

TAXONOMY, STRATIGRAPHY AND PHYLOGENY OF THE NEW GENUS *LANCEOPTYCHITES* (AMMONOIDEA, ANISIAN)

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Riassunto. Viene effettuato per la prima volta uno studio popolazionistico degli Ptychitidae compressi (Ammonoidea) raccolti strato-per-strato nel Calcare di Prezzo (Anisico superiore, Alpi meridionali). Si dimostra come in alcune popolazioni di Ptychitidi compressi durante l'ontogenesi si possa verificare una modificazione del ventre, che diventa subacuto/fastigato mentre la sezione del giro diventa lanceolata. Questo particolare sviluppo della zona ventrale non è dovuto ad anomalie di crescita, come talvolta riportato in letteratura, ma è un normale sviluppo ontogenetico. Gli Ammonoidi con questo tipo particolare di ontogenesi sono separati dal genere *Flexoptychites*, che comprende quindi gli Ptychitidi compressi con ventre arrotondato, ed inclusi nel nuovo genere *Lanceoptychites*. Il nuovo genere è un discendente secondario di *Flexoptychites* e comprende 4 specie: *L. velox* (tipo) sp. n., *L. styx* sp. n., *L. indistinctus* (Mojsisovics) e *L. charlyanus* (Diener). *L. styx* ed il suo discendente peramorfico *L. velox* sono specie stratofenetiche. Entrambe le specie sono istituite su materiale proveniente dal Calcare di Prezzo, dove sono limitate alla parte media della zona a *Paraceratites trinodosus* (Illyrico). *L. indistinctus* (Mojsisovics) e *L. charlyanus* (Diener) vengono rivisti sulla base dello studio dei tipi. Poiché non è disponibile nessuna informazione sulla distribuzione strato-per-strato dei tipi, questi taxa restano semplici morfospesie.

Abstract. For the first time a population analysis of compressed Ptychitidae (Ammonoidea) bed-by-bed collected from Prezzo Limestone (Upper Anisian, Southern Alps) is performed. The analysis allows to demonstrate that within some populations of compressed ptychitids during the growth the venter may become subacute/fastigate and the section lanceolate. This modification is not due to growth anomalies, as sometimes believed in literature, but is a normal ontogenetic development. The ammonoids with this peculiar ontogeny are moved from the genus *Flexoptychites*, that groups the compressed ptychitids with rounded venter, into the new genus *Lanceoptychites*. The new genus is a secondary descendent of *Flexoptychites* and comprises 4 species: *L. velox* (type) sp. n., *L. styx* sp. n., *L. indistinctus* (Mojsisovics) and *L. charlyanus* (Diener). *L. styx* and its peramorphic descendant *L. velox* are stratophenetic species. They are described from the Prezzo Limestone, where they are confined to the middle part of the *Paraceratites trinodosus* zone (Illyrian). No bed-by-bed information is available for *L. indistinctus* (Mojsisovics) and *L. charlyanus* (Diener). These morphospecies are revised on the basis of the type material.

Zusammenfassung. Anhand von horizontaliert aufgesammelten Fossilfolgen aus dem Prezzokalk (Südalpen), wird für flache Ptychitidae (Ammonoidea) erstmals eine Populationsanalyse durchgeführt.

Damit kann bewiesen werden, daß das Auftreten einer subakuten/fastigaten Externseite und eines lanzettförmigen Windungsquerschnitts während des Wachstums, bei flachen Ptychitidae, eine normale ontogenetische Entwicklung darstellt und dass es sich dabei nicht um Wachstumsanomalien handelt, wie manchmal in der Literatur vermutet wurde. Ammonoideen mit einer solch eigentümlicher Ontogenese werden nun aus der Gattung *Flexoptychites*, zu der nur noch flache Ptychitiden mit gerundeter Externseite gerechnet werden, ausgegliedert und zur neuen Gattung *Lanceoptychites* gestellt. Die neue Gattung ist eine sekundäre Abspaltung von *Flexoptychites* und umfasst zur Zeit aus vier Arten: *Lanceoptychites velox* sp. n. (Typusart), *L. styx* sp. n., *L. indistinctus* (Mojsisovics, 1882) und *L. charlyanus* (Diener, 1900). *L. styx* und seine peramorphe Abspaltung *L. velox* sind stratophenetische Arten aus dem Prezzokalk, wo sie auf den mittleren Abschnitt der Zone des *Paraceratites trinodosus* (Illyr) beschränkt sind. Über *L. indistinctus* (Mojsisovics, 1882) und *L. charlyanus* (Diener, 1900) gibt es keine gesicherten stratigraphische Angaben. Diese beiden Morphospezies werden anhand des Typenmaterials revidiert.

Introduction: summary of the knowledge on the west tethyan Ptychitidae.

The family Ptychitidae Mojsisovics, 1882 is a typical component of the open marine ammonoid assemblages during Anisian and in part Ladinian times. It groups leiostraca ammonoids with depressed to compressed coiling and a typical ammonitic suture line. The family is common in the Arctic, Pacific and Tethyan paleobioprovinces, while its episodic occurrence in epicontinental seas (Upper Muschelkalk: Urlichs & Kurzweil, 1997) is not surely related to living populations, but could be due to *post-mortem* drifting of the shells from the Tethys (Urlich & Mundlos, 1985). During the Pelsonian-Illyrian (Anisian) the family is represented in the Western Tethys by the genera *Ptychites* Mojsisovics, 1882, *Flexoptychites* Spath, 1951 and *Malleoptychites* Diener, 1916. The last genus is rare and restricted to red nodular limestones, while *Ptychites* and *Flexoptychites* are much more frequent and relatively facies-independent. Representatives of *Ptychites* and/or *Flexoptychites* are very abundant in red nodular limestones (i.e., Schreyeralm and Han-Bulog Limestones), but they can also be found

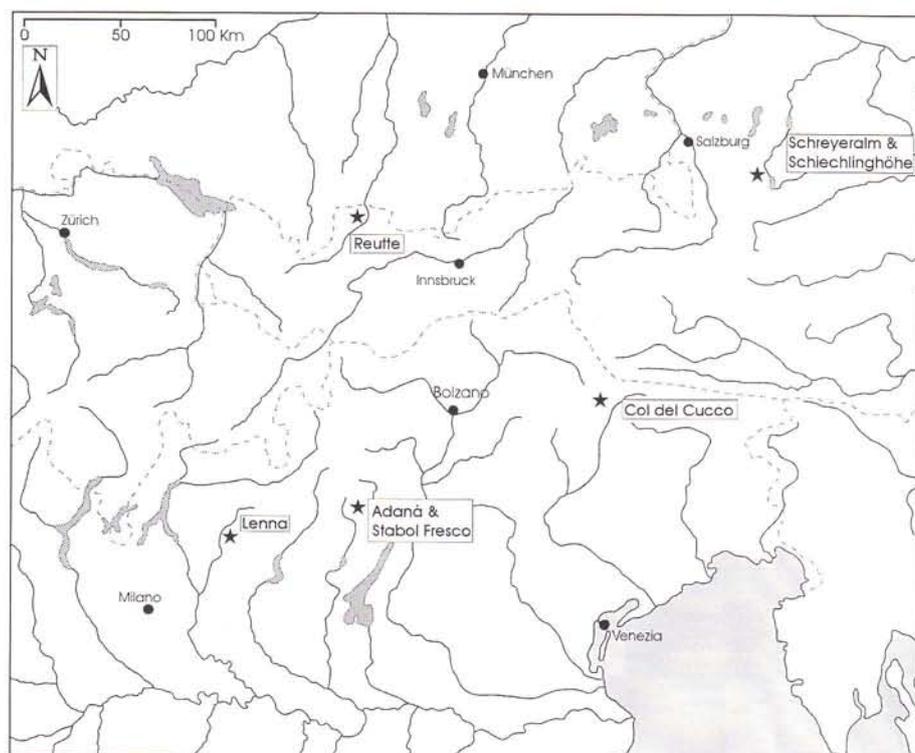


Fig. 1 - Location map of the most important Anisian localities of Southern and Northern Alps mentioned in the text.

in black or brown - bituminous limestones (i.e., Prezzo and Gutenstein Limestones), in sandy/silty limestones (i.e., Dont Formation) and in siliceous nodular limestones (i.e., Buchenstein Formation).

Despite the frequency in the stratigraphical record and the wide paleogeographic distribution, *Ptychites* and *Flexoptychites*, as the rest of the family Ptychitidae, are far from being well known. The history of the knowledge of the group is long and complex. *Ptychites* was formalized by Mojsisovics in 1875, and in a few years the genus grew including more and more species notably diverse in whorl section, coiling, size and suture line. The wide variety of species attributed to *Ptychites* was remarked by Mojsisovics (1882), who distinguished within the genus several groups of species. However the genus continued growing, and it gradually became a taxonomical basket, so large that in the Fossilium Catalogus 84 species were counted (Diener, 1915). Afterwards the content of that basket was gradually reduced by removing the most diverse species creating new genera, so that the taxonomy was shifted: the former genus *Ptychites* became a family composed by most of the previous groups of species raised to rank of genera. Much later (Tozer, 1981) moved *Discoptychites* Diener, 1916 (=Mojsisovics' group of *P. megalodiscus*) to the family Sturiiidae Kiparisova, 1958. Unfortunately this reorganization did not involve all the species formerly attributed to *Ptychites*, but only the more frequent and morphologically "extreme" forms. Several species, sometimes rare, often based on very few or single specimens, usually morphologically intermediate with respect to the leading forms of Mojsisovics' groups, were omitted.

phenological variability within true populations of individuals, but they were artificially assumed. At the present no good information on the stratigraphic relationships between the type specimens of these species is available. Therefore the problem of the understanding of the morphological features intermediate between different species cannot be solved because, the chronological and biological meaning of their relationships is unknown. All of these problems are common with Triassic ammonoids (Tozer, 1971), however in the case of Ptychitidae they are especially severe because the taxonomy of this family is much more influenced than that of other groups (i.e., the family Ceratitidae Mojsisovics, 1879) by collection from Anisian condensed red limestones (Schreyeralm and Han-Bulog Limestones), where three to four ammonoid zones are surely represented (Gaetani, 1969, p. 492).

The only way to solve these complex and inter-related taxonomical and stratigraphical problems should consist in the application of bed-by-bed (population) analyses to fossil-bearing sequences (stratophenetic approach s.l.: Gingerich, 1979; Dzik, 1987) possibly corresponding to historical localities. This paper shows the first result of the attempt at applying this technique to the Ptychitidae of two Illyrian sections of the Giudicarie (Southern Alps).

The new data from the Southern Alps.

Prezzo Limestone (Rosenberg, 1962; Assereto & Casati, 1965) is a southern alpine Middle Triassic formation known since the last century for its rich ammo-

noid fauna. In the study area (Fig. 1 and 2), which is located in the type area of the formation (Giudicarie), the Prezzo Limestone is about 80 m thick (Gaetani, 1969). The unit consists of rhythmic alternation of 10-20 cm thick dark grey marly limestones and equivalent thickness of dark grey to black marls or shales. In the upper 20 meters of the formation ammonoids and bivalves (*Daonella*) occur quite frequently in the limestone beds, while nautiloids, brachiopods and gastropods are rare. The limestone beds are very poor in sedimentological structures and textures. They do not show any features of the typical (proximal) tempestites or turbidites (erosional base, grading, cross lamination etc.), however this lack of structures should be compatible with both distal facies of event deposits or with cyclic sedimentation.

Two sections (Adanà and Stabol Fresco; Fig. 2) have been bed-by-bed sampled in the years 1989-1992 in the upper part of the Prezzo Limestone for a total amount of about 60 days of field work. All the limestone beds of Adanà section have been quantitatively sampled by mean of a motordriller, while Stabol Fresco has been quickly sampled by hammer for comparison. Some tens of fossil-bearing beds have been recognized. Except for the daonellids, which often occur in coquina-like layers, all the fossils found in the field have been kept and prepared in laboratory, even the poorly preserved ones. All the fossils collected in the same bed have been grouped into the same sample, which is named after the acronym of the section and the number of the bed. The samples are often composed by more than 100 cephalopods so that they are significant for the study of the original cephalopod assemblages.

Preservation of the ammonoids.

The specimens are preserved with the test. The phragmocones are almost completely filled by cements and the inner whorls are often recrystallized. The specimens do not show size-sorting within samples: very small to very large-sized specimens can be found, but the frequency distribution of the size is usually unimodal and the maximum frequency is at small size. The sediment infilling of the body chambers is identical to the rock matrix. The specimens are often slightly elliptical, due to fractureless lateral deformation (Seilacher et al., 1976). None of the features reported by Fernandez-Lopez (1985) as typical of taphonomic reworking (sensu Fernandez-Lopez & Melendez, 1994) have been observed. As a consequence the samples are not composed by mixed faunas, and their stratigraphic succession is a normal and undisturbed time sequence. Each sample is a chrono-assemblage of specimens which were living in the same interval of time. The time duration of the chrono-assemblages is at the present not defined, and depends on the time significance of the bedding: ~ 0 for distal tempestites/turbidites or $\gg 0$ (19-23ky) for cyclic bedding.

If the rich ammonoid record of the Prezzo Limestone is perfect from a theoretical point of view, from a practical point of view it is very difficult to study. A lot of specimens are broken during preparation because of the hardness of the rock and the recrystallization of the phragmocones. The likelihood of breakage is directly related to the size of the specimens, so that it is very difficult to prepare complete "mature" specimens. Lack of "mature" specimens prevents from the full understanding of the morphology of the very common young specimens. Moreover the study of the ontogeny of "mature" individuals is difficult because their recrystallized inner whorls cannot be exposed by preparation.

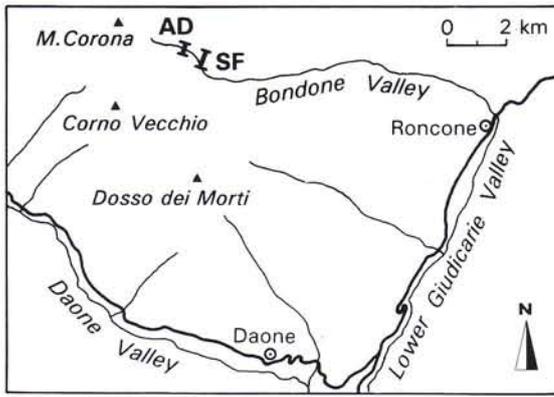
Distribution of Ptychitidae in the studied sections.

Ptychitidae are relatively common in Adanà and Stabol Fresco sections. Their abundance may change from bed to bed, but the average frequency is about 30-40% of the collected specimens. Most of the Ptychitidae can be ascribed to the genus *Flexoptychites* Spath, 1951, while very few specimens belong to the genus *Ptychites* Mojsisovics, 1882. In Adanà section *Ptychites* has been found in levels AD81 (2 specimens), AD87 (1 specimen) and AD93 (1 specimen). The first occurrence of *Flexoptychites* is recorded in bed AD88 (3 specimens), then the range of the genus continues up to the top of the section. In a similar way in Stabol Fresco section *Ptychites* is confined to the lower levels (SF85A, 2 sp.; SF92A, 1 sp., SF96A, 1 sp.), while *Flexoptychites* is much more common in the middle and upper part of the section (FO in level SF93A).

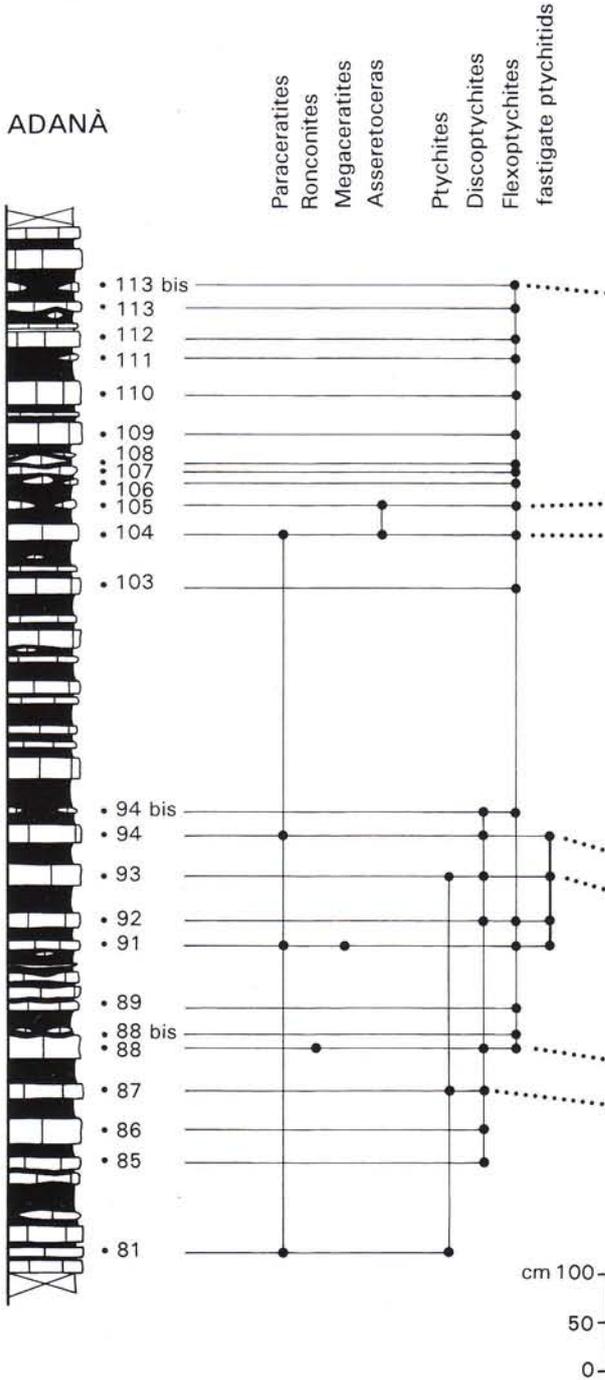
The rare occurrence of *Ptychites* does not allow any analysis of population variability. Moreover the small size of the specimens (diameter less than 3 cm) makes the comparison with the typical *Ptychites* from literature very difficult.

The attempt at studying the population variability of *Flexoptychites* leads to better results. The high frequency of *Flexoptychites* sometimes allows to overcome the problems of the above mentioned unperfect quality of the fossil record in the Prezzo Limestone. When a large number of specimens is available from the same sample it is possible to understand the ontogeny of the chrono-population by arranging the specimens in sequence of size. Then the comparison of specimens with the same size allows to check the intra-population variability.

The morphological differences between the *Flexoptychites* of the different levels are very faint. The whorl section is quite constant within a sample, but changes from sample to sample. It seems to have some taxonomical significance even if it does not seem to display a clear and continuous stratigraphic trend. On the contrary the sculpture of the very weak ribbing does not seem to have taxonomical significance, because it shows indi-



ADANÀ



STABOL FRESCO DUE

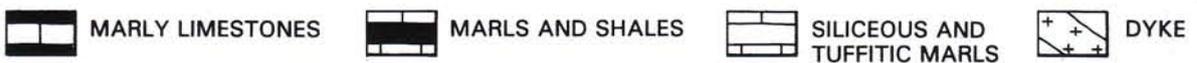
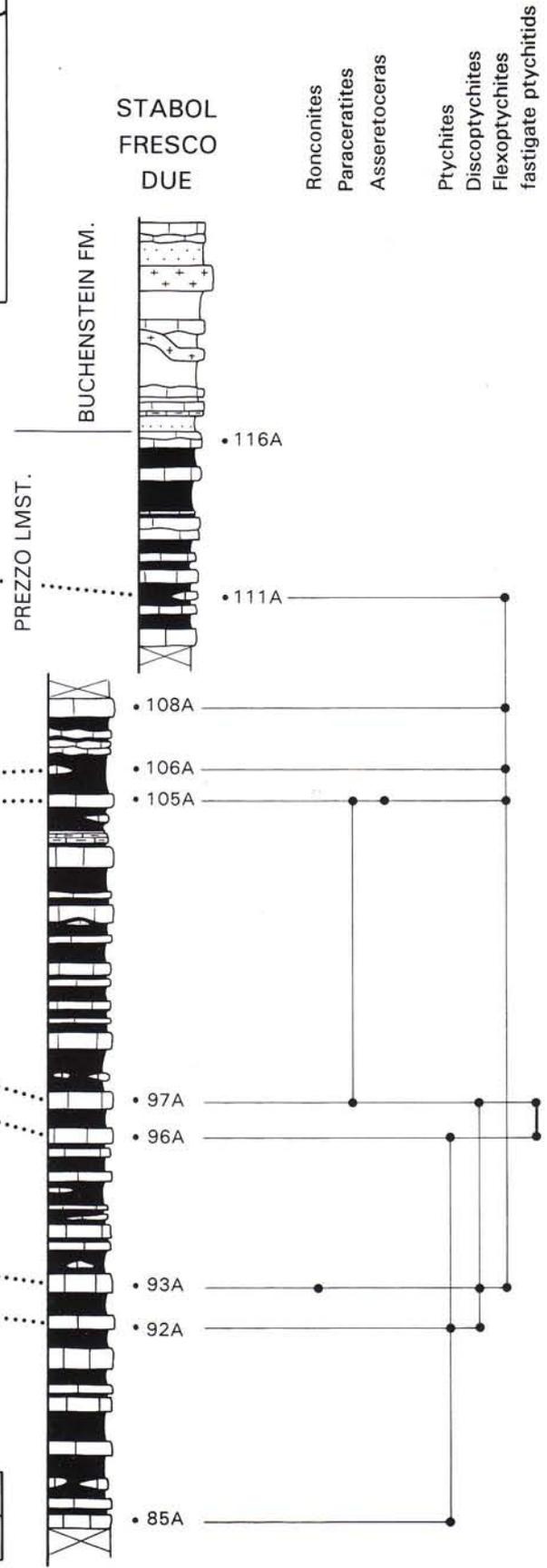




Fig. 3 - "Mature" *Flexoptychites* showing a modification of the body chamber close to the peristome. MPUM 8114 (SF94A-2), a) lateral view; b) ventral view. The arrow marks the beginning of body chamber. x 1.

vidual and ontogenetic variations within the same sample, without any significant difference from sample to sample. Much more difficult is to test the suture line and the umbilical area, because they are visible on a very few specimens within the samples (usually less than 10%). This restriction makes the classification of the specimens hard, because often in literature a great taxonomical weight is attributed to these characters. On the basis of the few observations of suture line and umbilical areas at the moment it is just possible to suggest a similarity between the lower samples (AD88-AD94b) and *Flexoptychites gibbus* (Benecke).

If the analysis of the variability of the classical taxonomical characters is complex, two new observations have been done. An unusual feature has been often observed on the "mature" specimens with preserved peristome. The body chamber of largest specimens from the levels AD89, AD112, AD113bis and SF94A shows a sudden narrowing followed by a widening near to the peristome that is produced by an undulation of the shell without any thickening of the test (Fig. 3). This development is similar to the constricted aperture of nauti-

loids (see Teichert, 1964) and is very unusual with respect to what is in general known on *Flexoptychites*. The interpretation of this feature is still open. Taking into account that complete "mature" specimens are extremely rare in the collection, the relative frequency of this modification is very high. Two possible explanations can be suggested: late ontogenetic epidemic pathologies or a "normal" origin. The latter can be a non-pathological feature of both males and females or a dimorphic character. In both the "normal" explanations it is very strange that the constriction has never been reported out of the Prezzo Limestone basin.

A second unusual feature has been observed within the samples of the interval AD91-AD94 and SF96A-SF97A. Here a group of compressed Ptychitidae looking like the classical *Flexoptychites* (group of *E. flexuosus*, type of the genus) in coiling, ornamentation and suture line, shows a quite complex ontogenetic modification of the ventral side. Quite early during the growth the venter becomes fastigate, then acute, while the whorl section becomes slender, sometimes lanceolate. This group has been analyzed in detail.

Fig. 2 - (facing page) Sketch of Adanà (AD) and Stabol Fresco Due (SF) stratigraphic sections, showing also the range of the ptychitids by comparison with the most important ceratitids. Numbers on the side of the sections are the identification numbers of the fossil bearing levels recognized within the interval of interest. Dotted lines draw bed-by-bed correlations of the most important fossiliferous levels of the two sections. The distance between the two sections is about 300 m.

Ontogeny and population variability of the fastigate ptychitids.

The composition of the samples from the levels AD91-AD94 is shown in Tab. 1. From a practical point

of view it is possible to include the very few specimens from Stabul Fresco section into the chrono-assemblages of Adanà. The two sections are very close and their levels can be physically and paleontologically correlated one by one (Balini, 1992a; Fig. 2).

Level	Total number of specimens	Fastigate Ptychitidae	<i>Flexoptychites</i>	<i>Ptychites</i>	<i>Discoptychites</i>	Ptychitidae ind.	Pinacocerataceae ind.
AD94	260	34	-	-	17	26	19
AD93	310	35	-	1	12	12	16
AD92	132	12	8	-	6	10	14
AD91	166	6	4	-	-	26	-

Tab. 1 - Total number of specimens collected in levels AD91-AD94 of Adanà section and classification of the ammonoids of the superfamily Pinacocerataceae. Very small or fragmentary specimens are classified only at family or superfamily level. Most of the specimens from level AD91 are crushed, then just a minor part of them has been classified at genus level.

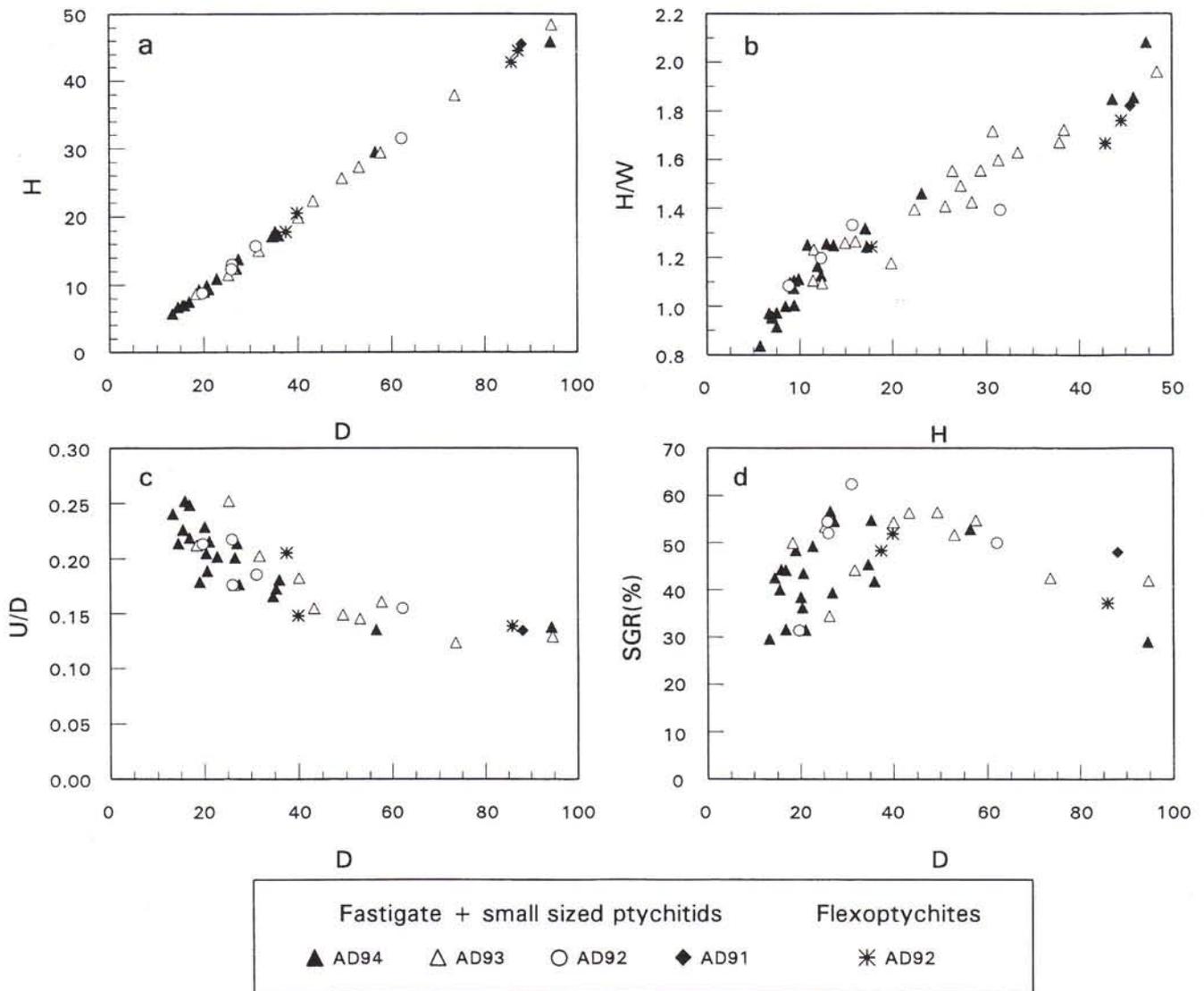


Fig. 4 - Biometrical analysis of the compressed ptychitids from chrono-assemblages AD91 to AD94. The fastigate ptychitids and very small specimens of AD93 and AD94 are grouped together (black and white triangles) because in these samples medium sized to "mature" *Flexoptychites* have not been found. For AD92 *Flexoptychites* (*) is instead separated from the fastigate and small sized ptychitids (5 sp.). The only specimen of AD91 is a fastigate form. The measurements that are not provided in the Systematic descriptions can be found in the Appendix.

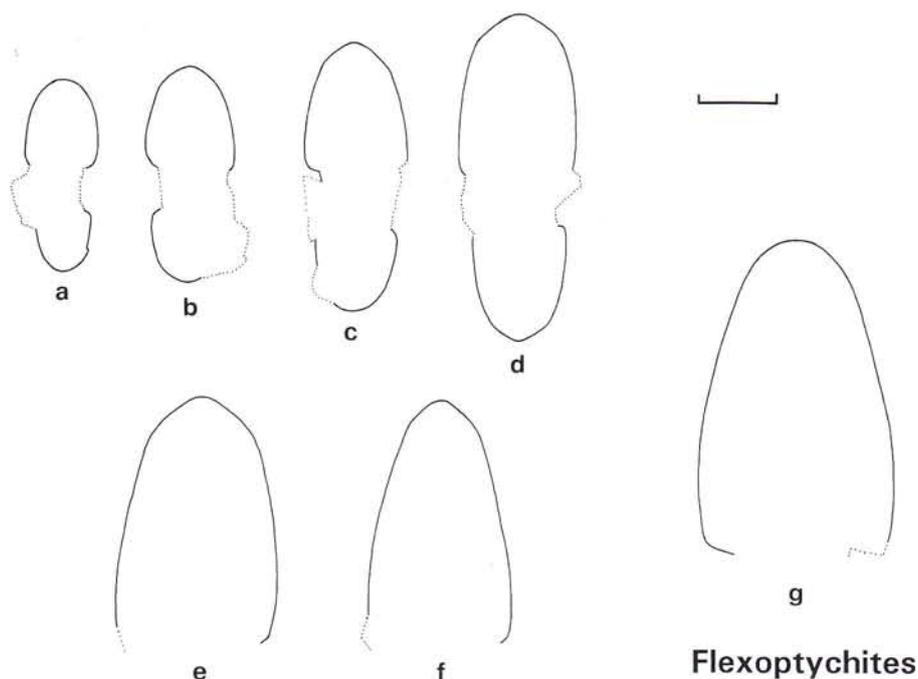


Fig. 5 - Whorl sections of the compressed Ptychitidae from chrono-assemblages AD92 to AD94. a) young Ptychitidae, MPUM 8104 (AD94-25); b) young Ptychitidae, MPUM 8105 (AD94-19); c) fastigate ptychitid showing on minor height semi-elliptical whorl section with rounded venter and subfastigate venter on the major height, MPUM 8106 (AD94-195); d) fastigate ptychitid, MPUM 8107 (AD94-194), the position of the diametral section is shown by asterisk on pl. 3, fig. 6a; e) thick variant of fastigate ptychitid, MPUM 8102 (AD93-4); f) compressed variant of fastigate ptychitid, MPUM 8103 (AD93-10); g) *Flexoptychites*, MPUM 8115 (AD92-1). Bar scale 1 cm.

Flexoptychites

Most of the information on fastigate ptychitids comes from the levels AD93 and AD94, for this reason the chrono-assemblages are treated in reverse stratigraphical order.

Chrono-assemblage AD94.

Within the wide range of size represented in this sample (Fig. 4a-d), approximately 1/6 of the specimens are of large size (some incomplete ones cannot be measured). The rest is mainly of small size, being the medium size scarcely represented. The size sequence analysis of the specimens leads to demonstrate that they are ontogenetically related. No classical *Flexoptychites* have been identified in the chrono-assemblage.

In the very inner whorls the coiling is slightly involute, the whorl shape is semi-elliptical and the venter is rounded (Fig. 5a-b). Until $D=22-27$ mm (H between 11 to 13-14 mm) the whorl width W increases more slowly than H (Fig. 4b). At $H=11-14$ mm the coiling and whorl shape change. H/W increases more slowly (Fig. 4b), the whorl section is still semi-elliptical, but the venter becomes subacute (specimens MPUM 8110 [AD94-14], MPUM 8106 [AD94-195], MPUM 8116 [AD94-7 and -24]). About a quarter of whorl further, at about 19-20 mm of H, the venter becomes fastigate (Fig. 5c-d). The beginning of the "mature" body chamber is at 40-50 mm of H (the specimens are slightly elliptical) where an umbilical egression occurs (specimens MPUM 8093 [AD94-1], MPUM 8094 [AD94-3], MPUM 8095 [AD94-4], MPUM 8092 [AD94-193]: not shown in Fig. 4). At the beginning of this final stage of growth the whorl section is still semi-elliptical with fastigate venter. Quickly the ventral side becomes acute and the whorl

section slender and lanceolate. In the last quarter of the body chamber the section becomes subrectangular by the appearance of rounded shoulders, and the venter becomes again fastigate (for more details and illustrations see Systematic descriptions). The end of the "mature" body chamber is marked by the constriction close to the peristome.

The conclusion of the geometrical analysis of the shell is that the fastigate ptychitids of the chrono-assemblage AD94 are one single group. At the present no subdivision is possible within this group on the basis of the ribbing and suture line. The ribbing is quite simple: rib-type is primary and intercalatory-bifurcate. Ribs are very weak to extremely weak. They are vanishing near to the periumbilical border and near to the ventral side or to the shoulder. For this reason the rib shape of small specimens sometimes looks convex. On the "mature" body chamber ribbing is always fading. The suture line is rarely well preserved, however it is almost equivalent to *Flexoptychites* with respect to the number of elements and the pattern of dentitions (Fig. 6).

Chrono-assemblage AD93.

This group is mainly composed by medium sized specimens. The specimens of this group are fully equivalent in ribbing and suture line (Fig. 6) to those of AD94.

The youngest stage of growth does not seem to be different with respect to AD94. The few measurements available overlap the values of the small specimens from AD94, and the specimen MPUM 8113 (AD93-27; not figured) shows the appearance of the subacute venter between 11.5 and 13 mm of H, as in AD94. The medium

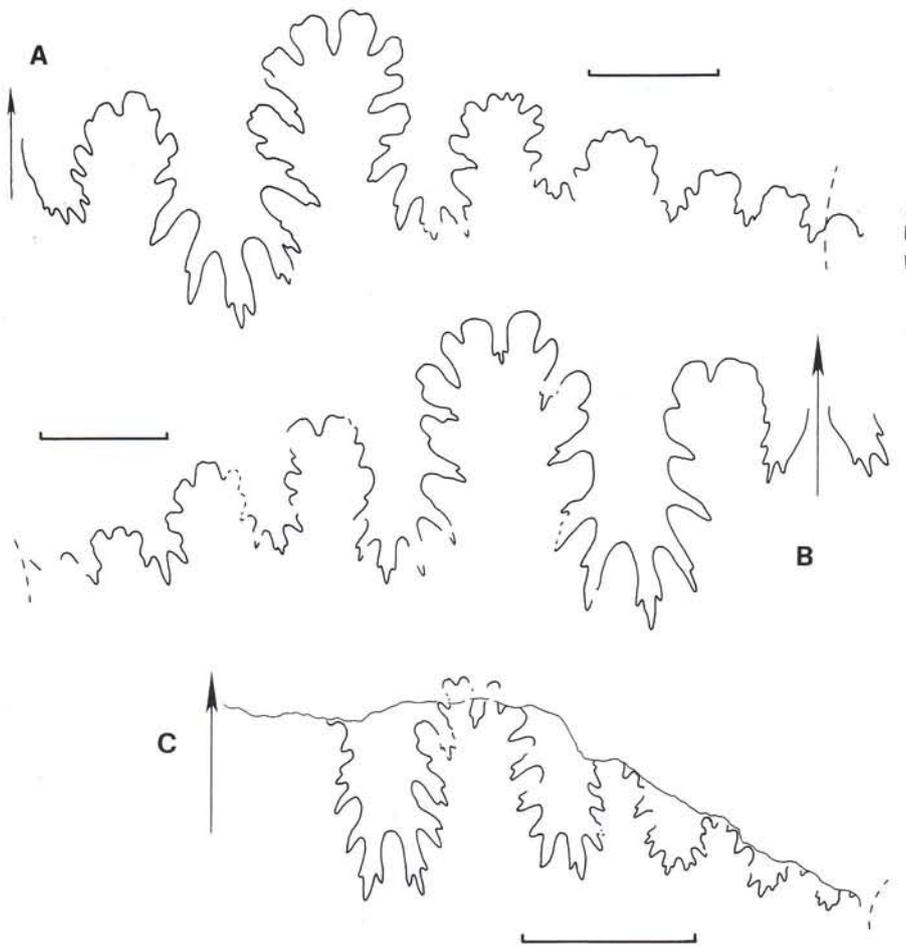


Fig. 6 - Suture lines of fastigate ptychitids from the Prezzo Limestone: A) specimen MCNSB 2694; B) specimen MPUM 8103 (AD93-4); C) specimen MPUM 8108 (AD94-8). Bar scale is always 0.5 cm.

Chrono-assemblages AD92 and AD91.

The scarce material from the levels AD91 and AD92 does not allow a true population analysis, however the few elements available can be compared to chrono-assemblages AD94 and AD93. From the biometrical point of view AD91 and AD92 are equivalent to AD93 and AD94 (Fig. 4a-d). The ornamentation and the suture lines are also similar. From young to intermediate stage of growth the ventral development does not differ from that of the same sized specimens of the chrono-assemblages AD93 and AD94. The development of the "mature" specimens is simplified with respect to AD94, as in the specimens from AD93. On 5 large sized but incomplete specimens 4 show the constriction on the body chamber.

sized individuals ($40 < D < 80$) show a fairly wide variability in the thickness of the venter (Fig. 5e-f) and in the value of H/W, so that it is possible to distinguish thicker and slender variants. The variation of H/W is about 20% (1.42-1.71, at 30 mm of H), however most of the specimens fall in the middle range of variation (Fig. 4b).

Up to the intermediate stage of growth the specimens of the chrono-assemblages AD93 and AD94 are fully similar. AD93 shows a wider variability, but this might be explained by the larger number of specimens available. On the contrary the "mature" body chamber is different in the two chrono-assemblages. The specimens available from AD93 display a more simplified modification of the venter. The semi-elliptical-fastigate stage is not followed by the sharpening of the venter as in AD94, moreover the section does not become slender. The venter may become subacute, sometimes also sublanceolate (just one very incomplete fragment: MPUM 8118 [AD93-305]) but the subrectangular-fastigate stage is never developed. At the end of the body chamber the venter turns back rounded and wider without any appearance of shoulders (for more details and illustrations see Systematic descriptions). The termination of the "mature" body chamber is underlined by the constriction, as in AD94 (Pl. 2, fig. 1a-b).

respect to AD94, as in the specimens from AD93. On 5 large sized but incomplete specimens 4 show the constriction on the body chamber.

Taxonomical position of the fastigate ptychitids.

After the bed-by-bed population analysis it is demonstrated that the unusual development of the ventral side shown by the compressed ptychitids of the interval AD91-AD94 is not anomalous (i.e., pathological) but is a normal character that appears during ontogeny. Then there are no drawbacks in the use of ventral ontogeny for taxonomical purposes. The rich literature on Ptychitidae leads to find that subacute or acute venters occur, even if rarely, in this group. Sometimes these features have been treated as anomalous developments of *Flexoptychites* (Spath, 1951; Venzo & Pelosio, 1968), but some other authors used them to separate species as *Ptychites indistinctus* Mojsisovics, 1882 and *Ptychites charlyanus* Diener, 1900. Both species are here revised on the basis of the study of type material (see Systematic descriptions). *P. indistinctus* has a subacute ventral side which becomes rounded on the "mature" body chamber, without any constriction. *P. charlyanus*, in the past regarded as a abnormal (pathological?) *Flexoptychites* (Spath, 1951, p. 150), has a lanceolate section already at juvenile stage of growth. Both species differ from the

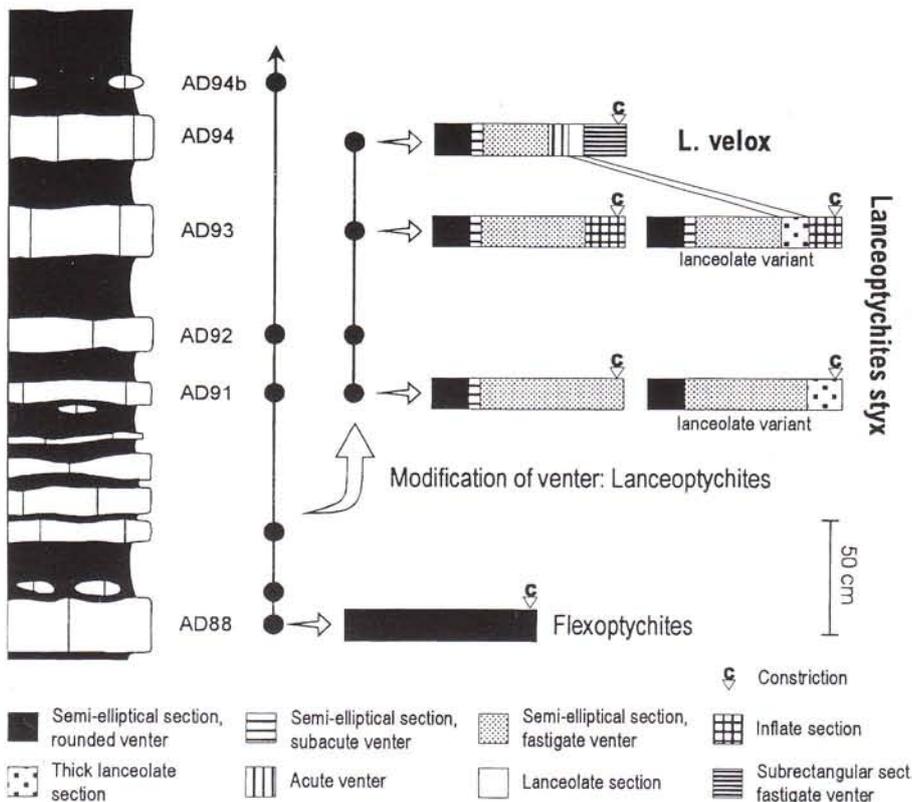


Fig. 7 - Morphological variability of compressed ptychitids from Giudicarie, compared with the bed-by-bed distribution. The reference section is Adanà, but the populations include also the specimens from Stabol Fresco Due section. Length of bar diagrams corresponds to "mature" size; relative length of stages is proportional, but not to scale. The method is summarized by Landman & Geysant, 1993, fig. 2.

specimens from the Prezzo Limestone, but altogether they support the erection of a new genus *Lanceoptychites*. On the basis of the morphology of the "mature" body chamber the specimens from Giudicarie are divided into two species. *L. velox* sp.n. (type-species of *Lanceoptychites*) groups the "mature" specimens from AD94 while *L. styx* sp. n. is based on the adult specimens from AD91-AD93. Small to medium sized specimens are not classified at species level.

At the first glance the default of a taxonomy in which species are classified on the basis of "mature" specimens is that small to medium sized individuals, sometimes quite abundant, cannot be fully classified. However, it must be pointed out that: a) small to medium sized specimens can be classified into the genus *Lanceoptychites* since 22-27 mm of diameter, which is a quite reasonably small size; b) the typical feature of the new genus (ventral side) is easy to be detected; c) the classification at species level of small to medium sized specimens ($30 < D < 40-50$ mm) is virtually impossible also within the very similar genus *Flexoptychites*; d) the stratigraphic range of *Lanceoptychites* is so short that even specimens with open classification at species level are useful for dating and correlating stratigraphic sections (see above).

Stratigraphical distribution and significance of *Lanceoptychites* gen. n.

Lanceoptychites has been identified from the Alps to Bulgaria (see Systematic descriptions), however bed-

by-bed data are available only from Giudicarie, where the range of the genus is confined to the middle part of the *Paraceratites trinodosus* zone (Fig. 2). This biozone is here understood as range zone based on *Paraceratites* s.s. (group of *P. elegans* [Mojsisovics, 1882] and *P. trinodosus* [Mojsisovics, 1882]). The lower boundary of this biozone is drawn between AD80 and AD81 in Adanà section, and between SF85A and SF86A in Stabol Fresco section. The upper boundary is respectively located between AD104 and AD105, and SF105A and SF106A (Balini, 1992a). The FO of *Lanceoptychites* is coeval to the occurrence of *Megaceratites fallax*, type-species of the genus *Megaceratites* Balini, 1992. The LO is older than the FO of the genus *Asseretoceras* Balini, 1992 (Balini, 1992b).

On the basis of the available data *Lanceoptychites* could be the only genus among the leiostraca ammonoids potentially useful as a guide fossil for the *Paraceratites trinodosus* zone. The new genus is easily distinguished and it is reported not only from the pelagic facies (red limestones) where the leiostraca are dominating elements of the assemblages, but also in more restricted (shallower?) environments (Reutte and Lombardia-Giudicarie), where the trachyostraca are much more frequent. However, the practical usefulness of *Lanceoptychites* depends on its frequency, that seems to be quite low in the red limestone, at least from literature. Among the several explanations for this rare occurrence (sampling, taxonomical mistakes in literature, reworking) I uphold the one related to the condensation of the red limestones. In this kind of highly condensed facies ammonoid biozones are recorded as cm-thin intervals (i. e., Krystyn, 1983), then the short time range of *Lanceoptychites* could be, from locality to locality, fully or in part equivalent to one of the several hiatuses.

Phylogeny of *Lanceoptychites* gen. n.

On the basis of the bed-by-bed data from the Giudicarie *Lanceoptychites* is here interpreted as a secondary descendant of the early *Flexoptychites* that develops a modification of the ventral side (Fig. 7). This interpretation is supported by the coiling and the whorl section of the inner whorls, the suture line, and the ribbing which are almost equivalent in the two genera. At species level *L. velox* seems to be a peramorphic descendant (Alberch et al., 1979) of *L. styx*. As the "mature" size of both species is identical the mode of evolution is the acceleration in the modification of the ventral area. More in details two trends can be recognized: appearance of new shapes and emphasizing.

The position of *L. indistinctus* and *L. charlyanus* in this model is at present open because no bed-by-bed information on their stratigraphic range is available. The ventral development of *L. indistinctus* and *L. charlyanus* compared with *L. styx* - *L. velox*, should suggest an earlier stage for *L. indistinctus*, and a final one for *L. charlyanus* (see Systematic descriptions). However this speculation does not take into account the problem of the understanding of the constriction close to the aperture of the *Lanceoptychites* from the Prezzo Limestone. At least *L. indistinctus* lacks this feature so that if the constriction is a normal ontogenetic character of the Prezzo Limestone compressed ptychitids, its lacking in *L. indistinctus* would make difficult the placing of *L. indistinctus* in between the sequence *Flexoptychites* - *L. styx*. A final solution should require stratophenetic information on the population of *Flexoptychites* from other areas, possibly from Han-Bulog-type red limestone. A possible polyphyletic status for *Lanceoptychites* could be also taken into consideration.

Systematic descriptions.

The family-group taxonomy is taken from Tozer (1981).

Figurations. Whorl sections have been drawn from photocopies of sectioned casts (Balini, 1994). All the suture lines have been drawn with x6 and x12 enlargements, then the relative size of saddles and lobes have been cross-compared with the specimen. All the specimens figured in the photographic plates have been whitened by Ammonium Chloride.

Acronyms. GBA=Sammlungen der Geologischen Bundesanstalt, Wien; NHWGPA=Naturhistorisches Museum, Wien; BSP=Bayerische Staatsammlung für Paläontologie, München; IGF=Museo di Paleontologia, Università di Firenze, Firenze; MCSNB=Museo Civico di Scienze Naturali "E. Caffi", Bergamo; MPUM=Museo di Paleontologia, Università di Milano, Milano;

MSNM=Museo di Storia Naturale, Milano; NMB=Naturhistorisches Museum, Berlin.

Numbering of the specimens from Prezzo Limestone. Every specimens mentioned in the text is identified by both registration number and collecting number. The latter, in brackets, reports the bed of collection and the individual number of the specimen (i.e., AD94-193: 193rd specimen from the bed 94 of Adanà section).

Dimensions. D=diameter (mm)=H+h+U; H=max. whorl height in D (mm); h=min. whorl height in D (mm); U=umbilicus in D (mm); W=whorl width in H (mm); SGR(%)=((H-h)/h)x100. If not otherwise specified all the measurements refer to internal mould (steinkern).

Order Ceratitida Hyatt 1884

Superfamily *Pinacocerataceae* Mojsisovics 1879

Family *Ptychitidae* Mojsisovics 1882

Genus *Lanceoptychites* gen. n.

Type-species *Lanceoptychites velox* sp. n.

Derivatio nominis. The name points out the lanceolate outline of the whorl section.

Diagnosis. Involute and compressed ptychitids equivalent to *Flexoptychites* in coiling, ornamentation and suture line, but showing more or less acute modifications of ventral side at intermediate to "mature" stage of growth.

The whorl section of the inner volutions until 11-14 mm of whorl height is semi-elliptical and the ventral side is rounded. Then the venter becomes subacute or fastigate. After this stage the development differs from species to species. The subacute/fastigate venter may persist on the first half of the "mature" body chamber, then the ventral side comes back rounded. In other species the whorl section evolves towards a lanceolate outline. This kind of section can be achieved at small-medium size or on large "mature" body chamber. In the latter case the lanceolate stage may regress towards a rounded venter or may evolve towards a subrectangular section with fastigate ventral side.

The ammonitic suture line shows six or six saddles and half between the ventral side and the periumbilical margin. The pattern of dentitions is almost equivalent to *Flexoptychites* Spath, 1951.

Composition of the genus: *Lanceoptychites velox* sp. n., *Lanceoptychites styx* sp. n., *Ptychites indistinctus* Mojsisovics, 1882, *P. charlyanus* Diener, 1900.

Discussion. Some species whose names could suggest morphological relations with the species belonging to *Lanceoptychites*, are instead excluded from the new genus.

Ptychites acutus Mojsisovics, 1882 is surely excluded from *Lanceoptychites* and confirmed in *Flexoptychites* Spath, 1951. Despite of its name, this species does not show acute ventral side, but compressed and slender whorl section with narrow but undoubtedly rounded venter (pers. observation on the type series housed in

PLATE I

- Fig. 1 - *Lanceoptychites velox* sp. n., holotype, MPUM 8092 (AD94-193): a) lateral view, b) ventral view; x 1.
 Fig. 2 - *Lanceoptychites velox* sp. n., paratype, MPUM 8096 (SF97A-15): a) lateral view, b) ventral view; x 1.
 Fig. 3 - *Lanceoptychites velox* sp. n., paratype, MPUM 8095 (AD94-4): a) lateral view, b) ventral view; x 1.



the NMB and in the GBA). A whorl section typical of the species is shown by Mojsisovics, (1882) on plate 64, figure 4b. This figure fits very well with the original, housed in Wien (GBA 1882/03/309).

The species *Ptychites fastigatus* Diener, 1900, is excluded from the new genus because its suture line, well figured by Diener (1900) on pl. 3 fig. 1c (pers. observation on the type: GBA 1900/03/35), is undoubtedly typical of the genus *Discoptychites* Diener, 1916.

Occurrence. The genus is surely reported from the dark limestone of Reutte (Tyrol), from the red limestone of Schreyeralm and Schiechlinghöhe (Salzkammergut), and from Golo-Bardo (SW Bulgaria). In the Southern Alps the genus is documented in the Prezzo Limestone of Giudicarie and Brembana Valleys and in the Ambata Formation of Anisei Valley (Dolomites). For more details see the occurrences of the species.

Age. The best bed-by-bed data are available only from the Prezzo Limestone, in the Southern Alps, where the range of the genus is restricted to the middle part of the *Trinodosus* Zone, Illyrian (Anisian, Middle Triassic).

Lanceoptychites velox sp. n.

Pl. 1, fig. 1-3; pl. 2, fig. 4a-b; fig. 8a-i

v ?1968 *Flexoptychites gibbus* - Venzo & Pelosio, p. 128, pl. 17, fig. 4a-c.

v ?1968 *Flexoptychites angusto-umbilicatus* - Venzo & Pelosio, p. 130, pl. 17, fig. 8a-b, 10, 11a-b.

Derivatio nominis. From the Latin *velox* -*velocis* (=fast).

Type series. Holotype: MPUM 8092 (AD94-193)(Pl. 1, Fig. 1; Fig. 8a-e). Paratypes (4 specimens): MPUM 8093 (AD94-1), 8094 (AD94-3), 8095 (AD94-4), 8096 (SF97A-15).

Stratum typicum and locus typicus. Prezzo Limestone, bed AD94 of Adanà section, laterally equivalent to bed SF97A of Stabol Fresco section. The locus typicus is Adanà section (Bondone Valley, Giudicarie).

Diagnosis. Large sized *Lanceoptychites* showing a slender lanceolate section on the "mature" body chamber, followed by the appearance of shoulders. At the end of the body chamber the whorl section becomes subrectangular with fastigate venter.

Description. In the holotype the height of the whorl at the beginning of the body chamber is 49.5mm. The venter is fastigate until 45° from the beginning of the body chamber (Fig. 8a), then it becomes acute and the section slender (Fig. 8b). At about 70° a lanceolate section is developed (Fig. 8c). The appearance of the shoulders is gradual and occurs at round 110° (Fig. 8d-e). In the paratypes the fastigate stage may be longer (90° in MPUM 8094 [AD94-3]) or shorter (MPUM 8095 [AD94-4] at 40° is already in the acute stage). The acute stage is always quite short: less than 40° in 8094 (AD94-4) and 25° in 8094 (AD94-3). The appearance of shoulders occurs in less than 30° in AD94-1. The length of the body chamber is 180-200°. The constriction is weak, but visible on MPUM 8093 (AD94-1) (not figured) and 8095 (AD94-4) (Pl. 1, fig. 3a).

The ribbing is extremely weak. On the paratypes 6-7 sinuous and simple ribs can be counted per half whorl. The ribs are fading towards both the umbilical border and the ventral area. On the holotype the ribbing is almost evanescent.

The suture line is not sufficiently well preserved to be drawn. The holotype displays at least 6 saddles on the lateral side. The pattern of the ammonitic frilling is *Flexoptychites*-like.

Dimensions.

	D	H	h	U	W	H/W	U/D	SGR
8092 (AD94-193)	130.10	57.40	50.20	22.50	-		0.172	14.34
8093 (AD94-1)		47.25			22.70	2.08		
8094 (AD94-3)		43.60			23.60	1.84		

Discussion. The morphology of the new species is so peculiar that the classification is simple, when almost complete large-sized specimens are available. The new species is similar to *L. styx* sp. n., that shows a slower change in the shape of the venter and in the whorl section. It must be pointed out that the two species belong to the same lineage, that is actually not continuous. The field of variation of the body chambers of *L. velox* do not overlap the variation of *L. styx*. *L. velox* shows always the acute slender and the subrectangular-fastigate stages (Fig. 8b, g; 8d-c, h-i) that are never displayed by *L. styx*. The discontinuity supports the separation of two stratophenetic species (Gingerich, 1979; Dzik, 1987).

Remarks on the synonymy. Some of the *Ptychitidae* from the Prezzo Limestone of Lenna (Brembana Valley) were not understood by Venzo & Pelosio (1968). Some small specimens showing the typical fastigate venter of the young *Lanceoptychites* were misplaced and classified as *Flexoptychites gibbus* (pl. 17, fig. 4) or as *Flexoptychites angusto-umbilicatus* (pl. 17, fig. 8, 10, 11). Due to the small size these specimens cannot be classified at species level. It is worth noting that better material was available to Venzo & Pelosio. Two large sized *Lanceoptychites* have been found in the unclassified part of their collection, housed in MCSNB. One (MCSNB 9190) is well preserved and is here attributed to *L. velox*, while the fragmentary preservation of the second (MCSNB 9189) prevents from a full classification.

Occurrence. The species is known from the Prezzo Limestone (Southern Alps). In the Giudicarie from Adanà section, level AD94, 4 specimens, and Stabol Fresco section, level SF97A, 1 specimen. In these sections the species is restricted to one level, in the middle part of the *Paraceratites trinodosus* zone. The species is also present in the Prezzo Limestone at Lenna (Brembana Valley). There, the fossil bearing levels are not only two, as reported by Venzo & Pelosio (1968), but many more (pers. obs.). Unfortunately the material studied by Venzo & Pelosio was not collected bed-by-bed.

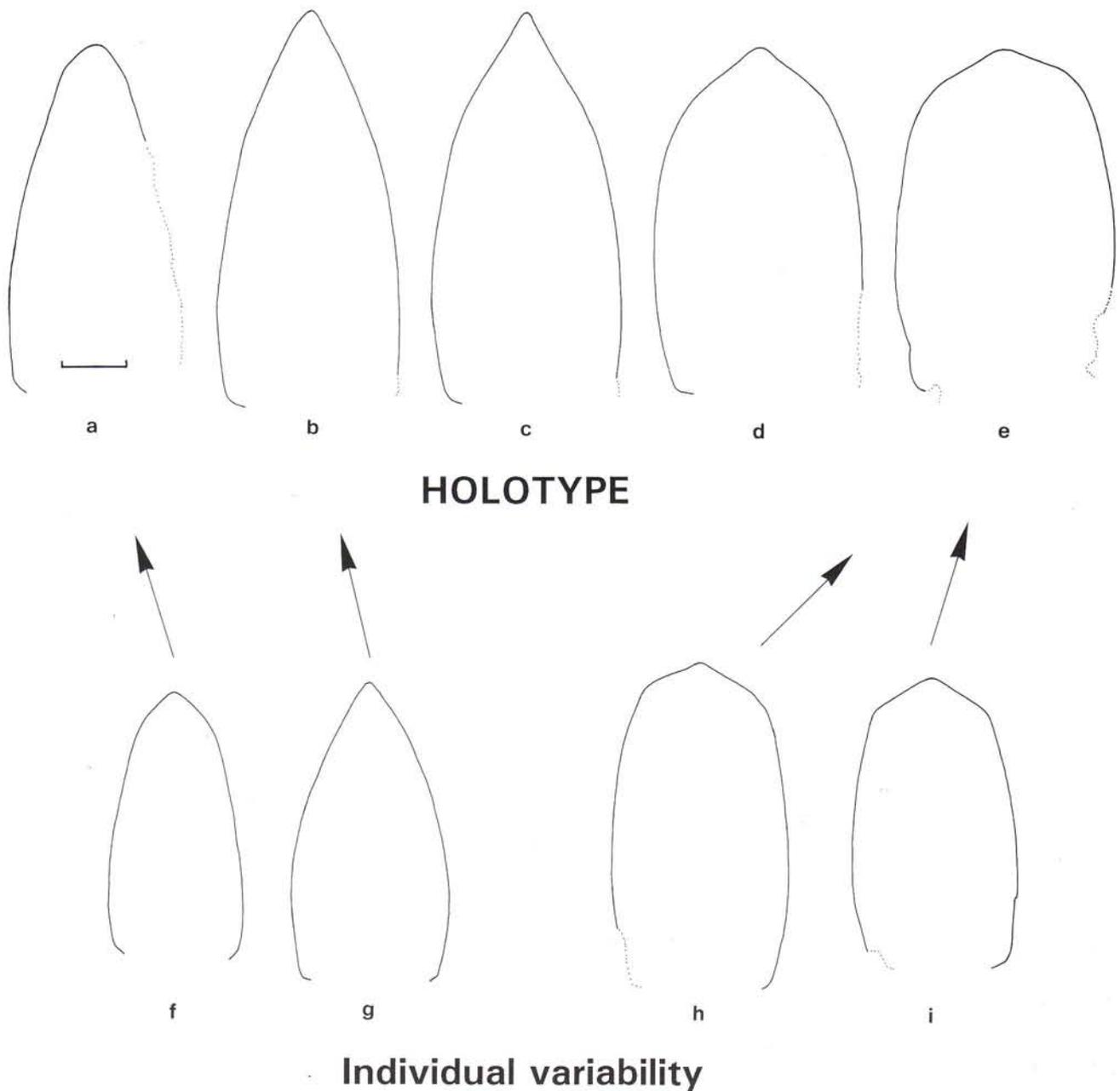


Fig. 8 - Whorl sections of *Lanceoptychites velox* sp. n. a) holotype, MPUM 8092 (AD94-193), example of semi-elliptical whorl section with fastigate venter (the position of the section is shown by asterisk on pl. 1, fig. 1a); b) same specimen, 35° after section a, example of acute venter; c) same specimen, lanceolate section 60° after a); d) same specimen, 108° after section a, the height is reduced with respect to the section c) because the specimen is elliptized; e) same specimen, 135° after section a, showing a fully developed subrectangular section with fastigate venter; f) paratype, MPUM 8094 (AD94-3) (see position marked with asterisk on pl. 2, fig. 4a); g) same specimen, 77° after the section f; h) paratype, MPUM 8095 (AD94-4) (see position marked with asterisk on pl. 1, fig. 3a); i) paratype, MPUM 8093 (AD94-1), section 150° from the last suture line. Bar scale 1 cm.

Lanceoptychites styx sp. n.

Pl. 2, fig. 1-3; fig. 9a-c

- v ? 1968 *Flexoptychites gibbus* - Venzo & Pelosio, p. 128, pl. 17, fig. 4a-c.
- v ? 1968 *Flexoptychites angusto-umbilicatus* - Venzo & Pelosio, p. 130, pl. 17, fig. 8a-b, 10, 11a-b.
- v 1968 *Flexoptychites angusto-umbilicatus* (Böckh) forma gerontica anomala - Venzo & Pelosio, p. 130, pl. 17, fig. 13a-e.

Derivatio nominis. From the Latin *Styx* -*Stigis* (mythological river).

Type series. Holotype: MPUM 8097 (SF96A-1)(Pl. 2, Fig. 1a-b; Fig. 9b-c). Paratypes: 6 more or less complete specimens MPUM 8100 (AD91-48), 8099 (AD91-49), 8101 (AD92-19 and AD92-101), 8098 (AD93-3).

Stratum typicum and locus typicus. Prezzo Limestone, bed SF96A of Stabol Fresco section (Giudicarie), laterally equivalent to level AD93 of Adanà section (Giudicarie). The locus typicus is Stabol Fresco section.

Diagnosis. Large sized *Lanceoptychites* showing fastigate venter on the "mature" body chamber. In some specimens the venter may gradually become rounded at the end of the body chamber. The ven-

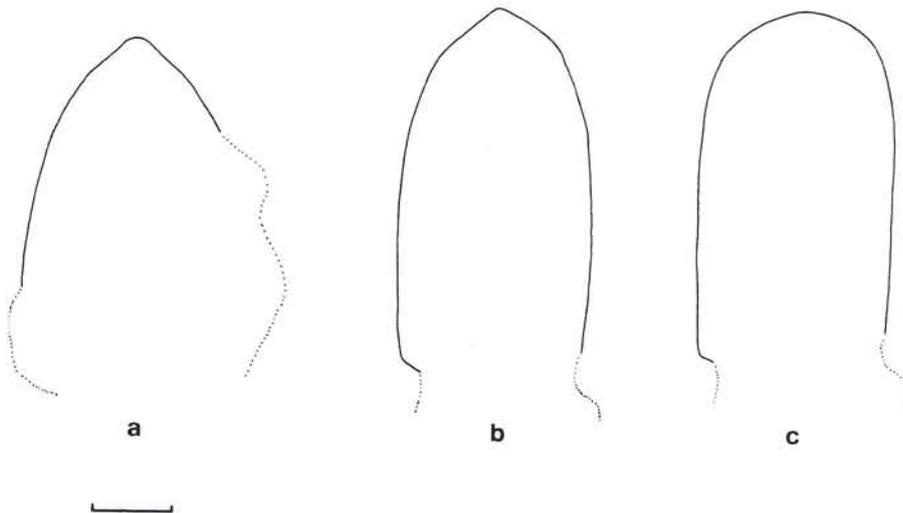


Fig. 9 - Whorl sections of *Lanceoptychites styx* sp. n.: a) paratype, MPUM 8099 (AD91-49), showing a faint sublanceolate section; b) holotype, MPUM 8097 (SF96A-1) (position shown by asterisk in pl. 2, fig. 1a) ; c) same specimen, section 37° after the section b. Bar scale 1 cm.

tral area is always rather thick (inflate) so that the whorl section is never as slender as in *L. velox* sp. n. More developed variants show a thick subacute stage and a sublanceolate section after the fastigate stage. However, there is no appearance of shoulders on the body chamber, and the subrectangular-fastigate stage is never displayed.

Description. The holotype only consists of the last 110-120° of a "mature" body chamber, but it is the most complete specimen within the type series. It shows the constriction and the peristome. In the first part of the preserved body chamber (30-40°) the whorl section is semi-elliptical and the venter fastigate (Fig. 9b). Then, in the remaining 80°, the venter becomes rounded and so broad that the lateral sides are almost parallel (Fig. 9c). The specimen MPUM 8098 (AD93-3) is submature and consists of a 220° long body chamber. At the end of the preserved body chamber (48-50 mm of H) the venter is still fastigate.

The "mature" paratypes from level AD91 do not show rounding of the venter. One of them shows a little more developed ventral area, because the fastigate venter seems to be followed by a weakly lanceolate section (Fig. 9a). In the "mature" paratypes from AD92 the rounding of the venter occur in the last 20° of body chamber.

Ribs are sinuous but evanescent. The suture line is not visible.

Dimensions (mm).

	D	H	h	U	W	H/W	U/D	SGR
8098 (AD93-3)	94.70	48.40	34.10	12.20	24.70	1.95	0.128	41.93

measurements corrected because of a calcite vein.

Discussion. *Lanceoptychites styx* sp. n. is morphologically intermediate between *L. velox* sp. n. and *L. indistinctus* (Mojsisovics, 1882). The separation between *L. styx* and the type species of the genus has been already discussed.

As regard the comparison with *L. indistinctus*, *L. styx* differs by the more complex modification of the whorl section. The whorl section of *L. indistinctus* is semi-elliptical but the venter is subacute, not fastigate. Moreover on the body chamber the venter becomes rounded, but the whorl section is always slender.

As regard the synonymy, the taxonomical position of the small specimens classified by Venzo & Pelosio (1968) as *Flexoptychites gibbus* and *F. angusto-umbilicatus* has been previously discussed. The larger specimen of plate 17, fig. 13 (MCSNB 2694), that was classified as gerontic and anomalous specimen by Venzo & Pelosio, is grouped together with the specimens collected from the Giudicarie, as lanceolate variant.

Occurrence. Prezzo Limestone (Southern Alps). In the Giudicarie the range of the species is restricted to the middle part of the *Paraceratites trinodosus* zone (Adanà section, bed AD91 to AD93; Stabol Fresco section, bed SF96A). The species is also known from Lenà (Brembana Valley), but no bed-by-bed information is available.

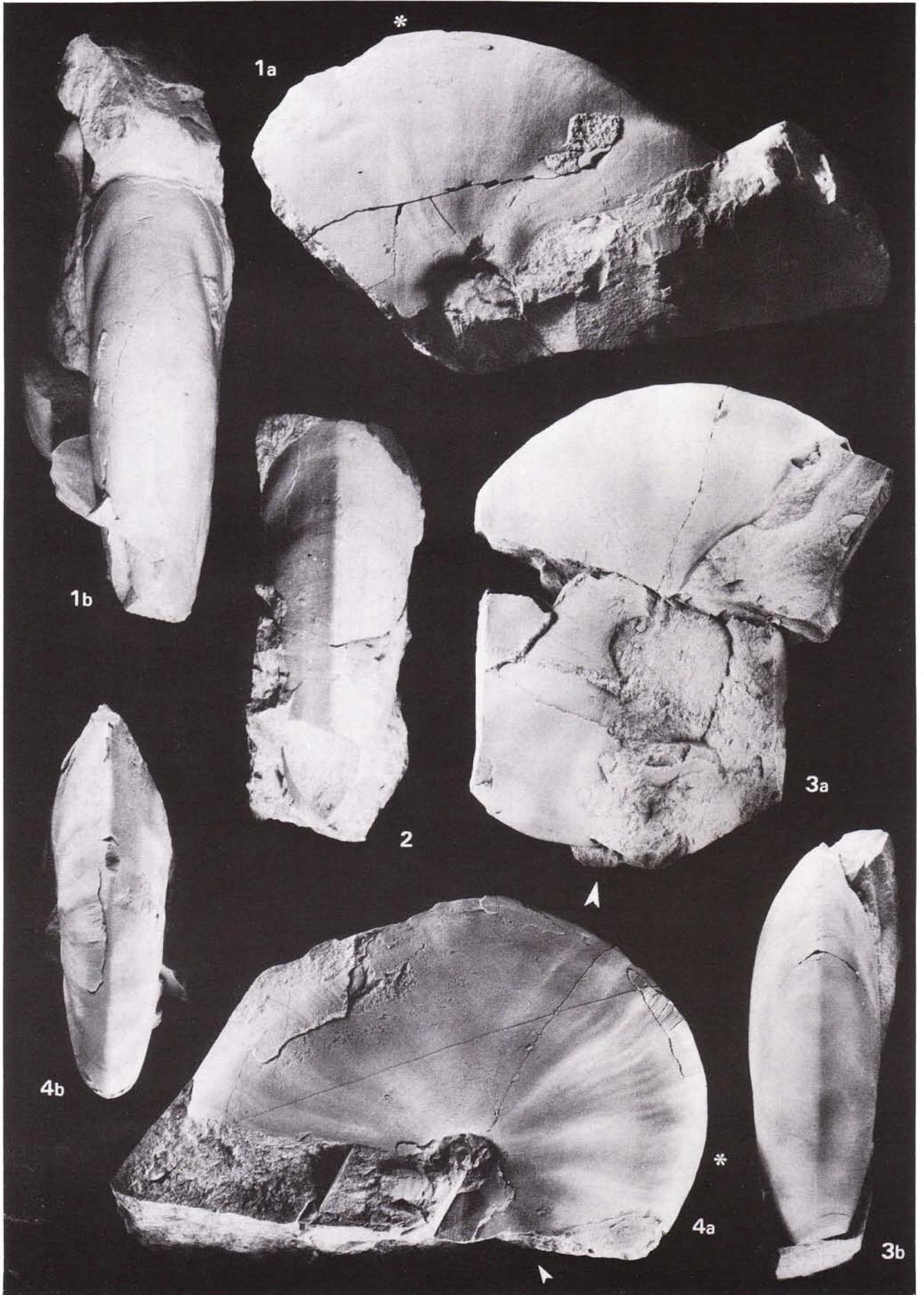
Lanceoptychites indistinctus (Mojsisovics, 1882)

Pl. 3, fig. 1a-b; fig. 10a-b, 11a-b

- v 1882 *Ptychites indistinctus* Mojsisovics, p. 263 *cum syn.*, pl. 67, fig. 1-2.
- v non1887 *Ptychites indistinctus* - Hauer, p. 45.
- ? 1900 *Ptychites* cf. *indistinctus* - Diener, p. 34.
- v non1904 *Ptychites* cf. *indistinctus* - Martelli, p. 130, pl. 12, fig. 3.
- 1912 *Ptychites* cf. *indistinctus* - Turina, p. 688.
- non 1916 *Ptychites indistinctus* - Kraus, p. 275.
- ? 1931 *Ptychites indistinctus* - Renz, p. 56 (nn).
- ? 1939 *Ptychites indistinctus* - Renz, p. 241 (nn).
- 1936 *Ptychites* cf. *indistinctus* - Stefanoff, p. 153, pl. 2, fig. 9.
- non 1964 *Ptychites indistinctus* - Celebic, p. 25, pl. 2 fig. 1a,1b.

PLATE 2

- Fig. 1 - *Lanceoptychites styx* sp. n., holotype, MPUM 8097 (SF96A-1): a) lateral view, b) ventral view; x 1.
- Fig. 2 - *Lanceoptychites styx* sp. n., paratype, MPUM 8099 (AD91-49), ventral view; x 1.
- Fig. 3 - *Lanceoptychites styx* sp. n., paratype, MPUM 8098 (AD93-3): a) lateral view, b) ventral view; x 1.
- Fig. 4 - *Lanceoptychites velox* sp. n., paratype, MPUM 8094 (AD94-3): a) lateral view, b) ventral view; x 1.



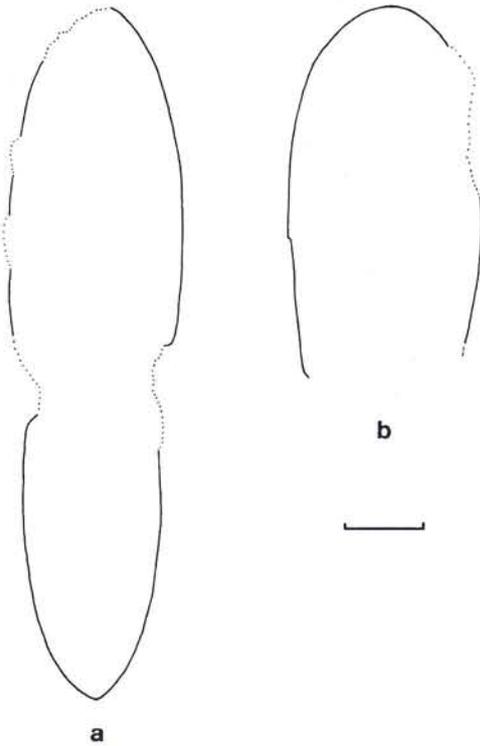


Fig. 10 - Whorl sections of *Lanceoptychites indistinctus* (Mojsisovics, 1882). Lectotype GBA 1882/03/310: a) diametral section showing semi-elliptical whorl section with subacute venter on the minor height (position shown by asterisk on pl. 3, fig. 1a); b) whorl section about 52° after the major height of the section a. Bar scale 1 cm.

- non 1972 *Ptychites (Flexoptychites) cf. indistinctus* - Brinkmann et al., p. 143 (nn).
 v 1982 *Flexoptychites indistinctus* - Fantini Sestini in Casati et al., p. 429 (nn).
 v 1982 *Flexoptychites flexuosus* - Fantini Sestini in Casati et al., p. 429 partim.

Type series. The type series was originally composed by four syntypes (Mojsisovics, 1882, p. 264): three from Schreyer Alm (Gosau) and one from Reutte (Tirol). Only one of the specimens from Schreyer Alm was figured, together with the specimen from Reutte. The type specimens have been searched for in the Institutions in Berlin, Budapest, München and Wien where most of Mojsisovics' collections are housed, but only the two figured specimens have been found: GBA 1882/03/310 (Mojsisovics' pl. 67, fig. 1) and BSP 1887 VII 501 (pl. 67, fig. 2). The largest one (GBA 1882/03/310) is here designated as lectotype (Mojsisovics, pl. 67, fig. 1; this paper Pl. 3, Fig. 1a-b; Fig. 10-11).

Stratum typicum and locus typicus. Schreyeralm Limestone at Schreyer Alm (Gosau, Austria).

Diagnosis. *Lanceoptychites* attaining large size, with semi-elliptical whorl section and subacute ventral side. On the "mature" body chamber the venter becomes rounded but the whorl section remains slender, *Flexoptychites*-like.

Revised description of the types.

Lectotype. The specimen is preserved as internal mould in part covered by recrystallized test. The last 200° of the outer whorl belongs to the body chamber. The surface of the phragmocone, especially on the right side, was grinded (probably by Mojsisovics) to make the suture line visible.

The coiling is involute ($U/D=0.14$) and the whorl section is compressed ($H/W=1.82-1.92$). Due to a breakage, the youngest visible whorl section is located at about 60° after the beginning of the outer whorl (95° before the last septum). There, at about 30 mm of whorl height, the section is semi-elliptical with subacute ventral side (see Fig. 10a). This shape of whorl section is kept until about 260° ($H \sim 42-43$ mm; about 115° after the last septum), then in less than 20° the ventral side becomes rounded (Fig. 10b). The periumbilical border, visible on the left side of the specimen which is not figured on plate 1, is a little rounded. The umbilical wall is subvertical.

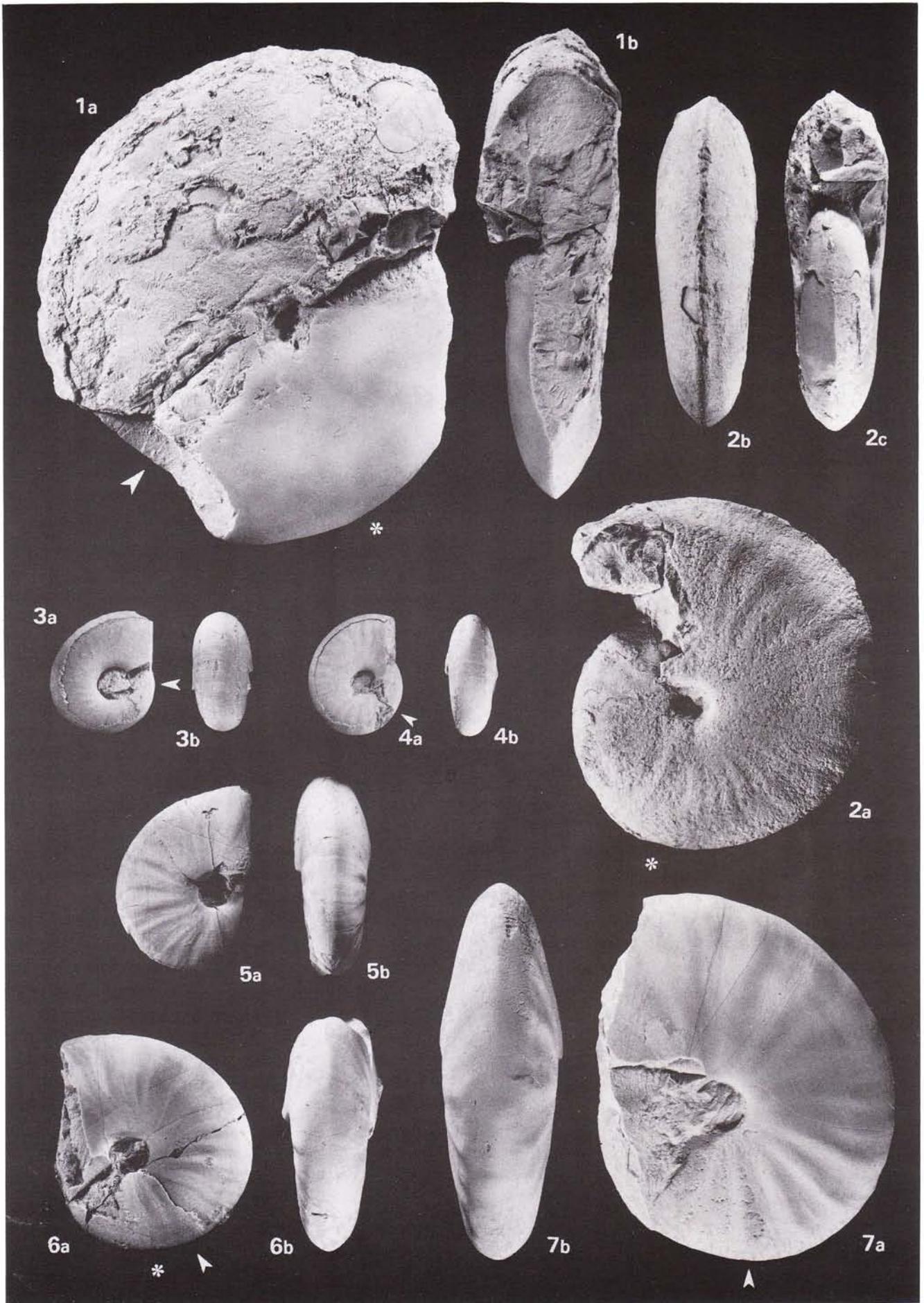
The ornamentation was probably represented by vanishing ribs. However, due to the bad preservation of the surface of the test combined with the smoothing for preparation of the suture lines, the ornaments are practically not visible.

The suture line is well exposed on both sides of the specimen. It is composed by 6 and a half saddles on the right side to which correspond 6 saddles on the left side (Fig. 11). The saddles are strongly frilled by *Flexoptychites*-like dentitions. The strong serration of the sutures leads to suppose a "mature" age of the specimen.

Paralectotype. The specimen is smaller, but similar to the lectotype in coiling, being U/D ratio equal (0.14) and SGR slightly higher (43.53). H/W ratio is lower but increasing (1.26 to 1.54) in the diameter. The whorl section is semi-elliptical. The ventral side is roun-

PLATE 3

- Fig. 1 - *Lanceoptychites indistinctus* (Mojsisovics, 1882), lectotype, GBA 1882/03/310: a) lateral view, b) ventral view; x 1.
 Fig. 2 - *Lanceoptychites charlyanus* (Diener, 1900), lectotype, GBA 1900/3/37: a) lateral view, b) ventral view, c) apertural view; x 1.
 Fig. 3-4 - Young Ptychitidae from the chrono-assemblage AD94.
 Fig. 3 - MPUM 8111 (AD94-208): a) lateral view, b) ventral view; x 1.
 Fig. 4 - MPUM 8112 (AD94-36): a) lateral view, b) ventral view; x 1.
 Fig. 5-6 - Young *Lanceoptychites* from the chrono-assemblage AD94. The light is optimized for ribbing, then the outline of the venter is not very well visible
 Fig. 5 - MPUM 8110 (AD94-14): a) lateral view, b) ventral view; x 1.
 Fig. 6 - MPUM 8107 (AD94-194): a) lateral view lacking of the last quarter of whorl, b) ventral view; x 1.
 Fig. 7 - Young *Lanceoptychites* from the chrono-assemblage AD93, MPUM 8109 (AD93-1): a) lateral view, b) ventral view; x 1.



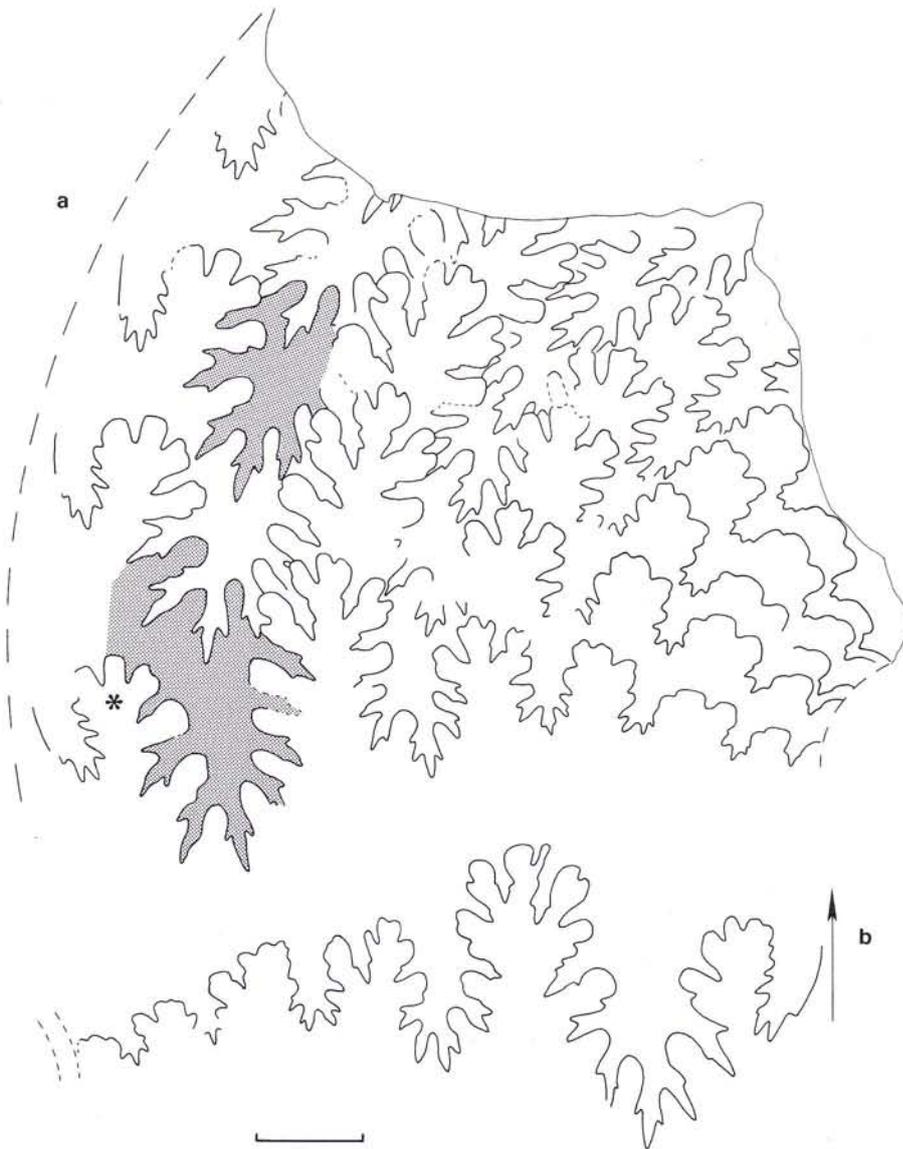


Fig. 11 - Suture line of *Lanceoptychites indistinctus* (Mojsisovics, 1882). Lectotype GBA 1882/03/310: a) sequence of sutures displaying a strong serration; b) left suture equivalent to the suture marked by asterisk in a). Bar scale 0.5 cm.

ded or rounded-subacuate in the first quarter of the outer whorl, then it becomes clearly subacuate in the last 110-120° of the outer whorl, after a breakage of the venter. The umbilical border is subangular and the umbilical wall is steep but not definitely vertical. The ornaments consist of extremely weak and sinuous ribs and the suture is *Flexoptychites*-like, with 6 saddles on the lateral side.

Dimensions (mm).

	D	H	h	U	W	w	H/W	U/D	SGR
GBA 1882/03/310	87.90	43.00	31.90	13.00	22.70	17.50	1.89	0.147	34.79
BSP 1887 VIII 501	57.20	28.85	20.10	8.25	18.70	15.90	1.54	0.144	43.53

Italic: measurement influenced by test remains.

Discussion. The two types are described separately because they came from two different localities then they do not belong to the same population. The missing of two of the types of *Lanceoptychites indistinctus* from Schreyer Alm probably prevents a more complete comparison between the lectotype and the paralectotype, which also do not have the same size.

The paralectotype, that is not "mature", is kept into *L. indistinctus* because its semi-elliptical whorl section with subacuate venter on the second part of the outer whorl fits well with the shape of the first part of the outer whorl of the lectotype. The classification of the paralectotype is done in some respects by exclusion, because at the present none of *Lanceoptychites* species develop these features at intermediate size. Lectotype and paralectotype differ a little in the periumbilical border, which is rounded in the former and subangular in the latter. Due to the scarce material at hand this difference cannot be tested (ontogeny, individual variability, different species). I have thought it of lesser importance with respect to the shape of the venter and I have removed it from the revised diagnosis.

Discussion of the synonymy. The revision of the synonymy reveals the low quality of most of the literature. The species was well described by Mojsisovics. He reported a list of features (fading of the ornamentation, vertical umbilical wall, the acute venter that becomes rounded on adults, suture with 6 saddles) that were also well visible in the figurations. Afterwards the list of features was not used as a whole, but some Authors selected one or two of them as diagnostic. Different choices lead the same name applied to sometimes very different specimens. All the identifications of *L. indistinctus* are here discussed in detail.

The synonymy provided by Mojsisovics (1882, p. 263) probably reports the previous attribution of the syntypes of his new species. As the two survived syntypes are not accompanied by pre-Mojsisovics labels, his synonymy cannot be definitely demonstrated.

The specimens classified by Hauer (1887) surely do not belong neither to the species *L. indistinctus* nor to the genus *Lanceoptychites*. Hauer's determination is based on the widening of the venter on the body cham-

ber of large sized specimens (Hauer, 1887, p. 45). Unfortunately all of the three specimens found in the Hauer collection at the Naturhistorisches Museum, Wien (NHWGPA 1888.II.334 and 1888.II.335) differ from *L. indistinctus* by having a regularly rounded *Flexoptychites*-like venter. At about 60-65 mm of whorl height the widening takes place in a way that the lateral sides gradually become parallel while the ventral side remains rounded.

Diener's identification cannot be fully tested because the original specimen has not been found. According to Diener (1900, p. 34) the specimen was damaged so that the most distinguishing feature (the venter) of the species could not be tested. The classification, by *confronta*, was then justified on the basis of the fading of the ornamentation, the umbilicus and the suture line with few elements. Actually these features seem to me a little weak for a classification. The ornamentation is never strong in compressed Ptychitidae. Moreover other species show the same kind of umbilicus (i.e., *Flexoptychites acutus* [Mojsisovics, 1882]) or a similar 6 saddled suture line (*Flexoptychites gibbus* [Benecke, 1866]).

The *Ptychites* cf. *indistinctus* described by Martelli (1904) cannot be ascribed neither to *L. indistinctus* nor to *Lanceoptychites*. His identification, by *confronta* due to the incomplete preservation of the specimen, is based on the umbilical wall, the ribbing, the shape of the lateral sides, the narrow ventral side and the suture line (Martelli, 1904, pp. 130-131). However, at the beginning of the outer whorl the ventral side of his specimen (IGF 3461E) is not damaged and it does not look narrow or subacute at all (pers. observation). On the contrary it is regularly rounded and as wide as the ventral side of *Flexoptychites*.

The identification by Turina (1912) is at the present accepted because the author in his very short description reports that the whorl section of his specimen is elliptical and the ventral side is acute.

On the contrary the classification by Kraus (1916) is very doubtful. His description deals with the dense ribbing and a suture with short external saddle and lobe. The former feature was also said to be visible on the original specimen of Mojsisovics, pl. 67, fig. 1 (the lectotype: sic!). The ventral side, which is the most significant character for a correct determination is not taken in great consideration. It is described as having an acute shape ("Zuschärfung") that disappears in the outer whorl. However this rounding does not fit with *L. indistinctus*, because it occurs at a diameter less than 6 cm, vs 8-9 cm in *L. indistinctus*. Probably the specimen can be included in the genus *Lanceoptychites*, but the species is open. A final decision cannot be taken because Kraus' specimen could not be studied directly. It should be housed in the Geologisches Institut of the Universität

Wien, but it is stored and not available for study (L. Krystyn, pers. comm.).

Renz's collections from Greece, nowadays housed in the Naturhistorisches Museum of Basel, have been studied, but neither specimens labelled as *P. indistinctus* nor specimens belonging to the species but accompanied by a different label, have been found. Unfortunately these collections are not complete (pers. obs.: some figured specimens are lacking), so that his determinations cannot be definitely verified.

Stefanoff's attribution is accepted because, despite of the poor quality of the lateral view (1936, pl. 2, fig. 9) and despite of the lack of a much more significant ventral or apertural views, the author clearly describes the sharp ventral side which becomes wider and rounded on the body chamber (p. 153). The complex frilling of the suture line is much more similar to *L. indistinctus* than to the *Lanceoptychites* from the Prezzo Limestone.

The specimen figured by Celebic (1964, pl. 2, fig. 1a-b) cannot be included into *L. indistinctus* because it shows a fully different coiling with low SGR and a excessively wide umbilicus. Moreover the ventral side does not fit neither with the species nor with the new genus, being regularly rounded.

The specimen/s quoted as *Ptychites (Flexoptychites)* cf. *indistinctus* in Brinkmann et al. (1972, p. 143) could not be found in Berlin, Bonn (Germany) and Izmir (Turkey). This notwithstanding I reject this attribution because it is not consistent with the rest of the ammonoid and conodont fauna of the Domuzkuru Beds. The unit is Olenekian-Lower Anisian in age.

The identification by Fantini Sestini (in Casati et al., 1982) is at the present the best one among the quite long synonymy of the species. The 7 specimens (MPUM 4146) show a semi-elliptical whorl section and a subacute venter. The largest one overlaps in size with the lectotype of *L. indistinctus* and shows the rounding of the venter at about 38-39 mm of whorl height. The rather bad preservation prevents from displaying them on plate figures. One specimen with the same morphology is unfortunately included in *Flexoptychites flexuosus* (MPUM 4149) together with six well identified specimens. Probably this specimen has been mixed by mistake with the true *Flexoptychites*, after classification.

Occurrence. The species is surely represented in the Schreyeralm Limestone at Schreyer Alm (Salzkammergut, Austria) and in the dark limestone at Reutte (Tirol, Austria) (Mojsisovics, 1882). It is also reported from the Ambata Formation at Col del Cucco (Dolomites, Italy) (Casati et al., 1982). Other occurrences are the Han-Bulog Limestone near Sarajevo (Turina, 1912), and the Anisian red limestone at Golo Bardo (SW Bulgaria; Stefanoff, 1936).

The fauna from Col del Cucco lacks of age-diagnostic ammonoids, and the datas from the other localities were not bed-by-bed collected. The fauna from Reutte is in general accepted as typical of the

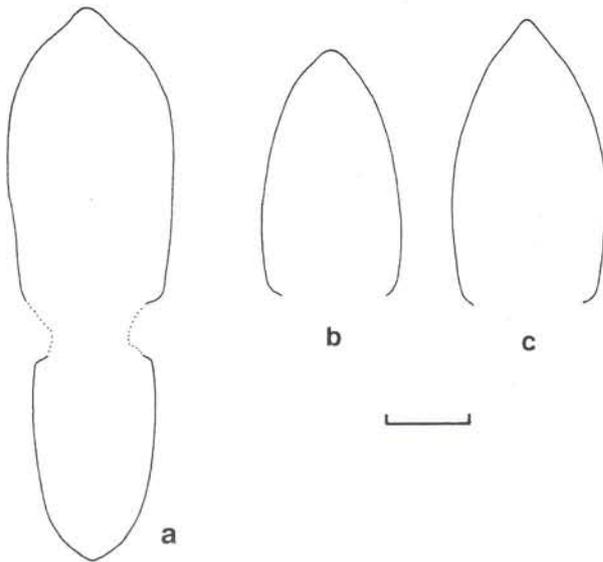


Fig. 12 - Whorl sections of *Lanceoptychites charlyanus* (Diener, 1900). Lectotype, GBA 1900/3/37: a) diametral section showing subacute venter on the minor height and lanceolate section on major height (position shown by asterisk in pl. 3, fig. 2a); b) whorl section 90° after the minor height of the section a; c) whorl section 135° after a. Bar scale 1 cm.

Paraceratites trinodosus zone (Illyrian), while the other localities yielded also younger or older ammonoids. The range of the Schreyeralm Limestone is Pelsonian by the occurrence of *Balatonites* but probably also Illyrian. The Han-Bulog Limestone in Bosnia yielded a very rich ammonoid fauna (i.e., Hauer, 1887, 1892 and 1896) containing elements of four biozones corresponding to the interval Balatonicus - Nevadites Zones. The fauna collected at Golo Bardo yields ammonoids of the *Paraceratites trinodosus* zone, but also elements (i.e., *Reitziites reitzi*: Stefanoff, 1936, p. 161) of the Reitzi-Kellnerites Zone (*sensu* Brack & Rieber, 1993).

Lanceoptychites charlyanus (Diener, 1900)

Pl. 3, fig. 2a-c; fig. 12a-c, 13

- v 1900 *Ptychites charlyanus* Diener, p. 31, pl. 3, fig. 2a-c.
1951 *Flexoptychites charlyanus* - Spath, p. 150 (nn).

Type series. The type-series of the species was originally composed of two specimens collected from the same locality (Schiechlinghöhe), but only one of them was figured (Diener, 1900, p. 31, pl. 3, fig. 2). After a survey in the GBA and in the NHWGPA, where Diener's collection should be housed (Diener, 1900, p. 3 and 4), only the figured specimen has been found. This specimen, registered under the number GBA 1900/3/37, is here designated as lectotype (Pl. 3, fig. 2; Fig. 12, 13).

Diagnosis. *Lanceoptychites* displaying lanceolate section on medium sized phragmocones (from 5-6 cm of diameter).

Revised description of the lectotype. The specimen is almost completely covered by recrystallized test. The test has been removed, probably by Diener, on the right side, then a little less than a quarter of whorl of phragmocone is exposed (Pl. 3, fig. 2c). The last septum is not visible.

The coiling is involute with very narrow umbilicus (U/D 0.09) and compressed whorl section (H/W 1.78). The periumbilical border is rounded but the umbilical wall is vertical. At the beginning of the outer whorl the shape of the whorl section is semi-elliptical and the ventral side is rounded. Then the ventral side becomes subacute (Fig. 12a-b). At about 45° from the end of the outer whorl the whorl section gradually becomes lanceolate (Fig. 12c and 12a), unlike Diener's figuration (Diener, 1900, pl. 3, fig. 2b) at the end of the outer whorl the whorl section is not slender, but thick.

The ornamentation is made of 14-16 very weak and slightly sinuous ribs per half whorl. The ribs appear on the lateral side, at about 1/4 of whorl height, then they fade on the ventral side.

The suture line of the lectotype is different from the illustration given by Diener (1900, pl. 3, fig. 2c). Diener's drawing is equivalent to an ink trace overdrawn directly on the side of the specimen. Actually this trace does not follow the true course of the suture. Fig. 13 displays the definite course of the suture, which has been re-exposed by removing the ink. The suture line is ammonitic. On the lateral side the suture is composed of 6 saddles. The relative width of the elements slightly changes from suture to suture without a definite trend, at least at the scale of the observed section of the phragmocone. The distance between septa and the degree of frilling of the sutures point to a relatively juvenile age for the specimen.

Dimensions.

	D	H	h	U	W	H/W	U/D	SGR
GBA 1900/03/37	65.65	34.9	24.4	6.35	19.5	1.78	0.096	43.03

Measurements refer to steinkern covered by test.

Remarks. The morphological variability and in part the ontogeny of this species are at the present unknown. However, the separation of *L. charlyanus* from the other species of the genus *Lanceoptychites* is sure. The species differs from *L. velox* by the ontogenetic change of the whorl section, which occurs at much smaller size. Moreover the umbilicus is narrower and falls out of the field of variability of the young *Lanceoptychites* of the Southern Alps. The change of the shape of the whorl section also allows the separation from *L. indistinctus*.

The correcting of Diener's illustration of the whorl section of the lectotype, cuts down the morphological similarities between *L. charlyanus* and *Ptychites fastigatus* Diener, 1900 (see Diener, 1900, pl. 3, fig. 1b and 2b). The whorl section now works together with the suture line in supporting the separation of the two species, also at generic rank (see previous discussion on the genus).



Fig. 13 - Suture line of *Lanceoptychites charlyanus* (Diener, 1900). Lectotype, GBA 1900/3/37. In the shaded areas the surface of the internal mould is more deeply incised by former preparation (Diener?) than the rest. In these areas the frilling is obviously artificially simplified and must not be taken into account. The 1st and 2nd lateral lobes of the 2nd suture, as well as the few exposed elements of the 1st and 5th suture were covered by shell. They have been prepared to check the significance of the damaged sutures. Bar scale 0.5 cm.

With respect to Spath's interpretation of *Ptychites charlyanus* as anomalous *Flexoptychites*, the new bed-by-bed data from the Giudicarie demonstrate that the development of subacute/fastigate ventral side in involute and compressed Ptychitidae cannot be explained as growth anomalies (see Ontogeny and population variability of the fastigate ptychitids).

Occurrence. This rare species is reported only by Diener (1900) from the Schreyeralp Limestone at Schiechlinghöhe, Salzkammergut (Northern Calcareous Alps). The fauna described by Diener should suggest an Illyrian to ?Lower Ladinian age of the unit. The range of *L. charlyanus* should fall within this interval, but most probably is Illyrian.

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