Lower Tithonian Microconchiate Simoceratins from Eastern Mexico: Taxonomy, Biostratigraphy, and Palaeobiogeography

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ANA B. VILLASEÑOR, FEDERICO OLÓRIZ, and CELESTINA GONZÁLEZ-ARREOLA

The precise record of simoceratins sampled bed-by-bed is first reported from Mexico (Mazatepec area in Puebla, central-eastern Mexico), as well as the existence of lappeted peristomes in these ammonites. Both *Pseudovolanoceras aesinense* and the subspecies *Pseudovolanoceras aesinense chignahuapense* are shown to occur among Mexican simoceratins. The European species and the Mexican subspecies share the same stratigraphic range in the studied sections, yet they differ in ephebic sculpture. Ecological adaptation to neritic seas corresponding to eastern Mexico areas is interpreted, forcing phenotypic deviation with geographic significance, i.e., subspeciation. The new subspecies would indicate stratigraphic horizons within the *Semiformiceras semiforme*/*Haploceras verruciferum* Chronozone in the Mediterranean Tethys. A revision of contemporaneous simoceratins in the Americas is founded on a comparative analysis with respect to the European species *P. aesinense*.

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Introduction

Upper Jurassic deposits from East-Central Mexico have long been investigated due to their importance for oil exploration. Cantú-Chapa (1967) gave valuable preliminary information about Middle Tithonian to Berriasian ammonites gathered from outcrops in the Mazatepec area, Puebla, Mexico. Cantú-Chapa (1989) proposed a type-section for the Tithonian–Berriasian boundary in the Mazatepec area, and Adatte et al. (1992) provided a precise biostratigraphy for calpionellids, indicating the Jurassic–Cretaceous boundary in the area. On the basis of calpionellid and ammonite biostratigraphy, Stinnesbeck et al. (1993) questioned the previous proposal for the Jurassic/Cretaceous boundary type-section made by Cantú-Chapa (1989). A further approach to sedimentology and diagenesis in Kimmeridgian deposits of the "San Andrés" Formation at Jonotla (Puebla) and Tlacolula (Veracruz), a region which includes the Mazatepec area, was made by Hernández De La Fuente (1996).

Institutional abbreviation.—BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CCS, Material housed in the Museo di Paleontologia del Servizio Geologico d'Italia, Roma, Italy; GPIBO, Goldfuss-Museum und Paläontologisches Institut der Universität Bonn, Germany; IGM, National Paleontological Collection (Museo Maria Carmen Perrilliat Montoya), Institute of Geology, Mexico City, Mexico; NS3Col, Museo di Paleontologia dell'Università di Roma, Italy; Rin, Collection housed in the Comune di Piobicco, Pesaro, Italy; SMNS, Staatlisches Museum für Naturkunde, Stuttgart, Germany; UNAM, Universidad Nacional Autónoma de México, Mexico; USNM, United States Natural Museum, New York, USA.

Other abbreviations.—Ac, A; Cantú-Chapa collection; C, number of constrictions; CT, Colle Tordina (Monti della Rossa, Appennino Marchigiano), Italy; Dm, measured shell diameter; M, macroconchs; m, microconchs; FAD, first occurrence datum; MTQ, Mazatepec Quesos section in the Apulco River area in Fig. 2; PS, periumbilical sculpture; PS/2, number of periumbilical sculptural elements, ribs, bullae or tubercles, per half-a-whorl; U, umbilical size; U/D, size ratio between the umbilicus and shell diameter; Wh, whorl height; Wh/D, size ratio between whorl height and shell diameter; specimen number a, b, letters refer to mould and cast of the same specimen.
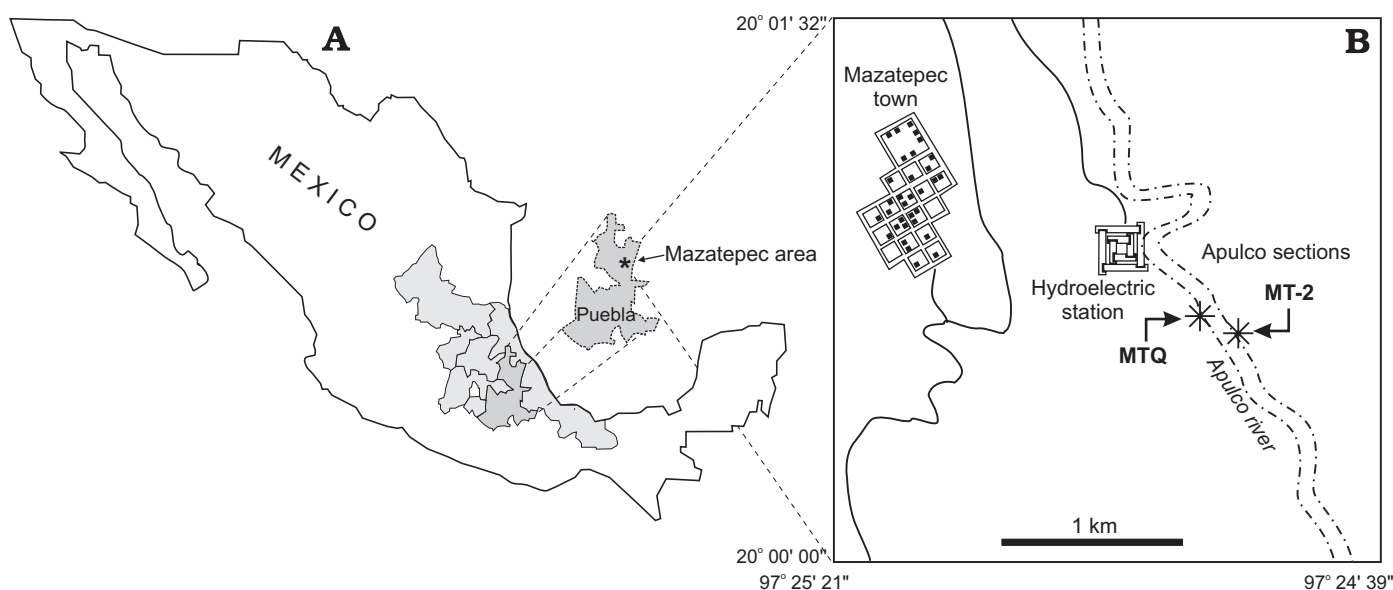
Fig. 1. Location of the studied sections. **A**. Regional location for Puebla state. **B**. Inlet for the precise location of the sections investigated on the banks of the Apulco River in the Mazatepec area.

Geological setting

The geological locality Apulco River section MT-2 lies within the Apulco Valley, Sierra Norte de Puebla, near the village of Mazatepec, Puebla (Figs. 1, 2). This mountainous region belongs to the geologic subprovince of Eastern Sierra Madre (López Ramos 1979a: 291, figs. 6-1, 6-8) and the Mexican Fold-and-Thrust Belt (Suter 1990; a geologic province according to Ortega-Gutiérrez et al. 1992) where NNW–SSE trending folds are interrupted southward by rocks of the Transmexican Volcanic Axis or Belt.

Upper Jurassic outcrops above the Apulco River banks are difficult to access due to dense forest coverage in the area near Mazatepec. The Upper Jurassic section shows a lower, coarse bedded part containing mid-shelf to lower-ramp carbonates (San Andres Formation; Hernández De La Fuente 1996). Overlying it are thinner bedded, brownish to grey-black siltstones with silty interbeds and occasional calcareous horizons showing common, mainly parallel, fine cross lamination (upper Lower Kimmeridgian and Tithonian Tamán Formation; see Cantú-Chapa 1971 for regional biostratigraphy and correlation). Regional deepening is 108° to 308° NE, and common faulting impedes precise lateral observation and correlation among outcrops. Evidence of synsedimentary sliding (slumps) and horizons containing more calcareous concretions are common in the Lower Tithonian succession. Coverage by alluvium (severe flooding during 1999) affects the Tithonian deposits. Cherty intercalations in grayish to darkish and more calcareous clayey limestones characterise the Pimienta Formation (López Ramos 1979b: 315).

The new Apulco section MTQ crops out along the west bank of the Apulco River, close to the hydroelectric station (Figs. 1, 2) and shows a 22 m thick succession made of brownish, more or less calcareous siltstones and silty limestones (Tamán Formation) containing decimetre to metre size concretions in the lower and middle part of the section.

Historical background

An overview of Upper Jurassic rocks and palaeoenvironments in the Apulco Valley, located in Sierra Norte de Puebla between Jonotla (Puebla) and Tlacolula (Veracruz), was given by Hernández De La Fuente (1996). In studying fossiliferous sections of the area, this author included some outcrops mentioned by Cantú-Chapa (1971: fig. 1). In his geological locality Apulco River, Hernández De La Fuente (1996) collected *Idoceras* sp., *Mazapilites* sp., and *Uhligites* sp. (without illustration), and mentioned the common occurrence of ammonites within the Tamán Formation.

Over the past ten years, two of us (ABV and FO) have studied outcrops around the Apulco River as part of a research programme focusing on sections of the San Andrés, Tamán, and Pimienta Formations, to provide a precise biostratigraphy based on bed-by-bed sampling (e.g., Villaseñor et al. 2000a, 2003; Villaseñor and Olóriz 2001, 2009; López-Caballero 2006; López-Caballero et al. 2007).

This paper presents the palaeontological analysis carried out on the first specimens of simoceratins collected bed-by-bed in Mexico from Lower Tithonian siltstones of the Tamán Formation cropping out along the Apulco River, Mazatepec, Puebla (Figs. 1, 2). The studied material was collected from Apulco section MT-2 (Villaseñor et al. 2003; López-Caballero et al. 2007; Villaseñor and Olóriz 2009) and the new MTQ section.
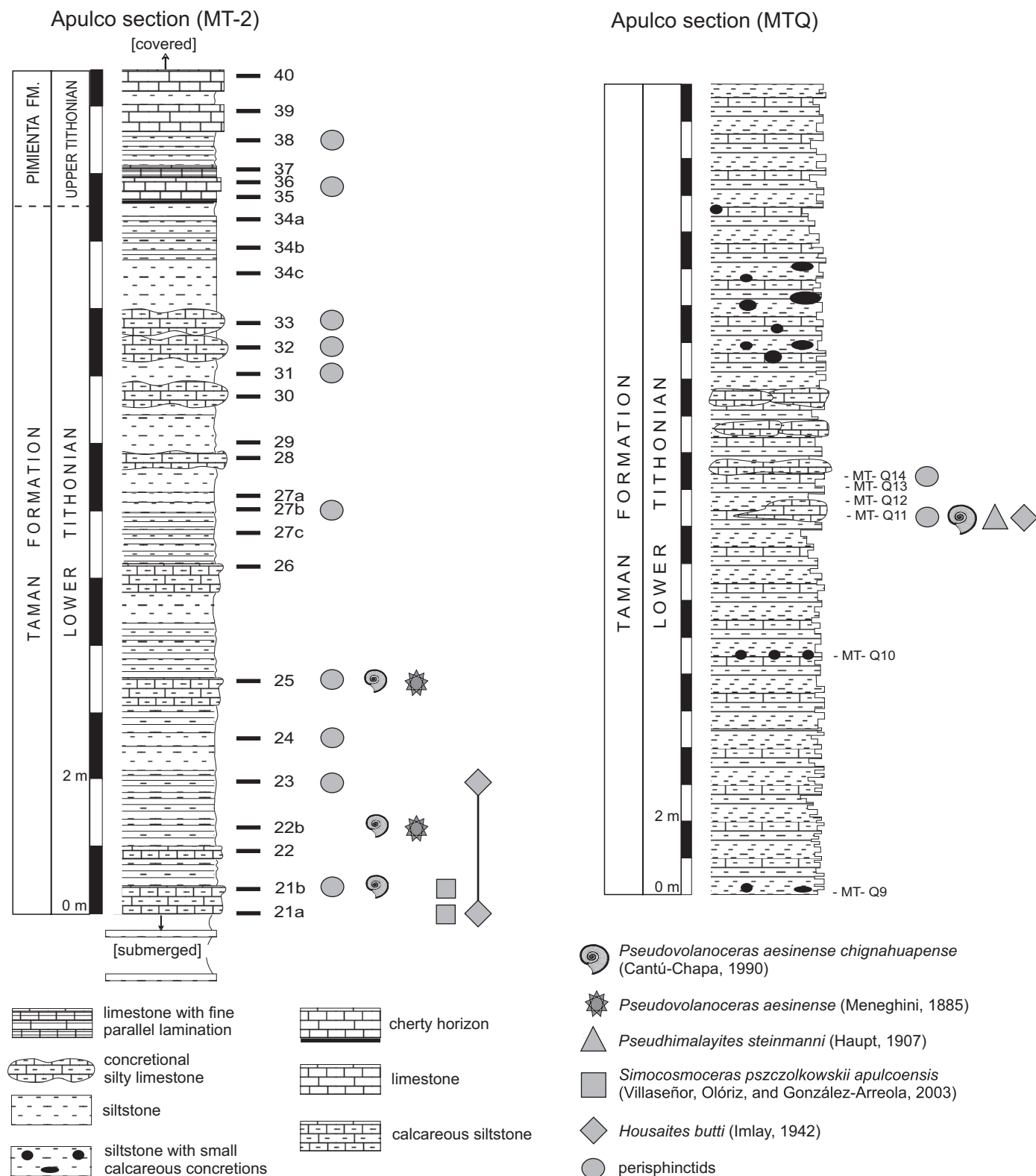
Fig. 2. Stratigraphic sections with indication of precise records of *Pseudovolanoceras aesinense* (Meneghini, 1885) and *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) in the Apulco sections MT-2 and MTQ. Note the occurrence of other ammonites significant for biostratigraphy and correlation.

Records of simoceratins from the Americas.—Precise information about the record of Lower Tithonian simoceratins from the Americas is rare, and to date only four specimens

have been reported with illustration, aside from some text citations. Krantz (1928) identified the southernmost record, from Argentina, while the other three records were reported by

Imlay (1942) from Cuba, and Verma and Westermann (1973), and Cantú-Chapa (1990) from Mexico. Among citations without illustrations, Leanza and Hugo (1977) alluded to Krantz's specimen and reported *Simoceras* aff. *S. volanense* Krantz, 1928 non Oppel (1863) from the same section or area studied by Krantz (1928); Leanza and Zeiss (1990, 1992, 1994) and Parent and Capello (1999) cited the occurrence of *Simoceras* in the Neuquen Basin, Argentina; Leanza (in Leanza and Zeiss 1990) cited *Volanoceras* from the same locality, and Parent (2001) and Parent et al. (2006) mentioned *Volanoceras krantzense* Cantú-Chapa, 1990. The mention without illustration made by Krantz (1928) of a geographically intermediate record of *Simoceras* in Peru (Welter 1913 in Krantz 1928: 13) was not taken into account in later revisions of simoceratins, and was unavailable for control. Based on the descriptions provided by all these authors, the following additional comments concern the interpretations made below.

Krantz (1928: pl. 3: 7) described *Simoceras* aff. *volanense* Oppel, 1863 from his locality 30 (surroundings of Barda Blanca, Argentina). The specimen was collected from clayey marls of the Middle Tithonian, together with *Aspidoceras* (*Pseudhimalayites*) *steinmanni* Haupt, 1907 and *Pseudolissoceras zitteli* Burckhardt, 1903, among other ammonites. Basically, Krantz (1928: 13–14) described his specimen of 85 mm in diameter as an extremely evolute and strongly sculptured form. In the outer whorl, radial periumbilical tubercles are connected by ribs with peripheral ones elongated towards the aperture. The beginning of the outer row of tubercles in the third whorl precedes that of the periumbilical tubercles. Krantz (1928) recognised differences between the Argentinean specimen and the European *Simoceras volanense* Oppel, 1863 (in Zittel 1870), namely the absence of the constrictions described by Zittel (1870), although he noted some more excavated inter-rib spaces in the Argentinean specimen. Krantz (1928) distinguished his specimen from *Simoceras schwertschlageri* Schneid, 1915 on the basis of its stronger, more radial sculpture. Later interpretations of this specimen include those of Santantonio (1986), Cecca (1999: 22) and Carlo Sarti in personal communication to Parent and Capello (1999), who reinterpret the Argentinean specimen as *Simoceras aesinense* (Meneghini, 1885); Fözy (1988) raises doubts about the species- and even genus-level meaning; Cantú-Chapa (1990) put forth the species *Volanoceras krantzense* Cantú-Chapa, 1990, a proposal followed by Parent (2001), Cecca (2002a), who considered *Simoceras* (*Pseudovolanoceras*) *krantzense* Cantú-Chapa, 1990 a genuine species after examination of a gypsum cast, Schweigert et al. (2002) and Parent et al. (2006); and Villaseñor et al. (2000b) foresee the possibility of revealing a local subspecies of *S. aesinense* (Meneghini, 1885) (see below).

Imlay (1942: pl. 3: 2–3) described *Simoceras* sp. juv. cf. *volanense* (Oppel, 1863) from the Viñales Limestone in the northeastern slope of Loma Sabanilla, Santa Clara Province, north-central Cuba, locality 268 of the Atlantic Refining Company of Cuba. Imlay (1942: pl. 3: 2–3) identified a very loose coiling, subquadrate whorl section with maximal thickness near the middle of gently convex flanks, and a coarse sculpture in the specimen 11 mm in size (note three-time magnification indicated by Imlay). This author also observed prominent and slightly prorsiradiate ribs terminating in coarse tubercles on the shoulders. Imlay (1942: 1446) noted the resemblance of the Cuban specimen with both the European *Ammonites volanense* (Oppel 1863: pl. 58: 2a, b), which was included in *Simoceras*, and the South American *Simoceras* aff. *volanense* Oppel in Krantz (1928: pl. 3: 7). Later, Cecca (1999: 22) interpreted the Cuban specimen as *S. aesinense* (Meneghini, 1885) while Schweigert et al. (2002: 8) reinterpreted this species as belonging to *Volanoceras*, a younger synonym of genus *Simoceras* according to Cecca (1999: 11).

Verma and Westermann (1973: 196, pl. 37: 2) described *Simoceras* cf. *S. volanense* (Oppel, 1863) from the Virgatosphinctinae Beds, upper part of the El Pastor Member, La Caja Formation, in locality 40C: a creek close to the small village of El Pastor in the southern part of Sierra de Catorce, San Luis Potosí, Mexican Altiplano. These authors recognised that the specimen was somewhat distorted, and they describe loose coiling, a subquadrate to depressed whorl section, and blunt ribs between two rows of tubercles in the specimen of 72 mm under study. They also observed a constriction at the end of the preserved inner mould, which they interpreted as a probable indication of complete growth, and the possible existence of constrictions in the inner whorls. Verma and Westermann (1973: 196–197) assumed a close affinity with *Simoceras* aff. *volanense* Oppel in Krantz (1928), which was considered synonymous with Oppel's (1863) original, and denser ribbing in *Simoceras* sp. juv. cf. *volanense* Oppel in Imlay (1942). Later interpretations considered the specimen described by Verma and Westermann (1973) as: *Simoceras* (*Volanoceras*) cf. *volanense* (Oppel, 1863) by Callomon (1992), who envisaged an age corresponding to the mid-to-upper Lower Tithonian in Europe; *Simoceras* close to *S. aesinense* (Meneghini, 1885) (Olóriz et al. 1999: 478); *S. aesinense* (Meneghini, 1885) (synonym *Simoceras schwertschlageri* Schneid, 1915) (Cecca 1999), *Simoceras* of the group of *S. aesinense* (Meneghini, 1885) (Villaseñor et al. 2000b), *S. aesinense* (Meneghini, 1885) (Villaseñor et al. 2000a: A-469) with the local subspecies *S. aesinense chignahuapense* (Cantú-Chapa, 1990) for eastern and north-central Mexico and doubts as to how many subspecies of *S. aesinense* (Meneghini, 1885) were in the Americas; and *Volanoceras krantzense* Cantú-Chapa, 1990 (Schweigert et al. 2002: 9).

Cantú-Chapa (1990: 41–45, fig. 2a–d) described *Volanoceras chignahuapense* sp. nov. from Lower Tithonian deposits that crop out in Chignahuapan, Puebla, central-eastern Mexico. The specimen of 40.13 mm in shell size was gathered from a calcareous concretion and magnified at 1.4 and 2.2 in Cantú-Chapa (1990: fig. 2a, b and 2c, d, respectively). This author noted a serpenticone shell with a rectangular whorl section, two to three constrictions per complete whorl, and simple, flattened ribs as wide as the inter-rib spaces. He also described periumbilical swelling of ribs and periumbilical tuber-

cles on the inner whorls (the latter unidentifiable in his illustrations), and ventrolateral termination of ribs in spiny, tangentially elongated tubercles. Cantú-Chapa (1990) indicated *Volanoceras* (Geyssant, 1985) as the most appropriate genus-level interpretation, and therefore made a detailed examination and comparative analysis of supposedly conspecific forms showing simple or bifurcate ribs on the inner whorls (as discussed in point d below). This author recognised a particular affinity with *Simoceras* aff. *volanense* Oppel in Krantz (1928) through ventrolateral tuberculation, and rightly remarked that the Argentinean specimen is distinguished by an absence of constrictions, a feature that he also used to differentiate *Ammonites volanense* in Oppel (1863) from the specimen described by Krantz (1928). Cantú-Chapa (1990) likewise proposed the interpretation of the specimen described by Krantz (1928) as *Volanoceras krantzense* sp. nov., and thus a separation from the European "*Simoceras* cfr. *volanense* Oppel, 1863 sp. var. *aesinense*" in Meneghini (1885), (= *Simoceras*, *Volanoceras* or *Pseudovolanoceras aesinense* Meneghini, 1885 of several authors). Cantú's (1990) proposal (Cantú-Chapa 1990: 43) assumed the occurrence of bifurcate ribs in *Volanoceras aesinense* (Meneghini, 1885); but they are absent from both the corresponding type specimens. Cantú-Chapa (1990: 43) rejected the conspecific relationships interpreted by Geyssant (1988) for the Italian species *V. aesinense* (Meneghini, 1885) with all simoceratin specimens referred to Tithonian *Simoceras* in the Americas. Concerning the small Cuban specimen (Imlay 1942), Cantú-Chapa (1990) stated that because it was a juvenile it would not be used for comparative analyses (but see point e below). Moreover, according to Cantú-Chapa, the Mexican specimen described by Verma and Westermann (1973) could not be interpreted at the species level because of poor preservation. Cantú-Chapa (1990: 43) rightly separated his Mexican specimen from *Simoceras volanense* Oppel in Zittel (1870) and *Simoceras schwertschlageri* in Schneid (1915). Finally, Cantú-Chapa (1990: 43, 45) outlined similarities and differences between *Volanoceras chignahuapense* sp. nov. and the closest species *V. aesinense* (Meneghini, 1885), indicating similarity in tuberculation and constrictions but absence of bifurcate ribs in the Mexican specimen. As commented above, the type of "*Simoceras* cfr. *volanense* Oppel, 1863 sp. var. *aesinense*" in Meneghini (1885: 376) does not show bifurcations, and both these forms furthermore show an exclusive character typical of the Meneghini' species, namely the longitudinal furrow between tubercles on the shoulders in moulds. This feature was not analysed by Cantú-Chapa (1990), but it is seen clearly in his fig. 2a, b. Later interpretations of Cantú's species *Volanoceras chignahuapense* Cantú-Chapa, 1990, refer to Cecca (1999: 26) and Schweigert et al. (2002), who assumed *Volanoceras chignahuapense* Cantú-Chapa, 1990 as conspecific with *Simoceras aesinense* (Meneghini, 1885) but belonging to different genera/subgenera (*Simoceras* and *Volanoceras*, respectively), whereas Villaseñor et al. (2000a) considered it to be the geographic subspecies *Simoceras aesinense chignahuapense* (Cantú-Chapa, 1990). Cecca (2002a) did not change his inter-

pretation at the species level (e.g., Cecca 1999), but included it in his new subgenus *Pseudovolanoceras*.

With regard to the hypotheses given below, this revision of interpretations of Lower Tithonian simoceratids from the Americas features some significant points:

(i) The early separation of the Argentinean specimen from the European species *S. volanense* Oppel, 1863 made by Krantz (1928), who compared two supposedly adult specimens.

(ii) The similarity Imlay (1942) found between his Cuban nucleus, assumed to be juvenile, the European species *S. volanense* Oppel, 1863, and the Argentinean specimen described by Krantz (1928). This does not indicate defective analysis, since the very nucleus (precisely the part that is barely observable in the Cuban specimen but crucial for interpretation) is not well preserved in the European *Ammonites volanense* in Oppel (1863) and *S. volanense* Oppel in Zittel (1870). The outer whorls in the latter were considered to belong to other species *V. aesinense* (Meneghini, 1885) by Geyssant (1985), a reinterpretation that could apply to the complete illustration (e.g., Santantonio 1986). In fact, true *A. volanense* Oppel, 1863 nuclei have been characterised by the occurrence of dominant bifurcates below ca. 20 mm, which was considered by Santantonio (1986) to be crucial for differentiation of the morphologically close species *S. aesinense* (Meneghini, 1885) and *S. volanense* (Oppel, 1863). The nucleus studied by Imlay (1942) basically coincides with that of the Argentinean specimen described by Krantz (1928). As mentioned above, the latter specimen was interpreted as *Volanoceras krantzense* Cantú-Chapa, 1990 by Schweigert et al. (2002) following Cantú-Chapa (1990), admitting the occurrence "pseudo-bifurcations" in nuclei and an intermediate, evolutionary place between *V. aesinense* (Meneghini, 1885) and *V. schwertschlageri* (Schneid, 1915). "Pseudo-bifurcations" for these authors (Schweigert et al. 2002: fig. 5a) refer to the sculptural structure resulting from the incidence of growth increments on ribbing orientation on the flanks. Connected to growth increments, these structures must show congruent orientation with adjacent, later simple ribs. However, it is not the sole case among interpreted *Volanoceras* illustrated by Schweigert et al. (2002; e.g., *V. krantzense* Cantú-Chapa, 1990 in pl. 2: 2 showing a specimen from Spain with an incorrect reference in the figure caption) and real bifurcate ribs occur (e.g., in the same illustration and in a later ontogenetic phase in *Volanoceras schwertschlageri* (Schneid, 1915, illustrated in their pl. 3: 1a)—i.e., in contrast to "pseudo-bifurcations", real bifurcate ribs show neither a congruence of rib projection on the flanks nor necessarily imply relation with more or less accentuated constrictions.

(iii) The interpreted affinity proposed by Verma and Westermann (1973) between their specimen collected from Sierra de Catorce, Mexico, and those described from Cuba (Imlay 1942) and Argentina (Krantz 1928), the latter being considered synonymous by these authors in contrast to some later interpretations (see above).

(iv) The artificial, compound character that Geyssant (1985: 679) interpreted for the illustration of *S. volanense* Oppel in Zittel (1870: pl. 32: 7), who interpreted the inner whorls as resembling *A. volanense* in Oppel (1863: pl. 58: 2a, b) while the outer evoked "*Simoceras* cfr. *volanense* var. *aesinense*" in Meneghini [1885 = *Volanoceras aesinense* (Meneghini, 1885) in Geyssant's (1985) interpretation]. Even if coinciding with Geyssant's (1985) observation (but see Santantonio 1986), assuming no difference in ribbing on the inner whorls among species of his new genus *Volanoceras*, the reference to Zittel's (1870) illustration does not help to clarify a crucial difference: the occurrence of bifurcate ribs on the inner whorls in *Ammonites volanense* Oppel, 1863 and the occurrence of simple ribs in *Simoceras aesinense* (Meneghini, 1885) (see above comments on "pseudobifurcations" sensu Schweigert et al. 2002). This distinction, unappreciated in interpretations subsequent to Oppel (1863: 232, pl. 58: 2a), was highlighted by Santantonio (1986), who described bifurcate ribs on the inner whorls of *Simoceras volanense* Oppel, 1863 (at least up to 18 mm) as he interpreted this taxon. In fact, close analysis of the nucleus in Oppel's illustration (1863: pl. 58: 2a) at less than 20 mm (see also Schweigert et al. 2002: pl. 4: 1 under magnification ×300) appears to reveal convergence of ribs close to the whorl overlap. Unfortunately, sculptural details in Zittel's (1870) illustration are unappreciable, most likely due to unfavourable preservation of the original specimen.

(v) Comments by Cantú-Chapa (1990) are relevant in two senses. Firstly, the close affinity between his Mexican species, the Argentinean specimen described by Krantz (1928) and *S. aesinense* (Meneghini, 1885) was soundly based on tuberculation, but he over-emphasised the sole difference in the development of constrictions with respect to the former, and did not observe the crucial shallow furrow recognisable in moulds of inner whorls of the species *S. aesinense* (Meneghini, 1885) as well as in the specimen he described (e.g., Cantú-Chapa 1990: fig. 2d). Other differences are minor or do not exist (e.g., bifurcate ribs in *S. aesinense* Meneghini, 1885). Secondly, he rightly interpreted that a sole nucleus (in reference to the Cuban specimen described by Imlay 1942) must not be used for comparative analysis at the species level (and, by extension, at the genus level); nevertheless, he worked with a potential juvenile and/or incomplete specimen showing probably less than one-fourth of the body chamber at 40.13 mm, and described his new species as included in the genus *Volanoceras* Geyssant, 1985. Villaseñor et al. (2000a) gave a preliminary interpretation as *S. aesinense chignahuapense* (Cantú-Chapa, 1990) for this incomplete specimen described by Cantú-Chapa (1990), while Cecca (2002a) proposed it as a junior synonym of the Meneghini (1885) species.

In addition to the above, we agree with the guidelines given by Santantonio (1986) for the precise differentiation of Tithonian simoceratin species, i.e., the occurrence of dominant bifurcate ribs vs. simple ribs in their nuclei. Hence, we assume a well established fact in the species group of *S. aesinense* (Meneghini, 1885) and *A. volanense* Oppel, 1863

—i.e., different nuclei with simple and bifurcate ribbing, respectively. Genus *Volanoceras*, as proposed by Geyssant (1985), is therefore polyphyletic, as it has been the common interpretation for *Simoceras*, even when the use of subgenera is restricted (e.g., Fözy 1988).

Material and methods

In both of the sections investigated bed-by-bed, macrofossils —mainly bivalves and ammonites (1200 specimens and fragments)—were found in discontinuous horizons within the stratigraphic interval containing simoceratins. In general, macrofossil preservation is moderate to poor (imprints and leaf preservation sensu Seilacher et al. 1976), and preservation in volume as inner moulds is rare. Haploceratidae, perisphinctids and simoceratins predominate in ammonite assemblages where most of the specimens can be identified only at the genus level.

The simoceratins described were found in the lowermost 3.5 m of the Apulco section MT-2, and in the upper 10 to 12 m of the new Apulco section MTQ (Fig. 2). The total number of identified specimens was twenty-one. Among stratigraphically collected specimens, fifteen belong to section MT-2, and six specimens were gathered from bed MTQ-11 in section MTQ.

Biochronostratigraphy was conducted according to the Secondary Standard of reference for the Tithonian (e.g., Geyssant 1997).

Preparation of the material and shell/mould measurement (in millimetres; see Appendix 1) was mainly performed in the Laboratory for Invertebrates of the UNAM, with complementary work carried out at the University of Granada, Spain.

Notes on Simoceratinae: systematics, taxonomy, and evolutionary patterns

Several proposals have been put forth over the past 30 years regarding systematics, taxonomy, and evolution in Lower Tithonian simoceratins above the species level (e.g., Olóriz 1978; Geyssant 1982, 1985, 1988; Santantonio 1986; Fözy 1988; Cecca 2002a; Schweigert et al. 2002). An abridged review is given below.

Olóriz (1978) interpreted a comprehensive genus *Simoceras* differentiated into morphologic, evolutionary subgenera according to basic phenotype differences through ontogeny, which starts with an initial perisphinctoid-stage followed by: (i) tuberculate or simoceroid-stage (subgenus *Simoceras*); (ii) shell smoothing or lytoceroid-stage (*Lytogyroceras*); or their combination (subgenus *Simolytoceras*). Olóriz (1978: 237) envisaged three potential interpretations of evolution at the subgenus level, which can be simplified in terms of: Iterative

evolution from a perisphinctoid nucleus (then considered as evidence of phylogenetic connection with Idoceratinae); and anagenetic and/or cladogenetic evolution from the basic simoceroid-stage. This author acknowledged difficulties with stratigraphic condensation in obtaining fine stratigraphy to clarify the relative FADs of *Simolytoceras* and *Lytogyroceras*, and did not study the species *S. aesinense* (Meneghini, 1885) among the rare (then considered *Simoceras volanense* Oppel, 1863 group) simoceratins collected from *Haploceras verruciferum* Biozone deposits in ammonitico rosso facies (*Semiformiceras semiforme/Haploceras verruciferum* Chronozone in the Secondary Standard for Tethyan areas; e.g., Geyssant 1997). In addition, this author identified a "simoceratin-like" morphology in one of the two groups interpreted as *Virgatosimoceras* (Olóriz 1978: 204), overemphasising their perisphinctoid nuclei resembling those shown by the older *Nebrodites* as well as the occurrence of *Idoceras*-like rib furcations.

Santantonio (1986) analysed abundant, well-preserved material, rightly typified traits' recognition for identification of Lower Tithonian simoceratin species, and considered common, defective preservation in ammonitico rosso facies as a major difficulty in separating *Simoceras aesinense* (Meneghini, 1885) from the *S. volanense* Oppel, 1863 group (genus level interpretation according to Santantonio 1986). He put forth *Virgatosimoceras* as a key-branch for evolution in Lower Tithonian simoceratins, potential polyphyly for the *S. volanense* Oppel (1863) group, as well as an obscure origin for *S. aesinense* (Meneghini, 1885), and recommended future separation of the latter at the genus or subgenus level. *S. aesinense* (Meneghini, 1885) was interpreted as a separate branch within the polyphyletic genus *Simoceras*.

Geyssant (1982, 1985, 1988) interpreted the evolutionary pattern in Lower Tithonian simoceratins and proposed punctuated equilibrium and palaeogeographic dynamics as the appropriate template for their interpretation. Geyssant (1982) interpreted genus *Simoceras* in a broad sense, as usual at the time, and identified "*Simoceras* n. sp. gr. *volanense* Oppel, 1863" from the *Semiformiceras semiforme* Biozone (equivalent to the *Haploceras verruciferum* Zone = *Semiformiceras semiforme/Haploceras verruciferum* Chronozone in the Secondary Standard for Tethyan areas; e.g., Geyssant 1997), envisaging a widespread geographic distribution (southern Europe, Cuba, Mexico, and Argentina). This author interpreted discontinuous in-situ evolution, allopatric speciation and recolonisation by species belonging to genus *Simoceras* in southern Europe and nearby northern areas (Franconia). Based on ICZN rules, Geyssant (1985) restricted the use of genus *Simoceras* to the *Simoceras admirandum* Zittel, 1869/ *Simoceras biruncinatum* Quenstedt, 1847 group and erected the new genus *Volanoceras* for Lower Tithonian simoceratins such as *V. aesinense* (Meneghini, 1885), *V. schwertschlageri* (Schneid, 1915), and *V. volanense* (Oppel, 1863). Implicit in Geyssant's (1985) interpretation is the polyphyletic character of her new genus *Volanoceras*, while *Simoceras* turned to be monophyletic. No particular comments about *V. aesinense* (Meneghini, 1885) were provided. Geyssant (1988) revisited

her punctuated equilibrium hypothesis, now applied to *Volanoceras* that she envisaged as a single monophyletic linage.

Fözy (1988) approached the interpretation of Simoceratinae promoting the use of assumed monophyletic taxa, and followed Geyssant (1985, 1988) when analysing *Volanoceras*, thus anticipating hypotheses later detailed by Schweigert et al. (2002). However, this author did not provide an evolutionary pattern at the subfamily level, and the degree of monophyly resulted heterogeneous in the taxa he identified in simoceratins. In his study of the material gathered from ammonitico rosso and related facies containing envisaged juveniles and adults, Fözy (1988) approached dimorphic couples at the subgenus level following Callomon (1969).

In 2002 the most recent reinterpretations of Tithonian simoceratins were published, in parallel, by Fabrizio Cecca and Günter Schweigert and collaborators. Schweigert et al. (2002) revisited Lower Tithonian simoceratins and reinterpreted *Volanoceras*' species, their stratigraphy, palaeobiogeography and evolution, partially based on bibliographic re-evaluations; they proposed invalidation of the oldest species related to the *S. aesinense* (Meneghini, 1885) group (*S. praecursor* in Santantonio 1986) and promoted recuperation of an old species name (*Ammonites perarmatiforme* Schauroth, 1865) for the youngest specimens reported. These authors envisaged a chronocline for *Volanoceras* and, following Geyssant (1985), did not recognise relevant differences in inner whorl sculpture between the *V. aesinense* (Meneghini, 1885) and *V. volanense* (Oppel, 1863) groups. Hence, the potential polyphyly derived from Santantonio's (1986) model was overlooked. Schweigert et al. (2002) interpreted *V. aesinense* (Meneghini, 1885) including European, Cuban, and east-Mexican records, and confirmed species-level status and conspecifity for the Argentinean and central Mexico records. On the other hand, Cecca (2002a) basically followed Santantonio (1986) and proposed the new subgenus *Pseudovolanoceras* for *S. aesinense* (Meneghini, 1885) and related species from the Americas. This author recognised difficulty with *Volanoceras*' evolution as proposed by Geyssant (1982), due to limitations forced by both the defective preservation of inner whorls and the precise biostratigraphic interpretation of some species crucial for Geyssant's (1982) interpretation. He therefore proposed species reorganisation among Lower Tithonian simoceratins, which were allocated in three morpho-evolutionary subgenera within genus *Simoceras*: *S.* (*Simoceras*) restricted to the *S. admirandum* Zittel, 1869/*S. biruncinatum* Quenstedt, 1847 group, *S.* (*Volanoceras*) for the *S. volanense* Oppel, 1863/*S. vicentinum* group, and *S.* (*Pseudovolanoceras*) for *S. aesinense* (Meneghini, 1885) and related species.

On the basis of all the above, we consider two alternative options for the present interpretation of Lower Tithonian simoceratins above the species level: (i) interpreting a comprehensive genus *Simoceras* subdivided in subgenera with evolutionary, not merely morphologic meaning (e.g., Olóriz 1978; Cecca 2002a); or (ii) interpreting evolutionary relevance at the genus level, meaning that no subgenera apply. In option (i) the

genus level is strictly nominal and provides the closest allusion to the immediately higher taxonomic level of reference (e.g., subfamily/family), and thus a higher level of polyphyly is assumed; whereas subgenera will provide phylogenetic information revealing relatively major phenotype breaks (innovations) within an assumed cohesive grouping of ammonites such as Simoceratinae. Alternatively, in option (ii) the genus level directly identifies these breaks in phenotype evolution (innovations forcing relative monophyly), with no direct information about the immediately higher level of taxonomic reference (family/subfamily level). At present, we favour option (ii), interpreting genus-level clade identification (through recognition of innovations) reinforcing taxonomy with evolutionary significance at this level—i.e., based on inner whorl sculpture as the crucial phenotype stage for the interpretation of higher-level taxonomy and evolution, and later morphological breaks (innovations) for clade-level, phylogenetic identification at the genus level.

This proposal is supported by (i) available information about precise biostratigraphy; (ii) iterative evolution of simoceratins from a "perisphinctoid", *Virgatosimoceras*-like or closely related branch as the main evolutionary pattern; (iii) difficulty in approaching genus-level monophyly sensu stricto some other way; (iv) the polyphyletic character of the latter genus-level taxon created for Simoceratinae (*Volanoceras* as interpreted by Geyssant 1985, 1988 and Schweigert et al. 2002); and (v) avoiding maintenance of genera as large, heterogeneous and presumably polyphyletic species complexes. Accordingly, and based on the available information, the genus-level taxonomy proposed points to approaching the least inclusive taxonomic unit at this level.

At the species level, our interpretation accords with postulates derived from: (vi) phenotype cohesion (e.g., Templeton 1989); (vii) relevance of dynamic biogeography, at least for determining subspecies (e.g., Nelson and Platnick 1981); and (viii) recognition of species-flock, species complex and metapopulation-metacommunity concepts and their enlightening potential for interpreting cephalopod diversity, biogeography and underlying dynamics at the population and species levels (e.g., Yacobucci 1999; Norman 2003; Yoshida et al. 2006; Bolstad 2009; Gillanders et al. 2009; Olóriz and Villaseñor 2010, and references therein). Thus, the species level is approached within the conceptual framework favouring the relevance of environmental forcing, of biogeographic range processes, and autapomorphy (e.g., Van Valen 1976 and Ridley 1989 to complement citations above).

Remarks on the simoceratin species *Simoceras aesinense* (Meneghini, 1885) sensu Santantonio (1986).—Some observations concerning the ontogenetic course of *Simoceras* cfr. *volanense* Oppel, 1863 sp. var. *aesinense* in Meneghini (1885) deserve mention here.

Meneghini (1885: 376–378) described a specimen of 62 mm in size (which accords with his illustration in pl. 20: 4a, b), identified the last whorl as the last one preserved, and recognised both difficulty in identifying constrictions on the inner whorls and their deepness on the outer whorl. In addition, Meneghini (1885) noted depressed tubercles on shell periphery (shoulders), pointed ones on the umbilical edge, ribs between these two rows that changed around the middle of the penultimate whorl (29–30 mm in his illustration) to become ventrally enlarged towards the outer whorl while showing a small, and delicate tuberculation on the inner whorls; he likewise reported suture line details from the third whorl. In comparison with the Lower Tithonian species *Ammonites volanense* Oppel, 1863, Meneghini (1885) found differences in coiling degree and rib density on the inner whorls, differential crowding of ribs and morphology of the peripheral tubercles with respect to *Simoceras volanense* (Oppel in Zittel 1870: 95, pl. 32: 7–9), and lesser similarity in both the looser coiling and gradual change in sculpture with respect to *A. volanensis* in Oppel (1863: pl. 58: 2a, b). On this basis, Meneghini (1885) formalised the recognition of his "*S.* cfr. *volanense* Oppel, 1863 sp. var. *aesinense*" as the most frequent among the *Simoceras* that he compared from Tithonian deposits in the Marche (central Italy), indicating that specimens larger than 45 mm show spiny periumbilical and peripheral tubercles on the outer whorl preserved. In this whorl, the author described two constrictions towards the end, the posterior one deep and bordered by an aboral simple, slightly finer rib concave forwards and terminating in the corresponding spiny tubercle on the shoulder. A similar constriction was identified by Meneghini (1885) closer to the end of the preserved outer whorl, as well as another two early in the same whorl, four in the penultimate whorl, and a few more irregularly spaced ones on the innermost whorls that show ribs with spiny tubercles on the shoulders. Finally, Meneghini (1885) stressed the absence of suture lines adorally from the outermost constriction described.

Santantonio (1986) indicated that Meneghini's (1885) type was lost during the Second World War, but was able to analyse a cast, and promoted the name *S. aesinense* (Meneghini, 1885) as a valid species. On the basis of abundant and well preserved material, this author accurately described the ontogeny in the *S. aesinense* (Meneghini, 1885) species and interpreted its morphologic variability. He recognised dimorphism on the exclusive basis of shell size within a range of small to medium sized individuals (up to 65 and 94 mm, respectively), and identified the beginning of the body chamber at around 60 mm in macroconchs (between 20 and 35 mm in microconchs). In addition, he observed subquadrate whorl sections, loose coiling that decreased throughout the ontogeny, and no difference in sculpture between sexual dimorphs other than those related to shell size. Santantonio (1986) did not describe the type of peristome in microconchs (see previous allusion to his comments about defective preservation in rosso ammonitico facies), but interpreted crowded constrictions at the end of preserved shells and moulds as an indication of complete individuals. This author established the following ontogenetic phases in the sculpture of the species *S. aesinense* (Meneghini, 1885): (i) below 15 mm, ribs are simple, wider than inter-rib spaces, slightly

concave adorally and terminating in small ventrolateral clavi that elongate tangentially during the ontogeny; (ii) at 30 mm, the periumbilical part of the ribs may have a comparatively higher relief, which coincides with their relative depression at the mid-flank, while ventrolateral clavi are prominent; (iii) around 40–45 mm the typical combination of progressive rib swelling, decreasing sculpture at the mid-flank, and the tangential expansion of clavi occurs, and typical individuals show radial-periumbilical bullae, a mid-flank depression with possible development of geminate ribs, and ventrolateral clavi elongated longitudinally. This third stage is accentuated in macroconchs larger than 60 mm, especially in development of bullae and the mid-flank germination of ribs. Santantonio (1986) gave fewer details about constrictions, but accurately noted their decreasing number (from around two in the inner whorls), their increasing excavation toward the outer whorls, and the persistent occurrence of relative sharp edges. In addition, he described the significant relief of clavi, which could be connected by subtle, wide folds of the ventral region. Santantonio (1986) placed special emphasis on the occurrence of a "cordone spirale" observable between clavi of well preserved shells, which determines an inter-clavi groove identifiable in phragmocones and body chambers preserved as inner moulds. Moreover, he mentioned small ribs (i.e., riblets) in the clavi walls of well-preserved specimens. In Santantonio's (1986) comparative analysis of the Lower Tithonian species *S. aesinense* (Meneghini, 1885) and *S. volanense* (Oppel, 1863) he stressed high variability in the change of bullae to periumbilical tubercles in specimens of greater size, and in their onset during the ontogeny (from 25–30 mm onwards), and gave the precise stratigraphic range for species *S. aesinense* (Meneghini, 1885) in coincidence with the Lower Tithonian *Haploceras verruciferum/ Semiformiceras semiforme* Chronozone in the Mediterranean Tethys.

Among the data provided by Meneghini (1885) and Santantonio (1986), the following points are of relevance for the interpretation of Lower Tithonian simoceratins from the Americas:

(i) Species *S. aesinense* (Meneghini, 1885) has small macroconchs (body chamber beginning as small as 60–70 mm). Recognition of the outer whorl in Meneghini's type as the last preserved (Meneghini 1885), and the clarification about a small final part without suture lines in the type (Meneghini 1985), indicate the possible existence of larger individuals (later confirmed by Santantonio 1986).

(ii) The noteworthy difference in recognition of constrictions indicates intra-species variability for this character.

(iii) Ribbing changes at ca. 30 mm, described by Meneghini (1885), coincide with the second ontogenetic stage described by Santantonio (1986), i.e., the beginning of periumbilical tuberculation together with mid-flank depression of ribbing. These two traits seem to be in co-variance.

(iv) Typical bituberculation comprising spiny-perpendicular and spiny-tangential elements above 45 mm (Meneghini 1885) agrees with the third ontogenetic stage of Santantonio

(1986), who added comments that support co-variation in shell features.

(v) Ontogenetic stages and variability affecting sculpture expression (timing for change from bullae to periumbilical tubercles included) as described by Santantonio (1986).

(vi) Occurrence of subtly ribbed clavi and "cordone spirale" in relation with good preservation, in particular the appearance of the latter as a groove on inner moulds of phragmocones and body chambers (Santantonio 1986).

(vii) Identification of the precise stratigraphic range of *S. aesinense* (Meneghini, 1885) within the Lower Tithonian (Santantonio 1986; genus-level interpretation according to this author).

(viii) Phenotypic expression of dimorphism. Interpreted on the basis of shell size without significant incidence in sculpture (Santantonio 1986), as commonly assumed for Lower Tithonian simoceratins (e.g., Geyssant 1988). No apertural structures are accurately known for macroconchs, and they are unknown in microconchs (in coincidence with Geyssant 1988). The sole reference to peristome in Tithonian simoceratins was made by Geyssant (1979: 15–16, text-fig. 15, pl. 2: 3), who envisaged a microconchiate peristome in correspondence with a small, pointed adoral projection separating dorsal and ventral concavities at the end of the shell in her Upper Tithonian genus *Baeticoceras* Geyssant, 1979, a younger synonym of *Cordubiceras* Olóriz and Tavera, 1979, as recently recognised by Benzaggagh et al. (2010).

Extensive reference to interpretations of Meneghini's (1885) species at the species level and higher ones is given above. At present, we interpret that "*S.* cfr. *volanense* Oppel, 1863 sp. var. *aesinense*" Meneghini, 1885 represents a widespread species, or species complex, inhabiting epioceanic environments in western Tethys but also, less commonly, epicontinental shelves in the area and the Americas, where geographical differentiation existed (see below).

Systematic palaeontology

Class Cephalopoda Cuvier, 1798

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Perisphinctoidea Steimann in Steimann and Doderlein, 1880

Family Simoceratidae Spath, 1924

Subfamily Simoceratinae Spath, 1924

Genus *Pseudovolanoceras* Cecca, 2002

Type species: *Simoceras aesinense* (Meneghini, 1885): Pelagic cephalopod limestone in central Appenines, Marche, Italy; Lower Tithonian.

Remarks.—Cecca (2002a: 363–364) erected *Simoceras* (*Pseudovolanoceras*) for the *Simoceras aesinense* (Meneghini, 1885) (sensu Santantonio, 1986) species group in Europe and the Americas, and designated the Meneghini (1885)

species as type-species. The Mexican species *Volanoceras chignahuapense* Cantú-Chapa, 1990 was considered a younger synonym, while the Argentinean species *V. krantzense* Cantú-Chapa, 1990 was accepted as a separate taxon at the species level.

Pseudovolanoceras aesinense chignahuapense (Cantú-Chapa, 1990)

Figs. 3A–E, 4A–G, 5A–D, 6C, 7, 8A, B.

?1973 *Simoceras* cf. *S. volanense* (Oppel 1863); Verma and Westermann 1973: 196, pl. 37: 2a, b.

1990 *Volanoceras chignahuapense* sp. nov.; Cantú-Chapa 1990: 41, fig. 2a–d.

1999 *Simoceras aesinense* (Meneghini, 1885); Cecca 1999: 7, 26 (partim).

2000a *Simoceras aesinense chignahuapense* (Cantú-Chapa, 1990); Villaseñor et al. 2000a: A469.

?2000b *Simoceras* group of *aesinense* (Meneghini, 1885); Villaseñor et al. 2000b: 257.

2002 *Volanoceras aesinense* (Meneghini, 1885); Schweigert et al. 2002: 8, non pl. 1: 1–4 (partim).

2002a *Simoceras* (*Pseudovolanoceras*) *aesinense* (Meneghini, 1885); Cecca 2002a: 364 (partim).

Material.—Twenty-one specimens labelled IGM 6085-2a and IGM 9541 to IGM 9559.

Measurements.—See Appendix 1. For approximate values note (*) for values obtained from specimens, or (**) when taken from illustrated specimens.

Emended diagnosis.—Loosely coiled shells. Simple ribs with more or less distinct reinforcement of ventral extremes on the inner whorls, and then two rows of tubercles. Low expression of geminate ribs on the flanks in macroconchs. Variable weakening of sculpture on the outer whorl in microconchs. Periumbilical tubercles indistinct to more or less bulliform to pointed structures. Peripheral tubercles elongated longitudinally, more or less flared with occasional riblets, connected by longitudinal ridge on well preserved shells, and the associated groove on preserved inner moulds. Macro- and microconchiate individuals. Lappets in microconchs and unknown adoral structures in macroconchs. Suture line incompletely known.

Description.—Twenty-one specimens and fragments with a size range of 23.12 mm to 95.2 mm, preserved as imprints except IGM 9543a, a crushed phragmocone with partial body chamber preservation in volume; the probably near-complete IGM 9544 gathered from a concretion; IGM 9548a, which is a flattened inner mould with only partial preservation of body chamber in volume; and IGM 9555, a fragmentary inner mould preserved in volume with shell remains and part of the body chamber. Note that flattening and related distortions probably determined the bias in some of the parameters and, therefore, curves showing the course of coiling and whorl height could be slightly affected.

Coiling is variable at smaller shell diameters (U/D = 37–59%) but tighter than above 20–30 mm shell diameter, except in the extremely evolute IGM 9541 (Fig. 4B), looser above 30 mm (U/D = 49–64%), and decreasing slightly during ontogeny (Fig. 5A, B).

Due to defective preservation, there are few precise data about the umbilical wall and the whorl section. When preservation in volume was possible, the umbilical wall seen to be gently vertical with rounded edge, or indistinct because of the gentle convexity of flanks towards the line of whorl-overlapping.

Due to common shell and/or mould crushing, equivalent estimation applies to whorl thickness. However, specimens preserved in volume allow for identification of subrectangular whorl sections. Thus, IGM 9555 shows a subrectangular whorl section with rather convex flanks (Fig. 3A); IGM 9543a allows for partial reconstruction of the body chamber showing subrectangular whorl section in correspondence with peripheral tubercles, and an oval whorl section between tubercles. A similar whorl-section design is found between ribs in other specimens, and gently convex flanks determine the maximum whorl-width placed close to the mid-flank.

Whorl-height values vary on the inner whorls (< 35 mm), and tend to stabilise through ontogeny (Fig. 5C). Thus, there are specimens in which whorl height values sharply decrease below 20 mm in shell size, then rise to ca. 25–30 mm and diminish at greater shell diameters (e.g., IGM 9551a, IGM 9544, IGM 9545a, IGM 9546a), although cases showing near-constant values were also identified (e.g., IGM 6085-2a).

Recognition of constrictions is variable, which might result from their usual course parallel to ribbing combined with the effect of flattening, but certainly provides information about inter-population biodiversity in constriction number, excavation and across flank course. Constrictions are more prorsiradiate in the nuclei. Thus two subsets of specimens were identified according to:

(i) Subtle constrictions, which are gently prorsiradiate between 20 mm and 27 mm of shell diameter but, while rare, seem to be better developed later in ontogeny (e.g., IGM 9545a shows a deep constriction, concave towards the aperture close to the end of the preserved imprint; Fig. 3C).

(ii) Constrictions are more frequent and well developed, concave to the aperture and more excavated, especially on the outer whorl (e.g., IGM 9541, IGM 9543a); two to three con-

Fig. 3. Simoceratin ammonoid *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) [M]. **A**. Left-side view of IGM 9555 from MTQ section, bed 11; arrows showing body chamber, and incipient longitudinal furrow between tubercles (see text for allusion to "cordone spirale"). **B–E** from the Apulco section (MT-2). **B**. Left-side view of IGM 9547a, bed 22b. **C**. IGM 9545a, bed 22b. **D**. IGM 9545b, bed 22b. **E**. IGM 9548a, bed 21b. **F**. *Simoceras* aff. *volanense* Oppel, 1863 [type of Krantz 1928: pl. 3: 7; GPIBO 1 = *Pseudovolanoceras aesinense krantzense* (Cantú-Chapa, 1990)]; slightly oblique, right-side view of plastic mold; arrows for longitudinal furrow between tubercles (see text for allusion to "cordone spirale"). **G**. *Simoceras* cf. *S. volanense* (Oppel, 1863) [type of Verma and Westermann 1973: pl. 37: 2; IGM 2764 = *Pseudovolanoceras aesinense* (Meneghini, 1885) transitional form between *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) and *Pseudovolanoceras aesinense krantzense* (Cantú-Chapa, 1990)], close up view; arrows for longitudinal furrow between tubercles (see text for allusion to "cordone spirale").
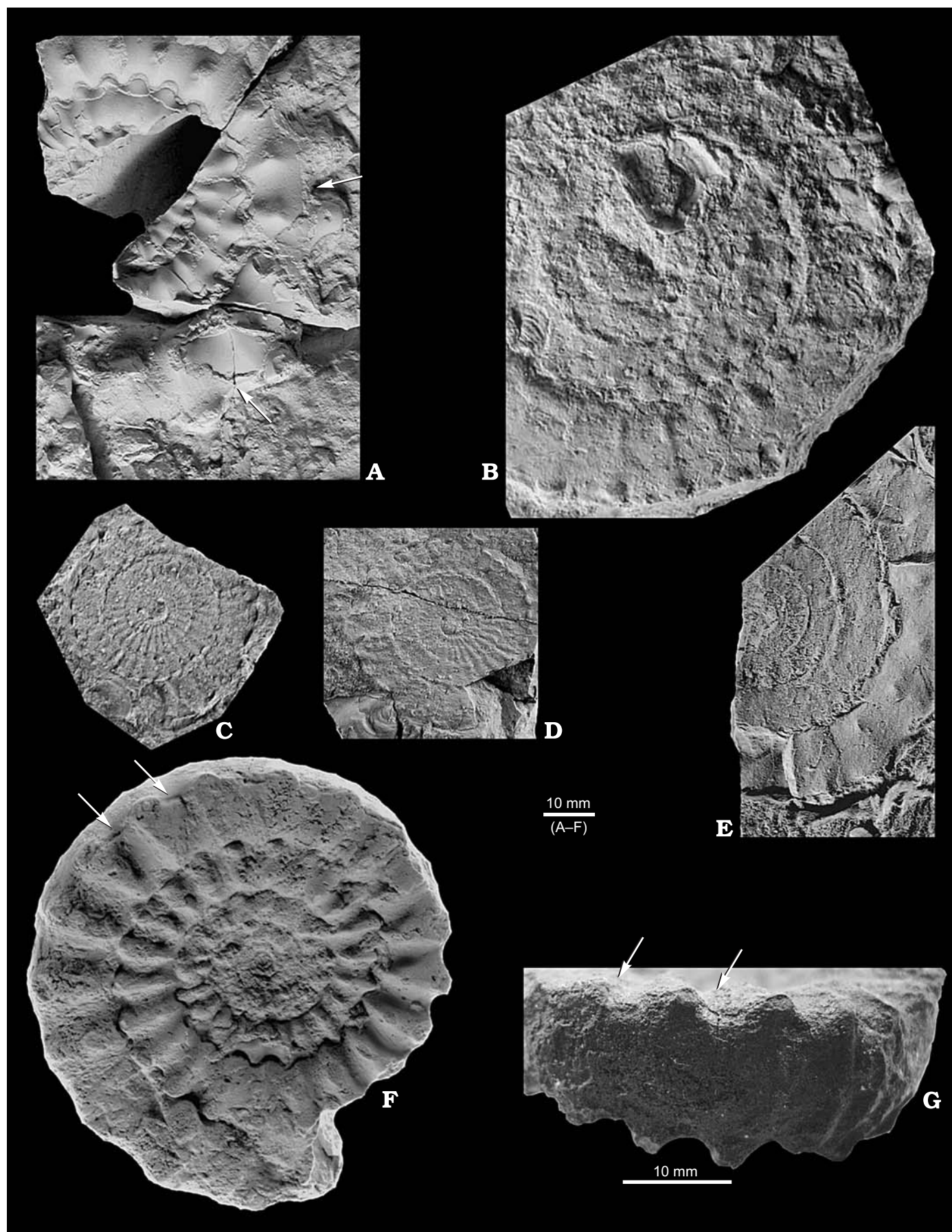
strictions per complete whorl in the middle whorls (e.g., IGM 9544), and three to four on the outer whorl; a constriction close to the end of the inner mould is the pre-apertural one, which is comparatively radial and straight (e.g., IGM 6085-2a).

Sculpture typically varies throughout ontogeny, and therefore, counting periumbilical ornamentation per half-a-whorl (PS/2 in Appendix 1) provides data on relative crowding during ontogeny, whatever its precise type. Figures 5D and 7 reveal initial, progressive decreases in crowding of sculpture and then a trend to stabilisation later in ontogeny. In general, on the inner whorls up to 16–22 mm in shell size, ribs are wider than the inter-rib spaces, simple, radial to slightly prorsiradiate, and slightly enlarged towards shell periphery. Their ventrolateral ends are reinforced as small, rounded tubercles, which are partially covered by the next whorl. Favourable but differential observation for analysing sculpture in the nucleus is found in some specimens. Up to 11 mm ribs are simple, prorsiradiate, slightly concave towards the aperture, wider than the inter-rib spaces and enlarge progressively toward the venter (IGM 6085-2a). However, rib crowding can persist up to 29–30 mm (e.g., IGM 9545a). Ventrolateral undulation due to the enlargement of clavi can occur from around 10 mm in shell size (e.g., IGM 9541, IGM 9544), and accentuates progressively to show typical *Pseudovolanoceras aesinense* (Meneghini, 1885)—typology with well-developed clavi, which are sometimes only evidenced through their impressions. At 19–20 mm the crowding of ribs diminishes, and ribs are much more swollen (IGM 6085-2a, IGM 9543a); but this observation could be partially obscured by preservation between 13–18 mm (IGM 6085-2a) and, therefore, the increasingly wide-convex relief could be more progressive than in IGM 9543a. Typical *P. aesinense* (Meneghini, 1885)—typology is seen ca. 20 mm in shell size and later in ontogeny (even in eroded specimens; e.g., IGM 9541), although it is doubtful to conclude about the incipient ribs' reinforcement close to the umbilical edge (e.g., observed in IGM 9544). A generalised change in sculpture occurs at around 30 mm with a marked increase in the enlargement of rib expansion towards the ventral extreme; ventrolateral clavi develop superimposing undulation on whorl junctions, and some cases of subtle periumbilical reinforcement of ribs in microconchs and stronger in macroconchs were observed (i.e., IGM 9545a and 9545b, IGM 9546a and 9546b, IGM 9546-2, IGM 9550b, IGM 9551a, IGM 9555).

In microconchs, a difference in rib crowding occurs and is considered as inter-population variability. Significant but variable weakening of the sculpture is typical (e.g., IGM 6085-2a, IGM 9543a, IGM 9544). It starts from 36–37 mm onwards in IGM 6085-2a, preceded by two sinuous ribs, which are wider towards the venter—i.e., the outer half-a-whorl preserved is comparatively smooth except for well developed peripheral tubercles elongated longitudinally. In contrast, IGM 9543a shows slight periumbilical reinforcement of two ribs around 32 mm in shell size, but the final part of the preserved inner mould reveals the ventral region in volume just after a deep constriction with a rounded posterior

edge and acute anterior one. Of special relevance is recognition in IGM 9543a and IGM 9544 of a very shallow groove between two successive ventrolateral tubercles elongated longitudinally (Fig. $4C_1$, G_3). This groove corresponds to the equivalent one characterising the well preserved inner mould of species *P. aesinense* (Meneghini, 1885), and is therefore interpreted as evidence of "cordone spirale" (sensu Santantonio 1986). Also relevant is the occurrence of riblets in clavi (Fig. $4G_2$), first appearing at 12.5 mm in diameter in IGM 9544 (Fig. $4G_4$), and likewise identified in IGM 9546a. This ornamentation seems to be related to, or forced by, clavi enlargement from around 13 mm in shell size, which accentuates progressively and is well developed with typical *P. aesinense* (Meneghini, 1885) typology from around 17 mm. In general, no ventral regions are observable due to flattening (horizontal settling dominant), and crushed flanks in moulds make it less probable to recognise the groove that corresponds to the "cordone spirale" (sensu Santantonio 1986).

In macroconchs, there is a generalised reinforcement of the sculpture from shell diameter of 37 mm to 45 mm onwards. Taking into account the common severe flattening, it is mainly evidenced by enlarged undulation on the whorl periphery, but in some cases periumbilical bullae or tubercles are affected (IGM 9545a, IGM 9547a, IGM 9551a, IGM 9554). The incomplete and comparatively coarse sculptured IGM 9545a shows relative smoothing on the outer whorl, with accentuated weakening of sculpture and a deep constriction concave to the aperture with prominent anterior edge (Fig. 3C, D). In the largest IGM 9547a, the outer whorl shows accentuation of inter-tubercle space that is concomitant with well-expressed periumbilical bullae and large peripheral tubercles. Given the state of preservation in almost all specimens, it is difficult to differentiate between blunt ribs and bullae or tubercles, which more or less progressively replace each other on the umbilical edge during ontogeny. However, the well and preserved in-volume IGM 9555 shows periumbilical spiny tubercles.

Body chamber recognition is obscured by common leaf-preservation in siltstones, but some cases of crushed phragmocones and filled body chambers preserved in-volume are known (e.g., IGM 9548a, IGM 9543a). Specimens collected from concretions are more favourable, even for local preservation of suture lines (e.g., IGM 9555). In general, preserved body chamber length extends from one- to three-quarters of the outer whorl (e.g., IGM 9543a, IGM 9544).

Nearly complete peristomial structures are first reported for microconchiate simoceratins in Mexico and the Americas. IGM 9546a shows pre-apertural constriction, comparatively radial and straight, which precedes the peristome with short, wide lappets that show convex corrugations inside (Fig. 4D, E). IGM 6085-2a preserves the pre-apertural constriction, which is wide, comparatively radial and straight, and also precedes the peristome with short, wide lappets that show convex corrugations inside (Fig. 4A). The occurrence of lappets in *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) validates the hypothesis of dimorphism
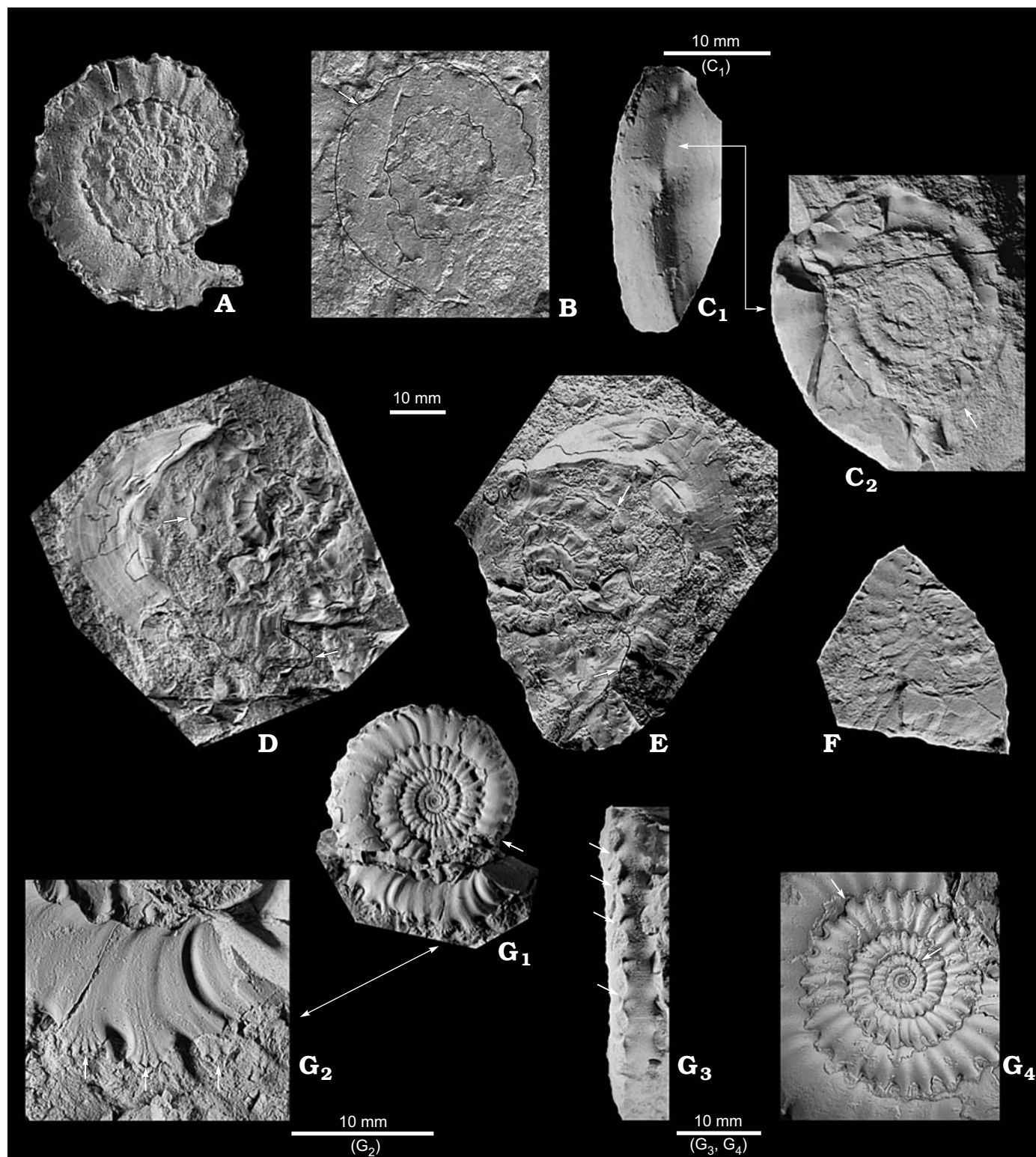
Fig. 4. Simoceratin ammonoid *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) [microconch]. **A–F**. From the Apulco section (MT-2). **A**. Right-side view of IGM 6085-2a showing lappet, bed 21b. **B**. Right-side view of IGM 9541; eroded and slightly distorted specimen, bed 21b. **C**. IGM 9543a, close-up view showing incipient longitudinal furrow between tubercles (C_1) (see text for allusion to "cordone spirale"); right-side view (C_2), bed 25. **D**, **E**. IGM 9546a and b, both from the same flattened inner mould. **D**. Imprint of the left side. **E**. Left-side view; arrows for lappet and tubercles showing riblets, bed 25. **F**. Left-side view of IGM 9542a, bed 21b. **G**. IGM 9544; G_1, right-side view, arrow showing the last suture line preserved; G_2, close-up view from the body chamber showing tubercles with riblets (arrows); G_3, ventral view showing longitudinal furrow between tubercles, arrows indicate the trace of the "cordone spirale" (see text for allusion to "cordone spirale"); G_4, close-up view of inner whorls showing tubercles with riblets (arrows); from MTQ section, bed 11.
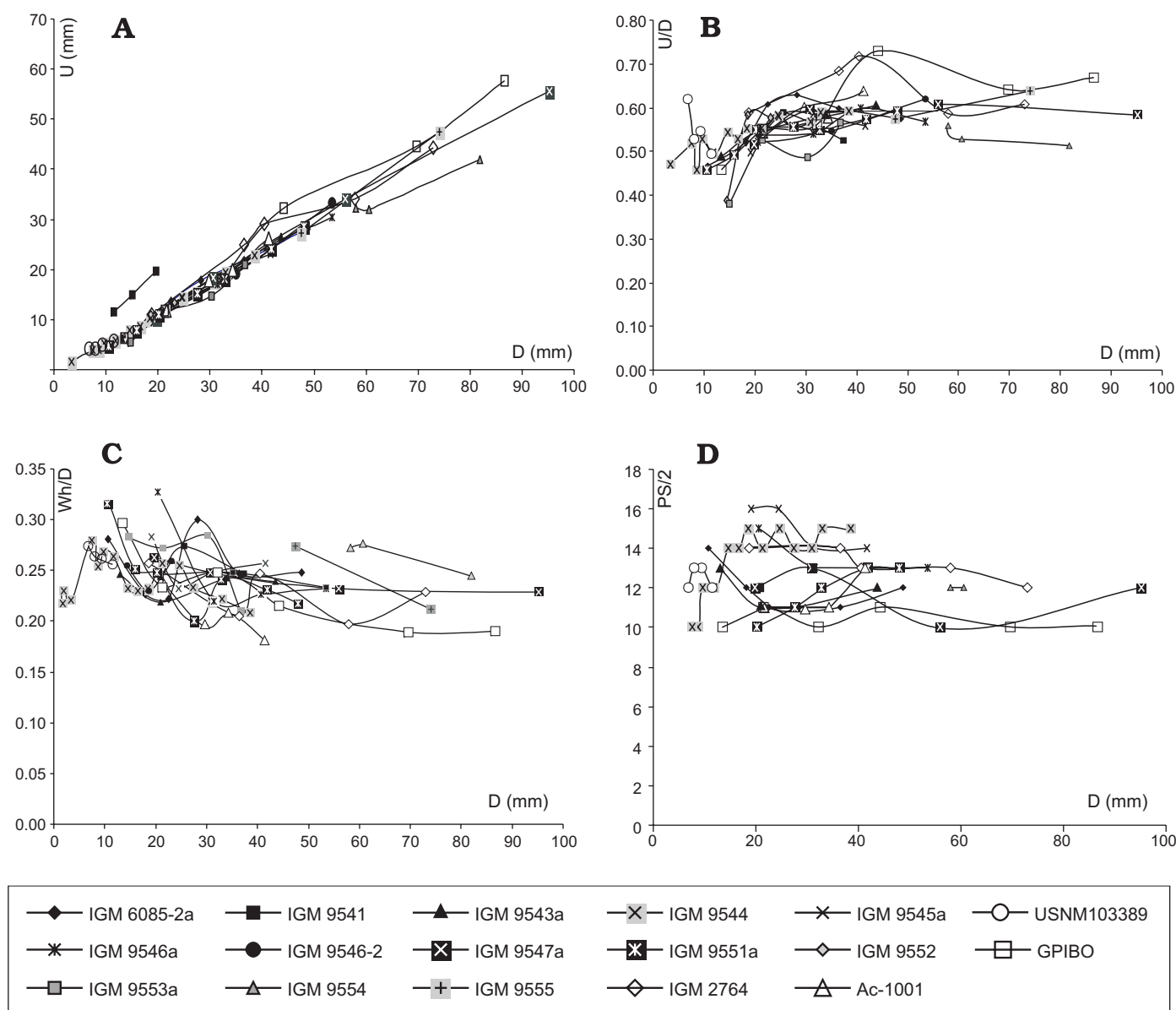
Fig. 5. Bivariate plots for shell features of simoceratin ammonoid *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) against shell diameter of Mexican, Cuban and Argentinean specimens. **A**. Umbilicus size (U). **B**. Size ratio between the umbilicus and shell diameter (U/D). **C**. Size ratio between whorl height and shell diameter (Wh/D). **D**. Periumbilical sculpture per half-a-whorl (PS/2). Shell diameter (D).

in Simoceratinae (e.g., Geyssant 1979; Santantonio 1986). Geyssant (1979) interpreted as microconchiate peristome the mid-flank pointed adoral projection separating two concavities identified in *Baeticoceras* (younger synonym of *Cordubiceras* Olóriz and Tavera, 1979), and envisaged the possibility of this projection being a rough-draft of lappet occurrence. Santantonio (1986) envisaged the existence of macro- and microconchs in *S. aesinense* (Meneghini, 1885), although he did not identify peristomial structuring for the Meneghini (1885) species and morphologically close ones. Thus, the reported evidence of lappeted peristome in *P. aesinense chignahuapense* (Cantú-Chapa, 1990) demonstrates a genus-level difference in peristomial structures for Tithonian microconchiate simoceratins.

The suture line preserved in specimens IGM 9555 and IGM 9544 (Fig. 8A, B) is simple and clearly similar to other suture lines of *Pseudovolanoceras aesinense* (Meneghini, 1885) species, or species complex, at similar diameters (see Santantonio 1986: fig. 3b, d, f).

Remarks.—The state of preservation forces serious limitations on the precise analysis of dominant ammonite imprints, including the description and comparison of delicate sculptures in the Mexican specimens [IGM 9547a, IGM 9546-2, interpreted as *Pseudovolanoceras* sp. cf. *aesinense* (Meneghini, 1885)]. The material described shows qualitative and quantitative features that clearly accord with those characterising the European species *P. aesinense* (Meneghini, 1885) (Figs. 6, 7; Appendix 1) here reinterpreted as belonging to
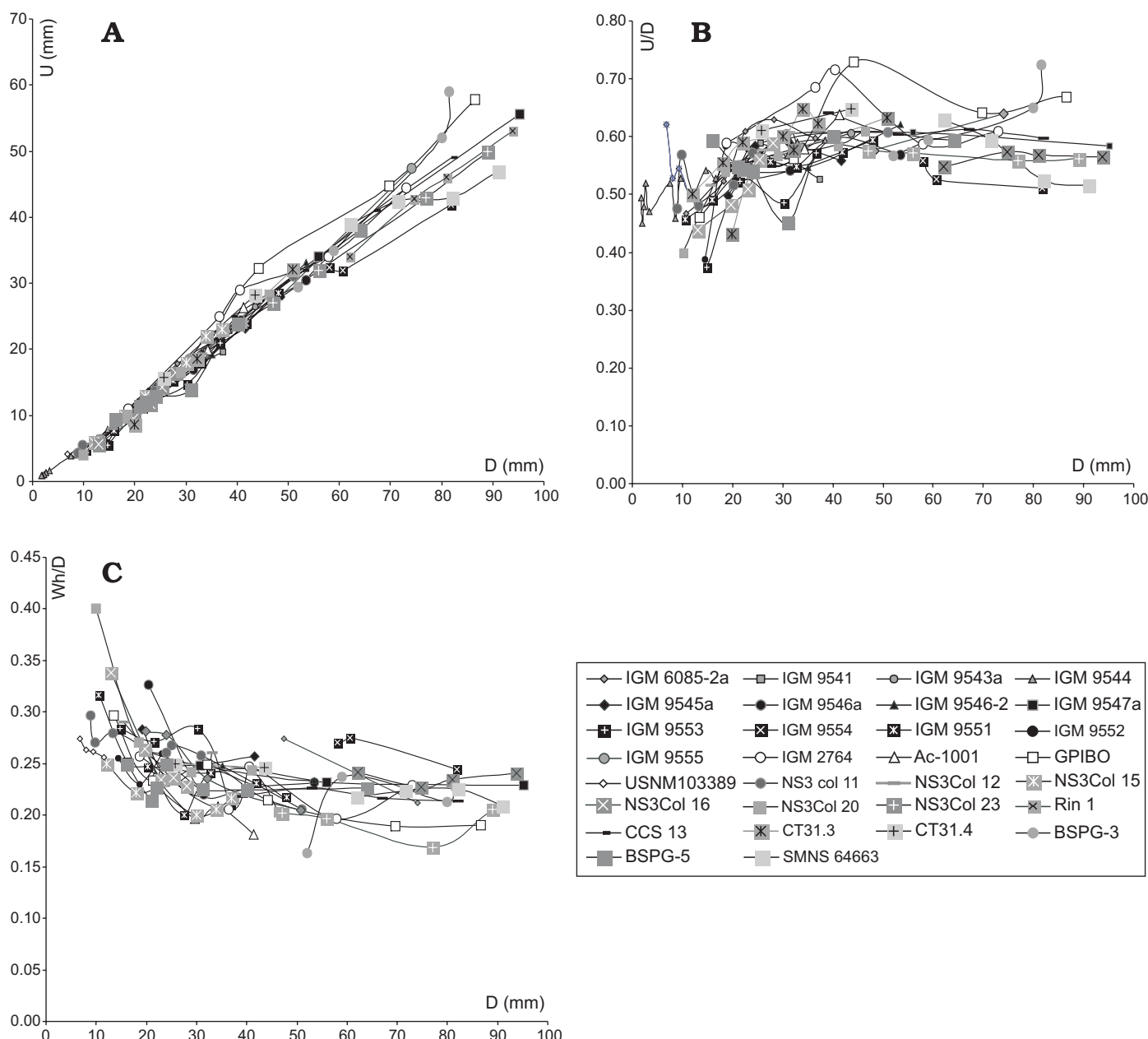
Fig. 6. Bivariate plots for shell features of simoceratin ammonoid *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) and *Pseudovolanoceras aesinense* (Meneghini, 1885)against shell diameter in American and European assemblages. **A**. Umbilicus size (U). **B**. Size ratio between the umbilicus and shell diameter (U/D). **C**. Size ratio between whorl height and shell diameter (Wh/D). Shell diameter (D).

the genus *Pseudovolanoceras* Cecca, 2002 (see also Cecca 2002a). Of special relevance is the simple ribbing identified below 22 mm in shell diameter, and the change in sculpture around 30 mm that results in the typical pattern of sculpture of *P. aesinense* (Meneghini, 1885) with undulating periphery and variable reinforcement of periumbilical sculpture, generally coarser from around 40 mm onwards. However, earlier development of clavi, lower reinforcement of periumbical sculpture, and typical weakening of flank sculpture on the outer whorl characterises microconchs of *P. aesinense chignahuapense* (Cantú-Chapa, 1990) in the studied area, a trait related to an accentuated decrease in rib density throughout ontogeny (Figs. 5D and 7).

All these differential traits are here interpreted as revealing local phenotype divergence from European representatives of the Meneghini (1885) species. In addition, observed traces consistent with occasional preservation (due to unfavourable dominant fossilisation in siltstones) of "cordone spirale" related structures (e.g., Santantonio 1986) in the material analysed (e.g., IGM 9543a, IGM 9544, IGM 9555) reinforce its interpretation as closely related to *Pseudovolanoceras aesinense* (Meneghini, 1885). The occurrence of riblets in external tubercles supports this hypothesis, since this bizarre sculpture was also identified in well preserved specimens of European *P. aesinense* (Meneghini, 1885) (e.g., Bernoulli and Renz 1970; Santantonio 1986). These two particular features, which
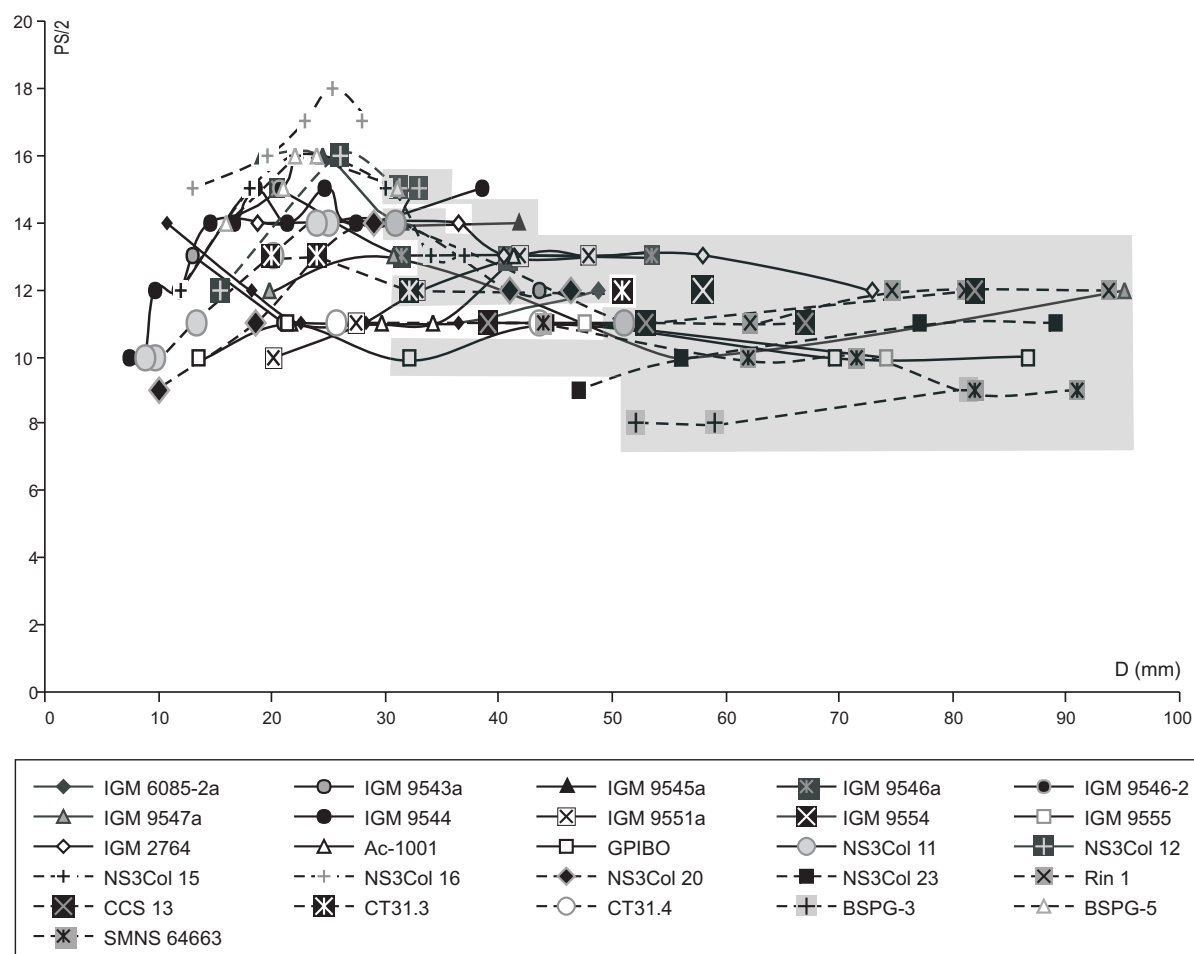
Fig. 7. Periumbilical sculpture per half-a-whorl against shell diameter (PS/D) (shadow area indicates tubercles as inner sculpture) in simoceratin ammonoid *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) and *Pseudovolanoceras aesinense* (Meneghini, 1885).

are known in the European species, are consistent with the favoured interpretation of relationships at the subspecies level. In addition to these qualitative and crucial phenotype traits for species identification, quantitative ones (Figs. 5–7) reinforce the interpretation of these Mexican simoceratins as closely related to the European species *P. aesinense* (Meneghini, 1885). As commented above, microconchs are not distinguishable on the exclusive basis of shell size (e.g., Santantonio 1986 for incomplete specimens of *P. aesinense* [Meneghini, 1885]) or small, pointed adoral projections at the mid-flank (e.g., Geyssant 1979 for microconchs of the younger *Cordubiceras*), but on the occurrence of real lappets, which are reported for the first time from subfamily Simoceratinae. Although based on a comparatively incomplete observation obtained from the Mexican material analysed (less common macroconchs collected) macroconchiate specimens show sculpture in agreement with stages above 40 mm described in Santantonio (1986).

The revision made of previous interpretations of Mexican simoceratins together with comments about the original description of "*Simoceras* cf. *volanense* Oppel, 1863 var. *aesinense*" in Meneghini (1885: 376) and later interpretations of

Simoceras, *Volanoceras*, or *Pseudovolanoceras aesinense* (Meneghini, 1885) (Santantonio 1986; Cecca 1999, 2002a; Villaseñor et al. 2000a, b; Schweigert et al. 2002), as well as the precise analysis of cast (Krantz 1928) and types (Verma and Westermann 1973) revealing occurrence of traces related to the "cordone spirale" (Fig. 3F, G), lend support to our interpretation of the occurrence of Tethyan species *P. aesinense* (Meneghini, 1885) in Mexico and the Americas. In fact, the synonymy list (mainly restricted to papers with illustration and unequivocal references) given in Appendix 2 demonstrates the special relevance given to variability in shell features that previously was underestimated; this led to different, comparatively restricted and/or general interpretations of the Meneghini (1885) species (e.g., Fözy 1988; Cantú-Chapa 1990; Cecca 2002a; Schweigert et al. 2002). Based on the conceptual approach presented (see Notes on Simoceratinae chapter), we agree with contemporaneous interpretations which more or less clearly accept the occurrence of *P. aesinense* (Meneghini, 1885) or *P. aesinense*-like forms as the typical simoceratins in the Americas, despite their being submitted to differential interpretations at the genus level (e.g., Fözy 1988; Cantú-Chapa 1990; Cecca 2002a; Schweigert et al. 2002).

As underlined earlier, the Argentinean specimen described by Krantz (1928) is without a doubt morphologically close to species *P. aesinense* (Meneghini, 1885) (Figs. 6, 7), even showing traces of the "cordone spirale" (sensu Santantonio 1986) as deduced from the plastic-cast examined (Fig. 3F). The intra-species variability we assume allows us to interpret this specimen as representing less constricted, heavier shell phenotypes showing coarser sculpture, most probably related to great size (as usually identified in neritic ammonites; cf. extreme phenotypes and the platform effect in Olóriz 1985; Olóriz et al. 1988; among others).

With the assumption of age-compatibility (e.g., Santantonio 1986; Olóriz and Tavera 1979; Cecca 1999, 2002a; Parent and Capello 1999; Villaseñor et al. 2000a, b; Schweigert et al. 2002), we interpret the Argentinean specimen as a local phenotype expression of *Pseudovolanoceras aesinense* (Meneghini, 1885)—i.e., the geographic subspecies *Pseudovolanoceras aesinense krantzense* (Cantú-Chapa, 1990).

The Cuban nucleus illustrated by Imlay (1942) is difficult to interpret, but the style of ribbing is easily comparable with that of species *P. aesinense* (Meneghini, 1885) (see above) rather than *S. volanense* Oppel, 1863, as interpreted by Imlay (1942). In fact, the latter species developed finer, bifurcate ribbing in the nucleus and then simple ribs with no equivalent difference in width across the flanks at the same ontogenic stage. The record of more complete individuals from Mexico, as demonstrated by the slightly larger individual from Puebla (species *Volanoceras chignahuapense* in Cantú-Chapa 1990) and the material described here from the Mazatepec area, reinforce this interpretation. The Cuban specimen would represent the first stage described by Santantonio (1986) for the species *Simoceras aesinense* (Meneghini, 1885) (genus level interpretation according to this author).

As noted above, the small *V. chignahuapense* in Cantú-Chapa (1990) is here reinterpreted at the genus and subspecies levels (*Pseudovolanoceras aesinense chignahuapense* [Cantú-Chapa, 1990]), based on the occurrence of simple ribbing in the nucleus and the delicate imprint of the "cordone spirale" (see above). Its sculpture accords closely with the second stage characterised by Santantonio (1986) for shells of *Simoceras* (here *Pseudovolanoceras*) *aesinense* Meneghini, 1885 below 40 mm in size, except for earlier and comparatively accentuated "flared" external tubercles. On the assumption of confidence in the precise evaluation of the chambered part made by Cantú-Chapa (1990), his specimen could be a mature but nearly complete microconch—i.e., it is not a nucleus.

The type of the Mexican specimen described by Verma and Westermann (1973) from the Alamitos section in north-central Mexico is slightly distorted, inducing doubts as to its interpretation; hence new material would be of great importance for this purpose. Later interpretations (see above) concluded close relationships with the here interpreted *P. aesinense* (Meneghini, 1885) (e.g., Cecca 1999; Olóriz et al. 1996, 1999; Villaseñor et al. 2000a, b) or *P. krantzense* (Cantú-Chapa, 1990) (Schweigert et al. 2002). Taking into
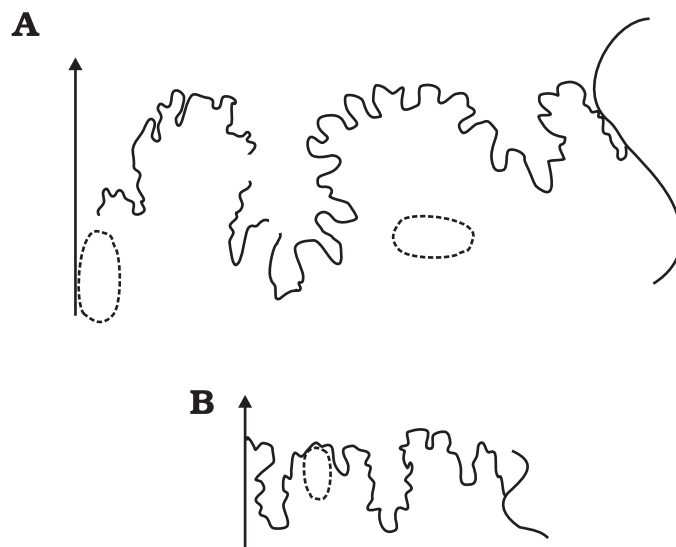

Fig. 8. Simoceratin ammonoid *Pseudovolanoceras aesinense chiagnahuapense* (Cantú-Chapa, 1990), suture lines. **A**. IGM 9555 [M], last incomplete suture at 70 mm of shell diameter. **B**. IGM 9544 [m], incomplete suture at 26.19 mm of shell diameter.

account the intra-species variability here interpreted for *P. aesinense* (Meneghini, 1885), including its geographical subspecies (see above), and the occurrence of traces of "cordone spirale" obscured by granular-phosphatic sediment preservation (Fig. 3G), two of the most typical "differences" argued for species level separation of this specimen become irrelevant. Thus, constrictions are astonishingly similar to those described by Meneghini (1885: 337), and variability in both periumbilical reinforcements and the timing of development (e.g., early outlined by Santantonio 1986) would clearly diminish problems when reinterpreting the specimen collected from Sierra de Catorce (north-central Mexico). In addition, close analysis of a plastic-cast of the Argentinean specimen and the type described by Verma and Westermann (1973) reveals closer resemblance of the latter with *P. aesinense* (Meneghini, 1885) in inner whorls coiling and ribbing, together with closer resemblance with the type described by Krantz (1928) in outer whorl sculpture and whorl section at the same shell size. All these observations support its reinterpretation as an intermediate phenotype between those identifiable in the types analysed by Meneghini (1885) and Krantz (1928), both of which are here held to evidence separate records of the same species resulting from biogeographical dynamics. As for the biochronostratigraphical interpretation of the Verma and Westermann (Verma and Westermann 1973) type gathered from the Rancho Los Alamitos section, San Luis Potosí, bed-by-bed sampled ammonite assemblages from the Virgatosphinctinae Beds allowed Olóriz et al. (1996, 1999) to identify discontinuous accumulation, most probably ranging from the late *Virgatosimoceras albertinum/Neochetoceras darwini* to the earliest *Richterella richteri* chronozones in the Mediterranean Tethys. Thus, the most probable age for the Verma and Westermann (1973) type corresponds

to the *Semiformiceras semiforme/ Haploceras verruciferum* Chronozone in the Secondary Standard for Mediterranean Tethys (e.g., Geyssant 1997).

Biochronostratigraphy.—The specimens described of *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990) were collected from beds 21b, 22b and 25 in the Apulco section MT-2 and bed 11 form the Apulco section MTQ. In bed 21b of the Apulco River section MT-2 they are assembled to *Simocosmoceras pszczolkowskii apulcoensis* (Villaseñor and Olóriz 2001; Villaseñor et al. 2003), and in bed 11 of the nearby Apulco section MTQ registered together with *Pseudhimalayites steinmanni* (Haupt, 1907) (Villaseñor and Olóriz 2004). *Housaites butti* (Imlay, 1942) (Villaseñor and Olóriz 2009) was collected from the same stratigraphic interval in these two sections, and associated ammonites are *Sublithaceras*, *Parapallasiceras*, *Danubisphinctes* (e.g., López-Caballero 2006) and haploceratids (*Haploceras*, *Pseudolissoceras*, and others) under study at present. The mentioned ammonite assemblages belong to a stratigraphic interval that correlates with an undetermined level within the *Semiformiceras semiforme/Haploceras verruciferum* Chronozone in the Mediterranean Tethys.

Remarks on palaeobiogeography

The occurrence of Lower Tithonian simoceratins in the Americas has been known since the early 20th century, and their relation with European (Tethyan) species has been progressively accepted. On the basis of present information, the occurrence of simoceratin species in the Americas is interpreted as relating the arrival of Tethyan (ubiquitous) taxa to available shelf environments in these areas, a phenomenon that largely involved ammonites throughout Jurassic times. This scenario is compatible with a general model for interpreting patterns of ammonoid biogeography (Olóriz 1985, 1990), identified in the Americas (Mexican areas included) under a rather variable degree of understanding (see Olóriz 1985, 1987, 1990, 1992; Leanza and Olóriz 1987; Olóriz et al. 1988, 1990; 1999; Leanza and Zeiss 1992; Cecca 1999; Parent and Capello 1999; Villaseñor et al. 2000a, 2003; Parent 2001; Villaseñor and Olóriz 2001, 2004, 2009, Parent et al. 2006, among others, for precise appliance of the model and/or compatible interpretations). A conceptual complement to this template is provided by assuming biogeographic dynamics as recognised from present cephalopods (e.g., Norman 2003; Yoshida et al. 2006; Bolstad 2009; Gillanders et al. 2009) and the potential application to past cephalopod records (e.g., Olóriz et al. 2006; Olóriz and Villaseñor 2010; and references therein)—see Notes on Simoceratinae chapter above.

The occurrence of simoceratins in the Americas is associated with the most significant flooding recorded during the Early Tithonian (e.g., Olóriz et al. 1997, 1999; Villaseñor et al. 2003; and see Parent 2001 for biogeographic expansion of

genus *Pseudolissoceras*). Support for this interpretation in Argentina are the records of *Pseudovolanoceras aesinense krantzense* (Cantú-Chapa, 1990) (Krantz 1928) together with *Pseudhimalayites steinmanni* (Haupt, 1907) (Krantz 1928) or with *Pseudolissoceras zitteli* Burckhardt, 1903 (Parent 2001), and of *Simocosmoceras adversum andinum* (Leanza and Olóriz, 1987), with *Pseudhimalayites steinmanni* (Haupt, 1907) (Leanza and Olóriz 1987), the latter reinterpreted as *Pseudhimalayites subpretiousus* (Uhlig, 1878) by Parent (2001). In Cuba, the only support available is the occurrence of *P. aesinense* (Meneghini, 1885) (nucleus illustrated by Imlay 1942) and *Simocosmoceras* sp. = *Simocosmoceras pszczolkowskii* Myczyński, 1989 (Myczyński 1989, 1990) according to the biochronostratigraphic interpretation made by Villaseñor and Olóriz (2001; see also Parent 2001). Villaseñor and Olóriz (2001) first described the occurrence of this genus in Mexico, later identified as *Simocosmoceras pszczolkowskii apulcoensis* Villaseñor, Olóriz, González-Arreola, 2003 (Villaseñor et al. 2003).

In Mexico, there are data and interpretations in accordance with the hypotheses related to the model mentioned above (Olóriz 1985, 1990), compatible as well with interpretations in the palaeobiogeographical overview provided by Cecca (1999). Of special relevance are: (i) the single specimen of *Simoceras* cf. *S. volanense* (Oppel, 1863) reported by Verma and Westermann (1973) from Sierra de Catorce; (ii) the biochronostratigraphic interpretation of the encasing Virgatosphinctinae Beds in Olóriz et al. (1999); (iii) the interpretation of these deposits as related to the Early Tithonian flooding mentioned above (Olóriz 1992; Olóriz et al. 1996, 1999; Villaseñor et al. 2000b); (iv) the interpretation of the specimen of Sierra de Catorce as evidence of the occurrence of *S. aesinense* (Meneghini, 1885) in Mexico (e.g., Geyssant 1988; Cecca 1999; Olóriz et al. 1999; Villaseñor et al. 2000b), here reinterpreted as *P. aesinense* (Meneghini, 1885), an intermediate phenotype between subspecies *P. aesinense chignahuapense* (Cantú-Chapa, 1990) and *P. aesinense krantzense* (Cantú-Chapa, 1990); (v) the reinterpretation of the record of a microconchiate simoceratin in Puebla (Cantú-Chapa 1990) as *P. aesinense chignahuapense* (Cantú-Chapa, 1990) and its close relationships to earlier interpretations concluding in close *P. aesinense* (Meneghini, 1885) affinity or even belonging to the latter species (e.g., Cecca 1999, 2002a; Villaseñor et al. 2000a, b; Schweigert et al. 2002); (vi) the combined record of *Simocosmoceras* and simoceratins in the Mazatepec area (Villaseñor and Olóriz 2001; Villaseñor et al. 2003); and (vii) the record of *Pseudhimalayites steinmanni* (Haupt, 1907) and the simoceratin species *P. aesinense* (Meneghini, 1885) (Villaseñor and Olóriz 2004; see above for their combined record in Argentina). All this information evidences the inter-related occurrence of Early Tithonian floodings in the Americas and the occurrence of Tethyan simoceratin species, here interpreted at the genus level as belonging to *Pseudovolanoceras*.

Whereas Mexico-Caribbean records of simoceratins (*Pseudovolanoceras*) and *Simocosmoceras*, assembled or not with *Pseudhimalayites*, accord with the hypothesis of faunal

influence via the Hispanic Corridor, the record of *Pseudovolanoceras aesinense krantzense* (Cantú-Chapa, 1990) in Argentina, together with records of *Simocosmoceras*, *Pseudhimalayites*, and *Pseudolissoceras* within the *Pseudolissoceras zitteli* Biozone requires a more intricate configuration supporting the known palaeobiogeographic pattern of distribution of the species, or species complex, *Pseudovolanoceras aesinense* (Meneghini, 1885), in accordance with the assumed pattern of marine currents (e.g., Leanza and Olóriz 1987 for *Simocosmoceras*).

The palaeobiogeographical pattern known for American simoceratins accords with the model proposed by Olóriz (1985, 1990), which was later acknowledged by Cecca (1999) and is compatible with more recent overviews on palaeobiogeographical interpretations (e.g., Cecca 2002b). Accordingly, incursions of peripheral populations of widespread cephalopods species, here the case of *Pseudovolanoceras aesinense* (Meneghini, 1885), into American neritic shelves would have occurred when and where these were available during relative sea-level rises, regardless of their palaeogeographic location within the range of marine influence of Tethyan water-masses, but according to the pattern of marine currents (e.g., Olóriz et al. 1997, 1999, 2000; Villaseñor et al. 2003; Olóriz and Villaseñor 2006). Widespread species, or species complexes without relevant phenotype differences, would be subjected to metacommunity and metapopulation dynamics (formally first proposed for ammonites by Olóriz et al. 2006, and treated in depth by Olóriz and Villaseñor 2010), and fragmentation of bioeographic ranges would depend on environmental dynamics. Aside from expatriation, rare relevant post-mortem transportation, and their combination, (perhaps the case of the single specimen registered of species *V. schwertschlageri* [Schneid, 1915], which is allocated inside giant *Aspidoceras*, as noted by Schweigert et al. 2002), vicariancy (fragmentation) and/or temporary, ancillary, selective vicariance (e.g., Olóriz et al. 2008) better explains local records of low-swimming cephalopods showing multispecies assemblies containing a variable percentage in combining local (i.e., endemics) and Tethyan and/or Tethyan-like taxa (i.e., ubiquitous colonisers with persistent phenotype expression).

In this context, the explanation of Mexico-Caribbean records agrees with the role usually assumed for the Hispanic Corridor, but providing a regional example of the general dynamics, which supports the model proposed by Olóriz (1985, 1990) and its complement derived from information from present cephalopods (e.g., Olóriz and Villaseñor 2010). Hence, faunal expansion during flooding of neritic shelves forced phenotype deviation in simoceratin colonisers of Argentinean shelves (see Parent 2001 for *Pseudolissoceras*). Faunal capture resulting in subspeciation processes is here favoured to explain the occurrence of comparatively massive shells in *Pseudovolanoceras aesinense krantzense* (Cantú-Chapa, 1990), and other deviations such as those registered in eastern Mexico *P. aesinense chignahuapense* (Cantú-Chapa, 1990). Both of these cases reinforce the implications of Olóriz's (1985, 1990) model in terms of palaeobiologic re-

sponse to a palaeobiogeographic dynamics promoting in situ evolution (e.g., Olóriz and Villaseñor 1999 for potential Early Tithonian example of species flock in neritic north-central Mexico, and Olóriz et al. 2000 for a lower level phenotype influence in the same area). The Argentinean case reveals extreme phenotype expression, which cannot be related to hypermorphosis but rather to early innovation promoting massive shells without conclusive evidence, at present, of relative gigantism. Mexican records indicate phenotype deviation throughout the combination of heterochronic processes (acceleration) in microconchs, interpreted as resulting in allometric heterochrony (sensu McKinney 1988) since no precise information exists about the growth rate and age in these ammonites, and post-embryonic, late innovation.

The case-study could thus reveal early phases of selective vicariance owing to the coeval co-existence of new and ancestral forms in a restricted part of the biogeographic range of the latter, with possible niche subdivision (ecospace reorganisation) and species fragmentation inside a heterogeneous environmental/palaeogeographical complex.

On the basis of all the above, future research is encouraged to realise bed-by-bed sampling followed by palaeobiological and eco-evolutive interpretations of these ammonites in Mexico and Tethyan areas within the framework of a combined geo-biological approach.

Acknowledgements

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Appendix 1

Measurements of *Pseudovolanoceras aesinense chignahuapense* (Cantú-Chapa, 1990), *Pseudovolanoceras aesinense krantzense* (Cantú-Chapa, 1990), and European specimens of *Pseudovolanoceras aesinense* (Meneghini, 1885) (e.g., Santantonio, 1986; Cecca et al. 1981, 1986; Schweigert et al. 2002).

Horizons	Repository	D	U	Wh	U/D	Wh/D	PS/2	C
MT-2-21b	IGM 6085-2a	48.70	28.00	12.10	0.57	0.25	12	2
		36.50	21.80	9.00	0.60	0.25	11	1
	*	28.30	17.80	8.50	0.63	0.30	11	1
	*	22.50	13.70	5.00	0.61	0.22	11	
	*	18.20	9.50	4.10	0.52	0.23	12	
	*	10.70	5.00	3.00	0.47	0.28	14	
MT-2-21b	IGM 9541	37.30	19.60	9.20	0.53	0.25	–	3
	*	25.50	15.00	7.00	0.59	0.27	8	
	*	21.00	11.50	5.12	0.55	0.24	12	
MT-2-25	IGM 9543a	*52.00	–	–	–	–	–	
	*	43.60	26.40	10.40	0.61	0.24	12	
	*	33.90	19.70	8.20	0.58	0.24	–	
	*	21.00	11.50	4.60	0.55	0.22	11	
	*	13.00	6.30	3.20	0.48	0.25	13	
MTQ-11	IGM 9544	38.50	22.86	8.04	0.59	0.21	15	2
		33.00	19.47	7.34	0.59	0.22	15	2
		30.87	17.51	6.77	0.57	0.22	14	2
		27.40	15.34	6.40	0.56	0.23	14	
	*	24.70	14.31	6.30	0.58	0.26	15	1
	*	21.35	11.82	5.50	0.55	0.26	14	2
	*	18.50	10.22	4.30	0.55	0.23	15	1
	*	16.60	8.77	3.82	0.53	0.23	14	1
	*	14.63	7.93	3.40	0.54	0.23	14	2
	*	11.77	5.85	3.10	0.50	0.26	12	
	*	9.70	5.12	2.60	0.53	0.27	12	
	*	8.66	3.97	2.20	0.46	0.25	10	
	*	7.50	3.90	2.10	0.52	0.28	10	
	*	3.40	1.60	0.75	0.47	0.22	0	
	*	2.70	1.40	0.65	0.52	0.24	0	
	*	2.30	1.10	0.56	0.48	0.24	0	
	*	2.00	0.90	0.46	0.45	0.23	0	
	*	1.70	0.84	0.37	0.49	0.22	0	
MT-2-22b	IGM 9545a	41.60	23.20	10.70	0.56	0.26	14	2
	*	31.50	18.50	7.80	0.59	0.25	14	
	*	24.50	14.30	5.70	0.58	0.23	16	
	*	19.10	9.50	5.40	0.50	0.28	16	
MT-2-25	IGM 9546a	53.50	30.40	12.40	0.57	0.23	13	
	*	40.70	24.40	9.20	0.60	0.23	13	
	*	31.40	17.00	6.90	0.54	0.22	13	
	*	20.50	10.70	6.70	0.52	0.33	15	
MT-2-25	IGM 9546-2	53.50	33.20	12.50	0.62	0.23	–	
	*	35.10	19.20	8.70	0.55	0.25	–	
	*	20.70	11.10	5.10	0.54	0.25	15	
MT-2-22b	IGM 9547a	95.20	55.60	21.80	0.58	0.23	12	
	*	56.00	34.00	13.00	0.61	0.23	10	
	*	30.70	18.30	7.60	0.60	0.25	13	
	*	19.80	10.20	5.20	0.52	0.26	12	

Horizons	Repository	D	U	Wh	U/D	Wh/D	PS/2	C
MTQ 11	IGM 9551a	48.00	28.50	10.45	0.59	0.22	13	
		41.85	24.00	9.68	0.57	0.23	13	
	*	32.80	18.00	7.90	0.55	0.24	12	
	*	27.50	15.30	5.50	0.56	0.20	11	
	*	20.20	11.10	5.00	0.55	0.25	10	
	*	15.90	7.80	4.00	0.49	0.25	0	
	*	10.50	4.80	3.32	0.46	0.32	0	
MTQ 11	IGM 9552	23.12	13.36	6.01	0.58	0.26	–	
		18.67	10.90	4.30	0.58	0.23	–	
		14.44	5.60	3.68	0.39	0.25	–	
MTQ 11	IGM 9553a	36.70	20.98	7.71	0.57	0.21	–	
		30.26	14.70	8.60	0.49	0.28	–	
		21.50	11.22	5.84	0.52	0.27	–	
		14.77	5.51	4.19	0.37	0.28	–	
MTQ 11	IGM 9554	*89	–	–	–	–	–	
		81.83	41.86	20.02	0.51	0.24	–	
		60.63	31.94	16.66	0.53	0.27	–	
		58.00	32.34	15.70	0.56	0.27	12	
MTQ 11	IGM 9555	74.15	47.39	15.69	0.64	0.21	10	
	*	47.50	27.28	13.03	0.57	0.27	11	
Loc. 40C	IGM 2764	73.00	44.40	16.70	0.61	0.23	12	1
	*	57.90	34.00	11.40	0.59	0.20	13	
	*	40.50	29.00	10.00	0.72	0.25	13	
	*	36.50	25.00	7.50	0.68	0.21	14	
	*	18.70	11.00	4.80	0.59	0.26	14	
Cantú-Chapa	Ac-1001	41.30	26.30	7.50	0.64	0.18	13	1
	**	34.28	19.85	7.14	0.58	0.21	11	2
	**	29.71	17.85	5.85	0.60	0.20	11	2
	**	21.70	11.70	5.14	0.54	0.24	11	1
Cuba	USNM103389	11.46	5.66	2.93	0.49	0.26	12	
	**	9.37	5.11	2.45	0.55	0.26	13	
	**	8.00	4.22	2.11	0.53	0.26	13	
	**	6.82	4.23	1.87	0.62	0.27	12	
Argentina	GPIBO 1	86.60	57.80	16.50	0.67	0.19	10	
		69.70	44.70	13.20	0.64	0.19	10	
	*	44.20	30.50	9.50	0.69	0.21	11	
	*	32.20	18.10	8.00	0.56	0.25	10	
	*	21.40	11.70	5.00	0.55	0.23	11	
	*	13.50	6.20	4.00	0.46	0.30	10	
Italy	NS3Col 11	51.00	31.00	10.50	0.61	0.21	11	
	**	30.85	18.61	7.97	0.60	0.26	14	
	**	25.00	14.09	6.70	0.56	0.27	14	
	**	23.90	13.67	6.22	0.57	0.26	14	
	**	20.22	10.42	5.31	0.52	0.26	13	
	**	13.29	6.38	3.72	0.48	0.28	11	
	**	9.78	5.55	2.65	0.57	0.27	10	
	**	8.93	4.25	2.65	0.48	0.30	10	
	NS3Col 12	33.00	19.30	8.60	0.58	0.26	15	
	**	31.30	19.00	6.90	0.61	0.22	15	
	**	26.00	15.00	6.00	0.58	0.23	16	
	**	15.50	8.00	4.50	0.52	0.29	12	
	NS3Col 15	37.00	23.00	8.00	0.62	0.22	13	

Horizons	Repository	D	U	Wh	U/D	Wh/D	PS/2	C
Italy	**	34.00	22.00	7.00	0.65	0.21	13	
	**	30.00	18.00	6.00	0.60	0.20	15	
	**	22.00	13.00	5.00	0.59	0.23	16	
	**	18.00	10.00	4.00	0.56	0.22	15	
	**	12.00	6.00	3.00	0.50	0.25	12	
	NS3Col 16	28.00	16.50	6.40	0.59	0.23	17	
		25.40	14.20	6.00	0.56	0.24	18	
	**	23.00	11.70	5.40	0.51	0.23	17	
	**	19.70	9.50	5.20	0.48	0.26	16	
	**	13.00	5.70	4.40	0.44	0.34	15	
	NS3Col 20	46.30	28.30	9.40	0.61	0.20	12	
	**	41.00	24.00	10.00	0.59	0.24	12	
	**	29.00	16.50	7.00	0.57	0.24	14	
	**	18.50	10.00	5.00	0.54	0.27	11	
	**	10.00	4.00	4.00	0.40	0.40	9	
	NS3Col 23	89.00	50.00	18.30	0.56	0.21	11	
	**	77.00	43.00	13.00	0.56	0.17	11	
	**	56.00	32.00	11.00	0.57	0.20	10	
	**	47.00	27.00	9.50	0.57	0.20	9	
	Rin 1	93.80	53.00	22.60	0.57	0.24	12	
	**	81.00	46.00	19.00	0.57	0.23	12	
	**	74.70	42.80	17.00	0.57	0.23	12	
	**	62.10	34.00	15.00	0.55	0.24	11	
	CCS 13	82.00	49.00	17.50	0.60	0.21	12	
	**	67.00	41.00	14.50	0.61	0.22	11	
	**	53.00	32.00	12.00	0.60	0.23	11	
	**	39.00	25.00	8.50	0.64	0.22	11	
	CT31.3	50.86	32.13	10.40	0.63	0.20	12	
	**	32.13	18.53	7.56	0.58	0.24	12	
	**	24.00	12.93	6.66	0.54	0.28	13	
	**	19.93	8.60	5.60	0.43	0.28	13	
	CT31.4	43.57	28.21	10.71	0.65	0.25	11	
	**	25.71	15.71	6.42	0.61	0.25	11	
Spain	BSPG-3	81.50	59.00	18.50	0.72	0.23	9	
	**	80.00	52.00	17.00	0.65	0.21	–	1
	**	59.00	35.00	14.00	0.59	0.24	8	
	**	52.00	29.50	8.50	0.57	0.16	8	
	BSPG-5	64.00	38.00	14.50	0.59	0.23	–	
	**	40.00	24.00	9.00	0.60	0.23	–	
	**	31.00	18.00	7.00	0.58	0.23	15	
	**	24.00	13.00	6.00	0.54	0.25	16	
	**	22.00	12.00	5.00	0.55	0.23	16	
	**	21.00	11.50	4.50	0.55	0.21	15	
	**	16.00	9.50	4.00	0.59	0.25	14	
	SMNS 64663	91.00	47.00	19.00	0.52	0.21	9	
	**	82.00	43.00	18.50	0.52	0.23	9	
	**	71.50	42.50	16.00	0.59	0.22	10	
	**	62.00	39.00	13.50	0.63	0.22	10	
	**	44.00	28.00	9.00	0.64	0.20	11	

Appendix 2

Annotated synonymy list for *Pseudovolanoceras aesinense* (Meneghini, 1885) including the geographic subspecies mentioned in text; exclusive for citations with illustrated specimens.

Pseudovolanoceras aesinense (Meneghini, 1885)

1870 *Simoceras volanense* Oppel, 1863; Zittel 1870: 95, pl. 32 [supplement: pl. 8]: 7 [macroconch; only outer whorls?], non 8, 9. From Lower Tithonian pelagic cephalopod limestone in central Apennines (Monte Catria, Marche), Italy.

1885 *Simoceras* cfr. *volanense* Oppel, 1863 sp. (var. *aesinense* nov.); Meneghini 1885: 376, pl. 20: 4a–d [macroconch]. From Lower Tithonian pelagic cephalopod limestone in central Appenines, Marche, Italy.

1928 *Simoceras* aff. *volanense* Oppel, 1863; Krantz 1928: 13, pl. 3: 7 [macroconch]. From the Lower Tithonian, *Pseudolissoceras ziteli* Chronozone (= *Semiformiceras semiforme/Haploceras verruciferum* Chronozone) calcareous horizons/concretion in the Vaca Muerta Fm., southern Mendoza, Argentina.

1942 *Simoceras* sp. juv. cf. *S. volanense* (Oppel, 1863); Imlay 1942: 1445, pl. 3: 2, 3 [juvenile, incomplete micro- or macroconch]. From the Lower Tithonian black to gray, siliceous, shaly and locally sandy Viñales Limestone Fm. in Santa Clara Provinve, Central Cuba.

1967 *Aspidoceras phoenicium* Gemmellaro, 1871; Colacicchi and Pialli 1967: 184–186, figs. 2e, 3b [macroconchs]. From Lower Tithonian, fossil rich interval (lumachella) in Monte Cucco, central Appenines; Umbria, Italy.

1970 *Simoceras* sp. group of *S. volanense* (Oppel, 1863); Bernoulli and Renz 1970: 600, pl. 5: 4–6 [macroconch]. From Lower Tithonian condensed, pelagic cephalopod limestone in Louros Valley, western Greece.

1973 *Simoceras* cf. *S. volanense* (Oppel, 1863); Verma and Westermann 1973: 196, pl. 37: 2a, b [macroconch]. From phosporitic, silty limestones (Virgatosphinctinae Beds) in Sierra de Catorce, north-central Mexico.

1977 *Aspidoceras phoenicium* Gemmellaro, 1871; Nicosia and Pallini 1977: pl. 2: 9 [macroconch]. From Lower Tithonian cephalopod limestones in central Appenines, Umbria-Marche, Italy.

1978 *Simoceras* (*Simoceras*) *volanense schwertschlageri* (Schneid, 1915); Olóriz 1978: 224, pl. 20: 3?, 6? (partim) [macroconchs]. From the upper *Haploceras verruciferum* Chronozone nodular limestone and the uppermost *Haploceras verruciferum*-to-lowermost *Richterella richteri* chronozones cephalopod-rich pelagic limestone (condensed horizon?) in the Middle and Internal Subbetic (southern Spain), respectively.

1983 *Simoceras* (*Simoceras*) *volanense* (Oppel, 1863); Cecca et al. 1983: 119, pl. 3: 1a, b [macroconch]. From the Lower Tithonian pelagic cephalopod limestone in central Appenines, Marche, Italy.

1984 *Simoceras* (*Simoceras*) *volanense* (Oppel, 1863); Rossi 1984: 115, pl. 35: 12 [macroconch]. From the Lower Tithonian cephalopod-rich pelagic limestone (Grigio Ammonitico) in central Appenines, Umbria-Marche, Italy.

1986 *Simoceras aesinense* Meneghini, 1885; Santantonio 1986: 15, pl.

1: 1–4 [figs. 1–3 macroconchs; fig. 4 microconch], pl. 2: 1–4, 6. [figs. 2, 3 and 6 macroconchs; figs. 1, 4 microconchs]. From Lower Tithonian *S. semiforme/H. verruciferum* Chronozone pelagic cephalopod limestones in central Appenines and nodular limestones in southern Alps Italy.

1986 *Simoceras aesinense* Meneghini, 1885; Cecca et al. 1986: 196, pl. 7: 1, 3 [macroconchs]. Lower Tithonian *S. semiforme/H. verruciferum* Chronozone pelagic cephalopod limestone in central Apeninnes, Marche, Italy.

1987 *Simoceras* aff. *volanense* (Oppel, 1863); Fözy 1987: pl. 1: 1 [= Fözy 1988: pl. 10: 2; macroconch]. From Lower Tithonian *S. semiforme/H. verruciferum* Chronozone red nodular limestone in Bakony Mountains, Hungary.

1988 *Volanoceras* (*Volanoceras*) *aesinense* (Meneghini, 1885); Fözy 1988: 73, pl. 8: 3, 4 [macroconchs; fig. 4 = Fözy 1990: pl. 3: 2], pl. 9: 1–3 [macroconchs], pl. 10: 2 [= Fözy 1987: pl. 1: 1; macroconch]. From Lower Tithonian *S. semiforme/H. verruciferum* Chronozone red nodular limestone in the Bakony and Gerecse Mountains, Hungary.

1990 *Volanoceras* (*Volanoceras*) *aesinense* (Meneghini, 1885); Fözy 1990: 327, pl. 3: 2 [= Fözy 1988: pl. 8: 4; macroconch]. From Lower Tithonian *S.semiforme/H. verruciferum* Chronozone red nodular limestone in Bakony Mountains, Hungary.

1990 *Volanoceras chignahuapense* Cantú-Chapa, 1990: 41, fig. 2a–d [microconch]. From Lower Tithonian loosed calcareous concretion in the Tamán Fm., Sierra Madre, eastern Mexico].

?1994 *Volanoceras* cf. *aesinense* (Meneghini, 1885); Fözy et al. 1994: 156, 158, pl. 2: 16 [fragmented nucleus of inconclusive interpretation]. From Lower Tithonian *S. semiforme/H. verruciferum* Chronozone, crinoid-ammonite coquina packestone (Hierlatz limestone) in the Gerecse Mountains, Hungary.

1998 *Simoceras aesinense* Meneghini, 1885; Caracuel et al. 1998: 240, 244, pl. 2: 4 [macroconch]. Lower Tithonian *S. semiforme/H. verruciferum* Chronozone red nodular limestone in the Venetian Alps, Italy.

2002 *Volanoceras aesinense* (Meneghini, 1885); Schweigert et al. 2002: 8, pl. 1: 1–4 [figs. 1–3 macroconchs; fig. 4 fragmented nucleus of macro- or microconch]. Lower Tithonian *S. semiforme/H. verruciferum* Chronozone red nodular limestone in External Subbetic (southern Spain), pelagic cephalopod limestone in central Apennines (Italy), and the Rogoźnik Coquina Mb. of the Czorsztyn Fm. in Polish Carpathians (Poland).

2002 *Volanoceras krantzense* Cantú-Chapa, 1990; Schweigert et al. 2002: 9, pl. 2: 1, non 2 (= fig. 1 in the plate caption) (partim) [macroconchs]. From the Lower Tithonian, *Pseudolissoceras zitteli* Chronozone (= *S. semiforme/H. verruciferum* Chronozone) calcareous horizon/concretion in the Vaca Muerta Fm., southern Mendoza, Argentina.