Morphometric and systematic study on three *Acanthocardia* species from the Mediterranean Pleistocene (Mollusca, Bivalvia, Cardiidae)

Rafael LA PERNA
Mauro D'ABRAMO
Università di Bari, Dipartimento di Geologia e Geofisica,
via Orabona 4, I-70125 Bari (Italy)
r.laperna@geo.uniba.it

La Perna R. & D'Abramo M. 2009. — Morphometric and systematic study on three *Acanthocardia* species from the Mediterranean Pleistocene (Mollusca, Bivalvia, Cardiidae). *Geodiversitas* 31 (3): 669-682.

ABSTRACT
The cardiids *Acanthocardia echinata* (Linnaeus, 1758), *A. deshayesii* (Payraudeau, 1826) and *A. lunulata* (Seguenza, 1879) co-occur in the Mediterranean Pleistocene and are closely similar to each other, even partially overlapping in shell morphology. Of these, only *A. echinata* is fairly well known. *Acanthocardia deshayesii* has been considered a subspecies or even a synonym of *A. echinata*, whereas *A. lunulata*, only known from the original description, has been confused with *A. deshayesii.* The univariate and multivariate morphometric analysis on six shell characters substantiates the distinct taxonomic status of the three species. *Acanthocardia mucronata* (Poli, 1791), *Cardium duregnei* Monterosato, 1891 and *C. bullatum* Locard, 1892 are considered synonyms of *A. echinata. Cardium propexum* Monterosato, 1891 is proved to be a synonym of *A. lunulata*, an extinct species probably endemic to the Mediterranean, like *A. deshayesii.*

KEY WORDS
Mollusca,
Bivalvia,
Cardiidae,
Acanthocardia,
morphometry,
systematics,
Mediterranean,
Recent,
Pleistocene.

RÉSUMÉ
Étude morphométrique et systématique de trois espèces du genre Acanthocardia *du Pléistocène méditerranéen (Mollusca, Bivalvia, Cardiidae).*
Acanthocardia echinata (Linnaeus, 1758), *A. deshayesii* (Payraudeau, 1826) et *A. lunulata* (Seguenza, 1879) apparaissent dans le Pleistocène méditerranéen et sont très similaires, la morphologie des coquilles se recouvrant parfois. Parmi ces espèces, seule *A. echinata* est bien connue. *Acanthocardia deshayesii* a été considérée comme une sous-espèce ou même un synonyme d'*A. echinata*, alors qu'*A. lunulata*, uniquement connue par la description originale, a été confondu avec *A. deshayesii.* L'analyse morphométrique univariée et multivariée porte sur six caractères de coquilles différentes et confirme les statuts taxonomiques des trois espèces. *Acanthocardia mucronata* (Poli, 1791), *Cardium duregnei* Monterosato, 1891 et *C. bullatum* Locard, 1892 sont considérés comme des synonymes d'*A. echinata. Cardium propexum* Monterosato, 1891 est synonyme d'*A. lunulata*, une espèce éteinte, probablement endémique de la Méditérannée, comme *A. deshayesii.*

MOTS CLÉS
Mollusca,
Bivalvia,
Cardiidae,
Acanthocardia,
morphométrie,
systématique,
Méditerranée,
Actuel,
Pléistocène.

INTRODUCTION

Acanthocardia Gray, 1853 is a European genus including medium sized, globose cardiids with strong radial, spiny ribs. Six extant species are currently assigned to this genus: *Acanthocardia aculeata* (Linnaeus, 1767), *A. spinosa* (Solander, 1786), *A. echinata* (Linnaeus, 1758), *A. deshayesii* (Payraudeau, 1826), *A. paucicostata* (Sowerby, 1841) and *A. tuberculata* (Linnaeus, 1758) (CLEMAM). Except for *A. deshayesii*, only known from the Mediterranean, the other species occur in the adjacent Atlantic too, with different ranges (Tebble 1966; Fischer-Piette 1977; Voskuil 1989; Voskuil & Onverwagt 1989). All of them are frequently cited also for the Mediterranean Plio-Pleistocene (e.g., Sacco 1899; Cerulli Irelli 1908; Monegatti & Raffi 2001).

Acanthocardia echinata is one of the most debated cardiid species, mainly because of its unclear relationships with *A. mucronata* (Poli, 1791). *Acanthocardia deshayesii* is not particularly well known and has been considered a subspecies or even a synonym of *A. echinata*. While studying a collection of Pleistocene cardiids (D'Abramo 2007), another *Acanthocardia* species was detected. It is *A. lunulata* (Seguenza, 1879), an extinct species which has been hitherto confused with *A. deshayesii*. *Acanthocardia echinata*, *A. deshayesii* and *A. lunulata* co-occurred in the Mediterranean Pleistocene, forming a group of closely similar species, partially overlapping in shell morphology. Based on a morphometric study on six shell characters, the present work mainly aims to infer if they can be actually kept as distinct species. The three species are also systematically treated, with comments on their synonymy, distribution and taxonomic problems.

MATERIAL AND METHODS

The present work is mostly based on Pleistocene material from public and private collections (Table 1). For *Acanthocardia deshayesii* some Recent material was also examined. Most of the studied material (103 valves) was used for a morphometric analysis on six characters (four quantitative, two qualitative), aimed to support the *a priori* classification into three species (*A. echinata*, *A. deshayesii* and *A. lunulata*): shell length, shell height, valve width, number of radial ribs, type of spiny projections and type of lunule. Complete shells (paired valves) were treated as single valves, by considering only the right valve. The software PAST (Hammer *et al.* 2001) was used for statistical analysis and multivariate ordination of morphometric data.

The spiny projections, or simply spines, of *Acanthocardia* consist of "enrolled scales", with the margins more or less closely sealed to each other dorsally. Depending on the extent of enrolling and sealing, spines may be conical or subcylindrical, straight or curved, with a deep dorsal notch (spine notch of Schneider 2002: 337) along the sealing line (type 1, Fig. 1A-C) or mostly open, spoon-like (type 2, Fig. 1D, G) or shovel-like (type 3, Fig. 1E, F, H, I). Types 2 and 3 were recognised within the study material and scored as 1 and 2, respectively (based on the prevailing adult sculpture). Another type of spines was found on a few specimens of *A. echinata*: they are similar to type 2, but larger and stronger. This case was assumed to be the same as type 2, since a gradual transition to smaller and weaker spoon-shaped spines was noticed. The knobby spines or tubercles of *A. tuberculata*, with an ill-defined notch, are thought to represent an extreme modification of the same constructional pattern. The spines of *Acanthocardia* and their common constructional pattern are then a useful taxonomic tool for defining the genus. This implies that *Rudicardium* Coen, 1914 ex Monterosato ms, with *Cardium tuberculatum* Linnaeus, 1758 as type species, should be considered a synonym of *Acanthocardia* Gray, 1853. This is not contradicted by the phylogenetic analysis published by Schneider (2002), who treated *Rudicardium* as a subgenus of *Acanthocardia*. Likewise, *Sphaerocardium* Coen, 1933 (type species *Cardium paucicostatum* Sowerby, 1841), with spoon-like or subcylindrical spines, should be also considered a synonym of *Acanthocardia.* Observations on the functional significance of radial and spiny sculpture of *Acanthocardia* were reported by Savazzi (1983, 1985). Data on shell microstructure, including spines, are available from Schneider & Carter (2001).

TABLE 1. — Material examined (asterisks indicate the specimens used for morphometric analysis).

Locality	Stage	Collection	Material	
***Acanthocardia echinata* (Linnaeus, 1758)**				
Monte Mario, Rome	Early Pleistocene (Calabrian)	MPUR, Cerulli Irelli coll.	13 vs, 2 shs	*
Cutrofiano, S Apulia	Early Pleistocene	Tommasi coll.	8 vs, 3 shs	*
Cutrofiano, S Apulia	Early Pleistocene	DGGB	2 vs	*
Gallipoli, S Apulia	Early Pleistocene	DGGB	14 vs	*
San Pietro in Lamis, S Apulia	Early Pleistocene	Tommasi coll.	5 vs	*
Grammichele, SE Sicily	Early Pleistocene	La Perna coll.	5 vs	*
Montalbano Jonico, S Basilicata	Early-Middle Pleistocene	D'Abramo coll.	2 vs	*
Francavilla Fontana, S Apulia	Early Pleistocene	DGGB	1 v	*
Asti Hills, Piedmont	Early-Middle Pliocene	MRSN, Bellardi & Sacco coll.	3 vs	
***Acanthocardia deshayesii* (Payraudeau, 1826)**				
Off Terracina, Latium, 50-80 m	Recent	La Perna coll.	7 vs, 2 shs	*
Cutrofiano, S Apulia	Early Pleistocene	Tommasi coll.	8 vs	*
Grammichele, SE Sicily	Early Pleistocene	La Perna coll.	1 v	*
Francavilla Fontana, S Apulia	Early Pleistocene	DGGB	1 v	*
Cava Tacconi, Pomezia, Latium	Early Pleistocene (Calabrian)	La Perna coll.	1 v	*
Gallipoli, S Apulia	Early Pleistocene	DGGB	1 v	*
Ficarazzi, Palermo	Early Pleistocene (Sicilian)	MZR, Monterosato coll.	1 sh	
***Acanthocardia lunulata* (Seguenza, 1879)**				
Ficarazzi, Palermo	Early Pleistocene (Sicilian)	MZR, Monterosato coll.	2 vs	
Monte Mario, Rome	Early Pleistocene (Calabrian)	MPUR, Cerulli Irelli coll.	11 vs, 3 shs	*
Monte Mario, Rome	Early Pleistocene (Calabrian)	MRSN, Bellardi & Sacco coll.	2 vs	
Cava Tacconi (Pomezia), Latium	Early Pleistocene (Calabrian)	La Perna coll.	8 vs	*
Cutrofiano, S Apulia	Early Pleistocene	Tommasi coll.	3 vs	*
Grammichele, SE Sicily	Early Pleistocene	La Perna coll.	1 v	*
Francavilla Fontana, S Apulia	Early Pleistocene	DGGB	1 v	*

As in most cardiids, the lunule is well distinct in the species herein examined. Three types of lunule were recognised: narrow and flattish (type 1), wide, flattish to slightly concave (type 2) and wide, markedly to strongly concave (type 3). These three types were scored as 1, 2 and 3 respectively.

ABBREVIATIONS

DGGB	Dipartimento di Geologia e Geofisica, Università di Bari (palaeontological collection);
MPUR	Museo di Paleontologia dell'Università di Roma "La Sapienza";
MRSN	Museo Regionale di Scienze Naturali, Turin;
MZR	Museo Civico di Zoologia, Rome;
coll.	collection;
sh(s)	complete shell(s);
v(s)	valve(s);
L	antero-posterior length;
H	dorso-ventral length;
W	valve width (tumidity);
nR	number of radial ribs;
tS	type of spine;
tL	type of lunule.

MORPHOMETRICS

The size range (L) of the studied material is reported in Figure 2A. One-way ANOVA was applied to test the difference in number of ribs and shell inflation. There is no significant difference in the number of ribs between "normal" specimens of *Acanthocardia echinata* and those with larger, stouter spines, as well as between fossil and Recent specimens of *A. deshayesii*. Conversely, significant differences occur among *A. echinata*, *A. deshayesii* and *A. lunulata*: ribs range from 19 to 22 in *A. echinata*, 20 to 24 in *A. deshayesii* and 21 to 26 in *A. lunulata* (Fig. 2B). Again, there is no significant difference within the specimens of *A. echinata* in shell inflation (L/W). The Recent specimens of *A. deshayesii* have a smaller

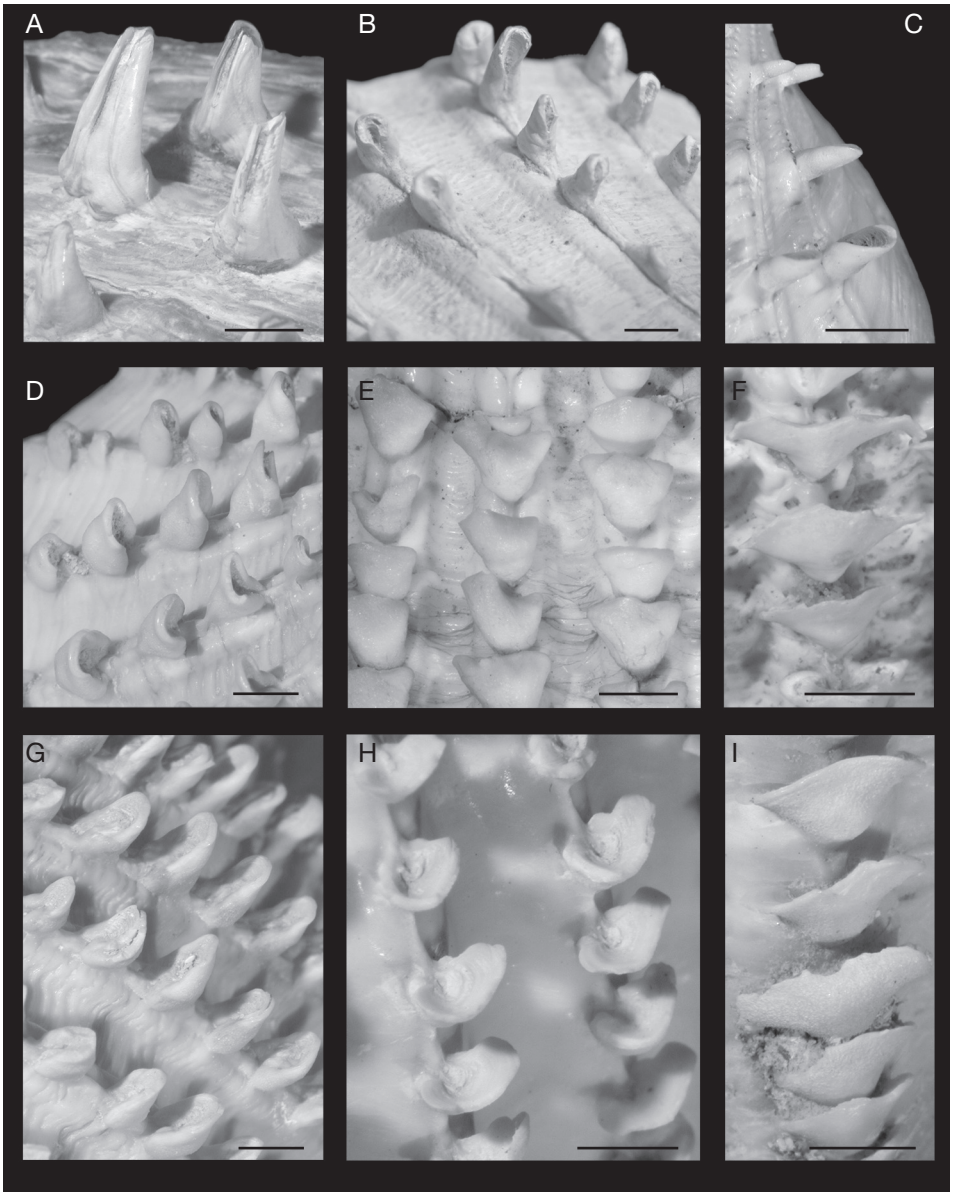

FIG. 1. — Spines in *Acanthocardia* Gray, 1853: **A**, *A. aculeata* (Linneaus, 1767), southern Adriatic (La Perna coll.), conical spines near the posterior margin (note the deep, narrow dorsal notch); **B**, *A. bianconiana* (Cocconi, 1873), Cerignola, northern Apulia, early Pleistocene (DGGB), subcylindrical spines near the antero-ventral margin (note the deep, wide dorsal notch); **C**, *A. echinata* (Linneaus, 1758), Gallipoli, southern Apulia, early Pleistocene (DGGB), subcylindrical spines near the antero-dorsal margin; **D**, *A. echinata*, Gallipoli, southern Apulia, early Pleistocene (DGGB), spoon-shaped spines near the ventral margin; **E**, *A. deshayesii* (Payraudeau, 1826), off Terracina, central-eastern Tyrrhenian, 50-80 m (La Perna coll.), shovel-shaped spines on the mid shell area; **F**, *A. lunulata* (Seguenza, 1879), Monte Mario, Rome, early Pleistocene (Cerulli Irelli coll., MPUR), shovel-shaped spines on the mid shell area; **G**, *A. echinata*, same as C, spoon-shaped spines on the mid shell area; **H**, *A. deshayesii*, Cutrofiano, southern Apulia, early Pleistocene (Tommasi coll.), shovel-shaped spines on the mid shell area; **I**, *A. deshayesii*, Cutrofiano, southern Apulia, early Pleistocene (Tommasi coll.), shovel-shaped spines on the mid shell area. Scale bars: 2 mm.

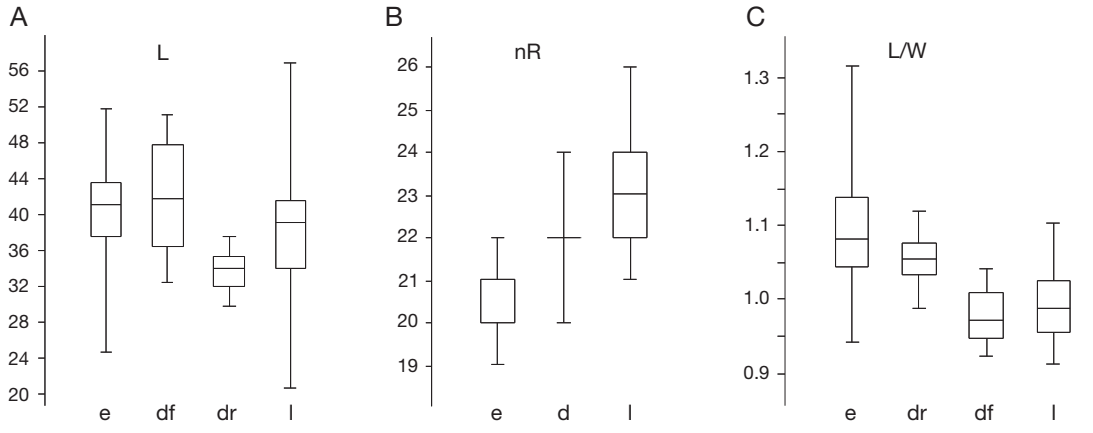

FIG. 2. — Box-plots for size range (**A**), number of ribs (**B**) and shell inflation (**C**) in the study material. Each box plot shows minimum, maximum, 25-75 percent quartiles and median. Abbreviations: **df**, fossil *Acanthocardia deshayesii* (Payraudeau, 1826); **dr**, Recent *A. deshayesii*; **e**, *A. echinata* (Linneaus, 1758); **l**, *A. lunulata* (Seguenza, 1879).

inflation, the same as *A. echinata*, whereas the fossil specimens of *A. deshayesii* are more inflate, as *A. lunulata* (Fig. 2C). Due to the high linear correlation (r = 0.96) between L and H for the entire dataset, these differences are also reflected by the H/W ratio.

No possibility of discriminating the three species is given by the bivariate analysis on L, H and W. The scatter-plots based on couples of these variables consist of a single, compact cloud of points. The L-L/W scatter-plot (entire dataset) shows no correlation and the species are loosely ordered from lower (*A. lunulata)* to higher (*A. echinata*) L/W values.

Principal Component Analysis (PCA) and Principal Coordinates Analysis (PCO), based on the six variables as above described, proved to be useful tools for better understanding the morphological separation of the studied species. In the plane of the first two PCA axes (about 90% of the total variance) the specimens form two clusters (Fig. 3A). Loadings are mostly given by L, H and W (positive values) on PCA1 and by nR, tL and tS (negative values) on PCA2. As usually in PCA, ordination along the first axis is based on size, with no differentiation among the species. Conversely, ordination along the second axis is based on decreasing number of ribs, narrower-flatter lunula (types 3 to 1) and narrower spines (types 3 to 2). A similar pattern was obtained through the PCO ordination (Fig. 3B): though the variance explained by the first two axes is smaller (about 70%) than in PCA, the two clusters are more clearly separated, in this case along the first axis (in PCO there is no relation of axes with the original variates). In both cases, *A. echinata* forms a well-defined cluster which includes the large-spined specimens. The other cluster consists of two subclusters, formed by *A. deshayesii* (fossil and Recent) and *A. lunulata* respectively, with a small overlap in PCA and no overlap in PCO. There is no separation between fossil and Recent specimens of *A. deshayesii*, but the latter are closely grouped within the main cluster, in the small size region (negative semi-axes of PCA). The Recent specimens of *A. deshayesii* thus differ from the fossil ones by being smaller and more inflate, but these differences do not produce a segregation in the multivariate morphospace. These results will be further discussed in the systematic part, but some considerations can be drawn here: 1) *A. echinata*, *A. deshayesii* and *A. lunulata* are morphologically distinct; 2) *A. deshayesii* and *A. lunulata* are much closer to each other than to *A. echinata*; and 3) the Pleistocene specimens of *A. deshaysii* are slightly different in size and inflation from the modern ones.

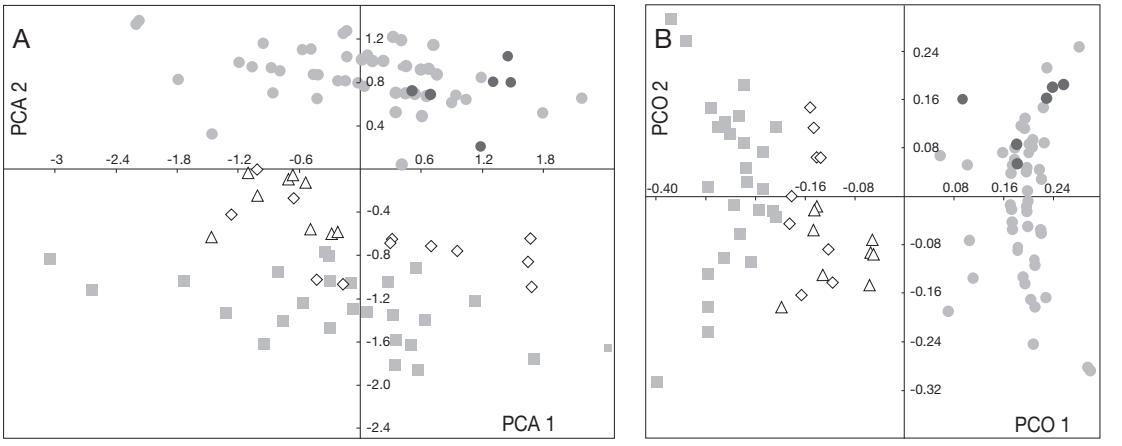

FIG. 3. — Multivariate ordination (103 specimens, variance-covariance matrix from standardized data): **A**, Principal Component Analysis: PCA 1 = 48.48 %, PCA 2 = 42.30 % of total variance; **B**, Principal Coordinates Analysis (Gower similarity index, transformation exponent c = 2): PCO 1 = 47.35 %, PCO 2 = 17.58 % of total variance. ●, *Acanthocardia echinata* (Linneaus, 1758); ●, *A. echinata* (large spine); ◇, *A. deshayesii* (Payraudeau, 1826) (fossil); △, *A. deshayesii* (Recent); ■, *A. lunulata* (Seguenza, 1879).

SYSTEMATICS

Family CARDIIDAE Lamarck, 1809
Subfamily CARDIINAE Lamarck, 1809

Genus *Acanthocardia* Gray, 1853

TYPE SPECIES. — *Cardium aculeatum* Linnaeus, 1758.

Acanthocardia echinata (Linnaeus, 1758)
(Figs 1C, D; 4)

Cardium echinatum Linnaeus, 1758: 679. — Bucquoy *et al*. 1892: 261, pl. 42, figs 1-3. — Fischer-Piette 1977: 105. — Hylleberg 2004: 845, unnumb. figs, 2nd and 3rd rows (syntypes).

Cardium mucronatum Poli, 1791: 59, pl. 17, figs 7, 8.

Cardium echinatum var. *mucronata* – Bucquoy *et al.* 1892: 266, pl. 42, figs 4, 5. — Cerulli Irelli 1908: 20, pl. 2, figs 10-15.

Cardium duregnei Monterosato, 1891 ex de Boury ms: 13.

Cardium bullatum Locard, 1892: 303.

Cardium echinatum var. *pliomucronata* Sacco, 1899: 39, pl. 9, fig. 9.

Cardium echinatum var. *gibba* Sacco, 1899: 38, pl. 9, figs 6-8.

? *Cardium novum* Coen, 1941: 170, figs 12-14.

Acanthocardia echinata (Linnaeus, 1758). — Voskuil 1989: 254, fig. 3. — Voskuil & Onverwagt 1989: 59, fig. 12.02.

MATERIAL EXAMINED. — See Table 1.

DISTRIBUTION. — *Acanthocardia echinata* has a wide distribution, ranging from Norway, Iceland south to Morocco and Canary Islands, including the Mediterranean (Bucquoy *et al.* 1892; Tebble 1966; Fischer-Piette 1977). It is common in the Mediterranean Plio-Pleistocene, in sandy-muddy deposits.

REMARKS

Three well-known works can serve to summarize the historical views about the relations between *Acanthocardia echinata* and *A. mucronata*: according to Bucquoy *et al.* (1892), *A. mucronata* is a Mediterranean "variety" of *A. echinata*, whereas they are separate species according to Dodge (1952) and synonyms according to Fischer-Piette (1977).

It may be worth reminding that Poli (1791) misinterpreted *Cardium echinatum* as *C. spinosum* Solander, 1786 (= *C. erinaceum* Lamarck, 1819) when describing *C. mucronatum,* as noticed by

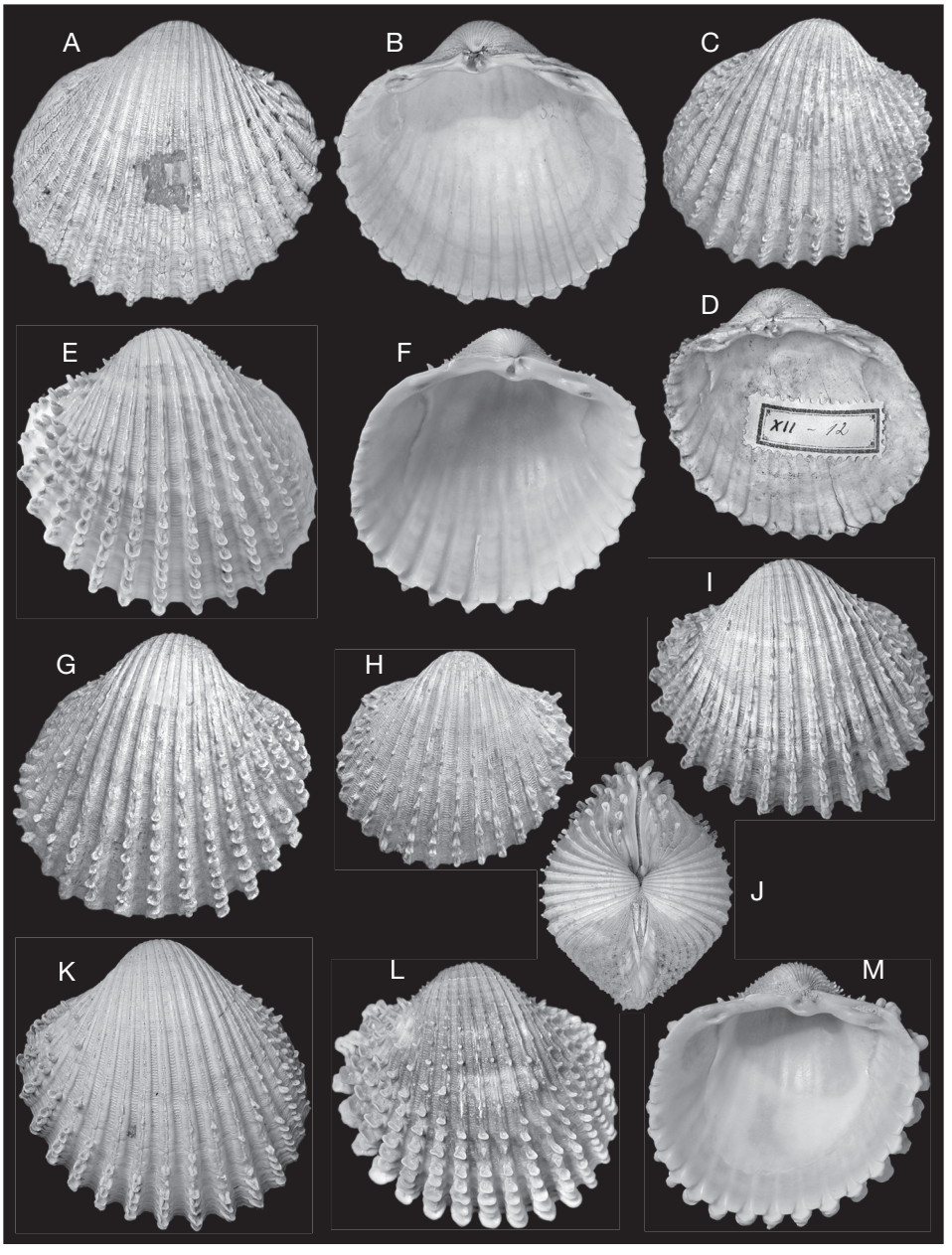

FIG. 4. — *Acanthocardia echinata* (Linnaeus, 1758): **A**, **B**, Asti Hills, Piedmont, Early-Middle Pliocene, syntype of *Cardium echinatum* var. *pliomucronata* Sacco, 1899, 49.6 mm (Bellardi & Sacco coll., MRSN BS.131.01.024), original illustration in Sacco (1899: pl. 9, fig. 9a); **C**, **D**, Monte Mario, Rome, early Pleistocene, 42.0 mm (Cerulli Irelli coll., MPUR), original illustration in Cerulli Irelli (1908: pl. 2, fig. 11); **E**, **F**, Gallipoli, early Pleistocene, 47.2 mm (DGGB); **G**, Monte Mario, Rome, early Pleistocene, 46.4 mm (Cerulli Irelli coll., MPUR), original illustration in Cerulli Irelli (1908: pl. 2, fig. 10); **H**, Monte Mario, Rome, early Pleistocene, 37.1 mm (Cerulli Irelli coll., MPUR), original illustration in Cerulli Irelli (1908: pl. 2, Fig. 13); **I**, Gallipoli, southern Apulia, early Pleistocene, 44.68 mm (DGGB); **J**, Cutrofiano, southern Apulia, early Pleistocene, 38.3 mm (Tommasi coll.); **K**, Cava Tacconi, Pomezia (Latium), early Pleistocene, 46.8 mm (La Perna coll.); **L**, **M**, Cutrofiano, southern Apulia, early Pleistocene, 44.3 mm (DGGB).

Coen (1941) and Hylleberg (2004: 482). Though *Acanthocardia spinosa* and *A. echinata* are well distinct, Poli's misinterpretation may have contributed to the idea that *A. mucronata* and *A. echinata* were different species. After the illustrations of the type material of *C. echinatum* (Linnean Society, London, one shell and two valves) by Hylleberg (2004), it should be clear that *C. echinatum* and *C. mucronatum* are the same species. One of the syntypes illustrated by Hylleberg (2004) shows the shell characters which are usually recognised for *A. mucronata*, i.e. sub-equilateral shape and larger spoon-like spines (e.g., Bucquoy *et al.* 1892; Coen 1941), whereas the others are more inaequilateral and with smaller, less developed spines, as generally recognised for *A. echinata*. Most probably, a clinal variation exists through the wide geographic range of *A. echinata*, with the sub-equilateral, coarsely spined form ("*mucronata*") prevailing at lower latitudes and in the Mediterranean.

In the literature on the Plio-Pleistocene Mediterranean molluscs, *A. mucronata* has been mostly regarded as specifically or subspecifically distinct from *A. echinata.* The latter has been even regarded as a northern immigrant in the Mediterranean during the Pleistocene glacial phases (Malatesta & Zarlenga 1986; Raffi 1986). *Acanthocardia echinata* was also present in the Mediterranean Pliocene, as proved by the material from the Asti area (Early-Middle Pliocene) in the Bellardi & Sacco collection (MRSN) (Fig. 4A, B) and by several well-illustrated Pliocene records, such as Palla (1966: 433, pl. 23, fig. 3a-c) and Cavallo & Repetto (1992: 202, fig. 601). *Cardium echinatum* var. *pliomucronata* Sacco, 1899 (Fig. 4A, B) is a synonym of *A. echinata.*

Cardium duregnei Monterosato, 1891 ex de Boury ms and *C. bullatum* Locard, 1892, both described from the Atlantic of France, have been synonymised with *A. echinata* (Bucquoy *et al.* 1892; Fischer-Piette 1977). A fully treatment of this case, including illustrations of the type material, will be reported elsewhere but the synonymy with *A. echinata* is confirmed in the present work. The shell of *Cardium duregnei* and *C. bullatum* is somewhat robust, with distinctly bipartite ribs, short, spoon-shaped spines and a slightly rugose surface, due to a poorly defined commarginal sculpture crossing radial ribs and interspaces. This morphology is interpreted as an ecophenotype of *A. echinata*, probably related with shallow, sheltered settings. The Plio-Pleistocene records of *Cardium duregnei* (Monterosato 1891; Foresti 1895) and *C. echinatum* var. *gibba* Sacco, 1899 from the Pliocene of Piedmont (Sacco 1899: 38, pl. 9, figs 6-8), similar to *C. duregnei* and *C. bullatum*, suggest that this form of *A. echinata* also occurred in the Mediterranean Plio-Pleistocene.

Cardium novum Coen, 1941, described from a single inaequilateral, oblique, slightly gaping shell with small spoon-like spines (Coen 1941: 170, figs 12-14) could be an abnormal specimen of *A. echinata* and is included, at least tentatively, in the synonymy of this species.

The identity of the fossil species *Cardium gibbum* and *C. mutabile*, both described by Defrance (1817: 107, 108), is doubtful. The former is from the Pliocene of Italy and might be a synonym of *A. echinata*. The identity of the latter, probably also from the Pliocene of Italy, is even more uncertain as its description recalls *A. echinata*, *A. deshayesii* and *A. lunulata.*

The examined material exhibits variability in shape and strength of spines (type 2), whereas the lunule is invariantly narrow and flattish (type 1). There is a gradual transition between shells with the look of *mucronata* (Fig. 4H, I) and those recalling *echinata* (Fig. 4C, K). All of the specimens identified as *A. echinata* fall into the same cluster (Fig. 3A, B). The specimens with unusually large, strong spines (Fig. 4L, M) also seem an extreme case of variability of *A. echinata*, as suggested by the morphometric analysis.

The hinge of *A. echinata* is similar to that of the congeners, as described and illustrated by Schneider (2002: 337, fig. 12C, D). The dorsal nymph flare (Schneider 2002: 337) is fairly well-developed, subrectangular to roughly triangular in shape.

Acanthocardia deshayesii (Payraudeau, 1826)
(Figs 4E, H, I; 5)

Cardium deshayesii Payraudeau, 1826: 56, pl. 1, figs 53-56. — Hidalgo 1870: 170, pl. 37, Fig. 3. — Bucquoy *et al.* 1892: 267, pl. 43, figs 6, 7. — Hylleberg 2004: 845, unnumb. figs, 1st row (syntype).

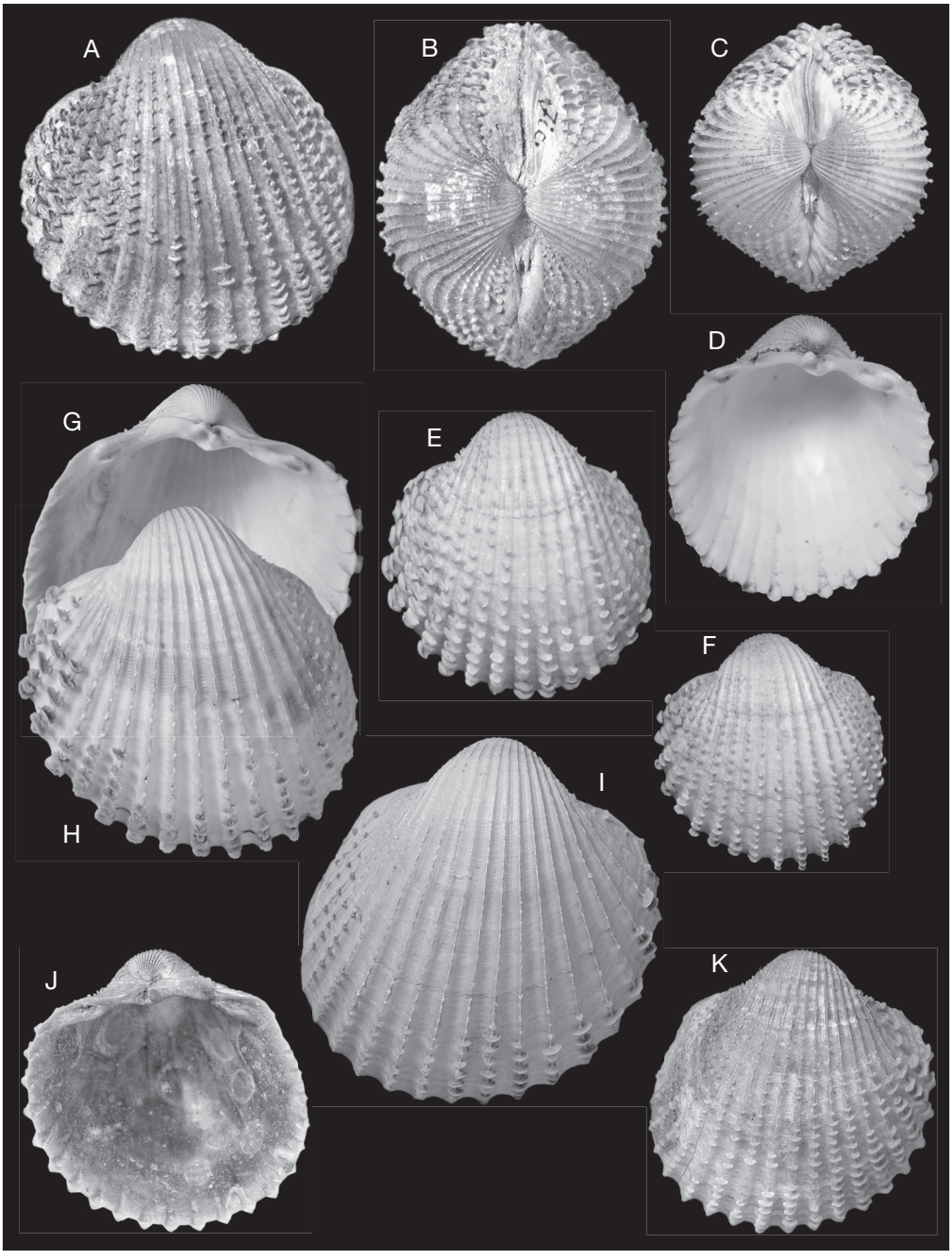

FIG. 5. — *Acanthocardia deshayesii* (Payraudeau, 1826): **A**, **B**, Ficarazzi, Palermo, early Pleistocene, 45.3 mm (Monterosato coll. ex Brugnone, MCZ 14742); **C**-**E**, off Terracina, central-eastern Tyrrhenian, 50-80 m, 35.3 mm (La Perna coll.); **F**, off Terracina, central-eastern Tyrrhenian, 50-80 m, 30.4 mm (La Perna coll.); **G**, **H**, Cutrofiano, southern Apulia, early Pleistocene, 44.8 mm (Tommasi coll.); **I**, Cutrofiano, southern Apulia, early Pleistocene, 47.6 mm (Tommasi coll.); **J**, **K**, Grammichele, southeastern Sicily, early Pleistocene, 38.5 mm (La Perna coll.).

Cardium (*Cerastoderma*) *deshayesii* Payraudeau, 1826. — Fischer-Piette 1977: 109.

MATERIAL EXAMINED. — See Table 1.

DISTRIBUTION. — *Acanthocardia deshayesii* was described from off southwestern Corsica (Payraudeau 1826) and most records are from the western Mediterranean, as a rare species (Hidalgo 1870; Locard 1886, 1892; Locard & Caziot 1900; Fischer-Piette 1977). There are also records from the eastern Mediterranean (Demir 2003; Zenetos *et al.* 2005; Vardala-Theodorou pers. comm.), but none from the Northeast Atlantic.

The fossil Mediterranean records are confusedly based on *A. deshayesii* and *A. lunulata*, both occurring in the Pleistocene.

REMARKS

Acanthocardia deshayesii has been considered a subspecies or even a synonym of *A. echinata* (see the nomenclatural history reported by Fischer-Piette [1977] and Hylleberg [2004: 467]). The Recent material studied in the present work matches the syntype of *Cardium deshayesii* (Muséum national d'Histoire naturelle, Paris) illustrated by Hylleberg (2004).

This species has more radial ribs than *A. echinata* (Fig. 2B), is more inflate (Fig. 2C), slightly higher dorso-ventrally, with a larger umbo and more clearly truncated posteriorly. Spines are wider, shovel-shaped and markedly concave dorsalward (type 3; Fig. 4E, H, I). This last character was finely described and illustrated by Payraudeau (1826). The lunule is moderately wide, flattish to slightly concave (type 2; Fig. 5B, C).

Though the Recent material of *A. deshayesii* examined in the present work is scant (Table 1), its size range (Fig. 2A) matches the records in literature (Payraudeau 1826; Hidalgo 1870; Locard 1892; Locard & Caziot 1900), with a shell length not exceeding 40 mm. The Pleistocene specimens are larger, with a maximum shell length slightly exceeding 50 mm and slightly less inflate (Fig. 2A; 5A, B, G-K), but shape, sculpture and wall thickness are the same as in the modern specimens (Fig. 5C-F). As discussed above, no segregation between Pleistocene and modern specimens of *A. deshayesii* resulted from the morphometric analysis (Fig. 3) and a taxonomic separation only based on minor differences in size and inflation cannot be proposed. However, these differences suggest the hypothesis that *A. deshayesii* has underwent minor morphological changes through its stratigraphic range.

Acanthocardia lunulata (Seguenza, 1879) (Figs 1F; 6)

Cardium lunulatum Seguenza, 1879: 280.

Cardium propexum Monterosato, 1891: 2. — Coen 1941: 169, fig. 11 (syntype).

MATERIAL EXAMINED. — See Table 1.

DISTRIBUTION. — At present, *Acanthocardia lunulata* is only known from the Mediterranean Pleistocene.

REMARKS

Seguenza (1879) described *Cardium lunulatum* from Pleistocene deposits on the Calabrian side of the Messina Strait, as follows: "a single valve of *Cardium* from Gallina somewhat resembling *C. echinatum* in shape and sculpture but clearly distinct. It is more rounded in shape; the ribs are 25 in number and ornamented with spoon-like papillae, anteriorly larger. However, the best distinguishing character is a cordate-ovate, wide, smooth, deeply excavated lunule. Length 20 mm. Width [height] 20.5 mm".

Monterosato (1891) briefly described *Cardium propexum* from the Pleistocene of Ficarazzi and Monte Pellegrino (Palermo) as differing from *C. deshayesii* by a greater number of ribs, a more transverse shape and the papillae closely leaning against each other. The material labelled as *C. propexum* in the Monterosato coll. (MZR) consists of four valves: one of *A. echinata* (sub-adult), one of *A. deshayesii* and two of a different species, somewhat corresponding to the description of *C. propexum* (Fig. 6A, B), all from Ficarazzi. A type valve of *C. propexum* from the same locality was illustrated by Coen (1941: fig. 11): this valve is clearly conspecific with the two valves in the Monterosato coll. corresponding to the original description. *Cardium propexum* has a deep, wide lunule, though this character was mentioned neither by Monterosato, nor by Coen. The "transverse" shape remarked by Monterosato is puzzling, as *C. propexum* is not more elongate than *A. echinata*. Probably, some confusion was made by

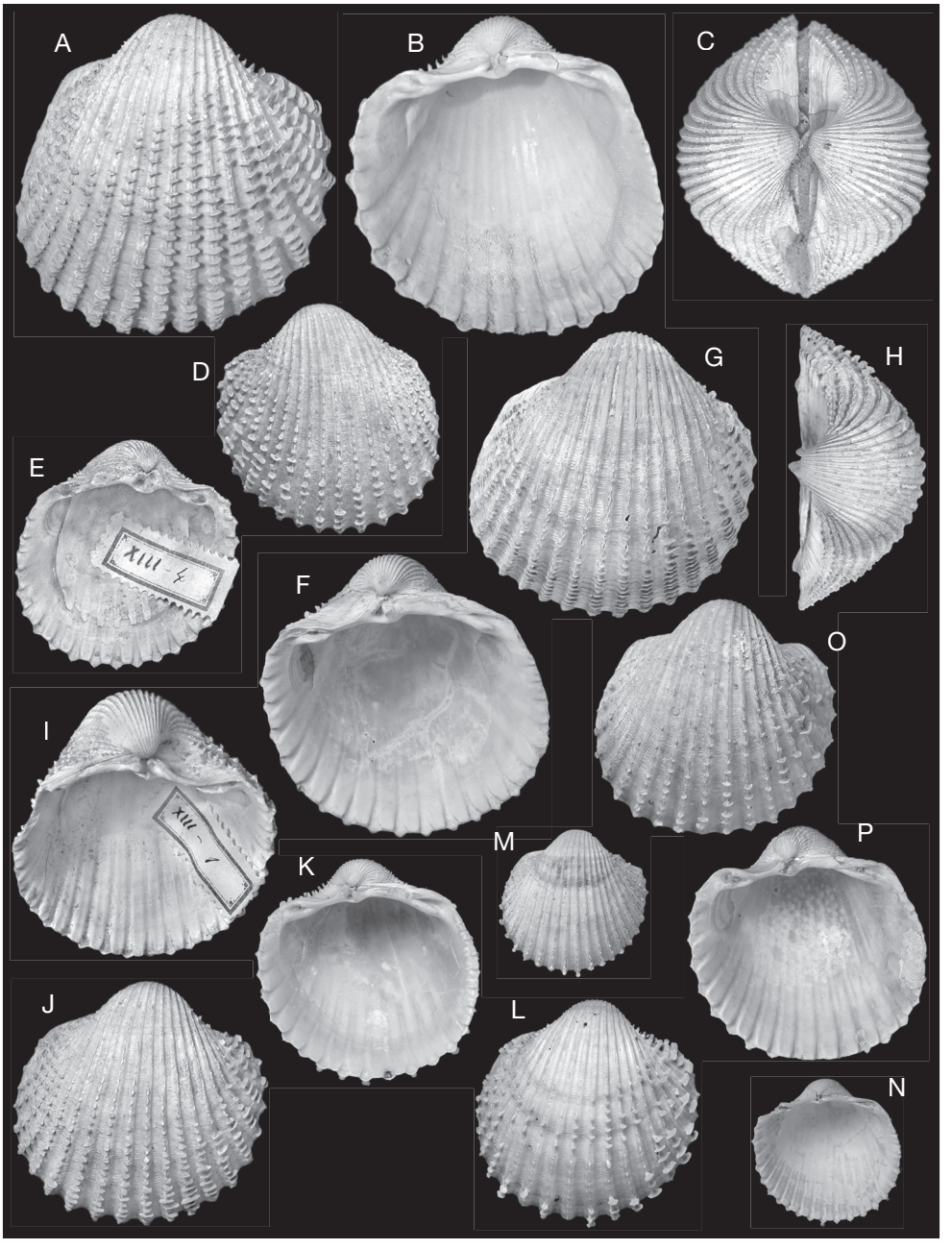

FIG. 6. — *Acanthocardia lunulata* (Seguenza, 1879): **A**, **B**, Ficarazzi, Palermo, early Pleistocene, syntype of *Cardium propexum* Monterosato, 1891, 50.2 mm (Monteosato coll., MZR 14744); **C**, Monte Mario, Rome, early Pleistocene, 43.5 mm (Cerulli Irelli coll., MPUR); **D**, **E**, Monte Mario, Rome, early Pleistocene, 35.0 mm (Cerulli Irelli coll., MPUR), original illustration in Cerulli Irelli (1908: pl. 3, fig. 4); **F**-**H**, Cava Tacconi, Pomezia (Latium), 44.9 mm; **I**, Monte Mario, Rome, early Pleistocene, 41.1 mm (Cerulli Irelli coll., MPUR), original illustration in Cerulli Irelli (1908: pl. 3, fig. 1); **J**, Monte Mario, Rome, 39.3 mm (Cerulli Irelli coll., MPUR); **K**, **L**, Cava Tacconi, Pomezia (Latium), 34.7 mm (La Perna coll.); **M**, **N**, Cava Tacconi, Pomezia (Latium), 23.1 mm (La Perna coll.); **O**, **P**, Grammichele, southeastern Sicily, early Pleistocene, 37.4 mm (La Perna coll.).

Monterosato when describing *C. propexum*, as seen in the material in collection. On the other hand, Monterosato (1891) thought that *C. propexum* was the same as *Cardium echinatum* var. *tenuis*, *costis angustioribus* of Mörch (1871) from the North Sea ("and of all authors on the Arctic fauna"). Similar comments were made by Coen (1941), reporting handwritten notes by Monterosato about the significance of *C. propexum* as a Northern migrant in the Mediterranean Pleistocene, "as *Cyprina islandica*". This recalls the records of *A. echinata* as a Northern immigrant in the Mediterranean Pleistocene, as discussed above.

Cerulli Irelli (1908: 20, pl. 3, figs 1-6) reported *Cardium deshayesi* (*sic*) from the Pleistocene of Monte Mario remarking a particularly distinct and deep lunule on his material. The material in the Cerulli Irelli coll. (MPUR) consists of a cardiid similar to *A. deshayesii* but with a deep, wide lunule, together with few misidentified valves of *A. echinata*. Material from Monte Mario corresponding to the same species with the deep lunule reported by Cerulli Irelli, is also present in the Bellardi & Sacco coll. (MRSN) (Sacco 1899: pl. 9, fig. 10).

It is obvious that Seguenza (1879), Monterosato (1891), Sacco (1899) and Cerulli Irelli (1908) dealt with the same species, i.e. *Acanthocardia lunulata* (Seguenza, 1879). Indeed, the main difference from *A. deshayesii* is the deep, wide lunule, particularly in larger specimens (Fig. 6I) but also seen in smaller ones (Fig. 6M, P), as that described by Seguenza (1879). Except for this difference, the two species are markedly similar to each other. The differences pointed out by the morphometric analysis (number of ribs and shell inflation) are statistically significant, but widely overlapping (Fig. 2B, C). Spines are similar in shape, size, orientation and distribution between the two species and the difference in spine density observed by Monterosato (1891) is not reliable. *Acanthocardia lunulata* seems more variable in shell outline than *A. deshayesii,* but no diagnostic difference in this character was found between the two species.

There are many records of *Cardium deshaysii* from the Mediterranean Plio-Pleistocene, but they could have been based either on *A. deshaysii* or on *A. lunulata.* Monterosato (1891) remarked that the fossil record of *C. deshayesii* by Philippi (1836: 53) was based on *C. propexum*, but there is no observation in Philippi's work useful to understand the species identity. The same can be said about the records by Coppi (1881), Ponzi & Meli (1887), Pantanelli (1893) and Foresti (1895). Gignoux (1913: 413, pl. 11, fig. 4) illustrated the external view of a Pleistocene cardiid as *C. echinatum propexum,* but it is not possible to understand if it is *A. deshayesii* or *A. lunulata*. Ruggieri (1953: 50) recorded *Cardium deshayesii propexum* from the Pleistocene of Calabria: it was said to differ from *C. deshayesii* only by its larger size and a less inaequilateral shape. These differences could point to the larger Pleistocene form of *A. deshayesii* but, once more, the record remains ambiguous.

CONCLUDING REMARKS

The separation of *Acanthocardia echinata*, *A. deshayesii* and *A. lunulata* may be troublesome, particularly for the last two, but there are strong evidences that they are distinct species. Apart from the shell characters considered in the present study, no diagnostic differences were observed among the three species in other shell characters, such as hinge, cross profile of the ribs, commarginal sculpture, etc.

More studies on a larger scale, on Recent and fossil material, are needed for better understanding the variability of *A. echinata* through its wide latitudinal and ecological range. This could be useful for assessing more clearly the taxonomic status of *A. deshayesii*, *A. lunulata* and of another closely related species, *A. sliggersi*, recently described from the Plio-Pleistocene of the North Sea Basin (Moerdijk & Ter Poorten 2007), hitherto misidentified as *A. echinata*.

Acknowledgements
Our thanks to Lionello Tringali (Rome), for the greatly appreciated donation of his own material of *Acanthocardia* and the kind assistance at the Monterosato coll. (MZR), to Luigi Tommasi (Museo di Storia Naturale del Salento, Calimera, Lecce) for the loan of material from his own collection, to

Daniele Ormezzano (MRSN) for his kind assistance at the Bellardi & Sacco coll. Serge Gofas (Universidad de Málaga). Jan Johan ter Poorten (Zoological Museum, Amsterdam) and an anonymous reviewer are acknowledged for critical reading, comments and suggestions.

Work supported by Fondi di Ricerca d'Ateneo 2006 (La Perna).

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Submitted on 2 February 2008;
accepted on 10 October 2008.