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Late Triassic and Early Jurassic Phylloceratids from the Salzkammergut (Northern Calcareous Alps)

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With 19 Text-Figures and 5 Plates

Oberösterreich
Steiermark
Salzkammergut
Nördliche Kalkalpen
Obertrias
Lias
Ammoniten

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Contents

Phylloceratiden aus der Obertrias und dem Unterlias des Salzkammergutes (Nördliche Kalkalpen)

Zusammenfassung

Gegenstand dieser Arbeit ist eine Revision der obertriadischen und liassischen phylloceratiden Ammoniten, die anhand des Originalmaterials von HAUER (1846), E. MOJSISOVICS (1873) and 1902), M. NEUMAYR (1879) und F. WÄHNER (1882–1898) durchgeführt wurde. Die beschriebenen Taxa werden in den Sammlungen der Geologischen Bundesanstalt und des Naturhistorischen Museums in Wien sowie der Bayerischen Staatssammlung in München aufbewahrt.

Außerdem wird das neue Ammonitengenus *Togaticeras* und *Fergusonites neumayri* sp.nov. beschrieben. Weiters werden phyllogenetische Probleme der obertriadischen und liassischen Phylloceratiden und deren mögliche Verwandtschaftsbeziehungen zu jurassischen Taxa diskutiert.

Abstract

This article deals with the reassessment of the Late Triassic and Early Jurassic Phylloceratid cephalopods which was carried out on the original specimens of F. HAUER (1846), E. MOJSISOVICS (1873 and 1902), M. NEUMAYR (1879) and F. WÄHNER (1882–1898). The subject specimens are deposited in the collections of GBA and NHM in Vienna (Austria) as well as in BSM in Munich (Germany). Included are the descriptions of a new genus *Togaticeras* gen.n. and a new species *Fergusonites neumayri* sp.n.

Discussed, further, are the problems of phyllogenesis of the Upper Triassic and Liassic Phylloceratid biota and their possible relationship with the Jurassic Ammonites.

1. Introduction

Late Triassic and Early Jurassic Phylloceratids, as a group, do not enjoy – with rare exceptions – any particular interest of contemporary ammonitologists.

Such a low status leads a curious observer to the assumption that the reason for this may be, in the first place, the remarkable, long-term stability of their external morphology, with barely perceptible changes. This feature earned the Phylloceratids the reputation of an " ... exceptionally persistent, conservative stock ... " (ARKELL et al., 1959).

Counter to such a general prejudice, however, stands the fact that the Phylloceratids are the only group of Am-

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monites to straddle the critical Triassic/Jurassic boundary! Further, as shown by numerous studies (POMPECKIJ, 1895; WÄHNER ,1882–98; DIENER, 1908, 1922; SPATH, 1914, 1924; ARKELL, 1951; GUEX, 1982) the Phylloceratids represent a group from which all subsequent Jurassic/Cretaceous Ammonites can be derived.

This contradictory situation – on the one hand the morphological conservatism, also described as "stasis" (KENNEDY, 1989) and an undeniable innovating potential of the "Front Runners" on the other, was for a long time arousing my curiosity while presenting an interesting challenge.

I must, however, humbly admit that, in view of the many pitfalls involved in the study of this particular group (of which I am painfully aware), my contribution can hardly solve all the problems concerning the Triassic/Jurassic Phylloceratids.

The objectives of the present work include:

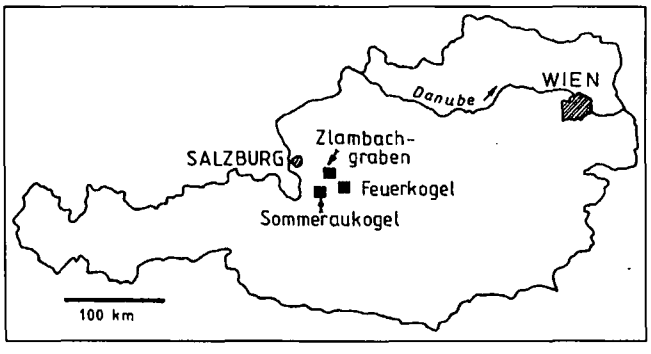
* Revision and re-drawing of the original material deposited in the collections of GBA and NHM in Vienna and BSM in Munich.
* Attempt at a phyllogenetic reconstruction of Late Triassic and Early Jurassic Phylloceratid biota.
* Discussion on the probable relationship with the Jurassic Ammonites.

During the revising studies problems were encountered with the identification of certain parts of the original material, mostly with species described by HAUER in 1846. Thanks to the information kindly provided by Dr. H. LOBITZER of the GBA it was possible to locate the "Metternich Collection". As it is known, HAUER based his description of several species, for example *Rhacophyllites debilis*, *R. neojurensis*, on specimens from this particular collection. The same collection was also used by MOJSISOVICS (1873 and 1902) in his monograph.

The revised material, unfortunately, is not horizoned. However, thanks to the meticulous work of the original authors the information on the labels is sufficient for the determination of the stratigraphic position.

The specimens assessed are in most cases well preserved and include a variety of growth stages. Both, subadult as well as adult individuals can be found often with the body chamber, or aperture preserved. Some forms, corresponding to micro and macroconchs could also be identified.

Lower Liassic Phylloceratids originate from "Psilonotenmergeln"("Psilonoten" marls) from the locality of "Zlambachgraben" (not to be mistaken for the "Zlambach" Formation of Norian–Rhaetian age) for which PLÖCHINGER (1982) introduced the term "Kendelbach Formation" of the Lower Hettangian age (*Planorbis* zone or *"Calliphyllum"* zone according to WÄHNER).



Text-Fig. 1.
Geographical position of the Ammonite finding sites.

In the summary an attempt will be made to sketch a phyllogenetic picture of the Late Triassic and Early Jurassic Phylloceratids with the objective to elucidate the possible relationship of the Upper Triassic Phylloceratida with the Jurassic Ammonitina. As we shall see this relationship can be directly proven only with great difficulties, no matter how logical it may appear.

Abbreviations – Terminology

GÚDŠ	Dionýz Štúr Institute of Geology Bratislava
GBA	Geologische Bundesanstalt Wien
NHM	Naturhistorisches Museum Wien
BSM	Bayerische Staatssammlung für Paläontologie München
D	total diameter
Wh	whorl height
Wt	whorl width
o	umbilicus diameter
v	vidi (latin); the author saw the original material
convolute	when successive whorls partly overlap and envelop preceding ones.

2. Systematic Part

Before dealing with the systematics it will be necessary to discuss the selection of the general diagnostic criteria of the Phylloceratids.

Degree of Coiling

The Late Triassic Phylloceratids are in general represented by convolute forms in which the overlapping of whorls is smaller than one half of their height. Phyllogenetically earlier forms (*Eophyllites*, *Leiophyllites*) are more evolute than the later ones (*Rhacophyllites*). We can also observe that *Simonyceras*, for example, shows a relatively long, subadult, evolute stage characterized by periodic, flare-type annulations.

Suture line

The suture line is, without doubt, one of the most characteristic and genetically most stable features of the Phylloceratida. The form of the saddles and the folioles, together with the lituitid inner lobe allow fast and reliable identification.

The primary, septal line of the Triassic Phylloceratids is quadrilobate (KULLMANN & WIEDMANN, 1970). The subadult and adult stages can be divided, according to the number of umbilical lobes, in two groups:

a) Group with one umbilical lobe
Lobe formula: $ELU_2:(U_1 = S)I_1$
(Discophyllitidae s.l.) b)

b) Group with several umbilical lobes:
$ELU_2U_3U_4 : U_1I_1$ (*Monophyllites*)
and
$ELU_2\,U_3\,U_5\,U_6 : U_4\,U_1\,I_1$ (*Eopsiloceras*) without septal lobe.

As mentioned earlier, the form, the way of splitting as well as the ending of the terminal part of the first (S_1) and second (S_2) lateral saddle demonstrate the changes taking place during the middle to late Triassic which have taxonomic value.

According to the termination of S_1 and S_2 altogether four types can be recognized (cf. Text Fig. 2):

a) Monophyllic-spherophyllic type: phyllogenetically the oldest, persisting with small modifications to the uppermost Triassic (*Eopsiloceras*). The terminal part of the saddle is formed by a spherophyllic foliole with a more (*Monophyllites*) or less (*Ussurites*) pinched base.

b) Monophyllic-subtriangular type: in fact a variation of the former type (a) characterized by a typically triangular form of the terminal foliole (*Simonyceras*). In both cases S_1 and S_2 are monophyllic.
c) Subdiphyllic type: in this case the terminal part of the saddle is asymmetrically split in two unequal folioles. The asymmetry is caused by a deep lateral incision into an originally spherophyllic foliole (*Rhacophyllites*, *Tragorhacoceras* and all Juraphyllidae).

The foliole contour of the Phylloceratids has a form which is characteristic for this group as well. An analogical dependence of the form of foliole on the age can also be observed. Phyllogenetically older taxa exhibit simpler folioles, less incised than the forms of the terminal Triassic. In both cases the folioles retain their typical spatular form.

Further, it can be noted, that the first lateral saddle (S_1) of the Upper Triassic Discophyllitids preserves the more primitive, monophyllic form longer than is the case with the second lateral saddle (S_2).

Ornamentation

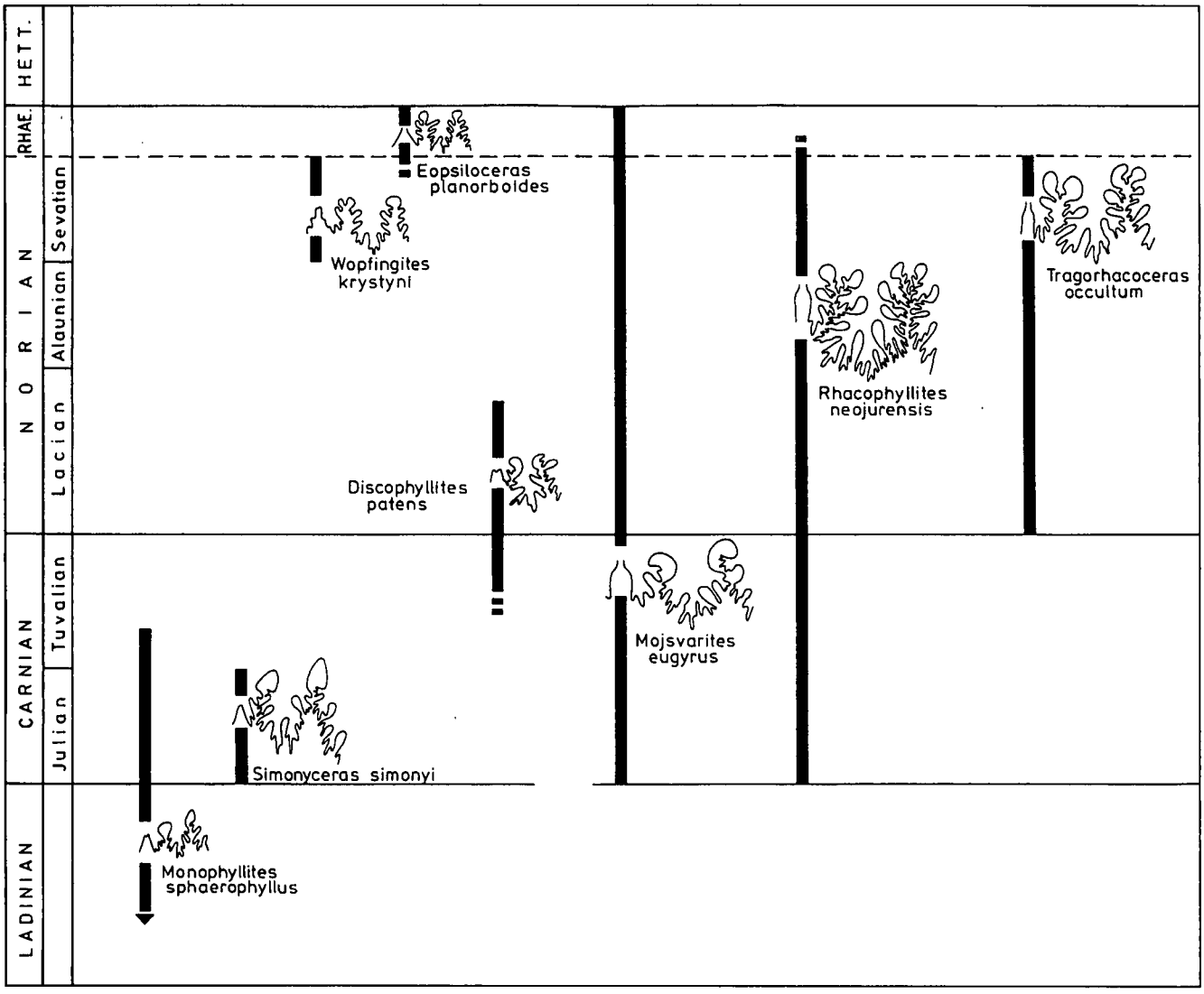
Late Triassic Phylloceratids are typically leiostracious forms with shells which are either smooth or covered only with the growth lines. These may be radial, sinuous or sigmoidal with a variable length of the ventral projection.

In only one case it is possible to observe the presence of flare annulations in juvenile stages, later rapidly disappearing (*Simonyceras*).

An exception to this general trend can be found with the *Tragorhacoceras*. It features a modified body chamber in which the ventral area is lined with transverse plications similar to those of *Tragophylloceras numismale* (POMP.). This new, hitherto unknown feature of the Discophyllitids seems to confirm the connection (relationship) with the Jurassic Juraphyllitids.

As distinct from the late Triassic Phylloceratids the Liassic representatives of this group show a quite pronounced ornamentation composed of ventro-lateral ribs, ventral plications and even a keel. Frequent are prorsiradiate constrictions which, in turn, in the upper Triassic representatives are completely absent.

Both, the Discophyllitids from the end of Triassic and the Jurassic Juraphyllitids include forms fulfilling the criteria of dimorphism. In most cases the dimorphism is of the "B" type in the sense of MAKOWSKI (1962). So, for example, the following species can be identified as microconchs: *Rhacophyllites invalidus* MOJ., *R. zitteli* (MOJ.), *Nevadaphyllites glaber-*



Text-Fig.2.
Phyllogeny of sutural elements S_1 and S_2 within Late Triassic Phylloceratids.

rimus (NEUM.). Macroconch criteria satisfy also *R. neojurensis* (QU. emend. HAUER), *Paradasyceras uermoesense* (HERB.). The distinguishing of dimorphous pairs, however, is up till now, scarcely possible because of the lack of suitable material.

Superfamily: Phylloceratacea ZITTEL, 1884
Family: Ussuritidae HYATT, 1900
Subfamily: Monophyllitinae SMITH, 1913

Diagnosis: The descendants of the ussuritid forms feature convolute coiling shells. The ornamentation includes delicate, sigmoidal growth lines. The septal line has primitive, monophyllic saddles. The number of umbilical lobes is great (6–7), however, without the sutural lobe; the internal lobe is lituitid. Middle–Upper Triassic.

Discussion: As opposed to TOZER (1981) it would seem useful to retain this subfamily in the sense given to it by WIEDMANN (1970). In this group we include the following taxa: *Monophyllites* MOJSISOVICS, 1879; *Simonyceras* WIEDMANN, 1970; *Eopsiloceras* SPATH, 1930 and *Mojsvarites* POMPECKIJ, 1895. However, the genus *Wopfingites* WIEDMANN, 1970, can be included here only with uncertainty because of the difference in the form of the growth lines and, mainly, the presence of a keel.

The above listed genera, characterized by the form of the septal line, its lobe formula and the type of ornamentation show a homogeneous grouping, easily distinguishable from Ussuritidae HYATT, 1900.

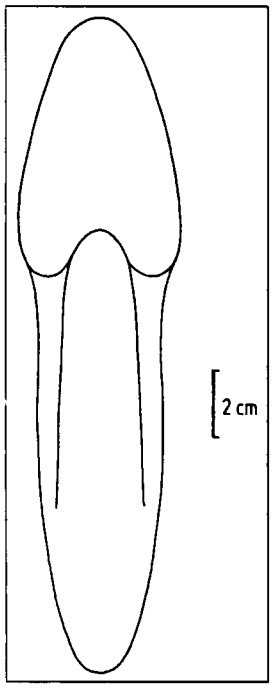
Genus: *Simonyceras* WIEDMANN, 1970

Type species: *Ammonites simonyi* HAUER, 1847.

Simonyceras simonyi (HAUER, 1847)

(Text-Fig. 3; Pl. 1, Fig. 1, 2, 4; Pl. 5, Fig. 1)

1847 *Ammonites simonyi* – HAUER; p. 270, Pl. 9, Fig. 4–6.
v 1873 *Lytoceras simonyi* HAUER – MOJSISOVICS; p. 32, Pl. 17, Fig. 1–6; Pl. 18, Fig. 1.
1902 *Monophyllites simonyi* (Fr. v. HAUER) – MOJSISOVICS; p. 316.
1934 *Monophyllites simonyi* (HAUER) – SPATH; p. 291, Text-Fig. 101.
1970 *Simonyceras simonyi* (HAUER) – WIEDMANN; p. 970, Pl. 2, Fig. 1, 2; Pl. 3, Text-Fig. 4b, 30B (cum syn.).



Text-Fig. 3.
Simonyceras simonyi (HAUER).
Cross-section of an adult specimen.
Loc. Feuerkogel (Aussee, Ausria).
Lower Carnian.

Holotype: As noted by WIEDMANN (1970, p. 971). The original material of HAUER has not been found so that the establishment of the Neotype, so far, could not be carried out.

Material: I had at my studies more than 13 specimens from the collections of GBA in Vienna. The material represents a variety of growth stages.

Dimensions:

	D	Wh	Wt	o
GBA	16,8	6,5	5,0	6,0
GBA 1873/5/48	27,0	10,5	≈ 9,6	9,8
GBA	36,5	18,8	10,5	11,6
GBA (no number)	84,5	35,0	22,32	28,8
GBA (no number)	100,0	40,0	–	34,5
GBA (no number)	105,0	42,0	27,02	32,0
GBA (no number)	141,5	59,5	≈38,0	45,0
GBA (no number)	147,0	63,5	≈38,0	53,0
GBA (no number)	151,0	64,0	–	50,0
GBA (no number)	186,0	77,0	46,52	59,4
GBA 1873/5/48 (MOJS., 1873 Pl. 17, Fig. 1)	208,0	78,0	≈55,0	68,8
GBA 1873/5/48 (MOJS., 1873 Pl. 17, Fig. 1)	234,0	89,0	–	68,0
GBA 1873/5/48 (MOJS., 1873 Pl. 17, Fig. 1)	≈248,0	111,0	≈55,0	82,0

Description: Because of the sufficient description presented quite recently by WIEDMANN (1970, p. 970) we shall deal here only with the early ontogenetic stage.

The ovoidal protoconch is dorso-ventrally compressed. The cross-section of the first whorl is also depressed; it is smooth, without annulations. The second to fourth whorls are evolute with a spheroidal cross-section.

Starting with the second whorl we can observe the presence of 5–6 radial annulations of a flarate type (Pl. I, Fig. 1, 2, 4). The sections between annulations show delicate growth lines.

On the fifth whorl the annulations become prorsiradiate, slightly sigmoidal. They are less pronounced and appear in clusters. (There are 9 of them on one half of a whorl). At the end of the fifth whorl they disappear completely being replaced by the growth lines. On the internal cast they appear as weak, sigmoidal constrictions (Pl. I, Fig. 2).

The whorl surfaces of subadult and adult stages are covered with characteristic, dense and regularly arranged growth lines. These are radiate up to the 2/3 of the whorl height. In the ventral (1/3) area the growth lines bend aperturally forming a large projection. This type of ornamentation persists also in adult individuals (Pl. 5, Fig. 1).

Remarks: *S. simonyi* belongs to the forms characteristic of the Lower Carnian. A reliable distinguishing of this species from the *Monophyllites sphaerophyllus* (HAUER, 1850) is quite a delicate matter requiring the identification of the complete septal line. Following detailed studies WIEDMANN (1970, p. 971) is inclined to conclude that this species already exhibits lobal affinity to the Eopsiloceratids. A unique feature of this species, as well as of all the Monophyllitid species, is the presence of annulations in juvenile stages. This feature in the late Triassic Phylloceratids is quite unique.

Stratigraphic range and geographic distribution: The species is found in the Northern Calcareous Alps (cf. HAUER, 1847 and SPATH, 1934), in the Western Carpathians (KOLLÁROVÁ-ANDRUSOVOVÁ, 1973), in Romania (SHEVYREV, 1990), Greece (RENZ, 1911), Lombardy (ALLASINAZ, 1968), Himalayas as well as Timor (cf. WIEDMANN, 1970). The stratigraphic span includes the Lower Carnian.

Genus: *Mojsvarites* POMPECKIJ, 1895

Type species: *Amm. (Ceratites) agenor* MÜNSTER, 1834 .

Discussion: Originally the genus was ranged to the family Ussuritidae (SPATH, 1934; ARKELL, 1957 and TOZER, 1981). In 1970 WIEDMANN re-ranged it to the family Discophyllitidae. WIEDMANN reasoned the re-rangement by the sutural position U_1 of *M. agenor* (MÜNST.) (l.c. Text-Fig. 7).

Although sutural lines depicted by WIEDMANN seem as a persuasive argument, I still regard the following facts as necessary:

1. The juvenile stages of both the monophyllitid and discophyllitid forms are so closely resemblant that it is practically impossible to find differences between them.
2. The sutural lines depicted by WIEDMANN were studied on juvenile specimens preventing reliable distinction.
3. The sutural line depicted in Text-Fig. 7c is evidently discophyllitid and shows evident tendency to form S_2 diphyllic!

Basing on this I suppose that sutural lines depicted by WIEDMANN belong actually to juvenile *Discophyllites* and not to *Mojsvarites*.

Our examination of MOJSISOVICS's original material shows that the external suture of *Mojsvarites agenor* (= *Lytoceras morloti* HAUER in MOJSISOVICS, 1873, Pl. 16, Fig. 1) shows typical monophyllic saddles! So in accordance with SPATH we regard *Mojsvarites* as a member of Ussuritidae.

In its external sculpture *Mojsvarites* as pointed out by WIEDMANN (1970, p. 977) shows affinity to smooth discophyllitid forms. Yet I think that the external similarity of *Mojsvarites* with *Discophyllites* is a matter of convergency and not of phyllogeny.

Stratigraphic range: Carnian–Rhaetian.

Mojsvarites agenor (MÜNSTER, 1834)

(Text-Fig. 4; Pl. 5, Fig. 2)

?1834 *Amm. (Ceratites) Agenor* MÜNSTER; p. 15, Pl. 2, Fig. 9.
1850 *Ammonites Morloti.* n.sp. – HAUER; p. 15, Pl. 2, Fig. 12–14 .
v1873 *Lytoceras Morloti* HAUER – MOJSISOVICS; p. 34, Pl. 16, Fig. 1, 2; Pl. 19, Fig. 11, 14, 15.
1882 *Monophyllites Agenor* (MÜNSTER) – MOJSISOVICS; p. 205, Pl. 78, Fig. 6–9.
1934 *Mojsvarites agenor* (MÜNSTER) – SPATH; p. 34, Text-Fig. 105c,d.
1970 *Mojsvarites agenor* (MÜNSTER) – WIEDMANN; p. 977, non Text-Fig. 7, Text-Fig. 30; Pl. 2, Fig. 3 (cum syn.).

Neotype: It was selected by WIEDMANN 1970, Pl. 2, Fig. 3. It is also depicted here in Pl. 5, Fig. 2.

Material: One complete specimen with preserved body chamber.

Dimensions:

	D	Wh	Wt	o
GBA 1873/5/51 Neotype	107,0	40,5	35,5	42,0

Remarks: This specimen was sufficiently described by WIEDMANN (1970) and it is not necessary to give here a new description. We only add here some observations.

The juvenile stage is evolute as we can observe on all monophyllitids. The whorl-section of the adult stage is ovoidal (Text-Fig. 3).

The surface of subadult and adult stages is characterized by the presence of fine but accentuated biconcave and periodic lines. On the body chamber interlines are denser than on the phragmocone. Between two periodic lines we can observe at oblique light the presence of very fine growth lines.

The suture line has a typically monophyllitic shape (Text-Fig. 4) with large terminal folioles. WIEDMANN's description (l.c. 1970) gives a large detailed review about this specimen. Our species differs from *D. eugyrus* (MOJSISOVICS, 1873) in more prominent periodic lines, whose ventral projection is distinctly smaller than those of *D. eugyrus*.

Stratigraphic range and geographic distribution: Lower Carnian (*Aonoides* zone) Northern Calcareous Alps (Goisern and Feuerkogel), Hungary and ?Himalaya.

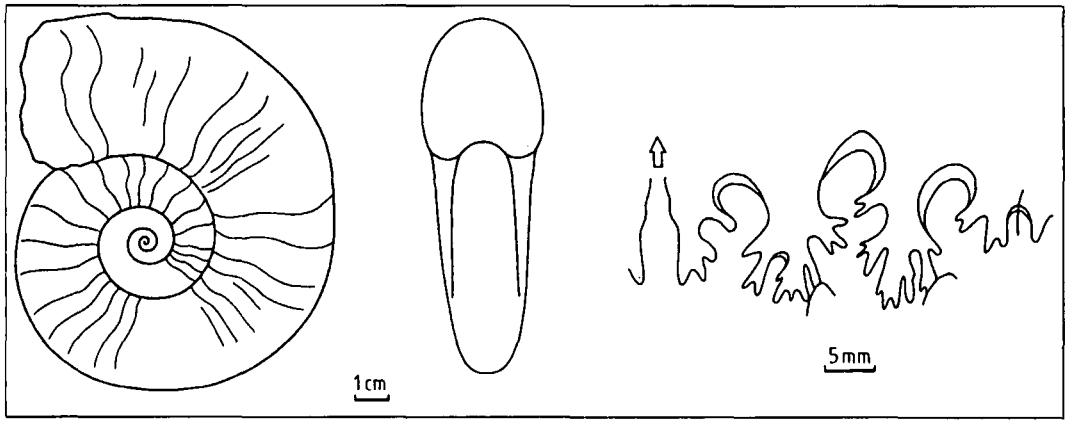
Genus: *Eopsiloceras* SPATH, 1930

Type species: *Ammonites planorboides* GÜMBEL, 1861.

Eopsiloceras planorboides (GÜMBEL, 1861)

(Pl. 1, Fig. 3)

1861 *Ammonites planorboides* GUEMB. – GÜMBEL, p. 410 .
v1895 *Monophyllites (Mojsvarites) planorboides* GÜMBEL sp. – POMPECKIJ; p. 16, Text-Fig. 2, 3c; Pl. 1, Fig. 1, 2.
1934 *Eopsiloceras planorboides* (GÜMBEL) – SPATH; p. 314, Text-Fig. 106a, b, e.
1970 *Eopsiloceras planorboides* (GÜMBEL – WIEDMANN; p. 972, Pl. 2, Fig. 5; Pl. 4, Fig. 3, 4; Pl. 6, Fig. 9, Text-Fig. 4c, d,19 (cum syn.).
v1977 *Eopsiloceras planorboides* (GÜMBEL) – MATHUR; p. 5, Text-Fig. 2a; Pl. 1, Fig. 1–3 (cum syn.).



Text-Fig. 4.
Mojsvarites agenor (MÜNSTER).
Cross-section, lateral view and suture line of an adult specimen.
Loc. Raschberg (Goisern, Austria).
Lower Carnian.

Neotype: WIEDMANN (1970, p. 973, Pl. 4, Fig. 4) designated as neotype the specimen originally depicted by POMPECKIJ 1895, Pl. 1, Fig. 1, 2 hereby repeatedly shown on Pl. 1, Fig. 3.

The specimen is deposited in the collections of the Bavarian State Museum under no. BSM AS I 702.

Remarks: This small, convolute form with a narrow-elliptical (high-oval) whorl cross-section and very subtle ornamentation above the body chamber has been described in some detail by WIEDMANN (1970) and MATHUR (1977).

The latter author described in his dissertation treatise the presence of relics of black melanine stains. It should be, however, noted that the position of these stains does not correspond to the original, biological location of spots in the body chamber.

Certain (nomenclatorial) difficulties may arise from the extent to which we shall make this species inclusive. WIEDMANN (1970) included in the species *E. planorboides* also the *Eopsiloceras clio* (MOJSISOVICS, 1893) which is quite similar to this species. We should note, however, that between *E. planorboides* and *E. clio* there are subtle differences:

- The course of *E. clio* growth lines is perceptibly more sigmoidal with larger ventral projection (according to WIEDMANN, 1970, Pl. 4, Fig. 3a, 3b).
- Certain differences exist also in the form of the terminal foliole of the second, lateral saddle (S_2).
- *E. clio* has been found, up till now, only in the upper Norian, Sevatian strata while the stratigraphic range of *E. planorboides* is Rhaetian, the zone of *Choristoceras marshi*.

Stratigraphic range and geographic distribution: Rhaetian, the zone of *Choristoceras marshi*. The area of occurrence of this species is very limited. The holotype comes from the vicinity of Garmisch-Partenkirchen, Lahnenwiesgraben locality, from the Kössen Formation.

Family: Discophyllitidae SPATH, 1930, sensu novo

Diagnosis: Medium large to giant, discoidal like, convolute forms with oval whorl cross-section always without constrictions. The ornamentation, without prominence, is represented by sigmoidal growth lines. The septal line is typically Phylloceratid with subdiphyllic and diphyllic saddles.

Discussion: The diagnostic description indicates that, as opposed to WIEDMANN (1970) and WIEDENMAYER (1977), in this family we shall include only smooth, unsculptured forms without constrictions during ontogeny.

Equally the last body chamber shows no signs of any significant morphological changes. In this family we are including the following genera: *Discophyllites* HYATT, 1900 and Rhacophyllites ZITTEL, 1884.

Genus: *Discophyllites* HYATT, 1900

Type species: *Lytoceras patens* MOJSISOVICS, 1873.

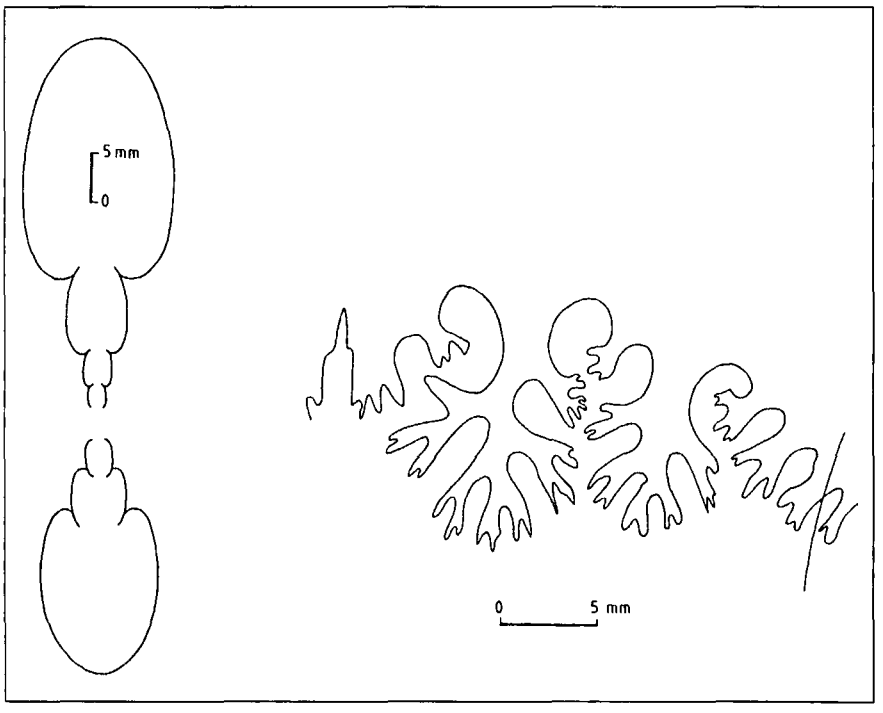
Discophyllites patens (MOJSISOVICS, 1873)

(Text-Fig. 5; Pl. 2, Fig. 6)

v1873 *Lytoceras patens* MOJSISOVICS – MOJSISOVICS; p. 34, Pl. 16, Fig. 3; Pl. 19, Fig. 17.
1927 *Rh.* (*Discophyllites*) *patens* MOJS. – J.P. SMITH; p. 100, Pl. 62, Fig. 1–13; Pl. 103, Fig. 4–6.
1934 *Discophyllites patens* (MOJS.) – SPATH; p. 317, Text-Fig. 107a, b.
1970 *Discophyllites patens* (MOJSISOVICS) – WIEDMANN; p. 981, Pl. 6, Fig. 8, Text-Fig. 22, 30C (cum syn.).

Holotype: WIEDMANN in 1970 selected for this purpose a specimen from the type-series GBA 1720 of MOJSISOVICS, depicted in Pl. 6, Fig. 8. The same individual is repeatedly shown here in Pl. 2, Fig. 6.

Material: One incomplete individual representing a phragmocone and, perhaps, part of the body chamber.



Text-Fig. 5.
Discophyllites patens (MOJSISOVICS) – Holotype.
Cross-section and suture line of an adult specimen.
Loc. Sommeraukogel near Hallstatt (Salzkammergut, Austria).
Norian.

Dimensions:

	D	Wh	Wt	o
GBA 1873/5/49 Holotype	55,0	24,0	16,0	22,0

Remarks: The species was described in detail by WIEDMANN (1970, p. 981) so that we shall deal here only with complementary observations.
In comparison with the rest of the species of the Discophyllitidae family the *D. patens* is perceptibly evolute. The whorl cross-sections of sub-adult stages are markedly elliptical and laterally compressed (Text-Fig. 5).
The septal line (Text-Fig. 5) is characterized by a subdiphyllic first lateral saddle (S_1) and diphyllic S_2 as well as a typical lateral incision of terminal folioles.

Stratigraphic range and geographic distribution: The species is known from the Northern Calcareous Alps and Northern America.
The stratigraphic range includes Norian (Lac).

Genus: *Rhacophyllites* ZITTEL, 1884

Type species: *Ammonites neojurensis* QUENSTEDT, 1845.

Rhacophyllites neojurensis (QUENSTEDT, 1845 emend. HAUER, 1846)

(Text-Fig. 6; Pl. 2, Fig. 1, 4, 5)

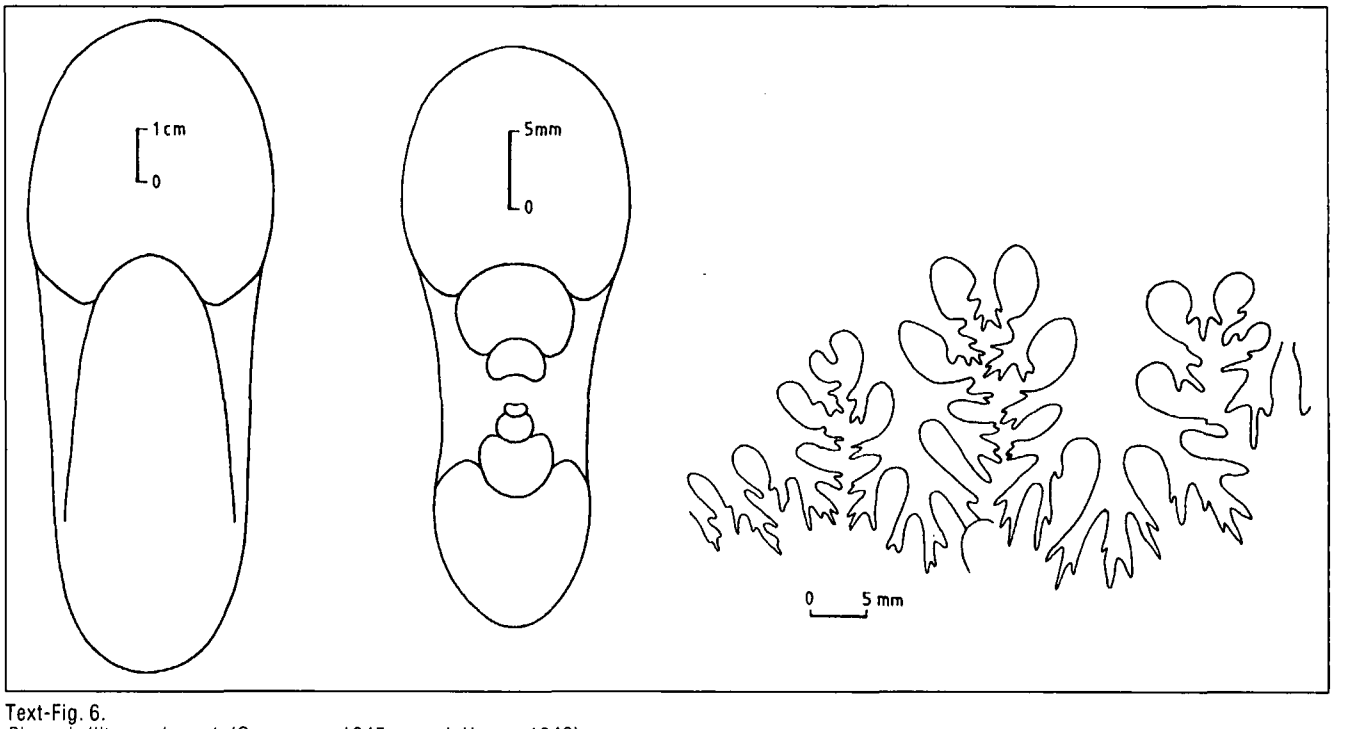
?1845 *Ammonites neojurensis* QUENSTEDT; p. 682 1846 *Ammonites neojurensis* QUENSTEDT. – HAUER; p. 8, Pl. 3, Fig. 2–4.
1873 *Phylloceras neojurense* QUENSTEDT sp. – MOJSISOVICS; p. 37.
v1902 *Rhacophyllites neojurensis* (QUENSTEDT) – MOJSISOVICS; p. 319, Pl. 17, Fig. 1; Pl. 23, Fig. 2, 3.
1934 *Diphyllites neojurensis* (QUENSTEDT) – SPATH; p. 319, Text-Fig. 109a, Pl. 4, Fig. 3.
1967 *Rhacophyllites neojurensis* (QU.) – ZAPFE; p. 456, Pl. 6, Fig. 2.
1970 *Rhacophyllites neojurensis* (QU.) (HAUER) – WIEDMANN; p. 982, ?Text.-Fig 6c, 23c, d (cum syn.).

Holotype: WIEDMANN (1970, p. 983) established as the holotype the specimen depicted by HAUER in 1846 in Tab. 3, Fig. 2–4. Unfortunately, its existence cannot be confirmed with unequivocal certainty, although the specimen in the GBA collections in Vienna is almost identical with the one depicted by HAUER. According to Dr. H. LOBITZER (personal communication) this particular individual originates from Metternich's collection and, with great probability, belongs to the original type-series studied by HAUER.
In case the above assumption will not be confirmed, another specimen depicted by MOJSISOVICS in 1902, Pl. 17, Fig. 1 could be designated as neotype. This individual is deposited in the GBA collections under no. 1706 and originates from the same locality. In addition it represents well all the substantial features of the species.

Material: I had at my disposal more than 20 individuals from the collections of GBA in Vienna, BMS in Munich and GÚDŠ in Bratislava. The studied material represents a variety of growth stages from sub-adult to adult individuals. As all these specimens originate from the same locality, their degree of preservation is quite similar. In most cases they are found as casts with calcified shells.

Dimensions:

	D	Wh	Wt	o
GÚDŠ 1615	26,0	12,0	11,0	8,0
GÚDŠ 1612	27,0	13,0	12,2	8,0
GÚDŠ 1613	28,0	14,0	13,0	–
GÚDŠ 1611	36,5	18,0	15,6	10,0
GÚDŠ 1614	36,6	17,0	–	10,0
GÚDŠ 1610	48,0	24,6	19,4	11,8
GBA 1902/3/277	79,0	38,2	43,4	21,0
GBA 1902/3/277	98,8	45,4	43,4	27,6
GBA 142	111,0	48,8	40,0	27,0
GBA 1902/3/277	117,4	54,0	47,0	35,0
GBA 1902/3/277	533,0	190,0	180,0	164,0



Text-Fig. 6.
Rhacophyllites neojurensis (QUENSTEDT, 1845 emend. HAUER, 1846).
Cross-sections and suture line of a subadult specimen.
Loc. Sommeraukogel (Hallstatt, Austria) – Lower Norian.

Description: The species is a large to giant convolutely coiled form. Juvenile stages (up to a diameter of cca 15 mm) are evolute-coiled with a depressed whorl cross-section. Approximately from the third whorl onwards the degree of coiling is increasing and with it changes also the relation between the width and height of whorls in favour of the latter. The cross-section of the whorls is becoming oval to wide-elliptical with a relatively wide ventrum (Text-Fig. 6).

Subadult and adult stages show robust, wide elliptical whorl cross-sections (Text-Fig. 6). The same type of the cross-section is retained also in the last body chamber of the largest individual preserved. The suture line is typically Phylloceratid with diphyllic saddles terminated by wide, spatular folioles. The external lobe is narrow, divided also by a narrow, secondary saddle.

The ornamentation is in all growth stages subtle to the extent that the shells can rather be described as smooth. Under oblique light, however, the delicate, sigmoidal, rursiradiate growth line can be recognized.

Remarks and relationship: The *"neojurensis"* species was described by HAUER (1846) and MOJSISOVICS (1873 and 1902) in sufficient details. The following remarks, therefore, are only complementary.

WIEDMANN (1970, p. 983) already pointed out the nomenclatural problem in connection with the prioritary authorship of the species. Although the species' name was first used by QUENSTEDT (1845, p. 682), we are in agreement with WIEDMANN (l.c., p. 983) that his description was by far inadequate to the point of being invalid. The first, palaeontologically sufficient description, together with the illustration, was made by F. HAUER (1846, p. 8, Pl. 3, Fig. 2–4) only one year after the name of the species was used for the first time. It is, therefore, recommended that HAUER's description is considered to be the prioritary authorship.

R. neojurensis has been frequently mistaken for or identified with the related, albeit well distinguishable species *R. debilis* (HAUER). The latter species differs from the one discussed mainly by a more robust whorl cross-section as well as a wider ventral area (Text-Fig. 5). Such a character becomes constant already in the sub-adult stage and is the most distinctive feature in the adulthood.

A certain distinguishing criterion seems to be provided also by the septal line, mainly its external lobe (E). This lobe in the "neojurensis" species is narrow and divided by a tall, narrow secondary saddle. In contrast, the external lobe (E) of *R. debilis* is much wider and the secondary saddle is wide-pyramidal. It should be noted, however, that a certain confusion may be caused by HAUER's illustration from 1846 (see Pl. 3, Fig. 4). The bottom drawing of the septal line in the area of the external lobe is significantly different from the next that follows. As all of the examined septal lines of *neojurensis* species exhibit the external saddle similar to the upper suture drawing it can be assumed that the lower drawing was added from a different specimen.

Dimorphism: The largest known individual in the the GBA collections bears the character of an adult macroconch with the aperture missing. The well preserved body chamber occupies 1/2 of the last coil. The microconch pair cannot be, at present, determined with certainty.

Stratigraphic range and geographic distribution: *R. neojurensis* is a form frequently found in the Tethys, mainly the Alpine Upper Triassic. Its Alpine occurrences, up to now, appear primarily in the Norian. It is possible, nevertheless, that the species reaches up to the Rhaetian. Besides the Alps the species was found in Hungary and Timor.

Rhacophyllites debilis (HAUER, 1846)

(Text-Fig. 7; Pl. 1, Fig. 8)

1846 *Ammonites debilis* HAUER; p. 10, Pl. 4, Fig. 1–3.
v1873 *Phylloceras debile* HAUER – MOJSISOVICS; p. 37, Pl. 22, Fig. 13.
1902 *Rhacophyllites debilis* (Fr.v. HAUER) – MOJSISOVICS; p. 313, Pl. 17, Fig. 2; Pl. 23, Fig. 4.
1934 *Diphyllites debilis* (HAUER) – SPATH; p. 323, Text-Fig. 109b.
1968 *Rhacophyllites debilis* (HAUER) – SHEVYREV; p. 230, Text-Fig. 92; Pl. 21, Fig. 5, 6.
1970 *Rhacophyllites debilis* (HAUER) – WIEDMANN; p. 984, ?Text-Fig. 23a, b.
1981 *Rhacophyllites* cf. *neojurensis* – BANDO & KOBAYASHI; p. 113, Pl. 3, Fig. 24; Text-Fig. 24a–c.
1990 *Rhacophyllites debilis* (HAUER, 1846) – SHEVYREV; p. 146, Text-Fig. 54, Pl. 8, Fig. 7, 8.

Lectotype: WIEDMANN (1970, p. 984) selected for this purpose a specimen described and illustrated by HAUER (1846,
Pl. 4, Fig. 1–3).

An individual figured by MOJSISOVICS (1902, Pl. 17, Fig. 2) now in the GBA collection was polished in a fashion similar to various ammonite specimens found in the Metternich collection. This particular specimen was fossilized by a yellow-gray biomicritic limestone as noted by HAUER. In respect to size it is almost similar to the 5 inch specimen mentioned by HAUER (l.c., p. 11a, 12). This individual was, in all probability, part of the type-series of F. HAUER and should be, therefore, considered as lectotype.

Material: 10 more or less complete specimens from the collections of GBA in Vienna and GÚDŠ in Bratislava were examined. They represent a variety of growth stages with one individual being, probably, an adult with a preserved body chamber (GBA 1705).

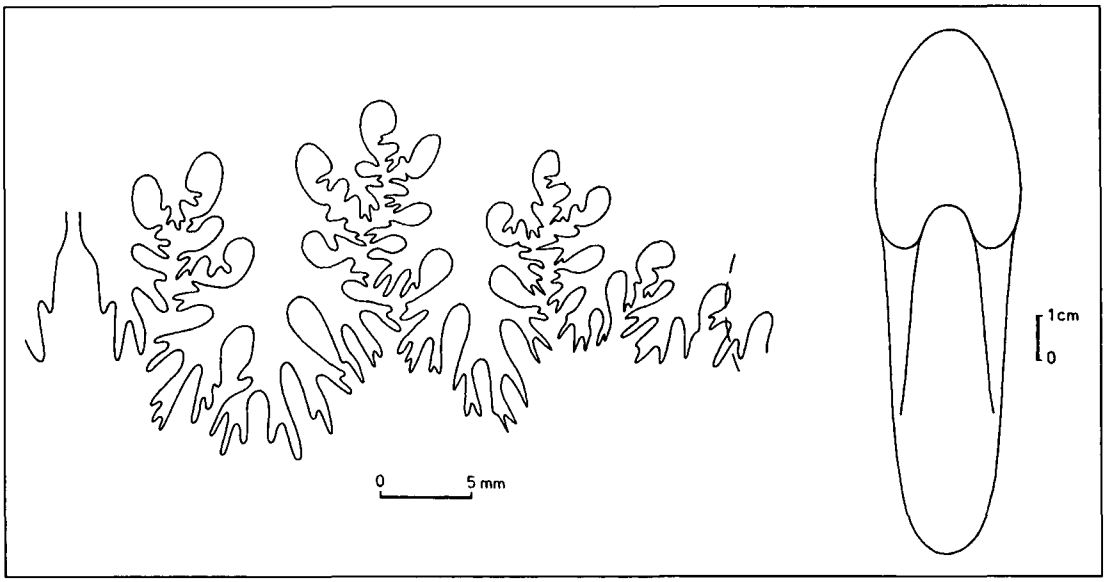
Dimensions:

	D	Wh	Wt	o
GBA (no number)	60,6	26,0	18,9	18,4
GÚDŠ (no number)	68,0	30,3	20,0	18,7
GBA 1902/3/276	80,0	34,0	26,4	25,0
GBA 1902/3/276 orig. MOJ. 1902, Pl. 17, Fig. 2	115,8	47,0	30,6	33,5

Description: It is a medium sized (the diameter of adult individuals does not exceed 120 mm), convolute, disc-like form. The whorl cross-section (Text-Fig. 7) is elliptical to subrounded-triangular. The ventral area is relatively narrow, formed by a small arch merging gradually with slightly bulging sides. The maximum whorl width is found in the periumbilical area. The septal line (Text-Fig. 6) is characterized by diphyllic saddles with wide-spatular folioles. The external lobe is relatively wide and split by a secondary, slightly incised saddle.

The ornamentation is very delicate, formed by sigmoidal, versiradiate (biconvex) growth lines visible only under oblique illumination.

Remarks: This easily recognizable form is frequently mistaken for *R. neojurensis*. From the latter it can be easily distinguished by sleek, subtriangular whorl cross-sections, smaller size and sleeker saddle bases. *D. zitteli* is a



Text-Fig. 7.
Rhacophyllites debilis (HAUER).
?Holotype.
Cross-section and suture line of an adult specimen.
Steinbergkogel near Hallstatt (Salzkammergut, Austria).
Norian.

quite similar-looking form distinguished, however, by its planparallel whorl sides.

Stratigraphic range and geographic distribution: *R. debilis* shows a much more extensive geographic distribution than the preceding species. It appears at many localities of the Northern Calcareous Alps, as well as in Bulgaria, NW Caucasus, SE Pamir, Tibet, West Verchoyan, West Chukchi Peninsula (see SHEVYREV, 1968, 1990), Timor, New Zealand, New Caledonia and Nevada. The stratigraphic range is Norian.

Rhacophyllites pumilus (MOJSISOVICS, 1873)

(Text-Fig. 8; Pl. 1, Fig. 5)

v1873 *Phylloceras pumilum* E. v. MOJSISOVICS – MOJSISOVICS, p. 40, Pl. 16, Fig. 8, 12.
1902 *Rhacophyllites pumilus* E. v. MOJSISOVICS – MOJSISOVICS, p. 318.

Holotype: The specimen depicted by MOJSISOVICS in 1873, Pl. 16, Fig. 8, 12 and repeatedly shown herein Pl. 1, Fig. 5.

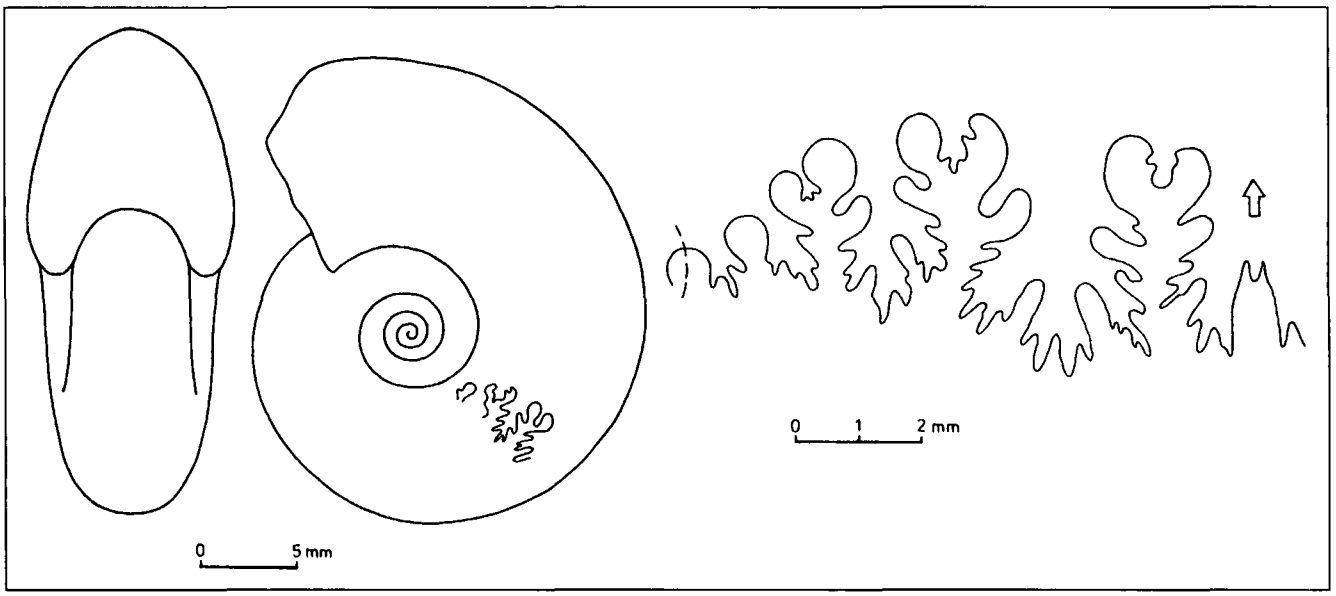
Material: One almost complete specimen with partly preserved body chamber.

Dimensions:

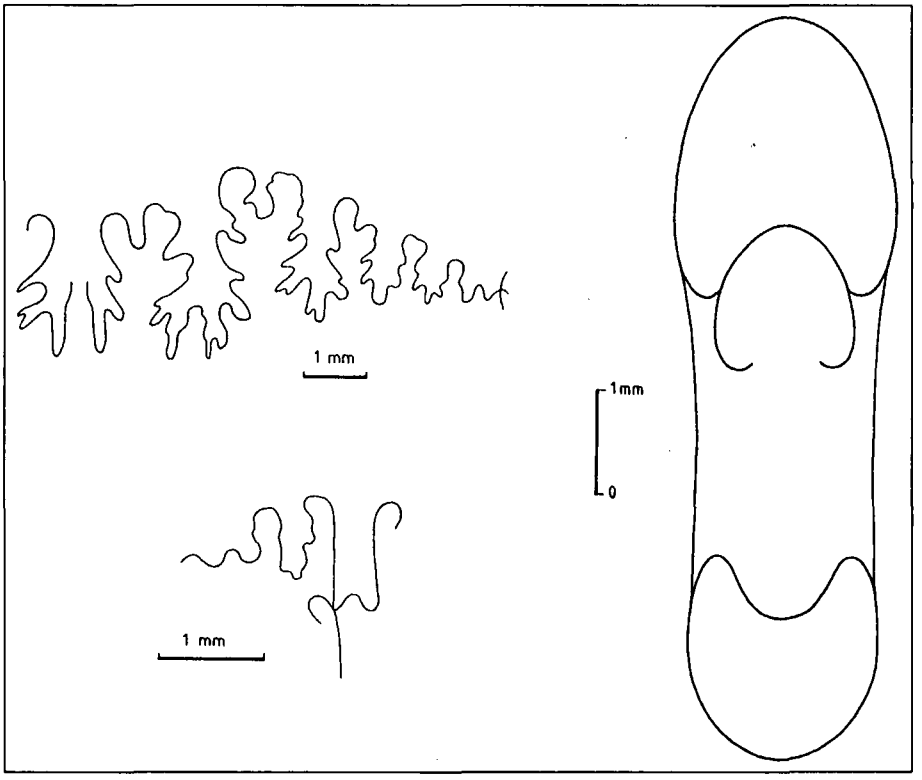
	D	Wh	Wt	o
GBA 1902/3/276	80,0	34,0	26,4	25,0
GBA 1873/5/57	22,7	10,0	9,5	6,0

Description: The form is small and convolute. The cross-section of the last, preserved whorl is wide-elliptical with bulging sides (Text-Fig. 8).
The septal line (Text-Fig. 8) is typically phylloceratid with diphyllic first saddles. The first lateral lobe (L) is much larger than the U_2. Compared to other species the septal line is less complex. The shell surface is smooth lacking any ornamentation.

Remarks: Regarding the size, an overall more simple septal line and the partially preserved body chamber we could consider our species being a microconch. However, because neither the telescoping of septal lines on the fragmocone, nor the unfolding of the last,



Text-Fig. 8.
Rhacophyllites pumilus (MOJSISOVICS) – Holotype.
Cross-section lateral view and suture line of an adult specimen.
Loc. Sandling (Salzkammergut, Austria) – Upper Carnian.



Text-Fig. 9.
Rhacophyllites invalidus (MOJSISOVICS).
Cross-section and suture line.
Loc. Goisern (Salzkammergut, Austria).
Upper Norian.

preserved whorl could be demonstrated we are inclined to believe that it is, in fact, a juvenile macroconch. In the form of the whorl cross-section this species resembles *R. neojurensis*.

Stratigraphic range and geographic distribution: The species is known only from the Northern Calcareous Alps from Upper Carnian to Lower Norian.

Rhacophyllites invalidus **(MOJSISOVICS, 1873)**

(Text-Figs. 9, 10; Pl. 1, Fig. 6)

1873 *Phylloceras invalidum* E. v. MOJSISOVICS – MOJSISOVICS; p. 39, Pl. 16, Fig. 7, 11; Pl. 19, Fig. 18.
v1902 *Rhacophyllites invalidus* E. v. MOJSISOVICS – MOJSISOVICS; p. 320, Pl. 19, Fig. 6.

Holotype: The specimen depicted by MOJSISOVICS in 1873 and 1902 in Pl. 19, Fig. 18 and repeatedly shown here in Pl. 1, Fig. 6.

Material: One complete specimen with preserved body chamber and two whorl fragments.

Dimensions:

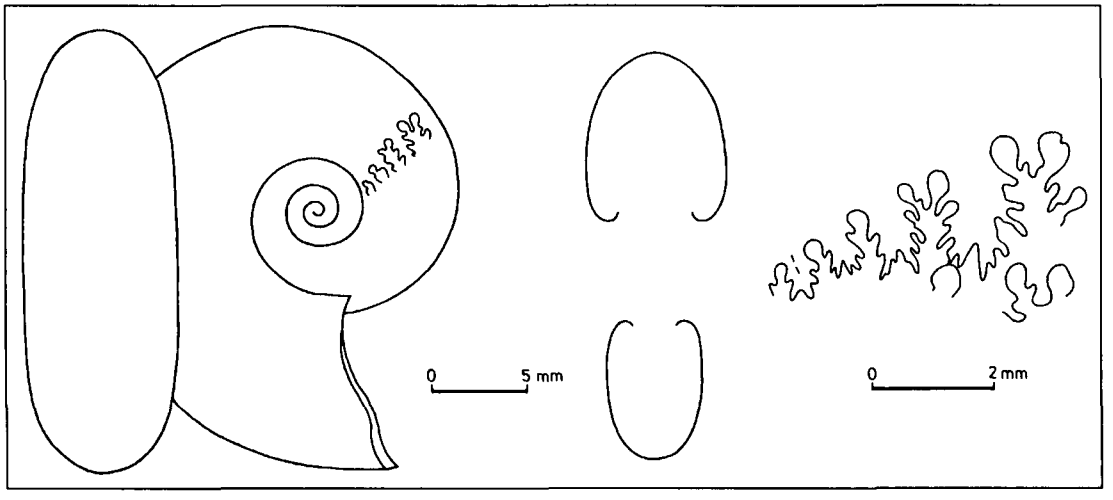
	D	Wh	Wt	o
GBA 1902/3/279 Holotype	22,0	8,6	6,5	6,0

Description: Small, convolute form with a diameter not exceeding 22 mm. Cross-sections of ontogenetically young whorls are elliptical with slightly convergent sides towards the ventrum (Text-Fig. 9). The cross-sections of the last whorl and the body chamber are wider-elliptical with flat, subparallel sides (Text-Fig. 10). The body chamber occupies 3/4 of the whorl with a clear tendency to unfolding. It is terminated by a simple peristome without a rostral protrusion. The septal line (Text-Figs. 9, 10), although simplified is typically phylloceratic. Relatively wide saddle bases are typical; S_1 and S_2 are diphyllic and little incised. The dorsal lobe is characteristically lituitid.

Remarks: The small size, unfolded body chamber ended by a peristome and the septal approximation sufficiently characterize this species as microconch. The matching macroconch pair, however, remained elusive.

Rh. invalidus, by its size, resembles the *Rh. pumilus* species from which it differs mainly in the dorso-ventrally more compressed whorl cross-section.

Stratigraphic range and geographic distribution: The species was, so far, identified only in the Northern Calcareous Alps. Stratigraphically it occurs in the Middle and Upper Norian.



Text-Fig. 10.
Rhacophyllites invalidus (MOJSISOVICS).
Holotype.
Lateral view, cross-section and suture line of an adult specimen.
Loc. Goisern (Salzkammergut, Austria).
Upper Norian.

Rhacophyllites zitteli MOJSISOVICS, 1902

(Text-Fig. 11; Pl. 1, Fig. 7; Pl. 2, Fig. 2, 3)

v1902 *Rhacophyllites zitteli* E. v. MOJSISOVICS – MOJSISOVICS; p. 318, Pl. 17, Figs. 3, 4.
1934 *Diphyllites zitteli* (MOJS.) – SPATH; p. 322.
1970 *Rhacophyllites zitteli* MOJSISOVICS – WIEDMANN, p. 986, pl. 1, Fig. 5.

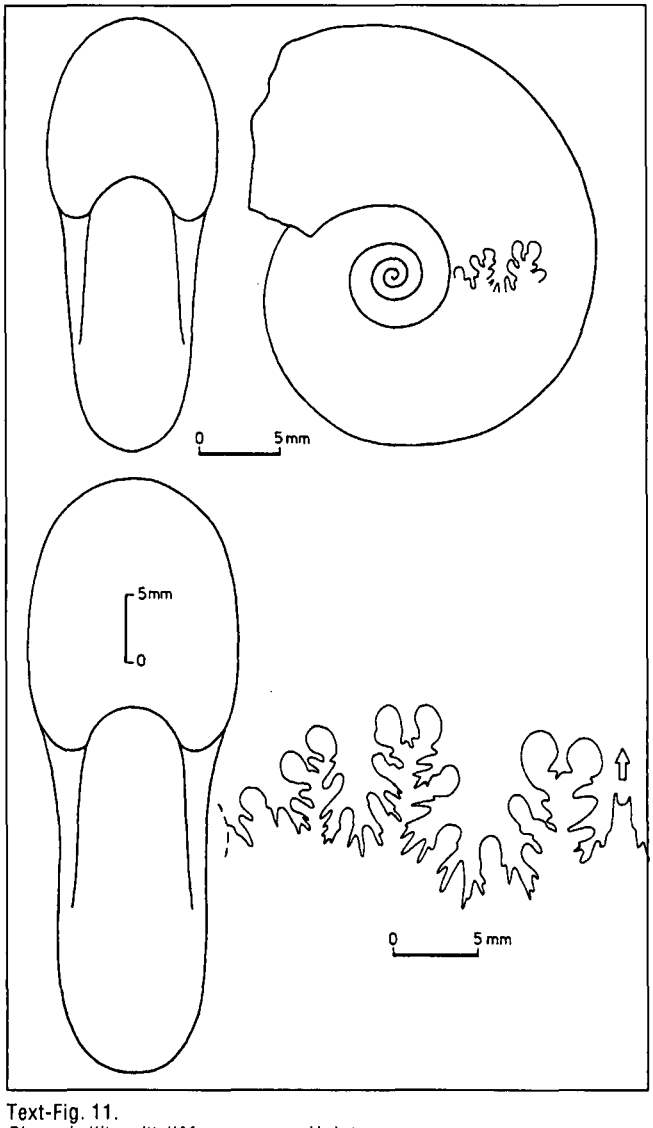
Holotype: Specimen originally depicted by MOJSISOVICS 1902, Pl. 17, Fig. 3 and repeatedly depicted here Pl. 1, Fig. 7.

Material: Three more or less completely preserved individuals.

Dimensions:

	D	Wh	Wt	o
GBA (no number)	13,0	5,4	4,6	4,0
GBA (no number)	22,0	9,4	8,6	6,0
GBA 1902/3/273	48,0	20,0	15,0	13,0

Description: This small form in the juvenile stage strongly resembles the *"pumilus"* species. Adult individuals, however, can be well distinguished by the cross-section of the body chamber characterized by planparallel sides (Text-Fig. 11). The body chamber occupies more than 1/2 of the whorl.
The shell surface is covered with delicate, sigmoidal growth lines.
The septal line (Text-Fig. 11) is characterized by a diphyllic saddle ending with wide terminal foliales.



Text-Fig. 11.
Rhacophyllites zitteli MOJSISOVICS – Holotype.
Lateral view, cross-section and suture line.
Loc. Feuerkogel (Aussee, Austria).
Lower Carnian.

Remarks: Shell size and the partially modified cross-section of the body chamber of *R. zitteli* suggest the possibility of the species being a microconch.
As shown by the description the differentiation of subadult stages from the rest of the *Rhacophyllites* species is very difficult.
This species is one of the oldest known representatives of the genus.

Stratigraphic range and geographic distribution: The species has been found, so far, only in the Northern Calcareous Alps, in the Lower Carnian–Julian.

Family: Juraphyllitidae ARKELL, 1950 pars Discophyllitidae sensu WIEDMANN, 1970 and WIEDENMAYER, 1977

Diagnosis: Derivatives of Discophyllitids characterized mainly by a modified body chamber (plications, ribs and keel) and in Liassic representatives also by constrictions. The septal line is phylloceratoid with diphyllic or triphyllic saddles.

Discussion: In comparison with other discophyllitid forms the most prominent feature of the Juraphyllitids is the modified body chamber. This feature is so characteristic that it enables a reliable distinguishing from the Discophyllitids. For the first time this feature appeared with the Upper Triassic *Tragorhacoceras*, however, it became dominant in the Liassic forms. Another distinguishing feature is the presence of constrictions which are absent in Discophyllitids.
In agreement with ARKELL et al. (1957) we are including here the following genera: *Tragorhacoceras* SPATH, 1927; *Juraphyllites* MÜLLER, 1939; *Paradasyceras* SPATH, 1923; *Dasyceras* HYATT, 1900; *Schistophylloceras* HYATT, 1900; *Togaticeras* gen.n., *Nevadaphyllites* GUEX, 1980; *Fergusonites* GUEX, 1980; *Tragophylloceras* HYATT, 1900; *Harpophylloceras* SPATH, 1927 and *Meneghiniceras* HYATT, 1900.
The last two genera are so different (featuring the keel – an exception with phylloceratids), that their separation as a distinct subfamily could be considered.
Galaticeras SPATH, 1938, originally included by ARKELL et al. (1957) with Juraphyllitidae was reclassified into Discamphiceratinae (GUEX & RAKÚS, 1991).

Genus: *Tragorhacoceras* SPATH, 1927

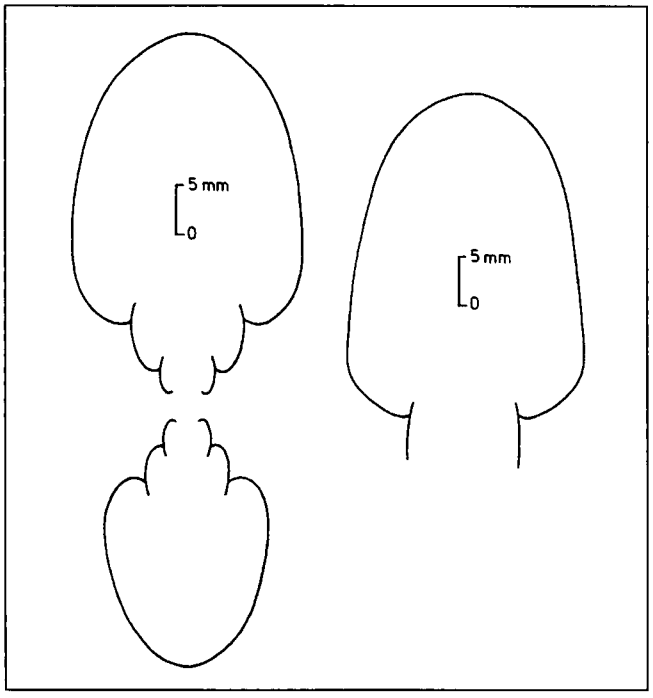
Type species: *Phylloceras occultum* MOJSISOVICS, 1873.

Tragorhacoceras occultum (MOJSISOVICS, 1873)

(Text-Figs. 12, 13; Pl. 2, Fig. 7, 8, 9)

v1873 *Phylloceras occultum* E. v. MOJSISOVICS – MOJSISOVICS; Pl. 16, Fig. 3–6.
1934 *Tragorhacoceras occultum* (MOJSISOVICS) – SPATH; p. 324, Fig. 111 (cum syn.).
1973 *Tragorhacoceras occultum* (MOJSISOVICS, 1873) – KOLLÁROVÁ-ANDRUSOVOVÁ; p. 106, Pl. 17, Fig. 2–9, 11–13, Text-Fig. 61–65.

Lectotype: The specimen depicted by MOJSISOVICS in 1873, Pl. 16, Fig. 4 and repeatedly shown here in Pl. 2, Fig. 8, 9.



Text-Fig. 12.
Tragorhacoceras occultum (MOJSISOVICS).
Cross section of an adult specimen.
Loc. Sandling (Salzkammergut, Austria).

Material: Two well preserved individuals whereby the Holotype includes an almost complete, well preserved body chamber.

Dimensions:

	D	Wh	Wt	o
GBA 1873/5/54	61,8	27,0	22,0	17,0
GBA 1873/5/54 Lectotype	70,0	29,0	24,0	21,3

Description: This small to medium large form is characterized by a smooth subadult stage similar to *R. neojurensis*. The whorl cross-section is elliptical with slightly convex sides (Text-Fig. 12). The last whorl, on the contrary, features a slightly compressed cross-section with straight sides (Fig. 12a).

The septal line (Text-Fig. 13) is typically phylloceratid with diphyllic saddles and wide-spatular, terminal foliales.

Ornamentation: Subadult stages are smooth. Adult stages exhibit a modified body chamber ornamented in the ventral area by blurred but, nevertheless, clearly visible plications similar to those of *Tragophylloceras numismale*.

Remarks: The presence of plications on the ventrum of the body chamber is being considered as a new, distinctive feature not previously known in the Discophyllitids. It indicates the relationship with Juraphyllitidae and the reason why we consider the *Tragorhacoceras occultum* to be at the beginning of the Juraphyllitid evolutionary line. This relationship to the Liassic *Juraphyllites* was noted already by SPATH (1934, p. 316).

Stratigraphic range and geographic distribution: The species is known from the Northern Calcareous Alps and the West Carpathians where it appears in the Upper Norian–Sevatian.

Genus: *Fergusonites* GUEX, 1980

Type species: *Fergusonites striatus* GUEX, 1980.

Fergusonites neumayri sp.n.

(Text-Fig. 14; Pl. 3, Fig. 5)

v1879 *Phylloceras* nov.form. cf. *partschi* STUR. – NEUMAYR; p. 22, Pl. 1, Fig. 18.

Holotype: The specimen here selected and depicted in Pl. 1, Fig. 6, was originally depicted by M. NEUMAYR (1879) Pl. 1, Fig. 18. The specimen is deposited in the GBA collections under no. 1879/3/5.

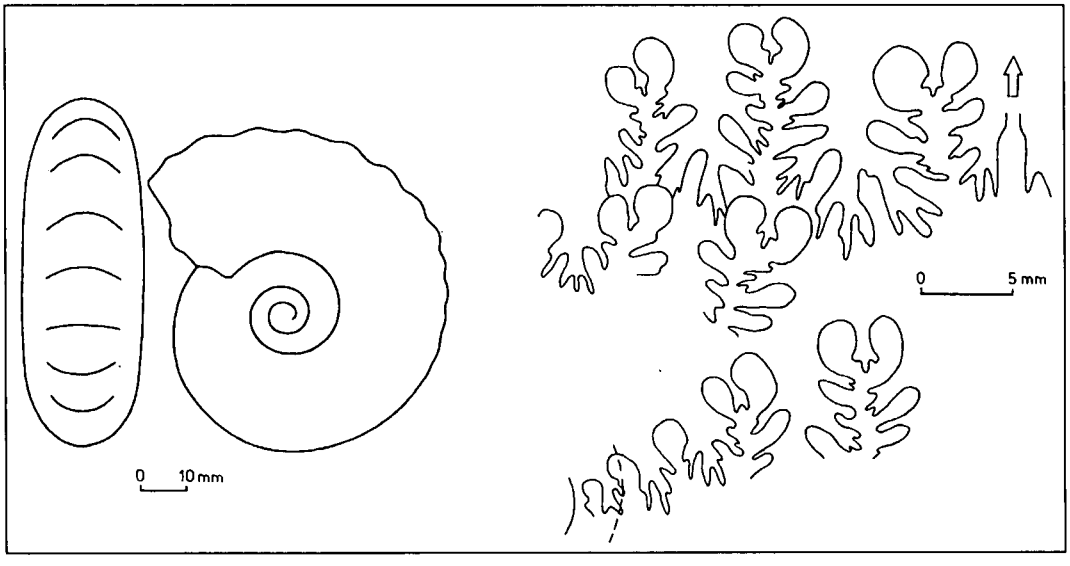
Derivatio nominis: In honor of M. NEUMAYR an outstanding expert on Jurassic Phylloceratids.

Locus et stratum typicum: Zlambachgraben (Northern Calcareous Alps), s.c. "Psilonotenmergel", Lower Hettangian, *Planorbis* zone.

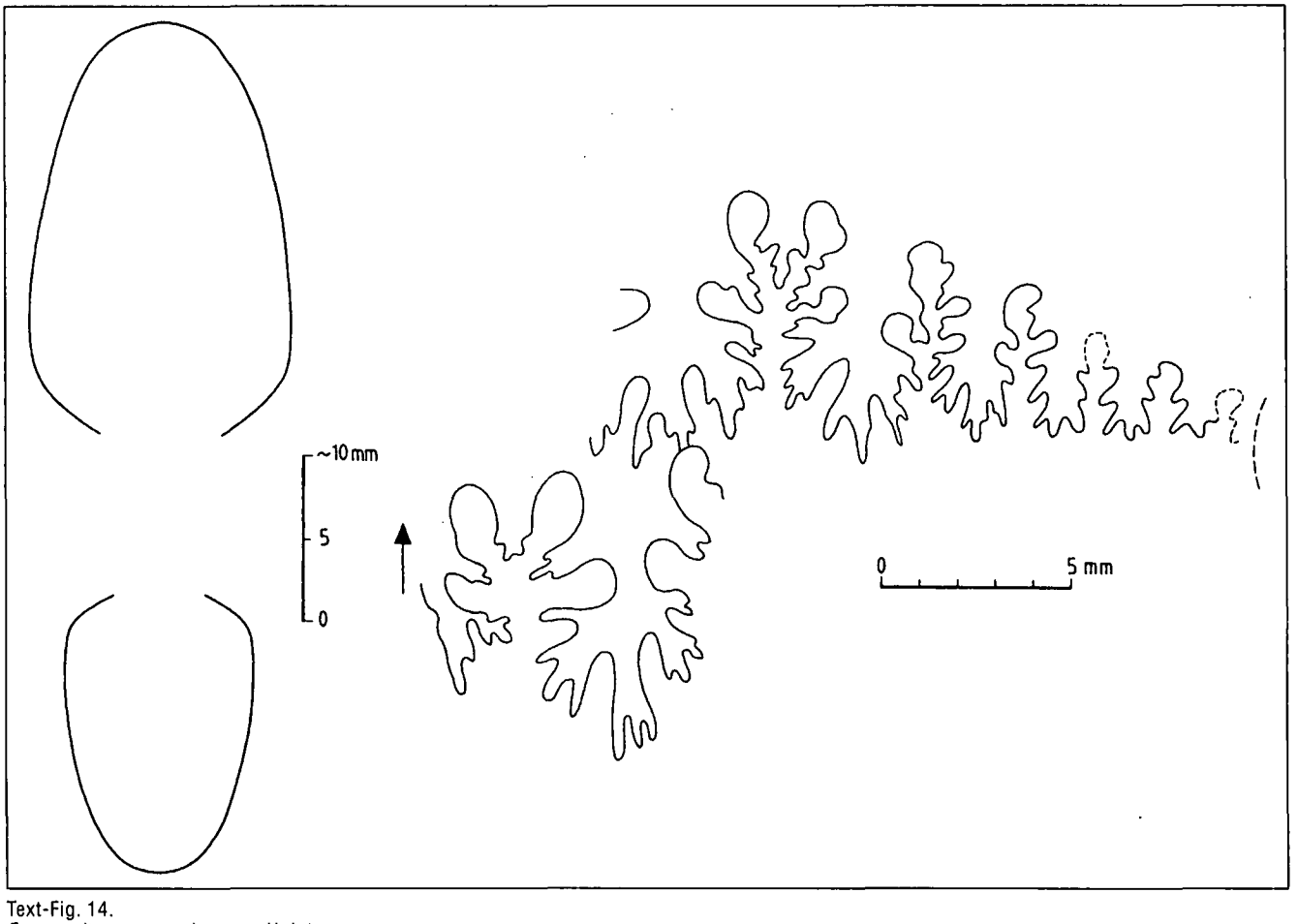
Material: One almost complete individual with preserved body chamber.

Dimensions:

	D	Wh	Wt	o
Specimen 1879/3/4; NEUMAYR; Pl. 1, Fig. 18	52,4	31,0	–	12,9



Text-Fig. 13.
Tragorhacoceras occultum (MOJSISOVICS).
Lectotype.
Lateral, ventral view and suture line of an adult specimen.
Loc. Sandling (Salzkammergut, Austria).
Norian.



Text-Fig. 14.
Fergusonites neumayeri n. sp. – Holotype.
Cross-section and suture line of an adult specimen.
Loc. Goisern (Salzkammergut, Austria) – Lower Hettangien.

Diagnosis: A small, convolute, laterally compressed form with elliptical whorl cross-sections; relatively wide umbilicum with slanted umbilical wall; modified body chamber features irregular, prorsiradiate ribs.

Description: The shell is small, convolutely coiled and laterally compressed. The cross-section of adult whorls (Text-Fig. 14, reconstruction) is elliptical with a relatively wide ventrum. The sides are slightly arched, running convergently towards the ventrum so that the maximum whorl width is found in the umbilical area. The umbilical wall is slanted towards the plane of symmetry. The whorl surface is smooth, except for the body chamber, which is covered by subdued, relatively irregular, slightly prorsiradiate and weakly sigmoidal "ribs". The ribs commence in the periumbilical area. They are, however, very delicate becoming more pronounced only in the ventral half of the coil increasing in thickness towards the ventrum which they traverse undiminished.

The septal line is typically Juraphyllitid (Text-Fig. 13). The first lateral saddle is lower and also more robust than the next. Both lateral saddles are diphyllic and widely spatular.

Remarks: This new species is a typical Juraphyllitid form, the individuality of which has been recognized already by NEUMAYR (1879, p. 22). He did, however, compare it to the species *Partschiceras partschi* STUR (= *P. striatocostatum* (MENEGHINI)). The new species differs from the latter, in the first place, by more evolute coiling and the ornamentation pattern of the body chamber.

Stratigraphic range and geographic distribution: So far the species is known from the Lower Hettangian, *Planorbis* zone of the Zlambachgraben locality in Austria.

Genus: *Togaticeras* gen. n.

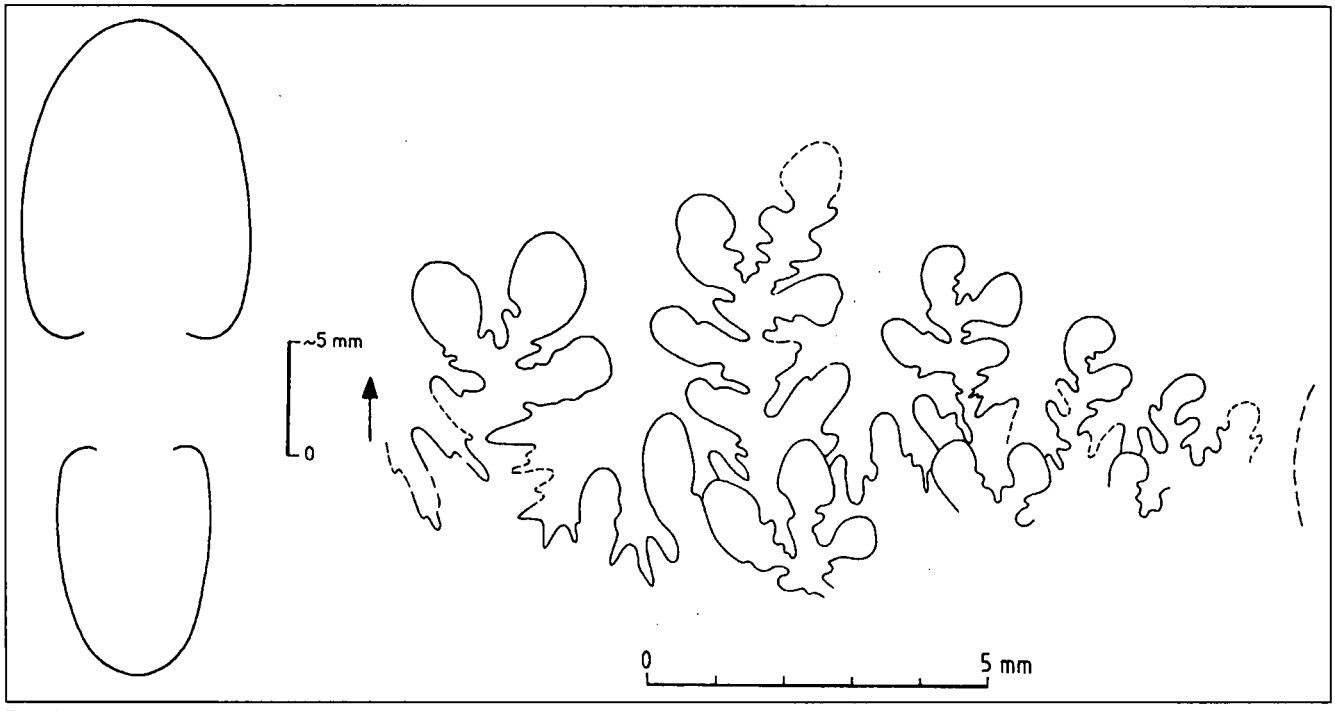
Type species: *Phylloceras togatum* NEUMAYR, 1879.

Diagnosis: Small to large, discoid, convolute to semi-involute forms with numerous, prorsiradiate, slightly sigmoidal constrictions. The subdued ornamentation consists of delicate, sigmoidal growth lines.

Discussion: The new genus *Togaticeras* differs sufficiently from all the rest of the Hettangian Juraphyllitids by the number and prominence of constrictions. It is the first and, phyllogenetically the oldest representative of Juraphyllitids in which the constrictions appear.

It was WÄHNER (1897, p. 175) who noted the similarity between *togatum* and *A. stella* SOW. species. His observations, however, escaped the attention of later researches and SPATH (1923, p. 291) created a considerable confusion when he introduced the taxon *Paradasyceras* for the group of *Rhacophyllites stella* (SOW.) ammonites, selecting as a typical species *Phylloceras ürmösense* (HERBICH) (Sic!).

WÄHNER (1897, p. 174) demonstrated quite convincingly that under the name of *Rhacophyllites stella* (SOW.) CANAVARI (1882 and 1886) depicted two different species: the first was the *stella* with triphyllic first lateral saddle and without constrictions.



Text-Fig. 15.
Togaticeras togatum (NEUMAYR) – Lectotype.
Cross-section and suture line of an adult specimen.
Loc. Zlambachgraben near Goisern (Salzkammergut, Austria) – Lower Hettangien.

Based upon these differences we are including the species *stella* in the genus *Togaticeras* and the species *uermoesense* in the genus *Paradasyceras*; the above mentioned characteristic features of these species fully correspond to the generic definition and bring stability into the systematic of the early Jurassic Juraphyllitids.

Stratigraphic range and geographic distribution: Hettangian to Lower Lotharingian of the Tethys province.

Togaticeras togatum (NEUMAYR, 1879)

(Text-Fig. 15; Pl. 3, Fig. 6,7)

v1879 *Phylloceras togatum* MOJSISOVICS in lit. – NEUMAYR; p. 21, Pl. 1, Fig. 16, 17.

Lectotype: The here included specimen is depicted in Pl. 3, Fig. 7; originally depicted also by M. NEUMAYR 1879, Pl. 1, Fig. 17. It is deposited in the GBA collections under no. 1879/3/4.

Locus and stratum typicum: Zlambachgraben (Northern Calcareous Alps) in s.c. "Psilonotenmergel", Kendelbach Fm., Lower Hettangian, *Planorbis* zone.

Material: Two slightly deformed casts. The Lectotype includes an almost completely preserved body chamber.

Dimensions:

	D	Wh	Wt	o
Specimen 1879/3/4; NEUMAYR; Pl. 1, Fig. 16	21,0	9,5	–	4,0
Lectotype 1879/3/4; NEUMAYR; Pl. 1, Fig. 17	34,8	15,5	10,0	7,5

Description: The shell is small, convolute, laterally compressed. The cross-section of the last, preserved whorl and the body chamber is wide elliptical (Text-Fig. 15, reconstruction). The ventrum is formed by a relatively wide arch merging gradually with arching sides. The umbilical "edge" and wall are made into one short arch.

The last, preserved whorl features approximately 8–10 strongly prorsiradiate constrictions with a large peristomal projection. Constrictions on the body chamber are slightly sigmoidal and less prominent. The shell surface is smooth except for the body chamber showing delicate growth lines with an orientation similar to the constrictions.

The septal line is typically Juraphyllitid (Text-Fig. 15). The first lateral saddle is lower and more robust than the second one. Both saddles are irregularly diphyllic and widely spatular folioles. The outer lobe is typically low and relatively wide.

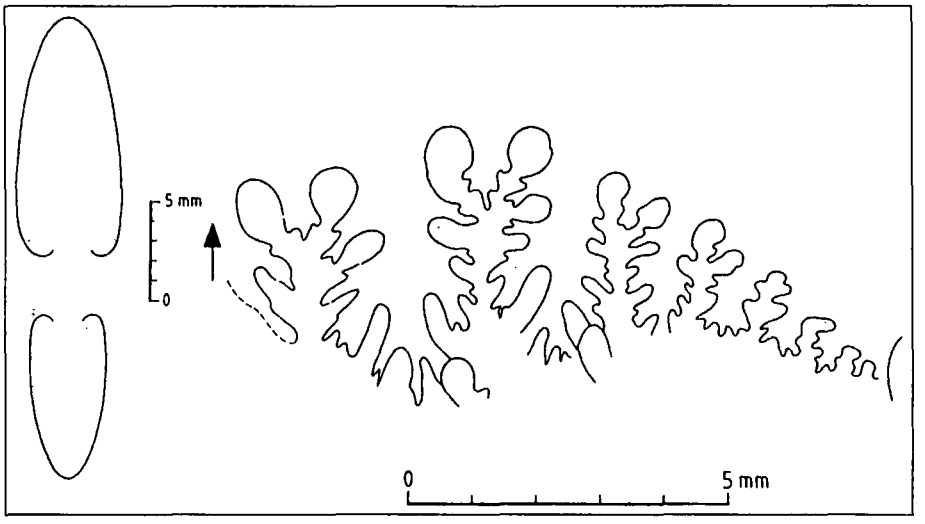
Remarks: The shape as well as the number of constrictions reliably distinguish this species from the rest of Hettangian Juraphyllitids. Considering the constriction stage of our species it bears the closest resemblance to the *T. stella* (SOW.) species as pointed out already by WÄHNER(1898) and SPATH (1914). *T. togatum* (MOJS.), however, differs from the *stella* species in a larger number of constrictions, their shape as well as in the rounded umbilical wall and edge.

Stratigraphic range and geographic distribution: The species is known only from the Lower Hettangian, *Planorbis* zone at the Zlambach locality.

Nevadaphyllites glaberrimus (NEUMAYR, 1879)

(Text-Fig. 16; Pl. 3, Fig. 4)

v1879 *Phylloceras glaberrimus* n.f. – NEUMAYR; p. 20, Pl. 2, Fig. 2 only = Lectotype; not Fig. 3!
1982 *Nevadaphyllites glaberrimus* (NEUM.) – GUEX; p. 136.



Text-Fig. 16.
Nevadaphyllites glaberrimus (NEUMAYR).
Lectotype.
Cross-section and suture line of an adult specimen.
Loc. Zlambachgraben near Goisern (Salzkammergut, Austria).
Lower Hettangian.

Lectotype: The specimen here selected is depicted in Pl. 1, Fig. 2 and by M. NEUMAYR 1879, Pl. 2, Fig. 2, deposited at GBA under no. 1879/3/6.

Locus et stratum typicum: Zlambachgraben, "Psilonotenmergel", Lower Hettangian, *Planorbis* zone.

Material: One specimen with partially preserved, calcified shell and body chamber with the peristome.

Dimensions:

	D	Wh	Wt	o
Specimen 1879/3/6 = NEUMAYR, Pl. 2, Fig. 2	28,6	15,0	–	3,0

Description: The shell is small, involute and strongly laterally compressed. Juvenile stages possess strongly encasing whorls which, however, are convolutely coiled (approximately up to a diameter of 6–8 mm). After that the shell becomes involute. The cross-section of adult whorls is high-elliptical (Text-Fig. 16) with a narrow but rounded ventrum. Flanks of the whorls are slightly arching. The umbilical edge and wall consist of one short arch.

The whorl surface is plain. The body chamber occupies a bit more than 1/2 of the whorl. The peristome is simple with peristomal thickening. The ventral rostrum is short.

The septal line is typically Juraphyllitid (Text-Fig. 16) the first and second lateral saddles (S_1 and S_2) are diphyllic with typical, spatular folioles.

Remarks: M. NEUMAYR included in his new species two individuals depicted in Pl. 2, Fig. 2 and 3. The revision of the original material has shown that with the *glaberrimus* species can also be included the specimen depicted in Tab. 2, Fig. 2. It is a complete specimen with a preserved body chamber. The chamber terminates in a peristome additionally emphasized by a peristomal constriction. This feature, together with the telescoping of septal lines suggests that the specimen was an adult microconch.

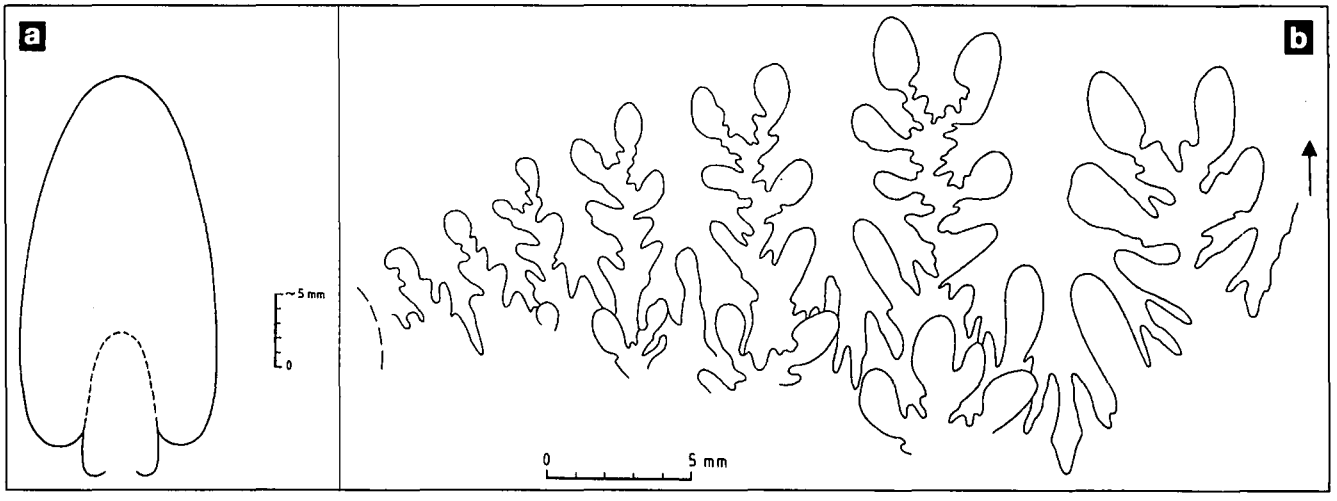
Our species is close to *N. compressus* GUEX, 1980 and *N. psilomorphus* (NEUM.). The differences from the first species were described by J. GUEX (l.c., p. 136). From the second species *N. glaberrimus* differs in the shape of S_1 and S_2 which are diphyllic in the whorl cross-section and, most of all, in the shape of the umbilical wall (see W. LANGE 1952, text end. 1, Fig. 1).

Stratigraphic range and geographic distribution: "Psilonotenmergel" in Zlambachgraben, Lower Hettangian, *Planorbis* zone.

Nevadaphyllites aff. *glaberrimus* (NEUM., 1879)

(Text-Fig. 17; Pl. 3, Fig. 3)

v pars 1879 *Phylloceras* glaberrimum n.f. – NEUMAYR; Pl. 2, Fig. 3 (not Fig. 2!).



Text-Fig. 17.
Nevadaphyllites aff. *glaberrimus* (NEUMAYR).
a) Cross-section of an adult specimen.
b) Suture line.
Loc. Zlambachgraben near Goisern (Salzkammergut, Austria) – Lower Hettangien.

Material: One incomplete, partially deformed, petrified cast.

Dimensions:

	D	Wh	Wt	o
Specimen no. 1879/3/6 = NEUMAYR 1879, Pl. 2, Fig. 3	54,0	27,0	14,0	9,0

Description: The shell is of medium size (total diameter up to 80 mm), involute, laterally compressed. The whorl cross-section is high-elliptical (Text-Fig. 17a). The ventrum is made of a short arch emerging into flat sides. The umbilical edge and wall consist of one single arch. The umbilicus is relatively open.

The surface of the phragmocone is covered with dense although unimpressive radiate plications which begin in the periumbilical area and traverse the ventrum crossing the total height of the whorl. The same ornamentation appears on the remnant of the body chamber.

Towards the end of the body chamber the intercalatory distance is increasing and several very delicate growth lines appear intercalated between the more prominent plication. The septal line (Text-Fig. 17b) is typically phylloceratoid. S_1 is diphyllic, S_2 irregularly triphyllic.

Remarks: M. NEUMAYR (1879, Pl. 2, Fig. 3a, b) depicted only a part of the phragmocone which he included with *N. glaberrimus* (NEUM.). In the GBA collections, however, there are two more fragments of the same (depicted) individual, one of which is part of the body chamber (cf. Pl. 2, Fig. 3). The assembled specimen represents an adult specimen which differs from the *N. glaberrimus* species, above all, by the presence of radiate plication both, on the phragmocone as well as on the body chamber. This feature distinguishes this specimen also from *N. psilomorphus* (NEUM.).

The presence of a body chamber with a modified sculpture and the tendency to unfold seem to indicate that the specimen could be a microconch.

Stratigraphic range and geographic distribution: "Psilonotenmergel" in the Zlambachgraben, Lower Hettangian, *Planorbis* zone.

Genus: *Paradasyceras* SPATH, 1923

Type species: *Phylloceras uermoesense* HERBICH, 1878.

Diagnosis: Medium to large size, discoid, convolute forms with a relatively wide umbilicus. The vertical umbilical wall is accentuated by a conspicuous umbilical edge. The whorl cross-section is oval with parallel to slightly convergent sides. The ornamentation is subdued consisting of delicate prorsiradiate, sigmoidal growth lines. Internal casts are without constrictions. The S_1 and S_2 saddles are diphyllic.

Discussion: It should be noted that, in spite of the very precise definition spelled out by WÄHNER (1898, p. 175), SPATH created a considerable confusion by the selection of genotype for his newly established genus *Paradasyceras*. The confusion stemmed from his erroneous interpretation of the species *Rhacophyllites stella* which, as we have demonstrated previously, does not belong to the genus *Paradasyceras*.

The genus *Paradasyceras* can be well distinguished from all the Hettangian Juraphyllitids and it would appear that it could be included with macroconchs.

Stratigraphic range: Hettangian to the lowest Sinemurian of the Tethys province.

Paradasyceras uermoesense (HERBICH, 1878)

(Pl. 4, Fig. 1, 2, 4)

1878 *Phylloceras üermösense* nov. sp. – HERBICH; p. 86, Pl. XXK, Fig. 1
1898 *Phylloceras uermösense* HERBICH – WÄHNER; p. 173, Pl. 66, Fig. 1–3, non Pl. 65, Fig. 3–5; Pl. 66, Fig. 4, 6–8!
1909 *Rhacophyllites ürmösensis*, HERB. sp. – VADASZ; p. 21, Pl. 6, Fig. 5.
1936 *Rhacophyllites ürmösensis* (HERBICH). – GUGENBERGER; p. 159 (cum syn.).
?1942 *Rhacophyllites ürmösensis* HERBICH. – KOVÁCS; p. 110, Pl. 2, Fig. 12.
1953 *Rhacophyllites* (*Paradasyceras*) *ürmösensis* HERB. – PREDA & RAILEANU; p. 56, Pl. 1, Fig. 1; Pl. 2, Fig. 1.
1957 *Paradasyceras uermoesense* (HERBICH) – ARKELL; p. 1192, Fig. 221, 3.

Neotype: As we are not sure about the existence of the HERBICH type we would propose, in agreement with ARKELL (1957), to designate as Neotype the specimen originally depicted by WÄHNER 1898, Pl. 66, Fig. 1 and repeatedly shown here in Pl. 4, Fig. 1.

Material: There are in total twelve, more or less preserved individuals in PANZER's and WÄHNER's collections. The specimens represent various growth stages, often with the body chamber. Calcified shells are relatively frequently preserved.

Dimensions:

	D	Wh	Wt	o
NHM 1897 I 39	27,4	10,6	8,0	8,1
NHM no number	35,6	16,0	9,7	8,5
NHM no number	43,0	18,0	11,4	11,0
NHM no number	44,0	19,0	9,0	10,8
NHM no number	53,5	24,0	16,0	14,0
NHM no number	56,5	27,4	14,0	14,0
NHM no number	61,4	28,0	15,0	14,0
NHM no number	69,0	30,0	17,0	16,8
NHM no number	76,0	35,8	22,8	21,7
NHM no number	98,0	43,0	23,5	26,4
NHM no number	114,0	52,4	28,6	28,0
NHM no number	127,6	59,0	32,0	29,4
NHM 1897 I 33 = WÄHNER 1898, Pl. 66, Fig. 2	133,0	59,0	32,0	36,0
NHM 1897 I 32 Neotype	196,0	73,4	42,0	52,0

Description: The form is of medium to large size, discoid and convolutely coiled. The cross-section of the whorls of subadult and adult specimens is elliptical with almost parallel sides. The maximum width of the cross-section is in the middle of its height. The sides in the periumbilical area are flat and parallel, even slightly concave. One specimen (Pl. 4, Fig. 2) exhibits a blunted keel located on the ventrum of the phragmocone (cf. WÄHNER, 1898, Pl. 66, Fig. 3a, b). The umbilical partition of the umbilical wall is perpendicular to the plane of symmetry and, during ontogenesis, was accompanied by a pronounced, sharp umbilical edge.

The septal line is typically Juraphyllitid. S_1 and S_2 are diphyllic, terminated by wide, spatular folioles.

The ornamentation is non-prominent, represented by sigmoidal (almost "harpoceratoid") growth lines.

Remarks: Our species distinguishes from the species of *T. stella* mainly in the perpendicular umbilical partition of the umbilical wall and the absence of constrictions.

From *Schistophylloceras aulonotum* (HERB.) it differs in its sharp umbilical edge as well as partition, missing a ventral furrow on the cast and in visibly smaller dimensions.

WÄHNER included in *P. uermoesense* an additional small form (cf. 1898, Pl. 66, Fig. 7). This form, however, differs from our species, in the first place, in a markedly more evolute coiling and the absence of an umbilical edge. It is an adult individual with the body chamber repreenting, in all probability, a microconch.

Stratigraphic range and geographic distribution: The species is known to occur from the Lower Hettangian to the lowermost Sinemurian. It is relatively widespread in the Alps, in the Tethys province (Schreinbach, Pfonsjoch) and in the Rumanian Mts. Persani.

Genus *Schistophylloceras* HYATT, 1900

Type species: *Phylloceras aulonotum* HERBICH, 1878.

Schistophylloceras aulonotum (HERBICH, 1878)

(Pl. 3, Fig. 1)

1878 *Phylloceras aulonotum* HERBICH – HERBICH; p. 115, Pl. 20G, Fig. 2.
1888 *Rhacophyllites stella* SOW. – CANAVARI; p. 91, Pl. 2, Fig. 5 only!
v1898 *Phylloceras uermösense* HERBICH – WÄHNER; p. 173, Pl. 65, Fig. 3, 4, 5; Pl. 66, Fig. 4, 6, 7, 8.
1908 *Rhacophyllites (Kochites) aulonotus* – VADASZ; p. 336, Pl. 6, Fig. 6.
1952 *Schistophylloceras aulonotum* (HERBICH) – LANGE; p. 79, Pl. 10, Fig. 1a, b (cum syn.).
1953 *Rhacophyllites (Schistophylloceras) aulonotus* HERB. – PREDA & RAILEANU; p. 57, Pl. 4, Fig. 1.

Lectotype: By a later designation (HYATT 1900, p. 568) was selected the specimen originally depicted by HERBICH (1878, Pl. 20G, Fig. 2). As we have no information concerning its existence, a replacement could be, justifiably, considered. As a Neotype could then be selected the specimen depicted by WÄHNER (1898, Pl. 23, Fig. 4) repeatedly shown here in Pl. 3, Fig. 1, deposited in the BSM in Munich under the number 1880, p. 529.

Material: Seven specimens from the type series of WÄHNER and one more from PANZER's collection. All specimens are very well preserved with calcite shells whereby the Neotype features the body chamber including aperture.

Dimensions:

	D	Wh	Wt	o
NHM 1897 I 38 = WÄHNER 1898, Pl. LXVI, Fig. 8	8,9 23,0	5,6	8,5	
BSM 1880 XV 529 = WÄHNER 1898, Pl. LXV, Fig. 5	25,0	11,0	6,5	6,5
NHM 1897 I 36 = WÄHNER 1898, Pl. LXVI, Fig. 6	60,0	26,0	16,4	14,6
NHM 1897 I 35 = WÄHNER 1898, Pl. LXVI, Fig. 4	66,5	≈30,6	18,8	15,8
NHM 1897 I 31 = W ÄHNER 1898, Pl. LXV, Fig. 3	71,0	30,0	18,0	16,0
BSM 880 XV 529 = WÄHNER 1898, Pl. LXVI, Fig. 4 = Neotype	82,0	33,0	–	21,0

Description: The shell is small, relatively evolute (in subadult stages) to convolute with an elliptical whorl cross-section. Internal casts feature a ventral furrow.

Juvenile stages (up to a diameter of cca 15 mm) are strongly compressed with a narrow but rounded ventrum. Starting at this point the interior cast features progressively a shallow ventral furrow (cf. CANAVARI 1888, Pl. 2, Fig. 5 or WÄHNER 1898, Pl. 23, Fig. 5b).

Subadult stages are characterized by a very prominent ventral furrow (WÄHNER 1898, Pl. 65, Fig. 4b, and LANGE 1952, Pl. 10, Fig. 1b). This furrow can be observed up to a shell diameter of cca 70 mm.

Above this diameter the furrow diminishes rapidly to the extent that its existence above the body chamber could not be ascertained.

The septal line is typically Juraphyllitid. S_1 and S_2 are di- and triphyllic with wide folioles.

The ornamentation is rather poor, albeit clearly designed. It appears as delicate, sigmoidal growth lines, periodically accentuated by more prominent lines.

The body chamber occupies 3/4 of the whorl. The peristome is without a peristomal thickening and its contour is identical with the course of the growth lines.

Remarks: WÄHNER (1898) considered this form equal to *Paradasyceras uermoesencs* (HERB.). From the latter our species is well distinguishable in a more pronounced arching of whorls, absence of the umbilical edge and the presence of the ventral furrow on the inner cast.

Stratigraphic range and geographic distribution: *Schistophylloceras aulonotum* occurs from the Lower Hettangian up to the Lower Sinemurian. It is found in the Northern Calcareous Alps (Pfonsjoch, Schreinbach, Zlambachgraben), in the North of the Apenninian peninsula (Spezia) and in the Rumanian Mts. Persani.

Family: Phylloceratidae ZITTEL, 1884
Subfamily: Phylloceratinae ZITTEL, 1884
Genus *Geyeroceras* HYATT, 1900

Type species: *Ammonites cylindricus* J. DE C. SOWERBY, 1831.

Geyeroceras subcylindricum (NEUMAYR, 1879)

(Text-Fig. 18; Pl. 3, Fig. 2)

v1879 *Phylloceras subcylindricum* n.f. – NEUMAYR; p. 22, Pl. 1, Fig. 15.
1839 *Geyeroceras subcylindricum* NEUM. – KOVACS, p. 304.
1952 *Phylloceras subcylindricum* NEUM. – LANGE; p. 83, textend. 2, Fig. 2; Pl. 10, Fig. 2.

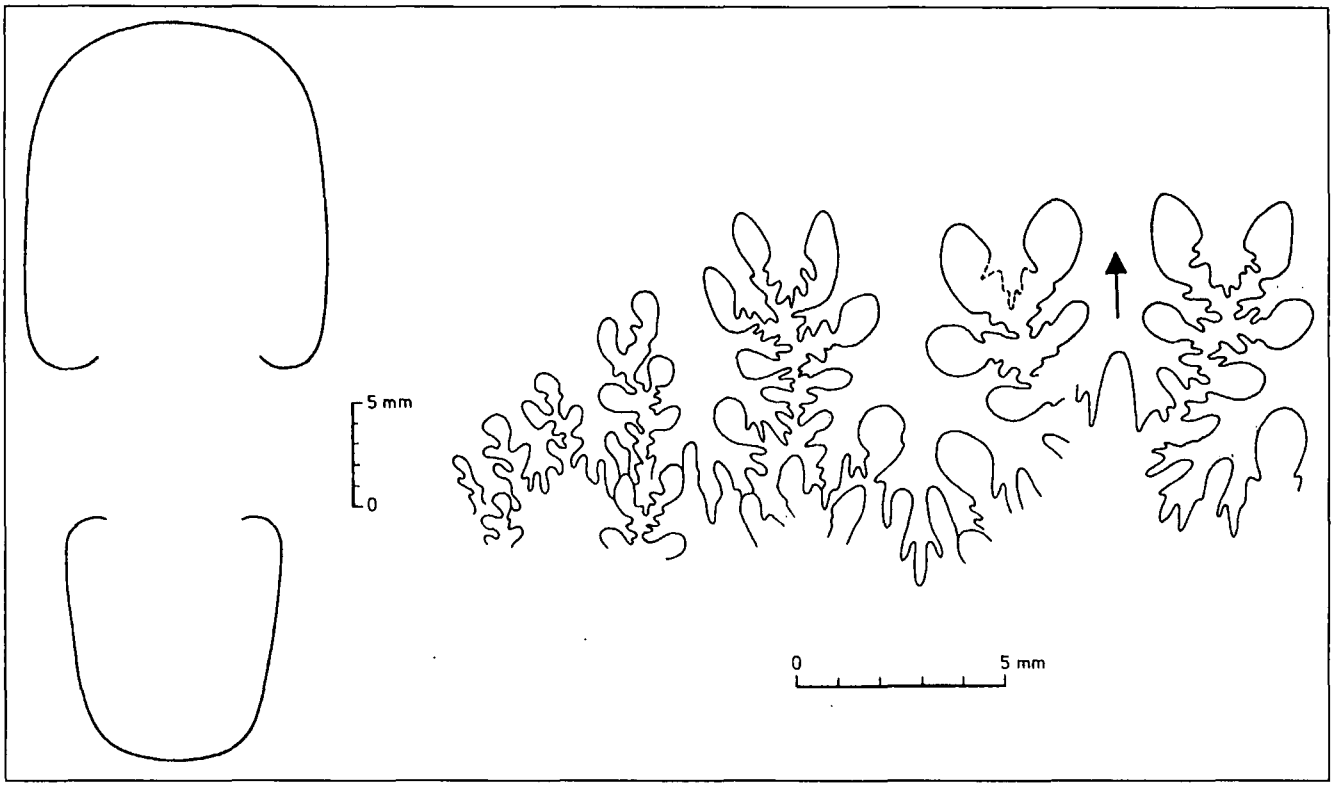
Lectotype: The specimen discussed is shown here in Pl. 3, Fig. 2. It was depicted also by NEUMAYR 1879, Pl. 1, Fig. 15. The specimen is deposited in GBA no. 1879/3/3.

Material: One incomplete, well preserved cast phragmocone.

Dimensions:

	D	Wh	Wt	o
Specimen 1879/3/3 = NEUMAYR, Pl. 1, Fig. 15	33,9	16,4	13,0	6,0

Remarks: NEUMAYR (1879, p. 22) and LANGE (1952, p. 83) amply characterized this species as typical with



Text-Fig. 18.
Geyeroceras subcylindricum (NEUMAYR) – Lectotype.
Cross-section and suture line of a subadult specimen.
Loc. Zlambachgraben near Goisern (Salzkammergut, Austria) – Lower Hettangien.

rounded, rhomboidal whorl cross-sections (Text-Fig. 18) and flat sides. These morphological features enable us to include it with certainty into the genus *Geyeroceras*. The septal line is typically phylloceratoid (Text-Fig. 18).

Stratigraphic range and geographic distribution: "Psilonotenmergel" in Zlambachgraben, Lower Hettangian, *Planorbis* zone.

3. Phyllogeny of the Late Triassic and Early Jurassic Phylloceratids and their Possible Relationship with Jurassic Ammonites

The first discophyllitid forms appeared at the beginning of the Carnian and survived to the uppermost Triassic–Rhaetian for a duration of approximately 20 Ma. During all this period the discophyllitids demonstrate a stable external morphology characterized by a more or less convolutely coiled shell with plain surface or only modest ornamentation consisting of growth lines.

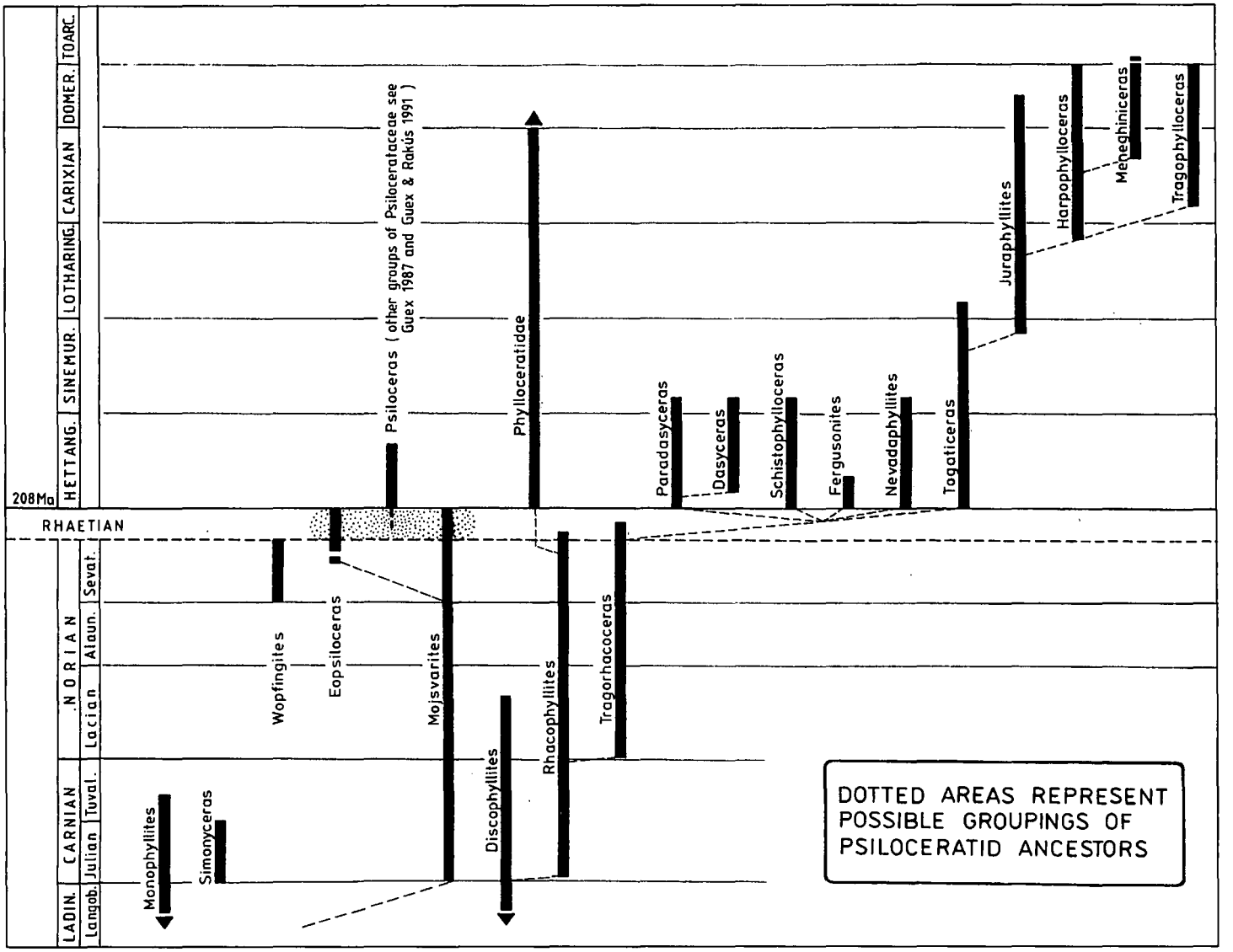
Whereas the external morphology was changing only slightly in the course of time the septal line shows more substantial change. Based on the complexity of its shape the Discophyllitids can be divided in two, parallel lines – Monophyllitinae with monophyllic saddles and Discophyllitidae s.str. with pseudodiphyllic or diphyllic saddles. These two parallel, evolutionary lines continued separately during the whole Upper Triassic. The descendants of these two lines became the basis of such important taxa as Phylloceratidae, Juraphyllitidae and Psiloceratidae.

The stabilized, external and internal organization of Discophyllitids is in a sharp contrast with other Upper Triassic ammonites. The question arises: what could have been the cause of such an organization? It appears that the answer to this question will be neither simple nor unequivocal. We shall, nevertheless, try to look more closely at some of the features and circumstances which could shed light on our problem.

The discophyllitids appear to be the only group capable to have occupied a particular ecological niche located in the upper level of the bathyal. The reasons, or special features, that made it possible (?like, maybe, the form of the septal line, width of the siphon, cf. WESTERMANN, 1987) are not well understood. The niches in question existed in narrow, but stable intra-platform basins of the Western Tethys. From this point of view, therefore, the area of Western Tethys may be considered as the most important focus or "radiation centre" of the Early Jurassic Ammonitina.

It appears that there should be a straight forward relationship between a simplified organization and an ecological niche. Such a relationship would have caused, obviously, a reduction of the ecological area and a simplified morphological organization. It would, on the other hand, accentuate the adaptive superiority of the Phylloceratid in face of other groups of ammonites. These characteristics would in the end lead to the evolutionary success of this group of cephalopods. Nevertheless, in our view, this simplified organization may only be a seeming one. In reality the organization was complex with a latent genetic potential as may be evident from the following features:

1) Phylloceratids are the only group of ammonoid cephalopods which straddles the critical Triassic/Jurassic boundary.



Text-Fig. 19.
Stratigraphical ranges and phyllogeny of the Late Triassic–Early Jurassic Phylloceratids and their possible relationship with Jurassic Ammonitina.

2) The stabilized organization with a considerable physiological tolerance during the approximate 19Ma must have accumulated a genetic potential which, during a short span of one ammonite zone (≈0,5–1,2 Ma), released an extraordinary evolutionary potential. A result of this diffusion was the "radiant boom" which followed in the Lower Liassic the roots of which must be traced to the Phylloceratid biota.
3) There was no time for the Phylloceratid biota to accumulate and encode genetically the features which were to be decisively favorable for the survival during the period of decimation by the end of the Triassic. The Phylloceratids thus were able to fix and retain features which they, eventually, did not make use of but which later during the Jurassic proved extremely useful for the Ammonitina.

In the critical time span of the Rhaetian three morphological groupings, within the Phylloceratid biota, can be distinguished:

- The first grouping is represented by the genus *Rhacophyllites*. It is the basic morphological form from which all the Jurassic Phylloceratids can be derived simply by the increasing speed of the coil widening, resulting in an involute shell.
- The second grouping represented by the genus *Tragorhacoceras* can be derived from *Rhacophyllites* with which it shares a common morphology of subadult stages. This grouping is important in the acquisition of a new feature on the body chamber – the transverse ventral plication. It is, thus, a "front runner" of the Liassic Juraphyllitids which suddenly appeared in the Lower Hettangian. With their "explosion" appears also another new feature – the constrictions. In the Lotharingian to Domerian period this grouping achieved a degree of ornamentation comparable to that of Ammonitina.
- Third, the grouping most difficult to define is represented by the following genera: *Eopsiloceras*, *Mojsvarites* and *"Phyllytoceras"* (Genus *Phyllytoceras* was based on an uncertain species [Species inquirenda] hence its status of "nomen dubiosum"!). The genus *"Phyllytoceras"* was given great importance by WIEDMANN (1972) who considered it to be a direct link between the Triassic Gymnitidae and Psiloceratidae. WIEDMANN (l.c.) included here two species: *"Phyllytoceras" intermedium* WIED. from Carnian sequences in Iran and *Ph. zlambachense* WIED. from Rhaetian of the Northern Calcareous Alps.

However, the comparison of septal lines of the two above mentioned species would indicate that their inclu-

sion in the same genus is disputable as the difference in the form of saddles would appear at the first glance. The *intermedium* species features saddles which are much more incised (including the interval one) than those of *zlambachense* which are typically wide and monophyllic.

The above differences were noted already by KRYSTYN (1974, p. 142), who considered the species *zlambachense* as belonging to *Rhacophyllites*.

The current state of knowledge indicates that within the Upper Triassic biota of Phylloceratid forms a type that could be designated as a direct ancestor of Psiloceratids or *Psiloceras* is not known. It would appear that the ancestors of *Psiloceras* should be sought in the vicinity of *Eopsiloceras* and *Mojsvarites* taxa (cf. Fig. 19).

As documented several times in the past as well as recently (GUEX, 1982) the Psiloceratids exhibit features, concerning mainly the septal line (phylloid folioles, lituitid I) attesting undoubtedly relationships with Phylloceratids. The fact that the Psiloceratids do not feature a sutural lobe sensu WIEDMANN would suggest affinities with Monophyllitinae rather than with Discophyllitidae s.str.

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Plate 1

Fig. 1: ***Simonyceras simonyi* (HAUER).**
Immature specimen representing a transition between late juvenile (annulated/flared) and subadult (fine ribbed) stage (or phase).
Lower Carnian, Feuerkogel (Aussee, Austria); 1×.
Coll. GBA 1993/3/1.

Fig. 2: ***Simonyceras simonyi* (HAUER).**
Juvenile specimen with typical annulated-flared stage, which is gradually but rapidly disappearing. On the internal mould (Fig. 2) we can see that flares correspond with sigmoidal "constrictions" which like the external ornamentation have disappeared.
Lower Carnian, Feuerkogel (Aussee, Austria).
Coll. GBA 1993/3/1.

Fig. 3: ***Eopsiloceras planorboides* (GUEMBEL).**
Neotype BSM ASI 702 (= POMPECKIJ, 1895, Pl. 1, Fig. 2).
Adult specimen with body chamber; Kössen fm. Rhaetian, *Choristoceras marshi* zone.
Lahnewiesgraben (Garmisch-Partenkirchen, Bayern), natural size.

Fig. 4: ***Simonyceras simonyi* (HAUER).**
Immature specimen representing a transition between late juvenile and subadult stage.
Lower Carnian, Feuerkogel (Aussee, Austria); 2×.
Coll. GBA 1873/5/48 (= MOJSISOVICS 1873, Pl. 17, Fig. 3).

Fig. 5: ***Rhacophyllites pumilus* (MOJSISOVICS).**
Holotype GBA 1873/5/57 (= MOJSISOVICS, 1873, Pl. 16, Fig. 12).
?Immature macroconch with partially preserved body chamber.
Upper Carnian. Layer with *Tropites subbullatus*, Sandling (Austria); 0,8×.

Fig. 6: ***Rhacophyllites invalidus* (MOJSISOVICS).**
Holotype GBA 1902/8/279 (= MOJSISOVICS, 1902, Pl. 19, Fig. 6).
Adult microconch with body chamber and peristome.
Upper Norian, layer with *Cochloceras*, Zlambach fm., Goisern (Austria); 0,8×.

Fig. 7: ***Rhacophyllites zitteli* MOJSISOVICS.**
Holotype GBA 1902/3/273 (= MOJSISOVICS, 1902, Pl. 17, Fig. 3).
Immature macroconch with partially preserved body chamber.
Lower Carnian (Julian), Feuerkogel (Aussee, Austria); 0,5×.

Fig. 8: ***Rhacophyllites debilis* (HAUER).**
?Holotype GBA 1902/3/276.
Mature specimen with body chamber.
Norian, Steinbergkogel near Hallstatt (Austria), natural size.

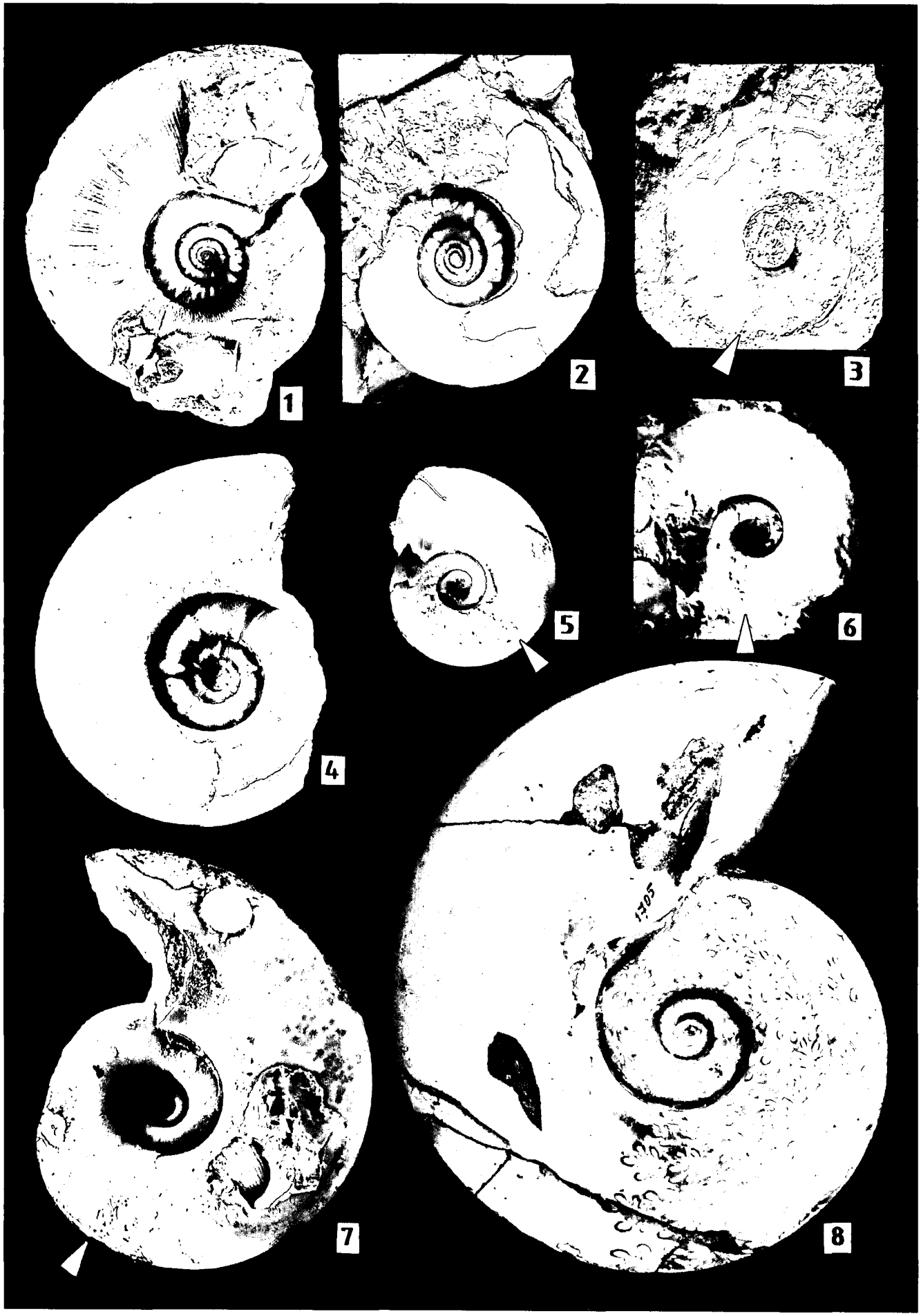


Plate 2

Fig. 1: ***Rhacophyllites neojurensis* (Qu. emend. Hauer).**
GBA without number, early subadult stage.
Lower Norian (Lacian).
Sommeraukogel (Hallstatt, Austria); 1×.

Figs. 2,3: ***Rhacophyllites zitteli.***
GBA 1902/3/273, Syntypes, subadult stages with body chamber partly preserved.
Lower Carnian (Julian).
Feuerkogel (Austria) 0,8×.

Fig. 4: ***Rhacophyllites neojurensis* (Qu. emend. Hauer).**
GUDS 1610, subadult stage.
Sommeraukogel near Hallstatt (Austria).
Lower Norian, natural size.

Fig. 5: ***Rhacophyllites neojurensis* (Qu. emend Hauer).**
Syntype GBA 1902/3/277 (= Mojsisovics, 1902, Pl. 17, Fig. 1).
Subadult stage.
Upper Norian (Sevatian), natural size.
Sommeraukogel near Hallstatt (Austria).

Fig. 6: ***Discophyllites patens* (Mojsisovics).**
Holotype GBA 1873/5/49 (= Mojsisovics, 1873, Pl. 16, Fig. 13 and Wiedmann, 1970, Pl. 6, Fig. 8).
Norian, slightly enlarged.
Sommeraukogel near Hallstatt (Austria).

Fig. 7: ***Tragorhacoceras occultum* (Mojsisovics).**
Syntype GBA 1873/5/54 (= Mojsisovics, 1873, Pl. 16, Fig. 5).
Subadult stage.
Norian, slightly enlarged.
Sandling (Austria).

Figs. 8,9: ***Tragorhacoceras occultum* (Mojsisovics).**
Holotype GBA (= Mojsisovics, 1873, Pl. 16, Fig. 4).
Adult specimen with modified body chamber, natural size.

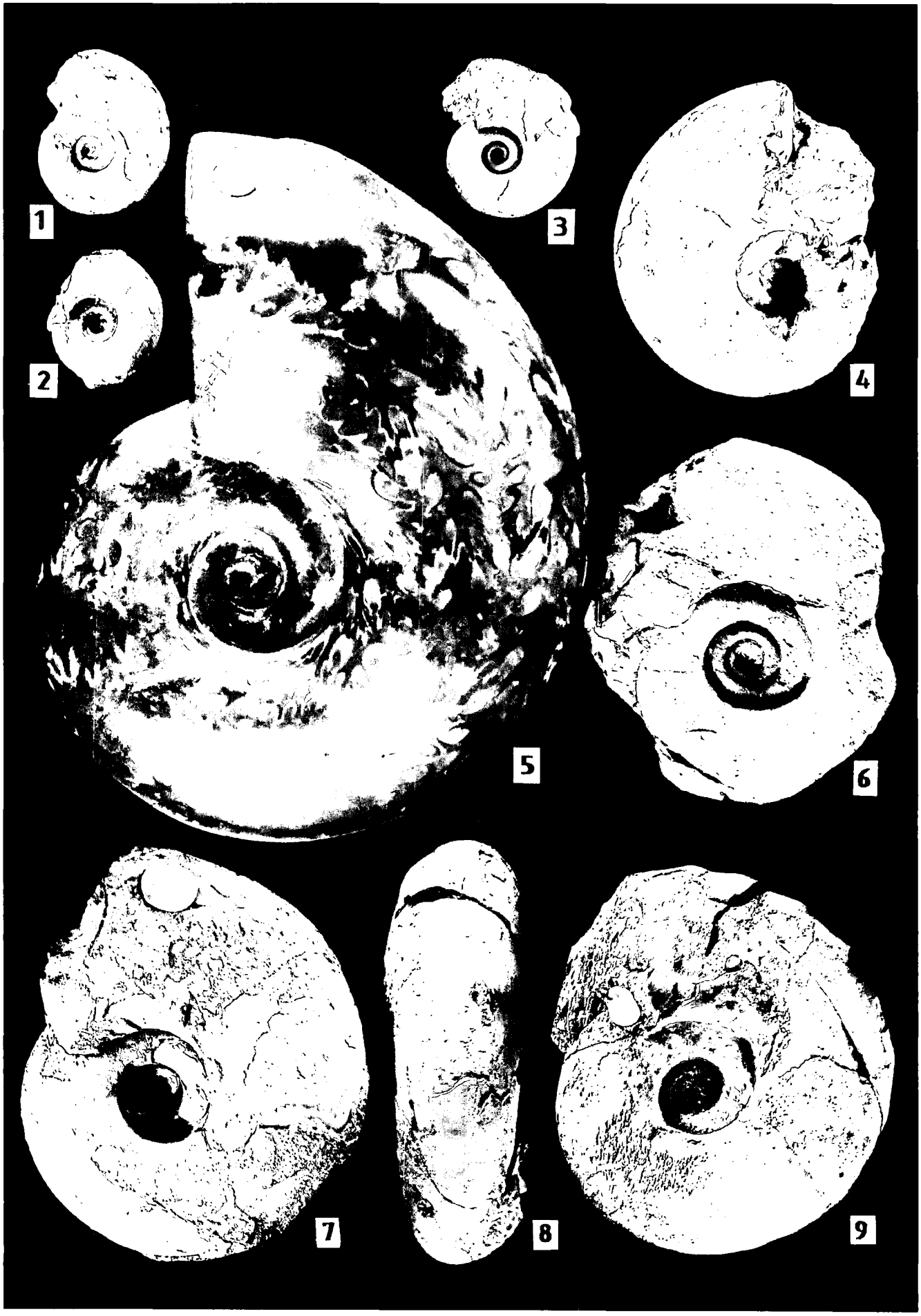


Plate 3

Fig. 1: ***Schistophylloceras aulonotum* (HERBICH).**
BSM 1880×; V 529 (= WÄHNER, 1898, Pl. 65, Fig. 4).
Adult specimen with body chamber and peristome.
Lower Hettangian, *Planorbis* zone.
Zlambachgraben near Goisern (Austria), natural size.

Fig. 2: ***Geyeroceras subcylindricum* (NEUMAYR).**
Holotype GBA 1879/3/3 (= NEUMAYR, 1879, Pl. 1, Fig. 15).
Subadult stage.
Lower Hettangian, *Planorbis* zone; 1×.
Zlambachgraben near Goisern (Austria).

Fig. 3: ***Nevadaphyllites* aff. *glaberrimus* (NEUMAYR).**
GBA 1879/3/6, originally one part of this phragmocone was figured by NEUMAYR 1879, Pl. 2, Fig. 3.
Adult specimen with partly preserved body chamber.
Zlambachgraben near Goisern (Austria), Lower Hettangian, *Planorbis* zone, natural size.

Fig. 4: ***Nevadaphyllites glaberrimus* (NEUMAYR).**
Holotype GBA 1879/3/6 (= NEUMAYR, 1879, Pl. 2, Fig. 2).
Adult microconch with body chamber and peristome.
Lower Hettangian, *Planorbis* zone, slightly enlarged.
Zlambachgraben near Goisern (Austria),

Fig. 5: ***Fergusonites neumayri* n.sp..**
Holotype GBA 1879/3/5 (= NEUMAYR, 1879, Pl. 1, Fig. 18).
Adult specimen with modified body chamber.
Lower Hettangian, *Planorbis* zone, natural size.
Zlambachgraben near Goisern (Austria).

Figs. 6,7: ***Togaticeras togatum* (NEUMAYR).**
Lectotype herein designed in figure 7 GBA 1879/3/4 (= NEUMAYR, 1879, Pl. 1, Fig. 17).
Adult specimen with body chamber, Fig. 6 (= NEUMAYR, 1879, Pl. 1, Fig. 16) is a phragmocone with typical prorsiradiate constrictions.
Lower Hettangian, *Planorbis* zone; 0,8×.
Zlambachgraben near Goisern (Austria).

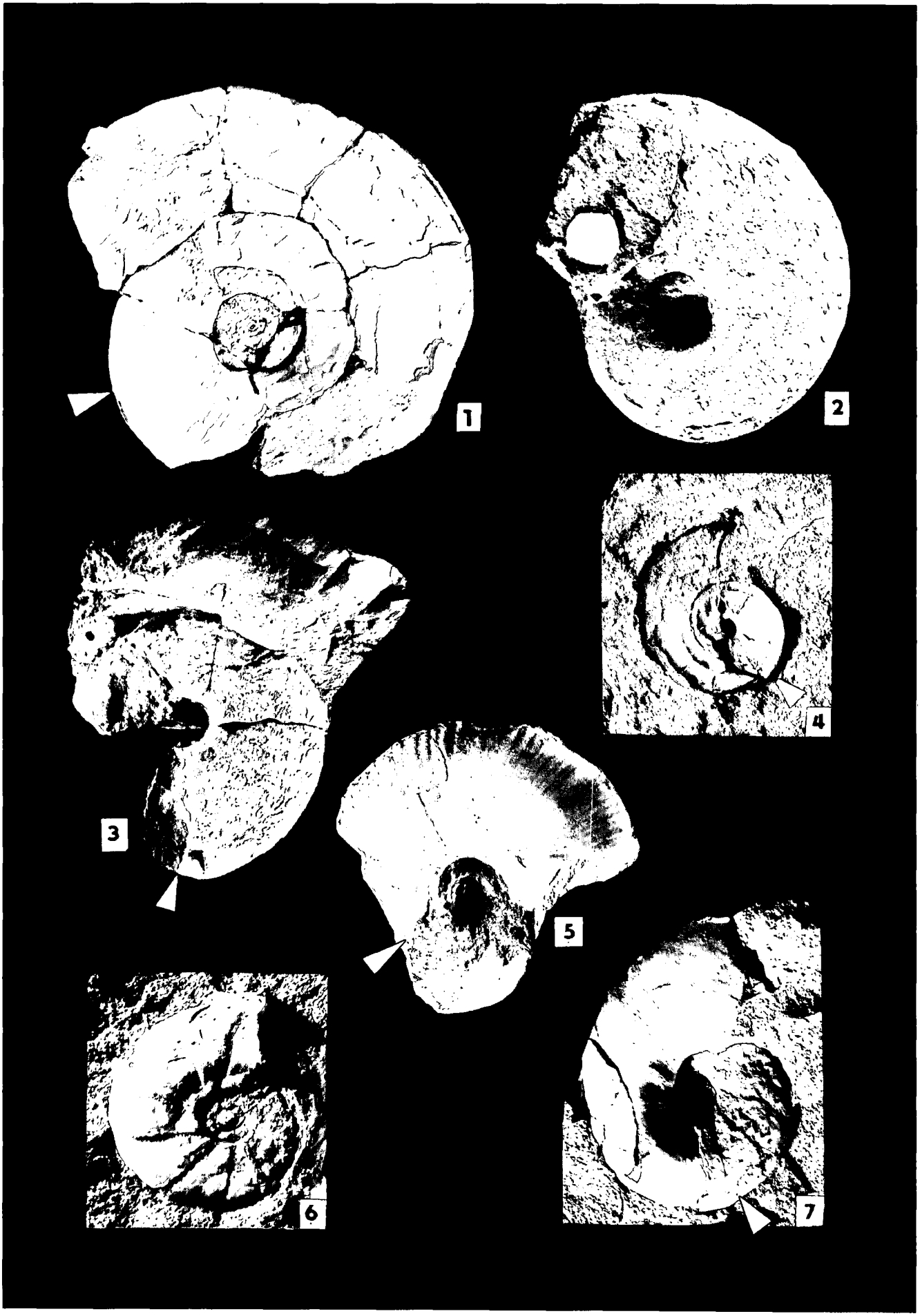


Plate 4

Fig. 1: ***Paradasyceras uermoesense* (HERBICH).**
Neotype NHMW 1898 (Pl. 66, Fig. 1).
Adult macroconch with body chamber.
Middle Hettangian, *Liasicus* zone diminuished; 0,8×.
Schreinbach near Wolfgangsee (Austria).

Figs. 2,4: ***Paradasyceras uermoesense* (HERBICH).**
NHM 1897 / 33 (= WÄHNER, 1898, Pl. 66, Fig. 2, 3).
Phragmocone with blunt keel (Fig. 2).
Middle Hettangian, *Liasicus* zone, natural size.
Schreinbach near Wolfgangsee (Austria).

Fig. 3: ***Schistophylloceras aulonotum* (HERBICH).**
NHM 1879 / 31 (= WÄHNER, 1898, Pl. 65, Fig. 3).
Adult specimen with body chamber; calcified conch with "fine ribs" or growth lines is without trace of ventral furrow.
Lower Hettangian, *Planorbis* zone, natural size.
Pfonsjoch (Austria).

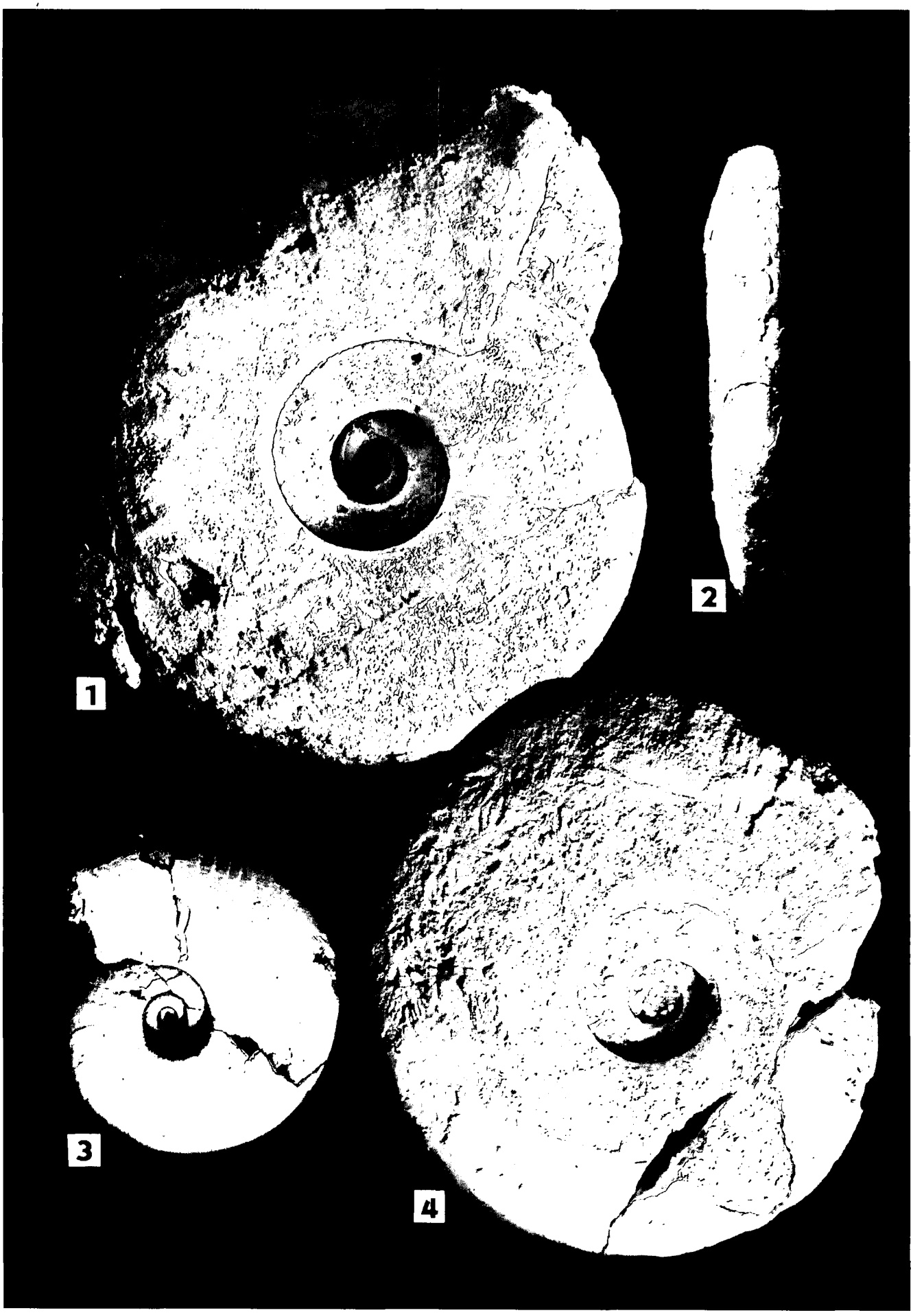
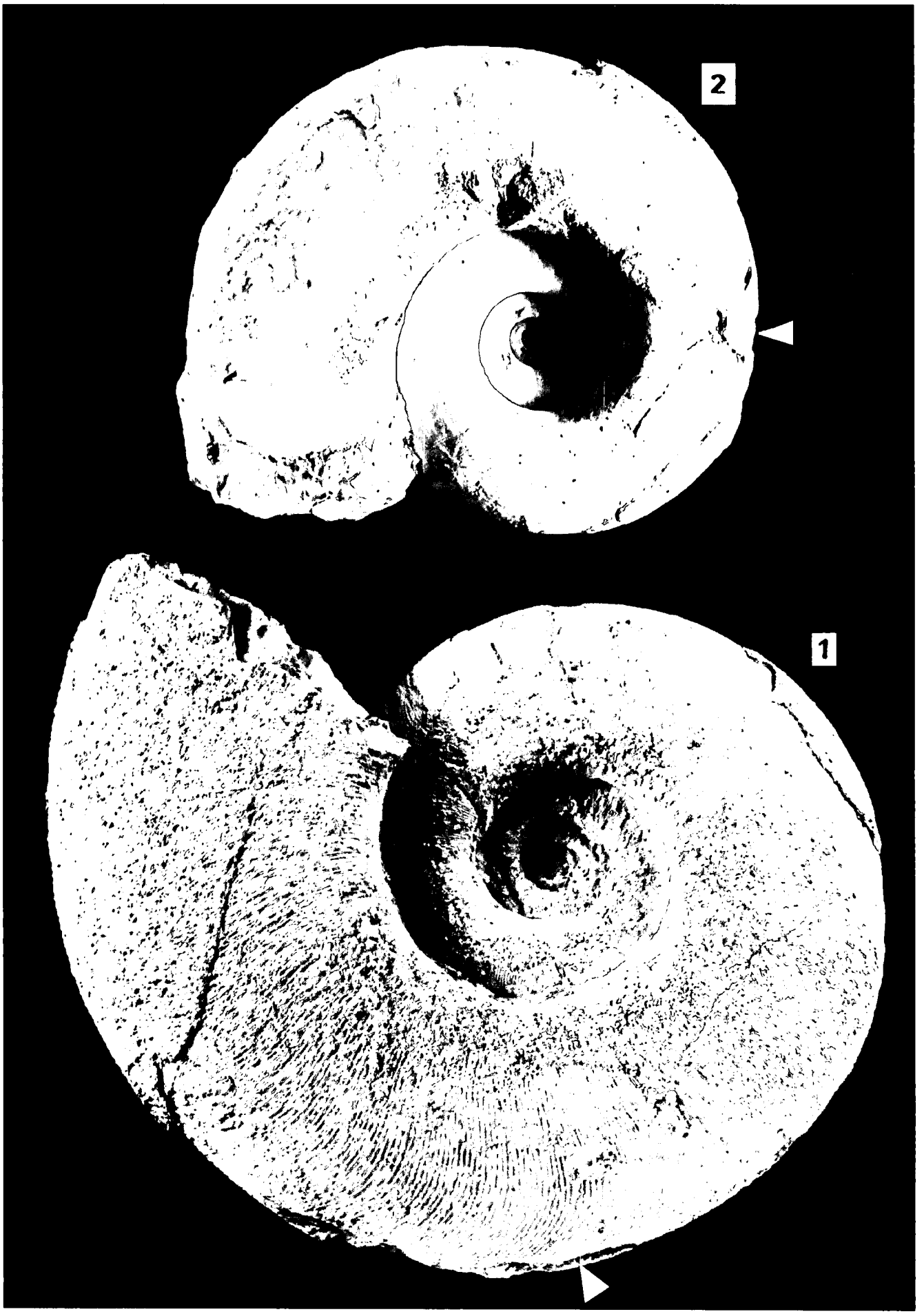


Plate 5

Fig. 1: ***Simonyceras simonyi* (HAUER).**
Syntype GBA 1873/5/48 (= MOJSISOVICS 1873, Pl. 17, Fig. 1).
Adult specimen with partially preserved body chamber.
Lower Carnian, Feuerkogel (Aussee, Austria); 0,8×.

Fig. 2: ***Mojsvarites agenor* (MÜNSTER, 1834).**
Neotype GBA 1873/5/51 (= MOJSISOVICS, 1873, Pl. 16, Fig. 1 sub *Lytoceras Morloti*) adult specimen with body chamber.
Lower Carnian, *sonoides* zone; Raschberg (Goisern, Austria), natural size.



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