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The genus *Caucasella* Moiseev, 1934 (Brachiopoda, Rhynchonellacea) in the Middle Jurassic of the French North-Tethyan Realm

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ABSTRACT – The study of numerous brachiopods (more than 700 specimens) collected in the Middle Jurassic of the French Border of the North-Tethyan Province (bordure vivaro-cévenole and Haut-Var) allows us to attribute to the genus *Caucasella* Moiseev the species *voulvensis* Oppel, *pseudoneumayri* De Brun and *trigona* Quenstedt described as *Gnathorhynchia* Buckman by previous authors. Thus, the definition of *Caucasella* is better specified. The palaeontological study of these three species compared with *Gnathorhynchia* *liostraca* Buckman, type-species of *Gnathorhynchia*, makes it possible to establish affinities and differences between *Caucasella* and *Gnathorhynchia* referred to the *Dimerellidae* family of *Rhynchonellacea* by Ager (1965). Lastly, the stratigraphical distributions of *C. voulvensis*, *C. pseudoneumayri* (latest Bajocian - earliest Bathonian) and *C. trigona* (Early Callovian), already given in the French Jurassic Zonation based on brachiopods (Almérés et al., 1991), are confirmed.

RIASSUNTO – [Il genere *Caucasella* Moiseev, 1934 (Brachiopoda, Rhynchonellacea, Dimerellidae) nel Giurassico medio del Dominio Nord-Tetideo francese] – Lo studio di abbondante materiale (più di 700 esemplari) raccolto nel Dogger del margine francese della Provincia Nord-Tetidea, ha permesso di attribuire al genere *Caucasella* Moiseev le specie *voulvensis* Oppel, *pseudoneumayri* De Brun e *trigona* Quenstedt, già descritte come *Gnathorhynchia* Buckman dagli autori precedenti. Viene così meglio specificata la diagnosi di *Caucasella*. Lo studio paleontologico di queste tre specie e la loro comparazione a *Gnathorhynchia* *liostraca* Buckman, specie tipo del genere *Gnathorhynchia*, rende possibile stabilire affinità e differenze tra i due generi, *Caucasella* e *Gnathorhynchia*, attribuiti da Ager (1965) alla famiglia *Dimerellidae* nei *Rhynchonellacea*.

Infine, viene confermata la distribuzione stratigrafica di *C. voulvensis*, *C. pseudoneumayri* e *C. trigona*, già prese in considerazione per la zonazione a brachiopodi del Giurassico della Francia (Almérés et al., 1991). La sottozona a *C. voulvensis*, prima sottozona della Zona a *Formosarhynchia* *dumortieri* (= Zona a *Cymatorhynchia* *reynesi*), viene correlata con la Zona ad ammoniti a *Parkinsoni* (Sottozona a *Bomfordi*) e a *Zigzag*. *Caucasella* *trigona* costituisce un elemento della fauna a brachiopodi caratterizzante la Zona a *Gracilis* del Calloviano inferiore.

RESUME – [Le genre *Caucasella* Moiseev, 1934 (Brachiopoda, Rhynchonellacea, Dimerellidae) dans le Dogger de la bordure vivaro-cévenole et du Haut-Var (bordure française de la Province nord-téthysienne)] – L'étude d'un abondant matériel (plus de 700 coquilles) collecté dans le Dogger de la bordure vivaro-cévenole et dans le Haut-Var (France) permet d'attribuer au genre *Caucasella* Moiseev les espèces *voulvensis*, *pseudoneumayri* et *trigona* rapportées à *Gnathorhynchia* Buckman par les auteurs antérieurs. L'acception du genre *Caucasella* est ainsi précisée. L'étude paléontologique de ces trois espèces comparées à *Gnathorhynchia* *liostraca* (Buckman), espèce-type de *Gnathorhynchia*, permet également de déduire les affinités et différences entre les deux genres. Enfin, l'extension verticale de *C. voulvensis*, *C. pseudoneumayri* et *C. trigona*, déjà prise en compte dans la zonation du Jurassique français par les brachiopodes, est confirmée. La sous-zone à *C. voulvensis*, première sous-zone de la zone à *Formosarhynchia* *dumortieri* (= zone à *Cymatorhynchia* *reynesi*) est corrélée avec les zones d'ammonites à *Parkinsoni* (sous-zone à *Bomfordi*) et à *Zigzag*. *Caucasella* *trigona* est un élément de la faune de brachiopodes caractérisant la zone à *Gracilis* du Callovien inférieur.

INTRODUCTION

The genus *Gnathorhynchia* was erected by Buckman (1917) for species showing a trigonal outline, posteriorly smooth valves (norelliform stage), a long and incurved beak, an oval pedicle-opening and disjunct deltidial plates. The other distinctive characters of *Gnathorhynchia* are septifer-type cruras, a strong medio-dorsal septum and a medio-dorsal sulcation developed in all ontogenetic stages. The type-species is *Rhynchonella* *liostraca* Buckman, 1886 = *Rhynchonella* *bilobata* Buckman, 1882, in Davidson, 1884, Pl. 19, figs. 18 and 19, from the Early Bajocian, Discites Zone of Dorset and Somerset.

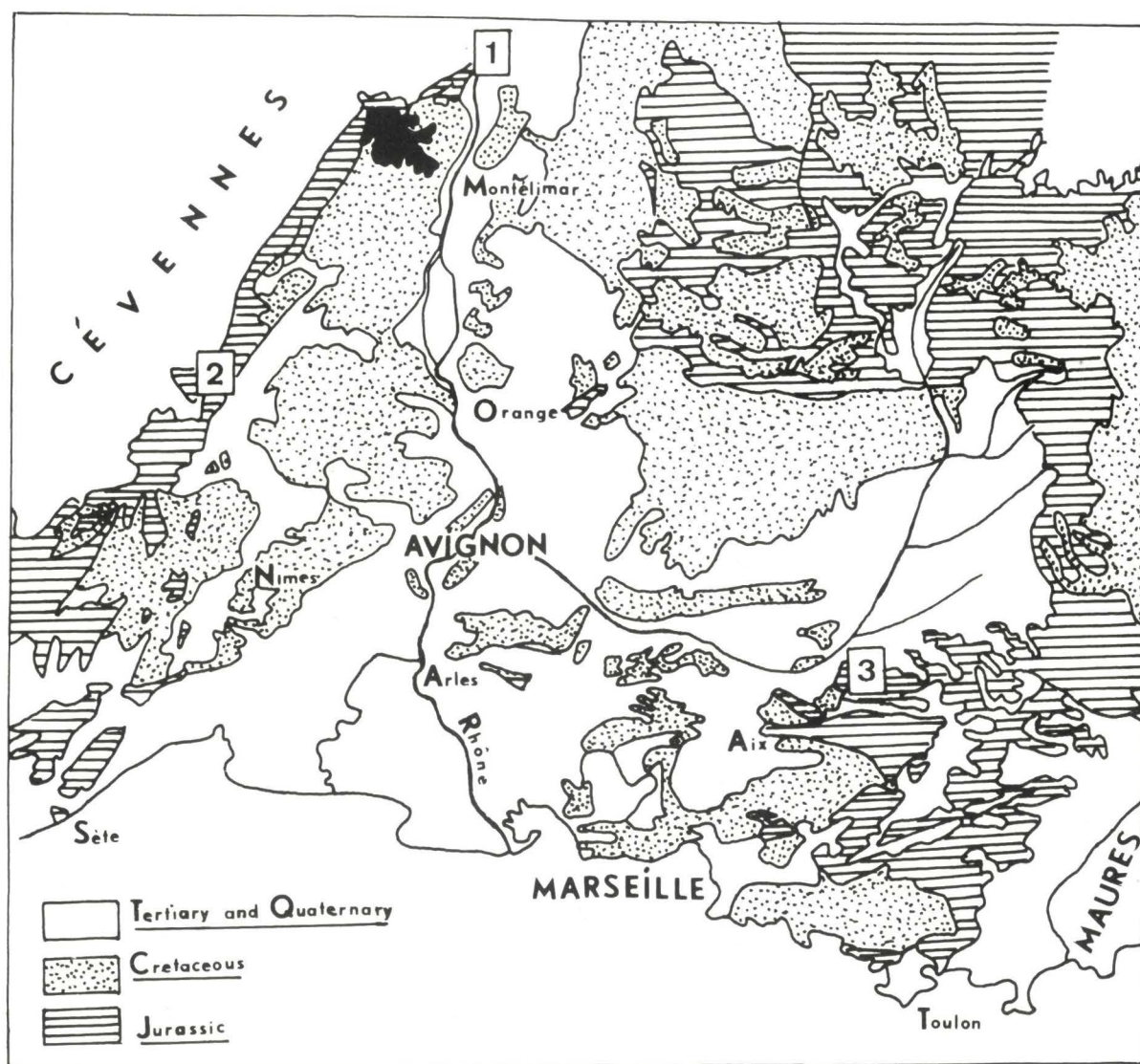
Rhynchonella *liostraca* is a small-sized species, which shows a dorsal sinus, a slightly bilobated anterior margin and the morphology of the genus *Holcorhynchia* Buckman. Buckman (1917, p. 228) considered the narrow specimen of Plate 19, fig. 19 as the lectotype of *liostraca* while the wide specimen (Pl. 19, fig. 18) was attributed to *Gnathorhynchia* *securiformis* (Rothpletz, 1886, Pl. 11, figs. 58-59) defined in the Aalenian of Vilser Alpen (Austria). In our opinion, these are two morphotypes showing a width variability in a single species, *G. liostraca*. The two species *liostraca* and *securiformis* were both created in 1886, so keeping the name *liostraca* allows us to preserve the choice of the type-species of *Gnathorhynchia*.

Whereas *G. liostraca* is a species with entirely smooth valves, only ribbed on the anterior margin, Buckman included, in his original diagnosis of the genus *Gnathorhynchia*, *Rhynchonella voutensis* Opeel, *R. trigona* Quenstedt and *R. trigonella* Rothpletz, which are species ribbed on the major part of the valves and whose medio-dorsal sulcation remains much more faint. The definition of *Gnathorhynchia* became more confused when Rothpletz quoted, in his original description of *R. trigonella*, references to *R. trigona* (Quenstedt, 1871, Pl. 40, figs. 72-73) and when *R. trigonella* was designated, in 1934, as the type-species of the genus *Caucasella* Moisseev, the main distinctive characters of which are septifer-type cruras and the lack of medio-dorsal septum (see Moisseev, 1934 and Kamyschan & Babanova, 1973).

This analysis leads us to clarify the relations between the genera *Gnathorhynchia* and *Caucasella* and also, to precise the generic attribution of the species *voutensis* and *trigona*, to which we add a third closely-related species, «*Rhynchonella*» *pseudoneumayri* De Brun. These problems of systematics have been resolved thanks to abundant brachiopod material from the Vivaro-Cévenole border and from the Haut-Var (713 specimens) (Text-fig. 1).

STRATIGRAPHY

The type-localities which have yielded the species *voutensis* (Pont-des-Etoiles, near Rompon, Ardèche department) and *pseudoneumayri* (Mont-



Text-fig. 1 - Location of the studied outcrops. Vivaro-Cévenole border: 1) Pont des Etoiles (Lauvie gully), near Rompon (Ardèche); 2) Montchaud, near Saint-Brès (Gard). Haut-Var: 3) Mont Major Woods, near Rians (Var).

chaud, near Saint-Brès, Gard department) are situated along the Vivaro-Cévenole border (Text-fig. 1).

The section of Pont des Etoiles (gully of Lauvie) has been described by Elmi (1967, p. 91). The brachiopods *Caucasella voutensis* (Oppel), *Cymatorhynchia* (*Formosarhynchia*) *dumortieri* (Szajnocha), *C. (F.) asymetrica* (Rollier), *C. (F.) haugi* (Rollier), *Antiptychina voutensis* (Rollier) can be abundant, grouped in nests scattered in the mass of a grey limestone including crinoïd ossicles (=«Brèche» à *Isocrinus nicoleti* of Sayn & Roman, 1928, bed 2). This «Brèche à crinoïdes» is an argillaceous limestone interbedded in thin and split banks often separated by shally marls. This facies is interpreted as a slope deposition along the paleorelief controlled by the La Voulte fault (Elmi *et al.*, 1993). There are no ammonites in the Pont-des-Etoiles outcrop, so it is difficult to establish its age. Laterally (ravin des Plaines, near Chamée; Elmi, 1967, p. 100), identical facies have yielded several *Parkinsonia parkinsoni* (Sowerby). Elsewhere (Celles-les-Bains; Elmi, 1967, p. 93), *Procerites subprocerus* Buckman has been collected in marl and limestone alternances with scattered crinoïd fragments (micrite with bioclasts), which represent a more distal environment. Thus, the age of the «Brèche à crinoïdes» varies in a time interval comprised between the latest Bajocian (Parkinsoni Zone) and the earliest Bathonian (Zigzag Zone) (Elmi *et al.*, 1993).

The section of Montchaud is located in the village of Saint-Brès, to the West of the Dieusse hamlet. It was recognized by Dumortier (1871, p. 8), described by Roman & De Brun (1909, p. 54) and recently revised by Elmi *et al.* (1989, p. 60). Above crinoidal limestones (*Isocrinus nicoleti*) referred to Late Bajocian with *Parkinsonia* gr. *parkinsoni*, there succeeds a pale-grey calcareous breccia with quartzitic and orthosic intraclasts. This breccia has yielded a rich fauna of ammonites and brachiopods of Early Bathonian. The matrix is a biomicrite or a pelmicrite crowded with thin-shelled pelecypods (*Bositra*), spicules of Porifera and scarce encrinurites. The facies indicates a deepening of the environment situated at the bottom of a paleorelief where erosion was active. The brachiopods, the shells of which are often worn and dotted with quartzitic intraclasts, are represented by *Caucasella pseudoneumayri* (De Brun) (type-locality), *Cymatorhynchia* (*Formosarhynchia*) *dumortieri* (Szajnocha), *C. (F.) asymetrica* (Rollier), «*Rhynchonella*» (*Ivanoviella*?) *ardescica* (Rollier), *Parvirhynchia balinensis* (Szajnocha), «*Rhynchonella*» *corculum* Dumortier, «*Terebratula*» *subeggensis* De Brun (type-locality), «*T.*» *pseudofylgia* De Brun (type-locality) and «*Zeilleria*» *subran-*

villiana De Brun (type-locality). The other species quoted or briefly described by De Brun (1935) and recently listed by Elmi *et al.* (1989), have not been observed.

The shells of *Caucasella trigona* (Quenstedt) studied in this paper come from the Haut-Var (Southern Provence). During the Late Bajocian and the Early Bathonian, whereas Provence was submitted to a epicceanic basin environment characterized by a significant marly-limestone sedimentation with no brachiopods, the Haut-Var formed a shoal with faint and intermittent sedimentation. This platform environment remained at the top of Early Bathonian, where a deposition of oolitic limestones and encrinuritic limestones, implying dolomitized levels, occurred. These beds were covered by a very irregular and ferruginous hard-ground supporting horizons dated, according to the outcrops, as Callovian or Oxfordian (Arnaud & Monleau, 1979, 1984). In the Woods of Mont Major, near Rians, this irregular hard-ground is overlaid by callovian encrinuritic limestones with brachiopods or by more or less glauconitic argillaceous limestones with ammonites. The Early Callovian brachiopods (Gracilis Zone) are abundant, they are referred to *Caucasella trigona* (Quenstedt), *Sphenorhynchia ferryi* (Deslongchamps), «*Rhynchonella*» *oppeli* (Szajnocha, non Deslongchamps), «*R.*» cf. *tremensis* Gilliéron, «*R.*» cf. *sublacunosa* Szajnocha, *Aromasithyris almerasi* Boullier, *Dictyothyris smithi* (Oppel), *Linguithyris bifrons* (Oppel), *L. vicaria* (Szajnocha), *Antiptychina teisenbergensis* (Winkler) and *Zittelina balinensis* (Szajnocha) (see also Alméras *et al.*, 1991, p. 15).

DESCRIPTION OF SPECIES

Super-family RHYNCHONELLACEA Gray, 1848

Family DIMERELLIDAE Buckman, 1917

Sub-family RHYNCHONELLININAE Ager, 1959

Genus CAUCASELLA Moisseev, 1934

Type-species – *Rhynchonella trigonella* Rothpletz, 1886.

CAUCASELLA VOUTENSIS (Oppel, 1865)

Pl. 1, figs. 1-19; Text-figs. 2-4; tabb. 1-3

1859a *Rhynchonella trigona* Quenstedt - DESLONGCHAMPS, p. 202; pl. 2, fig. 8 (holotype by monotypy).

pars 1859b *Rhynchonella trigona* Quenstedt - DESLONGCHAMPS, p. 45; non pl. 5, figs. 9-10 [= *Caucasella trigonella* (Rothpletz)].

1865 *Rhynchonella voutensis* nov. sp. Oppel, p. 317 (infrapaginal remark) = *Rhynchonella trigona* (pars) - DESLONGCHAMPS, 1859a, pl. 2, fig. 8.

- 1886 *Rhynchonella voutensis* Oppel - ROTHPLETZ, pl. 11, figs. 18, 25.
 pars 1917 *Rhynchonella voutensis* Oppel - COUFFON, p. 99; non pl. 2, figs. 12-13 (= *Caucasella trigona*).
 1917 *Rhynchonella voutensis* Oppel - ROLLIER, p. 116.
 1917 *Gnathorhynchia voutensis* (Oppel) - BUCKMAN, p. 29.
 non 1925 *Rhynchonella voutensis* Oppel - JEKELIUS, p. 50; pl. 1, fig. 1.
 1928 *Rhynchonella voutensis* Oppel - SAYN & ROMAN, p. 56.
 pars 1935 *Rhynchonella voutensis* Oppel - DE BRUN, p. 69; non pl. 3, figs. 29-31 [= *Caucasella pseudoneumayri* (De Brun)].
 1984 *Gnathorhynchia voutensis* (Oppel) - ALMÉRAS & ELMÍ, pl. 3, figs. 10-11.
 1991 *Gnathorhynchia voutensis* (Oppel) - ALMÉRAS *et al.*, p. 14.
 non 1995 *Caucasella voutensis* (Oppel) - VÖRÖS, p. 185; pl. 1, figs. 1-2 [= *Caucasella subtrigona* (Gilliéron)].

Holotype – It was given the erroneous name of *Rhynchonella trigona* Quenstedt by Deslongchamps in his «Note sur le Callovien de La Voulte» (1859, Pl. 2, fig. 8). Effectively, in 1865, Oppel erected *Rhynchonella voutensis* = *Rhynchonella trigona* (pars) in Deslongchamps, 1859a, Pl. 2, fig. 8 and he stated that this species characterizes the «Brèche à crinoïdes» from La Voulte, that is to say the «Brèche à *Isocrinus nicoleti*», which is broadly exposed at the Pont-des-Etoiles (gully of Lauvie), a type-locality situated in the commune of Rompon (Ardèche). So, the specimen figured by Deslongchamps (1859a) is the holotype of *voutensis* by monotypy.

Paratype – Pl. 1, fig. 19.

Studied material – 346 well preserved shells, 265 of which have been measured for biometrical study, and 127 specimens crushed or partially worn and

with incomplete valves. FSL 308198 to 308227 (Caillet, Geandey, Lissajous, Marin, De Riaz, Alméras, Clavel and Elmi collections).

Dimensions – 1. Dimensions of the specimens figured, Pl. 1, figs. 1-19: see Tab. 1.

2. Means and variation intervals of dimensions

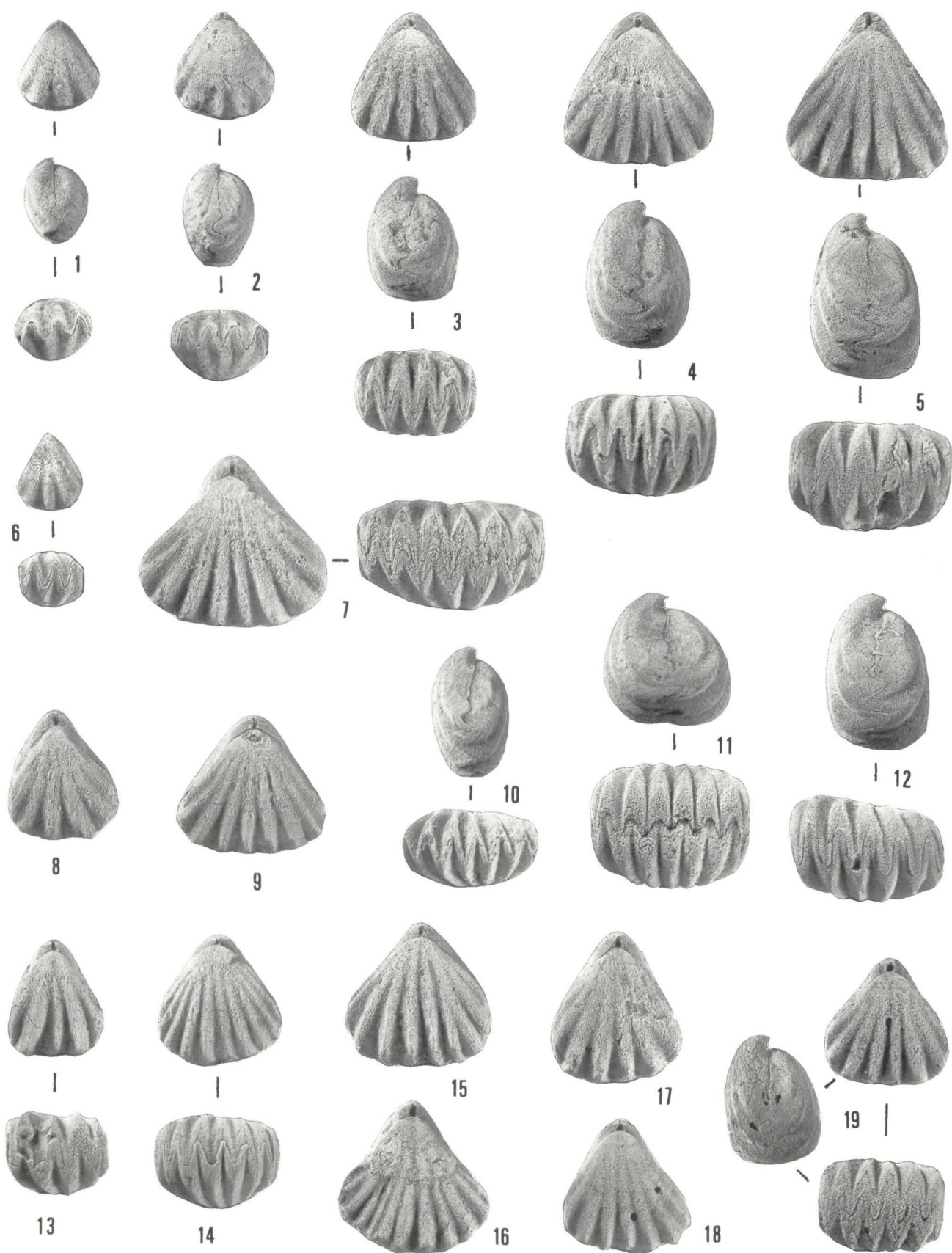
	L	I	E	I/L	lm/L	E/L	Ed/E	C1	C2	Nvd
Pl. 1, fig. 1	7.8	7.1	5.7	0.91	0.79	0.73	0.49	3.6	0.46	5
Pl. 1, fig. 2	9.7	9.0	6.7	0.93	0.74	0.69	0.49	4.5	0.46	6
Pl. 1, fig. 3	11.6	11.0	8.0	0.95	0.79	0.69	0.47	4.1	0.35	7
Pl. 1, fig. 4	14.0	13.5	9.5	0.96	0.81	0.68	0.48	4.8	0.34	9
Pl. 1, fig. 5	15.4	14.6	10.1	0.95	0.82	0.65	0.51	4.8	0.31	9
Pl. 1, fig. 6	7.0	6.0	5.1	0.86	0.78	0.73	0.43	2.2	0.31	5
Pl. 1, fig. 7	15.9	17.4	10.1	1.09	0.75	0.63	0.49	6.0	0.38	10
Pl. 1, fig. 8	12.3	10.1	7.0?	0.82	0.76	0.57?	0.46?	4.2	0.34	6
Pl. 1, fig. 9	12.8	14.0	8.1	1.09	0.76	0.63	0.44	4.9	0.38	9
Pl. 1, fig. 10	12.0	12.1	7.0	1.01	0.77	0.58	0.46	4.0	0.33	8
Pl. 1, fig. 11	13.2	14.3	11.6	1.08	0.86	0.88	0.49	3.8	0.29	9
Pl. 1, fig. 12	14.4	14.4	9.7	1.00	0.81	0.67	0.47	2.5	0.17	8
Pl. 1, fig. 13	10.9	9.5	7.3	0.87	0.73	0.67	0.46	3.3	0.30	5
Pl. 1, fig. 14	12.0	11.4	8.7	0.95	0.75	0.72	0.47	3.2	0.27	10
Pl. 1, fig. 15	13.4	13.3	9.6	0.99	0.77	0.72	0.50	3.6	0.27	9
Pl. 1, fig. 16	14.5	14.0	9.1	0.96	0.77	0.63	0.48	6.0	0.41	10
Pl. 1, fig. 17	13.9	12.0	9.2	0.86	0.79	0.66	0.48	3.9	0.28	6
Pl. 1, fig. 18	12.0	11.7	7.6	0.97	0.76	0.63	0.47	3.5	0.29	8
Pl. 1, fig. 19	11.9	11.4	8.5	0.96	0.75	0.71	0.48	4.2	0.35	7

Tab. 1 - Dimensions and number of costae of specimens in *Caucasella voutensis* (Oppel), figured Pl. 1, figs. 1-19. L, I, E = length, width and thickness of shells; I/L and E/L = relative width and thickness; lm/L = location of the maximal width; Ed/E = thickness of dorsal valve referred to the thickness of the shell; C1, C2 = location of the ribbing appearing (C1: measured from the beak; C2 = referred to the length of the ventral valve; C2 = C1/L); Nvd = number of costae on the dorsal valve (see Alméras, 1996, Fig. 1, A).

EXPLANATION OF PLATE 1

- Figs. 1-19 - *Caucasella voutensis* (Oppel). «Brèche à *Isocrinus nicoleti*». Uppermost Bajocian-lowermost Bathonian. Pont des Etoiles (Lauvie gully), near Rompon (Ardèche). Alméras collections, FSL 308198 to 308216.
 1-5) Five increasingly size shells illustrating the morphogenesis of the species (FSL 308198 to 308202).
 6-7) Size variability: L = 7.0 mm (Fig. 6, FSL 308203) and L = 15.9 mm (Fig. 7, FSL 308204).
 8-9) Width variability: I/L = 0.82 (Fig. 8, FSL 308205) and 1.09 (Fig. 9, FSL 308206). The maximal value of 1.09 exists also in the shell of Fig. 7.
 10-12) Thickness variability: E/L = 0.58 (Fig. 10), 0.88 (Fig. 11) and 0.67 (Fig. 12) (FSL 308207 to 308209). The maximal thickness of the ventral valve is located mid-length on the three specimens. The maximal thickness on the dorsal valve is comprised between the middle of the length (Fig. 10) and the anterior margin (Fig. 12).
 13-16) Ribbing variability: 5 costae (Fig. 13, FSL 308210) and 10 undivided costae (Fig. 14, FSL 308211). Fig. 15 (FSL 308212): Nvd = 9 costae, one intercalary of which appears towards the middle of the dorsal valve. Fig. 16 (FSL 308213): single specimen with 10 costae including 3 intercalary ones.
 17-18) More or less pronounced asymmetrical outline (FSL 308214 and 308215). Borings due to drilling gastropods (Fig. 18).
 19) Paratype, average shell according to its dimensions and its number of costae (FSL 308216).

The studied material is kept in the Collections of University Claude-Bernard, Lyon, with the references FSL 308198 to 308264. All the shells of plates 1 and 2 are represented in natural size.
 (Photographies: N. Podevigne.)



and of number of costae (265 measured shells): see Tab. 2.

Morphology – Shells of 7.0 mm (Pl. 1, fig. 6) to 15.9 mm in length (Pl. 1, fig. 7), with a more or less widened triangular outline. The anterior margin is slightly rounded or sometimes clearly truncated. The width is variable (Pl. 1, figs. 8, 9) and the widest shells, with a narrow cardinal region, have a fan-like appearance (Pl. 1, figs. 7, 9). Because of the trigonal outline of the shells, the maximal width is displaced towards the front, its average position is located at the anterior 8/10 of the length (Tab. 2). 21 specimens out of 265 have a more or less pronounced asymmetrical outline (Pl. 1, figs. 17-18). The average thickness is 0.69, but, as always in brachiopods, this dimension is also variable because of heterochonies of development: so, the specimens, Pl. 1, figs. 10-12, the sizes of which are very close, have very different E/L ratios. The maximal thickness of the ventral valve is situated at the middle of its length in 245 specimens, this position occurs slightly more posteriorly in the other 20 shells. The location of the maximal thickness is far more variable on the dorsal valve : at the middle of the length (129 specimens including the shell of Pl. 1, fig. 10), at the anterior third of the dorsal valve (119 specimens) or at the anterior fourth (24 shells) and also even on the anterior margin (3 specimens including the shell of Pl. 1, fig. 12). This displacement of the maximal thickness towards the anterior margin occurs during the growth of the shells. Effectively, the average length of shells showing their maximal thickness towards the middle of the dorsal valve is 11.3 mm whereas those of specimens reaching their maximal thickness towards the anterior third or fourth of the dorsal valve are respectively 12.8 and 13.2 mm. The anterior commissure is rectimarginate. There are neither fold nor sinus on the valves. We can observe only a shallow longitudinal hollow marked on the

dorsal umbo. The lateral commissures are always in a straight line.

Both valves bear between 5 and 11 strong and rounded costae, which become more and more pronounced towards the anterior margin where they show an appearance of *tetrahedra* to *quadrata*-type (*sensu* Ager, 1956, Text-fig. 4). The beak and the dorsal umbo are smooth, the ribbing appears only towards the posterior third of the valves (Tab. 2). These costae are undivided in 263 specimens. Two shells only (Pl. 1, figs 15, 16) show one and three intercalary costae differentiated towards the middle of their two valves.

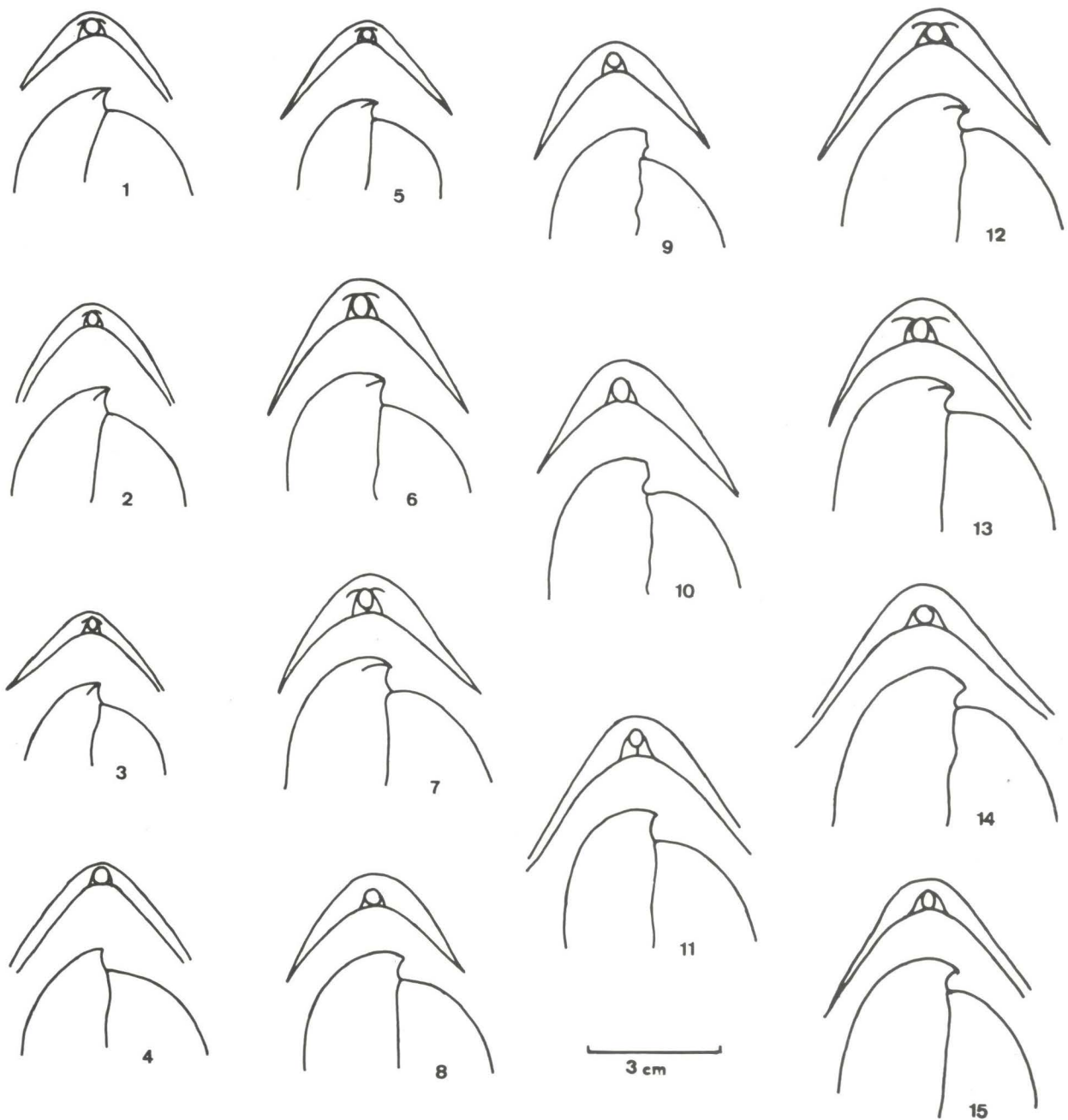
Quite strong and a little sharp beak. Short, rounded lateral beak-ridges can be observed mainly in young shells (79 specimens ; 31.5%). The beaks without lateral beak-ridges are predominant, especially in adult shells (172 specimens; 68.5 %). The sides of the shells are occupied by concave planes (planareas) developed from the beak to the anterior margin. The incurvation of the beak, the outline of the pedicle-opening and the appearance of the deltidium are very variable (Text-fig. 2). The study of 251 well preserved specimens allows us to quantify this variability (Tab. 3). The beak is rarely suberect (12 specimens; 4.8 %), it is quite often suberect to erect (50 specimens; 19.9%) or more often erect (164 specimens; 65.4 %) and even, sometimes, slightly incurved (25 specimens; 9.9%). The slightly incurved beaks are represented in the thick shells, showing the maximal thickness of their dorsal valve displaced towards the anterior margin. The pedicle-opening is more often oval (217 shells; 86.4 %) and rarely circular (34 shells; 13.6 %). The deltidial plates are disjunct as two small triangular pieces (213 shells; 84.9 %). The deltidial plates, just conjunct (12.3 %) or conjunct in a deltidium (2.8 %), are more rarely represented.

Some shells show small borings due to drilling gastropods (Pl. 1, fig. 18).

	N	L	I	E	I / L	Im / L	E / L	Ed / E
I	265	12,1 (7,0 - 15,9)	11,5 (6,0 - 17,4)	8,3 (4,8 - 11,6)	0,95 (0,76 - 1,09)	0,77 (0,68 - 0,86)	0,69 (0,55 - 0,88)	0,48 (0,42 - 0,58)
II	100	13,6 (5,8 - 17,3)	14,0 (5,8 - 18,9)	8,6 (3,2 - 11,0)	1,03 (0,82 - 1,22)	0,72 (0,64 - 0,80)	0,63 (0,44 - 0,77)	0,49 (0,41 - 0,57)
III	23	11,5 (9,3 - 13,3)	13,7 (11,0 - 16,4)	7,0 (5,9 - 8,7)	1,20 (1,05 - 1,42)	0,79 (0,75 - 0,83)	0,61 (0,53 - 0,76)	0,49 (0,43 - 0,55)

	Ribbing appearing (VV)		Nvd
I	4,3 (2,2 - 6,3)	0,37 (0,21 - 0,54)	7,4 (5 - 11)
II	3,2 (1,5 - 5,9)	0,23 (0,10 - 0,39)	8,6 (6 - 13)
III	4,7 (3,4 - 6,0)	0,41 (0,36 - 0,48)	11,6 (9 - 15)

Tab. 2 - Means and variation intervals of dimensions and of number of costae in different species referred to the genus *Caucasella* Moissev. I = *C. voutensis* (Oppel); II = *C. pseudoneumayri* (De Brun); III = *C. trigona* (Quenstedt). N = number of measured specimens. Symbols as in Tab. 1.



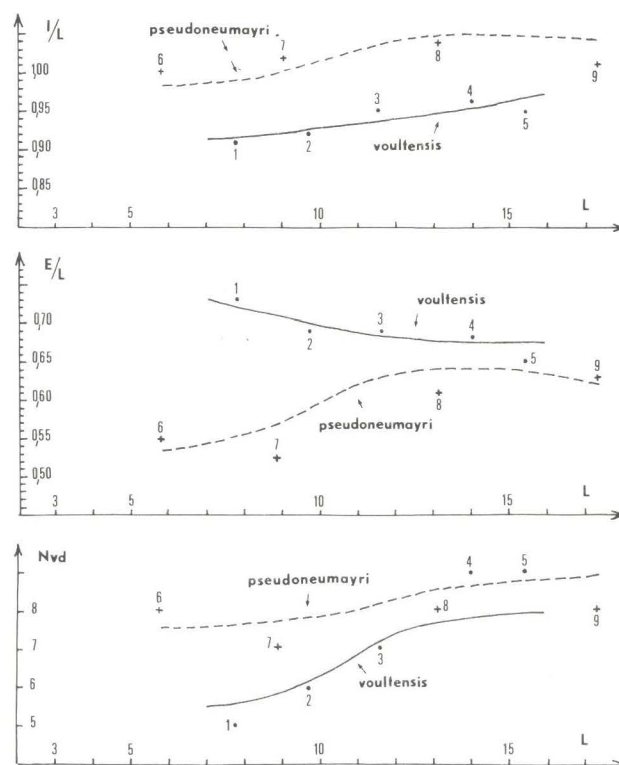
Text-fig. 2 - Variability of the beak incurvation, of the pedicle-opening outline and of the deltidium aspect ($\times 4$) in *Caucasella voutensis* (Oppel). «Brèche à *Isocrinus nicoleti*», uppermost Bajocian-lowermost Bathonian. Pont des Etoiles, near Rompon (Ardèche).
 1, 2, 3) Suberect beak, with slightly developed beak-ridges (Length L of the specimens: 10.7 mm, 10.5 mm and 9.6 mm). Circular pedicle-opening and disjunct deltidial plates (1). Oval pedicle-opening (2, 3). Disjunct (2) and just conjunct (3) deltidial plates.
 4) Suberect beak, without lateral beak-ridges. Circular pedicle-opening and disjunct deltidial plates (L = 10.9 mm).
 5, 6, 7) Erect beak, with slightly developed beak-ridges (L = 8.6 mm, 11.9 mm and 13.2 mm). Circular pedicle-opening and disjunct deltidial plates (5). Oval pedicle-opening (6, 7). Disjunct (6) and conjunct (7) deltidial plates.
 8, 9, 10, 11) Erect beak, without lateral beak-ridges (L = 11.2 mm, 11.0 mm, 12.0 mm and 12.2 mm). Circular pedicle-opening (8, 9). Disjunct (8) and just conjunct (9) deltidial plates. Oval pedicle-opening (10, 11). Disjunct (10) and conjunct (11) deltidial plates.
 12, 13) Slightly incurved beak with lateral beak-ridges (L = 14.2 mm and 13.2 mm). Circular pedicle-opening and disjunct deltidial plates (12). Oval pedicle-opening and disjunct deltidial plates (13).
 14, 15) Slightly incurved beak without lateral beak-ridges (L = 13.0 mm and 12.0 mm). Circular pedicle-opening and disjunct deltidial plates (14). Oval pedicle-opening and disjunct deltidial plates (15).

		pedicle opening	deltidial plates
suberect beak (12)	and with slightly developed beak-ridges (10)	circular (2)	disjunct (2)
		oval (8)	disjunct (3) just conjunct (5)
	and without lateral beak-ridges (2)	circular (2)	disjunct (2)
		oval (0)	
suberect to erect beak (50)	and with slightly developed beak-ridges (31)	circular (9)	disjunct (3) just conjunct (5) conjunct (1) disjunct (9)
			just conjunct (9)
			conjunct (4)
			disjunct (3)
	and without lateral beak-ridges (19)	circular (5)	just conjunct (2)
			disjunct (11)
			just conjunct (3)
erect beak (164)	and with slightly developed beak-ridges (29)	circular (2)	disjunct (2)
		oval (27)	disjunct (26) just conjunct (1)
	and without lateral beak-ridges (135)	circular (10)	disjunct (8) just conjunct (2)
			disjunct (119)
			just conjunct (4)
			conjunct (2)
slightly incurved beak (25)	and with slightly developed beak-ridges (9)	circular (1)	disjunct (1)
		oval (8)	disjunct (8)
	and without lateral beak-ridges (16)	circular (3)	disjunct (3)
		oval (13)	disjunct (13)

Tab. 3 - Statistics of the characteristics of beak, pedicle-opening and deltoidal plates in *Caucasella voultensis* (Oppel).

Ontogeny - The specimens, Pl. 1, figs. 1-5, illustrate the morphogenesis of the species. They are plotted on the curves (Text-fig. 3) which represent the average growth of the width and thickness of shells and also the increase in the number of costae on the dorsal valve. The increase in the number of costae is significant on 10 to 13 mm size shells whereas the growth of the width is much more progressive. Because of the great relative thickness of 7 to 10 mm size shells (Pl. 1, figs. 1, 2), the growth of the thickness decreases slightly. The specimen, Pl. 1, fig. 19, represents the average shape of the species by its dimensions and by the number of costae ; it has been chosen as paratype.

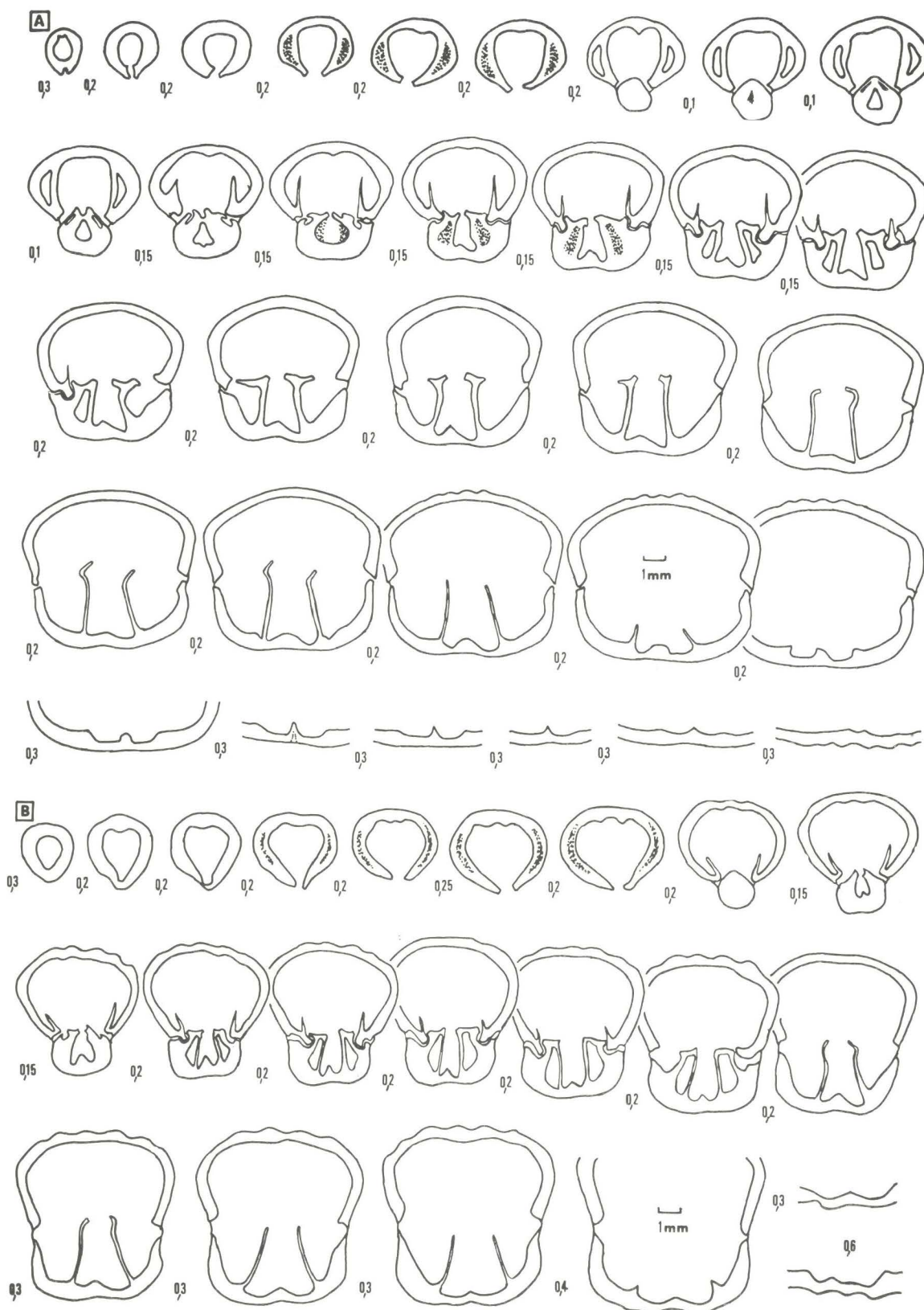
Internal characters (Text-fig. 4) - The ventral lateral cavities are only slightly developed and often obliterated by secondary calcifications. The thick dental plates rapidly split away from the walls of the ventral valve. One specimen (Text-fig. 4, A) shows an umbonal cavity. The hinge-plates are ventrally concave or subhorizontal. The septalium is lacking. The rectangular hinge-teeth fit into deep dental sockets ; the plane of articulation is well marked, but the presence of denticula and accessory sockets remains discrete. The inner socket-ridges of the dental sockets are not very differentiated. The dorsal sides of the hinge-plates are extended by septiform



Text-fig. 3 - Average trajectories of the width-growth (I/L), of the thickness-growth (E/L) and in the increase in the number of costae on the dorsal valve (Nvd) compared in *Caucasella voultensis* (Oppel) and in *Caucasella pseudoneumayri* (De Brun). 1 to 5) specimens *C. voultensis* figured on Pl. 1, figs. 1-5. 6 to 9) specimens *C. pseudoneumayri* figured on Pl. 2, figs. 1-4.

cruras which reach the floor of the dorsal valve. These cruras of septifer-type were described and figured for the first time in 1886 by Rothpletz with regard to *voultensis* (Pl. 11, fig. 18) and *Rhynchonella trigona*, later on considered (Moisseev, 1934) as the type-species of the genus *Caucasella* (Rothpletz, 1886, Pl. 8, fig. 50). The medio-dorsal septum is hardly outlined at all the level of the hinge ; soon, towards the anterior margin, it becomes a low, wide ridge separating two hollows in which the adductor muscles were inserted.

Affinities - *Caucasella voultensis* has been figured for the first time as *Rhynchonella trigona* (Deslongchamps, 1859a, Pl. 2, fig. 8). Deslongchamps (1859b) emphasized this confusion between the two species in his memoir on the Kelloway-Rock where, still under the name of *Rhynchonella trigona*, he gave the diagnosis of *C. voultensis* which he dated as Callovian from La Voulte. According to this author, *C. trigona*, very scarce in the callovian ferruginous



Text-fig. 4 - Internal characters of two shells referred to *Caucasella voutensis* (Oppel). Uppermost Bajocian-lowermost Bathonian. Pont des Etoiles, near Rompon (Ardèche). A = specimen FSL 308217 (L = 13.7 mm; l = 14.4 mm; E = 8.7 mm; Nvd = 10). B = specimen FSL 308218 (L = 12.3 mm; l = 11.8 mm; E = 9.8 mm; Nvd = 7).

bed from Montreuil-Bellay, also exists at La Voulte but with some morphological differences (larger and more inflated shells bearing coarser and less numerous costae). These differences were attributed by Deslongchamps to the specific variability. Couffon (1917) then made the same mistake as Deslongchamps; he described *C. vouldensis* (repeating Deslongchamps' diagnosis), but he figured (Pl. 2, figs. 12-13) *C. trigona* from the Callovian of Chalet, near Montreuil-Bellay. Rollier (1917) and Jekelius (1925) cleared up this taxonomic confusion, explaining that *vouldensis* was described from the «Brèche à crinoïdes» (Bathonian) of La Voulte whereas *trigona*, a closely-related but different species because of its finer and more numerous costae, is originated from the Callovian of Grossau, in the Enns valley (High-Austria). We must add that the morphology of the specimen collected in the callovian grey marly limestone of Pojana Tapului (Brassó) and figured by Jekelius (1925, Pl. 1, fig. 1), agrees neither with *vouldensis*, nor with *trigona*; the closest species to which it can be attributed will be *C. subtrigona*, which is nevertheless older (Klauss Schichten in the Monsalvens, Fribourg Alps). Lastly, De Brun (1935) summed up the differences between the two species: *vouldensis* «is thicker, more trigonal than *Rh. trigona* Quenstedt, it bears coarser and less numerous costae».

The two specimens from the Mecsek Mts. (Hungary) figured by Vörös (1995, Pl. 1, figs. 1-2) are very different from *C. vouldensis* in lateral views. The maximal convexity of their valves is reached

towards the posterior third of their length, or at most towards the middle of the length whereas *C. vouldensis* is characterized by the displacement of this maximal thickness towards the anterior margin. In our opinion, these two specimens the age of which is younger than that of *vouldensis* (Bathonian and even Late Bathonian for fig. 2) might be referred to *C. subtrigona* (Gilliéron) from the Klauss Schichten in the Monsalvens.

Distribution – Bordure ardéchoise. Pont des Etoiles, near Rompon: uppermost Bajocian-lowermost Bathonian (type-locality).

Western Algeria. Traras Mountains (Djebel Gorine) : Upper Bajocian (Almérás & Elmi, 1984).

CAUCASELLA PSEUDONEUMAYRI (De Brun, 1935)

Pl. 2, figs. 1-12; Text-figs. 3, 5-6; tabb. 2, 4-5

- 1935 *Rhynchonella pseudoneumayri* nov. sp. DE BRUN, p. 66; pl. 3, figs. 11-13 (holotype by monotypy).
 pars 1935 *Rhynchonella vouldensis* Oppel - DE BRUN, p. 69; pl. 3, figs. 29-31.
 1989 *Gnathorhynchia pseudoneumayri* (De Brun) - ELMI *et al.*, p. 60.
 1991 *Gnathorhynchia pseudoneumayri* (De Brun) - ALMÉRAS *et al.*, p. 14.

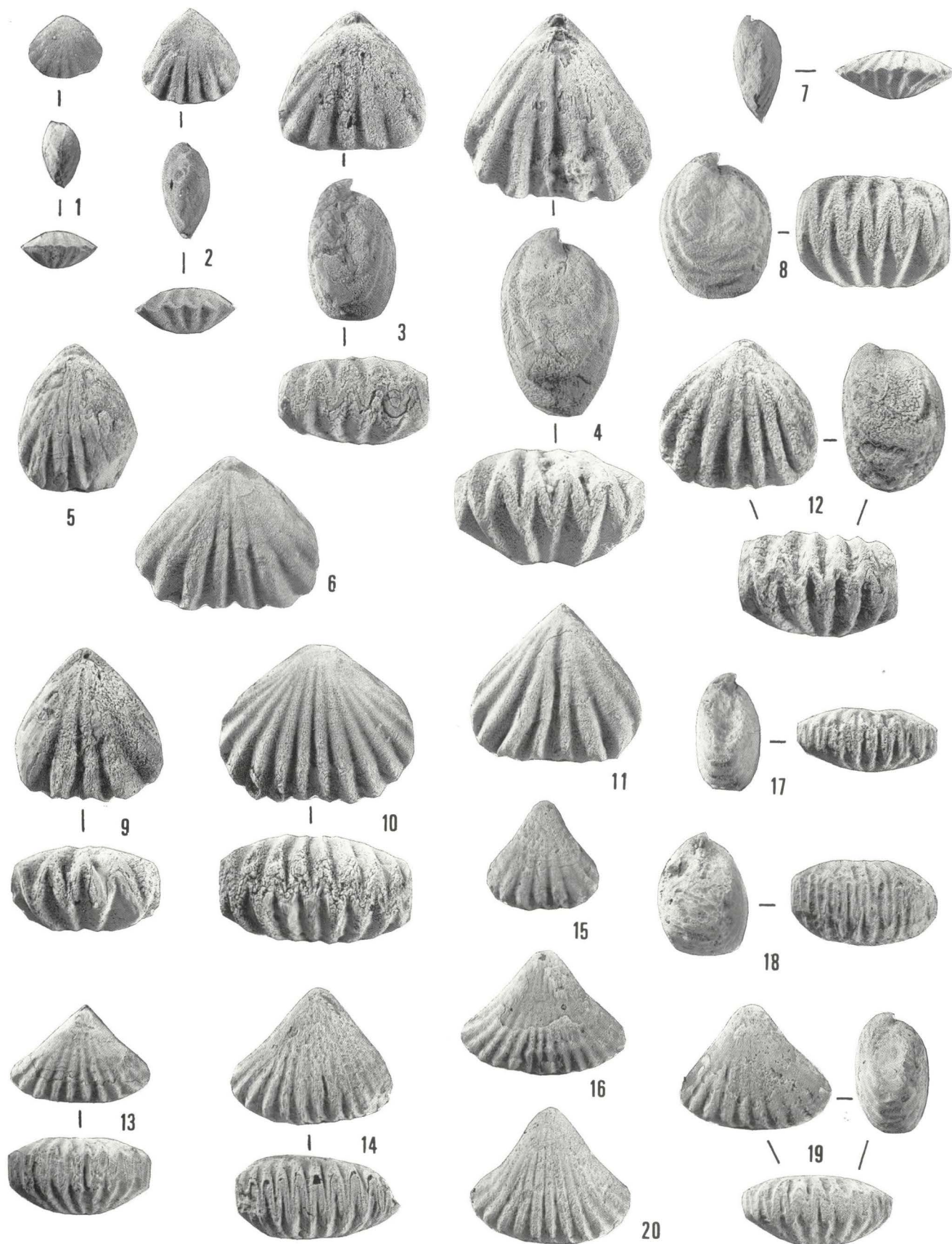
Holotype – De Brun, 1935, Pl. 3, figs. 11-13.

Paratype – Pl. 2, fig. 12.

Studied material – 100 shells measured for biometrical study and 116 incompletely preserved

EXPLANATION OF PLATE 2

- Figs. 1-12 - *Caucasella pseudoneumayri* (De Brun). Early Bathonian. Montchaud, near Saint-Brès (Gard). Almérás and Elmi collections, FSL 308228 to 308239.
 1-4) Four increasingly size shells illustrating the morphogenesis of the species (FSL 308228 to 308231).
 1 and 4. Size variability: $L = 5.8$ and 17.3 mm.
 5-6) Width variability: $l/L = 0.82$ (Fig. 5, FSL 308232) and 1.22 (Fig. 6, FSL 308233).
 7-8) Thickness variability: $E/L = 0.44$ (Fig. 7, FSL 308234) and 0.77 (Fig. 8, FSL 308235). On these two specimens, the maximal thickness on the ventral valve occurs at the posterior 2/5 of length whereas that of the dorsal valve is located mid-length.
 9-11) Ribbing variability: $Nvd = 6$ (Fig. 9, FSL 308236) and 13 (Fig. 10, FSL 308237). Very coarse costae ($Nvd = 8$) on the shell of Fig. 6. Fig. 11: $Nvd = 9$ costae comprising 2 dichotomous costae differentiated towards the middle of the two valves (FSL 308238).
 4 and 11. Asymmetry of outline.
 12) Paratype, average shell according to its dimensions and its number of costae (FSL 308239).
 Figs. 13-20 - *Caucasella trigona* (Quenstedt). Early Callovian, Gracilis Zone. Mont Major Woods, near Rians (Var). Almérás and Moulan collections, FSL 308248 to 308255.
 13-14) Size variability: $L = 9.3$ mm (Fig. 13, FSL 308248) and 12.9 mm (Fig. 14, FSL 308249). The shell, in Fig. 13, possesses the greatest relative width and thickness ($l/L = 1.42$; $E/L = 0.76$). The specimen, in Fig. 14, shows an asymmetrical outline.
 15-16) Variability of width and of number of costae: $l/L = 1.05$ and $Nvd = 9$ (Fig. 15, FSL 308250); $l/L = 1.33$ and $Nvd = 14$ (Fig. 16, FSL 308251).
 17-18) Thickness variability: $E/L = 0.53$ (Fig. 17, FSL 308252) and 0.72 (Fig. 18, FSL 308253).
 19) Paratype, average shell according to its dimensions and its number of costae (FSL 308254).
 20) Specimen showing a maximal lateral pinching in the beak region (FSL 308255).



	L	I	E	I/L	Im/L	E/L	Ed/E	C1	C2	Nvd
Pl. 2, fig. 1	5.8	5.8	3.2	1.00	0.79	0.55	0.47	2.0	0.34	8
Pl. 2, fig. 2	8.9	8.9	4.5	1.00	0.73	0.51	0.50	?	?	7
Pl. 2, fig. 3	13.1	13.7	8.0	1.04	0.72	0.61	0.51	?	?	8
Pl. 2, fig. 4	17.3	17.5	11.0	1.01	0.71	0.63	0.54	2.0	0.11	8
Pl. 2, fig. 5	14.0	11.5	8.7	0.82	0.73	0.62	0.53	3.5	0.25	9
Pl. 2, fig. 6	14.2	17.3	10.4	1.22	0.70	0.73	0.50	3.5	0.25	8
Pl. 2, fig. 7	10.0	10.5	4.4	1.05	0.72	0.44	0.55	2.5	0.25	13
Pl. 2, fig. 8	13.5	13.9	10.4	1.03	0.71	0.77	0.49	3.0	0.22	9
Pl. 2, fig. 9	14.3	13.7	8.1	0.96	0.68	0.57	0.46	2.7	0.19	6
Pl. 2, fig. 10	16.0?	17.9	10.1	1.12?	0.71?	0.63?	0.50	?	?	13
Pl. 2, fig. 11	14.9	15.6	9.2	1.05	0.74	0.62	0.52	2.8	0.19	9
Pl. 2, fig. 12	14.4	15.0	9.4	1.04	0.70	0.65	0.48	3.5	0.24	9

Tab. 4 - Dimensions and number of costae of specimens in *Caucasella pseudoneumayri* (De Brun), figured Pl. 2, figs. 1-12. Symbols as in Tab. 1.

specimens. FSL308228 to 308247, 308256 and 308257 (Elmi, Cassel and Alméras collections).

Dimensions - 1. Dimensions of the specimens figured Pl. 2, figs. 1-12: see Tab. 4.

2. Means and variation intervals of dimensions and of number of costae (100 measured shells): see Tab. 2.

Morphology - *Caucasella pseudoneumayri* is a trigonal species close to *C. voutensis*. 15 specimens out of 100 show a more or less asymmetrical outline (Pl. 2, figs. 14, 11). *C. pseudoneumayri* includes shells a little larger (average values) than that of *C. voutensis*, their length ranges from 5.8 to 17.3 mm (Tab. 2 and Pl. 2, figs. 1 and 4). It differs from *C. voutensis* by its wider and thinner shells (mean of I/L = 1.03 compared with 0.95; E/L = 0.63 compared with 0.69) and also by the more posterior position of maximal convexity on the dorsal valve. The maximal thickness on the ventral valve occurs towards the middle of the length in 24 shells and a little more posteriorly in the other 76. The maximal thickness of the dorsal valve also occurs mid-length in 78 shells and a little more posteriorly in the other 22. Unlike *C. voutensis*, we cannot observe the displacement towards the anterior margin of the maximal thickness in *C. pseudoneumayri*, the shells of which look thinner at their straight anterior margin. Moreover, the two valves are slightly depressed in their anterior part where a wide and very shallow medio-dorsal depression succeeds to the narrow hollow outlined on the dorsal umbo. We recall here that the valves of *C. voutensis* are slightly and regularly convex on all sides on their anterior part.

The valves bear between 6 and 13 costae (Pl. 2, figs. 9, 10). The ribbing is slightly denser and sharper than in *C. voutensis* (mean of Nvd = 8.6 compared

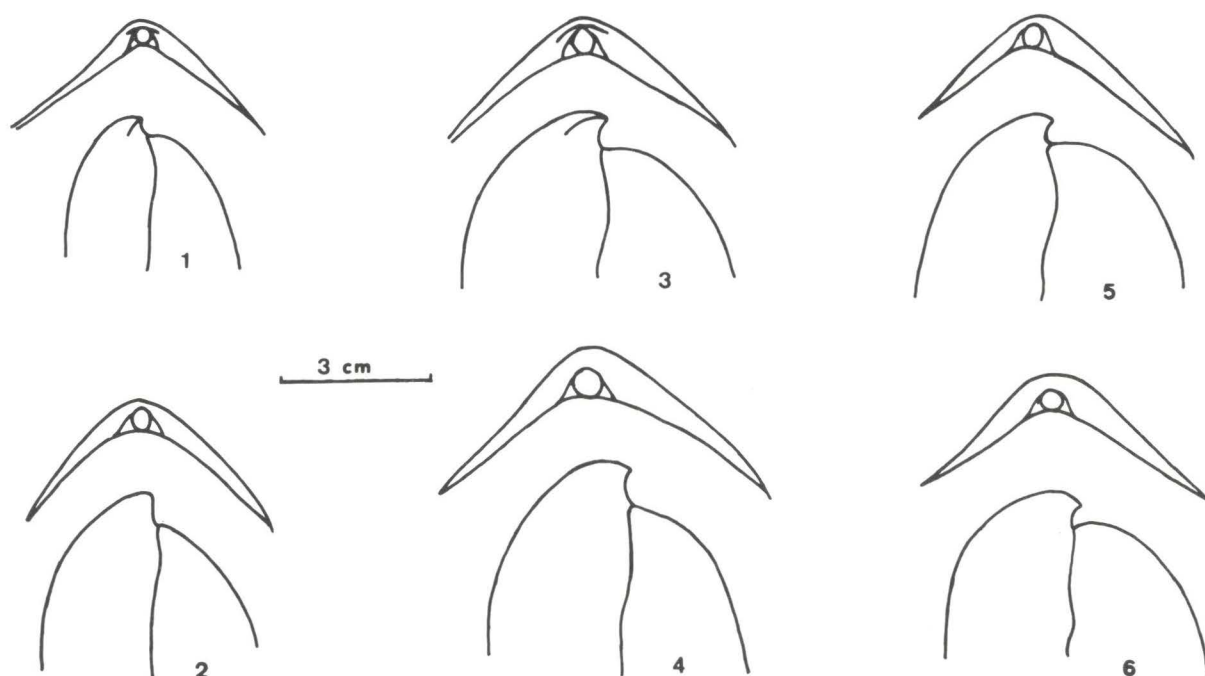
with 7.4 in *C. voutensis*). It occurs towards the posterior 2/10 of valves, that is to say sooner in ontogenetic stages than in *C. voutensis*. The costae become coarser when they are less numerous (Pl. 2, figs. 4, 6, 9). Another difference with *voutensis* concerns the more frequent development of intercalary costae; it can be observed in 20 specimens out of 100 (20 %) compared with two shells out of 265 (0.7 %) in *voutensis*. 17 specimens show an intercalary costa on their two valves whereas the other three (including the shell of Pl. 2, fig. 11) possess two intercalary costae. The appearing of intercalary costae occurs most often towards the middle of the valves (16 specimens), but also towards the anterior third or the posterior third of their length (4 shells).

The incurvation of the beak presents the same variability as in *C. voutensis* (Text-fig. 5 and Tab. 5). Beaks without lateral beak-ridges are predominant (53 shells out of 61). The percentages of circular pedicle-openings (49 specimens; 80.3 %) and oval pedicle-openings (12 specimens; 19.7 %) are inverted by comparison with *voutensis*. Lastly, deltidial plates are always disjunct (61 shells) whereas their aspect is much more variable in *C. voutensis*.

Ontogeny - The curves representing the average growth in width of shells and the increase in the number of costae show trajectories comparable to that of *C. voutensis*, but the I/L and Nvd values are greater all along the ontogeny (Text-fig. 3). Nevertheless, the increase in the number of costae seems more progressive in *C. pseudoneumayri*. The main difference between *voutensis* and *pseudoneumayri* concerns the thickness-growth of shells. The thickness-growth decreases in *voutensis* whereas *pseudoneumayri* shows a positive growth which is well marked up to 13 mm. Above this size, the thickness-growth stabilizes and even decreases slightly towards 15-16 mm. This difference is due to

		pedicle-opening	deltidial plates
suberect beak (5)	and with slightly developed beak-ridges (1)	circular (1)	disjunct (1)
	and without lateral beak ridges (4)	circular (3)	disjunct (3)
suberect to erect beak (27)	and with slightly developed beak-ridges (5)	oval (1)	disjunct (1)
	and without lateral beak ridges (22)	circular (2)	disjunct (2)
		oval (3)	disjunct (3)
erect beak (27)	and without lateral beak ridges (22)	circular (17)	disjunct (17)
	and with slightly developed beak-ridges (2)	oval (5)	disjunct (5)
		circular (2)	disjunct (2)
slightly incurved beak (2)	and without lateral beak ridges (25)	circular (24)	disjunct (24)
	and without lateral beak ridges (2)	oval (1)	disjunct (1)
		circular (2)	disjunct (2)

Tab. 5 - Statistics of the characteristics of beak, pedicle-opening and deltidial plates in *Caucasella pseudoneumayri* (De Brun).



Text-fig. 5 - Variability of the beak incurvation, of the pedicle-opening outline and of the deltidium aspect (x 4) in *Caucasella pseudoneumayri* (De Brun). Pale-grey calcareous breccia with quartzitic intraclasts. Early Bathonian. Montchaud, near Saint-Brès (Gard).

- 1) Suberect beak, with slightly developed beak-ridges. Circular pedicle-opening and disjunct deltidial plates (L = 11.1 mm).
- 2) Suberect beak, without lateral beak-ridges. Oval pedicle-opening and disjunct deltidial plates (L = 13.0 mm).
- 3) Erect beak, with slightly developed beak-ridges. Oval pedicle-opening and disjunct deltidial plates (L = 14.1 mm).
- 4, 5) Erect beak, without lateral beak-ridges (L = 14.4 mm and 13.7 mm). Circular pedicle-opening and disjunct deltidial plates (4). Oval pedicle-opening and disjunct deltidial plates (5).
- 6) Slightly incurved beak, without lateral beak-ridges. Circular pedicle-opening and disjunct deltidial plates (L = 12.6 mm).

the quite well marked convexity of valves in the young shells of *voultensis* whereas the young specimens of *pseudoneumayri* possess more flattened valves (compare Pl. 1, figs. 1-2 and Pl. 2, figs. 1-2). The shells, Pl. 2, figs. 1-4, illustrate the morphogenesis of the average form of the species. The specimen, Pl. 2, fig. 12, chosen as lectotype, represents an average shell according to its dimensions and its number of costae.

Internal characters (Text-fig. 6) - They agree with those of *C. voultensis* (Text-fig. 4). Some minor differences may be noticed: lack of umbonal cavity, subhorizontal hinge-plates, more developed denticula which reinforce the plane of articulation. A just outlined medio-dorsal septum remains anteriorly, after the disappearance of the septifer cruras.

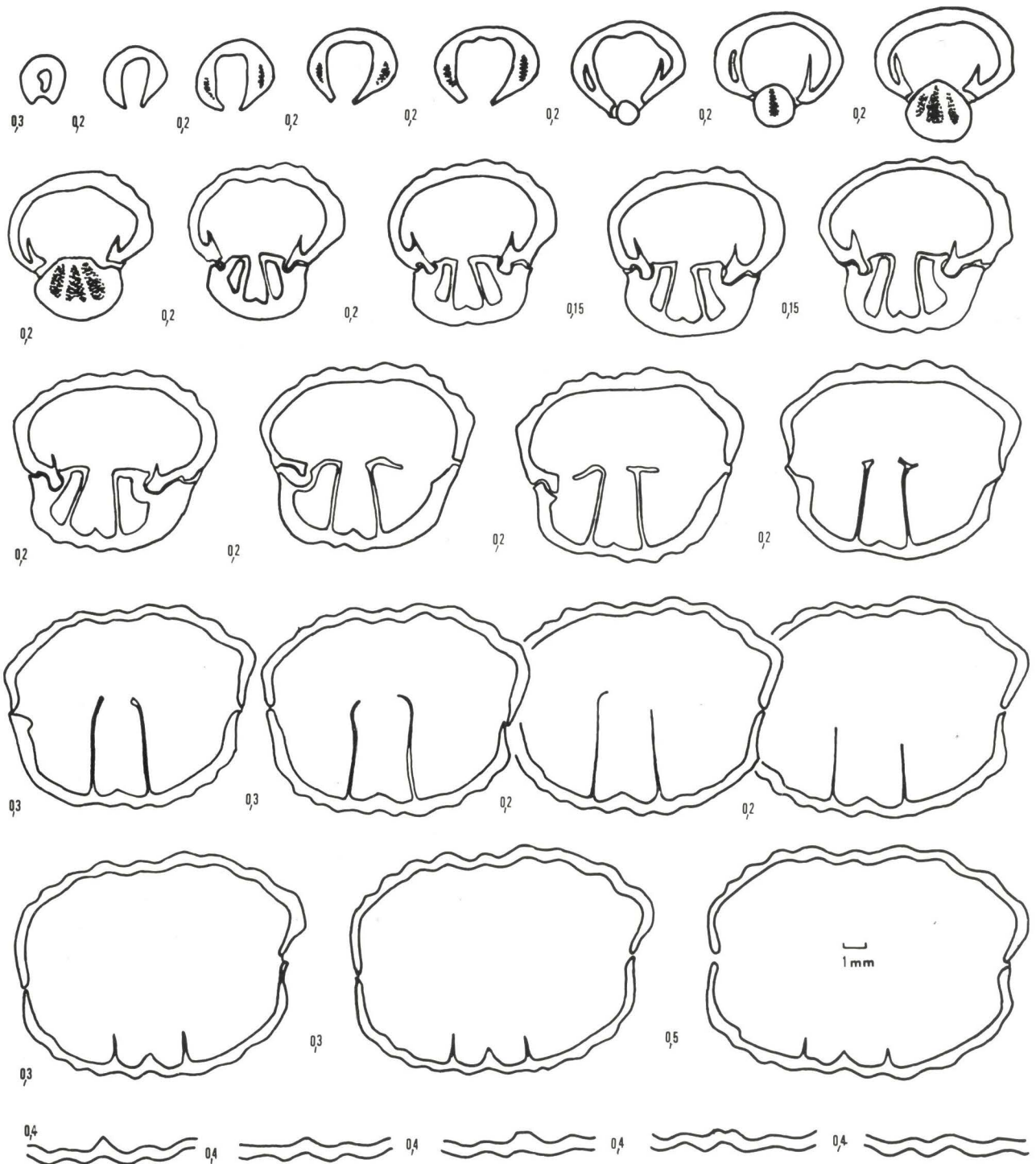
Affinities - *C. pseudoneumayri* and *C. voultensis* are two allied species. The morphology of *pseudoneumayri* has been described in comparison with that of *voultensis*.

The name *pseudoneumayri* is due, according to De Brun, to the likeness with flattened varieties of *Rhynchonella neumayri* Rollier. In fact, *R. neumayri*, the type of which is the shell from the reworked Bathonian-Callovian beds of Balin figured by Szajnocha (1879, Pl. 5, fig. 19) under the erroneous name of *Rhynchonella oppeli*, is a very different species characterized by thick and uniplicated shells bearing sharp, scarce costae. It is very close, if not identical to *Rhynchonella haugi* Rollier = *Formosarhynchia haugi* from the Early Bathonian of La Clapouze, near Saint-Etienne-de-Boulogne (Ardèche).

Distribution - Vivaro-Cévenole border. Montchaud, near Saint-Brès (Gard): Early Bathonian (type-locality).

CAUCASELLA TRIGONA (Quenstedt, 1852)
Pl. 2, figs. 13-20; Text-figs. 7-8; Tabb. 2, 6

1852 *Terebratula trigona* nov. sp. QUENSTEDT, p. 458; pl. 36, fig. 34.



Text-fig. 6 - Internal characters of a shell referred to *Caucasella pseudoneumayri* (De Brun). Early Bathonian. Montchaud, near Saint-Brès (Gard). Specimen FSL 308256 (L = 14.7 mm; l = 17.3 mm; E = 10.0 mm; Nvd = 10, one intercalary costa of which appears towards the middle of the two valves).

- | | | | |
|-----------|--|------------|---|
| 1856 | <i>Rhynchonella trigona</i> (Quenstedt) - DESLONGCHAMPS, p. 99. | pars 1859b | <i>Rhynchonella trigona</i> (Quenstedt) - DESLONGCHAMPS, p. 45; non pl. 5, figs. 9-10 [= <i>Caucasella trigonella</i> (Rothpletz)]. |
| 1857 | <i>Rhynchonella trigona</i> (Quenstedt) - OPPEL, p. 578. | | |
| non 1859a | <i>Rhynchonella trigona</i> (Quenstedt) - DESLONGCHAMPS, p. 202; pl. 2, fig. 8 (= <i>Caucasella voutensis</i>). | pars 1860 | <i>Rhynchonella trigona</i> (Quenstedt) - OPPEL, p. 37. |
| | | 1864 | <i>Rhynchonella trigona</i> (Quenstedt) - WINKLER, p. 310. |

- pars 1871 *Terebratula trigona* Quenstedt - QUENSTEDT, p. 145; pl. 40, fig. 71 only; non figs. 72-73 [= *Caucasella trigonella* (Rothpletz)].
- 1881 *Rhynchonella trigona* (Quenstedt) - SZAJNOCHA, p. 80.
- 1886 *Rhynchonella trigona* (Quenstedt) - ROTHPLETZ, p. 153; pl. 12, figs. 11-12.
- ? 1887 *Rhynchonella trigona* (Quenstedt) - CHOFFAT, p. 253.
- pars 1891 *Rhynchonella trigona* (Deslongchamps) - DE GROSSOURE, p. 254.
- 1917 *Rhynchonella trigona* (Quenstedt) - ROLLIER, p. 115.
- 1917 *Gnathorhynchia trigona* (Quenstedt) - BUCKMAN, p. 29.
- ? 1964 *Gnathorhynchia trigona* (Quenstedt) - PEVNY, p. 169; pl. 6, fig. 2.
- 1966 *Gnathorhynchia trigona* (Quenstedt) - SIBLIK, p. 155; pl. 3, fig. 1.
- 1969 *Gnathorhynchia trigona* (Quenstedt) - PEVNY, p. 146; pl. 28, fig. 2.
- 1970 *Caucasella trigona* (Quenstedt) - TCHORZEVSKIJ, p. 53, figs. 3-4; Text-fig. 3.
- 1991 *Gnathorhynchia trigona* (Quenstedt) - ALMÉRAS *et al.*, p. 15.
- 1994 *Caucasella trigona* (Quenstedt) - MIŠIK *et al.*, p. 263; pl. 4, fig. 1.

Holotype – Quenstedt, 1852, Pl. 36, fig. 34.

Studied material – Mont Major Woods, near Rians (Var): 23 measured specimens and two incompletely preserved shells. Lingouste, near Rians: one well preserved specimen. Almérás and Moulan collections, FSL 308248 to 308255, 308258 to 308263.

Dimensions – 1. Dimensions of the specimens figured Pl. 2, figs. 13-20: see Tab. 6.

2. Means and variation intervals of dimensions and of number of costae (23 measured shells): see Tab. 2.

Morphology – Trigonal shells, quite often asymmetrical like that of Pl. 2, fig. 14 (6 specimens out of 23), measuring 9.3 to 13.3 mm in length, smaller than in *voulensis* and, especially, than in *pseudoneumayri*. The width is variable (Pl. 2, figs. 15,

16, 13), but the shells are wider ($l/L = 1.20$) than in *pseudoneumayri* (1.03) and *voulensis* (0.95). The widest specimens show a laterally very spread outline in the anterior margin, which gives them a flabelliform aspect (Pl. 2, figs. 13, 16). This flabelliform outline is much more expressed when the width decreases rapidly in the beak region. This lateral pinching of the beak characterizes the species *trigona* (Pl. 2, fig. 20). The thickness is less than in *voulensis* (Tab. 2). The ventral valve is slightly and regularly convex in all sides. On the more flattened shells, the anterior half of the dorsal valve has a very shallow depression; this slightly sinuated aspect can be observed on the anterior views of the shells (Pl. 2, fig. 17). Lateral commissures in a straight line. Rectimarginate anterior commissure.

The costae are of the *quadrata*-type. They are sharp, finer and more numerous than in the two previously described species: mean of $Nvd = 11.6$ compared with 8.6 and 7.4 (Tab. 2). They also appear later, especially in comparison with *pseudoneumayri*, towards the posterior 4/10 of the length (Tab. 2). Their number is comprised between 9 and 15 (Pl. 2, figs. 15-16). The differentiation of intercalary costae is less frequent than in *pseudoneumayri*: 2 specimens out of 23, which is a percentage comparable to that observed in *voulensis*. These two shells possess an intercalary costa on their two valves, they appear at the middle or at the anterior third of the length.

Beaks without lateral beak-ridges are predominant. We have observed only one shell with a beak ornamented with quite long but only slightly marked lateral ridges (Text-fig. 7.2). The pedicle-opening is always oval and the deltidial plates are always disjunct (Text-fig. 7).

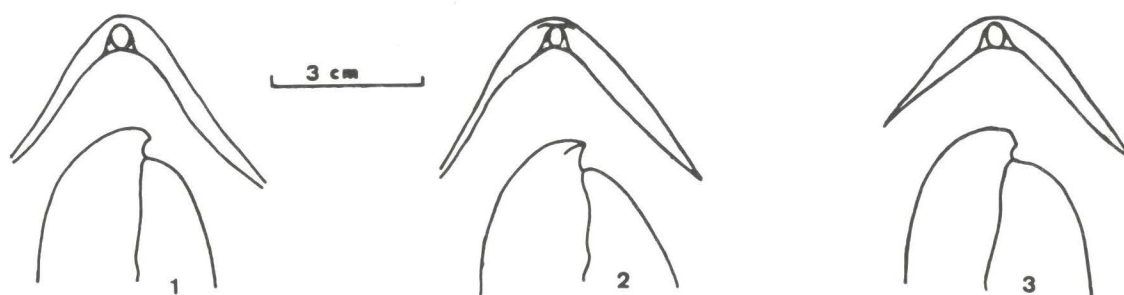
The low number of shells in our collections does not allow us to establish the average curves illustrating the ontogeny of *C. trigona*.

Internal characters (Text-fig. 8) – The internal characters are the same as in *C. voulensis* (Text-fig. 4) and in *C. pseudoneumayri* (Text-fig. 6). Minor differences concern better developed ventral lateral cavities and a square delthyrial cavity delimited by subvertical dental plates. The denticula are more (Text-fig. 8, A) or less differentiated (Text-fig. 8, B). The hinge-plates are dorsally inclined and the medio-dorsal septum is very reduced.

Affinities – Although Mišik *et al.* (1994) admit the synonymy, the presence of *C. trigona* in the Northern Carpathian Mountains (Pevny, 1964, Pl. 6, fig. 2) is not obvious because of the bad figuration of an incompletely preserved specimen bearing few costae

	L	I	E	I/L	Im/L	E/L	Ed/E	C1	C2	Nvd
Pl. 2, fig. 13	9.3	13.2	7.1	1.42	0.83	0.76	0.48	3.4	0.36	11
Pl. 2, fig. 14	12.9	15.2	8.0	1.18	0.80	0.62	0.50	4.7	0.36	12
Pl. 2, fig. 15	10.5	11.0	5.9	1.05	0.79	0.56	0.51	4.7	0.45	9
Pl. 2, fig. 16	11.4	15.2	6.0	1.33	0.77	0.53	0.52	4.5?	0.39?	14
Pl. 2, fig. 17	11.4	13.1	6.0	1.15	0.81	0.53	0.48	5.5	0.48	12
Pl. 2, fig. 18	10.9	13.5	7.9	1.24	0.76	0.72	0.45	?	?	10?
Pl. 2, fig. 19	11.7	14.0	6.8	1.20	0.81	0.58	0.48	4.4	0.38	11
Pl. 2, fig. 20	12.6	14.8	7.5	1.17	0.79	0.59	0.43	5.0	0.40	13

Tab. 6 - Dimensions and number of costae of specimens in *Caucasella trigona* (Quenstedt), figured Pl. 2, figs. 13-20. Symbols as in Tab. 1.



Text-fig. 7 - Variability of the beak incurvation, of the pedicle-opening outline and of the deltidium aspect ($\times 4$) in *Caucasella trigona* (Quenstedt). Early Callovian, Gracilis zone. Mont Major Woods, near Rians (Var).

- 1) Suberect to erect beak, without lateral beak-ridges. Oval pedicle-opening and disjunct deltidial plates ($L = 12.6$ mm).
- 2) Suberect to erect beak, with slightly developed beak-ridges. Oval pedicle-opening and disjunct deltidial plates ($L = 12.4$ mm).
- 3) Erect beak, without lateral beak-ridges. Oval pedicle-opening and disjunct deltidial plates ($L = 11.4$ mm).

and whose age is older (Bathonian). This older age (Bajocian-Bathonian) is also indicated by Pevny (1969) for shells from the Central Váh Valley, Klippen Belt, in the Biele Karpaty Mountains, the morphology of which (Pl. 28, fig. 2) entirely agrees with that of *C. trigona*.

Whereas *C. trigona* seems well defined in its original figuration with a marked pinching on its hinge-region (Quenstedt, 1852, Pl. 36, fig. 34), Quenstedt figured later (1871, Pl. 40, figs. 70-74) a much more variable species. Figs. 70 and 71 agree very well with *C. trigona* while Rothpletz (1886) has referred Quenstedt's figs. 72 and 73 to his new species, *Rhynchonella trigonella*, from the Callovian of Vils. This species later became the type-species of the genus *Caucasella* (Moisseev, 1934). It is not certain that *trigona* and *trigonella* are different species. Effectively, the dimensions of *C. trigonella* given by Rothpletz agree with those of *C. trigona* from the Haut-Var (Tab. 6). Moreover, *C. trigonella* (Rothpletz, 1886, Pl. 12, fig. 13) seems to differ from *C. trigona* (Rothpletz, 1886, Pl. 12, figs. 11-12) only by its more inflated valves. Now, the studied specimens of *C. trigona* show a much more variable thickness (see in this paper, Pl. 2, figs. 17-18).

Distribution – France (Maine-et-Loire, Haut-Var). Baviera, Tyrol, Carpathian Mountains. Early Callovian. Haut-Var : Gracilis Zone. Quoted without figuration (Choffat, 1887) from the Callovian with pyritous fossils of Southern Algarve (Portugal).

EMENDED DIAGNOSIS OF GENUS CAUCASELLA

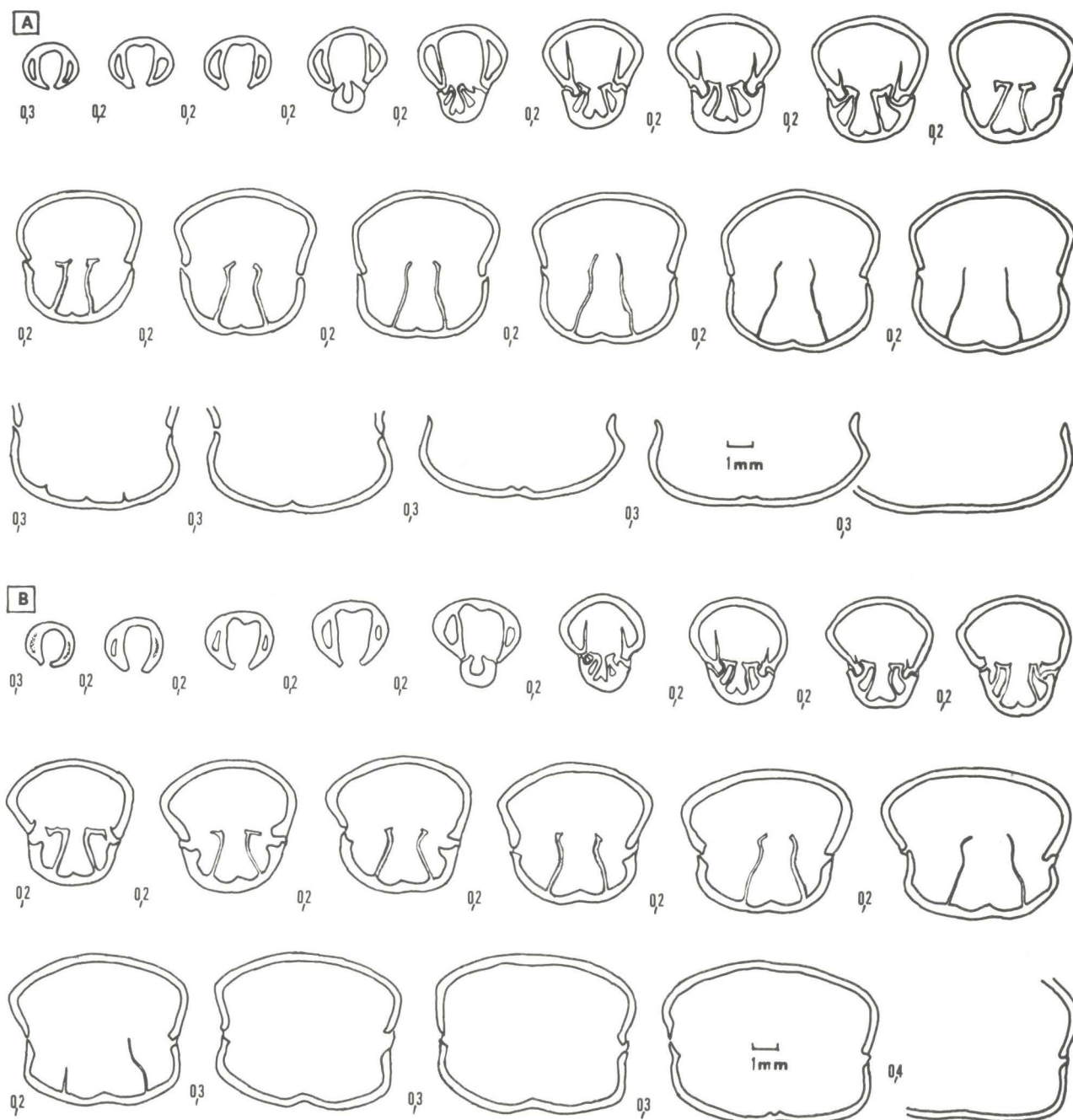
Their morphology and their internal characters allow us to refer to the genus *Caucasella* the species *voultensis*, *pseudoneumayri* and *trigona*. Their paleon-

tological study leads to a better definition of *Caucasella*.

Emended diagnosis – 5 to 18 mm size shells showing a triangular and sometimes asymmetrical outline more or less widened in the anterior margin. Rectilinear lateral commissures. Rectimarginate anterior commissure. A slight, narrow longitudinal hollow on the dorsal valve is sometimes extended with a wide, shallow depression developed to the anterior margin, which gives it a slightly sinuated aspect in frontal view. 5 to 15 undivided costae, more pronounced towards the anterior margin where they show a *tetrahedra* to *quadrata* appearance. More numerous and finer costae in *C. trigona* and in *C. subtrigona*. The intercalary costae are not very frequent. Smooth beak and dorsal umbo, the ribbing only appears between the posterior 2/10 and 4/10 of the valves length according to the species. Beak generally without lateral beak-ridges, suberect to erect, and even sometimes slightly incurved. Planareas are well developed from the beak to the anterior margin. Oval or circular pedicle-opening, according to the species. Disjunct deltidial plates.

Weakly developed lateral cavities in cross-section of the ventral valve. Umbonal cavity and septalium are lacking. The plane of articulation is well defined, but the inner socket-ridges of the dental sockets remain not very differentiated. Cruras of septifer-type. Medio-dorsal septum absent or very reduced.

Remarks – The valves are anteriorly flattened only in *C. pseudoneumayri* and in some specimens referred to *C. trigona*. So, contrary to Ager's diagnosis (1965, p. H 603), this flattening does not constitute a distinctive characteristic of the genus *Caucasella*. In the same way, the ribbing is not always so sharp and dense, as we can notice in *C.*



Text-fig. 8 - Internal characters of two shells referred to *Caucasella trigona* (Quenstedt). Early Callovian, Gracilis Zone. Mont Major Woods, near Rians (Var). A = specimen 308258 (L = 11.0 mm; l = 12.5 mm; E = 6.9 mm; Nvd = 12). B = specimen 308259 (L = 11.8 mm; l = 13.6 mm; E = 6.5 mm; Nvd = 10; asymmetrical outline).

voultensis and, to a lesser degree, in *C. pseudoneumayri*.

List of species -

Rhynchonella trigonella Rothpletz (1886, p. 154 ; Pl. 12, fig. 13 ; Pl. 8, fig. 50)
Rhynchonella voultensis Oppel

Rhynchonella pseudoneumayri De Brun
Rhynchonella subtrigona Gilliéron (1873, p. 244 ; Pl. 10, figs. 9-10)
Rhynchonella rectecostata Uhlig (1881, p. 421 ; Pl. 9, figs. 14, 16, 17)
Rhynchonella trigona (Quenstedt)
Caucasella pontica Moisseev (1934, p. 188 ; Pl. 16, figs. 16-17)

♀ *Rhynchonella nicolisi* Nicolis & Parona (1886, p. 56; Pl. 4, fig. 2).

The internal characters of *subtrigona*, *rectecostata* and *nicolisi* still remain unknown, and the attribution of these species to *Caucasella* is founded on the morphology of their shells only. *C. pontica* from the Late Jurassic of Caucasus has been referred to *Caucasella*, as early as its creation (Moisseev, 1934).

It is not certain that *C. trigonella* represents a species different from *C. trigona*. In this hypothesis, *C. trigonella* will have to be considered as synonymous with *trigona*, which will become the type-species of *Caucasella*.

Affinities – *Gnathorhynchia*, the genus to which two out of the three studied species have been referred (Buckman, 1917), differs from *Caucasella* by the smaller size of its shells which are entirely smooth (the frontal ribbing excepted), by its long and incurved beak, by a wide, well marked sinuate stage developed over all the dorsal valve and by a strong medio-dorsal septum. Ager (1965, p. H603) emphasizes the presence of this strong dorsal septum which constitutes the main characteristic differentiating *Gnathorhynchia* from *Caucasella* according to Moisseev (1934), Kamyschan & Babanova (1973) and Tchorzevskij (1970). We recall here that the internal characters of *G. liostraca*, the type-species of *Gnathorhynchia*, have not been figured as yet, according to our knowledge.

Caucasella show some morphological convergences with the genus *Lokutella* Vörös, 1983 from the Early and Middle Lias of the Mediterranean Province (Sicilia, Apennines, Southern Alps, Hungary) and whose type-species is *Rhynchonella palmaeformis* Haas (1912, p. 232; Pl. 19, figs. 2-4). Effectively, *Lokutella* comprises small to medium-size species, with a triangular or «axiniform» outline, with planareas, with no fold or sinus, but with a faint medio-posterior hollow which suggests a young sinuate stage. Nevertheless, the sharper ribbing, beak characters and, above all, the internal characters (see Vörös, 1983, Figs. 1 and 2) allow us to separate the two genera easily.

The genera *Caucasella*, *Gnathorhynchia* and *Holcorhynchia* belong to the Dimerellidae Buckman family and to the Rhynchonellinae Ager subfamily (Ager, 1965, p. H603). Now, this sub-family includes genera whose shells, with well developed septifer-type cruras, either lack a medio-dorsal septum or have one that is only slightly differentiated. On the contrary, this septum is strongly developed in *Gnathorhynchia*, which makes the attribution of this genus to the Rhynchonellinae subfamily doubtful.

Distribution – Middle European Platforms (France, Baviera, Fribourg Alps, Tyrol). Carpathian Mountains, Crimea, Caucasus. Late Bajocian - Callovian and until Late Kimmeridgian if «*Rhynchonella*» *nicolisi* from the Acanthicum Zone of Verona Province can effectively be referred to *Caucasella*.

CONCLUSIONS

The species *voultensis* and *trigona* were formerly referred to the genus *Gnathorhynchia* Buckman, the type-species of which is *Rhynchonella liostraca* (Buckman, 1917). Abundant material collected on the Vivaro-Cévenole border and in the Haut-Var has allowed us to study these two species and also, «*Rhynchonella*» *pseudoneumayri* De Brun. These three species are now referred to the genus *Caucasella* Moisseev whose type-species is «*Rhynchonella*» *trigonella* Rothpletz. The definition of *Caucasella* is thus precised and its diagnosis is emended. *Gnathorhynchia* differs from *Caucasella* by its smaller-sized shells that are entirely smooth (the frontal margin excepted), by its long and incurved beak, by a wide sinuate stage well developed over all the dorsal valve and by the presence of a strong medio-dorsal septum.

The vertical distribution of these three species, taken into account in the Jurassic Zonation according to brachiopods (Almérés *et al.*, 1991), is also confirmed. The *Caucasella voultensis* Subzone is the first Subzone of the *Formosarhynchia dumortieri* brachiopod Zone (= *Cymatorhynchia reynesi* Zone; see Almérés & Elmi, *in press*). It is correlated with the ammonite Parkinsoni Zone (Bombordi Subzone) and with the Zigzag Zone. *Caucasella trigona* belongs to the brachiopod fauna of the ammonite Gracilis Zone (Early Callovian).

The main environments in which have lived the three studied species of *Caucasella* are also evidenced: fault-controlled slopes along which mass flows have reworked brachiopods and crinoids (*C. voultensis*), bottom of paleorelief with pelagic influences and where erosion was active (*C. pseudoneumayri*), shoal (tilted blocks) with faint and intermittent sedimentation (*C. trigona*).

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