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LATE TRIASSIC MEGALODONTIDAE FROM NORTHERN CALABRIA (ITALY)

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Key-words: Megalodontidae (Bivalvia), Late Triassic, Southern Italy, Taxonomy, Functional morphology.

Riassunto. Da lumachelle raccolte nei dintorni di Castrovillari (Cosenza) e appartenenti all'Unità di Piattaforma Carbonatica del Triassico superiore della Calabria settentrionale sono state isolate numerose conchiglie di Megalodontacei. Tale conservazione, inusuale per questi bivalvi, ha permesso l'osservazione dei caratteri morfologici sia della conchiglia che del modello interno.

L'analisi biometrica ha consentito di descriverne la variabilità morfologica e di riconoscere nell'associazione due diversi morfogruppi, entrambi riferibili al genere *Triadomegalodon* e considerati appartenenti ad un'unica specie che presenta alcuni caratteri distintivi rispetto alle specie note. Tuttavia il cattivo stato di conservazione delle conchiglie, affette da disarticolazione, abrasione e frammentazione, induce prudenza nella creazione di un nuovo taxon [*Triadomegalodon* sp. n. aff. *tofanae* (Hörnes)].

Considerazioni morfofunzionali portano a ritenere che *Triadomegalodon* fosse un bivalve seminfaunale, non attivamente fossatore.

Abstract. Several shells of megalodontids have been extracted from densely packed coquinas coming from the Upper Triassic of northern Calabria (Southern Italy). Such a mode of preservation, which is unusual for these bivalves, has made it possible to detect the morphological characters regarding both the shell and inner mould.

Morphological variability has been identified by means of biometrical analysis, which allows them to be separated into two morpho-groups both belonging to the genus *Triadomegalodon.* Here they are considered to be the extreme morphotypes of a single species, which has some peculiar characteristics with respect to the known species. However, the bad state of the preservation of the shells, which are affected by disarticulation, abrasion and fragmentation, induces us to act with caution establishing a new taxon [*Triadomegalodon* sp. n. aff. *tofanae* (Hörnes)].

Some aspects of functional morphology led us to consider *Triadomegalodon* as a semi-infaunal bivalve, unable to burrow actively.

Introduction.

Recent studies on the structural framework of the junction between the Calabrian Arch and Apennine Chain (Ietto et al., 1992; Ietto & Barilaro, 1993; Ietto et al., in press) have consented the discovery of several fossiliferous localities in the Late Triassic carbonate platform of northern Calabria, the paleontological content of which is almost unknown. Among these, an outcrop located near Castrovillari (Cosenza) has provided several isolated, calcitized shells of megalodontids. Such a mode of preservation is unusual for these fossils because they generally occur in Late Triassic dolomitic formations (e.g. *Dolomia Principale* or *Hauptdolomit* facies) as internal moulds. Less frequently shells are found in limestone (e.g. *Dachsteinkalk* facies), but the hardness and recrystallization of the matrix generally hinders their isolation. Therefore, the majority of the megalodontid taxa have been created on internal moulds, and few on the shell. In the literature, the determination of specimens with a state of preservation opposite to that of the type-specimens is a source of great discrepancy between the different authors.

Systematic studies on the megalodontids from Southern Italy mostly regard the assemblages from the *Dolomia Principale* of Sicily (Di Stefano, 1912) and Campania (Galdieri, 1908). Little is known about shells preserved in limestone formations. As regards Calabria, only some citations had been made by Cortese (1895) and Di Stefano (1896).

The purpose of this paper is to contribute to the bio- and chronostratigraphic knowledge of the Late Triassic formations of Calabria and, due to the unusual preservation of the specimens, to approach some taxonomical and paleobiological aspects of the megalodontids.

In recent years, megalodontids have been object of various studies (Végh-Neubrandt, 1964, 1968, 1974, etc.; Zapfe, 1964, 1969; Allasinaz, 1965; Tichy, 1974; Allasinaz & Zardini, 1977; etc.). Recently, Végh-Neubrandt (1982) published the greatest taxonomical revision on the Triassic Megalodontidae, in which their evolutionary trends and complete references are reported. The classification used here will be mostly in accordance with that proposed by Végh-Neubrandt (1982).

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Stratigraphic setting and taphonomy.

The fossils come from a badly exposed sequence of carbonate platform located between the Cozzo della Paglia and Il Rotondello hills, about 2 km NW of Castrovillari (Cosenza), which represents the southern extremity of the Pollino Massif (Fig. 1).

The sequence consists of prevailing grey limestone sometimes dolomitized, and saccharoidal dark grey dolomite. It mainly forms the Cozzo della Paglia hill which is affected by several faults, and therefore an exact evaluation of the thickness of the sequence is impossible; it probably does not exceed 100 m. This sequence, which overlies the *Dolomia Principale*, yields several beds with *Griphoporella curvata* (Gümbel), particularly abundant in the lower part. The upper part is characterized by a rich foraminiferal assemblage with *Triasina hantkeni* Majzon and *Aulotortus* sp. (Ietto et al., in press).

A more detailed lithostratigraphic analysis, within the limits imposed by the tectonics and bad exposure conditions, allows us to recognize the following units (from top to bottom).

D) Thick layers of prevailing grey dolomitized limestone and loferitic dolomite intercalations. Some oolitic limestone beds yield frequent specimens of *T. hantkeni* and *Aulotortus* sp. Large megalodontids, about 20 cm in diameter (Fig. 2A) and algae (*Griphoporella curvata*) also occur (30-50 m thick).

C) Prevailing dark grey dolomite with grey limestone intercalations. The latter lithotype, with a grainstone matrix yields abundant forams, rare algae and scattered valves of megalodontids, 5-10 cm in diameter (about 10 m thick).

B) Grey limestone and dolomitic limestone with some megalodontid bearing coquinas, 10 to 30 cm in thickness, the matrix of which is a prevailing grainstone. The studied collection comes from these fossil concentrations. This unit, which also yields fragments of solitary and colonial corals, may have a thickness which does not exceed 30 m.

A) Prevailing grey loferitic limestone with intercalations of dark grey saccharoidal dolomite. Some beds are very rich with pyritized dasycladaceans, mainly represented by *Griphoporella curvata* (20-25 m thick).

The sequence belongs to the *Piattaforma Campano-Lucana* domain (D'Argenio et al., 1973). The megalodontid-bearing layers may correspond to the lower part of the *Calcari a Megalodus* of Cortese (1895) and Di Stefano (1896) who dated and correlated them to the Rhaetian Dachsteinkalk of the Alps. However, large discrepances occur in the literature on the litho- and chronostratigraphical meaning assigned to this unit, as its lithological limits and paleontological content were not defined exactly by Cortese (1895). For instance, Di Stefano (1904, p. 118) later denied the occurrence of the Rhaetian in this area and assigned the *"calcari con grandi Megalodus"* to the Dolomia Principale (Norian) and the *"facies del Dachsteinkalk"* to Liassic and Lower Cretaceous.

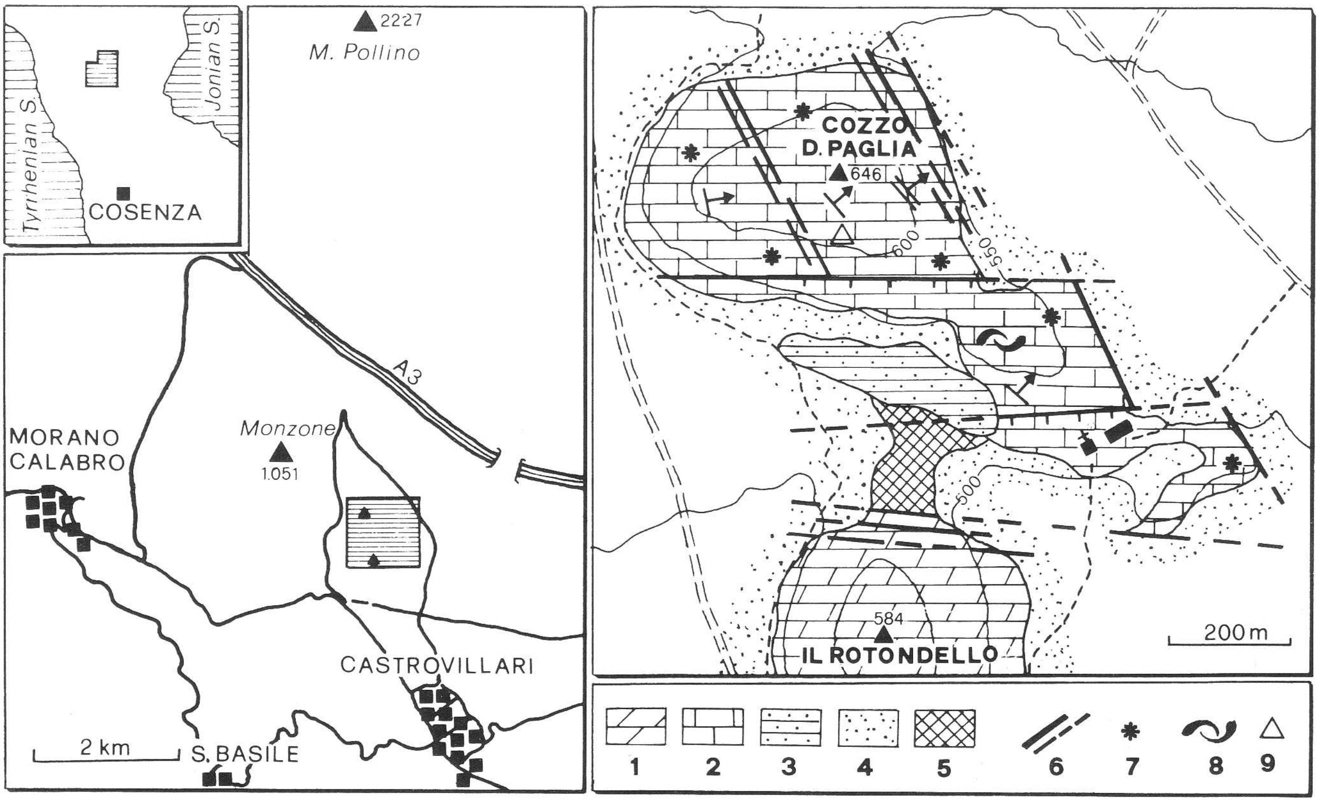


Fig. 1 - Geographical setting of the fossiliferous locality. Legend: 1) Dolomia Principale; 2) Limestone, dolomitic limestone and dolomite (Calcari a *"Megalodus"* Auctt. p.p.); 3) Miocene flysch; 4) detritus cover; 5) cataclastic rock; 6) main faults; 7) *Griphoporella* banks; 8) megalodontid bearing coquinas; 9) bank with large sized megalodontids, unit D (see Fig. 2A).

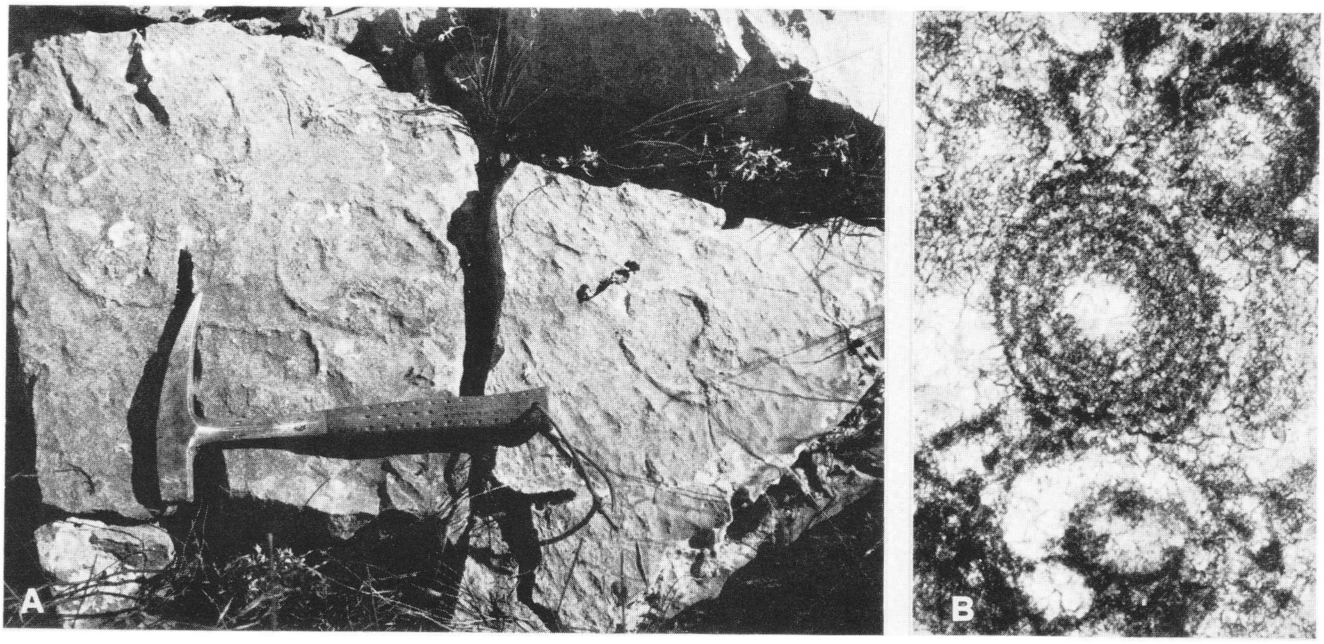


Fig. 2 - A) Large sized megalodontids from the upper part of the sequence (unit D); B) *Triasina hantkeni* Majzon in the matrix of the megalodontid bearing coquina, unit B (35 x).

T. hantkeni has been also found in the matrix of the megalodontid-bearing layers (Fig. 2B), and thus they belong to the *T. hantkeni* Range-zone which is considered, as a whole, to be Rhaetian in age (Zaninetti, 1976; Abate et al., 1984; De Castro, 1990). Such an age confirms the chronological setting of the lower part of the *Calcari a Megalodus* suggested by previous authors, especially by Cortese (1895).

Megalodontids are concentrated in densely packed coquinas found in small blocks which mostly contain disarticulated, fragmented and abraded valves with a grainstone-packstone matrix, light to dark grey in colour. Other clasts are represented by forams, algae remains (*Griphoporella* sp.), pellets and small rounded intraclasts. Such coquinas may be interpreted as storm wave concentrations. The ultimate burial of the megalodontids occurred after a period of bioclastic residence in shoal environments where fragmentation and abrasion took place.

These coquinas contain small and middle sized shell; the largest fragment, which mostly concerns umbonal and cardinal region, has a height of about 7 cm. The absence of larger shells is probably a result of sorting due to selective transport. Their occurrence in the biocoenosis may be presumed because articulated shells, about 10 cm in height, are yielded in the adjacent layers of the unit B, where the matrix and shell recrystallization impede their isolation. However, the lacking of larger shells (20 cm in diameter or more) must be also related to environmental and/or chronological factors, because very large specimens only occur in the upper part (Unit D) of the sequence.

The shell wall is made up of large neomorphic calcite crystals with relics of the original structure, and thus the specimens may be considered to be calcitized shells.

Biometrical analysis.

A statistical approach to analysing morphological variability can be performed on the Calabrian sample as some tens of specimens are available. However, the quantity and precision of the measurements vary on the basis of the selected character. In fact, some of them, such as the height and length of the shell, can be only estimated on the restored outline of few specimens, as the marginal thin anterior and ventral regions of shells are always broken and/or abraded. The measurements which are less influenced by the taphonomic factors

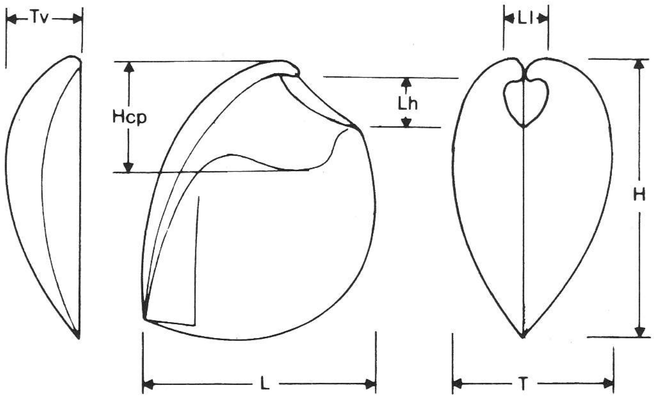


Fig. 3 - Morphometric parameters used in the biometrical analysis. Symbols: L) shell length; Ll) lunule length; Lh) lunule height; H) shell height; Hcp) distance between the ventral margin of the hinge plate and the umbo; T) shell thickness; Tv) valve thickness.

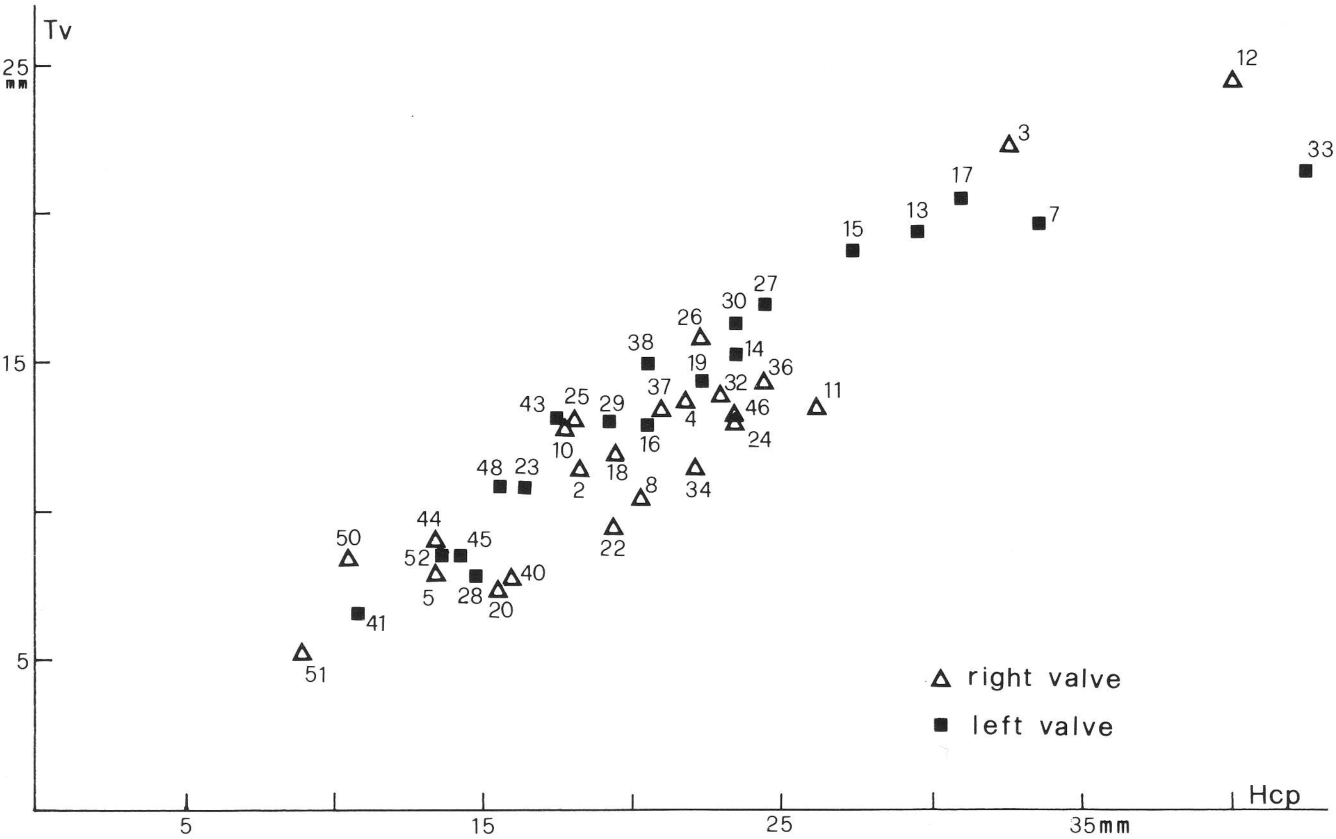


Fig. 4 - Scatter diagram in which the measurements (Tab. 1) of the valve thickness (Tv) and distance between the ventral margin of the hinge plate and the umbo (Hcp) are plotted.

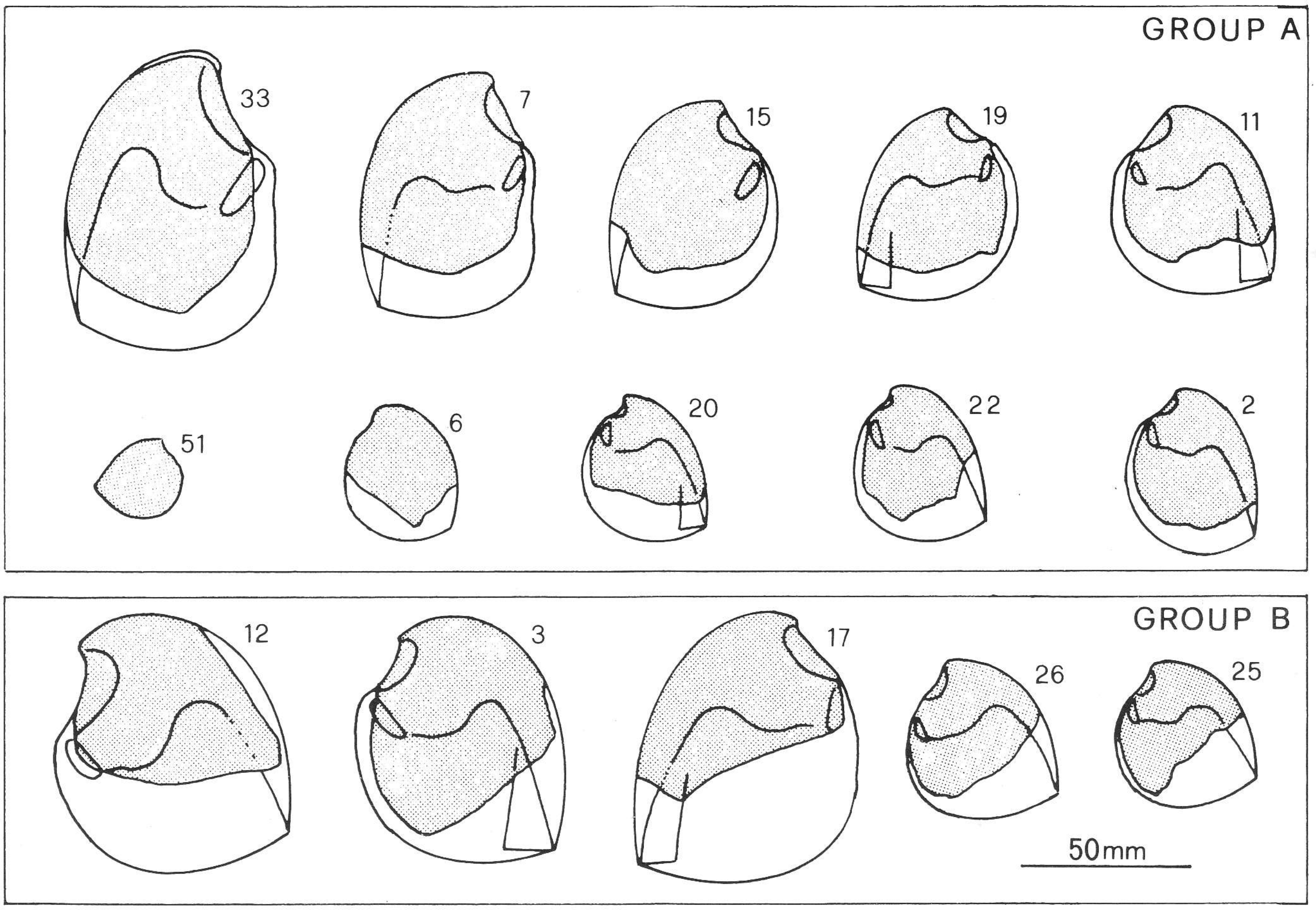


Fig. 5 - Restored outlines of some of the more complete specimens, the estimated measurements of which (Tab. 2) have been used in the diagrams of Fig. 6-8.

(fragmentation and abrasion) regard the distance between the ventral margin of the hinge plate and the umbo (Hcp) (Fig. 3), and the thickness of the valve (Tv). In order to describe the ontogenetic change in outline (cf. Campbell, 1957 fide Raup & Stanley, 1978, fig. 3-8), the length and height measured from the growth lines (Tab. 1) have been considered (Fig. 6).

The scatter diagram of Fig. 4 has been drawn considering the Hcp and Tv parameters. They provide the greatest quantity of available, objective measurements of the present sample. Thus, the results of this diagram can be considered with a greater statistical confidence in comparison with the others where estimated and a negligibile quantity of measurements are used. As is shown in Fig. 4, the left valve values are homogeneously distributed, while the scattering of the right valve values is more marked; this means that some right valves with equal Hcp differ in the Tv dimension.

In comparison with the left valves, the overlapping only regards the more inflated right valves, while the flattening is restricted to some specimens of right valves. This different distribution could be explained by the occurrence in the assemblage of a group of decidedly inequivalve specimens, with the right valve more flattened with respect to the left one. As a result in Fig. 4 the following right valves can be considered to be the extreme and typical morphotypes of a such group, here defined as group A: 8, 11, 20, 22, 34, 40. The occurrence of inequivalve shells is confirmed by the single double valved specimen of the sample (no. 6, Pl. 1, fig. 5). An other group (B) of right valves has measurements which overlap those of the left valves. For these specimens an equivalve condition may be proposed. However, the morphological analysis seems to exclude it (see later), and thus a higher degree of inflation of the right valve probably occurred in the specimens belonging to this group.

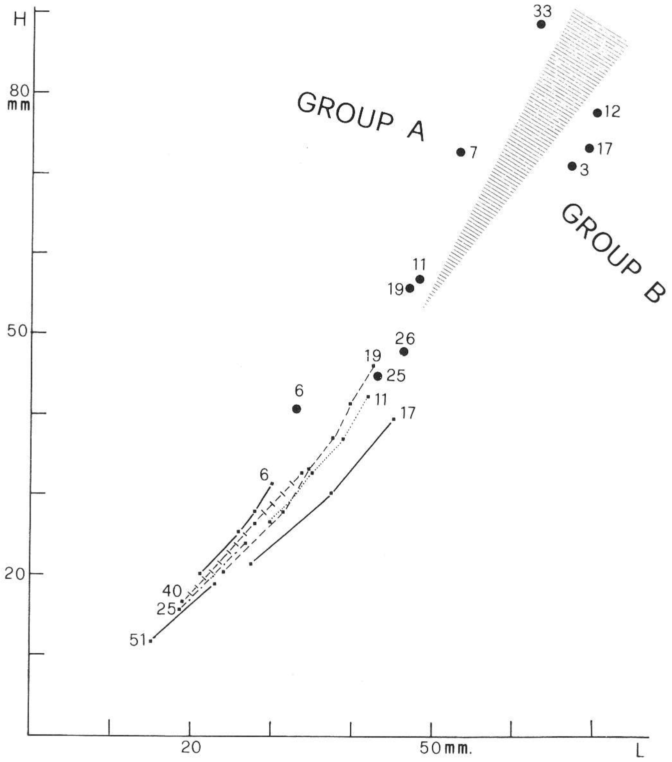


Fig. 6 - Ontogenetic change in shape described on the basis of the height (H) and length (L) measured from the growth lines of single, little abraded specimens (small points connected with lines, Tab. 1) and, where possible, H and L from restored outlines (black points, Tab. 2). This diagram allows us to separate the groups only in the late growth stages.

The better preserved and less fragmented right valves of group A (11, 20, 22, 40) have an elongated subtriangular outline in lateral view and a subcentral umbo, quite well developed in height. The right valves of group B show, at an adult stage, a subcircular outline with a lower and decidedly foreward directed umbo (specimens no. 3, 12, 25, 26) than those of group A. On

Left valves

no	Hcp	Tv
7	33.5	19.8
13	29.5	19.4
14	23.5	15.3
15	27.3	18.8
16	20.4	12.9
17	31.0	20.5
19	22.3	14.4
23	16.4	10.8
27	24.5	17.0
28	14.6	7.9
29	19.2	13.0
30	23.4	16.4
33	42.4	21.5
38	20.5	15.0
41	10.8	6.5
43	17.4	13.2
45	14.2	8.5
48	15.4	10.9
52	13.5	8.5

Right valves

no	Hcp	Tv
2	18.3	11.5
3	32.8	22.0
4	21.9	13.8
5	13.5	8.0
8	20.3	10.5
10	17.8	12.8
11	26.2	13.5
12	40.2	24.5
18	19.5	12.0
20	15.5	7.5
22	19.4	9.5
24	23.5	13.2
25	18.2	13.2
26	22.3	15.8
32	23.0	14.0
34	22.3	11.5
36	24.4	14.5
37	21.0	13.5
40	16.0	7.8
44	13.5	9.0
46	23.5	13.5
50	10.5	8.5
51	9.0	5.3

H and L measured on growth lines of single specimens

H	L
spec. no.17	
21.5	27.8
30.0	37.2
39.2	45.0
spec. no.19	
20.5	24.2
28.1	31.8
33.7	34.8
36.8	37.5
41.5	39.8
46.0	42.5
spec. no.51	
12.0	15.0
19.0	23.0
22.5	25.0

H	L
spec. no.11	
26.5	30.0
30.0	33.0
33.0	35.0
37.0	39.0
42.0	42.0?
spec. no.40	
16.5	19.0
22.3	24.5
26.5	28.0
30.0	31.5
33.0	34.0
spec. no.25	
15.5	18.5
24.0	27.0
spec. no. 6	
20.0	21.0
25.0	26.0
28.0	28.0
31.5	30.0

Tab. 1 - Measurements in mm of the Calabrian megalodontids studied. Abbreviations: no) specimen number; Hcp) distance between ventral margin of the hinge plate and umbo; Tv) valve thickness; H, L) height and length measured on the growth lines of single, little abraded specimens.

the basis of these morphological features, the left valves can be also separated into two groups. Specimens no. 7, 13, 15, 19, 33 can be referred to Group A, while specimens no. 17, 29, 30, 41, 48 to Group B.

Even if the diagram of Fig. 6 has little statistical value because of the negligible quantity of data, the two groups can be distinguished when the ontogenetic change of the outline expressed by the H and L measured on the growth lines of a few abraded valves (Tab. 1) and the estimated dimensions obtained from the restored outlines (Fig. 5) of the same or other specimens are taken into account. Fig. 6 shows that a boundary between the two groups is only detectable in the late growth stages. Therefore, the classification of the juvenile, small valves is not possible by means of this diagram. Juvenile specimens are scarcely represented in the assemblage and the limits of error increase in small size specimens with a bad state of preservation. In addition, the morphological method does not allow their classification; thus this difficulty may be related to both taphonomic, statistical and genetic factors.

Biometrical comparison with known species.

The Family Megalodontidae Morris & Lycett currently consists of the following 8 Triassic genera: *Ampezzania* Allasinaz, *Conchodon* Stoppani, *Gemmellarodus* Di Stefano, *Neomegalodon* Gümbel, *Paramegalodus* Cox, *Rhaetomegalodon* Végh-Neubrandt, *Rossiodus* Allasinaz, *Triadomegalodon* Végh-Neubrandt. Some of these genera have an imperfectly known shell morphology, as their type-species were erected on the basis of internal moulds, which can strongly differ from the outer shell shape and give little or no information on the hinge structure. On the other hand, when the type-specimens are represented by shell, little is known about their internal moulds. All this makes it difficult to construct a natural classification and to identify evolutionary trends within the megalodontids. For this reason, the following analysis will be mostly based on the comparison with the types.

A statistical approach was applied by Allasinaz (in Allasinaz & Zardini, 1977) and Végh-Neubrandt (1982) to provide for poorly available taxonomical characters, although with different emphasis, aim and conclusions. The former author reviewed the classification of the Megalodontids, both at species and at genus level, as well as their evolutive lineages, by means of numerical taxonomy. Since the material studied in Allasinaz's monograph was represented by internal moulds only, statistical comparison with the Calabrian material is impossible.

Végh-Neubrandt (1982) carried out a taxonomical revision, both at species and at genus level, mainly on the basis of the classical morphological method, although some diagrams showing the most important characters were included.

On the basis of the hinge structure, the great thickness of the shell wall in the dorsal region and the strong development of the posterior myophore platform from the juvenile stage onwards, the megalodontids examined can be ascribed to the genus *Triadomegalodon*. According to Végh-Neubrandt (1982), this genus includes 13 morphospecies which could be reduced, by applying the biological concept, to the following two: *T. damesi* (Hörnes) and *T. mojsvari* (Hörnes). The specimens collected fall within the first biospecies. Among its morphospecies, *T. damesi*, *T. gryphoides* (Gümbel) and *T. tofanae* (Hörnes) would represent the extreme morphotypes (morphospecies) of a coeval population, Norian to early Rhaetian in age. In fact, when Hörnes (1880) described these species, he noted the occurrence of transitional forms among them. Differences between the extreme morphotypes concern the lunule size and shape; shell outline and inflation; and the morphology of the anterior carinas bordering the lunule. Other morphospecies were considered by Végh-Neubrandt (1982) to be different evolutionary stages of *T. damesi*, starting from the late Carnian *T. cassianus* (Hörnes) to the Rhaetian *T. ampezzanus* (Hörnes). The phyletic trend of the *T. damesi* group consists mostly in an increase in size and an elongation of the shell in a ventral direction. Unlike the other megalodontids, the majority of the *Triadomegalodon* species were created on the basis of the shells, and thus their shell morphology and hinge plate structure are well known, even if little is known about their internal moulds.

In order to make an objective comparison with Hörnes' species, the following biometrical analysis has been made mainly according to the statistical methodology already proposed by Végh-Neubrandt (1982), in particular for the diagrams of Fig. 8. In addition, to make an homogeneous comparison between specimens with the same state of preservation only Hörnes' types have been considered. However, the small quantity of available measurements of the Calabrian sample does not consent a comparison which has a statistical value, and thus it must be supported by the classical morphological comparison which will be discussed in the systematic part of the present paper.

The diagrams of Fig. 7, in which the estimated measurements and their ratios obtained from some more complete specimens (Fig. 5; Tab. 2) are plotted, show ontogenetical changes in some of the most important taxonomical characters, such as elongation (Fig. 7A) and inflation (Fig. 7B) of the shell and the lunule shape (Fig. 7C, 7D). In these diagrams, the measurements of the type-specimens of the more closely related species of the *T. damesi* group and their transitional

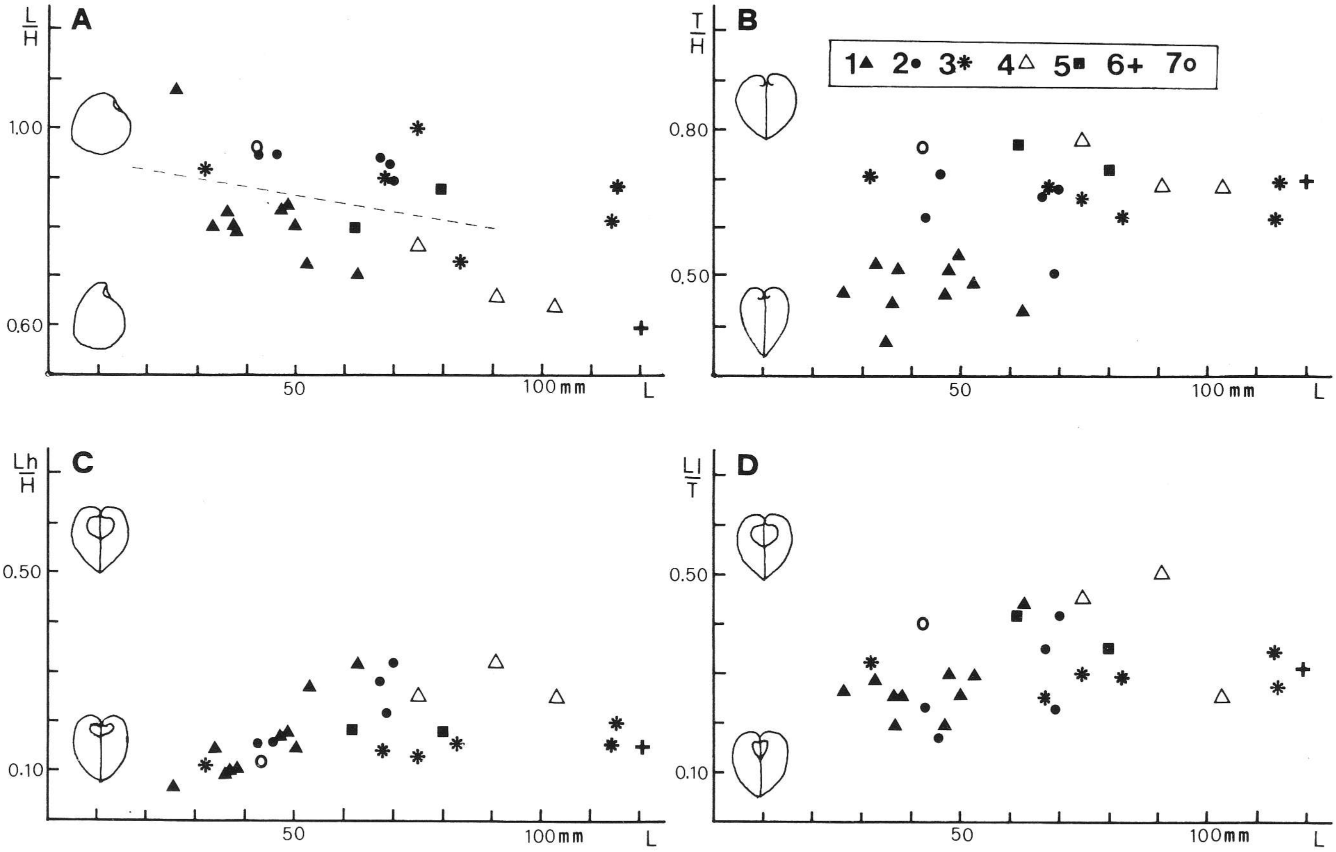


Fig. 7 - Biometrical comparisons between the Calabrian megalodontids (estimated dimensions of the outline, Fig. 5; Tab. 2) and some more closely related known *Triadomegalodon* species (figured types, Tab. 3). The diagrams show the changes of elongation (A) and inflation (B) of the shell, and the shape of the lunule (C, D) all versus length, that is through ontogeny. Legend: 1) Group A; 2) Group B; 3) *T. damesi* (Hörnes); 4) *T. tofanae* (Hörnes); 5) *T. damesi* - *T. tofanae* transitional forms; 6) *T. ampezzanus* (Hörnes); 7) *T. cassianus* (Hörnes).

forms are also used (Tab. 3). *T. gryphoides* has a large sized shell similar to that of *T. tofanae*; it differs from the latter as a result of the furrow which delimits the anterior lunule carinas from the lateral shell sides. Since such a feature does not occur in the Calabrian specimens, it has not been considered in the diagrams.

The diagram of Fig. 7A shows an allometric increase in the elongation (L/H) in a ventral direction during ontogeny, both in the Calabrian and the *T. damesi* group species. Here, apart the smallest specimen (no. 51), Groups A and B are clearly distinguishable. The specimens of Group B fall in the *T. damesi* group, while

Gr.	no.	H	L	Lh	Llv	Ll	Trv	Tlv	T	L/H	Lh/H	T/H	Ll/T
A	2r	48	38	5	3	6.5	11.5	(13.5)	25.0	.79	.10	.52	.26
B	3r	71	67	20	8	17.4	22.0	(25.9)	47.9	.94	.28	.67	.36
A	6s	41	33	6	-	6.5	10.0	11.8	21.8	.80	.14	.53	.29
A	7l	73	53	20	6	11.0	(16.6)	19.8	36.4	.72	.27	.49	.30
A	11r	57	48	10	4.2	9.1	13.5	(15.9)	29.4	.84	.17	.51	.30
B	12r	78	70	25	10.5	22.8	24.5	(28.9)	53.4	.89	.32	.68	.42
A	15l	62	50	9	5	9.2	(15.7)	18.8	34.5	.80	.14	.55	.26
B	17l	74	69	16	5.2	9.6	(17.3)	20.5	37.8	.93	.21	.51	.23
A	19l	56	47	9	3	5.5	(12.0)	14.4	26.4	.83	.16	.47	.20
A	20r	43	36	4	2	4.3	7.5	(8.8)	16.3	.83	.09	.37	.26
A	22r	46	37	5	2	4.3	9.5	(11.2)	20.7	.80	.10	.45	.20
B	25r	45	43	7	3.3	7.1	13.2	(15.5)	28.7	.95	.15	.63	.24
B	26r	48	46	8	3	6.5	15.8	(18.6)	34.4	.95	.16	.71	.18
A	33l	89	63	28	9.5	17.5	(18.0)	21.5	39.5	.70	.31	.44	.45
?A	51r	24	26	1.5	1.5	3.2	5.3	(6.2)	11.5	1.08	.06	.47	.27

Tab. 2 - Estimated measurements of some of the more complete specimens, the restored outlines of which are drawn in Fig. 5. All the shells are considered to be inequivalve, and thus their shell thickness and lunule length have been estimated on the basis of the articulated specimen no. 6, in which the left valve is 1.18% thicker than the right one. Abbreviations: Gr.) morpho-group; no.) specimen number; H) height; L) length; Lh) lunule height; Llv) lunule length of a valve; Ll) lunule length of the shell; Trv) thickness of the right valve; within parentheses the estimated thickness; Tlv) thickness of the left valve; T) shell thickness; r) right valve; l) left valve; s) double valved shell.

P	F	H	L	T	Ll	Lh	L/H	Ll/T	Lh/H	T/H
T. damesi (Hörnes, 1880)										
2	2	75	68	52	(13)	(11)	0.90	0.25	0.14	0.69
4	1	113	83	72	21	(18)	0.73	0.29	0.15	0.63
5	2	142	(114)	(88)	30	(22)	0.80	0.34	0.15	0.61
5	3	35	32	25	8	(4)	0.91	0.32	0.11	0.71
6	1	75	75	50	15	(10)	1.00	0.30	0.13	0.66
7	2	130	115	90	25	(25)	0.88	0.27	0.19	0.69
T. tofanae (Hörnes, 1880)										
2	1	160	(103)	(110)	(28)	(40)	0.64	0.25	0.25	0.68
4	3	137	91	95	48	44	0.66	0.50	0.32	0.69
6	3	98	75	77	35	(25)	0.76	0.45	0.25	0.78
T. damesi - ***T.tofanae*** transitional forms (Hörnes, 1880)										
4	2	77	62	60	25	(14)	0.80	0.41	0.18	0.77
6	2	90	80	65	(23)	(17)	0.88	0.35	0.18	0.72
T. ampezzanus (Hörnes, 1880)										
7	4	200	120	140	44	40	0.60	0.31	0.20	0.70
T. cassianus (Hörnes, 1880)										
1	7	45	43	35	14	6	0.95	0.40	0.13	0.77

Tab. 3 - Measurements of the figured types of some of the more closely related *Triadomegalodon* species inferred from the literature and estimated (within parentheses) in the original illustration. Abbreviations: P, F) plate and figure from Hörnes (1880); other symbols as in Tab. 2.

those of Group A are more closely related to *T. tofanae* or *damesi - tofanae* transitional forms.

Shell thickness has been estimated on the basis of the only articulated specimen (no. 6) in which the left valve is 1.18% thicker than the right one. As regards the degree of inflation, Fig. 7B shows that shells of Group A are flatter than all the known species, while Group B has an estimated inflation similar to that of *T. damesi.* The degree of inflation of the types figured in the literature seems to be roughly constant during ontogeny. However if more specimens are considered (cf. Végh-Neubrandt, 1982, fig. 49) the degree of inflation within the *T. damesi* group (*T. damesi, T. tofanae*, and *damesi - tofanae* transitional forms) decreases during ontogeny. On the basis of lunule dimensions (Fig. 7C, 7D), no clear distinction is possible between the two Calabrian groups.

The diagrams of Fig. 8 summarize the diagrams discussed above, without taking into account the ontogenetical stages. Where the degree of elongation and inflation are considered (Fig. 8A) a clear distinction is evident between the two groups: while Group B falls within the *T. damesi* range, Group A is well separated from all the known species. As previously noted, no clear di-

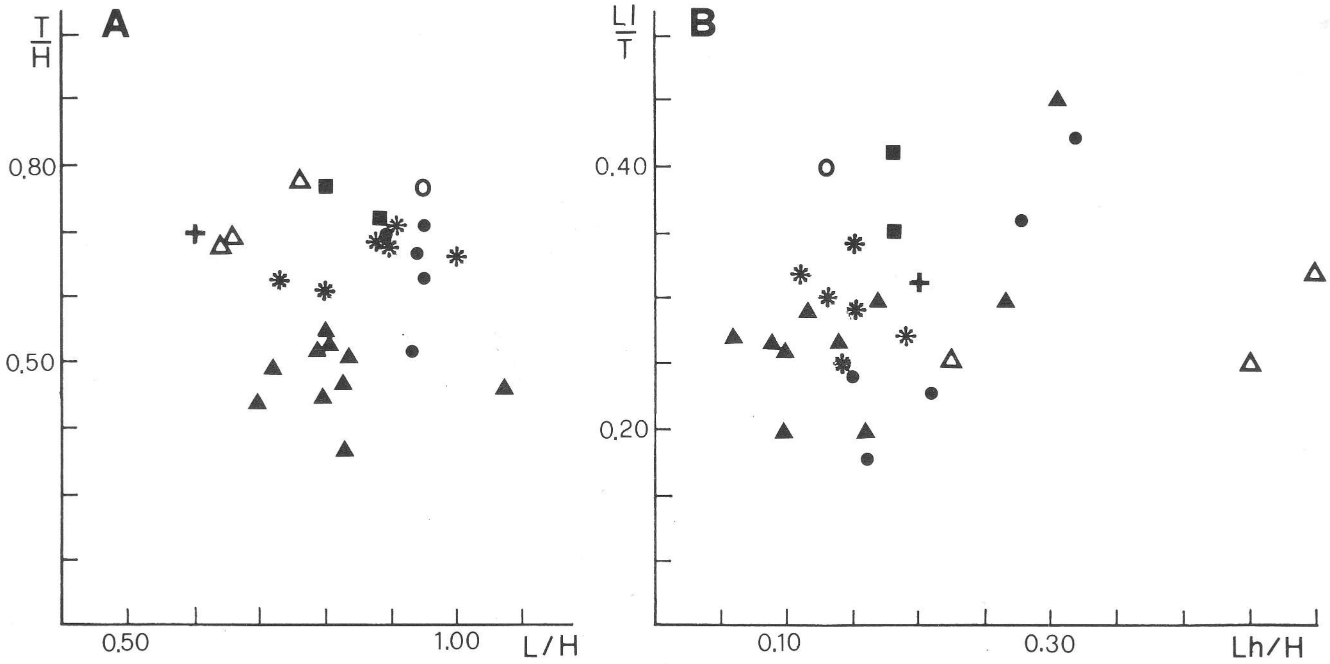


Fig. 8 - Biometrical comparison between the Calabrian megalodontids and some figured types of *Triadomegalodon* species, regarding shell inflation (T/H) and elongation (L/H) (Fig. 8A) and lunule shape (Fig. 8B). These diagrams, based on ratios, do not take into account the ontogenetic change of shape. Symbols as in Fig. 7.

stinction is possible if lunule dimensions are considered (Fig. 8B).

In conclusion, the Calabrian specimens of Group A can be related on the basis of elongation to *T. tofanae*, from which they differ in having a more flattened shell. Specimens of Group B have elongation and inflation degrees close to *T. damesi*, from which they differ in having a more arched posterior carina (see later). In addition, Hörnes' species have all equivalve shells, while those of both groups are inequivalve. Végh-Neubrandt (1982) considered the inequivalve condition to be a character with a value at specific level, and thus it could be used to propose new species.

However, several factors induce caution in the creation of new taxa. In particular, the confidence of the statistical analysis is low as taphonomic factors do not permit an objective knowledge of the shell shape, and consequently large errors in the measurements are very probable.

The morphological break between the two groups is detectable only among the larger specimens, but their quantity in the present sample is not statistically significant to display the variability.

Megalodontids are considered to be benthic recliners (Allasinaz, 1992) with a gregarious life habit. Thus a fairly wide ecomorphic variability probably occurred in such marine invertebrates. In particular, the occurrence of transitional forms between some *Triadomegalodon* species (i.e. between *T. damesi* and *T. tofanae*) supports the hypothesis that both the groups may belong to a single species.

Since Group A has morphological traits which are better known with respect to those of Group B, and since it is more closely related to the morphospecies *T. tofanae*, then both the groups will be compared, in open nomenclature, to this morphospecies. Juvenile, small size specimens, which group discrimination is questionable are tentatively classified within Group A.

Systematic Palaeontology

Class Bivalvia Linné, 1758
Subclass Heterodonta Neumayr, 1884
Order Pachyodontida Steinmann, 1903
Superfamily *Megalodontacea*
Morris & Lycett, 1853
Family *Megalodontidae* Morris & Lycett, 1853
Genus *Triadomegalodon* Végh-Neubrandt, 1974

Triadomegalodon sp. n. aff. **tofanae** (Hörnes)
Morphotype A
Pl. 1, fig. 1-10; Pl. 2, fig. 4

Description.

Medium-size shell, slightly inequivalve, RV more flattened than LV, inequilateral; outline anteriorly cordate compressed, laterally subtrigonal, more high than long (L=70% of H in the larger size specimens). Umbo erected, with prosogyrous beak, slightly outward curved in large specimens. Lunule cordate, relatively deep; its height varies from 10 to 25% of the shell height.

A sharp, posterior carina bounds the lateral surface from the posterior area, which is narrow lanceolate and relatively deep. The posterior carina creates a low arch in lateral outline. The right carina is slightly more backward protruding and the posterior right area is lesser inclined with respect to the commissure plane than that of the left valve. Ventral margin and posterior carina form nearly a right angle in the juvenile shell, and an obtuse angle in adult stage. Ventral and anterior margins form a curved, continuous line.

The shell wall is very thick, especially in the umbonal-cardinal region. The external skulpture is formed by growth lines, sometimes forming very low concentric folds. The wall is calcitized, made up by two layers: the outer is thinner than the inner one, the surface of which, detectable on scraped shells, has wide and shallow concentric folds and radial, slightly undulated, striae.

The posterior myophore platform has a triangular outline, with the dorsal apex starting from about the lower third of the shell height (Pl. 1, fig. 9). Myophore platform is already well developed in the juvenile stage and an acute, sharp step raises it from the valve pavement (Pl. 1, fig. 3). The posterior muscle scar is little impressed, probably subrectangular. The external valve surface, in correspondance with the myophore platform, is posteriorly furrowed by a very low radial sulcus, mostly limited to the left valve. The pallial line is whole and well impressed (Pl. 1, fig. 3).

At a adult stage, the hinge platform is very high and thick. Its height can reach about one third of the shell height. The ventral margin of the platform is sinuose, with a wide and relatively deep concavity in the posterior half, followed by an anterior convexity corresponding to the ventral extremities of the cardinal teeth.

The anterior muscle scar is very deep, with a narrow and elongated ovoidal outline. Its long axis is slightly foreward inclined; the dorsal extremity is located just below the ventral lunule limit.

The posterior element of the hinge platform in some LV consists of a very shallow triangular bulge, widely foreward arched, which may be interpreted as the rudiment of the posterior cardinal tooth. Its reliability is also proved by a shallow, but well distinguishable, furrow on some RV (e.g. no. 20). Its variable development may be related to the different degree of abrasion, even if a morphological variability cannot be excluded. The ligamental nymph with a narrow and elongated triangular outline is located on the dorsal hinge margin.

In the LV, anteriorly to the rudimentary posterior tooth is located the socket corresponding to the main cardinal tooth of the RV. The socket has an inverted comma-like outline, with the same orientation of the former tooth. Its concave pavement has two deeper areas, located close to the socket edges. The posterior pit is in a more dorsal position than the anterior one.

The two main cardinal teeth of the LV occur anteriorly. They are both dorsally pointed and separated by an elongated triangular socket, which gradually disappears in ventral direction so that, along the ventral margin of the hinge plate, these teeth are joined together. They are slightly dorsally convergent in juvenile stage, while they become parallel in large shells.

A small, triangular, relatively deep socket lies between the anterior cardinal tooth and the posterior margin of the anterior muscle scar.

On the RV a shallow and relatively wide furrow received the rudimentary tooth of the LV. The main cardinal tooth of the RV has a tusk-like shape. It is cut by a small groove, slightly oblique. Anteriorly, a wide subtrapezioidal socket is mesially divided by a ridge-like tooth, particularly developed toward the dorsal edge, clearly smaller and deeper than the adjacent cardinal teeth; it separates the main cardinal teeth of the LV. The anterior tooth has a triangular shape, with the apex ventrally directed. Its height is about half of the main cardinal tooth.

Triadomegalodon sp. n. aff. **tofanae** (Hörnes)

Morphotype B

Pl. 2, fig. 1-3

Description.

Medium size shell, probably inequivalve, inequilateral, strongly prosocline, beak prosogyrous, decidedly anterior; ovate in lateral outline; slightly more high than long (L= 90% of H). The lunule is high (about from 15 to 30% of shell height), cordate and deep.

The posterior carina is markedly arched. The right posterior area (no. 3, Pl. 2, fig. 2) is lesser inclined with respect to the commissure plane than that of the LV (no. 17, Pl. 2, fig. 3). This suggests that the inequivalve condition occurred also in this morphotype. The shell wall is very thick in the dorsal region. The exterior skulpture, shell architecture and hinge platform are similar to those of the previous group.

Remains of the posterior myophore platform are detectable on a RV (no. 3), in which it arises from the posterior vertical wall and on a LV (no. 17) where it originates from the posterior valve pavement.

Differences with the morphotype A concern the anterior tooth of the largest RV (no. 12, Pl. 2, fig. 1), which is not triangular but ovoidal with its long axis postero-dorsally directed. Moreover, in the LV the two main cardinal teeth are markedly mesially divided both in dorsal and in ventral directions; these teeth are nearly parallel (Pl. 2, fig. 3).

Internal moulds.

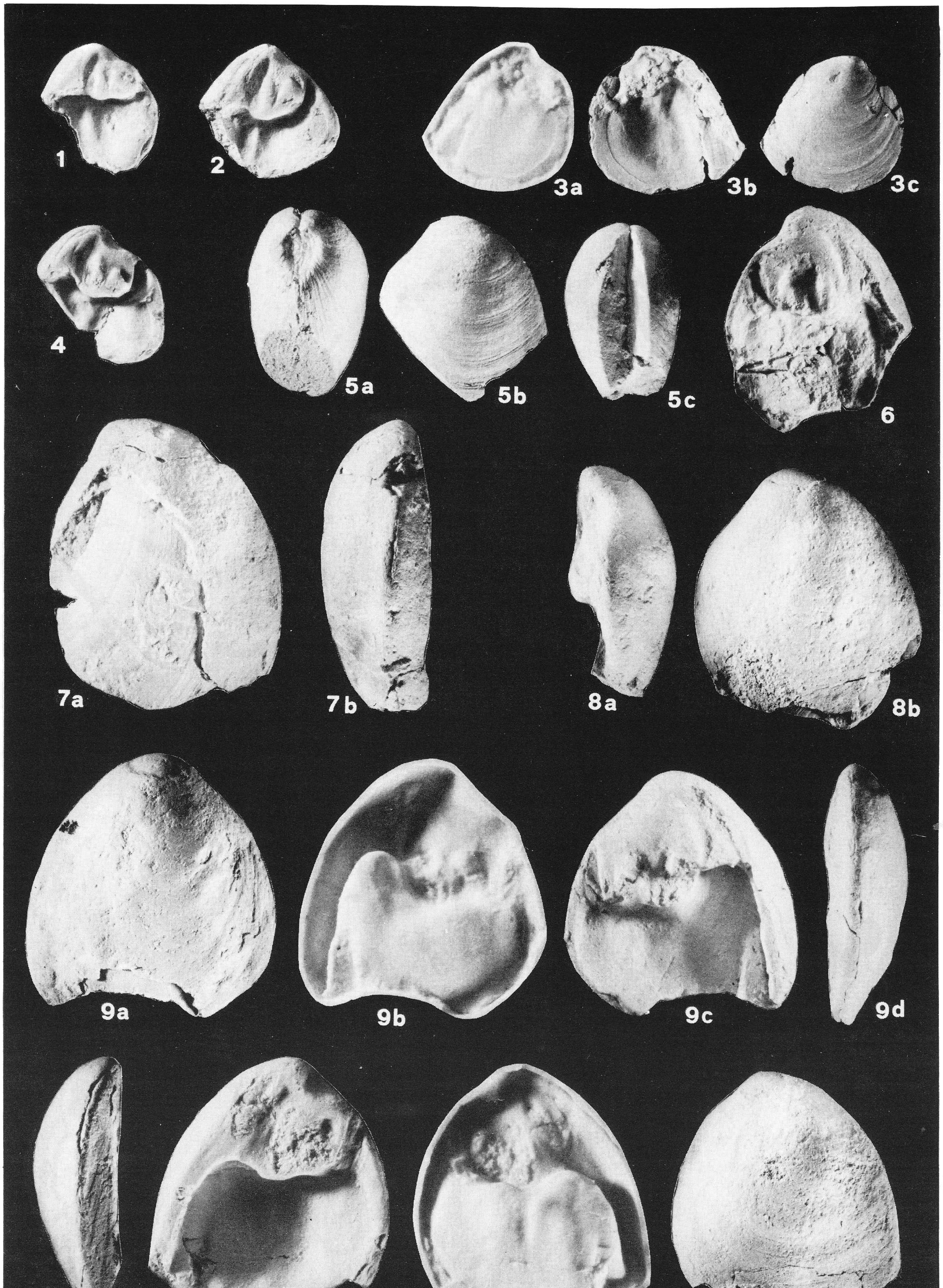
The description is based on some artificial internal moulds obtained with silicon rubber from 4 specimens (RV: no. 3, 11, 51; LV: no. 19). The internal moulds are strongly flattened, with a morphology very different from that of the external shell surface.

In a small-size specimen (no. 51, Pl. 1, fig. 3a), the group attribution of which is questionable, the umbo is very low, only just slightly higher with respect to the ventral lunule edge. The pallial line is well impressed and runs at about 3 mm from margin. The posterior myophore platform is well distinguished from the inner surface. On the lateral surface two shallow and wide rugae run from the ventral lunule edge, where they build up two small bulges, to the ventral margin. These rugae are parallel to the ridge bounding the myophore platform from the lateral surface.

PLATE 1

Triadomegalodon sp. n. aff. *tofanae* (Hörnes), morphotype A. Cozzo della Paglia, Castrovillari. All figures are natural size and specimens have been coated with magnesium powder.

Fig. 1 - Left valve, inner view, specimen no. 41.
Fig. 2 - Left valve, inner view, specimen no. 48.
Fig. 3 - Right valve, specimen no. 51; inner mould (a); inner (b) and outer lateral (c) views.
Fig. 4 - Left valve, inner view, specimen no. 52.
Fig. 5 - Articulated and unabraded shell, specimen no. 6; anterior (a), lateral (b) and posterior (c) views.
Fig. 6 - Right valve, inner view, specimen no. 22.
Fig. 7 - Left valve with the scraped outer layer, specimen no. 7; lateral (a) and posterior (b) views.
Fig. 8 - Left valve, specimen no. 15; anterior (a) and outer lateral (b) views.
Fig. 9 - Right valve, specimen no. 11; outer lateral (a), inner (c) and posterior (d) views; inner mould (b).
Fig. 10 - Left valve, specimen no. 19; posterior (a), inner (b) and lateral (d) views; inner mould (c). The umbonal cavity of this valve is again partially filled by of sediment.


1
2
3a
3b
3c
4
5a
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6
7a
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9b
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9d
10a
10b
10c
10d

In the late ontogenetic stages, the umbo is more elevated, almost straight and laterally flattened, with a rounded apex. The lunule is wide and deep and its anterior and ventral edges make it form an obtuse angle. A small knoll, corresponding to the dorsal extremity of the anterior ruga, protrudes from the ventral lunule edge. The height of the internal mould is about 70% of the restored shell height (sp. no. 11, shell height= 57 mm; Tab. 2). The posterior carina is nearly straight, and curves only near the apex.

The left mould (no. 19, Pl. 1, fig. 10c) is more inflated and the mesial rugae are better marked than in the right one (no. 11, Pl. 1, fig. 9b).

As regards Group B, only one inner mould is available (RV, no. 3, Pl. 2, fig. 2b). Its morphology is similar to that of the Group A, apart from the size which is a little larger. It shows a stronger development towards the umbo of the edge bounding the lateral surface from the myophore platform. Moreover, this edge is more posteriorly shifted, so that the "bitruncate" character of this internal mould appears better defined.

Comparisons.

Shell. On the basis of the lunule shape both the groups are more closely related to *T. tofanae* which also has a high, cordate lunule. Group A shares other features with this species, such as an erected umbo, a ventrally elongated lateral outline, and a posterior carina little arched in lateral view. Differences regard the degree of shell inflation, the value of which is also lower with respect to *T. damesi*, the most flattened of the group, and the inequivalve condition. All the species of the *T. damesi* group had been originally described as having equivalve shells. As regards the morphotype A, a lower inflation degree also with respect to *T. damesi* has been proposed by means of estimated measurements of the shell thickness. This peculiar character is confirmed by the comparison of similar size articulated shells, between the juvenile shell of *T. damesi* figured by Hörnes (1880) on plate 5, figure 3 and the single available double valved shell (no. 6, Pl. 1, fig. 5) of the studied collection.

Specimens of Group B have elongation values (L/H) which fall within the *T. damesi* range. However, the posterior carina in lateral view of the figured lectotype (Hörnes, 1880, pl. 2, fig. 2a) is very low arched, in contrast to the Calabrian specimen no. 12 in which it is markedly arched and the shell shape is more ovoidal.

The hinge structure does not show substantial differences between the two groups and the variability of the tooth size and shape may be related to ontogenetic development. As in the types illustrated by Hörnes (1880), the maximum variability of the hinge occurs in the late ontogenetic stages.

Internal mould. A part from the size, the inner moulds show some features in common with *T. tofanae* (Hörnes, 1880, pl. 2, fig. 1). These are: the large, deep and obtuse lunule; the erected and laterally flattened umbo with a very little arched posterior margin; and the position of the posterior myophore platform groove. The main differences regard the apex, which is pointed in Hoernes' species while it is rounded in the Calabrian moulds, and the great height of the umbo, which is probably related to the large size (H is about 12 cm) of the internal mould of the figured-type.

The internal mould of *T. damesi* was not illustrated by Hörnes (1880). According to Végh-Neubrandt (1982), it would be similar to that of *T. desioi* (Kutassy) (Kutassy, 1933, pl. 11, fig. 1, 2), which shows the strongest affinity with the Calabrian moulds. In this species the umbo is little developed in height, although its size (H= 5.8 cm) is greater than that of the material studied (in the highest specimen, H is 4.8 cm). However, in the Kutassy species the apex is also pointed.

The internal mould is strongly flattened so, it can be compared to that of *Neomegalodon complanatus* (Gümbel) (Gümbel, 1862, pl. 5, fig. 5, 6). However, no cast of the posterior myophore platform is detectable on the umbonal region of the Gümbel figured type. Moreover, the lunule is smaller, has a semicircular outline in lateral view and lacks the knoll protruding from the ventral lunule edge; even so, the main differences with the Gümbel species regard the hinge size and structure (see also Hörnes, 1880, pl. 1, fig. 8).

In conclusion, the Calabrian megalodontids have some peculiar characters such as inequivalve and low inflated shells which are not shared by the *T. damesi* group species. Inside the gen. *Triadomegalodon*, inequi-

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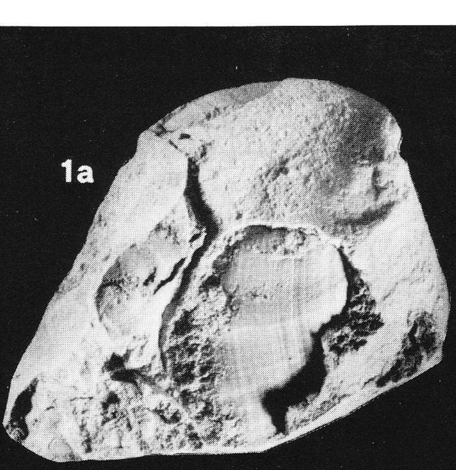
PLATE 2

Triadomegalodon sp. n. aff. *tofanae* (Hörnes). Cozzo della Paglia, Castrovillari. All figures are natural size and specimens have been coated with magnesium powder.

Morphotype B.
Fig. 1 - Fragment of the dorsal region of a right valve, specimen no. 12; lateral outer (a), anterior (b) and inner (c) views.
Fig. 2 - Right valve, specimen no. 3; lateral outer (a) and inner (c) views; inner mould (b).
Fig. 3 - Left valve, specimen no. 17; inner (a), lateral (b) and posterior (c) views.

Morphotype A.
Fig. 4 - Left valve, strongly abraded, specimen no. 33; inner (a), lateral outer (b) and anterior (c) views.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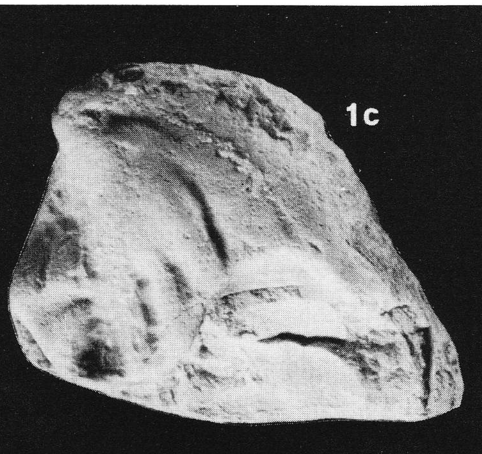
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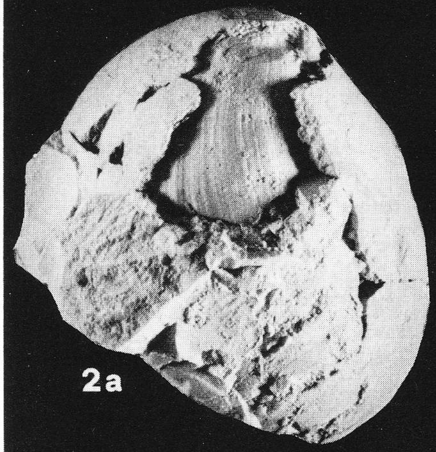
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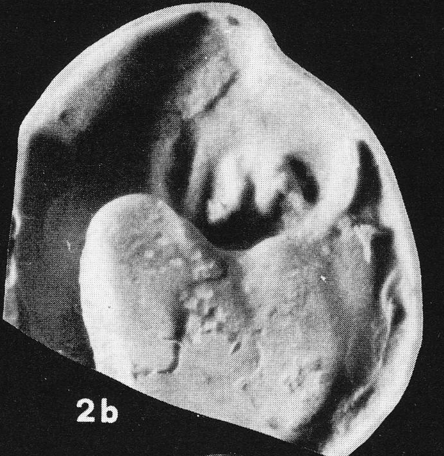
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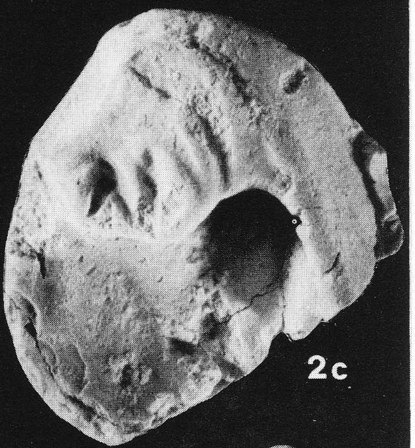
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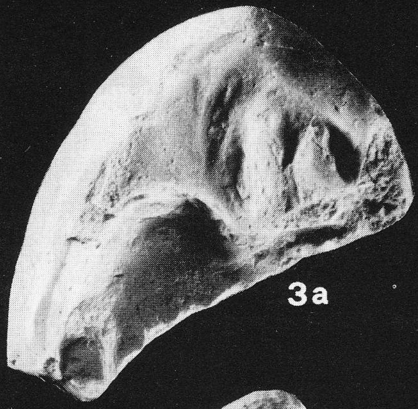
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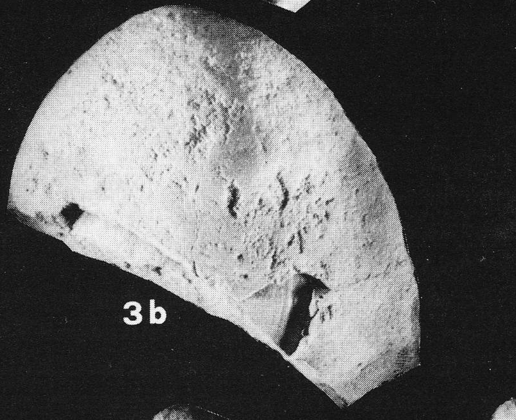
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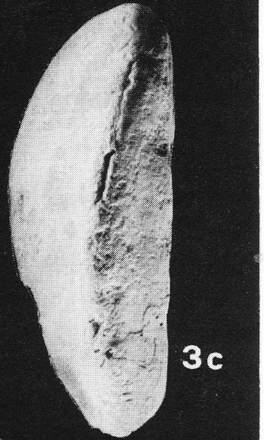
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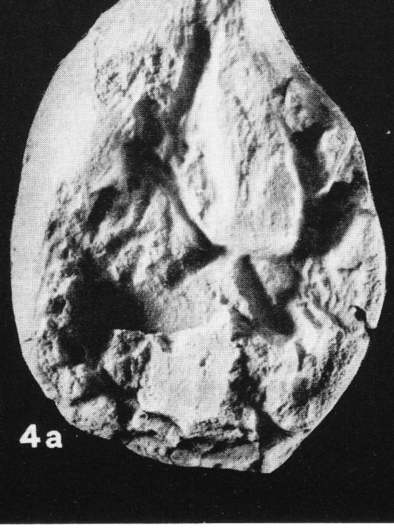
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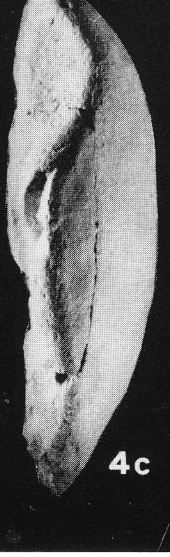
4c

valve shells occur in *T. ladakhensis* (Bittner) and *T. scutatus* (Schafhäutl), but these two species differ from the Calabrian material in the following characters. *T. ladakhensis* has a large shell with a subquadrangular outline; in *T. scutatus*, the inequivalve condition concerns the different height of the umbones while the degree of inflation of the two valves is nearly the same, so much so that Végh-Neubrandt (1982) advanced the hypothesis that the valves of holotype are slightly displaced.

The differences between Groups A and B mainly regard the lateral outline and the estimated degree of inflation. At present it is not possible to say whether such differences are related to an intra- or interspecific variability, even if an ecomorphic variability is more likely. However the bad state of preservation (fragmentation and abrasion), the allochthonous position, the small quantity of middle size specimens, and the lack of large sized shells comparable in dimensions with the types, induce caution in the creation of new taxa.

Functional morphology and morphological variability.

Zapfe (1957) proposed a semi-infaunal life habit for *Conchodon infraliasicus* Stoppani, an equivalve megalodontid. It rested on the substrate with the commissure plane perpendicular to the bottom and with the anterior region of the shell partially buried by the sediment.

In general, *Triadomegalodon* shows an ontogenetic and phylogenetic tendency to increase the shell elongation in a ventral direction. In addition the shell wall is very thick and heavy in the dorsal region. These features may be interpreted as adaptations towards a semi-infaunal mode of life, but with an orientation a little different with respect to *C. infraliasicus*. It rested with the heavy umbonal region inside the bottom, and with the ventral margin protruding from the substrate. Because the shell is little inequivalve, the commissure plane was probably slightly inclined towards the more inflated and heavy left valve.

The stabilization in the soft-bottom substrate was mainly guaranteed following a "heavy-weight strategy" (Seilacher, 1984), probably as a consequence of the loss of an active burrowing foot at the adult stage when large and very heavy shells were formed [e.g. *T. ampezzanus* (Hörnes)].

This mode of life was probably the reason for the wide variability regarding shell elongation, inflation and lunule shape. The bottom orientation and stabilization were guaranteed by means of the static (or passive) function of the shell, so small changes in the environmental factors (hydrodynamism, matrix texiture and bottom compactness) caused more or less wide morphological changes. On the basis of this hypothesis, elongated, subtriangular shells could have inhabited areas with a higher sedimentation rate with respect to those where the oval morphotypes occurred.

The bottom stabilization was also guaranteed by the wideness and shape of the support surface represented by the umbonal region, dorsal posterior area and lunule, the dimensions of which can all be related to the shell inflation. Thus, the morphological variability of these features could be related to a different degree of bottom compactness which could change both laterally with respect the bank and vertically, during the different stages of the bottom colonization.

The Calabrian megalodontids have thick and heavy shells. Such features indicate that they inhabited medium to high energy environments, where disarticulation and abrasion of the shells took place, similarly to those proposed by Di Stefano P. (1990, fig. 1) for the megalodontids of the Panormide sequence.

The *Triadomegalodon* species with ventrally elongated shells show a strong increase of the height of the shell and hinge platform, not accompanied in the same way by the enlargement of the body cavity volume, because of the dorsal increase in wall thickness (i.e. *T. tofanae*). Such growth mainly caused an elongation of the umbonal cavity, forming internal moulds similar to those of the *Rhaetomegalodon*, a genus derived, according to Végh-Neubrandt (1982), from *Triadomegalodon*.

Age.

The presence of *Triasina hantkeni* in the matrix of the megalodontid bearing coquinas permits us to include them in the *T. hantkeni* Range-zone, which is considered, as a whole, to be Rhaetian. This foram has already been cited both in the northern (Tre Croci D'Acerno; De Castro, 1990) and southern areas (Ietto et al., 1992) of the Campano-Lucana Carbonate Platform. The stratigraphical setting of these coquinas within the Cozzo della Paglia sequence, with respect to the underlying Dolomia Principale (? Norian) and the overlaying Rhaetian layers with very large sized megalodontids (unit D), and the small-middle size of the collected megalodontids in comparison with the large sizes of the typical Rhaetian megalodontids witness for a fairly probable lower Rhaetian age.

T. damesi group species (*T. damesi, T. tofanae, T. gryphoides*) and *T. ampezzanus* were considered by Frech (1904) and Végh-Neubrandt (1982) to be mostly Norian in age. However a wider stratigraphical range from Norian up to Rhaetian cannot be excluded. The Norian age assigned to these species by Végh-Neubrandt (1982), the types of which were found in the *Dachsteinkalk* of the Eastern Dolomites, arises from the belief that in the whole of the Southern Alps the Rhaetian would be represented by the Kössner Beds followed by the *Conchodon* Limestone or Dolomite. However, in the Southern Alps a lower shale-rich Rhaetian formation only occurs in the western part (Lombardian basin) (Gnaccolini, 1965; Jadoul, 1986; Masetti et al., 1988). In the Eastern Dolomites, the *Dachsteinkalk* directly overlies and intertongues with the *Dolomia Principale* and is mostly considered Rhætian in age (Casati et al., 1982; Bosellini & Hardie, 1988; De Zanche, 1990). This age is supported by the occurrence of *T. hantkeni* in the limestones bearing megalodontid (about 70 m thick) of the Sennes and Fanes (Cros & Neumann, 1964) and Sella Groups (Bosellini & Broglio Loriga, 1965). Thus a Rhaetian age, at least for the large *T. ampezzanus* as already proposed by Kutassy (1934), the type-bed and -locality of which are the upper *Dachsteinkalk* of Sorapiss (Eastern Dolomites) (Hörnes, 1880) is more probable.

Acknowledgements.

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