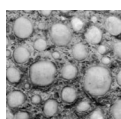


The first record of paguroids from the Eocene of Istria (Croatia) and further phylogenetic refinement of the Paguroidea (Crustacea, Anomura)

ROK GAŠPARIČ, RENÉ H.B. FRAAIJE, NINON ROBIN & ANTONIO DE ANGELI



A paguroid, *Lessinipagurus vasjamikuzi* sp. nov., is described from Eocene (upper Bartonian–lower Priabonian) of Istria, on the basis of a single right chela from Gračišće near Pazin, western Croatia. The specimen originates from beds of olistostrome breccias that formed in a bathyal setting. In addition, a new genus, *Prexylopagurus*, accommodated in the new family Xylopaguridae, is erected; based on a distinctive set of characters of the dorsal carapace, chelae, and operculate tergite of sixth abdominal somite. The phylogenetic relationships of the new family Xylopaguridae are discussed; it appears to have originated in the Tethyan Realm, possibly as early as the Jurassic, and displays a Tethyan distribution during the Cenozoic. Three extant species are transferred to the new genus, resulting in three new combinations: *Prexylopagurus anthonii*, *P. philippinensis*, and *P. caledonicus*. The palaeoecology and palaeobiogeography of the newly erected taxa are discussed. The bloom of diversity of *Lessinipagurus* during the late Eocene parallels the evolution and subsequent ecological expansion of grasses, especially of reed and bamboo, thus constituting a rare example of coevolution between land plants and marine organisms. The holotype of *Lessinipagurus vasjamikuzi* sp. nov. shows remains of an interesting *syn-vivo* balanomorph association; this is the earliest record of such barnacles on a decapod crustacean in the fossil record, and the sole record from an anomuran to date. • Key words: hermit crabs, Paguroidea, Paleogene, palaeoecology, coevolution.

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The present specimen constitutes the first fossil of an anomuran to be recorded from Eocene strata of Istria (Croatia, Slovenia). Coeval brachyurans have previously been described from several localities in Istria (Bittner 1880; Bachmayer & Nosan 1959; Mikuž 2002, 2003; Schweitzer *et al.* 2005) from the so-called “Marls with Crabs”. Despite the fact that the region could be expected to contain rich and diverse decapod crustacean assemblages, similar to those from the middle and upper Eocene of nearby Italy (*e.g.*, Beschin *et al.* 2010, Busulini *et al.* 2012), middle-late Eocene faunas in Istria are monotonous. Previously recorded fossil brachyurans belong predominantly to the genera *Harpactocarcinus* A. Milne-Edwards, 1862 and *Harpactoxanthopsis* Via, 1959, while specimens of *Lophoranina* Fabiani, 1910, are less common (Schweitzer *et al.* 2005, Mikuž 2010a).

The olistostrome breccia beds as exposed at Gračišće near Pazin are well known for their diverse Eocene macrofaunas that comprise plant remains, nummulitid foraminifera, coralline algae, corals, polychaetes, bivalves, gastropods and rare decapod crustaceans (Mikuž 2005, 2006, 2008a, b, 2010b; Mikuž *et al.* 2014). Until recently, only individuals of *Harpactoxanthopsis quadrilobata* (see Mikuž 2002), and *Lophoranina marestiana* (see Mikuž 2003) were recorded from the olistostrome levels at Gračišće.

The present hermit crab is assigned to the genus *Lessinipagurus* Beschin, De Angeli, Checchi & Zarantonello, 2012, which had been known exclusively from isolated chelipeds in Eocene strata of Italy (Beschin *et al.* 2012) that all resemble chelae of the extant genus *Xylopagurus* A. Milne-Edwards, 1880, all species of which

inhabit the Indo-Pacific and western Atlantic oceans (Forest 1997). Extant forms live in tube-shaped cavities such as pieces of driftwood, hollow pieces of reed or of bamboo (Lemaitre 1995). When lodged in its dwelling, these hermit crabs protect the anterior opening with their distinct strong and rounded right cheliped, while the posterior opening is tightly sealed off by the calcified operculate tergite of the sixth abdominal somite (Lemaitre & Campos 1993).

All species of *Lessinipagurus*, including the new one described below, are united by the highly characteristic gouge-shaped anterior morphology of the right cheliped which is due to the presence of a pseudo-fixed finger that extends parallel to the outer side of the dactylus. This phenomenon is also seen in extant species of *Xylopagurus*. Lemaitre (1995, p. 23) stated that, “several structures in species of *Xylopagurus* are unusual or unique among hermit crabs. The length of the linea d (= decalcified submassetic groove) as seen in *X. anthonii*, for example, is greater than is known in other hermit crabs. The most visible and striking structure found in species of *Xylopagurus* is the strongly calcified and operculate tergite of the sixth abdominal somite”. The same author also pointed out (p. 2) that, “on either side of the posterior region of the cephalic shield there is a shallow pit; they are referred to as the posterior gastric pits”. These gastric pits are also seen in illustrations provided in two other recent studies on *Xylopagurus* by Lemaitre & Campos (1993) and Forest (1997), albeit not mentioned in the descriptive part of those papers. Although *Xylopagurus* was assigned to the Paguridae Latreille, 1802 by de Saint Laurent-Dehancé (1966) and Provenzano (1971), the systematic position of this genus is still a matter of discussion (Lemaitre 1995).

Stratigraphical and geographical setting

Predominant Eocene strata in Istria comprise a clastic flysch sequence and pelagic foraminiferal limestones (Fig. 1A). The majority of known macrofossil localities are situated around the contact of both lithologies (Mikuž *et al.* 2014), where the foraminiferal limestones grade into the flysch and are therefore called “Transitional Beds”. These “Transitional Beds” (commonly called also “Marls with Crabs”) consist of calcareous marls, *Globigerina* marls, and breccias, which are conformably overlain by the more coarsely grained flysch beds (Živković & Glumac 2007). The 20-km-wide belt of flysch sediments extends from Ankarana (Slovenia) in the northwest, to Labin (Croatia) in the southeast (Mikuž *et al.* 2014).

The fossiliferous olistostrome breccia beds at Gračišće near Pazin formed in the Trieste-Pazin Basin. The Trieste-Pazin, a foreland basin of Alpine type with typical marine flysch deposits (Živković & Glumac 2007). The ba-

sin came into existence during the early to middle Eocene as a result of subduction and closure of the Tethys Ocean (Babić & Zupanič 1996). The transitional “Marls with Crabs” are interpreted to reflect a gradual deepening from a shelf carbonate platform to bathyal environments (Juračić 1979, Čosović *et al.* 2004). The upper part of these beds consists of several tens of metres of hemipelagic *Globigerina* marls, which are conformably overlain by coarser flysch beds, including the olistostrome breccia (Fig. 1B) discussed herein (Marinčić *et al.* 1996).

Nannoplankton analyses from the olistostrome breccia horizon were performed by Mikuž *et al.* (2014); these yielded a rich assemblage containing, amongst other taxa *Chiasmolithus solitus* (Bramlette & Sullivan 1961), *Sphenolithus obtusus* (Bukry 1971) and *Helicosphaera compacta* (Bramlette & Wilcoxon 1967). The co-occurrence of these coccolith species allows the assignment of the olistostrome breccia to the lower part of biozone NP17 (Martini 1971) or CP14b (Okada & Bukry 1980), which are dated as late Bartonian to early Priabonian (Pavšič & Premec Fuček 2000).

Institutional abbreviations

To indicate the repositories of specimens presented below, the following abbreviations are used: AO – Řlex Ossó fossil crab collection, Tarragona, Catalonia; MAB – Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; MCZ – Museo Civico “G. Zannato”, Montecchio Maggiore (Vicenza), Italy; NHMUK – The Natural History Museum, Department of Palaeontology, London, United Kingdom; RGA/SMNH – Slovenian Museum of Natural History, Ljubljana, Slovenia (R. Gašparič Collection).

Systematic palaeontology

Order Decapoda Latreille, 1802
 Infraorder Anomura MacLeay, 1838
 Superfamily Paguroidea Latreille, 1802

Family Xylopaguridae fam. nov.

Type genus. – *Xylopagurus* A. Milne-Edwards, 1880.

Included genera. – In addition to the type genus, *Lessinipagurus* Beschin, De Angeli, Checchi & Zarantonello, 2012 and *Prexylopagurus* gen. nov. The taxon *Paguritergites* Fraaije, Artal, Van Bakel, Jagt & Klompmaker, 2013, which was erected based on a sixth abdominal somite, also belongs here, but so far this somite type has not been linked to either a carapace or cephalic shield or chelae.

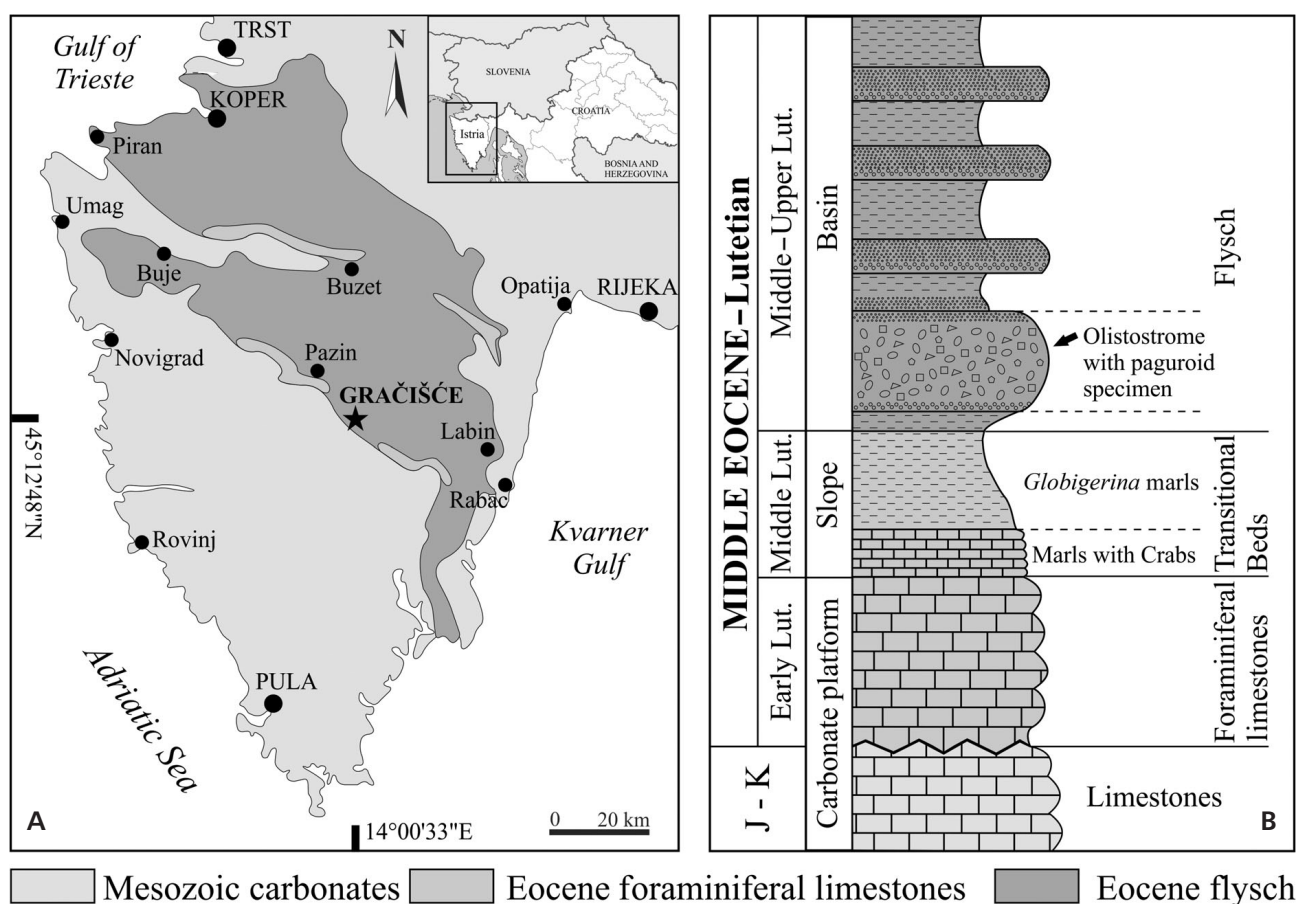


Figure 1. A – geographical position of the locality and simplified geological sketch of Eocene strata of Istria (after Živković & Glumac 2007).
 • B – stratigraphical column indicating the level of provenance of *Lessinipagurus vasmikuzi* sp. nov.

Stratigraphical range. – The earliest record of a xylopagurid is that of an abdominal tergite as recorded by Fraaije *et al.* (2013) from the upper Albian of northwest Spain. The type, and sole specimen known, is *Paguritergites yvonne-cooleae* Fraaije, Artal, Van Bakel, Jagt & Klompmaker, 2013; this constitutes a subquadratic, well-calcified and plate-like tergite divided into four subequal quadrants by anterior and posterior longitudinal median grooves and a median or transverse depression, similar to all known extant species of *Xylopagurus*.

Diagnosis. – Elongated subcylindrical carapace; shield longer than posterior part of carapace; gastric region shaped like an arrowhead pointing posteriorly with presence of gastric pits at about widest part; operculate, subquadratic, plate-like tergite of sixth abdominal somite strongly calcified, divided into four equal or subequal quadrants; chelipeds markedly dissimilar, right cheliped strong, massive with a pseudo-fixed finger extending parallel to the outer side of the dactylus.

Remarks. – Although *Xylopagurus* has previously been

placed, albeit provisionally, in the Paguridae, the systematic position of the genus still is under debate (Lemaitre 1995). Lemaitre’s landmark study of *Xylopagurus* noted several structures in its constituent species that were unusual or unique amongst extant hermit crabs. The combination of an elongated subcylindrical carapace, a shield that is longer than the posterior part of the carapace; a gastric region shaped like an arrowhead pointing posteriorly with the presence of gastric pits at about its widest part; a tergite of the sixth abdominal somite that is a strongly calcified, operculate, plate-like structure divided into four equal or subequal quadrants by anterior and posterior longitudinal median grooves and a median or submedian transverse depression; chelipeds that are markedly dissimilar; the strong, massive right cheliped with a pseudo-fixed finger extending parallel to the outer side of the dactylus (Fig. 2A–I), warrants the erection of the new paguroid family; Xylopaguridae.

A comparison of xylopagurid carapace morphology with the extensive record of carapaces of extinct paguroids discovered during the last decade (*e.g.*, Fraaije 2014) reveals a close affinity with the Parapylochelidae

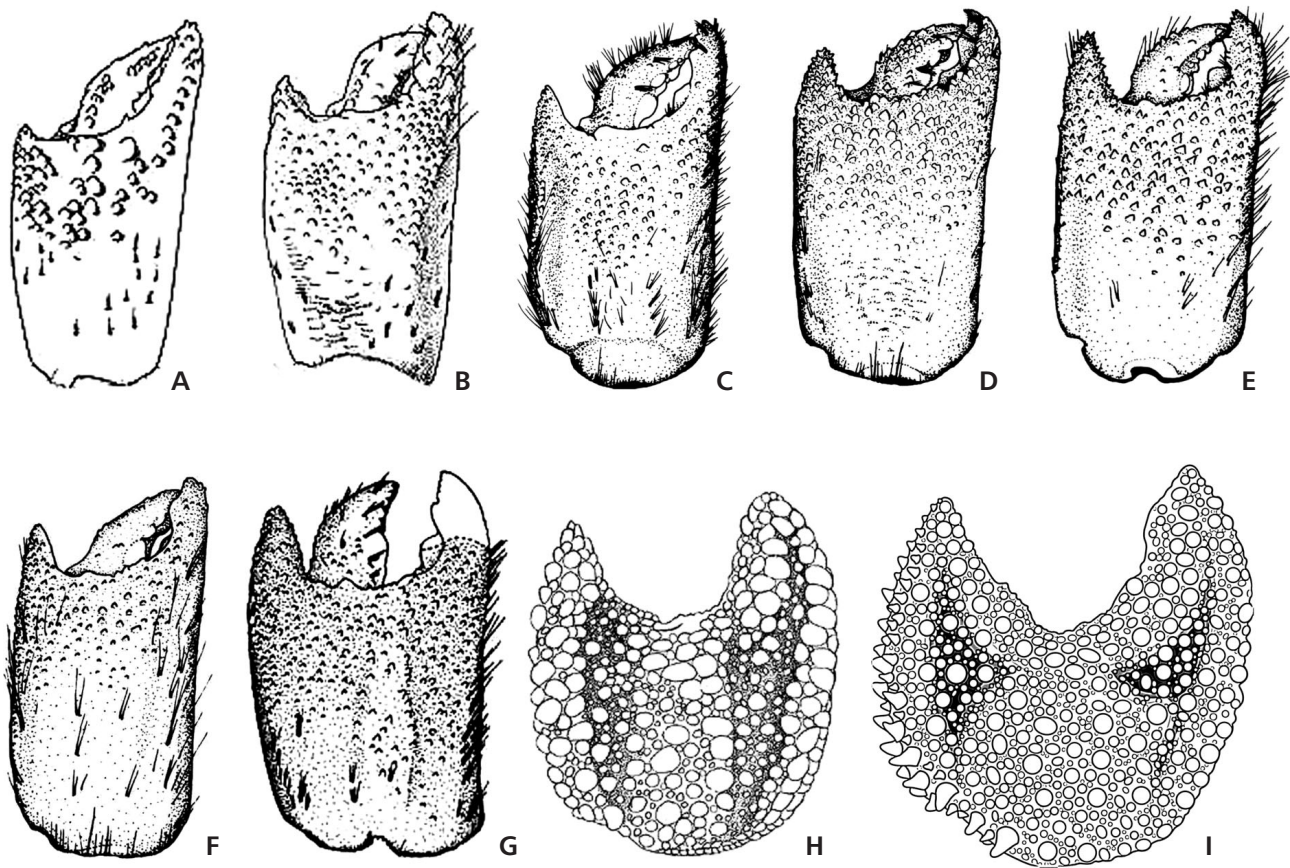


Figure 2. Comparison of right chelae of Xylopaguridae. • A – *Prexylopagurus philippinensis* (Forest, 1997). • B – *P. caledonicus* (Forest, 1997). • C – *P. anthonii* (Lemaitre, 1995). • D – *Xylopagurus rectus* A. Milne-Edwards, 1880. • E – *X. cancellarius* Walton, 1950. • F – *X. tenuis* Lemaitre, 1995. • G – *X. tayrona* Lemaitre & Campos, 1993. • H – *Lessinipagurus granulatus* Beschin, De Angeli, Checchi & Zarantonello, 2012. • I – *L. vasjamikuzi* sp. nov. Figures after: A, B – Forest (1997); C–F – Lemaitre (1995); G – Lemaitre & Campos (1993); H – Beschin *et al.* (2012).

(Fig. 3A–G). Fossil parapylochelids all have a down-pointed arrowhead shape of the gastric region within the posterior “arrow-tip” on either side a clear posterior gastric pit along with calcified posterior parts, and clear anterior branchial and massetic regions (see Fraaije *et al.* 2012, 2014; Fraaije 2014). The elongation and decalcification of the massetic regions and submassetic groove (*i.e.*, the line *d* in studies of extant hermit crabs) probably is an adaptation to inhabitation of long and narrow pieces of reed, bamboo and other comparable lodgings.

Interestingly, the calcified sixth abdominal tergite that was named *Paguritergites yvonnecooleae* by Fraaije *et al.* (2013) (Fig. 4H) co-occurs with numerous individuals of *Parapylocheles michaeljacksoni* and shows a morphology that is closely similar to the sixth abdominal tergites of species of *Xylopagurus* (Fig. 4A–J). This tergite probably constitutes the earliest record of this peculiar group of paguroids for which we propose a new family.

Based on the presence of a long decalcified submassetic groove the three extant species, *Xylopagurus anthonii*, *X. philippinensis*, and *X. caledonicus* are trans-

ferred to the new genus, *Prexylopagurus* (Fig. 4A–C). Species of *Xylopagurus* lack a submassetic groove.

Genus *Prexylopagurus* gen. nov.

Type species. – *Xylopagurus anthonii* Lemaitre, 1995.

Other species. – *Xylopagurus philippinensis* Forest, 1997, and *Xylopagurus caledonicus* Forest, 1997.

Etymology. – The Latin prefix *pre-* alludes to the probably earlier evolutionary origin.

Diagnosis. – Shield distinctly longer (1.5 times) than wide, evenly convex. Dorsal surface glabrous except for a few scattered minute setal pits, and low rostral ridge. Rostrum subtriangular, exceeding subtriangular lateral projections. Elongated massetic and submassetic regions of similar size. Massetic region laterally decalcified. Submassetic groove anteriorly ending just lateral of lateral projection.

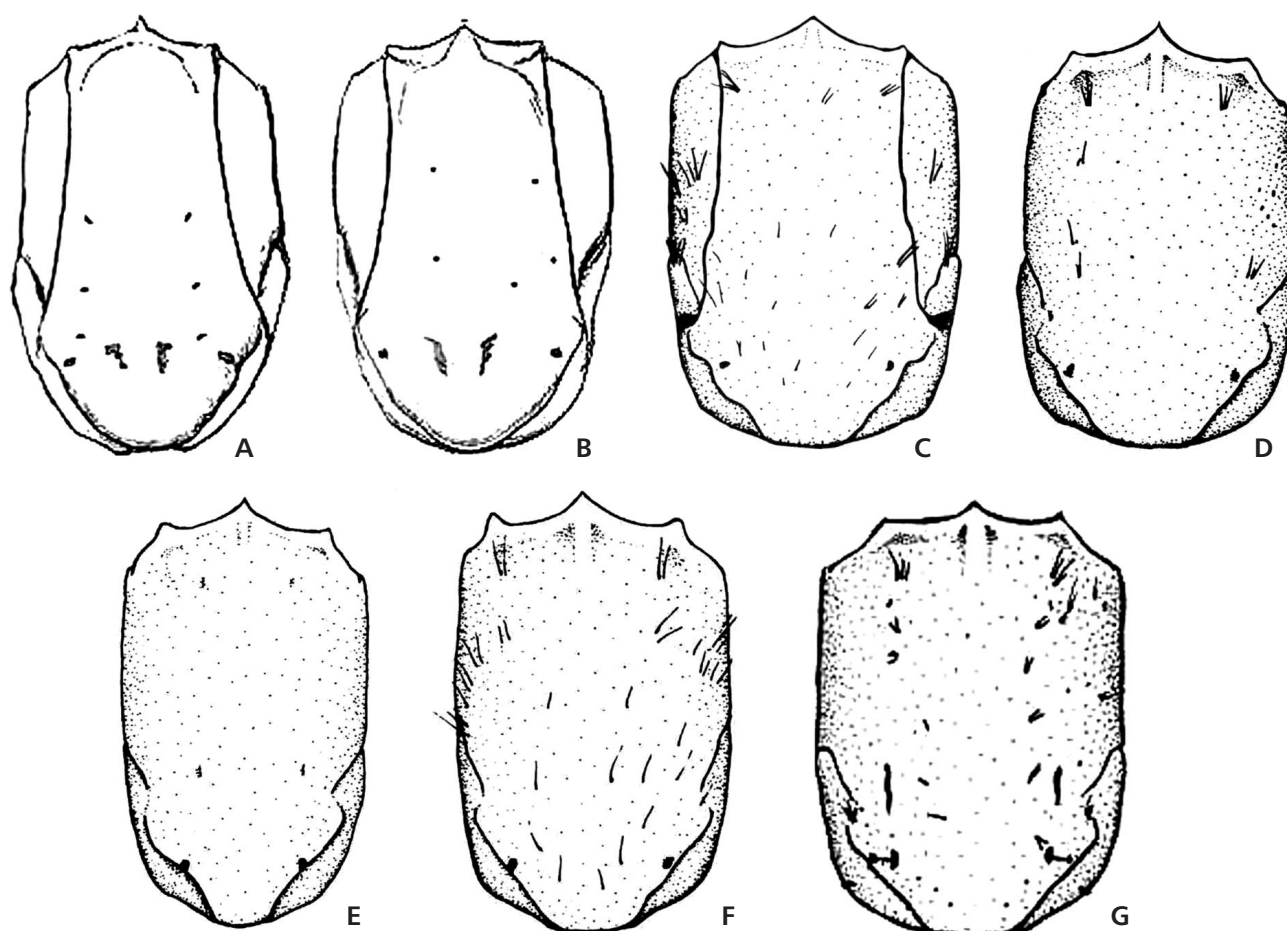


Figure 3. Comparison of thoracic shields. • A – *Prexylopagurus philippinensis* (Forest, 1997). • B – *P. caledonicus* (Forest, 1997). • C – *P. anthonii* (Lemaitre, 1995). • D – *Xylopagurus rectus* A. Milne-Edwards, 1880. • E – *X. cancellarius* Walton, 1950. • F – *X. tenuis* Lemaitre, 1995. • G – *X. tayrona* Lemaitre & Campos, 1993. Figures after: A, B – Forest (1997); C–F – Lemaitre (1995); G – Lemaitre & Campos (1993).

Gastric region shaped like an arrowhead pointing posteriorly with presence of gastric pits at about broadest part. Small keraial and anterior branchial regions.

Right cheliped strong, massive. Fingers each terminating in blunt calcareous claw. Dactylus with scattered, small spines and setal tufts on dorsal face, and row of setal tufts parallel to cutting edge; mesial margin with few tubercles and setal tufts. Fixed finger slightly overreaching dactylus. A “pseudo-fixed finger” extending parallel to the outer side of the dactylus gives the cheliped a typical gouge-like morphology; dorsal face with small spines or tubercles proximally; dorsolateral margin with row of small spines. Left cheliped slender, short, reaching to distal margin of carpus of right cheliped. Fingers distinctly longer than palm, terminating in corneous claw, opposing faces of fingers concave; cutting edge of fixed finger with closely spaced, minute corneous teeth; cutting edge of dactylus with row of minute, fused corneous teeth; dorsal and ventral surfaces with numerous setal tufts. Operculate tergite of sixth abdominal somite with raised crenulate margins bearing

evenly spaced tufts of long setae. Dorsal surface divided into four equal or subequal quadrants by anterior and posterior longitudinal median grooves and a median or submedian transverse depression.

Remarks. – This new genus can be distinguished immediately from *Xylopagurus* by the presence of decalcified submassetic grooves (linea d) on the shield and a decalcification of the lateral half of the massetic region. Morphologically, the shield of species of *Prexylopagurus* gen. nov. is in between that of a parapylochelid and of *Xylopagurus*. Within this lineage, there is an increase in the degree of decalcification of the massetic region.

***Prexylopagurus anthonii* (Lemaitre, 1995) comb. nov.**

Figures 2C, 3C, 4C

1995 *Xylopagurus anthonii* Lemaitre, 1995, p. 14, figs 7d, 11–13.

Original description. – The detailed description of several individuals of this species provided by Lemaitre (1995) need not be repeated here.

Remarks. – *Prexylopagurus anthonii* can be differentiated from its congeners by the possession of a straight postfrontal ridge; the sixth abdominal tergite is more evenly and regularly covered with rounded pits and tubercles.

***Prexylopagurus philippinensis* (Forest, 1997) comb. nov.**
Figures 2A, 3A, 4A

1997 *Xylopagurus philippinensis* Forest, 1997, p. 422, figs 1–3, 4a.

Original description. – The detailed description of several individuals of this species given by Forest (1997) need not be repeated here.

Remarks. – *Prexylopagurus philippinensis* differs from congeners in having a markedly spinose rostrum and a sub-circular postfrontal ridge; a very small “pseudo-fixed finger” and coarse ornamentation on the anterior part of the outer side of the right cheliped; the sixth abdominal tergite is more quadratic in outline than that of *P. anthonii* and less elongated than that of *P. caledonicus*.

***Prexylopagurus caledonicus* (Forest, 1997) comb. nov.**
Figures 2B, 3B, 4B

1997 *Xylopagurus caledonicus* Forest, 1997, p. 427, figs 4b, 5, 6.

Original description. – The detailed description of several individuals of this species presented by Forest (1997) need not be repeated here.

Remarks. – *Prexylopagurus caledonicus* is differentiated from congeners in having an oblique furrow that extends from the lateral side of the lateral projections towards the flanks of the curved postfrontal ridge.

Genus *Lessinipagurus* Beschin, De Angeli, Checchi & Zarantonello, 2012

Type species. – *Lessinipagurus granulatus* Beschin, De Angeli, Checchi & Zarantonello, 2012, by original designation.

Emended diagnosis. – Propodus with palm taller than long and a slightly inclined carpus-propodus articulation; palm

subsquarish to circular in outline; curved, divergent, upper and lower margins with convex profile; upper margin with two rows of large, forwardly directed tubercles lined up among smaller tubercles, and with prominent protuberance at mesial dorsodistal angle; tuberculated outer surface with two longitudinal depressions; convex inner surface, with small tubercles on the median part and larger tubercles on the lower and upper part; fixed finger shorter than palm, with several small rounded teeth on distal end of occlusal margin.

***Lessinipagurus vasjamikuzi* sp. nov.**
Figures 5A, B, 6A–D

Holotype. – Holotype, and sole specimen known to date, is RGA/SMNH 1987. It is a well-preserved right cheliped, measuring 21.5, 18.5, and 6.0 mm in length, height, and width, respectively.

Type horizon and locality. – Outcrop (45° 12' 48.5" N, 14° 00' 33.0" E) near Gračišće (Istria, Croatia), along the main road from Pazin to Labin; upper Eocene (upper Bartonian–lower Priabonian) olistostrome breccia horizon.

Etymology. – The specific epithet honours the Slovenian palaeontologist, Dr. Vasja Mikuž, in recognition of his considerable contributions to the palaeontological record of Slovenia and Istria.

Diagnosis. – Propodus with palm significantly taller than long; palm oval to ellipsoid in outline; curved, divergent, upper and lower margins with convex profile; upper margin with two rows of large, forwardly directed tubercles, ending in prominent, convexly diverging spiniform dorsomesial projection; tuberculated outer surface with two triangular longitudinal depressions; convex inner surface, with small flat tubercles; fixed finger almost as long as palm, with two larger, rounded teeth medially and four small rounded teeth on distal end of occlusal margin.

Description. – Right cheliped with ellipsoid oval outline, semi-circular in cross section; flat outer side and convex inner side, of large dimensions for the genus. Palm significantly taller than long, with inclined propodus/dactylus articulation, dorsal and ventral margins convex. Dorsal margin adorned with two rows of alternating, large, forwardly directed, spine-like, tubercles; one row positioned on the inner side, the other on the outer. Dorsal margin of cheliped ending in prominent, convexly diverging spiniform dorsomesial projection distally, protruding almost as far as fixed finger on the ventral margin, contributing to the ellipsoid oval appearance of the right cheliped (Fig. 5A, B).

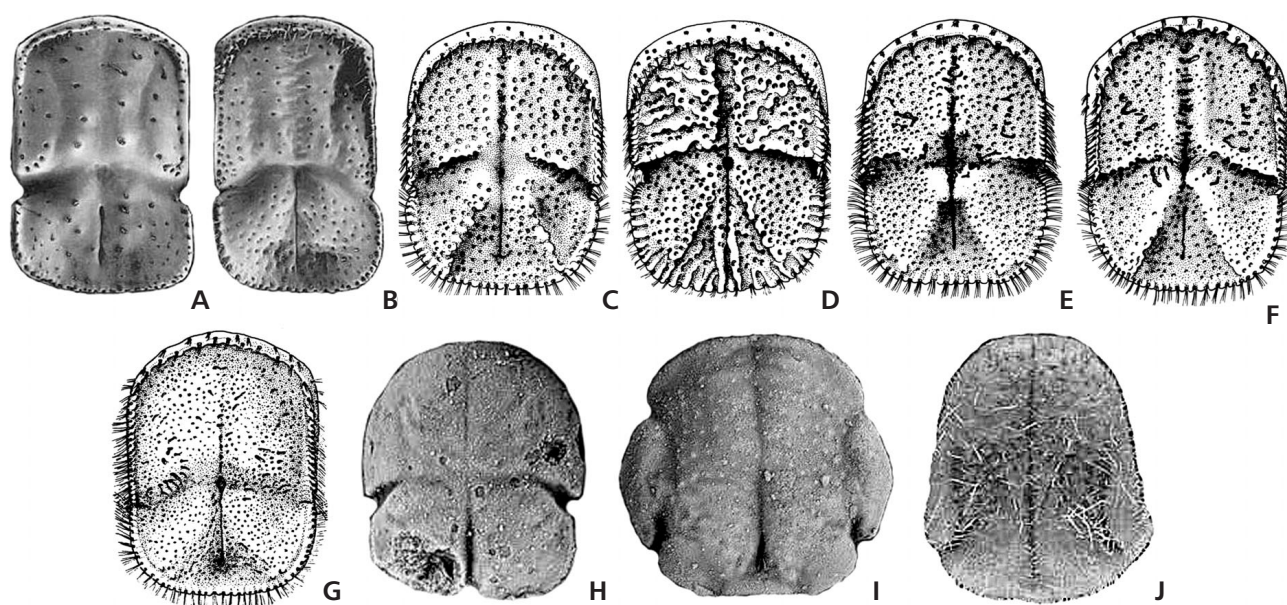


Figure 4. Comparison of sixth abdominal tergites. • A – *Prexylopagurus philippinensis* (Forest, 1997). • B – *P. caledonicus* (Forest, 1997). • C – *P. anthonii* (Lemaitre, 1995). • D – *Xylopagurus rectus* A. Milne-Edwards, 1880. • E – *X. cancellarius* Walton, 1950. • F – *X. tenuis* Lemaitre, 1995. • G – *X. tayrona* Lemaitre & Campos, 1993. • H – *Paguritergites yvonnecooleae* Fraaije, Artal, Van Bakel, Jagt & Klompmaker, 2013. • I – *Parapylochelitergites pustulosus* Fraaije, Artal, Van Bakel, Jagt & Klompmaker, 2013. • J – *Parapylocheles scorio* (Alcock, 1894). Figures after: A, B – Forest (1997); C–F – Lemaitre (1995); G – Lemaitre & Campos (1993); H–J – Fraaije et al. (2013).

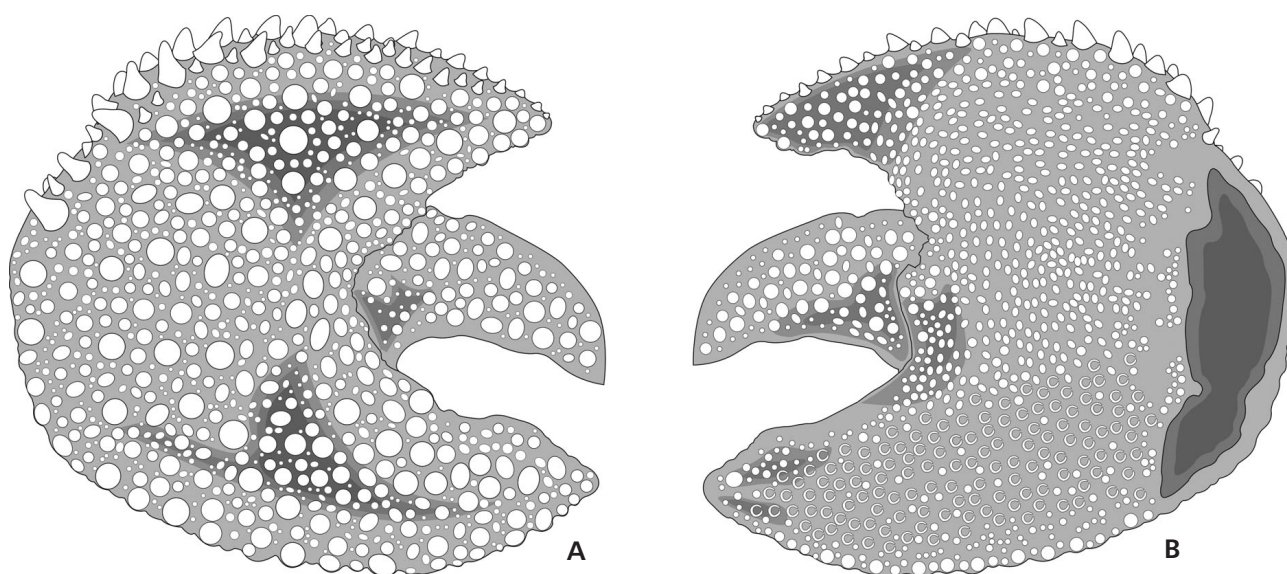


Figure 5. Reconstruction of the right chela of *Lessinipagurus vasjamikuzi* sp. nov. • A – outer side. • B – inner side of chela.

Ventral margin adorned with large rounded tubercles, interspersed with small tubercles. Fixed finger almost as long as palm, triangular, robust, convexly curved, ventral margin ornamented in similar fashion to palm, with alternating larger and smaller tubercles. Occlusal margin of fixed finger wide, hollowly concave at articulation rim, narrowing distally to a medially positioned two round teeth, distal part of cutting edge ending in four smaller

rounded teeth, flattened and straight distal end, slightly inclined to the inner side. Outer surface of right cheliped densely tuberculate. Large raised, round tubercles repeatedly alternating with smaller tubercles (Fig. 6A), more dense toward cheliped margins and along fixed finger length. Two elongated triangular depressions extending parallel to dorsal and ventral margins, continuing along fixed finger and dorsomesial projection. Outer surface

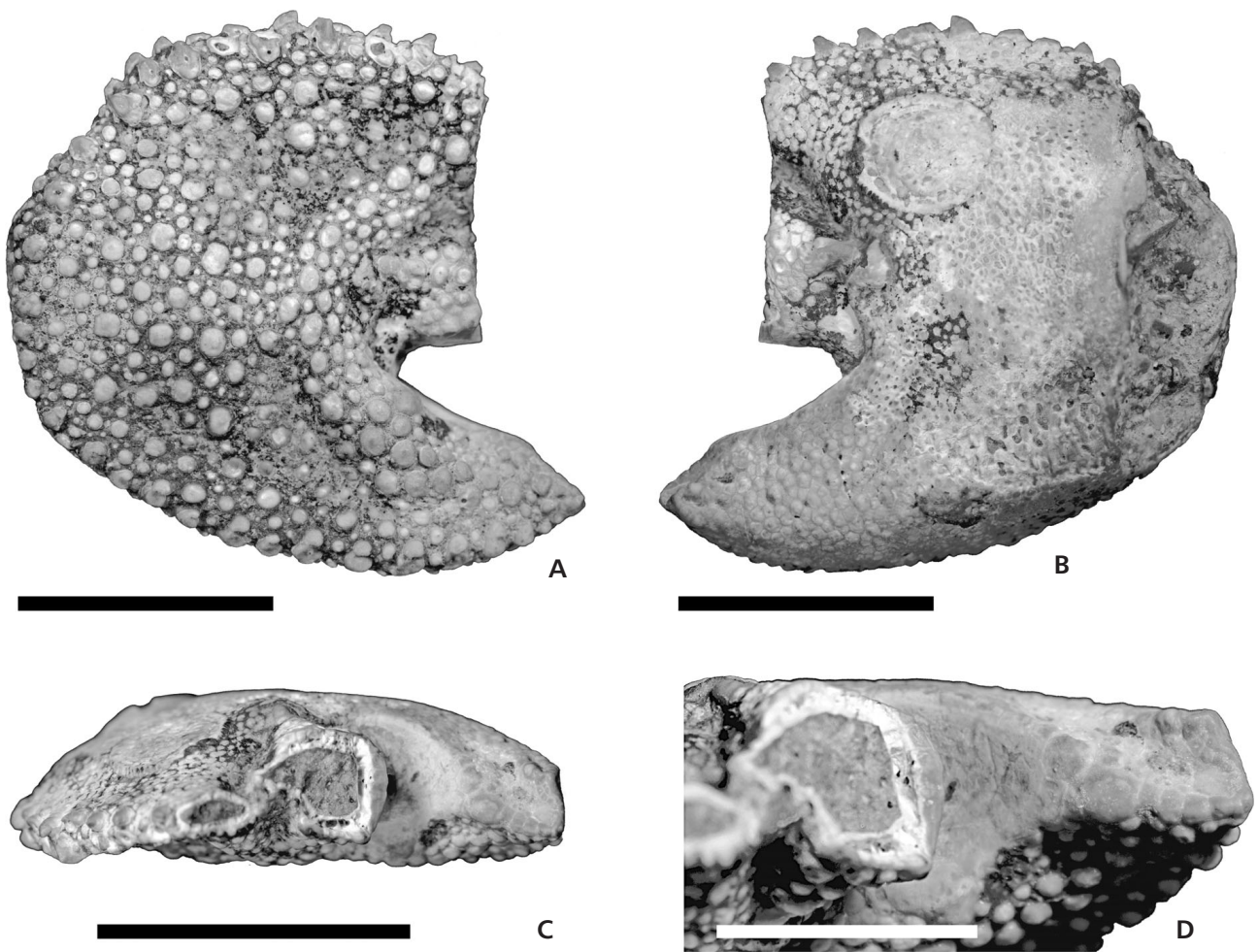


Figure 6. *Lessinipagurus vasjamikuzi* sp. nov. (holotype, RGA/SMNH 1987). • A – outer side. • B – inner side. • C – cross-section of dactylus. • D – close-up of occlusal margin. Scale bars: A–C = 10 mm; D = 5 mm.

margins rounded, margin along propodus/dactylus articulation swollen, inflated central palm area separating two triangular depressions. Inner surface of cheliped covered with small, flat, oval tubercles, sharply demarcated only on distal end and showing a pattern of imbrication, larger, rounded tubercles along ventral and dorsal inner margins (Fig. 6B). Dactylus only partially preserved, appearing stout, subsquarish in cross section (Fig. 6C), proximal part of occlusal margin forming a smooth molar-like tooth to fit in hollow of fixed finger, outer surface decorated with large round tubercles, inner surface with smaller, but distinct round tubercles (Fig. 6D).

Remarks. – This new form is assigned to *Lessinipagurus* on the basis of all morphological features as listed by Beschin *et al.* (2012). These include the circular outline of the tuberculated cheliped, with a palm that is taller than long and especially the prominent, spiniform dorsomesial projection on the distal dorsal margin.

In overall cheliped shape and ornamentation,

Lessinipagurus vasjamikuzi sp. nov. most closely resembles the type species, *L. granulatus*, but it can be differentiated from the latter by a unique set of characters. The greater size stands out, as the cheliped of the new species is significantly larger than individuals of *L. granulatus* (Table 1). The greater size might reflect different ontogenetic stages, but palm proportions demonstrate that, with a comparable palm length, palm height is approximately 1.35 times greater in the new species. In addition, the palm is much shorter in comparison to total propodus length, so that the cheliped in *L. vasjamikuzi* sp. nov. has a rounder ellipsoid outline. The fixed finger is wider proximally and triangular in shape, contrary to *L. granulatus*, rendering a V-shaped angle between the fingers rather than a U-shaped one as in *L. granulatus*. The two longitudinal depressions on the outer surface are less pronounced and triangular. The ornamentation of tubercles also differs slightly; on the outer surface, tubercles are evenly mixed: large round ones amidst an equal density of smaller tubercles, and more spaced than in the Italian material. The two rows of tuber-

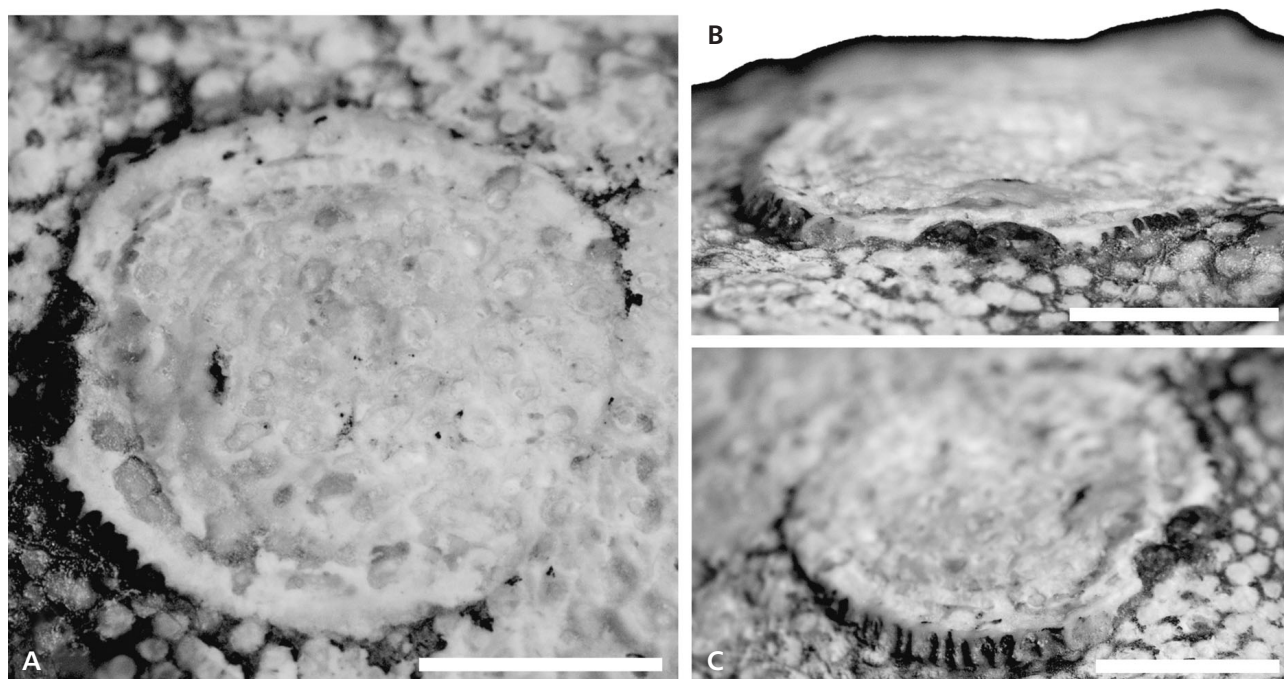


Figure 7. Close-up of epibiont attachment scar on *Lessinipagurus vasjamikuzi* sp. nov. (holotype, RGA/SMNH 1987). All scale bars = 2 mm.

Table 1. Morphometric comparison of *Lessinipagurus granulatus* Beschin, De Angeli, Checchi & Zarantonello, 2012 and *Lessinipagurus vasjamikuzi* sp. nov.

Species	Specimen No.	Propodus length (in mm)	Palm length (in mm)	Palm height (in mm)	Palm width (in mm)	Locality	Age
<i>Lessinipagurus granulatus</i>	MCZ 2732 (holotype)	14.9	11.2	12.9	6.1	Grola, Vicenza, Italy	middle Eocene, Lutetian
<i>Lessinipagurus granulatus</i>	MCZ 3109	10.0	8.0	8.7	4.4	Grola, Vicenza, Italy	middle Eocene, Lutetian
<i>Lessinipagurus granulatus</i>	MCZ 3044	13.0	9.0	11.6	na	Parona, Vicenza, Italy	late Eocene, Priabonian
<i>Lessinipagurus granulatus</i>	AO C-477/1	11.0	8.5	9.5	4.0	Arzignano, Vicenza, Italy	middle Eocene, Lutetian
<i>Lessinipagurus vasjamikuzi</i> sp. nov.	RGA/SMNH 1987	21.5	11.7	18.3	6.0	Gračiče, Istria, Croatia	late Bartonian–early Priabonian

cles on the dorsal margin are forwardly oriented and spine like in the Istrian specimen.

On the lateral proximal side, the propodus described shows remains of what appears to have been a balanomorph association (Fig. 6B). Indeed, the surface of the propodus reveals a tiny discoid structure that corresponds to an attachment scar.

Infraclass Cirripedia Burmeister, 1834
 Superorder Thoracica Darwin, 1854
 Order Sessilia Lamarck, 1818
 Infraorder Balanomorpha Pilsbry, 1916
 Figures 7A–C

Description. – The present regularly discoid scar is about 4.5 mm in diameter corresponds to a flat calcareous disc that displays concentric rings at some of its marginal points (Fig. 7A). These rings show very thin radial striations pointing toward the centre of the scar. At some points, the scar

reveals remains of a marginal wall in the form of paired striae (Fig. 7B, C). The central part of the scar appears to have been filled by a calcareous plug and does not reveal typical structures. Of note is a clear deformation of palm tubercles that underlie the scar (Fig. 7A).

Taxonomical remarks. – The concentric and thinner radial striations visible at the scar margin are typical of a balanomorph basal plate. The central aspect of this plate is here hidden by a calcareous layer. The remaining three-dimensional parts of the scar display the ornamentation of a balanomorph wall plate. The discoid shape of the scar is more or less typical of balanomorphs that grow in isolation on substrates. The specific nature of the balanomorph involved cannot be identified on the basal plate alone.

Taphonomical remarks. – The *post-mortem* or *syn-vivo* nature of the present association is difficult to determine on the basis of taphonomic aspects. However, although

recovered in isolation, the present propodus retains its articulation, which is indicative of a relatively brief interval of exposure of the hermit crab carcass prior to final burial. Indeed, this specific articulation site in decapod crustaceans is of pre-burial dislocation, *i.e.*, one of the first to become dislodged from the rest of the body (Briggs & Kear 1994, Locatelli 2012). This brief pre-burial exposure of the carcass would probably not have allowed *post-mortem* settlement and growth of a balanomorph of such dimension (4.5 mm).

However, the flattening of the tubercles appear to correspond to hindrance during the production of superficial cuticular layers (as already postulated in the case of ectosymbiotic bacterial colonies; see Robin *et al.* 2015) rather than to true abrasion of the tubercles that could have occurred as a result of *post-mortem* epibiont attachment. This would hardly be observed in a *post-mortem* association, but would more reliably be the result of a *syn-vivo* association with the anomuran. The average growth of balanomorphs is difficult to assess in detail, but in general varies from 10 to 160 µm per day, depending of growth stage and environment (Crisp & Bourget 1985). In this respect, a mean growth rate of 50 to 70 µm per day seems to be a convenient assessment of a classic adult balanomorph. This implies that such an association took place during the intermolt period of the host, demanding an average of about three months to reach such a size. This matches the intermolt duration of a subadult/adult anomuran of normal size. Indeed, studies on extant large-sized anomurans (Lithodidae; carapace length < 80 mm) have revealed that their intermolt duration may reach up to 13 months (Lovrich *et al.* 2003).

Remarks on partner encounter. – The genus *Lessinipagurus* is here shown to be related to extant *Xylopagurus*, which live in hollowed-out wooden structures and occupied gastropod shells. The perfectly round (of an estimated age of *ca* 80 days) growth of the balanomorph appears to have been possible because it was not affected by the chela rubbing against the inside the pagurid shelter (woody structure or other type). In their abodes, extant *Xylopagurus* often reveal extremities of their pereopods exposed outside of the wood shelter (Fig. 8A, B). This particular habit may have permitted the *syn-vivo* attachment and subsequent growth of the balanomorph on this (sub)adult *Lessinipagurus* during its intermolt period.

Contrary to what might be expected, records of balanomorph barnacles as epibionts of extinct decapod crustaceans are scarce. Cases recorded in the literature invariably correspond to indeterminate balanomorphs on crabs of the families Majidae (Glaessner 1960), Mathildellidae (Feldmann 2003), Atelecyclidae (Waugh *et al.* 2004) and Cancridae (Feldmann *et al.* 2006). All of these cases correspond to associations of Miocene age, which

means that the present case is the earliest report of similar barnacles attached on a decapod crustacean, of more or less comparable age to two balanomorph basal plates on the propodus of an Eocene (Ypresian) *Hoploparia gammaroides* (M'Coy, 1849) from the London Clay (NHMUK In.35300; see Robin 2015). However, the exact nature (either *post-mortem* or *syn-vivo*) of the latter has not been studied; the present example documents effective ectosymbiosis.

The present association may be related to the profusion of balanomorph larvae in the environment occupied by *Lessinipagurus* or to the assumedly muddy marine bottom of this setting, in which sunken wood fragments (and occasionally their occupants) provided suitable substrates for barnacle attachment and growth. Each sunken piece of driftwood may thus have corresponded to a local microenvironment (Hoyoux 2010) involving assemblages of decapod and thoracican barnacles.

Ecology

All extant xylopagurids known to date are found living in hollow pieces of reeds like bamboo, in open-ended cylindrical cavities (pieces of driftwood) or in empty polychaete tubes (Lemaitre 1995, Forest 1997). *Xylopagurus rectus* A. Milne-Edwards, 1880, *X. tayrona* Lemaitre & Campos, 1993, *Prexylopagurus anthonii* (Lemaitre, 1995) and *X. tenuis* Lemaitre, 1995 occur in the western Atlantic, while *X. cancellarius* Walton, 1950 inhabits the eastern Pacific. From the Indo-West Pacific *P. philippinensis* (Forest, 1997) and *P. caledonicus* (Forest, 1997) have been described. These species occur at depths ranging from several metres (*X. cancellarius*) to several hundreds of metres. *Prexylopagurus caledonicus* was dredged from a depth of 591 metres (Forest 1997).

Interestingly, the recently discovered bloom of *Lessinipagurus* (De Angeli 2016, in prep.) in the upper Eocene of northern Italy parallels the origin and evolution and subsequent ecological expansion of especially reed and bamboo (Poaceae) (*e.g.*, Strömberg 2011, Poinar & Columbus 2013, Wang *et al.* 2013).

There is a characteristic type of “pseudo-fixed” finger at the dorsal margin of the cheliped. The gouge-like morphology of the right cheliped with “pseudo-fixed” finger, dactylus and palm all covered with coarse, close-set spines and tubercles looks like a good rasping and stabbing tool to enlarge and smooth the inner side of hollow plants or other organic remains.

As a result of the elongation and decalcification of the massetic region and submassetic groove, these paguroid carapaces became more flexible so as to inhabit long and narrow pieces of reed, bamboo and other comparable lodgings.

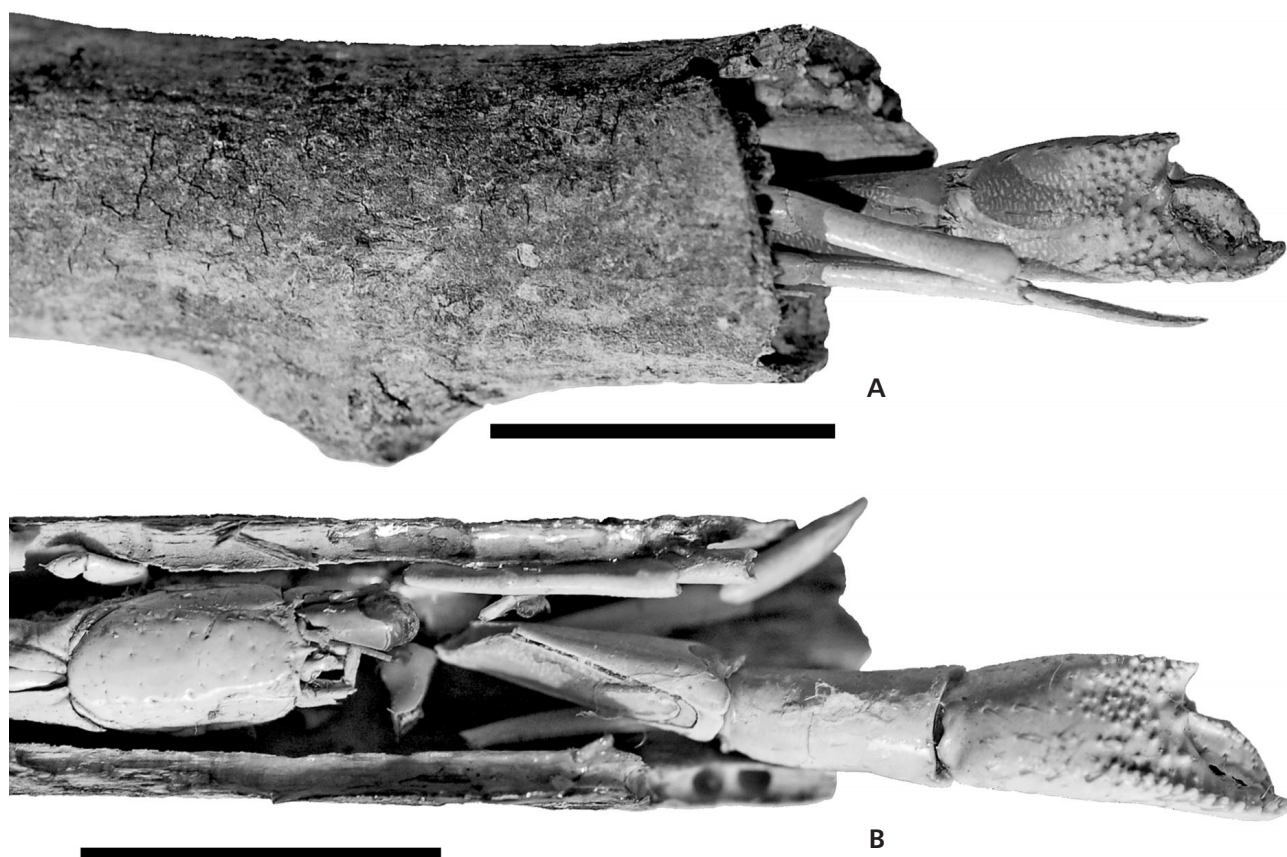


Figure 8. Extant *Prexylopagurus philippinensis* (Forest, 1997), specimen MAB k03567, Olango Island, Cebu, Philippines, inhabiting a hollowed sunken wood. • A – lateral view of exposed chelae. • B – dorsal view with the removed woody shelter. Both scale bars = 10 mm.

Palaeobiogeography

The newly erected family Xylopaguridae appears to have originated in the Tethyan Realm, perhaps as early as the Jurassic, and displays a Tethyan distribution throughout the Cenozoic. The distribution pattern of extant species of *Xylopagurus*, in the Indian Ocean and West Pacific on the one hand, and the Pacific and West Atlantic on the other, confirms the Tethyan origination and distribution (Forest 1997). Not unlike galatheoids (De Angeli & Garassino 2003), this taxon underwent rapid diversification and speciation in the Tethyan Ocean during the Eocene (De Angeli 2016, in prep.), possibly followed by another diversification in the Indo-Pacific region after the closure of Tethyan seaways (Renema 2007, Macpherson *et al.* 2010). This eastward shift of biodiversity is observed also in other marine organisms such as molluscs, fish, and mangroves, and indicates that tectonic changes are important drivers of modern biodiversity (Renema *et al.* 2008).

Conclusions

The first record of an Eocene paguroid, *Lessinipagurus vasjamikuzi* sp. nov., provides an opportunity to revise the

diversity of the genus and refine the phylogeny of the Paguroidea. This unique genus, up to now known exclusively from a single species from the Eocene of Italy, shows a wider palaeogeographical range and a higher diversity in the Tethyan Ocean during the Eocene than previously thought.

The type specimen of *Lessinipagurus vasjamikuzi* sp. nov. also reveals the remains of a *syn-vivo* balanomorph epibiotic association, which is the earliest record of such and the first to be described from an extinct anomuran. This interesting association most likely resulted from specific ecological conditions, where sunken pieces of wood and their occupants provided the only suitable substrate on a deep-water muddy sea floor.

We erect a new family, Xylopaguridae, on the basis of a distinctive set of characters of the dorsal carapace, chelae, and operculate tergite of the sixth abdominal somite. A new genus, *Prexylopagurus*, within this family, now accommodates three extant species, namely *P. anthonii*, *P. philippinensis* and *P. caledonicus*.

The new family appears to have originated in the Tethyan Realm, perhaps as early as the Jurassic. Increased speciation within the genus *Lessinipagurus* during the late Eocene parallels the evolution and ecological expansion of

grasses, especially reed and bamboo. As *Lessinipagurus* exclusively inhabited wood and bamboo fragments, this represents a rare example of coevolution between land plants and marine organisms.

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