

Taxonomic notes on some Barremian–Aptian cephalopods from the *Station de Cassis* section and surrounding sites, Bouches-du-Rhône, southern France

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Abstract. This paper describes and illustrates some of the cephalopod fossils (i.e., Ammonoidea and Nautiloidea) collected by the late Robert Busnardo (1926–2018) from the Barremian/Aptian boundary interval at the *Station de Cassis* section, and the surrounding sites, Bouches-du-Rhône, southern France. This collection is housed at the *Faculté des Sciences de Lyon* (Université Claude Bernard Lyon I, France). Figured specimens of the literature are also addressed, some of them being deposited in the collections of the *Musée de Paléontologie de Provence* (Aix-Marseille University). In the following taxonomic notes, emphasis is laid on the specific diagnosis, and ontogeny aspects of the Ancyloceratidae *Micrancyloceras breve*, *Pseudocrioceras mazierei* sp. nov., *Kutatissites pouponi*, and *Hoheneggericeras* sp., the Heteroceratidae *Calanquites* cf. *katsharavai*, *Martelites sarasini* and *Heteroceras baylei*, the Deshayesitidae *Deshayesites oglanlensis*, the Desmoceratidae *Pseudohaploceras* cf. *liptoviense*, the Barremitidae *Barremites* sp. (Ammonoidea), as well as on the Nautilidae *Cymatoceras neocomiense* and the Cenoceratidae *Heminautilus sanctaerucis* (Nautiloidea). We also address the potential sexual dimorphism in the lowermost Aptian Deshayesitidae *Deshayesites*, and we question its expression in the uppermost Barremian Ancyloceratidae *Micrancyloceras* and *Pseudocrioceras*, and the Heteroceratidae *Calanquites* as well. We here document an overlap of the genera *Martelites* and *Pseudocrioceras*; this has been overlooked so far. Moreover, the presence and stratigraphic range of *Pseudocrioceras waagenioides* should be regarded with caution at Cassis since the only two figured specimens are doubtful. The repeated use of *Pseudocrioceras waagenioides* as a marker of a total range subzone for characterising the uppermost Barremian (upper *Martelites sarasini* Zone) is, therefore, problematic. We here propose the dumping of the *Pseudocrioceras waagenioides* Subzone and its replacement by the *Pseudocrioceras mazierei* sp. nov. Subzone. The base of the new subzone is fixed at the first occurrence of the new nominative species, and its top is constrained by the first occurrence of the Deshayesitidae *Deshayesites oglanlensis* which marks the base of the Aptian in the standard Mediterranean ammonite scale. The new index species *Pseudocrioceras mazierei* sp. nov. is abundant and occurs in a short stratigraphic interval at the base of its nominative subzone, and can be easily identified. It is further regarded as a presumed descendant of *Micrancyloceras breve*, and merely forms the rootstock from which all other southern France *Pseudocrioceras* evolved.

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Keywords: Ammonoidea; Nautiloidea; Barremian; Aptian; Taxonomy; Cassis; Bouches-du-Rhône; France.

Notes taxonomiques sur quelques céphalopodes barrémo-aptiens de la coupe de la *Station de Cassis* et des sites environnants, Bouches-du-Rhône, Sud de la France

Résumé : Ce travail décrit et illustre certains céphalopodes fossiles (i.e., Ammonoidea et Nautiloidea) collectés par le défunt Robert Busnardo (1926–2018) dans l'intervalle de la limite Barrémien/Aptien dans la coupe de la *Station de Cassis* et des sites alentours, Bouches-du-Rhône, France. Cette collection est déposée à la *Faculté des Sciences de Lyon* (Université Claude Bernard Lyon I, France). Des spécimens figurés de la littérature, dont quelques-uns sont déposés dans les collections du *Musée de Paléontologie de Provence* (Université de Aix-Marseille), sont

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également traités. Dans l'étude taxonomique, l'accent est mis sur la diagnose spécifique et les aspects ontogénétiques des Ancyloceratidae *Micrancyloceras breve*, *Pseudocrioceras mazierei* sp. nov., *Kutatissites pouponi*, et *Hoheneggericeras* sp., des Heteroceratidae *Calanquites* cf. *katsharavai*, *Martelites sarasini* et *Heteroceras baylei*, du Deshayesitidae *Deshayesites oglanlensis*, du Desmoceratidae *Pseudohaploceras* cf. *liptoviense*, et du Barremitidae *Barremites* sp. (Ammonoidea), mais également du Nautilidae *Cymatoceras neocomiense* et du Cenoceratidae *Heminautilus sanctaerucis* (Nautiloidea). Nous abordons le potentiel dimorphisme d'ordre sexuel chez les Deshayesitidae de l'Aptien basal, et nous questionnons son expression chez les Ancyloceratidae *Micrancyloceras* et *Pseudocrioceras* du Barrémien terminal, et chez l'Heteroceratidae *Calanquites* également. Des nouvelles données sur l'extension stratigraphique des espèces de *Martelites* et de *Pseudocrioceras* sont apportées et ces dernières montrent un chevauchement des deux genres qui avait été jusqu'ici ignoré. De plus, la présence et la distribution stratigraphique de l'espèce *Pseudocrioceras waagenioides* doit être considérée avec prudence car les deux seuls spécimens rapportés à cette espèce sont douteux. L'utilisation de *Pseudocrioceras waagenioides* comme marqueur d'une sous-zone d'extension totale pour caractériser le Barrémien terminal (partie supérieure de la Zone à *Martelites sarasini*) est, de fait, problématique. Nous proposons ici l'abandon de la Sous-zone à *Pseudocrioceras waagenioides* et son remplacement par la Sous-zone à *Pseudocrioceras mazierei* sp. nov. La base de cette nouvelle sous-zone est fixée à la première occurrence de l'espèce index, et son sommet est contraint par la première occurrence du Deshayesitidae *Deshayesites oglanlensis* qui marque la base de l'Aptien dans l'échelle ammonitique standard méditerranéenne. La nouvelle espèce-index *Pseudocrioceras mazierei* sp. nov. est abondante et occupe un court intervalle stratigraphique à la base de sa sous-zone éponyme, et peut être facilement identifiée. L'espèce est en outre considérée comme un descendant probable de *Micrancyloceras breve*, et correspond à l'évidence au groupe initial duquel tous les autres *Pseudocrioceras* du Sud de la France ont évolué.

Mots-clés : Ammonoidea ; Nautiloidea ; Barrémien ; Aptien ; Taxonomie ; Cassis ; Bouches-du-Rhône ; France.

1. Introduction

This paper aims at describing and illustrating the cephalopods (i.e., Ammonoidea and Nautiloidea) that are of biostratigraphic relevance for characterising the Barremian/Aptian boundary interval at the *Station de Cassis* section, Bouches-du-Rhône, southern France. The studied material was collected in the eighties by the late Robert Busnardo (1926-2018) and re-examined at the *Faculté des Sciences de Lyon* (Université Claude Bernard Lyon I, France). Some of the specimens previously figured by Ropolo & Gonnet (1998), Cecca *et al.* (1999, 2000), Gonnet *et al.* (2000) and Ropolo *et al.* (1999, 2000a-b, 2006, 2008) from surrounding sites are also addressed. Few of them are deposited in the collections of the *Musée de Paléontologie de Provence* (Aix-Marseille University), and have been here re-examined.

2. Geological setting

2.1. Geological background

During the Early Cretaceous, the southeastern France palaeogeography embodies the northern palaeomargin of the Pyrenean–Valais oceanic realm, and houses the western appendage of the Alpine Tethys, the so-called Vocontian Basin (Dercourt *et al.*, 1993). The Vocontian Basin was bordered by extensive Urgonian carbonate platforms, the maximum development of which occurred during the Barremian (Frau *et al.*, 2017, 2018a-b) (Fig. 1A-B). The complex strain field regime induced by the developing Atlantic Rift resulted in the counterclockwise rotation

of Iberia in the upper Barremian and the opening of the V-shaped Bay of Biscay (Gong *et al.*, 2008). This large-scale tectonic deformation is regarded as the driving mechanisms of the N-S collapse of the southern part of the Urgonian Provence platform and the ensuing installation of a permanent intra-shelf basin, i.e., the South Provence Basin (Tendil *et al.*, 2018a). While the South Provence Basin was strongly subsident during the Barremian/Aptian boundary interval, the Urgonian carbonate producing ecosystems maintained in northern Provence up to the mid-early Aptian (Frau *et al.*, 2017, 2018a) (Fig. 1B).

The sedimentary succession recording the change from the Urgonian platform carbonates to the intra-shelf South Provence basinal deposits has a widespread record in southern Provence and can be followed over ~50 km through the Calanques and Nerthe massifs (Frau *et al.*, 2018a-b). The best outcropping successions are in the vicinity of the Cassis railway station (thereafter *Station de Cassis* section), halfway between the towns of Cassis and Roquefort-la-Bédoule (Fig. 1C-D). It forms the bottom part of the type succession of the lower Aptian Substage, former 'Bédoulien' of Toucas (1888).

2.2. Lithology, biofacies and ammonite-age zonal boundaries

The *Station de Cassis* section is ~20 m thick and exposes the uppermost part of the Urgonian limestones capped by the drowning and lowermost basinal sequences (Fig. 2A-B).

The Urgonian limestones are characterised by oolitic and micritic limestones, rich in small- to large-sized requieniid

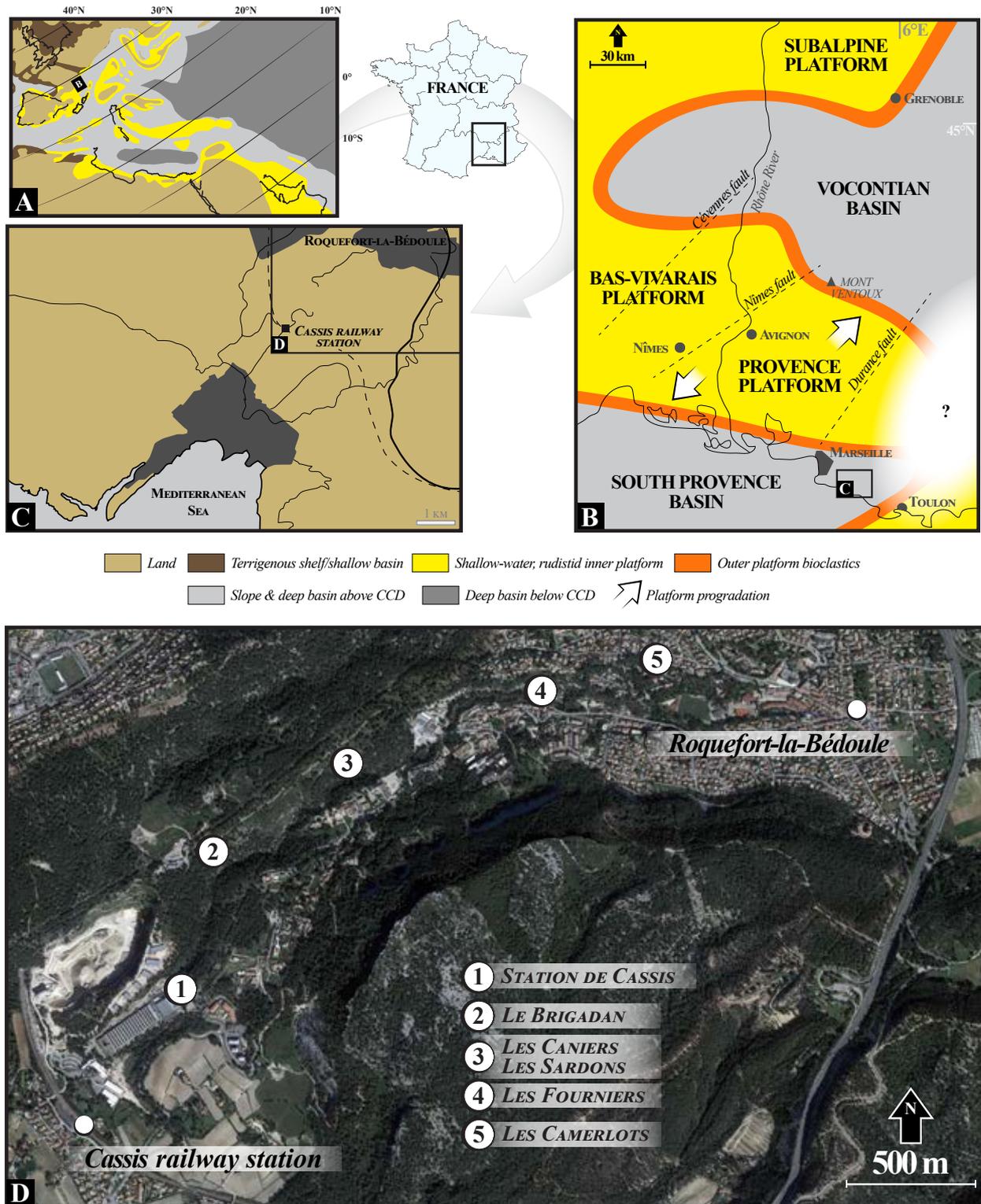


Fig. 1 - A: Barremian–Aptian palaeogeography of the Mediterranean Tethys (modified after Tendil *et al.*, 2018, and references therein). Position of Fig. 1B is noted; **B:** Uppermost Barremian palaeogeography reconstruction of southeastern France showing the Vocontian and South Provence basins separated by the Provence platform (modified from Frau *et al.*, 2018a). Black square indicates the position of Fig. 1C; **C:** Location of the *Station de Cassis* section, being halfway between the town of Cassis and Roquefort-la-Bédoule, Bouches-du-Rhône, southern France. Black square indicates the position of Fig. 1D; **D:** Location of the *Station de Cassis* section and the surrounding sites cited in the text (*Le Brigadan*, *Les Caniers/Les Sardons*, *Les Fourniers*, and *Les Camerlots*).

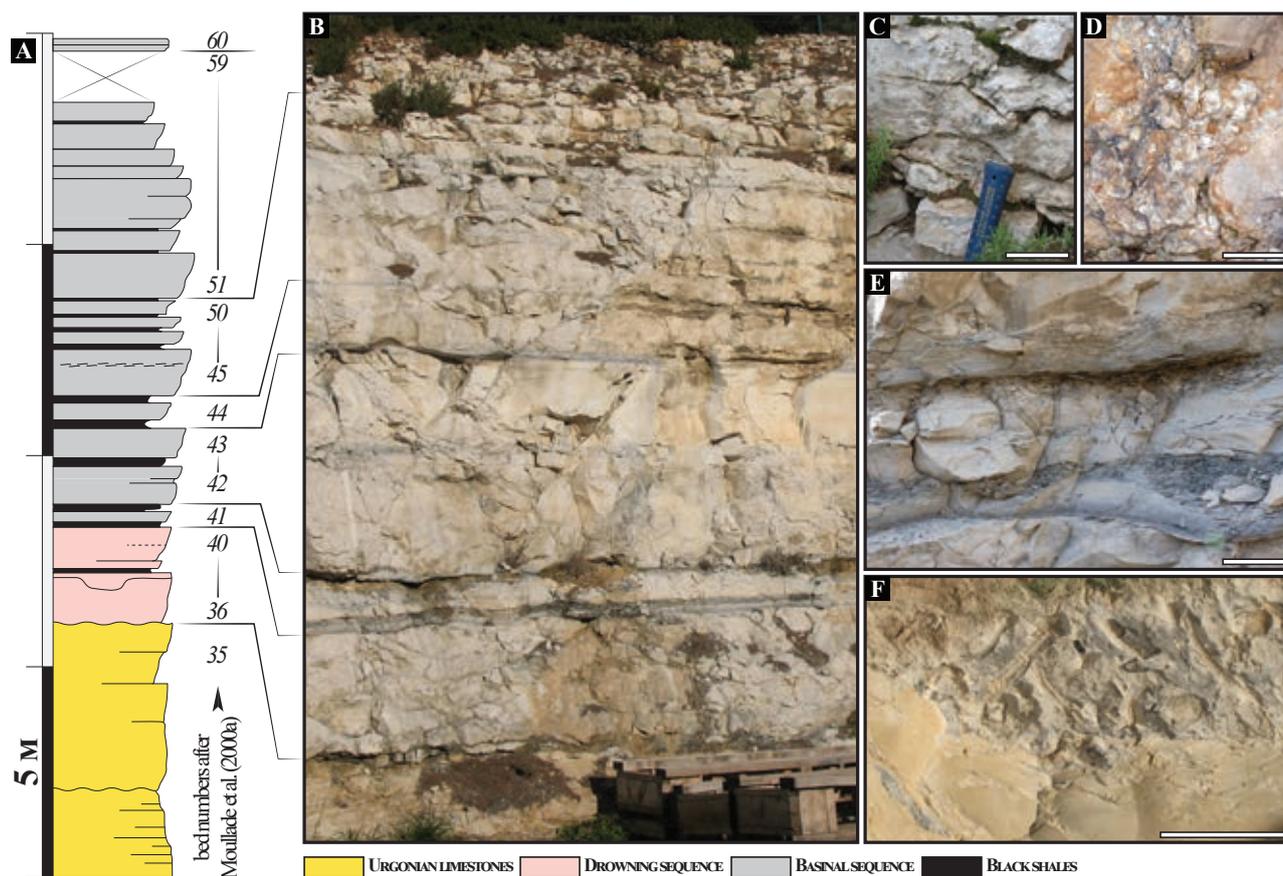


Fig. 2 - **A**: Litho-log of the *Station de Cassis* section, including, from bottom to top, the Urganian limestones, drowning and basinal sequences (modifier from Stein *et al.*, 2012); **B**: Field view of the section; **C**: Focus on the rudist-bearing bed 35; **D**: Photograph of rudists, brachiopods and serpulids accumulation at the top of bed 35 (= drowning discontinuity); **E**: The Niveau Taxy *sensu stricto* (bed 41); **F**: Serpulids accumulation at the top of bed 40 (modified from Stein *et al.*, 2012). Bed numbers follow Moullade *et al.* (2000).

rudists, as well as gastropods, miliolids and orbitolinids (**Fig. 2C**). This faunal assemblage likely indicates a palaeowater depth less than a metre (Fenerci-Masse *et al.*, 2004). This sequence is capped by an erosional hardground overlain by a condensed interval of varying thickness (15 to 35 cm), containing encrusted brachiopods, serpulids and rudists (Stein *et al.*, 2012) (**Fig. 2D**). This hardground marks the termination of the rudist-rich Urganian carbonate platform regime in southern France and the initiation of the tectonically induced intrashelf South Provence Basin (Masse & Fenerci-Masse, 2011; Tendil *et al.*, 2018). This is regionally assigned to the boundary between the upper Barremian *Gerhardtia sartousiana* and *Imerites giraudi* ammonite zones (Frau *et al.*, 2016, 2018a-b).

Above this drowning discontinuity, fossiliferous beds (beds 36 to 40), with red algae, orbitolinids, pycnodontid bivalves, and rhynchonellids (**Fig. 2A-B**). These beds form the drowning sequence *sensu stricto* (Masse & Fenerci-Masse, 2011; Frau *et al.*, 2016). Bed 37 records the inception of planktonic foraminifera illustrating a change toward deeper circalittoral conditions (Masse & Fenerci-Masse, 2011). Macsotay (1980) also reported a

rich gastropod assemblage in this bed, including diverse aporrhoids, procerithiids and nerinellids.

Bed 41 initiates the basinal sequence (**Fig. 2A-B**), and it marks the base of the uppermost Barremian *Martelites sarasini* Zone (Frau *et al.*, 2016). This sequence starts with an alternation of decimetre-thick, whitish, micritic basal limestones (beds 41 to 44), and thin, blue-grey black shales. These beds contain various bivalves, gastropods, serpulids, and sparse benthic and planktonic foraminifera (Moullade *et al.*, 2000; Masse & Fenerci-Masse, 2011; Stein *et al.*, 2012). Locally, black shales horizons occur. They can be darker and distinctly laminated at their base and burrowed at their top. Bed 41 refers to the ‘Niveau Taxy’ *sensu* Moullade *et al.* (2000) (**Fig. 2E**), which is easily recognisable on the field by the mass-occurrence of the minute bivalve *Astarte numismalis*, brachiopods and serpulids (**Fig. 2F**). Bed 44 ends at a burrowed surface marked by a bivalve-rich accumulation comprising astartid, pectinid, myalinid, pulvinitid, nuculanid, gryphaeid and venerid bivalves (Macsotay, 1980).

The overlying succession marks a change toward a limestone-dominated sequence, composed of

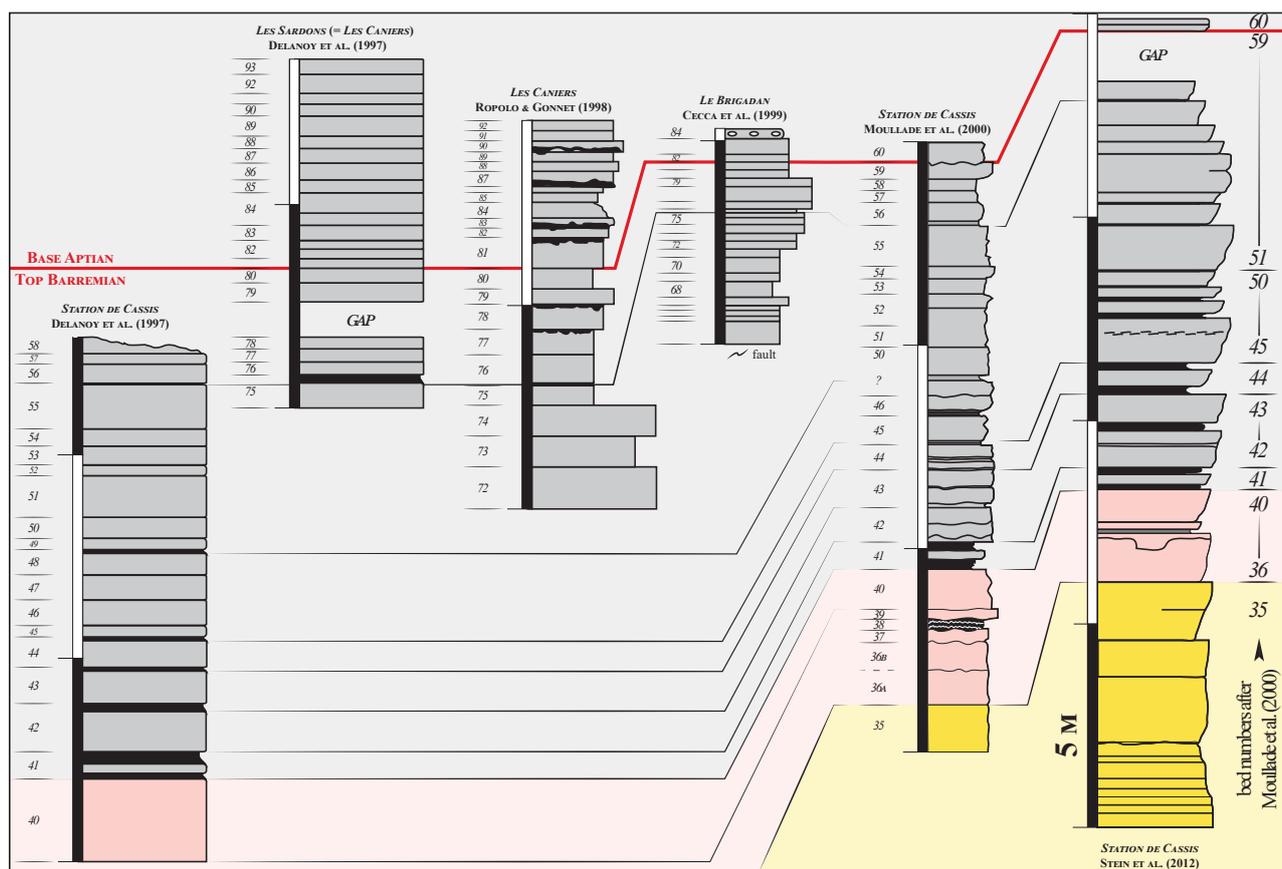


Fig. 3 - Putative lithological correlations between the published litho-logs of the *Station de Cassis* section and the surrounding sites (*Le Brigadan*, *Les Caniers/Les Sardons*). Facies colour legend follows Fig. 2.

decimetre-thick, bedded wackestones (from bed 45 upward) (**Fig. 2A-B**). These beds record the progressive disappearance of the shelly benthic fauna replaced by ammonites, nautiloids, belemnites and planktonic foraminifera indicating of hemipelagic depositional conditions (Moullade *et al.*, 2000). Bed 60 records the explosive appearance of deshaysitids ammonites, that is taken as the marker of the base of the Aptian Stage in the area (Delanoy *et al.*, 1997; Cecca *et al.*, 1999, 2000; Ropolo *et al.*, 1999, 2000a-b), and more generally in the Standard Mediterranean Ammonite Scale (SMAS of Reboulet *et al.*, 2011, 2014, 2018).

At least nine black shales horizons occur in the drowning and lowermost basinal sequences of the South Provence Basin (Stein *et al.*, 2012). These horizons form the Taxy black shales episodes in the sense of Föllmi (2012).

Various litho-logs of the *Station de Cassis* section and its surrounding sites (*Le Brigadan*, *Les Caniers/Les Sardons*) have been published in the literature (e.g., Delanoy *et al.*, 1997, fig. 2; Ropolo & Gonnet, 1998, fig. 2; Ropolo *et al.*, 1999, fig. 6; Cecca *et al.*, 1999, fig. 3; Moullade *et al.*, 2000, fig. 5; Masse & Fenerci-Masse, 2011, fig. 8; Stein *et al.*, 2012, fig. 3). Putative correlations are provided in **Fig. 3**. We here follow bed numbering of Moullade *et al.* (2000) for the *Station de Cassis* section.

3. Systematic paleontology

3.1. Conventions

In the following palaeontological study, the suprageneric classification is limited to the family level. Synonymy lists refer to the types and figured specimens from the South Provence Basin. This is distinguished as potential micro-[?m] and macroconchs [?M] for the Deshayesitidae. Unless otherwise mentioned, repository acronyms indicate:

- FSL – *Faculté des Sciences de Lyon*, Lyon, France.
- CNIGR – *Central scientific geological museum*, Saint-Petersburg, Russia.
- IJ – *Ivane Javakhishvili Tbilisi State University*, Georgia.
- MCGL – *Muséum Cantonal de Géologie de Lausanne*, Switzerland.
- MHNM – *Muséum d’Histoire Naturelle de Marseille*, France.
- MNHN – *Muséum National d’Histoire Naturelle*, Paris, France.
- MPP – *Musée de Paléontologie de Provence*, Marseille, France.

The coiling nomenclature and naming of the parts of the heteromorphic shells (i.e., spire/helix, proversum,

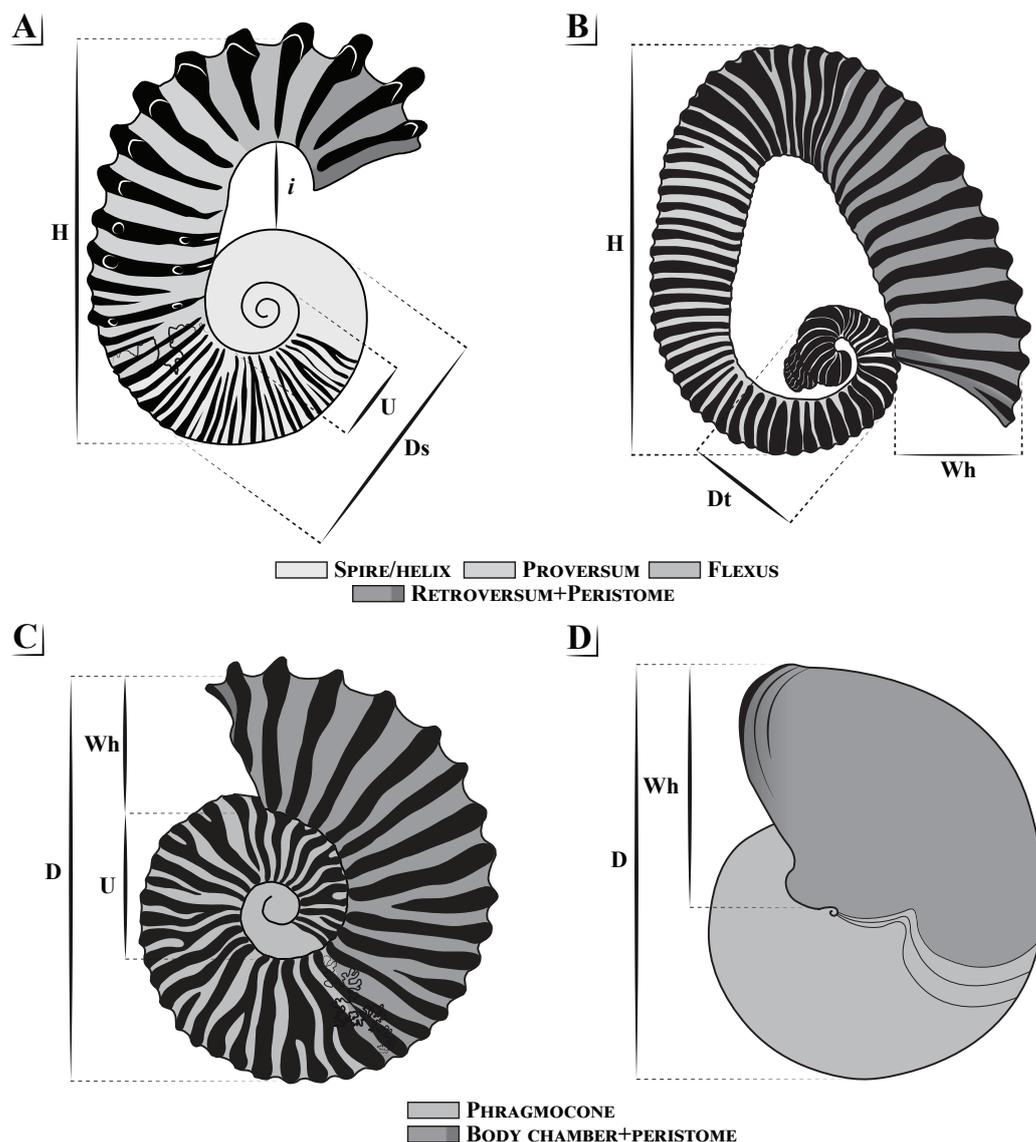


Fig. 4 - Shell parameter indices for (A) ancyloceratids (i.e., genus *Pseudocrioceras*), (B) heteroceratids (i.e., genus *Heteroceras*), (C) deshayesitids (i.e., genus *Deshayesites*) and other planispiral ammonites, and (D) nautiloids (i.e., genus *Heminautilus*) used in this work. The following abbreviations for heteromorphic shells indicate: H: total height, i: hiatus between the spire and the flexus, U: umbilicus width of the spire, Ds: diameter of the spire/helix; and those of planispiral ones are D: diameter; U: umbilicus width of the inner whorls; Wh: high of the whorl at the aperture or at the end of the last preserved whorl. Note that the whorl breath is often not considered due to sedimentary compaction.

flexus and retroversum) follow the terminology of Vašíček (1972) and Aguirre-Urreta (1986) (Fig. 4A-B). The following acronyms indicate H = total height of the shell, Ds = diameter of the spire, Dt = diameter of the turricones (when being present), U = width of umbilicus of the spire, and i = hiatus between the spire and the flexus. Measurement database of heteromorphic ammonites is taken from Ropolo & Gonnet (1998), Ropolo *et al.* (1999, 2000a), Delanoy (1997), Delanoy *et al.* (2000), Gauthier *et al.* (2006), Baudouin *et al.* (2012), and Frau *et al.* (2016). For *Deshayesites* and other planispiral ammonites (Fig. 4C), the measurement database derives from the works of Cecca *et al.* (1999, 2000), Ropolo *et al.* (2006), Bogdanova (1983). That of the nautiloids (Fig. 4D) is from

Baudouin *et al.* (2016). The following acronyms indicate D = total observed diameter, U = umbilical width, Wh = whorl length. In most cases, the whorl breath (Ww) is not considered due to sedimentary compaction.

A morphometric approach is performed on standard measurements for characterising the intraspecific variabilities and putative sexual dimorphism of the lowermost Aptian *Deshayesites* following the criteria of Bersac & Bert (2012, 2015). We performed univariate and bivariate analyses to highlight possible relationships between the variables and to study the evolution of the conch parameters through ontogeny following the guidelines of Klug *et al.* (2015).

3.2. Ammonoidea

Family Ancyloceratidae Gill, 1871

Genus *Micrancyloceras*Busnardo in Gauthier *et al.*, 2006

Type species: *Ancyloceras brevis* (d'Orbigny, 1842);
by original designation.

Remarks: The understanding of *Ancyloceras brevis* has long been based on the hand drawing of d'Orbigny (1842, p. 508, pl. 127, fig. 5-7), depicting a small-sized aspinoceratid ammonite with a crioconic spire from the “*couches moyennes supérieures du terrain néocomien du vallon de la Bédoule*”. The species has been subsequently transferred to the genus *Pseudocrioceras* Spath, 1924 by Ropolo & Gonnet (1998) and Ropolo *et al.* (1999, 2000a-b), and retained as a basal member of that genus. Re-examination of the holotype by monotypy of *A. brevis* shows that the d'Orbigny's hand drawing proved to idealised since the species is characterised by an aspinoceratid coiling with a tightly coiled spire, a uniform simple ribbing crossing the venter on the proversum and retroversum, and a sub-oval whorl section throughout most of the ontogeny (Busnardo in Gauthier *et al.*, 2006). As such, *A. brevis* lacks the typical *Pseudocrioceras* features characterised by sub-rectangular to subquadrate whorl section in the adult, with trituberculate primary ribs with elongated clavi on the ventro-lateral margins (thereafter *Pseudocrioceras* stage; see discussion below). For this reason, the species can hardly be assigned to *Pseudocrioceras*. To this respect, Busnardo in Gauthier *et al.* (2006) introduced the genus *Micrancyloceras*, based on *Ancyloceras brevis*, which is here retained as a valid genus.

Micrancyloceras brevis (d'Orbigny, 1842)

Fig. 5A-C, D, E

Type:

1842. *Ancyloceras brevis* d'Orbigny, p. 508, pl. 127, fig. 5-7
2006. *Micrancyloceras brevis* (d'Orbigny) - Busnardo in Gauthier *et al.*, p. 151, pl. 24, fig. 2a, b (= d'Orbigny, 1842, pl. 127, fig. 5, 6, 7)

Local synonymy:

1842. *Ancyloceras brevis* d'Orbigny, p. 508, pl. 127, fig. 5-7
- non. 1998. *Pseudocrioceras breve* (d'Orbigny) - Ropolo & Gonnet, p. 123, pl. 1, fig. 1, 2, 3, 4; pl. 2, fig. 1, 2 (= *Pseudocrioceras mazierei* sp. nov.)
- non 1999. *Acrioceras breve* (d'Orbigny) - Ropolo *et al.*, pl. 2, fig. 3 (= *Pseudocrioceras* aff. *mazierei* sp. nov.)
- non 2000a. *Acrioceras breve* (d'Orbigny) - Ropolo *et al.*, pl. 3, fig. 4 (= Ropolo *et al.*, 1999, pl. 2, fig. 3)
2006. *Micrancyloceras breve* (d'Orbigny) - Busnardo in Gauthier *et al.*, p. 151, pl. 24, fig. 2a, b (= d'Orbigny, 1842, pl. 127, fig. 5, 6, 7)

Type: The holotype by monotypy is specimen MNHN.F.R00728 (d'Orbigny collection) from Cassis. It is here illustrated (Fig. 5A-C).

Material: Plaster cast of specimens FSL.105076 (Fig. 5D) from the Busnardo collection. It comes from the *Station de Cassis* section. We also illustrate two photographs shared by P. Ropolo (pers. com. 2012) of specimens PR.1921 (Fig. 5E) and PR.1922 (Fig. 5F) from the Saludes collection. Locality of these specimens remains unknown.

Dimensions: See Table 1 and Fig. 6.

Description: The material at our disposal shows that *M. breve* includes two morphotypes characterised by:

- (1) Small-sized ($36 < H < 75$ mm; average equals to 55,3 mm) *Micrancyloceras* with an aspinoceratid coiling and a short retroversum. The *i* index is low and comprised between 4.7 and 9 mm (average equals to 7 mm). The spire is plane, tightly coiled, and proportionally large compared to the total diameter ($0.39 < Ds/H < 0.53$; average equals to 0.46). The umbilicus is very wide ($0.5 < U/Ds < 0.66$; average equals to 0.59) and shallow. On the spire, the whorl section is seemingly sub-rounded with indistinct umbilical wall. This whorl section is maintained in the adult, although the flanks flatten. The phragmocone ends at the transition of the spire and the proversum. The inner spire remains unknown, as well as aspect of the venter at this stage. Regarding the ornamentation, the outer spire bears

Collection numbers	Collections	Original ID	Illustration	Morpho- types	Localities	Beds	H	U	i	Ds
FSL.105076	Busnardo	<i>A. brevis</i>	/	1	<i>Station de Cassis</i>	48	36	9,3	4,5	14
MNHN.F.R00728	d'Orbigny	<i>A. brevis</i> (holotype)	d'Orbigny (1842; pl. 127, fig. 5-7)	1	<i>Cassis</i>	Unknown	55	15	9	25
PR.1921	Saludes	<i>P. breve</i>	/	1	<i>Cassis</i>	?50	75	19,8	7,6	40

Table 1. Dimensions of *Micrancyloceras brevis* (d'Orbigny, 1842).

strong, prorsiradiate, straight or slightly flexuous, mostly simple ribs, but rarely bifurcate ones occur (= thereafter Juvenile stage). The ribs then progressively develop discrete thickenings in the uppermost part of the flanks and the peri-ventral margin, through the transition of spire and the lower proversum (Sub-adult stage). The ribs become progressively sharp, spaced, and annular, pass the flank straight or with a slight convexity, and cross the venter with some strengthening in the upper proversum and retroversum (= thereafter *Micrancyloceras* stage). Ribs lose their strength approaching the aperture, and the peristome is marked by two sinuous attenuated ribs. The suture line remains unknown. This morphotype includes the holotype, as well as the specimens FSL.105076, and PR.1921. These specimens compare well to the holotype both regarding general morphology and ornamentation.

- (2) Based on the specimen PR.1922, this morphotype is defined as a moderate-sized (115 mm) *Micrancyloceras* with a distinctive ancyloceratid coiling and a short retroversum. The *i* index is greater and reaches 32 mm. The spire is similar but of smaller size compared to the total diameter ($Ds/H \sim 0.30$). The ornamentation conforms to that of the first morphotype, but the ribs become stronger, spaced and thickened from the lower proversum. They are enlarged and of subtriangular aspect in the retroversum.

Discussion: *Micrancyloceras breve* was previously considered as a basal member of the genus *Pseudocrioceras* by Ropolo & Gonnet (1998) and Ropolo *et al.* (1999, 2000a). However, the species lacks the typical *Pseudocrioceras* stage, and it mostly develops a simpler ribbing and sub-rounded whorl section in the adult. This supports the use of *Micrancyloceras* to keep separate these forms although our understanding of the type species is based on a very limited number of specimens. The material at our disposal is, nevertheless, rather homogeneous, exception made of the general size, coiling and strength of the ribbing in the adult of the second morphotype defined above. Both morphotypes share very similar succession of three ornamental stages, namely a Juvenile stage in the outer spire, a Sub-adult stage on the lower proversum, and a *Micrancyloceras* stage in the later growth stages (Fig. 7A). It is noteworthy that the variabilities observed in the shell of *M. breve* may conform to the expression of a morpho-dimensional dimorphism

of sexual nature including small-sized, aspinoceratid microconchs (1^{er} morphotype) and larger, ancyloceratid macroconchs (2nd morphotype). Revision on a sufficient palaeopopulation is, therefore, needed to confirm this hypothesis. As herein understood, the many individuals assigned to *Micrancyloceras breve* of Ropolo & Gonnet (1998) have been confused with *Pseudocrioceras mazierei* sp. nov. that is described below.

Occurrence: The type stratum of the holotype of *Micrancyloceras breve* remains unknown. Busnardo *in* Gauthier *et al.* (2006) pointed out that the matrix of the holotype is a creamy micrite limestone typical of the lowermost *Martelites sarasini* Zone at the *Station de Cassis* section. The topotype FSL.105076 here originates from bed 48. The bed occurrence of the two *Saludes*'s specimens remains unknown but bed 50 is acknowledged (Ropolo, pers. com., 2012). The species has been reported in beds 48, 50, and 52 by Delanoy *et al.* (1997) but the corresponding specimens were not illustrated and it is not known whether those individuals belong to *Micrancyloceras breve* or *Pseudocrioceras mazierei* sp. nov.

In the current state of knowledge, *Micrancyloceras breve* is considered to be endemic to the South Provence Basin. The endemism of this species should, nevertheless, be regarded with caution as there is still a gap in knowledge of various coeval ammonite assemblages from the uppermost Barremian of the Caucasus and the surrounding areas.

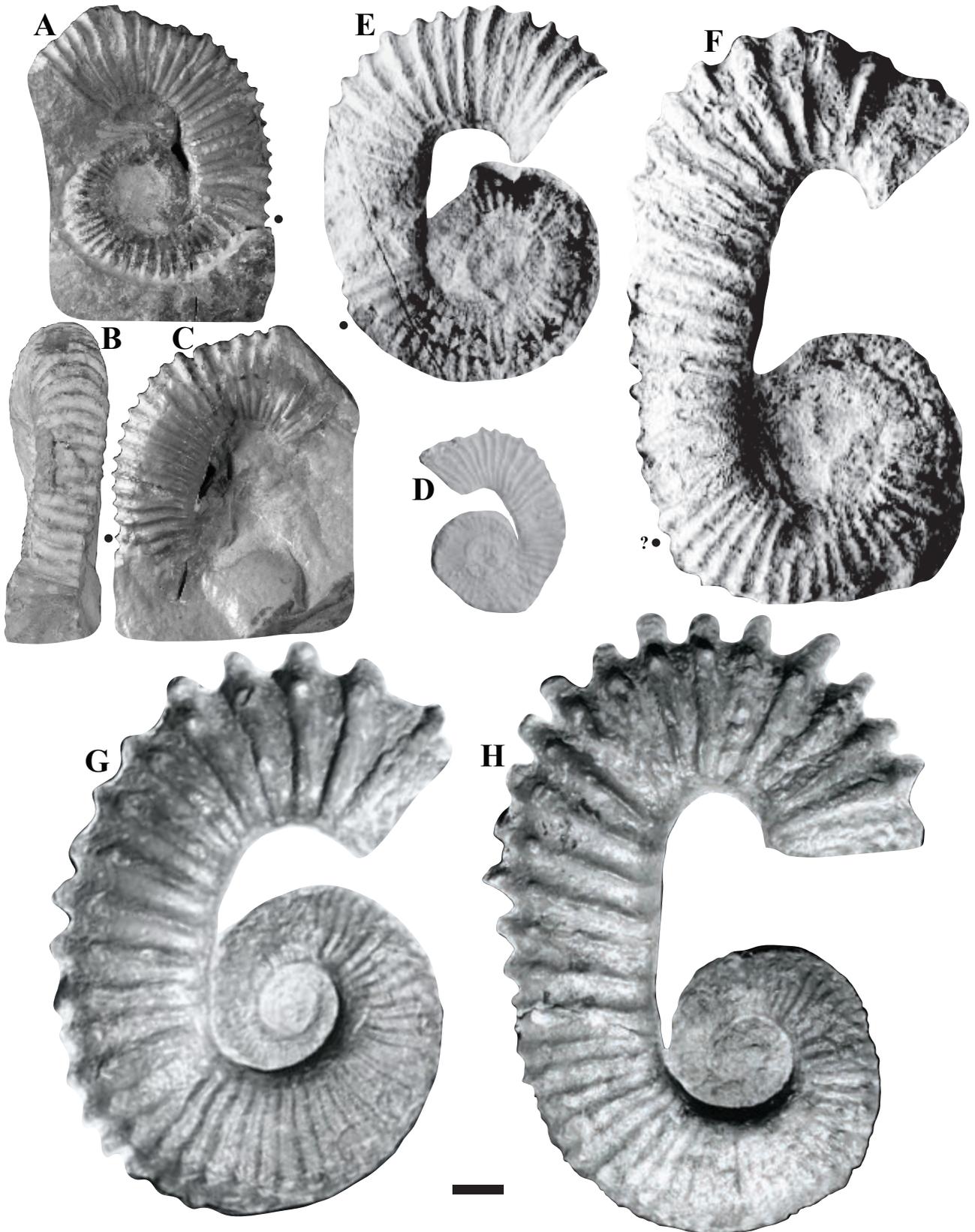
Genus *Pseudocrioceras* Spath, 1924

Type species: *Scaphites abichii* Batsevic, 1873;
by original designation.

Remarks: Understanding of the type species *Pseudocrioceras abichii* Batsevic, 1873 is based on the subsequent hand drawing of Simonovich *et al.* (1875, pl. IV, fig. a-b), illustrating an incomplete ancyloceratid individual from Kutaisi (Georgia) lacking the flexus and retroversum. The lack of a proper illustration introduced great confusions in the taxonomy of the genus *Pseudocrioceras*.

Ropolo & Gonnet (1998) and Ropolo *et al.* (1999, 2000a) reported twelve *Pseudocrioceras* species in southern France, gathered into four main morphological groups distinguished on the sculpture of the spire. This

Fig. 5 - Selected Ancyloceratidae from Cassis; *Micrancyloceras breve* (d'Orbigny, 1842) (A–F), and *Pseudocrioceras mazierei* sp. (E–F) nov. from Cassis–Roquefort-la-Bédoule: **A–C:** The holotype of *Ancyloceras brevis*, specimen MNHN.F.R00728 (d'Orbigny collection) of d'Orbigny (1842), unknown bed and locality of Cassis; **D:** Plaster cast of specimen FSL.105076 (Busnardo collection), bed 48 of *Station de Cassis*; **E–F:** Photographs of PR.1921 and PR.1922 (*Saludes* collection) shared by P. Ropolo (pers. comm. 2012), unknown bed and locality; **G:** The holotype here designed of *Pseudocrioceras mazierei* sp. nov., specimen RG.1477 (Gonnet collection) of Ropolo & Gonnet (1998, pl. 1, fig. 2), bed 75 of *Les Caniers/Les Sardons*; **H:** Paratype, specimen FG.520 (Gondran collection) of Ropolo & Gonnet (1998, pl. 2, fig. 2), bed 72 of *Les Caniers/Les Sardons*. Black dots indicate end of phragmocone. Scale bar is 10 mm.



classification does not consider the adult size, general coiling, succession and duration of the ontogenetic stages, aspect of the ventral area and sculpture of the retroversum. It is thus deficient with respect to the substantial variabilities observed in those *Pseudocrioceras* palaeopopulations. It should also be noted that the bed occurrences of the figured specimens vary in the papers of Ropolo and his collaborators (both in systematic descriptions, litho-logs, and plates), and the published litho-logs differ significantly from the type succession of Moullade *et al.* (2000) (see **Fig. 3**). As such, the distribution of the many *Pseudocrioceras* species at Cassis should be regarded with great caution.

Another problem concerns the synonymy between *Pseudocrioceras* and *Tonoceras* Hyatt, 1900, based on the species *Ancylloceras duvalianus* d'Orbigny, 1842 from Cassis. Indeed, Ropolo *et al.* (1999, 2000a) and Busnardo *in* Gauthier *et al.* (2006) assigned *A. duvalianus* to the genus *Pseudocrioceras*. According to Vermeulen (2006, note on page 119 *in* Klein *et al.*, 2007), this involves the priority use of *Tonoceras* against *Pseudocrioceras*. However, Busnardo *in* Gauthier *et al.* (2005, p. 149) indicated that the incomplete specimen MNHN.F.R00854 used by d'Orbigny for illustrating the species *Ancylloceras duvalianus* corresponds to the adult whorls (proversum and retroversum) of the spire that typifies the species *Pseudocrioceras fasciculare* (d'Orbigny) (see **Fig. 8A-B** and **8C-D**, respectively). The species *Ancylloceras duvalianus* should be thus considered as an objective synonym of *Pseudocrioceras fasciculare*. However, Busnardo *in* Gauthier *et al.* (2006) has designed a lectotype to maintain the name *Ancylloceras duvalianus* and the author selected the badly preserved specimen MNHN.F.R00868 among the d'Orbigny's syntypes (**Fig. 8E-F**). This designation is abusive with respect to the article 72.4.1.1 of the ICZN, and the lack of spire in the designed lectotype does not allow a precise understanding of that species. In agreement with the ICZN, we here consider *Ancylloceras duvalianus* as a *nomen dubium* and *Tonoceras* should be, therefore, abandoned since it is a *nomen nudum*.

In the following palaeontological notes, we describe the species *Pseudocrioceras mazierei* sp. nov., pending a proper taxonomic revision of the many *Pseudocrioceras* species occurring in the top *Martelites sarasini* Zone.

***Pseudocrioceras mazierei* sp. nov.**

Fig. 5G, H

Type:

1998. *Pseudocrioceras breve* (d'Orbigny) - Ropolo & Gonnet, p. 123, pl. 1, fig. 2

Local synonymy:

1998. *Pseudocrioceras breve* (d'Orbigny) - Ropolo & Gonnet, p. 123, pl. 1, fig. 1, 2, 3, 4; pl. 2, fig. 1, 2

? 1998. *Pseudocrioceras kutatisiense* (Rouchadzé) nov. var. *tuberculata* Ropolo & Gonnet, p. 124, pl. 2, fig. 3

? 1998. *Pseudocrioceras waageni rouchadzei* (Dimitrova) - Ropolo & Gonnet, p. 130, pl. 5, fig. 3

? 1999. *Acrioceras breve* (d'Orbigny) - Ropolo *et al.*, pl. 2, fig. 3 (= *Pseudocrioceras* aff. *mazierei* sp. nov.)

? 2000a. *Acrioceras breve* (d'Orbigny) - Ropolo *et al.*, pl. 3, fig. 4 (= Ropolo *et al.*, 1999, pl. 2, fig. 3)

Derivation of name: Named in honour of the amateur researcher Bruno Mazière (Ceyreste, France) for his invaluable, and still ongoing, contribution to the knowledge of the South Provence palaeontology, and his unfaltering commitment to the fieldtrip campaigns of the first author (CF).

Types and studied material: The holotype here designed is specimen RG.1477 (R. Gonnet collection) from Cassis (Bouches-du-Rhône, France). A re-illustration is given (**Fig. 5G**). Additional paratypes include specimens RG.1467, 1469, 1479, 1480, PR/AB.29, 51, FG.478, and 520 (**Fig. 5H**) that were figured by Ropolo & Gonnet (1998). All specimens from Cassis except RG.1467 from Lachau, Drôme. Only specimen FSL.105091 from the Busnardo collection can be doubtfully assigned to *Pseudocrioceras mazierei* sp. nov., but it is poorly preserved and not here illustrated.

<https://zoobank.org/d74d5f00-d2e4-42dd-ae50-59418d1fdc27>

Dimensions: See **Table 2** and **Fig. 6**.

Diagnosis: Small- to moderate-sized *Pseudocrioceras* including two morphotypes characterised by:

- (1) Small- to moderate-sized forms ($\sim 66 < H < \sim 115$ mm; average equals to ~ 93 mm) with an aspinoceratid to ancyloceratid coiling and a short retroversum. The *i* index is comprised between 13 and 29 mm (average equals to 18 mm). The spire is plane and proportionally large compared to the total diameter ($0.63 < D_s/H < 0.73$; average equals to 0,68). The umbilicus is wide ($0.22 < U/D_s < 0.38$; average equals to 0,30) and shallow. The whorl section on the spire is compressed, sub-oval with a low, convex umbilical wall, rounded venter with a discrete ventral band. It becomes subrectangular with a flattened dorsum and flattened venter in the adult. The inner spire remains unknown. Then, the outer spire bears equal, sometimes thicker ribs, straight to slightly flexuous, rarely rursiradiate, with or without a slight peri-umbilical retrocurvature. The ribs are mostly simple, but sometimes, secondary ribs occur and can branch, more or less distinctly, on the umbilical margin. In some specimens with an apparent depressed whorl section, ribbing of the spire can form indistinct bundle of rectiradiate primary ribs and secondaries (e.g., PR/AB.51 of Ropolo & Gonnet, 1998, pl. 1, fig. 3). The ribs become more spaced and sharper at the transition of the

Collection numbers	Collections	Original ID	Illustration	Morpho-types	Localities	Beds	H	U	i	Ds
PR.29	Ropolo	<i>P. breve</i>	/	1	?Les Sardons/Les Caniers	?72	66	15	16	47
PR.51	Ropolo	<i>P. breve</i>	Ropolo & Gonnet (1998, pl. 1, fig. 4)	1	Les Sardons/Les Caniers	72	79	19	18	50
RG.1479	Gonnet	<i>P. breve</i>	Ropolo & Gonnet (1998, pl. 2, fig. 1)	1	Les Sardons/Les Caniers	72	91	19	18	61
PR.28	Ropolo	<i>P. breve</i>	/	1	?Les Sardons/Les Caniers	?72	102	21	29	69
RG.1480	Gonnet	<i>P. breve</i>	Ropolo & Gonnet (1998, pl. 1, fig. 3)	1	Les Sardons/Les Caniers	72	102	16	15	74
RG.1477	Gonnet	<i>P. breve</i>	Ropolo & Gonnet (1998, pl. 1, fig. 2)	1	Les Sardons/Les Caniers	72	115	22	13	76
FSL.105091	Busnardo	<i>A. brevis in coll.</i>	/	1	Station de Cassis	52	/	/	/	/
FG.520	Gondran	<i>P. breve</i>	Ropolo & Gonnet (1998, pl. 2, fig. 2)	2	Les Sardons/Les Caniers	72	118	25	31	67
RG.1469	Gonnet	<i>P. waageni rou-chadzei</i>	/	2	Les Sardons/Les Caniers	72	121	23	45	55
FG.478	Gondran	<i>P. breve</i>	Ropolo & Gonnet (1998, pl. 1, fig. 1)	2	Les Sardons/Les Caniers	72	140	31	33	83
RG.1467	Gonnet	<i>P. kutatisiense tuberculata</i>	Ropolo & Gonnet (1998, pl. 2, fig. 3)	2	Lachau	Unknown	183	35	48	106
Unlabelled	Saludes	<i>P. aff. breve</i>	Ropolo et al. (1999, pl. 2, fig. 3)	1	Cassis	Unclear	68	55	26	38

Table 2. Dimensions of *Pseudocrioceras mazierei* sp. nov.

spire and the proversum. They progressively or abruptly develop small external and ventro-lateral bulges. These are closely similar to the Juvenile and Sub-adult stages of *Micrancyloceras breve*. As growth increases, the ribs are more spaced, and the bulges strengthen to form tubercles on the lower proversum and retroversum. The upper lateral tubercles are rounded and progressively enlarged while the peri-ventral ones take the form of small, then strong elongated clavi pinched along the axis of the coil (= thereafter *Pseudocrioceras* stage). The ribs cross the venter and can be looped on the external clavi. Secondaries ribs, starting at mid-flank, sporadically occur and cross the venter. On the retroversum, the ribbing is similar but thickened and spaced. Approaching the aperture, the last one or two ribs can lose their tubercles and become somewhat annular near the peristome with smooth interspaces. This is somewhat reminiscent to the latest evolution of the *Micrancyloceras* stage of *Micrancyloceras breve*.

- (2) Moderate- to large sized forms (~ 118 < H < ~ 183 mm; average equals to 141 mm) with a distinctly ancyloceratid coiling. The *i* index is comprised between 31 and 48 mm (average equals to 39 mm). The spire is smaller than the first morphotype ($0.45 < Ds/H < 0.59$; average equals to 0,55), but its umbilicus is slightly wider ($0.33 < U/Ds < 0.42$; average equals to 0,37). The ornamental stages – Juvenile, Sub-adult, and *Pseudocrioceras* – are similar to that of the first morphotype, but the

Pseudocrioceras stage can has a greater ornamental variability illustrated by the addition of peri-dorsal tubercles on the primary ribs, similar in size to the upper lateral ones, and/or intercalation of secondary ribs (one to two) between the primaries through most of the proversum. The tubercles of the *Pseudocrioceras* stage are more frequently thickened in certain individuals of the first morphotype. This gives a sub-hexagonal cross section to the primary ribs in particular when there is a slight centripetal evolution of the upper lateral tubercles on the flank along the upper proversum, flexus and/or retroversum. As for the first morphotype, the ribbing can change into somewhat annular ribs with smooth interspaces approaching the aperture. The peristome is not precisely known, but it seems to be composed of one to two simple ribs, sometimes approximated and sinuous.

The suture lines are of ancyloceratid type but not sufficiently preserved for further description.

Discussion: Majority of specimens identified to as *Pseudocrioceras breve* by Ropolo & Gonnet (1998) are here transferred to *Pseudocrioceras mazierei* sp. nov. In the first morphotype of *Pseudocrioceras mazierei* sp. nov. defined above, the length and strength of the Juvenile stage is variable and the transition with the succeeding *Pseudocrioceras* stage sometimes occurs in the outer spire. The second morphotype is best represented by specimen

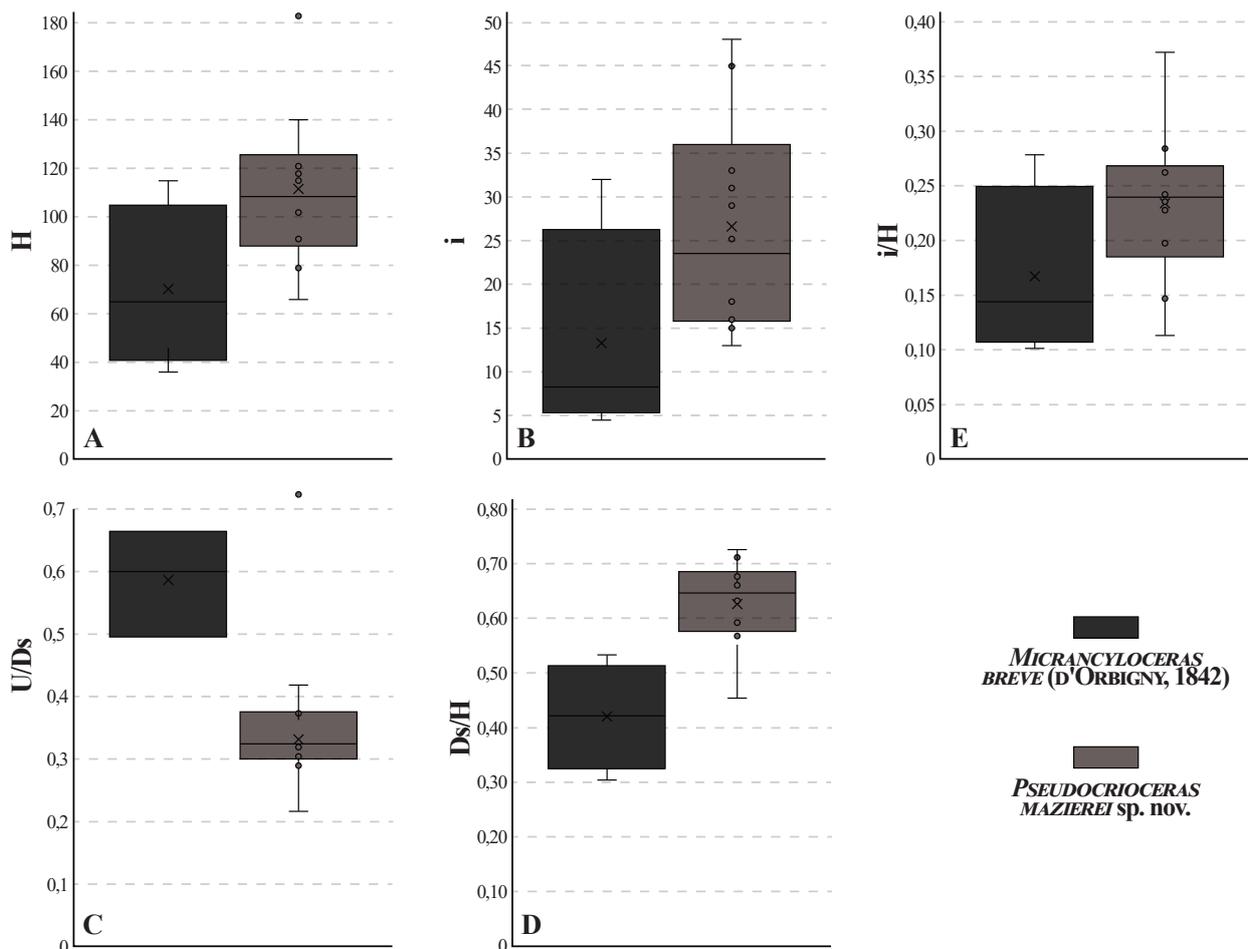


Fig. 6 - Selected morphometrics of *Micrancyloceras breve* (d'Orbigny, 1842) and *Pseudocrioceras mazierei* sp. nov. from Cassis: Box plots of conch parameters (A) H and (B) i, and shell shape ratios (C) U/Ds, (D) Ds/H, and (E) i/H. The boxes represent the interquartile range (i.e., the values ranging from the first to third quartiles, which are the 25th and 75th percentiles, respectively), the median value (black line), the extended interquartile range (whiskers) and the eventual outliers (isolated dots).

FG.478 from Ropolo & Gonnet (1998, pl. 1, fig. 1). This second morphotype may also include the specimens previously assigned to *Pseudocrioceras kutatsiense tuberculata* and *Pseudocrioceras waageni rouchadzei* of Ropolo *et al.* (1999, 2000a). The length of their ornamental stages is similar to the first morphotype, but the *Pseudocrioceras* stage can be characterised by addition of secondary ribs (*P. waageni rouchadzei*) or development of tubercles in the primary ribs (*P. kutatsiense tuberculata*). Note that the specimen of *Pseudocrioceras waageni rouchadzei* of Ropolo *et al.* (1999, 2000a) comes from the southeastern Vocontian margin and its age thus remains unclear with respect to the South Provence palaeopopulation of *Pseudocrioceras mazierei* sp. nov.

As herein documented, *Micrancyloceras breve* and *Pseudocrioceras mazierei* sp. nov. succeed around beds 49–50 and the two species are closely allied. The differences are found in increase in the general dimensions of *Pseudocrioceras mazierei* sp. nov. (Fig. 6A–B), the spire is distinctly larger with respect to the total diameter (Fig. 6D) but closer (Fig. 6C). Regarding the

ornamentation, the Juvenile and Sub-adult stages are rather similar to *Micrancyloceras breve* but this is followed by the development and strengthening of a characteristic *Pseudocrioceras* ribbing stage on the proversum and retroversum. It is evident that this *Pseudocrioceras* stage result from both strengthening and extension of the Sub-adult stage of *Micrancyloceras breve*, as evidenced by the exaggeration of the tubercles notably the peri-ventral ones that form strong elongated clavi pinched along the axis of the coil.

As further evidence, the strength of the *Pseudocrioceras* stage is variable among the figured specimens. For example, some individuals of the first morphotype of *Pseudocrioceras mazierei* sp. nov. has a large spire, and a reduced tuberculation on sharp primary ribs on the proversum and retroversum, that give a somewhat ribbing style resembling the *Micrancyloceras* adult stage of *Micrancyloceras breve* (e.g., specimen RG.1480 of Ropolo & Gonnet, 1998, pl. 1, fig. 4), although the bituberculation of the *Pseudocrioceras* stage is still present up to the end of the retroversum (Fig. 7B). Of interest is the unlabelled

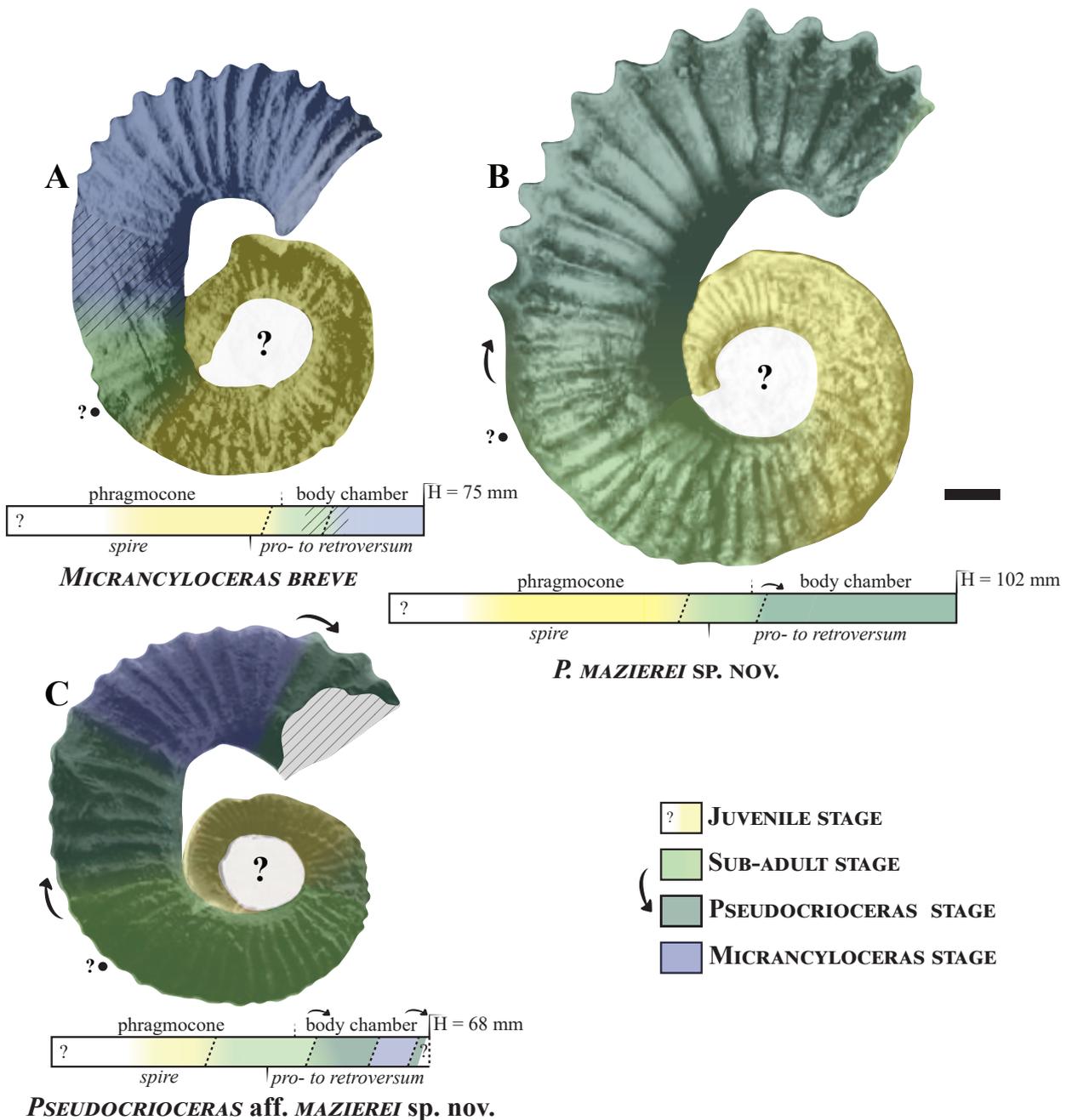


Fig. 7 - Schematic comparative ontogenetic development of *Micrancyloceras breve* (d’Orbigny, 1842) based on specimen PR.1921 (A); *Pseudocrioceras mazierei* sp. nov. based on specimen RG1477 (B); and *Pseudocrioceras aff. mazierei* sp. nov. based on the unlabelled Saludes’s specimen (C). Note the increase in size, innovation of the *Pseudocrioceras* adult stage and its acceleration in *Pseudocrioceras mazierei* sp. nov., which pinpoint a palingenetic evolutionary process. Black dots indicate end of phragmocone. Scale bar is 10 mm.

Saludes’s specimen of *Micrancyloceras breve* figured by Ropolo *et al.* (1999, pl. 3, fig. 4). This specimen has a small size and bears a gracile *Pseudocrioceras* stage with attenuated tubercles on the outer spire and proversum. It then develops a *Micrancyloceras* stage made of low annular ribs on the flexus that is similar to that of *M. breve*. It finally has a reminiscent *Pseudocrioceras* stage at the end of the retroversum (Fig. 7C). These observations suggest that the two species could be phyletically linked. On this basis, the evolution of *Pseudocrioceras mazierei* sp. nov.

from *Micrancyloceras breve* consists of a general increase in size (i.e., hypermorphosis), together with progressive strengthening and extension of the *Pseudocrioceras* ribbing style in the later growth stages. This refers to a typical palingenetic evolutionary process *sensu* Dommergues *et al.* (1986), in which the *Pseudocrioceras* stage consists of a late innovation plus an acceleration. By its unusual ontogenetic sequence, the Saludes’s specimen is here referred to as *Pseudocrioceras aff. mazierei* sp. nov. Finally, the recognition of two morphotypes in *Pseudocrioceras*

mazierei sp. nov. as observed in *Micrancyloceras breve* may similarly conform to the expression of a morpho-dimensional dimorphism of sexual nature including small-sized, aspinoceratid to ancyloceratid microconchs (1^{er} morphotype) and larger, ancyloceratid macroconchs (2nd morphotype).

Among the many species of the literature, *Pseudocrioceras mazierei* sp. nov. share affinities with *Pseudocrioceras kutatissense* (Rouchadzé, 1933); a species based on the holotype by monotypy of Rouchadzé (1933, pl. 8, fig. 1) from Kutaisi, Georgia. The ornamental sequence looks very similar but the species differs by a distinctive ancyloceratid coiling of larger adult size (H of 235 mm). By these features, *Pseudocrioceras kutatissense* has greater affinities with younger *Pseudocrioceras* forms that are recorded just above the *Pseudocrioceras mazierei*-bearing beds (e.g., such as the specimen identified to as *Pseudocrioceras densecostatum* Kakabadze by Ropolo & Gonnet, 1998, pl. 4, fig. 3 from bed 75 of the *Les Caniers* section).

Pseudocrioceras mazierei sp. nov. also share some affinities with the species *Pseudocrioceras massei* Ropolo & Gonnet, 1998, that is known by the two specimens from bed 75 of *Les Caniers* figured by Ropolo & Gonnet (1998, pl. 3, fig. 1= holotype, 2= paratype). *Pseudocrioceras massei* is thus younger than *Pseudocrioceras mazierei* sp. nov., and it has a larger adult size (H = 200–204 mm). The sculpture of its spire is, however, rather similar with that of our new species, but this ornamentation remains up to the mid-proversum. In the upper proversum, some ribs strengthen and bear peri-ventral tubercles, while number of secondaries decrease. This progressively changes into a typical *Pseudocrioceras* stage that is delayed through the flexus and retroversum. Note that the thickened ribs of the proversum can have bullae on the peri-dorsal margin from which a secondary rib is approximated or can branch on them.

By its size, and unusual ornamental sequence, *Pseudocrioceras massei* is fairly close to the species *Pseudocrioceras provinciale* (Matheron, 1878), although the holotype by monotypy of the latter lacks the later growth stages (i.e., flexus plus retroversum) for further confirmation (see Ropolo *et al.*, 1999, pl. 6, fig. 1-2). Increase in size is a diagnostic shell parameter to take into account for specific identification of *Pseudocrioceras* species and there is emerging evidence that a Cope's rule occurs in this lineage but this deserves special investigation.

Occurrence: The species *Pseudocrioceras mazierei* sp. nov. occurs in bed 52 at the *Station de Cassis* section (Busnardo *in coll.*). Maximum of abundance is in bed 72

at *Les Caniers/Les Sardons* (Ropolo & Gonnet, 1998), a level that correlates to bed 51 of the type succession according to our field experience. Indeed, this bed marks a change in the local lithology passing from chalky to massive micrite limestones and can be easily identified in the field. It should be noted that the unlabelled Saludes's specimen here assigned to *Pseudocrioceras* aff. *mazierei* sp. nov. was reported from the top of the *Pseudocrioceras*-bearing beds (= bed 78 or 79 of the *Le Brigadan* section depending the date of publication) according to Ropolo *et al.* (1999, 2000a). Despite our ongoing sampling at Cassis, no comparable specimen has been yet collected in these levels. The stratigraphic occurrence of this specimen is, therefore, doubtful.

Pseudocrioceras mazierei sp. nov. is known from the South Provence Basin (France), and doubtfully from the southeastern margin of Vocontian Basin (Lachau, Drôme). Its occurrence in the *Pseudocrioceras*-bearing localities of Georgia is suspected (Busnardo *in coll.*).

Genus *Kutatissites* Kakabadze, 1970

Type species: *Kutatissites bifurcatus* Kakabadze, 1970; by original designation.

Remarks: The genus *Kutatissites* is diversified at Cassis and represented by the many tripartite and recoiled species reported by Delanoy *et al.* (2000). There is no comprehensive study on the variabilities of the diverse *Kutatissites* species due to the low number of individuals. Delanoy *et al.* (2000) noticed out that a recoiling trend exists during the uppermost Barremian.

Kutatissites pouponi

Delanoy, Ropolo, Gonnet & Ebbo, 2000
Fig. 9A; Fig. 10A-B

Type:

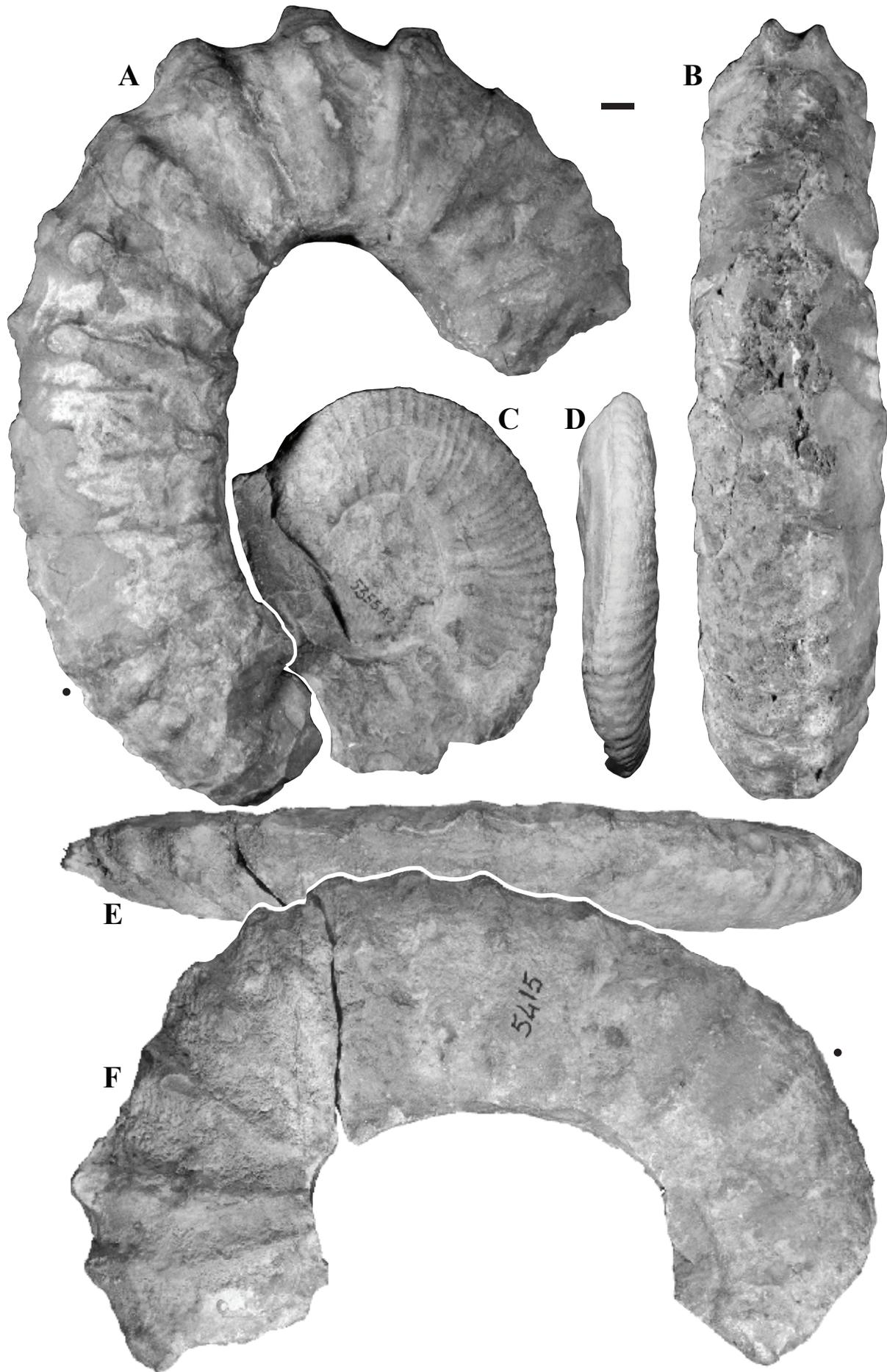
2000. *Kutatissites pouponi* Delanoy *et al.*, p. 27, pl. 1, fig. 1a-b

Local synonymy: None.

Type: The holotype by monotypy is specimen RG.1510 (Gonnet collection) from *Les Sardons*. It was illustrated by Delanoy *et al.* (2000, pl. 1, fig. 1a-b).

Material: Specimen FSL.105124 (**Fig. 9** and **10A-B**) from the Busnardo collection. Origin is unknown but *Les Caniers/Les Sardons* section is suspected.

Fig. 8 - A-D: Illustration of the proversum and retroversum (A–B), plus the spire (C–D) of specimen MNHN.F.R00854, lectotype of *Pseudocrioceras* (pro *Ammonites*) *fasciculare* (d'Orbigny, 1840); **E-F:** Specimen MNHN.F.R00868 that is the abusive lectotype of *Pseudocrioceras* (pro *Ancyloceras*) *duvalianum* (d'Orbigny, 1842) designed by Busnardo *in* Gauthier *et al.* (2006), unknown bed and locality of Cassis. Black dots indicate end of phragmocone. Scale bar is 10 mm.



Dimensions: See Table 3.

Description: Specimen FSL.105124 closely resembles the holotype of *Kutatissites pouponi*. Both consist of large-sized ammonites. The coiling is of ancycloceratid type with helicoidally coiled inner whorls in the holotype, and slightly curved proversum. The flexus is better preserved in specimen FSL.105124 than the holotype and is marked by a moderately long U-shaped aspect. The spire is proportionally large compared to the total diameter ($0.42 < Ds/H < 0.59$) and develops an inflated coronate whorl section. The umbilical wall is rounded, then steep and become elevated and rounded at the end of the spire. The whorl section changes into sub-rectangular with flattened and smoothed ventral band on the lower proversum. At least, six ornamental stages occur in the ontogeny of the holotype:

- A short Juvenile stage on the inner spire marked by strong, rectiradiate ribs branching indistinctly by three on a peri-dorsal bullae.
- This passes abruptly to a stage composed of strong uni-, but more frequently bituberculate primary ribs with strong, rounded peri-dorsal tubercles and more discrete upper lateral ones, together with irregular – generally one to three – atuberculate secondaries. Those secondaries start merging on the tubercles.
- A Fasciculate stage on the outer spire. Ribs start and strengthen on the umbilical wall, branch by one, then two or three, on prominent peri-dorsal tubercles with rounded bases and fasciculate (up to five ribs) on the flanks. The ribs become progressively trituberculate with marginal tubercles on the peri-ventral area. They are rectiradiate and progressively vanish on the venter with a slight weakening.
- A Subadult stage develops on the upper proversum. Secondary ribs here become slightly convex to prorsiradiate on the upper flanks and are more frequent. They are irregularly disposed by two or three, but up to five secondaries are noted. The primary ribs are distinctly stronger and trituberculate. The lower tubercles are variable in size but the always the smaller ones, and they are placed at the end of a unique dorsal rib, the lateral tubercles become thicker and they are high on the flanks, and the peri-ventral tubercles are clavi-like ones pinched along the axis of the ribs.

- An adult stage on the flexus and retroversum. Primary ribs strengthen, and they are still trituberculate. Secondaries are finer and by one or two. Ribs cross the venter but they are strongly attenuated on the siphonal area.
- Aspect of the Terminal stage (= peristome) remains unknown.

Ontogeny of specimen FLS.105124 starts with the second stage described above. Here the ribs are more distinctly bituberculate than the holotype. Then, there is a similar Fasciculate stage on the spire which changes into the Sub-adult stage up to the upper proversum. The later growth stages are worn but we observe the end of the adult stage on the flexus. Here secondaries tend to be replaced by large smooth interspaces between stronger and simpler primary ribs. The peristome is marked by a collared aperture formed by an attenuated rib.

Discussion: Specimen FSL.105124 is the second individual from Cassis that can be assigned to *Kutatissites pouponi*, but doubt remains since it lacks the diagnostic helicoidally inner whorls. It is worth noting that the specimen shares some affinities with the group of *Pseudocrioceras fasciculare* (d'Orbigny, 1840), including the two subspecies *P. fasciculare fasciculare* (d'Orbigny, 1840) and *P. fasciculare bituberculatus* Ropolo, Gonnet, & Conte, 1999. This group includes the largest *Pseudocrioceras* forms dominating the upper part of the *Pseudocrioceras*-bearing beds at Cassis (Ropolo *et al.*, 1999, 2000a; Frau, own data). On the spire, the ribs can either fasciculate on a single (*fasciculare* variety) or two tubercles (*bituberculatus* variety), mimicking the early stages of *Kutatissites pouponi* (e.g., compare for example with Ropolo *et al.*, 1999, pl. 1, fig. 2 and pl. 4, fig. 1). In the lack of the helicoidally inner whorls, the distinction is not that simple. The main criteria to be used is the inflated coronate spire of *Kutatissites pouponi*, with deep umbilicus, and whorl section becoming distinctly depressed and subrectangular in the adult with a large flattened venter. By contrast, the spire is more regularly coiled in typical *Pseudocrioceras fasciculare*, and the whorl section broadly remains compressed, subrectangular, then high sub-oval in the adult. Regarding the ornamentation, there is the early development of a typical *Pseudocrioceras* ribbing style in later growth stages of *Pseudocrioceras fasciculare* that could help in the identification.

Nevertheless, there is still problematic forms in the literature with intermediate coronate spire and *Kutatissites*-like ribbing style in the adult, such as the specimen of

Collection numbers	Collections	Original ID	Illustration	Localities	Bed occurrences	H	U	i	Ds	Dt
FSL.105124	Busnardo	<i>K. pouponi</i>	/	Cassis	Unknown	296	43	56	124	/
RG.1510 (holotype)	Gonnet	<i>K. pouponi</i>	Delanoy et al. (2000, pl. 1, fig. 1a-b)	Les Caniers/Les Sardons	76	245	/	/	144	45

Table 3. Dimensions of *Kutatissites pouponi* Delanoy, Ropolo, Gonnet & Ebbo, 2000.



Fig. 9 - Lateral view of specimen FSL.105124 (Busnardo collection) here assigned to *Kutatissites pouponi* Delanoy, Ropolo, Gonnet & Ebbo, 2000, unknown bed and locality of Cassis. Black dot indicates end of phragmocone. Size is reduced (80% of the total diameter). See **Fig. 11** for ventral and dorsal views.

Pseudocrioceras aff. *waagenioides* of Ropolo *et al.* (1999, pl. 11, fig. 1; = 2000a, pl. 10, fig. 1), either labelled to as PR.573 or PR.671 depending the date of publication. Direct re-examination is necessary for further interpretation, but there is hardly any doubt that this specimen does not fit at all with the Georgian species *Pseudocrioceras waagenioides* since it can be seen a bituberculate stage in the inner spire that is absent in the holotype (Rouchadzé, 1938, pl. V, fig. 2) or the related forms (Kakabadze, 1981, pl. XXII, fig. 2). By its features, the specimen PR.573/PR.671 of Ropolo *et al.* (1999, 2000a) shares greater affinities with tripartite *Kutatissites*, but its inner whorls are covered by matrix and the presence of a helix cannot be verified.

Occurrence: The holotype of *Kutatissites pouponi* is reported from bed 76 of *Les Sardons* (Delanoy *et al.*, 2000). This bed merely correlates to bed 56 (base) of the type succession (Fig. 3). Bed occurrence of the Busnardo's specimen remains unknown. Its matrix corresponds to a creamy micrite limestone typical of the lower (but non-lowermost) *Martelites sarasini* Subzone at Cassis.

In the current state of knowledge, *Kutatissites pouponi* is present in both the South Provence and Vocontian basins (Delanoy *et al.*, 2000).

Genus *Hoheneggericeras*

Delanoy, Baudouin, Gonnet, Bert, 2008

Type species: *Crioceras fallauxi* Uhlig, 1883;
by original designation.

Remarks: We report for the first time the Ancyloceratidae *Hoheneggericeras* at Cassis. The latter has so long been confused with *Audouliceras* by Ropolo *et al.* (1999, 2000a). It does not yet exist a comprehensive description of this genus, and the closely allied forms, from the South Provence Basin, although its members are not rare during the early Aptian (Ropolo *et al.*, 2000b; Frau, own data).

Hoheneggericeras sp.

Fig. 11A-B

Local synonymy: None.

Material: The single specimen MPP.12928/AB.303 from the Ropolo collection (Fig. 11A-B). It derives from the *Les Caniers* section.

Dimensions: None.

Description: Specimen MPP.12928/AB.303 is a large-sized (total estimated height > 300 mm) ancyloceratid ammonite lacking its spire, and most of the retroversum. The body chamber starts in the lower proversum. The latter is rather straight and marked by a distinct necking in its upper part. The flexus seems to be U-shaped. The whorl section is sub-oval, higher than wide, with convex

flanks. Regarding the ornamentation, the specimen has similar growth stages as those identified in the adults of *Hoheneggericeras*; namely a lower proversum marked by dense, simple ribs crossing the venter, followed by the progressive development of enlarged, trituberculate ribs with clavi, typical of the Ancyloceratidae, in the upper proversum and flexus, while the remanent simple ribs tend to vanish as growth increases.

Discussion: The specimen at our disposal conforms to the diagnosis of the genus *Hoheneggericeras* provided by Delanoy *et al.* (2008). The lack of the spire prevents further comparison with the type species *Hoheneggericeras fallauxi* although the later growth stages are closely similar.

Occurrence: The label of the Ropolo's specimen indicates an origin from the Barremian/Aptian boundary of *Les Caniers*. At Cassis, our own collection attests of the record of *Hoheneggericeras* in bed 59, in very few number, just below the massive flourishing of the Deshayesitidae that marks the base of the Aptian Stage (Frau, own data). This conforms to the age of *Hoheneggericeras fallauxi* in southern France (Delanoy *et al.*, 2008).

Family Heteroceratidae Spath, 1922

Genus *Calanquites*

Frau, Delanoy, Masse, Lanteaume, Tendil, 2016

Type species: *Imerites katsharavai* Rouchadze, 1933;
by original designation.

Remarks: The genus *Calanquites* was introduced by Frau *et al.* (2016) to separate a small group of uppermost Barremian species previously assigned to the Heteroceratidae genus *Paraimerites* Kakabadze, 1967. The type species *Calanquites katsharavai*, and the allied taxa listed by Frau *et al.* (2016), consist of small-sized imericone heteroceratids which are notably characterised by thin peri-siphonal tubercles on last whorl of the helix. They are mostly known from Georgia (Rouchadzé, 1933; Kotetishvili, 1970) and Turkmenia (Tovbina, 1963), but some of its members have been reported from certain localities (*Podestat-Pouli*, *Carry-le-Rouet*) of the South Provence Basin (Frau *et al.*, 2016). We identified a few crushed specimens of the Busnardo collection from the *Station de Cassis* section matching *Calanquites katsharavai*.

Calanquites cf. *katsharavai* (Rouchadzé, 1933)

Fig. 12A, B

Type:

1933. *Imerites katsharavai* Rouchadzé, p. 262, pl. 21, fig. 7.

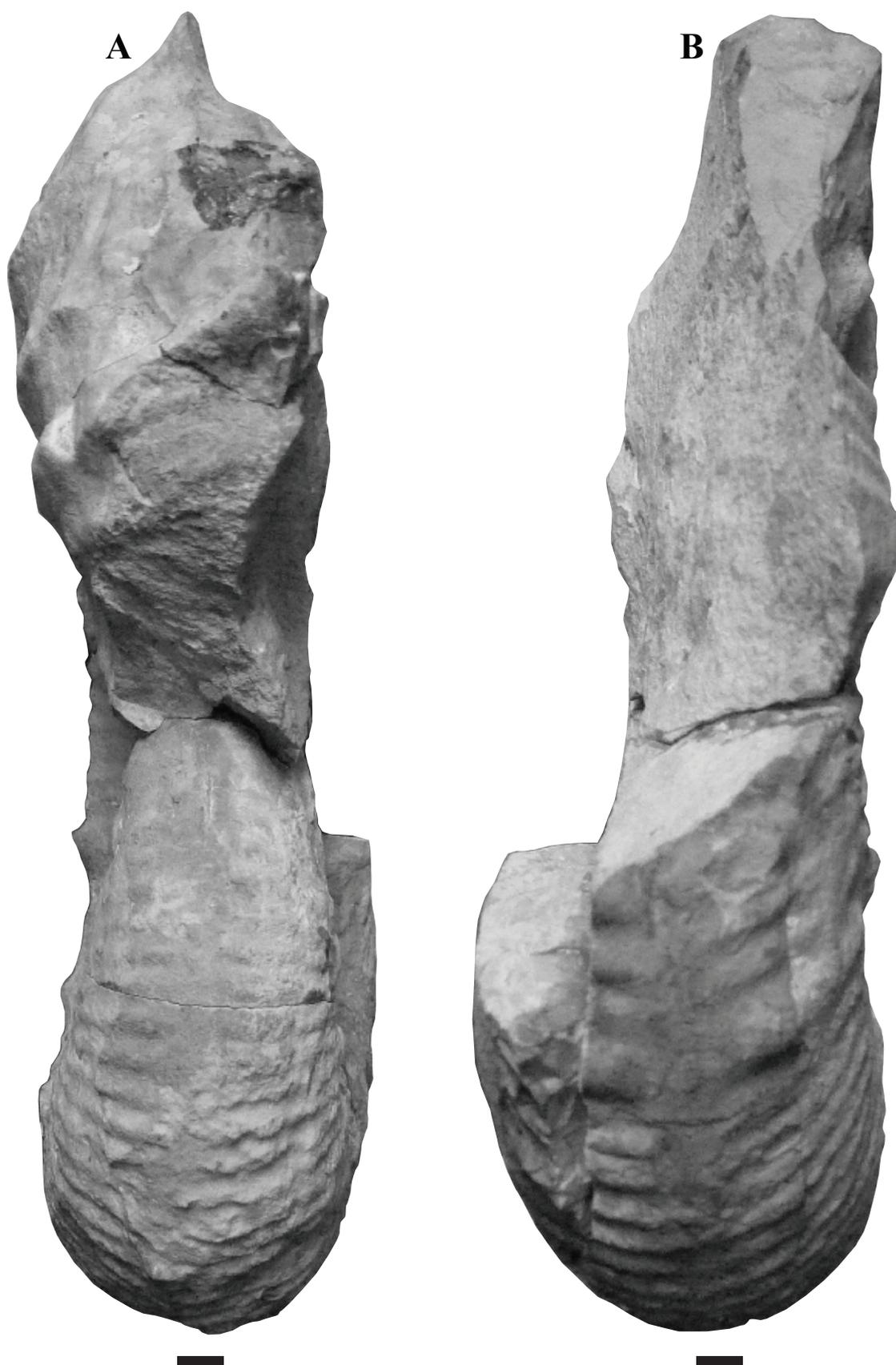


Fig. 10 - Dorsal (A) and ventral views (B) of specimen FSL.105124 (Busnardo collection) here assigned to *Kutatissites pouponi* Delanoy, Ropolo, Gonnet & Ebbo, 2000. Reduced in size as in Fig. 10. Scale bar is 10 mm.

Local synonymy:

- pars 1934. *Hoplites feraudi* (d'Orbigny, 1841) - Denizot, p. 156, pl. 5, non fig. 12 (= *H. feraudianus*), 13
 2016. *Calanquites katsharavai* (Rouchadzé) - Frau *et al.*, p. 209, pl. 1, fig. 1a-c, 2, 3a-b, 4; pl. 2, Fig. 1, 2, 3, 4; pl. 3, Fig. 9, 10
 2018b. *Calanquites* gr. *katsharavai* (Rouchadzé) - Frau *et al.*, fig. 5A, B

Type: According to Klein *et al.* (2007) and Frau *et al.* (2016), the lectotype of *Calanquites katsharavai* designed by Kakabadze (1971) must be specimen TSU485/1151 (Rouchadzé collection) from Nikortsminda, Georgia. It was properly illustrated by Frau *et al.* (2016, pl. 1, fig. 1a-c).

Material: Specimens FSL. 105035, 105036, 105037 (Fig. 12A), 105038 (Fig. 12B), 105039, and (?) 105145 from the Busnardo collection. All from *Station de Cassis*.

Dimensions: None.

Description: The few specimens from the Busnardo collection are represented by small-sized ammonites (estimation of D ~ 50 mm in specimens FSL.105038 and 105039; and D ~ 80 mm in specimen FSL.105037), but precise dimensions remain unclear due to incompleteness and crushing of the material at our disposal. The coiling is of imericone type with a slight uncoiled spiral part. Helix is lacking in most of the studied specimens except in specimen FSL.105037 (Fig. 12B). In the latter specimen, the last whorl of the helix is preserved and shows two lines of thin peri-siphonal tubercles typical of the species. Then, the ribbing on the phragmocone is not easily observable but seemingly made of simple, sometimes bifurcated, straight to slightly sinuous ribs, and rare irregular secondaries. The evolute planispiral part is mostly composed of 1,5 to 2 whorls. The body chamber approximately occupies the last ¾ part of the planispiral part. Ribs become mostly simple, spaced on the outer whorl.

Discussion: The Busnardo's specimens conform to the South Provence members of the species *Calanquites katsharavai*, although they are heavily crushed. It seems that their general size, shell morphology and ribbing style match the morphotype A of this species previously described by Frau *et al.* (2016). This morphotype may group the putative macroconchs of *Calanquites katsharavai* but this hypothesis lacks sufficient material to be confirmed (Frau *et al.*, 2016). Nevertheless, it is tempting to consider these forms as macroconchs since they share a larger size and a distinctive robust ribbing stage in the adult. They furthermore have a narrowing and regression of the whorl approaching the aperture that is not observed in the morphotype B (see for example specimens of Frau *et al.*, 2016, pl. 1, fig. 3a, and pl. 2, fig. 1). When complete, the aperture is made of a short stage with approximated fine lirae in both morphotypes, and the aperture modification cannot be thus used for separating the putative anti-dimorphs.

Occurrence: *Calanquites katsharavai* occurs in the second horizon with *Anglesites puzosianum* at *Podestat-Pouli*, and the species is thus dated to the lowermost part of the *Martelites sarasini* Zone (Frau *et al.*, 2016). The Busnardo's specimens from the *Station de Cassis* section are in bed 42 and slightly underlies the first occurrence of the index species *Martelites sarasini* (bed 44; see below). There is a lack of *Anglesites puzosianum* at the *Station de Cassis* section, and the base of the *Martelites sarasini* Zone is, therefore, floating. It has tentatively been fixed in bed 41 by local correlation with *Podestat-Pouli* (Frau *et al.*, 2016).

In the current state of knowledge, *Calanquites katsharavai* is present in the South Provence Basin (Frau *et al.*, 2016), Georgia (Rouchadzé, 1933; Kotetishvili, 1970) and Turkmenia (Tovbina, 1963).

Genus *Heteroceras* d'Orbigny, 1849

Type species: *Turrilites emericianus* d'Orbigny, 1842; by subsequent designation of Meek (1876).

Remarks: At Cassis, the genus *Heteroceras* has been mixed up with *Colchidites* by Ropolo *et al.* (1999, 2000a), and with *Argvethites* by Busnardo (*in coll.*). Identifications were revised by Frau *et al.* (2016) and majority of the individuals have been re-assigned to the species *Heteroceras baylei* Reynès, 1876.

***Heteroceras baylei* Reynès, 1876
 Fig. 12C**

Type:

1876. *Heteroceras baylei* Reynès, p. 107
 1990. *Heteroceras baylei* (Reynès) - Delanoy & Bulot, p. 17, pl. 2, fig. 4, 5, 6 (= Reynès, 1876, p. 107)

Local synonymy:

1999. *Colchidites* aff. *tsholashensis* (Rouchadzé) - Ropolo *et al.*, pl. 3, fig. 3a, b
 2000a. *Colchidites tsholashensis* (Rouchadzé) - Ropolo *et al.*, pl. 1, fig. 3 (= Ropolo *et al.*, 1999, pl. 3, fig. 3a)
 2016. *Heteroceras baylei* Reynès - Frau *et al.*, p. 215, pl. 6, fig. 1, 2, 3, 4, 5, 6

Type: The lectotype designed by Delanoy & Bulot (1990) is specimen MHN.1989-44 (Reynès collection) from Le Cheiron, Alpes-Maritimes, France.

Material: Specimens FSL.105041, 105042, 105043, 105044 (Fig. 12C), 105045, 105066, 105067, 105069, 105098 and doubtfully FSL.105093, 105094, 105095 from the Busnardo collection. All from *Station de Cassis*.

Dimensions: See Table 4.

Description: The Busnardo's material includes small- to very small-sized *Heteroceras* with a longiheterocone

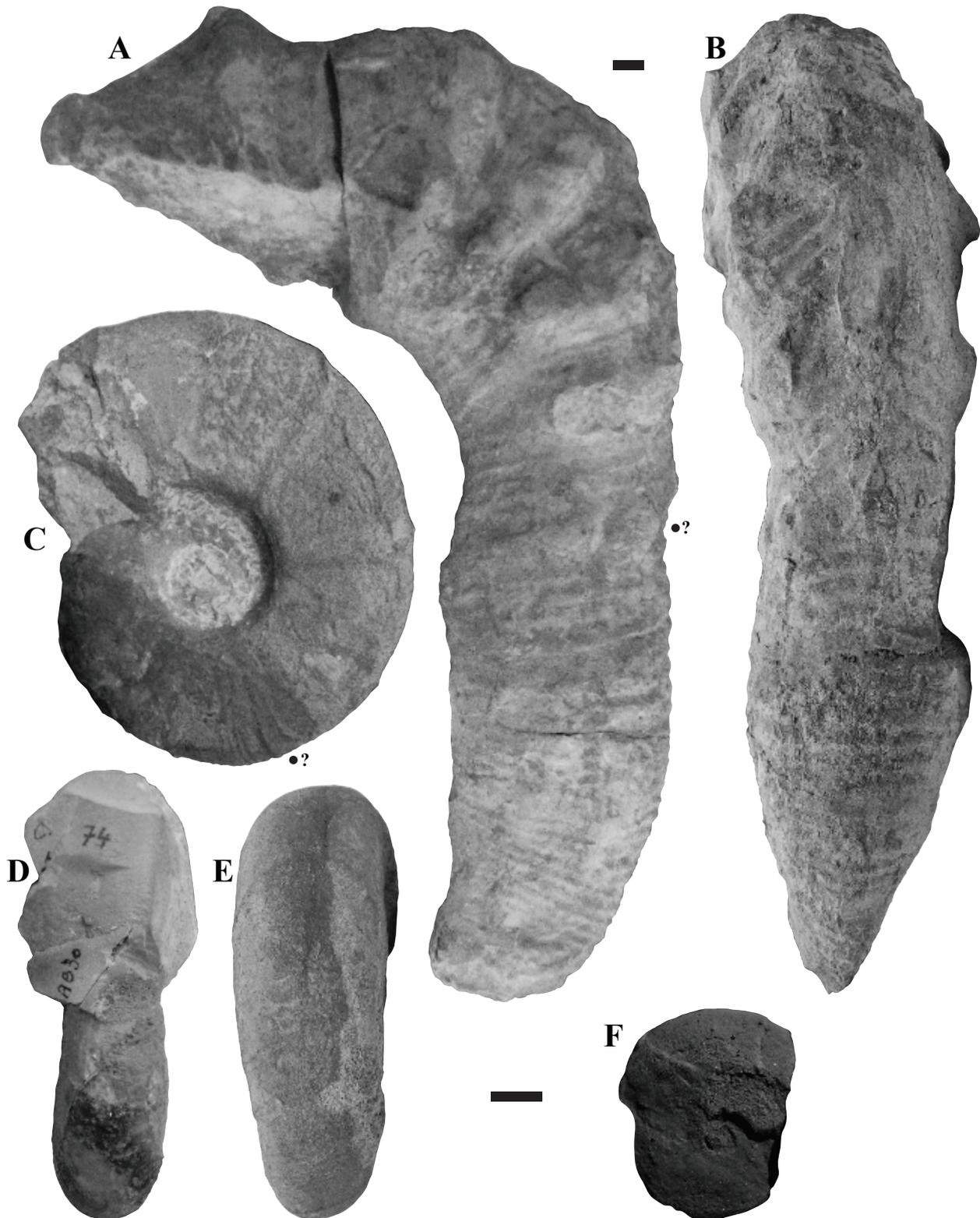


Fig. 11 - Selected Ancyloceratidae (A-B), Desmoceratidae (C-E), and Barremitidae (F) from Cassis. A-B: Lateral (A) and ventral views (B) of specimen MPP.12928/AB.303 (Ropolo collection) here assigned to *Hoheneggericeras* sp. from the Barremian/Aptian boundary of *Les Caniers*. Size is reduced (60% of the total diameter); C-E: Lateral (C) and ventral views (D-E) of specimen MPP.12.889/AB.30 (Ropolo collection) here assigned to *Pseudohaploceras* cf. *liptoviense* (Zeuschner, 1856), bed 74 of *Le Brigadan*; F: Plaster cast of specimen FSL.105083 (Busnardo collection) here assigned to *Barremites* sp., bed 50 of *Station de Cassis*. Black dots indicate end of phragmocone. Scale bar is 10 mm.

Collection numbers	Collection	Illustration	Locality	Beds	H	Dt	Wh
FSL.105041	Busnardo	/	Station de Cassis	Unknown	/	/	/
FSL.105042	Busnardo	/	Station de Cassis	44	/	/	/
FSL.105043	Busnardo	/	Station de Cassis	44	/	/	/
FSL.105044	Busnardo	/	Station de Cassis	44	46,5	10	18,3
FSL.105045	Busnardo	/	Station de Cassis	44	/	/	/
FSL.105066	Busnardo	/	Station de Cassis	45	/	/	/
FSL.105067	Busnardo	/	Station de Cassis	46	/	/	/
FSL.105069	Busnardo	/	Station de Cassis	Unknown	48	/	18
FSL.105098	Busnardo	/	Station de Cassis	52	/	/	/
FSL.105093	Busnardo	/	Station de Cassis	52	/	/	/
FSL.105094	Busnardo	/	Station de Cassis	52	/	/	/
FSL.105095	Busnardo	/	Station de Cassis	52	/	/	/

Table 4. Dimensions of *Heteroceras baylei* Reynès, 1876.

coiling. The ornamentation conforms to the two morphotypes (robust *versus* gracile) of that species identified by Frau *et al.* (2016), to which the reader is referred for further details.

Discussion: In the Busnardo collection, the individuals of *Heteroceras baylei* have been referred to as a new species of *Argvethites* Rouchadzé, 1933 (i.e., *A. massei* Busnardo *in coll.*). The type species *Argvethites minor* Rouchadzé, 1933 can be easily distinguished from the Busnardo's specimens by its small-sized heterocone shell with a large-sized turricon, long proversum and moderately short retroversum, flattened venter in the upper proversum with a ventral band bordered by small tubercles. Note that other individuals of *Heteroceras baylei* from Cassis have been mixed up with *Colchidites* aff. *tsholashensis* (Rouchadzé, 1933) by Ropolo *et al.* (1999, 2000a) as previously noticed out by Frau *et al.* (2016).

Occurrence: The species ranges from beds 44 to 52 at the *Station de Cassis* section.

Besides southern France (Vocontian and South Provence basins), the species *Heteroceras baylei* is recorded in Spain, Georgia, South Africa, and most probably in Bulgaria and Japan (Baudouin *et al.*, 2012).

Genus *Martelites* Conte, 1989

Type species: *Martelites marteli* Conte, 1989; by original designation.

Remarks: At Cassis, Busnardo (1984) mixed up *Martelites* with the Deshayesitidae *Prodeshayesites* (see discussion in Delanoy *et al.*, 1997; Ropolo & Gonnet, 1998; Cecca *et al.*, 1999, 2000; Ropolo *et al.*, 1999, 2000a-b; Frau *et al.*, 2016). This was further confirmed by Frau *et al.* (2018a) who illustrated for the first time a specimen from the Busnardo collection originating from the *Station de Cassis* section. A description of the many individuals from this collection is here provided, and a few new individuals are illustrated. These are tentatively assigned to the index species *Martelites sarasini* (Rouchadzé, 1933).

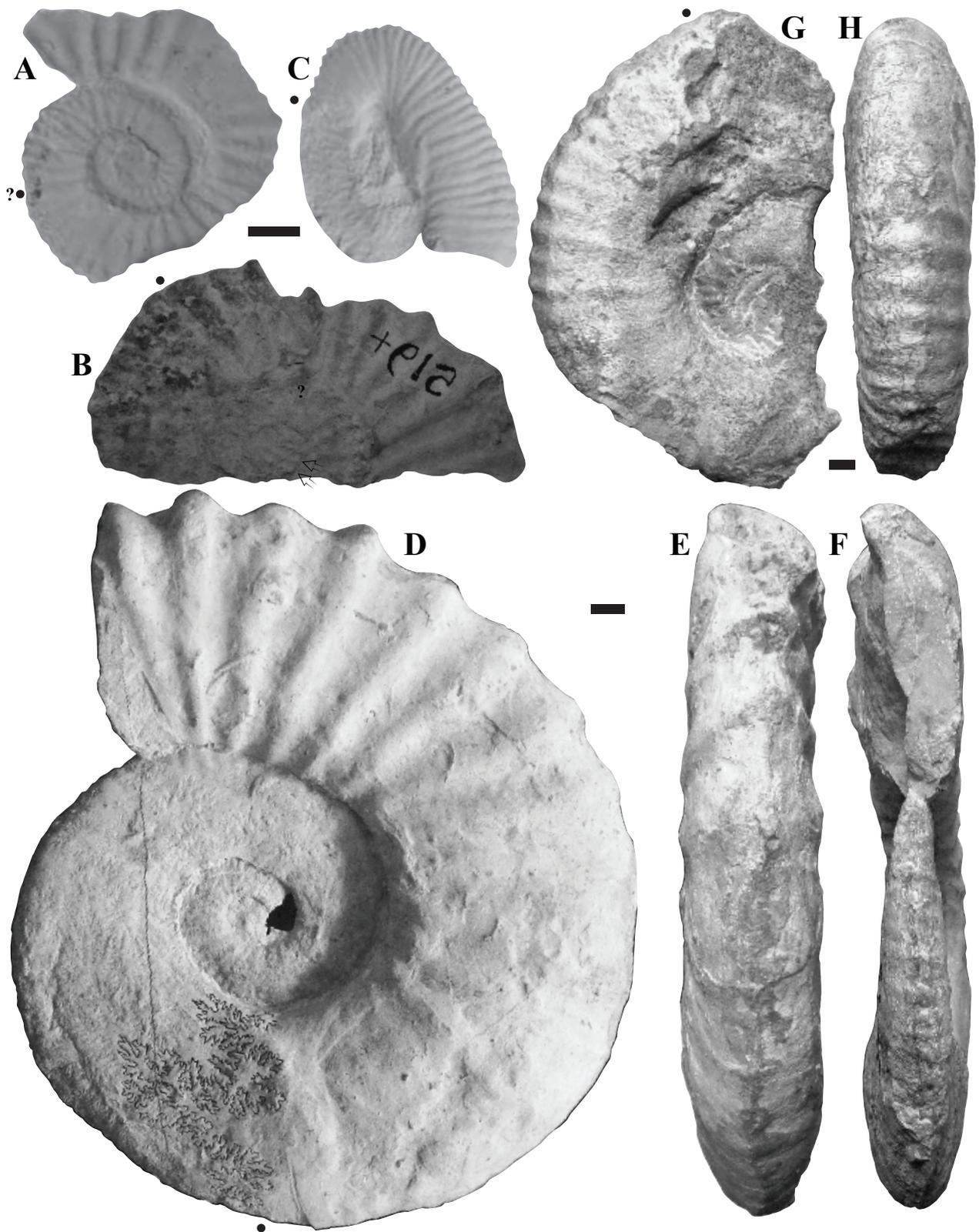
Martelites sarasini (Rouchadzé, 1933)

Fig. 12D-F, G-H; Fig. 13A-C, D-E; Fig. 14A-B, C

Type:

1933. *Colchidites sarasini* Rouchadze, p. 250, pl. XVIII, fig. 3; pl. XIX, fig. 1; text-fig. 49

Fig. 12 - A-H: Selected Heteroceratidae from Cassis. **A:** Lateral view of specimen FSL.105038 (Busnardo collection) here assigned to *Calanquites* cf. *katsharavai* (Rouchadzé, 1933), bed 42 of *Station de Cassis*; **B:** Lateral view of specimen FSL.105037 (Busnardo collection) here assigned to *Calanquites* cf. *katsharavai* (Rouchadzé, 1933), bed 42 of *Station de Cassis*; lateral; **C:** Lateral view of specimen FSL.105044 (Busnardo collection) here assigned to *Heteroceras baylei* Reynès, 1876, bed 44 of *Station de Cassis*; **D-F:** Lateral (**D**) and ventral views (**E-F**) of specimen FSL.105080 (Busnardo collection), here assigned to *Martelites sarasini* (Rouchadzé, 1933), bed 48 of *Station de Cassis*; **G-H:** Lateral (**G**) and ventral views (**H**) of specimen FSL. 105101 (Busnardo collection), here assigned to *Martelites sarasini* (Rouchadzé, 1933), bed 52 of *Station de Cassis*; Black dot indicates end of phragmocone. Scale bar is 10 mm.



Collection numbers	Collections	Illustration	Localities	Beds	D	U	Wh	Ww
PR.400	Ropolo	/	<i>Les Camerlots</i>	Unknown	/	/	/	/
PR.402	Ropolo	/	<i>Les Camerlots</i>	Unknown	273	83	99	/
D.II	?	/	Cassis area	Unknown	/	/	92,5	90
FSL.105040	Busnardo	/	<i>Station de Cassis</i>	44	/	/	/	/
FSL.105046	Busnardo	/	<i>Station de Cassis</i>	44	/	/	/	/
FSL.105047	Busnardo	/	<i>Station de Cassis</i>	44	/	/	/	/
FSL.105065	Busnardo	/	<i>Station de Cassis</i>	45	247,5	90	91	43
FSL.105070	Busnardo	Frau et al. (2018, fig. 12a)	<i>Station de Cassis</i>	Unknown	223	71,4	99,5	/
FSL.105073	Busnardo	/	<i>Station de Cassis</i>	48	/	/	/	/
FSL.105078	Busnardo	/	<i>Station de Cassis</i>	48	/	/	/	/
FSL.105079	Busnardo	/	<i>Station de Cassis</i>	Unknown	/	/	/	/
FSL.105080	Busnardo	/	<i>Station de Cassis</i>	48	264	98	94	/
FSL.105081	Busnardo	/	<i>Station de Cassis</i>	48	/	/	/	/
FSL.105085	Busnardo	/	<i>Station de Cassis</i>	50	/	/	/	/
FSL.105086	Busnardo	/	<i>Station de Cassis</i>	51	/	/	/	/
FSL.105099	Busnardo	/	<i>Station de Cassis</i>	52	/	/	/	/
?FSL.105100	Busnardo	/	<i>Station de Cassis</i>	52	/	/	/	/
FSL.105101	Busnardo	/	<i>Station de Cassis</i>	52	165,5	51	77	44
FSL.105104	Busnardo	/	<i>Station de Cassis</i>	54	/	/	/	/
FSL.105107	Busnardo	/	<i>Station de Cassis</i>	54	/	/	/	/

Table 5. Dimensions of *Martelites sarasini* (Rouchadzé, 1933).

Local synonymy:

2018a. *Martelites* gr. *sarasini* Rouchadzé – *marteli* Conte - Frau *et al.*, p. 232, fig. 12A

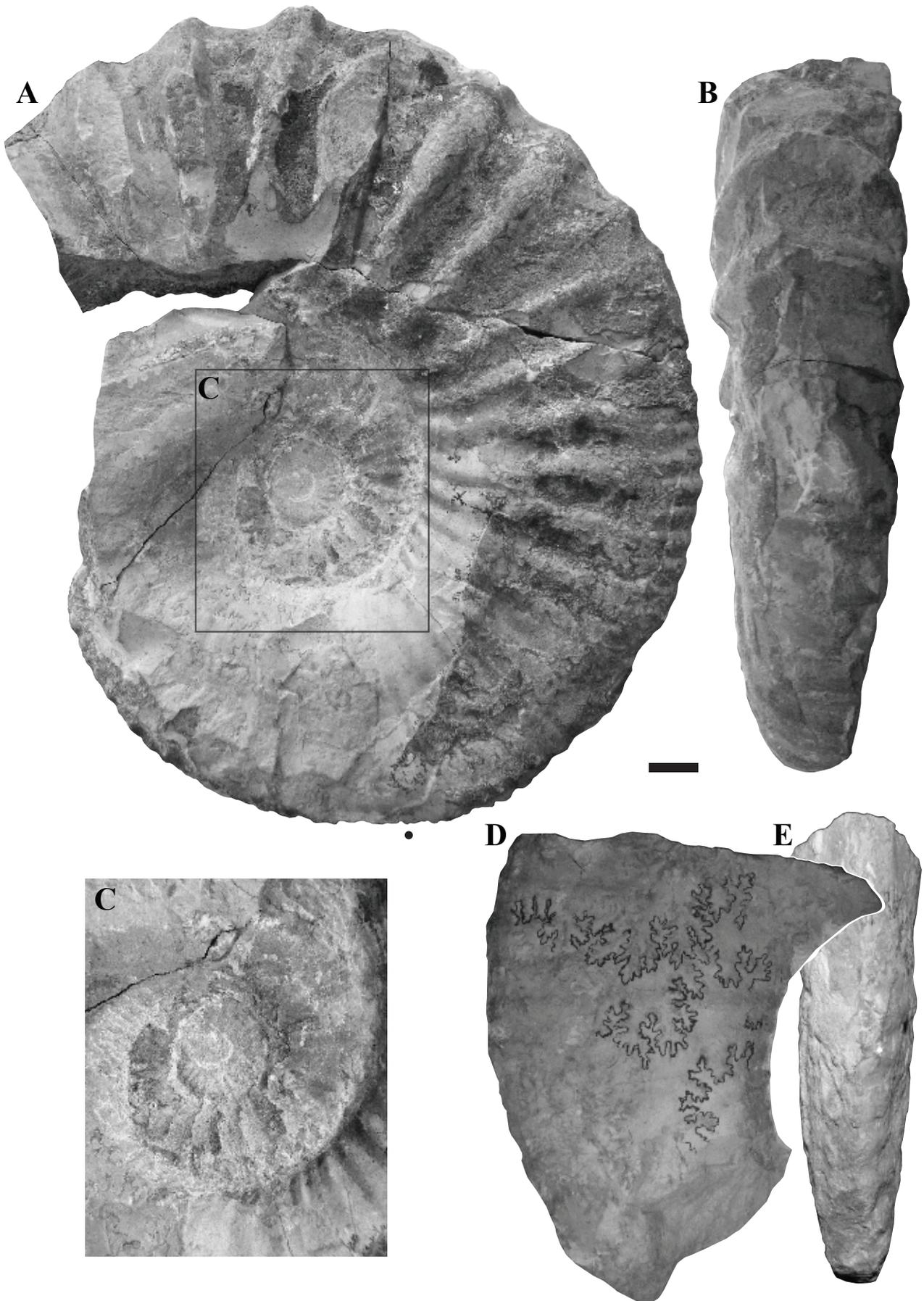
Type: The lectotype of *Martelites sarasini* designed by Kakabadze (1971) is specimen IJ.G.406/1072 (Rouchadzé collection) from Horecha, Georgia.

Material: Specimens MPP.12.872/PR.400, MPP.12.872/PR.402 (**Fig. 13A-C**), and MPP.D.II (**Fig. 14A-B**) from the Ropolo collection, and specimens FSL.105040, 105046 (**Fig. 13D-E**), 105047, 105065, 105070, 105073, 105078, 105079, 105080 (**Fig. 12D-F**), 105081, 105085, 105086, 105099, (?)105100, 105101 (**Fig. 12G-H**), 105104, 105107 from the Busnardo collection. All from *Station de Cassis*, and its surroundings.

Dimensions: See **Table 5**.

Description: The material at our disposal is composed of large-sized *Martelites* (D up to ~ 273 mm) with a small to moderate sized turricones compared to the total diameter (estimation of Dt ~ 17 mm for D ~ 273 mm in specimen MPP.12.872/PR.402; Dt ~ 22 mm for D ~ 223 mm in specimen FSL.107070). The turricones coiling is senestral in the two latter specimens, and characterised by mostly simple, somewhat rursiradiate ribs. The spiral part adapts the shape of the turricones (e.g., specimen FSL.105080; see Frau *et al.*, 2018a, fig. 13A), and has a sub-rectangular whorl section with a low rounded umbilical wall, slightly convex flanks, and rounded venter (e.g., specimen FSL.105101, **Fig. 12G-H**). The ribbing is composed of strong, somewhat clavate ribs, simple and sometimes bifurcate, and then secondaries occur. The ribbing distinctly vanishes at mid-flank as growth increases so that only ventral ribs are visible. Ribs can form a bulge on the umbilical margin, and they pass straight over the

Fig. 13 - A-E: Selected Heteroceratidae from Cassis. **A-C:** Lateral (**A**) and ventral views (**B**), and focus on the turricones (**C**) of specimen MPP.12.872/PR.402 (Ropolo collection) here assigned to *Martelites sarasini* (Rouchadzé, 1933), bed 51 of *Les Camerlots*; Lateral (**D**) and ventral views (**E**) of specimen FSL.105046 (Busnardo collection) also assigned to *Martelites sarasini* (Rouchadzé, 1933), bed 44 of *Station de Cassis*. Black dot indicates end of phragmocone. Scale bar is 10 mm.



venter with uniform thickening. This ribbing continues up to the end of the phragmocone and/or beginning of the body chamber. Secondary ribs progressively disappear, and the ribbing is then made of strong, simple, spaced ribs. It may exist a slight retrocurvature on the umbilical margin, but ribs are mostly straight on the flank, and cross the venter with progressive strong thickening (e.g., specimen MPP.12.872/PR.402, **Fig. 12A-C**; specimen MPP.D.II, **Fig. 14A-B**). The adult whorl section is compressed, sub-oval with flattened flank, and rounded venter. The umbilical wall becomes steeper with a rounded margin in the adult, but its height decreases approaching the aperture (e.g., specimen FSL.105080, **Fig. 12D-F**). The peristome is unknown. The suture lines are beautifully preserved in specimen FSL.105080 (see Frau *et al.*, 2018a, fig. 12A) and show a clear approximation approaching the end of the phragmocone.

Discussion: The inter- and intra-variabilities among the many *Martelites* taxa are not yet precisely quantified and sexual dimorphism is unclear (Delanoy, 1997; Baudouin *et al.*, 2012). According to the latter authors, the criteria used to separate taxa are not so diagnostic in isochronous palaeopopulations which show great variability in the adult size, dimension and orientation of the turricones, aspect of the spiral coiling surrounding the helix, as well as in the ribbing pattern, density, and flexuosity.

As an example, the *Martelites* specimens of the Busnardo collection differ from most typical *Martelites sarasini* by their larger adult size, the distinctive fading of the ribs at mid-flanks during the sub-adult stage, and a clear rib thickening in the adult. Nevertheless, the rib fading is also noted in many of its members from the nearby Vocontian Basin (e.g., Delanoy, 1997, pl. 52, fig. 2; pl. 54, fig. 2; pl. 57, fig. 1, 3; pl. 61, fig. 1, 5), and a similar form has been referred to as *Martelites* aff. *sarasini* by Baudouin *et al.* (2012, pl. XIV, fig. 1a-c). Of interest is the specimen of Delanoy (1997, pl. 57, fig. 1), that is large-sized mature individual possessing both a sub-adult fading and adult thickening of the ribs as in the Busnardo's specimens. The assumption can be made that they correspond to the average variation of *Martelites sarasini*, and they are thus not kept separate from the index species.

It should finally be noted that two *Martelites* individuals from Cassis were previously figured in the literature. The large-sized specimen of the Tourment collection from *Les Camerlots* has been assigned to *Martelites* aff. *vulanensis* since it would conform to that species by its general shell dimensions, and a slightly rursiradiate ribbing on the late phragmocone (Delanoy, 1997, pl. 51, fig. 1). The specimen has as a large turricones compared to its total diameter, and lacks the fading of the ribs in the sub-adult. It thus differs from the Busnardo's specimens here described. Nevertheless, it is established that the variability of *Martelites sarasini* expose a co-variation relationship between size of the turricones, strengthening of the subsequent ribbing, and the number of bifurcate and secondary ribs (Delanoy, 1997; Baudouin *et al.*, 2012). As an example, the individuals

with large turricones, develop a much more robust ribbing and tendency of rib fading is limited or delayed in the later growth stages. On this basis, there is an obvious possibility for considering the Tourment's specimen has another pole of variation of *Martelites sarasini*. However, its stratigraphic origin remains unknown (Delanoy, 1997), and this prevents further confirmation. Pending new collection, this form is kept separate and still assigned to *Martelites* aff. *vulanensis*.

The other specimen figured by Ropolo *et al.* (1999, pl. 15, fig. 1-2) was also assigned to *Martelites* aff. *vulanensis* but it obviously conforms to *Martelites sarasini* both regarding general shell morphology and ontogeny. It further has a rib fading in the outer whorl. It should, however, be noted that its preservation is rather unusual for the South Provence succession since it has a complete, non-distorted helix, visible on both faces, and does not show any sign of sedimentary compaction. The specimen is reported from bed 72 of *Le Brigadan* but none of specimens from this bed interval (i.e., beds 51–52) has a similar state of preservation (i.e., compare with **Fig. 12G-H** for example). It better agrees in its taphonomic characters with the Vocontian *Martelites*. We thus cast doubt on its origin and it is not included in the local synonymy list given above.

Occurrence: The index species *Martelites sarasini* first occurs in bed 44, and ranges up to bed 54 at the *Station de Cassis* section (Busnardo, *in coll.*). This is the first precise documentation of the stratigraphic range of the index species *Martelites sarasini* in the study area. The other specimens from the Ropolo's collection derives from bed 51 of *Les Camerlots* (MPP.12.872/PR.400 and MPP.12.872/PR.402) while specimen MPP.D.II is of doubtful origin.

Besides southern France (Vocontian and South Provence basins), the species *Martelites sarasini* is recorded in Spain, Georgia and the northwestern Caucasus (Baudouin *et al.*, 2012).

Family Deshayesitidae Stoyanow, 1949

Genus Deshayesites Stoyanow, 1949

Type species: *Ammonites deshayesi* d'Orbigny, 1841; by original designation.

Remarks: The taxonomy of the Deshayesitidae remains a matter of debate due to strict typological approaches, missing or imprecise stratigraphical data, preservation problems, and diverging concepts between authors, which clearly affects attempts to identify and compare taxa (e.g., Bersac & Bert, 2012, 2015; Moreno-Bedmar *et al.*, 2014). Despite the tremendous quantity of material illustrated, a critical review of the dataset shows that the picture one can build of the evolution of the Deshayesitidae from the South Provence Basin is far from being resolved. As an example, majority of the *Deshayesites* material



Fig. 14 - A-C: Selected Heteroceratidae from Cassis. **A-B:** Lateral (**A**) and ventral views (**B**) of specimen MPP.D.II (Ropolo collection) here assigned to *Martelites sarasini* (Rouchadzé, 1933), unknown bed and locality of Cassis; **C:** Lateral view of specimen FSL.105073 (Busnardo collection) also assigned to *Martelites sarasini* (Rouchadzé, 1933), bed 48 of *Station de Cassis*. Black dot indicates end of phragmocone. Scale bar is 10 mm.

(estimation at ~ 53,5 %) figured in the monograph of Ropolo *et al.* (2006) originate from *Les Fournier* section, but only a synthetic and stylised diagram of this outcrop, with its own bed numbering and estimated thickness, was provided by these authors. It is not possible to compare this drawing with the measured logs of tangible rock sequences outcropping southward at the *Station de Cassis* section. Bed-by-bed distribution of *Deshayesites* thus proves to be idealised throughout most of the lower Aptian in the type succession. Finally, it exists some misleading sample numbering in the works of Ropolo *et al.* (2006), putting in doubt the reliability of the information provided. A revision is out of the scope of this work and we here focus on the lowermost Aptian *Deshayesites*, mostly from *Le Brigadan*, that were mainly described by Cecca *et al.* (1999, 2000).

***Deshayesites oglanlensis* Bogdanova, 1983**

Fig. 15A, B-C, D, E, F, G-H; Fig. 16A-B, C-D; Fig. 17A-B

Type:

1983 *Deshayesites oglanlensis* Bogdanova, p. 136, pl. I, fig. 5, 6, 7, 8, 9a; text-fig. 5, 6

Local synonymy:

[m]

- 1999. *Deshayesites oglanlensis* Bogdanova – Cecca *et al.*, p. 278, pl. 1, fig. 2, 3, 4
- 1999. *Deshayesites* aff. *weissiformis* Bogdanova - Cecca *et al.*, p. 278, pl. 6, fig. 2, 3
- 1999. *Deshayesites* cf. *weissiformis* Bogdanova - Cecca *et al.*, p. 278, pl. 6, fig. 4
- ? 1999. *Deshayesites* aff. *normani* Casey - Cecca *et al.*, p. 279, pl. 7, fig. 2
- 1999. *Deshayesites* cf. *planicostatus* Bogdanova - Cecca *et al.*, p. 279, pl. 7, fig. 3
- 1999. *Deshayesites* n. sp. A Cecca *et al.*, p. 279, pl. 8, fig. 2, 3, 4
- 1999. *Deshayesites* n. sp. B Cecca *et al.*, p. 279, pl. 9, fig. 2, 3, 4
- pars 1999. *Deshayesites antiquus* Bogdanova - Ropolo *et al.*, p. 178, pl. 16, fig. 1, non fig. 2, 3
- 1999. *Deshayesites luppovi* Bogdanova - Ropolo *et al.*, p. 178, pl. 16, fig. 4, 5
- non 1999. *Deshayesites oglanlensis* Bogdanova - Ropolo *et al.*, p. 177, pl. 17, fig. 2
- 2000. *Deshayesites oglanlensis* Bogdanova - Gonnet *et al.*, p. 129, text-fig. 5b (= Bogdanova, 1983, text-fig. 6)
- 2000. *Deshayesites luppovi* Bogdanova - Gonnet *et al.*, p. 130, text-fig. 5c (= Bogdanova, 1983, text-fig. 8)
- 2000. *Deshayesites oglanlensis* Bogdanova - Gonnet *et al.*, p. 129, pl. 1, fig. 2 (= *D. luppovi* in Ropolo *et al.*, 1999, pl. 16, fig. 4); pl. 2, fig. 4 (= same specimen of pl. 1, fig. 2)

- 2000. *Deshayesites* gr. *tuarkyricus* Bogdanova - Gonnet *et al.*, p. 131, pl. 1, fig. 3
- 2000. *Deshayesites luppovi* Bogdanova - Gonnet *et al.*, p. 130, pl. 2, fig. 1 (= *D. oglanlensis* in Ropolo *et al.*, 1999, pl. 17, fig. 2), 2a-b; pl. 4, fig. 2 (= *D. luppovi* in Ropolo *et al.*, 1999, pl. 16, fig. 5)
- pars 2000. *Deshayesites antiquus* Bogdanova - Gonnet *et al.*, p. 129, pl. 3, fig. 2 (= *D. antiquus* in Ropolo *et al.*, 1999, pl. 16, fig. 1), non fig. 3 (= *D. antiquus* in Ropolo *et al.*, 1999, pl. 16, fig. 2)
- 2000. *Deshayesites oglanlensis* Bogdanova - Cecca *et al.*, pl. 1, fig. 2, 3, 4
- 2000. *Deshayesites* n. sp. A. - Cecca *et al.*, pl. 2, fig. 2
- 2000. *Deshayesites* cf. *planicostatus* Bogdanova - Cecca *et al.*, pl. 2, fig. 3
- 2000. *Deshayesites* aff. *weissiformis* Bogdanova - Cecca *et al.*, pl. 2, fig. 4
- 2006. *Deshayesites luppovi* Bogdanova - Ropolo *et al.*, p. 12, pl. 1, fig. 1 (= Gonnet *et al.*, 2000, pl. 3, fig. 2), 2, 4 (= Gonnet *et al.*, 2000, pl. 2, fig. 1), 12 (= *P. oglanlensis* in Ropolo *et al.*, 2006, pl. 1, fig. 13 with a different size)
- 2006. *Deshayesites* sp. aff. *luppovi* Bogdanova - Ropolo *et al.*, p. 12, pl. 4, fig. 1 (= *D. antiquus* in Gonnet *et al.*, 2000, pl. 3, fig. 4)
- pars 2006. *Paradeshayesites oglanlensis* (Bogdanova) - Ropolo *et al.*, p. 15, pl. 1, fig. 3 (= Gonnet *et al.*, 2000, pl. 1, fig. 2 and pl. 2, fig. 4), non fig. 11 (= *D. antiquus* in Ropolo *et al.*, 1999, pl. 16, fig. 2; in Gonnet *et al.*, 2000, pl. 3, fig. 3), 13
- 2006. *Paradeshayesites weissiformis* (Bogdanova) - Ropolo *et al.*, p. 17, pl. 1, fig. 5 (= Cecca *et al.*, 1999, pl. 2, fig. 4), 6; pl. 2, fig. 3 (= *D. n. sp. B* in Cecca *et al.*, 1999, pl. 9, fig. 2)
- 2006. *Paradeshayesites* sp. aff. *planicostatus* (Bogdanova) - Ropolo *et al.*, p. 16, pl. 1, fig. 7, 8 (= *D. sp.* in Gonnet *et al.*, 2000, pl. 4, fig. 1), 10
- 2006. *Paradeshayesites* sp. - Ropolo *et al.*, pl. 1, fig. 9 (= *D. gr. tuarkyricus* in Gonnet *et al.*, 2000, pl. 1, fig. 3)

[M]

- 1999. *Deshayesites bedouliensis* n. sp. Cecca *et al.*, p. 270, pl. 1, fig. 1; pl. 2; pl. 3, fig. 1, 2; pl. 4; pl. 5, fig. 1, 2; pl. 6, fig. 1; pl. 7, fig. 1; pl. 8, fig. 1
- 1999. *Deshayesites* aff. *consobrinus* (d'Orbigny) - Cecca *et al.*, p. 280, pl. 9, fig. 1
- 1999. *Deshayesites oglanlensis* Bogdanova - Ropolo *et al.*, p. 177, pl. 17, fig. 1
- 1999. *Deshayesites antiquus* Bogdanova - Ropolo *et al.*, p. 178, pl. 18, fig. 1
- pars 1999. *Deshayesites consobrinoides* (Sinzow) - Ropolo *et al.*, pl. 19, fig. 4 (= unprepared specimen of Cecca *et al.*, 1999, pl. 9, fig. 1); non pl. 18, fig. 2
- 1999. *Deshayesites weissiformis* Bogdanova - Ropolo *et al.*, p. 179, pl. 18, fig. 3 (= unprepared specimen of Cecca *et al.*, 1999, pl. 6, fig. 1)
- 2000. *Deshayesites oglanlensis* Bogdanova - Gonnet



Fig. 15 - A-H: Selected Deshayesitidae from Cassis here assigned to *Deshayesites oglanlensis* Bogdanova, 1983 from Cassis. **A:** Specimen MPP.BW.001 (Ropolo collection) of Cecca *et al.* (1999, pl. 9, fig. 2), bed 83 of *Le Brigadan*, [?m]; **B-C:** Specimen MPP.BW.005 (Ropolo collection) of Cecca *et al.* (1999, pl. 7, fig. 3), bed 83 of *Le Brigadan*, [?m]; **D:** Specimen MPP.BW.002 (Ropolo collection) of Cecca *et al.* (1999, pl. 1, fig. 2), bed 83 of *Le Brigadan*, [?m]; **E:** Specimen MPP.ABR.271 (Ropolo collection) of Ropolo *et al.* (2006, pl. 1, fig. 1), bed 84 of *Le Brigadan*, [?m]; **F:** Specimen MPP.BW.011a (Ropolo collection), bed 83 of *Le Brigadan*, [?m]; **G-H:** Specimen MPP.BW.112 (Ropolo collection) of Ropolo *et al.* (2006, pl. 2, fig. 1), bed 84 of *Le Brigadan*, [?M]. Black dots indicate end of phragmocone. All specimens x1 except (G-H) x3/4. Scale bar is 10 mm.

- et al.*, p. 129, pl. 1, fig. 1 (= Ropolo *et al.*, 1999, pl. 17, fig. 1)
2000. *Deshayesites* sp. aff. *weissiformis* Bogdanova - Gonnet *et al.*, p. 130, pl. 2, fig. 3 (= *D. weissiformis* in Ropolo *et al.*, 1999, pl. 18, fig. 3)
2000. *Deshayesites consobrinoides* (Sinzow) - Gonnet *et al.*, pl. 3, fig. 1 (= *D. consobrinoides* in Ropolo *et al.*, 1999, pl. 18, fig. 2)
2000. *Deshayesites* sp. aff. *consobrinoides* (Sinzow) - Gonnet *et al.*, pl. 7, fig. 1 (= *D. consobrinoides* in Ropolo *et al.*, 1999, pl. 19, fig. 4)
2000. *Deshayesites antiquus* Bogdanova - Gonnet *et al.*, p. 129, pl. 3, fig. 4 (= *D. antiquus* in Ropolo *et al.*, 1999, pl. 18, fig. 1)
2000. *Deshayesites* sp. - Gonnet *et al.*, pl. 4, fig. 1
2000. *Deshayesites bedouliensis* Cecca, Ropolo & Gonnet - Cecca *et al.*, pl. 1, fig. 1
- non 2000. *Deshayesites* aff. *consobrinus* (d'Orbigny) - Cecca *et al.*, pl. 2, fig. 1 (= Ropolo *et al.*, 1999, pl. 17, fig. 2)
2006. *Deshayesites bedouliensis* Cecca, Ropolo & Gonnet - Ropolo *et al.*, p. 6, pl. 2, fig. 1, ?2; pl. 3, fig. ?2, 3 (= *D. oglanlensis* in Gonnet *et al.*, 2000, pl. 1, fig. 1)
2006. *Deshayesites* sp. aff. *consobrinus* (d'Orbigny) - Ropolo *et al.*, p. 8, pl. 3, fig. 1 (= *D. aff. consobrinus* in Cecca *et al.*, 2000, pl. 2, fig. 1)

Type: The holotype of *Deshayesites oglanlensis* designed by Bogdanova (1983, pl. I, fig. 5) is specimen CNIGR.12/9442 (Bogdanova collection) from the Oglanly area, Bolshoi Balkhan, Turkmenistan.

Material: The Busnardo collection lacks lowermost Aptian *Deshayesites*. We here re-investigated the diverse specimens figured by Cecca *et al.* (1999, 2000), and Ropolo *et al.* (1999, 2000a, 2006) including MPP.ABR.30, 32, 33, 36, 37, 38, 40, 143, 271 (Fig. 15E), 272, 278, 279a-b, 280, 281, 282, 301, 1285, 2168, 2169, 2172, 2173, 2174, 2177, 4061, as well as MPP.BW.001 (Fig. 15A), BW.002 (Fig. 15D), BW.003, BW.004, BW.005a (Fig. 15B-C), and b, BW.006, BW.007, BW.011a (Fig. 15F), and b, BW.015 (Fig. 16C-D), BW.020, BW.021, BW.022, BW.023, BW.025, BW.050, BW.051, BW.052, BW.053, BW.054 (Fig. 16A-B), BW.055, BW.056, BW.057, BW.058, BW.061, BW.062, BW.063, BW.066, BW.067, BW.068, BW.069, BW.070, BW.071 (Fig. 17A-B), BW.073, BW.074, BW.075, BW.112 (Fig. 15G-H), BW.270, and RG.1456. All specimens from *Le Brigadan* and *Les Caniers/Les Sardons*.

Dimensions: See Table 6, and Fig. 18.

Description: Small to large-sized, possibly dimorphic *Deshayesites*.

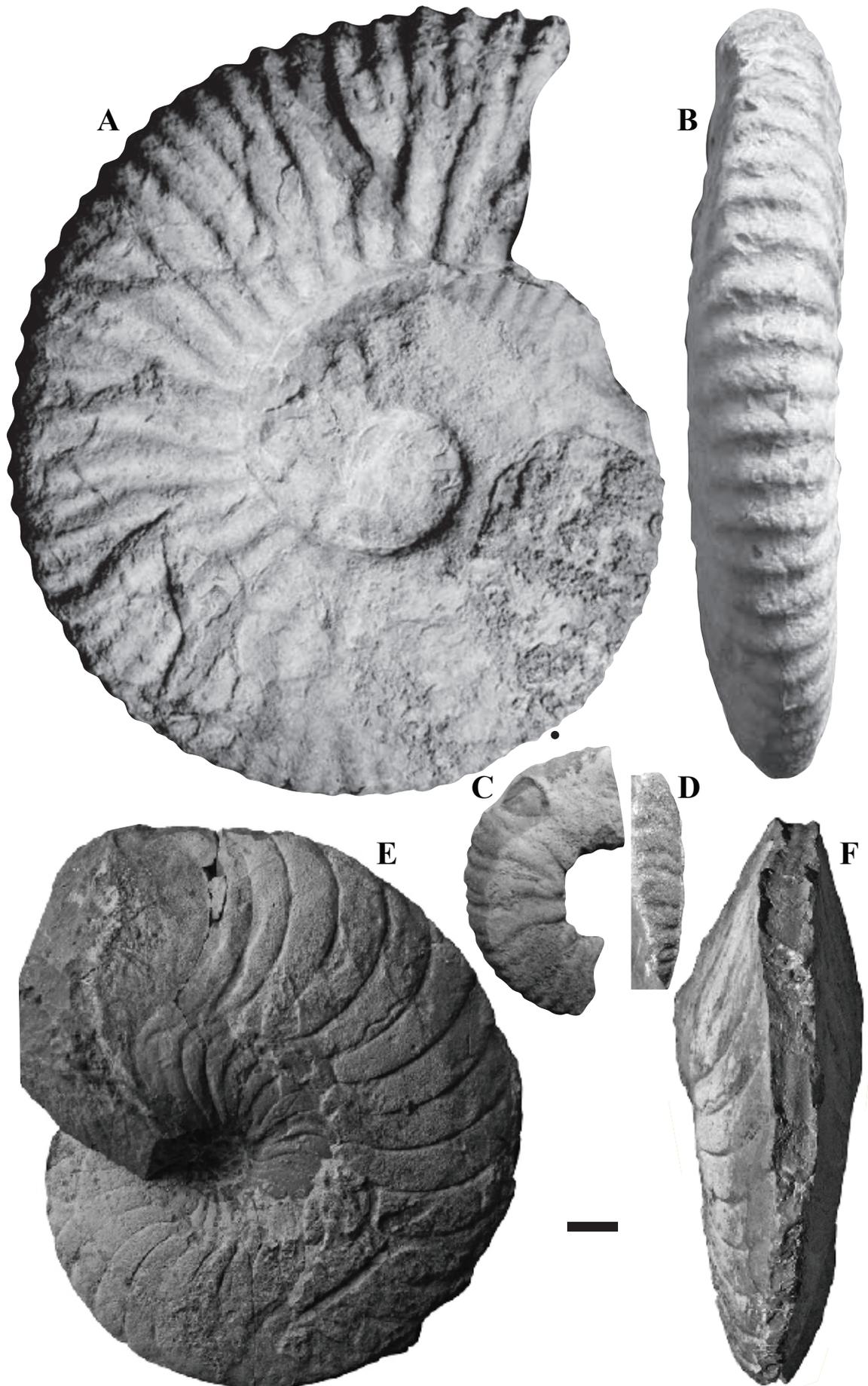
The putative microconchs are marked by a small-sized shell ($18 \leq D \leq 82$ mm; average of 40 mm), with an extremely discoidal ($0.08 \leq Ww/D \leq 0.24$; average ~ 0.15), strongly compressed ($0.19 \leq Ww/Wh \leq 0.46$; average ~ 0.31), very evolute ($0.25 \leq U/Wh \leq 1.07$; average ~ 0.67), discocone to virgacone coiling ($0.12 \leq Uw/D \leq 0.38$; average of ~ 0.29). The whorl section is compressed, high oval to sub-rectangular with narrow and rounded venter. The flanks are flattened, and the umbilical wall is steep and rounded. When complete, the body chamber approximately occupies half of the last whorl. The peristome is often worn and incomplete and there is no clear regression of the adult whorl that usually characterises some *Deshayesites* microconchs, such as in *Deshayesites fissicostatus* (Phillips) (compare with Casey, 1964, pl. LVIII, fig. 2 for example). The ornamentation is smooth up to ~ 7 – 10 mm in diameter (stage 1). There is a progressive appearance of ribbing with no clear evidence of attenuated or smooth siphonal band in the best-preserved individuals. Then, the ribbing is composed of more or less dense, sinusoidal, simple and/or bifurcate ribs with intercalate ones (stage 2a). The point of furcation of the ribs falls around mid-flank. At approximately $D = 20$ – 25 mm, the ribs originate from weak thickenings on the umbilical margin that strengthen as growth increases and form bullae in the adult (stage 2b). Primary ribs are progressively more spaced while the number of secondaries increases (3 to 5). The ribbing tends to be attenuated at mid-flank. After $D \sim 35$ mm, the interspaces between primary ribs and the number of intercalatories decrease. The branches of the ribs are smoothed (stage 3). Individual variations concern the length of the ornamental stages and relief of the ribbing.

We distinguished two main morphotypes:

- Small-sized ($D \leq 42$ mm), slightly involute, densely and finely ribbed forms that do not develop the final stages 2b and 3. This group includes the individuals from Cassis assigned to *Deshayesites weissiformis*, *Deshayesites* aff. *weissiformis*, *Deshayesites* cf. *weissiformis*, *Deshayesites oglanlensis* (pars), *Deshayesites* sp. and *Deshayesites* sp. B (Fig. 15A).

- Moderate-sized ($D \leq 82$ mm), moderately evolute, more or less strongly ribbed forms with complete ornamental sequence (stages 1 to 3). This group includes the typical forms of *Deshayesites oglanlensis* from Cassis and those assigned

Fig. 16 - Selected *Deshayesitidae* (A–D) and *Cenoceratidae* (E–F) from Cassis. **A–B:** Lateral (A) and ventral views (B) of specimen MPP.BW.054 (Ropolo collection) of Cecca *et al.* (1999, pl. 8, fig. 1) here assigned to *Deshayesites oglanlensis* Bogdanova, 1983, bed 83 of *Le Brigadan*, [?M]; **C–D:** Lateral (C) and ventral views (D) of specimen MPP.BW.013 (Ropolo collection), of doubtful identification, bed 60 of *Le Brigadan*, [?m]; **E–F:** Lateral (E) and ventral views (F) of specimen MPP.BW.599 (Gonnet collection) of Baudouin *et al.* (2016, pl. 12, fig. 2a and pl. 13, fig. 1a-b), previously assigned to *Heminautilus sanctaerucis* Conte, 1980, bed 78 of *Les Caniers/Les Sardons*. Black dot indicates end of phragmocone. Scale bar is 10 mm.



to *Deshayesites* cf. *planicostatus* and *Deshayesites* n. sp. A (Fig. 15B-C, D, E-F).

Among the putative microconch forms, there is an incomplete individual which is distinguished by a distinctly inflated ribbing style in the outer whorl that was referred to as *Deshayesites* aff. *normani* by Cecca *et al.* (1999, pl. 7, fig. 2) (see also Fig. 16C-D). Such specimen is of doubtful interpretation by its peculiar features that is not so frequent in the fossil record. It may illustrate an extreme robust pole of variation of *Deshayesites oglanlensis* but intermediate forms remain unknown for further confirmation.

The potential macroconchs are larger than the microconchs ($70 \leq D \leq 268$ mm; average of 160 mm) and develop an extremely discoidal ($0.15 \leq Ww/D \leq 0.22$; average ~ 0.19), weakly compressed ($0.41 \leq Ww/Wh \leq 0.66$; average ~ 0.53), very evolute ($0.38 \leq U/Wh \leq 1.30$; average ~ 0.91), and discocone to virgacone coiling ($0.19 \leq Uw/D \leq 0.42$; average of ~ 0.32). The whorl section is compressed subrectangular, with rounded venter that flatten in the adult. The flanks are rounded in the inner whorls and flatten in the adult. The umbilical wall is high and steep with a rounded margin. The venter is not observable in the early ontogeny. When complete, the body chamber occupies almost half of the last half whorl. The peristome is simple and sinuous with a discrete collared aperture. Cecca *et al.* (1999, 2000) previously documented a continuous variability in coiling – i.e., from relatively involute to evolute specimens – with a distinctive change of the sculpture in those macroconchs.

We here distinguished three morphotypes:

- Evolute morphotype with unattenuated ornamentation (Fig. 15G-H). The phragmocone is characterised by an extended stage 3. The ribs weaken on the flanks and increase in the upper part of the flank and on the venter. On the body chamber, the whorl height decreases and the whorl breadth increases while the umbilicus widens, thus producing both a narrowing and a regression of the whorl. The ribbing is composed of thick, rectiradiate to prorsiradiate, single or bifurcate ribs whose point of furcation falls at mid-flank. Few intercalatories occur and start at different heights on the flank. In the most evolute specimens, such as the holotype of *Deshayesites bedouliensis*, the body chamber touches the venter of the preceding whorl and the umbilical wall tends to disappear resulting in the loose of the general discoidal aspect of the shell.

- Involute morphotype with attenuated ornamentation (Fig. 16A-B). It is characterised by an involute, discoidal shell with an ovate, compressed whorl section, high and steep umbilical wall in the body chamber. The

ornamentation of the phragmocone is marked by spaced, strong, simple, and bifurcate ribs branching in the upper third of the flank. The ribs are prorsiradiate in the lower half of the flank and slightly rursiradiate in the upper half. This morphotype includes the specimen from Cassis assigned to *Deshayesites* aff. *consobrinus*.

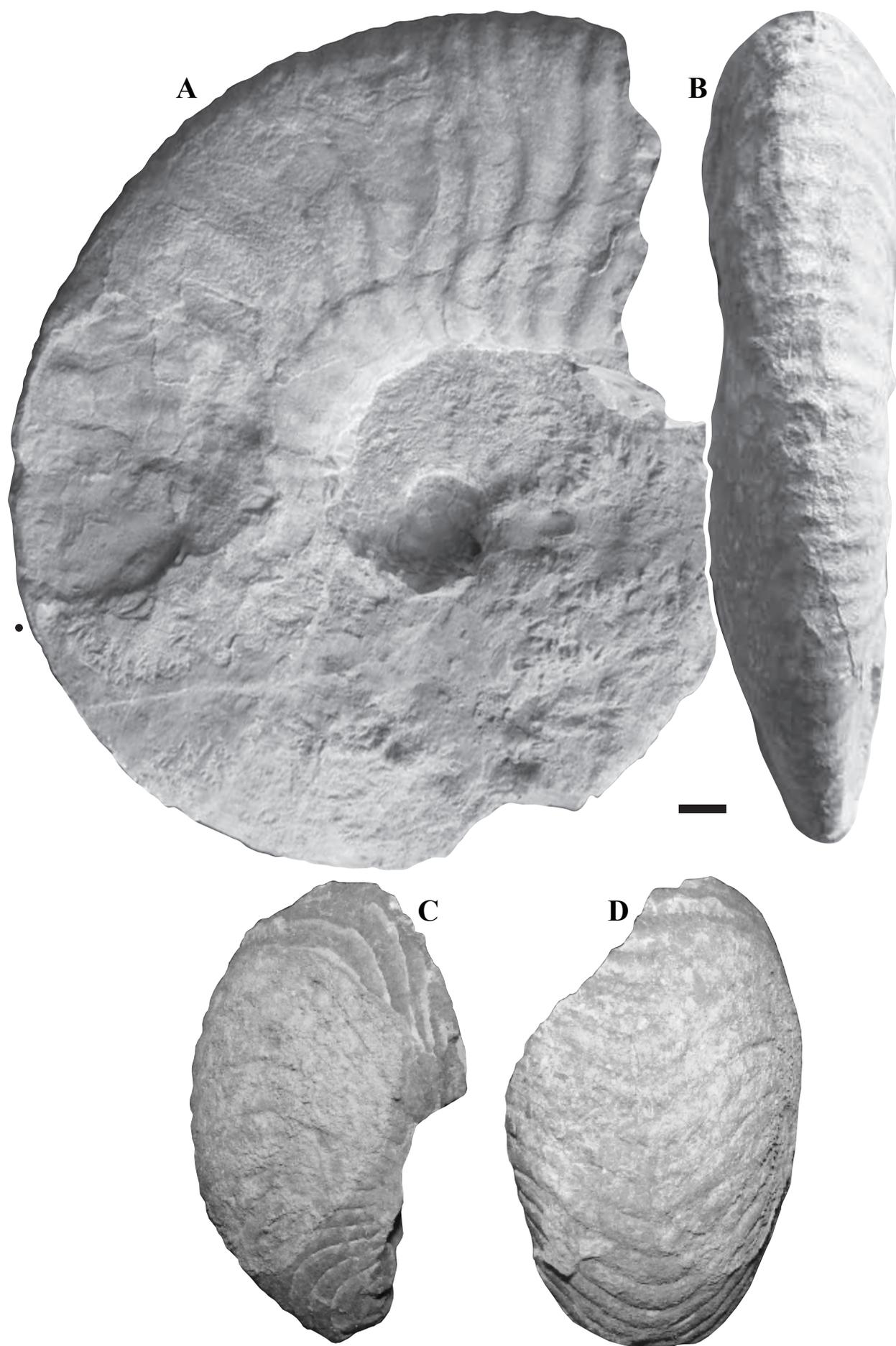
- Involute morphotype with a smooth ornamentation (Fig. 17A-B). Ribbing is vanished on the body chamber. Slight thickenings occur on the umbilical margin. On the body chamber, the ribbing is similar to the previous morphotype, but the ribs become rursiradiate at the furcation point and show a slightly adoral convexity on the venter.

Discussion: In agreement with Delanoy *et al.* (2008, p. 37), the many *Deshayesites* typological taxa from the base of the Aptian Stage at Cassis likely belong to a single dimorphic palaeopopulation. The documented variabilities support the sexual dimorphism hypothesis of Bersac & Bert (2012, 2015). The putative dimorphism is based on a change in the adult size in the range of four. The variability of alleged microconchs illustrates the first Buckman's law of covariation between whorl shape and robustness of the ornamentation. The individuals referred to as *Deshayesites oglanlensis* show all ornamental stages. They are more peramorphic than the individuals typologically referred to as *Deshayesites weissiformis*. These are herein considered as putative microconchs of the large-sized typological taxa *Deshayesites bedouliensis* and *Deshayesites* aff. *consobrinus* of Cecca *et al.* (1999). We also recognize a continuous chain from evolute morphotype with unattenuated ornamentation to involute morphotype with sub-smooth ornamentation in the putative macroconchs. In agreement with ICZN's rules, we here consider *Deshayesites bedouliensis* as a junior subjective synonym of *Deshayesites oglanlensis*. Among this palaeopopulation, the specimen assigned to *Deshayesites* aff. *normani* is of doubtful interpretation since it has a distinctly inflated ribbing style in the outer whorl which departs from the observed variabilities. It could, nevertheless, represent extreme, but rare ribbing style of microconchs.

The type series of *Deshayesites oglanlensis* illustrated by Bogdanova (1983) compares well with the Cassis palaeopopulation. As herein understood, this material consists of small-sized, moderately evolute putative microconchs with a complete ornamental sequence (stage 1 to 3 as defined above).

Occurrence: The group of *D. oglanlensis* largely dominates in bed 60 at the *Station de Cassis* section and

Fig. 17 - Selected *Deshayesitidae* (A-B) and *Nautilidae* (C-D) from Cassis. **A-B:** Lateral (A) and ventral views (B) of specimen MPP.BW.071 (Ropolo collection) of Cecca *et al.* (1999, pl. 4, fig. 1) here assigned to *Deshayesites oglanlensis* Bogdanova, 1983, bed 83 of *Le Brigadan*, [?M]; **C-D:** Lateral (C) and ventral views (D) of specimen FSL.105048 (Busnardo collection) here assigned to *Cymatoceras neocomiense* (d'Orbigny, 1840), bed 44 of *Station de Cassis*. Black dot indicates end of phragmocone. Scale bar is 10 mm.



Collection numbers	Collections	Original ID	Illustrations	Morpho- types	Localities	Beds	D	Wh	Ww	U	K
ABR1285	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	37	14	/	12	30
ABR143	Ropolo	<i>D. aff. weissiformis</i>	/	[?m]	<i>Le Bridagan</i>	60	31,5	/	/		40
ABR2168	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	82	34	/	25	33
ABR2169	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	39	18	/	13	28
ABR2172	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	35	14,5	/	13	30
ABR2173	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	28	13	/	10	28
ABR2174	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	26	11	/	7	28
ABR2177	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	26	10,5	/	9	27
ABR37	Ropolo	<i>D. aff. weissiformis</i>	/	[?m]	<i>Le Bridagan</i>	60	35,5	16	/	9	34
ABR38	Ropolo	<i>D. weissiformis</i>	/	[?m]	<i>Le Bridagan</i>	60	28	12,6	/	8	34
ABR40	Ropolo	<i>D. weissiformis</i>	/	[?m]	<i>Le Bridagan</i>	60	34	16	/	8	36
ABR4601	Ropolo	<i>D. luppovi</i>	/	[?m]	<i>Le Bridagan</i>	60	18,6	8	/	6,2	27
BW004	Ropolo	<i>D. oglanlensis</i>	/	[?m]	<i>Le Bridagan</i>	60	34	11,5	/	8	29
BW007	Ropolo	<i>D. oglanlensis</i>	/	[?m]	<i>Le Bridagan</i>	60	34	13	/	8	30
BW015	Ropolo	<i>D. antiquus</i>	/	[?m]	<i>Le Bridagan</i>	60	33	12	/	7	29
BW025	Ropolo	<i>D. n. sp. A</i>	/	[?m]	<i>Le Bridagan</i>	60	66	30,5	12	18	31
BW051	Ropolo	<i>D. antiquus</i>	/	[?m]	<i>Le Bridagan</i>	60	27	14	6,5	9	26
ABR272	Ropolo	<i>D. aff. weissiformis</i>	Ropolo et al. (2006, pl. 1, fig. 1)	[?m]	<i>Le Bridagan</i>	?64	41,5	18	/	10	38
ABR278	Ropolo	<i>D. aff. weissiformis</i>	Ropolo et al. (2006, pl. 1, fig. 6)	[?m]	<i>Les Caniers/ Les Sardons</i>	82	31	16	/	10	/
ABR280	Ropolo	<i>D. antiquus</i>	Ropolo et al. (1999, pl. 16, fig. 5)	[?m]	<i>Les Caniers/ Les Sardons</i>	81 or 82	/	/	/	/	/
ABR281	Ropolo	<i>D. oglanlensis</i>	Ropolo et al. (2006, pl. 1, fig. 11)	[?m]	<i>Les Caniers/ Les Sardons</i>	78	37	13	/	14	36
ABR282	Ropolo	<i>D. sp. aff. planicostatus</i>	Ropolo et al. (2006, pl. 1, fig. 1)	[?m]	<i>Les Caniers/ Les Sardons</i>	82	39,5	16,8	/	12,5	30
ABR30	Ropolo	<i>D. oglanlensis</i>	Ropolo et al. (2006, pl. 1, fig. 13)	[?m]	<i>Le Bridagan</i>	63	24	10	/	8	32
ABR301	Ropolo	<i>D. sp. aff. planicostatus</i>	Ropolo et al. (2006, pl. 1, fig. 8)	[?m]	<i>Les Caniers/ Les Sardons</i>	67	58	26	/	15	30
ABR32	Ropolo	<i>D. luppovi</i>	Ropolo et al. (2006, pl. 1, fig. 10)	[?m]	<i>Le Bridagan</i>	61	45,2	20,2	4	15	30
ABR33	Ropolo	<i>D. sp. aff. planicostatus</i>	Ropolo et al. (2006, pl. 1, fig. 7)	[?m]	<i>Le Bridagan</i>	63	42	19	4	12,5	30
ABR36	Ropolo	<i>D. luppovi</i>	Ropolo et al. (2006, pl. 1, fig. 12)	[?m]	<i>Les Caniers/ Les Sardons</i>	78	82	34	/	25	33
BW001	Ropolo	<i>D. n. sp. B</i>	Cecca et al. (1999, pl. 9, fig. 2)	[?m]	<i>Le Bridagan</i>	60	41	16,5	/	11,5	40
BW002	Ropolo	<i>D. oglanlensis</i>	Cecca et al. (1999, pl. 1, fig. 2)	[?m]	<i>Le Bridagan</i>	60	40	16	/	10,5	33
BW003	Ropolo	<i>D. aff. weissiformis</i>	Cecca et al. (1999, pl. 6, fig. 3)	[?m]	<i>Le Bridagan</i>	60	32,5	13	/	8	34
BW005	Ropolo	<i>D. cf. planicostatus</i>	Cecca et al. (1999, pl. 7, fig. 3)	[?m]	<i>Le Bridagan</i>	60	38	16	/	11	28
BW011a	Ropolo	<i>D. oglanlensis</i>	Cecca et al. (1999, pl. 1, fig. 3)	[?m]	<i>Le Bridagan</i>	60	35	/	/	/	/

BW020/22?	Ropolo	<i>D. aff. weissiformis</i>	Cecca et al. (1999, pl. 6, fig. 4)	[?m]	<i>Le Bridagan</i>	60	/	/	/	/	/
BW022	Ropolo	<i>D. aff. weissiformis</i>	Cecca et al. (1999, pl. 6, fig. 2)	[?m]	<i>Le Bridagan</i>	60	39	20	/	5	39
BW023	Ropolo	<i>D. n. sp. A</i>	Cecca et al. (1999, pl. 8, fig. 2)	[?m]	<i>Le Bridagan</i>	60	57	/	/	/	/
BW050	Ropolo	<i>D. oglanlensis</i>	Cecca et al. (1999, pl. 1, fig. 4)	[?m]	<i>Le Bridagan</i>	60	42	20	/	9	27
BW080	Ropolo	<i>D. sp. B</i>	Cecca et al. (1999, pl. 8, fig. 3)	[?m]	<i>Le Bridagan</i>	60	/	/	/	/	/
BW080	Ropolo	<i>D. sp. B</i>	Cecca et al. (1999, pl. 8, fig. 4)	[?m]	<i>Le Bridagan</i>	60	/	/	/	/	/
BW052	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	110	/	/	/	41
BW056	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	182	/	/	/	/
BW061	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	160	/	/	/	/
BW067	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	165	48	/	63	36
BW068	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	153,5	50	33	57,5	33
BW069	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	181,5	56,5	/	67,5	/
BW070	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	142	47	24	53	38
BW073	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	122	56	28	30	/
BW074	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	140	43,5	25	48	32
BW075	Ropolo	<i>D. bedouliensis</i>	/	[?M]	<i>Le Bridagan</i>	60	131	66	/	25	/
BW053	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 5, fig. 2)	[?M]	<i>Le Bridagan</i>	60	160	/	27	/	44
BW054	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 8, fig. 1)	[?M]	<i>Le Bridagan</i>	60	162	52	26,5	58	35
BW055	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 7, fig. 1)	[?M]	<i>Le Bridagan</i>	60	179	58	35	60	38
BW057	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 3, fig. 1)	[?M]	<i>Le Bridagan</i>	60	168	51,5	26	/	/
BW058	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 1, fig. 1)	[?M]	<i>Le Bridagan</i>	60	168	57	/	54,5	
BW062	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 4)	[?M]	<i>Le Bridagan</i>	60	205	/	/	/	/
BW063	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 6, fig. 1)	[?M]	<i>Le Bridagan</i>	60	178	61,5	30	58	38
BW066	Ropolo	<i>D. aff. consobrinus</i>	Ropolo et al. (2006, pl. 3, fig. 1)	[?M]	<i>Le Bridagan</i>	60	200	/	/	/	/
BW071	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 5, fig. 1)	[?M]	<i>Le Bridagan</i>	60	114	51,5	24	24	50
BW112	Ropolo	<i>D. bedouliensis</i>	Ropolo et al. (2006, pl. 2, fig. 1)	[?M]	<i>Le Bridagan</i>	60	268	86	/	112	/
BW270	Ropolo	<i>D. bedouliensis</i>	Ropolo et al. (2006, pl. 3, fig. 2)	[?M]	<i>Le Bridagan</i>	60	112	55	/	24,9	36
RG1456	Gonnet	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 2)	[?M]	<i>Le Bridagan</i>	60	225	/	/	/	/
BW021	Ropolo	<i>D. bedouliensis</i>	Ropolo et al. (2006, pl. 2, fig. 2)	[?M]	<i>Le Bridagan</i>	60	68	/	/	/	/
BW006	Ropolo	<i>D. bedouliensis</i>	Cecca et al. (1999, pl. 3, fig. 2)	[?M]	<i>Le Bridagan</i>	60	114,5	53	22	27,5	38

Table 6. Dimensions of *Deshayesites oglanlensis* Bogdanova, 1983.

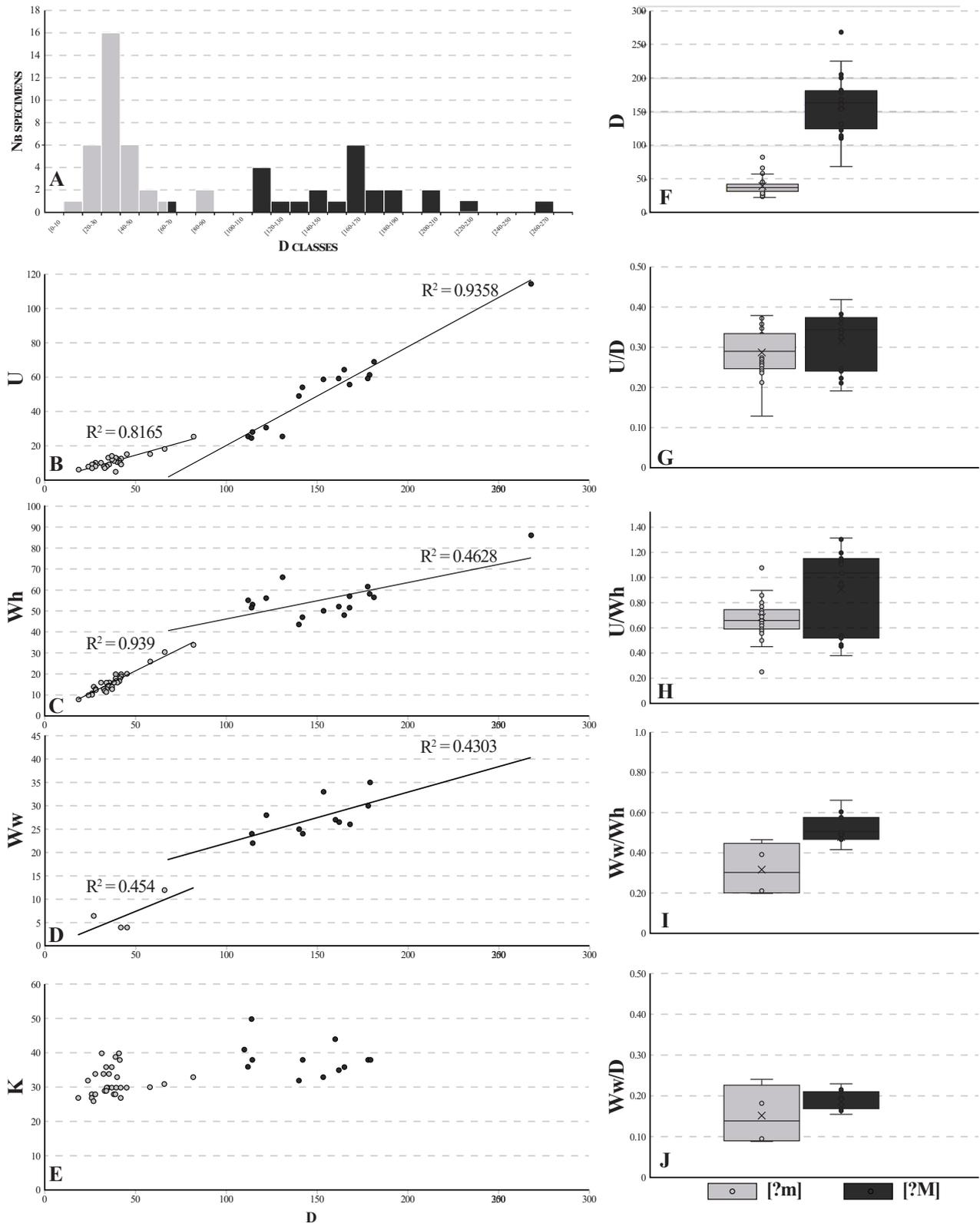


Fig. 18 - Selected morphometrics of *Deshayesites oglanlensis* Bogdanova, 1983 from Cassis. **A**: Histogram frequency of diameter of the studied simple showing a rather bimodal pattern; **B-E**: Bivariate diagrams of the conch parameters (**B**) U, (**C**) Wh, (**D**) Ww, and (**E**) Rv in function of D; **F-J**: Box plots of shell shape ratios (**F**) D, (**G**) U/D, (**H**) U/Wh, (**I**) Ww/Wh, and (**J**) Ww/D. The boxes represent the interquartile range (i.e., the values ranging from the first to third quartiles, which are the 25th and 75th percentiles, respectively), the median value (black line), the extended interquartile range (whiskers) and the eventual outliers (isolated dots).

its surroundings. Its evolution in the lower Aptian remains to be studied, but it is likely of short stratigraphic range since the species is only reported up to bed 64 according to Ropolo *et al.* (2006).

Besides southern France (Vocontian and South Provence basins), the species *Deshayesites oglanlensis* is recorded in Spain, Romania, Bulgaria, Iran, and Turkmenistan, its type locality (Klein & Bogdanova, 2013).

Family Desmoceratidae Zittel, 1895

Genus *Pseudohaploceras* Hyatt, 1900

Type species: *Ammonites liptoviensis* Zeuschner, 1856; by original designation.

Remarks: The genus *Pseudohaploceras* is rare in the Barremian/Aptian boundary interval at Cassis, but increases in abundance during the mid-early Aptian (Frau, own data). There is no comprehensive revision of the species *Pseudohaploceras matheroni* (d'Orbigny, 1841), whose holotype comes from an unknown level of the study area. We figure for the first time a *Pseudohaploceras* individual from the upper Barremian beds of Cassis. It is tentatively assigned to *Pseudohaploceras liptoviense* (Zeuschner, 1856).

Pseudohaploceras cf. liptoviense (Zeuschner, 1856)

Fig. 11C-E

Type:

1856. *Ammonites liptoviensis* Zeuschner, p. 181, pl. II, fig. 1a-c, 2a-b, 3a-b

Local synonymy: None.

Type: The lectotype designed by Vašíček (1972) is the specimen figured by Zeuschner (1856, pl. 2, fig. 1). According to Vašíček (1972) and Baudouin *et al.* (2012), it is lost and could have been destroyed during the WWII. None neotype has been yet designed.

Material: Specimen MPP.12.889/AB.30 from the Ropolo collection (Fig. 11C-E). It derives from *Le Brigadan*.

Dimensions: See Table 7.

Description: Specimen AB.30 is a medium-sized complete sub-desmoceratid individual, which is slightly deformed.

The coiling is seemingly subvirgacone with a sub-rounded whorl section, wider than high on the last preserved whorl, and slightly rounded flanks and venter. The umbilical wall is steep and slightly incurved with rounded margin. The ornamentation is rather erased but conform to that of *Pseudohaploceras*, marked by distinctive constrictions bordered by enlarged slightly sigmoid ribs, and variable number of intercalatories sometimes fasciculate on the primaries.

Discussion: The specimen at our disposal conforms to the diagnosis of *Pseudohaploceras liptoviense* given by Baudouin *et al.* (2012, p. 627) based on specimens from the Vocontian Basin, but its defective preservation of ribbing prevents further comparison. According to Baudouin *et al.* (2012), the species *Pseudohaploceras matheroni* is contemporaneous to that species, but differs by a more rounded whorl section, and a more rigid and less sigmoidal ribbing.

Occurrence: The specimen is said to originate from bed 74 of the *Le Brigadan* section (Ropolo, *in coll.*). Correlation with the type succession remains unclear, but this level may fall in bed interval 51 to 55 (Fig. 3).

Besides southern France (Vocontian and South Provence basins), the species *Pseudohaploceras liptoviense* has records in Spain, Georgia, Czech Republic, Slovakia, Romania, and most probably in Switzerland, Germany and the Caucasus (Baudouin *et al.*, 2012).

Family Barremitidae Breskovski, 1977

Genus *Barremites* Kilian, 1913

Type species: *Ammonites difficilis* d'Orbigny, 1841; by original designation.

Remarks: There is evidences of a *Barremites* lineage including *Barremites difficilis* (d'Orbigny, 184) → *Barremites hemiptychus* (Kilian, 1888) → *Barremites strettostoma* (Uhlig, 1883) during the latest Barremian (Busnardo *in* Gauthier *et al.*, 2006; Baudouin *et al.*, 2012). According to Avram (1997), *Barremites strettostoma* differs from the two other taxa by a discoid-compressed shell with narrow umbilicus, angular umbilical shoulder, flat subparallel sides in their inner half and convergent-depressed in their outer half, falcooid constrictions, bounded adapically in the depression area by short, crescent-shaped ribs, somewhere with irregular crescent-shaped riblets in between, suture line with wide and very dissymmetric

Collection number	Collection	Original ID	Illustration	Locality	Beds	D	U	Wh	Ww
AB.30	Ropolo	/	/	<i>Le Brigadan</i>	74	88,7	28,5	8,6	37

Table 7. Dimensions of *Pseudohaploceras cf. liptoviense* (Zeuschner, 1856).

Collection number	Collection	Original ID	Illustration	Locality	Beds	D	U	Wh	Ww
FSL.105083	Busnardo	<i>B. strettostoma</i>	/	Station de Cassis	50	43	8	21,7	/

Table 8. Dimensions of *Barremites* sp.

first lateral lobe. Avram (1997) introduced the genus *Barremitites* based on the Uhlig's species to group these forms.

A few barremitid ammonites from Cassis have been assigned to *Barremitites strettostoma* by Ropolo *et al.* (1999, 2000a). Those barremitids are small in size, heavily crushed and rare at the Barremian/Aptian boundary. Pending more material to be collected, they are here referred to as *Barremites* sp.

Barremites* sp.*Fig. 11F****Local synonymy:**

1999. *Barremites strettostoma* (Uhlig) – Ropolo *et al.*, pl. 12, fig. 3, 4
 2000a. *Barremites strettostoma* (Uhlig) - Ropolo *et al.*, pl. 3, fig. 3; pl. 9, fig. 3 (= Ropolo *et al.*, 1999, pl. 12, fig. 3, 4)

Material: Besides the figured Ropolo's forms, we add specimen FSL.105083 (**Fig. 11F**) from the Busnardo collection.

Dimensions: See **Table 8**.

Description: Small-sized, involute barremitid ammonite marked by an apparent compressed section, narrow umbilicus, and steep umbilical wall with angular margin. The ventral area seems to be narrow and rounded. The ornamentation of the phragmocone is smooth. The body chamber occupies the last whorl. It bears few indistinct falcoid primary ribs on the outer flanks. The aperture is not preserved.

Discussion: The specimen FSL.105083 and the other ones illustrated by Ropolo *et al.*, (1999, 2000a) has U/D ratio values close to *Barremites strettostoma* but the species can be distinguished by distinct sigmoidal constrictions at the same growth stage (compare with Avram, 1997, pl. 24.II).

The rather smooth ornamentation of the Cassis specimens better compare to *Barremites hemiptychus* but there is no the irregularly spaced falcoid ribs, between whom dense fine lirae occur, in the outer whorl that are typical of that species (Baudouin *et al.*, 2012).

Note finally that the Cassis individuals are represented by small-sized forms. Larger ones are missing, and their specific identification thus remains unclear.

Occurrence: The Busnardo's specimen of *Barremites* sp. originates from bed 50 of the *Station de Cassis* section, but closely similar forms occur sporadically throughout the uppermost Barremian and lowermost Aptian (Frau, own data).

The two specimens of Ropolo *et al.* (1999, 2000a) are reported from beds 76 and 79 of the *Les Caniers/Les Sardons* section. If this should prove correct, these beds fall in the top of the *Pseudocrioceras*-bearing beds (= ? beds 56 and 59 of the type succession).

3.3. Nautiloidea**Family Cenoceratidae Tintant & Kabamba, 1983****Genus *Heminautilus* Spath, 1927**

Type species: *Nautilus saxbii* Morris, 1848;
by original designation.

Remarks: The peculiar nautiloid *Heminautilus* is rare at the Barremian/Aptian boundary at Cassis, but increases in abundance during the mid-early Aptian (Baudouin *et al.*, 2016). Only a single specimen from the upper Barremian beds has been yet illustrated and identified to as *Heminautilus sanctaerucis* Conte, 1980.

Heminautilus sanctaerucis* Conte, 1980*Fig. 16E-F****Type:**

1980. *Heminautilus sanctaerucis* Conte, p. 138, pl. 1, fig. 1-2, 4a

Local synonymy:

2016. *Heminautilus sanctaerucis* Conte - Baudouin *et al.*, p. 72, pl. 12, fig. 2 (ventral view); pl. 13, fig. 1a-b (lateral views of the same specimen)

Type: The holotype designed by Conte (1980, pl. 1, fig. 1-2) is specimen MCGL.20747 (Pictet collection) from Sainte-Croix, Switzerland.

Material: Specimen MPP.BW.599 (**Fig. 16E-F**) from the Gonnet collection. It derives from *Les Caniers*.

Dimensions: See **table 9**.

Description: The reader is referred to Baudouin *et al.* (2016, p. 72) for a detailed description of this specimen.

Discussion: The only known specimen of *Heminautilus sanctaerucis* from Cassis conforms well to the description of that species given by Baudouin *et al.* (2016, p. 72).

Occurrence: The specimen is from bed 78 of *Les Caniers* (Baudouin *et al.*, 2016). Correlation with the type succession remains unclear, but this bed merely falls in bed interval 57-58 (Fig. 3).

Besides southern France, the species *Heminautilus sanctaerucis* has records in Bulgaria and Hungary (Baudouin *et al.*, 2016).

Family Nautilidae de Blainville, 1825

Genus *Cymatoceras* Hyatt, 1884

Type species: *Nautilus pseudoelegans* d'Orbigny, 1840; by original designation.

Remarks: The genus *Cymatoceras* is abundant in the South Provence Basin, but it, unfortunately, does not yet exist a comprehensive study of its members.

Cymatoceras neocomiense (d'Orbigny, 1840)

Fig. 17C-D

Type:

1840. *Nautilus neocomiensis* d'Orbigny, p. 74, pl. 11, fig. 1-3

2006. *Cymatoceras neocomiense* (d'Orbigny) - Tintant & Gauthier in Gauthier *et al.*, p. 20, pl. 2, fig. 3-4).

Local synonymy: None.

Type: The lectotype designed by Tintant & Gauthier in Gauthier *et al.* (2006, pl. 2, fig. 3, 4) is specimen MNHN.F.R04249 (d'Orbigny collection) from Escragnolles, Alpes-Maritimes, France.

Material: Specimen FSL.105048 (Fig. 17C-D) from the Busnardo collection, *Station de Cassis*.

Dimensions: None.

Description: Specimen FSL.105048 is a chambered nautiloid fragment with a sub-circular whorl section and distinctly rounded flanks and venter. The ornamentation is composed of simple ribs starting at the umbilical margin and increasing in thickness on the venter. They are slightly

flexuous on the flanks and form a slight rounded chevron on the venter. The suture line is slightly flexuous and concave on the flanks.

Discussion: The Busnardo's specimen conforms well to the definition of the species given by Delanoy *et al.* (2012), to which the reader is referred.

Occurrence: The specimen originates from bed 44 of the *Station de Cassis* section. This is the lowermost occurrence ever recorded, but it is worth noting that the species ranges throughout the uppermost Barremian and Aptian at Cassis (Frau, own data).

Besides southern France, the species *Cymatoceras neocomiense* has records in Algeria, Switzerland, Germany, Czech Republic, Bulgaria, Crimea, Turkmenistan and the Caucasus (Delanoy *et al.*, 2012).

4. Stratigraphic implications

The Ammonoidea and Nautiloidea species found at the *Station de Cassis* section, and the lateral equivalent outcrops, are here revised. The species distribution is here synthesised for the first time (Fig. 19).

The *Pseudocrioceras*-bearing beds were first referred to as the *Pseudocrioceras coquandi* Zone by Busnardo (1984) and placed between *Prodeshayesites*- and *Deshayesites*-bearing beds. The author assigned an early Aptian age to his *Pseudocrioceras coquandi* Zone (Fig. 20A), since the base of the Aptian was fixed at the FO of *Prodeshayesites* at that time (Birkelund *et al.*, 1984). It is actually clear that Busnardo (1984) mixed up his *Prodeshayesites* material with the Heteroceratidae *Martelites* (e.g., Delanoy *et al.*, 1997; Ropolo & Gonnet, 1998; Cecca *et al.*, 1999, 2000; Ropolo *et al.*, 1999, 2000a-b). The genus *Martelites* has long been retained as marker of the top Barremian (i.e., *Martelites sarasini* Zone) in the SMAS (Reboulet *et al.*, 2006, 2009, 2011, 2014, 2018). As such, the *Pseudocrioceras*-bearing beds should be regarded as the interval between *Martelites*- and *Deshayesites*-bearing beds (Fig. 20B); a similar pattern of distribution to that observed in the Caucasus and referred to as the *Pseudocrioceras waagenoides* Horizon by Kakabadze & Kotetishvili (1995).

Following the Georgian authors, Ropolo *et al.* (1999, 2000a-b, 2006, 2008) promoted the use of a *Pseudocrioceras waageni* Subzone (Ropolo & Gonnet, 1998; Ropolo *et al.*, 1999, 2000a-b) or a *Pseudocrioceras waagenoides* Subzone (Ropolo *et al.*, 2006, 2008) for characterising the top of the *Martelites sarasini* Zone at

Collection numbers	Collection	Original ID	Illustration	Localities	Beds	D	Wh	Ww	U
BW.599	Ropolo	<i>H. sanctaerucis</i>	Baudouin <i>et al.</i> (2016, pl. XII, fig. 2; pl. XIII, fig. 1)	Les Caniers/ Les Sardons	78	126.1	72.4	/	/

Table 9. Dimensions of *Heminautilus sanctaerucis* Conte, 1980.

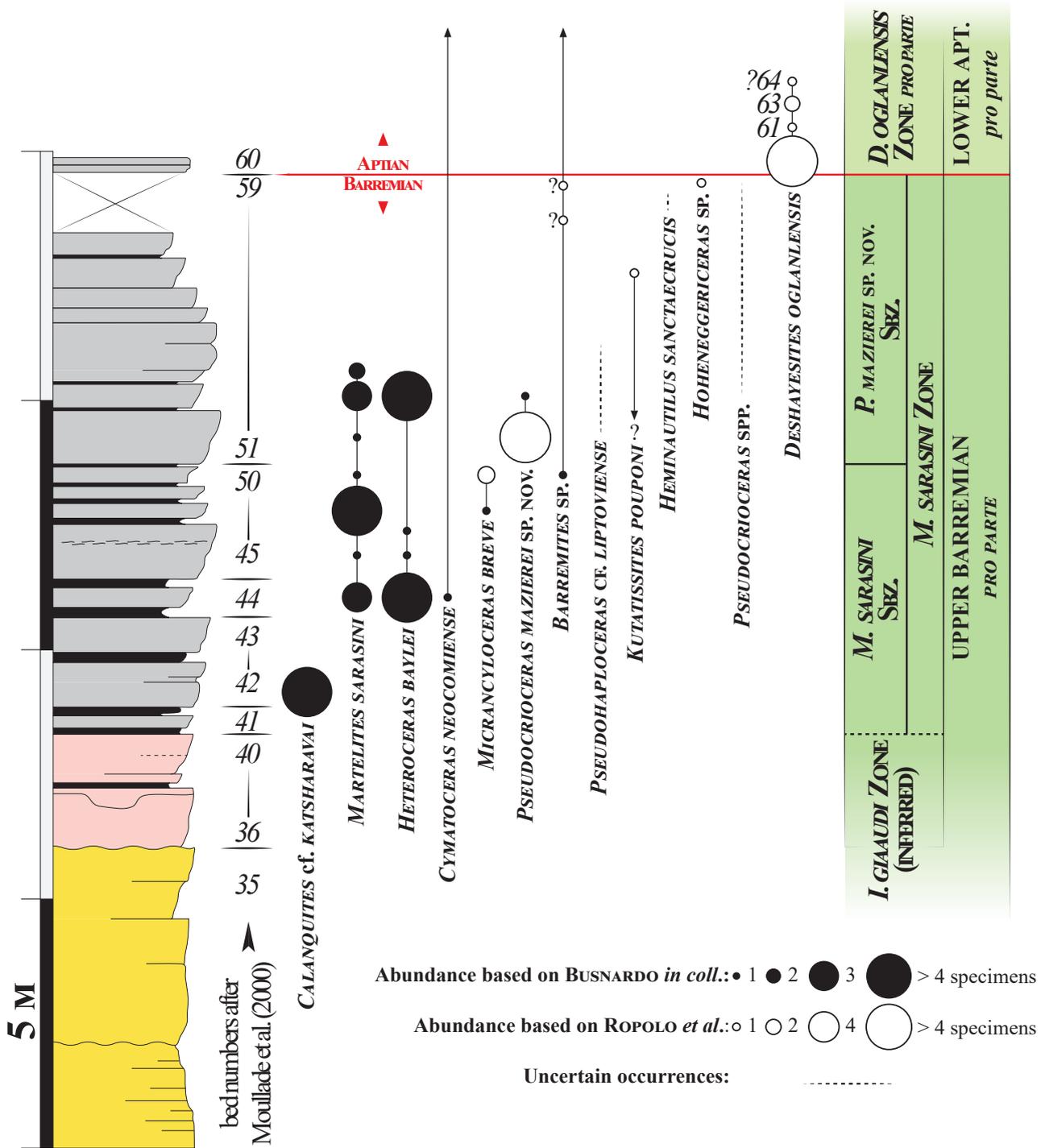


Fig. 19 - Stratigraphic distribution of the Ammonoidea and Nautiloidea species at the *Station de Cassis* section and its surrounding based on the collection of R. Busnardo, and the works of P. Ropolo *et al.* (op. cit.). The newly proposed zonation for the Barremian/Aptian boundary interval is indicated on the right. The base of the *Martelites sarasini* Zone remains unclear (see discussed in text). Facies colour legend follows **Fig. 2**. The stratigraphic range of the many *Pseudocrioceras* species is represented by a dashed lines pending new investigations.

Cassis. This subzone was fixed between beds 45 and 59 at the *Station de Cassis* section. Finally, the *Pseudocrioceras waagenoides* Subzone was introduced and maintained in the SMAS up to now (Reboulet *et al.*, 2006-2018).

Apart from the spelling error on the species name, our understanding of the index species *Pseudocrioceras*

waagenoides at Cassis is actually based on only two specimens; namely RG.1468 (Ropolo & Gonnet, 1998, pl. 5, fig. 2) and PR.573 (or PR.671?) (Ropolo *et al.*, 1999, pl. 11, fig. 1; = Ropolo *et al.*, 2000a, pl. 10, fig. 1). From our point of view, specimen RG.1468 better compares *Pseudocrioceras coquandi* (Matheron, 1878) and

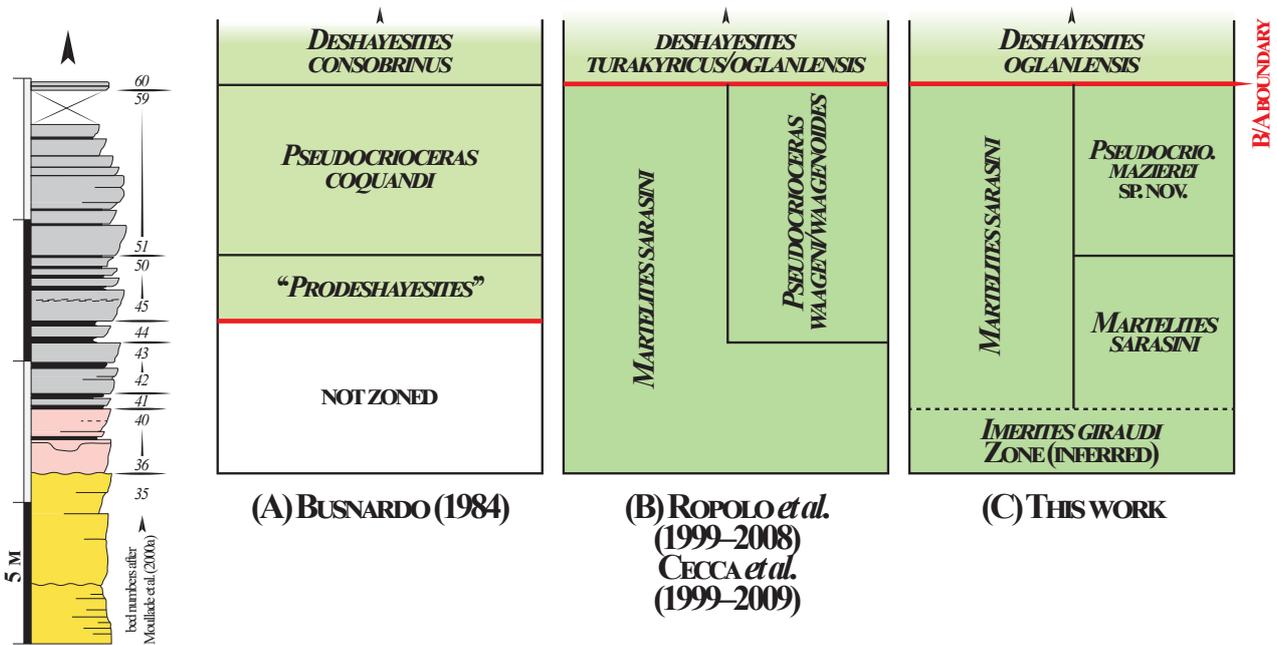


Fig. 20 - Evolution of the ammonite scales from around the Barremian/Aptian boundary at the *Station de Cassis* section, as proposed by (A) Busnardo (1984), (B) Ropolo *et al.* (1999–2008) and Cecca *et al.* (1999–2000), and (C) This work. The base of the *Martelites sarasini* Zone remains unclear (see discussed in text). We here propose the dumping of the *Pseudocrioceras waagenoides* Subzone *sensu* Ropolo *et al.* (op. cit.) and its replacement by the *Pseudocrioceras mazierei* sp. nov. Subzone for characterising the upper *Martelites sarasini* Zone. The position of the Barremian/Aptian boundary follows the current definition of the IUGS Lower Cretaceous Ammonite Working Group fixed at the first occurrence of the Deshayesitidae *Deshayesites oglanlensis* (Reboulet *et al.*, 2006–2018).

Pseudocrioceras provinciale (Matheron, 1878) since it can be seen a strong bituberculate stage on the proversum, with complex secondary ribbing typical of that to this species group, while specimen PR.573/671 has greater affinity with tripartite *Kutatissites* (see discussion above). The record of *Pseudocrioceras waagenioides* at Cassis should be, therefore, regarded with caution.

Furthermore, it was so far assumed that the total range of the genera *Martelites* and *Pseudocrioceras* are ordered in time at Cassis (Ropolo *et al.*, 1999, 2000a-b). However, our re-examination of the Busnardo's collection documents an overlap between beds 51 and 54 at the *Station de Cassis* section (Fig. 19). Also, we suggest that *Micrancycloceras* and *Pseudocrioceras* merely form a direct lineage. Divergence between these two genera is to be found in beds 49-50. There is no evidence that *Pseudocrioceras* could occur below these beds at Cassis.

All taken together, the use of *Pseudocrioceras waagenioides* as a marker of a total range zone is problematic. By contrast, the species *Pseudocrioceras mazierei* sp. nov. is the oldest *Pseudocrioceras* found at Cassis. The species is abundant, occurs in short stratigraphic interval, and can be easily identified. The species further forms the rootstock from which all other southern France *Pseudocrioceras* have evolved (Ropolo & Gonnet, 1998; Ropolo *et al.*, 1999, 2000a). We thus here propose the dumping of the *Pseudocrioceras waagenioides* Subzone

and its replacement by a *Pseudocrioceras mazierei* Subzone (Fig. 20C). Its base is fixed at the FO of the new nominative species (i.e., bed 51), and its top is constrained by the FO of *D. oglanlensis* (i.e., bed 60) which is actually taken as the marker of the Aptian base at the *Station de Cassis* section, and more generally in the SMAS (op. cit.).

5. Conclusions

Following the opening of the South Provence Basin, both Ammonoidea and Nautiloidea settle at the same time and spread through the Barremian/Aptian boundary interval. Notwithstanding their abundance and continuous distribution, their taxonomy remains poorly resolved. This is due to a lack of comprehensive systematic disputes and accurate stratigraphic occurrence for many taxa, deficient iconography, and low resolution of published lithologs. Re-examination of the Busnardo collection made at the *Station de Cassis* section brings new light on the specific diagnosis, ontogeny, and potential dimorphism of diverse taxa from this key area. New data is provided on the overlooked stratigraphic overlap of *Martelites* and *Pseudocrioceras* species. This supports the rejection of a *Pseudocrioceras waagenioides* Subzone as part of the SMAS, and its replacement by the *Pseudocrioceras mazierei* sp. nov. Subzone for characterising the uppermost Barremian (upper *Martelites sarasini* Zone).

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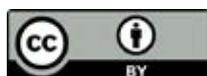
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