BAJOCIAN LISSOCERATINAE (HAPLOCERATOIDEA, AMMONITIDA) FROM THE MEDITERRANEAN-CAUCASIAN SUBREALM

GIULIO PAVIA1* & SIXTO R. FERNANDEZ-LOPEZ2

1*Corresponding author. Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, 10125 Torino, Italy. E-mail: giulio.pavia@unito.it
2Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Calle José Antonio Novais 12, 28040 Madrid, Spain. E-mail: sixto@ucm.es


IntroductIOn

The Middle Jurassic genus *Lissoceras* Bayle (1879) and its microconchiate counterpart *Microlissoceras* Sturani (1971) constitute a relatively common Tethyan haploceratoid couple, whose palaeobiogeographical distribution extends to the whole Tethys-Panthalassa Realm with pandemic diffusion throughout the Tethyan subrealms (Mediterranean-Caucasian, Indo-Pacific, East-Pacific and Arctic-Pacific: Westermann 2000; Fernandez-Lopez & Pavia 2015). These taxonomic groups were monographed in successive ammonite assemblages (e.g., Sturani 1971; Galácz 1980; Fernandez-Lopez 1985; Sandoval 1986; Schlögl et al. 2005; Pavia 2007; Zaton 2010) from the lower Bajocian *L. semicoastatum* Buckman to the Middle Bathonian *L. ferrifer* (Zittel) and the middle Callovian *L. ovalense* (Oppel).

The number of species assigned to *Lissoceras* is limited through the whole biocoronalogical range of the taxon. Particularly, for the Bajocian Stage, the literature lists six species most of which show wide biocronostratigraphical distribution; for instance, the most classical and cited species *Lissoceras oolithicum* (d’Orbigny) is recorded from the middle to the upper part of the stage. Such seemingly poor diversity of species with wide distribution depends on two general factors: (1) the genus *Lissoceras* usually represents a small fraction within the Middle Jurassic ammonite assemblages, and this fact hinders definition of convincing interspecific differences; (2) the morpho-structural simplicity of the platycone shells

Keywords: Lissoceratidae; Middle Jurassic; systematics; phylogeny; palaeobiogeography.

Abstract. A revision of the Bajocian Lissoceratinae is presented. The study of more than 500 lissoceratins from different sites of the Western Tethys (Northwest European, Sub-Mediterranean and Mediterranean bioprovinces) within the Tethys-Panthalassa Realm provided data useful to implement the systematics of these almost neglected, never deeply analysed ammonites. Two genera, *Lissoceras* Bayle and *Semilissoceras* n. gen., are described with 16 species, among which eight new species (four dimorphic, three macroconchiate and one microconchiate): *L. submediterraneum*, *L. maizetense*, *L. ovale*, *L. sturanii*, *L. maerteni*, *S. ellipticum*, *S. turgidulum* and *S. costellatum*. The neotype of *L. oolithicum* is established. The microconchiate genus *Microlissoceras* is regarded as the junior synonym of the macroconchiate *Lissoceras*. Taxa are discussed according to four groups that gather taxa sharing common morpho-structural features. They roughly relate to successive biocronostratigraphical intervals within the Bajocian Stage and are headed by species largely known in literature: *S. semicostulatum* (Buckman) with suboval to compressed whorl section and rectiradiate ribs on the outer half flank; *L. oolithicum* (d’Orbigny) with subtriangular to ovate whorl section, large and depressed ventral saddle, large suspensive lobe; *L. haugi* Sturani with ovate to globular whorl section, narrow lobe E and suspensive lobe; and *L. psilodiscus* (Schloenbach) with highly compressed whorl section, high ventral saddle and narrow lobe E. The phylectic relation of *Lissoceras* and *Semilissoceras* to the Aalenian-Bajocian Bradfordia-group is discussed, regarding *Semilissoceras* as the known stem-taxon of the subfamily Lissoceratinae.

Received: May 24, 2018; accepted: November 16, 2018
and the reduction to absence of ornaments, mostly represented by growth lines visible only on the shell, make difficult the systematic study. Therefore, the species of *Lissoceras* accredited by literature appear to be long-ranging within the Bajocian, and in general the Middle Jurassic. This evidence has discouraged any taxonomic and biostratigraphical speculation that further reduces the interest on these fossils because of their low biochrononstratigraphical resolution power.

The collection of a huge quantity of lissoceratins, during more than twenty years from the Bajocian Fe-oolitic limestones of Calvados (NW France: Pavia 1994; Pavia & Martire 2010; Pavia et al. 2013; Fernandez-Lopez & Pavia 2015; Pavia et al. 2015; Fernandez-Lopez & Pavia 2016), provided material useful to implement the systematic study of these ammonites. The direct comparison of Calvados specimens with fossils from different sites of the Western Tethys (Northwest European, Sub-Mediterranean and Mediterranean provinces) contributes to improve the project and let’s furnish a more detailed and partially innovative picture of the interspecific patterns of the Bajocian lissoceratins.

The present paper deals with the revision of the lissoceratins described in the Bajocian literature and with the proposition of new generic and specific taxa based on architecture, morphology and suture parameters. Further contributes concern the possible evolutive lineages within the subfamily Lissoceratinae and the phyletic relationship with Bradfordininae taxa.

Material and Methods

This study is based on the Bajocian ammonites coming from different stratigraphical contexts mainly pertaining to the central and western European and the Mediterranean areas known in literature within the Mediterranean-Caucasian Subrealm (Fernandez-Lopez & Pavia 2015; Pavia & Fernandez-Lopez 2016). Other morpho-structural studies published on lissoceratins integrate the systematic analysis leading to the definition of the species cited in this work (see the synonyms of the described taxa). Reviews on dimorphism, heterochrony, life-history strategies, and macroevolution in ammonoids have been published by Gould (1977, 2002), Callomon (1985), Dommergues et al. (1986, 1989), Dommergues (1990), Guex et al. (2003), Guex (2006, 2016), McNamara (2012), Ritterbush & Botjer (2012), Ritterbush et al. (2014) and Klug et al. (2015a, b), among others.

More than five hundred specimens of Bajocian lissoceratins are recorded in Appendix. They come from the outcrops listed below according to their palaeobiogeographical pertinence: 1 to 7 and 10, Northwest European Province (NW); 8-9 and 11-14, Sub-Mediterranean Province (SM); 15-16, Mediterranean Province (M); 17, Caucasian and North-Eastern Tethyan provinces (NET).
Bajocian Lissoceratinae from the Mediterranean-Caucasian Subrealm

Deux-Sirres, W France

Branger (1989) deeply described the Bajocian calcareous successions of this area.

8) Echiré, Malvalt, Thorigné, Viaduct de l'Egray. Patrick Branger (Cherveux) provided information and photographic reproduction of some specimens from the first three sites. As to the temporary outcrop at l'Egray, Gauthier et al. (2002) distinguished thirty-four beds referred to the Aalenian and Bajocian stages. The writers collected the fossils listed in Appendix according to their stratigraphical log.

Iberian Range, north-eastern Spain

9) Bajocian ammonite fossil assemblages from the outcrops of Masada Toyuela (Albarracin), Moscardon, Rambil La Gotera (Salden), Embalse San Blas (Gaude) and Cella (Teruel province) were studied by Fernandez-Lopez (1985, 2011a, 2012, 2014). The biostratigraphical and sedimentological features of the Bajocian and Bathonian deposits at Rielo (Zaragoza province) were described by Fernandez-Lopez & Aurell (1988).

Different sites in Germany länder

10) Bielefeld in the Nordrhein-Westfalen Länder. The fossiliferous locality and its ammonite assemblage were described by Wetzel (1911, 1950) and referred to as the Parkinsoni- and the Wuerttembergia-Schichten at the Bajocian-Bathonian transition.

11) Bopfingen, Eningen, Mössingen in the Baden-Württemberg Länder. The Bajocian successions of these sites in the Swabian Alb are well known in literature (e.g. Buck et al. 1966; Dietze & Dietl 2006, and references therein). The specimens listed in the present paper were described by Quenstedt (1858, 1886-87) and further illustrated by Schlegelmilch (1985).

12) Sengenthal in the Bavaria Länder. The classical paper of Callomon et al. (1987) describes in detail the succession at the Bajocian-Bathonian transition. Dietze et al. (2017b, and references therein) updated stratigraphical information on the Sengenthal Fm. The writers studied the fossils listed in Appendix according to their stratigraphical log.

Alpes-de-Haute-Provence, SE France

Two palaeostructural sectors distinguish the Bajocian successions: in the northern area the thick “Marno-calcaires à Cancellophycus” Formation is representative of the French Subalpine Basin (Graciansky et al. 1982, 1993; Pavia & Zunino 2012) whereas the calcareous facies develop southwards in the Provence Platform sector (Kerekhove & Roux 1976; Olivero 2007; Fernandez-Lopez et al. 2009a, b; Mariotti et al. 2012).

13) Bas Auran, Chaudon, La Palud. Fernandez-Lopez et al. (2009b, and references therein), Pavia & Zunino (2012, and references therein) and Innocenti et al. (1989) respectively described these Bajocian and Bathonian basin successions: their numberings are adopted for the lissoceratins described in the present paper.

14) Chiran, Teillon. The localities lay south- and westwards of Castellane and pertain to the Provence platform structural sector. Both fossiliferous sites are almost unknown and span respectively the Laeviuscula to Humphriesianum zones and the Garantiana to Parkinsoni zones. G. Pavia got field data respectively after suggestion by F. Atrops (Lyon) and Manassero’s thesis (1992).

Southern Alps, NW Italy

The “Paisosanna alpina beds” represent a well-defined, though discontinuous unit between the Toarcian-Aalenian San Vigilio Group and the upper Bajocian-Tithonian Rosso Ammonitico Formation in the Trento Plateau (Martire et al. 2006; Dietze et al 2017a, and references therein).

15) Several localities (Gelpach, Longara, Monte Meletta, Rotherbrunn, Troch) in the Asiago district provided rich fossil assemblages at the passage lower to upper Bajocian that were masterfully described by Sturani (1971).

Bakony Mountain, W Hungary

Galácz (1980) described several lissoceratins coming from the calcareous Rosso Ammonitico facies of Bajocian to Bathonian age.

16) Gynespuszta is the best-known site for Bajocian fossil assemblages.

North Caucasus (S Russia) and Great Balkhan (W Turkmenistan)

Besnosov & Mirta (1998 and 2000 respectively) discussed the ammonite assemblages of those basinal deposits in which lissoceratins are frequently represented.

17) Taxa cited from the Bajocian sites of the basin of the Kuban River, Zelenchuk District (Djangura Formation of Karach-Cherkessia, MItta & Sherstyukov 2014), Daturna, Akhvakhshtab, Gigatliurukh villages and Baceio mount (Tsudakhar Formation of Dagestan, Besnosov & Mirta 1993, 1998) on North slope of Caucasus, along with those of Chaloi and from the district southwards of the wells Karaman and Shorf (Tsudakhar Member of western Turkmenistan, Besnosov & Mirta 2000) on Great Balkhan could be directly compared by measurements with the material studied in the present paper.

The biochronostatigraphical rank assigned to each stratigraphical unit listed as “source” in Appendix derives from the literature related to the fossiliferous sites. The biochronostatigraphy scheme follows the classification proposed by Rioult et al. (1997) as it is accepted almost unanimously (see Sandoval et al. 2001, 2002; Callomon 2003; Pavia & Fernandez-Lopez 2016, and references therein). The standard ammonite zonation of the Bajocian Stage for the Mediterranean-Caucasian Subrealm is as follows from bottom up: (lower Bajocian) Diseites, Laeviuscula, Propinquans (nearly equivalent to Sauzei) and Humphriesianum (Romaini, umbilicile, Blagdeni subzones) zones; (upper Bajocian) Niortense (Banksi, Polygyralis, Baculata subzones), Garantiana and Parkinsoni zones.

A taphonomic analysis has been carried on the specimens directly studied by the writers. According to the diverse mechanisms of taphonomic alteration (Fernandez-Lopez 1991, 1995, 2007, 2011a, b; see also Fernandez-Lopez & Pavia 2015; Pavia et al. 2013, 2015) ammonites were distinguished between resedimented and reeleraborated (sensu Fernandez-Lopez 1991) fossils. Resedimented specimens correspond to taphonomic elements displaced on the sea floor prior to the burial; therefore, they are coeval to the encasing sediments. In contrast, reeleraborated specimens represent taphonomic elements exhumed and displaced on the sea floor before the final burial; therefore, with respect to the encasing sediments, they can be older than the event sedimentation or coeval to the background sedimentation, respectively. Such analysis results to be of fundamental importance for defining the biochronological interval of each taxon treated in this paper.

The morpho-structural terminology used in the following descriptions follow the glossary of the Treatise on Invertebrate Paleontology (Arkell et al. 1957) and other terms presented by Westermann (1996, 2005) and by Fernandez-Lopez (2014). Ammonite abbreviations and measurements in mm used in the text and in Appendix are as follows: shell diameter (D) at which the measurement was made on the body chamber (ch) or phragmocone (ph); whorl height (H); whorl width (W); umbilical diameter (U); whorl height/diameter ratio (h = H/D x100); whorl width/diameter ratio (w = W/D x100); umbilical diameter/diameter ratio (u = U/D x100); whorl width/whorl height ratio (W/H x100). The % values of h, w and u are also detailed in Appendix.
The palaeontological material described herein is housed in different public institutions or private collections with appropriate acronyms and sequential registration numbers: (AB) Alain Bonnet’s collection at Lasson, France; (BGS) British Geological Survey at Nottingham, Great Britain; (AB, CE, EB, G, M, MT, RC) Sixto R. Fernandez-Lopez at Madrid, Spain; (EM) Ecole Nationale supérieure des Mines at the University of Lyon, France; (FN) Fred Neurbauer’s collection at Balmannsweiler, Germany; (FSL) Collection Stratigraphique at the University of Lyon, France; (IGPT) Institut und Museum für Geologie und Paläontologie at the University of Tübingen, Germany; (IPM) Museum d’Histoire Naturelle at Paris, France; (J) Jurassic collection at the Eötvös Rolando University of Budapest, Hungary; (LM) Lionel Maerten’s collection at Ver-sur-Mer, France; (MG) Martin Görlich’s collection at Aldorf, Germany; (MAP) Museo Aragonés de Paleontología, Teruel, Spain; (MGP-PD) Museo di Geologia e Paleontologia at the University of Padova, Italy; (MSN-UP) Museo di Geologia e Paleontologia at the University of Pisa at Calc, Italy; (MGUPT-PU) Museo di Geologia e Paleontologia at the University of Torino, Italy; (MRSN) Museo Regionale di Scienze Naturali di Torino, Italy; (PB) Patrick Branger’s collection at Cherveux, France; (Sh-SL) Wessex Cephalopod Club Collection, London; (SMNS) Staatliches Museum für Naturkunde in Stuttgart, Germany; (UPMC) Université Pierre et Marie Curie of Paris, France; (VM) Palaeontological Institute of Russian Academy of Sciences in Moscow, Russia.

Lissoceratinae show a simple morphology without elements that may be definitively distinctive for taxa (neither ribbing except in a few cases nor keels and furrows) so that the possibility of taxonomic distinction is mainly reduced to the morpho-structural parameters and, where visible, the suture lines. In the present paper, the latter have been drawn everywhere possible. The architectural parameters and, where visible, the suture lines. In the present paper, the latter have been drawn everywhere possible. The architectural parameters and, where visible, the suture lines. In the present paper, the latter have been drawn everywhere possible. The architectural parameters and, where visible, the suture lines.

**Systematic Palaeontology**

**Class Cephalopoda** Cuvier, 1798

**Subclass Ammonoidea** von Zittel, 1884

**Order Ammonitida** Fischer, 1882

Superfamily Haploceratoidea von Zittel, 1884

Family Lissoceratidae Douvillé, 1885

Subfamily Lissoceratinae Douvillé, 1885

**Discussion.** The family Lissoceratidae (early Bajocian-middle Oxfordian: cf. Callomon in Donovan et al. 1981) was repeatedly treated in literature after Douvillé’s proposition. In general, it was synonymized by priority in favour of the family Haploceratidae Zittel, 1884 (e.g., Arkell 1951-1958; Arkell et al. 1957; Sturani 1971; Galácz 1980), whose typical representatives are aged to the Kimmeridgian-Hauterivian (cf. Callomon in Donovan et al. 1981) or reduced to a subfamily rank within the Haploceratidae (e.g., Fernandez-Lopez 1985; Sandoval 1986). Nevertheless, despite the morpho-structural similarities of *Lissoceras* Bayle, 1879 and *Haploceras* Zittel, 1870, the upper Oxfordian biostratigraphical gap between these two morpho-groups hinders from clarifying the phyletic relationships among the Middle and Late Jurassic haploceratoid taxa; possibly, such relationships do not exist, and the latter taxon developed analogous features deriving from a Late Jurassic haploceratoid independent of lissoceratids. Consequently, we follow Pavia’s proposition (1983, p 73; see also Zaton 2010, p. 94) that confirmed the lissoceratids at family rank after Douvillé (1885). In this systematic arrangement the subfamily Bradfordiinae (Callomon in Donovan et al. 1981) is also comprised that is represented by the late Aalenian to early Bajocian *Bradfordia* Buckman, (1910) with several subgenera (Sandoval 1986) or linked genera (Fernandez-Lopez 1985). Bradfordiinae span from the *Bradfordia*-group, supposed to be derived from late Aalenian hammatoceratids (Arkell et al. 1957, p. L274; Elmi 1967, p. 779; Geczy 1967, p. 224; Westermann 1969, p. 49-52; Sapunov 1971, p. 74; Galácz 1980, p. 55; Callomon in Donovan et al. 1981, p. 143; Fernandez-Lopez 1985, p. 173; Sadki 1989, p. 239) or graphoceratids (Sturani 1971, p. 89; Sandoval 1986, p. 451) to the early Bajocian taxa, in which the elevated umbilical edge common in the genus becomes feeble, indistinct or rounded. This last feature, beside the smooth and rounded venter, the peripheral ornamentation and some suture elements, such as the high and asymmetric saddle L/U2, supports the phyletic continuity between *Bradfordia* and *Lissoceras* in the earliest Bajocian (cf. Schindewolf 1965 in 1961-68) possibly via “Lissoceras” *semicostatum* Buckman (Arkell et al. 1957, p. L274; Sturani 1971, p. 90; Imlay 1973, p. 77).

*Lissoceras* Bayle, 1879 and *Lissoceratoides* Spath, 1923 are synonymized because the presumed gap between the two taxa at the passage Callovian-Oxfordian has been demonstrated to be inconsistent (Sandoval 1986, p. 438, and references therein).

Sturani (1971) and Fernandez-Lopez (1985; see also Sandoval 1986) indicated that *Taxambyites* Buckman, 1924 in 1909-1930, *Stegocyclites* Buckman, 1924 in 1909-1930 and *Poecilomorphus* Buckman,
1889 in 1886-1907 should be assigned to Haploceratidae, and thus to Lissoceratidae according to the preceding discussion. Sturani (1971, p. 90) also suggested the possibility that Toxamblyites derived in the earliest Bajocian from “Lissoceras” semiconcavatum, more likely than from some Bradfordia. If such phyletic lineage would be confirmed, Bradfordia L.s. assumes the role of stem-taxon of the whole Bajocian haploceratoids, which should pertain to the single family Lissoceratidae Douvillé 1895. The morpho-structural and biochronological continuity between the forms headed to Bradfordia and Lissoceras prevents the opportunity to separate these haploceratoids into the subfamilies Bradfordiinae Callomon 1981 and Lissoceritidae Douvillé 1885. However, waiting for a revision of bradfordiins, we prefer to maintain their distinction.

Dimorphism is well developed within lissoceratids. For the Bajocian, mainly based on Sturani’s paper (1971), the microconch Protococotraustes Spath, 1928 in 1927-1933 (presumed counterpart of Bradfordia l. s.), Microlisoscceras Sturani, 1971, Microcacoecilemoropus Sturani, 1971 and Microtoxamblyites Sturani, 1971 are accredited within the Lissoceratidae (Sandoval 1986). Some lissoceratins treated in the present paper are discussed as dimorphic pairs with distinction of [M] and [m] when both the morpho-structural features and the biochronological data support this solution; it is the case of L. inflatum, L. submediterraneum, L. sturanii and L. bangi. Other species are represented only by macroconchs ([M], e.g. L. oolithicum) or microconchs ([m], L. maerteni and L. pusillum) and are described in separate sheets waiting for future pairings. Such dimorphic evidence lets to group the lissoceratins treated herein in the single genus Lissoceras Bayle, 1879 and to regard the taxon Microlisoscceras Sturani, 1971 as junior synonym of the former.

**Genus Lissoceras Bayle, 1879**

**Synonym:** Lissoceratoids Spath, 1923; Microlissoceras Sturani, 1971

**Type species:** Lissoceras isidicus (Schloenbach, 1865) by original designation.

**Other species included:** Beside the type species, the genus Lissoceras comprises at least ten Bajocian species from the Mediterranean-Caucasian Subrealm. Five available species: L. inflatum Wetzel, L. oolithicum (d’Orbigny), L. melitensis (Parona), L. bangi Sturani and L. pusillum Sturani and five new species: L. submediterraneum, L. maerteni, L. ovale, L. sturanii and L. maerteni. The East-Pacific species L. bakeri Imlay (1962, p. A6, pl. 1, figs 1-6, 9-12), from the Bowser Member of the lower Tuxedni Formation, at Cook Inlet, Iniskin peninsula, S Alaska, upper Bajocian, Rotundum Zone, also belongs to this genus. Other available species referable to Lissoceras belong to the macroconch group such as L. badamui Seyed-Emami (1988, p. 78, figs 25-26) from the Badamu Formation at western Kerman, central Iran, lower Bajocian, Saueri Zone, and L. oolithicum Zaton & Marynowski (2006, p. 434, figs 3.11-13, from the uppermost Bajocian (Parkinsoni Zone, Bomfordi Subzone) and Lower Bathonian (Tenuiplicatus Zone) at Kawodrza Gorna, south-central Poland.

**Description.** Dimorphic taxon of small to medium size with macroconchs up to 200 mm (the early Bathonian L. magnum Galácz, 1980 and L. compressum Schlögl et al., 2005) and microconchs possibly reaching 50 mm (the dimorphic pair of L. magnum Galácz in the lower Bathonian of Bas Aur, Alpes-de-Haute-Provence: G. Pavia, field data). Macroconchs bear simple or sinuous aperture, and microconchs develop lateral lappets. Adult body chamber length between a half and three-quarters of the last whorl. The ontogenetic maturity is indicated by the uncoiling of the umbilical seam, with decreasing compression of the whorl section, associated with crowding and simplification of the last septal sutures.

Macroconchs are evolve to mid-involute, discocones to platycones or planorbicones, with compressed, ovate to subcircular or subtriangular whorl section (W/H= 130-45%), which becomes less compressed in the adult stage. The umbilicus is narrow (U/D= 15-45%), relatively deep, with steep wall and rounded edge. The flanks are gently convex to rounded, and converge to a convex, unkeeled venter, sometimes with flat ventral area and angular ventro-lateral margin. Ornamentation constituted by sigmoid and falcoide growth lines with peripheral projection, usually visible only on the shell. The suture line is quite simple to relatively complex, with short lobe E, very deep lobe L, saddle L/U asymmetrical and significantly higher than E/L, wide suspensive lobe with 3-4 auxiliary saddles (Fig. 1).

Microconchs are evolve platycones with shallow umbilicus. Whorl section compressed, oval or elliptical. Short umbilical wall. Convex venter. Ornamentation usually very reduced and represented by sigmoid growth lines that may show occasional relief in the middle flank. Aperture with pointed to stout lateral lappets and small ventral rostrum. The suture line has been described in very few cases (cf. Seyed-Emami 1988, fig. 10; Zaton & Marynowski 2006, fig 4c).
Remarks. The following systematic descriptions are organized according to morpho-structural groups that gather taxa showing some common features. These groups roughly relate to diverse bi-ochostron stratigraphical intervals and are headed by species largely known in literature: *Lissoceras psilodiscus*, highly compressed whorl section, narrow E and high ventral saddle; *L. oolithicum*, subtriangular to ovate whorl section, large and depressed ventral saddle at the bottom of lobe E, large suspensive lobe; *L. haugi*, depressed, ovate to globular whorl section, narrow E and suspensive lobe; “*L.* semicosulatum”, suboval to compressed whorl section, with rectiradiate ribs on the outer half-flank, is assigned here to the new lissoceratin genus *Semilissoceras*.

Dimorphic partnership for Middle Jurassic Lissoceratinae was definitively asserted since the institution of the taxon *Microlissoceras* Sturani, 1971 (type-species *M. pusillum* Sturani, 1971 by original designation) that gathered the microconchiate specimens coupling the macroconchiate *Lissoceras* of which it is regarded herein as the junior synonym of the former to constitute a dimorphic taxon. However, there is a still open question concerning the possible equivalence of the Bajocian-Callovian *Lissoceras* erato and *Glochiceras nimbatum* that would state the priority of *Glochiceras* on “*Microlissoceras*”.

Distribution. The earliest known representatives of macroconchiate *Lissoceras* date to the early Bajocian, Humphriesianum Chron: the most accepted founder by literature is *L. oolithicum* (d’Orbigny). The latest “classical” *Lissoceras* is *L. voultense* (Oppel 1862-1863) from the lower-middle Callovian (Galácz 1980, 2015; Sandoval 1986, 2016; Baborshkin et al. 2010). The taxon formerly referred to *Lissoceratoides*, such as *L. erato* (d’Orbigny, 1850), enlarge the distribution of the genus up to the upper Oxfordian (Enay & Gauthier 1994; Schlögl et al. 2009; Parent & Garrido 2015). Bajocian microconchiate *Lissoceras* are rarely reported in literature. Records of microconch lissoceratins are from the Bajocian-Bathonian transition in northern Germany (Westermann 1958, p. 55), in southern Poland (Zaton & Marynowski 2006, p. 434; Zaton 2010, p. 94) and in Great Balkan (Besnosov & Mitta 2000, p. 51), the basal upper Bajocian of Dorset (Parsons 1976, p. 126), Calvados (present paper) and the Iberian Range (Fernandez-Lopez 1985, p. 171), the top lower Bajocian on the Southern Alps (Surani, p. 1971) and the mid-lower Bajocian in Central Iran (Seyed-Emami 1988).

The palaeobiogeographical distribution of Bajocian *Lissoceras* spreads to the whole Tethys-Panthalassa Realm (Fig. 2) with pandemic diffusion throughout the different Tethyan subrealms (Westermann 2000):

1) Mediterranean-Caucasian Subrealm:

1a) NW European Province (d’Orbigny 1845 in 1842-1851; Schloenbach 1865; Bayle 1878; Buckman 1893 in 1886-1907; Buckman 1923 and 1925 in 1990-1930; Douvillé 1913; Wetzel 1950; Arkell...

1b) Sub-Mediterranean Province (Oppel 1862-63; Quenstedt 1886 in 1886-1887; Douvillé 1885; Bataller 1922; Fallot & Blanchet 1923; Dorn 1927; Roman & Pétouraud 1927; Stephanov 1927; Roman & Pétouraud 1927; Douvillé 1923; Pavia 1973, 1983, 2007; Fernandez-Lopez 1985; Schlegelmilch 1985; Cali- lomon et al. 1987; Sadki 1989, 1996; Galácz 1980, 1985, 1994, 1995b, 1999; Sand- oval 1986; Pavia & Cresta 2002; Schlögl et al. 2005; Hotsanyuk & Leschuch 2006; Bahrouni et al. 2016);


Mitta & Sherytuykov 2014);


2) Indo-Pacific Subrealm:

2a) Ethiopian Province (Douvillé 1916; Parnes 1988; Khalil 2003; Galácz 2015);

2b) Himalayan Province (Callomon & Rose 2000).

3) East-Pacific Subrealm:

3a) Andean Province (Stehn 1923; Covacevich & Piracés 1976; Sandoval & Westermann 1986; Fernandez-Lopez & Chong 2014);

3b) Shoshonean Province (Imlay 1973, 1986; Taylor 1988, 2014);

3c) Athabascan Province (Imlay 1962, 1964, 1982).

4) Arcto-Pacific Subrealm:

West Pacific Province (Sey & Kalacheva 1980, 2000; Sey et al. 2004).

Moreover, iterative Bajocian and early Bathonian events of occasional biodispersal along the western areas of the North Pacific into the Arctic–North American Province (Tuchkov 1972; Meledina 1991, 2014; Westermann 1992; Zakharov et al. 2018) support the pandemic distribution of lissoceratins in the Tethys-Panthalassa and Panboreal realms.

**Lissoceras psilodiscus** (Schloenbach, 1865) [M]

Figs 3, 4; Pl. 1, figs 12, 16

1852 *Ammonites Era* - Kudernatsch, p. 10, pl. 2, figs 7, 8 (only).

1865 *Ammonites psilodiscus* sp. nov. Schloenbach, p. 31, pl. 26, fig. 6.

1967 *Lissoceras psilodiscum* - Sturani, p. 23, pl. 3, fig. 17, pl. 4, fig. 11.

1968 *Lissoceras psilodiscum* - Hahn, p. 66, fig. 10, pl. 4, figs 1-2.

1980 *Lissoceras psilodiscum* - Galácz, p. 58, text-fig. 45, pl. 12, figs 1, 3 (cum syn., pars).

1985 *Lissoceras psilodiscum* - Fernandez-Lopez, p. 161 (pars; non text-fig. 15, 16/F, pl. 15, fig. 3 = *L. submediterraneum* n. sp.).

1986 *Lissoceras psilodiscum* - Sandoval, p. 440, text-fig. 4, pl. 1, figs 8-10 (cum syn.).

1998 *Lissoceras (Lissoceras) psilodiscus* - Besnosov & Mitra, p. 23, pl. 8, figs 5-7.

2005 *Lissoceras psilodiscus* - Schlögl et al., p. 342, pl. 3, figs 2, 3.

v 2008 *Lissoceras psilodiscus* - Pavia et al., p. 294.

**Diagnosis:** Sturani’s (1967) and Hahn’s (1968) papers allow compounding a diagnosis in absence of the original one: macroconchiate *Lissoceras*; discoidal, smooth shell, whorl section high, lanceolate with rounded venter, narrow umbilicus.

**Types:** Schloenbach (1865) stated that Kudernatsch’s specimen (1852, pl. 10, fig. 7, 8) represents the new taxon *Ammonites psilo- discus*.

**Material:** For the present research, only some selected specimens of *L. psilodiscus* from the uppermost Bajocian (Parkinsoni Zone)
and lowermost Bathonian (Zigzag Zone) have been studied, just to allow comparison with the Bajocian species *L. inflatum*. They come from outcrops of the Sub-Mediterranean Province: three specimens from Sengenthal in Bavaria, 13 specimens from different sites of the Alpes-de-Haute-Provence.

**Measurements**: See Appendix. Measured extremes for diameter: 24.7 - 74.6 mm. Values for h, w and u are summarized in Table 1.

**Description.** Many papers treated the species *Lissoceras psilodiscus*. For morphological description and details on the suture line we can refer to Hahn (1968), Galácz (1980) and Sandoval (1986).

**Remarks.** Wetzel (1950) distinguished the species *L. inflatum*, with two subspecies *decoratum* and *intrasculptum* that differentiate from *L. psilodiscus* for the larger whorl section. Hahn (1968) did not accept this proposition due to morphological continuity of these forms. Nevertheless, *L. psilodiscus* and *L. inflatum* differ by whorl section (Figs 3, 4), suture line and biochronostatigraphical position, so that it appears necessary to separate them at species rank as it discussed below.

**Distribution.** *L. psilodiscus* is a representative lower Bathonian ammonite distributed everywhere in the Mediterranean-Caucasian Subrealm. Doubtful records, however, are from the Bathonian at the Andean province in East-Pacific Subrealm (Stehn 1923) and Indonesia in the southwestern Pacific areas (Callomon & Rose 2000). The oldest record of *L. psilodiscus* is from the topmost Bajocian of the la Palud section in Alpes-de-Haute-Provence (Innocenti et al. 1990). Sturani (1967) reports the youngest specimens from the upper part of the lower Bathonian.

**Lissoceras inflatum** Wetzel, 1950 [M & m]

Figs 3-5; Pl. 1, figs 1-11, 13, 15, 17

1845 *Ammonites oolithicus* - d’Orbigny 1842-51, p. 383, pl. 124, fig. 3 (only).

1885 *Lissoceras psilodiscus* Douvillé, p. 34, text-fig. 14.

1886 *Ammonites complanatoides* Quenstedt 1886-87, p. 644, pl. 75, fig. 27 (only).

1913 *Lissoceras psilodiscus* - Douvillé, p. 72, text-fig. 5.

1913 *Lissoceras inflatum* - Roman & Petouraud, p. 48, pl. 5, figs 12, 14.

1927 *Lissoceras oolithicum* - Roman & Petouraud, p. 126.

1950 *Lissoceras inflatum* n. sp. Wetzel, p. 11, pl. 8, fig. 6.

1950 *Lissoceras inflatum decoratum* n. ssp. Wetzel, p. 11, pl. 8, fig. 7.

1976 *L. (L.) psilodiscus inflatum* - Parsons, p. 126.

1985 *Lissoceras psilodiscus* - Schlegelmilch, p. 68, pl. 21, fig. 3.

1994 *Lissoceras oolithicum* - Rioult in Fischer, p. 112, pl. 48, fig. 3.

2000 *Lissoceras oolithicum* - Besnosov & Mitra, p. 51, pl. 1, fig. 9.

2011 *Lissoceras oolithicum* - Rulleau, p. 68, pl. 30, fig. 1.

---

Tab. 1 - Synthesis of measurements and regression statistics for *Lissoceras psilodiscus* (Schloenbach, 1865), [M].

![Fig 3](image_url) - Plots of measurements for *Lissoceras psilodiscus* (Schloenbach), *L. inflatum* Wetzel and *L. submediterraneum* n. sp. with ontogenetic trajectories through ratios of the aperture shape (W/H). A) Whorl width/whorl height ratio (W/H x 100) versus shell diameter (D). B) Whorl width/whorl height ratio (W/H x 100) versus umbilical ratio (U/D x 100). Abbreviations: M, macroconch; m, microconch; h, holotype.
Diagnosis: The short description by Wetzel (1950) is a clear diagnosis for this species: macroconchiate and microconchiate *Lissoceras*; large, oval and lanceolate whorl section with steep umbilical wall.

Types: The syntype figured by Wetzel (1950, pl. 8, fig. 6) is here regarded as the lectotype of the species *L. inflatum*. It was housed at the Kiel Museum (Wetzel 1950, pl. 8, fig. 6 caption). At present, the type result to be missing in the palaeontological collections of the Geological Department of the Kiel University, possibly lost in the postwar reconstruction (personal communication by Mathias Alberti, Kiel). Many syntypes formed the type-series of “*Lissoceras inflatum* n. sp.” (Wetzel 1950, p. 11): 3 from Eimen and 14 from Bielefeld outcrops (originally housed in the Göttingen and Kiel collections, respectively) that were biochronologically referred to the passage Bajocian to Bathonian (obere Parkinsonien-Schichten and untere Württembergica-Schichten). Although the type is missing at present, the proposition of a neotype is not allowed for two reasons: it may be possible to find some residual syntypes in the future, and the differences between *L. psilodiscus* and *L. inflatum* are sufficiently clear (ICZN, art. 75c).

Material: Seventy-eight macroconch specimens from the upper Bajocian of different palaeobiogeographical sectors have been scheduled: 68 resedimented and reelaborated fossils from Calvados (67) and Dorset (1) sites, two resedimented fossils from the Iberian Range, two undefined fossils from Bielefeld (1) and Mössingen (1) in north and south Germany, five resedimented fossils from different sites in Asiago, Italian Southern Alps, two specimens from Gye-nespusza in Hungary. Five microconchs are added from the site of Sainte-Honorine-des-Pertes in Calvados.

Measurements: See Appendix. Measured extremes for diameter: [M] 8.5 - 76.0 mm; [m] 12.7 - 16.6 mm. Values for h, w and u are summarized in Table 2.

Description. Medium-sized ammonites with compressed, slightly rounded shell, steep umbilical wall and mid-open umbilicus. Dimorphism is well documented.

Tab. 2 - Synthesis of measurements and regression statistics for *Lissoceras inflatum* Wetzel, 1950, [M & m].

<table>
<thead>
<tr>
<th><em>L. inflatum</em> [M]</th>
<th>h = H/D x 100</th>
<th>w = W/D x 100</th>
<th>u = U/D x 100</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>105 measures</td>
<td>43.2 - 54.1</td>
<td>20.0 - 34.1</td>
<td>22.1 - 27.5</td>
<td>53.0 - 76.1</td>
</tr>
<tr>
<td>mean of 105</td>
<td>47.59</td>
<td>28.65</td>
<td>24.95</td>
<td>60.66</td>
</tr>
<tr>
<td>standard deviation</td>
<td>1.81</td>
<td>2.08</td>
<td>1.34</td>
<td>3.98</td>
</tr>
<tr>
<td>standard error</td>
<td>0.18</td>
<td>0.20</td>
<td>0.13</td>
<td>0.39</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>43.97 - 51.21</td>
<td>24.49 - 32.81</td>
<td>22.27 - 27.63</td>
<td>52.70 - 68.62</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>47.23 - 47.95</td>
<td>28.25 - 29.05</td>
<td>24.69 - 25.21</td>
<td>59.88 - 61.44</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>R² = 0.98 - y = 0.58x + 0.27</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><em>L. inflatum</em> [m]</th>
<th>h = H/D x 100</th>
<th>w = W/D x 100</th>
<th>u = U/D x 100</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 measures</td>
<td>42.5 - 45.3</td>
<td>22.8 - 27.1</td>
<td>27.6 - 30.0</td>
<td>52.2 - 60.0</td>
</tr>
<tr>
<td>mean of 5</td>
<td>44.36</td>
<td>24.64</td>
<td>28.64</td>
<td>55.60</td>
</tr>
<tr>
<td>standard deviation</td>
<td>1.14</td>
<td>1.66</td>
<td>1.06</td>
<td>2.99</td>
</tr>
<tr>
<td>standard error</td>
<td>0.51</td>
<td>0.74</td>
<td>0.47</td>
<td>1.33</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>42.08 - 46.64</td>
<td>21.32 - 27.96</td>
<td>26.52 - 30.76</td>
<td>49.62 - 61.58</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>43.34 - 45.38</td>
<td>23.16 - 26.12</td>
<td>27.70 - 29.58</td>
<td>52.94 - 58.26</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>R² = 0.98 - y = 0.70x - 0.90</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Macroconchs [M] - The whorl section varies from laterally compressed with planar flanks (MGPUT-PU 112704: Pl. 1, fig. 2; MGPUT-PU 112813: Pl. 1, fig. 17) to ovate (MGPUT-PU 112706: Pl. 1, fig. 1) or subtriangular with feebly convex flanks (MGPUT-PU 112885: Pl. 1, fig. 9). The umbilicus is deep with steep walls that pass to the flank by an angular to rounded umbilical edge. The maximum width of the whorl section lies in the inner third of flanks, which slope to the ventrolateral edge. The venter varies from narrow and acutely arched (MGPUT-PU 112859: Pl. 1, fig. 11) to relatively large and flat (MGPUT-PU 112701: Pl. 1, fig. 3). Sigmoidal growth lines are occasionally engraved on the shell (MGPUT-PU 112704: Pl. 1, fig. 2). The suture lines (Fig. 5) show a high saddle at the bottom of the short lobe E; the saddle E/L is symmetrically bipartite by a deep accessory lobe; the lobe L is narrow, tridif or bifid; the saddle L/U₂ is asymmetrical, coarsely branched and higher than E/L in the adult stage; the suspensive lobe occupies the inner third of the flank, bears 3 auxiliary saddles and shows a deep, slightly inclined and asymmetrically trifid U₂.

Microconchs [m] - The whorl section shows flat or planar flanks with rounded umbilical wall and regularly arched venter. The umbilicus is open. The aperture is slightly flared with deep constriction (MGPUT-PU 112722: Pl. 1, fig. 6); the peristome bears long, pointed lateral lappets and a small ventral rostrum.

Remarks. The names decoratum and intrasculptum proposed by Wetzel (1950) as subspecies of Lissoceras inflatum have no meaning as they refer only to evidence of growth lines on the shell. Despite the variability of the morpho-structural parameters in the present taxon, L. psilodiscus and L. inflatum are distinct based on whorl width and its regression on whorl height (Fig. 4). Tables 1 and 2 further evidence the distinction of the two species in numerical terms. Distinctive values are the means W/D and confidence intervals on standard error: respectively 28.65 and 25.55-26.31 for L. inflatum in comparison with 25.93 and 25.55-26.31 for L. psilodiscus. Further differences concern the suture line (Fig. 4): L. inflatum in adult stages shows shorter E/L saddle and wider suspensive lobe than L. psilodiscus (Krysyn 1972, fig. 16; Sandoval 1986, fig. 4/d).

Dense and projected ribs (costellae) ornament the outer flank of the specimen MGPUT-PU 35792 that was labelled as L. psilodiscus inflatum by Sturani (1971, p. 92) and comes from Monte Meletta in Asiago (Pl. 5, fig. 17): apart rib projection, this ornament recalls that of the coeval Semilissoceras costellatum n. sp. described below, but due to the fragmentary status of the specimen it is named S. aff. costellatum.

Distribution. Lissoceras inflatum is largely distributed in the Mediterranean-Caucasian Subrealm. Its biochronostratigraphical range is upper Bajocian. The oldest record is from the top of the Niortense Zone from both the Northwest European (Parsons 1976) and the Mediterranean provinces (Sturani 1971), and the youngest one is from the Parkinsoni Zone of Calvados (Appendix). The presence of the species in the basal Bathonian is based on the fossils that constitute the type-series (Wetzel 1950): nevertheless, the picture of the lectotype suggests that it deals with a reelaborated fossil so that the German datum needs confirmation.

Table 1

Figs 1-11, 13, 15, 17 - Lissoceras inflatum Wetzel, 1950. [M & m].
1) MGUPT-PU 112706, [M], Sully, upper Parkinsoni Zone. 2) MGUPT-PU 112704, [M], Sully, upper Parkinsoni Zone (see text-fig. 5A). 3) MGPUT-PU 112701, [M], Bretteville, upper Parkinsoni Zone. 4) MGUPT-PU 112725, [m], Sainte-Honorine-des-Pertes, upper Parkinsoni Zone. 5) MGUPT-PU 112723, [m], Sainte-Honorine-des-Pertes, upper Parkinsoni Zone. 6) MGUPT-PU 112722, [m], Sainte-Honorine-des-Pertes, upper Parkinsoni Zone. 7) MGUPT-PU 112724, [m], Sainte-Honorine-des-Pertes, upper Parkinsoni Zone. 8) MSNUP 117607, [M], Gelpach 4, Garantiana Zone. 9) MGPUT-PU 112885, [M], Sengenthal, topmost Bajocian. 10) MGPUT-PU 112718, Sully, upper Bajocian. 11) MGPUT-PU 112859, Evrey, Garantiana Zone. 12) MGPUT-PU SMNS 70396/9, [M], Burton Bradstock, Parkinsoni Zone. 13) RC132/32, Ricla, Garantiana Zone. 14) MGPUT-PU 112813, Bretteville, Niortense-Garantiana zones (see text-fig. 5B).

Figs 12, 16 - Lissoceras psilodiscus (Schloenbach, 1865). [M].
12) MGUPT-PU 111944, la Palud, lower Zigzag Zone. 16) MGUPT-PU 111445, Bas Auran, lower Zigzag Zone.

Fig 14 - Lissoceras submediterraneum n. sp. [M].
14) PB-189, paratype, Thorigné, Niortense Zone, photo provided by Patrick Branger.

Scale bars of plate and top-right panel equal 10 mm. Asterisk marks the beginning of the body chamber. Specimens were white-ned prior to photography, except fig. 14.
**Lissoceras submediterraneum** n. sp. [M & m]

Figs 3, 4, 6; Pl. 1, fig. 14; Pl. 2, figs 1-3, 5

1985 *Lissoceras psilodiscum* - Fernandez-Lopez, p. 161, text-figs 15, 16/F, pl. 15, fig. 3.

**Diagnosis:** Macroconchiate and microconchiate *Lissoceras*; extremely compressed shell, planar to feebly arched flanks, short, steep umbilical walls.

**Etymology:** From its occurrence in the western part of the Sub-Mediterranean Province.

**Types:** The holotype is the resedimented macroconch 8EB 167/9 (Pl. 2, fig. 2) from Embalse San Blas (Cauda, Iberian Range), Garantiana Zone, upper Bajocian. The allotype is the resedimented microconch 1EB 28/7 (Pl. 2, fig. 5) from Embalse San Blas (Cauda, Iberian Range), Garantiana Zone, upper Bajocian. Besides the allotype, three further paratypes are selected: the resedimented macroconch Pb-189 (Pl. 1, fig. 14) from Thorigné (Deux-Sèvres), Niortense Zone, upper Bajocian, and the reelaborated macroconchs MGPUT-PU 112855 (Pl. 2, fig. 1) and MGPUT-PU 112858 (Pl. 2, fig. 3) from Viaduc de l’Egray (Deux-Sèvres), Niortense Zone, upper Bajocian.

**Locus typicus:** The section-8 of Embalse San Blas (Cauda, Teruel), Iberian Range, Spain, described by Fernandez-Lopez (1985, p. 648, figs 91, 93, 95).

**Stratum typicum:** Bed BE167 in section-8 of Embalse San Blas, which contain resedimented ammonites belonging to the Robustus Biohorizon, upper Garantiana Zone (Fernandez Lopez, 1985), and to the uppermost El Pedregal Formation (Gomez & Fernandez-Lopez 2004).

**Material:** One resedimented and four reelaborated macroconch specimens from the Niortense Zone, upper Bajocian of Deux-Sèvres. One resedimented macroconch and one resedimented microconch specimens from the Garantiana Zone, upper Bajocian of Embalse San Blas (Cauda, Iberian Range).

**Measurements:** See Appendix. Measured extremes for diameter: [M] 26.1 - 45.4 mm; [m] 6.8 mm. Values for h, w and u are summarized in Table 3.

**Description.** Compressed, discoid, medium-sized ammonites with open umbilicus. Dimorphism is documented.

Macroconchs [M] - The whorl section is lanceolate with planar (8EB 167/9: Pl. 2, fig. 2) or feebly convex flanks (MGPUT-PU 112855: Pl. 2, fig. 1).

Microconchs [m] - The whorl section is sub-rectangular with rounded umbilical wall and regularly arched venter. The umbilicus is open. The aperture is not preserved in the single specimen EB 28/7.

**Remarks.** The microconch of *Lissoceras submediterraneum* n. sp. shows a comparable open umbilicus with those of *L. haugi* 32.40 for the former in comparison with 32.04 for the latter. They differ for the reduced dimension, the whorl width (26.50 vs 34.71) and the W/H ratio (62.10 vs 81.59) whereas the whorl section is rounded in *L. haugi* and very

---

**Tab. 3 - Synthesis of measurements and regression statistics for Lissoceras submediterraneum n. sp., [M & m].**
compressed, rectangular-like in the new species. On the other hand, in comparison with \textit{L. submediterraneum} n. sp., the umbilicus of \textit{L. inflatum} is closer (28.64 vs 32.40) and the umbilicus of \textit{L. sturanii} n. sp. is more open (means 37.70 vs 32.40). As to the macroconchs (Tables 1-3), the greatest differences concern \textit{L. psilodiscus}: the whorl width of \textit{L. submediterraneum} n. sp. is consistently narrower than in \textit{L. psilodiscus} (means 23.20 vs 28.65, confidence intervals on standard error 22.88/23.52 vs 25.55/26.31) and \textit{L. inflatum} (means 23.20 vs 28.65, confidence intervals on standard error 22.88/23.52 vs 28.25/29.05).

Besides, the umbilicus in \textit{L. submediterraneum} n. sp. is more open than in \textit{L. psilodiscus} (means 26.1 vs 22.9).

**Distribution.** \textit{Lissoceras submediterraneum} n. sp. is so far known only in the western sector of the Sub-Mediterranean Province, namely in the Iberian Range and Deux-Sèvres. It ranges through lower Sub-Mediterranean Province, namely in the Iberian Peninsula and in the Deux-Sèvres. It ranges through lower Sub-Mediterranean Province, namely in the Iberian Peninsula and in the Deux-Sèvres.

**Lissoceras oolithicum** (d’Orbigny, 1845) [M]

Figs 1, 7-11, 14; Pl. 2, figs 4, 6, 7, 9, 12

1845 \textit{Ammonites oolithicus} d’Orbigny 1842-51, p. 383, pl. 126, figs 1, 2, 4 (non fig. 3 = \textit{L. inflatum}).

1858 \textit{Ammonites oolithicus} - Quenstedt, p. 396, pl. 55, fig. 20 (= \textit{L. ovale} n. sp.).

1886 \textit{Ammonites oolithicus} - Quenstedt 1886-87, p. 563, pl. 69, fig. 4 (= \textit{L. ovale} n. sp.), fig. 5 (= \textit{L. bangi}).

1892 \textit{Lissoceras oolithicum} - Munier-Chalmas, p. 166.

1913 \textit{Lissoceras oolithicum} - Dournil, p. 72, text-fig. 4 (= \textit{L. bangi}).

1927 \textit{Lissoceras oolithicum} - Dorn, p. 245, pl. 7, fig. 3 (= \textit{L. bangi}).

1927 \textit{Lissoceras oolithicum} - Roman & Petrousl, p. 48, pl. 5, figs 12, 14 (= \textit{L. inflatum}), pl. 5, fig. 13 (= \textit{L. ovale} n. sp.).


1976 \textit{Lissoceras} (\textit{Lissoceras}) \textit{olithicus} - Parsons, p. 124-134.

1980 \textit{Lissoceras oolithicum} - Galác, p. 57, text-figs 43, 44, pl. 11, figs 3-5 (= \textit{L. ovale} n. sp.).

1983 \textit{Lissoceras oolithicum} - Pavia, p. 172, pl. 7, fig. 11.

1985 \textit{Lissoceras oolithicum} - Fernandez-Lopez, p. 164 (non text-figs 15, 16, E, pl. 15, fig. 2 = \textit{L. ovale} n. sp.).

1986 \textit{Lissoceras oolithicum} - Sandowal, p. 439, text-fig. 3, pl. 1, figs 6-7.

1994 \textit{Lissoceras oolithicum} - Fernandez-Lopez & Mouterde, p. 141, pl. 5, fig. 4 (= \textit{L. sturanii} n. sp.).

1995 \textit{Lissoceras oolithicum} - Galác, p. 124, pl. 18, figs 8-9.

1998 \textit{Lissoceras oolithicum} - Besnosov & Motta, p. 23, pl. 8, fig. 2 (= \textit{L. sturanii} n. sp.).

2000 \textit{Lissoceras oolithicum} - Besnosov & Motta, p. 51 (pl. 1, fig. 9 = \textit{L. inflatum}, pl. 1, figs 10-13 = \textit{L. sturanii} n. sp., pl. 3, fig. 2 = \textit{L. ovale} n. sp.).

2006 \textit{Lissoceras oolithicum} - Zaton & Marynowski, p. 433, text-fig. 4B, figs 3, 9-10 (= \textit{L. ferrifex}).

2010 \textit{Lissoceras oolithicum} - Zaton, p. 94, text-figs 11/0, pl. 6, figs G, H (= \textit{L. ferrifex}).

2011 \textit{Lissoceras oolithicum} - Rulleau, p. 68, pl. 30, fig. 1 (= \textit{L. inflatum}).

**Diagnosis:** The original diagnosis in Latin language (d’Orbigny 1845 in 1842-49, p. 383) states: compressed, smooth shell; high, slightly convex whorls; convex, rounded venter; oval aperture; suture line with 5 lateral lobes.

**Types:** As far as we know (Rioult in Fischer 1994, p. 112) two synonyms formed the series-type of \textit{“Ammonites oolithicus” d’Orbigny, 1845”}: among the fossils figured on d’Orbigny’s pl. 126, figs 1+2 and 4 concern the lectotype of \textit{L. oolithicum} (Schlegelmilch 1985, p. 68), whereas the specimen at fig. 3 was identified as \textit{L. psilodiscus} inflatum by Rioult (in Fischer 1994, p. 112). The first volume of the “Révision critique de la Paléontologie Française d’Alcide d’Orbigny” (Fischer 1994) initiated the process to review all the Jurassic ammonites collected and studied by d’Orbigny in 1842-49. The reviewers
concluded that some original name-bearing types were missing; at present they must be regarded as definitely lost. It is the case of the two sytypes of “Ammonites oolithicus” (Riout in Fischer 1994, p. 112). For this reason, in absence of the lectotype, the specimen MGPPUT-PU 112868 (Fig. 7) is selected as the neotype of Lissoceras oolithicum (d’Orbigny, 1845). It is here designated following the ICZN rules (Article 75) with the qualifying conditions specified below.

1) The designation of the neotype of L. oolithicum arises from the necessity to clarify the taxonomic status of the species in comparison with other congeneric taxa due to the misunderstanding of its architectural parameters as demonstrated by the above synonymes.

2) The most significant feature of L. oolithicum, according to the original diagnosis and figures by d’Orbigny (1845 in 1842-49, p. 383, fig. 4), is the compressed section with slightly convex whorls, maximum whorl width at the inner fourth of flank and high umbilical wall. This is different from the oval section shown in more recent descriptions (e.g., Galácz 1980; Schlegelmilch 1985).

3) The specimen MGPPUT-PU 112868, here selected as the neotype of L. oolithicum, comes from the condensed fossil assemblage of the Evrecy site that comprises both reworked and reealbored fossilis; it is referred to the upper Humphriesiaum Zone, top lower Bajocian (Pavia et al. 2013). A reworked, shelly arcid Paralheterodon sp. is strictly associated to the reealbored internal mould of the neotype (Fig. 6). Such features ensure identification of the fossil.

4) The neotype is consistent with d’Orbigny’s original description given of the former name-bearing type.

5) D’Orbigny (1845 in 1842-49, p. 383) indicated that he personally collected the specimens of “Ammonites oolithicus” from Bayeux and Moutiers-en-Cinglaís (Calvados). He figured two specimens at personally collected the specimens of “Four à Chaux” of Calvados (Pavia et al. 2015). At present, those ancient quarries are closed. Nevertheless, in the middle “Oolithe ferrugineuse de Bayeux” Fm of the sector southwards of Caen, from Bretteville-sur-Ordon to Maizet, Evrecy and Croisilles, a bed rich in Stephanoceratidae and subordinate Lissoceratidae is present (Pavia et al. 2013, 2015). The neotype of L. oolithicum was collected from this bed at Evrecy by Dieter Berger in 1994; the source-bed could be sampled after digging in the site at the coordinates 49°05’55” N - 0°30’31” E.

6) The neotype of L. oolithicum (d’Orbigny) was kindly transmitted by Dieter Berger (Wiesloch, Germany) to the palaeontological collections of the Dipartimento di Scienze della Terra at the Torino University, where it is stored with registration code MGPPUT-PU112868.

7) The neotype designation of L. oolithicum on the specimen MGPPUT-PU112968 should not arise any objection from Middle Jurassic ammonitologists. It has been supported by Patrick Branger (Cherveux, France), Robert Chandler (London, UK), Volker Dietze (Nordlingen, Germany), Raymond Enay (Lyon, France), András Galácz (Budapest, Hungary), Maria-Helena Henriques (Coimbra, Portugal), Vasily Mitra (Moscow, Russia), Horacio Parent (Rosario, Argentina), José Sandoval (Granada, Spain), Jan Schög (Bratislava, Slovakia), Guenter Schweigert (Stuttgart, Germany), Kazem Seyed Emami (Tehran, Iran), Michal Zaton (Sosnowiec, Poland).

Material: Eighteen specimens from different sites in Calvados and five from the Frogden Quarry in Dorset. One specimen from Échiré in Deux-Sèvres. One specimen from Moscardon (Teruel) in the Iberian Range. Four specimens from Chaudon, Alpes-de-Haute-Provence. Six specimens from the “Lumachella a Posidonia alpina” in Assigo

Measurements: See Appendix. Measured extremes for diameter: 12.1 - 75.6 mm. Values for h, w and u are summarized in Table 4.

**Description.** Medium-sized ammonites with planulate, compressed shell and moderately open umbilicus. The neotype is an adult specimen with approximate septa at 54 mm. The whorl section is subtriangular with slightly arched to planar flanks (Figs 11B, 11C); the maximum width lies at the inner fourth of the flank. The umbilicus is deep with approximate septa at 54 mm. The whorl section is subtriangular with slightly arched to planar flanks (Figs 11B, 11C); the maximum width lies at the inner fourth of the flank. The umbilicus is deep with vertical umbilical walls abruptly passing to the flank by a rounded edge. The venter is narrow, acutely

<table>
<thead>
<tr>
<th>L. oolithicum</th>
<th>[M]</th>
</tr>
</thead>
<tbody>
<tr>
<td>h = H/D x 100</td>
<td>w = W/D x 100</td>
</tr>
<tr>
<td>35 measures (min/max)</td>
<td>45.30 - 52.70</td>
</tr>
<tr>
<td>mean of 35 measures</td>
<td>49.69</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>1.49</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.22</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>46.71 - 52.67</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>49.25 - 50.13</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>R² = 0.99 - y = 0.30x + 1.40</td>
</tr>
<tr>
<td>correlation index and regression U on W:</td>
<td>R² = 0.96 - y = 0.67x - 0.40</td>
</tr>
</tbody>
</table>

Tab. 4 - Synthesis of measurements and regression statistics for Lissoceras oolithicum (d’Orbigny, 1845), [M].
arched, almost fastigate by marked ventrolateral edges. Sigmoidal growth lines are visible on the shell, whereas the internal mould is smooth. The suture line (Figs 1, 8) shows a large, flared saddle at the bottom of lobe E and a short, bipartite saddle E/L; the saddle L/U is asymmetrical and dominate on the deep, asymmetrical lobe L that is trifid; the wide suspensive lobe bears 4 auxiliary saddles with deep and slightly asymmetrical U.

Remarks. Any microconch is so-far known. Some authors treated d’Orbigny’s taxon differently from the original definition. They included it under the binomen *Lissoceras oolithicum* along with all the Bajocian lissoceratins lacking ribs and showing a whorl section neither inflated nor compressed (see the complex synonymic list). However, according to d’Orbigny’s diagnosis, the main characteristics consist of two architectural parameters: the compressed (subtriangular), slightly arched whorl section with vertical umbilical wall and the narrow venter. Features, such as the large ventral lobe and the four auxiliary lobes described in *L. oolithicum* are present also in other smooth forms that are equivalent to *L. oolithicum* as to the main architectural parameters W/H and U/D is concerned (Figs 9, 10). Nevertheless, two of these forms show different whorl sections: *Lissoceras maizetense* n. sp. with large and rounded venter (Fig. 11A), *Lissoceras ovale* n. sp. with inflated flanks (Fig. 11E). A third smooth form is *Lissoceras sturanii* n. sp. that Sturani (1971) assigned originally to d’Orbigny’s taxon; this species shows an arched-subrectangular whorl section (Fig. 11D) and a wider umbilicus and should be considered at most as linked to *L. oolithicum* (see Conclusions herein). For these reasons, it is impossible to confirm as conspecific the records for Normandy by Munier-Chalmas (1892, p. 166) and for Dorset by Parsons (1976, p. 124 to 134).

The small specimen referred by Seyed-Emami (1988, p. 79) to *L. oolithicum* from the Propinquans Zone of Central Iran needs confirmation because of the unusual biochronostratigraphical position in comparison with the bulk of specimens here described. The Mexican *Lissoceras cf. oolithicum* (Sandoval & Westermann 1986) from topmost lower Bajocian of the Oaxaca area is similar to d’Or-
**Lissoceras maizetense** n. sp. [M]

Figs 9-12; Pl. 2, figs 8, 10, 11, 13

**Diagnosis:** Macroconchiate *Lissoceras*; oval compressed shell, whorl becoming subrectangular in the adult stage with feebly inflated venter, light sigmoidal ribbing.

**Etymology:** The new species is dedicated to the ville of Maizet (Calvados, NW France) from where the bulk of the type-series comes.

**Types:** The holotype is the reelaborated macroconch MGPUT-PU 112804 (Pl. 2, fig. 8) from Maizet (Calvados), bed 5, upper Humphriesianum Zone. Two paratypes: the reelaborated macroconch MGPUT-PU 112966 (Pl. 2, fig. 11) from Maizet (Calvados), bed 5, upper Humphriesianum Zone; the reelaborated macroconch MGPUT-PU 112862 (Pl. 2, fig. 13) from Maizet (Calvados), bed 6, lower Niortense Zone.

**Locus typicus:** The section of Maizet, south of Caen, Calvados, NW France, where the “Oolithe ferrugineuse de Bayeux” Formation was described by Pavia et al. (2013).

**Stratum typicum:** Lower Bajocian, Humphriesianum Zone. Pavia et al. (2013, p. 142) indirectly referred the Maizet bed 5 to the late Humphriesianum Biochron. *L. maizetense* n. sp. is not present in bed 4 whose resedimented fossils refer to the lower Humphriesianum Zone, Romani Subzone. We can thus infer that the holotype of *L. maizetense* n. sp. pertains to the Umbilicum or Blagdeni subzones within the Humphriesianum Zone.

**Material:** Besides the type-series, two further specimens are assigned to *L. maizetense* from the Humphriesianum-Niortense zones of Maizet and Sully (Calvados).

**Measurements:** See Appendix. Measured extremes for diameter: 23.7 - 60.3 mm. Values for h, w and u are summarized in Table 5.

**Description.** Medium-sized ammonites with planulate, compressed shell and moderately open umbilicus. The whorl section is oval compressed; flanks are feebly arched with maximum width at the middle flank; the inner flank slopes to the acute umbilical edge. The umbilicus is shallow with short, vertical walls. The venter is narrow, acutely arched in the inner to middle whorls, with rounded ventrolateral edges. In the adult stage the venter enlarges and the whorl section becomes subrectangular, feebly inflated (Fig. 11A). Light sigmoidal ribbing is visible on the shell and on the external sector of the umbilicus.

---

**Plate 2**

Figs 1-3, 5 - *Lissoceras submediterraneum* n. sp. [M & m].
1) MGPUT-PU 112855, [M], paratype,Viaduc de l’Egray, Niortense Zone. 2) 8EB 16/7, [M], holotype, Embalse San Blas, Garantiana Zone. 3) MGPUT-PU 112888, [M], paratype, Viaduc de l’Egray, Niortense Zone (see text-fig. 5). 5) EB 28/7, [m], allotype, Embalse San Blas, Garantiana Zone.
4) Figs 4, 6, 7, 9, 12 - *Lissoceras oolithicum* (d’Orbigny, 1845). [M].
4) MGPUT-PU 112863, Maizet, Romani Subzone. 6) MGPUT-PU 112814, Baron-sur-Odon, Humphriesianum Zone. 7) SMNS 70396/7, Fagoden Quarry, Romani Subzone. 9) MGPUT-PU 112798, Croisilles, upper Garantiana Zone. 12) MGPUT-PU 112807, Evrecy, upper Humphriesianum Zone (see text-fig. 10C), specimen collected by Jean Dermeau.
8) Figs 8, 10, 11, 13 - *Lissoceras maizetense* n. sp. [M].
8) MGPUT-PU 112804, holotype, Maizet, upper Humphriesianum Zone (see text-fig. 10A). 10) MGPUT-PU 112740, Sully, Humphriesianum Zone. 11) MGPUT-PU 112966, paratype, Evrecy, upper Humphriesianum Zone (see text-fig. 12). 13) MGPUT-PU 112862, paratype, Maizet, Humphriesianum-Niortense zones.

Scale bar equals 10 mm, except fig. 5 with scale bar 5 mm. Asterisk marks the beginning of the body chamber. Specimens were whitened prior to photography.
internal mould (Plate 2, figs 8, 11); the external convex branch of ribs is slightly more carved. The suture line (Fig. 12) shows a large, flared saddle at the bottom of E lobe and a short, bipartite saddle E/L; the saddle L/U² is asymmetrical and dominates on the deep, symmetrical lobe L that is trifid; the wide suspensive lobe bears 4 auxiliary saddles with very deep and symmetrical U².

Remarks. No microconch is so-far known. As to other taxa, we have not found any equivalence with specimens described in literature. **L. ovale** n. sp. is similar to **L. maizetense** n. sp., but the former differs for the section enlarged on the mid-flank, the rounded venter and the suture line as described below. A possible comparison might be done with the small specimen described by Seyed-Emami (1988, p. 78) as **Lissoceras (Microlissoceras) badamui** n. sp. from the Propinquans Zone of Central Iran that shows slightly inflated flanks and depressed periumbilical area.

Distribution. All specimens of the new species are reeleraborated fossils that do not allow any definite biochronological statement. For the time being, **Lissoceras maizetense** n. sp. is considered to be limited to the Humphriesianum and at most to the lower Niortense Zone from Maizet and Sully (Calvados).

**Lissoceras ovale** n. sp. [M]

Fig. 9-11, 13; Pl. 3, figs 1, 8, 9, 11

1858 *Ammonites oolithicus* - Quenstedt, p. 396, pl. 55, fig. 20.
1886 *Ammonites oolithicus* - Quenstedt 1886-87, p. 563, pl. 69, fig. 4.
1927 *Lissoceras oolithicum* - Roman & Petouraud, p. 48, pl. 5, fig. 13.
1980 *Lissoceras oolithicum* - Galácz, p. 57, text-figs 43, 44, pl. 11, figs 5, 6.
1985 *Lissoceras oolithicum* - Schlegelmilch, p. 68, pl. 21, fig. 4.
2000 *Lissoceras oolithicum* - Besnosov & Mitta, p. 51, pl. 3, fig. 2.

**Diagnosis**: Macroconchiate *Lissoceras*; ovate shell, compressed in the middle whorls becoming regularly inflated in the adult stage with arched venter.

**Etymology**: The name of the new species refers to the ovate, regularly inflated whorls.

**Types**: The holotype is the reeleraborated macroconch 1CE2/1 (Pl. 3, fig. 1) from Cella (Teruel, Iberian Range), Garantiana Zone. Two paratypes: the reeleraborated macroconch MGPUT-PU 112966 (Pl. 3, fig. 9) from Croisilles (Calvados), lower Parkinsoni Zone; the reeleraborated macroconch PB-185 (Pl. 3, fig. 11) from Mal vault (Deux-Sèvres), Niortense Zone.

**Locus typicus**: The section-1 at Cella (Teruel), Iberian Range, Spain, described by Fernandez-Lopez (1985, p. 670, figs 101, 103).

**Stratum typicum**: Upper Bajocian, upper Garantiana Zone, Tetragona Subzone, Robustus Biohorizon, bed CE2 in section-1 at Cella, which contain reeleraborated ammonites (Fernandez Lopez 1985) and belongs to the uppermost El Pedregal Formation (Gomez & Fernandez-Lopez 2004).

**Material**: 6 specimens from diverse palaeobiogeographical sectors: 2 from Croisilles and Evrecy in Calvados, 1 from Mal vault in Deux-Sèvres, 1 from Cella (Teruel) in the Iberian Range, 1 from Eningen in southern Germany (Quenstedt 1858, pl. 55, fig. 20; Schlegelmilch 1985, pl. 21, fig. 4), 1 from Gyenespuszta in Bakony Mountains (Galácz 1980, pl. 11, fig. 5).

**Measurements**: See Appendix. Measured extremes for diameter: 22.8 - 66.0 mm. Values for h, w and u are summarized in Table 6.

**Description**: Medium-sized ammonites with planululate shell and moderately open umbilicus. The whorl section of the inner to medium whors is oval compressed; flanks are arched with maximum width at the middle flank; the umbilicus is shallow with short, rounded walls; the venter is narrow, acutely arched with rounded ventrolateral edge. In the outer
whorls the whorl section becomes ovate by homogeneous swelling of the flank, so that the venter becomes regularly arched and the umbilicus deep with high, rounded umbilical walls (Fig. 11E). Both shell and internal mould appear smooth except ghosts of sigmoidal growth lines. In the suture line (Fig. 13; see also Galácz 1980, text-fig. 44 and Schlegelmilch 1985, p. 68) the saddle at the bottom of lobe E is high and pointed in the middle; the saddle E/L is bipartite and the saddle L/U is high, asymmetrical and minutely branched; the symmetrical lobe L is trifid; the suspensive lobe shows an asymmetrically trifid U and bears 3 auxiliary saddles.

**Remarks.** No microconch is so far known. *Lissoceras ovale* n. sp. differs from the coeval *L. oolithicum* for the adult whorl shape and details of the suture line, namely the ventral saddle and the reduced number of auxiliary saddles of the suspensive lobe. The specimen slightly differs from the architectural scheme of *L. ovale* n. sp. because of the narrower venter; nevertheless, the maximum whorl width at the middle flank allows referring the specimen to the new species. *L. maizetense* n. sp. differs for the adult whorl shape and details of the suture line with depressed saddle at the bottom of lobe E. *Lissoceras bakeri* Imlay (1962: A6, pl. 1, figs 1-6, 9-12) from the upper Bajocian of Alaska differs for the fine external ribbing, whereas its subovate whorl section with rounded umbilical walls recall the morphological shape of *L. ovale* n. sp.

**Distribution.** *Lissoceras ovale* n. sp. is recorded from different sites through the Mediterranean-Caucasian Subrealm, where it is distributed in the upper Bajocian. The oldest records are from the lower Niortense Zone of Calvados and Deux-Sèvres, whereas the most recent specimen so far quoted is the readulted MGPUT-PU 112867 (Pl. 3, fig. 9) from the lowermost Parkinsoni zones of Croisilles (Pavia et al. 2015).

**Lissoceras sturanii** n. sp. [M & m]

Figs 9-11, 14; Pl. 3, figs 2-7, 10

v 1971 *Lissoceras olidithicum* - Sturani, p. 91, pl. 6, fig. 2.

v 1971 *Microlissoceras pusillum* - Sturani, p. 94, pl. 6, figs 8, 10 (non pl. 6, figs 7, 9; pl. 7, fig. 16 = *L. pusillum*).

v 1994 *Lissoceras olidithicum* - Fernandez-Lopez & Mouterde, p. 141, pl. 5, fig. 4.

1998 *Lissoceras olidithicum* - Besnosov & Mitta, p. 23, pl. 8, fig. 2.


2000 *Microlissoceras pusillum* - Besnosov & Mitta, p. 51, pl. 1, figs 15, 17, 18 (non figs 14, 16 = *L. pusillum*).

**Diagnosis:** Macroconchiate and microconchiate *Lissoceras*; planulate shell with subrectangular, slightly convex whorls, rounded venter and open umbilicus.

**Etymology:** The new species is dedicated to the late prof. Carlo Sturani who masterly described in 1971 the Bajocian ammonites from the “Posidonia alpina beds” of Asiago, NE Italy.

**Types:** The holotype is the readulted macroconch MGPUT-PU 112730 (Pl. 3, fig. 10) from Sully (Calvados), bed 5, upper
Bajocian. The allotype is the reelaborated microconch MGPUT-PU 112733 (Pl. 3, fig. 3) from Sainte-Honorine-des-Pertes (Calvados), bed 5, upper Bajocian. Besides the allotype, six paratypes are select ed: the resedimented macroconch MGPUT-PU 112732 (Pl. 3, fig. 6) from Sainte-Honorine-des-Pertes (Calvados), bed 5, upper Bajocian, the reelaborated macroconch MGPUT-PU 112849 (Pl. 3, fig. 7) from Maizet (Calvados), bed 9, Garantiana Zone, the resedimented macroconchs MGPUT-PU 36057 (Sturani 1971, pl. 6, fig. 2; see also this work at Pl. 3, fig. 2) and MGPUT-PU 112983 (Pl. 3, fig. 4) from Troch 1 (Asiago), Romani Subzone, the resedimented microconchs MGPUT-PU 36069 (Sturani 1971, pl. 6, fig. 8) and MGPUT-PU 36070 (Sturani 1971, pl. 6, fig. 10; see also this work at Pl. 3, fig. 5) from Troch 1 (Asiago), Romani Subzone.

**Locus typicus:** The section of Sainte-Honorine-des-Pertes, north of Bayeux, Calvados, NW France, where the “Oolithe ferrugineuse de Bayeux” Formation was described by Rioult (1964) and Pavia et al. (1994).

**Stratum typicum:** Upper Bajocian, Garantiana Zone. Pavia (1994, p. 142) attributed the Sully bed 5 to the upper Bajocian. Nevertheless, the reelaborated ammonites mixed in such taphonomically condensed fossil-assemblage refer to the Niortense up to the Garantiana zones. According to its state of preservation, the holotype of *Lissoceras sturanii* n. sp. has to be referred to the Garantiana Zone.

**Material:** The specimens of *Lissoceras sturanii* n. sp. here described come from two distinct areas. Six macroconchs were collected from the Calvados sites of Sainte-Honorine-des-Pertes, Sully, Maizet, and two microconchs from the surroundings of Bayeux and Maizet. Eight macroconchs and 41 microconchs come from the “*Posidonia alpina* beds” of Troch 1 in Asiago (Sturani 1971).

**Measurements:** See Appendix. Measured extremes for diameter: [M] 8.4 - 34.7 mm; [m] 7.3 – 10.9 mm. Values for h, w and u are summarized in Table 7.

**Description.** Small-sized ammonites with planulate, compressed shell and open umbilicus. Dimorphism is well documented.

Macroconchs [M] - The whorl section is sub-rectangular with arched flanks and maximum width in the middle part; the inner flank slopes to the rounded umbilical edge. The large umbilicus is shallow with short, vertical walls. The venter is large, regularly arched with rounded ventrolateral edges. Sigmoidal growth lines are visible on the shell; in the middle flank the inflexed lines are slightly raised. The suture line is poorly visible only on the holotype: the ventral lobe E is large and the saddle at E bottom is large, flared, high and acutely triangular; the saddle E/L is short and symmetrically bipartite; the saddle L/U is asymmetrical and much higher that E/L.

Microconchs [m] - The whorl section is sub-rectangular with broad venter. The umbilicus is very

---

<table>
<thead>
<tr>
<th><em>L. sturanii</em> [M]</th>
<th>h = H/D x 100</th>
<th>w = W/D x 100</th>
<th>u = U/D x 100</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>18 measures (min/max)</td>
<td>41.7 - 47.1</td>
<td>28.5 - 35.8</td>
<td>27.50 - 32.6</td>
<td>65.4 - 80.0</td>
</tr>
<tr>
<td>mean of 18 measures</td>
<td>44.26</td>
<td>32.21</td>
<td>29.39</td>
<td>72.78</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>1.34</td>
<td>2.00</td>
<td>1.37</td>
<td>4.33</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.32</td>
<td>0.47</td>
<td>0.09</td>
<td>1.02</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>41.58 - 46.94</td>
<td>28.21 - 36.21</td>
<td>26.65 - 32.13</td>
<td>64.12 - 81.44</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>43.62 - 44.90</td>
<td>12.31 - 13.90</td>
<td>29.21 - 29.57</td>
<td>70.74 - 74.82</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>( R^2 = 0.99 ) - y = 0.72x + 0.01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>correlation index and regression U on W:</td>
<td>( R^2 = 0.97 ) - y = 0.67x + 0.29</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><em>L. sturanii</em> [M]</th>
<th>h = H/D x 100</th>
<th>w = W/D x 100</th>
<th>u = U/D x 100</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>13 measures (min/max)</td>
<td>33.3 - 38.1</td>
<td>28.3 - 34.4</td>
<td>33.4 - 39.1</td>
<td>80.0 - 93.9</td>
</tr>
<tr>
<td>mean of 13 measures</td>
<td>35.75</td>
<td>30.80</td>
<td>37.70</td>
<td>86.18</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>1.29</td>
<td>1.70</td>
<td>1.87</td>
<td>4.50</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.31</td>
<td>0.47</td>
<td>0.52</td>
<td>1.25</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>33.17 - 38.33</td>
<td>27.40 - 34.20</td>
<td>33.96 - 41.44</td>
<td>77.18 - 95.18</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>35.13 - 36.37</td>
<td>29.86 - 31.74</td>
<td>36.66 - 38.74</td>
<td>83.68 - 88.68</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>( R^2 = 0.88 ) - y = 0.66x + 0.62</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

Fig. 14 - Bivariate scatter diagram of whorl width W and umbilical diameter U for *Lissoceras oolithicum* (d’Orbigny) and *L. sturanii* n. sp. Regression parameters are detailed in Tables 4 and 7 respectively.

Tab. 7 - Synthesis of measurements and regression statistics for *Lissoceras sturanii* n. sp., [M & m].
open with reduced umbilical walls. The body chamber occupies 3/5 of the last whorl. The aperture is slightly flared; the peristome bears short, pointed lateral lappets and a small ventral rostrum.

**Remarks.** Microconchs are known from Calvados in NW France, Southern Alps in Italy and Great Balkan in Turkmenistan. The specimens from Southern Alps belonged originally to the type-series of *Microlissoceras pusillum* Sturani that shows more rounded whorl section, slightly more open umbilicus and sigmoidal ribs on the body-chamber. The macroconchs of *Lissoceras sturanii* n. sp. differs from the other taxa of the *L. oolithicum* morpho-structural group for the small adult size, the subrectangular whorl section, the large and open umbilicus (Figs 11, 14); such reduced size suggests they are representatives of a micromorph species. They recall *L. ovale* n. sp. in the peculiarities of the suture line as it concerns the structure of the lobe E. The ammonites *Lissoceras* cf. *oolithicum* (d'Orbigny), described by Sandoval & Westermann (1986) from topmost lower Bajocian of the Oaxaca (S Mexico), shows a relatively open umbilicus and depressed umbilical edge, but its venter is narrow; the Mexican taxon looks like as the intermediate between *L. oolithicum* and *L. sturanii* n. sp.

**Distribution.** *Lissoceras sturanii* n. sp. ranges from the lower Humphriesianum Zone, Romani Subzone in both the Italian Southern Alps (Sturani 1971) and the western-central France (Fernandez-Lopez & Mouterde 1994) up to the Garantiana Zone in Calvados. The records from Daghestan (Besnosov & Mitra 1998) and Great Balkan (Besnosov & Mitra 2000) point to the middle part of the Bajocian (Humphriesianum and Niortense zones).

**Lissoceras haugi** Sturani, 1967 [M & m]

Figs 15-18; Pl. 3, figs 12-16; Pl. 4, figs 1-8, 12, 13, 15-17

1886 *Ammonites oolithicus* - Quenstedt 1886-87, p. 563, pl. 69, fig. 5.
1913 *Lissoceras oolithicum* - Douvillé, p. 72, text-fig. 4.
1927 *Lissoceras oolithicum* - Dorn, p. 225, pl. 7, fig. 3.
1935 *Lissoceras* sp. - Bircher, p. 137, text-fig. 17, pl. 9, fig. 8.
1967 *Lissoceras haugi* n. sp. - Sturani, p. 24, pl. 3, fig. 16.
1971 *Lissoceras oolithicum* - Sturani, p. 31 (pars).
1985 *Lissoceras monachum* - Fernandez-Lopez, p. 166, text-figs 15-16, pl. 15, figs 6-7;

Diagnosis: A diagnosis is synthesizable from Sturani’s work (1971) as follows: macroconchiate and microconchiate *Lissoceras*; whorl section stout with ovale shape, whorl side convex with rounded venter.

![Fig. 15 - Plots of measurements for Lissoceras meletense (Parona) and L. haugi Sturani, with ontogenetic trajectories through ratios of the aperture shape (W/H). A) Whorl width/whorl height ratio (W/H x 100) versus shell diameter (D). B) Whorl width/whorl height ratio (W/H x 100) versus umbilical ratio (U/D x 100). Abbreviations: M, macroconch; m, microconch; h, holotype; l, lectotype.](image-url)
Type: The holotype is the resedimented specimen MG-PUT-PU 31403 from the lowermost Zigzag Zone, lower Bathonian from Chaudon, Alpes-de-Haute-Provence (Sturani 1971, p. 24, pl. 3, fig. 16). Two topotypes were collected later from the same bed 1 of the Chaudon section (MGPUT-PU 112438, Pl. 3, fig. 16, and PU-112439).

Material: Besides the holotype and two topotypes, 127 macroconch specimens from the upper Bajocian of different palaeobiogeographical sectors have been scheduled in Appendix: 101 resedimented and reelaborated fossils from Calvados (100) and Dorset (1) sites, 11 resedimented fossils from Embalse San Blas (Teruel) in the Iberian Range, 12 resedimented fossils from IpF (1) and from Sengersathal (11) in southern Germany, 1 resedimented and 1 reelaborated fossil from Alpes-de-Haute-Provence, 1 resedimented fossil from the site Gelpach 2 in Asiago, Italian Southern Alps.

Fifteen microconchs are added: 14 specimens from different sites of Calvados and two specimens from Embalse San Blas (Teruel) in the Iberian Range.

Measurements: See Appendix. Measured extremes for diameter: [M] 7.7 - 57.6 mm; [m] 8.2 - 12.9 mm. Values for h, w and u are summarized in Tables 8.

Description. Medium-sized ammonites with ovate, rounded shell, high umbilical wall and mid-open umbilicus. Dimorphism is well documented.

Macroconchs [M] - The whorl section is highly variable from laterally compressed (MGPUT-PU 112792: Pl. 4, fig. 2) to subcircular wider than high (MGPUT-PU 112784: Pl. 4, fig. 13). The umbilicus...
is deep with high and rounded walls that pass to the flank by an arched umbilical edge. The maximum width of the whorl section lies in the inner fourth of flank, which varies from feebly convex to arched and slopes to the ventrolateral edge. The venter varies from large and rounded to acutely arched (MGPUT-PU 112827: Pl. 4, fig. 1). Sigmoidal growth lines are visible only on the shell. The suture lines (Fig. 17) show a relatively narrow lobe E with proportionally high saddle at the bottom; the saddle E/L is nearly symmetrical, stout, feebly bipartite; the lobe L is large, trifid and feebly asymmetrical; the saddle L/U is asymmetrical, a little higher than E/L and coarsely branched; the suspensive lobe occupies the inner third of the flank, bears 3 auxiliary saddles and shows a deep, inclined and asymmetrically trifid U₂.

Microconchs [m] - The whorl section is oval with rounded umbilical wall and regularly arched venter. The umbilicus is open. The body chamber occupies 3/5 of the last whorl. The aperture is slightly flared; the peristome bears stout lateral lappets and a small ventral rostrum (MGPUT-PU 112853: Pl. 4, fig. 5).

Remarks. *Lissoceras haugi* shows high intraspecific variability: at one side of the coiling spectrum there are plathycones with rounded flanks and narrow venter, in which W/D values are 34%, whereas at the opposite side the planorbicones with globular whorl show W/D values up to 54%. Between these two morphological extremes, there is a continuous gradation of specimens that cover this large morphological spectrum. Statistical analyses of the main shell parameters (the regression of the ratio W/H in Fig. 16 and the distribution of h, w, u in Fig. 18A-C) confirm the normal distribution of specimens with scattered extremes. The composite sample set (Fig. 17) show a relatively narrow lobe E with proportionally high saddle at the bottom; the saddle E/L is nearly symmetrical, stout, feebly bipartite; the lobe L is large, trifid and feebly asymmetrical; the saddle L/U is asymmetrical, a little higher than E/L and coarsely branched; the suspensive lobe occupies the inner third of the flank, bears 3 auxiliary saddles and shows a deep, inclined and asymmetrically trifid U₂.

Microconchs [m] - The whorl section is oval with rounded umbilical wall and regularly arched venter. The umbilicus is open. The body chamber occupies 3/5 of the last whorl. The aperture is slightly flared; the peristome bears stout lateral lappets and a small ventral rostrum (MGPUT-PU 112853: Pl. 4, fig. 5).

Remarks. *Lissoceras haugi* shows high intraspecific variability: at one side of the coiling spectrum there are plathycones with rounded flanks and narrow venter, in which W/D values are 34%, whereas at the opposite side the planorbicones with globular whorl show W/D values up to 54%. Between these two morphological extremes, there is a continuous gradation of specimens that cover this large morphological spectrum. Statistical analyses of the main shell parameters (the regression of the ratio W/H in Fig. 16 and the distribution of h, w, u in Fig. 18A-C) confirm the normal distribution of specimens with scattered extremes. The composite sample set
up for _L. bangi_ does not represent a palaeobiological entity; nevertheless, such variability is documented (see Appendix) in any set of fossils, independently from both source and age and quite apart from dimorphism (Fig. 18C). Similar extremely large variability in architectural parameters is documented in ammonoid literature; the paper of Dagsys & Weitschat (1993) on Triassic Noritaceae from Siberia may be assumed as a model for _L. bangi_.

The synonymy list contains many citations of _L. oolithicum_ whose figured specimens show, in fact, features referable to _L. bangi_ such as the rounded whorl sections (Riout in Fischer 1994; Rulleau 1997) or the short suspensive lobe (Douvillé 1913; Dorn 1927).

Besides the holotype, the ammonites here included in Sturani’s species were attributed in literature to _Lissoceras ferrifex_ (Zittel, 1868), _Lissoceras monachum_ (Gemmellaro, 1877) and _Lissoceras oolithicum_ (d’Orbigny, 1845). As to the latter, in the previous pages it has been demonstrated that the whorl section of d’Orbigny’s species is characterized by lightly arched to flattened whorl sections with vertical umbilical wall and by significant details in the suture line, such as large lobe E with flared saddle at the bottom and 4 auxiliary saddles in the wide suspensive lobe. _L. monachum_ is a lower to middle Bathonian species that shows a stout, subtriangular umbilicus with flared umbilical wall, the large venter arched umbilical edge. The maximum width of the suture line lies in the middle of flanks. The venter is depressed and large in continuity with the rounded-oval in shape.

**Distribution.** _Lissoceras bangi_ is recorded from different sites through the Mediterranean-Caucasian Subrealm, where it is distributed in the upper Bajocian. The holotype and two topotypes from Chaudon section testify the persistence of the species up to the lowermost Bathonian, at least in the Sub-Mediterranean Province.

**Lissoceras meletense** (Parona, 1896) [M]

Figs 15, 16, 18, 19; Pl. 4, figs 10, 11, 14

_v 1896 Lissoceras meletense_ Parona, p. 11, pl. 1, fig. 3.
_v 1971 Lissoceras meletense_ - Sturani, p. 92, text-fig. 29, pl. 6, figs 5, 6.

**Diagnosis:** A diagnosis is synthesizable from Sturani’s work (1971) as follow: macroconchiate _Lissoceras_ with extremely inflated whorl section, wider than high and depressed-oval in shape.

**Type:** Among 26 syntypes from the “Puzhdinia alpina beds” of Asiago (16 from Monte Meletta and 10 from Monte Longara) Sturani (1971, p. 92, pl. 6, fig. 6; see also this work at Pl. 4, fig. 11) designated as the lectotype the syntype MGPUT-PU 35789 from Monte Meletta already figured by Parona (1896, pl. 1, fig. 3). He further described as paralecotype the syntype MGP-PD 15069/F from Monte Longara (Sturani 1971, text-fig. 29; see also this work at Fig. 19A). An additional specimen of the type-series (MGUT/P-35790) is figured herein at Pl. 4, fig. 10.

**Material:** 2 specimens from Evrecy and Sully in Calvados. 32 specimens from the “Puzhdinia alpina beds” in Asiago, Southern Alps. 1 specimen from Karaiman-Shorli in Great Balkan.

**Measurements:** See Appendix. Measured extremes for diameter: 8.0 - 26.3 mm. Values for h, w and u are summarized in Table 9.

**Description.** Small-sized ammonites with depressed, rounded shell, high umbilical wall and moderately open umbilicus. The whorl section is subcircular, wider than high. The umbilicus is deep with high and rounded walls that pass to the flank by an arched umbilical edge. The maximum width of the whorl section lies in the middle of flanks. The venter is depressed and large in continuity with the rounded flanks without any defined ventrolateral edge. Sig-

---

<table>
<thead>
<tr>
<th><strong>L. meletense</strong> [M]</th>
<th><strong>h = H/D x 100</strong></th>
<th><strong>w = W/D x 100</strong></th>
<th><strong>u = U/D x 100</strong></th>
<th><strong>W/H x 100</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>21 measures (min/max)</td>
<td>44.9 - 52.9</td>
<td>54.5 - 63.5</td>
<td>21.3 - 25.3</td>
<td>111.7 - 127.4</td>
</tr>
<tr>
<td>mean of 21 measures</td>
<td>48.34</td>
<td>58.88</td>
<td>23.41</td>
<td>121.69</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>2.00</td>
<td>2.31</td>
<td>1.01</td>
<td>4.5</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.44</td>
<td>0.50</td>
<td>0.22</td>
<td>0.99</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>44.34 - 52.34</td>
<td>54.26 - 63.50</td>
<td>21.39 - 25.43</td>
<td>112.69 - 130.69</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>47.46 - 49.22</td>
<td>57.88 - 59.88</td>
<td>22.97 - 23.85</td>
<td>119.71 - 123.67</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>$R^2 = 0.99$</td>
<td>$y = 1.18x + 0.48$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Tab. 9 - Synthesis of measurements and regression statistics for _Lissoceras meletense_ (Parona, 1896), [M].
moidal growth lines are visible only on the shell. The suture lines (Fig. 19) show a relatively narrow lobe E with medium-sized saddle at the bottom; the saddle E/L is asymmetrical, slender, bipartite; the lobe L is trifid, large and lightly asymmetrical; the saddle L/U is nearly symmetrical, as high as E/L and coarsely branched; the suspensive lobe occupies the inner third of the flank, bears 3 auxiliary saddles, the external one very large, and shows a deep and asymmetrically trifid U.

Remarks. Specimen MGPUT-PU 112786 from Sully (Pl. 4, fig. 14) perfectly fits the lectotype in the whorl section and the paralectotype MGP-PD 15069/F in the suture line. The distinction of L. meletense from the more inflated specimens of L. haugi, apart the larger dimensions of the latter, is based on the maximum whorl width at the middle flank and the depressed venter of Parona’s taxon (cf. Pl. 4, figs 10, 11, 14, vs 13, 16) and it is supported by pattern of frequency and dispersion parameters (Figs 15, 16, 18). Distinctive values are the means W/D and U/D and the confidence intervals on standard error (see Tables 8 and 9); respectively 43.28 plus 42.10/44.46 and 24.45 plus 24.17/24.73 for L. haugi in comparison with 58.88 plus 57.88/59.88 and 23.41 plus 22.97/23.85 for L. meletense. Further differences concern the suture lines (Figs 17 vs 19): L. meletense shows larger lobe L and larger saddle L/U - L/U in the suspensive lobe.

Distribution. Lissoceras meletense is known through the upper Bajocian from different palaeobiogeographical contexts: Niortense and Garantiana zones in the NW European, the Mediterranean and the north-eastern Tethyan Border provinces; Sturani (1971, p. 93) quoted specimens also from the Parkinsoni Zone of Burton Bradstock in Dorset.

Lissoceras pusillum Sturani, 1971 [m]  
1971 Lissoceras (Microlissoceras) pusillum n. sp. Sturani, p. 94, pl. 6, figs 7, 79, pl. 7, fig. 16 (non pl. 6, figs 8, 10 = Lissoceras sturanii n. sp.).
2000 Microlissoceras pusillum - Besnosov & Mitta, p. 51, pl. 1, figs 14, 16 (non figs 15, 17, 18 = [m] of L. sturanii n. sp.).

Diagnosis: Sturani (1971, p. 94) did not give any diagnosis. Significant features may be summarized as follows: microconchiate Lissoceras; large evolute shell with vertical umbilical walls and oval whorl section

Types: The holotype is the resedimented MGPUT-PU 36068 (Sturani 1971, pl. 6, fig. 7; see also this work at Pl. 4, fig. 9) from the lower Humphriesianum Zone, Romani Subzone at the Troch 1 site of Asiago in Southern Alps (Sturani 1971). From the same outcrop came the paratype MGPUT-PU 36071 (Sturani 1971, pl. 7, fig. 16). The paratype figured by Sturani (1971, pl. 6, fig. 9) is missing in the collection of the Dipartimento di Scienze della Terra of the Torino University, most likely lost at Sturani’s time.

Material: By the present review of Sturani’s “Posidonia alpina beds” collection from Troch 1, only four specimens result to belong to L. pusillum. The other specimens are identified as the microconchs of Lissoceras sturanii n. sp.

Measurements: See Appendix. Measured extremes for diameter: 11.1 - 13.3 mm. Values for h, w and u are summarized in Table 10.

<table>
<thead>
<tr>
<th>L. pusillum [m]</th>
<th>h = H/D</th>
<th>w = W/D</th>
<th>u = U/D</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 measures (min/max)</td>
<td>32.2 - 34.0</td>
<td>29.0 - 32.3</td>
<td>39.5 - 43.1</td>
<td>85.3 - 95.5</td>
</tr>
<tr>
<td>mean of 4 measures</td>
<td>33.48</td>
<td>30.40</td>
<td>41.13</td>
<td>90.95</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>0.83</td>
<td>1.38</td>
<td>1.67</td>
<td>4.46</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.42</td>
<td>0.69</td>
<td>0.84</td>
<td>2.2</td>
</tr>
<tr>
<td>confidence intervals on sd</td>
<td>31.57 - 35.09</td>
<td>27.64 - 33.16</td>
<td>37.79 - 44.47</td>
<td>82.03 - 99.87</td>
</tr>
<tr>
<td>confidence intervals on se</td>
<td>32.59 - 34.27</td>
<td>29.02 - 31.78</td>
<td>39.45 - 42.81</td>
<td>86.55 - 95.35</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>R² = 0.95 - y = 0.70x + 0.60</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Description. Widely evolute shell with relatively deep umbilicus. Whorl section oval with convex flank, short and vertical umbilical wall, rounded umbilical edge and shoulder, regularly convex venter. Ornamentation consists of evanescent sigmoid growth lines with inflexion point in the inner third of flank; in the external branch they become stronger like ribs and are very convex. The body chamber occupies 3/5 of the last whorl. Peristome with short, pointed lateral lappets and small ventral rostrum.

The suture line is not available.

Remarks. Any dimorphic equivalence may be confirmed. The microconchs of *Lissoceras sturani* n. sp., some specimens of which come from the type-series of *L. pusillum*, show more flattened whorl section, slightly closer umbilicus and no sigmoidal ribs. As illustration is missing, the citation of *Lissoceras* (*Microlissoeras*) cf. *pusillum* Sturani by Parsons (1976, p. 126) cannot be confirmed.

Distribution. *Lissoceras pusillum* Sturani is so far known from the top lower Bajocian (Romani Subzone) of the Asiago district in Southern Alps and from the basal upper Bajocian (Niortense Zone) of Chaloi, in Great Balkan, western Turkmenistan (Besnosov & Mitta 2000, p. 51).

**Lissoceras maerteni** n. sp. [m]

*Fig. 8; Pl. 4, figs 18-19*

**Diagnosis.** Microconchiate *Lissoceras*; mid-evolute, serpenticone-like shell with compressed whorl section.

**Etymology.** The new species is dedicated to our friend Lionel Maerten, Ver-sur-Mer, who joined us during field trips on the Bajocian of Calvados and supplied the paratype MGPUT-PU 112999.

**Types.** The holotype is the reelaborated microconch MGPUT-PU 111998 (Pl. 4, fig. 18) from Sully (Calvados) collected by Mr. Pont and coming from bed 5 of Pavia’s stratigraphy (1994). A para

**Stratum typicum:** Upper Bajocian of Calvados, NW France, where the “Oolithe ferrugineuse de Bayeux” Formation was described by Pavia (1994).

**Material:** The holotype and paratype constitute the only specimens so far known.

**Measurements:** See Appendix. Measured extremes for diameter: 11.1 - 13.3 mm. Values for h, w and u are summarized in Table 11.

**Description.** Evolute platycone with shallow umbilicus. Whorl section compressed with slightly convex flank, short and inclined umbilical wall, rounded latero-ventral shoulder, convex venter. Ornamentation is represented by evanescent sigmoid growth lines with inflexion point in the inner third of flank; on the body chamber their external branch becomes a bit stronger. The body chamber occupies 3/5 of the last whorl. The aperture is flared; the peristome bears stout lateral lappets and a large ventral rostrum. The suture line is not available.

**Remarks.** No dimorphic equivalence can be confirmed. *Lissoceras maerteni* n. sp. might be coupled with one taxon of the *L. olitibicum* morpho-structural group: according to biochrononstratigraphy and whorl section the best candidate is *Lissoceras ovale* n. sp.

**Distribution.** Upper Bajocian of Calvados, NW France.

### Tab. 11 - Synthesis of measurements and regression statistics for *Lissoceras maerteni* n. sp. [m].

<table>
<thead>
<tr>
<th>L. maerteni</th>
<th>h = H/D</th>
<th>w = W/D</th>
<th>u = U/D</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 measures (min/max)</td>
<td>35.3 - 37.8</td>
<td>25.4 - 28.8</td>
<td>37.8 - 39.9</td>
<td>72.1 - 77.10</td>
</tr>
<tr>
<td>mean of 3 measures</td>
<td>36.50</td>
<td>27.40</td>
<td>38.53</td>
<td>75.13</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>1.25</td>
<td>1.78</td>
<td>1.18</td>
<td>2.67</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.72</td>
<td>0.97</td>
<td>0.68</td>
<td>1.54</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>34.00 - 39.00</td>
<td>23.84 - 30.96</td>
<td>36.17 - 40.89</td>
<td>69.79 - 80.47</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>53.06 - 37.94</td>
<td>25.46 - 29.34</td>
<td>37.17 - 39.89</td>
<td>72.05 - 79.21</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>R² = 0.99</td>
<td>y = 0.62x + 0.66</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Genus *Semilissoceras* gen. n.

**Type-species:** *Semilissoceras ellipticum* n. sp.

**Etymology.** Genus name combined with the prefix semi-, denoting partially ribbed and smooth.

**Other species included:** In addition to the type species, the genus *Semilissoceras* comprises at least four Bajocian species from the Mediterranean-Caucasian Subrealm. Two new species: *S. turgidulum*.
and S. castellatum; and two species previously assigned to the genus Lissoceras: S. seminulatum (Buckman) and S. depereti (Flamand). The species S. lydei (Imlay, 1973, p. 77, pl. 40, figs 24-33), from the Snowshoe Formation at the Izee area, Oregon, lower Bajocian, also belongs to this new genus.

**Description.** Dimorphic taxon of small to medium size. Macroconchs up to 85 mm, bearing simple or sinuous aperture. Microconchs reaching 35 mm, with lateral lappets. Adult body chamber length between a half and three-quarters of last whorl. Ontogenetic maturity indicated by the uncoiling of umbilical seam, with decreasing compression of the whorl section and development of secondary ribs without ventral interruption near the peristome, associated with crowding and simplification of the last septal sutures.

Mid-evolute to mid-involute, discocones to planorbicons. Shells are compressed with subelliptical to subtriangular whorl sections, which becomes less compressed in the adult stage (W/H=45-78%, Fig. 20A). The umbilicus is moderately open (U/D= 20-25%, Fig. 20B) and shallow to moderately deep, with moderately steep walls and somewhat rounded or distinct umbilical edge. The flanks are slightly convex, with inner flanks sloping towards the umbilical edge. Convex venter, sometimes with incipient ventrolateral edges. Ornamentation consisting of sigmoid or falcoïd and fasciculate ribs, and sigmoid radial growth lines with peripheral projection. The ribs are relatively homogeneous, commonly fine and dense, single and bifurcate, blunt and with low relief, very weak or absent on the inner half of the whorls, become stronger towards the ventrolateral area, with furcation point on the outer one-third of the flank. The primaries are sometimes bundled at about two-thirds whorl height. The number of external ribs increases from shell size less than 20 mm, reaching about 38-60 ribs per half whorl. The external ribs may represent bifurcation of primaries or intercalation, uniformly developed. Subradial, rursiradiate or slightly turned forwards, external ribs end abruptly on the edge of the periphery or meet about the central line of the periphery, alternate or opposite in the phragmocone, becoming continuous, subradial or slightly projected forwards at the ventrolateral area in adult stage. The suture line (Fig. 22) is relatively complex with short lobe E, deep lobe L, saddle L/U and suspensive lobe with U and U developed, beside other umbilical elements much smaller.

**Remarks.** The microconchs of *Semilissoceras* are discocones with more compressed whorl section, more evolute coiling and egression of the umbilical seam in the adult body chamber. The macroconchs of *Semilissoceras* differs from those of *Lissoceras* mainly by the presence of ribs. *Semilissoceras* differs from *Bradfordia* Buckman, 1910 (type species by original designation B. biuniforhalata Buckman, 1910 in 1909-1930, pl. 10, figs 4-5, holotype from the Inferior Oolite, “Fossil Bed” of Bradford Abbas, Dorset) commonly being more compressed with sharp or raised umbilical edge and simple suture, by the absence of spiral depression bordering the umbilical edge on the inner area of the whorl. *Etropolia* Sapunov, 1971 (type species by

---

**PLATE 4**

Figs 1-8, 12, 13, 15-17 - *Lissoceras bungii* Sturani, 1967. [M & m].
1) MGP-PU 112827, [M], Maizet, middle Garantiana Zone. 2) MGP-PU 112792, [M], Maizet, upper Garantiana Zone. 3) MGP-PU 112766, [m], Sainte-Honorine-des-Perthes, upper Parkinsoni Zone. 4) MGP-PU 112852, [m], Maizet, middle Garantiana Zone. 5) MGP-PU 112853, [m], Maizet, upper Garantiana Zone. 6) MGP-PU 112787, [M], Sainte-Honorine-des-Perthes, upper Parkinsoni Zone. 7) MGP-PU 112851, [m], Maizet, middle Garantiana Zone. 8) MGP-PU 112765, [m], Sainte-Honorine-des-Perthes, upper Parkinsoni Zone. 12) MGP-PU 112833, [M], Maizet, upper Garantiana Zone. 13) MGP-PU 112784, [M], Sully, upper Bajocian. 15) MGP-PU 112781 [M], Sainte-Honorine-des-Perthes, upper Parkinsoni Zone. 16) MGP-PU 112772, [M], Sully, upper Bajocian. 17) MGP-PU 112779, [M], Sully, upper Bajocian.

Fig. 9 - *Lissoceras pusillum* Sturani, 1971. [m].
9) MGP-PU 36068, holotype, Troch 1, Romani Subzone.
10) MGP-PU 35790, Monte Meletta, upper Niortense Zone.
11) MGP-PU 35789, lectotype, Monte Meletta, upper Niortense Zone. 14) MGP-PU 112786, Sully, upper Bajocian (see text-fig. 19B).

Figs 18, 19 - *Lissoceras meleteni* n. sp. [m].
18) MGP-PU 112998, holotype, Sully, upper Bajocian. 19) MGP-PU 112999, paratype, Sully, upper Bajocian.

Figs 20-26 - *Semilissoceras ellipticum* n. sp. [M & m].
20) AB104U80/2, [M], Murtenquelle, upper Laeviuscula Zone. 21) MAP-MT2c/279, [m], allotype, Masada Toyuela, lower Laeviuscula Zone. 22) M10U50/5, [M], paratype, Moscardon, lower Laeviuscula Zone. 23) MAP-MT2c/274, [M], paratype, Masada Toyuela, lower Laeviuscula Zone. 24) MAP-MT2d/277, [M], paratype, Masada Toyuela, upper Laeviuscula Zone. 25) MAP-MT2d/275, [M], paratype, Masada Toyuela, upper Laeviuscula Zone. 26) MAP-MT2d/273, [M], holotype, Masada Toyuela, upper Laeviuscula Zone.

Scale bars of plate and top-right panel equal 10 mm, except figs. 18, 19 with scale bar 5 mm. Asterisk marks the beginning of the body chamber. Specimens were whitened prior to photography.
original designation *Harpoceras blumius* De Gregorio, 1886, pl. 18, fig. 5, a synonym of *Oppelia platyomphala* Vacek 1886, pl. 9, fig. 8, after Geczy 1967, p. 227, and Westermann 1969, p. 47) is more evolute with ribbing more uniformly developed and saddle E/L higher than L/U. *Iokastelia* Renz, 1925 (type species by original designation *Oppelia (Iokastelia) hebenae* Renz 1925, pl. 2, figs 3, 3a, lectotype designated by Sapunov 1971, p. 79, from Monte San Giuliano/Erice, Western Sicily) shows raised umbilical edge bordered by a prominent funnel-like spiral depression, and rursiradiate ribs on the outer half of the whorls that become stronger towards the ventrolateral area. *Protoecotraustes* Spath, 1928 in 1927-1933 (type species by original designation *P. dundriensis* Spath, pl. 9, fig. 7, holotype also figured by Arkell et al. 1957, p. L272, fig. 315/7 and Sapunov 1963, pl. 1, fig. 8, from the Inferior Oolite of Dundry, Somerset, England, lower Bajocian, Sauzei Zone) shows smooth inner whorls and aperture with lappets, like the microconchs of *Semilissoceras* and *Lissoceras*, but develops sigmoid ribs ending at ventrolateral clavi and tabulate venter on the outer whorl.

*Toxamblyites* Buckman, 1924 (type species by original designation *T. arcifer* Buckman 1924 in 1909-1930, pl. 473, holotype from the “Ironshot Bed” of Dundry, Somerset, Dorset, lower Bajocian, Sauzei Zone) differs from *Semilissoceras* in having falcoid ribbing on the outer half of whorl sides that is projected as blunt chevrons over the venter.

*Amblyoxyites* Buckman, 1922 (type species by original designation *A. amblys* Buckman 1922 in 1909-1930, pl. 303, holotype from Stoford, Somerset, Dorset, lower Bajocian, Sauzei Zone) have more complex suture line, spiral depression on the inner area of the whorl and external ribs projected or forming blunt chevrons.

*Praeoppelia* Westermann, 1969 (type species by original designation *Bradfordia? (Praeoppelia) oppeliiformis* Westermann 1969, pl. 10, fig. 6 and pl. 20, holotype from the upper Kialagvik Formation at Wide Bay, Alaska Peninsula, lower Bajocian, Sowerbyi Zone or Widebayense Zone after Taylor 2014) is characterized by very involute coiling, with almost flat whorl sides and greatest whorl-breadth at the umbilical edge, and by narrow, rounded to fastigate and feebly keeled venter.

*Hebetoxyites* Buckman, 1924 (type species by original designation *Hebetoxyites heber* Buckman 1924 in 1909-1930, pl. 475, holotype from the Lower White Ironshot of Dundry in Avon, England) develops blunt fastigate venter on the mid and outer whorls, without ribs projected or forming chevrons over the venter.

**Distribution.** The oldest known species of *Semilissoceras* are *S. ellipticum* and *S. turgidulum*, from Moscardon and Masada Toyuela, Iberian Range, lower Bajocian, lower Laeviuscula Zone, Ovale Subzone. The youngest fossil of this genus is the specimen of *S. costellatum* known from Teillon, Alpes-de-Haute-Provence, upper Bajocian, Garantiana Zone. Diverse records of early Bajocian possible representatives in separate palaeobiogeographical provinces suggest a pandemic distribution of *Semilissoceras* in the Tethys-Panthalassa Realm: NW European (Buckman 1923 in 1909-1930; Dietze

**Semilissoceras ellipticum** n. sp. [M & m]

Figs 20-22; Pl. 4, figs 20-26

v 1983 *Bradfordia* (Praeoppelia) *cfr. gracilobata* (Vacek) - Pavia, pl. 7, fig. 9.

v 1985 Praeoppelia cf. gracilobata (Vacek) - Fernandez-Lopez, p. 182, pl. 15, fig. 6.

**Diagnosis:** Macroconchiate (Dmax over 60 mm) and microconchiate (Dmax over 35 mm) *Semilissoceras*. Very compressed shell (W/H = 45-59), planar or feebly arched flanks, umbilicus with short wall and distinct edge. Subradial or slightly turned forwards, homogeneous, fine and dense, external ribs on the outer forth of flank.

**Etymology:** After the form of an ellipse that characterize the whorl section of the species.

**Types:** The holotype MAP-MT2d/273 (Pl. 4, fig. 26) is from Masada Toyuela (Albarracin, Teruel), beds 2d in Fernandez-Lopez 2014, upper Laeviuscula Zone. Five paratypes: 4 from Masada Toyuela, upper Laeviuscula Zone (MAP-MT2d/275, 277, MAP-MT2e/274, 279: Pl. 4, figs 21, 23-25) and 1 from Moscardon, Lower Laeviuscula Zone (M10U50/5: Pl. 4, fig. 22). The microconch MAP-MT2e/279 is regarded as the allotype of the species. These six specimens are summarized in Table 12.

**Measurements:** See Appendix. Measured extremes for diameter: [M] 16.0 - 42.0 mm; [m] 35 mm. Values for h, w and u are summarized in Table 12.

**Description.** Adult shells of small to medium size, from macroconchs surpassing 60 mm of diameter to microconchs reaching 35 mm. Only one fragmentary microconch known (Pl. 4, fig. 21), with incomplete body chamber. Mid-evolute to mid involute discocones. Shells are compressed with subelliptical whorl section and maximum width at the middle of the flank. The umbilicus is moderately open (U/D = 22-25) and shallow, with somewhat rounded or distinct, but not sharp or raised, umbilical edge. The flanks are planar or slightly convex, with inner flanks sloping towards the umbilical edge. Convex venter, sometimes with incipient ventrolateral edges. Ornamentation consists of sigmoid or falcoidal and fasciculate ribs, very weak or absent on the inner half of the whorls and stronger towards the ventrolateral area. The ribs are relatively homogeneous, blunt, fine and dense, single and bifurcate, with furcation point on the outer third of the flank. The primaries are sometimes bundled at about two-thirds whorl height. The external ribs, subradial or slightly turned forwards, end on the edge of the periphery or meet about the central line of the periphery, alternate or opposite in the phragmocone (Pl. 4, fig. 26), becoming continuous, subradial or slightly projected forwards at the ventrolateral area in adult stage (Pl. 4, fig. 25). The suture line (Fig. 22A-C) is relatively complex with short lobe E, deep and asymmetrically trifid lobe L, saddle L/U, asymmetrical and higher that E/L, and suspensive lobe with inner flanks sloping towards the umbilical edge. Convex venter, sometimes with incipient ventrolateral edges. Ornamentation consists of sigmoid or falcoidal and fasciculate ribs, very weak or absent on the inner half of the whorls and stronger towards the ventrolateral area. The ribs are relatively homogeneous, blunt, fine and dense, single and bifurcate, with furcation point on the outer third of the flank. The primaries are sometimes bundled at about two-thirds whorl height. The external ribs, subradial or slightly turned forwards, end on the edge of the periphery or meet about the central line of the periphery, alternate or opposite in the phragmocone (Pl. 4, fig. 26), becoming continuous, subradial or slightly projected forwards at the ventrolateral area in adult stage (Pl. 4, fig. 25). The suture line (Fig. 22A-C) is relatively complex with short lobe E, deep and asymmetrically trifid lobe L, saddle L/U, asymmetrical and higher that E/L, and suspensive lobe with U₂ and U₃ developed beside other umbilical elements much smaller.

**Remarks:** Praeoppelia gracilobata (Vacek, 1886, p. 83, pl. 10, figs 1 and 4, only; lectotype designation by Sapunov, 1971, p. 80, from the “Oolite di San...
Vigilio", Lake Garda, N Italy) displays very involute coiling (U/D<13), with slightly raised umbilical edge and faint ribbing that fades out on the body chamber (cf. Galácz et al. 2015; Metodiev & Tsvetkova 2015).

Bradfordia liomphala (Buckman, 1910) shows spiral depression bordering the umbilical edge on the inner area of the whorl.

The specimen Lissoceras sp. described by Imlay (1973, p. 77, pl. 36, figs 5-7, 11-12) from the upper Weberg Member, Snowshoe Formation, lower-middle part of the Lower Bajocian at Oregon, show also compressed whorls and faint gently flexuous ribs; however, Imlay’s unnamed taxon show more involute coiling with simpler suture line.

Distribution. The type specimens recorded in the limestone beds of the upper Laeviuscula Zone at Masada Toyuela sections confirm the relatively common occurrence of Semilissoceras ellipticum in the upper Laeviuscula Zone. Furthermore, the specimen identified in the lower Laeviuscula Zone of Moscardon confirms the presence of this species in the Ovale Subzone. These results are corroborated by several representatives of this species from the Ovale and Laeviuscula subzones, respectively, identified at Beaumont, France (Pavia 1983, pl. 7, fig. 9) and Murtinheira, Cabo Mondego (Pl. 4, fig. 20).

Semilissoceras turgidulum n. sp. [M & m]
Figs 20-22; Pl. 5, figs 1-6
v 1985 Lissoceras semicostulatum - Fernandez-Lopez, text-fig. 15, pl. 15, fig. 5.

Diagnosis: Macroconchiate (Dmax over 60 mm) and microconchiate (Dmax over 35 mm) Semilissoceras. Compressed shell (W/H= 54-63), feebly arched flanks, shallow to moderately deep umbilicus with short wall and rounded edge; subradial or slightly turned forwards, homogeneous, fine and dense, external ribs on the outer forth of flank.

Etymology: After the slightly inflated, swollen or turgid form that characterize the whorls of the shell.

Types: The holotype (M9U50/1: Pl. 5, fig. 1) and the allootype (M9L20/2: Pl. 5, fig. 5) from Moscardon (Teruel, Iberian Range), lower Laeviuscula Zone. Three paratypes from the Iberian Range: a macroconch from Masada Toyuela, lower Laeviuscula Zone (MT2a/95: Pl. 5, fig. 3), a macroconch from Rambla La Gotera, Saldon, Teruel, Laeviuscula Zone (G10U70/4: Pl. 5, fig. 2) and a macroconch from Moscardon, Teruel, lower Laeviuscula Zone (M9L20/3: Pl 5, fig. 4). These five specimens are reelegant elements.

Locus typicus: The section of Moscardon, Teruel, Iberian Range.

Stratum typicum: Lower Bajocian, lower Laeviuscula Zone, Ovale Subzone, bed M9U50 from the section-1 at Moscardon (Fernandez-Lopez 1985) belonging to the El Pedregal Formation (Gomez & Fernandez-Lopez 2004).

Material: In addition to the five type specimens, an immature macroconch from the middle Laeviuscula Zone at Sanford Lane, Dorset (Pl. 5, fig. 6).

Measurements: See Appendix. Measured extremes for diameter: [M] 20.0 - 56.0 mm; [m] 33.6 mm. Values for h, w and u are summarized in Table 13.

<table>
<thead>
<tr>
<th>S. turgidulum</th>
<th>h = H/D x 100</th>
<th>w = W/D x 100</th>
<th>u = U/D x 100</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 measures (min/max)</td>
<td>43.0 - 51.1</td>
<td>23.9 - 28.8</td>
<td>21.5 - 23.4</td>
<td>54.3 - 62.5</td>
</tr>
<tr>
<td>mean of 6 measures</td>
<td>46.38</td>
<td>26.48</td>
<td>22.13</td>
<td>57.15</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>3.05</td>
<td>1.79</td>
<td>0.78</td>
<td>3.80</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>1.24</td>
<td>0.73</td>
<td>0.32</td>
<td>1.55</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>40.28 - 52.48</td>
<td>22.90 - 30.06</td>
<td>20.57 - 23.69</td>
<td>49.55 - 64.75</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>43.90 - 48.86</td>
<td>25.02 - 27.94</td>
<td>21.49 - 22.77</td>
<td>54.05 - 60.25</td>
</tr>
<tr>
<td>correlation index and regression W on H: R² = 0.96 - y = 0.55x + 0.29</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. turgidulum</td>
<td>h = H/D x 100</td>
<td>w = W/D x 100</td>
<td>u = U/D x 100</td>
<td>W/H x 100</td>
</tr>
<tr>
<td>1 measure</td>
<td>43.2</td>
<td>21.4</td>
<td>28.6</td>
<td>49.7</td>
</tr>
</tbody>
</table>
**Description.** Adult shells of small to medium size, from macroconchs surpassing 60 mm of diameter to microconchs reaching 35 mm. Mid-evolute to mid-involute, discocones. Shells are compressed with subelliptical to suboval whorl section and maximum width at the middle of the flank. The umbilicus is moderately open (U/D = 22-30, Fig. 20) and shallow, with rounded umbilical edge. The flanks are slightly convex, with inner flanks sloping towards the umbilical edge. Convex venter. Ornamentation consists of sigmoid or falcoide and fasciculate ribs, very weak or absent on the inner half of the whorls and stronger towards the ventrolateral area. The external ribs are subradial or slightly turned forwards, relatively homogeneous, blunt, fine and dense, single and bifurcate on the outer forth of the flank. They end on the edge of the periphery or meet about the central line of the periphery, and become continuous, subradial or slightly projected forwards at the ventrolateral area in adult stage. The suture line (Fig. 22D) is relatively complex with short lobe E, deep and asymmetrically trifid lobe L, saddle L/\(U_2\) asymmetrical and higher that E/L, and suspensive lobe with \(U_2\) and \(U_3\) developed beside other umbilical elements much smaller.

**Remarks.** *Semilissoceras ellipticum*, the type species of the new genus, is very similar to *S. turgidulum*. However, the latter taxon displays stouter whorls and more rounded umbilical edge. These two species are chronostratigraphically coincident at least in the middle Laeviuscula Zone, but *S. turgidulum* is dominant in the lower Laeviuscula Zone, Oval Subzone, whereas *S. ellipticum* is common in the upper Laeviuscula Zone at the Iberian Range.

*Semilissoceras* cf. *semicostulatum*, described by Imlay (1964, p. 39) from an ex-situ specimen at the top of the Red Glacier Formation, lower Bajocian, at northwest side of Cook Inlet, southern Alaska (roughly equivalent to the upper Laeviuscula and lower Propinquans zones: Westermann 1992, Taylor 2014), shows similar compressed whorl section and short homogeneous external ribs limited at the ventral shoulder; however, Imlay’s specimen reaches larger adult size. This Alaskan record is relevant from the palaeobiogeographical point of view as it is evidence of early lissoceratid dispersal throughout the whole Tethys-Panthalassa Realm, possibly via the so-called Hispanic Corridor, the Central-Atlantic seaway active during the Bajocian for bidirectional exchange of ammonite faunas between the East Pacific and the Mediterranean-Caucasian subrealms (Fernandez-Lopez & Pavia 2015, and references therein). The same meaning may be assigned to *Semilissoceras hydei* (Imlay 1973, p. 77, pl. 40, figs 24-33; Westermann 1992, p. 45) from the Crassico-status Zone of Oregon that, however, shows rursi-radiate and fasciculate ribs.

**Distribution.** The reelaborated fossils recorded in limestone beds of the lower Laeviuscula
Zone at Moscardon and Masada Toyuela sections confirm the occurrence of *Semilissoceras turgidulum* in the Ovale Subzone. Furthermore, the identified juvenile representative from Somerset (Pl. 5, fig. 6) confirms the persistence of this species in the middle Laeviuscula Zone.

**Semilissoceras depereti** (Flamand, 1911) [M]  
Fig. 20; Pl. 5, fig. 13

1911 Oppelia Depereti Flamand, p. 886, pl. 4, fig. 2.  
v 1985 Lissoceras depereti - Fernandez-Lopez, p. 168, pl. 15, fig. 4.  
1986 Lissoceras depereti - Sandoval, p. 438, text-fig. 2, pl. 1, figs 1-5  
.cum syn.).

v 1989 Lissoceras depereti - Fernandez-Lopez et al., text-fig. 2.

**Description.** Medium-sized macroconch (Dmax over 75 mm) with moderately open umbilicus. The whorl section is oval with maximum width at the inner fourth of the flank. The umbilical wall is relatively short with rounded edge; there is no trace of perumbilical depression. The outer forth of flank converges to the venter without any ventrolateral edge. The venter is narrow and regularly arched. Sigmoidal ornamentation is visible on both the shell and the internal mould. Ribs inflect in the middle side; the internal ribs are proverse and very light, whereas blunt ribs (52 on half-whorl at 45 mm diameter) form the external branch that show a recti- to rursiradiate course and fade at the ventral shoulder. The suture line shows a large saddle at the bottom of E lobe; according literature, the saddle E/L is short and L/U is high and asymmetrical.

**Remarks.** No microconch is so-far known. Sandoval (1986, p. 439) discussed the possibility to synonymize *Semilissoceras deperetii* and *S. semicostulatum*. The two species differ for architectural parameters and ribbing: the oval-subtriangular whorl section with narrow venter and the longer, slightly rursiradiate external ribs of *S. depereti* differ in comparison with the oval whorl section, the large venter, the perumbilical depression and the shorter rectiradiate external ribs of *S. semicostulatum*.

**Distribution.** The records from literature point to the lower Bajocian, upper Laeviuscula and lower Propinquans zones. The specimens studied from Albarracin and Murtinheira correspond to the upper Laeviuscula Zone.

**Semilissoceras semicostulatum** (Buckman, 1923) [M]  
Figs 20, 21, 23, 24; Pl. 5, figs 7, 8, 10.

v 1923 Lissoceras semicostulatum Buckman 1909-30, pl. 400.  
v 1983 Lissoceras semicostulatum - Pavia, p. 142 (pars; non pl. 7, figs 5-6 = *S. astellatum* n. sp.).  
non 1985 Lissoceras semicostulatum - Fernandez-Lopez, text-fig. 15, pl. 15, fig. 5 (= *S. turgidulum* n. sp.).  
non 1988 Lissoceras semicostulatum - Seyed-Emami, p. 78, text-fig. 24.  
non 1989 Lissoceras (Lissoceras) semicostulatum - Benshili, p. 174, pl. 21, fig. 11 (= *S. astellatum* n. sp.).  
non 1990 Lissoceras (Lissoceras) semicostulatum - Benshili, p. 77, pl. 1, fig. 3 (= *S. astellatum* n. sp.).  
non 1997 Lissoceras semicostulatum - Rulhuau, p. 7, pl. 4, figs 14-15 (= *S. astellatum* n. sp.).  
non 2006 Lissoceras semicostulatum - Rulhuau, p. 112, pl. 88, fig. 3 (= *S. astellatum* n. sp.).  
non 2007 Lissoceras? cf. semicostulatum - Dietze et al., p. 20, fig. 7c.  
non 2011 Lissoceras semicostulatum - Rulhuau, p. 68, pl. 30, fig. 3 (= *S. astellatum* n. sp.).  
v 2013 Lissoceras semicostulatum - Pavia et al., p. 142.  
2015 Lissoceras depereti - Chandler & Wircher, pl. 22, fig. 1.

**Material:** Two lower Bajocian specimens. A reelaborated macroconch from Masada Toyuela section, Albarracin, Iberian Range, uppermost Laeviuscula Zone (MT3/1: Pl. 5, fig. 13) and a re-sedimented macroconch (AB93b/1) from the Murtinheira section, uppermost Laeviuscula Zone.

**Material:** Besides the holotype, two specimens from the Sauzei (= Propinquans) Zone of Sandford Lane in Dorset: Sh-SL X40390 (Fig. 23B), SMNS 70396/3: Pl. 5, fig. 10, one fragmentary internal mould from the Maizet section (upper Humphriesianum Zone: MGPUT-PU 113011, Pl. 5, fig. 8), one shelly specimen from the Chiran outcrop (Propinquans Zone: MGPUT-PU 113031) and one compressed composite mould from the Chaudon section (lower Humphriesianum Zone: MGPUT-PU 113024: Pl. 5, fig. 7).

**Diagnosis:** In absence of the original diagnosis we propose the following: Macroconchiate *Semilissoceras* mid-evolute shell with suboval whorl section and arched venter; inclined umbilical wall; dense, blunt, slightly rursiradiate to rectiradiate ribs on the outer half flank.

**Types:** The holotype is the specimen described by Flamand (1911) from the Propinquans Zone of the NW Djebel-Malah, Mecheria, Algeria (Bassoullet 1973, p. 219; Fernandez-Lopez 1985, p. 169; Sandoval 1986, p. 439).

**Material:** In absence of the original diagnosis we propose the following: Macroconchiate *Semilissoceras* mid-evolute shell with suboval whorl section and arched venter; inclined umbilical wall; dense, blunt, slightly rursiradiate to rectiradiate ribs on the outer half flank.

**Types:** The holotype is the specimen described by Flamand (1911) from the Propinquans Zone of the NW Djebel-Malah, Mecheria, Algeria (Bassoullet 1973, p. 219; Fernandez-Lopez 1985, p. 169; Sandoval 1986, p. 439).

**Material:** Besides the holotype, two specimens from the Sauzei (= Propinquans) Zone of Sandford Lane in Dorset: Sh-SL X40390 (Fig. 23B), SMNS 70396/3: Pl. 5, fig. 10, one fragmentary internal mould from the Maizet section (upper Humphriesianum Zone: MGPUT-PU 113011, Pl. 5, fig. 8), one shelly specimen from the Chiran outcrop (Propinquans Zone: MGPUT-PU 113031) and one compressed composite mould from the Chaudon section (lower Humphriesianum Zone: MGPUT-PU 113024: Pl. 5, fig. 7).

**Measurements:** See Appendix. The measured diameter is 63.0 mm.
**Description.** Medium-sized macroconch with moderately open umbilicus. The whorl section is oval with maximum width in the middle flank. The umbilical wall is short, and the edge is rounded; a periumbilical depression is visible on the holotype. The outer third of flank converges to the venter without any ventrolateral edge. The venter is broad and regularly arched. Blunt ribs are present on the outer forth of flanks and visible both on the shell and the internal mould; they are relatively dense (47 on half-whorl at 50 mm diameter) and run rectiradiate up to the rounded ventrolateral edge of the flank. Feeble, proverse growth lines are visible on the shell up to the mid-flank. The suture line (cf. Fig. 23) shows a large saddle at the bottom of lobe E and a very short saddle E/L; the saddle L/U is dominant in the middle part of the suture line on the deep lobe L and on the relatively wide suspensive lobe that bears 4 auxiliaries saddles.

**Remarks.** No microconch has been attributed so far to *Semilissoceras semicostulatum*. The species is rarely figured in literature as shown by the short synonymy list. Other two species, *S. depereti* (Flamand) and *S. costellatum* n. sp. (see below for differences), show similar ribbing, so that quotations without figures can be accepted only with doubt; it is the case of Parson’s records (1974, p. 166 and 1976, p. 125, 133) from the Propinquans and Humphriesianum zones of Dorset.

**Distribution.** The holotype is a reebralorated fossil recorded from the Laeviuscula Zone of Dorset; this means that the appearance of *S. semicostulatum* might be also older than what reported in the literature. The specimen figured by Dietze et al. (2007, fig. 7c) came from the lower Laeviuscula Zone, Ovale subzone, bed 8bi, at Little Down Wood, Dundry Hill, Somerset. Further records are from the Propinquans Zone of Dorset (Chandler pers. comm.; Parsons 1974, 1976). The occurrence of this species was mentioned also from the upper Laeviuscula Zone at Murtinheira, Cabo Mondego (Fernandez-Lopez et al. 1989, fig. 2, bed 98). The most recent biochronological datum for *S. semicostulatum* is by the reseadimented fossil from the early Humphriesianum Zone (Romani Subzone) of Chaudon (Pavia 1983), whereas the record from

---

**Tab. 14 - Synthesis of measurements and regression statistics for [M] *Semilissoceras semicostulatum* (Buckman, 1923) [M].**

<table>
<thead>
<tr>
<th>S. semicostulatum [M]</th>
<th>h = H/D x 100</th>
<th>w = W/D x 100</th>
<th>u = U/D x 100</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 measures (min/max)</td>
<td>46.9 - 50.0</td>
<td>35.0 - 36.5</td>
<td>20.0 - 24.7</td>
<td>70.0 - 76.1</td>
</tr>
<tr>
<td>mean of 5 measures</td>
<td>48.58</td>
<td>35.82</td>
<td>22.66</td>
<td>73.72</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>1.38</td>
<td>0.54</td>
<td>1.75</td>
<td>2.60</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.62</td>
<td>0.24</td>
<td>0.78</td>
<td>1.16</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>45.82 - 51.34</td>
<td>34.74 - 36.90</td>
<td>19.16 - 26.16</td>
<td>70.52 - 76.92</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>47.34 - 49.82</td>
<td>35.34 - 36.30</td>
<td>21.10 - 24.22</td>
<td>71.40 - 76.04</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>( R^2 = 0.92 )</td>
<td>( y = 0.71x + 0.52 )</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

**Fig. 23 - *Semilissoceras semicostulatum* (Buckman, 1923), Laeviuscula Zone, Sandford Lane, Dorset, UK. (A) holotype BGS-47188 (Buckman, 1923, pl. 400), (B) Sh-SL X40390. Scale bar equals 10 mm. The authors wish to thank Robert Chandler for providing details and images of the specimens that are part of the Wessex Cephalopod Club collection.**
Calvados (Pavia et al. 2013) concerns a reelected fossil from the condensed fossil assemblage referred to as the upper Humphriesianum Zone.

**Semilissoceras costellatum** n. sp. [M]

Figs 20, 21, 24, 25; Pl. 5, figs 9, 11, 12, 14-16.

v 1971 Lissoceras sp. ind. aff. oolithicum - Surani, p. 91, pl. 6, figs 3-4.

v 1983 Lissoceras (Lissoceras) semicostulatum - Pavia, p. 71, pl. 7, figs 5-6.

1989 Lissoceras (Lissoceras) semicostulatum - Benshili, p. 174, pl. 21, fig. 11.

1990 Lissoceras (Lissoceras) semicostulatum - Benshili, p. 77, pl. 1, fig. 3.


2000 Lissoceras sp. - Besnosov & Mitta, p. 51, pl. 4, fig. 4.

2006 Lissoceras semicostulatum - Rulleau, p. 112, pl. 88, fig. 3.

2011 Lissoceras semicostulatum - Rulleau, p. 68, pl. 30, figs 3a, b.

**Diagnosis:** Macroconchiate *Semilissoceras*; mid-evolute shell with subtriangular whorl section and narrow venter; steep umbilical wall; dense, thin, fasciculate and reccordiat ridge on the outer half flank.

**Etymology:** From the thin ribs (costellae) that adorn the outer half flank.

**Types:** The holotype is the reelected macroconch MGPUT-PU 112835 (Pl. 5, fig. 9) from Maizet (Calvados), bed 5, upper Humphriesianum Zone. Five paratypes: the reelected macroconchs MGPUT-PU 112737 (Pl. 5, fig. 11) and MGPUT-PU 112736 (Pl. 5, fig. 14) from Sully (Calvados), bed 5a, Niortense-Garantiana zones; the rese dmend macroconch SMNS 70396/2 (Pl. 5, fig. 15) from Sandford Lane, Propinquans Zone; the rese dmend macroconch MGPUT-PU 113015 (Pl. 5, fig. 12) from Chaudon (Alpes-de-Haute-Provence), bed 397, Romani Subzone; the reelected macroconch MGPUT-PU 113010 (Pl. 5, fig. 16) from Teillon (Alpes-de-Haute-Provence), Garantiana Zone.

**Locus typicus:** The section of Maizet, south of Caen, Calvados, NW France, where the “Oolithe ferruginese de Bayeux” Formation was described by Pavia et al. (2013).

**Stratum typicum:** Lower Bajocian, Humphriesianum Zone. Pavia et al. (2013, p. 142) indirectly referred the Maizet bed 5 to the late Humphriesianum Biochron. *S. costellatum* n. sp. is not present in bed 4 whose rese dmend fossils refer to the lower Humphriesianum Zone, Romani Subzone. We can thus infer that the holotype of *S. costellatum* n. sp. pertains to the Umbilicum or Blageni subzones within the Humphriesianum Zone.

**Material:** 18 specimens from different sites in Calvados and 1 from Sandford Lane in Dorset. 10 specimens from Alpes-de-Haute-Provence; 9 from Chaudon and 1 from Teillon. 11 specimens from the “Pseudonida alpinei” beds in Asago. 1 specimen from Chalot, Great Balkan.

**Measurements:** See Appendix. Measured extremes for diameter: 11.9 - 42.9 mm. Values for h, w and u are summarized in Table 15.

<table>
<thead>
<tr>
<th><strong>S. costellatum</strong> [M]</th>
<th>h = H/D x 100</th>
<th>w = W/D x 100</th>
<th>u = U/D x 100</th>
<th>W/H x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>31 measures (min/max)</td>
<td>47.4 - 54.9</td>
<td>30.9 - 39.4</td>
<td>20.4 - 24.9</td>
<td>61.3 - 78.3</td>
</tr>
<tr>
<td>mean of 31 measures rec</td>
<td>50.05</td>
<td>35.14</td>
<td>22.85</td>
<td>70.28</td>
</tr>
<tr>
<td>standard deviation [sd]</td>
<td>1.58</td>
<td>1.80</td>
<td>1.18</td>
<td>3.98</td>
</tr>
<tr>
<td>standard error [se]</td>
<td>0.28</td>
<td>0.32</td>
<td>0.21</td>
<td>1.71</td>
</tr>
<tr>
<td>confidence interval on sd</td>
<td>46.89 - 53.21</td>
<td>31.54 - 38.74</td>
<td>20.49 - 25.21</td>
<td>62.32 - 78.24</td>
</tr>
<tr>
<td>confidence interval on se</td>
<td>49.49 - 50.61</td>
<td>34.5 - 35.78</td>
<td>22.43 - 23.27</td>
<td>68.86 - 71.70</td>
</tr>
<tr>
<td>correlation index and regression W on H:</td>
<td>R² = 0.98 - y = 0.62x - 1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Description.** Medium-sized form with moderately open umbilicus. The whorl section is rounded-subtriangular with maximum width at the inner third of the flank. The umbilical wall is steep, and the edge is rounded without periumbilical depression. The outer forth of flank converges to the venter without any ventrolateral edge. The venter is relatively narrow and regularly arched. Ornamentation is slightly sigmoidal. In the mid-flank it is represented by large, depressed ribs (73 on demi-tour 30.5 mm and 79 on demi-tour 32.5 mm diameters) that divide into thin ribs grouped in bundles of 2-3 at the outer forth of the flank; costellae run rectiradiate or slightly concave up to the rounded ventro-
Bajocian Lissoceratinae from the Mediterranean-Caucasian Subrealm
lateral edge. The suture line (Fig. 25) shows a large saddle at the bottom of lobe E and a short, deeply bipartite saddle E/L; the saddle L/U₂ is asymmetrical and dominate on the short saddle E/L and the deep, symmetrical lobe L; the relatively wide suspensive lobe bears 4 auxiliary saddles with deep and nearly symmetrical U₂.

**Remarks.** No microconch is so-far known. *Semilissoceras costellatum* n. sp. belongs to the morpho-structural group of *S. deperei* and *S. semicostulatum* for the external ribbing visible both on the shell and the internal mould; nevertheless, the new species differs for the shape and the intensity of such ornamentation characterized by fasciculate and thin ribs. Furthermore, *S. costellatum* shows a rounded-subtriangular whorl section with narrow venter against the suboval whorl section with large venter of *S. semicostulatum* (Fig. 24). The rib fasciculation of *Semilissoceras hydei* might recalls that of *S. costellatum* n. sp., but ribs in the north-American taxon are sharp and rursiradiate. *Lissoceras bukervi* Imlay (1962, p. A-6, pl. 1, figs 1-6, 9-12) from the upper Bajocian of Alaska shows a fine external ribbing; however, Imlay’s taxon has subovate whorl section with deep and narrow (u = 20,3) umbilicus.

*Semilissoceras costellatum* n. sp. is relatively common in the Bajocian “*Posidonia alpina* beds” of the Italian Southern Alps. Sturani (1971, p. 91) characterized *Lissoceras* sp. ind. aff. *oolithicum* as having “dense, fine falcate ribs”; this taxon from the lower HumphriesianZone of Troch locality fits well the new species. Furthermore, Sturani (1971, p. 92) assigned to *Lissoceras inflatum* Wetzel a specimen from the upper Niortense Zone of Monte Meletta (MGPUT-PU 35792: Pl. 5, fig. 17). Its fragmentary internal mould shows fine external ribs similar to those of *S. costellatum* n. sp., but its whorl section is more compressed; for this reason, this specimen is here recorded as *S. aff. costellatum*. Besides the material from Asiago, Sturani (1971, p. 92) mentioned a specimen from Bayeux that was housed in the palaeontological collections of Torino; this specimen is here listed with code MGPUT-PU 112738.

**Distribution.** The resedimented and re-elaborated fossils that constitute the type-series of *Semilissoceras costellatum* n. sp. range from the Propinquans Zone to the Garantiana Zone. Data from literature support this biochronostratigraphical range.

**CONCLUDING REMARKS**

The study of the conspicuous material of Lissoceratinae coming from different palaeobiogeographical areas of the Mediterranean-Caucasian Subrealm demonstrates that the Bajocian dimorphic lissoceratins during the Bajocian Stage differentiated in a number of taxa much greater than the records got from previous literature. At present, this number is almost triplicated (16 vs 6) with eight new species: *L. submediterraneun*, *L. maizetense*, *L. ovale*, *L. sturanii*, *L. maerteni*, *S. ellipticum*, *S. turgidulum*, *S. costellatum*. The dimorphism of Bajocian lissoceratins has been also discussed; the dimorphic pairing is described for *L. inflatum* Wetzel, *L. submediterraneun* n. sp., *L. sturanii* n. sp., *L. bangi* Sturani, *S. ellipticum* n. sp. and *S. turgidulum* n. sp., whereas it...
is still missing for two microconch taxa (L. maerteni n. sp., L. psilodiscus Sturani) and eight macroconchs taxa (L. psilodiscus (Schloenbach), L. oolithicum (d'Or-bigny), L. maizetense n. sp., L. ovale n. sp., L. meletense (Parona), S. depereti (Flamand), S. semicostulatum (Buckman), S. costellatum n. sp.).

From the morpho-structural and biochronological point of view, the Bajocian lissoceratins may be subdivided in four groups:

- **Semilissoceras semicostulatum**, S. depereti, S. ellipticum, S. turgidulum and S. costellatum, share suboval to compressed section and rectiradiate ribs on the outer half flank. Most taxa are limited to the lower Bajocian (Laeviuscula to Humphriesianum zones), whereas L. costellatum reaches the mid-upper Bajocian (Garantiana Zone).

- **Lissoceras oolithicum**, L. maizetense, L. ovale, L. sturanii show subtriangular to ovate whorl section, depressed ventral saddle at the bottom of the large lobe E and wide compressed lobe. The first two and the last taxa range from the top lower Bajocian (Humphriesianum zones) to the mid-upper Bajocian (Garantiana Zone) whereas L. ovale ranges through the whole upper Bajocian (Niortense to Parkinsoni zones). The microconchs L. pusillum and L. maerteni may be joined to the L. oolithicum morpho-group.

- **Lissoceras bangi** and L. meletense show ovate to globular whorl section, narrow lobe E, and narrow suspensive lobe. They are distributed through the upper Bajocian (Niortense to Parkinsoni zones) with L. bangi that reaches the lowermost Bathonian (basal Zigzag Zone).

- **Lissoceras psilodiscus**, L. inflatum and L. submediterraneum have highly compressed whorl section, narrow E and high ventral saddle. The last two taxa are distributed in the upper Bajocian; L. inflatum reaches the topmost Parkinsoni Zone where it is replaced by the lower Bathonian L. psilodiscus.

From a phylogenetic and microevolutionary point of view, such differentiated biochronological and morpho-structural features allow tracing several relationships among the Bajocian lissoceratins. The starting point is represented by **Semilissoceras ellipticum** and S. turgidulum followed by S. semicostulatum from the Laeviuscula Zone, the morphology of which (whorl section and ribs) leads back to the lowermost Bajocian forms of *Bradfordia* (see discussion below). As to the onset of diverse species of *Lissoceras*, after the contemporaneous S. depereti and S. semicostulatum, a crucial position seems to be assigned to S. costellatum for successive phyletic steps (Fig. 26):

1) the feeble ribs of L. maizetense may derive from those of S. costellatum in the lower Humphriesianum Zone;

2) L. oolithicum shows subtriangular whorl section similar to S. costellatum at the passage Pro-pinquans to Humphriesianum zones;

3) in the group of L. oolithicum, the morpho-structural similarities of L. sturanii and L. oolithicum suggest phylogenetic relationship, also supported by intermediate forms such as the specimen described as L. cf. oolithicum by Sandoval & Westermann (1986) from the topmost lower Bajocian of Oaxaca (S Mexico);

4) the resemblances of the suture line structure, namely the lobe E, the ventral region and the inflation of the shell between L. oolithicum and L. ovale confirm their close phylogenetic relationship;

5) from the morpho-structural point of view, L. sturanii represents a singular lissoceratin due to the small adult size and the low degree of ontogenetic and ontogenic variation;

6) the couple L. bangi and L. meletense is traceable to L. oolithicum by the intermediary of L. ovale that anticipates the rounded whorl section and the high saddle at the bottom of the ventral lobe E.

From a phyletic and macroevolutionary point of view (Fig. 26), Bajocian *Semilissoceras* and *Lissoceras* iteratively developed several lasting heterochronic trends of morpho-structural changes or peramorpholines, from moderately evolve discocones to platycones or planorbicones, more involute and more inflated (i.e., with larger values for shell inflation or thickness ratios), more weakly ornamented or smooth, with more frilled suture line and narrower lobe L. Three cases of such chronicles can be recognized among the following taxa:

1) *Semilissoceras ellipticum* < S. turgidulum < S. semicostulatum < S. costellatum, 2) *Lissoceras submediterraneum* < L. psilodiscus < L. inflatum, and 3) *Lissoceras oolithicum* < L. ovale < L. bangi < L. meletense. These successive species display increasing degrees of ontogenetic variation of morpho-structural features (e.g., as indicated by the ontogenetic trajectories through ratios of the aperture shape: Figs 3, 9, 15, 20) and higher degrees of ontogenetic variation with more involute and more inflated adult shells. Consequently, these diverse lineages underwent lasting palinge-
netic changes, eventually with similar peramorphic results, and represent iterative peramorphoclines. In this macroevolutionary context, *Lissoceras sturanii*, the micromorph species identified in the present study, can represent a paedomorphic lissoceratin belonging to the chronocline of *L. oolithicum*, originated from *S. costellatum* by progenesis and proterogenetic change with paedomorphic results. In contrast with the life-history strategy of *L. sturanii* as a progenic species, other proterogenetic taxa of Bajocian lissoceratins can represent neotenic species, such as *L. submediterraneum* and *S. ellipticum*, that display very low degrees of ontogenic and ontogenetic variation of morpho-structural features without evidence of reduced adult size.

As to the origin of *Semilissoceras* and *Lissoceras*, several authors (Sturani 1971; Fernandez-Lopez 1985; Sandoval 1986) pointed the attention on the genus-group *Bradfordia* Buckman, 1910 (see the general remarks on Lissoceratidae, herein): these genera share several morpho-structural elements such as the rounded venter without keel and the external ribs that are well marked in *Bradfordia s. l.* and in old species of *Semilissoceras*. The whorl section of most *Bradfordia* is compressed with depressed inner third of the flanks and elevated umbilical edge, being these last features absent in *Semilissoceras* and *Lissoceras*. However, among Bradfordiinae, the genus *Amblyocystites* Buckman, 1922 shows a high number of auxiliary saddles in the suspensive lobe and a short umbilical wall; such features, together with the external ribs, are in common with *Semilissoceras turgidulum*. These last morpho-structural features are well developed in the specimens here identified from the mid-Laeviuscula Zone of both Iberian Range and Dorset, that are here regarded as possible transitional haploceratoids between the Bradfordiinae typified by *A. amblys* and the Lissoceratinae represented by both the ribbed *Semilissoceras* and other taxa such as *Toxamblyites*. In this respect, the specimens cited by Parsons (1979, p. 141) as *L. aff. semicostulatum* and the juvenile figured by Dietze et al. (2007, fig. 7c) as *Lissoceras? cf. semicostulatum*, both from the lower Laeviuscula Zone at Dundry Hill, Somerset, might constitute a further intermediary in the lineage of the two subfamilies, or they can belong to *S. turgidulum*.

The genera *Semilissoceras* and *Lissoceras* are distinct monophyletic groups. The genus *Semilissoceras* represents a clade originated during the Aalenian/Bajocian transition, with species dispersal throughout diverse Tethyan subrealms during the early Bajocian. At least *Semilissoceras ellipticum* and *S. turgidulum* inhabited the eastern Iberian platform-system during the early Laeviuscula Chron, since they are recorded in the Iberian Range by polyspecific assem-

![Fig. 26 - Proposed phyletic relationships among diverse Bajocian Lissoceratinae from the Mediterranean-Caucasian Subrealm.](image-url)
blages dominated by pre-adult shells, including macroconchs and microconchs, that represent taphonic populations of type-2 (Fernandez-Lopez 2014, fig. 3) indicative of autochthonous biogenic production of shells by miotic taxa (i.e. shells recorded in an area occupied by active biodispersal, but where breeding does not occur as testified by the scarcity of adult or juvenile shells: Fernandez-Lopez 2014, fig. 3). Similar palaeoecological and palaeobiogeographical results have been obtained for Lissoceras bangi and L. ovale from the Garantiana Zone at the Iberian Range, whereas other species of Middle Jurassic lissoceratins are exclusively recorded by taphonomic populations of type-3 (Fernandez-Lopez 2014, fig. 3; i.e., monospecific or polyspecific shells, with unimodal or polynomials size-frequency distributions of negative asymmetry, adults dominant, juveniles absent, and dimorphism poorly represented) indicative of ademic or paradic morphologies that arrived at their present position by regional necrokinesis or passive biodispersal, respectively. Consequently, the oldest populations of Semilissoceras, belonging to Semilissoceras ellipticum and S. turgidulum from the early Laeviuscula Chron, Ovale Subchron, were Mediterranean-Caucasian and represent the known stem-taxa on which the subfamily Lissoceratinae is based.

Acknowledgements: This paper is devoted to our friend Maurizio Gaetani, who shared common interest on Jurassic stratigraphy during meetings in Alpes-de-Haute-Provence and Southern Alps.

Many friends and colleagues facilitated this research with assistance in the field, loan of material and photos of specimens: Mathias Alberti (Kiel, Germany), Dieter and Marianne Berger (Wiesloch, Germany), Alain Bonnet (Lasson, France), Patrick Branger (Chervaux, France), Robert Chandler (London, Great Britain), Aldo Defavi (Alessandria, Italy), Jean Dermeau (Saint Aubin-sur-Mer, France), Volker Dietze (Nördlingen, Germany), Mariagabriella Fornasiero and Stefano Castelli (Padova, Italy), Martin Görlich (Altendorf, Germany), Lionel Maerten (Ver-sur-Mer, France), Vasily Mitra (Moscow, Russia), Fred Neurbauer (Baltmannsweiler, Germany), Daniele Ormezzano (Turino, Italy), Marco Pavia (Torino, Italy), Isabelle Ruget (Paris, France), Emmanuel Robert (Lyon, France), Gunther Schweigert (Stuttgart, Germany), Chiara Sorbini (Pisa, Italy).

The clarity and impact of the final manuscript benefited from the action of an anonymous reviewer and of José Sandoval from Granada, Spain. The study was supported by G. Pavia’s personal grants and by S.R. Fernandez-Lopez research project CGL2011-23947 (MICYT) from the Spanish Ministry of Science and Innovation.

REFERENCES


Besnosov N.V. & Mitra V.V. (1993) - Late Bajocien and Bathonian ammonitids of Northern Caucasus and Middle Asia. Nedra, Moscow, 347 pp. [in Russian].


Buckman S.S. (1886-1907) - A monograph of the ammonites


De Gregorio A. (1886) - Monographie des fossiles de Ghelpa du Sous-horizon Ghelpin de Greg. (=Zone à *Posidonoma alpina* auctorum; =Zone à *Terebratula curvicauda* Oppel; (=Zone à Stephenoceras brugnarii Sow)). Louis Pedone Lauriel Edit. (Tip. Freres Verra), Palermo, 28 pp.


Fernandez-Lopez S.R. (1985) - El Bajociense en la Cordillera...
Bajocian Lissoceratinae from the Mediterranean-Caucasian Subrealm

Galácz A. (2012) - The Middle Jurassic ammonites of the Mecsek Mts (South Hungary) in the collection of the late Professor Lajos Kovacs. Földtani Közlöny, 142: 313-320.


