



**The Deshayesitidae (Ammonoidea, Ancyloceratina)
in the lower Aptian (Lower Cretaceous)
of the Les Ferres Aptian Basin (southeastern France)**

Stéphane BERSAC^{1, 3}

Didier BERT^{2, 3}

Abstract: In the present work, we study 335 specimens of Deshayesitidae (Ammonoidea) from the vicinity of the village of Les Ferres (SE France). The Deshayesitidae is the current key family for the ammonite biostratigraphy of the lower Aptian (Lower Cretaceous). Despite poorly preserved, the studied material could have been identified at species rank in most cases and allowed establishing the biostratigraphic frame of the lower Aptian of the study area. The results are as follows: (1) the studied samples range from the *Deshayesites forbesi* Zone to the *Dufrenoyia furcata* Zone; (2) their ontogenetic sequence is described; (3) their evolutionary patterns are consistent with those observed in other samples of Deshayesitidae; (4) no dimorphism is conspicuous; (5) the identified taxa are, from earliest to latest: *Deshayesites* sp. (*Deshayesites forbesi* Zone, rounded ventral area probably without smooth siphonal band), *Deshayesites multicosatus* SWINNERTON, 1935 (index of subzone, intermediate smooth siphonal band then rounded ventral area), *Deshayesites grandis* SPATH, 1930 (index of subzone, longer smooth siphonal band then subtabulate ventral area on phragmocone), *Dufrenoyia furcata* (J. de C. SOWERBY, 1836) (index of subzone and zone, even longer smooth siphonal band then subtabulate ventral area, onset of rounded to claviform latero-ventral tubercles in inner whorls) and *Dufrenoyia dufrenoyi* (ORBIGNY, 1841) (index of subzone, even more longer smooth siphonal band, latero-ventral tubercles claviform only).

Keywords:

- ammonites;
- *Deshayesites*;
- *Dufrenoyia*;
- biostratigraphy;
- intraspecific variability;
- evolution

Citation: BERSAC S. & BERT D. (2025).- The Deshayesitidae (Ammonoidea, Ancyloceratina) in the lower Aptian (Lower Cretaceous) of the Les Ferres Aptian Basin (southeastern France).- *Carnets Geol.*, Madrid, vol. 25, no. 9, p. 177-200. DOI: [10.2110/carnets.2025.2509](https://doi.org/10.2110/carnets.2025.2509)

Résumé : Les Deshayesitidae (Ammonoidea, Ancyloceratina) de l'Aptien inférieur (Crétacé inférieur) du Bassin Aptien de Les Ferres (SE de la France).- Dans le présent travail, nous étudions 335 spécimens de Deshayesitidae (Ammonoidea) provenant du secteur du village de Les Ferres (SE France). Les Deshayesitidae sont une famille clé pour la biostratigraphie par ammonites de l'Aptien inférieur (Crétacé inférieur). Malgré un état de conservation médiocre, le matériel étudié a pu être identifié au rang spécifique et a fourni une datation précise dans la plupart des cas. Les résultats sont les suivants: (1) les échantillons étudiés s'étendent de la Zone à *Deshayesites forbesi* à la Zone à *Dufrenoyia furcata*; (2) leur séquence ontogénique est décrite; (3) leur schéma évolutif est cohérent avec ceux observés dans d'autres échantillons de Deshayesitidae; (4) aucun dimorphisme n'est mis en évi-

¹ Corresponding author
geosteber@yahoo.com

² Réserve naturelle nationale géologique de Haute-Provence, Conseil départemental des Alpes de Haute-Provence, 13, rue du Docteur-Romieu, CS 70216, 04995 Digne-Les-Bains cedex 9 (France);
Univ. Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes (France)
didier.paleo@gmail.com

³ Laboratoire du Groupe de recherche en Paléobiologie et biostratigraphie des Ammonites (GPA), 65 Grand rue, F-04170 La Mure-Argens (France)





dence ; (5) les taxons identifiés sont, du plus ancien au plus récent: *Deshayesites* sp. (Zone à *Deshayesites forbesi*, région ventrale arrondie probablement sans bande siphonale lisse), *Deshayesites multicostatus* SWINNERTON, 1935 (indice de sous-zone, bande siphonale lisse de longueur intermédiaire puis région ventrale arrondie), *Deshayesites grandis* SPATH, 1930 (indice de sous-zone, bande siphonale lisse plus longue puis région ventrale subtabulée sur le phragmocône), *Dufrenoyia furcata* (J. de C. SOWERBY, 1836) (indice de sous-zone et de zone, bande siphonale lisse encore plus longue puis région ventrale subtabulée, apparition de tubercules latéro-ventraux arrondis à claviformes dans les tours internes) et *Dufrenoyia dufrenoyi* (ORBIGNY, 1841) (indice de sous-zone, bande siphonale lisse encore plus longue, tubercules latéro-ventraux claviformes uniquement).

Mots-clefs :

- ammonites ;
- *Deshayesites* ;
- *Dufrenoyia* ;
- biostratigraphie ;
- variabilité intraspécifique ;
- évolution

1. Introduction

The Les Ferres Aptian Basin (LFAB) is a small subsident basin presently located in the vicinity of the village of Les Ferres, in the Estéron valley (Alpes-Maritimes department, southeastern France, Fig. 1). A general presentation of this basin was published in an introductory article by BERSAC and BERT (2019). It is characterized by plurimetric deposits (Fig. 2) with abundant benthic and nectonic macrofossils, especially ammonites. The age of the lower Aptian series from this basin extends from the *Deshayesites forbesi* Zone (in the sense of BERSAC *et al.*, 2012, see Fig. 3) to the late *Dufrenoyia furcata* Zone (*Dufrenoyia dufrenoyi* Subzone). The LFAB provided many representatives of Deshayesitidae STOYANOW, 1949 (BERSAC & BERT, 2019). This ammonite family spans the whole lower Aptian and occurs over a wide geographic range (CASEY, 1964; YOUNG, 1974; ETAYO-SERNA, 1979; RENZ, 1982; BOGDANOVA & MIKHAILOVA, 2004; DUTOIR, 2005; ROPOLLO *et al.*, 2006; BARRAGAN & SZIVES, 2007; OBATA & MATSUKAWA, 2007; GARCÍA-MONDÉJAR *et al.*, 2009; MORENO-BEDMAR *et al.*, 2010, 2012, 2018, 2023; LEHMANN *et al.*, 2015; ROGOV & MIRONENKO, 2016; LEHMANN & BULOT, 2020). It is the key family for the ammonite biostratigraphy of the lower Aptian since it provided most or all of its index species for this interval of time according to the local zonal schemes (BARABOSHKIN, 2004; CASEY *et al.*, 1998; REBOULET *et al.*, 2018). In our introductory article on the ammonite fauna of the LFAB (BERSAC & BERT, 2019), we only quoted and figured the Deshayesitidae taxa we recognized in this area: *Deshayesites* sp., *Deshayesites multicostatus* SWINNERTON, 1935, *Deshayesites grandis* SPATH, 1930, *Dufrenoyia furcata* (J. de C. SOWERBY, 1836) and *Dufrenoyia dufrenoyi* (ORBIGNY, 1841). The purpose of the present article is to describe our sample of Deshayesitidae from the LFAB and to argue about their taxonomic assignation.

2. Material and method

Material

The material studied is represented by 335 specimens from 7 sections of the LFAB, namely Les Graous 1 section (GRS1), La Vallière section (VAL), La Graou section (GRO), Combe de Joinet section (CHP), Pont de la Cerise section (CLE), Combe de Marin section (CRS) and Pont Paire section (PPR) (Fig. 1). The lithostratigraphy, ammonite occurrence, and biostratigraphy of these sections are described and figured in BERSAC and BERT (2019). The specimens are preserved as marly limestone internal casts, mostly fragmented and deformed by compaction.

The specimens occur in various lithostratigraphic units from bottom to top (Fig. 2): the last bed of the Hauterivian-Aptian limestones, the Combe de Joinet Member (CJ), the *Ammonitoceras* Level (AL) of the Pont de la Cerise Member (*Deshayesites multicostatus* Subzone, *Deshayesites deshayesi* Zone) and the Les Graous Member (*Deshayesites grandis* Subzone, *D. deshayesi* Zone, and *D. furcata* Zone) and its basal *Toxoceratoides* Bed (TB).

The whole studied material belongs to Stéphane BERSAC's collection and is housed in the premises of the Réserve naturelle nationale géologique de Haute-Provence (RNNGHP, Digne-les-Bains, France). The database of the studied specimens is available in the supplementary appendix.

Method

We follow BERSAC and BERT (2012, 2015, p. 266, Figs. 1, 3) regarding the ontogenetic sequences of the flanks and the ventral area, the patterns of intraspecific variability and the criteria of taxonomic identification of the Deshayesitidae (based on the population concept of species, e.g., TINTANT, 1963; DZIK, 1985). They are summarized above.

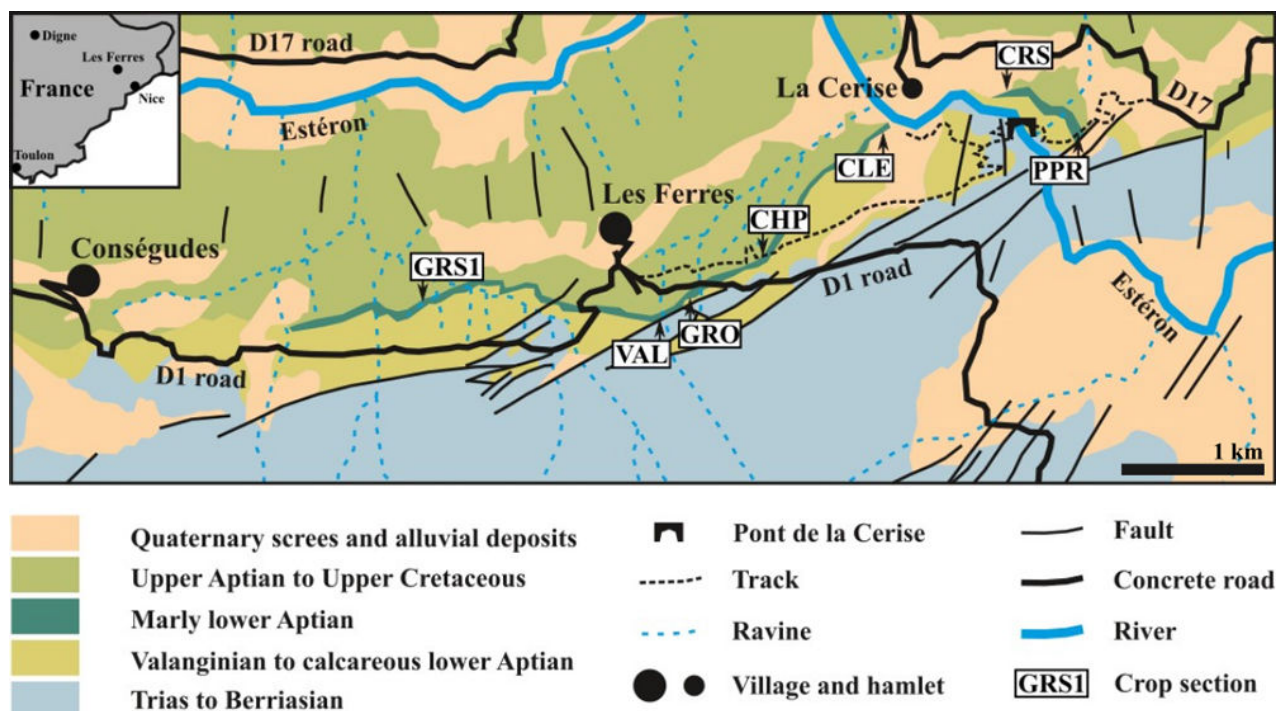


Figure 1: Map of the Les Ferres area with location of the sections quoted in the text.

The ontogenetic sequence of the inner whorls and the flanks is represented by 5 successive stages (Fig. 3):

- the Globular stage A,
- the stage B of *Kossmatella* type in the innermost whorls,
- the stage C with thin and dense main ribs, and with numerous intermediate ribs,
- the stage D with strong ribs with a more spaced and robust ornamentation, and less intermediate ribs,
- the adult stage E with spaced, strong, simple and straight ribs.

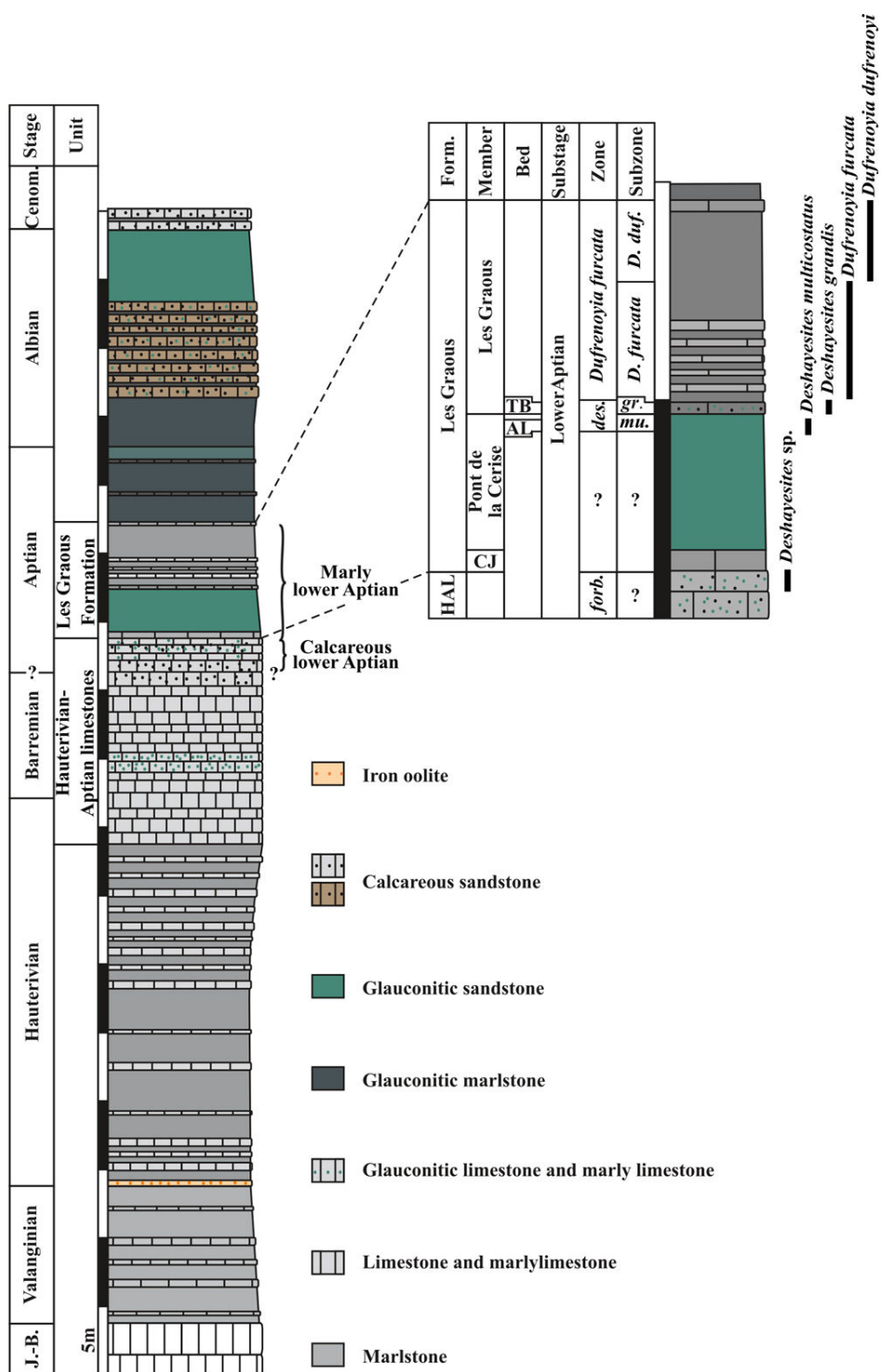
Three main patterns of intraspecific variability are recognised (Fig. 3):

- variability of type 1. It is determined by the duration of the stages C and D. All the morphologies coexist within an instantaneous population, between extremely robust individuals with absent stage C (and thus long stage D) and extremely slender individuals with a long stage C (and thus short stage D). This variability follows general 'laws' which were subject of several recent studies (BERSAC & BERT, 2012; BERT, 2013, 2019; BERT *et al.*, 2023; DE BAETS *et al.*, 2015, with references).
- variability of type 2. It relates exclusively to the intensity of ornamentation/relief of the ribs: the secondary attenuation of ornamentation (see BERT, 2013). All potential intermediates can be observed in a

same sample between individuals with ornamentation normally expressed to sub-smooth forms. This ornamental attenuation may concern all or part of the shell with exception of the ontogenetic stage E, which is never attenuated.

- probable sexual dimorphism with macroconchs and microconchs (these latter never express the stage E).

The evolution of the Deshayesitidae is characterized by the likely increasing complexity of the septal suture over time and by the onset of a new postembryonic stage (stage B) after the stage A in the inner whorls of the populations from the *Deshayesites fittoni* Subzone (*Deshayesites forbesi* Zone *sensu* BERSAC *et al.*, 2012) and of a smooth siphonal band in the populations from the *Deshayesites deshayesi* Subzone (*Deshayesites deshayesi* Zone *sensu* BERSAC *et al.*, 2012), then of latero-ventral tubercles from the *Dufrenoyia furcata* Subzone (*Dufrenoyia furcata* Zone, Fig. 4). Both these two last characters evolve through a neotenic process by expanding more and more on the venter of the shell over time (DUTOIR, 2005; BERSAC & BERT, 2012, 2015). Consequently, the key diagnostic characters of the Deshayesitidae are all evolutionary characters: the mean value of the end diameter of the smooth siphonal band (SSB) and of the latero-ventral tubercles measured in an isochronous population, the shape of these tubercles and the presence of a subtabulate ventral area (*i.e.*, ventral area flattened but without neat limit with the flanks) on the phragmocone.



◀ **Figure 2:** Synthetic log of the Lower Cretaceous of the Les Ferres area. J.-B.: Jurassic and Berriasian; Cenom.: Cenomanian; Form.: Formation; HAL: Hauterivian-Aptian limestones; CJ: Combe de Joinet Member; AL: *Ammonitoceras* Level; TB: *Toxoceratoides* Bed; forb.: *Deshayesites forbesi*; des.: *Deshayesites deshaysi*; mu.: *Deshayesites multicostatus*; gr.: *Deshayesites grandis*; D. duf.: *Dufrenoyia dufrenoyi*.

An additional pattern of variability of the Deshayesitidae is the intraspecific variability of the evolutionary characters recognized above: in a given isochronous population, these characters are not obviously all identical from a specimen to another, but vary - sometimes considerably - in a way assumed to be Gaussian (character value distribution represented by a bell/Gaussian curve). The species identification is based on the calculation of the mean value of these evolutionary characters in a given isochronous population (population concept of species, see Dzik, 1985).

The measured shell parameters are the diameter of the shell (D), the maximum whorl height (H), the rib density on the last half whorl (R), the end diameter of the smooth siphonal band (SSB) and the end diameter of the latero-ventral tubercles. Because of the deformation of the material, these parameters (given in the supplementary appendix) have to be taken as estimations. Consequently, no statistical analysis was performed apart from the mean values of SSB and R. Due to flattening of most of the specimens, the whorl width was not measured.

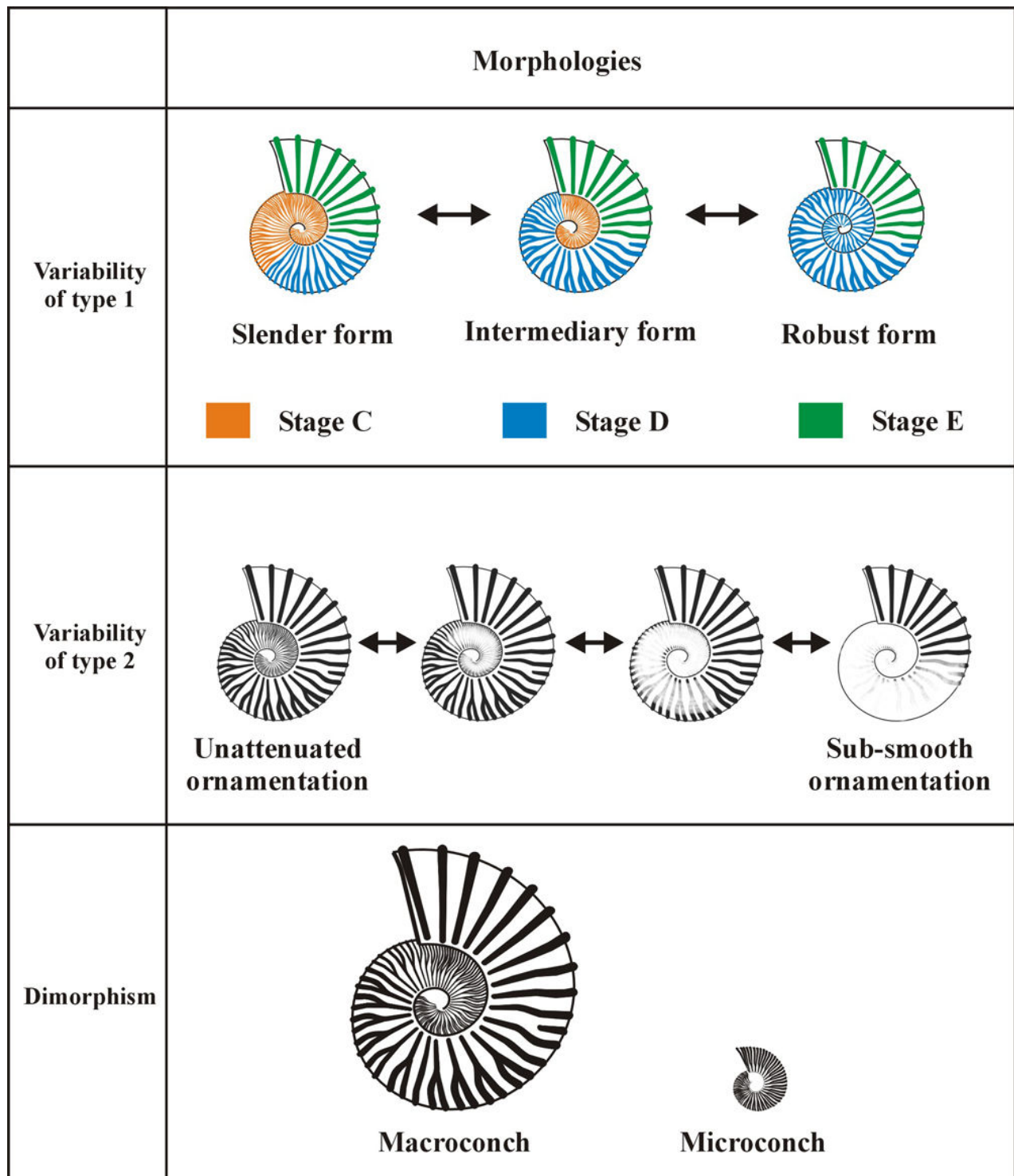


Figure 3: Patterns of intraspecific variability of the *Deshayesitidae*, after BERSAC & BERT (2012).

The synonymy lists we present only contain the works with the original description of the taxa here recognized, those containing their emended description and those quoting specimens from the LFAB.

3. Systematics

Ancyloceratina WIEDMANN, 1966
Deshayesitaceae STOYANOW, 1949
Deshayesitidae STOYANOW, 1949
Deshayestites KAZANSKY, 1914
***Deshayesites* sp.**
 Pl. 1, figs. A-E

? 1982 *Deshayesites* sp. - RAGAZZI, p. 74-75.
 ? 1982 *Deshayesites latelobata* (SINZOW) - RAGAZZI, p. 75.
 v 2019 *Deshayesites* sp. - BERSAC & BERT, p. 154, 157-158, 161, 167, Figs. 5, 10, 12, 14-15, Pl. 1, figs. 4-5.

Material studied: 12 specimens from the uppermost bed of the Hauterivian-Aptian limestones (*Deshayesites forbesi* Zone) of GRS1 (BERSAC & BERT, 2019, Fig. 5), CLE (*ibid.*, Fig. 12) and CRS (*ibid.*, Fig. 14). See the supplementary appendix for the complete list of the specimens with measurements.

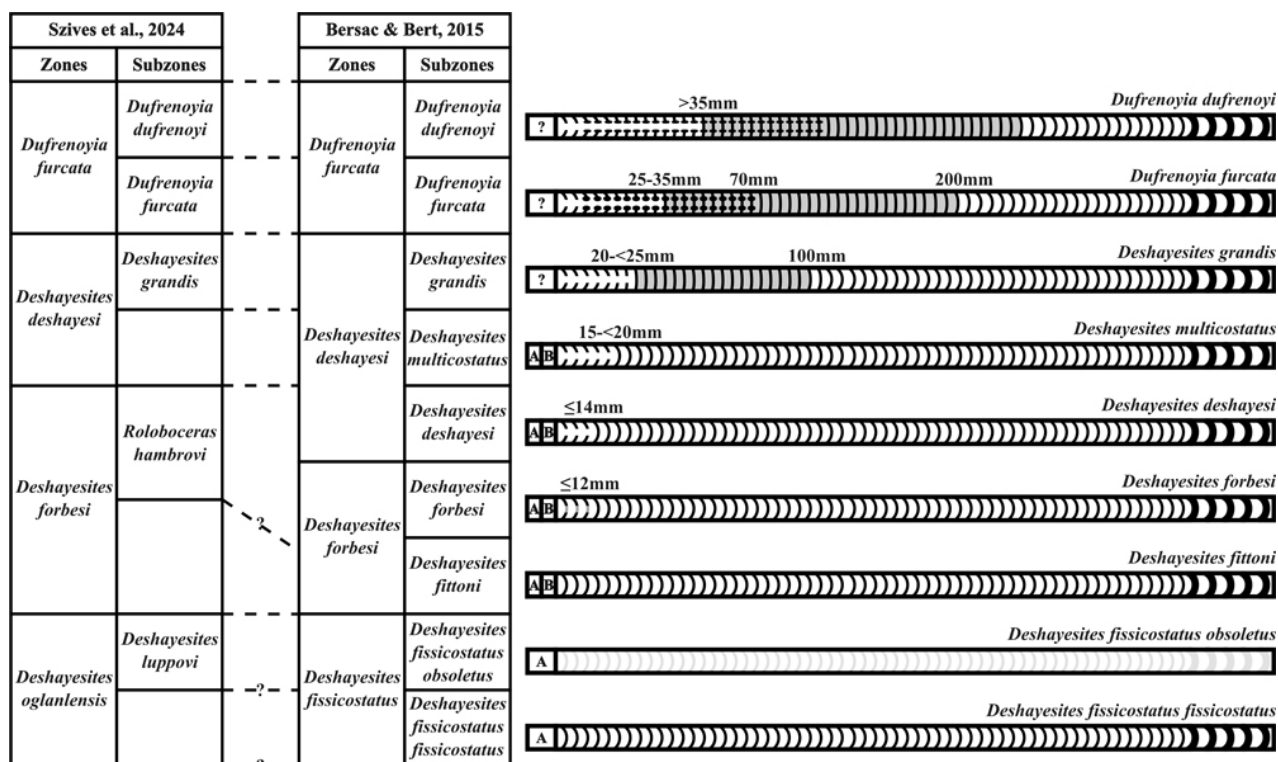


Figure 4: Biostratigraphic chart used in the present work (BERSAC & BERT, 2015) with characteristics of the ventral area of its index species, parallelized with the Standard Ammonite Zonation of the Western Tethys [*] Mediterranean Province (SZIVES *et al.*, 2024). Subtabulate ventral area is represented in clear grey. Stages C and D are not differentiated not to overburden the figure (see text for explanations).

Description: Most of the specimens are whorl fragments. Their shell is discoid to moderately evolute, with more or less covering whorls. The maximum observed D is 133 mm (Pl. 1, fig. A) and the maximum observed H is 63 mm. R was measurable on only two specimens (SBC.06061-00001/GRS115 and SBC.06061-00007/CLE030) and is respectively 21 and 27. The umbilical wall is steep and the flanks are flat or slightly convex. No specimen has its whorls observable below D=25 mm and the ontogenetic stages A and B cannot consequently be studied. The observable ontogenetic sequence of the shell flanks starts with the stage C having dense, more or less flexuous thin ribs, and more or less regular alternation between primary and intercalary ribs. Intercalary ribs are usually more numerous and emerge at various heights on the flanks. The stage D, that follows the stage C, presents thicker, less dense and less flexuous ribs, with a rather regular alternation between primary and intercalary ribs. No specimen shows a periumbilical rib thickening. The specimens are too small or fragmentary to exhibit the adult stage E. The transition between the stages C and D can be more or less sudden, the ribs are wedge shaped or not and the rib relief is sharp or more attenuated, especially in the middle part of the flanks. The shape of the specimens varies between a slender morphology with high rib density, high growth in whorl height and narrow whorl width and a robust morphology with lower rib density and lower growth in whorl height.

None of the specimens has its ventral area preserved below D=25 mm. From this diameter, the ventral area is always rounded with no rib attenuation. The septal suture is too poorly preserved to be described and no specimen has its peristome preserved.

Discussion: The range of variability seems to be continuous within the sample and similar to what is generally observed in monospecific samples of Deshayesitidae (DUTOIR, 2005; GARCIA & MORENO-BEDMAR, 2010; BERSAC & BERT, 2012, 2015; MORENO-BEDMAR *et al.*, 2014) and the sample is thus regarded monospecific. This sample exhibits no evidence of dimorphism but its fragmentary state prevents further discussion (expression of sexual dimorphism among Deshayesitidae is still under debate, see discussion in MORENO & COMPANY, 2007; BERSAC & BERT, 2012; MORENO-BEDMAR *et al.*, 2014; LEHMANN & BULOT, 2020; FRAU & DELANOY, 2022). The ventral area was not observed in any of the studied specimens before D=25 mm, and similarly, neither the smooth siphonal band, subtabulate ventral area nor latero-ventral tubercles are present. The absence of latero-ventral tubercles allows to assign unambiguously these Deshayesitidae to the genus *Deshayesites* KAZANSKY, 1914. The absence of a subtabulate ventral area allows to consider them as representatives of a species earlier than *Deshayesites grandis*. These specimens could belong to *Deshayesites deshayesi* (ORBIGNY, 1841) if they would have SSB<15mm, *Deshayesites multicostatus* if 15mm ≤ SSB ≤ 20mm or an even

[*] Editor's note: The wording 'Tethyan,' which was incorrect, was changed to 'Tethys' (see GRANIER, 2022).



earlier species such as *Deshayesites forbesi* CASEY, 1961, *Deshayesites fissicostatus* (PHILLIPS, 1829), *Deshayesites tuarkyricus* BOGDANOVA, 1983, etc. if they do not bear a smooth siphonal band. Because of the impossibility to observe the ventral area in inner whorls and thus to determine if a smooth siphonal band is present or not, the taxonomic identification cannot be carried further and these specimens are left in open nomenclature.

The co-occurring ammonite fauna can nevertheless help to estimate more precisely their biostratigraphic position: these *Deshayesites* occur with representatives of the genus *Procheloniceras* SPATH, 1923 (Douvilleiceratidae PARONA & BONARELLI, 1897) and small *Ancyloceras* ORBIGNY, 1842, assigned to *Ancyloceras rochi* SARKAR, 1955 (BERSAC & BERT, 2019, Pl. 1, figs. 2, 6-7). *Procheloniceras* is known probably up to the top of the *Deshayesites forbesi* Zone (in the sense of BERSAC *et al.*, 2012; see BERSAC & BERT, 2018) and small *Ancyloceras* such as *A. rochi* are present in the *D. forbesi* Zone (ROPOLO *et al.*, 1998). The suggested biostratigraphic position of these *Deshayesites* is thus the *D. forbesi* Zone. The absence of the biostratigraphically significant ammonite subfamily Roloboceratinae CASEY, 1961, in the uppermost bed of the Hauterivian-Aptian limestones, if not caused by sample bias or unfavorable paleoenvironment, may suggest a biostratigraphic position within the *D. forbesi* Zone lower than the *Roloboceras hambrovi* Subzone (see ROPOLO *et al.*, 2008; MORENO-BEDMAR *et al.*, 2009, 2010; BERSAC & BERT, 2012, 2015; FRAU *et al.*, 2017, 2023; FRAU, 2020; DELANOY *et al.*, 2022, for discussion on the biostratigraphic position of the Roloboceratinae).

Biostratigraphic distribution: *Deshayesites forbesi* Zone.

***Deshayesites multicostatus*
SWINNERTON, 1935**

Pl. 2, figs. A-C; Pl. 3, figs. A-C;

Pl. 4, figs. A-V; Pl. 5, figs. A-H

1935 *Deshayesites multicostatus* sp. nov. – SWINNERTON, Pl. 1, figs. 1a-c.

2015 *Deshayesites multicostatus* – BERSAC & BERT, p. 288.

v 2018 *Deshayesites* gr. *latelobatus/involutus* – DELANOY *et al.*, p. 38, Fig. 26B.

v 2018 *Deshayesites* aff. *grandis* – DELANOY *et al.*, p. 38, Fig. 9B.

v 2019 *Deshayesites multicostatus* – BERSAC & BERT, p. 154, 161, Figs. 5, 7, 10, 12, 15, Pl. 2, figs. 6-8, 13-15, 19.

Material studied: 71 specimens from the Pont de la Cerise Member: 30 from Bed 405 of VAL (BERSAC & BERT, 2019, Fig. 7), 1 from Bed 415 of PPR (*ibid.*, Fig. 15) and 40 from Bed 415 of CHP (*ibid.*, Fig. 10). See the supplementary appendix for the complete list of the specimens with measurements.

Description: The shell is discoid to moderately evolute, with more or less covering whorls. The umbilical wall is steep and the flanks are flat or slightly convex. The largest observed specimen is 273 mm in diameter (SBC.06061-00006/CHP241) but is deformed (BERSAC & BERT, 2019, Pl. 2, figs.

13-15). R is measurable on 26 specimens: it varies from 16 to 36 with an average value of 24.65. Innermost whorls ($D < 10$ mm) are never preserved on the studied specimens and the ontogenetic stages A and B cannot consequently be studied. The observable ontogenetic sequence of the shell flanks starts with the stage C and is followed by the stage D, which have characteristics similar to the corresponding stages of *Deshayesites* sp. previously described. The stage D is followed by the adult stage E with straight, simple and thick ribs. The transition between these stages is more or less sudden, similar to the above described specimens. All intermediate forms are present between slender specimens with high rib density, high growth in whorl height and narrow whorl width (Pl. 2, fig. A) and robust ones with lower rib density and lower growth in whorl height (Pl. 3, figs. A-B).

The ventral area below $D=30$ mm is rarely preserved. When it is the case, a smooth siphonal band or an absence of smothering of the ornamentation on this area can be present according to the specimens. The end diameter of the smooth siphonal band (SSB) is measurable on 4 specimens (see supplementary appendix): it ranges from 14-19 mm (respectively on the specimens Pl. 4, figs. Q-R, and Pl. 4, fig. P) and the average value is 16.5 mm. The rib relief then progressively reappears on the ventral area. Throughout the ontogeny, the ventral area is rounded, except on the specimen SBC.06061-00003/VAL009 (Pl. 4, figs. F-G), where it is subtabulate in inner whorls.

The septal suture on the few specimens on which it is observable, is too poorly preserved to be described. No specimen has its peristome preserved.

Discussion: The range of variability is continuous within the sample and similar to that of the above studied sample. Consequently, the sample is thus considered monospecific. Among the 71 specimens of the sample, the key diagnostic SSB is measurable on only 4 of them. The mean value of this character is 16.5 mm in this sample, which suggests a specific assignation to the index species *D. multicostatus*. However, this result is in itself of poor significance because it is based on very few specimens. No specimen has a SSB value larger than 20 mm: this element only suggests that this sample is earlier than the *D. grandis* Subzone. After the smooth siphonal band, the rest of the ventral area of the studied specimens is rounded with no relief attenuation and no latero-ventral tubercles, which also corresponds to a character predominant in samples of Deshayesitidae earlier than the *D. grandis* Subzone. Only one fragmentary specimen presents a subtabulate ventral area without latero-ventral tubercles (Pl. 4, figs. F-G), which is a character usually predominant in the *D. grandis* Subzone. On the basis of these elements, we consider that the sample has to be assigned to *D. multicostatus*. In our opinion, the presence in the sample of only one specimen with a subtabulate ventral area does not consti-



tute evidence of polysubzonal time averaging within this sample (*i.e.*, a mixture of *Deshayesitidae* from the *D. multicosatus* and the *D. grandis* subzones). Conspecific samples having specimens with primitive characters and specimens with derived ones were described in literature in various groups of Ammonoidea (*e.g.*, TINTANT, 1963; DZIK, 1985 – the 'GAUSS Bell effect') including *Deshayesitidae* (MORENO-BEDMAR *et al.*, 2014). Moreover, the assignation of the sample to the *D. multicosatus* Subzone is consistent with the co-occurring ammonite fauna (see discussion in BERSAC & BERT, 2019).

Biostratigraphic distribution: *Deshayesites multicosatus* Subzone, *Deshayesites deshayesi* Zone.

***Deshayesites grandis* SPATH, 1930**

Pl. 5, figs. I-N; Pl. 6, figs. A-G

1930 *Deshayesites grandis* sp. nov. – SPATH, Pl. XVII, figs. 2a, b.

2012 *Deshayesites grandis* – BERSAC & BERT, p. 251.

v 2019 *Deshayesites grandis* – BERSAC & BERT, p. 154, 165, Figs. 5, 10, 12, 15, Pl. 3, figs. 10-12.

Material studied: 22 specimens from the *Toxoceratoides* Bed of the Les Graous Member of GRS1 (BERSAC & BERT, 2019, Fig. 5), CHP (*ibid.*, Fig. 10) and CLE (*ibid.*, Fig. 12). See the supplementary appendix for the complete list of the specimens with measurements.

Description: The shell is discoid to moderately evolute, with more or less covering whorls. The umbilical wall is steep. The flanks are flat or slightly convex. The maximum observed diameter is 49 mm (SBC.06061-00001/GRS351, Pl. 6, figs. A-B). R is measurable on 10 specimens and varies from 18 to 31 with an average value of 23.4. Innermost whorls are never preserved on the studied specimens and the ontogenetic stages A and B cannot consequently be studied. Ornamentation is represented by more or less dense and flexuous ribs, with more or less regular alternation between primary and intercalary ribs. Intercalary ribs are usually more numerous and emerge at various heights on the flanks. The small size of the specimens prevents differentiation stage C from the stage D, and to observe the adult stage E. Periumbilical rib thickening are occasionally present. The ribs can be wedge shaped or not and the rib relief can be sharp or more attenuated, especially in the middle part of the flanks. Shape of the specimens vary between a slender morphology with high rib density, high growth in whorl height (Pl. 5, figs. M-N) and narrow whorl width and a more robust morphology with lower rib density and lower growth in whorl height (Pl. 5, figs. A-C).

When observable, the ventral area in inner whorls always presents a smooth siphonal band. SSB (Pl. 6, fig. E) was able to be measured on 7 specimens: ranging from 16 to 24 mm with an average value of 20.43 mm. After a brief attenuated siphonal band, the ventral area is subtabulate except for one poorly preserved specimen, where it is rounded (SBC.06061-00006/CHP361).

On the few specimens on which it is observable, the septal suture is too poorly preserved to be described. No specimen has its peristome preserved.

Discussion: The range of variability is continuous within the sample and similar to that of the above studied samples. Consequently, the sample is considered monospecific. Despite the small size of the specimens, the range of variability of R is similar to that of the sample of *D. multicosatus*. Taking into account that the studied material is deformed, the average value of SSB tentatively corresponds to the species *D. grandis*. The ventral area following the smooth siphonal band is subtabulate for most of the specimens, also characteristic of *D. grandis*. We consequently assign this sample to that species.

Biostratigraphic distribution: *Deshayesites grandis* Subzone, *Deshayesites deshayesi* Zone.

***Dufrenoyia* KILIAN & REBOUL, 1915**

***Dufrenoyia furcata* (J. de C. SOWERBY, 1836)**

Pl. 6, figs. H-X1; Pl. 7, figs. A-Z

1836 *Ammonites furcatus* sp. nov. – J. de C. SOWERBY in FITTON, Pl. XIV, fig. 17.

? 1971 *Dufrenoyia dufrenoyi* – COTILLON, 1971, p. 146.

? 1982 *Dufrenoyia furcata* – RAGAZZI, p. 74, 76.

2005 *Dufrenoyia furcata* – DUTOIR, Pl. 29, figs. 10-16.

v 2011 *Dufrenoyia* sp. – BERT & BERSAC, Fig. 41.

2012 *Dufrenoyia furcata* – BERSAC & BERT, p. 253.

v 2018 *Dufrenoyia dufrenoyi* – DELANOY *et al.*, Figs. 8D, 20E-H.

v 2019 *Dufrenoyia furcata* – BERSAC & BERT, p. 154, 165, Figs. 5, 9-10, 12, 15, Pl. 5, figs. 5-9.

Material studied: 210 specimens from the Les Graous Member of GRS1 (BERSAC & BERT, 2019, Fig. 5), GRO (*ibid.*, Fig. 9), CHP (*ibid.*, Fig. 10) and PPR (*ibid.*, Fig. 15). See the supplementary appendix for the complete list of the specimens with measurements.

Description: The shell is discoid to moderately evolute, with whorls covering about 50% of the flanks. The umbilical wall is steep. The flanks are flat or slightly convex. The maximum observed diameter is 190 mm (SBC.06061-00001/GRS437, on a poorly preserved specimen). No fragmentary specimens of potentially larger diameter seem to be present in the sample (*i.e.*, with a larger H than specimen SBC.06061-00001/GRS437). R was measured on 96 specimens; it varies from 9 to 30 with an average value of 17.67. Innermost whorls are never preserved on the studied specimens and the ontogenetic stages A and B cannot be studied. The observable ontogenetic sequence of the shell flanks starts with the stage C and is followed by the stage D, which have characteristics similar to those of the corresponding stages of the *Deshayesites* previously described. No specimen of the sample is enough developed to exhibit the adult stage E. The transition between the stages C and D can be more or less sudden. We observe a continuous variation between slender specimens with high rib density, high growth in whorl height and narrow whorl width (Pl. 7, figs. H-I) and very robust specimens with very low rib density, low growth in whorl height and wider whorl width (Pl. 7, figs. R-S).



The ventral area in the innermost whorls is flat, with a smooth siphonal band and without latero-ventral tubercles. These tubercles arise from approximately $D=10$ mm (Pl. 7, figs. V, X-Y). They are very discrete in slender specimens (Pl. 7, figs. T-U) and larger in the more robust ones (Pl. 6, figs. W1-X1). Their shape is variable, from conical with oval or rounded base (Pl. 6, figs. H1-I1), to claviform (Pl. 6, figs. S1-T1), this latter shape being less frequent. The smooth siphonal band is still present between the latero-ventral tubercles. SSB was measured on 18 specimens, all from beds 100, 102 and 104 of GRS1 section. It ranges from 16 to 37 mm and its average value is 24.89 mm. At bed level, SSB is 24.9 mm on average for Bed 100 (10 specimens), 24.5 mm for Bed 102 (6 specimens) and 26 mm for Bed 104 (2 specimens). There does not appear to be correlation between the SSB value and the robustness of the specimens. From the end of the smooth siphonal band, the ribs cross the ventral area between each pair of tubercles, with more and more relief (Pl. 7, figs. E-F). Then, the tubercles vanish and the venter becomes subtabulate without rib attenuation (Pl. 6, figs. W1-X1). Due to the fragmentary state of the studied material, the end diameter of the tubercles could have been measured for only two specimens and is 40 and 45 mm (Pl. 7, figs. C, J). Within the sample, various specimens have their tubercles present over $D=40-50$ mm and the few specimens larger than $D=80$ mm do not exhibit tubercles at this diameter.

On the few specimens on which it is observable, the septal suture is too poorly preserved to be described. No specimen has its peristome preserved.

Discussion: The range of variability is continuous within this sample and similar to that of the previously studied samples. Such variability has been already observed in different samples of *Dufrenoyia* (MARTIN, 2003; DUTOIR, 2005; GARCIA & MORENO-BEDMAR, 2010; LEHMANN & BULOT, 2020). Consequently, our sample is considered monospecific. It exhibits no evidence of dimorphism, as for the above studied samples. Specimens are abundant in CHP section and from Bed 98 to 105 in GRS1 section. The small value of 24.89 mm of SSB and the mostly rounded to oval latero-ventral tubercles of these specimens are primitive characters in *Dufrenoyia* (DUTOIR, 2005; BERSAC & BERT, 2012). The end diameter of the latero-ventral tubercles is also a diagnostic character in *Dufrenoyia*. It has a value of 40 and 45 mm in the only two specimens in which it could have been measured, which is very low (the limit between the primitive species *D. furcata* and its derived *D. dufrenoyi* is set at 70 mm for this character according to BERSAC and BERT, 2012). On the basis of these elements, we interpret these specimens from CHP and from the interval between the beds 98 and 105 of GRS1 as belonging to the primitive species *D. furcata*. It implies that some very slender specimens, of which the characters are similar to the taxon *Dufrenoyia transitoria* CASEY, 1961,

are here assigned to *D. furcata*. This is in line with a synonymy between *D. transitoria* and *D. furcata* (see discussion about the synonymy between these species in DUTOIR, 2005; BERSAC & BERT, 2012; LEHMANN & BULOT, 2020).

The average value of 24.89 mm for SSB in the herein studied sample is very close and consistent with the lowest average value of 25 mm retained for *D. furcata* according to BERSAC and BERT (2012, Fig. 18).

The absence of the adult stage E within the sample is due to the immaturity/fragmentary state of the specimens. DELANOY *et al.* (2018, Fig. 20E) figured a $D \approx 209$ mm specimen from their bed 110 of GRS1 section (here Bed 98 in the revised lithology; see BERSAC & BERT, 2019, for an explanation). This specimen is the largest *Dufrenoyia* found in the LFAB so far and exhibits the beginning of the adult stage E (the adult size of a *Dufrenoyia* seems to range from 250 to 420 mm, see CASEY, 1964, 1980; BERSAC & BERT, 2012, p. 233).

Biostratigraphic distribution: *Dufrenoyia furcata* Subzone, *Dufrenoyia furcata* Zone.

***Dufrenoyia dufrenoyi* (ORBIGNY, 1841)**

Pl. 7, figs. A1-B1

1841 *Ammonites dufrenoyi* sp. nov. - ORBIGNY, Pl. 33, figs. 4-6.

2005 *Dufrenoyia dufrenoyi* - DUTOIR, Pl. 29, figs. 10-16

v 2019 *Dufrenoyia dufrenoyi* - BERSAC & BERT, p. 154, 165-166, Fig. 5, Pl. 5, figs. 30-32.

Material studied: 20 specimens from the beds 110 (14 specimens) and 113 (6 specimens) of GRS1 (BERSAC & BERT, 2019, Fig. 5). See the supplementary appendix for the complete list of the specimens with measurements.

Description: The specimens are fragmentary and deformed. The largest specimen is estimated to be 37 mm in diameter (SBC.06061-00001/GRS 821, Pl. 7, fig. B1). R varies from 15 to 24. The size of the specimens is too small to differentiate the stage C from the stage D, and to express the adult stage E. All the specimens on which the ventral area is preserved exhibit a smooth siphonal band on the whole shell. Consequently, SSB could not be measured on any of them and it is obviously higher than 37 mm. The latero-ventral tubercles are all claviform. The septal suture is never preserved.

Discussion: Despite its poor preservation, the specimens of this sample have a variability included within the same scheme of the previously studied samples. We consequently regard these specimens as being conspecific until proven otherwise. Various elements suggest that this sample of *Dufrenoyia* presents derived characters: (1) the smooth siphonal band is present on the entirety of the preserved part of the shell of all the specimens, including the two largest ones (SBC.06061-00001/GRS819 with $D=34$ mm and SBC.06061-00001/GRS821, Pl. 7, fig. B1 with $D \approx 37$ mm), suggesting a high mean value of SSB in the sample and (2) the latero-ventral tubercles are always claviform. This latter element is characteristic of the species *D. dufrenoyi* ac-



cording to DUTOIR (2005), to which we therefore assign the sample. The range of variability of our sample is narrower than that of *D. furcata*, which is probably due to its smaller size.

Biostratigraphic distribution: *Dufrenoyia dufrenoyi* Subzone, *Dufrenoyia furcata* Zone.

4. Discussion and conclusions

In the present work, we studied a large sample of Deshayesitidae from a relatively wide stratigraphic interval of the LFAB. Despite the deformed and fragmentary state of most of the specimens, we confidently identified several biostratigraphically significant species and their corresponding biostratigraphy at subzonal level in most of the cases.

In the strata older than the *D. grandis* Subzone, the identification criteria used in the present work are restricted to the inner whorls only (septal suture is absent or too poorly preserved to be studied). If the samples from these levels are poorly preserved, their identification becomes particularly difficult. This is the case for the sample of the top of the Hauterivian-Aptian limestones of the LFAB, that we could not identify at species level (*Deshayesites* sp.). The age of its original bed was estimated by the co-occurring ammonite fauna. In the *Ammonitoceras* Level of the LFAB, no septal suture could be studied, but only 4 specimens, of the 71 collected have their inner whorls well enough preserved to be studied, allowing us to consider the sample to belong to the species *D. multicosatus*. In this case, the co-occurring ammonite fauna only helps to confirm the age and thus the identification of the sample (since *D. multicosatus* is a subzonal index).

In the more recent subzones, the taxonomic identification of the Deshayesitidae is generally easier because, due to their neotenic evolution, the identification characters occupy a larger part of the shell and thus are more visible and susceptible to be preserved (longer smooth siphonal band, subtabulate ventral area or latero-ventral tubercles on the phragmocone).

All these elements point out the necessity of identifying additional biostratigraphically significant ammonite taxa for the lower Aptian (as it is already the case with the Roloboceratinae), especially for levels below the *D. grandis* Subzone.

Acknowledgements

We warmly thank Mikel LÓPEZ-HORGUE (University of the Basque Country, Leioa), Antoine PICTET (Muséum cantonal des sciences naturelles, Lausanne) and an anonymous reviewer for their thorough reviews that improved the manuscript. We are grateful to Steven EAGAR for a linguistic correction of the manuscript.



Bibliographic references

- BARABOSHKIN E.J. (2004).- The Lower Cretaceous ammonite zonal standard of the Boreal Realm.- *Bulletin of Moscow Society of Naturalists*, t. 79, vol. 5, p. 44-68 [in Russian].
- BARRAGÁN R. & SZIVES O. (2007).- New records of *Mathoceras* CASEY (Deshayesitidae, Ammonoidea) from the Aptian (Lower Cretaceous) of Mexico and Hungary: Biostratigraphic and paleobiogeographic implications.- *Geobios*, Villeurbanne, vol. 40, p. 21-30.
- BERSAC S. & BERT D. (2012).- Ontogenesis, variability and evolution of the Lower Greensand Deshayesitidae (Ammonoidea, Lower Cretaceous, Southern England): Reinterpretation of literature data; taxonomic and biostratigraphic implications.- *Annales du Muséum d'Histoire Naturelle de Nice*, Nice, vol. 27, p. 197-270.
- BERSAC S. & BERT D. (2015).- Two ammonite species under the same name: Revision of *Deshayesites deshayesi* (d'ORBIGNY, 1841) based on topotype material (Lower Aptian, Lower Cretaceous, Northeast of France).- *Annales de Paléontologie*, Paris, vol. 101, p. 265-294.
- BERSAC S. & BERT D. (2018).- Revision of the lower Aptian (Lower Cretaceous) ammonite species *Chelonicerus cornuelianum* (d'ORBIGNY, 1841).- *Annales de Paléontologie*, Paris, vol. 104, p. 45-70.
- BERSAC S. & BERT D. (2019).- The lower Aptian ammonites of the Les Ferres Aptian Basin (Lower Cretaceous, Southeast of France). Part I: Introduction and biostratigraphy.- *Carnets Geol.*, Madrid, vol. 19, p. 149-183. DOI: 10.4267/2042/70292
- BERSAC S., BERT D. & MATRION, B. (2012).- Revision of the index-species *Deshayesites deshayesi* (Ammonoidea, lower Aptian, Lower Cretaceous): Taxonomic and biostratigraphic consequences. In: BERT D. & BERSAC S. (eds), First meeting of the Research Group for Paleobiology and Biostratigraphy of the Ammonites.- *Boletín del Instituto de Fisiografía y Geología*, Rosario, vol. 82, p. 31-33.
- BERT D. (2013).- Factors of intraspecific variability in ammonites, the example of *Gassendicerus alpinum* (d'ORBIGNY, 1850) (Hemihoplitidae, Upper Barremian).- *Annales de Paléontologie*, Paris, vol. 100, no. 3, p. 217-236
- BERT D. (2019).- Les lois de la variabilité intraspécifique chez les ammonites.- *Les Cahiers de la Réserve Naturelle de Sainte-Victoire*, Aix-en-Provence, numéro spécial congrès APF 2019, p. 12.
- BERT D. & BERSAC S. (2011).- Buts et méthodes du "levé de coupe".- *Fossiles*, Saint-Julien-du-Pinet, vol. 6, p. 49-61.
- BERT D., BERSAC S., CANUT L. & BELTRAND B. (2023).- Can the intraspecific laws of variation be used as a predictive model for understanding species with insufficient data? The example of the early Heteroceratidae in their evolutionary context (heteromorph ammonites, Tethys upper Barremian).- *Cretaceous Research*, vol. 151, 33 p.



- BOGDANOVA T.N. & MIKHAILOVA I.A. (2004).- Origin, evolution and stratigraphic significance of the superfamily Deshayesitaceae STOYANOW, 1949.- *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, Brussels, vol. 74, p. 189-243.
- CASEY R. (1964).- A monograph of the Ammonoidea of the Lower Greensand part. V.- *Palaeontographical Society* (1963), London, p. 289-398.
- CASEY R. (1980).- A monograph of the Ammonoidea of the Lower Greensand, part IX.- *Palaeontographical Society*, London, p. 633-660.
- CASEY R., BAYLISS H.M. & SIMPSON M.I. (1998).- Observations on the lithostratigraphy and ammonite succession of the Aptian (Lower Cretaceous) Lower Greensand of Chale Bay, Isle of Wight, UK.- *Cretaceous Research*, vol. 19, p. 511-535.
- COTILLON P. (1971).- Le Crétacé inférieur de l'Arc subalpin de Castellane entre l'Asse et le Var. Stratigraphie et sédimentologie.- *Mémoires du Bureau de Recherche Géologique et Minière*, Paris, no. 68, 313 p.
- DE BAETS K., BERT D., HOFFMANN R., MONNET C., YACOBucci M. & KLUG C. (2015).- Ammonoid intra-specific variability. In: KLUG C. et al. (eds.), *Ammonoid paleobiology: From anatomy to ecology*.- *Topics in Geobiology*, New-York - NY, vol. 43, p. 359-426.
- DELANOY G., BAUDOUIN C., PICTET A., DELATTRE P. & PÉNAGÉ E. (2018).- Ancyloceratidae (Ammonoidea, Ancyloceratoidea) nouveaux ou peu connus de l'Aptien inférieur des Alpes-Maritimes (Sud-Est de la France).- *Annales du Muséum d'Histoire Naturelle de Nice*, vol. 32, p. 35-90.
- DELANOY G., BAUDOUIN C., PICTET A., MORENO-BEDMAR J., FRAU C. & MATRION B. (2022).- The genera *Roloboceras* CASEY, 1954, and *Megatyloceras* HUMPHREY, 1949 (Ammonoidea, Ancyloceratina, Douvilleiceratidae), from the Lower Aptian of Ardèche (SE France) - Taxonomic and biostratigraphic implications.- *Carnets Geol.*, Madrid, vol. 22, no. 2, p. 7-109. DOI: 10.2110/carnets.2022.2202
- DUTOIR Y. (2005, unpublished).- Biostratigraphie, évolution et renouvellements des ammonites de l'Aptien supérieur (Gargasien) du bassin vocontien (Sud-Est de la France).- PhD thesis, Université Claude Bernard, Lyon 1, 280 p.
- DZIK J. (1985).- Typologic versus population concept of chronospecies: Implication for ammonite biostratigraphy.- *Acta Paleontologica Polonica*, Warsaw, vol. 30, no. 1-2, p. 71-92.
- ETAYO-SERNA F. (1979).- Zonation of the Cretaceous of Central Colombia by ammonites.- *Publicaciones geológicas especiales del Ingeominas*, Bogotá, no. 2, p. 1-186.
- FITTON W.H. (1836).- Observations on some of the strata between the Chalk and the Oxford Oolithe in the South-east England. Including: Appendix A, descriptive notes respecting the shells figured in Pls. XI-XXIII by J. de C. SOWERBY.- *Transactions of the Geological Society*, London, vol. IV, no. 2, p. 103-390.
- FRAU C. (2020).- Stable carbon-isotope chemostratigraphy versus ammonite biostratigraphy: Data from around the Barremian/Aptian boundary (Lower Cretaceous).- *STRATA*, Gaillac, série 2e, vol. 56, p. 1-31.
- FRAU C. & DELANOY G. (2022).- Taxonomic notes on some Barremian-Aptian cephalopods from the Station de Cassis section and surrounding sites, Bouches-du-Rhône, southern France.- *STRATA*, Gaillac, série 2e, vol. 58, p. 1-45.
- FRAU C., DELANOY G. & BAUDOUIN C. (2023).- A new insight into the lower Aptian Roloboceratinae CASEY, 1961 (Douvilleiceratidae, Ammonoidea) from southern France.- *STRATA*, Gaillac, série 2e, vol. 59, p. 1-21.
- FRAU C., PICTET A., SPANGENBERG J.E., MASSE J.-P., TENDIL A.J.-B. & LANTEAUME C. (2017).- New insights on the age of the post-Urgonian marly cover of the Apt region (Vaucluse, SE France) and its implications on the demise of the North Provence carbonate platform.- *Sedimentary Geology*, vol. 359, p. 44-61.
- GARCIA R. & MORENO-BEDMAR J.A. (2010).- *Dufrenoyia furcata* (SOWERBY, 1836), ammonite del Aptiense inferior (Cretácico inferior) del Perello (Tarragona). In: MORENO-AZANZA M., DIAZ-MARTINEZ I., GASCA J.M., MELERO-RUBIO M., RABAL-GARCÉS R. & SAUQUÉ, V. (eds.), VIII Encuentro de Jovenes Investigadores en Paleontología volumen de actas.- *Cidaris*, Elche, no. 30, p. 129-137.
- GARCÍA-MONDÉJAR J., OWEN H. G., RAISOSSADAT N., MILLÁN M. I. & FERNÁNDEZ-MENDIOLA P. A. (2009).- The early Aptian of Aralar (northern Spain): Stratigraphy, sedimentology, ammonite biozonation and OAE1.- *Cretaceous Research*, vol. 30, p. 434-464.
- GRANIER B. (2022).- Tethysian, Tethyan or ... Tethys Ocean and Tethys.- *Carnets Geol.*, Madrid, vol. 22, Editorial Note 1, p. 681-683. DOI: 10.2110/carnets.2022.22EN1
- LEHMANN J. & BULOT L.G. (2020).- A *Dufrenoyia* (Ammonoidea, Deshayesitidae) fauna from Germany: Evidence for *D. furcata* Zone deposits at the lower-upper Aptian boundary.- *Cretaceous Research*, vol. 116, article 104546, 14 p.
- LEHMANN J., BARGEN D. von, ENGELKE J. & CLABEN J. (2015).- Morphological variability in response to palaeoenvironmental change - a case study on Cretaceous ammonites.- *Lethaia*, Copenhagen, vol. 49, no. 1 (2016), p. 73-86
- MARTIN E. (2003).- Intraspecific variation of *Dufrenoyia furcata* SOWERBY (Ammonoidea, Ancylocerataceae, Deshayesitidae) from the Gargasien in the Vaucluse (Southern France).- *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, Hamburg, no. 87, p. 115-124.
- MORENO J.A. & COMPANY M. (2007).- Caracterización de dimorfismo morfodimensional en *Deshayesites deshaysi* (LEYMERIE in d'ORBIGNY) (Ancyloceratina, Ammonoidea).- XXIII Jornadas de la Sociedad Española de Paleontología,



- Libro de Resúmenes, Caravaca de la Cruz (Murcia), p. 153-154.
- MORENO-BEDMAR J.A., BARRAGAN R., DELANOY G., COMPANY M. & SALAS R. (2014).- Review of the early Aptian (Early Cretaceous) ammonoid species *Deshayesites deshayesi* (d'ORBIGNY, 1841).- *Cretaceous Research*, vol. 51, p. 341-360.
- MORENO-BEDMAR J.A., CASADOS-MONROY A., FRAU C., PICTET A., CHAVEZ CABELLO G. & ESQUIVEL-MACÍAS C. (2018).- Ammonite biostratigraphy of the Sierra del Patron section (Durango State, Mexico) and its bearing on the lower/upper Aptian boundary of the Central Atlantic Province.- *Cretaceous Research*, vol. 88, p. 100-110.
- MORENO-BEDMAR J.A., COMPANY M., BOVER-ARNAL T., SALAS R., DELANOY G., MARTÍNEZ R. & GRAUGES A. (2009).- Biostratigraphic characterization by means of ammonoids of the lower Aptian Oceanic Anoxic Event (OAE 1a) in the eastern Iberian Chain (Maestrat Basin, eastern Spain).- *Cretaceous Research*, vol. 30, p. 864-872.
- MORENO-BEDMAR J.A., COMPANY M., BOVER-ARNAL T., SALAS R., DELANOY G., MAURRASSE F.J., GRAUGES A. & MARTÍNEZ R. (2010).- Lower Aptian ammonite biostratigraphy in the Maestrat Basin (Eastern Iberian Chain, Eastern Spain). A Tethyan transgressive record enhanced by synrift subsidence.- *Geologica Acta*, Barcelona, vol. 8, no. 3, p. 281-299.
- MORENO-BEDMAR J.A., COMPANY M. & GUERRERO-SUASTEGUI M. (2023).- Un ammonite del género *Juandurhamiceras* del Aptiano de Campo Morado, Arcelia, estado de Guerrero, México.- *Paleontología Mexicana*, Mexico, vol. 12, no. 1, p. 1-8.
- MORENO-BEDMAR J.A., COMPANY M., SANDOVAL J., TAVERA J.M., BOVER-ARNAL T., SALAS R., DELANOY G., MAURRASSE F.J.-M.R. & MARTINEZ R. (2012).- Lower Aptian ammonite and carbon isotope stratigraphy in the eastern Prebetic Domain (Betic Cordillera, southeastern Spain).- *Geologica Acta*, Barcelona, vol. 10, no. 4, p. 333-350.
- OBATA I. & MATSUKAWA M. (2007).- Barremian-Aptian (Early Cretaceous) ammonoids from the Choshi Group, Honshu (Japan).- *Cretaceous Research*, vol. 28, p. 363-391.
- ORBIGNY A. d' (1841).- Paléontologie Française. Tome premier. Terrains crétacés. Céphalopodes.- Imprimerie Masson, Paris, p. 121-430.
- RAGAZZI M. (1982, unpublished).- L'Aptien dans les Alpes Maritimes: Stratigraphie, paléoécologie, sédimentologie.- PhD thesis, Université de Nice, 224 p.
- REBOULET S., SZIVES O., AGUIRRE-URRETA M.B., BARRAGAN R., COMPANY M., FRAU C., KAKABADZE M.V., KLEIN J., MORENO-BEDMAR J.A., LUKENEDER A., PICTET A., PLOCH I., RAISOSSADAT S. N., VAŠÍČEK Z., BARABOSHKIN E.J. & MITTA V.V. (2018).- Report on the 6th International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the "KILIAN Group" (Vienna, Austria, 20th August 2017).- *Cretaceous Research*, vol. 91, p. 100-110.
- RENZ O. (1982).- The Cretaceous ammonites of Venezuela.- Maraven Editor, Caracas, 132 p.
- ROGOV M.A. & MIRONENKO A.A. (2016).- Ammonite shell size changes in response of the Early Aptian anoxic event (preliminary data). In: BARABOSHKIN E.Y. (ed.), Cretaceous system of Russia and CIS countries: Problems of stratigraphy and paleogeography.- Proceeding of the 8th all-Russian meeting (26 September-3 October 2016, Republic of Crimea, Russian Federation).- ChernomorPRESS, Simferopol (Ukraine), p. 236-238.
- ROPOLO P., CONTE G., GONNET R., MASSE J.-P. & MOULLADE M. (1998).- Les faunes d'ammonites du Barrémien supérieur/Aptien inférieur (Bédoulien) dans la région stratotypique de Cassis-La Bédoule (SE France) : État des connaissances et propositions pour une zonation par Ammonites du Bédoulien-type.- *Géologie Méditerranéenne*, Marseille, t. XXV, no. 3-4, p. 167-175.
- ROPOLO P., MOULLADE M., GONNET R., CONTE G. & TRONCHETTI G. (2006).- The Deshayesitidae STOYANOV, 1949 (Ammonoidea) of the Aptian historical stratotype region at Cassis-La Bédoule (SE France).- *Carnets Geol.*, Madrid, Memoir 2006/01 (CG2006_M01), 46 p. DOI: 10.4267/2042/4744
- ROPOLO P., MOULLADE M., CONTE G. & TRONCHETTI G. (2008).- About the stratigraphic position of the Lower Aptian *Roloboceras hambrovi* (Ammonoidea) level.- *Carnets Geol.*, Madrid, Letter 2008/03 (CG2008 L03), 7 p. DOI: 10.4267/2042/18124
- SPATH L.F. (1930).- On some Ammonoidea from the Lower Greensand.- *Annals and Magazine of Natural History* (serie 10), London, no. 5, p. 417-464.
- SWINNERTON H. (1935).- The rocks below the Red Chalk of Lincolnshire and their cephalopod fauna. *Quaternary Journal of the Geological Society*, London, vol. XCI, 446 p.
- SZIVES O., MORENO-BEDMAR J.A., AGUIRRE-URRETA B., COMPANY M., FRAU C., LÓPEZ-HORGUE M., PICTET A., PLOCH I., SALAZAR C., BARRAGÁN R., LATIL J.-L., LEHMANN J., ROBERT E & REBOULET S. (2024).- Report on the 7th International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the KILIAN Group (Warsaw, Poland, 21st August 2022): State of the art on the current Standard Ammonite Zonation of the Western Tethyan Mediterranean Province.- *Cretaceous Research*, vol. 153, 14 p.
- TINTANT H. (1963).- Les Kosmocerotidés du Callovien inférieur et moyen d'Europe occidentale. Essai de paléontologie quantitative.- Publications de l'Université de Dijon, vol. XXIX, Les Presses Universitaires de France, Paris, 491 p.
- YOUNG K. (1974).- Lower Albian and Aptian (Cretaceous) ammonites of Texas.- *Geoscience and Man*, Baton Rouge - LA, vol. 8, p. 175-228.



Plates

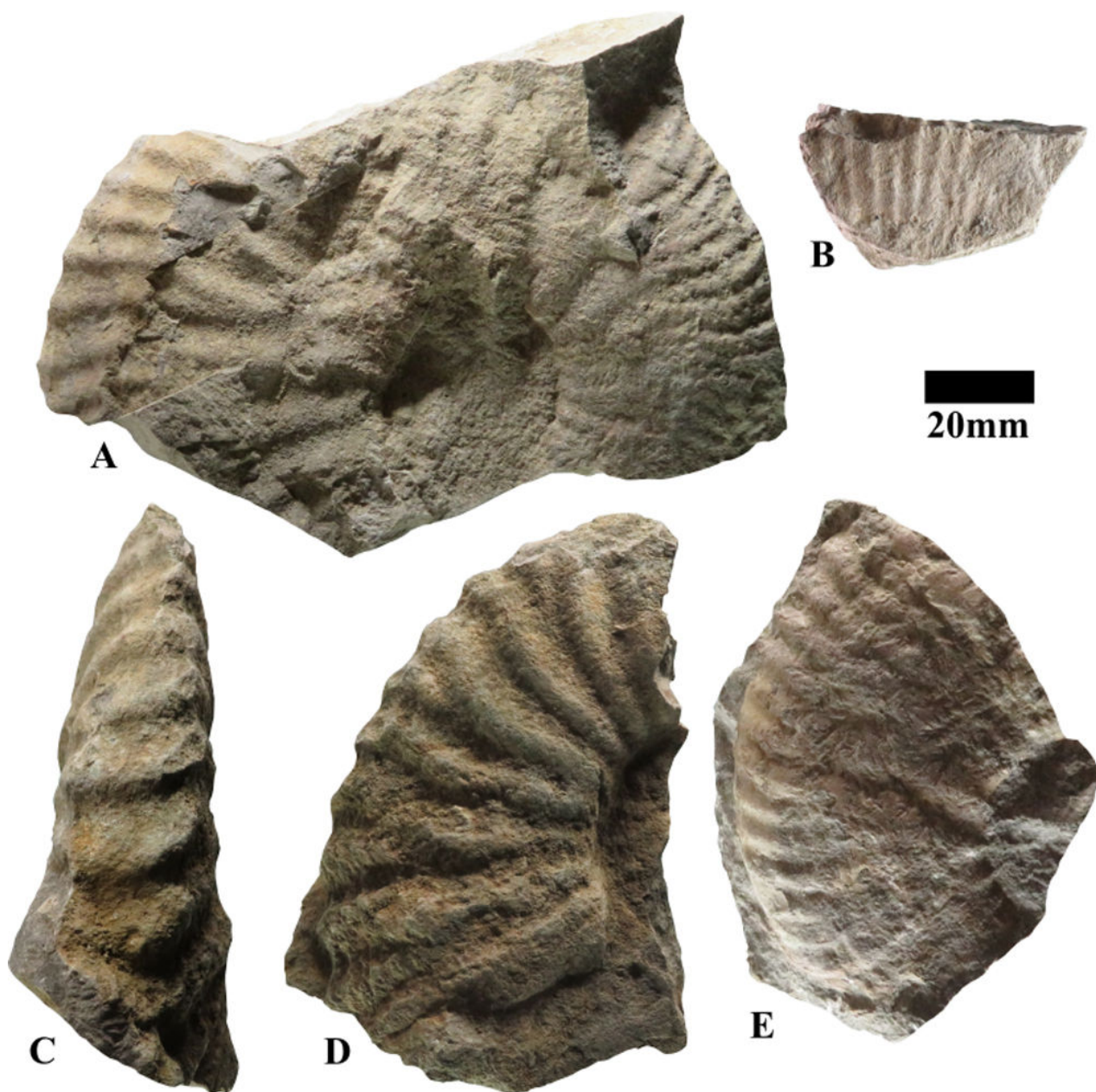


Plate 1: *Deshayesites* sp. from the last beds of the Hauterivian-Aptian limestones and of the Combe de Joinet Member (*Deshayesites forbesi* Zone) of CRS section. **A:** SBC.06061-00008/CRS017, Bed 399. **B:** SBC.06061-00008/CRS016, Bed 403. **C-D:** SBC.06061-00008/CRS019, Bed 400. **E:** SBC.06061-00008/CRS021, Bed 400.



Plate 2: *Deshayesites multicosatus* from the *Ammonitoceras* Level (top of the Pont de la Cerise Member, *Deshayesites deshayesi* Zone, *Deshayesites multicosatus* Subzone) of CHP section's Bed 415. **A:** SBC.06061-00006/CHP368. **B-C:** SBC.06061-00006/CHP373.



A


20mm



C



B



Plate 3: *Deshayesites multicosatus* from the *Ammonitoceras* Level (top of the Pont de la Cerise Member, *Deshayesites deshayesi* Zone, *Deshayesites multicosatus* Subzone) of CHP section's Bed 415. **A-B:** SBC.06061-00006/CHP371. **C:** SBC.06061-00006/CHP292.





Plate 4: *Deshayesites multicostatus* from the *Ammonitoceras* Level (top of the Pont de la Cerise Member, *Deshayesites deshayesi* Zone, *Deshayesites multicostatus* Subzone). **A-B:** SBC.06061-00006/CHP369, CHP section, Bed 415. **C:** SBC.06061-00003/VAL037, VAL section, Bed 405. **D-E:** SBC.06061-00003/VAL040, VAL section, Bed 405. **F-G:** SBC.06061-00003/VAL009, VAL section, Bed 405. **H-I:** SBC.06061-00003/VAL020, VAL section, Bed 405. **J-L:** SBC.06061-00003/VAL039, VAL section, Bed 405. **M-N:** SBC.06061-00003/VAL018, VAL section, Bed 405. **O-P:** SBC.06061-00003/VAL012, VAL section, Bed 405. **Q-R:** SBC.06061-00003/VAL017, VAL section, Bed 405. **S-T:** SBC.06061-00009/PPR004, PPR section, top of Bed 414. **U-V:** SBC.06061-00001/GRS115, GRS1 section, top of Bed 96.

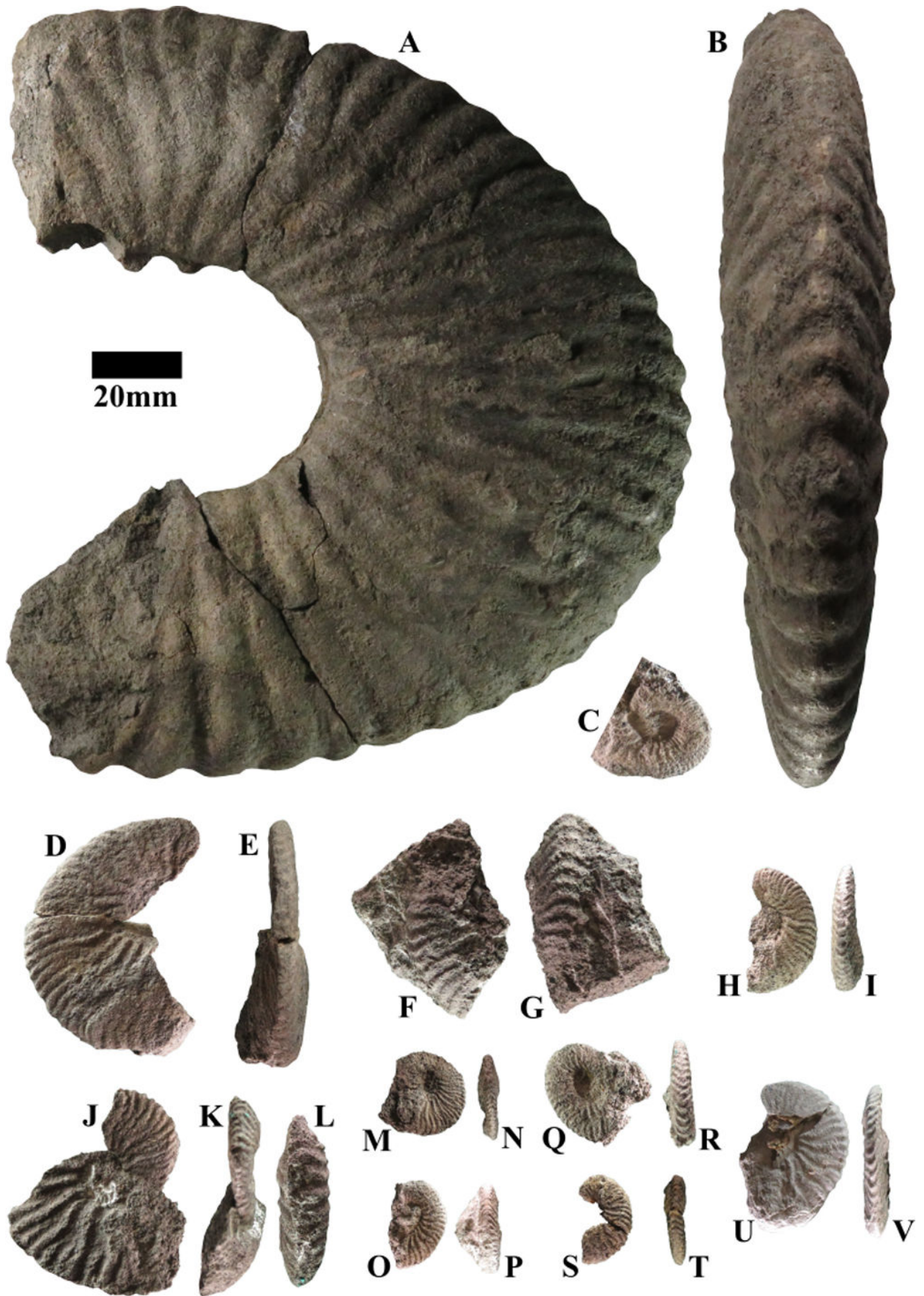




Plate 5: Black dot: last septal suture. **A-H:** *Deshayesites multicostatus* from the *Ammonitoceras* Level (top of the Pont de la Cerise Member, *Dehayesites deshayesi* Zone, *Deshayesites multicostatus* Subzone) of CHP section's Bed 415. **A-B:** SBC.06061-00006/CHP167. **C:** SBC.06061-00006/CHP294. **D:** SBC.06061-00006/CHP382. **E-F:** SBC.06061-00006/CHP385. **G-H:** SBC.06061-00006/CHP390. **I-N:** *Deshayesites grandis* from the *Toxoceratoides* Bed (base of Les Graous Member, *Dehayesites deshayesi* Zone, *Deshayesites grandis* Subzone) of CHP section's Bed 416. **I-J:** SBC.06061-00006/CHP391. **K-L:** SBC.06061-00006/CHP395. **M-N:** SBC.06061-00006/CHP392.

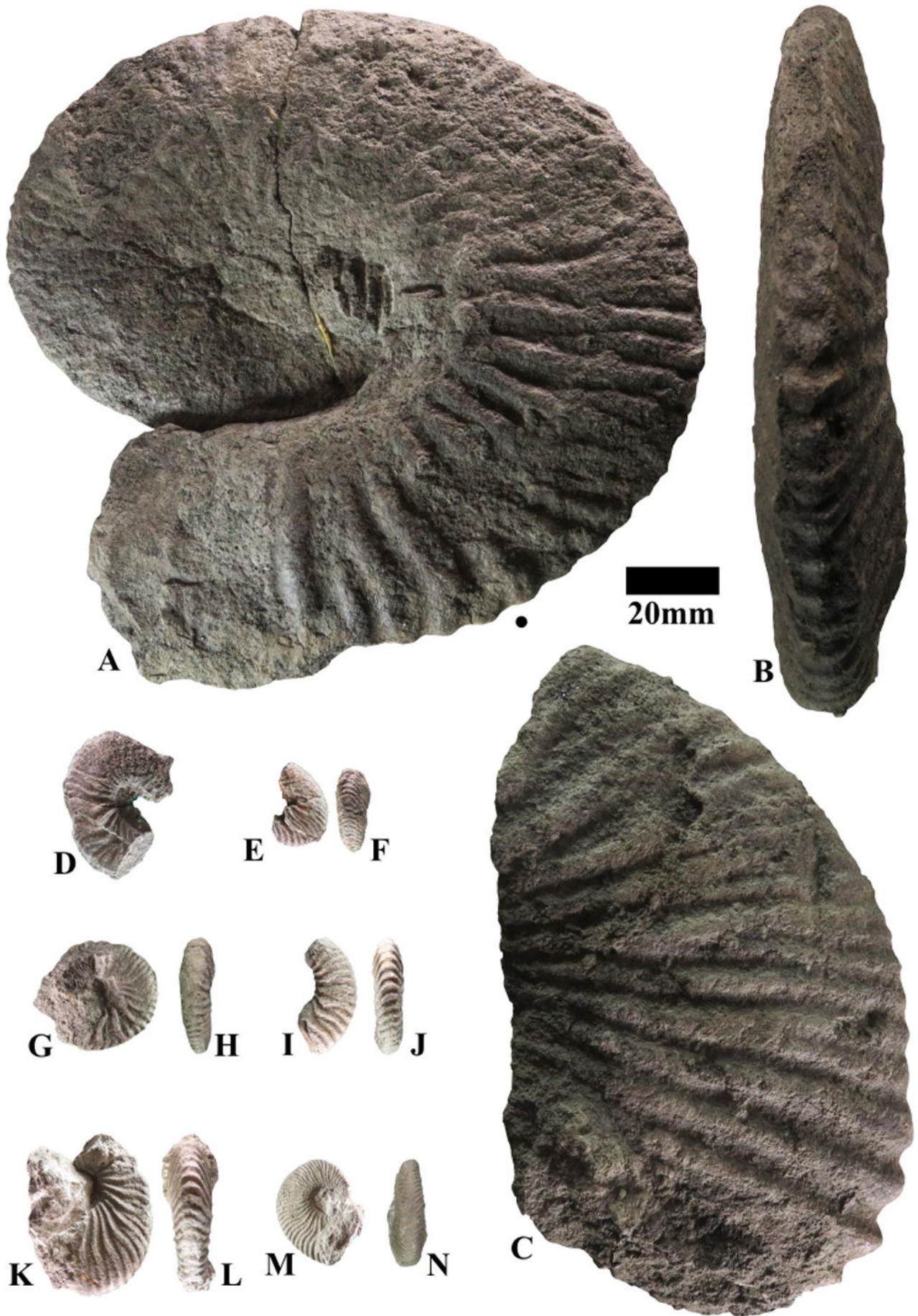




Plate 6: Black dot: last septal suture. **A-G:** *Deshayesites grandis* from the *Toxoceratoides* Bed (base of Les Graous Member, *Deshayesites deshayesi* Zone, *Deshayesites grandis* Subzone). **A-B:** SBC.06061-00001/GRS351, GRS1 section, Bed 97. **C:** SBC.06061-00001/GRS352, GRS1 section, Bed 97. **D-E:** SBC.06061-00001/GRS353, GRS1 section, Bed 97. **F-G:** SBC.06061-00006/CHP118, CHP section, Bed 416. **H-X1:** *Dufrenoyia furcata* from the Les Graous Member (*Dufrenoyia furcata* Zone, *Dufrenoyia furcata* Subzone). **H-O:** specimens from CHP section. **H-I:** SBC.06061-00006/CHP200, Bed 417. **J- K:** SBC.06061-00006/CHP163, Bed 418. **L:** SBC.06061-00006/CHP178, Bed 419. **M:** SBC.06061-00006/CHP198, Bed 421. **N-O:** SBC.06061-00006/CHP218, Bed 426. **P:** SBC.06061-00005/GRO075, Bed 418, GRO section. **Q-X1:** specimens from GRS1 section. **Q:** SBC.06061-00001/GRS077, Bed 98. **R-S:** SBC.06061-00001/GRS375, Bed 99. **T:** SBC.06061-00001/GRS426, Bed 99. **U-X1:** specimens from Bed 100. **U:** SBC.06061-00001/GRS084. **V-W:** SBC.06061-00001/GRS085. **X-Y:** SBC.06061-00001/GRS089. **A1-B1:** SBC.06061-00001/GRS156. **C1-D1:** SBC.06061-00001/GRS155. **E1-F1:** SBC.06061-00001/GRS170. **G1:** SBC.06061-00001/GRS168. **H1-I1:** SBC.06061-00001/GRS205. **J1-K1:** SBC.06061-00001/GRS305. **L1-M1:** SBC.06061-00001/GRS308. **N1:** SBC.06061-00001/GRS090. **O1-P1:** SBC.06061-00001/GRS650. **Q1-R1:** SBC.06061-00001/GRS738. **S1-T1:** SBC.06061-00001/GRS611. **U1-V1:** SBC.06061-00001/GRS825. **W1-X1:** SBC.06061-00001/GRS361.

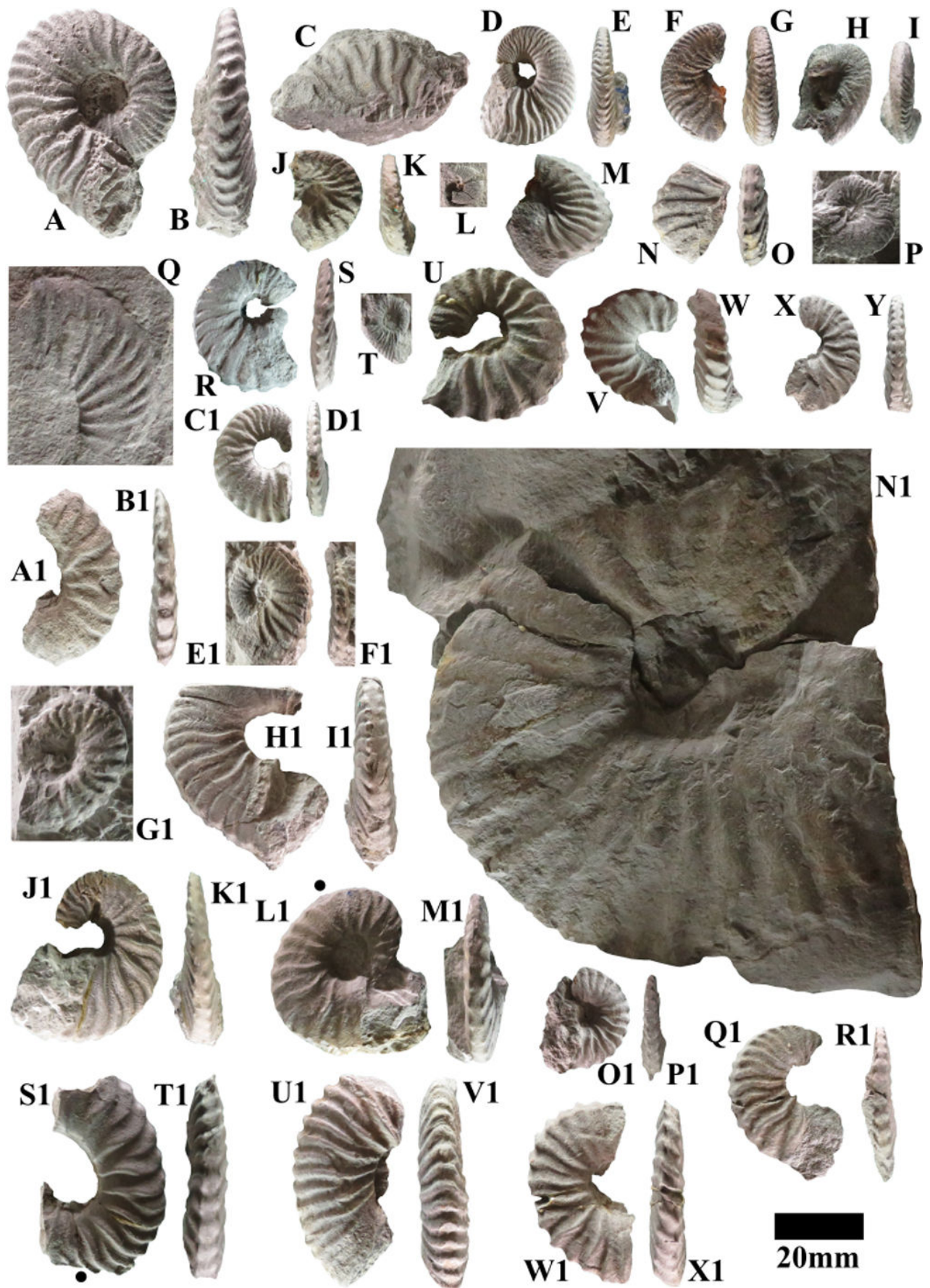




Plate 7: **A:** *Dufrenoyia* from GRS1 section (Les Graous Member, *Dufrenoyia furcata* Zone). Black dot: last septal suture. **A-Z:** *Dufrenoyia furcata* (*Dufrenoyia furcata* Zone, *Dufrenoyia furcata* Subzone). **A:** SBC.06061-00001/GRS668, Bed 100. **B:** SBC.06061-00001/GRS740, Bed 101. **C:** SBC.06061-00001/GRS744, Bed 101. **D-S:** specimens from Bed 102. **D:** SBC.06061-00001/GRS048 (in association with *Colombiceras crassicoatum*). **E-F:** SBC.06061-00001/GRS279. **G:** SBC.06061-00001/GRS272. **H-I:** SBC.06061-00001/GRS632. **J:** SBC.06061-00001/GRS227. **K:** SBC.06061-00001/GRS499. **L-M:** SBC.06061-00001/GRS556. **N:** SBC.06061-00001/GRS009. **O-P:** SBC.06061-00001/GRS275. **Q:** SBC.06061-00001/GRS767. **R-S:** SBC.06061-00001/GRS665. **T-Y:** specimens from Bed 104. **T, U:** SBC.06061-00001/GRS525. **V:** SBC.06061-00001/GRS486. **W:** SBC.06061-00001/GRS521. **X:** SBC.06061-00001/GRS402. **Y:** SBC.06061-00001/GRS536. **Z:** SBC.06061-00001/GRS494, Bed 106. **A1-B1:** *Dufrenoyia dufrenoyi* (*Dufrenoyia furcata* Zone, *Dufrenoyia dufrenoyi* Subzone) from Bed 110. **A1:** SBC.06061-00001/GRS751. **B1:** SBC.06061-00001/GRS821.





Appendix: List of the studied specimens

Total number of studied specimens: 335.

All specimens: BERSAC's collection, deposited in the Réserve naturelle nationale géologique de Haute-Provence (RNN-GHP, France).

Tables caption: N = number of specimens, D: diameter, H: whorl height, R: last half whorl rib density, SSB: end diameter of the smooth siphonal band, Subtab.: end diameter of the subtabulate ventral area, Tuberc.: end diameter of the latero ventral tubercles.

1. *Deshayesites* sp.

Identification number (N = 12)	Section	Bed	D	H	R	Subtab.	SSB	Figuration (N = 5)
SBC.06061-00001/GRS072	GRS1	96	?	63	?	No	No	
SBC.06061-00001/GRS115	GRS1	96	32	15	21	No	No	Pl. 4, figs. U-V
SBC.06061-00001/GRS773	GRS1	95	?	?	?	No	No	
SBC.06061-00007/CLE029	CLE	400	?	?	?	No	No	
SBC.06061-00007/CLE030	CLE	400	48	22	27	No	No	BERSAC & BERT, 2019, Pl. 1, figs. 4-5
SBC.06061-00007/CLE052	CLE	400	?	?	?	No	No	
SBC.06061-00008/CRS016	CRS	403	?	?	?	No	No	Pl. 1, fig. B
SBC.06061-00008/CRS017	CRS	399	133	?	?	No	No	Pl. 1, fig. A
SBC.06061-00008/CRS019	CRS	400	?	55	?	No	No	Pl. 1, figs. C-D
SBC.06061-00008/CRS020	CRS	400	57	26	?	No	No	
SBC.06061-00008/CRS021	CRS	400	?	52	?	No	No	Pl. 1, fig. E
SBC.06061-00008/CRS030	CRS	400	?	?	?	No	No	

2. *Deshayesites multicostatus* SWINNERTON, 1935

Identification number (N = 71)	Section	Bed	D	H	R	Subtab.	SSB	Figuration (N = 22)
SBC.06061-00003/VAL008	VAL	405	22	8.5	?	No	?	
SBC.06061-00003/VAL009	VAL	405	?	?	?	Yes	?	Pl. 4, figs. F-G
SBC.06061-00003/VAL012	VAL	405	22	8.9	26	No	19	Pl. 4, figs. O-P
SBC.06061-00003/VAL013	VAL	405	21	10.5	22	No	<20	
SBC.06061-00003/VAL014	VAL	405	?	9	?	No	?	
SBC.06061-00003/VAL015	VAL	405	?	9	?	No	?	
SBC.06061-00003/VAL017	VAL	405	24	10	23	No	14	Pl. 4, figs. Q-R
SBC.06061-00003/VAL018	VAL	405	19	9.5	26	No	?	Pl. 4, figs. M-N
SBC.06061-00003/VAL019	VAL	405	18	8.5	?	No	16	
SBC.06061-00003/VAL020	VAL	405	26.5	11.8	26	No	<15	Pl. 4, figs. H-I
SBC.06061-00003/VAL025	VAL	405	?	11.5	?	No	?	
SBC.06061-00003/VAL026	VAL	405	?	?	?	?	?	
SBC.06061-00003/VAL027	VAL	405	?	12	?	No	?	
SBC.06061-00003/VAL028	VAL	405	28	10	25	No	<16	
SBC.06061-00003/VAL029	VAL	405	?	8	?	No	?	
SBC.06061-00003/VAL030	VAL	405	?	?	?	?	?	
SBC.06061-00003/VAL031	VAL	405	?	?	?	No	?	
SBC.06061-00003/VAL032	VAL	405	?	14	?	No	?	
SBC.06061-00003/VAL033	VAL	405	20	9.2	21	No	17	
SBC.06061-00003/VAL034	VAL	405	28	13	22	No	<19	
SBC.06061-00003/VAL035	VAL	405	?	8	?	No	?	
SBC.06061-00003/VAL036	VAL	405	25	13	?	No	?	
SBC.06061-00003/VAL037	VAL	405	27	12	?	No	?	Pl. 4, fig. C
SBC.06061-00003/VAL038	VAL	405	?	14	?	No	?	
SBC.06061-00003/VAL039	VAL	405	45	20	?	No	<27	Pl. 4, figs. J-L
SBC.06061-00003/VAL040	VAL	405	52	26	29	No	?	Pl. 4, figs. D-E
SBC.06061-00003/VAL041	VAL	405	36	16	21	No	<18	
SBC.06061-00003/VAL042	VAL	405	13.5	?	28	No	>13.5	
SBC.06061-00003/VAL050	VAL	405	?	6.5	?	No	?	
SBC.06061-00003/VAL064	VAL	405	?	?	?	No	?	
SBC.06061-00006/CHP072	CHP	415	25	9	?	No	?	BERSAC & BERT, 2019, Pl. 2, fig. 19
SBC.06061-00006/CHP157	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP167	CHP	415	142	54	36	No	?	Pl. 5, figs. A-B
SBC.06061-00006/CHP168	CHP	415	125	65	31	No	?	BERSAC & BERT, 2019, Pl. 2, figs. 6-8
SBC.06061-00006/CHP241	CHP	415	273	103	19	No	?	BERSAC & BERT, 2019, Pl. 2, figs. 13-15



SBC.06061-00006/CHP255	CHP	415	?	65	?	No	?	
SBC.06061-00006/CHP266	CHP	415	215	?	22	No	?	
SBC.06061-00006/CHP290	CHP	415	?	55	?	No	?	
SBC.06061-00006/CHP292	CHP	415	70	34	33	No	?	Pl. 3, fig. C
SBC.06061-00006/CHP293	CHP	415	?	70	?	No	?	
SBC.06061-00006/CHP294	CHP	415	?	82	?	No	?	Pl. 5, fig. C
SBC.06061-00006/CHP295	CHP	415	62	22	?	No	?	
SBC.06061-00006/CHP352	CHP	415	?	14	?	No	?	
SBC.06061-00006/CHP368	CHP	415	248	85	?	No	?	Pl. 2, fig. A
SBC.06061-00006/CHP369	CHP	415	175	69	28	No	?	Pl. 4, figs. A-B
SBC.06061-00006/CHP370	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP371	CHP	415	267	95	17	No	?	Pl. 3, figs. A-B
SBC.06061-00006/CHP372	CHP	415	190	75	23	No	?	
SBC.06061-00006/CHP373	CHP	415	?	?	?	?	?	Pl. 2, figs. B-C
SBC.06061-00006/CHP374	CHP	415	24	?	?	No	?	
SBC.06061-00006/CHP375	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP376	CHP	415	?	88	?	No	?	
SBC.06061-00006/CHP377	CHP	415	155	55	31	No		
SBC.06061-00006/CHP378	CHP	415	?	63	?	No	?	
SBC.06061-00006/CHP379	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP380	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP381	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP382	CHP	415	31	12	25	No	?	Pl. 5, fig. D
SBC.06061-00006/CHP383	CHP	415	?	19	?	No	?	
SBC.06061-00006/CHP384	CHP	415	20	12	?	No	?	
SBC.06061-00006/CHP385	CHP	415	18	8.5	22	No	?	Pl. 5, figs. E-F
SBC.06061-00006/CHP386	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP386	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP387	CHP	415	27	15	26	No	?	
SBC.06061-00006/CHP388	CHP	415	32	?	21	No	?	
SBC.06061-00006/CHP389	CHP	415	?	11	?	No	?	
SBC.06061-00006/CHP390	CHP	415	25	10	22	No	< 18	Pl. 5, figs. G-H
SBC.06061-00006/CHP394	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP396	CHP	415	?	?	?	No	?	
SBC.06061-00006/CHP412	CHP	415	?	?	?	No	?	
SBC.06061-00009/PPR004	PPR	415	22	8.5	?	No	<12	Pl. 4, figs. S-T

3. *Deshayesites grandis* SPATH, 1930

Identification number (N = 22)	Section	Bed	D	H	R	Subtab.	SSB	Figuration (N = 9)
SBC.06061-00001/GRS350	GRS1	97	28	13	18	Yes	20	BERSAC & BERT, 2019, Pl. 3, figs. 9-10
SBC.06061-00001/GRS351	GRS1	97	49	23	20	Yes	24	Pl. 6, figs. A-B
SBC.06061-00001/GRS352	GRS1	97	?	18	?	Yes	?	Pl. 6, fig. C
SBC.06061-00001/GRS353	GRS1	97	27.5	14	24	Yes	20	Pl. 6, figs. D-E
SBC.06061-00001/GRS354	GRS1	97	20	10	?	?	>20	
SBC.06061-00001/GRS355	GRS1	97	?	?	?	Yes	?	
SBC.06061-00001/GRS509	GRS1	97	35	16	23	Yes	<23	
SBC.06061-00006/CHP059	CHP	416	?	13	?	Yes	?	
SBC.06061-00006/CHP084	CHP	416	?	13	?	Yes	?	
SBC.06061-00006/CHP099	CHP	416	?	18	?	Yes	?	
SBC.06061-00006/CHP117	CHP	416	13	6	24	?	>13	
SBC.06061-00006/CHP118	CHP	416	28.5	18	25	Yes	<20	Pl. 6, figs. F-G
SBC.06061-00006/CHP124	CHP	416	36	16	20	Yes	>21	BERSAC & BERT, 2019, Pl. 3, figs. 11-12
SBC.06061-00006/CHP158	CHP	416	27	13	?	Yes	20	
SBC.06061-00006/CHP361	CHP	416	42	17	?	No	16	
SBC.06061-00006/CHP391	CHP	416	?	?	?	Yes	?	Pl. 5, figs. I-J
SBC.06061-00006/CHP392	CHP	416	23	11.2	30	Yes	20	Pl. 5, figs. M-N
SBC.06061-00006/CHP393	CHP	416	?	?	?	Yes	?	
SBC.06061-00006/CHP395	CHP	416		15	?	Yes	?	Pl. 5, figs. K-L
SBC.06061-00007/CLE026	CLE	416	12	5	19	?	>12	
SBC.06061-00007/CLE040	CLE	416	21	9	31	Yes	19	
SBC.06061-00007/CLE046	CLE	416	?	5	?	?	?	

**4. *Dufrenoyia furcata* (J. de C. SOWERBY, 1836)**

Identification number (N = 210)	Section	Bed	D	H	R	Tuberc.	SSB	Figuration (N = 49)
SBC.06061-00001/GRS009	GRS1	102	?	19	?	?	?	Pl. 7, fig. N
SBC.06061-00001/GRS012	GRS1	102	36	?	19	>36	>36	
SBC.06061-00001/GRS017	GRS1	102	?	13	?	?	?	
SBC.06061-00001/GRS024	GRS1	102	30	15	19	>30	>30	
SBC.06061-00001/GRS042	GRS1	102	65	26	17	?	?	
SBC.06061-00001/GRS043	GRS1	102	37	18	18	?	?	
SBC.06061-00001/GRS048	GRS1	102	44	20	18	>44	29	Pl. 7, fig. D
SBC.06061-00001/GRS073	GRS1	100	75	36	19	?	<46	BERSAC & BERT, 2019, Pl. 5, fig. 5
SBC.06061-00001/GRS077	GRS1	98	?	10	?	?	?	Pl. 6, fig. Q
SBC.06061-00001/GRS084	GRS1	100	35	14.8	11	>35	?	Pl. 6, fig. U
SBC.06061-00001/GRS085	GRS1	100	27	12	12	>27	20	Pl. 6, figs. V-W
SBC.06061-00001/GRS086	GRS1	100	?	15	?	?	?	
SBC.06061-00001/GRS087	GRS1	100	?	?	?	?	?	
SBC.06061-00001/GRS089	GRS1	100	23	12	15	>23	>23	Pl. 6, figs. X-Y
SBC.06061-00001/GRS090	GRS1	100	116	48	21	?	?	Pl. 6, fig. N1
SBC.06061-00001/GRS091	GRS1	99	?	?	?	?	?	
SBC.06061-00001/GRS092	GRS1	100	30	12	16	?	?	
SBC.06061-00001/GRS093	GRS1	100	?	?	?	?	?	
SBC.06061-00001/GRS094	GRS1	100	26	12	18	?	?	
SBC.06061-00001/GRS107	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS113	GRS1	102	27	13	12	>27	>27	
SBC.06061-00001/GRS120	GRS1	99	?	11	?	?	?	
SBC.06061-00001/GRS124	GRS1	102	25	10	17	?	?	
SBC.06061-00001/GRS133	GRS1	102	35	13	9	?	?	
SBC.06061-00001/GRS143	GRS1	100	22	9	?	>22	>22	
SBC.06061-00001/GRS154	GRS1	100	?	14	?	?	?	
SBC.06061-00001/GRS155	GRS1	100	25.5	11.5	13	>25.5	>25.5	Pl. 6, figs. C1-D1
SBC.06061-00001/GRS156	GRS1	100	39	12	10	>39	?	Pl. 6, figs. A1-B1
SBC.06061-00001/GRS168	GRS1	100	27	12	12	>27	>27	Pl. 6, fig. G1
SBC.06061-00001/GRS169	GRS1	100	?	?	?	?	?	
SBC.06061-00001/GRS170	GRS1	100	26	13	15	>26	>26	Pl. 6, figs. E1-F1
SBC.06061-00001/GRS171	GRS1	100	28	13	12	>28	24	
SBC.06061-00001/GRS172	GRS1	100	26.5	14	15	?	?	
SBC.06061-00001/GRS185	GRS1	100	26.4	13.2	18	>26.4	>26.4	
SBC.06061-00001/GRS189	GRS1	100	25	10	11	>25	>25	
SBC.06061-00001/GRS190	GRS1	100	28	12.6	18	>28	>28	
SBC.06061-00001/GRS191	GRS1	100	32	12	10	>32	>32	
SBC.06061-00001/GRS192	GRS1	100	22	11.8	17	>22	20	
SBC.06061-00001/GRS194	GRS1	100	29	13	11	>29	>29	
SBC.06061-00001/GRS195	GRS1	100	36	16	16	>36	24	
SBC.06061-00001/GRS205	GRS1	100	?	14	?	?	?	Pl. 6, figs. H1-I1
SBC.06061-00001/GRS212	GRS1	102	?	20	?	?	?	
SBC.06061-00001/GRS214	GRS1	102	?	55	?	?	?	
SBC.06061-00001/GRS227	GRS1	102	118	?	21	45	?	Pl. 7, fig. J
SBC.06061-00001/GRS228	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS234	GRS1	102	?	21	?	?	?	
SBC.06061-00001/GRS235	GRS1	102	30	15	24	?	?	
SBC.06061-00001/GRS241	GRS1	102	17	8	18	>17	>17	
SBC.06061-00001/GRS272	GRS1	102	40	18	12	?	?	Pl. 7, fig. G
SBC.06061-00001/GRS273	GRS1	102	37	14	15	?	?	
SBC.06061-00001/GRS274	GRS1	102	18	9	?	>18	>18	
SBC.06061-00001/GRS275	GRS1	102	26	10	?	>26	18	Pl. 7, figs. O-P
SBC.06061-00001/GRS276	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS277	GRS1	102	30	14	15	?	?	
SBC.06061-00001/GRS278	GRS1	102	53	25	18	>53	<30	
SBC.06061-00001/GRS279	GRS1	102	34	15	18	?	16	Pl. 7, figs. E-F
SBC.06061-00001/GRS280	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS305	GRS1	100	38	18	18	>38	27	Pl. 6, figs. J1-K1



SBC.06061-00001/GRS306	GRS1	100	?	?	?	?	?	
SBC.06061-00001/GRS307	GRS1	100	28	16		>28	?	
SBC.06061-00001/GRS308	GRS1	100	38	17	15	>38	37	Pl. 6, figs. L1-M1
SBC.06061-00001/GRS309	GRS1	100	20	10	?	>20	>20	
SBC.06061-00001/GRS314	GRS1	100	19.7	8	13	>19.7	>19.7	
SBC.06061-00001/GRS316	GRS1	99	?	?	?	?	?	
SBC.06061-00001/GRS317	GRS1	100	?	?	?	?	?	
SBC.06061-00001/GRS318	GRS1	99	?	?	?	?	?	
SBC.06061-00001/GRS332	GRS1	100	?	17	?	?	?	
SBC.06061-00001/GRS333	GRS1	100	?	14	?	?	?	
SBC.06061-00001/GRS356	GRS1	100	24	13	?	?	?	
SBC.06061-00001/GRS357	GRS1	100	26	?	11	>26	>26	
SBC.06061-00001/GRS361	GRS1	100	41	15	13	>41	26	Pl. 6, figs. W1-X1
SBC.06061-00001/GRS363	GRS1	99	?	10	?	?	?	
SBC.06061-00001/GRS375	GRS1	99	30	15	13	>30	>30	Pl. 6, figs. R-S
SBC.06061-00001/GRS396	GRS1	99	?	?	?	?	?	
SBC.06061-00001/GRS399	GRS1	104	?	?	?	?	?	
SBC.06061-00001/GRS402	GRS1	104	11.5	5	27	?	>11.5	Pl. 7, fig. X
SBC.06061-00001/GRS403	GRS1	104	?	?	?	?	?	
SBC.06061-00001/GRS404	GRS1	104	?	11	?	?	?	
SBC.06061-00001/GRS405	GRS1	104	23	11	25	>20	>20	
SBC.06061-00001/GRS408	GRS1	104	25	12	14	>25	>25	
SBC.06061-00001/GRS409	GRS1	104	21	10	22	>21	>21	
SBC.06061-00001/GRS425	GRS1	99	?	10	?	?	?	
SBC.06061-00001/GRS426	GRS1		16	7.5	?	?	?	Pl. 6, fig. T
SBC.06061-00001/GRS431	GRS1	99	?	12	?	?	?	
SBC.06061-00001/GRS433	GRS1	99	124	55	28	?	?	
SBC.06061-00001/GRS437	GRS1	99	190	?	?	?	?	
SBC.06061-00001/GRS439	GRS1	104	34	15	?	?	?	
SBC.06061-00001/GRS440	GRS1	104	19	10	22	>19	>19	
SBC.06061-00001/GRS441	GRS1	104	21	9.5	30	?	?	
SBC.06061-00001/GRS442	GRS1	104	27	15	27	>27	>27	
SBC.06061-00001/GRS443	GRS1	104	?	12	?	?	?	
SBC.06061-00001/GRS445	GRS1	104	30	?	20	>30	>30	
SBC.06061-00001/GRS446	GRS1	104	?	11	?	?	?	
SBC.06061-00001/GRS447	GRS1	104	13	6	?	?	?	
SBC.06061-00001/GRS448	GRS1	104	?	?	?	?	?	
SBC.06061-00001/GRS450	GRS1	104	26	?	?	?	27	
SBC.06061-00001/GRS453	GRS1	104	25	12	19	>25	>25	
SBC.06061-00001/GRS454	GRS1	104	23	11.5	20	>23	>23	
SBC.06061-00001/GRS455	GRS1	104	31	13	17	?	?	
SBC.06061-00001/GRS456	GRS1	104	18	7	?	?	?	
SBC.06061-00001/GRS459	GRS1	104	26	?	30	>26	>26	
SBC.06061-00001/GRS461	GRS1	104	28	?	18	?	?	
SBC.06061-00001/GRS462	GRS1	104	?	10	?	?	?	
SBC.06061-00001/GRS470	GRS1	104	23	11	22	>23	<13	
SBC.06061-00001/GRS476	GRS1	104	22	9	?	?	?	
SBC.06061-00001/GRS479	GRS1	104	18	8.5	24	>18	>18	
SBC.06061-00001/GRS485	GRS1	104	?	9	?	?	?	
SBC.06061-00001/GRS486	GRS1	104	25	11	29	>25	>25	Pl. 7, fig. V
SBC.06061-00001/GRS487	GRS1	104	22	10	?	?	?	
SBC.06061-00001/GRS494	GRS1	106	?	?	?	?		Pl. 7, fig. Z
SBC.06061-00001/GRS495	GRS1	106	?	?	?	?		
SBC.06061-00001/GRS499	GRS1	102	80	37	18	?	?	Pl. 7, fig. K
SBC.06061-00001/GRS504	GRS1	104	18	8	20	>18	>18	
SBC.06061-00001/GRS515	GRS1	102	?	10	?	?	?	
SBC.06061-00001/GRS517	GRS1	102	33	15	?	?	?	
SBC.06061-00001/GRS520	GRS1	104	?	10	?	?	?	
SBC.06061-00001/GRS521	GRS1	104	26	?	?	?	?	Pl. 7, fig. W
SBC.06061-00001/GRS525	GRS1	104	30	13.8	23	>30	25	Pl. 7, figs. T-U
SBC.06061-00001/GRS536	GRS1	104	16	8	27	>16	>16	Pl. 7, fig. Y
SBC.06061-00001/GRS538	GRS1	104	?	?	?	?	?	



SBC.06061-00001/GRS540	GRS1	104	15	7	19	?	?	
SBC.06061-00001/GRS546	GRS1	104	?	10	?	?	?	
SBC.06061-00001/GRS551	GRS1	102	25	?	15	>25	>25	
SBC.06061-00001/GRS553	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS556	GRS1	102	?	?	?	?	?	Pl. 7, figs. L-M
SBC.06061-00001/GRS557	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS558	GRS1	102	40	16	?	?	>15	
SBC.06061-00001/GRS559	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS560	GRS1	102	?	12	?	?	?	
SBC.06061-00001/GRS563	GRS1	102	29	14	21	>29	25	
SBC.06061-00001/GRS565	GRS1	102	33	15	20	?	?	
SBC.06061-00001/GRS566	GRS1	102	27	12	?	>27	>27	BERSAC & BERT, 2019, Pl. 5, fig. 8
SBC.06061-00001/GRS578	GRS1	102	30	14	14	?	?	
SBC.06061-00001/GRS587	GRS1	109	15	6	26	?	?	
SBC.06061-00001/GRS588	GRS1	109	22	10	?	>22	>22	
SBC.06061-00001/GRS589	GRS1	109	?	?	?	?	?	
SBC.06061-00001/GRS597	GRS1	105	19	8	21	>19	>19	BERSAC & BERT, 2019, Pl. 5, fig. 9
SBC.06061-00001/GRS598	GRS1	105	?	8	?	?	?	
SBC.06061-00001/GRS599	GRS1	105	40	?	?	?	?	
SBC.06061-00001/GRS604	GRS1	102	35	15	16	>35	>35	
SBC.06061-00001/GRS608	GRS1	102	?	25	?	?	?	
SBC.06061-00001/GRS609	GRS1	100	30	15	?	>30	23	
SBC.06061-00001/GRS611	GRS1	100	45	17	14	>45	<30	Pl. 6, figs. S1-T1
SBC.06061-00001/GRS632	GRS1	102	38	16	25	>38	<24	Pl. 7, figs. H-I
SBC.06061-00001/GRS633	GRS1	102	36	15	14	>36	>36	
SBC.06061-00001/GRS635	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS636	GRS1	102	32	13	10	?	?	
SBC.06061-00001/GRS650	GRS1	100	27	13	13	>27	>27	Pl. 6, figs. O1-P1
SBC.06061-00001/GRS665	GRS1	102	44	16	9	?	?	Pl. 7, figs. R-S
SBC.06061-00001/GRS668	GRS1	100	40	20	18	>40	24	Pl. 7, fig. A
SBC.06061-00001/GRS683	GRS1	102	?	27	?	?	?	BERSAC & BERT, 2019, Pl. 5, figs. 6-7
SBC.06061-00001/GRS738	GRS1	100	35	16	15	?	24	Pl. 6, figs. Q1-R1
SBC.06061-00001/GRS739	GRS1	99	?	?	?	?	?	
SBC.06061-00001/GRS740	GRS1	101	22	10	?	?	?	Pl. 7, fig. B
SBC.06061-00001/GRS741	GRS1	101	18	8.5	?	>18	>18	
SBC.06061-00001/GRS742	GRS1	101	29	12	?	?	?	
SBC.06061-00001/GRS743	GRS1	101	?	16	?	?	?	
SBC.06061-00001/GRS744	GRS1	101	45	20	?	40	?	Pl. 7, fig. C
SBC.06061-00001/GRS745	GRS1	101	?	12	?	?	?	
SBC.06061-00001/GRS756	GRS1	107	?	?	?	?	?	
SBC.06061-00001/GRS757	GRS1	104	23	11	24	>23	>23	
SBC.06061-00001/GRS758	GRS1	108	?	?	?	?	?	
SBC.06061-00001/GRS759	GRS1	105	?	12	?	?	?	
SBC.06061-00001/GRS760	GRS1	105	?	?	?	?	?	
SBC.06061-00001/GRS763	GRS1	102	?	?	?	?	?	
SBC.06061-00001/GRS764	GRS1	102	25	12	16	>25	>25	
SBC.06061-00001/GRS765	GRS1	102	?	12	?	?	?	
SBC.06061-00001/GRS766	GRS1	102	?	5	?	?	?	
SBC.06061-00001/GRS767	GRS1	102	44	18	14	>44	33	Pl. 7, fig. Q
SBC.06061-00001/GRS768	GRS1	102	?	8	?	?	?	



SBC.06061-00001/GRS769	GRS1	100	32	15	14	?	?	
SBC.06061-00001/GRS812	GRS1	104	?	?	?	?	?	
SBC.06061-00001/GRS813	GRS1	105	?	?	?	?	?	
SBC.06061-00001/GRS814	GRS1	105	?	15	?	?	?	
SBC.06061-00001/GRS815	GRS1	105	?	?	?	?	?	
SBC.06061-00001/GRS816	GRS1	105	?	12	?	?	?	
SBC.06061-00001/GRS817	GRS1	105	?	?	?	?	?	
SBC.06061-00001/GRS818	GRS1	105	37	17	?	?	?	
SBC.06061-00001/GRS823	GRS1	100	30	15	17	>30	>30	
SBC.06061-00001/GRS824	GRS1	100	40	19.5	?	>40	?	
SBC.06061-00001/GRS825	GRS1	100	?	?	?	?	?	Pl. 6, figs. U1-V1
SBC.06061-00001/GRS826	GRS1	104	27	?	26	?	?	
SBC.06061-00001/GRS827	GRS1	100	32	13.5	11	>32	>32	
SBC.06061-00001/GRS828	GRS1	100	40	15	14	>40	>40	
SBC.06061-00001/GRS829	GRS1	102	36	17	15	>36	26	
SBC.06061-00005/GRO075	GRO	418	21	8	23	>21	>21	Pl. 6, fig. P
SBC.06061-00006/CHP037	CHP	418	22	8		>22	>17	
SBC.06061-00006/CHP080	CHP	418	25	8.2	17	>25	>25	
SBC.06061-00006/CHP081	CHP	418	19	8	21	>19	>19	
SBC.06061-00006/CHP163	CHP	418	24	12	14	>24	>24	Pl. 6, figs. J-K
SBC.06061-00006/CHP178	CHP	419	12	?	?	?	?	Pl. 6, fig. L
SBC.06061-00006/CHP179	CHP	419	?	7	?	?	?	
SBC.06061-00006/CHP181	CHP	421	35	12	?	>35	<22	
SBC.06061-00006/CHP187	CHP	419	37	15	?	?	?	
SBC.06061-00006/CHP188	CHP	419	17	7	?	?	?	
SBC.06061-00006/CHP195	CHP	421	?	?	?	?	?	
SBC.06061-00006/CHP198	CHP	421	23	10	13	>23	>23	Pl. 6, fig. M
SBC.06061-00006/CHP200	CHP	417	20	9	22	>20	>20	Pl. 6, figs. H-I
SBC.06061-00006/CHP211	CHP	426	18	7	20	>18	>18	
SBC.06061-00006/CHP213	CHP	426	21	?	?	?	?	
SBC.06061-00006/CHP214	CHP	426	18	7	14	>18	>18	
SBC.06061-00006/CHP215	CHP	426	?	14	?	?	?	
SBC.06061-00006/CHP216	CHP	426	27	12		>27	>27	
SBC.06061-00006/CHP217	CHP	426	14	?	?	?	?	
SBC.06061-00006/CHP218	CHP	426	23	12	?	>23	>23	Pl. 6, figs. N-O
SBC.06061-00006/CHP222	CHP	426	?	?	?	?	?	
SBC.06061-00006/CHP223	CHP	426	?	?	?	?	?	
SBC.06061-00006/CHP247	CHP	424	?	?	?	?	?	
SBC.06061-00006/CHP461	CHP	424	?	?	?	?	?	
SBC.06061-00009/PPR007	PPR	420	?	?	?	?	?	

5. *Dufrenoyia dufrenoyi* (ORBIGNY, 1841)

Identification number (N = 20)	Section	Bed	D	H	R	Tuberc.	SSB	Figuration (N = 4)
SBC.06061-00001/GRS592	GRS1	113	?	15	?	?	?	BERSAC & BERT, 2019, Pl. 5, fig. 32
SBC.06061-00001/GRS593	GRS1	113	24	11	24	>24	>24	
SBC.06061-00001/GRS594	GRS1	113	32	14	18	>32	>32	
SBC.06061-00001/GRS595	GRS1	113	18	?	?	?	?	
SBC.06061-00001/GRS596	GRS1	113	16	?	?	>16	>16	
SBC.06061-00001/GRS685	GRS1	110	?	16	?	?	?	BERSAC & BERT, 2019, Pl. 5, figs. 30-31



SBC.06061-00001/GRS746	GRS1	113	?	15	?	?	?	
SBC.06061-00001/GRS747	GRS1	110	?	?	?	?	?	
SBC.06061-00001/GRS748	GRS1	110	19	9	19	>19	>19	
SBC.06061-00001/GRS749	GRS1	110	?	14	?	?	?	
SBC.06061-00001/GRS750	GRS1	110	12	6.5	15	>12	>12	
SBC.06061-00001/GRS751	GRS1	110	22	10	22	>22	>22	Pl. 7, fig. A1
SBC.06061-00001/GRS752	GRS1	110	?	?	?	?	?	
SBC.06061-00001/GRS753	GRS1	110	23	11	?	?	?	
SBC.06061-00001/GRS754	GRS1	110	18	7	24	?	?	
SBC.06061-00001/GRS755	GRS1	110	?	?	?	?	?	
SBC.06061-00001/GRS819	GRS1	110	34	15	15	>34	>34	
SBC.06061-00001/GRS820	GRS1	110	?	?	?	?	?	
SBC.06061-00001/GRS821	GRS1	110	37	19	19	>37	>37	Pl. 7, fig. B1
SBC.06061-00001/GRS822	GRS1	110	?	?	?	?	?	