

***Deitanites* n. g. and other related ammonites. Their significance within the family Holcodiscidae (Lower Cretaceous, Mediterranean region)**

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With 2 figures

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Abstract: A new Barremian ammonite genus, *Deitanites* n. g., and two new species, *Deitanites labatlanensis* n. sp. and *Holcodiscus thomeli* n. sp. are described and illustrated. The genus *Almohadites* WIEDMANN, 1966 is also reviewed. The phylogenetic relationships between these taxa are analysed and their systematic position within the family Holcodiscidae is discussed.

Zusammenfassung: Es werden eine neue Ammonitengattung aus dem Barremium, nämlich *Deitanites* n. g., und zwei neue Arten, *Deitanites labatlanensis* n. sp. und *Holcodiscus thomeli* n. sp., beschrieben und abgebildet. Die Gattung *Almohadites* WIEDMANN, 1966 wird hierbei revidiert. Die phylogenetischen Beziehungen zwischen diesen Taxa werden analysiert und ihre systematische Position innerhalb der Familie Holcodiscidae wird diskutiert.

1. Introduction

Among the rich fossil assemblages yielded by the Lower Barremian pelagic sediments of the Betic Cordillera (south-eastern Spain) and the Gerecse Mountains (northern Hungary) we have identified some specimens belonging to a hitherto undescribed micromorph ammonite. The morphological features of this new taxon (*Deitanites labatlanensis* n. g. n. sp.) allow its assignment to the family Holcodiscidae, showing clear affinities with *Almohadites*, another small-sized member of this family. Both genera appear to constitute a collateral holcodiscid lineage that developed during the middle part of the Early Barremian and presumably derived from another as yet undescribed form, *Holcodiscus thomeli* n. sp. In this paper, we formally describe the new taxa and analyse their significance within the family Holcodiscidae.

2. Origin of the studied material

The Hungarian specimens were collected in the Bersek Hill quarry, near Lábatlan, in the Gerecse Mountains (Transdanubian Central Range). They come from the lower part of the Lábatlan Sandstone Formation (CSÁSZÁR 1997), a lithostratigraphic unit made up of yellowish, fine- to coarse-grained turbiditic sandstone levels alternating with calcareous and argillaceous marlstones. The specimens studied form a part of the so-called Fülöp József collection, gathered from the Bersek Hill by the staff of the Hungarian Geological Survey during the field seasons of 1963 and 1964. This collection, housed today in the Palaeontological Department of the Hungarian Natural History Museum

(HNHM), has remained undetermined for almost 40 years, but its rich cephalopod material has recently begun to be studied, and the first results have already been published (FÖZY & FOGARASI 2002; FÖZY 2004; JANSSEN & FÖZY 2004).

The Spanish material comes from several sections located in the hemipelagic domain (Internal Prebetic) as well as in the basin domain (Subbetic). The lithologic successions are similar in all these sections and are composed of marly limestone beds alternating with marlstone interbeds. The specimens studied have been collected by systematic samplings carried out by three of us (M.C., J.S. and J.M.T.) within the framework of an integrated biostratigraphic analysis of the Barremian stage in the Betic Cordillera (AGUADO et al. 1992, 1997, 2001; COMPANY et al. 1995). These specimens are stored in the palaeontological collections of the University of Granada (CPUG).

3. Systematic Palaeontology

Family Holcodiscidae SPATH, 1923

AGUIRRE-URRETA & RAWSON (2003) have recently provided a detailed historical review of the successive conceptions on the systematic emplacement, subdivision and generic content of the family Holcodiscidae. We agree with most of the conclusions of these authors, who placed the family Holcodiscidae within the superfamily Perisphinctoidea, and divided it into two subfamilies: Spitidiscinae and Holcodiscinae. The subfamily Spitidiscinae ranges from the *Olcostephanus nicklesi* Subzone (mid Late Valanginian) up to the *Plesiospitidiscus ligatus* Zone (early Late Hauterivian) and comprises the genera *Jeanthieulouyites* COOPER, 1981, *Spitidiscus* KILIAN, 1910, and *Holcoptychites* GERTH, 1921, while the subfamily Holcodiscinae is a Barremian group composed of *Holcodiscus* UHLIG, 1882 and related genera. In agreement with some authors (HOEDEMAEKER 1995; VERMEULEN & THIEULOY 1999), we believe that these two groups are linked by the genus *Abrytusites* NIKOLOV & BRESKOVSKI, 1969. On the contrary, we think that *Plesiospitidiscus* BREISTROFFER, 1947, a genus frequently included in this family, should rather be considered as the stem form of the superfamily Desmoceratoidea.

The subfamily Holcodiscinae ranges from the base of the Barremian up to the lower part of the *Toxancyloceras vandenheckii* Zone (Upper Barremian). The genera *Holcodiscus* UHLIG, 1882, *Astieridiscus* KILIAN, 1910, *Metahoplites* SPATH, 1924, *Parasaynoceras* BREISTROFFER, 1947, *Almohadites* WIEDMANN, 1966, *Avramidiscus* VERMEULEN, 1996, and *Taveraidiscus*, VERMEULEN & THIEULOY, 1999 (e.g. Fig. 1.1), are currently included in this subfamily. In addition, more than 70 nominal species have been assigned to these genera. Notwithstanding, we are convinced that a better understanding of the intraspecific variability of some morphological characters would drastically reduce the taxonomic complexity of this group.

Genus *Holcodiscus* UHLIG, 1882

Type species: *Ammonites caillaudianus* D'ORBIGNY, by original designation (UHLIG 1882: 93).

Holcodiscus thomeli n. sp.

Figs. 1.2-1.5

1990 *Holcodiscus* aff. *perezi* (D'ORB.). – THOMEL, pl. 12, figs. 5-7.

H o l o t y p e : Specimen CPUG XA₂.8.68 (Fig. 1.3)

D e r i v a t i o n o f n a m e : Dedicated to the French palaeontologist GERARD THOMEL.

T y p e l o c a l i t y : L'Almadrava (Section X.A₂, bed 8), northern flank of Serra del Sit (Petrer, Alicante province, SE Spain).

T y p e h o r i z o n : Lower Barremian, upper part of the *Taveraidiscus hugii* Zone.

P a r a t y p e s : 38 specimens. 36 of them come from several sections in SE Spain: one (CPUG XG.33.17) from Barranco de la Aguzadera (La Guardia, Jaén), three (CPUG XAg₄.48.36, 50.11, 50.52) from Río Argos (Caravaca, Murcia), three (CPUG XK_{v1}.28.21, 28.42, 28a.2) from Barranco de Cavila (Caravaca, Murcia), four (CPUG XV₁.34.24, 38.7, 39.7, 41.45) from Arroyo Gilico (Cehegín, Murcia), eight (CPUG XA₁.18.6, 21.10; CPUG XA₂.8.14, 8.56, 8.81, 8.130, 8.152, 8.297) from l'Almadrava (Petrer, Alicante), and 17 (CPUG X.Q₁.10.57, 10.74, 11a.43, 11a.45-50, R.26-33) from Barranc de la Querola (Cocentaina, Alicante). The other two specimens (CPUG XAH.45.5-6) come from Aït Hamouch (Agadir province, western High Atlas, Morocco).

D i m e n s i o n s : (D – diameter of the shell, H – height of the whorl, E – width of the whorl, O – diameter of the umbilicus, all in mm).

	D	H	E	O	H/D	E/H	O/D
CPUG XA ₂ .8.68	39.9	15.8	18.1	13.4	0.40	1.15	0.34
	31.8	13.1	15.2	11.2	0.42	1.16	0.35
CPUG XA ₂ .8.81	27.4	11.0	14.8	9.3	0.40	1.34	0.34
	19.5	8.9	12.3	6.5	0.46	1.38	0.33
CPUG XAg ₄ .50.11	36.4	13.3	–	13.4	0.37	–	0.37
	26.2	9.8	–	10.7	0.41	–	0.41
CPUG XAH.45.6	24.3	10.2	13.1	6.6	0.42	1.28	0.27

D e s c r i p t i o n . – Small- to medium-sized holcodiscids with inflated shells. The whorl section is reniform, wider than high, and has its maximum width at the middle of the flanks. The umbilicus is relatively wide and deep. The length of the body chamber is not known, but it occupies at least two thirds of a whorl.

In the innermost whorls (up to 6-8 mm diameter) the ornamentation consists of prorsiradiate umbilical ribs, which end in a small lateral tubercle, leaving a smooth, gently rounded venter. From this diameter, lateral tubercles give rise to pairs of ribs, which, together with some intercalatories, cross straight over the venter. As the ribs become progressively coarser, most lateral tubercles fade out. Only some of these (6-7 per whorl, regularly distributed) persist and even strengthen to constitute parabolic ridges bordering adorally the constrictions, which are almost imperceptible at first but gradually widen with age.

In the adult stage (from 15-20 mm diameter) many of the ribs become simple. Those bordering adapically the constrictions enlarge towards the ventral region and develop two prominent perisiphonal bullae. At the same time, the parabolic ridges tend to disappear on the adoral ribs.

R e m a r k s . – *H. thomeli* shows the closest affinities with *H. perezianus* (D'ORBIGNY, 1850). Shell structure and ornamentation are similar in both species. The most obvious difference between them is that, in *H. perezianus*, the parabolic nodes are placed on the same ribs which support the ventral bullae, at the adapical margin of the constriction.

O c c u r r e n c e : *H. thomeli* occurs from the *Psilotissotia colombiana* Subzone (upper part of the *T. hugii* Zone) up to the top of the *Nicklesia pulchella* Zone in the Betic Cordillera (SE Spain). Specimens attributable to this species have also been found at the same stratigraphic position in SE France and Morocco.

Genus *Almohadites* WIEDMANN, 1966

T y p e s p e c i e s : *Almohadites subcamelinus* WIEDMANN, by original designation (WIEDMANN 1966: 67). We regard this species as a junior synonym of *A. camelinus* (D'ORBIGNY).

E m e n d e d d i a g n o s i s : Small-sized holcodiscid with nearly equidimensional whorl section and a ventral furrow in the juvenile stages.

Almohadites camelinus (D'ORBIGNY, 1850)

Figs. 1.6-1.10

- 1850a *Ammonites Camelinus* D'ORB. – D'ORBIGNY, p. 100, n° 617.
1850b *Ammonites camelinus* D'ORB. – D'ORBIGNY, p. 197, pl. 8, figs. 1-4.
? 1923 *Kilianella camelina* D'ORB. – FALLOT & TERMIER, p. 44, pl.5, fig.1.
non 1937 *Ammonites Camelinus* D'ORB. – COTTREAU, p. 27, pl. 78, figs. 12-15.
1966 *Almohadites subcamelinus* nov. sp. – WIEDMANN, p. 69, pl. 2, fig. 5; pl. 3, figs.2, 5; text-figs. 20, 44b.
1966 *Almohadites evolutus* nov. sp. – WIEDMANN, p. 71, pl. 3, figs. 3-4; text-fig. 45.
1968 *Almohadites camelinus* (D'ORB.). – SORNAY, p. 6, pl. 1, figs. 7, 9, 10.

L e c t o t y p e : SORNAY (1968) reviewed the original syntypes of this species and designated as lectotype the specimen shown in his figure 10. It presumably corresponds to the strongly idealized fig. 3 of D'ORBIGNY (1850b). This specimen comes from the Barremian of Saint-Martin, near Escagnolles (Alpes-Maritimes, SE France).

M a t e r i a l : 69 specimens. 68 specimens of them come from several sections in SE Spain. Three (CPUG XKv₁.26.57, 27a.10, 28a.32) from Barranco de Cavila (Caravaca, Murcia), one (CPUG XV₁.39.3) from Arroyo Gilico (Cehegín, Murcia), 59 (CPUG XQ₁.11a.1-14, 11a.16-40, 12.39, 12a.7, R.2-7, R.9-20) from Barranc de la Querola (Cocentaina, Alicante) and five (CPUG XO.41.4-8) from Cantera de l'Almuixic (Oliva,

Valencia). The other specimen (CPUG XAH.45.4) comes from Aït Hamouch (Agadir province, western High Atlas, Morocco).

D i m e n s i o n s :

	D	H	E	O	H/D	E/H	O/D
CPUG XQ ₁ .11a.34	12.2	5.8	5.9	3.5	0.47	1.02	0.29
CPUG XQ ₁ .11a.40	12.6	5.8	6.3	4.1	0.46	1.09	0.33
CPUG XQ ₁ .11a.35	10.6	4.4	5.2	3.3	0.42	1.18	0.31
CPUG XQ ₁ .11a.12	8.9	3.5	4.3	2.9	0.39	1.23	0.33
CPUG XQ ₁ .11a.20	10.2	3.8	3.8	3.6	0.37	1.00	0.35
CPUG XQ ₁ .11a.4	9.4	3.8	4.1	3.4	0.40	1.08	0.36
CPUG XQ ₁ .R.7	8.8	3.9	5.0	3.5	0.44	1.28	0.40
CPUG XQ ₁ .R.12	11.5	4.0	4.4	4.1	0.35	1.10	0.36
CPUG XQ ₁ .R.20	14.5	6.0	6.9	4.5	0.41	1.15	0.31

D e s c r i p t i o n . – Small-sized ammonites (maximum diameter about 30-35 mm). The whorl section is subquadrate, varying from slightly depressed in the inner stages to slightly compressed in the adult, flanks being always gently convex. The umbilicus is wide and moderately deep. The length of the body chamber is unknown.

The ornamentation varies throughout ontogeny. Following a smooth initial stage, blunt prorsiradiate ribs, ending in a minute tubercle, appear in the inner half of the flank. From 6-7 mm diameter, lateral tubercles disappear and the ribs progressively extend into the outer part of the flanks. Some of the ribs bifurcate, and all of them end in a small ventro-lateral swelling, leaving a smooth siphonal furrow. Concurrently, deep oblique constrictions (6-9 per whorl) appear, normally in front of bifurcate ribs. The ribs immediately behind the constrictions develop a strong, radially elongated, lateral tubercle. In the adult stage (from 18-20 mm), the ventral furrow tends to fade out and the ribs cross straight over the venter.

R e m a r k s . – As WIEDMANN (1966) and SORNAY (1968) pointed out, the specimens attributed to this species by COTTREAU (1937, pl. 78, figs. 12-15) are very different from D'ORBIGNY's original figures. In fact, one of COTTREAU's specimens (fig. 12-13) was rightly referred by WIEDMANN (1966) to the Aptian cheloniceratids, whereas the other one (fig. 14-15) could be a *Holcodiscus*.

The two species described by WIEDMANN (1966), *A. subcamelinus* and *A. evolutus*, are hardly distinguishable from *A. camelinus*. Both are based exclusively on pyritised nuclei. The only difference that WIEDMANN clearly pointed out between *A. camelinus* and *A. subcamelinus* (i. e. a slightly depressed whorl section in the latter) is simply a juvenile character that changes with age. As regards *A. evolutus*, it does not seem to be more than a peculiar morphotype of this highly variable species.

O c c u r r e n c e : *A. camelinus* has been reported from SE Spain, the Balearic Islands, SE France and Morocco. VERMEULEN (1998a, b) used this species to characterise a biohorizon in the upper part of the *Kotetishvilia nicklesi* Zone in SE France. We have found it at the same level but also, and more frequently, in the lower part of the *N. pulchella* Zone.

Genus *Deitanites* n. g.

Type species: *Deitanites labatlanensis* n. sp.

Derivation of name: The generic name refers to the Deitani, a pre-Roman Iberian people who inhabited the interior of the Murcia region (SE Spain).

Diagnosis: Micromorph holcodiscid with very evolute coiling, compressed whorl section, dichotomous ribs and a ventral discontinuity.

Remarks. – Despite its singularities, this new taxon can be assigned, without many problems to the family Holcodiscidae, showing the closest affinities with the genus *Almohadites*. Both genera have in common the presence of a ventral discontinuity and the structure of the ribs bordering adapically the constrictions. Nevertheless, *Deitanites* differs from *Almohadites* in having a more evolute coiling and persistent bifurcate ribs. For the moment, only the type species is attributable to this new genus.

Deitanites labatlanensis n. sp.

Figs. 1.11-1.18

Holotype: Specimen HNHM 2004.170.1 (Fig. 1.17)

Derivation of name: From Lábatlan, where the holotype was found.

Type locality: Bersek Hill section (bed 132), near the village of Lábatlan (Komárom-Esztergom county, northern Hungary).

Type horizon: Lower Barremian, base of the *Kotetishvilia compressissima* Zone.

Paratypes: 25 specimens. Nine of them (HNHM 2004.168.1-2, 169.1-2, 170.2-6) come from the Bersek Hill quarry, near Lábatlan (Hungary). The other sixteen come from several sections in SE Spain: one (CPUG X.Ag4.56.14) from Río Argos (Caravaca, Murcia), five (CPUG X.Kv1.28.2, 29.26-28, 33.120) from Barranco de Cavila (Caravaca, Murcia), eight (CPUG X.V1.44.10, 44.25-29, 45.19) from Arroyo Gilico (Cehegín, Murcia), one (CPUG X.A1.34a.20) from l'Almadrava (Petrer, Alicante), and one (CPUG X.Q1.R.1) from Barranc de la Querola (Cocentaina, Alicante).

Dimensions:

	D	H	E	O	H/D	E/H	O/D
HNHM 2004.170.1	15.1	5.3	3.1	7.2	0.35	0.58	0.48
	11.8	4.1	2.9	6.0	0.35	0.70	0.51
HNHM 2004.169.1	15.4	4.5	–	8.0	0.29	–	0.52
	13.2	3.5	–	7.0	0.27	–	0.53
HNHM 2004.168.1	16.7	5.6	–	7.9	0.34	–	0.47
	9.5	3.6	–	4.5	0.38	–	0.47
CPUG XKv1.29.26	14.0	4.2	–	6.5	0.30	–	0.46
CPUG XKv1.33.120	14.6	3.4	–	7.8	0.23	–	0.54

Description. – Small-sized ammonite (maximum known diameter ~16 mm) with very wide, shallow umbilicus. The whorl section is rounded, varying from slightly depressed in the innermost stages to moderately compressed in the middle and outer whorls. The length of the body chamber is unknown, but it occupies, at least, half a whorl.

The innermost whorls (up to 2-3 mm diameter) are smooth. From this diameter, strong, distant, rectiradiate ribs appear. Most of them bifurcate at a point just below the middle part of the flank. The secondary ribs do not traverse the venter, leaving a smooth band, which is wide, occupying the entire ventral region, at the beginning, but quickly becoming much narrower. Constrictions (5-7 per whorl) are roughly parallel to costulation and, in the last whorls; they are adapically bordered by ribs flared on the venter sides. The suture line is not clearly visible in any specimen.

Remarks. – Moderate morphological variability has been detected within this species, affecting the relative width of the umbilicus, the shape of the whorl section and the ribbing. In general, the most evolute forms have thicker whorls and a larger proportion of simple ribs.

Occurrence: *D. labatlanensis* has been found in SE Spain and Hungary. It occurs from the lower part of the *N. pulchella* Zone up to the lower part of the *K. compressissima* Zone.

4. Discussion

The family Holcodiscidae is represented in the lowermost Barremian by the genus *Taveraidiscus*, here understood as including the species *Taveraidiscus hugii* (OOSTER, 1860) and *T. intermedius* (D'ORBIGNY, 1841), both appearing at the Hauterivian/Barremian boundary and disappearing in the lower part of the *K. nicklesi* Zone. According to our interpretation, the nominal species *T. oosteri* (SARASIN & SCHÖNDELMAYER, 1901) and *T. alcoyensis* (NICKLÈS, 1890) can be considered synonyms of *T. hugii*, whereas *T. vandeckii* (D'ORBIGNY, 1850), *T. heeri* (OOSTER, 1860), *T. kiliani* (PAQUIER, 1900) and *T. querolensis* (BUSNARDO in BUSNARDO & DAVID, 1957) should be synonyms of *T. intermedius*. This last species was assigned by VERMEULEN & THIEULOY (1999) to the genus *Avramidiscus*, together with the group of *A. gastaldianus* (D'ORBIGNY, 1850). However, as will be seen below, there is neither a direct phylogenetic relationship nor even a temporal connection between these two groups.

Taveraidiscus intermedius could be the ancestor of *Holcodiscus thomeli*, which appears in the upper part of the *T. hugii* Zone. In fact, the more evolute specimens of *T. intermedius* (corresponding to the *kiliani* and *querolensis* morphotypes) also show radially elongated swellings in front of the constrictions (see Fig. 1.1). The appearance of ventrolateral tubercles on the flared ribs bordering adorally the constrictions is an apomorphic feature that is shared by many other later members of the family (Fig. 2).

Almohadites camelinus, which has its first occurrence in the upper part of the *K. nicklesi* Zone, presumably derives from *H. thomeli*. Both species have similar innermost whorls, but *A. camelinus* displays some pedomorphic characteristics such as a reduced adult size and a simplified suture (see WIEDMANN, 1966). In addition, the ventral furrow

is a morphological novelty that, however, recalls the siphonal discontinuity of *Jeanthieuloyites*, the earliest holcodiscid.

In *D. labatlanensis*, descending from *A. camelinus* in the *N. pulchella* Zone and also possessing a smooth ventral band, the paedomorphic trend becomes more accentuated, leading to an even more reduced size and to the persistence of the bifurcate ribbing in the adult stage.

The short-lived lineage composed of *A. camelinus* and *D. labatlanensis* becomes extinct in the lower part of the *K. compressissima* Zone, apparently without giving rise to any descendent. Hence, we cannot agree with VERMEULEN & THIEULOY (1999), who regarded *A. camelinus* as the ancestor of the group of *Holcodiscus fallax* (MATHERON, 1878) (included by these authors in the genus *Metahoplites*). This latter species forms part (together with *H. perezianus* [D'ORBIGNY, 1850], *H. nicklesi* KARAKASCH, 1907, *Avramidiscus gastaldianus* [D'ORBIGNY, 1850], and *Astieridiscus morleti* [KILIAN, 1888]), of a holcodiscid radiation that took place at the base of the *K. compressissima* Zone. Despite the clear morphological differences existing between them, all these species show early ontogenetic stages very similar to those of *H. thomeli*, the species that, therefore, could be considered their ancestor.

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Fig. 1. 1: *Taveraidiscus intermedius* (D'ORBIGNY) (morphotype *kiliani*). CPUG XA₂.8.141, l'Almadrava (Petrer, Spain), *P. colombiana* Subzone, *T. hugii* Zone (Lower Barremian). ×1.

2: *Holcodiscus thomeli* n. sp. CPUG XA₂.8.81, l'Almadrava (Petrer, Spain), *P. colombiana* Subzone, *T. hugii* Zone (Lower Barremian). ×1.

3: dito, CPUG XA₂.8.68 (Holotype), l'Almadrava (Petrer, Spain), *P. colombiana* Subzone, *T. hugii* Zone (Lower Barremian). ×1.

4: dito, CPUG XAH.45.6, Aït Hamouch (Agadir province, Morocco), *K. nicklesi* Zone (Lower Barremian). ×1.

5: dito, CPUG XQ₁.11a.48, Barranc de la Querola (Cocentaina, Spain), *N. pulchella* Zone (Lower Barremian). ×2.

- 6: *Almohadites camelinus* (D'ORBIGNY). CPUG XQ₁.11a.40, Barranc de la Querola (Cocentaina, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 7: dito, CPUG XQ₁.11a.35, Barranc de la Querola (Cocentaina, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 8: dito, CPUG XQ₁.R.7, Barranc de la Querola (Cocentaina, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 9: dito, CPUG XQ₁.11a.20, Barranc de la Querola (Cocentaina, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 10: dito, CPUG XQ₁.R.20, Barranc de la Querola (Cocentaina, Spain), *N. pulchella* Zone (Lower Barremian). ×1.5.
- 11: *Deitanites labatlanensis* n. g. n. sp. CPUG X.Kv₁.29.26, Barranco de Cavila (Caravaca, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 12: dito, CPUG X.Kv₁.33.120, Barranco de Cavila (Caravaca, Spain), *K. compressissima* Zone (Lower Barremian). ×2.
- 13: dito, CPUG X.V₁.44.10, Arroyo Gilico (Cehegín, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 14: dito, CPUG X.Q₁.R.1, Barranc de la Querola (Cocentaina, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 15: dito, CPUG X.Kv₁.28.2, Barranco de Cavila (Caravaca, Spain), *N. pulchella* Zone (Lower Barremian). ×2.
- 16: dito, HNHM 2004.169.1, Bersek Hill (Lábatlan, Hungary), *K. compressissima* Zone (Lower Barremian). ×2.
- 17: dito, HNHM 2004.170.1 (Holotype), Bersek Hill (Lábatlan, Hungary), *K. compressissima* Zone (Lower Barremian). a) left lateral view, b) right lateral view; c) ventral view. ×2.
- 18: dito, HNHM 2004.168.1, Bersek Hill (Lábatlan, Hungary), *N. pulchella* Zone (Lower Barremian). ×2.

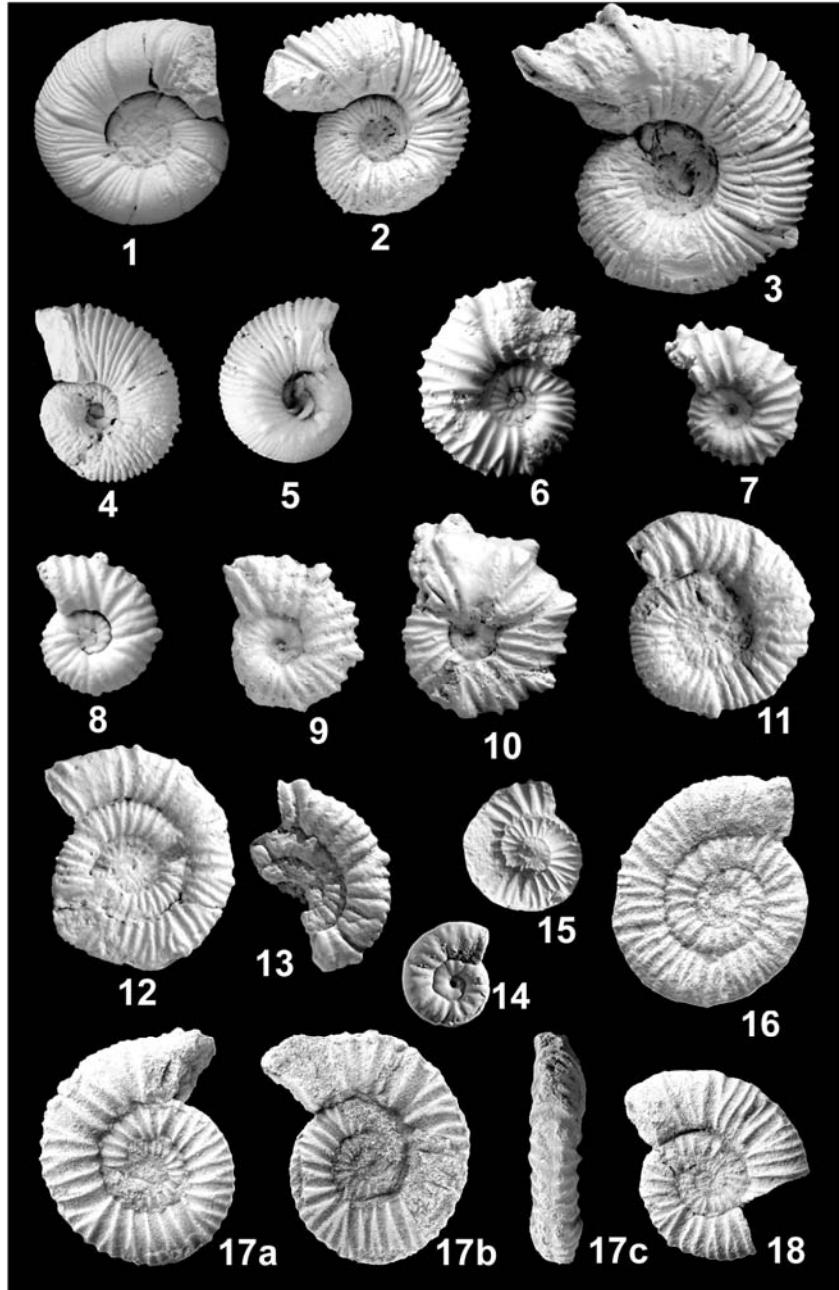


Fig. 2. Proposed phylogenetic relationships between the taxa discussed (calibrated against the Mediterranean standard zonation).

