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VERSITA

Palaeontology, taxonomic revision and variability of some species of the genus *Gassendiceras* Bert *et al.*, 2006 (Ammonitina, Upper Barremian) from southeastern France

DIDIER BERT[1], STÉPHANE BERSAC[1], GÉRARD DELANOY[2,1] AND LÉON CANUT[1]

[1]*Laboratoire du Groupe de recherche en Paléobiologie et biostratigraphie des Ammonites (G.P.A), Bois-Mésange, quartier St Joseph, F-04170 La Mure-Argens, France*
[2]*Department of Earth Sciences, University of Nice-Sophia-Antipolis, Sciences Faculty, 28 avenue Valrose, F-06108 Nice Cedex 2, France*

ABSTRACT:

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Bed-by-bed sampling of twelve Barremian sections in southeastern France from pelagic basin (Vocontian Basin) to neritic platforms (Arc of Castellane, Arc of Nice and Provençal Domain) has enabled the collection of isochronous samples of the ammonite genus *Gassendiceras*. Three poorly known species of the *Toxancyloceras vandenheckei* Zone (Upper Barremian) are revised: *G. alpinum*, *G. multicostatum* and *G. hoheneggeri*; two new species are described (*G. rebouleti* nov. sp. and *G. bosellii* nov. sp.). The intraspecific variability of particular species was recognised. This variability is between slender peramorphic and robust paedomorphic extreme morphologies, with the presence of all intermediates.

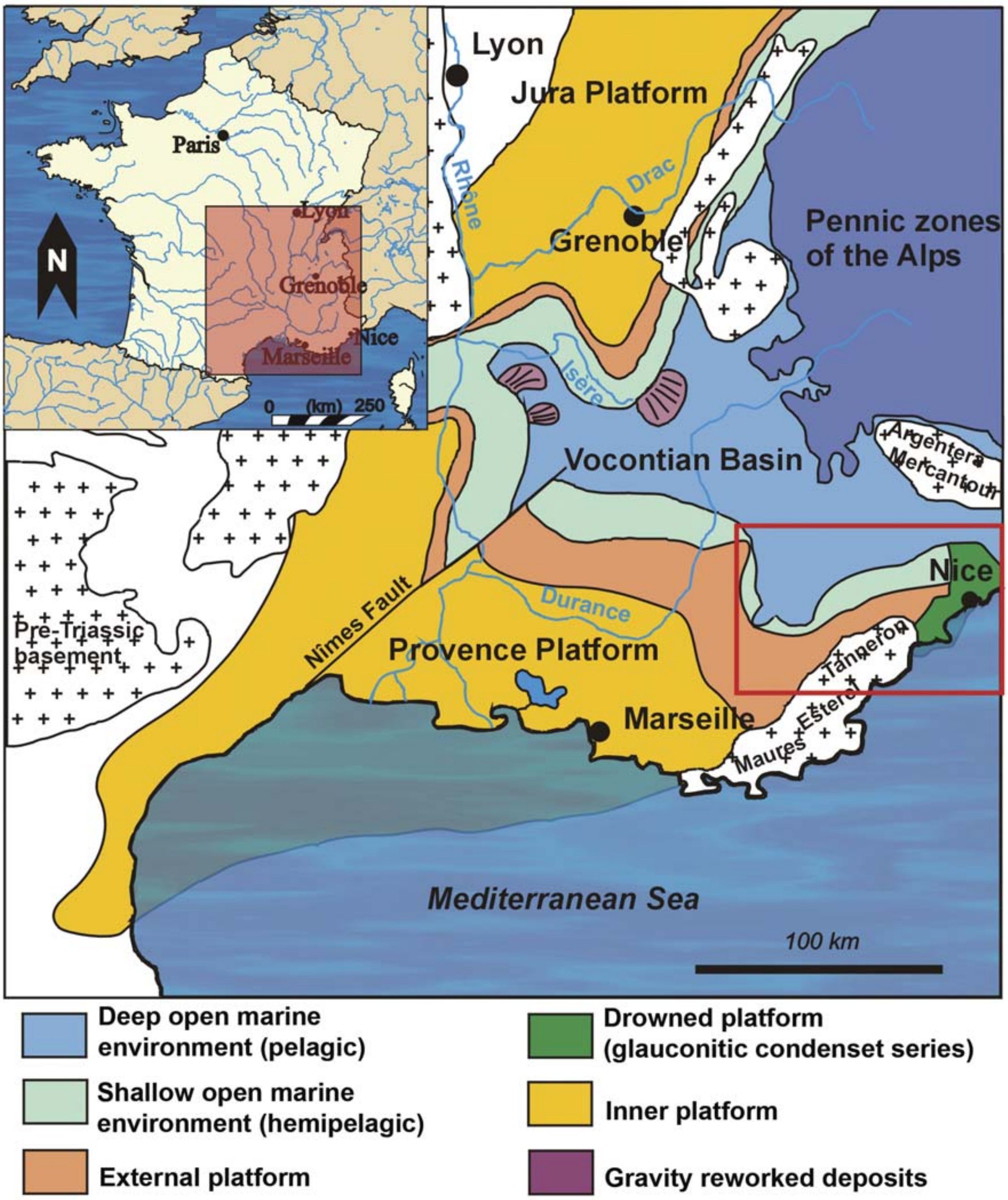
Key words: Ammonoidea; Gassendiceratinae; Upper Barremian; Southeastern France; Taxonomy; Intraspecific variability.

INTRODUCTION

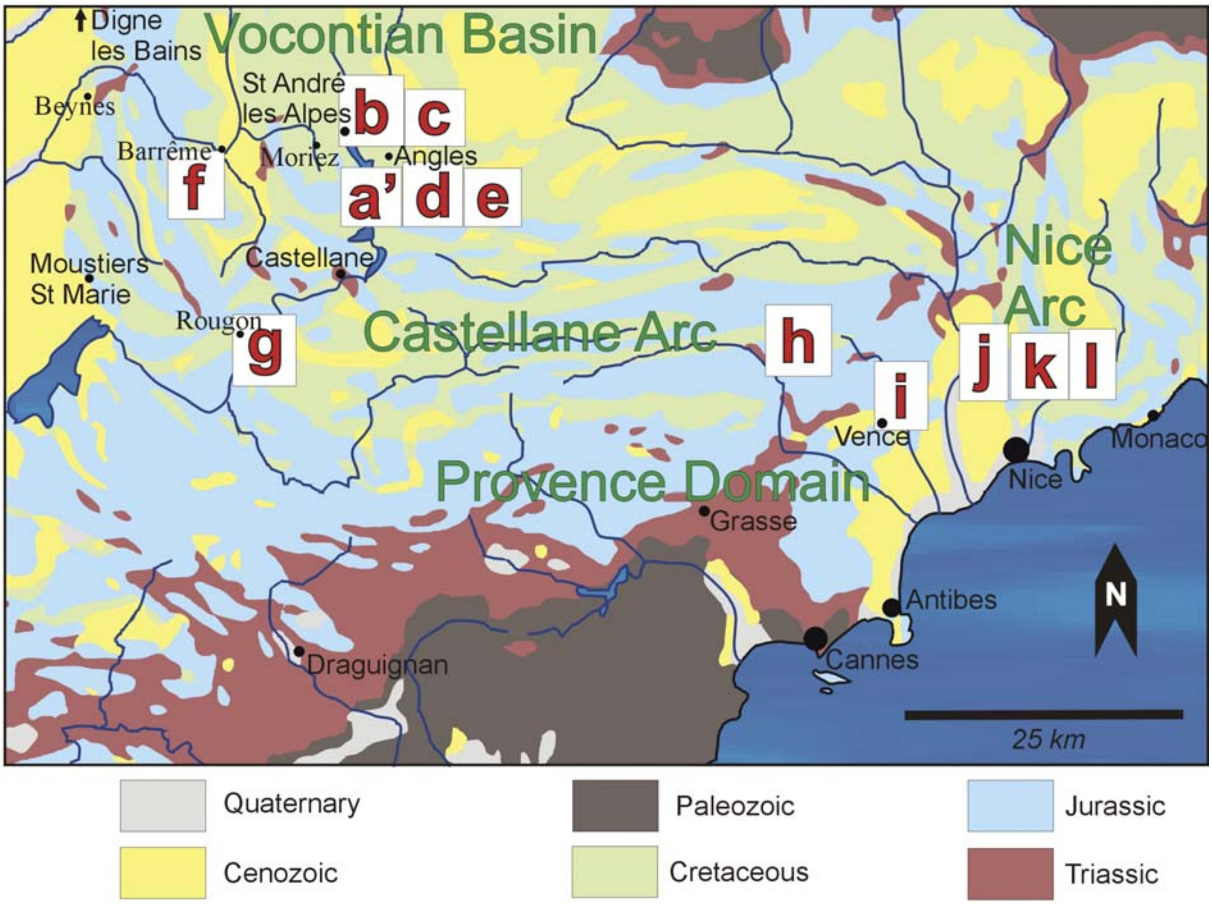
The rapid evolution and diversification of the family Hemihoplitidae Spath, 1924 make it a key group for the marine Upper Barremian (pro parte) in the North Tethyan margin (southeastern France). This group of ammonites was, however, relatively unknown until recently and it required taxonomic revision. This revision has been conducted by one of us (D.B.) over several years and numerous contributions have already been published (Bert and Delanoy 2000, 2009; Bert *et al.* 2006, 2008, 2009; Bert *et al.* 2010, 2011; Bert 2012b). New collections of ammonites have been made from levels previously reported as being poor in fossils in the upper part of the *Toxancyloceras vandenheckei* Zone, the *Gassendiceras alpinum* Subzone. The present work concerns the study of the genus *Gassendiceras* Bert *et al.*, 2006 (Gassendiceratinae Bert *et al.* 2006), of which many new specimens have been recently collected in sections from various environmental settings in southeastern France. This genus is characterized by a particularly distinctive robust ornamentation, with strongly trituberculate main ribs and smooth interribs. The intraspecies variability is recognised in this group its taxonomy is revised, being the first step in reconstructing the phylogeny of the genus (Bert and Bersac 2013).

GEOLOGICAL SETTING AND SECTIONS STUDIED

The studied specimens were collected by bed-by-bed sampling from twelve sections in both pelagic and neritic environments of southeastern France. The Lower Cretaceous of this area is marked by the evolution of a large intracratonic subsident area known as the Vocontian Basin (Paquier 1900; Text-fig. 1). The southern part of the Vocontian Basin, in the area of the historical Barremian stratotype (Angles-Barrême-Castellane area; Text-fig. 2), is usually less affected by gravity remodelling and the effects of the Alpine orogeny. It is bordered to the south by neritic platforms that were more or less open to the ocean. Six sections were studied in the southern Vocontian Basin in the stratotype area of the Barremian (pelagic environment), and six others on the southern edge of the peri-Vocontian platform (neritic environment). These are spread over the Arc of Castellane, the Provençal Domain and the Arc of Nice (Text-fig. 2).



Text-fig. 1. Palaeogeographic map of southeastern France to show the study area (from Arnaud 2005)



Text-fig. 2. Simplified geological map of the study area (Alpes-de-Haute Provence, Alpes-Maritimes and Var in southeastern France). Sections (see text): a'= A and A'; b = LAC; c = GRY; d = G12; E = G15; f = VIG2; g = SO; h = TAI; i = VA; j = SA; k = RS; l = TF

The stratigraphic framework of the Upper Barremian used in this work is the one proposed by the I.U.G.S Lower Cretaceous ammonite working group, the Kilian Group (Reboulet *et al.* 2007; Reboulet *et al.* 2009 – see Bert *et al.* 2008 for historical account), emended and supplemented by Bert *et al.* (2008), Bert and Delanoy (2009), and Bert *et al.* (2010, 2011).

Basinal sections

The Barremian of southeastern France is characterized by pelagic sedimentation with an alternation of marls and limestones in decimetric to metric beds. The continuous sedimentation and good palaeontological record reveal the ammonite succession in considerable detail. The deep marine conditions of the Vocontian Basin, largely opened to the Alpine Tethys, are reflected in the dominance of ammonites.

Sections A and A': Section A corresponds to the historical Barremian Stratotype of the Angles road. This section has been detailed by Busnardo (1965), its upper part by Delanoy (1994, 1997), and the entire section by Vermeulen (2005a). The lower part of the Upper Barremien (*s.l.*) succession is difficult to interpret; firstly because of poor exposure (access along a sloping road-cutting) and secondly, because of growth faults and depositional anomalies affecting the succession (Bert *et al.* 2008; Bert 2012a). Consequently, a new section (herein called A'), on the adjacent hill, was studied. Only the Vandenheckei Zone of this section, which yielded several specimens of *Gassendiceras*, is included in the present study (Text-fig. 4, *pars.*).

Sections LAC and GRY: The section was described by Bert *et al.* (2008) and it is the lateral continuation of the previously studied section MEO (Delanoy 1994, 1997; Bert *et al.* 2008). The nearby section GRY (Text-fig. 5) has never been previously mentioned. Both the LAC and

GRY sections have provided several specimens of *Gassendiceras* (this work) and perfectly complement the Angles' stratotype sections, being similar albeit slightly expanded.

Sections G12 and G15: Section G12 (Text-fig. 6) exposes well the lower Upper Barremian, in particular the Vandenheckei and Sartousiana zones, albeit the succession is slightly thinner than in the previous sections. Section G15, which represents a continuation of section G12, provided many of the *Gassendiceras* studied herein from the Alpinum Horizon. These sections are described here for the first time.

Section VIG2: Delanoy (1994, 1995, 1997) already described and figured the upper part of this section. A very good section of the basal beds of the Upper Barremian exposed a few hundred metres away and now formally designated VIG2, has never been described, albeit it provided some ammonites to Thomel (1964

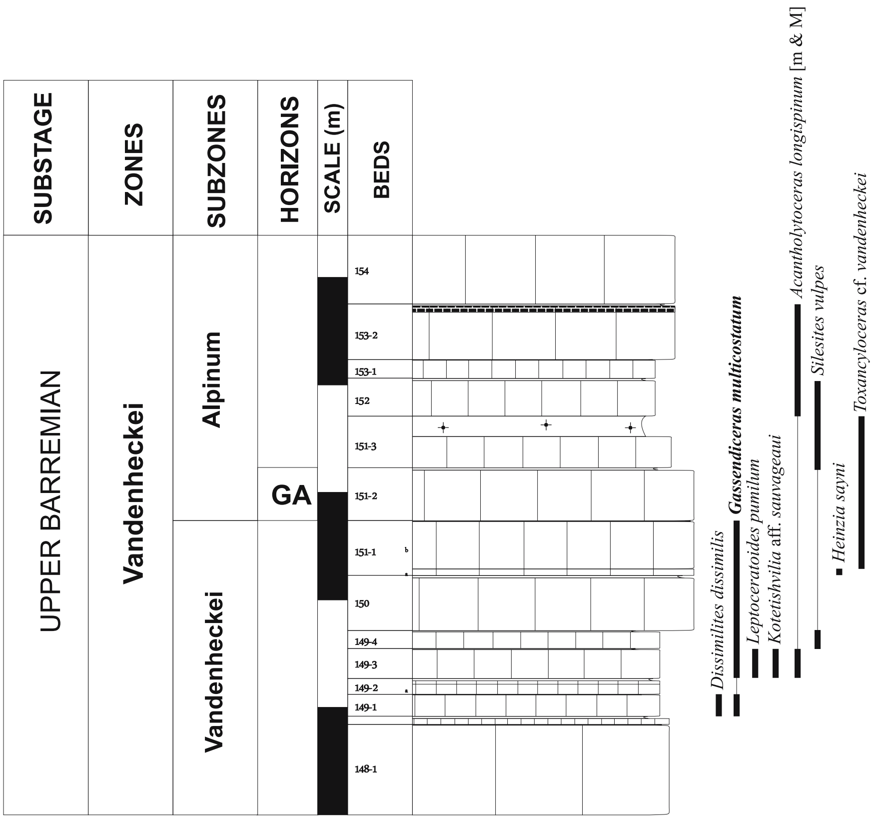
	Reboulet et al. 2009			This work		
Stages	**Zones**	**Sub-zones**	**Horizons**	**Horizons**	**Sub-zones**	**Zones**
Upper Barremian *pars*	*Imerites giraudi*	*Pseudocrioceras waagenoides*			*Pseudocrioceras waagenoides*	*Imerites giraudi*
		Martelites sarasini			*Martelites sarasini*	
			A. puzosianum	*A. puzosianum*		
		I. giraudi	*Heteroceras emerici*		*I. giraudi*	
				H. emerici		
			I. giraudi	*I. giraudi*		
				I. dichotomum		
	Gerhardtia sartousiana	*Hemihoplites feraudianus*		*P. autrani*	*Hemihoplites feraudianus*	*Gerhardtia sartousiana*
				P. bersaci		
				P. magnini		
				H. feraudianus		
		G. provincialis		*H. casanovai*	*G. provincialis*	
				G. provincialis		
		G. sartousiana		*G. sartousiana*	*Camereiceras limentinus*	
	Toxancyloceras vandenheckei	*Barrancyloceras barremense*		*C. limentinus*		
				C. marchandi	*Gassendiceras alpinum*	*Toxancyloceras vandenheckei*
				A. breistrofferi		
				G. alpinum		
		T. vandenheckei			*T. vandenheckei*	

Text-fig. 3. The Upper Barremian standard zonation (Reboulet *et al.* 2009) alongside the zonation used in this work (see Bert *et al.* 2008, Bert and Delanoy 2009, and Bert *et al.* 2010, 2011) and this work). The succession exposed is the most expanded (Text-fig. 7, pars) of all the sections described herein. It begins with a top surface of the bed at the base of the Vandenheckei Zone [*Toxancyloceras vandenheckei* (Astier) observed up to bed 250]. The bottom of this section is difficult to access and has yielded only rare Barremitidae and *Holcodiscus* (bed 256). Fragments of *T.* ex gr. *vandenheckei* were observed in scree. Beds 265 to 267 are more accessible and have yielded a limited ammonite fauna of which the most significant elements are *Gassendiceras alpinum* and *Kotetichvillia fischeuri* (Joleaud). Bed 266 yielded several fairly well preserved smaller specimens and a single very large adult specimen of *G. alpinum* (Pl. 1, Fig. 1; Pl. 2, Fig. 1).

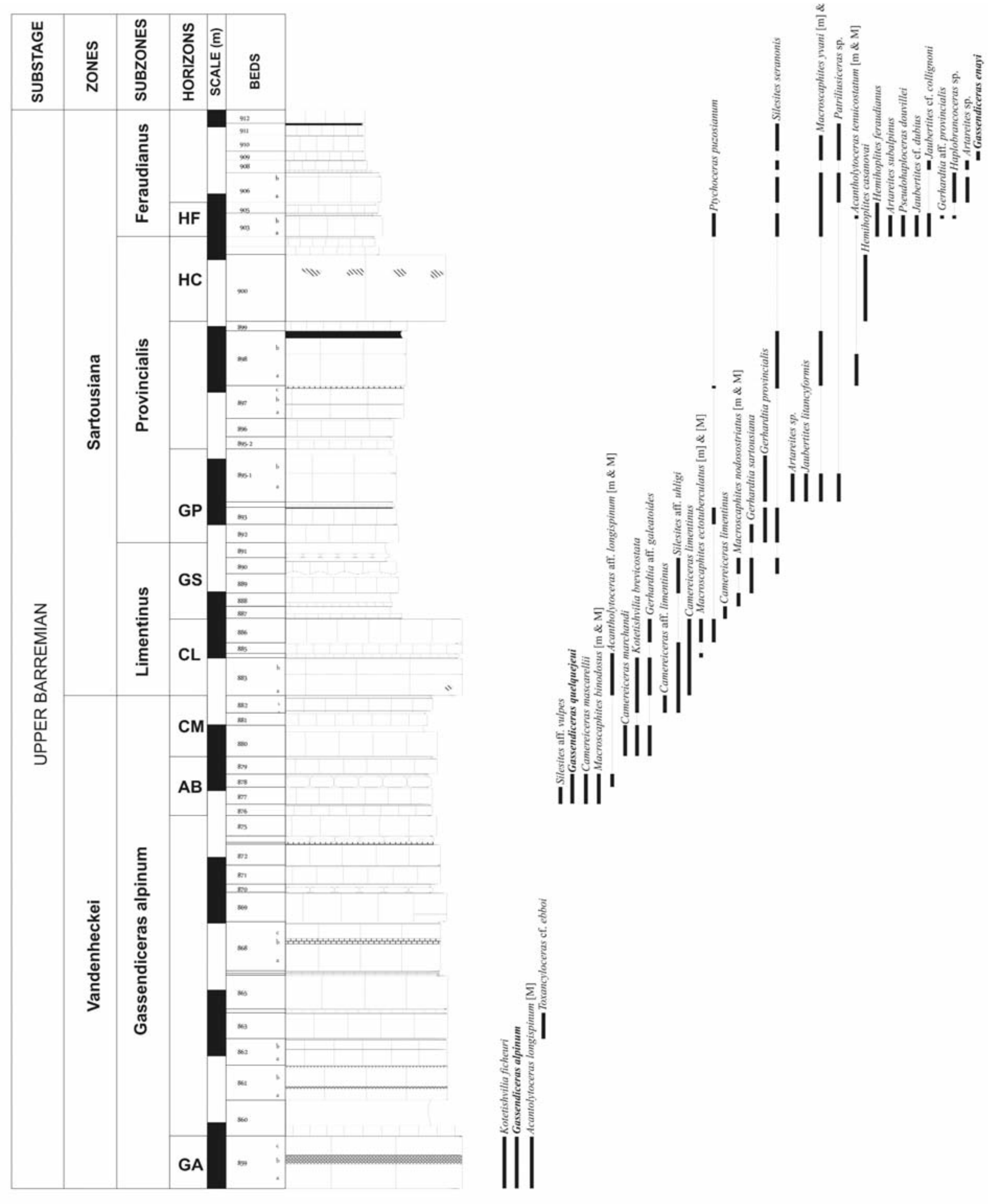
Neritic sections

The neritic domain of the South Vocontian Basin (Text-figs 1–2) is representative of a circalittoral marginal environment, rich in benthic faunas, and in cephalopods. The lateral continuity of the successions in the neritic area is lower than in the basin area because of high palaeotectonic activity (Cotillon *et al*. 2000). Sedimentation rates are generally low and subsidence is discontinuous compared to the pelagic domain (Cotillon 1971). Episodes of condensation and sedimentary gaps are noted (Bersac *et al*. 2010).

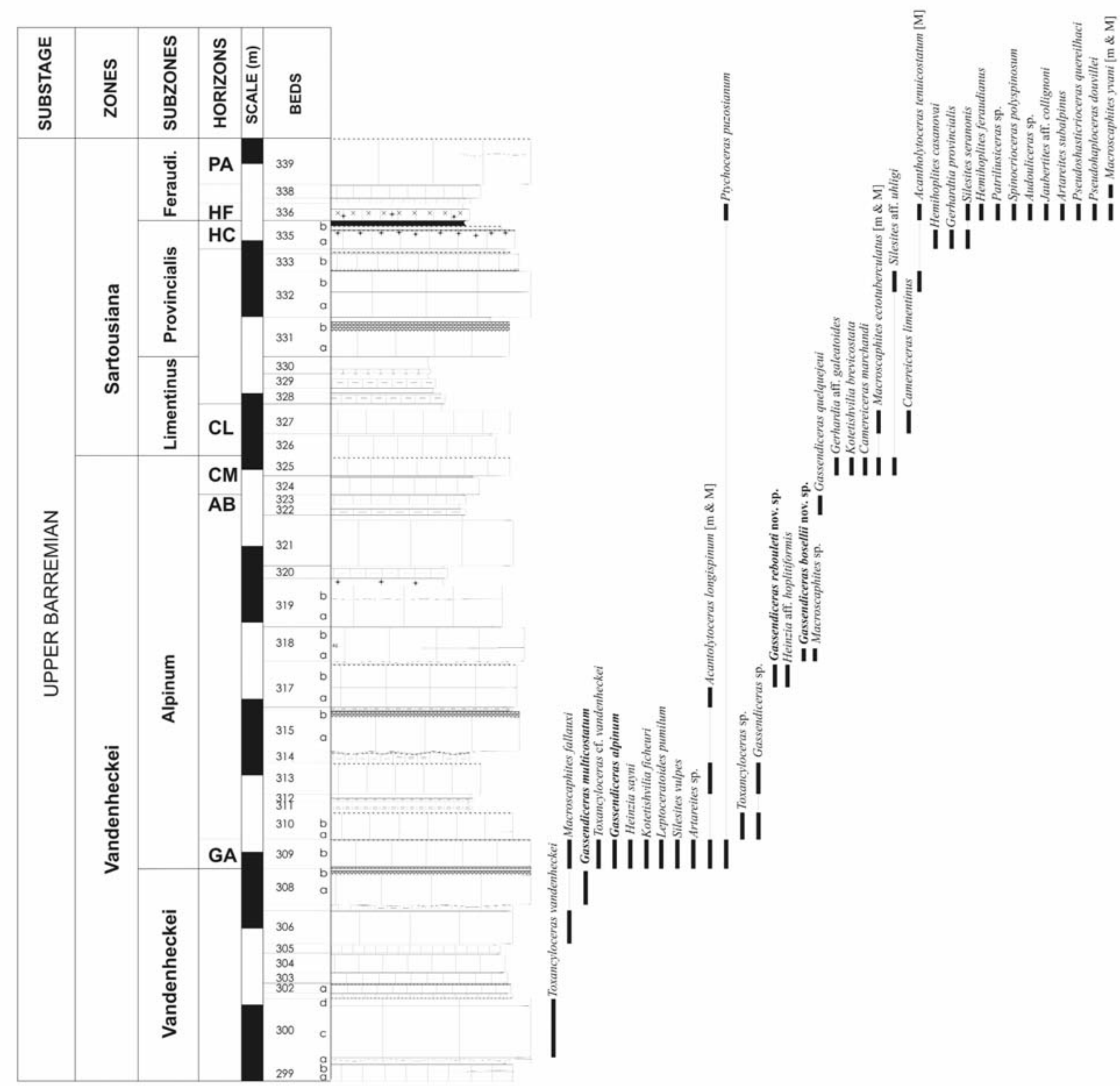
Section SO: Section SO is located in the distal limit of the peri-Provençal south Vocontian platform in the western part of the Arc of Castellane. The biostratigraphic framework was outlined by Busnardo and Cotillon (1964) and Cotillon (1971). The survey was carried out at the top of the Lower Cretaceous limestone formation. It includes a 17 m thick Barremian interval from the top of the Nicklesi Zone to the Sartousiana Zone (Feraudianus Subzone). The distribution of the ammonite faunas is given in Text-fig. 8, and their abundance allows recognition of the standard Tethyan ammonite zones and the establishment of reliable correlations with the Basin. The uppermost Barremian is always absent in this area because of truncation by the Aptian discontinuity (Cotillon *et al*. 2000), which separates the Eo-Cretaceous limestones from the Aptian–Albian marls. It may be noted that glaucony is present, especially in the levels of



Text-fig. 4. Range chart of the main ammonite species in section A' near Angles (complementary section of the Barremian stratotype), Alpes-de-Haute Provence, southeastern France. In the following Text-figs., MF/ND = Fallax and Didayana Horizon, Hco = Communis Horizon, GA = Alpinum Horizon, AB = Breistrofferi Horizon, CM = Marchandi Horizon, CL = Limentinus Horizon, GS = Sartousiana Horizon (acmeic horizon), GP = Provincialis Horizon, HC = Casanovai Horizon, HF = Feraudianus Horizon, PA = Autrani Horizon the Pulchella Zone. The appearance of *T. vandenheckei* and *Heinzia sayni* Hyatt in Bed 69-2 marks the base of the Upper Barremian. The presence in the same bed of *Gassendiceras multicostatum* (Sarkar) and *G. alpinum* suggests an episode of concentration / condensation in the lower part of the Vandenheckei Zone. Beds 72 to 74 are rich in "*small* Barremites" [*Barremites* aff. *charrierianum* (d'Orbigny) and *B. raspailli* Kilian] and correspond to the marker level described from Majastre (Bert 2009a). This particular level, located between the



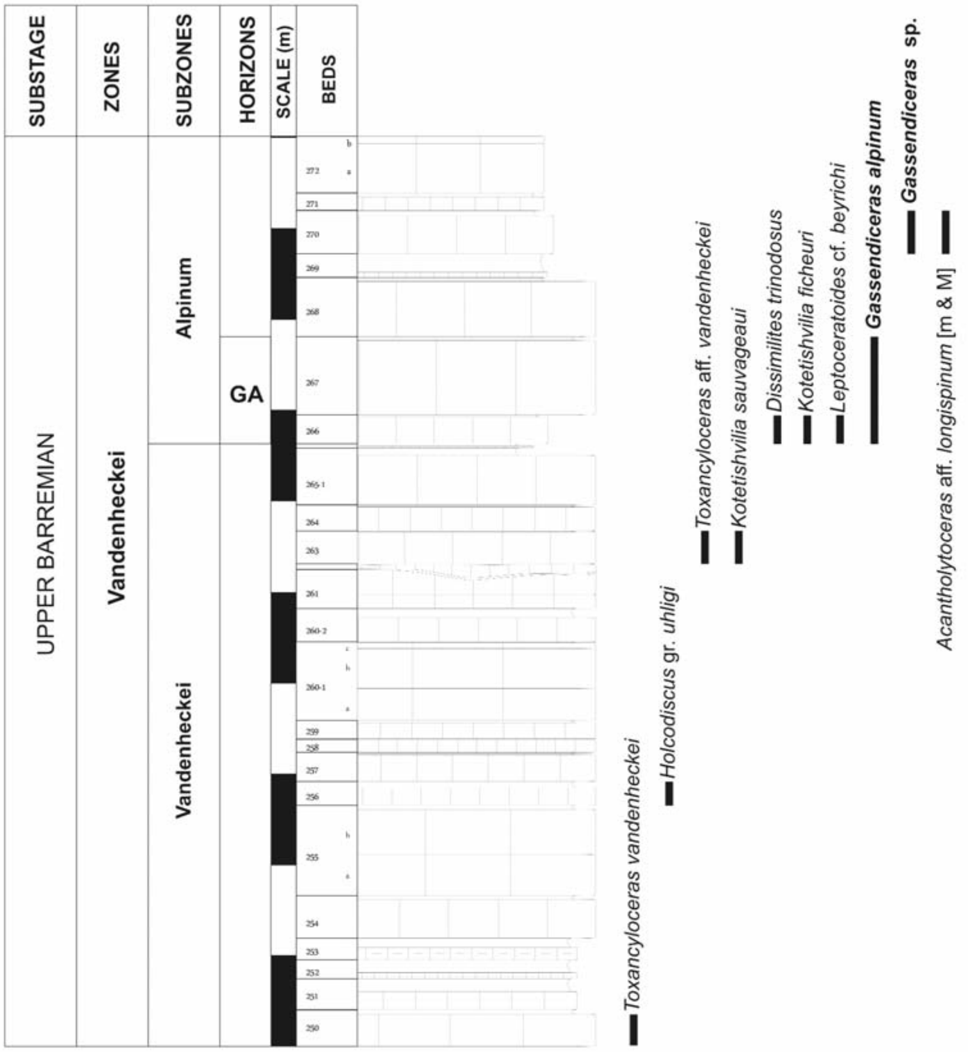
Text-fig. 5. Range chart of the main ammonite species in the section GRY near St André les Alpes, Alpes-de-Haute Provence, southeastern France



Text-fig. 6. Range chart of the main ammonite species in the section G12 near Angles, Alpes-de-Haute Provence, southeastern France

Alpinum and Breistrofferi horizons (top of the Vandenheckei Zone), provides an excellent datum on the south peri-Vocontian neritic platforms. The rest of the section is more calcareous, and is poorly fossiliferous up to the top of the Provincialis Subzone, which hinders recognition of the biostratigraphic horizons. However, a very large external mould attributed to *Gassendiceras* ex gr. *quelquejeui* Bert *et al*., a taxon that characterizes the top Vandenheckei Zone (Breistrofferi / Marchandi horizons) in southeastern France was observed in a lateral equivalent of beds 75-76. The presence of a large *Camereiceras* ex gr. *limentinus* (Thieuloy) in bed 80 indicates the position of the Limentinus Horizon, and thus the basis of the Sartousiana Zone (*sensu* Bert *et al*. 2008). The last bed of the section (83) is characterized by the presence of *Hemihoplites casanovai* Delanoy (Casanovai Horizon), while *H. feraudianus* (d'Orbigny) (Feraudianus Horizon) is confined to very glauconitic part immediately below the stromatolitic erosional surface of the Aptian discontinuity.

Section TAI: Section TAI belongs to the southeastern part of the Arc of Castellane. The Barremian is only a few metres thick and is represented by marly limestones at the top of the Lower Cretaceous limestone formation. The beds are rich in glaucony, broken fossils and omis-

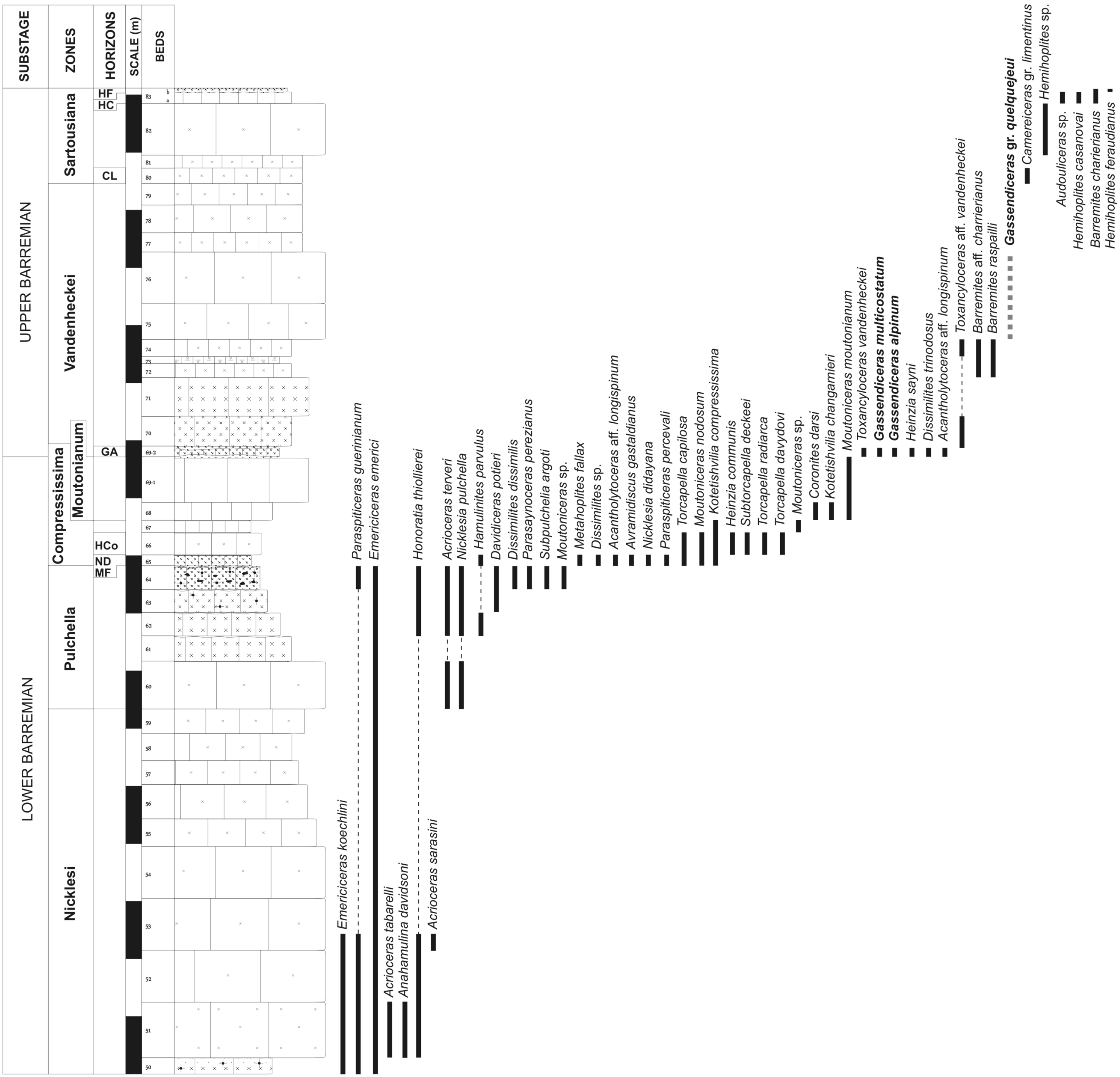


Text-fig. 7. Range chart of the main ammonite species in the section VIG2 near Barrême, Alpes-de-Haute Provence, southeastern France

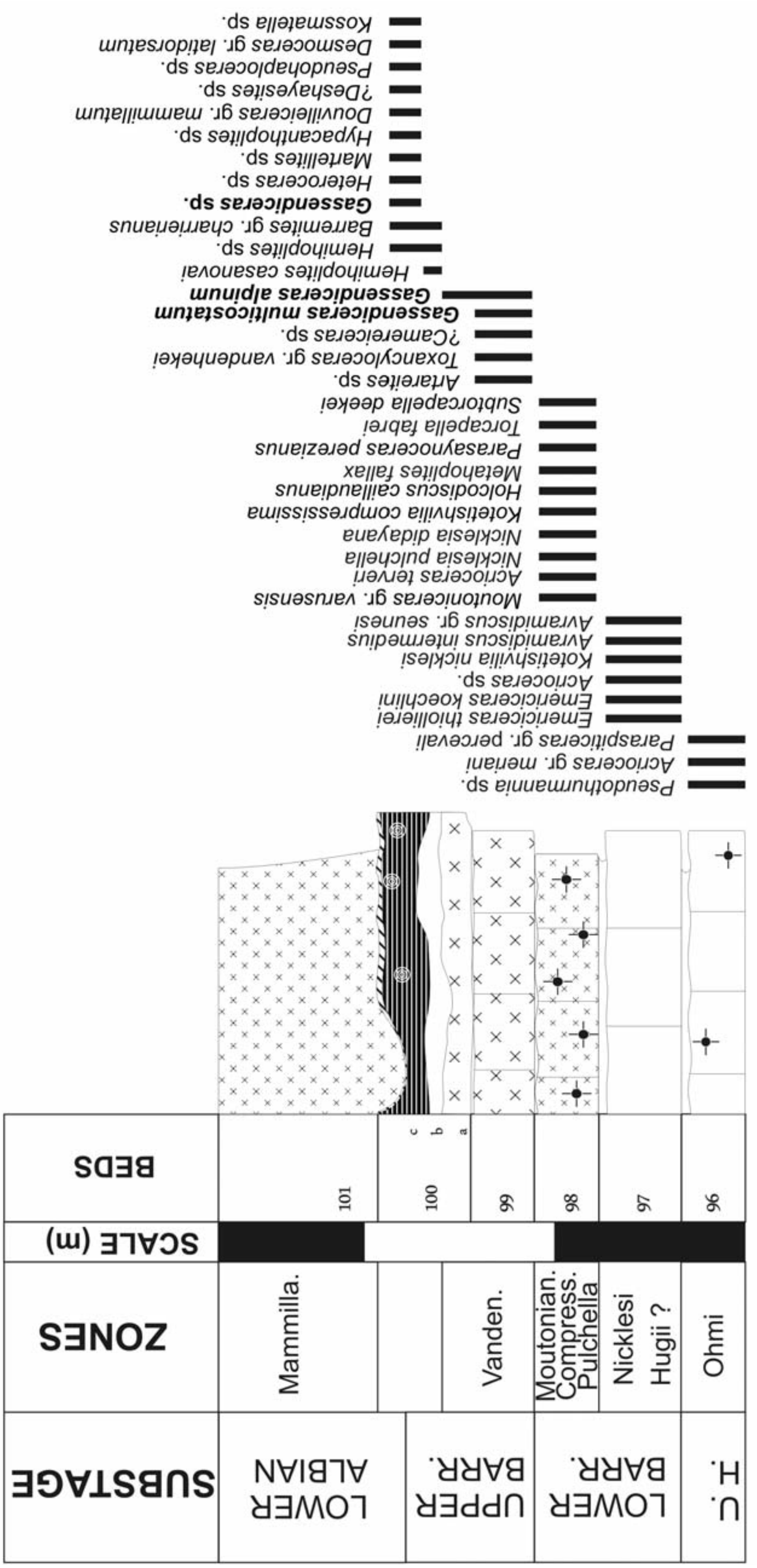
sion surfaces (Cotillon 1971; Bersac *et al*. 2010). The survey was carried out from the base of the Barremian to the top of the limestone formation. The distribution of the ammonites is illustrated in Text-fig. 9. The Upper Barremian starts with bed 99 documented by the appearance of *Toxancyloceras* ex gr. *vandenheckei*. The co-occurrence in this bed of *Gassendiceras alpinum* and *G. multicostatum* again indicates a probable episode of concentration / condensation at the base of the Vandenheckei Zone. Bed 100 varies in thickness, indicating disrupted sedimentation with high energy depositional episodes, and is composed of four levels. Level 100a (5–15 cm) yielded a reworked specimen of *Gassendiceras alpinum*. Level 100b (0–10 cm) is rich in undisturbed “*small* Barremites” [*Barremites* aff. *charrierianum* and *B. raspailli*] and represents the top of the Vandenheckei Zone between the Alpinum and Breistrofferi horizons (see Bert 2009a). Level 100c (5–15 cm) consists of a very heterogeneous glauconitic limestone with oncolithic and stromatolitic structures. Its reworked ammonite-fauna documents an interval between the Upper Barremian Vandenheckei Zone and the Lower Albian Mammillatum Zone. Level 100d (1–3 cm) bears stromatolitic structures and erosional surface at its top that ends the limestone series. Bed 100 is covered with Albian sandy-glauconitic marls (level 101).

Section VA: Section VA of the Provençal domain (Text-fig. 2) has been described and figured by Autran and Delanoy (1987). The glauconitic bed (11) is condensed and represents the Vandenheckei Zone. This bed yielded *Gassendiceras* specimens belonging to several taxa (this work): *G. alpinum*, *G. multicostatum*, *G. hoheneggeri* (Uhlig) and *G. bosellii* nov. sp. Part of the Sartousiana Zone (*sensu* Bert *et al*. 2008) is also represented in the uppermost part of the bed as a thin, highly glauconitic veneer.

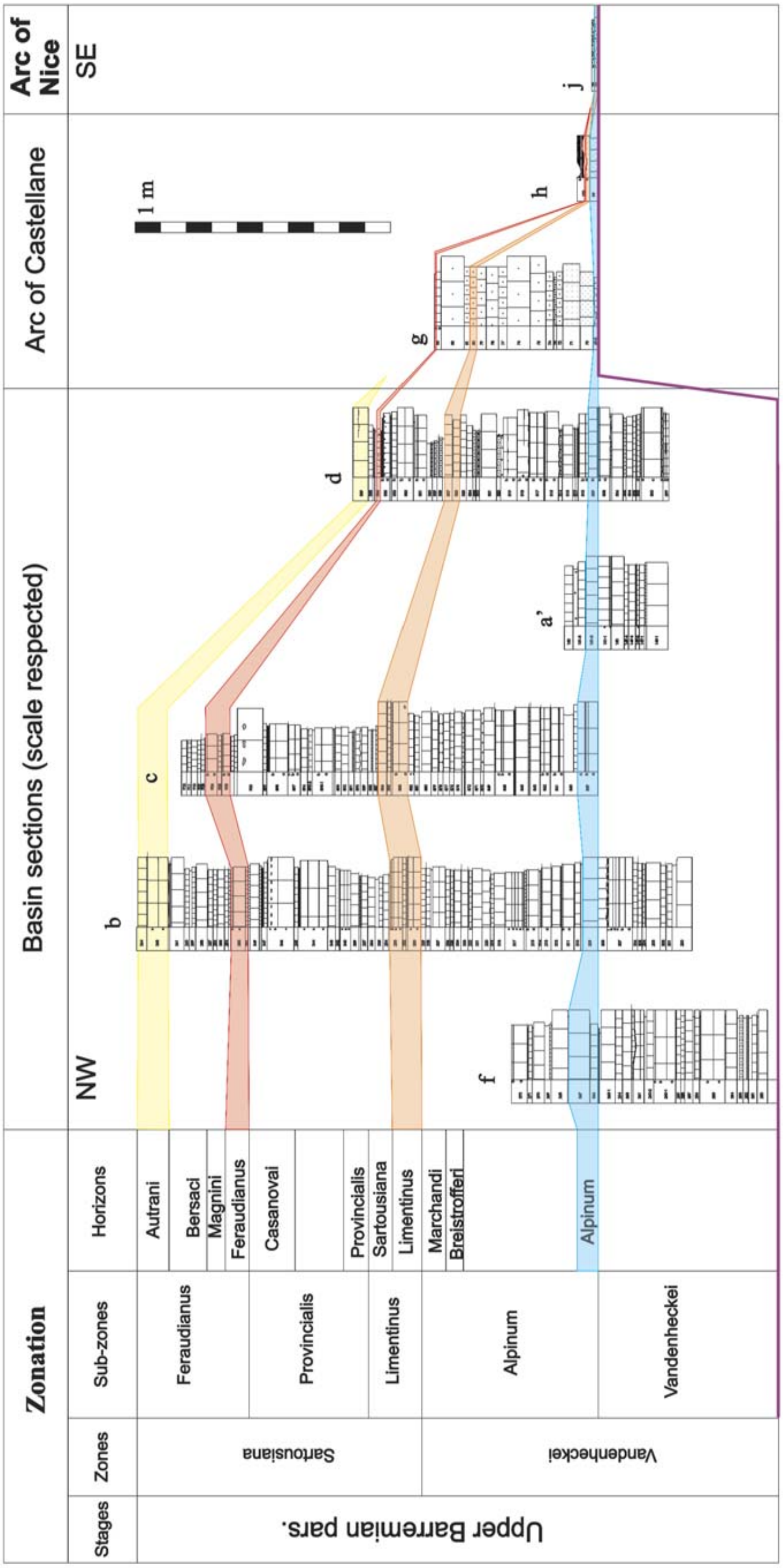
Text-fig. 8



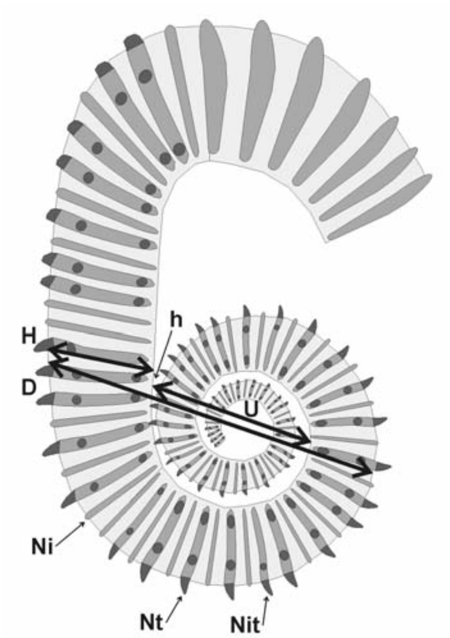
Text-fig. 8. Range chart of the main ammonite species in the section SO near Rougon, Var, southeastern France



Text-fig. 9. Range chart of the main ammonite species in the section TAI near Vence, Alpes-Maritimes, southeastern France



Text-fig. 10. Correlation chart of the main sections studied in southeastern France. The lower boundary of the Alpinum Horizon serves as horizontal datum



Text-fig. 11. Diagram illustrating measurements made on the *Gassendiceras*. D = diameter; H = height of the whorl; U = diameter of the umbilicus; h = spiral gap; Nt = number of trituberculate main ribs; Nit = number of weakly tuberculate intermediate ribs; Ni = number of smooth interribs

Sections SA, RS and TF: Upper Barremian sections SA, RS and TF are all located in the Arc of Nice (Text-fig. 2). They are represented by a single condensed bed rich in glaucony and phosphatic nodules. Section RS has already been studied and figured by Delanoy (1990), section SA by Bert and Delanoy (2000), and section TF will be described in a future work.

Text-fig. 10 shows correlations of the main sections studied in parallel with the zonation used in this work (see above). The Alpinum Horizon, present in all of the sections, provides a datum (blue horizontal line). The thickness of the Barremian deposits increases from east to west and from south to north (Text-fig. 2).

REPOSITORIES

The larger part of the ammonite material is actually housed in several French public institutions: the Museum National d'Histoire Naturelle of Paris (M.N.H.N), Université Pierre and Marie Curie (Jussieux) of Paris (U.P.M.C), Faculté des Sciences of Lyon (F.S.L), the collections of the Ecole des Mines de Paris (reposited at the Lyon Faculty of Sciences, France), the Institut Dolomieu of Grenoble (I.D), the Laboratory of the Groupe de recherche en Paléobiologie et biostratigraphie des Ammonites at La Mure-Argens (G.P.A), the Museum d'Histoire Naturelle de Nice (M.H.N.N), and the Barrême City Hall. However some specimens (a minority) are from private collections and as it is not possible to ensure their repository in an open institution, casts where reposited in the G.P.A's Laboratory when ever possible. The section's codes and the level number are added in brackets for every specimen. C.E.M is the abbreviation for Centre d'Etudes Méditerranéennes (St André les Alpes, France), which provided assistance in sampling the section VIG2.

SYSTEMATIC PALAEONTOLOGY

Measurements

The following conventional measurements (Text-fig. 11) were made in millimetres against diameter (D) for each specimen: the height of whorls (H), the maximum thickness of the whorls taken between ribs and tubercles (W), the diameter of the umbilicus (U), and the spiral gap (h). Some specimens have been disassembled and several sets of measurements (at several successive diameters) were performed whenever possible. The conventional ratios H/D (relative height), W/D (relative thickness), U/D (relative umbilicus), W/H (relative section) and U/H were calculated. The number of trituberculate main ribs (Nt), intermediate low tuberculate ribs (Nit), and smooth interribs (Ni) per whorl and half-whorl were also noted according to the diameter for each specimen (Text-fig. 11). All biometric data were then organized into bivariate diagrams to represent the evolution of quantitative parameters in relation to diameter, thus depending on the biological age of the specimens. The objective of this approach is to detect if one or more types of allometric relationships can be seen on the growth curves during ontogeny.

Definition of repeated ontogenic stages of ornamentation

Several ornamental stages recur frequently in most Hemihoplitidae at the different stages of their ontogenic development. They have been previously recognized (Bert and Delanoy 2000; Bert *et al.* 2006, p. 181; Bert and Delanoy 2009) and are represented in the genus *Gassendiceras*. They are (re)defined as follows (Text-fig. 12):

(1) *The Heberti stage* (Text-fig. 12a) is restricted to the earlier whorls of the shell and is recognizable in most Hemihoplitidae. It is characterized by a distinctive sub-octagonal whorl section that is scarcely higher than wide (Text-fig. 13-1). Its ornamentation

is more or less radial or slightly inclined backward and consists mostly of simple, regularly trituberculate, weakly differentiated thin ribs. The tubercles are small and conical.

(2) *The Barremense stage* (Text-fig. 12b) is characterized by an alternation of tuberculate and non-tuberculate ribs that are highly variable in appearance and in number. The whorl section is sub-circular to oval (umbilical wall high, peri-umbilical area gradually inclined to the rounded flanks then to the rounded venter – Text-figs 13-2 to 13-6, Text-figs 14 and 15-1). The main trituberculate ribs are slightly inclined backward and are wider at the top of the flanks than at their base (wedge-shaped). The ribs are thinner, more numerous and retroversed on the dorsal area. The tubercles are strong and are respectively located at the base, at the upper third, and in the peri-ventral areas of the flanks. They ribs increase in strength from the base to the top of the flanks, and the tubercles are topped with short massive spines partitioned near their base. On the flanks the spines are conical and slightly elongated in the direction of the ribs that support them. On the peri-ventral area the spines are pinched in the direction of coiling, making them flattened triangular in shape (claviform). On the venter the main ribs are very wide and blunt. The few intermediate ribs show reduced peri-ventral and lateral tubercles only. The interribs are relatively thin, smooth, non-tuberculate, and cross the venter without modification. These interribs can be more or less numerous depending on the species of *Gassendiceras* (see below the descriptions). The bifurcations are rare, and some main ribs can be looped.

(3) *The Simplified ornamental stage* (Text-fig. 12d) has a rounded whorl section but more compressed than in the Barremense stage (Text-fig. 13-7). The ornamentation becomes uniform compared to the latter stage. Smooth ribs become less numerous and stronger, while the main ribs are less wedge shaped due to the decrease in relative size of the lateral and peri-ventral tubercles.

(4) *The Irregular stage* (Text-fig. 12c) features an ornamentation close to that of the Barremense stage. It is more slender and irregular, with less pronounced and more uniform tubercles. The ribs are a little less wedge shaped. The venter is not as wide as in the Barremense stage; the whorl section is compressed but still rounded (Text-fig. 15-2).

(5) *The Camereiceras stage* (Text-fig. 12e) features a distinctive oval compressed whorl section with a broad base and flanks converging to the narrow venter (Text-figs 16-1 and 16-2). The ribs are less differentiated and blunter than in the Barremense stage. The tubercles are weak, particularly the lateral tubercles which tend to disappear. Peri-ventral tubercles, in contrast, are well marked and regular. They become smaller and their arrangement flanks the venter in a distinctive way.

(6) *The Adult late stage* (Text-fig. 12f) is characterized by a sudden strengthening of the ribs on the venter, just like the ribs on the hook of some tripartite ancyloceratids (Text-fig. 13-8 and 16-3). The tubercles are weak and are at first only a marked angulation of the rib, disappearing completely near the peristome. At this point the ribs are thinner, slightly approximated, and projected forward on the top flanks in order to make a proversal sinus on the venter.

Systematics

Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Ancyloceratoidea Gill, 1871
Family Hemihoplitidae Spath, 1924

The Upper Barremian family Hemihoplitidae is known in much of the Northern Tethyan Margin and the Essaouira-Agadir Basin (Morocco). It has three major developmental trends represented by three subfamilies (Bert *et al*. 2006): (1) the Gassendiceratinae Bert, Delanoy and Bersac, 2006, the stem group of the two other subfamilies, ranging from the base (*s.l.*) of the Upper Barremian to the base of the *Imerites giraudi* Subzone in the northern Tethyan margin; (2) The Hemihoplitinae Spath, 1924, ranging from the *Gassendiceras alpinum* Subzone to the *Hemihoplites feraudianus* Subzone; and (3) the Peirescinae Bert, Delanoy and Bersac, 2006, ranging from the *G. alpinum* Subzone to the top of the *I. giraudi* Subzone where it links with the genus *Procheloniceras* Spath, 1923 (first appearing at the base of the *Martelites sarasini* Subzone), which is the first Barremian member of the superfamily Douvilleiceratoidea Parona and Bonarelli, 1897 (see Bert *et al*. 2006, p. 223; Delanoy *et al*. 2008, p. 31; Bert 2012b).

Subfamily Gassendiceratinae Bert,
Delanoy and Bersac, 2006

This subfamily consists of the genera *Gassendiceras* Bert *et al*., 2006, *Pseudoshasticrioceras* Delanoy, 1998 and *Imerites* Rouchadze, 1933 (Bert *et al*. 2009, 2011; Bert 2012b). *Barrancyloceras* Vermeulen, 2000 is a genus based on a doubtful species (see Bert *et al*. 2010;

and discussion in Vermeulen 2010), *Crioceras barremense* Kilian, 1895, which remains an unusable *nomen dubium*. The new material of *G. alpinum* studied herein allows recognition of its large intraspecific variability and it includes the morphology expressed by Vermeulen's neotype of *B. barremense* [and by the type-specimens of *Leroyiceras mascarelli* (Vermeulen, 2005) and *Spinocrioceras sauvanae* Lepinay and Vermeulen, 2009].

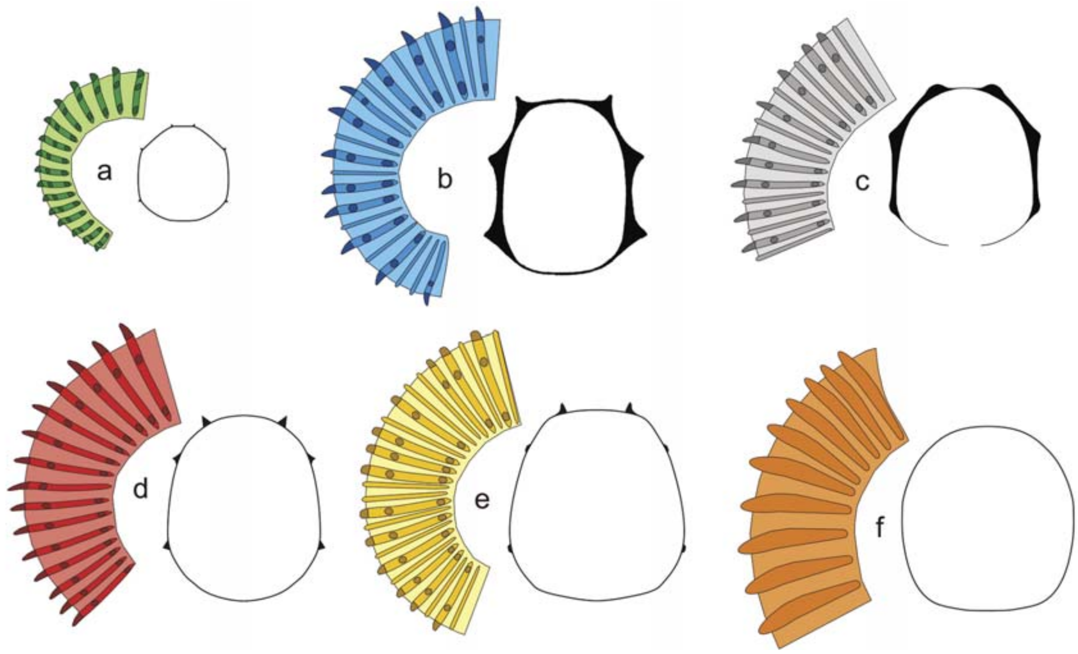
Genus *Gassendiceras* Bert, Delanoy and Bersac, 2006

TYPE SPECIES: *Gassendiceras quelquejeui* Bert, Delanoy and Bersac, 2006 (in Bert *et al.* 2006, pl. 3, fig. 3, pl. 4, figs 2–3, pls 5–6).

EMENDED DIAGNOSIS: Crioconic to ancyloceratic with all intermediates. Size medium to large. Ornamentation characterized by succession of several ontogenic stages: the Heberti stage in inner whorls always followed by the Barremense stage and then either by the Irregular and the Camereiceras stages depending on species. Growth ends with the Adult late stage.

Gassendiceras alpinum (d'Orbigny, 1850)
(Plates 1 to 8)

v 1850. *Crioceras alpinus* sp. nov.; d'Orbigny, p. 100, n°624.
v 1899. *Crioceras barremense* Kilian, 1895; Simionescu, p. 488, pl. 1, figs 4–5.
v 1937. *Crioceras alpinus* d'Orbigny, 1850; Cottreau, p. 63, pl. 78, figs 16–17.
? 1946. *Crioceras barremense* Kilian, 1895; Tzankov, pl. 12, fig. 2.
v 1955. *Emericiceras* cf. *barremense* (Kilian, 1895); Sarkar, p. 96, pl. 7, fig. 7.
v ? 1955. *Emericiceras dolloi* sp. nov.; Sarkar, p. 87, pl. 5, fig. 18.
? 1967. *Matheronites alpinus* (d'Orbigny, 1850); Dimitrova, p. 68, pl. 34, fig. 3.
? 1967. *Matheronites barremense* (Kilian, 1895); Dimitrova, p. 69, pl. 32, fig. 4.
v 1978. *Crioceratites (Crioceratites) alpinus* d'Orbigny, 1850; Immel, p. 53.
? 1981. *Paracrioceras barremense* (Kilian, 1895); Kakabadze, p. 89, pl. 15, fig. 1.
? 1981. *Paracrioceras dolloi* (Sarkar, 1955); Kakabadze, p. 89, pl. 3, fig. 4.
non 1989. *Emericiceras* cf. *barremense* (Kilian, 1895); Conte, p. 34, photo p. 36.
v 1990. *Emericiceras barremense* (Kilian, 1895); Delanoy, pl. 4, fig. 3.
v pars 1992. *Emericiceras barremense* (Kilian, 1895); Delanoy, p. 52, pl. 19, fig. 2.
v 1992. *Emericiceras* sp. gr. *barremense* (Kilian, 1895) forme 1; Delanoy, p. 54, pl. 19, fig. 3.
pars 1994. *Ancyloceras* ? aff. *barremense* (Kilian, 1895); Avram, pl. 16, fig. 1.



Text-fig. 12. Ornamentation and whorl section of ontogenic stage recognized in *Gassendiceras* (not to scale), after Bert and Bersac (2013, fig. 2). a: Heberti stage; b: Barremense stage; c: Irregular stage; d: Simplified ornamental stage; e: Camereiceras stage; f: Adult late stage

1995. *"Emericiceras" barremense* (Kilian, 1895); Company *et al.*, fig. 8e.
2004. *Barrancyloceras barremense* (Kilian, 1895); Vermeulen, pl. 4, fig. 1.
2005a. *Barrancyloceras barremense* (Kilian, 1895); Vermeulen, pl. 48, fig. 1.
2005b. *Barrancyloceras mascarellii* sp. nov.; Vermeulen, pp. 7–11, pl. 1, fig. 2.
? 2005. *Crioceratites (Paracrioceras) dolloi* (Sarkar, 1955) ; Kotetishvili *et al.*, p. 348, pl. 72, fig. 6.
v pars 2007. *Barrancyloceras alpinum* (d'Orbigny, 1850); Vermeulen and Lazarin, pp. 40–43, pl. 2, fig. 1, non fig. 2.
2007. *Barrancyloceras barremense* (Kilian, 1895); Vermeulen and Lazarin, pp. 33–37, pl. 2, fig. 3.
2008. *Barrancyloceras barremense* (Kilian, 1895); Company *et al.*, pl. 9, fig. a.
2009. *Spinocrioceras sauvanae* sp. nov.; Lepinay and Vermeulen, pp. 96–99, fig. 1.
v 2010. *Gassendiceras alpinum* (d'Orbigny, 1850); Bert *et al.*, pl. 1, fig. 2 ; pl. 3, figs 1–3 ; pl. 4, figs 1–2.

LECTOTYPE: The largest fragment of M.N.H.N R00833 (ex. No. M.N.H.N. 5406 – Pl. 5, Fig. 2a–c) of the d'Orbigny collection.

STATUS OF THE TYPE: d'Orbigny (1850, p. 100) briefly introduced *Crioceras alpinus* without any figure or designation of the type. Cottreau (1937, p. 63, pl. 78, figs 16–17) figured for the first time specimen M.N.H.N.R00833 in the revision of the *Prodrome Types of Universal stratigraphic paleontology* of d'Orbigny. This specimen is the only one actually attributed to this species in the d'Orbigny collection, but Cottreau did not designate it explicitly as the type. Vermeulen and Lazarin (2007, pl. 2, fig. 1) refigured this specimen and reported that it had been restored by cementing an inner whorl fragment to the outer whorl. They accepted that both fragments were parts of the same specimen and designated the external whorl fragment (the largest) as "holotype by monotypy" (p. 40–41). Bert *et al*. (2010, and this work) have, however, viewed this interpretation more circumspectly, as the growth in height of the whorl, coiling, and the type of preservation do not fit neatly between the two fragments, even assuming a missing fragment. These two fragments belong most probably to different specimens, and the designation "holotype" by Vermeulen and Lazarin (2007), followed by Bert *et al*. (2010), is inappropriate and should be replaced with lectotype (here designated). Inspection of these specimens has shown that the characters of the smallest fragment cannot be attributed to *G. alpinum*. The smooth interribs appear from D=52 mm only, which is a specific feature of *G. multicostatum* (see below).

Note: The genus *Leroyiceras* Vermeulen, 2006 was introduced in the same volume as *Gassendiceras*. As the type-species of the first (*L. mascarellii*) is a junior synonym of *G. alpinum*, and as the genus *Gassendiceras* is now revised and well recognised, we choose this latter genus to have priority (Bert *et al*. 2010, first reviser according to I.C.Z.N, art. 24.2.1 and 2).

TYPE LOCALITY: Angles, in the Alpes-de-Haute-Provence, southeastern France.

TYPE HORIZON: Not given in the original designation, but the species is richly represented in beds 151-2 of Angles (sections A and A', this work).

GEOGRAPHIC DISTRIBUTION: *Gassendiceras alpinum* is known in southeastern France (in both basinal and distal platform areas), in Romania, Spain, and probably also in Morocco, Bulgaria and Crimea.

STRATIGRAPHIC DISTRIBUTION: All of the specimens from the Vocontian Basin come from a marker bed in the Middle Vandenheckei Zone. This level was taken to be the Alpinum Horizon, at the base of the Alpinum Subzone (Bert *et al.* 2010).

DIAGNOSIS: Large adult shell (D>350 mm) criocone, slightly uncoiled, but with a break in growth at about D=150 mm. Whorl section rounded, slightly higher than wide. Ornamentation well marked but variable. Four successive stages during growth: (1) Heberti stage in innermost whorls; (2) Barremense stage from a diameter of 25 mm with relatively numerous smooth interribs (one or two between two main ribs on average); (3) Simplified ornamental stage from 170 mm diameter on average; and (4) Adult late stage from 320 mm up to peristome. Peristome simple, linear with little peak on venter. Suture line fairly denticulated of ancyloceratic type.

MATERIAL STUDIED (n=77): All specimens from southeastern France (Alpes-de-Haute-Provence, Var, and Alpes-Maritimes); 14 from the platform edges, 63 from more distal zone of the Vocontian Basin. See Appendix 1 for location details and Appendix 2a for measurements.

DESCRIPTION: Three specimens are more than 250 mm in diameter. Two of them have an adult body chamber and one is sub-adult; in addition, three other fragmentary specimens are parts of an adult body chamber. The adult body chamber starts at about 240 mm diameter and is a little more than a half whorl. G.P.A.AZ18 has its full development and preservation of the peristome at D=364 mm. The other specimens are either wholly septate nuclei, or juveniles. The shell is criocone, slightly uncoiled, sometimes with subjoined whorls (or joined in inner whorls). The spiral gap h is highly variable depending on the specimens (Appendix 3a); generally weak. It increases rapidly during growth up to a maximum of 13 mm for 200<D<250 mm, and decreases again thereafter (average relative umbilicus of U/D=0.47). The growth in height is rapid (Appendix 3b) with an average relative height of H/D=0.34 in the inner whorls, but it tends to decrease with respect to the diameter (H/D=0.31 for D>120 mm). The growth rate in thickness (Appendix 3b) remains low and decreases regularly with respect to the diameter, for the average thickness ratio is only W/D=0.30. The whorl section is very rounded (Text-fig. 13, Appendix 3c), it remains slightly higher than wide (W/H=0.91 on average for D<150 mm) except occasionally in the inner whorls where it can be sub-circular (D<60 mm), and it tends to be higher during growth (W/H=0.78 on average for D>150 mm – Appendix 2a). The average curves of the relationships between the measured values of H, W and U in relation to the diameter show disharmonic growth and the break of slope is at around 150 mm diameter (see Appendix 3a–d). In the inner whorls, growth is close to isometric (D<150 mm), while in the outermost whorls (D>150 mm) growth is in agreement with the allometric relationship $Y=bD^a$. This is linked to the increase in U/H with respect to the diameter progressing in the direction of a slower growth in height of the whorl associated with the widening of the umbilicus. The dispersion parameters reveal that in all cases the clouds of points are weakly scattered around the average and are homogeneous (very hight R^2 often more than 0.9, and standard deviations very low). We notice, however, that the coefficients of variation (Appendix 2a) present certain disparities (in all less than 15%), which can have multiple causes: (1) disharmonic growth, (2) the lack of measurements for the W values and other measurements beyond 200 mm diameter, and (3) the *post-mortem* differential compression, which is higher in basinal specimens than in those from the neritic area.

The ornamentation is always well marked and the total number of ribs (main ribs + intermediary ribs + smooth interribs) is stable during growth within the same individual specimen, but it varies greatly from one individual to another (from 9 to 27 ribs per half-whorl). The number of main ribs (Appendix 3e) is high in the inner whorls and decreases very rapidly until D=50 mm, increasing again gradually thereafter. In contrast, the number of intermediate ribs (Appendix 3f) and smooth interribs (Appendix 3g) increases rapidly to about 75 mm diameter and then decreases thereafter, making the number of smooth interribs inversely proportional to the number of tuberculate ribs. Four successive stages (see above for the complete descriptions) can be recognized during growth:

(1) The typical Heberti stage: the first observations were made from 8 mm diameter, but it is highly probable that the umbilicus is perforated to a diameter of 7 mm.
(2) The Barremense stage starts at a diameter of 25 mm on average. Smooth interribs are generally quite common (one to two smooth interribs per main rib on average) and, depending on the specimens, increase rapidly in number to about D=100 mm, decreasing again in number thereafter (Appendix 3g). Note that this stage is the only one shown on the lectotype of *G. alpinum*, which is preserved between 75 and 156 mm diameter.
(3) The Simplified ornamental stage: this stage appears gradually from an average of 170 mm diameter, and comprises a little over the last half-whorl of the phragmocone and most of the body chamber.
(4) The Adult late stage is visible on G.P.A. AZ18 and G.P.A.AZ23. It extends from 320 mm diameter up to the peristome (whorl length of about 70°). The peristome is simple, linear, and forms a little peak on the venter.

The suture line is very difficult to trace in most of our specimens (partial dissolution), but it is fairly denticulate and shows a trifid wide and deep lateral lobe. The ventral lobe appears bifurcated.

VARIABILITY: Robust specimens with wide whorl sections generally have fewer ribs (ribs are coarse) than compressed specimens with a more slender whorl-section (thinner ribs). This concerns the number of main trituberculate ribs and the number of smooth interribs: the specimens with the smoothest interribs are often more slender, and both the robust and gracile end-members of this polymorphism are linked by all possible intermediates.

This variability within slender and strong forms parallels variation in the ontogenetic sequence: the more slender specimens are also characterized by an earlier onset of the ontogenetic stages during growth. Their Heberti stage is on average shorter than in more robust specimens (20 mm *versus* 30 mm in diameter). Their Barremense stage, which is expressed earlier, is also more slender and determines the earlier onset of smooth interribs. The simplified ornamental stage also appears earlier in slender forms than in robust forms.

DIFFERENTIAL DIAGNOSIS: *G. alpinum* differs from *G. multicostatum* in several parameters: (1) the duration of its ontogenic stages, with a shorter Heberti stage, an earlier Barremense stage with the appearance of the smooth interribs from 15–30 mm diameter (D=30–40 mm for *G. multicostatum*), and a relatively early onset of the Simplified ornamental stage (average of 170 mm versus 200 mm in diameter for *G. multicostatum*); (2) more numerous intermediate ribs and smooth interribs, which are usually quite rare in *G. multicostatum*; (3) the spiral gap can reach a higher maximum value in *G. alpinum*; and (4) a break in growth in the early adult stage , never observed in *G. multicostatum*.

G. alpinum shows a Heberti stage close to that of *G. quelquejeui*, but its Barremense stage is longer (about 170 mm *versus* 100 mm diameter) and morphologically different (more robust with larger tubercles and less smooth interribs). There are two additional stages in *G. quelquejeui*, never present in *G. alpinum*: the Irregular and the Camereiceras stages. Finally, the growth in whorl height is greater in *G. quelquejeui* with no break.

Differences between *G. alpinum* and *G. enayi* Bert *et al.*, 2006 and *G. coulletae* Bert *et al.* 2006 are even greater, since they show a more compressed whorl section correlated with a shorter and slender Barremense stage, and the presence of the Camereiceras stage on a large part of the shell.

The spiral whorls of *G. hoheneggeri* are quite close to that of *G. alpinum*, but the former taxon has generally more interribs. *G. hoheneggeri* has in addition no Simplified ornamental stage, since the smooth interribs are present on the shaft until the Adult late stage (= Irregular stage). Finally, *G. alpinum* never shows tripartite coiling.

Gassendiceras multicostatum (Sarkar, 1955)
(Plates 9 to 11)

1955. *Emericiceras barremense multicostata* nov.; Sarkar, p. 85, pl. 6, fig. 3.
2007. *Barrancyloceras companyi* sp. nov.; Vermeulen and Lazarin, pp. 37–40, pl. 1, figs 1–2.
v pars 2007. *Barrancyloceras alpinum* (d'Orbigny, 1850); Vermeulen and Lazarin, pp. 40–43, pl. 2, fig. 2, non fig. 1.

LECTOTYPE: I.D.UJF.ID-111 (here designated – Pl. 10, Fig. 4a–b) is the only specimen illustrated by Sarkar (1955) in his original description, housed in the Institut Dolomieu in Grenoble, France.

TYPE LOCALITY: Not indicated in the original designation but the label associated with the lectotype says Trigance in the Haut-Var, southeastern France.

TYPE HORIZON: Not indicated in the original designation, but *G. multicostatum* was collected in bed 69-2 (Text-fig. 8) in the cross-section SO (Text-fig. 2) near the type locality.

GEOGRAPHIC DISTRIBUTION: *G. multicostatum* is known in southeastern France, in both basinal and distal platform areas, and probably in Morocco (unpublished data).

STRATIGRAPHIC DISTRIBUTION: All of the specimens from the Vocontian Basin come from beds immediately below the Alpinum Horizon. These levels are located at the top of the Vandenheckei Subzone (Vandenheckei Zone) of the Upper Barremian.

DIAGNOSIS: Large adult size (D about 350 mm), shell crioconic, slightly uncoiled. Ornamentation always well marked, with few smooth interribs. Four successive ontogenic stages recognized during growth: (1) the Heberti stage mostly in inner whorls; (2) the Barremense stage starts at onset of smooth interribs from D=30–40 mm on average; (3) the Simplified ornamental stage from about 200 mm diameter; and (4) the Adult late stage at end of growth with strengthened and raised ribs. Suture line of ancyloceratic type.

MATERIAL STUDIED (n=24): All the specimens are from southeastern France (Alpes-de-Haute-Provence, Var, and Alpes-Maritimes); 10 from the edges of the platform, and 13 from the more distal zone of the Vocontian Basin. See Appendix 1 for locality details and Appendix 2b for measurements.

DESCRIPTION: G.P.A.AZ32 reaches a diameter of 300 mm without having a complete development. The adult body-chamber of specimen UH starts at about 250 mm diameter, suggesting an adult diameter of approximately D=350 mm, with a body chamber of about a little more than half a whorl. The shell is criocone, weakly uncoiled, sometimes even with sub-joined whorls (or just joined in the inner whorls). The spiral gap h is highly variable depending on specimens (Appendix 4a); this parameter increases rapidly with growth, but remains below 7 mm maximum for 75<D<150 mm (average relative umbilicus of U/D=0.45). The growth in height is relatively rapid (Appendix 4b), with an average relative height of H/D=0.35. The whorl section is rounded (Text-fig. 14, Appendix 4c), it remains much higher than wide

(W/H=0.89), but it can become sub-circular in some specimens for 60<D<125 mm. The average curves of the measured values of H, W and U in relation to the diameter are always close to isometric (i.e. of $Y=bD$ type; see Appendix 4b-d). The dispersion parameters reveal that in all cases the clouds of points are weakly scattered around the average and are homogeneous. The coefficients of determination R^2 are still very high (>0.9), and the standard deviations (Appendix 2b) are very low. The coefficients of variation are a bit high for the thickness measurements (in all are less than 15%) but it is not surprising because of fewer values of W, and because of the frequent *post-mortem* compression of specimens collected in the basin.

The ornamentation is always well marked, and the total number of ribs is constant during growth (it varies from 10 to 15 ribs per half-whorl depending on the specimens – see Appendix 4e). The number of smooth interribs per half-whorl is still quite small (maximum 7 – Appendix 4f). Four successive ontogenic stages can be recognized:

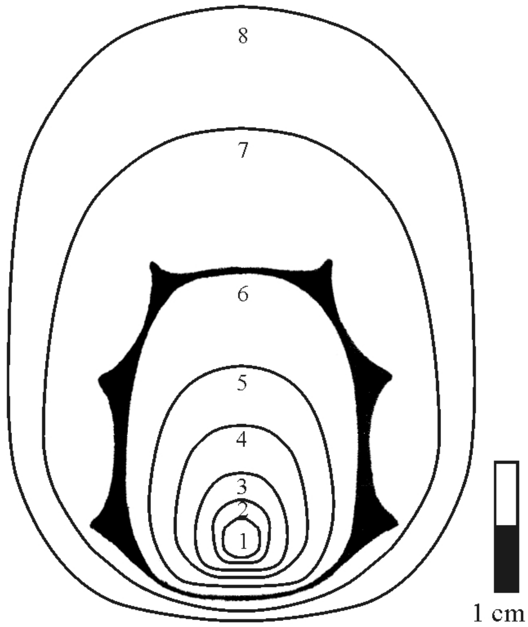
(1) the Heberti stage: the first observations were made from 13 mm diameter, but it is highly probable that the umbilicus is largely perforated. The ornamentation becomes more pronounced when approaching the next stage, which appears very gradually.

(2) The Barremense stage starts at the onset of the smooth interribs at around 30–40 mm diameter on average. These ribs are generally rare and are not always present between the main ribs. The number of smooth interribs varies depending on the specimens (Appendix 4e), but it increases rapidly from their appearance to about D=70 mm, decreasing again thereafter. The smooth interribs are generally little marked in the lower two-thirds of the flanks, and they pass across the venter without attenuation.

(3) The Simplified ornamental stage: one specimen studied (G.P.A.AZ32) shows the onset of this stage, but it is too fragmentary to be measured. Onset at 200 mm diameter seems likely, based on other specimens in which this stage is already visible at this diameter. This stage comprises the end of the phragmocone and most of the adult body chamber. The ornamentation becomes uniform compared to the previous stage (the Barremense stage), and the smooth interribs are rare or absent. The whorl section is more or less compressed depending on the specimens.

(4) The Adult late stage is only known on the fragmentary specimen G.P.A.AZ45. The ribs are strengthened and raised, while the tubercles are less dominant. The peristome is not known.

The suture line has not been studied in its entirety because of its often poor preservation on the specimens (partial dissolution), but as in *G. alpinum*, it looks fairly denticulate and shows a wide and deep trifid lateral lobe.



Text-fig. 13. Whorl sections of *Gassendiceras alpinum* (d'Orbigny, 1850). 1: AZ74 (D=20 mm); 2: AW66 (D=27 mm); 3: AW66 (D=45 mm); 4: AW67 (D=120 mm); 5: R00833 (*lectotype*, D=155 mm); 6: AZ41 (D=250 mm); 7: AZ18 (D=350 mm)

VARIABILITY: The morphological variability of *G. multicostatum* is between two (robust and gracile) end-members which are both extensively linked with all possible intermediates, as in *G. alpinum*. The more slender specimens of *G. multicostatum* are also slightly more peramorphic than the more robust specimens (e.g. the earlier onset of the smooth interribs is from D=30 mm *versus* D=40 mm).

DIFFERENTIAL DIAGNOSIS: The relationships and differences between *G. multicostatum* and *G. alpinum* have already been considered (see above). From *G. quelquejeui* the discussed *G. multicostatum* differs in its lower growth in whorl height, longer Heberti stage, less smoother interribs in the Barremense stage, and in the absence of the Irregular and the Camereiceras stages.

G. multicostatum differs from *G. enayi* and *G. coulletae* in its less compressed whorl section, a longer Barremense stage, and in the lack of the Irregular and Camereiceras stages.

G. hoheneggeri contains many more smooth interribs on the coil unlike *G. multicostatum*. The Simplified ornamental stage is here replaced by the Irregular stage. Finally, *G. multicostatum* never has tripartite coiling.

Gassendiceras hoheneggeri (Uhlig, 1883)
(Pl. 12)

1883. *Crioceras hoheneggeri* nov.; Uhlig, p. 263, pl. 31, pl. 32(?), fig. 2a–b.
non 1889. *Ancyloceras hoheneggeri* (Uhlig, 1883); Haug, p. 220, pl. 13, fig. 4.
non 1907. *Crioceras* aff. *hoheneggeri* Uhlig, 1883; Karakash, p. 137, pl. 4, fig. 3a–b.
non 1964. *Crioceratites (Emericiceras) hoheneggeri* (Uhlig, 1883); Thomel, p. 32, pl. 6, fig. 2–3.

LECTOTYPE: The specimen figured by Uhlig (1883, pl. 31). Researches in the collections of the Natural History Museum of Vienna (Alexander Lukeneder, pers. comm.) and in the Bayerische Staatssammlung für Paläontologie und Geologie Lehrstuhl für Paläontologie und Geobiologie of München (Winfried Werner, pers. comm.) have failed to find the lectotype of *Crioceras hoheneggeri* or any of the syntypes in the Hohenegger collection, which must be considered lost. Excavations undertaken in the type area (Vašíček, pers. comm.) have so far failed to find topotypes of *C. hoheneggeri*, making the establishment of a neotype impossible at present.

Moreover, there are some inconsistencies between the original illustration and the original description: Uhlig (1883, p. 263) described an alternation of main trituberculate ribs and thinner smooth interribs (1–2 by interval) on the coil of the lectotype, while the original illustration shows bituberculate main ribs. The whorls remain in contact late in the original figure, while the original description suggests that they are slightly disjoint. This suggests that the drawing of the specimen may be slightly idealized. Apart from these few points, the good overall quality of the figure and of the original description, as well as the discovery of a new complete specimen (this work), allow a reasonable understanding of this species.

TYPE LOCALITY: Grodischt (now Hradiště) in the Czech Republic.

TYPE HORIZON: The Hradiště Formation; details unknown.

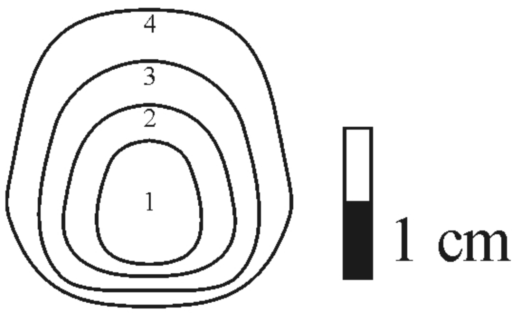
GEOGRAPHIC DISTRIBUTION: *G. hoheneggeri* is known in the Czech Republic, in southeastern France, and probably in Morocco.

STRATIGRAPHIC DISTRIBUTION: The Hradiště Formation (Uhlig 1883; Vašíček 2008 with bibliography) covers a stratigraphic interval ranging from the Lower Barremian to the Lower Aptian. The specimen from southeastern France comes from bed 11 of section VA, which is restricted to the base of the Upper Barremian (Vandenheckei Zone *sensu* Bert *et al*. 2008 – see above).

DIAGNOSIS: Shell tripartite (coil, shaft and hook); size large to very large ($320\ \text{mm}<D<540\ \text{mm}$). Adult body chamber comprises shaft and hook. Coil large, quite tight (about 180 to 200 mm in diameter). Hook low opened and relatively short. Shell section always rounded. Ornamentation always well marked. At least three successive stages during growth: (1) the Barremense stage is on the coil up to about D=150 mm. It is the first ornamental stage identified (inner whorl unknown until D=35 mm), with 1–3 smooth interribs between each main rib; (2) the Irregular stage is at the end of the coil and occupies the entire shaft; and (3) the Adult late stage starts from the top of the shaft.

MATERIAL STUDIED (n=1): The specimen (see Appendix 1) from southeastern France (Alpes-Maritimes). See Appendix 2c for measurements. We classify this specimen as *G. hoheneggeri* because its coiling and ontogenetic sequences are similar to the lectotype (figure and mostly description).

DESCRIPTION: The specimen studied is adult (maximum length 319 mm) with a complete tripartite shell (coil, shaft and hook). The adult body chamber comprises the entire shaft and the hook. The coil is large proportionally (about 180 to 200 mm in diameter), and the shaft is short and thickset (Pl. 12). The hook is open with a relatively short return. The winding of the coil is usually fairly tight with a gap (h) between 3 and 5 mm, but up to 11 mm approaching the shaft. The growth in whorl height on the coil is rapid (Appendix 2c, H/D>0.30), but it decreases on the shaft and the hook. The whorl section is rounded on the coil, sub-circular to oval, much higher than wide, with convex flanks and a rounded ventral area. The shell section is very rounded on the shaft.



Text-fig. 14. Whorl sections of *Gassendiceras multicostatum* (Sarkar, 1955). 1: AW50 (D=50 mm); 2: 28749 (D=70 mm); 3: AW50 (D=90 mm); 4: 1225 (D=130 mm)

At least three successive stages can be recognized during growth

(1) the Barremense stage is the first ornamental stage identified (the Heberti stage is probably present but the inner whorls are unknown until D=35 mm). There are one to three (usually two) smooth interribs between each main trituberculate rib. Bituberculate intermediate ribs are very rare.

(2) From D=150 mm, the Irregular stage is not very different at its onset from the previous stage, but the ornamentation becomes progressively less regular. The main ribs are weaker than on the coil, and the strength of the tubercles is more uniform. Intermediate ribs can sometimes be more frequent (Pl. 12). The number of smooth interribs decreases from the previous stage.

(3) The Adult late stage is found only on the hook. The ribs are spaced; smooth interribs are scarce and disappear completely at the end of hook. Tubercles tend to disappear completely too, especially late in the hook. The ventral area of the hook is worn and the ornamentation cannot be observed.

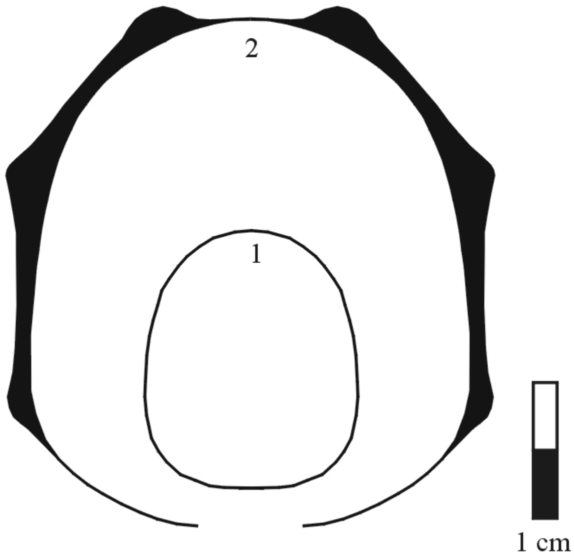
The suture line could not be studied.

VARIABILITY: It is currently not possible to know the variability of *G. hoheneggeri* based on the available material, but we consider the main difference (shaft length) between the studied specimen and the lectotype as intraspecific variability.

DIFFERENTIAL DIAGNOSIS: The coiling of *G. hoheneggeri* is very close to that of *G. alpinum* at an equivalent diameter, but it has generally more interribs in the Barremense stage, which is shorter. This difference in the Barremense stage also applies to *G. multicostatum*, which is still more robust. The Simplified ornamental stage is replaced with the Irregular stage in *G. hoheneggeri* (see fig. 6 in Bert & Bersac 2013). Finally, *G. alpinum* and *G. multicostatum* are never tripartite.

G. hoheneggeri, *G. rebouleti* nov. sp. and *G. bosellii* nov. sp. share a common tripartite coiling of the shell. It is, however, best expressed in *G. hoheneggeri*, which has a long and straighter shaft compared to the other species. The main ribs also remain strongly trituberculate on the shaft. *G. hoheneggeri* never shows the Camereiceras stage present in *G. rebouleti* nov. sp. and *G. bosellii* nov. sp.

G. quelquejeui, *G. coulletae* and *G. enayi* are entirely crioconic unlike *G.* aff. *hoheneggeri*, and their ontogenetic stages are earlier and leave room for development of the Camereiceras stage, which is absent in *G. hoheneggeri*.



Text-fig. 15. Whorl sections of *Gassendiceras* aff. *hoheneggeri* (Uhlig, 1883), un-numbered specimen from the Davoux collection. 1: 133.5 mm; 2: 214 mm (middle part of the shaft).

Gassendiceras rebouleti nov. sp.
(Pl. 13; Pl. 14, Fig. 2)

DERIVATION OF NAME: This species is dedicated to our colleague Stéphane Reboulet, Lecturer at the University of Lyon (France) and a specialist in Lower Cretaceous ammonites.

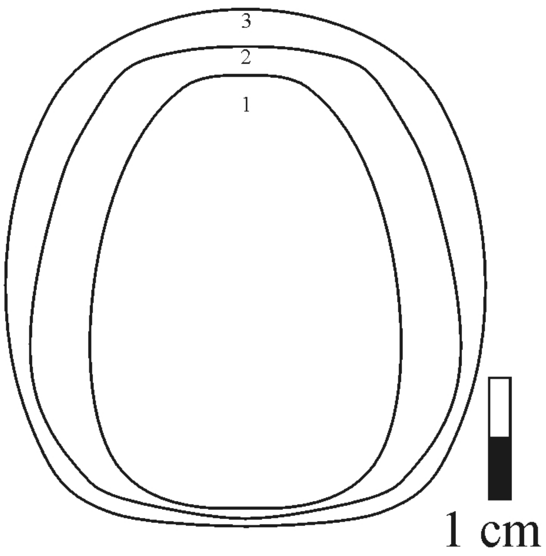
HOLOTYPE: G.P.A.AW43 (coll. Bert – Pl. 14, Fig. 2), which consists of a fragment of shaft and a plaster cast (made *in situ*) of the counterpart of the complete coil of the same specimen.

TYPE LOCALITY: Section G12 (Text-fig. 2) in the Barremian stratotype area (Angles, Alpes-de-Haute-Provence, France).

TYPE HORIZON: Bed 317b of the type section (G12 – Text-fig. 6).

GEOGRAPHIC DISTRIBUTION: *G. rebouleti* nov. sp. is known in southeastern France and probably in Morocco.

STRATIGRAPHIC DISTRIBUTION: All the specimens of the Vocontian Basin are from a bed in the middle part of the Alpinum Subzone, between the Alpinum and Breistrofferi horizons (top of the Vandenheckei Zone). This level appears stratigraphically very close to the level of “small Barremite*s*” (bed 108 of the Majastre section, Alpes-de-Haute-Provence) recently described and dated



Text-fig. 16. Whorl sections of *Gassendiceras bosellii* nov. sp. 1: AZ27 (D=200 mm); 2: 17252 (D=230 mm on the shaft); 3: 17252 (D=300 mm on the hook)

by Bert (2009a) in hemipelagic / neritic areas of southeastern France.

DIAGNOSIS: Shell large, tripartite (coil, shaft and hook – total height around 350 mm). Adult body chamber includes shaft and hook. Coil large (D about 200 mm), rather disjoint; shaft shorter proportionally. Hook open and fairly short. Whorl section rounded on coil, more compressed on shaft. At least four successive stages recognized during growth: (1) the Barremense stage (inner whorls unknown until D=55 mm) with rather numerous smooth interribs between each main rib; (2) the Irregular stage from 140 mm diameter up to beginning of shaft; (3) the Camereiceras stage on most of shaft; and (4) the Late adult stage which starts at top of shaft.

MATERIAL STUDIED (n=4): All specimens are from the Vocontian Basin of southeastern France. See Appendix 1 for locality details and Appendix 2d for measurements.

DESCRIPTION: Specimen M.H.N.N.104 (Pl. 13) has a full adult development showing the tripartition of the shell into coil, shaft and hook. A second specimen (G.P.A.AW43, Pl. 14, Fig. 2) shows the coil and the half shaft. Other specimens are fragments of coil or hook. The maximum total height of the shell reaches 346 mm (specimen M.H.N.N.104). The adult body chamber appears to be the entire shaft and the hook. The coil is generally quite disjoint with a spiral gap (h) up to 13 mm. The coil is large (up to 200 mm diameter), and the shaft is short in proportion. The hook is opened and fairly short. The growth in whorl height is rapid on the coil, but it becomes quite slow on the shaft and the hook (Appendix 1 – average relative height of H/D>0.30). The whorl section is rounded on the coil, much higher than wide, with convex flanks and a rounded ventral area. The whorl section tends to be compressed on the shaft.

The ornamentation is always well marked. At least four successive stages can be recognized during growth (see above the definition of recurring stages of ornamentation):

(1) The Barremense stage is the first ornamental stage identified (the Heberti stage is probably present but the inner whorls are unknown until D=55 mm). There are fairly numerous smooth interribs between each main trituberculate rib.
(2) The Irregular stage: there is a transition zone to the next stage from 140 mm diameter up to the beginning of the shaft.
(3) The Camereiceras stage comprises the majority of the shaft. The whorl section is compressed by flattening of the flanks that converge towards the venter; the ornamentation becomes less differentiated. The specimen M.H.N.N.104 shows pathological changes of the ornamentation at the top of the shaft.
(4) The Adulte late stage starts at the top of the shaft.

The suture line could not be observed.

VARIABILITY: Insufficient specimens are available for proper analyis of intraspecific variability. It may be noted, however, that the number of smooth interribs on the coil is correlated with the overall strength of the ornamentation, similarly as observed in *G alpinum*.

DIFFERENTIAL DIAGNOSIS: *G. rebouleti* nov. sp. differs from *G. multicostatum* and *G. alpinum* in its tripartite shell (coil, shaft and hook), and the much larger number of smooth interribs. It is distinguished also by a shorter Barremense stage, the lack of the Simplified ornamental stage and the new ontogenetic stage, the Camereiceras stage.

G. rebouleti nov. sp. is relatively close to *G. quelquejeui* and *G. coulletae* in the succession of their ontogenetic stages, but they appear later here. Finally, the latter two species do not have tripartite coiling, and the Camereiceras stage is more individualized.

G. hoheneggeri presents the same tripartite coiling of the shell, however, it has a lower spiral gap, fewer smooth interribs, and its main ribs remain trituberculate on the shaft. Moreover, it shows no Camereiceras stage.

Gassendiceras bosellii nov. sp.
(Pl. 14, Fig. 1; Pl. 15-16)

DERIVATION OF NAME: Dedicated to Patrick and Marc Boselli, fossil collectors from Valence (Drôme, France).

HOLOTYPE: G.P.A.AZ27 (Bert collection – Pl. 15, Fig. 1a-b).

TYPE LOCALITY: Section G12 (Text-fig. 2).

TYPE HORIZON: Bed 318a of section G12 (Text-fig. 6).

GEOGRAPHIC DISTRIBUTION: *G. bosellii* nov. sp. is known in southeastern France, in both basinal and distal platform areas, and in Morocco (unpublished data).

STRATIGRAPHIC DISTRIBUTION: All the specimens of the Vocontian Basin are from a bed in the middle Alpinum Subzone, between the Alpinum and Breistrofferi horizons (top of the Vandenheckei Zone). This level is located immediately above the bed that yielded *G. rebouleti* nov. sp. (see above).

DIAGNOSIS: Adult shell large, tripartite (coil, shaft and hook) (maximum height of about 300 mm). Coil large, (D about 190 mm), can be quite disjoint; shaft and hook rather short in proportion. Whorl section very rounded on most of coil and hook, but more compressed on end of coil and shaft. At least five successive stages can be recognized during growth: (1) the Heberti stage in innermost whorls; (2) the Barremense stage starts at about D=25 mm with numerous fairly systematic smooth interribs; (3) the Irregular stage from D=130 mm up to end of coil; (4) the Camereiceras stage on entire shaft; and (5) the Adult late stage begins at start of hook.

MATERIAL STUDIED (n=5): All the specimens are from southeastern France (Alpes-de-Haute-Provence, Alpes-Maritimes); two from the edges of platform, and three from more distal zone of the Vocontian Basin. See Appendix 1 for locality details and Appendix 2e for measurement.

DESCRIPTION: Specimen M.H.N.N.17252 (Pl. 16) has a tripartite full adult development (coil, shaft and hook) to a maximum height of 300 mm. G.P.A.AZ27 (Pl. 15, Fig. 1) is a portion of the coil with the beginning of the shaft; specimen. G.P.A.AW53 is a complete coil; G.P.A.AW41 (Pl. 14, Fig. 1) is a fragment with a portion of the coil and the beginning of the shaft; and G.P.A.AZ36 is a fragment of coil. The coil is large (around 190 mm in diameter) and usually quite disjoint (5 mm<h<10 mm). The shaft and the hook are quite short in proportion. The growth in whorl height is rapid on the coil, but it is reduced on the shaft and the hook (Appendix 2e – relative height average of H/D>0.32). The whorl section is rounded on most of the coil and the hook, but it tends to become compressed at the end of the coil and on the shaft (Text-fig. 16). Five successive stages can be recognized during growth:

(1) The Heberti stage: the inner whorls are known only in G.P.A.AW41.
(2) The Barremense stage starts at about 25 mm diameter. It has strongly trituberculate main ribs and relatively constant smooth interribs. G.P.A.AW41 locally shows fairly long spines when the next spiral whorl comes off to form the shaft.
(3) The Irregular stage is from about 130 mm diameter up to the end of the coil. The ornamentation becomes gradually less regular, and the tubercles lose their strength (except in G.P.A.AW41, which is significantly more robust than the others at this stage).
(4) The Camereiceras stage comprises the entire shaft. The ornamentation consists of ribs that are little differentiated: periumbilical tubercles gradually disappear and the lateral tubercles weaken considerably. The peri-ventral tubercles are connected by broad and blunt ribs and flank the almost flat venter.
(5) The Adult late stage begins early in the hook. The ribs are spaced and much strengthened. Near the peristome the ribs are approximated, raised and almost smooth.

The suture line is poorly preserved and could not be studied.

VARIABILITY: Insufficient specimens are available for proper analyis of intraspecific variability. However, it may be noted that the number of smooth interribs on the coil is correlated with the overall strength of the ornamentation and the thickness of the whorl section (compare the slender specimen. G.P.A.AZ27, Pl 15, Fig. 1 *versus* the robust specimen G.P.A.AW41, Pl 14, Fig. 1), as for *G. rebouleti* nov. sp.

DIFFERENTIAL DIAGNOSIS: *G. bosellii* nov. sp. is really close to *G. rebouleti* nov. sp. in its tripartite shell (a bit more coiled) and in the succession of its ontogenic stages. These stages may differ somewhat, first in their earlier appearence in *G. bosellii* nov. sp., and also in the Camereiceras stage, which starts at the beginning of the shaft and has a more uniform ornamentation than in *G. rebouleti* nov. sp.

G. bosellii nov. sp. and *G. hoheneggeri* have in common the tripartite coiling of the shell, but it is less well expressed in *G. bosellii* nov. sp. (shorter and curved shaft). *G. hoheneggeri* never shows the Camereiceras stage and its main ribs remain strongly trituberculate on the shaft.

G. quelquejeui and *G. coulletae* are also close to *G. bosellii* nov. sp. in the succession of their ontogenetic stages, but in *G. bosellii* nov. sp. the Barremense stage is shorter. G. *quelquejeui* and *G. coulletae* are never tripartite.

G. bosellii nov. sp. differs from *G. multicostatum* and *G. alpinum* in its tripartite shell, the much larger number of smooth interribs in the Barremense stage (which is also shorter), the absence of the Simplified ornamentation stage and in the additional presence of the Camereiceras stage.

VARIABILITY PATTERNS AND PROCESSES OF *GASSENDICERAS*

The study of *Gassendiceras* species show that the variability of shell size parameters and of the ornamentation is quite large, and always in the same way. The specimens with stouter cross-section (more robust) can have less tuberculate main ribs and especially smooth interribs, than the more compressed specimens (more slender). In general, the specimens with the smoother interribs are the most slender. This continuous variability allows to define a polymorphism framed by two robust and slender extremes both extensively connected by all possible intermediates. This type of variability looks to correspond to the 'laws' of covariation of Westermann (1966), based on Buckman's study (1892 in his work of 1887-1907) on the Sonninnidae (early Bajocian). The variability between robust and gracile morphologies is associated with a slight alteration of the ontogenetic sequence of the heterochrony type for each species of *Gassendiceras* where it was observed. These processes have long been known in the context of ontogeny / phylogeny relationships, but they can also be used as descriptors of intraspecific morphological variations. This is particularly true for accretionary building organisms such as ammonites (Dommergues *et al.* 1986; Meister 1989; Courville and Cronier 2003), which present all their growth stages on the same individual. In *Gassendiceras*, species in which ontogenetic stages appear earlier (peramorphic individuals) are of more gracile morphology, while those in which ontogenetic stages appear later (paedomorphic individuals) are of robust morphology.

Within each species of *Gassendiceras*, general coiling of the shell may also be highly variable due to the elasticity of the spiral gap (h). This variation can affect the same individual during its growth, or reflect a general trend in some specimens.

It is currently not possible, in the present state of knowledge and based on the material studied in this work, to report a sexual dimorphism as recognized for many ammonite groups (see Delanoy 1990, 1995 and Bert *et al.* 2006 for examples in the Hemihoplitidae).

TAXONOMIC DISCUSSION

Note on the genus *Toxancyloceras* Delanoy, 2003

The coil of some robust *Toxancyloceras* of the *T. vandenheckei* group may resemble some *Gassendiceras* coils from a strictly ornamental point of view, especially when there are many smooth interribs. This resemblance is, however, pure morphological convergence with no phyletic link (work in progress). In *Toxancyloceras* the uncoiling is more pronounced (spiral gap h higher), the growth in whorl height is lower, the coil is smaller in size, and smooth interribs are still more numerous. The shaft of *Toxancyloceras* is also more slender, straight and longer in proportion than in the few tripartite *Gassendiceras* species, and the hook is longer in *Toxancyloceras*. Lastly, the whorl section of the shell is more oval and commonly compressed in *Toxancyloceras*.

Note about the name of *T. vandenheckei*: the original spelling (Astier 1851) of this species is Vanden-Heckii. According to the *I.C.Z.N* article 32.5.2.3, this name has to be corrected into *vandenheckii*. But this species was dedicated to the Abbot Vanden-Hecke (Astier 1851, p. 452), so the name of the species should be *vandenheckei*. The terminal *-ii* is incorrect and corresponds probably to an inadvertant error (*lapsus calami*). The name therefore has to be corrected to *vandenheckei* wherever it appears (*I.C.Z.N* article 32.5.1).

Species previously classified as Gassendiceratinae

Several species have been classified as Gassendiceratinae in the recent taxonomic inventory conducted by Klein *et al.* (2007), but some of them belong to other families / taxa.

Immel (1978) compared *Emericiceras maghrebiensis* (Immel, 1978) to boreal species close to forms being classified as *Fissicostaticeras* Kakabadze and Hoedemaeker, 2010. *E. maghrebiensis* was then included in the genus *Barrancyloceras* by Klein *et al.* (2007) and by

Company *et al.* (2008), who regard this species as an ancestral representative of the Hemihoplitidae. However, according to Vermeulen (note 198, p. 225 in Klein *et al.* 2007), the type specimen of the Moroccan taxon *maghrebiensis* s. str. (*sensu* Immel non Company *et al.*) is a Lower Barremian *Emericiceras* unrelated to the Hemihoplitidae.

Crioceras klipsteini Uhlig, 1887 is only known from its original figure, and its type specimen appears to be lost. This species has been placed in the genus *Barrancyloceras* (see Klein *et al.* 2007). The whorl height and ornamentation of Uhlig's holotype (1887, pl. 3, fig. 3) differ from those of the Hemihoplitidae, and this species must therefore be excluded from the Gassendiceratinae. *C. klipsteini* could possibly be placed in the genus *Toxancyloceras* because of its characters. However, the fragmentary preservation of Uhlig's holotype and its unusual ornament (teratological?) led us to interpret this species as a *nomen dubium*.

Crioceras parolinianum Rodighiero, 1919 has always been considered close to the Hemihoplitidae of the "*Crioceras barremense*" group (*nomen dubium*, see Bert *et al.* 2010) since it was introduced. It was therefore placed tentatively in the genus *Barrancyloceras* by Klein *et al.* (2007). It is clear that the several authors (Sarkar 1955; Dimitrova 1967; Riccardi and Aguirre-Urreta 1989; Klein *et al.* 2007) saw this species as Barremian, while Rodighiero made it clear that the type specimen came from the Asiago Biancone (Val Frenzel, Padua in western Veneto region, northern Italy), which is a Valanginian–Hauterivian formation (Rodighiero 1919, p. 44–45). Moreover, the morphological characters of *C. parolinianum* resemble instead those of certain pseudothurmanniids (*sensu lato*) from the uppermost Hauterivian, such as *Sornayites lardyi* (Ooster, 1860), with which it may be possibly synonymous.

The taxon *Ammonites steinmani* Batsevich, 1873 was figured for the first time by Simonovitch *et al.* (1875, pl. 2, fig. A). Since then, Rouchadze (1933), Kakabadze (1977, 1981) and Kotetishvili *et al.* (2005) have confirmed its early Aptian age. *A. steinmani* was more recently placed in the Barremian Gassendiceratinae (Hemihoplitidae) by Klein *et al.* (2007), probably because of its ornamental features (alternation of trituberculate main ribs with smooth interribs). This style of ornament is, however, not restricted to the Hemihoplitidae (see Bert *et al.* 2010), and the taxon *A. steinmani* also has strong affinities with the inner whorls of other Lower Aptian groups such as *Proaustraliceras* Kakabadze, 1977, to which it may possibly belong.

Crioceras hammatoptychum Uhlig, 1883 was also classified in the genus *Barrancyloceras* by Klein *et al.* (2007). Its fragmentary lectotype comes from Tyrol (Uhlig 1883, pl. 30, fig. 1; Vašíček 1979, text-fig. 3, pl. 1, fig. 1a–b), but without any precise stratigraphic location it is difficult to decide on the classification of this form of which the ornamentation is reminiscent of some Upper Barremian Gassendiceratinae. The relatively frequent smooth interribs associated with the special aspect of the whorl section are characters known in the genus *Gassendiceras*.

Some of the specimens from the Barremian of Bir Lagamas (Sinai, Egypt) that Douvillé (1916) attributed to *Crioceras* (*Acanthodiscus*) *hammatoptychum* (especially EM1856 and perhaps also EM1853), appear at first sight morphologically quite close to the specimens figured by Uhlig (1883). The Egyptian material, preserved in the collections of the Ecole des Mines de Paris (deposited at the Lyon Faculty of Sciences, France), has been reexamined. This has shown that the flanks of the largest specimen converge towards the venter, which gives the whorl section the aspect of the Camereiceras stage, and the peri-umilical and lateral tubercles disappear earlier than on Uhlig's lectotype. These characters suggest that these Sinaï specimens could belong instead to the genus *Pseudoshasticrioceras*.

CONCLUDING REMARKS

Bed-by-bed sampling of several Upper Barremian sections in different depositional settings (both pelagic basin and distal platform) of southeastern France brought together a large number of ammonites of the genus *Gassendiceras*, particularly its poorly known species (*G. alpinum*, *G. multicostatum*, *G. hoheneggeri*) and those species whose representatives have sometimes been erroneously attributed to other taxa. Two new species are described (*G. rebouleti* nov. sp., *G. bosellii* nov. sp.). The abundance of *Gassendiceras alpinum* in the sections studied emphasizes its status as the index species for the Alpinum Horizon and the Alpinum Subzone in the upper part of the Vandenheckei Zone.

A palaeobiological approach with analysis of the ontogenetic stages of the species of *Gassendiceras* enabled the recognition of characters of strictly intraspecific variability. This variability occurs under the 'laws' of covariation theorized by Westermann (1966) and heterochronies of development. The intraspecific variability in *Gassendiceras* takes place between gracile peramorphic and robust paedomorphic extreme morphologies, with the presence of all intermediates. The evolutionary and phyletic relationships of the species under discussion tested by cladistics, as well as the influence of environment on their evolution, have been documented by Bert and Bersac (2013).

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REFERENCES

Arnaud, H. 2005. The South-East France Basin (SFB) and its Mesozoic Evolution. *Géologie Alpine*, Grenoble, série « Colloques et excursions », **7**, 5–28.

Astier, J.-E. 1851. Catalogue déscriptif des *Ancyloceras* appartenant à l'étage Néocomien d'Escragnolles et des Basses-Alpes. *Annales des Sciences Physiques et Naturelles, d'Agriculture et d'Industrie*, Lyon, **3**, 435–456.

Autran, G. and Delanoy, G. 1987. Mise en évidence d'un niveau à ammonites aptiennes dans la basse vallée du Var (Alpes-Maritimes, France). Conséquences paléogéographiques. *Géobios*, Villeurbanne, **20**, 415–422.

Avram, E. 1994. Lower Cretaceous (Valanginian-Early Aptian) ammonite succession in the Sviniţa region (SW Rumania). *Géologie Alpine*, **HS 20**, 113–167.

Bersac, S. and 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 Museum d'Histoire Naturelle de Nice*, **27**, 197–270.

Bersac, S., Bert, D. and Delanoy, G. 2010. Description, biostratigraphie et interprétation des séries condensées du Crétacé inférieur de la Montagne de Ruth, à l'extrémité sud orientale de l'Arc de Castellane (Alpes-Maritimes, sud-est de la France). *Annales du Muséum d'Histoire Naturelle de Nice*, **25**, 1–17.

Bert, D. 2009a. Description de *Artareites landii* nov. (Ammonoidea) du Barrémien supérieur de Majastre (Sud-Est de la France) et discussion sur les Helicancylidae Hyatt, 1894. *Annales de Paléontologie*, **95**, 139–163.

Bert, D. 2009b. Discussion, evolution and new interpretation of the *Tornquistes* Lemoine, 1910 (Pachyceratidae, Ammonitina) with the exemple of the Vertebrale Subzone sample (Middle Oxfordian) of southeastern France. *Revue de Paléobiologie*, **28**, 471–489.

Bert, D. 2012a. The Upper Barremian pro parte of the Angles stratotype (SE France). In: D. Bert and S. Bersac (Eds), First meeting of the resarch group for palaeobiology and biostratigraphy of the ammonites – communications. *Boletin del Instituto de Fisiografia y Geologia*, **82**, 23–26.

Bert, D. 2012b. Phylogenetic relationships among the Hemihoplitidae Spath, 1924 (Ammonoidea, Upper Barremian). In: D. Bert and S. Bersac (Eds), First meeting of the resarch group for palaeobiology and biostratigraphy of the ammonites – communications. *Boletin del Instituto de Fisiografia y Geologia*, **82**, 37–38.

Bert, D. and Bersac, S. 2013. Evolutionary patterns – tested with cladistics – and processes in relation to palaeoenvironments of the Upper Barremian genus *Gassendiceras* (Ammonitina, Lower Cretaceous). *Palaeontology*, **56**, 631–646.

Bert, D. and Delanoy, G. 2000. Considérations nouvelles sur quelques représentants barrémiens des Puchelliidae Douvillé, 1890 et des Hemihoplitidae Spath, 1924 (Ammonoidea). *Annales du Muséum d'Histoire Naturelle de Nice*, **15**, 63–89.

Bert, D. and Delanoy, G. 2009. *Pseudoshasticrioceras bersaci* nov. sp. (Ammonoidea, Gassendiceratinae), and new ammonite biohorizon for the Upper Barremian of southeastern France. *Carnets de Géologie / Notebooks on Geology*, Brest, article 2009/02 (CG2009_A02).

Bert, D., Delanoy, G. and Bersac, S. 2006. Descriptions de représentants nouveaux ou peu connus de la famille des Hemihoplitidae Spath, 1924 (Barrémien supérieur, Sud-est de la France): conséquences taxinomiques et phylétiques. *Annales du Muséum d'Histoire Naturelle de Nice*, **21**, 179–253.

Bert, D., Delanoy, G. and Bersac, S. 2008. Nouveaux biohorizons et propositions pour le découpage biozonal ammonitique du Barrémien supérieur du Sud-Est de la France. *Carnets de Géologie / Notebooks on Geology*, Brest, Article 2008/03 (CG2008_A03).

Bert, D., Delanoy, G. and Canut, L. 2009. L'origine des *Imerites* Rouchadzé, 1933: résultat d'une innovation chez les

Gassendiceratinae Bert, Delanoy et Bersac, 2006 (Ammonoidea, Ancyloceratina). *Annales de Paléontologie*, Paris, **95**, 21–35.

Bert, D., Busnardo, R., Delanoy, G. and Bersac, S. 2010. Problems in the identity of "*Crioceras*" *barremense* Kilian, 1895 (Ancyloceratida, Late Barremian), and their proposed resolution. *Carnets de Géologie / Notebooks on Geology*, Brest, Article 2010/01 (CG2010_A01).

Bert, D., Delanoy, G. and Bersac, S. 2011. The Dichotomus Horizon: proposal for a new bio-chronologic unit of the Giraudi Zone of the Upper Barremian of southeastern France, and considerations regarding the genus *Imerites* Rouchadzé (Ammonoidea, Gassendiceratinae). *Carnets de Géologie / Notebooks on Geology*, Brest, Article 2011/01 (CG2011_A01).

Buckman, S.S. 1887-1907. A monograph of the ammonites of the Inferior Oolite Series. *Palaeontographical Society*, London, **262**, 1–456.

Bunardo, R. 1965. Le stratotype du Barrémien. Lithologie et macrofaune. In : Colloque sur le Crétacé inférieur (Septembre 1963, Lyon). *Mémoires du Bureau des Recherches Géologiques et Minières*, Orléans, **34**, 101–116.

Busnardo, R. and Cotillon, P. 1964. Stratigraphie du Crétacé inférieur dans la région des gorges du Verdon (Basse-Alpes et Var). *Comptes Rendus Sommaires des Séances de la Société Géologique de France*, Paris, **8**, 321–322.

Callomon, J.H. 1963. Sexual Dimorphism in Jurassic Ammonites. *Transactions of the Leicester Literary and Philosophical Society*, **57**, 21–56.

Chaline, J. and Marchand D. 2002. Les merveilles de l'évolution, pp. 1–268. Editions Universitaires de Dijon.

Chandler, R. and Callomon, J H. 2009. The Inferior Oolite at Coombe Quarry, near Mapperton, Dorset, and a new Middle Jurassic ammonite faunal horizon, Aa–3b, *Leioceras comptocostosum* n. biosp. in the Scissum Zone of the Lower Aalenian. *Proceedings of the Dorset Natural History and Archaeological Society*, **130**, 99–132.

Company, M., Sandoval, J. and Tavera, J.M. 1995. Lower Barremian ammonite biostratigraphy in the Subbetic Domain (Betic Cordillera, southern Spain). *Cretaceous Research*, **16**, 243–256.

Company, M., Sandoval, J., Tavera, J.M., Aoutem, M. and Ettachfini, M. 2008. Barremian ammonite faunas from the western High Atlas, Morocco - biostratigraphy and palaeobiogeography. *Cretaceous Research*, **29**, 9–26.

Conte, G. 1989. Fossiles du plateau d'Albion. *Alpes de Lumière*, **99**, 1–72.

Cotillon, P. 1971. Le Crétacé inférieur de l'Arc subalpin de Castellane entre l'Asse et le Var, stratigraphie et sédimentologie. *Mémoires du Bureau des Recherches Géologiques et Minières*, Orléans, **68**, 1–313.

Cotillon, P., Banvillet, M., Gaillard, Ch., Grosheny, D. and Olivero, D. 2000. Les surfaces à *Rhizocorallium* de l'Aptien inférieur sur la bordure méridionale du Bassin vocontien (France, SE), marqueurs de dynamiques locales; leurs relations avec un évènement anoxique global. *Bulletin de la Société Géologique de France*, Paris, **171**, 229–238.

Cottreau, J. 1937. Types du Prodrome de paléontologie stratigraphique universelle de d'Orbigny. *Annales de Paléontologie*, **26**, 17–37.

Courville, P. and Crônier, C. 2003. Les hétérochronies du développement : un outil pour l'étude de la variabilité et des relations phylétiques? Exemple de *Nigericeras*, Ammonitina du Crétacé supérieur africain. *Comptes Rendus Palevol* **2**, 535–546.

Courville, P. and Crônier, C. 2005. Diversity or disparity in the Jurassic (Upper Callovian) genus *Kosmoceras* (Ammonitina): a morphometric approach. *Journal of Paleontology*, **79**, 944–953.

Delanoy, G. 1990. *Camereiceras* nov. gen. (Ammonoidea, Ancyloceratina) du Barrémien supérieur du Sud-Est de la France. *Géobios*, **23**, 71–93.

Delanoy, G. 1992. Les ammonites du Barrémien Supérieur de Saint-Laurent de l'Escarène (Alpes-Maritimes, Sud-Est de la France). *Annales du Muséum* D*'Histoire Naturelle de Nice*, **9**, 1–148.

Delanoy, G. 1994. Les zones à Feraudianus, Giraudi et Sarasini du Barrémien supérieur de la région stratotypique d'Angles-Barrême-Castellane (Sud-Est de la France). *Géologie Alpine*, Grenoble, **HS 20**, 279–319.

Delanoy, G. 1995. About some significant Ammonites from the Lower Aptian (Bedoulian) of the Angles-Barrême area (South-East of France). In Cecca, F. (Ed.), Proceeding of 3rd Workshop on Early Cretaceous Cephalopods. *Mem. Desc. Carta Geol. Italia*, **51**, 65–101.

Delanoy, G. 1997. Biostratigraphie des faunes d'Ammonites à la limite Barrémien-Aptien dans la région d'Angles-Barrême-Castellane. Etude particulière de la Famille des Heteroceratidae Spath 1922 (Ancyloceratina, Ammonoidea). *Annales du Muséum d'Histoire Naturelle de Nice*, **12**, 1–270.

Delanoy, G., Baudouin, C., Gonnet, R. and Bert, D. 2008. Sur les faunes d'ammonites (Crétacé inférieur) du niveau glauconieux de la carrière des Trois-Vernes, près de Crest (Drôme, Sud-est de la France). *Annales du Muséum d'Histoire Naturelle de Nice*, **23**, 11–65.

Dimitrova, N. 1967. Les fossiles du Bulgarie – IV Crétacé inférieur, Cephalopoda (Nautiloidea et Ammonoidea). *Académie Bulgare des Sciences*, 1–428.

Dommergues, J.-L., David, B. and Marchand, D. 1986. Les relations ontogénèse-phylogénèse : applications paléontologiques. *Geobios*, Villeurbanne, **19**, 335–356.

Douvillé, H. 1916. Les terrains secondaires dans le massif du Moghara à l'Est de l'Isthme de Suez d'après les explorations de M. Couyat-Barthoux. Paléontologie. *Mémoire de l'Académie des Sciences de l'Institut de France*, **54**, 1–184.

Haug, E. 1889. Beitrag zur Kenntniss der oberneocomen Ammonitenfauna der Puezalpe bei Corvara (Südtirol). *Beiträge zur Palaeontologie Oesterreich-Ungarns und des Orients*, **7**, 193–230.

Immel, H. 1978. Die Crioceratiten (Ancyloceratina, Ammonoidea) des mediterranen und borealen Hauterive-Barreme (Unterkreide). *Palaeontographica*, A**163**, 1–85.

Kakabadze, M.V. 1977. New and little-known Ancyloceratidae from the Caucasus. *Trudy Geologicheskog Instituta Akademiia Nauk Gruzinskoi SSR*, **58**, 128–151. [In Russian]

Kakabadze, M.V. 1981. The ancyloceratids of the South of the USSR and their stratigraphical significance. *Trudy Geologicheskog Instituta Akademiia Nauk Gruzinskoi SSR*, **71**, 1–221.

Karakash, N. 1907. Le Crétacé inférieur de Crimée et sa faune. *Travaux de la Société Impériale des Naturalistes de St Petersbourg*, **32**, 1–482.

Kennedy, W.J. and Cobban, W.A. 1976. Aspects of ammonite biology, biogeography, and biostratigraphy. *Special Papers in Paleontology*, **17**, 1−94.

Klein, J., Busnardo, R., Company, M., Delanoy, G., Kakabadze, M., Reboulet, S., Ropolo, P., Vašíček, Z. and Vermeulen, J. 2007. Lower Cretaceous Ammonites III Bochianitidae, Protancyloceratoidea, Ancyloceratoidea, Ptychoceratoidea. In: Riegraf W. (Ed.), Fossilium Catalogus I: Animalia, pp. 1–381. Backhuys Publishers; Leiden.

Kotetishvili, E.V., Kvantaliani, I.V., Kakabadze, M.V. and Tsirekidze, L.R. 2005. Atlas of Early Cretaceous Fauna of Georgia. *Georgian Proceedings of the Georgian Academy of Sciences*, A. Janelidze Geological Institute Tbilissi, **NS 120**, 1–788.

Lepinay, P. and Vermeulen, J. 2009. *Spinocrioceras sauvanae* sp. nov. et ses implications sur la compréhension phylogénétique du genre *Spinocrioceras* Kemper, 1973. *Annales du Muséum d'Histoire Naturelle de Nice*, **24**, 93–102.

Mahé, J. and Devillers, Ch. 1983. La chrono-espèce, conception chronodynamique de l'espèce, conséquence d'une stratégie de rupture au niveau de la spéciation. In: Chaline, J. (Ed.), Modalités, rythmes et mécanismes de l'évolution biologique, Université de Dijon, 145–152.

Marchand, D. 1986. L'évolution des Cardioceratinae d'Europe occidentale dans leur contexte paléobiologique (Callovien supérieur-Oxfordien moyen). Unpublished Ph.D. thesis, Université de Bourgogne, Dijon, 1–603.

Marchand, D. and Dommergues, J.-L. 2008. L'approche paléontologique des concepts biologiques de l'espèce : défi pour l'étude de la paléobiodiversité. L'exemple des ammonites jurassiques. In: Prat, D., Raynal-Roques, A., and Roguenant, A. (Eds), Peut-on classer le vivant ? Linné et la systématique aujourd'hui. Editions Belin, Paris, 203–214.

Masse, J.-P. and Fenerci-Masse, M. 2011. Drowning discontinuities and stratigraphic correlation in platform carbonates. The late Barremian-early Aptian record of southeast France. *Cretaceous Research*, **32**, 659–684.

Mayr, E. 1974. Populations, espèces et évolution, pp. 1–496. Hermann; Paris.

Mayr, E. 1982. The growth of biological thought. Diversity, evolution and inheritance, pp. 1–974. Belknap Press; Cambridge − Massachusetts.

Meister, Ch. 1989. Les ammonites du Crétacé supérieur d'Ashaka, Nigéria. *Bull. Centre Rech. Explor. Prod. elf-aquitaine*, **13**, 1–84.

Morard, A. and Guex, J. 2003. Ontogeny and covariation in the Toarcian genus *Osperleioceras* (Ammonoidea). *Bulletin de la Société Géologique de France*, **174**, 607–615.

Orbigny, A. d' 1850. Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique, 2ème volume pp. 1–432. Masson; Paris.

Paquier, M.V. 1900. Recherches géologiques dans le Diois et les Baronnies orientales. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de l'Université de Grenoble*, **5**, 149–556.

Reboulet, S. 2007 (reporter) and Atrops, F., Bert, D., Bulot, L., Busnardo, R., Delanoy, G., and Vermeulen, J. Compte rendu de la réunion des biostratigraphes français du Kilian Group IUGS Lower Cretaceous Ammonites Working Group, Digne-les-Bains (France), Mercredi 2 Mai 2007 (9H-17H). Parc St Benoît Réserve Géologique de Haute-Provence, France. Thème : zonation Hauterivien – Barrémien. 14 pp. (Unpublished).

Reboulet, S. and Klein, J. (reporters) and Barragan, R., Company, M., Gonzalez-Arreola, C., Lukeneder, A., Raisossadat, S.N., Sandoval, J., Szives, O., Tavera, J.M., Vašíček, Z. and Vermeulen, J. 2009. Report on the 3rd International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the "Kilian Group" (Vienna, Austria, 15th April 2008). *Cretaceous Research*, **30**, 496–502.

Riccardi, A.C. and Aguirre-Urreta, M.B. 1989. Hemihoplitid ammonoids from the Lower Cretaceous of Southern Patagonia. *Paleontology*, **32**, 447–462.

Rodighiero, A. 1919. Il sistema Cretaceo del Veneto occidentale compreso fra d'Adige e il Piave, con speciale riguardo al Neocomiano dei Sette Comuni. *Palaeontografica Italica*, **25**, 39–125.

Rouchadze, J. 1933. Les ammonites aptiennes de la Géorgie occidentale. *Bulletin de l'Institut Géologique de Géorgie*, **1**, 165–273.

Salvador, A. (Ed.) 1994. Internationnal Stratigraphic Guide. A guide to stratigraphic classification, terminology and procedure (2nd ed.), pp. 1–214. Geological Society of America, Boulder.

Sarkar, S. 1955. Révision des Ammonites déroulées du Crétacé inférieur du Sud-Est de la France. *Mémoires de la Société Géologique de France*, **N.S. 72**, 1–176.

Simionescu, I. 1899. Note sur quelques ammonites du Néocomien français. *Annales de l'Université de Grenoble*, **11**, 1–16.

Simonovitch, S.E., Batsevich, L.F. and Sorokin, A. 1875. Geological description of parts of the Kutais, Lechkhum, Senaks and Zughdid districts of the Kutais government. Materialy dlya Geologii Kavkaza (1874), 1–191. [In Russian]

Thomel, G. 1964. Contribution à la connaissance des céphalopodes crétacés du sud-est de la France. Note sur les ammonites déroulées du Crétacé inférieur vocontien. *Mémoires de la Société Géologique de France*, **101**, 1–80.

Tintant, H. 1952. Principes de la systématique. In: Piveteau, J. (Ed.), Traité de Paléontologie. Masson, Paris, **1**, 41–64.

Tintant, H. 1963. Les Kosmoceratidés du Callovien inférieur et moyen d'Europe occidentale. Thèse, Presse Universitaire de France, Paris, 1–500.

Tintant, H. 1965. La notion d'espèce en paléontologie. *Mises à jour scientifique* **1**, 273–294.

Tintant, H. 1966. Principes et méthodes d'une paléontologie moderne. *Bulletin d'Information des Géologues du Bassin de Paris*, **7**, 9–19.

Tintant, H. 1969. L'espèce et le temps. Point de vue du paléontologiste. *Bulletin de la Société Zoologique de France*, **94**, 559–576.

Tintant, H. 1976. Le polymorphisme intraspécifique en paléontologie (exemples pris chez les Ammonites). *Haliotis*, **6**, 49–69.

Tintant, H. 1980. Problématique de l'espèce en paléontologie. In: Les problèmes de l'espèce dans le monde animal. *Mémoire de la Société Géologique de France*, **40**, 321–372.

Tzankov, V. 1946. Etudes biostratigraphiques et paléoécologiques sur les formations géologiques en Bulgarie. In: Cohen, E.R., Dimitrov, S. and Kamenov, B.G. (Eds), Géologie de la Bulgarie, 1–390.

Uhlig, V. 1883. Die Cephalopoden der Wensdorfer Schichten. *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, **46**, 127–290.

Uhlig, V. 1887. Ueber neocome Fossilien vom Gardenazza in Südtirol nebst einen Anhang über das Neocom von Ischl. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt*, **37**, 69–108.

Vašíček, Z. 1979. Zwei neue faunistische Fundorte der Unterkreide in der Silesischen Einheit und Zusammenfassung der Revision d von V. Uhlig (1883) beschriebenen Ammoniten. *Sbornik vědeckých prací Vysoké školy báňské v Ostravě, řada hornicko- geologická,* **25**, 119–134.

Vašíček, Z. 2008. Barremian and Early Aptian ammonites from the Godula Facies of the Silesian Unit in the Outer-Western Carpathians, Czech Republic. *Acta Geologica Polonica*, **58**, 407–423.

Vermeulen, J. 2004. Vers une nouvelle classification à fondement phylogénétique des ammonites hétéromorphes du Crétacé inférieur méditerranéen. Le cas des Crioceratitidae Gill, 1871 nom. correct. Wright, 1952, des Emericiceratidae fam. nov. et des Acrioceratidae fam. nov. (Ancyloceratidaceae Gill, 1871). *Riviéra Scientifique*, **88**, 69–92.

Vermeulen, J. 2005a. Boundaries, ammonite fauna and main subdivisions of the stratotype of the Barremian. *Géologie Alpine*, **7**, 147–173.

Vermeulen, J. 2005b. Sur quatre espèces particulières d'ammonites du Barrémien du sud-est de la France. *Annales du Muséum d'Histoire Naturelle de Nice*, **20**, 1–24.

Vermeulen, J. and Lazarin, P. 2007. Nouvelles données sur les Ancyloceratoidea Gill, 1871 (Ancyloceratina Wiedmann, 1966 emend. Vermeulen, 2005) du Barrémien supérieur et de l'Aptien inférieur. *Annales du Muséum d'Histoire Naturelle de Nice*, **22**, 27–86.

Vermeulen, J. 2011. Discussion of: Problems in the identity of *„Crioceras" barremense* Kilian, 1895 (Ancyloceratida, Late Barremian), and their proposed resolution, by D. Bert *et alii* (CG2010_A01) [Alternative title: The nomenclatural status and the acceptation of the genus *Barrancyloceras* Vermeulen, 2000, and of its type species]. *Carnets de Géologie / Notebooks on Geology*, Brest, Article 2010/01_Reply (CG2010_A01R).

Westermann, G.E.G. 1966. Covariation and taxonomy of the Jurassic ammonite *Sonninia adicra* (WAAGEN). *Neues Jahrbuch für Geologie und Paläontologie Abteilung*, **124**, 289–312.

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Appendix 1.
List of the material

Gassendiceras alpinum **(d'Orbigny, 1850), list of the specimens (n=77):** the specimens No. R00833a (ex. No. 5406) from Angles, A. d'Orbigny' coll. (lectotype – *M.N.H.N*); 1279 from Barrême, Petitclerc's coll. (*U.P.M.C*); ID 161 et ID 162 from Méouille (*I.D*); G15-309b-01 and G15-309b-02 (G15/309b) C. Baudouin's coll. (G.P.A); LE 271 from Angles, L. Ebbo's coll. (a cast is in the D. Bert's collection under No. AZ19); Barr-11 from Angles, R. Quelquejeu's coll. (St. André les Alpes); F001 and an unnumbered specimen of the E. Pénagé's collection (VIG2/266) (C.E.M); CEM 2 (VIG2/266), G. Agostini's coll. (*C.E.M*); UH (SO/69-2), L. Canut's coll. (*G.P.A*); No. TAI63, TAI183, TAI184, TAI186, TAI190, TAI194 (TAI/99) and VLS005 (VA/11), S. Bersac's coll. (*G.P.A*); No. 1226 (A'/151-2), 28735 (A'/151-2) and 28734 (VIG2/266), G. Delanoy's coll. (*G.P.A*); No. AP46 (TF/15), AT36 (A'/151-2), AW44 (VA/11), AW57 (G12/309b), AW58 (GRY/859c), AW59 (LAC/209b), AW60 (A'/151-2), AW62 (VIG2/267), AW63 (G12/309b), AW64 (G15/309b), AW65 (A'/151-2), AW66 (GRY/859c), AW67 (G15/309b), AW68 (A'/151-2), AW69 (LAC/209), AW70 (LAC/209b), AW71 (G12/309b), AW72 (LAC/209c), AW74 (G15/309b), AW75 (A'/151-2), AW81 (G15/309b), AW82 (G15/309b), AW89 (G15/309b), AX10 (G12/309b), AX13 (G12/309b), AX17 (G12/309b), AX35 (LAC/209), AX36 (G12/309b), AY04 (G12/309b), AY05 (A'/151-2), AY10 (G12/309b), AY39 (G12/309b), AY40 (A/151-2), AY67 (GRY/859), AZ18 (VIG2/266), AZ21 (VIG2/266), AZ22 (LAC/209c), AZ23 (G12/309b), AZ24 (G12/309b), AZ25 (G12309b), AZ37 (SA/25), AZ38 (RS/8), AZ39 (G15/309b), AZ40 (G15/309b), AZ41 (G15/309b), AZ42 (G15/309b), AZ43 (G15/309b), AZ44 (G15/309b), AZ45 (RS/8), AZ46 (G15/309b), AZ47a-b (G15/309b) and AZ48 (G12/309b) D. Bert's collection (*G.P.A*); an unnumbered specimen from Rougon, P. Cotillon's collection (*F.S.L*); an unnumbered specimen from Moriez, P. Coullet's collection (Barrême); and an unnumbered specimen from Moriez, L. Maurel's collection (Town-hall of Barrême).

Gassendiceras multicostatum **(Sarkar, 1955), list of the specimens (n=24):** the specimen No. UJF.ID-111 (lectotype) from Trigance (*I.D*); the specimens No. UJ (SO/69-2), GJ (SO/69-2) L. Canut's coll. (*G.P.A*); TAI105 (TAI/99), TAI118 (TAI/99), TAI185 (TAI/99) S. Bersac's coll. (*G.P.A*); 136 (VA/11), 140 (VA/11), 1225 (A'/151-1), 28749 (TAI/99) G. Delanoy's coll. (*G.P.A*); AZ28 (A'/149-3), AW52 (A'/149-4), AW49 (A'/151-1), AZ26 (A'/151-1b), AZ30 (G12/308b), AX34 (G12/308a), AW45 (A'/151-1), AW48 (A'/151-1), AW50 (A'/150), AZ31 (SO/69-2), AZ32 (G5/99), AZ44 (G12/308a) D. Bert's coll. (*G.P.A*); the fragment No. R00833b (ex. No. 5406) from Angles, A. d'Orbigny collection (*M.N.H.N*); and an unnumbered specimen from Beynes, P. Cotillon's collection (*F.S.L*).

Gassendiceras hoheneggeri **(Uhlig, 1883), list of the specimens (n=1):** an unnumbered specimen (VA/11), J. Davoux' collection (Nice).

Gassendiceras rebouleti **nov. sp., list of the specimens (n=4):** No. AW43 (G12/317b - holotype), AZ33 (G12/317b) and AZ34 (G12/317b) D. Bert's coll. (*G.P.A*); and the No. 104 (VIG2/?), G. Thomel's collection (this specimen cannot be found in the collections of the *Natural History Museum of Nice* and it is considered lost).

Gassendiceras bosellii **nov. sp., list of the specimens (n=5):** No. AW41 (LAC/215 or 217), AZ27 (G12/318a - holotype) and AZ36 (G12/318a), D. Bert's coll. (*G.P.A*); No. 17252 (VA/11), G. Delanoy's coll. (*G.P.A*), and AW53 (TF/15), D. Bert's coll. (*G.P.A*).

Appendix 2a. Table of measurements for *Gassendiceras alpinum* (d'Orbigny, 1850)

No.	D	H	W	U	*H/D*	*W/D*	*U/D*	*W/H*	*U/H*	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
G.P.A.AZ18	364	97	70.7	184	0,27	0,19	0,51	0,73	1,90	5.5	-	18	-	1	-	0	
	287	86.3	56.2	146.7	0,30	0,20	0,51	0,65	1,70	11.5	-	20	-	2	-	0	105°
	248.5	78	-	126.2	0,31	?	0,51	?	1,62	8.7	-	-	-	-	-	-	75°
	162	48.2	-	77	0,30	?	0,48	?	1,60	8.3	27	14	-	-	-	-	200°
	128.5	38.5	-	59.5	0,30	?	0,46	?	1,55	8	24	13	-	-	-	-	90°
	100.5	28	-	47.7	0,28	?	0,48	?	1,70	7.5	22	12	-	-	-	-	90°
	78.6	23.4	-	38.3	0,30	?	0,49	?	1,64	5	21	11	-	-	-	-	90°
	62	20.8	-	32.2	0,34	?	0,52	?	1,55	2.5	19	10	-	-	-	-	90°
	44.7	142	-	23.4	0,32	?	0,52	?	1,65	2	19	9	-	-	-	-	90°
sp. Maurel's coll.	315	89.1	77.7	162	0,28	0,25	0,51	0,87	1,82	2.5	-	17	-	0	-	3	
	212	63.2	-	114	0,30	?	0,54	?	1,80	13	-	-	-	-	-	-	180°
G.P.A.AZ21	281	75.4	55.3	147.5	0,27	0,20	0,53	0,73	1,96	6.5	-	17	-	3	-	4	
	249	69.6	-	127	0,28	?	0,51	?	1,82	-	-	-	-	-	-	-	90°
	198	57	-	102	0,29	?	0,52	?	1,79	-	-	-	-	-	-	-	90°
G.P.A.AZ41	250	78.1	-	120	0,31	-	0,48	-	1,54	-	-	-	-	-	-	-	
	204	66.4	-	103.4	0,33	-	0,51	-	1,56	-	-	-	-	-	-	-	90°
	176	58	-	86.8	0,33	-	0,49	-	1,50	8	-	-	-	-	-	-	90°
	70	22	-	35	0,31	-	0,50	-	1,59	-	-	-	-	-	-	-	360°
G15-309b-01	165	59	43.5	68.8	0,36	0,26	0,42	0,74	1,17	8	25	13	6	3	19	8	
	129.3	47.6	41.4	54.3	0,37	0,32	0,42	0,87	1,14	5	21	12	2	2	22	10	90°
	98.2	37	31.7	42	0,38	0,32	0,43	0,86	1,14	2.9	20	11	2	2	21	11	90°
	78.5	29.6	-	32.8	0,38	-	0,42	-	1,11	2.9	21	9	1	1	21	12	90°
	57.6	19.3	-	26.2	0,34	-	0,45	-	1,36	2.2	28	9	0	0	14	10	90°
	46.2	16.4	-	21	0,35	-	0,45	-	1,28	-	-	12	-	0	-	9	90°
	36.2	12	-	18	0,33	-	0,50	-	1,50	-	-	19	-	0	-	4	90°
M.N.H.N.5406 (Lectotype)	156	51	48	65	0,33	0,31	0,42	0,94	1,28	-	-	12	-	1	-	9	
	130	45	-	60	0,35	?	0,46	?	1,33	-	-	12	-	2	-	7	90°
LE 271	156	50.9	-	71	0,33	?	0,46	?	1,40	3	21	11	6	5	11	5	
	128.5	44.5	41	56	0,35	0,32	0,44	0,92	1,26	2.8	22	13	2	2	11	5	90°
	102.7	34.9	34	46.7	0,34	0,33	0,45	0,97	1,34	2.6	19	10	2	1	15	6	90°
	79.6	28.2	25	35	0,35	0,31	0,44	0,89	1,24	1.4	19	9	1	0	14	6	90°
	67.4	22.1	20.5	29.8	0,33	0,30	0,44	0,93	1,35	1	20	9	1	1	17	9	90°
	50.3	17.9	-	22.4	0,36	?	0,45	?	1,25	0.6	21	10	1	1	19	8	90°
	43.2	14.7	-	19.9	0,34	?	0,46	?	1,35	0.3	25	11	0	0	15	8	90°
	31.6	10.3	-	15	0,33	?	0,48	?	1,46	0.1	33	11	0	0	13	11	90°
	27.8	8.5	-	13.6	0,31	?	0,49	?	1,60	-	-	14	-	0	-	7	90°
	20.7	6.5	-	10.7	0,31	?	0,52	?	1,65	-	-	22	-	0	-	2	90°
28735	153.9	47.8	36.6	74.2	0,31	0,24	0,48	0,77	1,55	5	-	9	-	2	-	8	
	102	32.8	-	53.7	0,32	?	0,53	?	1,64	3.1	-	-	-	-	-	-	180°
	65	24.8	-	33.5	0,38	?	0,52	?	1,35	1.5	-	10	-	-	-	-	360°

No.	D	H	W	U	*H/D*	*W/D*	*U/D*	*W/H*	*U/H*	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
28735	30.6	11.4	-	14.6	0,37	?	0,48	?	1,28	1.5	-	-	-	-	-	-	180°
	18.9	5.6	-	10	0,30	?	0,53	?	1,79	-	-	16	-	0	-	3	180°
1226	141	45.2	41.8	64.9	0,32	0,30	0,46	0,93	1,44	4.2	21	11	2	2	21	12	
	112.4	38.7	35.4	50.9	0,34	0,32	0,45	0,92	1,32	2.8	20	11	0	0	21	10	90°
	90.8	31.3	28.6	41.7	0,35	0,32	0,46	0,91	1,33	3.7	19	10	0	0	21	10	90°
	70.6	22.6	21.2	33.6	0,32	0,30	0,48	0,94	1,49	2	19	9	0	0	19	10	90°
	56.2	18.2	-	25	0,33	?	0,45	?	1,37	0.8	21	9	1	0	17	9	90°
	47.6	15.1	-	21.8	0,32	?	0,46	?	1,44	0.8	22	10	1	0	16	10	90°
G.P.A. AZ39	140.7	46.6	-	62.6	0,33	-	0,44	-	1,34	5.1	19	9	5	5	21	10	
	112.6	39.1	-	49.3	0,35	-	0,44	-	1,26	3.8	19	10	2	2	18	11	90°
	87.2	31.8	-	39.6	0,36	-	0,45	-	1,25	3.7	18	10	0	0	19	12	90°
	70.3	25.4	-	29.9	0,36	-	0,43	-	1,18	2.6	18	9	0	0	16	9	90°
	52.7	18.3	-	24.2	0,35	-	0,46	-	1,32	1.6	19	8	0	0	15	7	90°
	42.2	15	-	18.5	0,36	-	0,44	-	1,23	-	-	10	-	0	-	9	90°
	33.8	11.5	-	15.9	0,34	-	0,47	-	1,38	-	-	-	-	-	-	-	90°
G.P.A. AZ37	133.9	45.2	45.8	57	0,34	0,34	0,43	1,01	1,26	2.7	-	-	-	-	-	-	
	104.4	39.4	36.3	43.4	0,38	0,35	0,42	0,92	1,10	-	-	-	-	-	-	-	90°
	85.9	29.4	29.9	37.7	0,34	0,35	0,44	1,02	1,28	-	-	-	-	-	-	-	90°
G15-309b-02	129.1	38	-	61.7	0,29	-	0,48	-	1,62	7.9	21	11	3	3	11	5	
	103.1	33.5	-	48.2	0,32	-	0,47	-	1,44	5.2	18	10	2	2	14	5	90°
	80.3	26.8	-	37	0,33	-	0,46	-	1,38	3.2	18	10	0	0	15	7	90°
	63.9	21	-	29.9	0,33	-	0,47	-	1,42	2.4	18	8	0	0	16	9	90°
	49.6	16.5	-	23.2	0,33	-	0,47	-	1,41	2	19	8	0	0	14	8	90°
	39.7	12.6	-	20.1	0,32	-	0,51	-	1,60	1.6	25	8	0	0	9	7	90°
	31.5	9.8	-	15.6	0,31	-	0,50	-	1,59	0.4	32	11	0	0	7	7	90°
	25.8	7.8	-	13.2	0,30	-	0,51	-	1,69	0.3	44	14	0	0	3	3	90°
F001	127.4	-	-	-	?	?	?	?	?	-	22	11	0	0	11	4	
	113.6	36.2	32	51.9	0,32	0,28	0,46	0,89	1,43	4.5	22	11	0	0	8	4	45°
	89.1	29.1	27	48.6	0,33	0,30	0,55	0,93	1,67	3.5	21	10	1	0	7	3	90°
	69	24.6	20.5	32	0,36	0,30	0,46	0,83	1,30	2.3	22	10	2	0	9	5	90°
	56.6	19.6	15	24	0,35	0,27	0,42	0,77	1,23	1.7	25	10	4	1	6	4	90°
G.P.A. AZ42	127	46	-	59.1	0,36	-	0,47	-	1,28	4.6	-	-	-	-	-	-	
	78.5	25.4	-	33.4	0,32	-	0,43	-	1,31	2.5	-	-	-	-	-	-	200°
	52.8	19	-	22.5	0,36	-	0,43	-	1,18	1.6	-	-	-	-	-	-	150°
	33.2	11.8	-	15.2	0,36	-	0,76	-	2,14	-	-	8	-	0	-	13	170°
G.P.A. AW64	123.4	44.8	-	53.1	0,36	?	0,43	?	1,19	3.4	21	12	0	2	15	5	
	93.6	34.7	-	40.9	0,37	?	0,44	?	1,18	2	18	10	3	2	18	9	90°
	75.1	28	-	32.5	0,37	?	0,43	?	1,16	1.5	16	9	5	2	15	10	90°
	57.5	21.2	-	24	0,37	?	0,42	?	1,13	0.7	18	8	6	1	11	9	90°
	47.1	16.6	-	20.5	0,35	?	0,44	?	1,24	0.5	24	9	6	3	7	7	90°
	35.1	12.3	-	16.2	0,35	?	0,46	?	1,32	0.5	31	10	5	5	3	3	90°
	29.6	9.3	-	15	0,31	?	0,51	?	1,61	0.3	37	17	3	3	1	1	90°

No.	D	H	W	U	*H/D*	*W/D*	*U/D*	*W/H*	*U/H*	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
G.P.A. AW64	22.7	6.7	-	11.3	0,30	?	0,50	?	1,69	-	-	21	-	0	-	0	90°
G.P.A. AY67	119	43.1	-	52.4	0,36	?	0,44	?	1,22	2.4	20	11	1	0	10	8	
G.P.A. AT36	117.8	35.4	-	54	0,30	?	0,46	?	1,53	5.5	19	10	0	0	10	3	
	93.6	30.6	-	42.4	0,33	?	0,45	?	1,39	3.2	17	9	0	0	15	6	90°
	75.6	27.1	-	34.4	0,36	?	0,46	?	1,27	1.3	18	9	0	0	15	7	90°
	58.9	20.2	-	26.5	0,34	?	0,45	?	1,31	0	19	8	0	0	15	8	90°
	47.6	15	-	22.2	0,32	?	0,47	?	1,48	0	20	9	0	0	18	8	90°
	38	12	-	16.6	0,32	?	0,44	?	1,38	0	28	11	0	0	12	7	90°
28734	117.7	37.8	31.4	-	0,32	0,27	?	0,83	?	11	-	-	-	-	-	-	
	50.3	14.8	-	24.4	0,29	?	0,49	?	1,65	2.3	-	9	-	0	-	3	315°
	32.9	11	-	17	0,33	?	0,52	?	1,55	0.6	-	-	-	-	-	-	180°
	20.1	5	-	11.2	0,25	?	0,56	?	2,24	-	-	24	-	0	-	2	230°
G.P.A. AW82	113.4	37.1	-	47	0,33	?	0,42	?	1,27	2.6	-	10	-	1	-	4	
	71	25.8	23.5	29.5	0,36	0,33	0,42	0,91	1,14	0.7	-	-	-	-	-	-	180°
	44.5	16.4	16	19.9	0,37	0,36	0,45	0,98	1,21	-	-	8	-	1	-	10	180°
G.P.A. AZ40	110	35.5	-	48.7	0,32	-	0,44	-	1,37	4.1	19	11	4	4	-	-	
	88.6	32.3	-	34.9	0,36	-	0,39	-	1,08	-	-	8	-	2	-	-	90°
	50.9	17.3	-	24.6	0,34	-	0,48	-	1,42	1	-	-	-	-	-	-	180°
	43.8	14.7	-	19.9	0,34	-	0,45	-	1,35	0.6	-	-	-	-	-	-	90°
G.P.A. AW89	106.3	36	-	48.1	0,34	?	0,45	?	1,34	3	20	10	0	0	12	7	
	67.2	22.9	22.5	31.9	0,34	0,34	0,48	0,98	1,39	3	19	10	0	0	13	5	180°
	53.5	18.5	-	24.4	0,35	?	0,46	?	1,32	1.5	21	10	0	0	14	6	90°
	41.9	12.8	-	20.7	0,31	?	0,49	?	1,62	-	22	10	0	0	17	9	90°
G.P.A. AW75	105.5	35.5	25.4	51.6	0,34	0,24	0,49	0,72	1,45	7.2	-	-	-	-	-	-	
Barr-11	101.8	34.2	-	45.3	0,34	?	0,45	?	1,33	5	17	9	0	0	15	6	
	78	28.4	25.4	38.9	0,36	0,33	0,50	0,89	1,37	5.6	21	13	1	0	16	8	90°
G.P.A. AP46	99.3	34.9	-	45.9	0,35	?	0,46	?	1,32	7.3	26	14	0	0	26	15	
	81.4	29.3	27.9	38.2	0,36	0,34	0,47	0,95	1,30	5.9	26	13	0	0	23	14	90°
	58.1	20	-	28.1	0,34	?	0,48	?	1,41	2	25	12	0	0	21	13	90°
	46.5	15.2	-	20.9	0,33	?	0,45	?	1,38	2	28	12	0	0	13	9	90°
	36.2	11.7	-	17.1	0,32	?	0,47	?	1,46	1.8	31	13	0	0	10	7	90°
G.P.A. AY39	99	30.7	-	45.4	0,31	?	0,46	?	1,48	3.3	21	9	1	1	4	3	
	66.2	25.2	20.8	28.7	0,38	0,31	0,43	0,83	1,14	1.8	24	12	0	0	5	1	180°
G.P.A. AY04	93.7	33.3	25.4	44.7	0,36	0,27	0,48	0,76	1,34	4.2	-	10	-	0	-	6	
G.P.A. AZ22	93.3	29.1	-	44.7	0,31	?	0,48	?	1,54	6.3	24	13	0	0	5	1	
	75.7	23.7	-	37.3	0,31	?	0,49	?	1,57	4.5	23	12	1	0	4	1	90°
	58.3	20	-	27.2	0,34	?	0,47	?	1,36	2.4	24	11	1	0	5	3	90°

No.	D	H	W	U	*H/D*	*W/D*	*U/D*	*W/H*	*U/H*	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
G.P.A. AZ22	47.8	15.7	-	22.9	0,33	?	0,48	?	1,46	1.3	25	11	1	1	5	0	90°
	36.3	11.5	-	17.9	0,32	?	0,49	?	1,56	1.1	27	13	1	1	3	0	90°
	30.8	10	-	15.6	0,32	?	0,51	?	1,56	1	30	13	0	0	1	1	90°
UH	93.2	32.9	29.6	40.7	0,35	0,32	0,44	0,90	1,24	3.1	15	8	1	0	20	14	
	72.1	25.2	-	31.4	0,35	?	0,44	?	1,25	3.1	17	7	1	0	17	12	90°
	57.5	19.9	-	27.1	0,35	?	0,47	?	1,36	2.2	22	8	1	1	10	6	90°
	42.8	13.6	-	22.5	0,32	?	0,53	?	1,65	-	-	10	-	1	-	4	90°
	34.5	11.2	-	19.6	0,33	?	0,57	?	1,75	-	-	13	-	0	-	4	90°
G.P.A. AY10	92.1	33.2	25.6	37.3	0,36	0,28	0,41	0,77	1,12	1	15	8	0	0	25	15	
	74.7	29.1	22.5	29	0,39	0,30	0,39	0,77	1,00	4	15	7	3	0	21	13	90°
G.P.A. AZ38	92.1	32.9	-	39.1	0,36	-	0,42	-	1,19	2.5	-	-	-	-	-	-	
	72.2	26.8	-	29.5	0,37	-	0,41	-	1,10	1.8	-	-	-	-	-	-	90°
	56.1	20.7	-	23.8	0,37	-	0,42	-	1,15	1.5	-	-	-	-	-	-	90°
	42.2	15.1	-	18.6	0,36	-	0,44	-	1,23	0.9	-	-	-	-	-	-	90°
	33.1	11.8	-	15.4	0,36	-	0,47	-	1,31	-	-	-	-	-	-	-	90°
G.P.A. AW71	90.7	31	-	39.2	0,34	?	0,43	?	1,27	3.8	21	10	0	0	10	7	
	73.1	26	-	31.1	0,36	?	0,43	?	1,20	2	21	10	0	0	9	7	90°
	56.3	20.6	19	24.6	0,37	0,34	0,44	0,92	1,19	1.3	22	11	0	0	5	3	90°
	44.4	15.8	-	19.8	0,36	?	0,45	?	1,25	0.5	24	11	0	0	7	5	90°
	34.5	11.4	-	15.5	0,33	?	0,45	?	1,36	0.3	27	11	0	0	5	5	90°
	28.4	9.8	-	13.5	0,35	?	0,48	?	1,38	0	31	13	0	0	2	2	90°
	23	7.4	-	11.5	0,32	?	0,50	?	1,55	0	35	15	0	0	0	0	90°
	19	6	-	9.5	0,32	?	0,50	?	1,58	-	-	19	-	0	-	0	90°
G.P.A. VLS 005	88	30.8	30.6	38	0,35	0,35	0,43	0,99	1,23	-	-	-	-	-	-	-	
	39.1	12.7	14.1	17.5	0,33	0,36	0,45	1,11	1,38	0.2	-	11	-	2	-	2	320°
sp. Pénagé's coll.	86.8	29.7	23.3	40.7	0,34	0,27	0,47	0,79	1,37	2.2	19	10	5	0	11	4	
	66.8	21.9	18.3	30.7	0,33	0,27	0,46	0,84	1,40	0	16	9	10	0	12	9	90°
	57.2	17.4	16	25.7	0,30	0,28	0,45	0,92	1,48	0	19	6	9	6	12	9	90°
	43	15.1	13.6	19	0,35	0,32	0,44	0,90	1,26	0.1	35	12	8	6	2	2	90°
	39	12.7	9.9	18.7	0,33	0,25	0,48	0,78	1,47	-	-	18	-	4	-	0	90°
CEM 2	86	28.3	-	40.4	0,33	?	0,47	?	1,43	3	18	9	0	0	17	9	
	62.6	21	20	28.3	0,34	0,32	0,45	0,95	1,35	1.2	18	9	1	0	16	9	135°
	50.6	17.1	16.2	23	0,34	0,32	0,46	0,95	1,35	1	22	10	1	0	13	8	90°
	38.9	13.3	12.2	18.3	0,34	0,31	0,47	0,92	1,38	1	26	10	1	1	8	6	90°
	31.5	10.6	-	15.9	0,34	?	0,51	?	1,50	0.5	32	12	0	0	5	5	90°
G.P.A. AX17	83.4	30.6	-	37	0,37	?	0,44	?	1,21	3	19	9	1	1	18	12	
	60	22	-	26.5	0,37	?	0,44	?	1,21	1.5	20	9	0	0	17	10	90°
	47.6	15	-	23.7	0,32	?	0,40	?	1,58	2	29	11	0	0	7	6	90°
G.P.A. AW68	82.4	27	24.4	38.3	0,33	0,30	0,47	0,90	1,42	2.7	17	9	16	10	16	7	
	61.5	21.8	19	28.2	0,36	0,31	0,46	0,87	1,29	1.6	17	6	13	11	17	10	90°

No.	D	H	W	U	*H/D*	*W/D*	*U/D*	*W/H*	*U/H*	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
G.P.A. AW68	52.8	17.3	16	24.5	0,33	0,30	0,46	0,93	1,42	2.4	22	8	6	6	16	9	90°
	38.5	13	11.5	17.9	0,34	0,30	0,47	0,89	1,38	1	29	10	2	2	9	7	90°
	33.4	11	9.5	16	0,33	0,28	0,48	0,86	1,45	0.5	35	14	0	0	6	6	90°
	25.5	8.4	-	12.3	0,33	?	0,48	?	1,46	0.3	42	18	0	0	2	2	90°
G.P.A. AW60	80.6	28.6	-	35.7	0,36	?	0,44	?	1,25	1.7	-	-	-	-	-	-	
	47.1	16.3	13.9	20.6	0,35	0,30	0,44	0,85	1,26	-	-	-	-	-	-	-	220°
G.P.A. AW57	76.7	25.9	25.4	34.4	0,34	0,33	0,45	0,98	1,33	3.3	21	10	1	0	5	4	
	59.9	21	15.1	26.9	0,35	0,25	0,45	0,72	1,28	2.9	21	11	2	0	3	2	90°
	47	16.4	13	21.8	0,35	0,28	0,46	0,79	1,33	1.6	22	11	4	1	2	1	90°
	35.9	11.6	11.6	16.6	0,32	0,32	0,46	1,00	143,10	1.5	26	10	4	2	1	1	90°
	29.2	9.4	-	14.3	0,32	?	0,49	?	1,52	1	32	11	3	3	0	0	90°
	22.6	7.5	-	12.4	0,33	?	0,55	?	1,65	0.7	32	16	2	2	0	0	90°
	19.8	5.9	-	10	0,30	?	0,51	?	1,70	-	-	21	-	0	-	0	90°
I.D.161	71.1	26.2	-	29.4	0,37	?	0,41	?	1,12	3	-	10	-	0	-	11	
	28	10.3	-	12.4	0,37	?	0,44	?	1,20	0	30	13	0	0	1	1	360°
sp. Coullet's coll.	68.8	22.3	-	32.8	0,32	?	0,48	?	1,47	4.2	-	10	-	2	-	6	
	27.4	9.6	-	13.8	0,35	?	0,50	?	1,44	1	26	12	1	1	0	0	310°
G.P.A. AW72	68.4	24.5	19.9	30.6	0,36	0,29	0,45	0,85	1,25	3.2	-	9	-	0	-	11	
G.P.A. AW81	68.4	24.8	20.1	30.5	0,36	0,29	0,45	0,81	1,23	1.3	-	-	-	-	-	-	
	53.8	19.7	18.6	23.7	0,37	0,35	0,44	0,94	1,20	0.7	-	-	-	-	-	-	90°
	41.5	14.5	-	18.5	0,35	?	0,45	?	1,28	0.1	23	11	1	0	9	5	105°
	33.3	11.8	10	15.6	0,35	0,30	0,47	0,85	1,32	0.1	29	11	1	1	5	5	90°
	26.8	8	7.8	12.7	0,30	0,29	0,47	0,98	1,59	0	37	14	0	0	6	6	90°
G.P.A. AW62	63.8	20.8	-	29.3	0,33	?	0,46	?	1,41	-	-	7	-	1	-	4	
G.P.A. TAI 183	55.7	18.5	20.8	23.6	0,33	0,37	0,42	1,12	1,28	0	-	8	-	1	-	3	
	45.6	16.9	17.9	19.6	0,37	0,39	0,43	1,06	1,16	0	-	7	-	2	-	5	90°
G.P.A. AX10	55	19.4	-	25.1	0,35	?	0,46	?	1,29	1.5	23	11	0	0	15	7	
	46.4	15	-	22	0,32	?	0,47	?	1,47	2	28	11	0	0	11	8	90°
G.P.A. AW66	54.2	21	-	20.6	0,39	?	0,38	?	0,98	0.8	23	10	7	2	2	2	
	41	15.1	14	17	0,37	0,34	0,42	0,93	1,13	0.3	27	10	5	3	2	2	90°
	32.6	11.8	12.7	14.2	0,36	0,39	0,44	1,08	1,20	0.1	-	13	-	5	0	0	90°
G.P.A. TAI 190	52.5	17	18.6	24.1	0,32	0,35	0,46	1,09	1,42	0.5	/	10	/	0	/	10	
G.P.A. AW58	51.7	19.5	-	23.9	0,38	?	0,46	?	1,23	1.6	-	-	-	-	-	-	
G.P.A. AW65	39.7	14	15	16.7	0,35	0,38	0,42	1,07	1,19	-	-	-	-	-	-	-	

No.	D	H	W	U	*H/D*	*W/D*	*U/D*	*W/H*	*U/H*	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
G.P.A. AW74	31.8	10.8	-	15.2	0,34	?	0,48	?	1,41	0.2	32	14	1	1	4	4	
	25.5	8.5	-	12	0,33	?	0,47	?	1,41	0.1	37	17	0	0	0	1	90°
	21.2	6.6	-	10.6	0,31	?	0,50	?	1,61	0.1	44	18	0	0	0	0	90°
	16.8	5.6	-	8.6	0,33	?	0,51	?	1,54	0.1	48	21	0	0	0	0	90°
	14.7	4.2	-	8.1	0,29	?	0,55	?	1,93	-	-	25	-	0	-	0	90°
G.P.A. AX35	31.6	9.3	-	15.5	0,29	?	0,49	?	1,67	-	-	13	-	0	-	2	
G.P.A. AX13	25	8	-	12.6	0,32	?	0,50	?	1,58	-	-	17	-	0	-	0	
Mean					*0,34*	*0,31*	*0,47*	*0,89*	*1,40*								
Standard deviation					*0,03*	*0,04*	*0,04*	*0,10*	*0,20*								
coefficients of variation					*7,45*	*13,68*	*8,47*	*11,39*	*14,32*								

Appendix 2b. Table of measurements for *Gassendiceras multicostatum* (Sarkar, 1955)

No.	D	H	W	U	H/D	W/D	U/D	W/H	U/H	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
GJ	265	94	77,4	113,6	0,35	0,29	0,43	0,82	1,21	2	-	-	-	-	-	-	
	123,8	45,4	35,9	50,3	0,37	0,29	0,41	0,79	1,11	2	-	12	-	0	-	0	335°
1225	140,8	46,2	36,5	67,3	0,33	0,26	0,48	0,79	1,46	6	23	13	0	0	3	0	
	107	36,4	32,1	51,5	0,34	0,30	0,48	0,88	1,41	3	20	11	0	0	6	2	90°
	82,1	29,4	26,7	41,5	0,36	0,33	0,51	0,91	1,41	2,5	19	10	0	0	9	3	90°
	70,8	22,5	21	34,5	0,32	0,30	0,49	0,93	1,53	2,7	19	9	0	0	12	7	90°
	58,6	20,2	-	27,2	0,34	-	0,46	-	1,35	1,6	19	9	0	0	8	7	90°
	46,5	14,3	-	21,9	0,31	-	0,47	-	1,53	-	21	10	0	0	6	5	90°
UJ	132,2	48,1	-	54,7	0,36	-	0,41	-	1,14	3,9	-	-	-	-	-	-	
	105	39,8	31,3	46,3	0,38	0,30	0,44	0,79	1,16	-	-	-	-	-	-	-	90°
	78,9	29	21	33,7	0,37	0,27	0,43	0,72	1,16	-	-	-	-	-	-	-	90°
28749	125,4	42	40,5	56,5	0,33	0,32	0,45	0,96	1,35	5,3	25	13	0	0	0	0	
	102,7	38,2	34,9	46,5	0,37	0,34	0,45	0,91	1,22	4	24	12	0	0	1	0	90°
	78,8	28,7	26,5	35	0,36	0,34	0,44	0,92	1,22	1,7	24	12	0	0	2	0	90°
	62,7	21,5	-	28,5	0,34	-	0,45	-	1,33	1,3	26	12	0	0	2	1	90°
	48	16	-	22,5	0,33	-	0,47	-	1,41	1,1	28	12	0	0	2	2	90°
	38	13,6	-	18,8	0,36	-	0,49	-	1,38	-	-	14	-	0	-	1	90°
136	124,9	43,4	43,7	55,5	0,35	0,35	0,44	1,01	1,28	4	23	13	0	0	0	0	
	99,4	34,6	36,4	43,2	0,35	0,37	0,43	1,05	1,25	2,6	22	12	0	0	0	0	90°
	78,7	26,8	31,8	34,3	0,34	0,40	0,44	1,19	1,28	1,7	-	10	-	0	-	0	90°
	59	22,2	24	25,2	0,38	0,41	0,43	1,08	1,14	0,7	-	10	-	-	-	-	90°
	51	18,5	-	20,4	0,36	-	0,40	-	1,10	-	-	-	-	-	-	-	90°
AW48	111,1	36,8	-	49,4	0,33	-	0,44	-	1,34	6,5	22	11	1	1	8	5	
	88,7	30,4	24,4	39,8	0,34	0,28	0,45	0,80	1,31	6,6	22	10	1	1	9	4	90°
	67	23,6	17,5	29,7	0,35	0,26	0,44	0,74	1,26	3,7	25	11	0	0	6	4	90°
	51,9	18,8	15,7	23	0,36	0,30	0,44	0,84	1,22	1,6	26	12	0	0	5	5	90°
	40,5	13,8	12,2	18,4	0,34	0,30	0,45	0,88	1,33	1	30	14	0	0	2	2	90°
	31,9	10,4	7,2	15,3	0,33	0,23	0,48	0,69	1,47	-	-	15	-	0	-	0	90°
AW50	95	33,7	30,5	42,6	0,35	0,32	0,45	0,91	1,26	2,4	19	9	0	0	4	3	
	76,1	26,4	20,3	33,7	0,35	0,27	0,44	0,77	1,28	1,4	19	9	0	0	2	1	90°
	49,2	16,3	13,7	22,4	0,33	0,28	0,46	0,84	1,37	1	22	10	0	0	1	1	180°
	38,7	13	10,3	18	0,34	0,27	0,47	0,79	1,38	-	23	11	0	0	0	0	90°
	31,8	10,4	8	15,7	0,33	0,25	0,49	0,77	1,51	-	-	12	-	0	-	0	90°
140	93,3	31,6	32	42,3	0,34	0,34	0,45	1,01	1,34	-	-	10	-	0	-	1	
	73,4	25,6	26,6	33,1	0,35	0,36	0,45	1,04	1,29	-	-	12	-	0	-	2	90°
AW45	90	28,7	28,3	41,2	0,32	0,31	0,46	0,99	1,44	3	-	11	-	1	-	5	
	57,9	19,8	18	25,3	0,34	0,31	0,44	0,91	1,28	0,1	-	-	-	-	-	-	180°
Mean					0,35	0,32	0,45	0,90	1,29								
Standard deviation					0,02	0,05	0,03	0,12	0,12								
Coefficient of variation					4,95	14,62	5,90	13,24	9,63								

Appendix 2c. Table of measurements for *Gassendiceras* aff. *hoheneggeri* (Uhlig, 1883)

No.	D	H	W	U	H/D	W/D	U/D	W/H	U/H	h	α
	282,4	67,1	-	177	0,24	-	0,63	-	2,64	83,8	
	319	70,2	-	195	0,22	-	0,61	-	2,78	105,8	40°
sp. Davoux's coll.	285	73	-	184,9	0,26	-	0,65	-	2,53	102,4	25°
	214	70,5	-	119,7	0,33	-	0,56	-	1,70	38,3	30°
	c.183	c.	-	-	-	-		-	-	11,4	35°
	133.5	44.9	-	64.4	0,34	-	0,48	-	1,43	6,8	90°
	102.7	33.4	-	53.8	0,33	-	0,52	-	1,61	10,7	90°
	80.6	25	-	38.3	0,31	-	0,48	-	1,53	5,5	90°
	58.6	16.9	-	31.3	0,32	-	0,53	-	1,68	3,7	90°
	49.8	16.1	-	24.5	0,34	-	0,50	-	1,48	-	90°

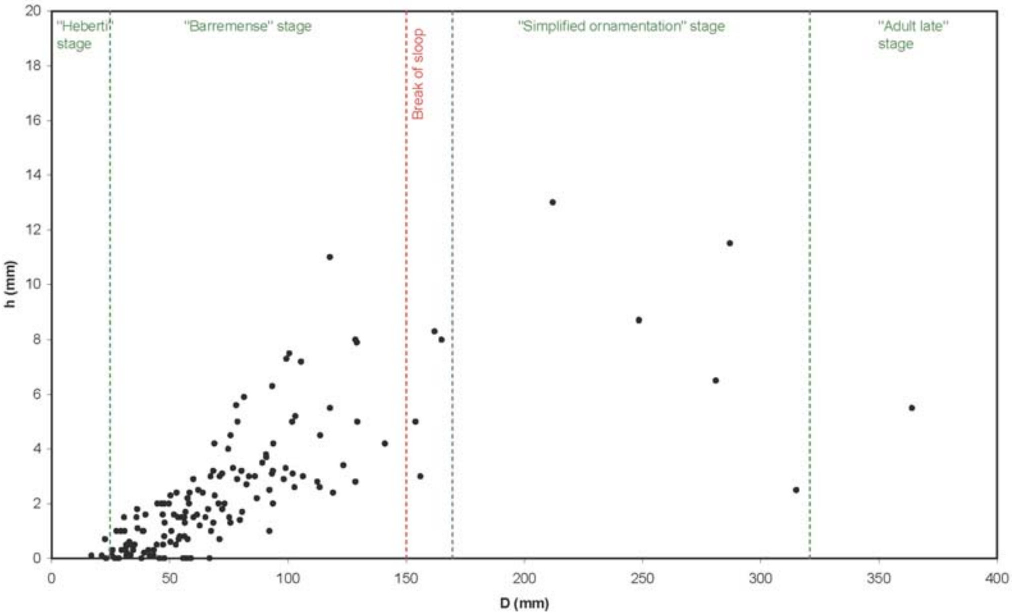
Appendix 2d. Table of measurements for *Gassendiceras rebouleti* nov. sp.

No.	D	H	W	U	H/D	W/D	U/D	W/H	U/H	h	Nt	Nt/2	Nit	Nit/2	Ni	Ni/2	α
	337	96	-	180	0,28	-	0,53	-	1,88	39	-	-	-	-	-	-	
	346	90	-	198	0,26	-	0,57	-	2,20	69	-	-	-	-	-	-	40°
	271	89	-	131	0,33	-	0,48	-	1,47	20,5	-	-	-	-	-	-	90°
104	203	67	-	100	0,33	-	0,49	-	1,49	12,6	-	-	-	-	-	-	90°
	158	48	-	75	0,30	-	0,47	-	1,56	12	-	-	-	-	-	-	90°
	125	37	-	63	0,30	-	0,50	-	1,70	-	-	-	-	-	-	-	90°
	98	35	-	44	0,36	-	0,45	-	1,26	-	-	-	-	-	-	-	90°
AW43 (holotype)	267	69	-	153	0,26	-	0,57	-	2,22	52	-	-	-	-	-	-	
	154	46	-	76	0,30	-	0,49	-	1,65	13	-	-	-	-	-	-	150°
Mean					0,30	-	0,51	-	1,71								

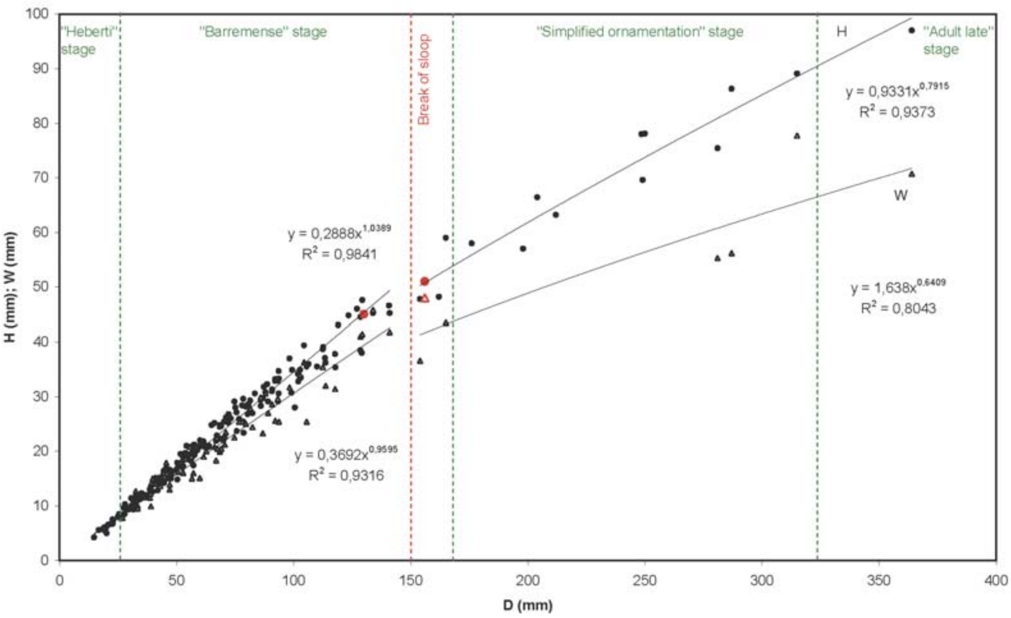
Appendix 2e. Table of measurements for *Gassendiceras bosellii* nov. sp.

No.	D	H	W	U	H/D	W/D	U/D	W/H	U/H	h	α
	294	88	77	141	0,30	0,26	0,10	0,88	1,60	29	
17252	301	85	78	149	0,28	0,26	0,15	0,92	1,75	44	40°
	278	83	70,5	135,5	0,30	0,25	0,15	0,85	1,63	42	40°
	167	68,7	55,8	80	0,41	0,33	0,05	0,81	1,16	9	90°
AZ27 (holotype)	210	69	46,7	98,5	0,33	0,22	0,47	0,68	1,43	19,7	
	77,2	18	-	44	0,23	-	0,57	-	2,44	-	310°
	165	55,1	-	79	0,33	-	0,48	-	1,43	8	
	125,5	44,7	-	59,2	0,36	-	0,47	-	1,32	5,8	90°
AW53	102,5	33,7	-	51,4	0,33	-	0,50	-	1,53	-	90°
	75	23	-	37,7	0,31	-	0,50	-	1,64	-	90°
	60,3	17,7	-	30,4	0,29	-	0,50	-	1,72	-	90°
Mean					0,32	0,27	0,36	0,83	1,61		

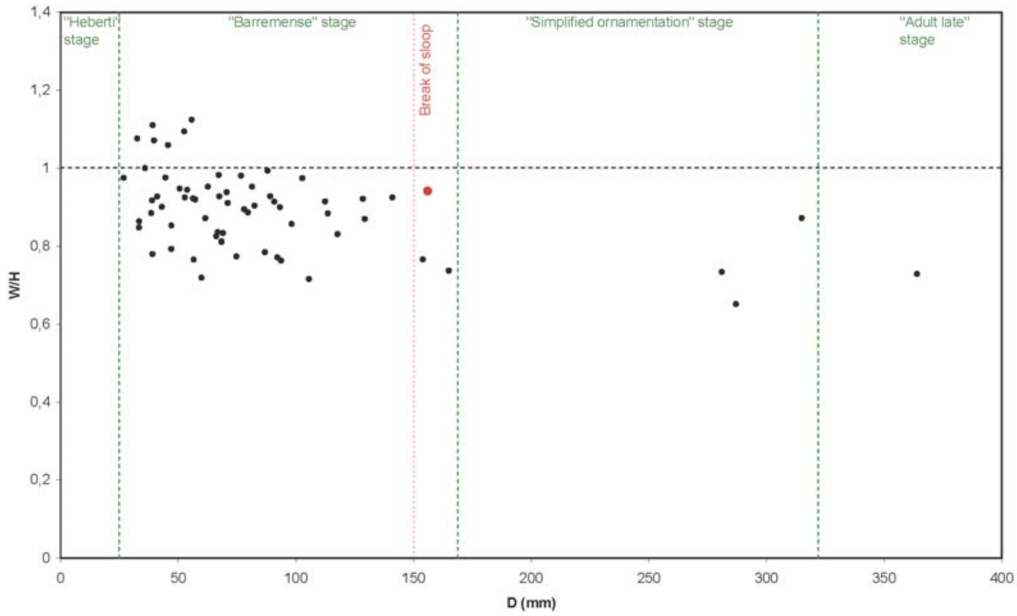
Appendix 3a. Crossplot of spiral gap (h, mm) against diameter (D, mm) for *Gassendiceras alpinum* (d'Orbigny, 1850)



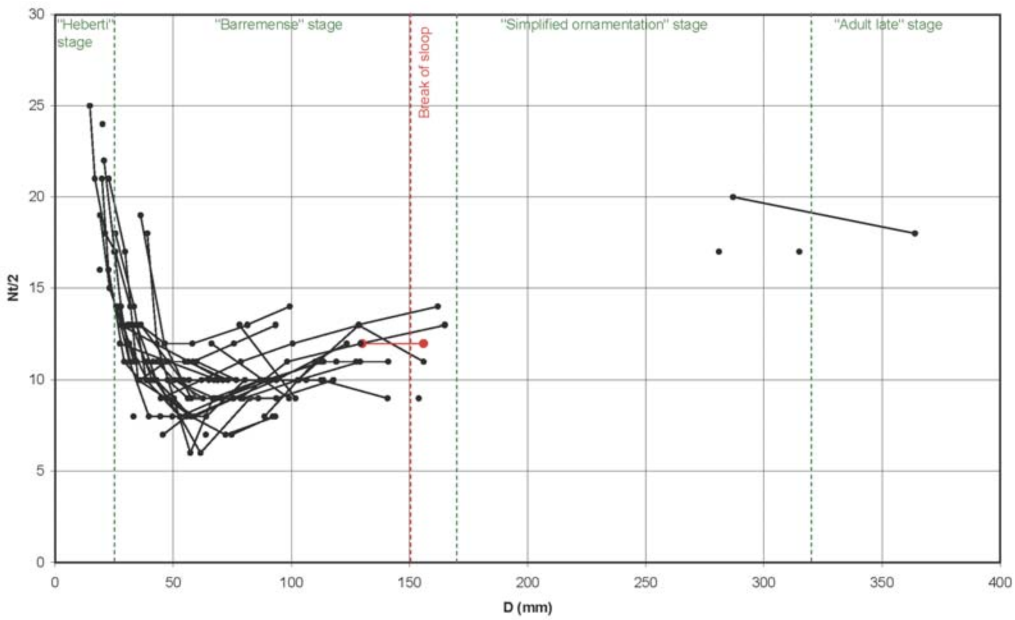
Appendix 3b. Crossplot of height (H, mm) and width (W, mm) against diameter (D, mm) for *Gassendiceras alpinum* (d'Orbigny, 1850). In red is the Lectotype



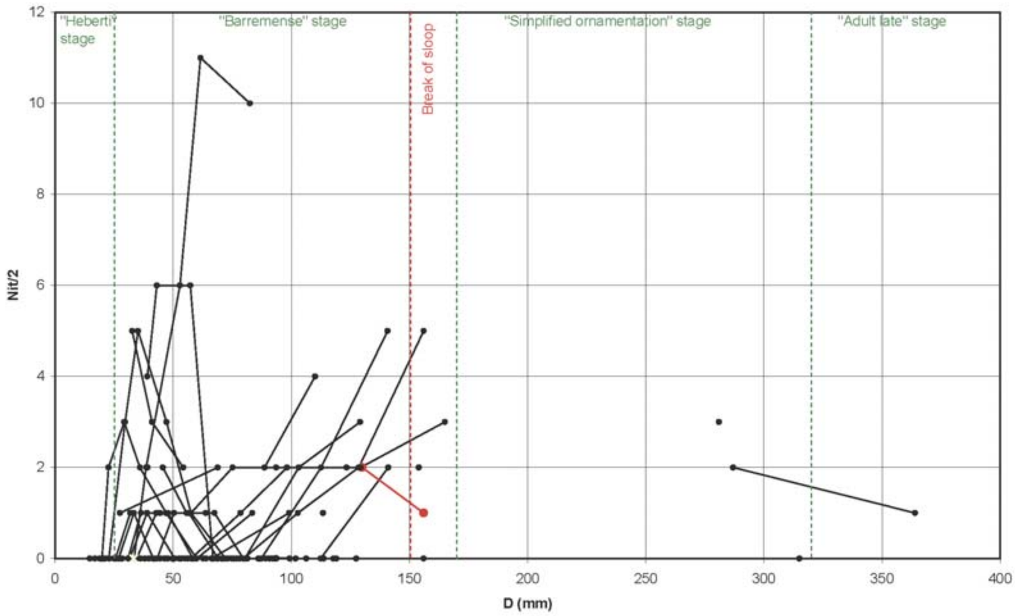
Appendix 3c. Crossplot of relative section (W/H) against diameter (D, mm) for *Gassendiceras alpinum* (d'Orbigny, 1850). In red is the Lectotype



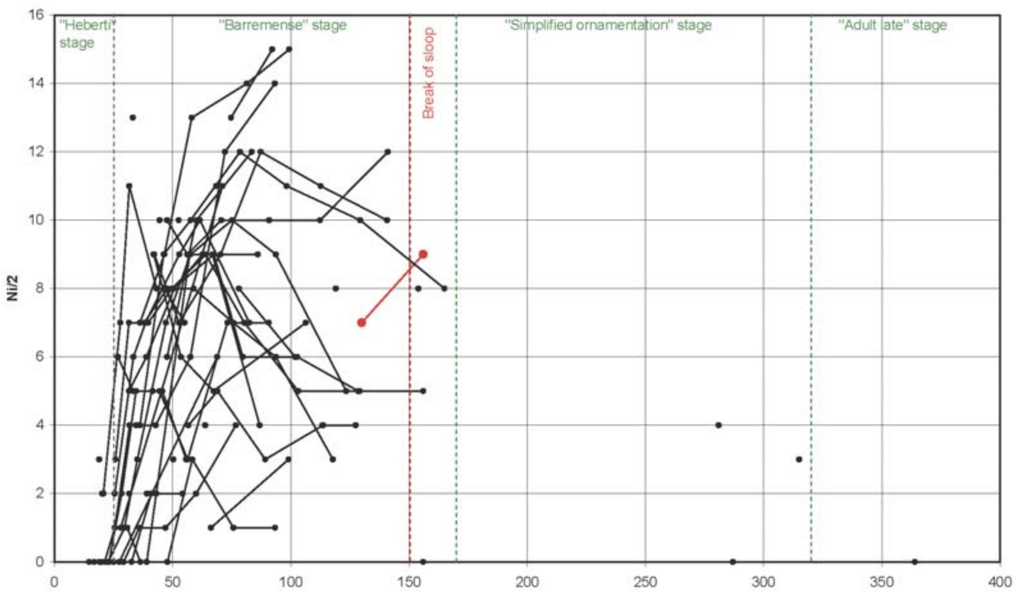
Appendix 3d. Crossplot of umbilicus (U, mm) against diameter (D, mm) for *Gassendiceras alpinum* (d'Orbigny, 1850). In red is the Lectotype



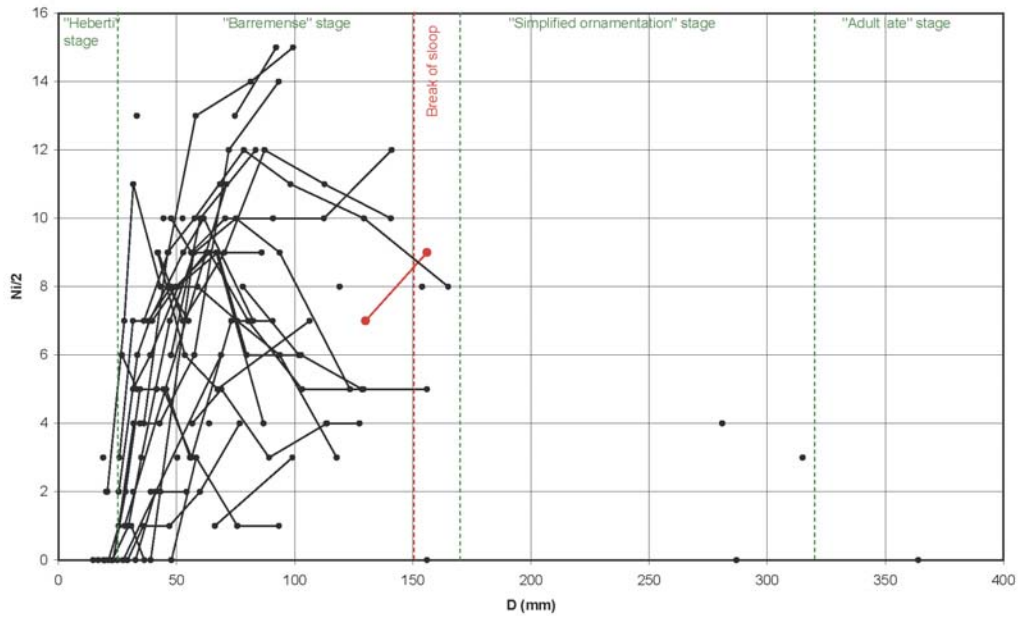
Appendix 3e. Number of main ribs (Nt/2) in function of diameter (D, mm) for *Gassendiceras alpinum* (d'Orbigny, 1850). In red is the Lectotype



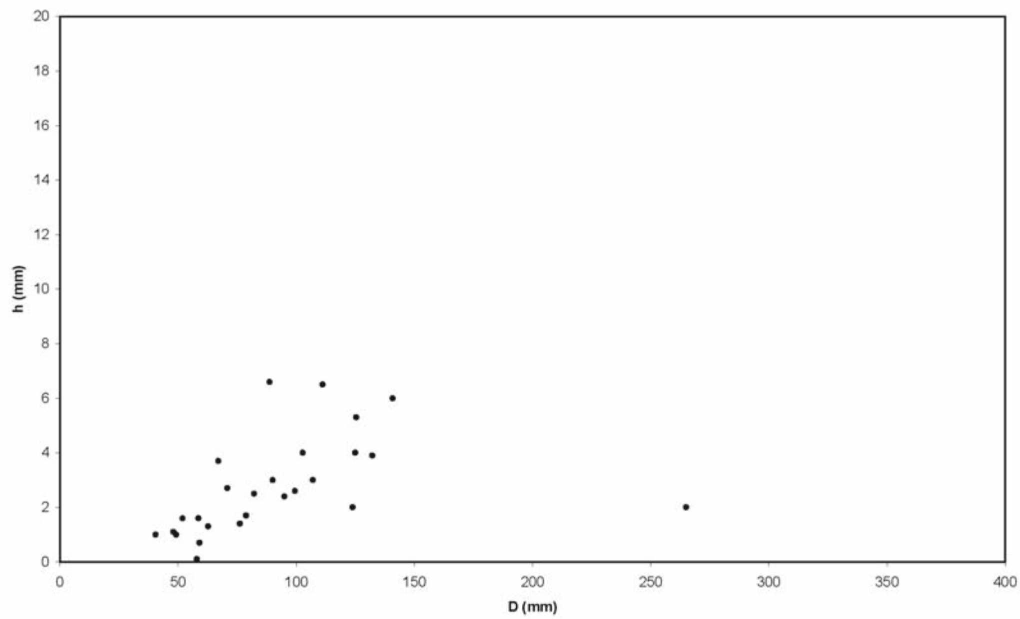
Appendix 3f. Crossplot of number of low tuberculate ribs (Nit/2) against diameter (D, mm) for *Gassendiceras alpinum* (d'Orbigny, 1850). In red is the Lectotype



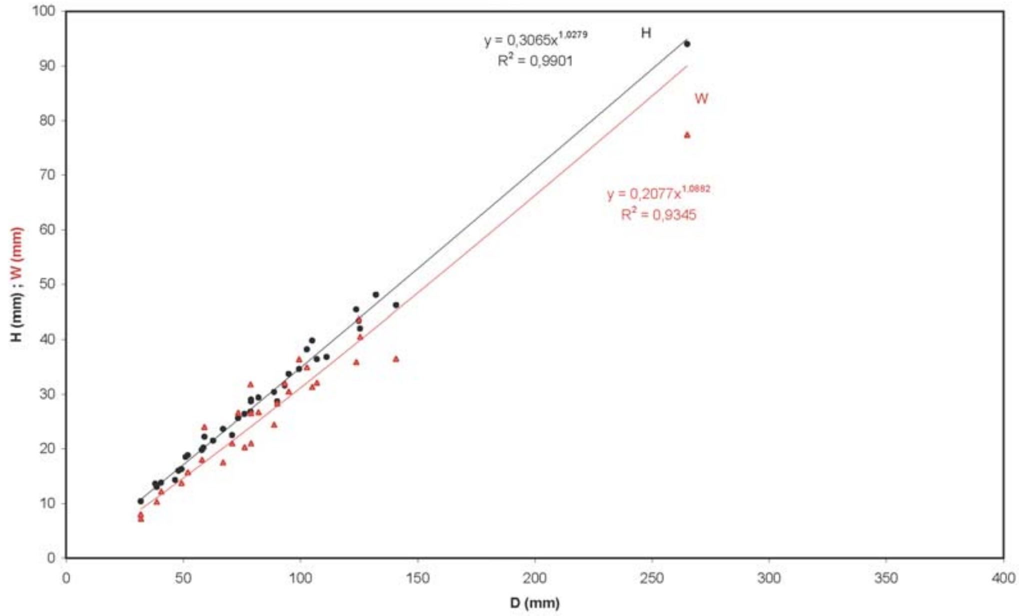
Appendix 3g. Crossplot of number of innermous interribs (N/2) against diameter (D, mm) for *Gassendiceras alpinum* (d'Orbigny, 1850). In red is the Lectotype



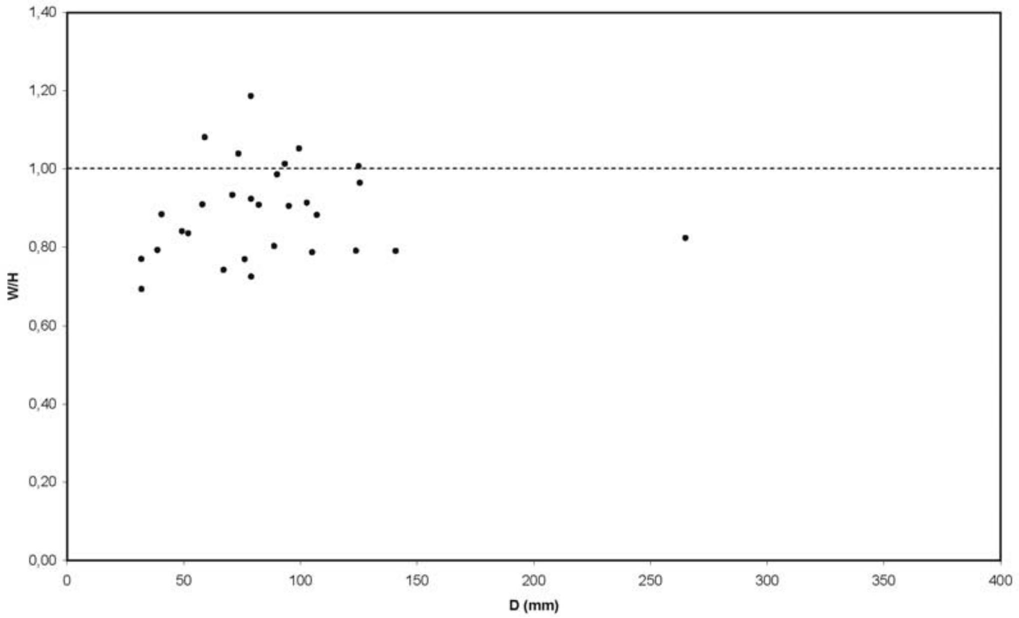
Appendix 4a. Crossplot of spiral gap (h, mm) against diameter (D, mm) for *Gassendiceras multicostatum* (Sarkar, 1955)



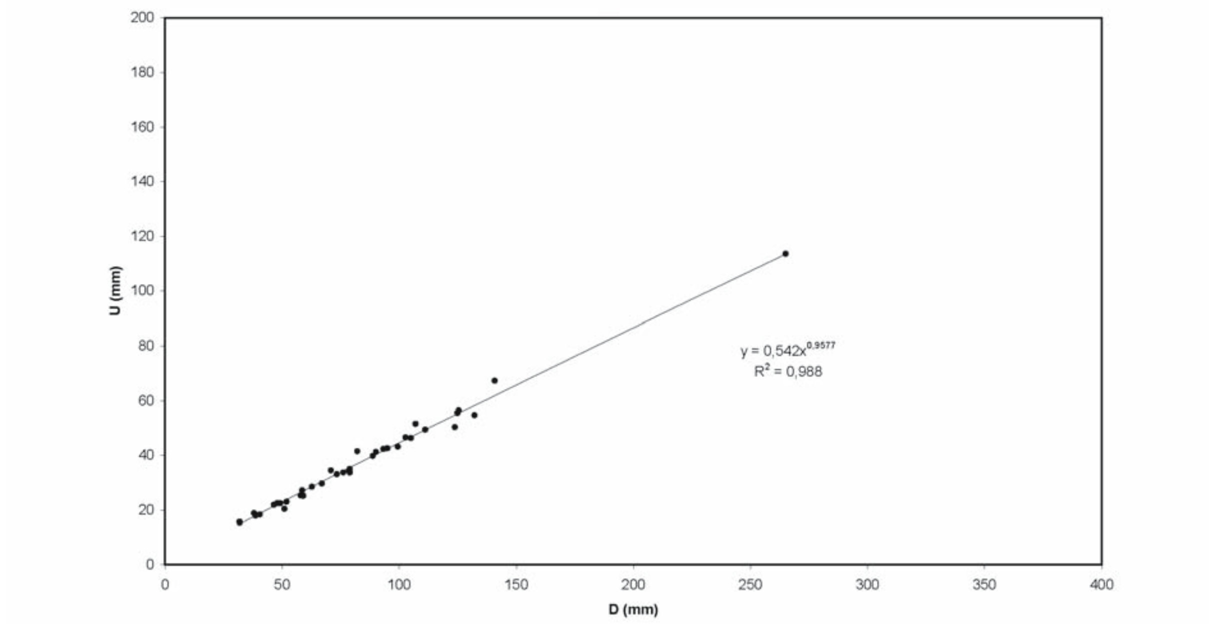
Appendix 4b. Crossplot of height (black circles - H, mm) and witdh (red triangles - W, mm) against diameter (D, mm) for *Gassendiceras multicostatum* (Sarkar, 1955)



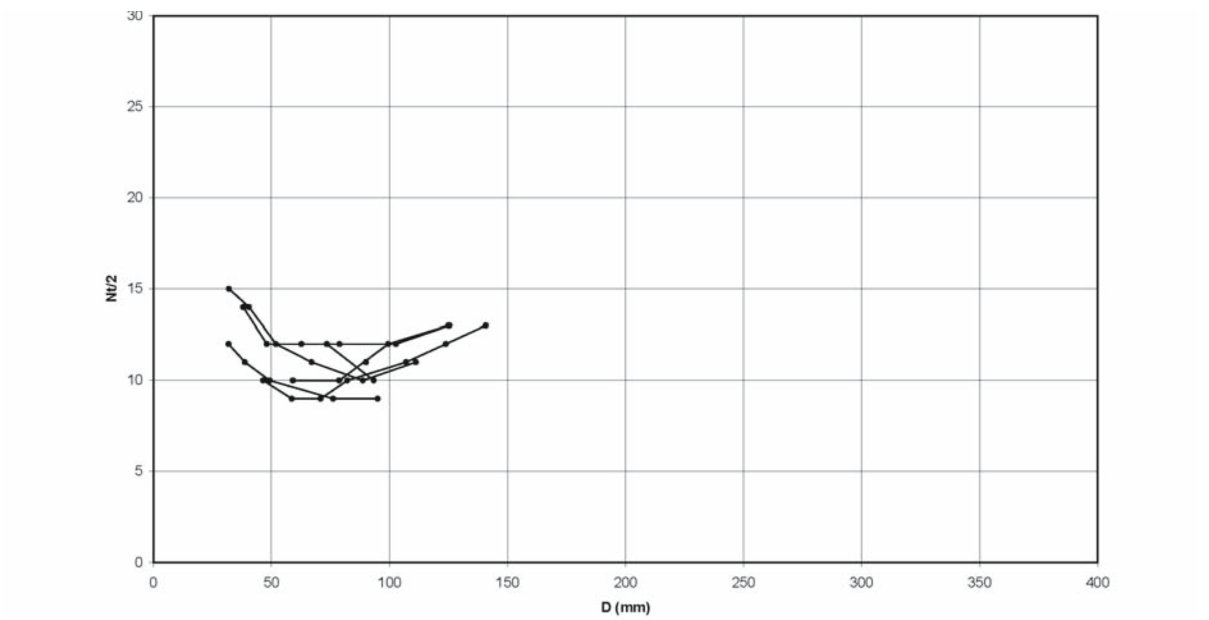
Appendix 4c. Crossplot of relative section (W/H) against diameter (D, mm) for *Gassendiceras multicostatum* (Sarkar, 1955)



Appendix 4d. Crossplot of umbilicus (U, mm) against diameter (D, mm) for *Gassendiceras multicostatum* (Sarkar, 1955)



Appendix 4e. Crossplot of number of main ribs (Nt/2) against diameter (D, mm) for *Gassendiceras multicostatum* (Sarkar, 1955)



Appendix 4f. Crossplot of number of innermous interribs (N/2) against diameter (D, mm) for *Gassendiceras multicostatum* (Sarkar, 1955)

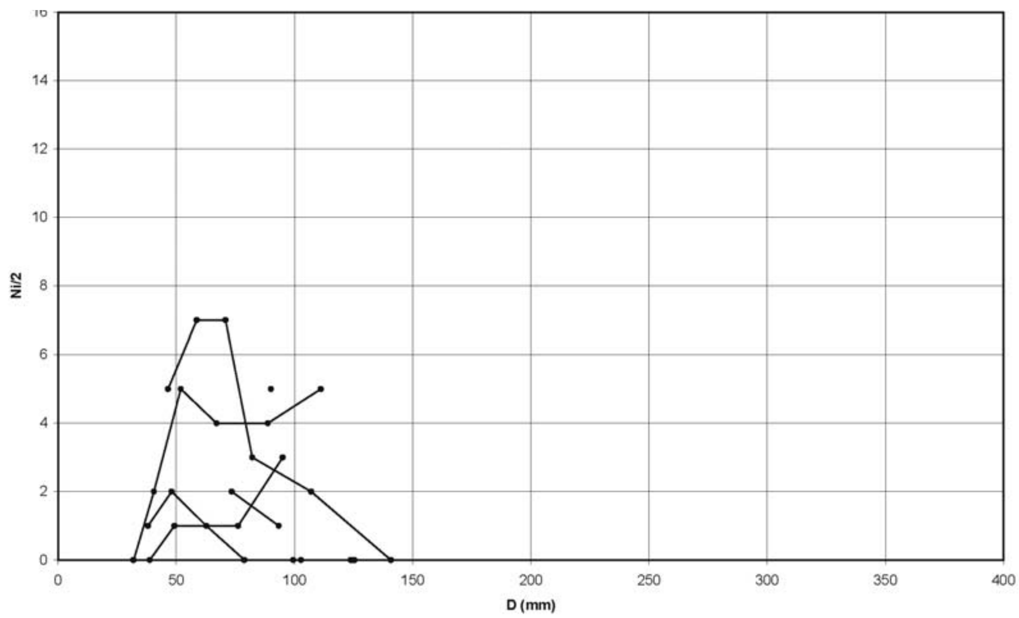


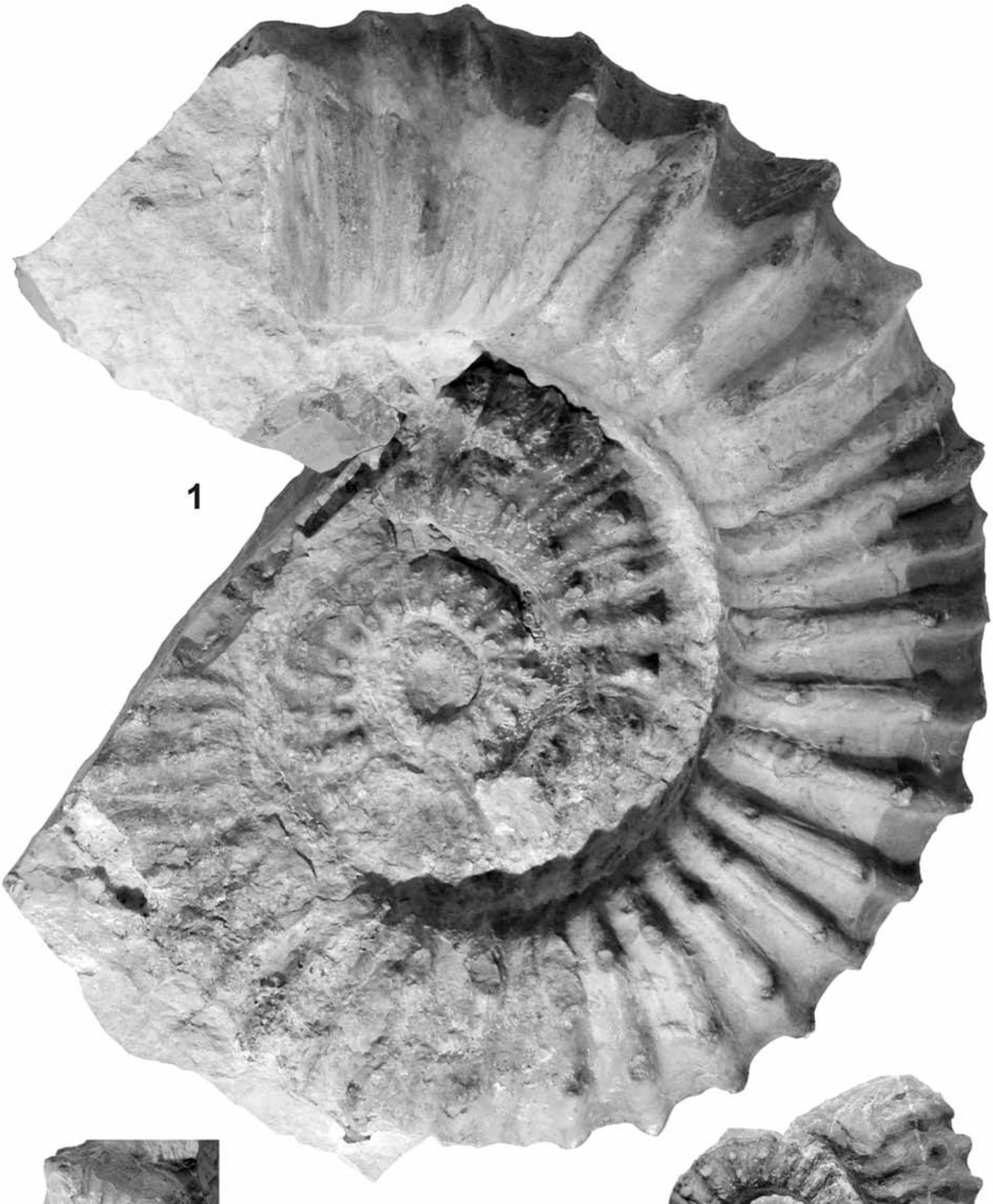
PLATE 1

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – AZ18 (G.P.A); section VIG2, level 266 (see. Pl. 2, Fig. 1); **2** – AW74 (G.P.A); section G15, level 309b; **3** – AW89 (G.P.A); section G15, level 309b.

Except Fig. 2 which is × 1, all specimens are × 0.5

1



2

3

PLATE 2

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – Ventral view of AZ18 (G.P.A); section VIG2, level 266 (see Pl. 1, fig. 1), Southeastern France) (see Pl. 3, fig. 1);
3 – AW57 (G.P.A); section G12, level 309b;
4 – AZ40 (G.P.A); section G15, level 309b;
5 – Barr-11, Quelquejeu collection (St André les Alpes); from Angles (southeastern France);
6 – AW82 (G.P.A); section G15, level 309b (see Pl. 3, fig. 2).

All specimens are × 0.5

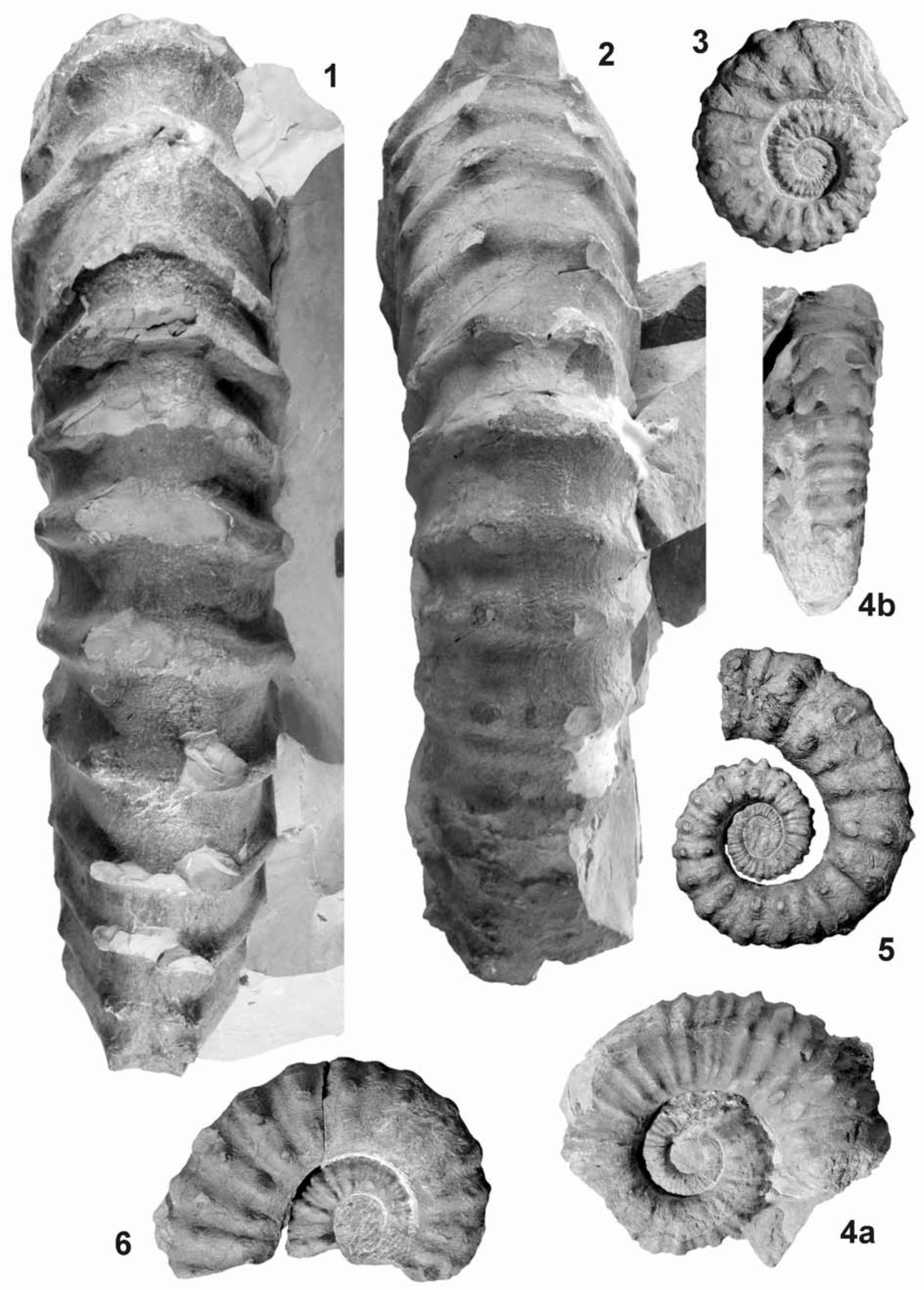

1
2
3
4b
5
6
4a

PLATE 3

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – Un-numbered specimen in the Maurel collection (Barrême), from Moriez (south-eastern France) (see Pl. 2, Fig. 2);
2 – AW82 (G.P.A); section G15, level 309b (see Pl. 2, fig. 6);
3 – AZ22 (G.P.A); section LAC, level 209c;
4 – AZ39 (G.P.A); section G15, level 309b.

All specimens are × 0.5

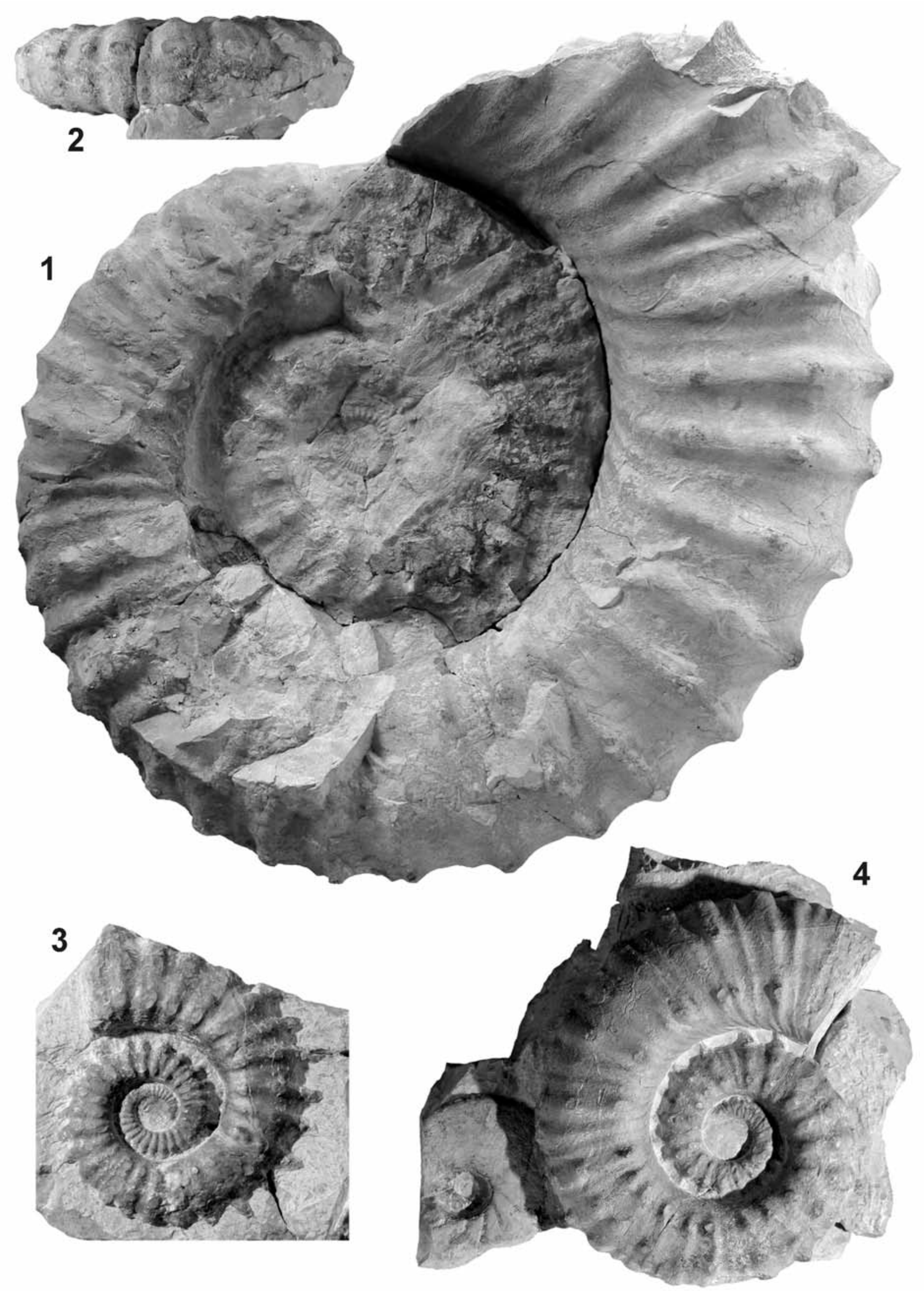

2
1
3
4

PLATE 4

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – AZ25 (G.P.A); section G12, level 309b;
2 – 28735 (G.P.A); section A', level 151-2;
3 – G15-309b-01 (G.P.A); section G15, level 309b;
4 – AW71 (G.P.A); section G12, level 309b.

All specimens are × 0.5

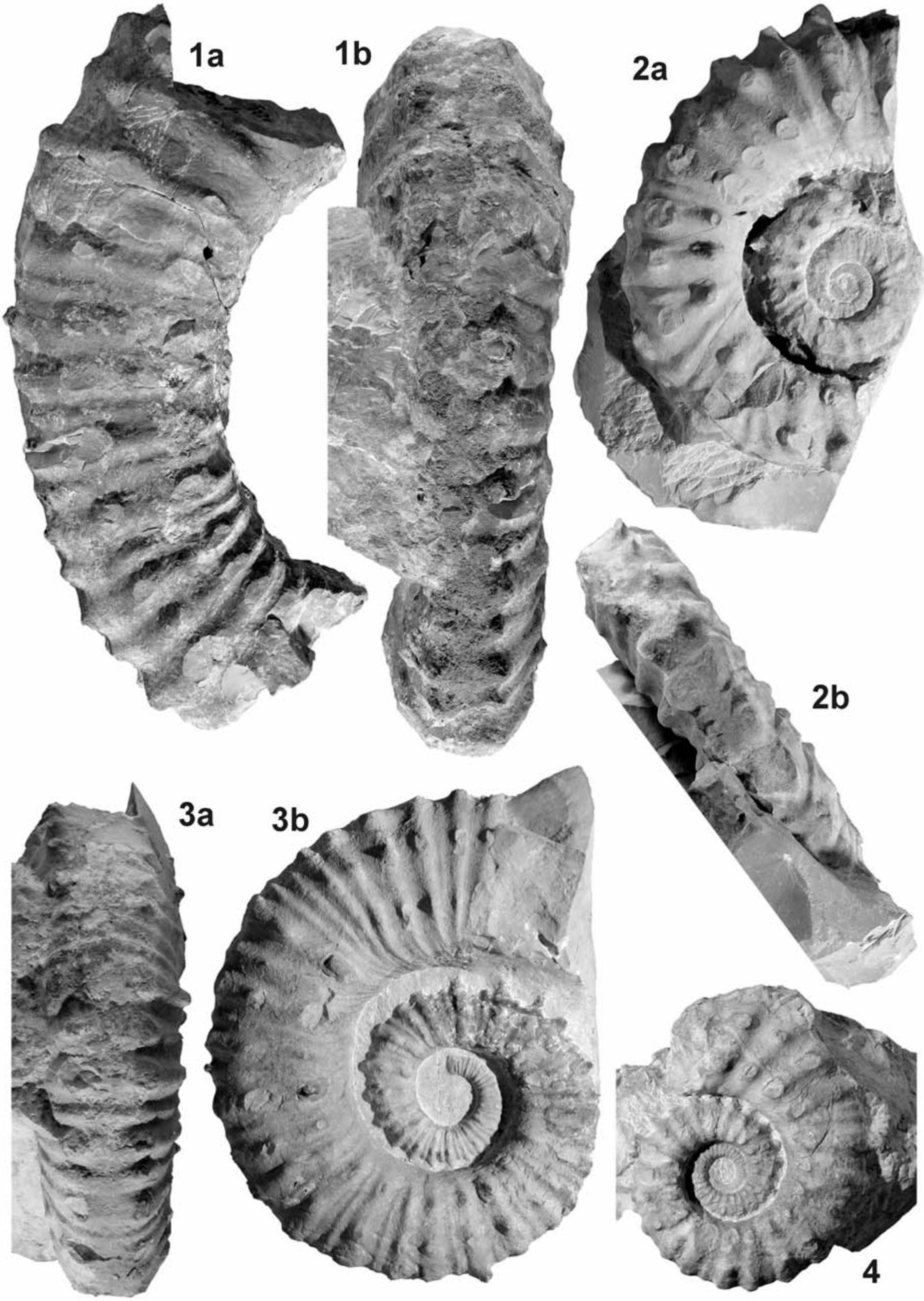
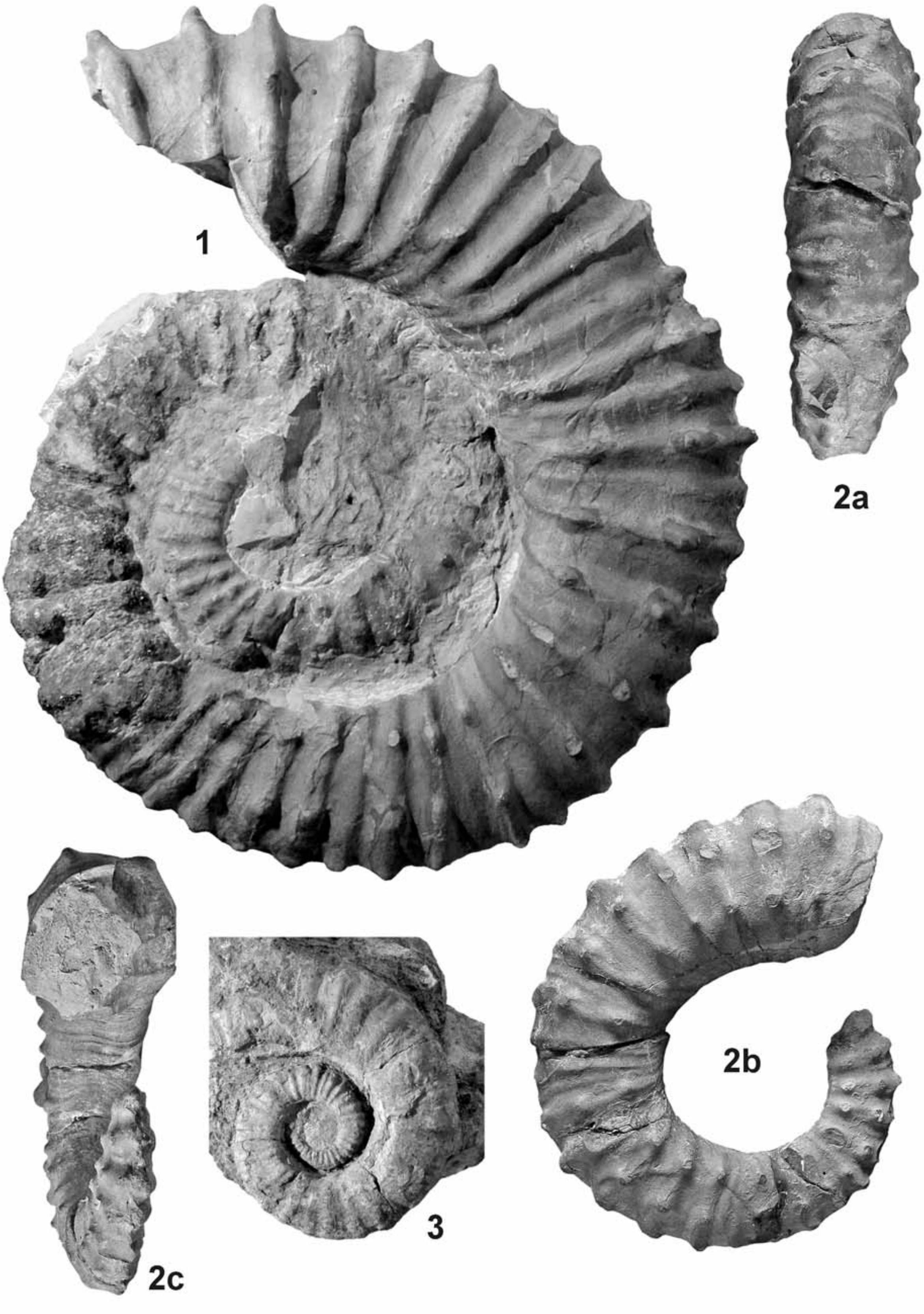

1a
1b
2a
2b
3a
3b
4

PLATE 5

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – AZ21 (G.P.A); section VIG2, level 266 (see Pl. 6, Fig. 1a-b);
2 – R00833a (ex. 5406) coll. d'Orbigny (lectotype – M.N.H.N); Angles;
3 – AZ38 (G.P.A); section SA, level 8.

All specimens are × 0.5



1
2a
2b
2c
3

PLATE 6

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – Ventral view of AZ21 (G.P.A); section VIG2, level 266 (see Pl. 5, Fig. 1);
2 – 1226 (G.P.A); section A', level 151-2;
3 – AW64 (G.P.A); section G15, level 309b.

All specimens are × 0.5

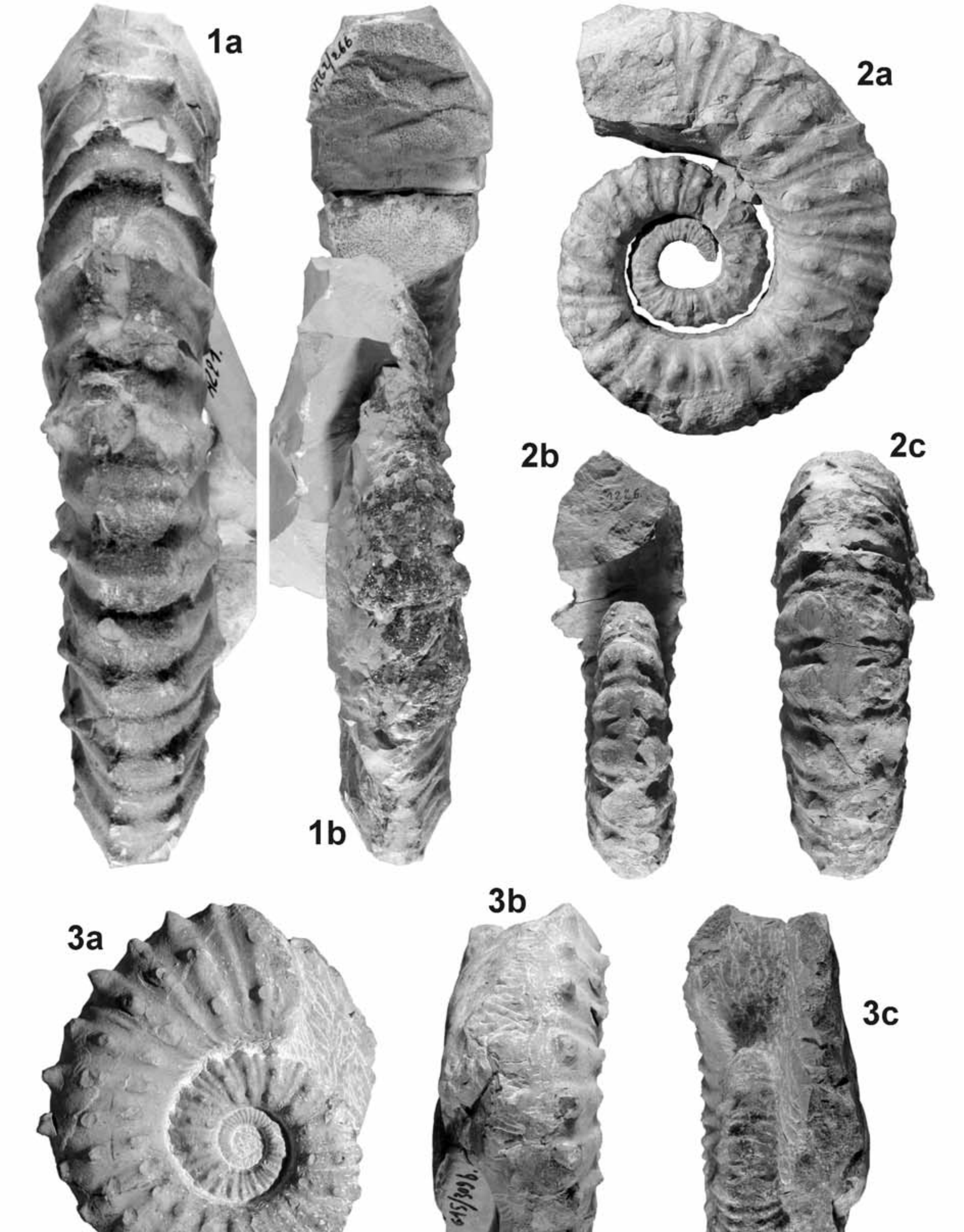

1a
1b
2a
2b
2c
3a
3b
3c

PLATE 7

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – LE 271 Ebbo collection (La Mure-Argens); from Angles (southeastern France);
2 – AW68 (G.P.A); section A', level 151-2;
3 – AW66 (G.P.A); section GRY, level 859c;
4 – F001 (C.E.M); section VIG2, level 266;
5 – G15-309b-02 (G.P.A); section G15, level 309b.

Except Fig. 3 which is × 1, all specimens are × 0.5

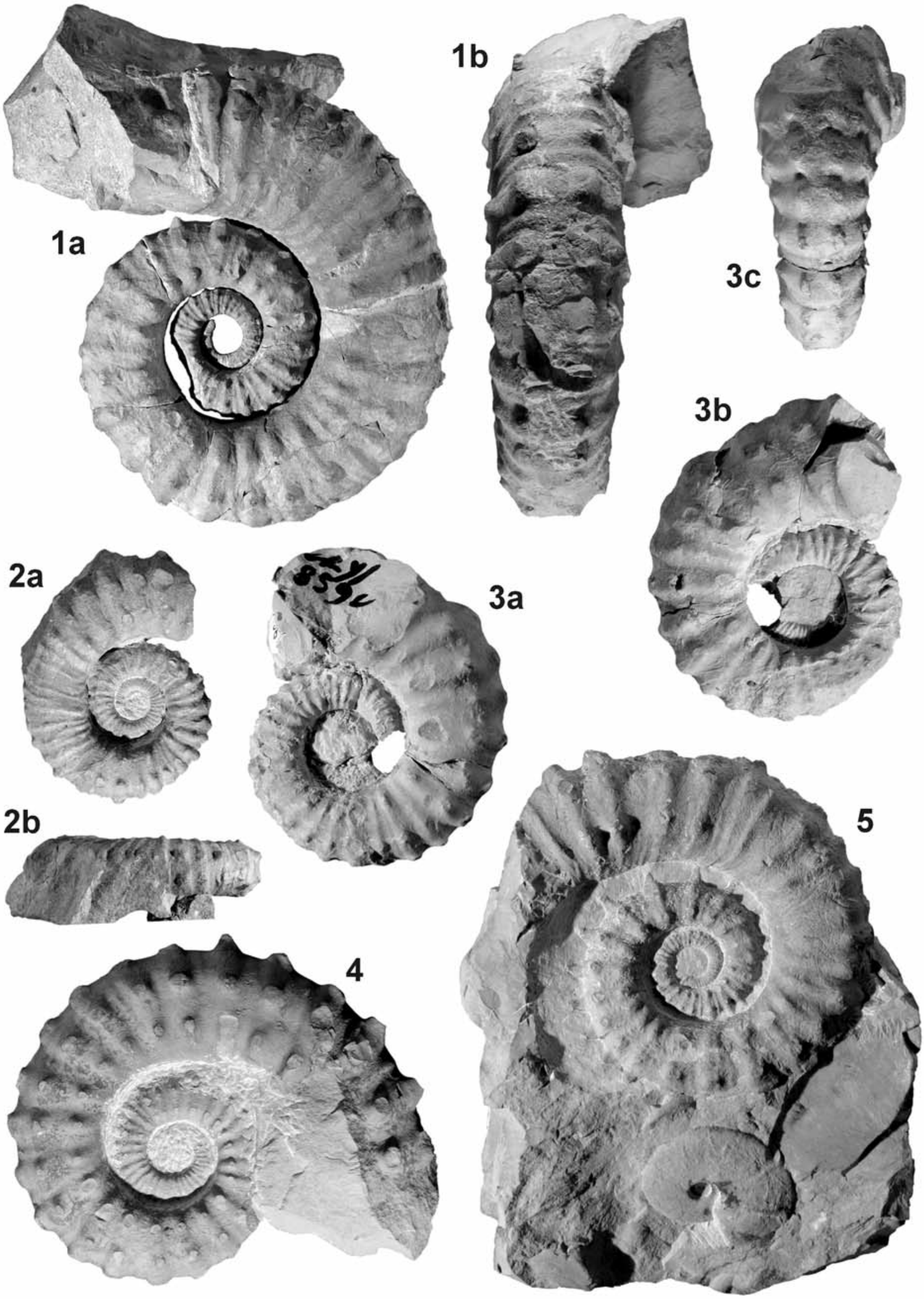

1a
1b
3c
3b
2a
3a
2b
5
4

PLATE 8

Gassendiceras alpinum (d'Orbigny, 1850); Upper Barremian, Vandenheckei Zone, Alpinum Subzone, Alpinum Horizon

1 – Un-numbered specimen in the Cotillon collection (*F.S.L*) from Rougon (southeastern France);
2 – CEM2 (*C.E.M*); section VIG2, level 266;
3 – 28734 (*G.P.A*); section VIG2, level 266;
4 – Un-numbered specimen in the Pénagé collection (*C.E.M*); section VIG2, level 266;
5 – AX17 (*G.P.A*); section G12, level 309b;
6 – UH (*G.P.A*); section SO, level 69-2.

All specimens are × 0.5

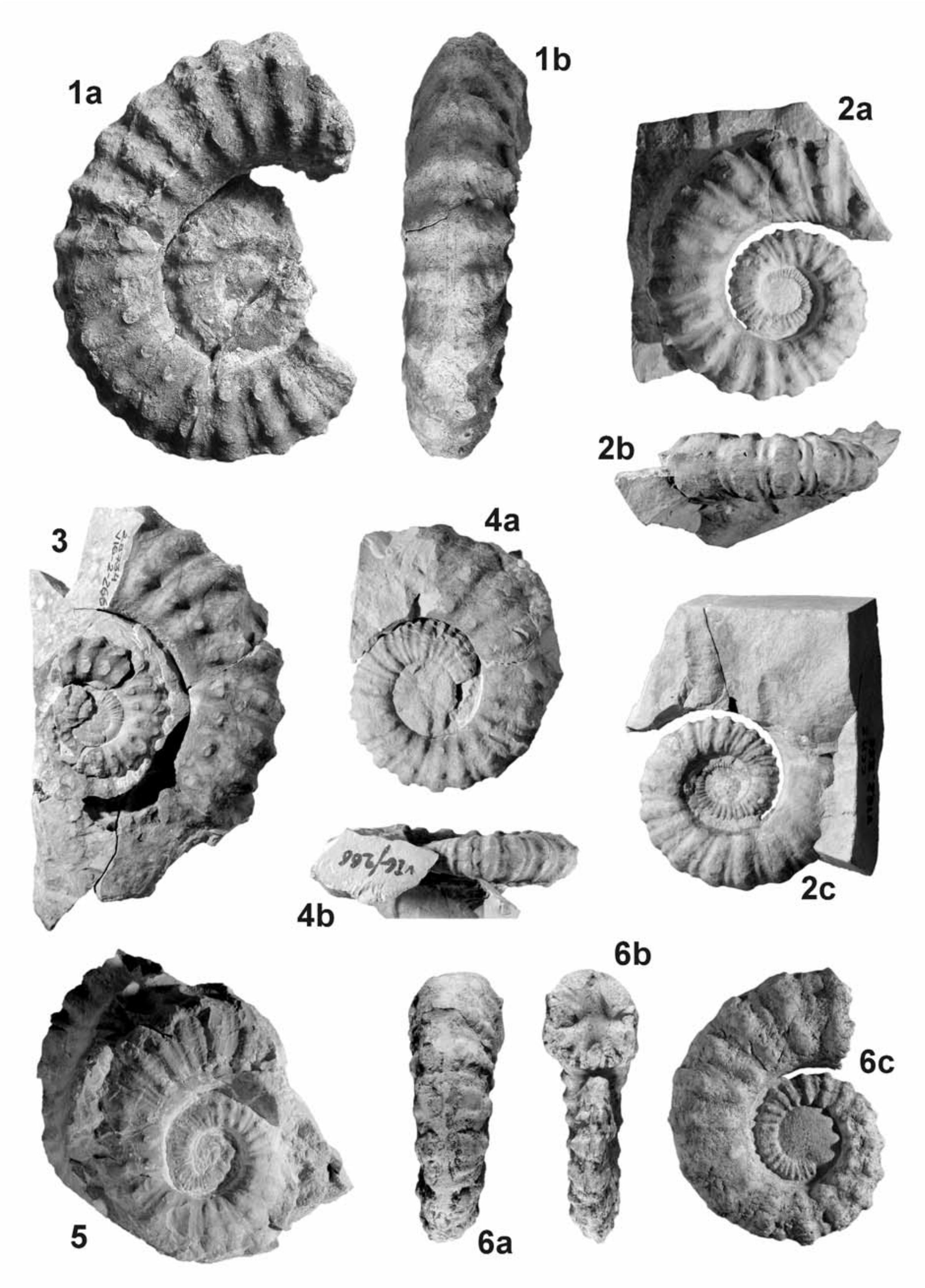

1a
1b
2a
2b
3
4a
2c
4b
5
6b
6c
6a

PLATE 9

Gassendiceras multicostatum (Sarkar, 1955); Upper Barremian, Vandenheckei Zone, top of the Vandenheckei Subzone

1 – AZ32 (G.P.A); section G5, level 99 (see Pl. 10, Fig. 1);
2 – R00833b (ex. 5406 – M.N.H.N) coll. A. d'Orbigny; from Angles; **3** – 28749 (G.P.A); section TAI, level 99

All specimens are × 0.5

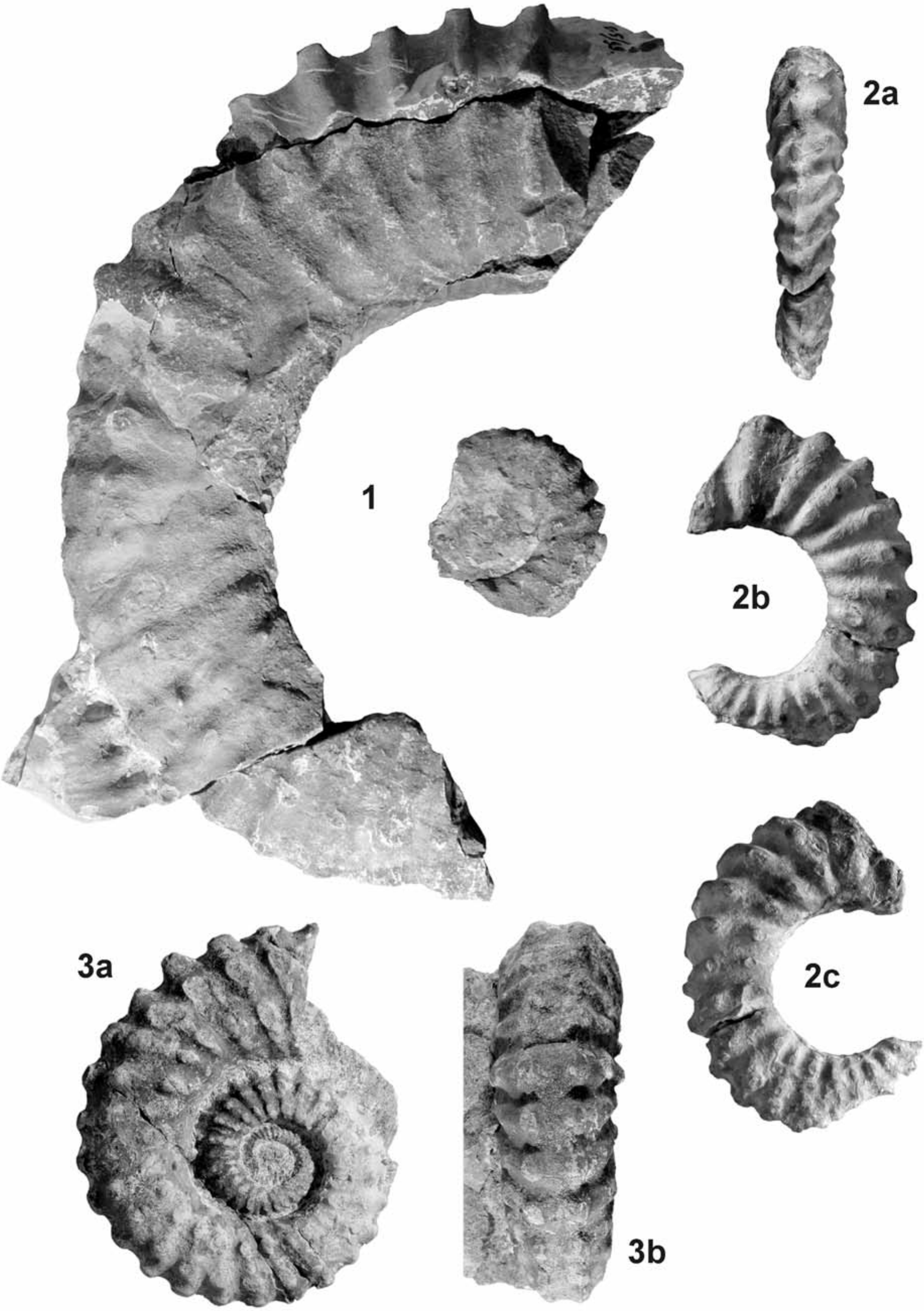

2a
1
2b
2c
3a
3b

PLATE 10

Gassendiceras multicostatum (Sarkar, 1955); Upper Barremian, Vandenheckei Zone, top of the Vandenheckei Subzone

1 – AZ32 (G.P.A); section G5, level 99 (see Pl. 9, Fig. 1);
2 – 1225 (G.P.A); section A', level 151-1;
3 – AW48 (G.P.A); section A', level 151-1 (see Pl. 11, Fig. 4);
4 – UJF.ID-111 (lectotype – I.D) from Trigance (southeastern France).

With exception of fig. 4a-b that is X1, all specimens are × 0.5

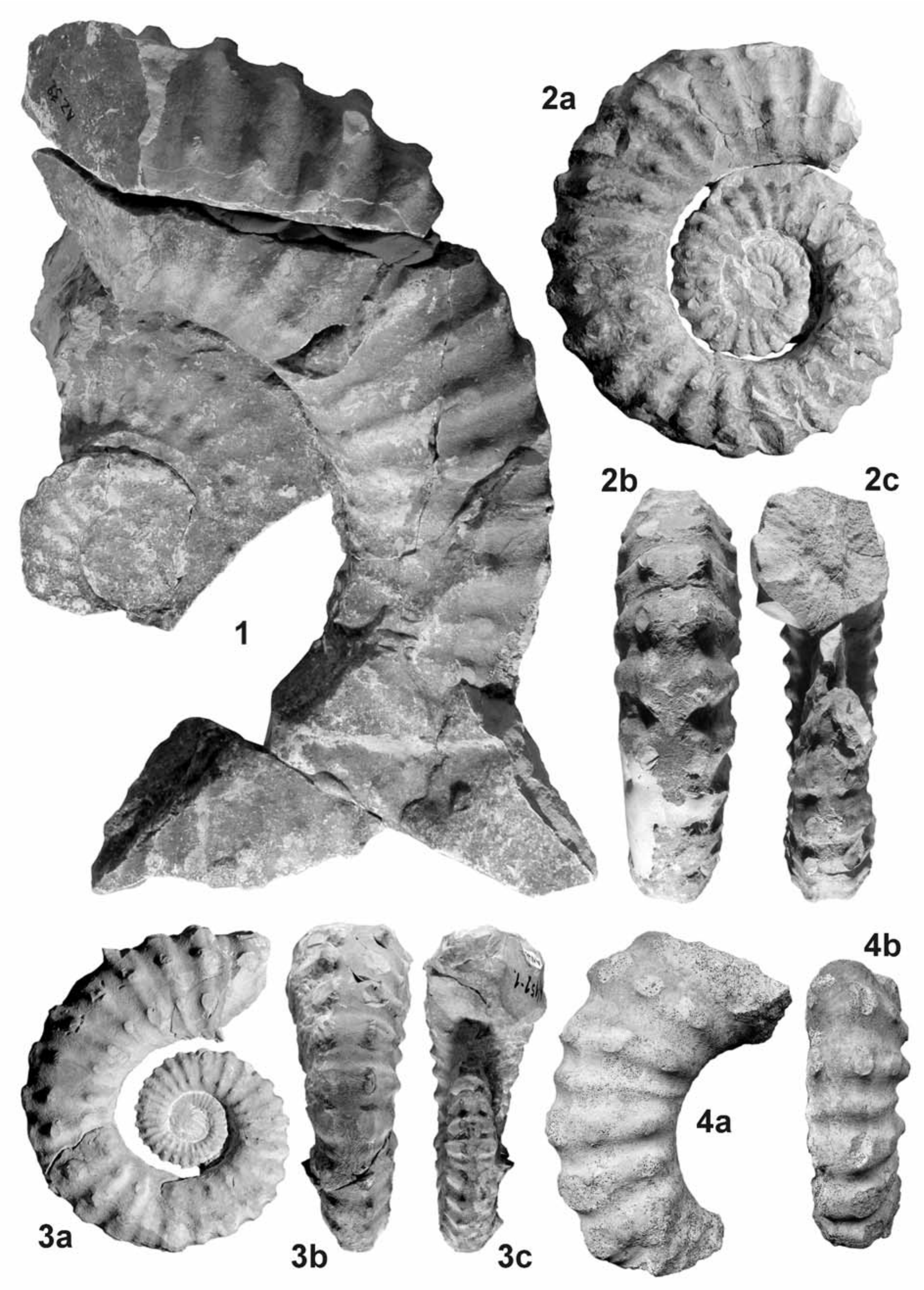

1
2a
2b
2c
3a
3b
3c
4a
4b

PLATE 11

Gassendiceras multicostatum (Sarkar, 1955); Upper Barremian, Vandenheckei Zone, top of the Vandenheckei Subzone

1 – GJ (G.P.A); section SO, level 69-2;
2 – AW45 (G.P.A); section A’, level 151-1.
3 – AW50 (G.P.A); section A’, level 150;
4 – Ventral view of inner whorls of AW48 (G.P.A); section A’, level 151-1 (see Pl. 10, Fig. 3a-c);

All specimens are × 0.5

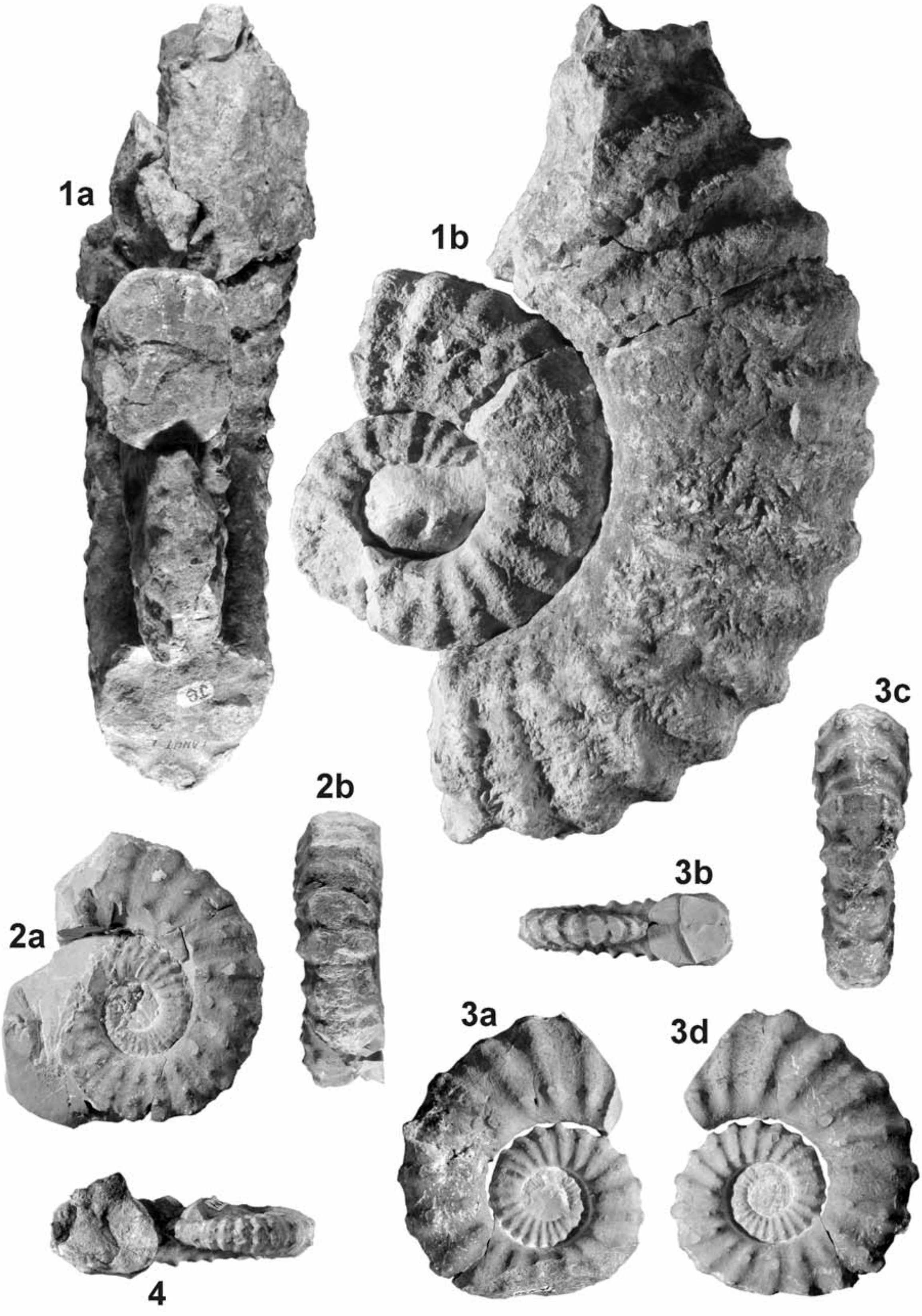

1a
1b
2a
2b
3a
3b
3c
3d
4

PLATE 12

Gassendiceras aff. *hoheneggeri* (Uhlig, 1883); un-numbered specimen in the Davoux collection; section VA, level 11; Upper Barremian, Vandenheckei Zone; × 0.5

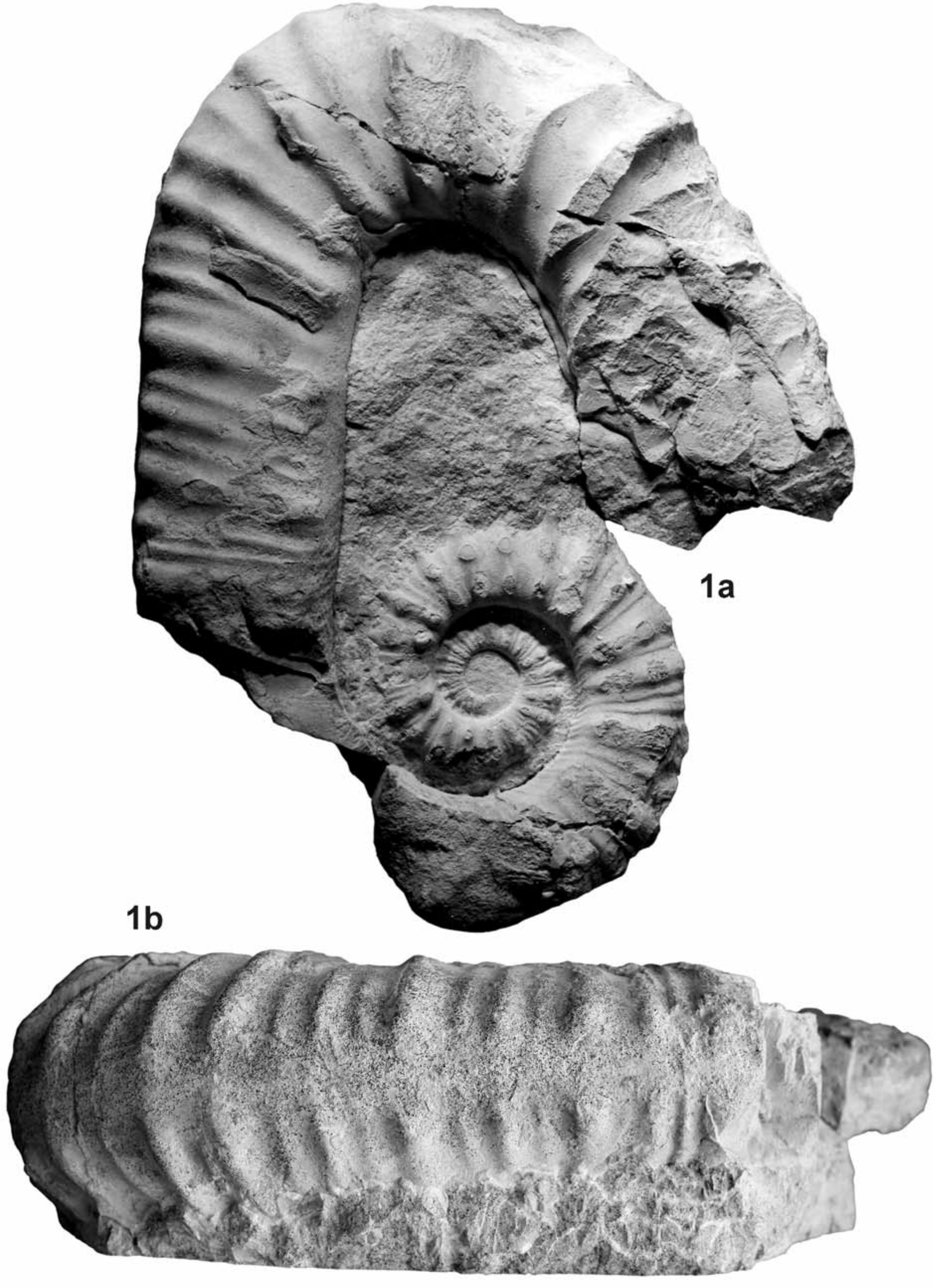

1a
1b

PLATE 13

Gassendiceras rebouleti nov. sp.; 104 (Thomel collection); section VIG2; Upper Barremian, Vandenheckei Zone, Alpinum Subzone; × 0.5


1

PLATE 14

1a-b – *Gassendiceras bosellii* nov. sp.; AW41 (G.P.A); section LAC, level 215 or 217; Upper Barremian, Vandenheckei Zone, Alpinum Subzone.

2 – *Gassendiceras rebouleti* nov. sp. (holotype); cast of specimen AW43 (G.P.A); section G12, level 317b; Upper Barremian, Vandenheckei Zone, Alpinum Subzone.

Both specimens are × 0.5

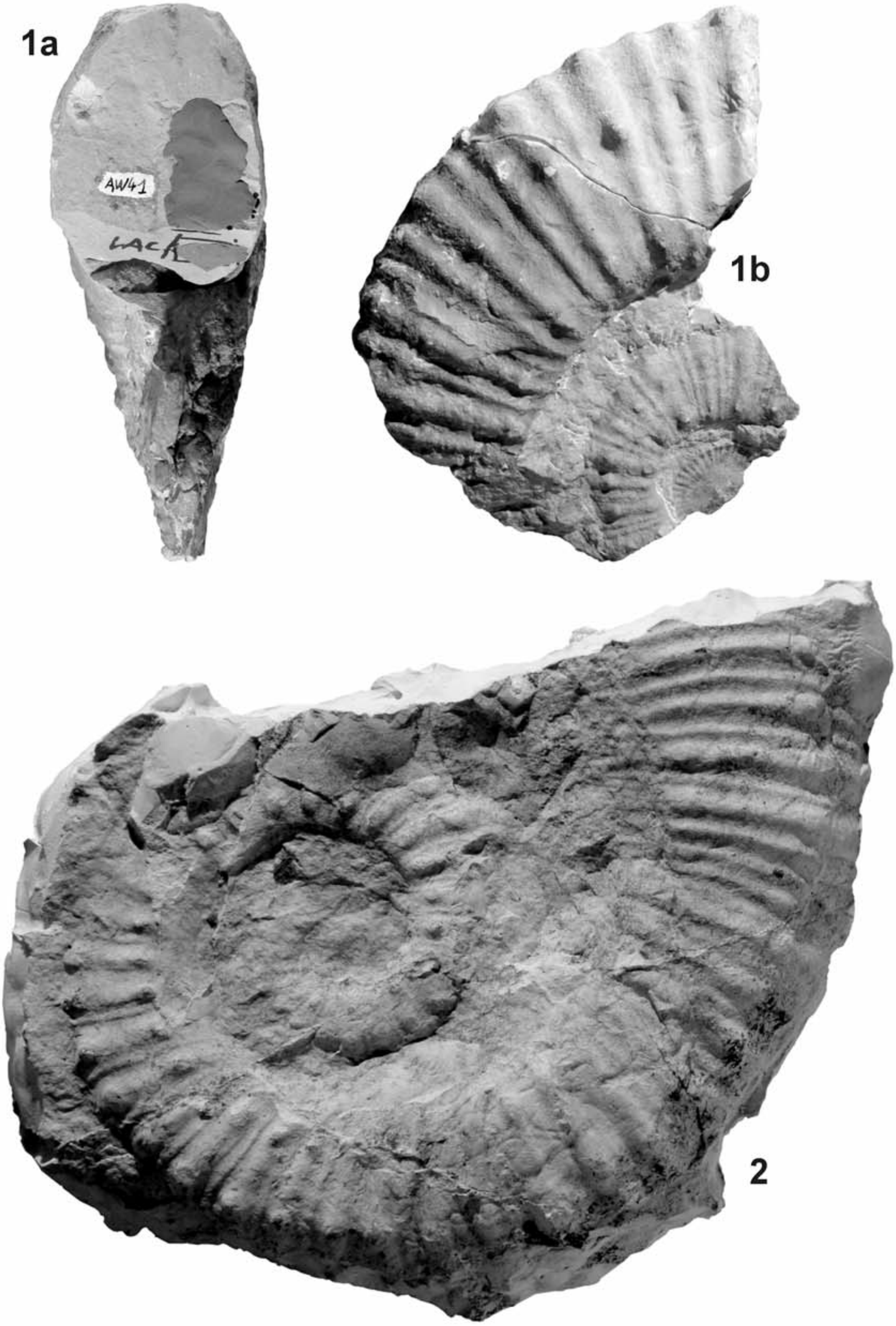

1a
AW41
LACK
1b
2

PLATE 15

1a-b – *Gassendiceras bosellii* nov. sp. (holotype); AZ27 (*G.P.A*); section G12, level 318a; Upper Barremian, Vandenheckei Zone, Alpinum Subzone.

2 – *Gassendiceras bosellii* nov. sp.; ventral view of 17252 (*G.P.A*); section VA, level 11; Upper Barremian, Vandenheckei Zone, Alpinum Subzone (see Pl. 16).

Both specimens are × 0.5

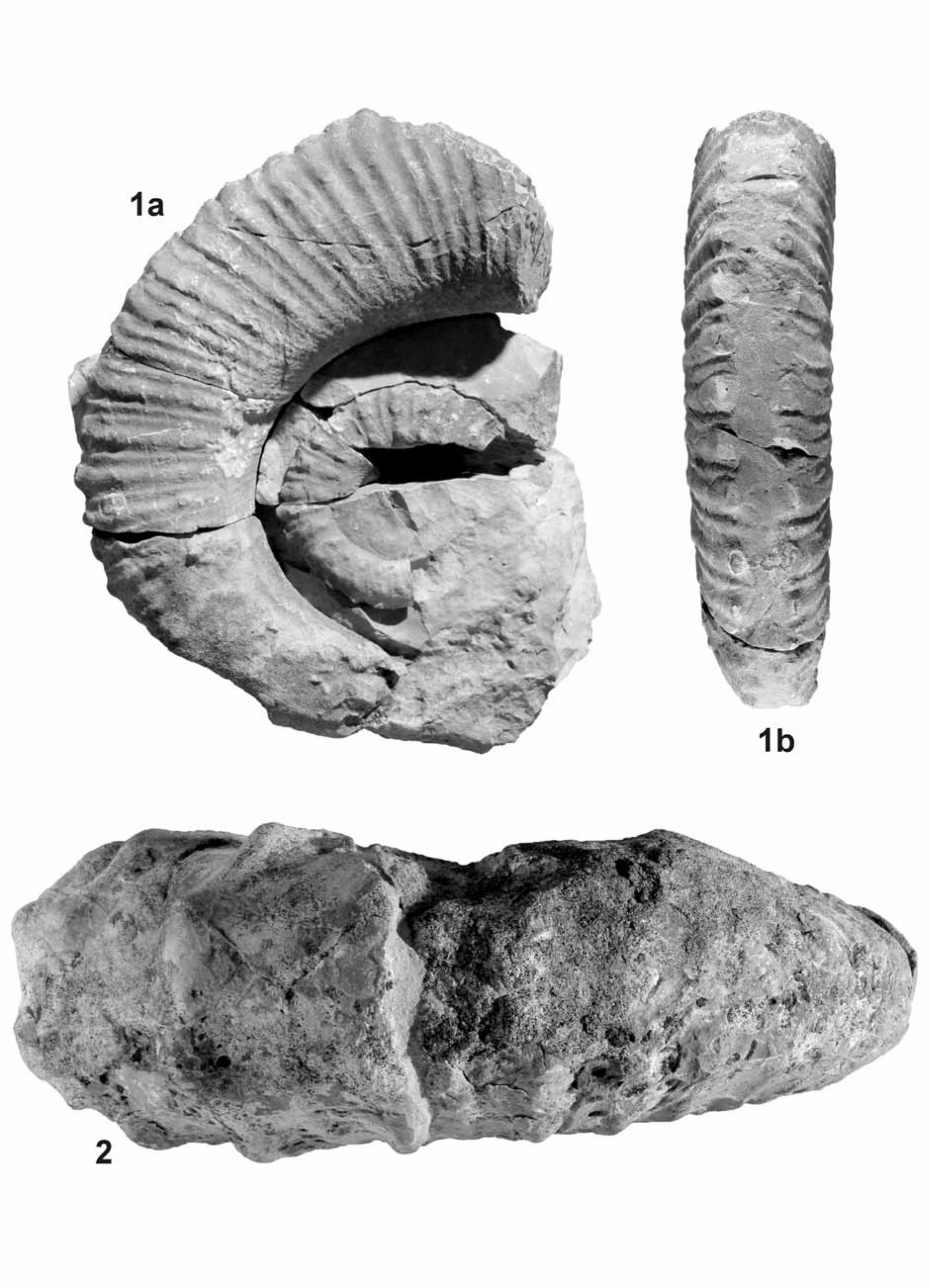
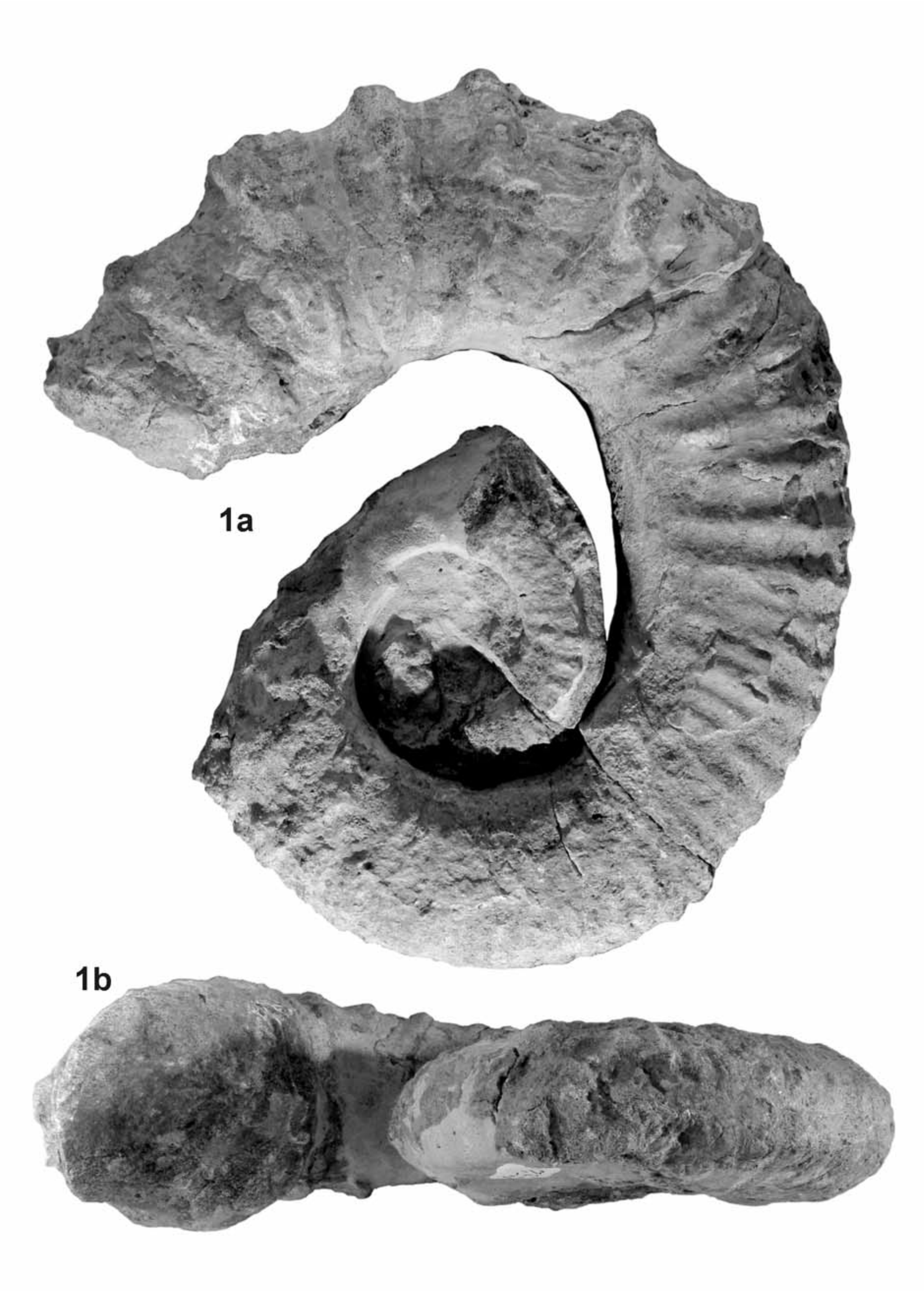

1a
1b
2

PLATE 16

Gassendiceras bosellii nov. sp.; lateral view (a) and adoral view (b) of 17252 (*G.P.A*); section VA, level 11; Upper Barremian, Vandenheckei Zone, Alpinum Subzone (see Pl. 15); × 0.5


1a
1b