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The *Volanoceras* lineage (Ammonoidea, Simoceratidae) – a tool for long-distance correlations in the Lower Tithonian

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With 8 plates, 7 figures and 1 table

Abstract

The allocation of the Tithonian ammonite species *Simoceras schwertschlageri* SCHNEID from the Neuburg Formation (Unterhausen Member) of southern Franconia to the genus *Volanoceras* GEYSSANT, 1985 is outlined. It represents a *Volanoceras* chronospecies of the Tethyan Fallauxi Standard Zone. Another species of this genus, *V. krantzense* CANTÚ CHAPA is rarely recorded from the uppermost Semiforme Zone, or its equivalents, respectively, of Argentina, Mexico, and from southern Spain. We interpret this taxon as a phyletic link between *Volanoceras aesianse* (MENEHINI) from the lower part of the Semiforme Zone and *V. schwertschlageri* (SCHNEID) from the Fallauxi Zone. Closer relations also exist with the still younger *V. volanense* (OPPEL) from the Ponti Zone of the uppermost Lower Tithonian.

A lectotype is designated for *Ammonites perarmatiformis* SCHAUROTH, 1865 which is included in *Volanoceras* and represents the youngest chronospecies of this genus.

As a result, the simoceratid genus *Volanoceras* GEYSSANT is demonstrated not to be an iterative offshoot of *Simoceras* s. str. and thus cannot be treated as a junior synonym of *Simoceras*.

Zusammenfassung

Die aus der Neuburg-Formation (Unterhausen-Subformation) der südlichen Frankenalb beschriebene Ammonitenart *Simoceras schwertschlageri* SCHNEID wird zur Gattung *Volanoceras* GEYSSANT, 1985 gestellt und als Chronospezies dieser Gattung aus der Fallauxi-Zone aufgefaßt. Eine andere Art dieser Gattung, *V. krantzense* CANTÚ CHAPA, ist aus der späten Semiforme-Zone bzw. deren zeitlichen Äquivalenten von Argentinien, Mexiko und von Südschpanien nachgewiesen. Wir sehen in ihr ein Bindeglied zwischen der älteren Form *V. aesianse* (MENEHINI) aus der Semiforme-Zone und *V. schwertschlageri* (SCHNEID) aus der Fallauxi-Zone. Letztere besitzt deutlich engere Beziehungen zu der noch jüngeren Chronospezies *Volanoceras volanense* (OPPEL) aus der Ponti-Zone des höchsten Unter-Tithonium als zu *Volanoceras aesianse* (MENEHINI).

Für *Ammonites perarmatiformis* SCHAUROTH, 1865 wird ein Lectotypus designiert. Die Art wird zu *Volanoceras* gestellt und repräsentiert die jüngste Chronospezies dieser Gattung.

Die Gattung *Volanoceras* GEYSSANT ist keine iterative Entwicklung aus *Simoceras* s. str.,

sondern ein davon unabhängiger Entwicklungszweig und kann folglich nicht als synonym angesehen werden.

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1. Introduction

In the Tithonian, strong faunal provincialism led to construction of several zonal schemes used in different areas which are not easy to correlate. For a good correlation it is necessary to investigate the ammonite successions in neighbouring areas in which faunal mixtures of two or more provinces are developed. This is evident in the Neuburg Formation of SW Germany, situated not far from the classical Tithonian outcrops of Solnhofen and Eichstätt, but younger in age. Hitherto, the Neuburg Formation and its ammonite fauna was the matter of many studies in which its age was estimated in comparison with data from the Tethyan Province in the South and the Subboreal Province in the East. A new approach already revealed that many of the perisphinctacean ammonites from the Neuburg Formation are more or less restricted to the Submediterranean Province, thus helping little in correlation. More useful are Tethyan immigrants, which provide a more reasonable correlation potential. This is implied by the citations of Neuburg ammonite taxa from many sections in Tethyan areas, e.g. southern Spain, northern Italy, and northern Africa. Already BARTHEL (1962), BARTHEL & GEYSSANT (1973), and CECCA (1988) focussed on the correlation with the Tethyan Province, but some conflicts soon became evident (see JELETZKY 1989) and still remain unsolved. In the present paper we focus on the ammonite genus *Volanoceras* GEYSSANT, 1985 of which only a single but significant specimen from the Neuburg section allows to make an important advance for the time scale of the Tithonian. There is no doubt that *Volanoceras* represents a simoceratid genus of Tethyan origin, but even the taxonomic status of this genus was explained by concurrent models (GEYSSANT 1985; SANTANTONIO 1986; CECCA 2002, in press). As discussed below, we favour a linear chronocline of the genus *Volanoceras*, in which the taxon *V. schwertschlageri* from the Neuburg Formation represents an age-diagnostic species.

Herein, we only deal with the macroconchs of *Volanoceras*. Their corresponding microconchs, still unnamed, are small individuals reaching only a diameter of few centimeters, but recalling the larger ones both in coiling and sculpture (see FÖZY 1988; SANTANTONIO 1996). Unfortunately, it was not possible to include the material formerly studied by SANTANTONIO (1986) in this revision because his collections are lost (pers. comm. F. CECCA, Marseille). Therefore, this study is mainly based on the syntypes of several *Volanoceras* species and additional material from southern

Spain which has been collected bed-by-bed by H. SEYFRIED and other colleagues of the University of Stuttgart. Further material comes from the collections of several other institutions.

Abbreviations

- d diameter of shell [mm]
- h height of last whorl [mm]
- w width of shell [mm]
- u width of umbilicus [mm]
- n/2 number of ribs per half a whorl
- BSPM Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
- GPIBO Goldfuss-Museum und Paläontologisches Institut der Universität Bonn, Germany
- ICPB Museo di Paleontologia, Università di Bologna, Italy
- NMC Naturkunde-Museum Coburg, Germany
- SMNS Staatliches Museum für Naturkunde Stuttgart, Germany

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2. Palaeobiogeographic distribution of *Volanoceras* GEYSANT, 1985

Palaeobiogeographic overviews on the ammonite genus *Volanoceras* have already been given by CANTÚ CHAPA (1990) and especially by CECCA (1999). Herein, we

Argentina	Mexico	Cuba	Southern Spain	Algeria	Sicily	Greece	Apennins	Southern Alps	Hungary	Western Alps	SE France	Carpathians	Franconia	Chronospecies	Age
			■					■						<i>V. perarmatiforme</i>	PONTI
			■					■						<i>V. volanense</i>	
			■							■				<i>V. schwertschlageri</i>	FALLAUXI/CILIATA
■			■											<i>V. krantzense</i>	SEMIFORME/ZITTELI*
■			■								?			<i>V. aecinense</i>	

Fig. 1. Geographic-chronologic distribution of the genus *Volanoceras* in the Tithonian (Semiforme – Ponti Zones). The *Zitteli* Biozone is approximately equivalent to the Semiforme Zone (PARENT & CAPELLO 1999). For palaeogeographic placement of localities see Figs. 2–3.

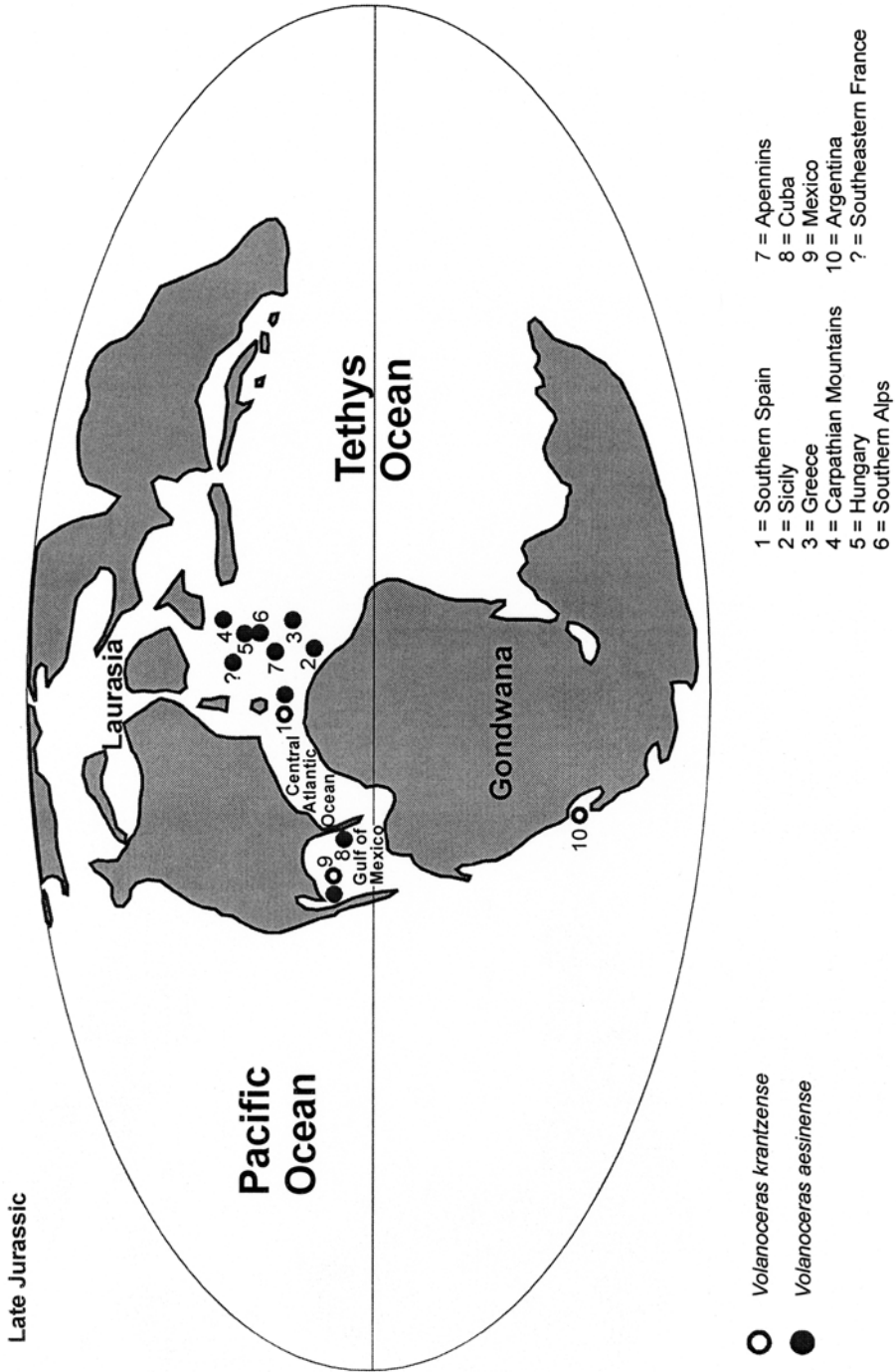


Fig. 2. Palaeobiogeographic record of *Volanoceras* during Semiforme Zone of the Tithonian. Map based on SCOTese (2002).

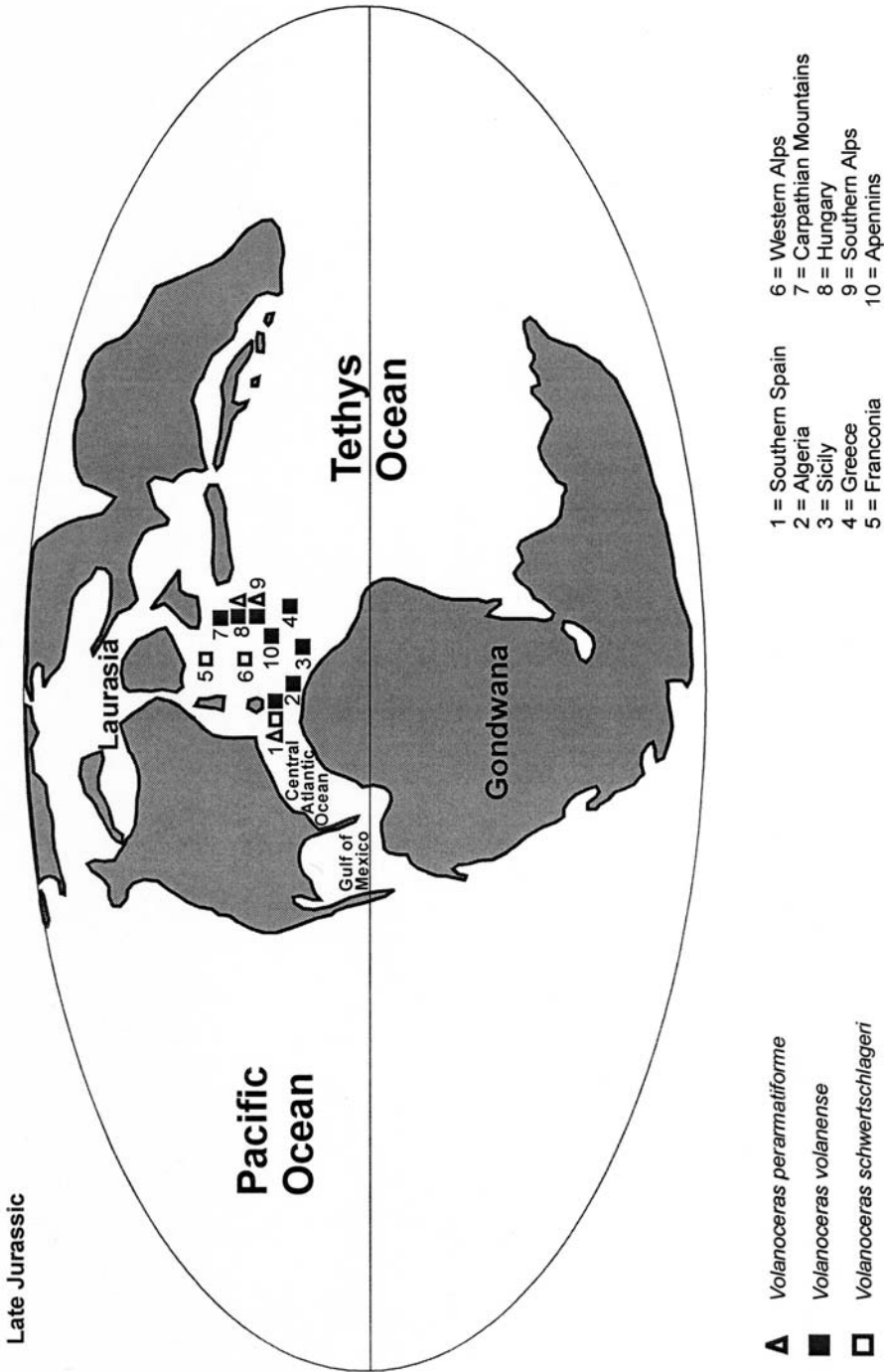


Fig. 3. Palaeobiogeographic record of *Volanoceras* during Fallauxi and Ponti Zones of the Tithonian. Map based on SCOTESE (2002).

present an updated review supported by a more accurate time resolution frame (Fig. 1–3). *Volanoceras* is recorded from the Southern Alps (OPPEL 1863; SCHAURROTH 1865; BENECKE 1866; SCHLOENBACH 1867; ZITTEL 1870; NICOLIS & PARONA 1885; PARONA 1888; DEL CAMPANA 1905; BENETTI 1977; SARTI 1985, 1986, 1995; CARACUEL et al. 1998; this study), the western Carpathian Mountains (ZITTEL 1868; this study), the Western Alps (Dept. Hautes-Alpes, THIEULOY 1963; ENAY et al. 1979); Ardèche area of south-eastern France (CECCA & ENAY 1991); the Apennines (ZITTEL 1870; COLACICCHI & PIALLI 1967; NICOSIA & PALLINI 1977; PALLINI & SCHIAVINOTTO 1980; SANTANTONIO 1986), Hungary (VIGH 1984; FÖZY 1987, 1988, 1994), Sicily (GEMMELLARO 1871; GEYSSANT & MASCLE 1970; CECCA 2002, in prep.), Greece (BERNOULLI & RENZ 1973), southern Spain (SCHLOENBACH 1867; ENAY & GEYSSANT 1975; OLÓRIZ & TAVERA 1975; OLÓRIZ 1978; SEYFRIED 1978; this study), Algeria (ROMAN 1936), southern Germany (SCHNEID 1915, 1916; BARTHEL & GEYSSANT 1973; SCHLEGELMILCH 1994; this study), Cuba (IMLAY 1942), Mexico (VERMA & WESTERMANN 1973; CANTÚ CHAPA 1990), and Argentina (KRANTZ 1926, 1928 and this study). Hence, *Volanoceras* seems to be restricted to the western Tethyan realm, the adjacent Caribbean area and the western south Pacific, the latter connected with the western Tethys by the “Hispanic Corridor”. Due to gaps in the stratigraphic record, collection bias, and the invasive character of occurrences in more marginal positions, the *Volanoceras* lineage is incompletely recorded in most areas. GEYSSANT (1985) interpreted one of these gaps which occurs in the Fallauxi Zone as an example of the “punctuated equilibrium” model of evolution. However, new data contradict her assumptions; nevertheless it is possible to reconstruct the complete *Volanoceras* succession based on well-horizoned material from many areas.

A single ammonite specimen mentioned as “*Simoceras* n. sp. aff. *volanense*” from submarine dykes of Sicily by WENDT (1971: 162) does not belong to the genus *Volanoceras*. It represents a still undescribed new species of the simoceratid genus *Ceratosphinctes*, most probably of much younger age than the type species *Simoceras rachistrophum* GEMMELLARO (= *Ammonites septenarius* QUENSTEDT).

From the Eastern Alps, TOULA (1907: 52) described “*Simoceras* n. sp., aff. *Simoceras volanense* OPP.”, but unfortunately, he did not figure this material, that consisted of four specimens. Hitherto, it was not possible to trace these specimens in the collections of the Natural History Museum of Vienna (pers. comm. Dr H. SUMMESBERGER, Vienna).

3. Systematics

Family Simoceratidae SPATH, 1924

Genus *Volanoceras* GEYSSANT, 1985

Type species: *Ammonites volanensis* OPPEL, 1863.

Remarks. – GEYSSANT (1985) and SANTANTONIO (1986) independently designated lectotypes for *Ammonites volanensis* OPPEL. The lectotype designated by GEYSSANT was the only specimen figured by OPPEL himself, this specimen, however, is lost since World War II. Nevertheless, this lectotype designation is valid (§ 74.4 of ICZN 1999). The paper of SANTANTONIO (1986) was published after GEYSSANT

(1985), although submitted much earlier for publication. Hence, his alternative “lectotype” is invalid, although this specimen is one of OPPEL’s syntypes and, moreover, still available. Despite of this taxonomic confusion, both syntypes belong to the same taxon, so that no further consequences will arise. Even SANTANTONIO (1986: 23) suggested to take the surviving specimen now as the neotype of *Ammonites volanensis*.

More confusion exists with the concept of the genus *Simoceras* ZITTEL, 1870 which was introduced without designation of a type species. Originally six species were attributed to this genus: *Ammonites strictus* CATULLO, *Simoceras lytogyrum* ZITTEL, *Ammonites biruncinatus* QUENSTEDT, *Simoceras admirandum* ZITTEL, *Ammonites volanensis* OPPEL, and *Simoceras catrianum* ZITTEL. In a short review on simoceratids, SPATH (1925) erroneously took FISCHER (1882) as the one who designated *Ammonites biruncinatus* QUENSTEDT as the type species of *Simoceras*, FISCHER only mentioned this species as an example of the genus. GEYSSANT (1986) clearly pointed out that according ICZN, it is now SPATH (1925) who has to be taken as author of this subsequent type designation, prior to that of ROMAN (1938).

In his thesis, OLÓRIZ (1978) argued that after ZITTEL’s intention, *Ammonites volanensis* OPPEL was the more frequent and typical species of *Simoceras*. As a consequence, he took *Ammonites volanensis* as the type species of *Simoceras* and tentatively included *Simoceras biruncinatus* in his new subgenus *Lytogyroceras*. Several authors followed this opinion. However, in the description of ZITTEL, there is no preference traceable for any of the listed species, so that the subsequent designation of SPATH must be accepted forever.

3.1. Taxonomic status of *Simoceras praecursor* SANTANTONIO, 1986

In his review of Tithonian simoceratids of the *volanense* group, now included in the genus *Volanoceras*, SANTANTONIO (1986) erected *Simoceras praecursor* n. sp. which he thought to represent an ancestor of the younger and much better known forms, like *S. aesinense* and *S. volanense*. This taxon is based on very poorly preserved and fragmentary material, the holotype figured therein as pl. 4, fig. 2–3, coming from the Darwini Zone of Monte Nerone, Apennines, Italy. The inner whorls of this holotype exhibit very wide-spaced, coarse and truly bifurcating ribs, a feature unknown from any other species of *Volanoceras* or *Simoceras*. The outer whorls are strongly weathered. In some aspects it resembles *Virgatosimoceras albertinum* (ZITTEL), which also occurs in the Darwini Zone (cf. “*Virgatosimoceras rothpletzi*” in CARACUEL et al. 1998: pl. 2, fig. 2), but differs from the latter in possessing small ventro-lateral nodules or thickenings of the ribs. The paratype of *Simoceras praecursor* is another corroded fragment of an outer whorl resembling a large simoceratid, but, in our opinion, also insufficient to characterize a new species. As a consequence, we take *Simoceras praecursor* SANTANTONIO as a nomen dubium.

3.2. Records of *Volanoceras* from the Semiforme Zone*Volanoceras aesinense* (MENEHINI)

Pl. 1, Figs. 1–4

- 1870 *Simoceras Volanense* OPP. – ZITTEL, p. 95, pl. 32, fig. 7, non figs. 8–9 [= *V. volanense*].
- *1885 *Simoceras* cfr. *volanense* OPP. sp. (var. *Aesinense* nov.). – MENEHINI, p. 376, pl. 20, fig. 4 a–d.
- 1938 *Simoceras volanense* OPPEL. – ROMAN, pl. 30, fig. 290 [refiguration of ZITTEL 1870, pl. 32, fig. 7].
- 1942 *Simoceras* sp. juv. cf. *S. volanense* (OPPEL). – IMLAY, p. 1445, pl. 3, figs. 2–3.
- 1967 *Aspidoceras phoenicium* GEMMELLARO. – COLACICCHI & PIALLI, p. 186, figs. 2e, 3b.
- 1970 *Simoceras* sp., group of *S. volanense* (OPPEL). – BERNOULLI & RENZ, p. 600, pl. 5, figs. 4–6.
- 1970 *Simoceras volanense* (OPP.). – GEYSSANT & MASCLE, p. 213.
- 1971 *Aspidoceras phoenicium* GEMM. – PASSERI, p. 104.
- 1975 *Simoceras* n. sp. gr. *volanense* (OPP.). – ENAY & GEYSSANT, p. 43.
- 1977 *Aspidoceras phoenicium* GEMMELLARO. – NICOSIA & PALLINI, p. 246 pars, pl. 2, fig. 9.
- 1980 *Simoceras volanense* (OPPEL). – PALLINI & SCHIAVINOTTO, p. 507.
- 1983 *Simoceras* (*Simoceras*) *volanense* (OPPEL). – CECCA et al., p. 119, pl. 3, fig. 1.
- 1984 *Simoceras* (*Simoceras*) *volanense* (OPPEL). – ROSSI, p. 115, pl. 35, fig. 12.
- 1986 *Simoceras aesinense* MENEHINI. – SANTANTONIO, p. 15, pl. 1, figs. 1–4, pl. 2, figs. 1–4, 6.
- 1986 *Simoceras volanense* (OPPEL). – CECCA et al., p. 191, tab. 7, fig. 1, 3.
- 1987 *Simoceras* aff. *volanense* (OppeL, 1863). – FÖZY, p. 70, pl. 1, fig. 1.
- 1988 *Volanoceras* (*Volanoceras*) *aesinense* (MENEHINI, 1855). – FÖZY, p. 73, pl. 8, fig. 3–4, pl. 9, fig. 1–3, pl. 10, fig. 2.
- 1989 *Volanoceras* (*Volanoceras*) *aesinense* (MENEHINI). – FÖZY, p. 327, pl. 3, fig. 2.
- 1990 *Volanoceras chignahuapense* sp. nov. – CANTÚ CHAPA, p. 41, figs. 2a–d.
- v ? 1991 *Volanoceras*. – CECCA & ENAY, p. 16.
- 1991 *Simoceras aesinense* MENEHINI. – CECCA et al., p. 97.
- ?1994 *Volanoceras* cf. *aesinense* (MENEHINI). – FÖZY et al., p. 158, pl. 2, fig. 16.
- 1998 *Simoceras aesinense* MENEHINI. – CARACUEL et al., pl. 2, fig. 4.

Holotype: The specimen figured by MENEHINI (1885, pl. 20, fig. 4a–d), formerly housed in the Museo di Paleontologia of Pisa, Italy, but destroyed during World War II. According to SANTANTONIO (1986), a cast of the holotype is housed in the Museo di Geologia e Paleontologia dell'Università di Firenze, no. IGF 507 E.

Type locality: Umbro-Marchean area, Central Italy.

Stratum typicum: Rosso Ammonitico lithofacies of Umbro-Marchean area (Semiforme Zone, Early Tithonian).

Occurrence: *Volanoceras aesinense* (MENEHINI) is recorded from northern and central Italy, Sicily, Greece, southern Spain, Hungary, Poland, Mexico, and Cuba.

Studied material: About 10 specimens from the Southern Alps and from the Apennines, 1 juvenile fragment from the Polish Carpathians.

Measurements: see SANTANTONIO 1986: 14.

Description. – See GEYSSANT 1985 and SANTANTONIO 1986. The innermost whorls exhibit simple but relatively wide-spaced ribs with very few constrictions and/or pseudo-bifurcations. For a very short distance ventrolateral nodes are developed which change gradually into elongate clavate ones. The diameter of onset of clavi is variable, but much earlier than in all other species of *Volanoceras*. The clavi are interconnected with a periumbilical row of nodes by very broad, or even fibulate ribs. The whorl section is subquadratic. Since hitherto no specimen with the peristome was found the final adult size is unknown. However, recorded diameters are much smaller than in younger species.

Remarks. – A juvenile specimen from the famous Rogoźnik area in the Polish Carpathians, previously mentioned as “*Simoceras* sp.” without specific determination (KUTEK & WIERZBOWSKI 1979, 1986; WIERZBOWSKI 1990) belongs to *Volanoceras aesinense* (Pl. 1, Fig. 4). The age of the finding level is confirmed as Semiforme Zone by several diagnostic ammonites, like the index *Semiformiceras semiforme* (OPPEL) and *Cyrtosiceras collegiale* (OPPEL), besides some additional longer ranging taxa, like *Sutneria asema* (OPPEL) and *Physodoceras neoburgense* (OPPEL).

Volanoceras krantzense CANTÚ CHAPA

Pl. 2, Figs. 1–2

- (?) 1925 *Simoceras* cf. *volanense* (OPPEL). – GERTH, p. 41.
 ? 1925 *Simoceras* sp. (ex aff. *S. volanense* OPPEL). – GERTH, p. 39.
 v 1926 *Simoceras* aff. *Volanense* OPP. – KRANTZ, p. 433.
 v 1928 *Simoceras* aff. *Volanense* OPP. – KRANTZ, p. 13, pl. 3, fig. 7.
 v 1956 *Simoceras* aff. *volanense* (OPPEL). – ARKELL, p. 582.
 ? 1959 *Simoceras* aff. *volanense* (OPPEL). – GROEBER, p. 424.
 1973 *Simoceras* cf. *S. volanense* (OPPEL). – VERMA & WESTERMANN, p.196, pl. 37, fig. 2.
 ? 1977 *Simoceras* aff. *volanense* KRANTZ, 1928 non OPPEL. – LEANZA & HUGO, p. 261.
 1977 *Simoceras* (*Simoceras*) *volanense schwertschlageri* (SCHN.). – OLÓRIZ, p. 224, pl. 20, fig. 6.
 1981a *Simoceras* aff. *S. volanense* (OPPEL). – LEANZA, p. 571.
 1981b *Simoceras* aff. *S. volanense* (OPPEL). – LEANZA, p. 80.
 1989 *Simoceras* sp. aff. *volanense*. – OLÓRIZ & TAVERA, p. 223.
 v *1990 *Volanoceras krantzense* n. sp. – CANTÚ CHAPA, p. 43.
 v 1999 *Simoceras aesinense* (MENEGHINI). – PARENT & CAPELLO, p. 352.
 1999 *Simoceras aesinense* (MENEGHINI). – OLÓRIZ et al., p. 478.

Holotype: The specimen figured by KRANTZ 1928, pl. 3, fig. 7, refigured herein, housed at the Palaeontological Institute, University of Bonn, Germany, GPIBO.

Type locality: Bardas Blancas, Prov. Mendoza, Argentina.

Stratum typicum: Formación Vaca Muerta, (*Zittelii* Biozone, Lower Tithonian).

Occurrence: *Volanoceras krantzense* CANTÚ CHAPA has been recorded from Argentina, Mexico, and southern Spain.

Studied material: The holotype and 1 specimen from southern Spain.

Measurements:

	d	h	u	w	n/2
Holotype	89.0	–	59	–	9
	86.0	18.2	58.0	19.3	10

Description. – *Volanoceras krantzense* exhibits a densely ribbed juvenile stage with few pseudo-bifurcations, followed by a longer persisting stage with pointed ventrolateral tubercles, which become clavate at a diameter of about 70 mm. Thus, it is morphologically intermediate between *V. aesinense* and *V. schwertschlageri*. In the latter, the clavate stage starts remarkably later in ontogeny. Proverse constrictions are not very distinctly developed but they are present both in the holotype and in specimens from Spain. The holotype of *V. krantzense* is an uncrushed specimen which hence exhibits a wider cross section than observable in many other specimens of the genus (but see *Volanoceras volanense* in FÖZY 1988, pl. 7, fig. 2–3).

Remarks. – The only specimen of the genus *Volanoceras* hitherto described from the Neuquén-Mendoza basin (West-Central Argentina and Northern Chile) was collected in Bardas Blancas (Fig. 5). It was originally described by KRANTZ

(1928: 13, pl. 3, fig. 7) as *Simoceras* aff. *volanense* (OPPEL), later SANTANTONIO (1986: 15) considered the specimen as a representative of *Simoceras aesinense* MENEGHINI; GEYSSANT (1988: 80) supported the specific identity but within the genus *Volanoceras* GEYSSANT, 1985, whereas FÖZY (1989: 69) even thought of its affiliation to a new genus. CANTÚ CHAPA (1990: 43) introduced the new taxon *Volanoceras krantzense* which is based on the specimen of Bardas Blancas. This specimen was cited by some authors with biostratigraphic purposes (LEANZA 1981a, 1981b; PARENT & CAPELLO 1999). GERTH (1925) cited *Simoceras* cf. *volanense* for the Middle Tithonian of Mendoza (most probably the same specimen later described by KRANTZ) and “*Simoceras* sp. (ex aff. *S. volanense* OPPEL)” from the Middle Tithonian of Cerro Lotena, Neuquén (Fig. 5). The latter specimen was not described and we were unable to trace it. LEANZA & HUGO (1977: 261) cited but did not illustrate *Simoceras* aff. *S. volanense* (OPPEL) sensu KRANTZ (1928) in the *Zitteli* Biozone of Bardas Blancas. The reference to KRANTZ (1928) suggests this specimen could belong to *V. krantzense* CANTÚ CHAPA. FUENZÁLIDA (in: GROEBER 1952: 424) cited *Simoceras* aff. *volanense* (OPPEL) from Baños del Flaco, Chile but no figuration exists of the specimen.

Since the holotype of *V. krantzense* constitutes an isolated record throughout all the basin it is useful to review the biostratigraphy of the type horizon in the type section at Bardas Blancas and the derived chronostratigraphy. KRANTZ (1928: 47) listed the association of *Pseudolissoceras zitteli* (BURCKHARDT), “*Neochetoceras*” *waageni* (ZITTEL), *Pseudhimalayites steinmanni* (HAUPT) [= *P. subpretiosus* (UHLIG, 1878), see SCHWEIGERT 1997 and PARENT 2001] and *Simoceras* aff. *volanense* (= *Volanoceras krantzense*). KRANTZ (1928: 15) gave a short comparative description of “*Neochetoceras*” *waageni*, without figuration, indicating very close resemblance with the type material, it can not contribute to correlation. Moreover, the observation of the original specimens showed that they do not belong to this species. In pure biostratigraphic terms the assemblage indicates the *Zitteli* Biozone, a range-biozone which, in the Neuquén-Mendoza basin, includes the rocks containing *Pseudolissoceras zitteli* (cf. BURCKHARDT 1900; LEANZA 1980; RICCARDI 1984). The age of this assemblage may be indicated as Semiforme Zone on the basis of the concurrent range of the species associated in comparison with occurrences in Europe (OLÓRIZ & TAVERA 1989; PARENT & CAPELLO 1999). In support to a late Semiforme Zone age is the occurrence of *V. krantzense* in southern Spain (surroundings of Cieza, Prov. Murcia), associated with *Physodoceras neoburgense* (OPPEL), *Pseudodiscosphinctes* aff. *bartheli* OLÓRIZ (cf. ZEISS et al. 1994, pl. 5, fig. 1), *Haploceras elimatum* (OPPEL), and overlain by beds yielding *V. schwertschlageri* (SCHNEID), *Toulisphinctes rafaelli* (OPPEL), “*Subplanitoides*” *pouzinensis* (TOUCAS), and *Lytoceras liebigei* (OPPEL).

3.3. Records of *Volanoceras* younger than Semiforme Zone

Volanoceras schwertschlageri (SCHNEID)

Pl. 3, Fig. 1, Pl. 4, Fig. 1–5

- v* 1915 *Simoceras schwertschlageri*. – SCHNEID, p. 92, pl. 4, fig. 6.
- v 1916 *Simoceras schwertschlageri*. – SCHNEID, p. 24.
- 1963 *Simoceras volanense* (OPPEL, 1863). – THIEULOY, p. 293, pl. 2, figs. 3a, 3b.
- v 1973 *Simoceras volanense schwertschlageri* SCHNEID. – BARTHEL & GEYSSANT, p. 33.
- non 1978 *Simoceras (Simoceras) volanense schwertschlageri* (SCHN.). – OLÓRIZ, p. 224, pl. 20, fig. 6 [= *Volanoceras krantzense* CANTÚ CHAPA].

- v 1978 *Simoceras* cf. *volanense* (OPPEL). – SEYFRIED, p. 41.
 v 1978 *Simoceras volanense* (OPPEL). – SEYFRIED, p. 73.
 1979 *Simoceras volanense* (OPP). – ENAY et al., p. 138.
 non 1984 *Simoceras (Simoceras) volanense schwertschlagerei* SCHN. – VIGH, p. 16, tab. 1(3) [= *V. volanense*].
 v 1985 *Volanoceras schwertschlagerei* (SCHNEID 1915). – GEYSSANT, p. 80.
 non 1987 *Simoceras schwertschlagerei* (SCHNEID). – FÖZY, pl. 2, fig. 5 [= *V. volanense*].
 non 1988 *Volanoceras (Volanoceras) volanense schwertschlagerei* (SCHNEID, 1915). – FÖZY, p. 72, pl. 8, fig. 1 [= *V. volanense*].
 v 1991 *Volanoceras schwertschlagerei* (SCHNEID). – SCHLAMPP, p. 64, pl. 15, fig. 7 [re-figuration of holotype].
 v 1994 *Volanoceras schwertschlagerei* (SCHNEID). – SCHLEGELMILCH, p. 116, pl. 61, fig. 2 [re-figuration of holotype].
 v 1999 *Volanoceras schwertschlagerei* (SCHNEID). – SCHERZINGER & SCHWEIGERT, p. 5.

Holotype: The specimen figured by SCHNEID (1915, pl. 4, fig. 6), housed in the collection of the BSPM 1913 IX 200.

Type locality: Unterhausen near Neuburg/Donau, Bavaria, SW Germany.

Type horizon: Neuburg Formation, Unterhausen Member, interval between beds 18 and 28 (according to lithology most probably from bed 26) in the section of BARTHEL (1962) (Lower Tithonian, *Ciliata* Biozone, *Penicillatum* horizon).

Occurrence: Southern Germany, southern Spain, Western Alps (Briançonnais).

Studied material: The holotype and 6 fragmentary specimens from southern Spain.

Measurements:

	d	h	u	w	n/2
Holotype	~90	~18.7	~55.5	~18.0	~11
	82.2	17.0	51.5	18.0	?

Description. – See SCHNEID (1915). Unfortunately the inner whorls of the holotype are rather imperfectly preserved so that it is not clear whether the simple ribs of the earliest stage exhibit pseudo-bifurcations or not. Taking into account the new material from southern Spain, it can be assumed that this earliest ribbing stage persists little longer than in *V. krantzense* and exhibits a higher number of pseudo-bifurcations, similar to *V. volanense*. *V. schwertschlagerei* mainly differs from *V. volanense* in its much earlier onset of clavate ventrolateral nodes, which are, in the latter chronospecies, only present in the adult stage. Moreover, it differs by much more pronounced periumbilical nodes interconnected with the ventrolateral ones by strongly developed ribs. In *V. volanense* the periumbilical nodes are rather weakly developed in the second ribbing stage but become stronger in the body chamber of adult specimens.

Remarks. – Since the original description of SCHNEID (1915) no further specimens of this exotic ammonite were recorded from the type area. According to SCHNEID, the holotype (only specimen) was discovered in the bodychamber of a giant *Toullisphinctes rafaelli* (OPPEL) which survived in the collection of BSPM. For the revision of the Tithonian ammonites from Neuburg (SCHERZINGER & SCHWEIGERT, in preparation) it became necessary to locate the type horizons of SCHNEID's material. The specimen of *Toullisphinctes rafaelli* in question comes from a level at the base of the Neuburg Formation (see SCHERZINGER & SCHWEIGERT 1999), biostratigraphically termed *Penicillatum* horizon. This faunal horizon yields the ammonite taxa listed below; it represents the most diverse faunal assemblage within the Neuburg Formation. The specific diversity of this horizon points to a great exchange rate at the northern Tethyan margin, possibly due to a sea level highstand. Other than in

Franconia, the *Penicillatum* horizon can be easily recognized at St. Concors near Chambéry, SE France (DONZE & ENAY 1961).

The ammonite species of the *Penicillatum* horizon are listed, synonyms are numerous and not mentioned here:

Sublithaceras penicillatum (SCHNEID) [M], "*Lemencia*" *pseudocontigua* (DONZE & ENAY) (m), *Franconites caespitosus* (SCHNEID) [M], *Paraberriassella blondei* DONZE [m], *Danubisphinctes danubiensis* (SCHLOSSER) [M], *Parapallasiceras praecox* (SCHNEID) [m], *Protancyloceras gracile* (OPPEL) [m], *Volanoceras schwertschlageri* (SCHNEID) [M], *Richterella richteri* (OPPEL) [m], *Virgatosimoceras rothpletzi* (SCHNEID) [M], "*Virgatosimoceras*" *broilii* (SCHNEID) [M], *Calliphylloceras* sp. [M], *Haploceras elimatum* (OPPEL) [M], *Haploceras carachtheis* (ZEJSNER) [m], "*Pseudolissoceras*" *concorsi* (DONZE & ENAY) [M], "*Glochiceras*" sp. [m], *Physodoceras neoburgense* (OPPEL) [M], *Sutneria asema* (OPPEL) [m], *Toulisphinctes rafaeli* (OPPEL) [M], *Sarmatisphinctes constrictor* (SCHNEID) [M], *Dorsoplanites lumbricarius* (SCHNEID) ?[M].

The new records of *V. schwertschlageri* from southern Spain confirm the tentative correlation of the Submediterranean Ciliata Zone with the Tethyan Fallauxi Zone. In the *Penicillatum* horizon of Franconia, ammonites from the Submediterranean, Tethyan, and Subboreal bioprovinces occur. Among the Tethyan elements we recognize forms like *Virgatosimoceras rothpletzi*, "*Virgatosimoceras*" *broilii*, *Haploceras carachtheis*, *Haploceras elimatum*, "*Pseudolissoceras*" *concorsi*, and *Toulisphinctes rafaeli*. The single record of *Richterella richteri* from the Neuburg section was found in a slightly higher bed (24) than the bulk of the *Penicillatum* horizon fauna (bed 18–22 in the section of BARTHEL 1962), which still comprises higher beds inclusive bed 28.

Sutneria asema and its dimorphic partner *Physodoceras neoburgense* have a larger stratigraphical range. They already occur in the Semiforme Zone and its equivalents. They have a remarkably wide palaeogeographic distribution which may be also used for correlation purposes. Both *Sutneria asema* and *Physodoceras neoburgense* occur in the Tithonian of Argentina (see KRANTZ, 1928, pl. 3, fig. 5; STEUER 1897, pl. 6, fig. 5), together with Tethyan aspidoceratids like *Pseudhimalayites steinmanni* and its local microconch *Simocosmoceras adversum andinum* LEANZA & OLÓRIZ, 1987 (see SCHWEIGERT 1997 and PARENT 2001), thus suggesting an almost world-wide sea level highstand in the Semiforme Zone.

Volanoceras volanense (OPPEL)

Pl. 5, Figs. 1–4

- non 1855 *Ammonites perarmatus*, SOWERBY – CATULLO, p. 204, pl. 1, fig. 4 [= *Euaspidoceras*, later erroneously interpreted as *V. volanense*]
- *1863 *Ammonites Volanensis* OPP. – OPPEL, p. 231, pl. 58, fig. 2.
- 1868 *Ammonites Volanensis* OPPEL. – ZITTEL, p. 116.
- 1867 *Ammonites Volanensis*. – SCHLOENBACH, p. 254.
- 1869 *Ammonites Volanensis* OPPEL. – ZITTEL, p. 148.
- pars 1870 *Simoceras Volanense* OPP. – ZITTEL, p. 95, pl. 32, figs. 8–9, non fig. 7 [= *V. aesinense*].
- 1871a *Simoceras Volanense* OPP., sp. – GEMMELLARO, p. 244.
- 1871b *Simoceras Volanense* OPP., sp. – GEMMELLARO, p. 63, pl. 2, fig. 5.
- 1871c *Simoceras Volanense* OPP., sp. – GEMMELLARO, p. 40, pl. 9, fig. 5.
- 1885 *Simoceras Volanense* OPPEL. – NICOLIS & PARONA, p. 10, 23, 59, 71.

- 1889 *Simoceras volanense* OPP. sp. – KILIAN, p. 658.
 pars 1905 *Simoceras Volanense* OPP. – DEL CAMPANA, p. 110, non pl. 6, fig. 9 (= HT of *Volanoceras vicentinum*). – [With further citations without figures]
 1936 *Simoceras* cf. *Rachystrophum* GEMMELLARO. – ROMAN, p. 19, pl. 1, fig. 4.
 ? 1939 *Simoceras volanense* OPP. – RAMACCIONI, p. 200.
 1970 *Simoceras volanense* (OPPEL, 1863). – BERNOULLI & RENZ, p. 599, pl. 6, fig. 2.
 1975 *Simoceras volanense* (OPP.). – OLÓRIZ & TAVERA, p. 97, 106.
 1975 *Simoceras volanense* (OPP.). – ENAY & GEYSSANT, p. 44.
 1977 *Simoceras lytogyrum* ZITTEL. – NICOSIA & PALLINI, p. 246, pl. 1, fig. 8.
 1977 *Simoceras volanense* OPP. – BENETTI, p. 236, fig. 32.
 1978 *Simoceras volanense* (OPPEL). – OLÓRIZ, p. 219, pl. 20, fig. 5.
 1978 *Simoceras volanense schwertschlagerei* (SCHNEID). – OLÓRIZ, p. 224.
 1978 *Simoceras* gen. nov., sp. nov. – OLÓRIZ, p. 243, pl. 18, fig. 2 [= pathological specimen, forma fastigata]
 1984 *Simoceras (Simoceras) volanense volanense* (OPPEL). – VIGH, p. 16, tab. 1(3).
 1984 *Simoceras (Simoceras) volanense schwertschlagerei* SCHN. – VIGH, p. 16, tab. 1(3).
 1986 *Simoceras volanense* (OPP.). – SARTI, p. 508, pl. 6, fig. 7.
 1986 *Simoceras volanense* (OPPEL). – SANTANTONIO, p. 17, pl. 2, fig. 5, pl. 3, figs. 1–5, pl. 4, fig. 1.
 1987 *Volanoceras (Volanoceras) volanense volanense* (OPPEL, 1863). – FÖZY, p. 69, pl. 7, Fig. 1–3, pl. 8, fig. 2.
 1988 *Volanoceras (Volanoceras) volanense schwertschlagerei* (SCHNEID, 1915). – FÖZY, p. 72, pl. 8, fig. 1.
 1989 *Volanoceras volanense* (OPPEL, 1863). – FÖZY, p. 143, pl. 4, fig. 2.
 1990 *Volanoceras volanense* (OPPEL 1863). – KAISER-WEIDICH & SCHAIRER, p. 362.
 1991 *Simoceras volanense* (OPPEL). – CECCA et al. p. 97.

Lectotype: The specimen figured by OPPEL (1863, pl. 58, fig. 2), originally housed in the collection of the BSPM, Munich, Germany, but destroyed during World War II.

Neotype: Specimen figured by SANTANTONIO (1986, pl. 5, fig. 1, syntype of OPPEL 1863), designated by SANTANTONIO (1986: footnote, p. 23), refigured herein Pl. 5, Fig. 4, housed in the collection of the BSPM, AS VIII 144. Interestingly, a thin section from the rock matrix of the back side of this neotype yielded numerous calpionellids (*Chitinoidella boneti* DOBEN) which were used for an integrated stratigraphical approach (KAISER-WEIDICH & SCHAIRER 1990).

Type locality: Volano, Trentino, northern Italy.

Stratum typicum: Rosso Ammonitico Superiore (“*Micracanthoceras*” *ponti* Zone, Lower Tithonian).

Occurrence: *Volanoceras volanense* (OPPEL) has been recorded from Italy, Sicily, Greece, southern Spain, Hungary, the Carpathian Mountains, and from Algeria.

Studied material: Survived type material, and about 15 additional specimens from several localities in southern Spain and northern Italy.

Measurements:

	d	h	u	w	n/2
Neotype	103.5	23.3	60.0	–	12

Description. – See SANTANTONIO (1986). Both, the lost lectotype and the neotype are not very indicative of this chronospecies, since the first one represents a juvenile specimen, whereas in the latter the inner whorls are strongly weathered. The innermost whorls exhibit moderately dense-spaced simple ribs with occasional pseudo-bifurcations. The following ribbing stage is characterized by a very pronounced row of pointed ventrolateral nodes, whereas the umbilical part of the flank is very weakly ornamented. At larger diameter, broad ribs starting from the ventrolateral nodes shift down the flank, where they end in periumbilical nodes. The whorl section is subquadratic or slightly higher than wide. One or two proverse constrictions per whorl are usually developed.

Remarks. – Adult specimens are mostly incompletely preserved, but according to some fragments, the final diameter seems usually smaller than in the slightly younger chronospecies *V. perarmatiforme* (SCHAUROTH). In the latest ribbing stage, just behind the aperture, *V. volanense* differs from *V. perarmatiforme* in developing the ribbing stage with ventrolateral clavi which are almost lacking in the latter.

Volanoceras perarmatiforme (SCHAUROTH)

Pl. 8, Figs. 1–2

- v pars *1865 *Ammonites perarmatiformis* n., n. sp. – SCHAUROTH, p. 148, pl. 30, fig. 4.
 1905 *Simoceras Volanense* OPPEL. – DEL CAMPANA, pl. 6, fig. 9.
 pars 1978 *Simoceras (S.) volanense magnum* subsp. nov. – OLÓRIZ, p. 228, pl. 19, fig. 1 [= holotype of *Cordubiceras maius* TAVERA], pl. 20, fig. 2. – [*magnum* = nomen nudum, see below]
 1979 *S. (Simoceras) volanense magnus*. – OLÓRIZ & TAVERA, fig. 1 [suture line].
 1984 *Simoceras (Simoceras) volanense magnum* OLÓRIZ. – VIGH, p. 16, pl. 2, fig. 1, tab. 1(3).
 ?1985 *Cordubiceras nexus* n. sp. – TAVERA, p. 42–43, pl. 1, fig. 5.
 1985 *Cordubiceras maius* n. sp. – TAVERA, p. 44, pl. 2, fig. 1; text-fig. 4b.
 1986 *Simoceras vicentinum* n. sp. – SANTANTONIO, p. 19, pl. 6, figs. 1–2, pl. 5, fig. 2.
 1989 *Volanoceras (Volanoceras) magnum* (OLÓRIZ). – FÖZY, p. 75, pl. 10, fig. 1.

Lectotype: The specimen figured on Pl. 8, Fig. 1, designated herein, housed in the collection of the NMC, no. 3771/1. For the taxonomic status of this taxon see chapter 3.4.

Paralectotype: The fragmentary specimen figured on Pl. 8, Fig. 2, housed in the collection of the NMC, no. 3771/2.

Type locality: Fondi, Sette Comuni, Vicentian Alps, northern Italy.

Stratum typicum: Rosso Ammonitico Veronese Superiore (most probably equivalent of “*Micracanthoceras*” *ponti* Zone, Uppermost Lower Tithonian).

Occurrence: *Volanoceras perarmatiforme* (SCHAUROTH) has been recorded from northern Italy, southern Spain, and Hungary.

Studied material: 2 specimens from northern Italy (= lectotype and paralectotype of *Ammonites perarmatiformis*).

Measurements:

	d	h	u	w	n/2
Lectotype	~23.5	51.0	~14	(–)	11

Description. – See SANTANTONIO (1986: 19) and TAVERA (1985: 44). OLÓRIZ (1978), when erecting *Simoceras volanense magnum* also included large macroconchs of *Volanoceras volanense* s.s. in his taxon. However, he did not designate a holotype, so that the original definition of this taxon is ambiguous and it is hence considered to be a nomen nudum according to ICZN 1999, Art. 13). TAVERA (1985) established a new taxon for the later forms with a trapezoidal section in the preadult growth stage, whereas SANTANTONIO (1986) simultaneously renamed the younger forms as *Simoceras vicentinum*. However, the oldest valid name for this species was already introduced by SCHAUROTH (1865). TAVERA (1985) included his taxon in *Cordubiceras* OLÓRIZ & TAVERA, 1979, because of a looped ribbing style (“*costillas geminadas*”) visible in the last half of the body chamber. However, this looped ribbing which we also observed in a large but fragmentary specimen of *V. volanense* (OPPEL) (SMNS 64852, approximate diameter 185 mm) from Vélez Blanco (Prov. Almería, southern Spain) and also in the lectotype of *Ammonites perarmatiformis* SCHAUROTH just recalls the looped ribbing of *Volanoceras aasinense* (MENEGHINI) or *V. schwertschlagerei* (SCHNEID) so that we do not hesitate to include *Ammonites*

perarmatiformis and its subjective younger synonyms within *Volanoceras*. Furthermore, the occurrence of bitubercular looped ribs is also recorded in adult stages of *Volanoceras schwertschlagerei* (SCHNEID) (see Pl. 4, Fig. 1) and *V. volanense* (OPPEL) from Italy (see SANTANTONIO 1986, pl. 4, fig. 1). Usually, the ventrolateral nodes are pointed rather than clavate depending on the width of the loops. Nevertheless, there is some resemblance with the macroconch *Cordubiceras principale* (GEYSSANT) which may represent an offshoot of *Volanoceras* developing around the Early/Late Tithonian boundary.

The innermost whorls of *V. perarmatiforme* are hitherto unknown, apart from the single and fragmentary *Cordubiceras nexus* TAVERA (1985, pl. 1, fig. 5) which may very likely represent a preadult specimen of *Volanoceras perarmatiforme*. Most likely, a similar simple-ribbed stage with occasional pseudo-bifurcations like in *V. volanense* is developed. Indeed, the holotype of "*Cordubiceras nexus*" shows exactly this supposed early ribbing stage. It is then followed by a ribbing stage with ventrolateral nodes and weak lateral rectiradiate ribs, whereas the periumbilical nodes developed at the umbilical shoulder arise later in ontogeny. In an intermediate ribbing stage the periumbilical and ventrolateral nodes or thickenings are interconnected by relatively sharp ribs typical of this chronospecies, which are often but not necessarily retrocostate. The periumbilical nodes of the adult stage tend to shift up towards the lower third of the flank. The cross sections of the whorl of the premature and adult stages become trapezoidal and do not remain subquadratic like in *V. volanense*. Proverse constrictions occur very rarely, mainly in the earlier stages. *V. perarmatiforme* reaches the largest diameters within the genus.

3.4. Taxonomic status of *Ammonites perarmatiformis* SCHAUROTH, 1865

In 1865, SCHAUROTH, the first curator of the collections of the Duke of Coburg, published a catalogue of fossils from this collection. In this catalogue he introduced a new ammonite taxon, *Ammonites perarmatiformis*, accompanied by a short description and idealised figures of the whorl section, and of the typical sculpture of this species. Only ZITTEL (1868) and GEMMELLARO (1871) cited this reference and both considered *Ammonites perarmatiformis* a junior synonym of *Ammonites volanensis* OPPEL. The syntypes of this taxon were made available by courtesy of E. MÖNNIG, Coburg. They comprise four specimens coming from the Vicentinian Alps. The first one (Pl. 8, Fig. 1) from which obviously the figure of the ribs, the section and the more detailed description was taken is indeed a *Volanoceras*. It is a very large, adult specimen comparable to another giant one figured by OLÓRIZ (1978, pl. 19, fig. 1), but only the body chamber is preserved, which bears 22 bituberculate ribs. The adult specimens of *Volanoceras perarmatiforme* (SCHAUROTH) differ from those of *Volanoceras volanense* (OPPEL) mainly by a larger diameter, a more trapezoidal section, and a sharper, wide-spaced ribbing with pointed ventrolateral nodes lacking clavi.

A further syntype (Pl. 8, Fig. 2) is a compressed fragment of a body chamber which also exhibits a ribbing sculpture typical of *Volanoceras perarmatiforme* (SCHAUROTH). The third syntype (Fig. 4) undoubtedly represents a *Simoceras biruncinatum* (QUENSTEDT). Although its inner whorls are not preserved, the ventral part clearly shows the elongate narrow-spaced and alternating elongate and clavate nodes

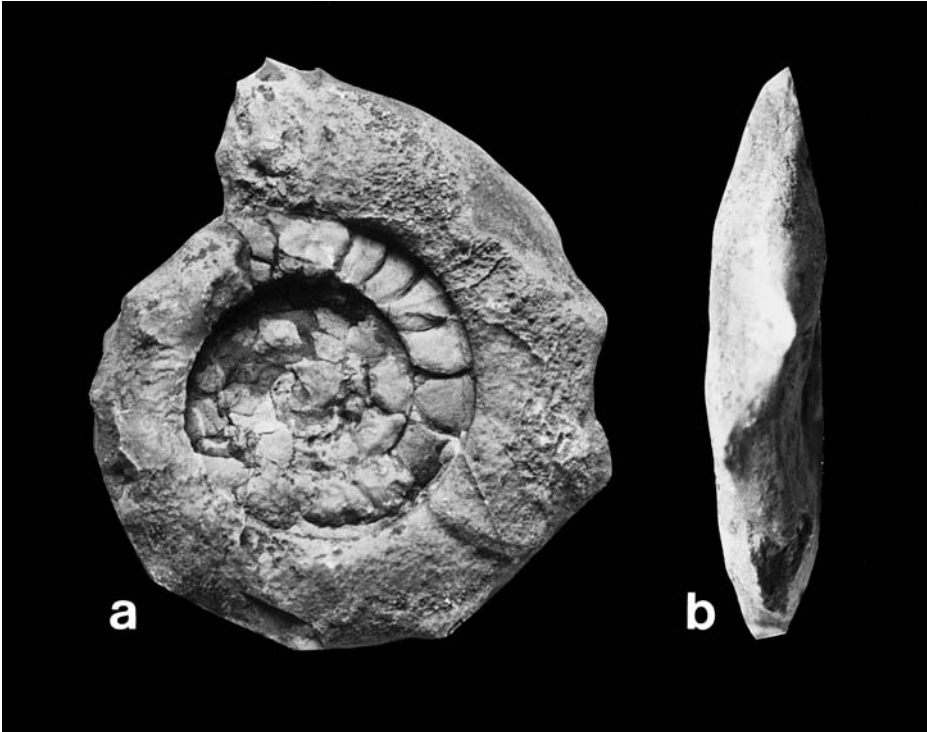


Fig. 4. *Simoceras biruncinatum* (QUENSTEDT) (= syntype of *Ammonites perarmatiformis* SCHAUROTH). Rosso Ammonitico Superiore, Fondi (Sette Comuni), Vicentian Alps, northern Italy; Lower Tithonian, Biruncinatum/Admirandum Zone. NMC no. 3771/3. – a: lateral view, b: ventral view. – x1.

typical of this species. Obviously, SCHAUROTH had erroneously taken this specimen as a juvenile specimen. The last syntype is an almost completely preserved, but much less evolute steinkern with very coarse and wide-spaced, but bifurcating ribs, the inner whorls partly restored by plaster. This latter specimen strongly resembles *Virgatosimoceras negrii* (DEL CAMPANA), which was described from the same area.

Herein, we take that syntype as the lectotype of *Ammonites perarmatiformis* from which the figure and whorl section was taken (Pl. 8, Fig. 1). The second syntype (Pl. 8, Fig. 2) which shows the sharp, rectiradiate to retroradiate ribbing style typical of the preadult stage is designated as the paralectotype. As a consequence, *Ammonites perarmatiformis* becomes a subjective senior synonym of *Volanoceras maius* (TAVERA) and also of the conspecific but later published *Volanoceras vicentinum* (SANTANTONIO). Although the taxon of SCHAUROTH was not used after 1899, it is no nomen oblitum in the sense of ICZN 1999, Art. 23.9 because it fulfils only Art. 23.9.1 but not 23.9.2.

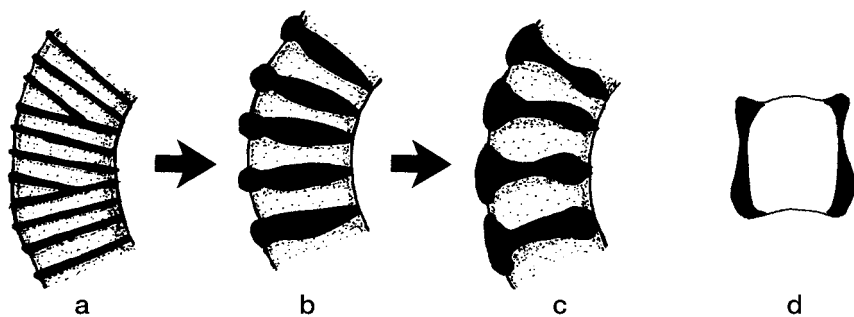


Fig. 5. Development of sculpture in succeeding ontogenetic stages of *Volanoceras*. – a: simple ribs with occasional pseudo-bifurcations, b: looped simple ribs with ventrolateral nodes, c: bituberculate simple ribs with clavate ventrolateral nodes, d: cross section.

4. Evolution of the *Volanoceras* lineage

The genus *Volanoceras* shows a characteristic change of ribbing stages during ontogeny, each stage persisting for a different portion of the ontogeny in succeeding chronospecies (Fig. 5). Another character that changes more gradually is the density of ribbing, which is very wide in specimens of *V. aesinense*, and during evolution becomes more and more narrow, then wide spacing being restricted to the adult stage. The last variable character is represented by the shape of the ventrolateral tubercles. These tubercles grade from pointed ventro-lateral nodes to more clavate ones both in ontogeny and phylogeny.

Within the chronocline of the genus *Volanoceras* the succeeding ribbing stages gradually tend to be displaced to larger diameters during phyletic evolution; moreover, according to present data, the final adult size gradually becomes larger. This clinal heterochronic change during morphologic evolution is a paedomorphic pattern by neoteny (McNAMARA 1982, 1986, 1992; DOMMERGUES 1987; KLINGENBERG 1998), and the lineage (chronocline) may be interpreted as a paedomorphocline (sensu McNAMARA 1982).

5. Further records of simoceratids from Middle and South America

The genus *Volanoceras* is rare not only in many parts of the Tethys but especially in America (for updated discussion see CECCA 1999). Besides the few specimens described in literature herein accounted, no further specimens are known. One of the authors (H. P.) has failed in collecting new specimens in the Tithonian of Bardas Blancas, Casa Pincheira, Mendoza and several localities of the Zapala area, Neuquén (Fig. 6). From the *Internispinosum* Biozone (approximately Ponti Zone in age) of El Ministerio, Zapala area, come two ammonites cited as *Simoceras* sp. or *Simoceras?* sp. by LEANZA & ZEISS (1990, 1992, 1994). Because of their fragmentary preservation status, a secure identification seems impossible, but they may belong to *Volanoceras* (pers. comm. A. ZEISS, Uttenreuth).



Fig. 6. Occurrence of simoceratids (*Volanoceras* spp.) in America.

In Cuba, after the *Volanoceras* specimen described by IMLAY (1942), it appears that no further specimens were recorded (R. MYCZYNSKI, personal communication 21-05-2001).

The ammonite fauna of Sierra Catorce, Mexico, described by VERMA & WESTERMANN (1973) is composed of taxa which are mainly restricted to Central and South America (e.g. "*Virgatosphinctes*", *Aspidoceras haupti*, *Pseudolissoceras zitteli*, "*Aula-*

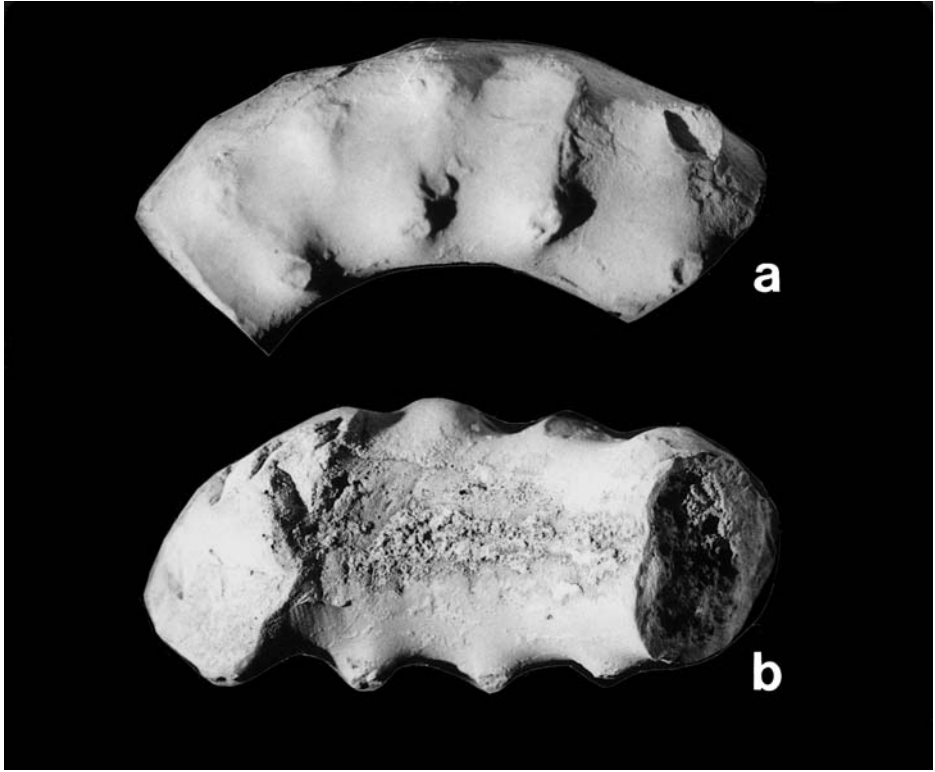


Fig. 7. *Hybonoticeras* ex gr. *crassicostatum/robustum*, lateral view (a) and internal view showing imprints of spines (b) of specimen figured by WELTER 1913, pl. 5, fig. 3. Upper Kimmeridgian/Lower Tithonian, Vale Ranch, northern Peru. GPIBO, without no. – x1.

cosphinctoides” *lauri*, “*Subdichotomoceras*”). The genus *Mazapilites* is endemic in Central America; its morphological affinities with European taramelliceratids like *Taramelliceras kiderleni* BERCKHEMER & HÖLDER are only homoemorphic and thus lacking phyletic or palaeobiogeographic relevance. To a lesser degree the fauna yields also Tethyan immigrants, like *Volanoceras krantzense* and *Physdoceras neoburgense*, which allow a correlation with the *Zitteli* Biozone of Argentina, or, in chronostratigraphic terms, with the (late) Semiforme Zone of the Tethyan standard zonation. Besides the single *Volanoceras* figured by VERMA & WESTERMANN (1973) from Mexico, CANTÚ CHAPA (1990: 41, fig. 2) described a single well preserved specimen of *Volanoceras* as *V. chignahuapense* CANTÚ CHAPA. Later, this specimen was assigned to *Volanoceras aesinense* (CECCA 1999; OLÓRIZ et al. 1999; VILLASEÑOR et al. 2000). We fully agree with this latter determination because of the typical coarsely ribbed inner whorls combined with the bituberculate adult stage.

From San Pedro de Gallo in the Durango District, Mexico, IMLAY (1939, pl. 6, fig. 2) determined an ammonite as “*Simoceras* sp.”. This evolute specimen, however, exhibits biplicate ribs with high diverging points, so that it is neither a *Volanoceras*, nor a *Simoceras* s. str.

An ammonite fragment from Peru figured as "*Simoceras* sp." by WELTER (1913: pl. 5, fig. 1) which exhibits an extremely broad, uncrushed cross section, is surely not a simoceratid as claimed before, but a *Hybonoticer* of the *crassicostatum/robustum* group. This is indicated by a rather weakly developed furrow on the venter, better visible on the print of the dorsal view of the last whorl. It shows perpendicularly arranged imprints of very long ventro-lateral spines (Fig. 7). This form represents, however, another interesting unique Tethyan element in South American Jurassic ammonite faunas. The age of this *Hybonoticer* is suggested to be Early Tithonian or, even more likely, latest Kimmerigian.

6. Remarks on the genus *Simoceras* ZITTEL, 1870

In the original paper of ZITTEL (1868), his newly erected genus *Simoceras* comprised a series of six species: *Ammonites strictus* CATULLO, *Simoceras lytogyrus* ZITTEL, *Ammonites biruncinatus* QUENSTEDT, *Simoceras admirandum* ZITTEL, *Ammonites volanensis* OPPEL, and *Simoceras catrianum* ZITTEL. No type species was designated. SPATH (1925) and ROMAN (1938) erroneously considered the mentioning of *Ammonites biruncinatus* QUENSTEDT of FISCHER (1882) as an example of *Simoceras* thus the type species designation. However, as already pointed out above, the subsequent type species designation is based on SPATH (1925). GEYSSANT (1975) excluded the group of *Ammonites volanensis*, together with *Simoceras schwertschlagerei* and *Simoceras aesinense*, from *Simoceras* and grouped them in a new genus *Volanoceras*, with *Ammonites volanensis* as its type species.

Ammonites biruncinatus QUENSTEDT, the type species of *Simoceras*, and *Simoceras admirandum* ZITTEL represent typical *Simoceras*. Both are said to occur in more or less the same stratigraphical interval, which is named the Admirandum/Biruncinatum Zone, an approximate equivalent of the Fallauxi Standard Zone. After examination of the surviving type material of both taxa, it became obvious, that they are closely related. The main difference seems to be the adult sculpture stage of *Simoceras biruncinatum* which consists of two narrow external rows of clavate nodes. In the preceding sculpture stage, specimens of *Simoceras biruncinatum* exhibit the same characters than in *Simoceras admirandum* with both rows of nodes being more distant and the nodes not clavate but pointed and often already starting to alternate. Another evolute simoceratid taxon is *Simoceras volanensis* VIGH, 1984 which is very closely related to the *admirandum-biruncinatum* group and may perhaps also be conspecific. Like even the type species of *Simoceras* itself, the latter was included in a separate (sub-)genus *Simolytoceras* or *Lytogyroceras* by several authors (OLÓRIZ 1978; VIGH 1984; FÖZY 1988).

While the holotype of QUENSTEDT's *Ammonites biruncinatus* and several specimens of the ZITTEL collection exhibit a rather involute coiling, others like the specimens from the SCHAUROTH collection (Fig. 4) are much more evolute. For these variable characters both taxa could represent either different chronospecies of the same lineage, sexual dimorphs or even extreme variants of a single biospecies. New material collected bed-by-bed is needed to decide which of these possibilities is more likely. According to SANTANTONIO (1986), the group of *Simoceras admirandum/biruncinatum* exhibits a biplicate juvenile ribbing stage (see CECCA et al. 1993, pl. 2, fig. 2), although it is not fully confirmed. In few specimens of *Simoceras*

ceras biruncinatum in which the inner whorls are preserved it is visible that the juvenile stage consists of rather dense, rectiradiate ribs followed by an almost smooth stage with strong prorsiradiate constrictions (Fig. 4, Pl. 6–7). Similar but better preserved specimens of *Simoceras biruncinatum*, however, were sometimes termed as *Simolytoceras volanensioides* (VIGH). Biplicate ribbing in the juvenile stage is clearly visible in *Simolytoceras subbeticum* OLÓRIZ, 1978. The supposed although not confirmed biplicate ribbing in *Simoceras* s. str. prompted SANTANTONIO (1986) to compare it with the “biplicate” ribbing in early whorls of *Volanoceras volanense* and corresponding microconchs. For this supposed synapomorphism, F. CECCA (pers. comm.) suggests *Ammonites volanensis* to represent a descendant of the *Simoceras biruncinatum/admirandum* group, thus being only homoeomorphic with the older *Simoceras aesinense*. As a consequence, he interprets *Volanoceras* as a junior synonym of *Simoceras* s. str. As pointed out above, the juvenile ribbing in *Volanoceras volanense* shows moderately narrow-spaced, simple ribs which often suddenly change their projection without developing pronounced constrictions at this stage. As a result, some ribs join the preceding ones forming “pseudo-bifurcations” (Fig. 5). The point of furcation of these ribs is highly variable depending on the angle and distance between the involved ribs. In *Volanoceras aesinense* the ribs of the juvenile stage are somewhat wider spaced so that such “pseudo-bifurcations” occur less frequently, and they were explicitly noticed by GEYSSANT (1985: 80). In the *Volanoceras* chronospecies which occur stratigraphically between *V. aesinense* and *V. volanense*, the ribbing density and also the number of “pseudo-bifurcations” in the initial stage is intermediate. The second sculptural stage in *Volanoceras volanense* is wholly different from that of *Simoceras admirandum/biruncinatum*, which is almost smooth, and also the later stages in both species have little in common other than the proverse simoceratid constrictions (see Table 1). A derivation of *Volanoceras volanense* from the *Simoceras* branch seems unlikely; the rare but now assured co-occurrence of

Table 1. Comparison of diagnostic features of *Volanoceras* GEYSSANT, 1985 and *Simoceras* ZITTEL, 1870.

Feature	<i>Volanoceras</i>	<i>Simoceras</i>
sculpture of innermost whorls	simple ribs, with occasional “pseudo-bifurcations”	biplicate ribbing
sculpture of juvenile/preadult stage	development of pointed ventro-lateral nodes, the latter may become clavate	flanks almost smooth, two rows of external nodes
sculpture of adult stage	bituberculate ribs	periumbilical nodes, clavate alternating tubercles on venter
position of external nodes	constant ventro-lateral position, not alternating	migrating to close ventral position, alternating
direction of external nodes	pointing ventrolaterally	pointing ventrally
cross section	subquadratic to trapezoidal	oval
constrictions	prorsiradiate	prorsiradiate
coiling	extremely evolute	moderately evolute
sexual dimorphism	observed but unnamed	unknown

Simoceras admirandum and *Volanoceras schwertschlageri* strongly favours our model of a *Volanoceras* chronocline beginning at the Semiforme Zone and reaching, at least, the Ponti Zone. This is concordant with GEYSSANT's view of the phylogeny of this genus.

The ancestors of *Volanoceras* are hitherto unknown. Some possibly related forms already occur in the late Early Kimmeridgian, e.g. "*Simoceras* nov. sp." figured by SARTI (1986, pl. 1, fig. 1) from the Divisum Zone of the Southern Alps. Descendants of *Volanoceras* are likely represented by the simoceratid genus *Cordubiceras* OLÓRIZ & TAVERA, 1979 which is characterized by a pronounced looped ribbing style, very similar to that of *Hybonotoceras*, and more abundant, rectiradiate constrictions.

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Plate 1

- Fig. 1. *Volanoceras aesinense* (MENEGHINI). Cabra, Prov. Cordoba, southern Spain; Lower Tithonian, Semiforme Zone. SMNS no. 64663. – x1.
- Fig. 2. *Volanoceras aesinense* (MENEGHINI). La Rocchetta near Arcevia, Central Apennines, Italy; Lower Tithonian, Semiforme Zone. BSPM no. 1964 XXIV 3. – x1.
- Fig. 3. *Volanoceras* cf. *aesinense* (MENEGHINI). La Rocchetta near Arcevia, Central Apennines, Italy; Lower Tithonian, Semiforme Zone. BSPM no. 1964 XXIV 5. – x1.
- Fig. 4. *Volanoceras aesinense* (MENEGHINI). Rogoźnik, Polish Carpathians, Czorsztyn Formation, Rogoźnik Coquina Member, bed 12 of section in KUTEK & WIERZBOWSKI 1986, table 2; WIERZBOWSKI 1990, fig. 3; Lower Tithonian, Semiforme Zone (photograph provided by courtesy of A. WIERZBOWSKI). – x2.

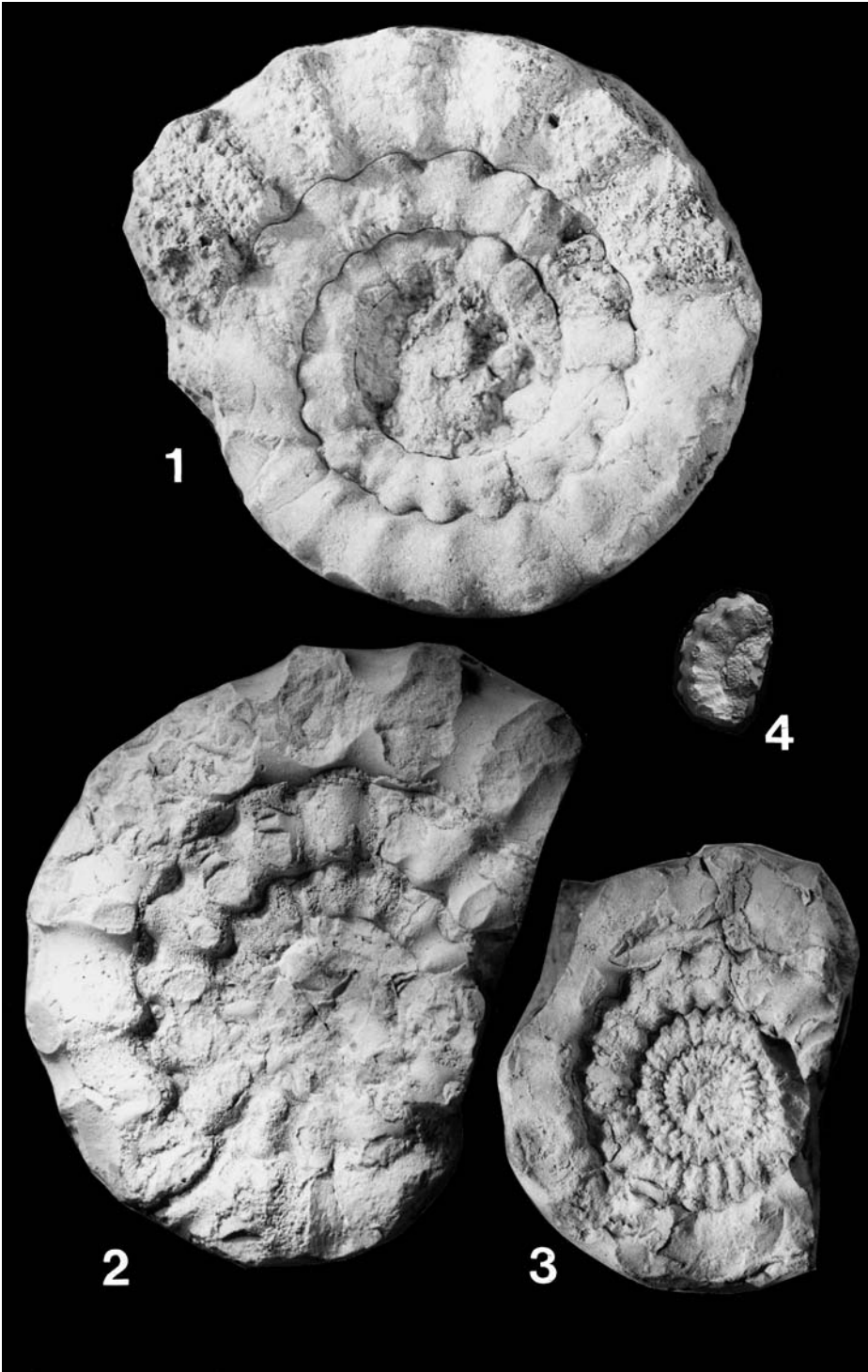


Plate 2

- Fig. 1. *Volanoceras krantzense* CANTÚ CHAPA. Llanos de la Vita SW Cieza, Prov. Murcia, Southern Spain; Lower Tithonian, late Semiforme Zone. a: lateral view, b: ventral view. SMNS no. 64664. – x1.
- Fig. 2. *Volanoceras krantzense* CANTÚ CHAPA, holotype (= *Simoceras* aff. *Volanense* OPP. in: KRANTZ 1928, pl. 3, fig. 7.). Las Brujas, Bardas Blancas, Prov. Mendoza, Neuquén-Mendoza Basin, Argentina; *Zitteli* Biozone (~ late Semiforme Zone); GPIBO. – x1.

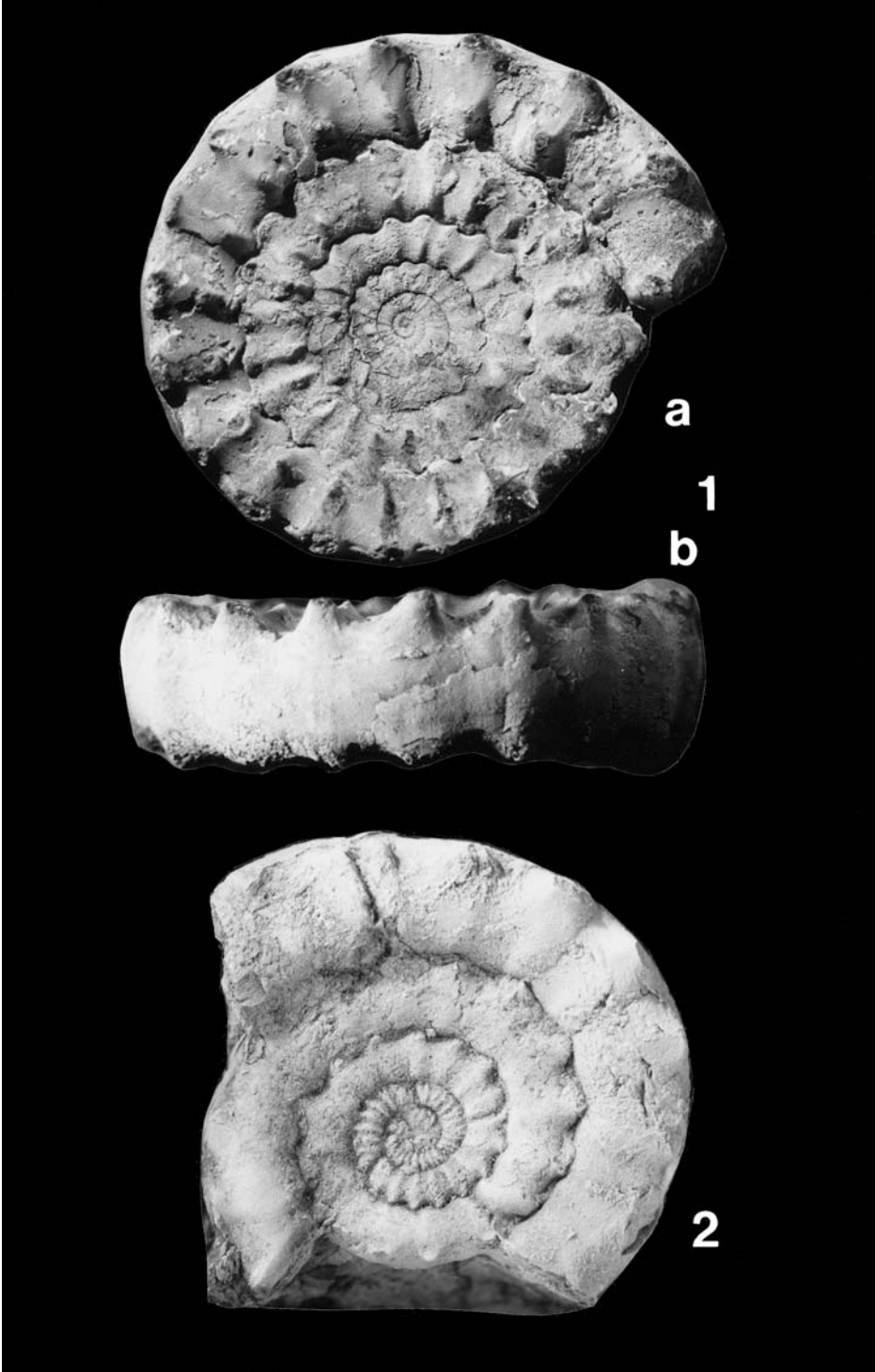


Plate 3

- Fig. 1. *Volanoceras schwertschlagerei* (SCHNEID), holotype. Neuburg Formation, Unterhausen member, bed x; Lower Tithonian, *Ciliata* Zone, *Penicillatum* horizon. BSPM no. 1913 IX 200. – x1.

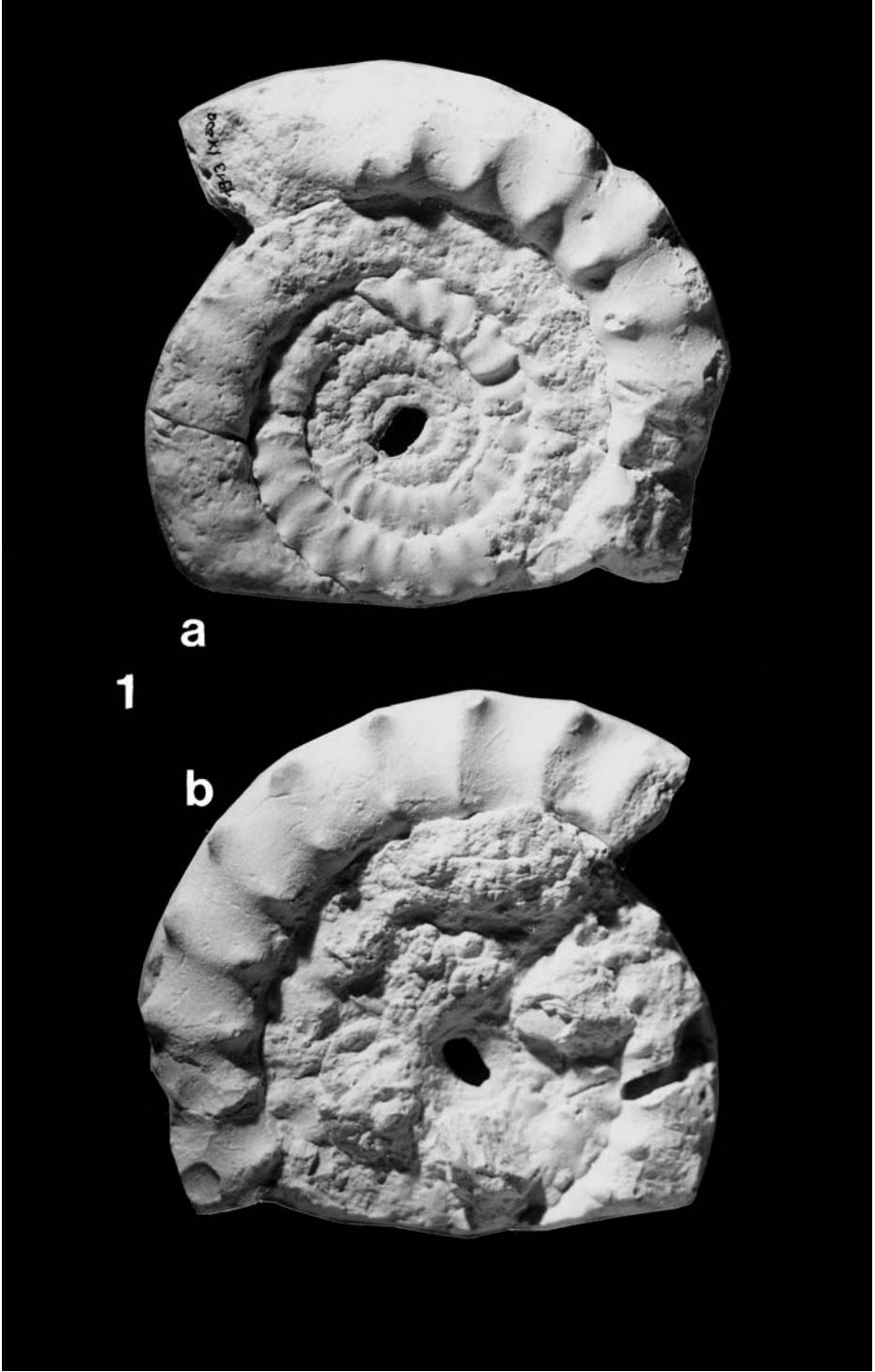


Plate 4

- Fig. 1–3. *Volanoceras schwertschlagerei* (SCHNEID). Barranco del Tollo near Caravaca, Prov. Murcia, southern Spain; Lower Tithonian, Fallauxi Zone (same bed as *Simoceras biruncinatum*, Pl. 6, Fig. 2). SMNS no. 64665/1–3. – x1.
- Fig. 4–5. *Volanoceras schwertschlagerei* (SCHNEID). Sierra de Ricote near Cieza, Prov. Murcia, southern Spain; Lower Tithonian, probably Fallauxi Zone. SMNS no. 64661/1–2. – x1.

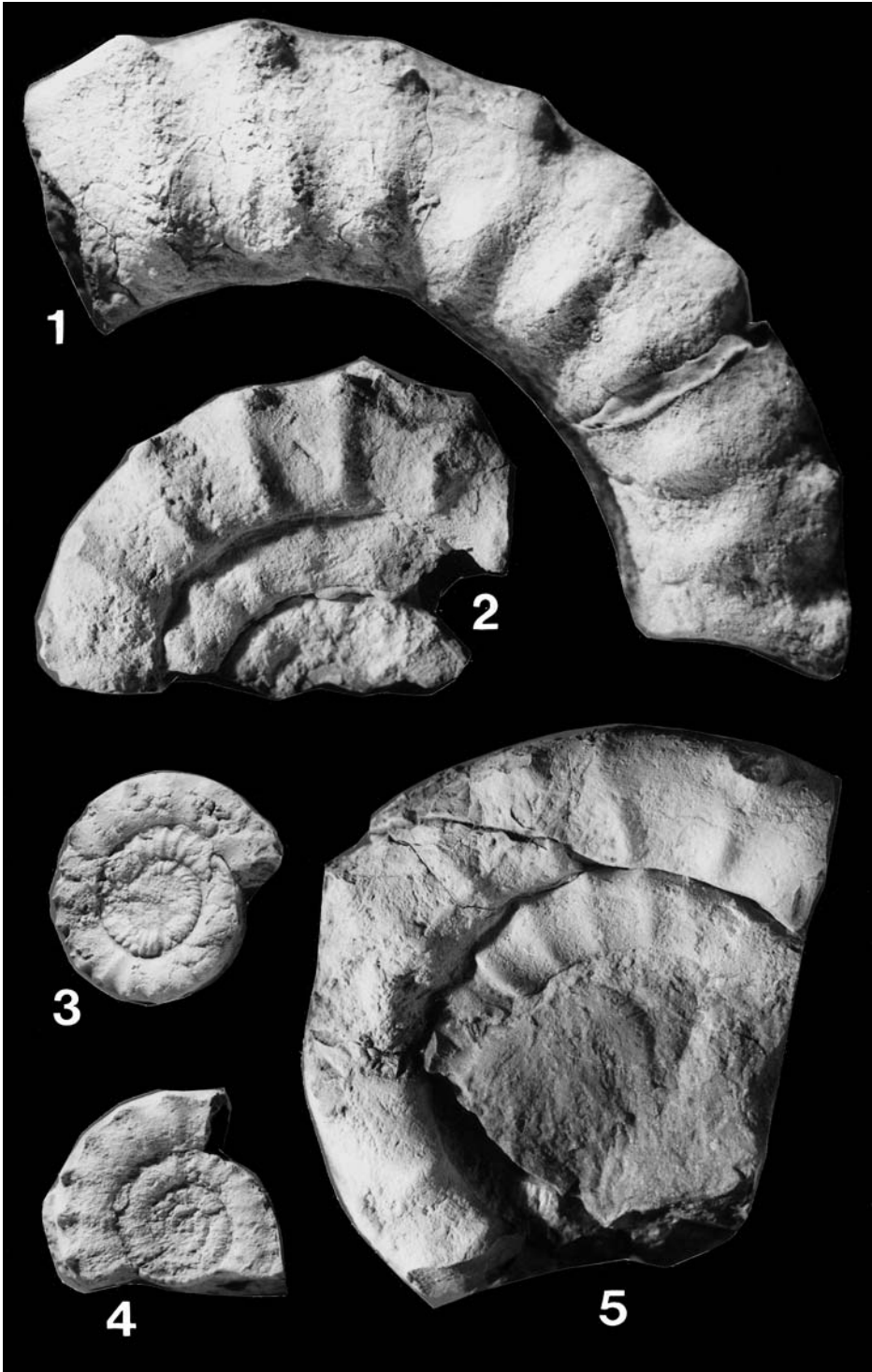


Plate 5

- Fig. 1. *Volanoceras volanense* (OPPEL), reproduction of the lectotype designated by GEYSSANT (1985) (from OPPEL 1863, pl. 58, fig. 2; specimen destroyed during World War II). Rosso Ammonitico Superiore, Volano near Rovereto, northern Italy. – x1.
- Fig. 2–3. *Volanoceras volanense* (OPPEL). Cabra, Prov. Cordoba, southern Spain; Lower Tithonian, Ponti Zone. SMNS no. 64662/1–2 (coll. H. SEYFRIED). – x1.
- Fig. 4. *Volanoceras volanense* (OPPEL), neotype. Rosso Ammonitico Superiore, Volano near Rovereto, northern Italy; Lower Tithonian, probably Ponti Zone. BSPM no. AS VIII 144. – x1.

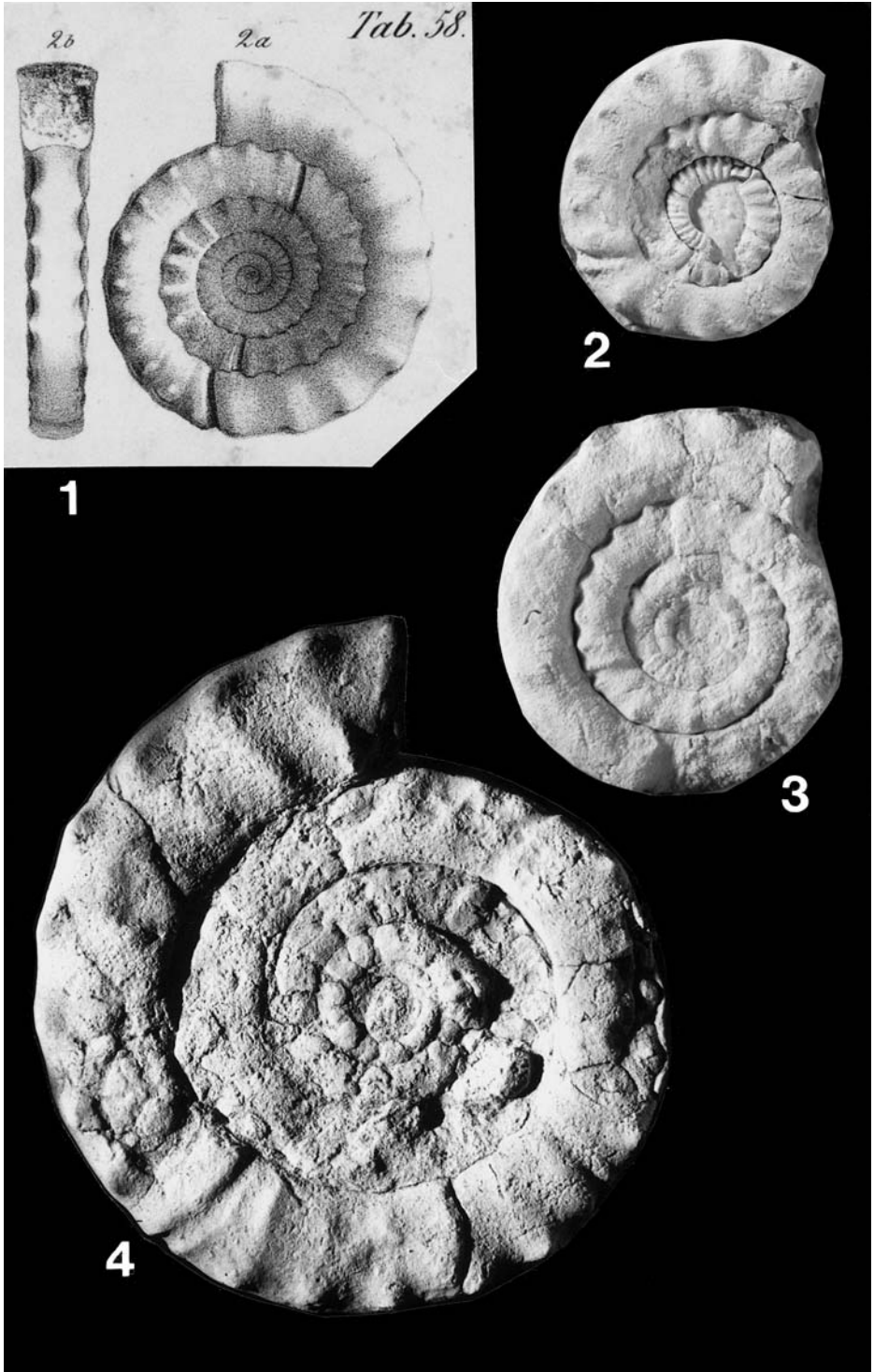


Plate 6

- Fig. 1. *Simoceras biruncinatum* (QUENSTEDT), Orig. ZITTEL 1870, pl. 7(31), fig. 6. Monte Catria, Apennines, Italy; Lower Tithonian, Biruncinatum/Admirandum Zone. BSPM no. AS 1868 X 95. – x1.
- Fig. 2. *Simoceras biruncinatum* (QUENSTEDT). Barranco del Tollo near Caravaca, Prov. Murcia, southern Spain; Lower Tithonian, Fallauxi Zone. SMNS no. 64667. – x1.
- Fig. 3. *Simoceras biruncinatum* (QUENSTEDT). 6.5 km N of Vélez Blanco, Prov. Almería, southern Spain; Lower Tithonian, Fallauxi Zone. a: lateral view, b: ventral view. SMNS no. 64666. – x1.

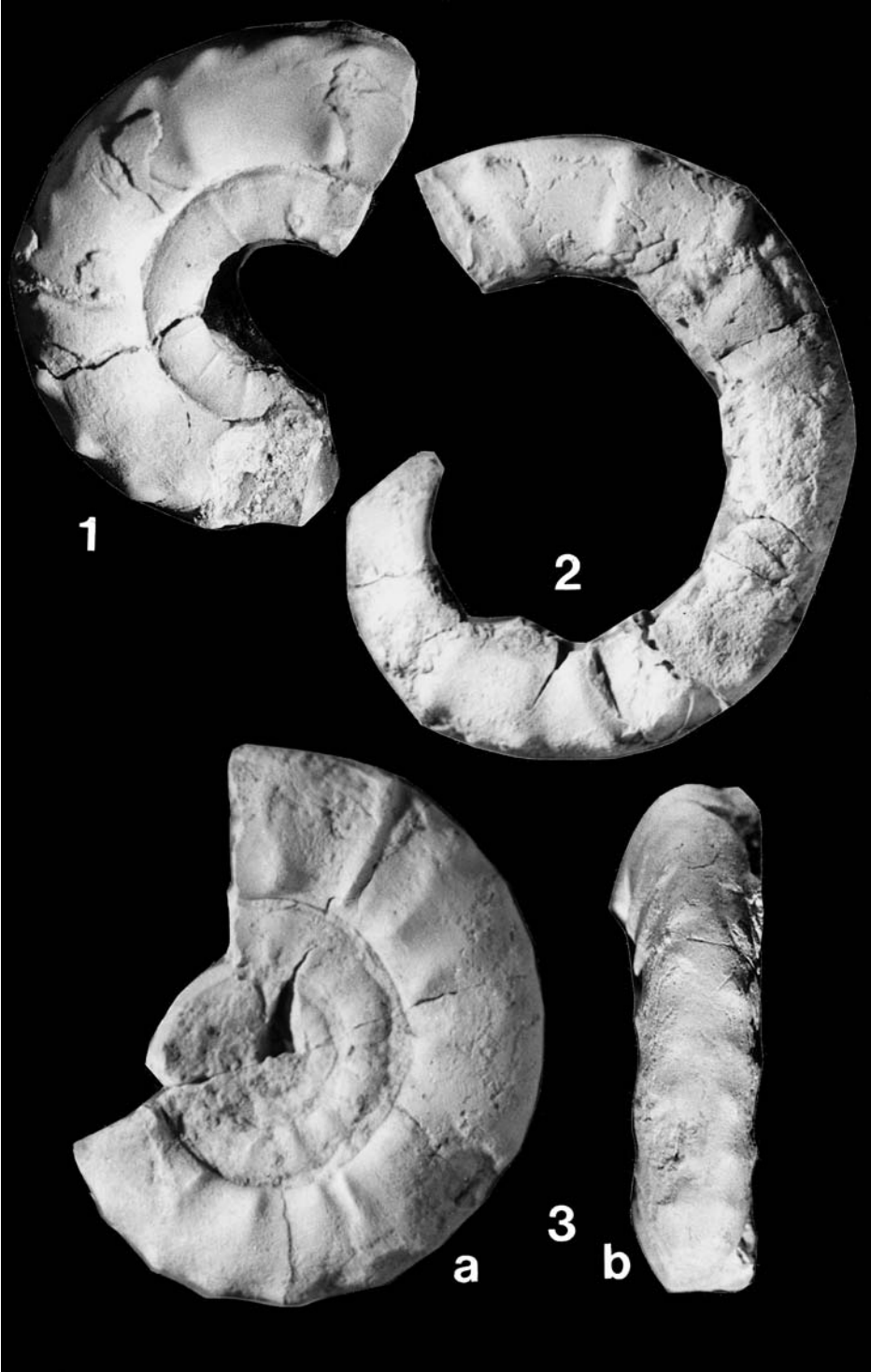


Plate 7

- Fig. 1. *Simoceras* cf. *biruncinatum* (QUENSTEDT). Mount Pasubio ("P"), Col Santino section ("A"). Southern Alps; Lower Tithonian, Biruncinatum/Admirandum Zone. ICPB no. P217A.
- Fig. 2. *Simoceras* cf. *biruncinatum* (QUENSTEDT). Mount Pasubio ("P"), Col Santino section ("A"). Southern Alps, northern Italy; Lower Tithonian, Biruncinatum/Admirandum Zone. ICPB no. P 270 A.
- Fig. 3. *Simoceras admirandum* ZITTEL. Brenzone, Mt. Baldo, northern Italy; Lower Tithonian, Biruncinatum/Admirandum Zone. IGPB, no. 1.

Fig. 1–3: Scale bar 4 cm.

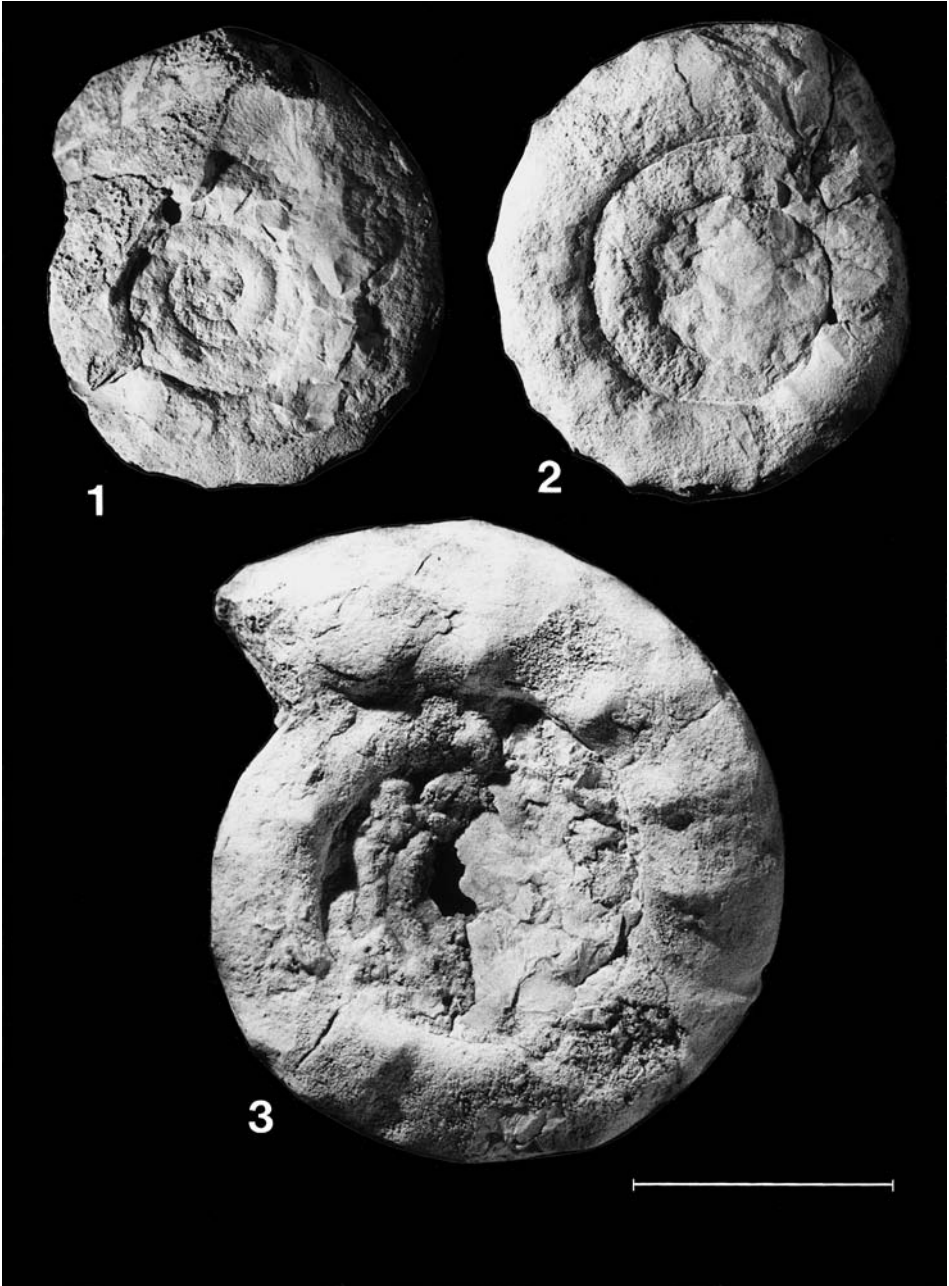
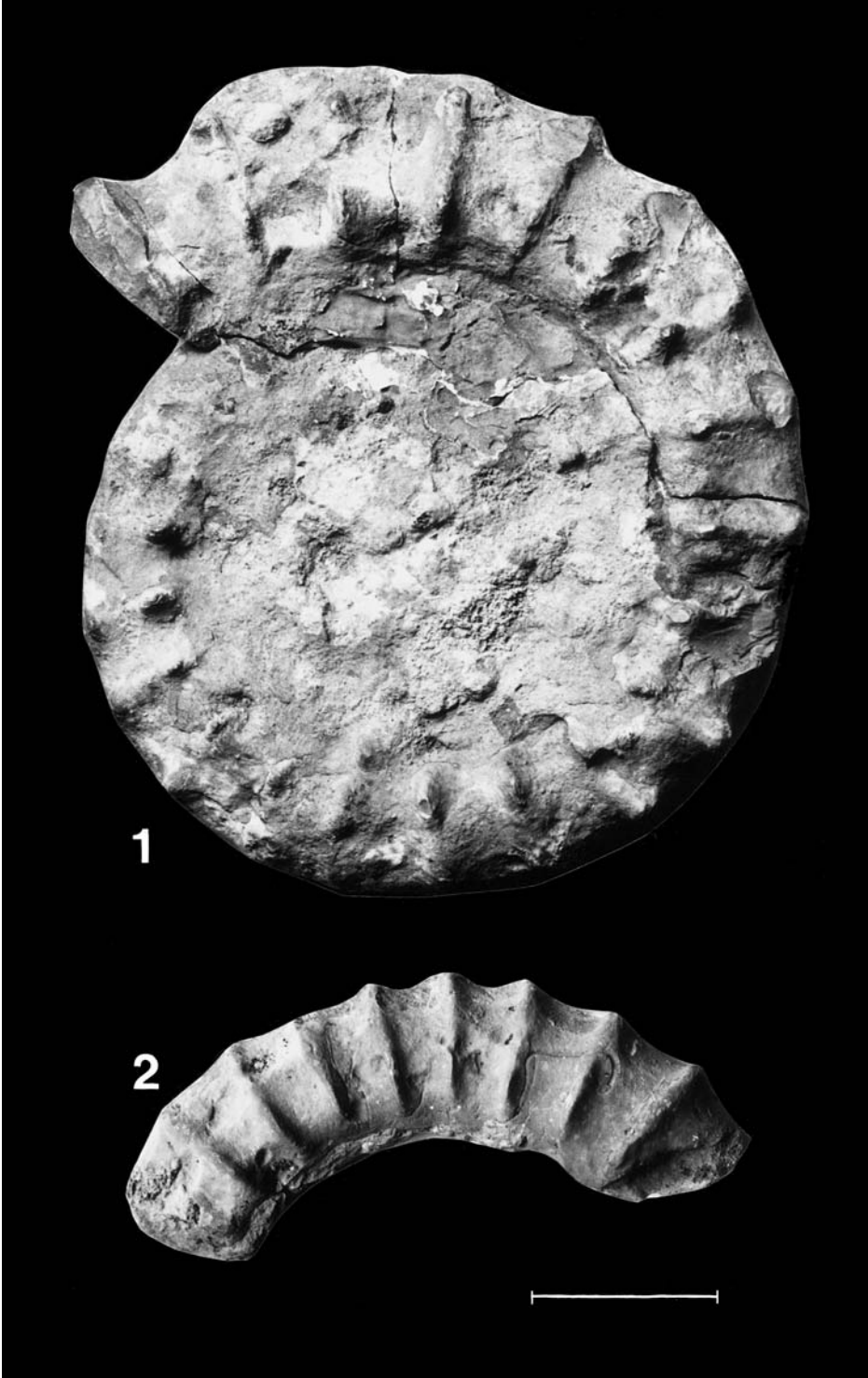


Plate 8

Fig. 1. *Volanoceras perarmatiforme* (SCHAUROTH), lectotype. Rosso Ammonitico Veronese Superiore, Fondi (Sette Comuni), Vicentinian Alps, northern Italy; Lower Tithonian, most probably equivalent of Ponti Zone. NMC no. 3771/1.

Fig. 2. *Volanoceras perarmatiforme* (SCHAUROTH), paralectotype. Rosso Ammonitico Veronese Superiore, Fondi (Sette Comuni), Vicentinian Alps, northern Italy; Lower Tithonian, most probably equivalent of Ponti Zone. NMC no. 3771/2.

Fig. 1–2: Scale bar 5 cm.



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