NEW SPECIES OF *FRANCHIA* AND *PROTOZIGZAGICERAS* (AMMONOIDEA, MIDDLE JURASSIC): THE PHYLETIC ORIGIN OF ZIGZAGICERATINAE

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Abstract: Three genera and seven species belonging to the subfamily Zigzagiceratinae (family Perisphinctidae) are described from the Lower Bathonian of France and Saudi Arabia. Intraspecific dimorphism is recognized. A revision of the genus *Franchia* proposed by Sturani (1967), based on the syntypes and new specimens from south-east France, is presented. *Franchia arkelli* Sturani, *Franchia subalpina* sp. nov., *Protozigzagiceras torrensi* (Sturani), *Protozigzagiceras tethycum* sp. nov., *Protozigzagiceras flexum* sp. nov. and *Protozigzagiceras densum* sp. nov. are described from the Digne–Castellane region of south-east France. *Megazigzagiceras subarabicum*, gen. et sp. nov. is described from the Dharma region of Saudi Arabia. The successive Early Bathonian species of *Franchia* and *Protozigzagiceras* herein identified in West Tethyan areas, as members of the Mediterranean–Caucasian Subrealm, formed lasting separate peramorphoclines characterized by increasing hydrodynamic coiling of the shell. In contrast, rapid proterogenesis originated and diversified the earliest Bathonian zigzagiceratin lineages, giving paedomorphic members, commonly neotenic and more scarcely progenetic. *Procerites–Siemiradzkia* seems to be the oldest zigzagiceratin member in the French Subalpine, Iberian and Lusitanian basins, branched off by paedomorphosis from leptosphinctins at the Bajocian–Bathonian transition. The Mediterranean–Caucasian genera *Franchia*, *Zigzagiceras*, *Zigzagites* and *Wagnericeras* branched from successive species of *Protozigzagiceras*, in turn, a direct derivative of *Procerites*. The oldest lineages of the clade Zigzagiceratinae evolved by iterative, rapid, paedomorphic changes and additional, lasting, peramorphic modifications during the Early Bathonian.

Key words: Ammonites, Perisphinctidae, Western Tethys, Ethiopian Province, Bathonian Global Stratotype Section and Point.

THE Early Bathonian genera *Franchia* and *Protozigzagiceras* characterize the Zigzag Zone, in particular the Parvum and Macrescens subzones of the French Subalpine Basin (Fig. 1A), although they are scarce components of the ammonite fossil assemblages (<5.0 per cent). The accurate biochronostratigraphy of these Perisphinctidae is crucial for calibration of the basal Bathonian Zigzag Zone and correlation of the Bathonian Global Stratotype Section and Point (GSSP), currently defined in the Ravin du Bès Section, Bas Auran area (Fig. 1B, Fernandez-Lopez *et al.* 2009*b*).

The specimens belonging to the subfamily Zigzagiceratinae studied herein have been collected, bed-by-bed, in several sections from the 'Marno-calcaires à *Cancellophycus*' Formation in south-east France, during the last five decades. Several tens of *in situ* Lower Bathonian *Franchia* and *Protozigzagiceras* from Digne–Castellane region have been identified to species level. Most of these specimens were determined by Sturani (1967) as *Franchia arkelli* and *Zigzagiceras torrensi*, assuming a high variability of sutural complexity in *Franchia* and of zigzag development in *Zigzagiceras*. Sturani (1967) and Torrens (1987) established the biochronostratigraphical foundations for the Lower Bathonian ammonoid succession of Digne–Castellane region. Complementary biostratigraphical information on Zigzagiceratinae was developed in graduate theses by Innocenti (1975), Puma (1975) and Romeo (1999). Innocenti *et al.* (1990) proposed the boundary stratotype of the Bathonian Stage based on a Bas Auran section. Fernandez-Lopez (2007) presented a taphonomic analysis of the ammonoid succession on the Bas Auran area at the Bajocian–Bathonian boundary and the palaeoenvironmental interpretation in terms of sequence stratigraphy. Fernandez-Lopez *et al.* (2007) published new data about the youngest members of the Bigotitinae and the oldest members of the Zigzagiceratinae,

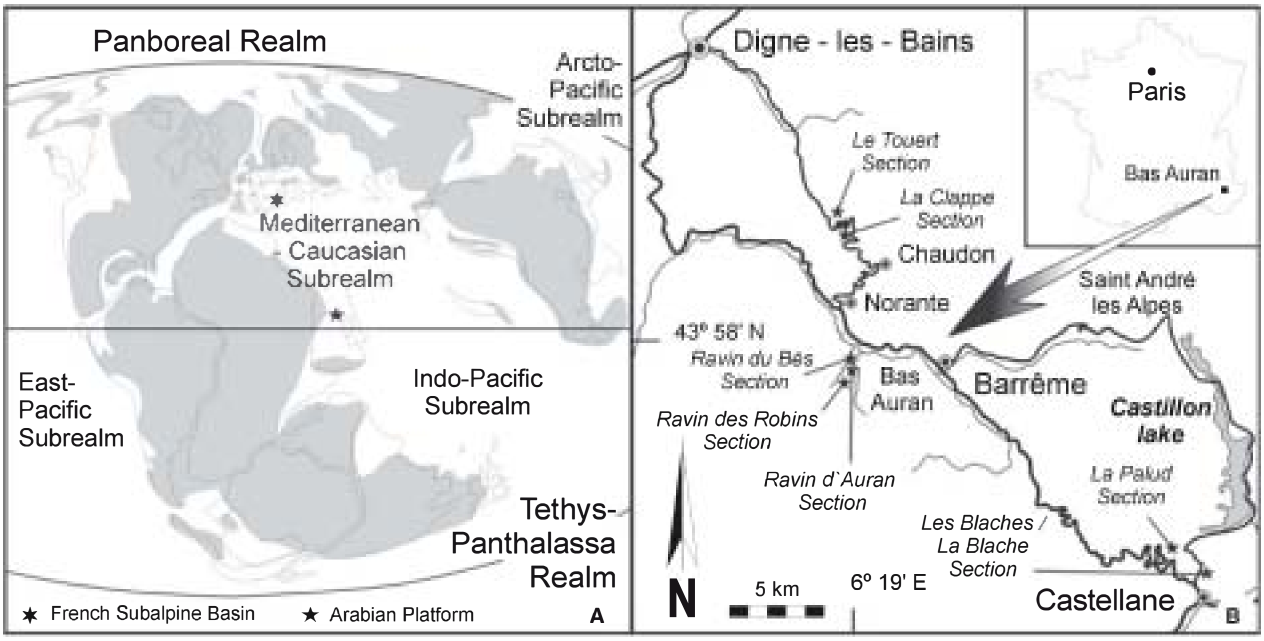

FIG. 1. Geographical positions of the localities mentioned in text. A, palaeogeographical position of the French Subalpine Basin in relation to the Arabian Platform during the Early Bathonian; palaeogeography modified from Fernandez-Lopez *et al.* (2009*b*), and Golonka (2011); palaeobiogeographical units according to Westermann (2000*b*). B, location map of the stratigraphical sections in the Digne–Castellane region (SE France).

of biochronostratigraphical importance for the subdivision and correlation of the basal Bathonian Zigzag Zone. Pavia *et al.* (2008) revised new information on the ammonoid biozonation in the Bas Auran area. Fernandez-Lopez *et al.* (2009*a*) formally proposed the Rabin du Bès Section as the GSSP of the Bathonian, and synthesized the regional biochronostratigraphical scales available for the Bajocian–Bathonian boundary. The Bathonian GSSP in the Ravin du Bès Section was approved by the International Commission of Stratigraphy (ICS) in June 2008 and ratified by the International Union of Geological Sciences (IUGS) in July 2008 (Fernandez-Lopez *et al.* 2009*b*).

The aims of this study were: (1) to provide a revision of the genus *Franchia* proposed by Sturani (1967) based on the syntypes and new specimens from south-east France, giving emphasis to the dimorphism of Zigzagiceratinae and its possible phyletic relationships with Leptosphinctinae or Bigotitinae; and (2) to interpret the palaeobiogeographical patterns and evolutionary trends of the oldest Zigzagiceratinae. The main new contribution concerns the phylogenetic relationships between Early Bathonian lineages of Zigzagiceratinae and the origination of the clade.

SPECIMEN REPOSITORY AND ABBREVIATIONS

Institutional abbreviations. The material described herein is housed at the collection of the Museo di Geologia e Paleontologia, Università di Torino (Italy), currently stored in the Dipartimento di Scienze della Terra. Specimens are marked with the acronym PU and a sequential registration number. Source of sampling, section and bed number indicated by abbreviations: BA, sections of the Bas Auran area (lithostratigraphical column of Sturani 1967); RB, Ravin du Bès Section; RA, Ravin d'Auran Section; RR, Ravin des Robines. The specimen from Dharma, Saudi Arabia, of Figure 19, is housed at the Claude-Bernard University of Lyon (France).

Ammonite abbreviations and measurements. M, macroconch; m, microconch; D, maximum shell diameter; H, whorl height; H/D, ratio of whorl height to diameter; W, whorl width; W/D, ratio of whorl width to diameter; U, umbilical diameter; U/D, ratio of umbilicus to diameter; W/H, ratio of whorl width to whorl height; Ni/2, internal ribs per half whorl; Ne/2, external ribs per half whorl; I, ratio of external to internal ribs. The measurements presented in Fernandez-Lopez and Pavia (2013) are given in mm and were measured at maximum shell diameter.

SYSTEMATIC PALAEONTOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: http://zoobank.org/References/F5576F2D-3C69-4CED-A6FD-1A4D677814CF

Class CEPHALOPODA Cuvier, 1798
Order AMMONITIDA Fischer, 1882
Superfamily PERISPHINCTOIDEA Steinmann, 1890
Family PERISPHINCTIDAE Steinmann, 1890

Remarks. The family Perisphinctidae is characterized by planulate shells, with retracted suspensive-lobe and egressive coiling at maturity, differentiated in two dimorphic groups: lappetted microconchs, with short body chamber ribbed to the end, and simple-aperture macroconchs with smooth or distantly ribbed, long body chamber (near 360 degrees; Lominadze *et al.* 1993; Shevyrev 2006; Page 2008; Howarth 2013).

Subfamily ZIGZAGICERATINAE Buckman, 1920

[as Zigzagiceratidae Buckman, 1920, TA-III, p. 30] [= Zigzagiceratinae Schindewolf, 1925, p. 319, 1962, p. 520; =Siemiradzkiinae Westermann, 1958, p. 75; = Gracilisphinctinae Beznosov, 1982, p. 54]

Remarks. The subfamily Zigzagiceratinae comprises micro- and macroconchs of small to large size (generally 30–600 mm), planorbicones to discocones. The whorls increase by segments between more or less marked pseudoconstrictions or constrictions. Depressed whorl section on the inner and middle whorls becomes rounded elliptical and more compressed on the outer whorls. The subfamily is mainly characterized by pseudocoronate early whorls that may be followed by a perisphinctoid stage, with blunt, bifurcate or trifurcate costae, lacking smooth band or groove on external region. The pseudocoronate stage, so-called zigzag-stadium or zigzag-ornament, may be composed of parabolic nodes, parabolic ribs, constrictions or pseudoconstrictions, megastriae, sigmoid ribs of greater strength upflank, and sharp ribs of variable strength and spacing (d'Orbigny 1846 in 1842–1851, pl. 129, figs 9–11; Siemiradzki 1898–1899; Buckman 1920 in 1909–1930, pl. 153; Arkell *et al.* 1957; Arkell 1958 in 1951–1958, pl. 20–22; Sturani 1967; Hahn 1969, pl. 2, figs 3–5, pl. 9, fig. 3; Mangold 1971; Torrens 1987). These ornamental features are due to resorption of the shell or local perturbation of the apertural growth field controlling the coiling and further growth of the shell during early-ontogenetic, immature or preadult growth stages (Bucher *et al.* 1996; Hammer and Bucher 2005; Doguzhaeva 2012). The evolutionary appearance of a new morphological feature in early ontogeny, such as the so-called zigzag-stadium, is a characteristic of the multiple phyletic lineages of Early Bathonian Zigzagiceratinae, distinguishing them from those of Leptosphinctinae and Bigotitinae. This criterion also corroborates the dimorphism of each phyletic lineage and allows the development of a primarily phylogenetic classification (Callomon in Donovan *et al.* 1981; Mangold 1988; Fernandez-Lopez *et al.* 2007).

The subfamily Zigzagiceratinae is known in the Tethys–Panthalassa Realm, mainly from the Bathonian. In Europe, it is a common component of Lower Bathonian assemblages (Mangold 1997). In North America, members of this subfamily are known from deposits of the Upper Bajocian – Lower Bathonian transition as relatively scarce components of certain ammonite assemblages (Westermann 1992; Evenchick *et al.* 2010). Very scarce records are known from Iran, Saudi Arabia, Chile, Argentina and Russia (Seyed-Emami *et al.* 1985, 1989; Poulton *et al.* 1992; Gröschke and von Hillebrandt 1994; Riccardi and Westermann 1999; Beznosov and Mitta 2000; Sey *et al.* 2004; Enay *et al.* 2007; Shams and Seyed-Emami 2010). The stratigraphical distribution of the oldest genera of Zigzagiceratinae in Bas Auran area (Ravin d'Auran and Ravin du Bès sections) is shown in Figure 2.

The diverse ontogenetic patterns of lateral ribs and megastriae in the zigzag-stadium among Early Bathonian Mediterranean–Caucasian zigzagiceratins correspond to an ordered multistate character that may be coded in the following three categories:

1. Zigzag-state 1: shortly developed in the nucleus up to a few mm in diameter, composed of proradiate to subradiate, straight to slightly bent ribs of variable strength and spacing (e.g. present in *Procerites* and *Siemiradzkia*; Fig. 3; Sturani 1967, pl. 18, fig. 3; Hahn 1969, pl. 4, fig. 4, pl. 9, fig. 4).
2. Zigzag-state 2: relatively well developed in the inner and intermediate whorls of the phragmocone (at least in the microconchs), firstly composed of proradiate to subradiate, straight to slightly bent ribs of variable strength and spacing; then appear proradiate to subradiate, sigmoid ribs of greater strength upflank and variably spaced; and finally with occasional proradiate to subradiate parabolic ribs of variable spacing that pass over the venter radially or with a gentle forward inclination (e.g. in *Franchia* and *Protozigzagiceras*; Fernandez-Lopez *et al.* 2007, figs 10–12).
3. Zigzag-state 3: developed in the phragmocone, and body chamber of the microconchs, firstly composed of proradiate to subradiate sigmoid ribs, of variable strength and spacing and of greater strength upflank and sharp, parabolic ribs; later, subradiate to rursiradiate, distant and sharp, parabolic ribs, projecting sharply forward on ventrolateral shoulder, polyfurcate and bent forward over the venter (e.g. in *Zigzagiceras* and *Procerozigzag*; Arkell 1958 in 1951–1958, pl. 20–22; Hahn 1969, pl. 2, figs 3–5, pl. 9, fig. 3).

The style of ribbing interpreted by Sturani (1967) as of *Zigzagiceras*, which passes through a stage transitional to *Siemiradzkia* before the parabolic nodes fade out, corresponds to the zigzag-state 2 herein distinguished. Accord-

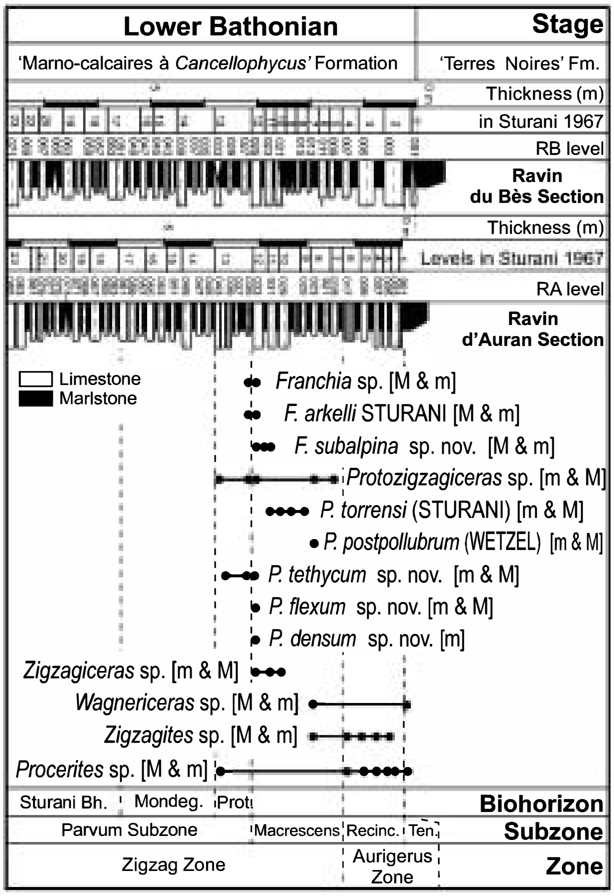

FIG. 2. Stratigraphical distribution of Lower Bathonian Zigzagiceratinae (*Franchia*, *Protozigzagiceras*, *Zigzagiceras*, *Wagnericeras*, *Zigzagites* and *Procerites*) in Ravin d'Auran and Ravin du Bes sections (France) according to the systematic revision presented in this paper. The range lines of the genera display the occurrence of fragmentary specimens of undeterminable species and their stratigraphical constancy through the sections. Logs from Fernandez-Lopez (2007) and Pavia *et al.* (2008). Standard chronostratigraphical zonation from Pavia *et al.* (2008) and Fernandez-Lopez *et al.* (2009*a*, *b*). For location of sites, see Figure 1B.

ing to the biochronostratigraphical information obtained in French Subalpine, Iberian and Lusitanian basins (Fig. 2; Fernandez-Lopez 2000; Fernandez-Lopez *et al.* 2007, 2009*a*; Pavia *et al.* 2008), these ontogenic modifications of zigzag-states in Early Bathonian zigzagiceratins of the western Tethys represent successive, derived or apomorphic conditions (Gould 1977, 2002; Dommergues *et al.* 1989; Dommergues 1990; Landman *et al.* 1991; Davis *et al.* 1996; Guex *et al.* 2003; Guex 2006). Therefore, these three early ontogenic, zigzag-states identified in the clade Zigzagiceratinae represent chronostratigraphically successive, apomorphic structures, for simplicity respectively characterized by: (1) straight ribs of variable strength; (2) sigmoid ribs of variable strength and spacing; and (3) distant, sharp, parabolic ribs.

On the basis of the syntypes of *Franchia* studied by Sturani (1967) and new specimens from south-east France, as well as a specimen from Saudi Arabia mentioned by Enay and Mangold (1994, Enay *et al.* 1987), seven species and three genera are described and interpreted below, belonging to *Franchia*, *Protozigzagiceras* and *Megazigzagiceras*. The genera of Zigzagiceratinae mentioned in text are listed in Table 1.

Genus FRANCHIA Sturani, 1967

Type species. Zigzagiceras (*Franchia*) *arkelli* Sturani, 1967 (p. 52, pl. 16, fig. 5, pl. 18, figs 2, 4), by monotypy.

Type level. Lower Bathonian, Zigzag Zone, Macrescens Subzone. Level BA12 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani 1967) and level RA033 of Ravin d'Auran Section (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran.

Type region. Alpes de Haute Provence (Bas Auran and Chaudon), south-east France.

Diagnosis. Conchs of small or medium size (40–260 mm). Moderately evolute to moderately involute planorbicones. Zigzag-state 2 developed in the phragmocone, firstly composed of proradiate to subradiate ribs of variable strength and spacing; then appear proradiate to subradiate, sigmoid ribs of greater strength upflank with variable spacing; and finally, occasional proradiate to subradiate, sharp, parabolic ribs of variable spacing. Coarse and blunt costae generally bifurcate. Relatively simple suture line, with broad lateral lobe.

Remarks. Franchia has been regarded as macroconchiate with a simple peristome. The counterpart microconch of *Franchia*, with lappets, is described here for the first time. Besides the type species, a new species is described and interpreted below. *Franchia* [M & m] is closely homeomorphic with some Lower Bathonian *Bigotites* Nicolesco [M & m] (1918; type species: *Bigotella petri* Nicolesco, 1917, p. 167, pl. 1, figs 4–5), especially in the coiling, the segmentary development of the whorls, the prominent primary ribs and the relatively simple suture line, but display zigzag-state 2. Other Early Bathonian Mediterranean–Caucasian macroconchiate zigzagiceratins display more complex suture lines. The leptosphinctins *Planisphinctes* Buckman [m] (1922; type species: *P. planilobus* Buckman, 1922 in 1909–1930, TA-IV, pl. 327), *Lobosphinctes* Buckman [M] (1923; type species: *L. intersertus* Buckman, 1923 in 1909–1930, TA-V, pl. 447) and *Phaulozigzag* Buckman [m] (1926 in 1909–1930; type species: *Phaulozigzag phaul-*

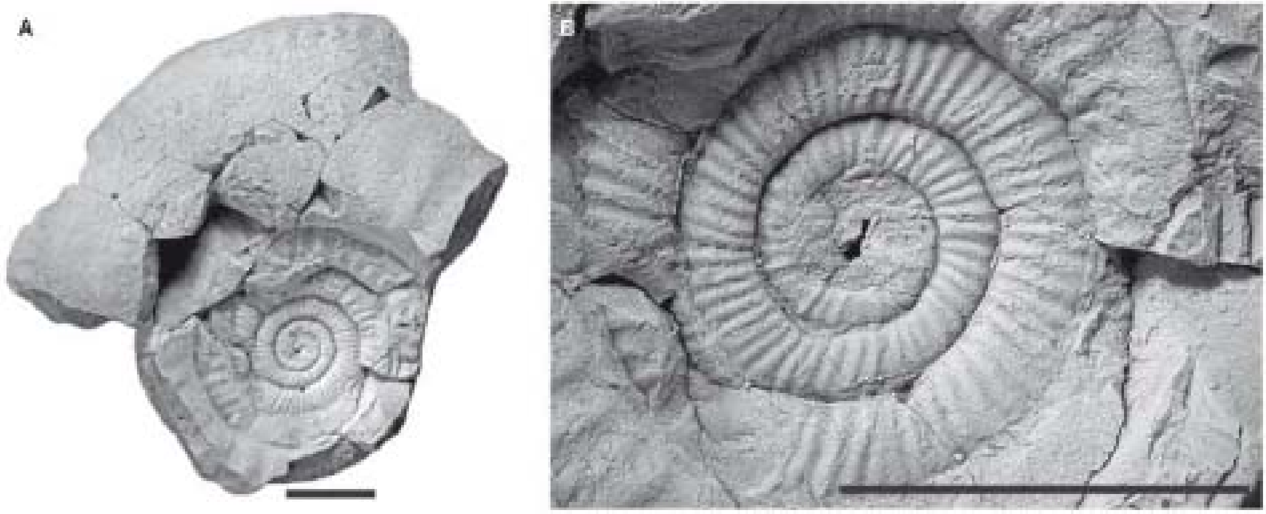

FIG. 3. *Procerites* sp. [M]. A, left-side view of incomplete, macroconch phragmocone; specimen PU112320, level BA12 or BA13 in Sturani (1967) and RR033 or RR035 in Pavia *et al.* (2008), Ravin des Robins Section, Bas Auran; lowest Macrescens Subzone or uppermost Parvum Subzone (Protozigzagiceras Biohorizon), Zigzag Zone. B, detail of the inner whorls showing a short stadium of proradiate to subradiate ribs of variable strength and spacing, up to a few mm in diameter. On this and following figures, all the specimens were whitened with magnesium oxide prior to photography. Scale bars represent 10 mm.

TABLE 1. Genera of Zigzagiceratinae mentioned in text.

Procerites Siemiradzki, 1898 [type, *Procerites procerus* Schloenbach, 1865; SD Buckman, 1914 (ICZN opinion 301)]
[= *Siemiradzkia* Hyatt, 1900, p. 582 (type, *Ammonites bakeriae* d'Orbigny, 1847; OD)]
Zigzagiceras Buckman, 1902, p. 7 [type, *Ammonites zigzag* d'Orbigny, 1846; OD]
[= *Procerozigzag* Arkell, 1953, p. 37 (type, *Zigzagiceras crassizigzag* Buckman, 1892; OD)]
Wagnericeras Buckman, 1921, p. 33 [type, *Ammonites wagneri* Oppel, 1857; OD]
Zigzagites Buckman, 1922, pl. 301 [type, *Zigzagites imitator* Buckman, 1922; OD]
Franchia Sturani, 1967, p. 32 [type, *Franchia arkelli* Sturani, 1967; OD]
Epizigzagiceras Frebold, in Frebold & Tipper 1973, p. 1119 [type, *Epizigzagiceras evolutum* Frebold, 1973; OD]
Protozigzagiceras Fernandez-Lopez *et al.*, 2007, p. 396 [type, *Zigzagiceras torrensi* Sturani, 1967; OD]
Megazigzagiceras Fernandez-Lopez & Pavia, gen. nov. [type, *Megazigzagiceras subarabicum* Fernandez-Lopez & Pavia, gen. et sp. nov.; OD]

omorphus Buckman, 1926 in 1909–1930, TA-VI, pl. 643) lack zigzag-stadium and display complex suture lines. *Procerites* Siemiradzki [M] (1898, p. 78; type species: *P. procerus* Schloenbach, 1865, by subsequent designation of Buckman 1914 and Opinion 301 of the International Commission on Zoological Nomenclature) and *Siemiradzkia* Hyatt [m] (1900, p. 582; type species *Ammonites bakeriae* d'Orbigny, 1847 in 1842–1851, p. 424, pl. 149, fig. 1) show zigzag-state 1 and a more complex suture line.

Sibirjakova (1961, p. 50, pl. 6, figs 1–2) described a new species *Procerites quenstedti* on the basis of two specimens from the 'Upper Bathonian sandstones' of Great Balkhan (Turkmenistan), but referred this species to *Ammonites gervillei grandis* Quenstedt (1886 in 1886-1887, p. 514, pl. 64, fig. 9 only, not figs 4–8, 10–12). Later, Beznosov described *Franchia quenstedti* (Sibirjakova; in Beznosov and Mitta 1993, p. 112) on the basis of five specimens (1 specimen figured in Beznosov and Mitta 1993, pl. 13, fig. 1), from the Lower Member of the Meulam Formation (Lower Bathonian, Zigzag Zone) also from Great Balkhan ridges, and six specimens of *Franchia* aff. *quenstedti* from the Upper part of Meulam Formation (also Zigzag Zone; in Beznosov and Mitta 1993, pl. 13, fig. 6). Beznosov wrote (in Beznosov and Mitta 1993, p. 113) that Sibirjakova had not selected a holotype and he designated as lectotype the specimen from Sibirjakova, 1961, pl. 6, fig. 2. Also, Beznosov noted that the indicated picture of Quenstedt (1886, pl. 64, fig. 9) is a representative of the Lower Bajocian genus *Emileia*. Later, Mitta (in Beznosov and Mitta 2000, p. 61) remarked that, according to the International Code (International Commission on Zoological Nomenclature 1999), the indication of Sibirjakova (1961) is valid as holotype identification for Quenstedt's specimen (i.e. *Emileia quenstedti* (Sibirjakova)), so that the species *F. quenstedti* is subsumed in the new name *Franchia sibirjakovae*, with holotype designated by Sibirjakova (1961, pl. 6, fig. 2). Therefore, the 'Upper Bathonian' syntypes of *F. sibirjakovae* are not justified as early zigzagiceratins or representatives of *Franchia*. The Lower Bathonian, relatively evolute, microconch figured as *F. quenstedti* (Sibirjakova) by Beznosov and Mikhailova (1981, pl. 6, fig. 5) and Beznosov and Mitta (1993, pl. 13, fig. 6), and newly described as *F. sibirjakovae* sensu Beznosov and Mitta (2000, pl. 7, fig. 5), shows zigzag-state 1 and probably belongs to the *Siemiradzkia* [m] group. The syntypes of *Franchia tlisiense* Beznosov (1993 in Beznosov and Mitta 1993, p. 113, pl. 13, fig. 4; pl. 14, fig. 4; 1998, p. 12, figs 2–3) display bifurcate and trifurcate, subradiate ribs, that pass over the venter radially, with occasional irregular-strength ribs between 20 and 30 mm in diameter, but lack sigmoid or parabolic, sharp ribs. In conclusion, all these Caucasian specimens allegedly belonging to genus *Franchia* seem to be zigzagiceratins of the *Procerites* [M] – *Siemiradzkia* [m] group.

Occurrence. *Franchia* is only known from the French Subalpine Basin, restricted to the Zigzag Zone, top of the Parvum Subzone (Protozigzagiceras Biohorizon) and lower part of the Macrescens Subzone. It can be regarded as an endemic group of the Submediterranean Province, in Subalpine areas of the northern border of western Tethys, phyletically derived from *Protozigzagiceras*.

Franchia arkelli Sturani, 1967
Figures 4, 5, 6D, 7A, 8, 9A D

1967 *Zigzagiceras* (*Franchia*) *arkelli* subgen. et. sp. nov. Sturani, p. 52, pl. 2, fig. 2; pl. 16, fig. 5 (paratype); pl. 18, figs 2a–b (paratype), 4a–b (holotype).

Type specimen. The holotype PU31689 [M] figured by Sturani (1967, pl. 18, fig. 4a–b) is refigured here in Figure 4A–B.

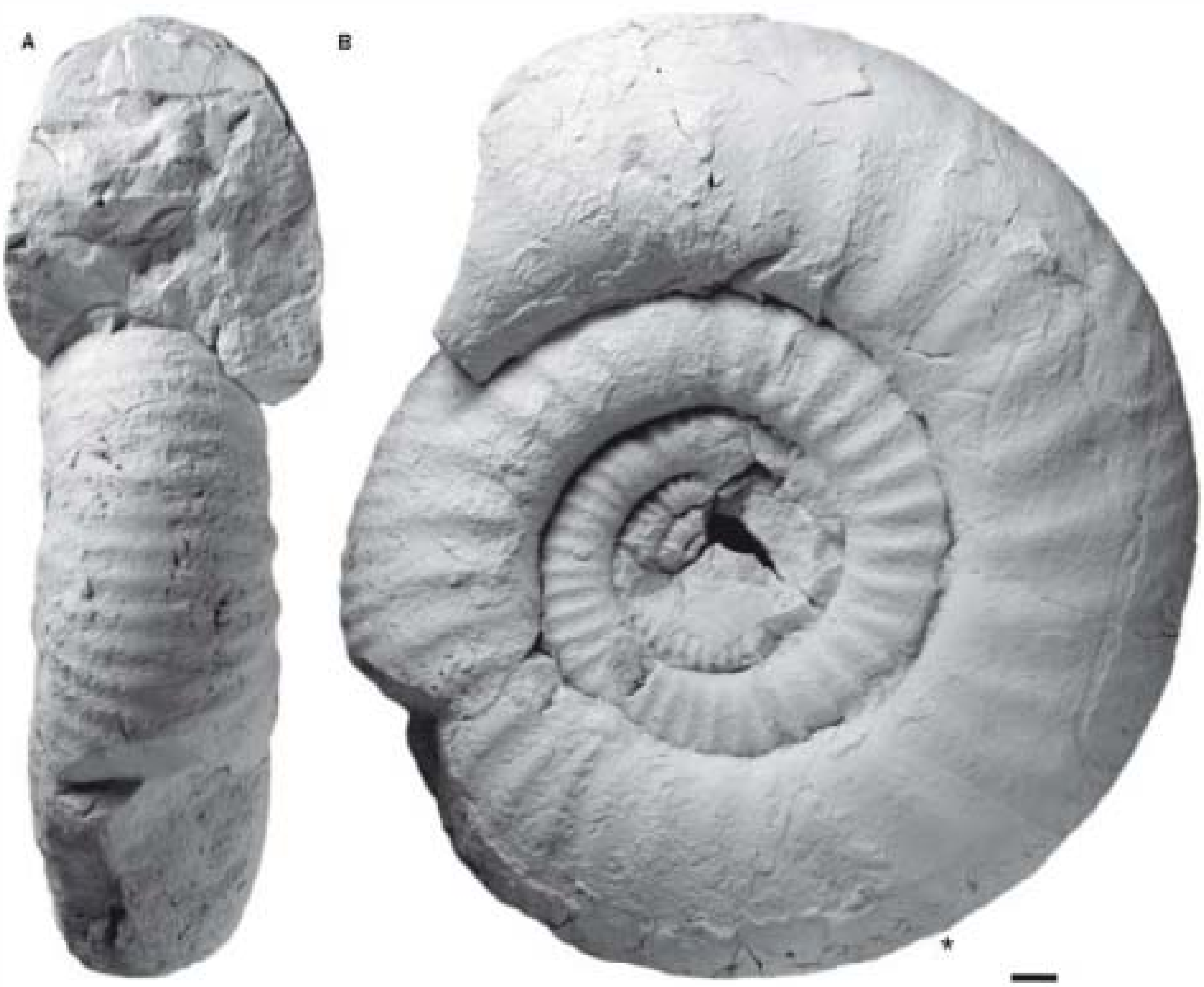

FIG. 4. *Franchia arkelli* Sturani; incomplete macroconch; holotype, specimen PU31689, level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008), Ravin d'Auran Section, Bas Auran; Macrescens Subzone, Zigzag Zone. A, oral view. B, right view. The end of the phragmocone is marked by a black asterisk. Scale bar represents 10 mm.

Type horizon. Lower Bathonian, Zigzag Zone, Macrescens Subzone. Level BA12 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani 1967) and level RA033 of Ravin d'Auran Section (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran, Alpes de Haute Provence, south-east France.

Material. Six specimens from Digne–Castellane region. Three specimens from the Parvum and Macrescens subzones of Bas Auran area: level BA12 (PU31689 [M], PU111325 [M]), level RR033 (PU112318 [m]). Two from Chaudon, Le Touert Section (Sturani 1967): PU31690 [M] and PU31691 [M]. One from the top Parvum Subzone of La Palud Section (Innocenti *et al.* 1990): PU112317 [M].

Syntypes. There are three syntypes from the Macrescens Subzone of Bas Auran area. The paratype PU31690 [M] figured by Sturani (1967, pl. 16, fig. 5) is refigured in Figure 5E–F. The paratype PU31691 [M] figured by Sturani (1967, pl. 18, fig. 2) is refigured in Figure 5A-C.

New material. Three specimens. Two topotypes of Bas Auran area: PU111325 [M], figured in Figure 6D, from Bas Auran, and PU112318 [m], figured in Figure 5D, magnified in Figure 7A, from level BA12 in Sturani (1967) and RR033 in Pavia *et al.* (2008), Ravin des Robins Section. One incomplete (outer whorls of phragmocone and body chamber, without inner whorls or peristomal portion) immature shell surpassing 100 mm in diameter, from top of Parvum Subzone of La Palud PU112317[M] (Innocenti *et al.* 1990; Romeo 1999).

Measurements. See Fernandez-Lopez and Pavia (2013).

Diagnosis. Evolute *Franchia* (U/D generally surpass 45 per cent in postjuvenile stages), macro- and microconchs, with coarse ribbing.

Description. Adult shells of small to medium size, from microconchs surpassing 40 mm of diameter (Fig. 5D) to adult macroconchs reaching 260 mm (Fig. 4). No specimens are known possessing complete body chamber, but umbilical suture surpasses 360 degrees in the macroconch holotype and 210 degrees in the incomplete, microconch topotype (Fig. 7A). Evolute coiling, with values of umbilical ratio ranging from 49 to 42 per cent, decreases in successive stages of ontogenic development (Fig. 8), except by egression of umbilical seam in adult body chamber (Fig. 4B). Whorls vary in section from low-oval to subcircular and high-oval contour, with convex flanks (Fig. 9A–D). Zigzag-state 2 developed in phragmocone, with sigmoid, sharp ribs of variable spacing (Figs 5C, 7A). Ulterior ornamentation to zigzag-state consists of relatively coarse, straight to slightly sinuous, rounded ribs. Primary ribs usually bifurcate, with additional free intercalatories that pass over the venter radially or with a gentle forward inclination. There are about 10–22 primaries per half whorl. Generally, secondary ribs are not interrupted on the middle of the venter (Figs 4A, 5F) nor displaced on both sides of a narrow smooth band as in *Bigotites*. Nevertheless, associated with the zigzag-stadium, a very shallow, narrow and ephemeral smooth band has been occasionally observed on ventral ribs (Fig. 5A; as indicated by Sturani 1967, p. 53). At maturity, ribs become sparser and blunter on upper flanks, but do not fade out on the venter. Shallow, broad and prorsiradiate constrictions are present; there is one or two every half a whorl at the outer whorls of the holotype. Suture line relatively simple, with suspensive lobe not strongly retracted (Figs 5E, 7A).

Occurrence. *Franchia arkelli* has been identified in the lower Macrescens Subzone in Bas Auran area and at the top of the Parvum Subzone (Protozigzagiceras Biohorizon) in La Palud. It is an endemic species of the Submediterranean Province, in Subalpine areas of the northern border of the western Tethys, phyletically derived from *Protozigzagiceras*.

Franchia subalpina sp. nov.
Figures 6A–C, 7B–C, 8, 9E–F

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2008 *Protozigzagiceras* [m] cf. *torrensi* (Sturani); Pavia *et al.*, pl. 3, figs 11, 12.
2008 *Franchia* sp. nov. ind.; Pavia *et al.*, pl. 3, fig. 13.
2009*a* *Protozigzagiceras* cf. *torrensi* (Sturani) [m]; Fernandez-Lopez *et al.*, fig. 6b.

Derivation of name. After the Subalpine Basin, the region inhabited by the species and that has yielded the syntypes.

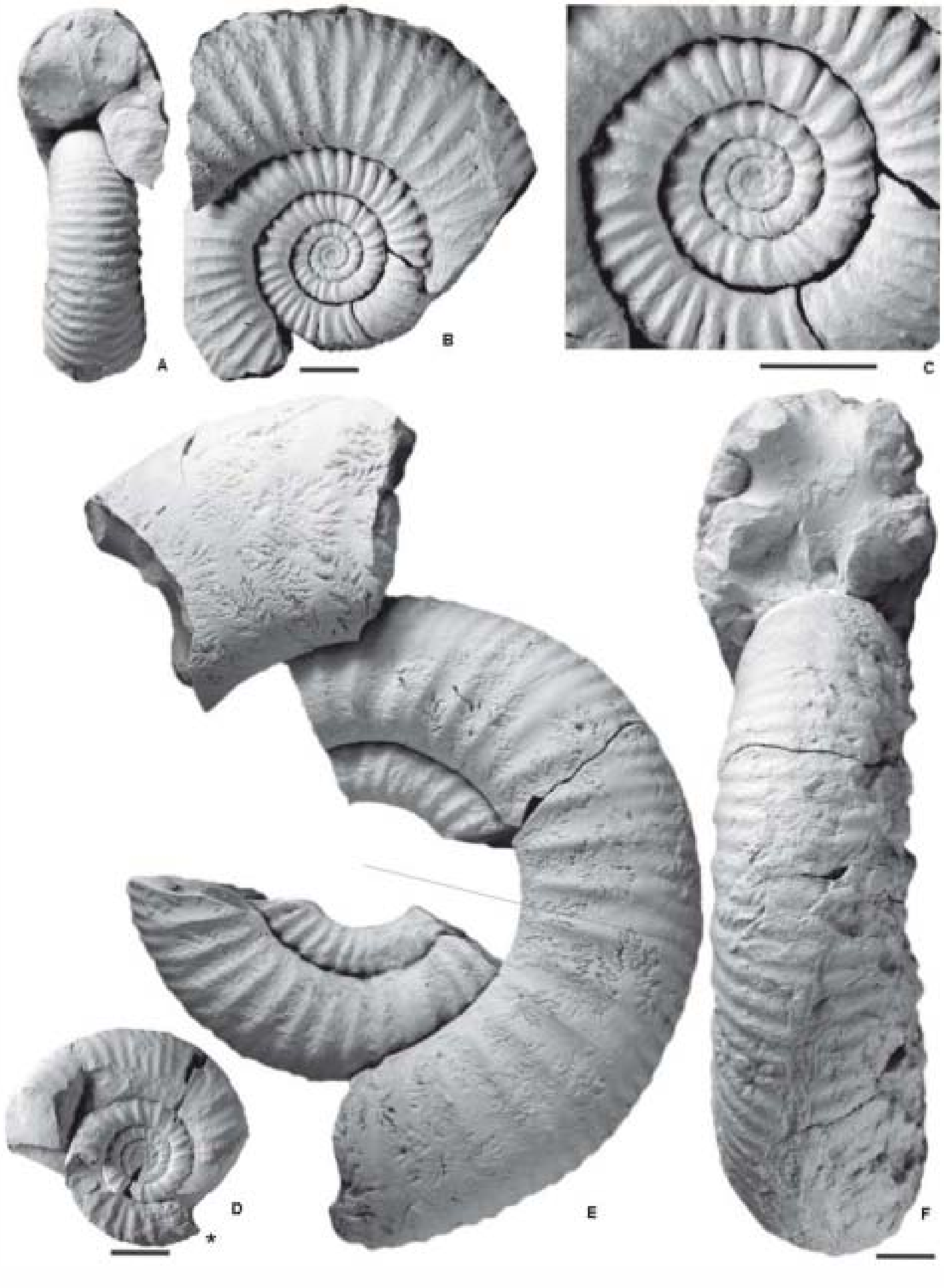
Type specimen. The holotype PU111399 [M] figured by Pavia *et al.* (2008, pl. 3, fig. 13) is refigured here in Figure 6A, from level BA11 in Sturani (1967).

Type horizon. Lower Bathonian, Zigzag Zone, Macrescens Subzone. Level BA11 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani 1967) and level RA031 of Ravin d'Auran Section (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran, Alpes de Haute Provence, south-east France.

Material. Three syntypes from the Macrescens Subzone of Bas Auran area. The paratype PU111573 [m] figured by Pavia *et al.* (2008, pl. 3, figs 11, 12) and Fernandez-Lopez *et al.* 2009*a*, fig. 6b) is refigured here in Figure 6B–C, magnified in Figure 7B-C, from level 12 in Sturani (1967) and RA033 in Pavia *et al.* (2008), Ravin d'Auran Section. The paratype PU111578 [M], a fragmentary nucleus *c.* 80 mm in diameter, shows zigzag-stadium in the right side, up to 30 mm D and 20 mm U.

Measurements. See Fernandez-Lopez and Pavia (2013).


A
B
C
D
E
F
*

Diagnosis. Moderately involute *Franchia* (U/D generally <45 per cent in postjuvenile stages), macro- and microconchs, with rounded and blunt ribbing.

Description. Adult shells of small to medium size, from microconchs surpassing 35 mm of diameter (Fig. 6B–C) to macroconchs reaching 140 mm of fully septate phragmocone and expected to surpass 250 mm in diameter (Fig. 8). Only one lappetted microconch known (Fig. 7B–C), with complete body chamber and umbilical egression but extremely short body chamber (130 degrees) indicative of preadult development. Moderately evolute coiling, with values of umbilical ratio ranging from 41 to 48 per cent, decreasing in successive ontogenic stages (Fig. 8B). Whorls vary in section from low-oval to subcircular and high-oval contour, with convex flanks (Fig. 9E–F). Zigzag-state 2 developed in phragmocone, with sigmoid, sharp ribs of variable spacing (Fig. 7C). Ulterior ornamentation to zigzag-state consists of relatively coarse, straight to slightly sinuous, rounded and blunt ribs (Fig. 6A). Primary ribs bifurcate or trifurcate, with additional free intercalatories that pass over the venter radially or with a gentle forward inclination, without interruption. There are about 10–19 primaries per half whorl. Looped, weak ribs, united on ventrolateral angle at a parabolic node, occur in the outer whorl of the microconch (Fig. 7C). At maturity, ribs become sparser and blunter on flanks, and eventually fade out, while still persisting on the venter. Shallow, broad and prorsiradiate constrictions are present in the holotype. Suture line relatively simple, with suspensive lobe not strongly retracted.

Remarks. Franchia arkelli Sturani, the type species of the genus, is the most similar representative. *F. subalpina*, however, shows stouter whorls and more involute coiling. These two species are chronostratigraphically coincident at the basal Macrescens Subzone, but *F. subalpina* persist into younger intervals, whereas *F. arkelli* occurs at the top of the precedent Parvum Subzone.

Occurrence. The syntypes of *F. subalpina* correspond to the Macrescens Subzone of the Bas Auran area. It is an endemic species of the Submediterranean Province, in Subalpine areas near the Provence–Ardeche platform system, in the northern border of the western Tethys, phyletically derived from *F. arkelli*.

Genus PROTOZIGZAGICERAS Fernandez-Lopez *et al.* 2007

Type species. Zigzagiceras torrensi (Sturani 1967, p. 47, pl. 21, fig. 3), by original designation of Fernandez-Lopez *et al.* 2007, p. 396.

Type level. Lower Bathonian, Zigzag Zone, Macrescens Subzone. Level BA9 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani 1967) and level RA024 of Ravin d'Auran Section (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran.

Type region. Alpes de Haute Provence (Bas Auran and Chaudon), south-east France.

Diagnosis. Micro- and macroconchs of small or medium size (40–300 mm). Planorbicones or discocones of moderately evolute to involute coiling. Zigzag-state 2 developed in the inner whorls, but surpassing 10 mm in diameter, firstly composed of proradiate to subradiate ribs of variable strength and spacing; then appear proradiate to subradiate, sigmoid ribs of greater strength upflank and variable spacing; and, finally, occasional proradiate to subradiate, sharp parabolic ribs of variable spacing. Numerous, blunt, bifurcate or trifurcate costae. Relatively complex suture line, with moderately broad and/or relatively short lateral lobe.

Remarks. Sturani (1967) regarded *Z. torrensi* and *Z. torrensi variecostatum* as microconchs of dimorphic macroconchs from the upper Macrescens Subzone, such as *Zigzagiceras* (*Procerozigzag*) *postpollubrum* Wetzel *garnieri*. However, *Zigzagiceras* Buckman [m] (1902, p. 7; type species: *Ammonites zigzag* d'Orbigny, 1846 in 1842–1851, p. 390, pl. 129, figs 9, 10) and *Procerozigzag* Arkell [M] (1953, p. 37; type species: *Stephanoceras crassizigzag* Buckman, 1892, pl. 14, figs 2, 3) display zigzag-state 3 and more complex suture lines. The distant parabolic ribs of *Zigzagiceras* [m & M] become strongly rursiradiate on lower and middle flanks, sharply projected forward on the ventrolateral shoulder, with parabolic tubercles or nodes, and the septal suture is strongly retracted with very narrow and long lateral lobe. Comparatively, *Protozigzagiceras* [m & M] is a lasting phyletic lineage of considerable morphological variability, and the source of the more specialized and briefer *Zigzagiceras* [m & M].

Both macroconchs and microconchs of *Franchia* also display zigzag-state 2, but show a simpler suture line, more planorbiconic coiling, shorter chronostratigraphical range and more restricted palaeogeographical distribution.

Zigzagiceras lenthayense [m] sensu Sturani (1967, p. 48, pl. 20, fig. 4) non Arkell (1958 in 1951–1958, p. 204, pl. 23, fig. 6a–b), from the level BA8, upper Macrescens

FIG. 5. *Franchia arkelli* Sturani. A–C, incomplete phragmocone of macroconch; paratype, specimen PU31691, level BA1 in Sturani (1967), Le Touert Section, Chaudon. D, complete microconch, topotype, specimen PU112318, level RR033 in Pavia *et al.* (2008) and level BA12 in Sturani (1967), Ravin des Robins Section, Bas Auran; for magnified view, see Figure 7A. E–F, incomplete phragmocone of macroconch; paratype, specimen PU31690, level BA1 in Sturani (1967), Le Touert Section, Chaudon. All specimens from the Macrescens Subzone, Zigzag Zone. Black asterisk marks the last septum of the phragmocone. Scale bars represent 10 mm.

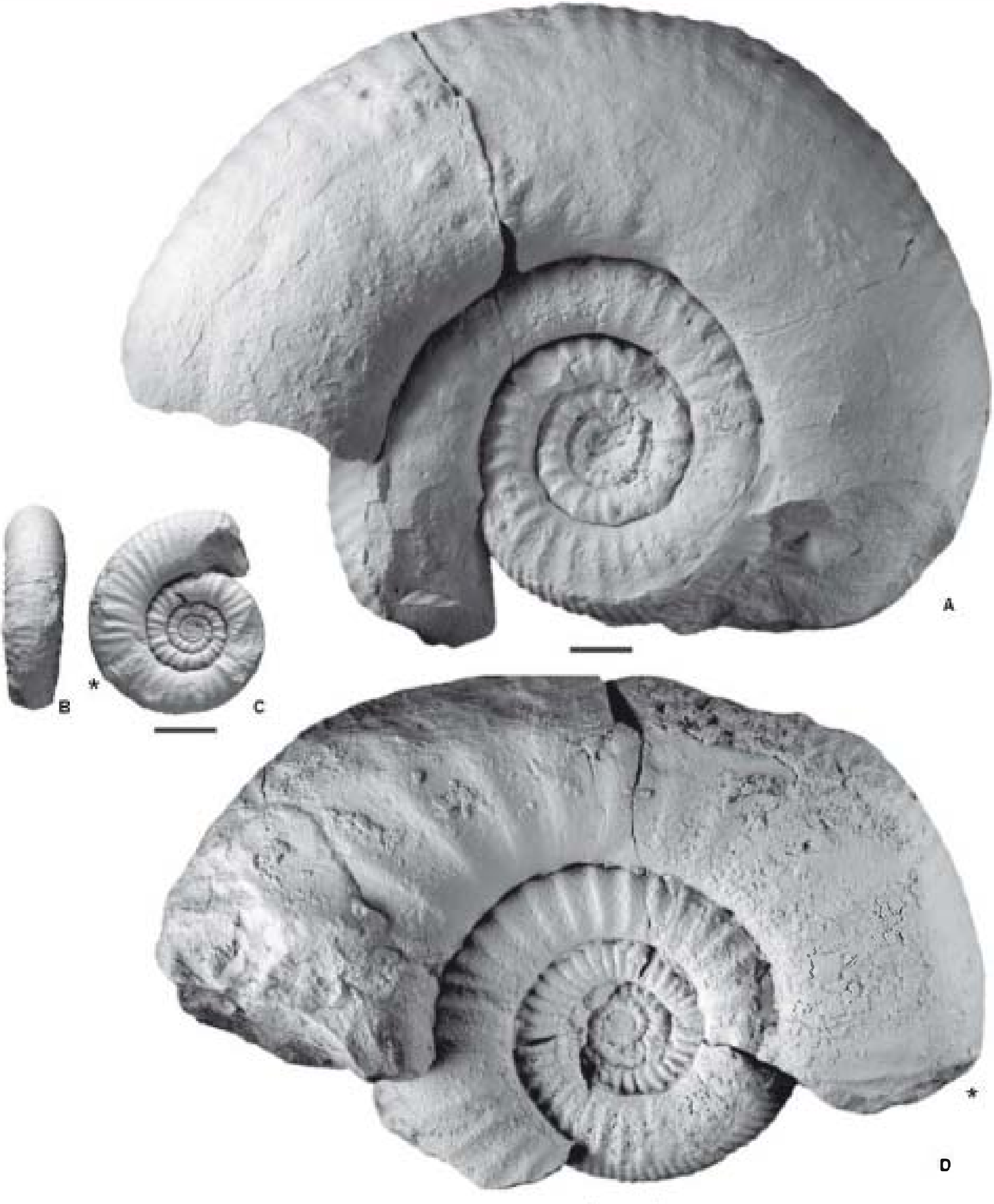


FIG. 6. *Franchia* spp. A, *Franchia subalpina* sp. nov.; incomplete phragmocone of macroconch; holotype, specimen PU111399, level RA030 in Pavia *et al.* (2008) and level BA11 in Sturani (1967). B–C, *F. subalpina* sp. nov.; complete microconch; paratype, specimen PU111573, level RA033 in Pavia *et al.* (2008) and level BA12 in Sturani (1967); for magnified view, see Figure 7B–C. D, *Franchia arkelli* Sturani; incomplete macroconch; topotype, specimen PU111325, level RA033 in Pavia *et al.* (2008) and level BA12 in Sturani (1967). All specimens from Ravin d'Auran Section, Bas Auran, Macrescens Subzone, Zigzag Zone. Black asterisk marks the last septum of the phragmocone. Scale bars represent 10 mm.

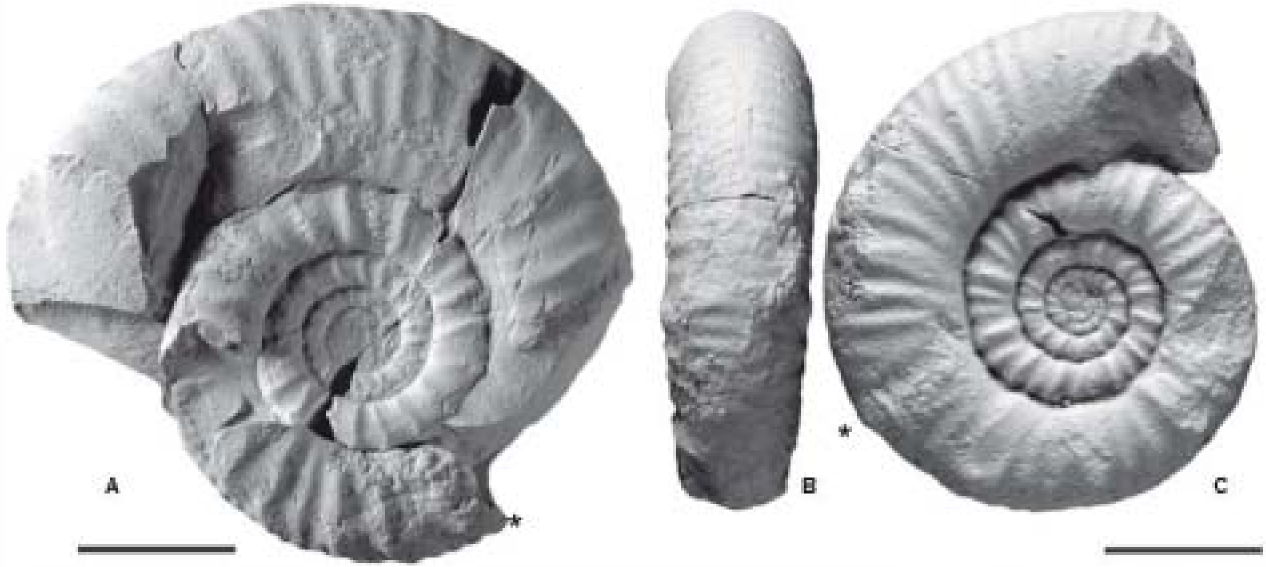


FIG. 7. *Franchia* spp. A, *Franchia arkelli* Sturani; incomplete microconch; topotype, specimen PU112318, level BA12 in Sturani (1967) and RR033 in Pavia *et al.* (2008), Ravin des Robins Section; Macrescens Subzone, Zigzag Zone. B–C, *Franchia subalpina* sp. nov.; complete microconch; paratype, specimen PU111573, level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008), Ravin d'Auran Section; Macrescens Subzone, Zigzag Zone. Black asterisk marks the last septum of the phragmocone. Note the occurrence of looped ribs, united on ventrolateral angle at a parabolic node, at 90, 165 and 240 degrees from the peristome. Scale bars represent 10 mm.

Subzone, and *Procerites imitator* Buckman [M] in Sturani (1967, p. 48, pl. 15, fig. 5) and Torrens (1987, pl. 7), from the levels BA1 to BA6, Aurigerus Zone, also display zigzag-state 2, but are more planorbiconic and of larger adult size. On the other hand, *Zigzagiceras* aff. *lenthayense* [m] sensu Sturani (1967, p. 49, pl. 12, fig. 2) from the marly interval BA8–7, upper Macrescens Subzone, displaying zigzag-state 1, belongs to the *Siemiradzkia* [m] group. *Procerites* [M]-*Siemiradzkia* [m] show zigzag-state 1 and more complex suture line than *Protozigzagiceras* [m & M].

Wagnericeras Buckman [M & m] (1921 in 1909–1930, TA-III, p. 33, type species: *Ammonites wagneri* Oppel, 1857 in 1856-1858, p. 477 [= *Ammonites planula* d'Orbigny, 1846 in 1842–1851, p. 416, pl. 144]) also occurs at the level BA8 in Bas Auran (Sturani 1967, p. 46, pl. 20, fig. 1), upper Macrescens Subzone, Zigzag Zone, but presents strong and blunt primary ribs, usually triplicate with additional free intercalatories.

Occurrence. Specimens belonging to the genus *Protozigzagiceras* have been described from Europe and Iran, although in most cases referred to the genera *Zigzagiceras* or *Procerozigzag*: Portugal (Fernandez-Lopez *et al.* 2007, fig. 11), France (Wetzel 1937; Sturani 1967, pl. 13, fig. 4, pl. 15, fig. 1, pl. 19, fig. 5, pl. 21, figs 1, 3, 7, pl. 22, fig. 1; Torrens 1987, pl. 8, figs 2–5; Fernandez-Lopez *et al.* 2007, figs 10, 12; Pavia *et al.* 2008, pl. 3, figs 6, 7, 9–12; Fernandez-Lopez *et al.* 2009*a*, fig. 6b), England (Buckman 1892, pl. 13, figs 1, 2; Dietze and Chandler 1997, pl. 1, figs 3, 4), Hungary (Galacz 1980, pl. 32), Betic Basin (Sandoval 1983, pl. 35, fig. 3), Carpathian (Schlögl *et al.* 2005, pl. 10, figs 4, 5, pl. 12, fig. 1) and Iran (Shafizadeh and Seyed-Emami 2005, figs 10, 11; Shams and Seyed-Emami 2010, p. 2, fig. 12; Table 2). Judging by these references, *Protozigzagiceras* occurs in the Early Bathonian, from Parvum to Recinctus subzones, Mediterranean-Caucasian Subrealm, along the whole of the northern border of the western Tethys, from Portugal through central Europe to Iran. Besides the type species, *P. torrensi*, three new species of *Protozigzagiceras* are described and interpreted below.

Protozigzagiceras torrensi (Sturani) 1967
Figures 10–13, 14A–D, 15

- 1967 *Zigzagiceras torrensi* sp. nov. Sturani, p. 47, pl. 2, fig. 4 (paratype); pl. 21, fig. 3 (holotype).
- 1967 *Zigzagiceras* (*Procerozigzag*) *postpollubrum* Wetzel *garnieri* n. ssp. Sturani, p. 51, pl. 15, fig. 1a,c; pl. 21, fig. 1, 7a–b, pl. 23, figs 4, 5.
- 1987 *Zigzagiceras* (*Procerozigzag*) *postpollubrum* Wetzel; Torrens, pl. 8, fig. 2a–b.
- 1987 *Zigzagiceras* (*Procerozigzag*) nov. sp.; Torrens, pl. 9, fig. 3a–b.
- 2007 *Protozigzagiceras* g. nov. *torrensi* (Sturani); Fernandez-Lopez *et al.*, p. 396, fig. 12 (holotype refigured).
- 2008 *Protozigzagiceras* [M] cf. *torrensi* (Sturani); Pavia *et al.*, pl. 3, figs 9, 10.

Type specimen. The holotype PU31676 [m] figured by Sturani (1967, pl. 21, fig. 3a–b) and Fernandez-Lopez *et al.* (2007, fig. 12) is refigured here in Figure 10A–D.

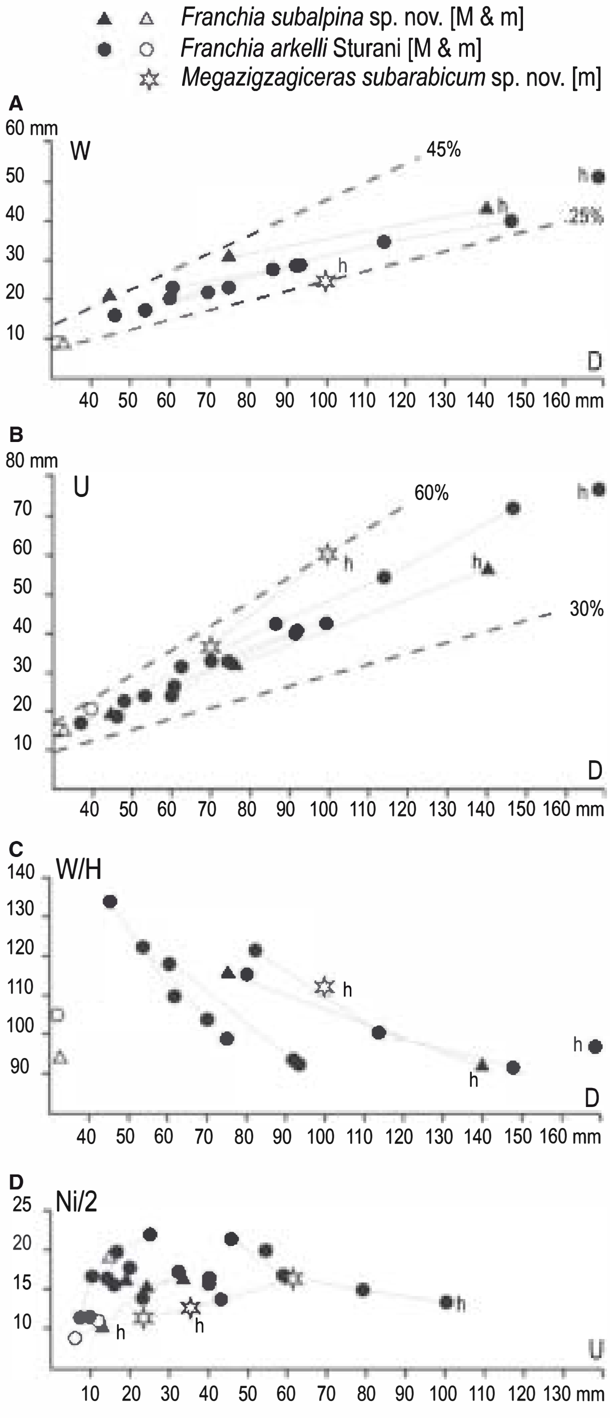


FIG. 8. Plots of measurements of *Franchia* and *Megazigzagiceras*. A, whorl width (W) versus shell diameter (D). B, umbilical diameter (U) versus shell diameter (D). C, whorl width/whorl height ratio (W/H) versus shell diameter (D). D, internal ribs per half whorl (Ni/2) versus umbilical diameter (U). h, holotype.

Type horizon. Lower Bathonian, Zigzag Zone, Macrescens Subzone. Level BA9 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani, 1967) and level RA024 of Ravin d'Auran Section (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran, Alpes de Haute Provence, south-east France.

Material. Eleven specimens from the Macrescens Subzone of Bas Auran area have been studied. Six specimens from level BA9 in Sturani (1967) and RA024 in Pavia *et al.* (2008), Ravin d'Auran Section: PU31676 [m], PU31677 [M?], PU31680 [m], PU31681 [m], PU31682 [m] and PU31719 [M]. Two specimens from level BA8 in Sturani (1967): PU311717 [M], which is the holotype of *Zigzagiceras* (*Procerozigzag*) *postpollubrum* Wetzel *garnieri* figured by Sturani (1967, pl. 21, fig. 7a–b) and refigured here in Figure 11, and PU311725 [M] collected by Sturani in 1972 and figured by Torrens (1987, pl. 9, fig. 3a–b). One specimen from level BA8 or BA9 collected by Sturani in 1972, PU31720 [M], and figured in Figure 12. One specimen from level BA9 or BA10 collected by Sturani (1967), PU311711 [M], and figured by Torrens (1987, pl. 8, fig. 2a–b). One specimen from level BA11 in Sturani (1967) and RA031 in Pavia *et al.* (2008), PU111577 [M], figured by Pavia *et al.* (2008, pl. 3, figs 9, 10).

Syntypes. There are two syntypes. The paratype PU31677 [M] described but not figured by Sturani (1967, p. 48) is figured here in Figure 10I–J.

New material. Four topotypes: PU31680 [m] figured in Figure 10G–H; PU31681 [m] in Figure 10E–F; PU31682 [m] in Figure 10K–M; and PU31720 [m] in Figure 12.

Measurements. See Fernandez-Lopez and Pavia (2013).

Diagnosis. Protozigzagiceras, planorbicones to discocones of moderately evolute to involute coiling, with straight to slightly concave, rounded and blunt, generally bifurcate ribs.

Description. Adult shells of small to medium size, from incomplete microconchs reaching 70 mm diameter (Fig. 10G–H) to macroconchs reaching 250 mm in diameter. Moderately evolute coiling, with values of umbilical ratio ranging from 49 to 41 per cent, decreasing insuccessive stages of ontogenic development (Fig. 13B). Whorls vary in section from low-oval to subcircular and high-oval, with convex flanks (Fig. 14A–D). Zigzag-state 2 developed in the inner whorls, composed of proradiate to subradiate, sigmoid ribs of greater strength upflank and variable spacing; and, finally, occasional, sharp parabolic ribs of variable spacing (Fig. 10D). Ulterior ornamentation consists of straight to slightly concave, rounded and blunt, generally bifurcate ribs that cross the venter with a gentle forward inclination. Simple primaries and intercalatories occur. There are about 19–26 primaries per half whorl. Generally, secondary ribs not interrupted on the middle of the venter. Shallow and prorsiradiate constrictions present exceptionally (Fig. 10B, J). Relatively complex suture line, with relatively short lateral lobe (Fig. 15).

Remarks. According to Sturani (1967), *Z. torrensi* is the microconch counterpart of *Procerozigzag postpollubrum garnieri*, and *Zigzagiceras postpollubrum* appears to be the end member of a wide chronospecies in which the

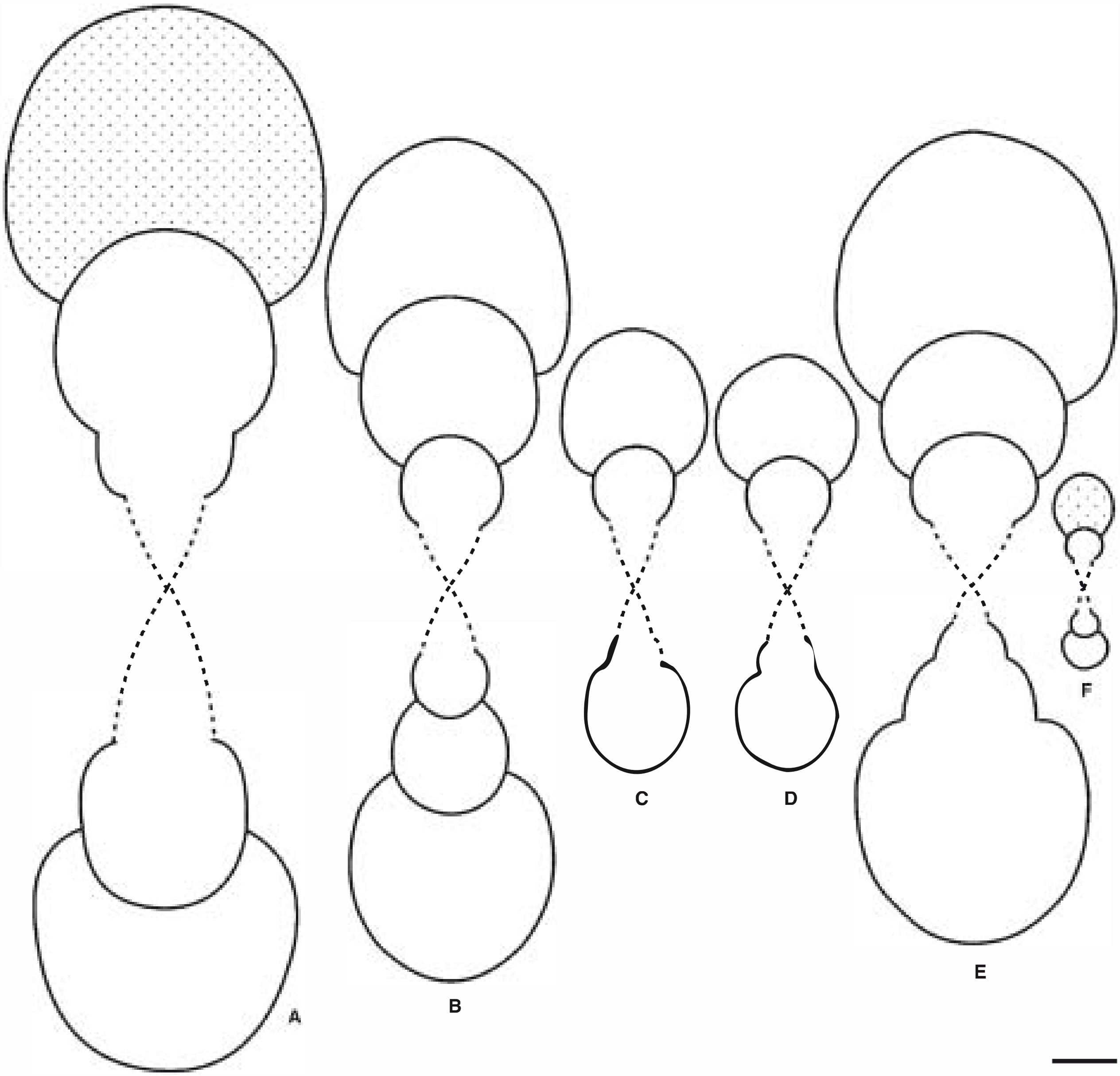


FIG. 9. Whorl shape cross-sections, through the phragmocone and body chamber (stippled), of *Franchia* spp. A–D, *Franchia arkelli* Sturani; A, holotype, PU31689 [M] (Fig. 4); B, paratype, PU31690 [M] (Fig. 5E–F); C, topotype, PU111325 [M] (Fig. 6D); D, paratype, PU31691 [M] (Fig. 5A–C). E–F, *Franchia subalpina* sp. nov.; E, holotype, PU111399 [M] (Fig. 6A); F, paratype, PU111573 [m] (Figs 6B–C, 7B–C). Scale bar represents 10 mm.

maximum size of full-grown specimens reaches 250 mm. In Bas Auran (Sturani 1967, pl. 22, fig. 1; Torrens 1987, pl. 8, figs 3–5), *Protozigzagiceras postpollubrum* (Wetzel 1937, p. 107, pl. 11, fig. 3a–b) comprises involute discocones with a very narrow and deep umbilicus (<24 per cent in adults), and with an earlier fade of primaries and secondaries at 80 and 120 mm, respectively, at the top of the Macrescens Subzone (level BA7 in Sturani and level RA019 in Pavia *et al.* 2008).

Zigzagiceras torrensi variecostatum Sturani (1967, p. 48, pl. 20, fig. 2a–b [holotype], pl. 2, fig. 5; pl. 13, fig. 4a,c; pl. 19, fig. 5) was based on four specimens from the beds succeeding that yielding the holotype of *P. torrensi* (BA8 and BA7). They show the zigzag-stage more densely ribbed and proportionally shorter, ending at 10 mm. On account of their biochronostratigraphical and morphological differences, this subspecies was regarded as transitional between typical *Zigzagiceras* and typical *Siemiradzkia*. However, the holotype is lost (H. Torrens, pers. comm.), the paratypes are fragmentary inner whorls, and new specimens similar to the holotype are unknown at present.

TABLE 2. Specimens published belonging to the genus *Protozigzagiceras* Fernandez-Lopez *et al.* 2007.

References	Occurrence
Buckman (1892, pl. 13, figs 1, 2)	England
Wetzel (1937, pl. 11, fig. 3)	France
Sturani (1967, pl. 13, fig. 4, pl. 15, fig. 1, pl. 19, fig. 5, pl. 21, figs 1, 3, 7, pl. 22, fig. 1)	France
Galacz (1980, pl. 32)	Hungary
Sandoval (1983, pl. 35, fig. 3)	Spain
Torrens (1987, pl. 8, figs 2–5)	France
Dietze and Chandler (1997, pl. 1, figs 3, 4)	England
Schlögl *et al.* (2005, pl. 10, figs 4, 5, pl. 12, fig. 1)	Slovakia
Shafizadeh and Seyed-Emami (2005, figs 10, 11)	Iran
Fernandez-Lopez *et al.* (2007, fig. 11)	Portugal
Fernandez-Lopez *et al.* (2007, figs 10, 12)	France
Pavia *et al.* (2008, pl. 3, figs 6, 7, 9–12)	France
Fernandez-Lopez *et al.* (2009*a*, fig. 6b)	France
Shams and Seyed-Emami (2010, p. 2, fig. 12)	Iran

Occurrence. *Protozigzagiceras torrensi* is known from the French Subalpine Basin, restricted to the Macrescens Subzone. It is common in the upper part of this subzone and scarce in the lower part. All the microconchs of Figure 10 come from the level BA9 in Sturani (1967) and RA029 in Pavia *et al.* (2008), Ravin d'Auran Section, but the macroconch published by Pavia *et al.* (2008, pl. 3, figs 9, 10) corresponds to the level RA031 (= Sturani's level BA11).

Protozigzagiceras tethycum sp. nov.
Figures 13, 14E–H, 16

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2007 *Protozigzagiceras* g. nov. sp. aff. *P. torrensi* (Sturani); Fernandez-Lopez *et al.*, p. 396, fig. 10.

Derivation of name. After the Neo-Tethys Ocean and the Peri-Tethyan sedimentary basins, where the species has been commonly recorded.

Type specimen. The holotype PU111574 [m] is figured in Figure 16J–L.

Type horizon. Lower Bathonian, Zigzag Zone, Parvum Subzone, Protozigzagiceras Biohorizon. Level BA13 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani 1967) and level RA035 of Ravin d'Auran (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran, Alpes de Haute Provence, south-east France.

Material. Six syntypes, all fully septate phragmocones, from the Parvum and Macrescens subzones of Bas Auran area. The paratype PU31694 [M] figured by Fernandez-Lopez *et al.* (2007, fig. 10) is refigured here in Figure 16H–I; both specimens from level BA13 in Sturani (1967) and RA035 in Pavia *et al.* (2008), Protozigzagiceras Biohorizon, Parvum Subzone. The paratypes PU31695 [m] figured in Figure 16A–D and PU111299 [m] figured in Figure 16E–G from level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008); Macrescens Subzone. Two fragmentary paratypes, PU111572 [m] and PU111300 [m], respectively, from levels BA12 (= RA033) and RA035.

Measurements. See Fernandez-Lopez and Pavia (2013).

Diagnosis. *Protozigzagiceras*, slim planorbicones of moderately evolute to moderately involute coiling, with straight, rounded and blunt, generally bifurcate ribs.

Description. Fully septate, discoid shells of small to medium size, from microconchs reaching 50 mm diameter (Fig. 16E–G) to presumed macroconchs surpassing 60 mm (Fig. 16H–I). Moderately evolute coiling, with values of umbilical ratio ranging from 49 to 39 per cent, decreases in successive stages of ontogenic development (Fig. 13B). Whorls vary in section from low-oval to subcircular and high-oval, with convex flanks (Fig. 14E–H). Zigzag-state 2 developed in the inner whorls, firstly composed of proradiate to subradiate ribs of variable strength and spacing; then appear proradiate to subradiate, sigmoid ribs of greater strength upflank and variable spacing (Fig. 16G). Ulterior ornamentation consists of straight to slightly concave, rounded and blunt, generally bifurcate ribs that cross the venter radially or with a gentle forward inclination. Simple primaries and intercalatories occur. There are about 19–23 primaries per half whorl. Generally, secondaries are not interrupted on the middle of the venter. Shallow and prorsiradiate pseudoconstrictions or constrictions are very scarce.

Remarks. Among the syntypes, the microconchs show a zigzag-state 2 clearly longer than the macroconch (Fig. 16H–I) as in other zigzagiceratin species. *Protozigzagiceras tethycum* comprises forms more planorbiconic and apparently smaller in size than *P. torrensi*. It differs from *Franchia* [M & m] by the more complex suture line, whereas *Siemiradzkia* [m] lacks zigzag-state 2 with sigmoid ribs. *Planisphinctes* [m] – *Lobosphinctes* [M] and *Phaulozigzag* [M & m] lack zigzag-stadium.

Occurrence. The holotype of *P. tethycum* corresponds to the Protozigzagiceras Biohorizon, upper Parvum Subzone, but other syntypes come from the lowermost Macrescens Subzone, Bas Auran area.

Protozigzagiceras flexum sp. nov.
Figures 13, 17

LSID. urn:lsid:zoobank.org:act:9E99C121-3A32-40E3-AB2F-665B256C76C2

Derivation of name. After the flexuous ribs that characterize the species.

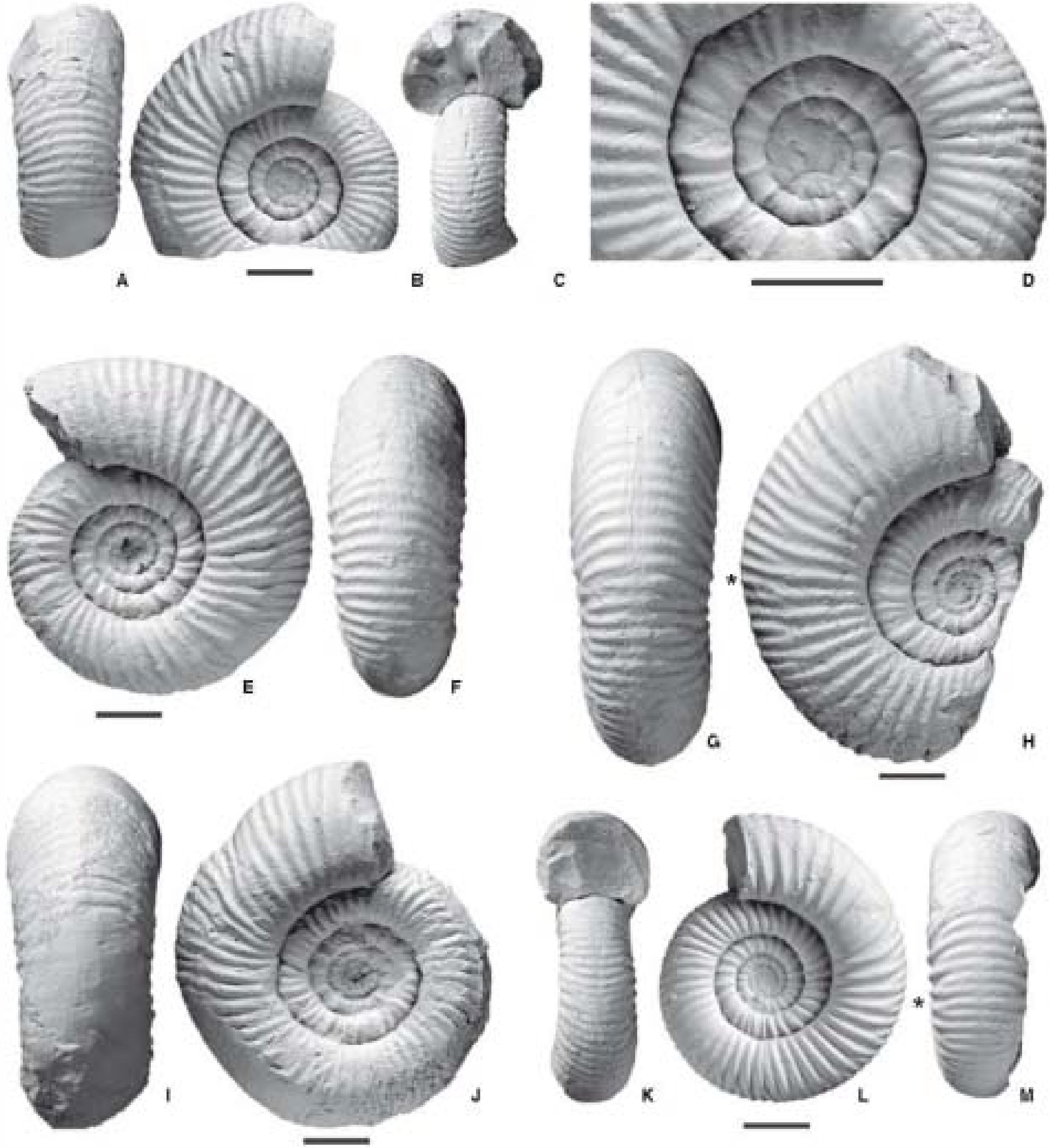

FIG. 10. *Protozigzagiceras torrensi* (Sturani). **A–D**, incomplete phragmocone; holotype, specimen PU31676. E–F, incomplete phragmocone; topotype, specimen PU31681. G–H, incomplete body chamber and phragmocone; topotype, specimen PU31680. I–J, incomplete phragmocone; paratype, specimen PU31677. K–M, incomplete body chamber and phragmocone; topotype, specimen PU31682. All microconch specimens from the level BA9 in Sturani (1967) and RA029 in Pavia *et al.* (2008), Ravin d'Auran Section, Bas Auran, Macrescens Subzone, Zigzag Zone. Black asterisk marks the last septum of the phragmocone. Scale bars represent 10 mm.

Type specimen. The holotype PU111326 [m] is figured in Figure 17A–D, from level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008), Ravin d'Auran Section, Bas Auran.

Type horizon. Lower Bathonian, Zigzag Zone, Macrescens Subzone. Level BA12 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani 1967) and level RA033

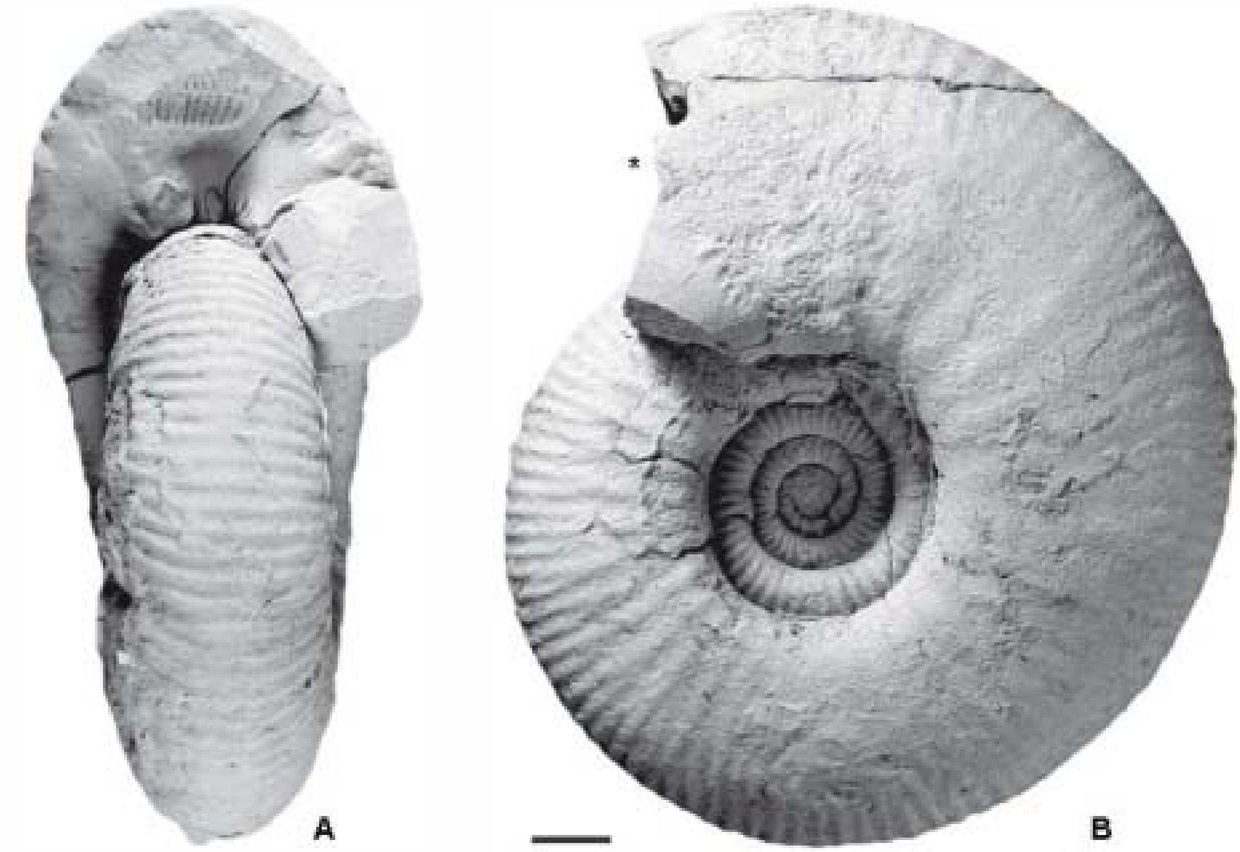

FIG. 11. *Protozigzagiceras torrensi* (Sturani); incomplete macroconch; specimen PU311717, holotype of *Zigzagiceras* (*Procerozigzag*) *postpollubrum* Wetzel *garnieri* Sturani; level BA8 in Sturani (1967) and RA023 in Pavia *et al.* (2008), Ravin d'Auran Section, Bas Auran; Macrescens Subzone, Zigzag Zone. A, oral view. B, right view. The end of the phragmocone is marked by a black asterisk. Scale bar represents 10 mm.

of the Ravin d'Auran Section (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran, Alpes de Haute Provence, south-east France.

Material. Two syntypes, all incomplete phragmocones, from the Macrescens Subzone of Bas Auran area. The paratype PU112319 [M] is figured in Figure 17E–F, from level BA12 in Sturani (1967) and RR033 in Pavia *et al.* (2008), Ravin des Robins Section.

Measurements. See Fernandez-Lopez and Pavia (2013).

Diagnosis. *Protozigzagiceras*, planorbicones to discocones of moderately evolute to moderately involute coiling, with flexuous, rounded and blunt, generally bifurcate ribs.

Description. Holotype is a fully septate, fragmentary microconch (Fig. 17A–D) surpassing 43 mm in diameter. Moderately evolute coiling, with values of umbilical ratio c. 48-46 per cent (Fig. 13B). Whorl section low-oval (W/H = 1.2 and W/D = 37 per cent), with convex flanks. Zigzag-state 2 clearly

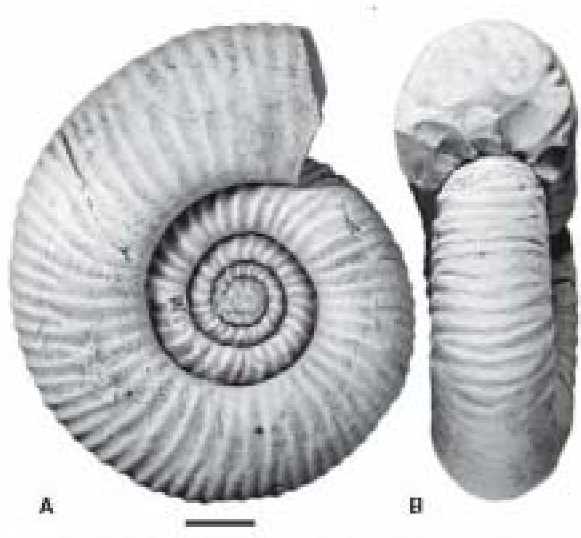

FIG. 12. *Protozigzagiceras torrensi* (Sturani); incomplete phragmocone of macroconch, showing pathological ornamentation in the last preserved whorl and complex suture line; specimen PU311720, level BA8 or BA9 in Sturani (1967), Bas Auran; Macrescens Subzone, Zigzag Zone. A, left view. B, oral view. Scale bar represents 10 mm.

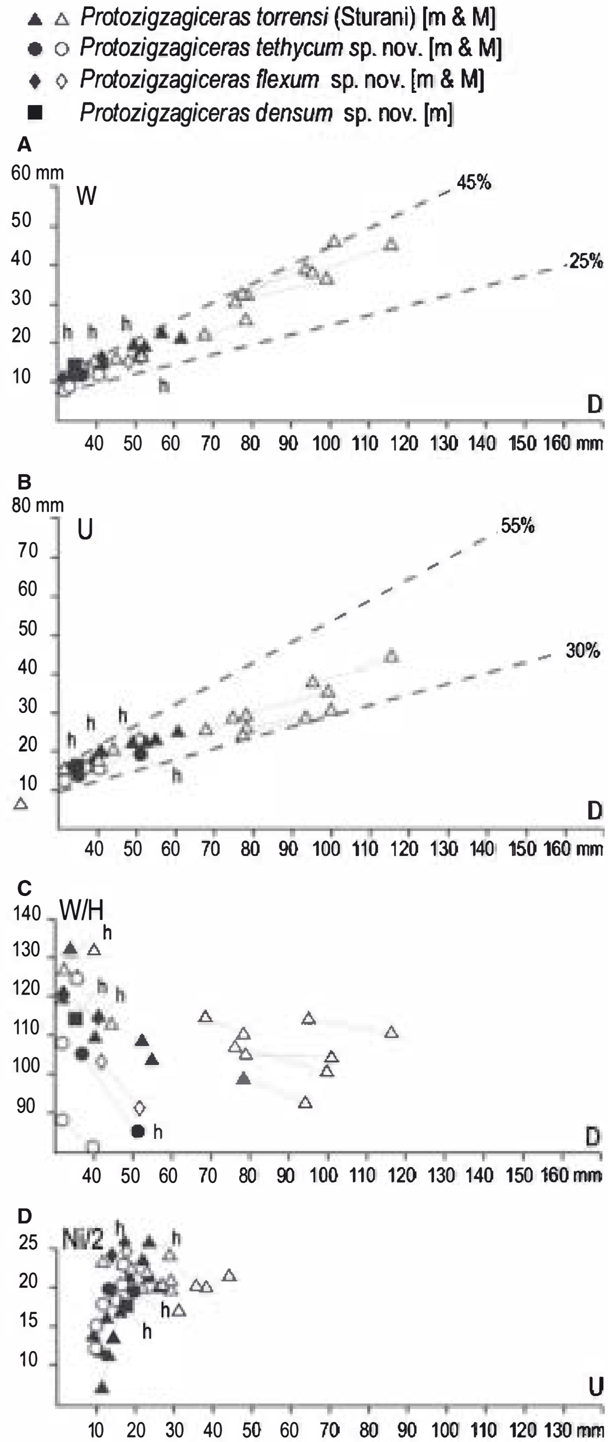

FIG. 13. Plots of measurements of *Protozigzagiceras*. A, whorl width (W) versus shell diameter (D). B, umbilical diameter (U) versus shell diameter (D). C, whorl width/whorl height ratio (W/H) versus shell diameter (D). D, internal ribs per half whorl (Ni/2) versus umbilical diameter (U). h, holotype.

developed in the inner whorls, up to 25 mm in diameter, with proradiate to subradiate, sharp sigmoid ribs of greater strength upflank and variable spacing; and, later, numerous, slightly convex, rounded and blunt, subradiate primary ribs with occasional parabolic ribs. In the last whorl, there are flexuous, rounded and blunt, subradiate primary ribs, generally bifurcate (Ni/2 = 21). Simple primaries and intercalatories occur. Secondary ribs cross the venter with a gentle forward inclination. Two shallow and prorsiradiate constrictions, diametrally opposite, are present in the last preserved whorl. Relatively complex suture line.

The paratype is an incomplete phragmocone of amacroconch (Fig. 17E–F) surpassing 100 mm in diameter. Moderately evolute, with proradiate to subradiate, flexuous ribs, rounded and blunt, generally bifurcate or trifurcate. Secondary ribs continue along the line of the primaries and bend forwards slightly over the venter.

Remarks. Protozigzagiceras flexum is close to *P. tethycum*, in its moderately evolute coiling, but differs in the more depressed whorl section and the flexuous ribs with forward inclination on the ventral region, instead straight ribs crossing the venter radially.

Zigzagites Buckman [M & m] (1922; type species: *Zigzagites imitator* Buckman, 1922 in 1909–1930, TA-IV, pl. 301), *Zigzagiceras lenthayense* [m] in Sturani (1967, p. 48, pl. 20, fig. 4) non Arkell (1958 in 1951–1958, p. 204, pl. 23, fig. 6a–b), from the upper Macrescens Subzone, Zigzag Zone, and *Procerites imitator* Buckman [M] in Sturani (1967, p. 48, pl. 15, fig. 5) and Torrens (1987, pl. 7) from the Aurigerus Zone, also display zigzag-state 2, but the phragmocone is more planorbiconic and of larger adult size. However, they could be counterpart dimorphs and paedomorphic taxa originated from a more involute and depressed species such as *P. flexum* during the Macrescens Subzone. Analogously, *Wagnericeras* could be a paedomorphic genus originating from this group of flexicostate zigzagiceratins during the Macrescens Subzone, taking into account of the relatively evolute specimen identified by Torrens (1987, p. 46, pl. 20, fig. 1) as *Wagnericeras*? sp. nov., collected by Sturani in bed BA8, and probably the earliest known representative of that genus.

Occurrence. Protozigzagiceras flexum is very scarce in the lowermost Macrescens Zone of Bas Auran, probably derived of *P. tethycum* at the latest Parvum Subzone (Protozigzagiceras Biohorizon).

Protozigzagiceras densum sp. nov.
Figures 13, 18

LSID. urn:lsid:zoobank.org:act:5656C765-CEE3-45A1-B82E-6FABA2AB4B8C

2008 *Franchia* [m] *arkelli* Sturani; Pavia *et al.*, pl. 3, figs 6, 7.

Derivation of name. After the dense ribbing that characterizes the species.

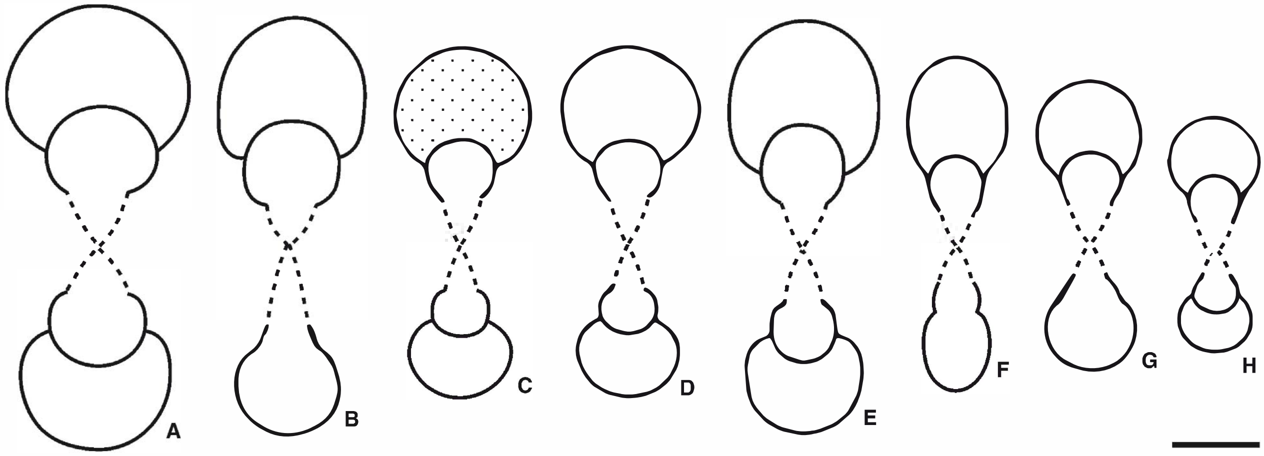

FIG. 14. Whorl shape cross-sections, through the phragmocone and body chamber (stippled), of *Protozigzagiceras* spp. [m & M]. A–D, *Protozigzagiceras torrensi* (Sturani); A, paratype, PU31677 [M?] (Fig. 10I–J); B, topotype, PU31681 [M] (Fig. 10E–F); C, topotype, PU31682 [m] (Fig. 10K–M); D, holotype, PU31676 [M] (Fig. 10A–D). E–H, *Protozigzagiceras tethycum* sp. nov.; E, paratype, PU31694 [M] (Fig. 16H–I); F, paratype, PU111299 [m] (Fig. 16E–G); G, paratype, PU111574 [m] (Fig. 16J–L); H, holotype, PU31695 [m] (Fig. 16A–D). Scale bar represents 10 mm.

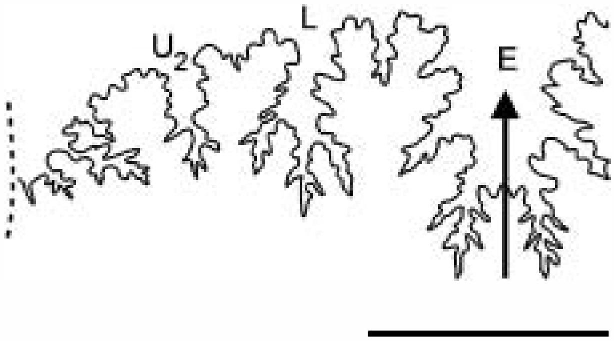

FIG. 15. Septal suture of *Protozigzagiceras torrensi* (Sturani), specimen PU31682 (Fig. 10K–M). E, external lobe; L, lateral lobe; U_2, second umbilical lobe. Scale bar represents 10 mm.

Type specimen. The holotype PU111322 [m], figured by Pavia *et al.* (2008, pl. 3, figs 6, 7) and refigured here in Figure 18A–D.

Type horizon. Lower Bathonian, Zigzag Zone, Macrescens Subzone. Level BA12 of the 'Marno-calcaires à *Cancellophycus*' Formation in Bas Auran area (Sturani 1967) and level RA033 of Ravin d'Auran Section (Pavia *et al.* 2008), indicated in Figure 2.

Type locality. Bas Auran, Alpes de Haute Provence, south-east France.

Material. One specimen, the holotype PU111322 [m], Figure 18A–D.

Measurements. See Fernandez-Lopez and Pavia (2013).

Diagnosis. Protozigzagiceras, planorbicones to discocones of moderately involute coiling, with straight to slightly sinuous, rounded and blunt, bifurcate and polyfurcate ribs.

Description. The holotype is a fully septate phragmocone of microconch (Fig. 18A–D) surpassing 40 mm in diameter and with moderately involute coiling, with values of umbilical ratio *c.* 45 per cent (Fig. 13B). Whorl section low-oval (W/H = 1.2 and W/D = 39 per cent), with convex flanks. Ornamentation, mainly ribbing and parabolic nodes, is very variable. Zigzag-state 2 developed in the inner whorls, but surpassing 30 mm in diameter, with proradiate to subradiate, sharp sigmoid ribs of greater strength upflank and variable spacing; and, later, occasional proradiate to subradiate parabolic ribs of variable spacing. Last half whorl displays numerous, straight to slightly concave, rounded and blunt, subradiate primary ribs (Ni/2 = 20). Secondary ribs, bifurcate or trifurcate, are quite weak, wiry, crossing the venter with forward inclination (Ne/2 = 53, i = 2.6). Whorl thickness is at its maximum just at the ventrolateral margin, where common parabolic nodes occur in the last preserved whorl. Shallow and prorsiradiate constrictions are locally present. Relatively complex suture line.

Remarks. Protozigzagiceras densum is the most involute, deeply navel and early polyfurcate species of the genus recorded in Bas Auran area at the transition between Parvum and Macrescens subzones. Moreover, the holotype is one of the specimens of this genus showing the largest number of parabolic nodes. This species clearly differs from species of *Zigzagiceras* [m] – *Procerozigzag* [M] in lacking zigzag-state 3, with distant and sharp, parabolic ribs. Another specimen, showing early polyfurcate ribs ventrally projected forwards, with zigzag-state 2 formed of sharp, sigmoid and parabolic ribs of variable spacing, has been figured from the Protozigzagiceras Biohorizon of Cap Mondego by Fernandez-Lopez *et al.* (2007, fig. 11). That Portuguese specimen is more planorbiconic and older than the holotype of *P. densum*, but it can represent a plesiomorph of the same phyletic lineage.

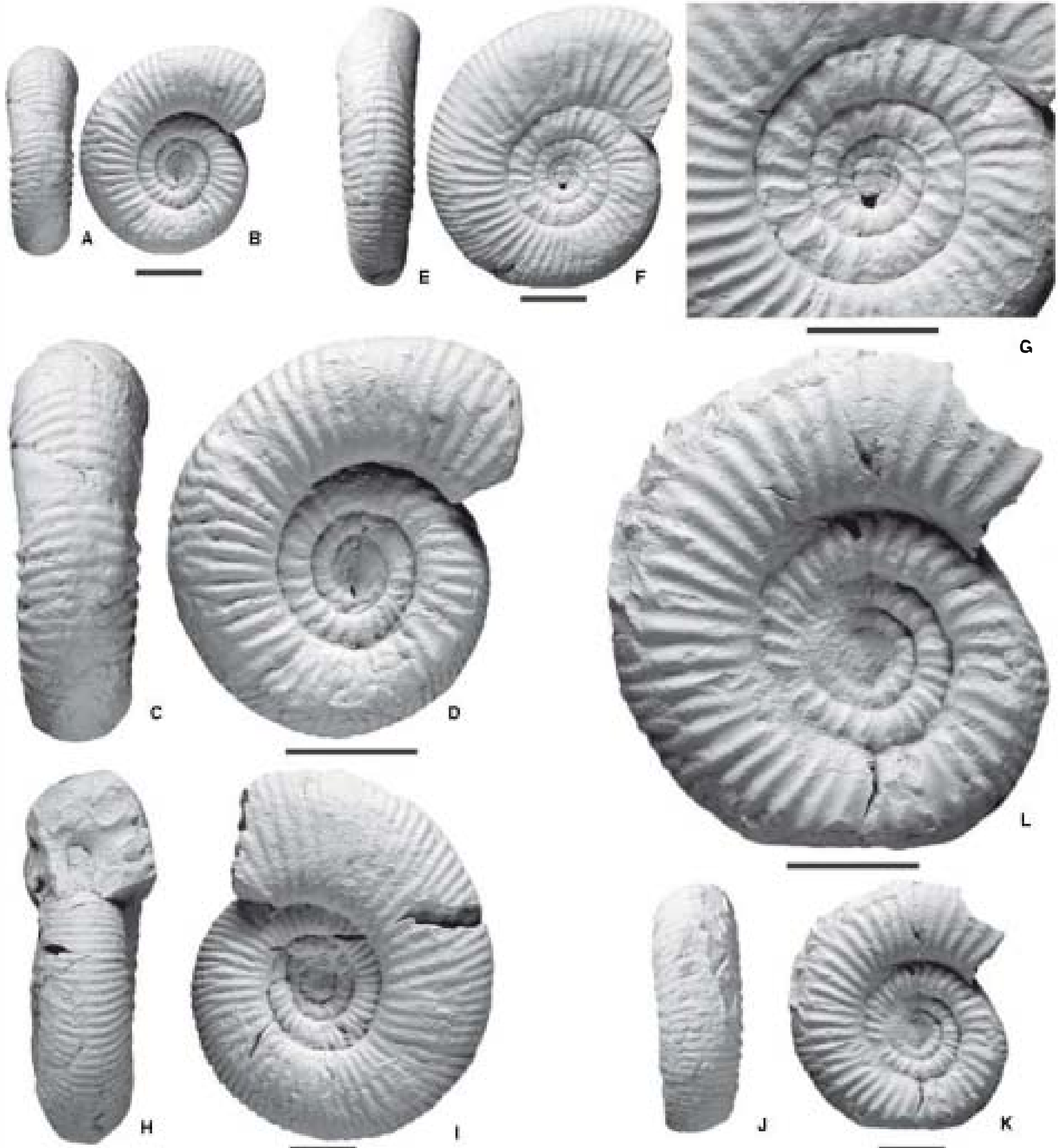

FIG. 16. ***Protozigzagiceras tethycum*** **sp. nov. A–D**, **incomplete phragmocone of microconch**; paratype, specimen PU31695, level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008); Macrescens Subzone. E–G, incomplete phragmocone of microconch; paratype, specimen PU111299, level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008); Macrescens Subzone. H–I, incomplete phragmocone of probable macroconch; paratype, specimen PU31694, level BA13 in Sturani (1967) and RA035 in Pavia *et al.* (2008); Protozigzagiceras Biohorizon, Parvum Subzone. J–L, incomplete phragmocone of microconch; holotype, specimen PU111574, level BA13 in Sturani (1967) and RA035 in Pavia *et al.* (2008); Protozigzagiceras Biohorizon, Parvum Subzone. All specimens from Ravin d'Auran Section, Bas Auran, Zigzag Zone. Scale bars represent 10 mm.

The two Chilean specimens taxonomically determined ?*Zigzagiceras* sp. (Gröschke and von Hillebrandt 1994, pl. 1, figs 4, 5; Gröschke 1996) from Aguada El Oro and W Sierra de Argomedo, Domeyko Cordillera, Lower Bathonian, correspond to immature or preadult, fragmentary shells. They display sigmoid ribs of variable strength and

FIG. 17. *Protozigzagiceras flexum* sp. nov. A–D, incomplete phragmocone of microconch; holotype, specimen PU111326, level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008), Ravin d'Auran Section. E–F, incomplete phragmocone of macroconch; paratype, specimen PU112319, level BA12 in Sturani (1967) and RR033 in Pavia *et al.* (2008), Ravin des Robins Section. All specimens from Bas Auran, Macrescens Subzone, Zigzag Zone. Scale bars represent 10 mm.

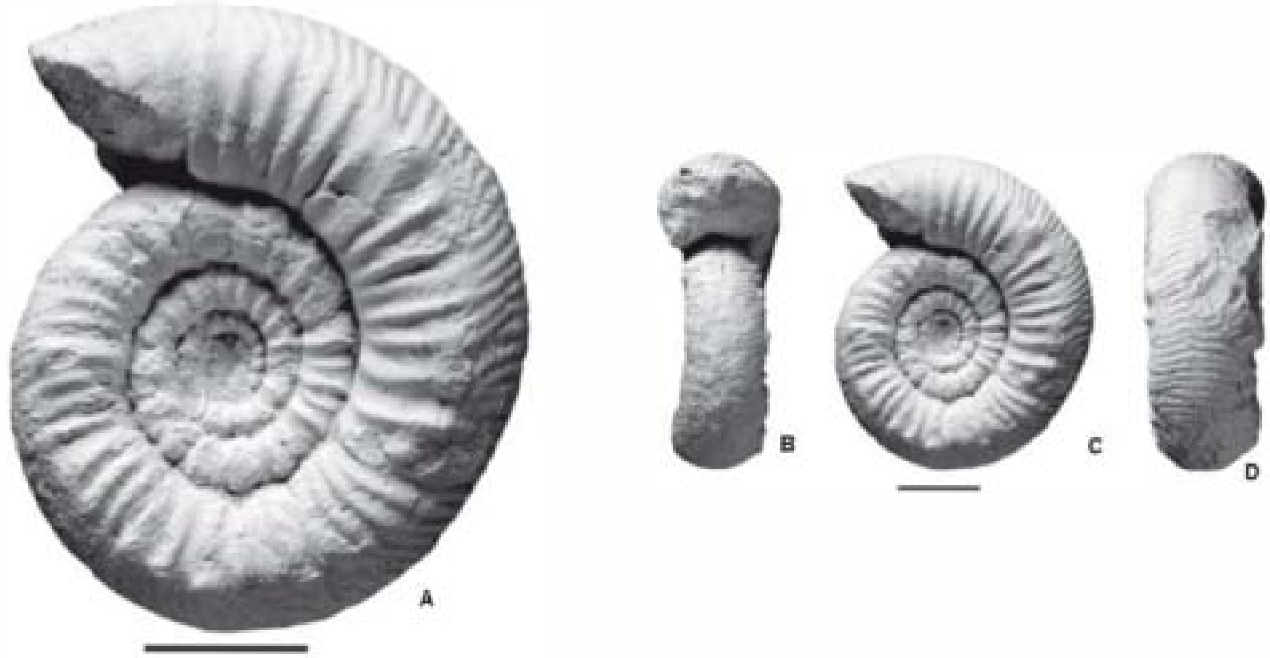

FIG. 18. *Protozigzagiceras densum* sp. nov.; incomplete phragmocone of microconch; holotype, specimen PU111322, level BA12 in Sturani (1967) and RA033 in Pavia *et al.* (2008), Ravin d'Auran Section; Macrescens Subzone, Zigzag Zone. A, C, right view. B, oral view. D, ventral view. Scale bars represent 10 mm.

spacing, bifurcate or trifurcate that cross the venter radially (therefore zigzag-state 2).

Occurrence. *Protozigzagiceras densum* is a very scarce species in the lowermost Macrescens Zone of Bas Auran, only recognized in the holotype, recorded at level BA12 and associated with the oldest representatives of *Zigzagiceras* [m] – *Procerozigzag* [M]. This stratigraphical coincidence, however, does not imply simultaneity of these two taxonomic groups nor sedimentary condensation in the stratigraphical interval, because the preservational features of this holotype are characteristic of a re-elaborated element included in an expanded deposit (Fernandez-Lopez 2007). Taking into account these features of the holotype, the species *P. densum* belongs to the earliest Macrescens and/or latest Parvum subzones. It possibly derives from *P. tethycum* through intermediate, plesiomorphic planorbicones, such as the above-mentioned Portuguese specimen (Fernandez-Lopez *et al.* 2007, fig. 11).

Genus MEGAZIGZAGICERAS, gen. nov.

LSID. urn:lsid:zoobank.org:act:E2DC3CC4-7969-4BB2-B19A-5972840923A6

Type species. *Megazigzagiceras subarabicum*, sp. nov.

Type level. Top of unit D3 and middle part of the Dhruma Formation (Enay *et al.* 1987, 2007; Enay and Mangold 1994; Almeras *et al.* 2010).

Type locality. Dhanna area, central Saudi Arabia.

Derivation of name. After the large size reached by the adults of the type species.

Diagnosis. Planorbicones of medium or large size (microconchs expected to surpass 100 mm in diameter). Zigzag-state 2 developed in the phragmocone, composed of proradiate to subradiate, blunt sigmoid ribs of greater strength upflank, but of variable strength and spacing. Relatively simple suture line, with broad lateral lobe.

Remarks. The holotype of the type species is the only specimen known of the genus *Megazigzagiceras*. The large size of the holotype and the presence of blunt, sigmoid ribs are distinctive features, differentiating it from other Tethyan microconch zigzagiceratins. It has a relatively simple suture line like *Franchia* [M & m]. *Protozigzagiceras* [m & M] also display zigzag-state 2 ribbing, but have a more complex suture line and more cadiconic or discoconic coiling. *Zigzagiceras* [m & M] display zigzag-state 3, a complex suture line and more cadiconic or discoconic coiling.

Certain Panthalassa zigzagiceratins such as *Epizigzagiceras* Frebold (1973 in Frebold and Tipper 1973; type species: *Epizigzagiceras evolutum* Frebold, 1973, p. 1119, pl. 1, figs 1–5) also reach a relatively large size. *Epizigzagiceras* comprises planorbicones, with zigzag-state 2 ribbing relatively developed in the phragmocone, composed of proradiate to

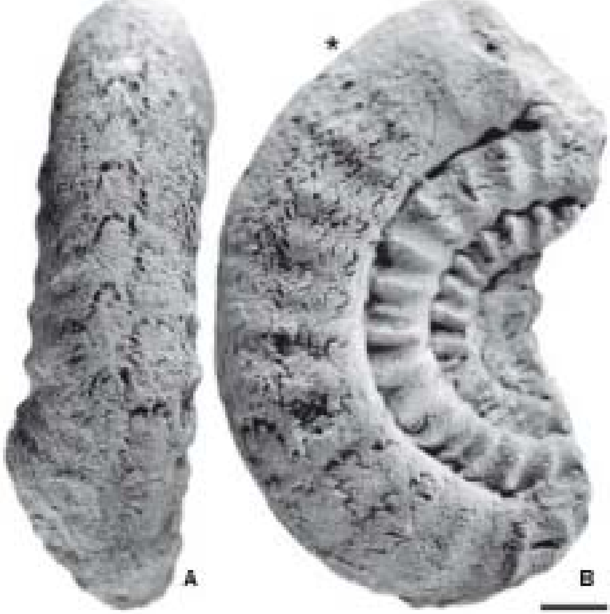

FIG. 19. *Megazigzagiceras subarabicum*, gen. et sp. nov.; phragmocone and incomplete body chamber of probable microconch; holotype, specimen JMA 82 285/FSL 177 639; top of unit D3 and middle part of the Dhruma Formation, Dharma area (central Saudi Arabia). A, ventral view. B, left view. Black asterisk marks the last septum of the phragmocone. Scale bar represents 10 mm.

subradiate, blunt sigmoid ribs of greater strength upflank, of variable strength and spacing, and occasional subradiate to rursiradiate, sharp parabolic ribs. In British Columbia, Canada, *E. evolutum* is associated with *Parareineckeia* spp. and was initially interpreted as equivalent in age to a similar Lower Bathonian ammonite association from southern Alaska described by Imlay (1962; Hall and Stronach 1981; Westermann 1981, 1993; Hall 1988; Poulton *et al.* 1992). *Epizigzagiceras crassicostatum* Frebold (1973 in Frebold and Tipper 1973, p. 1121, pl. 6, fig. 1) was recorded in an older ammonite assemblage assigned to the Bajocian, possibly Late Bajocian. The difference between these two species of *Epizigzagiceras* has been considered as nearly the same as that between *Zigzagiceras* Buckman and *Procerozigzag* Arkell, indicating that the absence of lappets in the syntypes of *E. evolutum* may be due to nonpreservation (Frebold and Tipper 1973, p. 1121). On the other hand, *Epizigzagiceras* has been considered as macroconchiate by several authors (Callomon 1984, p. 151). However, taking into account of the relatively developed zigzag-state in the phragmocone of these two evolute, planorbiconic holotypes, both are microconchs. Both species of *Epizigzagiceras* are associated with *Cobbanites talkeetnanus* Imlay, referred to Late Bajocian and used as regional zonal names in the Bowser Basin, now located in the interior of the Canadian Cordillera but belonging to the allochthonous terrane so-called Stikinia (Callomon 1984, fig. 3; Taylor *et al.* 1984; von Hillebrandt *et al.* 1992*a*; Palfy *et al.* 2000, fig. 1; Evenchick *et al.* 2010, fig. 3B; Shirmohammad *et al.* 2011, fig. 4). Generally, these species of *Epizigzagiceras* have been interpreted as East-Pacific endemic taxa, contemporaneous and/or older than *Zigzagiceras–Procerozigzag*. However, *Epizigzagiceras* is an Early Bathonian zigzagiceratin probably belonging to a Macrescens and/or post-Macrescens interval and would be very unlikely to occur in any Late Bajocian interval, according to the biochronostratigraphical and phylogenetic information of West Tethyan areas.

Occurrence. *Megazigzagiceras* is known only from the Middle Jurassic low palaeolatitude, shallow marine Arabian Platform (Enay *et al.* 2007; Enay 2011). As far as can be seen from the material currently known, it seems to be an endemic genus of the Ethiopian Province, in the southern border of the Central Tethys, probably derived from *Protozigzagiceras* at the latest Parvum and/or Macrescens subzones.

Megazigzagiceras subarabicum sp. nov.
Figures 8, 19

LSID. urn:lsid:zoobank.org:act:3E992DC2-CCE1-4A9E-9CC1-3F8966C40A7E

1987 *Zigzagiceras* (*Franchia*) sp. Enay *et al.*, p. 35, 41, 43.
1994 *Zigzagiceras* (*Franchia*) sp. Enay and Mangold, p. 170.

Derivation of name. After the outer marine environments, at the northern margin of the shallow Arabian Platform, the place that has yielded the holotype.

Type specimen. The holotype JMA 82 285/FSL 177 639 [m] (Fig. 19A–B).

Type horizon. Top of unit D3 and middle part of the Dhruma Formation, Lower Bathonian (Enay *et al.* 1987, fig. 2, tables 1, 2; Enay and Mangold 1994), correlated with the Parvum and Convergens subzones of the Submediterranean and NW European provinces (Enay *et al.* 2007; Alméras *et al.* 2010). As a whole, the age of unit D3 is Late Bajocian, Planus Zone of the Arabian Province (more or less equivalent with the Parkinsoni Zone), save the uppermost beds which have been dated as Lowermost Bathonian, Tuwaiqensis Zone on the basis of the occurrence of '*Franchia*' sp. and *Tulites* sp. (R. Enay, pers. comm. 2012).

Type locality. Wadi al Hisyan (24°45′N), Dharma Quadrangle (central Saudi Arabia).

Material. One specimen, JMA 82 285/FSL 177 639, the holotype [m] here figured in Figure 19.

Measurements. See Fernandez-Lopez and Pavia (2013).

Diagnosis. Moderately evolute *Megazigzagiceras*, with proradiate to subradiate, slightly sigmoid to straight, blunt ribs in the intermediate and outer whorls of phragmocone.

Remarks. The holotype is the internal mould of a fragmentary phragmocone and incomplete body chamber of probable microconch, reaching 80 mm and expected to surpass 100 mm in diameter (Fig. 19). Although it displays possible signs of maturity, such as egressive coiling and flattening of the body chamber, crowding of the last sutures is missing and so it probably represents a preadult individual.

Megazigzagiceras subarabicum differs from other Tethyan zigzagiceratins in having greater adult size, with subradiate, blunt, sigmoid ribs and relatively simple suture line. The holotype shows more depressed whorls and more evolute coiling than the known species of *Franchia* (Fig. 8).

Occurrence. The holotype comes from top of unit D3 and middle part of the Dhruma Formation, Lower Bathonian (Enay *et al.* 1987, fig. 2, table 2; Enay and Mangold 1994, p. 170, fig. 1; Almeras *et al.* 2010, fig. 2). It was mentioned as biostratigraphically related to the uppermost specimens of *Thambites planus* Arkell, '*Clydoniceras*' *avus* (Arkell) and *Clydoniceras pseudodiscus* Arkell, below *Tulites tuwaiqensis* Arkell (Enay *et al.* 1987, table 1). The basal levels of the Lower Bathonian Tuwaiqensis (*Tulites*) Zone of the Arabian Province have been correlated with the Parvum and Convergens subzones of the Submediterranean and NW European provinces (Enay *et al.* 2007). Upper Bajocian deposits of this area, with *Ermoceras*, *Thambites*, *Leptosphinctes* and *Spiroceras*, represent the Runcinatum (*Ermoceras*), Mogharense (*Ermoceras*) and Planus (*Thambites*) zones (Enay and Mangold 1994, 1996).

Megazigzagiceras subarabicum is interpreted here as an endemic species of the Ethiopian Province, of outer marine environments near the northern margin of the shallow Arabian Platform, in the southern border of the central Tethys, derived from *P. tethycum* probably belonging to the latest Parvum and/or Macrescens subzones.

PALAEOBIOGEOGRAPHICAL AND EVOLUTIONARY IMPLICATIONS

Zigzagiceratinae evolved from Leptosphinctinae in western Tethys and entered the eastern Pacific (Westermann 1993). Earliest Bathonian genera of Zigzagiceratinae spread to become in almost subrealms of the Tethys–Panthalassa Realm, but restricted in their palaeogeographical distribution to areas of only one hemisphere (Fig. 20). Similarly to *Franchia* [M & m] and *Protozigzagiceras* [m & M], *Zigzagiceras* [m] – *Procerozigzag* [M] are characteristic taxa of the Mediterranean–Caucasian Subrealm (Buckman 1892, 1909–1930; Thalmann 1925; Arkell *et al.* 1957; Westermann 1958; Hahn 1969, 1972; Krystyn 1972; Dietl 1977; Sandoval 1983; Schlegelmilch 1985; Seyed-Emami *et al.* 1985; Mangold 1994; Galacz 1995; Dietze and Chandler 1996; Page 1996; Mangold and Rioult 1997; Wierzbowski *et al.* 1999; Fernandez-Lopez 2000; Schlögl *et al.* 2005; Dietze and Dietl 2006; Zaton 2011). On the

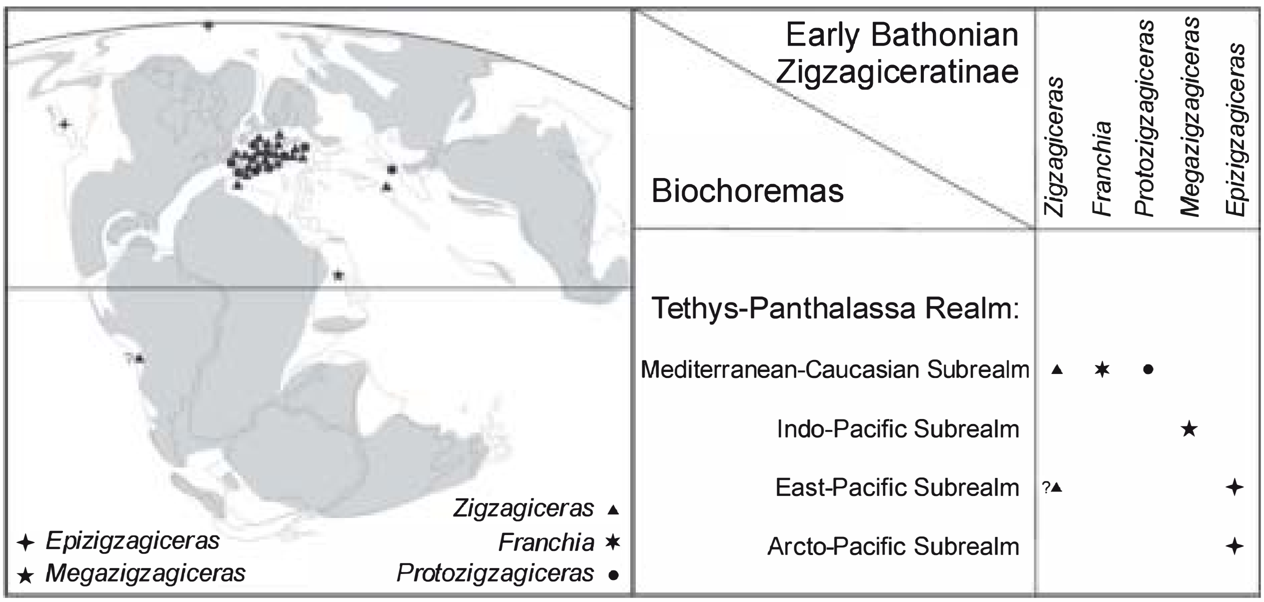

FIG. 20. Palaeobiogeographical distribution of some Zigzagiceratinae genera during Early Bathonian Zigzag Zone. Palaeogeography modified from Fernandez-Lopez *et al.* (2009*b*), Fernandez-Lopez and Chong Diaz (2011) and Golonka (2011); palaeobiogeographical units according to Westermann (2000*b*).

other hand, *Megazigzagiceras* [m] belongs to the Indo-Pacific Subrealm (Ethiopian Province; Enay 2007), whereas *Epizigzagiceras* [m & M?] characterizes the East-Pacific and Arcto-Pacific subrealms (Athabascan and Bering provinces; Frebold and Tipper 1973; Callomon 1984; von Hillebrandt *et al.* 1992*a*, *b*; Poulton *et al.* 1992; Sey *et al.* 1992, 2004; Zakharov *et al.* 1996; Sey and Kalacheva 2000; Evenchick *et al.* 2010). Therefore, the distribution of zigzagiceratin genera can be a diagnostic criterion to identify and to distinguish Bathonian biochoremas (Westermann 2000*a*, *b*; Cecca and Westermann 2003) as well as to test the palaeogeographical distribution of some plates and terranes (e.g. the North Tethyan position of the Iranian platform system during Early Bathonian; Stampfli & Borel 2002; Golonka 2011; Seton *et al.* 2012).

Several authors have considered *Bigotites* as the source of two main phyletic lineages of Bathonian perisphinctids, evolving in different directions: *Procerites* [M] – *Siemiradzkia* [m] progressing through *Planisphinctes* [m] – *Lobosphinctes* [M] and *Zigzagiceras* [m] – *Procerozigzag* [M] through *Franchia* [M & m] (Arkell *et al.* 1957; Arkell 1958 in 1951–1958; Sturani 1967; Hahn 1969; Mangold 1971; Galacz 1980; Callomon in Donovan *et al.* 1981; Sandoval 1983). However, in accordance with the sutural complexity, ornamentation and biochronostratigraphical distribution, it seems more probable that the dimorphic group *Planisphinctes* [m] – *Lobosphinctes* [M] represents a direct derivative of some Late Bajocian species of the group of *Vermisphinctes* [m] – *Prorsisphinctes* [M]. As suggested by Stephanov (1972), this dimorphic group can be included among the youngest Leptosphinctinae (Westermann 1956, 1958; Luppov and Druzschic 1958; Beznosov and Mikhailova 1981; Beznosov 1982; Torrens 1987; Innocenti *et al.* 1990; Beznosov and Mitta 1993, 1995, 1998; Fernandez-Lopez *et al.* 2006, 2007). The phylogenetic derivation of Zigzagiceratinae, in particular *Zigzagiceras* [m] – *Procerozigzag* [M] and *Franchia* [M & m], from *Bigotites* [M & m] as supported by Sturani (1967) and Torrens (1987), or from *Phaulozigzag* [m] – *Lobosphinctes*? [M] as suggested by Fernandez-Lopez *et al.* (2006), remains to be reassessed according to very accurate biochronological data and complementary morphological information (Fernandez-Lopez *et al.* 2006, 2007; Pavia *et al.* 2008).

Procerites [M] – *Siemiradzkia* [m], the oldest known Zigzagiceratinae with zigzag-state 1, probably branched off from the alleged Leptosphinctinae *Phaulozigzag* [m] – *Lobosphinctes*? [M] group (Fig. 21). The holotype of *P. phaulomorphus* Buckman (1926 in 1909–1930, TA-VI, pl. 643) lacks a zigzag-stadium, but is a very small adult (D = 56 mm), and the possible occurrence of parabolae in this taxonomic group needs further investigation.

Protozigzagiceras [m & M] and *Franchia* [M & m] represent progenetic zigzagiceratins, directly or indirectly branched off from *Procerites* [M] – *Siemiradzkia* [m],

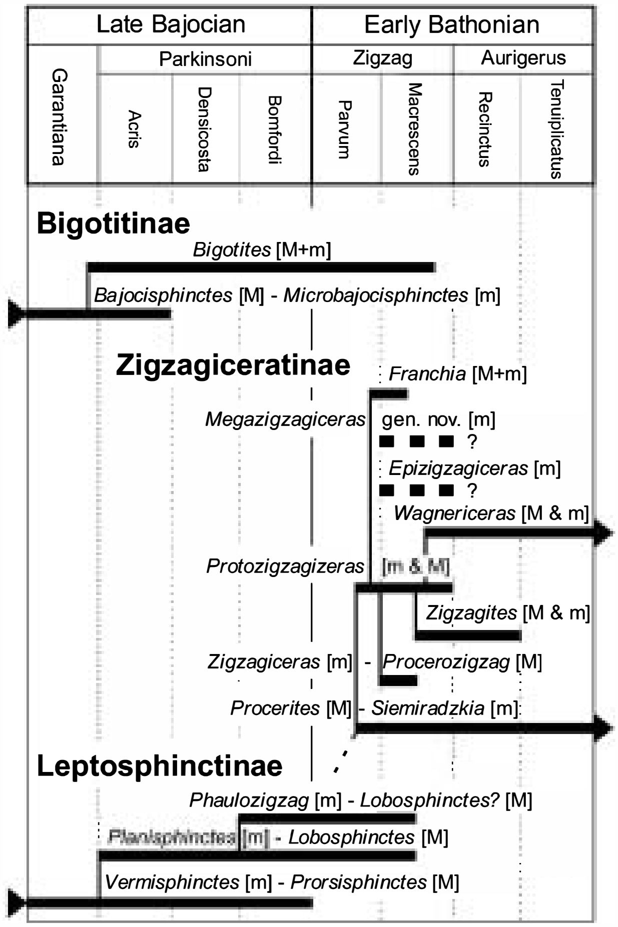

FIG. 21. Phylogenetic scheme of the Early Bathonian genera of Zigzagiceratinae, originated from Leptosphinctinae and diversified during Parvum and Macrescens subzones (Zigzag Zone, Early Bathonian), before the extinction of *Bigotites*. Geochronological divisions after Pavia *et al.* (2008) and Fernandez-Lopez *et al.* (2009*a*, *b*).

whereas *Zigzagiceras* [m] – *Procerozigzag* [M] represents a neotenic zigzagiceratin branched off from *Protozigzagiceras* [m & M]. *P. tethycum* and *F. arkelli* appear progenetic because they attain maturity at a relatively small size. *Protozigzagiceras* [m & M] and *Franchia* [M & m], besides zigzag-state 2, display morphological features characteristic of the earliest *Procerites* at a juvenile stage, such as relatively planorbiconic and evolute coiling with relatively simple suture lines. *Protozigzagiceras* [m & M] spreads in middle latitudes to many northern Peri-Tethyan basins, from Proto-Atlantic Ocean and Lusitanian Basin (Buckman 1892, pl. 13, figs 1, 2; Dietze and Chandler 1997, pl. 1, figs 3, 4; Fernandez-Lopez *et al.* 2007, fig. 11), through Alpine Ocean, Subalpine Basin and Tizia (Sturani 1967, pl. 13, fig. 4, pl. 15, fig. 1, pl. 19, fig. 5, pl. 21, figs 1, 3, 7, pl. 22, fig. 1; Galacz 1980, pl. 32; Sandoval 1983, pl. 35, fig. 3; Torrens 1987, pl. 8, figs 2–5; Schlögl *et al.* 2005, pl. 10, figs 4, 5, pl. 12, fig. 1; Fernandez-Lopez *et al.* 2007, figs 10, 12; Pavia *et al.* 2008, pl. 3, figs 6, 7, 9–12; Fernandez-Lopez *et al.* 2009*a*, fig. 6b), to the Iranian platform system (Shafizadeh and Seyed-Emami 2005, figs 10, 11; Shams and Seyed-Emami 2010). On the other hand, *Franchia* seems to be endemic to Subalpine areas, near the Provence–Ardeche platform system.

Zigzagiceras [m] – *Procerozigzag* [M], in addition to zigzag-state 3 ribbing and a complex suture line, displays a relatively planorbiconic and evolute coiling, in particular *Zigzagiceras euryodos* Schmidt [m] (1846, p. 106, pl. 43, fig. 6a–b) and *Zigzagiceras pseudoprocerum* Buckman [M] (1926 in 1909–1930, TA-VI, pl. 623). This dimorphic group becomes widely distributed along the northern border of Western Tethys. The primitive and evolute *Zigzagiceras*, in particular *Z. euryodos* [m & M], may be a direct neotenic derivative of *P. densum*, at the basal Macrescens Subzone. The group of *Z. imitator* Buckman [M] (1922 in 1909–1930, TA-IV, pl. 301) and *Z. lenthayense* [m] sensu Sturani (1967, p. 48, pl. 20, fig. 4) non Arkell (1958 in 1951–1958, p. 204, pl. 23, fig. 6a–b) was suggested as homeomorphic with *Procerites* by Torrens (1987). This group, and the stouter group of *Wagnericeras* Buckman [M & m] (1921 in 1909–1930, TA-III, p. 33), both recorded at the level BA8 (in Sturani 1967), may have originated by neoteny from more involute and depressed species such as *P. flexum* during the Macrescens Subzone. In this way, *Zigzagites* [M & m] and *Wagnericeras* [M & m] could be two neotenic zigzagiceratins, independently branched off from *Protozigzagiceras*. Also, *Megazigzagiceras* and *Epizigzagiceras*, showing zigzag-state 2 and lacking distant, sharp, parabolic ribs, can be regarded as neotenic groups phyletically derived from diverse species of *Protozigzagiceras*. Both derivative genera probably correspond to Macrescens and/or post-Macrescens intervals, being very improbable from any Late Bajocian interval (Fig. 21). The phyletic position of these two large-sized genera and the above-mentioned Chilean zigzagiceratins, however, still requires further investigation.

In summary, rapid proterogenesis gave rise to the earliest Bathonian zigzagiceratin lineages, producing paedomorphic members, commonly neotenic and more scarcely progenetic (Fig. 21). In contrast, the successive species of *Protozigzagiceras* (from *P. tethycum* to *P. torrensi* and *P. postpollubrum*) and *Franchia* (from *F. arkelli* to *F. subalpina*) show trends towards increasing involution of initially evolute planorbicones to more weakly ornamented discocones in the Bas Auran area. Other species of *Protozigzagiceras*, such as *P. densum* and *P. flexum*, show relatively complex suture line and novel structures (polyfurcate and flexuous ribs, respectively) in preadult ontogenic stages later developed in the adult phragmocone of *Zigzagiceras*, *Zigzagites* and *Wagnericeras*. A chronocline towards the more involute *Zigzagiceras zigzag* [m & M] has been recorded in Catalan Basin at the Macrescens Subzone (Fernandez-Lopez 2000, fig. 2, pl. 1, fig. 9). In turn, plesiomorphic representatives, older and more planorbiconic than *P. densum*, have been recorded in the uppermost Parvum Subzone of Cap Mondego. Therefore, most of the earliest Bathonian phyletic lineages of the clade Zigzagiceratinae developed lasting peramorphoclines with increasing hydrodynamic coiling of the shell and increasing adult size (at least, in the microconchs), in an opposite sense to the previous, rapid, paedomorphic changes.

In conclusion, the ancestor of the clade Zigzagiceratinae can be found in the genus *Procerites*, rapidly diversified in multiple phyletic lineages by iterative, paedomorphic changes and additional, lasting, peramorphic modifications during the Early Bathonian Zigzag Zone. The Mediterranean–Caucasian genera *Franchia*, *Zigzagiceras*, *Zigzagites* and *Wagnericeras* are phyletically derived of successive species of *Protozigzagiceras*, which is itself a direct derivative of *Procerites*. This evolutionary pattern produced numerous and brief phyletic lineages with common homeomorphisms. These new palaeontological results concerning the oldest Zigzagiceratinae are of biochronostratigraphical importance for calibration of the basal Bathonian and correlation of the Bathonian GSSP.

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New species of *Franchia* and *Protozigzagiceras* (Ammonoidea, Middle Jurassic): the phyletic origin of Zigzagiceratinae

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Measurements

A. Measurements for the specimens of *Franchia arkelli* Sturani, 1967

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	[illegible]
PU31689	Figs. 4A–B holotype	[M]	220.0	60.0	27.3%	61.2	27.8%	101.6	46.2%	1.02	14	35	2.5
			170.0	53.8	31.6%	52.0	30.6%	78.2	46.0%	0.97	15	–	–
PU31690	Figs. 5E–F	[M]	147.0	43.5	29.6%	40.0	27.2%	71.8	48.8%	0.92	–	–	–
			114.0	34.5	30.3%	34.7	30.4%	54.8	48.1%	1.01	20	45	2.3
PU112317	–	[M]	92.0	31.9	34.7%	29.4	32.0%	40.2	43.7%	0.92	16	–	–
PU31691	Figs. 5A–C	[M]	70.0	22.5	32.1%	22.0	31.4%	33.0	47.1%	0.98	–	–	–
			53.0	13.7	25.8%	16.8	31.7%	23.9	45.1%	1.23	22	–	–
PU111325	Fig. 6D	[M]	75.0	23.8	31.7%	23.3	31.1%	31.9	42.5%	0.98	17	–	–
PU112318	Figs. 4D, 7A	[m]	31.5	9.3	29.5%	9.8	31.1%	14.6	46.3%	1.05	–	–	–

B. Measurements for the specimens of *Franchia subalpina* sp. nov.

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	[illegible]
PU111399	Fig. 6A holotype	[M]	140.0	46.5	33.2%	43.0	30.7%	57.7	41.2%	0.92	–	45	–
			75.0	26.0	34.7%	30.0	40.0%	33.0	44.0%	1.15	16	–	–
PU111578	–	[M]	45.0	12.5	27.8%	20.1	44.7%	19.2	42.7%	1.61	16	–	–
PU111573	Figs.6B–C, 7B–C	[m]	32.0	10.5	32.8%	9.8	30.6%	15.3	47.8%	0.93	19	32	1.7

C. Measurements for the specimens of *Protozigzagiceras torrensi* (Sturani)

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	i
PU31725	Torrens 1987, pl. 9, fig. 3	[M]	115.6	41.0	35.5%	45.1	39.0%	43.8	37.9%	1.10	21	44	2.1
			94.4	33.7	35.7%	38.0	40.3%	37.7	39.9%	1.13	20	44	2.2
PU31717	Figs. 11A–B	[M]	105.7	46.2	43.7%	48.2	45.6%	30.5	28.9%	1.04	17	48	2.8
			79.0	30.0	38.0%	31.5	39.9%	26.5	33.5%	1.05	–	–	–
PU31711	Torrens 1987, pl. 8, fig. 2	[M]	98.9	38.0	38.4%	38.0	38.4%	36.0	36.4%	1.00	20	39	2.0
			75.9	27.4	36.1%	29.6	39.0%	29.2	38.5%	1.08	24	42	1.8
PU31719	Sturani 1967, pl. 15, fig. 1	[M]	93.3	42.8	45.9%	39.4	42.2%	28.6	30.7%	0.92	21	46	2.2
			77.9	31.8	40.8%	31.6	40.6%	24.6	31.6%	0.99	19	44	2.3
PU31720	Figs. 12A–B	[M]	67.4	23.5	34.9%	25.9	38.4%	28.7	42.6%	1.10	22	36	1.6
			52.0	18.1	34.8%	20.6	39.6%	22.9	44.0%	1.14	20	34	1.7
PU31680	Figs. 10G–H	[m]	61.0	21.5	35.2%	21.8	35.7%	25.0	41.0%	1.01	20	–	–
PU31677	Figs. 10I–J	[M?]	55.0	20.1	36.5%	23.5	42.7%	23.0	41.8%	1.17	26	–	–
PU31681	Figs. 10E–F	[m]	52.0	18.0	34.6%	19.5	37.5%	22.8	43.8%	1.08	21	36	1.7
			38.0	13.0	34.2%	14.2	37.4%	18.1	47.6%	1.09	20	31	1.6
PU31676	Figs. 10A–D holotype	[m]	49.0	15.6	31.8%	20.5	41.8%	21.2	43.3%	1.31	24	–	–
PU31682	Figs. 10K–M	[m]	44.0	15.0	34.1%	16.7	38.0%	20.5	46.6%	1.11	20	33	1.7
			33.0	10.0	30.3%	12.5	37.9%	16.1	48.8%	1.25	23	34	1.5
PU111577	Pavia *et al.* 2008, pl. 3, figs. 9–10	[M]	39.2	13.0	33.2%	17.0	43.4%	18.0	45.9%	1.31	22	–	–

D. Measurements for the specimens of *Protozigzagiceras tethycum* sp. nov.

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	i
PU31694	Figs. 16H–I	[M]	51.0	17.0	33.3%	17.0	33.3%	20.1	39.4%	1.00	20	39	2.0
			37.0	14.0	37.8%	14.0	37.8%	15.9	43.0%	1.00	21	–	–
PU111299	Figs. 16E–G	[m]	40.0	14.6	36.5%	11.6	29.0%	17.1	42.8%	0.79	23	46	2.0
			28.0	9.0	32.1%	8.1	28.9%	12.9	46.1%	0.90	19	–	–
PU111574	Figs. 16J–L holotype	[m]	36.0	10.0	27.8%	12.4	34.4%	17.4	48.3%	1.24	19	33	1.7
PU31695	Figs. 16A–D	[m]	30.0	9.7	32.3%	10.5	35.0%	13.6	45.3%	1.08	19	36	1.9
			33.0	10.0	30.3%	12.5	37.9%	16.1	48.8%	1.25	23	34	1.5

E. Measurements for the specimens of *Protozigzagiceras flexum* sp. nov.

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	i
PU112319	Figs. 17E–F	[M]	51.3	16.3	31.8%	14.9	29.0%	21.6	42.1%	0.91	–	–	–
			41.5	13.7	33.0%	14.1	34.0%	17.4	41.9%	1.03	24	46	1.9
PU111326	Figs. 17A–D holotype	[m]	41.0	13.1	32.0%	15.0	36.6%	19.0	46.3%	1.15	–	–	–
			30.0	9.2	30.7%	11.0	36.7%	14.6	48.7%	1.20	24	38	1.6

F. Measurements for the specimens of *Protozigzagiceras densum* sp. nov.

Specimens	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	i
PU111322	Figs. 18A–D holotype	[m]	35.6	11.5	32.3%	13.8	38.8%	16.1	45.2%	1.20	18	46	2.6

G. Measurements for the specimens of *Megazigzagiceras subarabicum* sp. nov.

Specimen	Figures		D	H	H/D	W	W/D	U	U/D	W/H	Ni/2	Ne/2	i
FSL 177 639	Figs. 19A–B holotype	[m]	100.0	22.3	22.3%	25.0	25.0%	60.0	60.0%	1.12	16	–	–