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A new hermit crab (Crustacea, Anomura, Paguroidea) from the Late Cretaceous (Cenomanian) of Lebanon

Abstract - A hermit crab from the Late Cretaceous (Cenomanian) is reported for the first time from Lebanon. The studied specimen has been ascribed to the superfamily Paguroidea Latreille, 1802, including *Striadiogenes frigerioi* n. gen., n. sp. (Diogenidae Ortmann, 1892). The discovery of *S. frigerioi* is very important because it is the first record of a hermit crab from the Late Cretaceous of Lebanon but, particularly, it represents the first complete fossil paguroid described to date, increasing substantially the knowledge of the poorly recorded Mesozoic forms of this superfamily.

Key words: Decapoda, Anomura, Paguroidea, Late Cretaceous, Lebanon.

Riassunto - Un nuovo paguro (Crustacea, Anomura, Paguroidea) del Cretacico superiore (Cenomaniano) del Libano.

Viene descritto un paguride del Cretacico superiore (Cenomaniano) del Libano. L'esemplare studiato è stato ascrivito alla superfamiglia Paguroidea Latreille, 1802 che comprende *Striadiogenes frigerioi* n. gen., n. sp. (Diogenidae Ortmann, 1892). La scoperta di *S. frigerioi* è molto importante in quanto è la prima segnalazione di un paguride nel Cretacico superiore del Libano e, in particolare, rappresenta il primo paguroide completo sinora descritto, incrementando notevolmente le conoscenze sulle forme Mesozoiche di questa superfamiglia, scarsamente documentate.

Parole chiave: Decapoda, Anomura, Paguroidea, Cretacico superiore, Libano.

Geological setting

The sublithographic limestones of Lebanon are well known for their rich and well preserved fossil assemblage ("Konservat-Lagerstätten") of the famous "fish-beds" layers, including vertebrates and invertebrates remains (particularly decapod crustaceans), from different localities as Haqel, Hadjula, Maifouk, Al-Namoura, and Sahel-Alma.

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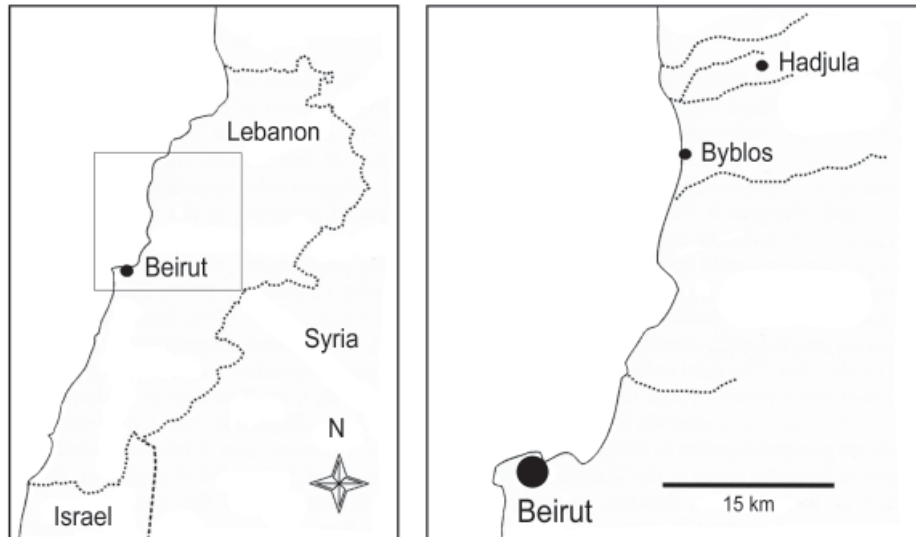


Fig. 1 – Geographic map with fossiliferous locality (after Fucks, 2006) / Carta geografica con la località fossilifera (elaborata da Fucks, 2006).

In the last 150 years many decapod species were reported and revised by various authors (Brocchi, 1875; Fraas, 1878; Dames, 1886; Whithers, 1928; Glaessner, 1945; Roger, 1946; Förster, 1984; Garassino, 1994, 2001; Larghi, 2004; Garassino & Schweigert, 2006).

Hadjula village is located about 10 km NE of Byblos, on the geographic ridges running parallel to the Mediterranean Sea coast, where the Late Cretaceous strata crop out (Fig. 1).

The biostratigraphical studies by Dubertret (1959, 1966), Hüchel (1969, 1970, 1974a, 1974b) and Saint Marc (1974) placed the sequences at Haqel, Hadjula, and Maifouk at the early-middle Cenomanian boundary. According to Hemleben (1977), Haqel and Hadjula are younger. In fact, the author dated these quarries to the late Cenomanian. Recently, Dalla Vecchia *et al.* (2002) considered the Hadjula assemblages to be lower late Cenomanian in age. On the basis of these data, we assigned our specimen to the late Cenomanian in generic terms (Late Cretaceous).

Previous records of Diogenidae from the Cretaceous

The studied specimen has been assigned to the Diogenidae Ortmann, 1892, in the infraorder Anomura MacLeay, 1838. The fossil record of Diogenidae in the Late Cretaceous is poorly documented and consists only of a few fragmentary or incomplete specimens from Europe, United States, and Antarctica Peninsula (indeterminate species not considered).

Rathbun (1935) reported *Paguristes* Dana, 1851, with *P. onachitensis* Rathbun, 1935 (one poorly preserved specimen) from the late Campanian of Arkansas (United States). Bishop (1983) reported *Paguristes* with *P. whitteni* Bishop, 1983 (25 chelipeds) from the early Maastrichtian of Mississippi (United States). Bishop (1986) placed *P. whitteni* (30 chelipeds) within a new genus *Parapaguristes* toge-

ther with a new species *P. tuberculatus* (4 chelipeds) from the middle Maastrichtian from Mississippi (United States). Feldmann *et al.* (1993) and Olivero & Aguirre-Urreta (1994) rejected Bishop's view.

Feldmann *et al.* (1993) reported *Paguristes santamartaensis* (2 chelipeds) from the ?late Santonian-middle Campanian of Antarctica.

Collins *et al.* (1995) reported *Paguristes* with *P. florae* Collins, Fraaye & Jagt, 1995 (10 incomplete chelipeds) from the Maastrichtian of The Netherlands. Fraaije *et al.* (2008) described the new genus *Annuntidiogenes* with *A. ruizdegaonai* Fraaije, van Bakel, Jagt & Artal, 2008 (one incomplete carapace) from the late Albian of Monte Orobe (Navarra, Spain) and *A. sunuciorum* Fraaije, van Bakel, Jagt & Artal, 2008 (one incomplete specimen *in situ*) from the Maastrichtian of The Netherlands. Finally Fraaije *et al.* (2009) reported a new coeval species of the same genus, *A. worfi* Fraaije, van Bakel, Jagt, Klompmaker & Artal, 2009 (one incomplete carapace), from the late Albian of Alsasua area (Navarra, Spain) only few kilometres south of Monte Orobe.

Material

One complete and articulated specimen in dorsal view (part and counter-part), with the soft body, exceptionally well preserved. It is compressed dorso-ventrally and flattened on the surface of the matrix.

The studied specimen was also investigated by UV light, to point out detailed phosphatised parts and soft tissues. The preparation was made by air gravers due to the hard nature of the surrounding rock. The perfect preservation allowed also a detailed reconstruction of the complete specimen. The studied specimen has been ascribed to the infraorder Anomura MacLeay, 1838, including *Striadiogenes frigerioi* n. gen., n. sp. (Diogenidae Ortmann, 1892). The carapace terminology used in this systematic description follows the scheme proposed by Forest *et al.* (2000) and Fraaije *et al.* (2008).

The specimen is housed in the Palaeontological Collections of the Museo di Storia Naturale, Milano (MSNM).

Abbreviations

P1-P4, first to fourth pereopods.

Measurements are given in millimetres (mm).

Systematic Palaeontology

Order Decapoda Latreille, 1802
 Infraorder Anomura MacLeay, 1838
 Superfamily Paguroidea Latreille, 1802
 Family Diogenidae Ortmann, 1892

Included fossil genera: *Annuntidiogenes* Fraaije, van Bakel, Jagt & Artal, 2008 (late Albian – Spain; Maastrichtian – The Netherlands); *Calcinus* Dana, 1851 (Lutetian – Italy; Pliocene – Italy); *Ciliopagurus* Forest, 1995 (Oligocene – Belgium; Badenian – Hungary); ?*Clibanarius* Dana, 1852 (?Late Eocene – Egypt); *Dardanus* Paulson, 1875 (Eocene – United States and Egypt; Oligocene – Asia; Lutetian – Italy; Miocene – Europe; Pliocene – Italy and Fiji; Pleistocene – United States); *Diogenes* Dana, 1851 (Ypresian – Italy); *Eocalcinus* Via Boada, 1959

(Eocene – Spain and Italy); *Eopaguropsis* van Bakel, Fraaije, Jagt & Artal, 2008 (late Oxfordian – Germany); *Paguristes* Dana, 1851 (?late Santonian-middle Campanian – Antarctic; Campanian, Maastrichtian – United States; Maastrichtian – The Netherlands; Paleocene – United States; Lutetian and Priabonian – Italy; Miocene – United States); *Petrochirus* Stimpson, 1859 (Late Cretaceous – United States; Lutetian and Priabonian – Italy; Oligocene – W India; Miocene – Panama, N America, and N Africa; Pliocene – N America) (updated after Glaessner, 1969).

Genus *Striadiogenes* nov.

Diagnosis: shield longer than broad; postantennal projections poorly developed; anterior region narrow and slightly raised centrally; subelliptic raised and calcified central part of shield marked by transverse and oblique striae medially and proximally, and divided by a short medial gastric groove proximally; proximal and medial sections of central part of shield flat, distal part inclined backwards marked by irregular roughness and divided by a thin medial ridge; pointed rostrum weakly developed; anterior margin weakly concave; anterolateral regions strongly raised and marked by a weak roughness mixed with small pits; posterolateral and posterior regions flat and well-marked by grooves; cervical groove and *linea transversalis* present and subparallel; ocular peduncles slightly longer than half length of shield; chelipeds equal and strong; chelipeds with chela longer than broad; fingers moderately curved ventromesially; merus and carpus of cheliped with corrugated striae partially superimposed and arranged vertically on outer face; palm of cheliped with small and flat tubercles on outer face; ambulatory legs strong and flat with corrugated dorsal and ventral margins; dactyli of ambulatory legs broadly curved, approximately as long as propodi; P4 semichelate; P4-P5 considerably smaller than P2-P3.



Fig. 2 – *Striadiogenes frigerioi* n. gen., n. sp., reconstruction of cephalic shield / ricostruzione dello scudo cefalico.

Etymology: combination of Latin, *stria*, *-ae* (*stria*), referred to the ornamentation with transverse striae of subelliptic raised and calcified central part of the shield and the generic name *Diogenes* Dana, 1852, denoting an early member of Diogenidae Ortmann, 1892.

Type species: *Striadiogenes frigerioi* n. gen., n. sp.

Description: as for the type species.

Striadiogenes frigerioi n. gen., n. sp.

Figs. 2-8

Diagnosis: as for the genus.

Etymology: the trivial name alludes to I. Frigerio who donated the studied specimen.

Holotype: MSNM i27213 (part and counter-part).

Type locality: Hadjula (Lebanon).

Geological age: Late Cretaceous (Cenomanian).

Material and measurements: one complete and articulated specimen in dorsal view.

MSNM i27213 – Supposed length of carapace: 18

Width of carapace: 8

Length of shield: 9

Width of shield: 7

Length of ocular peduncles: 5

Length of chela of left and right cheliped: 13

Length of palm of left and right chela: 10

Width of palm of left and right chela: 6

Length of merus of right P2: 14

Length of carpus of right P2: 6

Length of dactylus P3: 15

Length of abdomen: 13

Width of abdomen: 10

Antennular and antennal peduncles not preserved.

Description. Shield longer than broad; postantennal projections poorly developed; anterior region narrow and slightly raised centrally; subelliptic raised and calcified central part of shield marked by transverse and oblique striae medially and proximally, and divided by a short medial gastric groove proximally; proximal and medial sections of central part of shield flat, distal part inclined backwards marked by irregular roughness and divided by a thin medial ridge; pointed rostrum weakly developed; anterior margin weakly concave with ocular incisions weakly developed; anterolateral regions strongly raised and marked by a weak roughness mixed with small pits; posterolateral and posterior regions flat well marked by grooves; cervical groove and *linea transversalis* present and subparallel; posterior carapace with central calcified gastric tract preserved.

Ocular peduncles slightly longer than half length of shield; distal parts of left and right antennal flagellae preserved (visible by ultraviolet light).

Chelipeds equal and strong; subrectangular and elongate merus; subtriangular and short carpus; palm longer than broad with subtriangular fixed finger broad at base with rounded distal extremity; thin movable finger about as long as mesial margin

of palm; corrugated dorsal margin of left chela; merus and carpus of chelipeds with corrugated striae partially superimposed and arranged vertically; palm of chelipeds weakly tuberculate dorso-ventrally and with scale-like ornamentation centrally.

Left and right ambulatory legs equal, exceeding chelipeds by approximately 0.25 length of dactylus; corrugated dorsal and ventral margins; merus and carpus of P2-P3 with corrugated striae partially superimposed and arranged vertically; dactyli broadly curved approximately as long as propodi, and terminating in sharp corneous claws; proximal part of dactyli with one marked ridge extended medially; numerous small pits not aligned dorsally and distributed along all length of dactyli.



Fig. 3 – *Striadiogenes frigerioi* n. gen.; n. sp., reconstruction / ricostruzione.

Left and right P4-P5 visible by ultraviolet light; P4-P5 with merus, carpus, propodus, and dactylus thin and smooth; right P4 semichelate; P5 probably achelate; P4-P5 considerably smaller than P2-P3.

U-shaped uncalcified abdomen longer than broad with margins preserved as imprint (visible under ultraviolet light); abdomen curved on right side and shorter than carapace; calcified intestine tract preserved centrally extending for entire length of abdomen; telson and uropods poorly preserved.

Discussion. As reported by many authors, the systematics of Recent Paguroidea uses essentially morphological dorsal and ventral characters of the body to distinguish genera and species of each family. Since the studied specimen does not preserve ventral characters useful for its identification, only some dorsal diagnostic characters, such as the ornamentation of gastric region, the chelae of chelipeds, the ornamentation of chelipeds and ambulatory legs can be used for its taxonomic ascription.

As reported by McLaughlin (2003) the superfamily Paguroidea includes at present the following extant families, Coenobitidae Dana, 1851; Pylochelidae Bate, 1888; Diogenidae Ortmann, 1892; Lithodidae Samouelle, 1819; Pylojacquesidae McLaughlin & Lemaitre, 2001; Paguridae Latreille, 1802; and Parapaguridae Smith, 1882.

Comparing the general morphology of the carapace and chelipeds with the diagnostic characters of these families (McLaughlin & Lemaitre, 2001; Poore, 2004) the studied specimen is assigned to the Diogenidae.

Diogenidae is represented in the fossil record from the Cretaceous by two genera, *Paguristes* Dana, 1851, and *Annuntidiogenes* Fraaije, van Bakel, Jagt & Artal, 2008. The comparison between *Striadiogenes frigerioi* n. gen. n. sp. and the fossil representatives ascribed to *Paguristes* from United States, Antarctica, and Europe is difficult because the last named genus is represented by only isolated and fragmentary chelae. The ornamentation with strong tubercles aligned in parallel ridges on the palm in *P. whitteni* and in *P. ouachitensis*, the ornamentation with finely granulated ridges on the palm in *P. floriae*, the ornamentation with densely and uniformly spaced nodes on the palm in *P. santamartaensis*, and the ornamentation with tubercles interspersed with very small granules in random pattern on the palm in *P. tuberculatus* exclude the new genus from *Paguristes* because it has a weakly tuberculate dorso-ventral surface of the palm with a scale-like ornamentation centrally.

Annuntidiogenes, represented by three species (two from the late Albian of Spain and one from the Maastrichtian of The Netherlands) has an ovate cephalic shield divided into distinct regions, ornamented with scabrous, irregular pits, with an elongate anterior-gastric groove, and with the propodus of the chela covered with short transverse striae. *Annuntidiogenes sunuciorum* is the only Late Cretaceous species of the genus, preserved as one single incomplete carapace *in situ*. *Striadiogenes* n. gen. differs from this hermit crab from The Netherlands in having a subelliptic raised and calcified central part of shield marked by transverse and oblique striae, divided by a short medial gastric groove proximally, flat proximal and medial sections of the central part, distal section inclined backwards marked by irregular roughness and divided by a thin medial ridge.

Finally, among the Recent genera of Diogenidae, some genera, such as *Clibanarius* Dana, 1852, *Cancellus* H. Milne Edwards, 1836, and *Paguristes* Dana, 1851, show some morphological characters similar to those observed in the studied specimen, like the small, short rostrum and the equal chelipeds.

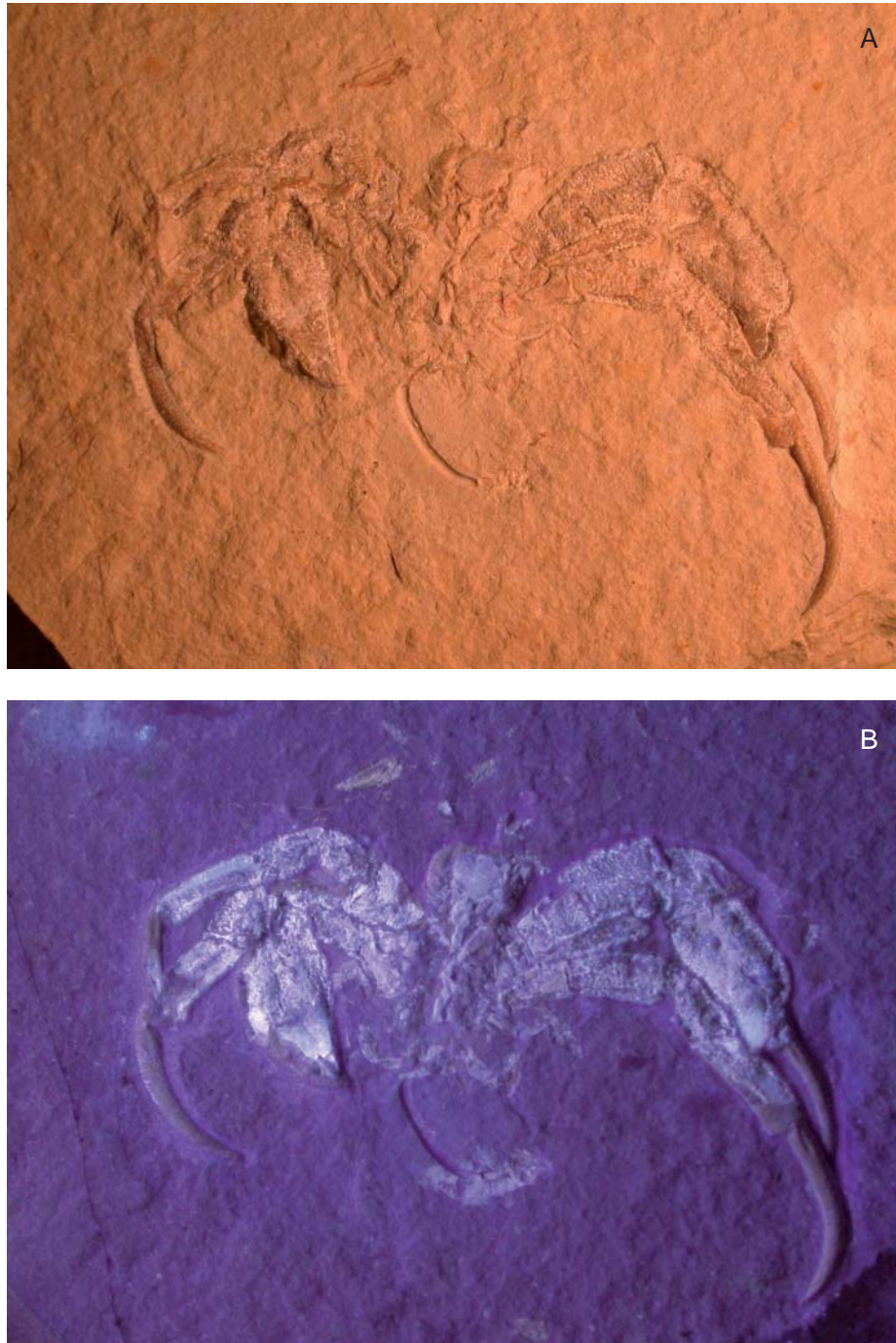


Fig. 4 – *Striadiogenes frigerioi* n. gen., n. sp., holotype / olotipo, MSNM i27213 (natural size / misura al naturale). A) specimen in natural light / esemplare a luce naturale. B) specimen in ultraviolet light / esemplare a luce ultravioletta.



Fig. 5 – *Striadiogenes frigerioi* n. gen., n. sp., detail of cephalic shield / dettaglio dello scudo cefalico (x 8.3).



Fig. 6 – *Striadiogenes frigerioi* n. gen., n. sp., detail of ornamentation of merus of P2 / dettaglio dell'ornamentazione del merus di P2 (x 9).



Fig. 7 – *Striadiogenes frigerioi* n. gen., n. sp., right chela of cheliped / chela destra del chelipede (x 8.3).



Fig. 8 – *Striadiogenes frigerioi* n. gen., n. sp., dactylus of P3 / dactylus di P3 (x 7.5).

Geological and palaeoecological notes

The representatives of the Recent Diogenidae inhabit various natural refuges, commonly gastropod shells, to protect the soft body (Walker, 1992).

The reports of hermit crabs *in situ* are rare in the fossil record, limited to a few incomplete specimens preserved in ammonite body chambers or in gastropod shells (Mertin, 1941; Hyden & Forest, 1980; Feldmann & Keyes, 1992; Fraaije, 2003; Jagt *et al.*, 2006; Fraaije *et al.*, 2008; van Bakel *et al.*, 2008; Garassino *et al.*, 2009).

Striadiogenes frigerioi n. gen., n. sp. is the first hermit crab with complete preservation, showing the uncalcified U-shaped abdomen and very reduced P4 and P5, both indicative characters of adaptation occupying solid protective structures.

Any track or remain of possible refuge is not present on the slab preserving the studied specimen.

The sublithographic limestones of Hadjula contain only sparse remains of shelled cephalopods, usually small sized, like some planispiral specimens belonging to the Acanthoceratidae de Grossouvre, 1894, one heteromorphic specimen belonging to the Anisoceratidae Hyatt, 1900, with *Allocrioceras* cfr. *annulatum* (Shumard, 1860) (Wippich & Lehmann, 2004), and one nautiloid, *Nautilus* sp. The gastropods are almost absent (Garassino, pers. comm., 2008). Because of the paucity and usually small size of shelled cephalopods and gastropods we infer that *Striadiogenes frigerioi* n. gen., n. sp. lived in a different environment inside the basin.

Roger (1946) interpreted the depositional environment to be a deep trough between rudist patch-reefs. Later Hüchel (1970) proposed a more complex model in which the shelf was collapsed locally forming a series of “pools” where mudstones were deposited under low energy and anoxic conditions.

If these reconstructions are correct, we can suppose that the life environment of *Striadiogenes* was into the crevices within the walls of the shelf or in crevices in the rudist-reef. Moreover the elongate valves of the rudists could also be a possible valid refuge.

Surely, the life environment of *Striadiogenes* was different from the depositional environment and its fossilization occurred only after its vertical fall into the bottom of the depositional pool of the basin.

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