

Ypresian Decapod Crustacean faunas from the coral-algal environments in the Eastern Lessini Mountains (Vicenza and Verona territory – NE Italy): a comparative analysis

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Abstract – A comparative analysis of the Crustacean faunas found in Ypresian bioconstructions cropping out in the Eastern Lessini Mountains is carried out. The fossiliferous sites are: Contrada Gecchelina at Monte di Malo, San Pietro Mussolino, Vestenanova, and the Bolca area (Vicenza; Verona – NE Italy). The high value of the Shannon-Weaver biodiversity index calculated for these buildups confirms the hypothesis of the existence during the Early Eocene of a large lagoon characterized by shallow water and patch reefs. Juvenile specimens of *Gecchelicarcinus lorigae* and *Alponella paleogenica* are described.

Keywords: Crustacea / Decapoda / Early Eocene / NE Italy / Paleoenvironment / Shannon-Weaver index

Résumé – Les faunes de crustacés décapodes yprésiens dans les environnements coralliens et algaires à l'est des Monts Lessini (provinces de Vicence et de Vérone – Italie du nord-est) : une analyse comparative. Une analyse comparative des faunes de crustacés découvertes dans les bioconstructions yprésiennes affleurant à l'est des Monts Lessini est réalisée. Les sites fossilifères sont : Contrada Gecchelina à Monte di Malo, San Pietro Mussolino, Vestenanova, et le secteur de Bolca (Vicence, Vérone – Italie du nord-est). La valeur élevée de l'indice de biodiversité de Shannon-Weaver calculé pour ces petits récifs fossiles confirme l'hypothèse de l'existence, pendant l'Éocène inférieur, d'une grande lagune caractérisée par des eaux peu profondes et des patchs récifaux. De jeunes spécimens de *Gecchelicarcinus lorigae* et d'*Alponella paleogenica* sont décrits.

Mots clés : Crustacea / Decapoda / Éocène inférieur / Italie du nord-est / paléoenvironnement / Indice de Shannon-Weaver

1 Introduction

The widespread presence of Ypresian coral-algal buildups in the Eastern Lessini Mountains (western Veneto, NE Italy) has been only recently discovered (Fig. 1). After the first report referred to a strongly recrystallized dome found in the quarry at Contrada Gecchelina (Monte di Malo – Vicenza) (Beschin *et al.*, 2000, 2007), methodical researches in coeval layers cropping out in the Chiampo and Alpone valleys allowed the identification of analogous structures in other quarries at San Pietro Mussolino (Vicenza) and Vestenanova (Verona) (Beschin *et al.*, 2015; Tessier *et al.*, 2011) and finally in the area around Bolca, the village famous all over the world for the coeval “Pesciara” and Monte Postale Fossil-Lagerstätten (De Angeli and Garassino, 2014;

Beschin *et al.*, 2016). These bioconstructions were dwelt by abundant crustacean faunas whose systematics has been studied; through the years more than 1300 specimens were collected and referred to over 140 taxa; they are housed in the Museo Civico “G. Zannato” at Montecchio Maggiore (Vicenza) (acronym MCZ) and in the Museo Civico di Storia Naturale in Verona (acronym VR). The remains consist of small carapaces with white cuticle, sometimes altered and dusty, or moulds, and a few parts of chelipeds.

A comparative analysis among the faunas is now proposed; it includes the relative abundance of the species common to almost all the studied outcrops, the Shannon-Weaver index that allows an evaluation of the biodiversity ascribable to these sites and a cluster analysis showing their statistical similarities. The availability of a high number of specimens, some of them measurable, made it possible to analyze the change of the shape of carapace during growth for some species.

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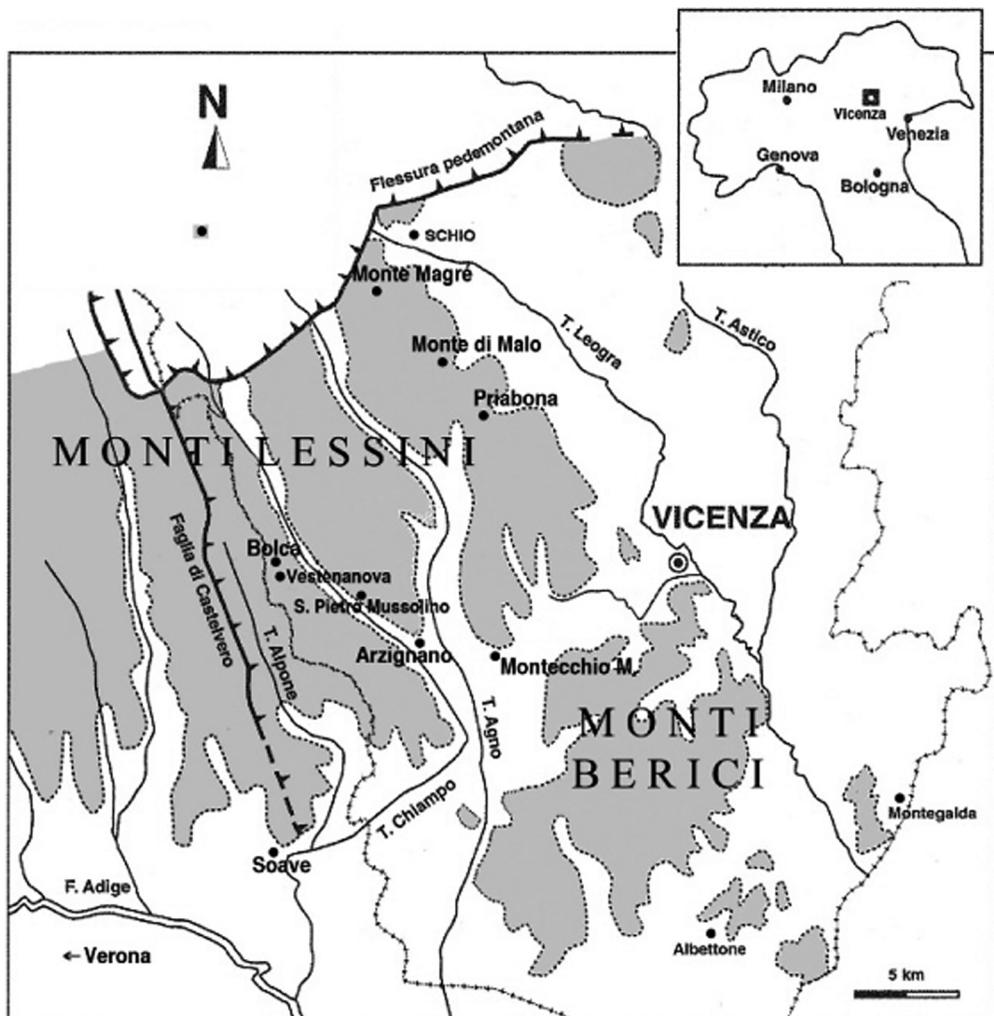


Fig. 1. Map of the sites of the studied crustacean-bearing bioconstructions.

2 Geological setting

In the Eastern Lessini Mountains located along the southern edge of the Alps in the western Veneto (NE Italy), marine sedimentary rocks crop out with an age ranging from the Early Cretaceous to Middle Eocene as well as volcanic rocks of Paleocene to Oligocene age characterized by a basaltic chemistry and referred to the well-known Venetian Tertiary Volcanism. The carbonate marine sedimentary rocks cropping out are represented by the “Maiolica”, “Scaglia Variegata Alpina”, “Scaglia Rossa Veneta” and “Calcare di Spilecco” formations and by the so-called “Nummulite Limestones”.

During the Cretaceous, the considered area was characterized by conditions of a submerged *plateau*. Afterwards, during the Paleogene, the bathymetric conditions have changed with the structuring of the so-called “Lessini Shelf” (Bosellini, 1989), an area characterized by shallow waters with prevalent carbonate deposits embedded with volcanic materials. The passage from the Cretaceous to Paleogene in the Eastern Lessini Mountains is marked by a depositional gap including large part of the Paleocene.

During the Early and Middle Eocene, and anyway during the quiet phases of volcanism, within the Alpone-Agno graben or semigraben, carbonate sediments were deposited, mostly limestones and organogenic calcarenites (Nummulite Limestones). The “Nummulite Limestones” are overlain by a thick layer of basaltic lavas and different kinds of volcanoclastic products that, during the Bartonian (late Middle Eocene), were subaerial. These lithologies are often associated with lignitic lenses and littoral/brackish deposits.

One of the most famous areas in the world for the Early Eocene fauna and flora is certainly Bolca (“Pesciara” and Monte Postale); fish and other vertebrates, worms, molluscs, insects, crustaceans but also plants are amazing for their excellent preservation. The paleoenvironment that produced these Fossil-Lagerstätten has been imagined as a lagoon or a coastal depression on the carbonate “Lessini Shelf” separated from the open sea by a ridge. The important carcinological researches recently carried out in this area (Beschin *et al.*, 2016) corroborate the recently proposed hypothesis of the existence of a true coral reef (Papazzone *et al.*, 2014a,b; Vescogni *et al.*, 2016); in the past the real existence of this structure had been only assumed on the basis of the peculiar



Fig. 2. Coralligenous dome cropping out in Contrada Gecchelina at Monte di Malo (no longer accessible).

faunistic associations there found. In particular, the lower Eocene rocks are represented by laminated shallow water carbonate sediments. It cannot be excluded that within the famous “Pesciara lagoon” and therefore in its inner but also in its outer part, patch reefs existed similar to the ones observed along the coasts of St. Croix Isle (Caribbean Sea).

In the last two decades in different lower Eocene outcrops in the Eastern Lessini Mountains, coral-algal buildups that yielded abundant crustacean faunas have been discovered mostly by one of the authors (CB). These biohermal limestones are distributed in the area at the boundary between the Vicenza and Verona territories and are also rich in larger foraminifera, bivalves, gastropods and fragments of echinoids (Fig. 1). Sites are presented from east to west. The quarry in Contrada Gecchelina at Monte di Malo (Vicenza) yielded a compact micritic-calcarenitic dome but it is unfortunately no longer accessible (Fig. 2). It was strongly recrystallized without a clear stratification, about 9 m wide and 3 m high and associated with small satellite buildups with a diameter of 2–3 m. A micropaleontological study clarified that its fossil association, middle-upper Ypresian in age, indicated an infraneric shallow-marine environment (Beschin *et al.*, 2000, 2007). The Bertocchi quarry at San Pietro Mussolini in the Chiampo Valley (Vicenza) has small buildups made of whitish micritic limestone that have been recognized as heteropic with Ypresian laminated limestones, with diameters of about 2 m. Incompletely exposed, they came into view for removing operations (Tessier *et al.*, 2011). The Braggi quarry at Vestenanova (Verona) has a large biohermal mound embedded between Ypresian laminated limestones and volcano-detrital deposits. It is very recrystallized, about 4 m high, but its lateral continuity is not apparent for the presence of abundant landfill (Beschin *et al.*, 2015). The Bolca area (Verona and Vicenza) yielded small isolated bioconstructions that have been found in several sites (Valecco, Monte Postale, Zovo, Laisi, Cracchi and Rama); their mutual relations are not clear but they are heteropic with the Ypresian laminated limestones which have already been the object of some studies (Barbieri and Medizza, 1969; Beschin *et al.*, 2016; Papazzoni *et al.*, 2014a,b). The stratigraphic closeness, even if in a different depositional facies, between the studied fauna and the “Pesciara” is confirmed by the discovery in the latter of a carapace on a limestone slab referred to *Eotrachynotocarcinus airaghii*

Beschin *et al.*, 2007 a species found in almost all the mentioned outcrops. All these findings hint at the existence of patch reefs within a large lagoon.

Ypresian coral-associated decapod remains have been found also in the Rossi quarry at Monte di Malo (a single specimen of Parthenopidae) (De Angeli *et al.*, 2010), and at Monte Magré di Schio (Vicenza) (Cecon and De Angeli, 2013; De Angeli and Cecon, 2012, 2013a,b, 2014, 2015, 2016) (Tab. 1); in both cases the crustaceans have been collected from layers of compact calcarenites with a decimetric lamination and not from buildups.

3 Analysis of the faunas

The crustacean faunas found in the described biohermal limestones have been carefully sampled and analyzed. The collecting of the specimens has been methodically made by one of the authors (CB); this operation has been carried out by removing big rocky blocks from the outcrops then broken into smaller pieces; from these fragments all the remnants of decapods have been retained with the help of a magnifying glass and sometimes of a stereomicroscope. In some fossiliferous sites the sampling has been negatively affected by the small areal extention of the outcrop.

In Table 1 all the species of fossil crustaceans (essentially decapods) found in Ypresian coralligenous levels in western Veneto are listed.

The richest site both for the number of specimens (647) and the number of species is Rama (Bolca territory): here 22 species of Anomura and 81 of Brachyura were recognized (an isolated chela determined as Porcellanidae gen. indet., sp. indet. and the carapace *Paguristes* sp. have not been considered in the number of species because they might be referred to already considered taxa). The Shannon-Weaver index of biodiversity (H') of this fauna has been calculated: its value is $H' = 4.00$. In the same outcrop also two specimens referred to *Sphaeroma gasparellai* De Angeli and Lovato, 2009 (Isopoda) were found (Beschin *et al.*, 2016). *Phlyctenodes multituberculatus* Beschin *et al.*, 2007 is the species with the highest relative abundance ($RA = 0.0912$); by contrast, the numerous taxa present with only one specimen have $RA = 0.0015$. Included among the most abundant species are not only the ones found in almost all the other here considered sites (Fig. 3), but also a few of the 51 taxa until now found exclusively in this outcrop (14 Anomura and 37 Brachyura) and namely *Bolcagalathea venetica* Beschin *et al.*, 2016 ($RA = 0.0526$), *B. corallina* Beschin *et al.*, 2016 (0.0479), *Tropicalia parva* Beschin *et al.*, 2016 ($RA = 0.0355$), *Rama lineatuberculata* Beschin *et al.*, 2016 ($RA = 0.0232$), *Acanthogalathea brogliei* Beschin *et al.*, 2016 ($RA = 0.0170$), *Phlyctenodes edwardsi* Beschin *et al.*, 2016 ($RA = 0.0155$). These species strongly characterize this site with their presence (Tab. 1).

In the quarry located in Contrada Gecchelina at Monte di Malo, 373 specimens have been collected and referred to 47 species (8 Anomura and 39 Brachyura; $H' = 3.07$). Also in this case we did not consider 3 isolated chelipeds not classified at a specific rank (Beschin *et al.*, 2007). The values of the relative abundance of the species of this bioconstruction show that the most represented taxa are the ones found also in other sites

Table 1. List of the crustaceans found in the Ypresian coral-algal outcrops in the Eastern Lessini Mountains with the number of specimens (X = number not given). Specimens consisting in: b = cephalothorax and abdomen; c = carapace; p = part of chelipeds; * = some infested by bopyrids.

In the systematic arrangement here adopted Martin and Davis (2001) have been followed for the Isopoda, Ahyong *et al.* (2010) for the Galatheoidea, Guinot *et al.* (2013) for the taxa at a higher rank than superfamily within the Brachyura, and in the other cases Schweitzer *et al.*, (2010) (Beschin *et al.*, 2016).

		Rama	Cracchi	Laisi	Zovo	Monte Postale	Valecco	Vestenanova	S. Pietro (Braggi quarry)	Monte Mussolini	Monte Magré	Monte di Malo (C. Bertocchi quarry)	Monte Gecchelina (Rossi quarry)	Monte di Malo
Bolca area														
ISOPODA														
Sphaeromatidae	<i>Sphaeroma gasparellai</i> De Angeli and Lovato, 2009	2												b
ANOMURA														
Chirostylidae	<i>Eouropythrus montemagrensis</i> De Angeli and Ceccon, 2012										1			c
Galatheidae	<i>Acanthogalathea brogliei</i> Beschin <i>et al.</i> , 2016	11												c
	<i>A. devechii</i> Beschin <i>et al.</i> , 2016	5				1	1					1		c
	<i>A. paucispinosa</i> Beschin <i>et al.</i> , 2016	3											3	c
	<i>A. squamosa</i> Beschin <i>et al.</i> , 2007								4					c*
	<i>Bolcagalathea corallina</i> Beschin <i>et al.</i> , 2016	31												c*
	<i>B. multispinosa</i> Beschin <i>et al.</i> , 2016	3				1								c
	<i>B. venetica</i> Beschin <i>et al.</i> , 2016	34												c*
	<i>Lessinigalathea regalis</i> De Angeli and Garassino, 2002	5	1	1	2				5	4	3	24		c*
	Galatheidae gen. indet., sp. indet.	2												c
Munididae	<i>Eosadayoshia bolcensis</i> Beschin <i>et al.</i> , 2016	6												c
	<i>Protomunida pentaspinosa</i> Beschin <i>et al.</i> , 2016	3												c*
Munidopsidae	<i>Eomunidopsis prealpina</i> Beschin <i>et al.</i> , 2016	7												c
	<i>Faxegalathea valeccensis</i> Beschin <i>et al.</i> , 2016	5						1						c
Porcellanidae	<i>Disipia sorbinii</i> Beschin <i>et al.</i> , 2016	12											1	c
	<i>Pachycheles dorsosulcatus</i> Beschin <i>et al.</i> , 2007													c
	<i>Paraporcellana fabianii</i> Beschin <i>et al.</i> , 2016	2												c
	<i>Petrolisthes lineatus</i> Beschin <i>et al.</i> , 2016	12	1				1		3					c
Diogenidae	Porcellanidae gen. indet., sp. indet.	1								3	2	8		p
	<i>Ciliopagurus tethysianus</i> Beschin <i>et al.</i> , 2007													p
	<i>Dardanus bayani</i> Beschin <i>et al.</i> , 2016	1												p
	<i>D. braggiensis</i> Beschin <i>et al.</i> , 2015	2							8					p
	<i>D. curtimanus</i> Müller and Collins, 1991	1												p
	<i>Dardanus suessi</i> Beschin <i>et al.</i> , 2016					1								p
	<i>Dardanus</i> sp.	1										1		p
	<i>Dardanus</i> sp. (1)											1		p
	<i>Diogenes</i> sp.											2		p
	<i>Paguristes extensus</i> Beschin <i>et al.</i> , 2007	3							3			2		p
	<i>P. paucituberculatus</i> Beschin <i>et al.</i> , 2016	2												p
	<i>Paguristes</i> sp.	1											1	c
	<i>Petrochirus minutus</i> Beschin <i>et al.</i> , 2016	1												p

Table 1. (continued).

		Rama	Cracchi	Laisi	Zovo	Monte Postale	Valecco	Vestenanova (Braggi quarry)	S. Pietro (Bertocchi quarry)	Monte Mussolini	Monte Magré	Monte di Malo (C.)	Monte Gecchelina	Monte di Malo (Rossi quarry)
		Bolca area												
BRACHYURA														
Goniodromitidae	<i>Biohermia chalmasi</i> Beschin <i>et al.</i> , 2016	1												c
	<i>Paradistefania piccoli</i> Beschin <i>et al.</i> , 2015				1				3					c
	<i>P. denticulata</i> Beschin <i>et al.</i> , 2016	4												c
	<i>Plagiophthalmus</i> sp.	1												c
Dromiidae	<i>Dromiopsis ceratoi</i> Beschin <i>et al.</i> , 2016	6				14	2							c
	<i>D. longitudovata</i> Beschin <i>et al.</i> , 2016	4							1					c
	<i>D. paleogenica</i> De Angeli and Ceccon, 2014									2				c
	<i>D. parvula</i> Beschin <i>et al.</i> , 2016	4												c
	<i>D. paucigranosa</i> Beschin <i>et al.</i> , 2007	24		2	1				6	1		10		c
Dynomenidae	<i>Acanthodromia zannatoi</i> Beschin <i>et al.</i> , 2016	3												c
	<i>Cracchidynomene areolata</i> Beschin <i>et al.</i> , 2016		1											c
	<i>Dynomene vetusta</i> Beschin <i>et al.</i> , 2016	3	1											c
	<i>Kromtits koberiformis</i> Beschin <i>et al.</i> , 2007	1			4				1	2		11		c
	<i>K. levigatus</i> Beschin <i>et al.</i> , 2007	14			1				1			3		c
	<i>K. subovatus</i> Beschin <i>et al.</i> , 2007	2				2			2			15		c
	<i>Metadynomene veronensis</i> Beschin <i>et al.</i> , 2015								1					c
	<i>Paradynomene antiqua</i> Beschin <i>et al.</i> , 2016	1												c
	<i>Paradynomene pentagonalis</i> (Müller and Collins, 1991)	1												c
Diaulacidae	? <i>Diaulax italicica</i> Beschin <i>et al.</i> , 2007										1			c
Etyidae	<i>Guinotosia tertaria</i> Beschin <i>et al.</i> , 2007										1			c
	<i>Guinotosia</i> sp.	1												c
Homolidae	<i>Latethicocarcinus italicus</i> De Angeli and Ceccon, 2013a										1			c
Dromiacea incertae sedis	<i>Cyamocarcinus angustifrons</i> Bittner, 1883	23	2		16				12	7	X	52		c*
	<i>C. budensis</i> Oppenheim, 1899	2	1						2	2		2		c
	<i>Eotrachynotocarcinus airaghii</i> Beschin <i>et al.</i> , 2007	15	1		1				19	3		23		c
Cyclodorippidae	<i>Tymolus italicus</i> Beschin <i>et al.</i> , 2016	1												c
Raninidae	<i>Antonioranina globosa</i> (Beschin <i>et al.</i> , 1988)			2										c
Calappidae	<i>Corallomursia eocaena</i> De Angeli and Ceccon, 2014								4			3		c
	<i>C. pauciornata</i> Beschin <i>et al.</i> , 2015								5					c
	<i>Paracorallomursia medizzai</i> Beschin <i>et al.</i> , 2016	3												c
	<i>Pseudocorallomursia barbierii</i> Beschin <i>et al.</i> , 2016	1												c
Leucosiidae	Leucosidae gen. indet., sp. indet.	1												p
Epiatlidae	<i>Bolcapisa giulianae</i> Beschin <i>et al.</i> , 2016	3												c

Table 1. (continued).

		Rama	Cracchi	Laisi	Zovo	Monte Postale	Valecco	Vestenanova (Braggi quarry)	S. Pietro (Bertocchi quarry)	Monte Mussolini	Monte Magrè	Monte Malo (C.)	Monte Gecchelina	Monte di Rossi
		Bolca area												
Inachoididae	<i>Vicetiulita granulata</i> De Angeli and Ceccon, 2015									2			c	
Parthenopidae	<i>Braggilambrus tani</i> De Angeli and Caporondo, 2016									1			c	
	<i>Daldorfia eocaena</i> Beschin et al., 2007										1		c	
	<i>Eogarthambrus guinotae</i> De Angeli et al., 2010										1	c		
	<i>Mesolambrus declinatus</i> Müller and Collins, 1991	4					1		5		2		c	
	<i>M. ypresianus</i> Beschin et al., 2015	4	3				1		7				c	
Cancridae	Parthenopidae gen. e sp. indet.										1		p	
	<i>Nicoliscarcinus rotundatus</i> Beschin et al., 2016	1										c		
	<i>Rama lineatuberculata</i> Beschin et al., 2016		15									c		
Corystidae	<i>Ypresicorystes expansus</i> Beschin et al., 2016	1										c		
Dairidae	<i>Daira sicula</i> (Di Salvo, 1933)	3						3		3		7		c
	<i>D. vestenanovensis</i> Beschin et al., 2015	1						26					c	
Carcinidae	<i>Miopipus zovensis</i> Beschin et al., 2016	1			2								c	
Macropipidae	<i>Boschettia giampietroi</i> Busulini et al., 2003										1		c	
	<i>Gecchelicarcinus lorigae</i> Beschin et al., 2007	6						5	1		7		c	
	<i>G. zanderigoi</i> Beschin et al., 2016	1										c		
	<i>Vestenanovia carinata</i> Beschin et al., 2015		7					3				c		
Portunidae	<i>Eocharybdis rugosa</i> Beschin et al., 2016		1								1		c	
	<i>Lessinithalamita gioiae</i> De Angeli and Ceccon, 2015	6									7		c	
	<i>Neptocarcinus dezanchei</i> Beschin et al., 2015							1				c		
Carpiliidae	<i>Braggicarpilius marginatus</i> Beschin et al., 2015		1					1					c	
	<i>Carpilius petreus</i> Beschin et al., 2007					1			2		4		c	
	<i>Corallicarpilius arcuatus</i> De Angeli and Ceccon, 2015										10		c	
	<i>Paraocalina multilobata</i> Beschin et al., 2007					1			13		2		c	
Palaeoxanthopsidae	<i>P. silviae</i> Beschin et al., 2016	6											c	
	<i>Frontelata spinacomposita</i> Beschin et al., 2016	3											c	
	<i>Latuxanthides dentatus</i> De Angeli and Ceccon, 2015										1		c	
Tumidocarcinidae	? <i>Lobulata</i> sp.	1									1		c	
	<i>Titanocarcinus raulinianus</i> A. Milne Edwards, 1863	1									3		c	
Pilumnidae	<i>Eumorphactaea convexa</i> Beschin et al., 2016	1											c	
	<i>Galenopsis depressa</i> A. Milne Edwards, 1872	3	1										c	
	<i>G. similis</i> Bittner, 1875	1			2			2		1	X	53	c*	
	<i>Glabropilumnus trispinosus</i> Beschin et al., 2016	1											c	

Table 1. (continued).

	Rama	Cracchi	Laisi	Zovo	Monte Postale	Valecco	Vestenanova (Braggi quarry)	S. Pietro (Bertocchi quarry)	Monte Mussolini	Monte Magré	Monte Malo (C.)	Monte Gecchelina	Monte di Rossi
	Bolca area												
	<i>Lobogalenopsis quadrilobata</i> (Lörenthey, 1898)	22		13	2		2	2		3			c
	<i>Palladiocarcinus brevidentatus</i> De Angeli and Ceccon, 2014	5					1		4				c
	? <i>Pilumnus</i> sp.									1			p
	<i>Prealpicarcinus dallagoi</i> De Angeli and Ceccon, 2015								6				c
	<i>P. laisensis</i> Beschin <i>et al.</i> , 2016	3	1	1	1				1				c
	<i>Santeella</i> sp.												c
	<i>Zovocarcinus muelleri</i> De Angeli and Garassino, 2014					1							c
Domeciidae	<i>Palmyria levigata</i> Beschin <i>et al.</i> , 2016	2				1							c
	<i>Tropicalia parva</i> Beschin <i>et al.</i> , 2016	23											c
Panopeidae	<i>Bittnereus vicentinus</i> (Bittner, 1875)	1			1					3			c
	<i>B. depressus</i> Beschin <i>et al.</i> , 2016	1											c
	<i>B. tumidus</i> Beschin <i>et al.</i> , 2016	6											c
	<i>Laevicarcinus lioyi</i> Beschin <i>et al.</i> , 2007	7	2		1			2	1		7		c
	<i>L. serratus</i> Beschin <i>et al.</i> , 2016				1								c
	<i>Panopeus incisus</i> Beschin <i>et al.</i> , 2007	7								9			c
	<i>P. postalensis</i> Beschin <i>et al.</i> , 2016	3				1							c
	<i>Sereneopeus humilis</i> Beschin <i>et al.</i> , 2007									2			c
Tetraliidae	<i>Eurotetralia loerentheyi</i> (Müller, 1975)									1			c
	<i>Scutata eocenica</i> Beschin <i>et al.</i> , 2016	5											c
	<i>Tetralia minuta</i> Beschin <i>et al.</i> , 2016	3											c
	<i>T. vicetina</i> De Angeli and Ceccon, 2013b									4			c
Trapeziidae	<i>Archaeotetra lessinea</i> De Angeli and Ceccon, 2013b	3		1	1					5			c
	<i>Eomaldivia trispinosa</i> Müller and Collins, 1991									4			c
	<i>Montemagralia lata</i> De Angeli and Ceccon, 2016									2			c
	<i>Paratetralia convexa</i> Beschin <i>et al.</i> , 2007	9	2	4	1			7	24	8	46		c
	<i>P. sulcata</i> De Angeli and Ceccon, 2013b	3								1			c
Xanthidae	? <i>Chlorodiella</i> sp.										1		c
	<i>Eoxanthops scutatus</i> Beschin <i>et al.</i> , 2016	3											c
	<i>Etisus arduinoi</i> Beschin <i>et al.</i> , 2007	39	1			1		1	2		5		c
	<i>Haydnella granosa</i> Beschin <i>et al.</i> , 2016	1		2									c
	<i>H. maladensis</i> Beschin <i>et al.</i> , 2007					2		2			2		c
	<i>Nanocassiope secretanae</i> Beschin <i>et al.</i> , 2016	1											c
	<i>Neoliomera minuta</i> Beschin <i>et al.</i> , 2015								1				c
	<i>N. paleogenica</i> Beschin <i>et al.</i> , 2007									6			c

Table 1. (continued).

		Rama	Cracchi	Laisi	Zovo	Monte Postale	Valecco	Vestenanova (Braggi quarry)	S. Pietro (Bertocchi quarry)	Monte Mussolini	Monte Magrè	Monte Malo (C.)	Monte Gecchelina	Monte di Rossi quarry)
		Bolca area												
	<i>Phlyctenodes tuberculosus</i> A. Milne Edwards, 1862	9												c
	<i>P. edwardsi</i> Beschin <i>et al.</i> , 2016	10												c
	<i>P. krenneri</i> Lörenthey, 1898	11	1					4						c
	<i>P. multituberculatus</i> Beschin <i>et al.</i> , 2007	59	1			1		7	2			27		c
	<i>Specocarcinus latus</i> Beschin <i>et al.</i> , 2016	4												c
Xanthoidea incertae sedis	<i>Actaeites lobatus</i> Müller and Collins, 1991				1			1				5		c
	<i>Muelleroplax minuscula</i> (Beschin <i>et al.</i> , 2007)					1			1			1		c
	<i>Pilumnomimus planidentatus</i> Müller and Collins, 1991	6										1		c
	<i>P. dorsocarinatus</i> Beschin <i>et al.</i> , 2016	4												c
	<i>P. miettoi</i> Beschin <i>et al.</i> , 2016	1												c
	<i>Prochlorodius ellipticus</i> Müller and Collins, 1991	29	2			1		11	1			5		c
	Xanthoidea fam., gen. e sp. indet. (1)											1		p
	Xanthoidea fam., gen. e sp. indet. (2)											1		p
Pseudoziidae	<i>Ramozius punctatus</i> Beschin <i>et al.</i> , 2016	1												c
Chasmocarcinidae	<i>Chasmocarcinus cf. guerini</i> (Vía, 1959)							1						c
Euryplacidae	<i>Alponella paleogenica</i> Beschin <i>et al.</i> , 2016	4												c
	<i>Coralliplax exigua</i> Beschin <i>et al.</i> , 2016	3						1						c
	<i>Prealpiplax lessinea</i> Beschin <i>et al.</i> , 2016	1												c
Mathildellidae	<i>Branchioplax cordata</i> Beschin <i>et al.</i> , 2016	6												c
	<i>B. parva</i> Beschin <i>et al.</i> , 2007		1					2				3		c
	<i>B. sulcata</i> Müller and Collins, 1991	4						1				1		c
	<i>Branchioplax</i> sp. (2)							1						c
Cryptochiridae	<i>Montemagrechirus tethysianus</i> De Angeli and Ceccon, 2015										3			c
Pinnotheridae	Pinnotheridae gen. indet., sp. indet.	1												c
Crossotonotidae	<i>Montemagrellus denticulatus</i> De Angeli and Ceccon, 2014										2			c
Plagusiidae	<i>Petrusia striata</i> Beschin <i>et al.</i> , 2016	1												c
Varunidae	<i>Brachynotus corallinus</i> Beschin <i>et al.</i> , 2007	6				1						1		c

(Fig. 3): the most abundant species is *Galenopsis similis* Bittner, 1875 (RA=0.1421); 10 species are exclusive for this outcrop (3 Anomura and 7 Brachyura) and all of them are represented by a very small number of specimens (RA=0.0027) excluding only *Neoliomera paleogenica* Beschin *et al.*, 2007, which shows a medium abundance (RA=0.0161). Twenty seven of these taxa have been found also at Rama.

In the Braggi quarry at Vestenanova 199 specimens have been found referred to 47 species (6 Anomura e 41 Brachyura; H'=3.39); the most abundant is *Daira vestenanovensis* Beschin *et al.*, 2015 (RA=0.1307), which is elsewhere an infrequent taxon. Seven species are known only for this outcrop. All of them, excluding *Corallomursia pauciornata* Beschin *et al.*, 2015, are represented by a single specimen

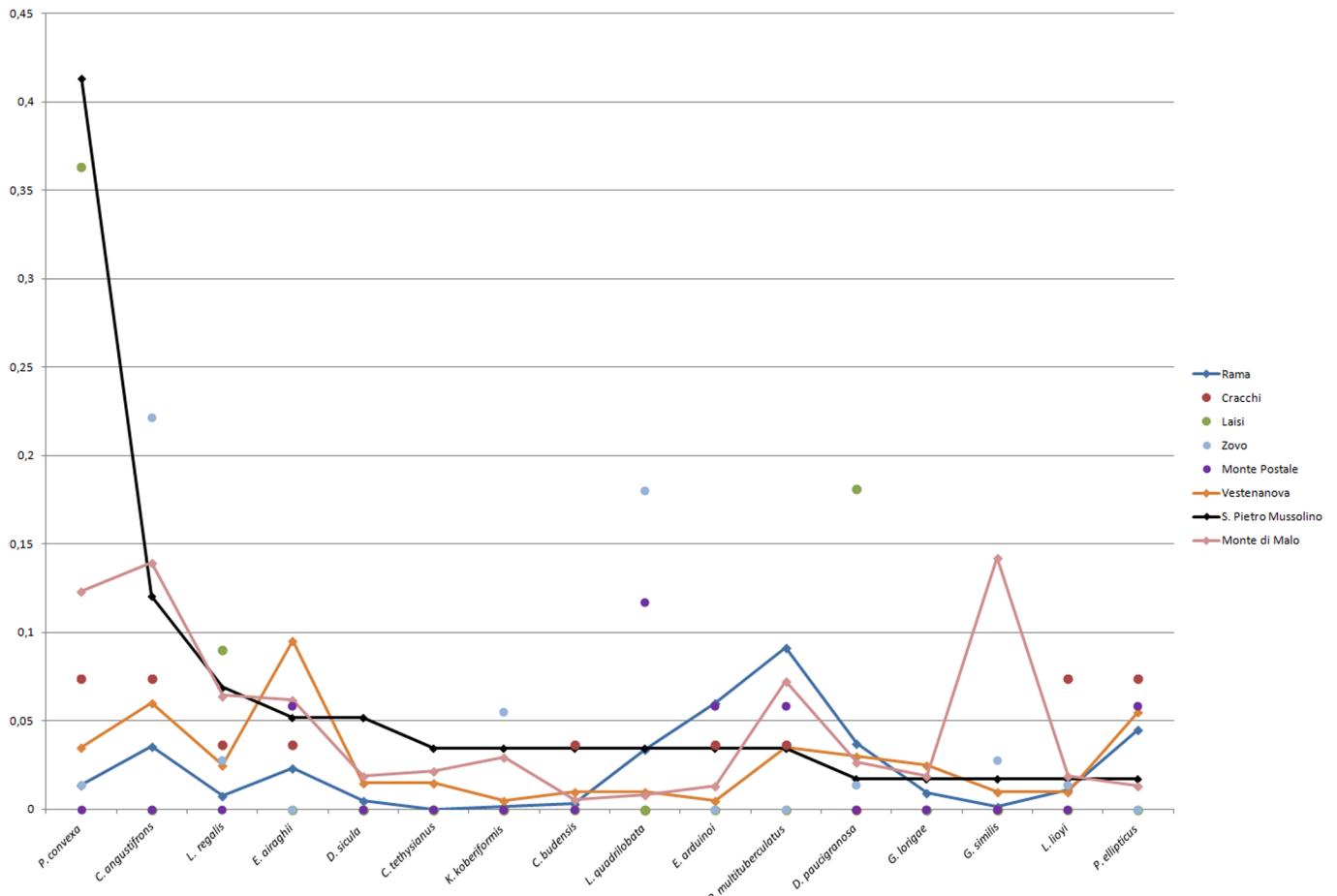


Fig. 3. Relative abundance of the species found in all sites.

(RA=0.0050) (Beschin *et al.*, 2015; De Angeli and Caporiondo, 2016). Twenty nine of these species have been found also at Rama, and 28 at Contrada Gecchelina.

The bioherms found in the Bertocchi quarry at San Pietro Mussolini have yielded 58 specimens referred to 2 species of Anomura and 14 of Brachyura ($H' = 2.16$) (Tessier *et al.*, 2011). Only one among them has not been found at Rama but all are present also at Contrada Gecchelina and in Braggi quarry. By far the most abundant species is *Paratetralia convexa* Beschin *et al.*, 2007. We note that all the species found in Bertocchi quarry are in the group of the most abundant taxa of the above considered outcrops and actually constitute a faunistic association that can be considered as typical for the Ypresian coral-algal buildups of the Eastern Lessini Mountains. It comprises among the Anomura *Lessinigalathea regalis* De Angeli and Garassino, 2002 and among the Brachyura *Dromiopsis paucigranosa* Beschin *et al.*, 2007, *Kromtthis koberiformis* Beschin *et al.*, 2007, *Cyamocarcinus angustifrons* Bittner, 1883 and *C. budensis* Oppenheim, 1899, *Eotrachynotocarcinus airaghii* Beschin *et al.*, 2007, *Daira sicula* (Di Salvo, 1933), *Gecchelicarcinus lorigae* Beschin *et al.*, 2007, *Galenopsis similis* Bittner, 1875, *Lobogalenopsis quadrilobata* (Lörenthey, 1898), *Laevicarcinus lioyi* Beschin *et al.*, 2007, *Paratetralia convexa* Beschin *et al.*, 2007, *Etisus arduinoi* Beschin *et al.*, 2007, *Phlyctenodes multituberculatus* Beschin *et al.*, 2007 and *Prochlorodius ellipticus* Müller and

Collins, 1991 (Fig. 3). Some of these species are long-lived and probably eurytopic; in fact they have been found in other outcrops in Veneto and in upper Eocene rocks in Budapest (Hungary) (*C. angustifrons*, *G. similis*, *L. quadrilobata*, *P. ellipticus*) (Müller and Collins, 1991) and, in a smaller number, in Sicilia (*C. angustifrons*, *G. similis*, *L. quadrilobata*, *D. sicula*) (Di Salvo, 1933).

Among the bioconstructions found in the Bolca area, also the Zovo outcropping has yielded a rich fauna (72 specimens) with 3 species of Anomura and 21 of Brachyura ($H' = 2.51$). This is the only site where some Raninoidea have been found. In fact Tessier *et al.* (2004) had already reported for this location a specimen referred to *Antonioranina globosa* (Beschin *et al.*, 1988) and the new further samplings have confirmed the presence of this species (Beschin *et al.*, 2016). The findings of these burrowing crustaceans which live in clastic bottoms suggest a *post mortem* transport from a different but adjoining environment. All the other species are not exclusive of the site excluding *Laevicarcinus serratus* Beschin *et al.*, 2016, known only from its holotype. Sixteen species from Zovo have been collected also at Rama, 16 also at Contrada Gecchelina, 13 also at Vestenanova and 8 also at San Pietro Mussolini. The most abundant species at Zovo are *Cyamocarcinus angustifrons* Bittner, 1883 (RA = 0.2222) and *Dromiopsis ceratoi* Beschin *et al.*, 2016 (RA = 0.1944). Among the species found at Zovo, Vestenanova and Contrada

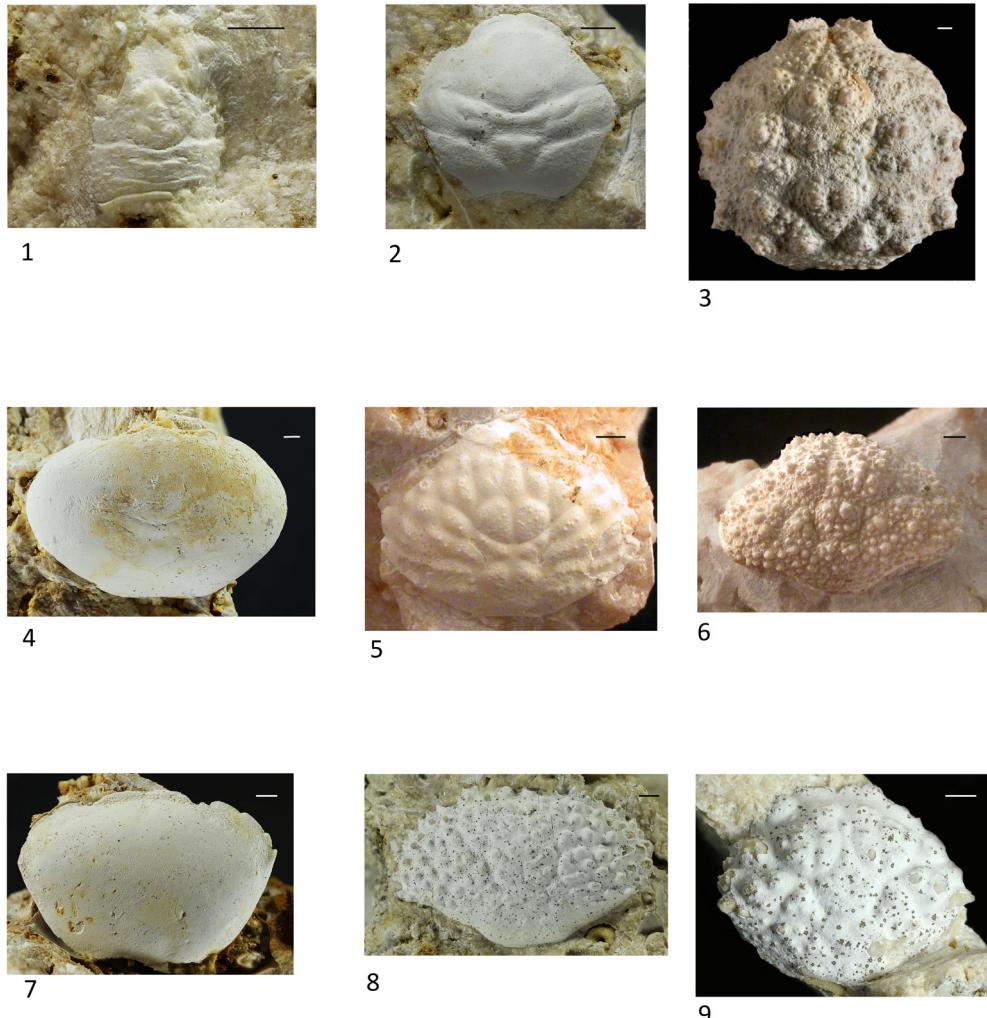


Plate 1. f. 1—*Faxegalathea valeccensis* Beschin et al., 2016; VR 93891; carapace: dorsal view; Rama di Bolca; W: 2.3; L: 2.9. f. 2—*Dromiopsis paucigranosa* Beschin et al., 2007; VR 93980; carapace: dorsal view; Rama di Bolca; W: 5.8. f. 3—*Kromititis koberiformis* Beschin et al., 2007; holotype MCZ 1927; carapace: dorsal view; Contrada Gecchelina at Monte di Malo; W: 18.5; L: 16.9. f. 4—*Cyamocarcinus angustifrons* Bittner, 1883; VR 94053; carapace: dorsal view; Rama di Bolca; W: 16.2. f. 5—*Eotrachynotocarcinus airaghii* Beschin et al., 2007; MCZ 3499; carapace: dorsal view; Braggi quarry at Vestenanova; W: 9.3; L: 7.1. f. 6—*Daira sicula* (Di Salvo, 1933); MCZ 3169; carapace: dorsal view; Bertocchi quarry at San Pietro Mussolini; W: 11.0; L: 7.4. f. 7—*Lobogalenopsis quadrilobata* (Lörenthey, 1898); VR 94212; carapace: dorsal view; Zovo; W: 12.2. f. 8—*Phlyctenodes multitudinatus* Beschin et al., 2007; VR 94315; carapace: dorsal view; Rama di Bolca; W: 12.8. f. 9—*Etisus arduinoi* Beschin et al., 2007; VR 94368; carapace: dorsal view; Rama di Bolca; W: 8.3; L: 6.1. Scale bars equal 1 mm; W = maximum width of carapace; L = maximum length of carapace.

Gecchelina, but not at Rama, are *Paraocalina multilobata* Beschin et al., 2007, *Haydnella maladensis* Beschin et al., 2007, *Acteites lobatus* Müller and Collins, 1991 and *Muelleroplax minuscula* (Beschin et al., 2007). *A. lobatus* is a long-lived species: in fact it was recognized for the first time in the Late Eocene of Hungary (Müller and Collins, 1991), but is present also in Oligocene rocks of the Vicenza territory (De Angeli and Beschin, 2008, De Angeli et al., 2010).

Despite its really small exposure, Cracchi is an interesting site. Here 27 specimens have been collected representing 2 species of Anomura and 18 of Brachyura ($H' = 2.92$); 16 of them have been found also at Rama; *Cracchidynomene areolata* Beschin et al., 2016, at the moment is exclusive for this outcrop.

Also at Monte Postale and Valecco the outcroppings have small areal extent. In the first site 2 species of Anomura and 12 of Brachyura have been found (17 specimens; $H' = 2.59$). The only species exclusive being *Panopeus postalensis* Beschin et al., 2016. At Valecco a single specimen of *Faxegalathea valeccensis* Beschin et al., 2016, a species found also at Rama, has been collected (clearly in this case the calculation of H' does not make sense) (Plate 1).

Laisi can be reached only with difficulty so at the moment only 11 specimens have been collected, 2 species of Anomura and 5 of Brachyura ($H' = 1.77$) all also known from Rama except *Paradistefania piccolii* Beschin et al., 2015.

A cluster analysis to compare these faunas has been carried out using the software PAST (Fig. 4). The dendrogram points

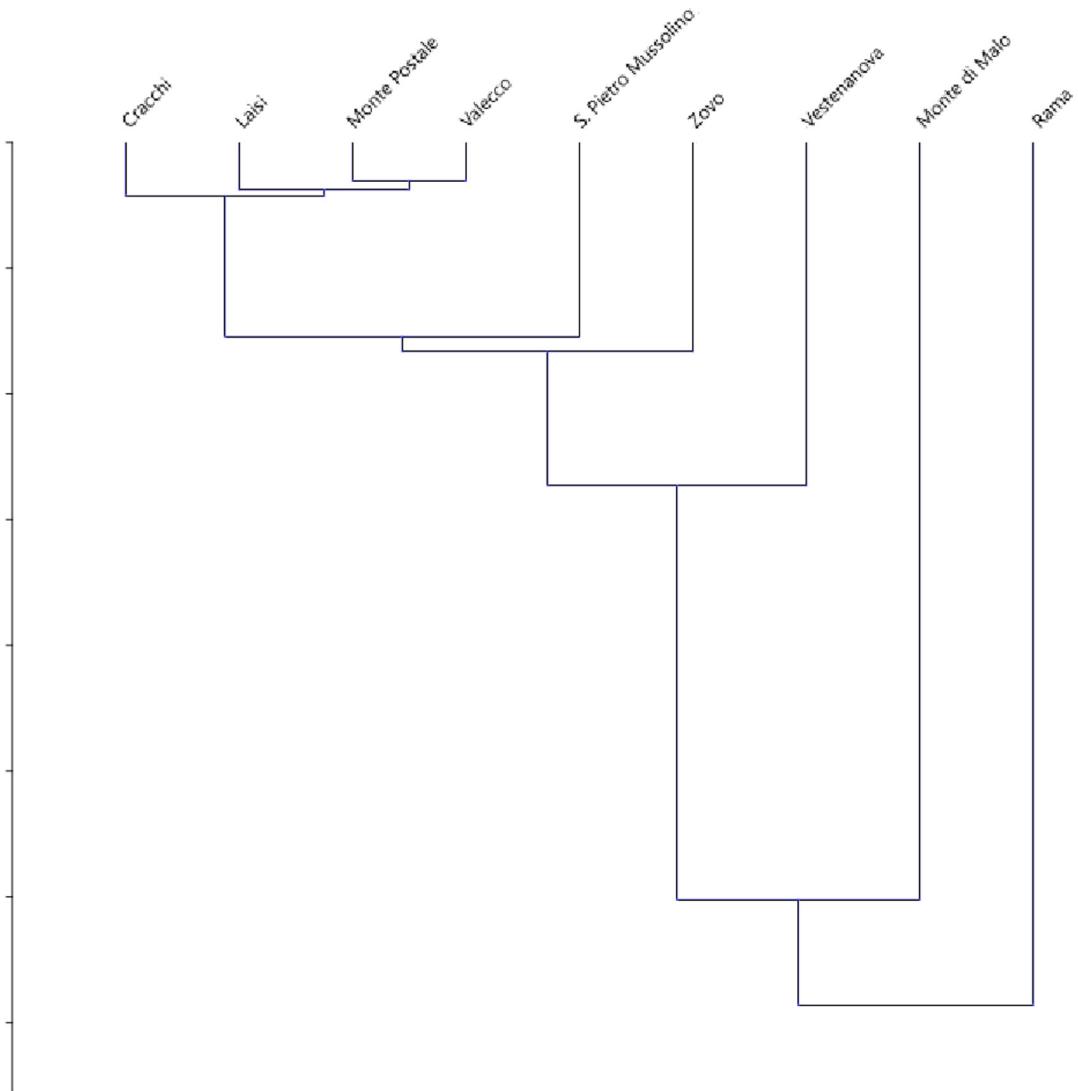


Fig. 4. Dendrogram showing the statistic similarities among the faunas found in all the considered sites (PAST's cluster analysis). Branch length is proportional to the distance.

out the distance among the decapod faunas from the considered sites depending on the number of specimens and of species; the results of this analysis prove that Rama fauna is much less similar to those from the other considered sites, as it can also be assumed on the basis of its abundance and its H' index.

Comparisons with the findings of Monte Magré cannot be made because the crustaceans have been collected there from stratified deposits and moreover their comprehensive overview was not given. In Figure 5 a comparison of the Shannon-Weaver indices calculated for the studied Ypresian sites, and the ones of two European coral-algal deposits with some faunistic affinities is reported: they are the Danian site of Faxe (Danmark) and the upper Eocene sites of Budapest (Hungary).

The high number of species recognized in the bioconstructions cropping out in the Eastern Lessini Mountains and the resulting high biodiversity index ($H' = 4.00$) can be compared with the ones of the faunas today dwelling in the shallower water coral buildups of the Central Pacific (Klompmaker *et al.*, 2016); this datum strengthens the

paleoenvironmental hypothesis proposed for the area of Bolca. Moreover, as a correlation exists between the wideness of the area that a community occupies and its biodiversity, the high value of the Shannon-Weaver index allows to support the idea of the existence of a vast territory occupied by patch reefs.

The site of Faxe has a Shannon index definitely lower ($H' = 1.71$) as Klompmaker *et al.* (2016) underlined justifying its value with a colder sea. Despite the diversities due to different age and paleoenvironmental conditions, clear faunistic affinities exist between the Danish and the western Venetian sites: the number of species of Galatheoidea is high in both and some genera have so far been found only in these locations such as *Protomunida* Beurlen, 1930 and *Faxegala-thea* Jakobsen and Collins, 1997. As far as the fauna from the upper Eocene in Budapest is concerned, the biodiversity index has been calculated using the data given by Müller and Collins (1991). Its value is weakly lower than the one found for the sites of Veneto. In this case the affinities are much higher and many species are present in both despite the different ages:

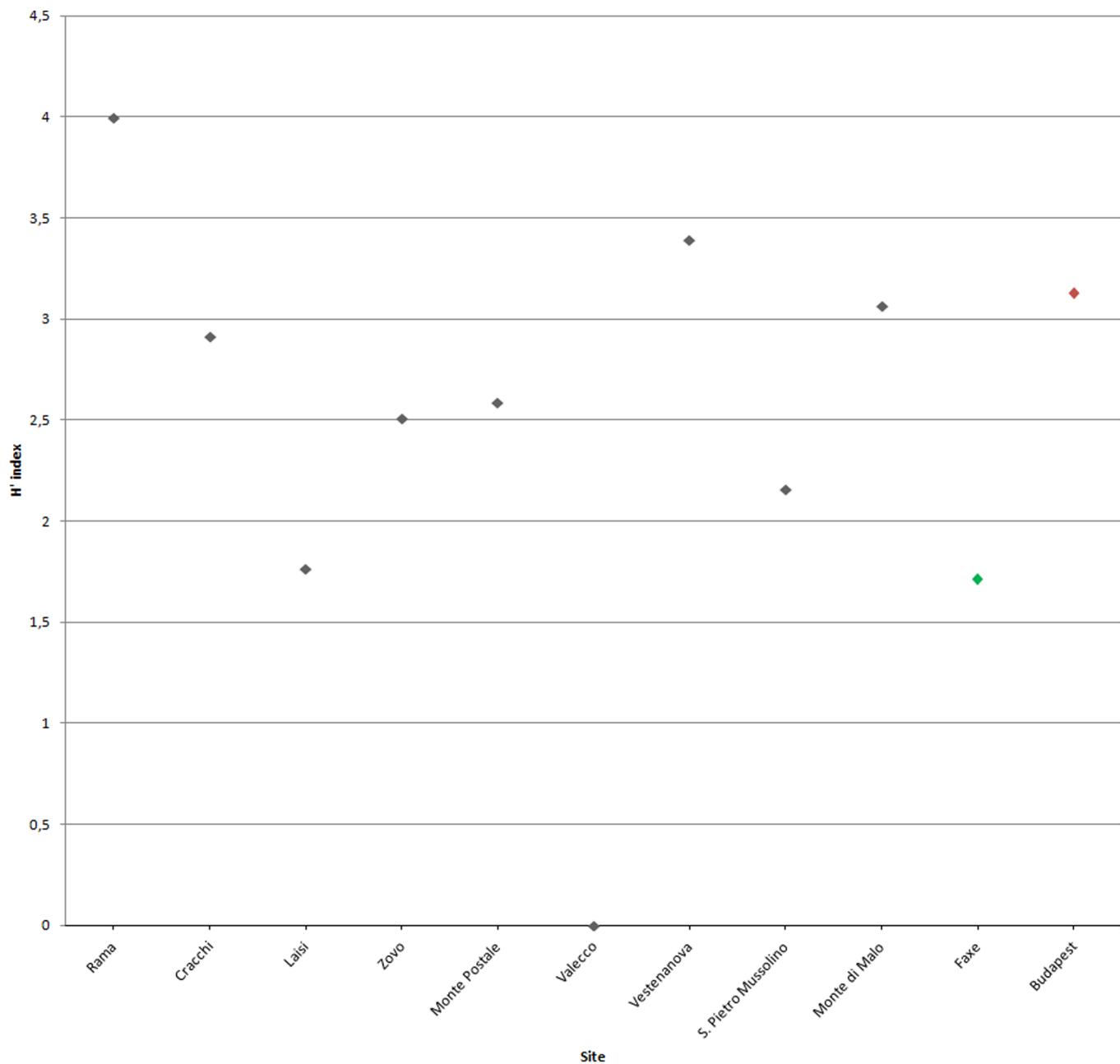


Fig. 5. Comparison of the Shannon-Weaver indices calculated for the studied Ypresian sites, for the Danian site of Faxe (Danmark) and for the upper Eocene sites of Budapest (Hungary).

Dardanus curtimanus Müller and Collins, 1991, *Paradynomena pentagonalis* (Müller and Collins, 1991), *Cyamocarcinus angustifrons* Bittner, 1883, *Mesolambrus declinatus* Müller and Collins, 1991, *Galenopsis similis* Bittner, 1875, *Lobogalenopsis quadrilobata* (Lörenthey, 1898), *Phlyctenodes krenneri* Lörenthey, 1898, *Actaeites lobatus* Müller and Collins, 1991, *Pilumnomimus planidentatus* Müller and Collins, 1991, *Prochlorodius ellipticus* Müller and Collins, 1991, *Branchioplax sulcata* Müller and Collins, 1991. A different kind of similarity is recorded between the Monte Magré and Budapest faunas.

The crustacean faunas here considered appear strongly associated to the shallow water coral-reef-ecosystems. The

living representatives of the Dynomenidae Ortmann, 1892, are often found associated with corals as their food consists of organic fragments from the substrate or mucous of corals (McLay, 1999): 9 species within the family are described for the Eastern Lessini Mountains. The recent Tetraliidae Castro *et al.*, 2004 and Trapeziidae Miers, 1886 (5 species from the analyzed bioconstructions) are typical symbionts of reef corals, and the genus *Tetralia* Dana, 1851 establishes obligate associations with many species of shallow water Scleractinia (Castro *et al.*, 2004).

Considering the size of the species found in these Ypresian coral-algal buildups, the tiny specimens are the most abundant, probably advantaged in finding shelter and food within the

Table 2. Dimensions (maximum Width and maximum Length) of all measurable *Cyamocarcinus angustifrons* carapaces found in the studied outcrops.

No.	W	L	W/L
VR 94060	3.30	3.00	1.100000
VR 94040	4.20	3.40	1.235294
VR 94061	4.80	3.50	1.371429
VR 94074	5.30	3.70	1.432432
VR 94069	5.50	4.80	1.145833
MCZ 3602	5.50	4.50	1.222222
VR 94041	5.50	3.80	1.447368
VR 94062	6.20	4.10	1.512195
MCZ 3604	6.50	5.10	1.274510
MCZ 1710	6.60	5.00	1.320000
VR 94042	6.90	4.60	1.500000
VR 94075	7.00	5.10	1.372549
VR 94043	7.00	4.60	1.521739
VR 94071	7.90	6.90	1.144928
VR 94044	8.00	5.70	1.403509
VR 94045	8.00	5.10	1.568627
VR 94067	8.10	4.30	1.883721
VR 94046	8.50	4.10	2.073171
VR 94070	8.90	6.70	1.328358
VR 94047	8.90	5.90	1.508475
VR 94072	9.00	6.80	1.323529
VR 94066	9.30	9.20	1.010870
VR 94063	9.40	6.60	1.424242
VR 94048	9.40	6.30	1.492063
MCZ 1711	9.60	6.80	1.411765
MCZ 1717	10.80	5.80	1.862069
VR 94077	11.20	10.50	1.066667
MCZ 1685	11.20	8.40	1.333333
VR 94049	11.70	8.30	1.409639
VR 94068	11.90	8.80	1.352273
VR 94050	11.90	8.10	1.469136
MCZ 3607	12.00	7.90	1.518987
MCZ 1693	12.30	8.80	1.397727
VR 94051	12.50	6.50	1.923077
MCZ 1697	12.80	8.00	1.600000
VR 94076	12.90	10.80	1.194444
MCZ 1679	13.00	10.40	1.250000
MCZ 1704	13.20	9.20	1.434783
VR 94078	13.60	10.90	1.247706
MCZ 1689	14.80	10.20	1.450980
MCZ 1687	15.10	9.50	1.589474
VR 94052	15.20	10.00	1.520000
MCZ 1701	15.50	11.80	1.313559
VR 94064	15.60	10.70	1.457944
VR 94053	16.20	10.90	1.486239
VR 94054	17.70	12.00	1.475000
VR 94055	17.80	11.80	1.508475
VR 94056	17.90	11.30	1.584071
MCZ 1702	18.50	12.80	1.445313
VR 94065	18.80	12.20	1.540984
VR 94079	19.30	14.80	1.304054
MCZ 1709	20.40	14.30	1.426573
MCZ 1706	20.50	14.60	1.404110
VR 94057	20.60	11.70	1.760684
MCZ 3609	21.50	13.60	1.580882

Table 2. (continued).

No.	W	L	W/L
VR 94073	21.70	16.90	1.284024
MCZ 1708	21.90	15.10	1.450331
MCZ 1688	22.50	15.20	1.480263
VR 94058	24.70	16.60	1.487952
MCZ 1696	25.20	17.30	1.456647
MCZ 1681	25.40	16.50	1.539394
MCZ 1699	26.60	13.60	1.955882
VR 94059	27.00	18.00	1.500000
MCZ 1721	30.40	21.40	1.420561
MCZ 1680	31.80	20.50	1.551220
MCZ 1677	34.00	24.00	1.416667
MCZ 1678	36.60	23.80	1.537815
MCZ 1937	39.90	26.10	1.528736

living or sometimes dead corals; however also larger carapaces have been collected (*Cyamocarcinus angustifrons*, *Kromtittis koberiformis*, *Galenopsis similis*). Probably the largest species lived along the edge of the coral reef and not within the corals.

The availability of so many specimens, some of them measurable, made it possible to analyze the change of the shape of carapace during growth for some species.

One hundred and twelve specimens of *Cyamocarcinus angustifrons* Bittner, 1883 (*Dromiacea incertae sedis*) have been collected with a carapace length range from 3.0 to 39.3 mm; for 68 of them it was possible to obtain both length and width (Tab. 2); Figure 6 shows that in this species the W/L increases with growth; instead in the small species *Bolcagallathea corallina* Beschin et al., 2016 (Galatheidae Samouelle, 1819) (width range 3.8 to 7.7 mm) the W/L ratio remains quite the same (W/L = 0.9).

In *Gecchelicarcinus lorigae* Beschin et al., 2007 (Macro-pipidae Stephenson and Campbell, 1960) and in *Alponella paleogenica* Beschin et al., 2016 (Euryplacidae Stimpson, 1871), the smallest specimens differ in some features from the largest ones, suggesting changes of the shape of carapace during growth (Plate 2). Nineteen specimens of *Gecchelicarcinus lorigae* have been collected in different sites in the Eastern Lessini Mountains (Tab. 1): the largest carapaces (length 8.1 to 18.6 mm) show a sinuous frontal margin with a deep open median notch, great development of the antero-lateral teeth, subdivided dorsal regions (particularly the gastric and cardiac ones) with granulated surface; the specimen VR 94151, collected at Rama, (length 3.1 mm) is probably a juvenile: it is much smaller than all the others and its carapace is subsquared with weakly swollen regions, the front is made of two lamellae with a just corrugated margin, the orbits are very large and situated at the anterolateral angle, the lateral spines are rudimentary; its attribution to *G. lorigae* is due to the similar convexity of the carapace, the analogous shape and ornamentation of the dorsal regions (very apparent the row of tubercles on the epibranchial lobes) and the equal number of lateral spines.

All the four specimens referred to *Alponella paleogenica* were found at Rama. The largest individual, the holotype, shows subhexagonal carapace, short subparallel anterolateral

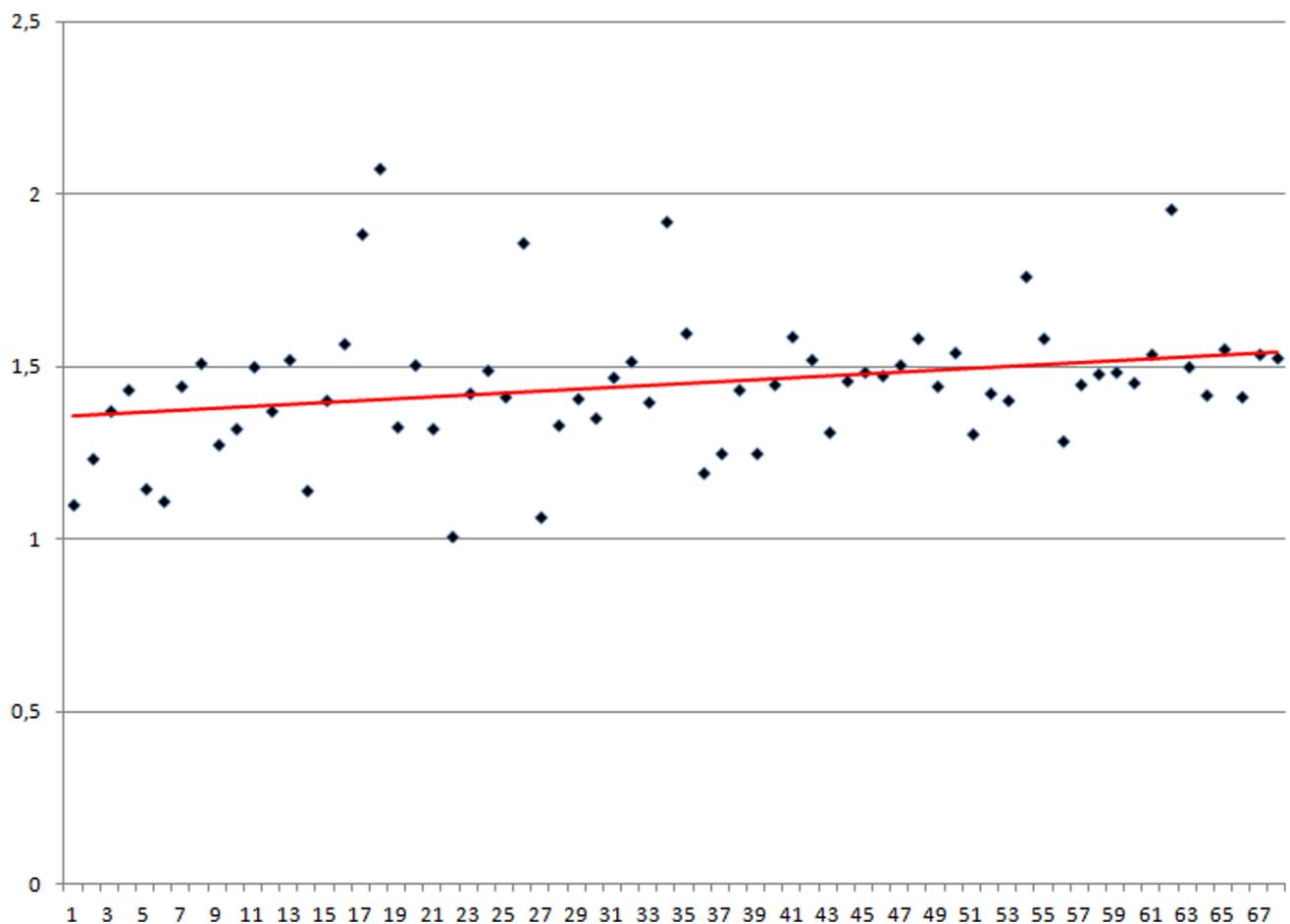


Fig. 6. Dimension dependent Width/Length ratio in *Cyamocarcinus angustifrons* carapaces, including linear regression.

margins with three tiny spines, longer convergent posterolateral margins; the smallest ones are more squared and more vaulted; the anterolateral spines are barely visible and their dorsal regions are more apparent but this might be caused by the fact that they are moulds; anyway these specimens are very small (about 2.0 mm) and were collected smashing the rock so their counterparts cannot be found. All the carapaces are referred to the same species for their wide front with a median longitudinal concavity and an almost straight margin, very large orbits situated at the anterolateral angle, and a similar structure of the dorsal regions, above all the posterior ones.

In both the considered species the overall shape of the carapace changes during growth: in the juveniles it appears more squared, the orbits are proportionally larger and more lateral, the lateral margins are shorter and the anterolateral spines poorly developed. The same set of characters is described by Schweitzer (2001) in the carapace that she proposed as a juvenile specimen of *Branchioplax washingtoniana* Rathbun, 1916 (Mathildellidae Karasawa and Kato, 2003) (Late Eocene; NW North America). Guinot (1989) analyzing the living species referred to *Carcinoplax* H. Milne Edwards, 1852 (Goneplacidae Macleay, 1838) could observe their growth pattern; also in most of these forms the general shape of carapace changes as the orbits become proportionally smaller and the anterolateral margins longer, but the antero-

lateral spines are usually less developed in the larger individuals.

The assignment of specimens with juvenile features to a fossil species cannot be certain, unless a growth series is available: it is the case of the specimens of *Ranina speciosa* Münster, 1840 (Raninidae De Haan, 1839) found in the Oligocene of Piemonte (NW Italy) showing an enlargement of the anterior portions of carapace and a greater development of the anterolateral spines during growth (Allasinaz, 1987), and of *Cancer sismondai* Meyer, 1843 (Cancridae Latreille, 1802) from the Pliocene of Puglia (SE Italy) whose larger carapaces are considerable flattened and enlarged than the smaller ones (Bonfiglio and Donadeo, 1982).

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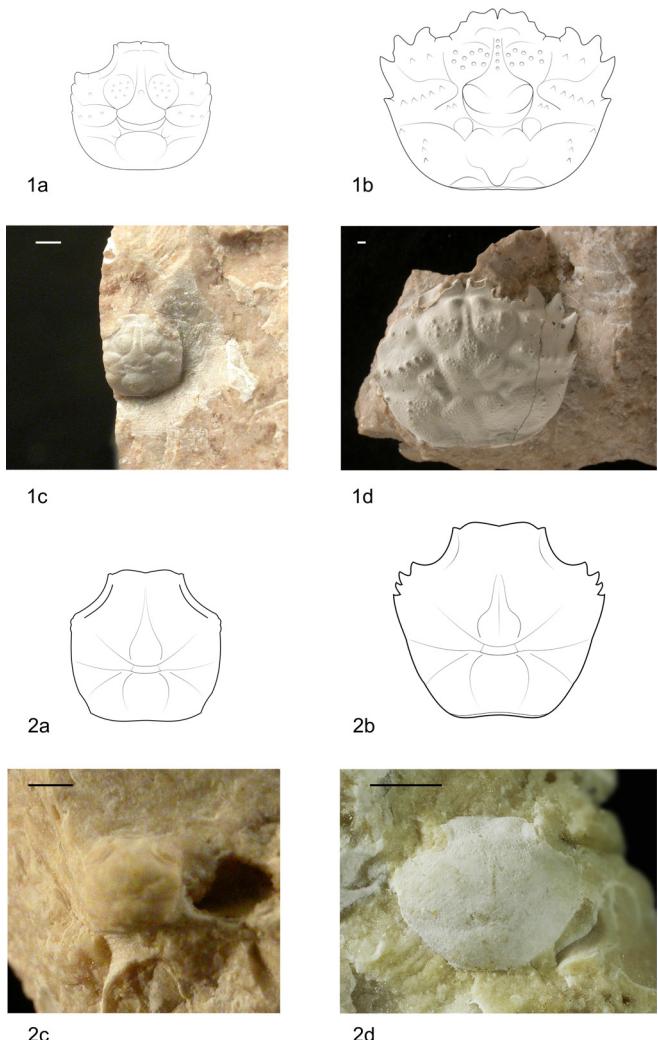


Plate 2. f. 1—*Gecchelicarcinus lorigae* Beschin et al., 2007; carapaces: dorsal view; a: line drawing of a juvenile specimen; b: line drawing of an adult specimen; c: VR 94151; Rama di Bolca; L: 3.1; d: holotype MCZ 1813; Contrada Gecchelina di Monte di Malo; W: 24.0; L: 18.6. f. 2—*Alponella paleogenica* Beschin et al., 2016; carapaces: dorsal view; a: line drawing of a juvenile specimen; b: line drawing of an adult specimen; c: VR 94534; Rama di Bolca; W: 2.1; d: holotype VR 94537; Rama di Bolca; W: 2.7. Scale bars equal 1 mm; W = maximum width of carapace; L = maximum length of carapace.

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