keinel *et al.*, 1995) of Malta are still extant in the Mediterranean and most have also been recorded from Maltese waters.



TEXT-FIG. 12. *Maja goltziana* D'Oliveira (extant) female, fished by net from the Malta/Gozo Channel.

Research into these extant species, in connection with this present study, has led to the discovery of yet another species from the Maltese Islands. Two *Maja* species have to date been recorded from waters around Malta, *M. squinado* and *M. crispata* (Medlycott 1870; Gulia 1873; Micallef and Evans 1968; Aquilina 1969; Lanfranco 1979; Schembri and Lanfranco 1984). *Maja goltziana* D'Oliveira, 1888 is here (Text-fig. 12, female), being recorded for the first time from Malta, with four specimens, two male and two female, fished by net from the Malta-Gozo channel and donated to one of the present authors (MG), by Mr Harry Farrugia of Tarxien, Malta. Other works on Maltese extant decapods (Despott 1930; Števčić 1979; Borg 1995) do not mention *M. goltziana* from Maltese waters.

Micippa, *Daira*, and *Carpilius* are the only genera which have been found associated with the Messinian patch-reefs of Malta, which are no longer extant in the Mediterranean.

Extant *Micippa* are confined to the Indo-West-Pacific faunal province. The extant *Micippa thalia* that is similar to *Micippa hungarica* lives at depths of 20–100 m on sand or broken shell substrates (Müller 1984*a*).

Daira perlata is widely distributed throughout the Indo-West-Pacific, Eastern Africa, Red Sea, including Japan, Hawaii and French Polynesia (Poupin 1994), while *Daira americana* has a distribution from the west coast of middle America, from lower California to Ecuador (Rathbun 1930). *Daira perlata* has been reported from low intertidal, shallow subtidal regions associated with coral reefs (Davie 2002), from the reef crest (Poupin 1994) and the reef front (Monteforte 1987), whilst *Daira americana* is known from under rocks and in *Pocillopora* corals (Garth 1946).

Carpilius currently includes three widely distributed species that inhabit tropical coral reefs and adjacent waters (Wetzer *et al.* 2002). *Carpilius maculatus* has been reported from the Hawaiian Islands, the far western Pacific where it is widespread, the Indian Ocean and the Red Sea at depths of around 25.5–27.3 m (Hawaii). *Carpilius convexus* is found from Hawaii, the Indo-Pacific, Indian Ocean south to Mozambique and South Africa and the Red Sea, at depths ranging from 25.6 to 58.5 m (Hawaii), while *Carpilius corallinus* is widespread throughout the Caribbean, the Gulf of Mexico, and the tropical western Atlantic, with records from Bermuda, the Gulf of Mexico off Texas, the Bahamas and off Sao Paulo, Brazil, at depths ranging from 3 to 20.4 m (Caribbean) (Wetzer *et al.* 2002).

All the other genera that have been found in the Messinian sites of Malta and that are still extant in the Mediterranean occur at widely varying depths (Text-fig. 13). A collective ecological analysis of these extant Mediterranean Sea and Indo-Pacific genera, however, shows that, with the exception of some species, the majority may be essentially found in shallow waters to depths in the region of 70 m. Depth preference is also within proximity of the 10–25 m water-depths suggested (Pedley 1978; Bosence and Pedley *in* Bosence 1991) for the Messinian patch-reefs of Malta. The abundant presence of *Daira speciosa* remains, may however, suggest even shallower depths for the patch-reefs, on account of extant *Daira* species that inhabit very shallow waters to depths of about 10 m.

Based on the decapod ecology discussed above (see also Text-fig. 13), and the association and taphonomy of specimens retrieved in the field, the following ecology may be envisaged for the Maltese patch-reefs. *Daira speciosa*, as the dominant species occupied the more exposed areas on the crest and front of the patch-reef associated with *Dromia* and occasionally *Xantho*. These species may have sought shelter in crevices and sheltered areas within the reef. Specimens of *Daira*, *Dromia*, and *Xantho* have been found in close proximity to each other in the Malta sites. The rock-boring bivalves *Lithophaga* and *Jouannetia*, *Creusia* barnacles, along with other molluscs including *Haliotis* and cidaroid echinoids, would have also thrived on the more-exposed frontal areas of the patch-reefs.

Dardanus could have occurred on the reef outer slope, as can be found in the extant species *Dardanus gemmatus* from French Polynesia. *Galathea*, *Carpilius*, *Panopeus*, *Pilumnus* and *Xantho*, on the other hand, preferred the more sheltered areas on the inner facet of the patch-reef. *Callianassa*, *Calappa*, *Xaiva* and *Micippa* would have occurred on the reef flat in more mobile sandy and bioclastic sediments along with brissid echinoids. *Maja* could be found on both sheltered areas of the patch reef or on sandy substrates.

Carapaces of the new species *Herbstia melitensis* were found embedded in the coarse-grained intra-framework

Species	Depth range	Habitat
Callianassa subterranea	20–30 m; occasionally up to1500 m	
Callianassa acanthura	10 m	
Callianassa truncata	40–60 m	
Callianassa tyrrhena	very common in 1 m waters	
Callianassa candida	rare - 10 m	sandy substrates
Galathea strigosa	up to 40 m, occasionaly 600 m	rocky substrates
Galathea rufipes	no data	
Galathea faiali	rare up to 300 m	
Galathea squamifera	few metres up to 30–70 m	
Galathea machadoi	100–750 m	rocky bottom or on corals
Galathea nexa	25–170 m	on colonies of *Corallium rubrum*
Galathea dispersa	very common 10–200 m, occasional 500 m	
Galathea bolivari	very common at few metres depths	on *Posidonia*
Galathea intermedia	abundant at 30–40 m	
Galathea cenarroi	at few metres depth	
Pagurus alatus	common 40–50 m	
Pagurus excavatus	common, 100–200 m	
Pagurus excavatus var. *meticolosus*	40–50 m	
Pagurus prideaux	very common at 30–40 m	
Pagurus chevreuxi	up to 12 m	
Pagurus carneus	very rare between 100–1000 m	
Pagurus bernhardus	very common at litoral to 500 m	
Pagurus anachoretus	very common 6–10 m depth, sometimes at 100 m	on *Posidonia*
Pagurus cuanensis	very common 25–50 m	
Pagurus sculptimanus	very common up to 70 m	
Dardanus arrosor	very common at 20–50 m	
Dardanus calidus	very common at 20–40 m	
Paguristes eremita	very common at 20–40 m	rocky bottom
Paguristes syrtensis	10–15 m	
Dromia personata	few metres depth, up to 70–75 m, occasionally at 100 m	rocky substrates and caves
Calappa granulata	very common from 30–150 m and sometimes even to depths of 250 m	on sandy and muddy substrates
Xaiva biguttata	very rare within the intertidal zone	inhabits sandy substrates
Panopeus africanus	litoral depths	common in lagoons and estuaries
Herbstia condyliata	commonly up to depths of 50 m	rocky substrates
Maja squinado	sublitoral zone at few metres and up to 60–70 m	rocky substrates
Maja goltziana	very rare at 15–200 m	sandy bottom
Maja crispata (syn. *M. verrucosa*)	common in few metres depth up to 40 m	rocky substrates
Pilumnus spinifer	common in depths of up to 40–100 m	rocky bottoms and calcareous algae
Pilumnus villosissimus	common in depths of a few metres	rocky bottoms and calcareous algae
Pilumnus hirtellus	very common at depths of 15–20 m	rocky bottoms and calcareous algae
Pilumnus aestuarii	rare at few metres depth	*Posidonia* meadows
Xantho pilipes	few metres to 100 m	
Xantho poressa	very common at few metres depth	amongst stones or boulders
Xantho incisus	common in few metres depth up to 30–40 m, also may be found at 100 m	

TEXT-FIG. 13. Extant decapod species inhabiting the Mediterranean, their depth range and habitat preference (Falciai and Minervini 1995), whose genera are represented in the Messinian reefal decapod assemblage of Malta.

sediments, not so closely associated with the patch-corals, which could suggest that the species may have frequented rocks and rubble on the reef flat rather than the patch-reef itself. The only representative of the genus *Herbstia* in the Mediterranean, *H. condyliata*, is also known to inhabit rocky substrates (Falciai and Minervini 1995). Likewise, other members of this genus which do not occur in the Mediterranean are known to inhabit similar habitats. *Herbstia parvifrons* (distribution, Monterey, California to Baja California) is reported from low intertidal to depths of 73 m, living under rocks and in crevices, most commonly found in shallow subtidal areas where fairly large rocks rest on other rocks (Jensen 1995). *Herbstia camptacantha* (distribution throughout the Gulf of Panama), reported from subtidal to 61 m depths, also inhabits subtidal rocks and rubble (Kerstitch 1989).

The only specimen discovered of *Pilumnus scaber* sp. nov. was found associated with specimens of *Panopeus muelleri* sp. nov., while no other decapod species were discovered in association with the other new species, *Micippa annamariae*.

Analysing the number of Miocene decapod species recorded associated with corals, a decrease is evident for the circum-Mediterranean region when compared with species recorded with reefal structures from Badenian locations in Poland and Hungary (Lower Badenian – 18/19 species respectively); in Austria (Middle Badenian, 15 species) and from Hungary (Upper Badenian, 16 species). The number of Messinian species recorded from the circum-Mediterranean areas is comparatevely rather low i.e. nine species from Spain, six from Algeria, and two from Morocco. The Maltese site with 19 species identified and the possibility of additional genera being recorded due to as yet unidentified material, mostly representing chela and movable fingers, is so far the richest location in decapod species from locations of a Messinian age. Although this may be indicative of less favourable environmental conditions in Tortonian and Messinian times when compared with the Badenian, this reduction in the number of species may also be biased merely through sampling and collecting practices. The generally small size of reef-dwelling decapods adds further difficulty to the discovery of additional taxa.

However, as in the case of the Maltese locality, where the original discovery of one species, *Daira speciosa*, led to the discovery of a more complex reefal decapod assemblage, extensive and intensive research into known Messinian locations would most likely yield further results. Different analytical interpretation of data could also influence results, whereby the same genera found associated with corals in one location are attributed to a different type of ecology from another.

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