Cretaceous Research 75 (2017) 31–44

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Amended diagnosis of *Colveraia variabilis* Klinghardt, 1921 (Bivalvia) from Friuli (NE Italy) and redescription of *Colveraia darendeensis* Karacabey, 1974 from Turkey: Taxonomy, comparisons and biogeography

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ARTICLE INFO

Article history:
Received 12 October 2016
Received in revised form
6 March 2017
Accepted in revised form 12 March 2017
Available online 14 March 2017

Keywords:
Rudist
Radiolitidae
Description
Late Campanian
Tethys

ABSTRACT

An examination of the historical material of *Colveraia variabilis* Klinghardt, 1921 housed in the collections of the Steinmann Institute of Palaeontology (Bonn, Germany) and of some newly collected specimens from the type area of Mt. Jouf (Friuli, NE Italy) has revealed many previously unknown characters of this radiolitid. Klinghardt had only large fragments of *Colveraia variabilis* at his disposal and he erred in some respects, mainly by mistaking the upper valve for the lower one. Representatives of the genus *Colveraia* have been collected at different localities of the Central-Eastern Mediterranean Tethys and the Arabian Plate, but the majority of these have never been described in detail or have been identified solely on the basis of transverse sections, except in Turkey, where many well-preserved specimens have been recovered. Historical and new examples of *Colveraia variabilis* from Mt. Jouf and the material recovered from Turkish localities show different external characters as far as radial zone, general shell shape and ornamentation are concerned. These lead us to assign all Turkish specimens to *Colveraia darendeensis* Karacabey, 1974, which is here described in detail. Comparisons with congeneric forms from the Central-Eastern Mediterranean Tethys and the Arabian Plate are also made.

1. Introduction

The radiolitid genus *Colveraia* was erected by the German palaeontologist Klinghardt almost a century ago (Klinghardt, 1921). The historical type locality of the genus discussed here is a small quarry near the Colvera torrent (Mt. Jouf area, Friuli, NE Italy), long since disused. In addition to Friuli, *Colveraia variabilis* has been recorded in Apulia, southern Italy (Sladić-Trifunović and Campobasso, 1980), Slovenia (Pleničar, 1963, 2005), Croatia (Sladić-Trifunović, 1981b, 1987; Moro et al., 2005), Bosnia-Herzegovina (Slišković, 1984), Romania (Lupu, 1970), Turkey (Karacabey, 1974, Karacabey-Öztemür, 1980; Özer, 1988b, 2002; Özer et al., 2008, 2009), Iran (Khazaei et al., 2010) and the United Arab Emirates (Morris and Skelton, 1995).

A number of specimens of *C. variabilis* recovered at different localities were identified solely on the basis of transverse sections (mostly left valve), except in Turkey, where entire, well-preserved examples were collected. There are a few significant morphological differences between the material of this species from Friuli and that from Turkey (Tarlao et al., 2014). Klinghardt (1921) was correct in assigning the genus *Colveraia* to the Radiolitidae. It is currently (Skelton, 2013a) placed in a group that includes also *Klinghardtites* Lupu, 1971, *Balabania* Karacabey-Öztemür, 1980, *Hatayia* Karacabey-Öztemür and Selçuk, 1981 and *Branislavia* Sladić-Trifunović, 1981a.

When screening figures and tables in Klinghardt's paper (1921), it can be noted that he had no intact, well-preserved specimens of *Colveraia variabilis* at his disposal, but only more or less large shell fragments. This explains why Klinghardt failed to describe all morphological features of this species adequately, and despite his punctilious diagnosis he erred in some respects, particularly when mistaking the upper valve for the lower one (Tarlao et al., 2014). It should also be noted that Klinghardt (1921) did not designate a holotype for *Colveraia variabilis*.

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http://dx.doi.org/10.1016/j.cretres.2017.03.012
0195-6671/

The aim of the present study is threefold: i) provide an amended diagnosis and taxonomic revision of *Colveraia variabilis* from the Mt. Jouf area on the basis of a single historical specimen housed in the Goldfuss Museum (Steinmann Institute of Palaeontology, Bonn) and a few newly collected examples from near Forcella di Pala Barzana (Mt. Jouf area), ii) compare material of *Colveraia variabilis* from Mt. Jouf with Turkish specimens that have previously been referred to as *Colveraia variabilis* and *Colveraia darendeensis* Karacabey, 1974, and iii) provide a brief discussion of other specimens and species of *Colveraia* from a number of countries.

2. Geological setting and stratigraphy

Geological data on the Mt. Jouf area and the Turkish regions are as follows:

2.1. Mt. Jouf, NE Italy

Specimens of *Colveraia variabilis* collected by Klinghardt (1921) and recently by ourselves stem from the Colvera torrent and near Forcella di Pala Barzana, respectively (Fig. 1). The most recent paper on the stratigraphic succession and rudist assemblages of the Mt. Jouf area is that by Swinburne and Noacco (1993). Most of the Mt. Jouf area consists of Cretaceous limestones assigned to the Calcari del Monte Cavallo Formation (?Albian–Campanian/Maastrichtian). This formation was subdivided by Swinburne and Noacco (1993) into four lithostratigraphic units. According to those authors, and on the basis of our own work, unit 4 (*c.* 45-m-thick) contains a rich and diverse fauna of radiolitids (among which, besides *Colveraia variabilis*, are *Joufia reticulata* Böhm, 1897, *Pseudopolyconites* sp., *Sauvagesia* sp.), less abundant hippuritids (*Pironaea polystyla* Pirona, 1868, *Hippuritella lapeirousei* Goldfuss, 1840), *Plagioptychus* sp. and rare requieniids. Unit 4 limestones are mostly coarse grained (rudstone, grainstone and packstone) and well washed, and consist of rudist fragments, echinoderm ossicles, micritised orbitoids and poorly preserved foraminifera, including *Siderolites* cf. *vidali* (see Swinburne and Noacco, 1993). Graded bioclastic, storm-related beds were also recognised. The texture of the coarse rudist-rich calcirudites and calcarenites of unit 4 indicates a high-energy subtidal depositional setting. An open-marine environment is suggested by the presence of rare planktonic foraminifera.

Unit 4 was dated by strontium isotope stratigraphy (SIS) of samples of rudist shells (Swinburne and Noacco, 1993). The numerical ages derived from geochemical analyses calibrated with the chronostratigraphy of the time suggested an age close to the Campanian/Maastrichtian boundary or earliest Maastrichtian ($^{87}Sr/^{86}Sr$ mean = 0.707682 and an age mean = 72.61 Ma). The contribution by Swinburne and Noacco (1993) represents one of the first pioneering studies that carried out SIS analysis, despite the fact that Steuber and Schlüter (2012) expressed some doubts over the overall quality of their data. Despite this, the rudist assemblage of unit 4 in the Mt. Jouf area may be reasonably placed in the *Hippuritella lapeirousei* interval zone (upper Campanian–lowermost Maastrichtian) as proposed by Steuber and Schlüter (2012) for rudist biozones of the Central-Eastern Mediterranean.

2.2. Turkey

Well-preserved specimens of *Colveraia* were collected mostly in eastern Anatolia around Hekimhan-Darende-Balaban-Yazıhan-Yeşilyurt in the Malatya Basin (Fig. 2). There are also some specimens from Gürün in the Sivas Basin (eastern Anatolia) and Çerkeş (Çankırı Basin, northeast-central Anatolia).

The Malatya Basin is located in the eastern part of the Anatolide-Tauride platform (or block) where the rudist-bearing Campanian–Maastrichtian transgressive mixed siliciclastic-carbonate sequences unconformably overlie ophiolitic, metamorphic and Mesozoic sedimentary rocks. From the bottom to the top, the diachronous sequence consists of reddish clastics, neritic limestones, sandy limestones with rudists and pelagic mudstones with planktonic foraminifera (Akkuş, 1971; Özer, 1983, 1988a, 2002; İzdar and Ünlü, 1985; Görmüş, 1990, 1992; Bozkaya and Yalçın, 1992; İnan et al., 1996; Meriç and İnan, 1997; Yıldız and Özdemir, 1999; Akyazı and Özgen-Erdem, 2003, 2009; Sarı et al., 2016). The clastic rocks are characterised by poorly to moderately sorted reddish, thick-bedded, matrix supported conglomerates, thin to thick-bedded, poorly sorted sandstones and thin to thick-bedded well-consolidated mudstones. Conglomerates predominate in this unit and interfinger with sandstones and mudstones. The thickness

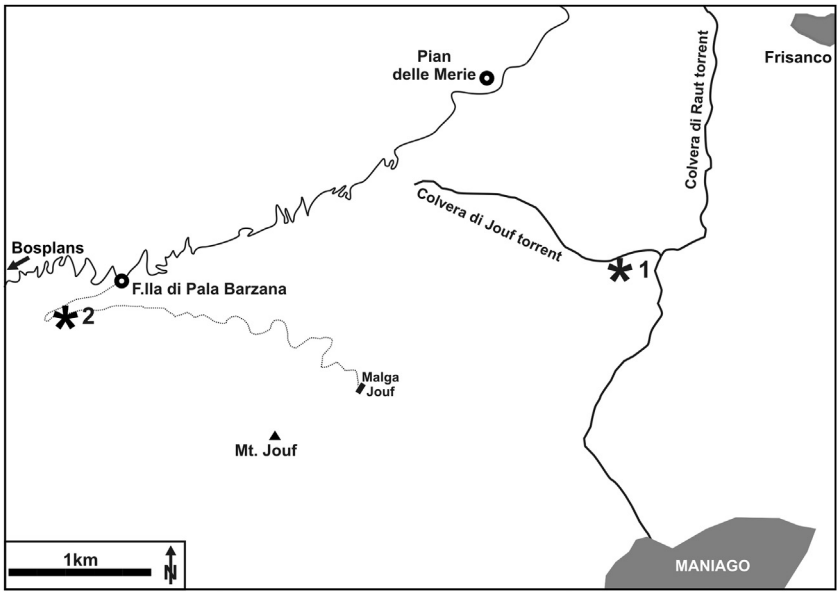

Fig. 1. Locality map of the Mt. Jouf area; 1. Old quarry near the Colvera torrent; 2. Poor outcrop of strata with specimens of *Colveraia variabilis* near Forcella di Pala Barzana.

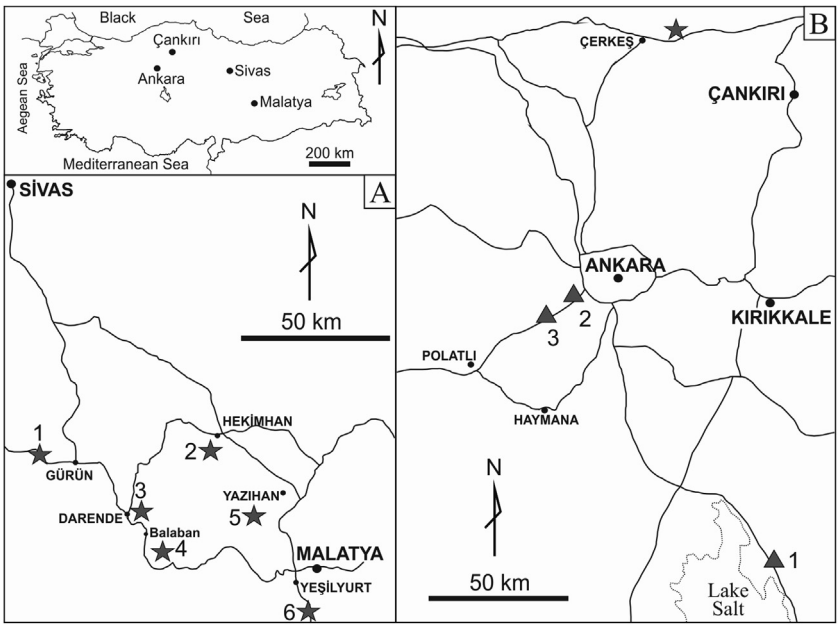

Fig. 2. Locality map illustrating the occurrence of *Colveraia darendeensis* in eastern and central Anatolia, Turkey (asterisk); A. Malatya and Sivas basins: 1. Sarıcalar-Gürün, 2. Hekimhan, 3. Darende, 4. Balaban, 5. Yazıhan. 6. Yeşilyurt. B. Çankırı Basin: Çerkeş. Localities in the Lake Salt and Haymana-Polatli basins are indicated by triangles: 1. Karapınar, 2. Yurtçu, 3. Malı.

of the reddish clastics varies from 20 to 100 m, but attains up to 350 m at some localities. This unit is barren of fossils but as it is characterised by lateral and vertical interfingerings with the lower part (e.g. grey-white mudstones, siltstones and sandy limestones with rare rudists) of the rudist-bearing units, so a late Campanian age for these clastics is proposed. The upper part of the rudist-bearing units consists of limestones and sandy limestones that are rich in rudists. The thickness of the formation is about 40–45 m. The rudist-bearing limestones are representative of the remarkable growth of rudists in these regions. Many species of hippuritids, radiolitids and caprinids were described from the matrix-free beds and well-preserved rudist specimens were observed (Woodward, 1855; Karacabey, 1969, 1970, 1972, 1974; Karacabey-Öztemür, 1976, 1979, 1980; Özer, 1988a,b, 1992, 2002, 2006; Özer et al., 2008). Gastropods, brachiopods, corals and larger benthic foraminifera are associated with the rudist fauna. The long-established subdivision on the basis of larger benthic foraminifera suggests a Maastrichtian age for the rudist-bearing formations in eastern Anatolia. However, a late Campanian date for rudist-bearing formations in the Malatya area was derived from Sr-isotope values of samples of rudist shells (Özer et al., 2008; Schlüter, 2008; Schlüter et al., 2008; Steuber and Schlüter, 2012). Recently, a detailed micropalaeontological study of planktonic foraminifera and nannoplankton has indicated a late Campanian–Maastrichtian age for pelagic mudstones that overlie the rudist-bearing formations in the Malatya area (Sarı et al., 2016), thus supporting the Sr isotope results for the rudists. In central Anatolia, the age of the rudists was indicated to be Maastrichtian on the basis of previous studies and larger benthic foraminifera.

In the Sivas Basin, the rudist-bearing sequences show architectural stratigraphical peculiarities that are similar to those of the Malatya Basin, but they have a sparse geographical distribution. A single specimen of *Colveraia* from Sarıcalar-Gürün (Sivas Basin) was described by Karacabey (1974). Sections of *Colveraia* that show the canals of the left valve have recently been observed by Poisson et al. (2016) in upper Campanian–Maastrichtian limestones with rudists on the top of ophiolitic rocks.

Some sections of left valves showing canals like the *Colveraia* were described from mixed siliciclastic-carbonate sequences of the Ankara region (villages of Yurtçu and Malı and east of Lake Salt) in central Anatolia by Özer (1985) (Fig. 2). Sr isotope values of samples of rudist shells from east of Tuz Gölü could not be considered reliable (T. Steuber pers. Comm., 2012). However, the presence of *Hippurites cornucopiae* Defrance, 1821 suggests a (late) Maastrichtian age for those sequences (Steuber and Schlüter, 2012).

The above-mentioned geographical and biostratigraphical data show that the well-preserved specimens of *Colveraia* described here are mainly located in the Malatya Basin and partially represented in the Sivas and Çankırı basins. Lastly, a late Campanian date is suggested for these specimens.

3. Material and methods

3.1. Klinghardt specimen

At the start of our research, there were no specimens of *Colveraia variabilis* in any Italian museum, nor in rich private collections. Consequently, we explored the zone of Mt. Jouf where unit 4 crops out, but the entire area is now extensively reafforested, which makes it difficult to find good exposures of rudist-bearing limestones. We did manage to recover a few large examples of *Colveraia variabilis* that mostly lack the outer shell layer after many surveys in the area. Problems arose when these seven new specimens were compared with those illustrated by Klinghardt (1921), because of their completeness. Thus, we examined Klinghardt's original specimens housed in the Goldfuss Museum, Bonn (Steinmann Institute of Palaeontology, STIBP).

The ten specimens attributed to *Colveraia variabilis* are together in a box (Fig. 3), but only three large fragments actually belong to *C. variabilis*. We wish to point out that none of the three specimens of *C. variabilis* housed in the Goldfuss Museum seems to belong to the syntypes illustrated by Klinghardt (1921). The specimen in the right-hand corner of the box was our "key" specimen at the time, because it comprised all features of the species which we know at

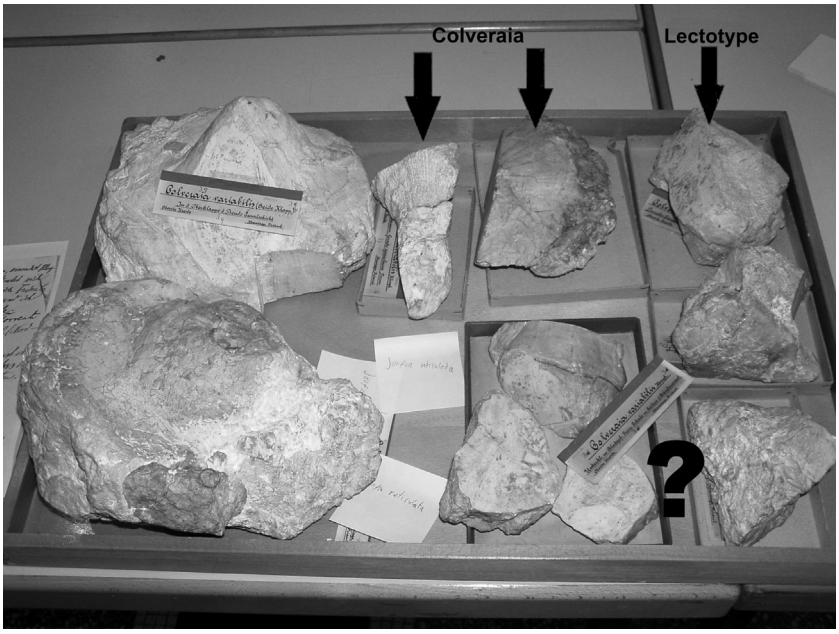

Fig. 3. Specimens originally attributed to *Colveraia variabilis* housed in the Goldfuss Museum, Bonn. Five examples marked by question marks cannot be classified, two on the left-hand side of the box belong to *Joufia reticulata* and only three very large fragments (arrows) belong to *Colveraia variabilis* (no. STIBP 3i, 3k and 3l). The specimen in the right-hand corner of the box is here designated lectotype of *C. variabilis*.

present (Tarlao et al., 2014) and is a historical example. Although this individual is not complete, we here designate it lectotype of the species, in the absence of any formally designated holotype (Fig. 4). Unfortunately, the lack of complete specimens in the rudist assemblage of unit 4 of the Calcari del Monte Cavallo Formation is quite common, being a result of abrasion and breakdown of their shells in a high-energy setting. In addition, the outer shell layer is almost always lost during extraction of the fossils from the hard rock.

The other four fragments (both large and small, and both genuine or presumed to be conspecific) of *Colveraia variabilis* illustrated by Klinghardt (1921, pl. 5, fig. 9; pl. 6, figs 1, 3; pl. 16, fig. 13) are housed in the collections of the Museum für Naturkunde (Berlin, MfN). Unfortunately, we did not have the opportunity to examine them due to construction works at the collection halls, which will last until 2018–2019 (Dr M. Aberhan, pers. comm. May 18, 2016). A pair of interesting historical examples of *Colveraia variabilis*, e.g., the specimen illustrated by Klinghardt (1921, pl. 1; pl. 16, fig. 12), appear to be missing.

The seven newly collected specimens of *Colveraia variabilis* (Fig. 5) are kept in the collections of the Museo Paleontologico Cittadino del Gruppo del Fante Monfalcone, Gorizia (Italy). All are more or less diagenetically altered, similar to the lectotype. Four examples, numbered I to IV, are referred specimens and were used by us for the amended diagnosis of the species. Referred specimen III is cut into three slices, of about 1.5 cm thick, parallel to the commissural plane, while specimen V is cut into four slices with different orientation. The transverse section of the left valve of referred specimen III is cut 7–8 mm below the commissural plane and the one of the right valve about 10 mm above it.

Lastly, we carefully read Klinghardt's (1921) long description of the characteristics of *Colveraia variabilis* and closely examined all illustrations of the species. After a careful study of available specimens of *Colveraia variabilis*, we are able to add further features and redescribe the species much more precisely, thus correcting a number of errors and incorrect descriptions published by Klinghardt (1921).

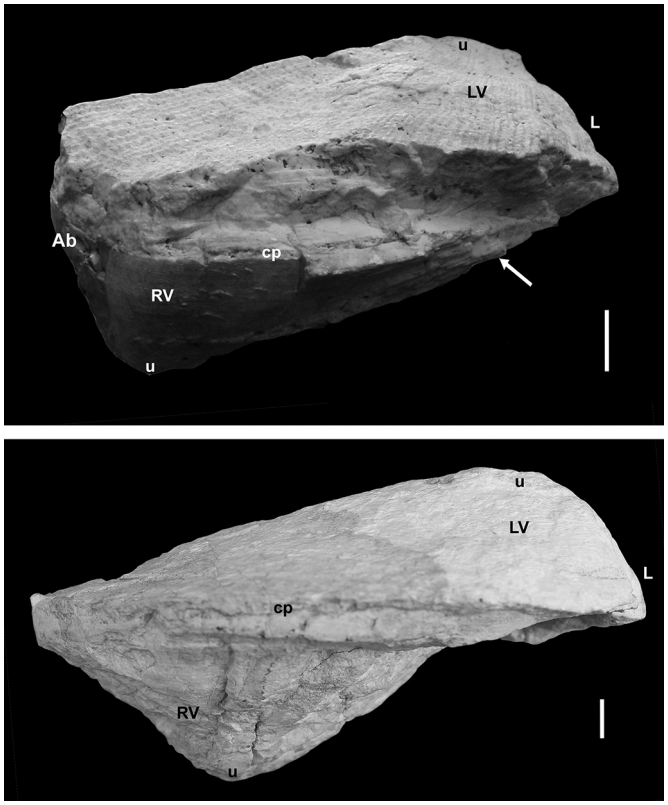

Fig. 4. Lectotype of *Colveraia variabilis* (no. STIBP 3l) (top) and the eroded, referred specimen I (no. 13850 Monfalcone) (bottom) for comparison. Both valves in lateral view. L = ligament, Ab = anterior band, cp = commissural plane, u = umbo. Note the marked displacements of the umbones of the upper and lower valves. The arrow marks a small area of the outer shell of RV of the lectotype that shows the cellulosprismatic structure. Scale bar equals 10 mm.

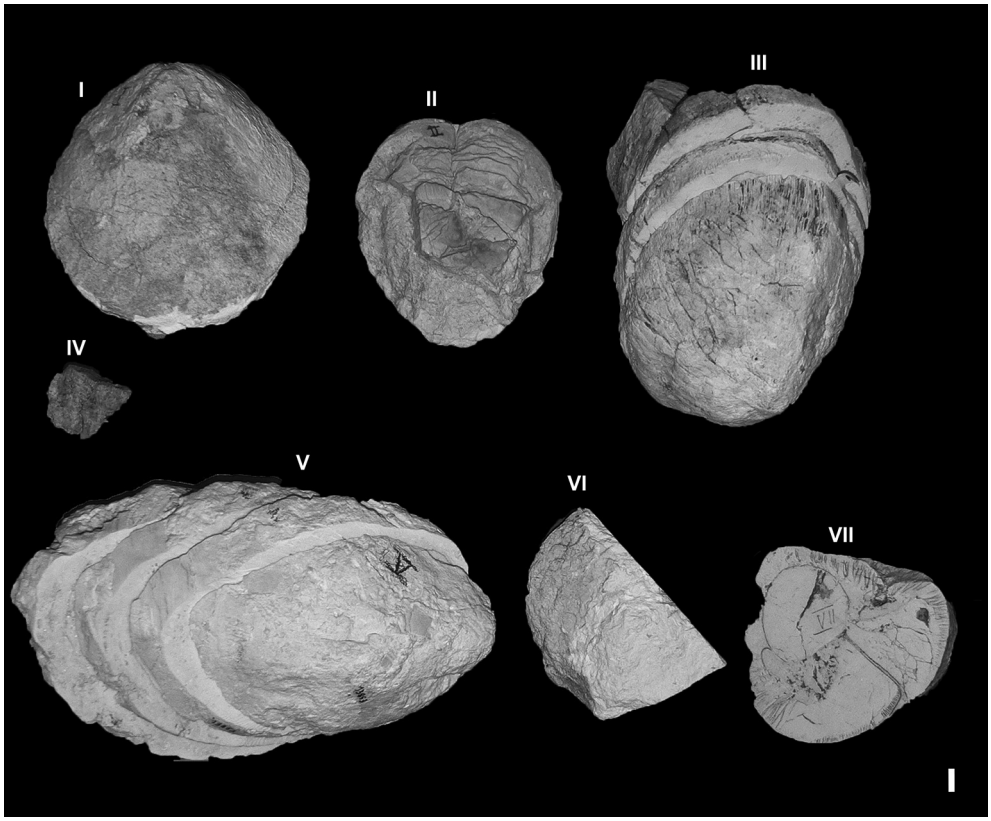

Fig. 5. Specimens of *Colveraia variabilis* housed in the Museo Paleontologico Cittadino di Monfalcone. Above, the examples numbered I to III (left to right) and fragment IV are considered referred specimens of the species (nos 13850, 13849, 13851 and 13856 Monfalcone). Below, examples V to VII (left to right, nos 13853, 13854 and 13852 Monfalcone). Scale bar equals 10 mm.

3.2. Turkish specimens

Previous research of rudists from nearly all regions in Turkey, including studies by one of us (SÖ), has shown that the material assignable to *Colveraia* comes only from eastern (Malatya and Sivas basins) and central Anatolia (Ankara region, Haymana-Polatlı and Lake Salt basins) (see Özer, 2002; Steuber, 2002; Özer et al., 2009). *Colveraia variabilis* was first recorded from Turkey by Karacabey (1974) on the basis of a single specimen with both valves from Gürün-Sivas and two other specimens from Çerkeş-Çankırı, one of which is fully articulated while the other retains only the right valve. Since these specimens were not numbered and Karacabey provided no data on their storage, they could not be found. The same author described a new species, *Colveraia darendeensis*, on the basis of a single specimen with both valves (holotype) and another one (paratype) with only the left valve from Darende-Malatya. Although it was not specified by Karacabey (1974) which photographs represent the holotype and which the paratype, we inferred that illustrations pertain to the holotype which retains both the valves. Only the number of the holotype, no. 2244, in the Museum of MTA (Ankara), was mentioned by Karacabey (1974, p. 83). The holotype and paratype were not traced by us, and are assumed not to be at the museum. In contrast, our description *Colveraia* is based on numerous articulated, well-preserved specimens collected mostly in eastern Anatolia by one of us (S. Ö). One of them (no. DM-86/10) is here designated neotype of *Colveraia darendeensis*; it is from Darende-Malatya, the type locality of the species.

Transverse sections of both valves were cut approximately 10 mm below and above the commissural plane, while radial sections refer to the opposite side with respect to the inclination of the LV passing just through the centre of the valve.

3.3. Repositories

Neo- and lectotype designations are based on the International Code of Zoological Nomenclature, ICZN (Ride et al., 1999). The lectotype housed in the Goldfuss Museum, Bonn, is STIBP-Klinghardt 3l, while the other two large fragments bear the numbers STIBP 3j and STIBP 3k (courtesy of Dr G. Heumann). Seven specimens and one dubious large fragment (not illustrated herein) are kept at the Museo Paleontologico Cittadino di Monfalcone. Referred specimens I, II, III (cut into three slices) and IV have inventory numbers 13850, 13849, 13851 and 13856 Monfalcone, respectively. Specimens V (cut into four slices), VI, VII and the dubious example VIII bear inventory numbers 13853, 13854, 13852 and 13857 Monfalcone, respectively (Fig. 5).

The neotype (DM-86/10) and referred specimens of *Colveraia darendeensis* described here are on display in museum showcases at the Geological Engineering Department of Dokuz Eylul University (İzmir), while additional referred specimens are housed in the Laboratory of Palaeontology of the same department.

4. Taxonomy

The classification scheme and terminology for higher taxa of rudists used here follows Skelton (2013a,b).

Abbreviations. LV, left valve; RV, right valve; Ab, anterior radial band; Pb, posterior radial band; Ib, interband; L, ligamental ridge; am, anterior myophore; pm, posterior myophore; at, anterior tooth; pt, posterior tooth; BC, body cavity; ol, outer shell layer; il, inner shell layer.

Class Bivalvia Linnaeus, 1758

Order Hippuritida Newell, 1965
Suborder Radiolitidina Skelton, 2013a
Superfamily Radiolitidea d'Orbigny, 1847
Family Radiolitidae d'Orbigny, 1847

Genus *Colveraia* Klinghardt, 1921
Type species: *Colveraia variabilis* Klinghardt, 1921

Colveraia variabilis Klinghardt, 1921
Figs. 3–8

1921 *Colveraia variabilis* Klinghardt, p. 23, text-fig. 7; pl. 5, figs 8–9; pl. 6, figs 1–10.
1928 *Colveraia variabilis* (n. sp.); Klinghardt, pl. 5, figs 8–9; pl. 6; pl. 13, fig. 6; pl. 14, fig. 6; pl.15, fig. 7; pl. 16.

4.1. *Amended diagnosis of* Colveraia variabilis

The length of the RV of the lectotype may be estimated to have been approximately 160 mm, while referred specimens I and V are 135 and 180 mm in length, respectively. The ol of the RV is largely lacking, with only a small area showing the celluloprismatic structure (Fig. 6A). The umbones are markedly displaced (Fig. 4); that of the LV projects towards L, while the one of the RV is close to the anterior part of the left valve. The LV is about 20 mm in height. Specimens of *Colveraia variabilis* invariably display an oval transverse section (Fig. 6B–C), which is unusual amongst radiolitids. The LV is characterised by a series of wrinkled, radially arranged, longitudinal, *c* 1.5-mm-large ribs starting from the umbo and spaced

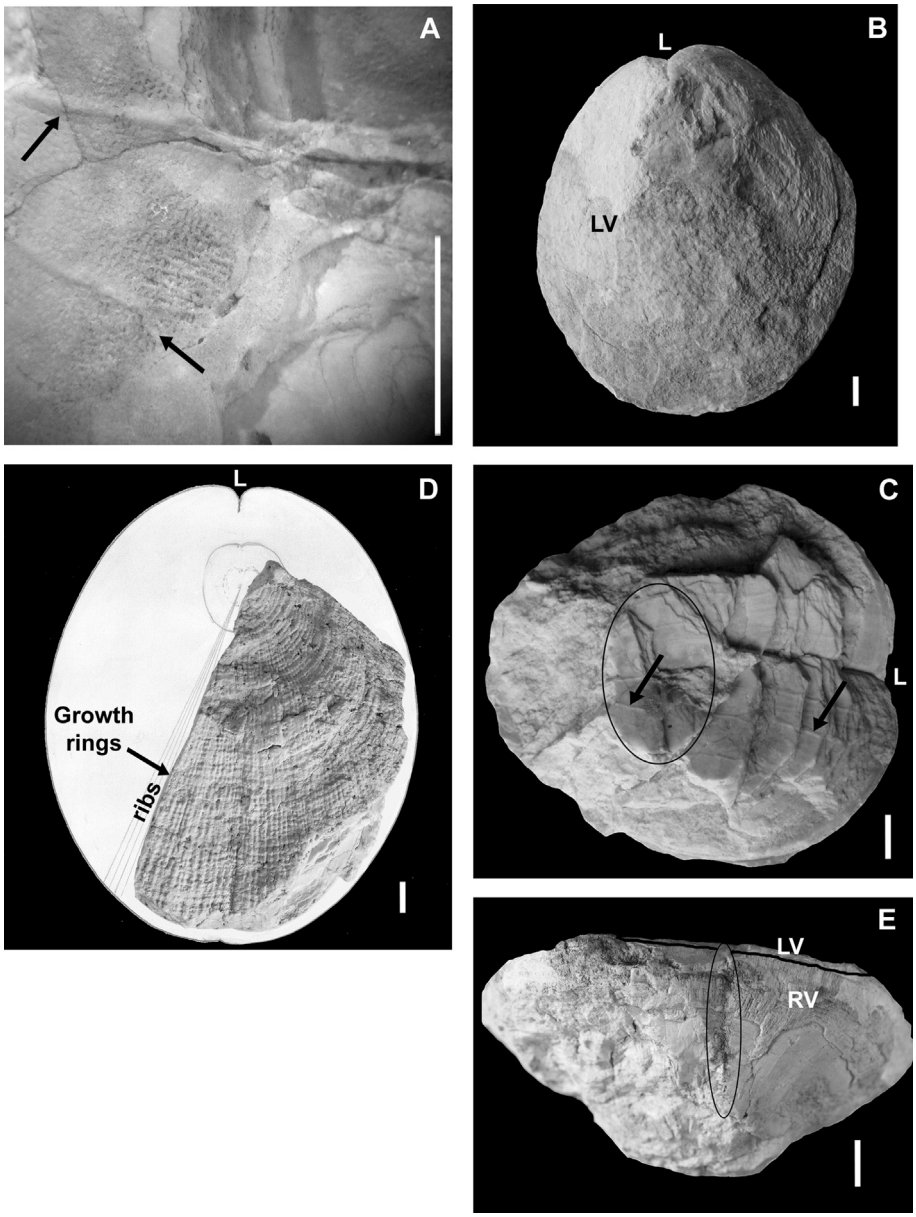

Fig. 6. *Colveraia variabilis*. A. Small area of ol of RV showing typical celluloprismatic structure; referred specimen II (no. 13849 Monfalcone); closeup of the ringed area of Fig. 6C. Note digitated calcite veins (arrows). B. Apical view of LV of referred specimen I (no. 13850 Monfalcone), exhibiting a marked oval shape. The arrows indicate growth rings. C. Apical view of RV of eroded referred specimen II, showing large growth lamellae. Arrows indicate calcite veins. D. Apical view showing reconstruction of incomplete LV of lectotype, tentatively proportioned on measurements made of the upper valve of referred specimen I, e.g., length and different widths, distance between the umbo centre and ligament. E. Antero-ventral view of both valves of eroded referred specimen I. Position of Ab in the centre of the ringed area. Scale bar equals 10 mm.

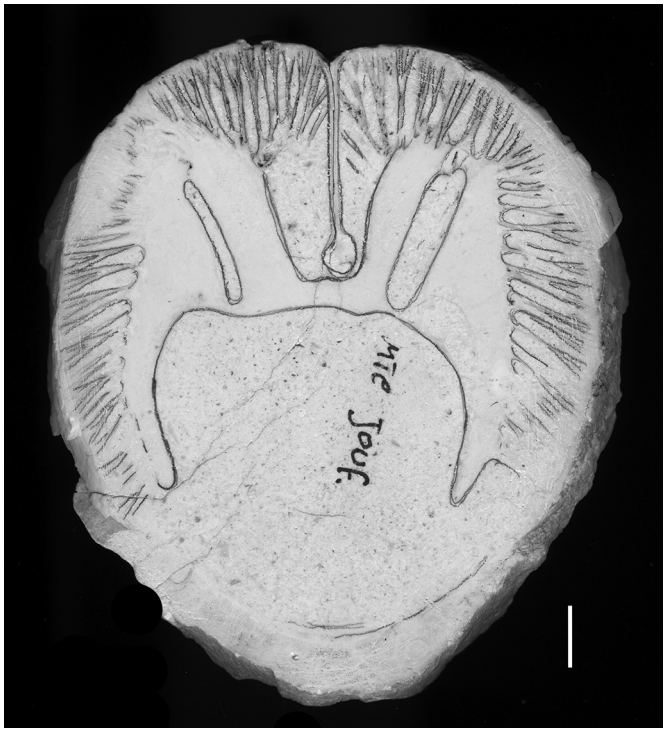

Fig. 7. Transverse section of RV of referred specimen III (no. 13851 Monfalcone), cut 7–8 mm below the commissural plane showing the cardinal apparatus, the laminae and the canal pattern which are clearly visible but their contour lines are intensified by pencil. Scale bar equals 10 mm.

by circular rings about 15 mm from each other marking the growth zones (Figs. 4, 6D). The RV apparently lacks ornament (see also Klinghardt, 1921, Nachtrag zu Teil I, pl. 6). A large furrow near the ligament zone, representing L, has been observed in all samples when looking towards the apex of the LV (Fig. 6B–C). Unfortunately, other characteristics of the ligament zone cannot be observed because of shell erosion.

The RV is characterised by smooth, large, superimposed growth lamellae (Fig. 6C) and by thin, often bifurcating or digitated calcite veins (i.e., Blutgefässe *sensu* Klinghardt, 1921) placed on the cellulosprismatic structure (Fig. 6A). The shape of the cellules in transverse section parallel to the growth lamellae seems to be regular and resembles the "penta-hexagonal" network of old. Klinghardt (1921) used the term "Aussenschicht" (a) for the cellulosprismatic structure when cellules in transverse section were seen to be parallel to the growth lamellae, and "Rindenschicht" when the orientation of the cut was tangential to the lamellae. Klinghardt employed the former term for describing morphological characteristics of *Radiolites styriacus* (Zittel, 1865) where such structure is clear.

A well-marked, invariably clear groove is considered here to be a radial band (Fig. 6E), presumably the Ab. In all samples examined, we never observed any clear trace of Pb. However, this should not be considered an exception to radiolitid morphology because a number of genera and species show only faint traces of the posterior band (e.g. *Radiolites angeiodes* Lapeirouse, 1781, *Biradiolites acuticostatus* d'Orbigny, 1842, *Gorjanovicia* and others).

Transverse sections cut along the commissural plane show the well-known configuration of the myocardinal apparatus (Fig. 7) with a long, well-developed L, robust expanded teeth matching the growth of the valve and large myophores following the growth of the external perimeter of the shell.

Lastly, the 'pseudocanals' *sensu* Klinghardt (1921) are always evident in the LV of the examined specimens. They appear as a series of digitated laminae or thin plates of about 0.7–0.8 mm, radially oriented, starting from the myocardinal apparatus and connecting the myophores (and teeth) with the inner border of the LV (Fig. 7). Each thin plate extends parallel to the contiguous ones for a short distance, after which all laminae ramify into two or more thin plates, thus isolating a series of tear-shaped spaces (Fig. 7). The

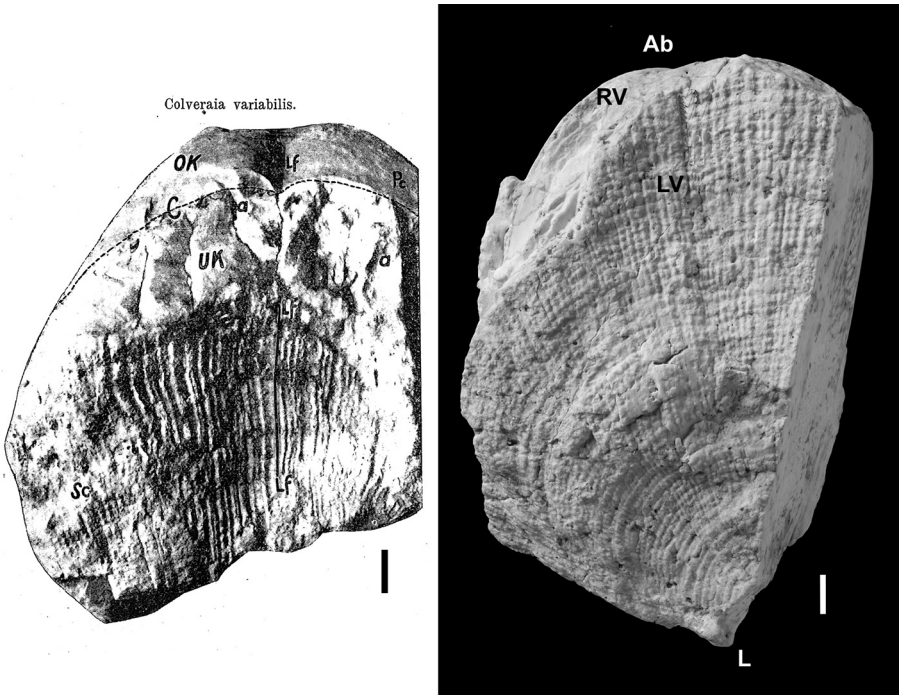

Fig. 8. Apical view of the most significant specimen chosen by Klinghardt (1921, p. 68) for describing external characters of *Colveraia variabilis* on the left. OK = LV, UK = RV, Lf = L, Pc = pseudocanal, C = commissure, a = Aussenschicht, Sc = ornamentation. Apical view of the lectotype on the right. Note that OK is not LV, but RV (see Ab, growth rings and umbonal position in the lectotype). Scale bar equals 10 mm.

branches of each thin plates join the inner wall of the LV characterised by tiny parallel laminae in transverse section (referred specimen IV). The canals do not appear to link with the external surface, e.g., with ribs. To sum up, the complex of thin plates and canals supports the myocardinal apparatus of the LV. According to Skelton (2013a), the distinction between canals and pseudocanals is meaningless, and for those found in the inner shell of canaliculate radiolitids he suggested the term pallial canals. This term was coined to describe the internal characters of caprinids; here, the simple term canal is preferred.

In his diagnosis of *Colveraia variabilis*, Klinghardt (1921) mistook the LV for the RV. By comparing the LV of a historical example with the one of the lectotype (Fig. 8), it is clear that the lower valve (his "uK") actually represents the upper valve (his "oK") and *vice versa*. The "Aussenschicht" cannot be present on the eroded upper part (LV) of the historical example. The ligament ridge (Lf = Ligamentfurche) is in fact the Ab, and L is situated on the lower part of the opposite side.

In addition to this error, from the text-figures it can be inferred that Klinghardt worked with some transverse sections that were cut irrespective of the orientation of the commissural plane or of the growth lamellae. In turn, this led to other errors, making it very laborious and misleading for modern scholars to understand the text and figures. Moreover, some examples do not seem to be significant and, in a number of cases, cannot be assigned to the species.

Not wishing to underestimate the punctilious work and the difficulties met by Klinghardt, we believe it is of use to list the errors and misinterpretations:

i) ornamentation characterises the LV, not the RV,
ii) the cellulo prismatic structure characterises the RV, not the LV,
iii) since we have never detected any "Aussenschicht" (always obscure in all original figures of Klinghardt's paper), we are inclined to consider this structure to be a forced interpretation,
iv) the radial band zone ("Siphonalzonen") seems not well developed; in particular, the pb and the interband were not observed in the samples examined,
v) the LV has no radial bands,
vi) the am and the pm are well developed and always evident provided that the cut is well oriented with respect to the commissure,
vii) the at and the pt are situated in the RV, not in the LV,
viii) sockets are absent,
ix) Km = "grob-feinmaschige Kalksubstanz" is not a peculiarity but only a calcite filling,
x) "pseudocanals" ("Pseudocanalschicht") are present in the LV, never in the RV, and not in the thickness of the shell layer.

Finally, Klinghardt noted variability in the shape of the valves, the myophores (more or less well developed), the teeth (more or less inclined), the shape of the cellulae and other features. This variability was probably due to the orientation of the transverse sections; we did not observe any significant variability of characters in *Colveraia variabilis*. Differences and similarities between *Colveraia variabilis* and the Turkish specimens are indicated in section 4.2 (Remarks).

4.2. **Colveraia darendeensis** *Karacabey, 1974*

Figs. 9–11

1974 *Colveraia variabilis* Klinghardt; Karacabey, p. 80, textfigs. 1-2, pl. 2, fig. 2a, b; pl. 3, figs 2-3; pl. 4, fig. 3; pl. 5, figs 1-2.
1974 *Colveraia darendeensis*; Karacabey, p. 83, text-fig. 3, pl. 3, fig. 1, pl. 4, fig. 2.
1980 *Colveraia variabilis* Klinghardt; Karacabey-Öztemür, p. 81, pl. 4, fig. 9.
1988 *Colveraia variabilis* Klinghardt; Özer, p. 332, text-fig. 3g.
2002 *Colveraia variabilis* Klinghardt; Özer, p. 174, pl. 3, fig. 1.

Type. Neotype, here designated, is DM-86/10 from Darende-Malatya (Figs. 9A–B, 11A, D–E).

Enlarged diagnosis. LV with beak slightly or markedly inclined towards ventral side and two ribs connecting with radial bands; RV conical, cylindro-conical or cylindrical, ornamented with longitudinal ribs, Ab and Pb salient as longitudinal ribs with thin rib and costules and Ib straight or slightly convex with rib and thin costules; RV ol with two parabolic arcs in radial band area.

Description. The RV is conical in the neotype and in some referred specimens (Fig. 9A–B, E–F). Most of the specimens are cylindro-conical or cylindrical, and slightly curved towards the ventral part (Figs. 9C–D, 11). The height is 30–40 mm in the conical valves and it is approximately equal to the diameter, but the latter is much wider in some specimens. The height of the robust cylindro-conical and cylindrical valves varies from 200 to 300 mm, and the diameter from 140 to 160 mm. The shell surface is ornamented with thin, regular longitudinal ribs and narrow furrows, 1–2 mm wide. Both the ribs and the furrows are rarely crossed by thin growth lines. The radial bands are distinct, Ab and Pb are salient and represented by a longitudinal rib (Figs. 9–10). Ab is wider (6–10 mm) and more salient compared to the other band. Thin longitudinal costules (two or six) are a bit hidden, especially those on the lateral faces of the radial bands. Ib is straight or slightly convex, three or sometimes four times wider (15–25 mm) than the other bands. It consists of three up to nine ribs showing similarities with those of the RV. The ribs of Ib show costules in some specimens. The radial bands are limited by a groove on both sides. The outer grooves are commonly deeper than the other ones. L is represented by a thin longitudinal furrow on the surface of the valve. The transverse section of the RV is generally circular or subcircular. The calcitic ol is 8–10 mm thick in the ventral part, and 15–20 mm thick in the dorsal, dorso-posterior and anterior sides. It consists of small, regular polygonal cells showing not uniformly developed growth lamellae. Two parabolic arcs (*sensu* Karacabey, 1974) separated from the ol by a thin lamella and related with the development of the radial bands can be observed in the ventral part of the valve (Fig. 11D). These structures (referred to as radial structures by Pons and Vicens, 2008) are very common in radiolitids. The anterior one is always wider and longer than the other one. Four or five lamellae welding to the outer lamella are also present inside the parabolas. They are slightly convex on their tops. The cells inside the parabolas resemble those of ol, but they are lined up parallel to the lamellae in the centre and at the top of the parabolas. Some cells towards the top of the parabolas are slightly elongated and larger compared to the others. L is long with a thin stem and enlarged with a subrectangular shape at the distal end, extending almost up to the centre of the valve. Two accessory cavities on either side of the L were observed in some specimens, but the posterior cavity is commonly preserved. The myocardinal apparatus is well developed and the teeth are symmetrically localised in connection with L and always extend up to the edge of the ol. The posterior myophore approaching the ventral part of the valve is more developed than the anterior one. The LV is convex, cap like and loosely or markedly inclined towards the ventral part. Four different shape types of LV were observed: (i) the slightly inclined valves are flattened and their apex is located very close to the centre of the valve or halfway between the margin and centre of the valve. The valves are 10–15 mm in height. (ii) Some valves

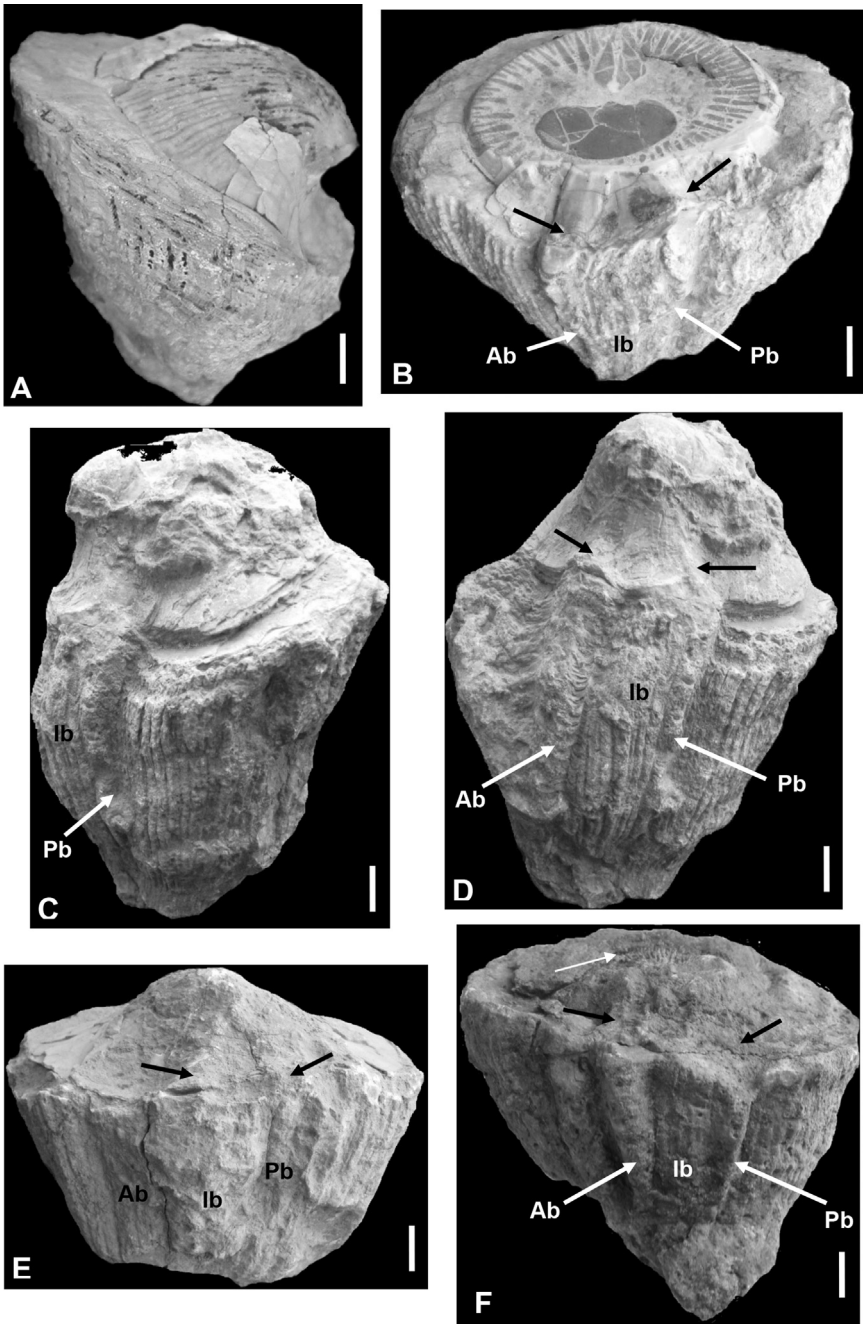

Fig. 9. *Colveraia darendeensis*, A–B. Neotype no. DM-86/10, Darende-Malatya, A. Both valves, antero-ventral view; RV conical, LV inclined towards ventral side. Note traces of canals of inner shell layer at eroded portions of thin outer shell layer of LV. B. Both valves showing radial bands and transverse section of LV. Note two prominent ribs connecting with radial bands and their lenticular apertures (black arrows). C–D. Specimen no. YM-07/41, Yazıhan-Malatya. C. Both valves. Note inclination and height of LV and its thick calcitic outer shell layer, postero-ventral side. D. Same specimen showing radial bands and LV. Black arrows indicate ribs of LV. E. Specimen no. HM-04/21A, Hekimhan-Malatya, both valves showing radial bands and thin calcitic outer shell layer of LV. Note that the apex is located approximately in the centre of the valve. Compare the thickness of outer shell layer with previous figures. Black arrows indicate ribs of LV. F. Specimen no. DM-86/22, Darende-Malatya, both valves showing radial bands. Canals are observed in the eroded portion of the thin ol of the LV (thin white arrow). Black arrows indicate ribs of LV. Scale bar equals 10 mm.

are also flattened, but their apex is more developed, inclined and closer to the ventral part compared to the previous specimens, and they are 15–25 mm in height. (iii) The valves, 40–45 mm tall, are hook like, the apex near aligned to the commissure. (iv) The robust valves are markedly inclined and go beyond the commissure, covering the upper part of the radial bands. The surface of the LV is smooth, and only two prominent ribs connecting with the radial bands are present (Figs. 9B–F, 10A–C). The anterior band is represented by a larger rib compared to the other one. The area between these ribs is flat or slightly concave with thin ribs in some specimens. Lenticular apertures in front of these ribs were observed. The transverse section is almost circular. The calcitic ol consists of fine lamellae arranged parallel to each other on the surface of the valve and is almost 3–7 mm thick in flattened valves, but can reach a thickness of 15 mm in robust valves. The canals of the il can be observed on the eroded parts of examples with thin ol (Fig. 9A). Tubular structures connected with the parabolic arcs of the RV were not observed in the ol around the ribs of the LV. The

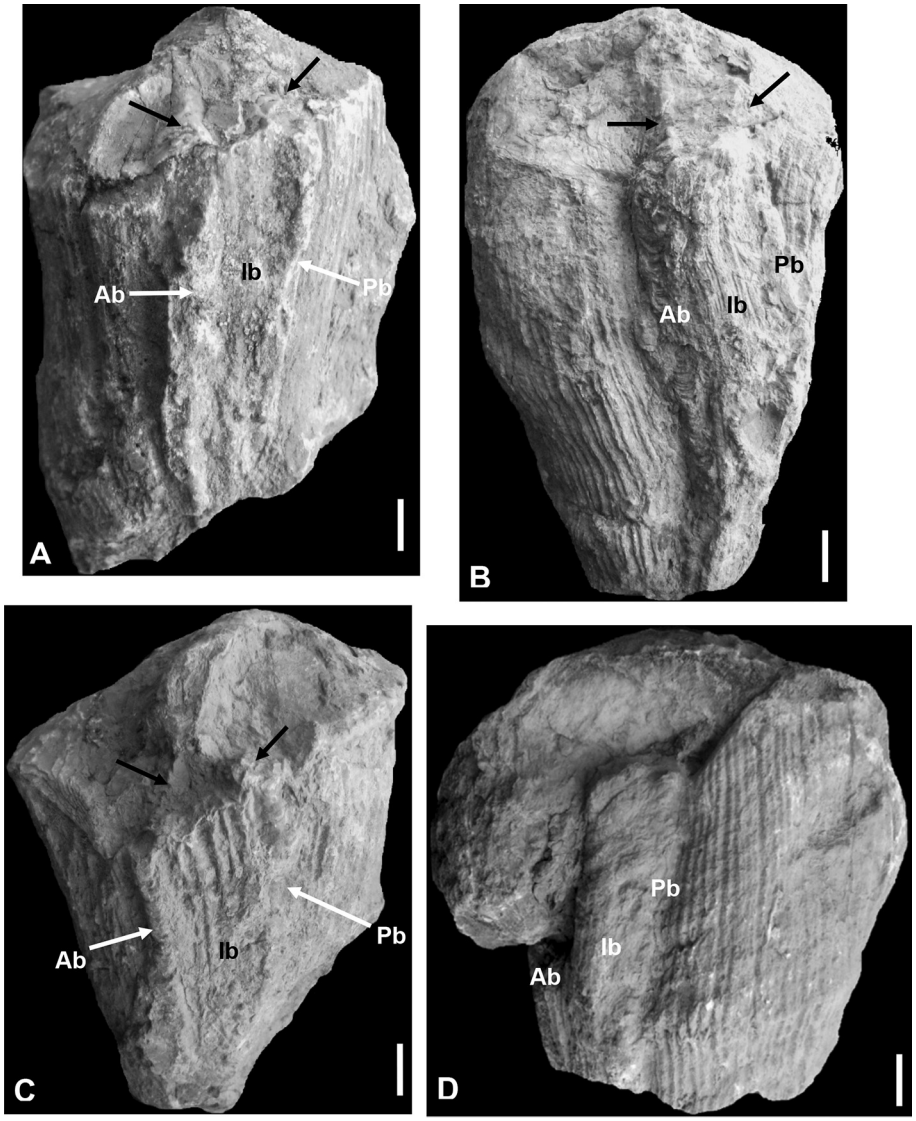

Fig. 10. *Colveraia darendeensis*, A–D. Both valves. Note variation in shape of LV from the apex located approximately in the centre of the valve, to form a hook and markedly inclined, with a very robust beak, towards the ventral side passing the commissure of the valve. Black arrows indicate ribs of LV. A. Specimen no. HM-86/22, Hekimhan-Malatya. B. Specimen no. DM-94/29, Darende-Malatya. C. Specimen no. HM-86/18, Hekimhan-Malatya. D. Specimen no. DM-94/32, Darende-Malatya. Scale bar equals 10 mm.

originally aragonitic il consists of fusiform canals showing a dichotomy as they are separated from each other by fine radial plates (Fig. 11A–B). The penetration of these canals into teeth and myophores was observed clearly in radial sections of both valves (Fig. 11C). The long L with subrectangular head, well-preserved teeth and myophores can be observed both in the transverse and radial sections (Fig. 11A–C).

Variabilities. The shape of both valves and structure of the radial bands show variation. The apex of the LV shows different features depending on whether it is very close to the centre of the valve or located between the centre and the margin of the valve and whether it is slightly or markedly inclined towards the ventral side. A robust LV, with a very high apex, that looks like a hook going beyond the commissure is fairly common. The conical RV is not long, while the cylindro-conical and cylindrical RVs are robust, long and slightly curved towards the ventral part. The thickness of the radial bands is also variable. For instance, Ab is generally three or four times wider than Pb, but in some specimens is narrower. Ib is not always straight, but at times slightly convex. Ib commonly has three ribs, but it may also bear many ribs.

The above-mentioned intraspecific variation is not used here to establish different new species, because all specimens examined reveal common features, such as two pronounced ribs of the LV inclined towards the ventral part, distinct radial bands, the calcitic ol of the RV with two parabolic arcs and the RV ornamented by regular longitudinal ribs.

Remarks. Some features of our specimens, such as the canals in the originally aragonitic il of the LV, the long L and the radiolitid type myocardinal apparatus, bear similarities to *Colveraia variabilis* as described from the original material of Klinghardt (1921) and as seen in the new Friuli examples housed in the Museo Paleontologico Cittadino del Gruppo del Fante Monfalcone, Gorizia (Italy). However, the amended diagnosis of that species (see above) indicates that the Turkish specimens differ from the ones from Friuli by a number of remarkable features, as follows:

(i) rather than projecting towards the dorsal part, the LV is inclined towards the ventral part,

(ii) the surface of the LV is smooth contrary to the radially arranged, longitudinal ribs of *Colveraia variabilis*,

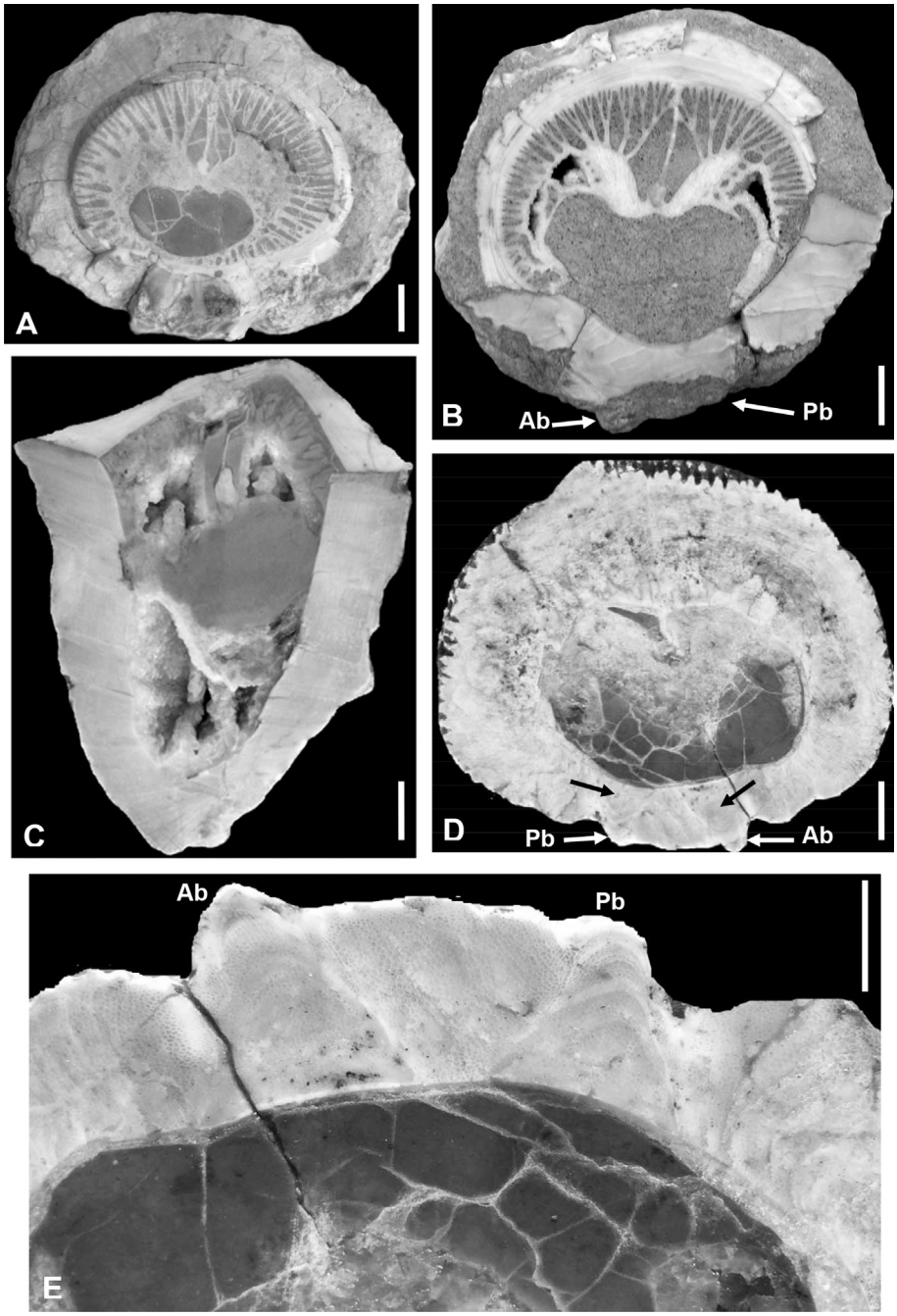

Fig. 11. *Colveraia darendeensis*, A–B. Transverse sections showing canals of inner shell layer, L and well-preserved cardinal apparatus of LV. Note thin calcitic outer shell layer of LV. A. Neotype no. DM-86/10, Darende-Malatya. B. Specimen no. MH-86, Hekimhan-Malatya. C. Specimen no. MH-68, Hekimhan-Malatya; radial section of both valves showing canal sections of inner shell layer of LV. Note the penetration of canals to teeth and myophores and the well-preserved L and dissolved cardinal apparatus. D. Specimen no. DM-86/10, Darende-Malatya; transverse section of RV passing 10 mm below commissure. The cardinal apparatus is well developed; black arrows indicate parabolic arcs (radial structures) illustrated in E. E. Enlarged part of the ol of the same specimen showing parabolic arc (radial structures) separated from the ol by thin lamella. Note interior of the parabolic arcs (radial structures), showing cells aligned in parallel to thin lamellae. Scale bar equals 10 mm.

(iii) the LV has two ribs related with radial bands,
(iv) the RV is ornamented with thin longitudinal ribs instead of showing a smooth surface,
(v) the radial bands are well-developed and clear,
(vi) the RV ol has two pronounced parabolic arcs in the radial bands area.

A new species, *Colveraia darendeensis*, was also described by Karacabey (1974). New material from the Darende-Malatya region has allowed us to typify this species. According to Karacabey, *C. darendeensis* differed from the specimens assigned to "*Colveraia variabilis*" found in Gürün-Sivas and Çerkeş-Çankiri by the strongly developed and inclined LV, the flatter Ib, the very salient Ab and Pb with the grooves located on their external lateral faces, which are much deeper and broader than the latter and the cylindro-conical shape of the RV. However, some of our specimens do not have a developed LV, but do show flattened Ib and/or salient radial bands or deep grooves in the external part of the radial bands; moreover, the LV apex is also variable (Figs. 9–10). These characters are of no taxonomic significance and must be considered to be within the

intraspecific variability of *Colveraia darendeensis*. There are many studies that have demonstrated that rudists were subject to intraspecific variability (Pons and Vicens, 1986; Pons and Sirna, 1994; Caffau et al., 1998; Steuber, 1999; Simonpiètri and Philip, 2000; Cestari, 2008; Özer, 2010; Săsăran et al., 2013).

5. Comparison with congeners and biogeography

In addition to *Colveraia variabilis* and *C. darendeensis*, another species of the same genus was established by Lupu (1970). This author described *C. secunda* from the Valea Neagra-Borod succession (northern Apuseni, Romania), which at the time was dated as Maastrichtian. The holotype of *C. secunda* is an incomplete, diagenetically altered specimen with a poorly preserved, eroded shell. Lupu (1970) provided poor or incomplete information as far as myocardinal apparatus, zone of the radial bands and ornamentation are concerned. *Colveraia secunda* shows a canal pattern that closely resembles the one described by Klinghardt (1921), and small areas of the outer shell reveal the cellulosprismatic structure. The main reason for Lupu (1970) to establish a new species was the short length (i.e., 6 mm) of the apparently truncated ligament. Minor differences between *C. secunda* and *C. variabilis* concern shell shape. In conclusion, the validity of Lupu's species is highly questionable because of the insufficient diagnosis, based on only few characters of a largely incomplete example.

Morris and Skelton (1995) described *Colveraia* aff. *variabilis* on the basis of three specimens from rudist-bearing beds at Qarn Mulayh, Qarn Murah and Jebel Faiyah (United Arab Emirates/Oman border region), of late Campanian(?)–earliest Maastrichtian and Maastrichtian age, representing the first record of the genus from the Arabian plate. These specimens bear a rare peculiarity, in that they show canals in the inner shell layer of both valves. In the RV, a single row of large subquadrate canals separates the sockets and the myophores from the outer shell layer. In the LV, the canals are somewhat narrower and radially elongate and penetrate the teeth and myophores. Moreover, in one specimen from Jebel Faiyah (Simsima Formation), the outer surfaces of both the teeth and myophores are longitudinally ridged, with the ridges apparently formed by the canal walls, which interdigitate with ridges on the muscle attachment surface of the opposing valve. These characters have not been noted by us in any specimen of *Colveraia darendeensis* or *C. variabilis*.

Material of *C. variabilis* was illustrated from the Maastrichtian of the Tarbur Formation (Zagros region, SW Iran) by Khazaei et al. (2010). These specimens show an ornamentation that differs from that of *C. variabilis* and *C. darendeensis*. Unfortunately, our knowledge of characters needed for a detailed description and hypothetical separation of the Iranian specimens is insufficient to date.

Other examples of radiolitids supposedly belonging to the genus *Colveraia* were recorded from elsewhere in Europe (e.g., Sladić-Trifunović and Campobasso, 1980; Sladić-Trifunović, 1981b; Slišković, 1984 and others), but in all these cases only incomplete examples were examined. For instance, records of *C. variabilis* from Poggiardo (Apulia, southern Italy) and from Brac Island (Croatia) were based only on small areas showing a canal pattern of the LV (Sladić-Trifunović and Campobasso, 1980). In addition, Sladić-Trifunovic (1987) admitted that the size of specimens recovered at Poggiardo and on Brac Island was much smaller compared to examples of *C. variabilis* found near Maniago (Friuli). Therefore, it is problematic to attribute these specimens to that species and, perhaps, also to the genus *Colveraia*.

6. Conclusions

The lectotype of *C. variabilis* Klinghardt, 1921 and newly referred specimens of the same reveal a number of unknown characters of this very rare radiolitid and allow to correct many mistakes Klinghardt made in his diagnosis of the species. In spite of the lack of entire specimens, it has been possible to evaluate almost the full range of external and internal characters of *C. variabilis* and to separate it from *Colveraia darendeensis* Karacabey, 1974. Although Klinghardt (1921) did note a marked range of variation in features of *C. variabilis*, the variability we have observed was not significant.

At present, genuine specimens of *C. variabilis* have been collected only from the Mt. Jouf area (Friuli, Italy). Other specimens were recorded from different localities in Europe, but their attribution to the species in question, based mostly on incomplete descriptions and poor photographs, is considered uncertain. Entire, well-preserved specimens of *Colveraia darendeensis* are known from numerous localities across Turkey; it differs from *C. variabilis* in the ornamentation of LV and RV, the radial band area and general shell shape.

The enigmatic *Colveraia* aff. *variabilis* described by Morris and Skelton (1995) and specimens of *Colveraia* from Iran (Khazaei et al., 2010) need to be re-examined and compared with congeners. New results and finds are also called for to understand the phylogenetic relationships among these particular radiolitids better.

Hopefully, the present note is a starting point for future research into the genus *Colveraia* and other genera belonging to the "*Colveraia* group" (Skelton, 2013a). Unfortunately, current knowledge of the precise stratigraphical distribution of these canaliculate radiolitids and of phylogenetic and evolutionary relationships within the group is largely insufficient.

Acknowledgements

We are grateful to Dr Georg Heumann and Mr Georg Oleschinski (Steinmann Institute of Palaeontology, Goldfuss Museum, Bonn, Germany) and Mr Armin Schmitt (former curator, Goldfuss Museum) for data and photographs and for providing access to the historical rudist material of Klinghardt. We also thank Dr Martin Aberhan (Museum für Naturkunde, Leibnitz Institute for Evolution and Diversity Science, Berlin, Germany), Cahit Dönmez (director of MTA Museum, Ankara, Turkey), Dr Liana Săsăran (Babeş-Bolyai University, Department of Geology, Cluj-Napoca, Romania) and Dr Ahmad Reza Khazaei (Department of Geology, University of Birjand, Iran). In addition, we are grateful to Nicol Grigo for the translation of Klinghardt's paper, Davide Trovò for improving the previous English text, Liana Săsăran and an anonymous reviewer for valuable comments on an earlier typescript and Elena Jagt-Yazykova, associate editor of the journal, for linguistic corrections and suggestions that helped improve our manuscript.

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