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First unequivocal occurrence of the genus Douvilleiceras (Douvilleiceratoidea, Ancyloceratina) in the Albian of Sinai (Egypt)

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Abstract :

Based on new material collected from the Risan Aneiza Formation at Gabal Maaza (Maghara area, Sinai), the occurrence of the cosmopolitan Albian genus Douvilleiceras is unequivocally documented for the first time in Egypt. Douvilleiceras orbignyi, a species known to characterise the middle to uppermost lower Albian of Western Europe, is identified. The taxonomy, palaeogeography and population dynamics of the hypernodose forms of Douvilleiceras, e.g. the “aequinodum” group of the literature are discussed.

Keywords : Cretaceous, Albian, Douvilleiceras, Ammonoids, Sinai, Egypt

Introduction. The first mention of *Douvilleiceras* from Sinai (Egypt) was made by Douvillé and Couyat-Barthoux (1914). Additionally, the occurrence of a small juvenile specimen from the upper oolitic horizon (H^2) of Talat el Felahin (now Gabal Maaza) was described by Douvillé (1916). As stated by Douvillé in his original description, the specimen does not show the typical double ventro-lateral tubercles that characterise the genus. As a consequence, the identification remains doubtful even though the general aspect of the specimen is closer to *Douvilleiceras* than to *Epicheloniceras*. The occurrence of *Douvilleiceras* from the Maghara mountain range was also mentioned by Moret and Mahmoud (1953), but the specimens were not documented.

Until the present material was collected from Gabal Maaza by one of the authors (MFA), no other *Douvilleiceras* was reported by palaeontologists who studied the Albian ammonoids of the Sinai (Mahmoud 1951, 1955; Aboul Ela et al. 1991, Hamama 1993; Hamama and Gabir 2001, Aly and Abdel-Gawad 2001, Abu Zied 2006, 2008; Latil and Aly 2012; El Qot 2018). The present contribution documents the first unequivocal occurrence of *Douvilleiceras* in the Albian of Sinai (Egypt). Four specimens are described and compared to material from the Anglo-Paris Basin, southern Africa and the Middle East. A new biostratigraphic interpretation of the associated fauna is proposed. Additionally, the palaeobiogeography and population dynamics of hypernodose *Douvilleiceras* is discussed.

Geological setting. During the Mesozoic Era, Egypt was progressively inundated from the north by the Tethys Sea. The Tethyan extensional tectonics and associated sinistral strike-slip movements, which were initiated during Early Mesozoic continued to influence the North African continental margin during Early Cretaceous times (El Hawat 1997). In North Sinai, many ENE- and NE-oriented doubly plunging anticlines represent the conspicuous highs and form a distinctive tectonic province in the area (Moustafa and Khalil 1990). These anticlines are part of the Syrian Arc System (Said 1962; Moustafa 2014, 2020). The Maghara dome represents one of the largest anticlines in north Sinai. By the beginning of Cretaceous times, most of the northern part of Egypt was under fully marine conditions. The marine Lower Cretaceous rocks, cropping out on the flanks of El Maghara area, are well known extending in north Sinai, Egypt (Fig. 1). These rocks unconformably overlie the shallow marine Upper Jurassic carbonates (Jenkins 1990).

The Aptian-Albian carbonate platform forms an elongated belt on the passive northern margin of the Arabo-Nubian Shield, extending from Syria in the northeast to Egypt in the southwest (Bachmann et al. 2010). The Lower Cretaceous fluvial facies is represented in Sinai by the Malha Formation, deposited in a proximal to distal braided-channel setting. These fluvial deposits changed into marine limestones of the carbonate platform margin northward near the present-day Mediterranean coastline (Kerdany and Cherif 1990).

According to El-Azabi and El-Araby (2005) the first marine transgression in North Sinai is of late Aptian-early Albian age, where these transgressive deposits are represented by the Risan Aneiza Formation. Based on ammonoids findings at the base of the formation, it is now established that the onset of the transgression is of late Barremian age (Aly and Abdel-Gawad 2001; Abu Zied 2006, 2008). The dolomitic limestone, chalky limestone, limestone and marl with interbedded shales that belong to the Halal Formation (late Albian-early Cenomanian) overlie conformably the Risan Aneiza Formation (Bachmann et al. 2010).

--------------- Figure 1 near here ---------------

The Aptian-Albian sequence of the Maghara area yielded rich macrofaunal assemblages (see Salama et al. 2020, with references), of which ammonoids are of particular interest. The studied Albian section at Gabal Maaza (MZ) is about 90 m thick. It is composed of fossiliferous oolitic limestones alternating with fossiliferous marls, sandstones and claystones. It represents the southernmost Lower Cretaceous section in the Maghara area (Fig. 1). The four *Douvilleiceras* specimens documented herein were collected from the lowermost part of the Risan Aneiza Formation that is well exposed at Gabal Maaza. They originate from a meter-thick bed of yolk-yellow oolitic limestone rich in *Knemiceras* and occasional phylloceratids. This level is equivalent to beds 28-33 (*Knemiceras gracile* Interval Zone) of the Manzour section published by Abu-Zied (2008, Fig. 12) (Fig. 1).

Systematic palaeontology.

Unless otherwise mentioned, the classification retained in this paper is the one of Wright et al. (1996). Description of the ammonoid conch follows the nomenclature of Arkell et al. (1957) amended by Klug et al. (2015).

Abbreviations: All the dimensions of the specimens are given in millimetres: D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter. Figures in parentheses are dimensions as a percentage of the diameter at the measurement point.

The following acronyms are used to indicate the repositories of the specimens mentioned in the text and captions: CUGM - Cairo University, Geological Museum, BM – Natural History Museum, London, OUM – University Museum, Oxford, FSL – Université Claude Bernard, Lyon, NARG – North African Research Group, University of Manchester, GD – Université de Bourgogne, Dijon, France.

Superfamily Douvilleiceratoidea Parona and Bonarelli 1897

Family Douvilleiceratidae Parona and Bonarelli 1897

Subfamily Douvilleiceratinae Parona and Bonarelli 1897

Genus *Douvilleiceras* de Grossouvre 1894

(= ?*Trinitoceras* Scott 1940, = ?*Eodouvilleiceras* Casey 1961a)

Type species. *Ammonites mammillatus* Schlotheim 1813, as interpreted by the neotype selected by Casey (1954, p. 250); ICZN specific name 764 (opinion 422, 1956).

Remarks. An extensive number of systematic studies have been published on the family Douvilleiceratidae since the nominal genus was introduced by de Grossouvre (1894). To date, 43 species and varieties belonging to the genus *Douvilleiceras* have been described (Klein and Bogdanova 2013; Futakami and Haggart 2018). This number increases if *Trinitoceras* and *Eodouvilleiceras* are considered as subjective junior synonyms of *Douvilleiceras* (see discussions *in* Bulot 2010; Latil 2011). Taking into consideration the recent discussion of Futakami and Haggart (2018) on these two genera, we suggest that they should be tentatively assigned to *Douvilleiceras* pending revision of the type material.

Following Cooper (1982), it has been outlined in recent years that the strict morphological criteria for differentiating the many *Douvilleiceras* species are unsatisfactory and fail to recognise the range of intraspecific and ontogenetic variation. Courville and Lebrun (2010) suggested that all described taxa of *Douvilleiceras* represent a single highly variable cosmopolitan species, *D. mammillatum*. Kennedy and Klinger (2015) suggested that the majority of previously named taxa can be regarded as junior synonyms of either *D. mammillatum* or *D. inaequinodum* (Quenstedt, 1846). A very similar view was already accepted by Amédro et al. (2014) in their systematic treatment of *Douvilleiceras*, but these authors did not develop their taxonomic opinions.

A more conservative approach was taken by Futakami and Haggart (2016, 2018). Based on the study of *Douvilleiceras* populations from Haida Gwaii (Canada), those authors assume that the most useful criteria for differentiating species are the mode of tuberculation, the pattern of ribbing, and the proportions of the shell in the middle growth stage (diameter of 50 to 100 mm). Applying those criteria to a more global revision of the genus, Futakami and Haggart (2018) retain seven nominal species, e.g., *Douvilleiceras mammillatum*, *D. inaequinodum*, *D. solitae* (d'Orbigny, 1853), *D. spiniferum* (Whiteaves, 1876), *D. offarcinatum* (White, 1887), *D. leightonense* Casey, 1962, and *D. alternans* Casey, 1962.

Latil (2008, 2011) preferred to adopt a typological approach since he pointed out that: "the phenotypic plasticity of shell form and ornament of the genus *Douvilleiceras* is well-known, but probably not yet well-understood”. He also outlined that the evolution of *Douvilleiceras* during the early Albian remains poorly constrained temporally and geographically. In our opinion, these conclusions are still largely valid, and the material described below illustrates the difficulty to assign isolated specimens to one typological taxon better than another.

Douvilleiceras orbignyi Hyatt 1903

Fig. 2.1-6

Preliminary remark. As a consequence of our taxonomic choice discussed below, the synonymy list has been intentionally reduced to the specimens from the literature that match our material from Sinai.

1878 *Acanthoceras mammillare* V. Schlotheim, sp., Bayle, Pl. LX, Fig. 4

1923 *Douvilleiceras mammillatum* (Schlotheim), var. *baylei* nov. Spath, p. 70

1923 *Douvilleiceras* aff. *inaequinodum* (Quenstedt), transitional to *D. mammillatum* var. *baylei* nov. Spath, Pl. IV, Fig. 5

1925 *Douvilleiceras mammillatum* (Schlotheim), var. *baylei* nov. Spath, Pl. V, Fig. 4

1962 *Douvilleiceras orbignyi* Hyatt – Casey, p. 279, pl. XL, fig. 6; Pl. XLII, Figs. 12-13, Text-Figs. 99a (= *Acanthoceras mammillare in* Bayle 1878, pl. LX, Fig. 4), 99b-c, 102h (sol)

1963 *Douvilleiceras* sp. indet. – Collignon, p. 109, Pl. CCLXXXIII, Fig. 1240

1977 *Douvilleiceras orbignyi* (Hyatt) – Kotetishvili, p. 64, Pl. XXXII, Fig. la-в

? 1980 *Douvilleiceras mammilatus* (Schloth.) – Krishna, p. 51, Pl. 1, Figs. 2, 6-7

1982 *Douvilleiceras inaequinodum* (Quenstedt) – Cooper, p. 284 (pars), Figs. 12G-H (sol)

? 1982 *Douvilleiceras orbignyi* Hyatt – Colleté et al. Pl. 15, Fig. 5

2000. *Douvilleiceras orbignyi* Hyatt – Matrion et al. Pl. 2, Figs. 10a-b

2005. *Douvilleiceras orbignyi* (Hyatt) – Sharikadze & Kotetishvili *in* Topchishvili et al. p. 389, Pl. 99, Fig. 2a-в (= Kotetishvili 1977, Pl. XXXII, Fig. la-в), Fig. 3a-в

2006. *Douvilleiceras inaequinodum* (Quenstedt) – Prins, p. 47, unnumbered Fig.

2014. *Douvilleiceras inaequinodum* (Quenstedt) – Amédro et al. Pl. X, Fig. 5

2015. *Douvilleiceras inaequinodum* (Quenstedt) – Kennedy and Klinger, p. 56 (pars), Figs. 5 (= *Acanthoceras mammillare in* Bayle, 1878, pl. LX, fig. 4), 11D–G (sol)

Neotype (designated by Casey, 1962, p. 279). The specimen illustrated by Bayle (1878, Pl. LX, Fig. 4) from Macheroméril (Ardennes, France). It is kept in the collections of the École des Mines, Paris, currently housed in the collections of the Université Claude-Bernard, Lyon (FSL EM 1168). It was recently re-illustrated by Kennedy and Klinger (2015). A ventral view is reproduced herein (Fig. 2.6).

Hyatt (1903, p. 110) originally designated the specimen of *Ammonites mammillaris* illustrated by d'Orbigny (1841, Pl. 73, Figs 1–3) as the holotype. The specimen is lost, its origin is unknown, and the original drawing might be idealised and based on a reconstruction from several specimens (Casey 1962, p. 169; Guérin-Franiatte 2006, p. 90-91).

Material. Two specimens from Gabal Maaza, Maghara area, North Sinai, Egypt. MZ/89/CUGM (Figs. 2.1a-b) and MZ/90/CUGM (Figs. 2.2a-b). Both specimens are preserved as oolitic limestone internal moulds.

Measurements (in mm):

Specimen	D	Wb	Wh	Wb/Wh
MZ/89/CUGM	~ 48	32	18	1.80
MZ/90/CUGM	~ 45	26	16	1.60

Description. MZ/89/CUGM and MZ/90/CUGM are represented by a partial whorl of a nucleus of an estimated diameter of 48 and 45 mm respectively. The whorl section is depressed (1.60 < Wb/Wh < 1.80) and marked by a U-shaped medial ventral sulcus moderately wide and deep. Venter is broadly rounded. The primary ribs are straight, strong, rectiradiate, and separated by interspaces wider than primaries. Five rows of tubercles are observed. The ribs arise at the umbilical seam and strengthen across the umbilical wall forming alternatively small bullae and spiny tubercles. Then, the ribs develop in a prominent conical lateral tubercle at mid-flank. All ribs bear large teat-like ventrolateral tubercles that are composed of three clavate swellings, forming distinct spiral ridges (= Set 1 *sensu* Futakami and Haggart 2018). Neither of the two specimens shows secondary rids. The suture line is not visible.

Discussion. The sculpture and ribbing style of our specimens compare well with the juvenile ornamental stage of specimens from the Anglo-Paris Basin described by Spath (1923), Casey (1962), Cooper (1982) and Kennedy and Klinger (2015). At equivalent diameter, the whorl shape and ornamentation of MZ/89/CUGM and MZ/90/CUGM matches that of the holotype of *Douvilleiceras baylei* Spath, 1923 (Casey 1962, Text-Fig 99b-c) (reproduced herein Figs 2.5a-b) and the neotype of *Douvilleiceras orbignyi* Hyatt, 1903 (Casey 1962, Text-Fig. 99a; Kennedy and Klinger 2015, Fig. 5). They also match well the specimen identified as *Douvilleiceras inaequinodum* by Cooper (1982, Fig. 12G-H) and Amédro et al. (2014, pl. 10, fig. 5).

--------------- Figure 2 near here ---------------

Outside Europe, Kennedy and Klinger (2015) illustrated specimens from KwaZulu-Natal (South Africa) that also show close similarity with the Egyptian material. This is especially true for the specimens illustrated in figures 11D and 11F-H (reproduced herein Figs. 2.4a-b). At a diameter of 50 to 55 mm, all the specimens listed above are characterised by the absence of intercalated ribs and the occurrence of teat-like ventrolateral tubercles that are composed of three clavate swellings. This morphology is perfectly expressed on the inner whorls of the neotype of *D. orbignyi* as illustrated by Kennedy and Klinger (2015, Fig. 5), to which *D. baylei* illustrated by Spath (1923, Pl. V, Fig. 4) likely represents the juvenile morphology. Though similar by its ornamentation, *Douvilleiceras alternans* differs by the occurrence of intercalatories at early ontogeny. It should be noted that the number of clavate swellings on the ventrolateral tubercle increases from 3 to 4 at a diameter of 60 to 65 mm.

Dimorphism and polymorphism. Based on a collection of 1500 specimens from Perchois-Ouest (Aube, Paris Basin, France), Destombes (1979) documented the complex structure of the *Douvilleiceras* populations from the Lower Albian (*C. floridum* Subzone). He recognised three species groups, namely, *D. mammillatum sensu lato*, *D. inaequinodum sensu lato*, and the group of *Douvilleiceras leightonense* Casey 1962 – *scabrosum* Casey 1962.

D. inaequinodum sensu lato includes morphologies that belong to the *inaequinodum – alternans – baylei – orbignyi* plexus. It represents 16% of the fauna (160 out of 1000 specimens) and includes individuals with a short body chamber (? immature adults) and specimens with a scaphitoid coiling (? microconchs). Besides, Destombes also outlined that the mean adult size of the populations was decreasing during the Lower Albian. Even so, Destombes mentioned the existence of microconch and macroconch forms. Neither the sex ratio nor the distinctive features of the antidimorphs are documented.

Taxonomy. Based on literature review, we agree with Casey (1962) that *D. baylei* is a subjective junior synonym of *D. orbignyi.* It is noteworthy that the teat-like tubercles of *D. baylei* show four clavate swelling at a younger stage than *D. orbignyi*. Besides, the holotype of *D. baylei* bears an isolated intercalated rib at what seems to mark the beginning of the body chamber. According to Owen (1988, p. 211) the specimen illustrated by Destombes (1979) as *D. orbignyi* is a misidentified *D. alternans*. We support this view.

We also agree with Casey (1962) that *D. orbignyi* was wrongly merged with *D. inaequinodum* since Spath (1923, p. 69-70).

Despite its extensive use in the literature (see Klein and Bogdanova, 2013), the true identity of *D. inaequinodum* remains unclear. It can only be interpreted on the basis of the original description and illustration since the type specimen is considered to be lost (Ingmar Werneburg, pers. com. 2020). The species was introduced as a variety of *D. monile* (= *D. mammillatum*). The original protograph was reproduced by Spath (1925, Text-Fig. 15a) and Casey (1962, Text-Fig. 95c). It illustrates a ventral view showing three strongly tuberculate ribs separated by two single intercalatories. The outer ventrolateral tubercles are divided into four spiral ridges. The ventral area is marked by a moderately wide sulcus. The ornamentation of the flanks is not illustrated. The original text mentions a single rounded lateral tubercle, and indicates that *D. monile* has two additional lateral tubercles that are not visible on var. *inaequinodum*. The specimen is entirely septate, and its early ontogenetic stages are unknown.

If Quenstedt's description is accurate, the primary ribs of the type specimen of *D. inaequinodum* would therefore bear five rows of tubercles (a lateral rounded one and a teat-like ventrolateral one subdivided into four spiral ridges). The only specimen of the literature that somewhat matches Quenstedt's original description is the fragmentary holotype of *Douvilleiceras magnodosum* Casey 1962. At present, we suggest that *D. inaequinodum* should be considered as a *nomen dubium*.

The taxonomic significance of the number of intercalated ribs was questioned by Cooper (1982). Based on material from the late Lower Albian (*Isohoplites eodentatus* Subzone) of Bully-Saint-Martin (France), he outlined transition forms between *D. alternans, D. orbignyi* and *D. inaequinodum*. Cooper's conclusions remain somehow unclear since he merged all three taxa under *inaequinodum* in his synonymy, but, pending a better understanding of the population structure of the *Douvilleiceras* from the Lower Albian, retained *orbignyi* as a subspecies of *inaequinodum* in the discussion.

A more drastic position was taken by Kennedy and Klinger (2015) who assume that the number of intercalated ribs represent no more than intraspecific variation. As a consequence, they regard *D. baylei*, *D. orbignyi* and *D. inaequinodum* as morphological variants of the same species. Similarly, the differences advocated by Casey (1962) to individualise *D. alternans* from *D. inaequinodum* were not considered sufficient by Kennedy and Klinger (2015). These opinions were largely adopted by Futakami and Haggart (2018). Nevertheless, those authors placed emphasis on the number tubercles per rib to keep *D. alternans* separate from *D. inaequinodum*. They suggested that confusion between the two species is common in the literature.

--------------- Figure 2 near here ---------------

In our view, many of the taxonomic opinions summarised above lack solid grounds. Conducting a biometric study based on material from successive horizons would be crucial to ascertain the identity of the taxa involved in the synonymy of the so-called "*inaequinodum*" group. Such a study cannot be based on types and topotypes alone since they originate from condensed deposits such as the "*niveau principal de Macheroménil*" (Ardennes, France), the "main *mammillatum* bed" at Folkestone (Surrey, UK), and the "*Grès glauconieux*" of the Nice area (Alpes-Maritimes, France) (Thomel and Lanteaume 1967; Casey 1961b; Owen, 1988; Amédro and Destombes 1975; Amédro 1985, 1992; Delanoy and Latil 1988). As already discussed above, Destombes (1979) presented a semi-quantitative approach of *Douvilleiceras* variability but he did not address a biometric study of the successive *Douvilleiceras* populations. Similarly, the ontogenetic sequence of the various typological taxa remains poorly understood. Pending such a study, our taxonomic approach is conservative. This is reflected by our synonymy list that refers only to specimens that match the holotype of *D. orbignyi*.

As discussed above, *Douvilleiceras alternans* differs by the appearance of simple intercalated ribs in early ontogeny (Figs. 3.4a-b). We agree with Futakami and Haggart (2018) that the species is valid even though we do not give the same importance to the number of umbilical and lateral tubercles. Many of the large specimens referred to *D. aequinodum* in the literature may represent the adults (? macroconchs) of *D. alternans*. This is the case of the specimens of *D.* gr. *orbignyi* illustrated by Destombes (1979) and Matrion (2010).

Douvilleiceras sp.

Fig 3.1a-c and 2a-c

cf. v. 2010 *Douvilleiceras* cf. *mammillatum* Schlotheim var. *aequinodum* (Quenstedt) *sensu* Cooper, Bulot, p. 186, Pl. 8.3-4.

Material. Two specimens from Gabal Maaza, Maghara area, North Sinai, Egypt. MZ/87/CUGM (Figs. 3.1a-c) and MZ/88/CUGM (Figs. 3.2a-c),

Measurements (in mm):

Specimen	D	Wb	Wh	Wb/Wh	U
MZ/87/CUGM	54 (100)	36 (0.67)	20 (0.37)	1.80	23 (0.43)
MZ/88/CUGM	53 (100)	24 (0.45)	19 (0.36)	1.30	20 (0.38)

Description. MZ/87/CUGM and MZ/88/CUGM are full whorls of respectively 53 and 54 mm in diameter. Both specimens are poorly preserved due to incrustation by oolitic grains. The umbilicus is large and comprises more than a third of the diameter (0.36 < U/D < 37). The ornamental features are essentially the same as those of MZ/89/CUGM and MZ/90/CUGM but the lateral and ventrolateral tubercles are weaker throughout ontogeny. MZ/88/CUGM is entirely septate and differs by its less depressed whorl section (Wb/Wh1 = 1.30). MZ/89/CUGM is marked by slightly rursiradiate ribs on the outer whorl. This change in ornamentation seems to coincide with the beginning of the body chamber at D ~ 26 mm. It is interesting to note that the development of rursiradiate ribs seems to indicate the adult stage of the microconch (see for example *Douvilleiceras mammillatum* var. *praecox* Casey 1962, Pl. 41, Fig. 5a-b and Destombes 1979, Fig. 4-21, Fig. 3a-b) (see also Fig. 3.5).

Discussion. Even though all the diagnostic characters of *Douvilleiceras* are present on the above specimens, their relatively poor preservation prevents identification at the specific level. To some extent, the Egyptian specimens match those identified from Kuh-e-Bangestan (South West Iran) such as the one illustrated by Bulot (2010, Pl. 8.3-4) (reproduced on Figs. 3.3a-b). The main difference lies in the lower number of clavate ventrolateral swellings (only two in the Iranian form). It should be also noted that the comparison of the specimens from Bangestan with *Douvilleiceras mammillatum* var. *aequinodum sensu* Cooper is likely erroneous. This point will be discussed in a forthcoming contribution on the Iranian faunas.

Biostratigraphy.

In Western Europe, the cosmopolitan ammonite genus *Douvilleiceras* is abundant in the *Douvilleiceras mammillatum* Superzone, but the stratigraphical range extends from the *Leymeriella tardefurcata* Zone (*Leymeriella acuticostata* Subzone) to the *Lyelliceras lyelli* Subzone of the *Hoplites (H.) dentatus* Zone (Owen 1988, 1999; Kennedy et al. 2000; Matrion 2010, with references).

Even so, most illustrated specimens originate from condensed sections. True *Douvilleiceras orbignyi* is documented from the middle Lower (middle part of the *Sonneratia chalensis* Zone) to upper Lower Albian (top of the *Otohoplites auritiformis* Zone) (see Figure 3). The species seems to be more common in the lower part of its range (*Cleoniceras (C.) floridum* to *Protohoplites (Hemisonneratia) pusozianus* subzones). Whether this reflects reality or collection failure is unknown.

--------------- Figure 4 near here ---------------

The South African *D. orbignyi* originate from Albian II-III of Kennedy and Klinger (1975). At Hluhluwe (locality 53), they are associated with *Tegoceras mosense* (d'Orbigny, 1841), a species that ranges from the *C. floridum* to the *P. puzosianus* subzones of the Lower Albian (Latil 1995; Kennedy and Klinger 2008).

As a consequence, the early Albian age of the *Knemiceras gracile* Interval Zone *sensu* Abu Zied (2008) is now firmly established. This time interval falls within the middle to the uppermost part of the *D. mammillatum* Superzone *sensu* Owen (1988) (= *D. mammillatum* Zone of Reboulet et al. 2011). A correlation with the *C. floridum* to *P. puzosianus* subzones is supported by the occurrence of *Beudanticeras revoili* Pervinquière 1907 in the *Knemiceras* assemblage of Gabal Manzour (Mahmoud 1955). In Tunisia, *Beudanticeras revoili* is reported from the upper part of the *Prolyelliceras gevreyi* Zone and *Buloticeras radenaci* Zone, a time equivalent to the *C. floridum* to *P. puzosianus* subzones of the Anglo-Paris Basin (see discussion in Latil 2011).

Palaeobiogeography and population dynamics.

The palaeobiogeographic distribution of *Douvilleiceras* with hypernodose ventrolateral tubercles, e.g. *D. orbignyi* and *D.* "*inaequinodum*" group of the literature, is presented in Figure 4. Throughout their palaeogeographic range, both taxa are minor elements of the faunal assemblages. When quantitative data are available, *Douvilleiceras* of the *mammillatum* group are always reported to dominate the populations (see Destombes 1979, for example). It is well established that *Douvilleiceras* is a cosmopolitan and major component of the lower Albian ammonoid faunas of the peri-Tethyan seas. Nevertheless, its abundance is very variable through space and time.

---------------- Figure 5 near here ---------------

In the Albian of the Anglo-Paris Basin, the oldest occurrences are poorly documented due to the condensed nature of the lowermost Albian deposits. Based on observations in Aube and Normandy, the genus represents between 70 and 80% of the total fauna in the middle part of the lower Albian, becoming less common in the uppermost lower Albian (12 to 20% of the fauna), and decreases to 5 to 6% of the fauna just before its extinction in lowermost middle Albian (Destombes 1970, 1973, 1979, Courville and Lebrun 2010, Amédro et al. 2014). Similar abundance has been reported from the UK, where the genus is a major component of the "main *mammillatum* bed" of the lower Albian of Folkestone (Casey 1961b, Owen 1988). *Douvilleiceras* is also reasonably common in the condensed deposits of the Dauphiné and Provence platforms (Castellane and Nice arcs; see Thieuloy and Girod 1964, 1965; Gebhard 1979).

Douvilleiceras also largely dominates the lower Albian assemblages of southern Africa (Cooper 1982, Tavares et al. 2007, Kennedy and Klinger 2015, LGB personal observations). A fairly large number of specimens were illustrated from the lower Albian of Madagascar by Besairie (1936), Breistroffer (1936) and Collignon (1950, 1963), but the genus is not the main component of the faunas. According to Collignon (1949, p. 103), at Ambarimaninga (Mahajanga Basin), *Douvilleiceras* represents only 11% of the fauna. A somehow higher percentage was reported from Hazara (Punjab, India), where *Douvilleiceras* represents 17% of the fauna (94 out of 550 specimens; see Spath 1930, p. 55).

North and Central American (including Colombia) abundances are difficult to appreciate since quantitative data are missing. In Brazil, the genus is well represented in the lower

Albian faunal assemblages (Zucon Ramos de Siquiera 2005). Conversely, the Peruvian assemblages are dominated by Engonoceratidae and *Douvilleiceras* are scarce (Robert 2002). The genus also occurs as a rarity on the southern margin of the Neo-Tethys. It was reported from Morocco, where it is represented by a handful of specimens that mostly occur in the lowermost Albian (Peybernès et al. 2013; Luber et al. 2017; Giraud et al. 2020). Spot occurrences from Algeria and Tunisia were documented by Latil (2011). In SW Iran, the genus is sporadically present in the deeper intra-shelf basin facies of the Bangestan anticline (Bulot 2010). Still, it is a rarity in the shallow water facies of the Khazdumi Formation characterised by the mass occurrence of *Knemiceras*. In Sinai, *Knemiceras* also dominates the assemblages and forms more than 90% of the assemblages (410 out of 440 ammonites at Gabal Manzour, according to Mahmoud 1955). The real abundance of the genus in Somalia is hard to appreciate, even though several *Douvilleiceras* were described by Tavani (1942, 1949).

Conclusions.

Even though *Douvilleiceras* was reported from Sinai in the literature, the genus was never unequivocally documented until the present contribution. The study of our material brought the following results:

1. The state of preservation of our material and a limited number of specimens do not allow us to state if more than one species is present in Sinai. Our best-preserved specimens are assigned to *Douvilleiceras orbignyi*, a species originally described from the middle to the uppermost lower Albian of the Anglo-Paris Basin. The early Albian age of the *Knemiceras gracile* Interval Zone *sensu* Abu Zied (2008) is now firmly established. Correlation with the *C. floridum* to *P. pusozianus* subzones (*D. mammillatum* Superzone *sensu* Owen 1988) of the standard ammonite scale of the Anglo-Paris Basin is proposed.
2. Evaluation of the intraspecific variability of *Douvilleiceras* is largely handicapped by the condensed nature of the lower Albian deposits of type localities in the Anglo-Paris Basin and Provencal Platform (Macheroméril, Folkstone and Nice area). Besides, the ontogenetic development of many typological species from the literature remains largely undocumented.
3. Careful re-examination of the literature has convinced us that the lumping of *D. orbignyi* in *D. inaequinodum* is questionable since the latter species is a *nomen dubium*. The systematic assignment of the material described as *D. inaequinodum* should be reconsidered. In our

current stage of knowledge, three nominal species, e.g. *Douvilleiceras orbignyi*, *D. alternans* and *D. magnodosum* would seem to accommodate them satisfactorily.

4. As herein understood, *D. orbignyi* is a fairly widespread species that is known from the Anglo-Paris Basin (France and UK), Sinai (Egypt), the Caucasus (Georgia), Mahajanga region (Madagascar), Rajasthan (India), KwaZulu-Natal (RSA) and Sergipe (Brazil).

5. The cosmopolitan distribution of *Douvilleiceras* during early Albian times must not overshadow the variability of its abundance through space and time. It is noteworthy that hypernodose morphologies (*orbignyi* and "*inaequinodum*" group) are unknown in the oldest and youngest populations. They represent a minor, thought constant element of the middle to late early Albian populations.

The present contribution also outlines the need for an exhaustive biometric study of the genus *Douvilleiceras* based on stratigraphically well-located populations such as the ones made by Destombes (1970, 1973, 1979) in the Anglo-Paris Basin.

The scarcity of *Douvilleiceras* in assemblages dominated by *Knemiceras* (Egypt and Iran) or *Parengonoceras sensu lato* (Peru) is intriguing. These three taxa favoured shallow water epicontinental seas and continental shelf environments. Westermann (1990, fig. 6) suggested a sluggish necto-benthic way of life in the shallow neritic zone for both Douvilleiceratidae and Engonoceratidae. Environmental changes are likely the main driving force that controlled the distribution of *Douvilleiceras*, *Knemiceras* and *Parengonoceras sensu lato*. Was the expansion of *Douvilleiceras* during early Albian times limited by thermal factors and/or hypersalinity that were more favourable to Engonoceratidae in the low latitudes?

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Captions.

Figure 1. A geological map of the studied area with localities and stratigraphic position of the *Knemiceras gracile* assemblage in the Manzour section (modified after Abu Zied 2008). The dark blue star indicates Gabal Maaza. The red stars indicate the location of the key Lower Albian sections of Gabal Lagama (Aly and Abdel-Gawad 2001) and Gabal Manzour (Aboul Ela et al. 1991, Abu Zied 2008).

Figure 2. *Douvilleiceras orbignyi* Hyatt, 1903. 1a-c, lateral and ventral views of MZ/89/CUGM, 2a-c., lateral and ventral views of MZ/90/CUGM; both from Gabal Maaza, Maghara area, North Sinai, Egypt; 3. ventral view of GSM 70425 from Copt Point, Folkestone, Kent, UK; 4a-b. lateral and ventral view of OUM KX4863 from south of the farm Izwehelia, north of Hluhluwe, KwaZulu-Natal, RSA (loc. 53 of Kennedy and Klinger 1977); 5a-b. lateral and ventral view of BM C12169, the holotype of *Douvilleiceras baylei* Spath, 1923 from Macheroméril, Ardennes, France. 6. Ventral view of the holotype of *Douvilleiceras orbignyi* from Macheroméril, Ardennes, France (FSL unnumbered specimen). All specimens in natural size.

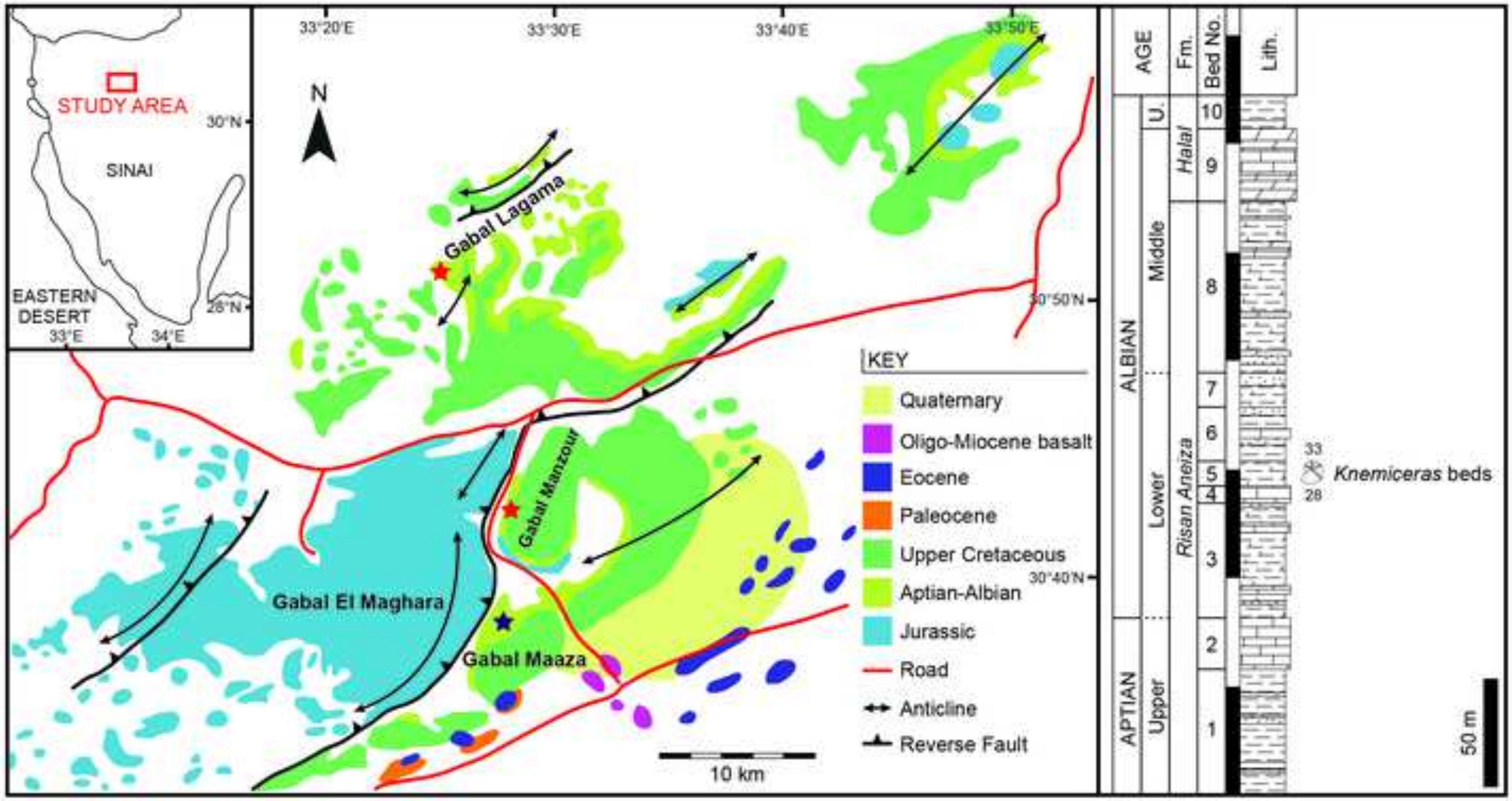
Figure 3. 1-2. *Douvilleiceras* sp. 1a-c, lateral and ventral views of MZ/87/CUGM, 2a-c, lateral and ventral views of MZ/88/CUGM; both from Gabal Maaza, Maghara area, North Sinai, Egypt; 3a-b. *Douvilleiceras* sp., lateral and ventral of NARG-LGB-BAN-92.1 from Kuh-e-Bangestan, Khuzestan, Iran; 4a-b. *Douvilleiceras alternans* Casey, 1962, lateral and ventral view of the holotype GSM 70426 from Copt Point, Folkestone, Kent, UK; 5. *Douvilleiceras mammillatum* var. *praecox* Casey, 1962, lateral view of GD 543 from Perchois-Est, Aube, France; All specimens in natural size.

Figure 3. Biostratigraphic distribution of the *Douvilleiceras* of the *orbignyi* group in the Anglo-Paris Basin. The ammonite zones and subzones are after Owen (188). The asterisk marks reference to the *H. benettianus* Zone *sensu* Amédro et al. (2014). 1. *S. (G.) perinflata*, 2. *S. kitchini*, 3. *C. floridum*, 4. *O. raulinianus*, 5. *P. (H.) puzosianus*, 6. *O. bulliensis*, 7. *P. (I.) steinmanni*, 8. *L. pseudolyelli*, *9. L. lyelli*. Ammonite ranges modified based on illustrated material only.

Figure 4. Palaeobiogeographic distribution of *Douvilleiceras orbignyi* and *D.* “*inaequinodum*” group based on illustrated material only (see synonymy and taxonomic discussion). The **?** indicates doubtful occurrences. Map modified after Scotese and Golonka (1992).

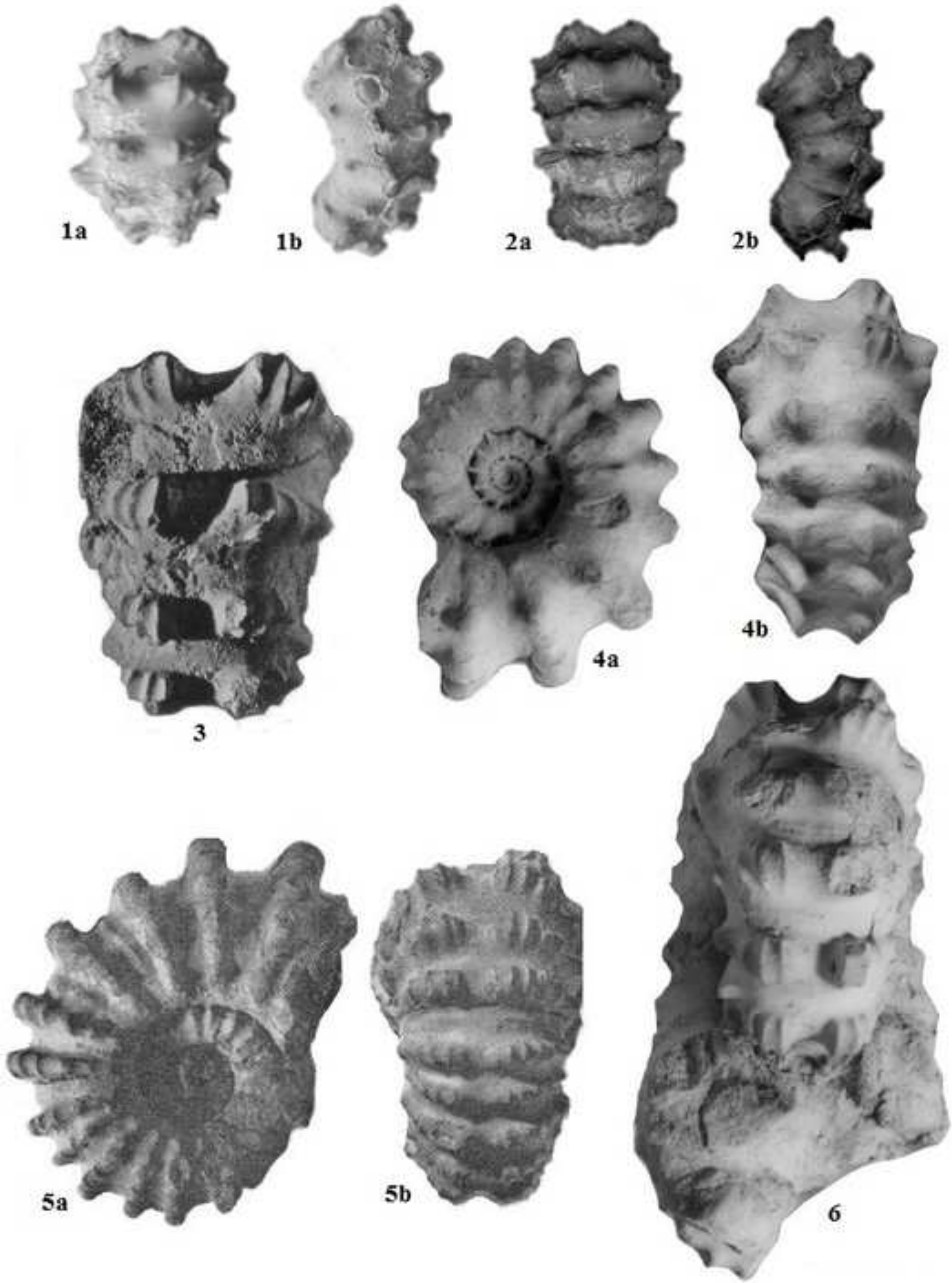
Location map

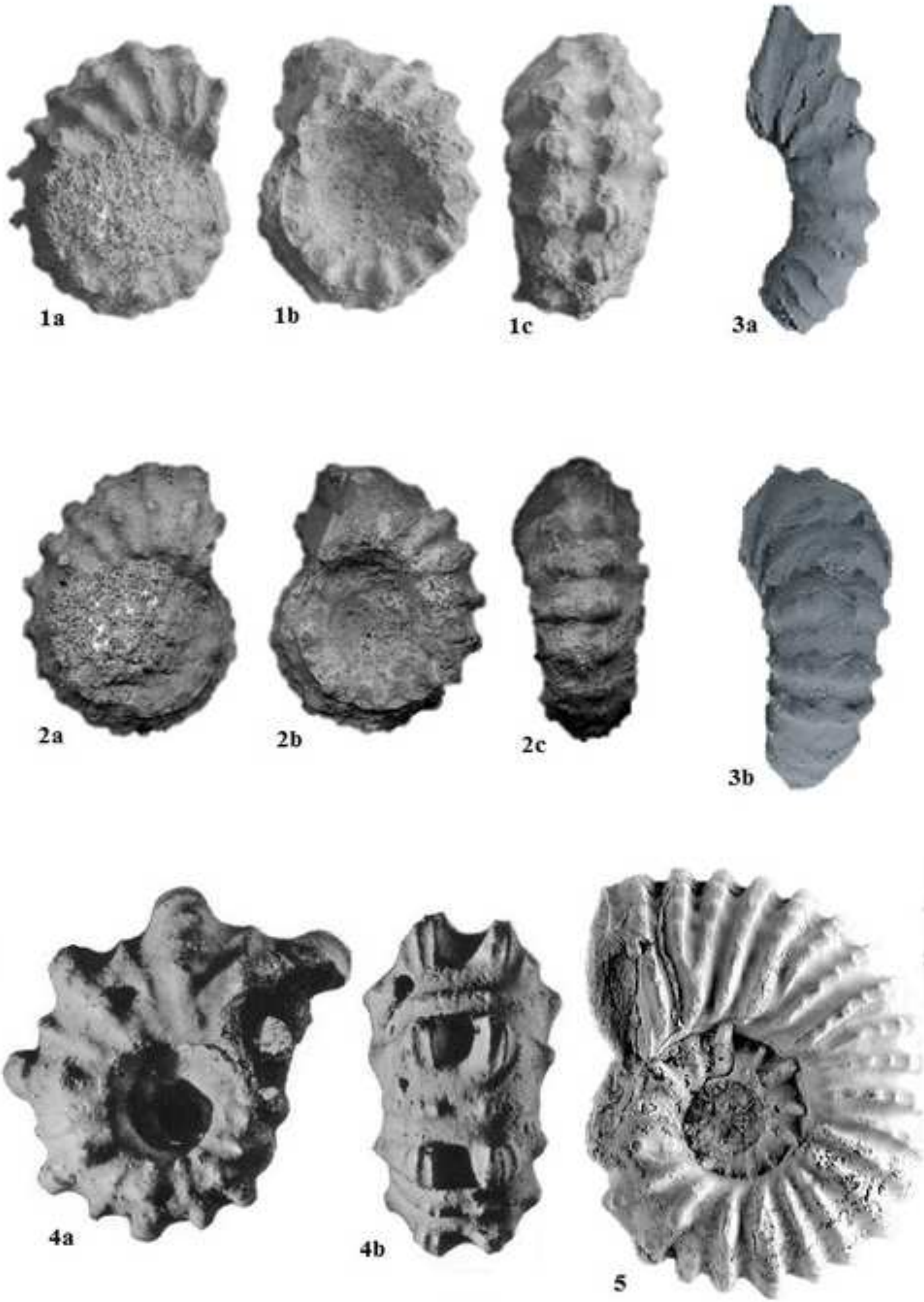
Click here to access/download;Figure;Fig. 1. Location map and log-01.tif



Photographic plate

Click here to access/download;Figure;Fig. 2. Plate ammonite Douvilleiceras orbignyi.jpg




1a
1b
1c
3a
2a
2b
2c
3b
4a
4b
5

	S. chalensis Zone			*L. auritiformis* Zone				*H. benettianus* Zone*	
	1	2	3	4	5	6	7	8	9
D. orbignyi		?	X	X	X	X	X		
D. magnodosum			X						
D. alternans			X	X	?				
"D. inaequinodum"							X	X	

Palaeobiogeographic map

Click here to access/download;Figure;Fig. 5. Paleobiogeography Douvilleiceras gr. inaequinodum-01.tif