



The affinities between the Lower Cretaceous Ammonoidea *Ammonites crassicostatus* d'Orbigny, 1841 and *Ammonites gargasensis* d'Orbigny, 1841

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Abstract

The present contribution provides a taxonomic reassessment of the Lower Cretaceous ammonite species *Ammonites crassicostatus* d'Orbigny (type species of *Colombiceras* Spath) and *Ammonites gargasensis* d'Orbigny (type species of *Gargasiceras* Casey) from the Aptian-type area (Apt, Vaucluse, southeastern France). Those nominal species represent two ornamental poles of a single population, here referred to *C. crassicostatum*. The genus *Gargasiceras* is, therefore, synonymised with *Colombiceras*. Implications on the taxonomy at the specific, generic, and supra-generic levels are discussed.

Keywords: Ammonite; Aptian; Cretaceous; Apt; Vaucluse; Taxonomy.

Resumen

El presente trabajo proporciona una reevaluación taxonómica de las especies de ammonites del Cretácico temprano *Ammonites crassicostatus* d'Orbigny (especie tipo de *Colombiceras* Spath) y *Ammonites gargasensis* d'Orbigny (especie tipo de *Gargasiceras* Casey) del área tipo del Aptiano (Apt, Vaucluse, sureste de Francia). Estas especies nominales representan dos polos ornamentales de una sola población, aquí referida como *C. crassicostatum*. Por lo tanto, el género *Gargasiceras* se sinonimiza con *Colombiceras*. Se discuten las implicaciones taxonómicas a nivel específico, genérico y supragénérico.

Palabras clave: Ammonites; Aptiano; Cretácico; Apt; Vaucluse; Taxonomía.

1. Introduction

The knowledge of Mediterranean ammonites during the upper Aptian (Lower Cretaceous) is substantial, and mostly concerns the super-families Douvilleiceratoidea Parona and Bonarelli, 1897, Parahoplitoidea Spath, 1922 and Acanthohoplitoidea Stoyanow, 1949. Despite the tremendous quantity of material illustrated in the literature, a critical review of the dataset shows that the picture one can have on the evolution of the Acanthohoplitoidea is far from being resolved (*e.g.* Dauphin, 2002; Bulot, 2010; Latil, 2011). This is linked to diverging concepts between

authors due to the lack of revision of the type material but also to preservation problems of the faunas which clearly affects attempts to identify and compare taxa (Bulot, 2010; Luber *et al.*, 2017).

This work focuses on the widely quoted acanthohoplitolitid taxa *Ammonites crassicostatus* d'Orbigny, 1841 and *Ammonites gargasensis* d'Orbigny, 1841, which respectively typify the genera *Colombiceras* Spath, 1923 and *Gargasiceras* Casey, 1954. Intermediate forms between both taxa have long been quoted in the literature (*e.g.* Jacob, 1907; Kilian, 1910; Dutour, 2005; Bulot, 2010) but their supposed affinities lack a comprehensive study. The present

contribution addresses this problem by the revision of the type specimens combined with a statistic approach based on material from the Apt–Gargas type area (Luberon UNESCO Geopark, Vaucluse, southeastern France, Fig. 1A).

This work follows the most recent standard Mediterranean ammonite scale for the Aptian Stage (Reboulet *et al.*, 2018).

2. Origin of the material

As designed by Delanoy in Gauthier *et al.* (2006, p. 74–75), the lectotypes of *Colombiceras crassicostatum* and *Gargasiceras gargasense* are, respectively, the pyritic nuclei MNHN-F.R4345 (Fig. 2A) and MNHN-F.R51910 (Fig. 2B), from the d'Orbigny collection deposited at the Muséum National d'Histoire Naturelle de Paris, France. They originate from the lower part of the blue-grey marls of the Apt–Gargas area, comprised in the Luberon UNESCO Geopark. Those marls characterize the former middle portion of the Aptian Stage (*i.e.* ‘Gargasien’) in the

sense of Leenhardt (1883), Kilian (1887), and Moullade (1965). Unfortunately, the historical outcrops of the Apt–Gargas area are no longer accessible because of extensive urbanization launched in the early sixties (Moullade, 1965). Nevertheless, surrounding localities of the Luberon Geopark provide better outcropping conditions, such as those of La Tuilière and Carniol (Dutour, 2005; Moullade *et al.*, 2006), and allow the collection of abundant quasi-topotypic individuals.

As documented by Dutour (2005), *C. crassicostatum* and *G. gargasense* both appear in the uppermost part of the *Dufrenoya furcata* Zone (uppermost lower Aptian) at La Tuilière and Carniol sections. The plexus represents a residual part of the ammonite spectrum, *i.e.* up to ~7% (Dutour, 2005). The abundance of the two taxa subsequently increases in the bottom part of the overlying *Epicheloniceras martini* Zone (lowermost upper Aptian), and reaches 10% (Carniol – Fig. 1B) to 40% (La Tuilière) of the total ammonite assemblage.

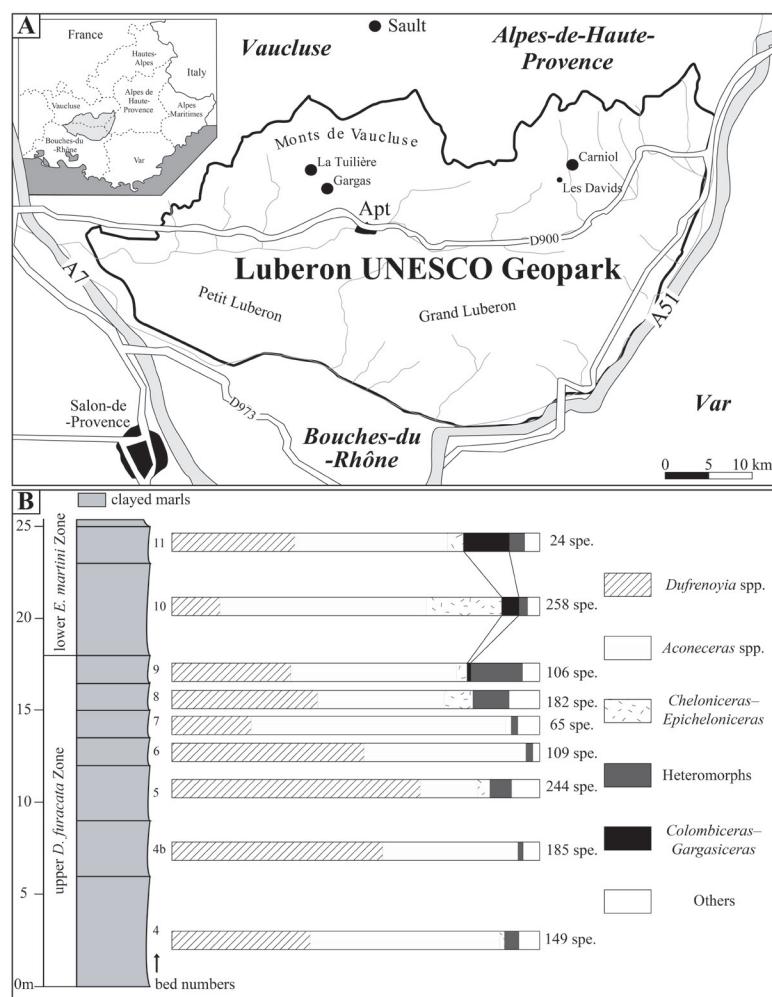


Figure 1. (A) The Luberon UNESCO Geopark (Vaucluse, southeastern France) including the localities cited in the text (modified from Frau *et al.*, 2017) and (B) the Carniol litho-log with the ammonite spectrum of the uppermost lower (*Dufrenoya furcata* Zone) and lowermost upper Aptian (*Epicheloniceras martini* Zone) documented by Dutour (2005). The location of the upper Aptian base follows Dutour (2005).

3. Material and methods

The close relationships between *C. crassicostatum* and *G. gargasense* have been repeatedly mentioned in the literature (Jacob, 1907; Kilian, 1910; Dutour, 2005; Bulot, 2010). A wide range of variabilities in robustness and length of the ontogenetic stages is observed in the topotypic population (Dutour, 2005); from robust nuclei with a low rib density (thereafter *C. crassicostatum* morphotype) to slender finely ribbed ones (thereafter *G. gargasense* morphotype). Such variability was tentatively interpreted as the expression of the Buckman's first law of covariation between conch shape and ribbing pattern (Dutour, 2005). Unfortunately, this assumption has never been statistically sustained on a sufficiently large sample. To our knowledge, the *C. crassicostatum*-*G. gargasense* plexus is known by only twelve figured specimens in its type area, including the two lectotypes (*i.e.* those figured by Roch, 1927; Thomel, 1980; Conte, 1989; Dutour, 2005; and Gauthier *et al.*, 2006).

The numerous pyritic nucleus collected in beds 9 to 11 at Carniol by the authors form the basis for a standard biometric study (Fig. 1B). Additional specimens from the nearby locality of Les Davids (Fig. 1A) are here included. Unless otherwise specified, the studied specimens belong to the collections of two of us (C.F. and A.P.), currently being deposited at the *Maison du Parc Naturel Regional du Luberon* (PNRL), Apt, France. This study also involves the type specimens of *A. gargasensis* var. *aptiensis*, *A. gargasensis* var. *recticostata* and *A. gargasensis* var. *attenuata* from the Apt-Gargas type area, previously introduced by Roch (1927, pl. XVIII, fig. 5–5a, 6–6a, 7–7a and 8–8a) and deposited in the paleontological collections of the Grenoble Alpes University (see Fig. 2C–E).

The conch shape has been quantified by standard measurements *D* (total observed diameter taken on top of the ribs), *U* (umbilical width), *Wh* (whorl height), *Ww* (whorl thickness). The associated ratios (*U/D*, *Wh/D*, *Ww/D*, *Ww/Wh* – Fig. 3) are investigated and compared to those of the type material (Table 1). All dimensions are given in millimetres. *Rv* indicates the number of ventral ribs on the half of the last preserved whorl. This study is combined with a qualitative analysis of the ontogeny of the material at our disposal. We performed univariate and bivariate analyses to highlight possible relationships between the variables and to study the evolution of the conch parameters through ontogeny. The suture terminology is that of Korn *et al.* (2003): *E* = external lobe; *A* = adventive lobe; *U* = umbilical lobe, *I* = internal lobe.

4. The Crassicostatum–Gargasense plexus from carniol

The studied material is composed of seventy-three specimens (Figs. 4, 5 and 6) originating from around the lower/upper Aptian boundary (*D. furcata*–*E. martini* zonal

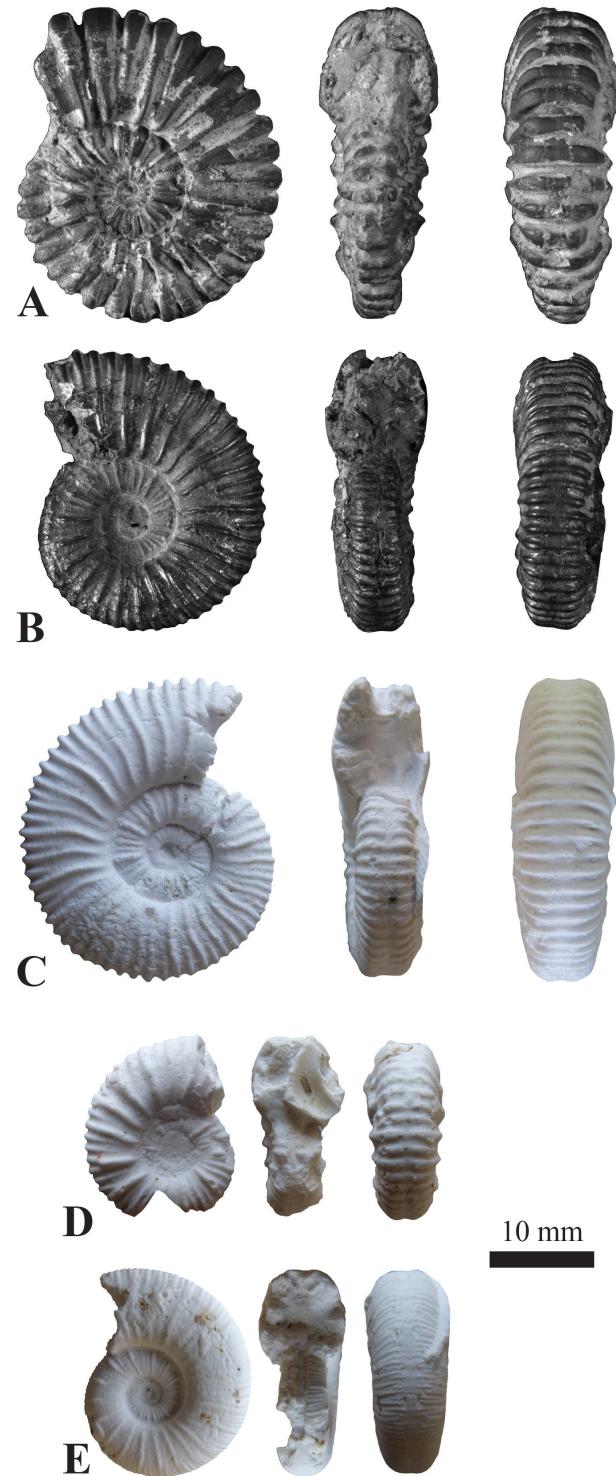


Figure 2. The lectotypes of (A) *Colombiceras crassicostatum* (d'Orbigny, 1841), specimen MNHN-F.R4345 (d'Orbigny coll.) and (B) *Gargasiceras gargasense* (d'Orbigny, 1841), specimen MNHN-F.R51910 (d'Orbigny coll.) designated by Delanoy in Gauthier *et al.* (2006, p. 74–75). Both from the Aptian marls of Gargas. Plaster cast of the type specimens of (C) *A. gargasensis* var. *aptiensis* Roch, 1927, specimen UJF-ID.1595 (Lory coll.) from Apt, (D) *A. gargasensis* var. *recticostata* Roch, 1927, specimen UJF-ID.1597 (Zürcher coll.) from Barrême, and (E) *A. gargasensis* var. *attenuata* specimen UJF-ID.1598 (Lory coll.) from the Aptian marls of Apt (Luberon UNESCO Geopark). Scale bar is 10 mm.

Table 1. Dimensions of the studied material from Carniol (CLR and CAR) and Les Davids (DAV), and the type specimens of *Colombiceras crassicostatum*, *Gargasceras gargasensis*, *G. gargasense* var. *aptiensis*, *G. gargasense* var. *recticostata* and *G. gargasense* var. *attenuata*.

Specimens	Collections	Morphotypes	Illustrations	D	U	Wh	Wb	Rv	U/D	Wh/D	Wb/D	Wb/Wh	U/Wh	coiling
<i>C. crassicostatum</i> lectotype MNHN-F.R4345	d'Orbigny coll.	Crassicostatum	Fig. 2A	31	12	11	12	16	0.387	0.355	0.3871	0.3871	1.091	subvirgacone
CAR.13	Pictet coll.	Crassicostatum	Fig.4B-B'	25	7.77	10.26		22	0.311	0.41			0.757	
CAR.14	Pictet coll.	Crassicostatum	Fig.4C-C'	18.36	6.69	7.29	6.92	17	0.364	0.397	0.3769	0.37691	0.918	subvirgacone
CAR.15	Pictet coll.	Crassicostatum	Fig.4D-D'	17.68	6.04	7.23	7.23	15	0.342	0.409	0.4089	0.40894	0.835	subvirgacone
CAR.16	Pictet coll.	Crassicostatum	/	21.2	7.9	7.87		20	0.373	0.371			1.004	
CAR.19	Pictet coll.	Crassicostatum	Fig.4F-F'	16.28	6.14	6.06	6.6	18	0.377	0.372	0.4054	0.40541	1.013	subvirgacone
CAR.21	Pictet coll.	Crassicostatum	Fig.4G-G'	14.59	5.35	5.82	5.79	19	0.367	0.399	0.3968	0.39685	0.919	subvirgacone
CAR.22	Pictet coll.	Crassicostatum	Fig.4I-I'	12.19	4.86	4.31	5.14	16	0.399	0.354	0.4217	0.42166	1.128	subvirgacone
CAR.23	Pictet coll.	Crassicostatum	/	13.9	4.6	5.94	4	17	0.331	0.427	0.2878	0.28777	0.774	virgacone
CAR.24	Pictet coll.	Crassicostatum	Fig.4J-J'	12.66	4.9	4.95	5.32	16	0.387	0.391	0.4202	0.42022	0.99	subvirgacone
CAR.25	Pictet coll.	Crassicostatum	/	14.14	4.96	5.66	6.42		0.351	0.4	0.454	0.45403	0.876	subvirgacone
CAR.29	Pictet coll.	Crassicostatum	Fig.4H-H'	12.15	3.96	4.82	4.81	21	0.326	0.397	0.3959	0.39588	0.822	subvirgacone
CAR.33	Pictet coll.	Crassicostatum	/	12.37	4.54	4.85	4.91	16	0.367	0.392	0.3969	0.39693	0.936	subvirgacone
CAR.36	Pictet coll.	Crassicostatum	/			7.45	6.73							
CAR.8	Pictet coll.	Crassicostatum	/	13.13	4.83	4.78	5.36		0.368	0.364	0.4082	0.40823	1.01	subvirgacone
CRL.14	Frau coll.	Crassicostatum	/	11	4	3.8	5.3	14	0.364	0.345	0.4818	0.48182	1.053	subvirgacone
CRL.3	Frau coll.	Crassicostatum	/			8.5	7.4							
CRL.4	Frau coll.	Crassicostatum	/			8.1	7.2							
CRL.5	Frau coll.	Crassicostatum	Fig.4E-E'	16.3	6.8	5.9	6	18	0.417	0.362	0.3681	0.3681	1.153	subphiocone
DAV.2	Pictet coll.	Crassicostatum	Fig.4A-A'			9.94	8.19							
CAR.26	Pictet coll.	Crassicostatum?	/	13.79	4.42	6.02	5.49	20	0.321	0.437	0.3981	0.39811	0.734	subvirgacone
CAR.34	Pictet coll.	Crassicostatum?	/			9.03	8.07							
CAR.51	Pictet coll.	Crassicostatum?	/			5.4	5.39							
<i>G. gargasense</i> lectotype MNHN-F.R51910	d'Orbigny coll.	Gargasense	Fig. 2B	31	11	12	10	28	0.355		0.3226	0.32258	0.917	subvirgacone
<i>G. gargasense</i> var. <i>aptiensis</i> holotype UJF-ID.1595	Lory coll.	Gargasense	Fig. 2C	28.31	11.23	9.83	8.73	32	0.397	0.398	0.3084	0.30837	1.142	subvirgacone
<i>G. gargasense</i> var. <i>recticostata</i> syntype UJF-ID.1597	Zürcher coll.	Gargasense	Fig. 2D	15.58	5.9	6.5	6.58	24	0.379	0.417	0.4223	0.42234	0.908	subvirgacone
CAR.1	Pictet coll.	Gargasense	Fig.5D-D'	15.38	5.26	6.05	5.58	30	0.342	0.393	0.3628	0.36281	0.869	subvirgacone
CAR.10	Pictet coll.	Gargasense	/	12.39	4.01	5.2	4.07	23	0.324	0.42	0.3285	0.32849	0.771	subvirgacone
CAR.11	Pictet coll.	Gargasense	/			6.21	6.1							
CAR.2	Pictet coll.	Gargasense	Fig.5A-A'		9.6	10.32	8.61	28						
CAR.28	Pictet coll.	Gargasense	Fig.5M-M'	10.74	3.65	4.47	4.73	23	0.34	0.416	0.4404	0.44041	0.817	subvirgacone
CAR.3	Pictet coll.	Gargasense	Fig.5C-C'	17.31	6.96	6.15	6.28	22	0.402	0.355	0.3628	0.3628	1.132	subvirgacone
CAR.30	Pictet coll.	Gargasense	Fig.5L-L'	11.96	4.08	5.47	5.38	22	0.341	0.457	0.4498	0.44983	0.746	subvirgacone
CAR.32	Pictet coll.	Gargasense	Fig.5K-K'	10.63	3.7				0.348					
CAR.35	Pictet coll.	Gargasense	/			6.38	5.21							
CAR.39	Pictet coll.	Gargasense	Fig.5P-P'	8.59	3.1	3.44	3.79	22	0.361	0.4	0.4412	0.44121	0.901	subvirgacone
CAR.4	Pictet coll.	Gargasense	Fig.5E-E'	14.41	5.25	5.73	5.53	25	0.364	0.398	0.3838	0.38376	0.916	subvirgacone
CAR.40	Pictet coll.	Gargasense	Fig.5N-N'	9.2	3.23	3.6	3.86	28	0.351	0.391	0.4196	0.41957	0.897	subvirgacone
CAR.41	Pictet coll.	Gargasense	/	9.75	2.64	4.22	3.96	22	0.271	0.433	0.4062	0.40615	0.626	subdiscocone
CAR.42	Pictet coll.	Gargasense	/	9.34	2.89	3.54	3.4		0.309	0.379	0.364	0.36403	0.816	subvirgacone
CAR.43	Pictet coll.	Gargasense	/			2.19								
CAR.44	Pictet coll.	Gargasense	/	8.75	3.49	3.14	3.27	20	0.399	0.359	0.3737	0.37371	1.111	subvirgacone
CAR.45	Pictet coll.	Gargasense	Fig.5Q-Q'	6.71	2.45	2.75	2.97		0.365	0.41	0.4426	0.44262	0.891	subvirgacone
CAR.46	Pictet coll.	Gargasense	/			6.03	6.25							
CAR.5	Pictet coll.	Gargasense	/	14.12	4.37	6.3	5.52	25	0.309	0.446	0.3909	0.39093	0.694	subvirgacone
CAR.50	Pictet coll.	Gargasense	/			6.82	6.94							
CAR.52	Pictet coll.	Gargasense	/			4.59	4.55							
CAR.6	Pictet coll.	Gargasense	/	12.7	4.37	5.56	5.1	24	0.344	0.438	0.4016	0.40157	0.786	subvirgacone
CAR.7	Pictet coll.	Gargasense	Fig.5I-I'	12.65	4.72	5.08	4.73	29	0.373	0.402	0.3739	0.37391	0.929	subvirgacone
CAR.9	Pictet coll.	Gargasense	/	11.73	3.25	5.11	5.08		0.277	0.436	0.4331	0.43308	0.636	subdiscocone
CRL.1	Frau coll.	Gargasense	Fig.5B-B'	24.2	9.9	9.2	7.9	25	0.409	0.38	0.3264	0.32645	1.076	subvirgacone
CRL.11	Frau coll.	Gargasense	Fig.5G-G'	12.4	4.4	5.3	5.1	24	0.355	0.427	0.4113	0.41129	0.83	subvirgacone
CRL.12	Frau coll.	Gargasense	/	12.1	4.1	5.2	4.3	20	0.339	0.43	0.3554	0.35537	0.788	subvirgacone
CRL.13	Frau coll.	Gargasense	Fig.5H-H'	11.8	4.4	4.3	4.6	21	0.373	0.364	0.3898	0.38983	1.023	subvirgacone
CRL.16	Frau coll.	Gargasense	/	10.1	3.6	4.1	4.1		0.356	0.406	0.40594	0.40594	0.878	subvirgacone
CRL.17	Frau coll.	Gargasense	Fig.5O-O'	9.1	3.3	3.6	3.6	22	0.363	0.396	0.3956	0.3956	0.917	subvirgacone
CRL.6	Frau coll.	Gargasense	/	15.9	5.5	5.8	4.9	22	0.346	0.365	0.3082	0.30818	0.948	subvirgacone
CRL.8	Frau coll.	Gargasense	/	16.3	4.9	6.8	5.9		0.301	0.417	0.362	0.36196	0.721	subvirgacone
CRL.9	Frau coll.	Gargasense	/	14.1	3.9	6.6	5.9	20	0.277	0.468	0.4184	0.41844	0.591	subdiscocone
DAV.1	Pictet coll.	Gargasense	/	10.32	3.6	3.67	4.02	20	0.349	0.356	0.3895	0.38953	0.981	subvirgacone
CAR.37	Pictet coll.	Gargasense?	/			8.75	7.46							
CAR.38	Pictet coll.	Gargasense?	/				9.09							
CAR.47	Pictet coll.	Gargasense?	/			6.49	6.37							
CAR.48	Pictet coll.	Gargasense?	/			7.12	6.71							
CAR.49	Pictet coll.	Gargasense?	/			6.95	6.51							
CRL.15	Frau coll.	Gargasense?	/			5.1	5.1							
DAV.3	Pictet coll.	pathological	Fig.5R-R'	14.57	4.93	5.73	4.76	17	0.338	0.393	0.3267	0.3267	0.86	subvirgacone
CAR.20	Pictet coll.	Transitional	Fig.6E-E'		5.86	6.63	6.43						0.884	
CRL.10	Frau coll.	Transitional	Fig.6D-D'	13.3	4.2	5.4	5.3	18	0.316	0.406	0.3985	0.3985	0.778	subvirgacone
CRL.2	Frau coll.	Transitional	Fig.6B-B'	22	7.5	9.7	8.1	22	0.341	0.441	0.3682	0.36818	0.773	subvirgacone
CAR.12	Pictet coll.	Transitional	Fig.6A-A'	28.48	9.77	11.99	10.29	22	0.343	0.421	0.3613	0.36131	0.815	subvirgacone
CAR.17	Pictet coll.	Transitional	Fig.6C-C'	17.68	6.31	7.26	6.44	20	0.357	0.411	0.3643	0.3643	0.869	subvirgacone
CAR.18	Pictet coll.	Transitional	/	18.09	6.09	7.54	6.94	18	0.337	0.417	0.3836	0.38364	0.808	subvirgacone
CAR.27	Pictet coll.	Transitional	/	14.3	4.52	5.4	5.47	20	0.316	0.378	0.3825	0.38252	0.837	subvirgacone
CAR.31	Pictet coll.	Transitional	/	11.24	3.71	4.92	4.73	18	0.33	0.438	0.4208	0.42082	0.754	subvirgacone
CRL.7	Frau coll.	Transitional	/	17.1	5.8	7	6.6	19	0.339	0.409	0.386	0.38596	0.829	subvirgacone
<i>G. gargasense</i> var. <i>attenuata</i> holotype UJF-ID.1598	Lory coll.		Fig. 2E	18.91	6.93	7.38	7.79	52	0.366	0.39	0.412	0.41195	0.939	subvirgacone

Note: Gray boxes indicate approximate measurements.

boundary). This material forms a statistically significant sample in the sense of De Baets *et al.* (2015) and can be considered as representative of a contemporaneous palaeopopulation which allows to test the conspecificity between *C. crassicostatum* and *G. gargasense*.

4.1. Size

The diameter of the studied sample ranges from ~6 mm to 31 mm with an average value equals to 14.6 mm. The size of the lectotypes of *C. crassicostatum* ($D = 30.5$ mm) and *G. gargasense* ($D = 27.6$ mm) falls into the size range of the material at our disposal. Unfortunately, only pyritic nuclei were collected, hence preventing the recognition of maturity and potential size differentiation of sexual significance. This is evidenced by the size-frequency histogram which is positively skewed and placed on specimens comprised between 10 to 20 mm (Fig. 7A).

To our knowledge, complete specimens from the Apt–Gargas area remain unknown. The most complete individuals of the *C. crassicostatum*–*G. gargasense* plexus are those figured by Salas and Moreno (2008, pl. 7, fig. C; pl. 9, fig. A) and Moreno-Bedmar *et al.* (2012, appendix fig. 8G) from the *D. furcata*–*E. martini* zonal boundary interval

of Spain. The diameter of those specimens suggests that the adult size does not exceed ~100 mm.

4.2. Conch shape and ornamentation

4.2.1. *C. crassicostatum* morphotype

This morphotype represents 30% of the studied population. Its diameter is comprised between 11 and 31 mm (average of ~16.2 mm). The conch shape is mainly subvirgacone ($0.31 < U/D < 0.42$; average of 0.36 – Fig. 8), rarely virgacone (specimen CAR.23) or subophiocone (e.g. specimen CRL.5), with a discoidal to extremely discoidal ($0.29 < Ww/D < 0.48$; average of 0.40), strongly compressed ($0.29 < Ww/Wh < 0.48$; average of 0.40), very evolute coiling ($0.73 < U/Wh < 1.15$; average of 0.94) (Fig. 9).

A succession of five ontogenetic stages is recognised from this morphotype and consists of (Fig. 4):

1. Embryonic (Ammonitella) stage occupies less than 1 mm. This stage is marked by a distinctive neponic constriction.
2. Post-embryonic stage marked by reniform whorl section, crateriform umbilicus, spaced and flat-topped ribs angulate at shoulders or bearing strong tubercles and smooth interspaces. This stage mimics

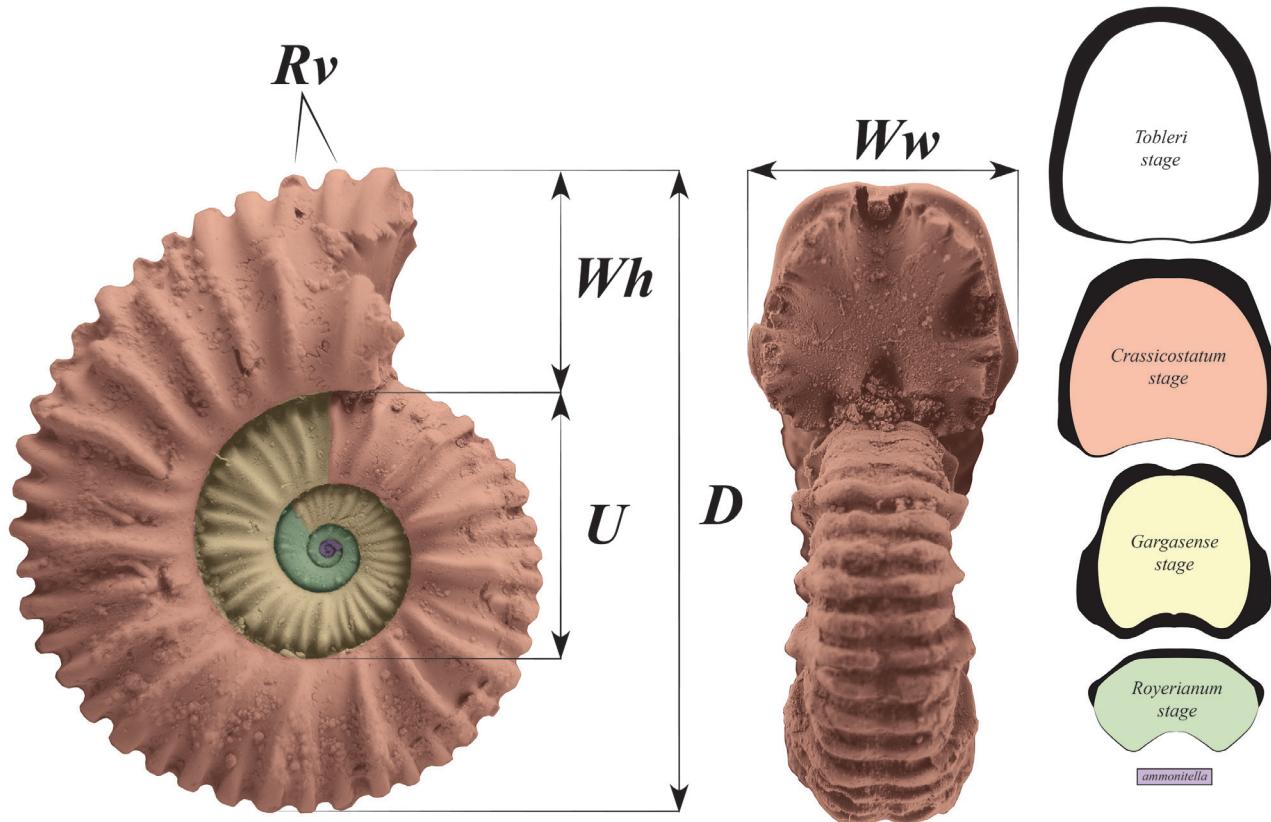


Figure 3. Explanatory diagram of the standard conch shape parameters measured, and illustration of the five ontogenetic stages and their schematised whorl sections (not to scale); namely (violet) Ammonitella, (green) Royerianum, (yellow) Gargasense, (red) Crassicostatum, and (white) Tobleri (not seen in our pyritic nuclei) on specimen CRL.1. Acronyms indicate D : diameter; Wh : whorl height; U : umbilical diameter; Ww : whorl width; Rv : number of ventral ribs on the half of the last preserved whorl.

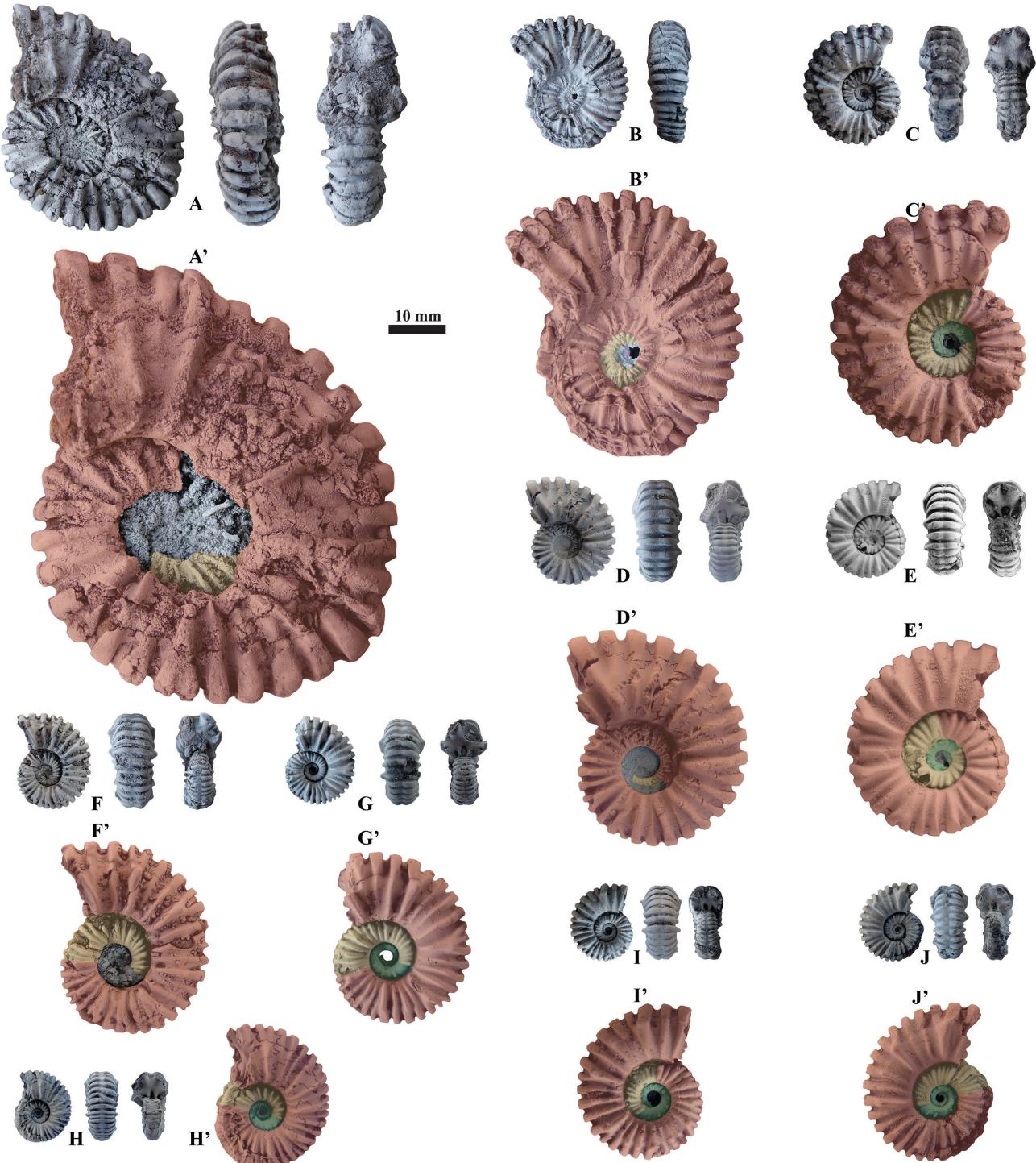


Figure 4. Selected specimens assigned to the *C. crassicostatum* morphotype from Carniol (CAR, CRL), and Les Davids (DAV), and illustration of the four ontogenetic stages on enlarged (x2) specimens. (A–A') DAV.2, (B–B') CAR.13, (C–C') CAR.24, (D–D') CAR.15, (E–E') CRL.5, (F–F') CAR.19, (G–G') CAR.21, (H–H') CAR.29, (I–I') CAR.22, and (J–J') CAR.24. All specimens were coated with ammonium chloride prior to photography. Scale bar is 10 mm. See Fig. 3 for colour legend of the four ontogenetic stages.



Figure 5. Selected specimens assigned to the *G. gargasense* morphotype from Carniol (CAR, CRL), and Les Davids (DAV), and illustration of the four ontogenetic stages on enlarged (x2) specimens. (A–A') CAR.2, (B–B') CRL.1, (C–C') CAR.3, (D–D') CAR.1, (E–E') CAR.4, (F–F') CAR.5, (G–G') CRL.11, (H–H') CRL.13, (I–I') CAR.7, (J–J') CRL.15, (K–K') CAR.32, (L–L') CAR.30, (M–M') CAR.28, (N–N') CAR.40, (O–O') CRL.17, (P–P') CAR.39, (Q–Q') CAR.45, and (R–R') DAV.3 (pathological specimen). All specimens were coated with ammonium chloride prior to photography. Scale bar is 10 mm. See Fig. 3 for colour legend of the four ontogenetic stages.

- the juvenile features of the Douvilleiceratidae *Procheloniceras–Cheloniceras* lineage known as the Royerianum stage in *litt.* (Ropolo *et al.*, 2008).
3. Gargasense juvenile stage (presents between $ca.2.7 < D < ca.3.8$ mm) marks a change from a reniform to a subquadrate whorl section with venter bearing a weak or moderately deep furrow. Following the Royerianum stage, the primary ribs maintain a tubercle on the upper flank, but secondaries – generally one to four – appear. The secondary ribs start at the peri-umbilical margin, they are simple albeit sometimes bifurcate or coalescent on the primaries at varying heights. The primary ribs are simple or rarely bifurcate. Those ribs become enlarged on the flank and can develop tubercles at the point of furcation. All ribs and branches tend to be flat-topped on the venter.
 4. Crassicostatum sub-adult stage starts between $ca.5.1 < D < ca.13.2$ mm and extends up to the end of the preserved outer whorls. The ornamentation continues the Gargasense juvenile stage, but the number of secondaries quickly decreases. The primary ribs become stronger, they are simple and bifurcate, rarely trifurcate, and commonly separated by a single secondary starting at varying heights.

The point of furcation is low, at the umbilical margin, or high on the flank and develop strong, elongated tubercles, and then strong thickenings. All ribs and branches are flat-topped or cuneiform on the venter. The ventral furrow is attenuated during the growth and progressively disappear because of ventral rounding.

5. The outer whorl ontogeny is not observed in the material at our disposal since it consists of pyritic nuclei. Nevertheless, the ribbing of the *C. crassicostatum* specimens illustrated by Salas and Moreno (2008, pl. 7, fig. C; pl. 9, fig. A), and Moreno-Bedmar *et al.* (2012, appendix fig. 8G) modifies into a regular alternation of strong, flexuous primary rib in the body chamber, with or without a slight retrocurvature at the umbilical margin, and one secondary starting at mid-flank. The whorl section is compressed, suboval, higher than wide, with a rounded venter. These features characterise the species *Colombiceras tobleri* (Jacob and Tobler, 1906); the latter being known as the potential direct descendant of *C. crassicostatum* (see discussion below). This stage is here referred to as the Tobleri adult stage (see also Fig. 3).

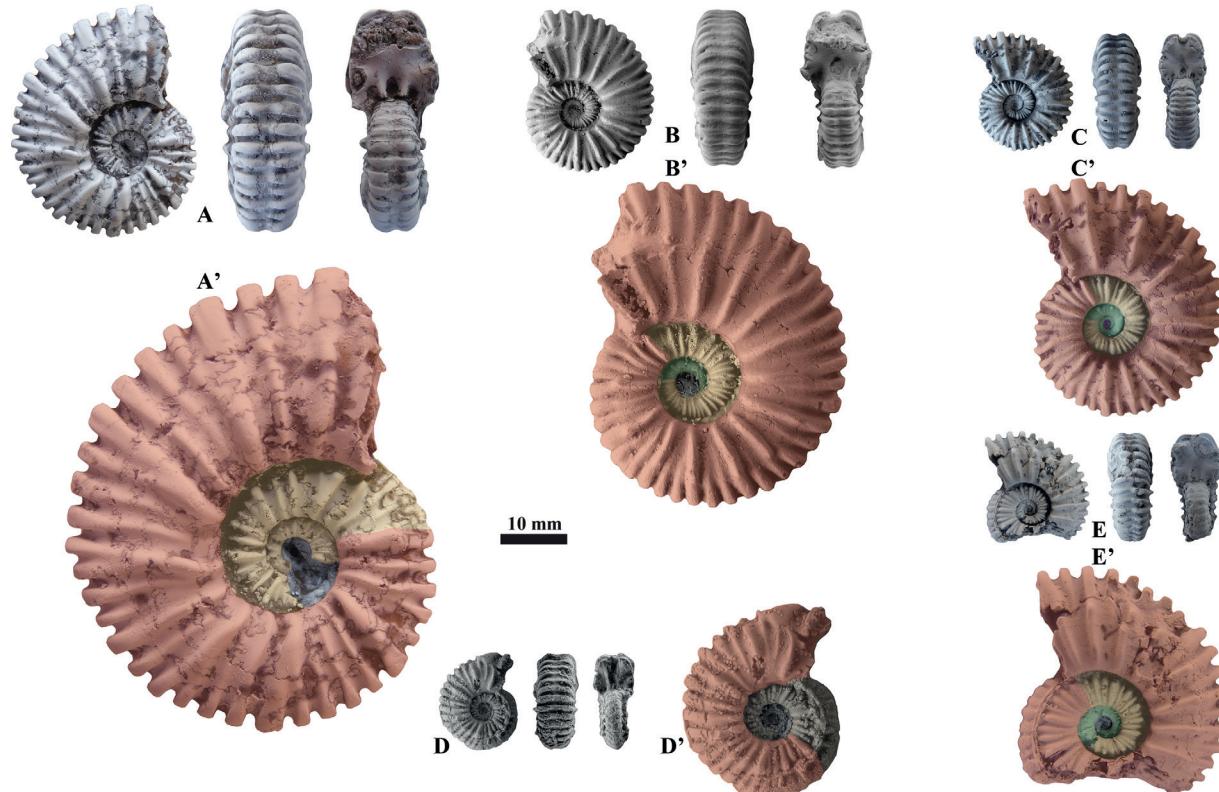


Figure 6. Selected specimens assigned to the transitional forms between the *C. crassicostatum* and *G. gargasense* morphotypes from Carniol (CAR, CRL), and Les Davids (DAV), and illustration of the four ontogenetic stages on enlarged (x2) specimens. (A–A') CAR.12, (B–B') CRL.2, (C–C') CAR.17, (D–D') CRL.10, (E–E') CAR.20. All specimens were coated with ammonium chloride prior to photography. Scale bar is 10 mm. See Fig. 3 for colour legend of the four ontogenetic stages.

4.2.2. *G. gargasense* morphotype

This morphotype represents 60% of the study sample. Its diameter is comprised between 6 and 28 mm (average of ~ 13.9 mm). The conch shape is mainly subvirgacone ($0.27 < U/D < 0.41$; average of 0.35) (Fig. 8), or rarely subdiscocone (e.g. specimens CAR.9, CAR.41, and CRL.9), with a discoidal to extremely discoidal ($0.31 < Ww/D < 0.45$; average of 0.38), strongly compressed ($0.31 < Ww/Wh < 0.45$; average of 0.38), evolute to very evolute coiling ($0.59 < U/Wh < 1.14$; average of 0.87) (Fig. 9).

This morphotype develops the four ontogenetic stages defined in the Crassicostatum morphotype but with major modifications of the Crassicostatum stage (Fig. 5):

- After the ammonitella, a similar Royerianum stage develops in most of specimens. However, this stage can sometimes be extended compared to the *C. crassicostatum* morphotype (e.g. Fig. 5D, H, N, O, P and Q). In those specimens, the ribbing is smoothed at the end of the stage and they develop a sub-rounded whorl section. Transition with the succeeding stage is more gradual as illustrated by the progressive appearance of the secondary ribs.
- The Gargasense juvenile stage appears between $ca.2.9 < D < ca.5.95$ mm. As a result, it appears slightly delayed and extended compared to the *C. crassicostatum* morphotype. The whorl section becomes distinctly subquadrate with flattened flanks and venter. The maximum thickness of the whorl

section is reached at the umbilical margin. Primary ribs are attenuated and tubercles at the point of furcation are mostly lacking or changed as slight thickenings (e.g. Fig. 5D). The ventral furrow is in most cases better expressed and can form a discrete smooth ventral band (e.g. Fig. 5O).

- The Gargasense juvenile stage progressively gives way to a modified Crassicostatum sub-adult stage consisting of finely ribbed, more or less regular alternation of simple, rarely bifurcate, primary ribs and generally one or secondaries starting at variable heights. All ribs and branches are sharp-edged and less cuneiform on the venter with progressively attenuated ventral furrow until its disappearance in larger specimens (such as in the lectotype, see Fig. 2B). This stage maintains a subrectangular whorl section with a flattened venter.
- Adult individuals of the *G. gargasense* morphotype are scarce in the literature and the presence of a Tobleri stage remains unclear.

Note that few specimens are transitional between the *C. crassicostatum* and *G. gargasense* morphotypes regarding conch shape and ribbing (see Fig. 6). These specimens maintain the compressed, subrectangular whorl section as those seen in *G. gargasense* sub-adult forms but develop a ribbing that better conform to the Crassicostatum stage.

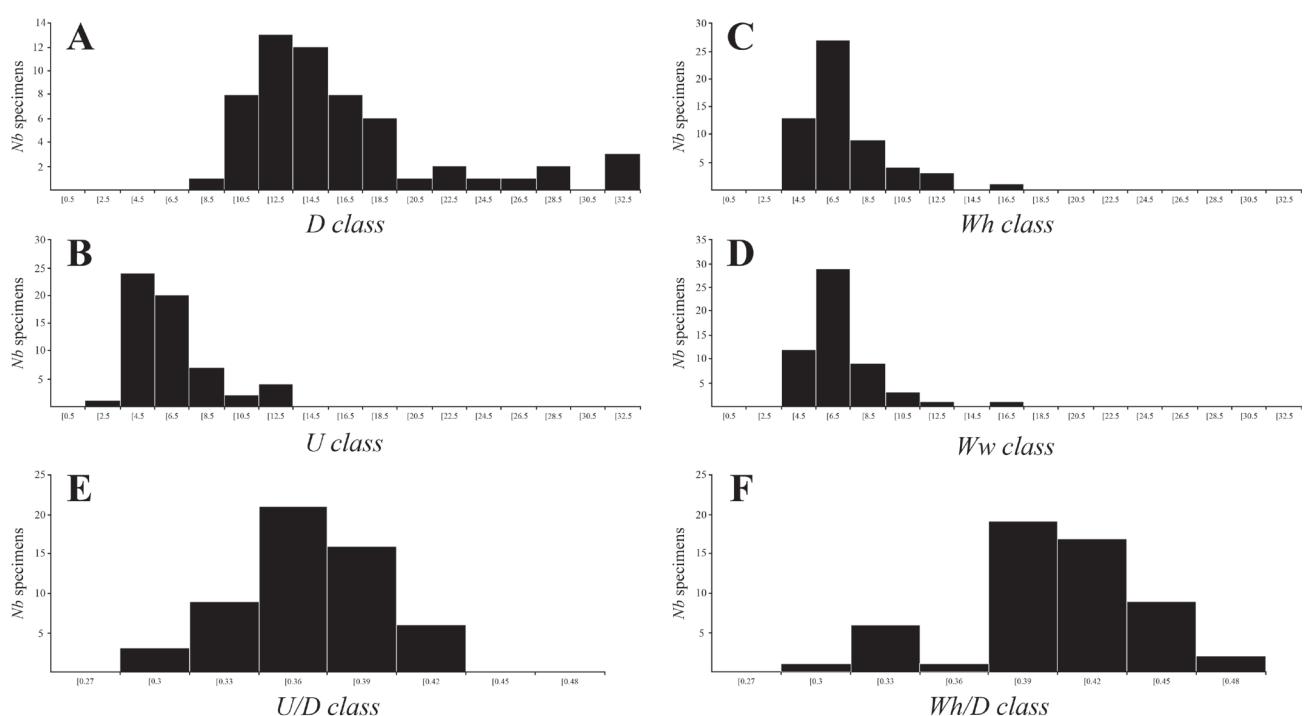


Figure 7. Frequency histograms of the conch shape parameters (D , U , Wh , Ww) and ratios (U/D , Wh/D) of the *C. crassicostatum* – *G. gargasensis* plexus from the Aptian-type area.

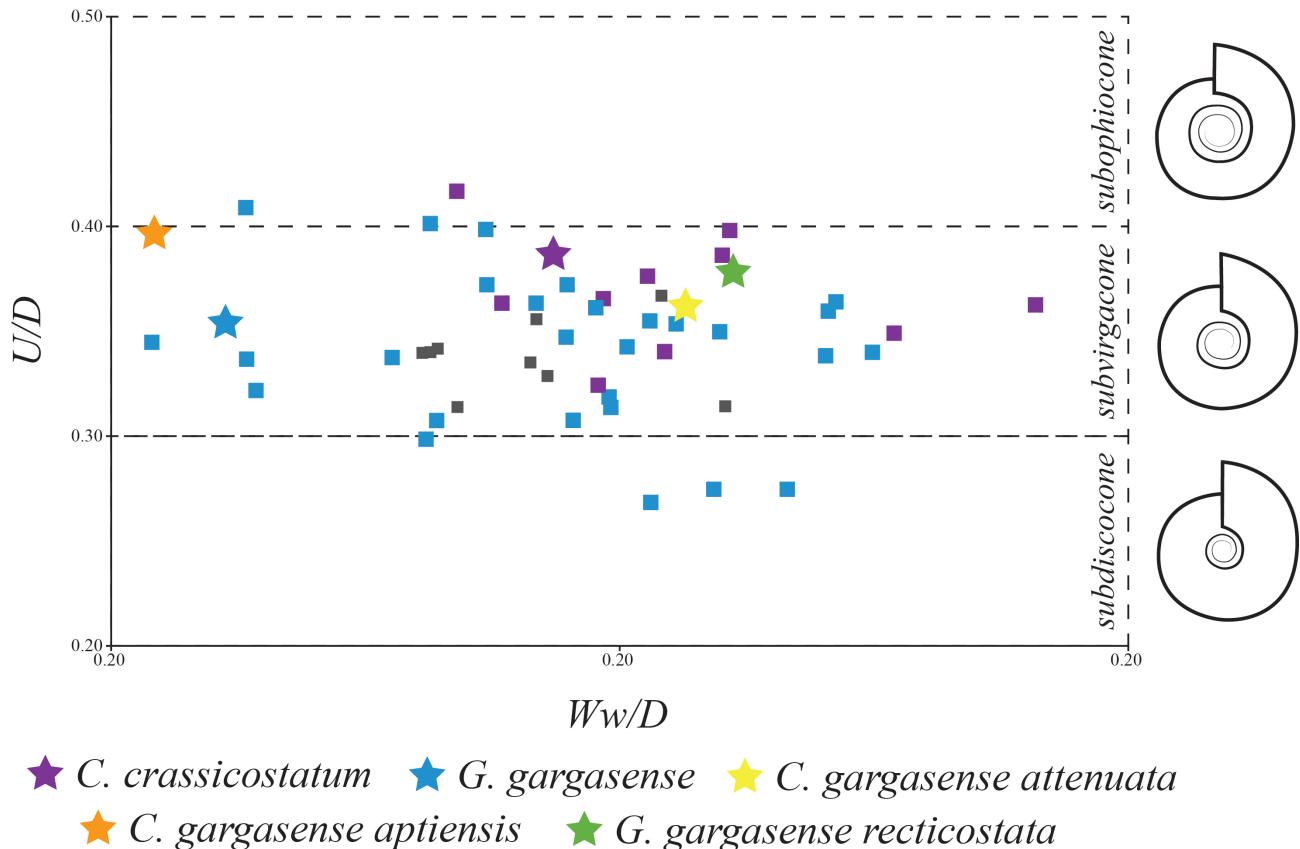


Figure 8. Relationships between the U/D and Ww/U ratios for describing the conch shape of the the *C. crassicostatum* (blue squares) and *G. gargasense* (green squares) morphotypes, and the transitional forms (grey squares), from Carniol and Les Davids, as well as those of the *C. crassicostatum*, *G. gargasense*, *G. gargasense* var. *aptiensis*, *G. gargasense* var. *recticostata*, and *G. gargasense* var. *attenuata* type specimens.

4.2.3. Biometric investigation

Although the distinction of two morphotypes can be a priori performed, the box plots of the four conch shape ratios (Ww/D , Ww/H , U/Wh and U/D – Fig. 9A–D) show that the two morphological groups do not differ significantly as indicated by their overlap. There is no major shell difference since the frequency histograms of the conch shape parameters D , U , Wh and Ww (Fig. 7A–D), as well as those of the ratios U/D and Ww/D (Fig. 7E and F) exhibit normal distributions. Finally, the investigation on the dimensional parameter growth of the shell (U , Wh and Ww in function of D - Fig. 10A–C; and Ww in function of Wh - Fig. 10D) of the seventy-three specimens show homogeneous scattering around the mean curve (with R^2 very high > 0.91), with a linear, isometric and harmonic growth which corresponds to the relationship $Y=bD$. Dense and homogenous scatter plots of the shell ratios U/D and Ww/Wh in function of D (Fig. 10E and F) are observed. Regarding the costal density on the venter, the values are comprised between 15 and 32 ventral ribs on the last preserved whorls of the studied specimens (including the types), except for the holotype of *G. gargasense* var. *attenuata* that reaches 52 ventral ribs and thus strongly deviates from the point cloud (Fig. 10G).

Taken together, the biometric investigation gives evidence of the sample homogeneity (except for *G. gargasense* *attenuata* regarding its ribbing), and the existence of a continuum in conch shapes. As such, the hypothesis of conch shape covariation proposed by Dutour (2005) for explaining the two morphotypes is unlikely.

4.3. Suture line

D'Orbigny (1841, pl. 59, fig. 3 and 7) provided hand-drawings of the suture lines of both *C. crassicostatum* and *G. gargasense* (here re-illustrated on Fig. 11A–B). The suture line of the *C. crassicostatum*–*G. gargasense* plexus shows the typical features of Cretaceous quinquelobate ammonites *sensu* Korn et al. (2003). The external lobe (E) is bifid with a bipartite median saddle while the adventive one (A) is trifid, more or less symmetrical with a long central branch. Between them, the saddle E/A is high, distinctly, or weakly asymmetrically, bifid. There are two umbilical lobes; the U2 is bifid while the U1 is shallow and trifid in both species but less distinct in *C. crassicostatum*. The saddle A/U2 is asymmetrical and narrower than the E/A one. D'Orbigny does not provided description of the internal (I) lobe.

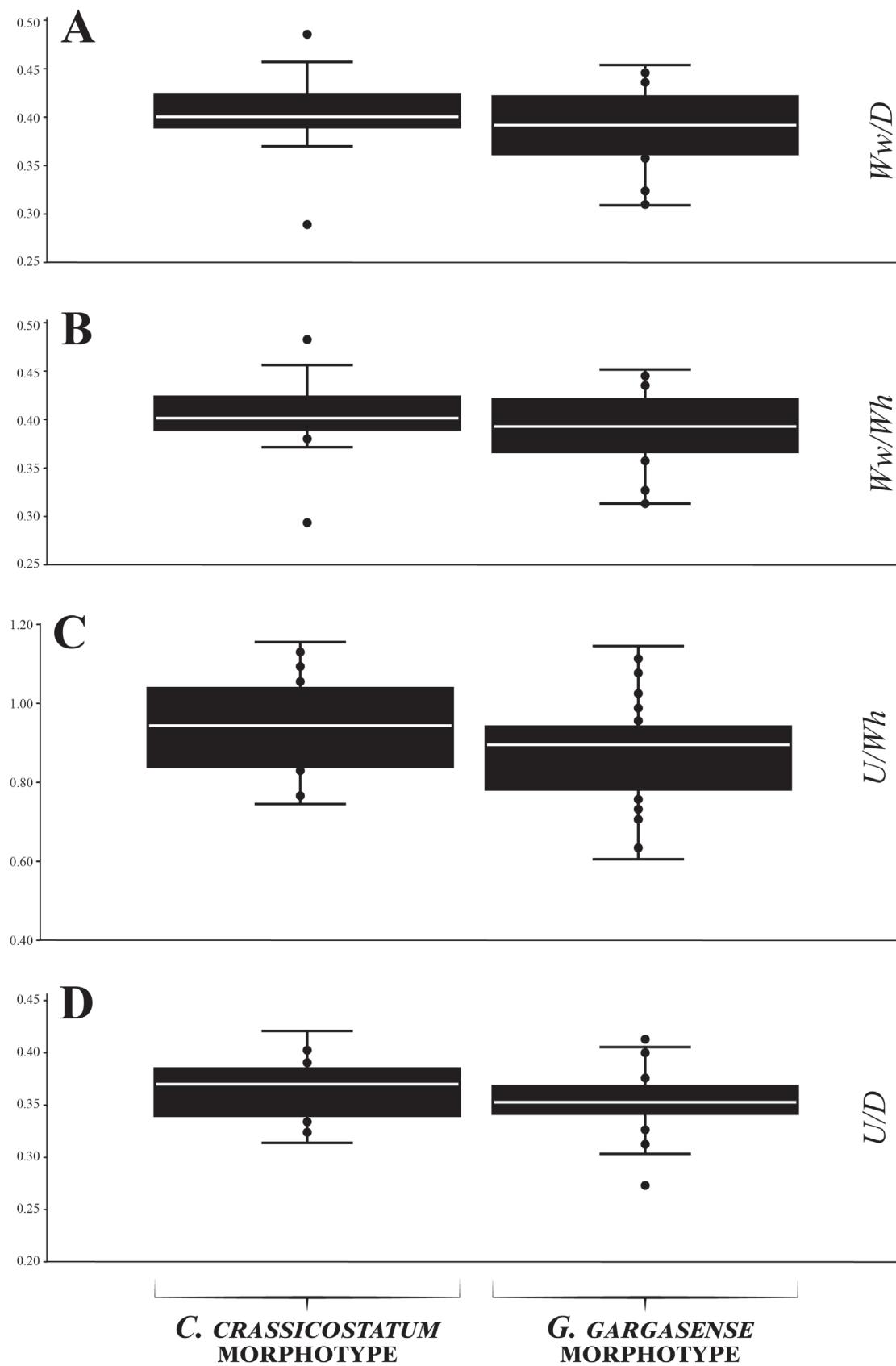


Figure 9. Box plots of shell shape ratios (A) Ww/D , (B) Ww/H , (C) U/Wh , and (D) U/D for the *C. crassicostatum* and *G. gargasense* morphotypes. The boxes represent the interquartile range (*i.e.* the values ranging from the first to third quartiles, which are the 25th and 75th percentiles, respectively), the median value (white line), the extended interquartile range (whiskers) and the eventual outliers (isolated black dots).

According to the revision of Bogdanova and Mikhailova (2016), it is deep, narrow and bifid with almost parallel serrated sides. The saddle U1/I is narrow bifid with a deep secondary lobe. Despite being observed on a limited number of specimens, these features do not appear to vary on the material at our disposal (Fig. 11C–F).

4.4. Pathology

In the material at our disposal, at least three specimens show pathologies (= 4% of the study sample):

- Specimen CAR.29 (Fig. 4H) shows a slight anomalous rib branching on the venter.
- Specimen DAV.3 (Fig. 5R) has a slightly deformed shell with a chaotic sculpture with respect to the ontogenetic stages defined above. This refers to the *chaotica forma*-type pathology *sensu* Keupp (1977) and could either be related to endo and exogenic causes (Hengsbach, 1996).
- Specimen CRL.10 (Fig. 6D) shows a conspicuous, temporary bulbous swelling of the external part of the venter. It corresponds to the *inflata forma*-type pathology as defined by Keupp (1976) and related to parasitism (Hengsbach, 1996).

5. Discussion

5.1. Species level

Our biometric investigation reveals a continuum of conch shapes between the *C. crassicostatum* and *G. gargasense* morphotypes. The variability observed mainly relates to accelerated/decelerated ornamental sequence. The *C. crassicostatum* morphotype develops earlier the Crassicostatum stage while the *G. gargasense* morphotype retains ribbing and conch shape of the Gargasense stage throughout most of the preserved subadult whorls. The variable duration of the ornamental stages accounted for the age-old taxonomic distinction between the *C. crassicostatum* and *G. gargasense* morphotypes. As such, *C. crassicostatum* and *G. gargasense* might be interpreted, respectively, as tachymorphic and bradymporphic forms *sensu* Besnozov and Mitta (1995) of a single palaeobiological entity. The lectotypes of *C. crassicostatum* and *G. gargasense* correspond to extreme representatives of the variation series (= typical tachy- and bradymporph as defined by Besnozov and Mitta, 1995). The two species can be, therefore, considered as synonym.

We thereafter retain *C. crassicostatum* as the senior subjective synonym of *G. gargasense* and its subspecies *aptiensis* and *recticostata*. In the lack of date priority between the two taxa, this synonymy is supported by the long quoting history of *C. crassicostatum* in the literature and its historical use as a zonal index of the Aptian in the Caucasus (Renngarten, 1951; Drushchits and Mikhailova,

1979; Drushchits *et al.*, 1985, 1986), Lesser Balkhan and Kyurendag (Bogdanova and Mikhailova, 2016 and references therein) and Vocontian through as well (Dauphin, 2002). Consequently, the genus *Gargasiceras* is here considered as junior subjective synonym of *Colombiceras* according to the ICZN's rules. Revision of the synonymy of *C. crassicostatum* is given in appendix 1. As herein understood, the species occurs in the Mediterranean-Caucasian Subrealm of the Tethyan Realm *sensu* Westermann (2000) and remains doubtful in Japan and the Caribbean domain.

Note that the taxon *G. gargasense* var. *attenuata* can be easily distinguished from the *C. crassicostatum* type population by its high costal density. Its generic assignment remains unclear and the taxon is provisionally kept in *Colombiceras* pending further refinements.

5.2. Genus level

5.2.1. Specific content

Based on the present results, the genus *Colombiceras* is here restricted to the following taxa:

- *C. crassicostatum* (and its junior subjective synonyms *G. gargasense*, *G. gargasense* var. *aptiensis*, and *G. gargasense* var. *recticostata*).
- *C. tobleri* and the closely allied, virtually coexisting taxa *Acanthohoplites tobleri* var. *discoidalis* Sinzow, 1908, *Acanthohoplites subpeltoceroides* Sinzow, 1908, *Acanthohoplites quadratus* Kazansky, 1914, *Acanthohoplites rectangularis* Kazansky, 1914, *Acanthohoplites sinzowi* Kazansky, 1914 and *Acanthohoplites subtobleri* Kazansky, 1914, *Colombiceras lecollei* Cantú-Chapa, 1963, *Colombiceras medellini* Cantú-Chapa, 1963, *Colombiceras bogdanovae* (Tovbina, 1982), *Colombiceras korotkovi* Bogdanova and Mikhailova, 2016 and doubtfully *Acanthohoplites subtobleri batinensis* Dimitrova, 1967. By comparison with the type species, the gathers of *C. tobleri* group taxa with Crassicostatum-like morphotype with earlier acquisition of a rounded whorl section, reduced Gargasense and Crassicostatum stages in the inner whorls, and a long Tobleri adult stage on the outer whorl (compare with Fig. 12A). The species is of younger age since it is reported in the middle to upper part of the *E. martini* Zone in the Mediterranean-Caucasian settings (Dauphin, 2002; Luber *et al.*, 2017). A direct phyletic relationship between *C. crassicostatum* and *C. tobleri* is likely and may correspond to a peramorphic evolution that deserves further investigation.
- *C. spathi* Humphrey, 1949 is based on a moderate-sized, calcareous mold from the Aptian of La Peña Formation of northern Mexico (see illustration of the holotype in Barragán *et al.*, 2016, Fig. 3) (Fig. 12B). The holotype lacks inner whorls,

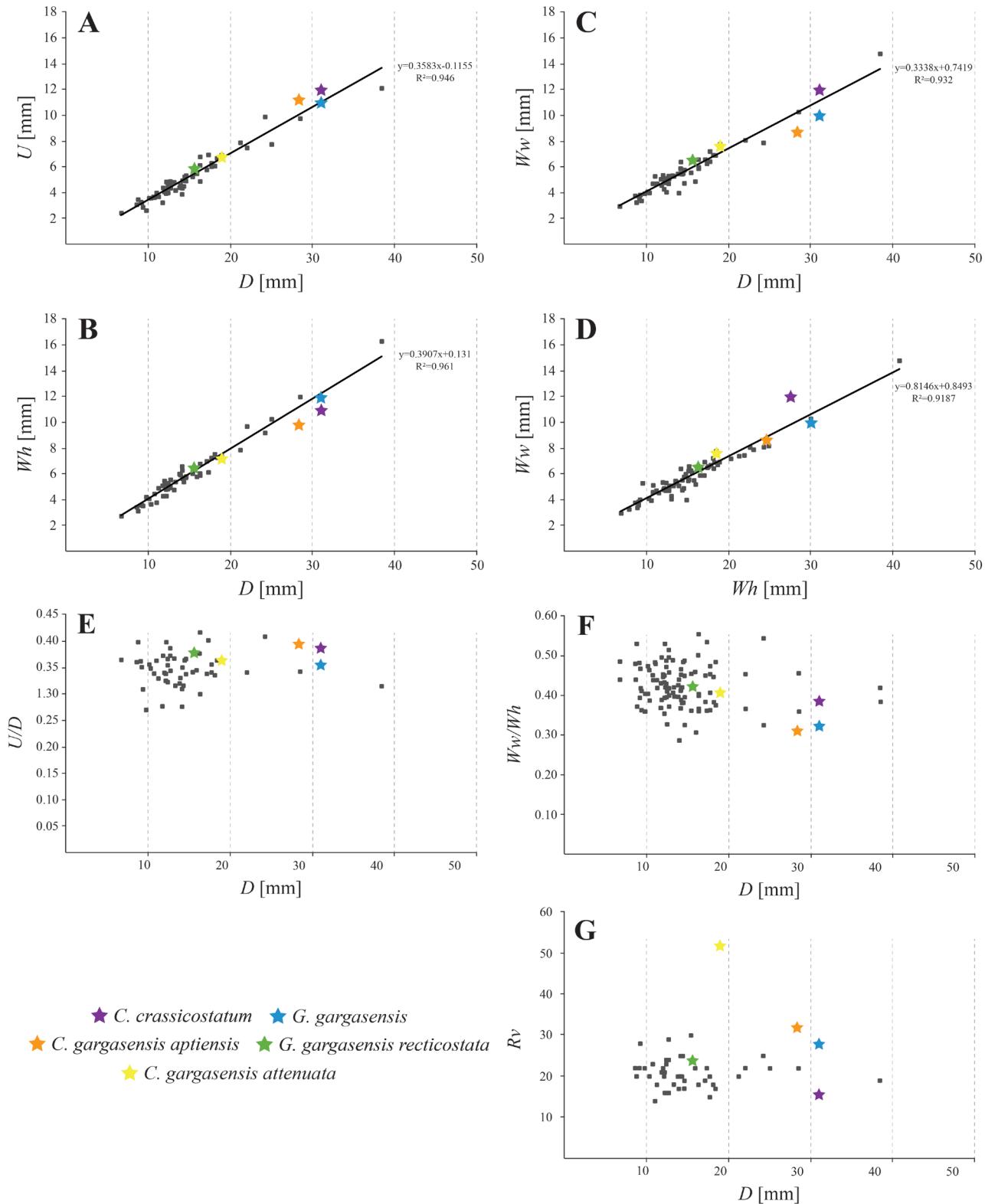


Figure 10. Bivariate diagrams of the conch parameters (A) U , (B) Wh , (C) Ww , and (G) Rv in function of D ; (D) Ww in function of Wh ; and the ratios (E) U/D , and (F) Ww/Wh in function of D for the 73 specimens of the *C. crassicostatum* – *G. gargasense* plexus from the Aptian-type area.

and this prevents further comparison with *C. crassicostatum*. Subsequent illustrations of northern Mexican colombiceratids assigned to *C. spathi* suggest that the species is closely related to the group of *C. tobleri* (compare for example Barragán *et al.*, 2016, fig. 1D and H and the typological taxa *Colombiceras subtobleri* and *C. quadratus*).

- *C. formosum* Sharikadze, Kakabadze and Hoedemaeker, 2004 is close to *C. crassicostatum* but develops a sub-rectangular whorl section in the adult with a flattened venter (see holotype in Fig. 12C). Its juvenile whorls are densely ribbed and then develop a Crassicostatum-like stage. It gives way to a short terminal stage on the outer whorls consisting of slightly prosiradiate primary ribs and secondaries.
- *C. satowi* Shimizu, 1931 from the Aptian of Japan has been recently regarded as a nomen dubium by Futakami (2018) since the holotype of this species “consists of an extremely small shell ($D = 17$ mm) which does not allow a sufficient comparison of morphological features with other species of the genus *Colombiceras*” (see holotype in Fig. 12D). Japanese colombiceratids figured by Futakami (2018) have been referred to *C. spathi*. From our point of view, the variability of the Japanese colombiceratids conform to those documented in *C.*

crassicostatum, with *gargasense* (Futakami, 2018, fig. 4 D–E, M–N, O; fig. 7C) and *crassicostatum* morphotypes (the others ones illustrated by Futakami, 2018). They similarly develop a moderate adult size (*ca.* 70 mm according to Futakami, 2018), sub-rectangular to sub-elliptical whorl section with a flattened venter. The affinities of this material with *C. satowi* and *C. crassicostatum* remains to be investigated.

- and doubtfully *C. attenuatum*.

Other taxa referred to as *Colombiceras* in the Fossilium Catalogus by Klein and Bogdanova (2013) belong to diverse acanthohoplid forms which deserve further investigation:

- *C. caucasicum* (Luppov, 1949) and the allied taxon *C. ellissoae* Kvartialiani, 1971 develop a short juvenile stage with strong ribs giving way to a Crassicostatum-like stage lacking tubercles. The whorl section is distinctly sub-rounded and lacks a ventral furrow. The two taxa are closely related, if not similar, to juveniles (or ?microconchs) of *Egoaniceras angulatum* (Egoian, 1969), the type species of *Egoaniceras* Avram, 1974 (compare for example with Avram, 1974, pl. 1, figs. 3, 4).
- *C. caucasicum tyrrhenicum* Wiedmann and Dieni, 1968 is based on a small-sized acanthohoplid fragment marked by a robust ornamentation with

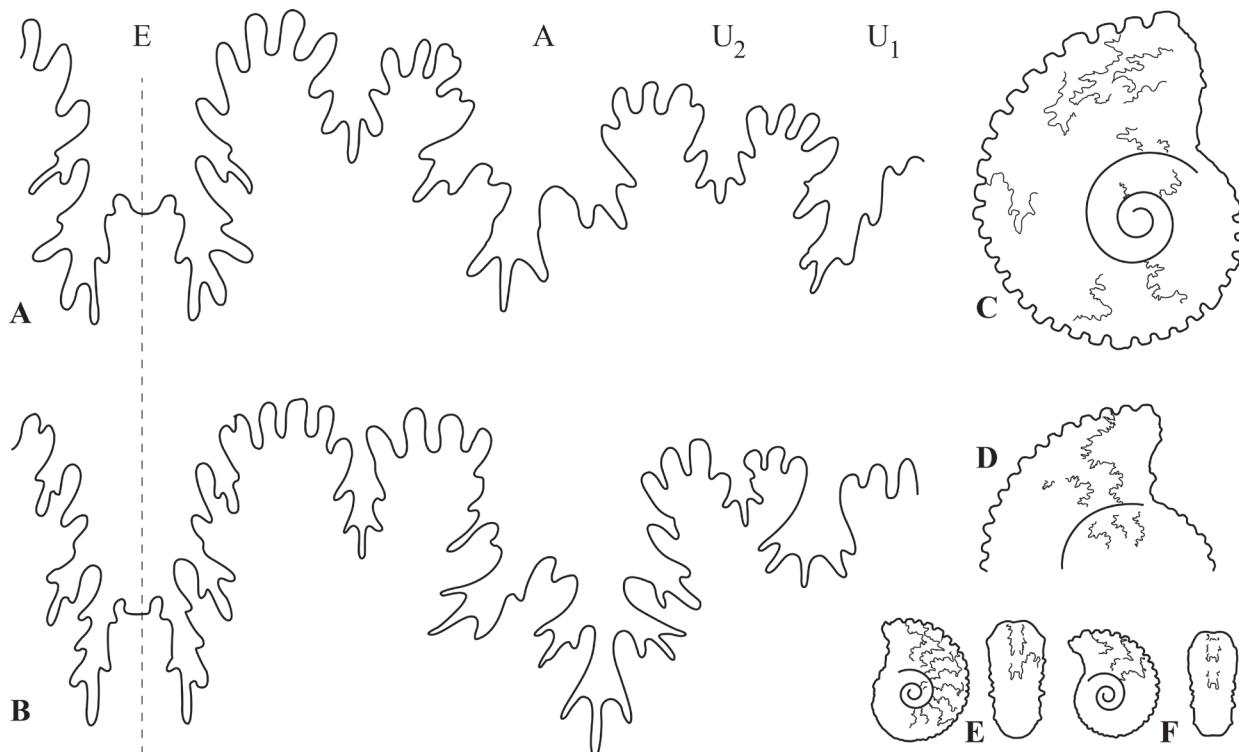


Figure 11. Comparison between the original suture lines of (A) *C. crassicostatum* and (B) *G. gargasense* hand-drawn by d'Orbigny (1841) and selected specimens from the Aptian-type area (C) CAR.12, (D) CRL.1, (E) CAR.29, (F) CAR.28. Not to scale.

flat-topped ribs and prominent tubercles at the point of furcation of the primary rib. These features differ from those observed in typical *C. caucasicum*. Considering that its complete ontogeny remains unknown, *C. caucasicum tyrrhenicum* should be considered as a nomen dubium pending new collection at its type locality (*i.e.* Orosei, Sardinia).

- *C. robustum* Scott, 1940 merely represents a juvenile and/or microconch of the Californian "*Hypacanthoplites*" *sensu* Young (1974).
- *C.? brumale* Stoyanow, 1949 is closely allied to *Immunitoceras immunitum* Stoyanow, 1949 that typifies the genus *Immunitoceras* Stoyanow, 1949.
- The taxonomy of *C. riedeli* Cantú-Chapa, 1963 remains unclear since its holotype lacks inner whorls.
- *C. strangulatum* Collignon, 1962 may represent a juvenile form of the "*Acanthoplites*" *sensu* Collignon (1962).
- *C. waageni* Spath, 1930 is based on a hand-drawing illustration. The species share general features of the adult *Colombiceras* (*i.e.* Tobleri stage). However, its juvenile morphology remains unknown and prevents further discussion. Validity of the species can only be established after re-examination of the type specimen.

The species previously assigned to the genus *Gargasiceras* (see Klein and Bogdanova, 2013) can be easily distinguished from *C. crassicostatum* by their morphological and ornamental features, age and

palaeobiogeographic distribution. The following species deserve further investigations:

- *Gargasiceras pulcher* (Riedel, 1938), *G. acutecostatum* (Riedel, 1938), *G. adkinsi* (Humphrey, 1949) *G. subpulcher* Sharikadze, Kakabadze and Hoedemaeker, 2004 and probably *G. interiectum* (Riedel, 1938) form a homogenous endemic group of the Caribbean domain (see discussion in Ovando-Figueroa *et al.*, 2015). These species closely resemble *Hypacanthoplites?* *rursiradiatus* Humphrey, 1949 which typify the genus *Penaceras* Cantú-Chapa, 1963.
- The subspecies *Gargasiceras lautum lautum* (Glazunova, 1953) and *Gargasiceras lautum laxa* (Glazunova, 1953), originating from the *P. melchioris* Zone *sensu lato*, are based on a very limited number of specimens from the Mangyshlak (Glazunova, 1953), Bulgaria (Dimitrova, 1967) and southeastern Spain (Moreno-Bedmar *et al.*, 2008). They show close affinities with the juveniles (or ?microconchs) of the type species *Egoaniceras angulatum* but with a higher rib density (compare with Egoian, 1969, pl. XII, fig. 8 and 9).
- *Gargasiceras (?) juanwyatti* Etayo-Serna, 1979 is based on a lower Albian micromorphic acanthohoplitid form. Its closest affinities are found with the inner whorls of the species *Juandurhamiceras juandurhami* Etayo-Serna, 1979 of same age and origin (Etayo-Serna, 1979, p. 108).

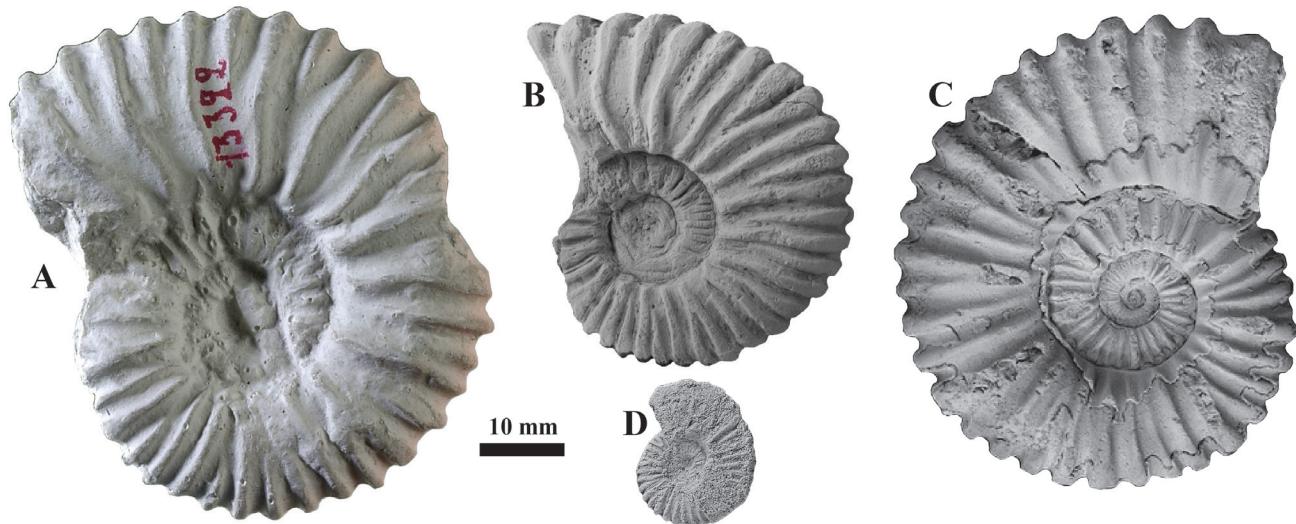


Figure 12. Re-illustration of (A) syntype of *Colombiceras tobleri* (Jacob and Tobler, 1906) (plaster cast FSL.13322 of the Faculté des Sciences de Lyon); (B) holotype UMM.P.24298 (University of Michigan Museum of Paleontology) of *Colombiceras spathi* Humphrey, 1949 (modified from Barragán *et al.*, 2016); (C) holotype RGM.283011 (Nationale Natuurhistorisch Museum, Leyde) of *C. formosum* Sharikadze, Kakabadze and Hoedemaeker, 2004 (modified from Sharikadze *et al.*, 2004), and (D) holotype IGPS.35387 (Tohoku University Museum, Sendai, Miyagi) of *Colombiceras satowi* Shimizu, 1931 (modified from Futakami, 2018). Scale bar 10 mm.

5.2.2. Subgenus

In the Fossilium Catalogus, Klein and Bogdanova (2013) identified two *Colombiceras* subgenera – *i.e.* *Colombiceras* and *Egoianiceras* – that have been considered as antidimorphs by Avram (1974). The subgenus *Egoianiceras* groups the species *Colombiceras (Egoianiceras) multicostatum* Avram, 1974 and *Colombiceras (Egoianiceras) angulatum* Egoian, 1969; the type species. The *Egoianiceras* relatives differ from *Colombiceras* by their rounded juvenile whorl section and the lack of ventral furrow. In those taxa, the Gargasense and Crassicostatum sub-adult stages are reduced and attenuated while a Tobleri stage extends over most of the ontogeny. As a result, these features better compare to late *Colombiceras* of the group of *C. tobleri*. However, the *Egoianiceras* relatives develop a more densely ribbed Tobleri stage ($Rv > 30$ in *C. (E.) multicostatum*). Moreover, the *Egoianiceras* relatives are known to flourish in the middle to upper part of the upper Aptian. This age is younger than that of *C. crassicostatum* and does not support the Avram's dimorphism hypothesis between the two subgenera. Pending further investigation, *Colombiceras* and *Egoianiceras* can be considered as two distinct valid genera.

5.3. Supra-generic level

In the current state of knowledge, *Procolombiceras* (including *P. antiquus* Sharikadze, 1979 and *P. aptus* Sharikadze, 1979, its type species) from the *D. furcata* Zone of Georgia corresponds to the most primitive Acanthohoplitidae. Its type species can be easily distinguished from *C. crassicostatum* by its douvilleiceratid shell morphology marked by moderately involute coiling with a deep umbilicus, depressed subrounded whorl section with rounded flanks and venter throughout ontogeny. The *P. aptus–antiquus* group is known by a limited number of specimens, most of them illustrated by Sharikadze (1979).

Both *Procolombiceras* and *Colombiceras* have been up to date classified in the subfamily Acanthohoplitiniae and in the family Parahoplitidae (Klein and Bogdanova, 2013). According to Spath (1931), Casey (1965), Wright *et al.* (1996) and Dutour (2005), the Acanthohoplitiniae have derived from late Deshayesitidae during the *D. furcata* Zone. However, this view has been subsequently challenged by some authors given the lack of intermediate forms and the strong discrepancy in the suture line between deshayesitid and acanthohoplitid ammonites, (*e.g.* Wiedmann, 1966; Tovbina, 1979; Sharikadze, 2015). Those authors favoured an evolution of the Acanthohoplitiniae within the Douvilleiceratidae. This would be supported by similar juvenile ontogenetic stage (*i.e.* Royerianum stage) and suture line shared by *C. crassicostatum* and the *Procheloniceras–Cheloniceras* lineage. According to Bogdanova and Mikhailova (2016), the morphogenesis of the suture of the basal *Colombiceras* relatives is similar to that observed in the Douvilleiceratidae over the first

two whorls and subsequently change as the result of the division of the *U2/U3* saddle. As further evidence, typical parahoplitid relatives (*Parahoplites*) markedly postdate the inception of both *Procolombiceras* and *Colombiceras* since they appear in the middle part of the upper Aptian (Casey, 1965; Dauphin, 2002; Bogdanova and Mikhailova, 2016). Ongoing study suggests that the genus *Parahoplites* has merely evolved from late *Epicheloniceras* of the group of *E. buxtorfi* (Jacob and Tobler, 1906) by accelerated hypermorphosis in the sense of Dommergues *et al.* (1986). As a result, we here considered that both acanthohoplitid and parahoplitid lineages iteratively evolved from the Douvilleiceratidae. The deep morphological and ornamental modifications, combined with deep changes in the suture line, support the separate use of the superfamilies Douvilleiceratoidea, Acanthohoplitoidea and Parahoplitoidea as suggested by Sharikadze (2015).

6. Conclusion

Based on a biometric study conducted on topotype material, we herein consider the Acanthohoplitidae *Colombiceras crassicostatum* and *Gargasiceras gargasense* as representative of a single palaeopopulation, in which their respective type specimens characterize two extreme ornamental poles, *i.e.* tachy- versus bradymorph, respectively. Both species are regarded as subjective synonyms and we retain *C. crassicostatum* as the valid name following historical precedence and *Gargasiceras* is, therefore, synonymised with *Colombiceras*. Revision of the specific content of both *Colombiceras* and *Gargasiceras* genera suggests an overlooked biodiversity in the Acanthohoplitidae that deserves comprehensive taxonomic investigations.

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Appendix 1. Revised synonymy list of *C. crassicostatum* (d'Orbigny, 1841)

- 1841 *Ammonites crassicostatus* d'Orbigny, p. 197, pl. 59, fig. 1-3, 4-4'.
 1841 *Ammonites Gargasensis* d'Orbigny, p. 199, pl. 59, fig. 5, 6, 7.
 1852 *Ammonites crassicostatus* d'Orbigny - Bronn, p. 322, pl. 32, fig. 12a-c (= d'Orbigny, 1841, pl. 59, fig. 1-3).
 1882 *Ammonites crassicostatus* d'Orbigny - Mallada, p. 21, pl. 8, fig. 3-4 (= d'Orbigny, 1841, pl. 59, fig. 1-2).
 1882 *Ammonites gargasensis* d'Orbigny - Mallada, p. 19, pl. 8, fig. 9, 10 (= d'Orbigny, 1841, pl. 59, fig. 5, 6); ?pl. 10, fig. 12, 13, 14.
 1897 *Hoplites gargasensis* (d'Orbigny) - Sarasin, p. 768, text-fig. 5.
 1913 *Acanthohoplites crassicostatus* (d'Orbigny) - Kilian, p. 346, pl. 11, fig. 6a-b, text-fig. 6 (= d'Orbigny, 1841, pl. 59, fig. 1-3).
 1913 *Acanthohoplites gargasensis* (d'Orbigny) - Kilian, p. 346, pl. 11, fig. 7a-b (= d'Orbigny, 1841, pl. 59, fig. 5, 6); pl. 11, text-fig. 7 left hand (= Sarasin, 1897, text-fig. 5).
 1915 *Acanthohoplites crassicostatus* (d'Orbigny) - Kilian and Reboul, p. 46, text-fig. 7 (= d'Orbigny, 1841, pl. 59, fig. 3).
 1915 *Acanthoplites gargasensis* (d'Orbigny) - Kilian and Reboul, p. 44, text-fig. 6 (= Sarasin, 1897, text-fig. 5).
 1927 *Acanthoplites gargasensis* var. *aptiense* - Roch, p. 292, pl. 18, fig. 5-5a, text-fig. 4.
 1927 *Acanthoplites gargasensis* var. *recticostata* Roch, p. 288, pl. 18, fig. 6-6a, 7-7a.
 1957 *Colombiceras crassicostatum* (d'Orbigny) - Arkell et al., p. L387, fig. 501: 1a-b (= d'Orbigny, 1841, pl. 59, fig. 1-2).
 1957 *Gargasiceras gargasense* (d'Orbigny) - Arkell et al., p. L387, fig. 501: 6a-b (= d'Orbigny, 1841, pl. 59, fig. 5-6).
 ? 1958 *Gargasiceras gargasense* var. *aptiensis* (Roch) - Luppov and Drushchits, p. 103, pl. 47, fig. 6A-B.
 non 1960 *Acanthohoplites gargasensis* (d'Orbigny) - Waitzman, p. 61, pl. 3, fig. 3a-b; pl. 5, fig. 4a-b (= Deshayesitidae indet.).
 non 1961 *Colombiceras crassicostatum* (d'Orbigny) - Eristavi, p. 66, pl. 4, fig. 5 (= *Colombiceras tobleri* juv.).
 1965 *Colombiceras crassicostatum* (d'Orbigny) - Casey, text-fig. 153a-b, 153c-d, 153e (= d'Orbigny, 1841, pl. 59, fig. 1-3, 4-4').
 1966 *Colombiceras* cf. *crassicostatum* (d'Orbigny) - Wiedmann, pl. 6, fig. 2a-b.
 1966 *Gargasiceras gargasense* (d'Orbigny) - Wiedmann, text-fig. 29.
 ? 1966 *Colombiceras* cf. *crassicostatum* (d'Orbigny) - Schindewolf, text-fig. 427a, 427b, 427c, 427d.
 non 1967 *Colombiceras crassicostatum* (d'Orbigny) - Dimitrova, p. 192, pl. 89, fig. 3 (= *Colombiceras* sp. gr. *tobleri*).
 non 1967 *Gargasiceras aptiense* (Roch) - Dimitrova, p. 189, pl. 90, fig. 10 (= "Acanthohoplites" lautum).
 non 1969 *Gargasiceras ex gr. gargasense* (d'Orbigny) - Egoian, p. 164, pl. 12, fig. 10a-b; pl. 23, fig. 35 (= *Diadochoceras* sp. juv.).
 1970 *Gargasiceras gargasense* (d'Orbigny) - Kullmann and Wiedmann, text-fig. 10 (= Wiedmann, 1966, text-fig. 29).
 1971 *Colombiceras crassicostatum* (d'Orbigny) - Kvataliani, p. 61, text-fig. 33-1, 33-2, 33-3 (= d'Orbigny, 1841, pl. 59, fig. 1-3).
 ?1975 *Gargasiceras gargasensis* (d'Orbigny) - Lillo Beviá, p. 87, pl. 2, fig. 10-11; pl. 4, fig. 3.
 non 1976 *Gargasiceras gargasensis* (d'Orbigny) - Peybernès, pl. 25, fig. 10 (= *Dufrenoyia* sp. juv.).
 ? 1977 *Gargasiceras gargasensis* (d'Orbigny) - Martínez, p. 25, pl. 3, fig. 7, 8, 9; pl. 4, fig. 1, 2, fig. 3 (= Lillo Beviá, 1975, pl. 4, fig. 3), 4, 5, 6, 7, 8, 9.
 ? 1979 *Gargasiceras gargasensis* (d'Orbigny) - Martínez, p. 344, pl. 1, fig. 3a-c (= Martínez, 1977, pl. 4, fig. 7, 8, 9).
 ? 1982 *Gargasiceras gargasensis* (d'Orbigny) - Martínez, p. 155, pl. 26, fig. 5a-c (= Martínez, 1977, pl. 3, fig. 7), text-fig. 25.
 1982 *Gargasiceras gargasense* (d'Orbigny) - Kullmann and Wiedmann, text-fig. 71 (= Wiedmann, 1966, text-fig. 29).
 non 1982 *Gargasiceras aptiense* (Roch) - Renz, p. 28, pl. 2, fig. 6a-b, text-fig. 16d (= Acanthohoplidae indet. juv.).
 ? 1982 *Gargasiceras* cf. *recticostatum* (Roch) - Renz, p. 27, pl. 2, fig. 11a-b, 12a-b, 13a-b, text-fig. 16c.
 ? 1983 *Colombiceras ex gr. crassicostatum* (d'Orbigny) - Mikhailova, fig. 66a-л.
 non 1988 *Gargasiceras* cf. *aptiense* (Roch) - Khalilov, p. 354, pl. 11, fig. 5a-6 (*Colombiceras* sp. juv.).
 1989 *Colombiceras crassicostatum* (d'Orbigny) - Conte, p. 49, fig. 9 on page 50.
 1996 *Colombiceras* (*Colombiceras*) *crassicostatum* (d'Orbigny) - Wright et al., p. 274, fig. 214.3a-b (= d'Orbigny, 1841, pl. 59, fig. 1-2).
 1996 *Gargasiceras* (*Gargasiceras*) *gargasense* (d'Orbigny) - Wright et al., p. 275, fig. 214.2a-b (= d'Orbigny, 1841, pl. 59, fig. 5-6).
 ? 2004 *Colombiceras* aff. *crassicostatum* (d'Orbigny) - Sharikadze et al., p. 388, pl. 56, fig. 2a-c.
 ? 2004 *Gargasiceras attenuatum* (Roch) - Sharikadze et al., p. 376, pl. 71, fig. 3a-c, 4a-b.
 non 2004 *Gargasiceras aptiense* (Roch) - Sharikadze et al., p. 377, pl. 72, fig. 1a-b (= "Gargasiceras" pulcher Riedel).
 ? 2004 *Gargasiceras recticostatum* (Roch) - Sharikadze et al., p. 378, pl. 72, fig. 2a-b.
 ? 2004 *Gargasiceras* aff. *recticostatum* (Roch) - Sharikadze et al., p. 381, pl. 72, fig. 3a-c, 4a-c, 5a-c.
 2005 *Colombiceras crassicostatum* (d'Orbigny) - Dutour, p. 206, pl. 18, fig. 9a-9d, 10a-c.
 2005 *Gargasiceras gargasense* (d'Orbigny) - Dutour, p. 209, pl. 18, fig. 12a-d.
 2006 *Colombiceras crassicostatum* - Delanoy in Gauthier et al., p. 74, pl. 32, fig. 6a-c (= lectotype).
 2006 *Gargasiceras gargasense* (d'Orbigny) - Delanoy in Gauthier et al., p. 74, pl. 32, fig. 7a-c.
 ? 2007 *Colombiceras* ex. gr. *crassicostatum* - Bogdanova and Mikhailova, text-fig. A.
 2007 *Colombiceras crassicostatus* (d'Orbigny) - Moreno-Bedmar, p. 29, pl. 2, fig. 4, text-fig. 34 (= d'Orbigny, 1841, pl. 59, fig. 1-3, 4-4'), text-fig. 35 (= Dutour, pl. 18, fig. 9a, d).
 2007 *Colombiceras crassicostatus* (d'Orbigny) - García et al., pl. 2, fig. 7.
 2008 *Colombiceras crassicostatum* (d'Orbigny) - Salas and Moreno-Bedmar, pl. 7, fig. C (= García et al., 2007, pl. 2, fig. 7); pl. 9, fig. A.
 2009 *Colombiceras crassicostatum* (d'Orbigny) - Moreno-Bedmar et al., pl. 1, fig. A (= Salas and Moreno-Bedmar, 2008, pl. 9, fig. A).
 2008 *Gargasiceras aptiense* (Roch) - Joly and Delamette, Fig. 6D.
 2012 *Colombiceras crassicostatum* - Moreno-Bedmar et al., appendix. fig. 8G (= García et al., 2007, pl. 2, fig. 7).
 ? 2016 *Colombiceras crassicostatum* - Matamales-Andreu and Moreno-Bedmar, p. 112, fig. 8. A1-2.