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SYSTEMATICS AND PALAEOBIOGEOGRAPHY OF *MEGACARDITA* SACCO IN THE NEOGENE OF EUROPE (BIVALVIA, CARDITIDAE)

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Abstract: *Megacardita* Sacco is a poorly known and misunderstood carditid genus in the subfamily Venericardiinae. The only species frequently reported from the Miocene of Europe is the type species *M. jouanneti* (Basterot), often considered to be a highly variable species. The genus also has been used for fossil and living species from disparate areas and ages. In addition to *M. jouanneti*, six other species were identified in the present work: *M. brocchii* (Michelotti), *M. guenterti* Pfister & Wegmüller, *M. hoernesi* sp. nov., *M. ignorata* Cossmann & Peyrot, *M. laeviplana* (Depéret) and *M. dertavicula* (Sacco). The new species is described from the Langhian of the Vienna Basin. The seven species cover a stratigraphic interval ranging from middle Burdigalian to Messinian, and a palaeogeographical area encompassing the north-east Atlantic, the Western and Central Paratethys, and the Mediterranean. The genus apparently radiated from the central European basins, but its evolutionary relations with other carditids remain unclear. Two additional species are also tentatively referred to *Megacardita*: *M.*? *laticosta* (Eichwald) from the Langhian of Ukraine and Poland, and *M.*? *redoniana* nom. nov. for *Cardita striatissima* auct. non Cailliaud *in* Mayer from the Messinian–Early Pliocene of France and Portugal. There is no evidence of a wider distribution of *Megacardita*, either stratigraphically or geographically.

Key words: Carditidae, Venericardiinae, *Megacardita*, systematics, Europe, Miocene.

As recently remarked by Huber (2010), Carditidae is one of the less well-studied bivalve families. The systematics of living and fossil carditids has been mostly neglected, and many or most species are still allocated in a few pigeonhole genera, such as *Cardita* Bruguière, 1792 and *Venericardia* Lamarck, 1801. This is not only because of the poor knowledge of these bivalves, but also due to the lack of suitable genera.

The living carditids are rather morphologically diverse: in size, from the minute species of *Pleuromeris* Conrad, 1867 to the large *Cardita crassicosta* Lamarck, 1819; in shape, from the strongly elongate species of *Carditamera* Conrad, 1838 to the orbicular ones of *Cyclocardia* Conrad, 1867; and in sculpture, from weakly sculptured, like *Coripia* de Gregorio, 1885, to strongly ribbed, often with beads, tubercles and projecting scales, as in most Carditinae. Such a morphological diversity, also seen in the fossil record, seems to reflect, at least in part, the wide range of life habits, from epifaunal byssally attached to endobyssate and free-burrowing (Yonge 1969; Stanley 1970, 1972; Heinberg 1993). In spite of their diversity, carditids are a rather conservative group, with frequent convergences among distinct subfamilies, families and genera, particularly in shape and sculpture. Also, a tendency to large, sturdy shells with a robust hinge is a recurrent theme in the evolutionary history of the family.

Megacardita Sacco, 1899 is an example of a very poorly known and misunderstood carditid genus. The only apparently well-known species is *Megacardita jouanneti* (Basterot, 1825), the type species, frequently cited from the Miocene of Europe thanks to its large size which allows it to be easily detected. It has often been considered to be highly variable, and a number of varieties and forms have been named. While *M. jouanneti*, with its cohort of varieties, included in the synonymy of *M. jouanneti* or totally forgotten, remained almost the only representative known for the genus in Europe, several species from disparate areas and ages, from the Oligo-Miocene of New Zealand, to the Miocene of the Russian Far East, the Mio-Pliocene of Japan, the Cenozoic of Patagonia and even from the modern seas of China and Australia, have been referred to *Megacardita*. In most cases, large size and similarities in shape and sculpture

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have been the only characters used to refer these carditids to *Megacardita*.

The present work tries to fill the gap in our knowledge of *Megacardita*, beginning with a comprehensive study of the type species. This study led to unexpected results: at least seven species are recognized here in *Megacardita,* ranging from the Burdigalian to the Messinian, through a rather wide area, including the north-east Atlantic, the Paratethys and the palaeo-Mediterranean.

It is hoped that this work will contribute significantly not only to the knowledge of the genus *Megacardita*, but also as an example for dealing with the study of the carditid bivalves, so disregarded and admittedly complex.

MATERIAL AND METHOD

The first step was careful bibliographical research to identify all the taxa with a possible systematic position in the genus *Megacardita*. This was followed by an extensive study of museum material, mostly coming from well-known fossil localities, mainly in Austria, Italy, France, Portugal and Switzerland, including type material whenever possible. Nine species are dealt with herein, two of which are only tentatively referred to *Megacardita*. After the type, species are listed in stratigraphical order.

Terminology follows Carter *et al.* (2012) as far as possible. Dentition terminology follows Bernard's system (Carter *et al.* 2012; Güller & Zelaya 2013).

A shape analysis was carried out on a sample of *Megacardita jouanneti* from Salles (SW France) and of another closely similar species from Gainfarn (Lower Austria), herein described as new, plus additional valves of the new species from various localities. The main goal of shape analysis was to quantify the differences in shell outline between *M. jouanneti* and the new species. More generally, it was meant to test the contribution of shell shape to the discrimination of species within the genus *Megacardita*. High resolution (400 dpi) images of the internal view of 62 valves (29 from Salles, 24 from Gainfarn, nine from other localities), in the range of about 40–70 mm in length, were obtained using a digital scanner. Left valve images were mirrored as right valves. Valve images were then transformed into outlines consisting of 100 evenly spaced points. Due to the difficulty in finding one distinct, easy to detect point along the shell outline, the starting point was fixed as the anterior intersection between the shell outline and the line connecting the two points where the pallial line joins with posterior and anterior muscle scars. Points and their coordinates were obtained with the software tpsDig 2.12 (Rohlf 2010). Shape analysis was performed using PAST 2.17 (Hammer *et al.* 2001): outlines were standardized, removing size, position and rotation (Procrustes fitting), then submitted to harmonic decomposition with the elliptic Fourier method. The coefficients of all harmonics were used in the principal component analysis (PCA), based on the covariance matrix.

Institutional abbreviations. MA, Auckland Museum, New Zealand; MHNBx, Museum d'Histoire naturelle, Bordeaux, France; MNHN, Museum national d'Histoire naturelle, Paris, France; MPUB, Museo di Paleontologia dell'Università di Bari, Italy; MRSN, Museo Regionale di Scienze Naturali di Torino, Italy; MSNUP, Museo di Scienze Naturali dell'Università di Pisa, Italy; NHMW, Naturhistorisches Museum Wien, Austria; NMB, Naturhistorisches Museum Basel, Switzerland; NMBB, Naturhistorisches Museum der Burgergemeinde Bern, Switzerland; TUG, Museum of Geology, University of Tartu, Estonia; ZNG PAN, Geological Museum of the Institute of Geological Sciences of the Polish Academy of Sciences, Kraków.

TAXONOMY OF *MEGACARDITA* SACCO, 1899

The genus *Megacardita* was introduced as a subgenus of *Cardita* Bruguière, 1792 by Sacco (1899, p. 9), who designated *Cardita jouanneti* Basterot, 1825 as type species. He discussed its relationship with *Cardita s.s.*, from which the new subgenus was distinguished by being larger and more robust, more regularly ovate, with radial ribs more uniform in strength and a less strongly anterior umbo.

Sacco considered *Megacardita* to be a living group, currently represented by *Cardita incrassata* (G. B. Sowerby, 1825) (= *Cardita turgida* Lamarck, 1819). It is one of the rather large, robust Australian carditids recently referred to *Megacardita* by Huber (2010). In gross shell shape, these species are actually reminiscent of *Megacardita,* but their sculpture, consisting of spaced, strong, often nodulose radial ribs with deeply excavated interspaces, is markedly different from the wide and moderately convex, mostly smooth ribs, with narrow and shallow interspaces of *M. jouanneti* (Fig. 1F, G). The hinge of *Cardita turgida* was illustrated by Lamy (1922, p. 292), who placed this species in *Venericardia* (*Megacardita*); it actually is similar to that of *Megacardita*, but weaker and differing in some details, such as a more slender tooth 3b, stouter 2a, and the occurrence of small, tubercle-shaped lateral teeth in the left valve (LA II and LP II), whereas only the small LA I is present in adult valves of *M. jouanneti* (Fig. 1D). The multilocus phylogenetic study of archiheterodont bivalves by González & Giribet (2015) showed that '*Megacardita*' *nodulosa* (Lamarck, 1819) and '*M.*' *preissii* (Menke, 1843), two of the robust Australian species used as representatives of *Megacardita*, form a distinct

monophyletic group, sister to *Carditamera* Conrad, 1838, although this genus has an elongate shell, weak radial sculpture and well-developed lateral teeth (Chavan 1969; González & Giribet 2012). The systematic position of the Australian species remains unclear, but a position in *Megacardita* is unlikely, due to their sculptural characters, at least.

In *Megacardita*, Sacco (1899) also included *Cardita arduini* Brongniart, 1823 and its varieties *truncata* Rovereto, 1898 and *corbuloides* Rovereto, 1898, all from the Tongrian (middle Oligocene) of Savona, Liguria. Similarly, Báldi (1973) placed early Egerian (Chattian, Late Oligocene) specimens of *Cardita arduini* from the Central Paratethys in *Megacardita*. However, *Cardita arduini* (Fig. 2G) has scaly radial ribs and a subterminal umbo, thus appearing much closer to *Cardita calyculata* (Linné, 1758; Fig. 2A, B), type species of *Cardita,* than to *Megacardita*. This species is therefore excluded from *Megacardita,* but has a possible position in the subfamily Carditinae.

A close relationship of *Megacardita* with *Venericardia* was proposed by Chavan (1969), who included it in the new subfamily Venericardiinae, described as follows: 'Outline subtrapezoidal to rounded trigonal, strongly prosogyrous beaks with penetrating lunule. Hinge with laminar 3a, other cardinals curved, laterals approximate, almost obsolete'. A comparison with *Venericardia imbricata* (Gmelin, 1791; Fig. 3), type species of *Venericardia*, from the Middle Eocene of the Paris Basin, confirms the systematic position of *Megacardita* in the Venericardiinae. The hinge of *V. imbricata* (Fig. 3A, C, E) is markedly similar to that of *M. jouanneti* (Fig. 1A–E), with a penetrating lunule (Figs 1C, 3E) and no lateral teeth, at least in the adult stages. The cardinal tooth 3a, small and laminar in *V. imbricata* (Fig. 3A), is rather stout in *M. jouanneti*, but ending as a ridge (Fig. 1E). Interestingly, the same tooth is very small and laminar in the juveniles (Fig. 4C). It is worth noting that *V. imbricata* has a tendency to allometric growth, leading to a relatively strong hinge (Fig. 4A, C). The juveniles of *M. jouanneti* have

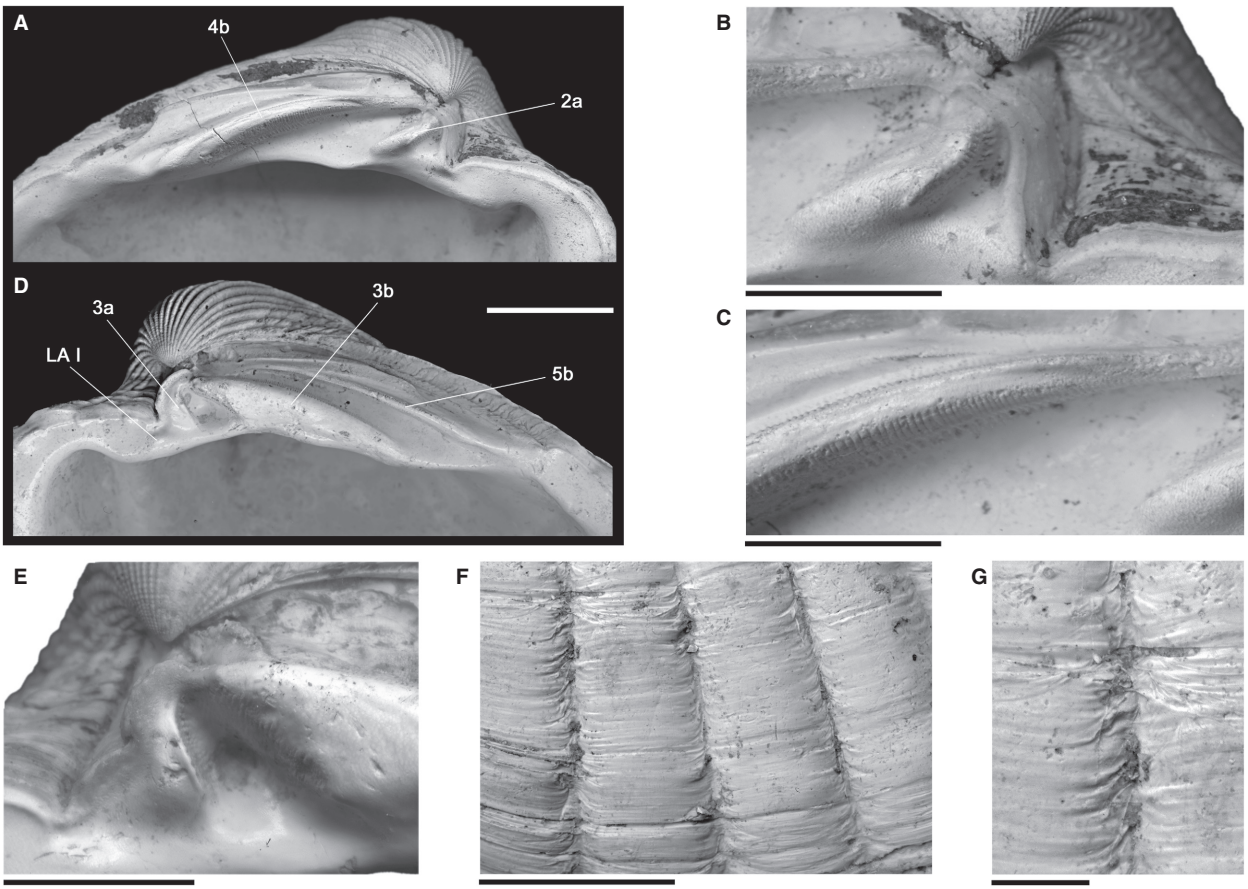

FIG. 1. *Megacardita jouanneti* (Basterot, 1825). A–C, hinge of left valve with details, Salles (MPUB 20016/10G). D, hinge of right valve, Salles (MPUB 20016/10F). E, anterior part of right hinge, Salles (MPUB 2016/10H). F–G, sculpture, Salles (MPUB 2016/10L). Dentition terminology follows Bernard's system (Carter *et al.* 2012; Güller & Zelaya 2013). Scale bars represent: 10 mm (A, D, F); 5 mm (B, C, E); 2.5 mm (G).

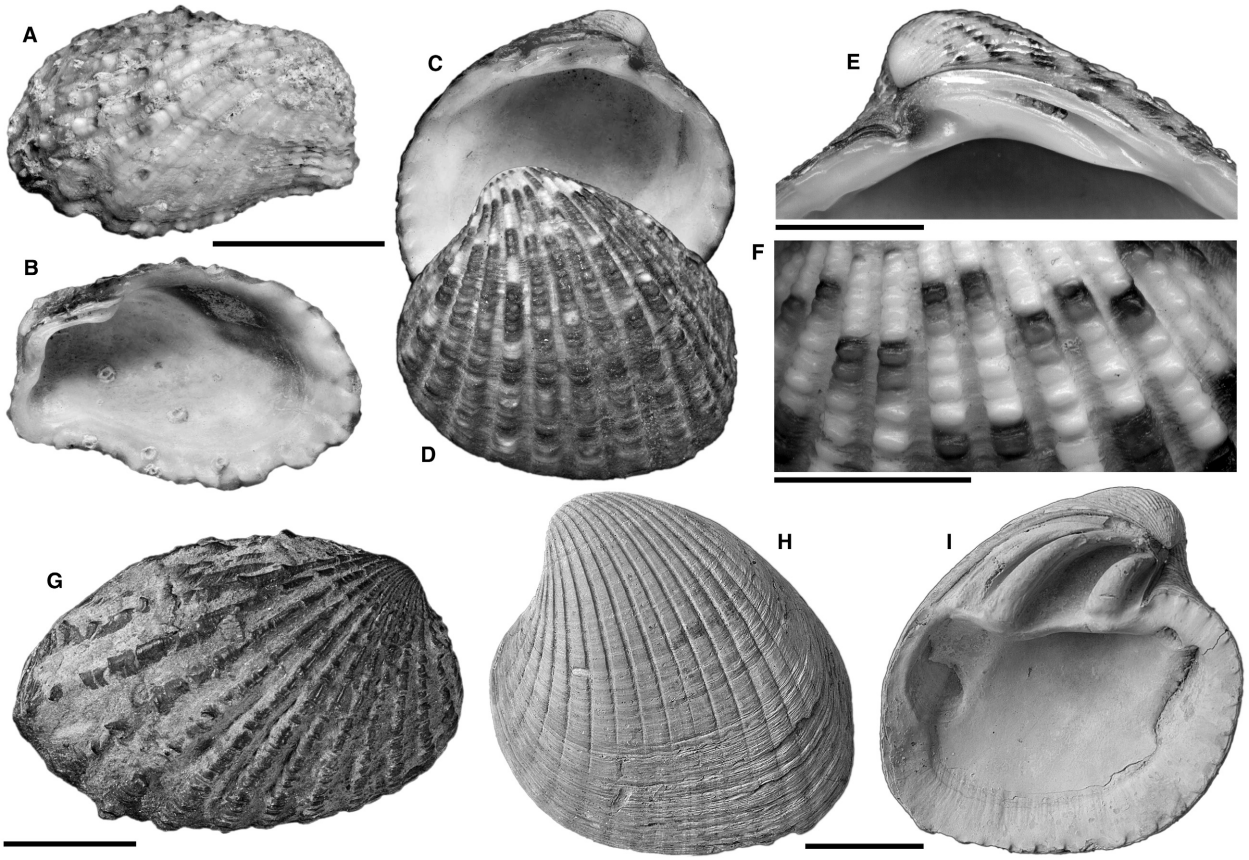

FIG. 2. Subfamilies Carditinae, Carditesinae and Venericardiinae. A, B, *Cardita calyculata* (Linné, 1758), Linnean specimen (The Linnean Society of London, A–F 0020061 www.linnean.org). C, D, *Cardites antiquatus* (Linné, 1758), Linnean specimen (The Linnean Society, A–F 0010035 www.linnean.org). E, F, *Cardites antiquatus* (Linné, 1758), Bari, Italy (La Perna coll.). G, *Cardita arduini* Brongniart, 1823, syntype (MNHN.F.R64082, photo J. Falconnet). H, I, *Venericor planicostata* (Lamarck, 1801), Bracklesham Bay, England (C. Andrew coll., photo C. Andrew). Scale bars represent: 10 mm (A–D, G); 5 mm (E, F); 30 mm (H, I).

small but clearly distinct lateral teeth (Fig. 4B, C), probably also present in other Venericardiinae, and beaded radial ribs (Fig. 4A, D, E). Such a juvenile beaded sculpture is more similar to that of *Venericardia imbricata* (Fig. 3F) than to the closely set, blunt tubercles of *Cardites antiquatus* (Linné, 1758; Fig. 2F), type species *Cardites* Link, 1807, in the subfamily Carditesinae Chavan, 1969. On the other hand, a position of *Megacardita* in the Carditesinae can be excluded, due to the lack of lateral teeth and of the cardinal 3a in this subfamily (Fig. 2E).

The hinge of *Megacardita* shows lateral striation on the cardinal teeth. They are better seen on both sides of the cardinal 4b (Fig. 1A, C) and on both sides of the fossette between teeth 3b and 5b (Fig. 1D, E). Such an unusual character, rarely described and apparently never discussed, also occurs in *V. imbricata*, but it is not known if it is a subfamily character or it has a wider occurrence in the Carditidae.

Glibert & Van de Poel (1970) considered *Megacardita* to be a complex of three subgenera: *Megacardita s.s.*, *Venericor* Stewart, 1930 and *Pacificor* Verastegui, 1953, in the Venericardiinae. *Venericor* and *Pacificor* include large, sturdily built carditids, more or less subtrigonal, with flattish radial sculpture and an unusually strong hinge. The best known representative of *Venericor* is the Eocene species *Venericardia planicosta* Lamarck, 1801, from the Paris Basis (Fig. 2H, I). There is a rather extensive literature on the Palaeogene carditids with flattish ribs, i.e. planicostate carditids *sensu* Stewart (1930), Verastegui (1953) and others, mostly from the USA (Cossmann 1901; Stewart 1930; Gardner & Bowles 1939; Verastegui 1953; Moore 1992; Sakakura *et al.* 2004; McClure & Lockwood 2015, etc.). Apart from the European Eocene, *Venericor* is also known from the Late Cretaceous – Eocene of North America, where it is mostly represented by the alleged subgenus *Leuroactis* Stewart, 1930, whereas *Pacificor* is known from both sides of the Pacific region, in the same stratigraphic range. There is no general agreement for keeping *Leuroactis* (with radial ribs becoming obsolete with growth) distinct from *Venericor* (with well-defined

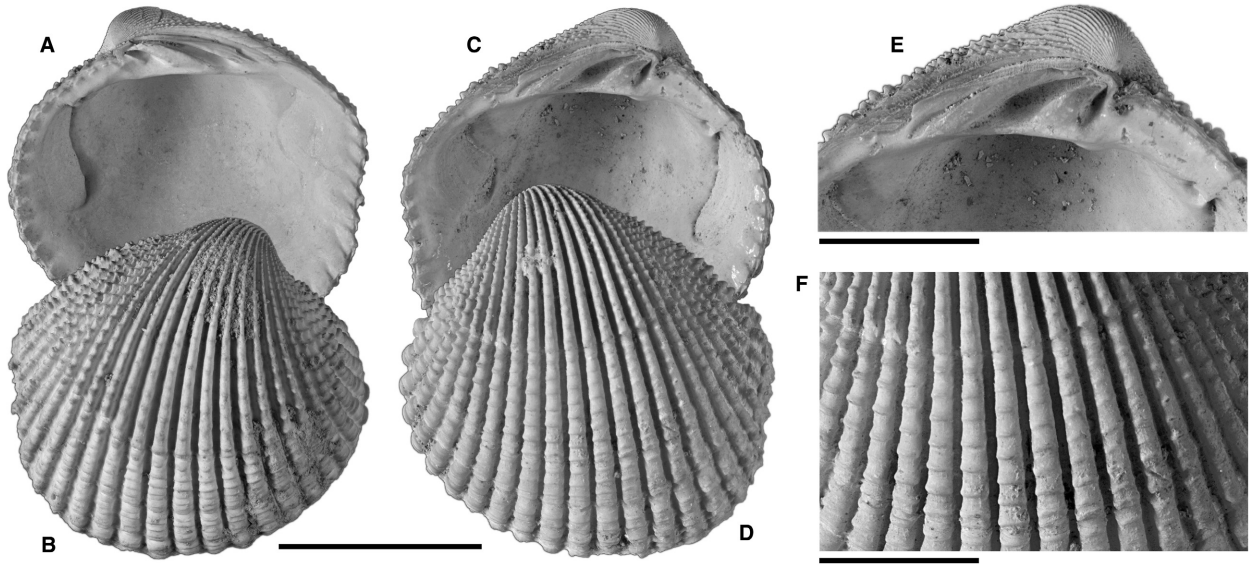

FIG. 3. *Venericardia imbricata* (Gmelin, 1791), Butte Saint-Léonard, France (Cossmann coll., MNHN.F.J07562, photo P. Massicard). Scale bars represent: 20 mm (A–D); 10 mm (E, F).

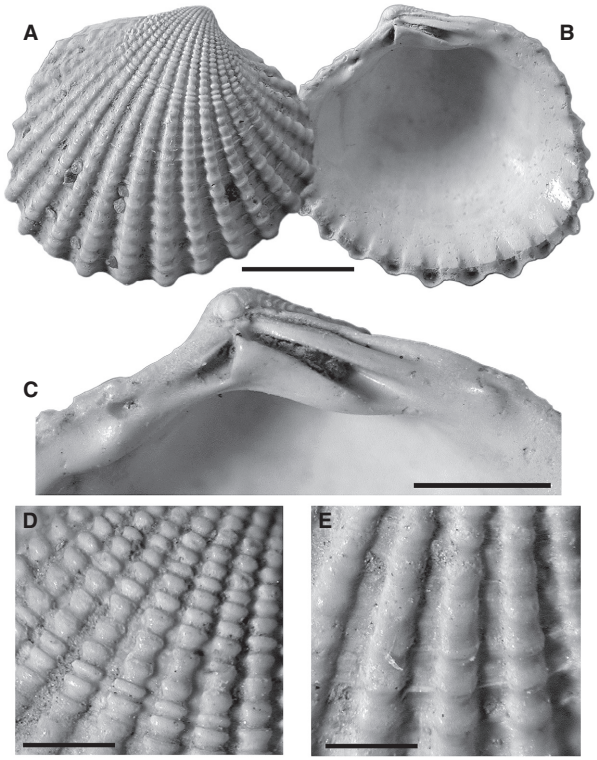

FIG. 4. *Megacardita jouanneti* (Basterot, 1825), juvenile valve and details, Mios (MPUB 2016/10M). Scale bars represent: 2 mm (A, B); 1 mm (C); 0.5 mm (D, E).

ribs all through the shell). *Pacificor* differs by having secondary riblets anteriorly, and by lacking an escutcheonal chord. *Megacardita*, *Venericor* and *Leuroactis* were considered by Stewart (1930, p. 151) to be subgenera of *Venericardia*. However, the relationships within these carditid groups are too poorly known and unclear for proposing any systematic arrangement, although it is worth noting that some characters are shared between *Megacardita* and *Venericor*/*Leuroactis*: large, sturdily built shell; strong hinge; flattish, wide radial ribs tending to become obsolete in some species; fine, flat commarginal sculpture; beaded radial ribs in the juvenile stages; long, deep escutcheon, mostly occupied by the ligament; etc. An attempt to separate a group of planicostate species from the Cenozoic of Patagonia, referred to *Neovenericor* Rossi de García *et al.*, 1980, from *Megacardita*, was recently proposed by Pérez *et al.* (2016).

None of the large and robust planicostate species have a character seen in *Megacardita*, namely the strong anterior thickening of the shell wall, seen clearly in cross-section (Fig. 5B), but also easily diagnosed morphologically thanks to the marked deepness of the anterior muscle scar (Fig. 5A). This character, although much less marked, is also seen in the juveniles (Fig. 4B), being evidently related to an allometric growth in shell thickness. The strong anterior thickening is herein considered to be an important taxonomic character of *Megacardita*, apparently not occurring in other large and robust carditids, more or less similar to this genus in other shell characters.

Two fossil species from New Zealand have also been referred to *Megacardita*: the Late Oligocene species *M. ponderosa* (Suter, 1913) and the Early Miocene species *M. squadronensis* (Powell, 1938) (Beu & Maxwell 1990). Actually, both species are notably similar to *Megacardita* in size, shape and sculpture, and the hinge is apparently the same. High resolution photographs of the holotype of

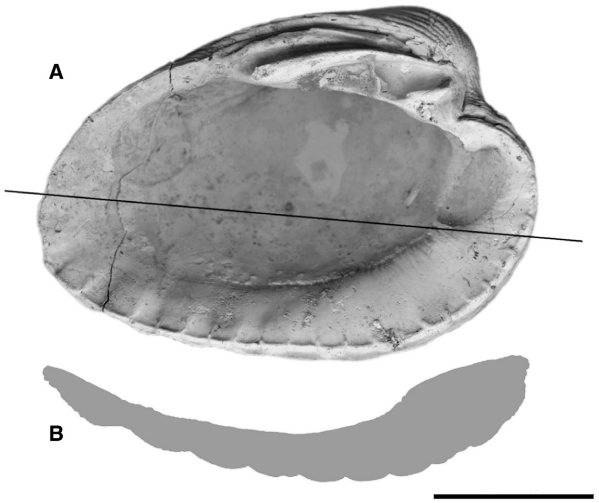

FIG. 5. *Megacardita jouanneti* (Basterot, 1825). A, left valve, Salles (MPUB 20016/10A). B, cross-section. Scale bar represents 10 mm.

Venericardia (*Megacardita*) *squadronensis* (MA72162, Auckland Museum) show widely spaced, elongate tubercles on the anterior ribs. A similar sculpture, mostly worn, can be faintly seen on the umbonal area as well. This character was reported in the original description, as 'weak folds surmounting the radials being present only on the first seven radials from the anterior end' (Powell 1938, p. 367). Interestingly, the anterior ribs of *Venericardia ponderosa* were also described as 'narrow and scaly' (Suter 1913, p. 296). In view of the homonymy of *V. ponderosa* Suter, 1913, not *V. jouanneti* var. *ponderosa* Cossmann & Peyrot, 1912, the name *Venericardia caelebs* Marwick, 1929 should be used for this species (Beu & Maxwell 1990). It is worth noting that the description of *V. caelebs* (Marwick 1929, p. 911), also reports 'prominent spaced spines' on the last posterior ribs. There is another fossil species from New Zealand, similar to *V. ponderosa* and *V. squadronensis*: the Danian (Early Paleocene) species *Venericardia fyfei* described by Finlay & Marwick (1937). High resolution photographs of the holotype (MA70821) show a large carditid, with moderately convex ribs covered by spaced, elongate tubercles, mainly on the umbonal area. This species was tentatively referred by Beu & Maxwell (1990) to *Purpurocardia,* proposed as a subgenus of *Venericarida* by Maxwell (1969) for a group of Pliocene to Recent carditids from New Zealand. The type species, *Purpurocardia purpurata* (Deshayes, 1854), is moderately large and robust, subequilateral, with well-spaced convex ribs covered by sharp, elongate tubercles. More recently, *Purpurocardia* has been considered a distinct genus related to *Centrocardita* Sacco, 1899 (Carditamerinae) according to Beu (2006), or in the subfamily Venericardiinae according to Huber (2010), whose view seems much more supported by the shell characters of *Purpurocardia*. It can be further hypothesized that *V. ponderosa* and *V. squadronensis*, together with *V. fyfei*, are Palaeogene representatives of *Purpurocardia*, or at least closely allied to it. None of them, apparently, has the anterior thickening of *Megacardita*, which on the other hand is never endowed with tubercles or spines on the radial ribs. Based on these considerations, *Megacardita* should be excluded from the Cenozoic fauna of New Zealand.

Popov (1983) maintained *Megacardita* in the Venericardinae and proposed a list of 20 species from Europe (France and Italy), the Russian Far East (Chukotka and Sakhalin), south to Japan, Taiwan, the Philippines and Indonesia, in the range Oligocene–Recent. Unfortunately, except for the type species *M. jouanneti*, none of the species listed by Popov (1983) can be considered unequivocally representative of *Megacardita,* although a discussion of each species is beyond the scope of the present study. Some species listed by Popov are from Japan and Taiwan, from which numerous Neogene records of *Megacardita* species are known (Ogasawara 1986; Shuto 1986; Masuda & Huang 1990; Nakamura *et al*. 1999; Matsukuma 2003; Matsubara 2011), for example the Miocene species *M. crenulicostata* (Nomura, 1933) and *M. granulicostata* (Nomura, 1933), the Early Pliocene species *M. panda* (Yokoyama, 1926), the extant species *M. ferruginosa* (Adams & Reeve, 1850), etc. These species, all markedly less inequilateral than *Megacardita* species, encompass a wide sculptural range: from strong, widely spaced ribs with square cross-section in *M. panda*, to weak, convex ribs in *M. ferruginosa*. *M. crenulicostata* and *M. granulicosta* share a well-defined commarginal sculpture of elongate tubercles on widely spaced ribs. Other species reported by Popov (1983), such as the Miocene species *M. chukotica* Popov, 1983 and the Oligocene species *M. matschigarica* (Khomenko, 1938), from the Russian Far East, differ markedly from *Megacardita* by their suborbicular shell, with a small umbo, and weak, spaced, radial ribs. Most probably, all of these species belong to distinct clades, more or less closely convergent with *Megacardita*, and only their careful revision could clarify composition, origin and systematic position of each group.

Megacardita has been reported also from north-west Africa, as *M. monodi* (Nicklès, 1953) (Huber 2010). Again, this species appears to be phylogenetically distant from *Megacardita*, due to its subtriangular, almost equilateral shape, with a small, somewhat pointed umbo. One of the species dealt with in the present work, from the Late Miocene – Early Pliocene of the north-east Atlantic, tentatively referred to *Megacardita*, seems similar to *M. monodi,* thus suggesting a common, distinct systematic position, which needs further investigation.

In the present study, *Megacardita* is considered to be endemic to the European area, with a distribution ranging from the Burdigalian to the Late Miocene of the (proto-)Mediterranean, the adjacent north-east Atlantic, and the Western and Central Paratethys. None of the species assigned to it from different areas and stratigraphic ranges share the character combination of *Megacardita* herein reported in the revised description.

SYSTEMATIC PALAEONTOLOGY

Family CARDITIDAE Férussac, 1822
Subfamily VENERICARDIINAE Chavan, 1969

Genus MEGACARDITA Sacco, 1899

Type species. Venericardia jouanneti Basterot, 1825, from the Serravallian of Salles, France.

Revised diagnosis. Shell medium-sized to large (*c.* 30–100 mm in length), equivalve, robust, normally convex, anteriorly thickened, subrectangular-ovate to subtrigonal, moderately to strongly inequilateral, weakly to moderately truncate posteriorly. Umbo large and broad, prominent, markedly prosogyrate, anterior to shell midline. Lunule small, well defined, heart-shaped, deeply sunken, penetrating into hinge plate; escutcheon lanceolate, narrow, elongate, deep, with steep walls, mostly occupied by external ligament. Posterior slope moderately wide, fairly well-defined; no keel. Hinge strong, allometrically increasing in strength with shell size. Right hinge: anterior cardinal (3a) small, rather stout with a laminar ridge; central cardinal (3b) strong, wide, triangular, slightly curved; posterior cardinal (5b) elongate, blade-like; small, deep, triangular fossette between 3a and 3b; narrow, elongate, slightly curved fossette between 3b and 5b. Left hinge: anterior cardinal (2a) short, robust; posterior cardinal (4b) elongate, robust, slightly curved; wide, obliquely triangular fossette between 2a and 4b. Small, tubercle-shaped lateral teeth only in juveniles; adults with only a small tubercle-shaped anterior lateral tooth in right valve (LA I). Sides of teeth finely striated. Sculpture mainly radial, consisting of *c.* 15–20 ribs, moderately to weakly convex to almost flat, rounded in cross-section; interspaces narrow to thread-like, shallow to moderately deep. Radial sculpture ventrally obsolete in some species; much weaker to poorly defined on posterior slope; slightly coarser anteriorly. Early radial ribs somewhat more convex and with deeper interspaces, bearing slightly elongate beads, better-defined anteriorly and centrally. Commarginal sculpture weak to poorly defined, consisting of close-set growth striae and laminae, usually irregular and somewhat wrinkled. Margin serrated, with short projections of outer ribs; internal crenulation coarse, stronger ventrally and anteriorly, weaker to almost obsolete posteriorly. Pallial line well-defined, regularly curved, entire, far from shell margin. Anterior muscle scar deeply impressed, wide, ovate; posterior one shallow, wide, roundish.

Megacardita jouanneti (Basterot, 1825)
Figures 1, 4, 5, 6, 7, 8, 15A–B

1825 *Venericardia jouanneti* Basterot, p. 80, pl. 5, fig. 3.
1899 *Cardita* (*Megacardita*) *jouanneti* (Basterot); Sacco, p. 9, pl. 3, fig. 1a, b.
1900 *Cardita jouanneti* var. *mayeri* Ivolas & Peyrot, p. 189, pl. 3, figs 3, 4.
1912 *Venericardia* (*Megacardita*) *jouanneti* var. *ponderosa* Cossmann & Peyrot, p. 197, pl. 3, figs 17–20.
1912 *Venericardia* (*Megacardita*) *jouanneti* var. *bearnensis* Cossmann & Peyrot, p. 198, pl. 4, figs 1–4.
1912 *Venericardia* (*Megacardita*) *jouanneti* var. *consobrina* Cossmann & Peyrot, p. 198, pl. 3, figs 5–6.
1913 *Cardita* (*Venericardia*) *laevicosta* (Lamarck); Dollfus & Dautzenberg, pl. 14, figs 24–28.
1963 *Cardita jouanneti jouanneti* (Basterot); Tavani & Tongiorgi, pl., 21, figs 2–2b.
1963 *Cardita jouanneti ponderosa* (Cossmann & Peyrot); Tavani & Tongiorgi, pl., 21, figs 3–10a (non pl. 22, figs 1–3a).

Material. Salles (France), 52 valves, 3 shells (MPUB). Mios (France), 8 shells, 6 valves (MPUB). Sallespisse (France), syntypes of *Venericardia (Megacardita) bearnensis* Cossmann & Peyrot, 1912, 3 valves (MNHN.F.J05629).

Description. The shape is elongate, ovate-subrectangular to ovate-subtrigonal, with the ventral margin moderately to slightly convex, and even almost straight. Ribs, numbering 17–20 (19 in most specimens), are wide, weakly convex to rather flattish, separated by narrow, shallow interspaces. On the posterior slope, which is fairly well defined, there are 5–6 ribs, narrower, weaker and slightly irregular in strength, poorly defined in some specimens. Anteriorly, 4–5 ribs are slightly coarser. In well-preserved shells, the beaded sculpture of the juvenile stage (Fig. 4) can be seen on the earliest part of the umbo. An obsolete commarginal sculpture, consisting of closely set, weakly defined lamellae and irregular growth marks, crosses the ribs (Fig. 1F, G). In many large valves (length 60–70 mm), the ventral margin shows a marked slope break, with dense lamellar sculpture (Fig. 7C). The maximum size is about 70 mm in the study material. Larger sizes reported in the literature, such as 90 mm (Sacco 1899) and 110 mm (Dollfus *et al.* 1903), are based on another species, *Megacardita laeviplana* (Depéret, 1839).

Remarks. Venericardia jouanneti was very briefly described as 'Testa transversa; costis planis; natibus scabriusculis', but finely illustrated (Basterot 1825, p. 80,

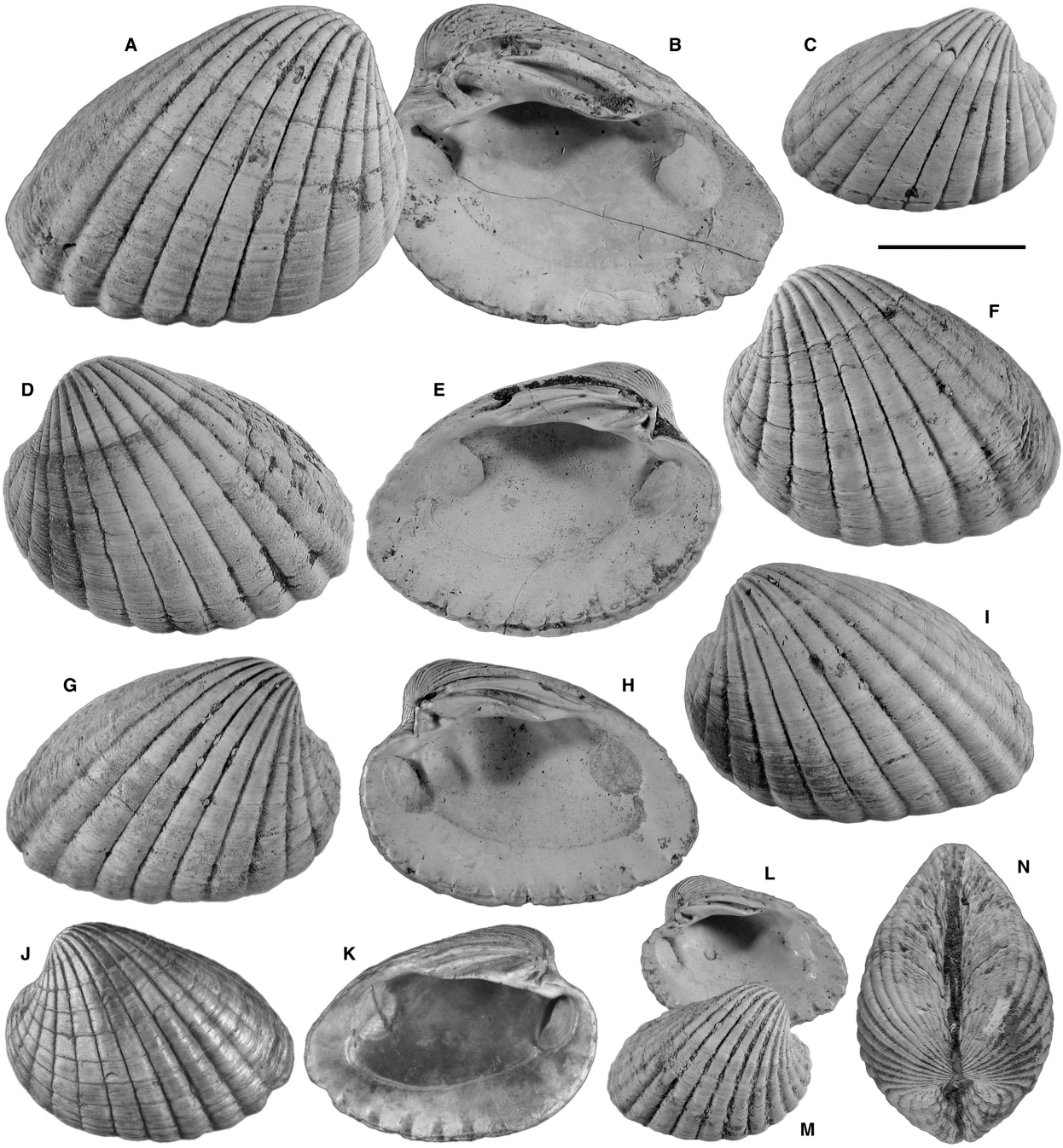

FIG. 6. *Megacardita jouanneti* (Basterot, 1825). A, B, Salles (MPUB 2016/10Q). C, Salles (MPUB 2016/10C). D, E, Salles (MPUB 2016/10E). F, Salles (MPUB 2016/10D). G, H, Salles (MPUB 2016/10I). I, Salles (MPUB 2016/10P). J, K, Sallespisse, syntype of *Venericardia (Megacardita) jouanneti* var. *bearnensis* Cossmann & Peyrot, 1912 (Cossmann & Peyrot 1912, pl. 4, figs 2, 3) (Cossmann coll., MNHN.F.J05629, photo P. Massicard). L, M, Salles (MPUB 2016/10B). N, Mios (MPUB 2016/10N). Scale bar represents 30 mm.

pl. 5, fig. 3). The only comment about the locality is: 'On trouve cette espèce assez abondamment dans un banc placé entre Léognan et la Brède avec la *Bulla lignaria*, var. β' (This species is very abundantly found in a bed located between Léognan and la Brède together with *Bulla lignaria* var. β). Léognan and La Brède are located a few kilometres south of Bordeaux, in the area of the Aquitanian and Burdigalian historical stratotypes (Cahuzac *et al.* 1997; Poignant *et al.* 1997*a, b*). However, in agreement with Basterot's remarks, the species was most probably described from the richly fossiliferous beds (*faluns*) of Serravallian age, overlying the Burdigalian deposits and

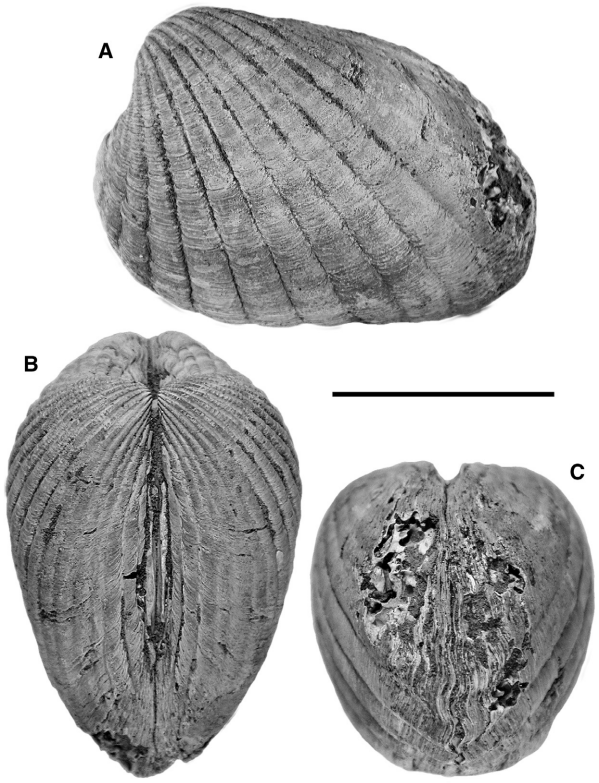

FIG. 7. *Megacardita jouanneti* (Basterot, 1825), Mios (MPUB 2016/10O). A, left valve; B, dorsal view; C, posterior view. Scale bar represents 30 mm.

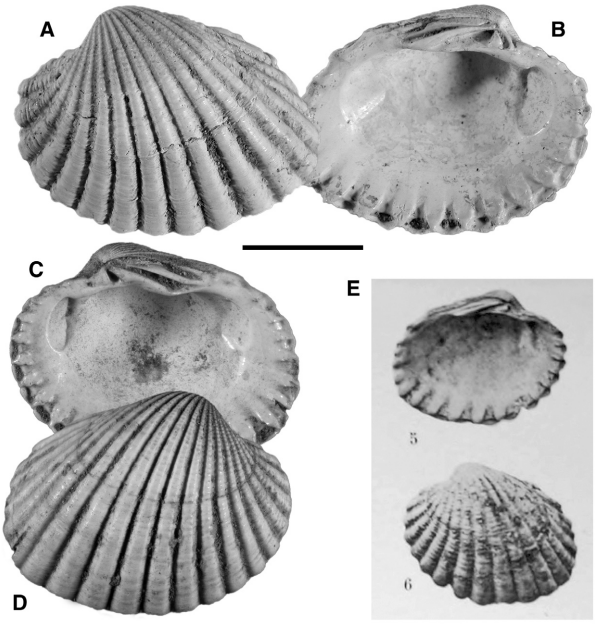

FIG. 8. *Megacardita jouanneti* (Basterot, 1825). A, B, Salles (MPUB 2016/10J). C, D, Sallespisse, syntype of *Venericardia (Megacardita) jouanneti* var. *bearnensis* Cossmann & Peyrot, 1912 (Cossmann & Peyrot 1912, pl. 4, figs 2, 3) (MNHN.F.J05629, photo P. Massicard). E, original illustration of *Venericardia (Megacardita) jouanneti* var. *consobrina* Cossmann & Peyrot, 1912 (pl. 3, figs 5, 6). Scale bar represents 10 mm (A–D).

containing large molluscs including *Megacardita* and *Glycymeris*, cropping out locally in the area of Saucats, particularly at Lassime south-west of La Brède (Poignant *et al.* 1997*b*, fig. 5; Cahuzac & Cluzaud 1999, fig. 3) and more widely in the nearby area of Salles, south-west of Bordeaux, type area of the Sallomacian (= Serravallian) Stage (Fallot 1893). The precise location of the outcrops from which the study material comes is not known, but several fossiliferous outcrops are known in the area of Salles and Mios (*c.* 10 km north of Salles), mostly along L'Eyre river and its tributaries (Folliot *et al.* 1993, fig. 1).

Megacardita jouanneti has been considered to be a highly variable species, and a number of varieties have been described and used (Depéret 1839; Sacco 1899; Ivolas & Peyrot 1900; Cossmann & Peyrot 1912; Mongin 1958; Tavani & Tongiorgi 1963; Glibert & Van de Poel 1970, etc.). Admittedly, *M. jouanneti* and most of the congeners dealt with in the present work exhibit a remarkable variability, mostly in shape. Sculpture, in particular number, shape, width, strength and spacing of radial ribs, and the width and depth of interspaces, is more constant and offers more useful characters for species discrimination. However, the much wider variability reported in the past literature resulted from confusing several distinct species mostly within the single species *M. jouanneti*. The present illustrations (Figs 6, 7), try to cover the shell variability in *M. jouanneti*. Another rich iconography, although with an out-dated nomenclature, was reported by Tavani & Tongiorgi (1963, pls 21–22).

For *Cardita* (*Megacardita*) *jouanneti*, Sacco (1899) listed the following varieties, all from the Miocene of the Turin Hills: *brocchii* Michelotti, 1839, *taurobrevis* Sacco, 1899, *dertavicula* Sacco, 1899, *laeviplana* Depéret, 1893, *dertobrevis* Sacco, 1899 and *dertolonga* Sacco, 1899. None of these varietal names is considered here to be a synonym of *jouanneti*, as discussed below.

Conversely, varieties *ponderosa*, *bearnensis* and *consobrina*, all described by Cossmann & Peyrot (1912) from outcrops in the area of Salles, are included in the synonymy of *M. jouanneti*. The first variety is represented by particularly large (up to 70 mm in length) and thick-walled shells (Cossmann & Peyrot 1912, pl. 3, figs 17–20; Fig. 6A, B, D, E), whereas var. *bearnensis* includes elongate shells (Cossmann & Peyrot 1912, pl. 4, figs 1–4; Fig. 6J, K), also falling in the variability range of *M. jouanneti* or representing, at least in part, different growth stages of this species. The third variety, *consobrina*, was based on a single, small valve (length 30 mm) from Salles 'Largileyre' (Cossmann & Peyrot 1912, p. 198, pl. 3, figs 5–6; Fig. 8E), described as thinner, flatter, with

a less inflated umbo and a narrower hinge plate, than the typical *M. jouanneti*. They considered var. *consobrina* to be a paedomorphic form of *M. jouanneti* ('Ce n'est pas une jeune *C. Jouanneti*, car le galbe est différent, mais vraisemblablement une forme qui est restée à un stade népionique') and added that the finding of additional material would allow this variety to be raised to the rank of a distinct species. However, the holotype valve of var. *consobrina* closely matches the juveniles of *M. jouanneti* of similar size: after an early roundish, subequilateral stage (up to a size of *c.* 15 mm; Fig. 4A, B), the shape becomes more and more elongate and inequilateral (Fig. 7A–D). Var. *consobrina* is considered to be a juvenile stage of *M. jouanneti.*

Ivolas & Peyrot (1900, p. 189, pl. 3, figs 3–4) described *Venericardia jouanneti* var. *mayeri* from the Middle Miocene of the Loire Basin (Touraine). It was said to differ from the Salles form by being smaller and more robust, with a sculpture of 21–23 ribs, instead of 19, less flat and separated by wider and deeper interspaces. According to them, var. *mayeri* is the only form of *jouanneti* occurring in the Middle Miocene of the Touraine. The same form, from the same localities (Manthelan, Sainte-Catherine-de-Fierbois, etc.), was reported by Dollfus & Dautzenberg (1913, pl. 14, figs 24–28) as *Cardita* (*Venericardia*) *laevicosta* (Lamarck, 1818). The identity of this species, described from the Touraine (Lamarck 1818, p. 384), is doubtful. Based on the illustrations of the Lamarckian fossil shells in Geneva by Favre (1914), Lamy (1916) concluded that *V. laevicosta* consists of more than a single species, among which are *Venericardia* (*Cardiocardita*) *turonensis* Ivolas & Peyrot, 1900 and *V.* (*Cardiocardita*) *alternas* Dujardin, 1837, both markedly different from *M. jouanneti*. Dollfus & Dautzenberg (1913) synonymized *Cardita rusticana* Mayer, 1861 with *V. laevicosta*, but the original description of this species (Mayer 1861, p. 361) suggests a carditid notably different from *M. jouanneti,* as confirmed by the recent illustration of a juvenile specimen from the Aquitanian of Saucats by Cahuzac *et al.* (2012, pl. 1, fig. 3). In conclusion, *V. laevicosta* and *C. rusticana* can be excluded from the synonymy of *M. jouanneti*. As for var. *mayeri*, the only remarkable differences seen in the good illustrations of Ivolas & Peyrot (1900) and those of Dollfus & Dautzenberg (1913) involve the radial ribs, slightly more numerous, narrower and with deeper interspaces than in valves from Salles. Further, the illustrations by Dollfus & Dautzenberg (1913) suggest some variability in these characters, apparently grading into the average morphology of the Salles material. Var. *mayeri* can therefore be considered to be a synonym of *M. jouanneti*.

Finally, it is worth noting that, contrasting with the material from Salles, which mostly consists of loose valves, often slightly worn (Fig. 6A–I, L, M), the material from Mios mainly consists of articulated, well-preserved shells (Figs 6N, 7), but many specimens are heavily bioeroded on the posterior tip (Fig. 7). Such bioerosion, which can be ascribed to boring polychaetes, was also reported on *M. jouanneti* (actually on *M. laeviplana*) from the Late Miocene of Portugal by Santos & Mayoral (2008). They interpreted the bioerosion as being produced during the lifetime of the bivalve, while it was buried in the substrate with the posterior tip emerging, but an alternative or additional explanation is that the endolithic colonization occurred shortly after the death of the bivalve, while preserved in life position. This explanation is in agreement with the fine substrate (sandy–muddy) of the Mios deposits (preserved inside the closed shells), suggesting quieter conditions than those of Salles, whose deposits are coarsely organogenic, with high disarticulation rate and abrasion. Facies similar to those outlined here were described and finely depicted by Folliot *et al.* (1993) for the areas of Mios and Salles, respectively.

Occurrence. In spite of the wide geographical distribution reported in the literature, including Aquitaine, Loire, Mediterranean and Western and Central Paratethys, *M. jouanneti* only occurs in the Serravallian of the Aquitaine and Loire basins.

Megacardita brocchii (Michelotti, 1839)
Figure 9

1839 *Cardita brocchii* Michelotti, p. 15.
1847 *Cardita jouanneti* (Basterot); Michelotti, p. 97.
1899 *Cardita (Megacardita) jouanneti* var. *brocchii* Michelotti; Sacco, p. 10, pl. 3 figs 2–4.
1899 *Cardita (Megacardita) jouanneti* var. *taurobrevis* Sacco, p. 10, pl. 3, fig. 5.
? 1952 *Megacardita jouanneti* var. *brocchii* (Michelotti); Mongin, p. 160, pl. 5, fig. 8.

Material. MRSN, Bellardi & Sacco coll.: Baldissero (Italy), 1 valve (BS.126.02.001); Albugnano (Italy), 1 valve (BS.126.02.001/01); Albugnano (Italy), 2 valves (BS.126.02.001/02); Albugnano (Italy), 2 valves (BS.126.02.001/03); Turin Hills (Italy), 1 valve (BS.126.02.002); Baldissero (Italy), 1 valve (BS.126.02.003); Baldissero (Italy), 2 valves (BS.126.02.003/01); Baldissero (Italy), 3 valves (BS.126.02.003/02); Albugnano (Italy), 2 valves (BS.126.02.003/03); Monte dei Cappuccini (Italy), 2 valves (BS.126.02.003/04); Turin Hills (Italy), 2 valves (BS.126.02.003/05); Turin Hills (Italy), 1 valve, syntype of *Cardita* (*Megacardita) jouanneti* var. *taurobrevis* Sacco, 1899 (BS.126.02.004); Turin Hills (Italy), 1 valve, syntype of *Cardita* (*Megacardita) jouanneti* var. *taurobrevis* Sacco, 1899 (BS.126.02.004/01). Baldissero (Italy), 2 valves (NHMW 1883.C.4190).

Description. The radial sculpture consists of 17–19 ribs, obscurely knotted in some specimens, stronger, more convex

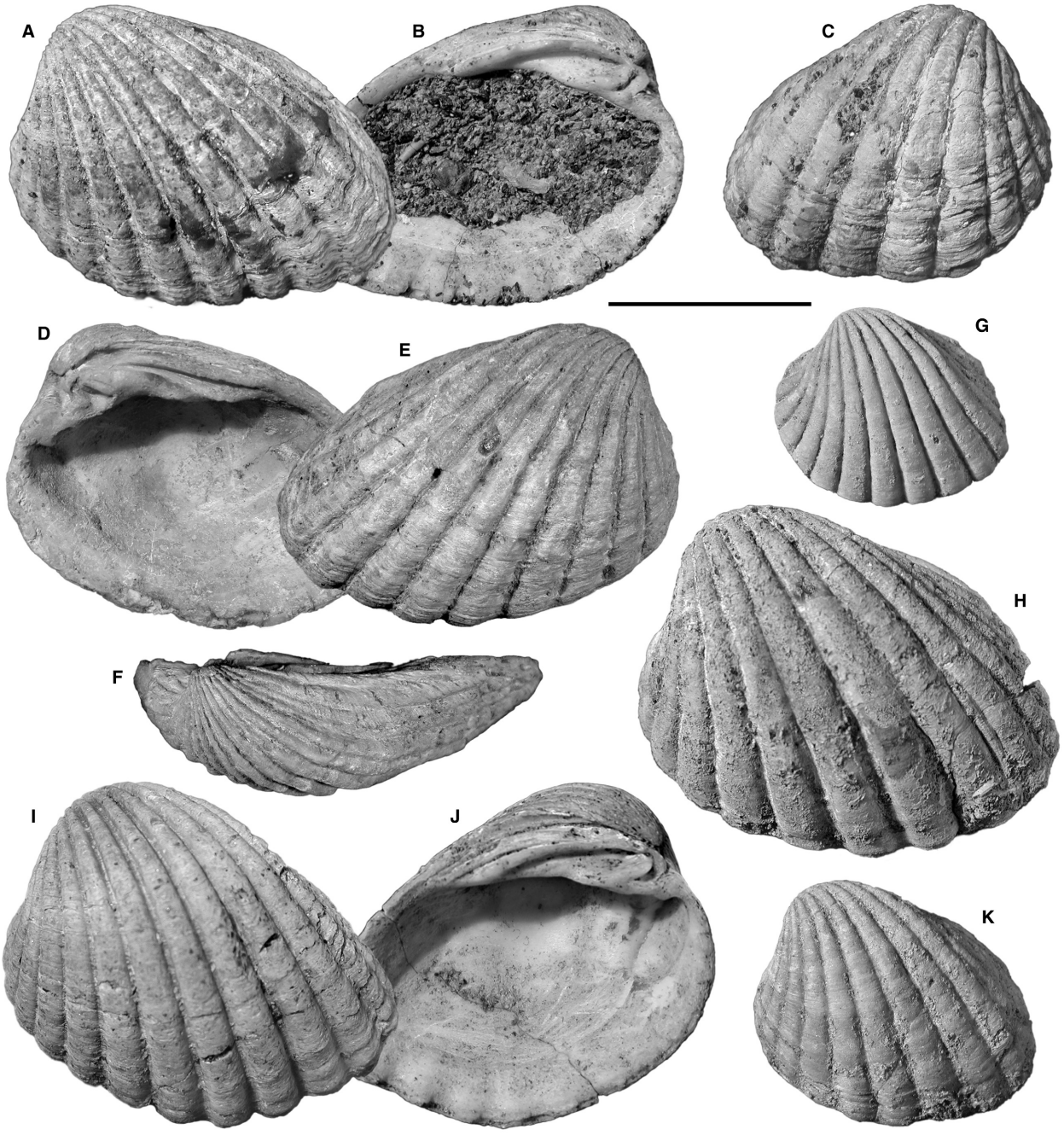

FIG. 9. *Megacardita brocchii* (Michelotti, 1839). A, B, Turin Hills (Sacco 1899, pl. 3, fig. 3) (MRSN BS.126.02.002). C, Turin Hills, syntype of *Cardita* (*Megacardita) jouanneti* var. *taurobrevis* Sacco, 1899 (Sacco 1899, pl. 3, fig. 5) (MRSN BS.126.02.004). D–F, Baldissero (MRSN BS.126.02.003/01). G, Albugnano (MRSN BS.126.02.003/03). H, Turin Hills (MRSN BS.126.02.003/05). I, J, Baldissero (Sacco 1899, pl. 3, fig. 4) (MRSN BS.126.02.003). K, Albugnano (MRSN BS.126.02.001/01). Scale bar represents 30 mm.

and separated by narrow and deeper interspaces than in *M. jouanneti*. Shell convexity is similar in both species (Figs 6N, 9F), but *M. brocchii* has a larger and broader umbo, giving a gibbose appearance to the shell. The two species are similar in size, probably slightly smaller in *M. brocchii* (maximum shell length *c.* 60 mm), with the hinge comparatively stronger than in *M. jouanneti,* and the posterior slope generally steeper. These differences may appear subtle and not discriminating, but a side-by-side comparison allows the two species to be separated.

The available material shows some variability in shape, which seems to be mostly, or in part, related to growth, as in *M. jouanneti.* After a subaequilateral juvenile stage (Fig. 9G), the shape

tends to become elongate, with a strongly posterior umbo (Fig. 9A, B, D–F), markedly similar to the average shape of *M. jouanneti*, while older shells tend to grow postero-ventrally (Fig. 9H–J), acquiring a subtrigonal-oblique shape, which is also shown by some smaller shells (Fig. 9K). Due to the generally poor preservation, it was not possible to see the beaded umbonal sculpture.

Remarks. Cardita brocchii was described from the Miocene of the Turin Hills, as: 'Testa ovato-transversa, latere antico, rotundato, postice sinuato, costis obsolete augulatis, laevigatis, bisulcatis' (Michelotti 1839, p. 15). The species was said to differ from *jouanneti* by having subangulose radial ribs ('costis obsolete augulatis') and granulations on the umbonal area. Actually, beaded umbonal sculpture occurs in *M. jouanneti,* as described above. Amongst the material from the Turin Hills in the Bellardi & Sacco coll. (MRSN), some radial ribs are obscurely angulose, particularly near the umbo. This material is generally poorly preserved and the subangulose radial ribs are thought to be due to slight compression and deformation. No mention was made in the comments about 'bisulcatis' (= with two grooves), leaving obscure the meaning of this character. In a following work, the same author reported *Cardita jouanneti* with a new description: 'C. testâ transversâ, ovatâ, longitudinaliter costata; costis planis, apice subgranulosis; cardine unidentato, altero bidentato; marginibus undato-dentatis' (Michelotti 1847, p. 97). He remarked that this species, whose original description was based on 'a very old shell', must synonymized with Basterot's species, and stated that he had also seen material from Bordeaux and Vienna, on which he noticed 'l'échelle des variétés de cette belle espèce'.

Var. *brocchii* was described by Sacco (1899) as being more convex and gibbose, with stronger ribs and deeper interspaces, compared to *M. jouanneti* ('Testa inflatior, gibbosior. Costae radiales perspicuiores, elatiores, inter se profundius disjunctae').

The material referred by Sacco (1899) to *Cardita* (*Megacardita) jouanneti* cannot be kept distinct from that of var. *brocchii*, both being also from the same outcrops: Albugnano, Baldissero, Monte dei Cappuccini or from a generic 'Helvetian' of the Turin Hills. Sacco was probably aware that the 'typical' form was not present in the Miocene of the Turin Hills, as he illustrated *M. jouanneti* with two valves from 'Bordeaux' (Sacco 1899, pl. 3, fig. 1a–b). On the other hand, among the carditids from the Miocene of the Turin Hills, *M. brocchii* is the most similar to *M. jouanneti,* and this supports the present interpretation of Michelotti's species.

Albugnano, Baldissero and Monte dei Cappuccini, the localities from which the study material comes, encompass a stratigraphic interval ranging from late Burdigalian (Baldissero) to Langhian (Albugnano, Monte dei Cappuccini) in age (Pavia 2000; Zunino & Pavia 2009; Festa *et al.* 2010).

Megacardita jouanneti var. *taurobrevis* Sacco, 1899 (p. 10, pl. 3, fig. 5) is included in the synonymy of *M. brocchii*. It is represented by two syntypes, both from the 'Helvetian' of the Turin Hills. One of them is a large fragment, with sculpture comparable with that of *M. brocchii*, whereas the other is a complete valve, filled with coarse, cemented sediment (Fig. 9C). The second specimen may appear different from *M. brocchii*, due to its wider, somewhat lamellose ribs, but there is no solid base for keeping it as a distinct species.

Var. *brocchii* reported by Dollfus *et al.* (1903, p. 54, pl. 20, figs 3–4) from the Tortonian of Adiça, Portugal, is clearly different from *M. brocchii,* as discussed below.

Mongin (1952, pp 160–161, pl. 5, fig. 8; 1958) reported both *Megacardita jouanneti* and var. *brocchii* from the Burdigalian of Provence, on very scarce, poorly preserved material. She only illustrated var. *brocchii*: a subtrigonal valve (or a large fragment). It is evidently a *Megacardita* species, which can be only tentatively identified as *M. brocchii*. The stratigraphy and age of the Burdigalian deposits of the Liguro-Provençal Basin are debated, but according to the most recent study (Oudet *et al.* 2010), they range from the latest early to middle Burdigalian.

Occurrence. Megacardita brocchii is known from the late Burdigalian to Langhian of Italy (Turin Hills). The records from the Burdigalian of Provence need confirmation.

Megacardita guenterti Pfister & Wegmüller, 1998
Figure 10

1928 *Venericardia* (*Megacardita*) *jouanneti* (Basterot); Rutsch, p. 152, pl. 9, fig. 43.
1998 *Megacardita guenterti* Pfister & Wegmüller, p. 470, pl. 8, figs 1–5.

Material. St Gallen (Switzerland), holotype (shell) (NMBB C88); St Gallen (Switzerland), paratype (shell) (NMBB B9421); Wikartswil (Switzerland), paratype (1 valve) (NMBB B9419); St Gallen (Switzerland), paratype (1 valve) (NMBB B9420); Aarwald (Switzerland), paratype (1 valve) (NMBB A4057); Chramburg (Switzerland), paratype (1 valve) (NMBB A9873); Imihubel (Switzerland), paratype (1 valve) (NMBB B9397); Imihubel (Switzerland), paratype (1 valve) (NMBB, B9398). St Gallen (Switzerland), 5 shells (NHMW 1847 XLVIII.47). Ermingen (Germany), 1 shell (NHMW 1853.XV.195).

Remarks. Megacardita guenterti was described from the middle Burdigalian deposits which crop out south and west of Bern, Switzerland (Pfister & Wegmüller 1998, p. 470, pl. 8, figs 1–5). Unfortunately, all the material so far known of this species is very poorly preserved, mostly as internal

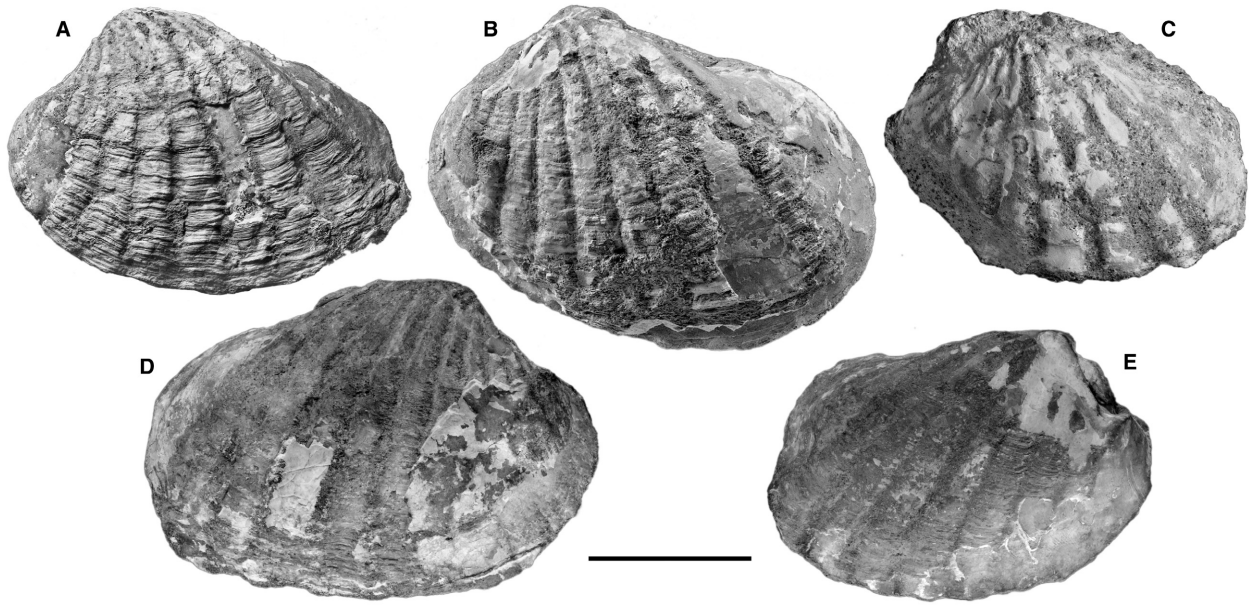

FIG. 10. *Megacardita guenterti* Pfister & Wegmüller, 1998. A, holotype, St Gallen (Pfister & Wegmüller 1998, pl. 8, fig. 1) (NMBB C88, photo NMBB). B, paratype, St Gallen (Pfister & Wegmüller 1998, pl. 8, fig. 3) (NMBB B9420, photo NMBB). C, paratype, Wikartswil (Pfister & Wegmüller 1998, pl. 8, fig. 2) (NMBB B9419, photo NMBB). D, St Gallen (NHMW 1847 XLVIII.47). E, St Gallen (NHMW 1847 XLVIII.47). Scale bar represents 30 mm.

moulds with some shell remains, as the fossil material from the Swiss Upper Marine Molasse generally is.

The holotype, a little better-preserved than most other material (Fig. 10A) is an elongate, moderately inequilateral shell, with wide, weakly convex radial ribs, and narrow, shallow interspaces, crossed by rather prominent commarginal wrinkles. Its length is about 50 mm. Pfister & Wegmüller (1998) reported 11–18 ribs on the specimens from St Gallen (Fig. 10A, B, D, E) and 11–16 ribs on the specimens from the Belpberg Formation, south of Bern, which were also described as generally smaller and with a somewhat shorter posterior area (Fig. 10C). The reported range in the number of ribs seems too wide, compared with the other species, but this is possibly due to the poor preservation, which makes it difficult to evaluate the number of ribs. The strongly wrinkled commarginal sculpture could be also, at least in part, an effect of preservation. Certainly, additional better-preserved material would be useful for a better understanding of this species.

In sculpture, *M. guenterti* is somewhat reminiscent of *M. brocchii*, but the former is distinctly more elongate (height/length *c.* 0.7) than the latter (height/length *c.* 0.8), subrectangular instead of tending to be trigonal, and with a smaller umbo. Its marked elongation and subrectangular shape also make *M. guenterti* distinctive compared with the other species treated in the present work.

As remarked by Pfister & Wegmüller (1998), *Venericardia* (*Megacardita*) *jouanneti* reported by Rutsch (1928, p. 152, pl. 9, fig. 43) from the Burdigalian of St Gallen is *M. guenterti*. The species was also reported by Höltke (2009, p. 81, fig. 20) from the middle Burdigalian of Ermingen, south-western Germany. Though based on a poorly preserved fragment, which leaves doubts about the species' identity, the occurrence of *M. guenterti* at Ermingen is confirmed by the examination of a better-preserved specimen from this locality (NHMW).

Pfister & Wegmüller (1998) compared their species with *Cardita zelebori* Hoernes, 1865, considered to be a *Megacardita* species. However, though similar to *Megacardita*, this species differs in several respects, as discussed below.

Occurrence. Megacardita guenterti is only known from the middle Burdigalian (Upper Marine Molasse) of Switzerland and Germany.

Megacardita hoernesi sp. nov.
Figures 11, 12, 13, 14, 15C–I

1865 *Cardita jouanneti* (Basterot); Hoernes, p. 266, pl. 35, figs 7–12.
1950 *Cardita (Megacardita) jouanneti* (Basterot); Csepreghy-Meznerics, p. 74, pl. 4, figs 8, 9.

1955 *Cardita (Megacardita) jouanneti* (Basterot); Moisescu, p. 86, pl. 4, figs 1–4.
1956 *Cardita* (*Megacardita*) *jouanneti* (Basterot); Sieber, p. 190, pl. 2, fig. 11, pl. 3, fig. 12a, b.
1959 *Cardita jouanneti* (Basterot); Eremija, pl. 4, figs 1–1b.
1963 *Megacardita jouanneti ponderosa* (Cossmann & Peyrot); Tavani & Tongiorgi, pl. 22, figs 1–4.
1981 *Megacardita jouanneti* (Basterot); Švagrovský, p. 78, pl. 24, fig. 1.
1985 *Megacardita jouanneti* (Basterot); Atanacković, p. 56, pl. 13, figs 1–3.
1998 *Megacardita jouanneti* (Basterot); Schultz, p. 94, pl. 41, fig. 5.
2003 *Megacardita jouanneti jouanneti* (Basterot); Schultz, p. 494, pl. 71, figs 6a–9b.

LSID. urn:lsid:zoobank.org:act:AF477230-E2FD-478F-A6E2-849F4B58D29B

Derivation of name. In honour of the Austrian palaeontologist Moriz Hoernes (1815–1868).

Diagnosis. Shape ovate-elongate, strongly inequilateral, posteriorly slightly truncate, ventrally convex. Umbo large, strongly anterior to shell midline. Posterior slope wide, fairly well defined. Radial sculpture of 17–18 wide, moderately convex ribs, weak to poorly distinct posteriorly; interspaces narrow, shallow. Radial ribs and interspaces crossed by some deeply incised, irregularly spaced growth striae.

Type material. Holotype, right valve, length 64 mm, height 52 mm, illustrated in Hoernes (1865, pl. 35, fig. 8) (NHMW 1855/0002/0062a). Paratype, left valve, length 65 mm, height 52 mm, illustrated in Hoernes (1865, pl. 35 fig. 7) (NHMW 1855/0002/0062b).

Type locality and age. Gainfarn (Austria), Vienna Basin; Middle Miocene, Badenian (late Langhian).

Description of holotype. Shell large, equivalve, robust, moderately convex, anteriorly thickened, ovate-elongate, strongly inequilateral. Anterior margin markedly convex; postero-dorsal margin long, barely convex; posterior margin obscurely truncate; ventral margin moderately convex, somewhat wavy due to radial sculpture. Umbo large, prominent, markedly prosogyrate, strongly anterior to shell midline. Lunule small, heart-shaped, deeply sunken, slightly penetrating into hinge plate; escutcheon lanceolate, narrow, elongate, deep, with steep walls, mostly occupied by external ligament. Posterior slope moderately wide, fairly well defined. Hinge strong; standard for the genus. Sculpture mainly radial, consisting of 18 wide, moderately convex ribs, separated by narrow, shallow interspaces. Radial ribs slightly stronger

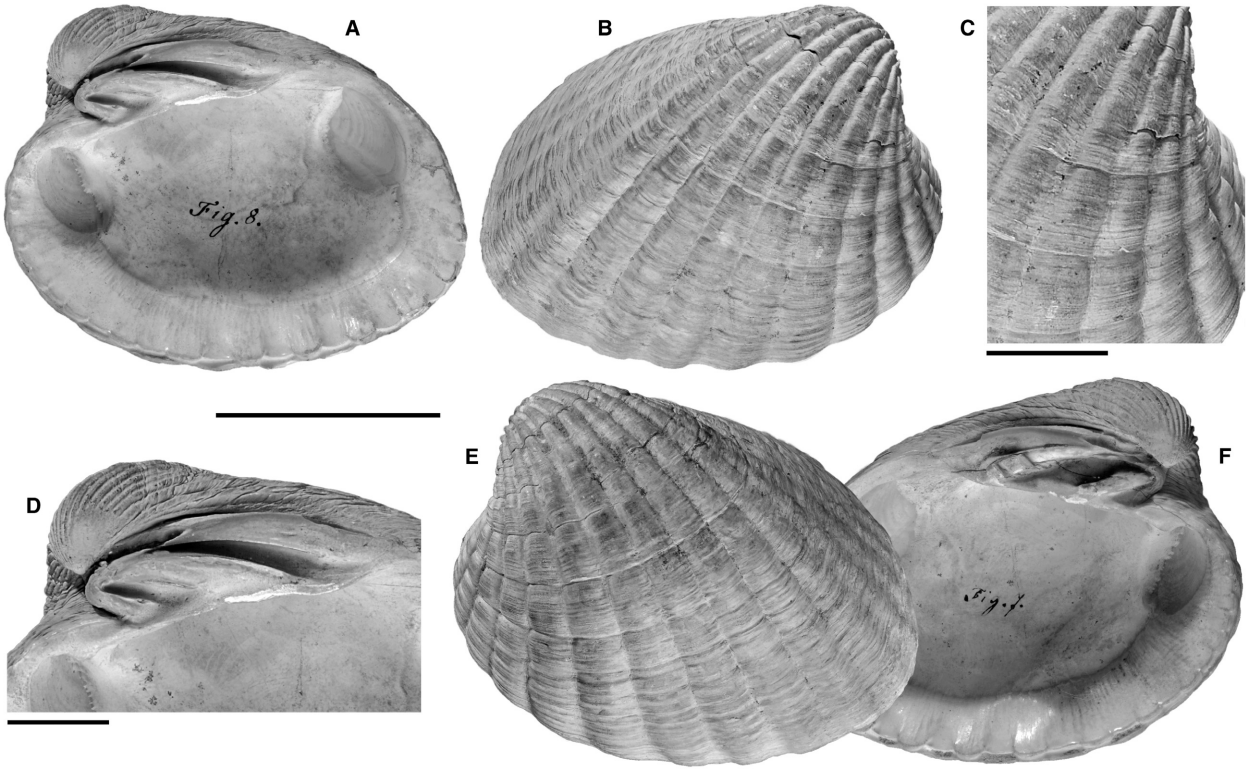

FIG. 11. *Megacardita hoernesi* sp. nov. A–D, holotype, Gainfarn (Hoernes 1865, pl. 35, fig. 8) (NHMW 1855/II/62). E, F, paratype, Gainfarn (Hoernes 1865, pl. 35, fig. 7) (NHMW 1855/II/62). Scale bars represent: 30 mm (A, B, E, F); 10 mm (C, D).

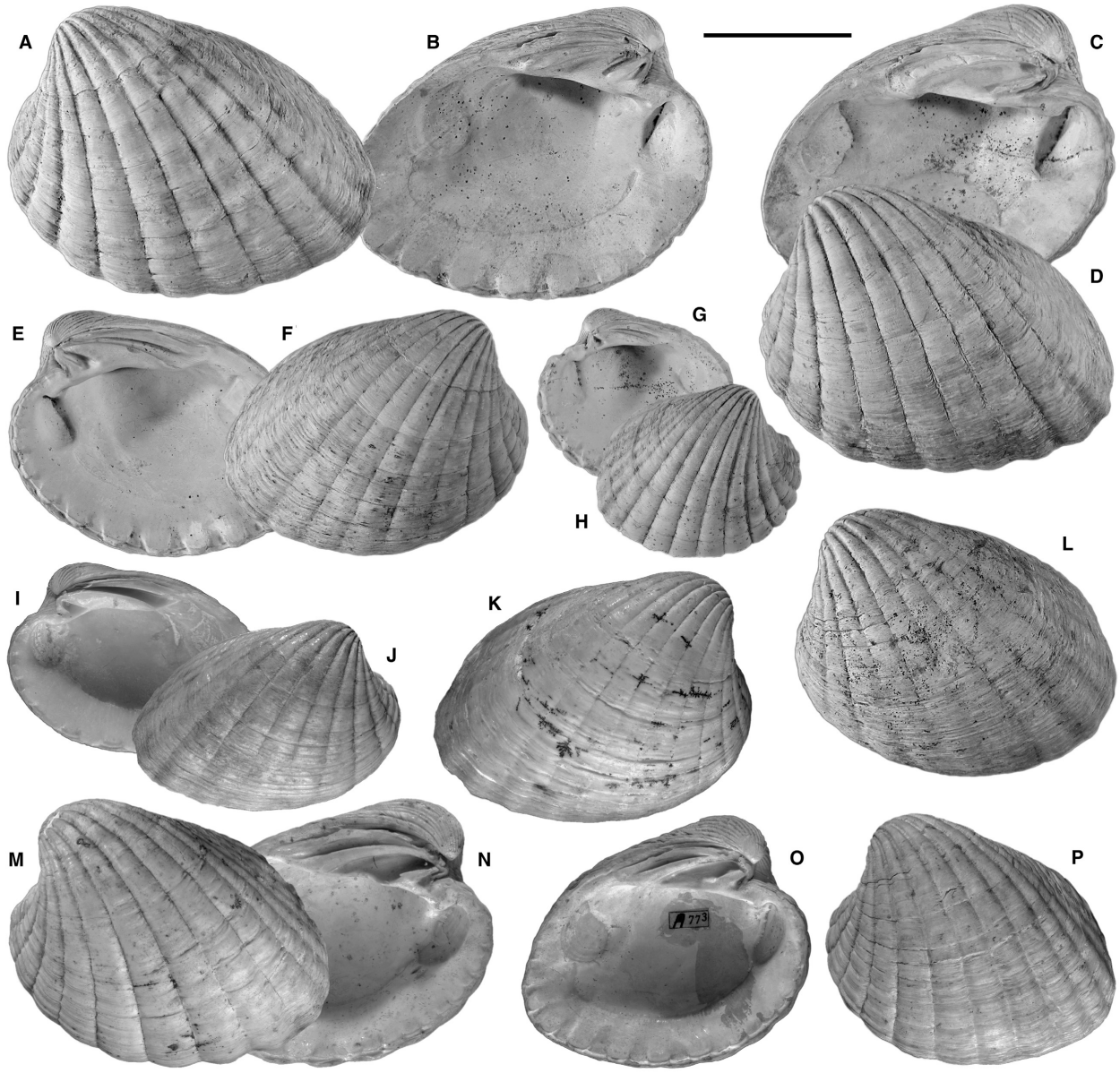

FIG. 12. *Megacardita hoernesi* sp. nov. A, B, Gainfarn (NHMW 2016/0254/0001). C, D, Gainfarn (NHMW 2016/0254/0005). E, F, Gainfarn (NHMW 2016/0254/0003). G, H, Gainfarn (NHMW 2016/0254/0002). I, J, Hidas (NHMW 1865/XXV/40). K, Mikulov/Kienberg (NHMW 1851/X/72). L, Gainfarn (NHMW 2016/0254/0004). M, N, Mikulov/Kienberg (NHMW 1851/X/72). O, P, Immendorf (NHMW A773). Scale bar represents 30 mm.

anteriorly, much weaker and on posterior slope. Early radial ribs beaded. Commarginal sculpture weak, consisting of close-set, somewhat lamellar growth striae, some of which more deeply incised and irregularly spaced, interrupting ribs. Margin serrated, with short projections of outer ribs; internal crenulation coarse, stronger ventrally, weaker anteriorly, poorly distinct posteriorly. Pallial line well impressed, regularly curved, entire. Anterior muscle scar deeply impressed, wide, ovate; posterior one shallow, wide, roundish.

Other material. Gainfarn (Austria), *c.* 40 valves, 9 shells (NHMW), Grund (Austria), 2 valves (NHMW). Immendorf (Austria), 4 valves (NHMW A773). Bad Vöslau (Austria), 1 valve (NHMW 1937.II.315). Steinebrunn (Austria), 14 valves (NHMW 1855.XL.306). Grinzing in Vienna (Austria), 6 valves (NHMW 1865.I.901). Ottakring in Vienna (Austria), 4 valves (NHMW A2287). Pötzleinsdorf in Vienna (Austria), 2 shells, 4 valves (NHMW 1868.I.190). Mikulov/Kienberg (Czech Republic), 6 valves (NHMW 1851.X.72). Lăpugiu de Sus (Romania), 2 valves (NHMW 1870.XXXIII.234). Degoj (Croatia), 3 valves (NHMW 1872.XXXI.23). Bujtur (Romania), 2 shells, 3 valves (NHMW 1862.L.589). Hidas (Hungary), 5 shells, 13 valves (NHMW 1862.XVIII.92; 1865.XXV.40; 1862.XVIII.91; 1859.XLII.73).

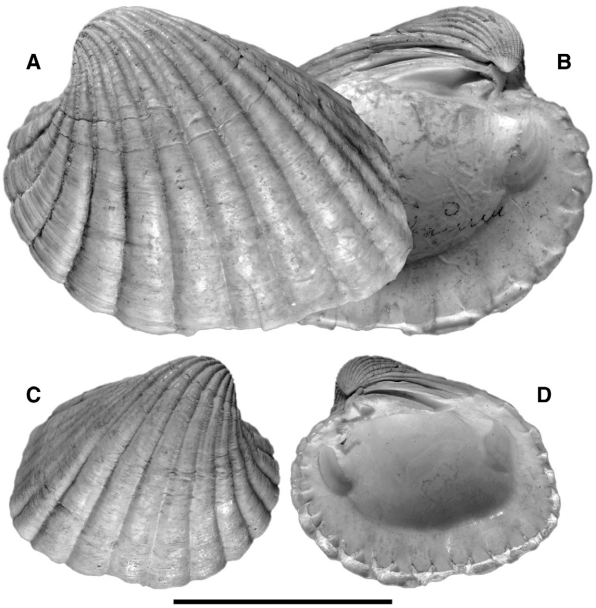

FIG. 13. *Megacardita hoernesi* sp. nov. A, B, Steinabrunn (NHMW 1855/XLV/306). C, D, Steinabrunn (NHMW 1855/XLV/306). Scale bar represents 30 mm.

Comparisons. Megacardita hoernesi sp. nov. is clearly similar to *M. jouanneti*, but a side-by-side comparison allows several distinctive characters to be recognized. The valves from Gainfarn are higher dorso-ventrally, more rounded in outline, with a sharper posterior truncation and a slightly more slender, more prominent and incurved umbo. These differences are shown graphically by the mean shape of the valves from Salles and Gainfarn used for the shape analysis (Fig. 16B).

Some remarkable differences also involve the sculpture. In *M. hoernesi* sp. nov., the radial ribs are wider, particularly near the ventral margin, and slightly less numerous (17–18 in the Gainfarn material), and generally much weaker to poorly distinct on the posterior slope, than in *M. jouanneti.* Deeply incised growth striae or incremental scars, interrupting the radial ribs are frequent in *M. hoernesi* sp. nov., whereas this character is absent or poorly developed in *M. jouanneti*. The radial sculpture tends to become obsolete near the ventral margin (Fig. 12L), where the sculpture is mainly commarginal, as also occurs in *M. jouanneti*. The maximum size is similar to that of *M. jouanneti, c.* 70 mm in length.

Sculptural differences between *M. jouanneti* and *M. hoernesi* sp. nov. are also seen in the juvenile stages; at a size of *c.* 15 mm, *M. jouanneti* has closely set radial ribs (Fig. 15B), whereas they are separated by wider interspaces in the new species (Fig. 15D). At this size, small differences in shape can be also seen (umbo more incurved in *M. hoernesi* sp. nov. etc.), but they are much more marked at a larger size; at 20–30 mm in length, *M. jouanneti* is distinctly elongate (Fig. 8A–D), whereas the shape is almost equidimensional in the new species (Fig. 15E, H).

As seen from the results of shape analysis (Fig. 16C), the valves from Salles (*M. jouanneti*) and Gainfarn (*M. hoernesi* sp. nov.) are well separated in the PCA 1–2

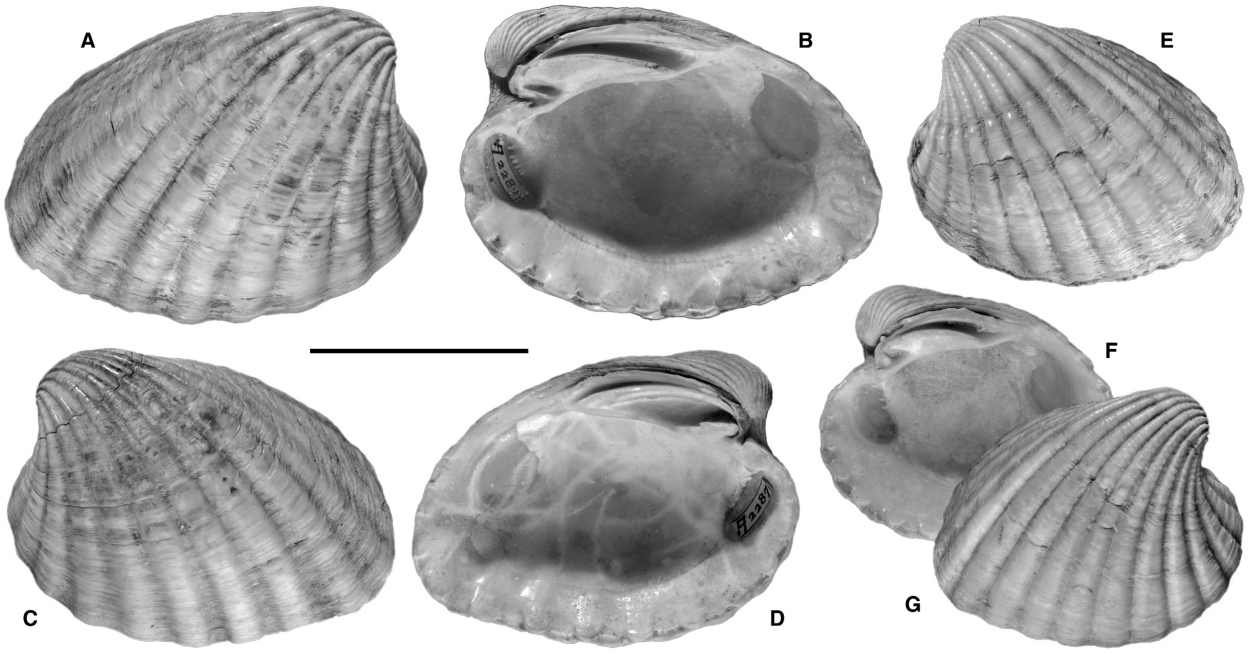

FIG. 14. *Megacardita hoernesi* sp. nov. A, B, Ottakring (NMHW A2287). C, D, Ottakring (NMHW A2287). E, Buituri (NMHW 1862/XXXIII/121). F, G, Buituri (NMHW 1862/XXXIII/121). Scale bar represents 30 mm.

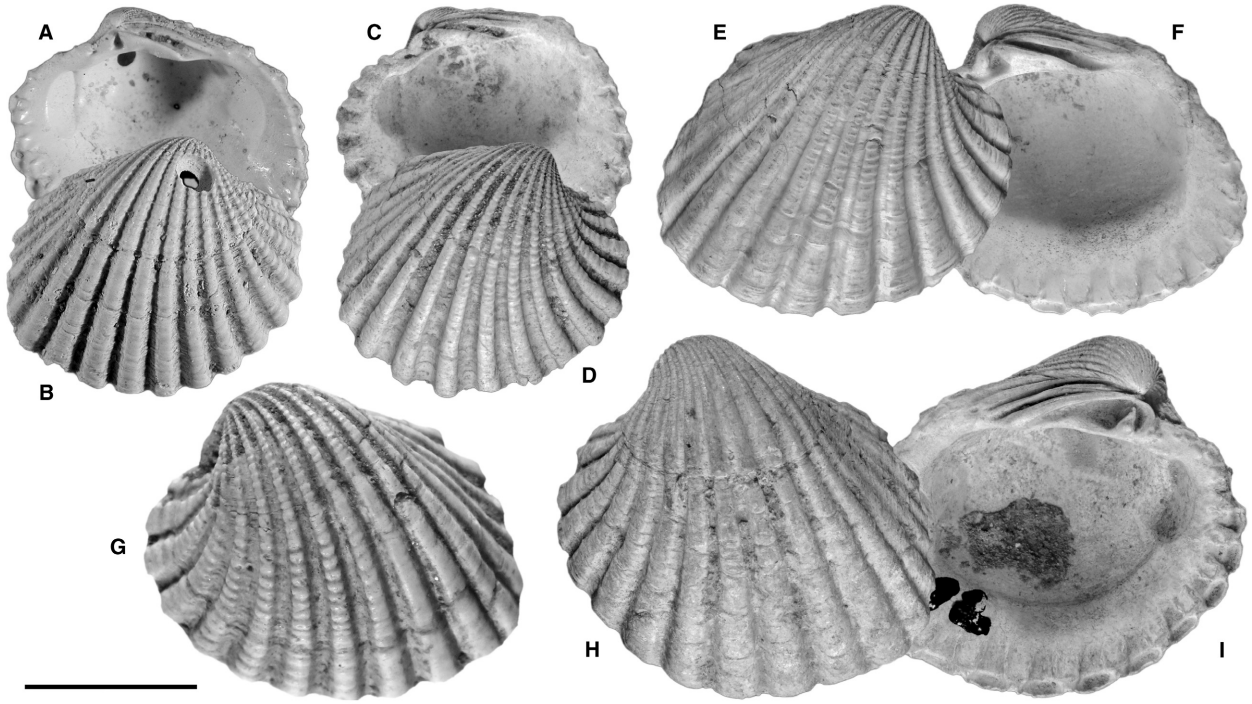

FIG. 15. Juvenile stages of *Megacardita* species. A, B, *Megacardita jouanneti* (Basterot, 1825), Mios (MPUB 2016/10K). C–F, *Megacardita hoernesi* sp. nov., Gainfarn (NHMW 1846/37/660). G, *Megacardita hoernesi* sp. nov., Buituri (TUG 1604-26 http://geokogud.info/specimen/240940). H, I, *Megacardita hoernesi* sp. nov., Grund (NHMW no catalogue number). Scale bar represents 10 mm.

morphospace, with only a small overlap. Dispersion is slightly higher for *M. jouanneti*, suggesting a wider variability than in *M. hoernesi* sp. nov. from Gainfarn. However, the variability of *M. hoernesi* sp. nov. and the overlap between the two species are markedly greater if the material from other Badenian localities in the Central Paratethys is considered, as discussed below.

Variability. Within the material from Gainfarn, the shell variability mainly involves the shape: more or less ovate and high, posteriorly slightly to barely truncate. Sculpture is also slightly variable in strength, but the number of ribs always is very close to 18.

Most material from the other localities differs in some respects from that from Gainfarn. Such variability was mostly observed in relatively scant material (3–15 valves or complete shells), which do not necessarily represent the main trend in their respective populations. Most valves from Hidas are markedly elongate and ovate (Fig. 12I, J), so that they fall in the PCA field of *M. jouanneti* (Fig. 16C), and with wider ribs; but some are very close to the mean shape recorded from Gainfarn. The valves from Immendorf and Steinebrunn (Figs 12O, P, 13A–D) tend to be more sharply truncate, and some specimens also have stronger sculpture. The material from Ottakring (Fig. 14A–F), Grinzing and Buituri (Fig. 14E–G), differs by having slightly more convex and stronger ribs, with wider and deeper interspaces. A case deserving special mention is represented by a valve from Buituri (Fig. 14F, G) that is much shorter, though apparently adult. The range of variability of *M. hoernesi* sp. nov. could be due to slight differences in age (e.g. the deposits of Gainfarn and Steinebrunn are about a million years younger than those of Immendorf), though all these localities are Badenian in age, or to different local conditions (depth, substrate etc.) or even, to geographically different populations.

Remarks. The type material of *Megacardita hoernesi* sp. nov. (Fig. 11) is from the material originally illustrated by Hoernes (1865, p. 266, pl. 35, figs 7–12) as *Cardita jouanneti*. The species was said to be particularly frequent at Gainfarn, and rarely occurring at other localities.

The occurrence of *Cardita jouanneti* in the Miocene of Austria was also discussed by Sieber (1956, p. 190, pl. 2, fig. 11; pl. 3, fig. 12a–b), who remarked on the general differences from some varieties reported by Sacco (1899). He also pointed out the occurrence of a possible distinct form, or subspecies, more heart-shaped and with the posterior margin more strongly truncate, at Immendorf and Bad Vöslau, of which he illustrated a right valve. Sieber's form is herein considered to be a variation of *M. hoernesi* sp. nov. as discussed above.

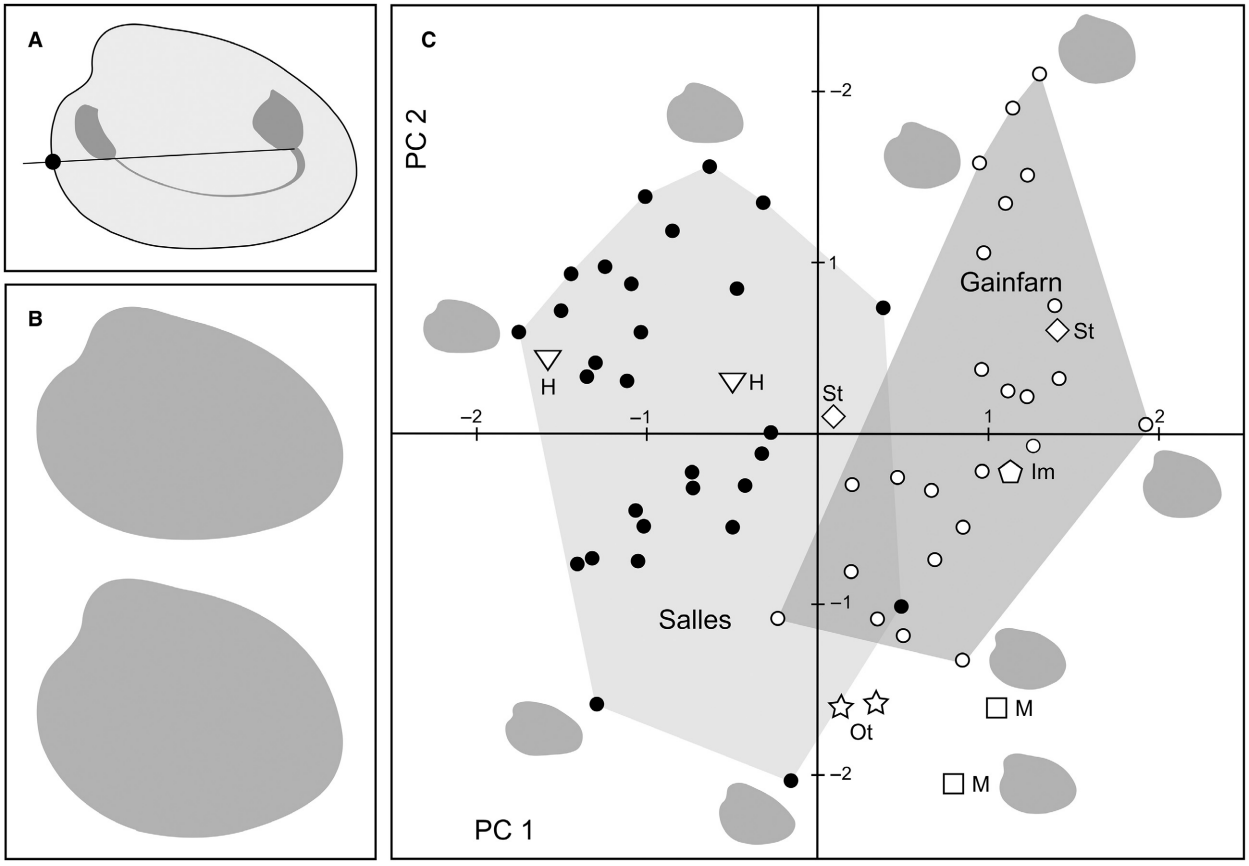

FIG. 16. Shape analysis of *Megacardita*. A, scheme illustrating the reference system for fixing a starting point on the shell outline. B, mean shape of the valves from Salles (top; 29 valves) and Gainfarn (bottom; 24 valves). C, PCA ordination of *Megacardita* specimens in the plane PC1–PC2 (*c.* 90% of total variance); shaded areas represent the convex hulls of Salles (*M. jouanneti*) and Gainfarn (*M. hoernesi* sp. nov.) samples; other material (*M. hoernesi* sp. nov.) abbreviated as follows: H, Hidas; Im, Immendorf; M, Mikulov/Kienberg; Ot, Ottakring; St, Steinabrunn.

Illustrations of specimens from Gainfarn were reported by Tavani & Tongiorgi (1963, pl. 22, figs 1–4), as *Megacardita jouanneti ponderosa*. More recently, Schultz (2003, pl. 71, figs 6a–9b) illustrated *Megacardita jouanneti jouanneti* from the Badenian of Austria based on material from NHMW: two valves from Gainfarn (figs 7a–b, 9a–b), one of which originally was illustrated by Hoernes (1865, pl. 35, fig. 12); one from Immendorf, originally illustrated by Sieber (1956, pl. 2, fig. 11), and one from Ottakring.

Most study material is from localities in the urban area of Vienna (Grinzing, Ottakring, Pötzleinsdorf) and from other localities in Lower Austria (Gainfarn, Bad Vöslau, Steinebrunn), all located in the Vienna Basin and representing middle to late Badenian transgressive–regressive cycles (Schultz 2005; Strauss *et al.* 2006), together with the locality of Mikulov/Kienberg (Czech Republic), also represented in the NHMW collection. Grund and Immendorf, both in Lower Austria, are located in the Alpine–Carpathian Foredeep Basin and represent the early Badenian cycle, dated at *c.* 15 Ma (Mandic 2004). Other material is from the Transylvanian Basin, namely from the early Badenian of Lăpugiu de Sus (= Lapugy) (Studencka *et al.* 1998) and from the late Badenian of Buituri (= Bujtur) (Studencka *et al.* 1998), both in Romania. Specimens from Buituri, identical to the NHMW specimens, were illustrated by Moisescu (1955). The NHMW collection also includes material from the Pannonian Basin, namely from the Badenian of Hidas near Pecs (Hungary), from which Csepreghy-Meznerics (1950) illustrated two specimens, and from Degoj (Croatia), one of the Badenian localities near Glina from which Pilar (1873) reported *Cardita jouanneti* as a very common species. Other illustrated records were reported by Eremija (1959) from Prijeka (Croatia), Švagrovský (1981) from Devinska Nova Ves-Sandberg (Slovakia) and Atanackovic (1985) from Prnjavor and Hrvaćani-Drenik (Bosnia and Herzegovina), all Badenian deposits.

Dollfus *et al.* (1903, pl. 20, figs 3–4) accurately illustrated two valves from the Tortonian of Adiça as *Cardita jouanneti* var. *brocchii*. They are large (up to 93 mm

long), with twelve wide ribs, the posterior one being obsolete, crossed by scattered, deeply incised growth striae. They are reminiscent of *M. hoernesi* sp. nov. but much larger and more orbicular, and their interpretation as a variation of *M. laeviplana*, definitely occurring in the Tortonian of Portugal, is even more difficult. Dollfus *et al.* (1903) suggested that they might represent a distinct species ('cette forme haute pourrait bien constituer une espèce distincte') and their hypothesis can be neither rejected nor supported.

There are also scant records of *Cardita jouanneti* from the Pliocene of northern Italy: Borzoli (Genoa) (Della Campana 1890) and Castell'Arquato (Modena) (Cocconi 1873), both doubtfully reported by Sacco (1899). A few specimens from 'Castell'Arquato' in the NHMW collections, bought from a private collector in the nineteenth century, can actually be referred to *M. hoernesi* sp. nov. but their state of preservation suggests that they originated from Gainfarn. It is assumed that old records from Castell'Arquato were based on misidentified species. For example, a relatively large, undetermined carditid, probably *Cardita pectinata* (Brocchi, 1814), which could be misidentified as a *Megacardita* species, was recently reported by Crippa & Raineri (2015, pl. 9, fig. 2a, b) from the Early Pleistocene deposits of the Castell'Arquato section.

Occurrence. Megacardita hoernesi sp. nov. is known from the Badenian of Austria, Czech Republic, Slovakia, Hungary, Romania, Croatia, Bosnia and Herzegovina.

Megacardita? *laticosta* (Eichwald, 1830)
Figure 17

1830 *Venericardia laticosta* Eichwald, p. 210.
1853 *Cardita laticosta* (Eichwald); Eichwald, p. 89, pl. 5, fig. 9a, b.
1936 *Venericardia* (*Megacardita*) *laticosta* Eichwald; Friedberg, p. 92, pl. 16, figs 11–13.

Material. Bogucice (Poland), 1 valve (Friedberg coll., ZNG PAN A-I-73/377); Stary Poczajów (Ukraine), 1 valve (Friedberg coll., ZNG PAN A-I-73/378); Zaleśce (Ukraine), 2 valves (Friedberg coll., ZNG PAN A-I-73/381). Zaleśce (Ukraine), 1 valve (NHMW 1859.XL.62); Kremenec' (Ukraine), 1 valve (NHMW 1981/8).

Remarks. Eichwald (1830, p. 210) described *Venericardia laticosta* from Shukowze (Zukowce) and Salisze (Zaleśce), Ukraine, as follows: 'Testa dilatata, crassa, costae latae, squamatae, squamis prope testae marginem approximatis, numerosis, margine dentato, latere cardinali valde prominulo'. The same species was then redescribed in more detail, commented and illustrated by Eichwald (1853, p. 89, pl. 5, fig. 9a, b): 'Testa incrassata exaltata, costata, costis planis, crassis, latis, undatim squamosis, squamis prope marginem approximatissimis, latioribus costarum interstistiis concavis, planis, margine cardinali posteriora versus exaltato, latitudo paullo major longitudine'. It was said to be similar to *Cardita* (*Venericardia*) *jouanneti*, with which it was compared. The main sculptural differences, according to Eichwald's comments, are: radial sculpture consisting of 17–18 wide ribs, whose interspaces are wider and deeper than in *M. jouanneti;* commarginal sculpture made up of 'écaillés grosses, bombées et serrées, qui sont ondulées, non aplaties, comme les écailles du *Cardita Jouanneti*'. He also remarked on the lack of granulations on the umbo, as differing from *M. jouanneti*, and commented that the fossil species reported from Volhynia as *Venericardia planicosta* by Pusch (1837, p. 183) is *C. laticosta*.

This species was studied on the basis of four valves (ZNG PAN), originally published by Friedberg (1936, pl. 16, figs 11–13), from Bogucice (Poland), Stary Poczajów and Zaleśce (Ukraine) (Fig. 17A–J) and two additional valves (NHMW) from Zaleśce and Kremenec' (Ukraine) (Fig. 17K–N), all late Badenian localities in the Carpathian Foredeep Basin (Porębski & Oszczypko 1999; Anistratenko & Anistratenko 2007).

The two largest valves (*c.* 50 mm), both badly worn (Fig. 17A–D), are apparently similar to *Megacardita* in most shell characters, including their large umbo, strong hinge, penetrating lunule, deep anterior muscle scar etc., but they differ by being markedly trigonal and relatively short, with squamose sculpture, particularly near the shell margin. Such sculpture was reported in Eichwald's descriptions and also remarked on in his comments: 'die zahlreichen wenig erhöhten Rippenschuppen zeigen den Wachstum der Schale an' (the numerous, gently raised scales on the ribs mark the growth stages of the shell) (Eichwald 1853, p. 89). It is also clearly seen in the original illustration by Eichwald (1853, pl. 5, fig. 9a, b) (Fig. 17J), apparently representing an adult shell, 48 mm in length (drawn at natural size).

Younger, better-preserved valves, 20–40 mm in length (Fig. 17F–N), have a markedly different shape, subquadrate or subtrapezoidal, strongly inequilateral with a long, almost straight postero-dorsal margin, subparallel to the ventral margin. The posterior margin is rather strongly truncate and obscurely sinuous. Their radial ribs increase in width rapidly from the anterior margin to the postero-ventral transition, where two or three particularly wide ribs are present. On the posterior slope, the radial ribs are still distinct and rather wide. This radial pattern, also seen in the largest valves, but slightly less evident, is somewhat different to that occurring in species of *Megacardita*, whose radial ribs increase in width more regularly

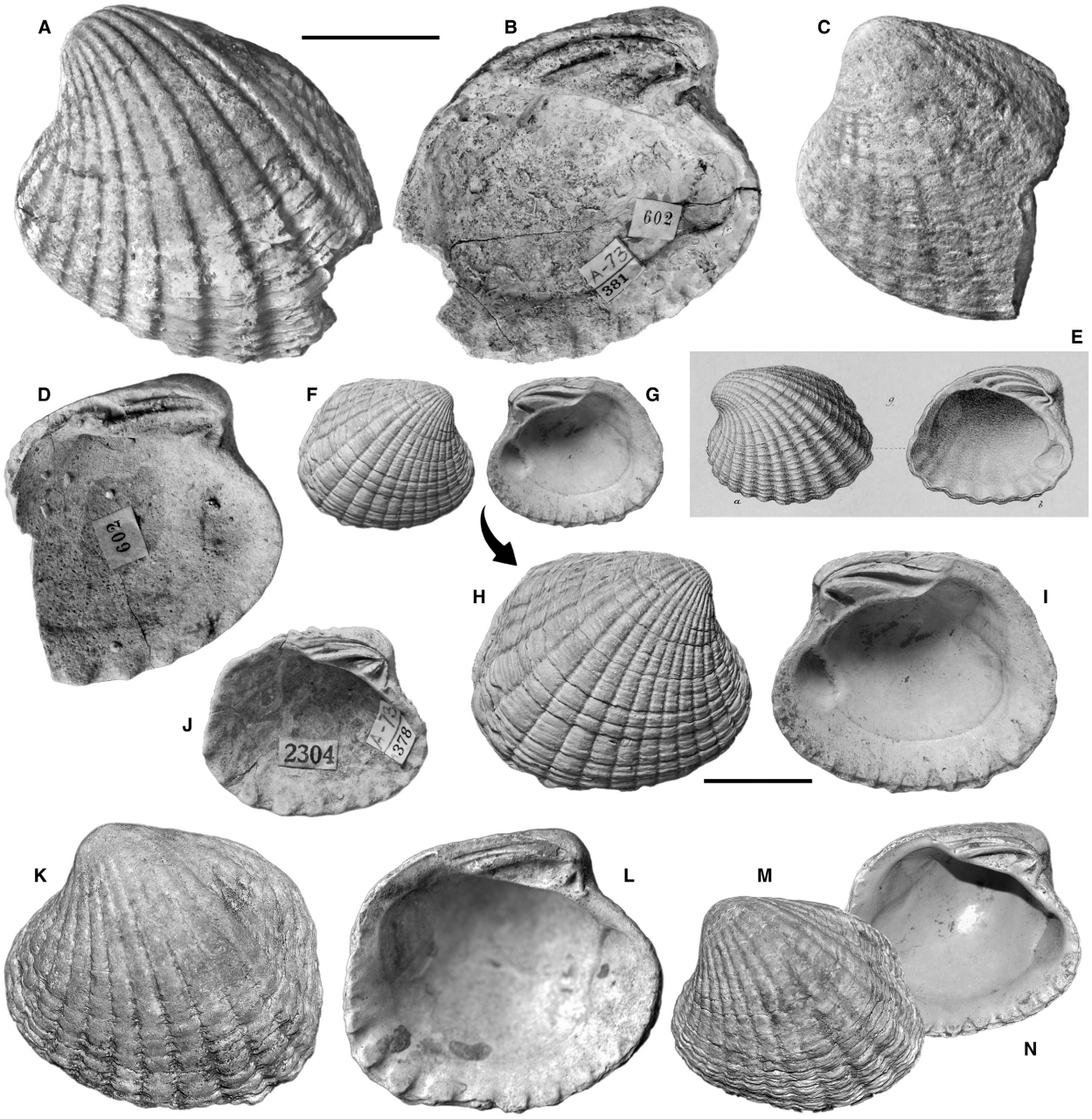

FIG. 17. *Megacardita*? *laticosta* (Eichwald, 1830). A, B, Zaleśce (Friedberg coll., ZNG PAN A-I-73/381, photo P. Olejniczak). C, D, Zaleśce (Friedberg coll., ZNG PAN A-I-73/381, photo P. Olejniczak). E, original illustration of *Cardita laticosta* Eichwald, 1830 (after Eichwald 1853, pl. 5, figs 9a, b). F–I, Bogucice (Friedberg coll., ZNG PAN A-I-73/377, photo P. Olejniczak). J, Stary Poczajów (Friedberg coll., ZNG PAN A-I-73/378, photo P. Olejniczak). K–L, Zaleśce (NHMW 1859.XL.62). M, N, Kremenec' (NHMW 1981/8). Scale bars represent: 20 mm (A–D, F, G, J–N); 10 mm (H–I).

antero-posteriorly, becoming particularly fine to almost obsolete on the posterior slope.

As remarked by Eichwald (1853), the present species apparently lacks beads or granulations on the umbo. Admittedly, this could be due to abrasion and it is also possible that the beaded sculpture is particularly fine and/or limited to the earliest stages, thus easily lost by wear.

For the time being, the present species seems to be closer to *Megacardita*, to which it is tentatively assigned, than to other carditid genera, but a distinct systematic position could be suggested by further study.

Studencka *et al.* (1998, p. 317) synonymized *Cardita crassa* var. *vindobonensis* Sacco, 1899 from the Badenian of Austria, with *M. laticosta,* based on the examination of

Eichwald's type material. Var. *vindobonensis* was proposed by Sacco (1899, p. 8) to keep the species reported by Hoernes (1865, p. 265, pl. 35, figs 1–6) as *Cardita scabricosta* Michelotti, 1847, distinct from Michelotti's species. Hoernes' illustrations show a large carditid similar in shape and sculpture to *M. laticosta*, but with robust radial ribs and markedly prominent, projecting scales and pointed tubercles, also present in the early growth stages. The examination of the type material of *C. crassa* var. *vindobonensis* (NHMW), which was illustrated by Schultz (2003, pl. 68, figs 2a–5b), confirms this sculpture: it is so prominent that it would be preserved, at least in part, even in worn shells and would have been remarked on in Eichwald's original description of *M. laticosta*. The records and illustrations of *Cardita crassa* var. *vindobonensis* by Schaffer (1910, p. 59, pl. 28, figs 2–3) from the Eggenburgian (Early Miocene) of Austria, of *Beguina (Mytilicardita) crassa vindobonensis* by Sieber (1956, p. 197, pl. 1, fig. 15) from the Badenian of Austria, and of *Cardita (C.) vindobonensis* by Freneix *et al.* (1987, p. 422, pl. 1, fig. 12a, b) from the Messinian of Algeria, all actually match the identity of var. *vindobonensis*. Also, the report of *M. laticosta* by Nevesskaja *et al.* (1993, p. 134, pl. 30, figs 7–9) from the late Badenian of Ukraine appears to be based on the same heavily sculptured carditid. Admittedly, these illustrations document some variability in the strength of scales and tubercles, from strong to weak, but the squamose sculpture of *M. laticosta* is never present. Unless *Cardita vindobonesis* is considered to be a species with an unusually wide variability, its synonymy with *M. laticosta* should be rejected. Nevertheless, the two species show remarkable similarities in shape and also in the radial pattern, with wider ribs at the transition from the median to the posterior area. These shared characters suggest a possible systematic closeness between *M. laticosta* and *C. vindobonensis* which should be investigated further.

Studencka *et al.* (1998) also synonymized *Beguina* (*Mytilicardia*) *crassa longata* Sieber, 1956 with *M. laticosta*, but Sieber's taxon is clearly different, much more elongate in shape and with a much narrower hinge.

In the same work, Studencka *et al.* (1998) listed *Megacardita tournoueri* (Mayer, 1871*a*), together with *M. jouanneti* and *M. laticosta*, among the Paratethyan bivalve fauna. However, *Cardita tournoueri*, described from the Aquitanian of Uzeste, south-east of Bordeaux (Mayer 1871*a*, p. 341, pl. 9, fig. 5), has tubercles and scales on the radial ribs, as clearly seen from the original description and illustration, definitely not characters of *Megacardita*.

Occurrence. Megacardita laticosta is known from the late Badenian of the Ukraine and Poland, Central Paratethys.

Megacardita ignorata (Cossmann & Peyrot, 1912)
Figure 18

1912 *Venericardia* (*Cardiocardita*) *ignorata* Cossmann & Peyrot, p. 181, pl. 4, figs 15–18.

Material. Salles 'le Minoy' (France), 3 valves, syntypes of *Venericardia* (*Cardiocardita*) *ignorata* (MNHN.F.J05628). Salles (France), 6 valves (MPUB 2016/10).

Remarks. Venericardia (*Cardiocardita*) *ignorata* was described from Salles 'le Minoy' and also reported from Salles, Largileyre and Saucats, as a rather common species (Cossmann & Peyrot 1912, p. 181, pl. 4, figs 15–18). It was compared with *Cardita partschi* Goldfuss, 1840, a species known from the Badenian of the Paratethys, notably different in shape and sculpture from the present species, with elongate tubercles on the radial ribs.

Most probably, Cossmann & Peyrot (1912) did not include this species in *Megacardita,* because of its small size (*c.* 30 mm) and weakly inequilateral shape. Nevertheless, they spent some words on a comparison with *M. jouanneti*, as follows: 'On distinguera aisément *C. ignorata* des jeunes *C. Jouanneti* par sa forme moins transverse, par son crochet plus gonflé, par sa dent 3b plus courte et plus épaisse et par ses côtes plus étroites séparées par des sillons plus larges'.

Both the type and other study material are slightly worn, as are most shells of *M. jouanneti* and of other species from Salles deposits.

Apparently, this species is more similar to some ribbed Neogene carditids, mostly poorly known, of moderate size and weakly inequilateral, such as *Cardita partschi*, *C. tournoueri* (both discussed above), *C. matheroni* Mayer, 1871*b,* etc. rather than to the *Megacardita* species treated in the present work. Nevertheless, the shell exhibits all the characters of *Megacardita*, except for large size and strongly inequilateral shape: (1) umbo large; (2) beaded ribs in the early stages; (3) closely set, convex radial ribs; (4) well-defined posterior slope with much finer ribs than elsewhere; (5) flat, weak commarginal sculpture; (6) shell robust, in particular anteriorly, with deeply impressed anterior muscle scar; (7) hinge relatively strong, closely matching the *Megacardita* hinge, including the penetrating lunule. Its 20–21 radial ribs are also compatible with the range known for *Megacardita*. The commarginal sculpture consists of incised striae, giving a weakly defined decussate pattern, herein considered a persistence of the beaded juvenile sculpture, becoming less and less regular towards the shell margin (Fig. 18G). This type of sculpture seems to be closely comparable with that of *M. jouanneti* and the other species so far discussed.

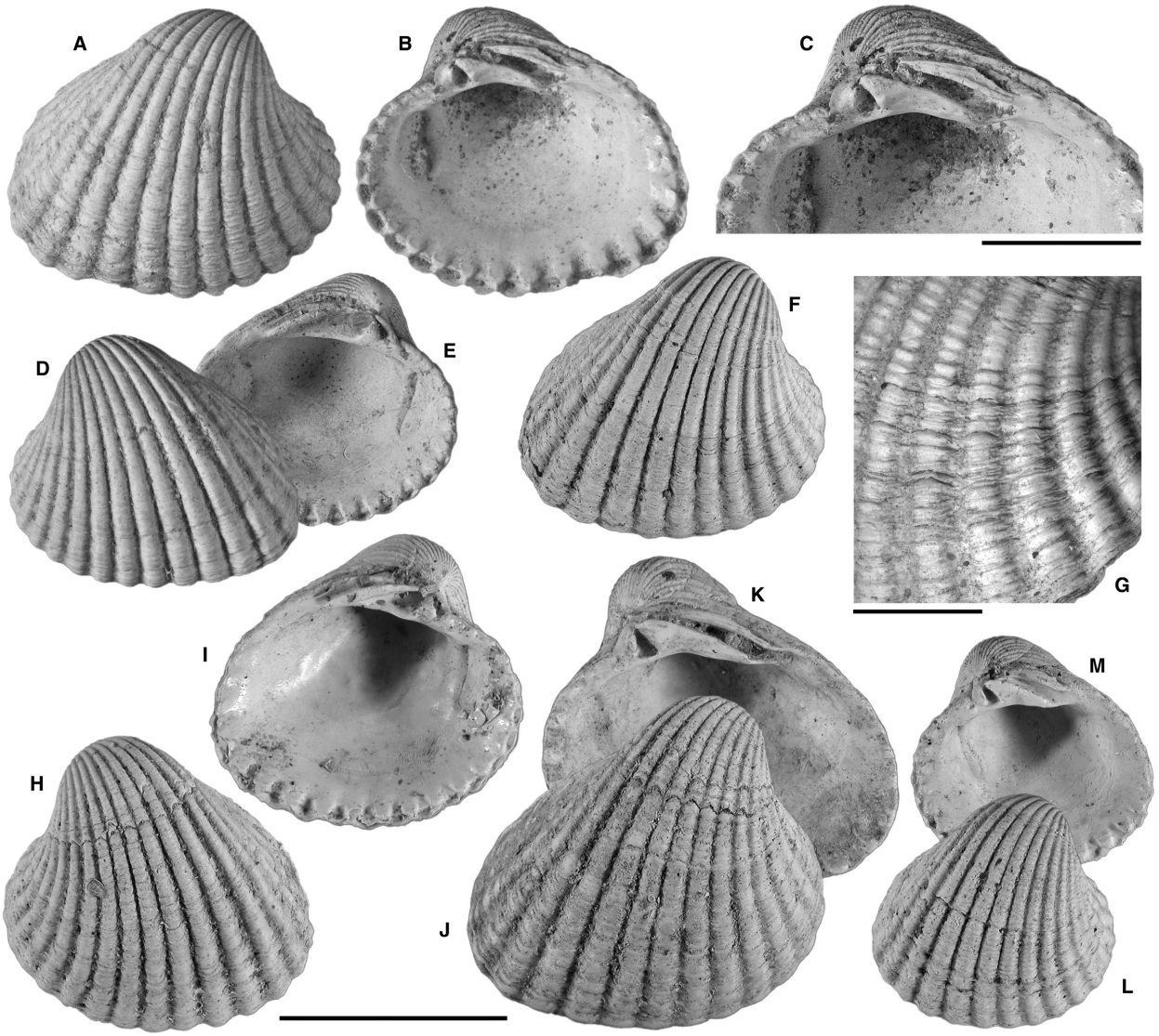

FIG. 18. *Megacardita ignorata* (Cossmann & Peyrot, 1912). A–D, Salles 'Le Minoy', syntype of *Venericardia (Cardiocardita) ignorata* Cossmann & Peyrot, 1912 (Cossmann coll., MNHN.F.J05628, photo P. Massicard). E, F, Salles 'Le Minoy', syntype of *Venericardia (Cardiocardita) ignorata* Cossmann & Peyrot, 1912 (Cossmann coll., MNHN.F.J05628, photo P. Massicard). G, Salles (MPUB 2016/10S). H, I, Salles (MPUB 2016/10T). J, K, Salles (MPUB 2016/10S). L, M, Salles (MPUB 2016/10R). Scale bars represent: 20 mm (A, B, D–F, H–M); 10 mm (C); 5 mm (G).

It is worth noting the increasingly inequilateral shape, due to prevalent antero-posterior rather than dorso-ventral growth, as seen in the largest valve (Fig. 18J, K), as well as the similarity in shape to the weakly inequilateral early stages of *M. jouanneti* (Fig. 8A–D).

Based on these observations, the present species is assigned to *Megacardita* as a case of marked size reduction, with preservation of the juvenile shape and, at least in part, also of the juvenile sculpture. With a maximum shell length of *c.* 35 mm, *M. ignorata* is the smallest species included in the genus.

The record of *Cardites ignoratus* by Lauriat-Rage (1981) from the Redonian of Anjou, not illustrated and only shortly commented, leaves doubts about its correct identification.

Occurrence. Megacardita ignorata is only known from the Serravallian of the Salles area.

Megacardita laeviplana (Depéret, 1839)
Figures 19, 20, 21, 22A–D

1839 *Cardita jouanneti* var. *laeviplana* Depéret; p. 256.
1897 *Cardita jouanneti* var. *laeviplana* Depéret; Brives, 1897, p. 17, pl. 5, figs 2–6.

1899 *Cardita* (*Megacardita*) *jouanneti* var. *laeviplana* Depéret, Sacco; p. 10, pl. 3, figs 9–12.
1899 *Cardia* (*Megacardita*) var. *dertobrevis* Sacco, p. 11, pl. 3, fig. 14.
1899 *Cardita* (*Megacardita*) var. *dertolonga* Sacco, p. 11, pl. 3, figs 15, 16 (*partim*?).
1903 *Cardita* (*Venericardia*) *jouanneti* (Basterot); Dollfus *et al.*; pl. 19, figs 1–1a; pl. 20, figs 1–2.
1958 *Megacardita jouanneti* var. *brivesi* Mongin, p. 236.
1963 *Cardita jouanneti laeviplana* Depéret; Tavani & Tongiorgi, pl. 23, figs 1–6; pl. 24, figs 1–8.

Material. MRSN (Bellardi & Sacco coll.): BS.126.02.008, Stazzano, 1 valve; BS.126.02.009, Stazzano, 1 valve; BS.126.02.010, Montaldo Torinese, 1 valve; BS.126.02.011, S. Agata Fossili, 1 valve; BS.126.02.012, Montaldo Torinese (Pilone), 1 valve; BS.126.02.012/02, Montaldo Torinese (La Moja), 1 valve; BS.126.02.012/03, Stazzano, 1 valve, 3 fragments, BS.126.02.012/04, Stazzano, 1 valve; BS.126.02.012/06, Moncucco, 1 fragment; BS.126.02.012, Montaldo Torinese, 1 valve; BS.126.02.013, Stazzano, syntype of *Cardita* (*Megacardita*) *jouanneti* var. *dertobrevis*, 1 valve; BS.126.02.014, Montaldo Torinese, syntype of *Cardita* (*Megacardita*) *jouanneti* var. *dertolonga*, 1 valve; BS.126.02.015, Turin Hills, syntype of *Cardita* (*Megacardita*) *jouanneti* var. *dertolonga*, 1 valve. NHMW: C.3867/1867, Cabrières-d'Aigues, 2 valves; 1886.IV.66, Adiça, 2 valves; 1862.II.45, Modena, 2 valves. Brunetti coll., Montegibbio, 1 valve; Rio di Bocca d'Asino, 1 valve. MSNP (Tavani & Tongiorgi coll.): Ponsano, I 8758, 1 valve; Ponsano, I 9417, 1 shell; Ponsano, I 9422, 1 shell; Ponsano, I 13575, 1 shell; Ponsano, I 13587, 2 shells; Ponsano, I 13596, 1 valve; Ponsano, I 13599, 1 shell.

Description. Megacardita laeviplana has the same rib pattern as *M. jouanneti* in the early stages, up to about 30–40 mm in shell length. Thereafter, the radial ribs tend to become flat, separated by thread-like interspaces, to almost lost near the ventral margin, where commarginal, wrinkled sculpture prevails. The extent of the radial ribs and their transition to a smoother sculpture represent the main aspect of the species' variability. Anteriorly,

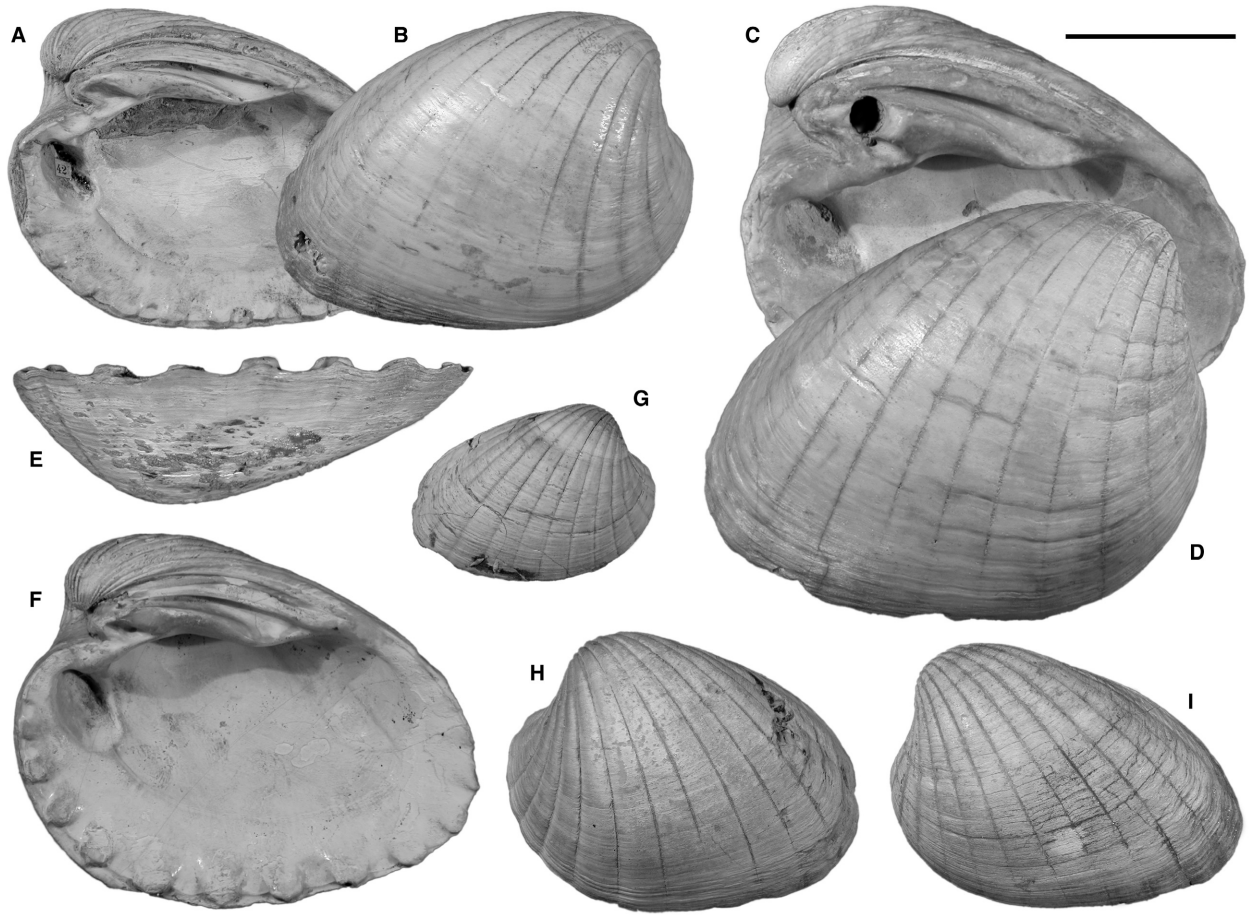

FIG. 19. *Megacardita laeviplana* (Depéret, 1839). A, B, Stazzano (Sacco 1899, pl. 3, fig. 9) (MRSN BS.126.02.008). C, D, Stazzano (MRSN BS.126.02.012/04). E, F, Stazzano (Sacco 1899, pl. 3, fig. 10) (MRSN BS.126.02.009). G, Montaldo Torinese, (Sacco 1899, pl. 3, fig. 13) (MRSN BS.126.02.012). H, Montaldo Torinese (Sacco 1899, pl. 3, fig. 11) (MRSN BS.126.02.010). I, S. Agata Fossili, (Sacco 1899, pl. 3, fig. 12) (MRSN BS.126.02.011). Scale bar represents 30 mm.

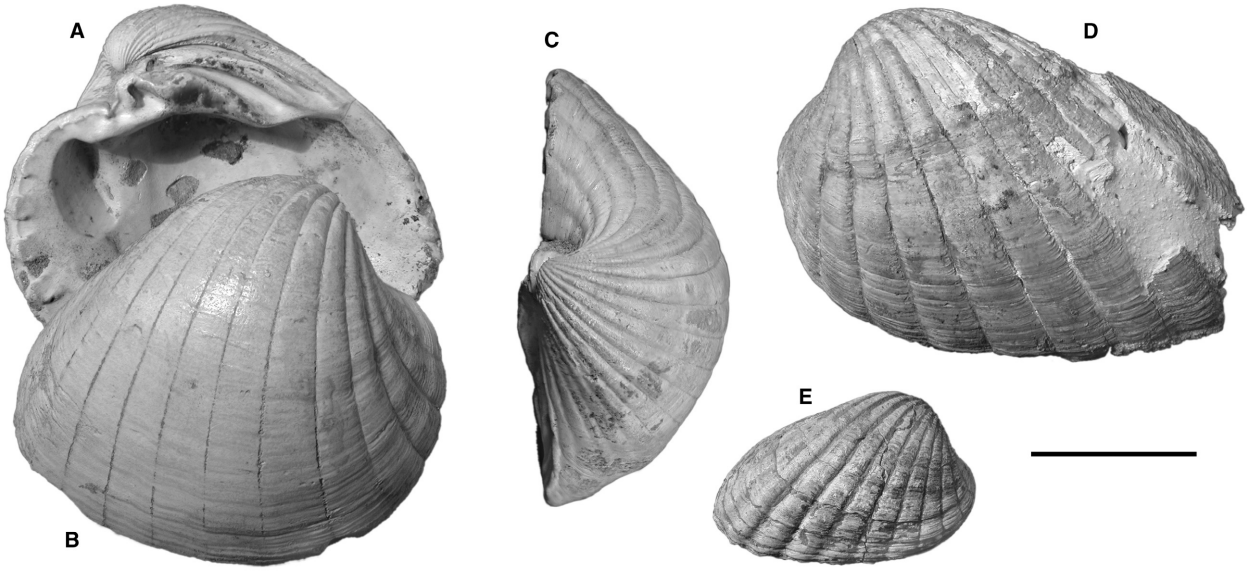

FIG. 20. *Megacardita* spp. A–C, Stazzano, syntype of *Cardita (Megacardita) jouanneti* var. *dertobrevis* Sacco, 1899 (pl. 3, fig. 14) (MRSN BS.126.02.013). D, Montaldo Torinese, syntype of *Cardita (Megacardita) jouanneti* var. *dertolonga* Sacco, 1899 (pl. 3, fig. 15) (MRSN BS.2602.014). E, Turin Hills, syntype of *Cardita (Megacardita) jouanneti* var. *dertolonga* Sacco, 1899 (pl. 3, fig. 16) (MRSN BS.126.02.015). Scale bar represents 20 mm.

the ribs tend to remain distinct, with a slight convex profile throughout growth, while they tend to be lost posteriorly. Ribs are slightly wider than in *M. jouanneti*, and slightly less numerous, generally 17–18. The shell outline is markedly more trigonal, with a long, regularly convex to almost straight postero-dorsal to posterior margin, while the ventral margin ranges from moderately to strongly convex.

This is the largest species in the genus, with a maximum shell length exceeding 100 mm, with a particularly thick shell and very strong hinge (Fig. 10C).

Remarks. Var. *laeviplana* was described by Depéret (1839, p. 256) in a footnote as follows: 'la forme à côtes plates et lisses du Tortonien d'Italie et de France mérite d'être distinguée à titre de variete sous le nome de *Cardita Jouanneti* var. *laeviplana*'. No indication of type locality was given, except for Tortonian of Italy and France.

Sacco (1899, p. 10, pl. 3, figs 9–12) reported var. *laeviplana* from the Tortonian of the Turin Hills (Montaldo Torinese, Moncucco, Stazzano, S. Agata Fossili) (Fig. 19), remarking that this variety could be considered as a distinct species, due to its unique shell characters and limited stratigraphical distribution.

Var. *dertobrevis* (Sacco, 1899, p. 11, pl. 3, fig. 14) is represented by a single valve from Stazzano (Fig. 20A–C). It has the same sculpture as large valves of *M. laeviplana*, but it is markedly smaller, *c.* 50 mm long, and convex. It could be considered to be a subadult specimen of *M. laeviplana*, but the early stages of this species are elongate and similar to the average shape of *M. jouanneti* (Fig. 19G–I). Var. *dertobrevis* could therefore be tentatively considered to be an extreme case of variability of *M. laeviplana*, if not a teratological or dwarfed specimen. On the other hand it comes from one of the Tortonian localities from which *M. laeviplana* was reported by Sacco.

The interpretation of var. *dertolonga* (Sacco 1899, p. 11, pl. 3, figs 15–16) is also somewhat troublesome; it is represented by two valves, one from the Tortonian of Montaldo Torinese (Fig. 20D), and the other is stated to be from the 'Helvetian' of the Turin Hills, without any details about the locality (Fig. 20E). The former most probably falls within the variation of *M. laeviplana*, although less trigonal than usual. The latter is much smaller, *c.* 20 mm long, markedly ovate-elongate and with relatively strong sculpture, both radial and commarginal. It seems rather far from the similarly sized valves of *M. laeviplana* and could be either a young specimen of *M. brocchii*, compatible with the 'Helvetian' (= Burdigalian and Langhian) age of the valve, or an unknown species.

Brives (1897, p. 17, pl. 5, figs 2–6) reported *Cardita jouanneti* var. *laeviplana* from the Sahelian of Algeria, remarking on the particularly large, thick shell with a robust hinge, and the radial sculpture lost on the ventral half of the valve, for which he suggested the need of a new variety. This opinion, criticized by Laffitte (1948), who found most material from the Sahelian of Algeria similar to that illustrated by Sacco (1899) from the Tortonian of Italy, was followed by Mongin (1958) with the creation of a var. *brivesi*. In the present work, the large

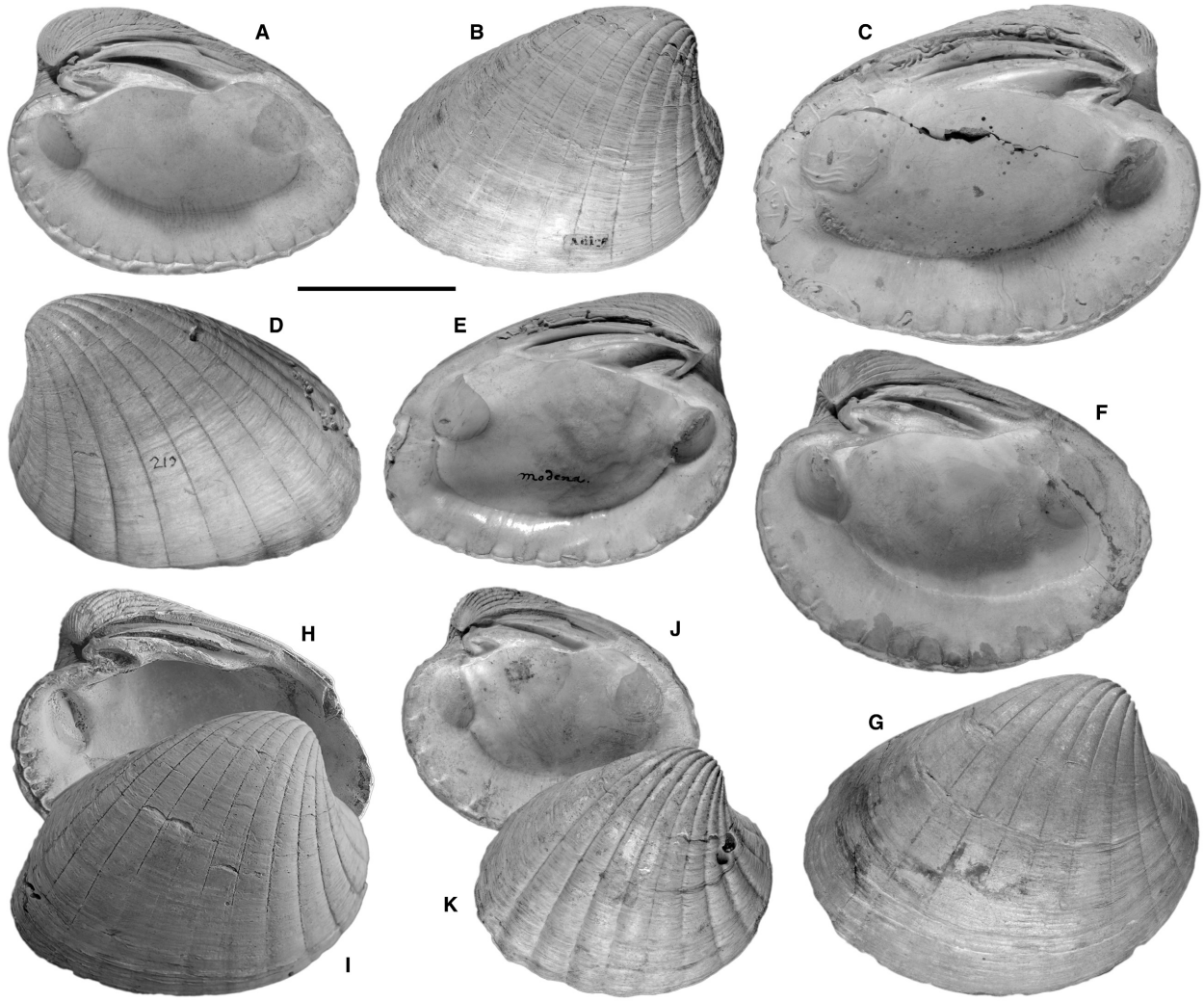

FIG. 21. *Megacardita laeviplana* (Depéret, 1839). A, B, Adiça (NHMW 1886.IV.66). C, Cacela (NHMW 1886.IV.66). D–G, Modena (NHMW 1862.II.45). H, I, Montegibbio (M. Brunetti coll.). J, K, Cabrières-d'Aigues (NHMW C.3867/1882). Scale bar represents 30 mm.

and sturdy Algerian form is considered to be within the range of variability and ontogenetic changes of *M. laeviplana*. Particularly large and sturdy shells of *M. laeviplana* are also known from the Tortonian of Italy (Fig. 19C, D) and, on the other hand, the old Sahelian Stage is now considered to correspond to the Tortonian (Berggren & van Couvering 1974).

Dollfus *et al.* (1903, pl. 19, figs 1–1a; pl. 20, figs 1, 2) illustrated and described *Cardita* (*Venericardia*) *jouanneti* from the Tortonian of Portugal (Adiça and Cacela): large, trigonal valves, exceeding 100 mm in length, with flattish ribs separated by poorly impressed interspaces ('une douzaine de côtes séparés par des sillons sans profondeur'). Large size, trigonal shape and weak sculpture all point to *M. laeviplana*, though the authors stated to have not illustrated var. *laeviplana*, of which specimens from Adiça were available. The valve from Adiça illustrated here (Fig. 21A, B) actually bears about 12 ribs, the posterior ones being almost totally lost. On the other hand, the modern illustrations of *M. laeviplana*, though under the name *M. jouanneti*, by Tavani & Tongiorgi (1963, pl. 23, figs 1–6; pl. 24, fig. 6) and Santos & Mayoral (2007, pl. 2, fig. 2a, b; 2008, fig. 7.1–3) from Cacela, and by Mocho *et al.* (2010, fig. 2h), from Foz de Rogo, testify to the occurrence of *M. laeviplana* in the Tortonian of Portugal, as also reported in older literature, such as Chavan (1940) and Glibert & Van De Poel (1970). Recently, Studencka & Zieliński (2013) dated some levels of the Cacela Formation, confirming the late Tortonian age suggested in the literature, but they also found early Messinian levels at Cabanas, from which they also reported *Megacardita jouanneti*, herein interpreted as *M. laeviplana*.

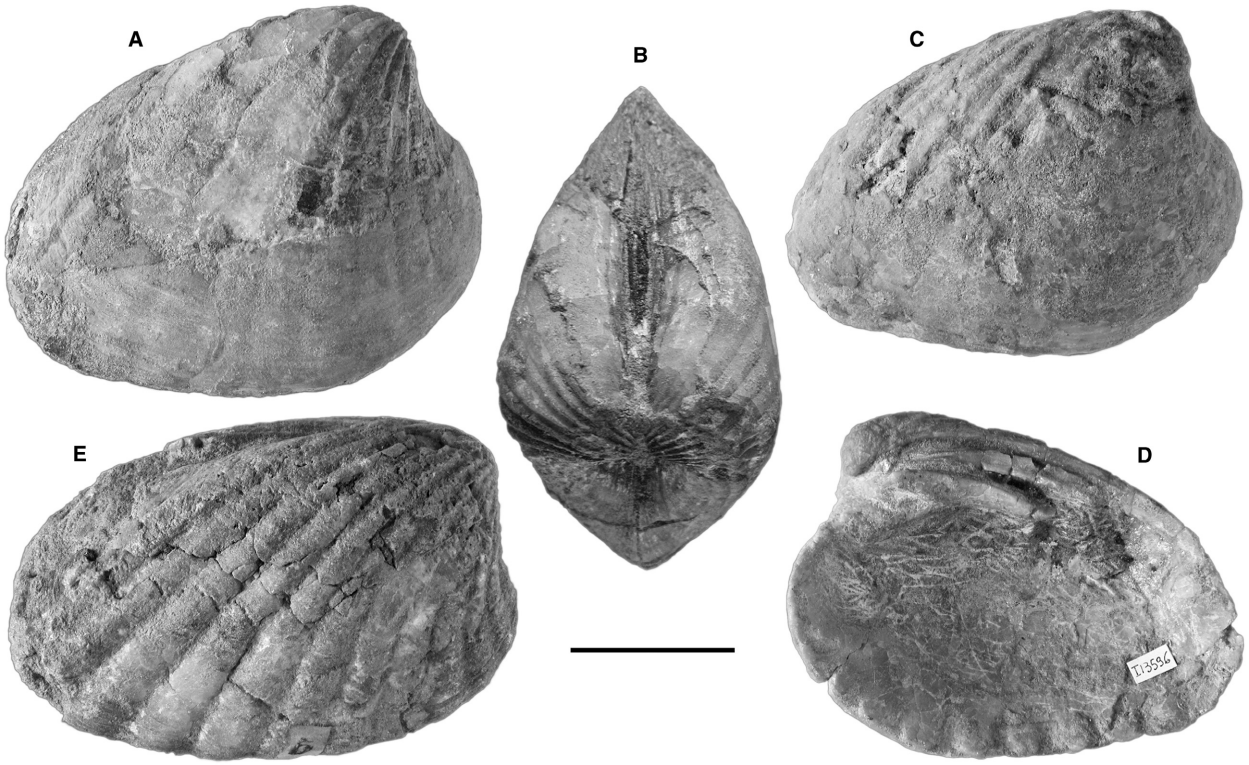

FIG. 22. *Megacardita* spp. A, B, *Megacardita laeviplana* (Depéret, 1839), Ponsano (Tavani & Tongiorgi, 1963, pl. 18, figs 2–3b) (MSNUP I.13587). C, D, *Megacardita laeviplana* (Depéret, 1839), Ponsano (Tavani & Tongiorgi 1963, pl. 18, figs 1–1b) (MSNUP I.13596). E, *Megacardita* sp., Ponsano (Tavani & Tongiorgi 1963, pl. 20, fig. 8). Scale bar represents 30 mm.

Megacardita jouanneti has also been reported from the Tortonian deposits of Provence (Cabrières-d'Aigues, Cucuron, Mont Luberon) (Fischer & Tournouër 1873; Fontannes 1878). The examination of material from Cabrières-d'Aigues (Fig. 21J, K) proved these records to be based on *M. laeviplana*.

Other records are from Montegibbio (Modena), a Tortonian locality in northern Italy (Tavani & Tongiorgi 1963, pl. 24, figs 1–4, 7, 8). Valves from Modena and Montegibbio are also illustrated herein (Fig. 21D–I).

The material of *Megacardita* from the Arenarie di Ponsano Formation, Tuscany, of early Tortonian age (Foresi *et al.* 1997, 2003), studied by Tavani & Tongiorgi (1963, pp 20–24, pls 18–24), is very poorly preserved; most shells are deformed, heavily recrystallized (when not preserved as moulds) and this makes their identification particularly difficult. The authors recognized a single species, *M. jouanneti*, consisting of intergrading forms, ranging from var. *ponderosa* Cossmann & Peyrot to var. *laeviplana* Depéret. The examination of this material led to the identification of *M. laeviplana* (Fig. 22A–D).

The Ponsano material includes another less common species (Fig. 22E), similar in shape to *M. jouanneti*, but with stronger and narrower ribs, lacking the large, and broad umbo of *M. brocchii*. The poor preservation does not allow further details to be examined and this material is left undetermined as *Megacardita* sp. The record of *Venericardia jouanneti* by Stefanini (1916, p. 143, pl. 4, fig. 3), from the Tortonian of Veneto, could be based on this undetermined species, as suggested by the strong ribbing. Concerning the occurrence of *Megacardita* in the Cenozoic sequence of north-eastern Italy, mainly Langhian–Messinian in age (Massari *et al.* 1986), it is worth remembering the 'horizon à *Cardita jouanneti*', in the area of Bassano del Grappa (Veneto), the molluscan fauna of which was studied by de Gregorio (1899). The identity of the *Megacardita* species characterizing this level is unknown.

Occurrence. Megacardita laeviplana is known from the Tortonian – early Messinian of Portugal and from the Tortonian of Italy, France and Algeria.

Megacardita dertavicula (Sacco, 1899)
Figure 23

1899 *Cardita* (*Megacardita*) var. *dertavicula* Sacco, p. 10, pl. 3, figs 6–8.

Material. MRSN (Bellardi & Sacco coll.), syntypes of *Cardita (Megacardita) jouanneti* var. *dertavicula*: BS.126.92.005, S. Agata

Fossili, 1 valve; BS.126.92.006, S. Agata Fossili, 1 valve; BS.126.92.007, S. Agata Fossili, 1 valve; BS.126.02.007/01, S. Agata Fossili, 2 valves, 3 fragments.

Description. The shell is markedly robust, relatively small, not exceeding *c.* 45 mm in length, subtrapezoidal, with strong sculpture consisting of 14–15 convex ribs with rather deep interspaces. The ribs are coarsely beaded on the umbo, becoming obscurely and irregularly nodulose with growth ('subgranosiores'), while near the ventral margin they are mainly crossed by growth striae. The beaded sculpture tends to persist on the anterior ribs.

Remarks. Cardita (*Megacardita*) var. *dertavicula* was described by Sacco (1899, p. 10, pl. 3, figs 6–8) from the Tortonian of S. Agata Fossili, Turin Hills, with the usual differential diagnosis from *Cardita (Megacardita) jouanneti*: 'Testa latitudine brevior; umbones strictiores et recurviores; costae radiales strictiores, subgranosiores, sulcis aliquantulum latioribus et profundioribus disjunctae' (Shell shorter, with smaller and more recurved umbo, radial ribs narrower, obsoletely beaded, separated by wider and deeper interspaces).

The original material (Fig. 23), all from the Tortonian of S. Agata Fossili, Turin Hills, is well preserved.

The sculpture of *M. dertavicula*, including the relatively deep radial interspaces, is similar to that of *M. ignorata* and is also considered to be a persistence of the juvenile sculpture. Most probably, it is not by chance that both species are markedly smaller than the other species, suggesting a heterochronic control (Alberch *et al.* 1979; Klingenberg 1998) in the evolution of both species.

It should be noted that *M. dertavicula* cannot be considered to be a young stage of the coeval *M. laeviplana*. All the available material of var. *dertavicula* (5 valves) is of similar size (40–45 mm); at this size *M. laeviplana* is much more elongate and with a larger umbo, while its sculpture consists of much wider and flatter ribs (Fig. 19G–I).

In some shell characters, *Megacardita dertavicula* seems to be particularly similar to *M. hoernesi* sp. nov. Both species have a well-defined umbo, slightly more slender and incurved than in the other species, and a distinct posterior truncation. In particular, *M. dertavicula* is similar to some Paratethyan forms that occur at Ottakring and Buituri (Fig. 14) due to their sculpture, with more convex ribs and deeper interspaces, and a well-defined posterior truncation. The closeness between the two species is more clearly shown by the short valve of *M. hoernesi* sp. nov. from Buituri (Fig. 14F, G), puzzlingly similar to *M. dertavicula* in shape and sculpture, although less robust.

Because of its relatively small size and short shape, *Megacardita dertavicula* most probably has been misidentified as one of the Neogene carditids with loosely similar

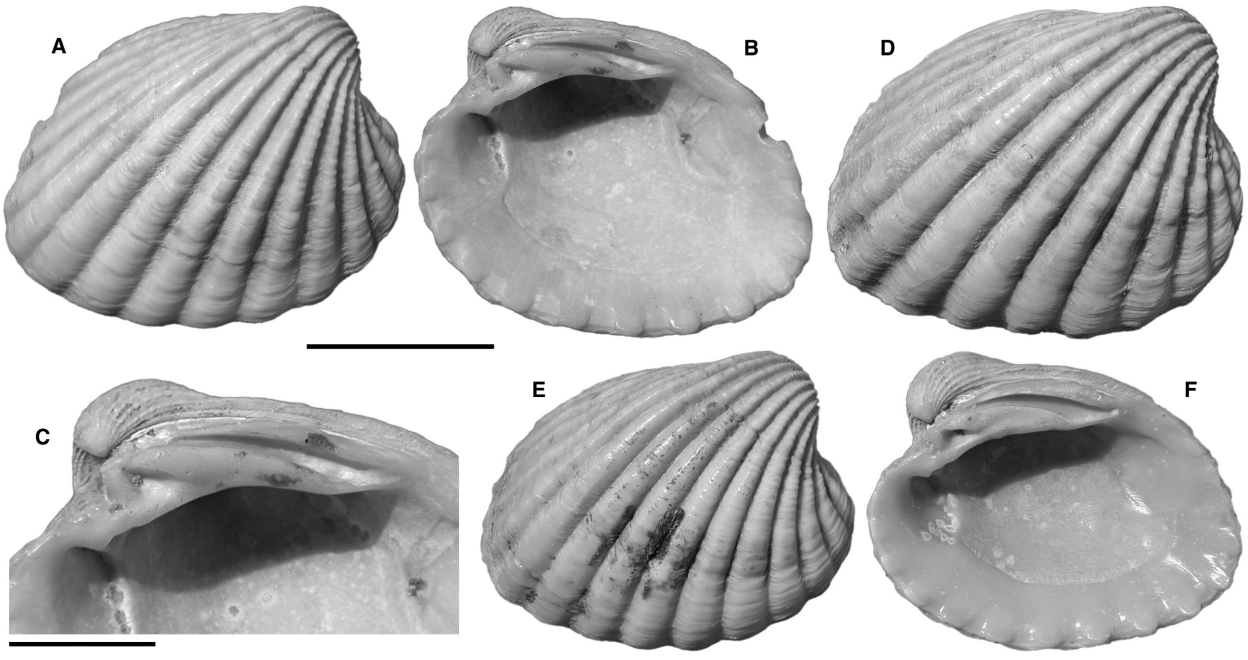

FIG. 23. *Megacardita dertavicula* (Sacco, 1899). A–C, S. Agata Fossili, syntype of *Cardita (Megacardita) jouanneti* var. *dertavicula* Sacco, 1899 (pl. 3, fig. 6) (MRSN BS.126.02.005). D, S. Agata Fossili, syntype of *Cardita (Megacardita) jouanneti* var. *dertavicula* Sacco, 1899 (MRSN BS.126.02.007/01). E, F, S. Agata Fossili, syntype of *Cardita (Megacardita) jouanneti* var. *dertavicula* Sacco, 1899 (pl. 3, fig. 7) (MRSN BS.126.02.006). Scale bars represent: 20 mm (A, B, D, F); 10 mm (C).

shape and sculpture, such as *Cardita pectinata* (Brocchi, 1814) or *C. intermedia* (Brocchi, 1814). However, the record of *Cardita jouanneti* var. *dertavicula* by Sangiorgi (1917) from the Tortonian of Valle dell'Idice, not far from the better known coeval locality of Montegibbio, seems to be correctly based on the present species, as suggested by his brief comments: radial ribs markedly convex, separated by deep and wide interspaces.

Occurrence. Only known from the Tortonian of northern Italy (Piedmont, Emilia Romagna).

Megacardita? *redoniana* nom. nov.
Figures 24, 25

1909 *Cardita striatissima* var. *abbreviata* Dollfus & Cotter, p. 48, pl. 5, fig. 16 (junior homonym of *Cardita abbreviata* Conrad, 1841, and of Emmons, 1858, etc.).
1909 *Cardita striatissima* Cailliaud *in* Mayer; Dollfus & Cotter, p. 48, pl. 5, figs 1–23.
1912 *Venericardia (Cardiocardita) striatissima* (Cailliaud *in* Mayer); Cossmann & Peyrot, p. 183 pl. 4, figs 13, 14.
1981 *Megacardita striatissima* (Cailliaud *in* Mayer); Lauriat-Rage, p. 71, pl. 10, fig. 11; pl. 11, figs 1–3.
1989 *Megacardita striatissima* (Cailliaud *in* Mayer); Lauriat-Rage *et al.*; pl. 4, figs 7, 8.

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Derivation of name. After the Redonian Stage used in the stratigraphy of north-western France.

Material. La Limouzinière, 1 valve (Viaud coll., MNHN.F.R52750); La Limouzinière, 1 valve (Viaud coll., MNHN.F.R52749). Saint-Denis-d'Oléron 'La Morelière', 1 valve (Lauriat-Rage coll., MNHN.F.R50775). Saint-Denis-d'Oléron, 1 valve (Degrange-Touzin coll., MHNBx 2014.10.3808). Saint-Denis-d'Oléron, 6 valves (Degrange-Touzin coll., MHNBx 2014.10.3809.0). Saint-Denis-d'Oléron, 5 valves (Degrange-Touzin coll., MHNBx 2014.10.3810.0).

Remarks. As discussed below, this species has been misidentified as *Cardita striatissima* Mayer, 1868. Dollfus & Cotter (1909, p. 48, pl. 5, fig. 16) described a short form from the Pliocene of Portugal as *C. striatissima* var. *abbreviata*, which is the first available name for the present species. However, *Cardita abbreviata* is multiply preoccupied and a replacement name (ICZN 57.2) is herein proposed: *Megacardita*? *redoniana*.

Mayer (1868, p. 187, pl. 7, fig. 4) described *Cardita striatissima* from several localities in the Loire Basin: Sceaux (Angers), Étangs (La Limouzinière), Dimerie (Saint-Julien-de-Concelles), Cléons (Haute-Goulaine), Vieillevigne. He discussed the age of these deposits, proposing that they could be coeval with the 'falun de Salles' (Serravallian) or with the 'mollasse de l'Anjou' (Tortonian).

Based on its type material (Fig. 26), *Cardita striatissima* proves to be a moderately large species (up to *c.* 30 mm in length), subequilateral, markedly orbicular and convex, not particularly robust, with *c.* 27 narrowly spaced, weakly convex ribs, crossed by closely set regular striae, giving a finely decussate pattern (Fig. 26C). The hinge is apparently similar to that of *Megacardita*, but weaker and differing in some details. Both muscle scars are poorly impressed. Evidently, it is not a *Megacardita* species, and it is also distinct from the species which has been reported, with various combinations (*Venericardia*, *Megacardita* etc.), under this name (Dollfus & Cotter 1909; Cossmann & Peyrot 1912; Lauriat-Rage 1981; Lauriat-Rage *et al.* 1989; to cite only the illustrated reports). The systematic position of *C. striatissima* is unclear, but it shows some resemblance, at least in sculpture, to a group of species with a northern distribution, usually referred to *Cyclocardia* Conrad, 1867 (Janssen & van der Slik 1972; Janssen & Moerdijk 2004; Huber 2010), of which *Scalaricardita* Sacco, 1899 may be a synonym.

In several citations (e.g. Lauriat-Rage 1981; Dollfus & Cotter 1909; Cossmann & Peyrot 1912) the authorship of *Cardita striatissima* has been referred to 'Nyst' or 'Nyst *in* Mayer'. It would appear that the mistake was made first by Dollfus (1901) in a communication to the French Geological Society. Dollfus & Cotter (1909) stated that the species was named by Nyst, on specimens sent to him by Cailliaud, but the first description was published by Mayer. However, there is no mention of this in Mayer (1868), who expressly stated the authorship of *C. striatissima* as 'Cailliaud *in* Mayer'.

The first identifiable record of *Megacardita redoniana* nom. nov., as *C. striatissima*, was by Dollfus & Cotter (1909, p. 48, pl. 5, figs 16–23), who found it to be very common in the Pliocene of the Mondego Basin, Portugal (Aguas Santas, Negreiro, Nabadoiro, Monte Real). They reported an average size of about 30 mm in length, with up to 32 ribs. On material from Negreiro, with smaller size, finer sculpture, shorter shape and thicker shell, they established var. *abbreviata* for which a size of 24 mm in length and 23 mm in height was reported. The species was compared with *Cardita matheroni* Mayer, 1871*b*, occurring in the same deposits, more orbicular and higher than '*striatissima*', with wider ribs, according to the species' interpretation by Dollfus & Cotter (1909). However, their illustrations (pl. 4, figs 21–26) seem to match the original description of *C. matheroni* (Mayer 1871*b*, p. 202). The age of the Pliocene deposits of the

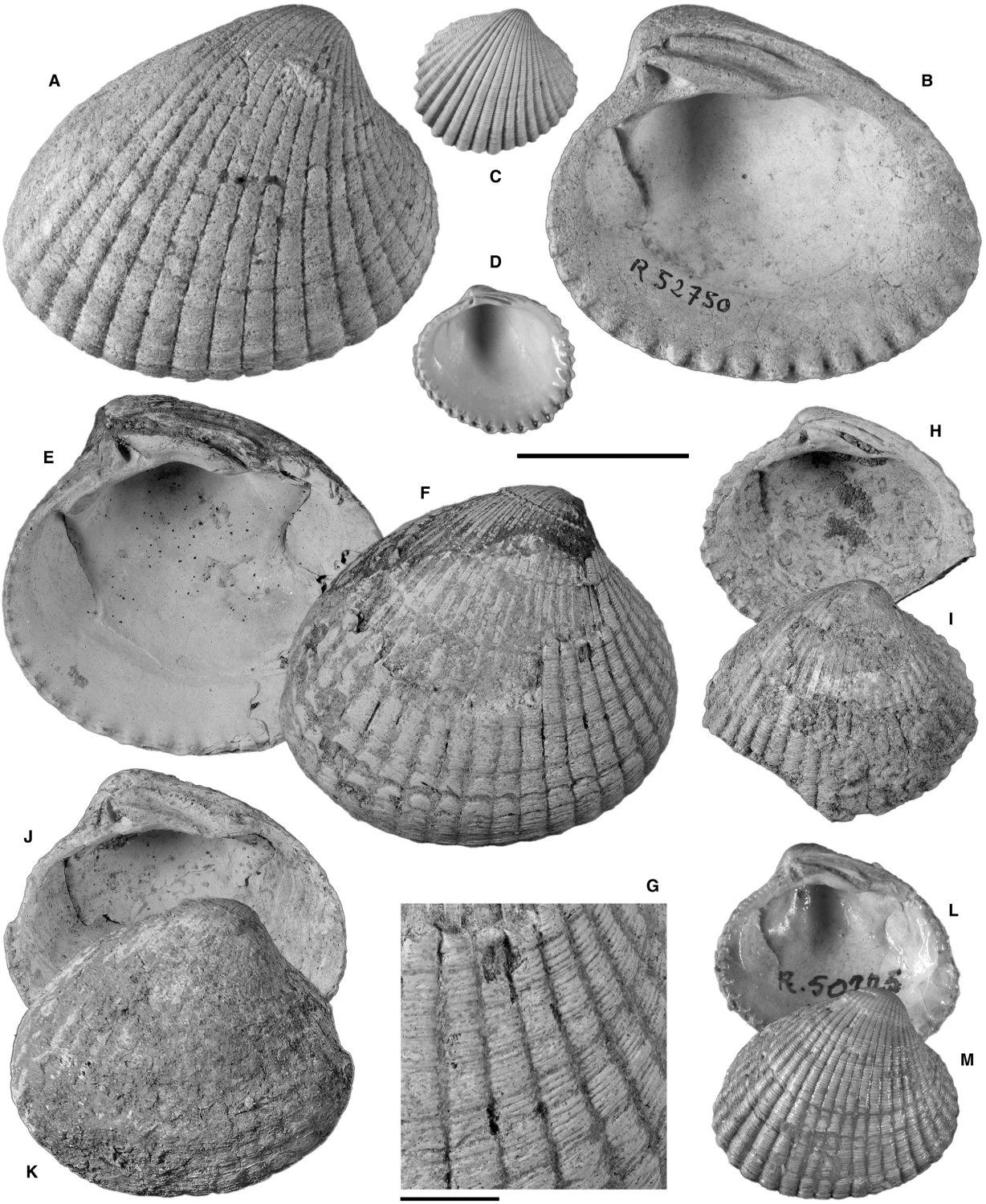

FIG. 24. *Megacardita*? *redoniana* nom. nov. A, B, La Limouzinière (Lauriat-Rage *et al.* 1989, pl. 4, figs 8a,b) (Viaud coll., MNHN.F.R52750, photo P. Massicard). C, D, La Limouzinière (Lauriat-Rage *et al.* 1989, pl. 4, figs 7a,b) (Viaud coll., MNHN.F.R52749, photo P. Massicard). E–G, Saint-Denis-d'Oléron (Cossmann & Peyrot 1912, pl. 4, fig. 13–14) (Degrange-Touzin coll., MHNBx 2014.10.3808, photo L. Charles). H, I, Saint-Denis-d'Oléron (Degrange-Touzin coll., MHNBx 2014.10.3809.3, photo L. Charles). J, K, Saint-Denis-d'Oléron (Degrange-Touzin coll., MHNBx 2014.10.3809.1, photo L. Charles). L, M, Saint-Denis-d'Oléron La Morelière (Lauriat-Rage 1981, pl. 11, fig. 2) (Lauriat-Rage coll., MNHN.F.R50775, photo P. Massicard). Scale bars represent: 20 mm (A–F, H–M); 5 mm (G).

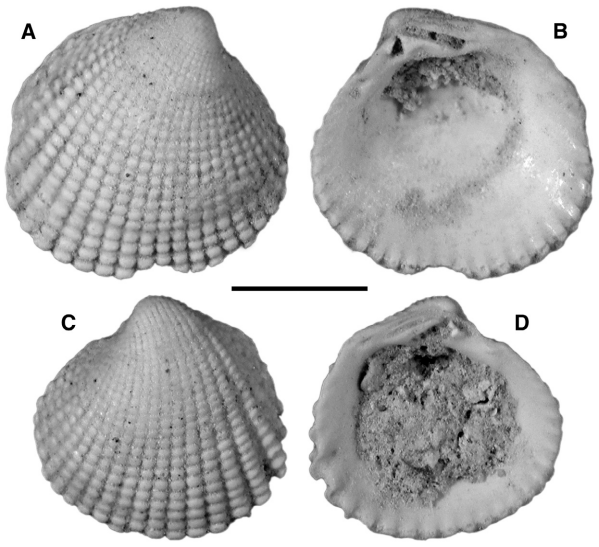

FIG. 25. *Megacardita*? *redoniana* nom. nov. A, B, Saint-Denis-d'Oléron (Degrange-Touzin coll., MHNBx 2014.10.3810.5, photo L. Charles). C, D, Saint-Denis-d'Oléron (Degrange-Touzin coll., MHNBx 2014.10.3810.4, photo L. Charles). Scale bar represents 2 mm.

Mondego Basin is now referred to the latest Zanclean – Piacenzian (Silva *et al.* 2010).

The next record was by Cossmann & Peyrot (1912, p. 183, pl. 4, figs 13, 14), as *Venericardia* (*Cardiocardita*) *striatissima*. For this species, which was said to be typical of the Redonian deposits of western France, they remarked on a rather wide variability: 'A Gourbesville, le galbe de la coquille varie beaucoup ... nous avons un individu presque identique à celui d'Oléron, sauf qu'il est plus fraîchement conservé, et à côté, des individus beaucoup plus globuleux, plus obliquement transverses. Dans la Loire-Inférieure ... le nombre des côtes est supérieur, la forme des valves est tout à fait oblique, et nous pensons qu'il s'agit d'une espèce différente'. They illustrated one valve from Saint-Denis-d'Oléron (Fig. 24E, F), notably larger (47 mm) than those of Dollfus & Cotter (1909). This is the largest valve among the material of '*Cardita striatissima*' in the Degrange-Touzin coll. (MNHBx), all from Saint-Denis-d'Oléron. Other valves (Fig. 24H–K) are in the range of 25–40 mm and are closely similar to the valves illustrated by Dollfus & Cotter (1909, p. 48, pl. 5, figs 16–23) from the Pliocene of Portugal. Smaller valves, 4–10 mm in length, are also present in the same lot (Fig. 25A–D).

Large valves from Palluau and La Limouziniere (both south of Nantes) were illustrated by Lauriat-Rage (1981) and Lauriat-Rage *et al.* (1989), as *Megacardita striatissima*, one of which is illustrated herein (Fig. 24A, B). These large and robust valves closely recall *Megacardita*, but they differ in shape by being trigonal, weakly elongate, not markedly inequilateral. The radial ribs are notably

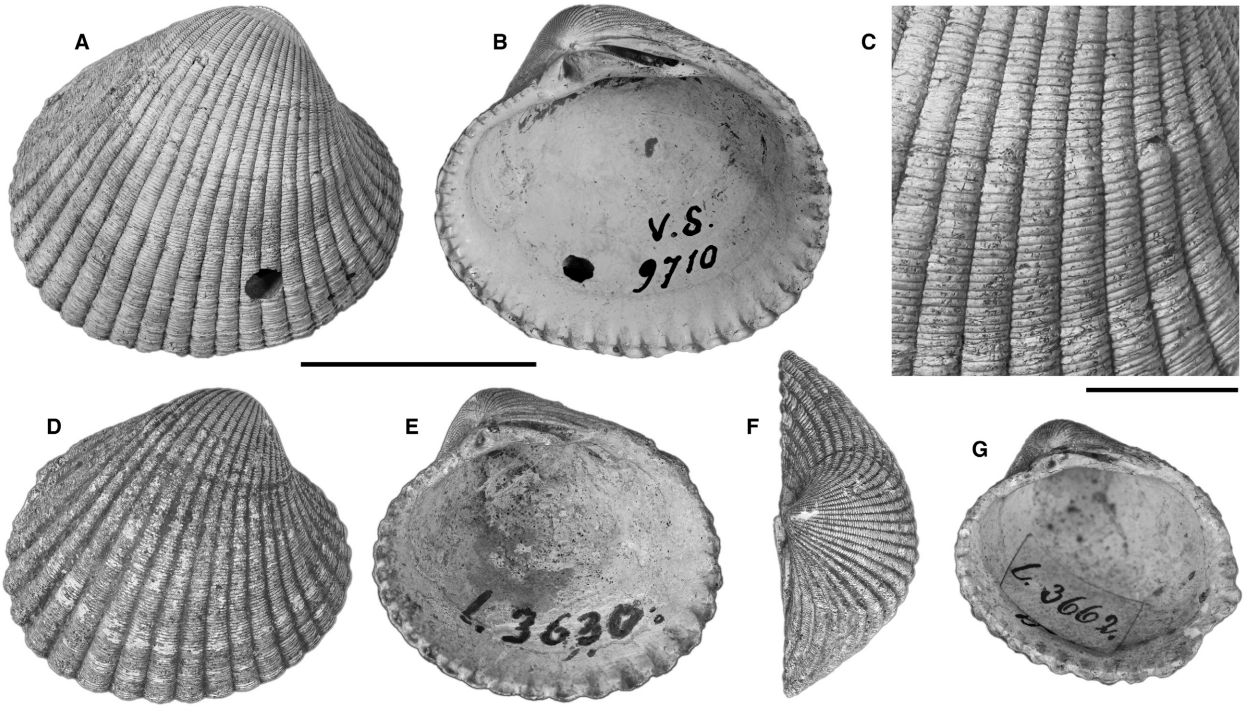

FIG. 26. *Cardita striatissima* Cailliaud *in* Mayer, 1868. A–C, Viellevigne, syntype (Mayer coll., NMB VS-9710, photo W. Etter). D–F, Viellevigne, syntype (Mayer, 1868, pl. 7, fig. 4) (Mayer coll., NMB L-3630, photo W. Etter). G, syntype (Mayer coll., NMB L-3662, photo W. Etter). Scale bars represent: 20 mm (A, B, D–G), 5 mm (C).

more numerous, *c.* 30, and narrower, while the posterior slope is much less distinct than in species of *Megacardita*. Although the anterior muscle scar is more deeply impressed than the posterior one, the difference is less marked than in the other species referred here. Other differences can be seen in the juvenile stages; although similar to the early sculpture of *M. jouanneti* (Figs 4, 15A–B) and of *M. hoernesi* sp. nov. (Fig. 15C, D), the beaded sculpture of *M. redoniana* nom. nov. is much more uniform and regular in strength all over the shell surface and the ribs are very closely set. The beaded sculpture becomes flatter and flatter with growth, producing the decussate pattern seen in the larger valves (Fig. 24G), which is similar to that of *C. striatissima* (Fig. 26C), but finer, less distinct and less regular. Conversely, in most of the other species referred to *Megacardita* the beaded sculpture disappears rapidly with growth, to be replaced by growth striae, with the partial exception of *M. ignorata* and *M. dertavicula*, where the beaded sculpture is more persistent with growth.

The shell characters so far commented on suggest a distinct position for this species, which is then only tentatively referred to *Megacardita*. It seems rather similar, particularly in its younger stages, to the living West African species *Cardita monodi* Nicklès, 1953. If this similarity is confirmed by further studies, the Redonian species could find a better systematic position in a distinct genus.

Further investigation of this species is also needed not only for better understanding its systematic position, but also to clarify the meaning of its variation, as reported in the literature. Lauriat-Rage (1981) remarked on the occurrence of geographical variations: smaller valves, with a more rounded shape, are found in the inner part of the Loire Basin, while larger, more elongate valves are found in deposits near the coast. It is not clear why Dollfus & Cotter (1909) reported only small valves from Portugal, in spite of the species' frequency in the Pliocene deposits. Likewise, it is not clear whether the variability recorded by Cossmann & Peyrot (1912) has something to do with that remarked on by Lauriat-Rage (1981), and whether such alleged variability could be due to the occurrence of distinct species.

According to Cossmann & Peyrot (1912), the species listed by Degrange-Touzin (1906) as '*Venericardia duboisi* Deshayes, 1852' from Ile d'Oléron is *Cardita striatissima* (i.e. *Megacardita redoniana* nom. nov.) However, *V. duboisi* was proposed by Deshayes (1857, p. 180) as a replacement name for *Venericardia intermedia* 'Basterot' by DuBois de Montpéreux (1831, pp 61–62, pl. 5, fig. 20), a name pre-occupied by *intermedia* Brocchi, 1814. However, Du Bois de Montpéreux's *intermedia*, illustrated well by Friedberg (1936, p. 95, pl. 17, figs 4–6) is clearly distinct from the present species.

A synthesis of the problem involving the age of the Redonian stage was recently provided by Monegatti & Raffi (2007, 2010). Based on a wide review of data in the literature, including studies of strontium isotopes (Néraudeau *et al.* 2003), they concluded that the Redonian of north-western France largely correlates with the Messinian and/or Zanclean.

Occurrence. Megacardita redoniana nom. nov. is known from the Redonian (Messinian–Zanclean) of western France, and the Early–Middle Pliocene of Portugal.

DISCUSSION

Origin and distribution

The origin of *Megacardita* remains obscure and only a deeper knowledge of fossil carditids could provide a sound basis for the systematics and evolutionary history of the European Venericardiinae, including *Megacardita*. The Palaeogene genus *Venericor* probably deserves a place in the ancestry of *Megacardita*, but closer relationships should be tracked down among the Oligocene and Early Miocene carditids. In this regard, the morphological similarities between *Megacardita* and *Cardita zelebori* Hoernes, 1865 (Hoernes 1865, p. 267, pl. 36, fig. 1a–d) from the middle Eggenburgian (early Burdigalian) of Loibersdorf, north-eastern Austria (Fig. 27) are worthy of remark. It is a moderately large species (up to *c.* 50 mm long), apparently similar to *Megacardita*, but differing in several respects: the umbo is much smaller and pointed; both muscle scars are of similar depth (i.e. no anterior thickening); and the shape is poorly elongate and much less inequilateral. The radial ribs are not markedly different from those of *Megacardita*, but are more numerous (*c.* 27), while the commarginal sculpture is more evident and somewhat lamellose. The hinge, not particularly well preserved in the study material, also seems to be similar to that of *Megacardita*, but the cardinal tooth 3a is antero-posteriorly elongate (instead of dorso-ventrally) and 3b is notably more elongate (instead of stout and strongly triangular) (Fig. 27G). Because of its poor state of preservation, it is not clear whether the early beaded sculpture of *Megacardita* is also present in *C. zelebori*. Schaffer (1910, p. 60, pl. 28, figs 5–12) described var. *planata* and var. *percostata* (Fig. 27C), both apparently falling within the variability range of *C. zelebori*. Recently referred to *Megacardita* by Pfister & Wegmüller (1998), this species most probably deserves a distinct genus. It is a representative of the Venericardiinae, as indicated by the hinge characters (the lunule is probably penetrating, but this character is not well seen). For the time being, *C. zelebori* seems the closest species to

Megacardita, not only morphologically, but also stratigraphically and geographically.

The oldest available records for *Megacardita*, those of *M. guenterti* from the middle Burdigalian of Switzerland and Germany (Western Paratethys), and of *M. brocchii* from the late Burdigalian of northern Italy (Piedmont–Liguria Basin) (Fig. 28A), with the addition of the records from the Burdigalian of Provence (Liguro–Provençal Basin), though of doubtful identity, point to the central European basins as the radiation centre for the genus (Fig. 28B). It should be remarked that all the Burdigalian records are from closely adjacent and well interconnected basins (Rögl 1998; Steininger & Wessely 2000), favouring the diffusion of benthic species lacking free larval stages, such as the Carditidae, many species of which brood their eggs (Yonge 1969; Jones & Thompson 1987).

The main documentation for the Langhian is represented by *Megacardita hoernesi* sp. nov., which occurred all through the Badenian, that is, early Langhian to middle Serravallian in the standard geological time scale (Piller *et al.* 2007) (Fig. 28A), of Central Paratethys, from the north-western sectors (Alpine–Carpathian Foredeep and Vienna Basins) east to the Transylvanian Basin (Fig. 28B). With this species, *Megacardita* reached its northernmost distribution, up to about 47°, most probably thanks to the favourable climatic conditions that characterized most of the Badenian interval, the Miocene Climatic Optimum (Harzhauser *et al.* 2011; La Perna 2016). The records of *M. brocchii* from the Langhian of the Turin Hills and of '*Cardita jouanneti*' from the Helvetian of Reggio Calabria (southern Italy) by Seguenza (1879, p. 74), testify to the occurrence of *Megacardita* in the Mediterranean during the early Middle Miocene (Fig. 28B).

By the Serravallian, *Megacardita* reached the north-eastern Atlantic (Aquitaine and Loire basins), evidently through the wide seaway between the Iberian Peninsula and North Africa (Fig. 28B). The north-eastern Atlantic species are *M. jouanneti* and the small *M. ignorata*, the former known from the Aquitaine and the Loire Basins, the latter only from the Aquitaine Basin.

The late Badenian (early–middle Serravallian) records of *M. hoernesi* sp. nov. from the Vienna Basin and other areas throughout central-eastern Europe represent the last occurrence of the genus in the Central Paratethys, before the transition of the Paratethys to restricted marine conditions in the late Serravallian (Piller & Harzhauser 2005; Popov *et al.* 2006). Conversely, during the Tortonian, *Megacardita* persisted in the Mediterranean (northern basins south to North Africa) and in the north-eastern Atlantic (Portugal), with *M. laeviplana*. It was the species with the widest geographical distribution, although apparently not as common and locally abundant in the molluscan assemblages as *M. hoernesi* sp. nov. and *M. jouanneti*. There is evidence that *M. laeviplana* ranged up to the early Messinian in the north-eastern Atlantic (Studencka & Zieliński 2013) and it was probably also present in the Mediterranean during most of the Messinian, since isolation from the Atlantic Ocean took place between 5.59 and 5.33 Ma, while the evaporitic deposition occurred 5.50–5.33 Ma, in the latest Messinian (Krijgsman *et al.* 1999).

Megacardita laeviplana was not the only species occurring in the Tortonian, as another species, the small *M. dertavicula*, is known from the Tortonian of northern Italy. However, our knowledge of the Late Miocene species is probably not complete, as suggested by the undetermined species from the Tortonian of Ponsano (*Megacardita* sp.), which could represent a distinct species. There are other Late Miocene records whose identity cannot be ascertained, such as those from southern Italy (Seguenza 1879), from north-eastern Italy (Stefanini 1916) and from southern Sardinia (Lovisato 1902; Barca *et al.* 2005). An additional species probably also occurred in the Tortonian of Portugal, as suggested by the large valves misidentified by Dollfus *et al.* (1903) as *Cardita jouanneti* var. *brocchii*.

Such a palaeobiogeographical distribution, within adjacent and interconnected basins, may explain the marked similarity between these species, whose morphology is partly overlapping, as seen in particular for *M. jouanneti* and *M. hoernesi* sp. nov. Exceptions are only represented by *M. ignorata* and *M. dertavicula*, which differ markedly mainly by their smaller size and less inequilateral shape. The same general morphological similarity prevents us from recognizing precise relationships among these species; it can only be supposed based on their stratigraphical and geographical distribution. *Megacardita hoernesi* sp. nov. probably evolved from one of the Burdigalian species, *M. brocchii* or *M. guenterti*, while *M. jouanneti* probably evolved from *M. hoernesi* sp. nov. The other Atlantic species, *M. ignorata*, can be considered an offshoot of *M. jouanneti*. The origin of *M. laeviplana* is unclear, as a tendency to obsolete radial sculpture is observed in both *M. jouanneti* and *M. hoernesi* sp. nov. If it is considered to be a shared character, *M. laeviplana* is more likely to be of Atlantic origin, from *M. jouanneti*. However, as discussed above, the Late Miocene species were probably more numerous than so far recognized, and thus *M. laeviplana* might have evolved from another, unknown ancestor. The other Tortonian species, *M. dertavicula*, appears to be more similar to *M. hoernesi* sp. nov., rather than to the coeval *M. laeviplana*, although a direct relationship between the Badenian species and the Tortonian one is difficult to explain.

Very little can be said about the Badenian *M.*? *laticosta* from the westernmost sectors of the Central Paratethys. It seems rather loosely related to the other species so far discussed, appearing instead morphologically closer to the

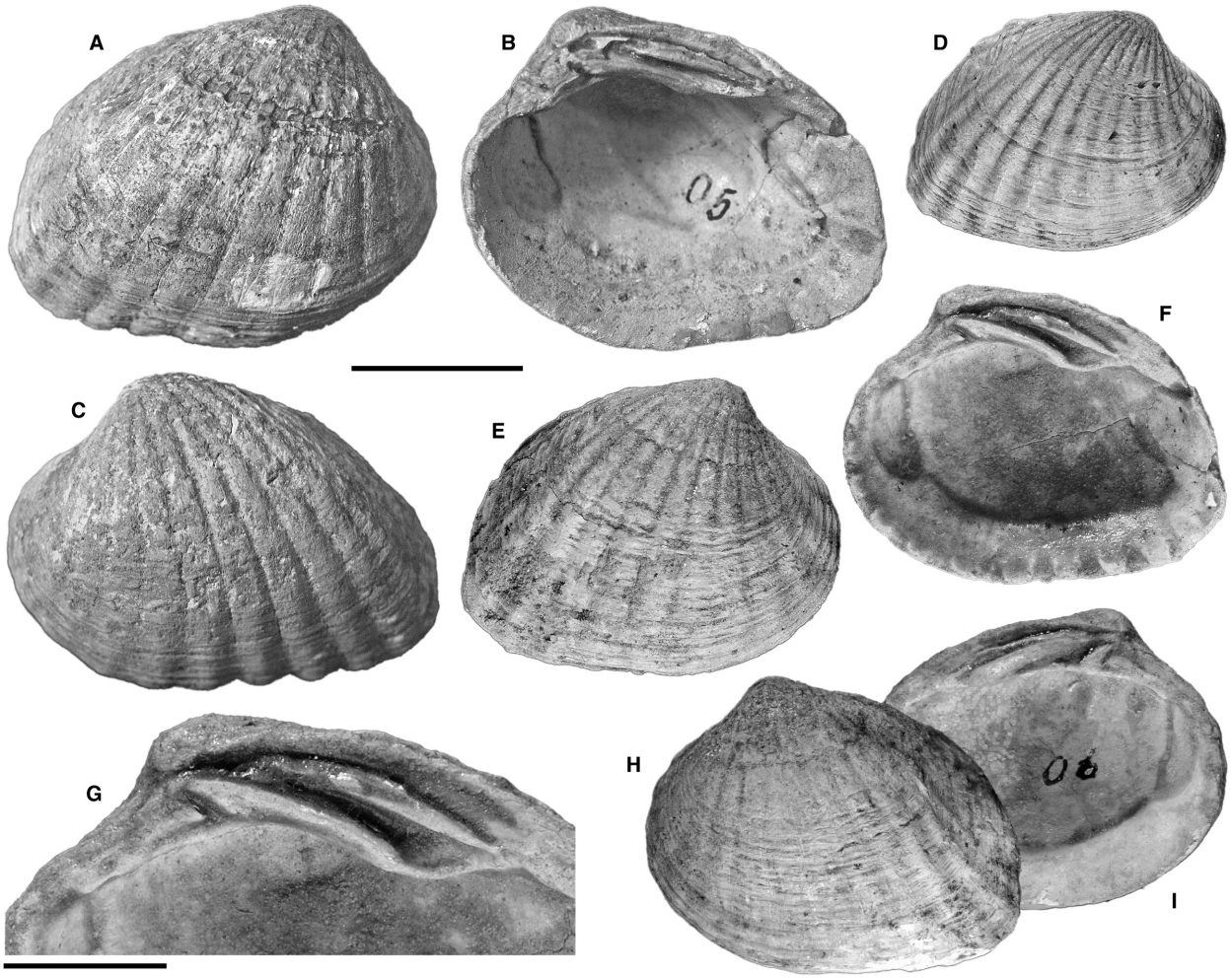

FIG. 27. *Cardita zelebori* Hoernes, 1865, Loibersdorf, syntypes (NHMW 1846.X.21). Scale bars represent: 20 mm (A–F, H, I), 10 mm (G).

Carditinae, as suggested by its radial sculpture. This subfamily only includes byssally-attached species (Yonge 1969; Stanley 1972; Huber 2010), mytiliform in shape and with a strong radial sculpture bearing tubercles, spines and scales. The morphological similarity of *M.*? *laticosta* to *Megacardita* is possibly the result of convergence, due to adaptation to an infaunal habit and this species could then represent an interesting case of free-burrowing adaptation in the Carditinae.

The other species doubtfully assigned to *Megacardita*, *M.*? *redoniana*, possibly represents another distinct lineage, tentatively considered to be related to the living species *Cardita monodi*.

Adaptive trends

Heinberg (1993) described the main adaptive pathway of the Carditidae as 'a pendulating evolutionary history with adaptational shifts from an infaunal mode of life to an epifaunal mode, and back again'. With *Megacardita*, the family reached one of its best adaptions to a free burrowing mode of life. This is clearly suggested by its elongate, streamlined shell with relatively weak radial sculpture, tending to be mostly lost in the latest representative, *M. laeviplana*. Interestingly, the oldest species *M. brocchii* and, most probably also *M. guenterti*, had markedly stronger ribs, compared with the Middle Miocene species, *M. jouanneti* and *M. hoernesi* sp. nov., which also show a tendency to obsolete radial ribs. In addition to large size and sturdy, heavy shell, evidently related to stability in soft bottoms (Seilacher 1984; La Perna 2006), *Megacardita* also possessed an unusual character: thickening of the anterior area (Fig. 5), producing a sort of 'ballasting effect' enhancing stability, most probably to compensate for the lack of a functional byssus in the adult stage. Apparently, the resulting stability was so great that the shells easily remained in life position after death, allowing

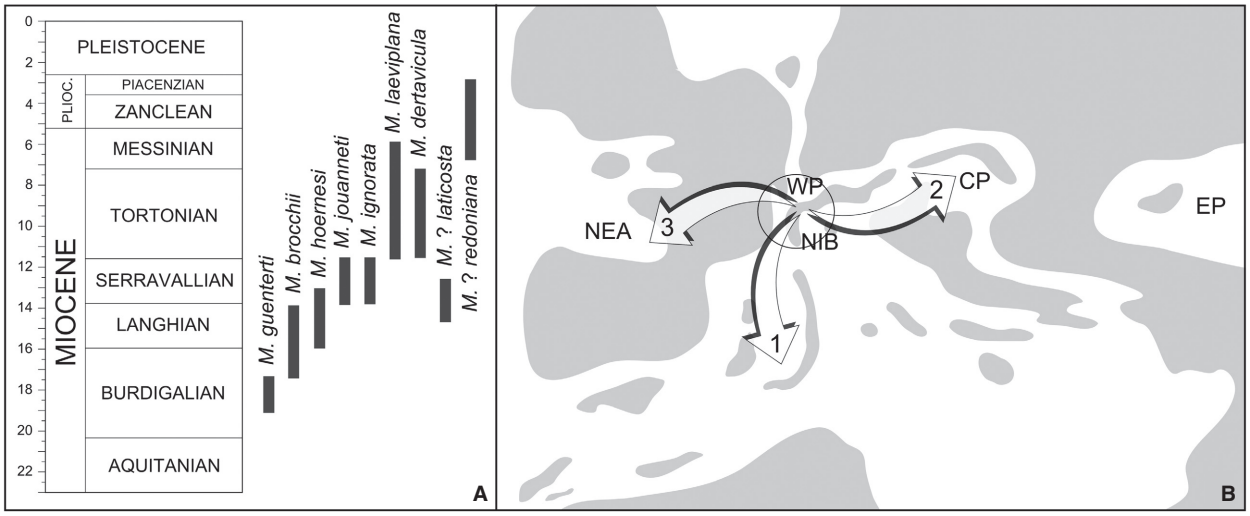

FIG. 28. A, stratigraphical distribution of *Megacardita* species. B, palaeogeographical scheme of the circum-Mediterranean area in the late Burdigalian (re-drawn after Rögl 1998) with the main directions of diffusion of *Megacardita* from the supposed radiation centre (circle). Legend: 1, Mediterranean (since late Burdigalian); 2, Central Paratethys (since Langhian); 3, Aquitaine and Loire basins (since Serravallian); NEA, north-east Atlantic; NIB, northern Italy basins; WP, Western Paratethys; CP, Central Paratethys; EP, Eastern Paratethys.

the posterior tip to be bioeroded strongly, as described for some shells of *M. jouanneti* (Fig. 7).

Conversely, the strongly ribbed and poorly elongate Tortonian species, *Megacardita dertavicula*, and at least in part also the Serravallian species *M. ignorata*, possibly represent a shift to a different burrowing strategy, more similar to that of most roundish, ribbed carditids, most of which are also smaller (Stanley 1972; Heinberg 1993), probably in relation to a coarser substrate.

A similar evolutionary pathway to free burrowing habits has been followed independently by other groups of carditids, leading to species morphologically similar to *Megacardita*. It is likely that most of the large fossil and living species previously referred to *Megacardita*, discussed above, are simply convergent with this genus, due to a similar free burrowing adaptation. Another example can be provided by the large and robust carditids referred by Popov (1983) to the new genus *Ainicardita*, from the Early Miocene of the Kamchatka Peninsula, grossly similar to *Megacardita* in sculpture and shape. Evidently, only careful comparative studies, aiming to point out shared characters and distributions, both geographically and stratigraphically, will help to reconstruct the evolutionary history of these distinct groups, providing a basis for their systematics.

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