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Implications of variation in coiling in some Hauterivian (Lower Cretaceous) heteromorph ammonites from the Vocontian basin, France

Implicazioni della variabilità dell'avvolgimento in alcune ammoniti eteromorfe dell'Hauteriviano (Cretaceo inferiore) del bacino voconziano, Francia

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343: Stratigraphic Correlations Basins of Peritethyan
362: Tethyan and Boreal Cretaceous

ABSTRACT - In many groups of ammonites that await revision, taxonomic divisions are often still based on morphology alone. Among the heteromorph ammonites, for example, the genera *Crioceratites*, *Subaspinoceras*, *Aspinoceras* and *Acrioceras* are separated from each other by their type of coiling, even if they are found together in the same bed and have identical sculpture and suture lines. Recent work on the mid Hauterivian suggested firstly that most species of *Crioceratites* evolved to a subaspinoceratid or an aspinoceratid type of coiling; secondly, that the old idea of sexual dimorphism could profitably be examined further. New material collected bed-by-bed, seems to confirm that in the Hauterivian, the association of *Crioceratites* with *Subaspinoceras/Acrioceras* and the morphological similarities between their early whorls, constitute a phenomenon of dimorphism which persists at least up to the Barremian. The stratigraphic position of each species is clearly stated. New dimorphic pairs are described.

KEY-WORDS: Heteromorph ammonites, morphology, dimorphism, Hauterivian, biostratigraphy.

RIASSUNTO - In numerosi gruppi di ammoniti, che non sono stati oggetto di revisioni recenti, le delimitazioni tassonomiche si basano spesso su criteri morfologici. Tra le ammoniti eteromorfe, per esempio, i morfotipi *Crioceratites*, *Subaspinoceras*, *Aspinoceras* e *Acrioceras* sono distinti soltanto in base al modo di avvolgimento della conchiglia e dunque appartengono, secondo la sistematica in uso, a generi diversi, nonostante l'ornamentazione e le linee di sutura siano simili e, soprattutto, la loro associazione negli stessi strati e nelle stesse località. Sulla base di recenti lavori sull' Hauteriviano medio si è cercato di dimostrare che la maggior parte delle forme spiralate di tipo *Crioceratites* evolvevano nelle Zone a *L. nodosoplicatum* e a *S. sayni* verso una disposizione tripartita di tipo aspinoceratitica o acrioceratitica della conchiglia e che l'idea di un eventuale dimorfismo avesse fondamento e quindi dovesse certamente essere presa in considerazione. Nuovo materiale, stratigraficamente localizzato con la più grande precisione, sembra confermare che nell' Hauteriviano questa trasformazione di struttura della conchiglia, dalla disposizione spiralata alla disposizione tripartita con asta ed uncino, appartenga spesso ad un fenomeno di dimorfismo riconoscibile almeno fino al Barremiano. La posizione stratigrafica delle specie è chiaramente illustrata e nuove coppie dimorfiche sono descritte. Il valore tassonomico dei generi a conchiglia tripartita dell' Hauteriviano *Acrioceras*, *Subaspinoceras* e *Protacrioceras* è ridiscusso. E' proposta la loro collocazione in sinonimia col genere *Crioceratites* che ha la priorità nomenclaturale.

PAROLE-CHIAVE: Ammoniti eteromorfe, morfologia, dimorfismo, Hauteriviano, biostratigrafia.

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1. - INTRODUCTION

The number and the variability of Lower-Cretaceous heteromorph ammonites seems to defy all attemps at classification. Moreover, phenomena of convergence and sometimes of dimorphism must be added, thus making the problem more difficult.

Ammonite palaeontologists of the last century delimited species and genera according to morphological criteria, referring only to an index-species, without considering the stratigraphical position of the taxa.

Present-day authors emphasize biostratigraphical analysis and also consider phyletic links and geographical distribution. Over the last few years, the study of those data has made considerable progress, particularly concerning the jurassic ammonites. Biometric methods allow us to appreciate more precisely the morphological variability of the shells. Biostratigraphical investigations enable us to estimate better the life span of different species and their geographical areas. Zonal schemes are now commonly used, and recently the new terms "Biozones" (THIEULOY, 1977; BUSNARDO, 1984) and "Biohorizons" (BULOT, 1990; THIEULOY *et alii*, 1990; BULOT & THIEULOY in BULOT *et alii*, 1992; BULOT, 1993; BULOT & THIEULOY in HOEDEMAKER & COMPANY, 1993), were introduced in the Upper Valanginian / Hauterivian ammonite scale, to facilitate the interpretation of the successive associations and to clarify better the chronostratigraphical zonation.

Unfortunatly, Hauterivian and Barremian systematic palaeontology has not always made the same progress. The evolution of some families, such as Ancyloceratidae, for example, is still badly known. The distinction between the Hauterivian taxa *Crioceratites* (LÉVEILLÉ, 1837), *Acrioceras* (HYATT, 1900), *Aspinoceras* (ANDERSON, 1938), *Paraspinoceras*, (BREISTROFFER, 1951), *Protacrioceras*, (SARKAR, 1955) and *Subaspinoceras* (THOMEL *et alii*, 1987) is still established according to morphological data and more precisely according to the differences in coiling patterns, although similarities in the early-whorls (ornamentation and suture lines) are clearly visible.

A full discussion on taxonomic divisions must be supported by good biostratigraphical analysis and material precisely collected bed-by-bed. This was not the case with SARKAR (1955), who proposed unsatisfactory subdivisions, many of them poorly defined on the stratigraphical level. His monograph, based on public and private collections, did not consider morphologically intermediate forms and gave the impression that crioceratitid populations had phylogenetic positions distinct from other genera of heteromorphs, often defined as successive grades: crioceratitid coiling evolving gradually through time, according to him, to other types of coiling perhaps by way of the aspinoceratic lineage.

His scheme was as follows:

1. *Crioceras* LÉVEILLÉ, 1837 - type species: *Crioceras duvali* LÉVEILLÉ, 1837 - crioceratitid coiling, major ribs mono-bi- or trituberculate.

2. *Emericiceras* SARKAR, 1955 - type species: *Emericiceras emerici* (LÉVEILLÉ, 1837) - crioceratitid coiling, strongly tuberculate forms, major ribs trituberculate separated by variable intermediaries that themselves may bear tubercles.

3. *Acrioceras s. s.* HYATT, 1900 - type species: *Acrioceras tabarelli* (ASTIER, 1851) - acrioceratid coiling, major ribs trituberculate.

4. *Acrioceras (Paraspinoceras)* BREISTROFFER, 1952 - type species: *A. (Paraspinoceras) pulcherrimum* (D'ORBIGNY, 1840) - acrioceratid coiling, major ribs, if present, non-tuberculate.

5. *Acrioceras (Paraspinoceras)* ANDERSON, 1938 - type species: *Aspinoceras hamlini*, (ANDERSON, 1938) - aspinoceratid coiling, major ribs non tuberculate.

6. *Acrioceras (Protacrioceras)* SARKAR, 1955 - type species: *A. (Protacrioceras) ornatum* (D'ORBIGNY, 1850) - aspinoceratid coiling, major ribs trituberculate.

Today, we know that though *Emericiceras* has a distinct crioceratid coiling, some specimens uncoil in the adult stage and may even form a recurved hook.

The result of this classification, still in common use and modified, but never simplified, by various subsequent authors was a multiplication of genera and species. THOMEL (1964), BRESKOVSKI (1966), DIMITROVA (1967), IMMEL (1978) did not clarify the interpretation of those populations which might have some importance in biostratigraphical scales, in spite of the disappearance of *Crioceratites duvali* as index species (Colloque sur le Crétacé Inférieur - Lyon 1963 - France).

IMMEL (1978) recognised five Mediterranean and three Boreal species groups in *Crioceratites*, but never considered morphological development nor intermediates and never referred to dimorphism, in spite of RAWSON's (1975) views, who three years before discussed ..."*generic distinction on coiling alone...*" (p. 282) and suggested that ..."*forms with aspinoceratid / ancyloceratid coiling may be dimorphs of larger crioceratitid forms...*" (p. 275).

The existence of dimorphism within ammonite populations was suggested in the middle of XIXth century, (DUCROTOY DE BLAINVILLE, D'ORBIGNY, WAAGEN, REYNÈS, QUENSTEDT). MUNIER-CHALMAS (1892) was the first to interpretate it as sexual. This hypothesis, too poorly argued at that time, was abandoned until the second part of the XXth century.

New indisputable facts allowed MAKOVSKI (1962), TINTANT (1963), CALLOMON (1963) and WESTERMANN (1964) to propose the issue of sexual dimorphism again. Those authors distinguished "microconch" and "macroconch" forms in dimorphic pairs. According to them, in almost all cases, the smaller adult microconch has stronger sculptures up to the body chamber aperture;the macroconch has a larger size the ornamentation fades away at the end of the phragmocone and on the body chamber.

Recent studies on the Lower-Cretaceous heteromorphs : *Macroscaphites* / *Costidiscus* (AVRAM, 1984)

- *Colchidites* (AGUIRRE-URRETA & KLINGER, 1986) - *Lytocrioceras* (DELANOY & POUPON, 1992), *Crioceratites / Acrioceras* (KLINGER & KENNEDY, 1992), *Crioceratites / Subaspinoceras* (ROPOLO, 1991; ROPOLO & SALOMON, 1992), and others on the Upper-Cretaceous (LANDMAN & WAAGE, 1993), provide good evidence of dimorphism, just as clearly demonstrated as for the Jurassic period.

The recognition of this phenomenon seems to be very important at the taxonomic level, because if we accept dimorphic pairs, we have to unite the subfamilies Crioceratitinae and Ancyloceratinae and regard *Crioceratites*, *Aspinoceras* and *Acrioceras* as synonyms, the oldest name, *Crioceratites* (LÉVEILLÉ, 1837) having priority.

2. - STRATIGRAPHY

It was essential to clarify the stratigraphical appearance of the different type of coiling and their deviation through time. We have chosen to use the Hauterivian ammonite zonation of the 2nd Workshop of the Lower Cretaceous Cephalopod Team of IGCP project 262, (Mula, SE of Spain, July 1992). (Fig. 1)

To support our research we have drawn up, bed by bed, the vertical distribution of heteromorphic ammonites and dimorphic pairs that we found in the Vocontian-Basin :

- on the North side of the Mont-Ventoux (Ravin du Croc - Ravin du Cave de Diou);
- at Curnier (Radiatus zone to Nodosoplicatum zone);
- at Le Poët-en-Percyp, near Buis-les-Baronnies.

In these sections, we paid special attention to the investigation of the microconch/macroconch morphotypes within each species and we noted that :

- in the Lower Hauterivian there first appears a dimensional dimorphism (*Crioceratites loryi* SARKAR - *Crioceratites matsumotoi* SARKAR: cf. pl. 1 and 2);
- this is followed by a morpho-dimensional dimorphism starting from the early Nodosoplicatum Zone. The Heteromorph microconchs seem to show at first during their ontogeny a peculiar coiling of the spiral with a tendency to a tripartite structure.

Stratigraphically higher, we collected some uncoiled specimens which form a shaft and a recurved hook (*Crioceratites curnieri* ROPOLO, *Crioceratites sornayi* SARKAR, *C. duvali* LÉVEILLÉ, *C.majoricensis* NOLAN, *C.shibaniae* SARKAR, *C.shibaae* SARKAR...; cf. pl. 3, 4, 5, 6). All these taxa are associated in the same beds and sometimes in the same nodules with larger crioceratitid partners (macroconchs).

We could clearly establish for the species *Protacrioceras ornatum* D'ORBIGNY, *Protacrioceras alpinum* SARKAR and *Protacrioceras puzosianum* D'ORBIGNY, an ontogenic development from a crioceratitid type of coiling to a tripartite type of coiling, always at the same stratigraphical levels. (ROPOLO & SALOMON, 1992)

HAUIERIVIAN

	ZONES	SUBZONES	HORIZONS
H7	P.angulicostata auct.	P. catulloi P. angulicostata auct.	
H6	B. balearis		
H5	P. ligatus		
H4	S. sayni		C. cruasense
H3	L. nodosoplicatum		
H2	C. loryi		O (J) jeannoti C. loryi
H1	A. radiatus		

H1 - H4: Lower Hauterivian

H5 - H7: Upper Hauterivian

Fig. 1 - Hauterivian zonation according to the last works of the 2nd Workshop of the Lower-Cretaceous Cephalopod Team of IGCP Project 262 - Mula (Spain), July 1992.
- Scala biostratigrafica dell' Hauteriviano secondo gli ultimi lavori del 2nd Workshop of the Lower-Cretaceous Cephalopod Team of IGCP Project 262 - Mula (Spagna), luglio 1992.

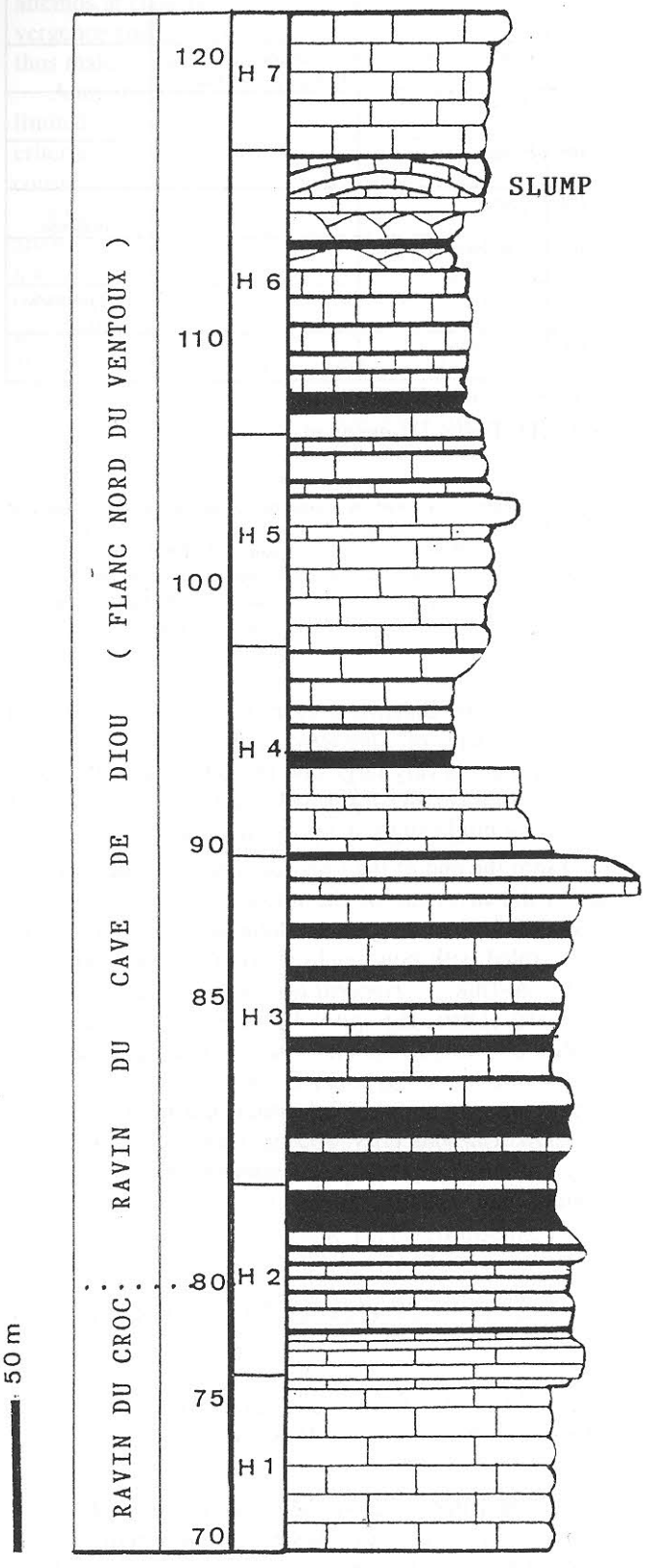
In the early Balearis Zone of Le Poët, we discovered two specimens of *Megacrioceras jourdani* (ASTIER). One of them is very large and the presence in the same horizon of a smaller form with a different juvenile part of coiling might suggest a possible dimorphism.

From the end of the Ligatus Zone, we noted the onset of the inversion of the uncoiling phenomenon. At first the shells are again moderately evolute, planispirally coiled with non touching whorls (*Binelliceras binelli* ASTIER, *Crioceratites pseudoangulicostatum* SARKAR). Then, the spiral tightens up with touching whorls (*Pseudothurmannia angulicostata* D'ORBIGNY - *Pseudothurmannia grandis* BUSNARDO). Aspinoceratid shapes become progressively rarer and the first *Megacrioceras/Garroniceras* appear (*Garroniceras seringuei* ASTIER - *Megacrioceras jourdani* ASTIER - *Megacrioceras doublieri* JAUBERT).

3. - LOCATION OF THE SECTIONS STUDIED

3.1. - RAVIN DU CROC - RAVIN DU CAVE DE DIOU, NORTH OF MONT VENTOUX (Fig. 2)

The Northern side of Mont-Ventoux, in front of Brantes and of the more western Mont-Serein, is very sheer. There is a continuous succession of beds along the forest road of the "col de Comte". Going up from this road in the ravines (Ravin du Croc, Ravin du Cave



Pseudothurmannia simionescui SARK.

Pseudothurmannia angulicostis(d'ORB.)
Acrioceras sp.
Binelliceras binelli (ASTIER)

Balearites balearis (NOLAN)
Balearites sp.

Crioceratites majoricensis(NOLAN)
(Crioceratitid and aspinoceratid forms)
Plesiospitidiscus rebouli(KILIAN)

Crioceratites shibaae SARKAR
(Crioceratitid and tripartite forms)

Plesiospitidiscus ligatus (d'ORB.)

Subsaynella mimica THIEUL. and BUL.

Crioceratites duvali LEVEILLE
(Crioceratitid and tripartite forms)
Subsaynella sayni (PAQUIER)
Crioceratites shibaniae sensu IMMEL
(Crioceratitid and tripartite forms)

Spitidiscus intermedius sensu THIEULOY non d'ORBIGNY

Protacrioceras puzosianum (d'ORB.)
Olcostephanus variegatus PAQUIER
Lyticoceras gr.nodosoplicatum (KILIAN and REBOUL)
Protacrioceras gr. alpinum SARK.
C. curnieri ROPOLO (Crioceratitid and subaspinoceratid forms)

Jeannoticeras jeannoti (d'ORB.)

Crioceratites loryi SARKAR

Olcostephanus sp.

Breistrofferella castellanensis (d'ORBIGNY)

Acanthodiscus radiatus (BRUG.)

Fig. 2 - Stratigrtaphical distribution of the Hauterivian heteromorph ammonites and dimorphic pairs in the North of Mont-Ventoux (S.E. of France).
- Distribuzione stratigrafica delle ammoniti eteromorfe e delle coppie dimorfiche nel versante nord del Mont-Ventoux (S.E. della Francia).

de Diou), it is possible to observe, from 750 m to 1150 m, strata of Hauterivian age.

Over a distance of roughly 50 m, the Radiatus Zone (H1) shows calcareous decimetric beds separated by schistose clays. A major fault cuts off these strata, which form a sort of anticlinal. The collected fauna (*Teschenites* aff. *paraplesius*, *Acanthodiscus radiatus*, *Breistrofferella castellanensis*) is characteristic of the basal Hauterivian.

Decimetric strata grouped together in bundles of 2 to 7m thick constitue the top of the Radiatus Zone and the base of the Loryi Zone. A synsedimentary landslip provides a marker for the new starting point of the section in the "Ravin du Cave de Diou". Limestone beds are separated by dark blue calcareous clays.

Crioceratites loryi, *Olcostephanus* sp., *Jeannoticeras jeannoti* and *Saynella clypeiformis* were collected (beds 80-83), indicating the Loryi Zone (H2).

In the lower Nodosoplicatum Zone (H3), appear crioceratitid and subaspinoceratid forms of *Crioceratites curnieri* with early specimens of *Olcostephanus variegatus* and of *Protacrioceras* gr. *alpinum* - (beds 84-86).

The Nodosoplicatum Zone (120 m) (H3) contains a very rich fauna: *Lyticoceras* gr. *nodosoplicatum/cryptoceras, Protacrioceras puzosianum, Spitidiscus intermedius, Protacrioceras ornatum, Crioceratites quenstedti, Crioceratites* gr. *nolani/sablieri*. As at Curnier, many morphological intermediates within the same species can be found in temporal and geographic associations. These intermediates all present similar sculpture in the early spiral whorls but differ in the type of coiling.

The Sayni Zone (90 m) (H4), shows the typical Hauterivian ribbon development; clays here are very dark. In the directly overlying strata were discovered many very interesting dimorphic pairs and particularly: *Crioceratites shibaniae* (bed 92) and, in the same nodules, *Crioceratites duvali* (presumed macroconch form) with a smaller tripartite shell which we suppose to be the microconch of this species (bed 95) (see e.g. Taxonomy and Systematics).

Over the next 50 metres calcareous blocks form a succession of beds. This is the Ligatus Zone (H5), yielding *Plesiospitidiscus ligatus* and *Crioceratites shibaae* (crioceratitid and aspinoceratid forms) (bed 103).

Over 70 metres, we could collect *Plesiospitidiscus rebouli* and many dimorphic specimens of *Crioceratites majoricensis* (beds 108-110).

In the beds 112-113, the Balearis Zone (H6) is marked by *Balearites balearis* and *Balearites* sp. In three slumped levels (113,114,116) we noted the presence of *Binelliceras binelli* and *Acrioceras* ind.

Acces to the outcrops now becomes difficult. After the last slump we found the Pseudothurmannia Zone (H7) with *Pseudothurmannia angulicostata* (117) and *Pseudothurmannia* gr. *simionescui* (120). Interbeds disappear, and an abrupt cliff does not allow us to collect more fossils, but the lithology and the stratigraphy indicate the top of Hauterivian.

3.2. - CURNIER (Fig. 3)

The geographical location and the biostratigraphy of the Valanginian / Hauterivian section of Curnier were given in previous articles (ROPOLO, 1991; BULOT & FUHR, 1990 in BULOT *et alii*, 1992). New investigations and new precisely located material allows us to complete the palaeontological survey of this section.

The visible strata of the Radiatus Zone (H1) begin in the thalweg made by the drained banks of the Argence brook. Over a thickness of 20 metres we collected: *Teschenites flucticulus*, *Teschenites pachydicranus*, *Breistrofferella varappensis* and *Breitrofferella castellanensis*, which characterize the first lower Hauterivian biohorizon. We could not individualize the Buxtorfi biohorizon defined for the first time by BULOT *et alii*, 1992. (Beds 250-253). Other species of lesser significance are *Neolissoceras grasi* and *Spitidiscus* gr. *rossfeldensis-menghini*.

In three decimetric calcareous beds we collected numerous *Crioceratites loryi*, microconchs and macroconchs (beds 254-255), *Oosterella cultrata* - *Phyllopachyceras winckleri* - *Crioceratites nolani*.

The thicker bed 256 (0,40 - 0,50 m thick) furnished *Crioceratites loryi*, *Olcostephanus astierianus*, *Olcostephanus* gr. *lamberti*, *Olcostephanus sayni* and *Saynella* gr. *neocomiensis*.

Bed 259-260-261 are grouped with thin interbeds. They represent the Jeannoti biohorizon with, *Crioceratites matsumotoi* (dimorphic pairs) and *Jeannoticeras jeannoti, Spitidiscus* aff. *rotula*, *Crioceratites quenstedti*. At the top of this horizon appears *Saynella clypeiformis*, which marks together with *Spitidiscus* gr. *pavlowi/mikadiensis* and *Abrytusites thieuloyi*, the boundary between the Loryi and the Nodosoplicatum Zones.

The faults in the Curnier area follow the eastern side of the Condorcet diapir. The very thick Nodosoplicatum Zone seems to be the consequence of a flattened fold and the repetition of the same beds would explain the exceptional abundance of fossils.

- Beds 264-265: *Lyticoceras nodosoplicatum*, *Olcostephanus variegatus*, *Crioceratites elegans*.

- Beds 266-267: *Lyticoceras nodosoplicatum*, *Crioceratites curnieri*, *Protacrioceras alpinum* (crioceratitid and tripartite forms), *Olcostephanus variegatus* and *Protacrioceras ornatum* (= *gignouxi* form, *sensu* SARKAR).

- Beds 268-269: *Crioceratites quenstedti*, *Lyticoceras gr. cryptoceras*.

- Beds 270-274: *Crioceratites curnieri* (crioceratitid and tripartite forms), *Crioceratites quenstedti*, *Olcostephanus variegatus* and *Abrytusites juliannii*.

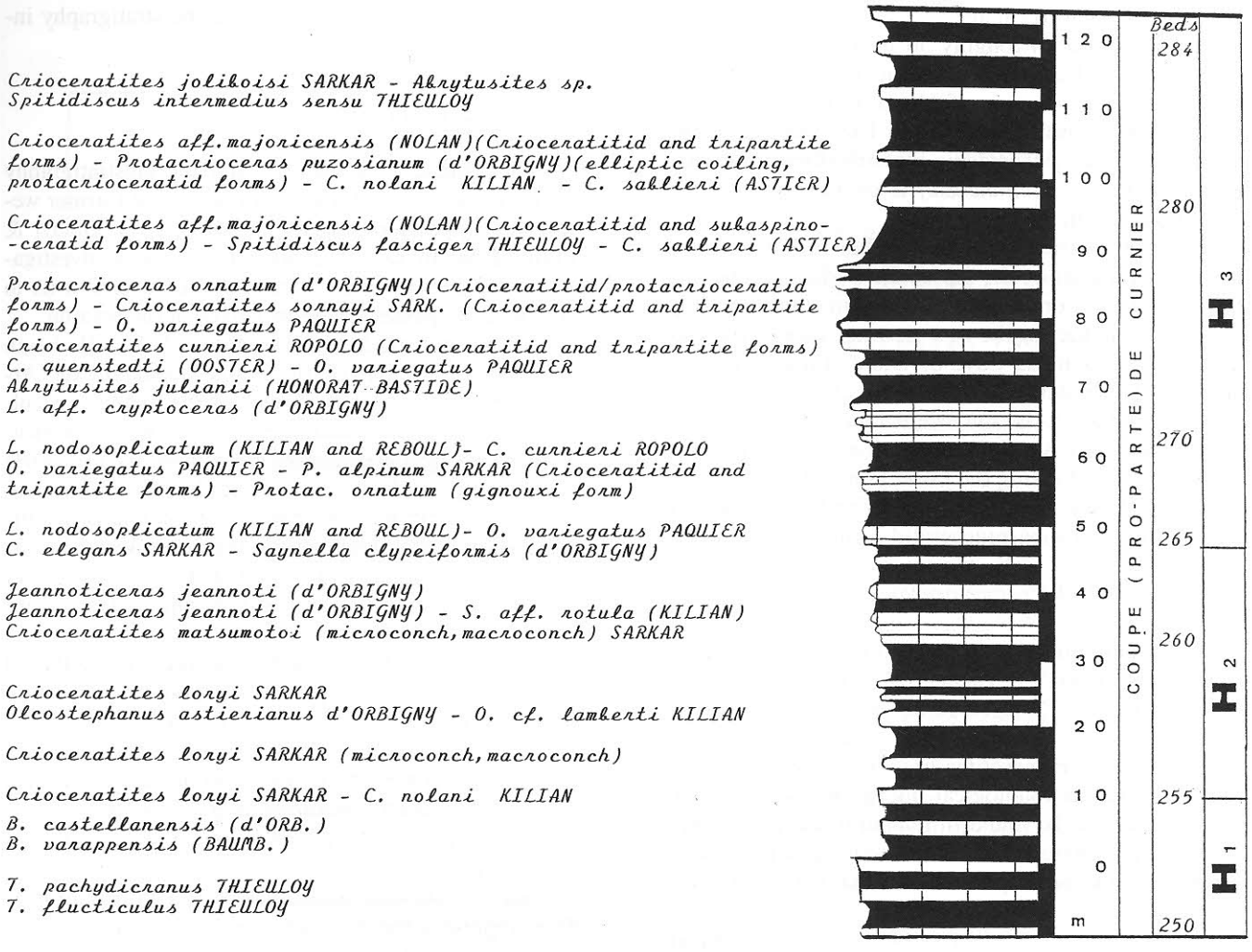


Fig. 3 - Stratigraphical distribution of the Lower Hauterivian heteromorph ammonites at Curnier (Vocontian Basin, France).
- *Distribuzione stratigrafica delle ammoniti eteromorfe nell'Hauteriviano inferiore di Curnier (Bacino Voconziano, Francia).*

- Bed 275: *Crioceratites quenstedti*, *Crioceratites curnieri* (microconch).

- Beds 276-277: *Olcostephanus variegatus*, *Crioceratites sornayi* (crioceratitid and tripartite forms).

- Beds 278-279: *Protacrioceras ornatum* (crioceratitid and protacrioceratid forms), *Crioceratites sornayi*.

- Beds 280-282: *Spitidiscus fasciger*, *Crioceratites* gr. *nolani/sablieri*, *Crioceratites sornayi*, (crioceratitid and aspinoceratid forms).- Bed 283: *Crioceratites* aff. *majoricensis* (crioceratitid and aspinoceratid forms), *Protacrioceras puzosianum* (elliptically coiled and protacrioceratid forms), *Crioceratites nolani*, *Crioceratites* gr. *nolani/sablieri*.

- Bed 284: *Crioceratites joliboisi*, *Abrytusites* sp. *Spitidiscus intermedius sensu* THIEULOY.

3.3. - LE POËT-EN-PERCYP (Fig. 4)

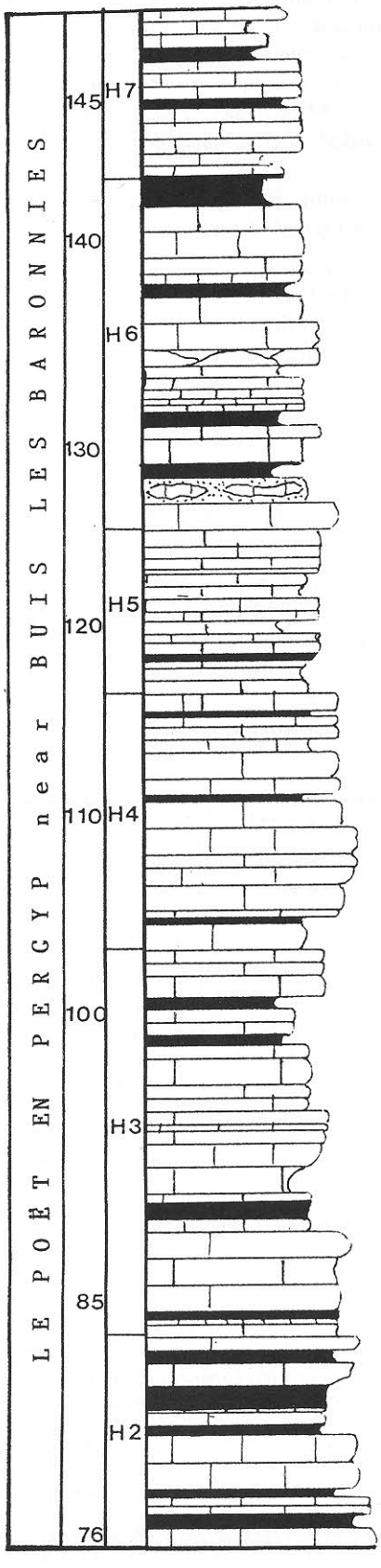
On the southern flank of the "Montagne de la Loube", just above the D.152 departmental road, east of Buis-les-Baronnies, the Le Poët deposit allows a good study of the different Hauterivian biostratigraphical levels, from the Loryi Zone to the Angulicostata Zone.

As in the above sections we collected what are probably dimorphic pairs for the following species *Crioceratites loryi*, *Crioceratites curnieri*, *Protacrioceras alpinum*, *Crioceratites shibaniae* and *Crioceratites majoricensis*.

In the first part of the Loryi Zone (H2), (beds 76-77-78) we collected in the decimetric calcareous beds many compressed macroconchs and microconchs of *Crioceratites loryi*, together with small *Olcostephanus* cf. *sayni*.

In the Jeannoti Subzone, appears *Saynella clypeiformis* (bed 82), with numerous small *Spitidiscus* gr. *pavlowi* and *Abrytusites thieuloyi* (bed 83-84).

The first appearance of *L. nodosoplicatum* (bed 85) marks the base of the following biozone. We found *Protacrioceras* gr. *alpinum* (crioceratitid and tripartite specimens: beds 87-88), *Crioceratites quenstedti*, *Crioceratites curnieri*, (dimorphic pairs) together with numerous *Olcostephanus variegatus*.



Pseudothurmannia simionescui SARKAR

Pseudothurmannia aff. grandis BUSNARDO

Pseudothurmannia angulicostata (d'ORBIGNY)

Pseudothurmannia aff. angulicostata (d'ORB.)

Binelliceras krenkeli (SARKAR)
Binelliceras binelli (ASTIER)

Balearites cf. monclusensis WIEDMANN
Balearites sp.

Balearites balearis (NOLAN)
Crioceratites majoricensis (NOLAN)
(crioceratitid and aspinoceratid forms)
Balearites balearis (NOLAN)

Megacrioceras jourdani (ASTIER)
Balearites balearis (NOLAN)

Crioceratites shibaae SARKAR
(Crioceratitid and tripartite forms)

Plesiospitidiscus ligatus (d'ORBIGNY)

Crioceratites duvali LEVEILLE
Subsaynella sp.
Crioceratites joliboisi SARKAR
Crioceratites duvali LEVEILLE

Subsaynella sayni (PAQUIER)
Crioceratites nolani KILIAN, morphe sablieri (ASTIER)

Spitidiscus intermedius sensu THIEULOY

Protacrioceras puzosianum (d'ORBIGNY)
Protacrioceras ornatum (d'ORBIGNY)

Olcostephanus variegatus PAQUIER
Crioceratites curnieri ROPOLO (Crioce--ratitid and tripartite forms)
Crioceratites quenstedti (OOSTER)
P. alpinum SARKAR (Crioceratitid and tripartite forms)

L. nodosoplicatum (KIL. and REB.)
Olcostephanus variegatus PAQUIER
Jeannoticeras jeannoti (d'ORBIGNY)
Saynella clypeiformis (d'ORBIGNY)

C. loryi SARKAR (macroconch and micr.)
C. loryi SARKAR (macroconchs)
Olcostephanus cf. sayni KILIAN

Crioceratites loryi SARKAR

Fig. 4 - Stratigraphical distribution of the Hauterivian heteromorph ammonites and dimorphic pairs in the Le Poët deposits (Drôme, Vocontian Basin, France).
- Distribuzione stratigrafica delle ammoniti eteromorfe e delle coppie dimorfiche a Le Poët (Drôme, bacino Voconziano, Francia).

- Beds 97-98: *Protacrioceras puzosianum* and *Protacrioceras ornatum*.

- Bed 101: *Spitidiscus intermedius sensu* THIEULOY is the last taxon collected in this biohorizon.

The Sayni Zone (H4) starts at beds 104 -105 with *Subsaynella sayni* and *Crioceratites* gr. *nolani/ sablieri*.

- Beds 110-113: *Crioceratites duvali*, *Crioceratites joliboisi* and what we believe to be a badly preserved *Subsaynella*.

- Bed 117: *Plesiospitidiscus ligatus* and four dimorphic specimens of *Crioceratites shibaae* (beds 120-121) are the only ammonites collected in the Ligatus biozone.

The Balearis Zone (beds 128-141) again shows successive strata with interbeds. The fauna is more abundant here, containing:

- Bed 128: *Balearites balearis*, *Crioceratites majoricensis*, *Megacrioceras jourdani*, (two specimens).

- Bed 130-131: *Balearites balearis*, *Crioceratites majoricensis* (crioceratidid and aspinoceratid forms).

- Beds 135-136: *Balearites* sp. and *Balearites montclusensis*.

- Beds 140-141: *Binelliceras krenkeli* and *Binelliceras binelli*.

Two biohorizons are clearly visible in the Angulicostata zone:

- Beds 142-145 with many *Pseudothurmannia angulicostata*, sometimes in the same nodule.

- Beds 146-150 with *Pseudothurmannia* cf. *grandis*, *Pseudothurmannia simionescui*, both characterizing the top of the Hauterivian.

4. - PALAEONTOLOGY

4.1. - POSSIBLE DIMORPHIC PAIRS

It is not always easy to identify dimorphic pairs within heteromorph ammonite populations with absolutely objective criteria. Some species have little or no detectable shell dimorphism. Certain microconchs change the orientation of the shell during their ontogeny and different stages of growth can be collected from the crioceratitid type of coiling to the aspinoceratid type of coiling. Others microconchs may be confused with macroconch juvenile or incomplete forms. For all those reasons identification must be based on :

- Material collected in one biostratigraphical horizon of one section.

-This material must be composed of adult and complete specimens, with similar initial whorls and identical sutural lines.

- A possible numerical ratio between the two supposed sexes can be introduced to confirm the above solution. However as extreme variation in sex-ratio may be caused by environmental conditions, by preservation, or by various processes of fossilization, (..."*The state of preservation of an ammonite may be greatly influenced by its absolute size, or by not yet clearly established other reasons*"... MAKOWSKI, 1962), such a criterion cannot be regarded as conclusive for the acceptance of dimorphism.

In the Taxonomy and Systematics' section we use standard morphological terms:

D = Shell diameter
H = Height of whorl
U = Width of umbilicus
H/D and U/D ratios characterize the shell coiling scheme.
I = Hiatus between the initial whorls and the oral part.

4.2. - TAXONOMY AND SYSTEMATICS

ORDER Ancyloceratida WIEDMANN, 1966
SUPERFAMILY Ancyloceratacea MEEK, 1876
FAMILY Ancyloceratidea MEEK, 1876
SUBFAMILY Crioceratitinae WRIGHT, 1952
GENUS ***Crioceratites*** LÉVEILLÉ, 1837
SUBGENUS ***Crioceratites*** LÉVEILLÉ, 1837
TYPE SPECIES: *Crioceratites duvali* LÉVEILLÉ, 1837

TAXA	Macroconch	Microconch	Strat. level
C. loryi SARKAR, 1955	Crioceratitid coiling	Crioceratitid coiling	Loryi Zone
C. matsumotoi SARKAR, 1955	Crioceratitid coiling	Crioceratitid coiling	Loryi Zone
C. curnieri ROPOLO, 1991	Crioceratitid coiling	Aspinoceratid coiling	Nodosoplicatum Zone
C. sornayi SARKAR, 1955	Crioceratitid coiling	Aspinoceratid coiling	Nodosoplicatum Zone
C. duvali LÉVEILLÉ, 1837	Crioceratitid coiling	Aspinoceratid coiling	Sayni Zone
C. shibaniae SARKAR, 1955	Crioceratitid coiling	Subaspinoceratid coiling	Sayni Zone
C. majoricensis NOLAN, 1894	Crioceratitid coiling	Subaspinoceratid coiling	Balearis Zone

Crioceratites (C.) loryi SARKAR, 1955

Pl. 1, fig. 1-4; pl. 2, fig. 3

1955 *Crioceras loryi* SARKAR, p. 40, pl. 5, fig. 2.
1955 *Balearites koechliniformis* SARKAR, p. 147, pl. 10, fig. 7.
1955 *Balearites tuberculatus* SARKAR, p. 146, pl. 11, fig. 3.
? 1955 *Balearites* cf. *balearis* NOLAN; SARKAR, p. 142, pl. 6, fig. 14.
1964 *Crioceratites (Crioceratites) duvali loryi* SARKAR; THOMEL, p. 12.
1964 *Crioceratites (Crioceratites) barrabei* SARKAR; THOMEL, p. 27, pl. 4, fig. 1.
1967 *Crioceratites arci* DIMITROVA, p. 43, pl. 16, fig. 4.
1972 *Crioceratites (Crioceratites) loryi* SARKAR; THIEULOY, p. 41, pl. 5, fig. 1, 5, fig. 4 q, r ,s, t.
1976 *Crioceratites (Crioceratites) loryi* SARKAR; MANDOV, pl. 6, fig. 3.

1978 *Crioceratites (Crioceratites) loryi* SARKAR; IMMEL, p. 42, pl. 1, fig. 4; pl. 4, fig. 2.
1986 *Crioceratites (Crioceratites) loryi* SARKAR; VASICEK & MICHALIK, p. 459, pl.1, fig. 4.

DESCRIPTION - All specimens are of medium size, well preserved and not deformed, which is rare in the Vocontian-Basin. Crioceraticonically coiled shells which have the three ornamental phases typical of this species:
INITIAL STAGE - Thin flexuous fasciculated ribs, sometimes with little median tubercles which disappear at the end of the first whorl. Short spines are periodically observable on the perimeter (one every 4 or 5 ribs).
INTERMEDIATE STAGE - Umbilical tubercles corresponding to spine bases appear on major ribs, which are separated by a variable number of intermediaries (4 to 7). All ribs are interrupted on the venter by a smooth siphonal band.
THE ADULT STAGE - Intermediate ribs tend to become as strong as main ribs which nevertheless remain more prominent. Bituberculation is now clearly visible. The main ribs bear variably developed ventro-lateral and umbilical tubercles. The latter are particularly prominent on the gently rounded umbilical rim. On the apertural part the whorl is as wide as high and the section subquadrate.
DIMORPHISM - It is not always easy to discern dimorphic pairs within the crioceratitid populations of the Loryi Zone. Dimorphic shell differences are barely detectable because inner whorls of microconchs and macroconchs are indistinguishable. However, the presence of adult specimens of different size in the same levels and the differing ratios between shells of larger size and those of modest size, justify the hypothesis of a dimensional dimorphism, probably of a sexual origin. We note that :
- generally the ornamentation of the microconch seems finer than that of the macroconch;
- at the end of the last whorl, the microconch often shows more numerous (5-6) and more flexuous intermediate ribs than the macroconch (3-4);
- while the growth rate of inner whorls tends to remain the same in both types, the height of the microconch increases more quickly than the height of the chamber of its dimorphic partner. This fact means probably that : "*...macroconchiate females took longer to mature than their microconchiate males...*" (WESTERMANN, 1990).

MATERIAL - Four specimens: macroconchs, pl. 1, fig. 2-4; microconchs, pl. 1, fig. 1-3: Loryi zone, bed 83 - Ravin du Cave de Diou, North side of Mont-Ventoux, France.

MEASUREMENTS

Specimen	D	H	U	H/D	U/D
Pl. 1, fig. 1	65	20.3	44	0.312	0.676
Pl. 1, fig. 2	72, 94	22.35	48.8	0.306	0.669
Pl. 1, fig. 3	55.2	16.47	33.52	0.302	0.607
Pl. 1, fig. 4	74.1	20	50	0.269	0.674

Crioceratites (C.) matsumotoi SARKAR, 1955
Pl. 2, fig. 1, 2

1955 *Crioceras matsumotoi* SARKAR, p. 74, pl.3, fig.2.
1962 *Crioceratites (Crioceratites) matsumotoi* SARKAR; WIEDMANN, pl. 8, fig. 2.
1964 *Crioceratites (Crioceratites) matsumotoi* SARKAR; THOMEL, p. 14.
1964 *Crioceratites (Crioceratites) krishnaae* SARKAR; THOMEL, pl. 1; fig. 4-5.
1967 *Crioceratites matsumotoi* SARKAR; DIMITROVA, pl. 17, fig.3.
1976 *Crioceratites (Crioceratites) villiersianum bituberculatum* SARKAR; MANDOV, pl. 6; fig. 4.
1976 *Crioceratites (Crioceratites) rodighieri* DIMITROVA; MANDOV, pl. 6, fig. 5-6.
1978 *Crioceratites (Crioceratites) matsumotoi* SARKAR; IMMEL, p. 37, pl.2, fig 5-6.
1992 *Crioceratites matsumotoi* SARKAR; BULOT *et alii*, Tabl. 10, p. 37; Tabl. 13, p. 48; Tabl. 14, p. 49.

DESCRIPTION

PRESUMED MACROCONCH SPECIMEN - A crioceraticonically coiled shell of relatively modest size (D = 63,91mm), moderately compressed, with flat or gently rounded flanks and a subrectangular section. The bituberculate spiral has a characteristically fine ornamentation. On the inner whorls the sculpture consists of thin, flexuous intermediate ribs (2-8) between slightly thicker main ribs. On the perimeter short spines appear periodically. Then the major ribs, which up to D = 63mm remained very discreet, gradually become more prominent. The three last ones are particularly strong at the end of the spiral. They are separated by 12-13 intermediate ribs. Five strong tubercles are preserved on the ventral edge. Sutural lines are clearly visible on the phragmocone.

PRESUMED MICROCONCH SPECIMEN - This ammonite differs from the other figured specimen by its smaller size and its peculiar involution. If the intermediate rib density is the same, the main ribs seem stronger on the phragmocone. The space between the aperture and the inner whorls is greater and the last whorl forms a sort of short shaft, which gives the impression of slight uncoiling.

Because of its long range (Loryi to Sayni Zones) *Crioceratites matsumotoi* is of no value as an index fossil.

MATERIAL - Two specimens (1.- macroconch - 2.- microconch) from the Loryi Zone, Jeannoticeras jeannoti biohorizon, bed 124 - Curnier, Drôme - France.

MEASUREMENTS

Specimen	D	H	U	H/D	U/D
Pl. 2, fig. 1	63.91	19.4	41.27	0.303	0.645
Pl. 2, fig. 2	45.07	14	28.10	0.299	0.623

Crioceratites (C.) curnieri ROPOLO, 1991
Pl. 3, fig. 1, 2, 3

1991 *Crioceratites (Crioceratites) curnieri* ROPOLO, p. 65, pl. 1, fig. A, B; pl. 2, fig. A, B; pl. 3, fig. A-C.

1992 *Crioceratites (Crioceratites) curnieri* ROPOLO; ROPOLO & SALOMON, p. 196, pl. 4, fig. 1-7.

non 1992 *Crioceratites curnieri* ROPOLO; BULOT *et alii*, p.42.

DESCRIPTION

PRESUMED MACROCONCH SPECIMEN - The specimen of pl. 3, fig. 1 is a crioceraticonically coiled shell with the typical three stages of ornamentation.

On the initial whorl, which is not entirely preserved, fine parallel ribs are visible. At diameter D = 25mm appear the first main ribs with a ventral and umbilical tuberculation. On the body chamber, major ribs and intermediates tend to become similar.

On the second and on the third ornamental stage there are 6 to 10 intermediate ribs between the main ribs; they can be radiate or flexuous. Major ribs bear fine ventral and umbilical tubercles. Flanks are flat or gently curved. The section is subrectangular.

Certain macroconch specimens tend to a tripartite structure with a marked space between the juvenile whorls and the last one.

In spite of some ornamental similarities, *Crioceratites curnieri* differs from *Crioceratites quenstedti* (OOSTER, 1860, *sensu* IMMEL, 1978) by its whorl section, its more evolute coiling and by its dimensional ratios:

Crioceratites curnieri, holotype (N° 1990/45 Muséum d'Histoire Naturelle, Marseille)

H/D = 0,259	I = 8,9	U/D = 0,530

Crioceratites curnieri, topotype (N° 1990/46 Muséum d'Histoire Naturelle of Marseille)

H/D = 0,269	I = 9,7	U/D = 0,544

Crioceratites quenstedti, holotype (in IMMEL, 1978, pl. 1, fig. 3)

H/D = 0,357	I = 4	U/D = 0,446

Crioceratites quenstedti (in IMMEL, 1978, pl. 3, fig. 1)

H/D = 0,366	I = 6	U/D = 0,500

PRESUMED MICROCONCH SPECIMENS - The group of small ancyloceratids variously referred to as *Acrioceras*, *Aspinoceras* or *Subaspinoceras* by previous authors is generally interpreted to have developed from crioceratiform ancestors. Therefore it seems surprising to collect tripartite shapes with similar sculpture and suture lines associated with crioceratitid partners. This fact suggests that the tripartite and crioceratitid forms may constitute dimorphic pairs.

The specimen of pl. 3, fig. 2 has a badly preserved aspinoceratid shell. It presents on the crioceratiform spiral, the hook and the straight shaft, the characteristic sculpture of *Crioceratites curnieri* with flexuous intermediate ribs and stronger bituberculate major ribs. The whorl height is low and increases very slowly. The flanks are moderately compressed with a subrectangular whorl section.

The well preserved specimen of pl. 3, fig. 3 has a better visible sculpture than the 2nd one, with prorsiradiate to rectiradiate intermediate ribs (6 to 10). The height of the last whorl increases moderately quickly and the terminal hook-shaped part is less curved than that of the previous specimen. The whorl section is subrectangular.

MATERIAL - Three specimens (pl. 3, fig. 1- macroconch; pl. 3, fig. 2, 3 microconchs) Nodosoplicatum Zone, bed 140 - Curnier (Drôme, France).

MEASUREMENTS

Specimen	D	H	U	H/D	U/D
Pl. 3, fig. 1	121	32	79	0.264	0.652
Pl. 3, fig. 2	79.2	20	31	0.252	0.391
Pl. 3, fig. 3	78	20	35.5	0.256	0.455

Crioceratites (C.) sornayi SARKAR, 1955
Pl. 3, fig. 4, 5

1955 *Crioceratites (Crioceratites) sornayi* SARKAR, p. 50, pl. 1, fig. 7.

1955 *Crioceras sornayi* var. *densicostata* SARKAR, p. 51, pl. 4, fig. 8.

1955 *Crioceras sornayi* var. *tuberculata* SARKAR, p. 51, pl. 4, fig. 15.

non 1978 *Crioceratites (Crioceratites) basseae* SARKAR; IMMEL, p. 50, fig. c; p. 48.

1992 *Crioceratites (Crioceratites) sornayi* SARKAR; ROPOLO & SALOMON, p. 196, pl. 5, fig. 1-5.

DESCRIPTION

PRESUMED MACROCONCH SPECIMEN (pl. 3, fig. 4) - A crioceraticonically coiled shell with a trituberculate juvenile part up to the early last whorl; here the sculpture changes and the major ribs become bituberculate; the lateral tubercle disappears on the body chamber and the intermediate ribs (4 to 8) tend to become as strong as the main ribs. The section is oval, the flanks are gently curved.

The whorl height increases moderately quickly though the whorls remain well separated, the last one being more evolute and forming a sort of incurved hook.

PRESUMED MICROCONCH FORM (pl. 3, fig. 5) - This specimen has a small but complete and well preserved shell. The first whorls (juvenile stage) are planispirally coiled whilst the gerontic part consists of an incurved shaft and of a sort of opened hook resulting in a subaspinoceratid type of coiling. On the phragmocone ma-

jor ribs bear three small tubercles. Then, on the body chamber, trituberculate ribs progressively bituberculate, the lateral tubercle disappearing. Intermediate ribs (4 to 10), often flexuous or concavely curved adorally; tend to be as strong as the major ribs on the terminal part. The whorl height increases moderately quickly, the flanks are gently curved. The section is subquadrate to oval.

MATERIAL - Two specimens (pl. 3, fig. 4 macroconch;pl. 3, fig. 5 microconch), Nodosoplicatum Zone, bed 142 - Curnier (Drôme - France).

MEASUREMENTS

Specimen	D	H	U	H/D	U/D
Pl. 3, fig. 4	133	34	84	0.255	0.631
Pl. 3, fig. 4	72	19.2	42.5	0.266	0.590

Crioceratites (C.) duvali LÉVEILLÉ, 1837
Pl. 4, fig. 1, 2, 3

1837 *Crioceratites duvali* LÉVEILLÉ, p. 313, pl. 22, fig. 1, 2.
1878 *Crioceras duvali* LÉVEILLÉ; BAYLE & ZEILER, pl. 97, fig. 1.
1902 *Crioceras duvali* LÉVEILLÉ; SARASIN & SCHÖNDELMAYER, p. 105, pl. 12, fig. 1.
1919 *Crioceras duvali* LÉVEILLÉ; RODIGHIERO, p. 110, pl. 5, fig. 4, 11.
1955 *Crioceras duvali* LÉVEILLÉ; SARKAR, p. 33, pl. 1, fig. 3; pl. 7, fig. 4.
1955 *Crioceras duvali* LÉVEILLÉ sp. var. *sarasini* SARKAR, p. 36.
1955 *Crioceras cf. duvali* LÉVEILLÉ sp. (forme n°1); SARKAR p. 36, pl. 5, fig. 6 and text fig. 4 A.
1955 *Crioceras baylei* SARKAR, p. 36 and Textfig. 4B.
1955 *Crioceras vishnui* SARKAR, p. 68, pl. 3, fig. 5.
1964 *Crioceratites (Crioceratites) duvali* LÉVEILLÉ; THOMEL, p. 10, pl. 1, fig. 1, 2.
1978 *C. (Crioceratites) duvali* LÉVEILLÉ; IMMEL, p. 36.
1989 *Crioceratites duvali* LÉVEILLÉ; AUTRAN, p. 211, pl. 13, fig. 7.

DESCRIPTION

MACROCONCH FORM (pl. 4, fig. 1) - The interpretation of *Crioceratites duvali* is beset with many difficulties, the holotype of LÉVEILLÉ being lost. SARKAR (1955) and THOMEL (1964) revised and figured this species again and we refer to them for identifying our specimens.

A crioceraticonically coiled shell, moderately compressed with well preserved sculpture and sutures. Ornamentation shows 23 major ribs with thin intermediate ribs (6 to 12): all are gently flexuous. Just before the end of the phragmocone, furrows appear which double the main ribs. 8 ventral tubercles are clearly visible on the 12 main ribs of the last whorl. This specimen corresponds to SARKAR's description of *Crioceratites duvali*.

The macroconch specimen of pl. 4, fig. 3 is a well preserved crioceraticonically coiled shell, larger than the specimen of pl. 4, fig. 1. On the juvenile whorls, thin intermediate ribs of uniform type are visible (6 to 14) between strong bituberculate major ribs. As in the specimen of pl. 4, fig. 1, this specimen corresponds entirely to SARKAR's description.

PRESUMED MICROCONCH SPECIMEN (pl. 4, fig. 2) - A complete and well preserved subaspinoceratid shell with a juvenile spirally coiled part, a short shaft and a curved hook. The sculpture shows 17 major ribs with gently flexuous intermediates (6 to 12). The sutures are indistinguishable from those of the dimorphic partner. On the shaft and on the hook the same furrows doubling the major ribs are particularly pronounced. The main ribs bear umbilical and ventral tubercles. The flanks are flat. On the spire the whorl height increases moderately quickly in relation to diameter, but diminishes at the end of the phragmocone.

MATERIAL - Three specimens (pl. 4, fig. 1 and 3 macroconchs;pl. 4, fig. 2 presumed microconch form) Sayni Zone - bed 95 - Ravin du Cave de Diou, North side of Mont-Ventoux, France.

MEASUREMENTS

Specimen	D	H	U	H/D	U/D
Pl. 4, fig. 1	140	44.55	89.1	0.318	0.636
Pl. 4, fig. 2	75	27	44.55	0.36	0.594
Pl. 4, fig. 3	156.6	47.25	99.9	0.301	0.637

Crioceratites (C.) shibaniae SARKAR, 1955
Pl. 5; fig. 1-4

1955 *Crioceras shibaniae* SARKAR, p. 49, fig. 9 and text. fig. 8 E.
1955 *Crioceras nowaki* SARKAR, p. 49, pl. 4, fig. 11 and text. fig. 8 B.
1955 *Crioceras karakashi* SARKAR, p. 48, pl. 4, fig. 13 and text. fig. 8 A.
1955 *Crioceras vialii* SARKAR, p. 44, pl. 4, fig. 19 and text. fig. 6 D.
1955 *Crioceras stahleckeri* SARKAR, p. 43, pl. 1, fig. 5 and text. fig 6 C.
1978 *C. (Crioceratites) shibaniae* SARKAR, in IMMEL, p. 51 and text. fig. d; p. 48.

DESCRIPTION

PRESUMED MACROCONCH SPECIMEN (pl. 5, fig. 1) - A crioceraticonically coiled shell of medium size with flat flanks and a narrow rounded venter. On the juvenile whorls of the spire up to a diameter of 52 mm the major ribs are trituberculate; the lateral tubercle is closer to the ventral one. At the end of the phragmocone, the lateral tubercle disappears and the main ribs become bituberculate. They are doubled by furrows on the body chamber. Intermediate ribs (6 to 12) are gently flexuous. The whorl height increases moderately quickly on the phragmocone but diminishes on the body chamber.

SUPPOSED MACROCONCH SPECIMEN (pl. 5, fig. 2) - This crioceraticonically coiled shell is smaller than that of

fig. 1 and presents a peculiar coiling which shows a faint tendency to aspinoceratid type of coiling because the increase of the whorl height is rather quick on the phragmocone but diminishes on the body chamber. This is interpreted as a macroconch characteristic.

SUPPOSED MICROCONCH SPECIMENS (pl. 5, fig. 3, 4) - The specimen of pl. 5, fig. 3 is a subaspinoceratid coiled shell with a juvenile crioceratiform part which tends to uncoil. The gerontic part forms a kind of short curved shaft. The whorl height increases moderately quickly. On the spire the major ribs bear three strong tubercles; at the end of the phragmocone, they become bituberculate and rarer. They are doubled by a furrow on the body chamber, whilst the number of intermediate ribs (6 to 20) between two main ribs increases.

The specimen of pl. 5, fig. 4 is a badly preserved aspinoceratid form has the same ornamental characteristics as the previous specimen. The flanks are flat and moderately compressed. On the straight shaft and on the hook the imperfectly preserved ribs are rather faint and indistinct, but become strong on the terminal part.

MATERIAL - Four specimens (pl. 5, fig. 1; 2 macroconchs; pl. 5, fig. 3, 4 microconchs) Sayni Zone - bed 92 - Ravin du Cave de Diou, North side of Mont Ventoux, France.

MEASUREMENTS

Specimen	D	H	U	H/D	U/D
Pl. 5, fig. 1	96	30	58.2	0.312	0.606
Pl. 5, fig. 2	78.9	28.3	49.8	0.358	0.631
Pl. 5, fig. 3	90	27	53	0.300	0.588
Pl. 5, fig. 4	81	22	39	0.271	0.481

Crioceratites (C.) majoricensis NOLAN, 1894
Pl. 6, fig. 1-5

1894 *Crioceras picteti* var. "*majoricensis*" NOLAN, p. 192, pl. 10, fig. 1a, 1b, 1d.
1894 *Crioceras angulicostatum* D'OREIGNY; NOLAN, p. 195, pl. 10, fig. 3 b, c.
1902 *Crioceras quenstedti* OOSTER; SARASIN & SCHÖNDELMAYER, p. 109, pl. 12, fig. 4-7.
1919 *Crioceras quenstedti* OOSTER; RODIGHIERO, p. 113, pl. 12, fig. 2.
1955 *Crioceras nolani* var. "*majoricensis*" NOLAN; SARKAR, p. 45.
1955 *Crioceras seitzi* SARKAR; p. 70, pl. 3, fig. 3.
? 1955 *Crioceras rogeri* SARKAR; p. 42, pl. 4, fig. 14 and text. fig. 6A.
1962 *Crioceratites (Crioceratites) majoricensis remanei* NOLAN; WIEDMANN, p. 118, pl. 8, fig. 3.
1962 *Crioceratites (Crioceratites) majoricensis*, NOLAN; WIEDMANN, p. 121, pl. 8, fig. 4; pl. 9, fig. 2.
1964 *Crioceratites (Crioceratites) majoricensis* NOLAN; THOMEL, p. 19, pl. 3, fig. 1.
1976 *Crioceratites (C) majoricensis majoricensis* NOLAN; MANDOV, pl. 4, fig. 1-3.
1976 *Crioceratites (C) majoricensis* WIEDMANN; MANDOV, pl. 5, fig. 4.
1978 *C. (Crioceratites) majoricensis* NOLAN; IMMEL, p. 49 and text. fig. b, p. 48.

DESCRIPTION

CRIOCERATITES MAJORICENSIS NOLAN CF. *REMANEI* WIEDMANN (pl. 6, fig. 1), **MACROCONCH** - This crioceraticonically coiled shell of medium size (D=116mm) forms an evolute spire, each whorl being more and more detached from the preceding one in relation with the diameter. This open crioceratitid coiling corresponds to NOLAN's (1894) pl. 10, fig. 3 b, c. Three ontogenetic stages are clearly visible: 1) on the juvenile stage the strongly trituberculate main ribs are separated by 4 to 5 flexuous intermediate ribs; 2) on the middle stage the lateral tubercle disappears and the umbilical one becomes more pronounced. Intermediates are biconcave towards the aperture; 3) on the adult stage only a strong ventral tubercle persists.

CRIOCERATITES MAJORICENSIS MAJORICENSIS NOLAN (pl. 6, fig. 2), **MACROCONCH** - This crioceraticonically coiled specimen bears exactly the same type of sculpture as the preceding one, but the form of the spiral differs; the whorl height increases more quickly than the specimen of pl. 6, fig. 1 and the section is subrectangular.

CRIOCERATITES MAJORICENSIS CF. *REMANEI* (pl. 6, fig. 3), PRESUMED **MICROCONCH** - Hook shaped aberrant shell with juvenile part coiled in free crioceratiform spire. The first ornamental stage (trituberculate major ribs with 4 to 5 inserted ribs) is here more pronounced and continues up to the end of the phragmocone on the early stage of the curved shaft. The next two main ribs are bituberculate and finally tubercles disappear on the hook, where the intermediate ribs tend to become as strong as the major ribs. The whorl height increases slowly on the phragmocone and more quickly on the hook.

CRIOCERATITES MAJORICENSIS MAJORICENSIS (pl. 6, fig. 4), PRESUMED **MICROCONCH** - An acrioceratiform specimen with a juvenile crioceratiform spire , a shaft and a curved hook. The sculpture shows the three typical stages of *C. majoricensis* (trituberculate, bituberculate, monotuberculate major ribs). On the hook, there is a section of alternating simple and dichotomous ribs. The whorl section is subquadrate.

CRIOCERATITES MAJORICENSIS CF. *REMANEI* (pl. 6, fig. 5), PRESUMED **MICROCONCH** - This tripartite shell has major trituberculate ribs separated by 4 to 5 intermediates on the spiral. On the straight shaft and on the curved hook the bituberculate and the monotuberculate stages are developed. At the transition of the shaft to the terminal hook occur ribs that bifurcate at medium flank height.

MEASUREMENTS

Specimen	D	H	U	H/D	U/D
Pl. 6, fig. 1	116	29	68	0.25	0.586
Pl. 6, fig. 2	101.2	28	58	0.276	0.583
Pl. 6, fig. 3	94.2	28	50	0.297	0.530
Pl. 6, fig. 4	92	25.5	49	0.277	0.532
Pl. 6, fig. 5	94	26	42	0.276	0.446

OCCURRENCE - All the specimens : Balearis Zone - (pl. 6, fig. 1, 3, 5, bed 110; pl. 6, fig. 2, 4, bed 111) Ravin du Cave de Diou - North side of Mont-Ventoux, France.

5. - TAXONOMIC IMPLICATIONS AND GENERAL CONCLUSIONS

The aim of this paper is to demonstrate that the phenomenon of dimorphism is a reality within heteromorph ammonite populations. The species described here reveal, for the same time and in the same beds, two structural types.

The first, larger, structure with crioceratitid coiling is probably the female of the species.

The second, smaller, structure with subaspinoceratid or aspinoceratid coiling would seem to correspond to the male.

However as our recent study suggests (ROPOLO & SALOMON, 1992) the variation of coiling or uncoiling does not seem to be reflect dimorphism alone, it takes on a second aspect.

Some species (*C. nolani* KILIAN var. *sablieri* ASTIER, *C. elegans*, D'ORBIGNY, *C. joliboisi*, SARKAR, etc.) reveal variations of coiling over time. These morphological transformations (a kind of biological "crisis") seem to correspond to transgressive or regressive periods with sea level variations (TINTANT *et alii* 1982; MARCHAND *et alii*, 1985; MARCHAND, 1992; DELANOY & MAGNIN, 1994).

Alternatively they could be explained by colder and warmer periods in which glacio-eutatism reached its maximum (KEMPER & WIEDENROTH, 1987). According to BULOT (1993, *cum bibl.*), recent investigations on bryozoan distribution and carbon isotopes seem to confirm this last hypothesis.

A further study to be published will include morphofunctional and biostratigraphic analyses in order to clarify our understanding of this second aspect of "uncoiling". In any case the appearance of morphological dimorphic differences or variations during evolution of the coiling seems to constitute a genetic response to physical and ecological changes induced by oceanic or climatic events.

The recognition of sexual dimorphism in Ancyloceratidae and of coiling evolution within heteromorph ammonites calls for a revision of the classification of the Lower Cretaceous genera and species. There is now no serious objection to uniting in the same genus large forms with crioceratitid coiling and smaller forms with subaspinoceratid / aspinoceratid or acrioceratid coiling. From a taxonomic point of view, a new classification suggested for many years by numerous eminent authors (MAKOWSKI, 1962; RAWSON, 1975; KLINGER & KENNEDY, 1992) would certainly mark a progress, because it seems evident now that conspecific large and small forms differing in sex must be assigned to the same genus or even the same species, and that generic separation based on criteria such as differences in coiling is untenable.

ACKNOWLEDGEMENTS

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PLATE 1

Supposed dimensional dimorphism.
Fig. 1, 3 - *Crioceratites loryi* SARKAR, 1955, microconchs - Loryi Zone, Ravin du Cave de Diou section (Northern side of Mont-Ventoux, France), bed 83.
Fig. 2, 4 - *Crioceatites loryi* SARKAR, 1955, macroconchs - Loryi Zone, same section and bed.
Collection GONNET - Avignon. Photos P. ROPOLO, x 1,5
An arrow indicates the beginning of the body chamber.

TAVOLA 1

Dimorfismo dimensionale presunto.
Fig. 1, 3 - Crioceratites loryi *SARKAR, 1955, microconchi - Zona a Lory, sezione di "Ravin du Cave de Diou" (versante settentrionale del Mont-Ventoux), strato 83.*
Fig. 2, 4 - Crioceatites loryi *SARKAR, 1955, macroconchi - Zona a Loryi, stessa sezione, stesso strato.*
Collezione GONNET - Avignon). Foto P. ROPOLO, x 1,5
La freccia indica l'inizio della camera d'abitazione.

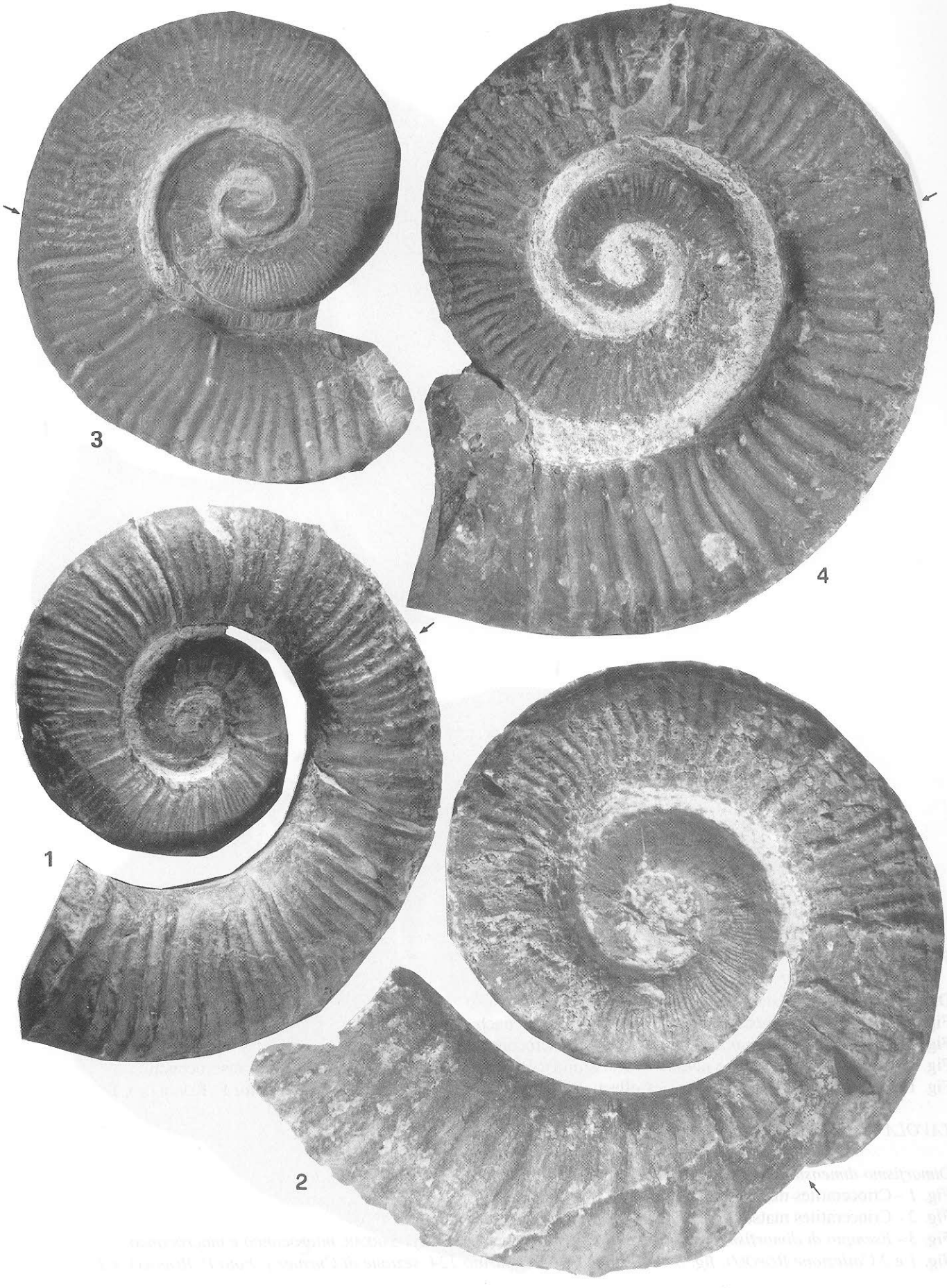
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PLATE 2

Dimensional dimorphism - Loryi Zone.
Fig. 1 - *Crioceratites matsumotoi* SARKAR, 1955, macroconch.
Fig. 2 - *Crioceratites matsumotoi* SARKAR, 1955, microconch.
Fig. 3 - Dimorphism in a same nodule - *Crioceratites loryi* SARKAR, 1955, microconch and macroconch.
Fig. 1 and 2 Collection ROPOLO; fig. 3 Collection POUPON (Bed 124, Curnier section). Photos P. ROPOLO, x 1

TAVOLA 2

Dimorfismo dimensionale - Zona a Loryi.
Fig. 1 - Crioceratites matsumotoi *SARKAR, 1955, macroconco.*
Fig. 2 - Crioceratites matsumotoi *SARKAR, 1955, microconco.*
Fig. 3 - Esempio di dimorfismo nello stesso nodulo - Crioceratites loryi *SARKAR, microconco e macroconco.*
Fig. 1 e 2 Collezione ROPOLO; fig. 3 Collezione POUPON (strato 124, sezione di Curnier). Foto P. ROPOLO, x 1

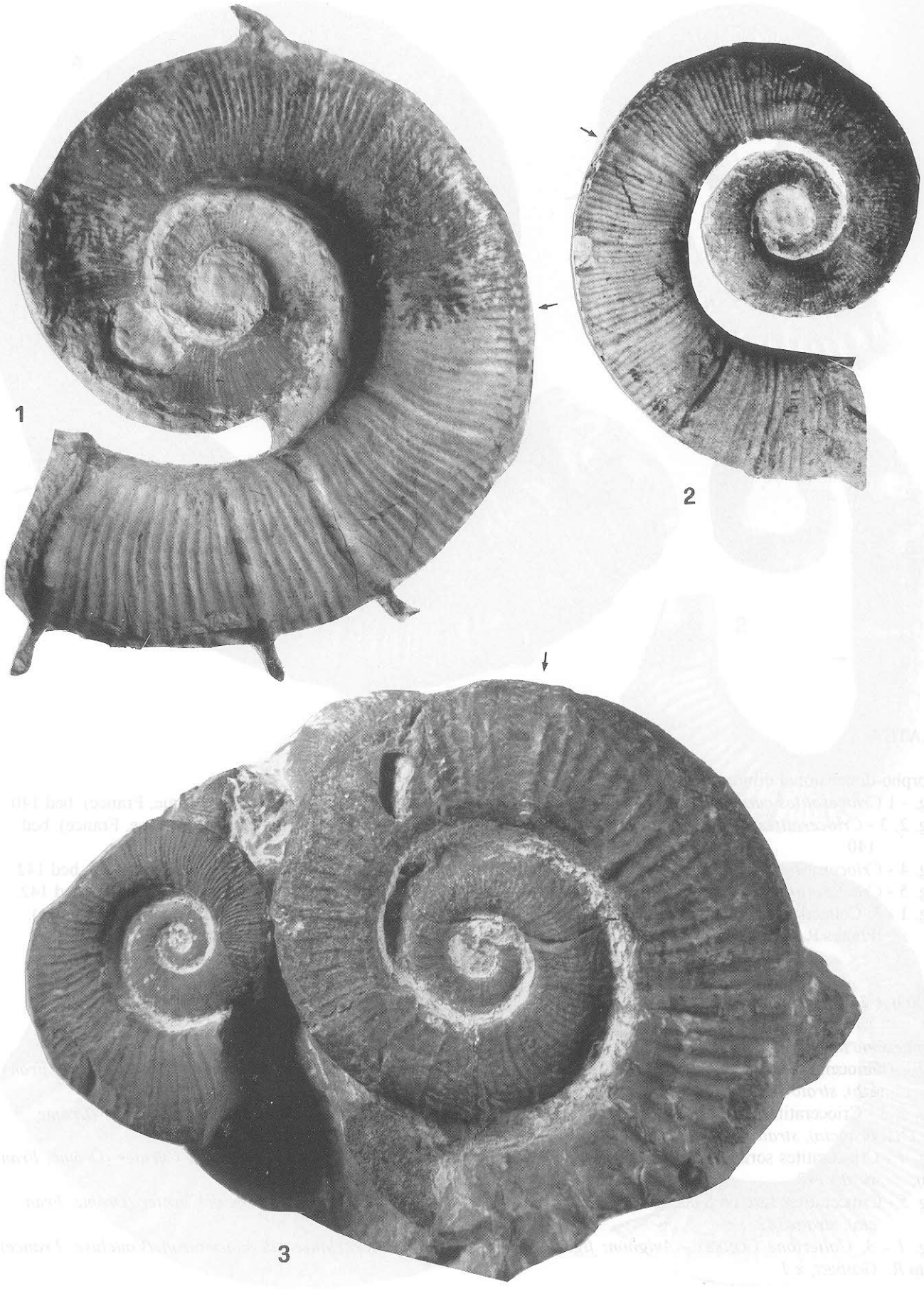
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PLATE 3

Morpho-dimensional dimorphism.
Fig. - 1 *Crioceratites curnieri* ROPOLO, 1991, macroconch - Nodosoplicatum Zone, Curnier (Drôme, France), bed 140.
Fig. 2, 3 - *Crioceratites curnieri* ROPOLO, 1991, microconchs - Nodosoplicatum Zone, Curnier (Drôme, France), bed 140.
Fig. 4 - *Crioceratites sornayi* SARKAR, 1955, macroconch - Nodosoplicatum Zone, Curnier (Drôme, France), bed 142.
Fig. 5 - *Crioceratites sornayi* SARKAR, 1955, microconch - Nodosoplicatum Zone, Curnier (Drôme, France), bed 142.
Fig. 1 - 3: Collection GONNET - Avignon; fig. 4, 5: Collection SALOMON, Musèe de Mormoiron, (Vaucluse, France). Photos R. GONNET, x 1

TAVOLA 3

Dimorfismo morfo-dimensionale.
Fig. - 1 Crioceratites curnieri *ROPOLO, 1991, macroconco - Zona a Nodosoplicatum, sezione di Curnier (Drôme, Fran cia), strato 140.*
Fig. 2, 3 - Crioceratites curnieri *ROPOLO, 1991, microconchi - Zona a Nodosoplicatum, sezione di Curnier (Drôme, Francia), strato 140.*
Fig. 4 - Crioceratites sornayi *SARKAR, 1955, macroconco - Zona a Nodosoplicatum, sezione di Curnier (Drôme, Francia), strato 142.*
Fig. 5 - Crioceratites sornayi *SARKAR, 1955, microconco - Zona a Nodosoplicatum, sezione di Curnier (Drôme, Fran cia), strato 142.*
Fig. 1 - 3: Collezione GONNET - Avignon; fig. 4, 5: Collezione SALOMON, Museo di Mormoiron (Vaucluse, France). Foto R. GONNET, x 1

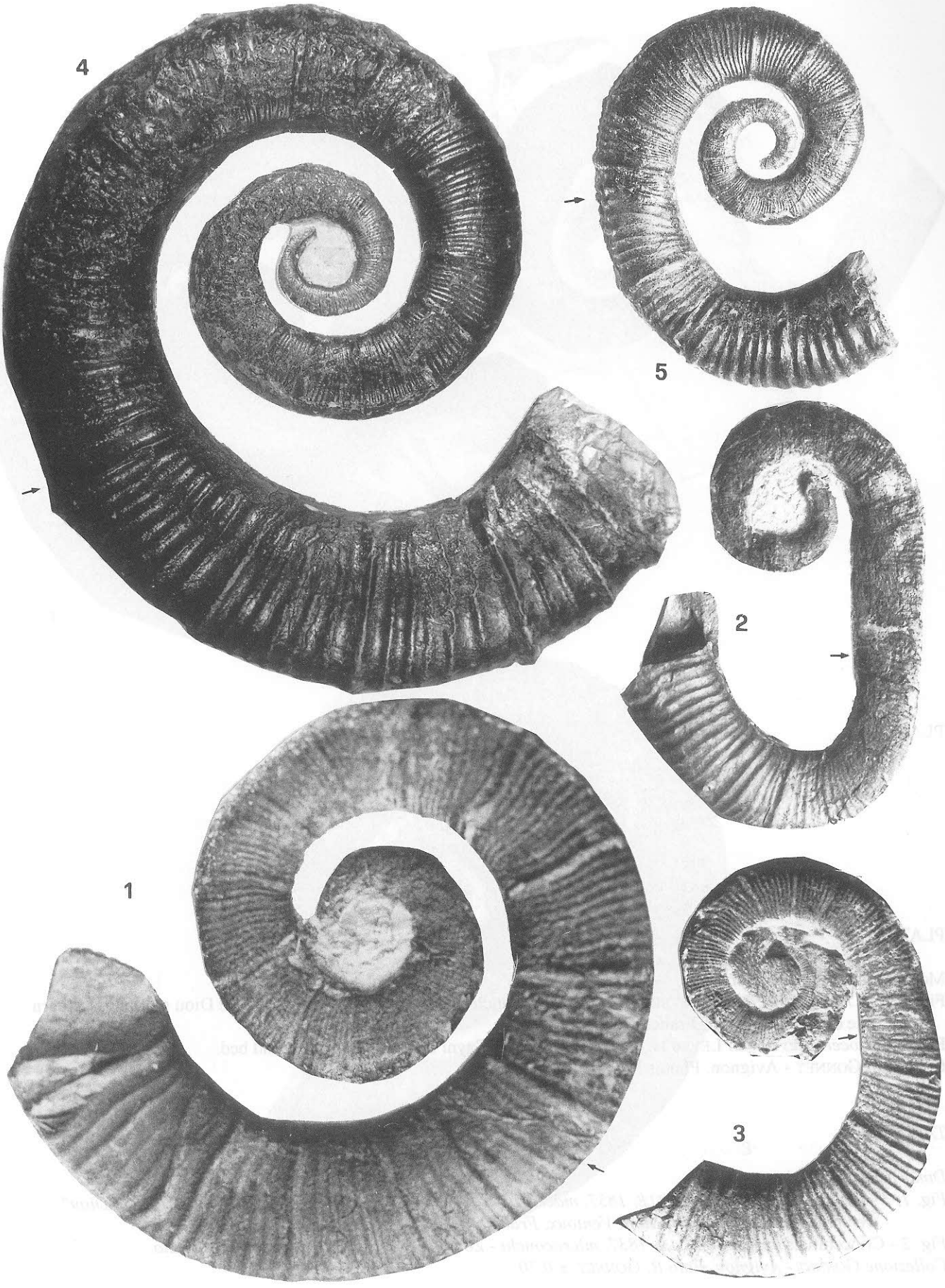
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PLATE 4

Morpho-dimensional dimorphism.
Fig. 1, 3 - *Crioceratites duvali* LÉVEILLÉ, 1837, macroconch - Sayni Zone, Ravin du Cave de Diou section (Northern side of Mont-Ventoux, France), bed 95.
Fig. 2 - *Crioceratites duvali* LÉVEILLÉ, 1837 microconch - Sayni Zone, same section and bed.
Collection GONNET - Avignon. Photos R. GONNET, x 0,70

TAVOLA 4

Dimorfismo morfo-dimensionale.
Fig. 1, 3 - Crioceratites duvali *LÉVEILLÉ, 1837, macroconchi - Zona a Sayni, sezione di "Ravin du Cave de Diou" (versante settentrionale del Mont-Ventoux, Francia), strato 95.*
Fig. 2 - Crioceratites duvali *LÉVEILLÉ, 1837, microconchi - Zona a Sayni, stessa sezione, stesso strato.*
Collezione GONNET - Avignon. Foto R. GONNET, x 0,70


1
2
3

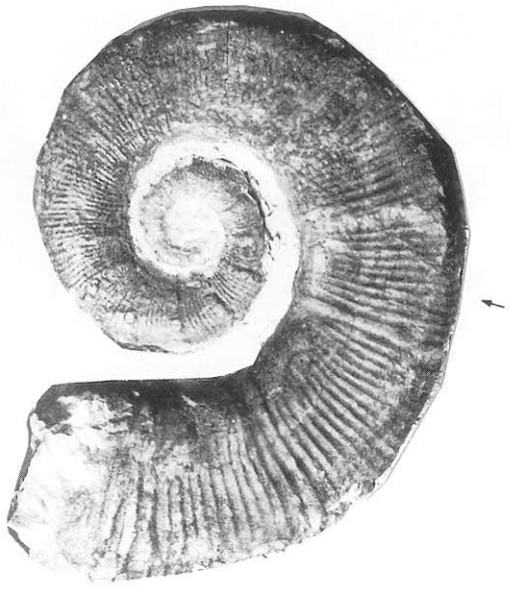
PLATE 5

Morpho-dimensional dimorphism
Fig. 1, 2 - *Crioceratites shibaniae* SARKAR, 1955, macroconchs - Sayni Zone, Ravin du Cave de Diou section (Northern side of Mont-Ventoux, France), bed 92.
Fig. 3, 4 - *Crioceratites shibaniae* SARKAR, 1955, microconchs - Sayni Zone, same section and bed.
Collection GONNET - Avignon. Photos R. GONNET, x 1

TAVOLA 5

Dimorfismo morfo-dimensionale.
Fig. 1, 2 - Crioceratites shibaniae *SARKAR, 1955, macroconchi - Zona a Sayni Zone, sezione di "Ravin du Cave de Diou" (versante settentrionale del Mont-Ventoux, Francia), strato 92.*
Fig. 3, 4 - Crioceratites shibaniae *SARKAR, 1955, microconchi - Zona a Sayni, stessa sezione, stesso strato.*
Collezione GONNET - Avignon. Foto R. GONNET, x 1

1



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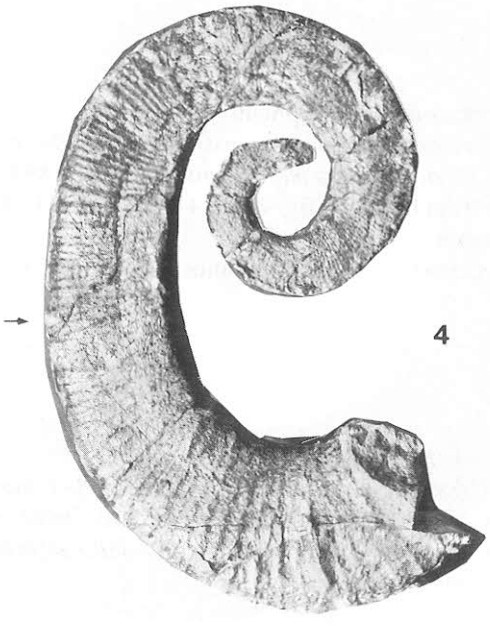

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PLATE 6

Morpho-dimensional dimorphism.
Fig. 1, 2 - *Crioceratites majoricensis* NOLAN, 1894, macroconch - Balearis Zone.
Fig. 3, 4, 5 - *Crioceratites majoricensis* NOLAN, 1894, microconchs - Balearis Zone.
Fig. 1, 3, 5 from bed 110; fig. 2 and 4 from bed 111, Ravin du Cave de Diou section (Northern side of Mont-Ventoux, France).
Collection GONNET - Avignon. Photos R. GONNET, x 1

TAVOLA 6

Dimorfismo morfo-dimensionale.
Fig. 1, 2 - Crioceratites majoricensis *NOLAN, 1894, macroconchi - Zona a Balearis.*
Fig. 3, 4, 5 - Crioceratites majoricensis *NOLAN, 1894, microconchi - Zona a Balearis.*
Fig. 1, 3, 5 strato 110, fig. 2, 4 strato 111 della sezione di "Ravin du Cave de Diou" (versante settentrionale del Mont-Ventoux, Francia).
Collection GONNET - Avignon. Foto R. GONNET, x 1

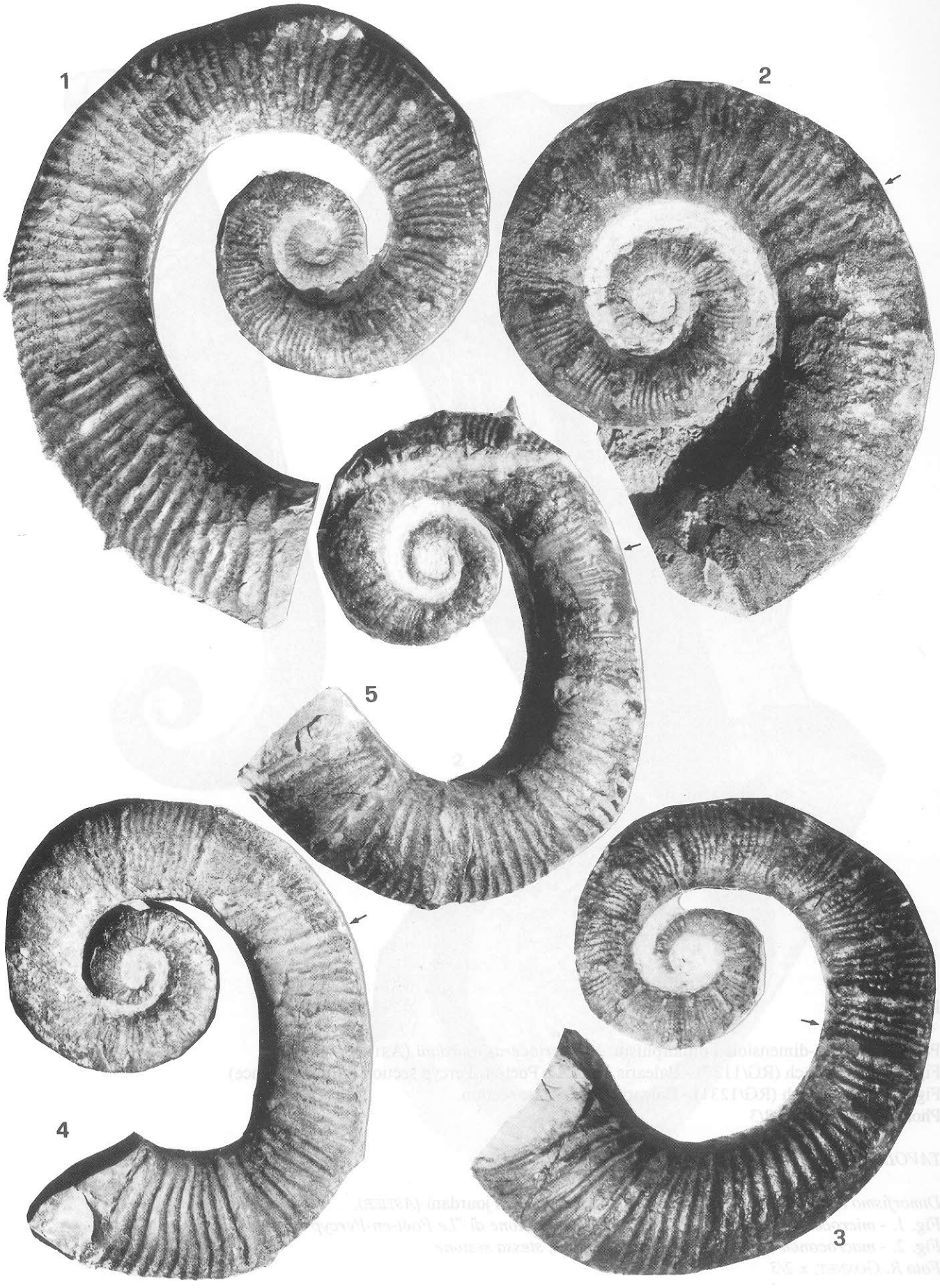
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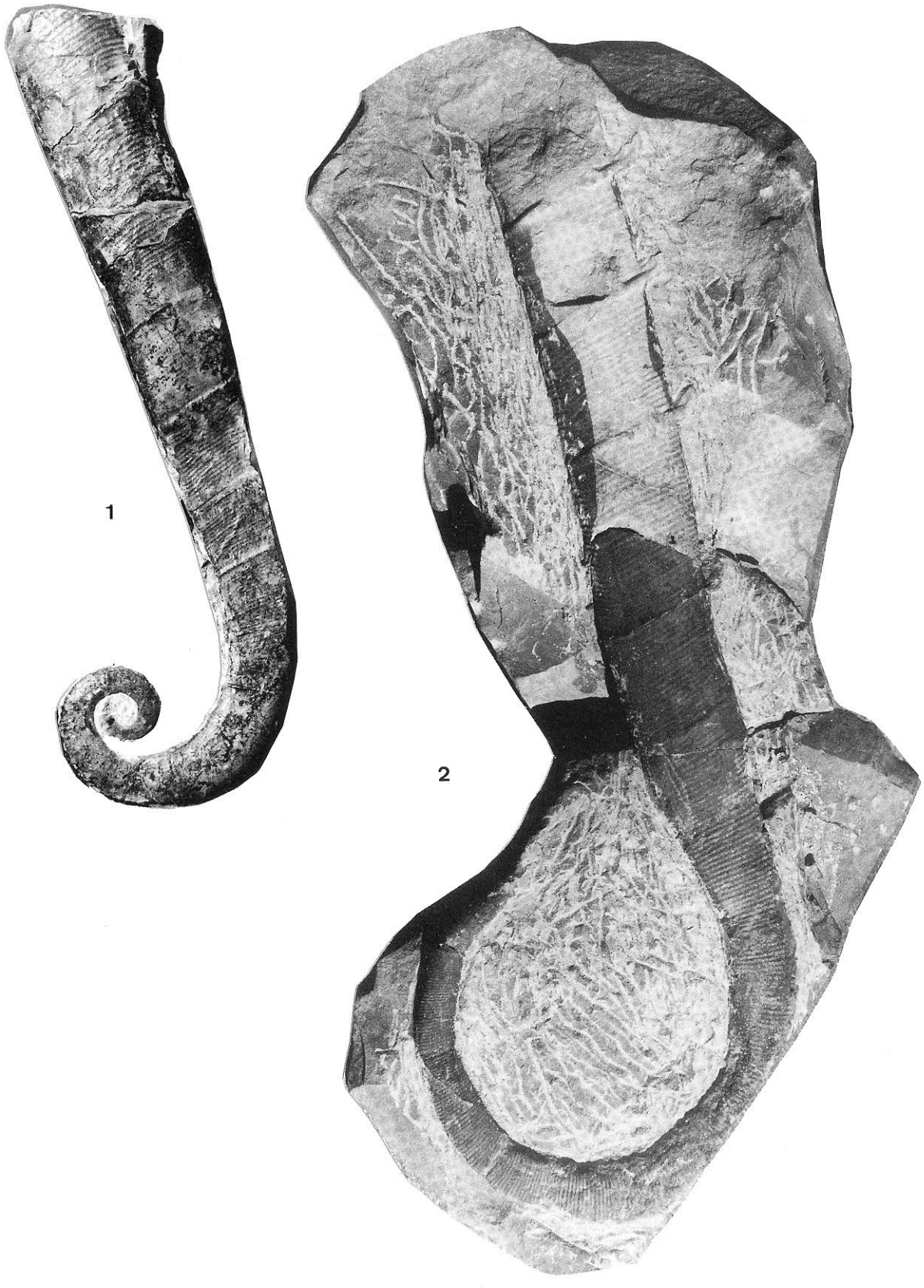
PLATE 7

Possible morpho-dimensional dimorphism: *Megacrioceras jourdani* (ASTIER).
Fig. 1. - microconch (RG/1127) - Balearis Zone, Le Poët-en-Percyp section (Drôme, France).
Fig. 2. - macroconch (RG/1231) - Balearis Zone, same section.
Photos R. GONNET, x 2/3

TAVOLA 7

Dimorfismo morfo-dimensionale presunto: Megacrioceras jourdani *(ASTIER).*
Fig. 1. - microconco (RG/1127) - Zona a Balearis, sezione di "Le Poët-en-Percyp" (Drôme, Francia).
Fig. 2. - macroconch (RG/1231) - Zona a Balearis, stessa sezione.
Foto R. GONNET, x 2/3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