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The ammonite genus *Vascoceras* CHOFFAT, 1898  
(family Vascoceratidae DOUVILLÉ, 1912)  
in the Iberian Trough, Spain

by

FERNANDO BARROSO-BARCENILLA and ANTONIO GOY, Madrid

With 5 plates and 6 text-figures



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# The ammonite genus *Vascoceras* CHOFFAT, 1898 (family Vascoceratidae DOUVILLÉ, 1912) in the Iberian Trough, Spain

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## Zusammenfassung

Die zu der Gattung *Vascoceras* zugeschriebenen Ammoniten der Sammlungen von WIEDMANN (Universität Tübingen, Deutschland) sowie GOY, CARRETERO und MELÉNDEZ (Universidad Complutense de Madrid, Spanien), die aus dem Ober Cenoman und dem Unter Turon des Iberischen Trogs stammen, sind revidiert worden. Anschließend neue Vertreter der Arten *Vascoceras gamai*, *V. charoni* sp. nov., *V. barcoicense*, *V. durandi*, *V. cauvini*, *V. amieirensense*, *V. harttii* und *V. kossmati* sind studiert und präsentiert worden. Untersuchungen über die Morphologie sowie die geographische und stratigraphische Verteilung dieser Ammoniten haben geführt schließlich zu der Feststellung verschiedener phylogenetischer Beziehungen zwischen ihnen und zu der Unterscheidung von zwei Hauptphasen in der Entwicklung der Familie Vascoceratidae die durch die aufeinanderfolgende Dominanz von "primitiven" und von "entwickelten" *Vascoceras* gekennzeichnet sind.

**Schlüsselwörter:** ober Cenoman – unter Turon – Ammonoidea – Vascoceratidae – *Vascoceras* – neue Art – Iberischer Trog – Spanien

## Summary

The ammonites assigned to the genus *Vascoceras* of the WIEDMANN (Universität Tübingen, Germany) and GOY, CARRETERO and MELÉNDEZ (Universidad Complutense de Madrid, Spain) collections obtained from the upper Cenomanian and lower Turonian of the Iberian Trough have been revised. Subsequently, new representatives of the species *Vascoceras gamai*, *V. charoni* sp. nov., *V. barcoicense*, *V. durandi*, *V. cauvini*, *V. amieirensense*, *V. harttii* and *V. kossmati* have been studied and presented. Finally, studies of the morphologies and the geographical and stratigraphical distributions of these ammonites have led to the identification of several phylogenetic relationships between them, and to distinguishing two main phases in the evolution of the family Vascoceratidae, characterised by the successive dominance of the "primitive" *Vascoceras* and of the "evolved" *Vascoceras*.

**Key words:** upper Cenomanian – lower Turonian – Ammonoidea – Vascoceratidae – *Vascoceras* – new species – Iberian Trough – Spain

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## Introduction

In this paper, firstly, a revision of the ammonites assigned to the genus *Vascoceras* CHOFFAT, 1898, obtained from the upper Cenomanian and lower Turonian of the Iberian Trough that are held in the Universität Tübingen (UT), Germany, and the Universidad Complutense de Madrid (UCM), Spain, is presented. These centres hold the WIEDMANN (JW), GOY (AG), CARRETERO (CM) and MELÉNDEZ (MH) collections, which now contain the largest number of representatives of the family Vascoceratidae DOUVILLÉ, 1912, collected from the Iberian Trough. Secondly, a taxonomic analysis of the members of this genus obtained during this research is developed. Geographically, the field work was carried out in the upper Cenomanian and lower Turonian outcrops situated in the localities of Puente de y (PU), in the north of the province of Burgos, of Fuentetoba (FT), in the centre of Soria, and of Cantalojas (CC), Galve de Sorbe (CG), Condemios (CA; CB), Somolinos (CS) and Tamajón (TA), in the north of Guadalajara, Spain (Text-fig. 1).

Stratigraphically, the ammonites presented here were mainly collected from the Margas de Puente de y (FLOQUET et al. 1982) and Margas de Picofrentes (FLOQUET et al. 1982) formations, deposited in the inner and the marginal environments of the platform, respectively. These formations are remarkable for con-

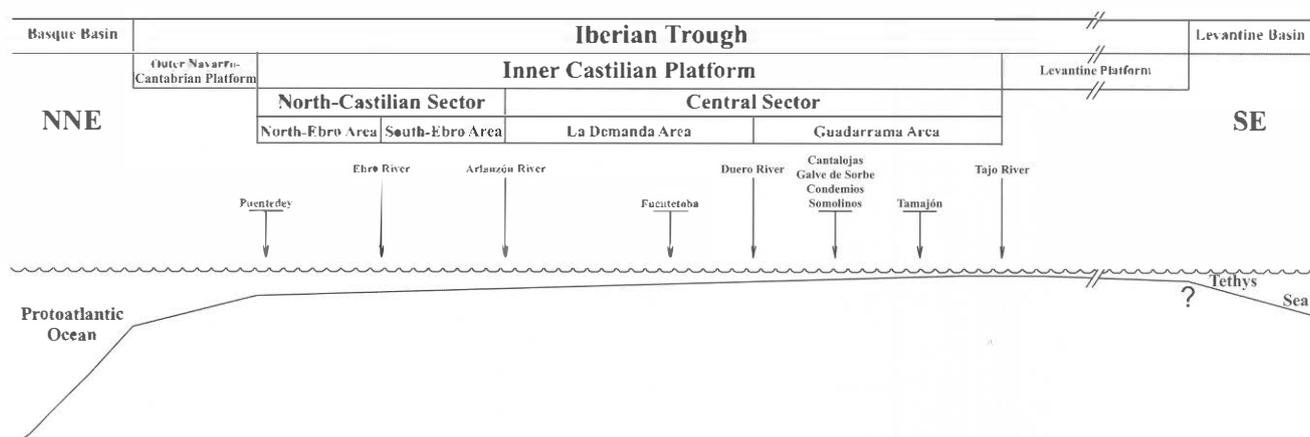
taining the most complete and typical marls of the studied interval in the Iberian Trough, as asserted by FLOQUET et al. (1982), FLOQUET (1991), SANTAMARÍA-ZABALA (1991, 1992, 1995) and SEGURA et al. (1993). In order to establish a more precise taxonomic classification, the original types attributed to this family that are held in the Museu do Instituto Geológico e Mineiro de Lisboa, Portugal, and the Musée National d'Histoire Naturelle de Paris, France, were also studied. Thirdly, the obtained data are interpreted, and several conclusions concerning the systematic, distribution and evolution of the Vascoceratidae are presented. In the present paper, the palaeogeographical division (Text-fig. 2) and the ammonite zonation (Text-fig. 3) for the upper Cenomanian and lower Turonian of the Iberian Trough proposed by BARROSO-BARZENILLA et al. (2009) have been followed.

## Historical background

From the beginning of the 20<sup>th</sup> century many cephalopods have been collected from the upper Cenomanian and lower Turonian, not only in the Iberian Trough but in the whole of Spain, and assigned to the family Vascoceratidae DOUVILLÉ, 1912. KARREBERG (1935) identified a significant number of representatives of the genus *Vascoceras* CHOFFAT, 1898, in the Outer Navarro-Cantabrian Platform and the



Text-fig. 1. Geographic provenance of the specimens presented in this paper.



Text-fig. 2. Divisions followed in the Iberian Trough, the approximate locations of the outcrops studied and the geographic boundaries between their different palaeogeographic areas.

North-Castilian Sector. WIEDMANN (1960, 1964) obtained numerous members of the group in the Outer Navarro-Cantabrian Platform and the North-Castilian and Central sectors, many of them in Puente de Ebro, Fuentetoba and Somolinos. WIEDMANN (1975) presented several ammonite sequences containing various representatives of *Vascoceras* from the Upper Cretaceous of the Central Sector. MOJICA & WIEDMANN (1977) analysed some ammonite sequences from the Cenomanian of the Central Sector, which included several members of the genus. WIEDMANN & KAUFFMAN (1978) and WIEDMANN (1979) identified numerous ammonites attributed to *Vascoceras* in the Outer Navarro-Cantabrian Platform, the North Castilian Sector and the La Demanda Area. CARRETERO-MORENO (1982) collected some representatives of the genus in several outcrops of the Levantine Platform, and in Cantalojas, Galve de Sorbe, Condemios and Somolinos. MELÉNDEZ-HEVIA (1984) identified numerous members of *Vascoceras* in Condemios, Somolinos and Tamajón. FLOQUET (1991) cited some representatives of the genus in the northern half of the Iberian Trough and in the Basque Basin, in the north of Spain. SEGURA et al. (1993) analysed several stratigraphic sequences deposited in the Cenomanian-Turonian transition of some parts of the Central Sector, one of them in Somolinos, and mentioned various representatives of the genus. BARROSO-BARCENILLA (2004) identified several members of *Vascoceras* in the upper Cenomanian and lower Turonian of the northern margin of the North-Castilian Sector, specifically in Puente de Ebro. His conclusions on the genus were con-

trasted with the ones obtained in other regions of the Iberian Trough by BARROSO-BARCENILLA (2006) and have been presented here.

Other relevant contributions to the knowledge of the upper Cenomanian and lower Turonian cephalopods in the Iberian Trough and in other adjoining and closely related palaeogeographical regions, such as the North-Cantabrian and the Pyrenean basins, both located in the north of Spain, were reported by BARROSO-BARCENILLA (2007), BARROSO-BARCENILLA & GOY (2007, 2009) and BARROSO-BARCENILLA et al. (2009).

### Revision of *Vascoceras* from the Iberian Trough in the Universität Tübingen and the Universidad Complutense de Madrid

Regarding the revision of the ammonites assigned to the genus *Vascoceras* CHOFFAT, 1898, obtained from the Iberian Trough that are held in the WIEDMANN (Universität Tübingen, Germany) and GOY, CARRETERO and MELÉNDEZ (Universidad Complutense de Madrid, Spain) collections, it is important to emphasize certain remarks. It has not been possible to find specimens of all the members of *Vascoceras* cited by WIEDMANN (1960, 1964, 1975, 1979), MOJICA & WIEDMANN (1977) and WIEDMANN & KAUFFMAN (1978) in the UT. Therefore, the results of the investigation at this research centre are based exclusively on the specimens that are now hosted in the JW Collection. Likewise, the method by which the fossils of the CM Collection have been numbered and identified has hindered an adequate

Substage	Standard ammonite zonation. Based on KENNEDY (1984), TRÖGER & KENNEDY (1996), BENGTSSON (1996) and GRADSTEIN et al. (2004)	Iberian Trough, Spain. BARROSO-BARCENILLA et al. (2009)	
		Zones	Subzones
Lower Turonian	<i>Mammites nodosoides</i>	<i>Mammites nodosoides</i>	<i>Wrightoceras munieri</i> <i>Mammites nodosoides</i>
	<i>Watinoceras devonense</i>	<i>Spathites (Ingridella) malladae</i>	<i>Chuffaticeras (Leoniceus) luciae</i> <i>Spathites (Ingridella) malladae</i>
		<i>Chuffaticeras (Chuffaticeras) quausi</i>	
Upper Cenomanian	<i>Neocardioceras juddii</i>	<i>Spathites (Jeanrogericeras) subconciliatus</i>	
	<i>Metioceras gestinianum</i>	<i>Metioceras gestinianum</i>	<i>Vascoceras gamai</i> <i>Metioceras gestinianum</i>
	<i>Calycoceras (Proeucalycoceras) guerangeri</i>	<i>Neolobites vibrayeanus</i>	<i>Metioceras mosbyense</i> <i>Neolobites vibrayeanus</i>
		<i>Eucalycoceras rowei</i>	<i>Calycoceras (Calycoceras) naviculare</i> <i>Eucalycoceras rowei</i>

Text-fig. 3. Biostratigraphic zonation followed in this work and its correlation with the standard scale.

and individualized tracking of its ammonites. Therefore, the revision of the taxa cited by CARRETERO-MORENO (1982) has only been partially carried out, and the references to her work in the synonymy of the taxonomic section are necessarily imprecise. In spite of these difficulties, some conclusions on the present situation of the *Vascoceras* in the JW, AG, MH and CM collections have been reached and presented here (Text-fig. 4).

### New data on *Vascoceras* in the Iberian Trough

In this section, a systematic description of the new records of the genus *Vascoceras* CHOFFAT, 1898, obtained during field work carried out by the first author as well as of the unpublished members of the group identified in the AG and MH collections is given. The terminology used for the descriptions is based on the glossary of morphological terms proposed by BARROSO-BARCENILLA (2008). Measurements have been made with an adjustable caliper, and are given in tenths of millimetre and in percentages of the diameter of the shell. For comments or location of specimens, the following abbreviations are used here: UT, Universität Tübingen, Germany; ICZN, International Code of Zoological Nomenclature; MNHN, Musée National

d'Histoire Naturelle, Paris, France; SGP, Serviços Geológicos de Portugal, Lisboa, Portugal; UCM, Universidad Complutense de Madrid, Spain. All the specimens presented here are held in the Departamento de Paleontología of the UCM.

## Systematic Palaeontology

### Family Vascoceratidae DOUVILLÉ, 1912

#### Neoptychitinae COLLIGNON, 1965a (p. 70)

**Diagnosis:** Genera with spires showing variable sections and degrees of involution that rapidly become smooth. Maturity with smooth surfaces, or maintaining only umbilical or ventrolateral tubercles, or some spaced ribs. Sutural elements usually shallow, although in some genera these may be deep and differentiated.

**Discussion:** CHOFFAT (1898) defined the genus *Vascoceras*, and suggested the possible relationship between his new group and *Ammonites superstes* KOSSMAT, 1897. HYATT (1903) included the genera *Vascoceras*, *Tolypeceras* HYATT, 1903, and *Barroisiceras* DE GROSSOUVRE, 1894, within the family Cosmocerotidae HYATT, 1900. DOUVILLÉ (1912) differentiated the “vascoceratinés” between the forms with normal first lateral lobe derived from the “pulchelliidés”.

<i>Vascoceras</i> CHOFFAT, 1898, and related groups				
Original classification	Collection	Stratigraphical origin	Geographical origin	Remarks
<i>V. gamai</i> CHOFFAT, 1898, and <i>V. cf. gamai</i>	JW, AG, CM and MH	Almost all <i>V. gamai</i> Subzone	Mainly Guadarrama Area, but also North-Castilian Sector and La Demanda Area	-
<i>V. mundaе</i> CHOFFAT, 1898	AG	<i>V. gamai</i> Subzone	Central Sector, mainly Guadarrama Area	Specimen of MELÉNDEZ-HEMERA (1984, p. 88, pl. 3, fig. 3 a-b) with narrow umbilici and persistent ribs: <i>V. harcoicense</i>
<i>V. cf. mundaе</i>	JW	<i>V. gamai</i> Subzone	Central Sector	-
<i>V. grossouvrei</i> CHOFFAT, 1898	JW	<i>S. (I.) malladae</i> Zone, <i>M. nodosoides</i> Subzone and, with doubts, <i>W. munieri</i> Subzone	Inner Castilian Platform	Dimensions close to <i>V. grossouvrei</i> , but by possible ribbing and high stratigraphical origin is advisable to reject the specific assignment of these ammonites
<i>V. cf. barcoicense</i> CHOFFAT, 1898	JW	<i>S. (I.) malladae</i> Zone and <i>M. nodosoides</i> Subzone	North-Castilian and Central sectors	Subgival and compressed section, tectiform venter, narrow umbilicus, complex suture (with four saddles) and stratigraphical range close to evolute and compressed <i>Choffaticeras</i> ( <i>Choffaticeras</i> ) HYATT, 1903
<i>V. durandi</i> (THOMAS & PERON, 1889) and <i>V. cf. durandi</i>	JW	From <i>C. (C.) quaasi</i> Zone to <i>M. nodosoides</i> Subzone	North-Castilian and Central sectors	-
<i>V. douvillei</i> CHOFFAT, 1898, and <i>V. cf. douvillei</i>	JW	From <i>C. (C.) quaasi</i> Zone to <i>M. nodosoides</i> Subzone	North-Castilian and Central sectors	-
<i>V. cf. douvillei</i>	CM	-	Guadarrama Area	-
<i>V. cavini</i> CHUDEAU, 1909	CM	-	Guadarrama Area	-
<i>V. cf. amietrense</i> CHOFFAT, 1898	JW	<i>S. (J.) subconciiliatus</i> Zone and lower Turonian	North-Ebro Area and Central Sector	Most of these specimens are attributable to other taxa, such as the number 957 that may be assigned to <i>V. durandi</i> , but some other ammonites could be transitional <i>Vascoceras</i>
<i>V. harttii</i> (HYATT, 1870)	AG and MH	Upper part of <i>C. (C.) quaasi</i> Zone and <i>S. (I.) malladae</i> Subzone	Guadarrama Area	-
<i>V. cf. harttii</i>	JW	Lower Turonian	La Demanda Area	-
<i>V. kossmati</i> CHOFFAT, 1898, and <i>V. cf. kossmati</i>	JW	<i>S. (I.) malladae</i> Zone and <i>M. nodosoides</i> Subzone	South-Ebro and La Demanda areas	-
<i>V. harttiforme</i> CHOFFAT, 1898, and <i>V. cf. harttiforme</i>	JW	Mainly <i>S. (I.) malladae</i> and <i>M. nodosoides</i> zones	Mainly Central Sector, but also South-Ebro Area	-
<i>V. cf. carteri</i> (BARBER, 1957)	AG and MH	<i>S. (I.) malladae</i> Subzone	Guadarrama Area	Specimens that should be assigned to <i>V. kossmati</i>
<i>V. globosum</i> (REYMENT, 1954b)	JW	<i>S. (I.) malladae</i> Zone and <i>M. nodosoides</i> Subzone	South-Ebro Area	-
<i>V. triangulare</i> FARAUD, 1940, and <i>V. cf. triangulare</i>	JW	<i>S. (I.) malladae</i> Zone and <i>M. nodosoides</i> Subzone	South-Ebro Area	<i>V. triangulare</i> must be considered as a synonym of <i>Choffaticeras</i> ( <i>Choffaticeras</i> ) <i>douvillei</i> (PERON, 1896), as indicated by BARROSO-BARCENILLA & GOY (2007)
<i>V. silvanense</i> CHOFFAT, 1898, and <i>V. cf. silvanense</i>	JW	<i>S. (I.) malladae</i> and <i>M. nodosoides</i> zones	-	<i>V. silvanense</i> seems restricted to the upper Cenomanian (CHOFFAT, 1898; KENNEDY et al., 1989) and, thus, the stratigraphical distribution attributed by WIEDMANN to these specimens may be incorrect
<i>V. rumeau</i> (COLLIGNON, 1957)	CM	-	Guadarrama Area	Two morphologies: ammonites with the proportions, narrow umbilici and juvenile ornamentation of <i>V. barcoicense</i> ; specimens with the dimensions and lack of ornamentation of <i>V. durandi</i>
<i>V. (Pachyvascoceras) crassum</i> (FURON, 1935)	JW	-	La Demanda Area	Globose and involute ammonites close to <i>V. kossmati</i>
<i>Paravasoceras</i> spp.	AG and MH	From <i>S. (J.) subconciiliatus</i> Zone to <i>S. (I.) malladae</i> Subzone	Guadarrama Area	Specimens from <i>S. (J.) subconciiliatus</i> and <i>C. (C.) quaasi</i> zones with rounded and depressed section: <i>V. durandi</i> ; ammonites from <i>C. (C.) quaasi</i> Zone and <i>S. (I.) malladae</i> Subzone with triangular and compressed section: <i>V. amietrense</i>
<i>Plesiovascoceras</i> sp.	AG	Upper part of <i>V. gamai</i> Subzone	Guadarrama Area	Specimens with the diagnostic features of <i>V. charoni</i> sp. nov.
-	AG	Upper part of <i>V. gamai</i> Subzone and lower part of <i>S. (J.) subconciiliatus</i> Zone	Guadarrama Area	Not previously classified ammonites with narrow umbilici, early lack of umbilical tubercles and persistent ribs: <i>V. barcoicense</i>

Text-fig. 4. Ammonites attributed to the genus *Vascoceras* CHOFFAT, 1898, and related groups in the WIEDMANN (JW), GOY (AG), CARRETERO (CM) and MELÉNDEZ (MH) collections.

Within the "vascoeratinés" he included the genera *Vascoceras* and *Fagesia* PERVINQUIÈRE, 1907. SPATH (1925) suggested Vascoceratidae as the name for this group, which was finally accepted, and included the genera *Vascoceras*, *Thomasites* PERVINQUIÈRE, 1907, and *Plesiovascoceras* SPATH, 1925, within the family. REYMENT (1954a) integrated the genera *Vascoceras*, *Paramammites* FURON, 1935, *Nigericeras* SCHNEEGANS, 1943, *Neoptychites* KOSSMAT, 1895, and *Ezilloella* REYMENT, 1954a, within the Vascoceratidae. KUMMEL & DECKER (1954) described the genus *Spathites*, assigning it to this same family. WRIGHT in MOORE (1957) stated that the genera *Nigericeras*, *Spathites*, *Gombeoceras*, *Ezilloella*, *Paravasoceras* FURON, 1935, *Pachyvascoceras*, *Vascoceras*, *Paramammites*, *Plesiovascoceras*, *Fagesia* and *Neoptychites* belong to the Vascoceratidae.

BARBER (1957) attributed to this family the same genera as WRIGHT in MOORE (1957), although he considered *Paracanthoceras* and *Pachyvascoceras* to be synonyms of *Paravasoceras*. WIEDMANN (1960, 1964) asserted that the subfamily Pseudotissotiinae HYATT, 1903, in which he included Coilopoceratidae HYATT, 1903, should be integrated into the Vascoceratidae. Furthermore, he stated that *Discovasoceras* COLLIGNON, 1957, shows a strong resemblance to *Choffaticeras* HYATT, 1903. KENNEDY et al. (1980) transferred *Spathites*, and its synonym *Fallotites* WIEDMANN, 1960, to Mammitinae HYATT, 1900. WRIGHT & KENNEDY (1981) divided the family into the Vascoceratinae, with normally rounded ventral area without keels, and the Pseudotissotiinae, with relatively involute whorls and flat flanks. CHANCELLOR (1982) presented a summary of the modifications established in the taxonomic organisation of the Vascoceratidae, since the work of WRIGHT in MOORE (1957) until the year in which his study was written. RENZ (1982) proposed the inclusion of *Paramammites* within Acanthoceratidae DE GROSSOUVRE, 1894. KENNEDY et al. (1989) and COBBAN et al. (1989) suggested that *Nigericeras* should be included within the Acanthoceratidae. CHANCELLOR et al. (1994) stated that the pseudotissotiids seemed to be derived directly from the acanthoceratids, and therefore recognised the family status of the former group, as KENNEDY (1994). ZABORSKI (1996) assigned *Paravasoceras* and his new genus *Pseudovasoceras* to the Acanthoceratidae. WRIGHT in KAESLER (1996) included *Vascoceras*, *Ezilloella*, *Neoptychites*, *Fagesia*, *Infabricaticeras* COBBAN et al., 1989, *Rubroceras* COBBAN et al., 1989,

and ?*Microdiphascoceras* COBBAN et al., 1989, within the family of DOUVILLÉ.

Regarding the phylogeny of the Vascoceratidae, REYMENT (1955) considered that the origin of the family could be located in *Nigericeras*. However, in 1979 the same author stated that several of the Acanthoceratidae taxa could be involved in the origins of the Vascoceratidae, and therefore he indicated that the latter group could be considered as a polyphyletic family. COOPER (1979) indicated that *Vascoceras diartianum* (D'ORBIGNY 1850) gave rise to *Paravasoceras* and *Vascoceras*. WRIGHT & KENNEDY (1981) considered that Vascoceratidae derived from Acanthoceratidae by ornamental reduction and sutural simplification. ZABORSKI (1996) also defended the common origin of *Paravasoceras* and *Vascoceras*, indicating that both groups seemed to have originated from *Nigericeras*, and maintained that his new genus *Pseudovasoceras* could derive from *Cunningtoniceras* COLLIGNON, 1937.

**Distribution:** From the upper Cenomanian to the upper Turonian of many countries, mainly belonging to the palaeogeographical environment of the Tethys. The earliest records of the family correspond to North American specimens of *V. diartianum* from the *Sciponoceras gracile* Zone, almost equivalent to the *Metoicoceras geslinianum* standard Zone. In the Iberian Trough, the Vascoceratidae have been identified from the *V. gamai* Subzone to the middle Turonian.

#### Genus *Vascoceras* CHOFFAT, 1898

*Pachyvascoceras* FURON, 1935, p. 58, type species *Pachyvascoceras crassum* FURON, 1935, by subsequent designation of REYMENT, 1954b, p. 257.

*Paracanthoceras* FURON, 1935, p. 59, type species by original designation *Vascoceras (Paracanthoceras) chevalieri* FURON, 1935.

*Paravasoceras* FURON, 1935, p. 60, type species by original designation *Vascoceras cauwini* CHUDEAU, 1909.

*Broggiiceras* BENAVIDES-CÁCERES, 1956, p. 469, type species by original designation *Broggiiceras olsoni* BENAVIDES-CÁCERES, 1956.

*Greenhornoceras* COBBAN & SCOTT, 1972, p. 84, type species by original designation *Vascoceras (Greenhornoceras) birchbyi* COBBAN & SCOTT, 1972.

*Provasoceras* COOPER, 1979, p. 123, type species by original designation *Ammonites diartianus* D'ORBIGNY, 1850.

*Nannovasoceras* RENZ & ÁLVAREZ, 1979, p. 978, type species by original designation *Nannovasoceras intermedium* RENZ & ÁLVAREZ, 1979.

**Type species:** *Vascoceras gamai* CHOFFAT, 1898. Although some authors stated that the designation of this species as

genotype corresponds to CHOFFAT (1898) or ROMAN (1938), the first author who explicitly mentioned *V. gamai* as the type of *Vascoceras* was DIENER (1925, p. 182), as indicated by CHANCELLOR et al. (1994).

**Diagnosis:** Variable morphology with oval, subtriangular or rounded embracing whorl section, subacute, arched or plane ventral region, steep umbilici, and generally globose and involute adult cadicone. Only the first whorls may show umbilical tubercles and also, in some species, small and rounded ribs crossing the ventral area, constrictions and feeble ventrolateral tubercles. The ornamentation disappears progressively during ontogeny, although the umbilical tubercles can remain until maturity. Quite simple and irregular suture lines, with three bifid or indented lobes and wide saddles on each flank. The first lobes are wide and low, with palm-shaped terminations.

**Discussion:** CHOFFAT (1898) established the genus *Vascoceras* and noted that the species he described and included in this group could be divided into four conjuncts. The first is composed of taxa with only one type of tubercles and wide umbilici, such as *V. gamai*, including its variety *subtriangularis*, and *V. mundae*. The second comprises subglobose species with rounded umbilical margins, such as *V. silvanense*, *V. douvillei* and *V. adonense*. The third is composed of globose taxa with sharp umbilical margins, such as *V. amieirense* and *V. kossmati*. Finally, the fourth comprises the multituberculate species *V. subconciatius*. This author remarked, however, that some specimens with intermediate features cannot be clearly assigned to any of these four categories.

PERVINQUIÈRE (1907) considered that *V. douvillei* is a synonym of *V. durandi*, and suggested that *V. amieirense* might be included within the morphological variability of *V. durandi*. FURON (1935) differentiated four subgenera in *Vascoceras*. The first one, *Pachyvascoceras*, includes globose and involute species with umbilical tubercles, deep umbilici and lack of ornamentation at maturity, such as *V. silvanense*, *V. douvillei*, *V. adonense*, *V. amieirense*, *V. barttiforme* and *V. kossmati*. The subgenus *Paramammites* groups nonglobose and tuberculate taxa, such as *V. subconciatius* and *V. polymorphum* PERVINQUIÈRE, 1907. The subgenus *Paracanthoceras* includes involute and nonglobose species, less ornamented and with complex suture lines, such as his new species *V. chevalieri*. Finally, the subgenus *Paravasoceras* groups compressed and involute taxa with ribs and simple suture lines and without tubercles, such as *V. cauwini* CHUDEAU, 1909.

SCHNEEGANS (1943) considered the subgenera *Paracanthoceras* and *Pachyvascoceras* as synonyms of *Paravasoceras*. He also gave generic status to *Paravasoceras*, and suggested that this group should include the species with the typical suture lines of *Vascoceras*, with oval whorl section and with ribs. REYMENT (1954b) considered that the name *Paracanthoceras* should maintain priority over the term *Paravasoceras*, but later he (1955) again preferred the designation *Paravasoceras* for this group. BENAVIDES-CÁCERES (1956) described the species *B. olssoni* and *B. humboldti*, which show smooth inner whorls and adult ornamentation composed of strong ribs, and on the basis of these features he proposed the genus *Broggioceras*.

WIEDMANN (1960, 1964), taking *Ammonites reveliereanus* COURTILLER, 1860, as type, described *Fallotites*, the group in which he included *V. subconciatium*. COLLIGNON (1965b) maintained *Paravasoceras* as a different genus. FREUND & RAAB (1969) did not consider *Discovasoceras* COLLIGNON, 1957, as a differentiated genus, and included it in *Paravasoceras*, together with *Paracanthoceras* and *Pachyvascoceras*. COBBAN & SCOTT (1972) described *Vascoceras* (*Greenhornoceras*) as the most recent subgenus of *Vascoceras*. These authors indicated that this subgenus differs from *V. (Vascoceras)* in developing a larger involution grade and maintaining a subrectangular whorl section. SCHÖBEL (1975) concluded that several species should be considered as synonyms of *V. cauwini*, whereas *Pachyvascoceras* should be included in *Paravasoceras*, which for this author maintained the generic status. BERTHOU & LAUVERJAT (1975) studied the Vascoceratidae in its type region, and BERTHOU et al. (1975) included in the genus *Vascoceras* the groups of *V. gamai-mundae*, of *V. barcoicense*, of *V. douvillei* and *V. amieirense*, of *V. kossmati* and of *V. subconciatius*. The first is composed of specimens with evolute and quite compressed shell, umbilical tubercles that disappear near the adult body chamber, rounded or subtriangular whorls and feeble ribs during early ontogeny. The group of *V. barcoicense* comprises more involute specimens with feeble plications on the adult body chamber. The group of *V. douvillei* and *V. amieirense* is characterised by specimens that differ in the whorl section. The group of *V. kossmati*, a taxon considered indistinguishable from *V. barttiforme*, comprises involute and globose specimens with narrow umbilici and flattened whorls of subrounded or subtriangular section. The fifth and last group includes *V. subconciatius*. Finally, BERTHOU et al. (1975) con-

cluded that, with the exception of *V. subconciatus*, all the original material of CHOFFAT (1898) could be assigned to *Vascoceras*, and that this genus should only be divided into *V. s. str.* and *V. (Pachyvascoceras)*, which includes the species *V. douvillei*, *V. amieirensis* and *V. kossmati*.

COOPER (1978) considered *Greenhornoceras* as a synonym of *Vascoceras*. REYMENT & CHANCELLOR (1978) studied the common occurrence of members of *Vascoceras* in Spain and West Africa. RENZ & ÁLVAREZ (1979) described *Nannovascoceras* on the basis of several tiny ammonites with certain constrictions during their young stages. COOPER (1979) proposed *Provascoceras* as a new genus for small Cenomanian specimens with marked ribs on the ventral area and numerous tubercles on the adult body chamber. WRIGHT & KENNEDY (1981) considered that the diagnostic features of *Provascoceras* did not justify its generic status. RENZ (1982) included *Greenhornoceras* in the synonymy of *Pseudoneoptychites* LEANZA, 1967. BERTHOU et al. (1986) included in the genus of CHOFFAT the species *V. diartianum* (D'ORBIGNY 1850), *V. harttii* (HYATT 1870), *V. gamai*, *V. barcoicense*, *V. kossmati*, *V. cauwini* CHUDEAU, 1909, *V. pioti* (PERON in FOURTAU 1904), *V. birchbyi* COBBAN & SCOTT, 1972, and, as a possible synonym of HYATT's taxon, *V. durandi* (THOMAS & PERON 1889). They considered *V. amieirensis* and *V. douvillei* to be conspecific forms of *V. durandi*; *V. munda*, *V. adonense* and *Ammonites* (?*V.*) *grossouvrei* of *V. gamai*; and *V. harttiforme* of *V. kossmati*. These authors also indicated that *V. silvanense* CHOFFAT, 1898, *V. tavense* FARAUD, 1940, and *V. triangulare* FARAUD, 1940, are *nomina dubia*. Finally, BERTHOU et al. (1986) highlighted the complexity of the classification of the Nigerian species assigned to *Vascoceras*. KENNEDY (1994) excluded *V. (Pachyvascoceras) triangulare* from this genus, attributing it to *Choffaticeras* HYATT, 1903, as he considered this species as a synonym of *Choffaticeras (Choffaticeras) douvillei* (PERON 1896). ZABORSKI (1996) proposed the genus *Pseudovascoceras*, designating *V. nigeriense* WOODS, 1911, as its type species. Within his new group he included specimens without tubercles during mid and advanced ontogeny and often with strong ventral ornamentation, and integrated *Pseudovascoceras* and *Paravascoceras* in the Acanthoceratidae DE GROSSOUVRE, 1894.

On the basis of the above remarks, there would seem to be insufficient grounds for maintaining the separation of *Pachyvascoceras*, *Paracanthoceras*, *Brog-*

*gioceras*, *Greenhornoceras*, *Provascoceras* and *Nannovascoceras*. Regarding *Paravascoceras*, there is no doubt that its type, *V. cauwini*, is an unusual species among those of the genus of CHOFFAT, as it follows a slightly different ontogenetic development. Nevertheless, this species lacks the juvenile ornamentation of the Acanthoceratidae, and shows simple suture lines. Therefore, it seems to be more appropriate to assign *V. cauwini*, and consequently *Paravascoceras*, to the family Vascoceratidae, specifically to the genus *Vascoceras*.

As regards the phylogeny of the group, although for many years it was believed that the origin of *Vascoceras* was in *Nigerioceras* SCHNEEGANS, 1943, WRIGHT & KENNEDY (1980) and KENNEDY & WRIGHT (1994) indicated that the genus of CHOFFAT could be derived directly from *Protacanthoceras* SPATH, 1923. CHANCELLOR et al. (1994) concluded that the origin of *Vascoceras*, and therefore of the Vascoceratidae, was in *Protacanthoceras proteus* WRIGHT & KENNEDY, 1980, exactly in *P. proteus vascoceratoides* WRIGHT & KENNEDY, 1987, by loss of the ventrolateral and siphonal tubercles. ZABORSKI (1996), observing the ornamentation and the bifid form of the first lateral saddles of *V. diartianum*, indicated that this species is transitional between the Acanthoceratidae and the Vascoceratidae.

**Distribution:** Upper Cenomanian and lower Turonian of Portugal, France, Spain, the UK, Germany, Croatia, north, west and east of Africa, Madagascar, the Middle East, Brazil, Peru, Colombia, Mexico, Venezuela, the USA and Japan. Its oldest records occur in the *S. gracile* Zone, almost equivalent to the *M. geslinianum* standard Zone. In the Iberian Trough, the genus ranges from the base of the *V. gamai* Subzone to the upper part of the *S. (I.) malladae* Subzone of the Inner Castilian Platform. Nevertheless, *Vascoceras* is better represented in the Central Sector than in the North-Castilian Sector.

*Vascoceras gamai* CHOFFAT, 1898

(Plate 1, figs. A–L; Text-fig. 5 A)

- 1898 *Vascoceras gamai* CHOFFAT, p. 54, pl. 7, figs. 1–4; pl. 8, fig. 1; pl. 10, fig. 2; pl. 21, figs. 1–4.
- 1898 *Vascoceras gamai* var. *subtriangularis* CHOFFAT, p. 55, pl. 7, fig. 5; pl. 21, fig. 5.
- 1898 *Vascoceras munda* CHOFFAT, p. 56, pl. 10, fig. 1; pl. 8, figs. 2–4; pl. 21, figs. 6–8, 10.
- 1898 *Vascoceras adonensis* CHOFFAT, p. 59, pl. 9, fig. 3; pl. 21, fig. 12 a–b.

- 1898 *Ammonites* (?*Vascoceras*) *grossouvrei* CHOFFAT, p. 68, pl. 9, figs. 1–2; pl. 22, figs. 37–38.
- ? 1898 *Ammonites* (?*Vascoceras*) cf. *barcoicensis* CHOFFAT, p. 67, pl. 16, fig. 11; pl. 22, fig. 36.
- aff. 1920 *Vascoceras* aff. *gamai* CHOFFAT – BÖSE, p. 216, pl. 15, figs. 3–5, text-fig. 3.
- 1928 *Vascoceras gamai* CHOFFAT – DOUVILLÉ, p. 13, fig. 3; pl. 1, fig. 4.
- ? 1957 *Vascoceras gamai* CHOFFAT – COLLIGNON, p. 122, pl. 2, fig. 2.
- cf. 1960 *Vascoceras* cf. *gamai* CHOFFAT – WIEDMANN, pp. 712, 720.
- ? non 1960 *Vascoceras* (*Pachyvascoceras*) *grossouvrei* CHOFFAT – WIEDMANN, pp. 712, 720.
- 1960 *Vascoceras* (*Vascoceras*) *gamai* CHOFFAT – WIEDMANN, p. 723.
- cf. 1960 *Vascoceras* (*Vascoceras*) cf. *mundae* CHOFFAT – WIEDMANN, p. 723.
- cf. 1964 *Vascoceras* (*Vascoceras*) cf. *gamai* CHOFFAT – WIEDMANN, pp. 111, 115.
- ? non 1964 *Vascoceras* (*Pachyvascoceras*) *grossouvrei* CHOFFAT – WIEDMANN, pp. 111, 115.
- 1964 *Vascoceras* (*Vascoceras*) *gamai* CHOFFAT – WIEDMANN, p. 116.
- cf. 1964 *Vascoceras* (*Vascoceras*) cf. *mundae* CHOFFAT – WIEDMANN, p. 116.
- 1965b *Vascoceras gamai* CHOFFAT – COLLIGNON, p. 183 (21), figs. 5–7.
- 1967 *Vascoceras gamai* CHOFFAT – POLSAK, p. 137, pl. 83, fig. 3.
- 1967 *Vascoceras* (*Pachyvascoceras*) *grossouvrei* CHOFFAT – POLSAK, p. 137, pl. 83, fig. 1.
- cf. 1975 *Vascoceras* cf. *gamai* CHOFFAT – WIEDMANN, p. 141.
- 1977 *Vascoceras* ex. gr. *V. gamai* CHOFFAT – MOJICA & WIEDMANN, p. 749, pl. 1, fig. 1.
- 1978 *Vascoceras gamai* CHOFFAT – WIEDMANN & KAUFFMAN, pl. 7, fig. 1.
- cf. 1978 *Vascoceras* cf. *gamai* CHOFFAT – WIEDMANN & KAUFFMAN, p. 2.
- 1979 *Vascoceras gamai* CHOFFAT – WIEDMANN, pl. 7, fig. 1.
- ? non 1979 *Pachyvascoceras grossouvrei* CHOFFAT – WIEDMANN, pp. 193, 205.
- cf. 1979 *Vascoceras* cf. *gamai* CHOFFAT – WIEDMANN, p. 203.
- 1981 *Vascoceras gamai* CHOFFAT – WRIGHT & KENNEDY, text-fig. 29 g–i.
- cf. 1982 *Vascoceras* cf. *gamai* CHOFFAT – CHANCELLOR, p. 97, figs. 26–28.
- 1982 *Vascoceras gammai* [*sic*] CHOFFAT – CARRETERO-MORENO, p. 255.
- 1984 *Vascoceras gamai* CHOFFAT – MELÉNDEZ-HEVIA, p. 85, pl. 2, fig. 1 a–b; pl. 3, figs. 1–2.
- 1984 *Vascoceras mundae* CHOFFAT – MELÉNDEZ-HEVIA, p. 88 (only).
- 1986 *Vascoceras gamai* CHOFFAT – BERTHOU et al., p. 66, pl. 2, figs. 1–12; pl. ?3, figs. 1–3, 5–7, 10, 13–14.
- 1989 *Vascoceras gamai* CHOFFAT – LUGER & GRÖSCHKE, p. 378, pl. 40, figs. 5, 7, text-fig. 6 c.
- ? 1989 *Vascoceras* cf. *gamai* CHOFFAT – COBBAN et al., p. 45, figs. 44, 87 w–aa, ee–rr.
- 1992 *Vascoceras gamai* CHOFFAT – THOMEL, p. 228, pl. 121, figs. 1–2; pl. 121, fig. 4.
- 1996 *Vascoceras gamai* CHOFFAT – AMÉDRO et al., p. 213, fig. 17 a–d.
- 2001 *Vascoceras gamai* CHOFFAT – CALLAPEZ & FERREIRA, p. 51, pl. 5, figs. 3–6; pl. 6, figs. 1–2, text-figs. 16.4–11, 20.9.
- 2001 *Vascoceras adonense* CHOFFAT – CALLAPEZ & FERREIRA, p. 64, pl. 8, figs. 4–5; pl. 9, figs. 1–2, text-figs. 19.2–3, 19.5–6, 19.8–10.
- ? 2005 *Vascoceras* gr. *gamai* CHOFFAT – MEISTER & ABDALLAH, p. 134, pl. 13, figs. 1–2, 4, text-fig. 25.
- 2006 *Vascoceras gamai* CHOFFAT – BARROSO-BARCENILLA, p. 220, pl. 28, figs. a–l; pl. 29, figs. a–c, text-fig. 66.

Type: The holotype designated by CHOFFAT (1898, p. 54, pl. 7, fig. 1; pl. 21, fig. 1) was destroyed. Among the paratypes conserved in the SGP, BERTHOU et al. (1986) selected as neotype the specimen 808-2 of CHOFFAT (1898, pl. 7, fig. 2), from Meirinhas de Baixo, Portugal.

Material: 19 specimens; CA-R-397, CA-S-151, CA-S-496, CA-S-497, CC-R-207, CC-R-208, CC-R-235, CG-R-529, CS-S-149, TA-R-107, TA-R-430, TA-R-613, TA-R-654, TA-S-100, TA-S-102, TA-S-103, TA-S-104, TA-S-105 and TA-S-108.

#### Dimensions:

	D	H (%)	E (%)	O (%)
Range	1245–408	548–169 (49–32)	587–185 (56–23)	445–124 (41–29)
Mean	963	376 (39)	364 (39)	327 (34)

**Description:** Specimens with slightly compressed or depressed rounded whorl section, evolute coiling, convex ventral area, convergent flanks, and relatively wide umbilici with subvertical and low walls, and nar-

row and rounded margins. In early ontogeny they show 5–7 large and rounded umbilical tubercles per whorl. From each of these can grow 1–2 sinuous, divergent and slightly prorsiradiate ribs, which become

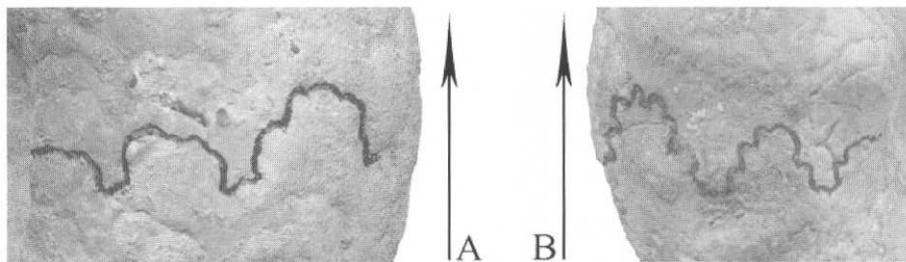
stronger after crossing the ventral area. When present, the accessory ribs grow from the flanks, intercalated at regular intervals. During ontogeny the whorl section becomes slightly compressed, the flanks flatten and the ornamentation disappears, leaving the adult body chamber completely smooth and with a certain tendency to uncoiling.

**Discussion:** CHOFFAT (1898) included *V. gamai* within the forms of the genus he called monotuberculate with wide umbilici, and described other close taxa, such as *V. mundaе*, *V. adonensis* and *Ammonites* (?*V.*) *grossourei*. The possibility that *V. mundaе*, *V. adonensis* and *A.* (?*V.*) *grossourei* were synonyms of *V. gamai* was first suggested by BERTHOU et al. (1975). These authors stated that it is impossible to establish a limit between *V. gamai* and *V. mundaе*, and considered that *V. gamai* var. *subtriangularis*, *V. gamai* var. *lissa* CHOFFAT, 1898, *V. adonense* and *A.* (?*V.*) *grossourei* could be included in the morphological variability of the first taxon. BERTHOU et al. (1986) regarded *V. gamai* var. *subtriangularis* CHOFFAT, 1898, *V. mundaе*, *V. adonense* and *A.* (?*V.*) *grossourei* as synonyms of *V. gamai*. They integrated nearly all of the most evolute, compressed and monotuberculate forms of the genus in this species, and indicated that the slight differences in the ornamentation, the degree of involution and the outline of the suture lines of *V. mundaе*, *V. adonense* and *A.* (?*V.*) *grossourei* do not justify their specific separation. Finally, the same authors also stated that the outline of the suture lines cannot be accepted as a feature for classifying the members of *Vascoceras*, and they considered that the slightly tabulate form of the ventral area of some juvenile specimens of this genus reveals the existence of a close relationship with *Spathites* KUMMEL & DECKER, 1954.

The coincidence of the geographical and stratigraphical distributions of *V. gamai* and *V. mundaе* in the Iberian Trough, as well as the great similarity between both forms, supports the conclusions of BERTHOU et al. (1986) in this respect. Likewise, after having observed in SGP that the types of *V. adonense* and *A.* (?*V.*) *grossourei* present the typical features of *V. gamai*, in this paper both taxa have also been included in the synonymy of *V. gamai*. On the contrary, *V. gamai* var. *mahafalensis* COLLIGNON, 1965a, excluded from the synonymy of *V. gamai* by BERTHOU et al. (1986), shows persistent and strong umbilical tubercles and complex suture lines, and seems to be closer to the groups *Spathites* or *Pseudaspidoceras* HYATT, 1903, than to the genus *Vascoceras*.

The evolute *Ammonites* (?*V.*) cf. *barcoicensis* of CHOFFAT (1898, pl. 16, fig. 11; pl. 22, fig. 36) lacks ribs and shows an umbilical width closer to *V. gamai*. The fragmented *V. gamai* of COLLIGNON (1957) has some features of the same species, but they are not significant enough to make a precise taxonomic determination. Some of the *V.* cf. *gamai* of COBBAN et al. (1989) show quite narrow umbilici, weak umbilical tubercles and persistent ribs. These features are close to those of *V. barcoicense*, suggesting that these ammonites may be transitional forms between this species and *V. gamai*.

**Distribution:** This species has been identified in the upper Cenomanian, where it reaches its maximum abundance, and in the base of the lower Turonian of Portugal, Egypt, Algeria, Spain, Croatia, France and, possibly, Mexico and the USA. In the Iberian Trough, it has been collected from the *V. gamai* Subzone of the Inner Castilian Platform.



Text-fig. 5. Suture lines. A, *Vascoceras gamai* CHOFFAT, 1898, TA-S-105, from the *Vascoceras gamai* Subzone of Tamajón. B, *Vascoceras charoni* sp. nov., MS-3, holotype, from the *Vascoceras gamai* Subzone of Tamajón. Both are  $\times 3/2$ .

*Vascoceras charoni* sp. nov.

(Plate 2, figs. A–F; Text-fig. 5 B)

- 1984 *Plesiovascoceras* sp. MELÉNDEZ-HEVIA, p. 95, pl. 3, figs. 4 a–b, 5 a–b.  
 2006 *Vascoceras* nov. sp. BARROSO-BARCENILLA, p. 226, pl. 29, figs. d–i, text-fig. 67.

**Types:** Holotype is specimen MS-3, and paratypes are specimens TA-R-655, TA-S-95, TA-S-122 and TA-S-556.

**Derivation of the name:** The name comes from the mythological ferryman who carries souls across the river Acheron to the realm of Hades.

**Material:** 5 specimens; MS-3, TA-R-655, TA-S-95, TA-S-122 and TA-S-556.

**Dimensions:**

	D	H (%)	E (%)	O (%)
Range	838–405	342–199 (49–32)	548–295 (76–58)	275–134 (44–30)
Mean	589	237 (41)	391 (68)	199 (34)

**Diagnosis:** Small or medium globose specimens, strongly ornamented for the genus *Vascoceras* CHOFFAT, 1898, and with semicircular or subreniform whorl section and relatively wide umbilici. They present 6–8 strong umbilical tubercles and 20–25 marked ribs of triangular section and the same number of semicircular interspaces per whorl. From each umbilical tubercle grow one or two main ribs. Each radial band without umbilical tubercles has two or three accessory ribs, which grow from the outer limit of the umbilical margins. The ribbing crosses the flanks without changing, but as it approaches the ventral area it is usually less pronounced, and it may even disappear on the siphonal line. During early ontogeny the most characteristic features are the rounded ventral ridges produced by a siphon located at a very outer position, and the feeble and elongated ventrolateral tubercles located over the main and the accessory ribs, which disappear quickly with growth. During ontogeny the ornamentation becomes more distant, the umbilical tubercles get stronger and more rounded, and the ribbing and the siphonal ridge tend to decrease. The whorl section during ontogeny maintains the normal tendency of *Vascoceras* of becoming more compressed, although its height is always by far surpassed by its width. These specimens show the typical suture lines of this genus, with broad and high first lateral saddles, and wide and low second lateral saddles.

**Discussion:** Few species of *Vascoceras* present a relatively wide whorl section and a marked ornamentation. Most of the more ornamented forms, such as *V. diartianum* (D'ORBIGNY 1850), *V. gamai* CHOFFAT, 1898, *V. barcoicense* CHOFFAT, 1898, *V. cauvinii* CHUDEAU, 1909, *V. bulbosum* (REYMENT 1954a) and *V. obscurum* BARBER, 1957, show elevated and compressed whorl sections. On the other hand, the wider and more compressed taxa, such as *V. harttii*

(HYATT 1870), *V. kossmati* CHOFFAT, 1898, *V. globosum* (REYMENT 1954b), *V. proprium* (REYMENT 1954b), *V. robustum* BARBER, 1957, *V. polygonum* BARBER, 1957, and *V. ellipticum* BARBER, 1957, do not normally have strong ornamentations, and follow the tendency to adopt almost smooth surfaces. Among the few forms of this genus with relatively wide and ornamented whorls, *V. costatum* (REYMENT 1954b) shows strong ribs, but it has a highly involute coiling and lacks the characteristic tubercles of *V. charoni*. *V. nigriense* WOODS, 1911, presents strongly marked ventrolateral tubercles, which can modify the whorl section to the extent of developing a subpolygonal contour, and notably different ornamentation. *V. silvanense* CHOFFAT, 1898, also has relatively wide whorl section and strong umbilical tubercles, but during early ontogeny it lacks ribs. *V. rumeauui* (COLLIGNON 1957) is one of the most ornamented taxa of *Vascoceras*. Nevertheless, it presents subtriangular section, has narrower umbilici, lacks umbilical tubercles and shows ribs only during advanced ontogeny. Finally, it has been observed that during early ontogeny, the oldest specimens of *V. durandi* can show feeble vestiges of umbilical tubercles, and therefore exhibit a relatively similar appearance to the representatives of *V. charoni*. This new species, however, presents much more robust and persistent ornamentation, broader whorl section, slightly more complex suture lines and lower stratigraphical distribution than *V. durandi*.

Among the Cenomanian members of *Vascoceras*, a tendency towards the progressive loss of umbilical tubercles and ribs has been observed. *V. charoni* constitutes an atypical form within this process, because its morphology becomes similar to that of the genus *Fagesia* PERVINQUIÈRE, 1907. This new species may therefore be one of the taxa from which the earliest representatives of this group originated. An example

of these first members of *Fagesia* is *F. catinus* (MANTPELL 1822), whose lowest records were reported by COBBAN et al. (1989) from the *N. juddii* Zone of the USA. This biostratigraphic unit is stratigraphically close to the *V. gamai* Subzone and the *S. (J.) subconciatus* Zone of Spain, from whose levels *V. charoni* has been collected.

**Distribution:** This new species occurs in the levels 10, 11 and, possibly, 12 of BARROSO-BARCENILLA (2006) of the upper part of the *V. gamai* Subzone and the lower part of the *S. (J.) subconciatus* Zone of Tamajón, in the Guadarrama Area of the Iberian Trough, Spain.

*Vascoceras barcoicense* CHOFFAT, 1898

(Plate 2, figs. G–K)

- 1898 *Ammonites* (?*Vascoceras*) *barcoicensis* CHOFFAT, p. 67, pl. 17, fig. 1; pl. 22, fig. 35 [only].  
 ? 1907 *Vascoceras* cf. *barcoicensis* CHOFFAT – PERVINQUIÈRE, p. 335.  
 ? 1914 *Vascoceras barcoicensis* CHOFFAT – ECK, p. 203, pl. 14, fig. 1.

**Dimensions:**

	D	H (%)	E (%)	O (%)
Range	993–534	415–234 (48–42)	571–304 (58–46)	228–129 (26–19)
Mean	737	325 (44)	384 (52)	173 (24)

**Description:** Involute specimens with subelliptical or subrectangular whorl section whose greatest breadth is close to the umbilical margins. They have an arched ventral region, flat or slightly convex flanks and quite small umbilici with rounded margins. Their ornamentation appears on the ventral region and the outer half of the flanks, and is composed of several slightly prorsiradiate ribs, although certain specimens can also have some small umbilical tubercles on the inner whorls, which disappear quite quickly. The adult body chamber presents a scaphitoid aspect and a broad aperture. They show variable suture lines with proximate septa.

**Discussion:** CHOFFAT (1898) described this species and included it in his new genus *Vascoceras*. In contrast, SCHNEEGANS (1943) integrated *V. barcoicense* in *Panvascoceras* FURON, 1935, and AMARD et al. (1981) included it in *Nigericeras* SCHNEEGANS, 1943. However, as shown by CHOFFAT (1898, pl. 12, fig. 35), the suture lines of this species show the typical pattern of *Vascoceras*.

- 1967 *Vascoceras barcoicense* CHOFFAT – POLSAK, p. 136, pl. 83, fig. 2.  
 1981 *Nigericeras barcoicense* (CHOFFAT) – AMARD et al., p. 54, pl. 4, fig. 16 a–b.  
 1984 *Vascoceras mundaie* CHOFFAT – MELÉNDEZ-HEVIA, p. 88, pl. 3, fig. 3 a–b [only].  
 1986 *Vascoceras barcoicense* CHOFFAT – BERTHOU et al., p. 70, pl. 4, figs. 1–3.  
 1989 *Vascoceras barcoicense* CHOFFAT *exile* COBBAN et al., p. 47, pl. 87, figs. q–s; pl. 89, figs. m–g.  
 ? 1994 *Vascoceras durandi* (THOMAS & PERON) – CHANCELLOR et al., p. 48, pl. 10, figs. 1–2 [only].  
 2001 *Vascoceras barcoicense* CHOFFAT – CALLAPEZ & FERREIRA, p. 67, pl. 6, figs. 3–5; pl. 7, figs. 1–2, text-figs. 20.1–3, 20.5.  
 2006 *Vascoceras barcoicense* CHOFFAT – BARROSO-BARCENILLA, p. 228, pl. 30, figs. a–i.

**Type:** The holotype designated by CHOFFAT (1898, pl. 17, fig. 1 a–c) was destroyed. Among the paratypes conserved in the SGP, BERTHOU et al. (1986) selected as neotype the non-illustrated specimen 831 of CHOFFAT, from Almoxarife, Portugal.

**Material:** 6 specimens: TA-R-106, TA-R-634, TA-R-652, TA-R-99, TA-S-567 and TA-S-572.

The *V. cf. barcoicensis* of PERVINQUIÈRE (1907, p. 335) was considered a strongly ribbed *Vascoceras durandi* (THOMAS & PERON 1889) by BERTHOU et al. (1986) and CHANCELLOR et al. (1994). After studying in the MNHN this specimen, figured by CHANCELLOR et al. (1994, pl. 10, figs. 1–2), it has been observed that its features, such as the whorl section, which is only slightly wider than higher, the umbilical width, which only reaches 20 % of the diameter of the shell, and the ornamentation are closer to those of *V. barcoicense* than to those of *V. durandi*. The *V. barcoicense* of ECK (1914) was considered a doubtful *V. durandi* by BERTHOU et al. (1986). This specimen has a relatively depressed whorl section, as indicated by BERTHOU et al. (1986), and in our opinion their features may correspond to a wide *V. barcoicense*. The *Panvascoceras* cf. *barcoicensis* of SCHNEEGANS (1943) was considered an evolute *V. cauwini* CHUDEAU, 1909, by SCHÖBEL (1975). This opinion was not rejected by BERTHOU et al. (1986, p. 72), who, nevertheless, maintained it in the synonymy of *V. barcoi-*

*cense*. The same ammonite was later attributed to *V. (Paravascoceras) cauwini* by MEISTER et al. (1992), and with some reservations to *Pseudovascoceras nigeriense* (WOODS 1911) by ZABORSKI (1996). This doubtful specimen, recently studied at the MNHN, presents 25–30 weak ribs per whorl but reaches a relatively high umbilical width, which ranges 26–29 % of the diameter of the shell, depending on the measured flank. For this reason, it is difficult to consider this ammonite a member of *V. barcoicense*. Finally, the *N. barcoicense* of AMARD et al. (1981) was considered a possible *Paravascoceras cauwini* by ZABORSKI (1996). In our opinion, this specimen of the MNHN seems to present the typical features of *V. barcoicense*.

In view of the difficulties encountered in distinguishing *V. barcoicense* from *V. gamai* and from *V. cauwini*, BERTHOU et al. (1975, 1986) emphasised that the main problem in identifying and establishing the taxonomic status of the the former species lies in the ignorance of the morphology and ornamentation of the inner whorls of its holotype. BERTHOU et al. (1986) also remarked that if this missing holotype in its early ontogeny had presented some umbilical tubercles, or a nearly smooth external surface, it would be difficult to maintain the specific separation between *V. barcoicense* and *V. gamai*, in the first case, or between *V. barcoicense* and *V. cauwini*, in the second.

Regarding the separation between *V. barcoicense* and *V. cauwini*, BERTHOU et al. (1986) stated that the former species has compressed and involute morphology and, apparently, lacks umbilical tubercles during early ontogeny. However, they maintained this specific distinction because *V. cauwini* shows a subtriangular and more involute whorl section and a strong ribbing at maturity. ZABORSKI (1996) separated both species on the basis of the reduced ornamentation of *V. barcoicense* during maturity. Apart from these features, the different ontogenetic tendencies followed by *V. barcoicense* and *V. cauwini* also make it possible to differentiate between these two species. Whereas the former loses ornamentation during ontogeny, as can be observed in the specimens presented in this paper, the latter develops stronger ribbing during growth. Therefore, the notable morphologic differences and the dissimilar ontogenetic development of *V. barcoicense* and *V. cauwini* support the taxonomic separation of these taxa. Specimens with small umbilici whose ornamentation disappears during ontogeny correspond to CHOFFAT's species, whereas specimens with an almost smooth surface in the earlier stages of growth

and with strong ribbing in the later stages belong to CHUDEAU's species. Similarly, the presence of ornamentation in some of the smallest specimens presented in this paper clearly distinguishes *V. barcoicense* from *V. cauwini*, but places the former species close to *V. gamai*. However, the narrowness of the umbilici, the robustness of the ribbing and the early lack of ornamentation near the umbilical area of these immature specimens of *V. barcoicense* distinguish them from the more evolute members of the genus. *V. barcoicense* loses its small umbilical tubercles earlier than its strong ribbing, whereas *V. gamai* loses its weak ribbing quickly and maintains its strong umbilical tubercles until advanced ontogeny. On the basis of these features, it is advisable to maintain the specific status of *V. barcoicense*. Phylogenetically, *V. barcoicense* is also close to *V. gamai*, from which it seems to have evolved by weakening and early disappearance of the umbilical tubercles, and increasing involution of the whorls.

**Distribution:** *V. barcoicense* occurs in the upper Cenomanian and lower Turonian of Portugal, Croatia, Algeria, Spain, the USA, and, possibly, Tunisia and Egypt. In the Iberian Trough, it has been identified in the upper part of the *V. gamai* Subzone and the lower part of the *S. (J.) subconciatus* Zone of the Guadarrama Area.

*Vascoceras durandi* (THOMAS & PERON, 1889)

(Plate 3, figs. A–G; Plate 4, figs. A–B; Text-figure 6 A)

- ‡ aff. 1889 *Pachydiscus* aff. *peramplus* (MANTELL) – THOMAS & PERON in PERON, p. 25, pl. 18, figs. 1–2.
- 1889 *Pachydiscus durandi* THOMAS & PERON in PERON, p. 27, pl. 18, figs. 5–8.
- 1896 *Pachydiscus durandi* THOMAS & PERON – PERON, p. 44, pl. 4, fig. 1; pl. 5, fig. 1; pl. 17, fig. 5.
- 1898 *Vascoceras dowillei* CHOFFAT, p. 59, pl. 10, fig. 6; pl. 11, figs. 2–5; pl. 21, figs. 13–15.
- aff. 1898 *Vascoceras* sp. aff. *dowillei* CHOFFAT, p. 60, pl. 10, fig. 3; pl. 21, fig. 16.
- 1903 *Vascoceras durandi* (THOMAS & PERON) – PERVINQUIÈRE, pp. 98–99.
- 1903 *Vascoceras dowillei* CHOFFAT – PERVINQUIÈRE, p. 99.
- 1907 *Vascoceras durandi* (THOMAS & PERON) – PERVINQUIÈRE, p. 332, pl. 21, fig. 1 a–b, text-fig. 125.
- 1914 *Vascoceras durandi* (THOMAS & PERON) – ECK, p. 202.
- ‡ 1915 *Vascoceras durandi* (THOMAS & PERON) – GRECO, p. 210, pl. 18, figs. 2–3.
- ‡ aff. 1920 *Vascoceras* sp. nov. ex. aff. *adonense* CHOFFAT – BÖSE, p. 214, pl. 14, fig. 4; pl. 17, fig. 2, text-fig. 2.

- 1928 *Vascoceras* sp. D●UVILLÉ, p. 15, pl. 1, fig. 6.
- 1934 *Vascoceras durandi* (THOMAS & PERON) – FARAUD, pl. 20, fig. 8.
- 1940 *Vascoceras (Pachyvascoceras) durandi* (THOMAS & PERON) – FARAUD, p. 43, pl. 2, figs. 1–2; pl. 8, fig. 1.
- cf. 1960 *Discovascoceras* cf. *dowillei* (CHOFFAT) – WIEDMANN, pp. 712, 721, 723.
- 1960 *Vascoceras (Pachyvascoceras) durandi* (THOMAS & PERON) – WIEDMANN, pp. 714, 720.
- cf. 1960 *Vascoceras (Pachyvascoceras)* cf. *durandi* (THOMAS & PERON) – WIEDMANN, p. 714.
- cf. 1964 *Discovascoceras* cf. *dowillei* (CHOFFAT) – WIEDMANN, pp. 111, 115–116.
- 1964 *Vascoceras (Pachyvascoceras) durandi* (THOMAS & PERON) – WIEDMANN, pp. 111, 115.
- cf. 1964 *Vascoceras (Pachyvascoceras)* cf. *durandi* (THOMAS & PERON) – WIEDMANN, p. 111.
- ? aff. 1965a *Vascoceras (Pachyvascoceras)* aff. *dowillei* CHOFFAT – *durandi* (THOMAS & PERON) – COLLIGNON, p. 43, pl. 394, fig. 1676.
- 1969 *Vascoceras durandi* (THOMAS & PERON) – FREUND & RAAB, p. 30, text-fig. 6 h–i.
- ? 1969 *Vascoceras harttiforme* CHOFFAT – FREUND & RAAB, p. 31, text-fig. 6 j.
- cf. 1969 *Vascoceras* cf. *V. adonense* CHOFFAT – FREUND & RAAB, p. 32, pl. 5, fig. 1, text-fig. 7 a–b.
- ? aff. 1973 *Vascoceras* sp. aff. *durandi* (THOMAS & PERON) – MATSUMOTO, p. 29, pl. 8, fig. 1, text-fig. 1.
- 1975 *Pachyvascoceras durandi* (THOMAS & PERON) – WIEDMANN, p. 142.
- ? aff. 1978 *Vascoceras* sp. aff. *V. durandi* (THOMAS & PERON) – MATSUMOTO & MURAMOTO, p. 281, text-fig. 1 a–b.
- 1979 *Vascoceras* cf. *dowillei* CHOFFAT – WIEDMANN, p. 199.
- 1984 *Paravascoceras* sp. 2 MELÉNDEZ-HEVIA, p. 102, pl. 7, fig. 2 a–c [only].
- 1984 *Paravascoceras* sp. 4 MELÉNDEZ-HEVIA, p. 102, pl. 8, figs. 1 a–c, 2 [only].
- 1986 *Vascoceras durandi* (PERON) – BERTHOUS et al., p. 72, pl. 4, figs. 4–9; pl. 6, figs. 1–6.
- 1989 *Vascoceras durandi* (THOMAS & PERON) – LUGER & GRÖSCHKE, p. 376, pl. 43, figs. 1–2, text-fig. 8 a.
- 1991 *Vascoceras durandi* (PERON) – KENNEDY & SIMMONS, p. 138, pl. 5 a–b.
- 1994 *Vascoceras durandi* (THOMAS & PERON) – CHANCELLOR et al., p. 48, pl. ?2, fig. 1; pl. 10, figs. 3–4; pl. 11, figs. 1–2; pl. 12, figs. 1–3; pl. 13, figs. 3–4; pl. ?14, figs. 2, 5 [only].
- ? aff. 1996 *Vascoceras (Paravascoceras)* aff. *durandi* (THOMAS & PERON) – MEISTER & ABDALLAH, p. 10, pl. 4 fig. 1; pl. 5, fig. 2, text-fig. 5 c.
- 2001 *Vascoceras dowillei* CHOFFAT – CALLAPEZ & FERREIRA, p. 69, pl. 9, figs. 3–8; pl. 10, fig. 1, text-figs. 20.8–11, ?21.1, 21.2.
- 2001 *Vascoceras durandi* (THOMAS & PERON) – CALLAPEZ & FERREIRA, p. 78, pl. 11, figs. 3–4; pl. 12, figs. 1–2, text-figs. 21.3–6.
- 2005 *Vascoceras durandi* (THOMAS & PERON) – MEISTER & ABDALLAH, p. 135, pl. 14, fig. 1 [only].
- cf. 2006 *Vascoceras* cf. *durandi* (THOMAS & PERON) – EL QOT, p. 118, pl. 25, fig. 4; pl. 26, fig. 1 a–b.
- 2006 *Vascoceras durandi* (THOMAS & PERON) – BARROSO-BARZENILLA, p. 232, pl. 30, fig. j; pl. 31, figs. a–d; pl. 32, figs. a–e, text-fig. 68.

**Type:** The lectotype designated by CHANCELLOR et al. (1994) is the specimen 1901–11 from Ain Settara, Tunisia, described by PERON (1889, p. 25, pl. 18, fig. 5), and currently held in the MNHN with the number R7937.

**Material:** 17 specimens; CA-R-28, CB-R-659, CC-R-194, CC-R-199, CC-R-203, CC-R-206, CC-R-225, MS-4, TA-R-101, TA-R-418, TA-R-621, TA-R-624, TA-S-432, TA-S-568, TA-S-573, TA-S-575 and TA-S-85.

#### Dimensions:

	D	H (%)	E (%)	O (%)
Range	1310–676	500–282 (45–34)	770–392 (63–44)	485–210 (38–28)
Mean	1000	396 (40)	545 (55)	337 (34)

**Description:** Slightly involute specimens, almost without ornamentation, and with quite variable, depressed and rounded, subtriangular or subogival whorl section, which is always wider than higher. They have wide umbilici with steep and subvertical walls and blunt umbilical angles. Juveniles may present 6–8 small umbilical tubercles per whorl, disappearing quickly during ontogeny. They show a tendency to adopt a subtriangular whorl section that becomes

more acute in the approach to maturity. Their first lateral saddles are large, whereas the remaining saddles are relatively small.

**Discussion:** CHOFFAT (1898) emphasised the strong resemblance between *Vascoceras durandi* (THOMAS & PERON 1889) and his new species *Vascoceras dowillei*, and based their taxonomic separation on the smaller size and the strong ventral ribbing of the latter. PERVINQUIÈRE (1907) included *V. dou-*

*villei* in the synonymy of *V. durandi*. BERTHOU et al. (1986) remarked that many specimens with intermediate features can be observed, and concluded that *V. douvillei* should be considered as a synonym of *V. durandi*. The interpretations made by PERVINQUIÈRE (1907) and BERTHOU et al. (1986) concerning *V. durandi* and *V. douvillei* have been confirmed by the Spanish records of both taxa, and the latter has also been considered here as a synonym of the former.

BERTHOU et al. (1986) regarded the separation between *V. durandi* and *Vascoceras amieirensis* CHOFFAT, 1898, as being based only on the involution and the contraction of the body chamber, and they considered that the second taxon is conspecific with the first one. Likewise, these authors highlighted the morphologic proximity between *V. durandi* and *Vascoceras harttii* (HYATT 1870). They stated that the *Paravascoceras* aff. *harttii* of CHANCELLOR (1982, p. 101, fig. 34) shows a high umbilical width, with dimensions close to those of *V. douvillei*, and that this specimen, which could represent an intermediate form between the species of HYATT and of THOMAS & PERON, seems to provide evidence of the close phylogenetic relationship between these two taxa. BERTHOU et al. (1986) also suggested that *V. durandi* could be a possible synonym of *V. harttii*. Nevertheless, they maintained the specific division of both taxa, on the basis of the narrower umbilical width of *V. harttii*. The new data for *V. amieirensis* and *V. harttii* presented in this paper support their specific separation, as explained below.

Some compressed juvenile specimens of *V. durandi*, such as that presented by PERVINQUIÈRE (1907), can be hard to differentiate from those of *V. gamai*, especially when their umbilical tubercles are maintained. However, the members of *V. gamai* develop a less wide whorl section and a more evolute coiling, and present striking and strong umbilical tubercles. On the other hand, *Vascoceras cauwini* CHUDEAU, 1909, shows a more compressed whorl section, a less wide umbilical width and a different adult ornamentation, whereas *Vascoceras angermannii* BÖSE, 1920, and *Vascoceras crassum* FURON, 1935, have narrower umbilici than *V. durandi*.

The *Pachydiscus* aff. *peramplus* (MANTELL 1822) of THOMAS & PERON (1889) is a poorly preserved ammonite that, as indicated by CHANCELLOR et al. (1994), could be a compressed and highly ornamented *V. durandi*. The *Vascoceras harttiforme* CHOFFAT, 1898, and *V. cf. Vascoceras adonense* CHOFFAT, 1898,

of FREUND & RAAB (1969) also present a morphology quite similar to that of *V. durandi*, as noted by BERTHOU et al. (1986) and CHANCELLOR et al. (1994), who attributed these specimens to the species of THOMAS & PERON. The *V. cf. V. adonense* of FREUND & RAAB (1969) are closer to *V. durandi* than the *V. harttiforme* of the same authors. The *V. durandi* of GRECO (1915), the *V. (Pachyvascoceras)* aff. *douvillei-durandi* of COLLIGNON (1965a), and the *V. sp. aff. durandi* of MATSUMOTO (1973) and MATSUMOTO & MURAMOTO (1978) have a whorl section and a reduced umbilical width that seem to separate these specimens from the species of THOMAS & PERON, as stated by BERTHOU et al. (1986) and CHANCELLOR et al. (1994). The *V. sp. nov. ex. aff. adonense* of BÖSE (1920) has a notable whorl breadth and lacks umbilical tubercles, which seems to indicate that it is slightly closer to *V. durandi* than to *Vascoceras gamai* CHOFFAT, 1898. Finally, the *V. (P.) aff. durandi* of MEISTER & ABDALLAH (1996) exhibits a very persistent ribbing that is notably different from that of the species of THOMAS & PERON.

Studying the phylogeny of *V. durandi*, BERTHOU et al. (1986) and CHANCELLOR et al. (1994) indicated that the juvenile specimen of *V. harttii* previously cited by CHANCELLOR (1982, p. 118) presents a tricarinate ventral region, similar to that of the members of the species assigned by COLLIGNON (1957, 1965b) to his new genus *Discovascoceras*. These authors also indicated that this morphologic similarity could reveal a certain phylogenetic relationship between the species *V. durandi* and the bicarinate taxon *Thomasites madagascariensis* COLLIGNON, 1965a. In this regard, it should be noted that within the morphological variability of *Vascoceras* CHOFFAT, 1898, as can be observed in *V. gamai*, particularly in its variety *subtriangularis*, and in *V. durandi*, forms exist with a relatively sharp triangular whorl section. Therefore, the small ammonite cited by CHANCELLOR (1982) may be a member of *Vascoceras* with a more or less triangular whorl section. Likewise, it has been noted that in the Iberian Trough *V. durandi* follows an ontogenetic development similar to that of *V. gamai*. This coincidence and the existence of specimens with intermediate features, such as ammonite TA-S-568 (Pl. 3, figs. A-B), could also indicate that the origin of *V. durandi* might be in *V. gamai*.

**Distribution:** *V. durandi* has been collected from the upper Cenomanian and lower Turonian of Tunisia, Algeria, Portugal, Egypt, France, Spain, Israel,

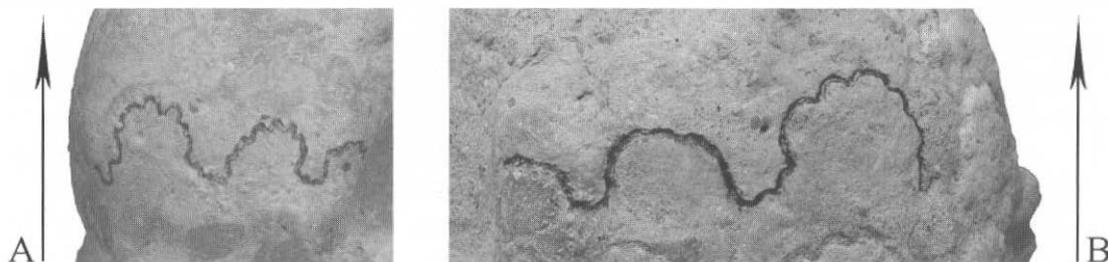
Oman and, probably, Mexico, Madagascar and Japan. In the Iberian Trough, it is common in the Inner Castilian Platform, within the *S. (J.) subconciatus* and *C. (C.) quaasi* zones. Within the latter biostratigraphic unit, the morphological variability of *V. durandi* increases progressively. The stratigraphical distribution of this species observed in Spain is equivalent to that determined by CHOFFAT (1898) and BERTHOU et al. (1986) in Portugal. In fact, the lowest Iberian records are among the oldest ones in the world assigned to *V. durandi*.

BERTHOU et al. (1986) noticed a progressive increase in the whorl breadth from the earlier to the later representatives of *V. durandi*. They also indicated that the amplitude of the umbilical tubercles seems to depend on the palaeogeographical origin of the specimens, because members of *V. durandi* collected in Portugal show thicker tubercles than those obtained in North Africa. From the earlier to the later Spanish specimens of *V. durandi* presented in this paper it can be observed that the whorl breadth increases gradually as the size and persistence of the vestigial tubercles decreases. In fact, the umbilical tubercles seem to be primitive structures in *V. durandi*, probably evolved from *V. gamai*, and their thickness and persistence are possibly related to the stage of evolution of the specimen considered. For this reason the tubercles reduce progressively, until they disappear in the later members of *V. durandi*. These observations are similar to those of BERTHOU et al. (1986), because the Portuguese specimens of *V. durandi*, which are older, show stronger umbilical tubercles than the African ones, which are earlier.

*Vascoceras cauwini* CHUDEAU, 1909

(Plate 4, fig. C)

- 1909 *Vascoceras cauwini* CHUDEAU, p. 68, pls. 1–2; pl. 3, figs. 1–2, 4.  
 1921 *Thomasites cauwini* (CHUDEAU) – CHUDEAU, p. 463, fig. 1.  
 1933 *Vascoceras cauwini* CHUDEAU – FURON, p. 268, pl. 9, fig. 17.  
 ? 1935 *Vascoceras (Paracanthoceras) chevalieri* FURON, p. 59, pl. 4, fig. 1 a–b.  
 ? 1935 *Vascoceras (Paracanthoceras) chudeaui* FURON, p. 60, pl. 4, fig. 2.  
 1935 *Vascoceras (Paravascoceras) cauwini* CHUDEAU – FURON, p. 60, pl. 5, fig. 1.  
 1935 *Vascoceras (Paravascoceras) cauwini* CHUDEAU var. *semiglabra* FURON, p. 61, pl. 4, fig. 3.  
 1943 *Paravascoceras cauwini* (CHUDEAU) – SCHNEEGANS, p. 128, pl. 5, fig. 2, text-fig. 9.  
 1943 *Paravascoceras cauwini* (CHUDEAU) var. *evoluta* SCHNEEGANS, p. 130, pl. 8, fig. 2, text-figs. 10–11.  
 1943 *Paravascoceras cauwini* (CHUDEAU) var. *inflata* SCHNEEGANS, p. 131.  
 aff. 1957 *Paravascoceras* aff. *cauwini* (CHUDEAU) – BARBER, p. 37, pl. 14, figs. 2–3; pl. 32, figs. 8–9.  
 1969 *Paravascoceras cauwini* (CHUDEAU) – FREUND & RAAB, p. 20, pl. 3, figs. 1–3.  
 ? 1969 *Paravascoceras tavense* (FARAUD) – FREUND & RAAB, p. 23, pl. 2, fig. 9, text-fig. 5 e–g.  
 1975 *Paravascoceras cauwini* (CHUDEAU) – SCHÖBEL, p. 119, pl. 4, figs. 1, ?2, 3; pl. 5, figs. 1–4.  
 1982 *Paravascoceras cauwini* (CHUDEAU) – CARRETERO-MORENO, p. 253.  
 1989 *Vascoceras cauwini* CHUDEAU – LUGER & GRÖSCHKE, p. 374, pl. 40, figs. 3, 6, 8–9; pl. 41, figs. 1–4; pl. 42, fig. 1, text-figs. 6 g–h, 8 c.  
 cf. 1989 *Vascoceras* cf. *cauwini* CHUDEAU – LUGER & GRÖSCHKE, p. 376, pl. 42, fig. 2; pl. 43, fig. 3, text-figs. 6 f, 8 b.  
 1989 *Vascoceras cauwini* CHUDEAU – KENNEDY et al., p. 82, figs. 9 g, 20 c–g.  
 1990 *Vascoceras cauwini* CHUDEAU – ZABORSKI, figs. 8 a–b, 12–15.



Text-fig. 6. Suture lines. A, *Vascoceras durandi* (THOMAS & PERON 1889), TA-S-575, from the *Choffaticeras (Choffaticeras) quaasi* Zone of Tamajón. B, *Vascoceras kossmati* CHOFFAT, 1898, TA-R-624, from the *Spathites (Ingridella) malladae* Subzone of Tamajón. Both are  $\times 3/2$ .

- 1992 *Vascoceras* (*Paravascoceras*) *cauwini* CHUDEAU – MEISTER et al., p. 71, pl. 4, fig. 6; pl. 5, figs. 1–3; pl. 6, figs. 1–4; pl. 7, figs. 1–2, 4–5, text-fig. 16.
- 1996 *Paravascoceras cauwini* (CHUDEAU) – ZABORSKI, p. 65, figs. 2–8.
- 1996 *Vascoceras cauwini* CHUDEAU – AMÉDRO et al., p. 215, fig. 18.
- 2002 *Vascoceras cauwini* CHUDEAU – EL-HEDENY, p. 406, figs. 4b–c, 7f.
- 2006 *Vascoceras cauwini* CHUDEAU – EL QOT, p. 117, pl. 25, figs. 2–3, 5.
- 2006 *Vascoceras cauwini* CHUDEAU – BARROSO-BARCENILLA, p. 238, pl. 33, fig. a.

Type: The lectotype designated by KENNEDY et al. (1989) is a specimen of CHUDEAU (1909), from Gjadjidouma, Niger, and held in the MNHN with the number R52488.

Material: 1 specimen; PU-S-312.

#### Dimensions:

D	H (%)	E (%)	O (%)
690	316 (46)	~245 (58–46)	228–129 (26–19)

**Description:** Moderately involute and small specimen, with a compressed and subelliptical whorl section. It presents rounded ventral region, flat or slightly convex flanks, and subvertical umbilical walls with blunt margins. Its visible surface is smooth and its suture lines have a reduced number of elements with clearly divided saddles.

**Discussion:** CHUDEAU (1909) described this species in comparison with *Vascoceras durandi* (THOMAS & PERON 1889). He stated that the first whorls of both taxa are very similar, and emphasised that, in contrast to *V. cauwini*, none of the closer forms, such as *Vascoceras dowillei* CHOFFAT, 1898, and *Vascoceras amieirensis* CHOFFAT, 1898, retain their ornamentation into the maturity. CHUDEAU (1921) asserted that *Vascoceras nigeriense* WOODS, 1911, may possibly be a synonym of *V. cauwini* whilst, in contrast, REYMENT (1954b) affirmed that the second species could be a synonym of the first one. SCHÖBEL (1975) considered *Vascoceras* (*Pachyvascoceras*) *crassum* FURON, 1935, *Vascoceras* (*Paracanthoceras*) *chevalieri* FURON, 1935, *Vascoceras* (*Paravascoceras*) *chudeaui* FURON, 1935, *Vascoceras* (*Paravascoceras*) *cauwini* var. *semiglabra* FURON, 1935, *Nigericeras jacqueti* SCHNEEGANS, 1943, *Paravascoceras crassum* var. *bullata* SCHNEEGANS, 1943, *Paravascoceras cauwini* var. *evoluta* SCHNEEGANS, 1943, *Paravascoceras cauwini* var. *inflata* SCHNEEGANS, 1943, *Broggioceras humboldti* BENAVIDES-CÁCERES, 1956, *Broggioceras olssoni* BENAVIDES-CÁCERES, 1956, and *Paravascoceras rumeaui* COLLIGNON, 1957, as synonyms of *V. cauwini*.

BERTHOU et al. (1986) indicated that *V. cauwini* could be a synonym of *Vascoceras barcoicense* CHOFFAT, 1898, but maintained their specific separation on the basis of their different ontogenetic development

of the whorl section and of the ornamentation. LUGER & GRÖSCHKE (1989) considered *Vascoceras rumeaui* a slightly different species from *V. cauwini*. MEISTER et al. (1992) differentiated in *V. cauwini* the forms “*cauwini* s.s.”; “forme lisse”, which is smooth or nearly smooth and includes the “*nigeriensis*” and “*tavense*” styles; “forme comprimée”, which is compressed and involute; and “forme *crassum*”, which is globose. They also recognised a transitional form between the “forme *crassum*” and the species *Vascoceras* (*Paravascoceras*) *proprium* (REYMENT 1954b). AMÉDRO et al. (1996) considered the taxon *P. rumeaui* to be conspecific with *V. cauwini*, whereas ZABORSKI (1996) included within the synonymy of this species *V. (P.) chevalieri*, *V. (P.) chudeaui*, *V. (P.) cauwini* var. *semiglabra*, *P. cauwini* var. *evoluta*, *P. cauwini* var. *inflata* and *Vascoceras depressum* BARBER, 1957. He also stated that *P. rumeaui* and *Vascoceras costellatum* AMARD et al., 1981, could be regional variants of *V. cauwini*. The same author only considered as conspecific with *V. cauwini* the taxa assigned to the forms “*cauwini* s.s.”, “lisse” and “comprimée” by MEISTER et al. (1992).

The relatively compressed whorl section and the notably strong adult ribbing of this species make its identification easier. Nevertheless, at least *V. (P.) chevalieri* and *V. (P.) chudeaui* seem to be indistinguishable from *V. cauwini*. With regard to the specific separation between *V. barcoicense* and *V. cauwini* it should be emphasised, as indicated by ZABORSKI (1996) and detailed above, that the former lacks the mature ribbing of the latter. The *Paravascoceras tavense* (FARAUD 1940) of FREUND & RAAB (1969) should be assigned to *V. cauwini*, as observed by SCHÖBEL (1975) and BERTHOU et al. (1986), because even the smallest of them has no ornamentation. The *V. cauwini* of KENNEDY et al. (1989) were considered as a possible

*V. barcoicense* exile COBBAN et al., 1989, by ZABORSKI (1996). These ammonites lack ornamentation, despite being immature specimens, and seem to correspond to *V. cauwini*. Regarding its phylogeny, ZABORSKI (1996) indicated that *V. cauwini* could be derived from *N. gadeni* by progressive loss of the juvenile ornamentation, simplification of the suture lines and development of the adult ribbing.

**Distribution:** This species has been identified in the upper Cenomanian of Niger, the Sudan, Israel, Spain, Egypt, the USA, Nigeria and Algeria, in biostratigraphic units equivalent to the *M. geslinianum* and *N. juddii* standard zones. However, ZABORSKI (1996) observed that the ammonites collected from the *M. geslinianum* Zone of Israel and classified as *V. cauwini* by LEWY et al. (1984) present many similarities with the members of the genus *Nigericeras* SCHNEEGANS, 1943, and that they may be transitional specimens. In the Iberian Trough, the ammonite presented here has been obtained at the top of the *S. (J.) subconciatus* Zone of the North-Ebro Area, and other specimens were recorded by CARRETERO-MORENO (1982) in undetermined levels of the Guadarrama Area.

#### Dimensions:

	D	H (%)	E (%)	O (%)
Range	1400–968	649–380 (46–39)	550–435 (50–37)	382–258 (35–26)
Mean	1105	461 (42)	489 (45)	322 (30)

**Description:** Relatively compressed ammonites with subtriangular whorl section and without ornamentation. They have rounded ventral area, slightly arched and convergent flanks and not too wide umbilici with subvertical walls and rounded margins.

**Discussion:** CHOFFAT (1898) highlighted the subtriangular whorl section and the lack of umbilical tubercles as the main features of his new species *Vascoceras amieirensis*. He also stated that it presents higher whorls and broader umbilici than *Vascoceras hartiformis* CHOFFAT, 1898. COLLIGNON (1957) included *V. amieirensis* within his new genus *Discovascoceras*, although this interpretation was rejected by COBBAN & SCOTT (1972). The latter authors also noticed that the specimens they had classified as *Vascoceras* sp. have features in common with *V. amieirensis*. BERTHOU et al. (1975), although recognising the great similarity between *V. amieirensis* and *Vascoceras*

#### *Vascoceras amieirensis* CHOFFAT, 1898

(Plate 4, figs. D–E)

- 1898 *Vascoceras amieirensis* CHOFFAT, p. 61, pl. 12, figs. 1–2; pl. 13, figs. 1–2; pl. 21, figs. 17–21.  
 cf. 1914 *Vascoceras* sp. cf. *amieirensis* CHOFFAT – ECK, p. 201.  
 cf. 1957 *Vascoceras* (*Discovascoceras*) cf. *amieirensis* CHOFFAT – COLLIGNON, p. 124.  
 cf. 1960 *Discovascoceras* cf. *amieirensis* (CHOFFAT) – WIEDMANN, pp. 712, 714, 721.  
 cf. 1964 *Discovascoceras* cf. *amieirensis* (CHOFFAT) – WIEDMANN, pp. 111, 115.  
 cf. 1969 *Vascoceras* cf. *V. amieirensis* CHOFFAT – FREUND & RAAB, p. 32, text-fig. 6 k–l.  
 ? 1972 *Vascoceras* sp. COBBAN & SCOTT, p. 83, pl. 36, figs. 3–4, text-fig. 41 a.  
 cf. 1975 *Discovascoceras* cf. *amieirensis* (CHOFFAT) – WIEDMANN, p. 142.  
 1984 *Paravascoceras* sp. 2 MELÉNDEZ-HEVIA, p. 102, pl. 7, fig. 1 a–c [only].  
 1984 *Paravascoceras* sp. 3 MELÉNDEZ-HEVIA, p. 102, pl. 6, fig. 3.  
 2006 *Vascoceras amieirensis* CHOFFAT – BARROSO-BARCENILLA, p. 242, pl. 33, figs. b–c.

**Type:** The holotype is specimen 825 of the SGP, the original of CHOFFAT (1898, pl. 12, fig. 1 a–b; pl. 13, fig. 1; pl. 21, figs. 17, 20), from the lower Turonian of Amieira, Portugal.

**Material:** 6 specimens; CA-R-598, CB-R-542, CC-S-211, TA-S-570, TA-S-571 and TA-S-578.

*durandi* (THOMAS & PERON 1889), maintained their specific separation. On the basis of morphometric analysis, BERTHOU et al. (1986), and other authors such as CHANCELLOR et al. (1994), considered *V. amieirensis* as a synonym of *V. durandi*.

Nevertheless, as can be seen in the diagram by BERTHOU et al. (1986, p. 61, fig. 5), the dimensions of the holotype of *V. amieirensis* are at the morphological extreme of the group designated *V. durandi* by these authors. We therefore agree with the interpretation made by BERTHOU et al. (1975) concerning the comparison of the specimens of *V. amieirensis* and *V. durandi*. Accordingly, we have maintained the specific division of *V. amieirensis* and of *V. durandi*, as they differ in their whorl section and in their umbilical width. This conclusion is supported by the fact that *V. amieirensis* occurs in higher levels than *V. durandi* in the Iberian Trough, an observation also made by BERTHOU

et al. (1975) in Portugal, who remarked that the stratigraphical distribution of *V. douvillei* coincides with that of *V. subconciatus*, and is lower than that of *V. amieirensis*, which occurs with *V. kossmati*.

With regard to the specimens classified as *Vascoceras* sp. by COBBAN & SCOTT (1972), BERTHOUE et al. (1986) stated that these ammonites probably belong to *V. durandi*, and CHANCELLOR et al. (1994) added that they may be compressed variants of the same species. In our opinion, although the specimen of COBBAN & SCOTT (1972, pl. 36, figs. 1–2) is too deformed to permit a precise taxonomic classification, in general, the ammonites classified by these authors as *Vascoceras* sp. exhibit several features close to those of *V. amieirensis*.

Phylogenetically, *V. amieirensis* seems to have originated from some of the latest members of *V. durandi*, by modifications in the width and the contour of the whorl section. In fact, PERVINQUIÈRE (1907) had already suggested the possible existence of transitional specimens between both species, and LUGER & GRÖSCHKE (1989) highlighted the fact that their representatives of *V. durandi* have several features close to those of the members of *V. amieirensis*. Likewise, the *V. durandi* and *V. cf. amieirensis* of FREUND & RAAB (1969) seem to be examples of these ammonites with intermediate features.

**Distribution:** *V. amieirensis* has been obtained in the lower Turonian of Portugal, Spain and, possibly, Egypt, Algeria, Israel and the USA. In the Iberian Trough, it has been found in the upper part of the *C. (C.) quaasi* Zone and in the lower part of the *S. (I.) malladae* Subzone of the North-Ebro and Guadarrama areas.

*Vascoceras harttii* (HYATT 1870)

(Plate 5, figs. A–E)

- 1870 *Ceratites harttii* HYATT, p. 386.  
 1875 *Buchiceras harttii* (HYATT) – HYATT, p. 370.  
 1887 *Ammonites (Buchiceras) harttii* (HYATT) – WHITE, p. 226, pl. 19, figs. 1–2; pl. 20, fig. 3.  
 1903 *Vascoceras harttii* (HYATT) – HYATT, p. 103, pl. 14, fig. 16.

Dimensions:

	D	H (%)	E (%)	O (%)
Range	1125–516	421–200 (48–31)	795–420 (87–61)	335–155 (38–25)
Mean	794	303 (39)	587 (75)	245 (31)

- 1937 *Vascoceras harttii* (HYATT) – MAURY, p. 247, pl. 22, figs. 1–2.  
 cf. 1940 *Vascoceras (Pachyvascoceras) cf. harttii* (HYATT) – FARAUD, p. 48, pl. 4, fig. 2; pl. 5, fig. 2; pl. 9, figs. 1–2.  
 cf. 1960 *Vascoceras (Pachyvascoceras) cf. harttii* (HYATT) – WIEDMANN, p. 712.  
 cf. 1964 *Vascoceras (Pachyvascoceras) cf. harttii* (HYATT) – WIEDMANN, p. 111.  
 1969 *Pachyvascoceras harttii* (HYATT) – DE OLIVEIRA & BRITO, p. 220, pl. 2, figs. 1–2 [only].  
 1977 *Paravasoceras harttii* (HYATT) – CHANCELLOR et al., p. 96, fig. 20.  
 1982 *Paravasoceras harttii* (HYATT) – CHANCELLOR, p. 98, figs. 2 b, 29–33.  
 ? aff. 1982 *Paravasoceras aff. harttii* (HYATT) – CHANCELLOR, p. 101, fig. 34.  
 1984 *Paravasoceras harttii* (HYATT) – MELÉNDEZ-HEVIA, p. 99, pl. 4, figs. 1 a–b, 2 a–b, 3 a–b.  
 1985 *Vascoceras (Paravasoceras) harttii* (HYATT) – HOWARTH, p. 100, fig. 25.  
 1989 *Vascoceras harttii* (HYATT) – COBBAN et al., p. 49, figs. 49, 91 a–d, g–k.  
 ? 1989 *Fagesia superstes* var. *levis* RENZ – MEISTER, p. 37, pl. 16, fig. 2, text-fig. 26.  
 ? 1992 *Vascoceras* gr. *globosum* (REYMENT) ou *Fagesia* sp. COURVILLE, pl. 9, fig. 1.  
 1996 *Vascoceras harttii* (HYATT) – ZABORSKI, p. 81, figs. 58, 60.  
 2006 *Vascoceras harttii* (HYATT) – EL QOT, p. 118, pl. 26, fig. 2 a–b.  
 2006 *Vascoceras harttii* (HYATT) – BARROSO-BARCENILLA, p. 244, pl. 34, figs. a–f; pl. 35, figs. a–c.

**Type:** Although HYATT (1870) did not provide illustrations of this species, WHITE (1887, pl. 19, figs. 1–2; pl. 20, fig. 3) illustrated a specimen that possibly corresponds to one of the original syntypes. According to article 33a of the ICZN, the terminations *-ii* and *-i* are allowed alternatives, which is why the specific names of *harttii* and *hartti* are both valid. In the present work, however, we have used the first one, as it coincides with the original denomination of HYATT (1870).

**Material:** 24 specimens; CA-S-509, CB-R-552, CB-R-855, CC-R-11, CC-R-197, CC-R-228, CC-R-8, CC-S-226, CG-R-533, CS-R-591, CS-R-592, TA-R-412, TA-R-426, TA-R-574, TA-R-617, TA-R-645, TA-R-656, TA-R-750, TA-R-751, TA-S-431, TA-S-608, TA-S-648, TA-S-649 and TE-S-587.

**Description:** Slightly involute and globose cadicones with depressed half moon-shaped whorl section. Medium-sized, very deep and steep umbilici with subvertical or oblique walls and sharp margins. Ornamentation is reduced to about twenty non-persistent and broad ventral juvenile plications per whorl, irregularly distributed and slightly orientated towards the body chamber. The first whorls can present a subtriangular section, and the adult spires almost hide the rest of these ammonites. Simple and rounded suture lines, each one with four wide lateral saddles.

**Discussion:** After being described by HYATT (1870), the species *Ceratites harttii* was included by CHOFFAT (1898) in his new genus *Vascoceras*. HYATT (1903) indicated that this species is related to the taxa *Vascoceras harttiformis* CHOFFAT, 1898, *Vascoceras amieirensis* CHOFFAT, 1898, and *Vascoceras kossmati* CHOFFAT, 1898. PERVINQUIÈRE (1907) observed great similarities between *Vascoceras harttii* and *Vascoceras durandi* (THOMAS & PERON 1889), although he added that both species can be distinguished by the presence of umbilical tubercles and the complexity of the suture lines of the latter. FURON (1935) described a species with a similar morphology, named *Vascoceras (Pachyvascoceras) crassum*. BARBER (1957) remarked that *V. harttii*, as well as *V. harttiforme*, is more globose than *Vascoceras nigeriense* WOODS, 1911, but less involute, more compressed and with steeper umbilical walls than *Vascoceras robustum* BARBER, 1957. CHANCELLOR (1982) stated that the species *V. harttii* is close to some globose taxa with a narrow umbilicus of the same genus, such as *V. angermannii* BÖSE, 1920, and *V. carteri* (BARBER 1957). He classified a specimen from Mexico, with an umbilical width reaching approximately 57 % of the diameter of the shell, as *Paravasoceras* aff. *harttii*. This ammonite was considered by BERTHOU et al. (1986) as a possible specimen of *V. durandi*, and excluded by HOWARTH (1985) and ZABORSKI (1996) from the synonymy of *V. harttii*. CHANCELLOR (1982) also indicated that the *V. harttii* of WILLARD (1966, pl. 41, fig. 2; pl. 42, fig. 1) is close to the *V. amieirensis* of LISSON (1908). This ammonite was subsequently considered by BERTHOU et al. (1986) as a possible specimen of *Vascoceras cauvinii* CHUDEAU, 1909. BENGTSON (1983) and HOWARTH (1985) assigned the specimens of *Pachyvascoceras harttii* of DE OLIVEIRA & BRITO (1969, p. 220, pl. 2, fig. 3) and REYMENT & TAIT (1972) to the genus *Fagesia* PERVINQUIÈRE, 1907. HOWARTH (1985) also emphasised that *V. harttii* is only slightly different

from *V. harttiforme*. KENNEDY et al. (1987) stated that the species of HYATT is very similar to *Vascoceras globosum* (REYMENT 1954b) and to certain specimens of *Vascoceras proprium* (REYMENT 1954b), but asserted that *V. harttii* shows a more evolute coiling and a steep umbilical wall. ZABORSKI (1996), however, included within the species of HYATT all the specimens classified as *Fagesia superstes* var. *levis* RENZ, 1982, by MEISTER (1989, p. 37, pl. 16, fig. 2, text-fig. 26) and as *V. gr. globosum* or *Fagesia* sp. by COURVILLE (1992, pl. 9, fig. 1).

Regarding the separation between *V. harttii* and *V. harttiforme*, it can be deduced from the Spanish material that the distributions of these species are different, as the former occurs in higher levels than the latter. These facts are consistent with those observed by other authors, such as CHANCELLOR (1982) in Mexico, and support the specific division of these two taxa. The high depression of the whorl section of *V. harttii* enables its differentiation from other forms of the genus with higher whorls, such as *V. durandi* and *Vascoceras ellipticum* BARBER, 1957. The umbilical width can also be considered an important feature in order to differentiate *V. harttii*, being wider than that of *V. globosum*, and narrower than that of *V. durandi*. In addition to the important differences between *V. harttii* and *V. globosum* stated by KENNEDY et al. (1987), the Spanish specimens of the first species show a more triangular and less rounded whorl section and a flatter umbilical wall than those of the second one. Likewise, due to its globose aspect it is easy to confuse *V. harttii* with some members of the genus *Fagesia*, although this species follows the typical ontogenetic development of the group *Vascoceras*, as emphasised by ZABORSKI (1996), and exhibits a simpler outline of the septa. The *F. superstes* var. *levis* of MEISTER (1989) and the *V. gr. globosum* or *Fagesia* sp. of COURVILLE (1992) show important similarities with *V. harttii*. Likewise, the *F. superstes* var. *levis* of MEISTER (1989) seems to lack the umbilical tubercles of the taxon of RENZ. Phylogenetically, *V. harttii* was apparently originated from the more depressed, involute and globose members of *V. durandi*, such as the specimen CC-R-199 (Plate 4, figs. A–B).

**Distribution:** Cited in the lower Turonian of Brazil, Mexico, Spain, Angola, the USA, Nigeria, Egypt and, possibly, France. The members of *V. harttii* from the Iberian Trough have been located in the lower part of the *S. (I.) malladae* Subzone of the Central Sector.

- Vascoceras kossmati* CHOFFAT, 1898  
(Plate 5, figs. F–H; Text-figure 6 B)
- 1898 *Vascoceras harttiformis* CHOFFAT, p. 61, pl. 12, fig. 3; pl. 13, figs. 3–6; pl. 21, figs. 22–24.
- 1898 *Vascoceras kossmati* CHOFFAT, p. 63, pl. 13, figs. 8–9; pl. 14, figs. 1–2; pl. 21, figs. 26–27.
- 1914 *Vascoceras kossmati* CHOFFAT – ECK, pp. 182, 202.
- 1934 *Vascoceras harttiformis* CHOFFAT – FARAUD, p. 9, fig. 6.
- aff. 1935 *V. aff. harttiformis* CHOFFAT – KARREBERG, p. 140, pl. 31, fig. 11.
- 1960 *Vascoceras (Pachyvascoceras) harttiforme* (CHOFFAT) – WIEDMANN, pp. 712, 723.
- cf. 1960 *Vascoceras (Pachyvascoceras) cf. harttiforme* (CHOFFAT) – WIEDMANN, pp. 712, 714.
- 1960 *Vascoceras (Pachyvascoceras) crassum* FURON – WIEDMANN, p. 712.
- 1960 *Vascoceras (Pachyvascoceras) kossmati* (CHOFFAT) – WIEDMANN, p. 723.
- 1964 *Vascoceras (Pachyvascoceras) harttiforme* (CHOFFAT) – WIEDMANN, pp. 111, 116.
- cf. 1964 *Vascoceras (Pachyvascoceras) cf. harttiforme* (CHOFFAT) – WIEDMANN, p. 111.
- 1964 *Vascoceras (Pachyvascoceras) crassum* FURON – WIEDMANN, p. 111.
- 1964 *Vascoceras (Pachyvascoceras) kossmati* (CHOFFAT) – WIEDMANN, p. 116.
- 1975 *Pachyvascoceras (Pachyvascoceras) harttiforme* (CHOFFAT) – WIEDMANN, p. 142.
- cf. 1979 *Pachyvascoceras cf. harttiforme* (CHOFFAT) – WIEDMANN, p. 203.
- 1984 *Paravasoceras cf. carteri* (BARBER) – MELÉNDEZ-HEVIA, p. 100, pl. 5, figs. 1 a–c, 2 a–b.
- 1986 *Vascoceras kossmati* CHOFFAT – BERTHOU et al., p. 76, pl. 5, figs. 1–9.
- 1992 *Paravasoceras kossmati* (CHOFFAT) – THOMEL, p. 225, pl. 119, figs. 2–3.
- ? aff. 1992 *Paravasoceras aff. kossmati* (CHOFFAT) – THOMEL, p. 225, pl. 118, figs. 1–2.
- ? 2005 *Vascoceras durandi* (THOMAS & PERON) – MEISTER & ABDALLAH, p. 135, pl. 26, fig. 1; pl. 27, fig. 1.
- 2006 *Vascoceras kossmati* CHOFFAT – BARROSO-BARCENILLA, p. 248, pl. 35, figs. d–f, text-fig. 70.

Type: Among the syntypes, BERTHOU et al. (1986) designated as lectotype the specimen 827-1 of CHOFFAT (1898, pl. 13, fig. 8; pl. 14, fig. 1), collected from Costa d'Arnes, Portugal, and held in the SGP. In spite of recognising that page priority corresponds to *Vascoceras harttiformis* CHOFFAT, 1898, BERTHOU et al. (1975) used the name *Vascoceras kossmati* CHOFFAT, 1898, for this species, after observing that the types of this taxon are in a better state of preservation.

Material: 5 specimens; CB-R-21, CB-R-554, PU-R-455, TA-R-644 and TE-S-588.

#### Dimensions:

	D	H (%)	E (%)	O (%)
Range	1193–685	546–334 (47–41)	840–500 (73–64)	225–141 (24–14)
Mean	896	426 (45)	619 (69)	175 (19)

**Description:** Globose and highly involute ammonites with depressed whorl section. They show rounded or slightly subtriangular ventral region, and deep and narrow umbilici with vertical walls and sharp margins. Juvenile specimens may show weak and slightly prorsiradiate ribs that become stronger as they reach the ventral region. Adult specimens lack ornamentation, and have a body chamber that gradually reduces in width and becomes slightly less involute. They exhibit suture lines with short saddles.

**Discussion:** CHOFFAT (1898) justified establishing *V. harttiformis* as a new species on the grounds that it exhibited wider whorl section and narrower umbilici than his new taxon *Vascoceras amieirensis*. FREUND & RAAB (1969) emphasised the strong resemblance between *V. harttiforme*, *Vascoceras durandi* (THOMAS & PERON 1889) and *Vascoceras harttii* (HYATT 1870). BERTHOU et al. (1975) remarked that they were not able to observe the umbilical tubercles

of the types of *V. kossmati* described by CHOFFAT (1898), and demonstrated that this species cannot be distinguished from *V. harttiforme*. BERTHOU et al. (1986) considered that, among the species of the genus *Vascoceras* CHOFFAT, 1898, occurring in Portugal, *V. kossmati* is the most globose and involute and has the deepest umbilici. They specified that the cadicones of *Vascoceras angermanni* BÖSE, 1920, which totally lacks ornamentation, and of *Vascoceras carteri* (BARBER 1957) present an even more spherical aspect than those of *V. kossmati*.

Besides the impossibility of determining a morphological limit between *V. kossmati* and *V. harttiforme*, in the Iberian Trough it has been observed that the geographical and stratigraphical distributions of both taxa are coincident. Due to the subspherical shape, the small umbilical width and the highly depressed whorl section of *V. kossmati*, this species can easily be differentiated from other related members of

the genus, such as *V. durandi* and *V. harttii*. Nevertheless, there are certain doubtful specimens, such as the ammonite classified as *V. durandi* by MEISTER & ABDALLAH (2005, pl. 26, fig. 1; pl. 27, fig. 1). Although this specimen exhibits seemingly eroded umbilical areas, it shows notably wide and involute whorls and presents dimensions close to those of *V. kossmati*. A close phylogenetic relationship might be established between the latest and most involute members of *V. harttii* and the earliest and the most evolute specimens of *V. kossmati*.

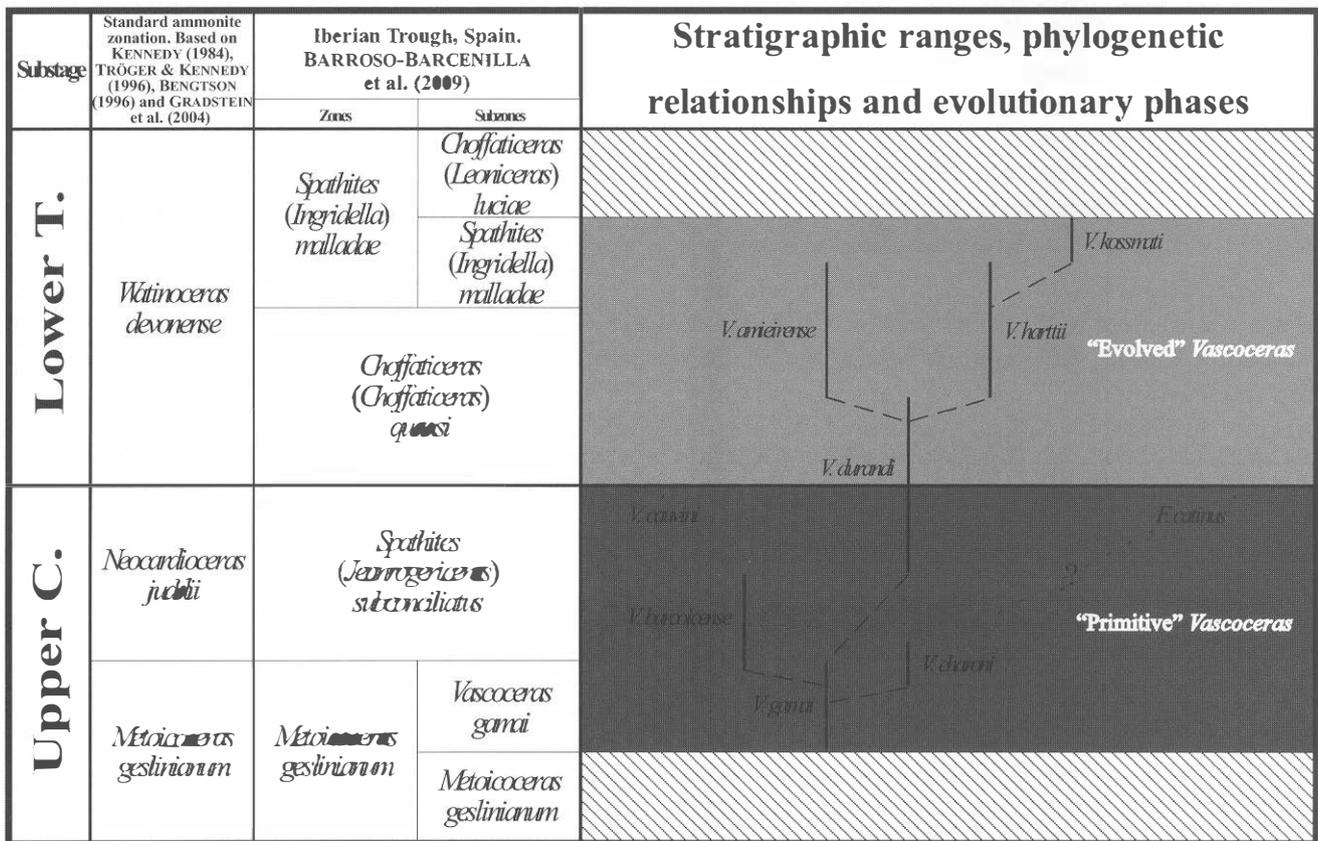
**Distribution:** Lower Turonian of Portugal, Egypt, France and Spain. In the Iberian Trough, in the upper part of the *S. (I.) malladae* Subzone of the Inner Castilian Platform.

### Conclusions

In the present work, new specimens from the Iberian Trough have been described and assigned to the species *Vascoceras gamai*, *V. charoni*, *V. barcoicense*, *V. cauwini*, *V. durandi*, *V. amieirensense*, *V. harttii* and

*V. kossmati*. Although all these taxa had already been cited, with the logical exception of the new species, *V. barcoicense*, *V. durandi*, *V. amieirensense* and *V. kossmati* had never previously been properly classified nor illustrated for this palaeogeographical region. During the developed revision, the presence of specimens attributable to *V. silvanense* and, possibly, *V. globosum* and *V. crassum* has been observed in the collections of the UT and the UCM. On the other hand, the specimens of these research centres regarded as *V. triangulare*, a taxon that may be a synonym of *Choffaticeras (Choffaticeras) douvillei*, should be assigned to the Pseudotissotiidae. Therefore, it can be assumed that the Vascoceratidae are represented, among others, by the genus *Vascoceras* in the Iberian Trough, where the species *V. gamai*, *V. charoni*, *V. barcoicense*, *V. cauwini*, *V. durandi*, *V. amieirensense*, *V. harttii*, *V. kossmati*, *V. silvanense* and, probably, *V. globosum* and *V. crassum* have been properly identified.

Furthermore, the distribution of the new members of the family Vascoceratidae presented here has been determined (Text-fig. 7). The records of the ge-



Text-fig. 7. Stratigraphical ranges of the species of *Vascoceras* identified in this work, and their inferred phylogenetic relationships and evolutionary phases in the Iberian Trough.

nus *Vascoceras* extend from the *V. gamai* to *S. (I.) malladae* subzones. Among its species, *Vascoceras gamai* is the first taxon of the genus, and of the family, established in this palaeogeographical region. Many specimens of this species have been obtained in the *V. gamai* Subzone. In the upper part of the *V. gamai* Subzone, and the lower part of the *S. (J.) subconciliatus* Zone, *V. charoni* and *V. barcoicense* have been identified. Although these two species show partially coincident vertical distributions, that of the latter is slightly higher than that of the former. *V. durandi* has been obtained in the upper part of the *S. (J.) subconciliatus* Zone and the lower part of the *C. (C.) quaasi* Zone. The occurrence of *V. cauvinii* seems to be restricted to the top of the *S. (J.) subconciliatus* Zone. *V. amieirensis* and *V. barttii* have been obtained from the upper part of the *C. (C.) quaasi* Zone and the lower part of the *S. (I.) malladae* Subzone. Finally, within the upper part of the *S. (I.) malladae* Subzone, *V. kossmati* has been identified. This is the most recent species of *Vascoceras* collected in the Iberian Trough.

In terms of the phylogeny of the group, one possible evolutionary lineage joining *V. gamai*, *V. durandi*, *V. barttii* and *V. kossmati* has been identified within the genus *Vascoceras* (Text-fig. 7). It becomes progressively more involute and depressed, with less ornamented forms. Likewise, the representatives of *V. charoni* and of *V. barcoicense* seem to be phylogenetically close to the wider or more involute specimens of *V. gamai* with persistent ornamentation, from which they could respectively be derived. The members of *V. amieirensis* possibly originated from some of the more compressed specimens of *V. durandi*.

After observing the distribution of the family in the Iberian Trough, two main evolutionary phases can be distinguished. These are characterised by the successive dominance of the "primitive" *Vascoceras* and of the "evolved" *Vascoceras* (Text-fig. 7). The first one has been identified in the *V. gamai* Subzone and the *S. (J.) subconciliatus* Zone. During this phase the family is mainly represented by upper Cenomanian species of *Vascoceras* with umbilical tubercles, at least during early ontogeny, such as *V. gamai*, *V. charoni*, *V. barcoicense* and the first specimens of *V. durandi*. Their most numerous members also show compressed sections and evolute coilings, and their morphologies can be considered as "primitive". The second phase has been identified in the *C. (C.) quaasi* Zone and the *S. (I.) malladae* Subzone. During this phase the family is predominantly represented by lower Turonian species

of *Vascoceras* without umbilical tubercles, such as the typical specimens of *V. durandi*, *V. amieirensis*, *V. barttii* and *V. kossmati*. Their most abundant members also exhibit depressed sections and involute coilings, and their morphologies can be considered as "evolved". These two evolutionary phases seem not only to coincide with the evolutionary intervals followed by the family in other palaeogeographical regions, but also by any other groups, as indicated by BARROSO-BARCENILLA & GOY (2005).

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**Plate 1**

*Vascoceras gamai* CHOFFAT, 1898 – A, B, C, D, E, F, G, H, I, J, K, L, ventral, lateral and apertural (complete), ventral, lateral and apertural (without a fragment of body chamber), ventral, lateral and apertural (without body chamber), and ventral, lateral and apertural (without body chamber and a fragment of phragmocone) views of CA-S-151, from the *Vascoceras gamai* Subzone of Condemios, × 3/4.



**Plate 2**

*Vascoceras charoni* sp. nov. – A, B, lateral and apertural views of MS-3, holotype, from the *Vascoceras gamai* Subzone of Tamajón, × 1.  
C, D, E, F, lateral, apertural, lateral and ventral views of TA-S-556, paratype, from the *Vascoceras gamai* Subzone of Tamajón, × 1.  
*Vascoceras barcoicense* CHOFFAT, 1898 – G, H, lateral and ventral views of TA-R-106, from the *Vascoceras gamai* Subzone of Tamajón,  
× 1. I, J, K, apertural, lateral and ventral views of TA-R-634, from an unknown level of Tamajón, × 1.

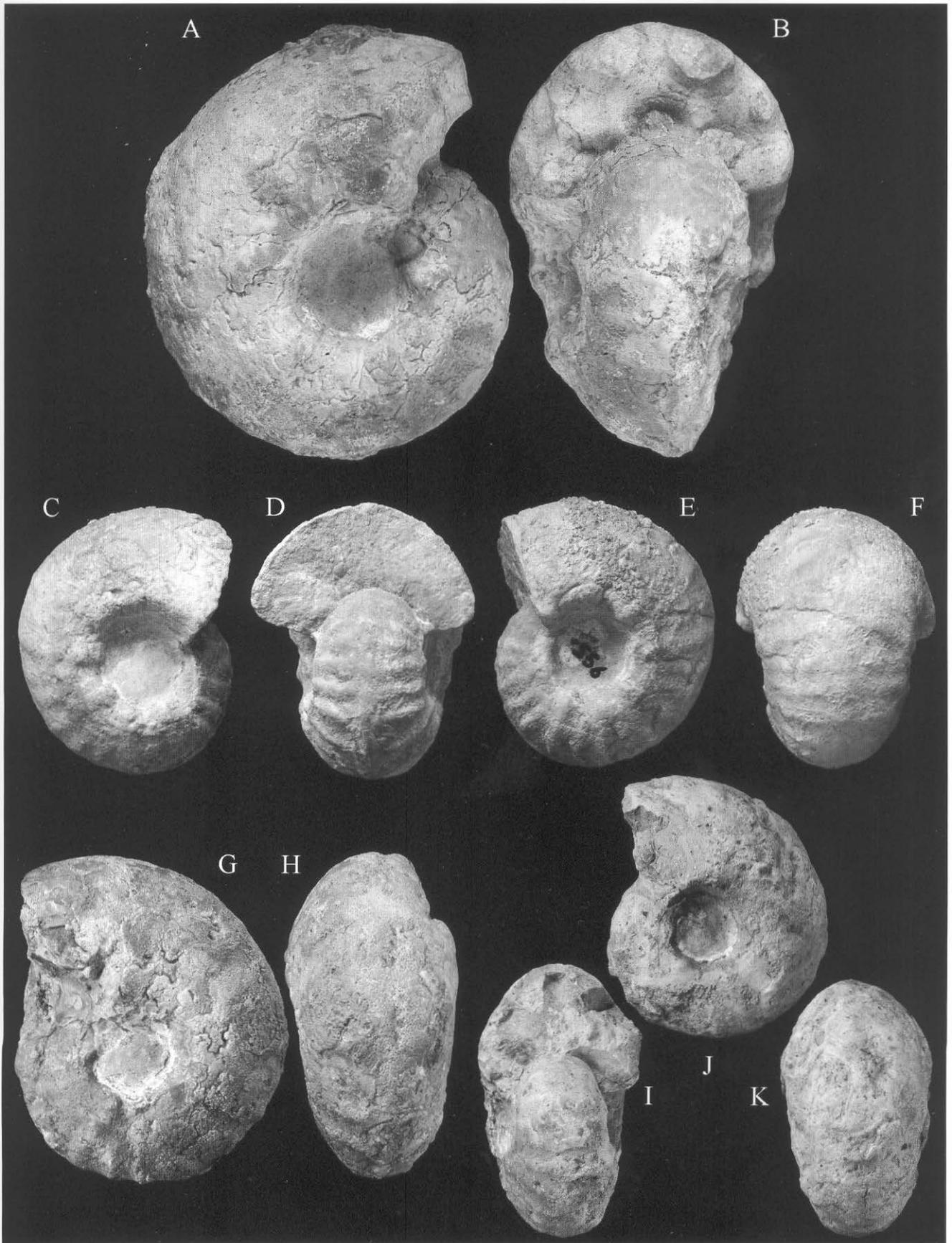


Plate 3

*Vascoceras durandi* (THOMAS & PERON 1889) – A, B, lateral and apertural views of MS-4, from the *Spathites* (*Jeanrogericeras*) *subconciliatus* Zone of Tamajón. C, D, ventral and lateral views of TA-S-568, from the *Spathites* (*Jeanrogericeras*) *subconciliatus* Zone of Tamajón. E, F, G, apertural, lateral and ventral views of TA-S-573, from the *Choffaticeras* (*Choffaticeras*) *quaasi* Zone of Tamajón, × 5/6.

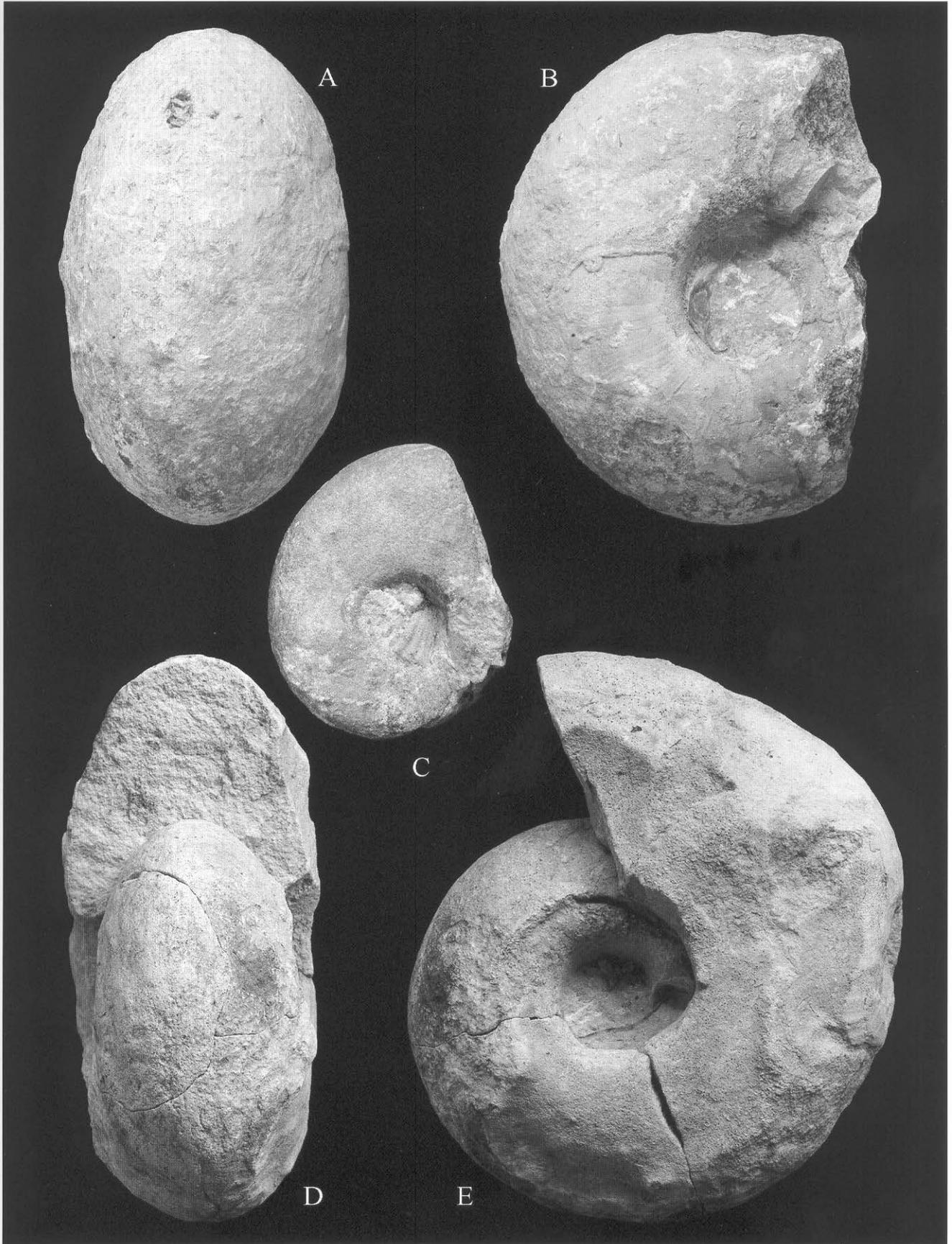


**Plate 4**

*Vascoceras durandi* (THOMAS & PERON, 1889) – A, B, ventral and lateral views of CC-R-199, from an unknown level of Cantalojas, × 5/6.

*Vascoceras cauwini* CHUDEAU, 1909 – C, lateral view of PU-S-312, from the *Spathites* (*Jeanrogericeras*) *subconciatus* Zone of Puentedey, × 5/6.

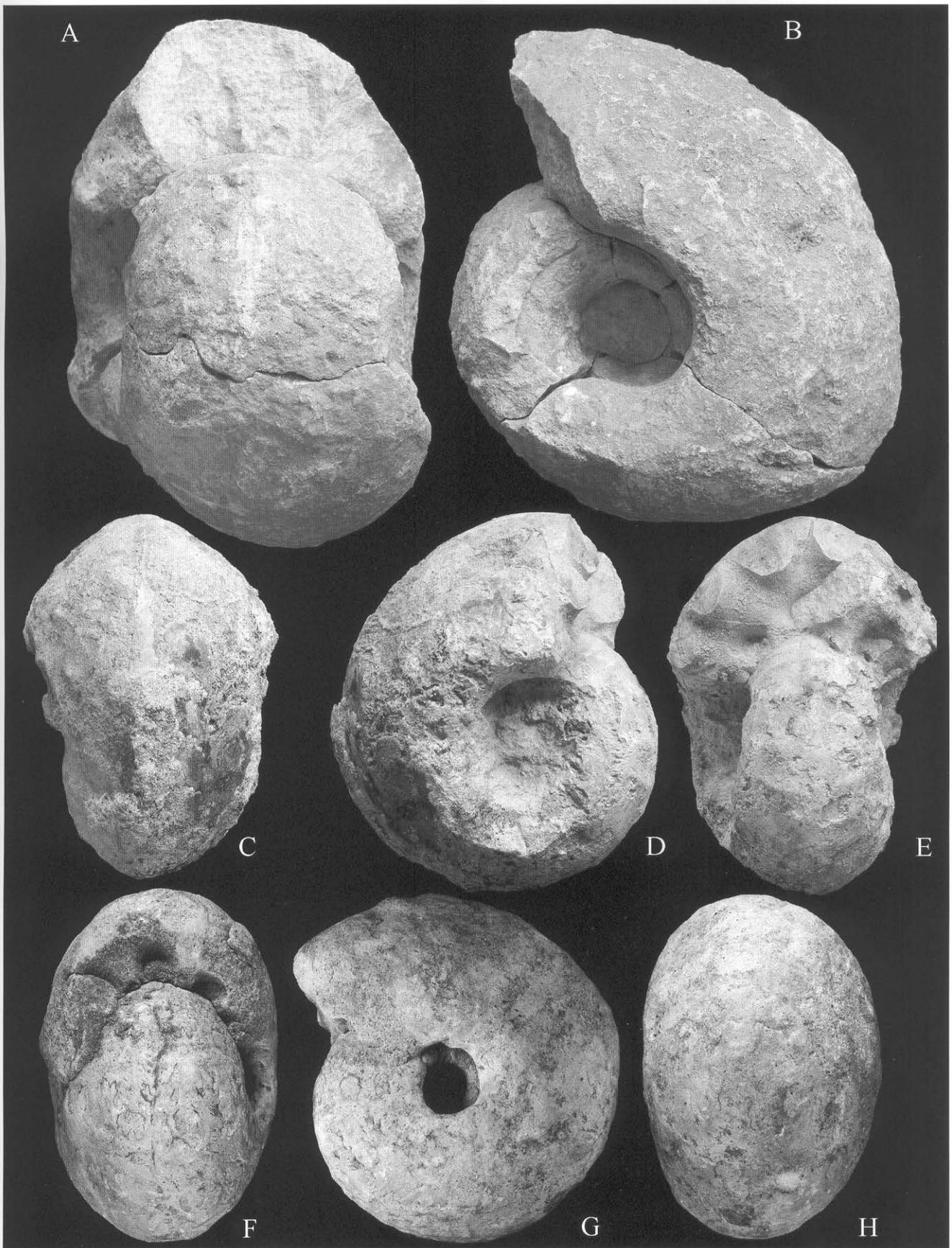
*Vascoceras amieirensense* CHOFFAT, 1898 – D, E, apertural and lateral views of CA-R-598, from the *Spathites* (*Ingridella*) *malladae* Subzone of Condemios, × 5/6.



**Plate 5**

*Vascoceras harttii* (HYATT 1870) – A, B, apertural and lateral views of CC-S-226, from the *Spathites (Ingridella) malladae* Subzone of Cantalojas, × 1. C, D, E, ventral, lateral and apertural views of CB-R-855, from the *Spathites (Ingridella) malladae* Subzone of Condemios, × 1.

*Vascoceras kossmati* CHOFFAT, 1898 – F, G, H, apertural, lateral and ventral views of PU-R-455, from the *Spathites (Ingridella) malladae* Zone of Puente dey, × 1.



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