The genus *Phlyctenodes* Milne Edwards, 1862 (Crustacea: Decapoda: Xanthidae) in the Eocene of Europe

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ABSTRACT

A systematic review of the crab genus Phlyctenodes Milne Edwards, 1862 is carried out. Based on carapace features, this taxon is placed in the subfamily Actaeinae, family Xanthidae MacLeay, 1838. Species attributed to this genus are known from Eocene reef environments in Europe. Preservation of crustacean remains in this kind of environment is very rare, and it could explain scarcity of specimens of this genus. For the first time, pictures of types of this genus described during the XIX century and the first decades of the XX century are presented. A study of recently collected specimens from the Eocene of Veneto (Italy) allows to clarify relationships between Phlyctenodes krenneri Lörenthey, 1898 and P. dalpiazi Fabiani, 1911. Presence of P. tuberculosus Milne Edwards, 1862 among the new material is documented. The other known species of this genus, P. hantkeni Lörenthey, 1898 is placed in Pseudophlyctenodes new genus on the basis of differences in morphological features.

Key words: Crustacea, Decapoda, Phlyctenodes, systematic review, Eocene, Italy.

RESUMEN

Se presenta una revisión sistemática del género de cangrejo Phlyctenodes Milne Edwards, 1862. Con base en las características del caparazón, este taxon es ubicado en la subfamilia Actaeinae, familia Xanthidae MacLeay, 1838. Las especies de este género son conocidas de ambientes arrecifales en el Eoceno de Europa. La preservación de restos de crustáceos en este tipo de ambiente en muy rara, lo que podría explicar la escasez de especímenes de este género. Se presentan por vez primera fotografías de ejemplares tipo de este género descritos durante el siglo XIX y las primeras décadas del siglo XX. El estudio de especímenes recolectados recientemente en el Eoceno de Veneto (Italia) permite aclarar las relaciones entre Phlyctenodes krenneri Lörenthey, 1898, y P. dalpiazi Fabiani, 1911. Se documenta la presencia de P. tuberculosus Milne Edwards, 1862 entre los ejemplares recolectados. La otra especie conocida de este género, P. hantkeni Lörenthey, 1898, es ubicada en Pseudophlyctenodes nuevo género, con base en diferencias en las características morfológicas.

Palabras clave: Crustacea, Decapoda, Phlyctenodes, revisión sistemática, Eoceno, Italia.

INTRODUCTION

Fossil crabs housed in the Museo civico "G. Zannato" (Montecchio Maggiore, Vicenza, Italy) and discovered in the Colli Berici (Berici Hills, NE Italy) –precisely at San Feliciano and Campolongo di San Germano (Vicenza)– represent four species referred to the genus *Phyctenodes* Milne Edwards, 1862, including *P. dalpiazi* Fabiani, 1911, *P. krenneri* Lörenthey, 1898, *P. steinmanni* Lörenthey, 1902, and *P. tuberculosus* Milne Edwards, 1862. The fossils were collected in Late Eocene limestones rich in corals, algae and crustaceans remains (De Angeli and Garassino, 2002).

The new findings have prompted to carry out a review of *Phlyctenodes* Milne Edwards, 1862, represented by a small number of Eocene species, all of them distributed only in Europe (Figure 1). This study is suitable for publication of a photographic testimony of all type specimens referred to species of *Phlyctenodes*, previously known only by drawings. *P. krenneri* Lörenthey, 1898 and *P. steinmanni* Lörenthey, 1902 were reported from several localities, represented by a small number of specimens. Only holotypes are known for *P. pustulosus* Milne Edwards, 1862, and *P. nicolisi* Bittner, 1884. *P. tuberculosus* Milne Edwards, 1862, the generic type species, and *P. dalpiazi* Fabiani, 1911 were in the same situation, but new specimens of these two species are herein documented.

Scarcity of findings is probably caused by the low preservation potential for crustacean remains of the coral environment where these species lived. This paleoenvironment is confirmed by several studies (Lörenthey and Beurlen, 1929; Di Salvo, 1933; Müller and Collins, 1991; Beschin *et al*., 2000). Reports of this genus are also scarce in Eocene outcrops from Veneto, Italy, most of them from the Lessini Mounts. After the studies of Bittner (1884) on *P. nicolisi* and of Fabiani (1911) on *P. dalpiazi*, in the last decades the genus has been found again in Middle Eocene deposits at "Main" quarry (Arzignano, Vicenza) (Busulini *et al*., 1982), at "Boschetto" quarry (Nogarole Vicentino, Vicenza) (Beschin *et al*., 1994), and many specimens referred to the taxon found at "contrada Gecchelina" (Monte di Malo, Vicenza) from Early Eocene limestones are being studied (Beschin *et al*., 2000).

Some species originally referred to *Phlyctenodes* must be placed within other genera: for *P. hantkeni* Lörenthey, 1898 found in Eocene levels of Hungary and Sicily, Italy, *Pseudophlyctenodes* gen. nov. is herein erected. *Daira depressa* (Milne Edwards, 1865), originally referred to the genus *Phlyctenodes* and commonly found in Oligocene outcrops in Veneto, Italy, is briefly discussed here.

SYSTEMATIC PALEONTOLOGY

Systematic arrangement proposed by Martin and Davis (2001) is here adopted. Measurements (width = W; length = L) are given in millimeters (mm). Specimens are deposited in the Museo civico "G. Zannato", Montecchio Maggiore, Vicenza (Italy) under acronym MCZ.

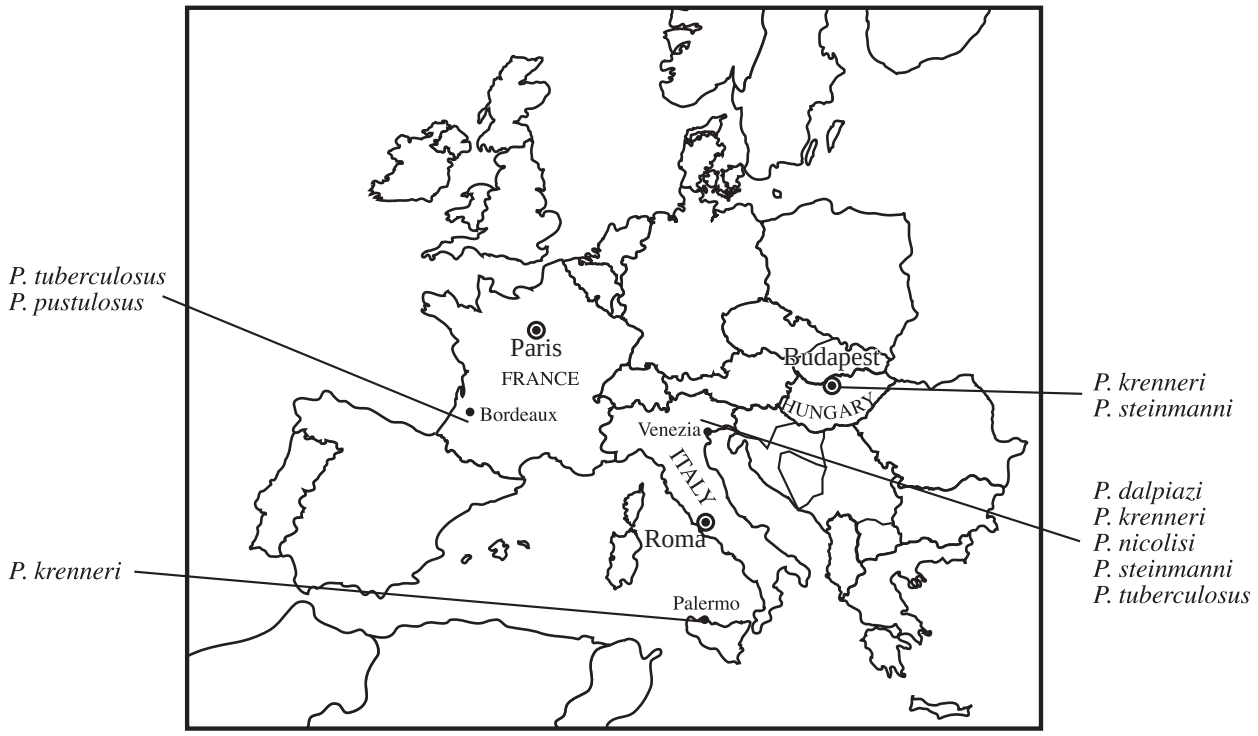

Figure 1. Distribution of the species referred to the genus *Phlyctenodes* Milne Edwards, 1862.

Superfamily Xanthoidea MacLeay, 1838
Family Xanthidae MacLeay, 1838
Subfamily Actaeinae Alcock, 1898
Genus *Phlyctenodes* Milne Edwards, 1862

Type species. *Phlyctenodes tuberculosus* Milne Edwards, 1862, Eocene, France.

Description. Carapace ovate, wider than long, vaulted longitudinally especially in the anterior part; dorsal surface with large tubercles, round and more or less isolated, never fused, more numerous and apparent on the anterior part of the carapace; regions not well defined. Front wide with four or more tubercle-like teeth (excluding inner-orbital spines); orbits large, subcircular, rimmed, without upper orbital fissures; frontal and anterolateral margins forming a wide, regular arch; anterolateral margins thick, with tubercles whose number and size change with the species; lateral angle underlined by a short little dorsal ridge usually tuberculate; posterolateral margins converging posteriorly, almost straight to concave, smooth and thick; posterior margin straight to a little convex, a little shorter than fronto-orbital margin. Pereiopods, sternum and abdomen unknown.

Frontal, epi- and protogastric regions fused, not distinguishable; the part of the carapace corresponding to these regions is herein indicated as "interorbital regions".

Discussion. The systematic position of the genus *Phlyctenodes* Milne Edwards, 1862 has always been problematic, also because its fossil remains consist only of the carapaces. Milne Edwards (1862) put it among the carpiliids and observed that no other representative of this group shows large and isolated tubercles on the dorsal part of the carapace, a feature typical of this genus. He asserted that it resembles the genera *Actaea* de Haan, 1833 and *Actaeodes* Dana, 1851, but also noted that the features of the rich ornamentation of the species of these two extant genera are different from those of *Phlyctenodes*: actually, the tubercles on the carapace of *Actaea savignyi* (H. Milne Edwards, 1834) are made up of little granules or tubercles and show a raspberry-like structure (Barnard, 1950).

Some authors have observed the resemblance between the genus *Phlyctenodes* Milne Edwards, 1862 and the genus *Daira* de Haan 1833 (Guinot, 1967; Via, 1969). *Daira*, initially placed within the Xanthidae MacLeay, 1838, is now referred to the family Dairidae Ng and Rodriguez, 1986, superfamily Parthenopoidea, MacLeay, 1838 (Martin and Davis, 2001). Formerly, Guinot (1978) had already placed *Daira* within the Parthenopoidea. Guinot (1967) thought that the genus *Daira* represents an advanced evolutionary stage among the parthenopoids as it has evolved to a "xanthiforme" direction and assumes an intermediate position between these two groups. She noted that it is difficult to say if *Phlyctenodes* has more characters of *Daira* than of *Actaea*. The genus would have differentiated from an ancestral form, the same from which *Daira* would descend and that would represent also the stock from which some species referred to *Actaea* could have arisen. From a more ancient form, one evolutionary branch originated the parthenopoids with the fossil genus *Phrynolambrus* Bittner, 1893 and the living one *Dairoides* Stebbing, 1920; a second branch, already differentiated during the Eocene, gave rise to *Daira*: this genus appears as a living fossil; a third branch, similar to the others and precociously differentiated (with forms like *Phlyctenodes*) would have produced more groups of xanthids: one with *Glyptoxanthus* Milne Edwards, 1879, *Euxanthus* Dana, 1851, *Hypocolpus* Rathbun, 1897, *Carpoporus* Stimpson, 1871 and *Edwardsium* Guinot, 1967 and another one with *Actaea*.

Even if *Phlyctenodes* and *Daira* appear very similar, some important differences can be noted; in *Phlyctenodes* the lateral angle is more apparent than in *Daira*: in this second genus the antero- and posterolateral margins are not clearly distinct and the posterolateral margins begin in the posterior quarter of the carapace; in *Phlyctenodes* the ornamentation is made up of tubercles that appear isolated, never fused and become less apparent on the axial and posterior regions, while in *Daira* there are larger and flat nodules developed also on the posterior regions; in *Phlyctenodes* the front is wide with four or more tubercle-like teeth whereas in *Daira* it is bilobed and deflected; in *Phlyctenodes* the dorsal regions are not well defined and a large, pentagonal mesogastric region can be observed; on the contrary, in *Daira* the same region is relatively narrower with an anterior process well developed and directed forward to the front.

In many studies, *Phlyctenodes* is placed within the Xanthidae (Glaessner, 1969; Via, 1969; Busulini *et al*., 1982; Müller and Collins, 1991; Beschin *et al*., 1994) and, at last, it has been referred to the Carpiliidae Ortmann, 1893, again by Beschin *et al*. (2004).

The observation of the features of the carapace, when chelipeds and ventral parts lack, makes it difficult to establish with certainty the systematic position of this genus. Anyway, recent studies (see for example Schweitzer, 2003) have shown that some characters of the dorsal carapace can be considered as diagnostic at the family and generic level even if the ventral parts are not preserved.

Schweitzer (2003) studied in detail fossil records of the Carpiliidae and on the basis of their features clarified that they possess carapaces wider than long that may be ornamented with large and flat nodes, regions moderately to poorly defined, grooves usually not developed, front usually with bilobed median projection and blunt inner-orbital spines, orbits circular, entire, rimmed or beaded; anterolateral margins long and convex, posterolateral margins short, straight or slightly concave, posterior margin narrow, nearly straight. The analysis of all the species referred to *Phlyctenodes* shows that this genus cannot be placed within the carpiliids. In *Phlyctenodes* the front is almost straight,

generally with a median notch, adorned with tubercles and the carapace shows a typical ornamentation made of tubercles above all on the anterior and lateral regions (among the carpiliids the carapace has sometimes only flat nodes as in *Ocalina floridana* Rathbun, 1929 characterized by broad, low swellings and large tubercles on the frontal and anterolateral margins).

The dorsal peculiarities of the carapace of *Phlyctenodes* allow to place the genus within the heterogeneous superfamily Xanthoidea MacLeay, 1838, apparently with close relationships with the subfamily Actaeinae Alcock, 1898 (family Xanthidae MacLeay, 1838) whose representatives possess carapaces usually divided into distinct regions, granulate, tuberculate or spinous, with a bilobed and spinous front (Serène, 1984). Certain affinities can be observed above all between the genus *Phlyctenodes* and some species referred to the genus *Actaea* de Haan, 1833, as some authors have pointed out (Milne Edwards, 1862; Guinot, 1967). This is true above all for those species characterized by an ornamentation constituted by isolated tubercles such as *Actaea polyacantha* (Heller, 1861) living in coral environments in the Red Sea, the Indian and Pacific Oceans (Serène, 1984).

The species now referred to the genus *Phlyctenodes* Milne Edwards, 1862 constitute a fairly homogeneous group. They are distinguishable because of the arrangement of the tubercles and the degree of definition of the regions on the dorsal carapace. In the past, several authors have thought they ought to be divided into two groups: the first one with the complete carapace covered with tubercles, the second one with the posterior and median part almost smooth. Airaghi (1905) and afterward Fabiani (1911) referred to the first group "*P. depressus*" Milne Edwards, 1865 and "*P. hantkeni*" Lörenthey, 1898 and, to the second one, *P. dalpiazi* Fabiani, 1911, *P. krenneri* Lörenthey, 1898, *P. nicolisi* Bittner, 1884, *P. pustulosus* Milne Edwards, 1862, *P. steinmanni* Lörenthey, 1902, and *P. tuberculosus* Milne Edwards, 1862. Lörenthey and Beurlen (1929) also made a similar consideration, but their subdivision didn't agree with the preceding one: in fact they put in the first group "*P. depressus*", "*P. hantkeni*", *P. nicolisi* and *P. steinmanni* and in the second one *P. dalpiazi*, *P. krenner*i and *P. tuberculosus* while *P. pustulosus* would be in an intermediate position. These attempts at subdivision are baseless: in all the species the tubercles become smaller and less apparent in the posterior part of the carapace but are always present as can be deduced from the diagnoses and the figures; moreover "*P. depressus*" and "*P. hantkeni*" are currently placed within other genera. The first one is referred to the genus *Daira* de Haan, 1833. A new genus, *Pseudophlyctenodes* gen. nov., is here erected for the second one. *P. nicolisi* Bittner, 1884 differs slightly from the other species; in fact, its small tubercles don't have regular arrangement: this character could bring it near to *P. pustulosus*. The holotype of this second species is very damaged so it is not possible a certain observation of the disposition of the tubercles; anyway, the ornamentation on the posterior regions of the carapace is almost absent and the furrows typical of *P. nicolisi* are not apparent.

Ristori (1896) described *P. irregularis* from Middle Miocene rocks of Piemonte, NW Italy, from a fragment of carapace; its assignment is very difficult but he observed that some of the irregularly arranged tubercles are fused; this would exclude the attribution of the fragment to the genus *Phlyctenodes*: this species, therefore, is not considered in the present analysis.

***Phlyctenodes tuberculosus* Milne Edwards, 1862**

Figures 2.1 - 2.3

Phlyctenodes tuberculosus Milne Edwards, 1862, p. 193, pl. 7, fig. 2.

Description. Carapace longitudinally vaulted with hardly defined regions; frontal margin wide with four tubercle-like teeth (excluding inner-orbital spines); orbits rimmed without upper orbital fissures; anterolateral margins with five tubercles; numerous isolated tubercles on the anterior and lateral regions of the carapace, smaller on the axial ones; four longitudinally rows of four tubercles on intraorbital regions; one small tubercle on each anterolateral angle of the mesogastric region; two series of four tubercles concentric to anterolateral margins; a transverse row of little tubercles on the lateral angle constitutes a little dorsal ridge; posterior branchial and cardiac regions almost smooth.

Discussion. *Phlyctenodes tuberculosus* Milne Edwards, 1862 has been erected with a sole carapace specimen found near Hastingues (Landes, France) in "terrain nummulitique" (probably Middle Eocene). Comparing the figure published in 1862 and the photo of the holotype (Figure 2.1) some important differences are apparent: the posterolateral margins are less concave and there are some tubercles on the cardiac region that, according to the original description given by Milne Edwards, would be smooth. A second specimen is described here. It has been found in Late Eocene rocks at San Feliciano (Vicenza, Italy) and it is very similar to the holotype in the general shape of the carapace, even if it is smaller, and in the arrangement of the tubercles that are isolated. Clearly shown on the right anterolateral margin are the five tubercles described by Milne Edwards; because of the better preservation they project forward and are pointed.

P. tuberculosus has great affinities with *P. dalpiazi* Fabiani, 1911 and *P. krenneri* Lörenthey, 1898 because of the presence of four longitudinal rows of tubercles on the interorbital regions, but in the type species, the regions are not defined and the tubercles are clearly isolated and form rows that don't diverge from the axial line; moreover there is a little tubercle on each anterolateral angle of the mesogastric region.

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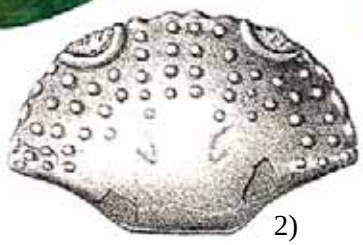

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Material examined. Holotype (cast and photographs) R03826, Muséum National d'Histoire Naturelle, Paris; one specimen (MCZ 2456 W 13.6 L 9.2) from San Feliciano (Colli Berici, Vicenza).

Occurrence. Middle Eocene: SW France; Late Eocene: Veneto, NE Italy.

Phlyctenodes dalpiazi Fabiani, 1911
Figures 2.4 - 2.6

Phlyctenodes dalpiazi Fabiani, 1911, p. 4, fig. 1.

Description. Carapace vaulted in the anterior half, axial regions fairly defined. Frontal margin with four tubercles (excluding inner-orbital spines), orbits rimmed, with sparse and little granules; anterolateral margins tuberculate; posterolateral margins a little concave; posterior margin a little wider than frontal one, straight, rimmed. Tubercles present on anterior and lateral regions. Interorbital regions with four longitudinal rows, diverging posteriorly, each composed of four, contiguous, broad, blunt tubercles. Irregularly arranged tubercles on the lateral regions. Mesogastric region pentagonal, fairly defined; cardiac and posterior branchial regions almost smooth.

Discussion. *Phlyctenodes dalpiazi* Fabiani, 1911 has been erected with only one specimen collected in limestone levels at San Feliciano (Vicenza, Italy) that Fabiani attributed to the Early Oligocene. More recent studies show them to be Late Eocene (Ungaro and Bosellini, 1965; Ungaro, 1978; De Angeli and Garassino, 2002). Fabiani (1911) described also the propodus of a small claw preserved on the same rocky fragment and suggested that it could be a part of the same individual: the features of this propodus make his hypothesis unlikely.

Some specimens referred to the species are housed in the Museo civico "G. Zannato" (Montecchio Maggiore, Vicenza): two of them have been found in the type locality (San Feliciano) and one in coeval levels at Campolongo di San Germano (Vicenza). They preserve the frontal margin, lacking in the holotype: it has four small tubercles. It is possible to confirm the differences between *P. dalpiazi* and *P. krenneri* Lörenthey, 1898 regarding the lack of well defined tubercles on the mesogastric region (and usually on the cardiac one) and the features of the tubercles (Fabiani, 1911).

Material examined. Holotype, MGPD 23654, Museo Geologico e Paleontologico, Università di Padova; two specimens (MCZ 2458, L 7.0; MCZ 2459, W 9.1, L 7.0) from San Feliciano (Vicenza) and one (MCZ 2457, W 11.8, L 8.2) from Campolongo di San Germano (Vicenza).

Occurrence. Late Eocene: Veneto, NE Italy.

Phlyctenodes krenneri Lörenthey, 1898
Figures 2.7 - 2.10

Phlyctenodes krenneri Lörenthey, 1898, p. 46, pl. 2, fig. 9.
Phlyctenodes krenneri; Checchia-Rispoli, 1905, p. 312, pl. 1, fig. 10.
Phlyctenodes krenneri; Lörenthey and Beurlen, 1929, p. 201, pl. 12, fig. 9.
Phlyctenodes krenneri; Di Salvo, 1933, p. 20.
Phlyctenodes krenneri; Müller and Collins, 1991, p. 76, pl. 5, fig. 9, pl. 6, fig. 1.

Description. Carapace longitudinally vaulted with poorly defined regions. Front wide with four small tubercles (excluding inner-orbital spines); anterolateral margins tuberculate; posterolateral margins a little curved; posterior margin straight, rimmed. Furrows between gastric and hepatic regions. Surface covered with pointed tubercles on anterior regions; four longitudinal rows of tubercles on interorbital regions; four small tubercles in transverse row on pentagonal mesogastric region; three small tubercles constituting a triangle on wide, transversely ovate cardiac region; series of large tubercles on the hepatic and anterior branchial regions concentric to anterolateral margins. Posterior regions almost smooth.

Discussion. *Phlyctenodes krenneri* differs from *P. dalpiazi* in the constant presence of four tubercles in a transverse row on the mesogastric region, with three others forming a triangle on the cardiac region and in the features of the tubercles on the dorsal surface that appear definitely pointed and isolated (Fabiani, 1911). The species has been found also in Sicily: Checchia-Rispoli (1905) reported a damaged specimen (Figure 2.8) and later Di Salvo (1933) reported six specimens: examination of the photographs of these specimens housed in the Museo geologico "G.G. Gemmellaro" (Palermo) allows to confirm their attribution and also to validate the persistence of the typical features of the species with a carapace varying in size; the length

Figure 2. 1: *Phlyctenodes tuberculosus* Milne Edwards, 1862, holotype, R03826 Musèum National d'Histoire Naturelle, Paris (W 27.0, L 17.0); 2: *P. tuberculosus*, line drawing (from Milne Edwards, 1862) (W 27.0, L 17.0); 3: *P. tuberculosus*, MCZ 2456 (W 13.6, L 9.2), San Feliciano (Vicenza); 4: *Phlyctenodes dalpiazi* Fabiani, 1911, holotype, 23654, Museo Geologico e Paleontologico, Università di Padova (W 10.5, L 6.3); 5: *P. dalpiazi*, line drawing (from Fabiani, 1911) (W 10.5, L 6.3); 6: *P. dalpiazi*, MCZ 2457 (W 11.8; L 8.2), Campolongo di San Germano (Vicenza); 7: *Phlyctenodes krenneri* Lörenthey, 1898, holotype (cast) (W 12.5, L 9.0); 8: *P. krenneri*, GABA015, Museo Geologico "G.G.Gemmellaro", Palermo (W 11.8, L 8.5); 9: *P. krenneri*, line drawing (from Lörenthey and Beurlen, 1929) (W 12.5, L 9.0); 10: *P. krenneri*, MCZ 2460 (L 9.3), Campolongo di San Germano (Vicenza).

ranging from 2.5 to 10.0 and the width respectively from 4.0 to 13.2 (Di Salvo, 1933).

Material examined. Holotype (cast), Magyar Állami Földtani Intézet, Budapest; photographs of specimens BAGA006, BAGA015, BICH2, PILU002, PILU004, Museo Geologico "G.G. Gemmellaro", Palermo (Italy); one specimen (MCZ 2460, L 9.3) not well preserved from Campolongo di San Germano (Vicenza, Italy).

Occurrence. Middle Eocene: Sicily, Italy; Late Eocene: Hungary, Veneto (NE Italy).

Phlyctenodes nicolisi Bittner, 1884
Figures 3.1, 3.2

Phlyctenodes nicolisi Bittner, 1884, p. 5, pl. 1, fig. 5.

Description. Carapace ovate, vaulted with fairly evident axial regions; frontal margin wide, tuberculate, with a median notch; orbital margins inflated and beaded; anterolateral margins with seven tubercles (including outer-orbital angle); posterolateral margins concave, very thick, smooth; posterior margin almost straight; branchiocardiac furrows clear, reaching the posterior margin. Dorsal surface covered with many small, round, irregularly arranged tubercles; they are larger and forward directed near anterior margins; smaller on the posterior regions. Cardiac region with three tuberculate swellings forming a triangle.

Discussion. Only the holotype of this species is known: it was collected near Avesa (Verona). It preserves the orbito-antennal region, described by Bittner (1884); it is possible to observe a fairly wide, transverse basal segment of antennula and a narrow antennal fissure on the infraorbital margin.

One specimen reported in Beschin *et al*. (2000) from the Early Eocene of "contrada Gecchelina" (Monte di Malo, Vicenza) has been formerly attributed to the species but it is under study and its assignement is not certain yet.

Material examined. Holotype 1982, Museo Civico di Storia Naturale di Verona, Italy.

Occurrence. Middle Eocene: Veneto, NE Italy.

Phlyctenodes pustulosus Milne Edwards, 1862
Figures 3.3, 3.4

Phlyctenodes pustulosus Milne Edwards, 1862, p. 194, pl. 7, fig. 1.

Description. Carapace ovate, regions hardly distinguishable; axial furrow separating protogastric regions; branchiocardiac furrows visible. Frontal margin wide with four (or six) tubercles; six tubercles increasing in size toward lateral angle. Many isolated tubercles on anterior and lateral regions, smaller in posterior regions; posterior part of carapace nearly smooth; tubercles constituting a row concentric to anterolateral margins.

Discussion. The holotype, and sole specimen found at Nousse (Landes, France), is a carapace emerging from a marly limestone. The comparison of the specimen to the original figure suggests the specimen has been probably damaged after the publication and some of the characters described by Milne Edwards are not observed.

Material examined. Holotype (cast and photographs) A24551, Muséum National d'Histoire Naturelle, Paris.

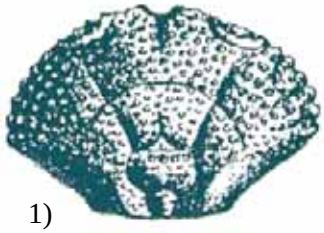
Occurence. Middle Eocene: SW France.

Phlyctenodes steinmanni Lörenthey, 1902
Figure 3.5 - 3.7

Phlyctenodes steinmanni Lörenthey, 1902, p. 111, pl. 1, fig. 4.
Phlyctenodes steinmanni; Lörenthey and Beurlen, 1929, p. 200, pl. 12, fig. 2.
Phlyctenodes steinmanni; Müller and Collins, 1991, p. 76, pl. 5, fig. 9, pl. 6, fig. 1.
Phlyctenodes steinmanni; Beschin, Busulini, De Angeli and Tessier, 1994, p. 188, pl. 9, fig. 3.

Description. Carapace ovate with well defined regions; frontal margin with four spines; orbital and anterolateral margins spinous; posterolateral margins straight, smooth; posterior margin rimmed. Median furrows present on both front and protogastric regions; branchiocardiac furrows visible. Dorsal surface covered with pointed tubercles

Figure 3. 1: *Phlyctenodes nicolisi* Bittner, 1884, line drawing (from Bittner, 1884) (W 28.0, L 20.0); 2: *P. nicolisi*, holotype, 1982, Museo Civico di Storia Naturale, Verona (W 28.0, L 20.0); 3: *Phlyctenodes pustulosus* Milne Edwards, 1862, holotype, A24551, Muséum National d'Histoire Naturelle, Paris (W 25.5, L 17.5); 4: *P. pustulosus*, line drawing (from Milne Edwards, 1862) (W 25.5, L 17.5); 5: *Phlyctenodes steinmanni* Lörenthey, 1902, MCZ 2461 (W 13.6, L 11.0), Campolongo di San Germano (Vicenza); 6: *P. steinmanni*, holotype (cast) (W 25.0, L 18.0); 7: *P. steinmanni*, MCZ 2462 (W 11.5, L 8.0), San Feliciano (Vicenza); 8: *Daira depressa* (Milne Edwards, 1865), MCZ 2463 (L 16.1), Montecchio Maggiore (Vicenza); 9: *Pseudophlyctenodes hantkeni* (Lörenthey, 1898), GABA003, Museo Geologico "G.G. Gemmellaro", Palermo (W 26.0, L 17.0); 10: *P. hantkeni*, line drawing (from Lörenthey and Beurlen, 1929) (W 11.0, L 8.0).



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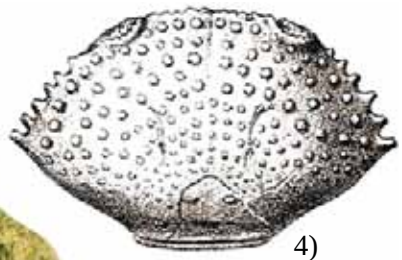

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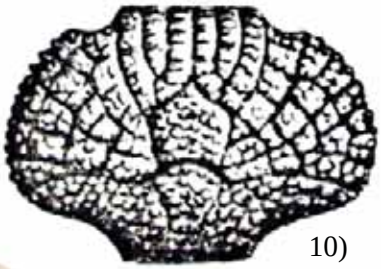

10)

larger on the anterior regions. Three longitudinal rows of tubercles on each protogastric region; longitudinal rows of tubercles on branchial regions; mesogastric regions with four rows of small tubercles; cardiac region triangular with very small, irregularly arranged tubercles; metabranchial regions smooth, anteriorly delimited by a transverse row of small tubercles forming a dorsal ridge; intestinal region with smooth, transverse, slightly concave ridge.

Discussion. Specimens referred to this species have been found frequently, but the individuals mentioned herein allow a complete description of the posterior part of the carapace, damaged in the holotype; the presence of a transverse ridge on the intestinal region is significant.

Material examined. Holotype (cast) Magyar Állami Földtani Intézet, Budapest; two specimens (MCZ 2461, W 13.6, L 11.0; MCZ 2465, W 11.7, L 8.4) from Campolongo di San Germano (Vicenza, Italy) and two (MCZ 2462, W 11.5, L 8.0; MCZ 2466) from San Feliciano (Vicenza).

Occurrence. Middle Eocene: Veneto, Italy; Late Eocene: Hungary and Veneto (NE Italy).

Genus *Pseudophlyctenodes* gen. nov.

Type species. *Phlyctenodes hantkeni* Lörenthey, 1898, Eocene, Hungary and Italy.

Etymology. *Pseudophlyctenodes* (m.) from ψευδο (gr.) = false, and the similar genus *Phlyctenodes*.

Diagnosis. As for type species.

***Pseudophlyctenodes hantkeni* (Lörenthey, 1898)**
comb. nov.
Figures 3.9, 3.10

Phlyctenodes hantkeni Lörenthey, 1898, p. 44, pl. 2, fig. 10.
Phlyctenodes hantkeni; Lörenthey and Beurlen, 1929, p. 199, pl. 12, fig. 8.
Phlyctenodes hantkeni; Di Salvo, 1933, p. 21, pl. 2, fig. 1.

Description. Carapace ovate, wider than long, strongly longitudinally vaulted with fairly defined regions. Frontal and anterolateral margins forming a regular arch. Frontal margin wide. Orbits large, orbital margins poorly swelled, tuberculate. Anterolateral margins tuberculate; posterolateral margins strongly concave, very thick, almost smooth; posterior margin straight, rimmed. Furrows dividing gastric and cardiac regions from fused hepatic and branchial ones. Mesogastric region pentagonal. Protogastric regions large, separated by an axial furrow and reaching frontal margin. Dorsal surface covered with close, large, composite tubercles. Three longitudinal rows of composite tubercles on each protogastric region. Rows of tubercles on the hepatic and branchial regions diverging like rays from mesogastric region. Tubercles smaller, irregularly arranged on axial and metabranchial regions.

Discussion. This species, characterized by a very close, composite tuberculation, appears to be in an intermediate position between the representatives of the genus *Phlyctenodes* and those of *Daira*. *Pseudophlyctenodes hantkeni* (Lörenthey, 1898) is very similar to *Daira*, as Lörenthey and Beurlen (1929) have suggested, in the general carapace shape with antero- and posterolateral margins almost continuous. Definitely different, and near to *Phlyctenodes*, is the mesogastric region proportionally wider without a developed anterior process; the protogastric regions are separated only by an axial furrow. On the other hand, the species shows a rich ornamentation made up of assembled tubercles, very different from the individual tubercles typical of *Phlyctenodes*. The assignement to the new genus *Pseudophlyctenodes* gen. nov. allows to give this species a more adequate systematic position.

Material examined. Casts of type series, Magyar Állami Földtani Intézet, Budapest; photographs of specimens BAGA001, BAGA003, BAGA004, BAGA005, PILU003 Museo Geologico “G.G. Gemmellaro”, Palermo (Italy).

Occurrence. Middle Eocene: Sicily, Italy; Late Eocene: Hungary.

Superfamily Parthenopoidea MacLeay, 1838
Family Dairidae Ng and Rodriguez, 1986
Genus *Daira* de Haan, 1833

Type species. *Cancer perlatus* Herbst, 1790, Recent, Indo-Pacific.

***Daira depressa* (Milne Edwards, 1865)**
Figure 3.8

Phlyctenodes depressus Milne Edwards, 1865, p. 367, pl. 33, fig. 2.
Phlyctenodes depressus; Bittner, 1877, p. 446.
Phlyctenodes depressusv Bittner, 1883, p. 15.
Phlyctenodes depressus; Airaghi, 1905, p. 205, pl. 4, fig. 3.
Daira depressa; Glaessner, 1929, p. 135.
Daira depressa; Beschin *et al.*, 2001, p. 20, pl. 2. figs. 2, 4.

Material examined. Two specimens (MCZ 2463, L 16.1, MCZ 2464) from Montecchio Maggiore (Vicenza, Italy).

Description. Carapace ovate, wider than long, almost flattened; orbits small; frontal margin tuberculate; frontal

and anterolateral margins forming a wide arch; antero- and posterolateral margins not clearly distinct one another; posterolateral margins shorter than anterolateral ones and concave; regions moderately defined; dorsal surface covered with large tubercles very close one another, the largest on the anterior regions; tubercles longitudinally arranged on gastric regions: two longitudinal rows on each protogastric regions and an axial one on long, narrow anterior mesogastric process; mesogastric region pentagonal, relatively narrow; tubercles arranged in transverse rows on posterior regions of the carapace.

Discussion. The general shape of the carapace with anterolateral margins not clearly distinct from the posterolateral ones, the structure and the arrangement of the tubercles, and the mesogastric region relatively narrow with the anterior process very apparent, allow to attribute this species to the genus *Daira* as Bittner (1877, 1883) has already suggested. Particular affinities can be noted between *Daira depressa* and *Daira speciosa* (Reuss, 1871) of the Miocene of Europe. *Daira depressa* has been found frequently in Early Oligocene rocks of Veneto (see Beschin *et al.*, 2001, for a detailed analysis).

Occurrence. Early Oligocene: Veneto, NE Italy.

ACKNOWLEDGEMENTS

We wish to thank R. Ghiotto (Museo Civico "G. Zannato", Montecchio Maggiore, Vicenza) for providing the study material housed in his museum; M. Fornasiero (Museo Geologico e Paleontologico, Università di Padova) for providing access to the type originally described by Fabiani at her institution, and S. Castelli for the photographs of the same specimen; A. Vaccari (Museo Civico di Storia Naturale, Verona) for providing access to the type originally described by Bittner at her institution and the photographs of that specimen; L. Galletti (Museo Geologico "G.G.Gemmellaro", Università di Palermo) for providing photographs of some specimens originally studied by Checchia-Rispoli and Di Salvo; J.M. Pacaud (Muséum National d'Histoire Naturelle, Paris) for providing casts of the holotypes originally studied by Milne Edwards. We are very grateful to D. Guinot (Muséum National d'Histoire Naturelle, Paris) for her kind advice and to P. Müller (Magyar Állami Földtani Intézet, Budapest) for casts and information concerning Hungarian specimens studied by Lörenthey.

Many thanks to F. Vega Vera (Instituto de Geología, UNAM) for his kind and thoughtful review of our manuscript and to R.H.B. Fraaije (Oertijdmuseum, Boxtel), G.A. Bishop (Museum of Geology, South Dakota) and H. Karasawa (Mizunami Fossil Museum) for their critical reviews. Thanks also to A. Checchi (Associazione Amici del Museo "G. Zannato") for his field work and to A. De Angeli (Associazione Amici del Museo "G. Zannato") for providing photographs of the holotypes studied by A. Milne Edwards. For their patient "linguistic assistance" thanks to I. Bozza and M. Busulini and to F. Turio for his photographic help.

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Manuscript received: September 2, 2005
Corrected manuscript received: January 17, 2006
Manuscript accepted: January 25, 2006