

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

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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. sturani*, *L. maerteni*, *S. ellipticum*, *S. turgidulum* and *S. costellatum*. The neotype of *L. oolithicum* is established. The microconchiate genus *Microilissoceras* 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 biochronostratigraphical intervals within the Bajocian Stage and are headed by species largely known in literature: *S. semicostulatum* (Buckman) with suboval to compressed whorl section and retriradiate 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. bangi* 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 phyletic relation of *Lissoceras* and *Semilissoceras* to the Aalenian-Bajocian *Bradfordia*-group is discussed, regarding *Semilissoceras* as the known stem-taxon of the subfamily Lissoceratinae.

INTRODUCTION

The Middle Jurassic genus *Lissoceras* Bayle (1879) and its microconchiate counterpart *Microilissoceras* 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 Arcto-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; Za-

ton 2010) from the lower Bajocian *L. semicostulatum* Buckman to the Middle Bathonian *L. ferrifex* (Zittel) and the middle Callovian *L. vouttense* (Oppel).

The number of species assigned to *Lissoceras* is limited through the whole biochronological range of the taxon. Particularly, for the Bajocian Stage, the literature lists six species most of which show wide biochronostratigraphical 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

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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 biochronostratigraphical resolution power.

The collection of a huge quantity of lissoceratins, during more than twenty years from the Bajocian Fe-oolithic 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 Bradfordiinae 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 synonymies 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 & Botjter (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).

Calvados, NW France

In the western sector of the Calvados Department, the Bajocian Stage is represented by the “Malière”, the “Oolithe ferrugineuse de Bayeux” (OFB) and the “Calcaire à Spongiaires” formations that crop out in the permanent cliff of Sainte-Honorine-des-Pertes and in many other occasional sites (Rioult et al. 1991). Lissoceratins come from the OFB Formation.

1) Bayeux, Sainte-Honorine-des-Pertes, Sully. The condensed section of OFB is known in literature since the mid-Eighteenth Century by d'Orbigny (1842-1851, 1849-1852, 1850-1852). Rioult (1964) described in detail the section of Sainte-Honorine, and Pavia (1994) studied the temporary outcrop of Sully where the Fe-oolithic succession totals over 60 cm in thickness. The section of Sully with 7 beds is assumed herein as the reference for the whole area (cf. Pavia 1994, fig. 2). Most fossils listed from Sully and Sainte-Honorine were collected in situ by the writers and are referred herein to as from the Sully beds 3-6 with details for their lower (a) and upper (b) parts. In addition, some specimens listed from Sully and those referred indefinitely to as from Bayeux concern fossils of old (e.g. Lyon and Paris) or private collections for which there is no location nor stratigraphic details: according to lithofacies, they are quoted to Sully beds with brackets in Appendix.

2) Feuguerolles-Bully: the OFB is exposed in the Feuguerolles quarry and was studied by Gauthier et al. (1995, 1996) who described four beds with details of lower (a), middle (b) and upper (c) parts. The writers collected the fossils listed in Appendix according to the stratigraphical log of those authors.

3) Baron-sur-Odon, Bretteville-sur-Odon: the writers sampled in detail the section of Bretteville when the ring road of Caen was under construction. At present the oolitic succession is hidden. Beds 3-16 pertain to the OFB (Pavia & Martire 2010). Fernandez-Lopez & Pavia (2015, 2016) and Pavia & Fernandez-Lopez (2016) carried on further studies on the Bretteville collection. The site of Baron-sur-Odon is equivalent in terms of bed succession (G.P., personal field study): brackets (e.g. “7-8”) in Appendix specify the bed equivalence.

4) Evrecy, Maizet: the section of Maizet was deeply sampled in 2010 (Pavia et al. 2013) and 2013 (Fernandez-Lopez & Pavia 2016, and reference therein). Beds 3-12 pertain to the OFB. Their lissoceratin specimens constitute the bulk of the present paper. The temporary section of Evrecy is equivalent in terms of bed succession (G.P., personal field study): brackets (e.g. “5”) in Appendix indicate the bed equivalence.

5) Croisilles: the section “Les Fours à Chaux” was repeatedly sampled since 2015. Beds 3-14 pertain to the OFB (Pavia et al. 2015; Pavia & Fernandez-Lopez 2016).

Dorset, S England

The Inferior Oolite Formation represents the Bajocian succession of the Dorset County in South-western England (Arkel 1933). Many localities result from literature: Callomon & Cope (1995 and references therein) described them in detail and very recently Chandler et al. (2017) further precised their biostratigraphical classification. Volker Dietze (Nördlingen) transmitted on loan the specimens studied in the present paper, whereas Robert Chandler (London) furnished information and photographic reproduction of specimens. The fossils come from the following districts:

6) Burton Bradstock on the coast of the English Channel. Callomon & Chandler (1990, fig. 2) and Callomon & Cope (1995, fig. 9) reported the stratigraphical log after Richardson (1928-1930) and Torrens (1969).

7) Sandford Lane, Frogden Quarry and Loose Hill of the Sherborne district in the central Dorset. Callomon & Chandler (1990, fig. 4), Callomon & Cope (1995, figs 11, 12) and Chandler et al. (2017, figs 3, 5) described their stratigraphical logs.

Deux-Sèvres, W France

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

8) Echiré, Malvault, 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 (Albarracín), Moscardon, Rambla La Gotera (Saldón), Embalse San Blas (Caude) 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 Ricla (Zaragoza province) were described by Fernandez-Lopez & Aurell (1988).

Different sites in Germany länders

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 Württembergica-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 reference 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 (Kerckhove & 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 "*Posidonia 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 Mountains, W Hungary

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

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

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

Besnosov & Mitta (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 Karachay-Cherkessia, Mitta & Sherstyukov 2014), Datuna, Akhvakhshab, Gigatliurukh villages and Bacelo mount (Tsudakhar Formation of Dagestan, Besnosov & Mitta 1993, 1998) on North slope of Caucasus, along with those of Chaloi and from the district southwards of the wells Karaiman and Shorli (Tsudakhar Member of western Turkmenistan, Besnosov & Mitta 2000) on Great Balkhan could be directly compared by measurements with the material studied in the present paper.

The biochronostratigraphical rank assigned to each stratigraphical unit listed as "source" in Appendix derives from the literature related to the fossiliferous sites. The biochronostratigraphy 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) Discites, Laeviuscula, Propinquans (nearly equivalent to Sauzei) and Humphriesianum (Romani, Umbilicum, Blagdeni subzones) zones; (upper Bajocian) Niortense (Banksii, 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 reelaborated (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, reelaborated 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 ($h = H/D \times 100$); whorl width/diameter ratio ($w = W/D \times 100$); umbilical diameter/diameter ratio ($u = U/D \times 100$); whorl width/whorl height ratio ($W/H \times 100$). 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 Neubauer's collection at Baltmannsweiler, 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 of Paris, France; (J) Jurassic collection at the Eötvös Roland University of Budapest, Hungary; (LM) Lionel Maerten's collection at Ver-sur-Mer, France; (MG) Martin Görlich's collection at Altdorf, 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 Calci, Italy; (MGUPT-PU) Museo di Geologia e Paleontologia at the University of Torino, Italy; (MRSN) Museo Regionale di Scienze Naturali of 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 H, W, U, their relative values h, w, u and the ratios W/H serve to describe the whorl shape of specimens and thus are used to distinguish taxa. These architectural values, calculated for the studied specimens, are detailed in Appendix and summarized in parametric tables, one for each described taxon. Statistical elaborations, necessary for improving taxonomic distinction, consist of distribution histograms and bivariate analyses for each taxon as to dispersion and regression are concerned; in particular, the bivariate scatter diagrams W/H state the sample homogeneity, whereas the plots for W/H vs D and W/H vs U/D serve to identify ontogenetic trajectories through ratios of the aperture shape and the umbilical exposure.

SYSTEMATIC PALAEOLOGY

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*" *semicostulatum* Buckman (Arkell et al. 1957, p. L274; Sturani 1971, p. 90; Imlay 1973, p. 77).

Lissoceras Bayle, 1879 and *Lissoceratoidea* 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 *Toxamblyites* Buckman, 1924 in 1909-1930, *Stegoxyites* 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*" *semicostulatum*, 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 Lissoceratinae 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 *Protoecotraustes* Spath, 1928 in 1927-1933 (presumed counterpart of *Bradfordia* l. s.), *Microlissoceras* Sturani, 1971, *Micropoecilomorphus* 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. sturani* and *L. haugi*. 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 *Microlissoceras* Sturani, 1971 as junior synonym of the former.

Genus *Lissoceras* Bayle, 1879

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

Type-species: *Lissoceras psilodiscus* (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. meletense* (Parona), *L. haugi* Sturani and *L. pusillum* Sturani and five new species: *L. submediterraneum*, *L. maizetense*, *L. ovale*, *L. sturani* 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 microconch group such as *L. badammi* Seyed-Emami (1988, p. 78, figs 25-26) from the Badamu Formation at western Kerman, central Iran, lower Bajocian, Sauzei Zone, and *L. solitarium* 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 Auran, 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 evolute 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 falcooid 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_2 asymmetrical and significantly higher than E/L , wide suspensive lobe with 3-4 auxiliary saddles (Fig. 1).

Microconchs are evolute 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).



Fig. 1 - Suture line of *Lissoceras oolithicum* (d'Orbigny), MGPUP-PU 112809, upper Humphriesianum Zone, Maizet, bed 5.

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 biostratigraphical 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. bangi*, depressed, ovate to globular whorl section, narrow E and suspensive lobe; "*L.*" *semicostulatum*, 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 *Microilissoceras* 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 microconchiate *Lissoceras* ("*Microilissoceras*") with the Oxfordian-Tithonian *Glochiceras* Hyatt, 1900 (type-species *Am. nimbatus* Oppel, 1863 in 1862-1863). The latter was repeatedly regarded as the dimorphic partner of different Late Jurassic hap-

locerataceans such as *Lissoceratooides* Spath, 1923 (type-species *Am. erato* d'Orbigny, 1850 in 1842-51), *Haploceras* Zittel, 1870 (type-species *Am. elimatus* Oppel in Zittel, 1868) and even *Ochetoceras* Haug, 1885 (type-species *Am. canaliculatus* von Buch, 1831) or *Taramelliceras* Del Campana, 1904 (type species *Am. trachinotus* Oppel, 1863 in 1862-1863) (cf. Callomon in Donovan et al. 1981, p. 145). If the synonymy of *Lissoceras* and *Lissoceratooides* (see the general discussion herein for Lissoceratidae) is accepted, the nomenclatural problem connected with the relationships "*Microilissoceras*" to *Glochiceras* (Galácz 1980, p. 56; Fernandez-Lopez 1985, p. 160) may be reduced to ascertain the dimorphic pairing between *Lissoceras erato* and *Glochiceras nimbatus* that would state the priority of *Glochiceras* on "*Microilissoceras*".

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. voutlense* (Oppel 1862-1863) from the lower-middle Callovian (Galácz 1980, 2015; Sandoval 1986, 2016; Baraboshkin et al. 2010). The taxa formerly referred to *Lissoceratooides*, 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 (Sturani, 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 1909-1930; Douvillé 1913; Wetzel 1950; Arkell

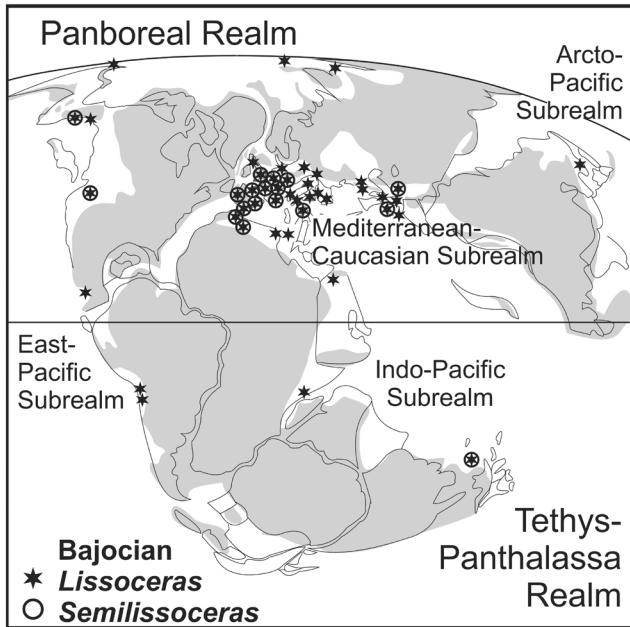


Fig. 2 - Palaeobiogeographical distribution of Bajocian Lissoceratinae. Palaeogeography based on Golonka (2011) and Fernandez-Lopez and Pavia (2015). Palaeobiogeographical units or biochoremas according to Westermann (2000).

1951-1958; Arkell et al. 1957; Westermann 1958; Morton 1971; Callomon & Chandler 1990; Fernandez-Lopez & Mouterde 1994; Fischer 1994; Rioult 1994; Callomon & Cope 1995; Gauthier et al. 1996; Rioult et al. 1997; Dietze et al. 2007; Chandler & Whicher 2015; Chandler et al. 2017);

1b) Sub-Mediterranean Province (Opper 1862-63; Quenstedt 1886 in 1886-1887; Douvillé 1885; Bataller 1922; Fallot & Blanchet 1923; Dorn 1927; Roman & Pétouraud 1927; Stephanov 1961; Sapunov 1963, 1971; Buck et al. 1966; Elmi 1967; Sturani 1967; Hahn 1968; Pavia 1973, 1983, 2007; Fernandez-Lopez 1985; Schlegelmilch 1985; Callomon et al. 1987; Sadki 1989, 1996; Galácz 1995, 2012; Rulleau 1997, 2006, 2011; Dietze & Dietl 2006; Zaton & Marynowski 2006; Pavia et al. 2008; Fernandez-Lopez et al. 2009a, b; Zaton 2010; Dietze et al. 2014, 2017; Metodiev & Tsvetkova 2015);

1c) Mediterranean Province (Kudernatsch 1852; Gemmellaro 1877; De Gregorio 1886; Parona 1896; Popovici-Hatzeg 1905; Bircher 1935; Passendorfer 1935; Wendt, 1963; Sturani, 1964, 1971; Rakus 1965; Geczy 1967; Krystyn 1972; Linares et al. 1979; Galácz 1980, 1985, 1994, 1995b, 1999; Sandoval 1986; Pavia & Cresta 2002; Schlögl et al. 2005; Hotsanyuk & Leschuch 2006; Bahrouni et al. 2016);

1d) Caucasian Province (Azaryan 1982; Rostovtsev 1985; Besnosov & Mitta, 1993, 1998, 2000;

Mitta & Sherstyukov 2014);

1e) NE Tethyan Province (Seyed-Emami et al. 1985, 1989, 1991, 2018; Seyed-Emami 1988).

2) Indo-Pacific Subrealm:

2a) Ethiopian Province (Douvillé 1916; Parnes 1988; Khalil 2003; Galácz 2017);

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) Athabaskan 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; Medina 1991, 2014; Westermann 1992; Zakharov et al. 1996; Shurygin 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 Erato* - Kudernatsch, p. 10, pl. 2, figs 7, 8 (only).

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

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

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

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

v 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 & Mitta, 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 psilodiscus*.

Material: For the present research, only some selected specimens of *L. psilodiscus* from the uppermost Bajocian (Parkinsoni Zone)

<i>L. psilodiscus</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
21 measures (min/max)	46.8 - 52.1	24.1 - 27.3	21.1 - 24.3	50.4 - 55.5
mean of 21 measures	48.93	25.93	22.87	53.03
standard deviation [sd]	1.11	0.88	0.86	1.74
standard error [se]	0.24	0.19	0.19	0.38
confidence interval on sd	46.71 - 51.15	24.17 - 27.69	21.15 - 24.59	49.55 - 56.51
confidence interval on se	48.45 - 49.41	25.55 - 26.31	22.49 - 23.25	52.27 - 53.79
correlation index and regression W on H:	$R^2 = 0.99$ - $y = 0.53x + 0.01$			

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

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 biostratigraphical 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 An-

dean province in East-Pacific Subrealm (Stehn 1923) and Indonesia in the southwestern Pacific areas (Calomon & 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.
- 1927 *Lissoceras oolithicum* - Roman & Petouraud, p. 48, pl. 5, figs 12, 14.
- 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.
- 1950 *Lissoceras inflatum intrasculptum* n. ssp. Wetzel, p. 12, pl. 8, fig. 8.
- v 1971 *Lissoceras psilodiscus inflatum* - Sturani, p. 92, pl. 6, fig. 1.
- 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 & Mitta, p. 51, pl. 1, fig. 9.
- 2011 *Lissoceras oolithicum* - Rulleau, p. 68, pl. 30, fig. 1.

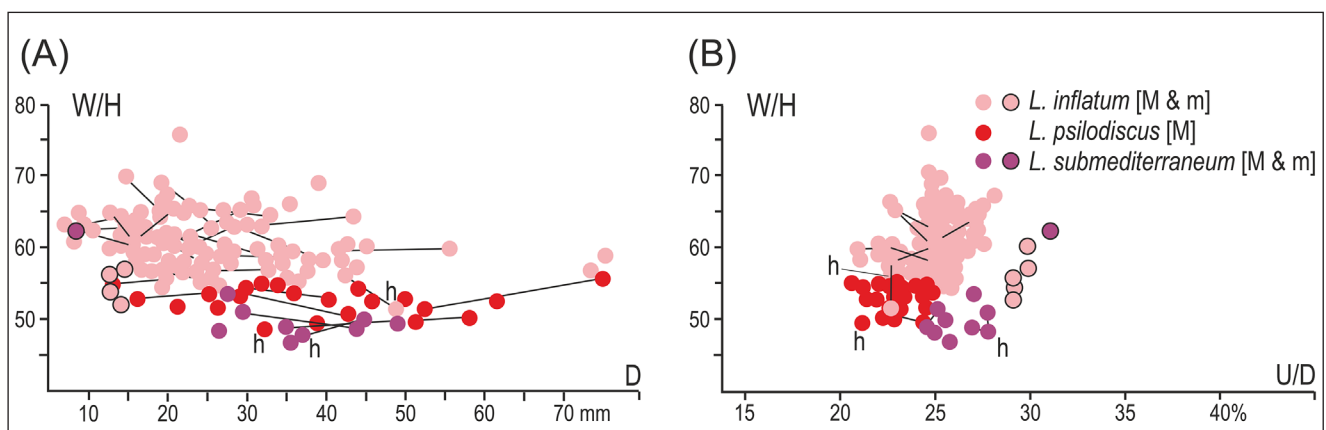


Fig. 3 - Plots of measurements for *Lissoceras psilodiscus* (Schloenbach), *L. inflatum* Wetzel and *L. submediterraneum* n. sp. with ontogenetic trajectories through ratios of the aperture shape (W/H). A) Whorl width/whorl height ratio (W/H x 100) versus shell diameter (D). B) Whorl width/whorl height ratio (W/H x 100) versus umbilical ratio (U/D x 100). Abbreviations: M, macroconch; m, microconch; h, holotype.

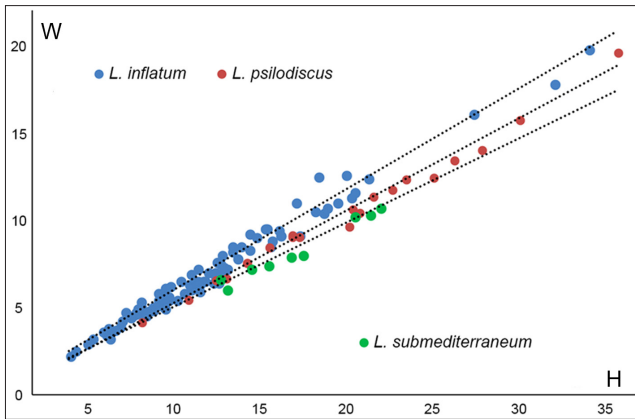


Fig. 4 - Bivariate scatter diagram of whorl height H and whorl width W for *Lissoceras psilodiscus* (Schloenbach), *L. inflatum* Wetzel and *L. submediterraneum* n. sp. Regression parameters in Tables 1 to 3.

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

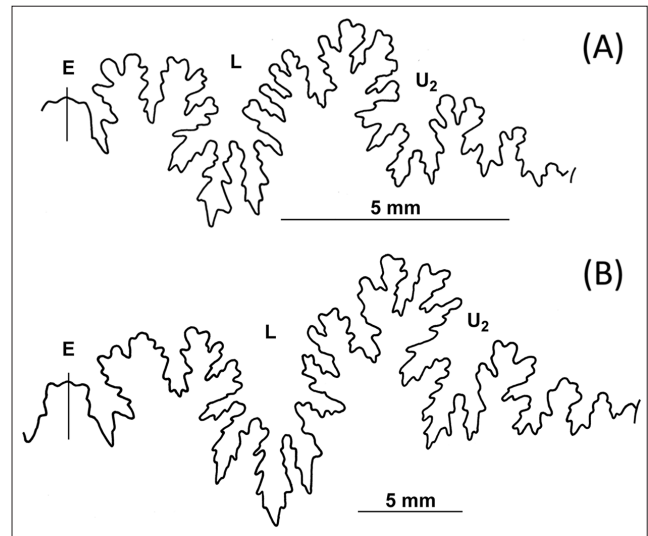


Fig. 5 - Suture lines of *Lissoceras inflatum* Wetzel. A) Specimen MG-PUT-PU 112704, upper Parkinsoni Zone, Sully, bed 6. B) Specimen MGP-PUT-PU 112813, Niortense-Garantiana zones, Bretteville, bed 9.

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 Gyenespuszta 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].

<i>L. inflatum</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
105 measures (min/max)	43.2 - 54.1	20.0 - 34.1	22.1 - 27.5	53.0 - 76.1
mean of 105 measures	47.59	28.65	24.95	60.66
standard deviation [sd]	1.81	2.08	1.34	3.98
standard error [se]	0.18	0.20	0.13	0.39
confidence interval on sd	43.97 - 51.21	24.49 - 32.81	22.27 - 27.63	52.70 - 68.62
confidence interval on se	47.23 - 47.95	28.25 - 29.05	24.69 - 25.21	59.88 - 61.44
correlation index and regression W on H:	$R^2 = 0.98 - y = 0.58x + 0.27$			
<i>L. inflatum</i> [m]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
5 measures (min/max)	42.5 - 45.3	22.8 - 27.1	27.6 - 30.0	52.2 - 60.0
mean of 5 measures	44.36	24.64	28.64	55.60
standard deviation [sd]	1.14	1.66	1.06	2.99
standard error [se]	0.51	0.74	0.47	1.33
confidence interval on sd	42.08 - 46.64	21.32 - 27.96	26.52 - 30.76	49.62 - 61.58
confidence interval on se	43.34 - 45.38	23.16 - 26.12	27.70 - 29.58	52.94 - 58.26
correlation index and regression W on H:	$R^2 = 0.98 - y = 0.70x - 0.90$			

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, trifid 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 28.25-29.05 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* (Krystyn 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.

PLATE 1

Figs 1-11, 13, 15, 17 - *Lissoceras inflatum* Wetzel, 1950. [M & m].

- 1) MGPUT-PU 112706, [M], Sully, upper Parkinsoni Zone. 2) MGPUT-PU 112704, [M], Sully, upper Parkinsoni Zone (see text-fig. 5A). 3) MGPUT-PU 112701, [M], Bretteville, upper Parkinsoni Zone. 4) MGPUT-PU 112725, [m], Sainte-Honorine-des-Pertes, upper Parkinsoni Zone. 5) MGPUT-PU 112723, [m], Sainte-Honorine-des-Pertes, upper Parkinsoni Zone. 6) MGPUT-PU 112722, [m], Sainte-Honorine-des-Pertes, upper Parkinsoni Zone. 7) MGPUT-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, Evrecy, Garantiana Zone. 13) SMNS 70396/9, [M], Burton Bradstock, Parkinsoni Zone. 15) RC132/32, Ricla, Garantiana Zone. 17) MGPUT-PU 112813, Bretteville, Niortense-Garantiana zones (see text-fig. 5B).

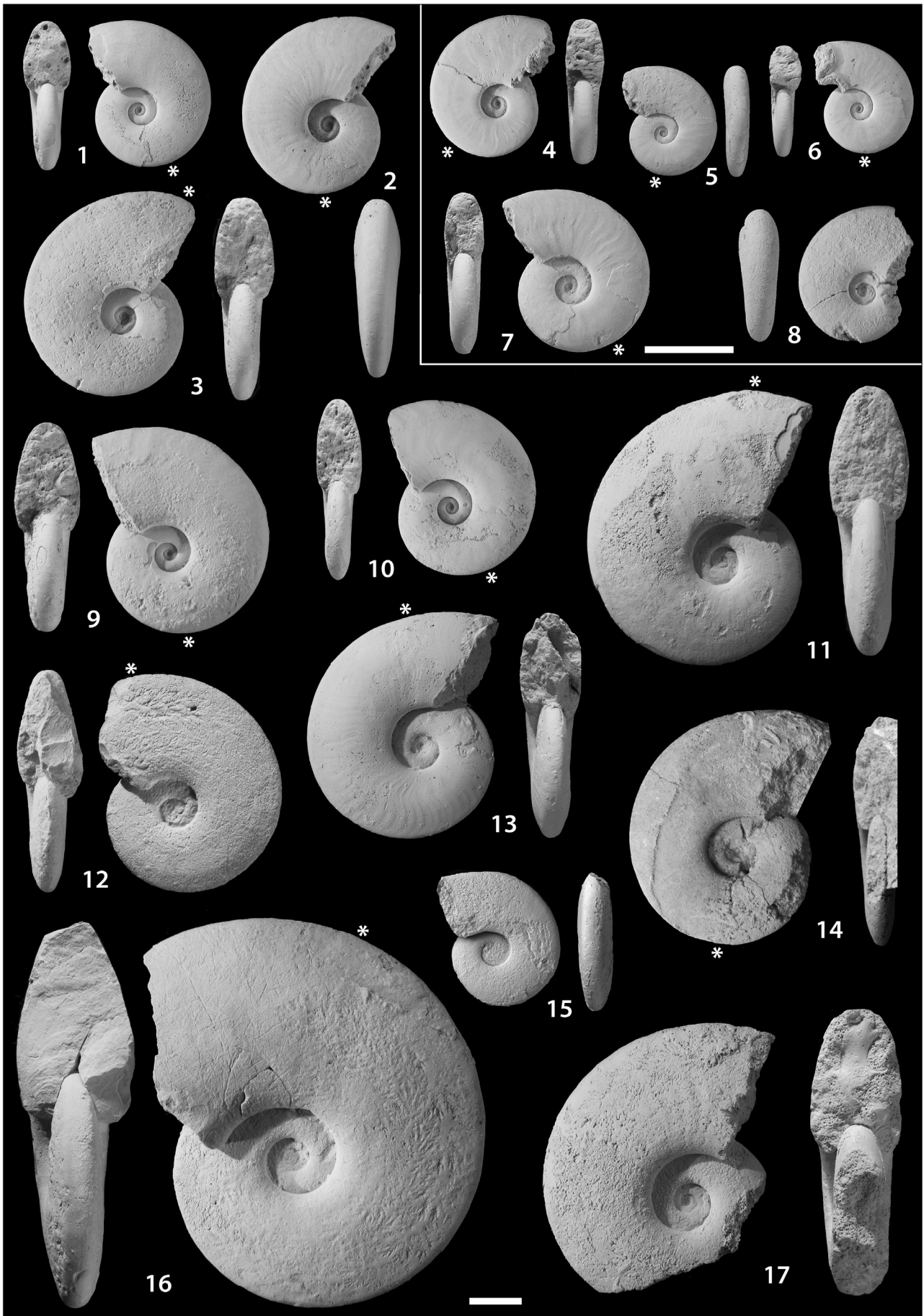
Figs 12, 16 - *Lissoceras psilodiscus* (Schloenbach, 1865). [M].

- 12) MGPUT-PU 111944, la Palud, lower Zigzag Zone. 16) MGPUT-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 whitened 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

v 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 (Caude, Iberian Range), Garantiana Zone, upper Bajocian. The allotype is the resedimented microconch 1EB 28/7 (Pl. 2, fig. 5) from Embalse San Blas (Caude, 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 MGPU-T-PU 112855 (Pl. 2, fig. 1) and MGPU-T-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 (Caude, 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 (Caude, 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).

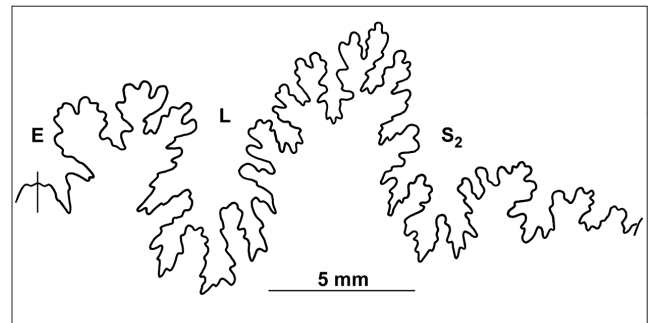


Fig. 6 - Suture line of *Lissoceras submediterraneum* n. sp. Paratype MGPU-T-PU 112858, Niortense Zone, Viaduc de l'Egray.

The umbilicus is shallow with short, steep walls that pass to the flank by an angular umbilical edge. The maximum width of the whorl section lies in the inner fourth of flanks, which gently slope to the narrow and acutely arched venter. Sinuous growth lines are occasionally observable on the shell and engraved on the internal mould. The suture line (Fig. 6) shows a short saddle at the bottom of lobe E; the saddle E/L is slender and asymmetrically tripartite; the lobe L is asymmetrically trifid; the asymmetrical saddle L/U₂ is large, coarsely branched and much higher than E/L; the suspensive lobe occupies the inner third of the flank, bears 3 auxiliary saddles and shows a deep and asymmetrically trifid U₂.

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

<i>L. submediterraneum</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
9 measures (min/max)	44.7 - 49.8	21.9 - 25.3	24.5 - 28.0	47.1 - 54.0
mean of 9 measures	46.63	23.20	26.23	49.80
standard deviation [sd]	2.19	0.49	0.64	1.63
standard error [se]	0.73	0.16	0.21	0.54
confidence interval on sd	42.25 - 51.01	22.22 - 24.18	24.95 - 27.51	46.54 - 53.06
confidence interval on se	45.17 - 48.09	22.88 - 23.52	25.81 - 26.65	48.72 - 50.88
correlation index and regression W on H:	R ² = 0.97 - y = 0.48x + 0.24			
<i>L. submediterraneum</i> [m]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
1 measure	42.60	26.50	32.40	62.10

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 *L. submediterraneum* n. sp., the umbilicus of *L. inflatum* is closer (28.64 vs 32.40) and the umbilicus of *L. sturani* n. sp. is more open (means 37.70 vs 32.40). As to the macroconchs (Tables 1-3), the greatest differences concern *L. psilodiscus*: the whorl width of *L. submediterraneum* n. sp. is consistently narrower than in *L. psilodiscus* (means 23.20 vs 25.93, confidence intervals on standard error 22.88/23.52 vs 25.55/26.31) and *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 *L. submediterraneum* n. sp. is more open than in *L. psilodiscus* (means 26.1 vs 22.9).

Distribution. *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 and middle upper Bajocian, i.e. Niortense and Garantiana zones.

Lissoceras oolithicum (d'Orbigny, 1845) [M]

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

- 1845 *Ammonites oolithicus* d'Orbigny 1842-51, p. 383, pl. 126, figs 1, 2, 4 (non fig. 3 = *L. inflatum*).
 non 1858 *Ammonites oolithicus* - Quenstedt, p. 396, pl. 55, fig. 20 (= *L. ovale* n. sp.).
 non 1886 *Ammonites oolithicus* - Quenstedt 1886-87, p. 563, pl. 69, fig. 4 (= *L. ovale* n. sp.), fig. 5 (= *L. haugii*).
 1892 *Lissoceras oolithicum* - Munier-Chalmas, p. 166.
 non 1913 *Lissoceras oolithicum* - Douvillé, p. 72, text-fig. 4 (= *L. haugii*).
 non 1927 *Lissoceras oolithicum* - Dorn, p. 245, pl. 7, fig. 3 (= *L. haugii*).
 non 1927 *Lissoceras oolithicum* - Roman & Petouraud, p. 48, pl. 5, figs

- 12, 14 (= *L. inflatum*), pl. 5, fig. 13 (= ? *L. ovale* n. sp.).
 1971 *Lissoceras oolithicum* - Morton, p. 270, pl. 40, figs 1-2.
 v 1971 *Lissoceras oolithicum* (d'Orbigny) - Sturani, p. 91 (pars) (non pl. 6, fig. 2 = *L. sturani* n. sp.).
 ? 1976 *Lissoceras (Lissoceras) oolithicum* - Parsons, p. 124-134.
 non 1980 *Lissoceras oolithicum* - Galácz, p. 57, text-figs 43, 44, pl. 11, figs 5-6 (= *L. ovale* n. sp.).
 v 1983 *Lissoceras oolithicum* - Pavia, p. 172, pl. 7, fig. 11.
 v 1985 *Lissoceras oolithicum* - Fernandez-Lopez, p. 164 (non text-figs 15, 16/E, pl. 15, fig. 2 = *L. ovale* n. sp.).
 non 1985 *Lissoceras oolithicum* - Schlegelmilch, p. 68, pl. 21, fig. 4 (= *L. ovale* n. sp.).
 1986 *Lissoceras oolithicum* - Sandoval, p. 439, text-fig. 3, pl. 1, figs 6-7.
 non 1994 *Lissoceras oolithicum* - Fernandez-Lopez & Mouterde, p. 141, pl. 5, fig. 4 (= *L. sturani* n. sp.).
 1994 *Lissoceras oolithicum* - Rioult in Fischer, p. 112 (non pl. 48, fig. 2 = *L. haugii*; non pl. 48, fig. 3 = *L. inflatum*).
 1995 *Lissoceras oolithicum* - Galácz, p. 124, pl. 18, figs 8-9.
 non 1998 *Lissoceras oolithicum* - Besnosov & Mitta, p. 23, pl. 8, fig. 2 (*L. sturani* n. sp.).
 non 2000 *Lissoceras oolithicum* - Besnosov & Mitta, p. 51 (pl. 1, fig. 9 = *L. inflatum*, pl. 1, figs 10-13 = ? *L. sturani* n. sp., pl. 3, fig. 2 = ? *L. ovale* n. sp.).
 non 2006 *Lissoceras oolithicum* - Zaton & Marynowski, p. 433, text-fig. 4B, figs 3. 9-10 (= ? *L. ferrifex*).
 non 2010 *Lissoceras oolithicum* - Zaton, p. 94, text-fig. 11/O, pl. 6, figs G, H (= ? *L. ferrifex*).
 non 2011 *Lissoceras oolithicum* - Rulleau, p. 68, pl. 30, fig. 1 (= *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 syntypes formed the series-type of "*Ammonites oolithicus* d'Orbigny, 1845": among the fossils figured on d'Orbigny's pl. 126, figs 1+2 and 4 concern the lectotype of *L. oolithicum* (Schlegelmilch 1985, p. 68), whereas the specimen at fig. 3 was identified as *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



Fig. 7 - Neotype MGPUP-PU 112868 of *Lissoceras oolithicum* (d'Orbigny), upper Humphriesianum Zone, Evrechy, bed "5". The authors wish to thank Dieter and Marianne Berger who collected and provide details of the specimen.

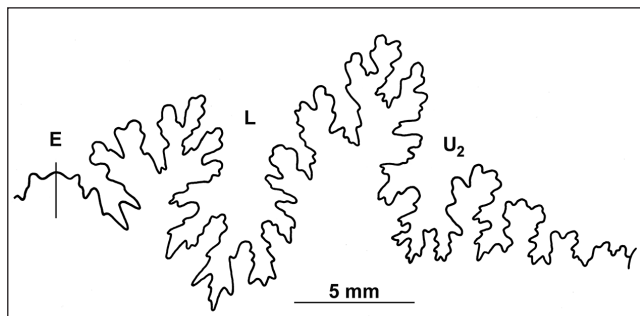


Fig. 8 - Suture line of *Lissoceras oolithicum* (d'Orbigny), specimen MGPOT-PU 112809, upper Humphriesianum Zone, Maizet, bed 5.

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 syntypes of “*Ammonites oolithicus*” (Rioutl in Fischer 1994, p. 112). For this reason, in absence of the lectotype, the specimen MGPOT-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 synonymies.

2) The most significant feature of *L. oolithicum*, according to the original diagnosis and figures by d'Orbigny (1845 in 1842-1849, 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 MGPOT-PU 112868, here selected as the neotype of *L. oolithicum*, comes from the condensed fossil assemblage of the Evrecy site that comprises both resedimented and reelaborated fossils; it is referred to the upper Humphriesianum Zone, top lower Bajocian (Pavia et al. 2013). A resedimented, shelly arcid *Paralobodon* sp. is strictly associated to the reelaborated 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-Cinglais (Calvados). He figured two specimens at pl. 126: figs 1, 2 and 4 represent the lectotype of *L. oolithicum*, whereas Rioutl (in Fischer 1994, p. 12) referred fig. 3 to as *L. psilodiscus inflatum*. According to what is known of the Bajocian successions and ammonite assemblages of Calvados (Rioutl 1964; Pavia 1994;

Pavia et al. 2013, 2015), we can state that the specimen of fig. 3 came from a locality of the surroundings of Bayeux (e.g. Sully) whereas the lectotype pertains to Moutiers where, at d'Orbigny's time, some limestone quarries delivered large quantities of fossils, e. g. from the “Fours à Chaux” of Croisilles (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-Odon 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 MGPOT-PU112868.

7) The neotype designation of *L. oolithicum* on the specimen MGPOT-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 (Nördlingen, Germany), Raymond Enay (Lyon, France), András Galácz (Budapest, Hungary), Maria-Helena Henriques (Coimbra, Portugal), Vasily Mitta (Moscow, Russia), Horacio Parent (Rosario, Argentina), José Sandoval (Granada, Spain), Jan Schlögl (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 Frogden Quarry in Dorset. One specimen from Echiré in Deux-Sèvres. One specimen from Moscardon (Téruel) in the Iberian Range. Four specimens from Chaudon, Alpes-de-Haute-Provence. Six specimens from the “*Lumachella a Posidonia alpina*” in Asiago.

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 vertical umbilical walls abruptly passing to the flank by a rounded edge. The venter is narrow, acutely

<i>L. oolithicum</i> [M]	$h = H/D \times 100$	$w = W/D \times 100$	$u = U/D \times 100$	$W/H \times 100$
35 measures (min/max)	45.30 - 52.70	29.90 - 38.10	15.60 - 25.60	60.10 - 78.80
mean of 35 measures	49.69	33.75	21.47	68.02
standard deviation [sd]	1.49	1.94	1.68	4.05
standard error [se]	0.22	0.29	0.25	0.60
confidence interval on sd	46.71 - 52.67	29.87 - 37.63	18.11 - 24.83	59.92 - 76.12
confidence interval on se	49.25 - 50.13	33.17 - 34.33	20.47 - 22.47	66.82 - 69.22
correlation index and regression W on H:	$R^2 = 0.99 - y = 0.60x + 1.40$			
correlation index and regression U on W:	$R^2 = 0.96 - y = 0.67x - 0.40$			

Tab. 4 - Synthesis of measurements and regression statistics for *Lissoceras oolithicum* (d'Orbigny, 1845), [M].

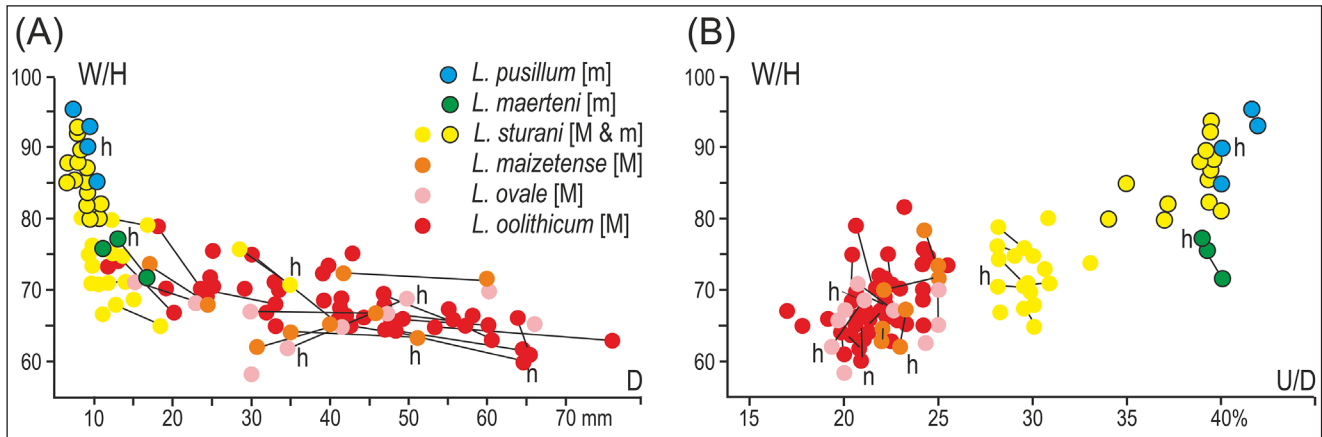


Fig. 9 - Plots of measurements for *Lissoceras oolithicum* (d'Orbigny), *L. ovale* n. sp., *L. maizetense* n. sp., *L. sturani* n. sp., *L. maerteni* n. sp. and *L. pusillum* Sturani, with several ontogenetic trajectories through ratios of the aperture shape (W/H). A) Whorl width/whorl height ratio (W/H 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; n, neotype.

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/U₂ 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 U₂.

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 sturani* 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 biostratigraphical 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-

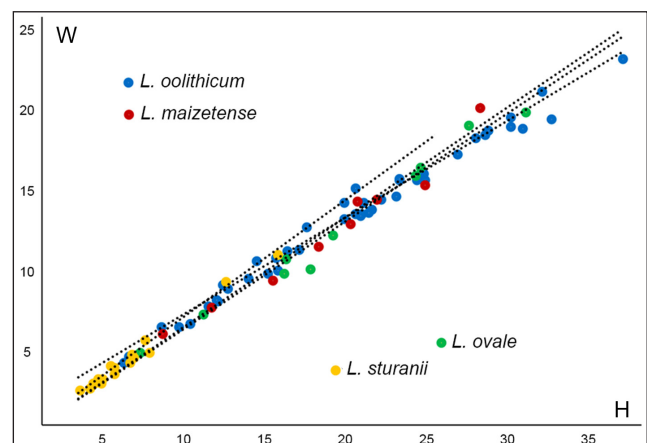


Fig. 10 - Bivariate scatter diagram of whorl height H and whorl width W for *Lissoceras oolithicum* (d'Orbigny), *L. maizetense* n. sp., *L. ovale* n. sp. and *L. sturani* n. sp. Regression parameters in Tables 4-7. Note the diagnostic inconsistency of parameters H and W to distinguish among these taxa; conversely the whorl shape cross sections of Fig. 11 make possible their distinction.

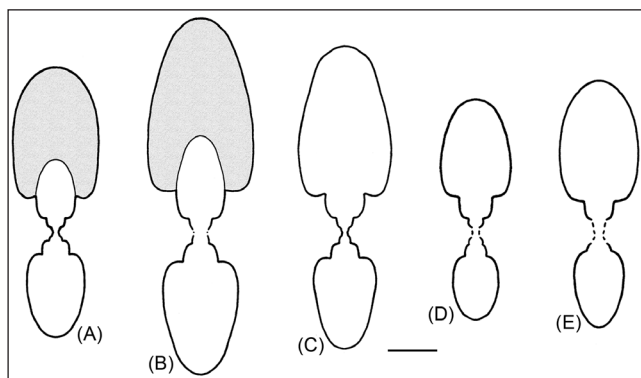


Fig. 11 - Whorl shape cross sections through the phragmocone and body chamber (stippled). A) *Lissoceras maizetense* n. sp., holotype, MGPUPT-PU 112804. B) *L. oolithicum* (d'Orbigny), neotype MGPUPT-PU 112868. C) *L. oolithicum*, MGPUPT-PU 112807. D) *L. sturani* n. sp., holotype MGPUPT-PU 112730. E) *L. ovale* n. sp., holotype 1CE2/1. Scale bar equals 10 mm.

bigny's taxon except for the depressed periumbilical edge and the open umbilicus. *Lissoceras bakeri* Imlay (1962, p. A6, pl. 1, figs 1-6, 9-12) from the upper Bajocian of Alaska differs for the fine external ribbing, the subovate whorl section with rounded umbilical walls and the narrow umbilicus ($u = 20.3$).

Distribution. As far as it is presently confirmed, *Lissoceras oolithicum* is largely represented throughout the entire Western Tethys. The oldest record is from the lower Humphriesianum Zone (Romani Subzone) of Dorset (Frogden Quarry herein) and Alpes-de-Haute-Provence (Chaudon, Pavia 1983). Specimens of the taxon from the Propinquans Zone of Iran (Seyed-Emami 1988) might suggest an origin of the species from the eastern part of the Mediterranean-Caucasian Subrealm. Recent records repeatedly list *L. oolithicum* in fossil-assemblages of the upper Bajocian, up to the Garantiana Zone where it is confirmed by the specimens studied in the present paper.

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 MGPUPT-PU 112804 (Pl. 2, fig. 8) from Maizet (Calvados), bed 5, upper Humphriesianum Zone. Two paratypes: the reelaborated macroconch MGPUPT-PU 112966 (Pl. 2, fig. 11) from Maizet (Calvados),

bed 5, upper Humphriesianum Zone; the reelaborated macroconch MGPUPT-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

PLATE 2

Figs 1-3, 5 - *Lissoceras submediterraneum* n. sp. [M & m].

1) MGPUPT-PU 112855, [M], paratype, Viaduc de l'Egray, Niortense Zone. 2) 8EB 167/9, [M], holotype, Embalse San Blas, Garantiana Zone. 3) MGPUPT-PU 112858, [M], paratype, Viaduc de l'Egray, Niortense Zone (see text-fig. 5). 5) EB 28/7, [m], allotype, Embalse San Blas, Garantiana Zone.

Figs 4, 6, 7, 9, 12 - *Lissoceras oolithicum* (d'Orbigny, 1845). [M].

4) MGPUPT-PU 112863, Maizet, Romani Subzone. 6) MGPUPT-PU 112814, Baron-sur-Odon, Humphriesianum Zone. 7) SMNS 70396/7, Frogden Quarry, Romani Subzone. 9) MGPUPT-PU 112798, Croisilles, upper Garantiana Zone. 12) MGPUPT-PU 112807, Evrecy, upper Humphriesianum Zone (see text-fig. 10C), specimen collected by Jean Dermeau.

Figs 8, 10, 11, 13 - *Lissoceras maizetense* n. sp. [M].

8) MGPUPT-PU 112804, holotype, Maizet, upper Humphriesianum Zone (see text-fig. 10A). 10) MGPUPT-PU 112740, Sully, Humphriesianum Zone. 11) MGPUPT-PU 112966, paratype, Evrecy, upper Humphriesianum Zone (see text-fig. 12). 13) MGPUPT-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.



<i>L. maizetense</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
9 measures (min/max)	46.8 - 51.8	30.7 - 36.8	20.7 - 24.6	62.3 - 73.3
mean of 9 measures	49.37	33.16	22.77	67.20
standard deviation [sd]	1.55	1.92	1.42	4.05
standard error [se]	0.52	0.64	0.47	1.35
confidence interval on sd	46.27 - 52.47	29.32 - 37.00	19.93 - 25.61	59.10 - 75.3
confidence interval on se	48.33 - 50.41	31.88 - 34.44	21.83 - 23.71	64.5 - 69.90
correlation index and regression W on H:	$R^2 = 0.97 - y = 0.68x - 0.21$			

Tab. 5 - Synthesis of measurements and regression statistics for *Lissoceras maizetense* n. sp., [M].

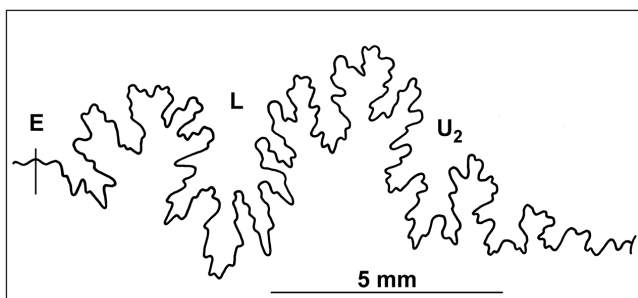


Fig. 12 - Suture line of *Lissoceras maizetense* n. sp., paratype MGPUP-PU 112966, upper Humphriesianum Zone, Maizet, bed 5.

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/ U_2 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 U_2 .

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) badammi* 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 reelaborated 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]

Figs 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.
 v 1985 *Lissoceras oolithicum* - Fernández-López, p. 164, text-figs 15, 16, pl. 15, fig. 2.
 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 resedimented macroconch 1CE2/1 (Pl. 3, fig. 1) from Cella (Teruel, Iberian Range), Garantiana Zone. Two paratypes: the reelaborated macroconch MGPUP-PU 112867 (Pl. 3, fig. 9) from Croisilles (Calvados), lower Parkinsoni Zone; the reelaborated macroconch PB-185 (Pl. 3, fig. 11) from Malvault (Deux-Sèvres), Niortense Zone.

Locus typicus: The section-1 at Cella (Teruel), Iberian Range, Spain, described by Fernández-López (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 resedimented ammonites (Fernández López 1985) and belongs to the uppermost El Pedregal Formation (Gomez & Fernández-López 2004).

Material: 6 specimens from diverse palaeobiogeographical sectors: 2 from Croisilles and Evrecy in Calvados, 1 from Malvault 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 planulate shell and moderately open umbilicus. The whorl section of the inner to medium whorls 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

Tab. 6 - Synthesis of measurements and regression statistics for *Lissoceras ovale* n. sp., [M].

<i>L. ovale</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
10 measures (min/max)	45.8 - 53.0	29.4 - 35.90	18.8 - 25.0	58.1 - 70.80
mean of 10 measures	49.08	32.35	21.72	65.97
standard deviation [sd]	2.68	2.07	2.32	3.73
standard error [se]	0.85	0.66	0.73	1.18
confidence interval on sd	43.72 - 54.44	28.21 - 36.49	17.08 - 26.36	58.51 - 73.43
confidence interval on se	47.38 - 50.78	31.03 - 33.67	20.26 - 23.18	63.61 - 68.33
correlation index and regression W on H:	R ² = 0.98 - $y = 0.68x - 0.20$			

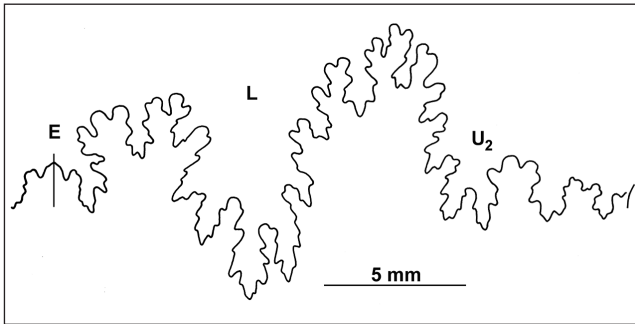


Fig. 13 - Suture line of *Lissoceras ovale* n. sp., paratype PB-185, Niortense Zone, Malvault.

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/U₂ is high, asymmetrical and minutely branched; the symmetrical lobe L is trifid; the suspensive lobe shows an asymmetrically trifid U₂ and bears 3 auxiliary saddles.

Remarks. No microconch is so-far known. *Lissoceras ovale* n. sp. differs from the coeval *L. oolithicum* for the whorl shape, regularly rounded in the adult stage in comparison with the compressed, subtriangular whorls of d'Orbigny's taxon (Fig. 11), and for details of the suture line, namely the ventral saddle and the reduced number of auxiliary saddles of the suspensive lobe. The specimen MGPU-PU112864 is a reelaborated fossil from the lower Niortense Zone of Evrecy (Pl. 3, fig. 8); this biostratigraphical datum means that MGPU-PU112864 must be referred to the upper Humphriesianum Chron or at most to the earliest Niortense Chron. This 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 reelaborated MGPU-PU 112867 (Pl. 3, fig. 9) from the lowermost Parkinsoni zones of Croisilles (Pavia et al. 2015).

Lissoceras sturani n. sp. [M & m]

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

- v 1971 *Lissoceras oolithicum* - 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 oolithicum* - Fernandez-Lopez & Mouterde, p. 141, pl. 5, fig. 4.
- 1998 *Lissoceras oolithicum* - Besnosov & Mitta, p. 23, pl. 8, fig. 2.
- 2000 *Lissoceras oolithicum* - Besnosov & Mitta, p. 51, pl. 1, figs 10-13.
- 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 reelaborated macroconch MGPU-PU 112730 (Pl. 3, fig. 10) from Sully (Calvados), bed 5, upper

<i>L. sturanii</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
18 measures (min/max)	41.7 - 47.1	28.5 - 35.8	27.50 - 32.6	65.4 - 80.0
mean of 18 measures	44.26	32.21	29.39	72.78
standard deviation [sd]	1.34	2.00	1.37	4.33
standard error [se]	0.32	0.47	0.09	1.02
confidence interval on sd	41.58 - 46.94	28.21 - 36.21	26.65 - 32.13	64.12 - 81.44
confidence interval on se	43.62 - 44.90	32.31.27 - 33.1	29.21 - 29.57	70.74 - 74.82
correlation index and regression W on H:	$R^2 = 0.99 - y = 0.72x + 0.01$			
correlation index and regression U on W:	$R^2 = 0.97 - y = 0.67x + 0.29$			
<i>L. sturanii</i> [m]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
13 measures (min/max)	33.3 - 38.1	28.3 - 34.4	33.4 - 39.1	80.0 - 93.9
mean of 13 measures	35.75	30.80	37.70	86.18
standard deviation [sd]	1.29	1.70	1.87	4.50
standard error [se]	0.31	0.47	0.52	1.25
confidence interval on sd	33.17 - 38.33	27.40 - 34.20	33.96 - 41.44	77.18 - 95.18
confidence interval on se	35.13 - 36.37	29.86 - 31.74	36.66 - 38.74	83.68 - 88.68
correlation index and regression W on H:	$R^2 = 0.88 - y = 0.66x + 0.62$			

Tab. 7 - Synthesis of measurements and regression statistics for *Lissoceras sturanii* n. sp., [M & m].

Bajocian. The allotype is the reelaborated microconch MGPU-PU 112733 (Pl. 3, fig. 3) from Sainte-Honorine-des-Pertes (Calvados), bed 5, upper Bajocian. Besides the allotype, six paratypes are selected: the resedimented macroconch MGPU-PU 112732 (Pl. 3, fig. 6) from Sainte-Honorine-des-Pertes (Calvados), bed 5, upper Bajocian, the reelaborated macroconch MGPU-PU 112849 (Pl. 3, fig. 7) from Maizet (Calvados), bed 9, Garantiana Zone, the resedimented macroconchs MGPU-PU 36057 (Sturani 1971, pl. 6, fig. 2; see also this work at Pl. 3, fig. 2) and MGPU-PU 112983 (Pl. 3, fig. 4) from Troch 1 (Asiago), Romani Subzone, the resedimented microconchs MGPU-PU 36069 (Sturani 1971, pl. 6, fig. 8) and MGPU-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/U₂ is asymmetrical and much higher than E/L.

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

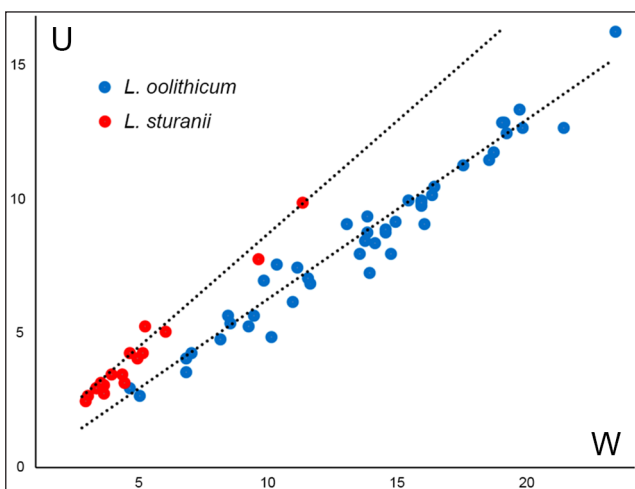


Fig. 14 - Bivariate scatter diagram of whorl width W and umbilical diameter U for *Lissoceras oolithicum* (d'Orbigny) and *L. sturanii* n. sp. Regression parameters are detailed in Tables 4 and 7 respectively.

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 (Fernan-

dez-Lopez & Mouterde 1994) up to the Garantiana Zone in Calvados. The records from Daghestan (Besnosov & Mitta 1998) and Great Balkhan (Besnosov & Mitta 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* - Douvill e, 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.
- v 1967 *Lissoceras haugi* n. sp. - Sturani, p. 24, pl. 3, fig. 16.
- v 1971 *Lissoceras oolithicum* - Sturani, p. 91 (pars).
- v 1985 *Lissoceras monachum* - Fernandez-Lopez, p. 166, text-figs 15-16, pl. 15, figs 6-7.
- v 1985 *Lissoceras haugi* Sturani - Fernandez-Lopez, p. 170, text-figs 15-16.
- v 1985 *Microlissoceras* sp. - Fernandez-Lopez, p. 171, pl. 15, fig. 8.
- 1985 *Lissoceras ferrifex* - Schlegelmilch, p. 68, pl. 21, fig. 5.
- 1994 *Lissoceras oolithicum* - Rioult in Fischer, p. 112, pl. 48, fig. 2.
- 1997 *Lissoceras oolithicum* - Rulleau, p. 7, pl. 4, figs 12-13.
- 1998 *Lissoceras haugi* - Besnosov & Mitta, p. 23, pl. 8, figs 3-4.
- 2000 *Lissoceras haugi* - Besnosov & Mitta, p. 51, pl. 4, fig. 14.
- ? 2006 *Lissoceras ferrifex* - Dietze & Dietl, p. 22, pl. 1, fig. 3.
- 2006 *Lissoceras oolithicum* - Rulleau, p. 112, pl. 4, fig. 4.
- v 2007 *Lissoceras haugi* - Pavia, p. 221, pl. 1, fig. 4.
- v 2007 *Lissoceras ferrifex* - Pavia, p. 221, pl. 1, fig. 7.
- 2011 *Lissoceras* aff. *L. monachum* - Rulleau, p. 68, pl. 30, fig. 2.
- 2014 *Lissoceras haugi* - Mitta & Sherstyukov, pl. 3, fig. 3.

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.

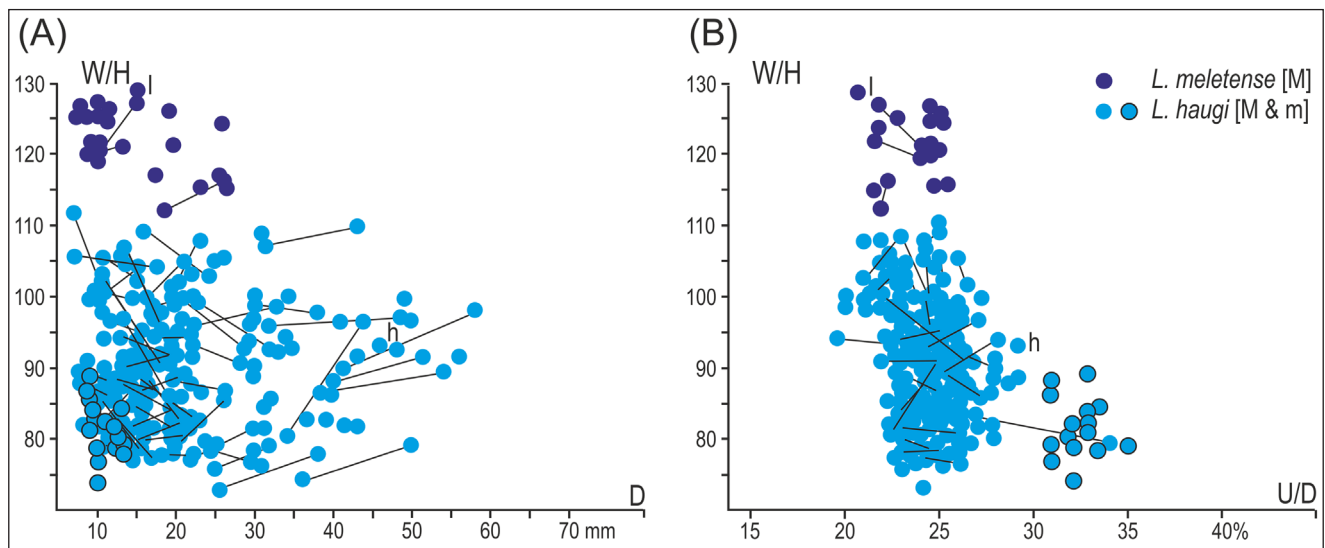


Fig. 15 - Plots of measurements for *Lissoceras meletense* (Parona) and *L. haugi* Sturani, with ontogenetic trajectories through ratios of the aperture shape (W/H). A) Whorl width/whorl height ratio (W/H x 100) versus shell diameter (D). B) Whorl width/whorl height ratio (W/H x 100) versus umbilical ratio (U/D x 100). Abbreviations: M, macroconch; m, microconch; h, holotype; l, lectotype.

<i>L. haugi</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
184 measures (min/max)	35.6 - 63.7	34.6 - 60.1	18.5 - 34.2	73.4 - 111.4
mean of 184 measures	47.67	43.28	24.45	90.49
standard deviation [sd]	2.62	4.96	1.85	8.71
standard error [se]	0.19	0.59	0.14	0.64
confidence intervals on sd	42.43 - 52.91	33.60 - 52.00	20.75 - 28.15	73.70 - 107.91
confidence intervals on se	47.29 - 48.05	42.10 - 44.46	24.17 - 24.73	89.21 - 91.77
correlation index and regression W on H:	$R^2 = 0.95 - y = 0.91x - 0.07$			
<i>L. haugi</i> [m]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
15 measures (min/max)	38.8 - 45.1	31.0 - 40.2	28.9 - 35.1	73.8 - 89.2
mean of 15 measures	42.53	34.71	32.04	81.59
standard deviation [sd]	1.43	2.28	1.31	4.34
standard error [se]	0.37	0.60	0.39	1.12
confidence intervals on sd	39.67 - 45.39	30.15 - 39.27	29.42 - 34.66	72.91 - 90.27
confidence intervals on se	41.79 - 43.27	33.51 - 35.91	31.26 - 32.82	79.35 - 83.83
correlation index and regression W on H:	$R^2 = 0.85 - y = 0.67x + 0.63$			

Tab. 8 - Synthesis of measurements and regression statistics for *Lissoceras haugi* Sturani, 1967, [M & m].

Type: The holotype is the resedimented specimen MGPUT-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 reelaborated fossils from Ipf (1) and from Sengenthal (11) in southern Germany, 1 resedimented and 1 reelaborated fossils 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

PLATE 3

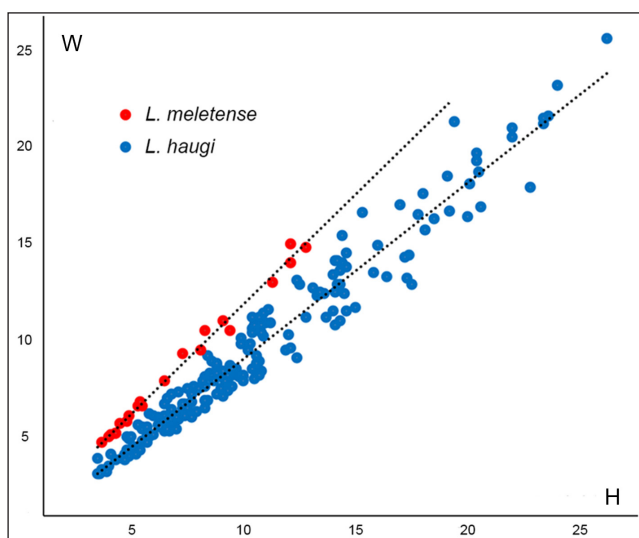


Fig. 16 - Bivariate scatter diagram of whorl height H and whorl width W for *Lissoceras haugi* Sturani and *L. meletense* (Parona). Regression parameters in Tables 8 and 9.

Figs 1, 8, 9, 11 - *Lissoceras ovale* n. sp. [M].

- 1) ICE2/1, holotype, Cella, Garantiana Zone (see text-fig. 11E).
- 8) MGPUT-PU 112864, Evrecy, lower Niortense Zone.
- 9) MGPUT-PU 112867, paratype, Croisilles, lower Parkinsoni Zone.
- 11) PB-185, paratype, Malvault, Niortense Zone.

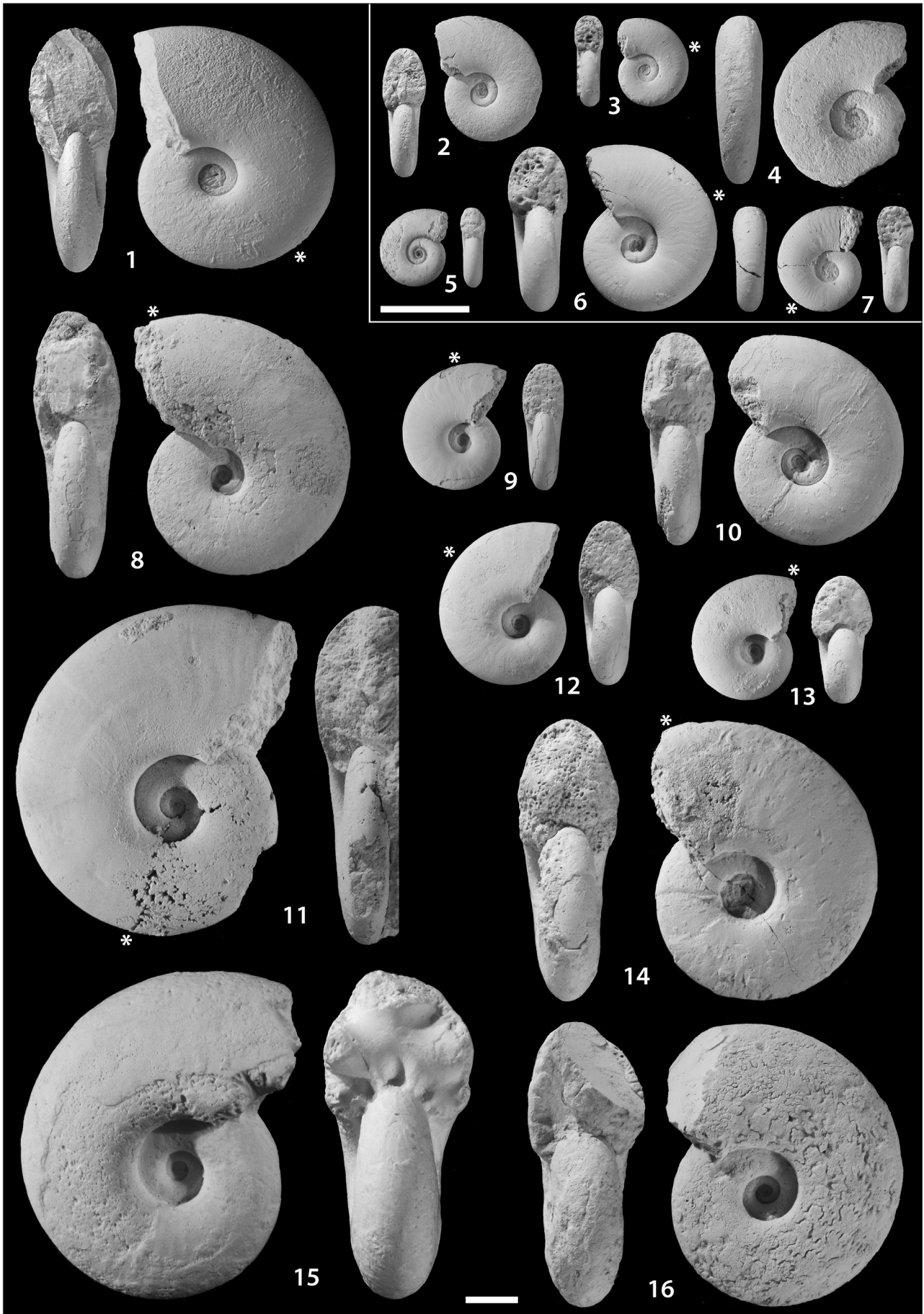
Figs 2-7, 10 - *Lissoceras sturani* n. sp. [M & m].

- 2) MGPUT-PU 36057, [M], paratype, Troch 1, Romani Subzone.
- 3) MGPUT-PU 112733, [m], allotype, Sully, Niortense-Garantiana zones.
- 4) MGPUT-PU 112983, [M], paratype, Troch 1, Romani Subzone.
- 5) MGPUT-PU 36070, [m], paratype, Troch 1, Romani Subzone.
- 6) MGPUT-PU 112732, [M], paratype, Sainte-Honorine-des-Pertes, upper Bajocian.
- 7) MGPUT-PU 112849, [M], paratype, Maizet, middle Garantiana Zone.
- 10) MGPUT-PU 112730, [M], holotype, Sully, upper Bajocian (see text-fig. 10D).

Figs 12-16 - *Lissoceras haugi* Sturani, 1967. [M].

- 12) MGPUT-PU 112829, Maizet, middle Garantiana Zone.
- 13) MGPUT-PU 112776, Sully, upper Parkinsoni Zone.
- 14) MGPUT-PU 111515, Sully, upper Bajocian (see Pavia 2007, pl. 1, fig. 7, and text-fig. 17B herein).
- 15) EM-589, plaster cast, Bayeux, upper Bajocian.
- 16) MGPUT-PU 111438, topotype, Chaudon, lowermost Zigzag Zone.

Scale bars of plate and top-right panel equal 10 mm. Asterisk marks the beginning of the body chamber. Specimens were whitened prior to photography.



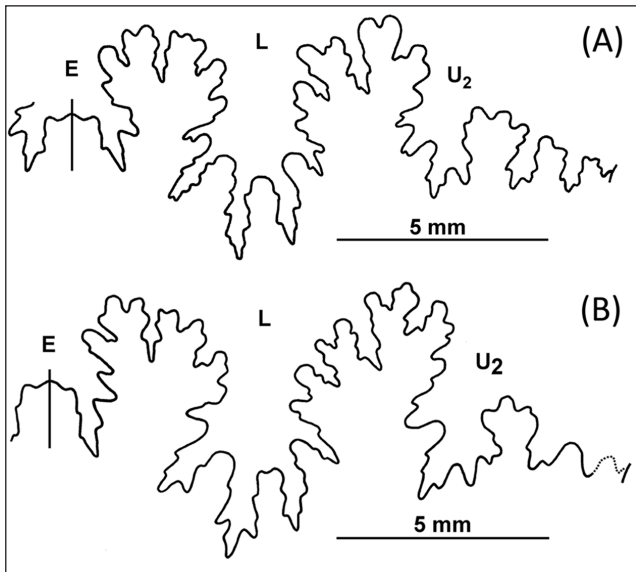


Fig. 17 - Suture lines of *Lissoceras haugi* Sturani. A) Specimen MGPUP-PU 111514 with large, rounded whorl section, upper Bajocian, Sully, bed 5. B) Specimen MGPUP-PU 111515 with narrow, compressed whorl section, upper Bajocian, Sully, bed 5.

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 (MGPUP-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_2 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 U_2 .

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 (MGPUP-PU 112853: Pl. 4, fig. 5).

Remarks. *Lissoceras haugi* shows high intraspecific variability: at one side of the coiling spectrum there are platycones 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

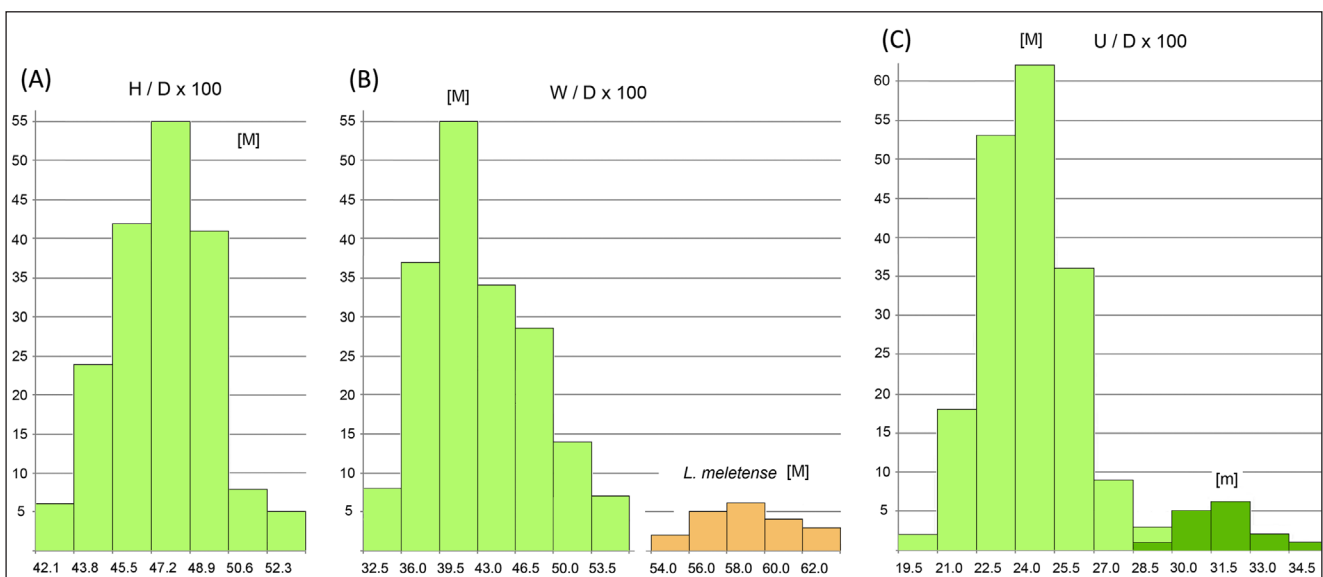


Fig. 18 - Whorl-size frequency histograms for *Lissoceras haugi* Sturani showing the number of specimens for successive ranges of H/D, W/D and U/D. The frequency values delineate a normal distribution of the sample formed by the 184 macroconchs listed in Appendix. In the histogram B the record distribution of *L. meletense* (Parona) is also inserted on equivalent size values to support the independence of the two species. In the histogram C the distribution of 15 specimens of [m] *L. haugi* emphasizes the importance of the umbilical diameter in the distinction of the two dimorphic partners.

up for *L. haugi* 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 Dagens & Weitschat (1993) on Triassic Noritaceae from Siberia may be assumed as a model for *L. haugi*.

The synonymy list contains many citations of *L. oolithicum* whose figured specimens show, in fact, features referable to *L. haugi* 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 whorl section and more branched primary elements of the suture line (Pavia 2007, and references therein). *L. ferrifex* is also a Bathonian species that shows high similarities with *L. haugi*, except for the wider umbilicus with flared umbilical wall, the large venter and a very narrow L lobe in the suture line (Krystyn 1972; Galácz 1980; Pavia 2007).

L. haugi is largely represented in the Munier-Chalmas' collection at the Université Pierre et Marie Curie of Paris. Their original labels register the name "*Moeristoceras simplex* Munier-Chalmas", but this binomen must be regarded as unavailable

because it was never published and does not appear in any paper of Munier-Chalmas (1891, 1892).

Distribution. *Lissoceras haugi* 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 *Lytoceras meletense* Parona, p. 11, pl. 1, fig. 3.

v 1971 *Lissoceras meletense* - Sturani, p. 92, text-fig. 29, pl. 6, figs 5, 6.

2000 *Lissoceras meletense* - Besnosov & Mitta, p. 51, pl. 1, fig. 19.

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 "*Posidonia 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 MGPU-PU 35789 from Monte Meletta already figured by Parona (1896, pl. 1, fig. 3). He further described as paralectotype 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 (MGUPT-PU 35790) is figured herein at Pl. 4, fig. 10.

Material: 2 specimens from Evrecy and Sully in Calvados. 32 specimens from the "*Posidonia 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-

Tab. 9 - Synthesis of measurements and regression statistics for *Lissoceras meletense* (Parona, 1896), [M].

<i>L. meletense</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
21 measures (min/max)	44.9 - 52.9	54.5 - 63.5	21.3 - 25.3	111.7 - 127.4
mean of 21 measures	48.34	58.88	23.41	121.69
standard deviation [sd]	2.00	2.31	1.01	4,5
standard error [se]	0.44	0.50	0.22	0.99
confidence interval on sd	44.34 - 52.34	54.26 - 63.50	22.39 - 25.43	112.69 - 130.69
confidence interval on se	47.46 - 49.22	57.88 - 59.88	22.97 - 23.85	119.71 - 123.67
correlation index and regression W on H:	$R^2 = 0.99 - \gamma = 1.18x + 0.48$			

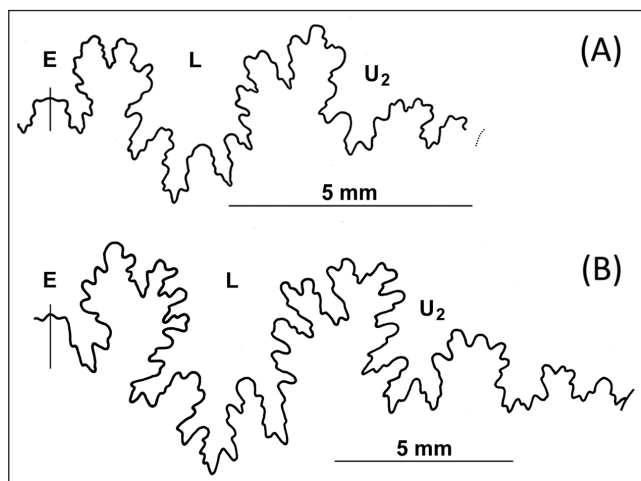


Fig. 19 - Suture lines of *Lissoceras meletense* (Parona). A) Paralectotype MGP-PD 15069/F, upper Niortense Zone, Monte Longara (from Sturani 1971, p. 92, text-fig. 29). B) Specimen MG-PUT-PU 112786, upper Bajocian, Bayeux, bed "5".

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_2 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_2 .

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_2 - L/ U_3 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]

Fig. 8; Pl. 4, fig. 9

1971 *Lissoceras* (*Microlissoceras*) *pusillum* n. sp. Sturani, p. 94, pl. 6, figs 7, ?9, 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.

<i>L. pusillum</i> [m]	h = H/D	w = W/D	u = U/D	W/H x 100
4 measures (min/max)	32.2 - 34.0	29.0 - 32.3	39.5 - 43.1	85.3 - 95.5
mean of 4 measures	33.43	30.40	41.13	90.95
standard deviation [sd]	0.83	1.38	1.67	4.46
standard error [se]	0.42	0.69	0.84	2,2
confidence intervals on sd	31.57 - 35.09	27.64 - 33.16	37.79 - 44,47	82.03 - 99.87
confidence intervals on se	32.59 - 34.27	29.02 - 31.78	39.45 - 42.81	86.55 - 95.35
correlation index and regression W on H:	$R^2 = 0.95 - y = 0.70x + 0.60$			

Tab. 10 - Synthesis of measurements and regression statistics for *Lissoceras pusillum* Sturani, 1971, [m].

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 (Microlissoceras) 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 Balkhan, western Turkmenistan (Besnosov & Mitta 2000, p. 51).

Lissoceras maerteni n. sp. [m]

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

Diagnosis: Microconchiate *Lissoceras*; mid-evolute, serpentine-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 paratype possibly with the same source is the reelaborated microconch MGPUT-PU 111999 (Pl. 4, fig. 19).

Locus typicus: The section of Sully, north of Bayeux, Cal-

vados, NW France, where the "Oolithe ferrugineuse de Bayeux" Formation was described by Pavia (1994).

Stratum typicum: Upper Bajocian, Garantiana Zone. Pavia (1994, p. 142) attributed the bed 5 of Sully section to the upper Bajocian because the reelaborated ammonites mixed in such taphonomically condensed fossil-assemblage refer to the Niortense up to the Parkinsoni zones. Nevertheless, according to the state of preservation, both the holotype and the paratype of *Lissoceras maerteni* n. sp. have to be referred to the Garantiana Zone.

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. oolithicum* morpho-structural group: according to biochronostratigraphy and whorl section the best candidate is *Lissoceras ovale* n. sp.

Distribution. Upper Bajocian of Calvados, NW France.

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*

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

<i>L. maerteni</i> [m]	h = H/D	w = W/D	u = U/D	W/H x 100
3 measures (min/max)	35.3 - 37.8	25.4 - 28.8	37.8 - 39.9	72.1 - 77.10
mean of 3 measures	36.50	27.40	38.53	75.13
standard deviation [sd]	1.25	1.78	1.18	2.67
standard error [se]	0.72	0.97	0.68	1.54
confidence interval on sd	34.00 - 39.00	23.84 - 30.96	36.17 - 40.89	69.79 - 80.47
confidence interval on se	53.06 - 37.94	25.46 - 29.34	37.17 - 39.89	72.05 - 79.21
correlation index and regression W on H:	$R^2 = 0.99 - \gamma = 0.62x + 0.66$			

and *S. costellatum*, and two species previously assigned to the genus *Lissoceras*: *S. semicostulatum* (Buckman) and *S. depereti* (Flamand). The species *S. hydei* (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 planorbicones. 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 falcoid 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/U₂ asymmetrical and higher than E/L, and suspensive lobe with U₂ and U₃ 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. liomphala* 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 bangi* Sturani, 1967. [M & m].

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

Fig. 9 - *Lissoceras pusillum* Sturani, 1971. [m].

- 9) MGPU-PU 36068, holotype, Troch 1, Romani Subzone.

Figs 10, 11, 14 - *Lissoceras meletense* (Parona 1896). [M].

- 10) MGPU-PU 35790, Monte Meletta, upper Niortense Zone. 11) MGPU-PU 35789, lectotype, Monte Meletta, upper Niortense Zone. 14) MGPU-PU 112786, Sully, upper Bajocian (see text-fig. 19B).

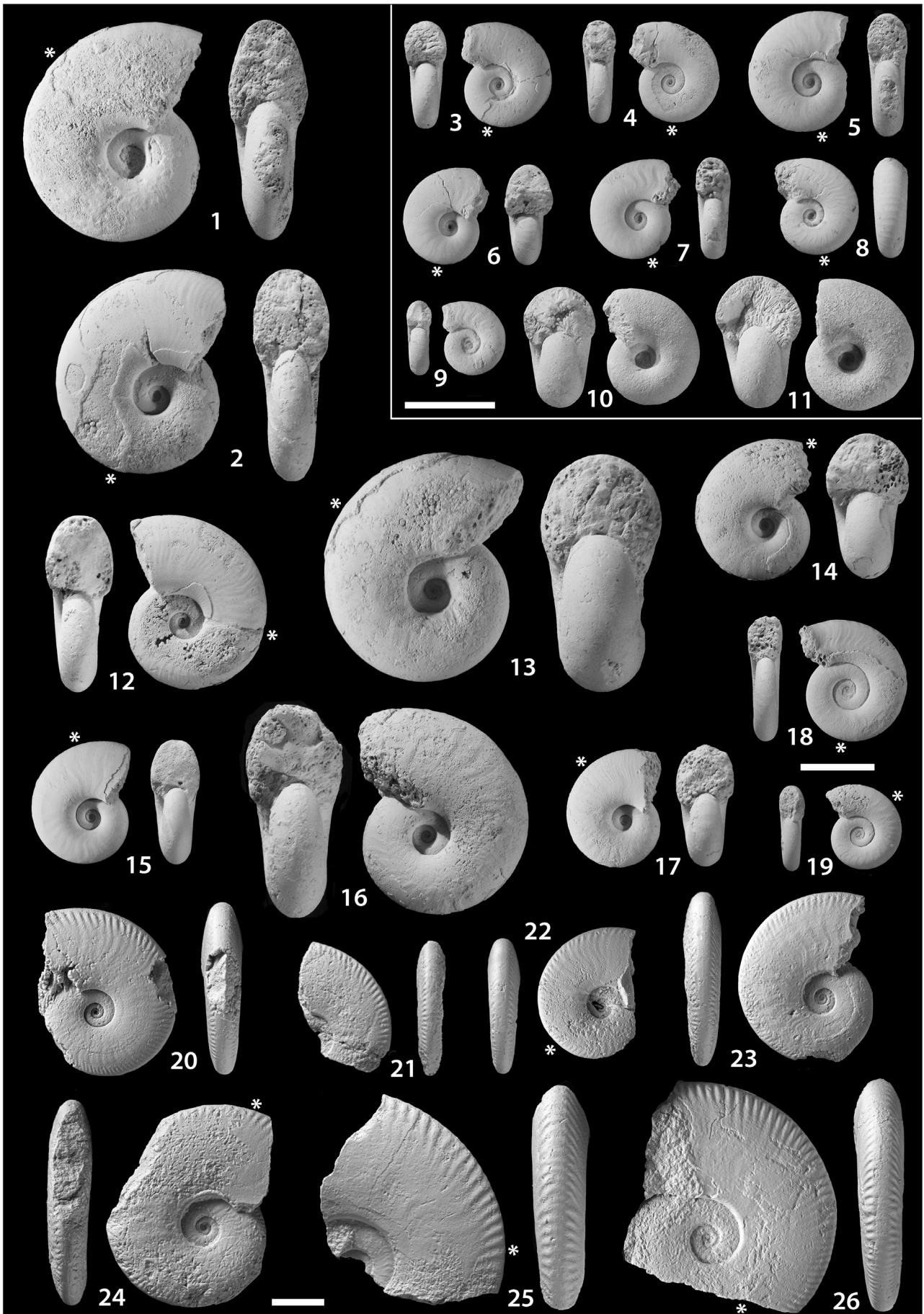
Figs 18, 19- *Lissoceras maerteni* n. sp. [m].

- 18) MGPU-PU 112998, holotype, Sully, upper Bajocian. 19) MGPU-PU 112999, paratype, Sully, upper Bajocian.

Figs 20-26 - *Semilissoceras ellipticum* n. sp. [M & m].

- 20) AB104U80/2, [M], Murtinheira, upper Laeviuscula Zone. 21) MAP-MT2c/279, [m], allotype, Masada Toyuela, upper Laeviuscula Zone. 22) M10U50/5, [M], paratype, Moscardon, lower Laeviuscula Zone. 23) MAP-MT2c/274, [M], paratype, Masada Toyuela, middle 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.



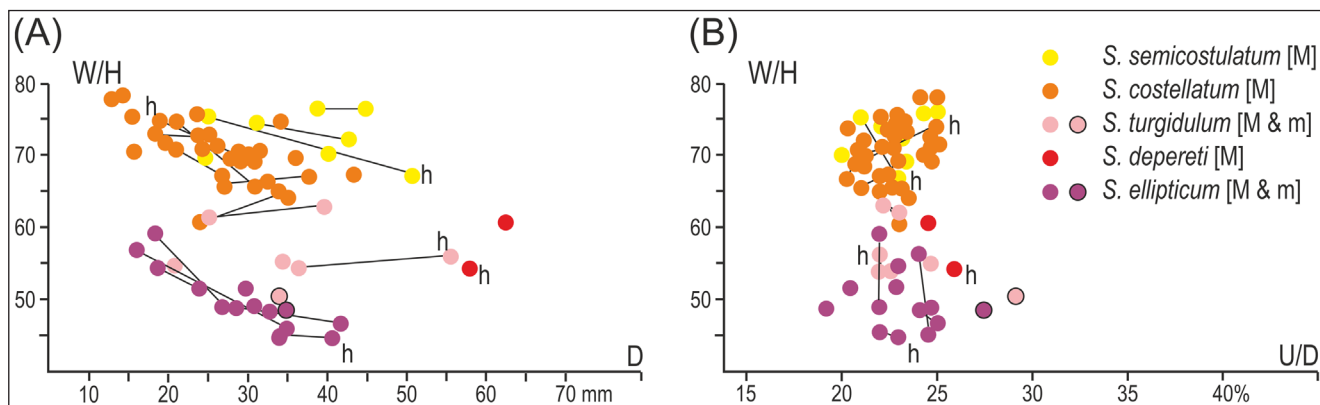


Fig. 20 - Plots of measurements for *Semilissoceras semicostulatum* (Buckman), *S. costellatum* n. sp., *S. turgidulum* n. sp., *S. depereti* (Flamand) and *S. ellipticum* n. sp., with several ontogenetic trajectories through ratios of the aperture shape (W/H). A) Whorl width/whorl height ratio (W/H 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.

original designation *Harpoceras blumius* De Gregorio, 1886, pl. 18, fig. 5, a synonymous 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/U₂. *Iokastelia* Renz, 1925 (type species by original designation *Oppelia (Iokastelia) helena* 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 falcooid 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, Som-

erset, 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 hebes* 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

Tab. 12 -Synthesis of measurements and regression statistics for *Semilissoceras ellipticum* n. sp. [M & m].

<i>S. ellipticum</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
11 measures (min/max)	44.6 - 48.6	20.20 - 27.2	21.90 - 25.0	45.2 - 59.0
mean of 11 measures	46.66	23.51	23.20	50.32
standard deviation [sd]	1.35	2.46	1.04	4.64
standard error [se]	0.41	0.74	0.31	1.40
confidence interval on sd	43.96 - 49.36	18.59 - 28.43	21.12 - 25.28	41.04 - 59.60
confidence interval on se	45.84 - 47.48	22.03 - 24.99	22.58 - 23.82	47.52 - 53.12
correlation index and regression W on H:		$R^2 = 0.99 - y = 0.37x + 1,61$		
<i>S. ellipticum</i> [m]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
1 measure	43.4	21.1	27.4	48.7

et al. 2007), Sub-Mediterranean (Flamand 1911; Pavia 1983; Fernandez-Lopez 1985; Benshili 1989, 1990; Fernandez-Lopez et al. 1989; Rulleau 1997, 2006, 2011), Mediterranean (Sturani 1971; Sandoval 1986), NE Tethyan (Seyed-Emami 1988), Himalayan (Westermann & Callomon 1988), Shoshonean (Imlay 1973) and Athabascan (Imlay 1964) bioprovinces.

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 fourth 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-MT2c/274, 279; Pl. 4, figs 21, 23-25) and 1 from Moscardon, Lower Laeviuscula Zone (M10U50/5; Pl. 4, fig. 22). The microconch MAP-MT2c/279 is regarded as the allotype of the species. These six specimens are reelaborated elements.

Locus typicus: The section Masada Toyuela at Albarracin, Teruel, Iberian Range.

Stratum typicum: Lower Bajocian, upper Laeviuscula Zone, bed 2c from Masada Toyuela (Fernandez-Lopez 2011a, 2014), belonging to the El Pedregal Formation (Gomez & Fernandez-Lopez 2004).

Material: In addition to the six type specimens, six macroconchs: 4 fragmentary specimens from Masada Toyuela (MAP-MT2d/280, 281, 287, MAP-MT2c/272), 1 from Moscardon (M10U130/2) and 1 from Murtinheira, Cabo Mondego (AB104U80/2; Pl. 4, fig. 20; fig. 21/B-C), all of them from the upper Laeviuscula Zone, 1 from Beaumont (MGUPT-PU 112296) from the lower Laeviuscula Zone.

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 falcoid 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/U₂ asymmetrical and higher than 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

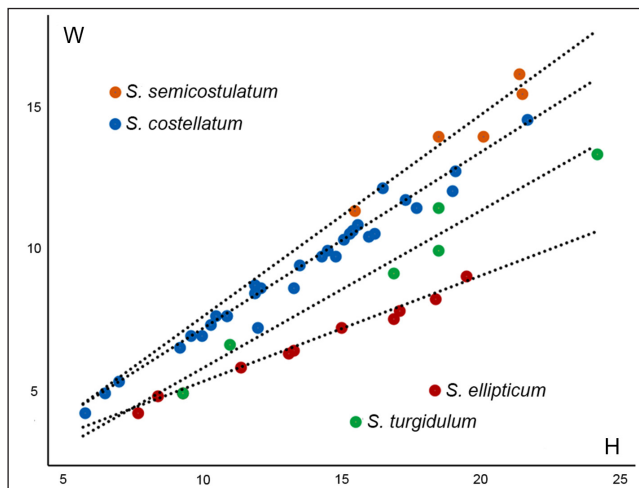


Fig. 21 - Bivariate scatter diagram of whorl height H and whorl width W for *Semilissoceras ellipticum* n. sp., *S. turgidulum* n. sp., *S. semicostulatum* (Buckman) and *S. costellatum* n. sp. Regression parameters in Tables 12-15.

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. Galacz 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* - Fernández-López, 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 allotype (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 microconch from Moscardon, Teruel, lower Laeviuscula Zone (M9L20/3: Pl. 5, fig. 4). These five specimens are reelaborated 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 (Fernandez-Lopez 1985) belonging to the El Pedregal Formation (Gomez & Fernandez-Lopez 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.

<i>S. turgidulum</i> [M]	$h = H/D \times 100$	$w = W/D \times 100$	$u = U/D \times 100$	$W/H \times 100$
6 measures (min/max)	43.0 - 51.1	23.9 - 28.8	21.5 - 23.4	54.3 - 62.5
mean of 6 measures	46.38	26.48	22.13	57.15
standard deviation [sd]	3.05	1.79	0.78	3.80
standard error [se]	1.24	0.73	0.32	1.55
confidence interval on sd	40.28 - 52.48	22.90 - 30.06	20.57 - 23.69	49.55 - 64.75
confidence interval on se	43.90 - 48.86	25.02 - 27.94	21.49 - 22.77	54.05 - 60.25
correlation index and regression W on H:	$R^2 = 0.96 - y = 0.55x + 0.29$			
<i>S. turgidulum</i> [m]	$h = H/D \times 100$	$w = W/D \times 100$	$u = U/D \times 100$	$W/H \times 100$
1 measure	43.2	21.4	28.6	49.7

Tab. 13 - Synthesis of measurements and regression statistics for *Semilissoceras turgidulum* n. sp. [M & m].

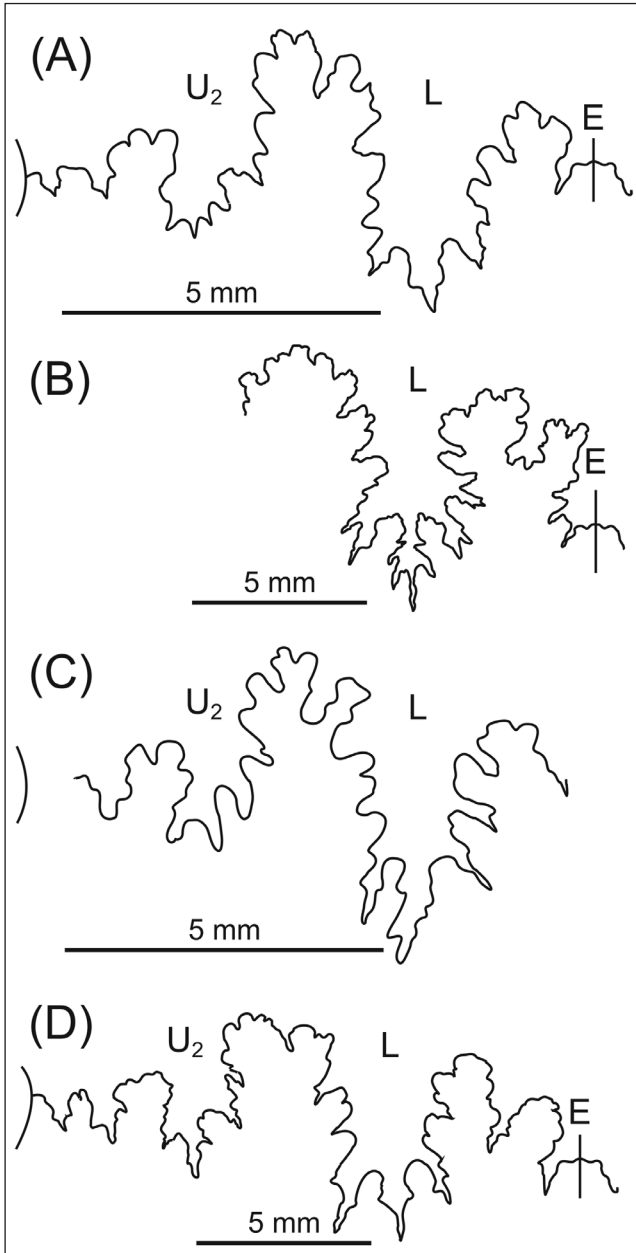


Fig. 22 - Suture lines of *Semilissoceras* gen. nov. A) *S. ellipticum* n. sp. [M], M10U50/5, paratype, Moscardon, Teruel, lower Laeviuscula Zone. B-C) *S. ellipticum* sp. nov. [M], AB104U80/2, Murtinheira, Cap Mondego, upper Laeviuscula Zone. D) *S. turgidulum* sp. nov. [m], M9L20/3, paratype, Moscardon, Teruel, lower Laeviuscula Zone.

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 falcid 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 fourth 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 trifold lobe L, saddle L/U₂ asymmetrical and higher than E/L, and suspensive lobe with U₂ and U₃ 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, Ovale 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.

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: 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 resedimented macroconch (AB93b/1) from the Murtinheira section, Cabo Mondego, Portugal, upper Laeviuscula Zone (Fernandez-Lopez et al. 1989, text-fig. 2, bed 93).

Measurements: See Appendix. The measured diameter is 63.0 mm.

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 periumbilical depression. The outer fourth 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/U₂ is high and asymmetrical.

Remarks. No microconch is so-far known. Sandoval (1986, p. 439) discussed the possibility to synonymize *Semilissoceras depereti* 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 periumbilical depression and the shorter rectiradiate external ribs of *S. semicostulatum*.

Semilissoceras hydei (Imlay, 1973) from the Cras-sicostatus Zone of Oregon shows more retro-inflexion of ribs that appear fasciculate.

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. costellatum* n. sp.).

non 1985 *Lissoceras semicostulatum* - Fernandez-Lopez, text-fig. 15, pl. 15, fig. 5 (= *S. turgidulum* n. sp.).

1988 *Lissoceras semicostulatum* - Seyed-Emami, p. 78, text-fig. 24.

non 1989 *Lissoceras* (*Lissoceras*) *semicostulatum* - Benshili, p. 174, pl. 21, fig. 11 (= *S. costellatum* n. sp.).

non 1990 *Lissoceras* (*Lissoceras*) *semicostulatum* - Benshili, p. 77, pl. 1, fig. 3 (= *S. costellatum* n. sp.).

non 1997 *Lissoceras semicostulatum* - Rulleau, p. 7, pl. 4, figs 14-15 (= *S. costellatum* n. sp.).

non 2006 *Lissoceras semicostulatum* - Rulleau, p. 112, pl. 88, fig. 3 (= *S. costellatum* n. sp.).

2007 *Lissoceras*? cf. *semicostulatum* - Dietze et al., p. 20, fig. 7c.

non 2011 *Lissoceras semicostulatum* - Rulleau, p. 68, pl. 30, fig. 3 (= *S. costellatum* n. sp.).

v 2013 *Lissoceras semicostulatum* - Pavia et al., p. 142.

2015 *Lissoceras depereti* - Chandler & Witcher, pl. 22, fig. 1.

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

Types: The holotype is the specimen BGS-47188 from the lower Bajocian, Laeviuscula Zone of Sandford Lane, Dorset, figured by Buckman (1923 in 1909-30, pl. 400, see also Fig. 23A herein).

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. Measured extremes for diameter: 40 - >60 mm. Values for h, w and u are summarized in Table 14.

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

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

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 fourth 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 rectiradial 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/U₂ 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 reelaborated 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 resedimented fossil from the early Humphriesianum Zone (Romani Subzone) of Chaudon (Pavia 1983), whereas the record from



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.

<i>S. costellatum</i> [M]	h = H/D x 100	w = W/D x 100	u = U/D x 100	W/H x 100
31 measures (min/max)	47.4 - 54.9	30.9 - 39.4	20.4 - 24.9	61.3 - 78.3
mean of 31 measures record	50.05	35.14	22.85	70.28
standard deviation [sd]	1.58	1.80	1.18	3.98
standard error [se]	0.28	0.32	0.21	0.71
confidence interval on sd	46.89 - 53.21	31.54 - 38.74	20.49 - 25.21	62.32 - 78.24
confidence interval on se	49.49 - 50.61	34.5 - 35.78	22.43 - 23.27	68.86 - 71.70
correlation index and regression W on H:	$R^2 = 0.98$ - $y = 0.62x - 1.00$			

Tab. 15 - Synthesis of measurements and regression statistics for [M] *Semilissoceras costellatum* n. sp. [M].

Calvados (Pavia et al. 2013) concerns a reelaborated 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* - Sturani, 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.
 1997 *Lissoceras* *semicostulatum* - Rulleau, p. 7, pl. 4, figs 14-15.
 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 rectiradial ribs on the outer half flank.

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

Types: The holotype is the reelaborated macroconch MGPUT-PU 112835 (Pl. 5, fig. 9) from Maizet (Calvados), bed 5, upper Humphriesianum Zone. Five paratypes: the reelaborated 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 resedimented macroconch SMNS 70396/2 (Pl. 5, fig. 15) from Sandford Lane, Propinquans Zone; the resedimented macroconch MGPUT-PU 113015 (Pl. 5, fig. 12) from Chaudon (Alpes-de-Haute-Provence), bed 397, Romani Subzone; the reelaborated 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 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. *S. costellatum* 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 *S. costellatum* n. sp. pertains to the Umbilicum or Blagdeni 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 "Posidonia alpine beds" in Asiago. 1 specimen from Chaloi, 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.

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 fourth 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 fourth of the flank; costellae run rectiradial or slightly concave up to the rounded ventro-

PLATE 5

Figs 1-6 - *Semilissoceras turgidulum* n. sp. [M & m].

- 1) M9U50/1, [M], holotype, Moscardon, Laeviuscula Zone. 2) G10U70/4, [M], paratype, Saldon, Laeviuscula Zone. 3) MT2/95, [M], paratype, Masada Toyuela, lower Laeviuscula Zone. 4) M9L20/3, [m], paratype, Moscardon, lower Laeviuscula Zone. 5) M9L20/2, [m], allotype, Moscardon, lower Laeviuscula Zone. 6) SMNS 70396/10, [M], Sandford Lane, middle Laeviuscula Zone.

Figs 7, 8, 10 - *Semilissoceras semicostulatum* (Buckman, 1923). [M].

- 7) MGPUT-PU 113024, Chaudon, Romani Subzone. 8) MGPUT-PU 113011, Maizet, upper Humphriesianum Zone. 10) SMNS 70396/3, Sandford Lane, Propinquans Zone (see text-fig. 24B).

Figs 9, 11, 12, 14-16 - *Semilissoceras costellatum* n. sp. [M].

- 9) MGPUT-PU 112835, holotype, Maizet, upper Humphriesianum Zone. 11) MGPUT-PU 112737, paratype, Sully, Niortense-Garantiana zones. 12) MGPUT-PU 113015, paratype, Chaudon, Romani Subzone. 14) MGPUT-PU 112736, Sully, Niortense-Garantiana zones. 15) SMNS 70396/2, Sandford Lane, Propinquans Zone. 16) MGPUT-PU 113010, paratype, Teillon, Garantiana Zone.

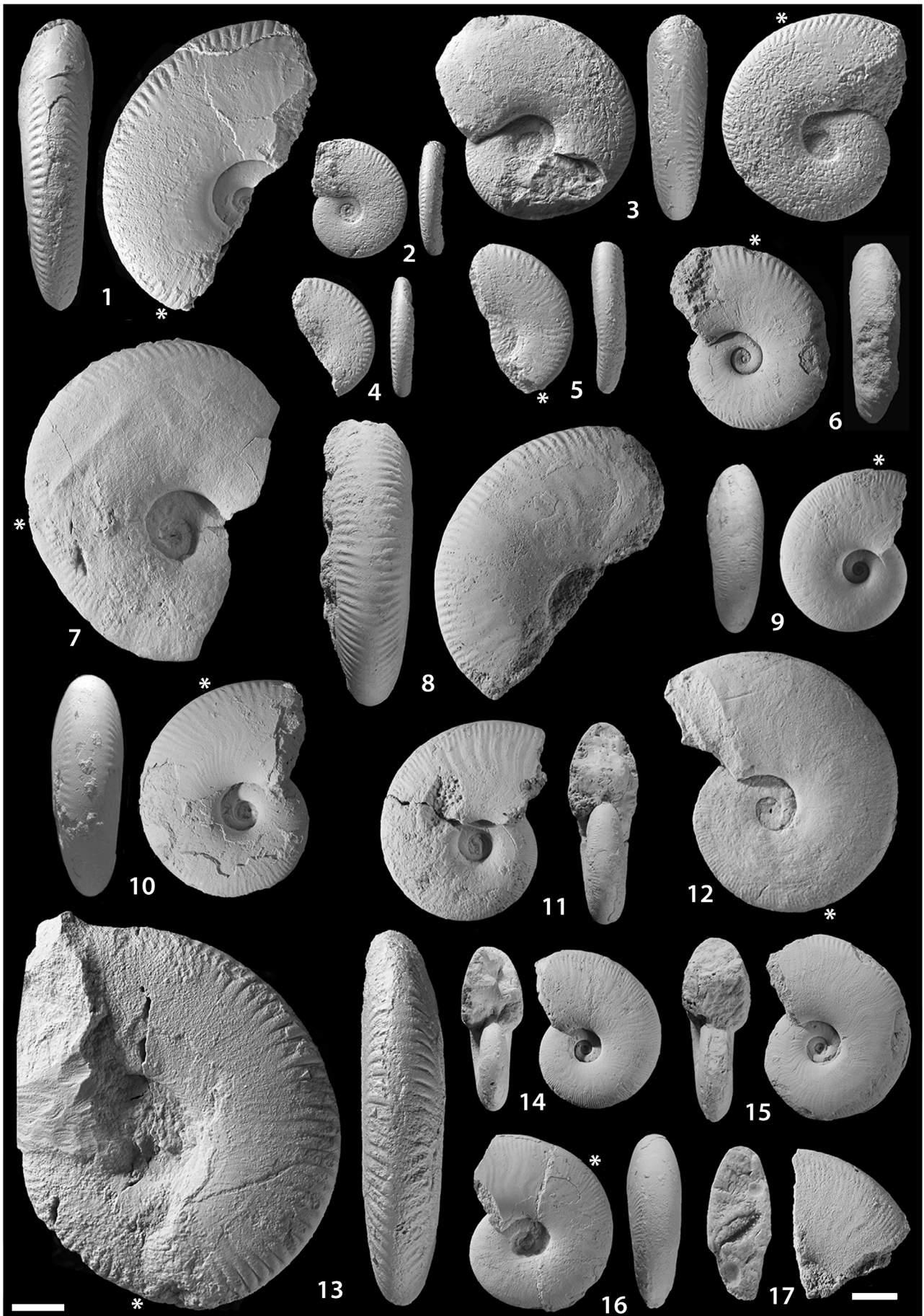
Fig. 13 - *Semilissoceras depereti* (Flamand, 1911). [M].

13) MT3/4, Masada Toyuela, uppermost Laeviuscula Zone.

Fig. 17 - *Semilissoceras* aff. *costellatum* n. sp. [M].

- 17) MGPUT-PU 35792, Monte Meletta, Niortense-Garantiana zones.

Scale bars of plate equal 10 mm, except fig. 17 with scale bar 5 mm. Asterisk marks the beginning of the body chamber. Specimens were whitened prior to photography.



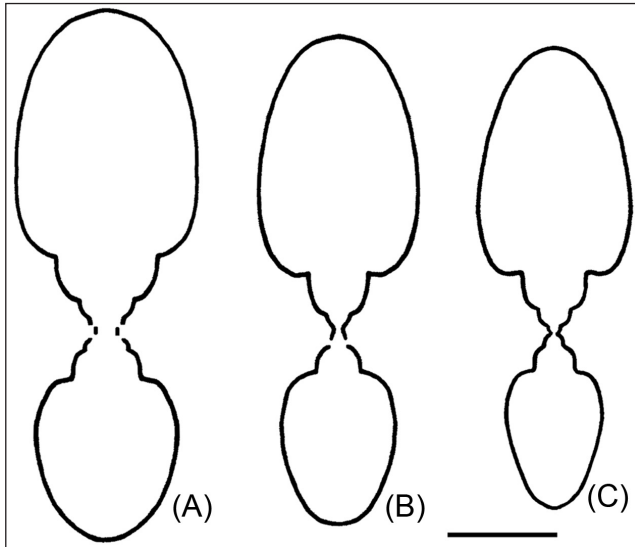


Fig. 24 - Whorl shape cross sections through the phragmocone. A) *Semilissoceras semicostulatum* (Buckman) holotype BGS-47188. B) *S. semicostulatum* (Buckman), SMNS 70396/2. C) *S. costellatum* n. sp., paratype EM-588. Scale bar equals 10 mm.

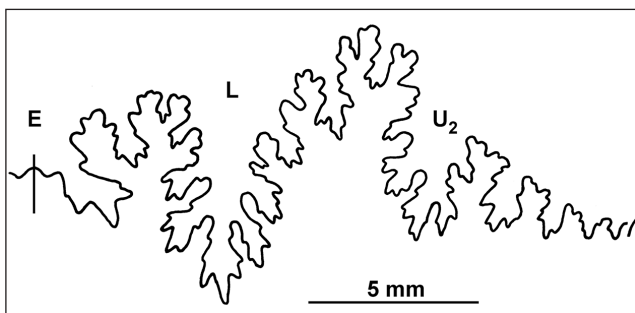


Fig. 25 - Suture line of *Semilissoceras costellatum* n. sp., paratype MG-PUT-PU 112735, Niortense-Garantiana zones, Bayeux area, bed "5a".

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/ U_2 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 U_2 .

Remarks. No microconch is so-far known. *Semilissoceras costellatum* n. sp. belongs to the morpho-structural group of *S. depereti* 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

rounded 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 bakeri* 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 Humphriesianum Zone 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 reelaborated 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 Lissocerotinae coming from different palaeobiogeographical areas of the Mediterranean-Caucasian Subrealm demonstrates that the Bajocian dimorphic lissocerotins 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. submediterraneum*, *L. maiyetense*, *L. ovale*, *L. sturani*, *L. maerteni*, *S. ellipticum*, *S. turgidulum*, *S. costellatum*. The dimorphism of Bajocian lissocerotins has been also discussed: the dimorphic pairing is described for *L. inflatum* Wetzel, *L. submediterraneum* n. sp., *L. sturani* n. sp., *L. haugi* Sturani, *S. ellipticum* n. sp. and *S. turgidulum* n. sp., whereas it

is still missing for two microconch taxa (*L. maerteni* n. sp., *L. pusillum* Sturani) and eight macroconchs taxa (*L. psilodiscus* (Schloenbach), *L. oolithicum* (d'Orbigny), *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. sturani* show subtriangular to ovate whorl section, depressed ventral saddle at the bottom of the large lobe E and wide suspensive 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 haugi* 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. haugi* 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 ribbing) 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 Propinquans to Humphriesianum zones;

(3) in the group of *L. oolithicum*, the morpho-structural similarities of *L. sturani* 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. sturani* represents a singular lissoceratin due to the small adult size and the low degree of ontogenetic and ontogenic variation;

(6) the couple *L. haugi* 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 peramorphoclines, from moderately evolute 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 chronoclines 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. haugi* < *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-

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 miademic 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 taphonic populations of type-3 (Fernandez-Lopez 2014, fig. 3; i.e., monospecific or polyspecific shells, with unimodal or polymodal size–frequency distributions of negative asymmetry, adults dominant, juveniles absent, and dimorphism poorly represented) indicative of ademic or parademic taxa that arrived at their present location by regional nekrokinosis 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.

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