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New Heteroceratidae (Ammonoidea) from the late Barremian deepening succession of Marseille (Bouches-du-Rhône, France)

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ABSTRACT:

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Investigation of the late Barremian deepening succession of the Provence platform, cropping out south of Marseille (Bouches-du-Rhône, France), has yielded a new ammonite fauna belonging to the *Martelites sarasini* Subzone (*Martelites sarasini* Zone). The fauna is dominated by representatives of the Heteroceratidae Spath, characterized by different patterns of coiling, high intraspecific variabilities and dwarfism. These heteroceratids are distinctive and utterly different from all previously known taxa, and this justifies the introduction of the new taxa *Heteroceras denizoti* sp. nov., *Heteroceras veratiae* sp. nov., *Calanquites* gen. nov., based on *Imerites katsharavai* Rouchadzé; *Giovaraites* gen. nov., based on *Giovaraites massiliae* gen. et sp. nov., *Barguesiella* gen. nov., based on *Barguesiella goudesense* gen. et sp. nov. and the closely allied *Barguesiella mantei* gen. et sp. nov. The occurrence of the latter species at the top of the Maiolica Formation in Italy questions its early Aptian age assumed in the literature. The newly described fauna could be considered as the first case of micromorphy in the Heteroceratidae. Its biostratigraphy, palaeoenvironmental and palaeobiogeographical significance are discussed.

Key words: Ammonoidea; Heteroceratidae; Upper Barremian; Marseille; Southeast France; Micromorphy; Biostratigraphy.

INTRODUCTION

The Early Cretaceous succession of Provence (southeast France) consists of Valanginian to early Aptian deposits of carbonate platforms of the so-called Urgonian facies (Masse 1976). During Barremian–Aptian times, the northward progradation of the Provence platform, on the southern margin of the Vocontian Basin, was punctuated by four deepening events (Masse 1976; Masse and Fenerci-Masse 2011, 2013). The first event led to the development of an intra-shelf basin centred on the Cassis–La Bédoule area (Bouches-du-Rhône) that houses the unit-stratotype of the lower Aptian, formerly called *Bedoulian* by Toucas (1888). The deepening suc-

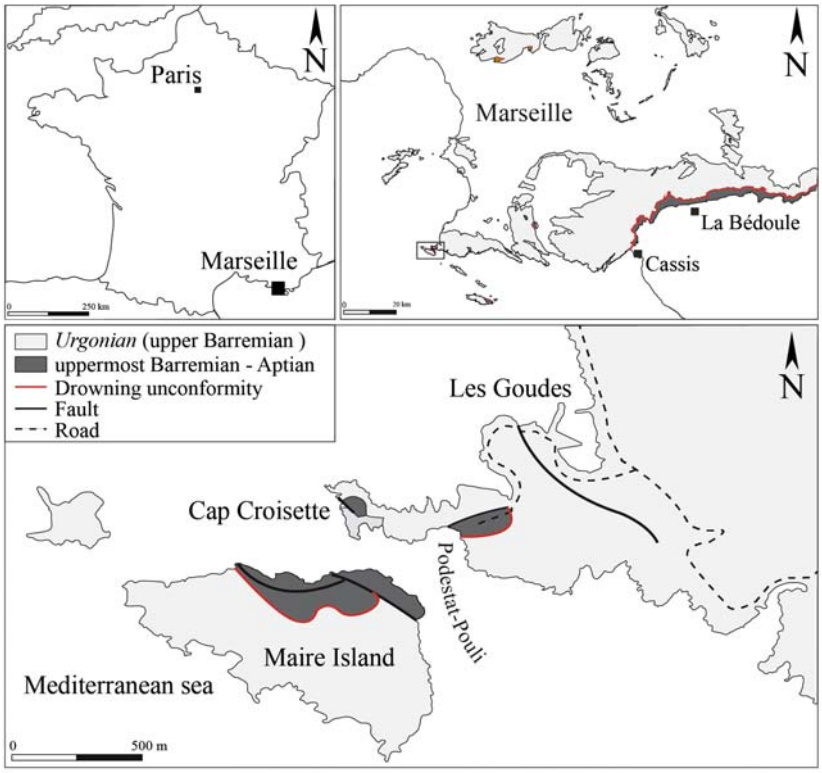
cession has been called the "*Heteroceras* horizon" after the late Barremian ammonites it apparently contains (Denizot 1934). But until recently, this palaeontological material had never been described, which is explained by the extreme rarity and poor preservational state of this fauna in the type area (Fabre-Taxy *et al*. 1963). Ropolo and Gonnet (1998) and Ropolo *et al*. (1998a, 1999) were the first to illustrate typical late Barremian ammonites from Cassis and La Bédoule. These authors reported an heteroceratid assemblage at the base of the *Pseudocrioceras waagenoides* Subzone that typifies the upper part of the *Martelites sarasini* Zone of the uppermost Barremian (in the Mediterranean standard zonation; see Reboulet *et al*. 2014). However, this heteroceratid assemblage is only known from a very limited number of specimens, together with ancyloceratids of the genus *Pseudocrioceras* Spath, 1924 which also dominate this interval. It should be noted that the validity of the *P. waagenoides* Subzone has been much debated because this genus is considered to be spatially restricted to the proximal margins of Tethyan basins (Bert *et al*. 2008; Reboulet *et al*. 2006, 2011, 2014).

Our investigation of a laterally equivalent upper Barremian section in the vicinity of Marseille (Bouches-du-Rhône, France) has revealed new heteroceratids-rich assemblages in the deepening succession. The detailed examination of the fauna has led to the introduction of new micromorphic heteroceratid genera and species. Their biostratigraphic, palaeoenvironmental and palaeobiogeographic significance are discussed below.

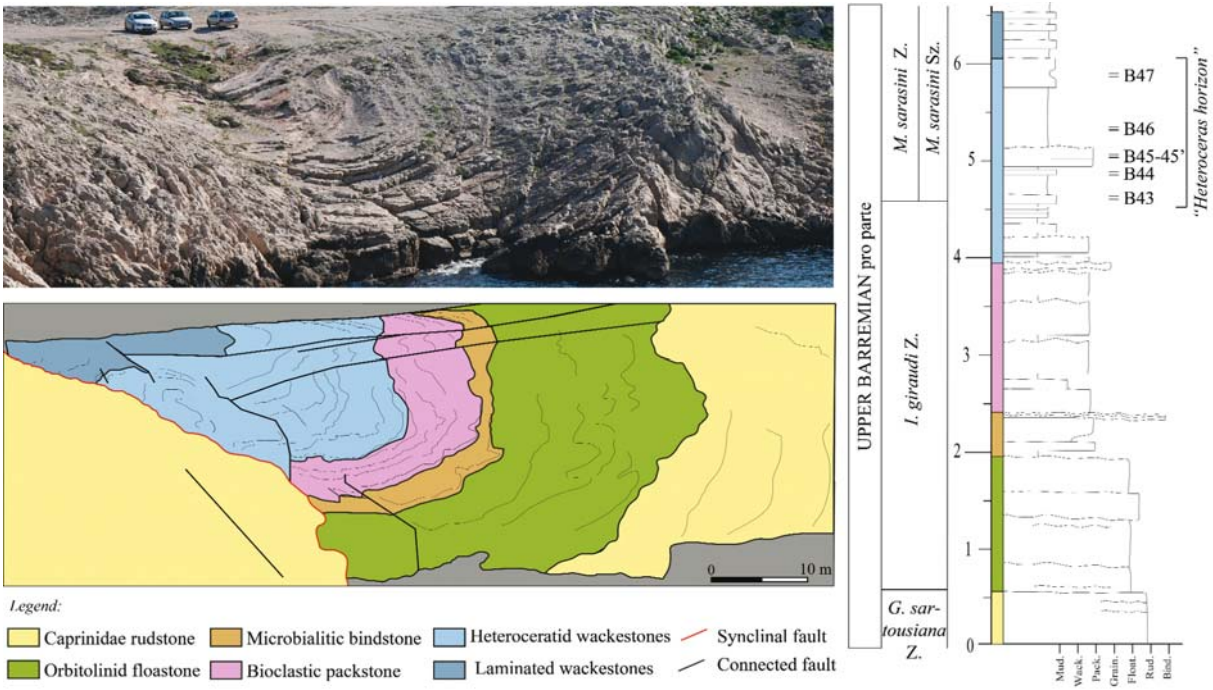
GEOLOGICAL SETTING

This study focuses on the Barremian deepening succession that crops out in the small, faulted syncline of the Podestat–Pouli cove on Cap Croisette in the Massif des Calanques (Marseille, France). This cove is located in front of the Maïre Island (Text-fig. 1).

Podestat–Pouli (Text-fig. 2) is considered as a reference section for the first deepening event of the late Barremian Provence Platform (Denizot 1934; Blanc 1960; Masse 1976) that overlaps a thick carbonate succession (units 11 to 8 *in* Blanc 1960) marked by a well-stratified caprinid-rich interval with oolithic, peloidal and schizophytoidic-rich levels. The lowest beds caused by the drowning event are medium-bedded orbitolinid-rich limestones (units 7 and 6 *in* Blanc 1960) with a burrowed surface. The top of this interval is marked by a microbialithic mamelloned crust. The fifth unit is composed by brachiopod- and serpulid-rich limestone beds, with red interbedded clays.



Text-fig. 1. Geological map of the Barremian–Aptian interval of the Cap Croisette at the south of Marseille, and its location inside southeast France. The studied area is marked by a black rectangle



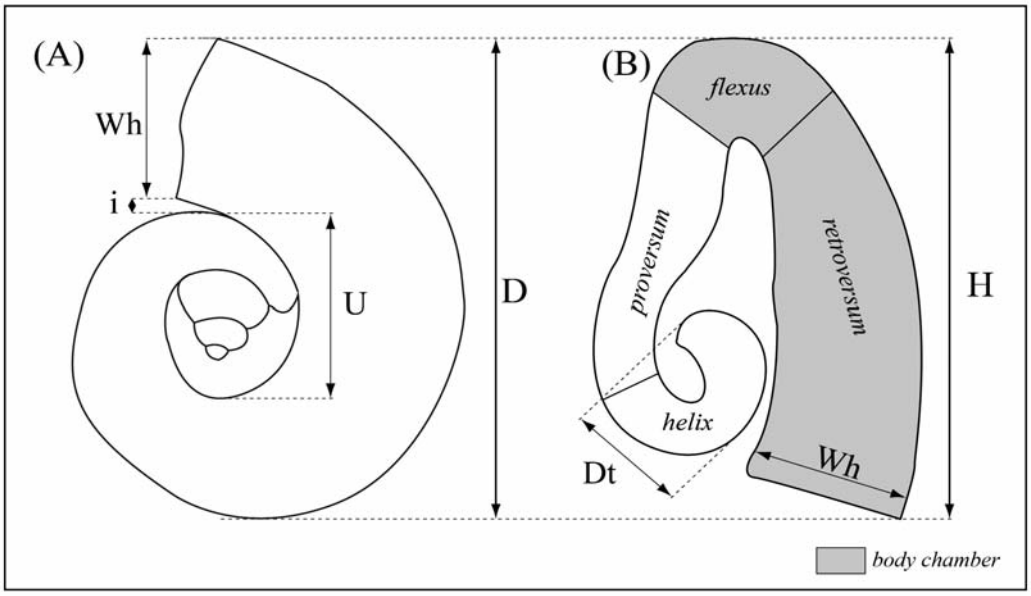
Text-fig. 2. Photograph and interpretative setting of the upper Barremian of Podestat–Pouli and its litho-, biostratigraphic scheme

As herein understood, the "*Heteroceras* horizon" is restricted to beds B43 to B47 (see Text-fig. 2) characterized by alternations of finely laminated grey micritic limestone beds, and chalky pinkish interbeds. The first ammonite assemblage (B43) is composed of numerous specimens of *Anglesites puzosianum* (d'Orbigny, 1841) and *Calanquites* gen. nov. aff. *semituberculatus* (Rouchadzé, 1933). Scarce *Calanquites* gen. nov. sp. and *Heteroceras veratiae* sp. nov. were collected from another micritic limestone bed (B44). The next assemblage (B45) is characterized by a highly fossiliferous taphocenosis of *Calanquites* gen. nov. *katsharavai* (Rouchadzé, 1933) with scarce *Heteroceras* sp. and ?*Martelites* sp. The top of this bed (B45') contains another specimens of *A. puzosianum*. The overlying chalky inter-bed (B46) contains a rich fauna composed by *Giovaraites massiliae* gen. et sp. nov., *Heteroceras veratiae* sp. nov., *Heteroceras baylei* Reynès, 1876, *Heteroceras* sp. and *Barguesiella mantei* gen. et sp. nov. A thick white limestone bed (B47) ends the „*Heteroceras* horizon*"* and contains *Barguesiella goudesense* gen. et sp. nov. and *Heteroceras denizoti* sp. nov. Above the „*Heteroceras* horizon", the section is ended by several limestone beds lacking body fossils (units 1 *in* Blanc 1960) affected by small-scale, synsedimentary breccias.

Reboulet *et al.* 2014			
Stages	**Zones**	**Subzones**	**Horizons**
upper Barremian	*M. sarasini*	*P. waagenoides*	
		M. sarasini	
			A. puzosianum
	I. giraudi	*H. emerici*	
		I. giraudi	
	G. sartousiana	*H. feraudianus*	
		G. provincialis	
		G. sartousiana	

Text-fig. 3. The upper Barremian (*pro parte*) standard zonation (Reboulet *et al.* 2014) used in this work

In terms of biostratigraphy, this work confirms the occurrence of the index-species *A. puzosianum* at the base of the "*Heteroceras* horizon", as originally reported by Masse (1976). This species actually typifies the base of the late Barremian *M. sarasini* Subzone (*Martelites sarasini* Zone) of the Mediterranean standard zonation



Text-fig. 4. Shell parameter indices for quasi-planispiral (A) and tripartite (B) heteromorph forms. The following abbreviations indicate: D: diameter of the shell; Dt: diameter of the helix; U: diameter of the umbilicus; Wh: high of the whorl at the aperture or at the end of the preserved whorl ; H: total length; i: hiatus between the aperture and the inner whorl

(Reboulet *et al*. 2014) (see Text-fig. 3). Following Masse and Fenerci-Masse (2011), we agree that the deepening event is coeval with the "*Heteroceras* marls" episode *sensu* Paquier (1900), recorded in the nearby Vocontian Basin, and dated to the boundary between the *G. sartousiana* Zone and the *I. giraudi* Zone (Bert *et al*. 2008).

CONVENTIONS

The ammonite specimens described herein were collected during the summer of 2010. The creation of the *Parc National des Calanques* (spring 2012) now legally preserves these deposits against the damaging excavations they have suffered previously. The material collected is housed in the Frau collection at the *Musée de Paléontologie de Provence* (Aix-Marseille University), and numbered accordingly to these abbreviations: FCC for "*Frau Cap Croisette*", LCC for "*Lanteaume Cap Croisette*", with sample numbers.

The following acronyms of repositories indicate FSL: Université Claude Bernard, Lyon-I; MHNM: Muséum d'Histoire Naturelle de Marseille; and TSU: Ivane Javakhishvili Tbilisi State University.

Our specimens are preserved as crushed internal moulds which prevent us from giving other measurements than those reported below (Text-fig. 4). The types of heteroceratids coiling used in this work are based on those of Vašíček (1972), Kakabadzé (1988) and Delanoy (1997). The term "dwarf" is used in the sense of an adult of atypically small size, and does not refer to any genetically controlled arrest of growth.

SYSTEMATIC PALAEONTOLOGY

Class Cephalopoda Cuvier, 1797
Subclass Ammonoidea von Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Ancyloceratataceae Gill, 1871
Family Heteroceratidae Spath, 1922
Genus *Calanquites* gen. nov.

TYPE SPECIES: *Imerites Katsharavai* Rouchadzé, 1933.

DERIVATION OF NAME: Refers to the so-called *Massif des Calanques* to the south of Marseille.

INCLUDED SPECIES: Based on the original descriptions and pending new studies on the inter- and intraspecific variabilities of the Georgian species, *Calanquites* gen. nov. comprises the taxa *Imerites katsharavai* Rouchadzé, 1933, *I. microcostatus* Rouchadzé, 1933 and *I. semituberculatus* Rouchadzé, 1933. The species *I. ladjanuriensis* Rouchadzé, 1933 and *I. tcholashensis* Rouchadzé, 1933, based on poorly preserved type specimens, doubtfully belong to *Calanquites* gen. nov.

DIAGNOSIS: Small ammonite with imericone coiling marked by small helix composed of 4-6 whorls followed by evolute planispiral part of 1 to 2 whorls. Whorl height increasing slowly. Body chamber approximately occupying last half of adult whorl. Whorl section subrectangular, higher than wide on phragmocone, becoming sub-elliptical on body chamber. After helicoidal part, venter flattened, rounded progressively at diameter of about 35-40 mm. Convex umbilical wall. Ornamentation of helix composed of dense, sinuous simple ribs. Thin peri-siphonal tubercles appear on last whorl of helix. Ventro-lateral ends of ribs strengthened on last part of phragmocone. On planispiral part, ribs simple and bifurcated, more or less spaced, crossing venter.

DISCUSSION: In the current literature, the species *I. katsharavai* is usually referred to the genus *Paraimerites* Kakabadzé, 1967, based on the poorly-known species *Heteroceras densecostatum* Renngarten, 1926 from the North Caucasus. The genus *Paraimerites* was mostly quoted from the upper Barremian of Georgia (Drushchits 1960; Tovbina 1963; Kotetishvili 1970; Kakabadzé 1971) and actually groups small to large, unituberculate imericone, heterocone and martelicone ammonites. As a result, this genus is in many ways a discarded taxon.

Paraimerites densecostatum (Renngarten, 1926) is based on four incomplete specimens. The better preserved one, illustrated by Renngarten (1926, fig. 16a–c), is here designated as lectotype. It is here re-illustrated (Pl. 1, Fig. 5a–c). The lectotype is an incomplete phragmocone of about one whorl surrounding a large helix proportional to the total diameter. The helix is dextral and bears strong sigmoid ribs with a strong forward inclination and a slight reduction of the thickness of the ribs on the siphonal area. On the last whorl of the helix, the ventro-lateral tubercles appear on both sides of the venter. After the helicoidal part, the planispiral portion is marked by a fast growth rate and an oval whorl section, higher than wide. The ornamentation is composed by dense, slightly flexuous, simple ribs that can branch with the intercalated ones. A bituberculate stage starts at the end of the helix and continues briefly on the planispiral part up to a diameter of 37 mm. These morphological and ornamental features clearly differ from the species group of *I. katsharavai* and they support the introduction of *Calanquites* gen. nov. In our view, the genus *Paraimerites* should be limited to its type species and probably the taxon *I. planus* Kotetishvili, 1970 non Rouchadzé, 1933.

Calanquites katsharavai (Rouchadzé, 1933)
(Pl. 1, Figs 1a–c, 2, 3a, b, 4; Pl. 2, Figs 1, 2, 3, 4; Pl. 3, Figs 9, 10)

1933. *Imerites Katsharavai*; Rouchadzé; p. 262, pl. 21, fig. 7.

pars 1934. *Hoplites Feraudi* (d'Orbigny, 1841); Denizot, p. 156, pl. 5, non fig. 12 (= *H. feraudianus*), 13.

1955. *Colchidites (Imerites) katsharavai* (Rouchadzé); Eristavi, p. 129.

1963. *Imerites* aff. *katsharavai* (Rouchadzé); Tovbina, p. 108, pl. 3, fig. 3.

1970. *Imerites katsharavai* (Rouchadzé); Kotetishvili, p. 87, pl. 15, fig. 2a, 2b.

1971. *Paraimerites katsharavai* (Rouchadzé); Kakabadzé, p. 87, pl. 22, fig. la, 1b (= Kotetishvili 1970, pl. 15, fig. 2a, 2b)

TYPE: As noticed by Klein *et al*. (2007), the designation of the type specimen by Kakabadzé (1971, p. 87) was done without referring to an illustration. According to the authors, the lectotype should be specimen no. TSU485/1151 illustrated by Rouchadzé (1933, p. 262, pl. 21, fig. 7), and is re-illustrated herein on Pl. 1, Fig. 1a–c.

TYPE LOCALITY: Nicortsminda, Racha region, western Georgia. The type horizon is not documented originally.

MATERIAL: Fifteen specimens: LCC 3, 9, 11, 13, 14 and FCC 2, 3, 4, 28, 29, 30a, 30b, 30c, 36, 37 from B45.

DESCRIPTION: A detailed examination of the material collected at Podestat–Pouli allows the distinction of two morphotypes, which differ in their size and ornamentation.

Morphotype A: These are medium forms (Dmax ~ 40–60 mm) with imericone coiling. The ornamentation is composed of dense, sinuous, simple ribs and thin peri-siphonal tubercles on the last part of the helix that are generally poorly-preserved on the material at our disposal.

The planispiral part is evolute, more or less elliptical, and consists of about two whorls in which the body chamber occupies approximately the last half. The ornamentation consists of simple, sometimes bifurcated, straight to slightly sinuous ribs throughout the ontogeny that cross the venter. On the phragmocone, the ribs show ventro-lateral thickening and they disappear at a diameter of about 35–40 mm. Then, the ribbing strengthens in the adult whorl. The aperture is characterized by a slight reduction in the height of the adult whorl and the presence of two joined ribs at the peri-umbilical margin. In some specimens, the second half of the body-chamber is slightly uncoiled.

Morphotype B: This morphotype represents smaller forms (Dmax < 25–40mm) with denser ribbing at all ontogenetic stages. The helix of this morphotype is unknown. The planispiral part of the shell is composed approximately of two whorls. The ornamentation consists of dense, thin, straight, rectiradiate or prorsiradiate, simple ribs (e.g. almost 40 ribs at a diameter of 20mm). Some ribs are bifurcated on the outermost flank. All the ribs are of regular thickness and cross the venter.

On the body chamber, the ornamentation is composed by more spaced, simple ribs that are slightly rursiradiate on the lower flank and then rectiradiate. When preserved, the aperture is as in morphotype A.

MEASUREMENTS (mm):

Morphotype A			
Specimen	D	U	Wh
LCC 9	54.0	25.2	17.0
FCC 36	*c*.52.0	24.0	17.0
LCC 3	45.0	16.0	16.5
FCC 4	*c*.40.0	25.5	13.5
Morphotype B			
Specimen	D	U	Wh
FCC 28	38.0	17.0	11.4
FCC 30a	36.5	14.5	14.0
FCC 30c	35.5	14.0	14.2
FCC 37	35.0	16.7	10.0
FCC 30b	34.4	14.0	12.4
FCC 3	21.5	11.2	10.4

DISCUSSION: Morphotype A of *Calanquites katsharavai* matches well the original description and illustration of the type specimen of the species. It should be noted that Morphotype B differs by its smaller adult size, and its denser and uniform ribbing, especially on the body chamber. This morphotype shares great morphological and ornamental affinities with morphotype B of *Calanquites* aff. *semituberculatus* (Rouchadzé 1933), described below. The latter form differs in having a flexuous ribbing on the planispiral part and the presence of fine intercalated and bifurcated ribs on the body chamber.

The co-occurrence of the two morphotypes of *C. katsharavai* in level B45 could be related to intraspecific variability or sexual dimorphism. In the latter case, morphotype A should be considered the macroconch. The sampling of a larger population and its study with a palaeobiologic approach could solve this problem.

OCCURRENCE: At Podestat–Pouli, *C. katsharavai* first occurs in the second level (e.g. B45) with *A. puzosianum* (*M. sarasini* subzone, *M. sarasini* Zone). Beside this report, *C. katsharavai* also occurs in the heteroceratid-rich assemblage of the „*Colchidites*“ *securiformis* Zone of Georgia (Kakabadzé 1971, 1989; Kakabadzé and Kotetishvili 2003). This occurrence is considered below in great detail.

Calanquites aff. *semituberculatus* (Rouchadzé, 1933) (Pl. 2, Figs 5, 6, 7, 8)

1933. *Imerites semituberculatus*; Rouchadzé, p. 263, pl. 21, fig. 10.

TYPE: As noticed by Klein *et al*. (2007), the designation of a neotype (specimen no. TSU374/45 from the Kakabadzé collection) by Kakabadzé (1971, p. 84) has been done without description and illustration. Our concept of the species is herein based on the specimen illustrated by Rouchadzé (1933, p. 263, pl. 21, fig. 10).

TYPE LOCALITY: Nicortsminda, Racha region, western Georgia. The type horizon is not documented originally.

MATERIAL: Six specimens: FCC 44, 45, 46 47, 48 and 49 from B43.

DESCRIPTION: The material at our disposal allows the recognition of two morphotypes.

Morphotype A: This morphotype is known from only one specimen, with a diameter of 67 mm. Its helix and inner whorls are covered by matrix and this does not allow the description of morphological and ornamental features. The last-preserved portion of the whorl only shows thin and rectiradiate ribs. At the end of the phragmocone, the ribs are thicker, rectiradiate, simple or bifurcated. The maximum thickness of the ribs occurs on the upper part of the flanks. On the body chamber, the ornamentation is comprised of sinuous, simple ribs that are strongly rursiradiate on its first half and beginning rectiradiate on its second. The aperture is marked by two bifurcated ribs from the peri-dorsal margin with a sinuous peristome.

Morphotype B: These are small forms (Dmax ~ 40mm), with denser ribbing throughout the phragmocone and at the beginning of the body chamber. No helix is preserved. The planispiral part of the shell is composed of almost two whorls. On the phragmocone, the ornamentation consists of dense, rursiradiate and/or rectiradiate, simple ribs that may bifurcate on the upper flank. The ribbing regularly strengthens from the

peri-umbilical margin to the venter, which it crosses with its maximum thickness. Small tubercles seem to arise on the latero-ventral margin throughout the phragmocone. On the body-chamber, the ribbing strengthens moderately, but at first it is similar to that on the phragmocone. Then, the ribbing becomes more irregular and is composed of uniform, sinuous, simple and bifurcated ribs with thin, irregularly disposed intercalatories.

MEASUREMENTS (mm):

Morphotype A			
Specimen	D	U	Wh
FCC 47	67.0	28.3	23.4
Morphotype B			
Specimen	D	U	Wh
FCC 45	41.0	18.4	18.9
FCC 48	37.0	18.4	12.0
LCC 44	36.0	14.5	13.0
FCC 49	33.3	13.3	11.7
FCC 46	25.0	10.3	8.0

DISCUSSION: Morphotype A of *C.* aff. *semituberculatus* differs from morphotype A of *C.* gen. nov. *katsharavai* by having dense, sinuous ribs on the body chamber and probably, also on all the inner whorls. Morphotype B of *C.* aff. *semituberculatus* shows great morphological and ornamental affinities with *Imerites microcostatus* Rouchadzé and *I. semituberculatus* Rouchadzé, that were synonymised by Kakabadzé (1971). Morphotype B of *C. katsharavai* differs by the frequent presence of sinuous ribs and in having intercalatory and bifurcated ribs on the planispiral part of the shell.

OCCURRENCE: At Podestat–Pouli, *C.* gen. nov. aff. *semituberculatus* comes from the first horizon of *A. puzosianum* (*M. sarasini* subzone, *M. sarasini* Zone). Beside this report, *C. katsharavai* was also reported from the heteroceratid-rich assemblage of the „*Colchidites*“ *securiformis* Zone of Georgia (Kakabadzé 1971, 1989; Kakabadzé and Kotetishvili 2003).

Genus *Barguesiella* gen. nov.

TYPE SPECIES: *Barguesiella goudesense* gen. et sp. nov.

DERIVATION OF NAME: Named in honour of Bonnie Bargues (of Marseille) for her help in the field and continuous support to one of us (C.F.) during the preparation of this work.

INCLUDED SPECIES: This new genus contains its type species and *Barguesiella mantei* gen. et sp. nov.

DIAGNOSIS: Small ammonite with small to medium helix followed by strong to moderately open coiling, composed of about one whorl. After helicoidal part, whorl section suboval in all ontogenetic stages, with slightly convex umbilical wall. Ornamentation of helix composed of slightly flexuous and simple ribs. On uncoiled whorl, ornamentation composed by simple and/or bifurcate or intercalatory ribs, straight or slightly flexuous. All ribs crossing venter at all ontogenetic stages.

DISCUSSION: The combination of small size, very open coiling and atuberculate ribbing distinguishes *Barguesiella* gen. nov. from the great majority of heteroceratid species in the *M. sarasini* Zone.

The general features of *Barguesiella* gen. nov. can be confused with those of the leptoceratid species *A. puzosianum* but the new genus strongly differs in the presence of a helix in the inner whorls and the very open criocone coiling comprising only one adult whorl. In addition, none of the studied specimens shows acrioceratid coiling as the kind sometimes encountered in *A. puzosianum*.

Barguesiella goudesense gen. et sp. nov.
(Pl. 3, Figs 1, 2, 3, 4, 5)

TYPE: The holotype (Pl. 3, fig. 3) is specimen no. LCC.14a from bed B47.

DERIVATION OF THE NAME: Name refers to the port of Les Goudes of the Massif des Calanques.

TYPE LOCALITY: Podestat–Pouli, Cap Croisette (Marseille, southeast France).

MATERIAL: Five specimens: LCC 11, 13, 14a, 14b and 50 from B47.

DIAGNOSIS: Typical *Barguesiella* with dense, more or less flexuous ribs. Some intercalatory and/or secondary ribs are present on the uncoiled adult whorl.

DESCRIPTION: *Barguesiella goudesense* gen. et sp. nov. is a small ammonite (Dmax ~ 45 mm) marked by a small helix followed by only one open, more or less elliptical crioconic adult whorl with a slow grow rate. The body chamber constitutes the last half of the last whorl. The helix is composed by 2-3 whorls with rounded, thin, slightly flexuous ribs. There is no rib bifurcation on

the flanks of the helix. On the last whorl, the ornamentation is composed by dense, more or less prorsiradiate, more or less flexuous, single ribs. Some intercalatory ribs occur that originate from the middle or third quarter of the flanks. In some specimens, the ribs are strongly inclined forward on the upper flank. The ribs become thicker on the second half of the body chamber. The peristome is unknown.

MEASUREMENTS (mm):

Specimen	D	U	Wh
FCC 50	*c*.43.0	20.5	*c*.11.0
LCC 13	39.0	29.0	10.0
LCC 14b	37.0	16.8	10.5
LCC 11	35.0	16.5	11.0
LCC 14a	34.5	17.5	10.0

DISCUSSION: At Podestat–Pouli, *Barguesiella goudesense* gen. et sp. nov. follows *Barguesiella mantei* gen. et sp. nov. in the succession. *B. mantei* differs from our new species in the ornamentation of its last criocone whorl, which bears distant, elevated simple ribs with marginal thickening at their latero-ventral ends.

OCCURRENCE: To date, the species is only known from one stratigraphic level (B47) at Podestat–Pouli above the two horizons with *A. puzosianum* (*M. sarasini* Subzone, *M. sarasini* Zone).

Barguesiella mantei gen. et sp. nov.
(Pl. 3, Figs 7, 8, 9)

2000. *Leptoceratoides hoheneggeri* (Vašíček and Wiedmann); Landra, Cecca and Vašíček, p. 38, pl. 2, figs 1–4.

TYPE: The holotype (Pl. 3, Fig. 7) is the specimen no. FCC.13 from B46.

DERIVATION OF NAME: Named in honour of Alain Mante (Conservatoire d'espaces naturels de Provence-Alpes-Côte d'Azur, Marseille) for his help in the field undertaken in the Massif des Calanques.

TYPE LOCALITY: Podestat–Pouli, Cap Croisette (Marseille, southeast France).

MATERIAL: Three specimens: FCC 13, 15a and LCC 8 from B46.

DIAGNOSIS: Typical *Barguesiella* with distant, robust, more or less straight, simple ribs on criocone adult whorl. Ribs with more or less pronounced thickening on latero-ventral margin.

DESCRIPTION: *Barguesiella mantei* gen. et sp. nov. is a small ammonite composed of a small helix followed by only one open criocone adult whorl with a slow grow rate. The body chamber comprises the second half of the last whorl. The helix is similar to those of *B. goudesense* gen. et sp. nov. The ornamentation of the final whorl is composed of more or less straight, simple ribs that become slightly prorsiradiate at the end of the body chamber. The ribs number is about 40 on the last whorl. Bifurcate ribs are very rare. The ribs bear small thickenings on the latero-ventral margin before crossing the venter and they thicken strongly as they cross the venter. The peristome is unknown.

MEASUREMENTS (mm):

Specimen	D	U	H
FCC 13	38.0	19.5	10.0
FCC 15a	36.0	21.0	10.5
LCC 8	*c*.23.5	12.4	7.5

DISCUSSION: The specimens illustrated by Landra *et al*. (2000, pl. 2, figs 1–4) under *Leptoceratoides hoheneggeri* (Vašíček and Wiedmann, 1994) from the top of the Maiolica Formation (Lombardy, Italy) match well the type material of *Barguesiella mantei* gen. et sp. nov. In this connection, Delanoy and Busnardo (2007) previously considered that these specimens were typical representatives of the Heteroceratidae, because of the presence of the helix in the inner whorls (e.g. the last whorl of a helix is visible on the specimen N. 8234 (K 126), see Landra *et al*. 2000, pl. 2, fig. 2), a characteristic that had been overlooked by the authors. Thus, the occurrence of *Barguesiella mantei* gen. et sp. nov. brings into question the age of the top of the *Maiolica* Formation repeatedly assigned to the lower Aptian. The biostratigraphic implications of this observation are discussed further below.

OCCURRENCE: B46 of the Podestat–Pouli section, base of the *M. sarasini* Subzone (*M. sarasini* Zone) above the two horizons with *A. puzosianum*. The new species is only known to date in southeast France and northern Italy.

Genus *Martelites* Conte, 1989

TYPE SPECIES: *Martelites marteli* Conte, 1989, by original designation.

?*Martelites* sp.
(Pl. 4, Fig. 11)

MATERIAL: One specimen: FCC 5 from B45.

DESCRIPTION: Very small specimen with a medium helix, as a proportion to the total diameter followed by a short surrounding planispiral whorl that probably corresponds to a part of the body chamber. The helix is dextral, with rounded, simple, rursiradiate ribs. On the planispiral part, the ornamentation changes, to straight, relatively strong and simple ribs with scarce intercalatories or bifurcations.

MEASUREMENTS (mm):

Specimen	D	U	Wh
FCC 5	*c*.31.0	13.5	*c*.19.0

DISCUSSION: With some reservations, we assign a poorly-preserved specimen to *Martelites*, a genus introduced for large recoiled heteroceratids from the upper Barremian of the Plateau d'Albion (Vaucluse Department, France). It was subsequently amended by Delanoy (1994, 1997) to group small to large martelicone species, some of which had been originally included in the genus *Colchidites* Djanélidzé, 1926. In the Vocontian Basin, the genus is well represented in the lower part of the *M. sarasini* Subzone by its index species (Delanoy 1994, 1995, 1997). At Cassis–La Bédoule, Ropolo *et al*. (1999) reported and illustrated large specimens of *M*. aff. *vulanensis* Egoian, 1965 and *M*. gr. *marteli* Conte, 1989 in the uppermost Barremian. However, the specimen of *Martelites* sp. B is too poorly preserved to allow a specific determination and a comparison with these forms. Also, we cannot state if ?*Martelites* sp. is an incomplete juvenile or a dwarf adult. The suture lines are too poorly preserved to provide an answer.

OCCURRENCE: At Podestat–Pouli, ? *Martelites* sp. originates from the second level with *A. puzosianum*, at the base of the *M. sarasini* Subzone (*M. sarasini* Zone).

Genus *Giovaraites* gen. nov.

TYPE SPECIES*: Giovaraites massiliae* gen. et sp. nov.

DERIVATION OF NAME: Named in honour of Dr. Robin Giovara (La Ciotat) for his continuous support during the fieldtrips of the first author.

INCLUDED SPECIES: The new genus is monospecific.

DIAGNOSIS: Small heteroceratid ammonite with elliptical martelicone coiling. Medium helical part, comprising 3-4 whorls, surrounded by planispiral part of about one whorl. Body chamber occupying almost half of last whorl. Slightly uncoiled adult whorl. Height of whorl increases progressively throughout ontogeny. Ornamentation composed of straight to slightly concave, simple or bifurcated ribs crossing venter at all ontogenetic stages. Intercalate ribs noticed.

DISCUSSION: *Giovaraites* gen. nov. possesses a general martelicone coiling with a loosely coiled and moderately projected adult whorl. The peculiar morphology of the shell shares some affinities with the species *Heteroceras blaronense* Delanoy and Bert, 2006, but it differs in its smaller size, tightened coiling, higher growth rate and strong rectiradiate ribs near the aperture. Also, *H. blaronense* occurs only at the top of the *H. feraudianus* Zone.

Giovaraites gen. nov. shows also some affinities with the group of "*Colchidites" securiformis* that occurs in the heteroceratid-rich assemblage of Georgia. "*Colchidites" securiformis* was previously referred with a doubt to the genus *Martelites* by Delanoy (1997). However, Delanoy (1994) had previously stated that the species should be removed from the *Martelites* because of its general morphological features and ecological preferences. In any case, "*Colchidites" securiformis* differs from *Giovaraites* gen. nov. by its evolute martelicone coiling, the presence of a lateral marked 'ripple' on the helix and progressive ornamental change throughout the ontogeny.

Finally, *Giovaraites* gen. nov. shares strong morphological and ornamental affinities with the smaller representatives of the genus *Martelites*, which can be distinguished by its typical martelicone coiling with tightly coiled whorls. Some confusion may exist with incomplete *Martelites* specimens but the earlier development of the body chamber and peculiar morphology make it possible to easily distinguish *Giovaraites* gen. nov.

Giovaraites massiliae sp. nov.
(Pl. 3, Fig. 6; Pl. 5, Figs 1, 2, 3, 4, 5; Pl. 6, Fig. 7)

TYPE : The holotype (Pl. 5, Fig. 4) is the specimen FCC FO from B46.

DERIVATION OF NAME : After the ancient Greek name of the town of Marseille.

TYPE LOCALITY: Podestat–Pouli, Cap Croisette (Marseille, southeast France).

MATERIAL: Twenty specimens: FCC 28x from bed 45; FCC FO and LCC 6, 7, 9, 12, 15b, 16a, 17, 18, 20, 22, 23a, 27, 30, 31, 32, 33, 34a from B46 and FCC 51 from B47.

DIAGNOSIS: As for the genus.

DESCRIPTION: This is a small-size heteroceratid ammonite with more or less elliptical martelicone coiling. The helix is of medium size compared to the total diameter, and composed by 3-4 whorls. The ornamentation of the helix is hardly distinguishable, but seems to be composed of sinuous, rounded ribs. The transition between the helix and the planispiral whorl almost forms a short, slightly curved proversum (e.g. pseudo-shaft). The body chamber begins in or after the curved portion that follow the pseudo-shaft. The body-chamber is markedly convex, in contact with the last whorl of the helix before markedly uncoiled at the aperture. The ornamentation of the phragmocone consists of rursiradiate or prorsiradiate, simple and bifurcate ribs. Intercalate ribs are sometimes observed. On the pseudo-shaft, the ribs are simple and more or less straight. All ribs cross the venter with a limited strength. At the beginning of the body-chamber, the ribs are stronger and progressively spaced. They are more or less flexuous, rursiradiate and they often bifurcate at mid flank.

MEASUREMENTS (mm):

Specimen	D	U	Wh	i
FCC 28x	46.5	16.5	28.5	–
FCC 31	62.0	27.0	18.5	3.0
FCC FO	*c*.60.0	22.0	*c*.21.0	5.5
FCC 22	54.5	22.7	18.0	3.0
FCC 17	*c*.49.0	22.0	*c*.16.5	1.8
FCC 27	48.5	16.0	18.0	0.0
FCC 12	46.0	20.5	16.0	2.0
FCC 30	*c*.44.5	19.0	16.0	4.6
FCC 51	45.0	21.5	13.5	–
FCC 9	42.0	16.0	14.0	0.5
LCC 7	38.0	17.0	14.5	0.0
FCC 16a	36.0	16.0	17.0	0.0

DISCUSSION: By its peculiar morphological and ornamental features, *Giovaraites massiliae* gen. et sp. nov. can easily be distinguished from the new genera and species herein described.

A coiling variation occurs on the last adult whorl, that may be more or less loosely uncoiled from the inner helicoidally whorls.

OCCURRENCE: *Giovaraites massiliae* gen. et sp. nov. occurs in a great number at the base of the *M. sarasini* Subzone (*M. sarasini* Zone) above the *A. puzosianum* horizon but it is rare in the last bed (bed 45) of this horizon. The species is only known to date in southeast France.

Genus *Heteroceras* d'Orbigny, 1850

TYPE SPECIES: *Turrilites Emericianus* d'Orbigny, 1842, by subsequent designation of Meek (1876).

Heteroceras baylei Reynès, 1876
(Pl. 6, Figs 1–6)

1876. *Heteroceras baylei* sp. nov.; Reynès, p. 107.
1955. *Leptoceras* (? *Lytocrioceras*) *sabaudianum* Pictet and de Loriol sp. var *non tuberculata* nov. Sarkar, p. 140, pl. 10, fig. 14.
1964. *Anahamulina subcylindrica* (d'Orbigny); Nikolov, p. 126, pl. 4, fig. 6; pl. 5, fig. 1, 2.
1980. *Heteroceras astieri* d'Orbigny; Thomel, p. 54, fig. 93.
1988. *Heteroceras elegantoides* Kakabadzé, p. 451, text-fig. 2.25.
pars 1989. *Heteroceras* cf. *elegans* Rouchadzé; Conte, p. 41, ? figs 9–12,
1990. *Heteroceras baylei* Reynès; Delanoy and Bulot, p. 17, pl. 2, fig 4–6 [lectotype].
1992. *Heteroceras baylei* Reynès; Delanoy, p. 119, pl. 36, figs 2, 3, 4, 6.
1994. *Heteroceras baylei* Reynès; Delanoy, pl. 1, figs 2, 4.
1997. *Heteroceras baylei* Reynès; Aguado *et al*., p. 313, fig. 5c.
pars 1997. *Heteroceras baylei* Reynès; Delanoy, p. 95, pl. 9, fig. 3a, 3b; pl. 13, figs 4, 5; pl. 14, figs 4–7; pl. 16, ? fig. 3; pl. 20, figs 2–4; pl. 50, figs 4, 8; pl. 51, figs 2, 3, 4, 5, 6a, b, 6e, 7, 8; text-figs 58, 59.
1997. *Heteroceras* aff. *baylei* Reynès; Delanoy, pl. 19, fig. 2.
1997. *Heteroceras* gr. *baylei* Reynès; Delanoy, pl. 50, figs 6, 7.
1998. *Heteroceras* gr. *baylei* Reynès; Arnaud *et al*., pl. 5, fig. 13, pl. 6, figs 2, 3 (= Delanoy, 1997, pl. 50, fig. 6, 7), pl. 5, fig. 11.
?1998a. *Colchidites* aff. *tsholashensis* (Rouchadzé); Ropolo, Gonnet and Conte, p. 86, pl. 1, fig. 3.
?1999. *Colchidites* aff. *tsholashensis* (Rouchadzé); Ropolo, Gonnet and Conte, p. 161, pl. 3, fig. 3a, b.
2012. *Heteroceras baylei* Reynès; Baudouin *et al*., p. 647, pl. 7, figs 8, 9.

TYPE: The lectotype no. MHNM.1989-44 from the Reynès collection.

TYPE HORIZON: Le Cheiron (Alpes–de–Haute–Provence Department, France).

MATERIAL: Ten specimens: FCC 29 from B45; FCC 10, 11a, 14a, b ,16b, 23a, 23b, 24, and LCC 25 from B46.

DESCRIPTION: Small- to very small-sized *Heteroceras* with longiheterocone coiling. The shell is composed of a helix, a proversum and a long retroversum which joins the helix. The helix is generally crushed on our specimens and therefore not observable. The proversum is elongated and more or less straight or short, straight, curved or arched. Its ornamentation consists of numerous, single, regularly spaced and generally rectiradiate ribs. The flexus is more or less open. The ribs of the retroversum are similar by their shape to the ones of the proversum but they very frequently bifurcate at different heights on the flanks. Near the aperture, the ribs are single and quickly become thicker. The peri-apertural area is indicated by two ribs bifurcating from the dorsal margin.

MEASUREMENTS (mm):

Specimen	H	Dt	Wh
FCC 24	*c*. 44.5	15.0	–
FCC 10	47.0	19.0	15.0
FCC 11a	35.5	11.0	12.0
FCC 14a	34.0	13.0	12.0
FCC 16b	27.0	10.5	9.7
FCC 14b	26.2	–	9.8
FCC 16b	23.0	10.5	11.0
FCC 23b	23.0	11.0	–
FCC 23a	22.0	11.0	10.0
FCC 29	22.0	–	6.5
LCC 25	20.0	9.5	8.0

DISCUSSION: Small heteroceratid specimens with a longish final retroversum have repeatedly been referred to *H. baylei*, and the species has been widely quoted from the upper Barremian all over the world. However, it is noteworthy that the typological use of the species has neglected the existence of homeomorphy and convergence phenomenon. For example, the re-examination of the cast of the type specimen of *Heteroceras elegans* Rouchadzé, 1933 by one of us (G.D.) confirms that the Georgian species differs from *H. baylei* in its marked heterocone coiling. This challenges relevant literature (see synonymic list in Klein *et al*. 2007) that has repeatedly considered *H. elegans* as a minor subjective synonym of *H. baylei*.

Delanoy and Bulot (1990) described the lectotype of *H. baylei* from Le Cheiron (Alpes-de-Haute-Provence Department, France) and Delanoy (1997) illustrated several topotypes. Among the illustrated specimens from southeast France, several differ from the lectotype in their smaller size, a short proversum and retroversum (see for example Delanoy 1997, pl. 51, fig. 6). Similar forms also occur at Podestat–Pouli (see Pl. 6, Figs 4–6), and these are herein considered as dwarf morphotypes of *H. baylei*. It should be noted that Ropolo *et al*. (1998a, pl. 1, fig. 3; 1999, pl. 3, fig. 3a, b) illustrated under *Colchidites tsholashensis* (Rouchadzé, 1933) a specimen that only differs from the dwarf form of *H. baylei* by its greater size (H ~ 50 mm) and its marked elliptical coiling. This specimen shares great affinities with *Heteroceras eristavii* Kakabadzé, 1975 from the „*Colchidites*“ *securiformis* Zone of Georgia that can be distinguished by a proportionately large helix. New paleaontological studies are necessary to determine the relationship between *H. baylei* and this form, and if they could be fit into the intraspecific variability of *H. baylei*.

OCCURRENCE: At Podestat–Pouli, *H. baylei* was found at the base of the *M. sarasini* Subzone (*M. sarasini* Zone), within and above the two *A. puzosianum* horizons. *H. baylei* has been reported from southeast France, Bulgaria, Spain and Georgia.

Heteroceras veratiae sp. nov.
(Pl. 4, Figs 5A, B, 6–8)

TYPE: The holotype (Pl. 4, Fig. 4) is specimen FCC.8A from B44.

DERIVATION OF THE NAME: Named in honour of Chrystèle Verati, geochronologist at the Nice–Sophia Antipolis University, France.

MATERIAL: Eight specimens: FCC 7, 8a, 8b, 27a, 27b, 38, 39, 40 from B44.

DIAGNOSIS: Very small *Heteroceras* with slender to robust heterocone coiling marked by long helix, straight to slightly curved proversum and short retroversum, with dense, simple, straight to slightly sinuous, prorsiradiate ribs, coarsening at end of retroversum. Ribs bifurcating on retroversum. Aperture with two simple ribs joined on peri-dorsal margin.

DESCRIPTION: This is a very small *Heteroceras* with a heterocone coiling. Its general morphology varies from slender to slightly stockier forms. The helix is composed of 3-4 whorls tightly in contact and directly linked to the base of the proversum. The proversum is more or less straight or slightly curved. The angle of the flexus is more or less open. The retroversum is moderately short. The ribbing is composed of dense (e.g. 9 and12 ribs in one centimetre in the middle proversum), simple, straight to slightly sinuous, prorsiradiate ribs that are coarser at the end of the retroversum. The ribs bifurcate on the retroversum. The aperture is characterized by two simple ribs joined on the peri-dorsal margin.

MEASUREMENTS (mm):

Specimen	H	Dt	Wh
FCC 39	38.0	–	11.0
FCC 27b	35.5	14.5	*c*.10.0
FCC 8a	33.0	11.0	9.0
FCC 7	32.5	10.4	8.0
FCC 27a	29.5	*c*.11.0	9.0
FCC 8b	29.3	–	10.0

DISCUSSION: According to Delanoy (1994, 1997), the last representatives of the genus *Heteroceras* markedly declined at the base of the *Martelites sarasini* Subzone of the Vocontian Basin, where only *H. baylei* and the poorly-known *H. fuhrae* Delanoy, 1997 have been recorded.

H. veratiae sp. nov. differs from *H. baylei* in its smaller average size, marked heterocone coiling with a short final retroversum and a rapid increase in growth rate. However, incomplete specimens of dwarf *H. baylei* can be confused with the new species.

H. fuhrae is distinguished by a greater size, a moderately large helix, and a generally robust morphology. Also, the ornamentation of its helix is marked by strong sigmoid ribs with a shallow 'ripple' at mid–flank.

Heteroceras veratiae sp. nov. is close to *Heteroceras elegans* Rouchadzé, 1933 in its size and heterocone coiling. The new species differs in its stockier morphology with a short proversum, medium helix and open flexus.

OCCURRENCE: At Podestat–Pouli, *H. veratiae* sp. nov. is found in several levels at the base of the *M. sarasini* Subzone (*M. sarasini* Zone) above the two horizons of *A. puzosianum*. The new species is known to date only in southeast France.

Heteroceras denizoti sp. nov.
(Pl. 5, Fig. 6, 7; Pl. 6, Fig. 8, 9)

TYPE: The holotype (Pl. 5, Fig. 6) is specimen FCC.25 from B47.

DERIVATION OF NAME: Named in honour of Georges Denizot (1889-1979), who greatly contributed to the knowledge of the geology of the Marseille and its surrounding areas.

MATERIAL: Four specimens: LCC 12, FCC 25, 52 and 53 from bed B47.

DIAGNOSIS: Small to very small *Heteroceras* with heterocone coiling, medium helix, curved proversum and open flexus. Ribbing uniform on proversum and flexus.

DESCRIPTION: The shell exhibits a heterocone coiling. The helix comprises three to four whorls in contact. The ornamentation of the helix is barely visible, but the ribs seems to be slightly sinuous. The proversum is more or less long, curved and marked by dense, moderately thin, more or less prorsiradiate simple ribs. The flexus is quite open with a relatively short retroversum. The same ribbing continues on the flexus. Any strengthening of the ribbing is visible on the return. On the retroversum, ribs are simple or bifurcate. On the return, ribs are also simple or bifurcate, straight to slightly sinuous. The aperture is marked by two bifurcate ribs on the peri-dorsal margin.

MEASUREMENTS (mm):

Specimen	H	Dt	Wh
LCC 12	*c*.31.0	–	*c*.5.5
FCC 25	26.0	*c*.9.0	*c*.4.0

DISCUSSION: *Heteroceras denizoti* sp. nov. shows great morphological affinities with *H. veratiae* sp. nov. but differs in that it has a more open flexus, uniform ribbing almost throughout the ontogeny. In addition, the species is stratigraphically younger than *H. veratiae* sp. nov.

Heteroceras gonneti Delanoy, 1997 shares some morphological affinities with *H. denizoti* sp. nov. but differs in its greater size and coarser ornamentation. The species is stratigraphically older since it occurs at the base of the *Imerites giraudi* Zone.

Heteroceras isocostata Kakabadzé, 1975 can be easily distinguished by its very uniform ribbing and its greater size.

Heteroceras vermiforme Rouchadzé, 1933 is based

on a poorly-preserved specimen, which prevents further comparison with *H. denizoti* sp. nov. In our opinion, and according to ICZN's rules, *H. vermiforme* must be considered as a *nomen dubium* because of its state of preservation.

OCCURRENCE: At Podestat–Pouli, *Heteroceras denizoti* sp. nov. is found at the base of the *M. sarasini* Subzone (*M. sarasini* Zone) above the two levels of *A. puzosianum*.

Family Ancyloceratidae Gill, 1871
Subfamily Leptoceratoidinae Thieuloy, 1966
Genus *Anglesites* Delanoy and Busnardo, 2007

TYPE SPECIES: *Crioceras pusozianum* d'Orbigny, 1841, by original designation of Delanoy and Busnardo (2007).

Anglesites puzosianum (d'Orbigny, 1841)
(Pl. 4, Figs 1–4)

1842. *Crioceras puzosianus*; d'Orbigny, p. 466, pl. 115 bis, figs 1, 2.
1995. *Leptoceratoides puzosianum* (d'Orbigny); Delanoy, pl. 7, figs 4, 5.
1995. *Leptoceratoides* aff. *puzosianum* (d'Orbigny); Delanoy, pl. 7, fig. 3.
1997. *Leptoceratoides puzosianum* (d'Orbigny); Delanoy, pl. 8, fig. 5; pl. 14; fig. 8; pl. 20, fig. 5; pl. 30, fig. 4.
?1998. *Parancyloceras meridionale* sp. nov. Avram *in* Avram and Melinte, p. 1127, text-fig. 4a, b, pl. 1, figs 1, 2.
2006. *Leptoceratoides puzosianum* (d'Orbigny); Busnardo and Delanoy *in* Gauthier *et al*., p. 137, pl. 23, fig. 10 [neotype].
2007. *Anglesites puzosianus* (d'Orbigny); Delanoy and Busnardo, p. 4, figs 1–4 [neotype], 6, 7, text–fig. 2.
2011. *Anglesites puzosianum* (d'Orbigny); Masse and Fenerci-Masse, fig. 9.

TYPE: The neotype FSL.85331.1 from the Busnardo collection, designated by Delanoy and Busnardo (2007).

MATERIAL: Eight specimens: LCC 1, 2, FCC 41, 42, 43 from B43 and LCC 5, 6, 15, from bed B45'.

DESCRIPTION: Small ammonite with a criocone to hoplocrioceratid–like coiling. Among the criocone specimens, the growth of the whorls is very regular until the body chamber where it is more loosely coiled. The other specimens are smaller and exhibit a short, slightly curved retroversum. In both morphotypes, the ornamentation is smooth on the innermost whorls. Regular, simple, slightly flexuous ribs progressively appear and cross the venter throughout the ontogeny. On the body-chamber, ribs are ended by a small thickening on the latero-ventral margin.

MEASUREMENTS (mm):

Crioceratic forms			
Specimen	D	U	Wh
FCC 6	31.0	*c*.13.0	11.5
FCC 42	30.0	14.6	9.7
Hoplocrioceratic forms			
Specimen	H	U	Wh
FCC 43	*c*.22.5	14.0	–
LCC 2	18.8	10.3	5.4
FCC 41	18.5	10.0	6.4

DISCUSSION: The specimens of *A. puzosianum* from bed B43 match well those from the Vocontian Basin described by Delanoy and Busnardo (2007). The co-occurrence of crioceratic and hoplocrioceratic forms supports the hypothesis of sexual dimorphism as suggested by those authors. In both areas, reports of this species are marked by a full-fletched mass-occurrence that has been used as a stratigraphic horizon in the upper Barremian of southeast France (Busnardo 1965; Delanoy 1994, 1997; Bert *et al*. 2008). It should be noted that *A. puzosianum* is also recorded in another level (e.g. B45') at Podestat–Pouli. Both populations are homogenous, but the younger one is significantly less rich. The palaeoenvironmental and biostratigraphic significance of the levels with *A. puzosianum* are discussed below.

OCCURENCE: *Anglesites puzosianum* was found at two levels (e.g. B43 and B45') at Podestat–Pouli. The species is reported in southeast France and perhaps in Tunisia and Romania.

BIOSTRATIGRAPHIC IMPLICATIONS OF THE NEW FAUNA

South Provençal Basin

At Podestat–Pouli, we document two horizons with *A. puzosianum* for the first time in association with martelicone heteroceratid forms that are herein referred to *Calanquites* gen. nov. As discussed above, the first occurrence of *A. puzosianum* marks the base of the *M. sarasini* Zone according to the standard ammonite zonation of the upper Barremian (Reboulet *et al*. 2014, p. 131). The first level with *A. puzosianum* from Podestat–

Pouli was previously recognized by Masse (1976) and tentatively correlated with bed 43 of the composite reference section at Cassis–La Bédoule by Ropolo *et al*. (1998b). The correlation was based on the co-occurrence of re-coiled heteroceratids at this level (see Text-fig. 5). However, the Cassis–La Bédoule ammonites were never illustrated and therefore the fixing of the lower boundary of the *M. sarasini* Zone remains unclear in the area of the unit-stratotype.

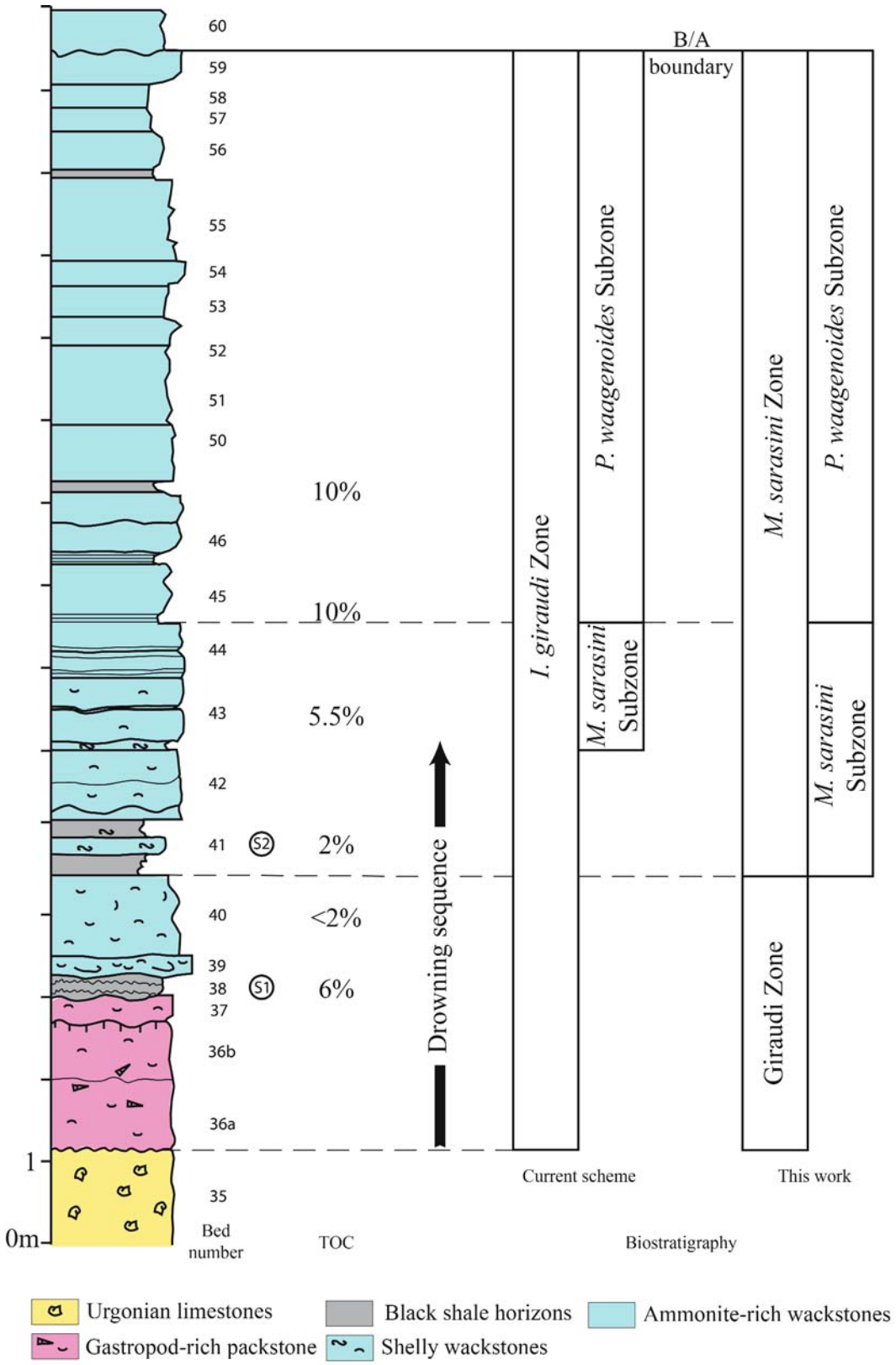
Following Vašíček and Klajmon (1998), Lukeneder (2005) showed that the recurrent mass-occurrence of small criocone ammonites during the Lower Cretaceous is commonly recorded in dark, laminated, marly limestone levels linked to short-lived episodes of oxygen-depletion conditions. The author assumed that these conditions enhanced the explosion of such ammonite form by their opportunistic mode of life and adaptation to dysaerobic sea water. In this regard, the deepening succession at Cassis–La Bédoule is characterized by several organic-rich horizons, called sapropel S1 and S2 (= "Taxy levels") by Moullade *et al*. (1998). According to Machhour *et al*. (1998), these levels are the result of intermittent dysaerobic conditions favoured by the palaeogeography of the intra-shelf basin. In our opinion, the laminated beds with numerous *A. puzosianum* recorded at Podestat–Pouli are closely linked to these palaeoenvironmental conditions and can be correlated with the "Taxy levels". This is also supported by the common occurrence at this level of both sections of the hypoxia-tolerant bivalve *Astarte numismalis* d'Orbigny (Machhour *et al*. 1998). Pending the finding of *A. puzosianum* in the stratotypical area, we support that the base of the *M. sarasini* Subzone should be fixed in bed 41 (Text-fig. 5). Interestingly, the first occurrence of the index species *M. sarasini* is reported in bed 42 of the stratotypical succession (Frau, unpublished data).

Western Georgia

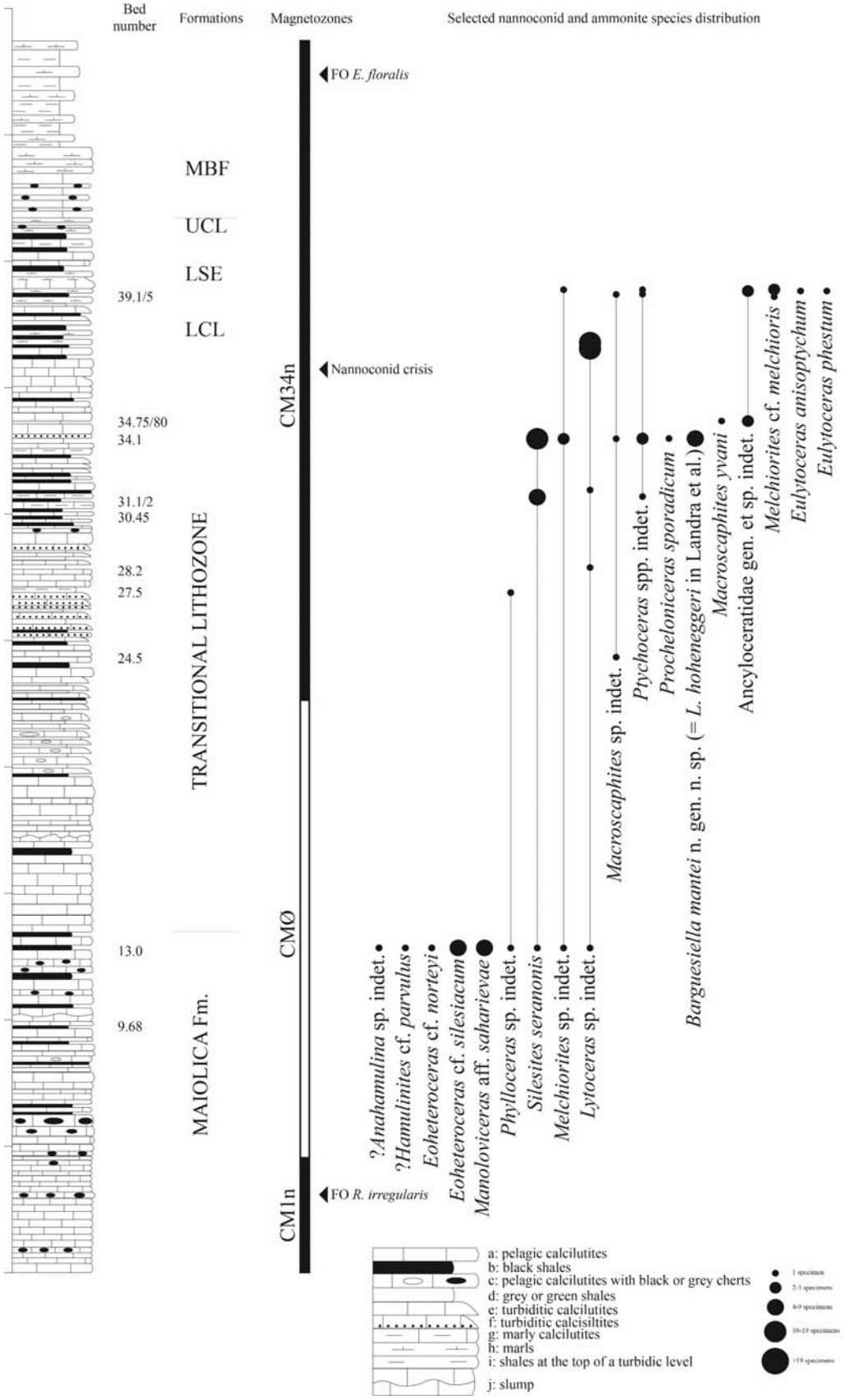
The ammonite assemblage of the base of the *M. sarasini* Zone of Podestat–Pouli is unique, but shows an apparent similarity with coeval heteroceratid faunas of western Georgia (see for example Rouchadzé 1933; Kakabadzé and Kotetishvili 1995). At a specific level, *Heteroceras baylei* and *Calanquites* gen. nov. *katsharavai* co-occur in the interval referred usually to the "*Colchidites*" *securiformis* Zone. According to Kakabadzé and Kotetischvili (1995, 2003), this zone is sandwiched in the Tvishi reference section between the *I. giraudi* Zone below and the *P. waagenoides* horizon above, and it corresponds to almost 20 m of medium-bedded grey to whitish-grey, compact limestones with common "*Colchidites*" *securiformis* (Simonovich *et al.* 1875) and "*C*." *ratshensis* Rouchadzé, 1933. From the published data, we can assume that the upper boundary of the "*C*." *securiformis* Zone is defined by the last occurrence of representatives of the genus „*Colchidites*" and the radiation of large U-shaped ancyloceratids *Pseudocrioceras* of the *P. waagenoides* horizon. Such faunal pattern is rather similar to the uppermost Barremian of the South Provençal Basin (Ropolo *et al*. 1998b). However, no detailed ammonite distribution is yet available for the Tvishi section and a lack of integrated sedimentological/biostratigraphical analysis exists in all the other reference sections of western Georgia. Thus, the stratigraphic correlation between Georgian sections and other parts of the Mediterranean Tethys remains unclear. Ivanov and Idakieva (2013) suggested that the heteroceratid assemblages of the "*C*." *securiformis* Zone of western Georgia and its equivalent, the "*Colchidites*" *ratshensis* horizon of the *Turkmeniceras turkmenicum* Zone of the Transcaspian region, are marked by a strong facies-controlled distribution that has caused it to be confused with the western Mediterranean *M. sarasini* Zone . These zones have been repeatedly correlated with one another, but no author have been put them in synonymy since the introduction of the standard late Barremian *M. sarasini* Zone (Reboulet *et al*. 2006).The current knowledge of the distribution of late Barremian ammonites shows that the ammonite assemblage of the *M. sarasini* Subzone is rather similar in the whole Mediterranean-Caucasian Subrealm and the adjacent part of the Boreal-Atlantic Subrealm, with consequent great potential for biostratigraphic correlation (Reboulet *et al*. 2014 with references). In the light of this study, there is no doubt that the peculiar heteroceratids faunas shared by the Podestat-Pouli and Tvishi sections correspond to the environmentally proximal assemblages of the base of the *M. sarasini* Subzone. Therefore, in our view, there is no doubt that the *M. sarasini* Subzone should be given preference in western and eastern Mediterranean settings, thus following the recommendation of Ivanov and Idakieva (2013).

Central Italy

The co-occurrence of *Barguesiella mantei* gen. et sp. nov. in southeast France and northern Italy raises questions about the age of the so-called Maiolica Formation. Landra *et al*. (2000, fig. 3) reported the specimens which are herein referred to *B. mantei* gen. et sp. nov. in bed 34.1 in section C at Cesana Brianza (Text-fig. 6). This section corresponds to the well-bedded limestone succession punctuated by several organic–



Text-fig. 5. The late Barremian drowning succession of Cassis–La Bédoule with the current and revised biostratigraphic scheme and TOC content (modified after Masse and Fenerci-Masse 2011)


Bed number
Formations
Magnetozones
Selected nannoconid and ammonite species distribution
FO E. floralis
Nannoconid crisis
FO R. irregularis
MBF
UCL
LSE
LCL
TRANSITIONAL LITHOZONE
MAIOLICA Fm.
39.1/5
34.75/80
34.1
31.1/2
30.45
28.2
27.5
24.5
13.0
9.68
CM34n
CMØ
CM1n
?Anahamulina sp. indet.
?Hamulinites cf. parvulus
Eoheteroceras cf. norteyi
Eoheteroceras cf. silesiacum
Manloviceras aff. saharievae
Phylloceras sp. indet.
Silesites seranonis
Melchiorites sp. indet.
Lytoceras sp. indet.
Macroscaphites sp. indet.
Ptychoceras spp. indet.
Procheloniceras sporadicum
Barguesiella mantei n. gen. n. sp. (= L. hoheneggeri in Landra et al.)
Macroscaphites yvani
Ancyloceratidae gen. et sp. indet.
Melchiorites cf. melchioris
Eulytoceras anisoptychum
Eulytoceras phestum
a: pelagic calcilutites
b: black shales
c: pelagic calcilutites with black or grey cherts
d: grey or green shales
e: turbiditic calcilutites
f: turbiditic calcisiltites
g: marly calcilutites
h: marls
i: shales at the top of a turbidic level
j: slump
1 specimen
2-3 specimens
4-9 specimens
10-19 specimens
>19 specimens

rich levels at the top of the Maiolica Formation. Bed 34.1 (e.g. top of the Transitional lithozone *sensu* Landra *et al*. 2000) is situated almost three metres below a bundle of organic-rich horizons that are considered to be a local equivalent of the Livello Selli Event (LSE), usually referred to the early Aptian Ocean Anoxic Event 1a (Erba 1996 for references). It should be noted that Erba (*in* Cecca and Landra 1994) previously reported the first occurrence of the calcareous nannofossil *R. irregularis* Thierstein at 2.95 m, and Channell *et al.* (1995) recognized the base of the reversed magnetozone CM0r between 4.5 m and meter 23 m at section C of Cesana Brianza. Both micropalaeontological and magnetostratigraphic markers have repeatedly been used to define the base of the Aptian Stage in the Maiolica Formation (Erba 1996).

It should be noted that the discovery of a unique specimen of *Prodeshayesites* sp. in the reversed interval of magnetozone CM0r of the Gorgo a Cerbara (Umbria–Marche Basin) reference section has supported this definition of the Barremian/Aptian boundary (Cecca *et al*. 1995). Some doubts stated by Rawson (com. pers. *in* Cecca *et al*. 1995) and Aguado *et al*. (1997) led to the re-examination of this specimen, and its revision as *Deshayesites* sp. In any case, the first appearance datum of the genus *Deshayesites* actually marks the lower boundary of the lower Aptian by means of ammonites in the Tethyan Realm (Cecca *et al.* 1998, 1999). However, a re-examination of the illustration of this poorly-preserved specimen shows that its morphological features can be easily confused with representatives of the heteroceratid genus *Martelites* since the inner whorls of this specimen are poorly preserved. A similar confusion has already been reported by Delanoy *et al*. (1997) concerning material from the reference section of Cassis-La Bédoule, where representatives of this genus were historically confused with the genus *Prodeshayesites* by Busnardo (1984).

At Cesana Brianza, most of the ammonite specimens were reported from levels stratigraphically higher than 23 m. Therefore, the ammonite assemblage was considered as indicating an early Aptian age because they fell within the 'normal' interval (i.e. magnetozone C34n) above magnetozone CM0r (Landra *et al*. 2000, p. 42). However, in our view, none of the ammonites illustrated by Landra *et al*. (2000) support an early Aptian age for the top of the Maiolica Formation. The Italian ammonite faunas are characteristic of the *Martelites sarasini* Zone as it is seen in the nearby Vocontian Basin (see for example Delanoy 1994, 1995, 1997; Bert *et al*. 2008). Also, the occurrence of *B. mantei* gen. et sp. nov. below the LSE is a new evidence that the age of the "transitional lithozone" should be reconsidered. Such considerations imply that the stratigraphic correlation of the magnetozone CM0r at the base of the Aptian stage is highly doubtful. As herein understood, it should fall within the uppermost Barremian in term of ammonite biostratigraphy. These preliminary observations need to be re-evaluated by the integration of litho-, bio and magnetostratigraphic markers.

SIGNIFICANCE OF THE NEW FAUNA

Recent works devoted to the Heteroceratidae have illustrated their rapid evolution and phenotypic plasticity, linked to sea-level changes. For example, Delanoy (1994, 1997) shows that the *I. giraudi* Subzone in the Vocontian Basin is characterized by the diversification of small to large U-shaped heteroceratids species during a 3rd order transgressive period followed by a rapid decline at the base of the *M. sarasini* Subzone. This decline is marked by the transition from U-shaped *Heteroceras* to the recoiled *Martelites* that was probably linked to a change from quasiplanktonic to a nekton-benthic mode of life. This morphological change had probably helped their establishment in shallower platform settings (Delanoy 1994).

In the case of the new heteroceratid genera and species herein described, no similar or closely related forms are known in basinal settings of the same age in southeast France. In fact, they are marked by diversified types of coiling and a high level of intraspecific polymorphism. Also, the specimens are characterized by small to very small size, and no evidence suggests taphonomically-induced size limitation. In our view, the small heteroceratids species from Podestat–Pouli could be interpreted as micromorph ammonites.

The small size of micromorph ammonites is usually explained by adaptative response to a less than optimal environment (Bucher *et al*. 1996). This phenomenon has occasionally been reported in the literature on Cretaceous ammonites and led to several taxonomic problems at the genus and supra-generic levels (see for example Kennedy and Cooper 1977; Wright and Kennedy 1979; Kennedy and Cobban 1990).

Such forms are commonly recorded from organic-rich sediments which have been linked to regional and/or global oxygen-depleted conditions in the water

Text-fig. 6. Stratigraphic log of Section C, Cesana Brianza (northern Italy) with magnetostratigraphy and distribution of selected nannoconid and ammonites species. The following abbreviations indicate LCL= Lower Critical Level; LSE= Livello Selli Equivalent; UCL= Upper Critical Level; MBF= Marne di Bruntino Formation (modified after Cecca and Landra 1994; Landra *et al*. 2000)

column (Mancini 1978). To our knowledge, the micromorph heteroceratids, described herein, occur only in the deepening succession of the *Massif des Calanques*, south of Marseille, that corresponds to a deeper area than Cassis–La Bédoule (Masse *et al*. in prep). Therefore, we assume that conditions in the Podestat–Pouli area permitted the entrenchment of heteroceratids, and this was predated by dysaerobic conditions in shallower water areas centred on Cassis–La Bédoule.

According to data of Kotetishvili (1989) and Kakabadzé and Kotetishvili (1995), the comparable heteroceratid assemblage from western Georgia existed in a deep environment. In this connection, Marchand *et al*. (2002) already suggested that open environments, rich in organic material, can lead to the development of micromorphic ammonites. Thus, there is no evidence that the heteroceratids recorded at Podestat–Pouli are the result of an *in-situ* (e.g. development among the older heteroceratid stock of the *I. giraudi* Zone, or *ex-situ* (e.g. migration from Georgia) evolutionary process. This remains unclear since the knowledge of latest Heteroceratidae is still limited and there is no detailed data on the lithological succession and faunal assemblages of western Georgia.

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PLATE 1

1-4 – *Calanquites* gen. nov. *katsharavai* (Rouchadzé, 1933), morphotype A; 1a, b – TSU485/1151, re-illustration of the lectotype TSU485/1151 (Rouchadzé collection) from Nicortsminda, Georgia; 2 – LCC 3, level B45 from Podestat–Pouli section; 3a–b – FCC 36, idem as above; 4 – FCC 9, idem as above.

5 – *Paraimerites densecostatus* (Renngarten, 1926. 5a–c – reproduction of the lectotype illustrated by Renngarten (1926, pl. 2 fig. 16a–c) from Naltchik.

> indicates beginning of the body chamber. Scale bar is 1 cm

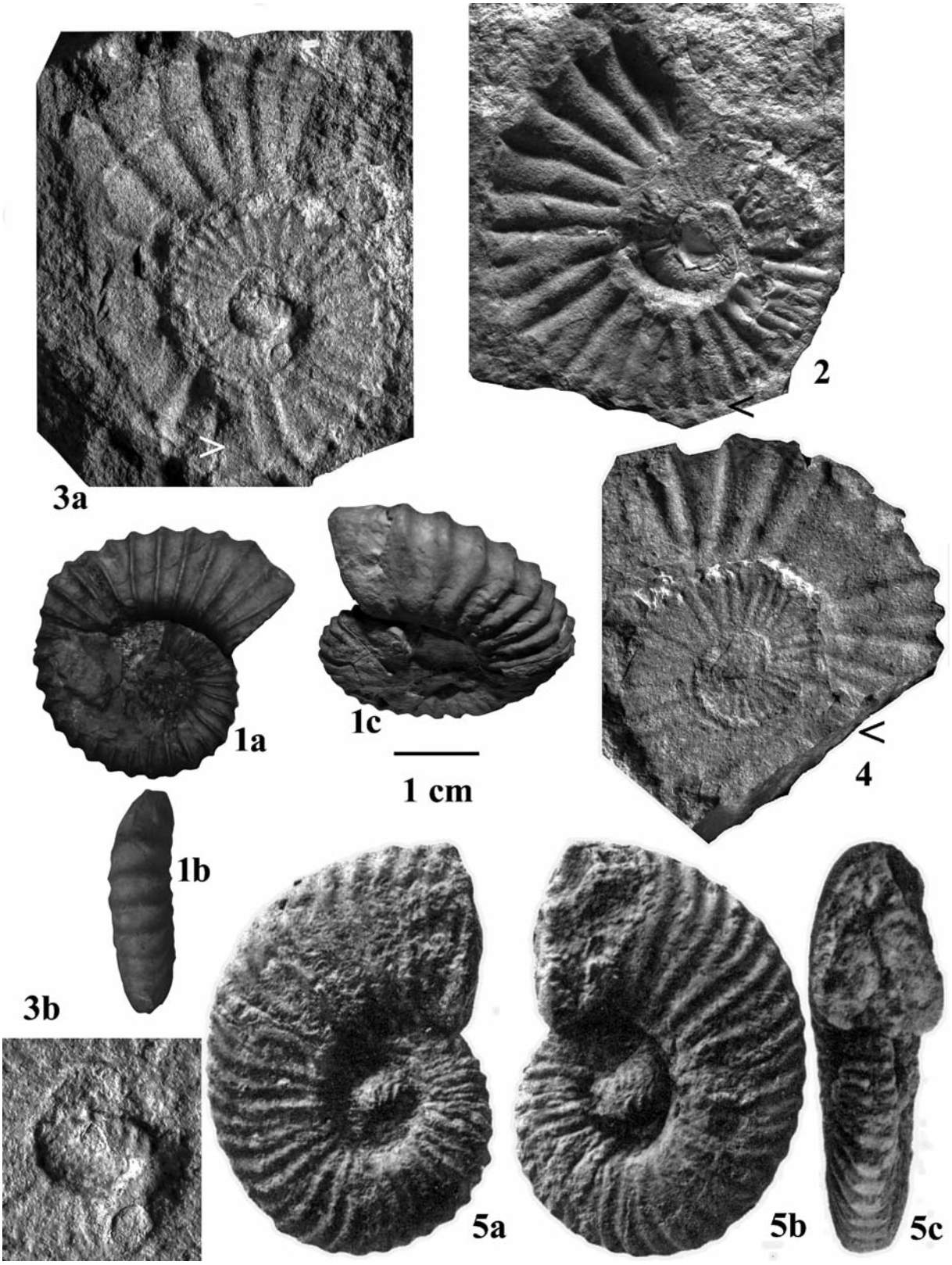

3a
2
1a
1c
1 cm
4
1b
3b
5a
5b
5c

PLATE 2

1 – *Calanquites* gen. nov. *katsharavai* (Rouchadzé, 1933) morphotype A; LCC 9, level B45 from Podestat–Pouli section.

2-4 – *Calanquites* gen. nov. *katsharavai* (Rouchadzé, 1933) morphotype B; 2– FCC 28, level B45 from Podestat–Pouli section; 3a–b – FCC 37, idem as above; 4 – FCC 3, idem as above.

5, 7, 8 – *Calanquites* gen. nov. aff. *semituberculatus* (Rouchadzé, 1933) morphotype A: 5 – FCC 47, level B43 from Podestat–Pouli section; 7 – FCC 48, idem as above; 8 – FCC 45, idem as above.

6 – *Calanquites* gen. nov. aff. *semituberculatus* (Rouchadzé, 1933) morphotype B; FCC 46, level B43 from Podestat–Pouli section.

> indicates beginning of the body chamber. Scale bar is 1 cm

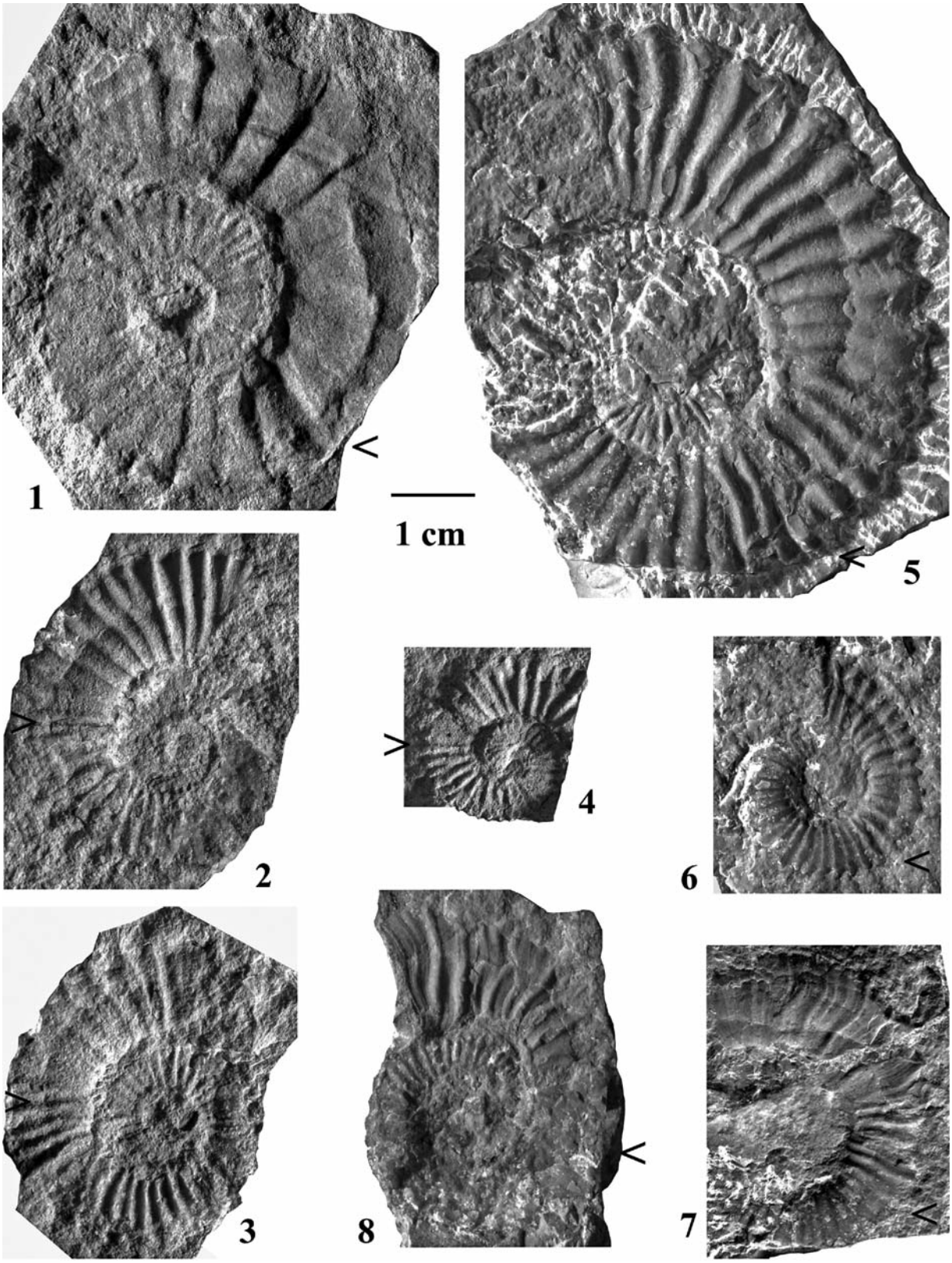

1
1 cm
5
2
4
6
3
8
7

PLATE 3

1-5 – *Barguesiella goudesense* gen. et sp. nov., level B47 from Podestat–Pouli section; 1 – FCC 50; 2 – LCC 11; 3 – LCC 14a (holotype); 4 – LCC 13; 5 – LCC 14b.

7-9 – *Barguesiella mantei* gen. et sp. nov., level B46 from Podestat–Pouli section; 7 – FCC 13 (holotype); 8 – FCC 15; 9 – LCC 8.

> indicates beginning of the body chamber. Scale bar is 1 cm

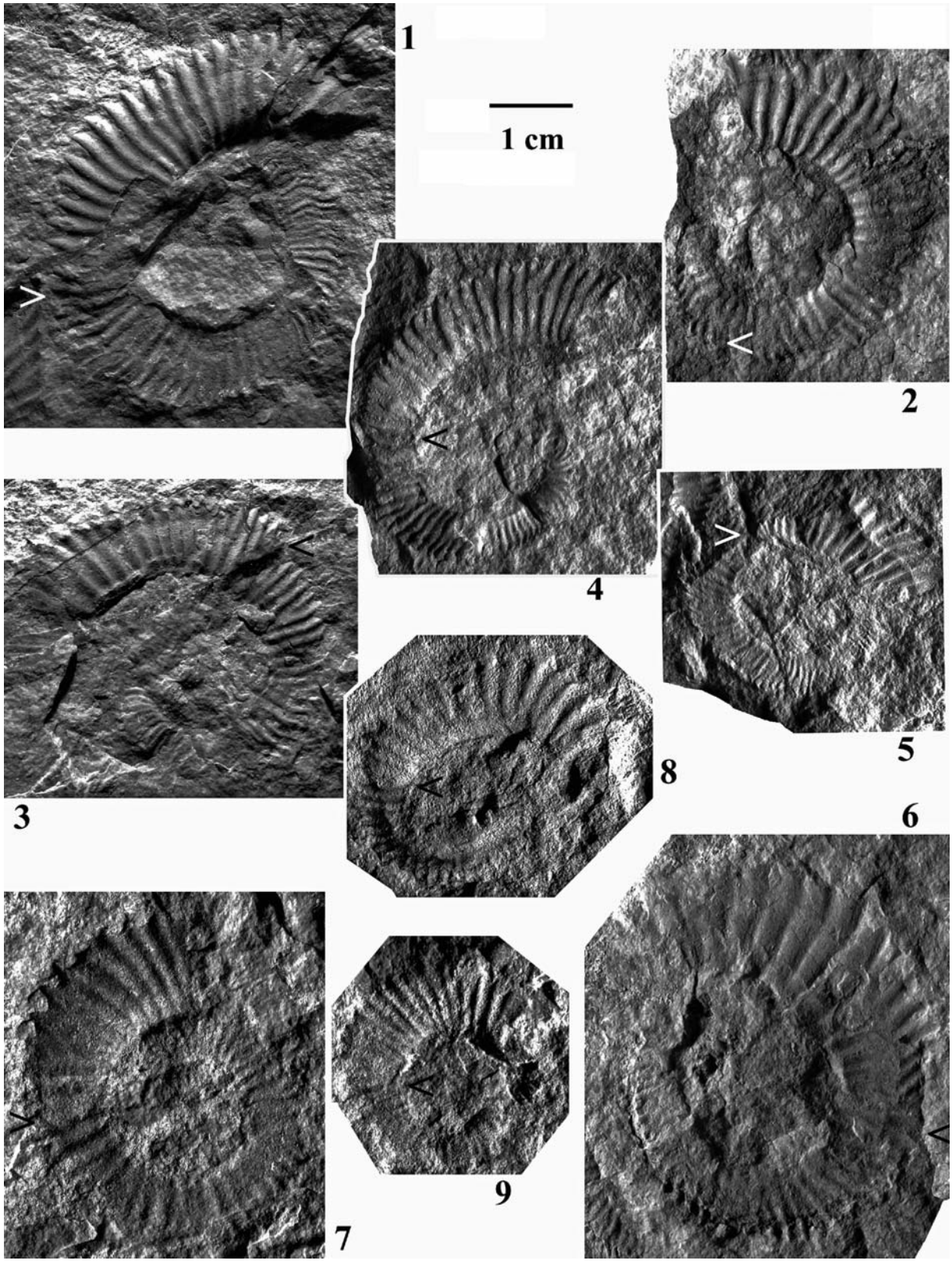

1
1 cm
2
3
4
5
6
7
8
9

PLATE 4

1-4 – *Anglesites puzosianum* (d'Orbigny, 1841), Podestat–Pouli section; 1 – FCC 42, level B43; 2 – FCC 41, level B43; 3 – FCC 43, level B43; 4 – LCC 5, level B45.

5-8 – *Heteroceras veratiae* sp. nov.; 5 – FCC 8a (holotype) and FCC 8b, level B44 from Podestat–Pouli section; 6 – FCC39, idem as above; 7 – FCC 7, idem as above; 8 – FCC 27, idem as above.

9, 10 – *Calanquites* gen. nov. *katsharavai* (Rouchadzé, 1933) morphotype B; 9 – FCC 30b, level B45 from Podestat–Pouli section; 10 – FCC 30a, idem as above.

11 –?*Martelites* sp., 11 – FCC 5, level B45 from Podestat–Pouli.

> indicates beginning of the body chamber. Scale bar is 1 cm

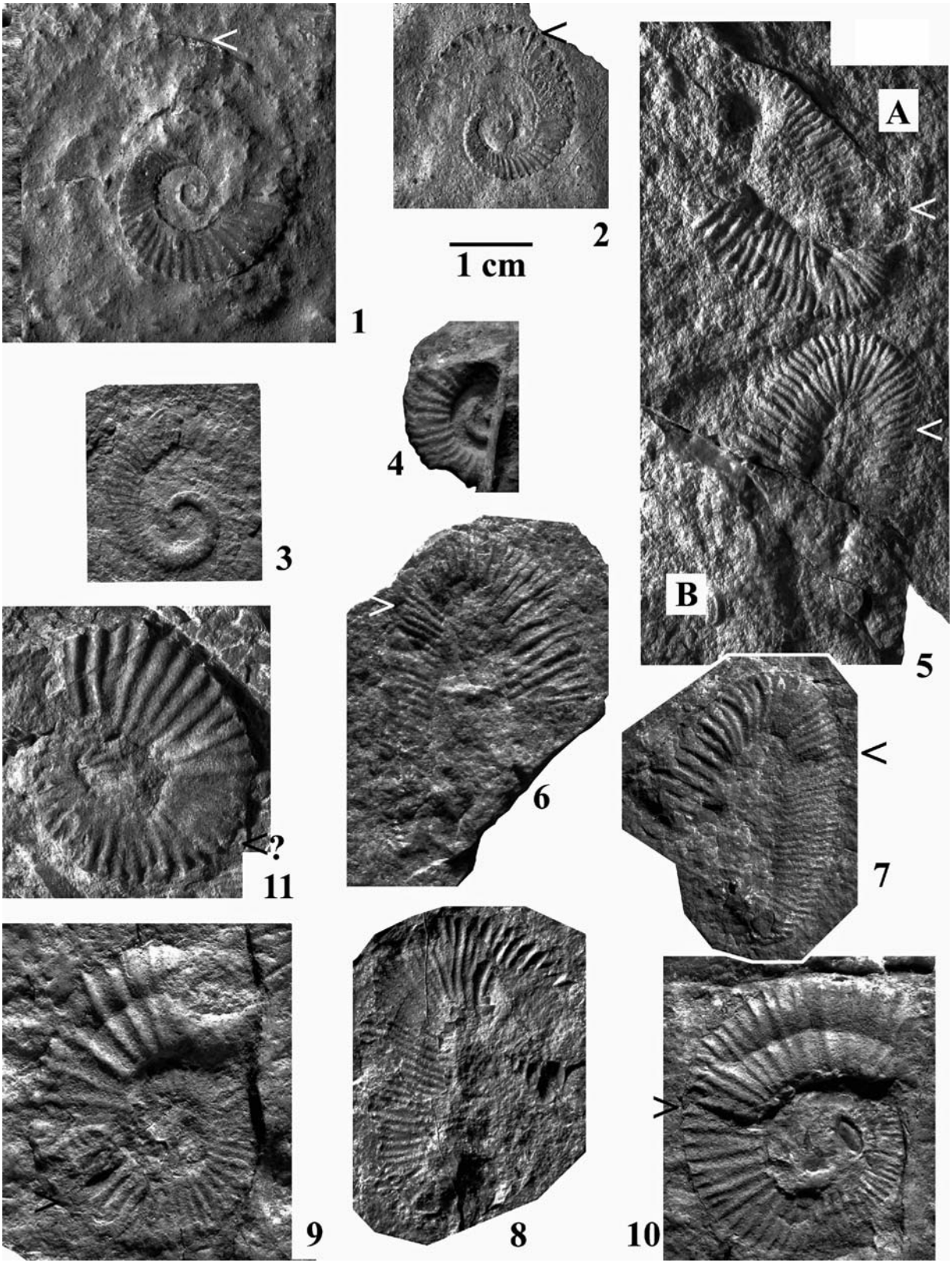

1
2
1 cm
A
B
3
4
5
6
7
11
?
8
9
10

PLATE 5

1-5 – *Giovaraites massiliae* gen. et sp. nov., level B46 from Podestat–Pouli section; 1 – FCC 22; 2 – FCC 12; 3 – FCC 27; 4 – FCC FO (holotype); 5 – FCC 30.

6, 7 – *Heteroceras denizoti* sp. nov., level B47 from Podestat–Pouli section; 6 – FCC 25 (holotype); 7 – LCC 12.

> indicates beginning of the body chamber. Scale bar is 1 cm

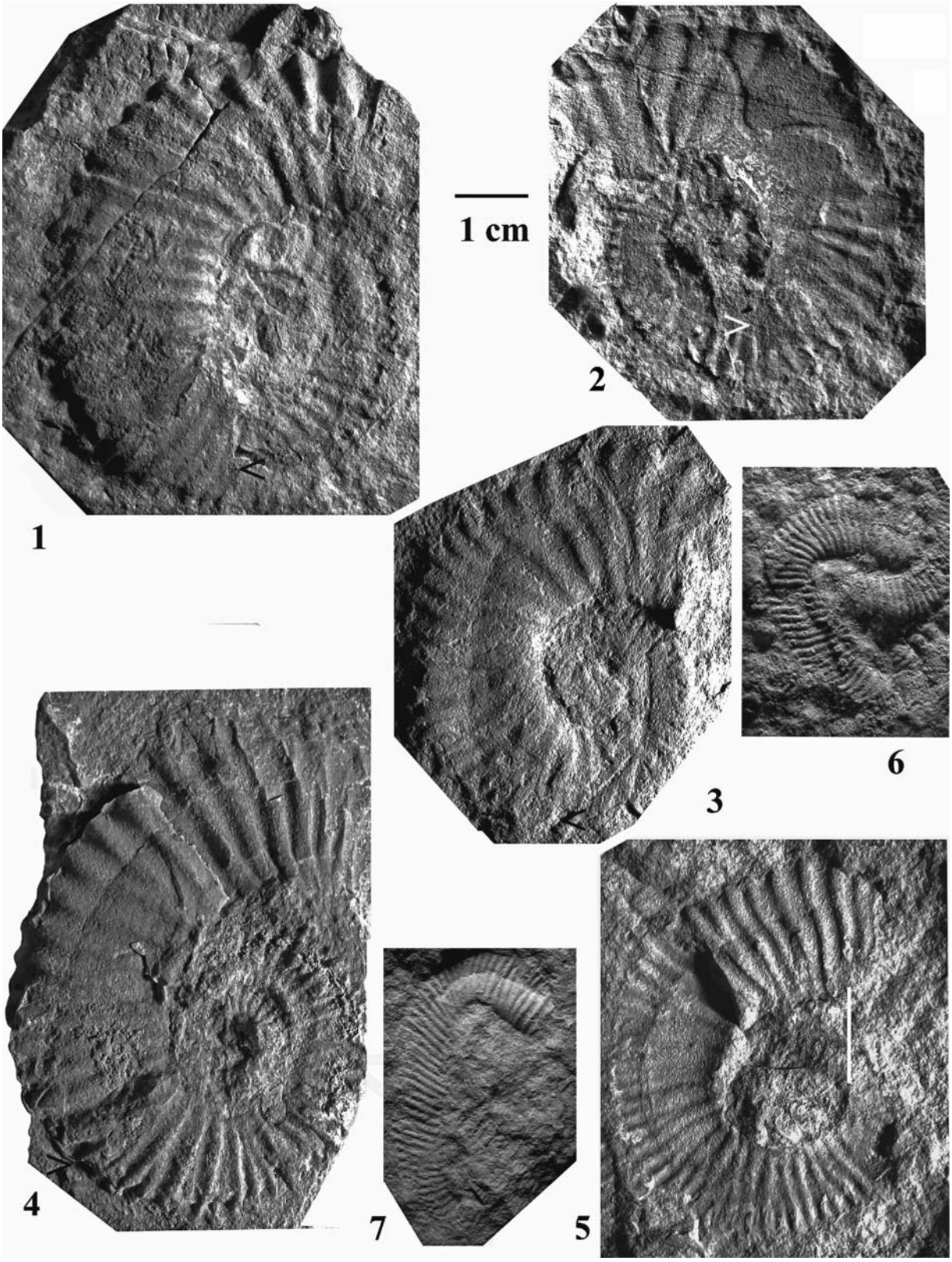

1 cm
1
2
3
4
5
6
7

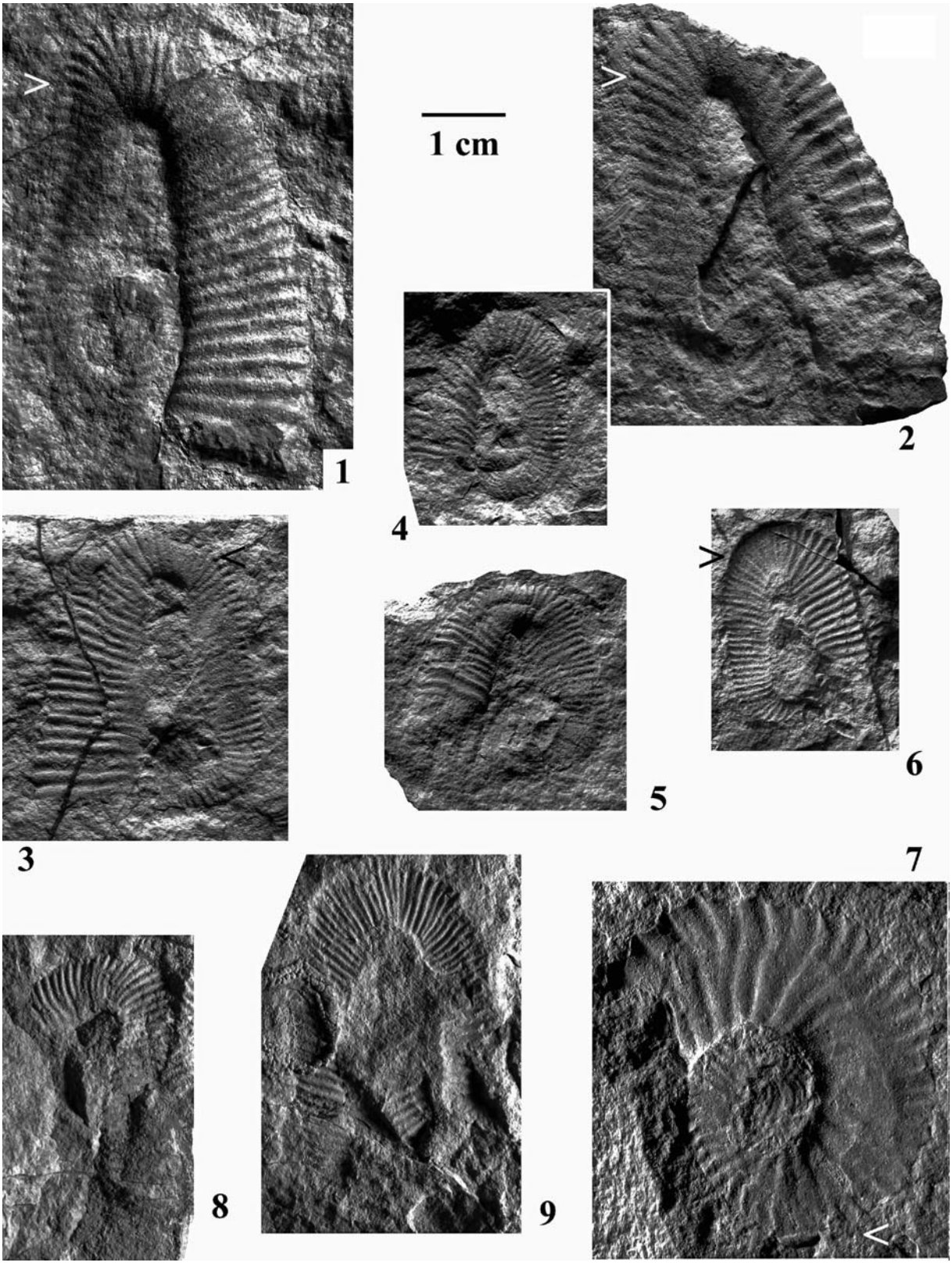
PLATE 6

1-6 – *Heteroceras baylei* (Reynès, 1876), level B46 from Podestat–Pouli section; 1 – FCC 10; 2 – FCC 24; 3 – FCC 14; 4 – FCC 16b; 5 – FCC 23a; 6 – FCC 14b.

7 – *Giovaraites massiliae* gen. et sp. nov., level B45 from Podestat–Pouli section: 7 – FCC 28x.

8, 9 – *Heteroceras denizoti* sp. nov., level B47 from Podestat–Pouli section: 8 – FCC 53; 9 – FCC 52.

> indicates beginning of the body chamber. Scale bar is 1 cm


1 cm
1
2
3
4
5
6
7
8
9