

A new genus of nautiloid in the Toarcian of the Iberian peninsula (Spain and Portugal)

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Key-words. – Nautiloidea, New genus, Lower Jurassic, Toarcian, Iberian peninsula, Spain, Portugal.

Abstract. – Historically, most of the nautiloids arisen during the Early Jurassic have been assigned initially to the genus *Nautilus* LINNAEUS, 1758, and subsequently to *Cenoceras* HYATT, 1884. At present, a tendency to rehabilitate other genera or to describe new ones predominates among the few authors who try to classify and to group these problematic cephalopods. In the present work, the new genus *Ligeiceras* has been described for remarkably small and involute nautiloids with notably retrogressive suture lines. It has a smooth or slightly ornamented external surface, limited to thin tenuous, ventrally retroverse and distant growth lines and longitudinal and transversal striae. This group, seemingly, appeared after the biotic crisis of the end of the Tenuicostatum/Polymorphum Zone, evolved during the radiation of the Early Toarcian Serpentinum/Levisoni Zone and the Late Toarcian, and survived at least until the Aalenian. New specimens from the Iberian peninsula (Basque-Cantabrian and Iberian basins, Spain; and Lusitanian basin, Portugal), belonging to the taxa *Nautilus fourneti* DUMORTIER, 1874 (selected as type species), *Nautilus inornatus* d'ORBIGNY, 1843, *Nautilus anomphalus* PIA, 1914, *Nautilus jurensis* QUENSTEDT, 1846-49, and, with doubts, *Cenoceras globulus* RULLEAU, 2008, have been collected, described and assigned to this systematic group. Although some of these species have already been cited in the literature, *Ligeiceras fourneti*, *Ligeiceras jurensis* and *Ligeiceras? globulus* have never been previously clearly described or illustrated, and their stratigraphic distribution has not been determined accurately for the Iberian peninsula, as has been done here for these taxa and for *Ligeiceras inornatus* and *Ligeiceras anomphalus*. Therefore, the present work on the new genus *Ligeiceras* constitutes a notable advance in the knowledge of these nautiloids, and seems to confirm that the dwarfism could have been a relatively generalized tendency in the Upper Toarcian of southwestern Europe, possibly due to palaeoenvironmental causes.

Un nouveau genre de nautilé dans le Toarcien de la Péninsule ibérique (Espagne et Portugal)

Mots-clés. – Nautiloidea, Nouveau genre, Jurassique inférieur, Toarcien, Péninsule ibérique, Espagne, Portugal.

Résumé. – Les nautilés surgis durant la radiation du Jurassique inférieur qui a suivi l'extinction en masse de la fin du Trias sont difficiles à classer et à grouper. Historiquement, la plupart d'entre eux ont d'abord été assignés au genre *Nautilus* LINNAEUS, 1758, et par la suite à *Cenoceras* HYATT, 1884 (parfois divisé en quelques sous-genres). Actuellement, la tendance à réhabiliter d'autres genres ou à en décrire de nouveaux groupes prédomine chez les rares paléontologues qui essaient de classer et de grouper dans un système logique et pratique ces problématiques et encore peu étudiés céphalopodes. Dans le présent travail, le nouveau genre *Ligeiceras* a été créé pour des nautilés de petite taille (rarement de plus de dix centimètres de diamètre) présentant une forte involution et des lignes de suture nettement rétroverses. Ce groupe systématique présente une surface externe totalement lisse ou légèrement ornée, qui se limite aux lignes de croissance minces et stries longitudinales et transversales très fines. Il semble que le même groupe soit apparu après la crise biotique de la fin de la zone à Tenuicostatum/Polymorphum, qu'il se soit développé (pouvant être même relativement abondant) durant la radiation du Toarcien inférieur (zone à Serpentinum/Levisoni) et du Toarcien supérieur, et qu'il aurait survécu, au moins, jusqu'à l'Aalénien. Les nouveaux spécimens rattachés au genre *Ligeiceras* dans le présent travail ont été récoltés dans plusieurs coupes de référence du Toarcien de la Péninsule ibérique (Camino, dans le Bassin basque-cantabrique, et Muro de Aguas, Paniza, Moneva, Muniesa, Ariño, Ribarredonda, Maranchón, Turmiel et Fuentelsaz, dans le Bassin ibérique, en Espagne, et Coimbra et Alvaizere, dans le Bassin lusitanien, au Portugal) enregistrées, malgré les divers contextes paléogéographiques de chaque bassin, sous forme de sédiments carbonatés marins très riches en macrofaune benthique et nectonique (avec l'occurrence remarquable des nombreuses ammonites) qui permettent un contrôle biostratigraphique très détaillé. Ils ont été rapportés à *Nautilus fourneti* DUMORTIER, 1874 (sélectionnée comme espèce-type de ce nouveau groupe proposé sur la base des caractéristiques morphologiques et des distributions stratigraphiques), *Nautilus inornatus* d'ORBIGNY, 1843, *Nautilus anomphalus* PIA, 1914, *Nautilus jurensis* QUENSTEDT, 1846-49, et, avec doute, *Cenoceras globosus* RULLEAU, 2008. Parmi ces espèces, déjà mentionnées dans la littérature, *Ligeiceras fourneti*, *Ligeiceras jurensis* and *Ligeiceras? globulus* n'ont jamais été clairement décrits ou figurés et leur répartition biostratigraphique n'a jamais été déterminée avec précision, en particulier dans la Péninsule ibérique. Précisément, *Ligeiceras fourneti* a été identifié dans la zone à Aalensis des branches aragonaise et castillane de la Cordillère

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ibérique (Bassin ibérique). *Ligeiceras inornatum* a été récolté dans la zone à Serpentinum de la branche aragonaise, la zone à Bifrons de la branche castillane, et la zone à Levisoni du Bassin lusitanien. *Ligeiceras anomphalus* a été identifié dans la zone à Aalensis de la Cordillère cantabrique (Bassin basque-cantabrique), les zones à Dispanum, Aalensis et Murchisonae de la branche aragonaise, et dans les niveaux indéterminés du Toarcien de Vélez Rubio. *Ligeiceras jureense* a été récolté dans la zone à Serpentinum de la branche aragonaise. *Ligeiceras ? globulus* a été identifié dans la zone à Serpentinum de la branche aragonaise, dans les niveaux indéterminés du Toarcien inférieur, les zones à Serpentinum et Bifrons de la branche aragonaise, et la zone à Bifrons du Bassin lusitanien. En somme, le présent travail vise à combler quelques lacunes taxonomiques et biostratigraphiques importantes, et constitue une avancée notable dans la connaissance d'un groupe de céphalopodes trop souvent négligé par les paléontologues, et semble confirmer que le nanisme pourrait être une tendance relativement généralisée dans le Toarcien supérieur du Sud-Ouest de l'Europe, peut-être, causée principalement par des causes paléoenvironnementales.

INTRODUCTION

The nautiloids arisen during the radiation of the Early Jurassic that followed the mass extinction of the end-Triassic are difficult to classify and to group. Historically, most of them have been assigned initially to the genus *Nautilus* and subsequently to *Cenoceras*. This genus, originally considered as a unity [e.g. Kummel, 1956], has been subsequently divided into several subgenera [e.g. Tintant, 1984]. At present, a tendency to rehabilitate other genera or to describe new ones predominates among the few authors who try to classify and to group in a logical and practical system these problematic cephalopods [e.g. Chirat, 1997; Rulleau, 2008].

In this study of the nautiloids from the Toarcian of the Iberian peninsula (Basque-Cantabrian and Iberian basins, Spain, and Lusitanian basin, Portugal), we report several new observations that, after comparison with data presented by other authors in different basins, have provided new tools that can help to solve the difficult systematic attribution of these invertebrates. Specifically, we have noticed that certain small nautiloids, likely related to the radiation occurring between the Early Toarcian (Serpentinum/Levisoni zone) and the Aalenian, after the biotic crisis characterising the end of the Tenuicostatum/Polymorphum zone, are relatively abundant in the geological record and may constitute a taxonomic group.

HISTORICAL BACKGROUND

Since the genus *Nautilus* was defined by Linnaeus [1758], numerous species of Lower Jurassic nautiloids were proposed, and for many years most of them were assigned to this group. In fact, Montfort [1808] proposed *Bisiphytes* for nautiloids with two siphuncles and selected as type his new species *B. reticulatus*, but most of authors continued assigning the Lower Jurassic nautiloids to *Nautilus* until the study of Hyatt [1884] was published.

Hyatt [1884] defined *Cenoceras* and designated as its type the species *Nautilus intermedius* SOWERBY, 1816, [sensu d'Orbigny, 1843]. Unfortunately, due to the shortness of the diagnosis and the deficiencies of the illustration of *N. intermedius*, *Cenoceras* was interpreted in very different ways. Hyatt [1894] defined *Digonioceras* for medium to large sized nautiloids with depressed semicircular or suboval section, slightly involute coiling and nearly straight suture lines and selected as type his new species *D. rotundum*, subsequently mainly considered as a synonym of *Nautilus excavatus* SOWERBY, 1826.

Prinz [1906], on the basis of the differences of *N. intermedius* presented by Sowerby [1816] and d'Orbigny [1843], considered these two forms as two different species, and proposed for the latter the name *Nautilus orbignyi*. This author also established *Nautilites* for medium to large sized nautiloids with depressed suboval or rounded subtrapezical section, slightly involute coiling and moderately sinuous suture lines, and included in it the species *N. excavatus*, among others. Spath [1927] proposed *Ophionutilus* for *Nautilus burtonensis* FOORD & CRICK, 1890, *Sphaeronutilus* for *Nautilus pisanus* FUCINI, 1895, and *Procymatoceras* for *Nautilus subtruncatus* MORRIS & LYCETT, 1850, but he did not provide diagnosis for these groups.

Kummel [1954] included *Cenoceras* as a subgenus of *Bisiphytes* as an attempt to express the homogeneity of these two groups. Kummel [1956] included within the synonymy of *Cenoceras* the groups *Digonioceras*, *Nautilites*, *Ophionutilus*, and *Sphaeronutilus*, and due to the ambiguity connected with its type species, in agreement with Teichert [1940], considered *Bisiphytes* as an invalid name. The same author considered as the type of *Cenoceras* the species *N. orbignyi*. Kummel [1964] included within the synonymy of *Cenoceras* the groups *Digonioceras*, *Nautilites* ZIETEN, 1830 (*non* PALLAS, 1771), *Ophionutilus* and *Sphaeronutilus*. This author considered as the type of *Cenoceras* the species *N. intermedius*, but figured as representative of this group the specimen of d'Orbigny [1843].

Tintant [1969], in agreement with the general tendency after Kummel [1956, 1964], considered that nearly all the Lower Jurassic nautiloids must be assigned to *Cenoceras*, and included in it the Middle Jurassic group *Procymatoceras* as a subgenus. Tintant [1984] redefined *Cenoceras*, and divided it into three subgenera on the basis of the ornamentation of the shell. The same author proposed the subgenera *Cenoceras s. st.* for the forms that maintain longitudinal ornamentation in the adult stage, *Hemicenoceras* (type species *Nautilus semistriatus* d'ORBIGNY, 1843) for those that present longitudinal ornamentation only over the ventral and the umbilical regions, and *Metacenoceras* (type species *Nautilus inornatus* d'ORBIGNY, 1843) for those that totally or practically lack longitudinal ornamentation. This author also redefined the species *N. intermedius* on the basis of several specimens of the Sinemurian of Bourgogne, France. Tintant [1994] differentiated in *Cenoceras* the four subgenera *C. (Cenoceras)*, *C. (Hemicenoceras)*, *C. (Metacenoceras)* and *C. (Digonioceras)*. The same author did not find the original specimen of *N. orbignyi*, and considered that this name is non-utilizable.

Chirat [1997] did not distinguish subgenera within *Cenoceras*, rehabilitated the genera *Digonioceras* and *Ophionautilus*, and proposed the gen. nov.? A: for the group of *Nautilus austriacus* HAUER, 1856, and the gen. nov.? B: for the group of *Nautilus araris* DUMORTIER, 1869. Finally, Rulleau [2008] neither differentiated subgenera within *Cenoceras*, maintained the validity of the genera *Digonioceras* and *Ophionautilus*, proposed the new genus *Belmonticeras*, type species *Nautilus subsinuatus* d'ORBIGNY, 1850, for compressed nautiloids with narrow umbilicus and markedly sinuous suture line, and considered the group of "*Nautilus*" *araris* as a different group for very compressed specimens, with wide umbilicus and nearly straight suture line.

GEOGRAPHICAL AND GEOLOGICAL CONTEXT

Field work has been carried out in several outcrops with mainly Toarcian sequences of the Iberian peninsula (Spain and Portugal). Among them, the here presented representatives of this new genus have been obtained from outcrops situated in the localities of Camino, in the Cantabrian ranges, of Muro de Aguas, Paniza, Moneva, Muniesa and Ariño, in the Aragonese branch of the Iberian ranges, and of Ribarredonda, Maranchón, Turmiel and Fuentelsaz, in the Castilian branch of the Iberian ranges, Spain; and of Coimbra and Alvaíazere, in the Lusitanian basin, Portugal (fig. 1 A-C).

During the Early Jurassic, the current Iberian peninsula was a relatively independent tectonic unit, named Iberian subplate. Its particular structural layout and its privileged palaeogeographical location enabled that the eustatic cycles were registered in several epicontinental flooded regions of the Iberian subplate, such as the Basque-Cantabrian, the Iberian and the Lusitanian basins, containing both Boreal fauna, coming from the Protoatlantic ocean, and Meridional fauna, arrived from the Tethys sea. Likewise, as these basins constituted relatively confined environments, endemic fauna arose in their waters as well.

Specifically, the Toarcian of the Basque-Cantabrian basin is made up mainly by a succession of black to grey limestones or marly limestones and marlstones of epicontinental carbonated platform. Specifically, these materials were deposited in an outer-middle platform environment and nowadays correspond to the Castillo Pedroso formation [Robles *et al.*, 2004]. In the same way as in the Iberian ranges, several levels with ammonoids have been recognized and this has enabled to identify all the standard cronozones [Goy *et al.*, 1994].

The Toarcian of the Iberian basin is constituted mainly by a succession of mudstone limestones and marlstones that currently are attributed to the Turmiel formation [Goy *et al.*, 1976]. This lithostratigraphic unit exceeds 80 m thickness in the depocentres of Moreal and Azuara, both in the Aragonese branch of the Iberian ranges, and in extensive regions of the basin it is replaced in the Upper Toarcian by limestones of shallow platform nowadays included in the Casinos formation [Gómez and Goy, 2004, 2005]. In the Castilian branch of the Iberian ranges, especially near the Iberian plateau, the base of the Toarcian corresponds to the upper part of the Barahona formation. Locally, such as in Fuentelsaz, the Turmiel formation continues up to the

Aalenian [Goy and Ureta, 1990]. Mainly in the centre of the Iberian ranges numerous levels with ammonoids have been differentiated and this has made possible to recognize all the standard cronozones and subcronozones [Goy and Martínez, 1990; Comas-Rengifo *et al.*, 1996].

The Toarcian of the Lusitanian basin corresponds, generally, to a thick (around 100 m to more than 200 m) marly limestone succession, rich in benthic and nektonic fauna [Duarte, 1997], deposited on a homoclinal carbonate ramp [Duarte, 2007]. These hemipelagic units, included in the São Gião formation [Duarte and Soares, 2002] and, partially, in the Póvoa da Lomba formation, are controlled by an accurate ammonite [e.g. Rocha *et al.*, 1987; Elmi *et al.*, 1989] and calcareous nannofossil [Perilli and Duarte, 2006] biostratigraphy.

As a whole, in the studied areas nautiloids are extremely scarce (< 1 % of the collected cephalopods), immature specimens being nearly non-existent (only 1 exemplar of the here presented new genus). Possibly, these nautiloids did not inhabit the Iberian basin and arrived to this palaeogeographic area during the transgressive episodes of the T-R cycles, especially in the biocrones Serpentinum-Bifrons, Dispansum and Aalensis. In the Basque-Cantabrian and the Lusitanian basins, these nautiloids have been recorded in the lower part of the Aalensis zone, and in the middle part of the Levisoni zone and the upper part of the Bifrons zone, respectively (fig. 2 A-B, 3 A-C).

PALAEONTOLOGICAL STUDY

In this section is presented a systematic description of new mainly Toarcian nautiloids from the Iberian peninsula, obtained during field work carried out by the authors, belonging to the Antonio Goy and María José Comas-Rengifo (G&C) and Luís Vítor Duarte (LVD) collections, nowadays held in the Universidad Complutense de Madrid, Spain, and the Universidade de Coimbra, Portugal, respectively. In this study is also included a revision of previously published Toarcian nautiloids [Martínez and Rábano, 1999], nowadays held in the Instituto Geológico y Minero, Spain.

Conventions

The terminology used to describe the different specimens studied is based on the glossary of morphological terms for post-Triassic nautiloids and ammonoids proposed by Barroso-Barcenilla [2008]. To indicate the location of several specimens, the following acronyms and abbreviations are used throughout the text: Instituto Geológico y Minero (IGME), Madrid, Spain; Musée des Confluences (MCL), Lyon, France; Musée National d'Histoire Naturelle (MNHN), Paris, France; Universidade de Coimbra (UC), Coimbra, Portugal; Universidad Complutense de Madrid (UCM), Madrid, Spain.

Measurements were made with an adjustable calliper, and are given in tenths of millimetre and as percentages of the diameter of the shell. The dimensions used in the analysis are defined as follows: diameter of the shell (D), maximum distance between two diametrically opposite ventral extremes, measured perpendicularly to the coiling axis; whorl height (H), maximum distance between the ventral extreme and the most distanced point of the dorsal wall, taken parallel to the plane of bilateral symmetry; whorl

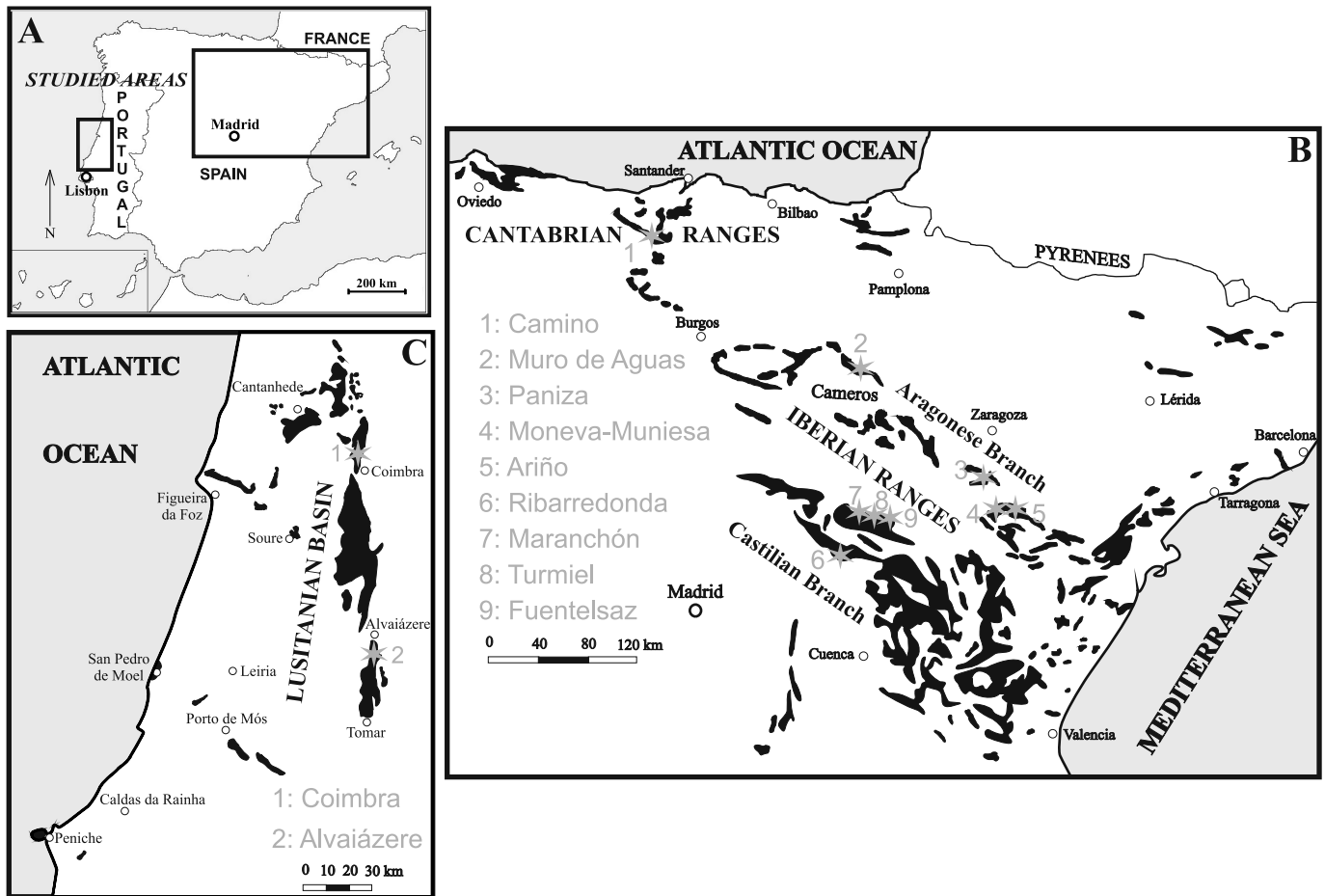


FIG. 1. – A, Geographic location of the studied areas (general). B, Geographic location of the Spanish studied area (detailed). C, Geographic location of the Portuguese studied area (detailed).

FIG. 1. – A, Emplacement géographique de la région étudiée (général). B, Emplacement géographique de la région espagnole étudiée (détaillée). C, Emplacement géographique de la région portugaise étudiée (détaillée).

breadth (B), maximum distance between both flanks, measured perpendicularly to the coiling axis; umbilical width (U), maximum distance, taken perpendicularly to the coiling axis, separating two diametrically opposite umbilical margins of the same whorl. All the specimens presented here are nowadays held in the Departamento de Paleontología of the UCM, the Departamento de Ciências da Terra of the UC and the Museo Geominero of the IGME.

Systematic palaeontology

Class Cephalopoda Cuvier, 1797
 Subclass Nautiloidea Agassiz, 1847
 Order Nautilida Agassiz, 1847
 Family Nautilidae de Blainville, 1825

Genus *Ligeiceras* nov. gen. (BARROSO-BARCENILLA)

Type species. *Nautilus fourneti* DUMORTIER, 1874.

Derivation of the name. It comes from the mythological siren Ligeia, whose name entitled a short story written by Edgar Allan Poe [1838].

Diagnosis. Group with representatives of small adult size (rarely of more than ten centimetres in diameter), with moderately compressed or depressed from subquadrate to

subrounded section and markedly involute coiling. Numerous septa with fairly plicate but considerably retroverse suture lines. Smooth or slightly ornamented external surface, limited to thin tenuous, ventrally retroverse and distant growth lines and longitudinal and transversal striae.

Discussion. Regarding the rank of this new group, according to the extensive but broad original description of *Cenoceras* given by Hyatt [1884, p. 300], and the short but also broad interpretation of the same genus written by Kummel [1964, p. K449], certainly, nearly all the Lower Jurassic nautiloids could be included within the wide morphological variability of this genus, as historically it has happened. Nevertheless, to get a more useful, concise and practical division of these cephalopods, it seems to be not only suitable but also necessary to divide these cephalopods by creating subgenera in *Cenoceras*, as proposed by Tintant [1984], or by rehabilitating previous genera or describing new ones, as proposed by Chirat [1997] and Rulleau [2008], among others. With this purpose a new genus is proposed here on the basis of morphological features and stratigraphical distributions.

According to its diagnosis, *Ligeiceras*, besides its type species, could include *Nautilus inornatus* d'ORBIGNY, 1843,

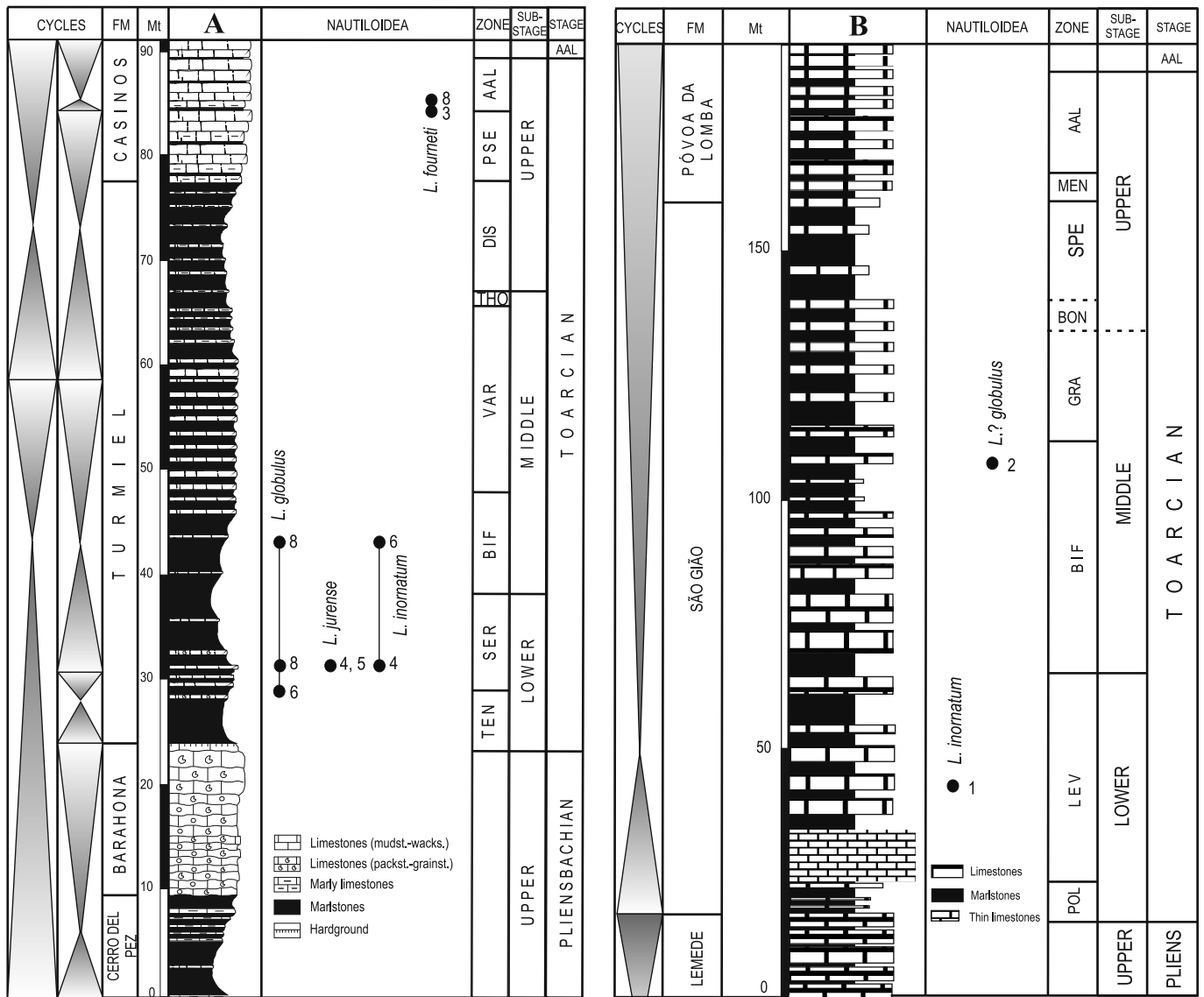


FIG. 2. – A, Chronostratigraphic ranges of the collected specimens of the new genus *Ligeiceras* in the centre of the Iberian ranges. Zone abbreviations : TEN: Tenuicostatum, SER: Serpentinum, BIF: Bifrons, VAR: Variabilis, THO: Thouarsense, DIS: Dispansum, PSE: Pseudoradiosa, AAL: Aalensis. B, Chronostratigraphic ranges of the collected specimens of the new genus *Ligeiceras* in the Lusitanian basin. Zone abbreviations: SPI: Spinatum, POL: Polymorphum, LEV: Levesquei, BIF: Bifrons, GRA: Gradata, BON: Bonarelli, SPE: Speciosum, MEN: Meneghinii, AAL: Aalensis. Outcrops are indicated with numbers of fig. 1.

FIG. 2. – A, Distribution chronostratigraphique des spécimens du nouveau genre *Ligeiceras* recueillis dans le centre de la Cordillère ibérique. Abréviations de zones : TEN : Tenuicostatum, SER : Serpentinum, BIF : Bifrons, VAR : Variabilis, THO : Thouarsense, DIS : Dispansum, PSE : Pseudoradiosa, AAL : Aalensis. B, Distribution chronostratigraphique des spécimens du nouveau genre *Ligeiceras* recueillis dans le Bassin lusitanien. Abréviations de zones : SPI : Spinatum, POL : Polymorphum, LEV : Levesquei, BIF : Bifrons, GRA : Gradata, BON : Bonarelli, SPE : Speciosum, MEN : Meneghinii, AAL : Aalensis. Les affleurements sont indiqués avec les nombres de la fig. 1.

Nautilus anomphalus PIA, 1914, *Nautilus jurensis* QUENSTEDT, 1846-49, and, possibly, *Cenoceras globulus* RULLEAU, 2008. As already suggested by Rulleau [2008, p. 39], in the Upper Toarcian can be identified in different groups other species of small adult size, such as *Digoniceras terebratum* (DUMORTIER, 1874), that seem to reveal that dwarfism could be a relatively generalized tendency in this substage, possibly mainly due to palaeoenvironmental causes.

Ligeiceras shares several species with those assigned to the group *Cenoceras* (*Metacenoceras*) of Tintant [1984], whom his author remitted, besides numerous Sinemurian

and Pliensbachian taxa, *Nautilus fischerianus* FOORD & CRICK, 1890, *Nautilus toarcense* d'ORBIGNY, 1850, *N. inornatum*, *N. anomphalus*, *N. jurensis* and *N. fourneti*. Nevertheless, using the ornamentation as main feature to differentiate Lower Jurassic nautiloids, such as in *C. (Metacenoceras)*, does not seem to be suitable, as this characteristic can easily be alterable by numerous *post-mortem* agents and, therefore, its actual appearance strongly depends of the preservational state of each specimen.

Occurrence. Lower (part), Middle and Upper Toarcian and Middle (part) Jurassic of southwestern Europe (to date, France, Germany, Spain and Portugal). Specifically, it

seems that this new group appeared after the biotic crisis of the end of the Early Toarcian Tenuicostatum/Polymorphum zone, evolved during the radiation that began in the Serpentinum/Levisoni zone, and survived, at least, until the Aalenian.

Ligeicerasourneti (DUMORTIER, 1874)

Plate I, A-F.

1874 *Nautilusourneti* DUMORTIER, p. 45, pl. 8, figs. 1-3.

1914 *Nautilusourneti* DUMORTIER; Pia, p. 30 [12], ? 74 [56], pl. 4, figs. 4a-b; ? pl. 8, fig. 19.

? 1956 *Cenocerasourneti* (DUMORTIER); Kummel, text-fig. 8 t.

1998 *Cenoceras (Metacenoceras)ourneti* (DUMORTIER); Tintant, p. 39, pl. 4, figs. 3-4, text-fig. 5.

2006 *Cenocerasourneti* (DUMORTIER); Rulleau, p. 118, text-fig. 30/5.

2008 *Cenocerasourneti* (DUMORTIER); Rulleau, p. 39, pl. 9, figs. 2-3; pl. 12, fig. 2; text-fig. 7/11.

Type: Among the two representatives of this species figured by its author, nowadays held in the MCL, Tintant [1998] designated as lectotype the ML-9177 of Dumortier [1874, p. 45, pl. 8, figs. 1-2], from the Upper Toarcian of La Verpillière, France.

Material and dimensions:

	D	H (%)	B (%)	U (%)
G&C-861	677	404 (60)	404 (60)	.
G&C-1131	789	442 (56)	475 (60)	121 (15)
	610	337 (55)	398 (65)	107 (18)
G&C-1281	585	340 (58)	412 (70)	72 (12)

Description: Small to medium sized specimens with moderately depressed from subquadrate or subtrapezoidal to subcircular section of progressively ventrolateral and sharply umbilical rounded margins, and markedly involute coiling. Their venter is tabulate or slightly arched, their flanks are flat or moderately convex, and their umbilici are very small and deep, occasionally closed before maturity, and have subvertical walls. The siphuncle is clearly lower than the central position of the septa. The adult body chamber can show a sudden increase of the breadth and the roundness of the whorl section. Each whorl has from sparse to dense moderately plicate suture lines, with a wide and shallow ventral lobe, and a retrogressive and deep lateral lobe and a long and low lateral saddle per side. The ornamentation is nearly non-existent, and is limited to delicate and sinuous growth lines and tenuous and serrate transversal striae that describe a retroverse "u" over the venter.

Discussion: The schematic section of Pia [1914, p. 74 (56), pl. 8, fig. 19], refigured by Kummel [1956, text-fig. 8 t] seems to show too rounded section and too high siphuncle to be a representative of this taxon, as already noted by Tintant [1998]. Few species of Toarcian nautiloids can be confused with *L.ourneti*. Specifically, *Ligeiceras inornatus* (d'ORBIGNY, 1843) and *Ligeiceras jurense* (QUENSTEDT, 1846-49) present less involute coilings, and *Ligeiceras anomphalus* (PIA, 1914) reaches smaller adult sizes. Other small species of the Upper Toarcian, such as *Ligeiceras? globulus* (RULLEAU, 2008) and *Digonioceras terebratum* (DUMORTIER, 1874) have more rounded sections and wider umbilici. Regarding its phylogeny, Tintant [1998] suggested that this species may be derived from *D. terebratum* by progressive disappearance of the spiral ornamentation.

Distribution: Upper Toarcian and, possibly, Aalenian of France, Germany and Spain. It has been also cited but not figured in Hungary (Cserny, Bakony) and Austria (Piszk, Adnet) by Prinz [1906], as reported by Pia [1914]. In the present work this species has been identified in the Aalensis zone of Fuentelsaz (G&C-861, specifically Aalensis subzone) and Turmiel (G&C-1131), both in the Castilian branch of the Iberian ranges, and of Paniza (G&C-1131, specifically Pseudoradiosa or Aalensis subzones), in the Aragonese branch of the Iberian ranges.

Ligeiceras inornatum (d'ORBIGNY, 1843)

Plate I, G-I; Plate II, A-B.

1843 *Nautilus inornatus* d'ORBIGNY, p. 152, pl. 28, figs. 1-2.

1867 *Nautilus inornatus* d'ORBIGNY; Quenstedt, p. 413, pl. 33, fig. 21.

1878 *Nautilus inornatus* d'ORBIGNY; Mallada, pl. 3, figs. 5-6.

1884 *Nautilus inornatus* d'ORBIGNY; Mallada, p. 228 (figured in 1878, pl. 3, figs. 5-6).

non 1890 *Nautilus inornatus* d'ORBIGNY; Foord and Crick, p. 281, figs. 12 a-b.

1893 *Nautilus inornatus* d'ORBIGNY; Geyer, p. 62, pl. 9, figs. 6-7 (non 5).

1914 *Nautilus inornatus* d'ORBIGNY; Pia, p. 71 [53], pl. 9, fig. 14.

1956 *Cenoceras inornatus* (d'ORBIGNY); Kummel, text-fig. 9 o (non pl. 5, figs. 1-2).

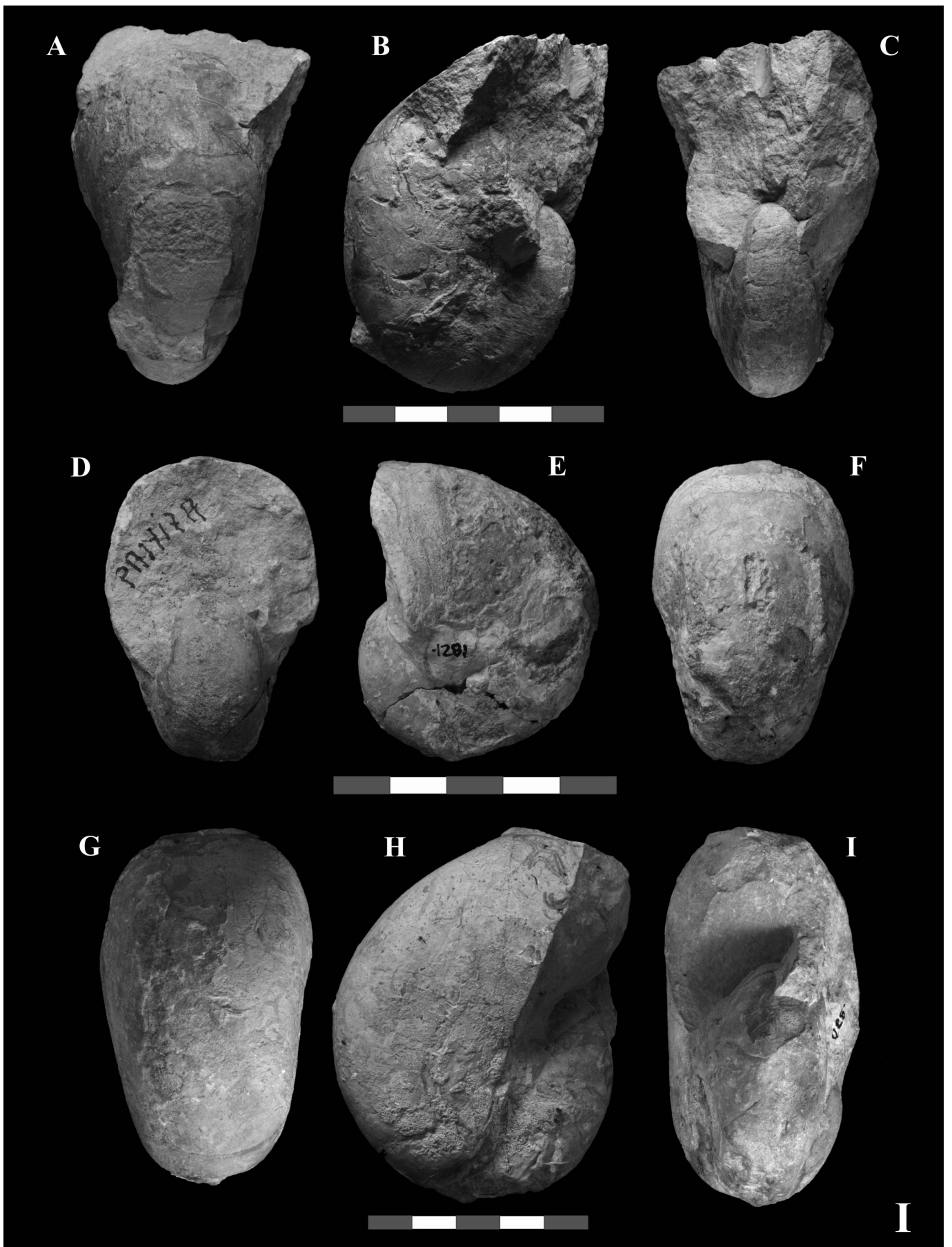
1994 *Cenoceras (Metacenoceras) inornatum* (d'ORBIGNY); Tintant, p. 28, pl. 8, figs. 1 a-b, fig. 2; text-figs. 5 a-b.

non cf. 1999 *Cenoceras (Metacenoceras) cf. inornatus* (d'ORBIGNY); Martínez and Rábano, p. 418, pl. 2, fig. 4, pl. 4, fig. 7.

non 2006 *Cenoceras inornatum* (d'ORBIGNY); Rulleau, p. 118, pl. 105, fig. 1; text-fig. 30/8.

PLATE I. – A-C, *Ligeicerasourneti* (DUMORTIER, 1874), specimen G&C-861, Aalensis Zone (Aalensis Subzone) of Fuentelsaz, ventral, lateral and apertural views. D-F, *L.ourneti*, specimen G&C-1281, Aalensis zone (Pseudoradiosa or Aalensis subzone) of Paniza, apertural, lateral and ventral views. G-I, *L. inornatum* (d'ORBIGNY, 1843), specimen G&C-870, Bifrons zone (Bifrons subzone) of Ribarredonda, ventral, lateral and apertural views. Scale bars are 5 cm.

PLATE I. – A-C, *Ligeicerasourneti* (DUMORTIER, 1874), specimen G&C-861, zone à Aalensis (sous-zone à Aalensis) de Fuentelsaz, vues ventrale, latérale et aperturale. D-F, *L.ourneti*, specimen G&C-1281, zone à Aalensis (sous-zone à Pseudoradiosa ou sous-zone à Aalensis) de Paniza, vues aperturale, latérale et ventrale. G-I, *L. inornatum* (d'ORBIGNY, 1843), specimen G&C-870, zone à Bifrons (sous-zone à Bifrons) de Ribarredonda, vues ventrale, latérale et aperturale. Échelle graphique : 5 cm.



Type: Although d'Orbigny [1843] cited several representatives of his new species in his original work, he described and figured only one specimen (p. 152, pl. 28, figs. 1-2) collected by Guibal from the Toarcian of the area of Nancy, France, that can be considered as lectotype. Unfortunately, the present whereabouts of the Guibal Collection is unknown. Tintant [1994] selected the nautiloid 1901 E-1 of the d'Orbigny Collection, obtained from Saint-Maixent, France, and nowadays housed in the MNHN, to redescribe this species.

Material and dimensions

	D	H (%)	B (%)	U (%)
G&C-870	897 646	507 (57) 377 (58)	511 (58) 439 (68)	98 (11) .
G&C-1149	.	391	.	129
LVD-230-1	790	430 (54)	455 (58)	155 (20)
LVD-230-2	645	370 (57)	385 (60)	~145 (23)

Description: Small to medium sized specimens with depressed subquadrate section of rounded but conspicuous ventrolateral and umbilical margins, and notably involute coiling. Their venter is tabulate or slightly arched, their flanks are flat or moderately convex, and their umbilici are small and deep and have subvertical walls. The siphuncle is in a slightly low but nearly central position over the septa. Each whorl has numerous relatively plicate suture lines, with a wide and shallow lobe on the venter and a retrogressive and deep lobe and a long and shallow saddle per side. The ornamentation is nearly non-existent and, if present, is limited to delicate and sinuous growth lines.

Discussion: Regarding the diagnosis of this species there are certain differences between the original description of d'Orbigny [1843] and the subsequent redescription of Tintant [1994]. The specimen studied by d'Orbigny [1843] exhibits higher density of septa, greater sinuosity of suture lines and a siphuncle in a slightly more elevated location than that analysed by Tintant [1994]. The Bajocian nautiloid assigned by Foord and Crick [1890, figs. 12 a-b] to *N. inornatus* and refigured by Kummel [1956, pl. 5, figs. 1-2] was renamed by Tintant [1994] as *Cenoceras (Metacenoceras) foordi*. The Pliensbachian specimen classified by Martínez and Rábano [1999] as *Cenoceras (Metacenoceras) cf. inornatus* has an umbilicus too wide to be a representative of this taxon. The Aalenian nautiloid considered by Rulleau [2006] as *Cenoceras inornatum* and subsequently classified by Rulleau [2008] as *Cenoceras aff. multiseptatum* (FOORD and CRICK, 1890), exhibit morpho-

logical features and stratigraphic range that exclude it of the species of d'Orbigny.

Ligeiceras anomphalus (PIA, 1914) shows a more compressed whorl section and a more involute coiling, with convex venter and nearly closed umbilici. *Ligeiceras fourneti* (DUMORTIER, 1874) can reach a slightly bigger adult size, and has a more rounded section and a more involute coiling. *Cenoceras toarcense* (d'ORBIGNY, 1850) reaches notably larger adult size and exhibits markedly deeper ventral lobe. *Cenoceras geyeri* (PRINZ, 1906) shows a semicircular section, with angular umbilical margins, and a less involute coiling.

Distribution: Lower (part), Middle and Upper Toarcian of France, Germany, Spain and Portugal. It has been also cited but not figured in Switzerland, Austria and Italy by different authors, as reported Foord and Crick [1890] and Pia [1914]. Tintant [1994] considered this taxon vaguely as Toarcian but, specifically, the new specimens presented here have been collected exclusively in the Bifrons zone (Bifrons subzone) of Ribarredonda (G&C-870), in the Castilian branch of the Iberian ranges, the Serpentinum zone (Elegantulum subzone) of Moneva (G&C-1149), in the Aragonese branch of the Iberian ranges, and the Levisoni zone of Coimbra (LVD-230-1 and LVD-230-2), in the Lusitanian basin.

Ligeiceras anomphalus (PIA, 1914)

Plate II, C-H.

1843 *Nautilus truncatus* SOWERBY; d'Orbigny, p. 153, pl. 29, figs. 1-2.

1914 *Nautilus anomphalus* PIA, p. 77 [59], pl. 10, fig. 9. cf. 1914 *Nautilus cf. anomphalus* PIA, p. 30 [12].

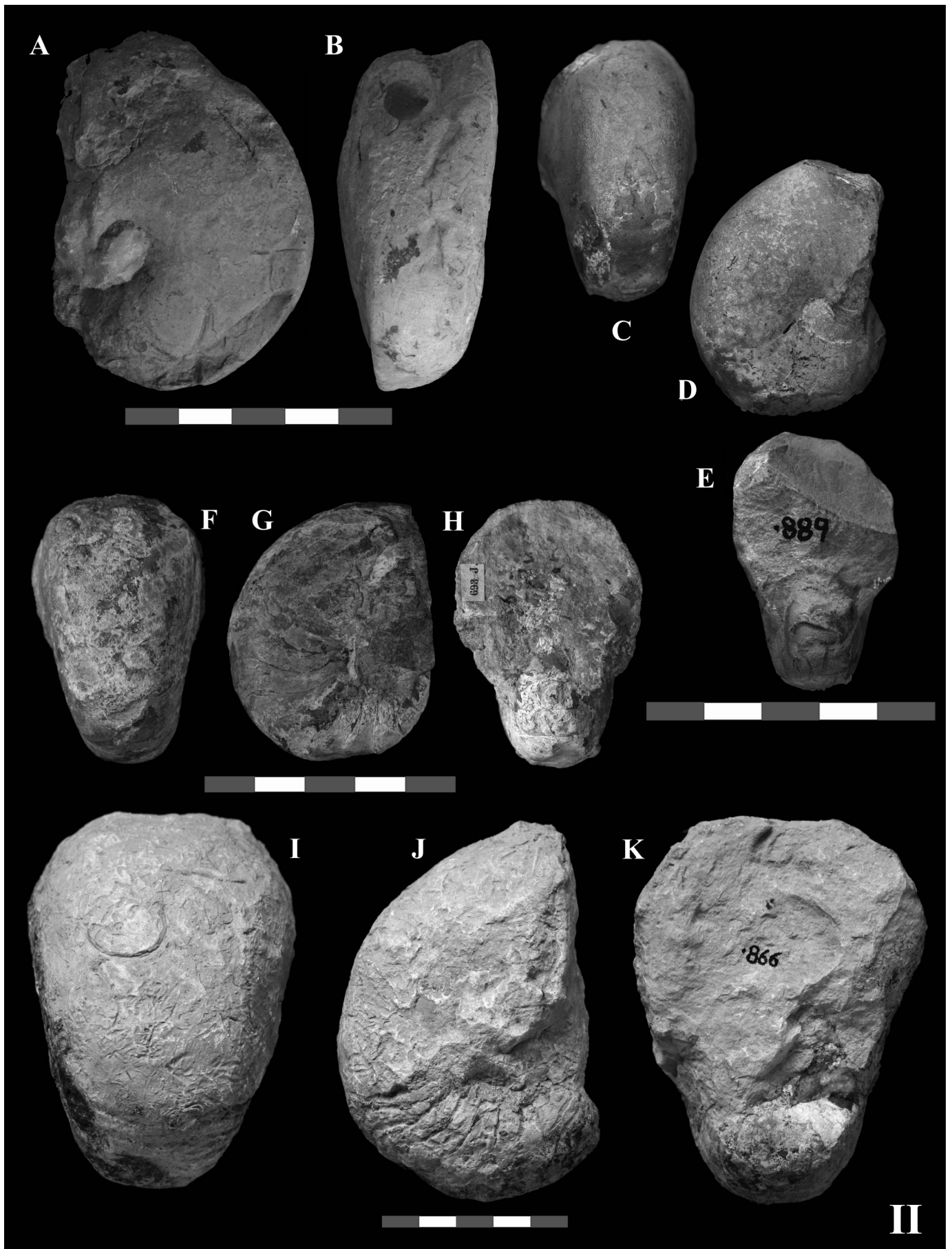
1994 *Cenoceras (Metacenoceras) anomphalus* (PIA); Tintant, p. 29, pl. 8, figs. 3 a-b; text-figs. 6 a-b.

1999 *Cenoceras (Metacenoceras) anomphalus* (PIA); Martínez and Rábano, p. 418, pl. 1, fig. 3, pl. 4, fig. 4.

Type: D'Orbigny [1843] cited several representatives of *Nautilus truncatus* SOWERBY, 1816, in his original work, and figured one specimen (p. 153, pl. 29, figs. 1-2) collected by him from the Toarcian of the environs of Millau, France. Unfortunately, the present whereabouts of this nautiloid, used by Pia [1914] to define *Nautilus anomphalus*, is unknown. Tintant [1994] selected the specimen 1902 of the d'Orbigny Collection, obtained from the same locality and nowadays housed in the MNHN, to redescribe this species.

PLATE II. – A-B, *Ligeiceras inornatum* (d'ORBIGNY, 1843), specimen G&C-1149, Serpentinum zone (Elegantulum subzone) of Moneva, lateral and ventral views. C-E, *L. anomphalus* (PIA, 1914), specimen G&C-889, Murchisonae zone of Muro de Aguas, ventral, lateral and apertural views. F-H, *L. anomphalus*, specimen IGME-693J, undetermined Toarcian levels of Vélez Rubio, ventral, lateral and apertural views. I-K, *L. jurense* (QUENSTEDT, 1846-49), specimen G&C-866, Serpentinum zone of Ariño, ventral, lateral and apertural views. Scale bars are 5 cm.

PLATE II. – A-B, *Ligeiceras inornatum* [d'ORBIGNY, 1843], specimen G&C-1149, zone à Serpentinum (sous-zone à Elegantulum) de Moneva, vues latérale et ventrale. C-E, *L. anomphalus* (PIA, 1914), specimen G&C-889, zone à Murchisonae de Muro de Aguas, vues ventrale, latérale et aperturale. F-H, *L. anomphalus*, specimen IGME-693J, niveaux indéterminés du Toarcien de Vélez Rubio, vues ventrale, latérale et aperturale. I-K, *L. jurense* (QUENSTEDT, 1846-49), specimen G&C-866, zone à Serpentinum de Ariño, vues ventrale, latérale et aperturale. Échelle graphique : 5 cm.



Material and dimensions

	D	H (%)	B (%)	U (%)
G&C-887	686	333 (49)	.	72 (11)
G&C-888
G&C-889	425	254 (60)	271 (64)	.
	314	169 (54)	194 (62)	.
G&C-903	480	302 (63)	362 (75)	25 (5)
	418	177 (42)	252 (60)	.
IGME-693J	565	329 (58)	370 (65)	67 (12)
	433	279 (65)	263 (61)	.

Description: Small sized specimens with compressed or moderately depressed from subrectangular to subquadrate, or even subtapered, section of conspicuous ventrolateral angles and rounded umbilical margins, and extremely involute coiling. Their venter is slightly concave or tabulate, their flanks are flat or moderately convex, and their umbilici are nearly or completely close, with subvertical and deep walls. Numerous and moderately plicate suture lines, with a wide and nearly straight lobe on the venter and a retrogressive, asymmetrical and shallow lobe and a long and low saddle per side. The ornamentation, when preserved, is limited to thin growth lines, and delicate, retroverse and distant transversal striae over the venter and the flanks and slight longitudinal striae over the venter.

Discussion: The species *Nautilus truncatus* was defined by Sowerby [1816], who selected as type a large British specimen with low siphuncle (p. 153, pl. 29, figs. 1-2). D'Orbigny [1843] assigned to this species several small French nautiloids. On the basis of the deficiencies in the original description, and the doubts regarding the systematic assignation (*Cenoceras* or *Paracenoceras*) and the stratigraphic provenance (Lias or Dogger) of *N. truncatus*, Prinz [1906] proposed for the specimens of d'Orbigny the name *Nautilus subtruncatus*, previously used by Morris and Lycett [1850] for a Bathonian *Procyatoceras*. Pia [1914] proposed the new name *Nautilus anomphalus* for the nautiloids of d'Orbigny. Finally, Tintant [1994] redescribed this species on the basis of the recovered specimens of the d'Orbigny Collection. *Ligeiceras inornatum* (d'ORBIGNY, 1843) also has a small size, a subquadrate section and a nearly smooth surface, but exhibits depressed section and wider umbilici.

Distribution: From Lower Toarcian (part) to Aalenian of France and Spain. It has been also cited but not figured by different authors, such as d'Orbigny [1850], Giebel [1852] and Prinz [1906]. Tintant [1990] indicated that this species ranges from the Serpentinum zone to, probably, the Aalenian, and Tintant [1994] again considered this taxon vaguely as Toarcian. The specimens presented here have been collected in the Dispansum, Aalensis and Murchisonae zones of Muro de Aguas (G&C-887, G&C-888, G&C-889),

in the Aragonese branch of the Iberian ranges, in the Aalensis zone (Aalensis Subzone) of Camino (G&C-903), in the Cantabrian ranges, and in undetermined Toarcian levels of Vélez Rubio (IGME-693J).

Ligeiceras jureense (QUENSTEDT, 1846-49)

Plate II, I-K; Plate III, A-C.

1846-49 *Nautilus aratus jurensis* QUENSTEDT, p. 56, pl. 11, fig. 9.

1858 *Nautilus jurensis* QUENSTEDT, p. 284, pl. 41, fig. 1.

1914 *Nautilus jurensis* QUENSTEDT; Pia, p. 32 [14], 79 [61], pl. 4, fig. 2; pl. 5, fig. 2; pl. 9, fig. 2.

1956 *Cenoceras jurensis* (QUENSTEDT); Kummel, text-fig. 9 b. aff. 1987 *Cenoceras* (*Metacenoceras*) nov. sp. aff. *jurensis* (QUENSTEDT); Tintant, p. 72, pl. 1, fig. 1, text-fig. 2.

Type: Without designation.

Material and dimensions

	D	H (%)	B (%)	U (%)
G&C-866	109	655 (60)	775 (71)	.
G&C-901	804	387 (48)	658 (82)	93 (12)

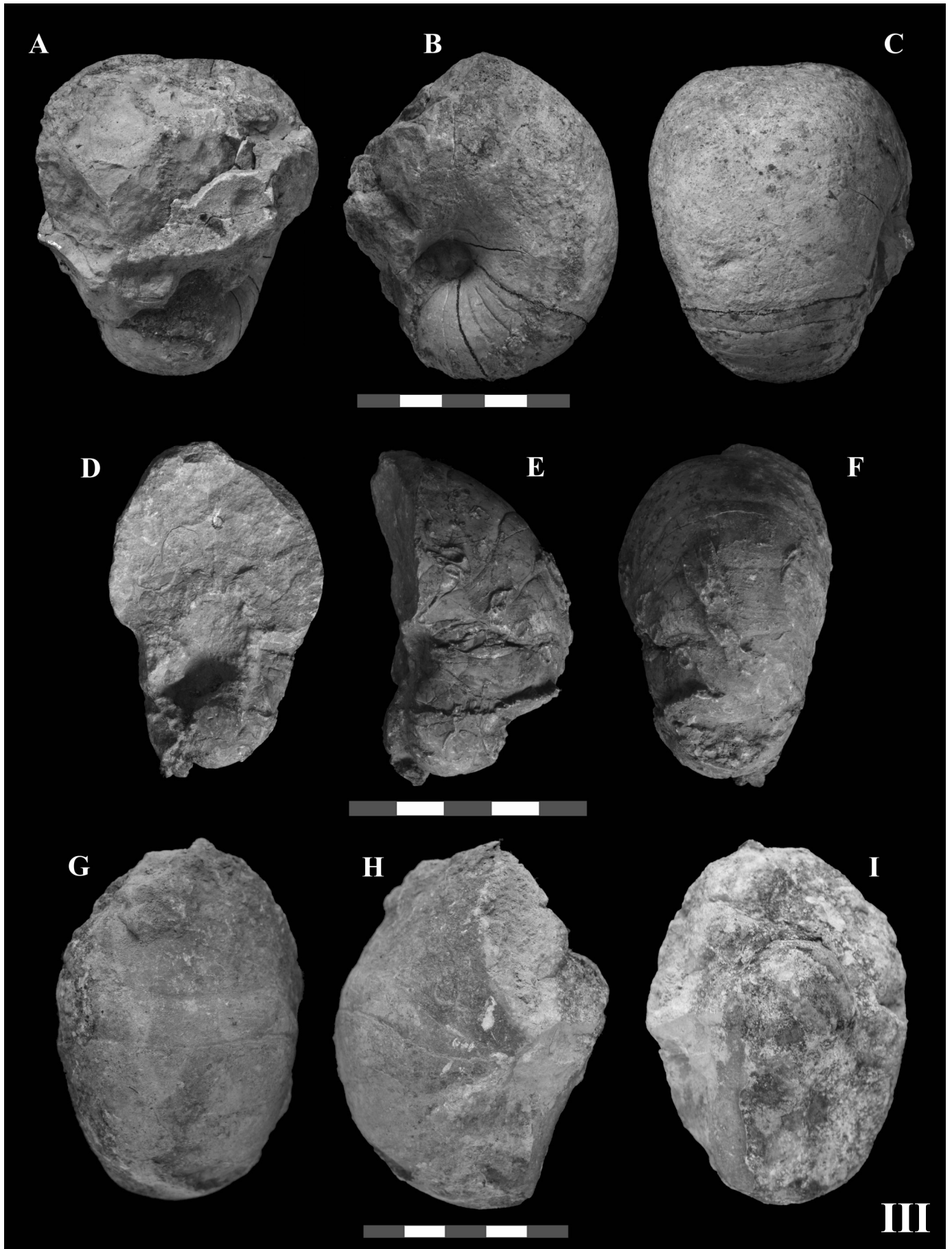
Description: Small to medium sized specimens with markedly depressed subtapered or subreniform section of rounded but conspicuous ventrolateral and umbilical margins, and markedly involute coiling. Their venter is tabulate or slightly arched, their flanks are flat or moderately convex, and their umbilici are considerably small and deep and have subvertical walls. The siphuncle is in a nearly central position over the septa. Each whorl has relatively plicate suture lines, with a wide and shallow lobe on the venter, and a retrogressive and deep lobe and a long and shallow saddle per side. The ornamentation is nearly non-existent.

Discussion: Quenstedt [1846, pl. 2, fig. 9; 1858, pl. 49, fig. 1] presented two notably different schematic figurations for this species and, therefore, Rulleau [2008] considered that the name *jurensis* should be avoided until a detailed revision of its types is carried out. *Ligeiceras inornatum* (d'ORBIGNY, 1843) is, probably, the closest species, but it has a smaller adult size, a more squared section and a wider umbilicus. The small specimens from the Lower Toarcian (Serpentinum zone) of Saudi Arabia classified by Tintant [1998] as *Cenoceras* (*Metacenoceras*) nov. sp. aff. *jurensis* (QUENSTEDT, 1846) has a more compressed section, a less arched venter, more straight suture lines and a lower siphuncle.

Distribution: From Lower Toarcian (part) to, possibly, Aalenian of Germany and Spain. It has been also cited but not figured in different countries, among them the UK (Yorkshire) by Tate and Blake [1876] and Austria (Adnet) by Prinz [1906], as reported by Pia [1914]. Tintant [1990]

PLATE III. – A-C, *Ligeiceras jurensis* (QUENSTEDT, 1846-49), specimen G&C-901, Serpentinum zone of Muniesa, apertural, lateral and ventral views. D-F, *L.? globulus* (RULLEAU, 2008), specimen CG-1136, Serpentinum zone of Turmiel, apertural, lateral and ventral views. G-I, *L.? globulus*, specimen LVD-287, Bifrons zone of Alvaizere, ventral, lateral and apertural views. Scale bars are 5 cm.

PLATE III. – A-C, *Ligeiceras jurensis* (QUENSTEDT, 1846-49), specimen G&C-901, zone à Serpentinum de Muniesa, vues aperturale, latérale et ventrale. D-F, *L.? globulus* (RULLEAU, 2008), specimen CG-1136, zone à Serpentinum de Turmiel, vues aperturale, latérale et ventrale. G-I, *L.? globulus*, specimen LVD-287, zone à Bifrons de Alvaizere, vues ventrale, latérale et aperturale. Échelle graphique : 5 cm.



indicated that this species ranges from the Variabilis zone to the Thouarsense zone and Branger [2004], on the basis of suggestions of the Groupe Français d'Etudes du Jurassique reported by Cariou and Hantzpergue [1997], extended its distribution until the Aalenian (Murchisonae zone). Nevertheless, the new specimens presented here have been collected in the Serpentinum zone of Ariño (G&C-866) and Muniesa (G&C-901), both located in the Aragonese branch of the Iberian ranges.

***Ligeiceras? globulus* (RULLEAU, 2008)**
Plate III, D-I

1998 *Cenoceras* (*Cenoceras*) *globulus* TINTANT (*in schedis*).
2008 *Cenoceras globulus* RULLEAU, p. 40, pl. 12, fig. 4, text-fig. 8/3.
Type: The holotype designated by Tintant is the specimen ML-8759 of the Dumortier Collection, collected, possibly, in the Middle Toarcian of La Verpillière, France, and nowadays held in the MCL.

Material and dimensions

	D	H (%)	B (%)	U (%)
G&C-867	379	.	305 (80)	.
G&C-872	~672	~368 (55)	~506 (75)	~96 (14)
G&C-893	237	115 (49)	166 (70)	~38 (16)
G&C-1134	645	~332 (52)	~487 (74)	.
G&C-1136	729	398 (55)	493 (68)	~10 (14)
LVD-287	805	~450 (56)	500 (62)	~95 (12)

Description: Small sized specimens, with depressed subsemicircular section and moderately involute coiling. Their venter, ventrolateral margins and flanks are arched, and their umbilici are deep and have suboblique walls and markedly rounded margins. Each whorl has numerous and scarcely plicate suture lines. The ornamentation is composed by growth lines and longitudinal striae.

Discussion: The globular aspect of this species makes it easy to differentiate them from other Toarcian nautiloid forms. Among them, *Cenoceras toarcense* (d'ORBIGNY, 1850) reaches larger adult size, wider umbilicus of more



FIG. 3. – Chronostratigraphic ranges of the collected specimens of the new genus *Ligeiceras* in the Cantabrian ranges: Camino section (A), and the external parts of the Iberian ranges: Muro de Aguas (B) and Fuentelsaz (C) sections. Zone abbreviations: DIS: Dispansum, PSE: Pseudoradosa, AAL: Aalensis, OPA: Opalinum. Subzone abbreviations: IN: Insigne, LE: Levesquei, PS: Pseudoradosa, MA: Mactra, AA: Aalensis, OP: Opalinum, CO: Comptum.

FIG. 3. – *Distribution chronostratigraphique des spécimens du nouveau genre Ligeiceras recueillis dans la Cordillère cantabrique : section de Camino (A), et les parties externes de la Cordillère ibérique : sections de Muro de Aguas (B) et de Fuentelsaz (C). Abréviations de zones : DIS : Dispansum, PSE : Pseudoradosa, AAL : Aalensis, OPA : Opalinum. Abréviations de sous-zones : IN : Insigne, LE : Levesquei, PS : Pseudoradosa, MA : Mactra, AA : Aalensis, OP : Opalinum, CO : Comptum.*

angulous wall, and more distant septa. *Digoniceras terebratum* (DUMORTIER, 1874) exhibit a wider umbilicus with conspicuous umbilical angle, and more sinuous suture lines.

Distribution: Toarcian of France, Spain and Portugal. Specifically, the French specimens come from the Bifrons and Thouarsense zones, the Spanish exemplars come from the Serpentinum zone of Ariño (G&C-867), in the Aragonese branch of the Iberian ranges, from undetermined Lower Toarcian levels of Maranchón (G&C-872), the Tenuicostatium zone (Semicelatium subzone) or Serpentinum zone (Elegantulum subzone) of Ribarredonda (G&C-893), and the Bifrons zone (G&C-1134) and Serpentinum zone (G&C-1136) of Turmiel, in the Castilian branch of the Iberian ranges, and the Portuguese specimens come from the Bifrons zone of Alvaizere, in the Lusitanian basin.

CONCLUSIONS

In the present work, the new genus *Ligeiceras* has been created to describe remarkably small and involute nautiloids with notably retrogressive suture lines. This group, seemingly, appeared after the biotic crisis of the end of the Tenuicostatium/Polymorphum zone, evolved during the radiation that began in the Early Toarcian Serpentinum/Levisoni zone and continued in the Late Toarcian, and survived, at least, until the Aalenian. New specimens from the Iberian peninsula (Basque-Cantabrian and Iberian basins, Spain, and Lusitanian basin, Portugal), belonging to the taxa *Nautilus fourneti* DUMORTIER, 1874 (selected as type species), *N. inornatus* d'ORBIGNY, 1843, *N. anomphalus* PIA, 1914, *N. jurensis* QUENSTEDT, 1846-49, and, with doubts, *Cenoceras globulus* RULLEAU, 2008, have been collected, described and assigned to this new systematic group. Although some of these species have already been cited in the literature, *L. fourneti*, *L. jurensis* and *L.? globulus* have

never been previously clearly described or illustrated, and their stratigraphic distribution has not been determined accurately for the Iberian peninsula. Specifically, *L. fourneti* has been identified in the Aalensis zone of the Aragonese and the Castilian branches of the Iberian ranges (Iberian basin). *L. inornatum* has been collected in the Serpentinum zone of the Aragonese branch, the Bifrons zone of the Castilian branch, and the Levisoni zone of the Lusitanian basin. *L. anomphalus* has been identified in the Aalensis zone of the Cantabrian ranges (Basque-Cantabrian basin), the Dispansum, Aalensis and Murchisonae zones of the Aragonese branch, and undetermined Toarcian levels of Vélez Rubio. *L. jurensis* has been collected in the Serpentinum zone of the Aragonese branch. Finally, *L.? globulus* has been identified in the Serpentinum zone of the Aragonese branch, undetermined Lower Toarcian levels, the Serpentinum and Bifrons zones of the Castilian branch, and the Bifrons zone of the Lusitanian basin. The morphological features and the stratigraphical distribution of the new genus *Ligeiceras* seem to confirm that dwarfism could have been a relatively generalized tendency in the Upper Toarcian of southwestern Europe, possibly mainly due to palaeoenvironmental causes.

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