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THE GEN. *COMELICANIA* FRECH, 1901 (BRACHIOPODA) FROM THE SOUTHERN ALPS: MORPHOLOGY AND CLASSIFICATION

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Riassunto. *Comelicania* è un brachiopode di grandi dimensioni caratteristico nell'area dolomitica degli strati sommitali della Formazione a Bellerophon. Di questo brachiopode, conosciuto da oltre un secolo ed utilizzato nel passato come marker del Dorashamiano inferiore, si descrivono per la prima volta i caratteri morfologici interni, riguardanti in particolar modo i cardinalia ed il brachidio. Questi caratteri confermano l'attribuzione di *Comelicania* Frech alla Superfam. Athyridoidea Davidson e permettono di completare la diagnosi della Fam. Comelicaniidae Merla. L'indagine morfologica è stata condotta su numerosi esemplari sia della specie-tipo *C. megalotis* (Stache) che di altre specie congeneriche delle Alpi Meridionali. Essa ha permesso di evidenziare notevoli differenze dei caratteri interni (p.e. struttura del processo cardinale, delle flange cardinali, etc.) rispetto ai Comelicaniidi del Dorashamiano inferiore della Transcaucasia che giustificano l'attribuzione di quest'ultimi ad un diverso genere (*Gruntallina* Waterhouse & Gupta).

I numerosi esemplari a disposizione consentono di evidenziare un'ampia variabilità dei caratteri esterni, che interessa sia il contorno della conchiglia e sia la morfologia della regione mediana dorsale. La variabilità del contorno, derivante probabilmente dalla mancanza di un peduncolo funzionale, trae origine dalle diverse strategie adattative degli individui per la loro stabilizzazione su substrati di differente consistenza. Le indagini biometriche mostrano che le diverse specie di *Comelicania* avevano stadi giovanili con contorno molto simile. La differenziazione, per una sensibile allometria di crescita, si realizzava solo nello stadio adulto. Solo in questo stadio ontogenetico gli individui acquisivano i caratteri peculiari della specie di appartenenza.

La revisione tassonomica a livello specifico porta a ridurre le undici specie istituite nel passato nelle Alpi Meridionali, secondo un rigido concetto tipologico, a sole due specie: *C. megalotis* (Stache) e *C. haueri* (Stache). Viene inoltre proposta la nuova specie *C. merlai*.

Abstract. Analysis of the internal characters, especially the cardinalia and brachidium, of the brachiopod *Comelicania* Frech from the Southern Alps, confirmed the attribution of this genus to the Superfam. Athyridoidea Davidson and provided a more complete taxonomic description of the Fam. Comelicaniidae Merla. This family includes two genera which differ in the morphology of their cardinalia, i.e. *Gruntallina* Waterhouse & Gupta, type-species *Gruntallina triangularis* (Grunt) from the lower Dorashamian of Transcaucasia and *Comelicania*, type-species *Comelicania megalotis* (Stache) from the uppermost Bellerophon Fm. of the Southern Alps.

The study of a collection composed of more than a hundred specimens highlighted a broad variability of the morphological characters and a pattern of ontogenetic development which demonstrates that classification at the species level is possible only when using mature specimens. Taxonomic revision at the specific level reduced the eleven species of *Comelicania* from the Southern Alps, described by previous authors, to: *C. megalotis* (Stache) and *C. haueri* (Stache). In addition a new species, *C. merlai*, which characterises the upper *Comelicania* beds, is proposed.

Introduction.

Comelicania Frech, 1901 is a large athyridoid brachiopod characteristic of the Late Permian Bellerophon Fm. of the Southern Alps (Stache, 1878; Merla, 1930; Broglio Loriga et al., 1986; 1988). Its classification was recently discussed by several authors (Grunt, 1986, 1989; Waterhouse & Gupta, 1986; Posenato, 1988a) since its taxonomic position in the Treatise on Invertebrate Palaeontology (Moore, 1965, p. H863) is uncertain at both order and family levels, due to a lack of data on its internal features. Grunt (1986, 1989) placed *Comelicania* in the Superfam. Athyridacea, Fam. Spirigerellidae, Subfam. Spirigerellinae, while Waterhouse & Gupta (1986) placed it into what they considered a new Family, Comelicaniidae. However, such a name had already been proposed by Merla (1930) as Subfam. Comelicaniidae (sic). Questions concerning the priority of nomenclature for the Fam. Comelicaniidae were discussed by Posenato (1988a), who attributed the family name to Merla (1930).

Comelicania has also an important chronologic value since Upper Permian formations in the Southern Alps generally lack ammonoids, and thus brachiopods represent one of the most important groups for chronostratigraphic correlations. Its chronologic value resulted from the discovery of *Comelicania triangularis* Grunt, 1965 in the *Phisonites* beds of the lower Dorashamian of

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Transcaucasia (Grunt in Ruzhentsev & Sarytcheva, 1965; Rostovtsev & Azaryan, 1973) with which the *Comelicania* beds of the Southern Alps were correlated (Assereto et al., 1973).

Waterhouse & Gupta (1986?) described the occurrence of Comelicaniids from Spiti (Himalayas), but this finding was later rejected (Gaetani et al., 1990; Posenato, 1991) because of the strong suspicion that the material had been collected originally in the Dolomites by Gupta, known for his habit of falsifying the locality of the finding (Talent, 1989). Gupta had the opportunity to collect some Comelicaniids from the Sass de Putia section (Dolomites) on July 7th, 1986 during the Field Conference of Project n. 203. These specimens were probably re-proposed as coming from Spiti in a back-dated paper (Waterhouse & Gupta, June 1986). If they really come from Spiti, it is questionable why Gupta did not present the already published paper during the Field Conference. In the same paper, Waterhouse & Gupta (1986) proposed three new genera of Comelicaniidae based on a debatable taxonomic review. They created the genera *Gruntallina* for the Transcaucasian Comelicaniids (type species *Comelicania triangularis*), *Alatothyris* (type species *Spirifer (vultur) haueri* Stache from the Alps) and the (?) Himalayan *Spitispirifer*, already considered a junior synonym of *Comelicania* (Posenato, 1988a), for the specimens possibly coming from the Dolomites.

So far only the internal characters of *C. triangularis* are known (Grunt, 1986), while few data are available for the Alpine species, among which the type species of *Comelicania* (*Spirifer megalotis* Stache) occurs. These data concern the morphology of the cardinalia detected in disarticulated valves (Posenato, 1988a). Additional internal characters detected in serial sections from Alpine specimens are reported here to complete the description of this genus, allowing comparisons between Alpine and Transcaucasian Comelicaniids and clarifying whether their distinction at the genus level is justified. The taxonomic revision of the numerous species described in the past in the Southern Alps is provided as well.

Material and methods.

Comelicaniids from the Dolomites are relatively rare. The present collection, composed of about 150 specimens and housed in the Museum of the Dipartimento di Scienze Geologiche e Paleontologiche of Ferrara University (MDSGF), originates mostly from three localities: Sass de Putia (PK), Val Brutta (Valsugana, VB) and Passo di Monte Croce di Comelico (MC) or Kreuzberg in German toponymy, the type locality of most of the species created by Stache (1878) and Merla (1930). Additional material comes from Piz da Peres (PZ) and Agordo (AG). Preservation is not always good and depends on both the stratigraphic setting and the geographic provenance of the material. The numerous specimens found in Val Brutta (Fig. 1) are represented mostly by articulated shells, even though they are frequently deformed within their marly lithology. In the Sass de Putia section (Fig. 1), *Comelicania* is frequent in the marly intercalations of the lower *Comelicania* beds, but it is represented mostly by disarticulated and compressed valves (Gupta's material probably would have been collected in these beds). In the overlying black massive limestone, shells are well preserved but not frequent. In the outcrop of Passo di Monte Croce Comelico the specimens are relatively frequent, preserved in a massive black limestone, but generally have recrystallized shells; unfortunately, the majority of these specimens was collected in the talus.

Internal characters were observed directly on about twenty disarticulated and cleaned valves (Sass de Putia), on open shells (e.g. Val Brutta, no. VB61) or on internal moulds. Serial transverse sections were made on seven specimens from several localities. The polished sections were reproduced with acetate peels from which negative, enlarged photographs were used to reconstruct the internal characters.

The collections of Stache (1878) and Merla (1930) were examined also. They are housed in the Museum of the Geologische Bundesanstalt of Wien (MGBW) and in the Museum of the Dipartimento di Geologia, Paleontologia e Geofisica of Padova University (MDGP) respectively.

Biodiversity of *Comelicania* in the Southern Alps.

Comelicaniids from the Southern Alps are characterised by a broad morphologic variability which induced previous authors to create 11 species, all coming from a thin unit (0.3-1.5 m in thickness) located at the top of the Bellerophon Formation (Caneva, 1906; Broglio Loriga et al., 1986; 1988). Considering the short vertical and relatively narrow horizontal distribution of Comelicaniids in the Southern Alps, this large number of species is probably disproportionate using the modern concept of species.

The majority of Merla's species were not recognised in the large collection studied here. Using a typological concept of species, the present collection yields also some individuals for which additional new "species" might be proposed. For these reasons, the majority of *Comelicania* species must be considered as extreme morphotypes of a few species with a rather broad morphologic variability.

The taxonomic characters used by Merla (1930) to erect his own species consisted primarily of the outline and inflation of the shell, the shape and inclination of

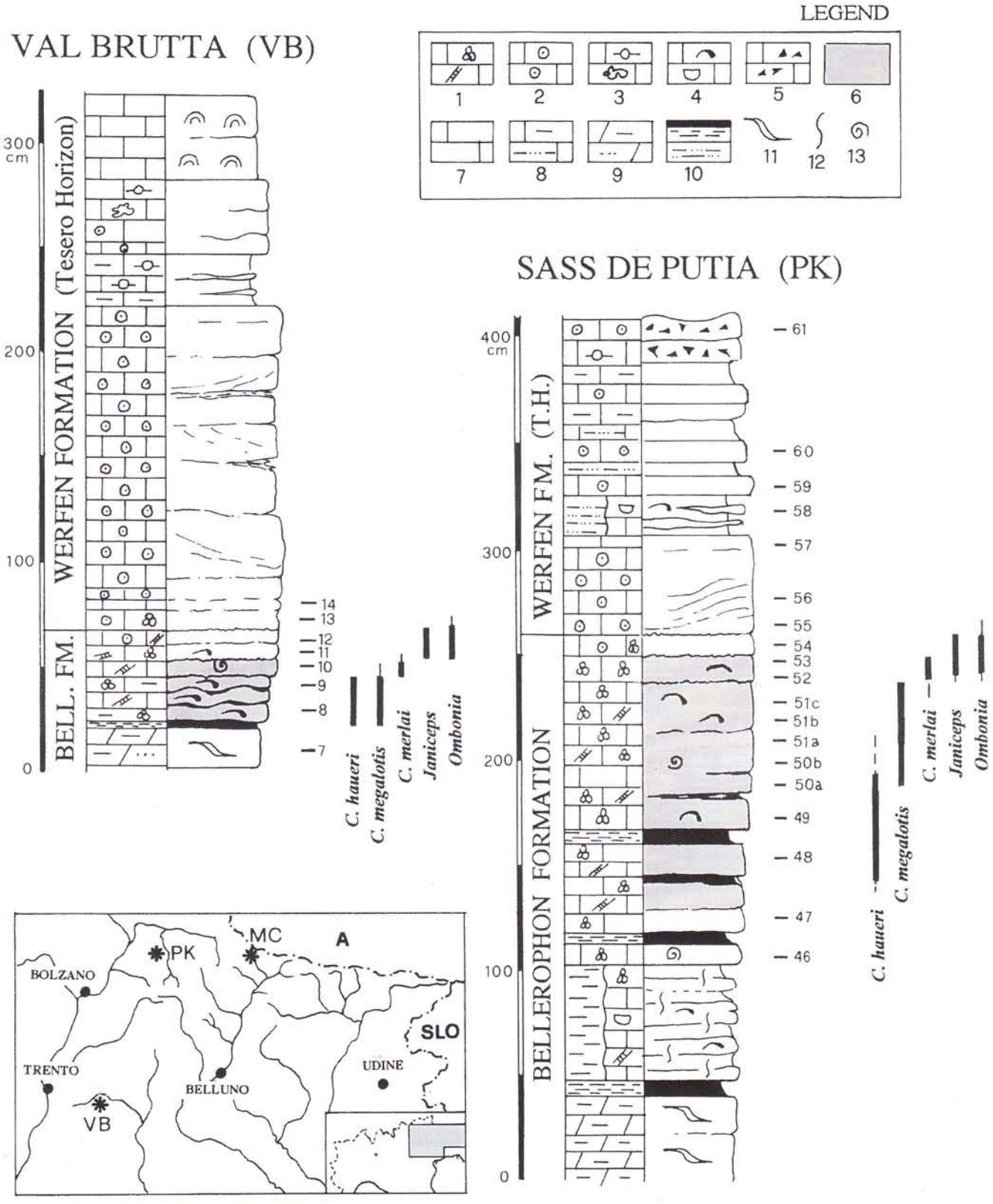


Fig. 1 - Stratigraphic setting and vertical range of *Comelicania* in Val Brutta (Valsugana, Trento) and Sass de Putia (Dolomites, Bolzano) sections. Legend: 1) bioclastic limestone with foraminifers and algae; 2) oolitic limestone; 3) peloid and oncolitic limestone; 4) bioclastic limestone with brachiopods, bivalves and ostracods; 5) intraclastic limestone; 6) *Comelicania* beds; 7) micritic limestone; 8) marly and silty limestone; 9) marly and silty dolomite; 10) marl and silty marl; 11) fenestrae; 12) bioturbation; 13) Bellerophontid; MC) Passo di Monte Croce Comelico. Sass de Putia column adapted from Broglio Loriga et al. (1988), Val Brutta column from unpublished data of Neri & Posenato.

the cardinal ridges, the morphology of the cardinal surface and the shape of the median ridges. The majority of these characters must be considered within the intraspecific variability, because they are frequently detectable only in the illustrated types, while they do not always occur all together or in the same arrangement in the other syntypes. Only the shell outline and degree of elongation seem to have a chronostratigraphic value and therefore have been used as taxonomic characters to gather the known species into the following three groups (Posenato, 1988a, b):

- *C.* gr. *haueri* (Stache): large, strongly transverse and alate shells, with very long and pointed alae gradually connected to the anterior margin. It includes: *C. avis* Merla, *C. dalpiazi* Merla, *C. haueri* (Stache), *C. macroptera* Merla, *C. vespertilio* Merla.

- *C.* gr. *megalotis* (Stache): large and transverse shells with alae well defined from the shell in the adult stage. It includes: *C. doryphora* Merla, *C. megalotis* (Stache), *C. rostrata* Merla, *C. vultur* (Stache).

- *C.* gr. *ladina* (Stache): moderately transverse shells with short and pointed alae; width of the cardinal margin similar to or greater than the anterior margin. It includes: *C. ladina* (Stache) *sensu* Merla, ? *C. insana* (Stache).

The reasons for the broad morphologic variability of *Comelicania* at the specific level probably arose from its free-lying mode of life. This behaviour is suggested by the absence of a foramen, the dorsal umbo inserted in the delthyrial cavity and a great thickening of the posterior region. The stabilisation of the shell on the soft bottom was guaranteed by its weight, resulting from the considerable thickening of the posterior region and the development of a wide resting surface, represented by a relatively wide cardinal surface and long lateral alae. The alae probably did not act like siphons because their extremities are closed; their function was mainly to increase the resting surface on muddy substrates, with a ski-like function as has already been proposed for *Mucrospirifer* (Rudwick, 1970). This interpretation is supported also by the occurrence of individuals with very short alae (*C.* gr. *ladina*) in the packstone-grainstones transitional to the oolite bank of the Tesero Horizon, where little or no risk of sinking into the substrate existed. Therefore, strongly transverse shells such as those of the *C. haueri* group probably represent an adaptation to muddy substrates of free-lying brachiopods. In contrast, *C.* gr. *ladina*, with very short alae and a slightly transverse shell, represents an adaptation to coarser substrates.

The stratigraphic data based on the Sass de Putia section (Fig. 1), where *Comelicania* beds are about 1.5 m thick, show that the lower, middle and upper *Comelicania* beds are characterised by the dominance of individuals belonging to *C.* gr. *haueri*, *C.* gr. *megalotis* and *C.* gr. *ladina* (= *C. merlai* sp. n., see below) respectively. These groups could be considered as three different species (Fig. 2). The lithology of the *Comelicania* beds shows a transition from the lower marls (*C. gr. haueri* beds), to the middle bioclastic wackestone-packstones (*C.* gr. *megalotis* beds) to the upper packstone-grainstones (*C.* gr. *ladina* beds). This sedimentary evolution suggests that the rapid change of the *Comelicania* species may be linked mainly to a change of texture resulting from an increase in hydrodynamic energy, an event recorded in all the sequences of the eastern Southern Alps located at the boundary between the Bellerophon and Werfen Formations.

In the Val Brutta section (Fig. 1) the *Comelicania* beds are thin (0.3 m thick). In this "condensed" section, the lower *Comelicania* beds (beds VB8-9, 0.2 m thick), composed mostly of marly, slightly nodular wackestones (beds VB8-9,), bear all the proposed *Comelicania* groups of species. However, in this section *C.* gr. *ladina* is represented by large individuals, while middle-sized shells of this group characterise the overlying packestone-grainstones (bed VB10). The *Comelicania* assemblage of Val Brutta suggests that the specimens of beds 8-9 are ecomorphotypes of a single species (*C. megalotis*), since the occurrence of transitional forms prevents a clear distinction between the three groups based on the outline. Therefore, only two species occurred (*C. megalotis* and small-sized individuals of *C.* gr. *ladina*) in the Val Brutta section. The high intraspecific diversity of the population of beds 8-9 could be due to the rather variable lateral stability of the bottom caused by spots of dead shells buried in the mud, resulting from a relatively dense population.

The systematic hypothesis derived from the stratigraphic data of the Val Brutta section seems to be supported by biometric analysis (Fig. 2) which allows the distinction of only two clearly different groups of individuals. One group (*C. ladina sensu* Merla) is represented by middle-sized shells of *C. gr. ladina* and is restricted to the upper *Comelicania* beds, while the other group (*C. megalotis*), including *C.* gr. *haueri*, *C.* gr. *megalotis* and large individuals of *C.* gr. *ladina*, is found in the middle-lower beds. In fact, the scatter diagram obtained from their outline shows that an area of overlap exists among *C. haueri* and *C. megalotis*, and that the allometric changes of the outline can occur during different ontogenetic stages (e.g. specimen no. VB67; see Fig. 2).

However, at present it is preferable to keep *C. haueri* distinct from *C. megalotis*, because of the still imprecise correlation between beds 8-9 of the Val Brutta section, bearing the *C.* gr. *megalotis*, *C.* gr. *haueri* and the large *C.* gr. *ladina* assemblage and those of the Sass de Putia section. In fact, it is not possible to demonstrate that the lower *C. haueri* beds of the Sass de Putia

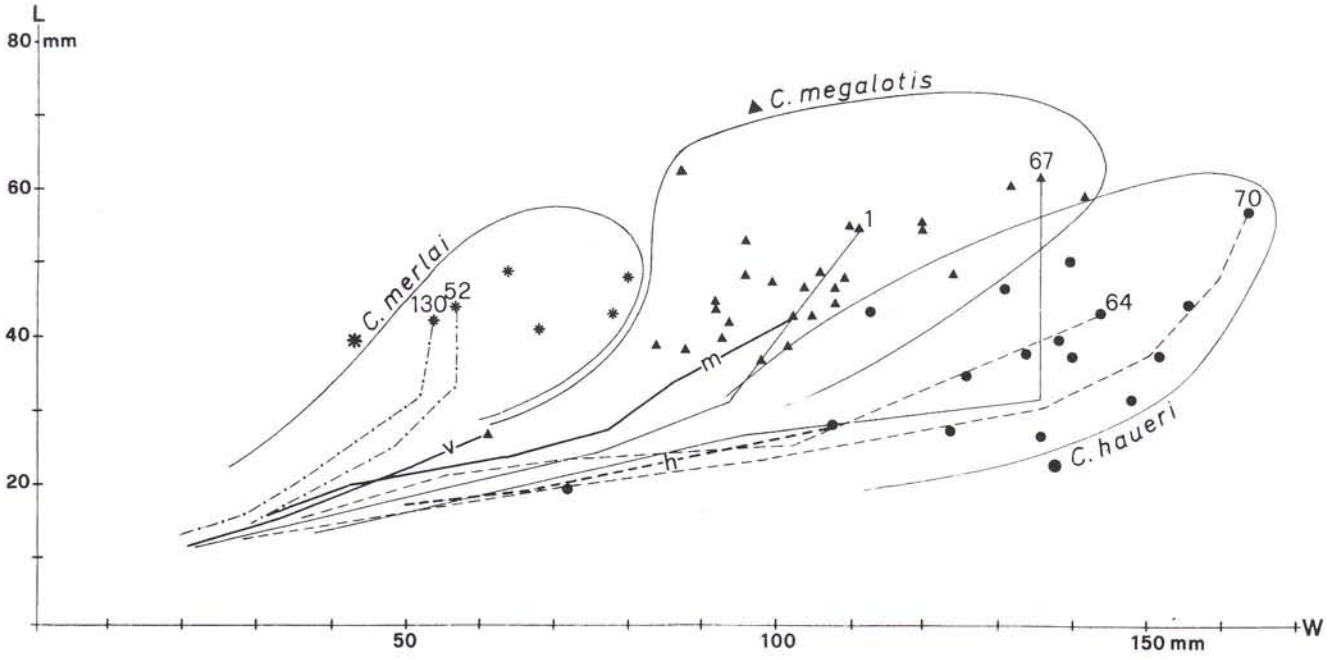


Fig. 2 - Scatter diagram of the MDSGF collection and growth variations of some individuals based on measuring concentric growth lines which show that allometric growth occurs in all species. The species have a very similar shell elongation during the early growth stage, which makes distinctions at this stage difficult. An area of overlap occurs between *C. megalotis* and *C. haueri*; shells occurring in this area are classified on the basis of the degree of distinction of the ears from the lateral margins. Abbreviations: h) lectotype of *C. haueri* (Stache, 1878, pl. 3, fig. 3; Pl. 1, fig. 1); m) holotype of *C. megalotis* (Stache) (Pl. 3, fig. 7); v) holotype of *C. vultur* (Stache) (Pl. 1, fig. 8); W) width of the shell; L) length of the ventral valve.

section are of the same age or older than the lower *Comelicania* beds of the Val Brutta section. The latter section was located towards the margins of the Bellerophon basin so, for instance, during the time of the middle *Comelicania* beds (*C.* gr. *megalotis* beds) the transgression might have reached this area later than the Sass de Putia, which was in a more open marine environment.

Furthermore, the distinction between *C. haueri* and *C. megalotis* is preferable due to the imprecision of the statistical analysis discussed previously, which results from the following factors: a) the majority of the dimensions are estimates because they were obtained from the reconstruction of the outline of broken shells; b) it is difficult to identify coeval assemblages with a sufficient number of individuals for a valid statistical analysis, since the types of Merla and Stache species and some well preserved individuals of the collection studied here have no precise stratigraphic position within the *Comelicania* beds. These constraints prevent us from understanding objectively whether a clear morphologic division between the two groups really existed.

In conclusion, the following three species are proposed: *C. haueri, C. megalotis* and *C. ladina sensu* Merla. For this last taxon the new species *C. merlai* sp. n. is proposed. The great variability in the outline of *C. megalotis* allows a subdivision into four morphogroups with different patterns of growth, which will be discussed in the systematic part.

Systematic description.*

(* supra-ordinal classification according to Williams et al., 1996)

Phylum **Brachiopoda** Duméril, 1806

Subphylum **Rhynchonelliformea** Williams, Carlson, Brunton, Holmer & Popov, 1996

Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996

Order Athyridida Boucot, Johnson & Staton, 1964

Suborder Athyrididina Boucot, Johnson & Staton, 1964

Superfamily *Athyridoidea* Davidson, 1881

Family *Comelicaniidae* Merla, 1930

Type-genus *Comelicania* Frech, 1901

Diagnosis.

Biconvex, smooth shell, strophic at adult stage, slightly to markedly transverse and alate, without foramen; ventral and dorsal sulcus present; dental plates lacking or feebly developed; delthyrium open; cardinal plate high and posteroanteriorly elongated, with a middle furrow or flat and bearing two posteroventrally elevated cardinal flanges; jugal saddle and stem present, accessory lamellae terminating between the 1st and 2nd volutions of the spiralia; shell impunctate.

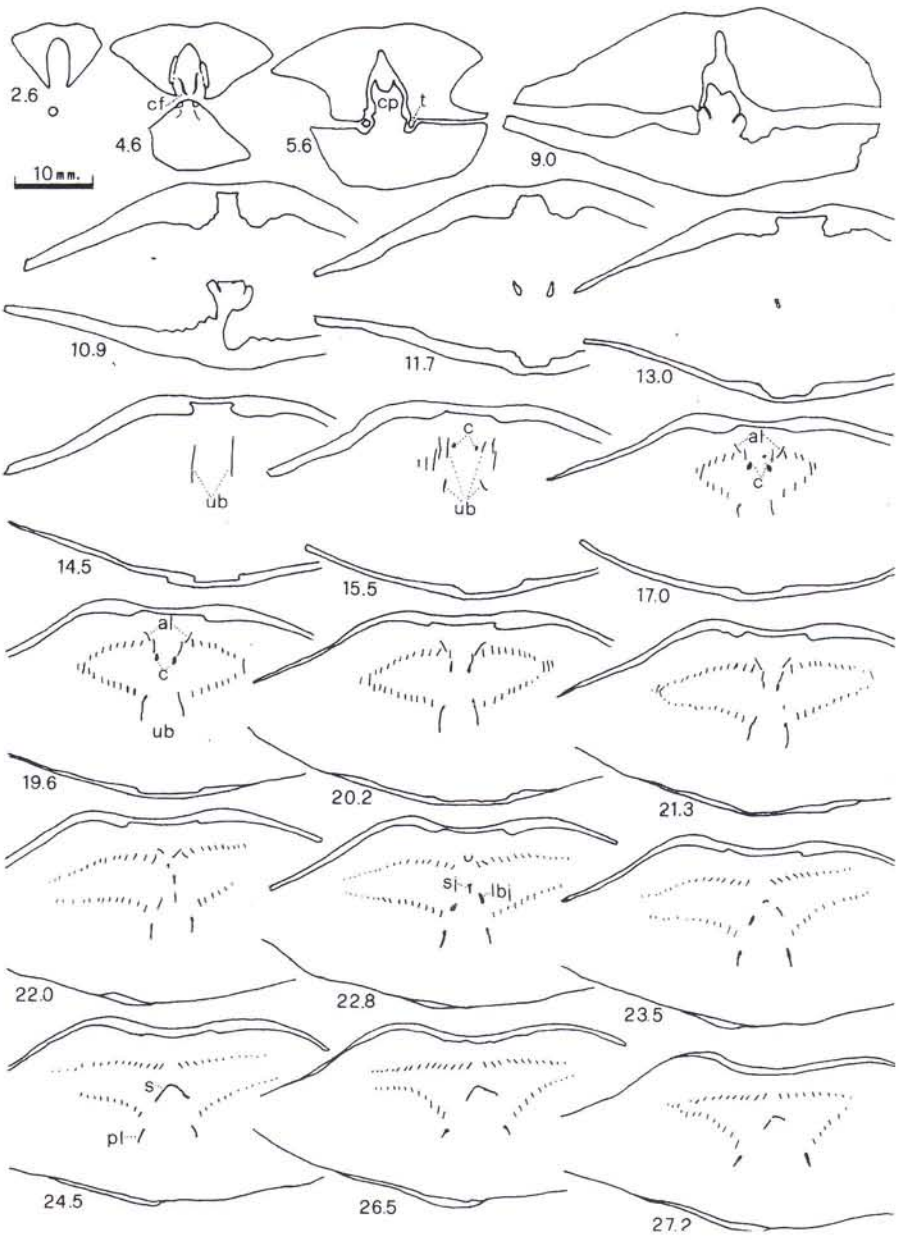


Fig. 3 - Serial transverse sections of *Comelicania* sp., specimen no. VB110 (MDSGF); uppermost Bellerophon Fm., Val Brutta. This specimen is lacking the lateral and anterior regions. Abbreviations: al, accessory lamellae; c, crura; cp, cardinal plate; cf, cardinal flange; lbj, lateral branch of jugum; pl, primary lamella; s, saddle; sj, stem of jugum; t, tooth; ub, umbonal blades.

Discussion.

Comelicania was placed by Grunt (in Ruzhentsev & Sarytcheva, 1965) in the Subfam. Athyridinae Phillips, and later placed in the Fam. Spirigerellidae Grunt, Subfam. Spirigerellinae Grunt (Grunt, 1986, 1989). However, *Comelicania* is characterised by some peculiar characters (e.g. strophic condition, very wide hinge line, absence of foramen, etc.) which do not completely fulfill the taxonomic characters of the groups quoted above. In fact, several differences exist between *Comelicania* and *Spirigerella* Waagen, 1883 (type genus of Fam. Spirigerellidae); among others, *Spirigerella* has an ovoidal, nonstrophic shell, generally with an open foramen. These external features could be used to separate *Comelicania* from the Fam. Spirigerellidae. A distinct family might be identified, like the already proposed Fam. Comelicaniidae Merla, which can be placed, following the classification of the Order Athyridida proposed by Grunt (1986), in the Superfam. Athyridoidea. Among the internal characters, the brachidium is similar to that of *Spirigerella* even if this genus has a median septum on the saddle and cardinal flanges unified posteriorly (Brunton et al., 1996, fig. 19), which *Comelicania* lacks (Fig. 3, 4).

According to Merla (1930) the Fam. Comelicaniidae is characterised by the lack of "area", delthyrium and dental plates. Both of the last two features are present, even if the delthyrium is concealed by the dorsal umbo and the dental plates are short and almost completely buried laterally by secondary shell deposits which fill the lateral cavities of the ventral umbo (Fig. 5B).

The lack of the cardinal area was also reported by Frech (1901, p. 551), who created the subgenus *Comelicania* on the basis of this character. The adult shell is strophic with the dorsal umbo tucked into the delthyrium, as to create an umbonal region which can be considered "rostrate" (Fig. 6), a typical feature of non-strophic shells (Rudwick, 1959). Therefore, the ventral "cardinal area" is not triangular but is subdivided by the umboes into two lateral lancet-like surfaces, more or less separated from the lateral surface by umbonal ridges, which vanish before they reach the alae. The early growth lines on this cardinal surface are not parallel to the posterior margin but form an acute angle with it (Fig. 6). The dorsal area is not present, as the dorsal umbo reaches the cardinal margin so that the umbonal ridges, sometimes not clearly defined, form a low arch on each lateral side. The inclination relative to the posterior margin of the growth lines on the cardinal area suggests that non-strophic shells occurred in the early

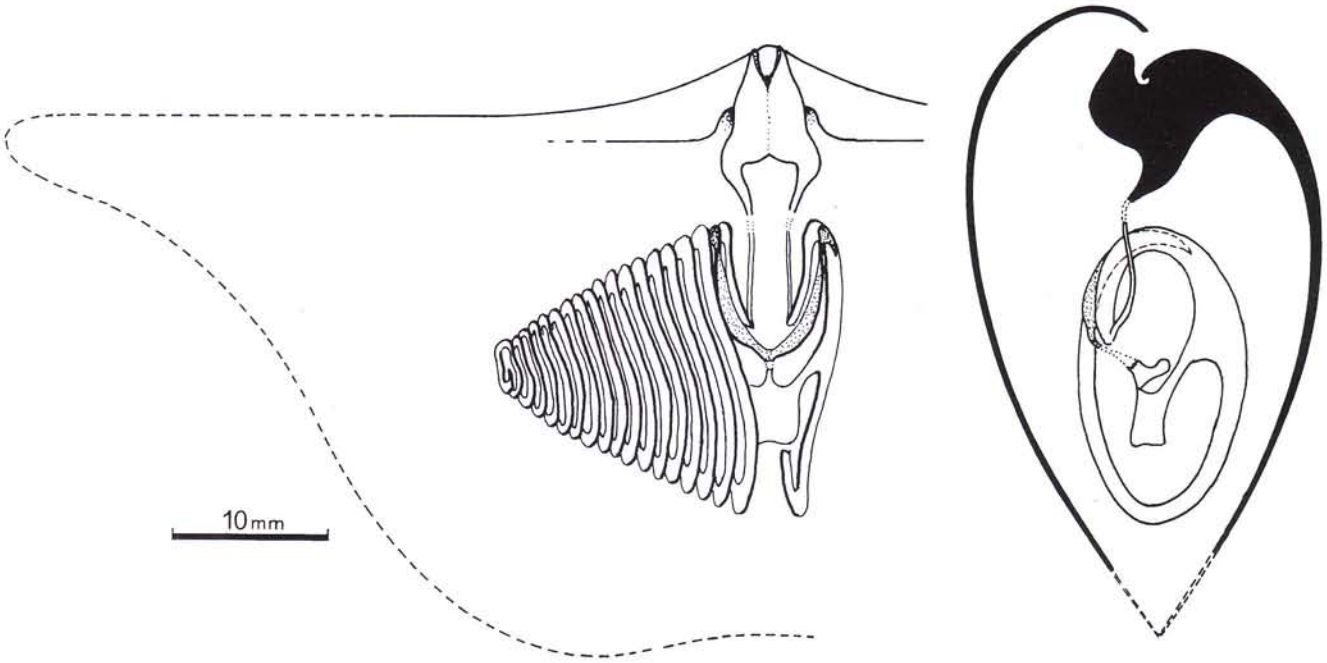


Fig. 4 - *Comelicania* sp. Reconstruction of the internal characters of the dorsal valve, mainly based on the serial sections of specimen no. VB110 (MDSGF); uppermost Bellerophon Fm., Val Brutta. The outline of the valve, the connection of the crura with cardinal plate and jugum stem with accessory lamellae are tentative. Scale bar 10 mm.

ontogenetic stages. In fact, juvenile individuals have a slightly curved posterior margin. *Comelicania* probably derives from a non-strophic athyridacean stock (?Spirigerellidae), from which it differs on the basis of its straight dorsal margin and the development of a peculiar palintrope which is here named the "cardinal surface", a term already proposed by Stache (1878) and adopted by Merla (1930). Among athyridoid brachiopods, the strophic shell is recorded also in other groups, for instance in the Late Triassic *Clavigera* Hector from New Zealand and New Caledonia, which has an external morphology similar to that of *Comelicania*. Waterhouse (1975) advanced the hypothesis that *Clavigera* may derive from a non-strophic precursor. In *Comelicania* such an hypothesis is supported by the early growth lines of large and strophic specimens, and juvenile non-strophic individuals which are, however, uncommon in the Dolomites.

Genus *Comelicania* Frech, 1901

Type-species ?*Spirifer megalotis* Stache 1878*

*) original name used by Stache in the text (p. 139). The type-species was named as *Spirifer (vultur) megalotis* n. f. (? *Spirigera*) on pl. 3, fig. 1 (Stache, 1878).

Syn.: *Spitispirifer* Waterhouse & Gupta, 1986 (*nomen nullum*); *Alatothyris* Waterhouse & Gupta, 1986 (junior syn.).

Description.

External characters. Large, biconvex shell with a very thick posterior wall, reaching about 15-18 cm in width; slightly to markedly transverse and alate; strophic at maturity, with a maximum width corresponding with the hinge line. Cardinal extremities pointed. Shell surface smooth, with only growth lines. The ventral valve is slightly more convex than the dorsal one. Each valve has a median sulcus bordered by smooth ridges. Sometimes the median sulcus of the brachial valve is placed on a fold-like swelling with a wide and low plication on each side. Anterior commissure poorly known (rectimarginate to uniplicate ?). Cardinal surface with a double lancet-like shape separated by rostrate umboes; it is separated from the lateral surface by an arcuate, smooth umbonal ridge which tends to be inconspicuous laterally to the umbonal region; a consistent ridge appears on the alae, where it slightly diverges from the cardinal margin to form a slightly convex surface sloped posteriorly and anteriorly. The ala thus has a rhomboidal outline in transversal section.

Ventral umbo broad and relatively strong, curved beyond the hinge line and covering the beak of the dorsal umbo; delthyrium open, large but concealed by the dorsal umbo. Dorsal umbo small and weakly curved close to the ventral umbo, tucked within the delthyrium.

Internal characters. The internal morphology was reconstructed from disarticulated valves and from serial sections of specimens 10-12 cm wide. Dental plates are short, about 5 mm long from the beak, forming a subelliptical mid chamber in transversal section; lateral cavities of the ventral umbo are almost completely filled by secondary shell thickening. Hinge-teeth are cyrtomatodont, smooth with the apex curved posteriorly within

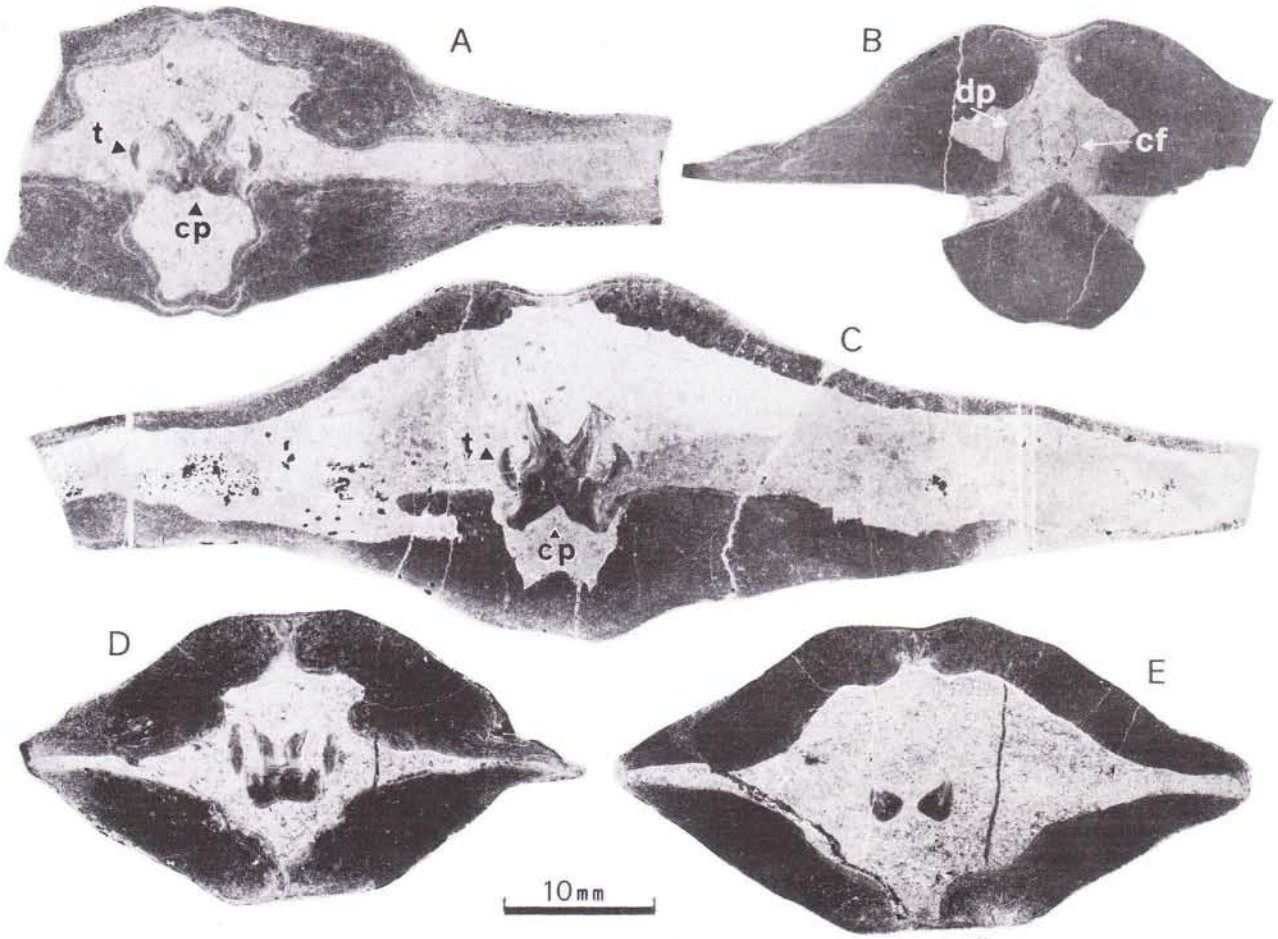


Fig. 5 - A) *Comelicania megalotis* (Stache), morphotype B, specimen no. MC109 (MDSGF), topotype (Pl. 3; fig. 1); uppermost Bellerophon Fm., Passo di Monte Croce Comelico. Transverse section through cardinal process at 6.4 mm from the umbo. Ventral valve at the top. B, C) *C. megalotis* (Stache), morphotype A, specimen no. VB111 (MDSGF) with slightly open shell; uppermost Bellerophon Fm., Val Brutta (Valsugana): B) transverse section through ventral umbonal cavity with the anterior portion of the dental plates (dp) and cardinal flange (cf), at 5.3 mm from the umbo; C) transverse section through the cardinal plate (cp) and teeth (t) at 8.3 mm from the umbo. D, E) *Comelicania merlai* sp. n., specimen no. PK130 (MDSGF); uppermost Bellerophon Fm., Sass de Putia: transverse sections at 7.0 and 8.5 mm from the umbo.

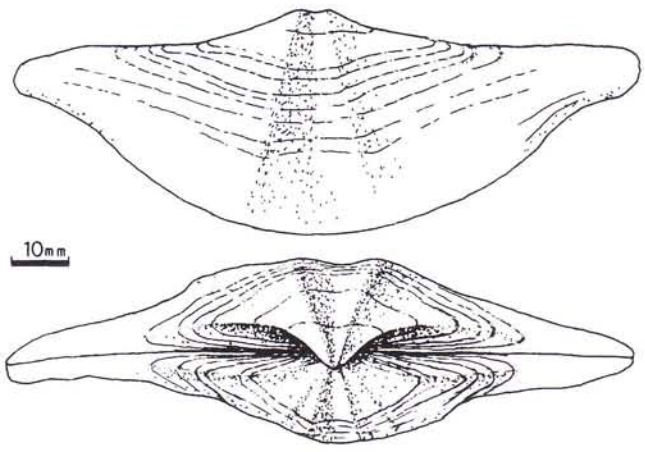


Fig. 6 - Ventral and posterior views of *Comelicania haueri* (Stache), specimen no. VB83 (MDSGF); uppermost Bellerophon Fm., Val Brutta (Valsugana). This anteriorly compressed and slightly divaricated shell has well-marked growth lines which show that *Comelicania* had non-strophic early growth stages.

the sockets. Dorsal and ventral umbonal cavities without median septa.

Cardinal plate longitudinally elongated, subrectangular to subtrapezoidal in outline, anterodorsally sloped and mesially grooved. Its posterior extremity, which extends beyond the dorsal beak, bears two cardinal flanges (*sensu* Brunton et al., 1996); they thin distally to form slightly arched blades gently convergent towards the commissure plane. Cardinal flanges are posteriorly crenulated on the side facing the sagittal plane, while they are smooth on the lateral side. Anterior edge of the cardinal plate bears two tubercles (crural basis), sometimes elongated to originate laterally flattened blades which extend anteroventrally, diverging from the median plane.

Muscle field deeply impressed, fusiform in outline, and divided by a low myophragm which extends for three quarters or more of the length of the valve, vanishing anteriorly. The posterolateral sides of the shell floor have shallow and irregular pits (gonocoel marks ?).

Jugum similar in pattern to that of *Athyris* (Moore, 1965, fig. 108). Jugal saddle present and relatively long, without median septum. Accessory lamella short, not exceeding in length the umbonal blade. Stem poorly known, but probably with a short posterodorsally directed blade. Spiralia directed laterally; adult spiralia have up to 18 whorls on shells of about 10 cm in width (Fig. 4).

Remarks.

The distinction of Alpine Comelicaniids into *Comelicania* Frech, 1901 (type species ?*Spirifer megalotis* Stache, 1878) and *Alatothyris* Waterhouse & Gupta, 1986 (type species *Spirifer Haueri* Stache, 1878) was proposed by Waterhouse & Gupta (1986) only on the basis of the shell outline. At present, this character does not seem to have a taxonomic value at the genus level because there is no sharp morphologic boundary between the two genera. *C. megalotis* can be identified generally only at an adult or senile stage because at juvenile stages it shows similarities with *C.haueri* (Fig. 2). Considering the internal characters, the cardinal plate of *C. megalotis* has the same structure as that of *C. haueri*; differences concern only the size and a different elongation of the cardinal flanges and crural basis. At present, the lack of data on their respective brachidia hinders the comparison of this character.

The lack of specimens among the sectioned shells with the brachidium connected to the cardinal plate led to the hypothesis that these structures could be loosely connected, as already proposed in some athyridoids (Rudwick, 1970) like *Diplospirella* (Benigni & Ferliga, 1990).

Comparison between *Comelicania* and *Gruntallina*

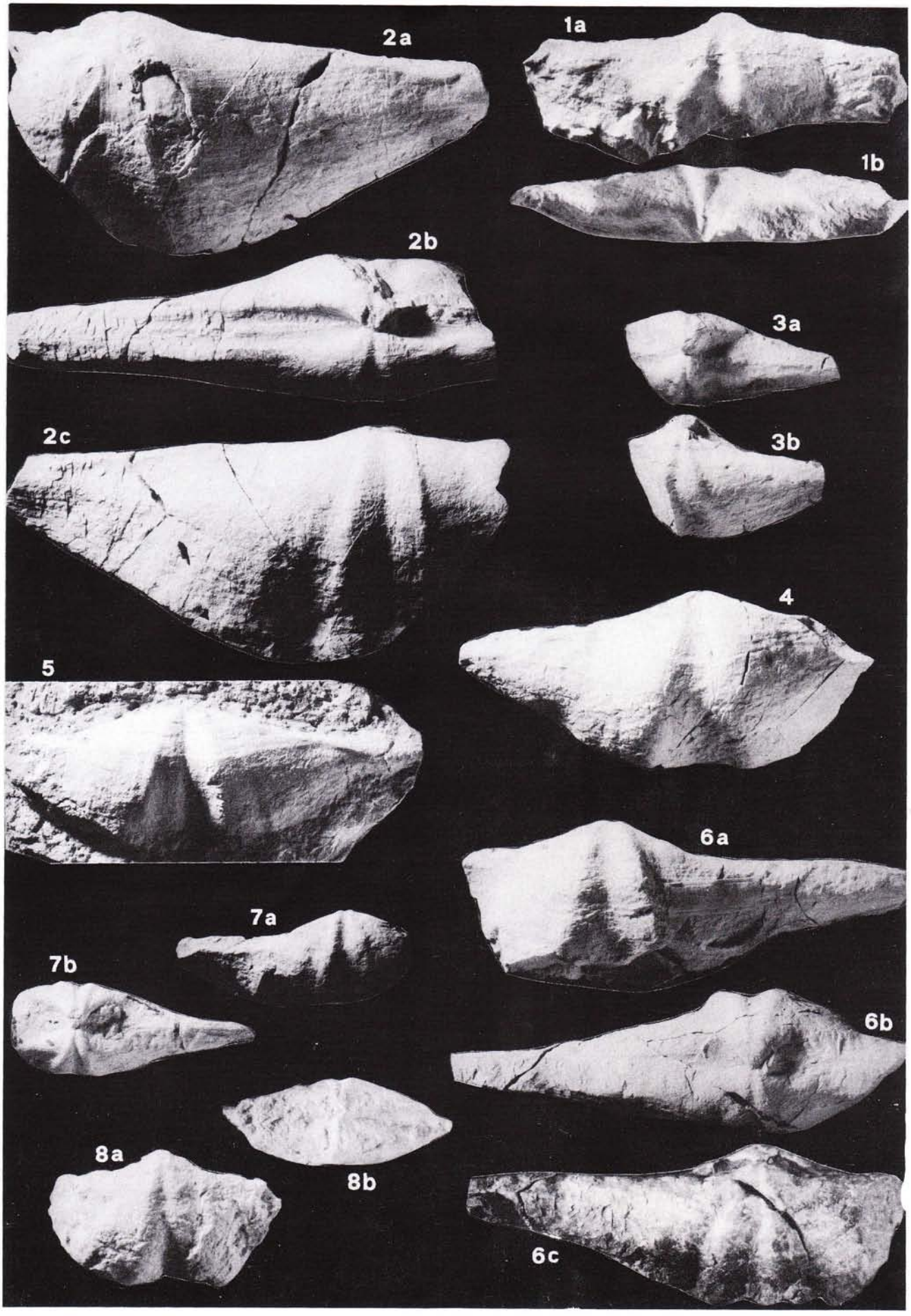
The genus *Gruntallina* (type-species *Comelicania triangularis* Grunt, 1965) was "distinguished from *Comelicania* by the elevated median part of the ventral valve, which is massively swollen." (Waterhouse & Gupta, 1986, p. 51). Besides such an external character, additional differences can be detected among the external and internal features, which strongly justify the distinction at the genus level. Alpine Comelicaniids have large dimensions (up to 180 mm in width), while Transcaucasian specimens are decidedly smaller (up to 40 mm in width; Grunt in Ruzhentsev & Sarytcheva, 1965). Although some distinctive characters could be correlated with the difference in size, i.e. the number of spires (18-20 whorls in *Comelicania* vs. 5-7 in *Gruntallina*) and the occurrence, in *Comelicania*, of short dental plates which in *Gruntallina* are reduced to "low dental rims" (Waterhouse & Gupta, 1986) not connected with the valve wall, the main differences affect the morphology of the cardinalia and in particular that of the cardinal flanges. On the basis of Grunt's figures (Grunt in Ruzhentsev & Sarytcheva, 1965, figs. 47, 48; Grunt, 1986, fig. 59), *Gruntallina* shows short, laterally elongated and nearly flat cardinal flanges, parallel to the commissural plane, while in *Comelicania* they are longer and strongly inclined or nearly perpendicular to the commissure plane. In *Gruntallina* the cardinal plate has an anteriorly projected, underlying median septum, located inside the dorsal umbonal cavity (Grunt in Ruzhentsev & Sarytcheva, 1965, fig. 48; Grunt, 1986, fig. 59), which is lacking in *Comelicania*. A median, anteriorly projected tubercle was detected only in a dorsal valve (no. PK23), but it is placed at the base of the mas-

PLATE 1

Fig. 1-3, 5-7 - *Comelicania haueri* (Stache), Bellerophon Fm., Dorashamian (x 1).
Fig. 4, 8 - *Comelicania megalotis* (Stache), Bellerophon Fm., Dorashamian (x 1).
1) Plaster replica of the lectotype of *C. haueri* (Stache), ventral valve (Stache, 1878, pl. 3, fig. 3a, b); a, b) ventral and posterior views; Kreuzberg (= Monte Croce di Comelico), MGBW 3785. 2, 4) *C. macroptera* Merla: (2) lectotype (Merla 1930, pl. 4, fig. 1a, b); a-c) ventral, posterior and dorsal views; Monte Croce di Comelico, MDGP 24804; (4) paralectotype (Merla 1930, pl. 4, f. 4), ventral view; Monte Croce di Comelico, MDGP 24805. 3) *C. avis* Merla, lectotype (Merla 1930, pl. 3, fig. 6a-c); a, b) posterior and dorsal views; Monte Croce di Comelico, MDGP 24807. 5) *C. vespertilio* Merla, lectotype (Merla 1930, pl. 4, fig. 3), ventral valve, Monte Croce di Comelico, MDGP 24808. 6, 7) *C. dalpiazi* Merla: (6) lectotype (Merla 1930, pl. 3, fig. 4a, b); a-c) ventral, posterior and dorsal views; Monte Croce di Comelico, MDGP 24800; (7) paralectotype (Merla 1930, pl. 3, fig. 5); a, b) ventral and posterior views; Monte Croce di Comelico, MDGP 24801. 8) *C. vultur* (Stache); plaster replica of the holotype (Stache 1878, pl. 4, fig. 2a, b); a, b) ventral and posterior views; Pitschberg, St. Ulrich, MGBW 3800.

PLATE 2

Fig. 1-7 - *Comelicania megalotis* (Stache), Bellerophon Fm., Dorashamian (x 1). 1) *C. doryphora* Merla, lectotype (Merla 1930, pl. 3, fig. 2a, b); a-c) ventral, posterior and dorsal views; Monte Croce di Comelico, MDGP 24803. 2, 3) *C. rostrata* Merla: (2a-c) ventral, posterior and dorsal views of a paralectotype not illustrated, MDGP 24980; (3) lectotype (Merla 1930, pl. 4, fig. 5a, b); a, b) ventral and posterior views of ventral valve, MDGP 24824; all from Monte Croce di Comelico. 4) *C. vultur* (Stache); a-c) ventral, posterior and dorsal views of a shell depicted by Merla (1930, pl. 2, f. 5); Monte Croce di Comelico, MDGP 24792. 5) *C. megalotis* (Stache); a-c) ventral, posterior and dorsal views of a shell depicted by Merla (1930, pl. 2, f. 1a, b); Monte Croce di Comelico, MDGP 24797. 6) Morphotype A, MDSGF MC90 Passo di Monte Croce di Comelico, posterior view. 7) Morphotype A, MDSGF MC91, Passo di Monte Croce di Comelico, dorsal view.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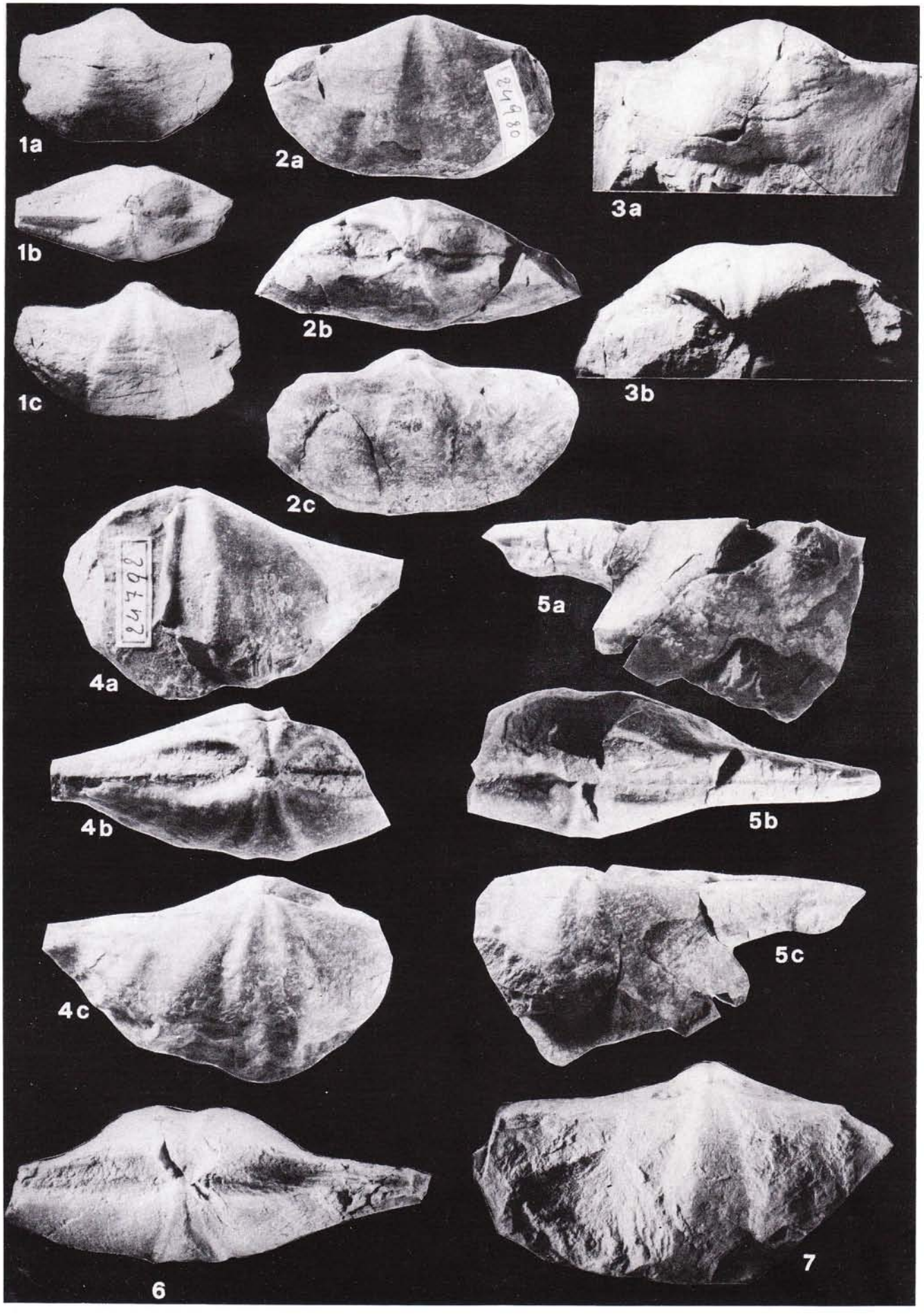
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sive cardinal plate, close to the shell wall. Moreover, *Gruntallina* has a low cardinal process which tends to be flattened anteriorly and a ventral umbonal cavity devoid of secondary shell material.

Comelicania megalotis (Stache, 1878)

(Pl. 1, fig. 4, 8; Pl. 2, fig. 1-7; Pl. 3, fig. 1-8; Pl. 4, fig. 1, 2; Pl. 5, fig. 3, 4; Pl. 6, fig. 2, 3, 7)

v 1878 *? Spirifer megalotis* Stache, p. 139, pl. 6, fig. 1a-c.
v 1878 *Spirifer vultur* Stache, p. 136, pl. 7, fig. 2a, b.
v 1878 *Spirifer (vultur)* var. *ladinus* Stache, p.137, pl. 4, fig. 1.
?v 1878 ? *Spirifer insanus* Stache, p. 138, pl. 2, fig. 24a, b.
1901 *Athyris (Comelicania) megalotis* - Frech, p. 551, pl. 67, fig. 12 a, b.
v 1930 *Comelicania megalotis* - Merla, p. 42, pl. 1, fig. 11, pl. 2, fig. 1a, b.
v 1930 *Comelicania* cfr. *megalotis* - Merla, p. 43, pl. 2, fig. 2.
v 1930 *Comelicania vultur* - Merla, p. 40, pl. 2, fig. 5, 6a-d.
v 1930 *Comelicania doryphora* Merla, p. 47, pl. 3, fig. 1, 2a, b.
v pars1930 *Comelicania macroptera* Merla, p. 48, pl. 4, fig. 4.
v 1930 *Comelicania rostrata* Merla, p. 49, pl. 4, fig. 5a, b.
? 1958 *Comelicania vultur* - Ramovs, p. 539, pl. 8, fig. 3.
? 1963 *Spirifer (Comelicania) vultur* - Schreter, p. 133, pl. 7, fig. 6a-e.
v 1988 *Comelicania* gr. *megalotis* - Posenato, pl. 50, fig. 2.

Material and dimensions (in mm).

Holotype. Specimen illustrated by Stache (1878) on pl. 6, fig. 1a-c and housed in the Museum of the Geologische Bundesanstalt, Wien with catalogue no. 3780 (Pl. 3, fig. 7).

Type locality and stratum. Monte Croce Comelico or Kreuzberg, Dolomites, Southern Alps, Italy. Uppermost Bellerophon Formation.

Age. Late Permian, Dorashamian or Changxinghian.

Diagnosis.

Large, transverse, subtriangular to subrectangular in outline; wings separated from shell by a more or less deep concavity of lateral margins. L/W ratio ranging from 0.37 to 0.70.

Description.

External characters. Large, triangular to subrectangular transverse shell with long and slender alae separated from the lateral margins at the mature stage; inclination of the lateral margins variable both during ontogenesis and among mature individuals: it varies from straight and anteriorly converging with a strongly transverse shell (*C. haueri* stage), mostly occurring in the juvenile stage (up to 20 mm in length) to anteriorly di-

Specimen	layer	shell	mor. type	Wm*	Wm	Wo	Lv*	Lv	Ld	T	Lv/Wm	sinal angle
1	PK51	S	B	**111**	111	78	**54**	54	46	36	0.49	28
20	PK51	D	D	**86**	86	80	**-**	-	57	17	-	-
21	PK51	V	C	108	108	58	46	46	-	16	0.42	33
30	PK51	S	A	**93**	93	-	**39**	39	33	26*	0.42	25
46	VB8-9	S	B	**116**	96	96	**48**	54	45	33?	0.41	30
47	VB8-9	V	D	**88**	84	76	**62**	62	-	17	0.70	20
49	VB8-9	D	D	**84**	84	72	**61**	61	55	12	-	-
50	VB8-9	D	D	**106**	100	86	**-**	-	57	14	-	-
55	VB8-9	V	A	**106**	106	-	**42**	42	-	-	0.40	30
60	VB8-9	S	B	**110**	96	80	**47**	47	-	23*	0.43	30
61	VB8-9	S	B	**84**	74	55	**38**	35	36	23?	0.45	-
62	VB9	V	B	**96**	96	80	**52**	52	-	17	0.54	-
67	VB8-9	S	B	**136**	136	114	**61**	61	-	35?	0.45	30
69	VB8-9	V	B	**124**	124	90	**48**	48	-	14	0.39	30
71	VB10	V	A	**94**	94	-	**41**	41	-	12	0.44	30
72	VB10	S	A	**114**	114	76	**46**	46	37	-	0.40	-
75	VB8-9	S	B	**96**	96	74	**48**	48	-	-	0.50	30
76	VB8-9	S	B	**110**	96	92	**54**	62.5	56	29	0.49	30
88	MC	S	B	**120**	120	88	**55**	62	50?	28?	0.46	25
90	MC	S	B	**98**	98	66	**36**	36	29	28*	0.37	35
91	MC	S	A	**88**	88	72	**37**	37	32	25*	0.42	25
92	MC	S	C	**142**	142	80	**58**	58	51	32?	0.41	30
93	MC	S	A	**108**	108	84	**44**	44	39	28.5	0.41	30
94	MC	V	C	**120**	94	84	**54**	54	-	19	0.45	30
97	AG	V	B	**132**	132	88	**60**	68	-	-	0.45	35
108	PZ	S	A	**92**	88	72	**43**	43	40	28.5	0.47	35
109	MC	S	B	**92**	74	68	**44**	46	41	24	0.48	30
111	VB8-9	S	A	**102**	102	-	**38**	35	-	25*	0.37	30

Tab. 1 - Measurements in mm of *Comelicania megalotis* (Stache) housed in the Museum of the Dipartimento di Scienze Geologiche e Paleontologiche, Ferrara University (MDSGF). Abbreviations: S - shell; V - ventral valve; D - dorsal valve (not considered in the scatter diagram of Fig. 2); Wm - width of shell; Lv - length of ventral valve; Ld - length of dorsal valve; T - thickness; * - estimated measurements of broken and/or deformed specimens, plotted in Fig. 2. Since the shells are frequently incomplete and/or deformed, the width was obtained by doubling the measurement of the better preserved half.

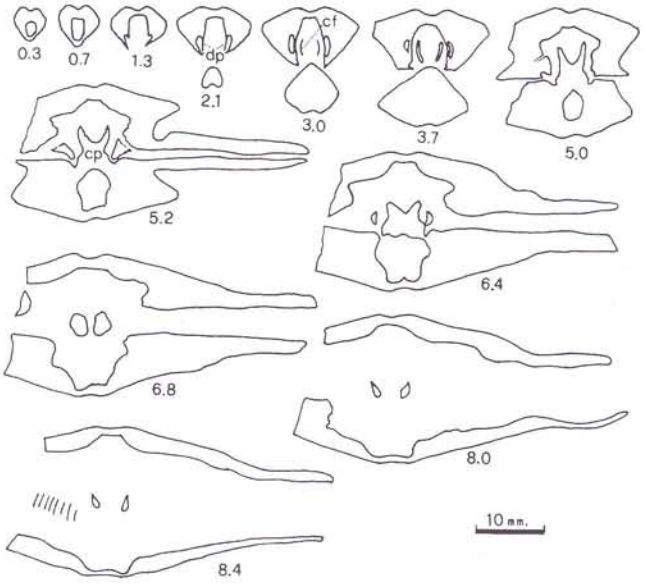


Fig. 7 - Serial transverse sections of *Comelicania megalotis* (Stache), morphotype B, specimen no. MC109 (MDSGF) (Pl. 3, fig. 1); uppermost Bellerophon Fm., Passo di Monte Croce Comelico. For abbreviations see Fig. 2, 3.

verging in the senile stage with well separated alae. Ventral valve more inflated than the dorsal. Ventral umbo large, curved beyond the commissure plane and covering the dorsal umbo. Delthyrium open but covered by dorsal umbo; foramen absent. Ventral sulcus with concave floor and sinal angle of 25-35°. Sinal ridges smooth, sometimes slightly distinguished from the lateral umbonal regions by a hardly perceptible furrow, which vanishes anteriorly. Dorsal valve with only a median sulcus (no. PK1; Pl. 3, fig. 2b) or with a fold-like swelling which bears a middle sulcus (no. PZ108; Pl. 3, fig. 4); occasionally, a relatively large groove occurs on each side of the fold (no. MC109; Pl. 3, fig. 1b). The ridges defining the dorsal sulcus are slightly rounded in the umbonal region, while they are not well defined anteriorly. Cardinal surface relatively narrow, with a double lancet-like outline, separated along the median plane by rostrate umboes and from the lateral shell surface by rounded umbonal ridges (*costole umbonali* of Merla, 1930), which are well defined only in the umbonal region; the posterior walls range from concave, in the umbonal region, to convex outwards, where no clear separation between cardinal surface and lateral regions is detectable. A middle ridge occurs on the alae; it is directed laterally and subparallel to the cardinal margins; lateral extremities of wings closed. Sculpture only represented by growth lines, which sometimes form irregular concentric corrugations of the shell (e.g. in the holotype).

Internal characters (Fig. 7-9). Dental plates short and buried laterally by a thick secondary shell deposit which fills the lateral cavities of the ventral umbo. Cardinal plate anteroposteriorly elongated, highly raised from the hinge plate and subrectangular in outline; its posterior extremity bears two thin cardinal flanges perpendicular to the commissural plane and gently concave towards the mid-plane. The anterior part of the cardinal plate has two anteroventrally directed blades, which are sometimes reduced to small tubercles (crural basis). Ventral muscle field (Pl. 6, fig. 2, 3) elongated and drop-like in outline with a low myophragm in the posterior half; dorsal muscle field ovoidal elongated with a middle low ridge; both are deeply impressed on the valve; adductor and diductor scars on ventral valve are not clearly discernible.

Morphotypes and Remarks.

C. megalotis shows a considerable morphologic variability which allows this species to be split into four main morphotypes, distinguished on the basis of their

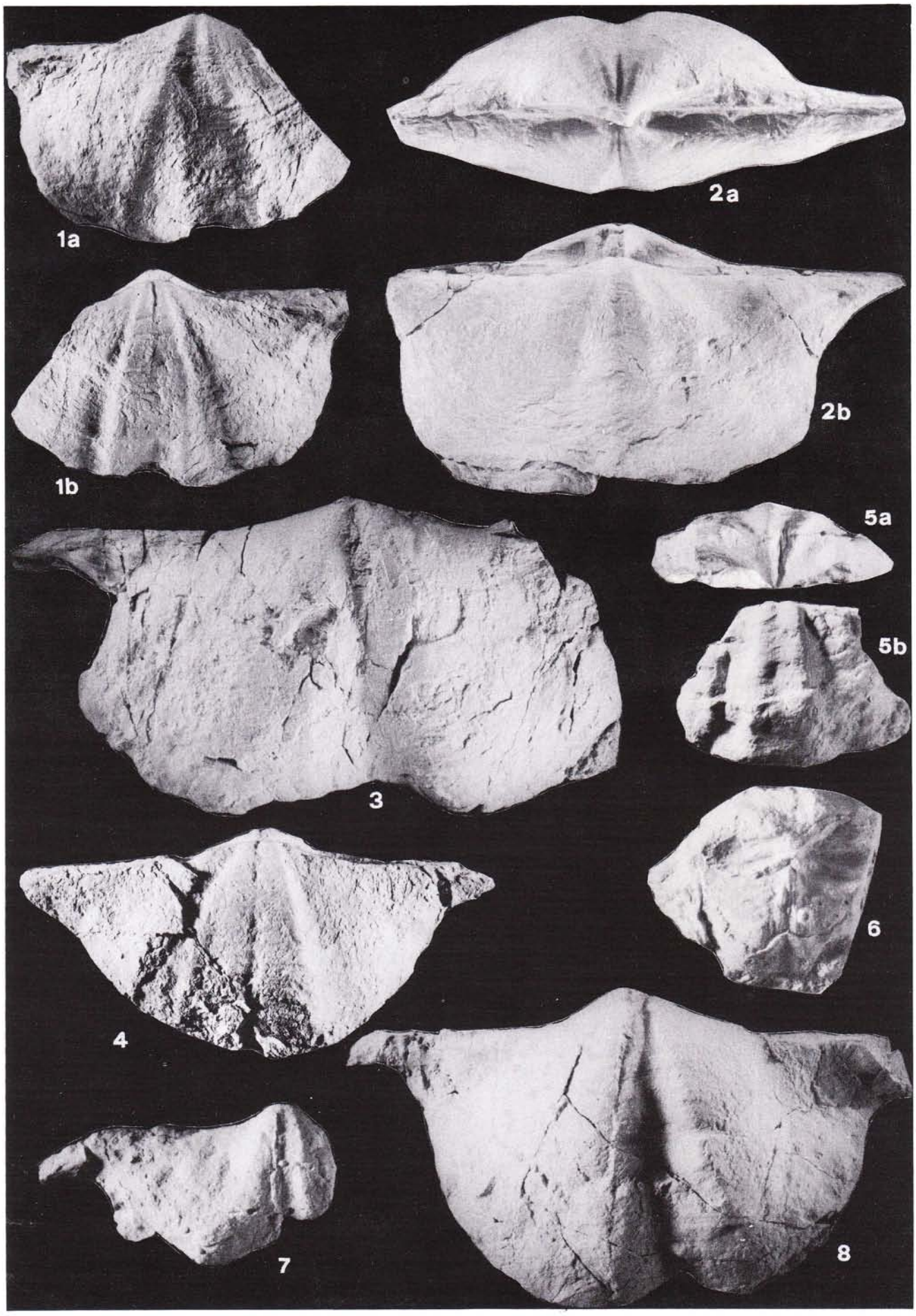
PLATE 3

Fig. 1-8 - *Comelicania megalotis* (Stache), Bellerophon Fm., Dorashamian (x 1).1a, b) Morphotype B, ventral and dorsal views of a sectioned shell (Fig. 5A, 7); Monte Croce di Comelico, MDSGF MC109. 2a, b) Morphotype B, posterior and dorsal views; Sass de Putia, MDSGF PK1. 3) Morphotype B, ventral view of the largest specimen yet found; Val Brutta, MDSGF VB67. 4) Morphotype A, dorsal view; Piz da Peres, MDSGF PZ108. 5) *C. insana* (Stache), plaster replica of the holotype (Stache, 1878, pl. 2, fig. 24); a, b) posterior and dorsal view of dorsal valve; Monte Croce di Comelico, MGBW 3793. 6) *C. ladina* (Stache), plaster replica of the holotype (Stache 1878, pl. 4, fig. 1), an open shell with deformed ventral valve; Ruefenberg (Sass de Putia Group), MGBW 3778. 7) Ventral view of the holotype of *C. megalotis* (plaster replica) (Stache 1878, pl. 3, fig. 1 a-c); Monte Croce di Comelico, MGBW 3780. 8) Morphotype B, ventral view; Monte Croce di Comelico, MDSGF MC88.

PLATE 4

Fig. 1, 2 - *Comelicania megalotis* (Stache), Bellerophon Fm., Dorashamian (x 1).
1) Morphotype D, ventral valve, Val Brutta, MDSGF VB47. 2) Morphotype D, dorsal valve; Sass de Putia, MDSGF PK20.

Fig. 3-9 - *Comelicania merlai* sp. n., Bellerophon Fm., Dorashamian, x 1. 3-5) Specimens of Merla's collection classified as *C. ladina*: (3) ventral valve (Merla, 1930, pl. 2, fig. 4), MDGP 24795a; (4) ventral valve (?) (Merla, 1930, pl. 2, fig. 3), MDGP 24795b; (5) a dorsal valve, not illustrated, of Merla's collection, MDGP 24794. All from Monte Croce di Comelico. 6a-d) Ventral, posterior, dorsal and lateral views of specimen no. PK130 (MDSGF) with broken wings. 7) Ventral valve, MDSGF PK52. 8) Ventral valve, MDSGF VB66. 9) ventral view of the specimen no. VB65 (MDSGF).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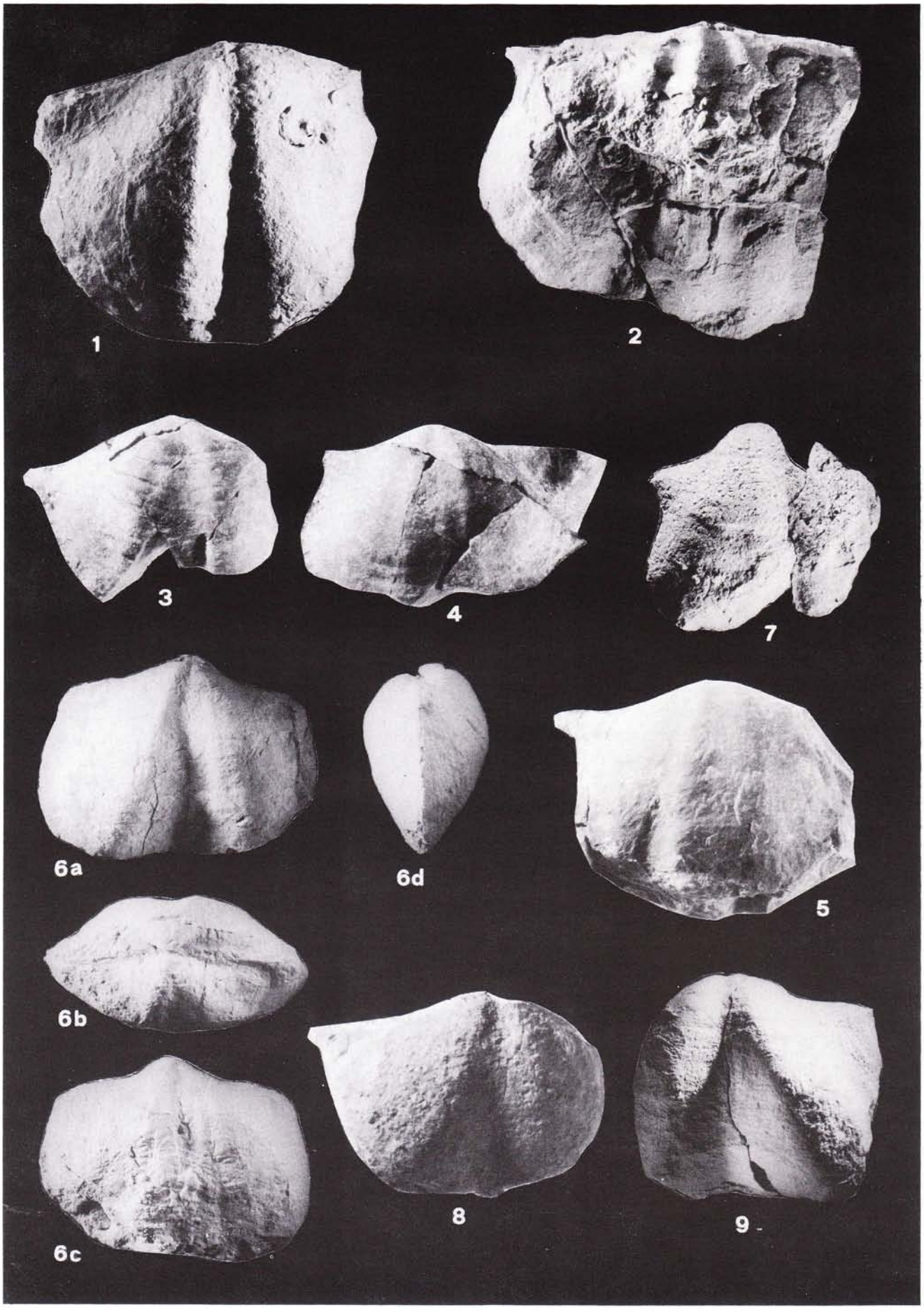
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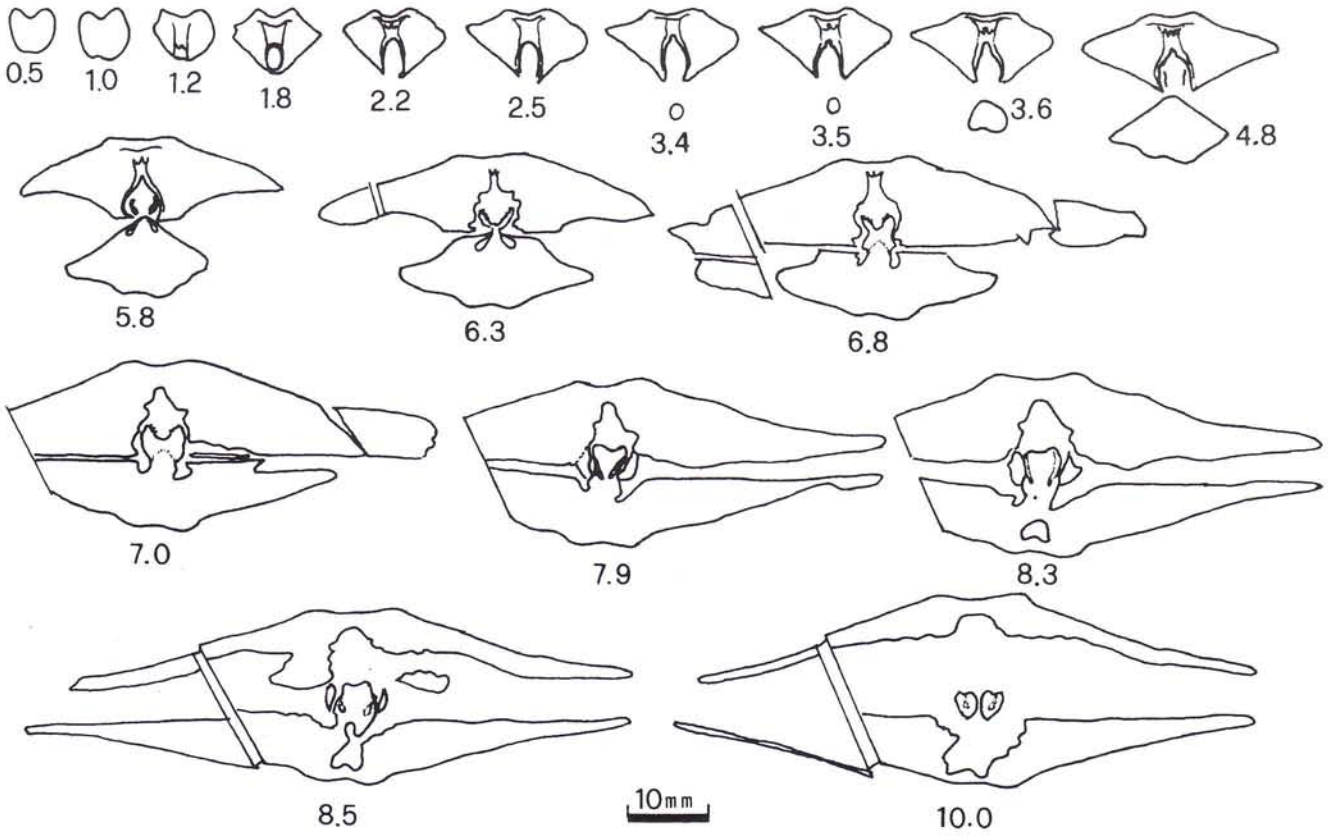


Fig. 8 - Serial transverse sections of *Comelicania megalotis* (Stache), morphotype A, specimen no. PZ108 (MDSGF) (Pl. 3, fig. 4); uppermost Bellerophon Fm., Piz da Peres.

relative widths and the degree of alae distinction from the shell (Fig. 10, 11). These morphotypes highlight the degree of variability and aid in the discussion of the species and its synonyms. The large individuals previously attributed to the *C.* gr. *ladina* (Posenato 1988a) are included in this species. All morphotypes occur in the same layers, and therefore must be considered as belonging to the same population, which does not seem to show significant geographic differences in the various areas of the Southern Alps.

Morphotype A.

The lateral margins of morphotype A converge anteriorly during the the course of ontogenetic development, as in *C. haueri,* and the alae are indistinct from the lateral margins. This morphotype shows transitional features with *C. haueri* from which it differs in having less transverse shells (higher L/W ratio). It includes specimens no. PK30, VB55, VB71, VB72, MC91 (Pl. 2, fig. 7), MC93, PZ108 (Pl. 3, fig. 4), etc. of the MDSGF collection (Tab. 1), some of which, represented by middle-sized shells, should be considered as an immature stage of morphotype B.

Morphotype A includes the specimens of *C. vultur* depicted by Merla (1930, pl. 2, fig. 5, 6) and the syntype of *C. doryphora* Merla illustrated by Merla (1930) on pl. 3, fig. 2 (Pl. 2, fig. 1). It is a small-sized shell with an outline similar to that of *C. vultur* from which it differs by its more acute cardinal ridges and a wider cardinal surface. These peculiar characters are well developed only in this syntype, while they are less marked in the others syntypes (e.g. Merla 1930, pl. 3, fig. 1) represented by larger and incomplete shells, always falling within the variability of *C. megalotis*, in which the lack of a detectable outline prevents its attribution to a definite morphotype.

Morphotype B.

Morphotype B yields the holotype of *C. megalotis* and that of *C. vultur*; furthermore, it includes specimens PK1 (Pl. 3, fig. 2), the sectioned specimen MC109 (Pl. 3, fig. 1) and nos. VB46, VB60, VB67 (Pl. 3, fig. 3), MC90 (Pl. 2, fig. 6), etc. (see Tab. 1). The holotype of *C. vultur* (Pl. 1, fig. 8) is represented by a shell of medium size with an outline and growth pattern corresponding with that of *C. megalotis*. Therefore, the former species must be considered a synonym of *C. megalotis*, type-species of *Comelicania*.

C. ladina (Stache) (Pl. 3, fig. 6) was placed in this morphotype for reasons which will be discussed later (see *C. merlai* sp. n.). *C. insana* (Stache) was assigned tentatively because its holotype (Pl. 3, fig. 5) is repre-

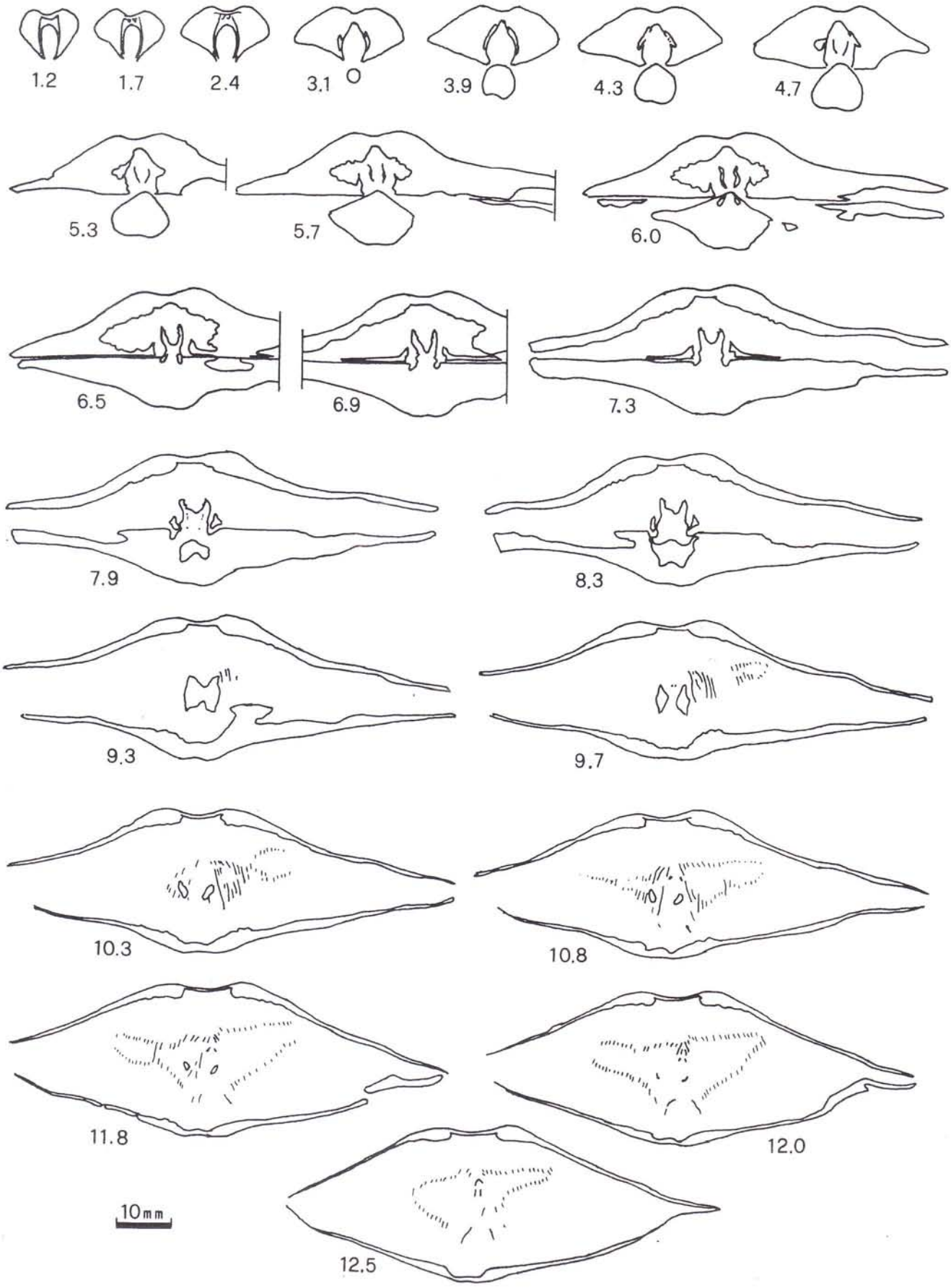


Fig. 9 - Serial transverse sections of *Comelicania megalotis* (Stache), morphotype A, specimen no. VB111 (MDSGF) slightly open, complete shell,; uppermost Bellerophon Fm., Val Brutta.

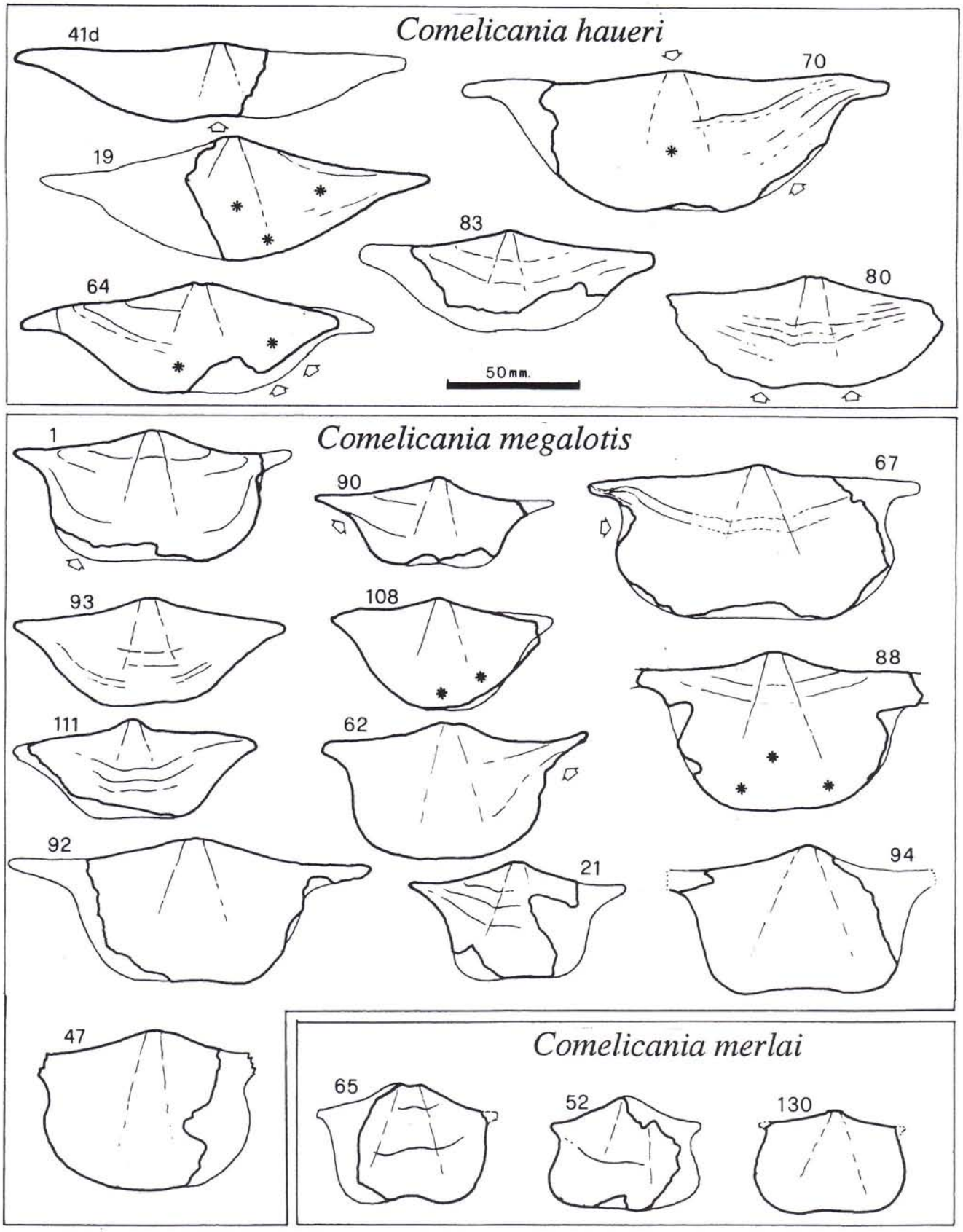


Fig. 10 - Outlines of the more complete *Comelicania* specimens of the collection housed in the Museum of the Dipartimento di Scienze Geologiche e Paleontologiche, Ferrara University (MDSGF). Thin lines show the reconstruction of the outline of broken or strongly deformed specimens; arrows indicate the direction of deformation; asterisks indicate a strong compression, perpendicular to the commissure plane. d) dorsal valve or dorsal view of the shell. For stratigraphic and geographic setting see Tab. 1, 2, 3.

sented by a deformed dorsal valve lacking the lateral regions. The morphology of the middle region, a raised swelling with a middle sulcus, is similar to that of specimen no. MC109 (Pl. 3, fig. 1), but the absence of the lateral margin does not allow a positive classification.

Morphotype C.

The specimens assigned to this morphotype (no. PK21, MC92, MC94; Pl. 6, fig. 7) are similar to those classified by Merla (1930, pl. 1, fig. 11) as *C. megalotis*. They have a ventral umbo that is larger than that of morphotype B and show an outline transitional to that of *C. merlai* which, in turn, has middle-sized shells, very short alae and a faster growth of the anterior region which may coincide with the maximum shell width.

C. rostrata Merla is placed tentatively in this morphotype, due to the incompleteness of the illustrated type (Merla 1930, pl. 4, fig. 5), which is represented by an isolated ventral valve with broken lateral and anterior margins, making its complete outline unknown (Pl. 2, fig. 3). Its peculiar features are a large, rostrate umbo and sharp umbonal ridges.

The specimens from the Bükk Mts. (Hungary) and Slovenja, classified by both Schreter (1963) and Ramovs (1958) as *C. vultur*, were not examined and therefore their taxonomic position, both at the species and genus level, is uncertain.

Geographic distribution. Passo di Monte Croce Comelico (Kreuzberg), Sass de Putia, Piz de Peres, Monte Pitsch, Solschedia, Agordo, Val Brutta (Southern Alps).

Comelicania haueri (Stache, 1878)

(Pl. 1, fig. 1-3, 5-7; Pl. 5, fig. 1; Pl. 6, fig. 4, 6)

v 1878 *Spirifer (vultur) Haueri* Stache, p. 140, pl. 6, fig. 2a, b, 3a, b.
1910 *Comelicania Haueri* - Kossmat & Diener, p. 300, pl. 15, fig. 14a, b.
v 1930 *Comelicania Haueri* (?) - Merla, p. 44, pl. 3, fig. 3.
v 1930 *Comelicania avis* Merla, p. 48, pl. 3, fig. 6a-c, pl. 4, fig. 2.
v 1930 *Comelicania Dalpiazi* Merla, p. 45, pl. 3, fig. 4a, b, 5.
v *pars*1930 *Comelicania macroptera* Merla, p. 48, pl. 4, fig. 1a, b.
v 1930 *Comelicania vespertilio* Merla, p. 50, pl. 4, fig. 3.
v 1988a *Comelicania* gr. *haueri* - Posenato, pl. 50, fig. 1.

Material and measurements (in mm).

specimen	layer	shell	Wm*	Wm	Wo	Lv*	Lv	Ld	T	Lv/Wm	sinal angle
3	PK<50	S	140	134	-	37	37	31	31*	0.26	35
4	PK<50	S	148	144	-	31	31	-	24*	0.21	30
5	PK<50	V	136	136	-	26	25	-	-	0.19	30
9	PK<50	S	126	126	-	34	39	-	-	0.27	30
19	PK<50	S	156	156	108	44	48.5	44	-	0.28	33
31	PK<50	V	124	124	90	27	25	-	-	0.22	-
41	PK<50	S	152	152	122	37	37	29	27*	0.24	-
54	VB8-9	D	132	132	-	-	-	40	-	-	-
64	VB8-9	S	144	144	108	43	48	40.5	27	0.30	28
70	VB8-9	S	164	164	136	57	59	-	28?	0.35	30
77	VB8-9	S	138	138	76	39	38.5	-	31*	0.28	25
80	VB8-9	S	132	120	-	46	43	-	31*	0.35	23
82	VB8-9	S	140	130	-	50	50	-	30*	0.36	30
83	VB8-9	S	113	107.6	-	43	37.5	-	24*	0.38	30
89	MC	S	134	118	100	37	37	32	22	0.28	30
115	VB8	S	126	126	80	-	-	34	28*	-	-

Tab. 2 - Measurements in mm of *Comelicania haueri* (Stache) housed in the Museum of the Dipartimento di Scienze Geologiche e Paleontologiche, Ferrara University (MDSGF). For abbreviations see Tab. 1.

Morphotype D.

It includes large individuals characterised by short alae and a L/W ratio ranging from 0.60 to 0.75, falling in the range of *C. merlai*. However, the specimens of this morphotype (PK20 - Pl. 4, fig. 2, VB50, VB49, VB47 - Pl. 4, fig. 1), placed previously in the *C.* gr. *ladina* (Posenato, 1988a), differ from *C. merlai* in having a larger size, a narrower median sulcus (VB47), and a *haueri* outline of the growth lines, which almost reach the maximum width (PK20).

Lectotype. Specimen depicted by Stache (1878) on pl. 6, fig. 3a, b and housed in the Museum of the Geologische Bundesanstalt, Wien with catalogue no. 3785 (Pl. 1, fig. 1).

Type locality and stratum. Monte Croce di Comelico or Kreuzberg, Dolomites, Southern Alps, Italy. Uppermost Bellerophon Formation.

Age. Late Permian, Dorashamian or Changxinghian.

Diagnosis.

Large, strongly transverse and alate shell; alae not separated from lateral margins. L/W ratio ranging from 0.19 to 0.38.

Description.

Large and strongly transverse shell with very long and slender alae, gradually connected to the lateral margins. Ventral valve more inflated than the dorsal. Ventral umbo curved beyond the commissure plane, on average more acuminate than that of *C. megalotis*. Cardinal ridges varying from sharp and elongated in the alae to rounded, restricted to the umbo. Sinal ridges range from rounded, more or less elevated from the lateral region, to sharp. Dorsal valve with a middle sulcus limited laterally either by raised rounded ridges, separated from the lateral regions by a shallow groove, or by smooth but not raised ridges. Other external and internal characters as in *C. megalotis*, with the exception of a shorter cardinal plate.

Remarks.

Merla (1930) attributed only a few broken specimens of his large collection to *C. haueri* because, in adopting a strict typologic concept of species, he considered the anterolateral direction of the umbonal ridge and the limited shell swelling as its main taxonomic characters. In the lectotype of *C. haueri* these characters are due to the diagenetic deformation which compressed the ventral valve. Furthermore, according to Merla (1930) *C. haueri* is characterised by a small and short umbo. However, this feature was misused by Merla, as his illustrated specimen was incorrectly considered a ventral, rather than a dorsal valve, which has a short umbo, and was dubiously attributed to *C. haueri* (Merla 1930, pl. 3, fig. 3). If the characters of *C. haueri* caused by deformation are excluded from the classification, *C. avis* Merla can be considered as its junior synonym, since it does not show any remarkable difference with Stache's species.

According to Merla (1930), *C. dalpiazi* differs from *C. haueri* in having a more inflated shell. This character is accentuated by an anteroposterior deformation in the illustrated types (Pl. 1, fig. 6, 7). The great swelling of the shells and median ridges is also due to the fact that the valves are slightly open (Merla, 1930, pl. 3, fig. 3). This species also has rounded median ridges and an inconspicuous umbonal ridge. These characters are shared by specimen no. VB80 (Pl. 6, fig. 6) of the MDSGF collection which is associated with typical individuals of *C. haueri*. Therefore, *C. dalpiazi* falls within the intraspecific variability of *C. haueri*.

C. macroptera includes two illustrated but quite different syntypes. This species was differentiated mostly on the basis of the great width of the wings, although the two shells have a quite different degree of elongation (L/W ratio). In particular, the small sized syntype (Pl. 1, fig. 4) has a lower relative shell width compared with the larger syntype (Pl. 1, fig. 2). This allometric development is reversed with respect to the ontogenetic trend detected in the individuals studied. Therefore, the small-sized syntype (Merla, 1930, pl. 4, fig. 4) is removed from this species and attributed, on the basis of the outline and degree of elongation, to morphotype A of *C. megalotis*. The other syntype (Merla, 1930, pl. 4, fig. 1, not to scale in Merla's figure, see Pl. 1, fig. 2) is characterised by a low inflated shell, large umbo, and a narrow and long cardinal surface, distin-

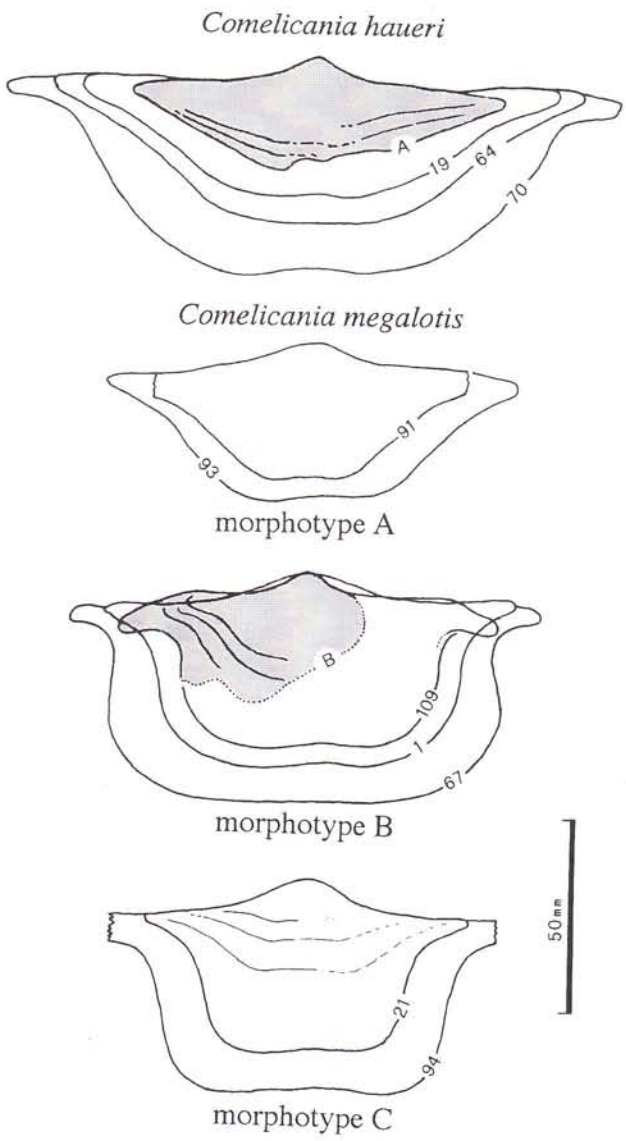


Fig. 11 - Outline variability of *C. haueri* and *C. megalotis*. Each morphotype of *C. megalotis* yields specimens with a similar outline, but not always with the same ontogenetic growth-pattern. Outlines and growth lines of the types of *C. haueri* (A) and *C. megalotis* (B) are drawn in those groups with a similar pattern of growth. Growth lines drawn in morphotype C belong to specimen PK21. The different morphotypes of *C. megalotis* are distinguished on the basis of shell elongation and time of appearance of alae well separated from the lateral margins. Morphotype D was not drawn due to the scarcity of available ventral valves. The largest specimen (no. VB67; Pl. 3, fig. 3) has a senile outline which is classified in *C. megalotis* even if an *haueri* growth-pattern persists during most of ontogeny (see Fig. 2).

guished from the lateral region by sharp umbonal ridges. Sharp umbonal ridges and a narrow cardinal surface are also present in the lectotype of *C. haueri* (Pl. 1, fig. 1). Its large umbo may depend on the large size of the shell and therefore falls within the ontogenetic variability of *C. haueri.*

C. vespertilio is represented in Merla's collection by two, strongly transversal, ventral valves. The type depicted (Pl. 1, fig. 5) is characterised by a sulcus with a sharp mid furrow and sharp sinal ridges, with adjacent shallow and narrow radial grooves. Radial grooves are absent in the other syntype, not illustrated (MDGP no. 24979). Relatively sharp sinal ridges, only slightly elevated from the lateral regions, occur in the lectotype of *C. haueri.* In this case, the populations of *C. haueri* would have a ventral sulcus rather variable in shape, with sinal ridges ranging from broad, rounded and moderately elevated from the lateral regions (*C. dalpiazi* morphotype), to rounded but not elevated (*C. avis* morphotype) and less frequently, sharp (*C. vespertilio* morphotype). The same variability is also detectable among the *C. megalotis* population.

Geographic distribution.

Passo di Monte Croce Comelico, Sass de Putia, Ortisei, Val Brutta (Southern Alps); Vrzdenec (Slovenja).

Comelicania merlai sp. n.

(Pl. 4, fig. 3-9)

v 1930 *Comelicania ladina* - Merla, p. 41, pl. 2, fig. 3, 4.
v 1988a *Comelicania* gr. *ladina* (Stache) *sensu* Merla - Posenato, pl. 50, fig. 3.

Material and measurements (in mm).

specimen	layer/ collection	shell	Wm*	Wm	Wo	Lv*	Lv	Ld	T	Lv/Wm	sinal angle
24795a	Merla	V	**58.4**	58.4	51	**38**	36	-	14	0.65	32
24795b	Merla	D	**49**	49	43	-	-	36	13	-	-
24794	Merla	D	**60**	60	50	-	-	38	12	-	-
48	VB10	V	**68**	56	55	**40**	40	-	14	0.59	35
51	VB10	V	**64**	64	56	**48**	45	-	14	0.75	-
52	PK53	V	**57**	57	57	**43**	41	-	12	0.75	35
65	VB10	S	**80**	60	60	**47**	47	41	30	0.59	35
66	VB10	V	**78**	78	72	**42**	42	-	14	0.54	35
130	PK53	S	**54**	54	46	**41**	41	39	26.2	0.75	40

Tab. 3 - Measurements in mm of *Comelicania merlai* sp. n. of the Merla's collection (Museum of the Dipartimento di Geologia, Paleontologia e Geofisica, Padova University, MDGP) and Museum of the Dipartimento di Scienze Geologiche e Paleontologiche, Ferrara University (MDSGF). For abbreviations see Tab. 1.

PLATE 5

Fig. 1 - *Comelicania haueri* (Stache). Large shell with a very thick umbonal wall; Bellerophon Fm., Val Brutta, MDSGF VB70; a) ventral view (x 1); b) portion of the ventral internal mould with the mould of the delthyrium cavity limited by the dental plates (x 1); c) interior view of the shell fragment with the umbonal region (x 2).

Fig. 2 - *Comelicania* sp. Fragment of the dorsal umbonal region with the cardinalia. a) interior view with broken crural basis; b) exterior view with cardinal flanges projecting beyond the dorsal umbo; Bellerophon Fm., Sass de Putia, MDSGF PK128 (x 2).

Fig. 3 - *Comelicania megalotis* (Stache). Cardinalia and teeth of an articulated specimen (Posenato 1988a, fig. 1C); ventral valve at the top; Bellerophon Fm., Val Brutta, MDSGF VB56 (x 2).

Fig. 4 - *Comelicania megalotis* (Stache). Cardinalia and teeth of an articulated shell (Posenato 1988a, fig. 1B); Bellerophon Fm., Val Brutta, MDSGF VB61 (x 2).

PLATE 6

Fig. 1 - *Comelicania* sp. Shell and internal mould of the middle region with muscle fields; a, b) ventral and dorsal views (x 1); c) detail of the interior dorsal valve with muscle field and a low myophragm (x 2); Bellerophon Fm., Val Brutta, MDSGF VB84.

Fig. 2 - *Comelicania megalotis* (Stache). Ventral internal mould with muscle field; Bellerophon Fm., Val Brutta, MDSGF VB68 (x 1).

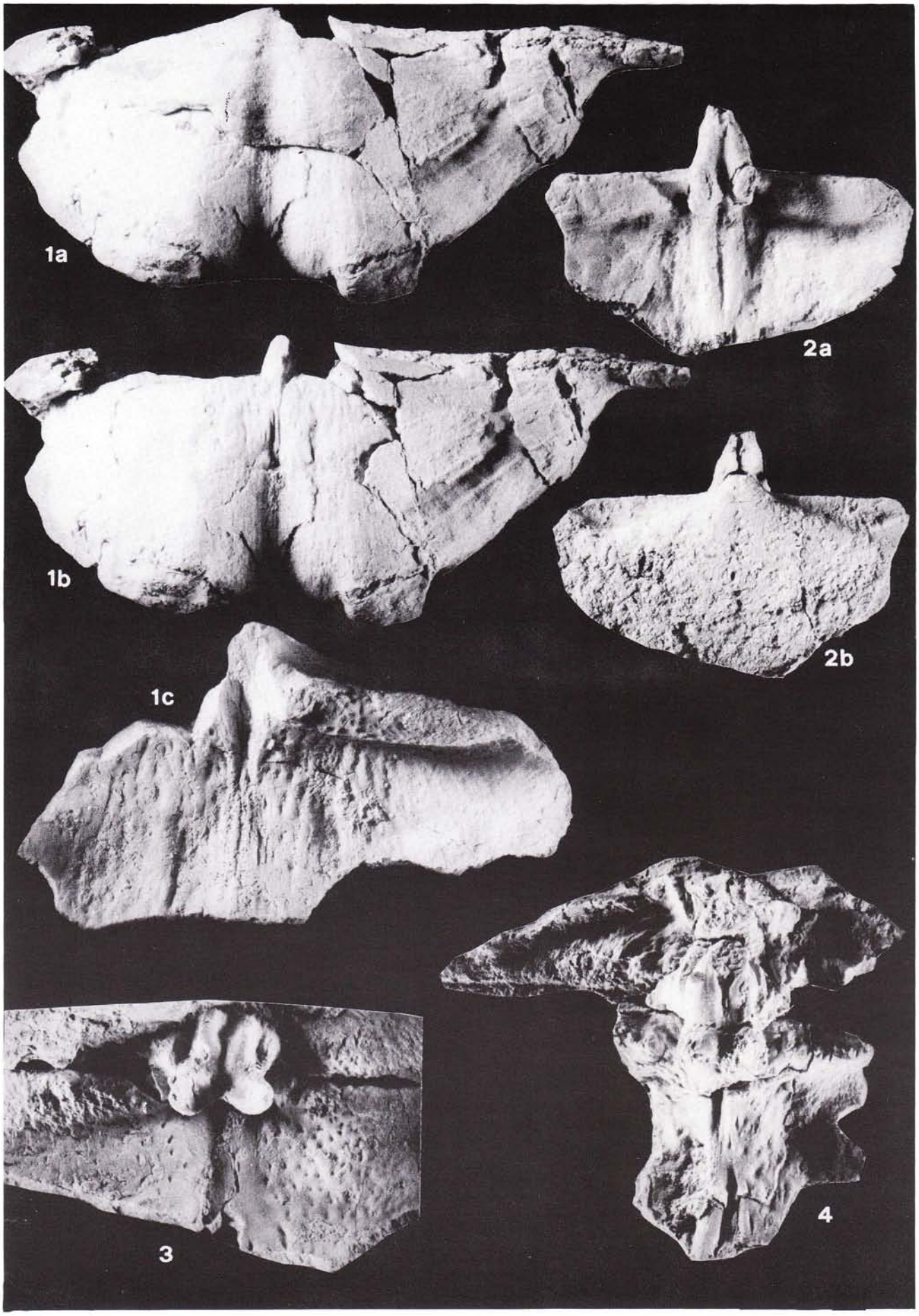
Fig. 3 - *Comelicania megalotis* (Stache). Internal mould with muscle field. a, b) dorsal and ventral views; Bellerophon Fm., Val Brutta, MDSGF VB61 (see cardinalia on Pl. 5, fig. 4) (x 1).

Fig. 4 - *Comelicania haueri* (Stache). Dorsal internal mould with muscle field; Bellerophon Fm., Val Brutta, MDSGF VB115 (x 1).

Fig. 5 - *Comelicania* sp. Ventral view of an internal mould of a ventral valve with muscle field; the pitted surfaces on each side of the umbonal region may represent gonocoel marks; Bellerophon Fm., Sass de Putia, MDSGF PK18 (x 1).

Fig. 6 - *Comelicania haueri* (Stache). Posterior view of the external surface of an articulated, slightly open, shell; Bellerophon Fm., Val Brutta, MDSGF VB80 (x 1).

Fig. 7 - *Comelicania megalotis* (Stache). Morphotype C; exterior view of a ventral valve; Bellerophon Fm., Monte Croce di Comelico, MDSGF MC94 (x 1).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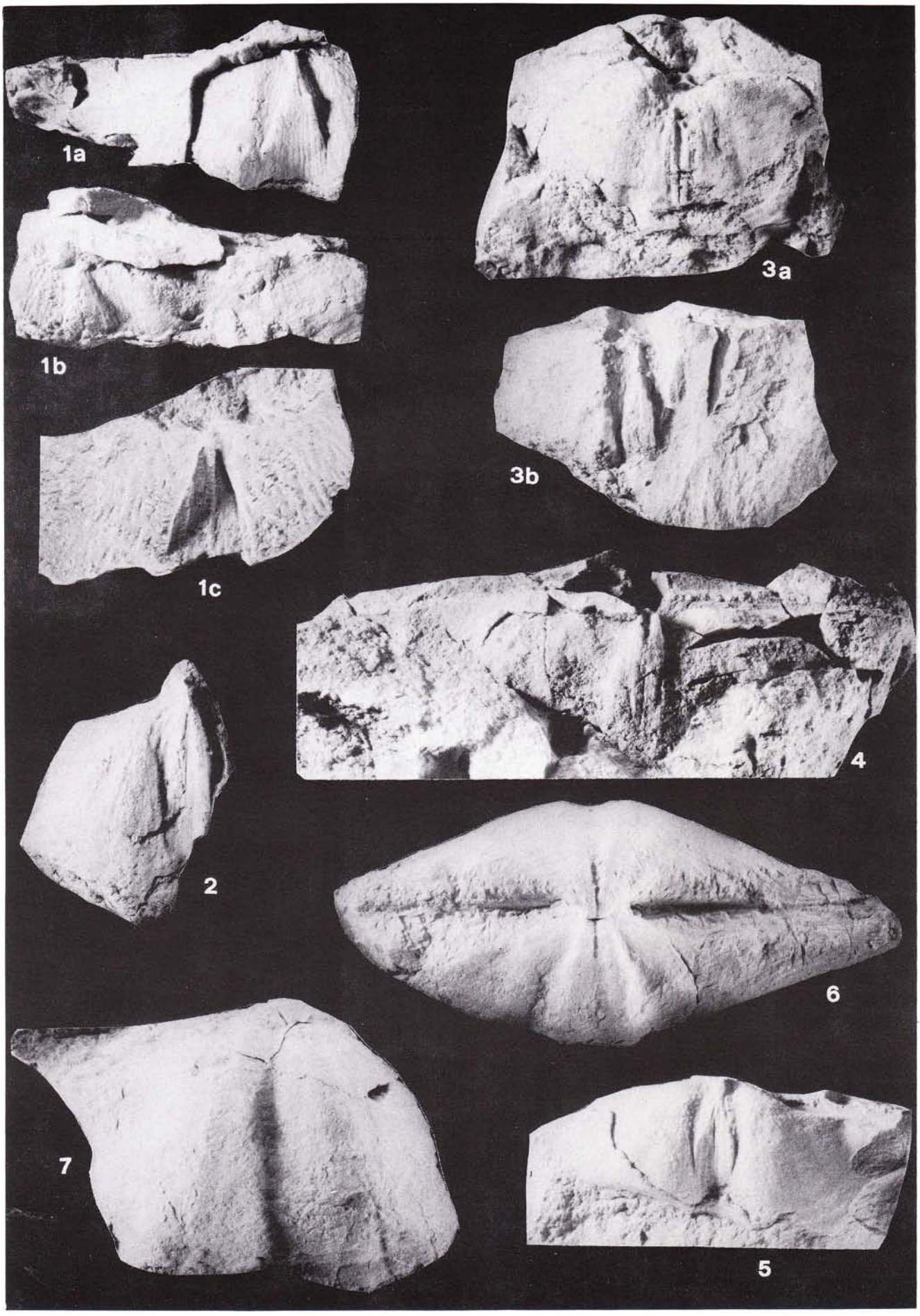
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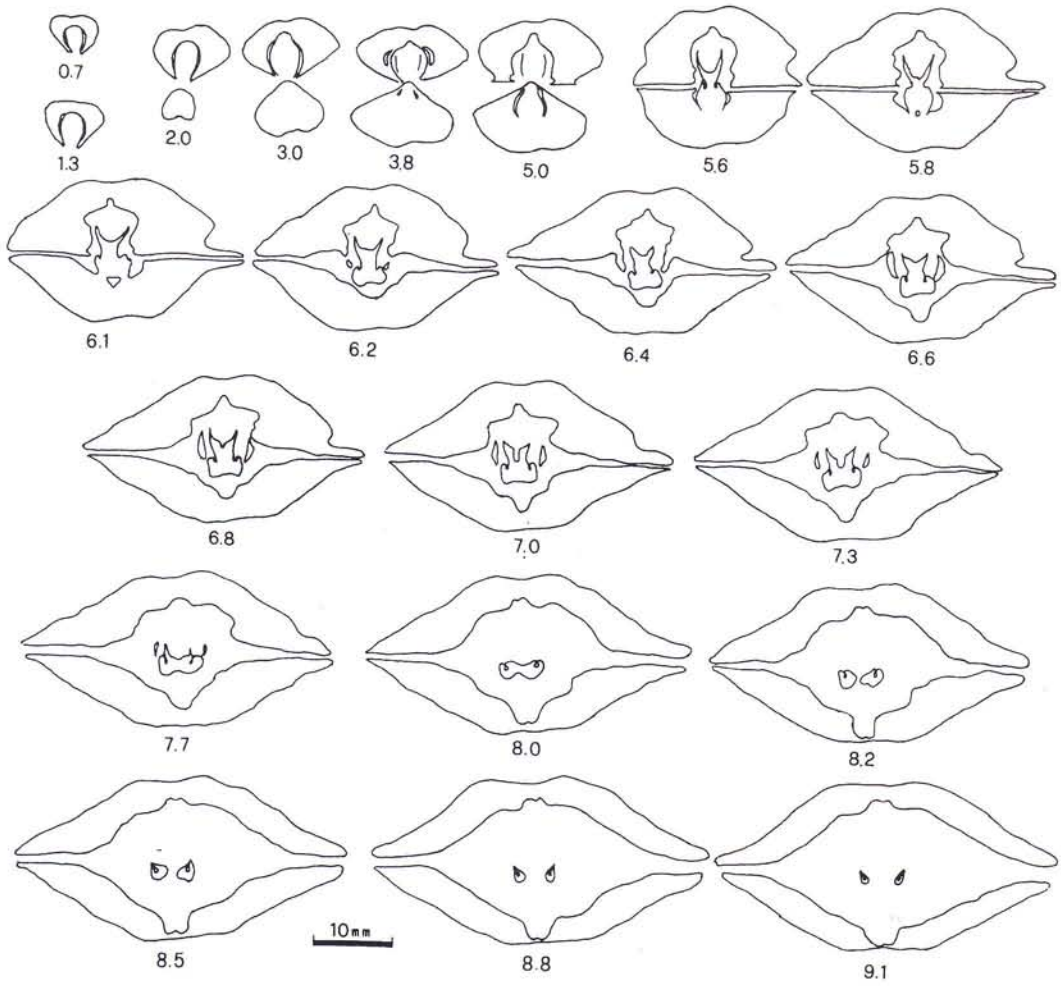

Fig. 12 - Serial transverse sections of *Comelicania merlai* sp. n., specimen no. PK130 (MDSGF) (Pl. 4, fig. 6); uppermost Bellerophon Fm., Sass de Putia.

Type series. Holotype (Pl. 4, fig. 7), specimen no. PK52 from the Sass de Putia section, layer 53, housed in the Museum of the Dipartimento di Scienze Geologiche e Paleontologiche, Ferrara University (MDSGF). It is an isolated ventral valve.

Paratypes consisting of a single ventral valve (Merla, 1930, pl. 2, fig. 4, MDGP no. 24795: Pl. 4, fig. 3) and two dorsal valves of Merla's collection (Merla, 1930, pl. 2, fig. 3, MDGP no. 24795b: Pl. 4, fig. 4, and a specimen not illustrated, MDGP no. 24794: Pl. 4, fig. 5). Collection of MDGF: two shells (no. VB65, PK 130), three ventral valves (VB48, VB51, VB66).

Origin of the name. The new species is named after Giovanni Merla for his contribution to the knowledge of the brachiopods of the Bellerophon Formation.

Type locality and stratum. Sass de Putia, Dolomites, Southern Alps, Italy. Uppermost Bellerophon Formation, beds 52, 53 (Fig. 1).

Age. Late Permian, Dorashamian or Changxinghian.

Diagnosis.

Middle-sized shell for the genus, outline subrectangular to subpentagonal with large umbo, wings very short, maximum width corresponding to posterior margin or to anterior third of length at adult ontogenetic stage; ventral sulcus broad with sinal ridges smoothed. L/W ratio ranging from 0.54 to 0.75.

Description.

Shell of middle size for the genus with very short or absent alae and thick wall. It is the least transverse shell among the species described. Shell inflation is stronger than in the other species, convexity of dorsal valve equal to or slightly lower than that of the ventral valve. Outline ranging from subrectangular to subpentagonal. The latter outline characterises the mature stage. The growth lines show that the shell reached a subrectangular outline rapidly during ontogeny: lateral margins became parallel already at a shell width of 40-50 mm, when the alae were not yet developed. Umbo large and projected beyond the hinge line; cardinal surface narrow and poorly distinct from the lateral regions. Ventral sinus broad, with an angle of about 35-40$, limited laterally by smooth ridges. Dorsal valves are poorly represented in the collections examined, making it impossible to delineate their variability; the dorsal valve is poorly preserved in the holotype, while in Merla's collection a dorsal valve (not depicted, MDGP no. 24794) has a very shallow mid-dorsal sulcus, located on a raised fold laterally limited by shallow grooves (Pl. 4, fig. 5).

The cardinalia follow the same pattern as those of *C. megalotis*. Slight differences consist of a stronger dorsoventral flattening of the anterior part of the cardinal plate and narrower dorsal and ventral umbonal cavities (Fig. 5D, 12).

Remarks.

This species includes the specimens classified previously by Posenato (1988a, b) in the *C. ladina* (Stache) *sensu* Merla group, which characterises the upper *Comelicania* beds. The holotype of *C. ladina* is represented by a mid-sized, strongly deformed, open shell (Pl. 3, fig. 6). The outline of the ventral valve is not detectable due to its strong distortion. The dorsal valve, mostly represented by the internal mould, has a subtrapezoidal outline with a maximum width corresponding to the posterior margin; alae seem to be short, but it is impossible to define their original extension because the lateral extremities are broken. The considerable transversal extension of the cardinal margin relative to the short anterior margin suggests a strong resemblance between the holotype of *C. ladina* and that of *C. vultur*, as formerly proposed by Stache (1878). *C. vultur* is here considered a juvenile stage of *C. megalotis*. Furthermore, the L/W ratio of the holotype of *C. ladina* (about 0.45) falls within the range of *C. megalotis*. The strong deformation of the holotype would suggest that it comes from the marly intercalations of the lower *Comelicania* beds.

The specimens classified by Merla as *C. ladina* differ from the holotype of this species mostly on the basis of the limited difference between the anterior and posterior width and a higher L/W ratio (equal or higher than 0.65). Sometimes the anterior width exceeds the posterior (e.g. the specimen illustrated by Merla, 1030, pl. 2, fig. 3: Pl. 4, fig. 4). Because these Comelicaniids have a morphology quite different from the other known species and a stratigraphic range restricted to the upper *Comelicania* beds, a new species is proposed here.

Geographic distribution.

Passo di Monte Croce Comelico, Sass de Putia, Val Brutta (Southern Alps), Velence Lake (Central Hungary).

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