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THE ATHYRIDOIDS OF THE TRANSITIONAL BEDS BETWEEN BELLEROPHON AND WERFEN FORMATIONS (UPPERMOST PERMIAN, SOUTHERN ALPS, ITALY)

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Riassunto. I livelli transizionali tra le formazioni a Bellerophon e di Werfen, spessi pochi centimetri e di età permiana finale, contengono una fauna a brachiopodi con una associazione di athyridoidi relativamente ricca, della quale *Janiceps* è il genere più comune e caratteristico. Vengono qui descritti per la prima volta i caratteri interni della specie-tipo (*J. peracuta*) e viene avanzata la revisione tassonomica delle specie del Sudalpino. E' proposta la nuova sottofamiglia Janicepsinae comprendente *Janiceps* ed il nuovo genere *Comelicothyris*; nell'ambito di quest'ultimo genere si propone la nuova specie *Comelicothyris laterosulcata*. Sono inoltre designati ed illustrati i lectotipi delle seguenti specie: *Spirigera janiceps* Stache, *S. confinalis* Stache, *S. bipartita* Stache, *S.* ? *archimedis* Stache, *Spirifer* ? *sextensis* Stache, *Athyris irregularis* Merla, *A. semilunaris* Merla e *A. janiceps* var. *globulus* Merla.

Gli athyridoidi degli strati transizionali sono caratterizzati da un'ampia variabilità morfologica che indusse i passati Autori ad istituire numerose specie e varietà create generalmente su un unico o pochi individui. Per quanto riguarda *Janiceps*, delle 14 specie e 7 "varietà" citate nella letteratura delle Alpi Meridionali, solo quattro specie vengono considerate valide. Esse sono: *J. peracuta* (Stache), *J. cadorica* (Stache), *J. papilio* (Stache) e *J. bipartita* (Stache). Vengono inoltre descritte le seguenti quattro specie: *Comelicothyris recticardinis* (Merla), *Septospirigerella* ? sp., Spirigerellinae gen. et sp. indet. e *Comelicania merlai* Posenato.

Abstract. The transitional beds between Bellerophon and Werfen formations, few centimetres thick and latest Permian in age, contain a brachiopod fauna with a relatively rich athyridoid assemblage, among which *Janiceps* is the most common and characteristic genus. The internal morphology of the type species (*J. peracuta*) is here described for the first time, and a taxonomical revision of the South Alpine species is proposed. The new subfamily Janicepsinae is proposed, which contains *Janiceps* and the new genus *Comelicothyris*. Among the latter genus, *Comelicothyris laterosulcata* n. sp. is suggested. Lectotypes are selected and illustrated for *Spirigera janiceps* Stache, *S. confinalis* Stache, *S. bipartita* Stache, *S.* ? *archimedis* Stache, *Spirifer* ? *sextensis* Stache, *Athyris irregularis* Merla, *A. semilunaris* Merla, and *A. janiceps* var. *globulus* Merla.

The athyridoids of the transitional beds are characterized by a broad morphological variability which induced past authors to create many species and "varieties", generally on the basis of a single or few individuals. As concerns *Janiceps*, only four species -versus the 14 species and 7 "varieties" cited in the literature of the Southern Alps- are here considered valid [*J. peracuta* (Stache), *J. cadorica* (Stache), *J. papilio* (Stache), and *J. bipartita* (Stache)]. Besides, other four species are identified here; these are: *Comelicothyris recticardinis* (Merla), *Septospirigerella* ? sp., Spirigerellinae gen. et sp. indet., and *Comelicania merlai* Posenato.

Introduction.

The brachiopod fauna of the Upper Permian Bellerophon Fm. of the eastern Southern Alps is dominated by athyridoids (Fig. 1). In the Dolomites, brachiopods appear only in the uppermost black limestone of the formation, few metres thick, near the contact with the base of the Werfen Fm., which is represented by oolitic grainstones of the Tesero Member (Fig. 2). This brachiopod fauna was studied in the classical works of Stache (1878) and Merla (1930). *Comelicania* and *Janiceps* represent the most common and characteristic genera of this thin stratigraphical segment. *Comelicania*, common in the lower part of the brachiopod-bearing beds with the species *C. haueri* (Stache) and *C. megalotis* (Stache), has been the object of a recent taxonomical revision (Posenato, 1998), while knowledge of *Janiceps* is very scarce: in particular the internal characters of its type species [*J. peracuta* (Stache)] are unknown. *Janiceps* is common above the *C. haueri* and *C. megalotis* beds, in the transitional layers between Bellerophon and Werfen Fms. (Fig. 2). The transitional nature of the formational boundary makes it difficult to define the lithostratigraphical setting of the *Janiceps* beds few centimetres thick, constituted of bioclastic and ooid packstone and grainstone, dark to light grey or yellowish in colour. Before the precise definition of the base of the Werfen Fm., placed at the first appearance of oolitic grainstones (Bosellini, 1964), all previous authors ascribed them to the Bellerophon Fm. (e.g. Stache, 1878; Merla, 1930). After Bosellini (1964), many authors placed the transi-

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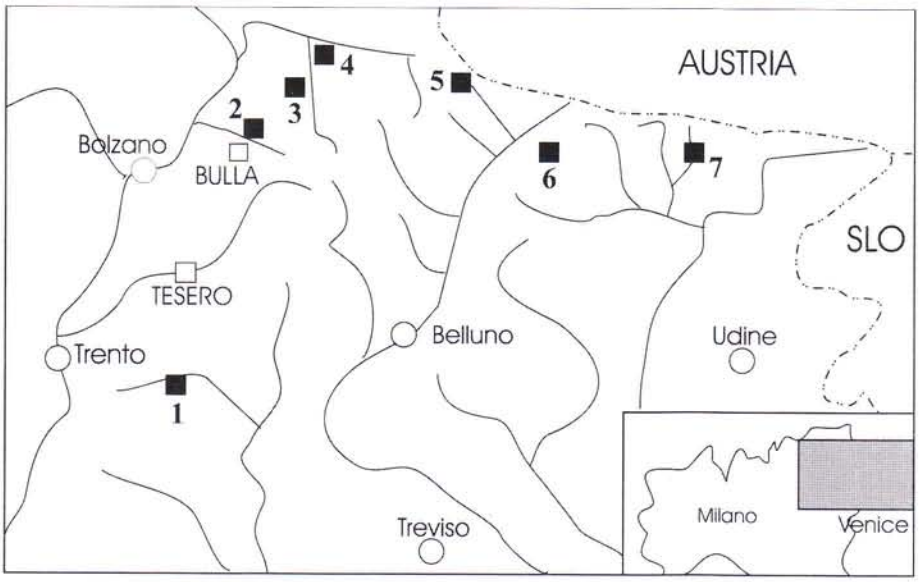


Fig. 1 - Localities of eastern Southern Alps from which the studied material was collected. 1 - Val Brutta; 2 - Ortisei; 3 - Sass de Putia; 4 - Piz da Peres; 5 - Passo di Monte Croce Comelico; 6 - Casera Federata; 7 - Paularo.

tional beds (= *Janiceps* beds = *Ombonia* and *Orthothetina* beds) at the base of the Werfen Fm. (e.g. Cirilli et al., 1998; Farabegoli & Perri, 1999; Neri & Posenato, 1999) while others considered them at the top of Bellerophon Fm. (e.g. Broglio Loriga et al., 1988; Wignall & Hallam, 1992). The transitional beds, which represent the "current event" of Sholger et al. (2000) and recorded in entire Dolomite area, are here considered as the base of Tesero Member (Werfen Fm.).

Despite the very low taxonomical diversity of the *C. haueri* and *C. megalotis* beds, in which only rare individuals of *Janiceps* may occur, the transitional beds contain a relatively diversified brachiopod fauna which, besides the orthotetid *Ombonia* and *Orthothetina*, contains several species of athyridoids studied in the present work. Another important difference regards the sizes of the brachiopod shells. In the *C. haueri* and *C. megalotis* beds these are very large, up to 15 cm in width, while shells are few centimetres wide in the transitional beds. Here the shells are frequently disarticulated and abraded, probably due to the high water turbulence of the depositional environment.

The aim of this work is to characterize the internal characteristics of *Janiceps* and associated athyridoid genera, and to determine the taxonomical diversity of this brachiopod fauna of the transitional beds; in fact, in literature there are numerous species created by Stache (1878) and Merla (1930), frequently on the basis of a single specimen, many of which would not be valid according to a modern species concept. This fauna is a sample of the latest Permian biota very close to the P/Tr mass extinction, thus the recognition of their biodiversity is fundamental to studying this event. The taxonomical analysis considers both the material of the type collections of Stache and Merla, and new recently discovered specimens coming from several sections of the eastern Southern Alps (Italy) (Fig. 1).

Stratigraphic position

The studied material has been mainly collected in the transitional beds between Bellerophon and Werfen Fms., whose thickness ranges from 0.1 to 0.3 m in the different sections. The material comes from many sections of the eastern Southern Alps, among which the richest are Passo di Monte Croce Comelico, type locality of the majority of species created by the previous authors, Val Brutta and Sass de Putia (Fig. 1).

Few specimens have been found in the upper *C. haueri* and *C. megalotis* beds (Unit A, Fig. 2), 0.5-2 m thick, constituted by an alternation of thin blackish carbonaceous marls and thick nodular wackestone, with bioclastic packstone showing quite a diverse foraminiferal assemblage. This unit, which shows a moderate coarsening-upward evolution, represents the topmost Bellerophon beds or parasequence 1 of Neri & Posenato (1999).

The transitional beds (Unit B, Fig. 2) are a thin horizon, 0.1-0.3 m thick, made up of bioclastic (algae and foraminifers) grainstone and packstone, and are characterized by the co-occurrence of *Ombonia* and *Orthothetina*. No significant change of the microbiofacies is detectable with respect to the underlying unit. This unit, representing the base of parasequence 2 (Neri & Posenato, 1999), is overlain by an oolitic grainstone, belonging to Unit C, in which the size of ooids increases from 150-200 μm at the base to 800 μm at the top. Athyridoids are more frequent in the deeper part of the basin (e.g. Sass de Putia, Passo di Monte Croce Comelico), while at the basin margins they are rare or absent [e.g. Bulla and Tesero sections respectively (Fig. 2); in

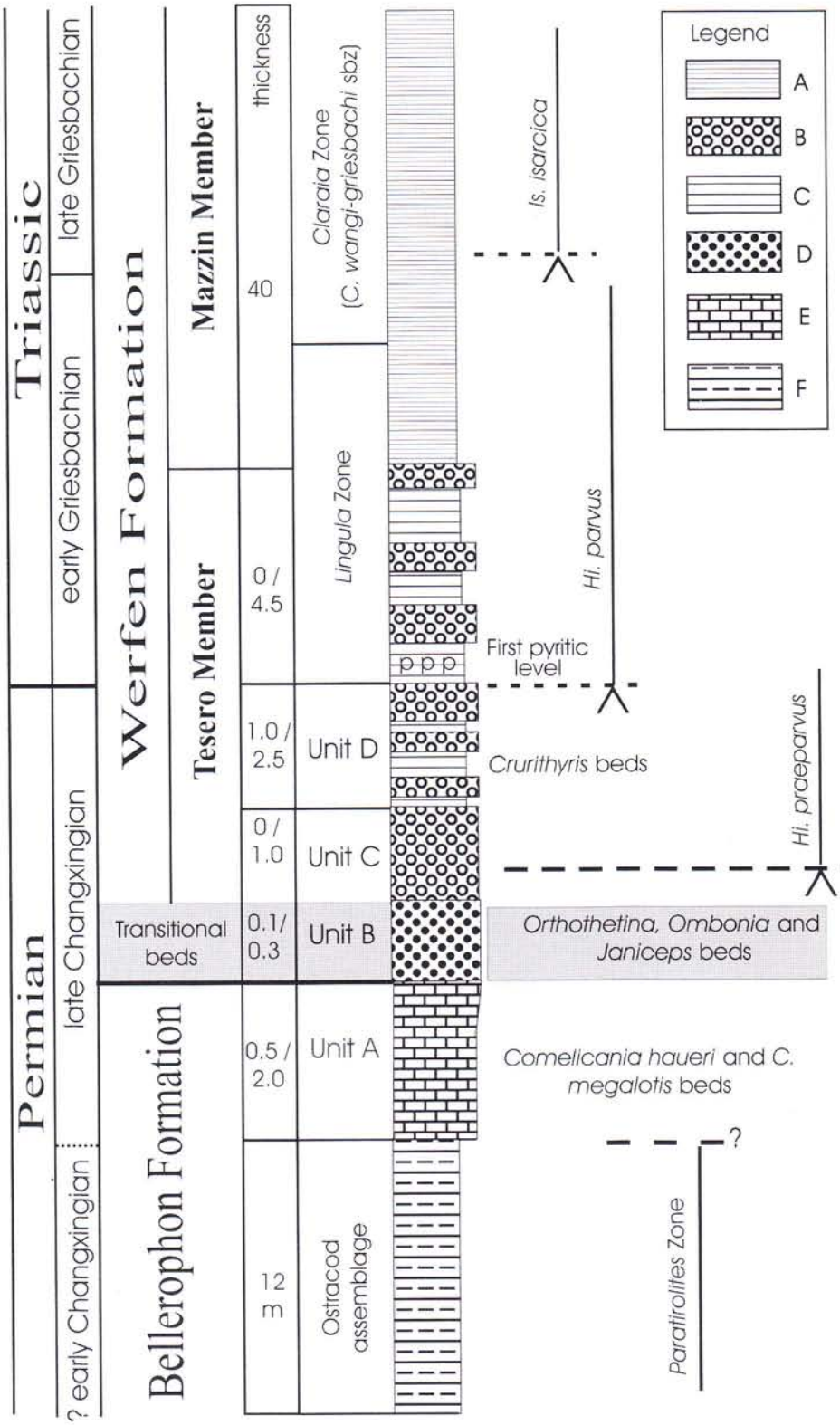


Fig. 2 - Stratigraphic setting and chronostratigraphic framework of the transitional beds (*Ombonia, Orthothetina* and *Janiceps* beds) in the eastern Southern Alps. A - marly mudstone; B - oolitic grainstone; C - marls, micritic and microbialitic limestone; D - bioclastic grainstone and packstone; E - wackestone and packstone; F - marly limestone and silty dolomites. Conodont data after Farabegoli & Perri (1998) and Nicora & Perri (1999).

the latter section only *Ombonia* and *Orthothetina* are present].

The oolitic grainstone, of the lower Tesero Member (Werfen Fm.), forms a bank (Unit C, Fig. 2) whose thickness ranges from 1 m (western Dolomites, e.g. Tesero section) to few centimetres or zero in the eastern Dolomites (e.g. Passo di Monte Croce Comelico). It represents the top of parasequence 2 (Neri & Posenato, 1999). Here, the first individuals of *Bellerophon vaceki* Bittner appear, brachiopods are only represented by rare specimens of *Ombonia*, and the richness and abundance of the microbiofacies strongly decreases (Broglio Loriga et al., 1988; Posenato 1988; Neri & Posenato, 1999).

The basal oolitic bank of the Tesero Member is overlain by a 1-2.5 m thick unit with alternating oolitic-bioclastic grainstone and wackestone, micritic limestone, microbialitic laminites and marls (Unit D, Fig. 2). The marly interlayers yield the *Crurithyris* fauna (Tesero and Bulla sections) and *Eumorphotis*-like bivalves (e.g. Sass de Putia section) (Neri & Pasini, 1985; Broglio Loriga et al., 1988; Posenato, 1988; Wignall & Hallam, 1992). This unit belongs to parasequence 3 of Neri & Posenato (1999).

Chronostratigraphic framework

The chronostratigraphic framework of the upper Bellerophon Fm. has been tentatively defined on the basis of brachiopods (Assereto et al., 1973; Posenato, 1988), foraminifers (Pasini, 1985; Broglio Loriga et al., 1988), and palynomorphs (Cirilli et al., 1998), because fossils with chronostratigraphic value (ammonoids and conodonts) are

very rare. The ages obtained from these fossils are often poorly defined and lack a general consensus among different authors. However, the recent discovery of a specimen of *Paratirolites*, probably coming from the Ostracod Assemblage located below the *C. haueri* and *C. megalotis* beds (Posenato & Prinoth, 1999) (Fig. 2), has made it possible to recognize in the Dolomites the *Paratirolites* Zone. According to some authors (e.g. Tozer, 1979), this is the last Permian ammonoid zone while, according to others, it is followed by the *Pseudotirolites-Pleuronodoceras* Zone, latest Changxingian in age (e.g. Zakharov, 1988; Yin, & Tong, 1998; Kozur, 1998).

No ammonoid or conodont markers have yet been discovered within the *C. haueri* and *C. megalotis* beds and transitional beds, thus a precise chronostratigraphical position of these units is not possible, even if Cirilli et al. (1998) recently proposed for the transitional beds a basal Triassic age on the basis of palynomorphs.

The age of the transitional beds cannot be directly determined because conodont markers only appear few centimetres above the base of Tesero Member. However, they are surely Permian in age because they are located below the FO of *Hi. parvus* (Kozur & Pjatakova), marker of the basal Triassic (Yin, 1993; 2000) after the recent ratification by the IUGS of the GSSP at the base of bed 27c of Meishan section (Orchard, 2001). In the Dolomites, the older appearance of *Hi. parvus* is recorded in the Bulla section at 1.30 m above the base of the Tesero Member (Farabegoli & Perri, 1998). Here, a further conodont zone occurs in the basal Tesero Member, just above the transitional beds. It is the *Hi. praeparvus* Zone, the last Permian conodont zone, which lower boundary is located about 0.3 m above the base of the Tesero Member in the Bulla and Tesero sections (Farabegoli & Perri, 1998; Nicora & Perri, 1999, respectively) (Fig. 2). In conclusion, the transitional beds are located between the *Paratirolites* and *Hi. praeparvus* zones, with an undifferentiated upper Changxingian age.

Material and methods

The present collection is composed of more than a hundred specimens and housed in the Museum of the Dipartimento di Scienze della Terra, Ferrara University (MDTF). Most of the specimens originate from three localities: Val Brutta (Valsugana, VB), Sass de Putia (western Dolomites, PK) and Passo di Monte Croce Comelico (eastern Dolomites, MC) or Kreuzberg in German toponomy. Additional material comes from Piz da Peres (western Dolomites, PZ), Ortisei (western Dolomites, OR), Casera Federata and Paularo (Carnia, CF, PA) (Fig. 1).

The shells are often disarticulated and sometimes abraded since the depositional environment was located within the wave base. In the outcrops specimens are not frequent, and many of them were collected in the talus. Fortunately, the lithology of this horizon is easily recognizable, thus making it possible to understand their stratigraphical origin.

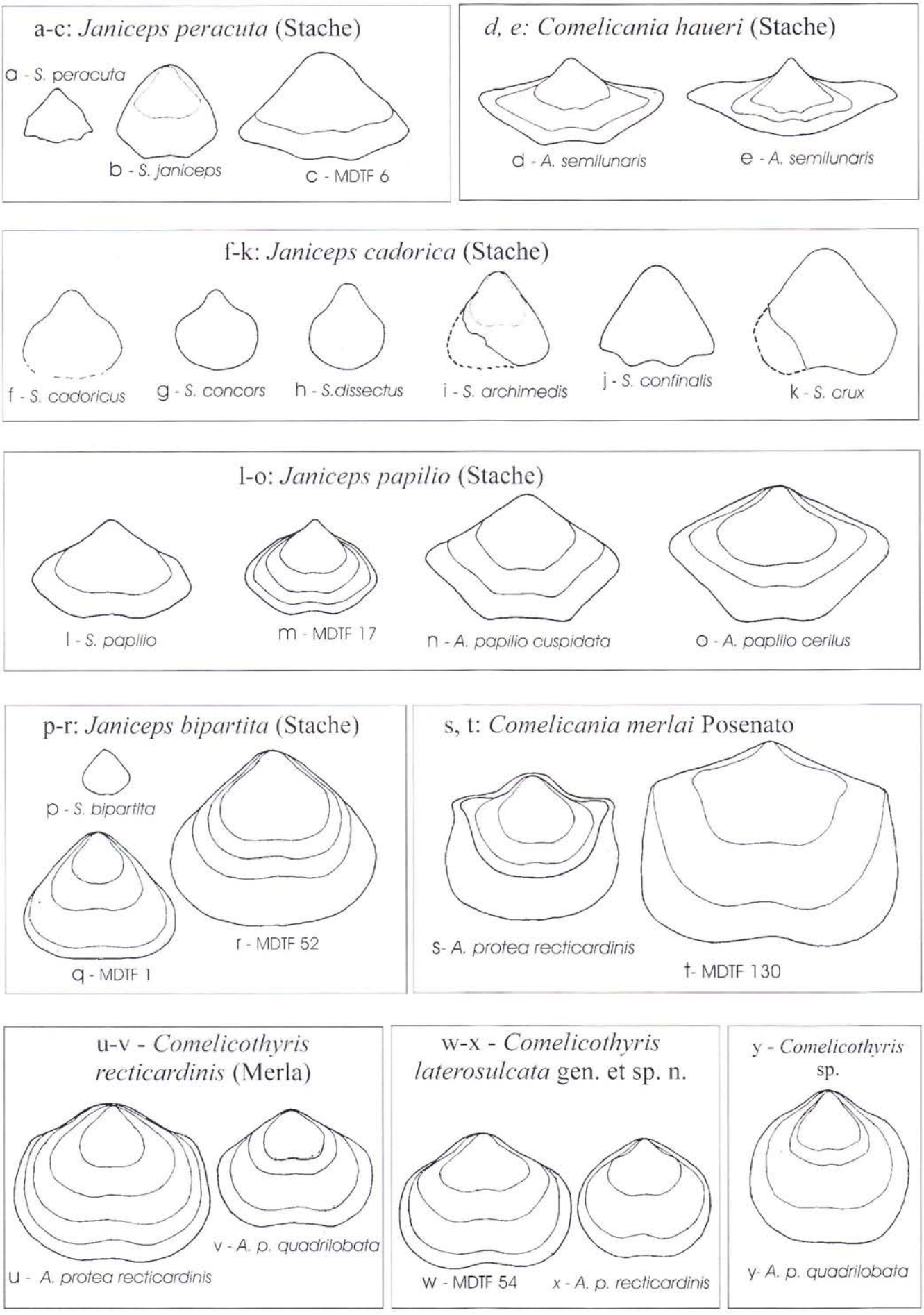
Serial transverse sections were made on about ten specimens. The polished sections were reproduced with acetate peels from which enlarged negative photographs were used to reconstruct the internal characters.

The types of Stache's collection of the Geologische Bundesanstalt of Wien (MGBW) and Merla's collection of the Dipartimento di Geologia, Paleontologia e Geofisica of Padova University (MDGP) have also been examined.

Biodiversity of the uppermost Permian athyridoids in the Southern Alps

The athyridoids of the transitional beds are characterized by a broad morphological variability: this is the cause of the high number of species and "varieties" proposed by the former authors. Stache (1878) created 14 species, of which 13 were grouped in two main species-groups: five into *Spirifer cadoricus* Stache and eight into *Spirigera janiceps* Stache (Tab. 1). The species were proposed on the basis of a single or at most two specimens, therefore following a rigid typological concept of species. Merla (1930) added two new species and eight "varieties": one "variety" in the *Athyris cadorica* group and six "varieties" and one species (*A. semilunaris* Merla) in *A. janiceps* group. Besides, he introduced a fur-

Fig. 3 - Ontogenetical changes of outline of some specimens discussed in the text. To make possible the comparison between specimens of different sizes, the outline of each stage is drawn with horizontal commissural plane and viewed ventrally (all about x 1). a - lectotype of *Spirigera peracuta* Stache, 1878, pl. 3, fig. 6; b - lectotype of *S. janiceps* Stache, 1878, pl. 2, fig. 22; c - MDTF specimen no. 6; d - paralectotype of *Athyris semilunaris* Merla, 1930, pl. 6, fig. 6; e - lectotype of *A. semilunaris* Merla, 1930, pl. 6, fig. 5; f - holotype of *Spirifer cadoricus* Stache, 1878, pl. 2, fig. 17; g - holotype of *Spirifer concors* Stache, 1878, pl. 2, fig. 18; h - holotype of *Spirifer dissectus* Stache, 1878, pl. 2, fig. 19; i - lectotype of *Spirigera archimedis* Stache, 1878, pl. 2, fig. 21; j - lectotype of *Spirigera confinalis* Stache, 1878, pl. 3, fig. 4; k - holotype of *Spirifer crux* Stache, 1878, pl. 2, fig. 20; l - holotype of *Spirigera papilio* Stache, 1878, pl. 2, fig. 23; m - MDTF specimen no. 17; n - holotype of *Athyris papilio cuspidata* Merla, 1930, pl. 5, fig. 22; o - holotype of *A. papilio cerilus* Merla, 1930, pl. 5, fig. 26; p - lectotype of *Spirigera bipartita* Stache, pl. 3, fig. 12; q, r - MDTF specimens nos. 1 and 52; s - *Athyris protea recticardinis* Merla, 1930, pl. 6, fig. 12; t- MDTF specimen no.130; u - *A. protea recticardinis* (Abich), Merla, 1930, pl. 6, fig. 11; v- *A. protea quadrilobata* (Abich), Merla, 1930, pl. 6, fig. 7; w - MDTF specimen no. 54; x - *A. protea recticardinis* Merla, 1930, pl. 6, fig. 13, 14; y - *A. protea quadrilobata* (Abich), Merla, 1930, pl. 6, fig. 9.


a-c: *Janiceps peracuta* (Stache)
a - S. peracuta
b - S. janiceps
c - MDTF 6
d, e: *Comelicania haueri* (Stache)
d - A. semilunaris
e - A. semilunaris
f-k: *Janiceps cadorica* (Stache)
f - S. cadoricus
g - S. concors
h - S.dissectus
i - S. archimedis
j - S. confinalis
k - S. crux
l-o: *Janiceps papilio* (Stache)
l - S. papilio
m - MDTF 17
n - A. papilio cuspidata
o - A. papilio cerilus
p-r: *Janiceps bipartita* (Stache)
p - S. bipartita
q - MDTF 1
r - MDTF 52
s, t: *Comelicania merlai* Posenato
s- A. protea recticardinis
t- MDTF 130
u-v - *Comelicothyris recticardinis* (Merla)
u - A. protea recticardinis
v - A. p. quadrilobata
w-x - *Comelicothyris laterosulcata* gen. et sp. n.
w - MDTF 54
x - A. p. recticardinis
y - *Comelicothyris* sp.
y- A. p. quadrilobata

STACHE, 1878	MERLA, 1930	POSENATO, this work
Spirifer cadoricus Stache	*Athyris cadorica* Stache	***Janiceps cadorica***
	A. cadorica var. *ornata* Merla	= *J. cadorica*
Spirifer crux Stache	*A. crux* Stache	= *J. cadorica*
Spirifer dissectus Stache	*A. dissecta* Stache	= *J. cadorica*
Spirifer concors Stache	*A. concors* Stache	= *J. cadorica*
?*Spirifer sextensis* Stache	*A. sextensis* Stache	= *J. peracuta*
Spirigera janiceps Stache	*Athyris janiceps* Stache	= *J. peracuta*
	A. janiceps var. *globulus* Merla	= *J. cadorica*
	A. janiceps var. *humeralis* Merla	= *J. cadorica*
	A. janiceps var. *sagitta* Merla	= *J. cadorica*
	A. janiceps var. *rhomboidea* Merla	= *J. cadorica*
Spirigera papilio Stache	*Athyris papilio* Stache	***J. papilio***
	A. papilio var. *cuspidata* Merla	= *J. papilio*
	A. papilio var. *cerilus* Merla	= *J. papilio*
Spirigera aquilina Stache	*Athyris aquilina* Stache	= *J. papilio*
	Athyris semilunaris Merla	= *Comelicania haueri*
Spirigera peracuta Stache	*Athyris peracuta* Stache	***J. peracuta***
Spirigera confinalis Stache	= *Athyris peracuta* Stache	= *J. cadorica*
Spirigera pusilla Stache	*Athyris pusilla* Stache	= *J. cadorica*
?*Spirigera archimedis* Stache	= *Athyris pusilla* Stache	= *J. cadorica*
Spirigera bipartita Stache	*Athyris bipartita* Stache	***J. bipartita***
Spirigera faba Stache		***"Spirigera ?" faba***
	Athyris protea var. *quadrilobata* Abich	= ***Comelicothyris recticardinis Comelicothyris laterosulcata* sp. n.** and ***Comelicothyris* sp.**
	Athyris protea var. *recticardinis* Merla	= ***Comelicothyris recticardinis, Comelicothyris laterosulcata* sp. n.** and ***Comelicania merlai* Posenato**
	Athyris irregularis Merla	= *J. cadorica*
		***Septospirigerella* ? sp.**
		Spirigerellinae gen. et sp. indet.

Tab. 1 - List of the athyridoid species and varieties of the Southern Alps studied in the present paper; species considered valid are in boldface.

sther group of athyridoids, named *Athyris protea* (Abich), split in two "varieties" and one new species (*A. irregularis* Merla). Merla (1930) proposed the following taxonomical characteristics to distinguish the groups:

- *Athyris cadorica* Group: shell with a more or less rounded outline, maximum width situated at mid-length, sinus not laterally delimited by sharp ridges;
- *Athyris janiceps* Group: shell with a more or less triangular outline, maximum width situated near the anterior margin; sinus delimited by sharp ridges and often by lateral grooves;
- *Athyris protea* Group: shell with a rounded outline, umbo short and stocky, valves inflated; sinus sometimes very shallow and not delimited by sharp ridges;

Merla (1930) remarked that the specific determination of these species is very difficult because of their broad morphological variability and the occurrence of transitional forms between different species which impede recognition of "good species". Therefore, he pointed out that his classification has a "conventional

value" because the characteristics (e.g. outline, depth of sinus, sharpness of sinus ridges, inflation of valves) used to recognize a species are variable, and thus they do not repeat in the same manner in the individuals belonging to the same taxon.

Transitional forms also occur between different groups and different athyroidid genera in the Southern Alps, so their identification is not always objective on the basis of external characteristics. The classification of small sized individuals of *Janiceps*, which represent the majority of the types of Stache (1878), is very difficult as different adult forms may have similar juvenile stages. For instance, juvenile growth lines of *Janiceps peracuta*-type are also present in large sized shells of *Athyris semilunaris* Merla [= *Comelicania haueri* (Stache)] and in a specimen of *Athyris protea quadrilobata* (Abich) Merla (1930) [= *Comelicothyris* sp.] (Fig. 3d,e and 3y). Therefore, the specific name of small sized types (e.g. *J. peracuta*) is here applied to those large shells in which the juvenile shape persists throughout the ontogenetical development (Fig. 3c).

Some species show transitional external features between different genera. For instance, *Spirigera papilio* Stache have an adult rhomboidal outline (Fig. 3 l-o) which is intermediate between *Janiceps peracuta* (Stache) and middle sized shells of *Comelicania*.

The holotype of *J. cadorica* Stache is represented by an umbonal fragment of a ventral valve which has a transverse fracture in the anterior region. Stache's figure (Stache, 1878, pl. 2, fig. 17) does not report these breakages and his reconstructed outline probably does not correspond to the original shape, which was not so different from that of the *J. janiceps* group.

J. janiceps was proposed by Stache (1878) as the main form of the homonymous group. In fact, this species was created on two syntypes, one of which, the lectotype (Stache, 1878, pl. 2, fig. 22), is represented by an articulated, well preserved specimen which clearly illustrated the mean morphological characteristics of the group. Unfortunately, Schuchert & Le Vene (1929) indicated *J. peracuta* Stache as the type species of *Janiceps* Frech, 1902. Because, the latter species was created on two syntypes, Schuchert & Le Vene (1929) chose as type specimen the shell figured by Stache (1878) in pl. 3, fig. 4. This specimen, considered by Stache a variety of the species, consists of a diagenetically compressed, small, articulated shell. Deformation accentuated the sharpness of the lateral and anterior margins, the characteristic used by Stache to separate *J. peracuta* from *J. janiceps* which has lateral regions perpendicular to the commissural plane. The other syntype of *J. peracuta*, which is not deformed and is about half the size of the lectotype of *J. janiceps*, has lateral surfaces scarcely inclined outwards. Because they share the same other characteristics (i.e. umbonal angle, lateral grooves, sharp sinus ridges), they are here considered as synonymous. *J. peracuta* is the valid species, because it has already been proposed as the type species of *Janiceps*.

The broad variability of external features and the occurrence of specimens with transitional characteristics between the groups could suggest joining *J. peracuta* and *J. cadorica* groups in a single valid species. However, the internal characteristics detected in the sectioned specimens show some slight differences. These mostly concern the morphology and orientation of the cardinal flanges, which are blade-like, dorsally converging and crenulated on the side facing the sagittal plane in *J. peracuta*, and triangular in section, with ventrally directed crenulated side in *J. cadorica*. Therefore, these differences suggest both *J. cadorica* and *J. peracuta* be considered as two different species. However, the identification of these two species on the basis of their external characters is not always easy possible. For this reason a conventional taxonomical characteristic, namely the umbonal angle, is here used to distinguish the two species (Fig. 4). In this way, *Spirigera confinalis* Stache, already considered synonomous of *J. peracuta* by Merla (1930), is here placed within *J. cadorica*, because it has an umbonal angle of 65° versus 82° of the paralectotype of *J. peracuta*. *J. bipartita* (Stache) is a further valid species; it has a rounded triangular outline similar to *J. cadorica*, but with a wider umbonal angle (from 83° to 91°) and larger adult shells.

As concerns the *Athyris protea* group of Merla, this is formed by large sized specimens in comparison with the *Janiceps* types, which do not belong to *Araxathyris protea* (Abich) because the genus *Araxathyris* Grunt has quite different internal characters (see below). Merla's group contains nearly strophic, transversely ovoidal or subrectangular shells. The majority of them differ from *Comelicania* for a hinge margin shorter than the maximum shell width and for the absence af alae, two typical characteristics of this genus. Since these specimens have an internal shell morphology similar to *Comelicania*, they probably originated from this genus, as occurs for *Janiceps*. However, in comparison with *Janiceps*, characterized by astrophic, subtriangular to rhomboidal shells, these specimens of *Athyris protea* Merla's group acquired quite a different, subrectangular, adult outline. These differences make it possible to propose the new genus *Comelicothyris*, which contains the following species: a) *Comelicotyris recticardinis* (Merla), with a transversely elongated subrectangular shell, in which dental plates are almost joined to the umbonal wall; b) *Comelicothyris laterosulcata* sp. n., which is distinguishable from the former species for the occurrence of lateral grooves and dental plates clearly separated from the umbonal wall. c) *Comelicothyris* sp. with a subequidimensional shell. One specimen of *Athyris protea* Merla's group has a subpentagonal strophic shell with short alae (Merla, 1930, pl. 6,

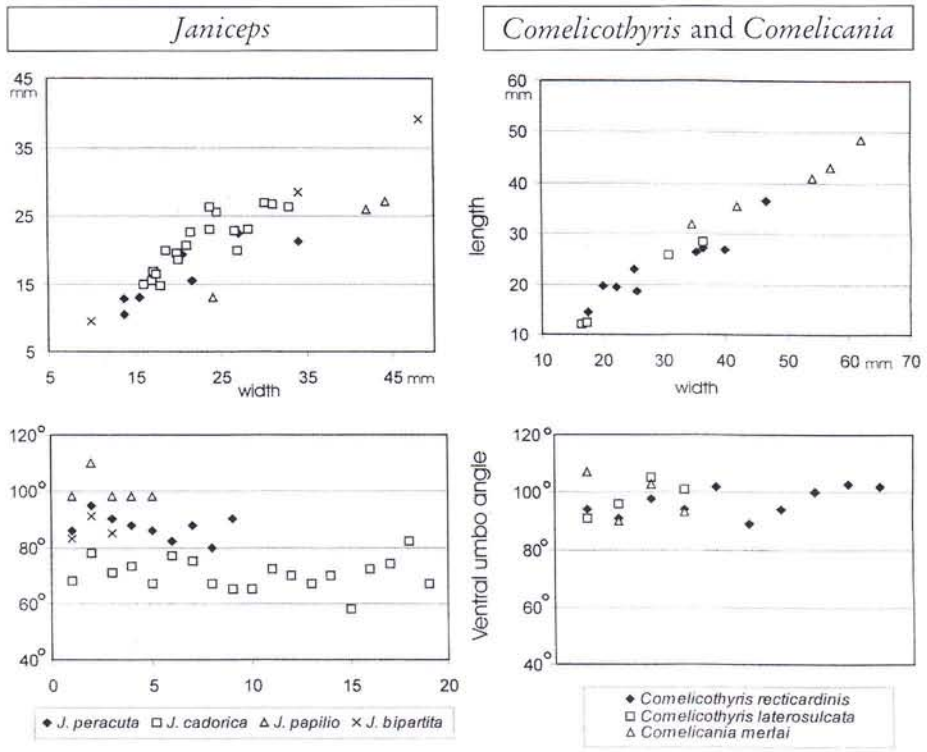


Fig. 4 - Distribution of shell dimensions (top, bivariate scatter diagrams) and ventral umbonal angle (below, univariate diagrams) for *Janiceps*, *Comelicothyris* and *Comelicania* species.

fig. 12), and is attributed to *Comelicania merlai* Posenato.

Investigation of the internal characters has permitted the recognition of two other genera, belonging to fam. Spirigerellinae, each represented by a single sectioned specimen: one ovoidal shell has a strong dorsal septum similar to *Septospirigerella* Grunt, while the other subcircular shell has internal characters different from the known athyridoid genera (Spirigerellinae gen. et sp. indet.). Even if these specimens could be attributed to new genera and species, the scarcity of the available material suggests prudence in creating new taxa.

In conclusion, the athyridoids of the transitional beds determined here consist of four valid species of *Janiceps* [*J. peracuta* (Stache), *J. cadorica* (Stache), *J. papilio* (Stache), and *J. bipartita* (Stache)] versus the 14 species and 7 "varieties" cited in literature; three species of the new genus *Comelicothyris* [*Comelicothyris recticardinis* (Merla), *C. laterosulcata* sp. n. and *Comelicothyris* sp.)], and a further three species, of which two belonging to the subfam. Spirigerellinae (*Septospirigerella* ? sp., Spirigerellinae gen. et sp. indet.) and one to the subfam. Comelicaniidae (*Comelicania merlai* Posenato) (Tab. 1).

Systematic palaeontology*

*supra-ordinal classification according to Williams et al. (1996); sub-ordinal classification according to Alvarez et al. (1998).

Phylum **Brachiopoda** Duméril, 1806

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

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

Order Athyridida Boucot, Johnson, and Staton, 1964

Suborder Athyrididina Boucot, Johnson, and Staton, 1964

Superfamily Athyridoidea Davidson, 1881

Family Athyrididae Davidson, 1881

Subfamily Janicepsinae subfam. n.

Diagnosis. Small to moderate sized, subtrigonal to subrectangular, astrophic to almost strophic and biconvex shell with ventral sulcus and dorsal sulcate fold; lateral plications may be developed; pedicle support absent; dental plates thin and relatively short; cardinal plate subquadrangular and thick; inner socket ridges high; dorsal foramen absent; dorsal myophragm or septum absent; jugum as in *Athyris* with short accessory jugal lamellae.

Occurrence. Uppermost Permian.

Genera included. *Janiceps* Frech, 1902; *Comelicothyris* gen. n.

Remarks

Grunt (1986) placed *Janiceps* in the Subfam. Spirigerellinae Grunt. Alvarez et al. (1998) adopted the same classification, but with reservation, since no recent systematic review was available to them at that time.

The internal characters described here could suggest ascribing it to the Subfam. Spirigerellinae. However, the internal characters of *Janiceps* show strong simi-

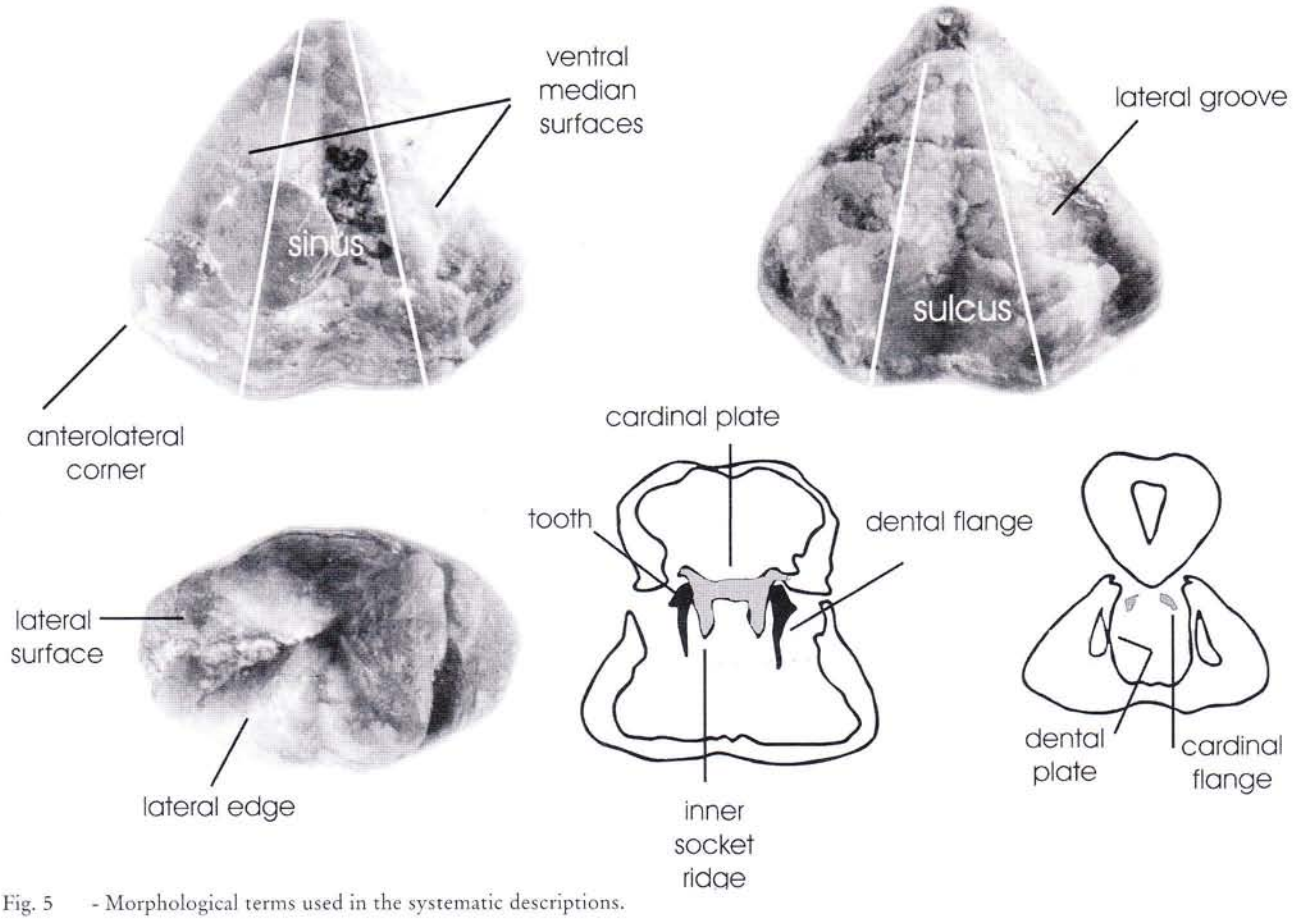


Fig. 5 - Morphological terms used in the systematic descriptions.

larities with *Comelicania* (Subfam. *Comelicaniinae* Merla). In the Bellerophon Fm., *Janiceps* appears in the *Comelicania* beds and becomes frequent in younger beds. The outline of some *Janiceps* species (e.g. *J. peracuta, J. aquilina*) is very similar to juvenile *Comelicania* shells, a stage at which the latter genus has an astrophic shell (Posenato, 1998). Very small specimens (less than 10 mm in width), already determined as *Janiceps* and found in the *Comelicania* beds, could probably represent juvenile shells of *Comelicania*. These facts support the hypothesis that *Janiceps* may be a paedomorphic descendant of *Comelicania*. However, *Janiceps* has an external form quite different from adult Comelicaniinae, which have large, transverse and alate shells, with greatest shell width at hinge margin (Alvarez et al., 1998; Posenato, 1998). If *Janiceps* was included, on the basis of its internal characteristics, within Spirigerellinae, then this subfamily should have a polyphyletic origin. For this reason, the genera *Janiceps* and *Comelicothyris* gen. n., both derived from *Comelicania*, are here included in the new subfamily Janicepsinae. Older occurrences of "*Janiceps*" from Transcaucasia [*J. emarginatiformis* Grunt from upper Djulfian, *J. ogbinensis* (Grunt) from Upper Djulfian to lower Dorashamian, and *J. lozovskyi* from lower Dorashamian] (Grunt, 1986) and China (*J. janiceps* from Wuchiapingian and Changxingian) (Liao, 1980) need systematic review. There is the doubt, at the light of the present investigation concerning the internal characters of *Janiceps* type species, that these extralpine species could belong to genera different from *Janiceps* (T. Grunt, pers. com.).

Genus ***Janiceps*** Frech, 1902

Type-species *Spirigera peracuta* Stache, p. 152, pl. 3, fig. 6a-d.

Diagnosis. Small to medium sized, subtrigonal, biconvex and astrophic shell with ventral sulcus and dorsal sulcate fold, lateral grooves may be developed; anterolateral extremities pointed or rounded; umbo small, recurved and pointed; only very fine growth lines; pedicle support absent; dental plates thin and short, mostly buried in secondary shell material; cardinal plate subquadrangular and thick; inner socket ridges high; dorsal foramen absent; cardinal flanges variably developed; dorsal myophragm or septum absent; jugum as in *Athyris* with short accessory jugal lamellae.

Janiceps peracuta (Stache, 1878)

(Fig. 6, 7; Pl. 1, Fig. 1-10)

v 1878 *Spirigera peracuta* Stache, p. 60, pl. 3, fig. 5a-c, 6a-d.
v 1878 *Spirigera Janiceps* Stache, p. 58, pl. 2, fig. 22a-e, 25.
v 1878 ? *Spirifer Sextensis* Stache, p. 54, pl. 2, fig. 14a-e
v 1902 *Athyris (Janiceps) peracuta* Stache - Frech, p. 551, pl. 6, fig. 6.
v 1930 *Athyris Janiceps* Stache - Merla, p. 56, pl. 5, fig. 15-18.
v 1930 *Athyris peracuta* Stache - Merla, p. 63, pl. 5, fig. 27.
v 1988 *Janiceps aquilina* (Stache) - Broglio Loriga et al., p. 11, pl. 1, fig. 6.

Diagnosis. Small, triangular shell with ventral umbonal angle

specimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/ ew
MDTF 6	VB	S	86	100	29.6+	34.0	21.4	21.4				20.6	0.63
MDTF 38	VB	V	95		27.0+	?	18.2+	?		8.9			
MDTF 55	PK	S	90	104	19.5	21.6	15.4	15.4	13.4			10.3	0.71
MDTF 71	PK	V	88		12.7		10.6	10.6		4.0			
MDTF 77	MC	D		104	25.0+	29.0			19.5		8		
MDTF 79	MC	D		102	17.8+	20.8			12.5		3.9		
MDTF 84	PZ	V	86		12.4	15.6	13.0	13.0		3.5			0.83
MDTF 87	PZ	D		99	21.4+	23.8			21.1		8.5		
MDTF 91	CF	D		98	26.7+	28.4			20.3		6.6		
S. peracuta, fig. 5 MGBW 1878/1/50b	MC	S	82	95	13.8	13.8	12.8	12.8	12			4.1	0.92
S. peracuta, fig. 6 MGBW 1878/1/50a	MC	S	88	105	13.8	13.8	10.4	10.4	9.5			3.2	0.75
S. janiceps, fig. 22 MGBW 1878/1/47a	MC	S	80	89	20.5	20.5	19.4	19.4	16.4			12	0.88
S. janiceps, fig. 25 MGBW 1878/1/47b	MC	V	90		27.0	27.0	22.5	22.5		10.5			0.83

Tab. 2 - Measurements in mm of *Janiceps peracuta* (Stache). Abbreviations: Loc. - locality, Vß - ventral umbonal angle, Dß - dorsal umbonal angle, W - measured width, eW - estimated width of incomplete shell, Lv - measured length of ventral valve, eLv - estimated length of incomplete ventral valve, Ld - length of dorsal valve, Tv - thickness of the ventral valve, Td - thickness of the dorsal valve, Ts - thickness of the shell, S - articulated shell, V - ventral valve, D - dorsal valve, VB - Val Brutta, PK - Sass de Putia, MC - Monte Croce di Comelico, ND - Niederdorf, PZ - Piz da Peres, CF - Casera Federata, OR - Ortisei, PA - Paularo.

ranging from 80° to 95°; maximum shell width near anterior margin; anterolateral extremities pointed; lateral edges almost sharp; ventral median surfaces generally with lateral grooves and sinus, whose angle ranges from about 20° to 30°; dorsal sulcus shallow and laterally limited by raised radial folds; lateral surfaces perpendicular to commissural plane. Dental plates short; subrectangular cardinal plate with crura dorsally convergent towards middle plane, forming an obtuse angle; cardinal flanges short, low and dorsally convergent.

Material and dimensions - See Tab. 2

Description

External characters. The shell has a triangular outline, with the ventral umbonal angle ranging from 80° to 95°; this angle is slightly smaller than the dorsal one (from 89° to 105°). The anterior margin is straight or feebly arcuated and connected to the laterals by means of acute and pointed corners. The maximum shell width is situated near the anterior shell margin. The external ornamentation is only constituted of growth lines.

The ventral umbo is small and slightly recurved (Pl. 1, fig. 1d). Delthyrium concealed by the dorsal umbo, and the foramen seems to be absent. The ventral median surface is flat or slightly convex, generally with shallow radial lateral grooves, easily detectable in specimens wider than 1-2 cm. The ventral and dorsal median surfaces are connected to the lateral surfaces by acute or slightly rounded lateral edges. The lateral surfaces are nearly perpendicular to the commissure plane. Each valve has a median groove: the ventral one (sinus) is slightly broader than the dorsal (sulcus). The sinus, with an angle variable from about 20° to 30°, is laterally limited by rounded ridges which, in the lectotype (Pl. 1, Fig. 8), are slightly protruding along the anterior margin; the sulcus is laterally limited by raised folds, followed by broad and shallow lateral grooves.

Internal characters. The dental plates are short and parallel, separated anteriorly from the lateral umbonal wall (Fig. 6). The teeth are cyrtomatodont, strong and inserted within U-shape sockets. The cardinal plate is trapezoidal in outline, wider than longer, with short cardinal flanges dorsally converging and crenulated on the side facing the sagittal plane. The anterior part of the cardinal plate is thinner and wider than the posterior one. Inner socket ridges are very high. The crura are dorsally convergent with an angle of about 120°. The jugal saddle is present, but without median septum, and jugal stem is vertical. Accessory lamella short, their length not exceeding the umbonal blade. Spiralia directed laterally, with 14 whorls on shell about 3 cm in width (Fig. 6, 7).

specimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/ eW
MDTF 3	VB	V	67		31.0	31.0	26.7	26.7		8.7			0.89
MDTF 12	VB	V	70		32.2	33.0	26.4	26.4		9.2			0.80
MDTF 14	VB	V	58		23.7	23.7	23.0	23.0		10.7			0.97
MDTF 16	VB	S	72	82	23.7	26.8	17.5	20.0				17.6	0.74
MDTF 29	VB	S	74	85									-
MDTF 35	VB	S	82		26.6	26.6	22.8	22.8				15.9	0.86
MDTF 44	VB	V	67		16.6	18.5	18.5	20.0		7.8			0.93
MDTF 61	PK	D		85	18.6	19.8	19.5	19.5			4.0		0.98
MDTF 63	PK	V	68		18.8	20.0	18.5	18.5		6.9			0.93
MDTF 75	PK	V	78		16.9	18.0	14.7	14.7		5.1			0.82
MDTF 80	MC	V	71		14.3	16.0	14.9	14.9		6.0			0.93
MDTF 88	PZ	D		77	16.9	16.9	15.5	15.5			6.5		0.92
S. cadoricus, fig. 17 MGBW 1878/1/41	MC	V	73		20.5		17.4			7.8			
S. archimedis, fig. 21 MGBW 1878/1/54	MC	V	67		18.0	21.0	20.7	20.7		7.8			0.98
S. crux, fig. 20 MGBW 1878/1/43	MC	V	77		26.0	30.0	27.0	27.0		7.6			0.90
S. concors, fig. 18 MGBW 1878/1/44	MC	V	75		17.2	17.2	16.9	16.9		7.0			0.98
S. dissectus, fig. 19 MGBW 1878/1/42	MC	V	67		17.4	17.4	16.5	16.5		7.4			0.95
S. confinalis, fig. 4 MGBW 1878/1/53	MC	S	65	72	21.5	28.2	23.1	23.1	21.0			13.8	0.82
A. janiceps globulus, fig. 19 MDGP 24818	MC	D		82	18.0	19.0			19.1		5.7		
A. j. sagitta, fig. 21 MDGP 24822	MC	V	65		21.5	21.5	22.7	22.7		6.5			1.05
A. j. humeralis, fig. 23 MDGP 24820	MC	V	72		24.4	24.4	25.6	25.6		12.1			1.05
A. cadorica ornata, fig. 14 MDGP 24813	MC	D		85	20.4	25.5			19.8		6.3		
A. irregularis, fig. 15 MDGP 24839	MC	S	70	85	23.6	23.6	25.3	26.4	22.1			16.3	1.19

Tab. 3 - Measurements in mm of *Janiceps cadorica* (Stache). For abbreviations see Tab. 2.

Remarks

Janiceps peracuta (Stache) was based on two syntypes represented by small, juvenile shells. The syntype figured by Stache (1878) in pl. 3, fig. 6 was later designated (Schuchert & Le Vene, 1929) as the type species of *Janiceps* Frech. However, it is represented by a shell compressed during diagenesis (Pl. 1, Fig. 8), and thus it does not fully record the original characteristics of the species. For instance, compression has accentuated the thinning and sharpness of the anterior margins and caused distortion of the lateral margins, which are laterally sloped. The latter character was indicated by Stache (1878) as a taxonomical character to distinguish *J. peracuta* from *J. janiceps*.

The original shell morphology of *J. peracuta* is easily detected in the other syntype (Stache, 1878, pl. 3, fig. 5), in which the lateral surfaces are almost perpendicular to the commissure plane (Pl. 1, Fig. 7), as occur in *J. janiceps* lectotype (Pl. 1, Fig. 1) and in all examined mature specimens. The lectotype of *J. janiceps* (here designed, Stache, 1878, pl. 2, fig. 22) mostly differs from that of *J. peracuta* in its narrower triangular outline (ventral umbonal angle of 80° versus 88°). Considering the different outline within the intraspecific variability, the two species are here considered as synonyms. In particular,

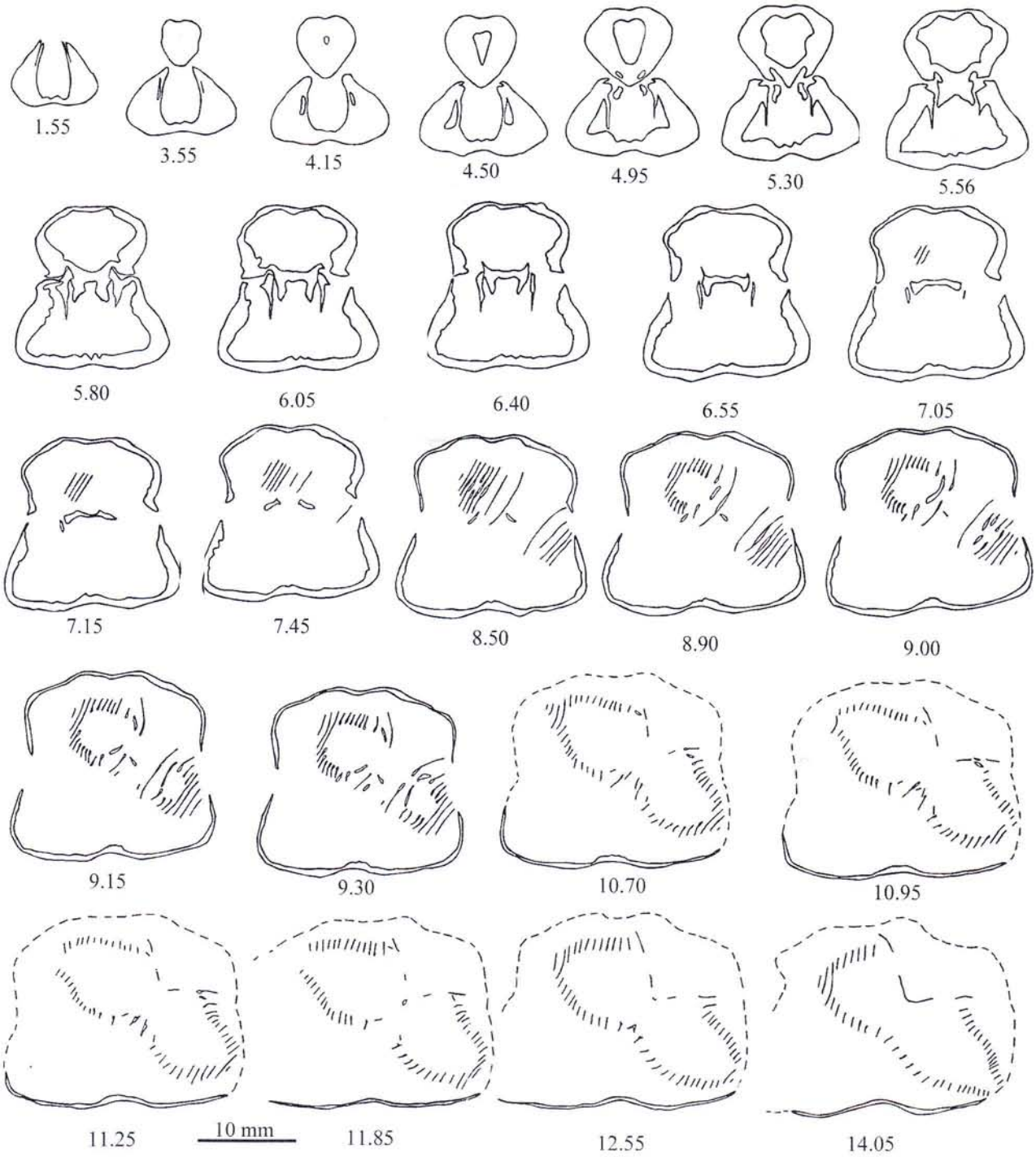


Fig. 6 -Transverse serial sections of *Janiceps peracuta* (Stache), MDTF specimen no. 6 (Pl. 1, Fig. 2), transitional beds, Val Brutta. Numbers refer to the distances in mm from the ventral beak.

they have in common: radial lateral grooves, sharp lateral edges and raised radial dorsal folds.

As already recorded, both *J. peracuta* syntypes are represented by juvenile shells. Among the examined collections, larger individuals with a *J. peracuta* juvenile stage acquired the following, quite different, outlines:

A - Triangular, astrophic and thick shell, which maintains (e.g. outline) and develops (e.g. lateral grooves) some of the juvenile characters of *J. peracuta* (Fig. 3c); the lateral surfaces are perpendicular to the commissure plane (e.g. no. 6: Pl. 1, Fig. 2; 38: Pl. 1, Fig. 5, 91: Pl. 1, Fig. 4). These specimens, in which juvenile characters persist in adult shells, are here determined as *J. peracuta.*

B - Subequidimensional and strophic shell, with a short cardinal margin (Fig. 3y). This outline is recorded in a single specimen of Merla's collection (Merla, 1930, pl. 6, fig. 9), which was classified as *Athyris protea* var.

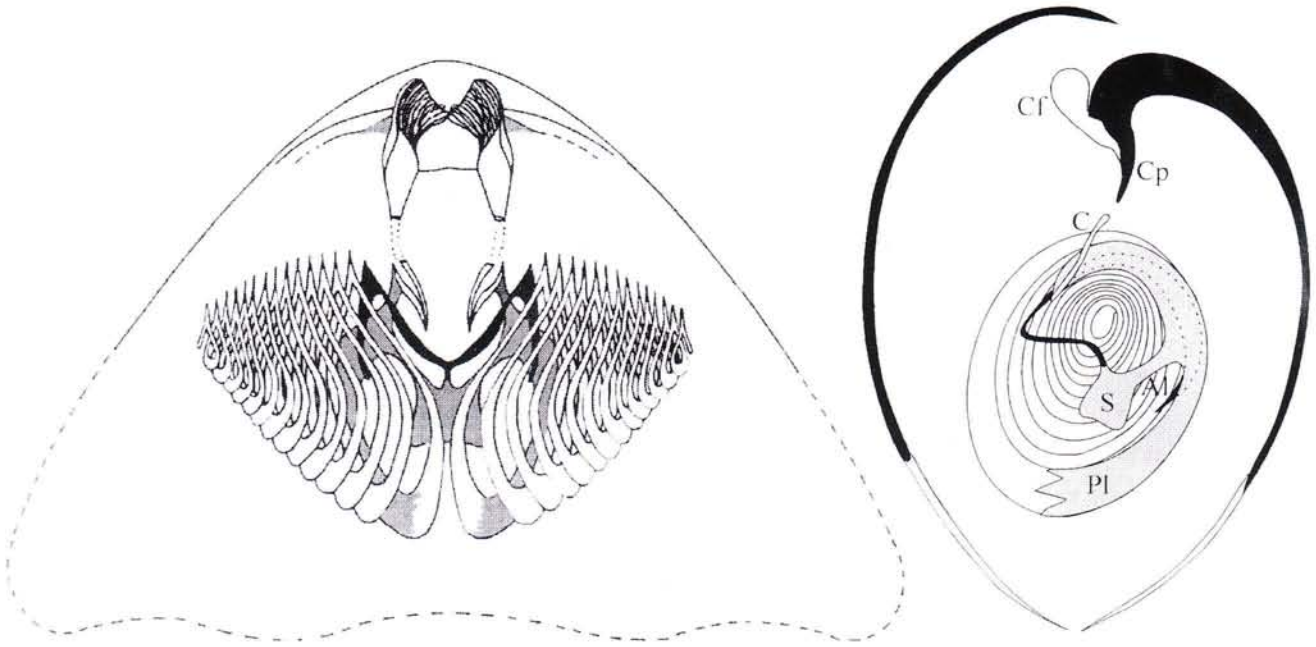


Fig. 7 - *Janiceps peracuta* (Stache). Reconstruction of the internal characters of the dorsal valve, ventrally and laterally viewed, based on the serial section of MDTF specimen no. 6 (Fig. 6). Abbreviations: Al - accessory lamella, C - crus, Cf - cardinal flange, Cp - cardinal plate, Pl - primary lamella, S - saddle (x 3.5).

quadrilobata Abich (see Pl. 3, Fig. 14). Here, shallow lateral grooves are only present in the umbonal region, while they disappear in the mature stage. Lateral surfaces are perpendicular to the commissure plane in the juvenile stage until about 15 mm shell width. This specimen is determined as *Comelicothyris* gen. n., sp. ind. (see below).

C - Strongly transverse, almost strophic, alate shells (Fig. 3d, e). The ventral umbonal angle of these specimens (Pl. 1, Fig. 11, 12), belonging to Merla's collection (*Athyris semilunaris* Merla), is greater (about 105°) than that of the *J. peracuta* lectotype. Also in these shells, the juvenile lateral margins are perpendicular to the commissure plane. *A. semilunaris* is here considered a juvenile stage of *Comelicania haueri* (Stache), therefore it is a junior synonym of this species.

Janiceps sextensis (Stache) was created on two deformed and incomplete specimens (e.g. Pl. 1, Fig. 6). On the basis of the ventral umbonal angle (about 90°), triangular outline and pronounced sinal and lateral edges, it is here considered a synonym of *J. peracuta.*

Janiceps cadorica (Stache, 1878)

(Fig. 8; Pl. 2, Fig. 1-22)

v 1878 *Spirifer cadoricus* Stache, p. 51, pl. 2, fig. 17a-c.
v 1878 *Spirigera confinalis* Stache, p. 62, pl. 3, fig. 4a-d, 7a-d.
v 1878 ? *Spirigera Archimedis* Stache, p. 62, pl. 2, f. 21a-c, tav. 3, fig.9.
v 1878 *Spirigera pusilla* Stache, p. 61, pl. 3, fig. 10a-d.
v 1878 *Spirifer cadoricus* concors Stache, p. 54, pl. 2, fig. 18a,b.
v 1878 *Spirifer cadoricus crux* Stache, p. 53, pl. 2, fig. 20a,b.
v 1878 *Spirifer cadoricus dissectus* Stache, p. 52, pl. 2, fig. 19a,b.
v 1930 *Athyris cadorica* Stache - Merla, p. 54, pl. 5, fig. 1-7, 9-13.
v 1930 *Athyris cadorica* var. *ornata* Merla, p. 55, tav. 5, fig. 14.
v 1930 *Athyris Janiceps* var. *globulus* Merla, p. 56, pl. 5, fig. 19.
v 1930 *Athyris Janiceps* var. *humeralis* Merla, p. 57, pl. 5, fig. 23.
v 1930 *Athyris Janiceps* var. *sagitta* Merla, p. 57, tav. 5, fig. 21.
v 1930 *Athyris irregularis* Merla, p. 67, pl. 6, fig. 15-17.
v 1930 *Athyris pusilla* Stache - Merla, p. 63, pl. 5, fig. 24.

Diagnosis. Triangular, small to medium sized shell; umbo small with pointed beak; ventral umbonal angle ranging from 58° to 82°; maximum shell width at or in the anterior third of shell length; anterolateral extremities from rounded to pointed; ventral median surfaces flat or slightly convex, generally without lateral grooves; sinal and lateral ridges of variable shape; lateral surfaces generally perpendicular to the commissural plane; sulcus very shallow. Cardinal flanges low, triangular in section, with crenulated side ventrally directed.

Material and dimensions - See Tab. 3

Description

External characters. The shell is triangular, astrophic, with the anterolateral extremities ranging from pointed (lectotype of *Spirigera confinalis*: Pl. 2, Fig. 1 and no. 14: Pl. 2, Fig. 9) to rounded (holotype of *Spirifer crux*: Pl. 2, Fig. 3 and no. 35: Pl. 2, Fig. 11). The maximum shell width is placed at or in the anterior third of shell length. The external ornamentation consists only of growth lines; radial riblets occur only in the inner shell layers. The ventral umbo is pointed and covers the beak of the dorsal umbo (Pl. 2, Fig. 13). The foramen is absent and the delthyrium is like that of *J. peracuta.*

The ventral sinus is variable in width: its angle

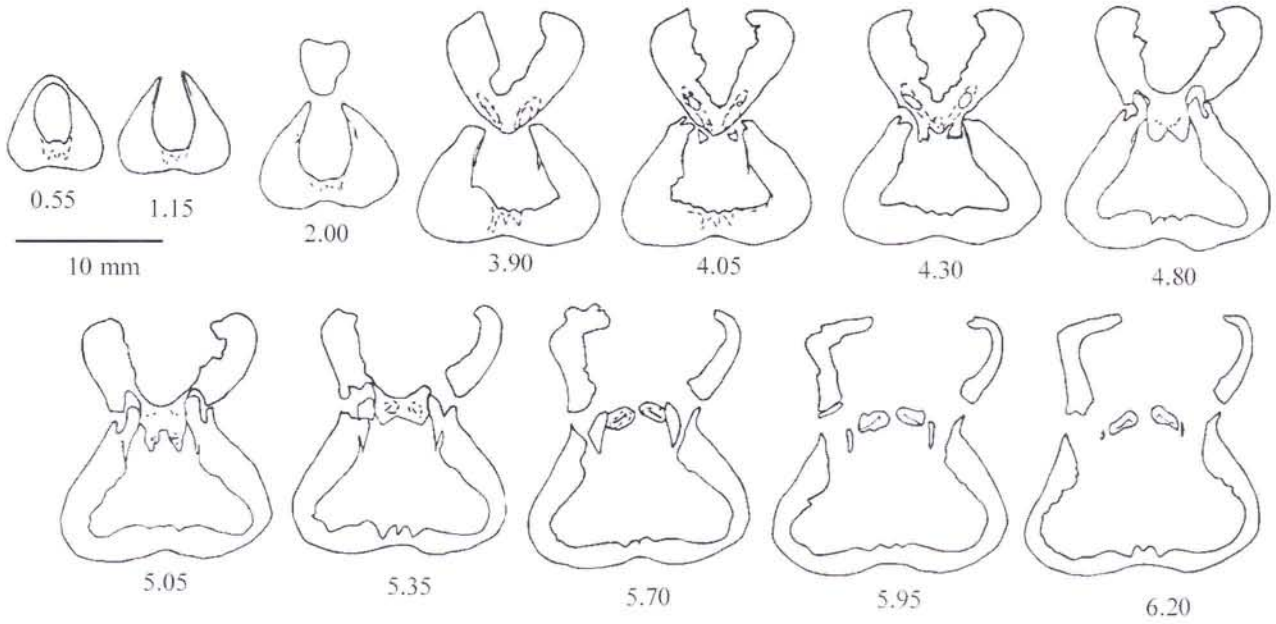


Fig. 8 - Transverse serial sections of *Janiceps cadorica* (Stache), MDTF specimen no. 29 (Pl. 2, Fig. 13), transitional beds, Val Brutta. Numbers refer to the distances in mm from the ventral beak.

ranges from 18 (no. 3: Pl. 2, Fig. 14) to 32° (no. 12: Pl. 2, Fig. 8). In some specimens (no. 16: Pl. 2, Fig. 12; holotype of *J. cadorica*: Pl. 2, Fig. 7; ? *Spirigera archimedis*: Pl. 2, Fig. 6; *Spirifer cadoricus dissectus*: Pl. 2, Fig. 5; *Spirigera confinalis*: Pl. 2, Fig. 2), the sinus is gradually connected to convex (*J. cadorica*: Pl. 2, Fig. 7, no. 16: Pl. 2, Fig.12; no. 35: Pl. 2, Fig. 11) or flattened (?*Spirigera archimedis*, and no. 29: Pl. 2, Fig. 13; no. 63, etc.) median surfaces; more rarely, it is delimited by a smoothed radial ridge (e.g. spec. no. 29: Pl. 2, Fig. 13; holotypes of *Spirifer cadoricus crux*: Pl. 2, Fig. 3 and *Spirifer cadoricus concors*: Pl. 2, Fig. 4). The lateral surfaces are gradually connected to median ones (no. 16: Pl. 2, Fig. 12; *J. cadorica*: Pl. 2, Fig. 7; *Spirifer cadoricus crux*: Pl. 2, Fig. 3) or are delimited by a rounded corner (no. 29: Pl. 2, Fig. 13; ? *Spirigera archimedis*: Pl. 2, Fig. 6). The lateral surfaces range from perpendicular with respect to the commissural plane to laterally sloped. The dorsal valve has a shallow median sulcus, which passes to the median surfaces without the interposition of radial folds.

Internal characters. The dental plates are very short and parallel, joined to the umbonal wall (Fig. 8). The teeth are cyrtomatodont, strong and inserted within U-shape sockets. The cardinal plate is subrectangular in

PLATE 1

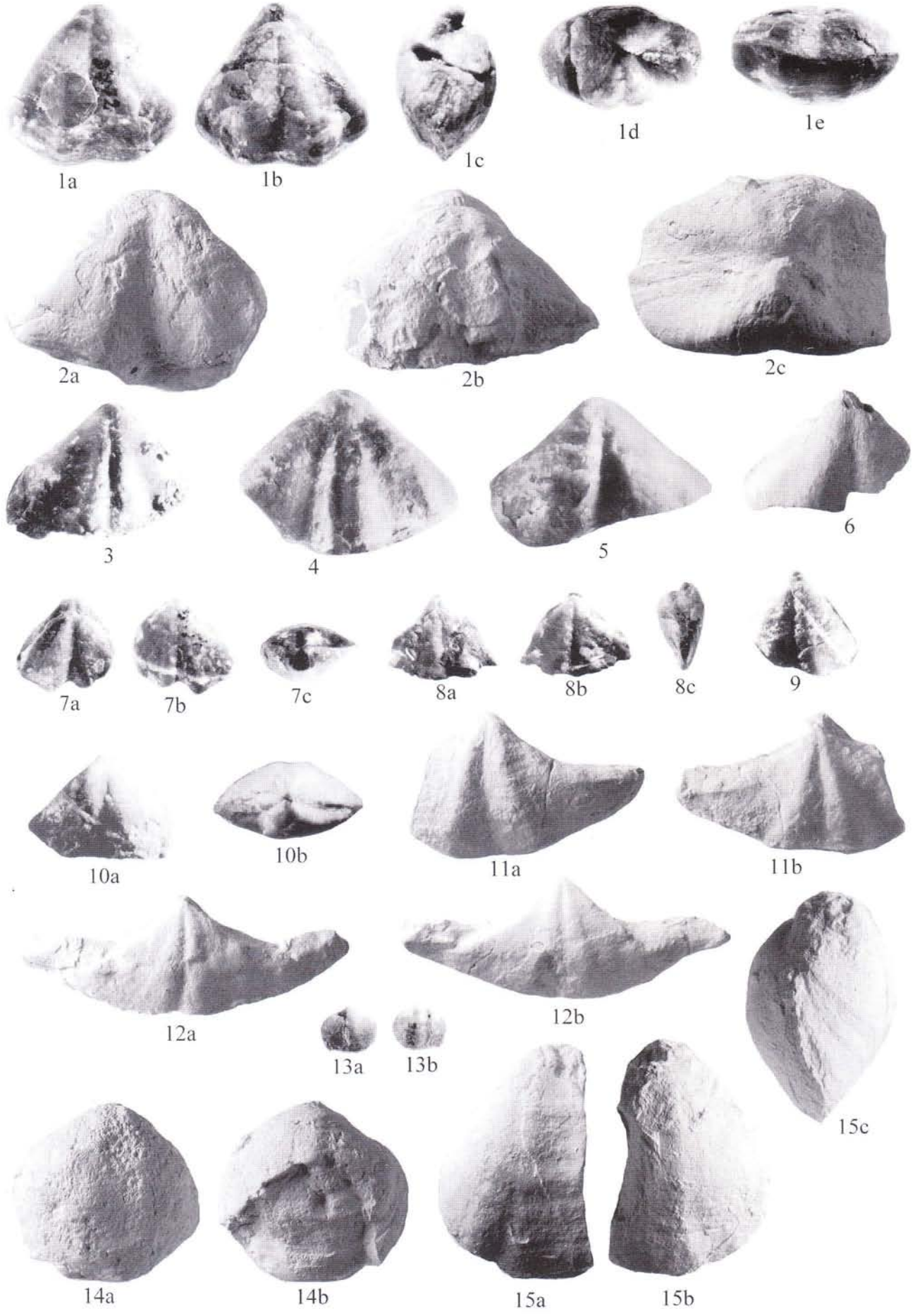
Fig. 1-10 - *Janiceps peracuta* (Stache), all x 1.5. Fig. 1- Lectotype of *Spirigera janiceps* Stache, 1878, pl. 2, fig. 22, MGBW no. 1878/1/47a, ven -tral (1a) dorsal (1b) lateral (1c), posterior (1d) and anterior (1e) views, Monte Croce Comelico. Fig. 2 - Articulated shell, MDTF no. 6, ventral (2a) dorsal (2b) and posterior (2c) views, Val Brutta (Trento); see its transverse sections in Fig. 6. Fig. 3 - Dorsal valve, MDTF no. 77, Passo di Monte Croce Comelico (Belluno). Fig. 4 - Dorsal valve, MDTF no. 91, Casera Federata (Udine). Fig. 5- Ven -tral valve, MDTF no. 38, Val Brutta (Trento). Fig. 6 - Lectotype of ?*Spirifer sextensis* Stache, 1878, pl. 2, fig. 14, MGBW no. 1878/1/45b, Monte Croce Comelico. Fig. 7 - Paralectotype of *Spirigera peracuta* Stache, 1878, pl. 3, fig. 5, MGBW no. 1878/1/50 b, ventral (7a), dorsal (7b) and posterior (7c) views, Monte Croce Comelico. Fig. 8 - Lectotype of *Spirigera peracuta* Stache, 1878, pl. 3, fig. 6, MGBW no. 1878/1/50a, ventral (8a), dorsal (8b) and lateral (8c) views, Monte Croce Comelico. Fig. 9- Ventral valve, MDTF no. 84, Piz da Peres (Bolzano). Fig. 10- Articulated shell, MDTF no. 55, Sass de Putia (Bolzano), ventral (10a) and posterior (8c) views.

Fig.11,12 - *Comelicania haueri* (Stache), all x 1.5. Fig. 11- Paralectotype of *Athyris semilunaris* Merla, 1930, pl. 6, fig. 6, MDGP no. 24828b, ven -tral (11a) and dorsal (11b) views, Monte Croce Comelico. Fig. 12 - Lectotype of *Athyris semilunaris* Merla, 1930, pl. 6, fig. 5, MDGP no. 24828a, dorsal (12a) and ventral (12b) views, Monte Croce Comelico.

Fig. 13 - "*Spirigera* ?" *faba* (Stache). Holotype, Stache, 1878, pl. 4, fig. 7, MGBW no. 1878/1/61, ventral (13 a) and dorsal (13b) view of an artic lated shell, Monte Croce Comelico, x 1.

Fig. 14 - Spirigerellinae gen. et sp. indet., MDTF no. 2, ventral (14 a) and dorsal (14b) views of an articulated shell, Val Brutta (Trento), x 1. See its transverse sections in Fig. 12.

Fig. 15 - *Septospirigerella* ? sp., MDTF no.11, ventral (15a), dorsal (15b) and lateral (15c) views of an articulated, but brocken shell, Val Bruta (Trento), x 1. See its transverse sections in Fig. 13.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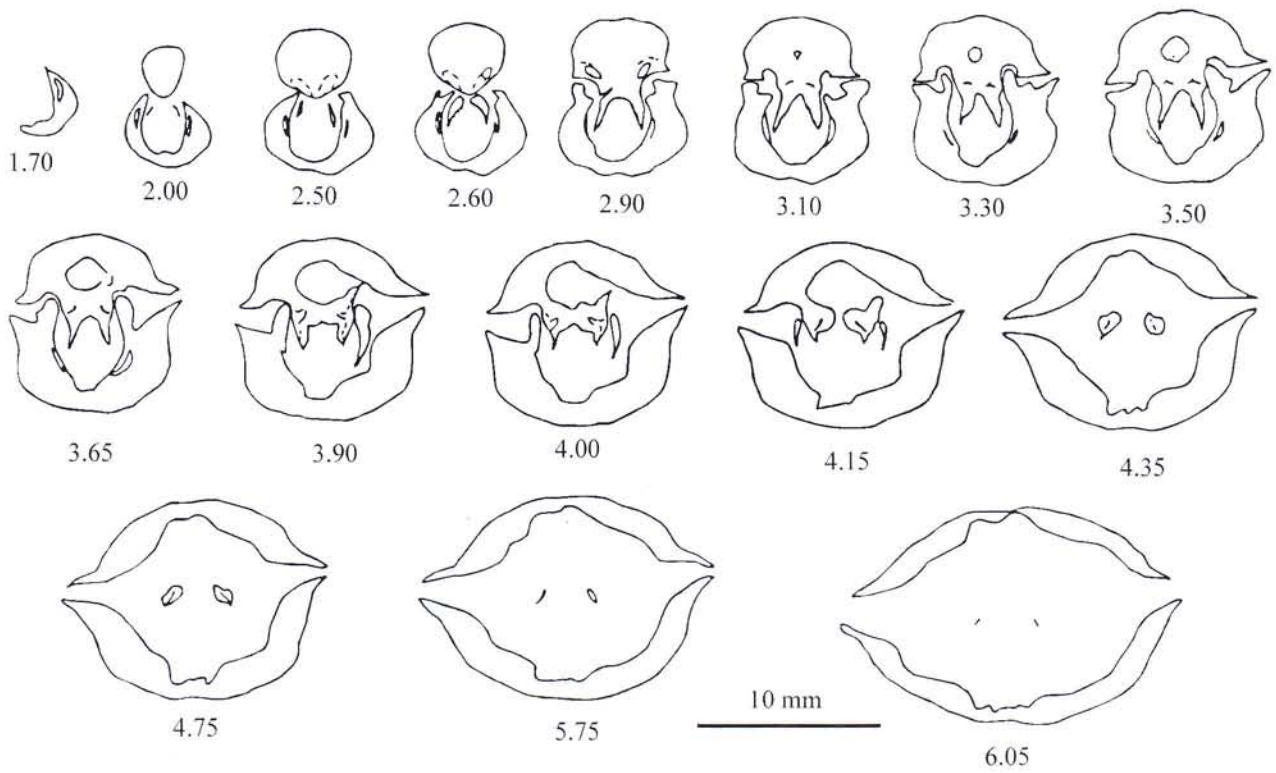


Fig. 9 - Transverse serial sections of *Janiceps papilio* (Stache), MDTF specimen no. 17 (Pl. 3, Fig. 1), transitional beds, Val Brutta. Numbers refer to the distances in mm from the ventral beak.

outline, wider than it is long, with short cardinal flanges, triangular in section. They are characterized by the crenulated side oriented towards the ventral valve. The crura are dorsally convergent with an angle of about 120°, and their bases are large.

Remarks

This taxon includes the majority of the "species" and "subspecies", belonging to *Janiceps*, created by Stache (1878) and Merla (1930). Many of these "species" have distinctive characteristics which can be used as taxonomical features at species level only following a typological species concept. According to this taxonomical method, other new "species" could be proposed here. However, the occurrence of "species" or individuals with a mixture of characters peculiar to other "species" induces us to consider *J. cadorica* as a species with a

spécimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/eW
MDTF 17	VB	S	98	105	26.5+		20.1+		19.1			12.2	
MDTF 26	VB	S	110	118	32.1+		22.9+		20.4			14.5	
MDTF 59	PK	D		110	23.0	23.0			14.6		4.2		
MDTF 101	MC	S		113	28.1	34.0			18.5			18.8	
S. papilio, Fig. 23	MC	D		106	30.0	30.0			18.0		10.0		
S. aquilina, Fig. 4 MGBW 1878/1/49	ND	S	98	107	15.1	24.0	13.0	13.0	11.5			9.0	0.54
A. papilio cerilus, Fig. 26 MDGP 24825	MC	V	98		36.0	44.2	27.2	27.2		12.0			0.62
A. papilio cuspidata, Fig. 22 MDGP 24826	MC	S	98		38.4	42.0	25.9	25.9	22.2			15.5	0.62
A. janiceps rhomboidea, Fig. 20 MDGP 24821	MC	D		105	37.3	37.3			29.4		9.4		

Tab. 4 - Measurements in mm of *Janiceps papilio* (Stache). For abbreviations see Tab. 2.

broad morphological variability, in which the following main "morphotypes" can be recognized.

"Morphotype A" (umbonal angle from 65° to 75°). Shells with flat ventral median surfaces and nearly sharp lateral edges. The anterolateral corner is pointed, and the lateral surfaces are perpendicular to the commissure plane (no. 3: Pl. 2, Fig. 14; no. 12: Pl. 2, Fig. 8; no. 29: Pl. 2, Fig. 13; no. 44: Pl. 2, Fig. 10; no. 63; lectotype of ? *Spirigera archimedis*: Pl. 2, Fig. 6, and *S. confinalis*: Pl. 2, Fig. 1). Inside group A, the shape of the sinal edges ranges from rounded (the sinus is gradually connected to median surfaces, no. 44: Pl. 2, Fig. 10) to sharp (no. 3: Pl. 2, Fig. 14). The lateral grooves are present in some asymmetrical shells, such as no. 14: Pl. 2, Fig. 9, and in the lectotype of S. confinalis: Pl. 2, Fig. 1. This characteristic is also present in *J. peracuta*, but the asymmetrical specimens have a decidedly smaller umbonal angle, the taxonomical character used here to distinguish them. As concerns the lectotype of *Spirigera confinalis*, it is represented by a deformed shell with the right anterior side of the ventral valve compressed and broken: a breakage not recorded in Stache's illustration.

"Morphotype B" (umbonal angle from 67°-72°). Shells with convex ventral median surface and rounded lateral edges. The anterolateral corner is rounded (holotypes of *J. cadorica*: Pl. 2, Fig. 7, *Spirifer dissectus*: Pl. 2, Fig. 5, and no. 16: Pl. 2, Fig. 12).

"Morphotype C" (umbonal angle from 77-82°). Similar to morphotype B, but with sharper sinal edges and wider umbonal angle, which ranges from 77° (*Spirifer crux*: Pl. 2, Fig. 3) to 82° (no. 35: Pl. 2, Fig. 11).

The holotype of *J. cadorica* (by monotipy) is represented by a fractured ventral valve and lacking of anterior and lateral margins, so it is impossible to detect its original size and anterior outline. However, this species was proposed by Stache (1878) as the main representative of triangular shells with a rounded anterior margin; therefore, it is here considered as a valid species containing individuals with this, or similar, morphology.

Some specimens of *J. cadorica* have external characteristics (e.g., pointed anterolateral corners, acute lateral edges, flat median surfaces, lateral grooves, not occurring contemporaneously in the same shell) in common with *J. peracuta* which make difficult a clear distinction between the two species, when the shells have an umbonal angle of similar value. However, the specimens of *J. cadorica* with a wide umbonal angle have rounded anterior lateral margins (e.g., specimen no. 35: ventral umbonal angle of 80°) or lack a of lateral grooves, and present smoothed lateral edges (e.g., specimen no. 75: ventral umbonal angle of 78°). The occurrence of these shells, with their mixture of characteristics of the two species, could suggest uniting them in a single species. However, their distinction is based on the different shape of the cardinal flanges of the sectioned *J. peracuta* and *J. cadorica* specimens (Fig. 6, 8).

Janiceps papilio (Stache, 1878)

(Fig. 9; Pl. 3, Fig. 1-5)

v 1878 *Spirigera papilio* Stache, p. 59, pl. 2, fig. 23a,b.
v 1878 *Spirigera aquilina* Stache, p. 59, pl. 4, fig. 4a-c, 5.
v 1930 *Athyris papilio* Stache - Merla, p. 57, pl. 5, fig. 28-31.
v 1930 *Athyris papilio* var. *cerilus* Merla, p. 59, pl. 5, fig. 26.
v 1930 *Athyris papilio* var. *cuspidata* Merla, p. 59, pl. 5, fig. 22.
v 1930 *Athyris aquilina* Stache - Merla, p. 59, pl. 6, fig. 1-3.
v 1930 *Athyris janiceps* var. *rhomboidea* Merla, p. 57, pl. 5, fig. 20

Diagnosis. Shell rhomboidal, astrophic, with short alae in mature specimens. Umbo relatively small and pointed; umbonal angle from 98 to 110°. Ventral sinus shallow, laterally limited by smoothed ridges; dorsal sulcus on a raised fold; lateral surfaces concave and externally projected, forming an acuminate posterolateral corner. Dental plates small and close to umbonal wall; cardinal flanges short, low and dorsally convergent; cardinal process subrectangular and completely separated from the dorsal umbonal wall. Crura dorsally converging with an angle of about 70°.

Material and dimensions - See Tab. 4

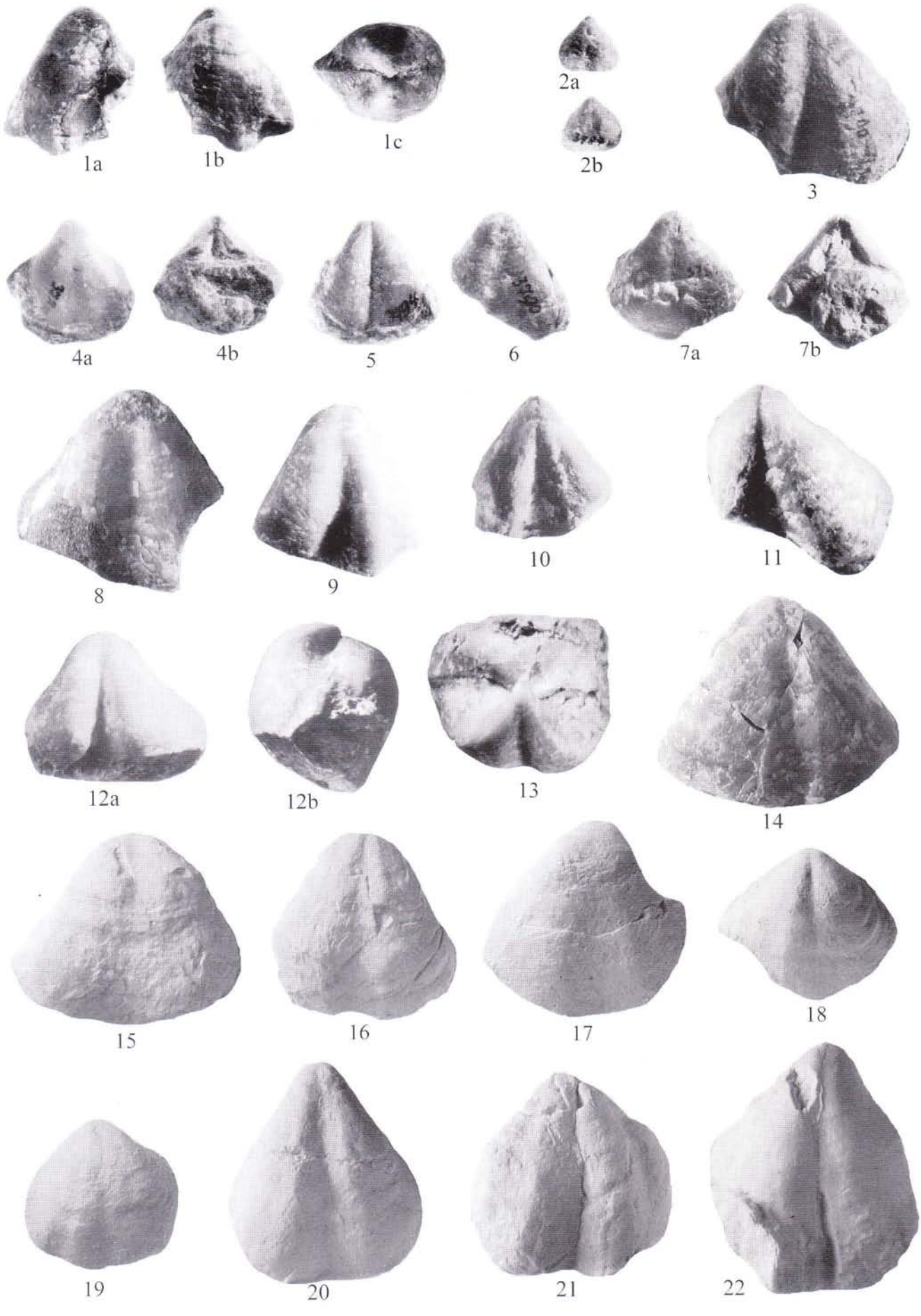
Description

External characters. The shell has a transversely elongated rhomboidal outline, with an obtuse ventral umbonal angle, which ranges from 98 to 110°. In mature individuals, the maximum width is placed at midlength and the lateral extremities form short alae. The lateral edges have a variable shape, from almost acute to rounded. The sinus is limited by low, smoothed folds. The dorsal sulcus is laterally limited by raised folds. The external ornamentation consists only of growth lines, and radial riblets are only present in the inner shell layers.

Internal characters. The dental plates are small and joined to a relatively thick umbonal wall (Fig. 8). The cardinal flanges are thin and dorsally convergent. The cardinal socket ridges are very high. The cardinal plate is high and thick; its anterior portion is thinner and has a butterfly-like shape in cross section. The dorsal umbonal cavity is subcircular to rhomboidal in cross section.

Remarks

Spirigera papilio was created on a single dorsal valve (Stache, 1878, pl. 2, fig. 23). The specimen preserved in the collections of the Geologische Bundesanstalt Museum (cat. no. 1878/1/48) is an isolated, incomplete and probably deformed, ventral valve. With the exception of the short, almost strophic cardinal margins, all the remaining marginal regions are missing;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specimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/ eW
MDTF 15	VB	S	94	104	25.3	25.3	23.0	23.0	20.0			14.8	0.91
MDTF 18	VB	S	91		18+	20.0	19.7	19.7	16.7			12.3	0.99
MDTF 34	VB	V	98		29+	36.4	27.2	27.2					0.75
MDTF 36	VB	S	94	105	20.3	22.4	19.5	19.5				14.3	0.87
MDTF 57	PK	S	102		31.2	40.1	25.5	27.0	24.4			12.9	0.67
MDTF 60	PK	V	89		17+	22.0	17.1			6.5			0.77
MDTF 90	PA	V	94		25.6	25.6	18.5	18.5		7.6			0.72
MDTF 94	OR	V	100		15.8	17.6	14.3	14.3		4.6			0.81
MDTF 96	OR	D		107	29.2	29.2			20.8		5.6		
MDTF 99	OR	D		115	33.2	33.2			23.6		7.9		
A. p. quadrilobata, Fig. 7 MDGP 24834	MC	V	103		35.2	35.2	26.4	26.4		9.7			0.75
A. p. recticardinis, Fig. 11 MDGP 24840	MC	V	102		44+	46.8	36.6	36.6		13.8			0.78

Tab. 6 - Measurements in mm of *Comelicothyris recticardinis* (Merla). For abbreviations see Tab. 2.

Gen. **Comelicothyris** gen. n.

Derivation of name. After the combination of the name of the Comelico area, type-area of the type species, and the suffix "thyris", for its belonging to the fam. Athyrididae.

Diagnosis. Moderate-sized biconvex shell; adult stage transverse subrectangular, almost strophic, width of hinge margin shorter than maximum shell width, which is located at about mid-length; alae absent; ventral sinus relatively deep and dorsal sulcus on a slightly raised fold. Dental plates thin and well distinct from the lateral walls; other internal characteristics as in *Comelicania*.

Type-species. *Athyris protea* var. *recticardinis* Merla, 1930, p. 67, pl. 6, fig. 11, from the upper Bellerophon Formation of the Comelico area (Southern Alps, Italy), uppermost Permian.

Species assigned. *Comelicothyris recticardinis* (Merla), *Comelicothyris laterosulcata* sp. n., *Comelicothyris* sp.

Occurrence. Uppermost Permian, in eastern Southern Alps.

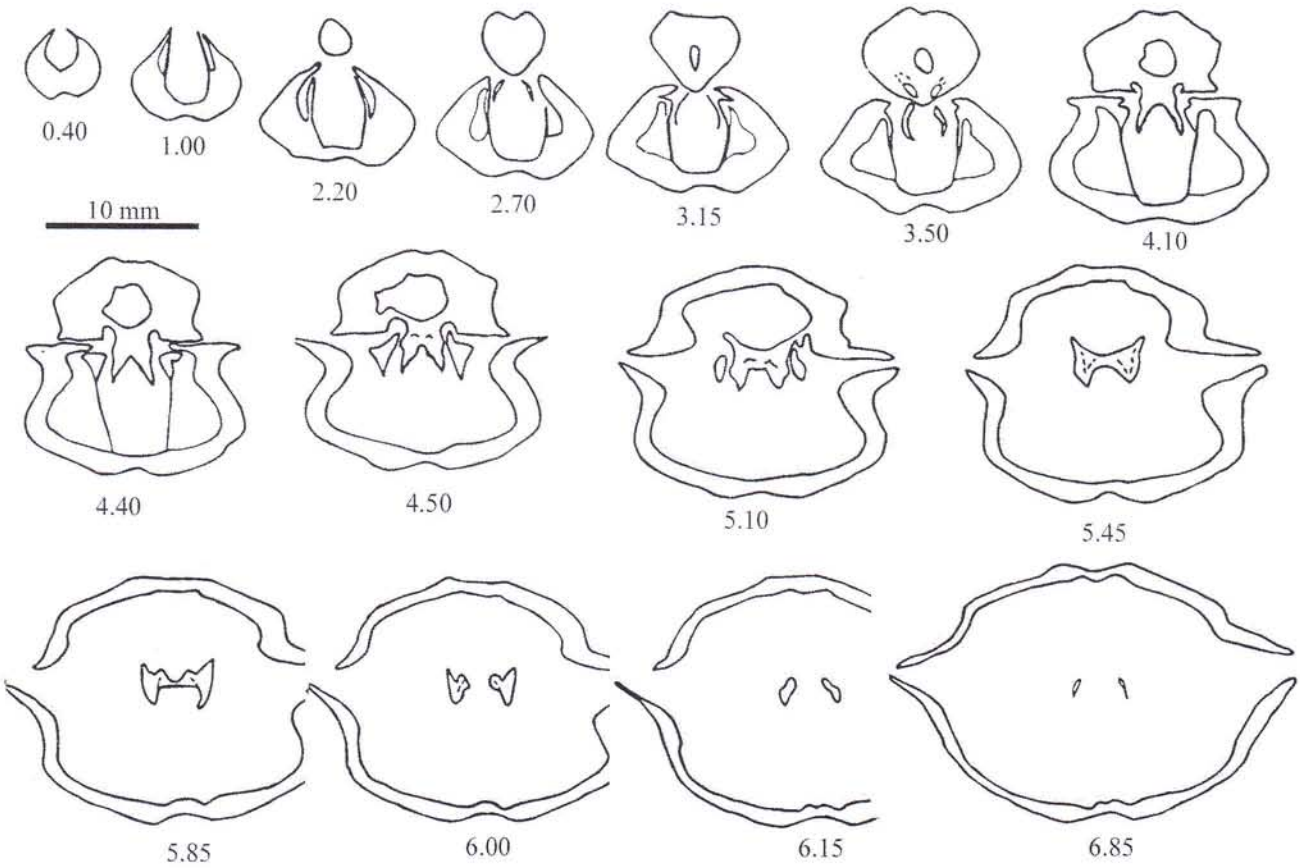


Fig. 11 - Transverse serial sections of *Comelicothyris laterosulcata* sp. n., MDTF specimen no. 54 (Pl. 3, Fig. 12), transitional beds, Val Brutta. Numbers refer to the distances in mm from the ventral beak.

Remarks

Athyris protea recticardinis Merla is a variety created before 1961; it thus has a subspecific rank (ICZN, 1999, Article 45.6.4), and is here elevated to specific level. Its generic position is matter of discussion because *Athyris protea*, similar in external morphology to our specimens, is now attributed to the gen. *Araxathyris* Grunt, whose internal characters are different from those seen in the sectioned specimens. Grunt's genus has larger dental plates, lower cardinal flanges, presence of dorsal foramen, thinner cardinal plate and low median dorsal septum. These differences suggest a different generic position for Merla's species.

This new genus has exterior characteristics transitional between *Janiceps* and *Comelicania*. Juvenile shells have a rounded subtriangular *Janiceps*-like outline, while adult specimens [i.e. one specimen of *Athyris protea* var. *recticardinis* Merla (1930, pl. 6 , fig. 11) and specimen no. 54: Pl. 3, Fig. 12 a-d] developed a transverse subrectangular outline with an almost straight posterior margin, but shorter than the maximum shell width. This mature outline is similar to late *Comelicania* species (e.g. *C. merlai* Posenato), from which it differs for the absence of alae and a shorter posterior margin. In fact, Comelicaniidae are characterized by transverse and alate shells with greatest shell width at hinge margin. These differences suggest the new genus *Comelicothyris*, to be placed within the new subfam. Janicepsinae, due to its derivation from the subfam. Comelicaniidae.

Comelicothyris recticardinis (Merla, 1930)

(Fig. 10; Pl. 3, Fig. 9-11, 16)

v pars 1930 *Athyris protea* var. *recticardinis* Merla, p. 67, pl. 6, fig. 11 (not fig. 12 = *Comelicania merlai* and fig. 13-14 = *Comelicothyris laterosulcata* sp. n.).
v pars 1930 *Athyris protea quadrilobata* Abich - Merla, p. 66, pl. 6, fig. 7, 8 (not fig. 9 = *Comelicothyris* sp. and 10 = *Comelicothyris laterosulcata* sp. n.).

Diagnosis. Middle sized shell; juvenile stage with a rounded triangular outline, adult stage transverse subrectangular, almost strophic with a hinge margin shorter than maximum shell width, which is situated at about mid-length; ventral median surfaces convex; sinus wide, laterally delimited by rounded edges, without lateral grooves; dorsal valve with a median shallow groove on a slightly raised fold.

Material and dimensions - See Tab. 6

Description

At the juvenile stage (up to 35 mm in width) the shell is astrophic, with a rounded subtrigonal outline (Fig. 3u, v). The adult outline becomes subrectangular with an almost strophic shell, even if with a hinge margin shorter than maximum shell width (Pl. 3, Fig. 9). The sinus has an angle of about 30°, and is laterally delimited by rounded edges. Lateral grooves are absent in both ventral and dorsal valves. The maximum shell thickness is situated in the posterior third of length. The foramen is absent and the delthyrium is open. The dental plates are thin, short and almost joined to the lateral walls (Fig.10). The cardinal flanges are relatively high and dorsally converging, with the crenulated side facing the sagittal plane. The cardinal plate is thick, subtrapezoidal in outline and grooved by a median, broad sulcus. The crura are dorsally convergent and form an angle of 54°. The dorsal umbonal cavity has a rhomboidal outline in transverse section.

Remarks

When Merla (1930) erected *A. protea recticardinis* on the basis of three specimens, he pointed out that this variety is not morphologically homogeneous. Only the syntype of pl. 6, fig. 11 (Merla, 1930), is here considered within this species, for which it represents the lectotype. The second specimen (Merla, 1930, pl. 6, fig. 12: Pl. 3, Fig. 17), with broken anterior margin, has growth lines at about 20 mm in shell length, which show a subpentagonal outline with forward-converging lateral margins (Fig. 3s); at this growth stage the shell is already strophic and has a small, short ala, which can be seen in the left cardinal region. This latter specimen is here classified within *Comelicania merlai* Posenato. The third specimen, an articulated shell (Merla, 1930, pl. 6, fig. 13 and 14: Pl. 3, Fig. 13), is characterized by shallow lateral grooves. Since one sectioned specimen (specimen no. 54: Pl. 3, Fig. 12) with the same outer morphology as Merla's third specimen has dental plates well distinct

specimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/ eW
MDTF 8	VB	S	91	105	15.6	16.4	12.1	12.1	10.5			7.6	0.74
MDTF 54	PK	S	96	110	36.4	36.4	28.6	28.6	25.7			17.9	0.79
MDTF 56	PK	S	105	119	17.3	17.3	12.3	12.3	11.2			7.3	0.71
A. p. recticardinis, Fig. 13, 14 MDGP 24836	MC	S	101	117	28.9	30.8	25.8	25.8	23.4			19.2	0.84

Tab. 7 - Measurements in mm of *Comelicothyris laterosulcata* sp. n. For abbreviations see Tab. 2.

specimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/eW
MDTF 2	VB	S	120	126	34.7	34.7	33.4	33.4	32.2			23.4	0.96

Tab. 8 - Measurements in mm of *Spirigerellinae* gen. et sp. indet. For abbreviations see Tab. 2.

from the lateral walls (Fig. 11), a different specific attribution is here proposed for it (*Comelicothyris laterosulcata* sp. n., see below).

Comelicothyris laterosulcata sp. n.

(Fig. 11, Pl. 3, Fig. 12, 13)

Type series. Holotype (Pl. 3, Fig.12 a-d), specimen no. MDTF 54 from the Sass de Putia section, layer 53, housed in the Museum of the Dipartimento di Scienze della Terra, Ferrara University. It is an articulated shell.

Paratypes consisting of two articulated shells illustrated by Merla [*A. protea quadrilobata* Abich, Merla, 1930, pl. 6, fig. 10 (not found in Merla's collection) and *A. protea recticardinis* Merla, 1930, pl. 6, fig. 13: Pl. 3, Fig. 13 a-d] and two small sized articulated shells: from Sass de Putia section, no. MDTF 56 and Val Brutta section, no. MDTF 8.

Derivation of name. From the presence of lateral grooves in the umbonal region.

Type locality and stratum. Sass de Putia, Dolomites, Southern Alps, Italy. Uppermost Bellerophon Formation, bed 53.

Age. Uppermost Permian, late Changxingian.

Diagnosis. Middle sized shell with a narrow ventral sinus, laterally delimited by rounded ridges and lateral grooves in the umbonal-middle region. Dorsal valve with median groove on a slightly raised fold and lateral grooves. Juvenile stage astrophic, with a transversally rhomboidal to ovoidal outline; adult stage almost strophic and subrectangular in outline. Dental plates thin and well distinct from the lateral walls.

Material and dimensions - See Tab. 7

Description

At the juvenile stage (up to 35 mm in width) the shell is astrophic, with a rhomboidal or transversely ovoidal outline (Fig. 3 w, x). The adult outline becomes subrectangular with an almost strophic shell; the hinge margin is relatively wide, but shorter than maximum shell width (Pl. 3, Fig. 12). The sinus is laterally delimited by rounded edges, which are followed by shallow grooves, mostly detectable in the umbonal region (Pl. 3, Fig. 12, 13). Juvenile growth lines have a *J. papilio* outline.

The foramen is absent and the delthyrium is open. The dental plates are thin, short and well distinct from the lateral walls, giving rise to large lateral umbonal cavities (Fig. 11). Cardinal flanges and cardinal plate as in *Comelicothyris recticardinis*.

Remarks

Comelicothyris laterosulcata sp. n. is distinguishable from *Comelicothyris recticardinis* for both the exterior and interior characteristics. In particular, the former species has lateral shallow grooves, sharper lateral edges, and longer dental plates, which are clearly distinct from the umbonal wall.

One specimen of *A. protea quadrilobata* (Merla, 1930, pl. 6, fig. 9: Pl. 3, Fig. 14), with a *Janiceps peracuta* juvenile stage (Fig. 3y) and lateral grooves in the umbonal region, acquires a subequidimensional adult outline with a short, almost straight hinge margin. Shell width (estimated 34.5 mm) is slightly greater than length (33.6 mm), and hinge margin width is 16 mm, about 45% of maximum shell width, versus 75% of the lectotype of *Comelicothyris recticardinis* (Merla). As this *A. protea quadrilobata* specimen has some characteristics (i.e. a subdimensional outline and short hinge margin), which distinguish it from the other specimens of *Comelicothyris laterosulcata*, it is here placed in open nomeclature within *Comelicothyris* and classified as *Comelicothyris* sp. ind.

Subfamily Spirigerellinae Grunt, 1965

Spirigerellinae gen. et sp. indet.

(Fig. 12; Pl. 1, Fig. 14)

Diagnosis. Biconvex, subcircular, astrophic shell with a broad, shallow sinus and low, wide dorsal fold; median surfaces slightly convex. Dental plates short, well separated from a thick umbonal wall. Cardinal process high and strong with cardinal flanges perpendicular to commissural plane; dorsally converging crura, forming an angle of 68°; no septum on the saddle.

Material and dimensions - See Tab. 8

Description

External characters. The shell is medium-sized, biconvex with a subcircular outline and an umbonal angle of 120°. The ventral umbo is short and broad. The dorsal fold is low and not sulcate. The anterior commissure is slightly sulcate. The ventral sinus is shallow and gradually connected to the median surfaces. The lateral ridges are smoothed.

Ornamentation is composed of growth lines and shallow commarginal corrugations which are only clear

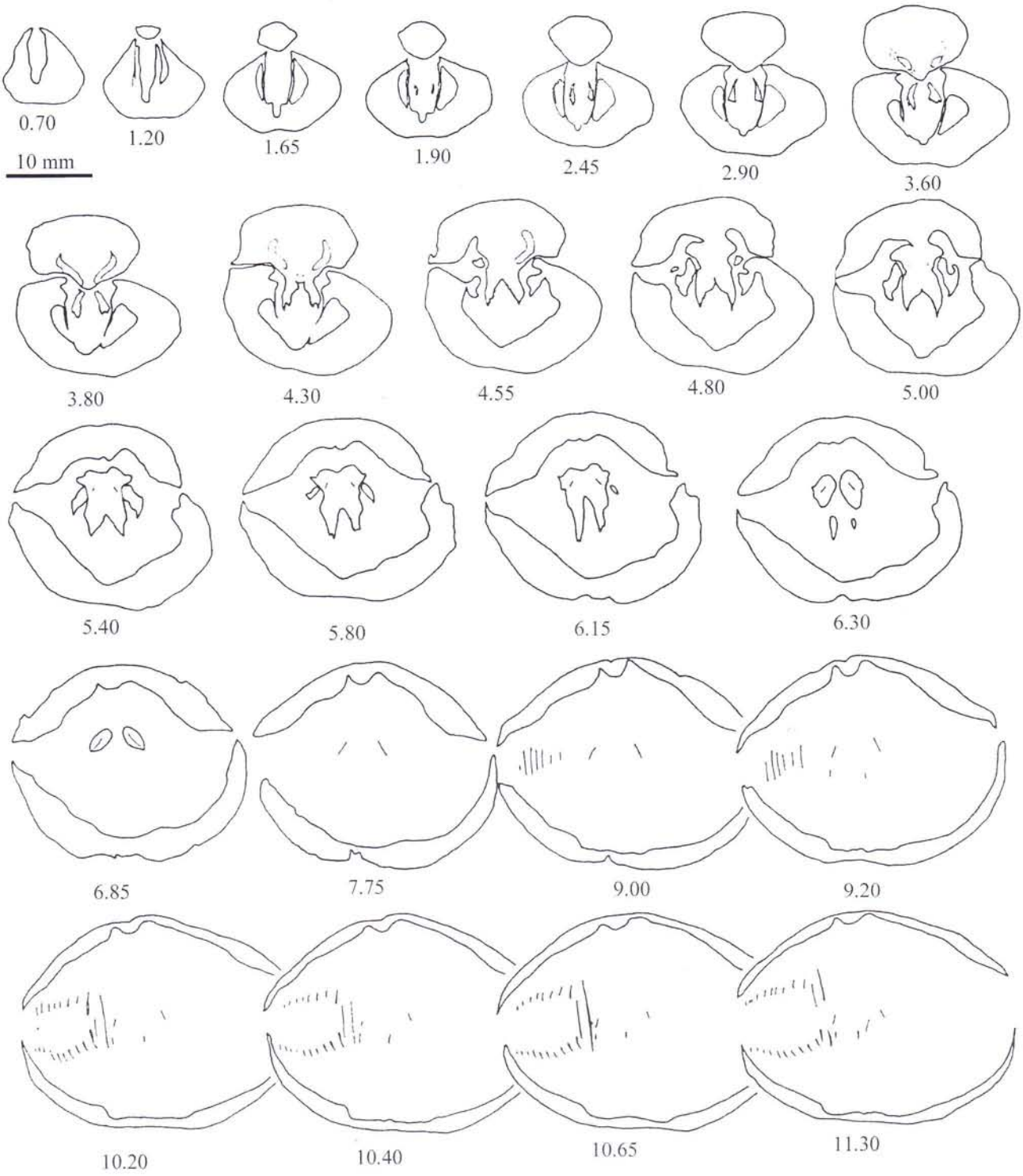


Fig. 12 - Transverse serial sections of Spirigerellinae gen. et sp. indet., MDTF specimen no. 2 (Pl. 1, Fig. 14), transitional beds, Val Brutta. Numbers refer to the distances in mm from the ventral beak.

towards the anterior margin.

Internal characters. The dental plates are relatively short (4.3 mm long), parallel and well separated from the thick umbonal wall. The cardinal flanges have a comma-like shape, with the distal anterior parts parallel and perpendicular to the commissural plane (Fig. 12). Their crenulated side is directed towards the sagittal plane.

The inner socket ridges are very high. The cardinal plate is very thick and high, and has a V-shaped median groove which becomes deeper and deeper towards the front. Dorsal umbonal region, below the cardinal plate, is heavily thickened posteriorly. Crura are dorsally converging, forming an angle of 68°. The accessory lamellae

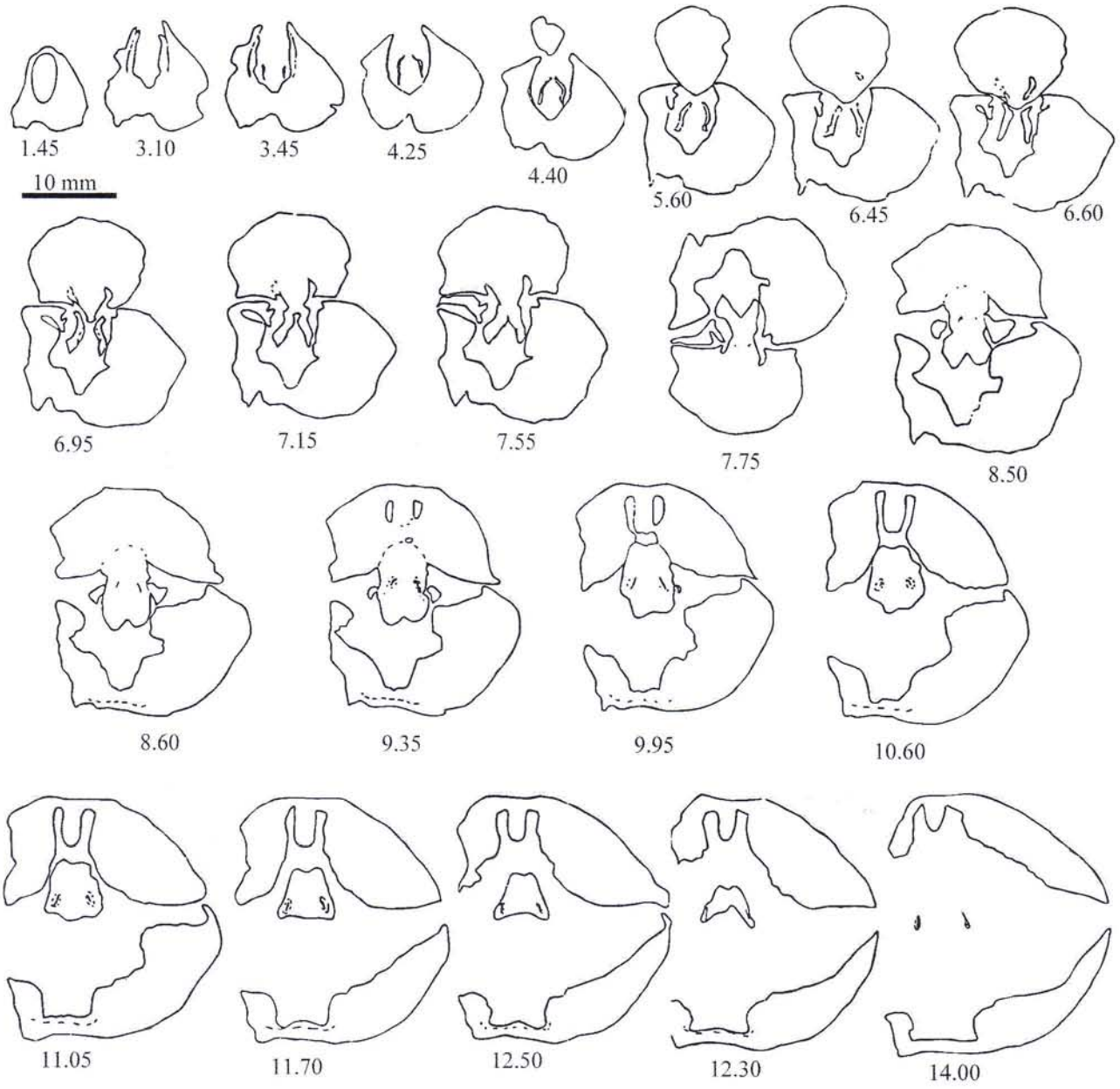


Fig. 13 - Transverse serial sections of *Septospirigerella* ? sp., MDTF specimen no. 11 (Pl. 1, Fig. 15), transitional beds, Val Brutta. Numbers refer to the distances in mm from the ventral beak.

are short. Laterally directed spiralia, with 12 whorls. No septum is present on the saddle.

Remarks.

Only a single specimen is attributed to this species: it is an articulated shell with the outer surface and umbonal region poorly preserved (Pl. 1, Fig. 14). Besides, the middle-anterior region of the dorsal valve is fractured and deformed. This specimen has exterior (i.e., subcircular outline, dorsal fold without sulcus) and interior (i.e., high and massive cardinal plate) quite different from the other athyridoids of the transitional beds. In literature, only *Spirigera* ? *faba* Stache has a subcircular outline. The holotype of this species is a very small shell, 11 mm in width (Pl. 1, Fig. 13), of which the internal features are unknown. In the present specimen, no growth line is detectable at the same growth stage, therefore a comparison at this ontogenetic stage is impossible.

As concerns the generic position, the specimen's subcircular outline prevents its classification within *Janiceps*. A subcircular to ovoidal outline is common in *Spirigerella* Waagen, which has a strong, high massive cardinal plate and absence of median sulcus on the dor-

specimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/eW
MDTF 11	VB	S	85	100	32.4	45.0	44.0	44.0	39.0			27.2	0.98

Tab. 9 - Measurements in mm of *Septospirigerella* ? sp. For abbreviations see Tab. 2.

sal fold, all features occurring in this Southalpine specimen. However, *Spirigerella* is characterized by: absence of dental plates; cardinal flanges almost parallel to commissural plane (see *S. grandis*: Grunt, 1986, fig. 55); occurrence of a septum on the jugal saddle and a complete pedicle collar. None of these features occur in the sectioned specimen (Fig. 12).

Spirigera ? faba has an outer morphology similar to *Araxathyris araxensis minor* Grunt from the Dorashamian beds of Transcaucasus. Unfortunately, the internal caracteristics of this Grunt's species are unknown and the genus *Araxathyris* Grunt has some characteristics different from the specimen here described (e.g. median furrow on the dorsal fold and a smaller, lower cardinal plate, dorsal foramen on the cardinal plate). These differences do not allow classification at either genus and species level and the scarcity of the available material suggests prudence in creating new taxa.

Gen. ? *Septospirigerella* Grunt, 1965

Septospirigerella ? sp.

(Fig. 13; Pl. 1, Fig. 15)

Diagnosis. Biconvex, astrophic, ovoidal shell; sinus wide and shallow, delimited from median surfaces by a narrow furrow; lateral edges rounded; dorsal valve with a wide and low median fold. Delthyrium open, short dental plates; cardinal flanges range from parallel and perpendicular to commissure plane backwards to slightly dorsally convergent forwards; cardinal plate high and massive, subrectangular to trapezoidal in transverse section; dorsal umbonal cavity with a large median septum.

Material and dimensions - See Tab. 9

Description

External characters. The shell is astrophic, subtrigonal-ovoidal in outline, with an umbonal angle of about 85°. The external ornamentation is made up of shallow concentric undulations and growth lines. The maximum shell width is placed near the midlength. The ventral valve is thicker than the dorsal valve and has a large, shallow, feebly concave sinus, laterally delimited by narrow grooves, particularly detectable in the anterior region. The median surface is connected to the lateral region by a rounded edge. The ventral umbonal region is poorly preserved. Dorsal valve with a broad median fold; the lateral regions are undistinguishable from the median dorsal surface.

PLATE 3

Fig. 1-5 - *Janiceps papilio* (Stache), all x 1. Fig. 1- Articulated shell, ventral (1a), dorsal (1b) and posterior (1c) views, MDTF no. 17, Val Bruta (Trento); see its transverse section in Fig. 9. Fig. 2 - Holotype of *Athyris papilio cerilus* Merla, 1930, pl. 5, fig. 26, MDGP no. 24825, exterior ventral valve, Monte Croce Comelico. Fig. 3 - Holotype of *Athyris papilio cuspidata* Merla, 1930, pl. 5, fig. 22, MDGP no. 24826, exterior ventral view, Monte Croce Comelico. Fig. 4 - Holotype of *Athyris janiceps rhomboidea* Merla, 1930, pl. 5, fig. 20, MDGP no. 24821, dorsal valve exterior, Monte Croce Comelico. Fig. 5 - *Athyris papilio* (Stache), Merla, 1930, pl. 5, fig. 31, MDGP no. 24823b, ventral view of an articulated shell, Monte Croce Comelico.

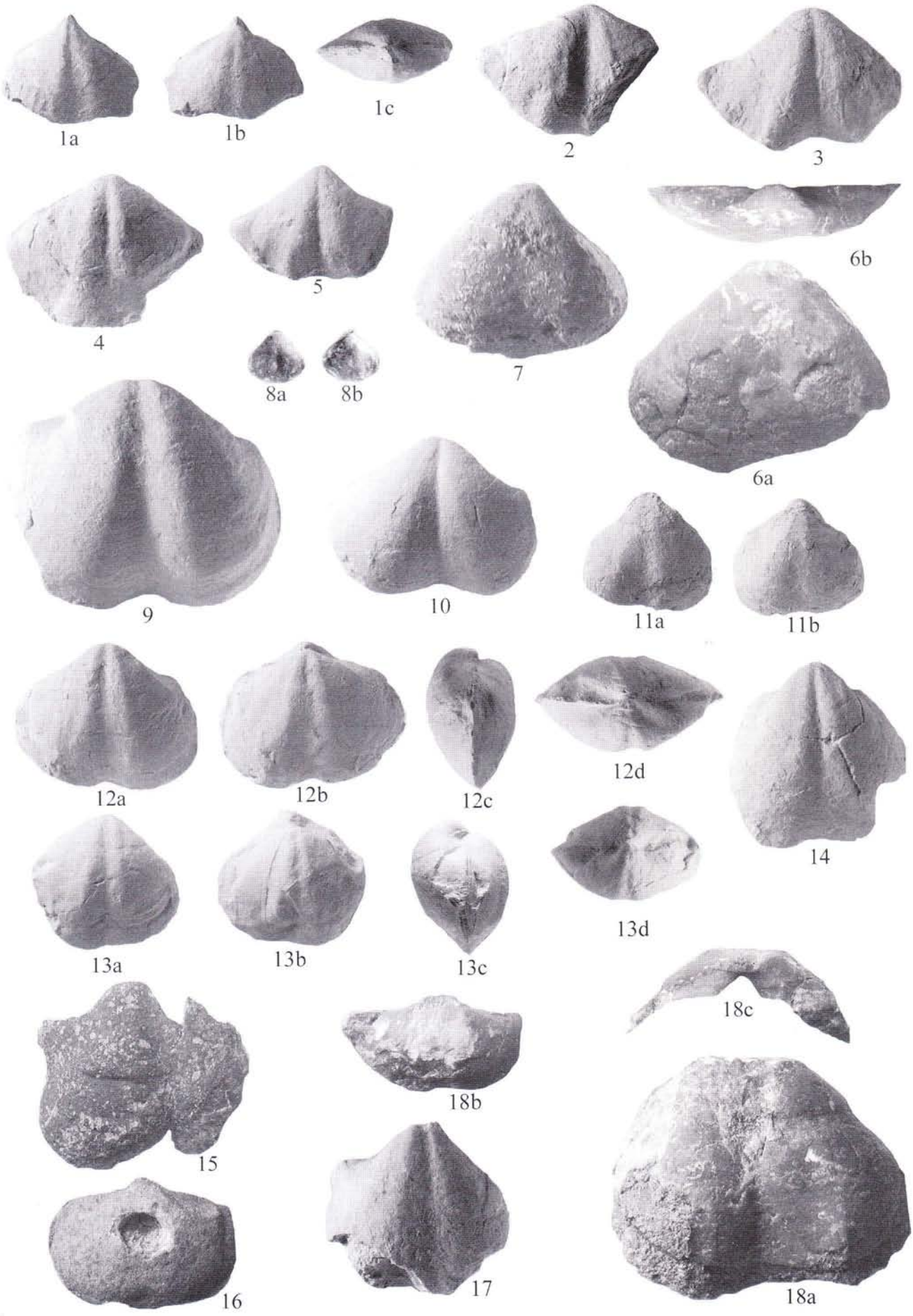
Fig. 6-8 - *Janiceps bipartita* (Stache), all x 1. Fig. 6 - Ventral valve, MDTF no. 52, ventral (6a) and posterior (6b) views, Val Brutta (Trento). Fig. 7 - Ventral valve, MDTF no. 1, Val Brutta (Trento). Fig. 8- *Lectotype of Spirigera bipartita* Stache, 1878, pl. 3, fig.12, MGBW no. 1878/1/51a, articulated shell, ventral (8a) and dorsal (8b) views, Monte Croce Comelico.

Fig. 9-11, 16 - *Comelicothyris recticardinis* (Merla), all x 1. Fig. 9- Lectotype of *Athyris protea recticardinis* Merla, 1930, pl. 6, fig. 11, MDGP no. 24840, ventral valve, Monte Croce Comelico. Fig. 10 - *Athyris protea quadrilobata* (Abich), Merla 1930, pl 6, fig. 7, MDGP no. 24834, ventral valve, Monte Croce Comelico. Fig. 11 - Articulated shell, MDTF no. 15, ventral (15a) and dorsal (15b) views, Val Brutta (Trento); see its transverse section in Fig. 10. Fig. 16 - Dorsal valve, MDTF no. 99, Ortisei (Bolzano).

Fig. 12-13 - *Comelicothyris laterosulcata* sp. n., all x 1. Fig. 12 - Articulated shell, MDTF no. 54, ventral (12a), dorsal (12b), lateral (12c) and posterior (12d) views, Sass de Putia (Bolzano); see its transverse section in Fig. 11. Fig. 13 - *Athyris protea recticardinis* Merla 1930, pl. 6, fig. 13, 14, MDGP no. 24836, articulated shell, ventral (13a), dorsal (13b), lateral (13c) and posterior (13d) views, Monte Croce Comelico.

Fig. 14 - *Comelicothyris* sp.; *Athyris protea quadrilobata* (Abich), Merla 1930, pl 6, fig. 9, MDGP no. 24837, ventral view of an articulated shell in which only the cardinal region of the dorsal valve is preserved, Monte Croce Comelico.

Fig.15, 17, 18 - *Comelicania merlai* Posenato, all x 1. Fig. 15 - Holotype of *Comelicania merlai* Posenato, 1998, pl. 4, fig. 7, ventral valve, MDTF no. PK52, Sass de Putia (Bolzano).Fig. 17 - *Athyris protea recticardinis* Merla, 1930, pl. 6, fig. 12, MDGP no. 24842, Monte Croce di Comelico, exterior view of ventral valve. Fig. 18 - Ventral valve of a slightly deformed or asymmetrical individual, MDTF no. 85, ventral view (18a), particular of the juvenile stage in which short asymmetrical ears are detectable (18b) and posterodorsal view in which a large and open delthyrium is present, Piz da Peres (Bolzano).


1a
1b
1c
2
3
4
5
6b
6a
7
8a
8b
9
10
11a
11b
12a
12b
12c
12d
13a
13b
13c
13d
14
15
16
17
18a
18b
18c

specimen	loc.	shell	Vß	Dß	W	eW	Lv	eLv	Ld	Tv	Td	Ts	eLv/eW
MDTF 52	PK	V			57	57	41	43		12			0.75
MDTF 69	PK	V			34.7	42.0	35.6	35.6		11.5			0.85
MDTF 85	PZ	V	107		56	62	46.2	48.5		20.9			0.78
MDTF 100	PK	V	90		41.4	50.1			47.0*				
MDTF 130	PK	S	103		54	54	41	41				26.2	0.76
A. p. recticardinis, fig. 12 MDGP 24842	MC	S	93		32.7	34.7	30.5	32.0		9.4			0.92

Tab. 10 - Measurements in mm of *Comelicania merlai* Posenato. For abbreviations see Tab. 2.

Internal characters. The dental plates are very short and joined to the thick umbonal wall. The posterior extremities of dental flanges are parallel to one another and perpendicular to commissure plane; they become dorsally convergent forwards. The cardinal plate is thick and its transverse section, in the anterior part, has a trapezoidal outline (Fig. 13, section 12.50). The inner socket ridges form a V-shaped median groove, which becomes shallower and shallower anteriorly until it disappears. The crura form an angle of 35°.

The dorsal umbonal cavity is narrow and has a large, strong median septum, which only in the posterior extremity is joined to the cardinal plate. The septum also occurs in the thick dorsal umbonal wall, where it is submerged by shelly material.

Remarks

Only a single specimen is available. It is an articulated shell, lacking the right lateral region (Pl. 1, Fig. 15). The peculiar morphology of the ventral sinus and the presence of the dorsal median septum make possible a clear differentiation from the other athyridoids of the transitional beds.

The occurrence of a dorsal median septum is a characteristic in common with *Septospirigerella* Grunt (Grunt 1986, p. 110). The exterior morphology of this specimen is similar to *Septospirigerella megridagica* Grunt. However, the genus *Septospirigerella* has: a shorter and thinner, blade-like, median dorsal septum; a lower cardinal plate; a very shallow ventral sinus which is undistinguishable from the median surface.

On the basis of these differences, a new genus could be proposed for this specimen, but at present, the scarcity of the available material induces us to be cautions about erecting a new taxon, at both a generic and specific level.

Subfamily Comelicaniinae Merla, 1930

Gen. *Comelicania* Frech, 1902

Comelicania merlai Posenato, 1998

(Pl. 3, Fig. 15, 17, 18)

v 1930 *Comelicania ladina* Stache - Merla, p. 41, pl. 2, fig. 3,4.
v pars 1930 *Athyris protea* var. recticardinis Merla, p. 67, pl. 6, fig. 12 (not fig. 11, 13, 14 = *Comelicothyris recticardinis*)
v 1988 *Comelicania* gr. *ladina* (Stache) sensu Merla - Posenato, pl. 50, fig. 3.
v 1998 *Comelicania merlai* Posenato, p. 63, pl. 4, fig. 3-9.

Diagnosis. Biconvex, bisulcate shell, subpentagonal to subrectangular in outline; strophic at mature stage with short, pointed alae; maximum width placed at the hinge line or close to it; sinus wide, gradually connected to median surfaces; concentric growth lines and some concentric corrugations. Cardinal plate higher than wider, detached from dorsal umbonal wall; crura dorsally converging, forming an angle of 72°.

Description

External characters. The shell is of middle size and has a transversely elongated outline with short alae and thick posterior wall. The convexity of the dorsal valve is equal to or slightly lower than that of the ventral valve. The outline ranges from subrectangular to subpentagonal (Fig. 3 s, t). The ventral umbo is large; the posterior surface is narrow and poorly distinct from the lateral regions. The sinus is broad, with an angle of about 35-40°, laterally delimited by smooth ridges. The dorsal mid-sulcus is shallow and located on a raised fold.

Internal characters. The dental plates are short and close to a thick umbonal wall. The ventral umbonal cavity is small. The cardinal flanges are nearly parallel, slightly arcuated, and joined to the cardinal plate, which is posteriorly very high, with well raised inner socket ridges (see Posenato, 1998, fig. 12) The cardinal plate becomes more and more flattened forwards. The crura are dorsally convergent, forming an angle of 72°.

Remarks

This species has been proposed by the author in a

recent revision (Posenato, 1998) of *Comelicania*. Some new individuals (i.e. Pl. 3, Fig. 18) have been found since then, including a specimen of Merla's collection, already ascribed by him to *Athyris protea recticardinis* (Pl. 3, Fig. 17). The reasons for this specific determination as already been detailed in the previous discussion on *Comelicothyris recticardinis*.

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