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

By Renato Posenato 1)

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 ultimely *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 évèments à ammonïdes enregistrés dans la section de Muć (Dalmatie, Yugoslavie), 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 premieres 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. illy-ricus*, 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 mode 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 refences 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 (Broglio 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 (Broglio 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).

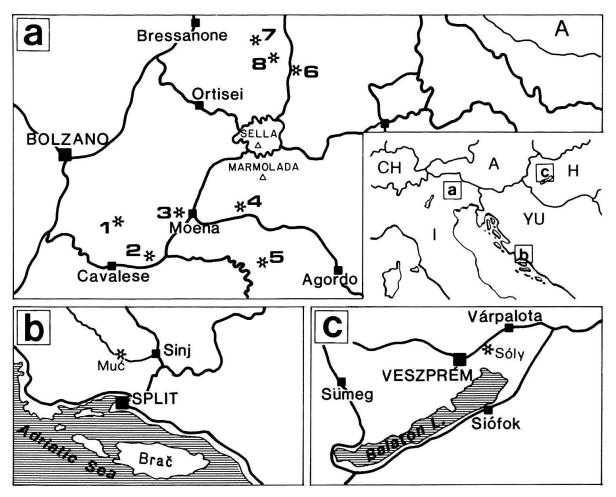


Fig. 1. Geographical setting of the quoted localities. Dolomites: 1-Butterloch, 2-Val Averta, 3-Moena, 4-Costabella, 5-Val Venegia, 6-Val Badia (SS 244), 7-Col Vercin, 8-Grones.

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 *Bakevellia*, *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 ocurrences 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*.

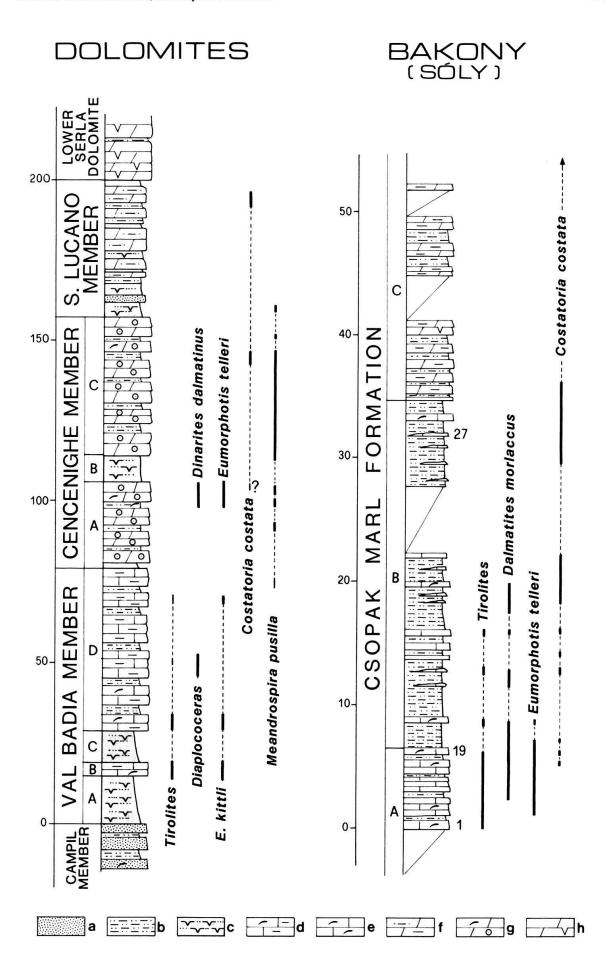
The San Lucano Member, consisting of fine-grained sandstone, marl and marly dolomite, is very poor in fossil content, because of its prevalent peritidal conditions. *Meandrospira pusilla* disappears at the base of this member, which yields rare specimens of *Costatoria costata* and *Natiria costata*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



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 frequence 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.

Unfortunatly, 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 speciments 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 (Hmax/Hmin = 1.10–1.15).

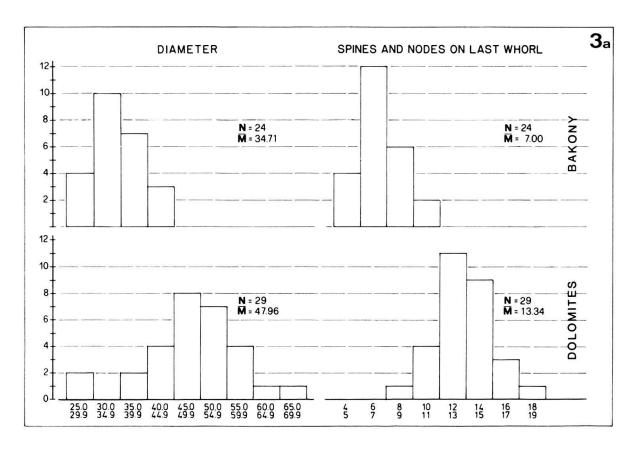
3.3. Biometrical and morphological analysis

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



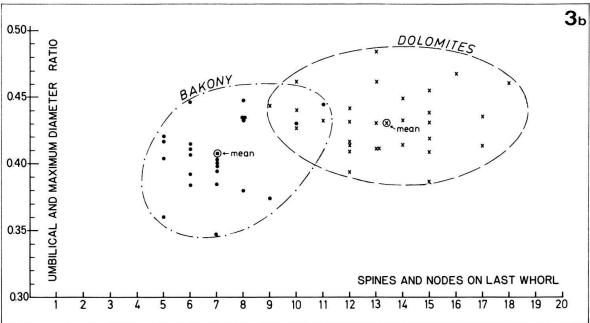


Fig. 3. Diagrams of comparison between Dolomite and Bakonian populations. 3a = Histograms of measurements of maximum diameter (left) and total amount of spines and/or nodes on the last whorl (right). 3b = Scatter diagrams of umbilical/maximum diameter ratio versus total amount of spines and/or nodes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

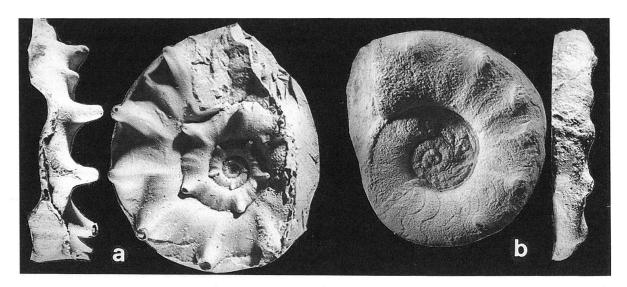


Fig. 4. Comparison between Tirolitids of similar size from Dolomites and Bakony. 4a = artificial mould of the external cast (specimen no. 19) from the Butterloch section, lower Val Badia Member (Werfen Formation, Dolomites). 4b = internal mould (specimen no. 45) from the Sóly section, lower unit (Csopak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

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* senus 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. Unfortunatly, 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)

Posenato R. Posenato

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

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

- the dissolution of the internal moulds with sculpture simplification and pseudosutures (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. kerneri (8), T. prior (11) and T. rectangularis (15), are located in Figure 5 a 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 compactation, so that T. rect-

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

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.

angularis must be invalidated. T. kerneri 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.

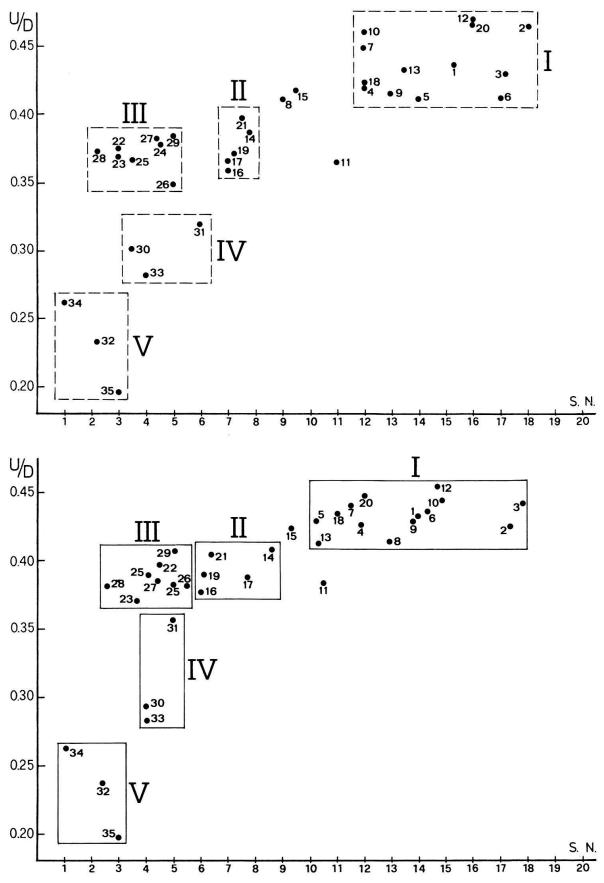


Fig. 5a (top) and 5b (bottom).

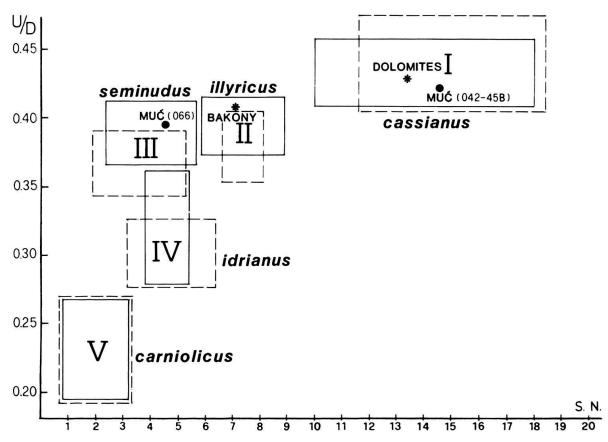


Fig. 5c. Scatter diagrams regarding: 5a = means of figured types of Kittl's collection, 5b = means of figured and not figured specimens of Kittl's collection, 5c = means of populations coming from Dalmatia (Muć), Dolomites and Bakony (Sóly). Numbers of the morpho-species as Table 1.

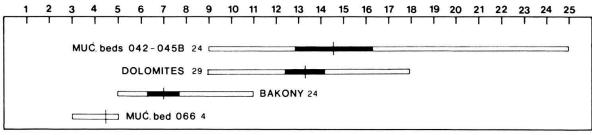
The graph of Figure 6, concerning the range and confidence limits of spines/nodes on last whorl, permits to distinguish T. cassianus from T. illyricus, that is species with evolute or feebly involute shells. However, it does not allow a good distinction between seminudus, idrianus and carniolicus population-species.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

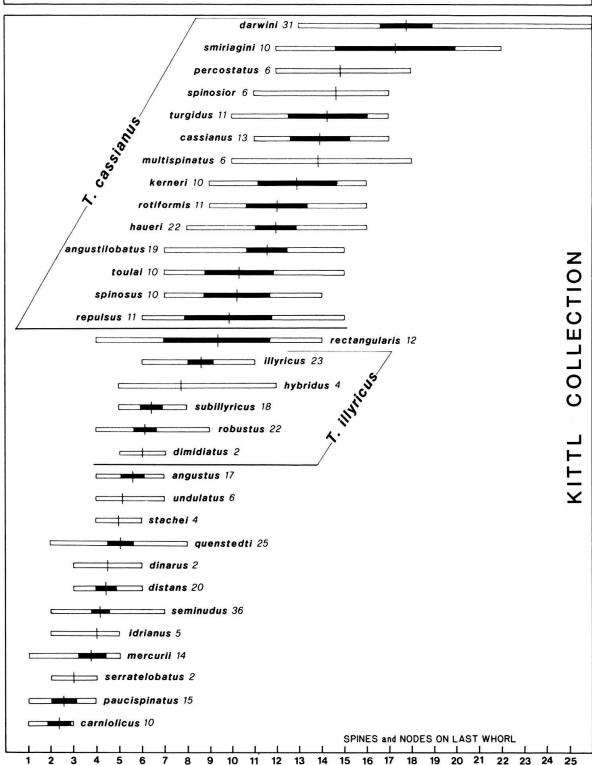
According to the methodology used, the Hungarian population can be assigned, at a specific level, to *T. illyricus*. As this species has never yet been noted, apart from in Dalmatia originating from an unknown stratigraphical level, it needs to be established whether it can be recognized in the Muć sequence, 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" (Broglio 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 (Broglio 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 (Broglio Loriga et al. 1983, 1986), Bakony (Broglio 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.

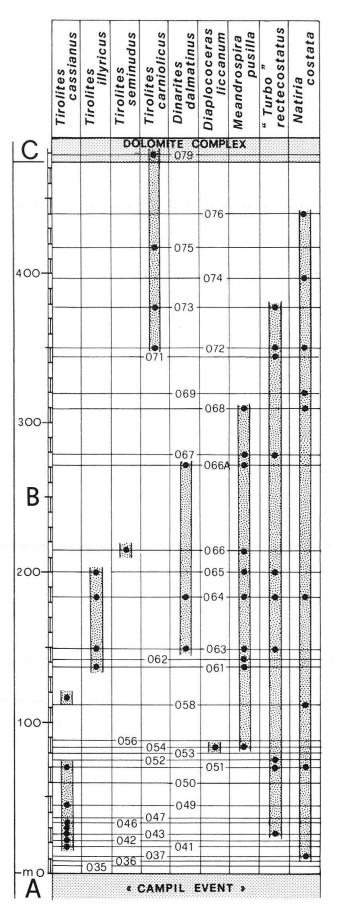


Fig. 7. Vertical distribution of molluscs and forams at Muć, Dalmatia (from Herak et al. 1983, modified).

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 *Dia-*plococers (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*.

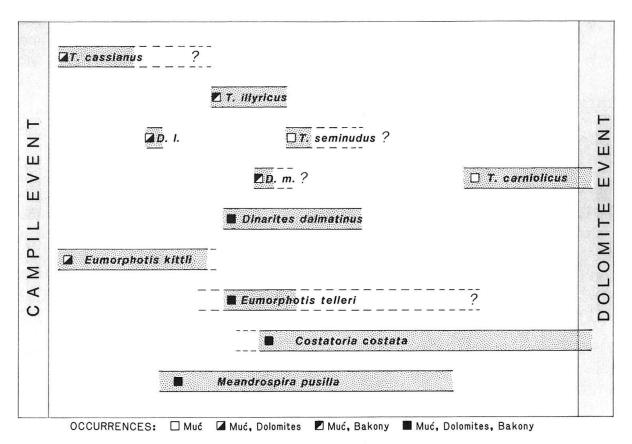


Fig. 8. Tentative correlation between the ammonoid events and benthic markers in the European Late Scythian sequences. Abbreviations: D.l.-Diaplococeras liccanum; D.m.-Dalmatites morlaccus.

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* subzone) can be correlated to *T. illyricus* beds. The disappearance of *Tirolites* from the Dolomites seems to be 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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Manuscript received 18 July 1991 Revision accepted 29 June 1992 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

٠.	D	U	нм	W	SN	U/D	bed	D	U	нм	SN	U/
L	VERCIN						042	39.9	16.0?		10	.40
2	55.2	24.3	17.2	14.0	10	.440	••	48.3	20.8?	14.7?	14	.43
5	49.5	19.2	18.0?	9.9	15	.387	•	39.0	16.4?	13.0?	11?	. 42
,	63.4	27.3	21.4	22.6	15?	.430	"	36.5	15.0?	12.0?	9?	. 41
)	47.6	19.5	17.6	13.0	15?	.409	**	38.0	16.0	12.5	9	. 42
)	40.9	17.7	14.5	8.1	11	.432	••	37.7	15.1	15.3	13	.40
5	48.6	20.9?	15.4	14.7	13	.430	••	44.3	18.9	14.8	12?	. 43
1	65.0	26.9	22.5	13.9	17?	.413	••	46.3	19.8?	-	14?	. 4
							**	41.0	18.8?	_	11?	. 4
L	BADIA (S.S.244)									
2	51.3	23.7?	16.2	15.2	13	.461	044	61.5	29.5?	20.0?	25	. 4
	52.0	23.7	17.8	13.7	15	.455	••	41.4	17.3	13.0	21	. 4
	46.2	21.6	15.2	12.4	16?	.467						
	56.7	24.7	19.6	13.8	17?	.435	045A	48.5	19.8	18.8	14	. 4
	49.3	22.7	15.7	10.0	18	.460	.,	47.5	21.4	14.4	22	. 4
	54.2	22.2	20.0?	14.5	12	.409	**	31.3	13.9	_	15	. 4
							•	42.5	18.8	16.0	18?	. 4
10	IES						••	44.4	18.5?	14.0?	14	. 4
Ü.	45.1	20.8	14.1	13.6	10	.461	.,	33.5	15.8	10.5	18	. 4
	50.5	20.8	18.1	10.5?	13	.411						
	50.1	20.6	16.6	13.3	13?	.411	045B	35.2	14.5?	11.4	13	. 4
Œ	40.8	18.0	14.4	7.0?	12	.441	"	49.0	22.0?	18.5?	15	. 4
	55.5	24.0	19.5	18.2	14	.432	••	45.2	16.5	15.5	11	. 3
	46.6	22.6	14.0	13.6	13?	.484		40.5	15.0	13.5	14	. 3
	52.0	21.8	17.6	16.0	15?	.419	••	51.2	19.9	16.9	17	. 3
	41.5	17.2	14.1	7.2	12	.414		41.5	17.4	12.3	15	. 4
	27.1	12.0	8.3	6.7	9	.442	100	47.7	18.4	15.7	15	. 3
	35.9	15.5	10.9?	10.3	12	.431			10.,			
	48.8	21.9	17.4	9.2	14	.448	046	40.5?	15.0	13.7	13	. 3
	38.0	15.8	13.3	9.1	12	.415	040	40.5.	13.0	2011		
		20.0	20.0			1122	066	42.7	18.6	13.5	5	. 4
SI	CABELLA						"	33.2	11.8?	12.0?	3	. 3
	52.0	20.5	18.3	10.6	12	.394	**	33.4	12.4?	12.4	5?	. 3
	56.9	23.6	19.1	13.5	14?	. 414	"	41.0?	17.5	14.6?	5	. 4
ΒN	IA.						072	60.0	19.3	22.9?	1	. 3
	42.0	18.4	15.0	-	15?	.438						
							073	57.0	15.4?	23.5	2	. 2
TI	TERLOCH							45.0	11.5	19.7	2	. 2
	28.0	12.0	9.0	-	10	.428						
							079	61.0	15.2?	25.4	3	. 2

Sòly (Bakony, Hungary)

bed	no.	D	U	нм	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
н	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

Appendix, Table 2

Tirolites measurements of Kittl's collection. pl.-fig. = Kittl's figured types, plate and figure; n.f. = not figured specimens; * = Mojsisovics's figured type; other symbols as Figure 1.

	KITTL 1903	D	U	нм	SN	U/D	7		n f	45.0	19.9	13.6	13?	.442
1	plfig	•					8		nf nf	44.9	20.0 15.2	14.3 11.2	14? 12	.445
Ti	rolites	angus	tiloba	tus KI	TTL 1	903	1	0	n f	36.4	15.0	11.9	11 15	.412
1	8-19	41.0	18.0	13.8	11	.439		1 2	n f n f	48.8	22.1	15.8	17	.452
2	9-1	47.7	22.5	14.2	14	.471	1	3	n f	33.8	15.3	11.1	17	.452
3 4	9-2 9-3	46.6	21.1	15.0 16.6	12 11	.452 .437							13.9	.432
			gured		12		<u>T</u>	ir	olites	darwi	<u>ni</u> MOJ	SISOVI	CS 18	82
5	n f	46.0	21.6		13	.469			10 /	, , ,	21.0	1/ 2	20	171
6 7	nf nf	40.0	18.0 16.9	13.1	9 12	.450	1 2		10-4 10-5	45.5 46.2	21.0	14.2 16.1	20 15	.461
8	nf	44.0	18.2	15.0	12	.413	3		11-1	64.3	28.5	21.7	14	.443
9	n f	40.9	16.1	14.4	10	.393	4		11-2	63.7	27.5	22.4	20	.431
10 11	n f	41.1	18.4	14.2	10?	.447	5		11-3	37.4	14.2	13.3	17	.379 .2430
12	n f n f	41.0	15.8 17.8	15.3 13.4	7? 11	.392	6		n £	59.5	27.9	17.8	17	.468
13	n f	41.4	18.5	12.7	15	.446	7		n f	61.0	26.3	21.0	19?	.431
14	n f	43.5		14.1	11	.471	8		n £	68.0	29.5	22.9	15	.433
15 16	n f n f	49.4	22.8	16.0	12 10	.461 .470	9	0	n f n f	54.4 58.3	25.3	17.9 19.9	17 21	.465 .457
17	n f	40.0	16.6	13.4	13	.415		1	nf	59.5	25.9	21.4	13	.435
18	n f	39.5	16.4	14.1	13	.415	1	2	n f	73.2	34.0	23.5	20	.464
19	n f	49.3	23.0	15.8	13	.466		3	n f	49.9	19.9	17.4	13	.398
	ans of		d and	not	11 6	.440		5	n f n f	50.1	22.5	15.3 19.7	17 16	.449
111	gured t	ypes			11.5	.440		6	n f	55.0	25.0	18.0	18	.454
Ti	rolites	angus	tus KI	TTL 19	03		1	7	n f	54.8	25.0	17.0	17	.456
		atto pated to						8	n f	50.0	22.1	14.9	16	.442
1	7-12	42.4	14.8	15.2	5	.349		9	n f n f	55.1	23.4	17.5	15 16	.424
2	n f	44.2	15.5	17.0	-5 4	349 .350		1	n f	63.0	26.0?		18	.412
3	nf	40.2	15.5	14.4	6	.385		2	n f	67.8	31.0?		20?	.457
4	n f	52.4	20.2	20.2	5	.385		3	n f	45.0	20.0?		18?	. 444
5	nf	36.1	14.7	12.9	7	.407		4	n f	49.5	21.8	_	26	.440
6 7	nf nf	40.2 37.2	14.9	15.0	6	.370		6	n f n f	48.3	23.4 17.7	- 15.0	25 15	.484
8	nf	37.8	13.4	15.5 15.0	5 7	.360 .351		7	n f	53.0	27.3	15.0	22	.515
9	nf	51.2	18.3	18.7	4	.357		8	n f	35.7	15.0	12.0	15	.420
10	n f	45.7	17.8	16.3	5	.389		9	n f	61.5	28.0	20.8	19	.455
11	nf		17.2	17.5	7	.373		0	n f n f	48.6 54.0	22.0	15.3 16.5	17 21?	.452
12 13	nf nf	42.6	16.0	16.0 14.2	5 6	.375	3	1	n r	34.0	24.0	10.5	$\frac{21:}{17.8}$.444
14	nf	45.0	19.0	15.5	7	.422								
15	n f	38.0	16.0	12.9	6	.421	Ti	ir	olites	dimid	iatus K	CITTL 1	903	
16	nf	38.7		14.2	5	.423							-	240
17	n f	36.0	15.0	12.0	5 5	$\frac{.416}{.381}$	1	1	8-15	48.0	17.3	17.0	7 -7	.360
					3.3	. 301	2		n f	43.1	17.0	16.0?		.394
Tir	olites	carni	olicus	MOJSI	SOVIC	S 1882							6	.377
1	5-1	57.8	11.5	17.7	2	.198	т	i r	alitee	dinar	us MOJS	SISOVIC	S 181	3.2
2	5-2	59.8	15.7	24.0	3	.262	4.1	11	JIICES	armar	45 11035	7150110	5 100	,,,
3	5-3	53.7	13.1	24.2	1	.243	1	:	2-9*	40.0	15.0	-	3	.375
4	5-4	52.9	12.3?	22.4	3	.232							-3	375
	6	57 2	12.5	28.4		2233	2		n f	40.0	16.7	13.5	6 5	$\frac{.417}{.396}$
5 6	n f n f	57.2 51.2	15.0	21.0	3 2	.292							4.5	. 370
7	n f	59.9	14.6	25.9	3	. 243	T.	ir	olites	dista	ns KIT	rl 1903	3	
8	n f	51.5	12.7?		3	.246			2					.07
9	nf	56.0	13.6	25.0	2	. 242	1		6-12	45.6	18.6 14.8	17.3 18.5	5 4	.407 .367
10	n f	59.5	11.7	28.2	$\frac{2}{2.4}$	<u>.196</u> .237	2		6-13 6-14	40.3	17.5?		6	.392
						. 207	4		6-15	37.4	14.6?		4	.390
Tir	olites	cassi	anus (QUENST	EDT 1	849)	5		6-16	37.5	15.0	12.9	3?	.400
							6		7-7	38.7	13.9	16.0	5	.359
1	9-4	50.3	22.3	17.6	16	.443	7		7-8	46.6	17.0	19.1	4	.364
2	9-5 9-6	42.2	18.1 19.3	15.0 14.2	16 14	.442	8		n f	43.0	17.0	14.8	3	.395
~	•					.3437	9		n f	35.2	13.9	13.0	5	.394
4	n f	45.3	19.3	17.2	14	.426	10		n £	36.0		14.1?	4	.383
5	nf	44.0	18.9	14.4	11	.429	1		n f	41.8 41.4	15.1 14.6	16.1 16.0	3? 4	.361
6	n £	33.6	14.0	11.4	11	.416	1	2	n f	41.4	14.0	10.0	•	. 332

13	n f	36.3	13.5	12.7	5	.371	13	n f	40.5	18.2	13.3	8	.449
14		37.7	13.2	13.4	5	.350	14		42.9	17.4	15.7	8	.405
15		34.4	14.1	12.5	6?	.409	15		45.5	18.2	16.0	8	.400
16 17		35.7 40.5	13.8	11.8	5 4	. 386	16 17		44.0 40.8	17.0	15.5	8 10	.386
18		40.3	16.4 16.6	13.5	3	.404	18		34.0	16.9 15.4	14.3	9	.414
19		34.8	13.6	11.7	5	.390	19		39.6	15.73			.396
20		44.2	17.5	13.1	5	.395	20		40.3	17.33		9?	.429
						.384	2 1		30.0	12.3	9.5	10	.410
							22	n f	36.0	15.8	11.6	10	.438
Ti	rolites	hauei	<u>ci</u> MOJS	SISOVI	CS 188	2	23	n f	34.6	13.9	12.4	8	.401
	9-8	/ O 2	22.0	15.5	1.7							8.6	.407
1 2	9-0	49.3	22.8	15.5	16 12	.462	Тi	rolites	kerne	eri KIT	тт. 190) 3	
3	9-10	59.3	24.5	20.3	10?	.413							
4	9-11	47.0	19.5	16.8	10	.414	1	11-8	49.6	20.4	17.3	9	.411
5	9-12	50.0	20.6	18.1	12	.412						- 9	411
6	9-13	51.0	23.0	16.5	13	.450	2	n f	52.0	19.6	19.7	13	.376
7	10-1	46.0	18.0?	17.8	12	.391	3	n f	43.0	17.7	15.5	11?	. 411
8	10-2	39.0	17.0	13.9	8	.435	4	n f	57.5	26.0	17.4	13?	. 452
9	10-3	45.1	18.3	16.0	15	.405	5 6	n f	45.2 52.5	18.9	15.5 18.0	15	.418
			100			.0420	7	n f n f	57.7	20.9	16.3	16 10	.398
10 11		46.8	19.8	15.8	12 12	.423	8	n f	37.2	16.4	11.5	14	.440
12		49.4	20.6	17.0	13	.433	9	n f	38.0		11.5	12	.421
13		47.2		15.9	10	. 404	10	n £	40.0	18.0	12.5	16	.450
14		46.0	19.8	15.2	12	.430						12.9	
15		41.2	17.9	13.5	8	.434							
16	n f	49.1	22.9	15.5	10	.466	Ti	rolites	mercu	rii MO	JSISOV	ICS 1	882
17	n f	51.9	21.5	16.8	11	. 414				nama nama		1001	trace of trace
18		55.6		18.5	13	.476	1	5-10	45.1		18.0	4	.343
19	n f	49.9	20.7	18.0	14	. 414	2	5-11	46.9		17.1	4	.360
20		46.8		17.0	12	.416	3	6-2	56.4	23.0	19.2	1 -3	.407 370
21 22	nf	54.9	24.2	18.3	13	.440	4	n f	52.0	20.9	18.1	3	.401
22	n f	51.3	22.2	22.5	15	.432 .426	5	nf	35.7	13.9	13.5	4	.389
					11.7	.420	6	n f	33.5		11.5?		.411
т:,	rolites	hatar	o n h a n u	c KITT	1 1903	ı	7	nf	52.0	19.0	19.0	5	.365
111	olices	necet	opnanu	2 KIII	ь 1703	,	8	n f	39.7	15.4	15.0	5	.387
1	5-7	56.3	15.9	23.6	4	.282	9	nf	38.3	12.6	15.0	4	.328
•		50.0	23.7	20.0	-4	282	10	nf	44.0	15.8	15.5	5	.359
							11	nf	39.0	14.1	14.4	4	.361
Ti	rolites	hybri	dus KI	TTL 19	03		12	n f	35.8	12.8 13.8?	14.0	4?	.357
1000	F28 10-17	B 102 112	140 THE SEC.	numer or			13 14	nf nf	37.4 43.1	15.8:	15.8	4 <u>3</u>	.368
1	8-2	53.0	19.5	20.5	7	.367	14	11 L	43.1	13.2	13.0		.370
2	£	5 / O	10 5	10 0	-7 52	367						3.,	
2	nf nf	54.0 39.0	19.5 16.0	19.8 14.5	5 ? 7	.361	Til	rolites	monop	tychus	KITTL	1903	
4	n f	65.5	27.3	23.6	12	.416							
S1#		00.0		20.0		.388	1	4-9	62.2	16.3	25.4	1	.262
												1	.262
Ti	rolites	idria	nus (H	AUER 1	865)		т:.	colites	m., 1 + i	cninat	VIT	TI 10	12
846			00 0	20.0		201	111	OTICES	marci	SPINAL	us KII	16 17	, ,
1 2	1-1* 5-8	68.0 58.4	20.0 18.0	30.0	5 2	.294	1	11-9	54.4	22.7	19.4	13?	.417
2	3-0	30.4	10.0	24.3	-3.5	301						13	417
3	n f	66.0	19.8	27.3	5?	.300	2	n f	37.0	14.8	13.2	10	.400
4	nf	53.8	16.4	23.0	5	.304	3	n f	40.2	17.1	12.8	12	.425
5	n f	61.5	16.2	23.3	3	.263	4	n f	44.7	20.0?		18	.447
					4	.293	5	nf	53.0	23.0	18.0	15	.433
							6	n f	38.0	17.2	12.7	15	.452
Ti	colites	illyr	icus M	OJSISO	VICS 1	.882						13.8	. 4 2 9
1	8-3	45.6	17.6	16.0	6	.385	Tir	olites	pauci	spinat	us KIT	TL 190	3
1 2	8-4	49.0	19.5	17.0	7	.397			A-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2				
3	8-6	38.4	14.4	13.4	9	.375	1	6-11	41.4	14.8	15.8	3	.357
4	8-7	41.0	15.3	16.0	8	.373	2	7-4	41.5	15.3	15.3	2	.368
5	8-8	44.2	16.3	16.0	8	.368	3	7-5	39.0	14.3	17.0	3	.366
6	8-9	36.0	15.3	12.9	9	.425	4	7-6	41.9	16.9	14.7	1	.403
1000	10.000	10 mm	No. 121 15500	SACTORY TO MAKE	-7.8	387	5	n f	44.1	15.4	10 0	-2.2	373
7	n f	34.3	14.8	10.7	10	.431	6	n f	44.1	17.2	19.0 17.0	4 2?	.349
8	nf	39.5	16.4	13.8	9	.415	7	n f	37.1	14.5	13.5	1	.390
9 10	nf nf	40.5	16.4 16.9	15.0 16.3	7 10	.404	8	nf	43.6	16.6	16.0	2	.380
11	n f	40.5	15.3	14.0	11	.377	9	n f	32.0	13.6	11.5	3?	.425
12	nf	40.4	17.5	14.0	10	.433	10	n f	38.3	15.0	13.5	2?	.391

11 nf 36.8 14.0 12.1 2 .380	Tirolites repulsus KITTL 1903
12 nf 36.0 13.7 12.4 4 .380	Titotices repuisus kille 1903
13 nf 41.0 15.2 15.3 3 .370	1 8-5 42.7 16.2 15.9 11 .379
14 nf 35.9 13.4 12.7 3 .373	2 8-10 38.6 16.2 13.3 15 .419
15 nf 36.0 14.8 11.9 4 .411	
2.6 .381	
	4 8-14 28.0 12.9 9.0 9 .460
Tirolites percostatus KITTL 1903	12422
Potostatas Milia 1700	5 nf 27.6 12.3 9.0 12 .445
1 10-6 47.2 21.8 15.0 12 .461	6 nf 35.2 15.0 12.0 11 .426
12461	7 nf 34.6 16.5 11.5 7 .476
2 nf 45.0 21.7 14.7 18 .482	8 nf 34.2 14.9 11.3 <u>10?</u> <u>.435</u>
	11.0 .434
	Tirolites robustus KITTL 1903
5 nf 48.3 21.8 17.0 14 .451	
6 nf 54.0 23.0? - 15 .425	1 7-9 42.6 14.2 17.4 7 .333
14.8 .445	2 7-10 45.5 16.9 17.6 7 .371
	3 7-11 35.5 13.7 12.8 9 .385
The second secon	4 8-1 49.8 19.7 17.5 6 .395
<u>Tirolitoides prior</u> (KITTL 1903)	-7.237
	5 nf 36.4 13.7 14.1 5 .376
1 11-3 54.6 20.0 21.0 11? .366	6 nf 52.5 20.7 20.0 6 .394
11366	7 nf 42.6 15.7 16.0 5 .368
2 nf 61.3 22.2 23.3 9? .362	
3 nf 50.7 19.8 18.2 9 .390	1 11 11 11 11 11 11 11 11 11 11 11 11 1
4 nf 26.0 10.8 - 13 .415	The second secon
10.5 .383	10 nf 39.5 16.0 14.0 6 .405
	11 nf 56.3 22.4 19.7 7 .397
Tirolites quenstedti MOJSISOVICS 1882	12 nf 44.6 18.1 16.4 7 .405
TITOTICO QUENOCOCI NOCOLIO INCO	13 nf 40.0 16.7 13.0 6? .417
1 6-19 50.5 19.1 17.6 5 .378	14 nf 40.7 17.0 13.6 7 .417
2 6-20 47.3 18.0 17.9 4 .380	15 nf 40.0 16.9 15.5 7 .422
-4.5379	16 nf 42.9 16.8 15.6 5 .391
	17 nf 35.6 14.2 12.5 7 .398
3 nf 48.5 19.4 17.6 4 .400	18 nf 44.0 15.8 16.8 6 .359
4 nf 44.5 16.8 18.0 4 .377	19 nf 49.0 21.0 18.0 5 .428
5 nf 37.8 14.0 14.4 6 .370	20 nf 42.4 17.9 14.2 5 .422
6 nf 37.0? 14.4 14.5 6 .389	21 nf 44.6 18.0 16.2 6 .403
7 nf 44.9 15.7 17.1 5 .349	22 nf 40.1 15.1 14.3 <u>4</u> <u>.376</u>
8 nf 45.6 17.6 18.0 6 .385	6.1 .389
9 nf 44.0 15.6 18.3 5 .354	0.1 .507
10 nf 33.0 13.0 12.0 6 .393	Tirolites rotiformis KITTL 1903
11 nf 38.2 16.2 12.8 7 .424	THOTICES TOUTIONIES KITTE 1905
12 nf 32.6 12.5 12.0 8 .383	1 8-12 44.2 21.8 13.6493
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	1641
16 nf 35.3 14.1 12.3 5 .399	3 nf 38.0 16.3? 13.0 14 .428
17 nf 55.4 22.9 21.0 2 .413	4 nf 35.0 15.3 11.7 11? .437
18 nf 46.4 18.2 17.0 6 .392	5 nf 32.7 13.8 11.0 9? .422
19 nf 37.0 14.0 15.0 6? .378	6 nf 35.7 16.8? 11.5 13 .470
20 nf 24.5 10.4 7.7 4 .424	7 nf 31.3 15.8 9.4 12 .504
21 nf 60.5 21.4 22.2 3? .353	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
24 nf 46.5 18.5 15.6 5 .397	12 nf 28.9 12.6 9.1 13 .435
25 nf 42.3 15.5 15.0 5 .366	12 .447
5.0 .382	
-1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -	Tirolites seminudus MOJSISOVICS 1882
Tirolites rectangularis MOJSISOVICS 1882	
	1 6-3 50.0 19.7 18.4 2 .394
1 8-16 44.4 19.0 19.1 11 .427	2 6-4 44.9 16.9 16.0 5 .376
2 8-17 41.5 17.0 14.2 8 .409	3 6-5 40.3 14.3 15.9 2 .354
9.5418	
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 6-8 43.3 16.2 17.0 4 .374
6 nf 43.3 16.7 - 7? .385	7 6-9 34.2 13.4 12.0 3 .391
7 nf 42.1 18.3 13.8 4 .436	8 6-10 29.8 11.3 10.7 4 .379
	9 6-17 31.6 12.0 11.2 4? .379
	10 6-10 /2 2 15 1 17 2 5 257
	10 6-18 42.2 15.1 17.2 5 .357
9 nf 48.2 20.0 17.4 10 .414	-3.536
10 nf 58.0 26.0? 19.0 14 .448	-3.536 11 nf 45.1 15.7 17.4 3 .348
10 nf 58.0 26.0? 19.0 14 .448 11 nf 39.0 18.0 12.0 14? .461	-3.536
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	-3.536 11 nf 45.1 15.7 17.4 3 .348
10 nf 58.0 26.0? 19.0 14 .448 11 nf 39.0 18.0 12.0 14? .461	-3.536 11 nf 45.1 15.7 17.4 3 .348 12 nf 42.1 17.2 15.2 5 .408

15	n f	36.8	15.4	12.5	5	.418	Ti	rolites	stach	ci KIT	TL 190	3	
16	n f	38.9	14.8	14.6	6	.380					8.0 8		2000
17	n f	36.3	14.0	13.1	5	.385	1	7 - 1 4	58.3	18.7	24.0	6	.320
18	n f	34.5	13.2	12.2	6	.382	7627	20	12 21 12			- 6	320
19	nf	56.5	23.0	20.5	3	.407	2	n f	52.0	18.3	19.4	4	.351
20	n f	46.0	18.5	16.4	3	.402	3	n f	45.1	17.3	16.6	5	.383
21	n f	37.0	15.5	13.3	4	.418	4	n f	42.5	16.0?	-	5 0	$\frac{.376}{.357}$
22 23	n f	36.4	12.3	16.0	5 5 ?	.337						3.0	. 557
24	n f n f	41.3	15.5 16.5	15.5	3	.375	т;	rolites	cubi 1	1	c KITT	r 190	3
25	n f	37.2	13.4	$13.4 \\ 14.0$	4	.409 .360	11	TOTICES	SUDII	Lyticu	<u>5</u> KIII	1, 190	3
26	n f	35.0	13.4	13.4	3	.382	1	7-15	44.0	17.8	15.3	7	.404
27	n f	37.3	15.4	12.7	5	.412	2	7-16	33.8	13.3	12.5	8	. 393
28	n f	41.9	19.0	13.9	4?	.435	-	, ,,	33.0	13.3	12.5		5398
29	n f	46.3	16.3	16.7	6	.352	3	n f	38.4	15.3	14.0	6	.398
30	n f	39.4	16.3	13.0	4	.413	4	n f	44.8	19.1	16.5	6	.426
31	n f	43.0	17.0	13.8	4	.395	5	n f	41.4	17.0	15.2	6	.410
32	n f	44.0	18.6	15.2	4	.422	6	n f	30.0	11.7	11.0	6	.390
33	n f	40.4		15.0	4	.400	7	n f	38.3		13.7?	8	. 446
34	n f	38.6	15.7	14.0	4	.406	8	n f	39.0	13.9	15.3	7	.356
35	n f	44.5	17.0	17.0	7	.382	9	n f	44.4	16.2	17.5	7	.364
36	n f	40.0	16.2	15.0?	5	.405	10	n f	41.7	17.4	13.8?	6	.417
					4.1	.389	11	n f	33.2	12.8	12.0	6	.385
							12	n f	40.7	16.8	14.9	5?	.412
Ti	rolites	serra	teloba	tus KI	TTL 1	903	13	n f	41.5	18.6?		6	. 448
							14	n f	41.2	15.6	14.7	6	.378
1	5 - 5	54.3	9.9	26.2	2	.182	15	n f	35.0	13.9	12.2	7	.397
2	5-6	55.7	11.9	23.1	4	.213	16	n f	41.8	17.1	14.4	8	.409
					3	.197	17	n f	40.0	17.4	14.2	5	.435
			9 191				18	n f	44.3	17.9	12.9	6	.404
T11	rolites	smiri	agini	(AUERB	ACH)							6.4	. 404
1	11-6	47.4	22.0	15.5	18	.464	т;,	colites	toulo	; к ттт	1 1003		
		47.4	22.0	13.3	18	464	111	Olices	toura	T KILL	L 1703		
2	n f	51.2	23.1	18.5	13	.451	1	11-11	59.1	26.0	21.7	15	.439
3	n f	39.5	17.3	12.8	19	.437	2	11-12	46.7	20.0	15.0	12	.428
4	n f	42.2	18.4?		13	.436							.5433
5	n f	42.0	18.6	14.5	15	.442	3	n f	50.4	19.9	18.5	7?	.394
6	n f	40.5	16.6	13.0	12	.409	4	n f	47.0	20.0	16.5	10	.425
7	nf	36.4	14.4	12.8	22	.395	5	n f	47.2	20.3	16.8	10	.430
8	n f	51.4	22.3	16.2	22	.433	6	nf	38.7	14.4	14.0	10	.372
9	n f	47.4	19.3	16.0	19	.407	7	n f	44.8	18.8	14.0	11	.419
10	n f	40.8	15.7	14.7	20	.384	8	n f	37.0	14.3	12.0	9	.386
					17.3	.425	9	n f	42.9	18.2	13.8	9	.424
							10	nf	44.1	17.8	15.2	10	.403
Tir	rolites	spino	sior K	ITTL 1	903							10.3	.412
1	11_5	74 0	25 7	25 (1.0		m:			J MO	ICTCOV.	r.cc 10	000
1	11-5	76.0	35.7	25.6	16 16	.469 469	111	olites	turgi	dus Mo.	J3130V	103 10	002
2	n f	44.1	18.2?		13?	.412	1	10-8	58.6	24.2	20.0	1.7	.412
3	nf	51.8		16.6?		.471	•	10 0	30.0	24.2	20.0		7412
4	n f	60.5	28.0?		15	.462	2	n f	61.5?	25.6	20.5	11	.416
5	nf	67.4	30.4	20.6		.451	3	n f	53.4	23.9?		16	.447
6	n f	61.8	28.3?	-	16	.457	4	n f	50.5	22.3	12.5	10	.441
					$\frac{10}{14.6}$	-	5	n f	56.8	24.0	20.2	12?	.422
							6	n f	58.2	24.2?		17?	.415
Tir	olites	spino	sus MO.	JSISOV	ICS 18	382	7	n f	46.9	19.2	16.3	12?	.409
			1853500 1				8	n £	56.0	24.5	20.3	15	.437
1	9-7	57.9	23.9	19.4	14	.412	9	n f	38.4	19.0	13.2	16	.494
					14	412	10	n £	47.6	21.0	16.0	14	.441
2	nf	37.3	15.4	12.8	9	.412	11	n f	47.0	21.6	14.5	17	.459
3	n f	61.6	30.4	19.8	11	.493						14.2	.435
4	n f	36.6	15.6?	14.3	10	.426							
5	n f	49.5	22.0	16.9	12	. 444	Tir	olites	undula	tus Kl	TTL 19	03	
6	n f	48.4	18.8	18.3	12	.388							
7	n f	46.2	19.9	15.6	9	.430	1	7-13	55.0	21.2	18.3	5	.385
8	n f	40.8	17.3?	13.5	7	.424						-5	385
9	n f	35.2	15.8	11.4	10	.448	2	n f	52.7	21.5	17.9	5?	.407
10	n f	38.6	16.2	12.8		.419	3	n f	60.6	24.4	20.4	4	.402
					10.2	.429	4	n f	38.0	14.0	14.0	7	.368
							5	n f	44.5	16.3	15.5	5	.366
							6	n É	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.

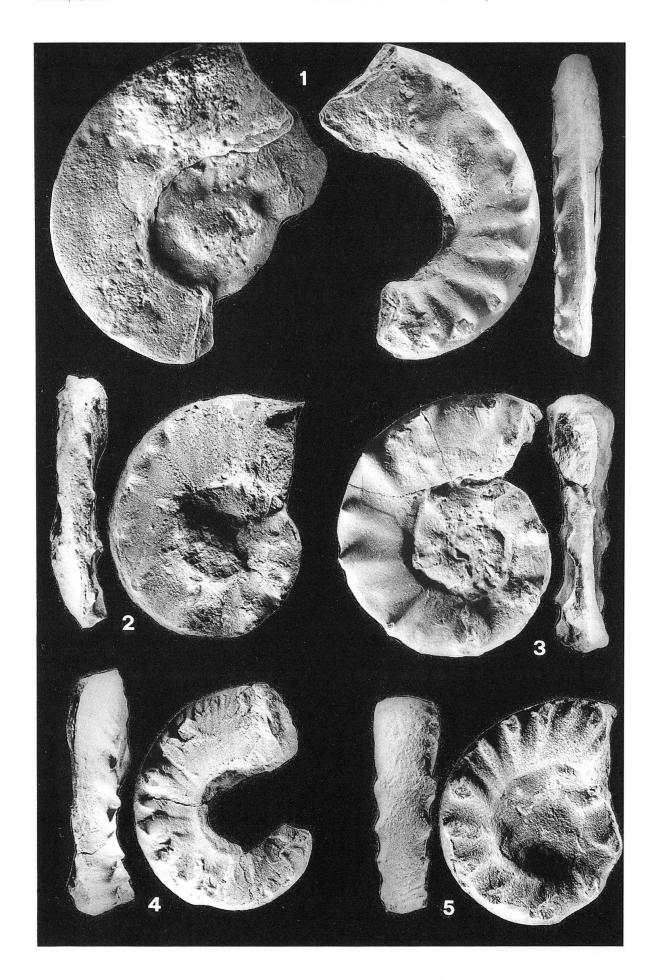


Plate 3

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.

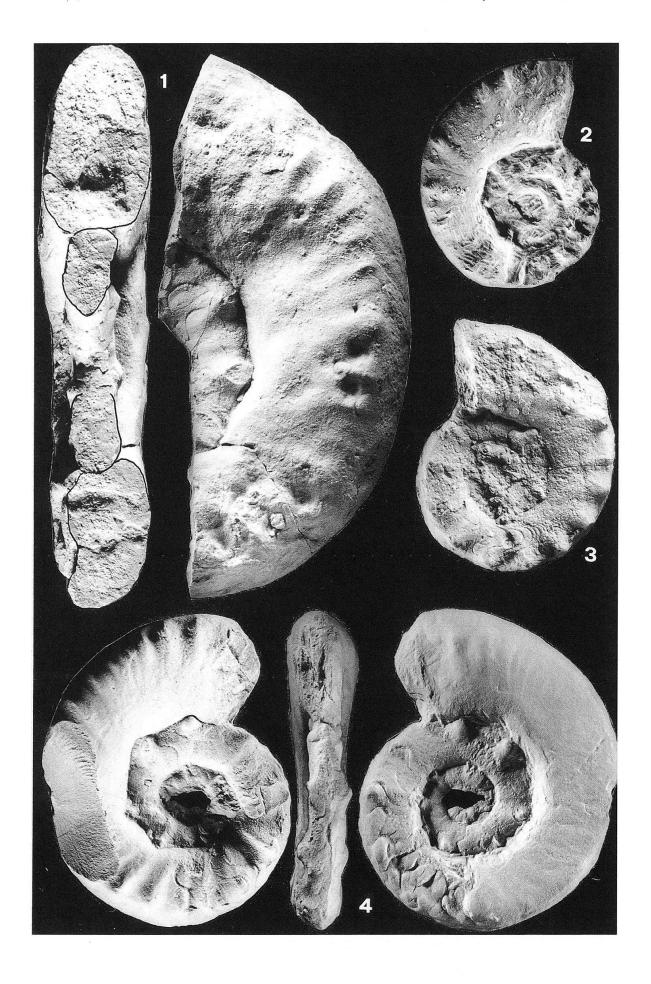


Plate 4

All figures natural size

- Fig. 1-9. *Tirolites illyricus* Mossisovics from the unit a of the Csopak Marl Formation, Sóly 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, Sóly section, Bakony.

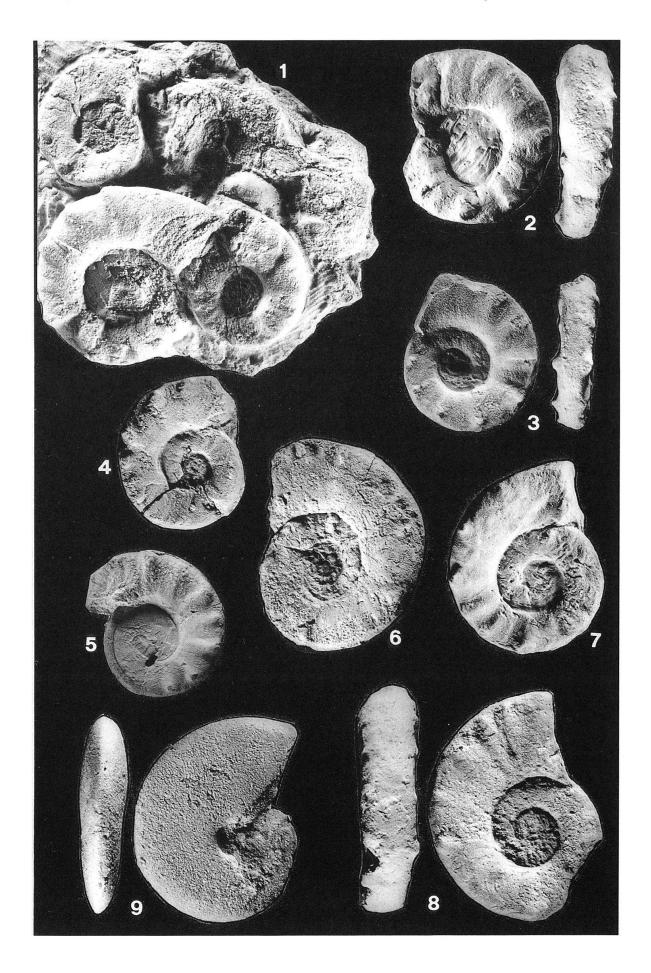


Plate 5

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.

