



*Heteroceras gracile* sp. nov.,  
a new species of *Heteroceras* ORBIGNY, 1849,  
from the upper Barremian of Morteiron  
(Alpes de Haute-Provence, France)

Cyril BAUDOUIN <sup>1, 2</sup>

G rard DELANOY <sup>2, 3</sup>

Gr goire BOURNAUD <sup>4</sup>

Roland GONNET <sup>2, 5</sup>

**Abstract:** The species *Heteroceras gracile* sp. nov. is described; it is a small and slender species, with a small helix and hamuliniform morphology, previously considered as an atypical variant of *Heteroceras baylei* (REYN S, 1876). In southeast France, it is mainly known in the Morteiron section (Alpes de Haute-Provence, France), but the species is also present in Bulgaria and possibly in Japan.

**Key-words:**

- Ammonoidea;
- upper Barremian;
- *Heteroceras*;
- Alpes de Haute-Provence;
- France

**Citation:** BAUDOUIN C., DELANOY G., BOURNAUD G. & GONNET R. (2018).- *Heteroceras gracile* sp. nov., a new species of *Heteroceras* ORBIGNY, 1849, from the upper Barremian of Morteiron (Alpes de Haute-Provence, France).- *Carnets Geol.*, Madrid, vol. 18, no. 6, p. 155-165.

**R sum  :** *Heteroceras gracile* sp. nov., une esp ce nouvelle d'*Heteroceras* ORBIGNY, 1849, du Barr mien sup rieur de Morteiron (Alpes de Haute-Provence, France).- L'esp ce *Heteroceras gracile* sp. nov. est cr e e ; elle est repr sent e par des formes de petite taille,   enroulement fr le et petit turric ne, de morphologie hamuliniforme, pr c demment consid r es comme des morphes atypiques d'*Heteroceras baylei* (REYN S, 1876). Dans le sud-est de la France, elle est essentiellement connue dans la coupe de Morteiron (Alpes de Haute-Provence, France), mais l'esp ce est aussi pr sente en Bulgarie et hypoth tiquement au Japon.

**Mots-clefs :**

- Ammonoidea ;
- Barr mien sup rieur ;
- *Heteroceras* ;
- Alpes de Haute-Provence ;
- France

<sup>1</sup> 6, rue Fr d ric Mistral, 26200 Mont limar (France)  
cyril.baudouin@gmail.com

<sup>2</sup> Centre d' tudes M diterran ennes, 04170 St-Andr -l s-Alpes (France)

<sup>3</sup> D partement des Sciences de la Terre, Universit  de Nice-Sophia-Antipolis, Facult  des Sciences, 28 avenue Valrose, 06108 Nice Cedex 2 (France)  
delanoy@unice.fr

<sup>4</sup> 7, impasse du Clos, 04200 Peipin (France)

<sup>5</sup> Chemin de Dard ne, La Barthelasse, 84000 Avignon (France)



### I. Introduction

The genus *Heteroceras* ORBIGNY, 1849, includes forms of very diverse size, from a few centimeters for the species *Heteroceras baylei* (REYNÈS, 1876), *H. elegans* ROUCHADZÉ, 1933, *H. eristavii* KAKABADZE, 1975, and *H. veratiae* FRAU *et al.*, 2016, to 60 cm or more in *Heteroceras coulleti* DELANOY, 1995. The small forms of southeast France have been the subject of several recent studies (DELANOY & BULOT, 1990; DELANOY, 1997; DELANOY & BERT, 2006; FRAU *et al.*, 2016). The existence in bed no. 3 of the Morteiron section (Alpes de Haute-Provence, France) of a population of small individuals with hamuliform morphology and bearing a long and slender *proversum*, was described by DELANOY (1997, p. 98). It was then considered as a variant of *Heteroceras baylei* (REYNÈS, 1876), and linked to particular

ecological conditions. The collection and study of new specimens showed, however, very marked morphological differences with *Heteroceras baylei* (REYNÈS, 1876), including slender coiling, with a long *proversum* and a relatively short *retroversum* that is not in contact with the helix, leading us to consider this population as a distinct species.

### II. Paleontological and systematic study

The biozonation scheme of the Lower Cretaceous employed here (Fig. 1) is the one developed by the IUGS Lower Cretaceous Ammonite Working Group (REBOULET *et al.*, 2011, 2014). We retain the tripartite division of the *Imerites giraudi* Zone at the top of the Barremian (BERT *et al.*, 2008, 2011; REBOULET *et al.*, 2011).

Stages	Zones	Subzones	Horizons
Barremian	Upper	<i>Imerites giraudi</i>	<i>Pseudocrioceras waagenoides</i>
			<i>Martelites sarasini</i>
		<i>Imerites giraudi</i>	<i>Anglesites puzosianum</i>
			<i>Heteroceras emericianum</i>
			<i>Imerites giraudi</i>
			<i>Imerites dichotomus</i>
			<i>Pseudoshastrioceras autrani</i>
			<i>Pseudoshastrioceras bersaci</i>
		<i>Gerhardtia sartousiana</i>	<i>Pseudoshastrioceras magnini</i>
			<i>Hemihoplites feraudianus</i>
	<i>Hemihoplites casanovai</i>		
	<i>Gerhardtia provincialis</i>		
	<i>Toxancyloceras vandenheckii</i>	<i>Gerhardtia provincialis</i>	<i>Gerhardtia provincialis</i>
			<i>Gerhardtia sartousiana</i>
		<i>Camereiceras limentinus</i>	<i>Camereiceras limentinum</i>
			<i>Camereiceras marchandi</i>
		<i>Gassendiceras alpinum</i>	<i>Ancylezeiceras breistrofferi</i>
			<i>Gassendiceras alpinum</i>
	Lower	<i>Toxoceras moutonianum</i>	<i>Toxancyloceras vandenheckii</i>
			<i>Heinzia caicedi</i>
<i>Kotetishvilia compressissima</i>		<i>Coronites darsi</i>	
		<i>Subtorcapella defayae</i>	
		<i>Heinzia communis</i>	
		<i>Nicklesia didayana</i>	
<i>Nicklesia pulchella</i>		<i>Holcodiscus fallax</i>	
<i>Kotetishvilia nicklesi</i>			
<i>Taveraidiscus hugii auctorum</i>	<i>Psilotissotia colombiana</i>		
	<i>Taveraidiscus hugii auctorum</i>		

Figure 1: Biozonation of the Barremian (according to BERT *et al.*, 2008, 2011, and REBOULET *et al.*, 2011, 2014).

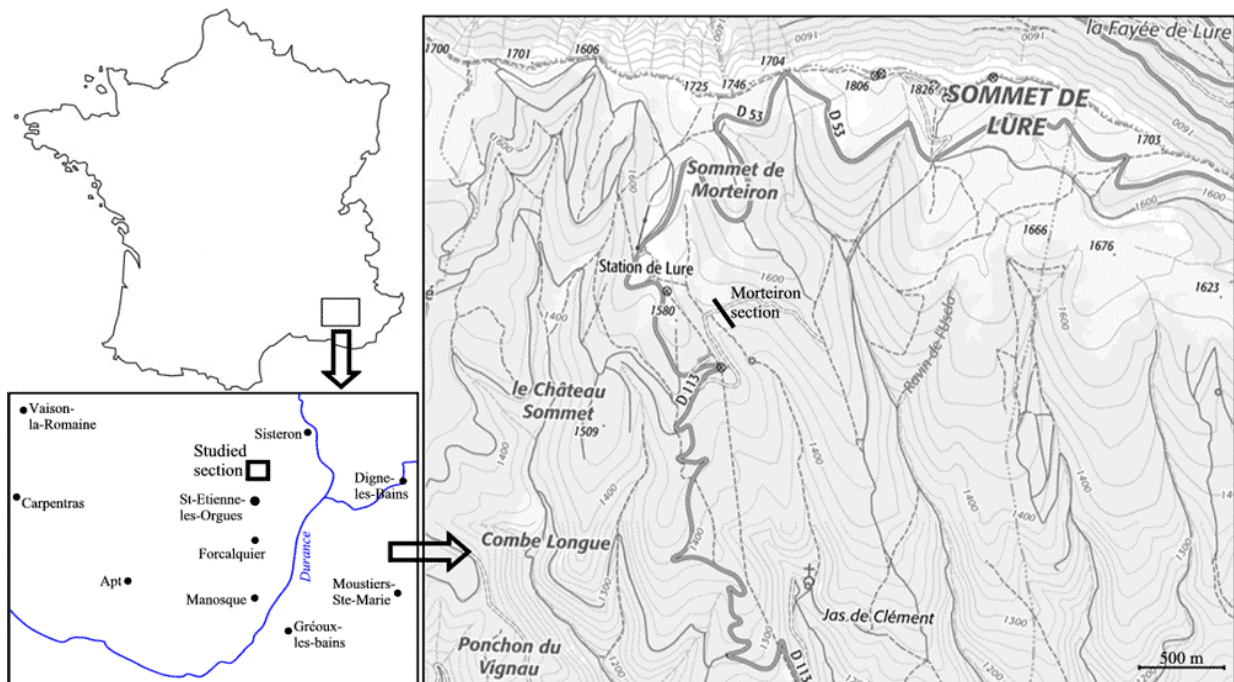


Figure 2: Geographical location of the studied section (source: [www.geoportail.gouv.fr](http://www.geoportail.gouv.fr)).

All the specimens studied in this work come from the Morteiron section (Fig. 2), located in the commune of Saint-Étienne-lès-Orgues (Alpes de Haute-Provence, France). The important Heteroceratidae fauna of this section was first reported by KILIAN (1889) and described in detail by DELANOY (1997), DELANOY & EBBO (2000) and DELANOY & BERT (2006). Two levels in particular are remarkable for the diversity and abundance of the representatives of this family: bed no. 3, with *Heteroceras emericianum* ORBIGNY, 1842, and its morphotypes, *H. gracile* sp. nov. (= *H. baylei* (REYNÈS, 1876) in DELANOY, 1997), *Rouchadzeites mascarellii* (DELANOY & EBBO, 2000), *Egoianites mikhaili* DELANOY & BERT, 2006, *Paraimerites* ? sp., *Argvethites* sp., and bed no. β, with *Heteroceras emericianum* ORBIGNY, 1842, *H. moulladei* DELANOY & BERT, 2006, *H. gracile* sp. nov., *H. gonneti* DELANOY, 1997, *H. baylei* ? (REYNÈS, 1876) and several forms of *Heteroceras* sp. which will be the subject of a future study.

The terminology of the different parts of the shell is the one used by FRAU *et al.* (2016, Fig. 4).

The measurements (Fig. 3 and Tab. 1) were carried out according to the protocol employed by DELANOY (1997, p. 18, fig. 2 and p. 26) for the measurements *N* (ribbing density), and *C<sub>p</sub>* and *C<sub>c</sub>* (growth rate). On incomplete specimens, measurement *H* corresponds to the height of the preserved part of the shell. The *h<sub>2</sub>* measurement was performed at the last suture if it was visible. If the last suture is not visible, *h<sub>2</sub>* was measured at the top of the *proversum*, at the level where the boundary between the phragmocone and the body chamber is usually observed. In order to allow the calculation of the growth rates *C<sub>p</sub>* and *C<sub>c</sub>*

on the maximum number of specimens, where *h<sub>1</sub>* or *h<sub>3</sub>* are not measurable (incomplete specimens), additional measurements *h<sub>1</sub>\** or *h<sub>3</sub>\** (as well as the *l<sub>p</sub>\** and *l<sub>c</sub>\** lengths of the corresponding shell segments) were carried out, corresponding respectively to the lowest measurable whorl height on the phragmocone and to the highest measurable whorl height on the body chamber.

Table 1: Abbreviations used in the text.

<i>H</i>	Total length
<i>L</i>	Total width
<i>D<sub>t</sub></i>	Turricone diameter
<i>h<sub>1</sub></i>	Whorl height at the end of the turricone
<i>h<sub>1</sub>*</i>	Whorl height at the base of the preserved part of the <i>proversum</i> (when <i>h<sub>1</sub></i> is not measurable)
<i>h<sub>2</sub></i>	Whorl height at the last suture
<i>h<sub>3</sub></i>	Whorl height at the end of the body chamber
<i>h<sub>3</sub>*</i>	Whorl height at the end of the preserved part of the body chamber (when <i>h<sub>3</sub></i> is not measurable)
<i>l<sub>p</sub></i>	Length of the phragmocone (without the turricone)
<i>l<sub>p</sub>*</i>	Length of the preserved part of the phragmocone (when <i>l<sub>p</sub></i> is not measurable)
<i>l<sub>c</sub></i>	Length of the body chamber
<i>l<sub>c</sub>*</i>	Length of the preserved part of the body chamber (when <i>l<sub>c</sub></i> is not measurable)
<i>C<sub>p</sub></i>	Relative growth in whorl height of the phragmocone: $C_p = (h_2 - h_1) \div l_p$ (or of the preserved part of the phragmocone when it is incomplete: $C_p = (h_2 - h_1^*) \div l_p^*$ )
<i>C<sub>c</sub></i>	Relative growth in whorl height of the body chamber: $C_c = (h_3 - h_1) \div l_c$ (or of the preserved part of the body chamber when it is incomplete: $C_c = (h_3^* - h_1) \div l_c^*$ )
<i>N</i>	Number of ventral ribs belonging to a longitudinal interval of length <i>h</i> , where <i>h</i> is the whorl height in the middle of this interval

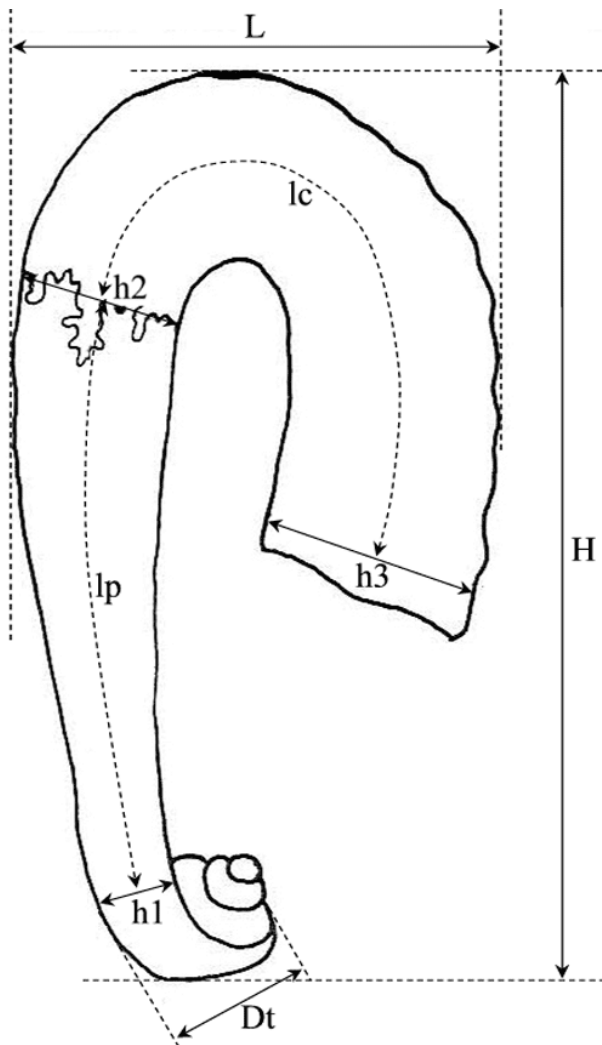


Figure 3: Explanatory diagram of the measurements made on the specimens studied.

**Suborder Ancyloceratina**  
WIEDMANN, 1966

**Superfamily Ancyloceratoidea**  
GILL, 1871

**Family Heteroceratidae SPATH, 1922**

**Genus *Heteroceras* ORBIGNY, 1849**

(= *Lindigia* KARSTEN, 1858; *Atopoceras* JAUBERT in KILIAN, 1889, *nomen nudum*; *Hemibaculites* HYATT, 1900, *nomen dubium*; ? *Dirrymoceras* HYATT, 1900, *nomen dubium*; *Colchidites* DJANÉ-LIDZÉ, 1926; ? *Santandericeras* ROYO y GOMEZ, 1945)

**Type species:** *Turrilites emericianus* ORBIGNY, 1842 (by subsequent designation of MEEK, 1876, p. 477).

***Heteroceras gracile* sp. nov.**

(Pl. 1, figs. 1-12)

- ? 1964 *Anahamulina subcylindrica* (ORBIGNY, 1850). - NIKOLOV, p. 126, Pl. 4, fig. 6; non Pl. 5, figs. 1-2 (= *Heteroceras* sp.)
- ? 1976 *Acrioceras* (?) aff. *julivertii* ETAYO-SERNA, 1968. - OBATA & OGAWA, Pl. 4, fig. 6
- 1989 *Heteroceras* cf. *elegans* ROUCHADZÉ, 1933. - CONTE, p. 39, fig. 9 ?, 10 ?, 11
- pars 1997 *Heteroceras baylei* (REYNÈS, 1876). - DELANOY, p. 95, Pl. 13, fig. 4; Pl. 16, fig. 3; Pl. 20, figs. 3-4; Pl. 50, fig. 3; non Pl. 9, fig. 3; Pl. 13, fig. 5; Pl. 14, figs. 4-7; Pl. 20, fig. 2; Pl. 50, figs. 4, 8; Pl. 51, figs. 2-8 [= *Heteroceras baylei* (REYNÈS, 1876)]
- 2013 *Heteroceras baylei* (REYNÈS, 1876). - IVANOV & IDAKIEVA, fig. 6.E ?, F-G

**Holotype:** Specimen no. FSL13388, coll. Claude Bernard University, Lyon, France. Examination of the matrix indicates that the holotype comes from bed no. 3 of the Morteiron section (Alpes-de-Haute-Provence, France).

**Derivatio nominis:** In reference to the slender and hamuliniform character of this new species.

**Locus-typicus:** Morteiron, Saint-Étienne-lès-Orgues (Alpes-de-Haute-Provence, France).

**Stratum-typicum:** Upper Barremian, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon.

**Geographical and stratigraphical distribution:** *H. gracile* sp. nov. is mainly known in the *Heteroceras emericianum* Horizon of the Morteiron section (Alpes-de-Haute-Provence, France), more precisely in beds no. 3 and  $\beta$  (DELANOY, 1997, p. 255).

*H. gracile* sp. nov. also appears to be present in Bulgaria in the *Heteroceras astierianum* Zone of NIKOLOV (1964, Pl. 4, fig. 6). Its presence seems certain at the base of the *Martelites sarsini* Subzone of the Opaka section (IVANOV & IDAKIEVA, 2013, p. 55 and Fig. 6).

Its presence in Japan is still hypothetical and is based on the morphological affinities between *Acrioceras* (?) aff. *julivertii* ETAYO-SERNA, 1968, figured by OBATA & OGAWA (1976, Pl. 4, fig. 6) and *H. gracile* sp. nov.

**Material and dimensions (N=29):** Specimens no. FSL13388, coll. Claude Bernard University (Lyon, France), mot02, mot03, mot04, mot05, mot06, mot07a, mot07b, mot09, mot10, mot11, mot12, mot13, mot14, mot16, mot17, mot18, mot19, mot20, coll. BAUDOUIN, 28824, 28838, 28839, 28840, coll. DELANOY, MOT GBD 01, MOT GBD 02, coll. BOURNAUD, bed no. 3, upper Barremian, *Imerites giraudi* Zone, *Imerites*



**Table 2:** Morphometric measurements of *Heteroceras gracile* sp. nov. (Bold italic type indicates that these values were measured on photographs).

no.	"H"	L	h1	h1*	h2	h3	h3*	Dt	lp	lp*	lc	lc*	Cp	Cc
FSL13388	65.9	24.5	3.8	-	8.2	13.7	-	4.8	58.3	-	48.4	-	7.5	11.4
mot02	50.9	-	-	3.9	8.2	-	-	-	-	39.6	-	-	10.9	-
mot03	59.6	24.3	-	4.3	8	12.3	-	-	-	47.8	30.2	-	7.7	14.2
mot04	57.3	23.2	-	2.9	7.8	13.9	-	-	-	48.3	49.7	-	10.1	12.3
mot05	51.4	20.7	-	4.6	7.2	-	11.6	-	-	39.6	-	29.5	6.6	14.9
mot06	55.5	-	-	4.7	7.7	-	-	-	-	39.6	-	-	7.6	-
mot07a	80	29.5	-	5.2	9.7	16.2	-	-	-	60.3	34.9	-	7.5	18.6
mot07b	69.3	-	-	-	-	-	-	-	-	-	-	-	-	-
mot09	83.3	28.2	3.5	-	10.7	15.5	-	-	75.2	-	51.5	-	9.6	9.3
mot10	59	-	4.1	-	c9.8	-	-	c8.1	52	-	-	-	11.0	-
mot11	56.9	25.1	-	4.1	7.8	16.2	-	-	-	42.8	44.3	-	8.6	19.0
mot12	72.6	36.4	-	6.4	10.2	18.4	-	-	-	58.3	48.2	-	6.5	17.0
mot13	45.3	27.9	-	5.2	7.4	15.4	-	-	-	38.4	50.9	-	5.7	15.7
mot14	67.9	23.4	-	5.3	9.1	-	-	-	-	45	-	-	8.4	-
mot16	55.3	24.5	-	6.6	8.5	13.8	-	-	-	37.3	63	-	5.1	8.4
mot17	56.7	28.3	-	6	9.1	13.7	-	-	-	42.3	44.9	-	7.3	10.2
mot18	34.4	26	-	-	7.9	12.8	-	-	-	-	42.1	-	-	11.6
mot19	49.6	21.6	-	4.8	7.6	12.3	-	-	-	39.6	47.5	-	7.1	9.9
mot20	50.9	27.6	-	3.9	6.7	13.4	-	-	-	42.6	49	-	6.6	13.7
RG419a	62.9	23.9	4.2	-	7.6	11.6	-	-	51.2	-	50.3	-	6.6	8.0
RG419b	55.8	20	-	-	6.7	-	-	-	-	-	-	-	-	-
MOT GDB 01	58.4	23.5	-	7	9.3	-	11.8	-	-	42.2	-	29.8	5.5	8.4
MOT GDB 02	65.6	25.3	3.4	-	8	c13	-	9.4	53.5	-	50.1	-	8.6	10.0
MOT GDB 03	46.7	25.2	-	5.5	8.4	14.9	-	-	-	34.1	57	-	8.5	11.4
MOT GDB 06	37.5	16.8	-	3.4	5.3	9.6	-	-	-	31	43.2	-	6.1	10.0
22839	55	21.9	-	5	8.6	-	10.8	-	-	37.7	-	22.8	9.5	9.6
28840	61	-	-	6.6	10.4	17.1	-	-	-	45.8	46	-	8.3	14.6
<i>Heteroceras baylei</i> , holotype no. MHNM 1989-44	65.7	-	-	8.6	11.7	16.7	-	-	-	34.3	62	-	9.0	8.1
<i>Heteroceras elegans</i> , holotype no. GIT 350/1016	53.1	28	8.1	-	9.4	14.8	-	13.6	29.8	-	39.7	-	4.4	13.6
<i>Heteroceras veratae</i> , holotype no. FCC.8A	33	-	<b>5.7</b>	-	<b>7.4</b>	9	-	11	<b>16.2</b>	-	<b>25.1</b>	-	10.5	6.4

*giraudi* Subzone, *Heteroceras emericianum* Horizon, Morteiron, Saint-Étienne-lès-Orgues (Alpes-de-Haute-Provence, France); no. RG419a, RG419b, coll. BAUDOUIN leg. GONNET, bed no. β, upper Barremian, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, Morteiron, Saint-Étienne-lès-Orgues (Alpes-de-Haute-Provence, France); no. MOT GDB 03, MOT GDB 06, coll. BOURNAUD, bed no. β ?, upper Barremian, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, Morteiron, Saint-Étienne-lès-Orgues (Alpes-de-Haute-Provence, France). See Tables 2 and 3 for dimensions.

The holotype no. FSL13388 and specimens no. 28839 and no. 28840, as well as casts of specimens no. mot09 and no. mot10 (registered as UCBL-FSL 391837 and UCBL-FSL 391838) are deposited in the collections of the Claude Bernard University, Lyon 1 of Villeurbanne (France).

**Diagnosis:** Small *Heteroceras* ORBIGNY, 1849, of hamuliniform morphology with a relatively slow growth rate, having a small helix, a long and thin *proversum* and a *retroversum* approximately half the length of the shell. The ribbing is very regular and consists of simple ribs on most of the shell, with bifurcated ribs present only on or near the *flexus*.



**Table 3:** Ribbing density measurements of *Heteroceras gracile* sp. nov.

no.					
FSL13388	<i>h</i> 4.2	6.3	8.6	13.7	
	<i>N</i> 4	5	6	8	
mot02	<i>h</i> 6.4				
	<i>N</i> 6				
mot03	<i>h</i> 4.6	6.5	8.5	11.8	
	<i>N</i> 4	5	6	6	
mot04	<i>h</i> 3.7	8.4	11.5		
	<i>N</i> 5	11	9		
mot05	<i>h</i> 4	7.2	11.1		
	<i>N</i> 4	7	7		
mot06	<i>h</i> 5.1	7.6			
	<i>N</i> 5	6			
mot07a	<i>h</i> 4.9	8.2	10.7	14.9	
	<i>N</i> 5	7	10	9	
mot07b	<i>h</i> 3.2	6.6			
	<i>N</i> 3	6			
mot09	<i>h</i> 4	6.1	10.7	13.2	
	<i>N</i> 5	5	9	8	
mot10	<i>h</i> 4.4	5.5	8.8		
	<i>N</i> 5	5	6		
mot11	<i>h</i> 5.2	7.2	14.4		
	<i>N</i> 5	5	7		
mot12	<i>h</i> 7.5	10.9	17.3		
	<i>N</i> 7	9	10		
mot13	<i>h</i> 8	14.2			
	<i>N</i> 6	8			
mot14	<i>h</i> 5.5	9.4	11.6		
	<i>N</i> 5	6	6		
mot16	<i>h</i> 7.3	8.7	13.8		
	<i>N</i> 6	6	6		
mot17	<i>h</i> 6.5	9.3	13.5		
	<i>N</i> 7	8	8		
mot18	<i>h</i> 7.1	12.4			
	<i>N</i> 5	6			
mot19	<i>h</i> 5.1	7.2	11.7		
	<i>N</i> 5	6	7		
mot20	<i>h</i> 5.4	13			
	<i>N</i> 5	8			
RG419a	<i>h</i> 4.6	7.4	12.6		
	<i>N</i> 6	8	7		
RG419b	<i>h</i> 11.2	10.6			
	<i>N</i> 5	6			
MOT GDB 01	<i>h</i> 6.8	9.2			
	<i>N</i> 6	6			
MOT GDB 02	<i>h</i> 3.4	7.6	12		
	<i>N</i> 4	6	8		
MOT GDB 03	<i>h</i> 7.2	8.8	13.8		
	<i>N</i> 6	7	8		
MOT GDB 06	<i>h</i> 3.6	5.3	9.2		
	<i>N</i> 4	5	7		
28839	<i>h</i> 6.5	8	11		
	<i>N</i> 6	6	6		
28840	<i>h</i> 7	10	16		
	<i>N</i> 6	7	9		
<i>Heteroceras baylei</i> , holotype no. MHNM 1989-44	<i>h</i> <b>9.3</b>	<b>16.7</b>			
	<i>N</i> <b>5</b>	<b>5</b>			
<i>Heteroceras elegans</i> , holotype no. GIT 350/1016	<i>h</i> 8.5	9.3	14.9		
	<i>N</i> 5	6	6		
<i>Heteroceras veratiae</i> , holotype no. FCC.8A	<i>h</i> <b>5.7</b>	<b>8.6</b>			
	<i>N</i> <b>5</b>	<b>6</b>			

**Description:** Shell of small size and hamulini-form morphology. The whorl section, rarely visible in its entirety, appears to be subcircular to suboval, higher than wide. The helix, rarely preserved, is small, with whorls in contact and with both dextral (specimen no. mot10, Pl. 1, fig. 4) and sinistral coiling (specimen no. FSL13388, Pl. 1, fig. 6). The *proversum* is long, straight or slightly curved, with a relatively moderate whorl height growth (*C<sub>p</sub>* between 5.7% and 11%). On specimens with visible sutures, the body chamber begins at the top of the *proversum*, at the junction with the *flexus*. The *retroversum* is straight, half to two thirds of the total length of the shell. Growth in whorl height is increasing, particularly on the *flexus* and the start of the *retroversum*, with a *C<sub>c</sub>* growth rate of between 8% and 18%. The gap between the *proversum* and the *retroversum* is generally narrow, especially in specimens with straight *proversum*.

On the helix, the ribs are simple or sometimes bifurcated from the umbilical shoulder.

For most of the *proversum*, the ornamentation consists solely of straight, simple and regular, slightly prorsiradiate, more or less fine and dense ribs, *N* varying between 5 and 11 at whorl height *h* between 6 and 10 mm (Fig. 4). The ribs appear in the dorsal region where they can be relatively attenuated. During growth, the ribbing gradually strengthens, and, in the upper third of the *proversum*, bifurcated ribs appear, with the bifurcation point generally lying between the lower third and the middle of the flanks. The number of bifurcated ribs increases gradually.

On the *flexus*, the proportions of bifurcated and single ribs are highly variable; however, bifurcated ribs are most often predominant, with single ribs isolated and irregularly arranged, or even absent.

On the *retroversum*, the ribbing becomes even stronger and the ribs are then slightly rursiradiate, sometimes rectiradiate. It again consists mostly of simple ribs; bifurcated ribs, however, are present in the lower half of the *retroversum* where they may be dominant (specimen no. mot17, Pl. 1, fig. 7).

The peristome is not preserved on any of the specimens studied. At the approach of the peristome, the rib pattern seems to become slightly prorsiradiate again (specimens no. mot04, Pl. 1, fig. 1; no. mot09, Pl. 1, fig. 3; no. RG419a, Pl. 1, fig. 9).

Suture lines are difficult to observe in detail. They show, however, a relatively deep and feebly incised, trifid lateral lobe (specimen no. MOT GDB 02; Fig. 5).

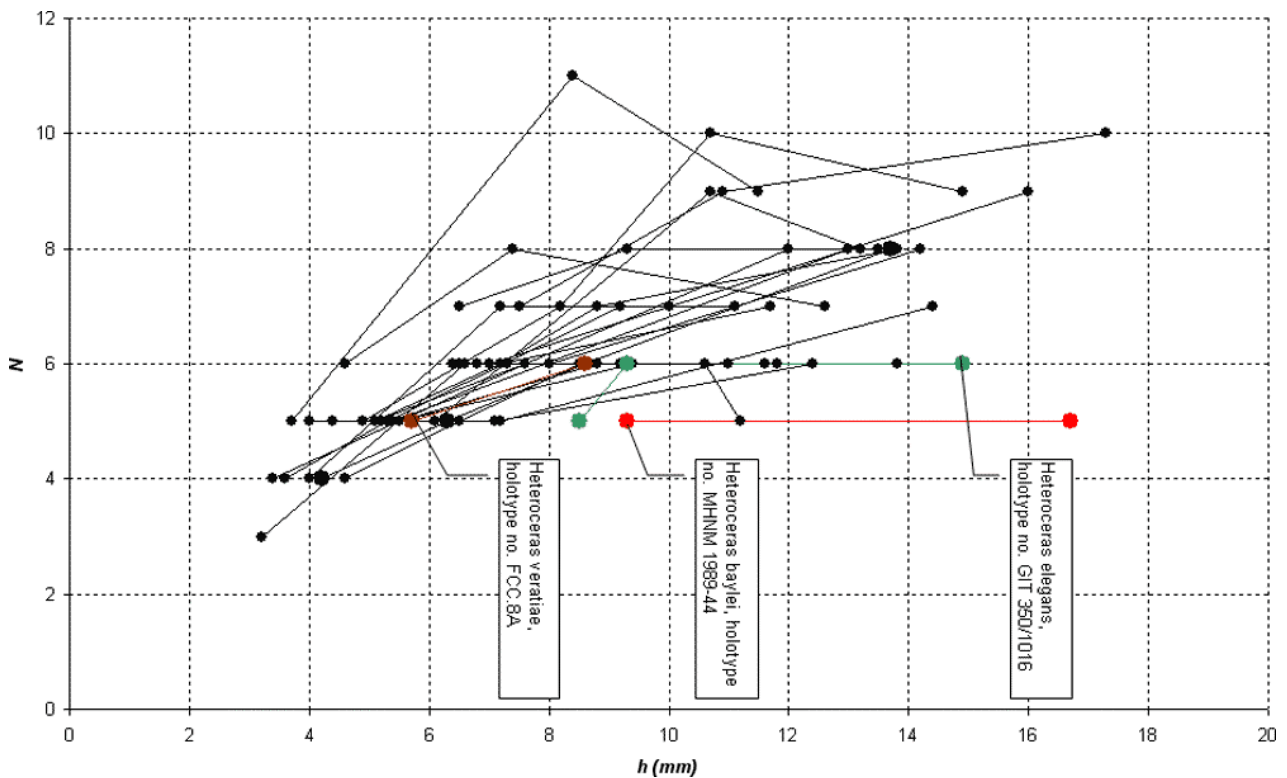


Figure 4: Ribbing density  $N$  in function of  $h$  in *Heteroceras gracile* sp. nov. (see Table 2).

#### Discussion and comparisons:

*Heteroceras gracile* sp. nov. is close to *Heteroceras baylei* (REYNÈS, 1876), of which it was considered a variant, and linked to particular ecological conditions by DELANOY (1997, p. 98). *Heteroceras gracile* sp. nov. is distinguished by its generally more hamuliform and slender form, with a much longer *proversum* and a relatively short *retroversum* that never comes into contact with the helix, as well as by its much denser ribbing (Fig. 4).

*Heteroceras gracile* sp. nov. is also close to *Heteroceras elegans* ROUCHADZÉ, 1933, whose type-specimens come from the upper Barremian ("Colchidites securiformis Zone", KAKABADZE, 1975, p. 89) of Goresha (Georgia). *Heteroceras gracile* sp. nov. differs from it by its larger size and more slender morphology, with a significantly smaller helix and a much longer and thinner *proversum*, and by its denser ribbing (Fig. 4).

*Heteroceras helicoceroides* (KARSTEN, 1858) is a small form from the upper Barremian of Colombia, known only from the original picture of KARSTEN. This makes it difficult to establish the specific characteristics of this taxon, which appears to differ from *Heteroceras gracile* sp. nov. by its less slender morphology and the chevron-like ribbing on its ventral region.

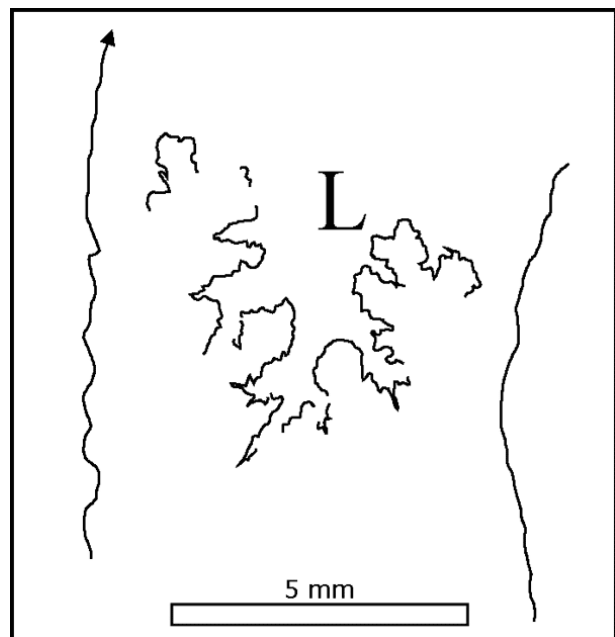


Figure 5: Detail of the suture line (lateral lobe) of *Heteroceras gracile* sp. nov. (specimen no. MOT GBD 02).



*Heteroceras vermiforme* ROUCHADZÉ, 1933, of the upper Barremian ("Colchidites securiformis Zone", KAKABADZE, 1975, p. 90) of Georgia, is known only from its holotype, which has many similarities to *Heteroceras gracile* sp. nov., in particular, a rather long *proversum* and quite similar ribbing. The very incomplete state of this holotype, figured by ROUCHADZÉ (1933, Pl. 13, fig. 5) and KAKABADZE (1975, Pl. 3, fig. 6), makes it difficult to compare the two taxa; the general morphology of the Georgian species seems less slender than that of *H. gracile* sp. nov.

*Heteroceras veratiae* FRAU *et al.*, 2016, a species known only in the *Martelites sarasini* Subzone of Cape Croisette (Marseille, France), differs from *Heteroceras gracile* sp. nov. primarily in its much smaller size which does not exceed 38 mm, and its less slender morphology. Its *proversum* and *retroversum* are clearly divergent instead of subparallel.

### III. Conclusion

The particular morphological characteristics of the specimens studied (slender and almost hamuliniform shell, long *proversum* and relatively short *retroversum*) justify the creation of the taxon *Heteroceras gracile* sp. nov. This new species makes it possible to complete the inventory of the genus *Heteroceras* ORBIGNY, 1849, particularly for small taxa. These still poorly known species are often difficult to characterize on the basis of incomplete and/or poorly stratigraphically located specimens, which preclude us from appreciating their great morphological diversity and establishing clear specific distinctions.

### Acknowledgements

We would like to thank Emmanuel ROBERT (Co-director of Geological Collections, University Lyon 1, France) for his hospitality during our investigations of the collections of the Claude Bernard University, and both Keith P. MINOR (University of Texas at Austin, USA) and Stephen CAREY (Federation University, University of Ballarat, Australia) for the improvement of the English text. We also warmly thank our reviewers Miguel COMPANY (Granada University, Spain) and Zdeněk VAŠIČEK (Academy of Sciences, Czech Republic) for their constructive remarks.

### Bibliographic references

- BERT D., DELANOY G. & BERSAC S. (2008) – Nouveaux biohorizons et propositions pour le découpage biozonal ammonitique du Barrémien supérieur du Sud-Est de la France.- *Carnets Geol.*, Madrid, vol. 8, no. A03 (CG2008\_A03), 18 p.
- BERT D., DELANOY G. & S. BERSAC (2011) - The Dichotomus Horizon: Proposal for a new biochronological unit of the Giraudi Zone of the Upper Barremian of southeastern France, and considerations regarding the genus *Imerites* ROUCHADZÉ (Ammonoidea, *Gassendiceratinae*).- *Carnets Geol.*, Madrid, vol. 11, no. A01 (CG2011\_A01), 12 p.
- CONTE G. (1989) - Fossiles du plateau d'Albion.- *Les Alpes de Lumière*, Forcalquier, no. 99, 75 p.
- DELANOY G. (1997) - Biostratigraphie des faunes d'ammonites à la limite Barrémien-Aptien dans la région d'Angles-Barrême-Castellane. Étude particulière de la Famille des Heteroceratidae SPATH, 1922 (Ancyloceratina, Ammonoidea).- *Annales du Muséum d'Histoire Naturelle de Nice*, t. XII, 270 p.
- DELANOY G. & BERT D. (2006) - Nouvelles unités taxonomiques de la Famille des Heteroceratidae SPATH, 1924.- *Annales du Muséum d'Histoire Naturelle de Nice*, t. XXI, p. 255-295.
- DELANOY G. & BULOT L.G. (1990) - Révision des types et figures des collections MATHERON et REYNÈS 3. Genres: *Acrioceras*, *Heteroceras*, *Kutatissites* et *Pseudocrioceras* (Ancyloceratina, Cephalopoda).- *Mésogée*, Marseille, vol. 50, p. 15-21.
- DELANOY G. & EBBO L. (2000) - Une nouvelle espèce d'*Heteroceras*: *H. mascarelli* sp. nov. (Ancyloceratina, Ammonoidea) dans le Barrémien du SE de la France.- *Annales du Muséum d'Histoire Naturelle de Nice*, t. XV, p. 1-17.
- FRAU C., DELANOY G., MASSE J.-P., LANTEAUME C. & TENDIL A.J.B. (2016) - New Heteroceratidae (Ammonoidea) from the late Barremian succession of Marseille (Bouches-du-Rhône, France).- *Acta Geologica Polonica*, Warszawa, vol. 66, no. 2, p. 205-225.
- IVANOV M. & IDAKIEVA V. (2013) - Lower Aptian ammonite biostratigraphy and potential for further studies of OAE 1a in Bulgaria.- *Cretaceous Research*, vol. 39, p. 47-69.
- KAKABADZE M.V. (1975) - Lower Cretaceous heteroceratids of Georgia and adjacent regions.- *Trudy geologicheskogo Instituta Akademii Nauk GSSR* (new series), Tbilissi, vol. 47, p. 62-131.
- KARSTEN H. (1858) - Über die geognostischen Verhältnisse des Westlichen Colombien der heutigen Republiken Neu Granada und Ecuador.- *Amtlicher Bericht über Versammlung Deutscher Naturforscher und Ärzte zu Wien*, vol. 32, p. 80-117.
- KILIAN W. (1889) - Description géologique de la Montagne du Lure (Basses-Alpes).- Masson, Paris, 458 p.
- MEEK F.B. (1876) - A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri Country.- *Report of the United States Geological and Geographical Survey of the Territories*, Washington, vol. IX, 629 p.





- NIKOLOV T.G. (1964) - Barremian ammonites from north-eastern Bulgaria.- *Travaux sur la Géologie de Bulgarie* (série paléontologie), Sofia, vol. 6, p. 117-141.
- OBATA I. & OGAWA Y. (1976) - Ammonites Biostratigraphy of the Cretaceous Arida Formation, Wakayama Prefecture.- *Bulletin of the National Science Museum* (series C), Tokyo, vol. 2, no. 2, p. 93-110.
- ORBIGNY A. d' (1840-1842) - Paléontologie française, description zoologique et géologique de tous les animaux mollusques et rayonnés fossiles de France. Terrains Crétacés, Vol. I. Céphalopodes.- Masson, Paris, 662 p.
- REBOULET S., RAWSON P.F., MORENO-BEDMAR J.A., AGUIRRE-URRETA M.B., BARRAGÁN R., BOGOMOLOV Y., COMPANY M., GONZÁLEZ-ARREOLA C., IDAKIEVA STOYANOVA V., LUKENEDER A., MATRION B., MITTA V., RANDRIANALY H., VAŠÍČEK Z., BARABOSHKIN E.J., BERT D., BERSAC S., BOGDANOVA T.N., BULOT L.G., LATIL J.-L., MIKHAILOVA I.A., ROPOLO P. & SZIVES O. (2011) - Report on the 4th International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the "KILIAN Group" (Dijon, France, 30th August 2010).- *Cretaceous Research*, vol. 32, p. 786-793.
- REBOULET S., SZIVES O., AGUIRRE-URRETA B., BARRAGÁN R., COMPANY M., IDAKIEVA V., IVANOV M., KAKABADZE M.V., MORENO-BEDMAR J.A., SANDOVAL J., BARABOSHKIN E.J., ÇAĞLAR M.K., FÓZY I., GONZÁLEZ-ARREOLA C., KENJO S., LUKENEDER A., RAISOSSADAT S.N., RAWSON P.F. & TAVERA J.M. (2014) - Report on the 5th International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the KILIAN Group (Ankara, Turkey, 31st August 2013).- *Cretaceous Research*, vol. 50, p. 126-137.
- ROUCHADZÉ J. (1933) - Les Ammonites aptiennes de la Géorgie occidentale.- *Bulletin de l'Institut géologique de Géorgie*, Tbilissi, vol. I, fasc. 3, p. 165-273.



## Plate

**Plate 1:** All specimens are from Morteiron, Saint-Étienne-lès-Orgues (Alpes de Haute-Provence, France).

Fig. 1: *Heteroceras gracile* sp. nov. Specimen no. mot04, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 2: *Heteroceras gracile* sp. nov. Specimen no. mot07a, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 3: *Heteroceras gracile* sp. nov. Specimen no. mot09, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 4: *Heteroceras gracile* sp. nov. Specimen no. mot10, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 5: *Heteroceras gracile* sp. nov. Specimen no. mot12, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 6: *Heteroceras gracile* sp. nov. Holotype no. FSL13388, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. University Claude Bernard collection (Lyon, France).

Fig. 7: *Heteroceras gracile* sp. nov. Specimen no. mot17, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 8: *Heteroceras gracile* sp. nov. Specimen no. mot16, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 9: *Heteroceras gracile* sp. nov. Specimen no. RG419a, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no.  $\beta$ . BAUDOUIN collection (donated by R. GONNET).

Fig. 10: *Heteroceras gracile* sp. nov. Specimen no. mot11, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3. BAUDOUIN collection.

Fig. 11: *Heteroceras gracile* sp. nov. Specimen no. MOT GBD 02, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon. BOURNAUD collection.

Fig. 12: *Heteroceras gracile* sp. nov. Specimen no. 28840, *Imerites giraudi* Zone, *Imerites giraudi* Subzone, *Heteroceras emericianum* Horizon, bed no. 3, Morteiron, Saint-Étienne-lès-Orgues (Alpes de Haute-Provence, France). DELANOY collection.

