# A new insight into the lower Aptian Roloboceratinae Casey, 1961 (Douvilleiceratidae, Ammonoidea) from southern France

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**Abstract.** The present paper presents a new insight into the ammonite subfamily Roloboceratinae (Family Douvilleiceratidae) from the lower Aptian – former 'Bédoulien' – unit-stratotype area of Cassis–Roquefort-la-Bédoule, Bouches-du-Rhône, southern France. Additional material comes from a nearby locality of Martigues, called *Gueule d'Enfer*. Our bed-by-bed collection documents the occurrence of the Roloboceratinae *Roloboceras hambrovi*, *Roloboceras* aff. *hambrovi* and *Megatyloceras* cf. *coronatum* in the lower part of the Marly Calcareous Member. Their stratigraphic distribution is correlated with major trends in the carbon-isotope curve resulting from the mid-early Aptian Oceanic Anoxic Event 1a. This allows comparison with the Roloboceratinae record from SE France and to question their reliability as reliable biological markers.

**Keywords:** Roloboceratinae; Ammonoidea; Aptian; OAE 1a; Tethys; France.

**Un éclairage nouveau sur la sous-famille des Roloboceratinae (Douvilleiceratidae, Ammonoidea) du Sud de la France**

**Résumé :** Le présent travail apporte un éclairage nouveau sur la sous-famille des Roloboceratinae (Famille Douvilleiceratidae) de l'aire stratotypique de l'Aptien inférieur – anciennement 'Bédoulien' – situé à Cassis–Roquefort-la-Bédoule, Bouches-du-Rhône, Sud-Est de la France. Du matériel supplémentaire provient d'une localité voisine des environs de Martigues, nommée *Gueule d'Enfer*. Notre récolte banc-à-banc documente la présence des Roloboceratinae *Roloboceras hambrovi*, *Roloboceras* aff. *hambrovi* et *Megatyloceras* cf. *coronatum* dans la partie inférieure du Membre Marno-Calcaire. Leur distribution stratigraphique est corrélée avec les grandes tendances de la courbe isotopique du carbone résultant de l'Evènement Océanique Anoxique 1a daté de l'Aptien inférieur moyen. Cette démarche permet non seulement une comparaison des occurrences de Roloboceratinae du Sud-Est de la France, mais aussi de questionner leur fiabilité en tant que marqueurs biologiques.

**Mots-clés :** Roloboceratinae ; Ammonoidea ; Aptien ; OAE 1a ; Téthys ; France.

## 1. Introduction

The ammonite-rich sedimentary series cropping out north of the Cassis railway station (Bouches-du-Rhône, southern France) consists of the unit-stratotype of the 'Étage Bédoulien' (Toucas, 1888). This series was deposited in the narrow intra-shelf South Provence Basin located on northwestern margin of the Mediterranean Tethys (**Fig. 1A-B**). The 'Bédoulien' has long been identified as the lower portion in the tripartite division of the Aptian Stage (e.g., Fabre-Taxy *et al.,* 1965), but for now, the term should be abandoned according to the IUGS Lower Cretaceous Ammonite Working Group, and the stage is preferentially divided into two parts – lower and upper – in the current Standard Mediterranean Ammonite Scale (SMAS of Reboulet *et al.*, 2011, 2018).

The first data on the lower Aptian ammonites from the South Provence Basin were notably provided by Roch (1927), Conte (1975), Fabre-Taxy *et al.* (1965), Busnardo (1984), Cecca *et al.* (1999), Ropolo *et al*. (1999, 2000a-b,

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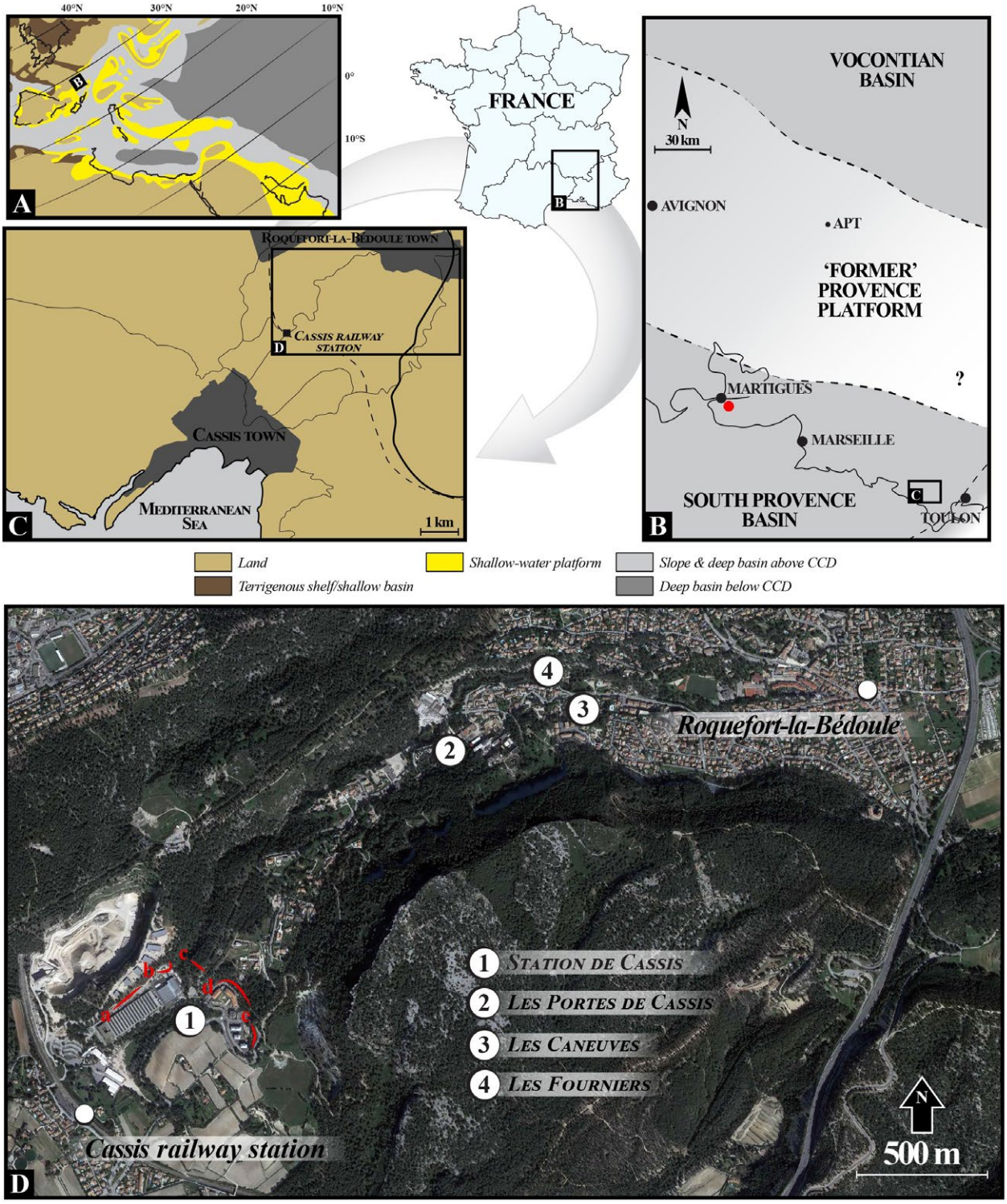



**Fig. 1 – A:** Barremian–Aptian (palaeo-) geography of the Mediterranean Tethys (modified after Tendil *et al.,* 2018, and references therein). Position of Fig. 1B is noted; **B:** Lower Aptian palaeogeography reconstruction of southeastern France showing the position of the Vocontian and South Provence basins, separated by the 'former' Provence platform. Position of Fig. 1C is noted. The locality of *Gueule d'Enfer* (city of Martigues) is indicated by a red circle; **C:** Location of the *Station de Cassis* section, located halfway between Cassis and Roquefort-la-Bédoule, Bouches-du-Rhône, southern France. Position of Fig. 1D is noted; **D:** Location of the *Station de Cassis* section and the surrounding localities cited in the text (*Les Portes de Cassis*, *Les Caneuves*, and *Les Fourniers*).

2006, 2008a-b, 2009a-b), to which can be added the subsequent contributions of Frau *et al*. (2015, 2016, 2017, 2018a-c), and Frau & Delanoy (2022). A brief look at those papers identifies a patchy ammonite record, especially regarding deshayesitid taxa, during the mid-early Aptian (see for example Ropolo *et al*., 2000a, fig. 3; 2008b, fig. 3). The cause of this decline remains unclear but links with the palaeoceanographic disturbances of the so-called Ocean Anoxic Event (OAE) 1a, that is recorded worldwide at that time, cannot be excluded (Frau, 2020). However, there is no sedimentological and geochemical evidences of anoxic deposits in the 'Bédoulien' sedimentary succession (Stein *et al.,* 2012), and the OAE 1a is here only reflected by the typical prominent negative carbon isotope excursion followed by a rapid increase of values and a long plateau (Kuhnt *et al*., 2000; Stein *et al.*, 2012).

Of interest is the record of rare roloboceratid ammonites during this carbon anomaly (Ropolo *et al*., 2006, 2008a-b, 2009a-b). This includes the two genera of the subfamily Roloboceratinae Casey, 1961; namely *Roloboceras* Casey, 1954 (Type species *Roloboceras hambrovi* Forbes, 1845) and *Megatyloceras* Humphrey, 1949 (Type species *Megatyloceras coronatum* Rouchadzé, 1933). These Roloboceratinae were previously identified by Roch (1927) and Busnardo (1984) and the latter author himself considered that they should typify a stratigraphic unit labelled to as the *Roloboceras hambrovi* Zone; being between beds 148 and 160 of the 'Bédoulien' sedimentary succession (**Fig. 2A**).

The life habit of Roloboceratinae on slopes or marginal basins of the Tethys was first mentioned by Ropolo *et al.* (2008b) to explain the supposed diachrony between the Roloboceratinae-bearing beds of the 'Bédoulien' unit-stratotype with those of the Great Britain, Ardèche (southern France), and Spain. However, many ammonite determinations of Ropolo and collaborators do not stand up well when comparisons and verification are attempted between the different deshayesitid assemblages (e.g., Moreno-Bedmar *et al*., 2008, 2009, 2010, 2012; Frau *et al.,* 2015, 2017; Delanoy *et al.,* 2022). The stratigraphic position of those Roloboceratinae-bearing beds has been subsequently much debated by ammonite specialists and their placement as a subzone in the upper part of the *Deshayesites forbesi* Zone or the *Deshayesites deshayesi* Zone is still an open question even in the SMAS (e.g., compare Reboulet *et al.*, 2011, 2014, 2018). Conflicting views regarding the definition of the two index species *Deshayesites forbesi* and *Deshayesites deshayesi* unfortunately persist among the ammonite specialist community (Bersac & Bert, 2012, 2015), and this prevents a consensus to emerge.

Bed-by-bed collection made by the first author (CF), and re-examination of historical collections, enable us to update the Roloboceratinae record from the 'Bédoulien' unit-stratotype. This is compared to the local carbon-isotope chemostratigraphy; a tool allowing long-distance correlation and examination of the Roloboceratinae as reliable stratigraphic markers.

## 2. Geological setting

Majority of the collected Roloboceratinae originates from the *Station de Cassis* section (or Comte Quarry *in litt*.), located in the vicinity of the Cassis railway station (**Fig. 1B-C**). This area contains five outcrops – labelled *a*, *b*, *c*, *d, e* – forming the composite 'Bédoulien'-type sedimentary succession of Moullade *et al.* (2000) (**Fig. 1D**). These outcrops encompass the Calcareous Mb. (Outcrops *a*, *b*, *c*) and Marly Calcareous Mb. (Outcrop *d, e*) of Moullade *et al*. (2000). A revised distribution of the Roloboceratinae from outcrop *d* is here provided (**Fig. 2A**).

Another studied locality is *Les Caneuves*, located ~ 1 km north of the Cassis railway station (**Fig. 1D**). Urbanisation works in the year 2016 opened a superb outcrop at the transition between the Calcareous and Marly Calcareous members (**Fig. 2B** and **3**). This allowed detailed examination of the "*discontinuité intra-bédoulienne*" of Moullade *et al.* (2000) marking a clear boundary between the two corresponding members, although a set of minor syn-sedimentary faults occur. This discontinuity correlates to base of bed 129 of the *Station de Cassi*s section (**Fig. 2B**). A few Roloboceratinae individuals were found just above this discontinuity at *Les Caneuves*.

Finally, the locality of *Gueule d'Enfer*, in the vicinity of Martigues, has provided a single Roloboceratinae individual that is actually housed at the Musée des Amis de Castrum Vetus, Châteauneuf-les-Martigues, France. This locality crops out in the northern limb of the Nerthe Massif, located ~ 45 km east of Cassis (**Fig. 1B**). This locality is currently under investigation and its description is out of the scope the paper. But it is worth noting that the Aptian sedimentary succession from the Nerthe Massif shows great similarities with that of the *Station de Cassis* section and its surroundings (Frau *et al*., 2018a-b; Tendil *et al.,* 2018).

## 3. Conventions

Our study is based on specimens collected *in situ* by the first author (C.F.). Specimens of the Frau collection are being deposited at the Muséum d'Histoire naturelle d'Aix-en-Provence. We also re-examined the material collected by:

- Robert Busnardo deposited at the Geological Collections of the Université Claude Bernard-Lyon-I (UCBL-FSL).
- Gabriel Conte and Pierre Ropolo deposited at the Muséum de Paléontologie de Provence (MPP), Aix-Marseille Université.
- Maurice Dérognat deposited at the Université Joseph Fourier – Institut Dolomieu (UJF-ID).

- The unlabelled collection of the Musée des Amis de Castrum Vetus (MACV).

Bed numbering of the 'Bédoulien'-type sedimentary succession follows Moullade *et al.* (2000). The synonymy lists are limited to the figured individuals from the 'Bédoulien' unit stratotype including those of Roch (1927), Conte (1975), Ropolo *et al*. (2006, 2008a-b, 2009a-b). The reader is referred to the work of Delanoy *et al.* (2022) for complete synonymy lists.

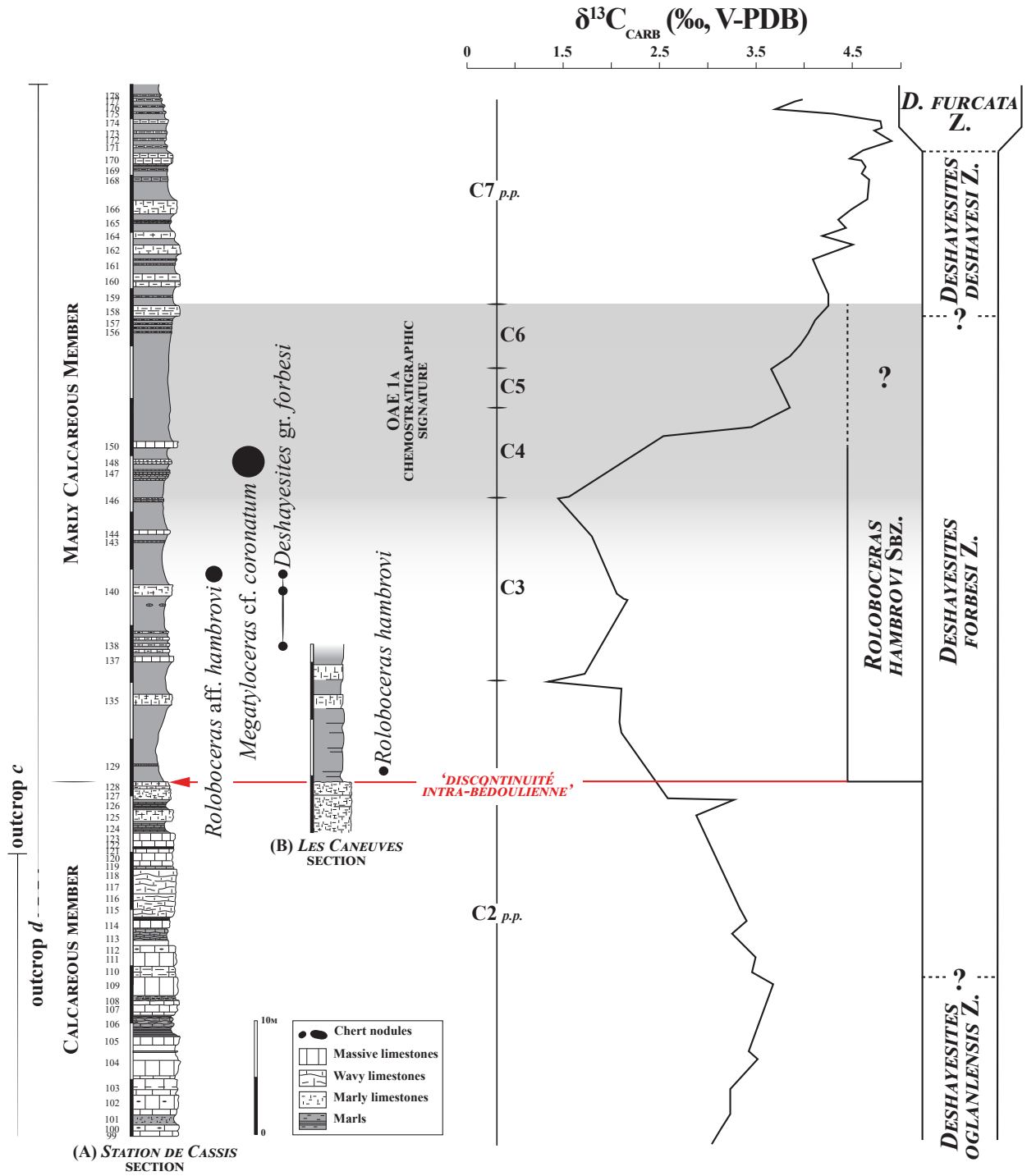



**Fig. 2 – A:** Litho-log of *Station de Cassis* (modified from Moullade *et al.,* 2000); **B:** litho-log of *Les Caneuves* (this work) with distribution of the collected roloboceratid and deshayesitid species.
The lithostratigraphy of Moullade *et al.* (2000), and the position of the "*discontinuité intra-bédoulienne*" (red line) is noted. Correlation to the lower Aptian ammonite biozonation *pro parte* of Frau *et al*. (2015) is given. Comparison with the carbon-isotope curve ($\delta^{13}C_{carb}$) of Kuhnt *et al.* (2000) is added together with indication of the Menegatti's segments (C2 to C7 *pro parte*) as interpreted by Frau (2020).

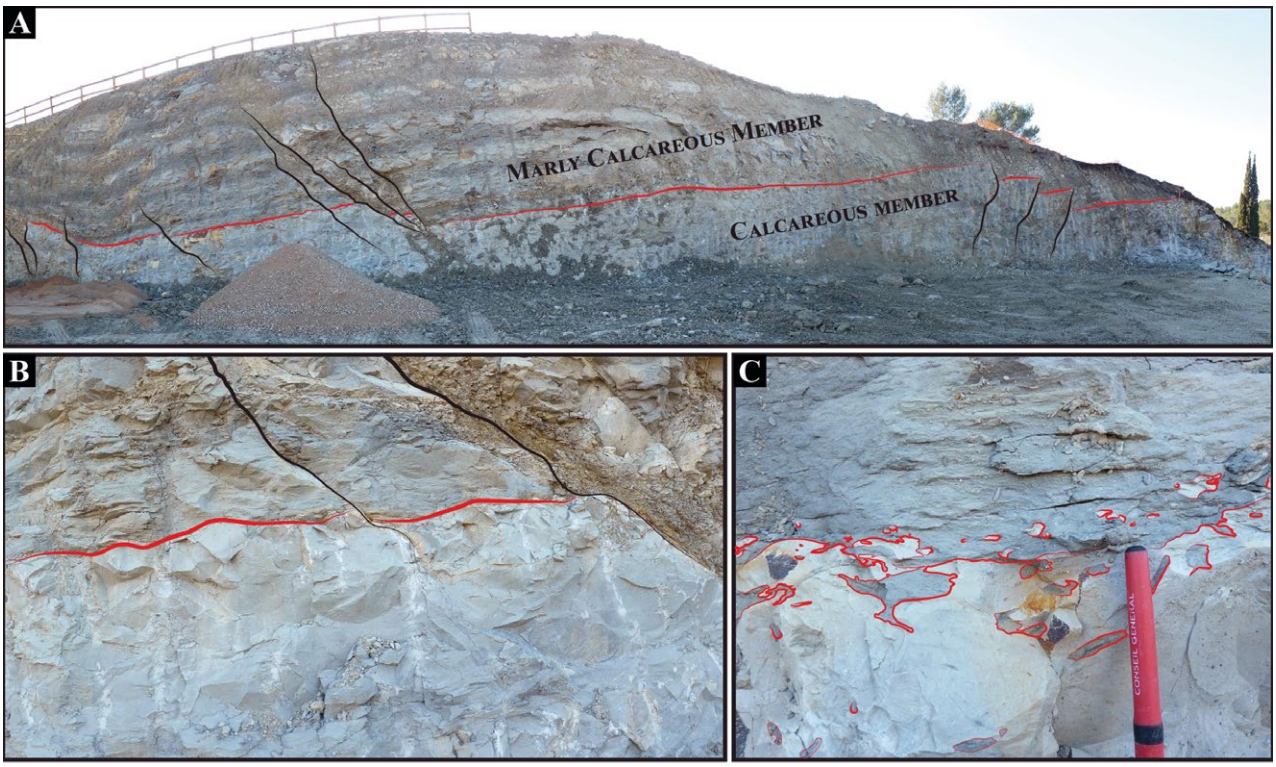



**Fig. 3 –** Panoramic views of the *Les Caneuves* section during urbanisation work in the year 2016. **A:** Wide field panoramic photography of the main outcrop showing transition between the Calcareous and Marly Calcareous members, separated by the "*discontinuité intra-bédoulienne*" of Moullade *et al*. (2000). Note the synsedimentary faulting (black lines). **B and C:** Close-up views on this discontinuity related to a major deepening event (Renard & De Rafaélis, 2000).

In the paleontological description, shell shape and coiling terminology follows Klug *et al.* (2015). Measurements of dimensional characters were possible only on a few individuals due to the poor state of preservation resulting from incompleteness, crushing, and distortion. The following abbreviations indicate: D: total diameter; U: umbilical width; Wh: whorl height; Ww: whorl wight. All dimensions are given in millimetres.

In the following, the use of the *Roloboceras hambrovi* Subzone complies with the definition of Frau *et al*. (2017) including the succeeding stratigraphic ranges of the genera *Roloboceras* and *Megatyloceras*. This is correlated to the Menegatti's carbon-isotope segments of the local $\delta^{13}C_{carb}$ curve previously published by Kuhnt *et al.* (2000), and revised by Frau (2020).

## 4. Systematic palaeontology

**Order Ammonoidea Zittel, 1884**
**Superfamily Douvilleiceratoidea**
**Parona & Bonarelli, 1897**
**Family Douvilleiceratidae Parona & Bonarelli, 1897**
**Subfamily Rolobоceratinae Casey, 1961**

**Genus *Roloboceras* Casey, 1954**

**Type species:** *Ammonites hambrovi* Forbes, 1845; by original designation of Casey (1954, p. 114).

***Roloboceras hambrovi* (Forbes, 1845)**
**Fig. 4A-B, 5A-B, 6A-C**

**Local synonymy:**

non 1927. *Douvilleiceras* cf. *hambrovi* (Forbes) - Roch, p. 2, pl. I, fig. 3 (= *Megatyloceras* aff. *coronatum*).

non 2006. *Roloboceras hambrovi* (Forbes) - Ropolo *et al*., pl. 11, fig. 2 (= *Cheloniceras* sp.).

non 2008a. *Roloboceras hambrovi* (Forbes) - Ropolo *et al*., p. 26, pl. 6, fig. 2 (= Ropolo *et al.*, 2006, pl. 11, fig. 2).

non 2008a. *Roloboceras horridum* Casey - Ropolo *et al.,* p. 27, pl. 12, fig. 3 (= *Cheloniceras* sp.).

non 2009b. *Roloboceras hambrovi* (Forbes) - Ropolo *et al*., pl. 6, fig. 2 (= Ropolo *et al.*, 2006, pl. 11, fig. 2).

non 2009b. *Roloboceras horridum* Casey - Ropolo *et al.,* p. 149, pl. 12, fig. 3 (= Ropolo *et al.*, 2008a, pl. 12, fig. 3).

**Type:** The lectotype designated by Casey (1961) is specimen BGSM.Geol.Soc.Coll.2295 housed at the Geological Survey Museum, Nottingham, UK. It was first represented by the hand-drawn of Forbes (1845, pl. V, fig. 4; right-hand specimen) and then properly illustrated by Casey (1961, pl. XXXII, fig. 5) and Delanoy *et al.*

(2022, pl. 1, fig. 3a-d). It comes from the Lower Lobster Bed Member (lower Aptian) of Atherfield, Isle of Wight, Great Britain.

**Studied material:** Specimens B-CAO3 (**Fig. 4A-B**) and B-CAO1 (**Fig. 5A**) from *Les Caneuves* (Frau collection); the unlabelled specimen of the Dérognat collection (**Fig. 5B-D**) from unknown locality of the 'Bédoulien' unit-stratotype; and specimen MACV.433 (**Fig. 6A-C**) from *Gueule d'Enfer*, Nerthe Massif.

**Description:** Specimen B-CAO3 (**Fig. 4**) is represented by a fairly well-preserved, large-sized calcareous internal mold (approximative D ~ 185 mm). Its shell shape is characterized by a discoidal (Ww/D ~ 0.42), weakly depressed (Ww/Wh ~ 1.09), very evolute (U/Wh ~ 0,92), subvirgacone coiling (U/D ~ 0.35). The whorl section is slightly distorted but it seems to be distinctly depressed and coronate in the inner whorls. The umbilical wall is slightly convex, then subvertical. The flanks and the venter are merged into a broad, domed lateroventral region in the outer whorl. The whorl expansion rate is high and with moderately embracing whorls. The body chamber approximately occupies the half of the last whorl. The first observable part of the ontogeny starts with the *Roloboceras* stage (*sensu* Delanoy *et al.*, 2022) made of short and blunt ribs with periumbilical nodes. These nodes degenerate into radially-elongated bulges with deep costal interspaces. Mostly three ribs branch on the bulges. A few indistinct intercalate ribs occur and fade out in the intercostal grooves. On the last half whorl, the tubercles abruptly change into strong bullae, from which originate one, sometimes two, thick and rounded ribs. Irregular intercalate ribs occur and branch at different heights on the flank. The ribbing becomes more uniform approaching the end of the whorl with alternating simple and intercalate ribs. This matches the senile stage of Delanoy *et al.* (2022). The peristome is not preserved.

Specimen MACV.433 (**Fig. 6A-B**) is represented by a fairly well-preserved, large-sized calcareous internal mold (approximative D ~ 142 mm). Its shell is slightly crushed laterally but it seems characterized by an extremely discoidal (Ww/D ~ 0,34), weakly compressed (Ww/Wh ~ 0,83), very evolute (U/Wh ~ 0,79), subvirgacone coiling (U/D ~ 0.32). The general shell shape is closely similar to that of specimen B-CAO3. It is seemingly depressed and coronate in the inner whorls and changes into semicircular in the outer whorl. The umbilical wall is first low in the innermost whorls, tends to be slightly convex, and then subvertical, in the outer whorl. The body chamber approximately occupies the ¾ of the last whorl. The general ornamental sequence is closely similar to the specimen described above. It starts with the *Roloboceras* stage composed of short and blunt ribs with the progressive development of periumbilical nodes, becoming bulges during a short stage. These bulges are significantly less robust than in specimen B-CAO3 (**Fig. 4**). On the outer whorl, the ribbing changes into thick and rounded, simple and bifurcate ribs with attenuated peri-umbilical bullae, and irregular secondaries. Ribbing similarly becomes more uniform (senile stage) approaching the end of the whorl.

The unlabelled specimen of the Dérognat collection consists of an incomplete, large-sized, calcareous internal mold (**Fig. 5B-D**). It bears prominent bulges with deep costal interspaces, typical of the Roloboceras stage. The ribbing is erased on the outer whorls but the presence of uniform ribs over the venter testifies of the senile stage.

Specimen B-CAO1 (**Fig. 5A**) is represented by a large-sized, vertically crushed body chamber bearing the senile stage of Delanoy *et al*. (2022).

**Discussion:** The material at our disposal conforms well to the shell morphology and ornamentation of *Roloboceras hambrovi* as revised by Delanoy *et al.* (2022). Roch (1927, pl. I, fig. 3) first reported the presence of *Roloboceras* (pro *Douvilleiceras*) cf. *hambrovi* in the 'Bédoulien' unit-stratotype but he illustrated a specimen from Ardèche as an example. This specimen has been re-assigned to *Megatyloceras* aff. *coronatum* by Delanoy *et al.* (2022). This is evidenced by the presence of large radially pinched tubercles at the beginning of the last whorl characterising well that species. The other specimen cited by Roch (1927, p. 22) corresponds to the unlabelled Dérognat's specimen described above. This specimen corresponds well to *Roloboceras hambrovi* as it bears the *Roloboceras* stage of Delanoy *et al.,* (2022) visible in the inner whorls.

None of the subsequent reports of *Roloboceras* individuals from the 'Bédoulien' unit-stratotype does not appear valid. These are discussed below:

Specimen MPP-C.104/12.580 of Conte (1975, fig. 2-3) identified to as *Roloboceras* sp. gr. *transiens* was refigured under the same name by Ropolo *et al*. (2008a, pl. 8, fig. 2; Ropolo *et al*., 2009a, pl. 8, fig. 2). It is here properly illustrated in **Fig. 7A-D**. This is said to come from bed 158 of the *Les Fourniers* section. Its origin is actually located thousands of metres southwest of *Les Caneuves* according to the map of Conte (1975, fig. 1), and it derives from the outcrops comprised into the camping *Les Portes de Cassis* according to the Conte's label (**Fig. 7E**). Furthermore, the bed occurrence of this specimen is unclear unlike of the opinion of Ropolo *et al.* (op. cit.)., since a correlation between the litho-log of Conte (1975) and the type succession of Moullade *et al.* (2000) is almost impossible. Furthermore, this specimen does not compare to *Megatyloceras transiens* by the lack of a stage with radially pinched tubercles typical of that species. It better conforms to *Roloboceras* both regarding its general shell morphology and dimensions but we find that its ornamentation is distinctly less robust during the *Roloboceras* stage. Pending the finding of a similar individual *in situ*, we here assign this specimen to as *Roloboceras* sp.

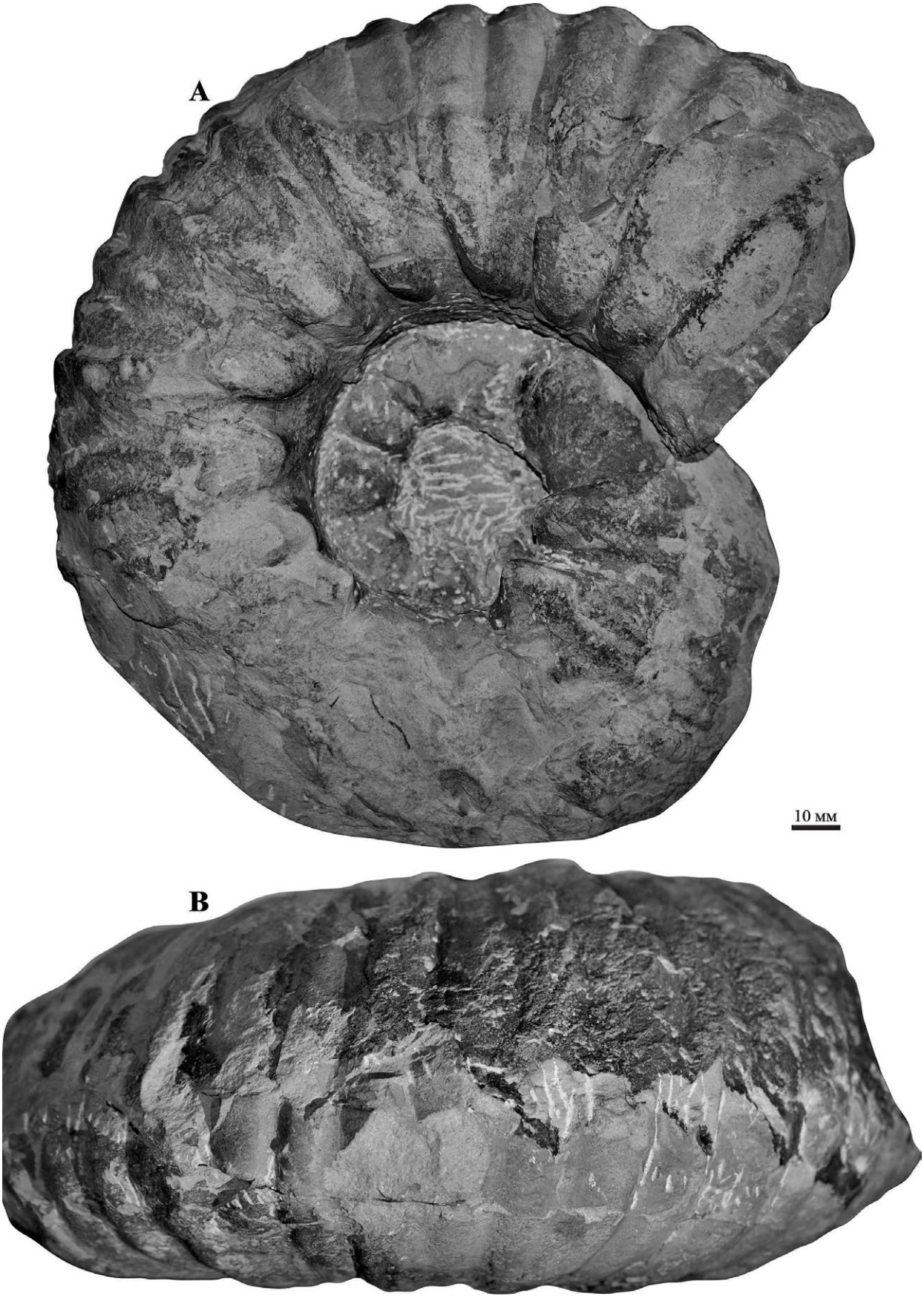



**Fig. 4.** ***Roloboceras hambrovi*** **(Forbes, 1845)**. Lateral (**A**) and (**B**) ventral views of specimen B-CA03 (Frau collection) from *Les Caneuves* (equivalent of bed 129). Scale bar is 10 mm.

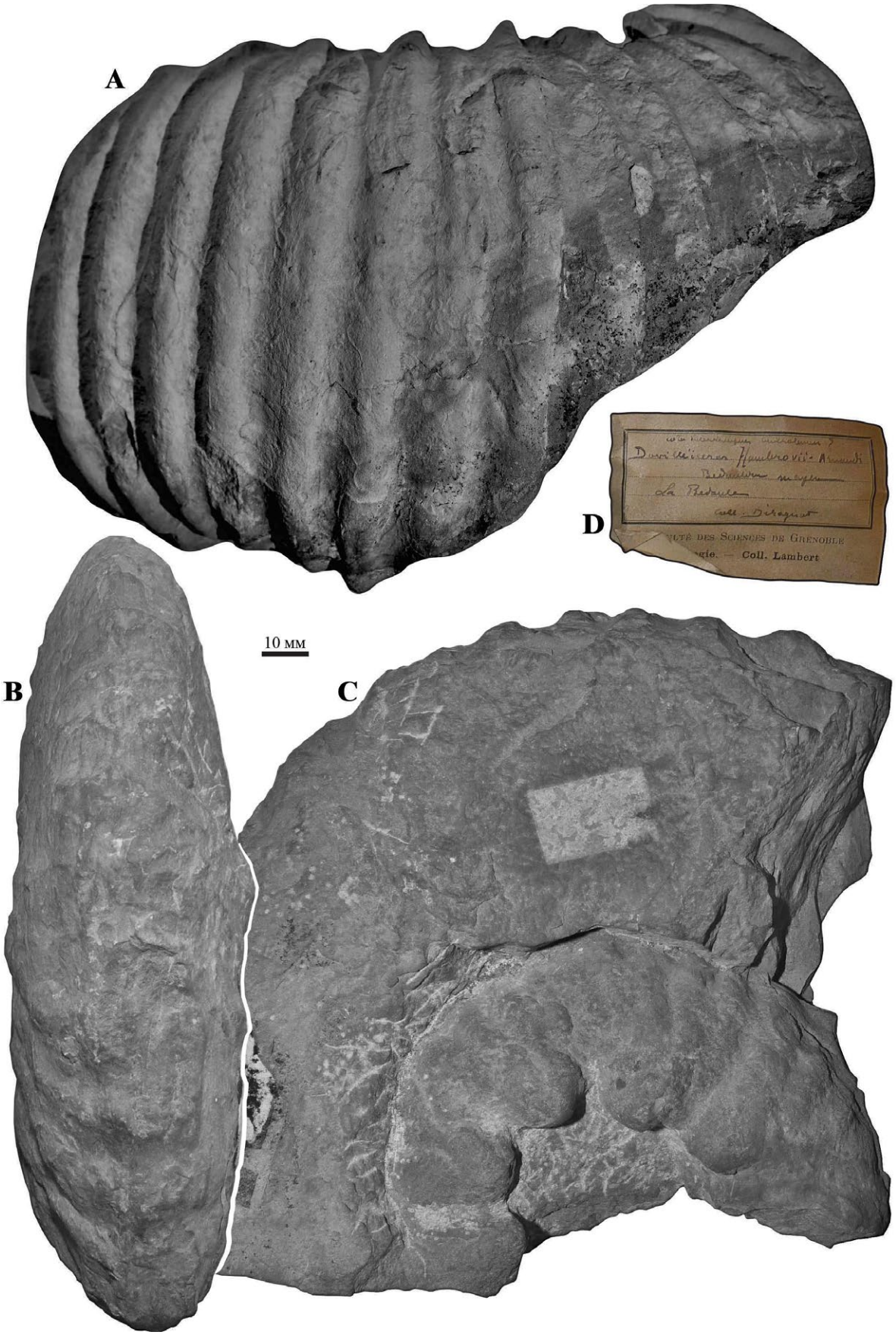



**Fig. 5.** ***Roloboceras hambrovi*** **(Forbes, 1845)**. **A:** ventral view of specimen B-CA01 (Frau collection) from *Les Caneuves* (equivalent of bed 129); **B-D:** ventral (**B**) and (**C**) lateral views of the unlabelled Dérognat's specimen from an unknown bed and locality of the 'Bédoulien' unit-stratotype, and (**D**) its original label. Scale bar is 10 mm.

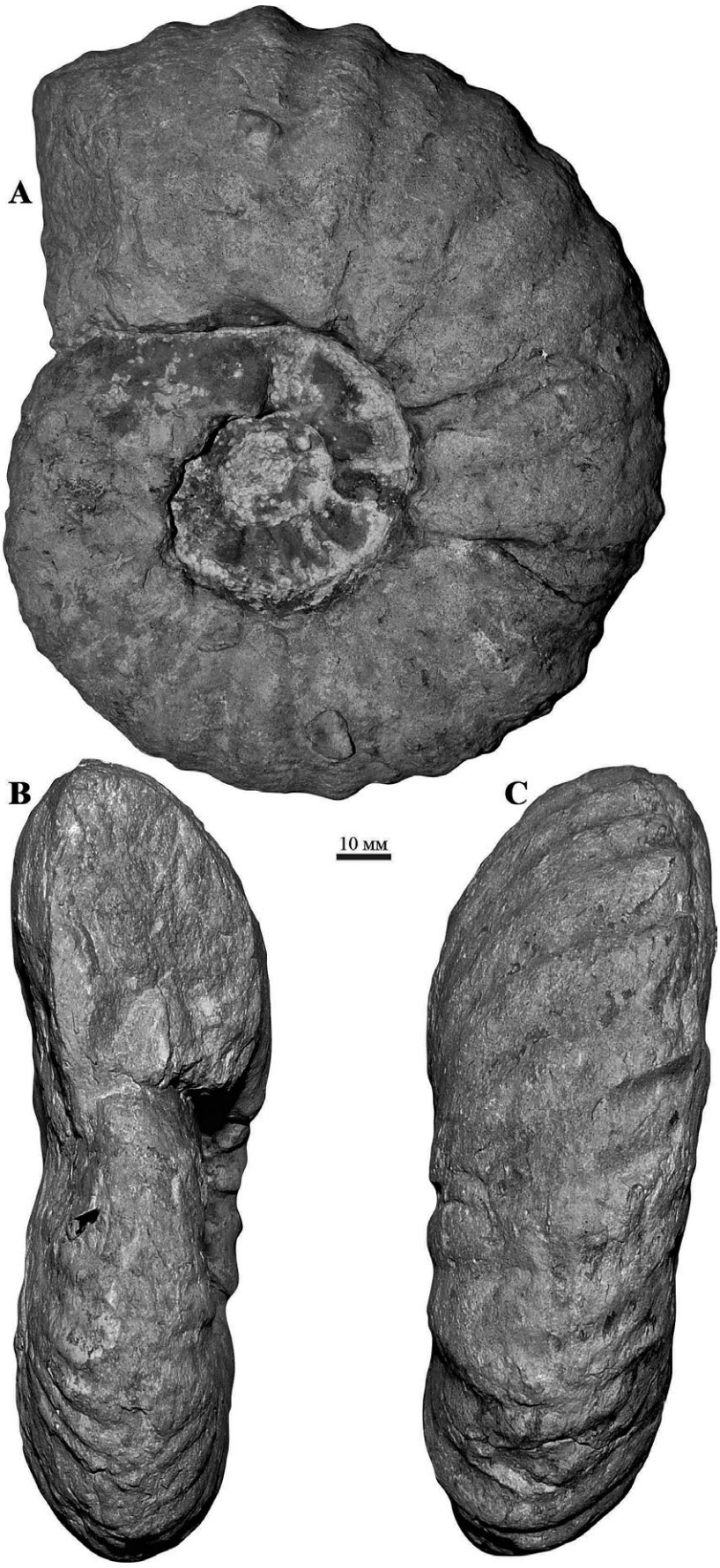



**Fig. 6.** ***Roloboceras hambrovi*** **(Forbes, 1845)**. Lateral (**A**) and (**B-C**) ventral views of specimen MACV.433 (Musée des Amis de Castrum Vetus collection) from *Gueule d'Enfer*, near Martigues. Scale bar is 10 mm.

Specimen MPP-PRA1430 (reported from bed 148 of the 'Bédoulien' unit-stratotype (= *Roloboceras hambrovi* in Ropolo *et al.*, 2006, pl. 11, fig. 2; Ropolo *et al*., 2008a, pl. 6, fig. 2; Ropolo *et al.,* 2009a, pl. 6, fig. 2) has been re-interpreted to as *Cheloniceras* sp. by Delanoy *et al.* (2022). This view is here followed since the corresponding specimen lacks the large and strong periumbilical tubercles characterising the sub-adult ontogeny of *Roloboceras hambrovi*. It should, furthermore, be noted that the specimen actually belongs to the Gabriel Conte collection (coll. number is MPP-281/12.531) and comes from the lower Aptian locality of *Serviers-La-Baume*, Gard, France (**Fig. 7F-I**). Both the collection number and locality have been mixed up in the works of P. Ropolo.

Specimen MPP-PRA1455 reported from bed 170 of the 'Bédoulien' unit-stratotype (= *Roloboceras horridum* in Ropolo e*t al.*, 2008a, pl. 12, fig. 3; Ropolo *et al*., 2009a, pl. 12, fig. 3) has also been re-interpreted to as *Cheloniceras* sp. by Delanoy *et al.* (2022). This view is also followed here since the specimen illustrates well the royerianum stage that characterises the juveniles of *Cheloniceras* (see Frau *et al.,* 2020). Only its ventral view was illustrated in the works of P. Ropolo (op. cit.). Nevertheless, there is hardly any doubt that the illustration of that specimen depicts a small-sized pyritic specimen. After more than fifteen years of fossil collecting at Cassis–Roquefort-la-Bédoule by the first author (CF), it is evident that such pyritic material does not occur in the Marly Calcareous Mb. It is thus more than likely that the locality of that specimen has also been mixed up in the works of P. Ropolo.

**Dimorphism:** A putative morpho-dimensional dimorphism of sexual nature has been hypothesised by Delanoy *et al.* (2022) in the *Roloboceras hambrovi* palaeopopulations from Ardèche. By their size, the best-preserved specimens B-CAO3 (**Fig. 4**) and MACV.433 (**Fig. 6**) fall in the diameter range of the putative microconchs. However, their ornamental sequence better corresponds to that of macroconchs as they show a typical *Roloboceras* stage followed by a senile stage marked by the progressive change of the large periumbilical tubercles into more or less pinched tubercles and then into bullae approaching the peristome. This unusual character combination does not cast doubt on the dimorphism criteria used by Delanoy *et al.* (2022) since one should considered that significant adult-size variations occur in Cretaceous ammonoid palaeopopulations of a same species related to distinct – i.e., basin *versus* platform – environments (Reboulet, 2001 and references therein). Indeed, the life habit of the *Roloboceras hambrovi* individuals from the 'Bédoulien' unit-stratotype is distinctly deeper than their equivalents from Ardèche flourishing in distal outer platform environments (Delanoy *et al.,* 2022). For that reason, our putative *Roloboceras hambrovi* macroconchs have a distinctly reduced size. The lack of putative microconch findings here prevents further confirmation.

**Occurrence:** Specimens B-CAO3 (**Fig. 4**) and B-CAO1 (**Fig. 5**) assigned to *Roloboceras hambrovi* come from base of the Marly Calcareous Mb. that cropped out at *Les Caneuves*. This is correlated to bed 129 of the *Station de Cassis* section. This bed marks the base of the *Roloboceras hambrovi* Subzone of Frau *et al.* (2017), and falls in the upper part of the C2 carbon-isotope segment (**Fig. 2**). Origin of the unlabelled Dérognat and MACV's specimens remains unknown but their matrix conforms to lithology from the base of the Marly Calcareous Mb.

### *Roloboceras* aff. *hambrovi* (Forbes, 1845)
### Fig. 7J-K, L-N

**Studied material:** Specimens B-EM.211 (**Fig. 7J-K**) and B-EM.206 (**Fig. 7L-N**) (Frau collection) from outcrop *d* of the *Station de Cassis* section.

**Description:** The specimens B-EM.206 and 211 are incomplete and moderate in size (i.e., estimated diameters of 50 and 85 mm, respectively). Although distorted, it can be recognised a very evolute subvirgacone coiling (U/D and Wh/D are both estimated between 0,3 and 0,4). The whorl section is likely depressed, with a subvertical to slightly convex umbilical wall. The flanks and the venter are seemingly merged into a broad, domed lateroventral region. Regarding ornamentation, specimen B-EM.206 (**Fig. 7L-N**) shows the end of the third stage of *Roloboceras hambrovi* (perli-stage of Spath, 1930) bearing strong main, sometimes bifurcate, and intercalary ribs and more or less thorny peri-umbilical tubercles. This then changes to the ornamentation typical of *Roloboceras hambrovi* consisting in thick, low, rounded ribs, simple or arising in pairs from large obtuse periumbilical tubercles. This stage occupies the whole preserved whorl of specimen B-EM.211 (**Fig. 7J-K**). In this specimen, the main ribs sometimes arise by three from the periumbilical tubercles while few intercalary ribs develop near them. The tubercles become as prominent bulliform at end of the whorl. There are 11 tubercles counted on the half whorl, and at least 20 ribs occur near the lateroventral region. The sutures are not properly observed in both specimens.

**Discussion:** The two specimens at our disposal match the general shell morphology and ornamentation of *Roloboceras hambrovi* as revised by Delanoy *et al.* (2022). They differ from the type species by their much smaller size, and a greater number of ribs and tubercles during the fourth *Roloboceras* ontogenetic stage of Delanoy *et al.* (2022). The specimens are here referred to as *Roloboceras* aff. *hambrovi* pending more material to be collected.

**Dimorphism:** The small number of individuals, and their poor state of preservation, do not allow recognition of a putative sexual dimorphism in *Roloboceras* aff. *hambrovi*. Nevertheless, it is worth noting that the two studied specimens have somewhat miniaturised size compared to their equivalents from Great Britain and Ardèche.

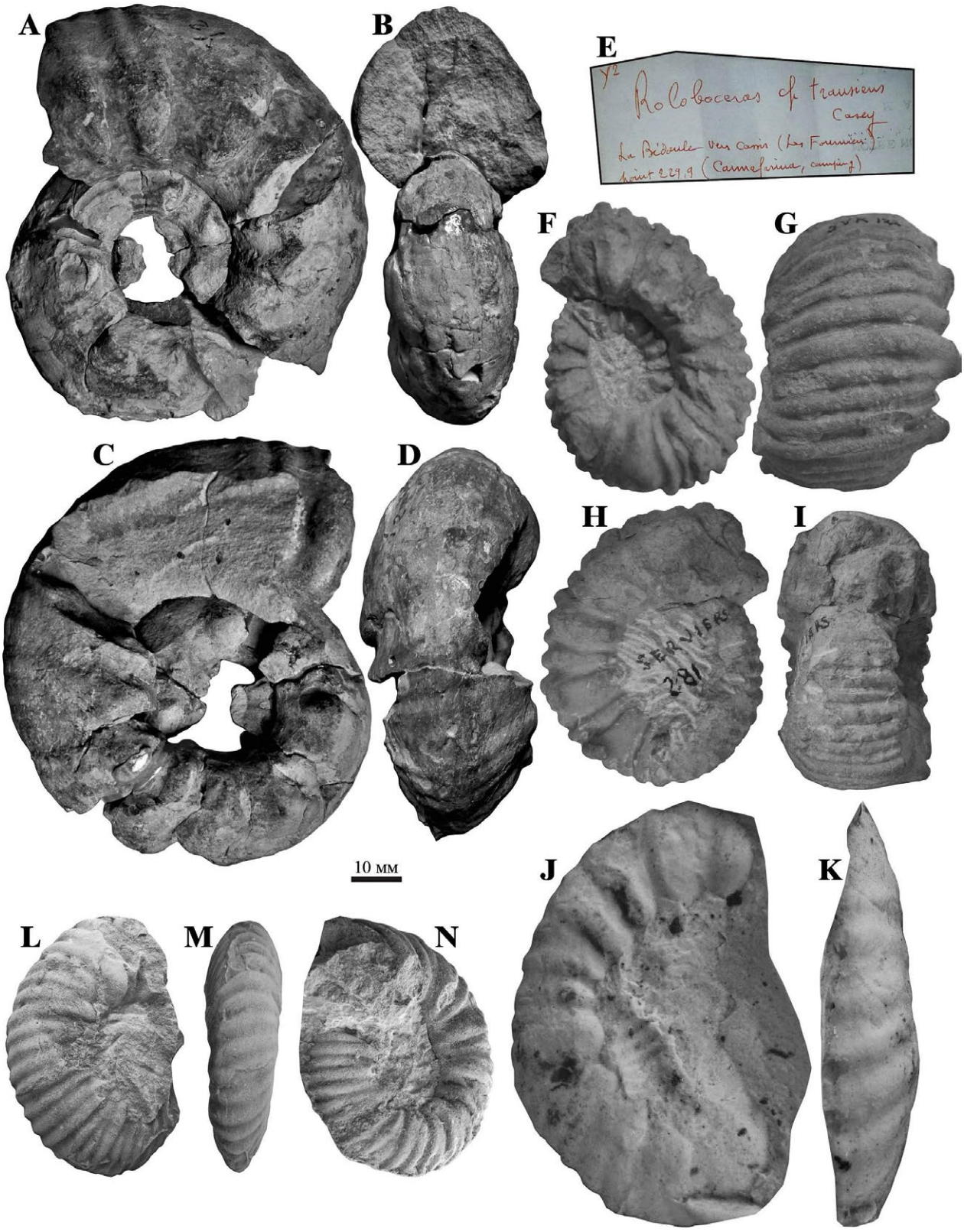



**Fig. 7. A-E: *Roloboceras* sp.** Lateral (**A, C**) and (**B, D**) ventral views of specimen MPP-C.104/12.580 (Conte collection) from *Les Portes de Cassis* camping, and (**E**) its original label.

**. F-I: *Cheloniceras* sp.** Lateral (**F, H**) and (**G, I**) ventral views of specimen MPP-281/12.531 (Conte collection) from *Serviers-La-Baume*, Gard.

**. J-N: *Roloboceras* aff. *hambrovi* (Forbes, 1845). J-K:** lateral (**J**) and (**K**) ventral views of cast B-EM.211 (Frau collection) from *Station de Cassis* (bed 142) ; **L-N:** lateral (**L, N**) and (**M**) ventral views of cast B-EM. 206 (Frau collection) from *Station de Cassis* (bed 142). Scale bar is 10 mm.

**Occurrence:** *Roloboceras* aff. *hambrovi* occurs in bed 142 (base) from outcrop *d* of the *Station de Cassis* section. This bed falls in the *Roloboceras hambrovi* Subzone of Frau et al. (2017) and correlates to the mid-C3 carbon-isotope segment (**Fig. 2**).

### Genus *Megatyloceras* Humphrey, 1949

**Type species:** *Douvilleiceras coronatum* Rouchadzé, 1933 by original designation of Humphrey (1949).

### *Megatyloceras* cf. *coronatum* (Rouchadzé, 1933)
### Fig. 8A-I

**Local synonymy:**

? 1927. *Douvilleiceras* cf. *hambrovi* (Forbes) - Roch, p. 22, pl. I, fig. 3 (= *Megatyloceras* aff. *coronatum*)

? 2008a. *Megatyloceras ricordeanum* (d'Orbigny) - Ropolo *et al*., pl. 9, fig. 4.

non 2008a. *Megatyloceras ricordeanum* (d'Orbigny) - Ropolo *et al.,* pl. 11, fig. 3 (= *Cheloniceras* sp.).

non 2008c. *Megatyloceras ricordeanum* (d'Orbigny) - Ropolo *et al.,* fig. c-d (= juvenile of *Cheloniceras cornuelianum*).

? 2009a. *Megatyloceras ricordeanum* (d'Orbigny) - Ropolo *et al.,* pl. 9, fig. 4 (= Ropolo *et al*., 2008a, pl. 9, fig. 4).

non 2009a. *Megatyloceras ricordeanum* (d'Orbigny) - Ropolo *et al*., pl. 16, fig. 1 (= Ropolo *et al*., pl. 11, fig. 3).

**Types:** According to Delanoy *et al.* (2022), the valid lectotype is specimen from the Bayern collection figured by Rouchadzé (1938, pl. 3, fig. 4) and designed by Casey (1961). It derives from the lower Aptian beds of Kharagoüli, Horecha, Georgia. A proper illustration of the lectotype is given in Delanoy *et al.* (2022, pl. 13, fig. 1a-b).

**Studied material:** Specimens B.EM.73 (**Fig. 8A-C**), 74 (**Fig. 8D**), 78 (**Fig. 8F**), 80 et 298 (**Fig. 8I**) (Frau collection); and specimens UCBL-FSL 105265 (**Fig. 8G-H**), and 105267 (**Fig. 8E**) (Busnardo collection); all from outcrop *d* of the *Station de Cassis* section.

**Description:** The studied material is composed of heavily distorted and incomplete individuals but they illustrate well the ontogeny and ornamentation of *Megatyloceras*. They have a width and strongly depressed, coronate shell morphology together with a deep umbilicus with subvertical and smooth umbilical wall, and broad and rounded ventral region in the internal whorls. Furthermore, the main ontogenetic stages, following the embryonic one, characterising *Megatyloceras coronatum* are recognised in the many individuals from the *Station de Cassis* section:

- The Ricordeanum stage – consisting in prominent bosses, elliptical in section, the longer axis parallel to the umbilical spiral – is observed in specimens B-EM.73, 74 (**Fig. 8A-C, D**).
- The two next stages – characterised by highly conical tubercles becoming radially pinched – is present in specimens B.EM. 78 (**Fig. 8F**), UCBL-FSL.105267 (**Fig. 8E**). As noticed out by Delanoy *et al.* (2022), the tubercles give rise to groups of 3, more rarely 4, rounded broad ribs, which cross the latero-ventral region with their maximum thickness. This is also characterised by few intercalate ribs emerging on or near the umbilical margin. Note that the strength of tubercules in specimen B-EM.73 differs on both faces, and its whorl section is apparently more rounded (**Fig. 8A-C**). This observation is likely a result of syn-sedimentary distortion but teratology cannot be excluded due to the poor state of preservation.
- The two adult stages – in which the tubercles develop as periumbilical bullae and then give way to a simple or bifurcate ribbing – is only seen in the medium-sized specimen B.EM.298 (**Fig. 8I**). The presence of irregularly arranged intercalary ribs is also noted.

The sutures are not properly observable.

**Discussion:** The material at our disposal matches well the general shell morphology and ornamentation of *Megatyloceras coronatum* as revised by Delanoy *et al.* (2022). The main difference with the type specimens, and those from Ardèche, is their reduced size. The reports of *Megatyloceras coronatum*, and allied forms, from the 'Bédoulien' unit-stratotype are rare in the literature and in need of clarifications:

Illustration of Ropolo *et al.* (2008a, pl. 8, fig. 3) is a ventral view of a *Megatyloceras* specimen that was identified to as *Megatyloceras ricordeanum* and said to come from bed 150 of the *Station de Cassis* section. However, Ropolo *et al.* inadvertently figured a specimen of *Megatyloceras* aff. *coronatum* of the C. Baudouin collection from *Le Teil*, Ardèche (see Delanoy *et al.,* 2022, pl. 24, fig. 1). The *corrigendum* of Ropolo *et al.* (2008c, fig. c-d) subsequently illustrated specimen MPP-PRA.1424. This specimen is actually a small-sized pyritic ammonite. This contradicts with the scale bar provided by Ropolo *et al.* (2008c, fig. c), and still questions its origin and locality since it is established that no pyritic ammonite occurs in the Marly Calcareous Mb. of the 'Bédoulien' unit-stratotype. According to Delanoy *et al.* (2022), the specimen MPP-PRA.1424 likely illustrates a juvenile *Cheloniceras* of the group of *C. cornuelianum*. This view is here followed, but doubt still remains on both its origin and locality.

Specimen MPP-C.865/12.574 (**Fig. 8J-L**) of the Gabriel Conte collection was first illustrated by Ropolo *et al.* (2008a, pl. 9, fig. 4; 2009a, pl. 9, fig. 4) and assigned to *Megatyloceras ricordeanum*. It is said to come from bed 158 of the *Station de Cassis* section, but once again, the specimen lacks data regarding its

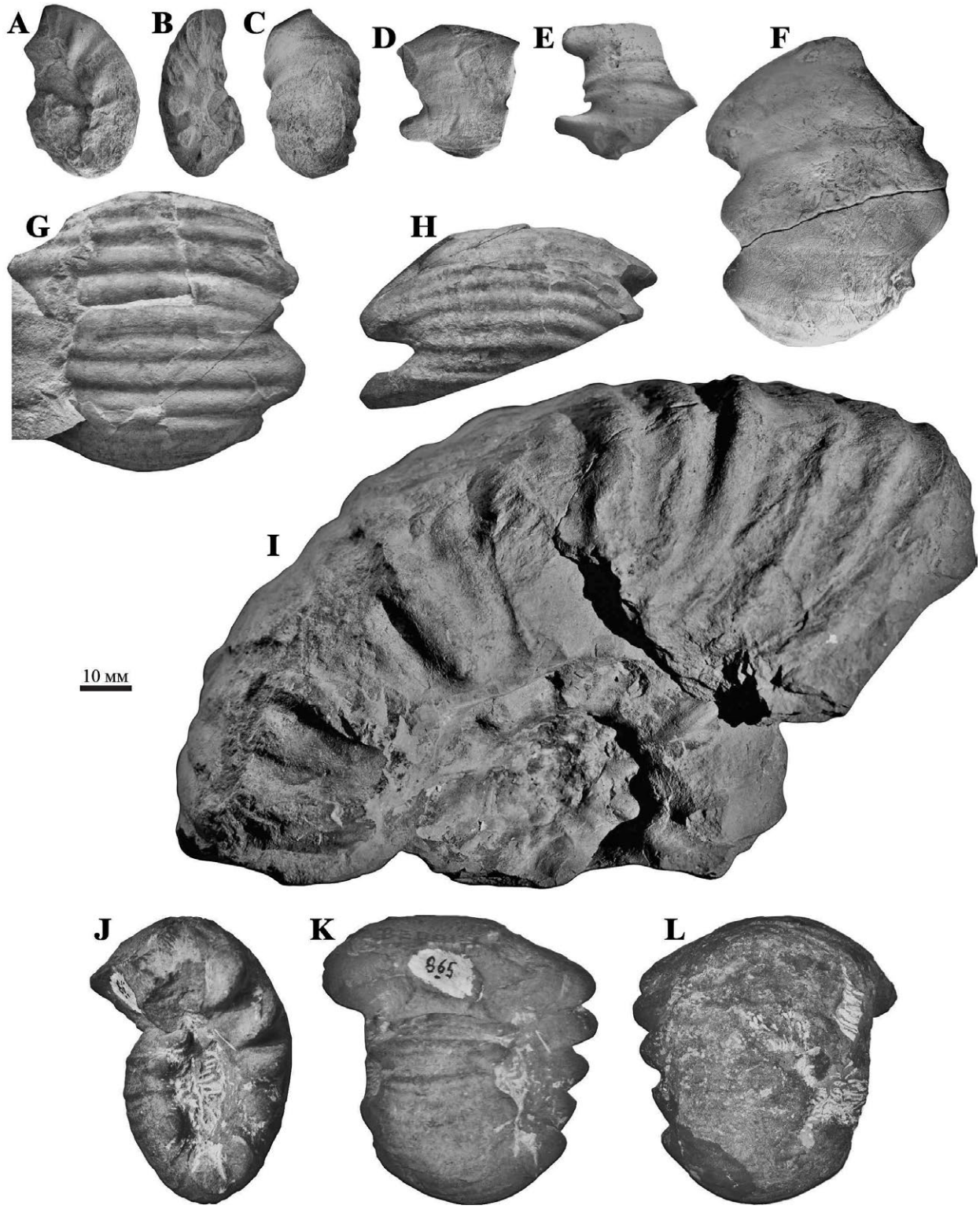



**Fig. 8. A-I:** ***Megatyloceras*** **cf.** ***coronatum*** **(Rouchadzé, 1933).** **A-C:** lateral (**A, B**) and (**C**) ventral views of specimen B.EM.73 (Frau collection) from *Station de Cassis* (bed 148); **D:** ventral view of specimen B.EM.74 (Frau collection) from *Station de Cassis* (bed 148); **E:** ventral view of specimen UCBL-FSL.105267 (Busnardo collection) from *Station de Cassis* (bed 148); **F:** ventral view of specimen B.EM.78 (Frau collection) from *Station de Cassis* (bed 148); **G-H:** ventral view of specimen UCBL-FSL.105266 (Busnardo collection) from *Station de Cassis* (bed 148); **I:** lateral view of specimen B.EM.298 (Frau collection) from *Station de Cassis* (bed 148).
**. J-L:** ***Megatyloceras*** **sp.** Lateral (**J**) and (**K-L**) ventral views of specimen MPP-C.865/12.574 (Conte collection) from unknown locality of La Bédoule. Scale bar is 10 mm.

locality, and bed occurrence. There is no label in the Conte collection, and it is only indicated that it comes from "La Bédoule". Its pale beige matrix, and vertically crushed state of preservation, nevertheless, conform to the *Megatyloceras coronatum* individuals we collected in bed 148 at the *Station de Cassis* section (**Fig. 2**). The specimen was re-interpreted to as *Megatyloceras* sp. by Delanoy *et al*. (2022).

Specimen MPP-PRA.1425 was illustrated by Ropolo *et al.* (2008a, pl. 11, fig. 3; 2009a, pl. 11, fig. 3) and assigned to *Megatyloceras ricordeanum*. It is said to come from bed 158 of the *Station de Cassis* section. The specimen is illustrated under the name *Cheloniceras cornuelianum* in the same works (Ropolo *et al*., 2008a, pl. 16, fig. 1; Ropolo *et al*., 2009a, pl. 16, fig. 1) and assigned to the Gabriel Conte collection (coll. number assigned is C.890). It is further said to come from bed 169 of the *Station de Cassis* section. After verification at MPP collection, the corresponding specimen truly belongs to the Conte collection (coll. number is actually MPP-GACO.001) but it derives from bed 170 of the *Station de Cassis* section according to its original label. Here once more, there is evidence that bed number and locality has been mixed up in the works of Ropolo *et al.* (op. cit.). Following Delanoy *et al.* (2022), we contend that the specimen is a crushed fragment of *Cheloniceras* of doubtful identification.

**Dimorphism:** A putative morpho-dimensional dimorphism of sexual nature has been hypothesised by Delanoy *et al*. (2022) in the *Megatyloceras coronatum* palaeopopulations from Ardèche. We lack sufficient and well-preserved material for further comparison but one should observe that the larger specimen B-EM.298 (**Fig. 8I**) conforms well to the putative *Megatyloceras coronatum* macroconchs of Delanoy *et al.* (2022) as it shows a strong and long conical and pinched tuberculate stage, and thus a later appearance of the adult stage (**Fig. 8I**). However, the adult size seems to be distinctly reduced than the macroconch equivalents from Ardèche.

**Occurrence:** *Megatyloceras* cf. *ricordeanum* occurs in beds 148 of outcrop *d* of the *Station de Cassis* section. This bed falls in the upper part of the *Roloboceras hambrovi* Subzone of Frau *et al.* (2017) and correlates to the mid-C4 carbon-isotope segment (**Fig. 2**).

## 5. Discussion

### *5.1. Stratigraphic significance of Roloboceratinae in the 'Bédoulien' unit-stratotype*

Our bed-by-bed collection documents the presence of *Roloboceras hambrovi* at the base of the Marly Calcareous Mb. at *Les Caneuves* section. This correlates to base of bed 129 of the 'Bédoulien' unit-stratotype sedimentary succession (**Fig. 2**). Closely-allied forms, here assigned to *Roloboceras* aff. *hambrovi*, have further been identified in bed 142 at the unit-stratotype section. Reports of *Roloboceras* above this level as indicated in the works of Ropolo *et al.* (2006, 2008a-b, 2009a-b) are considered incorrect. We explain this by confusion of bed occurrences, localities, and collection numbers of the figured specimens.

The same misleading applies to the record of *Megatyloceras coronatum* figured by Ropolo *et al.* (op. cit.); none of the identifications does not appear valid, and all localities and bed occurrences are obviously mixed up. Our bed-by-bed collection only documents the presence of *Megatyloceras* cf. *coronatum* in bed 148 at the *Station de Cassis* section (**Fig. 2**).

The reports of Roch (1927) and Conte (1975) belong to *Roloboceras* sp. and *Megatyloceras coronatum* but the bed occurrences of those specimens remain unclear unlike of the opinion of Ropolo *et al*. (op. cit.).

It is here established that the species *Roloboceras hambrovi*, *Roloboceras* aff. *hambrovi*, and *Megatyloceras* cf. *coronatum* have succeeded in time in the 'Bédoulien' sedimentary succession. In detail, our data brings down the first occurrence of *Roloboceras hambrovi* to almost 10 metres compared to the previous record of Ropolo *et al.* (2006, 2008a-b, 2009a-b) in the 'Bedoulian' sedimentary succession. It is worth noting that *Deshayesites* of the group of *D. forbesi* Casey, 1964 were previously reported in bed 138 of the 'Bédoulien' sedimentary succession (Frau *et al.,* 2015), to which we add further specimens from bed 140 (**Fig. 9A**) and 142 (**Fig. 9B**). This brings more evidence that most of the *Roloboceras*-bearing beds, and thus the base of the *Roloboceras hambrovi* Subzone of Frau *et al.* (2017), fall in the *Deshayesites forbesi* Zone *auctorum* although precise location of its lower boundary remains unclear (**Fig. 2**). Above, only poorly-preserved fragments of deshayesitids were found in beds 143 to 157. The relative dating of the *Megatyloceras*-bearing beds, and thus the top-boundary of the *Roloboceras hambrovi* Zone of Frau *et al.* (2017), remains equivocal with either the top of the *Deshayesites forbesi* Zone or the base of the *Deshayesites deshayesi* Zone pending new material to be collected.

### *5.2. Palaeoecological significance of Roloboceratinae in the 'Bédoulien' unit-stratotype*

It turns out that *Roloboceras hambrovi* settles in the intrashelf South Provence Basin just above a distinctive discontinuity – i.e., base of bed 129 matches the "*discontinuité intra-bédoulienne*" of Moullade *et al.* (2000) – interpreted as the consequence of a supra-regional deepening event (Renard & De Rafaélis, 2000) (**Fig. 2**). This is in contradiction with the views of Ropolo *et al*. (2008b) arguing of a delayed appearance of Roloboceratinae in this intrashelf basin because of ecological restriction. This view is hereby abandoned.

Furthermore, it is to note that the Roloboceratinae individuals from the 'Bédoulien' unit-stratotype are reduced in size (*Roloboceras hambrovi*) or somewhat miniaturised (*Roloboceras* aff. *hambrovi* and *Megatyloceras* cf.

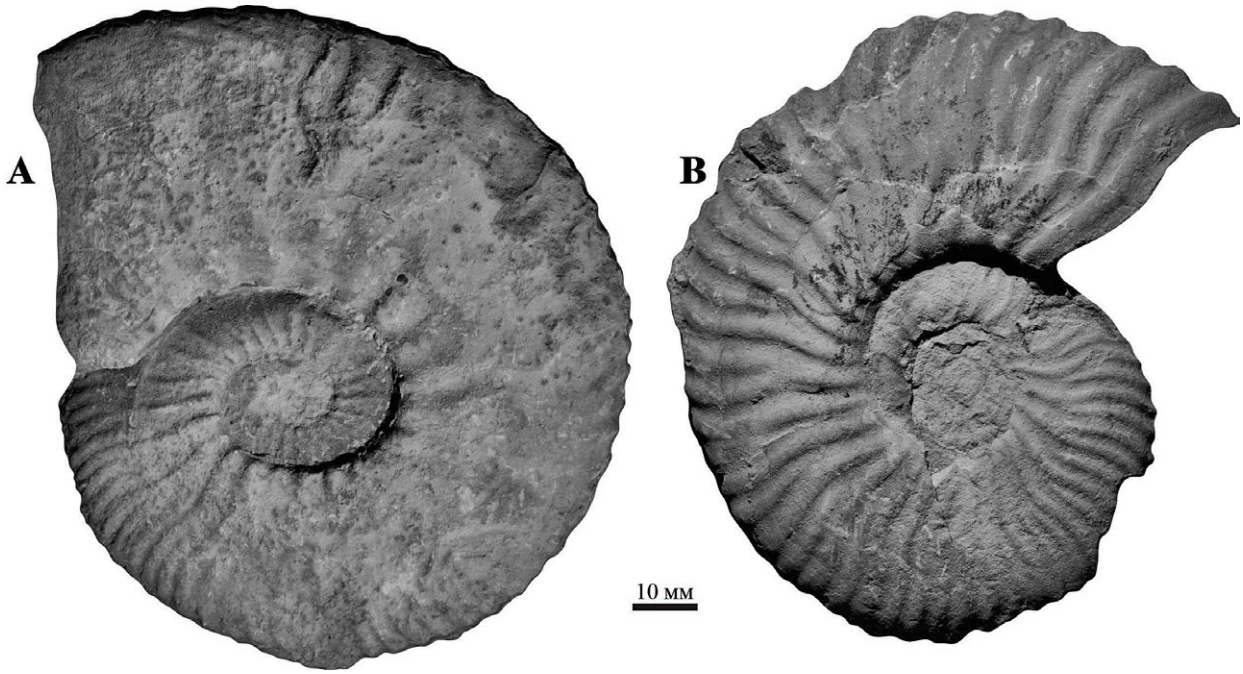



**Fig. 9.** ***Deshayesites* gr. *forbesi* Casey, 1964**. **A:** Lateral view of specimen B.EM.159 (Frau collection) from *Station de Cassis* (bed 140); **B:** lateral view of specimen B.EM.114 (Frau collection) from *Station de Cassis* (bed 142). Scale bar is 10 mm.

*coronatum*) compared to their equivalents from Great Britain and Ardèche (compare with Casey *et al.,* 1998; Delanoy *et al.,* 2022). Sampling biases excluded, the main reason is their life habit in deeper basinal settings compared to their equivalents from distal outer platform environments (see similar cases *in* Reboulet, 2001). There is also emerging evidence that miniaturisation occurs in Deshayesitidae and Aconeceratidae during the unfavourable conditions of the OAE 1a in Russia (Rogov *et al.,* 2019). The lack of sufficient and well-horizonted palaeopopulations actually prevents confirmation of such a process in the South Provence Roloboceratinae.

### *5.2. Comparison with others Roloboceratinae records*

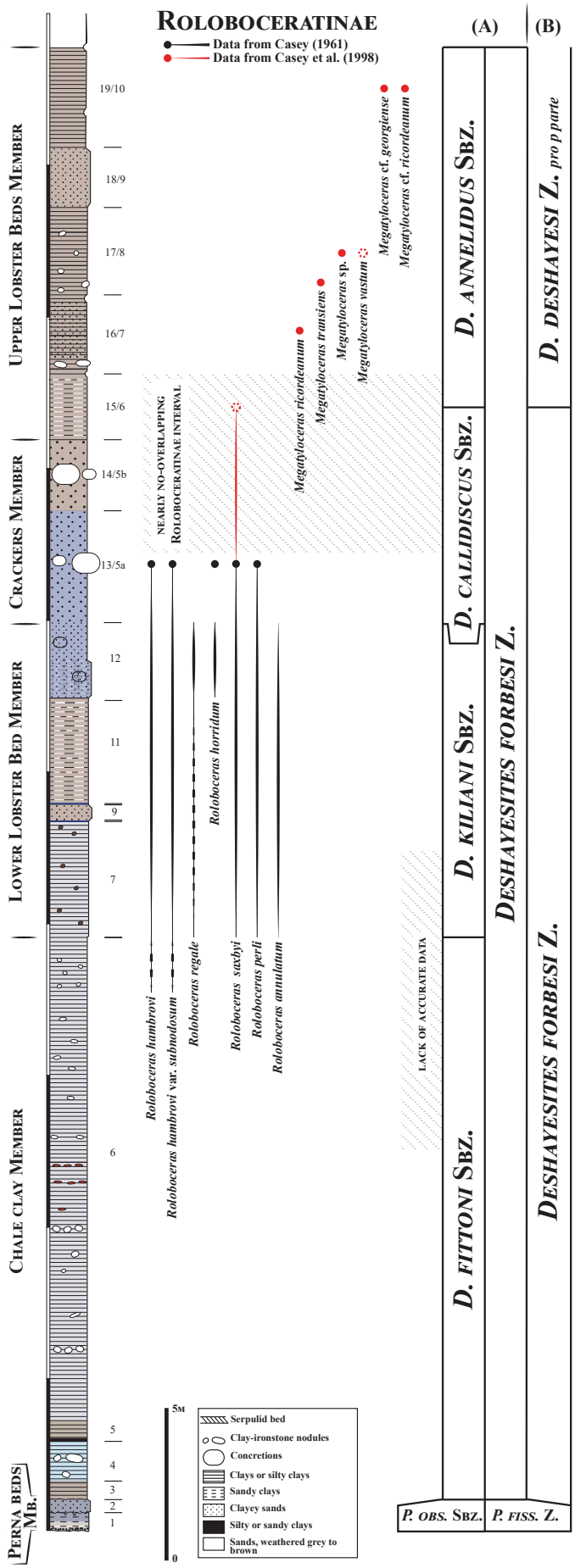
#### *Atherfield, Great Britain*

In Great Britain, the Atherfield costal cliffs of the Isle of Wight expose a beautifully outcropping Lower Greensand sedimentary succession, deposited in the norther margin of the Anglo-Paris Basin, which is "*unrivalled in for its contribution to* [Roloboceratinae]*, both in numbers and variety and in excellence preservation*" (Casey, 1961, p. 178).

Here, *Roloboceras* taxa range throughout the Lower Lobster Bed Mb. and the lower part of the Crackers Mb. of the Atherfield Clay series (*sensu* Simpson, 1985) (**Fig. 10**). According to Casey (1961, p. 182), crushed individuals doubtfully assigned to *Roloboceras hambrovi* occur in the top of the underlying Chale Bay Mb., but the corresponding material lacks illustration for further confirmation. The lowest *Roloboceras* occurrence thus falls at, or close to the lower boundary of the Lower Lobster Beds Mb.; the latter being dated to the base of the *Deshayesites kiliani* Subzone of Casey *et al.* (1998). There are still some confusions surrounding this biostratigraphical boundary (Simpson, 1985, p. 26). Firstly, it has until now never been properly defined, and secondly ammonites through the basal part of the formation have never been figured. There is, nevertheless, a consensus to consider that this level falls somewhere in the *Deshayesites forbesi* Zone regardless of the contrasting definitions of this zone at Atherfield (e.g., Casey, 1961; Casey *et al.,* 1998; Bersac & Bert, 2012, 2015) (**Fig. 10**). This *Roloboceras* distribution fits well with the picture here identified in the 'Bédoulien' unit-stratotype.

The co-occurrence of *Roloboceras* and *Megatyloceras* at Atherfield was first suggested by Casey (1961, p. 191) due to the report of the eroded holotype of *Megatyloceras vastum* from the Lower Lobster Bed Mb. However, this holotype was picked up on the foreshore exposure and it better agrees in its taphonomic characters with the fauna found at the base of bed 17/8 of the Upper Lobster Beds Mb. (Casey *et al.,* 1998). This is the member that yields all other *Megatyloceras* faunas (Casey *et al.,* 1998).

The same authors also came to the conclusion that *Roloboceras* and *Megatyloceras* strictly succeeded in time with no clear overlap (**Fig. 10**). Indeed, there is barren Roloboceratinae interval between the top-Crackers Mb. and lower Upper Lobster Beds Mb., exception made of a single, non-illustrated report of *Roloboceras saxbii* at one level (bed 15/6). According to Casey *et al.* (1998), the *Megatyloceras*-bearings beds cover the Upper Lobster Beds Mb., and date the *Deshayesites annelidus* Subzone. The latter


ROLOBOCERATINAE
Data from Casey (1961)
Data from Casey et al. (1998)
(A)
(B)
ATHERFIELD CLAY FORMATION
PERNA BEDS MB.
CHALE CLAY MEMBER
LOWER LOBSTER BED MEMBER
CRACKERS MEMBER
UPPER LOBSTER BEDS MEMBER
19/10
18/9
17/8
16/7
15/6
14/5b
13/5a
12
11
9
7
6
5
4
3
2
1
NEARLY NO-OVERLAPPING ROLOBOCERATINAE INTERVAL
Megatyloceras cf. georgiense
Megatyloceras cf. ricordeanum
Megatyloceras ricordeanum
Megatyloceras transiens
Megatyloceras sp.
Megatyloceras vastum
Roloboceras hambrovi
Roloboceras hambrovi var. subnodosum
Roloboceras regale
Roloboceras horridum
Roloboceras saxbyi
Roloboceras perli
Roloboceras annulatum
LACK OF ACCURATE DATA
D. ANNELIDUS SBZ.
D. CALLIDISCUS SBZ.
D. KILIANI SBZ.
D. FITTONI SBZ.
DESHAYESITES FORBESI Z.
DESHAYESITES FORBESI Z.
D. DESHAYESI Z. pro p parte
P. OBS. SBZ.
P. FISS. Z.
5M
0
Serpulid bed
Clay-ironstone nodules
Concretions
Clays or silty clays
Sandy clays
Clayey sands
Silty or sandy clays
Sands, weathered grey to brown

is a marker of the top-*Deshayesites forbesi* Zone of Casey. However, a recent study has suggested that *Deshayesites annelidus* could be a synonym of *Deshayesites deshayesi*, and that the two species are temporally coeval (Bersac & Bert, 2015). Here diverging taxonomic interpretation of *Deshayesites* taxa clearly affects attempts to identify the top-boundary of the *Roloboceras hambrovi* Subzone of Frau *et al.* (2017) with respect to either the *Deshayesites forbesi* Zone or *Deshayesites deshayesi* Zone.

***Ardèche, France***

The lower Aptian marine deposits from southern Ardèche, deposited along the eastern margin of the Vocontian Basin, yield rich Rolobocerati nae faunas in post-Urgonian marly deposits known as the Chabert Fm. (Pictet & Delanoy, 2017). Delanoy *et al.* (2022, fig. 19) here identified diverse *Roloboceras* and *Megatyloceras* taxa through the Violette Mb. and Rouvière Rocherenard Mb. It has been further identified that the Rolobocerati nae distribution is regionally controlled by paleodepth along a proximal–distal platform gradient, and only the most distal setting, such as at the Chabert section, exposes a rather complete vertical record of the Rolobocerati nae (Delanoy *et al*., 2022). Of major interest is the brief overlap of *Roloboceras* and *Megatyloceras* taxa in the lower part of the Rocherenard Mb. at the Chabert section (**Fig. 11**). This is contrasted with the 'Bédoulien' and Atherfield records discussed above.

According to Delanoy *et al.* (2022), the total range of Rolobocerati nae from Ardèche falls in the *Deshayesites forbesi* Zone *auctorum*. However, deshayesitid ammonites from the top-Rocherenard Mb. remain rare (Pictet & Delanoy, 2017), and their assignment to the *Deshayesites deshayesi* Zone is barely hypothetical except in its topmost beds. There is therefore much work to be done to locate the top-boundary of the *Roloboceras hambrovi* Subzone of Frau *et al.* (2017) with respect to either the *Deshayesites forbesi* Zone or *Deshayesites deshayesi* Zone.

### *5.3. Chemostratigraphy of the Rolobocerati nae-bearing beds*

The vertical range of the Rolobocerati nae from the 'Bédoulien' unit-stratotype provided by Frau (2020) is here updated and calibrated to the OAE 1a isotopic excursion previously published by Kuhnt *et al*. (2000). It is established that *Roloboceras* taxa range through the upper C2 segment to the mid-C3 segment, while *Megatyloceras coronatum* falls in the segment C4 segment only (**Fig. 2**). The species *Roloboceras hambrovi*, *Roloboceras* aff. *hambrovi*, and *Megatyloceras coronatum* have thus succeeded in time during the most negative carbon-isotope values of the OAE 1a, and its early build-up stage.

A more complete Rolobocerati nae record is documented in Ardèche (Delanoy *et al*., 2022). *Roloboceras hambrovi* and *Roloboceras* aff. *hispanicum* here appear at two different level in the upper C2 segment, and the index species ranges up to the C5 segment (**Fig. 11**). Sporadic occurrence of *Roloboceras* aff. *hambrovi* and *Roloboceras* aff. *hispanicum* are reported in the C4 and C5 segments. As expected, the group of *Megatyloceras coronatum* appears later – in the mid-C4 segment – and ranges up to the bottom-C6 segment. The newly introduced species *Megatyloceras leteilensis* occurs through the top-C4 segment to the bottom-C6 segment. Of interest is the overlapping of both *Roloboceras hambrovi* and *Megatyloceras coronatum* through the build-up stage – mainly during the C4 and C5 segments – of the OAE 1a. Moreover, there is a stepped extinction of *Roloboceras* and *Megatyloceras* species during the last portion of the OAE 1a build-up stage; all *Megatyloceras* taxa being extinct from around the C5/C6 carbon-isotope segment boundary

By contrast, only sporadic occurrences of Rolobocerati nae are reported in the Iberian sections during the OAE 1a (Frau, 2020 based on data from Moreno-Bedmar *et al*., 2008, 2009, 2010, 2012). Elsewhere, the Rolobocerati nae record are not calibrated by carbon-isotope stratigraphy; this is the case in Bulgaria and Georgia to mention only the main area of distribution of the Rolobocerati nae. Comparison with the Rolobocerati nae record from the Lower Greensand is difficult since there is a lack of accurate carbon-isotope signal associated with the Rolobocerati nae-bearing beds (Frau, 2020 based on data from Gröcke *et al*., 1999). There is, however, evidence that the *Megatyloceras*-bearing beds could fall in C5 segment to (?) lower C6 segment. There seems to be a disappearance of Rolobocerati nae above those levels as observed in Ardèche.

## 6. Conclusion

This work provides a new insight into the taxonomy and stratigraphic distribution of the ammonite subfamily Rolobocerati nae from the 'Bédoulien' unit-stratotype, and its surroundings. It is here established that the species *Roloboceras hambrovi*, *Roloboceras* aff. *hambrovi*, and *Megatyloceras coronatum* have succeeded in time during the most negative carbon-isotope values of the OAE 1a, and its early build-up stage. The total range of

**Fig. 10 –** Litho-log of the Atherfield Clay Series *pro parte* at Atherfield, UK (modified from Simpson, 1985) – including, from bottom to top, the Perna Beds, Chale Clay, Lower Lobster Bed, Crackers, and Upper Lobster Beds members – and the interpreted occurrence of Rolobocerati nae according to data from Casey (1961), and Casey *et al.* (1998). Bed number and colours on litho-log refer to the work of Simpson (1985). This is correlated to the conflicting lower Aptian ammonite biozonation *pro parte* of (**A**) Casey *et al.* (1998) and (**B**) Bersac & Bert (2015).

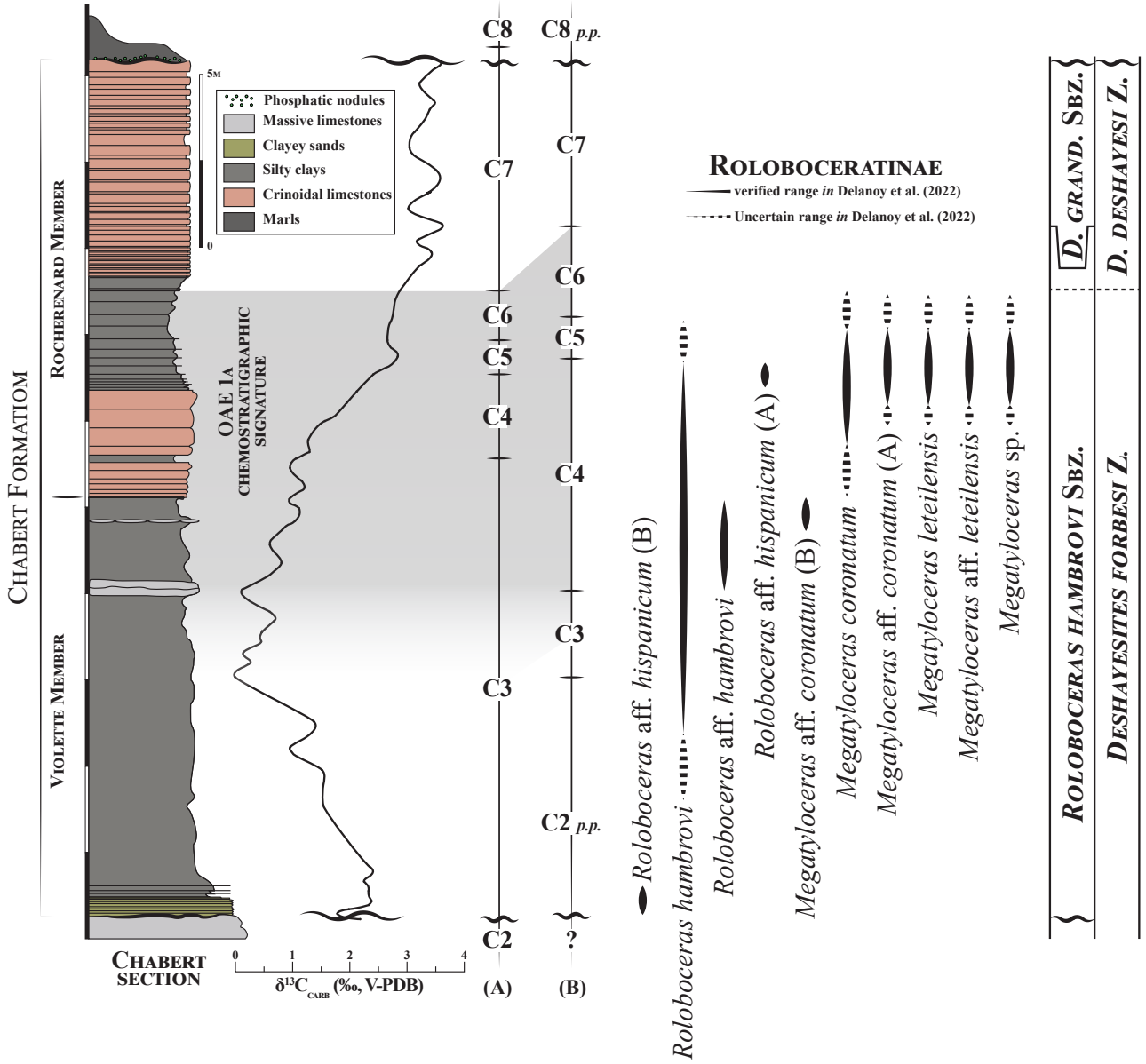



**Fig. 11 –** Litho-log of the Chabert Formation at Chabert, France – including, from bottom to top, the Violette and Rocherenard members – and the documented occurrence of Roloboceratinae according to Delanoy *et al.* (2022). Correlation to the lower Aptian ammonite biozonation *pro parte* of Delanoy *et al.* (2022) is given. Comparison with the carbon-isotope curve ($\delta^{13}C_{carb}$) of Pictet *et al.* (2015) is added together with indication of the Menegatti's segments (C2 to C7 *pro parte*) as interpreted by (**A**) Pictet *et al.* (2015) and (**B**) Frau (2020).

the *Roloboceras hambrovi* Subzone of Frau *et al.* (2017) seemingly encompasses the top-C2 segment to the bottom-C6 segment based on SE France record. We confirm that the base of the *Roloboceras hambrovi* Subzone falls in the *Deshayesites forbesi* Zone *auctorum*, but doubt still persists on the location of its top-boundary with respect to the *Deshayesites deshayesi* Zone. This observation is in need of confirmation through the distribution area of the Roloboceratinae; much of the Mediterranean record lack accurate data and carbon-isotope chemostratigraphic calibration.

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