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Tirolites (Ammonoidea) from the Dolomites, Bakony and Dalmatia: Taxonomy and biostratigraphy

By RENATO POSENATO¹⁾

ABSTRACT

This paper concerns the taxonomy and biostratigraphy of the genus *Tirolites*, one of the more typical Late Scythian ammonoids of the European Werfen beds.

Tirolitids from the upper Werfen Formation of the Dolomites (Southern Alps, Italy) have been compared with those occurring in the Csopak Marl Formation of Bakony (Transdanubian Mid-mountains, Hungary), using the ammonoid events of the Muć section (Dalmatia, Yugoslavia), which have already been proposed as a standard Upper Scythian sequence in Europe, as reference point.

Taxonomical analysis has been carried out according to the fossil population concept of species, due to the wide variability of morphological characters, often influenced by diagenetic-deforming factors, responsible for the great splitting of *Tirolites* at species level.

The Dolomite and Bakonian populations, clearly distinguishable with both biometrical and typological methods, have been classified into two different species, respectively: *T. cassianus* and *T. illyricus*. The phylogenetic trend of *Tirolites* and the associated benthic markers show that *T. cassianus* is older than *T. illyricus*, and that they represents the early stages of Tirolitid evolution, which would be followed by *T. seminudus*, *T. idrianus* and *T. carniolicus*. The last three evolutionary species, mostly recorded in the Dalmatian sequences, are missing in the Dolomites and Bakony because of the ultimately *Tirolites* disappearance.

T. cassianus beds belong to *Eumorphotis kittli* subzone, whilst *T. illyricus* beds, which record the appearance of *Costatoria costata* and *Dalmatites morlaccus*, belong to *Meandrospira pusilla* Zone (or *Eumorphotis telleri* subzone). The Bakonian *Tirolites* beds can be roughly correlated with the *Dinarites dalmatinus* beds of the Cencenighe Member of the Dolomites.

RÉSUMÉ

Dans cette étude sont prises en examen la taxonomie et la biostratigraphie du genre *Tirolites*, un ammonoïde typique du Scythien supérieur des Couches de Werfen européennes.

Les Tirolitides de la partie haute de la Formation de Werfen des Dolomites (Alpes méridionales, Italie) ont été comparés avec ceux provenant de la Formation des Csopak Marl de la Bakonie (Transdanubie, Hongrie), en utilisant comme point de référence les évènements à ammonoïdes enregistrés dans la section de Muć (Dalmatie, Yougoslavie), déjà proposée comme séquence-standard du Scythien supérieur en Europe.

L'analyse taxonomique a été conduite d'après la notion d'espèce-population fossile, étant donné la grande variabilité des caractères morphologiques, souvent influencés par des facteurs diagénétiques-déformatifs, responsables de la fragmentation des *Tirolites* à niveau spécifique.

Les populations dolomitiques et bakoniques, bien distinguables soit avec les méthodes biométriques que typologiques, ont été classifiées en deux espèces distinctes, respectivement: *T. cassianus* et *T. illyricus*. Le trend phylogénétique des *Tirolites* et les markers benthiques associés indiquent que ces deux espèces représentent les premières stades de l'évolution des Tirolitides, qui est probablement suivie par *T. seminudus*, *T. idrianus* et *T. carniolicus*. Ces dernières espèces, enregistrées principalement dans la séquence dalmate, sont absentes dans les Dolomites et en Bakonie, à cause de la précoce disparition des *Tirolites*.

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Les couches à *T. cassianus* appartiennent à la subzone à *Eumorphotis kittli*, tandis que les couches à *T. illyricus*, qui enregistrent l'apparition de *Costatoria costata* et *Dalmatites morlaccus*, appartiennent à la Zone à la Zone à *Meandrospira pusilla* (ou subzone à *Eumorphotis telleri*). Les couches à *T. illyricus* peuvent grosso modo être mises en relation avec les couches à *Dinarites dalmatinus* du «Membro di Cencenighe» des Dolomites.

1. Introduction

In Europe, the marine Lower Triassic is represented by terrigenous-calcareous units which, since the last century, have been known as "Werfen beds". Within these beds, ammonoids have only been recorded in the upper part (Campil beds). They are characterized by the occurrence of *Tirolites*, a ceratitid which includes *Tirolites cassianus* (QUENSTEDT) amongst its more peculiar species, which was used by Mojsisovics (1882) to mark a zone which embraces the whole of the Alpine Upper Scythian.

After a series of early works in the last century (Hauer 1856, Mojsisovics 1882), some areas, such as the Dolomites and Dalmatia, became of great interest for the study of the Campil bed ammonoids. In Dalmatia, near the village of Muć, material was collected for the publication by Kittl (1903), which became the basic work about the ammonoids of upper Werfen beds. Unfortunately, this material was collected without stratigraphical references and was classified according to strictly morphological criteria. Using this method, he described 33 morphological species of *Tirolites*, 18 of which were new.

It was not until recently that more research into the Muć section was been carried out, by Krystyn (1974) and Herak et al. (1983). These works have made it possible to establish the stratigraphical range of some species of *Tirolites* and to approach their taxonomical revision, according to a population species concept. From this, a new biozonation has been proposed, in which the Mojsisovics zone has been divided into two units, a lower *T. cassianus* Zone and an upper *T. carniolicus* Zone (Krystyn 1974).

In the Dolomites, the revision of the lithostratigraphical units of the Werfen beds (= Werfen Formation; Bosellini 1968) (Bosellini 1968; Farabegoli et al. 1977; Pisa et al. 1979) and detailed biostratigraphical studies (Broglia Loriga et al. 1983, 1986, 1990; Neri & Posenato 1985) have made it possible to detect the vertical range of ammonoids plus the associated benthos. According to the above authors, the *T. cassianus* beds are located in the Val Badia Member, whilst in the overlaying Cencenighe Member only *Dinarites dalmatinus* (HAUER) has been found. During this research, quite a notable collection of ammonoids was made, which will be studied in this work.

Another collection of *Tirolites* was made in the course of research projects in the Scythian sequences of Transdanubia (Central Hungary), which have also concerned the outcrops of *Tirolites* beds in the area surrounding the Balaton Lake (Balaton Highland or Bakony). Although *T. cassianus* is mentioned in the geological literature from this area as well (Frech 1907), the associated benthic molluscs show a stronger affinity with those from the Cencenighe Member rather than with those from the Val Badia. For this reason, the Bakonian *Tirolites* beds have been considered as younger than the Dolomite ones (Broglia Loriga et al. 1990).

The aim of this work is a comparison of the two *Tirolites* collections (both ascribed to the same species in the past geological literature, but from different stratigraphical levels), in order to identify any morphological difference which exist and to define their taxonomical position.

The comparison will be made using the fossil population concept (Sylvester-Bradley 1958), due to the wide variability of shell ornamentation and whorl section, often influenced by diagenetic factors. A statistical methodology will be used to achieve this, because of the high number of *Tirolites* described in literature and because of the fairly good availability of specimens.

Finally, the correlation between the ammonoid events, with particular reference to *Tirolites*, and the main benthic events, used in free-ammonoid beds will be tested, in an attempt to understand the late Scythian biostratigraphy of the Werfen beds in Europe.

2. Examined occurrences of *Tirolites*

2.1. *Tirolites* beds, upper Werfen Formation, western Dolomites

In this section, there will be a description of the vertical range of *Tirolites* and of the main ammonoid and benthic events of the upper Werfen Formation (Val Badia, Cencenighe and San Lucano Members), according to Broglio Loriga et al. (1983, 1990) and Neri & Posenato (1985).

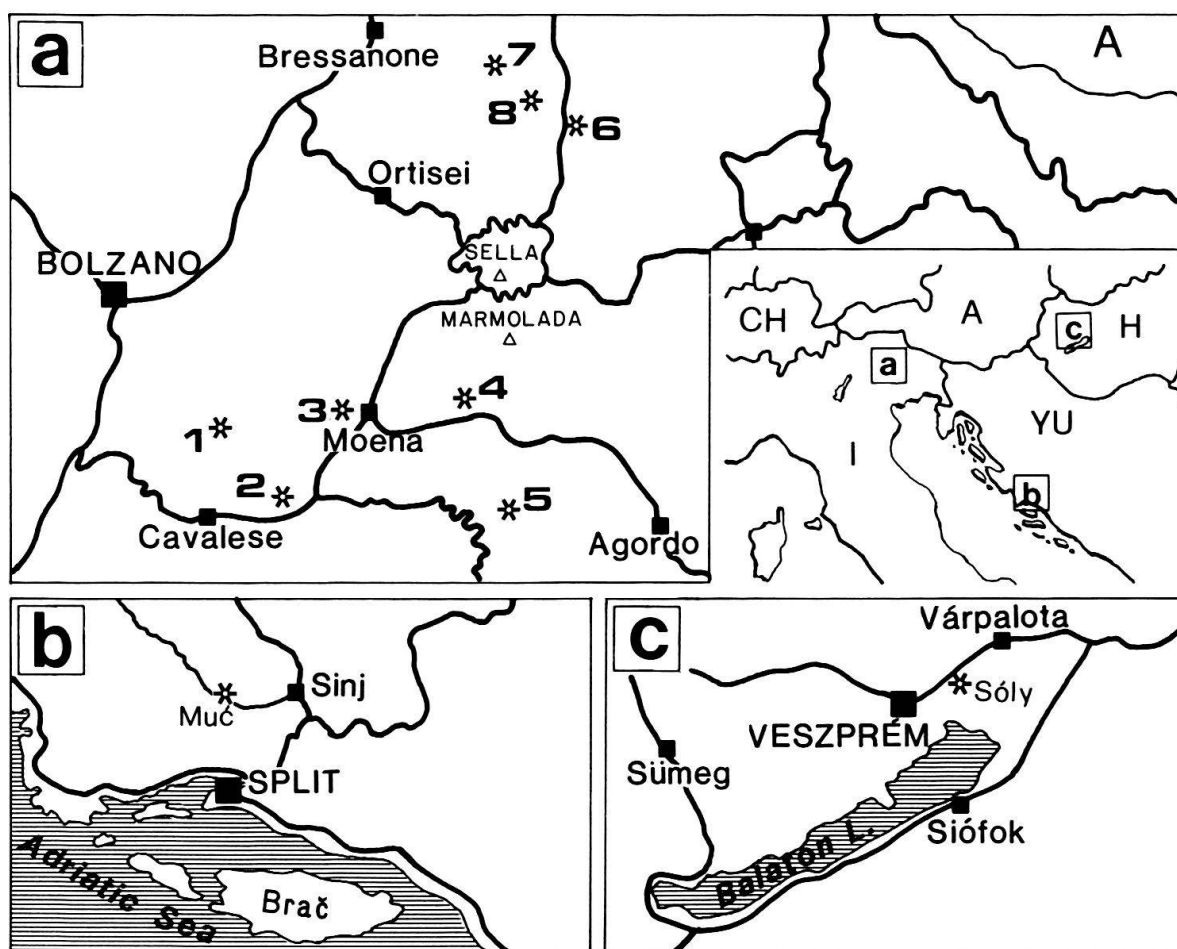


Fig. 1. Geographical setting of the quoted localities. Dolomites: 1-Butterloch, 2-Val Averta, 3-Moena, 4-Costa-bella, 5-Val Venegia, 6-Val Badia (SS 244), 7-Col Vercin, 8-Grones.

In the western Dolomites (Fig. 1), *Tirolites* is located in the Val Badia Member, with a higher frequency in the lower part, corresponding to unit B and lowest unit D (Fig. 2). The specimens studied in this work are from these beds (referred to here as *Tirolites* beds), which are about 10 meters thick and separated by the barren, peritidal unit C. They are contained in greenish sediments composed of marly limestone alternating with bioclastic calcarenite (storm-layers) and marl.

The *Tirolites* beds yield the bivalves *Eumorphotis kittli* (BITTNER), frequent specimens of *Bakevella*, *Neoschizodus* and the gastropods *Natiria costata* (MÜNSTER) and “*Turbo*” *rectecostatus* HAUER.

The middle part of unit D is characterized by the occurrence of *Diaplococeras liccanum* (HAUER) and very rare specimens of *Tirolitoides prior* (KITTL) (Val Venegia section). The upper part of unit D yields rare specimens of “*Meekoceras*” *caprilense* MOJSISOVICS (Grones section) and smooth dinaritids (Col Vercin section). There are scattered occurrences of *Meandrospira pusilla* (HO) at the top of the member. *Tirolites* becomes very rare in the *Diaplococeras* beds, and they disappear completely at the end of the Val Badia Member.

The lower unit of the Cencenighe Member (unit A) is made up of oolitic-bioclastic calcarenite, alternating with sandstone and siltstone, sometimes with mud-crack structures. Unit A yields the *Dinarites dalmatinus* beds, with a notable fossiliferous occurrence in the upper part. It is from this interval that the more diversified fauna of the whole Werfen Formation has been collected. It is characterized by the abundance of *Eumorphotis telleri* (BITTNER), which here is its acme zone.

Although the sampling accuracy, the occurrence of *Costatoria costata* (ZENKER) in *D. dalmatinus* beds cannot be confirmed, as only one doubtful specimen has been collected. It is definitely present in the upper Cencenighe Member (unit C), in oolitic-encrinitic layers, where only one specimen of ammonoid, a smooth dinaritid, has been found (Malga Fosse section). In unit C of the Cencenighe Member there is the acme zone of *Meandrospira pusilla*.

The San Lucano Member, consisting of fine-grained sandstone, marl and marly dolomite, is very poor in fossil content, because of its prevalent peritidal conditions. *Meandrospira pusilla* disappears at the base of this member, which yields rare specimens of *Costatoria costata* and *Natiria costata* up to the top.

2.2. *Tirolites* beds, Csopak Marl Formation, Bakony

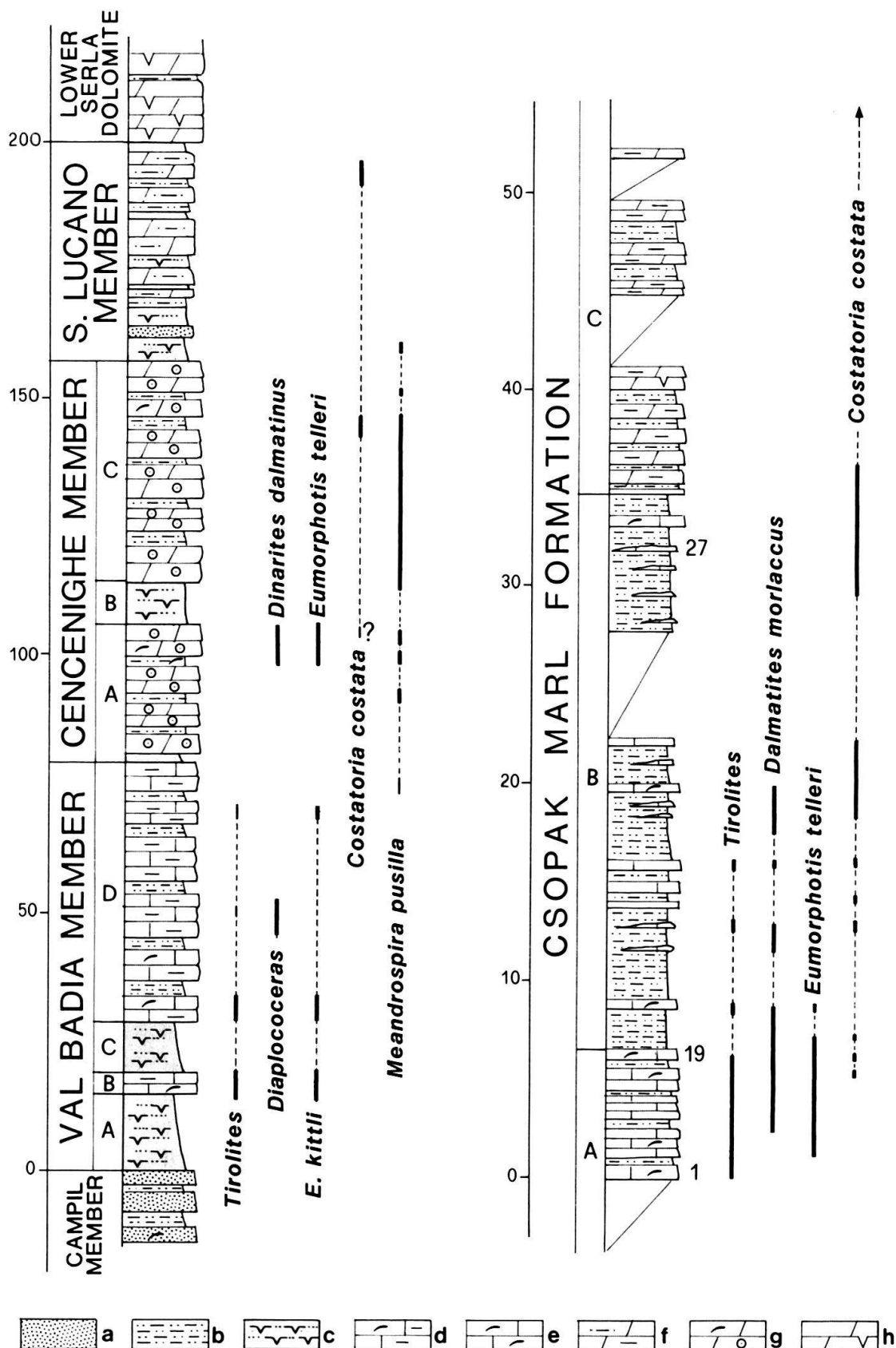
In the Balaton Highland (Fig. 1), the *Tirolites* beds are located in the Csopak Marl Formation, with its lower boundary formed by the Hidegkút Formation and the Aszófő Dolomite at the top. Csopak Marl has recently been divided into three units,

Fig. 2. Lithostratigraphy and vertical range of ammonoids and benthic markers, upper Werfen Formation and Csopak Marl Formation. Dolomites: composite column from Costabella (Val Badia Member) and Val Sorda (Cencenighe and San Lucano Members) sections, respectively adapted from Broglio Loriga et al. 1986, Neri & Posenato 1985. Bakony: Soly column adapted from Broglio Loriga et al. 1990.

Legend: a-sandstone, b-marl and marly siltstone, c-siltstone with mud cracks (peri- supratidal events), d-marly limestone, e-micritic limestone, f-marly and silty dolomite, g-oolitic dolomite, h-fine grained dolomite.

DOLOMITES

BAKONY (SÓLY)



consisting of: yellowish marly limestone and bioclastic limestone alternating with silty marl (lower unit, A); prevailing red siltstone with bioclastic limestone intercalations (middle unit, B); greenish-gray marly limestone and silty marl (upper unit, C) (Haas et al. 1988; Broglio Loriga et al. 1990).

Tirolites is very frequent in the upper part of unit A, with scattered specimens occurring in the lower part of unit B. The lower boundary of *Tirolites* beds cannot be ascertained in detail, because of the scarcity of outcrops in the middle-lower part of unit A, where the finding of a *Dinarites dalmatinus* specimen from detritus is worthy of note.

The *Tirolites* specimens studied in this work have been collected from the basal five meters of the Sóly section, which is a part of the uppermost unit A (Fig. 2). Here, the benthic assemblage is characterized by the abundance of *Eumorphotis telleri*.

The ammonoid *Dalmatites morlaccus* KITTL occurs also in the *Tirolites* beds, even though its appearance starts from a few meters above the early *Tirolites*, more or less coinciding with the first specimens of *Costatoria costata*.

The lower part of unit B has an assemblage which is comparable to the ones in the underlying unit, but with a considerable decrease in the frequency of ammonoids. Although the *Dalmatites morlaccus* range is slightly wider than the *Tirolites*, both of these disappear in the middle part of unit B. The *Costatoria costata* acme occurs in the upper part of unit B.

No ammonoids are observed in unit C, whereas *Costatoria costata* is present once more, and ranges up to as far as the Aszófó Dolomite.

3. Comparison between Dolomite and Bakonian Tirolitids

3.1. Methodology

The comparison between the two populations has been carried out using a biometric-statistics methodology based on the phylogenetic trend of *Tirolites*, as proposed by Krystyn (1974). It consists of the transition from evolute shells with a high number of spines and nodes (*T. cassianus*), to involute shells, with a small number of nodes or spines limited to the body chamber (*T. carniolicus*). This means to say that the following characteristics can be observed in the genus *Tirolites* with the passage of time: increased involution, increased whorl height and a simplifying of ornamentation.

Unfortunately, the scanty occurrence of specimens in both areas made it impossible to collect a sufficient number of *Tirolites* from any single bed, from a statistical point of view. The Dolomite specimens were collected from an interval about 20 m thick, and the Bakonian ones from 5 m. However, the two populations can be considered as sufficiently homogeneous from an evolutionary point of view, considering that the Muć sequence, where Krystyn (1974) studied the *Tirolites* evolution, is 450 m thick, and anyone of the three considered sequences was formed in pelagic environment.

3.2. Choice of biometric characters for comparison

The condition of preservation, mostly of the Dolomite specimens, is generally not good. The compactation of sediment, due to marly lithologies, has deformed the major-

ity of the shells, in particular those from more terrigenous sediments. As regards the shells lying parallel to the surface layer, they are flattened, to a greater or lesser extent. The whorl width, therefore, is influenced by diagenetic factors rather than by genetic ones. Consequently, this dimension cannot be used as character for comparison amongst specimens collected in sediments of different composition (Pl. 1, Fig. 1, 2).

The occurrence of spines rather than nodes or tubercles sometimes depends on taphonomy. In fact, the preservation of the spines occur on the lateral side, thrust into the more calcareous fraction of the layer, whilst on the opposite side, which faces a marl intercalation, the ornamentation is more or less worn (Pl. 3, Fig. 4), to the point of being completely absent. The internal mould of many of the Dolomite specimens is deeply dissolved to the point of the quatorial plane (Pl. 2, Fig. 1). This was probably caused by an early dissolution of the shell at the water/sediment contact surface during periods characterized by a low buried rate.

Generally, only the internal mould of the body chamber and the phragmocone of the last whorl are preserved, whilst the internal whorls are seen to be entirely flattened (Pl. 1, Fig. 6).

The choice of characters for the comparison has been made, therefore, with an emphasis on measurements less influenced by diagenetic or deforming processes, such as: maximum and umbilical diameters, maximum whorl height, the total amount of marginal spines and nodes on the last whorl. Other characters, such as the minimum whorl height, have not been used, as the peristome region is often badly preserved: if this character had been used, it would have considerably reduced the size of the available populations. As regards the degree of involution, the Dolomite specimens have evolute shells, whereas the Bakonian ones have a low involution ($H_{\max}/H_{\min} = 1.10-1.15$).

3.3. Biometrical and morphological analysis

Following a biometrical analysis of the measurements, (appendix, Tab. 1), the following conclusions can be drawn (Fig. 3): the Dolomite Tirolitids have a wider maximum diameter, a higher number of spines, and nodes on last whorl and a higher umbilical/maximum diameter ratio as compared to the Bakonian ones.

The low number of nodes on the last whorl of the Bakonian specimens could be correlated to their small sizes, but this hypothesis is not confirmed by the comparison of similar size specimens (Fig. 4). In this case, the Hungarian forms tend to have smooth internal whorls and a low number of nodes on the last whorl, whilst, on the contrary, the Dolomite specimens have spines starting from the initial phragmocone whorls. With the latter specimens, the radial sculpture tends to degenerate apically, with the exciting of feeble ribs on the lateral side and without any nodes or spines on the ventral-lateral shoulder. (Pl. 2, Fig. 4). This character has already been observed in the Dalmatian population of *T. cassianus* (Krystyn 1974).

Table 1. List of the examined *Tirolites* species and changes of their taxonomical position according to Mojsisovics 1882 (1), Kittl 1903 (2), Kummel 1969 (3), Krystyn 1974 (4), Posenato this paper (5). CP = *Ceratites* (*Paraceratites*), CR = *T. carniolicus*, CS = *T. cassianus*, D = *Dinarites*, H = *Hololobus*, INV = invalided species, ID = *T. idrianus*, IL = *T. illyricus*, SE = "Gruppe der *seminudi*", SP = "Gruppe der *spinosi*", SS = *T. seminudus*, TH = *Tirolites* (*Hololobus*).

	1		2		3			4		5				
	SP	SE	SP	SE	CS	ID	CR	CS	CR	CS	IL	SS	ID	CR
1 - <i>T. cassianus</i> (QUENSTEDT, 1849)	+		+		+			+		+				
2 - <i>T. smiriagini</i> (AUERBACH, 1871)	+		+		+			+		+				
3 - <i>T. darwini</i> MOJSISOVICS, 1882	+		+		+			+		+				
4 - <i>T. haueri</i> MOJSISOVICS, 1882	+		+		+			+		+				
5 - <i>T. spinosus</i> MOJSISOVICS, 1882	+		+		+			+		+				
6 - <i>T. turgidus</i> MOJSISOVICS, 1882	+		+		+			+		+				
7 - <i>T. angustilobatus</i> KITTL, 1903			+		+			+		+				
8 - <i>T. kernerii</i> KITTL, 1903			+		+			+		+				
9 - <i>T. multispinatus</i> KITTL, 1903			+		+			+		+				
10 - <i>T. percostatus</i> KITTL, 1903			+		+			+		+				
11 - <i>T. prior</i> (KITTL, 1903)			CP		+			+						
12 - <i>T. spinosior</i> KITTL, 1903			+		+			+		+				
13 - <i>T. toulai</i> KITTL, 1903			+		+			+		+				
14 - <i>T. illyricus</i> MOJSISOVICS, 1882		+		+		+		+			+			
15 - <i>T. rectangularis</i> MOJSIS., 1882		+		+		+		+			INV			
16 - <i>T. dimidiatus</i> KITTL, 1903				+		+		+			+			
17 - <i>T. hybridus</i> KITTL, 1903				+		+		+			+			
18 - <i>T. repulsus</i> KITTL, 1903				+		+		+		+				
19 - <i>T. robustus</i> KITTL, 1903				+		+					+			
20 - <i>T. rotiformis</i> KITTL, 1903				+		+		+		+				
21 - <i>T. subillyricus</i> KITTL, 1903				+		+					+			
22 - <i>T. dinarus</i> MOJSISOVICS, 1882	+			+		+							+	
23 - <i>T. mercurii</i> MOJSISOVICS, 1882		+		+		+							+	
24 - <i>T. quenstedti</i> MOJSISOVICS, 1882		+		+		+							+	
25 - <i>T. seminudus</i> MOJSISOVICS, 1882		+		+		+							+	
26 - <i>T. angustus</i> KITTL, 1903				+		+							+	
27 - <i>T. distans</i> KITTL, 1903				+		+							+	
28 - <i>T. paucispinatus</i> KITTL, 1903				+		+							+	
29 - <i>T. undulatus</i> KITTL, 1903				+		+							+	
30 - <i>T. idrianus</i> (HAUER, 1865)		+		+		+								+
31 - <i>T. stachei</i> KITTL, 1903				+		+								+
32 - <i>T. carniolicus</i> MOJSIS., 1882		+		+			D		+					+
33 - <i>T. heterophanus</i> KITTL, 1903				+			D		+				+	
34 - <i>T. monoptychus</i> KITTL, 1903			TH				H		+					+
35 - <i>T. serratelobatus</i> KITTL, 1903				+			D		+					+

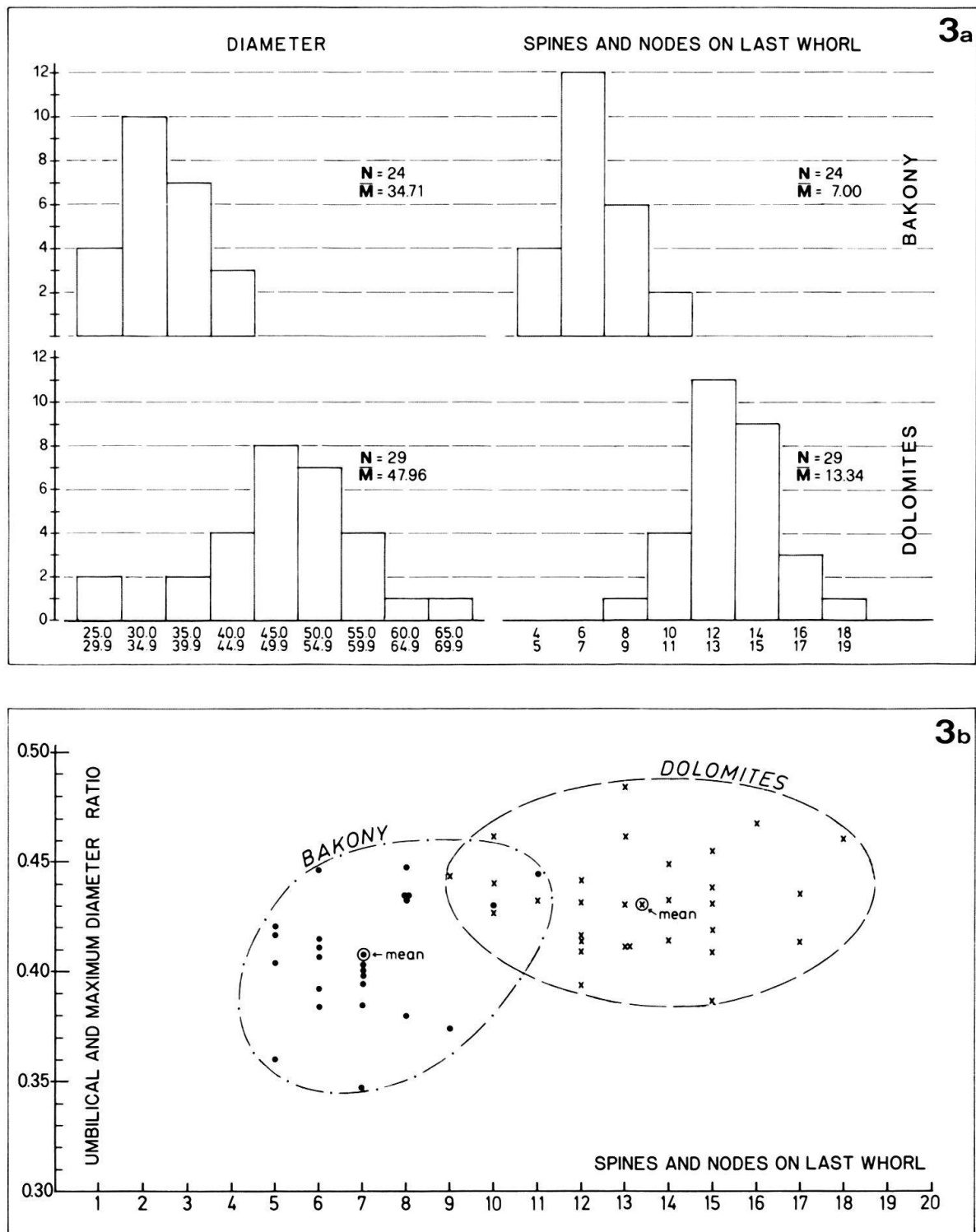


Fig. 3. Diagrams of comparison between Dolomite and Bakonian populations. 3a = Histograms of measurements of maximum diameter (left) and total amount of spines and/or nodes on the last whorl (right). 3b = Scatter diagrams of umbilical/maximum diameter ratio versus total amount of spines and/or nodes on last whorl.

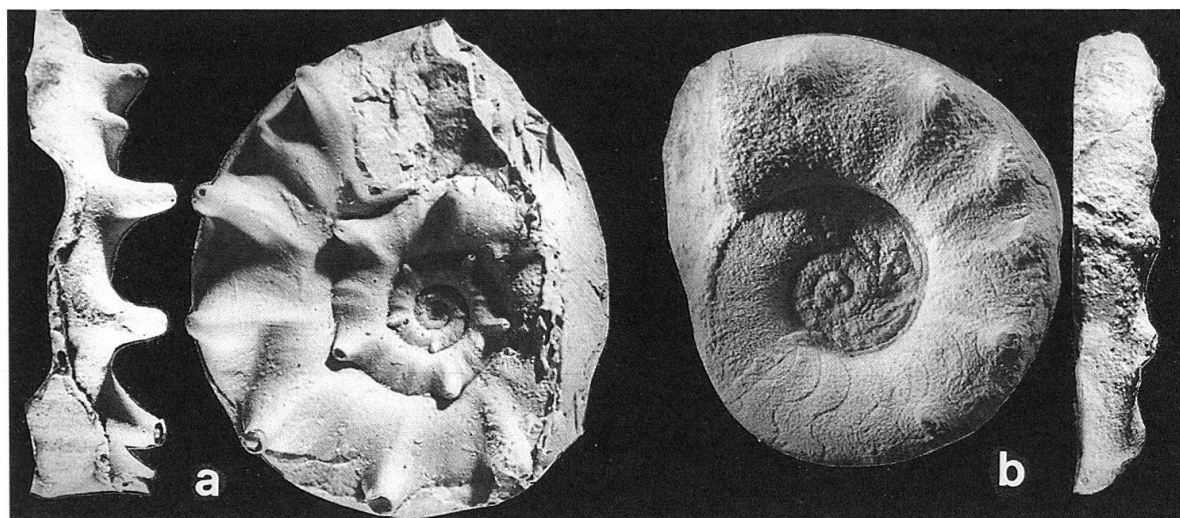


Fig. 4. Comparison between Tirolitids of similar size from Dolomites and Bakony. 4a = artificial mould of the external cast (specimen no. 19) from the Butterloch section, lower Val Badia Member (Werfen Formation, Dolomites). 4b = internal mould (specimen no. 45) from the Sóly section, lower unit (Csopak Marl Formation, Bakony) (all $\times 1.7$)

The tendency of increasing whorl height in the Bakonian specimens is accompanied by a slight increase in shell involution, as compared to the Dolomite specimens, which are wholly evolute.

The sample collected in the Dolomites has a number of nodes (9–18, mean 13.34) similar to the range of *T. cassianus* from Dalmatia (12–22, mean 16.3; Krystyn 1974).

Therefore, the Dolomites sample is characterized by: occurrence of spines on inner whorls, high number of spines/nodes on last whorl and wholly evolute shells. All these features permit to ascribed them to *T. cassianus*, according to the past geological literature (Tommasi 1895; Wittenburg 1908; Leonardi 1935; Broglio Loriga et al. 1983, etc.).

According to the Tirolitid evolution, the differences detected make it possible to ascertain that the Bakonian population is younger than the Dolomite one.

Of the series of graphics in Figure 3, the scatter diagram (Fig. 3b) which takes into account the main biometric features associated with the Tirolitid evolution, seems to be the better technique for separating the two samples. This result, however, does not allow the classification of the Bakonian Tirolitids. In fact, these have a number of nodes which is still high and a low involuted shell, when compared to the younger species of Tirolitids, such as *T. idrianus* or *T. carniolicus* sensu KRYSTYN (1974) or *T. seminudus* sensu KITTL (1903). As for these features, they have a closer affinity with *T. cassianus*, differing in the absence of sculpture on the inner whorls, the feature used by Mojsisovics (1882) to distinguish *seminudi* group from *spinosi* group.

Therefore, in order to classify the Hungarian specimens, a study needs to be made of the morpho-species that have been recorded in the literature, using the chosen statistical methodology.

4. Taxonomical revision of *Tirolites*

4.1. The genus *Tirolites*

The morphological species of *Tirolites* from the Alps and Dalmatia noted in the literature number more than 35. A number as large as this cannot possibly be in agreement with the modern concept of biological species. In fact, some authors have already attempt to group them, by applying the population concept (Kummel 1969; Krystyn 1974).

At the time when Mojsisovics (1882) published his work, 14 species were known, divided into the *seminudi* and *spinosi* groups (Tab. 1). Following this, Kittl (1903), using strictly morphological criteria, created 20 new species. In addition to the Mojsisovics' groups, he proposed the following, distinguished at the subgenus level (Tab. 2): *Hololobus* (1 species), *Svilajites* (2 species) and *Bittnerites* (3 species); all of which were later raised to the generic rank (Spath 1934, Kummel in Arkell et al. 1957).

None of the specimens examined belong to the last three groups, so these will not be dealt with this work. As regards *Hololobus monoptychus*, Krystyn's proposal (1974) to consider it as a younger synonym of *T. carniolicus* is accepted.

Kummel (1969) assigned Kittl's *spinosi* group, with the addition of *Ceratites* (*Paraceratites*) prior KITTL, to the single *T. cassianus* species; Kittl's *seminudi* group was assigned to *T. idrianus*, with some exceptions located in the "*Dinarites*" *carniolicus* (Tab. 1). As noted by Krystyn (1974), Kummel's revision was based on the Kittl's collection, which was collected without any stratigraphical references. Therefore, it cannot be considered as a homogeneous population.

Following this, stratigraphical research studies were carried out by Krystyn (1974) in the classical section of the Muć (Dalmatia). As a result of this work the vertical distribution of some Tirolitids was defined, and a collection was made of homogeneous populations from the lower (*T. cassianus* Zone) and upper (*T. carniolicus* Zone) parts of the sequence, the former of which was examined by means of biometrical analysis. The taxonomical conclusions are shown in Table 1. Unfortunately, some species of the *seminudi* group have not been considered, probably because of the lack of data in the middle part of the sequence.

More recent biostratigraphical work in the Muć sequence (Herak et al. 1983) led to the finding of *T. seminudus* (bed 066) in the middle part. However, this has not been followed up with a systematic meaning being given to this species. The presence of a further species between the two species recognized by Krystyn (1974) indicate the possibility of the intermediate evolutionary species occurring between *T. cassianus* and *T. carniolicus*, which explains their preservation.

4.2. From the morphological to the population concept of species. –

The Kittl collection

As has been recorded formerly, the splitting of the *Tirolites* at species level, is due to the following causes:

- plastic deformation of the moulds, either laterally (e.g. *T. rectangularis*) or dorso-ventrally (e.g. *T. turgidus*)

Table 2. Groups and subgenera of *Tirolites* used by Kittl (1903), and results of Kummel's taxonomical revision (1969).

KITTL 1903		KUMMEL 1969	
1-	"GRUPPE DER SEMINUDI"	<i>Tirolites idrianus</i>	<i>Dinarites carniolicus</i>
2-	"GRUPPE DER SPINOSI"	<i>Tirolites cassianus</i>	
3-	SUBGENUS <i>Hololobus</i> (<i>H.monoptychus</i>)	<i>Hololobus monoptychus</i>	
4-	SUBGENUS <i>Svilajites</i> (<i>S.cingulatus</i>) (<i>S.tietzei</i>)	<i>Tirolites cingulatus</i>	<i>Tirolites cassianus</i>
5-	SUBGENUS <i>Bittnerites</i> (<i>B.bittneri</i>) (<i>B.malici</i>) (<i>B.telleri</i>)	<i>Bittnerites bittneri</i>	" "

- the dissolution of the internal moulds with sculpture simplification and pseudo-sutures (e.g. *H. monoptychus*; see Krystyn 1974)
- intraspecific variability
- evolution changes

Naturally, all the species created on the basis of the first two taphonomic factors must be invalidated. In fossil populations, intraspecific variability is not easily recognizable and the results of taxonomical revision are substantially subjective.

The Kittl collection, taken mostly from Muć and kept in the Wien Natural History Museum, consists of several hundred specimens of *Tirolites*, including the Kittl species types, the plesiotypes of Mojsisovics's species and species from other authors, as designed by Kummel (1969). This made it possible to measure more than 400 specimens from the 35 species under consideration (appendix, Tab. 2).

The means of the measurements for each species (total amount of spines and/or nodes on the last whorl and umbilical/maximum diameter ratio) have been plotted on two scatter diagrams (Fig. 5a, b). In the first diagram (Fig. 5a), only the figured types of Kittl are included, and in the second (Fig. 5b), all the specimens, both figured and non-figured, have been considered. In both diagrams, the species can be grouped into five areas.

Area I includes species belonging to the *spinosi* group of Kittl, with node number means ranging from 10 to 18 (Fig. 5b), considered as synonyms of *T. cassianus* by Kummel (1969) and Krystyn (1974). The Dolomite population is located within area I (Fig. 5c). This confirms the classification of the population from the lower Val Badia Member as *T. cassianus*.

Some species, such as *T. kernerii* (8), *T. prior* (11) and *T. rectangularis* (15), are located in Figure 5a between areas I and II. Kittl's specimens of the last species have number of node means ranging from 4 to 14. It is likely, therefore, that specimens such as these come from different stratigraphical levels. The distinctive features of this taxon, mostly based on the whorl section, are strongly controlled by compaction, so that *T. rect-*

Table 3. Some statistical parameters of examined samples. Symbols: SN-total amount of spines and/or nodes on last whorl, U/D-umbilical and maximum diameter ratio. For measurements see appendix Table 1.

	DOLOMITES (N=29)		BAKONY (N=24)		MUC 42-45B (N=24)	
	SN	U/D	SN	U/D	SN	U/D
mean	13.34	431.41	7.00	406.00	14.58	421.08
standard deviation	2.26	22.65	1.56	27.85	4.01	28.98
standard error	0.42	4.21	0.32	5.68	0.82	5.92
median	13.00	431.00	7.00	405.50	14.00	419.50
min. value	9.00	387.00	5.00	349.00	9.00	365.00
max. "	18.00	484.00	11.00	447.00	25.00	479.00

angularis must be invalidated. *T. kernerii* can be considered as synonymous with *T. cassianus*, as the mean of the whole collection falls within area I (Fig. 5b).

T. prior (11) is separated from the two areas in both the diagrams. This species, classified by Kittl (1903) as *Ceratites* (*Paraceratites*) *prior* is the genotype of *Tirolitoides* Spath 1934, characterized by nodes on the latero-ventral shoulder as well as on the umbilical side. A specimen with this feature has been found in the middle Val Badia Member, where Tirolitids are very rare. As this species is seen to have a high number of nodes in relation to the U/D ratio and a different, clearly detectable, ornamentation as compared to *Tirolites*, it is preferable to separate it at genus level, thus preserving the "Treatise" classification (Kummel in Arkell et al. 1957) to which it is assigned to the gen. *Tirolitoides*.

Area II yields some species of Kittl's *seminudi* group, considered by Krystyn (1974) as being synonyms of *T. cassianus* (1). They have node number means ranging from 6 to 9 (Fig. 5b). This area is not clearly distinguishable from area III, especially in Figure 5b, so they could be joined together. The Hungarian population, however, as regards the number of nodes, falls within the area (Fig. 5c). As the Bakonian Tirolitids are yielded in a fossil assemblage with a different age to the Dolomites Tirolitids, it has been preferred to separate them into a specific level. The area II species are considered synonyms of *T. illyricus* (14), the older species of the group, and well represented in the Kittl collection in terms of number of specimens.

The area III species have a U/D ratio similar to area II, but differs in the means of node number, ranging from 2 to 6 (Fig. 5b). The species yielded in this area are considered synonyms of *T. seminudus* (25), the older and better represented species, in terms of number of specimens, in the group. Furthermore, it has been noted in the Muć section from the bed 066, located above the *T. cassianus* beds (Herak et al. 1983) (Fig. 5c).

The last two areas have only 3 species each, with very few specimens in the collection. The lack of Tirolitids from the Dolomites and Bakony, from these groups, and the scarcity of material in the Kittl collection make it impossible to define their variability. At present, it is better to separate *T. idrianus* (area IV) from *T. carniolicus* (area V). The latter species is characterized by more involute shell with only a few spines (1–3), limited to the body chamber. On the basis of these characters, *T. heterophanus* (33) can be considered as synonymous of *T. idrianus* (30), as the holotype is seen to have nodes on the inner whorl and a U/D ratio closely related to *T. idrianus*.

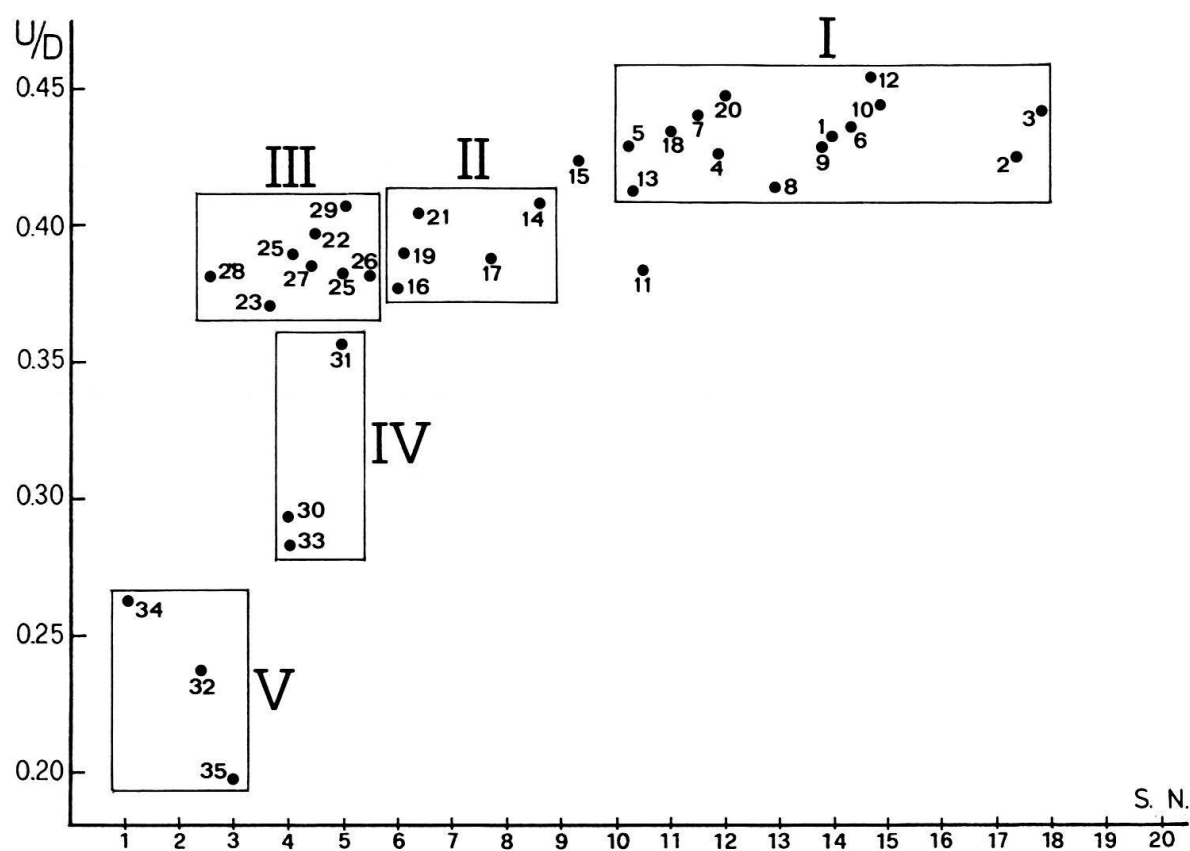
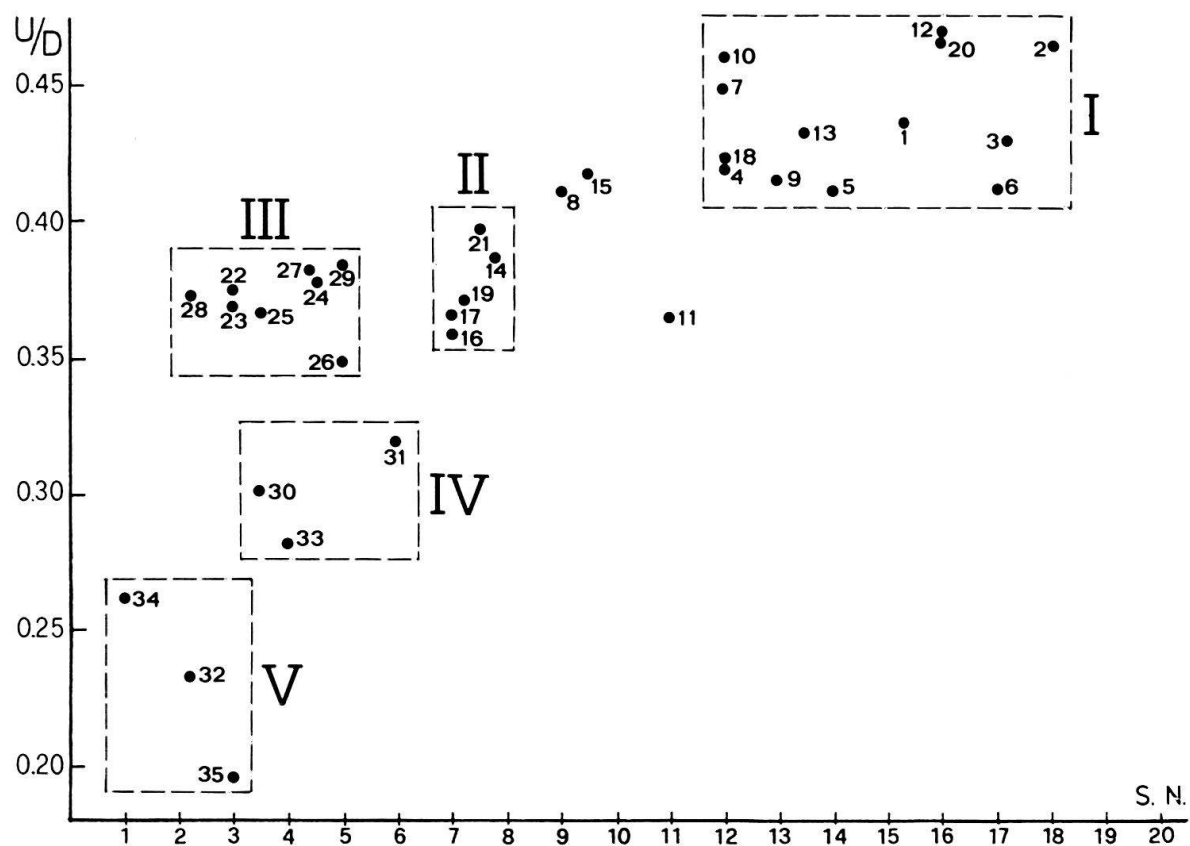


Fig. 5a (top) and 5b (bottom).

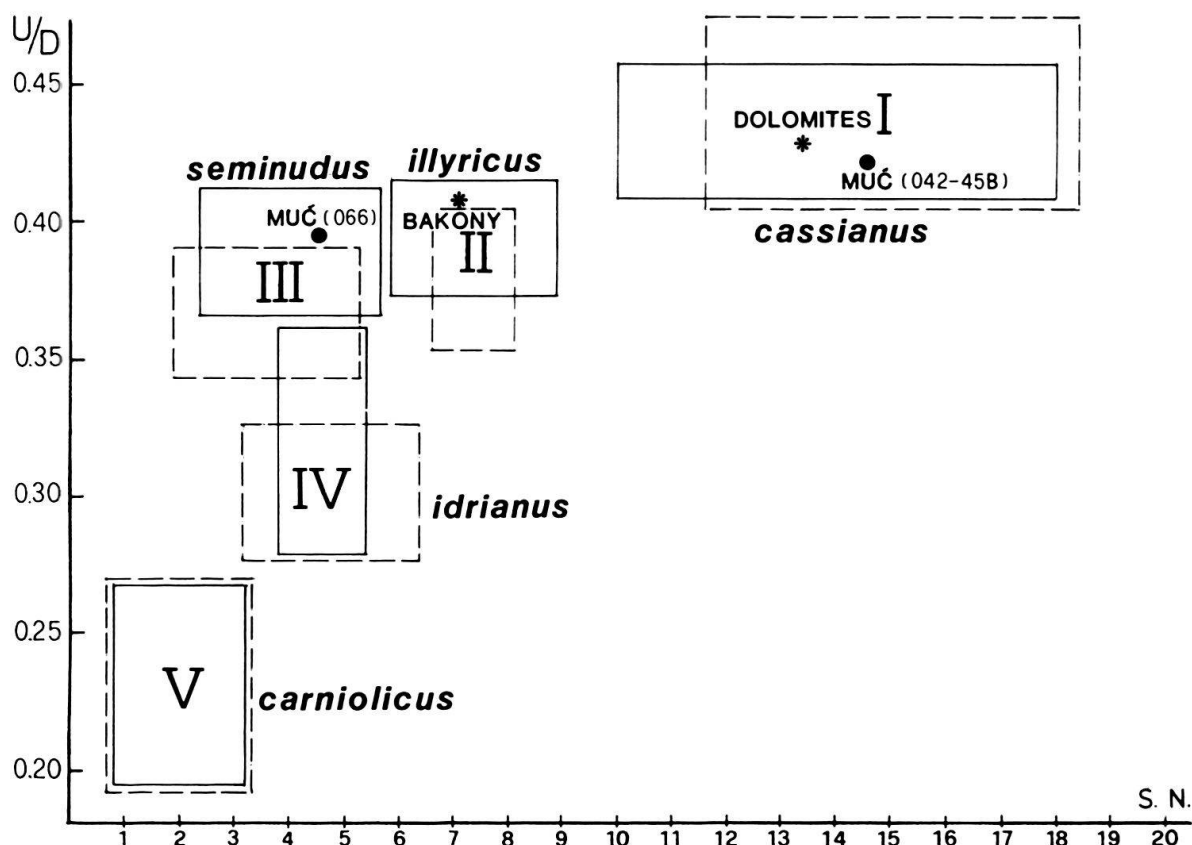


Fig. 5c. Scatter diagrams regarding: 5a = means of figured types of Kittl's collection, 5b = means of figured and not figured specimens of Kittl's collection, 5c = means of populations coming from Dalmatia (Muć), Dolomites and Bakony (Sóly). Numbers of the morpho-species as Table 1.

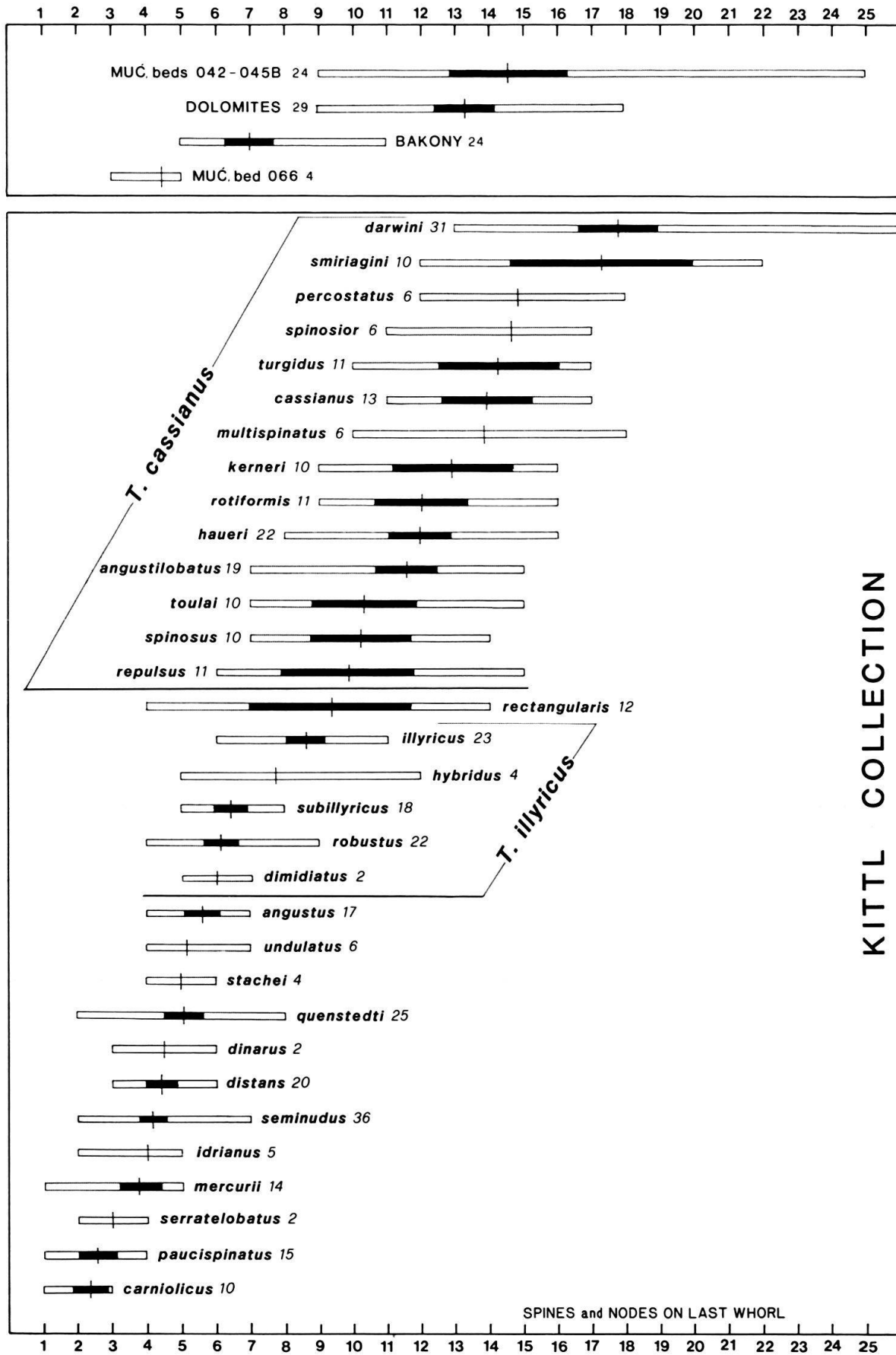
The graph of Figure 6, concerning the range and confidence limits of spines/nodes on last whorl, permits to distinguish *T. cassianus* from *T. illyricus*, that is species with evolute or feebly involute shells. However, it does not allow a good distinction between *seminudus*, *idrianus* and *carniolicus* population-species. In these last three species the degree of involution, in some extent represented by U/D ratio, must be also considered (see Fig. 5).

According to the methodology used, the Hungarian population can be assigned, at a specific level, to *T. illyricus*. As this species has never yet been noted, apart from in Dalmatia originating from an unknown stratigraphical level, it needs to be established whether it can be recognized in the Muć sequence, and where it is settled.

4.3. From the population to the evolutionary species. – The Herak et alii collection.

This collection was made during the course of a biostratigraphical survey in the Muć section (Herak et al. 1983), and is kept in the Zagreb Natural History Museum. It should be noted that the specimens are not adequately prepared, so the measurements, especially the umbilical diameter, must be considered with care.

To obtain a significant sample, from the statistical point of view, the specimens collected in bed 042 to 045 B (Fig. 7) have been combined. The mean of node number of this population falls within the *T. cassianus* variability range, even though it is



slightly higher than the Dolomite number (Fig. 5c, 6). This depends on the specimens coming from beds 044–045 B, which are characterized by a high number of nodes and ribs. Considering the morphological concept of species, they could be classified with *T. darwini* which has the largest number of ribs of all *Tirolites* species.

A few, badly preserved Tirolitids are available between beds 045 B and 065, which were classified by Herak et al. (1983) as *T. cassianus* (beds 046–063) or *T. cassianus* – *T. seminudus* transitional forms (bed 065). The specimens which occurred in the beds 046 and 059 can be assigned to *T. cassianus*. Those from beds 061 to 065 have node numbers ranging from 5 to 7, whilst other have a higher number of ribs on the body chamber. On the whole, these Tirolitids can be regarded as belonging to *T. illyricus*.

The bed 066 sample (4 specimens) falls within the *T. seminudus* variability range (Fig. 5c, 6), thus confirming the classification given by Herak et al. (1983).

The following findings are recorded as coming from bed 072, with the appearance of *T. carniolicus*, which also occurs in beds 075 and 079. The low number of specimens (1 for each bed) does not allow them to link them phylogenetically with *T. seminudus* and population variability.

This collection, therefore, seems to confirm the phylogenetic trend of *Tirolites*, from *cassianus* to *seminudus*, with an intermediate evolutionary species represented by *T. illyricus*. It does not, however, make it possible to ascertain the evolutionary relationships between *seminudus* and *carniolicus* via *idrianus*, due to the lack of available specimens ascribed to the latter species. These relationships can only be presumed on the basis of *idrianus*–*carniolicus* transitional forms, which would have preceded the appearance of *carniolicus* (Krystyn 1974).

5. Biostratigraphy

In the “Werfen beds” (Northern Italy, Austria, Hungary and Dalmatia) the ammonoid bearing layers are bounded by two sedimentary events, known as the “Campil event” (Broglia Loriga et al. 1990) at the base, and the “Dolomite event” at the top (Krystyn 1974). In this interval, the occurrence of ammonoids is strongly controlled by the environmental and tectonic evolution of the different basins. In some area (e.g. Dolomites, Bakony), peritidal events did not allow a continuous, permanent presence of ammonoids. Therefore, because of the fragmentary nature of the ammonoid events, a biozonation based on benthic markers has been used (Broglia Loriga et al. 1983, 1990).

At present, the more complete ammonoid sequence of the upper “Werfen beds” in Europe has been noted only in Dalmatia. On the basis of data acquired in the Dolomites (Broglia Loriga et al. 1983, 1986), Bakony (Broglia Loriga et al. 1990) and Dalmatia (Herak et al. 1983), it is possible to test a correlation between the *Tirolites* events and benthic biozonation.

Fig. 6. Range of spines and/or nodes on last whorl and confidence limits (at 0.975%) of mean for samples with more than 9 specimens.

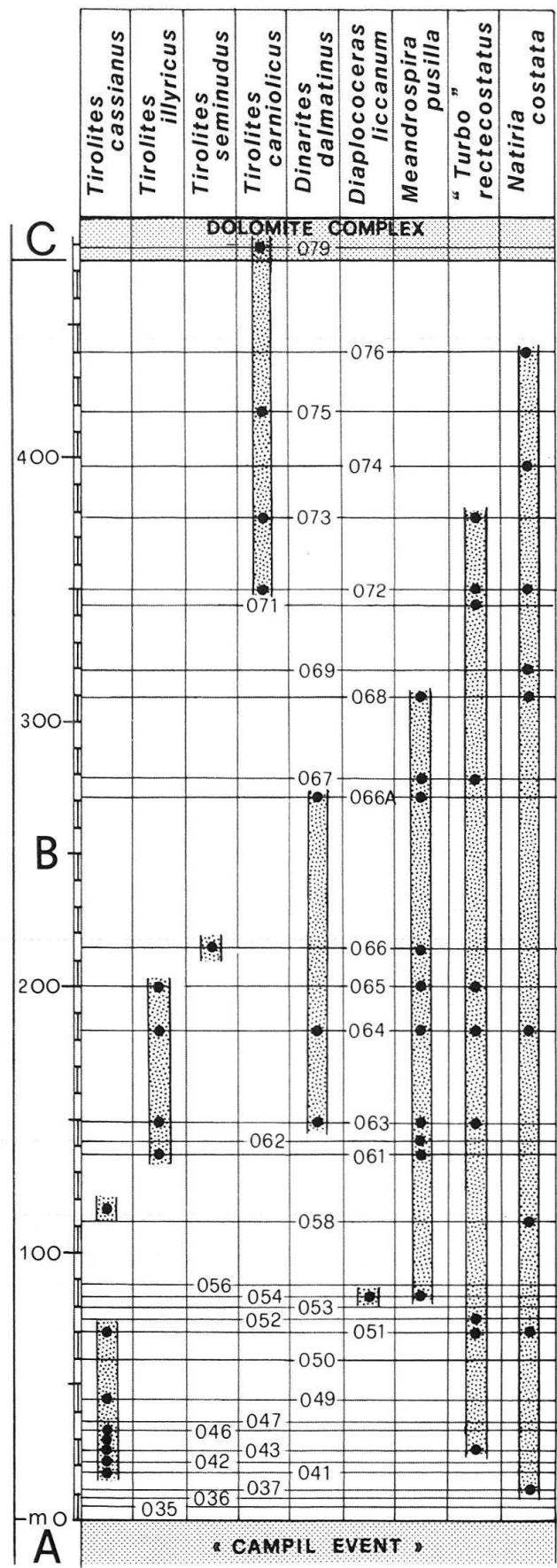


Fig. 7. Vertical distribution of molluscs and forams at Muć, Dalmatia (from Herak et al. 1983, modified).

Tirolites cassianus beds

The occurrence of this unit is well documented in the Dolomites (Fig. 8). It corresponds to the lower part of the Val Badia Member, belonging to *Eumorphotis kittli* subzone. At present, it is not possible to demarcate its upper boundary, as Tirolitids became very rare from the middle part of the Member (*Diaplococeras* beds). This means that they cannot be classified with biometrical methods.

In Dalmatia the unit definitely corresponds to beds 042–052, which underlie *Diaplococeras* (bed 053), this last coinciding with the appearance of *Meandrospira pusilla*. Also in this area, for the reason given above, it is not possible to define the upper boundary. Further studies are needed to detect the occurrence and distribution of *T. cassianus* above *Diaplococeras* beds.

T. cassianus beds have not been found in the Balaton Highland. They can probably be correlated to the lower part of Unit A of Csopak Marl, yielding a fauna dominated by Lingulids, noted only in boreholes.

Tirolites illyricus beds

In the Balaton Highland, this unit is represented by the uppermost part of unit A and the lower part of unit B of Csopak Marl. They yield a rich benthic fauna characterized by *Eumorphotis telleri* with the appearance of *Costatoria costata* and *Dalmatites morlaccus*.

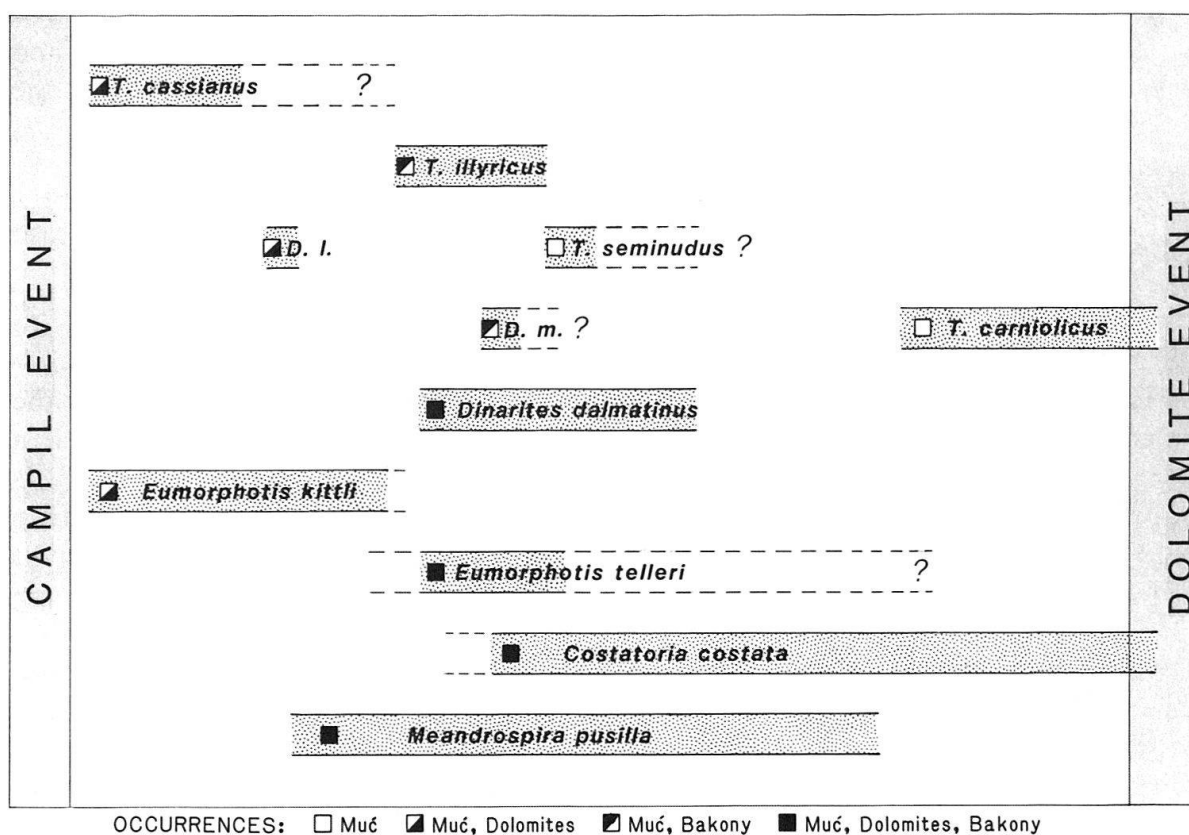


Fig. 8. Tentative correlation between the ammonoid events and benthic markers in the European Late Scythian sequences. Abbreviations: D.l.-*Diaplococeras liccanum*; D.m.-*Dalmatites morlaccus*.

In Dalmatia, this can be correlated to the middle part of *M. pusilla* beds (beds 061 to 065), in which the appearance of *Dinarites dalmatinus* is worthy of note.

In the Dolomites, this event has not been recorded since the disappearance of Tirolitids. On the basis of benthic markers (*E. telleri*, *M. pusilla*) and ammonoids (*D. dalmatinus*), the *D. dalmatinus* beds of the lower Cencenighe Member (*E. telleri* sub-zone) can be correlated to *T. illyricus* beds. The disappearance of *Tirolites* from the Dolomites seems to have been caused by a local environmental change, rather than by chronological factors.

Tirolites seminudus beds and *Tirolites idrianus* beds

Up to present, a *seminudus* bed has only been noted in Dalmatia (bed 066). Its punctuated occurrence makes it impossible to establish either its vertical range or a precise correlation with other localities.

As regards *T. idrianus* beds, their presence has only been presumed, on the basis of Krystyn's work, but no stratigraphical data on their position in the Herak et alii column is available. The Muć sequence, located between beds 066 (*T. seminudus* bed) and 072 (*T. carniolicus* bed) is about 130 m thick. It mostly corresponds to the upper part of *M. pusilla* beds. In this way, the upper parts of the Cencenighe Member and Unit B of Csopak Marl and the lowermost parts of the San Lucano Member and Unit C of Csopak Marl could be correlated to these units.

Tirolites carniolicus beds

These have only been recorded in the upper Muć sequence, between beds 072 and 079, in which *M. pusilla* and *D. dalmatinus* have already disappeared. Therefore, the Dolomite and Bakonian sequences located between the Dolomite unit and *M. pusilla* beds can be roughly correlated to *T. carniolicus* beds.

6. Conclusions

The comparison between Dolomite and Bakonian Tirolitids has made it possible to distinguish the two populations by means of both an elementary statistical methodology and a classical morphological approach, such as the occurrence of nodes on the inner whorls and shell involution. The results seem to bear out the distinction at a specific level.

The benthic associated markers prove that the Dolomite Tirolitids (*T. cassianus*) are older than the Bakonian ones (*T. illyricus*). In this way, these species, on the basis of the population concept, can also be regarded as evolutionary species, which represent the first two stages of *Tirolites* phylogenetic trend.

Correlation between Krystyn's biozonation and the proposed *Tirolites* beds is not possible, since the limit between *T. cassianus* Zone and *T. carniolicus* Zone was not defined.

The early disappearance of Tirolitids, both from the Dolomites and Bakony, does not allow the verification of the last stages of Tirolitid evolution, as displayed in the Dalmatian sequence. The proposal of Herak et al. (1983), therefore, to consider the Muć profile as a standard section for the Late Scythian of the Werfen beds is approved.

In the light of this, new biostratigraphical studies need to be made in the Dalmatia sequence to establish the vertical range of some benthic markers, such as *Eumorphotis* and *Costatoria*, which will be useful in forming correlations with other ammonoid-free sequences and in clarifying the phylogenetic relationships among the younger stages of the Tirolitid evolution.

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Measurements of *Tirolites* specimens from Dolomites, Bakony and Dalmatia. D = maximum diameter, U = umbilical diameter, HM = maximum whorl height, W = whorl width, SN = total amount of spines and/or nodes on the last whorl.

Dolomites (Italy)							Muć (Dalmatia) HERAK et al. (1983) collection					
no.	D	U	HM	W	SN	U/D	bed	D	U	HM	SN	U/D
COL VERCIN							042	39.9	16.0?	-	10	.401
2	55.2	24.3	17.2	14.0	10	.440	"	48.3	20.8?	14.7?	14	.430
5	49.5	19.2	18.0?	9.9	15	.387	"	39.0	16.4?	13.0?	11?	.420
6	63.4	27.3	21.4	22.6	15?	.430	"	36.5	15.0?	12.0?	9?	.410
9	47.6	19.5	17.6	13.0	15?	.409	"	38.0	16.0	12.5	9	.421
10	40.9	17.7	14.5	8.1	11	.432	"	37.7	15.1	15.3	13	.400
15	48.6	20.9?	15.4	14.7	13	.430	"	44.3	18.9	14.8	12?	.426
17	65.0	26.9	22.5	13.9	17?	.413	"	46.3	19.8?	-	14?	.427
							"	41.0	18.8?	-	11?	.458
VAL BADIA (S.S.244)							044	61.5	29.5?	20.0?	25	.479
22	51.3	23.7?	16.2	15.2	13	.461	"	41.4	17.3	13.0	21	.417
24	52.0	23.7	17.8	13.7	15	.455						
25	46.2	21.6	15.2	12.4	16?	.467						
46	56.7	24.7	19.6	13.8	17?	.435	045A	48.5	19.8	18.8	14	.408
50	49.3	22.7	15.7	10.0	18	.460	"	47.5	21.4	14.4	22	.450
51	54.2	22.2	20.0?	14.5	12	.409	"	31.3	13.9	-	15	.444
							"	42.5	18.8	16.0	18?	.442
GRONES							"	44.4	18.5?	14.0?	14	.416
29	45.1	20.8	14.1	13.6	10	.461	"	33.5	15.8	10.5	18	.471
32	50.5	20.8	18.1	10.5?	13	.411						
34	50.1	20.6	16.6	13.3	13?	.411	045B	35.2	14.5?	11.4	13	.411
35	40.8	18.0	14.4	7.0?	12	.441	"	49.0	22.0?	18.5?	15	.448
47	55.5	24.0	19.5	18.2	14	.432	"	45.2	16.5	15.5	11	.365
48	46.6	22.6	14.0	13.6	13?	.484	"	40.5	15.0	13.5	14	.370
49	52.0	21.8	17.6	16.0	15?	.419	"	51.2	19.9	16.9	17	.388
55	41.5	17.2	14.1	7.2	12	.414	"	41.5	17.4	12.3	15	.419
57	27.1	12.0	8.3	6.7	9	.442	"	47.7	18.4	15.7	15	.385
58	35.9	15.5	10.9?	10.3	12	.431						
59	48.8	21.9	17.4	9.2	14	.448	046	40.5?	15.0	13.7	13	.370
60	38.0	15.8	13.3	9.1	12	.415						
COSTABELLA							066	42.7	18.6	13.5	5	.435
27	52.0	20.5	18.3	10.6	12	.394	"	33.2	11.8?	12.0?	3	.355
70	56.9	23.6	19.1	13.5	14?	.414	"	33.4	12.4?	12.4	5?	.371
							"	41.0?	17.5	14.6?	5	.426
MOENA							072	60.0	19.3	22.9?	1	.321
45	42.0	18.4	15.0	-	15?	.438						
BUTTERLOCH							073	57.0	15.4?	23.5	2	.270
19	28.0	12.0	9.0	-	10	.428	"	45.0	11.5	19.7	2	.255
							079	61.0	15.2?	25.4	3	.249

Söly (Bakony, Hungary)

bed	no.	D	U	HM	Hm	W	SN	U/D
2	24	29.8	11.9	9.9	8.8	7.8	7?	.399
"	22	33.9?	14.6	11.2	10.0	8.7	10	.430
3	2	41.6	18.5	14.0	-	-	6?	.447
"	3	28.5	11.2	10.5	-	-	6?	.392
4-5	8	32.2	14.3	10.4	-	6.8?	11?	.444
6	21	34.1	14.2	11.1	-	6.3	6?	.416
"	16	37.8	15.8	12.2	-	10.1	5	.417
"	7	37.2	16.2	12.9	-	10.1	8	.435
9-10	5	34.6	12.1	13.5	-	10.0	7?	.349
"	45	28.4	11.7	9.6	-	8.5	6	.411
"	12	31.7	13.8	10.2	-	7.3	8	.435
"	6	35.2	12.7?	12.7	-	6.4	5?	.360
11-12	19	37.4	14.0?	12.8?	-	8.5	9?	.374
12	10	29.4	11.9	10.0	8.7	7.7	5	.404
"	14	34.0	13.1	11.6	-	8.3	7?	.385
12-13	23	36.0?	13.7	13.0	-	7.3	8	.380
"	25	34.3	13.2	12.0	10.4	9.4	6	.384
"	20	35.5	14.2	12.6	-	8.5	7?	.400
"	29	41.5	16.7	14.2	-	8.7	7	.402
PR2	43	44.7	19.4	15.8	-	11.0	8	.434
15-16	33	30.7	11.4	10.5	-	5.2	7	.371
16	17	32.4	13.2	10.8	-	8.6	6?	.407
"	4	38.0	17.0	11.8	-	10.3	8?	.447
"	9	34.2	14.4	12.0	-	9.7	5?	.421

1	6-12	45.6	18.6	17.3	5	.407
2	6-13	40.3	14.8	18.5	4	.367
3	6-14	44.6	17.5?	15.5	6	.392
4	6-15	37.4	14.6?	14.0	4	.390
5	6-16	37.5	15.0	12.9	3?	.400
6	7-7	38.7	13.9	16.0	5	.359
7	7-8	46.6	17.0	19.1	4	.364
					-4.4	-.382
8	nf	43.0	17.0	14.8	3	.395
9	nf	35.2	13.9	13.0	5	.394
10	nf	36.0	13.8?	14.1?	4	.383
11	nf	41.8	15.1	16.1	3?	.361
12	nf	41.4	14.6	16.0	4	.352

13	nf	36.3	13.5	12.7	5	.371
14	nf	37.7	13.2	13.4	5	.350
15	nf	34.4	14.1	12.5	6?	.409
16	nf	35.7	13.8	11.8	5	.386
17	nf	40.5	16.4	15.2	4	.404
18	nf	40.2	16.6	13.5	3	.412
19	nf	34.8	13.6	11.7	5	.390
20	nf	44.2	17.5	13.1	5	.395
					4.4	.384

Tirolites haueri MOJSISOVICS 1882

1	9-8	49.3	22.8	15.5	16	.462
2	9-9	56.7	22.9	20.0	12	.403
3	9-10	59.3	24.5	20.3	10?	.413
4	9-11	47.0	19.5	16.8	10	.414
5	9-12	50.0	20.6	18.1	12	.412
6	9-13	51.0	23.0	16.5	13	.450
7	10-1	46.0	18.0?	17.8	12	.391
8	10-2	39.0	17.0	13.9	8	.435
9	10-3	45.1	18.3	16.0	15	.405
					--12.0	-.420
10	nf	46.8	19.8	15.8	12	.423
11	nf	56.0	24.3?	20.0	12	.433
12	nf	49.4	20.6	17.0	13	.417
13	nf	47.2	19.1?	15.9	10	.404
14	nf	46.0	19.8	15.2	12	.430
15	nf	41.2	17.9	13.5	8	.434
16	nf	49.1	22.9	15.5	10	.466
17	nf	51.9	21.5	16.8	11	.414
18	nf	55.6	26.5?	18.5	13	.476
19	nf	49.9	20.7	18.0	14	.414
20	nf	46.8	19.5?	17.0	12	.416
21	nf	54.9	24.2	18.3	13	.440
22	nf	51.3	22.2	22.5	15	.432
					11.9	.426

Tirolites heterophanus KITTL 1903

1	5-7	56.3	15.9	23.6	4	.282
					-4	-.282

Tirolites hybridus KITTL 1903

1	8-2	53.0	19.5	20.5	7	.367
					-7	-.367
2	nf	54.0	19.5	19.8	5?	.361
3	nf	39.0	16.0	14.5	7	.410
4	nf	65.5	27.3	23.6	12	.416
					7.7	.388

Tirolites idrianus (HAUER 1865)

1	1-1*	68.0	20.0	30.0	5	.294
2	5-8	58.4	18.0	24.3	2	.308
					-3.5	-.301
3	nf	66.0	19.8	27.3	5?	.300
4	nf	53.8	16.4	23.0	5	.304
5	nf	61.5	16.2	23.3	3	.263
					4	.293

Tirolites illyricus MOJSISOVICS 1882

1	8-3	45.6	17.6	16.0	6	.385
2	8-4	49.0	19.5	17.0	7	.397
3	8-6	38.4	14.4	13.4	9	.375
4	8-7	41.0	15.3	16.0	8	.373
5	8-8	44.2	16.3	16.0	8	.368
6	8-9	36.0	15.3	12.9	9	.425
					-7.8	-.387
7	nf	34.3	14.8	10.7	10	.431
8	nf	39.5	16.4	13.8	9	.415
9	nf	40.5	16.4	15.0	7	.404
10	nf	42.3	16.9	16.3	10	.399
11	nf	40.5	15.3	14.0	11	.377
12	nf	40.4	17.5	14.0	10	.433

13	nf	40.5	18.2	13.3	8	.449
14	nf	42.9	17.4	15.7	8	.405
15	nf	45.5	18.2	16.0	8	.400
16	nf	44.0	17.0	15.5	8	.386
17	nf	40.8	16.9	14.3	10	.414
18	nf	34.0	15.4	10.5	9	.452
19	nf	39.6	15.7?	14.5?	6?	.396
20	nf	40.3	17.3?	14.1	9?	.429
21	nf	30.0	12.3	9.5	10	.410
22	nf	36.0	15.8	11.6	10	.438
23	nf	34.6	13.9	12.4	8	.401
					8.6	.407

Tirolites kernerii KITTL 1903

1	11-8	49.6	20.4	17.3	9	.411
					-9	-.411
2	nf	52.0	19.6	19.7	13	.376
3	nf	43.0	17.7	15.5	11?	.411
4	nf	57.5	26.0	17.4	13?	.452
5	nf	45.2	18.9	15.5	15	.418
6	nf	52.5	20.9	18.0	16	.398
7	nf	57.7	21.4	16.3	10	.370
8	nf	37.2	16.4	11.5	14	.440
9	nf	38.0	16.0?	11.5	12	.421
10	nf	40.0	18.0	12.5	16	.450
					12.9	.414

Tirolites mercurii MOJSISOVICS 1882

1	5-10	45.1	15.5?	18.0	4	.343
2	5-11	46.9	16.9?	17.1	4	.360
3	6-2	56.4	23.0	19.2	1	.407
					-3	-.370
4	nf	52.0	20.9	18.1	3	.401
5	nf	35.7	13.9	13.5	4	.389
6	nf	33.5	13.8?	11.5?	3	.411
7	nf	52.0	19.0	19.0	5	.365
8	nf	39.7	15.4	15.0	5	.387
9	nf	38.3	12.6	15.0	4	.328
10	nf	44.0	15.8	15.5	5	.359
11	nf	39.0	14.1	14.4	4	.361
12	nf	35.8	12.8	14.0	4?	.357
13	nf	37.4	13.8?	14.7	4	.368
14	nf	43.1	15.2	15.8	3	.352
					3.7	.370

Tirolites monoptychus KITTL 1903

1	4-9	62.2	16.3	25.4	1	.262
					1	.262

Tirolites multispinatus KITTL 1903

1	11-9	54.4	22.7	19.4	13?	.417
					--13	-.417
2	nf	37.0	14.8	13.2	10	.400
3	nf	40.2	17.1	12.8	12	.425
4	nf	44.7	20.0?	-	18	.447
5	nf	53.0	23.0	18.0	15	.433
6	nf	38.0	17.2	12.7	15	.452
					13.8	.429

Tirolites paucispinatus KITTL 1903

1	6-11	41.4	14.8	15.8	3	.357
2	7-4	41.5	15.3	15.3	2	.368
3	7-5	39.0	14.3	17.0	3	.366
4	7-6	41.9	16.9	14.7	1	.403
					-2.2	-.373
5	nf	44.1	15.4	19.0	4	.349
6	nf	45.0	17.2	17.0	2?	.382
7	nf	37.1	14.5	13.5	1	.390
8	nf	43.6	16.6	16.0	2	.380
9	nf	32.0	13.6	11.5	3?	.425
10	nf	38.3	15.0	13.5	2?	.391

11	nf	36.8	14.0	12.1	2	.380
12	nf	36.0	13.7	12.4	4	.380
13	nf	41.0	15.2	15.3	3	.370
14	nf	35.9	13.4	12.7	3	.373
15	nf	36.0	14.8	11.9	4	.411
				2.6		.381

Tirolites percostatus KITTL 1903

1	10-6	47.2	21.8	15.0	12	.461
					--12	--.461
2	nf	45.0	21.7	14.7	18	.482
3	nf	55.9	23.4	24.1	15	.418
4	nf	56.5	24.8?	17.5?	15?	.438
5	nf	48.3	21.8	17.0	14	.451
6	nf	54.0	23.0?	-	15	.425
				14.8		.445

Tirolitoides prior (KITTL 1903)

1	11-3	54.6	20.0	21.0	11?	.366
					--11	--.366
2	nf	61.3	22.2	23.3	9?	.362
3	nf	50.7	19.8	18.2	9	.390
4	nf	26.0	10.8	-	13	.415
					10.5	.383

Tirolites quenstedti MOJSISOVICS 1882

1	6-19	50.5	19.1	17.6	5	.378
2	6-20	47.3	18.0	17.9	4	.380
					-4.5	--.379
3	nf	48.5	19.4	17.6	4	.400
4	nf	44.5	16.8	18.0	4	.377
5	nf	37.8	14.0	14.4	6	.370
6	nf	37.0?	14.4	14.5	6	.389
7	nf	44.9	15.7	17.1	5	.349
8	nf	45.6	17.6	18.0	6	.385
9	nf	44.0	15.6	18.3	5	.354
10	nf	33.0	13.0	12.0	6	.393
11	nf	38.2	16.2	12.8	7	.424
12	nf	32.6	12.5	12.0	8	.383
13	nf	39.2	13.1	15.0	6	.334
14	nf	44.8	18.8	16.4	4	.419
15	nf	39.5	13.5	17.0	5	.341
16	nf	35.3	14.1	12.3	5	.399
17	nf	55.4	22.9	21.0	2	.413
18	nf	46.4	18.2	17.0	6	.392
19	nf	37.0	14.0	15.0	6?	.378
20	nf	24.5	10.4	7.7	4	.424
21	nf	60.5	21.4	22.2	3?	.353
22	nf	57.5	21.5	21.0	6	.373
23	nf	54.5	20.8	20.0	3	.381
24	nf	46.5	18.5	15.6	5	.397
25	nf	42.3	15.5	15.0	5	.366
					5.0	.382

Tirolites rectangularis MOJSISOVICS 1882

1	8-16	44.4	19.0	19.1	11	.427
2	8-17	41.5	17.0	14.2	8	.409
					--9.5	--.418
3	nf	41.8	17.2	-	5	.411
4	nf	40.0	17.8	-	10	.445
5	nf	37.0	15.5	-	4	.418
6	nf	43.3	16.7	-	7?	.385
7	nf	42.1	18.3	13.8	4	.436
8	nf	41.6	17.0	14.4	13	.408
9	nf	48.2	20.0	17.4	10	.414
10	nf	58.0	26.0?	19.0	14	.448
11	nf	39.0	18.0	12.0	14?	.461
12	nf	37.0	16.0	11.0	12	.432
					9.3	.424

Tirolites repulsus KITTL 1903

1	8-5	42.7	16.2	15.9	11	.379
2	8-10	38.6	16.2	13.3	15	.419
3	8-11	43.1	18.7	14.9	13	.433
4	8-14	28.0	12.9	9.0	9	.460
					--12	--.422
5	nf	27.6	12.3	9.0	12	.445
6	nf	35.2	15.0	12.0	11	.426
7	nf	34.6	16.5	11.5	7	.476
8	nf	34.2	14.9	11.3	10?	.435
					11.0	.434

Tirolites robustus KITTL 1903

1	7-9	42.6	14.2	17.4	7	.333
2	7-10	45.5	16.9	17.6	7	.371
3	7-11	35.5	13.7	12.8	9	.385
4	8-1	49.8	19.7	17.5	6	.395
					-7.2	--.37
5	nf	36.4	13.7	14.1	5	.376
6	nf	52.5	20.7	20.0	6	.394
7	nf	42.6	15.7	16.0	5	.368
8	nf	36.2	13.1	13.2	6?	.361
9	nf	42.3	15.1	15.7	6	.356
10	nf	39.5	16.0	14.0	6	.405
11	nf	56.3	22.4	19.7	7	.397
12	nf	44.6	18.1	16.4	7	.405
13	nf	40.0	16.7	13.0	6?	.417
14	nf	40.7	17.0	13.6	7	.417
15	nf	40.0	16.9	15.5	7	.422
16	nf	42.9	16.8	15.6	5	.391
17	nf	35.6	14.2	12.5	7	.398
18	nf	44.0	15.8	16.8	6	.359
19	nf	49.0	21.0	18.0	5	.428
20	nf	42.4	17.9	14.2	5	.422
21	nf	44.6	18.0	16.2	6	.403
22	nf	40.1	15.1	14.3	4	.376
					6.1	.389

Tirolites rotiformis KITTL 1903

1	8-12	44.2	21.8	13.6	-	.493
2	8-13	30.6	13.5	9.8	16	.441
					--16	--.441
3	nf	38.0	16.3?	13.0	14	.428
4	nf	35.0	15.3	11.7	11?	.437
5	nf	32.7	13.8	11.0	9?	.422
6	nf	35.7	16.8?	11.5	13	.470
7	nf	31.3	15.8	9.4	12	.504
8	nf	34.5	16.0	10.2	11	.463
9	nf	36.0	15.5	12.6	12	.430
1	nf	32.3	14.0	9.5	9	.433
1	nf	32.2	13.5	10.3	12	.419
12	nf	28.9	12.6	9.1	13	.435
					12	.447

Tirolites seminudus MOJSISOVICS 1882

1	6-3	50.0	19.7	18.4	2	.394
2	6-4	44.9	16.9	16.0	5	.376
3	6-5	40.3	14.3	15.9	2	.354
4	6-6	41.6	16.8	14.6	4	.403
5	6-7	43.3	15.8	14.7	2?	.364
6	6-8	43.3	16.2	17.0	4	.374
7	6-9	34.2	13.4	12.0	3	.391
8	6-10	29.8	11.3	10.7	4	.379
9	6-17	31.6	12.0	11.2	4?	.379
10	6-18	42.2	15.1	17.2	5	.357
					-3.5	--.36
11	nf	45.1	15.7	17.4	3	.348
12	nf	42.1	17.2	15.2	5	.408
13	nf	36.2	14.5	13.9	4	.400
14	nf	41.1	16.6	13.8	3?	.403

15	nf	36.8	15.4	12.5	5	.418
16	nf	38.9	14.8	14.6	6	.380
17	nf	36.3	14.0	13.1	5	.385
18	nf	34.5	13.2	12.2	6	.382
19	nf	56.5	23.0	20.5	3	.407
20	nf	46.0	18.5	16.4	3	.402
21	nf	37.0	15.5	13.3	4	.418
22	nf	36.4	12.3	16.0	5	.337
23	nf	41.3	15.5	15.5	5?	.375
24	nf	40.3	16.5	13.4	3	.409
25	nf	37.2	13.4	14.0	4	.360
26	nf	35.0	13.4	13.4	3	.382
27	nf	37.3	15.4	12.7	5	.412
28	nf	41.9	19.0	13.9	4?	.435
29	nf	46.3	16.3	16.7	6	.352
30	nf	39.4	16.3	13.0	4	.413
31	nf	43.0	17.0	13.8	4	.395
32	nf	44.0	18.6	15.2	4	.422
33	nf	40.4	16.2?	15.0	4	.400
34	nf	38.6	15.7	14.0	4	.406
35	nf	44.5	17.0	17.0	7	.382
36	nf	40.0	16.2	15.0?	5	.405
					4.1	.389

Tirolites serratelobatus KITTL 1903

1	5-5	54.3	9.9	26.2	2	.182
2	5-6	55.7	11.9	23.1	4	.213
					3	.197

Tirolites smiriagini (AUERBACH)

1	11-6	47.4	22.0	15.5	18	.464
					--18	--.464
2	nf	51.2	23.1	18.5	13	.451
3	nf	39.5	17.3	12.8	19	.437
4	nf	42.2	18.4?	14.5	13	.436
5	nf	42.0	18.6	14.5	15	.442
6	nf	40.5	16.6	13.0	12	.409
7	nf	36.4	14.4	12.8	22	.395
8	nf	51.4	22.3	16.2	22	.433
9	nf	47.4	19.3	16.0	19	.407
10	nf	40.8	15.7	14.7	20	.384
					17.3	.425

Tirolites spinosior KITTL 1903

1	11-5	76.0	35.7	25.6	16	.469
					--16	--.469
2	nf	44.1	18.2?	-	13?	.412
3	nf	51.8	24.4?	16.6?	11?	.471
4	nf	60.5	28.0?	-	15	.462
5	nf	67.4	30.4	20.6	17	.451
6	nf	61.8	28.3?	-	16	.457
					14.6	.453

Tirolites spinosus MOJSISOVICS 1882

1	9-7	57.9	23.9	19.4	14	.412
					--14	--.412
2	nf	37.3	15.4	12.8	9	.412
3	nf	61.6	30.4	19.8	11	.493
4	nf	36.6	15.6?	14.3	10	.426
5	nf	49.5	22.0	16.9	12	.444
6	nf	48.4	18.8	18.3	12	.388
7	nf	46.2	19.9	15.6	9	.430
8	nf	40.8	17.3?	13.5	7	.424
9	nf	35.2	15.8	11.4	10	.448
10	nf	38.6	16.2	12.8	8	.419
					10.2	.429

Tirolites stachei KITTL 1903

1	7-14	58.3	18.7	24.0	6	.320
					-6	--.320
2	nf	52.0	18.3	19.4	4	.351
3	nf	45.1	17.3	16.6	5	.383
4	nf	42.5	16.0?	-	5	.376
					5.0	.357

Tirolites subillyricus KITTL 1903

1	7-15	44.0	17.8	15.3	7	.404
2	7-16	33.8	13.3	12.5	8	.393
					-7.5	--.398
3	nf	38.4	15.3	14.0	6	.398
4	nf	44.8	19.1	16.5	6	.426
5	nf	41.4	17.0	15.2	6	.410
6	nf	30.0	11.7	11.0	6	.390
7	nf	38.3	17.1?	13.7?	8	.446
8	nf	39.0	13.9	15.3	7	.356
9	nf	44.4	16.2	17.5	7	.364
10	nf	41.7	17.4	13.8?	6	.417
11	nf	33.2	12.8	12.0	6	.385
12	nf	40.7	16.8	14.9	5?	.412
13	nf	41.5	18.6?	-	6	.448
14	nf	41.2	15.6	14.7	6	.378
15	nf	35.0	13.9	12.2	7	.397
16	nf	41.8	17.1	14.4	8	.409
17	nf	40.0	17.4	14.2	5	.435
18	nf	44.3	17.9	12.9	6	.404
					6.4	.404

Tirolites toulai KITTL 1903

1	11-11	59.1	26.0	21.7	15	.439
2	11-12	46.7	20.0	15.0	12	.428
					--13.5	--.433
3	nf	50.4	19.9	18.5	7?	.394
4	nf	47.0	20.0	16.5	10	.425
5	nf	47.2	20.3	16.8	10	.430
6	nf	38.7	14.4	14.0	10	.372
7	nf	44.8	18.8	14.0	11	.419
8	nf	37.0	14.3	12.0	9	.386
9	nf	42.9	18.2	13.8	9	.424
10	nf	44.1	17.8	15.2	10	.403
					10.3	.412

Tirolites turgidus MOJSISOVICS 1882

1	10-8	58.6	24.2	20.0	17	.412
					--17	--.412
2	nf	61.5?	25.6	20.5	11	.416
3	nf	53.4	23.9?	12.9	16	.447
4	nf	50.5	22.3	12.5	10	.441
5	nf	56.8	24.0	20.2	12?	.422
6	nf	58.2	24.2?	21.5	17?	.415
7	nf	46.9	19.2	16.3	12?	.409
8	nf	56.0	24.5	20.3	15	.437
9	nf	38.4	19.0	13.2	16	.494
10	nf	47.6	21.0	16.0	14	.441
11	nf	47.0	21.6	14.5	17	.459
					14.2	.435

Tirolites undulatus KITTL 1903

1	7-13	55.0	21.2	18.3	5	.385
					-5	--.385
2	nf	52.7	21.5	17.9	5?	.407
3	nf	60.6	24.4	20.4	4	.402
4	nf	38.0	14.0	14.0	7	.368
5	nf	44.5	16.3	15.5	5	.366
6	nf	38.5	13.3	13.5	5	.345
					5.1	.407

Plate 1

All figures natural size

Fig. 1–6. *Tirolites cassianus* (QUENSTEDT) from the lower Val Badia Member, Werfen Formation, Dolomites.

Localities and number of the specimen.

- 1: Grones, Val Badia (Bolzano), 55.
- 2: S.S. 244 della Val Badia (Bolzano), 24.
- 3: Col Vercin, Val Badia (Bolzano), 51.
- 4: Col Vercin, Val Badia (Bolzano), 17.
- 5: Grones, Val Badia (Bolzano), 49.
- 6: Col Vercin, Val Badia (Bolzano), 9.

Plate 1



Plate 2

All figures natural size

Fig. 1–5. *Tirolites cassianus* (QUENSTEDT) from the lower Val Badia Member, Werfen Formation, Dolomites.

Localities and number of the specimen.

- 1: Col Vercin, Val Badia (Bolzano), 1.
- 2: Costabella, P. so S. Pellegrino (Trento), 27.
- 3: Col Vercin, Val Badia (Bolzano), 2.
- 4: Col Vercin, Val Badia (Bolzano), 8.
- 5: Col Vercin, Val Badia (Bolzano), 15.



Plate 3

All figures natural size

Fig. 1–4. *Tirolites cassianus* (QUENSTEDT) from the lower Val Badia Member, Werfen Formation, Dolomites.

Localities and number of the specimen.

1: Col Vercin, Val Badia (Bolzano), 18; the largest specimen, till now found in the Dolomites.

2: Grones, Val Badia (Bolzano), 59.

3: Grones; Val Badia (Bolzano), 32.

4: Col Vercin, Val Badia (Bolzano), 3.

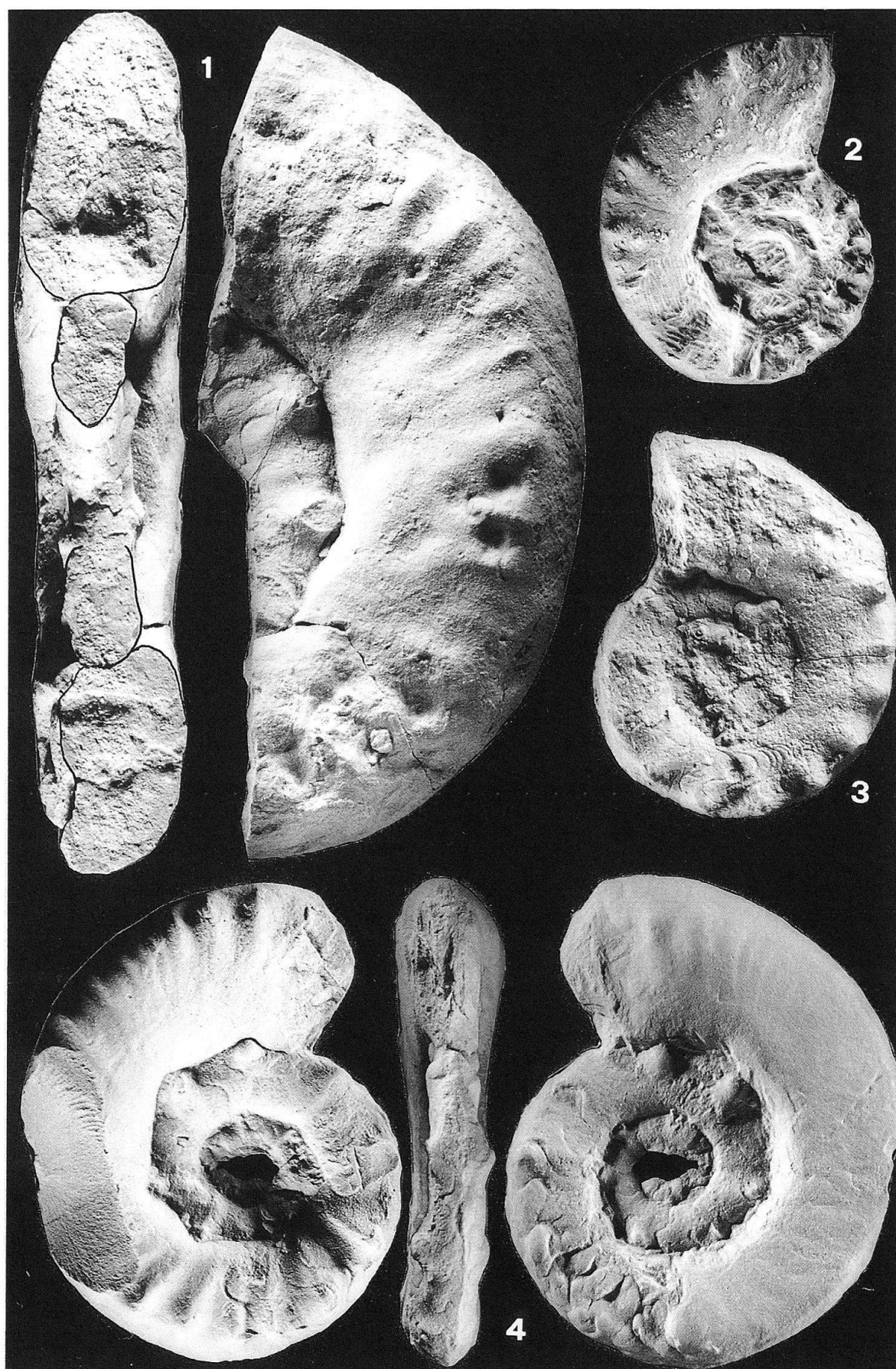


Plate 4

All figures natural size

Fig. 1–9. *Tirolites illyricus* MOJSISOVICS from the unit a of the Csopak Marl Formation, Soly section, Bakony.

Beds and number of the specimen.

1: bed 3; 1, 2, 3.

2: bed 6; 7.

3: bed 2; 22.

4: bed 9–10; 12.

5: bed 2; 24.

6: bed PR 2; 43.

7: bed 16; 4.

8: bed 11–12; 18.

Fig. 9. *Dalmatites morlaccus* KITTL, lower unit of the Csopak Marl Formation, Soly section, Bakony.

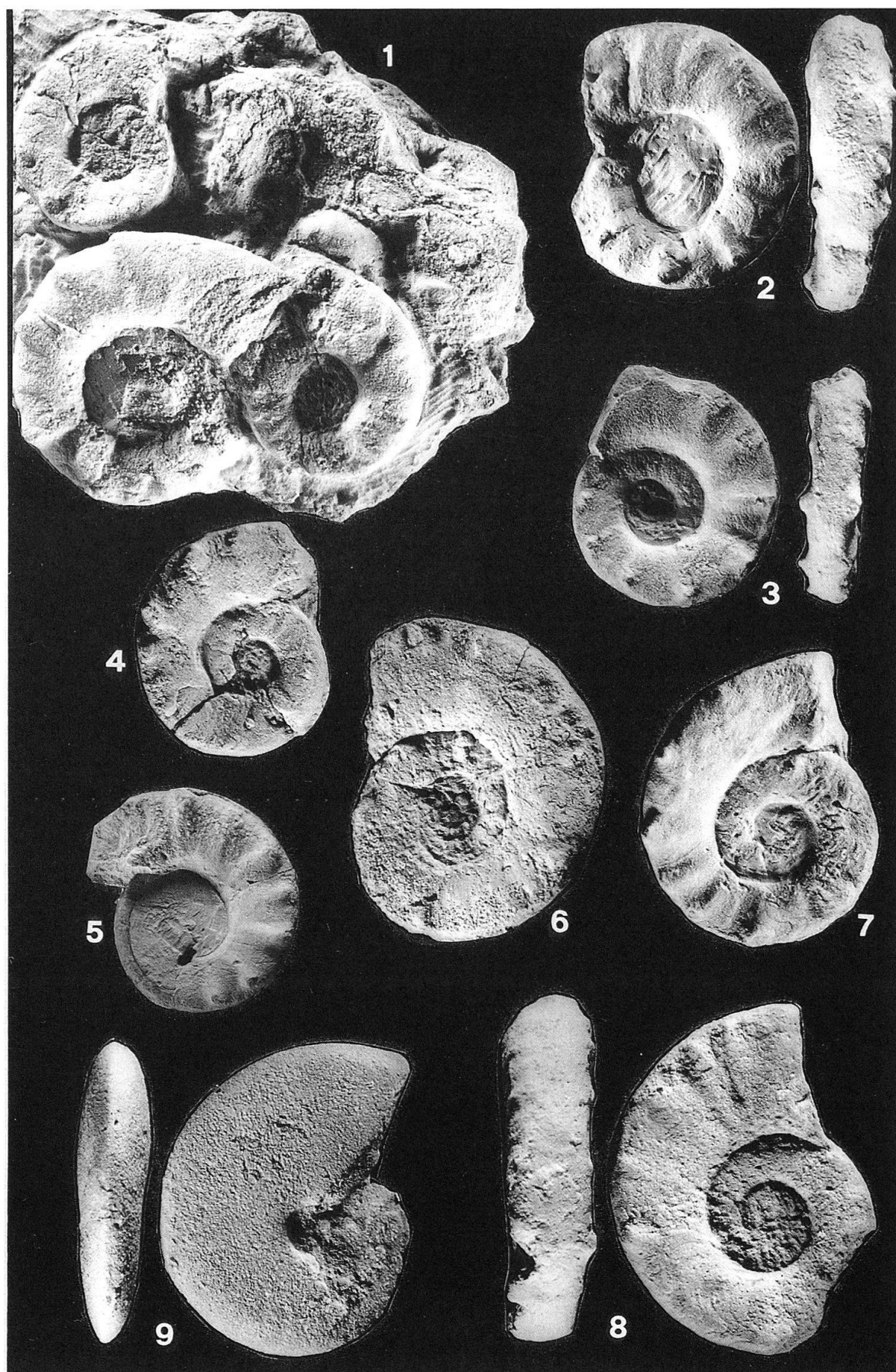


Plate 5

All figures natural size

Fig. 1–2. *Dinarites dalmatinus* (HAUER), unit a of the Cencenighe Member, Werfen Formation, Dolomites.

1: Val Sorda, Predazzo (Trento).

2: P. so di Lusia, Moena (Trento).

Fig. 3–4. *Diaplococeras liccanum* (HAUER), middle part of unit d of the Val Badia Member, Werfen Formation, Dolomites.

3: Costabella, P. so San Pellegrino (Trento).

4: Butterloch, Egna (Bolzano).

Fig. 5. “*Meekoceras*” *caprilense* MOJSISOVICS, topmost unit d of the Val Badia Member (Werfen Formation); Col Vercin, Dolomites.

Fig. 6. *Tirolitoides prior* (KITTL), unit d of the Val Badia Member (Werfen Formation); Val Venegia, P. so Rolle, Dolomites.

