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MARMARONIA ANGIOLINII, NEW GENUS AND NEW SPECIES OF BAKEVELLIIDAE (PTERIOIDA, BIVALVIA) FROM THE MIDDLE PERMIAN OF CHIOS (GREECE)

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Riassunto. I "Calcari a Gymnocodiacee" guadalupiani (Permiano Medio), affioranti nella parte nordorientale dell'isola Greca di Chio (Egeo orientale), sono tra i più fossiliferi della Tetide occidentale. Essi contengono ricche associazioni a coralli, brachiopodi, molluschi, alghe calcaree, foraminiferi e ostracodi, tuttavia, mentre i brachiopodi e i foraminiferi sono stati oggetto di studi sistematici, scarsa attenzione è stata dedicata, sino ad ora, alle faune a molluschi.

Nel presente lavoro viene istituito il nuovo genere *Marmaronia* con specie tipo *Marmaronia angiolinii* n. sp. per comprendere alcuni bivalvi della famiglia delle Bakevelliidae King, 1850, rinvenuti nelle successioni del Guadalupiano medio della località di Marmaro. *Marmaronia angiolinii* n. gen. n. sp. é fortemente inequivalve, con valve che differiscono per convessità, sviluppo degli umboni e ornamentazione. La valva sinistra presenta un solco radiale che partendo dall'umbone giunge al margine ventrale ed é ornata da robuste coste radiali; la valva destra presenta rughe di crescita concentriche e debolissime coste radiali visibili nella parte posteriore della conchiglia dei primi stadi di crescita di alcuni esemplari; entrambe le valve mostrano un'ala posteriore espansa.

Nel presente lavoro vengono inoltre discusse brevemente due ipotesi riguardanti un possibile adattamento epi- o endobissato di *Marmaronia*.

Abstract. The Guadalupian (Middle Permian) "Gymnocodiacean Limestones" cropping out in the north-eastern part of the Greek island of Chios (eastern Aegean Sea) are amongst the most fossiliferous in the western Tethys. They contain rich assemblages of corals, brachiopods, molluscs, calcareous algae, foraminifers and ostracods. Scant attention was given till now to mollusc faunas compared with brachiopods and foraminifers. In the present paper the new genus *Marmaronia*, with type-species *M. angiolinii* n. sp., is established to distinguish some bivalves of the Bakevelliidae King, 1850, from the middle Guadalupian successions of the Marmaro locality in Chios Island.

M. angiolinii n. gen. n. sp. is strongly inequivalve, with valves differing in convexity, umbo development and ornamentation. The left valve shows a radial furrow running from the anterior part of the umbonal region anteroventrally and is ornamented by strong radial costae; the right valve is ornamented by concentric sculpture and by thin rugae in the first growth stages of the posterior part of the shell. Both valves have a wide posterior wing.

Two hypotheses concerning the epi- or endobyssate adaptation of *Marmaronia* are also discussed briefly in the present paper.

Introduction

The study of Permian bivalves of the Tethyan province was neglected compared with other fossil groups such as foraminifers, conodonts and brachiopods. The majority of the limited literature addresses the Eastern Tethys (see Hayami & Kase 1977; Nakazawa & Newell 1968; Wanner 1922, 1940); Permian bivalves in the western part of the Tethyan province were described by Gemmellaro (1892), Termier et al. (1977), Boyd & Newell (1979) and recently by Dickins (1999).

In the last few decades the importance of Permian bivalve faunas in the fields of palaeoecology, palaeobiogeography and biostratigraphy has been recognized.

The discovery of a connection between the cold water *Eurydesma* fauna and the late Paleozoic Gondwanan glaciations, for example, was useful for the interpretation of Permian climate changes, as well as for global correlations (Harrington 1955; Dickins 1957, 1978, 1984).

Moreover, the bivalve assemblages associated with the transgression on the mid-Permian unconformity, are found in many parts of the world, including Australia, New Zealand, the northern Russian Region, the central and southern United States and recently Oman (Dickins 1997, 1999). These faunas are characterised by the appearance of new pectinacea and permophorids, and by the development of multivincular pterioid forms such as *Bakevellia* (Dickins 1997).

From a biostratigraphic point of view, some genera discovered for the first time in the Permian successions have acquired today a great importance not only in the Permian, but also in the Lower Triassic.

Some species attributed to the genus *Towapteria* Nakazawa & Newell, 1968, for example, have now a great biostratigraphic importance in the Tethyan province. In particular *T. schytica* (Wirth) was men-

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Fig. 1 - Location map of Chios in the Aegean area.

tioned for the first time in the Eastern Tethys deposits of western China (Wirth 1936) and later in the Dolomites (Broglio Loriga et al. 1983). Later this species presence was confirmed in the basal Lower Triassic of south-western China (Chen 1980). Today *T. schytica* is considered an important index for Lower Triassic global correlations (Shen et al. 1995, Yin & Tong 1998; Kozur 1998).

Today the knowledge on bivalves in some areas of the Tethys is almost non-existent and according to Yancey (1985), a high degree of endemism shown by some Permian faunas could be only the result of lack of knowledge. Perhaps new studies on bivalves will permit to discover new taxa useful for the correlations of Permian benthonic faunas.

This work is part of wider investigations on the Palaeozoic successions of Chios Island, involving many researchers from the Dipartimento di Scienze della Terra of the Università di Milano and from other Italian and European Universities.

Previous works and geological setting.

The island of Chios, one of the largest in Greece, is located in the eastern Aegean Sea a few kilometres from the Turkish coast of the Karaburun peninsula (Fig. 1).

According to many authors (Herget & Roth 1968, Besenecker et al. 1968, 1971) two tectono-stratigraphical units can be distinguished on Chios Island: an autochthonous unit and an overthrust of an allochthonous unit. The lower unit consists of a thick Palaeozoic succession, composed of terrigenous rocks, cherts, volcanics and limestones (the last dated from Silurian to Carboniferous), which is overlain by a Meso-Cenozoic succession. The allochthonous unit comprises an Upper Carboniferous to Upper Permian sequence, underlying a Liassic shallow-water carbonate platform. Red siltstones of uncertain age separate them (Kauffmann 1969; Besenecker et al. 1968). The study area described in this paper belongs to the allocthonous unit.

A Middle Permian carbonate sequence crops out specifically near Marmaro, Agrelias and Parpanda. These very fossiliferous limestones were called "Gymnocodiacean limestones" (Gymnocodiaceen-Kalke) by Kauffmann (1969) (Fig. 2). Fossils consist of calcareous algae, corals, molluscs, echinoids, brachiopods, fusulinids, smaller foraminifers, ostracods and conodonts.

Flajs et al. (1996a) provided a list of the most frequent algae which are *Gymnocodium bellerophontis, Permocalculus texanum, Mizzia velebitana* and *Pseudovermiporella sodalica*, but until now no systematic study of these algae has been produced. On the contrary, the systematics of the rich assemblage of silicified brachiopods from some levels of the "Gymnocodiacean limestones" near Marmaro, was studied by Grant (1993).

An age for the "Gymnocodiacean limestones" was given by Kahler (1987) who studied foraminifers sampled by Kauffman during his doctoral thesis. He mentioned the presence of the foraminifers *Nankinella inflata* and *Eoverbeekina intermedia*, that correspond to the Middle Permian, in the "Gymnocodiacean limestones" of the Marmaro section.

According to Flajs et al. (1996a) the "Gymnocodi-

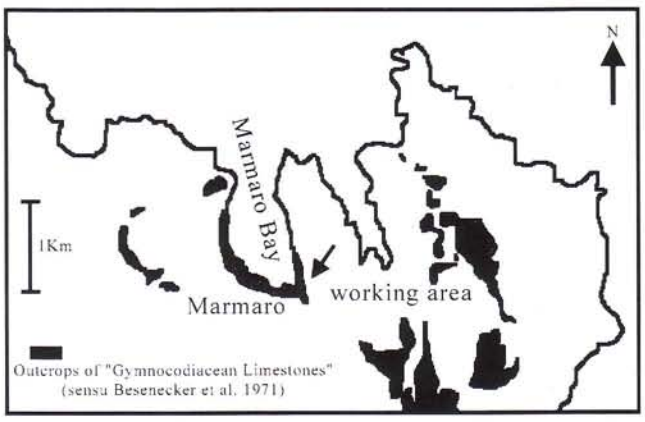


Fig. 2 - Simplified geological map of northeastern Chios (rectangle in fig. 1) showing the investigated area and the outcrops of "Gymnocodiacean limestones" (from Flajs et al. 1996a, modified).

acean limestones" exposed in the Marmaro section belong either to the Verbeekina Zone or to the Neoschwagerina Zone, which correspond to the middle Guadalupian.

No work was devoted to the mollusc faunas up to now.

The Marmaro section.

One of the best exposed outcrops of the "Gymnocodiacean limestones" is located on the eastern side of the Marmaro beach (Fig. 2).

The Marmaro section (Fig. 3), approximately 32 meters thick, was divided into 5 Units by Flajs et al. (1996a). The stratigraphy of the present paper is based on that work. Unit 1 reaches a thickness up to three meters. This unit is composed of dark grey to black or brown thin-bedded limestones, which include mudstones, wackestones, packstones, floatstones and framestones. It consists of 30-60 cm thick individual layers of yellow-brown limestones with corals (*Multithecopora* sp.) and intercalations of brachiopods and black limestones with molluscs and foraminifers; the amount of corals decreases towards the top of the unit, while at the base corals form biostromes. Foraminifers, calcareous algae and a variety of encrusting micro-organisms form the bulk of the microfossiliferous assemblage. Some coquina beds suggest tempestite deposits and red and green algae, which locally form algal packstones, indicate moderate water depths (Flajs et al. 1996b).

Unit 2 consists mainly of grey to brown calcareous marls up to 2 m thick. Abundant richtofeniid brachiopods, many bryozoans, echinoderms and kirkbyacean and bairdiacean ostracods, which are supposed to indicate calm water conditions (Flajs et al. 1996b), are present locally.

Richthofeniids in the upper levels form a massive reef limestone up to 6 m thick, called Unit 3.

Calcareous marls with a very high fossil content (Unit 4) separate the richthofeniid bank from regularly bedded limestones containing calcareous algae and oncoids (Unit 5) which represent the end of the Marmaro Permian sequence.

Many specimens of a single species of bivalve can be collected in all the units of the "Gymnocodiacean limestones", except for Unit 3. Systematics analyses showed that these bivalves belong to a new genus and a new species for which the name *Marmaronia angiolinii* is introduced. The Types of *Marmaronia angiolinii* n. gen. n. sp. were collected in the upper part of Unit 1 (fig. 3).

Some specimens of *Marmaronia angiolinii* (MPUM8605A-D) were collected also by L. Angiolini and L. Carabelli (Dipartimento di Scienze della Terra, Università degli Studi di Milano) in the locality of sample USMN9592 of section II, described by Grant (1993) in the region of Agrelia (Parpanda).

Faunal and sedimentological features in the mudstones and marls of Unit 1 (the Stratum Typicum of *Marmaronia angiolinii* n. gen. n. sp.) suggest calm waters and a lagoonal environment, but probably the coquinas of this unit indicate that this environment was subjected to periodically heavy and deep-reaching storms. Bivalved specimens of *Marmaronia* are present in the mudstones of Unit 1, together with spines of large quasi-infaunal brachiopods. On the contrary, in the coquinas valves are always disarticulated, often selected by transport (actually some fossil concentrations are composed exclusively of right valves).

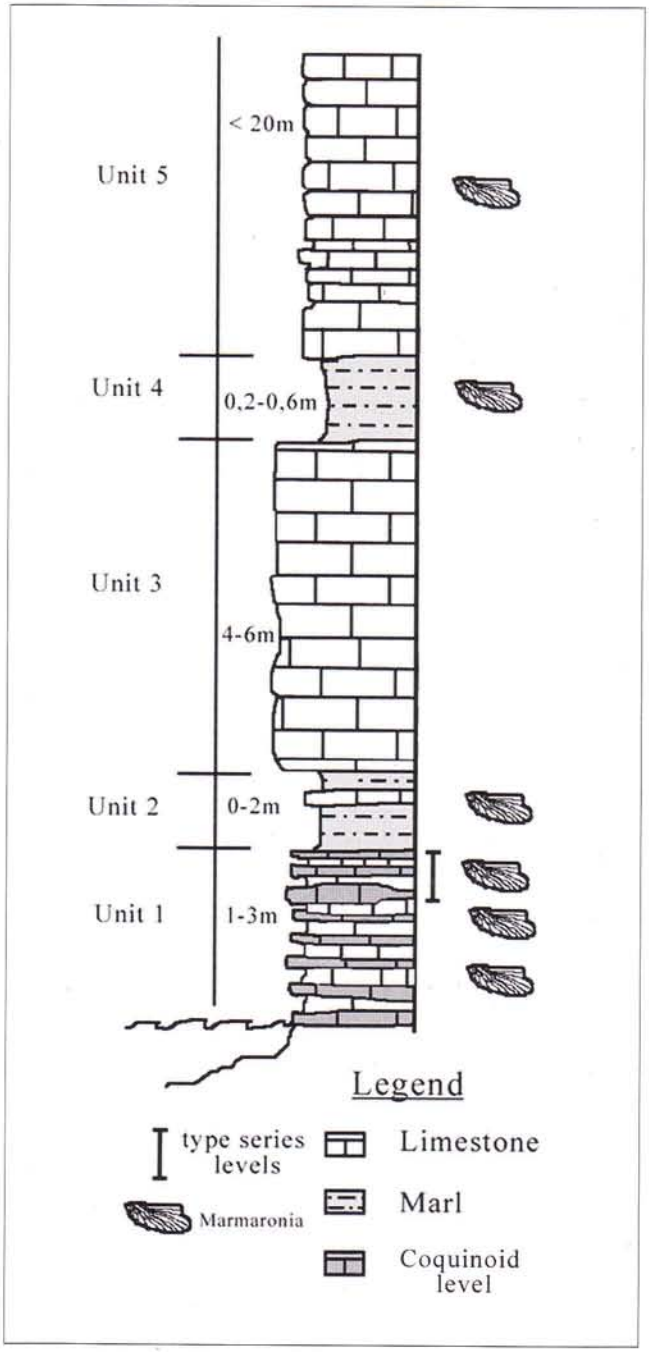


Fig. 3 - Stratigraphical section of "Gymnocodiacean Limestones" outcropping in the Marmaro bay (from Flajs et al. 1996a, modified).

Systematic Paleontology.

Illustrated and described specimens are housed in the collections of the Dipartimento di Scienze della Terra, Università degli Studi di Milano, Museo di Paleontologia, via Mangiagalli 34, Milano, Italy (numbers with the prefix MPUM).

Phylum **Mollusca**

Class **Bivalvia** Linné, 1758 (Buonanni, 1681)

Subclass **Pteriomorpha** Beurlen, 1944

Order Pterioida Newell, 1965

Suborder Pteriina Newell, 1965

Superfamily Pteriacea Gray, 1847 (1820)

Family Bakevelliidae King, 1850

Preliminary remarks

The important family of Bakevelliidae (King, 1995), which includes highly inequilateral Pterioida with a usually rhombic to trapezoidal outline, originated in the Permian and flourished in the Cretaceous.

According to Muster (1995) important diagnostic features of the family are the outline (defined by parameters diagonal, maximum length of the body, length of the posterior wing, and obliquity), shell ornamentation, wing shape, position and shape of the umbones, hinge, and muscle scars.

Marmaronia n. gen., showing all the features of this family, represents one of the most ancient members of this group.

Marmaronia n. gen. is similar to some genera of Cassianellidae Ichikawa, 1958, for the presence of a well-developed radial furrow on the left valve; however, the internal septum, important character of the Cassianellidae, is absent.

The records of Cassianellidae in the Permian successions are still sporadic and based on incomplete specimens in which the important internal characters are often not visible.

Genus *Marmaronia* n. gen.

Type species *Marmaronia angiolinii* n. sp.

Etymology. Genus named from the locality of Marmaro (Μαρμαρο), island of Chios, Greece.

Composition of the genus. At present the genus is composed only by the type species *Marmaronia angiolinii* n. sp.

Diagnosis. Shell small, oblique, prosocline, from rhombic to trapeziform, inequilateral and posteriorly alate, strongly inequivalve; shell sinuated for byssus in the antero-ventral margin.

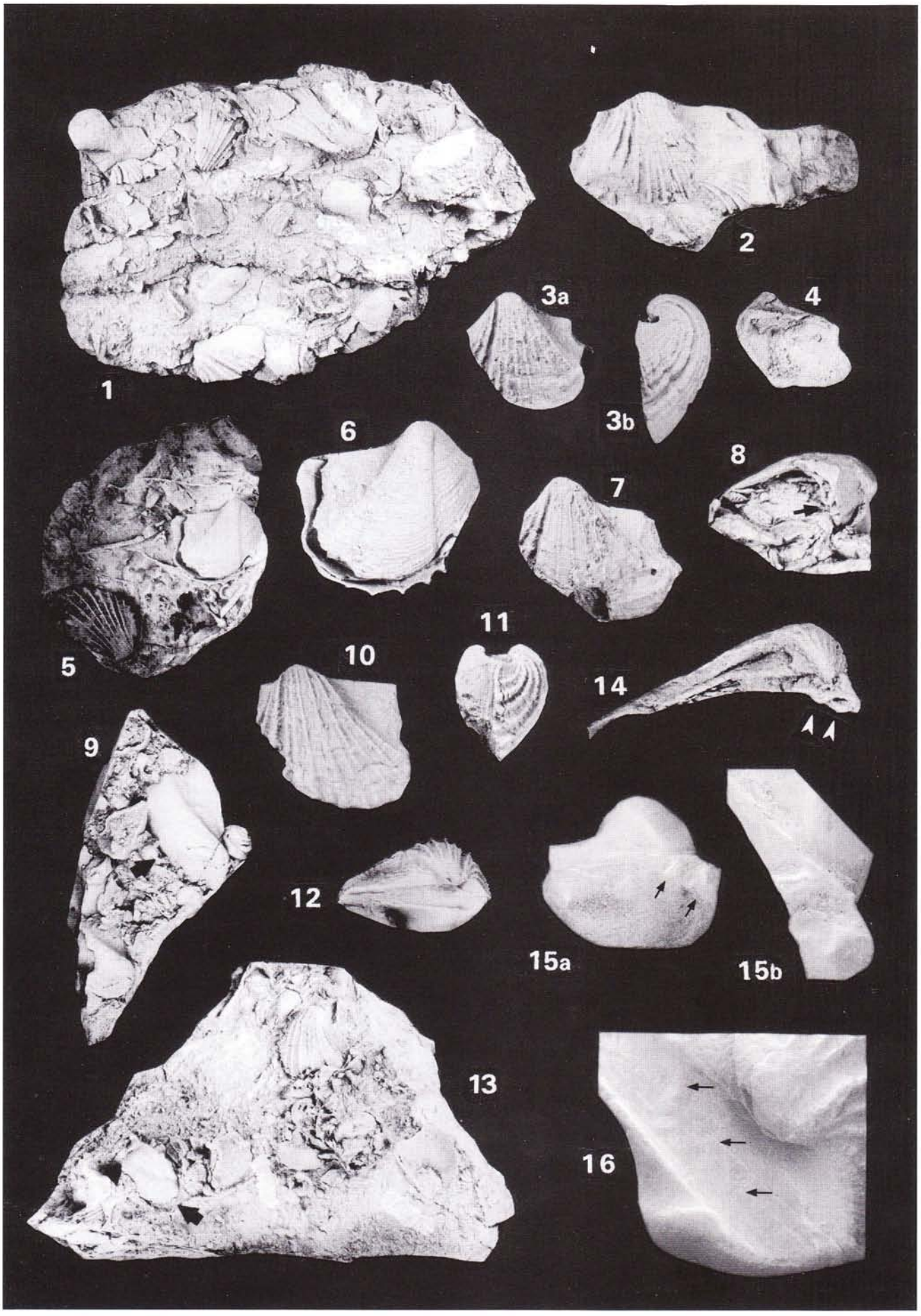
Left valve strongly convex, with prominent umbo ornamented by strong radial costae, anterior not lobate but with a radial furrow running from the anterior part of the umbonal region to the ventral margin. Right valve less convex, with prominent umbo, without a true anterior auricle, but with an anterior lobe depressed in comparison with the umbonal region; right valve ornamented by a concentric sculpture and by few, thin, filiform costae in the posterior part of the shell body, present only in the first growth stages; hinge consisting of two (or perhaps three in the right valve) cardinal teeth and one slender, long, posterior lateral tooth parallel to the hinge margin. Ligament area straight and rather wide, ligament multivincular.

Discussion. The new genus is similar to the genus *Towapteria* Nakazawa & Newell, 1968 established on the basis of some specimens from the Japanese Middle Permian associations of the Tenjinnoki and Kanokura Formations (Nakazawa & Newell, 1968), and later discovered in other Permian and Lower Triassic localities of the Western and Eastern Tethys.

Muster (1995), in his emended diagnosis of the genus *Towapteria*, defined this genus as a Bakevellidae without radial ribs on the anterior wing. However, this is true only for the right valve because the holotype of the type species *T. nipponica* Nakazawa & Newell, 1968 (Pl.3 fig.8), which is a left valve, shows radial ribs in the anterior part of the shell (which does not have a real anterior wing or lobe, also according to the original

PLATE 1

Fig. 1 - Little slab from the coquinoid levels (upper part of Unit 1, Marmaro section) with valves of *Marmaronia angiolinii* n. gen. n. sp. (x 1).
Fig. 2 - *Marmaronia angiolinii* n. gen. n. sp., left valves from Agrelia (x 1).
Fig. 3a, b - *Marmaronia angiolinii* n. gen. n. sp., paratype MPUM8603N, left valve; 3a: lateral view (x 1.5); 3b: frontal view (x 2).
Fig. 4- *Marmaronia angiolinii* n. gen. n. sp., paratype MPUM8604D, right valve, internal view (x 1.5).
Fig. 5 - Little slab from the upper part of Unit 1, Marmaro section, on the right the paratype MPUM8602 (the same specimen in fig. 6)(x 1.5).
Fig. 6 - *Marmaronia angiolinii* n. gen. n. sp., paratype MPUM8602, articulated specimen, lateral view of the right valve (x 3).
Fig. 7 - *Marmaronia angiolinii* n. gen. n. sp., paratype MPUM8603M, left valve, lateral view (x 1.5).
Fig. 8 - *Marmaronia angiolinii* n. gen. n. sp., paratype MPUM8604G, right valve, oblique view of the partially broken hinge (see arrow) (x 2).
Fig. 9 - Little slab with right valves of *Marmaronia angiolinii* n. gen. n. sp., the arrow indicates the paratype MPUM8604A (x 1.5).
Fig. 10-12, 16 - *Marmaronia angiolinii* n. gen. n. sp., holotype MPUM8601, articulated specimen; 10: lateral view of the left valve (x 2); 11: frontal view (x 2); 12: dorsal view (x 2); 16: ligament area showing the ligamental pits (marked by arrows) (x 8).
Fig. 13 - Little slab from the coquinoid levels (upper part of Unit 1, Marmaro section), with valves of *Marmaronia angiolinii* n. gen. n. sp., the arrow indicates the paratype MPUM8604G (see also fig. 8) (x 1).
Fig. 14 - *Marmaronia angiolinii* n. gen. n. sp., paratype MPUM8604G, left valve, hinge area with cardinal teeth marked by arrows (the tooth on the left is broken) (x 3).
Fig. 15a, b - *Marmaronia angiolinii* n. gen. n. sp., paratype MPUM8603W, left valve; 15a: internal view with cardinal teeth marked by arrows (x 8); 15b: enlargement of the hinge (x 20).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description by Nakazawa & Newell 1968; p. 58).

The original diagnosis of *Towapteria* by Nakazawa & Newell (1968) can be considered still valid.

The new genus *Marmaronia* is distinguished from *Towapteria* in the less pteriiform outline (because of the presence of a more expanded posterior wing, with a less incised sinus), in a wider ligament area, in the prominent umbo of the right valve (beak located above the hinge margin) and in the ornamentation of the right valve.

The radial costulation is very slight in the first growth stages and absent in the adult stage.

Costigervillia Cox & Arkell, 1948 differs from *Marmaronia* in the outline, in the more developed obliquity of the shell, in the presence of an anterior wing on the left valve and of few but strong ribs on the right valve.

Single valves of *Marmaronia* n. gen. are similar to the valves of some genera such as *Arcavicula* Cox, 1964 (right valve) or *Oxytoma* Meek, 1864 (left valve).

Occurence. "Gymnocodiacean limestones" sensu Kauffmann (1969) of Chios Island (Greece).

Age. Middle Guadalupian (Middle Permian).

Marmaronia angiolinii n. sp.

(Plate 1)

Material. Total: 43 specimens. 39 specimens from Marmaro (MPUM8601, 2; MPUM8603A-Z, α, ß; MPUM8604A-L) and 4 specimens From Agrelia (MPUM8605A-D).

Type series (28 specimens).

Holotype. A bivalved complete specimen: MPUM8601 (Pl. 1, fig.10-12, 16).

Paratypes. Bivalved complete specimen: MPUM8602; left valves (16 specimens): MPUM8603A, B, D-F, J, K, M, N, O-Q, U, Y, W, Z; right valves (10 specimens): MPUM8604A-L.

Etymology. Species named in honour of Lucia Angiolini.

Stratum Typicum and Locus Typicus. The locus typicus is the Marmaro section and the Stratum Typicum is the upper part of Unit 1 sensu Flajs et al. (1996a).

Diagnosis. As for the Genus.

Description. Shell small, oblique, prosocline, from rhombic to trapeziform, inequilateral and posteriorly alate. Ratio of height to length about 0.9. Strongly inequivalve, left valve strongly convex, anterior not lobate, but with a radial furrow running from the anterior part of the umbonal region to the ventral margin; right valve less convex, without a true anterior auricle, but with an anterior lobe depressed in comparison with the umbonal region.

Both umbones are narrowly rounded, protruding and placed anteriorly. Dorsal margin long and straight, a little shorter than the length of the shell.

Valves discordant, right valve smaller than the left. No subauricular notch, only faint traces of a sinuation in the antero-lateral margin.

Posterior wing very wide separated from the body of the shell by a very shallow sinus.

Ligament area rather developed, perpendicular to the commissure plane of valves, wider in the right valve than the left, even if the left is wider and more convex. Ligament multivincular, with several weak, subrectangular or rarely subtrigonal pits; on some specimens (MPUM8601, MPUM8603N) the pits are at least five, and one of them is located under the beaks.

Hinge consisting of two cardinal teeth on the left valve, (one under the beak and one strong anterior cardinal, Fig. 4) and one slender, long, posterior lateral tooth parallel to the hinge margin. On the right valve hinge consisting of two (or three) cardinal teeth and, like in the left valve, one slender, long, posterior lateral tooth parallel to the hinge margin.

Surface of left valve sculptured by radial costae of one or two orders and by concentric costae over shell body and posterior wing, radials more or less scaly and sometimes nodose at intersections with concentric costae. On the larger specimens there are 6-9 costae near the ventral margin, between the radial umbonal sulcus and the posterior margin of the shell body (which separates the body margin from the posterior wing). Before the sulcus there are 7-8 strong radial costae; the posterior wing has a reticulate ornamentation because of the intersections between 7-8 weak radial costae and the growth rugae. There are costae of the first and second order, the latter rare and present only in specimens larger than 7 mm.

Right valve ornamented by concentric growth rugae and in some specimens, in the first growth stages, by few very thin costae near the posterior margin of the shell body (this radial costulation is perhaps present

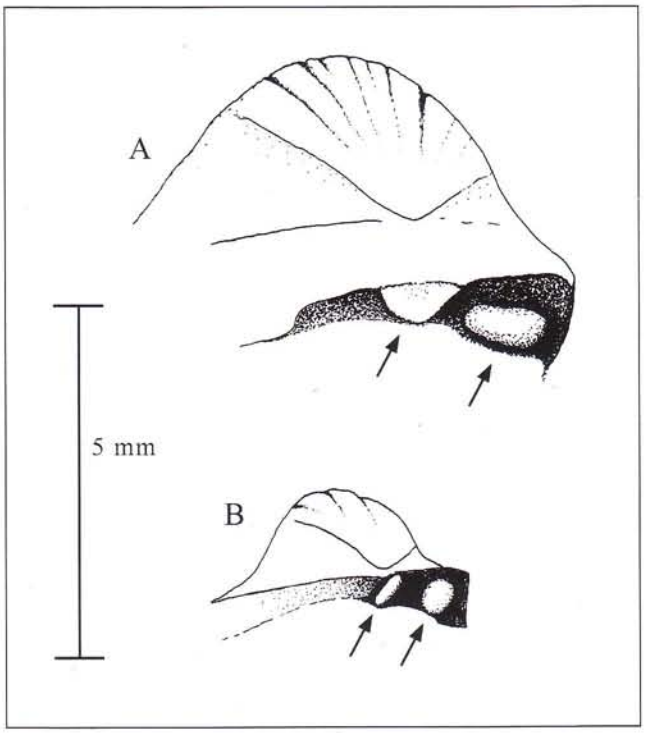

Fig. 4 - Reconstruction (from camera-lucida, shaded) of the cardinal teeth (marked by arrows) in two left valves, A: specimen 8603D, B: specimen 8603W.

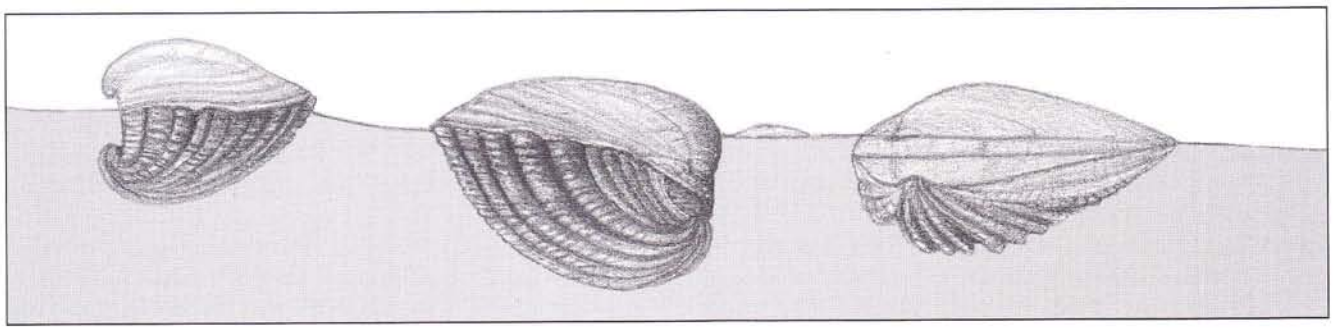

Fig 5 - Hypothetical endobyssate life habit of *Marmaronia*.

only in few specimens because it has been removed by abrasion or weathering).

A displacement of the radial ornaments visible on the MPUM8603F specimen might indicate that the organism survived a trauma.

Muscle scars and pallial line not observed.

Dimensions (in cm).

Specimen	Length	Height	Thickness
MPUM8601 (Holotype, bivalved specimen)	1.4	1.3	0.8
MPUM8602 (paratype, bivalved specimen)	1	0.9	-
MPUM8603M (paratype, left valve)	1.9	1.7	0.6
MPUM8603N (paratype, left valve)	1.4	1.3	0.4
MPUM8604D (paratype, right valve)	1.3	1.1	-

Discussion. Apart for the generic characters, *Towapteria nipponica* Nakazawa & Newell, 1968 differs from *Marmaronia angiolinii* n. gen. n. sp. in having more numerous and differentiated (to 3rd order) radial costae on the left valve.

There are some similarities between the first ontogenetic stages of *Gervillaria alaeformis* (Sowerby, 1819) and *Marmaronia angiolinii* n. gen. n. sp. but the left valve of this species shows a distinct anterior wing.

Marmaronia angiolinii n. gen. n. sp. is similar externally to *Cassianella decussata* (Muenster, 1834), but the latter shows a developed anterior auricle.

Only the right valve of *Marmaronia angiolinii* n. gen. n. sp. is similar to the right valve of *Bakevellia ceratophaga* (Schlotheim, 1816), but can be distinguished by a more prominent umbo and a wider posterior wing.

Occurrence and Age. The same as the genus.

Palaeoecological remarks

Like the others Bakevelliidae, *Marmaronia* probably lived fixed to the sea floor temporarily or permanently by byssal attachment. In agreement with the "Gymnocodiacean limestones" fossil assemblage of corals, brachiopods and calcareous algae, it lived in very shallow waters.

The morphology of *Marmaronia* suggests two possible different strategies of byssal attachment: epibyssate or endobyssate habit.

Following the model of Kauffman (1969) which correlates the shell shape with the exposure to currents, *Marmaronia* shows a rather hydrodinamically streamlined shell. Perhaps *Marmaronia* lived as an epibyssate in the most exposed lagoonal environments or in coralline patch reefs, attached to the biostromes made up of syringoporid corals (*Multhitecopora* sp.), brachiopods and calcareous algae. Yet this epibyssate habit is most suitable for bivalves which have, unlike *Marmaronia*, a developed anterior auricular sulcus and a byssal sinus (see also: Stanley 1972).

The model proposed by Seilacher (1983) for the byssate Bakevelliidae seems most suitable for *Marmaronia*. According to this model *Marmaronia* was endobyssate, partly buried in mud. It would have lived reclined flatly in the sediment, and the strongly inequivalved shell could be evidence of this way of life. *Marmaronia* rested on the left valve, which is more convex and bears stronger sculpture to increase adhesion to the sediment (Fig. 5). The ligament area of *Marmaronia* is more developed than in similar epibyssate forms because the ligament must have acted against the sediment pressure.

This way of life seems to be confirmed by taphonomic analyses: the mud levels of the upper part of Unit 1, in which bivalved specimens can be collected, could represent the levels in which the bivalves lived.

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