La publication de cette note a subi un long retard, puisque le premier manuscript a été déposé en 1990.

Durant ce temps, de notables modifications ont été apportées à la biozonation du Barrémien. Ainsi, la position stratigraphique du taxon *Emericiceras sp. nov.?* est actuellement : zone à Sartousiana, niveau à Limentinus.

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The publication of this paper has been suffered a long delay, the first manuscript being submitted in 1990.

During this time, some modifications have been effected in the biozonation of the Barremian. So, the stratigraphic position of *Emericiceras sp. nov.?* is actually : *Heinzia sartousiana* Zone, level with *Camereiceras limentinus*.

G. Delanoy
On the Genus *Spinocrioceras*, KEMPER, 1973
(Ammonoidea, Ancyloceratina)

GÉRARD DELANOY & PATRICK FÉRAUD

Ancyloceratidae (Spinocrioceras, Emericiceras), Barremian, stratotype, shell, biometry, ornamentation, biologic evolution, biogeography, Tethys, boreal zone

French Alps (Angles, Vergons), Alpes de Haute Provence, Northwest German Lowlands (Gehrden), Lower Saxony, Caucasus

TK 25: Nr. 3623

Abstract: Bed-by-bed collecting of specimens in some sections in the stratotype area of the Barremian in the southeastern part of France has yielded a small population of *Spinocrioceras polyspinosum* KEMPER, 1973. This taxon was previously known only from the holotype material from the Lower Saxony Basin of northwestern Germany. This study sheds new light on this poorly known species present in the *Hemihoplites feraudianus* Zone in southeast France.

An original form of *Emericiceras* is described; it may represent an ancestor of the genus *Spinocrioceras*. In this case, considering the different stratigraphic occurrences of this taxon, *Spinocrioceras* may represent a Tethyan genus that migrated to northwest Europe. The problems of stratigraphic correlation and migration are discussed at the end of this study.

[Über die Gattung *Spinocrioceras* KEMPER, 1973 (Ammonoidea, Ancyloceratina)]


Diese Untersuchung wirft ein neues Licht auf diese wenig bekannte Art, die in der *Hemihoplites feraudianus*-Zone in Südost-Frankreich vorkommt.

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Es wird ein Exemplar von Emericiceras beschrieben, das zu den Vorfahren der Gattung Spinocrioceras gehören könnte. Wäre dies der Fall, und zieht man außerdem die verschiedenen stratigraphischen Vorkommen dieses Taxons in Betracht, würde Spinocrioceras eine Tethys-Gattung repräsentieren, die bis in den Nordwesten Europas migrierte.

Die Probleme stratigraphischer Korrelation und der Migrationen werden am Ende dieser Untersuchung diskutiert.

[O p o n e Spinocrioceras Kemper, 1973 Ammonoidea, Ancyloceratina]

Резюме: В результате последнего опробования некоторых разрезов в области стратотипа баррема (Юго-Восточная Франция) была получена небольшая популяция Spinocrioceras polyspinosum Kemper. Ранее этот таксон был известен только в стратотипе Северо-Западной Германии (Нижнеасиасский бассейн).

Данное исследование проливает новый свет на этот слабо известный вид, который встречается в зоне Hemihopliites feraudanus в Юго-Восточной Франции.

Описан экземпляр Emericiceras, который возможно, относится ко предкам рода Spinocrioceras. Если это справедливо, то, принимая во внимание различные стратиграфические местонахождения этого таксона, Spinocrioceras представлял собой тетисский род, мигрировавший вплоть до северо-запада Европы.

В заключение обсуждаются проблемы стратиграфической корреляции и миграций.

Contents

1 Introduction ........................................ 202
2 Paleontological Study .................................... 203
3 The Problems of Correlation and Migration ............ 210
4 References ............................................. 212

1 Introduction

In 1973, Kemper described a new species of ammonite with a very peculiar ornamentation; this species became the type species of a new genus: Spinocrioceras polyspinosum. The creation of this new taxon was based on a single specimen collected in a clay pit near Gehrden, a village between Hannover and the Deister hills in northern Germany. Another specimen, more fragmentary, was also attributed without certainty to this new genus. The author gave an upper Barremian age to these ammonites: Lower Parancyloceras bidentatum Zone.

No other specimen has been described or figured since Kemper's paper, and Spinocrioceras appeared to be only a subboreal genus. In recent years, bed-by-bed collection of specimens in the Barremian stratotype area in southeastern France (Fig. 1) has yielded a small population of Spinocrioceras in a level at which Hemihopliites feraudanus (O'K.) occurs. In spite of some differences, this population can be identified as Spinocrioceras polyspinosum Kemper.

2 Paleontological Study

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1960
Super Family Ancylocerataceae Gill, 1871
Family Ancyloceratidae Gill, 1871
Genus Spinocrioceras Kemper, 1973

Type species: Spinocrioceras polyspinosum Kemper, 1973, p. 47, pl. 1, figs. 2a–b

Diagnosis: Medium-sized ammonites with a very evolute coiling. The whorls overlap slightly. The whorl section is more or less square; the venter is broad and flattened. After a short bituberculate stage, the ornamentation is very regular, composed of simple, prominent, thick, trituberculate ribs which cross the venter without interruption. There are no secondary ribs except in very rare cases. The suture line is of ancyloceratic type with relatively simple elements.
Spinocrioceras polyspinosum Kemper, 1973

(Plate 1, figs. 1 & 2; Plate 2; Plate 3, figs. 2 & 3; Plate 4; Plate 5, figs. 1 & 2; Text figs. 2b-e)

1970 - Emericiceras(?) sp. Kupisch, p. 71, pl. IX, figs. 3a-b
1973 - Spinocrioceras polyspinosum n. gen. & n. sp. Kemper, p. 47, pl. 1, figs. 2a-b
1973 - Spinocrioceras(?) sp. Kemper, p. 49, pl. 1, figs. 8a-b

Holotype (monotypic): The specimen described and figured by Kemper (1973, pl. 1, figs. 2a-b) (NLFB type catalog, No. Kb 11) is from the upper Barremian at Gehren (Lower Paramyloceras bidentatum Zone).

Studied material: Cast of the holotype (kbll, NLFB catalog) and specimen no. 27871, Delanoy Collection, upper Barremian, St. Laurent de l'Escarene, near Nice (Alpes Maritimes); no. 28516, Delanoy Collection, upper Barremian, Hemihoplites feraudianus Zone, La Baume, near Castellane (Alpes de Haute Provence); nos. 28616 and 28617, Delanoy Collection, upper Barremian, Hemihoplites feraudianus Zone, Vergons (Alpes de Haute Provence); no. 28618, Delanoy Collection, upper Barremian, Hemihoplites feraudianus Zone, Barrême (Alpes de Haute Provence); nos. 28619 and 28620, Delanoy Collection, upper Barremian, Hemihoplites feraudianus Zone, Vergons (Alpes de Haute Provence); nos. 28621 and 28622, Delanoy Collection, upper Barremian, Hemihoplites feraudianus Zone, Vergon (Alpes de Haute Provence); nos. 28623 and 28624, Delanoy Collection, upper Barremian, Hemihoplites feraudianus Zone, Vergons (Alpes de Haute Provence); unregistered specimen in the Nury Collection, Digne, Hemihoplites feraudianus Zone(?), Moriez (Alpes de Haute Provence).

Dimensions (in mm):

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<th>Wh/D</th>
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<td>1.01</td>
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</tbody>
</table>

D = diameter, Wh = whorl height, Wb = whorl width, U = umbilicus

* Casts of these specimens are in Delanoy's collection (Centre d'Études Méditerranéens, Museum d'Histoire Naturelle) under nos. 28673 and 28680, respectively.

Description: Medium-sized ammonite, probably adult, about 250 mm in diameter, very evolute (U/D = 0.47-0.52), the whorls overlap slightly. The ornamentation of the more internal whorls of the shell, observed from 2 to 2.5 mm (holotype and specimen no. 28616), is composed of indistinct bituberculate ribs with a round umbilical tubercle and a marginal tubercle extended radially. In later whorls, the umbilical tubercle is observed to migrate ventrally to the middle of the whorl side. This migration is followed by the appearance of a third tubercle in the periumbilical area (Wh about 6 mm). The ribs become thicker and broaden out into a wedge between the lateral and marginal tubercles. The latter is always longer than the others, but it also becomes broad and flattened, sometimes the middle part is marked by a small radial furrow. Very rarely it is possible to observe a discrete inermous intercalary rib. Afterwards, the ornamentation rapidly assumes a regular appearance over the entire shell (phragmocone and body chamber). This regular appearance results from simple, thick, prominent, straight, more or less rursiradiate ribs separated by intercostal spaces of the same width. At the convex umbilical wall, these ribs begin develop into the first angular, sharp-pointed tubercle. A second tubercle with the same appearance is present in the middle

Fig. 2: a = whorl section of Emericiceras sp. nov.? no. PF29, X1
b, c, d, e = whorl sections of Spinocrioceras polyspinosum Kemper, 1973; b = no. 28621,
c = unpublished specimen from Nury Coll., d = no. 28621; e = no. PF30, X1.
of the whorl side. Beginning at this tubercle, the ribs broaden into a wedge up to the claviform marginal tubercle. On the older specimens, this tubercle changes into a large, angular tuberculiform swelling. All of the ribs pass through the very wide, flattened, convex ventral region without becoming lower and thinner. In most of the collected specimens, the whorl section shows a considerable change in size during ontogenic development. The whorl section is approximately square and nearly as high as it is broad, up to a shell diameter of 50 mm. The width then becomes greater than the height, and the last whorls on the large specimens have a very distinct depressed section (Figs. 2b, d–e). Nevertheless, this could be somewhat variable, as indicated by the unpublished specimen from Nury’s collection, which show a very depressed whorl section at a shell diameter of 61.5 mm (microconch?).

Discussion: The population collected in the southeastern part of France shows a certain uniformity in its ornamentation. It differs, however, from the holotype in that it shows more prominent ornamentation at all growth stages. Generally speaking, the ribs are thicker and more prominent than those of the holotype, and they are rursiradiate. The tubercles are larger, even in the juvenile stage.

The specimen from Kouthais in the Caucasus mountains of Georgia interpreted by Kotetichvili (1970: 71, pl. IX, figs. 3a–b), like Emericiceras? sp., presents all the ornamental characteristics of Spinocrioceras polyspinosum Kemper (prominent, regularly spaced trituruberculate ribs, lack of intercalary ribs, very broad ventral region), and we consider it as an authentic member of this taxon.

The differences between the holotype and the specimens presented here do not seem to exceed the limits of intraspecies variability. These differences are perhaps heightened by spatial and temporal displacement of the populations, perhaps also by a slight post-mortem compression of the holotype.

Procheloniceras amadei (Uhlig 1883), of which we have seen a cast of the holotype figured by Vasicek (1979), shows interesting ornamental and sutural similarities to S. polyspinosum. The bituberculate ribs of P. amadei (Uhlig) are the main difference between the two. It would be of interest to know whether the similarities are due simply to homomophy or to phyletic relationships, leading eventually to modification of the generic attributes.

Geographic and stratigraphic occurrences: Spinocrioceras polyspinosum Kemper, 1973, is an upper Barremian species identified in the Hemihoplites feraudianus Zone in the southeastern part of France, in the Imerites giraudii Zone in the Caucasus (Georgia), and in the lower part of the Paracyloceras bidensatum Zone in the Lower Saxony Basin of northern Germany.

Genus Emericiceras Sarkar, 1954

Type-species: Crioceratites emerici Leveille, 1837 (p. 314, pl. 23, figs. 1a–b)

Emericiceras sp. nov.? (pl. 3, fig. 1; text fig. 2a)

Sutuded material: Specimen no. PF29, Collection Féraud, upper Barremian, Emericiceras barremensis Zone, Vergons (Alpes de Haute Provence).

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Dimensions (in mm):

<table>
<thead>
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<th>Wh/D</th>
<th>U</th>
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</table>

* A cast of specimen PF29 is in DELANOY’s collection (Centre d’Etudes Méditerranéennes, Museum d’Histoire Naturelle) under no. 28674.

** number of disjunction hiatuses

Description: Small ammonite with crioceratitic coiling, the small uncoiled whorls increasing slowly in height, noteworthy owing to the presence of two successive stages of prominent and contrasting ornaments. The phragmocone is initially ornamented with bituberculate ribs, the ventral tubercle being wider than the dorsal one. In later whorls, the trituruberculate primary ribs appear very quickly (H = 3.5 mm), increasing in strength during growth. On the umbilical border, these ribs form a rounded tubercle, from which they widen out to a second, lateral tubercle on the third of the whorl side nearest the venter. The ribs continue widening up to the shoulder of the ventral region, where they form a third, broad tubercle elongated in the direction of coiling. This third tubercle is very large in the last stage of development of the phragmocone. This ribs cross the venter with moderate relief. In addition, the marginal ventral tubercles join the dorsal region of the next whorl. Between these primary ribs there are one to three simple intercalated ribs; these ribs do not appear to be present under a whorl height of about 3.5 mm in the initial stage of shell development.

A rapid change is observed in the ornamentation on the body chamber: The intercalary ribs disappear; the trituruberculate ribs are closer, and the thickness of the ribs and the strength of the tubercles gradually become more regular. Thus, at the beginning of the chamber, the ribs are still wedge-shaped, broader than high, and the prominence of the lateral tubercle is the same as that of the periumbilical tubercle; but at the end of the body chamber, the ribs are more prominent, and nearly as wide as they are high (the width is increased by the periumbilical tubercle). The ribs then cross the venter without losing their strength and the marginal tubercles correspond to clavi that are not as prominent and large as those on the phragmocone and at the beginning of the body chamber.

The pre-peristomial area is missing and the suture line is not usable.

The restored whorl section also shows some evolution; It is practically circular on the phragmocone, whereas on the body chamber it is elliptic, higher than wide (Fig. 2a).

Stratigraphic occurrence: This remarkable ammonite specimen was collected near Vergons (Alpes de Haute Provence) in the upper Barremian Emericiceras barremensis Zone, several meters below the Hemihoplites feraudianus Zone.

Discussion: The ornamentation of this specimen differs from all known members of the genus Emericiceras and it could perhaps be a new species. However, this specimen is not unique enough for us to create a new species.
The ribbing and the tubercles of the phragmocone (wedge-shaped ribs, marginal triangular tubercles) show that this form is a descendant of the *Emericiceras barremense-alpimum* group. On the other hand, the original characteristics that appear at the end of the phragmocone are particularly interesting, as they remind us of the ornamentation of *Spinocrioceras polyspinosum* Kemper (simple, prominent ribs with angular umbilical and lateral tubercles and claviform marginal tubercles).

On the Genus *Spinocrioceras* Kemper, 1973 (Ammonoidea, Ancyloceratina)

Thus we see in this *Emericiceras* a possible ancestor of *Spinocrioceras*; the transition between these two genera could be considered in terms of heterochrony (Dommergues et al. 1986; Marchand & Dommergues 1988). The *Spinocrioceras*-like ornaments present on the body chamber of *Emericiceras* sp. nov.? spread to practically the entire shell of *S. polyspinosum* in an evolutionary process similar to accelerated hypermorphosis (peramorphosis) (see discussion by McNamara 1986). The bituberculate stage of the first whorls of *Emericiceras* sp. nov. is present in *S. polyspinosum* only in the most internal whorls.

The passage between these two taxa could be associated with a major restructuring of the shell. The early appearance of the *Spinocrioceras* morphology at the expense of the large bituberculate *Emericiceras* stage could have been accompanied by complete recoiling of the shell (except probably of the first whorl) with displacement of the marginal ventral tubercle towards the more external part of the ventral region.

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**Fig. 3:** Possible phylogenetic relationship between *Emericiceras* sp. nov.? and *Spinocrioceras polyspinosum*; the evolution of the former to the latter could result from accelerated hypermorphosis. Intermediary forms are not known at present, however.

1 = bituberculate stage, 2 = trituberculate *Emericiceras*-like stage,
3 = trituberculate *Spinocrioceras*-like stage, 4 = uncoiled stage, 5 = coiled stage

The scale refers to the photograph of the ammonite.

The bar graphs indicate whorl height for the different stages of growth.

**Fig. 4:** Distribution of *Spinocrioceras polyspinosum* Kemper, 1973, during the Barremian (after Barron 1986 and Tyson & Funnel 1986); grey = land areas at that time.
3 The Problems of Correlation and Migration

All of the specimens we collected in the southeastern part of France come from the Hemihoplites feraudianus Zone - more precisely, from the beds containing this index species. The holotype of Spinocrioceras polyosinum KEMPER, collected in an abandoned clay pit near Gehrdten, must have been taken from the lower part of the Paracyloceras bidetatum Zone, even if the true level which it was collected is not known with precision (KEMPER 1990, pers. comm.). It is tempting to correlate the Hemihoplites feraudianus Zone with the Paracyloceras bidetatum Zone of the boreal realm, but this would certainly be an oversimplification. Moreover, the fragmentary specimen from Kouthais figured by KOTETCHOVLI (1970) was collected from the Immites giraudi Zone, which suggests spatial and temporal displacement of the species. If this is so, then it migrated somewhat later into the Lower Saxony Basin.

The boundaries of these zones might also be redefined on the basis of the presence of the boreal ammonites Paracrucoceras denckmanni (KOENEN) and P. stadlaenderi (KOENEN) in the upper Barremian in the Caucasus. KARABADZE (1983) has correlated the Paracrucoceras denckmanni Zone in northern Germany with the Hemihoplites souleri-Silesites seranonis Zone in the Caucasus on the basis of these ammonites. The latter zone was later correlated with the Hemihoplites feraudianus Zone (KARABADZE 1983; 1987; DELANOY 1990). It should be possible now - in view of the presence of Spinocrioceras in Georgia - to correlate the lower part of the Paracyloceras bidetatum Zone with the upper part of the Immites giraudi Zone or the base of the Colchidites gr. sarasinii Zone of southeastern France (DELANOY 1990). Such a scheme would agree with the one figured by HAQ et al. (1987).

But the presence of Spinocrioceras polyosinum KEMPER in the Lower Saxony Basin and the more southern basins of the Tethys raises an interesting problem with respect to the marine connection between the boreal realm and the Tethys realm during the late Barremian. Many studies have revealed exchanges of ammonites between these two realms during the Valanginian and the Hauterivian (RAWSON 1973; KEMPER et al. 1981; THEBULOY 1973, 1977). The main connection at that time was the Danish-Polish Furrow, which joined the Lower Saxony Basin with the Carpathian region, which itself was at the northern margin of the Tethys.

A global regression began during the upper Hauterivian, continuing throughout the Barremian. This regression was partly responsible for the closing of the south end of the Danish-Polish Furrow (RAWSON 1973; RACZINSKA 1979; KEMPER et al. 1981; MAREK 1989; MICHALIK & VASICEK 1989), preventing any direct connection between northwest Europe and the Tethys. This limits the possibilities for migration of S. polyosinum from the Tethys to the Lower Saxony Basin.

MUTTERLOSE & HARDING (1987) in a study of the paleontological contents of the Blätterton horizons point out the episodic presence of flora and fauna of Tethys origin in the lower Barremian in northern Germany. They found Tethyan elements among cephalopods (Hibolites jaculoides SWÄTANSON), foraminifers, nanoplankton, and dinocysts (Rhyncho-

On the Genus Spinocrioceras, KEMPER, 1973 (Ammonoidea, Ancyloceratina) 211

niopsis fimбриata (DUXBURY) SARGENT, a common form in the Barremian and Aptian deposits of the Angles section) in the Hauptblätterton of the Oxytethus sp. Zone (upper Barremian). No Tethyan components were found in the Blätterton horizons of the upper Barremian in the Oxytethus brunswicensis, O. germanica, and O. depressa Zones. The episodic presence of Tethyan organisms in the Barremian of northern Germany (IMMEL & MUTTERLOSE 1980; MUTTERLOSE & HARDING 1987; MUTTERLOSE 1990; DELANOY & FERUAID, this paper) and of boreal ammonites in some parts of the Tethys (MOORE: ROCH 1930; CAUCASUS: KARABADZE 1981, 1983) seems to prove the existence of connections between the two realms.

There are three possible hypotheses:

1. A seaway to the east via the North Sea, the Norwegian Sea, and the arm of the sea connecting the Petchora region (in the eastern part of the Baltic Shield) with the Caucasian seas through the Moscow Basin and the Lower Volga region (RAWSON 1983). This hypothesis is supported by the presence of the genus Spinocrioceras (KARABADZE 1981, 1983) in the boreal heteromorphs Paracrucoceras stadlaenderi (KOENEN) and P. denckmanni (KOENEN) (a form already noted in Morocco by ROCH in 1930) in the Hemihoplites souleri-Silesites seranonis Zone.

2. A seaway to the west via the North Atlantic, northern Scotland, and the North Sea. This hypothesis was proposed by IMMEL & MUTTERLOSE (1980) on the basis of the presence in Morocco of boreal Barremian Crioceratidae elegans (KOENEN) and C. roerveri (KOENEN) (ROCH 1930).

3. A more direct connection would have sporadically joined the Caucasian basins with the Lower Saxony Basin via Poland. Direct evidence (sediments of late Barremian-Aptian age) is lacking in the key region around Lublin according to the paleogeographical reconstructions presented by RAWSON (1983), RACZINSKA (1979), KEMPER et al. (1981), MAREK (1989), and MICHALIK & VASICEK (1989). KEMPER in this vol., however, supports the idea of a seaway in the area of Lublin because the Aptian ammonite associations on the Isle of Wight, in northwestern Germany, and in the Caucasus are identical, and hence a long-distance connection seems unlikely. He considers such faunal similarities to be more important than the accidental preservation of sediments. It is of interest to note that these faunal exchanges occurred during the time of the Tethyan Hemihoplites feraudianus Zone, which is characterized by a relatively major transgression (HAQ et al. 1987), reaching a maximum during the time of the Immites giraudi Zone (equivalent in part to the Heteroceras astieri Zone of HAQ et al. 1987).

Acknowledgements: We wish to particularly thank E. KEMPER (Hannover) for the interest he has taken in this work and for his support. Thanks are also due E. ALZIAR (Nice) for the translation of several German text and J. DEAY (Nice) for her help in preparing the figures and photographs, provided by G. THIEMEL (Nice). We are particularly indebted to G. SCHAER (Munich) who furnished us with a cast of the holotype of Procheloniceras amadei (UdLC), and to Y. NUTR, who provided a sample from his collection.
4 References


Plate I

Fig. 1: Cast of the holotype, NLfB Type Catalog No. kb11, Upper Barremian (Lower Paracyloceras bidentatum Zone), Gehden near Hannover, Germany; x1.

Fig. 2: No. 28621, Delany Coll., Upper Barremian (Hemihoplites feraudianus Zone), Angles, Alpes de Haute Provence, France; x1.
Plate 2

(a) No. 28616, Delany Coll., Upp Barremian (Hemihoplites feraudianus Zone),
Vergons, Alpes de Haute Provence, France;
(b) Hemihoplites feraudianus (d’Orbigny, 1841); x1.
Plate 3

Fig. 1: *Emericeras* sp. nov.? - No. PF29, FÉRAUD Coll., Upper Barremian (Upper *Emericeras barremense* Zone), Vergons, Alpes de Haute Provence, France; x1.

Fig. 2: *Spinocrioceras polyspinosum* Kemper, 1973. - No. 28619, DELANOV Coll. Upper Barremian (*Hemihoplites feraudianus* Zone, Bergons, Alpes de Haute Provence, France; x1.

Fig. 3: *Spinocrioceras polyspinosum* Kemper, 1973. - Unregistered specimen, Nury Coll., Upper Barremian (*Hemihoplites feraudianus* Zone?), Moriez, Alpes de Haute Provence, France (?microconch); x1.
Plate 4

No. PF30, Féraud Coll., Upper Barremian (Hemikoptites feraudianus Zone?), Vergons, Alpes de Haute Provence, France; x1.
Plate 5

Fig. 1: *Spinocrioceras polyspinosum* Kemper, 1973.
No. 27871, Delanoy Coll., Upper Barremian (condensed level),
St. Laurent de l'Escarène near Nice, Alpes Maritimes, France; x0.66.

Fig. 2: *Spinocrioceras polyspinosum* Kemper, 1973.
No. 28516, Delanoy Coll., Upper Barremian (*Hemihoplites feraudianus* Zone),
La Baume near Castellane, Alpes de Haute Provence, France; x1.