

***Geczyceras* (Hammatoceratidae, Ammonoidea) in the western Tethys: biostratigraphic analysis between Northwest European Province (Iberian Range) and Mediterranean Province (Betic Cordillera)**

Gemma MARTÍNEZ¹, José SANDOVAL², Soledad URETA¹, & Antonio GOY¹

¹Departamento y UEI de Paleontología, Facultad de C.C. Geológicas e Instituto de Geología Económica (UCM-CSID),
C/José Antonio Novais 2, 28040, Madrid. E-mail: gemmamar@geo.ucm.es

²Departamento de Estratigrafía y Paleontología, Universidad de Granada, Av. Fuentenueva s/n, 18002, Granada, Spain

Abstract

The stratigraphic record of the different species belonging to genus *Geczyceras* MARTÍNEZ, 1992 once found in the Iberian Range and Betic Cordillera stretches from the Variabilis/Gradata Zone to the Aalensis Zone of the Toarcian. Most of the species, including *G. speciosum* (JANENSCH), *G. perplanum* (PRINZ), *G. porcarellaense* (BONARELLI) and *G. allobrogense* (DUMORTIER), are represented in both mountain ranges. *Geczyceras costulosum* (MERLA) and *G. cf. tipperi* (SEYED-EMAMI) are, however, only represented in the Betic Cordillera, while *G. costatum* (GABILLY), *G. clausum* (GABILLY) and *G. gabillyi* MARTÍNEZ are only represented in the Iberian Range. The present work compares the biostratigraphic distributions of the species of this genus identified in these domains, and notes differences between the first and last records for the most common.

Keywords: *Geczyceras*, *Hammatoceratinae*, *Ammonitina*, *Toarcian*, *Jurassic*, *Spain*

Introduction

In agreement with its original diagnosis, genus *Geczyceras* MARTÍNEZ (1992b, p. 65) includes hammatoceratids with evolute shells, the inner whorls of which are rounded in cross-section, and the outer whorls are subovate and compressed. Their flanks are parallel or subparallel, and the umbilicus is shallow. They have moderate ornamentation with regular tubercles and sinuous ribbing. The septal suture is complex. L is long, narrow and branched, and the U lobes well-developed and retracted. These morphological characters differentiate the genus from others of the family Hammatoceratidae such as *Hammatoceras* HYATT and *Crestaites* RULLEAU & ELMÍ, as well as those of the closely related Erycitidae, e.g., *Erycites* GEMMELLARO, and *Cagliceras* RULLEAU & ELMÍ.

Hammatoceras speciosum JANENSCH (1902, pl. 4, fig. 4, pl. 10, fig. 1) was originally designated by MARTÍNEZ (1992b) as the type species of *Geczyceras* since it was deemed that best reflected the diagnostic features of the genus. However, RULLEAU et al. (2001) and RULLEAU (2009) proposed a new type species, *Hammatoceras porcarellaense* BONARELLI, 1898, which appeared in MENEGHINI (1867–1881, pl. 14, fig. 3). The present authors, however, believe that *Geczyceras speciosum* should be the type species given its original designation (ICZN) and worldwide distribution in basin and platform

environments (see MARTÍNEZ 1992b, CRESTA 1994, RULLEAU 2009, KOVÁCS 2009, SANDOVAL et al. 2011).

It should be noted that RULLEAU & ELMÍ (in RULLEAU et al. 2001) proposed the genus *Crestaites* (type species *Hammatoceras meneghinii* BONARELLI, 1899, in MENEGHINI 1867–1881, pl. 13, fig. 1) to separate the clearly tuberculate forms from those only ribbed. This new genus included three species considered by MARTÍNEZ (1992b) to belong to *Geczyceras*: *Geczyceras meneghinii* (BONARELLI), *Geczyceras victorii* (BONARELLI) and *Geczyceras goyi* MARTÍNEZ. They also considered *Crestaites* to include “*Hammatoceras*” *tipperi* SEYED-EMAMI, although later, KOVÁCS (2009) in his detailed study of the subfamily Hammatoceratinae, would return it to *Geczyceras*. The fact that *Crestaites* includes non-tuberculate forms, and the recognition that these are generally stratigraphically more recent, would justify the proposal of this genus. However, these species show the septal suture typical of *Geczyceras*, and both genera may therefore be part of a single evolutionary line within the notable adaptive radiation shown by the family Hammatoceratidae from the Late Toarcian (see MARTÍNEZ et al. 2010, fig. 1).

In the Iberian Range, the standard scale used as the chronostratigraphic reference for the Upper Toarcian in the interval between the Bifrons and Pseudoradosa Zones, is that proposed by ELMÍ et al. (1997) and PAGE (2003). In the Betic

Cordillera, the proposal of SANDOVAL et al. (2012) is contemplated for the interval between the Bifrons and Meneghini Zones, while the zonation proposed by SANDOVAL et al. (2001) has been adopted for the latest Toarcian (Aalensis Zone) in both ranges.

Among the recent systematic and biostratigraphic studies of *Geczyceras*, the following are particularly notable: ELMI & RULLEAU (1993), MARTÍNEZ (1992a, b, 1996), GOY et al. (1994, 1995), CRESTA et al. (1995), RULLEAU (1996, 2007, 2009), RULLEAU et al. (2001), PETTINELLI et al. (1997), VENTURI & FERRI (2001), VENTURI & ROSSI (2003), BÉCAUD et al. (2005), CARACUEL et al. (2006), ELMI et al. (1997, 2007), GÉCZY & SZENTE (2007), EL HAMMACHI et al. (2009), GÉCZY et al. (2008), KOVÁCS (2009), KOVÁCS & GÉCZY (2008), MARTÍNEZ et al. (2010, 2012) and SANDOVAL et al. (2011).

Geczyceras in the Iberian Range and Betic Cordillera

In the Iberian Range (Figure 1), the Upper Toarcian is represented by rhythmic successions of marls and limestones (mudstones/wackestones) (with a predominance of marls), giving rise to the Turmiel Formation (GOY et al. 1976). Sedimentation probably occurred in a platform or shallow and well-communicated, open, external ramp environment where the hydrodynamic conditions were relatively tranquil, and below the level of the wave base (GABALDÓN et al. 1991, GÓMEZ & GOY 2005). Ammonoids are common in this sediment. However, the record for *Geczyceras* is scarce and discontinuous.

In the Betic Cordillera (Figure 1), *Geczyceras* is more commonly represented at localities within the Median Subbetic domain, the only Betic domain showing more or less continuous pelagic or hemipelagic sedimentation over the entire Toarcian. The dominant sediments are formed by alternations of marls and grey marl-limestones, although some grey limestone intervals exist (sometimes containing chert nodules), as do some of red, nodular limestone. *Geczyceras* has also been recorded in condensed facies of nodular limestones within the Maláguide Complex of the Internal Zones of the Betic Cordillera (CARACUEL et al. 2006).

Analysis of different representatives of *Geczyceras*

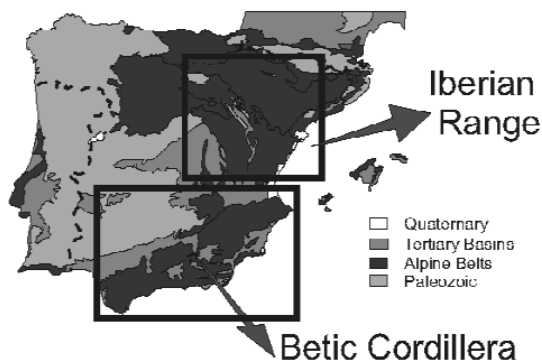


Figure 1. Geographic situation of Iberian and Betic Ranges in the Iberian Peninsula

collected from the Iberian Range and Betic Cordillera shows that the common species of both domains are *G. speciosum* (JANENSCH), *G. porcarellaense* (BONARELLI), *G. perplanum* (PRINZ) and *G. allobrogense* (DUMORTIER). The Iberian Range also contains records of *G. costatum* (GABILLY), *G. clausum* (GABILLY), *G. gabillyi* MARTÍNEZ and *G. aff. bonarellii* (PARISH & VIALE), while the Betic Cordillera (Subbetic domain) contains (although in very small numbers) *G. cf. tipperi* (SEYED-EMAMI) and *G. costulosum* (MERLA). Figure 2 shows the biostratigraphic positions of these species in both areas.

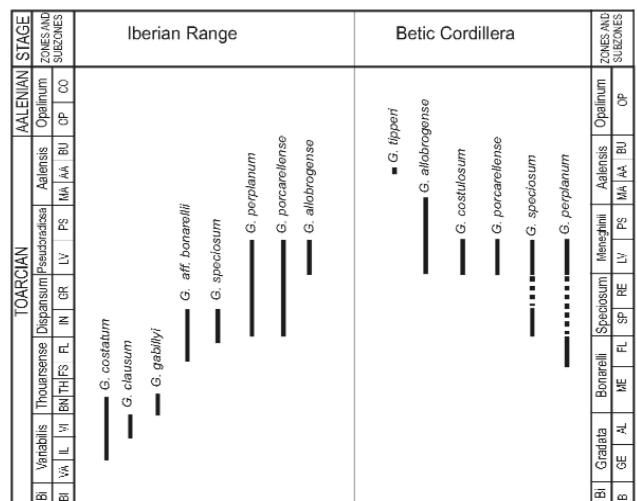


Figure 2. Biostratigraphic distribution of *Geczyceras* species recorded in the studied areas. Abbreviations: BI, Bifrons; VA, Variabilis; IL, Illustis; VI, Vitiosa; BN, Bingmanni; TH, Thouarsense; FS, Fascigerum; FL, Fallaciosum; IN, Insigne; GR, Gruneri; LV, Levesquei; PS, Pseudoradiosa; MA, Maetra; AA, Aalensis; BU, Buckmani; OP, Opalinum; CO, Comptum; GE, Gemma; AL, Alticarinatus; ME, Mediterranean; SP, Speciosum; RE, Reynesi. Zonal Scale adopted from ELMI et al. 1997, Page 2003 and SANDOVAL et al. 2012 for Upper Toarcian (excepted Aalensis Zone) and SANDOVAL et al. 2001 for uppermost Toarcian (Aalensis Zone)

Systematic palaeontology

Superfamily Hammatoceratoidea SCHINDEWOLF, 1964
 Family Hammatoceratidae BUCKMAN, 1887
 Subfamily Hammatoceratinae BUCKMAN, 1887

Genus *Geczyceras* MARTÍNEZ, 1992

Type species by original designation: *Hammatoceras speciosum* JANENSCH, 1902. The type species (JANENSCH 1902, pl. 10, fig. 1) was designated by MARTÍNEZ (1992b, p. 65).

Geczyceras costatum (GABILLY, 1973) (Plate 1, fig. 1)

1973 *Hammatoceras costatum* nov. sp.; GABILLY, p. 421, pl. 67, figs 1–3.

1992b *Geczyceras? costatum* (GABILLY, 1973) (M); MARTÍNEZ, p. 66, p. 68, text-fig. 8, pl. 1, figs 1–2.

Description: Coiling evolute. Flanks convex and convergent, varying from subrounded to subgival

throughout ontogeny. Ventral region rounded. Keel slightly differentiated, thick, less raised. Umbilicus wide and shallow. Ornamentation prominent, involving thick primary ribs arising from the umbilical wall; these reach their maximum width at the umbilical margin and run approximately half the length of the flank. These primary ribs are straight, proverse and somewhat thicker than the intercostal spaces. The inner whorls bifurcate or rarely trifurcate into secondary ribs also thicker than the intercostal spaces. The secondary ribs are also proverse, concave (especially the anterior ones), and disappear before reaching the ventral region, leaving a smooth band instead of keel. The peripheral projection of the ribs is very short and very marked.

Stratigraphic distribution: Iberian Range, Variabilis Zone (Illustis Subzone) – Thouarsense Zone (Bingmanni Subzone).

Geczyceras clausum (GABILLY, 1973)
(Plate 1, fig. 2)

1973 *Hammatoceras clausum* nov. sp.; GABILLY, p. 432, pl. 66, figs 7–8.

1992b *Geczyceras? clausum* (GABILLY, 1973); MARTÍNEZ, p. 69, p. 70, text-fig. 9; pl. 1, fig. 3.

Description: Coiling moderately involute until the last whorl, at which a notable uncoiling is apparent. Slightly depressed in cross-section, and varying from subrounded to subovate. Ventral region rounded with a fine, slightly elevated keel. Flanks gently convex and convergent; maximum width of the cross-section in the lower part of the flank. Umbilicus narrow, quite deep, with a mildly convex and abrupt wall with a rounded margin. Ornamentation fine to moderate, including primary ribs with thickened bases reminiscent of tubercles. They originate at the umbilical wall, close to the margin; rectiradiate or slightly proverse, thick, short, and wider than the intercostal spaces. Just at the end of the internal third of the flank they divide into three secondary ribs of lesser relief but still wider than the intercostal spaces. Sinuous and faintly proverse. At the end of the flank they project forwards. Their peripheral projection is short, but approaching the keel. The sinuosity of the ribs becomes attenuated along of last visible whorl.

Stratigraphic distribution: Iberian Range, Variabilis Zone (Vitiosa Subzone).

Geczyceras gabillyi MARTÍNEZ, 1992
(Plate 2, fig. 1)

1973 *Hammatoceras* aff. *victorii* BONARELLI; GABILLY, p. 435, pl. 68, figs 3–4.

1992b *Geczyceras? gabillyi* n. sp. (M); MARTÍNEZ, p. 71, p. 72, text-fig. 10; pl. 2, fig. 1.

Description: Coiling evolute, cross-section subovate, compressed. Slightly convex and convergent flanks. Maximum width of the cross-section in the lower part of the flanks. Ventral region rounded with a less differentiated keel

appearing as a smooth, fine band. Umbilicus wide, wall slightly convex and abrupt, margin rounded. Strong ornamentation including thick, rounded tubercles located a little above the umbilical margin; tubercles regularly spaced and about as wide as the inter-tubercular spaces. From the tubercles originate three slightly convex, proverse ribs. On the upper third of the flank, these curve forward but have a short peripheral projection. They are dense and somewhat thicker than the intercostal spaces. On the last visible whorl, the ornamentation is considerably attenuated, and the tubercles substituted by primary ribs that give rise to secondary ribs, which reach the ventral region. In the last half whorl, the loss of ornamentation becomes more pronounced, and the spiral uncoils rapidly.

Stratigraphic distribution: Iberian Range, Thouarsense Zone (probably Bingmanni Subzone).

Geczyceras aff. *bonarellii* (PARISCH et VIALE, 1906)
(Plate 1, fig. 3)

1906 *Hammatoceras Bonarellii* n. sp.; PARISCH & VIALE, p. 159, pl. 10, figs 1–4.

1992b *Geczyceras* aff. *bonarellii* (PARISCH & VIALE); MARTÍNEZ, p. 74, p. 75, fig. 11, pl. 3, fig. 1.

Description: Coiling evolute, subovate in cross-section, compressed, somewhat more rounded on the inner whorls. Flanks convex. Umbilicus wide and quite shallow. Ornamentation moderate, with small tubercles on the umbilical margin. Each tubercle gives rise to three ribs, sometimes one intercalated, all rectiradiate and very dense. The ribs reach the keel but their peripheral projection is very short. The septal suture is complex with E long, thin and slightly branched, covering over two thirds the length of L. L narrow, symmetrical, with oblique branches, quite ramified. SL1 is narrow but not very complex, with a thick, slightly branched accessory lobe. SL2 is rather larger with three small, accessory lobes.

Stratigraphic distribution: Iberian Range, Thouarsense Zone (Fallaciosum Subzone) – Dispansum Zone (Insigne Subzone).

Geczyceras speciosum (JANENSCH, 1902)
(Plate 3, fig. 1; Plate 5, fig. 1)

1902 *Hammatoceras speciosum* n. sp.; JANENSCH, p. 102, pl. 4, fig. 4, pl. 10, fig. 1.

1992b *Geczyceras speciosum* (JANENSCH); MARTÍNEZ, p. 75, p. 78, text-fig. 12, pl. 3, figs 2–3, pl. 4, figs 1–2, pl. 5, figs 1–2, pl. 6, fig. 1, pl. 7, fig. 1, pl. 8, fig. 1.

Description: Coiling moderately evolute. Sub-circular in cross-section; depressed in the first three whorls, becoming compressed and subovate with growth. Flanks convex until the third whorl, after which they become flatter, parallel and gently convergent. Ventral region rounded; keel fine, slightly elevated. During ontogeny it becomes progressively sharper and the keel thicker and more raised. Umbilicus wide, shallow. Ornamentation moderate, com-

posed of tubercles situated above the umbilical margin. These are rounded, coming to a point, and very regularly spaced; width the same as the inter-tubercular spaces. The tubercles give rise to two or three sinuous, dense secondary ribs wider than the intercostal spaces, gently proverse, and with only a short peripheral projection. Septal suture rather complex; E long, reaching three quarters of the length of L and with four visible branches. L is long, straight and branched; branches symmetrical, slightly oblique. U3 and U2 oblique, long and directed towards the tip of L. SL2 narrow with two notable accessory lobes. SL1 also narrow and complex with a long accessory lobe.

Stratigraphic distribution: Iberian Range, Thouarsense Zone (Fallaciosum Subzone) – Dispansum Zone (Insigne Subzone); Betic Cordillera: Speciosum Zone (Speciosum Subzone) and Meneghinii Zone (Levesquei Subzone).

Geczyceras perplanum (PRINZ, 1904)

(Plate 4, fig. 1; Plate 5, figs 2–3; Plate 6, fig. 1)

1867–1881 *Ammonites insignis* SCHÜBLER, MENEGHINI, p. 55, pl. 12, fig. 3.

1904 *Hammatoceras insigne* SCHÜBLER, mut. nov. *perplana*; PRINZ, p. 72.

1992b *Geczyceras perplanum* (PRINZ); MARTÍNEZ, p. 87, p. 89, text-fig. 15, pl. 12, figs 2–4.

Description: Coiling evolute, tending towards serpenticone during growth. Subtrapezoid in cross-section, compressed. Inner whorls more rounded, becoming depressed. Flanks rounded in the inner whorls, becoming almost flat and convergent in the outermost whorls. Ventral area rounded with a fine, slightly elevated keel. Maximum width of the whorl reached in the internal third of the flank. Large umbilicus, becoming more accentuated with growth, flat, rather shallow. Ornamentation generally strong; primary ribs short and thick, arising from below the umbilical margin. Rounded tubercles present above the umbilical margin, elevated, very regular, giving rise to two or three straight secondary ribs, somewhat proverse and clearly thicker than the intercostal space. Reaching the ventral region they project slightly forward and disappear before the keel. On the outer whorls the tubercles are thicker and of less conspicuous relief, as are the ribs. Septal suture rather complex; E not so thin, covers more than three quarters of the length of L. L long, thin, complex, practically symmetrical; U lobes long, thick, slightly branching, somewhat oblique and approaching one another, and directed towards the tip of L. SL1 narrow but not complex and with an accessory lobe. SL2 rather larger, also with accessory lobes but somewhat larger and more complex.

Stratigraphic distribution: Iberian Range: Dispansum Zone (Insigne Subzone) – Pseudoradiosa Zone (Levesquei Subzone); Betic Cordillera: Bonarellii Zone (Fallaciosum Subzone) and Meneghinii Zone (Levesquei Subzone).

Geczyceras porcarellense (BONARELLI, 1899)

(Plate 1, fig. 4; Plate 6, fig. 4)

1867–1881 *Ammonites insignis* SCHÜBLER; MENEGHINI, p. 58, pl. 14, fig. 3, pl. 16, fig. 1.

1899 *Hammatoceras porcarellense* n. sp.; BONARELLI, p. 209 [refigured of MENEGHINI (1867–1881), pl. 14, fig. 3].

1992b *Geczyceras porcarellense* (BONARELLI); MARTÍNEZ, p. 83, p. 85, text-fig. 14, pl. 11, figs 2–4.

Description: Coiling varies from moderately involute to evolute with growth. Cross-section subovate, depressed in the inner whorls, becoming subovate and compressed in the outer whorls. Flanks clearly convex in innermost whorls, becoming progressively flatter. Ventral region rounded with a fine, slightly elevated keel that widens with ontogeny. Umbilicus moderately narrow, rather shallow; umbilical wall convex, abrupt and with a rounded margin. Ornamentation includes small tubercles very close to the umbilical margin. Tubercles are dense, rounded, regular, somewhat thicker than the intertubercular spaces, well-differentiated in the outermost whorls but hardly visible in the innermost. Tubercles bifurcate, sometimes trifurcate, giving rise to very dense, fine, straight and slightly proverse ribs. In the upper third of the flank these ribs curve slightly forwards but have a very short peripheral projection; they disappear before reaching the keel, leaving two fine, lateral bands. Septal suture complex, E reaches little beyond the first half of L. L long and thin with oblique, asymmetrical branches. U lobes oblique, approaching one another, directed towards the tip of L. SL1 and SL2 rather narrow and with numerous accessory lobes.

Stratigraphic distribution: Iberian Range: Dispansum Zone (Insigne Subzone) – Pseudoradiosa Zone (Levesquei Subzone); Betic Cordillera: Meneghinii Zone (Levesquei Subzone).

Geczyceras allobrogense (DUMORTIER, 1874)

(Plate 4, fig. 2; Plate 6, figs 2–3, 5)

1874 *Ammonites Allobrogensis* n. sp.; DUMORTIER, p. 79, pl. 19, figs 1–2.

1992b *Geczyceras allobrogense* (DUMORTIER); MARTÍNEZ, p. 104, p. 106, text-fig. 20, pl. 18, figs 2–6.

Description: Coiling moderately evolute. Cross-section varies from subrounded in the inner whorls to subovate compressed in the outermost. Ventral region rounded, keel fine and somewhat elevated in the inner whorls, becoming thicker and more elevated in the outermost. Flanks convex, with maximum cross-section width towards the lower half of the flanks. Umbilicus moderately wide and deep, margin rounded, wall smooth and strongly inclined. Ornamentation composed of tubercles located above the umbilical margin. On the inner whorls they arise close to the margin and are small, pointed, very dense and rather regular. On the outermost they arise at the end of the first third of the flank; they are clearly visible, thick, rounded, with high relief, and regularly spaced. From them in turn arise three ribs, two external and one intercalated. On the inner whorls these ribs are fine, dense and

straight, and reach the keel, they show no peripheral projection. On the outer whorls they appear thicker, sinuous, and in the upper third of the flank they become proverse. They disappear before reaching the keel, and show only a short peripheral projection. Septal suture shows a long E that slightly exceeds half of the length of L, thin and moderately branched. L long, thin, and with oblique, asymmetrical lateral branching. U lobes long and slightly branched, oblique, directed towards the tip of L. SL1 and SL2 rather narrow, each with a long but slightly complex branch.

Stratigraphic distribution: Iberian Range: Pseudoradiosa Zone (Levesquei Subzone). Betic Cordillera: Meneghinii Zone (Levesquei and Pseudoradiosa Subzones) and Aalensis Zone (Mactra Subzone).

Geczyceras costulosum (MERLA, 1934)
(Plate 6, fig. 6)

1934 *Hammatoceras costulosum* n. sp.; MERLA, p. 13, pl. 1, figs 3–4.

1995 *Geczyceras costulosum* (MERLA); GOY et al. p. 100, pl. 12, fig. 1.

Description: The Subbetic specimen is of medium size; complete phragmocone reaches approximately 100 mm in diameter. Coiling moderately evolute with narrow and deep umbilicus on the innermost whorls, becoming wider and shallow on the last preserved whorl. Cross-section subcircular in the inner whorls, becoming ovate-ogival and compressed at the phragmocone end and in the body chamber. On the outermost whorls, the umbilical wall and umbilical margin are slightly developed. Flanks slightly convex with ventrolateral shoulders and a rounded ventral area. Short, proverse primary ribs originate at the base of the umbilical wall; near the umbilical shoulder they divide into two or three secondary ribs, finer than the primaries and arched forward. They reach the ventral area where they fade away on both sides of the keel. Secondary ribs are fine, well-marked on the inner whorls but becoming wider and more widely spaced on the middle and outer whorls. Keel slightly marked, disappearing at the body chamber end. The ventral area is rounded on the inner and middle whorls. Septal suture, rather with erycitid character, has short E and retracted U lobes.

Stratigraphic distribution: Betic Cordillera: Meneghinii Zone (Levesquei Subzone).

Geczyceras cf. tipperi (SEYED-EMAMI, 1967)
(Plate 6, fig. 7)

1967 *Hammatoceras tipperi* n. sp.; SEYED-EMAMI, p. 72, pl. 2, figs 16–17; pl. 9, figs 1–2.

Description: The only specimen available is incomplete and laterally squashed, making a proper identification and description very difficult. Coiling moderately evolute. Cross-section (though deformed) ovate, compressed, with convex flanks and with maximum width in the lower third of the flank. Ventral region has a fine keel, somewhat elevated.

Umbilical margin rounded; confounded with the umbilical wall. Ornamentation involves primary ribs, very short and radial, almost tuberculiform, but not very marked. Near the umbilical margin they divide into two, rarely three, radial secondary ribs. These are well marked, relatively dense, and curve slightly forwards near the keel. Septal suture not preserved. The specimen (with a diameter of about 61 mm) is very similar in size to the holotype of “*Hammatoceras tipperi*” described by SEYED-EMAMI (l.c.). The only small difference is that the Iranian holotype has more clearly marked primary ribs on the internal whorls than does the Subbetic specimen.

Stratigraphic distribution: Betic Cordillera: Aalensis Zone (Aalensis Subzone).

Discussion and conclusions

The origin of *Geczyceras* is uncertain, although it might be related to some primitive members of Hammatoceratidae that inhabited the Tethys. The genus shows clear affinity with the earliest members of the Erycitidae (*Cagliceras*) (SANDOVAL et al. 2015). Starting at the Dispansum/Speciosum Zone it probably gives rise to species belonging to genera *Hammatoceras*, *Bredyia*, and *Eudmetoceras*, which are typical of platform environments. It is also related to *Crestaites* and *Accardia*, which are more common in basin environments (MARTÍNEZ et al. 2010).

From a palaeobiogeographic standpoint, *Geczyceras* is typical and abundant in basin environments of the western Tethys. However, it has also been found in platforms of NW Europe and America (Figure 3), although the record of the

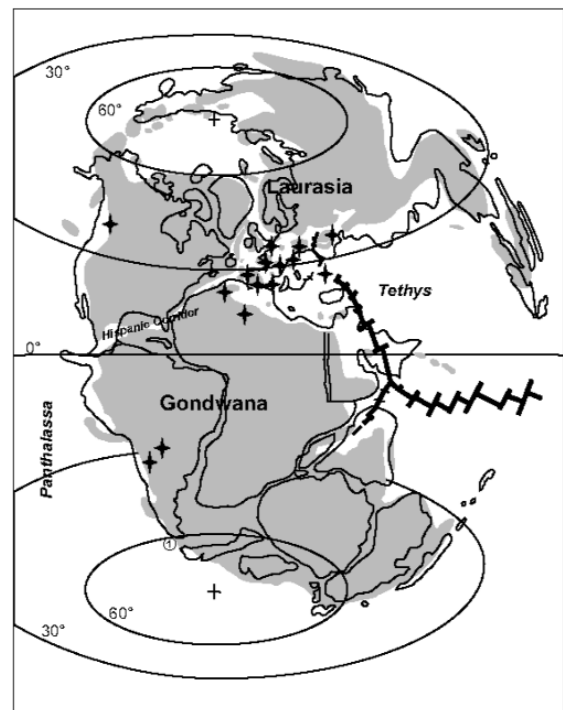


Figure 3. Palaeobiogeographic distribution of *Geczyceras* genus. (From MARTÍNEZ et al. 2012 and modified from DAMBORENEA 2002: Paleogeographic reconstruction for the Pliensbachian–Toarcian period)

genus in these last two areas does not imply (from a palaeobiological point of view) that colonization was very effective (MARTÍNEZ 1992b, p. 291, 1996).

In areas where *Geczyceras* has an ample and continuous record, e.g. in Morocco, Portugal, France, Spain (Iberian Range), Italy and Hungary, different authors (see KOVÁCS 2009) report similar distributions for the different species, but looking more closely their stratigraphic ranges are not exactly the same. In the Iberian Range (Figure 2), the oldest species (*G. costatum*, *G. clausum* and *G. gabillyi*) appear mainly in the Variabilis Zone. Above these appear *G. aff. bonarellii*, *G. speciosum*, *G. porcarellense* and *G. perplanum*, the stratigraphic positions of which correspond about to the Thouarsense and Dispansum Zones. The most recent species (*G. allobrogense*) appears in the Pseudoradiosa Zone. However, in the Subbetic domain of the Betic Cordillera, the genus covers a somewhat different position. *G. perplanum*, although it is found in the Fallaciosum Subzone (one specimen), is common in the Meneghini Zone (Levesquei Subzone). *G. speciosum* is very scarce; indeed, only two specimens have been recorded in the Betic Cordillera, one from the Speciosum Zone (belonging to the Internal Zones of the Betic Cordillera) (CARACUEL et al. 2006), and one from the base of the Meneghini Zone (Levesquei Subzone). *G. porcarellense* and *G. costulosum* are restricted to the Meneghini Zone (Levesquei Subzone) while *G. allobrogense* appears until to the Aalensis Zone (Mactra Subzone). Finally, *G. cf. tipperi* is found in the Aalensis Zone (Aalensis Subzone) (Figure 2).

Though *Geczyceras* has been cited mainly for the western Tethys (from Iran to Portugal and from France to Morocco), it is in Portugal, France, Spain (Iberian Range) and Hungary where its stratigraphic range is most extended, that it reaches its greatest diversity. However, associations are more numerous in the Tethyan basins (Italy and Hungary). This suggests that the origin of the genus is more linked to basin environments, which are more favourable for colonization and evolutionary development over extended periods. The fact that *Geczyceras* appears in platform areas such as the Iberian Range, Portugal and France, among others, suggests that communication routes existed that facilitated the migration of these ammonoids, with or without effective colonization. The Subbetic area, which is linked to deeper

environments, might have offered conditions suitable to their development, although to date the record for *Geczyceras* is scarce and restricted mainly to the Meneghini Zone. This scarcity in the record of the Betic Cordillera has several possible explanations: 1) Although the Toarcian of the Betic Cordillera (mainly the Subbetic) is generally well-understood, many of the sampling have been restricted to the Lower and Middle Toarcian (JIMÉNEZ & RIVAS 1991, 1992). 2) On the Subbetic swells (Internal and External Subbetic) the last part of the Middle Toarcian and the Upper Toarcian generally coincide with stratigraphic hiatuses. In addition, in many areas of the Median Subbetic domain (which clearly coincides with the deepest parts of the Subbetic basin for this interval of time) there are stratigraphic hiatus for the upper part of the Gradata Zone through to the Reynesi Subzone. Finally, 3) In other areas of the Median Subbetic domain, the materials of the Middle Toarcian are mainly marl and siliceous marl-limestone facies in which aragonitic ammonoid shells are not preserved. Thus, the absence of *Geczyceras* and its irregular stratigraphic distribution in the Subbetic is not a result of the different species of this genus never arriving, but a lack of sedimentation, taphonomic preservation, or even sampling problems.

In conclusion, *Geczyceras* has a generally homogeneous stratigraphic distribution in the different basins of the western Tethys. Its members were especially abundant in the Variabilis/Gradata Zone, and particularly between the Thouarsense/Bonarellii and Pseudoradiosa/Meneghini Zones. Thus, its presence in platform and basin environments provides a useful tool for comparing and correlating the different basins of the western Tethys.

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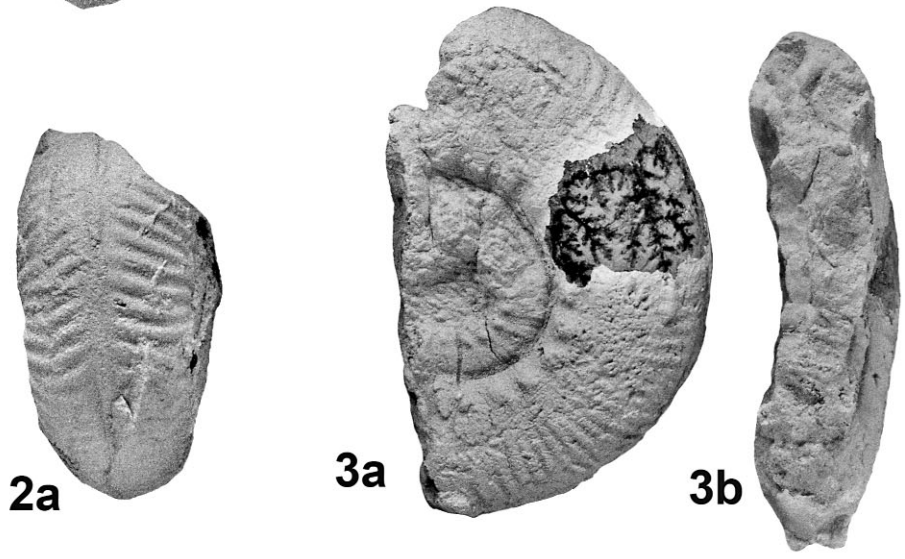
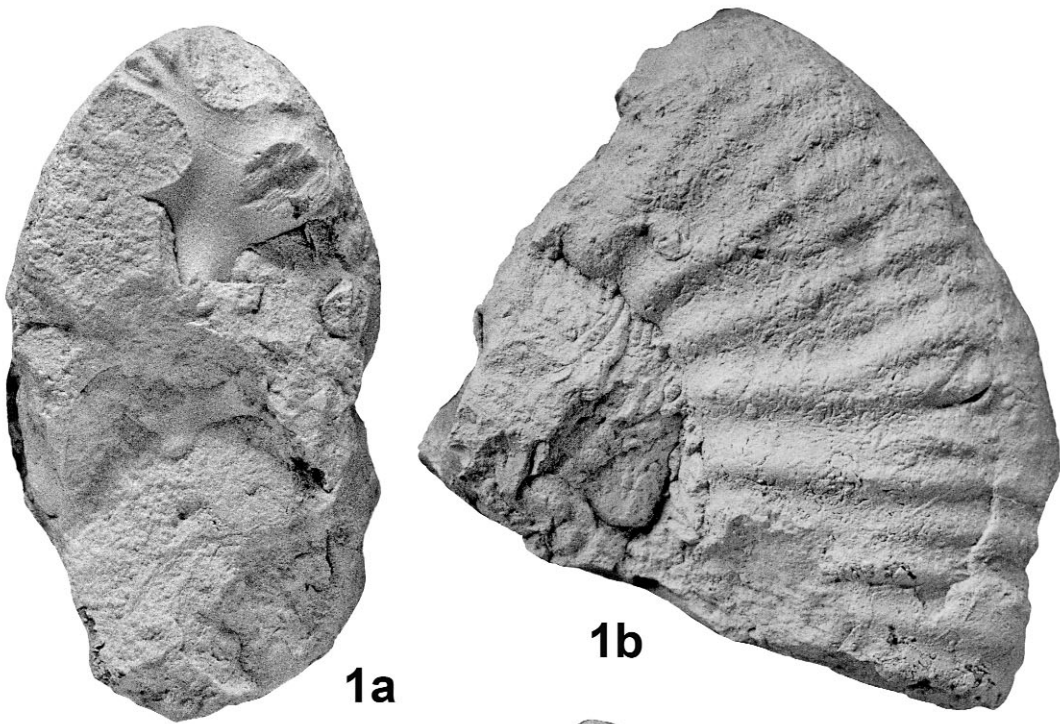
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Plate 1

- Figure 1. *Geczyceras costatum* (GABILLY). SP359/2. Variabilis Zone (Vitiosa Subzone). Iberian Range.
- Figure 2. *Geczyceras clausum* (GABILLY). SP359/1. Variabilis Zone (Vitiosa Subzone). Iberian Range.
- Figure 3. *Geczyceras* aff. *bonarellii* (PARISCH & VIALE). Fz1.3/13. Thouarsense Zone. Iberian Range.
- Figure 4. *Geczyceras porcarellense* (BONARELLI). My40/6. Dispansum Zone (Insigne Subzone). Iberian Range.

Graphic scale: 1 cm. All specimens have been previously figured in MARTÍNEZ, 1992b.



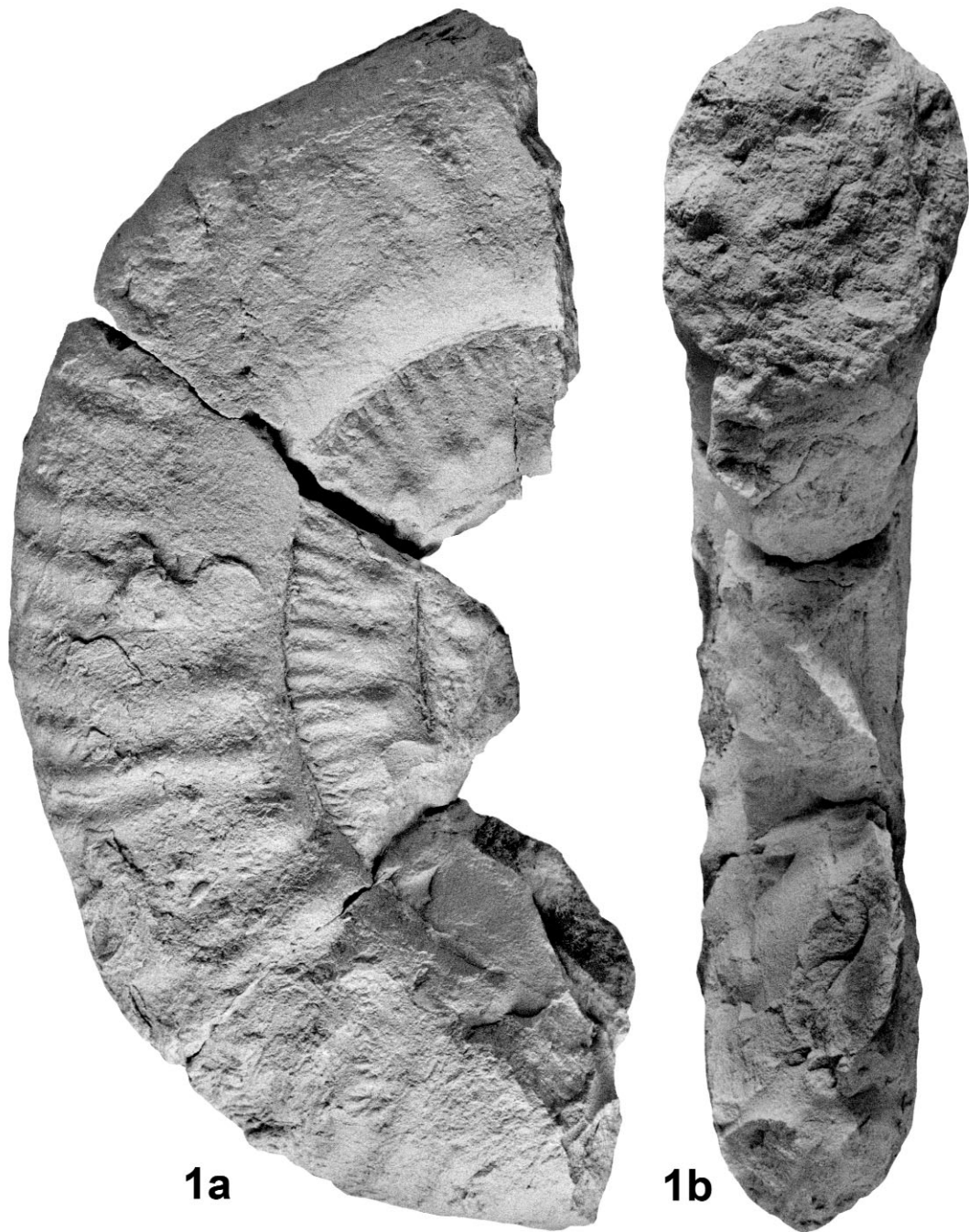
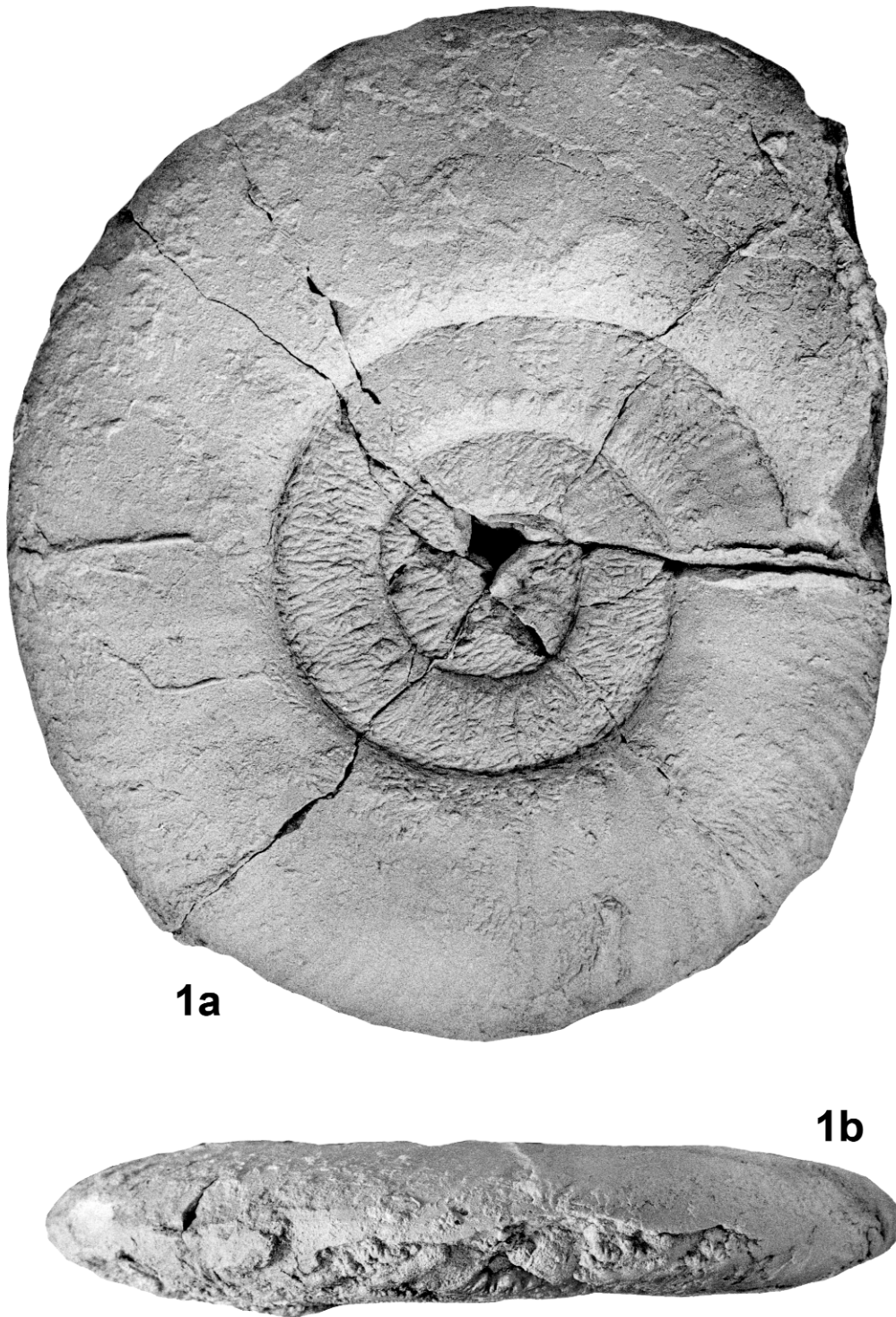


Plate 2

Figure 1. *Geczyceras gabillyi* MARTÍNEZ. Ph411/1. Thouarsense Zone (Bingmanni Subzone). Iberian Range.

Graphic scale: 1 cm. Specimen previously figured in MARTÍNEZ, 1992b.



1a

1b

Plate 3

Figure 1. *Gecyceras speciosum* (JANESCH). My37/2. Thouarsense Zone (Fallaciosum Subzone). Iberian Range.

Graphic scale: 1 cm. Specimen previously figured in MARTÍNEZ, 1992b.

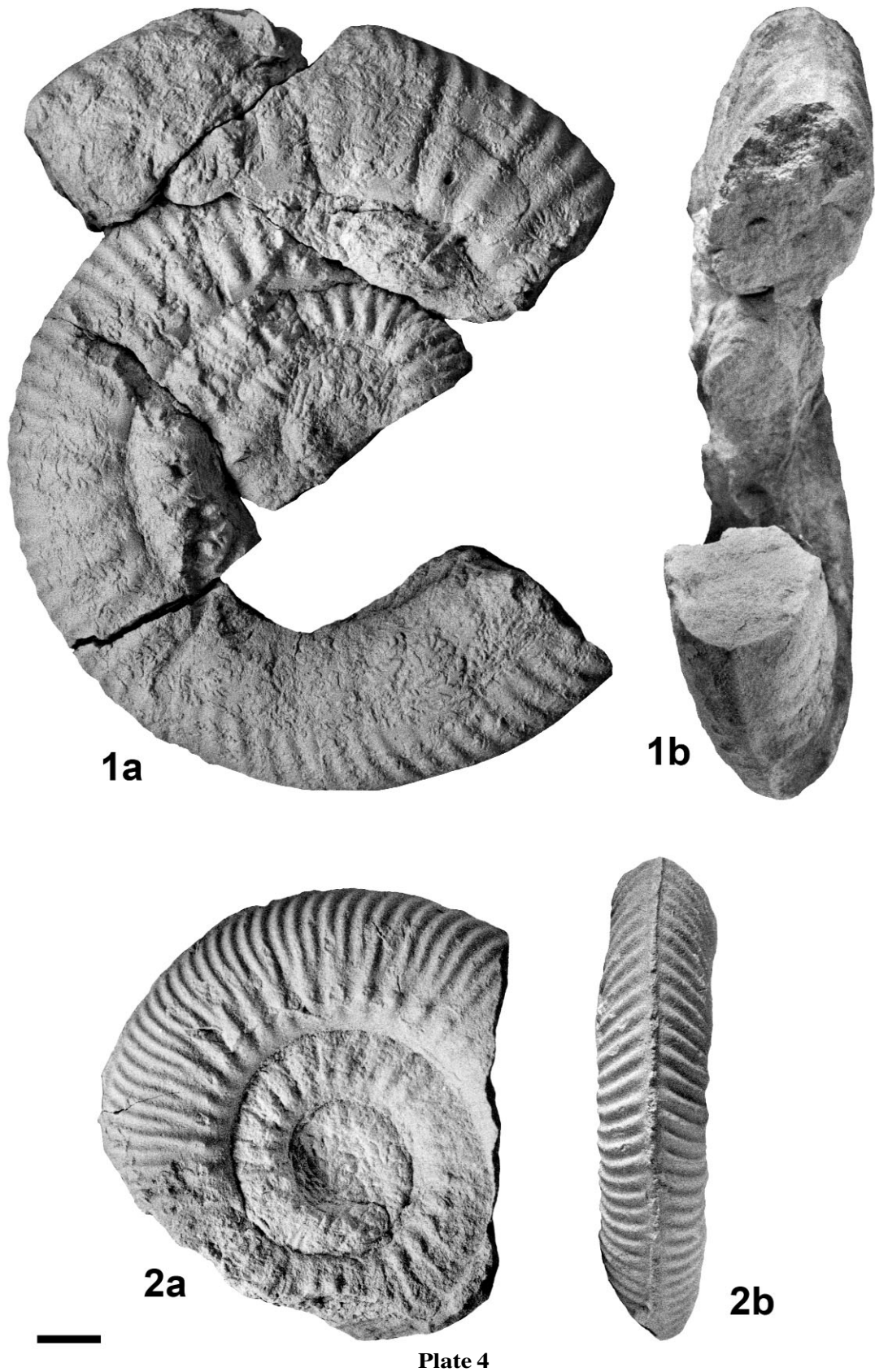


Figure 1. *Geczyceras perplanum* (PRINZ). Fz6/2. Dispansum Zone (Insigne Subzone). Iberian Range.

Figure 2. *Geczyceras allobrogense* (DUMORTIER). Bo6/8. Pseudoradosa Zone. Iberian Range.

Graphic scale: 1 cm. All specimens have been previously figured in MARTÍNEZ, 1992b.

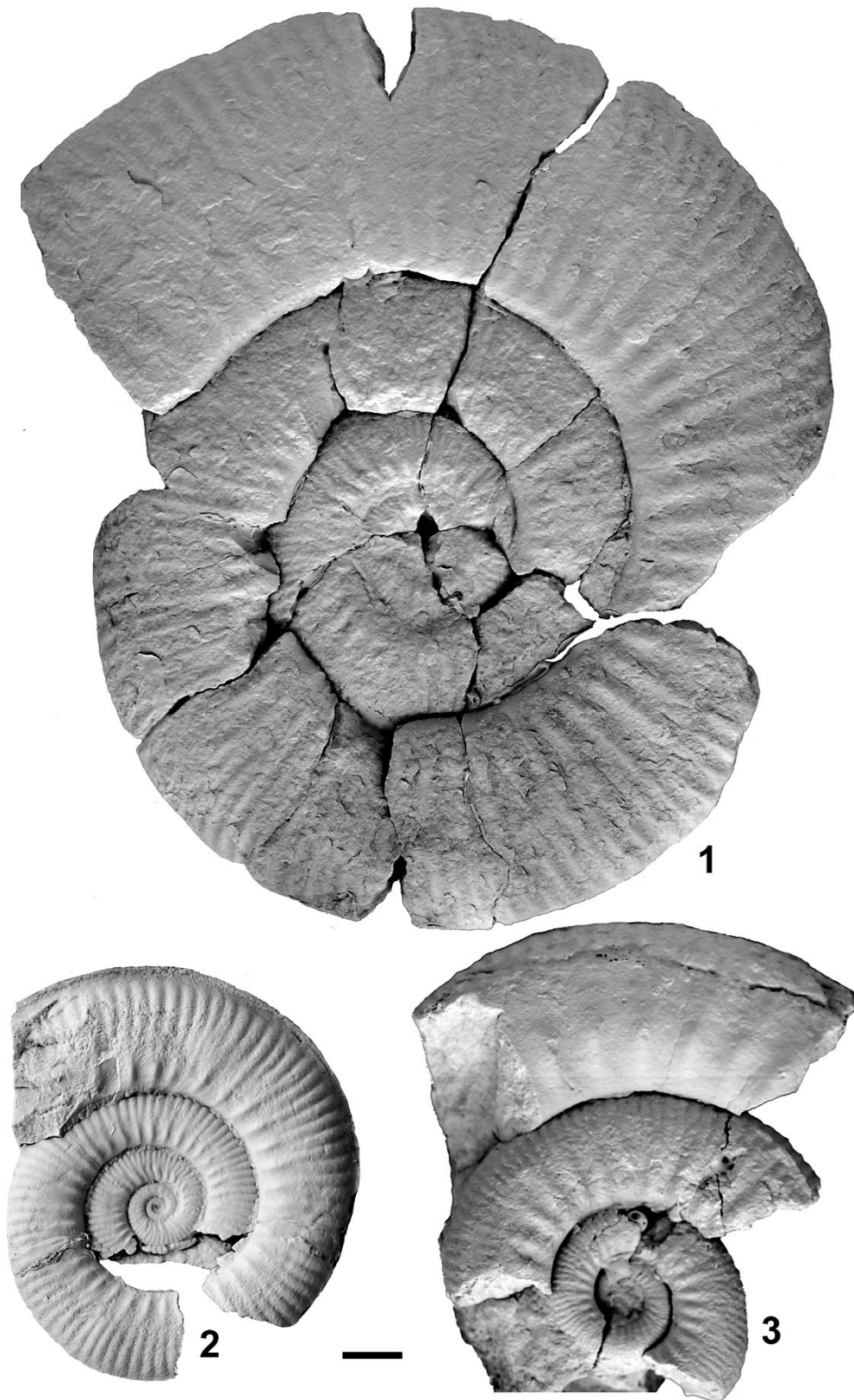


Plate 5

Figure 1. *Geczyceras speciosum* (JANENSCH). CM1.23.1. Meneghinii Zone. Betic Cordillera.

Figure 2. *Geczyceras perplanum* (PRINZ). CM1.12.1. Thouarsense Zone (Fallaciosum Subzone). Betic Cordillera.

Figure 3. *Geczyceras perplanum* (PRINZ). CM1.22.1. Meneghinii Zone. Betic Cordillera.

Graphic scale: 9.2 mm.

Plate 6

- Figure 1. *Geczyceras perplanum* (PRINZ). CM1.19.1. Thouarsense Zone (Fallaciosum Subzone). Betic Cordillera.
Figure 2. *Geczyceras allobrogense* (DUMORTIER). CM.28.1. Meneghinii Zone (Pseudoradiosa Subzone). Betic Cordillera.
Figure 3. *Geczyceras allobrogense* (DUMORTIER). JRi1.26.1. Meneghinii Zone. Betic Cordillera.
Figure 4. *Geczyceras porcarellaense* (BONARELLI). CM1.22.3. Meneghinii Zone. Betic Cordillera.
Figure 5. *Geczyceras allobrogense* (DUMORTIER). CM.35B.1 (External mould). Aalensis Zone, (Mactra Subzone). Betic Cordillera.
Figure 6. *Geczyceras costulosum* (MERLA). CM1.22.2. Meneghinii Zone. Betic Cordillera. (Refigured of Sandoval et al. 2011: fig. 10. 1)
Figure 7. *Geczyceras* cf. *tipperii* (SEYED-EMAMI). CM.51.1. Alalensis Zone (Aalensis Subzone). Betic Cordillera.

Graphic scale: 1 cm.

