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Genus *Pseudothurmannia* Spath, 1923 and related subgenera *Crioceratites* (*Balearites*) Sarkar, 1954 and *C.* (*Binelliceras*) Sarkar, 1977 (Lower Cretaceous Ammonoidea)

Philip HOEDEMAEKER[1]

Abstract

In order to avoid confusion and to keep stability in zoological nomenclature, article 70.3.2 of the fourth edition of the ICZN permits palaeontologists to choose as type species of *Pseudothurmannia* the specimen that was designated, but misidentified, by Spath (1923) as *Pseudothurmannia angulicostata* d'Orbigny, and that was renamed *Pseudothurmannia picteti* by Sarkar. A systematic overview is given of genus *Pseudothurmannia* Spath, which is characterized by having two ventrolateral rows of small uniform clavi without fibulation, by having (at least their inner) whorls in contact, and by the absence of lateral tubercles on the inner whorls. *Ammonites angulicostatus* d'Orbigny, 1841, which according to earlier editions of the International Code of Zoological Nomenclature should have been the type species of *Pseudothurmannia*, cannot be considered congeneric with the latter genus, and is here considered to belong to genus *Crioceratites*, because of the crioconic whorls, the presence of trituberculate main ribs in early growth stages, and the frequent fibulation with the ventrolateral tubercles. These features do not occur in *Pseudothurmannia.*

In this paper the genus *Pseudothurmannia* (16 species) is subdivided into three subgenera. *Pseudothurmannia* (*Pseudothurmannia*) Spath, 1923, type species *Pseudothurmannia picteti* Sarkar, 1955, *Pseudothurmannia* (*Parathurmannia*) Busnardo, 2003, type species *Pseudothurmannia sarasini* Sarkar, 1955, and *Pseudothurmannia* (*Kakabadziella*) subgen. nov., type species *Ammonites Mortilleti* Pictet & de Loriol, 1858. *Pseudothurmannia* (*Pseudothurmannia*) *picteti* exhibits lateral nodes on the main ribs of the adult whorls, which implies that the group of species with trituberculate ribs in late ontogenetic stages constitutes the typical group of *Pseudothurmannia*, instead of a separate generic group, as it has been regarded over the last 40 years (*Sornayites* Wiedmann, 1962, or *Prieuriceras* Vermeulen, 2004). All the ammonites described here form part of the collection of the Naturalis Biodiversity Center in Leiden, The Netherlands.

The following nine new species and subspecies are described in the present article: *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata*, *P.* (*P.*) *perevoluta*, *Pseudothurmannia* (*Parathurmannia*) *dissiticostata*, *Pseudothurmannia* (*Kakabadziella*) *caravacaensis*, *P.* (*K.*) *ohmi valbonnettensis*, *P.* (*K.*) *tornajensis*, *Crioceratites* (*Balearites*) *oicasensis*, *C.* (*B.*) *theodomirensis*, and *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.

The phylogeny, the stratigraphic ranges and the biostratigraphy of the species of *Pseudothurmannia* and related subgenera *Crioceratites* (*Balearites*) (four species) and *Crioceratites (Binelliceras)* (seven species) are elaborately discussed, and in addition the age of the Faraoni Level, which is situated within the *Pseudothurmannia* beds.

Keywords

Ammonites, *Pseudothurmannia*, *Balearites*, *Binelliceras*, phylogeny, systematics, biostratigraphy, Faraoni Level.

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[1] *Naturalis Biodiversity Center, Postbox 9517, 2300A Leiden, The Netherlands. E-mail: flip.hoedemaeker@naturalis.nl*

1. INTRODUCTION

A systematic overview, the phylogeny and the biostratigraphy of the species of *Pseudothurmannia* Spath, 1923, are given; also the systematics, phylogeny and biostratigraphy of related generic groups *Balearites* Sarkar, 1954, and *Binelliceras* Sarkar, 1977, are discussed. The latter two groups have some morphological characteristics in common with *Pseudothurmannia*, viz. rows of small ventrolateral tubercles, the small number of intermediate ribs between every two main ribs, and the whorls being in contact or nearly in contact with each other; therefore, they have often been included in *Pseudothurmannia*, or their species have been synonymized with species of *Pseudothurmannia*.

The overview given in this monograph is necessary in view of the disagreement about the type species. Moreover, there is an apparent difficulty in identifying the various species as a result of the inadequate preservation of the holotypes, which are often juvenile specimens; therefore, there is chaos in the systematics as demonstrated by the synonymy lists. The great numbers of specimens collected by the author make it possible to follow the ontogenetic development from young to adult specimens, and to become aware of the great variability of the various species.

All the measurements are in millimetres; the numbers between brackets are percentages of the diameter; the author used the abbreviations D (diameter), Wh (whorl height), wh (whorl height at 180 degrees), U (width of the umbilicus), and Wt (whorl thickness). In the new species the letter “s” means syntype.

All the specimens described here form part of the ammonite collection of the Naturalis Biodiversity Center including the plaster casts of the types sent from other museums. All these specimens have been given museum numbers beginning with the letters RGM or GIA. These specimens originally formed part of the former State Museum of Geology and Mineralogy (RGM) and of the former Geological Institute of the University of Amsterdam (GIA), respectively, but now form part of the Naturalis collection.

The majority of the specimens described in this article were collected from outcrops of the Lower Cretaceous sedimentary rocks in Spain, viz. along the Río Argos, west of Caravaca (Province of Murcia), from the Sierra de la Muela north of Moratalla (Province of Murcia) and from the north flank of the Tornajo Mountain in the northern part of the district of Lorca (Province of Murcia). Also included are some specimens from Angles (St.-André-les-Alpes, Alpes-de-Haute-Provence, France), from the section along the road to Col de Rousset north of Chamaloc (Die, Drôme, France), from the section at the place of an old farm called Chamateuil near Castellane (Alpes-de-Haute-Provence, France), and a few specimens from other countries. Along the Río Argos the *Pseudothurmannia* beds could only be encountered in the sections A, C, D, E, F, J, K, and W. The bed numbers from sections C-K correspond to those of section A. Only section W has different numbers. Section A and W are 5 km apart (Fig. 1).

The Lower Cretaceous outcrops along the Río Argos, in the Sierra de la Muela and in the northeastern flank of the Tornajo Mountain are situated in the Betic Cordillera in southeastern Spain. Those along the Río Argos near Caravaca form part of the Subbetic Zone, more precisely in the tectonic unit of the Frontal Subbetic Zone in which the Cretaceous rocks were deposited in a rather deep water (upper bathyal) environment. The Sierra de la Muela, 20 km north of the Río Argos, forms part of the Prebetic Zone in which the Cretaceous rocks were deposited on a shallow platform. The Lower Cretaceous sedimentary rocks of the Tornajo Mountain, 18 km south of the Río Argos, were deposited in a deeper shelf (neritic) environment. The Tornajo Mountain forms a huge overturned block (2-3 km^3) of Jurassic and Cretaceous rocks transported towards the west over a great distance along the large Crevillente Fault, a large ENE-WSW directed wrench fault. The original location of the displaced Tornajo rocks during the Early Cretaceous is not yet known.

Locality codes: The various localities were given the following numbers in the explanations of the figures and plates:

1: Río Argos, (west of Caravaca, Prov. of Murcia, Spain)
1A: Section A near the Molino de Las Oicas de Abajo
1B: Section B, 400 m east of Molino de Las Oicas de Abajo
1C: Section C, 500 m east of Molino de Las Oicas de Abajo
1D: Section D, 150 m east of Molino de Las Oicas de Abajo
1E: Section E, 175 m east of Molino de Las Oicas de Abajo
1F: Section F, 275 m east of Molino de Las Oicas de Abajo
1J: Section J, 550 m east of Molino de Las Oicas de Abajo
1K: Section K, 875 m east of Molino de Las Oicas de Abajo
1W: Section W, 250 m west of Casa de Alguacil
(In section W the author also collected many ammonites from large loose blocks, which contained ammonites. The blocks were produced by making an underground irrigation pipe, and could only be derived from beds W35-46. The blocks were given the letters A-N)
2: Basal condensed bed of the Barremian Bolos Formation, 1000 m north of the Cortijo de la Tosca (north of Moratalla, Prov. of Murcia, Spain)
3: Cretaceous outcrops northeast of Tornajo Mountain (north of Lorca, Prov. of Murcia, Spain)

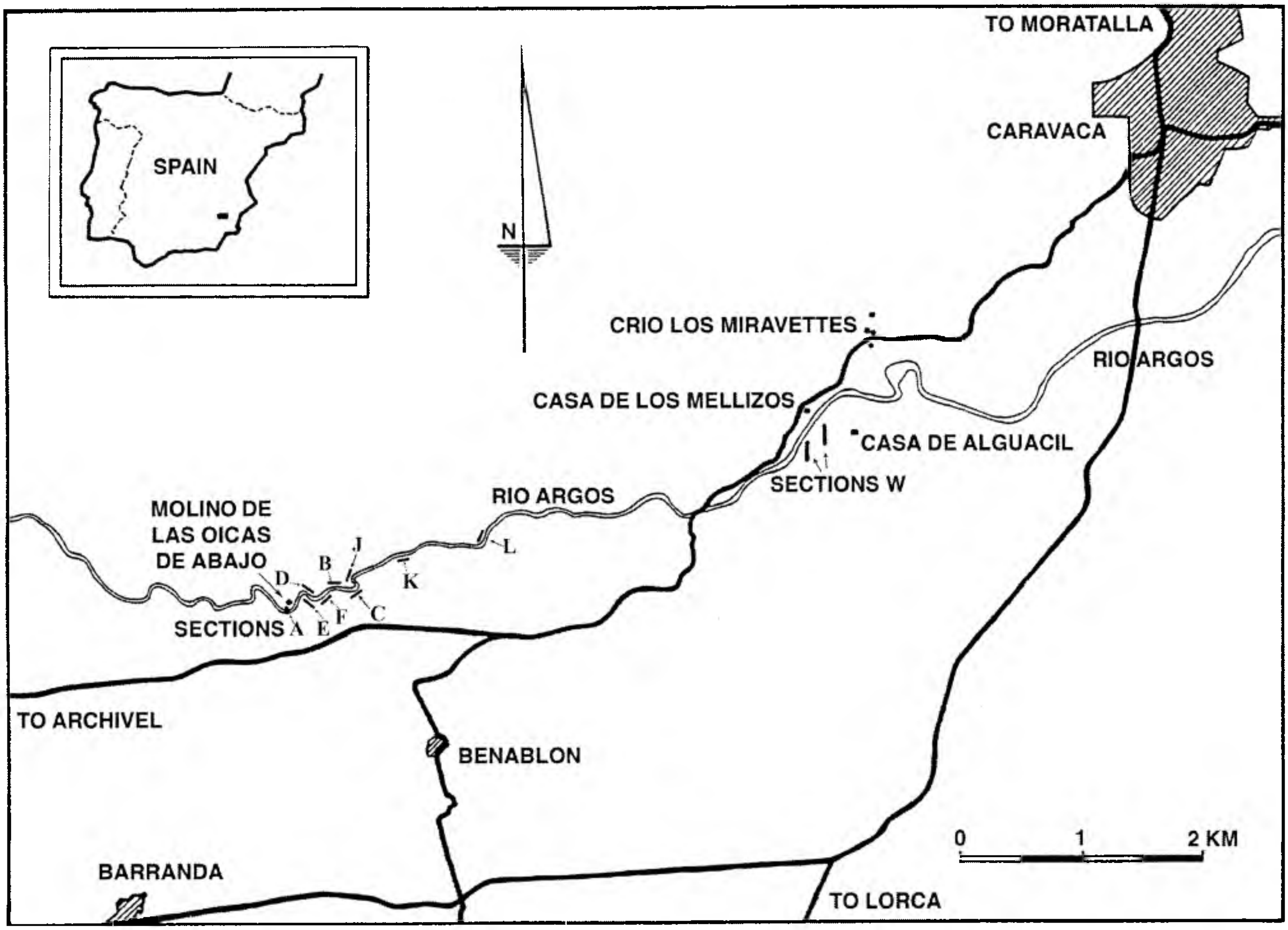


Fig. 1: Geographic distribution of the various sections in the Lower Cretaceous outcrops along the Río Argos mentioned in the text. Main coordinates of Caravaca (La Templeta) are: 1°50' 38" W – 38° 06' 17" N.

3A: Section 2A
3B: Section B
3C: Section C
3T: Section T
4: Section near Ermita de la Virgin de Los Cuadros (Bedmar, Prov. of Jaén, Spain)
5: Section along the road to Angles (St.-André-les-Alpes, Alpes-de-Haute-Provence, France)
6: Section along the road to the Col de Rousset north of Chamaloc (Die, Drôme, France)
7: Section in the locality called Chamateuil (Castellane, Alpes-de-Haute-Provence, France)
8: The Crimea, Ukraine
9: Section along the Lackbach, 25 km WSW of Unken (Salzburg, Austria)
10: Section near Aftas Imsouane, Morocco

2. TYPE SPECIES

2.1. Former type species of *Pseudothurmannia* Spath, 1923

The figure of the holotype of *Ammonites angulicostatus* in d'Orbigny's *Paléontologie française* (1841, pl. 46, figs. 3, 4) is a restoration. A specimen corresponding to the figure has never been found; the restoration, especially of the inner whorls, was therefore considered erroneous. Moreover, the holotype was lost for a long time, so that only the restored drawing was available for comparison. The holotype was recovered 20 years ago by Busnardo (Hoedemaeker & Bulot, 1990).

When Spath (1923, p. 66, footnote 1) introduced the genus *Pseudothurmannia*, he originally designated the specimen depicted by Pictet (1863) on pl. 1 bis, fig. 1a-b under the name *Ammonites angulicostatus* d'Orbigny as type species of the genus. He considered this specimen conspecific with *Ammonites angulicostatus* d'Orbigny (personal communication in Sarkar, 1955, p. 155). Spath had the custom of furnishing all his type species with a reference to a figure and he generally chose, in accordance with the recommendation of that time, the figure of the largest adult representative of the species instead of that of the first name-bearing specimen. This procedure is, unless the figured specimen is deliberately stated as a misidentification, against the rules of zoological nomenclature, which prescribe that only the nominal species could be the type species (art. 67) and, since the nominal species is based on the holotype, this holotype is implicitly also the type on which the genus is based. The nominal species is *Ammonites angulicostatus* d'Orbigny. This change of type species was at first a mere formality, because the specimen of plate 1 bis, fig. 1a, b of Pictet (1863) was considered by all authors before 1955, also by Spath, to be conspecific with d'Orbigny's specimen and a full-grown representative of the species; d'Orbigny's specimen was not regarded as full-grown. The concept of *P. angulicostata* (d'Orbigny) and the diagnosis of the genus *Pseudothurmannia* Spath, 1923, therefore remained firmly based on the generic characteristics displayed by the figure of Pictet. However, the specimen of Pictet was also inadequately depicted on pl. 1 bis, fig. 1a-b. Therefore, the genus *Pseudothurmannia* was at that time diagnosed as having compressed rectangular whorls, which are in contact or overlapping each other, and which are ornamented with flexuous main ribs, which may be provided with umbilical bullae; the main ribs are separated by a few shorter intermediate ribs, which have the same strength as the main ribs when they pass uninterruptedly over the venter; characteristic are the ventrolateral rows of fine uniform clavi. Lateral tubercles are absent. The species with lateral tubercles in the adult stage, formerly grouped within *Pseudothurmannia*, would constitute a separate genus.

Sarkar (1955, p. 155), however, recognized that the specimen of pl. 1 bis, fig. 1 of Pictet (1863) could not possibly be conspecific with *P. angulicostatus* (d'Orbigny). This is because the whorls of Pictet's specimen grow more rapidly in height, the whorl section is markedly higher, and the last whorl is thickest in the lower part of the flanks instead of the middle, which renders the whorl section rather high and subtrapzoidal than subquadratic. At the umbilical border the main ribs are provided with a pointed umbilical tubercle, and there are two rows of small ventrolateral clavi, which remain clearly visible up to the end of the last preserved whorl. Sarkar (1955) renamed the specimen of pl. 1 bis, fig. 1 of Pictet (1863) as *Pseudothurmannia picteti*.

The present author agrees with Sarkar's conclusion. The last whorl of the plaster cast of the specimen of fig. 1 (Muséum d'Histoire naturelle de Genève, Collection Pictet, No 16849), kindly sent to the author by Dr. D. Decrouez, additionally shows distinct lateral knobs at midflank on each main rib in the adult stage. The main ribs are very prominent in the lower half of the flanks, but abruptly diminish in height above the nodal swellings. Although described by Pictet (1863, p. 13) in his text, these tubercle-like knobs are not depicted on the drawing on pl. 1 bis. This renders the figure quite different from the real appearance of the specimen. These lateral nodes are absent on the penultimate whorl and on the inner whorls; these whorls only show umbilical tubercles and ventrolateral clavi. The involution is approximately one third of the penultimate whorl. This means that *Pseudothurmannia picteti* Sarkar, 1955, belongs to one of the groups of species with trituberculate ribs in the adult.

2.2. Holotype of *Ammonites angulicostatus* d'Orbigny, 1841

Because of the loss of the holotype of *A. angulicostatus* d'Orbigny, Lapeyre (1974) tried to collect specimens of *A. angulicostatus* d'Orbigny from the *locus typicus*, Chamateuil (just south of Castellane, Alpes-de-Haute-Provence), with the purpose of selecting a neotype from them. The inner whorls of most specimens found in Chamateuil are, at best, badly preserved. According to Lapeyre, this situation would cast doubts on the faithfulness of the drawing of the inner whorls of the holotype by d'Orbigny. He considered the specimens collected in Chamateuil conspecific with *A. angulicostatus* d'Orbigny, because they would have approximately the same measurements as the holotype, and the ribbing of the last whorl is similar. Nevertheless, Lapeyre noted some differences with d'Orbigny's drawing, viz. the forwardly convex passage of the ribs over the venter and the presence of two rows of weak ventrolateral clavi, which were not drawn on d'Orbigny's type. According to Lapeyre, the latter may have been hardly visible on the lost holotype and may therefore have escaped the attention of the draughtsman, Mr. J. Delarue. The neotype that he finally selected (Muséum d'Histoire Naturelle de Nice, Collection C.E.M., No 14110) is the best preserved specimen among a homogenous population of topotypes found within a few beds; it shows only half a whorl and the inner whorls are not preserved as they are in the holotype. However, with the publication of this neotype, the species *P. angulicostatus* d'Orbigny and the genus *Pseudothurmannia* Spath seemingly became firmly established, at last. Moreover, Lapeyre was, after 1955, the only author who still considered *P. picteti* Sarkar, 1955, to be conspecific with his neotype and a junior synonym of *P. angulicostata* (d'Orbigny).

However, the holotype of *Ammonites angulicostatus* d'Orbigny was recovered, and this caused much confusion. Busnardo himself freed the penultimate whorl from the surrounding rock and announced that *A. angulicostatus* has trituberculate inner whorls (pers. comm., 1990, during the meeting of the Lower Cretaceous Cephalopod Team of the IGCP-project 262 in Digne, France; Hoedemaeker & Bulot, 1990). The author obtained, through the kind intervention of Dr. L. Bulot (Université de Provence, Marseille, France), a plaster cast of the holotype with the penultimate whorl visible; and, through the kind intervention of Dr. M. Wippich also obtained a plaster cast of the holotype as it had lain before d'Orbigny when he described the species, with only less than half of the last whorl visible. It now appears that d'Orbigny's restoration of the holotype was wrong, as was already surmised for a long time. Features not visible on d'Orbigny's drawing are the following. The whorls of the holotype are just not touching each other, and the involution drawn in d'Orbigny's figure is erroneous. The last part of the penultimate whorl shows straight main ribs with prominent umbilical bullae separated by 2-3 long intermediate ribs, without umbilical bullae; the inner whorls are adorned with strong trituberculate ribs separated by 2-3 intermediate ribs. On the last whorl, a faint row of uniform ventrolateral tubercles is visible. The whorl section of the last whorl is thick, subquadrate, and the measurements published by d'Orbigny (whorl height 17 mm, whorl thickness 15 mm) are correct. This is a characteristic feature of *A. angulicostatus* d'Orbigny. The holotype of *A. angulicostatus* d'Orbigny was badly refigured by Hoedemaeker (1995b, pl. 4, fig. 5a-c) and Vermeulen (2002, pl. 57, fig. 3), but better by Busnardo (2003, pl. 29, figs. 2-3), Busnardo & Gauthier (2006, pl. 16, fig. 5a-b) and Vermeulen (2004, pl. 1, fig. 2).

2.3. *A. angulicostatus* d'Orbigny belongs to genus *Crioceratites* Léveillé, 1837

The ornamentation of the inner whorls of *Ammonites angulicostatus* d'Orbigny is totally different from the ornamentation drawn on d'Orbigny's figure, and from that of all other species currently assigned to *Pseudothurmannia*, including Lapeyre's neotype and *P. picteti* Sarkar. The combination of slightly crioconic inner whorls with prominent trituberculate main ribs is unknown in the other species of *Pseudothurmannia*, but common in *Crioceratites*. On account of this combination of characteristics, the author is of the opinion that *A. angulicostatus* d'Orbigny has to be included in the genus *Crioceratites* Léveillé, 1837, whereas the other species currently assigned to *Pseudothurmannia* should be separated from *Crioceratites* as a separate genus. Here we are dealing with a case of misinterpretation, not misidentification, of the holotype of *A. angulicostatus* d'Orbigny. The latter is not congeneric with *A. angulicostatus* Pictet, *non* d'Orbigny (= *Pseudothurmannia picteti* Sarkar, 1955), nor with Lapeyre's neotype of *P. angulicostatus* d'Orbigny [= *Pseudothurmannia ohmi* (Winkler, 1868)], nor with any other species currently assigned to *Pseudothurmannia*.

A second specimen identical to *A. angulicostatus* d'Orbigny has not yet been figured in literature. This implies that this species is rare. In 1971 to 1973, the author sampled many specimens currently assigned to *Pseudothurmannia* from Chamateuil (near Castellane, Alpes-de-Haute-Provence), with the same purpose as Lapeyre, but none of the specimens found could be considered identical to the holotype of d'Orbigny. The specimen chosen by Lapeyre as the neotype of *Pseudothurmannia angulicostata* (d'Orbigny) can now be identified as *Pseudothurmannia ohmi* (Winkler, 1868). Of all species of *Pseudothurmannia*, the appearance of the latter species approaches most closely to the erroneous drawing of *Ammonites angulicostatus* in d'Orbigny's *Paléontologie française*.

However, in the Tornajo Mountain (municipal district of Lorca, Spain) the author found a second specimen of *Crioceratites angulicostatus* d'Orbigny, which perfectly exhibits the ornamentation of the inner whorls. It has the same adult ornamentation as the holotype including the faint ventrolateral rows of tubercles, the same measurements and the same subquadratical whorl section, which is diagnostic for the species. The whorls are just not in contact.

2.4. Legitimate type species of *Pseudothurmannia* Spath, 1923

As to the type species of the genus group *Pseudothurmannia* there are now two options. The first option is that the newly recovered holotype of the nominal species *Ammonites angulicostatus* d'Orbigny, 1841, should remain the type species. This would have been the normal procedure before 2000 and in accordance with the third edition of the *International Code of Zoological Nomenclature* (1961). After 2000 this option was chosen by Vermeulen (July 2002, 2004), Vermeulen *et al.* (November 2002), and Busnardo (2003). This option has, however, the disadvantage that genus *Pseudothurmannia* would then merely embrace the three species of the *angulicostata* group, which consist of species that are totally different from the group of 16 species that over the past 80 years have been considered to belong to *Pseudothurmannia*.

To avoid confusion and to maintain stability in nomenclature, it would be better to retain the name *Pseudothurmannia* for this latter group. This second option is preferred here. Before 2000 this possibility would have only been possible through the intervention of the ICZN (International Commission on Zoological Nomenclature). Sarkar's (1955) proposal to regard the holotype of *Pseudothurmannia picteti* Sarkar, 1955, as type species of *Pseudothurmannia* was, therefore, in conflict with the code of zoological nomenclature then. However, in the fourth edition of the code (1999), which became effective on 1st January 2000, a new article (article 70.3) was inserted, permitting the author, in the interest of stability in nomenclature, to fix as type species the non-deliberately misidentified nominal species that has previously been fixed as such. This means that *Pseudothurmannia picteti* Sarkar may now legitimately be considered the type species of *Pseudothurmannia* without the intervention of the ICZN. This second option has been followed by Company *et al.* (June 2002, p. 84, 2003) and is endorsed by the author.

There is still a problem, because both options for designating the type species of *Pseudothurmannia* are simultaneously valid. The *International Code of Zoological Nomenclature* (1999) failed to state that, if it can be demonstrated that the original type species is misidentified as being conspecific with the nominal species, then article 70.3.2. (misidentified type species) automatically overrules article 70.3.1. (nominal type species). The author holds this view. This omission of the *Code* would mean that the first author, who designates the type species after the 1st of January 2000, still has priority. This is illogical and cannot be the purpose of this article. However, in designating the type species of *Pseudothurmannia* after 2000, Company *et al.* (June 2002) still have priority over Vermeulen (July 2002).

In 2009 Vermeulen considered *Pseudothurmannia picteti* Sarkar, 1955 to be a *nomen nudum*, because Sarkar did not formally indicate a holotype, did not specify the distinguishing characters and did not give a diagnosis nor a description of the new species. However, every author is entitled to give a described and figured specimen a new name, if he is able to substantiate that the original identification is wrong, and that is what Sarkar did.

Since Company *et al.* (2002), in accordance with the new article, designated *Pseudothurmannia picteti* Sarkar as type species of *Pseudothurmannia* Spath, the species *Ammonites angulicostatus* d'Orbigny automatically lost its status of type species, and can, without violating the rules, be considered to belong to the species *Crioceratites*. *Pseudothurmannia picteti* Sarkar is also the type species of *Pieuriceras* Vermeulen, 2003, which renders *Prieuriceras* a junior objective synonym of *Pseudothurmannia*. However, as the type species of *Pseudothurmannia* belongs to the group of species with lateral nodes on the main ribs in middle and late ontogenetic stages, this also means that this group has to be regarded as *Pseudothurmannia sensu stricto*. In this article this group is given the status of subgenus and referred to as *Pseudothurmannia* (*Pseudothurmannia*). This group has been regarded by Wiedmann (1962) and Busnardo (1970, 2003) as not belonging to *Pseudothurmannia*; they grouped them into a separate subgenus *Crioceratites* (*Sornayites*) Wiedmann, 1962. Wiedmann (1962, p. 140) stated that the species of this group have trituberculate ribs in all stages of development. Wiedmann chose *Emericiceras paronai* Sarkar, 1955, as type species of *Sornayites*, which is not congeneric with the laterally tuberculated species of *P.* (*Pseudothurmannia*). *Emericiceras paronai* is adorned with long ventrolateral spines on the main ribs, which are absent in *P* (*Pseudothurmannia*); *E. paronai* also lacks the ventrolateral rows of small uniform clavi, which characterize *P.* (*Pseudothurmannia*), and has lateral tubercles on the inner whorls, which, in contrast to the assumption of Wiedmann, are absent in *P.* (*Pseudothurmannia*). However, Wiedmann did not include *Pseudothurmannia picteti* Sarkar nor *Pseudothurmannia pseudomalbosi* Sarasin & Schöndelmayer, 1901, in *Sornayites*, because he saw that these species lack lateral tubercles on the inner whorls.

Busnardo (2003) followed Wiedmann (1962) in separating the species with lateral tubercles in the adult as *Sornayites* from the species without them. However, Busnardo (2003, p. 72) proposed *Pseudothurmannia simionescui* Sarkar, 1955, to be the type species of genus *Sornayites*, because the type of the latter could not be found. This proposal is not in accordance with the *International Code of Zoological Nomenclature* (1999), because *Pseudothurmannia simionescui* Sarkar, 1955, cannot be considered the neotype of *Sornayites paronai* (Sarkar, 1955). Thomel (1965b) also separated the species with trituberculate ribs in middle to late ontogenetic stages from the other species of *Pseudothurmannia,* not as *Sornayites*, but as *Crioceratites*, because he rightly regarded *Sornayites* as a problematic genus.

The above sketched misinterpretations of the type species are merely due to the wrong illustrations of *Ammonites angulicostatus* by d'Orbigny (1841) and Pictet (1863), for in both figures the lateral tubercles have not been depicted.

3. SUBGENERA

In this monograph the author distinguishes five subgenera; two within the genus *Crioceratites* and three within the genus *Pseudothurmannia* (Fig. 2). They are distinguished on the ground of differences in the ontogenetic development of the ornamentation of the ammonites. The author is of the opinion that, in heteromorphic ammonites, the ontogenetic development of the ornamentation has a greater validity in distinguishing generic groups than the accidental likeness or unlikeness of the variable ornamentation of the adult stage. Similarity of ornamental ontogeny presupposes phylogenetic kinship. We return to this subject when discussing the probable phylogenetic relations of the subgenera. It is the experience of the author that each species of *Crioceratites* has its own specific fixed measure of uncoiling and that the narrowness of the distance between the whorls at a certain diameter varies only within narrow limits.

3.1. Subgenus *Pseudothurmannia (Pseudothurmannia)* Spath, 1923

The group of species within *Pseudothurmannia* that develops lateral tubercles on middle to late ontogenetic

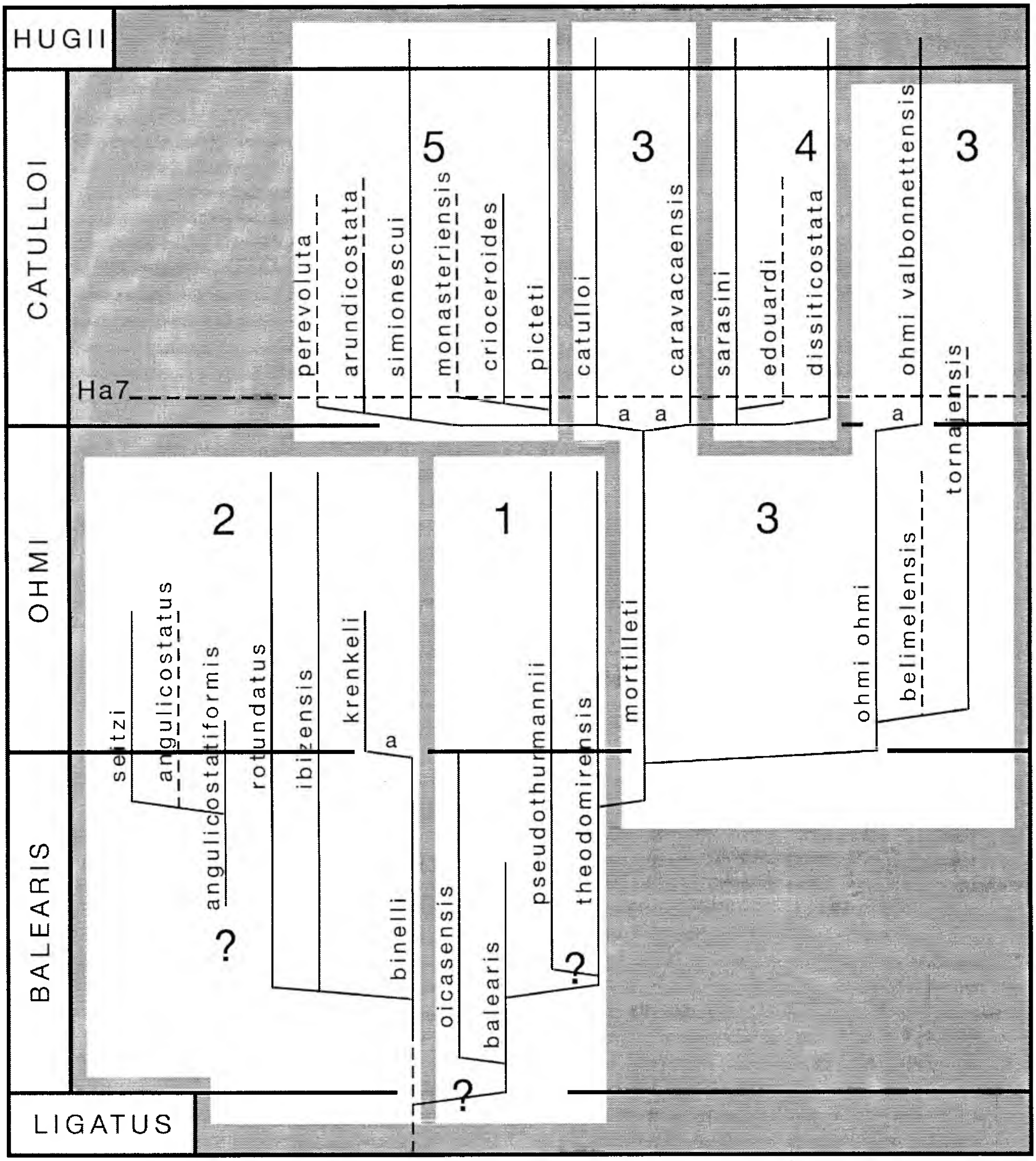


Fig. 2: Phylogenetic tree of *Pseudothurmannia* and related generic groups. 1. Subgenus *Crioceratites* (*Balearites*). 2. Subgenus *Crioceratites* (*Binelliceras*). 3. Subgenus *Pseudothurmannia* (*Kakabadziella*). 4. Subgenus *Pseudothurmannia* (*Parathurmannia*). 5. Subgenus *Pseudothurmannia* (*Pseudothurmannia*). Note the great radiation of species of *Pseudothurmannia* that have trituberculate main ribs in late ontogenetic stages at the base of the Catulloi Zone. In 1995 the author showed that this renewal in the ammonite fauna includes also many other species, and took place during the Falling Stage Systems Tract (formerly the late Highstand Systems Tract) preceding major sequence boundary Ha7.

stages may be separated (with the exception of a few species around *Pseudothurmannia sarasini* Sarkar, 1955) as *Pseudothurmannia* (*Pseudothurmannia*) Spath, 1923, from the group that lacks lateral tubercles in all ontogenetic stages. The species within subgenus *Pseudothurmannia* (*Pseudothurmannia*) lack lateral tubercles on the inner whorls, but lateral tubercles are present in middle to late growth stages. The lateral tubercles of *P.* (*P.*) *picteti* Sarkar, 1955, type species of this group, occur only in the middle growth stage. *P.* (*Pseudothurmannia*) lacks the fine-ribbed inner whorls and more distantly spaced ribs. The main ribs are markedly more prominent below the lateral tubercle than above it, and have ventrolateral rows of small uniform clavi up to the aperture; fibulation (two ribs unite in one ventrolateral tubercle) is absent. Weak constrictions may be present in the latest growth stage.

Since Vermeulen (2004) did not recognize *P. picteti* as type species of genus *Pseudothurmannia*, he had to invent a new name for this group of species, viz. *Prieuriceras*. The author considers this name an objective synonym of *Pseudothurmannia* (*Pseudothurmannia*), because both generic groups have the same type species.

The species within the subgenus *Pseudothurmannia* (*Pseudothurmannia*) have so many characteristics in common, that a close kinship can be assumed. In the chapter on phylogeny it will be shown that they form a nice cladogenetic peramorphocline with *P* (*P.*) *picteti* as aperamorphic species. In the same chapter arguments will be given that *Pseudothurmannia catulloi* Parona, 1897, is the probable ancestor of the subgenus.

The following six species are included in *Pseudothurmannia* (*Pseudothurmannia*): *arundicostata* sp. nov.; *crioceroides* Torcapel, 1884 (= *pseudomalbosi* Sarasin & Schöndelmayer, 1901 = *angulicostata* var. *tuberculata* Sarkar, 1955); *monasteriensis* Simionescu, 1899; *perevoluta* sp. nov.; *picteti* Sarkar, 1955, type species (= *grandis* Busnardo, 1970 = *lurensis* Busnardo, 1970 = sp. A Busnardo, 1970); and *simionescui* Sarkar, 1955.

3.2. Subgenus *Pseudothurmannia* (*Parathurmannia*) Busnardo, 2003

Like *P picteti*, *Pseudothurmannia sarasini* Sarkar, 1955, also has generally been misinterpreted, for example, by Cecca *et al.* (1998) and Busnardo (2003), because the holotype is a juvenile specimen which does not show the adult ornamentation. The adult ornamentation of the large specimen of *P. sarasini* from the Río Argos shows small, pointed lateral tubercles over a quarter of a whorl. Busnardo (2003) restricted the name *Pseudothurmannia* to the species around *Ammonites angulicostatus* d'Orbigny, which exhibits lateral tubercles on the inner whorls. Therefore, Busnardo (2003) was compelled to rename the group of species that do not exhibit lateral tubercles in any ontogenetic stage; he chose the name *Parathurmannia* for this group. However, he erroneously chose *P. sarasini* as type species, which does have lateral tubercles in the middle growth stage. He also included *Hoplites pseudomalbosi* Sarasin & Schöndelmayer, 1901 (conspecific with *Ammonites crioceroides* Torcapel, 1884), which develops lateral tubercles in the adult stage, in *Parathurmannia*. The group of species without lateral tubercles in any ontogenetic stage should, therefore, be separated from *Parathurmannia*; the present author gave it the status of subgenus under the name *Pseudothurmannia* (*Kakabadziella*) subgen. nov.

Nevertheless, there is a small group of species around *Pseudothurmannia sarasini*, which is also characterized by the presence of lateral tubercles in middle to late ontogenetic stages, but which shows several conspicuous differences from the subgenus *Pseudothurmannia* (*Pseudothurmannia*). The main differences between *P.* (*Pseudothurmannia*) and the *sarasini* group are the strong, relatively closely spaced, main ribs with 2-3 intermediate ribs in the former group, and the fine, notably wide-spaced main ribs with 3-6 intermediate ribs in the latter. These differences suggest a different ancestry for the *sarasini* group. This group may, therefore, be treated as a separate generic group for which the name *Parathurmannia* Busnardo, 2003, is available. In this article the concept of the subgenus *P.* (*Parathurmannia*) is, as a matter of course, entirely different from the concept of Busnardo (2003), and the diagnosis should be totally altered. However, *P.* (*Parathurmannia*) *sarasini* remains the type species.

The species within the subgenus *Pseudothurmannia* (*Parathurmannia*), as it is conceived herein, have so many characteristics in common, that a monophyletic origin seems the most plausible solution. In the chapter on phylogeny it will be argued that *P.* (*K.*) *caravacaensis* sp. nov. is the probable ancestor of the subgenus.

The following three species are included in *Pseudothurmannia* (*Parathurmannia*): *dissiticostata* sp. nov.; *eduardi* Honnorat-Bastide, 1889; and *sarasini* Sarkar, 1955, type species.

3.3. Subgenus *Pseudothurmannia* (*Kakabadziella*) subgen. nov.

This group of species without lateral tubercles in any ontogenetic stage has for a long time been considered to constitute the core of the genus *Pseudothurmannia*, because the drawing of *Ammonites angulicostatus* in d'Orbigny's *Paléontologie française* (1841, pl. 46, figs. 3, 4) does not show lateral tubercles. Nobody has ever doubted that these species belong to the genus *Pseudothurmannia*. This group formerly contained the species *C. angulicostata* d'Orbigny and *P. picteti* Sarkar, because their holotypes were figured without lateral tubercles, but now the group consists only of the species *P. mortilleti* Pictet & De Loriol, *P. ohmi* Winkler, *P. catulloi* Parona, *P. belimelensis* Dimitrova and two new species. The species of this group still belong to *Pseudothurmannia*, because they show the diagnostic ventrolateral rows of small uniform clavi, which are finer and may easily wear off; constrictions, fibulation of ribs and lateral tubercles on the first whorl are absent. However, weak constrictions may be present in some adult macroconchs. For this group of species a new subgeneric name should be found, because *P.* (*Pseudothurmannia*) and *P.* (*Parathurmannia*) are not available. The author proposes to call this group *Kakabadziella* in honour of the well-known Georgian palaeontologist and specialist of heteromorphic ammonites, Prof. Dr. Micheil Kakabadze. As type species, the author chose *Ammonites Mortilleti* Pictet & De Loriol, 1858, because it is the most common *Pseudothurmannia* and the main stem from which all other species of *Pseudothurmannia* are derived. Wiedmann (1962) designated as lectotype of *Pseudothurmannia mortilleti* the well-preserved specimen from the neighbourhood of Nice, which Pictet & De Loriol used in their description in addition to the specimens from Voirons. The subsequent designation by Busnardo (2003) of the specimen from Voirons as lectotype of *P mortilleti* is, therefore, invalid. Vermeulen (2004) included *P. mortilleti* in the genus *Balearites*. The author cannot endorse this view because of the lack of thick ribs alongside constrictions in the adult of *P. mortilleti* and the absence of lateral tubercles on the first whorl.

Busnardo (2003) reserved the name *Pseudothurmannia* for the group of species that have trituberculated inner whorls, that is, the group around the former type species of *Pseudothurmannia*, viz. *Ammonites angulicostatus* d'Orbigny. However, he included in this group *Pseudothurmannia picteti* Sarkar, 1955, which has no trituberculated ribs on the inner whorls, but only trituberculated ribs in the adult stage. In the present article *Ammonites angulicostatus* d'Orbigny is provisionally included in *Crioceratites* (*Binelliceras*) Sarkar, 1977.

To *Pseudothurmannia* (*Kakabadziella*) belong the following seven species: *belimelensis* Dimitrova, 1967; *catulloi* Parona, 1897; *caravacaensis* sp nov.; *mortilleti* Pictet & De Loriol, 1858 (= *renevieri* Sarasin & Schöndelmayer, 1901); *ohmi* Winkler, 1868 (= *biassalensis* Dimitrova, 1967); *ohmi valbonnettensis* subsp. nov. [= *angulicostata* Lapeyre, 1974 ('neotype'), *non* d'Orbigny, 1841]; and *tornajensis* sp. nov.

3.4. Subgenus *Crioceratites (Balearites)* Sarkar, 1954

When Sarkar (1954) introduced the genus *Balearites*, he chose *Crioceras baleare* Nolan, 1894, as type species (fixed by monotypy). He stressed its close affinity with *Pseudothurmannia,* as Nolan (1894) and Sarasin & Schöndelmayer (1901) did before him. Nolan stated that the whorls are in contact, but tend to become disconnected near the aperture. Therefore, Sarasin & Schöndelmayer (1901) included this species in *Hoplites*. Sarkar (1955) and Vermeulen (2004), on the other hand, put emphasize on the tendency of the whorls to become loose near the aperture, and included many crioconic species with fine, flexuous ribbing in *Balearites*. The present author restricts *Balearites* to those species that have their whorls in contact, and expelled the species with crioconic whorls from it.

Balearites balearis (Nolan, 1894) has generally been regarded as closely related to *Pseudothurmannia*, because it shows a combination of crioceratitic and pseudothurmannian features.

Typical crioceratitic features are, (1) the presence of constrictions alongside coarse ribs in the adult stage; this feature is common in *Crioceratites*, but does not occur in *Pseudothurmannia* except weakly in the latest ontogenetic stage of some macroconchs. (2) The presence of ventrolateral rows of small, uniform, rounded tubercles, which may or may not continue up to the aperture; the ventrolateral rows in *Pseudothurmannia* consist of small, uniform clavi and continue up to the aperture. (3) The first whorls of the species here included in *Balearites* are provided with lateral tubercles; *Pseudothurmannia* lacks lateral tubercles in any ontogenetic stage. Although the first whorl of the holotype of *B. balearis* has never been made visible, the variety *shankariae* of this species has lateral tubercles on the first whorl. Because of the latter feature, the author considers *Balearites* a subgenus of *Crioceratites*.

Typical pseudothurmannian features of *Crioceratites* (*Balearites*) are the combination of two characteristics: (1) the whorls being in contact with each other, and (2) the presence of ventrolateral rows of fine uniform tubercles without fibulation. Fibulation is absent in *Pseudothurmannia*, but occurs only in *Crioceratites*. *Crioceratites* (*Balearites*) clearly forms the phylogenetic link between *Crioceratites* and *Pseudothurmannia* (*Kakabadziella*).

Vermeulen (2004) includes the fine-ribbed species *Pseudothurmannia* (*Kakabadziella*) *mortilleti* Pictet & De Loriol, 1858, and "*P.* (*K.*) *caravacaensis* Hoedemaeker sp. nov." in *Balearites*. However, these species lack lateral tubercles on the first whorl, lack constrictions alongside thick ribs in the adult, and have small uniform ventrolateral clavi up to the aperture. They have all the characteristics of *Pseudothurmannia* (*Kakabadziella*), which has *P* (*K.*) *mortilleti* as type species. Vermeulen (2004) also included *Crioceratites krenkeli* (Sarkar, 1955) in *Balearites*. However, *C. krenkeli* has crioconic whorls, shows lateral tubercles up to a diameter of 15 mm, and exhibits strong fibulation on the inner whorls, which are characteristic features of *Crioceratites* (*Binelliceras*).

Species here considered belonging to subgenus *Crioceratites* (*Balearites*) are: *balearis* Nolan, 1894, [which includes variety *shankariae* Sarkar, 1955, and the cotype of *Crioceratites binelli* (Astier, 1851) figured by Sarkar, 1955, on pl. 2, fig. 6 under the name *C. binelli*];

oicasensis sp. nov. [= *Pseudothurmannia* (*Balearites*) nov. sp. A in Hoedemaeker, 1995b]; *pseudothurmannii* Dimitrova, 1967; *theodomirensis* sp. nov.

3.5. The subgenus *Crioceratites* (*Binelliceras*) Sarkar, 1977

Sarkar (1977) designated *Ancyloceras binelli* Astier, 1851 (pl. 2, fig. 2), as type species of his new genus *Binelliceras*. Earlier, in 1955, he designated the same specimen as lectotype of the species *Crioceras binelli* Astier, 1851. *Binelliceras* Sarkar, 1977, is here regarded as a subgenus of *Crioceratites* because of crioconic whorls, the presence of lateral tubercles on the inner whorls and the frequent presence of fibulation. The close relation between *Crioceratites* (*Balearites*) and *Crioceratites* (*Binelliceras*) can be exemplified by one of the cotypes of *C. binelli*, which was figured by Sarkar (1955, pl. 2, fig. 6) under the name *Crioceras binelli* Astier. This specimen can be identified as *Crioceratites* (*Balearites*) *balearis* variety *shankariae* Sarkar. The relation of *binelli* with *balearis* is based on the peculiar ornamentation of closely spaced, fine, S-shaped ribs in both species. Besides, it is quite possible that *C.* (*Bi.*) *binelli* is the ancestor of *C.* (*B.*) *balearis*. The differences between *C.* (*Binelliceras*) and *C.* (*Balearites*) are (1) the whorls being in contact in *Balearites* and crioconic in *Binelliceras*; (2) the presence of lateral tubercles up to a diameter of 7-10 mm in *Balearites*, whereas lateral tubercles disappear between diameters of 10-16 mm in *Binelliceras*; (3) the absence of fibulation in *Balearites*, which is frequently present in *Binelliceras*.

The number of characteristics that the species of the group around *C.* (*Bi.*) *binelli* have in common with the species of the group around *Crioceratites angulicostatus* (d'Orbigny) is much greater. Both groups (1) have crioconic whorls; (2) have lateral tubercles up to rather large diameters; (3) have ventrolateral tubercles exhibiting frequent fibulation on the inner whorls; and (4) the amount of fibulation diminishes with growth, so that in a later ontogenetic stage every rib ends in a ventrolateral tubercle. The ventrolateral tubercles become weaker or disappear towards the aperture. *Balearites* lacks all these characteristics.

There are, nevertheless, some important differences between the species of the *binelli* group and the *angulicostatus* group: (1) in the *binelli* group lateral tubercles are absent at diameters greater than 16 mm, whereas in the *angulicostatus* group they are present up to diameters of 16-23 mm; (2) in the *angulicostatus* group the ribbing is coarser than in the *binelli* group; finally, (3) the inner whorls of the species of the *binelli* group have a more or less extended part with fine, undifferentiated ribbing; fasciculation is common in this fine-ribbed part. Such a fine undifferentiated ribbing is absent in the *angulicostatus* group.

The species that are morphologically closest to *Crioceratites angulicostatus* (d'Orbigny) are *Crioceratites seitzi* Sarkar, 1955 (pl. 3, fig. 3), and *Ammonites angulicostatus* Pictet, 1863 (pl. 1 bis, fig. 3a-b), *non* d'Orbigny, of which Dr. D. Decrouez from the Muséum d'Histoire naturelle de Genève sent a plaster cast (No. 16850) to the author. All three species are crioconic. The main difference between the *C. seitzi* and *C. angulicostatus* (d'Orbigny) is the more compressed whorl section of the former. The inner whorls of the crioconic *Ammonites angulicostatus* Pictet have, like *C. angulicostatus* (d'Orbigny), thick trituberculated main ribs separated by 2-3 thinner, non-tuberculate intermediate ribs; these are not depicted in Pictet's figure. Kilian (1888, p. 212; 1910, pp. 222, 224) separated Pictet's crioconic *Ammonites angulicostatus* from d'Orbigny's (at that time, supposedly) non-crioconic, *Ammonites angulicostatus*, and renamed it *Crioceras angulicostatum* Kilian, 1888. This species should be renamed again. The author proposes the name *Crioceratites angulicostatiformis* nom. nov.

The similarity in the characteristic and ontogeny of the ornamentation in the *binelli* and *angulicostatus* groups is great. It is the author's opinion that the number of characteristics they have in common is great enough to unite provisionally these groups into one subgenus, *Crioceratites* (*Binelliceras*) Sarkar, 1977, instead of looking for a new subgeneric name; the name *Pseudothurmannia* is not available for this group anymore. Vermeulen (2004) also was of the opinion that the *binelli* and *angulicostatus* groups had a close phyletic liaison. On the other hand, the differences between these groups are great enough to keep them apart as distinct groups within *Crioceratites* (*Binelliceras*). The *angulicostatus* and *binelli* groups may have a common ancestor within the group of *Crioceratites* with trituberculate main ribs on the inner whorls, such as *C. nolani* Kilian, 1910, *C. karakaschi* Sarkar, 1955, *C. shibaniae* Sarkar, 1955, *C. sornayi* Sarkar, 1955, *C. majoricensis* Nolan, 1894.

The seven species here considered to belong to *Crioceratites* (*Binelliceras*) are: *binelli* Astier, 1851 (= *nowaki* Sarkar, 1955); *krenkeli* Sarkar, 1955; *ibizensis* Wiedmann, 1962; *rotundatus* Sarkar, 1955; *angulicostatus* d'Orbigny, 1841; *angulicostatiformis* nom. nov. (for *Crioceras angulicostatum* Kilian, 1888); *seitzi* Sarkar, 1955. Sarkar (1977) also included *Crioceras rogeri* Sarkar, 1955, and *Aegocrioceras densiradiatum* Rawson, 1975 in the subgenus *Binelliceras*, but both *C. rogeri* and *A. densiradiatum* lack lateral tubercles on the inner whorls, and *Aegocrioceras* is restricted to the Boreal Realm and to the basalmost part of the upper Hauterivian.

3.6. Different interpretations of the systematic position of *Pseudothurmannia* and *Balearites*

There are several different taxonomic interpretations as to the systematic position and mutual relation of the genera *Balearites, Pseudothurmannia*, and *Crioceratites*.

1. *Balearites* was considered a separate genus next to *Pseudothurmannia* and *Crioceratites* by Sarkar (1955). These genera were put into two separate families; the first two into Hemihoplitidae, the latter into Ancyloceratidae (this interpretation was followed by Dimitrova, 1967).
2. *Balearites* and *Pseudothurmannia* were considered separate genera by Arkell *et al.*, 1957, but the first was transposed into Ancyloceratidae, whereas the latter was kept in Hemihoplitidae.
3. *Balearites* and *Pseudothurmannia* were considered separate genera by Sornay (1968), but the first was considered a subgenus of *Crioceratites*, whereas the latter was considered a separate genus apart from *Crioceratites*, but still within the family of the Ancyloceratidae.
4. *Balearites* has been put in synonymy with *Pseudothurmannia* by Wiedmann (1962) and the latter was considered a subgenus of *Crioceratites* within the family Ancyloceratidae (this interpretation is followed by Baccelle & Lucchi Garavello, 1967; Braga *et al.*, 1982; Adamikova *et al.*, 1984). Wiedmann was the first to separate the forms around *Pseudothurmannia edouardi/simionescui/crioceroides* with lateral tubercles on the middle and late ontogenetic stages from *Crioceratites* (*Pseudothurmannia*), and united them in a separate subgenus *Crioceratites* (*Sornayites*), unaware that *Pseudothurmannia picteti* Sarkar (1955), also belongs to that group. This idea was followed by Busnardo (1970).
5. Thomel (1965b) considered *Sornayites* a problematic subgenus and preferred to put the *P. edouardi/simionescui* group into *Crioceratites*.
6. Lapeyre (1974) designated a topotype specimen that he collected from Chamateuil as the lectotype of *Pseudothurmannia angulicostata* (d'Orbigny). He considered *Pseudothurmannia picteti* Sarkar a synonym of *P. angulicostata* (d'Orbigny).
7. *Balearites* and *Pseudothurmannia* were kept separate by Immel (1979b), but both were kept within Ancyloceratidae; he synonymized *Balearites* with *Crioceratites*, whereas *Pseudothurmannia* was considered a subgenus of *Crioceratites* (this interpretation was followed by Avram, 1995). Immel followed Thomel (1965b) as to the *P. simionescui/edouardi* group.
8. *Balearites* was considered a subgenus of *Pseudothurmannia* by Kakabadze (1981) and kept in Ancyloceratidae. Hoedemaeker (1995b) and Vašíček & Faupl (2000) followed this idea.
9. Borza *et al.* (1984), Michalík & Vašíček (1989), Vašíček (1989), Vašíček *et al.* (1994), Vašíček (1995, 1997), and Vašíček & Michalik (1999) considered *Pseudothurmannia* a separate genus next to *Crioceratites*, and *Balearites* to be a synonym of *Pseudothurmannia*. They considered all these genera members of the family Ancyloceratidae.
10. Hoedemaeker (1995) regarded *Ammonites angulicostatus* d'Orbigny as a species of the genus *Crioceratites* (this idea was followed by Company *et al.*, 2003), and he proposed *Ammonites Ohmi* Winkler, which is the true identity of the specimen that Lapeyre (1974) designated as the lectotype of *Pseudothurmannia angulicostata* d'Orbigny, to be the type species of *Pseudothurmannia* of which *Balearites* was considered a subgenus.
11. Wright (1996) considered *Balearites* a subjective synonym of *Pseudothurmannia*. The latter was regarded as a separate genus next to *Crioceratites*, but was, in contrast to Arkell (1957), included in the subfamily Crioceratitinae Gill, 1871, family Ancyloceratidae Gill, 1871.
12. Avram (*in* Avram & Melinte, 1998) considered *Balearites* a separate genus next to *Pseudothurmannia* and *Crioceratites*, all within the family Ancyloceratidae.
13. Company *et al.* (2002, 2003) considered *Balearites* to be synonymous with *Crioceratites*, and *Ammonites angulicostatus* d'Orbigny to be a species of the genus *Crioceratites*. *Pseudothurmannia picteti* Sarkar, 1955, was redesignated as the type species of *Pseudothurmannia* (this is followed herein) and this was regarded as a separate genus within the family Ancyloceratidae.
14. Vermeulen (2002) considered *Ammonites angulicostatus* d'Orbigny to be the type species of *Pseudothurmannia*. He considered *Pseudothurmannia*, *Balearites* and *Crioceratites* separate species within the family Ancyloceratidae. He included the species of the *P. simionescui/crioceroides* group with trituberculate main ribs in the middle and adult growth stages in *Pseudothurmannia*.
15. Busnardo (2003) considered *Ammonites angulicostatus* d'Orbigny to be the type species of *Pseudothurmannia*, which means that all species (except the holotype) that formerly constituted this genus were transferred into a new genus *Parathurmannia* with the exception of the group of species around *P. simionescui/eduardi* with trituberculate main ribs in the middle and adult growth stages. Busnardo followed Wiedmann (1962) and still assigned this group to the genus *Sornayites*. He chose *Pseudothurmannia sarasini* Sarkar, 1955, as type species of *Parathurmannia*, unaware of the fact that adult *P. sarasini* shows a transient stage with trituberculate main ribs. *Balearites* was regarded as a separate genus. *Pseudothurmannia, Parathurmannia, Sornayites,* and *Balearites* are all considered genera of the family Ancyloceratidae.
16. Vermeulen (2004) regarded *Ammonites angulicostatus* d'Orbigny as the type species of *Pseudothurmannia*, and regarded *Pseudothurmannia, Balearites* and *Binelliceras* as independent genera next to *Crioceratites*. He invented the genus group name *Prieuriceras* for all species of the *simionescui/crio-*

ceroides group, which he still included in *Pseudothurmannia* in 2002.

17. Vermeulen (2009) considered *Ammonites angulicostatus* d'Orbigny, forme à tours emboités in Pictet, (1863, pl. 1bis, fig. 1a, b) as the type species of *Pseudothurmannia*, but regarded *Pseudothurmannia picteti* as a *nomen nudum*.
18. In this paper, *Pseudothurmannia picteti* Sarkar, 1955, which has a transient stage with trituberculate ribs, is considered the type species of the genus *Pseudothurmannia* Spath, 1923, which was kept in the family Ancyloceratidae. The former type species of *Pseudothurmannia*, viz. *Ammonites angulicostatus* d'Orbigny, 1841, was considered to belong to the genus *Crioceratites* Léveillé, 1837, and provisionally to form part of the subgenus *Crioceratites* (*Binelliceras*) Sarkar, 1977, type species *Ancyloceras Binelli* Astier, 1851. The group around *P. picteti* is brought back into *Pseudothurmannia*, and constitutes the typical subgenus *Pseudothurmannia* (*Pseudothurmannia*). The group around *P. sarasini* Sarkar, 1955, which has a transient stage with trituberculate ribs, is maintained as subgenus *Pseudothurmannia* (*Parathurmannia*) Busnardo, 2003. *Balearites* Sarkar, 1954, type species *Crioceras baleare* Nolan, 1894, is also considered a separate subgenus of *Crioceratites*. The group of *Pseudothurmannia* without lateral tubercles in any ontogenetic stage, formerly regarded as the typical group of that genus, is renamed *Kakabadziella* subgen. nov., type species *Ammonites Mortilleti* Pictet & De Loriol, 1858, and is regarded as a subgenus of *Pseudothurmannia*.

4. ONTOGENY AND PHYLOGENY

The author has reflected a long time on possible phylogenies of the species and subgenera mentioned in this article, but when the systematics and stratigraphical ranges became gradually clearer, the phylogeny advocated here presented itself as the most probable (Fig. 2). First, the author provides some of the basic assumptions with respect to the phylogenetic relation of the subgenera *Crioceratites* (*Binelliceras*), *Crioceratites* (*Balearites*), *Pseudothurmannia* (*Kakabadziella*), *Pseudothurmannia* (*Parathurmannia*) and *Pseudothurmannia* (*Pseudothurmannia*) and of their species. These subgenera are distinguished on the grounds of different ontogenetic developments of their shape and ornamentation.

The genus *Pseudothurmannia* is generally thought to be derived from *Crioceratites* because of the presence of some crioceratitic features, such as a crioconic first whorl, which produces a perforated umbilical centre; a quadrilobate suture line similar to that of *Crioceratites*; and a fully developed outer conch wall at the dorsum with outer prismatic layer and nacrous layer (in normally coiled ammonites the dorsal wall lacks the outer prismatic layer and nacrous layer), even when the whorls are in contact or overlapping. This implies that the feature of crioconic whorls in young ontogenetic stages is ancestral to the feature of overlapping whorls in young ontogenetic stages. Finally, the crucial criterion is, of course, that the ancestral subgenera should start their ranges earlier than the descendant subgenera.

If one endeavours to perform a phyletic analysis, one has to take account of two aspects; first, the stratigraphic ranges of the species and the relation of these ranges to each other; second, the presence and nature of heterochrony.

In general, the ranges of fossil species are not reliable, because palaeontologists are often severely hampered by collection failure, i.e. the inability of collecting enough specimens of a species necessary to get a reliable picture of the total range of the species. This is a normal phenomenon when collecting macrofossils. However, the reliability of the ranges of *Pseudothurmannia* (*Kakabadziella*) *mortilleti*, *P.* (*K.*) *ohmi*, *P.* (*K.*) *catulloi*, and *P.* (*K.*) *caravacaensis* along the Río Argos are quite good in relation to the reliability of the ranges of the other species discussed in this paper. This is because the stratigraphic distance between the distinct samples in this continuously deposited succession is quite short; in nearly every bed within the range, one or more specimens were found, and the calculus of probability demonstrates that in such cases the first and last appearances in the field are very close to the real first and last appearances in time. Also it has never been demonstrated that the ranges of *Balearites balearis* and *Pseudothurmannia* (*Kakabadziella*) *mortilleti* are overlapping, or that species of *Pseudothurmannia* (*Pseudothurmannia*) and *P.* (*Parathurmannia*) occur below the base of the Catulloi Zone.

The presence of heterochrony is not always unequivocal. Therefore one has to define successive ontogenetic stages within the ornamentation and within the shape of the conch of all species concerned. A cladogenetic mosaïc heterochronocline (McNamara, 1982, 1990) was determined in a stepped lineage extending from *Balearites balearis* to *Pseudothurmannia* (*Kakabadziella*) *tornajensis*; a stepped cladogenetic dissociated peramorphocline was determined within the subgenus *Pseudothurmannia* (*Pseudothurmannia*), and another stepped cladogenetic peramorphocline in the *angulicostatus* group of the subgenus *Crioceratites* (*Binelliceras*). Four small anagenetic lineages could be indicated, from *P.* (*K.*) *mortilleti* to *P.* (*K.*) *caravacaensis*, from *P.* (*K.*) *mortilleti* to *P.* (*K.*) *catulloi*, from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *ohmi valbonnettensis*, and from *C.* (*Bi.*) *binelli* to *C.* (*Bi.*) *krenkeli*. However, several species could not be inserted in a heterochronocline, and these are considered to represent individual side branches.

The author calibrated the ontogeny of the ornamentation and the shape of the shell with the size of the conch (diameter). This is only justified if the sizes are of the same order. The ontogenies of shape and ornamentation are considered to be somatic, because the shell is the product of glands along the apertural rim of the mantle. It must be mentioned that the author used only macroconchs in his analysis in order to enhance clarity in mutual comparison, because many microconchs are still unknown or questionable. Macroconchs are conservative in their development, whereas microconchs are progressive and do not show all ornamental stages.

4.1. Stepped cladogenetic mosaïc heterochronocline from *C.* (*B.*) *balearis* to *P.* (*K.*) *tornajensis* (Fig. 3)

The first part of this mosaïc heterochronocline is a dissociated peramorphocline; the last part is a dissociated paedomorphocline.

Ancestry of *C.* (*B.*) *balearis*: The ornamentation of the inner whorls of *Crioceratites* (*Binelliceras*) *binelli* are quite similar to *Crioceratites* (*Balearites*) *balearis* var. *shankariae* with this difference, that young *C.* (*Bi.*) *binelli* has crioconic whorls and lateral tubercles up to a diameter of 15 mm, whereas young *C.* (*B.*) *balearis* has its whorls in contact and lateral tubercles up to a diameter of 7 mm. As species with crioconic whorls in the young are considered more primitive than the species with overlapping whorls in the young, and as a late disappearance of lateral tuberculation is considered more primitive than an early disappearance, *C.* (*Bi.*) *binelli* is considered more primitive than *C.* (*B.*) *balearis* and could possibly be the ancestor of the latter; the laterally tuberculated ornamental ontogenetic stage of the former species is accelerated in relation to the equivalent stage in the latter. *C.* (*Bi.*) *binelli* appears close to the appearance

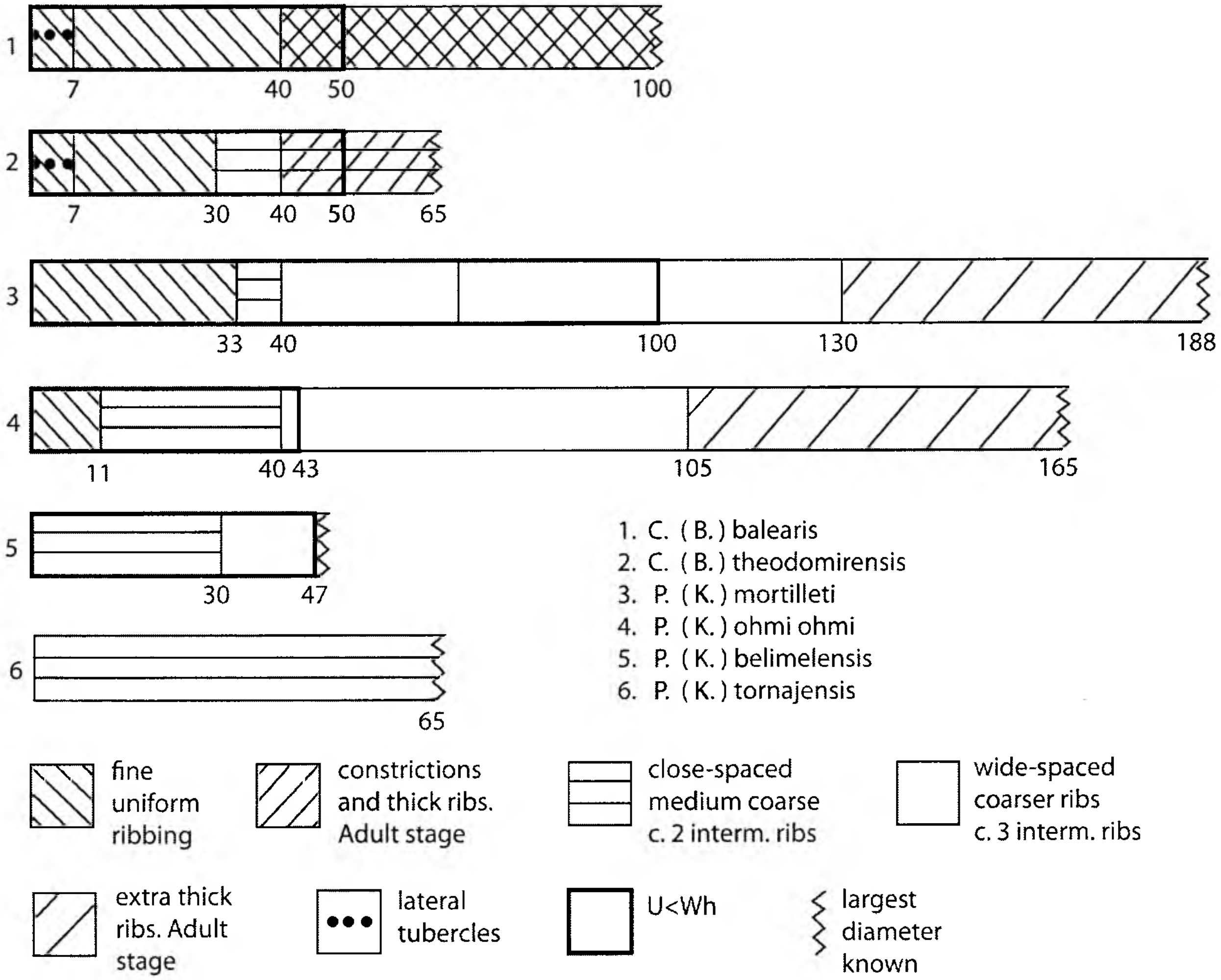


Fig. 3: Diagram showing the ontogenetic stages of the ornamentation and conch shape of the species forming the cladogenetic mosaïc heterochronocline from *Crioceratites* (*Balearites*) *balearis* to *Pseudothurmannia* (*Kakabadziella*) *tornajensis*. Species 1-4 form a stepped cladogenetic dissociated heterochronocline affected by different peramorphic processes. The change-over from *Crioceratites* to *Pseudothurmannia* is made between species 2 and 3. The stage with fine *balearis*-like ribs accelerates step by step and disappears in species 5. The presence of constrictions lined by thick ribs is considered to be an adult variation. Species 3 is an example of hypermorphosis on account of the appreciable shift in the start of adulthood from a diameter of 40 mm to 130 mm. Species 4-6 form a stepped cladogenetic paedomorphocline. Species 6 is an example of progenesis.

of *C.* (*B.*) *balearis*, but has never found yet in beds earlier than the appearance of the latter. However, the exact ranges of these two species are still insufficiently known.

***Crioceratites* (*Balearites*) *balearis*:** This species is regarded as the ancestral aperamorphic species of this mosaïc *heterochronocline*. Two ornamental ontogenetic stages could be defined.

1. A first fine uniformly ribbed stage with lateral tubercles and uniform ventrolateral tubercles on every rib up to a diameter of 7 mm.
2. A long second stage characterized by fine dense uniform ribbing without lateral tubercles up to a diameter of 40 mm, but with uniform ventrolateral tubercles on every rib up to a diameter of 30-40 mm.
3. The adult growth stage with distantly spaced constrictions lined by thick ribs appearing amidst the fine dense uniform ribbing up to the aperture. The constrictions with thick ribs are here interpreted as an 'adult variation,' because this ornamentation remains restricted to the adult in the descendants, and does not exhibit heterochrony. In many other species of *Crioceratites* this type of ornamentation is present in the adult stage.

As for the ontogeny of the shape of the conch; the whorl height equals the umbilical width at a diameter of c. 50 mm. At smaller diameters the umbilicus is narrower than the whorl height, at larger diameters wider. The largest specimen has a diameter of 101 mm.

***Crioceratites* (*Balearites*) *theodomirensis*:** This species is interpreted as the first descendant of *C.* (*B.*) *balearis* in this heterochronocline, because its ornamentation is closest to that of *C.* (*B.*) *balearis*. It shows three ornamental ontogenetic stages.

1. The first stage is characterized by a fine dense uniform ribbing with lateral tubercles and small ventrolateral tubercles on every rib; this stage ends at a diameter of 7 mm.
2. The second stage is called the *balearis* stage and is characterized by fine dense uniform ribbing without lateral tubercles, but with ventrolateral tubercles on every rib; the appearance of umbilical bullae, which mark the future main ribs, begins at a diameter of 13 mm. This fine-ribbed stage ends at a diameter of c. 30 mm and is much shorter than in the ancestor through the process of acceleration.
3. The third stage is an 'innovation' characterized by a gradual coarsening and a distinct differentiation of the ribbing.
4. Thick ribs lined by constrictions begin to appear at a diameter of 36-40 mm. This is the 'adult variation' which characterizes all species of *Crioceratites* (*Balearites*).

Ventrolateral tubercles are present on every rib up to the aperture. This extension of the rows of ventrolateral tubercles up to the aperture can be interpreted as the result of the process of 'progressive deviation' in the ontogeny of the descendant. Progressive deviation has been defined as the process in which "a character, which makes its appearance in the young stage of an ancestral animal, may in the ontogeny of the descendant appear in the young and adult stage, producing a substitution of a new adult condition for the old condition" (De Beer, 1930; Gould, 1977). No heterochrony is involved.

The whorl height equals the umbilical width at a diameter of 50 mm. There is no heterochrony in the shape of the conch in relation to the aperamorphic ancestor. The size of a full-grown specimen is not known; the largest diameter found in the material of the author is 60-65 mm.

***Pseudothurmannia* (*Kakabadziella*) *mortilleti*:** This species is the second descendant of this heterochronocline and considered to belong to another genus than the first descendant, because it lost the crioceratitic initial ornamental stage with lateral tubercles (this loss is interpreted as the product of persistent acceleration of the first ornamental stage of its ancestor until it has disappeared) and it lost the typical crioceratitic adult ornamental variation with constrictions lined by thick ribs. Besides, this species has fine uniform ventrolateral clavi on every rib instead of rounded tubercles, it displays a strong sexual dimorphism, the macroconch reaches a large size, and the young specimen has strongly overlapping whorls and a narrow umbilicus. Nevertheless, the ornamentation of the inner whorls is similar to that of *C.* (*B.*) *theodomirensis*, and that is the reason why the author is convinced that the change-over from *Crioceratites* to *Pseudothurmannia* is made from *C.* (*B.*) *theodomirensis* to *P.* (*K.*) *mortilleti*.

In the macroconch of *P.* (*K.*) *mortilleti* four ontogenetic stages were defined.

1. A fine, uniformly ribbed *balearis* stage, which ends at a diameter of 20 mm; umbilical bullae appear at a diameter of 15 mm, which is not significantly different from their appearance in *C.* (*B.*) *theodomirensis*; later in this stage, the umbilical bullae become more prominent, the ribs slightly more pronounced and differentiated into 3-5 intermediate ribs to one main rib; this stage is equivalent to the later part of stage two of *C.* (*B.*) *theodomirensis* and ends at a diameter of c. 33 mm, which is not significantly different from that diameter in *C.* (*B.*) *theodomirensis*.
2. The second stage is characterized by slightly wider spaced ribs with mainly two intermediate ribs to one main rib and ends at a diameter of c. 40 mm, which is not significantly different from the diameter at the end of the equivalent stage three in *C.* (*B.*) *theodomirensis*.
3. In the third stage the number of intermediate ribs increases to mainly 3-4 to one main rib.
4. The adult stage starts at a diameter of c. 130 mm with the addition of distantly spaced, extra thick ribs separated by 5-7 intermediate ribs per interval. Small uniform ventrolateral clavi occur on every rib in all ontogenetic stages.

Up to a diameter of 40 mm *P. (K.) mortilleti* is quite similar to *C. (B.) theodomirensis* except for the shape of the conch, which is more involute in *P. (K.) mortilleti*. In *C. (B.) theodomirensis* the adult ornamentation starts at a diameter of 40 mm, in *P. (K.) mortilleti* at a diameter of c. 130 mm. The largest macroconch of *P. (K.) mortilleti* reaches a diameter of 188 mm, and has two ornamental ontogenetic stages more than *C. (B.) theodomirensis* of which the largest specimen known has a diameter of 65 mm.

As for the ontogeny of the shape of the conch: the point where the whorl height equals the umbilical width is at a diameter of c. 100 mm, which is at a smaller size than the start of the adult ornamentation. In *C. (B.) theodomirensis* this point is reached at a diameter of 50 mm, which is a larger diameter than the start of the adult ornamentation. This means that in *P. (K.) mortilleti* this point has reached in an earlier ontogenetic stage than in *C. (B.) theodomirensis*. This means that this point accelerated in the ontogeny of *P. (K.) mortilleti*, not retarded as it seems at first sight. It means furthermore that the ornamental ontogenetic stages 1-3 also accelerated with respect to those in the ontogeny of *C. (B.) theodomirensis*. In view of the additional two ornamental ontogenetic stages in *P. (K.) mortilleti*, the type of heterochrony between the ontogenies of *C. (B.) theodomirensis* and *P. (K.) mortilleti* could be interpreted as hypermorphosis.

***Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi*:** This species is the third descendant species in the peramorphic part of the heterochronocline, but also the first apaedomorphic species of the paedomorphic part of the mosaïc heterochronocline; it has four ornamental ontogenetic stages:

1. The *balearis* stage with fine dense uniform ribbing ends at a diameter of 11 mm, and is accelerated in relation to the ontogeny of the ancestor.
2. The second stage, which has coarser and differentiated ribbing with two intermediate ribs to one main rib, is equivalent to stage two in *P. (K.) mortilleti*. The ornamental stages one and two in combination with a small umbilicus are united in the so-called *mortilleti* stage, which ends at a diameter of c. 40 mm. Stage two merges into the third stage.
3. This third stage is characterized by more intermediate ribs per main rib and by an irregular distribution of main and intermediate ribs. This irregularity is an acceptable variation with respect to the more regular distribution in ontogenetic stage three of *P. (K.) mortilleti*; it ends at a diameter of c.105 mm. This early end may be a small heterochrony in the ontogeny of the second and third descendant produced by acceleration.
4. The adult ornamentation of the macroconch consists of very strong distant main ribs with distinct umbilical tubercles separated by 6-7 intermediate ribs.

The young stage of *P. (K.) ohmi ohmi* below a diameter of 25 mm closely resembles *P. (K.) mortilleti*, and can with difficulty be distinguished from the latter. The early egression of the whorls differentiates them. Small uniform ventrolateral clavi occur on every rib in all ontogenetic stages.

As for the ontogeny with respect to the shape of the conch: the diameter at which the umbilical width is equal to the whorl height occurs at a diameter of 41-43 mm. This means that also in the ontogeny of proportions acceleration has occurred. The largest macroconch sampled has a diameter of 165 mm and is of the same size order as that of *P. (K.) mortilleti*. This species marks the end the peramorphic part and the beginning of the paedomorphic part of the mosaic heterochronocline towards *P. (K.) tornajensis*.

***Pseudothurmannia* (*Kakabadziella*) *belimelensis*:** This species is provisionally regarded as the fourth descendant species of the heterochronocline, because it most resembles evolute *P. (K.) ohmi ohmi*, and because the latter is the only possible and most appropriate ancestor for *P. (K.) belimelensis*. However, the age of its appearance in relation to that of *P (K.) ohmi ohmi* is unknown, and possible adult features and size also are unknown. This species probably remained small. It totally lost the ornamental ontogenetic *balearis* and *mortilleti* stages, which may have disappeared through persistent acceleration; all the whorls, also the innermost, are advolute. Two ornamental ontogenetic stages could be recognized:

1. The ribbing of the first stage consists of two intermediate ribs to one main rib. This stage can be compared with stage two of *P. (K.) ohmi ohmi*.
2. The ribbing of the second stage consists of 3-5 intermediate ribs to one main rib. These stages may be compared with stage three of *P. (K.) ohmi ohmi*. No heterochrony in the ornamental ontogenetic stages can be detected between the two species. Small uniform ventrolateral clavi occur on every rib probably in all ontogenetic stages.

The diameter at which the umbilical width is equal to the whorl height is 47 mm, which means that there is no significant heterochrony in the ontogeny of the shape of the conch in comparison with *P. (K.) mortilleti*. However, the adult size is probably significantly less than the adult size of *P. (K.) ohmi ohmi*. The presumed smaller size and the loss of the two last ornamental stages may indicate the ontogenetic process of progenesis in relation to the ontogeny *P. (K.) ohmi ohmi*._

***Pseudothurmannia* (*Kakabadziella*) *tornajensis*:** This species may be regarded as the fifth and last descendant species in this heterochronocline. It is not likely that *P. (K.) tornajensis* would be the young of *P. (K.) belimelensis*, because its ornamentation is more irregular than that of young *P. (K.) belimelensis*. Moreover, the advolute whorls of *P. (K.) tornajensis* increase much slower in height than those of *P.* (*K.*) *belimelensis*. Therefore *P.* (*K.*) *tornajensis* cannot be the microconch of the latter. It is interpreted as a descendent of *P.* (*K.*) *belimelensis*, which exhibits only one ornamental ontogenetic stage, which is similar to the first ornamental stage in *P.* (*K.*) *belimelensis*, but a little more irregular. The only possibility seems to be that one has to do with the phenomenon of dwarfism (nanism) by ontogenetic progenesis (precocious sexual maturation for acquiring a demographical strategy of type r). Because of its smallness it could have been a favourite prey for predators.

The phylogeny of *Crioceratites* (*Balearites*) *oicasensi*: The first ornamental ontogenetic stage of this species is characterized by fine, dense ribbing like *C.* (*B.*) *balearis* and by the presence of lateral tubercles. As in *C.* (*B.*) *balearis* lateral tuberculation stops at a diameter of 10 mm, and between this diameter and a diameter of 20 mm there is only fine, dense ribbing. The difference with *C.* (*B.*) *balearis* is the appearance of slightly thicker, widely spaced ribs with small pointed umbilical tubercles from a diameter of 20 mm. These main ribs become more and more distant and are lined by constrictions from a diameter of 31 mm. *C.* (*B.*) *balearis* also has wide-spaced main ribs lined by constrictions from a diameter of 35-40 mm. One may consider the appearance of main ribs earlier in the ontogeny of *C.* (*B.*) *oicasensis* as a case of predisplacement. If so, then *C.* (*B.*) *oicasensis* could be interpreted as a descendant of *C.* (*B.*) *balearis*. This species does not belong to the heterochronocline, but forms an individual phylogenetic side branch departing from *C.* (*B.*) *balearis*.

The phylogeny of *Crioceratites* (*Balearites*) *pseudothurmannii*: The ornamentation of this species fits best with the ornamentation of *C.* (*B.*) *theodomirensis*, and this is the reason why the author included it in subgenus *Crioceratites* (*Balearites*) as an individual side branch departing from *C.* (*B.*) *theodomirensis*. The heterochrony between the ontogenies of *C.* (*B.*) *pseudothurmannii* results from the process of acceleration of the ornamental ontogenetic stages one and two; the latter stage ends at a diameter of 22 mm instead of 36 mm.

Conclusion: Fig. 3. One may say that in this stepped cladogenetic mosaïc heterochronocline only the link between *P.* (*K.*) *ohmi ohmi* and *P.* (*K.*) *belimelensis* is uncertain. The five successive steps are not in contradiction to the starting points of the stratigraphic ranges of the various members of the heterochronocline. The heterochronocline consists of a first part from *C.* (*B.*) *balearis* to *P.* (*K.*) *ohmi ohmi* consisting of a stepped cladogenetic dissociated heterochronocline affected by different peramorphic processes, and a second part from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *tornajensis* consisting of a stepped cladogenetic paedomorphocline. The presence of *C.* (*B.*) *balearis* as well as *P.* (*K.*) *mortilleti* in the same heterochronocline does not mean that they should necessarily belong to one and the same genus, as many authors suggested.

The main distinction between the genera *Crioceratites* and *Pseudothurmannia* is the presence or absence of lateral tubercles in the first ontogenetic stage respectively. However, their presence in one and the same heterochronocline does support their close relationship, which has already been surmised by Nolan (1894). The author is convinced that the overstepping from *Crioceratites* to *Pseudothurmannia* is made from *C.* (*B.*) *theodomirensis* to *P.* (*K.*) *mortilleti*. The genus *Pseudothurmannia* forms a monophyletic group of species. A polyphyletic origin as advocated by Busnardo (2003) is untenable. In the course of the heterochronocline there is a remarkable increase in size from *C.* (*B.*) *theodomirensis* to *P.* (*K.*) *mortilleti* (a case of hypermorphosis), and a decrease in size from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *tornajensis* (a case of progenesis). The evolutionary tendency within the subgenus *Pseudothurmannia* (*Kakabadziella*) is from an involute to an evolute conch shape. *C.* (*B.*) *oicasensis* and *C.* (*B.*) *pseudothurmannii* are interpreted as individual side branches.

4.2. Anagenetic transitions: *mortilleti-catulloi*, *mortilleti-caravacaensis* and *ohmi ohmi-ohmi valbonnettensis* (Fig. 4)

Ancestry of *P.* (*K.*) *catulloi* and *P.* (*K.*) *caravacaensis*: These species closely resemble *P.* (*K.*) *mortilleti*. In 1995 the author (Hoedemaeker, 1995) referred to the specimens that are herein united in *P.* (*K.*) *caravacaensis* as a variety or chronosubspecies of *P.* (*K.*) *mortilleti*. On the other hand, Vermeulen *et al.* (2002) and Company *et al.* (2003) considered *P.* (*K.*) *catulloi* a junior synonym of *P.* (*K.*) *mortilleti*. Both *P.* (*K.*) *catulloi* and *P.* (*K.*) *caravacaensis* have a small umbilicus, which is even slightly smaller than the umbilicus of *P.* (*K.*) *mortilleti*. The latter is the only species with a small umbilicus among the potential ancestors occurring before the first appearance of *P.* (*K.*) *catulloi* and *P.* (*K.*) *caravacaensis*. *P.* (*K.*) *mortilleti* is, therefore, the only possible ancestor of these two species. It should be emphasized that there are no intermediate forms between *P.* (*K.*) *catulloi* with strong, regularly distributed ribs and *P.* (*K.*) *caravacaensis* with fine, irregularly distributed ribs. The morphological separation is total, and they can, therefore, be considered separate species. These species are both anagenetically descended from one and the same ancestor at the same time and in the same sea. Do we have a case of sympatric or parapatric speciation?

***Pseudothurmannia* (*Kakabadziella*) *catulloi*:** It was not possible to detect a significant heterochrony in the ornamental ontogeny between the chronospecies *P.*

(*K.*) *mortilleti* and *P.* (*K.*) *catulloi*. The latter has four ornamental ontogenetic stages.

1. The *balearis* stage, which ends at a diameter of 20 mm as in *P.* (*K.*) *mortilleti*.
2. The second stage is characterized by differentiated ribs with 1-3, but mainly 1-2, short intermediate ribs to one main rib. It is equivalent to stage two of *P.* (*K.*) *mortilleti*.
3. In *P.* (*K.*) *catulloi* the third stage is a strong-ribbed prolongation of stage two. The ribs become slightly more distant, thicker, blunter and more sigmoidal, and there are generally not more than 1-2, rarely three, commonly short, intermediate ribs between every pair of main ribs; umbilical bullae are absent. These features are consistent and are the prelude to the ornamentation of *Pseudothurmannia* (*Pseudothurmannia*) *picteti*. In *P.* (*K.*) *mortilleti* this third stage has more than two thin intermediate ribs to one main rib. This clear ornamental distinction between the third stages of *P.* (*K.*) *mortilleti* and *P.* (*K.*) *catulloi* can be interpreted as the product of 'adult variation', which does not involve heterochrony. Adult variation has been defined as a character present in the adult stage of an ancestor, which may in the ontogeny of a descendant reappear in the adult stage with the kind of difference that distinguishes varieties, races and chronospecies (De Beer, 1930; Gould, 1977). The new ornamentation of stage three of *P.* (*K.*) *catulloi* has been substituted for the ornamentation of stage three of *P.* (*K.*) *mortilleti*, the ancestor.
4. Stage four represents the adult ornamentation and begins at a diameter of c. 130-140 mm, which is the same as in *P.* (*K.*) *mortilleti*, that is, the appearance of extra thick ribs separated by 4-5 long ribs and a few short intercalatory ribs. *P.* (*K.*) *catulloi* may reach an adult size of more than 300 mm. There is no heterochrony in the ontogeny of the ornamentation with respect to that of *P.* (*K.*) *mortilleti*.

There is, however, a heterochrony in the shape of the conch; the egression in the macroconchs of *P.* (*K.*) *catulloi* begins at a larger diameter of c. 100 mm, and the equality of umbilical width and whorl height is also reached at a larger diameter of c. 125 mm. There is a clear heterochrony in the shape of the conch. The ontogeny of the shape of the macroconch of *P.* (*K.*) *catulloi* is retarded through the process of neoteny with respect to that of *P.* (*K.*) *mortilleti*, its ancestor. This retardation is correlated with the slightly smaller umbilical width and the greater whorl height of *P.* (*K.*) *catulloi* in comparison with *P.* (*K.*) *mortilleti*. Such narrowing of the umbilicus often occurs in evolutionary lineages and this trend can be explained by obtaining a better streamlining by finer sigmoidal ribbing and by more compressed shapes with smaller umbilici.

Pseudothurmannia* (*Kakabadziella*) *caravacaensis: It was not possible to detect a significant heterochrony between the ornamental ontogenies of the two chronospecies *P.* (*K.*) *mortilleti* and *P.* (*K.*) *caravacaensis*. In the latter, four ornamental ontogenetic stages could be distinguished:

1. The *balearis* stage ends at a diameter of 20 mm like in *P.* (*K.*) *mortilleti*.

2-3. There exists a clear ornamental distinction between the middle ontogenetic stages of *P.* (*K.*) *mortilleti* and *P.* (*K.*) *caravacaensis*. The ribbing remains fine, bundling of ribs is more frequent, the umbilical parts of the intermediate ribs become effaced, the number of intermediate ribs to one main rib is highly variable and varies from 1-6, and the distance between the main ribs can often be very great. It is difficult to make a distinction between these two middle ontogenetic stages; with growth, the distribution of main and intermediate ribs seems to increase in irregularity in the course of these stages, and the lower parts of intermediate ribs become more and more effaced. Just like *P.* (*K.*) *catulloi*, this ornamental change can be interpreted as the product of 'adult variation,' because it does not involve heterochrony.

4. This stage is not preserved in the material of the author.

There is, however, a clear heterochrony in the shape of the conch; the egression in *P.* (*K.*) *caravacaensis* begins much earlier in the ontogeny than in *P.* (*K.*) *mortilleti*, viz. at a diameter of c. 30-40 mm instead of 80-90 mm. The equality of umbilical width and whorl height is reached at a diameter of c. 70 mm instead of c. 100 mm. It is evident that the ontogeny of the conch shape has accelerated with respect to that of *P.* (*K.*) *mortilleti*, the ancestor. The early start of egression is a feature that makes *P.* (*K.*) *caravacaensis* readily distinguishable from *P.* (*K.*) *mortilleti*.

Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis: It was possible to detect significant heterochronies in the ornamental ontogenies at the anagenetic transition from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *ohmi valbonnettensis*. Four ornamental ontogenetic stages can be distinguished in the latter species.

1. The *balearis* stage, which ends at a diameter of 13 mm.
2. The *mortilleti* stage, which ends at a diameter of 55 mm. The stages one and two end later in the ontogeny than in *P.* (*K.*) *ohmi ohmi*. This retardation in the ornamental ontogeny results in a slightly finer and denser ribbing of *P.* (*K.*) *ohmi valbonnettensis* in contrast to *P.* (*K.*) *ohmi ohmi*.
3. Stage three shows an irregular disposition of 1-4 intermediate ribs to one main rib and the presence of umbilical bullae on the main ribs, which are absent in *P.* (*K.*) *ohmi ohmi*; this stage is equivalent to stage three in *P.* (*K.*) *ohmi ohmi* and ends at a diameter of 98 mm, which is not significantly earlier in the ontogeny than in *P.* (*K.*) *ohmi ohmi*.

4. The adult ornamentation shows extra thick, broad main ribs and prominent umbilical bullae.

There is also a clear heterochrony in the shape of the conch. The whorl height equals the umbilical width at a diameter of 56 mm, which is significantly later in the ontogeny than in *P.* (*K.*) *ohmi ohmi*. This retardation in the ontogeny of the conch shape is correlated with the slightly smaller umbilicus of *P.* (*K.*) *ohmi valbonnettensis* in comparison with *P.* (*K.*) *ohmi ohmi*. A smaller umbilicus and more sigmoid ribs promote swimming velocity.

The retardation in the ontogeny of the conch and ornamentation is indicative of the process of 'neoteny.' The evolutionary trend of the anagenetic transition from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *ohmi valbonnettensis* is a paedomorphic one. The differences between *P.* (*K.*) *ohmi ohmi* and *P.* (*K.*) *ohmi valbonnettensis* are too small to warrant the introduction of a new species, but the recognition of this subspecies is a way to identify the Catulloi Zone. The rapid transformation from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *ohmi valbonnettensis* probably occurred during the time span of the same precession of the equinoxes as the transition from *P.* (*K.*) *mortilleti* to *P.* (*K.*) *catulloi* and *P.* (*K.*) *caravacaensis*.

Conclusions: Fig. 4. The evolutionary trend of the anagenetic transition from *P.* (*K.*) *mortilleti* to *P.* (*K.*) *catulloi* is characterized by a paedomorphic tendency, the one from *P.* (*K.*) *mortilleti* to *P.* (*K.*) *caravacaensis* by a peramorphic one. In contrast to speciation by branching (cladogenesis), anagenesis is the tendency for a lineage to achieve greater functional efficiency owing to natural selection, that is, evolutionary improvement. Commonly, a gradual transition (gradualism) is implied, but in the cases described here the sea-level fall preceding major sequence boundary Ha7 caused the phyletic transition to become punctuated. As the morphological separation of the ancestor and descendant within the lineage is total, that is, without intermediate forms, both parts of the lineage can be considered genuine species, chronospecies, instead of subspecies.

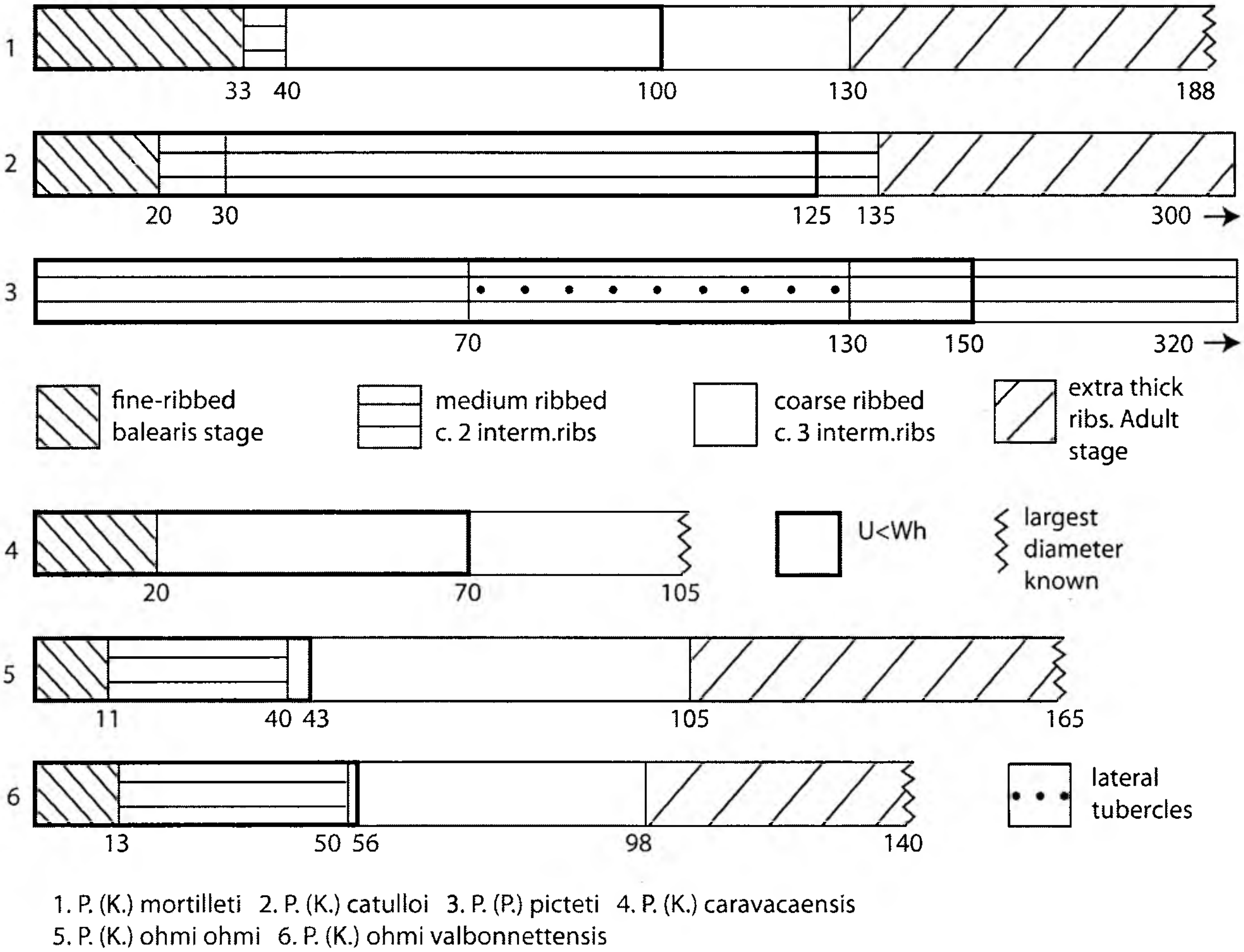


Fig. 4: Diagram showing the ontogenetic stages of the species involved in the anagenetic transitions from species 1→2 (paedomorphosis), from species 1→4 (peramorphosis) and from species 5→6 (paedomorphosis). The total paedomorphocline (partly anagenetic, partly cladogenetic) from *P.* (*K.*) *mortilleti* to *Pseudothurmannia* (*Pseudothurmannia*) *picteti* (1→2→3) is added to show the close relationship between *Kakabadziella* and *Pseudothurmannia*; the innovation of lateral tubercles in *P (P.) picteti* is shown.

The transition from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *ohmi valbonnettensis* is, like in *P.* (*K.*) *catulloi*, characterized by a paedomorphic tendency.
This transition from *P.* (*K.*) *mortilleti* to the chronospecies *P.* (*K.*) *catulloi* or *P.* (*K.*) *caravacaensis* and from *P.* (*K.*) *ohmi ohmi* to *P.* (*K.*) *ohmi valbonnettensis* occurred in a very short time geologically, probably not longer than the time span of one precession of the equinoxes, 20.000 years, because the change took place in a deep water (upper bathyal) environment (implying no hiatus) between two successive beds at the boundary between the Ohmi and Catulloi zones, and because intermediate forms were not found. The change was induced by the major sea-level fall, that is, during the Falling Stage Systems Tract that precedes major sequence boundary Ha7. As a consequence of this deep sea-level fall many biotopes of ammonite species were pushed over the shelf edge and severely telescoped. This reduction of the extension of their biotopes would have enhanced selection pressure and ultimate extinction (Hoedemaeker, 1995a).

4.3. Stepped cladogenetic dissociated peramorphocline within subgenus *Pseudothurmannia* (*Pseudothurmannia*) (Fig. 5)

It should be stressed that species of the subgenera *Pseudothurmannia* (*Pseudothurmannia*) and *Pseudothurmannia* (*Parathurmannia*) were never found below the base of the Catulloi Zone. All nine species with trituberculate main ribs in the adult are restricted to the Catulloi Zone, which begins just one or two orbital precessions earlier than major sequence boundary Ha7. This could be confirmed along the Río Argos, along the River Veveyse, in the Angles section, in the Tornajo section, in the Vergons section, in the Chamaloc section and in the Valbonnette section. In this basal bed (bed A153) along the Río Argos *P.* (*K.*) *caravacaensis*, *P.* (*K.*) *catulloi*, *P.* (*K.*) *ohmi valbonnettensis*, *P.* (*Pa.*) *dissiticostata*, *P.* (*Pa.*) *sarasini*, and *P* (*P.*) *picteti* start their ranges. There is a strong radiation of *Pseudothurmannia* at the base of the Catulloi Zone.

Ancestry of *P.* (*P.*) *picteti*: The first ornamental ontogenetic stage of *P.* (*P.*) *picteti* closely resembles the second ornamental ontogenetic stage of *P.* (*K.*) *mortilleti* and *P.* (*K.*) *catulloi*; *P.* (*P.*) *picteti* has, like *P.* (*K.*) *mortilleti*, a truncated venter. The last argument may indicate that *P.* (*P.*) *picteti* could be a direct descendant of *P.* (*K.*) *mortilleti*. Moreover *P.* (*P.*) *picteti* has a small umbilicus and strongly overlapping whorls like *P.* (*K.*) *catulloi* and *P.* (*K.*) *mortilleti*. However, the slightly wider spacing of the ribs makes the resemblance with the ribbing of the second and third stages of *P.* (*K.*) *catulloi* so great, that many specimens of this species figured in literature have been identified as *P. picteti*. Moreover *P.* (*K.*) *catulloi* and *P.* (*P.*) *picteti* start their ranges in the same bed (Río Argos bed A153). All these arguments make it probable that *P.* (*P.*) *picteti* have descended from *P.* (*K.*) *catulloi* at the same time or just after the latter succeeded *P.* (*K.*) *mortilleti* as chronospecies.

***Pseudothurmannia* (*Pseudothurmannia*) *picteti*:** This species is the aperamorphic ancestor of this peramorphocline. The ornamentation of young *P.* (*P.*) *picteti* lacks the ornamental ontogenetic *balearis* stage, which may have disappeared through persistent acceleration. Only two ornamental ontogenetic stages could be distinguished.

1. The first stage of *P.* (*P.*) *picteti* is similar to the second stage of *P.* (*K.*) *catulloi*, and consists of rather wide-spaced main ribs and of 1-3 short intermediate ribs between every two main ribs. This stage ends at a diameter of c. 60 mm.
2. In the second stage, the ribbing coarsens and there are mainly 1-2 intermediate ribs to one main rib; this stage is similar to the third ornamental stage of *P.* (*K.*) *catulloi*. This uniform and regular ornamentation continues up to the adult aperture, which means that *P.* (*P.*) *picteti* lacks the distinct adult ornamentation which is present in its ancestor, *P.* (*K.*) *catulloi*. This also means that adult *P.* (*P.*) *picteti* has an ornamentation which characterizes a younger ontogenetic stage of the ancestor. The ornamental ontogeny of *P.* (*P.*) *picteti* is, therefore, retarded with respect to its ancestor, and caused by the heterochronic process of neoteny, because the adult size of *P.* (*P.*) *picteti* of 320 mm is of the same order as that of *P.* (*K.*) *catulloi*.

On the other hand, in *P.* (*P.*) *picteti* a new ornamental character was introduced, which has been passed down to all subsequent members of the subgenus *Pseudothurmannia* (*Pseudothurmannia*), viz. the development of lateral tubercles on main ribs. This ornamental 'innovation' starts at a diameter of 75 mm, but disappears at a diameter of 130 mm; the lateral tubercles are only present over three quarters of a whorl, and merely occur in a transitional ontogenetic stage.
There is a clear heterochrony with respect to its ancestor in the shape of the conch; the umbilical width of *P.* (*P.*) *picteti* equals the whorl height at a diameter of 150 mm, which is significantly later than *P.* (*K.*) *catulloi* (at D = 123 mm). This means that the ontogenetic development of the shape of the conch is also retarded. This heterochrony is probably caused by neoteny. This paedomorphic evolutionary trend (paedomorphocline, which is partly anagenetic and partly cladogenetic) in fact proceeds from *P.* (*K.*) *mortilleti* via *P.* (*K.*) *catulloi* to *P.* (*P.*) *picteti*; the latter is, however, the aperamorphic species of the peramorphocline within the subgenus *Pseudothurmannia* (*Pseudothurmannia*).

***Pseudothurmannia* (*Pseudothurmannia*) *simionescui*:** This species is the first descendant of the stepped cladogenetic dissociated peramorphocline, and its ornamentation closely resembles that of *P.* (*P.*) *picteti*. It has two ornamental ontogenetic stages.

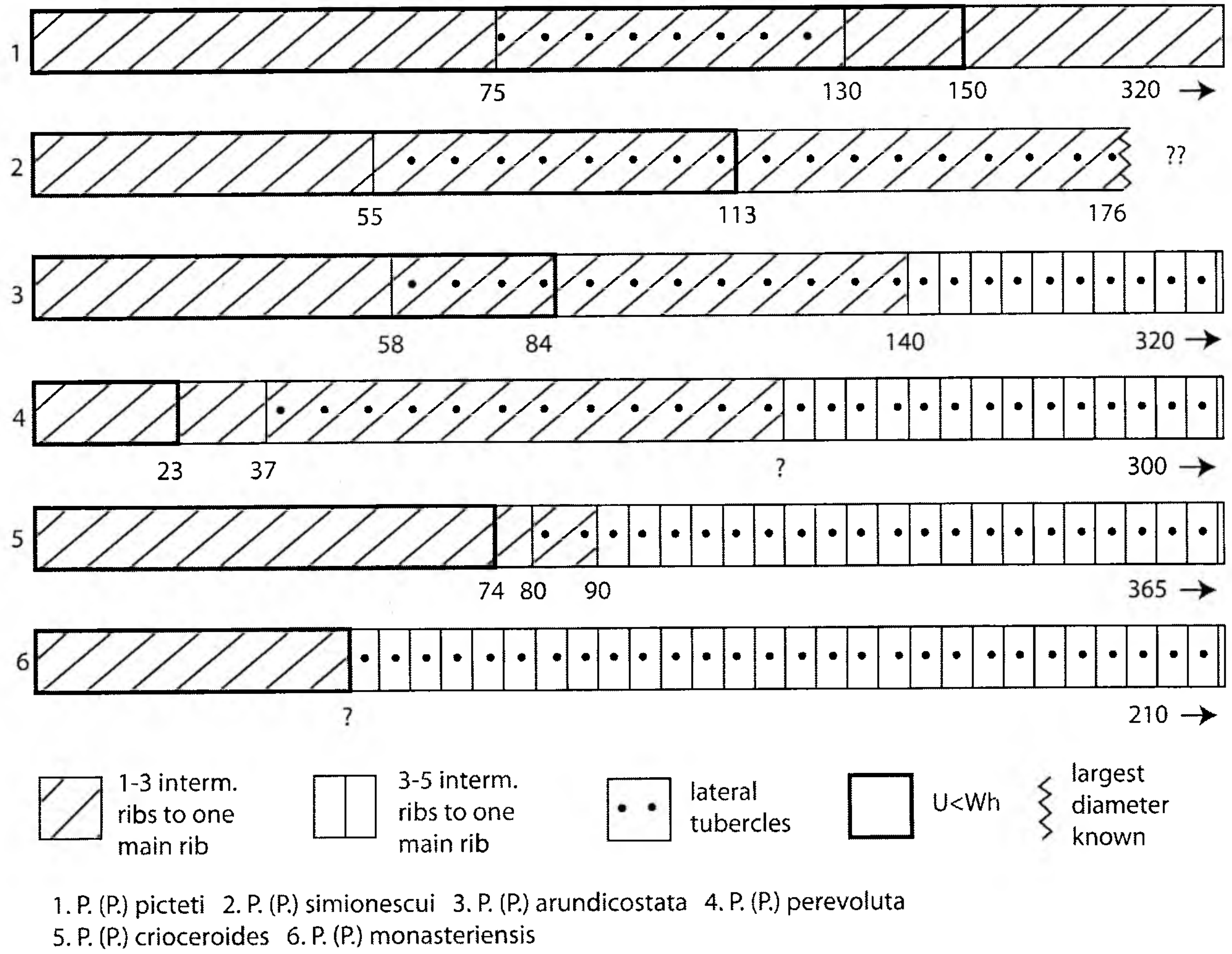


Fig. 5: Diagram showing the ontogenetic stages in the ornamentation and conch shape of the species involved in the stepped cladogenetic dissociated peramorphocline within subgenus *Pseudothurmannia* (*Pseudothurmannia*) (species 1-4). It becomes clear that *P.* (*P.*) *crioceroides* and *P.* (*P.*) *monasteriensis* (species 5-6) do not comply with the peramorphocline and probably form a separate phylogenetic branch. The heterochrony in the start of lateral tuberculation is interpreted as a process of predisplacement. The heterochrony in the shape of the conch and the start of the adult ornamentation are interpreted as processes of acceleration.

1. The first stage consists of 1-3 intermediate ribs to one main rib and is equivalent to stage one of *P.* (*P.*) *picteti*.
2. In the second stage the ribbing gradually becomes stronger, rather uniform and regular, with mainly two intermediate ribs to one main rib; it begins at a diameter of 65 mm, is equivalent to stage two of *P.* (*P.*) *picteti* and continues at least to a diameter of 176 mm.
3. It is not known whether this species has a third stage with a *crioceratites*-like ornamentation as all the other descendants have, for the largest known *P.* (*P.*) *simionescui* has a diameter of only 176 mm, while all other members of the subgenus *Pseudothurmannia* (*Pseudothurmannia*) have an adult diameter of more than 300 mm and a third adult ornamental stage. Nevertheless, it is quite possible that a similar ornamental stage exists in *P.* (*P.*) *simionescui*.

The lateral tubercles inherited from *P.* (*P.*) *picteti* appear at a diameter of 55 mm, which is much earlier than in *P.* (*P.*) *picteti*, and continue up to the aperture. The apertural extension of the lateral tuberculation can be explained by 'progressive deviation.' This phenomenon does not produce heterochrony. However, the earlier start of the lateral tuberculation is interpreted to be due to the heterochronic process called 'predisplacement' (Alberch *et al.*, 1979). Predisplacement concerns the beginning of a structure, which starts earlier in the ontogeny of the descendant than in the ancestor; the result of this heterochrony is the same as the process of acceleration.
There is a clear heterochrony in the shape of the conch; the inner whorls overlap only a little, and the whorl height equals the umbilical width at a diameter of 113 mm, which is earlier in the ontogeny than in *P.* (*P.*) *picteti* (at D = 150 mm). This could be interpreted as heterochrony produced by acceleration. Moreover, the

last whorl becomes detached from the preceding whorl and is weakly crioconic; it is difficult to judge where the whorls stop touching each other. This detachment is a late innovation of the shape of the conch and the prelude to the *crioceratites*-like ornamentation in the adult of the descendants. Perhaps *P.* (*P.*) *simionescui* already has this ornamentation.

***Pseudothurmannia* (*Pseudothurmannia*) *arundicostata*:** This species is the second descendant species in this peramorphocline and has three ornamental ontogenetic stages.

1. The first stage has a similar ornamentation as *P.* (*P.*) *picteti* without lateral tubercles up to a diameter of 58 mm.
2. The second stage has a similar ornamentation as *P.* (*P.*) *simionescui* with lateral tubercles up to a diameter of 140 mm. So there is no 'predisplacement' of the start of the lateral tubercles as in *P.* (*P.*) *simionescui*.
3. The last stage is characterized by a late 'ornamental innovation,' viz. from a diameter of 140 mm begins a *crioceratites*-like ornamentation consisting of thick trituberculate ribs separated by 3-4 long intermediate ribs; this ornamentation continues up to the aperture. The *simionescui*-like ornamentation stops earlier than in *P.* (*P.*) *simionescui*, which can be interpreted as heterochrony through acceleration of the ontogeny in relation to *P.* (*P.*) *simionescui*. The innovation of the *crioceratites*-like ornamentation is presumably a case of hypermorphosis, since the adult size of *P.* (*P.*) *arundicostata* is more than 320 mm. Perhaps *P.* (*P.*) *arundicostata* returns to a crioceratitic way of life. As it is not clear whether *P.* (*P.*) *simionescui* has a *crioceratites*-like ornamentation, the author cannot assess where this innovation has occurred for the first time, in *P.* (*P.*) *simionescui* or in *P.* (*P.*) *arundicostata*.

There is a clear heterochrony in the shape of the conch. In *P.* (*P.*) *arundicostata* the diameter at which the umbilical width equals the whorl height is 84 mm instead of 113 mm in *P.* (*P.*) *simionescui*, the ancestor. This can be attributed to heterochrony by the process of acceleration. The early whorls of *P.* (*P.*) *arundicostata* are in touch with each other, the later whorls are just not in touch; it is difficult to judge where the whorls stop touching each other. It seems as if crioconic whorls go together with crioceratitic ornamentation.

***Pseudothurmannia* (*Pseudothurmannia*) *perevoluta*:** This species is the third and last descendant of the cladogenetic peramorphocline. The ribbing of *P.* (*P.*) *perevoluta* can be considered an acceptable variation of the *picteti*/*simionescui*-like ribbing, as it consists of long ribs separated by one or two shorter ribs. However, not all the long ribs are main ribs; the main ribs are provided with umbilical and later also lateral tubercles, and have thicker lower parts. The adult part figured by Dimitrova (1967) shows *crioceratites*-like ornamentation with 4-5 intermediate ribs to one trituberculate main rib. There is a clear heterochrony in the shape of the conch. The whorls are not touching each other, probably with the exception of the innermost whorls, and the whorl height grows very slowly. The whorl height equals the umbilical width already at a diameter of 23 mm. The early start of the egression and the diameter at which the shell becomes crioconic may be attributed to heterochrony by the process of acceleration. The lateral tubercles already begin at a diameter of 37 mm, and this earlier start of the lateral tuberculation is considered to be due to the process of 'predisplacement.' The ornamental innovation set in by *P.* (*P.*) *arundicostata*, is inherited by *P.* (*P.*) *perevoluta*. The largest known specimen of *P.* (*P.*) *perevoluta* is 290 mm, but the species may reach a diameter of more than 300 mm).

***Pseudothurmannia* (*Pseudothurmannia*) *crioceroides*:** This species does not fit in the cladogenetic peramorphocline of *Pseudothurmannia* (*Pseudothurmannia*). *P.* (*P.*) *crioceroides* has two ornamental ontogenetic stages.

1. A *picteti*-like stage with commonly 2-3 intermediate ribs to one main rib, including a very short stage with 1-2 intermediate ribs to one main rib, ends at a diameter of 80-90 mm.
2. A second stage characterized by a *crioceratites*-like ornamentation with commonly 3-5 intermediate ribs between every two thick trituberculate main ribs. This late ontogenetic innovation possibly indicates a return to a crioceratitic way of life during the adult stage. This late innovation continues up to the aperture at a diameter of more than 365 mm. The interpretation given for this deviating ontogenetic development is that *P.* (*P.*) *crioceroides* forms a side branch of the peramorphocline, which descended directly from *P.* (*P.*) *picteti*. The strongly overlapping whorls and the small umbilicus in the young ontogenetic stage are arguments in favour of this derivation.

With respect to the shape of the conch, the whorls start egressing much earlier than in *P.* (*P.*) *picteti*, and the umbilical width equals the whorl height at a diameter of 74 mm. This can be ascribed to heterochrony by the process of acceleration. In a variety of *P.* (*P.*) *crioceroides* [which might belong to *P.* (*P.*) *monasteriensis*] the trituberculation begins earlier, a case of predisplacement.

***Pseudothurmannia* (*Pseudothurmannia*) *monasteriensis*:** This species looks like *P.* (*P.*) *crioceroides* and may be a variety of the latter, but it has a different shape (rounded whorls), thicker sturdier ribs and an earlier start of lateral tubercles. The latter start at a diameter of c. 50 mm, whereas in the typical *P.* (*P.*) *crioceroides* they start at a diameter of 80-90 mm, with the exception of the variety that has an early start of the lateral tubercles. The ontogeny of this variety and of *P.* (*P.*) *monasteriensis* would show heterochrony with respect to the ontogeny of *P.* (*P.*) *crioceroides* through the process of 'predisplacement.'

The shape of the conch is quite similar to the conch of *P.* (*P.*) *crioceroides* with the exception of the rounded whorl section, but whether this is due to the process of acceleration or retardation in the ontogeny is not clear.

Conclusion: Fig. 5. It can be concluded that the peramorphosis in the shape of the shells in the successive steps of the cladogenetic *Pseudothurmannia* (*Pseudothurmannia*) peramorphocline is produced by the acceleration of the start of the egression of the whorls to ever younger ontogenetic stages. U = Wh at a diameter of 150 mm, 113 mm, 84 mm, and 37 mm in *P.* (*P.*) *picteti*, *P.* (*P.*) *simionescui*, *P.* (*P.*) *arundicostata* and *P* (*P.*) *perevoluta* respectively. This means that also the umbilicus becomes wider at the same diameter. Also *P.* (*P.*) *crioceroides* and *P* (*P.*) *monasteriensis* yielded to the same trend with D = 74 mm and D = 50 mm respectively, though they form a side branch of the main lineage. The overall trend is to become slightly crioconic. This trend is also recognizable in the late ontogenetic return to a *crioceratites*-like ornamentation consisting of thick trituberculate main ribs with many long intermediate ribs. Perhaps this is connected with a return to a crioceratitic way of life. The author also observed predisplacement of the beginning of lateral tuberculation, which moved in the successive ontogenies from D = 75 mm in *P.* (*P.*) *picteti* via D = 55-58 mm in *P.* (*P.*) *simionescui* and *P.* (*P.*) *arundicostata* to D = 37 mm in *P.* (*P.*) *perevoluta*. This is not a case of acceleration, because all the species of the subgenus *Pseudothurmannia* (*Pseudothurmannia*) have comparable sizes of more than 300 mm.

The ontogeny of the aperamorphic ancestral species, *P.* (*P.*) *picteti*, shows a neotenic heterochrony with respect to the ontogeny of *P.* (*K.*) *catulloi*, its ancestor, which in its turn shows a neotenic heterochrony with respect to *P.* (*K.*) *mortilleti* (Fig. 4). So, starting from *P.* (*K.*) *mortilleti* the first appearing species of *Pseudothurmannia*, and following the phylogenetic line to *P* (*P.*) *perevoluta* one has to do with a stepped mosaïc heterochronocline with an early paedomorphic part and a later peramorphic part. The polyphyletic origin of the non-tuberculate species and the tuberculated species of *Pseudothurmannia* (Busnardo, 2003, p. 62, table 6) is untenable; the latter group originated from the former.

4.4. Evolutionary trends in subgenus *Pseudothurmannia* (*Parathurmannia*) (Fig. 6)

Ancestry of *P.* (*Pa.*) *Sarasini*: The ornamentation of the inner whorls of *Pseudothurmannia* (*Parathurmannia*) *sarasini* does not resemble the ornamentation of *P.* (*K.*) *catulloi* or *P.* (*P.*) *picteti* in any sense. However, *P.* (*Pa.*) *sarasini* has a small umbilicus, and the only remaining small-umbilicated ancestors are *P.* (*K.*) *mortilleti* and *P.* (*K.*) *caravacaensis*. The ribbing of the inner whorls of *P.* (*Pa.*) *sarasini* is fine and dense, but regularly spaced umbilical bullae are already present at a diameter of 8 mm. This means that the ornamental ontogenetic stage with fine uniform *balearis*-like ribbing is absent, for in *P.* (*K.*) *caravacaensis* and *P.* (*K.*) *mortilleti* umbilical bullae appear at the end of the *balearis* stage. Young *P.* (*Pa.*) *sarasini* have regularly, but widely spaced main ribs separated by 4-5, sometimes even six intermediate ribs. This feature is characteristic for all species of *Pseudothurmannia* (*Parathurmannia*). Wide spacing of main ribs in potentially ancestral species occurs only in *P.* (*K.*) *caravacaensis* in which irregularly spaced main ribs are commonly separated by 1-2, but also by 3-4, and even by 6-7 intermediate ribs; this wide separation of the main ribs is not rare. The presence of more than four intermediate ribs between two main ribs in young specimens is an exclusive characteristic of the subgenus *Parathurmannia*. This implies that *P.* (*K.*) *caravacaensis* is likely the ancestor of *P* (*Pa.*) *sarasini*. The latter species must have split off at much the same time as the origination of *P.* (*K.*) *caravacaensis* from *P.* (*K.*) *mortilleti*, that is, at the base of the Catulloi Zone when the sea level was rapidly falling to a very low level and the decreasing biotope caused severe selection pressure.

***Pseudothurmannia* (*Parathurmannia*) *sarasini*:** In this species, umbilical bullae appear much earlier than in *P.* (*K.*) *caravacaensis*, which means that the ontogenetic stage with the *balearis*-like ornamentation has disappeared, possibly through persistent acceleration. *P.* (*Pa.*) *sarasini* has four ornamental ontogenetic stages:

1. The first stage consists of 4-5, rarely six, flexuous intermediate ribs to one main rib.
2. The second stage begins at a diameter of 40 mm and consists of rather coarse, less flexuous ribbing with two intermediate ribs to one main rib. In this stage small lateral tubercles on the main ribs appear; they disappear with the beginning of the third ornamental stage, at a diameter of 68 mm.
3. The third stage has strong, widely separated main ribs, every two of which are separated by 3-4 intermediate ribs.
4. The fourth stage begins at a diameter of 83 mm, is situated on the living chamber, and is considered the adult stage. In this stage the intermediate ribs become more or less effaced below midflank as in *P.* (*K.*) *caravacaensis*.

The umbilical width becomes equal to the whorl height at a diameter of 100 mm. The largest specimen hitherto found is 107 mm in diameter.

***Pseudothurmannia* (*Parathurmannia*) *dissiticostata*:** In this species only three ontogenetic stages could be established:

1. The first stage is similar to the first one of *P.* (*Pa.*) *sarasini*, and consists of flexuous main ribs with 4-6 intermediate ribs between every two main ribs. This stage ends at a much larger diameter than in *P.* (*Pa.*) *sarasini*, viz. at a diameter of c. 70 mm.

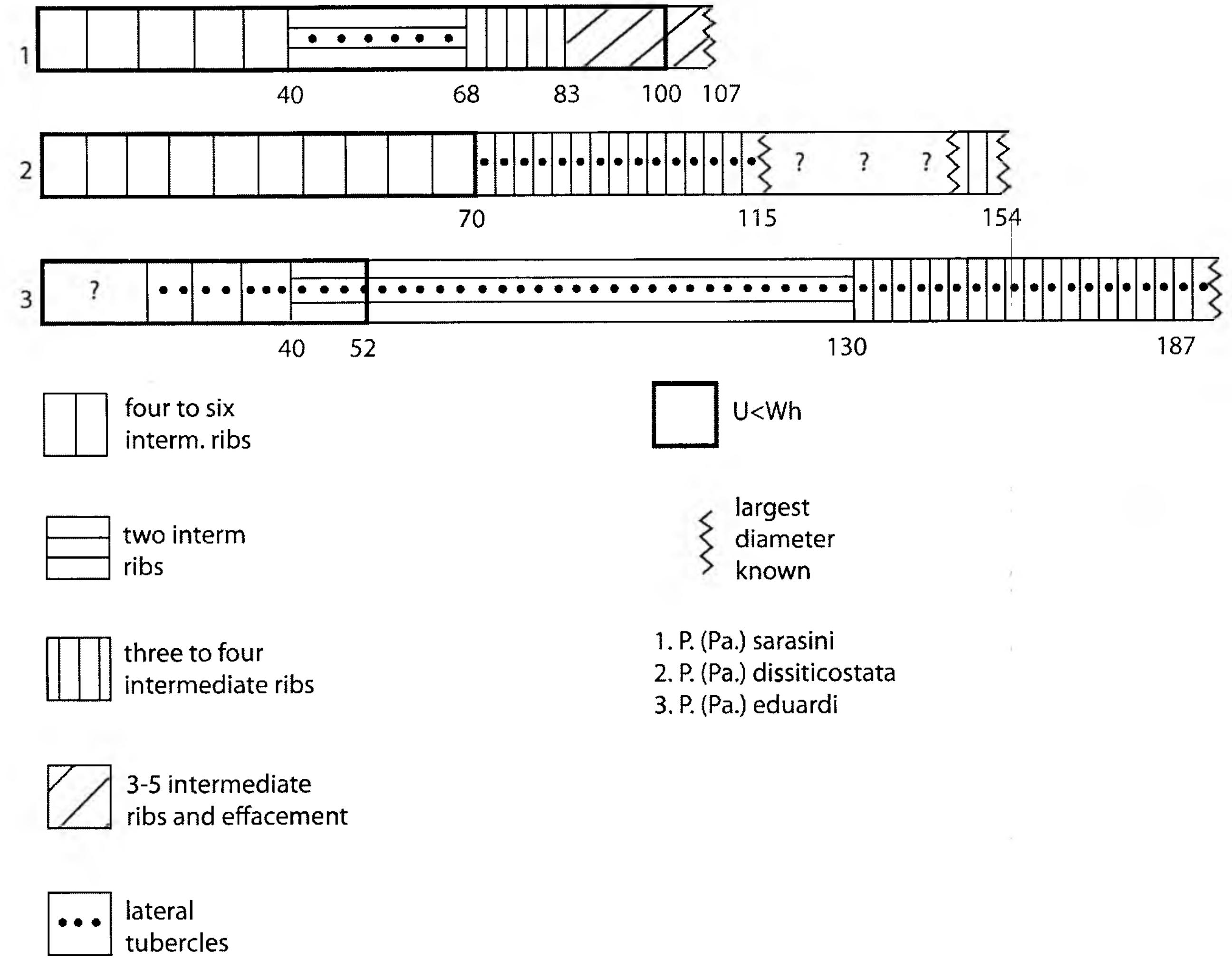


Fig. 6: Diagram showing the ontogenetic stages in the ornamentation and conch shape of the species within subgenus *Pseudothurmannia* (*Parathurmannia*). The heterochrony in the shape of the conch seems to display a stepped cladogenetic peramorphocline, but the heterochrony in the ornamental ontogenetic stages does not comply with this peramorphocline. Species 2 and 3 are, therefore, considered to form two independent phylogenetic branches originating from species one.

2. The second stage consists of 3-4 intermediate ribs to one main rib. Lateral tubercles appear on the main ribs and continue to be present at least up to a diameter of 115 mm. Thus also the end of the second stage is clearly retarded in relation to the second stage in *P.* (*Pa.*) *sarasini*.
3. The author collected a whorl fragment belonging to a specimen at least 150 mm in diameter with 2-4 flexuous intermediate ribs to one main rib; this stage is equivalent to stage three of *P.* (*Pa.*) *sarasini*. However, it ends at a much larger diameter and is retarded in relation to *P.* (*Pa.*) *sarasini*. As all the stages of *P.* (*Pa.*) *dissiticostata* are longer than the equivalent stages of *P.* (*Pa.*) *sarasini*, one may have to do with 'proportioned gigantism,' which is caused by more rapid growth with a constant rate of somatic (= ornamental) development.

There is a clear heterochrony in the shape of the conch. The inner whorls are overlapping and have a small umbilicus, and the diameter at which the umbilicus is equal to the whorl height is c. 70 mm, which is smaller than in *P.* (*Pa.*) *sarasini*. This diameter has shifted from 100 mm to 70 mm, which is indicative of the process of acceleration. The author is not sure whether it is possible that one species can show two opposite evolutionary trends.

***Pseudothurmannia* (*Parathurmannia*) *edouardi*:** This species shows three ornamental ontogenetic stages.

1. The first stage is equal to the first one of *P.* (*Pa.*) *sarasini* and consists of fine ribbing with 5-6 long intermediate ribs between every two main ribs. Within this stage (at a diameter of c. 20 mm) small lateral tubercles appear which gradually become more prominent. These tubercles appear in an earlier stage than in *P* (*Pa.*) *sarasini*, and this early appearance may be the result of the heterochronic process of predisplacement.

2. Stage two begins at a diameter of 40 mm, and consists of coarse, straight main ribs of which every pair is separated by two intermediate ribs. This stage is equivalent to stage two of *P.* (*Pa.*) *sarasini*, and begins at the same diameter as in *P.* (*Pa.*) *sarasini*, but significantly earlier in the ontogeny than in *P.* (*Pa.*) *dissiticostata*. It ends at a diameter of 130 mm [in the specimen of *P.* (*Pa.*) *edouardi* described by Thomel, 1965b].
3. The third stage exhibits strong main ribs with three intermediate ribs to one main rib. This stage is equivalent to stage three of *P.* (*Pa.*) *sarasini*. This implies that stage two proceeds to a larger diameter than in *P.* (*Pa.*) *sarasini*, but does not show significant ontogenetic difference with *P.* (*Pa.*) *dissiticostata*. This is probably a case of 'progressive deviation', which does not involve heterochrony.

The whorls of *P.* (*Pa.*) *edouardi* are not in contact and it is not known whether the inner whorls are in contact or not. The equality of whorl height and umbilical width is reached at a diameter of 52 mm, which is much earlier than in *P.* (*Pa.*) *sarasini*, but also earlier than in *P.* (*Pa.*) *dissiticostata*. This may be interpreted as the heterochronic process of acceleration.

Conclusion: Fig. 6. There is only one peramorphic trend apparent that involves all species of subgenus *Pseudothurmannia* (*Parathurmannia*), viz. the acceleration of the start of the egression of the whorls monitored by the shift of the diameter at which the whorl height equals the umbilical width. In this trend the whorls of the successive species become more and more evolute and slightly crioconic in the end, as in subgenus *Pseudothurmannia* (*Pseudothurmannia*). This means that *P.* (*Pa.*) *sarasini* is the ancestral stock. There may also be a tendency to increase in size. With respect to the shape and size of the successive species, one could possibly think of a peramorphocline.

However, as to the ornamental (= somatic) ontogenetic development, there is no clear heterochrony. Their ornamental ontogeny does not change in steps in one direction.

Be that as it may, it became clear that the three species *P.* (*Pa.*) *sarasini*, *P* (*Pa.*) *dissiticostata* and *P.* (*Pa.*) *edouardi* are closely related, because they have similar ornamentations in the same ontogenetic order. But whether the three species form one lineage is not probable. It is more probable that *P.* (*Pa.*) *dissiticostata* and *P.* (*Pa.*) *edouardi* originate independently from *P* (*Pa.*) *sarasini*.

4.5. Evolutionary trends in the *binelli* group of subgenus *Crioceratites* (*Binelliceras*)

Ancestry of *C.* (*B.*) *binelli*: This species may be the ancestor of *C.* (*B.*) *balearis*. *Crioceratites* (*Binelliceras*) begins close to, or at the base of, the Balearis Zone, and has its roots in the large group of species of *Crioceratites* with trituberculate main ribs on the inner whorls, especially in the group of *C. sornayi* Sarkar, 1955, *C. sornayi* var. *tuberculata* Sarkar, 1955 and *C. majoricensis* Nolan, 1894. Vermeulen (2004) introduced the name *Davouxiceras* for the group of *Crioceratites* with trituberculate main ribs, type species *C. nolani* Kilian, 1910, but the present author hesitates to use this name, because he cannot yet judge whether this group of completely or partly trituberculate *Crioceratites* constitutes a monophyletic or a polyphyletic group (iterative origination). He suspects it to be an artificial species. Within *Crioceratites* (*Binelliceras*), there also seems to be a gradual reduction of the fine uniform ribbing of the young stage in the course of the phylogeny of the subgenus.

***Crioceratites* (*Binelliceras*) *binelli*:** This species is regarded as the ancestor of all species in the *binelli* group and probably also of *C.* (*B.*) *balearis*. This species has three ornamental ontogenetic stages:

1. The first stage has 5-6 intermediate ribs to one main rib. The main ribs are provided with lateral tubercles up to a diameter of 15 mm.
2. The second stage consists of thin, uniform ribs with 6-8 intermediate ribs to one main rib. Fasciculation from umbilical bullae and fibulation toward the ventrolateral tubercles frequently occur.
3. The third adult ornamental ontogenetic stage begins at a diameter of 45-50 mm. The irregularly spaced main ribs are slightly thicker than the 3-16 intermediate ribs to one main rib. They are bordered by shallow constrictions. The largest phragmocone ends at a diameter of 74 mm, which implies (Wh : wh = 7 : 4) a total diameter of c. 125 mm.

***Crioceratites* (*Binelliceras*) *krenkeli*:** This species mostly resembles *C.* (*Bi.*) *binelli* and could be typified as a coarse issue of *C.* (*Bi.*) *binelli*. However, they do not occur together, but follow each other in time in the Río Argos succession and in the Angles section (observation of the author). Therefore, they presumably represent two chronospecies of an anagenetic lineage. *C.* (*Bi.*) *krenkeli* has three ornamental ontogenetic stages.

1. The first stage consists of 1-3 intermediate ribs to one trituberculated main rib. Large ventrolateral tubercles are present. The first trituberculate stage ends at a diameter of 16 mm and gives room for stage two.
2. Stage two consists of fine uniform flexuous ribbing. The umbilical bullae give rise to fascicules, and between every two fascicules are c. seven intermediate ribs.
3. From a diameter of 42 mm the third stage begins with 2-3 intermediate ribs to one main rib. With growth, the main ribs become more and more differentiated from the intermediate ribs and become more wide-

ly spaced. This results in an adult ornamentation of well-differentiated, regularly-separated, widely-spaced main ribs, of which every two are separated by 4-6 intermediate ribs. So, the inner whorls, up to a diameter of 42-45, are similar to *C.* (*Bi.*) *binelli*, but after this diameter, the ribbing becomes gradually coarser and more regularly differentiated into main and intermediate ribs. This change in ribbing can be interpreted as 'adult variation' by which varieties, races and chronospecies can be distinguished. No heterochrony is involved.

***Crioceratites* (*Binelliceras*) *ibizensis*:** This species has three ornamental ontogenetic stages.

1. The first stage has, like *C.* (*Bi.*) *binelli*, 3-6 intermediate ribs to one main rib; fibulation frequently occurs; the main ribs are provided with lateral tubercles up to a diameter of 15 mm.
2. The second stage consists of main and intermediate ribs, which are only slightly differentiated; fasciculation from umbilical bullae occurs. There are 6-8 intermediate ribs to one main rib.
3. In the third stage, which begins at a diameter of c. 23-25 mm, the main ribs gain in prominence and are irregularly spaced; there are 2-6 intermediate ribs between every two main ribs. The irregularity concerns not only the distribution of main and intermediate ribs, but also their curvature, the variable presence of forking, the variable presence of fasciculation, the variation in the height of the origination of intermediate ribs and the variation in prominence and effacement of ribs. Ventrolateral tubercles are present on every rib. This third ontogenetic stage begins earlier in the ontogeny than in *C.* (*Bi.*) *binelli*. This acceleration of ornamental stage two is possibly the only heterochrony in the ontogeny of *C.* (*Bi.*) *ibizensis* in relation to that of *C.* (*Bi.*) *binelli*. It could also be due to this small size of *C.* (*Bi.*) *ibizensis* in relation to *C.* (*Bi.*) *binelli*. The largest specimen of *C.* (*Bi.*) *ibizensis* found has a diameter of 64 mm and is almost half the size of *C.* (*Bi.*) *binelli*. The phragmocone ends at a diameter of 40 mm.

***Crioceratites* (*Binelliceras*) *rotundatus*:** Three ornamental ontogenetic stages could be recognized in this species.

1. The first stage consists of trituberculate main ribs with five intermediate ribs. Fibulation frequently occurs. This stage ends at a diameter of 10-11 mm. This stage ends earlier in the ontogeny than in the ontogenies of *C.* (*Bi.*) *ibizensis* and *C.* (*Bi.*) *binelli*.
2. This stage is followed by a second stage with fine, almost uniform ribbing up to a diameter of 25-30 mm. Fasciculation occurs. The second stage also ends earlier in the ontogeny than in *C.* (*Bi.*) *binelli*. The shifts in the ends of the first and second ornamental ontogenetic stages are the only heterochronies between the ontogenetic developments of *C.* (*Bi.*) *rotundatus* and *C.* (*Bi.*) *binelli*, and are probably due to acceleration.
3. Then follows the third stage, which persists up to the aperture and consists of prominent, rather regularly distributed main ribs, with 3-4 intermediate ribs to one main rib, rarely two or six. The largest *C.* (*Bi.*) *rotundatus* found is 127 mm in diameter. Small ventrolateral tubercles are present on every rib up to the aperture.

Conclusion: The species united by the author in the *binelli* group of the subgenus *Crioceratites* (*Binelliceras*) have the same succession of similar ornamental ontogenetic stages. This unites the group. Apart from the anagenetic transition from *C.* (*Bi.*) *binelli* to *C.* (*Bi.*) *krenkeli* (Fig. 9), the other two species, *C.* (*Bi.*) *ibizensis* and *C.* (*Bi.*) *rotundatus*, do not show a harmonious heterochronocline with *C.* (*Bi.*) *binelli*. Therefore the author believes that these species do not form a heterochronocline with *C.* (*Bi.*) *binelli*, but represent two independent branches originating from *C.* (*Bi.*) *binelli*. There is an apparent evolutionary tendency from fine uniform ribbing to coarser differentiated ribbing in the *binelli* group of the subgenus *Crioceratites* (*Binelliceras*).

4.6. Stepped cladogenetic peramorphocline in the *angulicostatus* group of subgenus *Crioceratites* (*Binelliceras*) (Fig. 7)

The species of the *angulicostatus* group are here provisionally included in the subgenus *Crioceratites* (*Binelliceras*), because the ontogeny of their ornamentation resembles the ornamental ontogeny of the species of the *binelli* group. However they show some primitive traits, viz. the presence of lateral tubercles up to a greater diameter, and the coarseness of their ribbing. They lack the fine-ribbed part with fasciculation of the ribs that characterizes the *binelli* group, and apparently do not have the close relation with *Crioceratites* (*Balearites*) *balearis* that the *binelli* group and *Pseudothurmannia* have. However, they exhibit rows of small ventrolateral tubercles, which are considered typical for *Pseudothurmannia*, *Crioceratites* (*Balearites*) and the *binelli* group of *Crioceratites* (*Binelliceras*). Nevertheless, their phylogenetic relation to the latter three taxa is still obscure.

Vermeulen included *C.* (*Bi.*) *angulicostatiformis* and *C.* (*Bi.*) *seitzi* in *Spathicrioceras* Sarkar, 1955, because of the similarities in the ornamentation, but Sarkar (1955) stressed the loose crioconic coiling of his new genus, while *C.* (*Bi.*) *angulicostatiformis*, *C.* (*Bi.*) *seitzi* and *C.* (*Bi.*) *angulicostatus* are characterized by a tight crioconic coiling. Their closest relatives are doubtless the species of the *binelli* group. Therefore the author inserted them

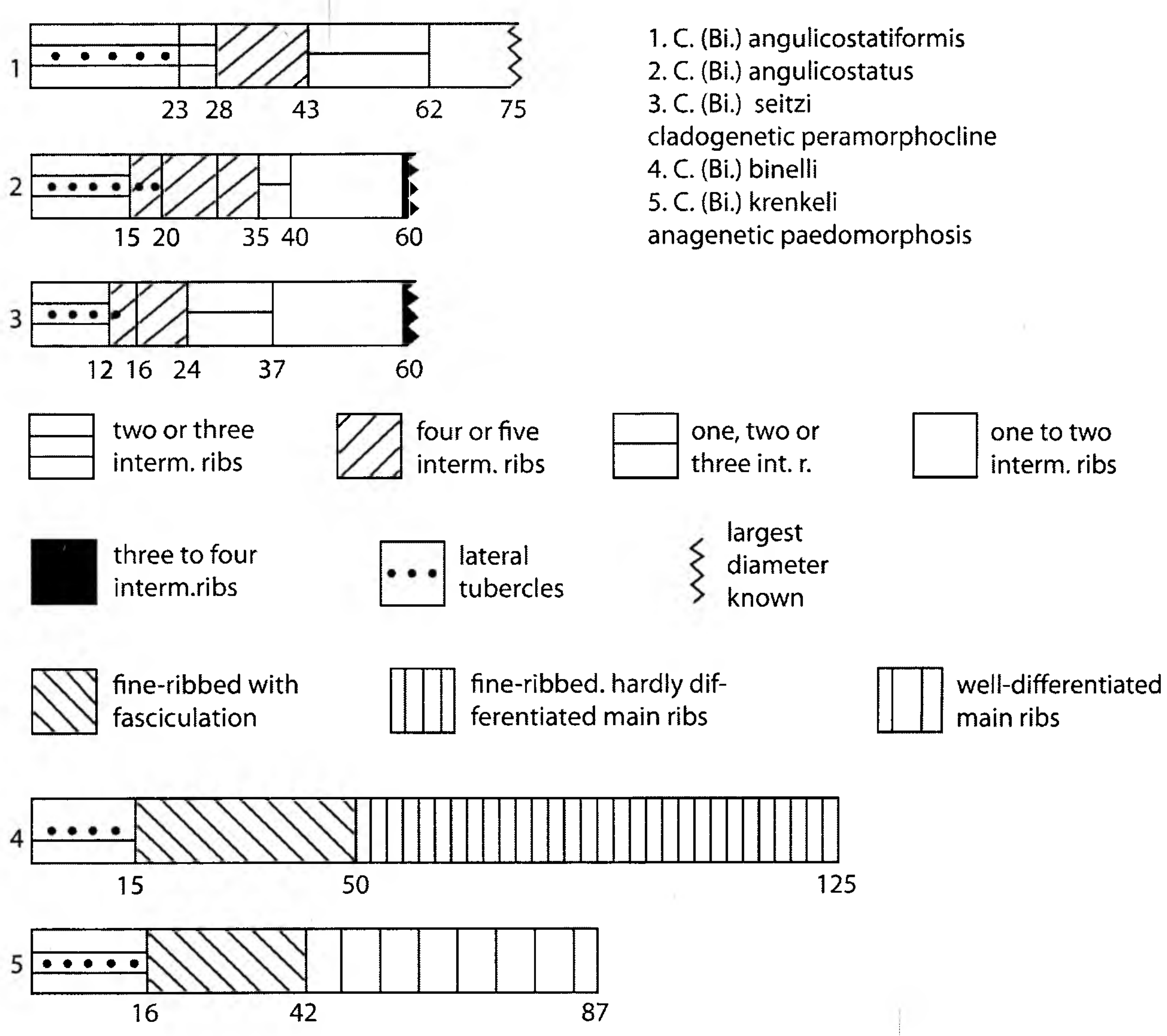


Fig. 7: Diagram showing the ontogenetic stages in the ornamentation of the species (1-3) of the Angulicostata Group within *Crioceratites (Binelliceras)* and the species (4-5) involved in the anagenetic transition from *Crioceratites* (*Binelliceras*) *binelli* to *C.* (*B.*) *krenkeli*. The heterochrony in the ornamentation of the species 1-3 form a nice stepped cladogenetic peramorphocline showing acceleration in the ornamental ontogenetic stages; that of species 4-5 also exhibits acceleration.

provisionally into *Crioceratites* (*Binelliceras*) as a separate group, the *angulicostatus* group.

Crioceratites* (*Binelliceras*) *angulicostatiformis: This species is considered the ancestral aperamorphic species of the peramorphocline and exhibits four ornamental ontogenetic stages.

1. A stage with one short intermediate rib between every two long ribs. The long ribs are provided with lateral tubercles. However every other long rib is a main rib provided with an umbilical bulla, whereas every long rib in between them is thinner and lacks the umbilical bulla. First the thinner long ribs lose their lateral tubercles. Later, at a diameter of 23 mm the main ribs also lose their lateral tubercles.
2. From a diameter of 28 mm there are two intermediate ribs to one long rib, but in fact there are five intermediate ribs between two main ribs, because the intermediate rib in the middle is long.
3. From a diameter of 43 mm there are three intermediate ribs to one main rib; the middle intermediate rib is the longest. From a diameter of 50 mm this long intermediate rib becomes a main rib again; it strengthens and obtains an umbilical bulla. Between every pair of main ribs is now one intermediate ribs, rarely two.
4. From a diameter of 62 mm every two thick main ribs are separated by 2-3 intermediate ribs. Forking is not rare.

Crioceratites* (*Binelliceras*) *angulicostatus: This species has four ornamental ontogenetic stages.

1. The first stage has two intermediate ribs to one thick rib with a lateral tubercle. Later, every second thick rib obtains an umbilical bulla; every other main rib becomes weak, loses its umbilical bulla, but still keeps its lateral tubercle. The two intermediate ribs unite into one ventrolateral tubercle (fibulation). This stage corresponds to stage one of *C.* (*Bi.*) *angulicostatiformis*, but it ends at a smaller diameter of 15 mm due to acceleration of the ontogeny in relation to *C.* (*Bi.*) *angulicostatiformis*.
2. The second stage consists of four intermediate ribs between every main rib. Fibulation is still present. From a diameter of 20 mm the lateral tubercles disappear. Between every two main ribs are 3-4 intermediate ribs. This stage is equivalent to stage two of *C.* (*Bi.*) *angulicostatiformis*, but ends earlier in the ontogeny, viz. at a diameter of 33 mm. This implies an acceleration of the ontogeny in relation to *C.* (*Bi.*) *angulicostatiformis*.
3. From a diameter of 33 mm, the number of intermediate ribs between every two main ribs is two. This third stage is equivalent to stage three of *C.* (*Bi.*) *angulicostatiformis* and ends at a diameter of 40 mm; it has accelerated in relation to the corresponding stage in *C.* (*Bi.*) *angulicostatiformis*.
4. From a diameter of 40 mm there are 1-2 intermediate ribs to one main rib. Forking occurs. Only just before the aperture, this number suddenly augments to three or four.

Crioceratites* (*Binelliceras*) *seitzi: This species has four ornamental ontogenetic stages:

1. The ribbing of the first stage consists of two intermediate ribs to one main rib, and the main ribs are provided with lateral tubercles. This stage is equivalent to stage one of *C.* (*Bi.*) *angulicostatus*. This stage ends at a diameter of 12 mm, which is earlier in the ontogeny than in *C.* (*Bi.*) *angulicostatus*; it has therefore accelerated in relation to the ontogeny of the latter species.
2. The ribbing of the second stage consists of 3-5 intermediate ribs to one main rib. The lateral tubercles disappear at a diameter of 16 mm. This stage is equivalent to stage two in *C.* (*Bi.*) *angulicostatus*, and ends at a diameter of 24 mm, that is, earlier in the ontogeny than in *C.* (*Bi.*) *angulicostatus*. It has accelerated in relation to the ontogeny of the latter species.
3. In this third stage every two main ribs are separated by three intermediate ribs. Splitting of ribs occurs. This stage ends at a diameter of 37 mm, which is earlier in the ontogeny than the equivalent stage three in *C.* (*Bi.*) *angulicostatus*. Therefore, this stage also has accelerated in relation to the corresponding stage of the ancestor.
4. The ribbing of the last stage has only 1-2 ribs to one main rib. Only just before the aperture this number suddenly augments to 3-4; a similar increase in number of intermediate ribs occurs just before the aperture of *C.* (*Bi.*) *angulicostatus*.

Conclusion (Fig. 7): The three species of the *angulicostatus* group form a harmonious, stepped cladogenetic peramorphocline. Owing to the rarity of these species, their total ranges are obscure, but thanks to this peramorphocline their phylogeny became clear. The ancestor of this group is not known, but should be sought for in the neighbourhood of the ancestor of *C.* (*Bi.*) *binelli*.

5. DISTRIBUTION AND BIOSTRATIGRAPHY

5.1. Distributional peculiarities

Different assemblages along the Río Argos: The outcrops of the Lower Cretaceous along the Río Argos (Caravaca, Murcia, Spain) extend over two subbasins separated by what the author interpreted as a swell. This becomes clear if one follows the rocks of the chronostratigraphic interval that includes the uppermost Hauterivian and lower Barremian from west (section A) to east (section W) over a distance of 5 km (Fig. 1). Going from section A to section K, halfway between A and W, one can observe a gradual decrease in thickness of this chronostratigraphic interval; the marlstone interbeds become appreciably thinner and several marly limestone beds disappear. The result is that rocks of this chronostratigraphic interval in section K are half as thick as in section A. However, between the adjacent sections K and L there is an abrupt increase in thickness of the chronostratigraphic interval; the limestone beds are separated again by thick marlstone interbeds. There is apparently an important fault between outcrops K and L. From here the chronostratigraphic interval stays thick with thick marlstone intervals up to its easternmost outcrop in section W. It is the opinion of the author that these changes in thickness should be interpreted as two subbasins separated by a swell. The siliciclastic clay fraction could hardly be deposited on the swell, where mainly pelagic limestones (consisting of calacareous nannoplankton) were deposited almost without siliciclastic marlstone interbeds. The two subbasins belong to the same sea. The author called the western subbasin the Las Oicas basin, the eastern one the Los Miravetes basin.

The rocks in the Las Oicas basin contain much more limestone beds than those of the Miravetes Basin. In the latter basin the marlstone beds clearly dominate over the limestone beds, whereas in the Oicas basin the quantities of marlstone and limestone are approximately equal. The author is of the opinion that the Oicas basin was deeper than the Miravetes basin.

It appears that the two subbasins contain different *Pseudothurmannia* assemblages. In the eastern Los Miravetes subbasin, *P.* (*K.*) *ohmi ohmi* and *P.* (*K.*) *mortilleti* are absent, and *P.* (*K.*) *ohmi valbonnettensis* and *P* (*K.*) *catulloi* rather rare, but *P.* (*K.*) *caravacaensis* is abundant. On the other hand, in the western Las Oicas subbasin *P.* (*K.*) *ohmi ohmi*, *P.* (*K.*) *mortilleti*, *P.* (*K.*) *ohmi P.* (*K.*) *valbonnettensis* and *P.* (*K.*) *catulloi* are abundant, whereas *caravacaensis* is rare (three specimens). In the Los Miravetes subbasin several specimens with lateral tubercles in the adult occur, viz. *P.* (*P.*) *crioceroides* and *P.* (*P.*) *arundicostata*, some specimens of *P.* (*Pa.*) *dissiticostata* and *P.* (*Pa.*) *sarasini*, and one specimen of *P.* (*P.*) *picteti*. In the Las Oicas subbasin, on the contrary, only three specimen of *P.* (*P.*) *picteti* and one of *P.* (*Pa.*) *sarasini* were sampled. This is a remarkable faunal difference over a distance of only 5 km in the same sea and the same facies. Also with respect to the species of the subgenera *Crioceratites* (*Binelliceras*) and *Crioceratites* (*Balearites*), a difference exists between the faunas of the Miravetes and Oicas basins. In the former basin, *C.* (*B.*) *pseudothurmannii* and *C.* (*B.*) *ibizensis* are abundantly present, whereas these species are absent in the Oicas basin, except for one specimen of *C.* (*B.*) *ibizensis*.

Remarkable also are the rapid faunal changes in section A of the Las Oicas Basin. Bed A144 of the Río Argos succession, for instance, yielded almost exclusively specimens of *P.* (*K.*) *ohmi ohmi* in great abundance (58 specimens sampled), whereas the following bed, A145, produced almost exclusively specimens of *P.* (*K.*) *mortilleti,* also in great abundance (40 specimens sampled). It is very intriguing to observe these rapid changes in faunal composition, which occurred within 20.000 years (duration of one precession).

In the platform deposits of the same chronostratigraphic interval of the same sea outcropping in the Sierra de la Muela, Moratalla, about 20 km north of the Río Argos, *P.* (*P.*) *crioceroides* was not found. On the other hand, many specimens of *P.* (*P.*) *picteti* occur on the platform, whereas this species is rare in the basins. There is an abundance of *P* (*K.*) *catulloi.* Also, it is striking that on the platform the *Pseudothurmannia* fauna is dominated by large specimens, whereas in the basins the specimens of *Pseudothurmannia* are much smaller. This difference in size between basinal and platform specimens is also obvious for *Emericiceras thiollieri*, *Taveraidiscus*, *Barremites* and *Phylloceras*. Why ammonites of old age prefer to live and die in shallow water and the specimens of younger age in the deep open sea is not clear.

Remarkable in this respect is also the absence of *P.* (*K.*) *catulloi* and *P.* (*K.*) *caravacaensis* in the Catulloi Zone of Chamateuil (near Castellane) in southeastern France. These differences in the composition of the *Pseudothurmannia* fauna indicate that every species has its own different biotope.

Presence of either a Catulloi or an Ohmi zonal assemblage, or of both: Quite a different distributional peculiarity is the presence of either an Ohmi zonal ammonite assemblage or a Catulloi zonal ammonite assemblage instead of the presence of both assemblages. From several localities, only species of *Pseudothurmannia* (and other genera) from the Catulloi zonal assemblage were mentioned, for instance, by Karakasch (1907) and Baraboshkin (personal communication, 1995) from the Crimea in Russia, by Avram (1995) and Simionescu (1898) from Roumania, by Cecca *et al.* (1994, 1995, 1998), Cecca & Pallini (1995) and Faraoni *et al.* (1995, 1996) from several localities in Italy, and by Busnardo (2003) from the banks of the river Veveyse near Châtel-St-Denis, Switzerland. The author found only species of the Catulloi zonal assemblage in the Sierra de la Muela (Moratalla, southeast Spain) and in Chamateuil (Castellane, Alpes-de-Haute-Provence, France), both rather shallow platform deposits. Specimens of *Pseudothurmannia* (and other genera) of the Ohmi zonal assemblage appear to be absent.

On the other hand, Dimitrova (1967) and Mandov (1976) mentioned species from both Ohmi and Catulloi zones from Bulgaria, Company *et al.* (2003) and the author found the ammonite assemblages of both biozones in the outcrops along the Río Argos, and ammonite species of both assemblages have been reported from the Chamaloc section along the road from Chamaloc to the Col de Rousset (Drôme, France).

Finally, Vašiček (1989 to 2002) mentioned only species of *Pseudothurmannia* (and other genera) that occur in the Ohmi Zone from the western Carpathians in Slovakia and Vermeulen (2002, 2005) reported only specimens from the Ohmi Zone in the Angles section (Alpes-de Haute-Provence, France). In these cases at least a part of the Catulloi Zone should be present in higher stratigraphic levels.

This peculiar distribution of the species of *Pseudothurmannia* can be explained by the presence of a major sequence boundary (Ha7) a little above the base of the Catulloi Zone (along the Río Argos on top of bed A155). In platform environments the newly deposited sediments of the Ohmi zone became emergent and were eroded away when the sea regressed. During late Catulloi times sedimentation was resumed, and mixed as a consequence of wave action, so that only sediments of Catulloi age were preserved as a condensed deposit. In deeper parts of the shelf, but still above wave base, sediments of Ohmi Age remained preserved. Permanent sedimentation was resumed when the sea began to transgress and started earlier than in the shallower parts of the sea. In still deeper environments below wave base, sediments of both Ohmi and Catulloi ages remained preserved. With increasing depth ammonites become extremely rare. However, during the Falling Stage Systems Tract a shallower, ammonite-bearing facies may have shifted into the basin, giving rise to relatively ammonite-rich beds within an almost ammonite-barren succession. This is how the author explains the ammonite richness of the Faraoni Level in the Umbria-Marche Apennines in Italy, an ammonite-bearing marker bed amidst the almost ammonite-barren Maiolica Formation in Italy. This level yielded (besides many other genera) a *Pseudothurmannia* assemblage of the basal Catulloi Zone (Cecca *et al.*, 1998) exclusively consisting of *Pseudothurmannia* (*Kakabadziella*) *caravacaensis*.

5.2. Biozonation of the *Balearites* and *Pseudothurmannia* beds; Faraoni Level (Figs. 8A-B, 9A-B)

The biozonation presented here is in essence the same as that which the author proposed in 1995, and is based on the chronostratigraphic distribution of the ammonite species in the Hauterivian-Barremian boundary beds exposed along the Río Argos (west of Caravaca, Province of Murcia, Spain). However, the identification of the species and their ranges has been revised subsequently. The proposed zonation has been adopted by the Lower Cretaceous Ammonite Working Group of the IUGS Subcommission on Cretaceous Stratigraphy and used in "A Geologic Time Scale 2004" (Gradstein *et al.*, 2004).

The author distinguished a Balearis Zone below, an Ohmi Zone in the middle, and a Catulloi Zone above, characterized by the first occurrences of *Crioceratites* (*Balearites*) *balearis*, *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* and *Pseudothurmannia* (*Kakabadziella*) *catulloi*, respectively. The boundaries are still the same as in the author's publication in 1995b; the base of bed A124 for the Balearis Zone, the base of bed A 142 for the Ohmi Zone, and the base of bed A153 for the Catulloi Zone.

The zonations published by Vermeulen (2002, 2004, 2005), Vermeulen *et al.* (2002) and Company *et al.* (2003, 2005) differ in many respects from the one proposed by the author. The differences are probably due to collection failure, a normal case in palaeontological collecting of macroinvertebrates, which causes incomplete stratigraphic ranges, but are also due to deviating identifications of ammonites, mainly owing to the inadequate preservation of holotypes, which caused the different concepts of the species. These failures became apparent because of the great numbers of specimens collected by the author. As Company *et al.* (2003) set up their zonation in the same section A as the author did along the Río Argos, the zones and subzones of Company *et al.* could be calibrated exactly with the author's zonation. Vermeulen's (2005) ammonite zones defined in the section along the road to Angles could also be correlated fairly well with the section Argos Section A (Fig. 8A-B), because the author sampled a small collection of ammonites from the same interval in the Angles section, but especially because the sequence boundary Ha7 and the isotopic signal of the lower black shale of the Faraoni Level can be clearly identified in the Argos Section A (Company *et al.*, 2005) and in the Angles section.

Correlation with the Faraoni Level: The Faraoni Level is a 0.3 m thick ammonite-rich group of seven beds, A-G, within the *Pseudothurmannia* beds. The type section is situated along the River Bosso (Umbria, Italy). The ammonite association of bed D was published by Cecca *et al.* (1998), and correlates with the ammonite association of beds A153-154 of the Río Argos succession. The latter beds harbour a unique ammonite association; they contain the end of some ammonite ranges as well as the beginning of some other ammonite ranges. The author established the concurrence of the first *Pseudothurmannia caravacaensis* sp. nov., *P. catulloi* (Parona), *P. sarasini* Sarkar, *P. dissiticostata* sp. nov., *P. arundicostata* sp. nov., *Emericiceras thiollierei* (Astier), *Acrioceras tabarelli* (Astier), *Protetragonites crebrisulcatus* (Uhlig), *Lytoceras densifimbriatum* (Uhlig), *Abritusytes neumayri* (Haug), *Paraspiticeras* sp. and *Anahamulina subcylindrica* (d'Orbigny), with the last *Neolissoceras grasianum subgrasianum* (Drushchits & Kudrjavtsev), *Phyllopachyceras winkleri* (Uhlig), *Lytoceras subfimbriatum* (d'Orbigny), *Protetragonites quadrisulcatus* (d'Orbigny), *Plesiospitidiscus subdifficilis* (Karakasch), and *Lamellaptychus*. This important concurrent association of 15 ammonites occurs exclusively in these beds, which are the two basal beds of the Catulloi Zone.

It is most remarkable that the concurrence of the same species also has been established in the thick bed D halfway between the two black shale beds of the type Faraoni Level from which a large ammonite fauna was described by Cecca *et al.* (1998). It becomes clear that bed A154 and bed D can exactly be correlated with each other. As such a concurrence of so many ranges cannot be repeated in time, the author concludes that the beds A153-155 represent the Faraoni Level *sensu stricto*.

Along the Río Argos the isotopic signal of the Faraoni Level has been established in the paper-shale between beds A147 and A149 (Company *et al.*, 2005), which is high in the Ohmi Zone, four meters below bed A154 and five metres below sequence boundary Ha7. This level does not show the unique occurrence of ranges of the Faraoni Level *sensu* stricto. Therefore there seems to be a discrepancy between the age of the Faraoni Level according to stable isotopes, and its age according to fossils. In the section along the route d'Angles, the isotopic signal of the Faraoni Level occurs at the same stratigraphic position as along the Río Argos, 4 m below sequence boundary Ha7 (Bodin *et al.*, 2005); this sequence boundary is interpreted at the top of bed 64 of the Angles section (Fig. 68).

There is another paper-shale level in the Río Argos succession between beds A160 and A162, four metres above sequence boundary Ha7 within the Catulloi Zone. This paper shale can also be found in section W between beds W37 and W38, 2.5 m above sequence boundary Ha7 on top of bed W36. This paper shale level corresponds to the Couche à Poissons (bed 92.2), assigned to the Faraoni Level in the *Pseudothurmannia* beds along the River Veveyse near Châtel-St.-Denis (Fribourg, Switzerland; Busnardo *et al.*, 2003, Bodin *et al.*, 2006b, Godet *et al.*, 2006) (Fig. 69). Those species of *Pseudothurmannia* that were figured with bed numbers by Busnardo *et al.* (2003), all characterize the Catulloi Zone (Fig. 69). The following species were identified by the author (see synonymy lists of these species in the Systematics part, and Busnardo, 2003):

1. *P. caravacaensis* sp. nov. occurs in beds 91.1, 92.3, 93.5, 94.5, 94.6 and was figured by Busnardo *et al.*, 2003 under the names *Parathurmannia* sp. A on pl. 9, figs. 4, 9, *Parathurmannia* gr. *sarasini* on pl. 15, fig. 6, *Pseudothurmannia* (*l.s.*) sp. C on pl. 15, fig. 12 and *Pseudothurmannia* (*l.s.*) *rugosa* n. sp. (= microconch of *P. caravacaensis*) on pl. 21, figs. 2, 7.
2. *P. catulloi* (Parona, 1897) occurs in beds 92.1, 93.4 and was figured by Busnardo *et al.* under the names *Parathurmannia* gr. *sarasini* on pl. 12, fig. 1 and *Parathurmannia mortilleti* on pl. 6, fig. 1.
3. *P. ohmi valbonnettensis* subsp. nov. occurs in bed 92.3 and was figured by Busnardo *et al.* under the name *Parathurmannia* cf. *biassalensis* on pl. 15, figs. 3, 8.
4. *P. sarasini* Sarkar, 1955 occurs in beds 91.3, 93.5 and was figured by Busnardo *et al.* under the names *Parathurmannia renevieri* on pl. 9, fig. 8 and *Pseudothurmannia* (*l.s.*) sp. D on pl. 19, fig. 1.
5. *P. dissiticostata* sp. nov. occurs in bed 94.5 and was figured by Busnardo *et al.* under the name *Pseudothurmannia* (*l.s.*) sp. E on pl. 19, fig. 6.

Remarkable is the presence of *Sabaudiella* Vašíček, May 2003 (= *Sabaudiella* Busnardo, June 2003), which is restricted to the Couche à Poissons (bed 92.2). Specimens of this opportunistic genus occur in similar stratigraphic positions along the Río Argos (*Sabaudiella argosensis* Vašíček, 2003 in parallel section W) and in the section along the route du Col de Rousset north of Chamaloc (Die, Drôme, France), i.e. in the lower part of the catulloi Zone. This level does not show the unique concurrence of ranges of the Faraoni Level *sensu stricto*. Sequence boundary Ha7 is interpreted as being situated on top of bed 91, which is 4.5 m below the Couche à Poissons (Fig. 69).

It is not possible to correlate the Couche à Poissons with the Faraoni Level determined by Company *et al.* (2005) in the Rio Argos, nor with the level in the section along the route d'Angles. The latter two levels have a clear Ohmi zonal assemblage, whereas the Couche à Poissons has a clear Catulloi zonal assemblage. It should also be noted that the Couche à Poissons and the Faraoni equivalents in the Angles and Río Argos sections are single black layers, whereas the outcrops of the Faraoni Level in the Umbrian Mountains and in the Vergons section show all the layers A to G (Baudin *et al.*, 1999, 2002) and have a basal Catulloi zonal age.

As for the Angles section, Bodin *et al.* (2005) explained that a decrease in the Phosphorous Accumulation Rate (PAR) encountered in the Angles section may be caused by a decease in continental weathering rates, or by a spread of dysaerobic to anoxic bottom waters, or the combined effect of both processes. The beginning of the rather sharp decrease of the PAR in the Angles section coincides with the Faraoni equivalent in bed 53. The PAR minimum ends rather abruptly at the base of bed 72, which is the base of the Hugii Zone. This would mean that the same dysaerobic condition prevailed during the whole Catulloi Zone and during the last part of the Ohmi Zone, and that this condition may have extended as far as southeastern Spain. In the Angles section the same interval is in addition characterized by a conspicuous low in siliciclastic detritus, i.e. a minimum presence of detritus consisting of phyllosilicates, quartz, K-feldspar and Na-plagioclase. In this case the minima in the PAR and detritus are apparently linked and seem to designate the absence of significant water movements. During this long period of dysaerobic conditions many local subsidiary paper shales with varying organic Carbon contents and isotopic signals could have been formed. This period would have lasted, roughly estimated, c. 360,000 years being c. 18 precessions of the equinoxes, which are represented by the limestone/marlstone couplets of approximately one meter thickness in the Río Argos succession (Sprenger & Ten Kate, 1992). Inexplanable remains the fact that the Cutulloi Zone in the Angles section is only 3.5 metres thick (Fig. 68), whereas it is 15 m thick (Fig. 8B) in the Río Argos Succession and c. 22 m thick (Fig. 69) along the River Veveyse. In the Angles section something must be missing; there is probably a hiatus at sequence boundary Ha7.

The author is of the opinion that in Río Argos section A the Faraoni Level *sensu stricto* is represented by the beds A153-155 on account of the unique concurrence of 15 ammonite ranges in these beds. The marly interbeds between these limestone beds are not developed into black shales as in the type Faraoni Level. The two paper shale levels, four metres above and five metres below the sequence boundary, are subsidiary paper shale layers. They should not be considered Faraoni equivalents, because this would cause unacceptable correlation errors.

Stratigraphic position of sequence boundary Ha7 in various Mediterranean sections: The *Pseudothurmannia* fauna that characterizes the Catulloi Zone makes an explosive start in the Falling Stage Systems Tract preceding sequence boundary Ha7. The sequence boundery was interpreted to be situated on top of bed A155 in the Río Argos succession (Caravaca, Murcia, Spain) (Figs. 8 and 9); on top of bed 91 in the River Veveyse near Châtel-Saint-Denis (Switzerland) (Fig. 69); in the Angles section (Alpes-de-Haute-

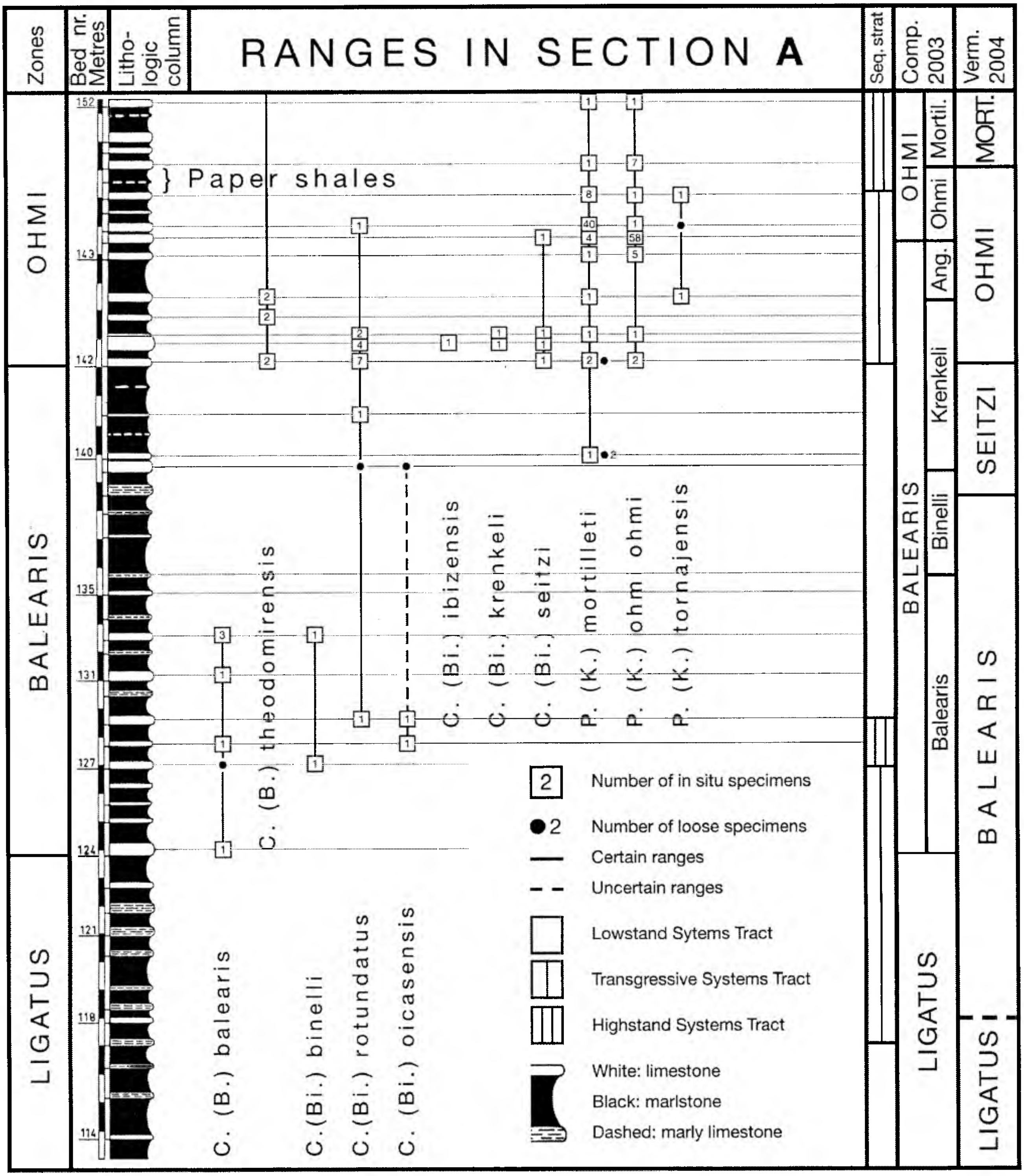
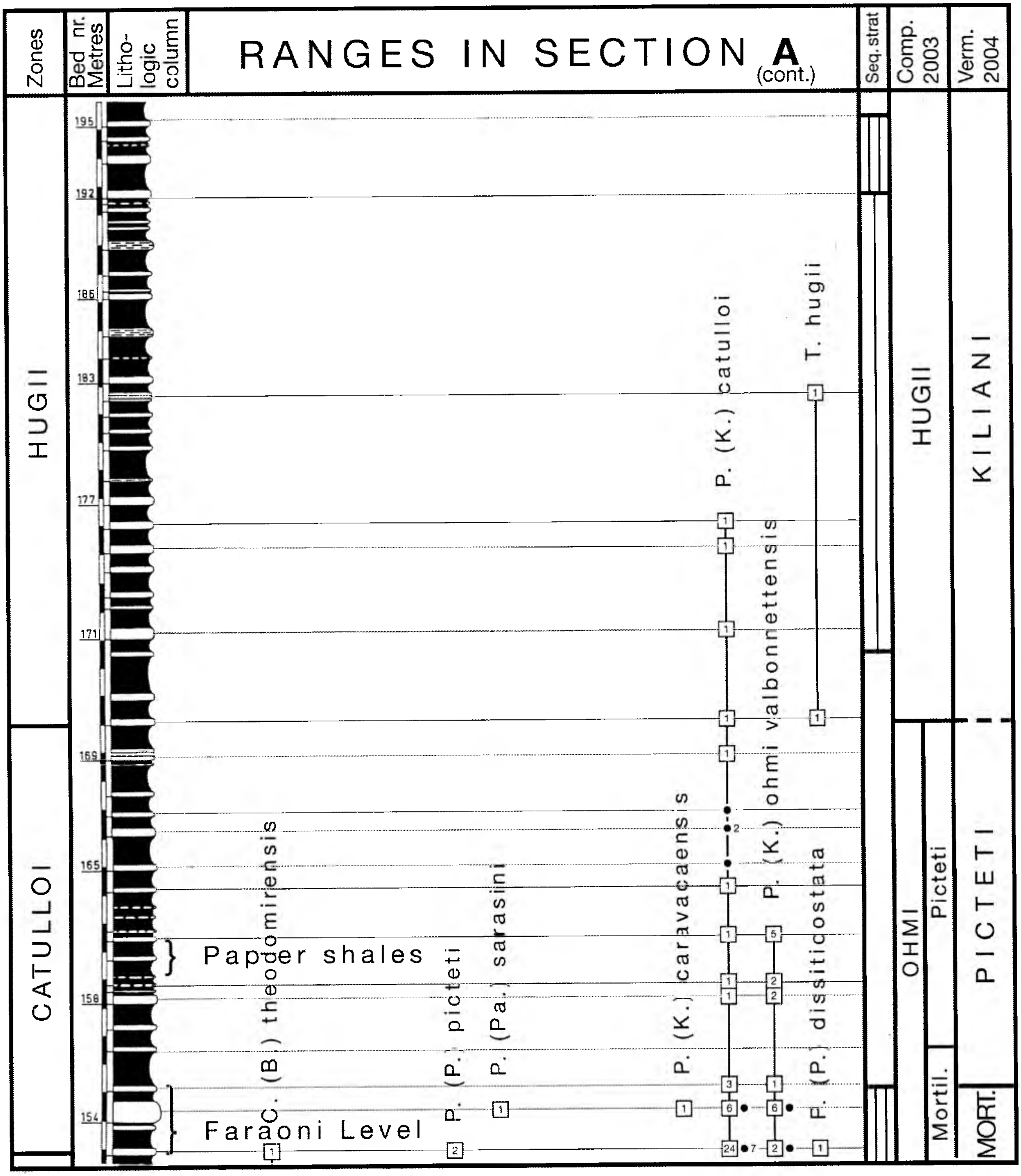


Fig. 8: Ranges of the species of genus *Pseudothurmannia* and subgenera *Crioceratites* (*Balearites*) and *Crioceratites* (*Binelliceras*) in the Balearis-Catulloi zonal interval in section A and six parallel sections along the Río Argos. The zonation advocated by the author is compared with the latest zonations of Company *et al.* (2003, 2006) and Vermeulen (2005). The sequence stratigraphy of the studied interval is shown (Hoedemaeker, 1995a, 1998, 2002, 2003; Hoedemaeker & Leereveld, 1995). A (p. 32), lower part; B (p. 33), upper part.


Zones
Bed nr. Metres
Litho-logic column
RANGES IN SECTION A (cont.)
Seq. strat
Comp. 2003
Verm. 2004
HUGII
CATULLOI
195
192
186
183
177
171
169
165
158
154
Paper shales
Faraoni Level
C. (B.) theodomirensis
P. (P.) picteti
P. (Pa.) sarasini
P. (K.) caravacaensis
P. (K.) catulloi
P. (K.) ohmi valbonnettensis
T. hugii
P. (P.) dissiticostata
1
2
1
1
24
7
2
1
6
6
3
1
1
1
2
2
1
5
1
2
1
1
1
1
1
1
1
HUGII
OHMI
Picteti
Mortil.
KILIANI
PICTETI
MORT.

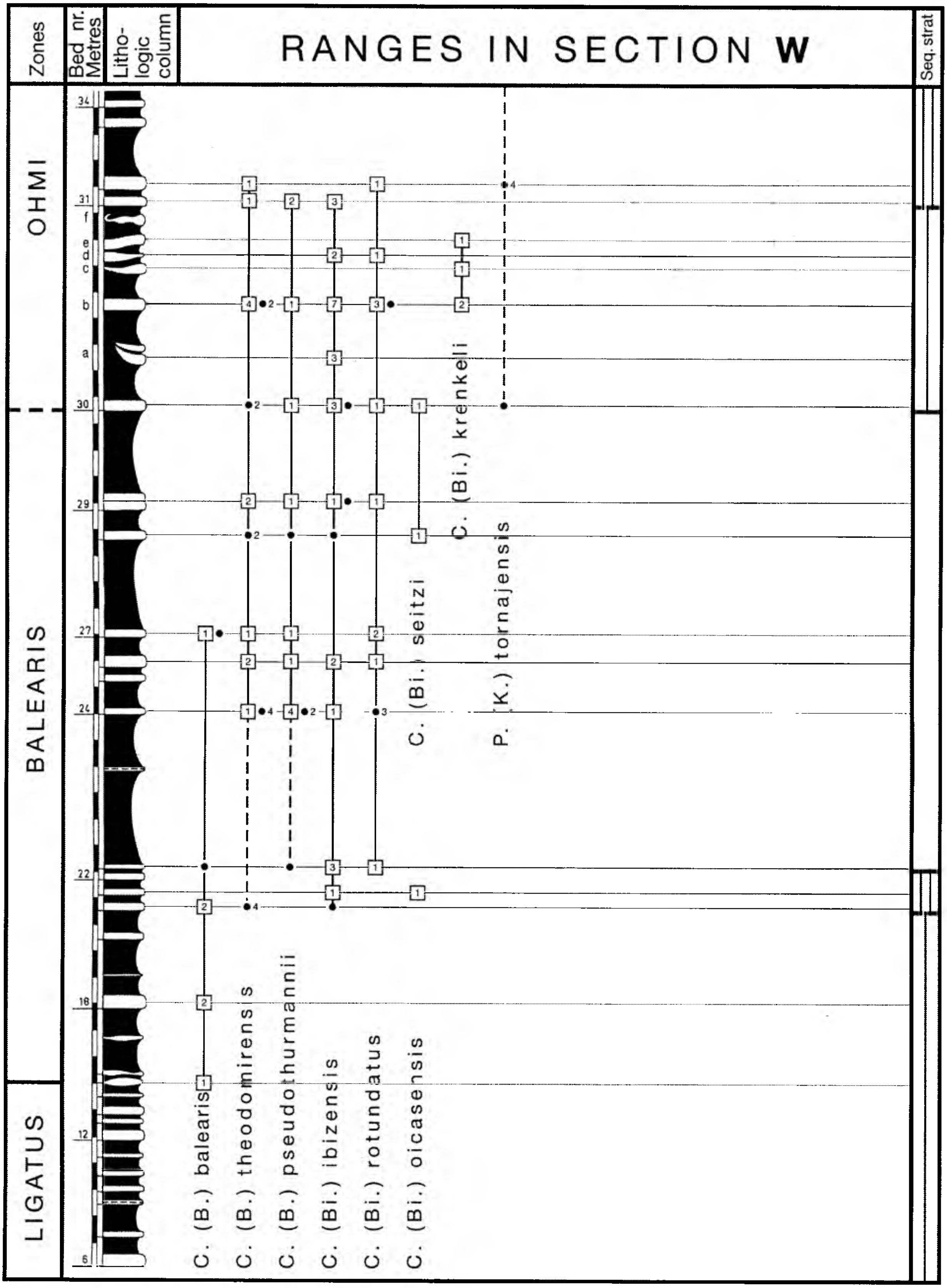
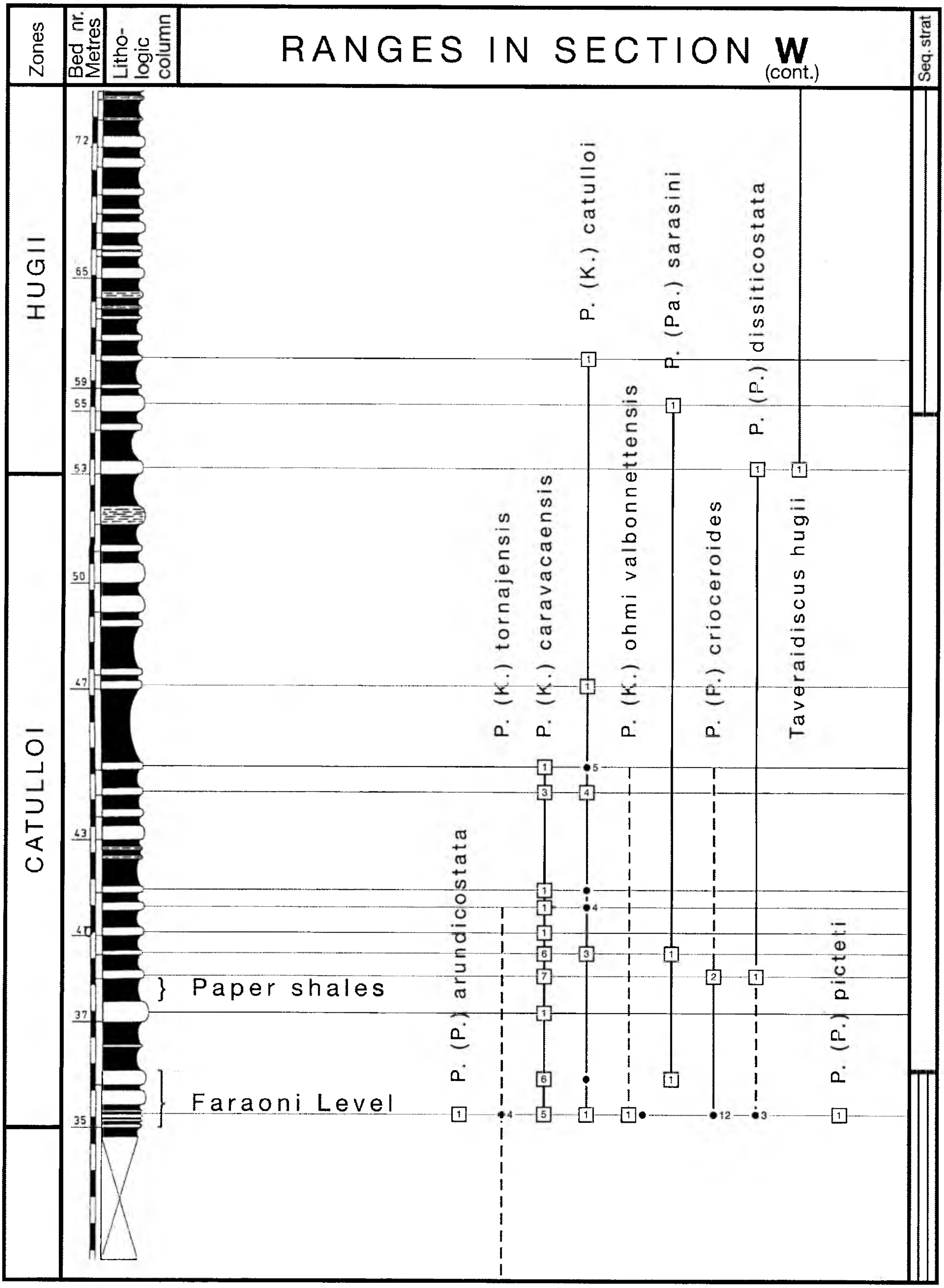


Fig. 9: Ranges of species of genus *Pseudothurmannia* and the subgenera *Crioceratites* (*Balearites*) and *Crioceratites* (*Binelliceras*) in the Balearis-Catulloi zonal interval in section W, 5 km west of section A along the Río Argos. The sequence stratigraphy of the studied interval is shown. Note that the ammonite assemblage in section W is rather different from section A (Fig. 3). A (p. 34), lower part; B (p. 35), upper part.


Zones
Bed nr.
Metres
Litho-logic column
RANGES IN SECTION W
(cont.)
Seq. strat
HUGII
CATULLOI
72
65
59
55
53
50
47
43
40
37
35
Paper shales
Faraoni Level
P. (P.) arundicostata
P. (K.) tornajensis
P. (K.) caravacaensis
P. (K.) catulloi
P. (K.) ohmi valbonnettensis
P. (Pa.) sarasini
P. (P.) crioceroides
P. (P.) dissiticostata
Taveraidiscus hugii
P. (P.) picteti
1
3
4
5
6
7
2
12

Provence) several levels have been indicated for Ha7, viz. on top of bed 64 (Hoedemaeker, 1998) (Fig. 67), on top of bed 65 (Magniez-Jannin, 1991), at the base of bed 66 (Jaquin, 1993), or at the base of bed 67 (Arnaud, 2005), so somewhere in the 1.5 m between the top of bed 64 and the base of bed 67; on top of bed 209 in the valley of the Valbonnette near Barrême (Alpes-de-Haute-Provence); on top of bed 321 in the Chamaloc section (Drôme); and on top of bed 196 in the Vergons section (Alpes-de-Haute-Provence); on top of bed D of the Faraoni level in the Umbria-Marche succession in Italy. It is remarkable that the black shales of the Faraoni Level coincide with a major sequence boundary. Just as during a sea level highstand the sea level also remains unchanged for several ten thousands of years during a sea level lowstand.

5.3. Comparison with the zonations of Company *et al.* (2003, 2005) and Vermeulen (2005)

In this paragraph the author compares the limits and ranges of the ammonite zones proposed by Company *et al.* (2003, 2005), who set up their zonation in the same section as the author did (section A along the Río Argos), with the limits and ranges determined by the author. The zonation proposed by Vermeulen (2005) is also correlated with the ammonite ranges found by the author in section A and W (Figs. 8A-B, 9A-B). Section W is seven kilometres east of section A.

Mortilleti Zone: Fig. 8A. Company *et al.* (2003) mentioned the first *Pseudothurmannia* (*Kakabadziella*) *mortilleti* from bed A149 of the Río Argos succession, which is on top of the paper shale that produces the isotopic signal of the Faraoni Level. In France, Vermeulen (2005) collected the first *P.* (*K.*) *mortilleti* in bed 54 of the Angles section, also on top of the bed with the Faraoni isotopic signal (Fig. 68). The author, however, sampled the first *P.* (*K.*) *mortilleti* in bed A140 along the Río Argos, which is 10 m below the top of the paper shale with the Faraoni isotopic signal; the acme of this species is in bed A145, and the end of the range is in bed A152. Finally, in France, the author found *P..* (*K.*) *mortilleti* in bed 50 of the Angles section, which is below the base of Vermeulen's (2005) Mortilleti Zone. So, the author concludes that the Mortilleti Zone begins much lower than indicated by Company *et al.* (2003, 2005) and Vermeulen (2005).

In the Río Argos succession, the range of *P.* (*K.*) *mortilleti* begins earlier (in bed A140) than that of *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (in bed A142), which could be expected on account of the proposed phylogeny (see above). This would mean that in the French Angles section, the range of *P.* (*K.*) *mortilleti* also would start below the first *P.* (*K.*) *ohmi ohmi*. The author collected the latter species in bed 42 of the Angles section, one bed below the base of Vermeulen's Ohmi zone (Fig. 67). It is even probable that *P.* (*K.*) *mortilleti* starts its range near bed 33 of the Angles section, in which the author collected two specimens of *C.* (*Bi.*) *krenkeli*; along the Río Argos the latter species begins, almost together with *P.* (*K.*) *mortilleti*, in bed A139 (range of Company *et al.*, 2003, range in section W). If this is the case, then *P.* (*K.*) *mortilleti* could probably be found in beds in the neighbourhood of bed 33 of the Angles section. This implies that the Mortilleti Subzones of Company *et al.* (2003, 2005) and Vermeulen (2005) merely represent the small upper part of the total range of *P.* (*K.*) *mortilleti*.

An additional complication is that these two authors consider *P.* (*K.*) *catulloi* a junior synonym of *P.* (*K.*) *mortilleti*, so that a small part of the Catulloi Zone was incorporated into the Mortilleti Zone *sensu* Company *et al.* (2003). Along the Río Argos the ranges of *P.* (*K.*) *mortilleti* and *P.* (*K.*) *catulloi* do not overlap. In the Río Argos succession, *P.* (*K.*) *catulloi* ranges from bed A153 into the basal Hugii Zone. The young specimens of *P.* (*K.*) *mortilleti* and *P.* (*K.*) *catulloi* closely resemble each other so the putting in synonymy of these two species is quite understandable. With the exception of the specimen in the paper of Braga *et al.* (1982), the author would identify all the specimens that Company *et al.* (2003, 2005) figured under the name *P. mortilleti*, as *P.* (*K.*) *catulloi*. On the other hand Vermeulen never figured a specimen that the author would call *P.* (*K.*) *catulloi*. The author will amply unfold his concept of *P.* (*K.*) *mortilleti* and *P.* (*K.*) *catulloi* in the systematic palaeontology part.

Ohmi Zone: Fig. 8A. The range of *P.* (*K.*) *ohmi ohmi* figured by Company *et al.* (2003, 2005) comprises only a few beds, viz. from bed A144 up to bed A147. According to the author's collection, the range of *ohmi ohmi* begins in bed A142, has its acme in bed A144 and ends in bed A152; in bed A153 begins the range of chronosubspecies *P.* (*K.*) *ohmi valbonnettensis*, which ranges up to bed A162. So, the Ohmi Subzone of Company *et al.* covers only the small upper part of the Ohmi Zone of the author. The range of *P.* (*K.*) *ohmi ohmi* figured by Vermeulen (2002, fig. 8; 2005, fig. 77) (Fig. 67) also covers only a part of the total range of this species. The Ohmi Subzone *sensu* Company *et al.* (2003, fig. 6.4; 2005, fig. 4D) comprises the basal part of their total Ohmi Zone, the Picteti Subzone *sensu* Company *et al.* the upper part. The only reason for extending the Ohmi Zone up to the base of the Hugii Zone is to unite all the beds with *Pseudothurmannia* into one zone.

Taking up this idea, it might be considered to replace the author's Ohmi Zone by the Mortilleti Zone, because *P.* (*K.*) *mortilleti* is the first appearing species of *Pseudothurmannia*.

Picteti Zone: Fig. 8B. Vermeulen (2002, 2004, 2005), Vermeulen *et al.* (2002) and Company *et al.* (2003, 2005) introduced a Picteti Subzone, which according to Company *et al.* begins in bed A156 where they sampled the first *P.* (*P.*) *picteti*. Therefore, Company's subzone covers almost the entire Catulloi Zone of the author. In fact, all species of *Pseudothurmannia* (*Pseudothurmannia*) with lateral tubercles in the adult stage occur in the Catulloi Zone, and it would be obvious to choose one of these as index species; *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955, would be a good choice, as it starts its range together with *P.* (*K.*) *catulloi* in bed A153. However, species of the subgenus *Pseudothurmannia* (*Pseudothurmannia*) are rare in the Río Argos succession and in the deeper parts of the Vocontian trough (Vergons and Angles sections). Vermeulen (2002, 2005) (Fig. 67) mentioned only one specimen of *P.* (*P.*) *picteti* from the Angles section, and the author found only three specimens in the Río Argos succession. This occurrence is too rare for introducing a biostratigraphic zone. Moreover, the only specimen figured by Company *et al.* (2003) under the name *P. picteti* was identified by the author as a young *P* (*P.*) *arundicostata* sp. nov.

P. (*P.*) *picteti* occurs frequently only in shallow water environments. For instance, the author found many specimens in the platform deposits of the Sierra de la Muela (Moratalla, Murcia, Spain) and Busnardo (1970) described four specimens from the platform deposits of the Montagne de Lure (Alpes-de-Haute-Provence), which he called *Pseudothurmannia grandis*, *Pseudothurmannia lurensis* and *Pseudothurmannia* sp. A, but which are all representatives of *Pseudothurmannia* (*Pseudothurmannia*) *picteti*. The scarcity of *P.* (*P.*) *picteti* in the Río Argos succession compelled the author (Hoedemaeker, 1995) to choose *P.* (*K.*) *catulloi* as index species, because this species occurs in great abundance in the rather deep-water deposits of the Río Argos succession as well as in the platform deposits of the Sierra de la Muela. Unfortunately, *P.* (*K.*) *catulloi* is not present in all localities. For instance, it was neither collected from the platform deposits of the Chamateuil section, nor from the deep shelf deposits of the Angles section.

Angulicostatus Subzone: Fig. 8A. The Angulicostatus Subzone of Company *et al.* (2003) should have the rare *Crioceratites* (*Binelliceras*) *angulicostatus* d'Orbigny as index species. However, the specimens from bed -2 and -4 of the Arroyo Gillico section (Cehegín, Murcia, Spain) and figured under that name by Company *et al.* (2003) were identified by the present author as *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler) and as *Crioceratites* (*Binelliceras*) *seitzi* Sarkar, respectively. The Angulicostatus Subzone of Company *et al.* (2003) is therefore not based on *Crioceratites* (*Binelliceras*) *angulicostatus* d'Orbigny, but probably on *C. (Bi.) seitzi*, which is very similar to *C.* (*Bi.*) *angulicostatus* and occurs in the same beds as those that Company *et al.* (2003) have designated as the Angulicostatus Subzone in the Río Argos succession.

Binelli and Krenkeli Subzones: Fig. 8A. Finally, Company *et al.* (2003, 2005) introduced a Binelli Subzone and a Krenkeli Subzone as two successive subzones in the upper part of the Balearis Zone. *Crioceratites* (*Binelliceras*) *binelli* indeed occurs mainly in beds older than *C.* (*Bi.*) *krenkeli*. According to the ranges given by Company *et al.* (2003) in the Río Argos succession, *C.* (*Bi.*) *krenkeli* replaces *C.* (*Bi.*) *binelli* in the same double bed (A139-140) in which *P.* (*K.*) *mortilleti* begins its range. According to their ranges in the outcrops along the Barranco Gillico (Cehegín, Murcia, Spain), the two species have even slightly overlapping ranges. The ranges of the author are: the lower part of the Balearis Zone for *C.* (*Bi.*) *binelli* and lower Ohmi Zone for *C.* (*Bi.*) *krenkeli*. The author also collected *C.* (*Bi.*) *binelli* in the lower part of the Balearis Zone in the Angles section (beds 12 and 20, Fig. 67). He also collected two specimens of *C.* (*Bi.*) *krenkeli* from bed 33 of the Angles section (Fig. 67), that is, just below the base of the Seitzi Zone of Vermeulen (2005). The Binelli and Krenkeli Subzones may have some reason for existence, but the ranges of the index species should be determined more precisely before one can properly define the subzones.

Seitzi Zone: Vermeulen (2005) introduced this zone representing the interval between the first appearances of *'Pseudothurmannia' seitzi* (in bed 36 of the Angles section) and *'Parathurmannia' ohmi* (in bed 42) respectively. Along the Río Argos the range of *Crioceratites* (*Binelliceras*) *seitzi* begins in bed W28 (= equivalent to bed A138) and that of *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* begins in bed A142. The present author has two specimens of *Crioceratites* (*Binelliceras*) *krenkeli* from bed 33 of the Angles section (Fig. 68). This means that the first appearance of *C.* (*Bi.*) *krenkeli* is close to that of *C.* (*Bi.*) *seitzi*. Company *et al.* (2003) also collected his first *C.* (*Bi.*) *krenkeli* in bed A139 adjacent to the correlatable bed W28 (= A128) in which the author found his first *C.* (*Bi.*) *seitzi*, but also adjacent to the first *P.*. (*K.*) *mortilleti* in bed A140. This means that Vermeulen's Seitzi Zone for the greater part overlaps the Krenkeli Subzone of Company *et al.* (2003), and that one of the two biostratigraphic units is superfluous. Moreover *P.* (*K.*) *mortilleti* should be present at the base of the Seitzi Zone. The subzones in the report of the Kilian Group (Reboulet *et al.*, 2008, 2011) should be revised.

Conclusion: The author is compelled to conclude that, for the time being, the biostratigraphic subdivision of the *Balearites* and *Pseudothurmannia* beds should still be a Balearis Zone at the base, an Ohmi Zone in the middle, and a Catulloi Zone at the top.

5.4 Hauterivian-Barremian boundary

The Hauterivian-Barremian boundary advocated by the International UIGS Working Group of lower Cretaceous ammonites is put at the base of the Hugii Zone, that is, above the *Pseudothurmannia* beds. However, Hoedemaeker (1995b, 1996) advocates that this boundary could be better placed at the base of the Catulloi Zone at the base of bed A153, because of the almost complete change of the ammonite fauna within the few boundary beds between the Ohmi and Catulloi zones, and because the latter zone contains many species that have hitherto been considered to characterize the Barremian Stage. This almost complete change of fauna means that the zones on either side of the zonal boundary can easily be distinguished from each other; species whose ranges cross the boundary are rare. The almost complete faunal change is apparently caused by the major sequence boundary, Ha7, near the boundary between the Ohmi and Catulloi zones. The change was brought about by the major sea-level fall during the deposition of the Falling Stage Systems Tract that precedes major sequence boundary Ha7. As a consequence of this sea-level fall many biotopes of ammonite species were pushed over the shelf edge and severely telescoped. This reduction of the extension of their biotopes would have enhanced selection pressure and induced ultimate extinction (Hoedemaeker 1995a). As the change took place in deep water environment (upper bathyal), there is no hiatus at the boundary. It would be an excellent place for a golden spike.

The base of the Catulloi Zone, though defined by the appearance of *P.* (*K.*) *catulloi*, is in addition characterized by the sudden appearance of many new ammonite species. Owing to the sea-level fall, their appearance is punctuated, which makes it relatively easy to recognize the zonal boundary, even when the index species is not present.

5.5 Geographical distribution of genus *Pseudothurmannia*

This genus is restricted to the Mediterranean Faunal Province, and has been reported from Morocco, Spain, France, Italy, Switzerland, southern Germany, Austria, Slovakia, Hungary, Roumania, Bulgaria, Ukraine (The Crimea) and Georgia.

There are several reports of *Pseudothurmannia* outside the Mediterranean Faunal Province. From the western hemisphere three species can be cited. The first one is from the lower Barremian of Colombia and has been named *Crioceratites* (*Pseudothurmannia*) *portarum* Etayo Serna, 1968 (p. 57, pl. 3, figs. 1-3). Because of the fine ribbing on the inner whorls, Etayo-Serna compares the specimen with several species that have been included in *Balearites* by Sarkar (1955). However, this specimen does neither belong to *Pseudothurmannia*, nor to *Balearites*, but to an unknown group within *Crioceratites sensu lato*, which is probably endemic in the Andean Faunal Province. The second and third species occur in California. Imlay (1960, p. 199, 200) thought that *Neocomites russelli* Anderson, 1938 (p. 165, pl. 27, fig. 3) and *Thurmannia jupiter* Anderson, 1938 (p. 162, pl. 31, fig. 1), had better be assigned to *Pseudothurmannia* because of their association with *Hoplocrioceras*, which only occurs in the late Hauterivian, while neocomitids became extinct at the end of the early Hauterivian. Anderson (1938, p. 162), however, assigned these two species to the Valanginian stage. They do not look at all like *Pseudothurmannia*.

From the eastern hemisphere two species have been published. The first is from the Barremian Hanoura Shale on the island of Shikoku (Japan), and has been named *Pseudothurmannia hanouraensis* Shimizu, 1932 (p. 29, pl. 1, figs. 20-24, pl. 3, fig. 11). This species does not belong to *Pseudothurmannia* because of the absence of ventrolateral clavi, the frequency of forking of the ribs, the broadening of the ribs towards the venter, and the near absence of differentiation of the ribs; the ribs cross the venter without weakening. The second species is from Irian Jaya (Indonesia) from the Barremian rocks of the Taminabua area and has been named *Pseudothurmannia* (*Ornicephalites*) *indonesiana* Skwarko & Thieuloy, 1989 (p. 31, pl. 2, figs. 3-4, 7-9). These cannot be included in *Pseudothurmannia* because of the absence of ventrolateral clavi, the presence of forking and splitting of ribs, the broadening of the ribs towards the venter, and the near absence of differentiation of the ribs; the ribs are weakened on the venter. The Japanese and Indonesian species are apparently closely related to each other. The only difference is that the Indonesian species has a narrower umbilicus than the Japanese, and shows a ventral weakening of the ribs. The Japanese and Indonesian species probably belong to the very same genus for which the name *Ornicephalites* Skwarko & Thieuloy, 1989, is available. This genus of the Pacific Faunal Realm is presumably related to *Hemihoplites*.

6. SYSTEMATIC PALAEONTOLOGY

Suborder Ancyloceratina Wiedmann, 1966
Superfamily Ancyloceratoidea Gill, 1871
Family Ancyloceratidae Gill, 1871
Subfamily Crioceratitinae Gill, 1871
7. Genus *Pseudothurmannia* Spath, 1923

Type species: *Pseudothurmannia picteti*, Sarkar, 1955.

Planospiral shells with evolute, advolute or slightly crioconic whorls. The first whorl is uncoiled and leaves an open umbilicus. The whorls egress during ontogeny (excentric umbilicus). The whorl section is compressed with flat to slightly convex parallel flanks, and has a flattened to arched ventral side. The dorsal side of the whorls is flat to deeply concave, and has the same three-layered constitution as the shell on the flanks and venter. In the earliest ontogenetic stages the ribs are simple and fine to moderately fine; lateral tubercles are lacking. With growth they become coarser and differentiate into main ribs and intermediate ribs. The main ribs are prominent only near the umbilicus, where they may have umbilical bullae; on the venter all ribs are characteristically equal or virtually equal in thickness except in the adult stages of a few species of the subgenus *Pseudothurmannia* (*Pseudothurmannia*). There are characteristically only a few, generally short, intermediate ribs between every two main ribs, normally 1-4, rarely five or six. On the innermost whorls the ribs are weakened at mid-venter, on the outer whorls they are not. Small uniform clavi are present on each rib forming two delicate rows on the ventral shoulders, which continue to be present up to the aperture. The suture line consists of four trifid lobes and bifid saddles. The saddle L/U is higher than E/L. For several species sexual dimorphism is established; the macroconchs are markedly larger than the coarse-ribbed microconchs.

Remarks: The main diagnostic characteristics, by which *Pseudothurmannia* can be distinguished from the other species of laterally tuberculate Crioceratitinae, are their having at least the inner whorls in contact; the absence of lateral tubercles on the innermost whorl; the absence of constrictions alongside thick ribs (except for weak constrictions in the latest growth stage of some large macroconchs); and, last but not least, the presence of small uniform clavi instead of tubercles on each rib forming two rows on the ventrolateral shoulders, which continue up to the aperture. The smallness of these clavi is the reason for their defective preservation.

In *Pseudothurmannia* the shell of the dorsal side of a whorl does not consist, as in normally coiled ammonites, of merely an inner prismatic layer (Runzelschicht), but has the same three-layered constitution as the shell of the flanks and ventral side; it consists of an outer prismatic layer, a nacreous layer and an inner prismatic layer. The two outer prismatic layers, one of the dorsal side of the outer whorl and one of the ventral side of the inner whorl, are not welded together, but merely in contact, or not (Fig. 40C-D); there is no real umbilical seam, but a more or less deep fissure. It is, therefore, not possible to judge whether the whorls are really in contact or not. When the dorsal side is concave, the whorls may exhibit an overlap, but may easily be separated from each other. The significance of the remarks 'touching each other', or 'not touching each other', or 'slightly crioconic' is not really relevant. A three-layered dorsal side is probably a feature of most heteromorphic ammonites. The three-layered dorsal side of the whorls, the perforate umbilicus, and the quadrilobate suture lines betray the heteromorphic nature of *Pseudothurmannia* and a systematic position within the Crioceratitinae.

As to sexual dimorphs, the macroconchs are markedly larger than the microconchs and may return to crioceratitic features in late ontogenetic stages. In microconchs, the egression of the whorls starts markedly earlier that in the macroconchs of the same species, and exhibit a coarsening and a greater irregularity of the ornamentation.

The genus *Pseudothurmannia* is here subdivided into three subgenera, namely *Pseudothurmannia* (*Pseudothurmannia*) Spath, 1923, *Pseudothurmannia* (*Parathurmannia*) Busnardo, 2003, and *Pseudothurmannia* (*Kakabadziella*) subgen. nov. In the ideas of ammonitologists, the latter subgenus includes the species that, with the exception of *Ammonites angulicostatus* d'Orbigny, 1841, and *Pseudothurmannia picteti* Sarkar, 1955, always have formed part of the genus *Pseudothurmannia*, and that lack lateral tubercles in any ontogenetic stage. Subgenus *Pseudothurmannia* (*Pseudothurmannia*) consists of species that do not match the former fixed idea of how *Pseudothurmannia* should look; the presence of lateral tubercles in the late growth stages was not considered characteristic of *Pseudothurmannia*, but of *Crioceratites*. Subgenus *Pseudothurmannia* (*Pseudothurmannia*), together with the small subgenus *Pseudothurmannia* (*Parathurmannia*), first has been renamed *Sornayites* by Wiedmann (1962) and later *Prieuriceras* by Vermeulen (2004). However, this group of species appears to be the typical group of *Pseudothurmannia*, because it includes the type species *P.* (*P*) *picteti* Sarkar. Only the late ontogenetic part of large macroconchs of the species of *Pseudothurmannia* more or less returns to a *Crioceratites*-like morphology, the start of which accelerates during phylogeny. This shows that it is embedded within the family Ancyloceratidae.

7.1. Subgenus *Pseudothurmannia* (*Kakabadziella*) subgen. nov.

Type species: *Ammonites Mortilleti* Pictet & De Loriol, 1858, designated herein.

Diagnosis: Lateral tubercles are absent in any ontogenetic stage. Simple, flexuous ribs developed in middle and late ontogenetic stages; the ribs are of moderate strength, and are differentiated into main and intermediate ribs In the earliest growth stages the ribbing is very fine, dense and non-differentiated; this is followed by a stage with differentiated ribbing and a regular or irregular distribution of main and intermediate ribs. The main ribs arise at the umbilical seam and may, or may not, have umbilical bullae, whereas the intermediate ribs originate on the flanks. The species may be moderately involute to evolute. For all species of *Pseudothurmannia* (*Kakabadziella*), sexual dimorphism is established; the macroconchs are much larger than the microconchs. The microconchs develop coarse, irregular, more distantly spaced ribs and forking may occur.

Remarks: There is a group of two small species which have very evolute whorls from the first whorl onward, which lack the very fine, dense ribbing on the innermost whorls, and for which no sexual dimorphism has been established yet. As lateral tubercles are totally absent, they are included in *Pseudothurmannia (Kakabadziella)*, but they clearly form a separate group.

7.1.1. *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858)

Figs. 10-15; Pl. I; Tab. I

v* 1858. *Ammonites Mortilleti* Pictet & De Loriol, p. 21, pl. 4, fig. 2a-d.

1868. *Ammonites Mortilleti* Pictet & De Loriol.– Winkler, p. 3, pl. 1, fig. 2.

? 1868. *Ammonites angulicostatus* d'Orbigny.– Winkler, p. 5, pl. 1, fig. 7, 7a-b.

pars 1901. *Hoplites Mortilleti* Pictet & De Loriol.– Sarasin & Schöndelmayer, p. 84, pl. 11, only fig. 5 (= lectotype), *non* figs. 3 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* Winkler, 1868], 4 (= *Crioceratites* sp. indet.).

1901. *Hoplites Renevieri* nov. sp.– Sarasin & Schöndelmayer, p. 89, pl. 11, fig. 1-2 (= macroconch).

non 1962. *Crioceratites* (*Pseudothurmannia*) *mortilleti mortilleti* (Pict. & De Lor.).– Wiedmann, p. 132, pl. 7, fig. 5a-b [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* ? sp. nov.].

pars 1967. *Balearites mortilleti* (Pictet & De Loriol).– Dimitrova, p. 76, pl. 36, fig. 6, *non* fig. 5 [= Probably *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955].

non 1968. *Pseudothurmannia mortilleti* (Pict. & De Lor.).– Sornay, p. 4, pl. 1, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1971. *Pseudothurmannia* cf. *mortilleti* (Pictet & De loriol).– Thomson, p. 160, fig. 3i (= unidentified ammonite).

non 1974. *Pseudothurmannia* cf. *mortilleti* (Pictet & De Loriol).– Thomson, p. 14, pl. 2, fig. i-j (= unidentified ammonite; umbilicus very wide, ribs very sinuous, no mention of ventrolateral clavi).

? 1976. *Pseudothurmannia mortilleti* (Pictet & Lor.).– Mandov, p. 64, pl. 8, fig. 3.

1979b. *Crioceratites* (*Pseudothurmannia*) *mortilleti* (Pictet & Loriol).– Immel, p. 67, pl. 1, fig. 2.

non 1981. *Pseudothurmannia* cf. *mortilleti* (Pictet & De Loriol).– Thomson, p. 290, pl. 1, fig. 5 (= unidentified ammonite).

non 1981. *Crioceratites* (*Pseudothurmannia*) aff. *mortilleti* (Pictet & De Loriol).– Nagy, p. 73, pl. 2, fig. 2 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

non 1981. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Kakabadze, p. 91, pl. 1, fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.] *non* fig. 8 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

pars 1982. *Crioceratites* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Braga *et al.*, p. 685, pl. 1, fig. 4, *non* fig. 5 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

1984. *Crioceratites* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Adamíková *et al.*, p. 606, pl. 2, fig. 3.

non 1986. *Crioceras* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Darga & Weidich, p. 103, pl. 3, fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], fig. 5 [= *Pseudothurmannia* (*Kakabadziella*) *tornajensis* sp. nov.].

non 1987. *Crioceratites* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Immel, p. 117, pl. 12, fig. 1. [= refigured '*Hoplites angulicostatus*' Richarz, 1905, *non* d'Orb. = *Pseudothurmannia* (*Kakabadziella*) *tornajensis?* sp. nov.].

non 1989. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Michalík & Vašíček, p. 518, pl. 2, fig. 5 [= *Pseudothurmannia* (*Balearites*) *theodomirensis* sp. nov.].

non 1994. *Pseudothurmannia mortilleti* morphotype *catulloi* (Parona).– Cecca *et al.*, p. 560, fig. 5c [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., microconch].

non 1994. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Cecca *et al.*, p. 560, fig. 5d [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., var. *fissicostulata*].

pars 1995b. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Hoedemaeker, p. 229, only pl. 1, fig. 4, pl. 2, fig. 1, *non* figs. 2-3 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., var. *fissicostulata*], *non* fig. 4-5 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov. macroconchs], *non* fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., microconch].

non 1995. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Cecca & Pallini, p. 212, pl. 1, fig. 14 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1995. *Pseudothurmannia mortilleti mortilleti* (Pictet & De Loriol).– Cecca *et al.*, p. 198, pl. 1, fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., var. *fissicostulata*].

non 1995. *Pseudothurmannia mortilleti catulloi* (Parona).– Cecca *et al.*, p. 198, pl. 1, figs. 3-4 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., microconchs].

non 1995. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Vašíček, pl. 4, fig. 6 [= *Pseudothurmannia* (*Balearites*) *theodomirensis* sp. nov.].

non 1995. *Pseudothurmannia* aff. *mortilleti* (Pictet & De Loriol).– Ambrosi *et al.*, p. 63, pl. 3, fig. 2 [*Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

non 1997. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Vašíček, p. 237, pl. 2, fig. 3 [= *Crioceratites* (*Balearites*) *theodomirensis* sp. n.].

non 1998. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Cecca *et al.*, p. 94, pl. 5, figs. 1-2, 7, 12-13 [*Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov. macroconchs), figs. 3-4, [= *P.* (*Kakabadziella*) *caravacaensis* sp. nov. microconchs], *non* figs. 5, 6, 8-11 [*P.* (*Kakabadziella*) *caravacaensis* sp. nov., var. *fissicostulata*].

non 1999. *Pseudothurmannia mortilleti* (Pictet & De Loriol) *sensu* Hoedemaeker.– Baudin *et al.*, p. 490, fig. 3E [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

2000. *Pseudothurmannia* (*Pseudothurmannia*) cf. *mortilleti* (Pictet & De Loriol).– Vašíček & Faupl, p. 604, pl. 6, figs. 3, 4.

2001. *Pseudothurmannia* cf. *mortilleti* (Pictet & De Loriol).– Avram & Gradinaru, p. 139, pl. 2, fig. 1.

2002. *Pseudothurmannia sarasini* Sarkar.– Bodrogi & Fogarasi, p. 304, *non* pl. 1, fig. 1 [= *Pseudothurmannia (Kakabadziella) caravacaensis* sp. nov.], *non* fig. 2 [= probably *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].

non 2002. *Pseudothurmannia* cf. *mortilleti* (Pictet & De Loriol).– Bodrogi & Forgarasi, p. 304, pl. 2, fig. 5 (= inner whorl of *Pseudothurmannia* (*Pseudothurmannia*) sp.).

2002. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Vermeulen *et al.*, p. 77, pl. 1, fig. 2.

2002. *Pseudothurmannia* aff. *sarasini* (Sarkar).– Vermeulen *et al.*, p. 77, pl. 3, fig. 4.

pars 2003. *Parathurmannia mortilleti* (Pictet & De Loriol).– Busnardo, p. 69, pl. 32, fig. 2a, b (= paralectotype, = var. *tenuicostata*), 4 (= lectotype); *non* pl. 16, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* Parona, 1897, microconch]; *non* pl. 16 fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* Parona, 1897, macroconch].

pars 2003. *Parathurmannia renevieri* (Sarasin & Schöndelmayer).– Busnardo, pl. 17, fig. 1; pl. 18, fig. 2 (= ambo macroconchs), *non* pl. 9, fig. 8 [= juvenile *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884].

non 2003. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Company *et al.*, p. 691, fig. 6.4. [= *Pseudothurmannia* (*Kakabadziella*) *catulloi*, microconch].

non 2004. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Kakabadze, p. 384, pl. 2 figs. 2-3 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], *non* fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* Parona, 1897].

non 2005. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Kakabadze, p. 350, pl. 72, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 2005. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Company *et al.*, p. 188, fig. 4D [= *Pseudothurmannia* (*Pseudothurmannia*) *catulloi* (Parona, 1897), microconch].

non 2006a. *Balearites* aff. *mortilleti* (Pictet & De Loriol).– Bodin *et al.*, p. 160, fig. 3A [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

non 2006a. *Balearites* sp. gr. *mortilleti* (Pictet & De Loriol).– Bodin *et al.*, p. 170, fig. 3G (= *Pseudothurmannia* sp.).

Lectotype: The specimen from the Pictet collection from the Neocomian of Nice, designated by Wiedmann (1962), deposited in the Museum of Natural History in Genève (nr 16862) and figured by Sarasin & Schöndelmayer, 1901, pl. 11, fig. 5 (Fig. 10 herein). A plaster cast was kindly sent to the author by Dr. Max Wippich. The lectotype designated 41 years later by Busnardo (2003, pl. 32, fig. 2a, b), that is, the specimen from Voirons (Les Hivernages) depicted by Pictet & De Loriol (1858), Pictet collection nr 30929, is not legitimate. The drawing given by Pictet & De Loriol largely reproduces the well-preserved Nice specimen instead of the defectively preserved specimen from Voirons.

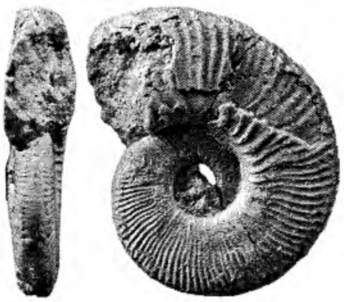


Fig. 10: *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858), plaster cast of lectotype (designated by Wiedmann, 1962), young specimen from the neighbourhood of Nice. A, apertural view; ×1. B, lateral view; ×1.

Material: One hundred and five specimens. France: Gypsum cast of lectotype (Neocomian of Nice), two specimens from the Angles section (bed 50, Coll. Hoedemaeker; nr. 43374 of the Coll. J. Klein) and two specimens from Chamaloc (beds 320, 321). Spain: Lorca (Tornajo Mountain): sections B and 2A (37 specimens), Caravaca (Río Argos succession): section A, from bed A140 to A152 (63 specimens, including a population of 40 specimens from bed A145).

Emended diagnosis: Fine-ribbed *Pseudothurmannia* (*Kakabadziella*) provided with prominent umbilical bullae at regular distances. The fine prorsiradiate ribs are only slightly flexuous and consist of 1-3, rarely four or five, intermediate ribs to one main rib. This species has the most compressed conch of all species of *Kakabadziella*, the flanks are almost flat and parallel; the young conch resembles a thick coin. The almost flat venter is adorned with two ventrolateral rows of very small, uniform clavi. The umbilicus is small, about three quarters of the whorl height before the beginning of the egression of the outer whorl of the macroconchs at a diameter of 75 mm. The ribbing of adult macroconchs remains fine and only slowly increases in coarseness with age; it still consists of weakly S-shaped main ribs separated by 0-5, commonly 3-4, intermediate ribs. *Hoplites renevieri* Sarasin & Schöndelmayer, 1901, is considered the macroconch of *P.* (*K.*) *mortilleti* and may reach a diameter of 188 mm. Possible microconchs are much smaller and the outer whorl starts to egress at a diameter of 23 mm. From here the ribs are much coarser and more distant from each other.

Description: Very compressed planulate conchs with flat, almost parallel flanks, flat to slightly arched venter, and rounded umbilical rim; the ventrolateral shoulders are well developed, giving the shell a flat rectangular section like a thick coin. The umbilicus is small, about three quarters of the whorl height. The whorl section is thickest at one third of the flank height. The ribs are fine, prorsiradiate and straight to slightly flexuous.

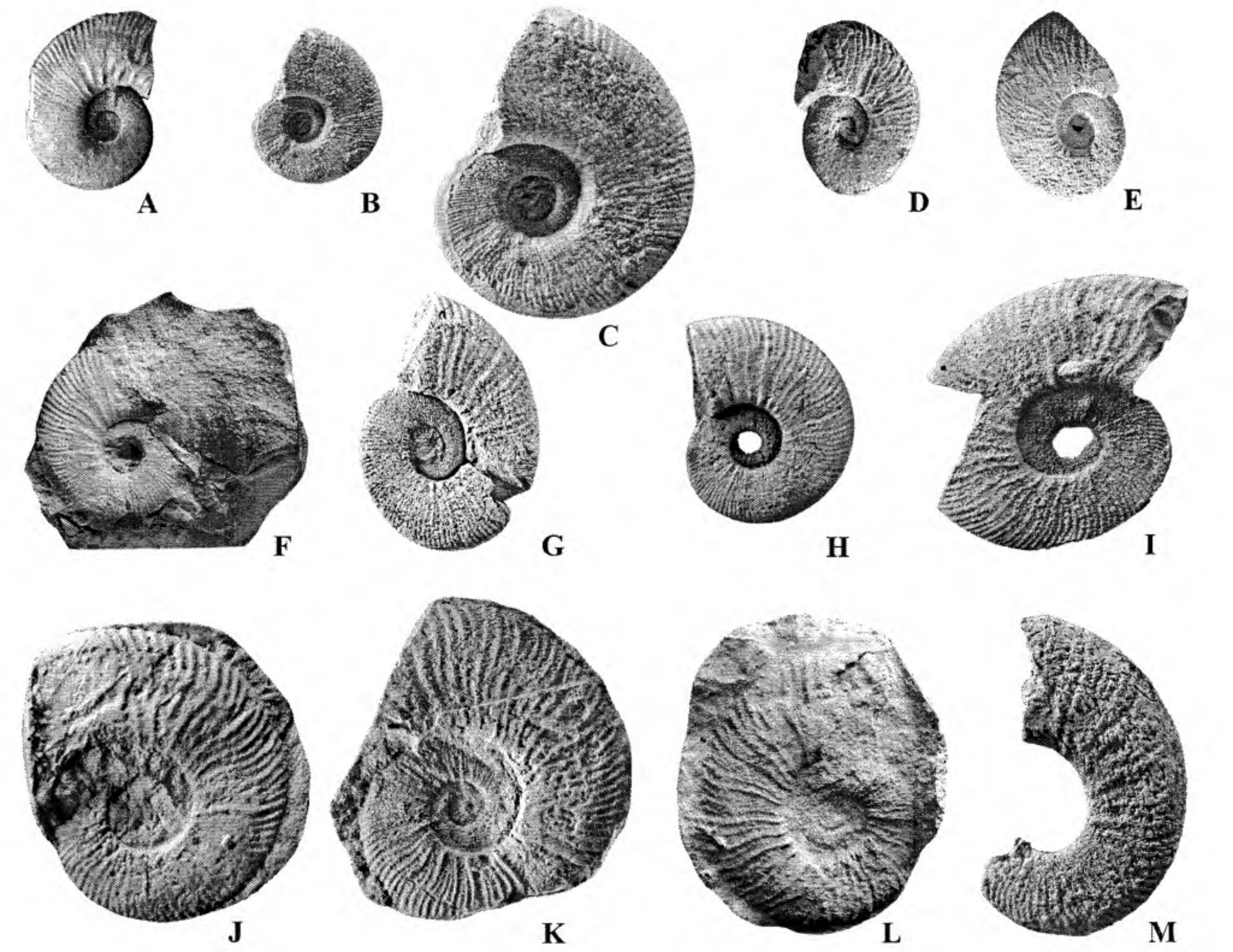


Fig. 11: A-M, *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858), young specimens. A, RGM 542260, locality 5, bed 50; ×1. B, RGM 541831, locality 3B, bed B202; ×1. C, same specimen; ×2. D, RGM 541841, locality 3A, bed 1; ×1. E, RGM 541828, locality 3B, bed B200; ×1. F, RGM 542028, locality 1A, bed A152; ×1. G, RGM 542079, locality 1A, bed A145; ×1. H, RGM 387962, locality 1A, bed A145; ×1. I, RGM 541835, locality 3B, bed B200; ×1. J, RGM 387657, locality 1A, bed A145; ×1. K., RGM 387889, locality 1A, bed A145; ×1. L, RGM 542031, locality 1A, bed A145; ×1. M, RGM 542073, locality1A, bed A145; ×1.

The innermost whorls are only preserved from a diameter of 3.5 mm (RGM 541831, Fig. 11C). The first ribs are widely spaced, but the ribbing becomes very fine, dense and uniform from a diameter of 5 mm. All the ribs are virtually equal in thickness; some of them develop weak umbilical bullae on the umbilical rim or are slightly thicker. From this diameter many ribs start from the umbilical seam, single or in twos (fascicle); some ribs start in the lower part of the flanks. The ribs weaken on the ventral side leaving the middle of the venter smooth. On the ventrolateral shoulders every rib is provided with a small clavus; the clavi form two rows, like serrated keels, on each side of the venter.

From a diameter of 15 mm, the umbilical bullae become more prominent and regularly distributed; they mark off the main ribs. There are 3-5 intermediate ribs to one main rib. All the ribs have the same thickness on the upper half of the flanks. The differentiation in main and intermediate ribs begins at a diameter of 20 mm. The comma-shaped bullae are situated at the umbilical rim and may give rise to two ribs; the intermediate ribs originate on the umbilical rim and, later, just above the rim. On the upper two thirds of the flank the ribs are equal in thickness. On the umbilical wall the bullae often have a rursiradiate direction. All the ribs pass the flanks in a nearly straight to slightly S-shaped manner, are 1 mm apart and cross the venter straight without diminishing in thickness; later, they cross the venter with a convex forward curve. The tiny ventrolateral clavi are still visible on the marked shoulders, but become insignificant in relation to the thickness of the ribs.

From a diameter of 33 mm the somewhat S-shaped ribs become a little coarser and slightly more distant from each other; the bullae give rise to only one main rib, and these are separated by 1-3, but generally two intermediate ribs, some of which may appear at midflank. This ornamentation can just be seen on the lectotype.

Suture line: The typical crioceratitic suture line has four lobes (Fig. 12A-C), viz. external, lateral, umbilical and internal. The large, trifid lateral lobe has a wide throat and is a little deeper than the ventral lobe, whereas the trifid umbilical lobe is broad and much shallower. The side arms of the lateral lobe are not extending far sideways and leave the saddles broad-necked. The external lobe has a short median saddle. All saddles are asymmetrically bifid and broad necked; the external part of saddle E/L has three upright branches, whereas the internal part has only two. Both parts of saddle L/U have three upright branches; the branches of the internal part are separated by a rather deep incision. Saddle L/U is slightly higher than saddle E/L, and saddle U/I is much lower. Busnardo (2003) depicted the suture line of '*Parathurmannia renevieri*' [= macroconch of *P.* (*K.*) *mortilleti*], which equally shows the wide throat of the lateral lobe and the broad necks of the saddles. The suture line figured by Busnardo, 2003 (p. 70, fig. 25) has narrow throated lobes and narrow necked saddles and belongs to *P.* (*K.*) *caravacaensis* sp. nov., not to *P.* (*K.*) *mortilleti*.

Macroconchs: Most specimens figured in the literature do not exceed 40 mm in diameter; this is the diameter of the lectotype, which lacks a living chamber. How *P.* (*K.*) *mortilleti* should look when it is larger than 40 mm is not known. However, in the Tornajo Mountain (in the north of the communality district of Lorca, Murcia, Spain) the author collected a series of specimens from small to large dimensions and he interpreted the larger specimens as macroconchs of *P.* (*K.*) *mortilleti* (Pl. I). The ribs remain fine and only slowly increase in coarseness with age; they still consist of somewhat S-shaped main ribs separated by 1-5, commonly 3-4, intermediate ribs. The main ribs are still provided with comma-shaped or curved umbilical bullae, which are rursiradiate on the umbilical wall; the intermediate ribs start at various heights on the flanks. All the ribs cross the venter without weakening and still show faint ventrolateral clavi up to the aperture. The main ribs are slightly thicker than the intermediate ones on the lower two thirds of the flank; on the upper third they are of the same thickness as the intermediate ribs. At a diameter of about 75 mm the whorl begins to egress, increasing the ratio of the umbilical width. The largest macroconch collected in the Tornajo Mountain by the author has a diameter of 118 mm. The

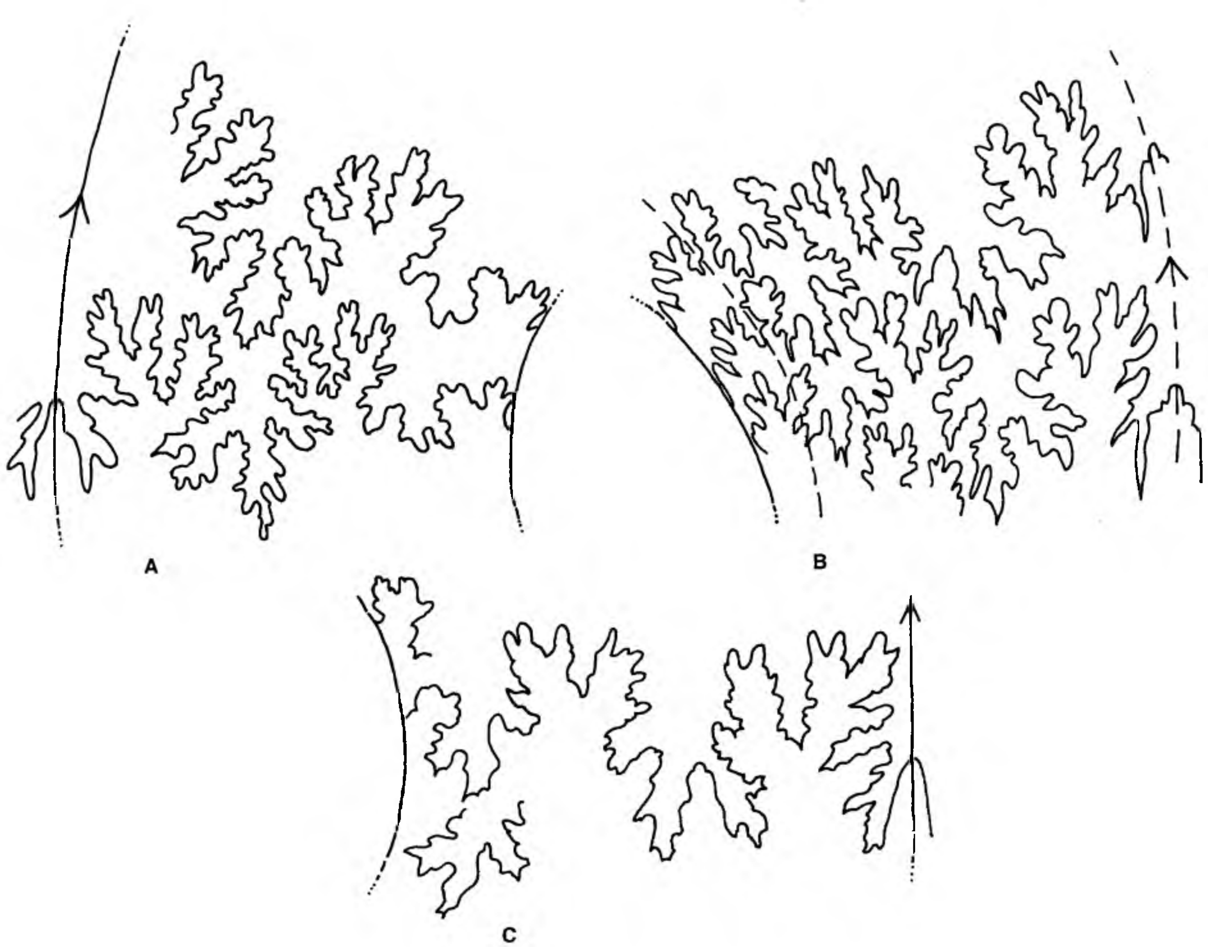


Fig. 12: A-C, *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858), suture lines. A, RGM 542073, at Wh 14 mm; ×4. B, RGM 542026, at Wh 13 mm; ×4. C, RGM 542022, at Wh 18 mm; ×3.8.

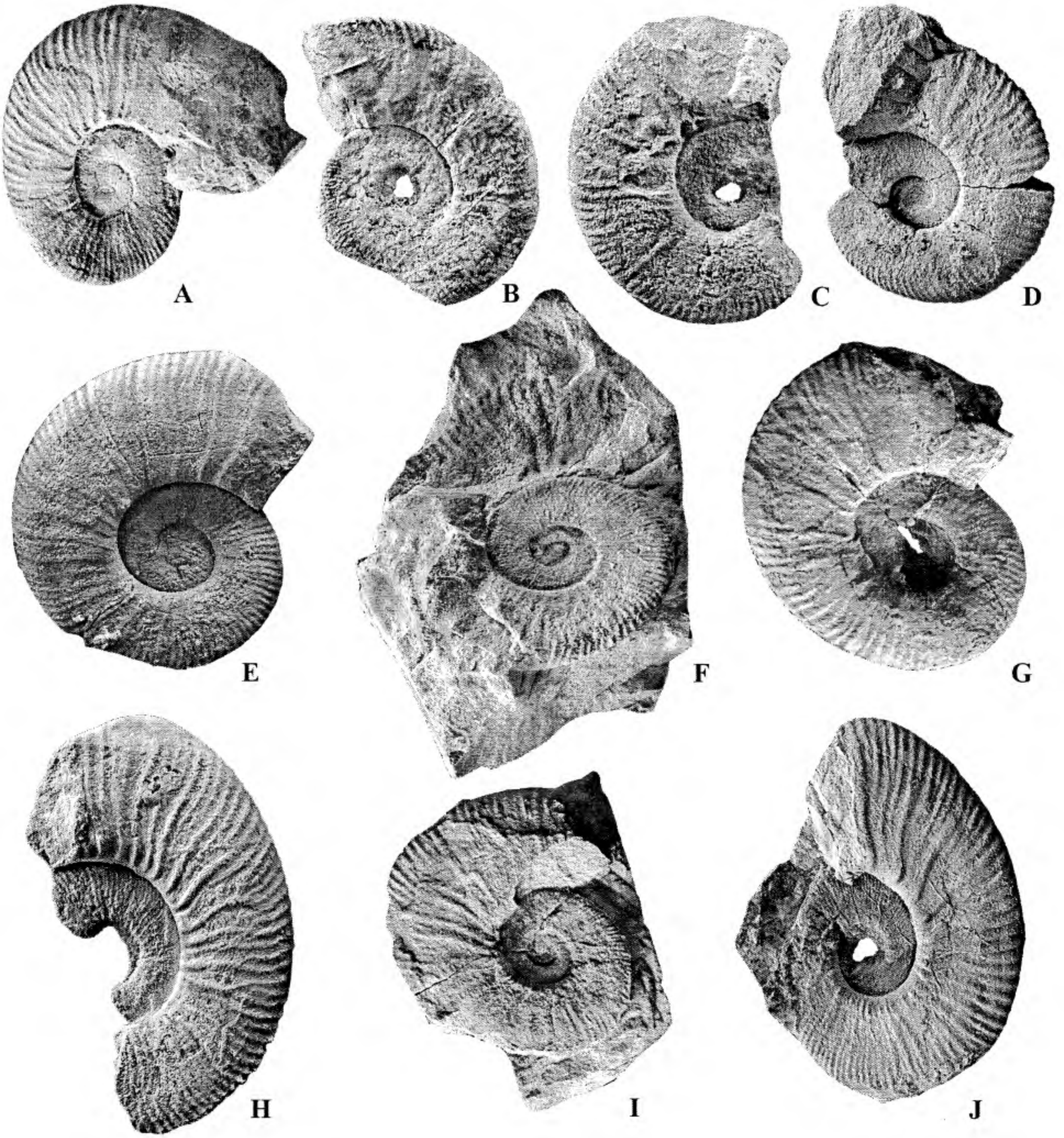


Fig. 13: A-J, *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858), small macroconchs. A, RGM 541857, locality 3B, bed B200; ×1. B, RGM 542027, locality 1A, bed A145; ×1. C, RGM 542038, locality 1A, bed A147; ×1. D, RGM 541833, locality 3B, bed B201; ×1. E. RGM 542025, locality 1A, bed A144; ×1. F, RGM 541822, locality 3; ×1. G, RGM 541832, locality 3B, bed B200; ×1. H, RGM 541830, locality 3B, bed B200; ×1. I, RGM 542270, locality 3C; ×1. J, RGM 541823, locality 3B, bed B200; ×1.

ornamentation of the large specimens is identical to *Pseudothurmannia renevieri* (Sarasin & Schöndelmayer, 1901), which is, therefore, considered the macroconch of *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858). This means that the macroconchs of *P.* (*K.*) *mortilleti* may reach a diameter of at least 188 mm.

Variety *tenuicostata*: There are several specimens that remain fine-ribbed at least up to a diameter of 50 mm (Fig. 14). The specimen of the Pictet collection (Muséum d'histoire naturelle de Genève, nr 30929) from Les Voirons (Les Hivernages, France) and figured by Busnardo (2003, pl. 32, fig. 2a, b), belongs to this variety. The ribs of the lectotype are much coarser at this diameter. As there are transitional specimens, these fine-ribbed specimens are considered a variety of *P.* (*K.*) *mortilleti*.

Possible microconchs: If the specimens described below (Fig. 15) are really microconchs of *P.* (*K.*) *mortilleti*, then all specimens on which the fine ribbing continues at diameters greater than 25 mm are macroconchs.

From a diameter of 15 mm rather prominent umbilical bullae appear at regular distances from which one or a fascicle of two ribs may part. The main ribs do not differ in thickness from the intermediate ribs. Between every two main ribs or fascicles are one or two intermediate ribs, rarely three, which are shorter than the main ribs. All ribs are weakened at mid-venter.

At a diameter of 23-25 mm, the ribs rather suddenly appreciably coarsen, but the intercostal distance remains equal to the thickness of the ribs. The ribs become markedly S-shaped. The one or two intermediate ribs that occur between every two main ribs become still shorter and differ in length. The main ribs are provided with umbilical bullae. All the ribs cross the venter equal in strength, and small ventrolateral clavi are still well visible. The whorls begin to egress at the same diameter and only slowly grow in height.

I suspect these specimens to be young microconchs of *P.* (*K.*) *mortilleti*, because one would expect them to have more or less similar ornamentation to *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* and *P.* (*K.*) *catulloi*. As they all occur in the Ohmi Zone instead of the Catulloi Zone and as they markedly differ from the microconchs of *P.* (*K.*) *ohmi ohmi*, they should be the microconchs of *P.* (*K.*) *mortilleti*.

Remarks: *Pseudothurmannia* (*Kakabadziella*) *mortilleti* differs from *Crioceratites* (*Balearites*) *theodomirensis* sp. nov., which has often been mistaken for *P.* (*K.*) *mortilleti*, mainly in having more prominent, comma-shaped umbilical bullae, a larger whorl height, a smaller umbilicus, and a slightly flattened ventral side, which creates a flat rectangular whorl section. *Pseudothurmannia* (*Kakabadziella*) *mortilleti* is interpreted as the most primitive *Kakabadziella*, because it still shows the fine ribs that this species inherited from *Crioceratites* (*Balearites*); the ribs become slightly coarser with age, but remain rather fine.

Pseudothurmannia (*Kakabadziella*) *mortilleti* differs from *Pseudothurmannia* (*Kakabadziella*) *catulloi*, which is interpreted herein as a direct descendant of *P.* (*K.*) *mortilleti*, in the persistence of fine ribbing, in the presence of bullae [absent in *P.* (*K.*) *catulloi*] and in the more compressed, flat-sided early whorls [the whorls of *P.* (*K.*) *catulloi* are thicker and have more convex flanks]. It does not generate the coarse ribbing of *P.* (*K.*) *catulloi* at larger diameters. At larger diameters (50-100 mm) *P.* (*K.*) *mortilleti* generally has 3-4 intermediate ribs between every two main ribs, whereas *P.* (*K.*) *catulloi* has normally only 1-2 intermediate ribs between every two

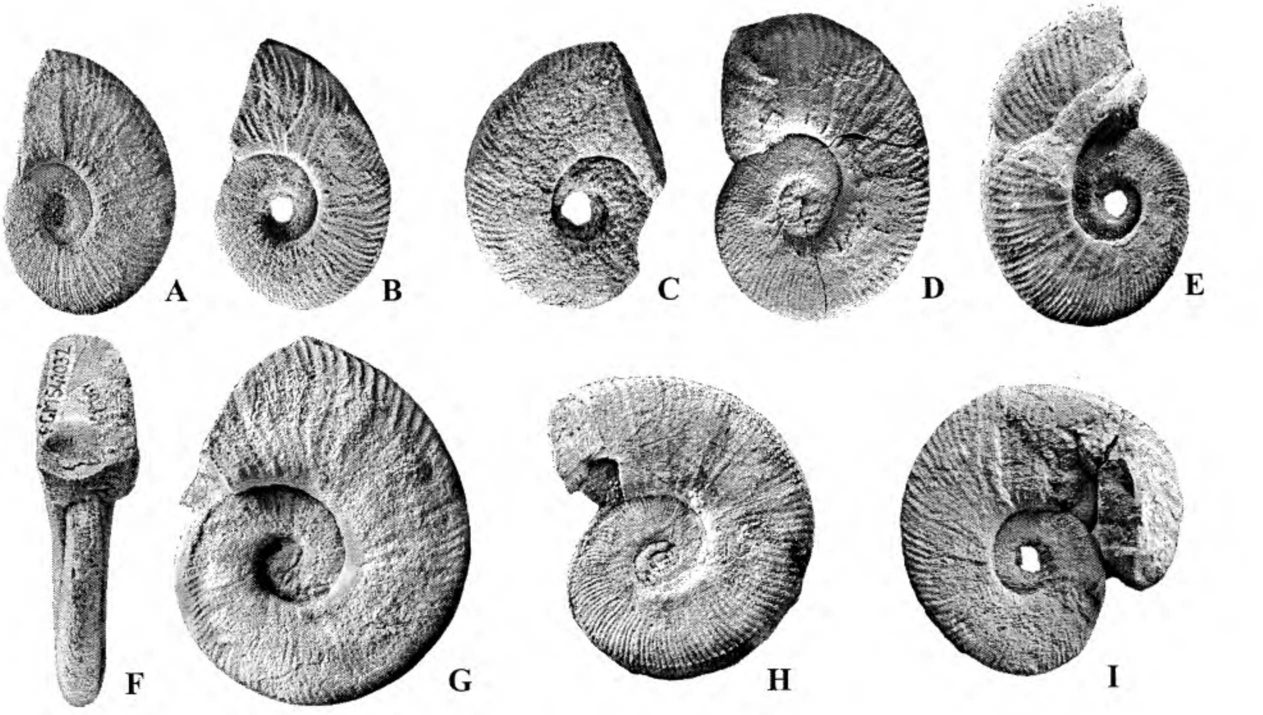


Fig. 14: A-I, *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858) var. *tenuicostata*. A, RGM 541827, locality 3B, bed B201; ×1. B, RGM 541834, locality 3B, bed B200; ×1. C, RGM 542068, locality 1A, bed A145; ×1. D, RGM 541829, locality 3B, bed B200; ×1. E, RGM 541836, locality 3B, bed B201; ×1. F, RGM 542032, apertural view, locality 1A, loose from beds A139-151; ×1. G, same specimen, lateral view; ×1. H, RGM 542030, locality 1A, bed A144; ×1. I, RGM 541837, locality 3B, bed B208; ×1.

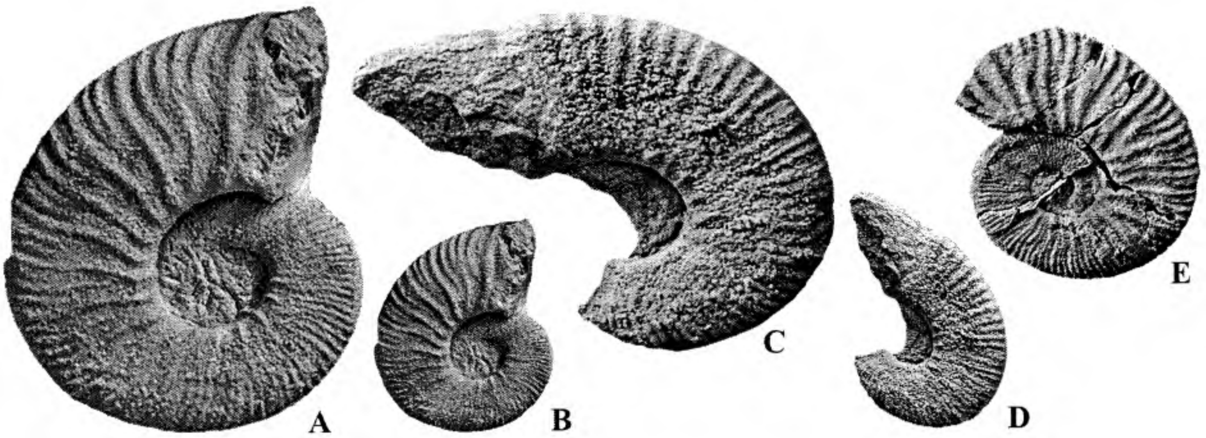


Fig. 15: A-F, *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858), possible small microconchs. A, RGM 541826, locality B3, bed B200; ×2. B, same specimen; ×1. C, RGM 541852, locality 3B, bed B201; ×2. D, same specimen; ×1. E, RGM 541853, locality 3A, bed 1; ×1.

main ribs. The lateral lobe of *P.* (*K.*) *catulloi* has a narrow throat, whereas *P.* (*K.*) *mortilleti* has a wide-throated lateral lobe.

Pseudothurmannia (*Kakabadziella*) *mortilleti* differs from *Pseudothurmannia* (*Kakabadziella*) *caravacaensis*, which is here interpreted as a direct descendant of *P.* (*K.*) *mortilleti*, in its greater regularity in the distribution of the ribs, in the rarity of fasciculation and splitting of ribs, and in the absence of rib effacement. In *P.* (*K.*) *caravacaensis,* main ribs with umbilical bullae appear in an earlier growth stage than in *P.* (*K.*) *mortilleti*; their distance is irregular and often great, occasionally with six intermediate ribs in between them. The whorls of *P.* (*K.*) *caravacaensis* egress much more rapidly (umbilicus much more excentric) than in *P.*(*K.*) *mortilleti*. The lateral lobe of *caravacaensis* has a narrow throat, whereas *P.* (*K.*) *mortilleti* has a wide-throated lateral lobe.

Range: Highest Balearis Zone and Ohmi Zone (bed A 140 to A152).

Geographical distribution: France (Nice, Angles, Chamaloc), Spain (Rio Argos, Tornajo, La Guardia de Jaén, Ermita de la Virgin de Cuadros), Slovakia (Polomec Quarry), The Crimea (Verkhoreche), Switzerland [La Veveyse (Les Crases)], and Austria (northeast of Geisshorndl), Georgia (River Ritseula).

7.1.2. *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.
Figs. 16-20; Pl. II; Tab. II

pars 1919. *Parahoplites angulicostatus* (d'Orbigny).– Rodighiero, p. 103, pl. 25 (11), fig. 4, *non* fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

1960. *Pseudothurmannia picteti* Sarkar.– Drushchits & Kudrjavtsev, p. 228, pl. 30, fig. 6.

1964. *Balearites* sp.– Fülöp, pl. 9, fig. 7.

1967. *Crioceratites* (*Pseudothurmannia*) *mortilleti catulloi* (Parona).– Bacelle & Lucchi Garavello, p. 137, pl. 3, fig. 4.

1968. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Sornay, p. 4, pl. 1, fig. 1.

1976. *Pseudothurmannia belimelensis* Dimitrova.– Mandov, p. 66, pl. 9, fig. 1.

pars 1981. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Kakabadze, p. 91 pl. 1, only fig. 7, *non* fig. 8 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

1982. *Crioceratites* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Braga *et al.*, p. 685, pl. 1, fig. 5 (var. *fissicostulata*), *non* fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858)].

pars 1986. *Crioceratites* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Darga & Weidich, p. 103, pl. 3, fig. 4, *non* fig. 5 [= *Pseudothurmannia (Kakabadziella) tornajensis* sp. nov.].

1994. *Pseudothurmannia belimelensis* Dimitrova.– Cecca *et al.*, p. 560, fig. 5a.

1994.. *Pseudothurmannia mortilleti* morphotype *catulloi* (Parona).– Cecca *et al.*, p. 560, fig. 5c (microconch).

1994. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Cecca *et al.*, p. 560, fig. 5d (= var. *fissicostulata*).

pars 1995b. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Hoedemaeker, p. 230, pl. 2, figs. 2-3 (= var. *fissicostulata* nov.), 4-5 (= macroconchs), fig. 6 (= microconch), *non* pl. 1, fig. 4, pl. 2, fig. 1 [= ambo *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858)].

pars 1995b. *Pseudothurmannia belimelensis* Dimitrova.– Hoedemaeker, p. 230, pl. 2, only fig. 7 (= var. *gracilis* nov.), *non* fig. 9 [*Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* (Torcapel, 1884)].

1995. *Pseudothurmannia sarasini* Sarkar.– Cecca *et al.*, p. 198, pl. 1, fig. 1 (microconch).

1995. *Pseudothurmannia mortilleti catulloi* (Parona).– Cecca *et al.*, p. 198, pl. 1, figs. 3-4 (microconchs).
1995. *Pseudothurmannia belimelensis* Dimitrova.– Cecca *et al.*, p. 198, pl. 1, fig. 5 (macroconch).
1995. *Pseudothurmannia mortilleti mortilleti* (Pictet & De Loriol).– Cecca *et al.*, p. 198, pl. 1, fig. 6 (var. *fissicostulata*).
1995. *Pseudothurmannia mortilleti catulloi* (Parona).– Cecca & Pallini, p. 212, pl. 1, figs. 9-10 (microconchs).
? 1995. *Pseudothurmannia angulicostata* (d'Orbigny).– Cecca & Pallini, p. 212, pl. 1, fig. 11.
1995. *Pseudothurmannia belimelensis* Dimitrova.– Cecca & Pallini, p. 212, pl. 1, fig. 13 (macroconch).
1995. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Cecca & Pallini, p. 212, pl. 1, fig. 14 (variety *fissicostulata*).
1995. *Pseudothurmannia sarasini* Sarkar.– Cecca & Pallini, p. 212, pl. 1, fig. 12 (microconch).
1995. *Pseudothurmannia angulicostata Auctt*.– Faraoni *et al.*, p. 230, pl. 2, fig. 11 (microconch).
1996. *Pseudothurmannia sarasini* Sarkar.– Cecca *et al.* p. 418, fig.3 (macroconch).
pars 1996. *Pseudothurmannia catulloi* (Parona).– Faraoni *et al.* 1996, p. 253, pl. 2, figs. 4-5, 7, *non* figs. 6, 8 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].
1998. *Pseudothurmannia* sp. cf. *catulloi*? (Parona).– Cecca *et al.*, p. 94, pl. 5, fig. 14.
1998. *Pseudothurmannia sarasini* Sarkar var. *belimelensis* Dimitrova.– Cecca *et al.*, p. 93, pl. 5, fig. 17, 18.
1998. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Cecca *et al.*, p. 94, pl. 5, figs. 1-13. (figs. 1-2, 7, 12-13, macroconchs; figs. 3-4, microconchs; figs. 5-6, 8-11, var. *fissicostulata*).
1998. *Pseudothurmannia sarasini* Sarkar.– Cecca *et al.*, p. 92, pl. 5, figs. 15-25, 15, 22-25 (microconchs), figs. 17-18 (var. *gracilis*), 16, 19-21 .
1999. *Pseudothurmannia mortilleti sensu* Hoedemaeker.– Baudin *et al.*, p. 491, fig. 3E (macroconch).
1999. *Pseudothurmannia* sp.– Baudin *et al.*, p. 490, fig. 3B (macroconch).
pars 2002. *Pseudothurmannia sarasini* Sarkar.– Bodrogi & Fogarasi, p. 304, pl. 1 fig. 1, *non* fig. 2 [= probably *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].
2003. *Parathurmannia* sp. A.– Busnardo, p. 71, pl. 9, figs. 4, 9 (macroconchs).
pars 2003. *Parathurmannia* gr. *sarasini* (Sarkar).– Busnardo, p. 69, pl. 15, fig. 6 (microconch), pl. 32, figs. 3, 5-6, *non* pl. 9, fig. 2 (= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar); *non* pl.12, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* Parona], *non* figs. 2, 9 (= *Crioceratites* sp. indct); pl. 15, fig. 1 [= probably *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].
2003. *Pseudothurmannia* (*l.s.*) sp. C.– Busnardo, p. 68, pl. 15, fig. 12 (macroconch).
2003. *Pseudothurmannia* (*l.s.*) *rugosa* n. sp.– Busnardo, p. 68, pl. 21, figs. 2, 7 (microconchs).
pars 2003. *Pseudothurmannia ohmi* (Winkler).– Company *et al.* p. 691, fig. 6.1. (macroconch), *non* fig. 6.2 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* Winkler, 1868].
pars 2004. *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol).– Kakabadze, p. 384, pl. 2, fig. 2-3, *non* fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* Parona, 1897].
2004. *Pseudothurmannia (Balearites)* cf. *balearis* (Nolan, 1894).– Kakabadze, p. 387, pl. 2, figs. 4, 6 (probably inner whorls).
2005. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Kakabadze, p. 350, pl. 72, fig. 1.
2005. *Pseudothurmannia* (*Balearites*) *balearis* (Nolan).– Kakabadze, p. 351, pl. 72, fig. 2.

Syntypes: Four macroconchs (Figs. 16A-D) of what the author considers the typical variety derived from section W; (1) from a bed between beds W34-36 (RGM 387907), (2) from bed W38 (RGM 541930), (3) from block B (RGM 387884), and (4) from block D (RGM 541931). The blocks are derived from beds between W35 and W46. Deposited in Naturalis diversity Center, Leiden The Netherlands.

Locus typicus: Section W along the Río Argos Succession, 250 m west of Cortijo de Alguacil, near Caravaca, Province of Murcia, Spain. Very well exposed in 1973-1975, now overgrown by an orchard of fruit trees.

Derivation of name: After the nearest town, Caravaca de la Cruz (province of Murcia, Spain).

Material: One hundred and thirteen specimens in total. One hundred and four specimens from the Río Argos succession (Caravaca, Murcia, Spain); the first is derived from bed W35, and the last from bed W46. Eight specimens from the Bolos Formation in the Sierra de la Muela (Moratalla, Murcia, Spain). One specimen from Casas Les Fontanelles (Biar, Alicante, Spain).

Diagnosis: *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* exhibits fine ribs on the inner whorls, which are, however, not as uniform as in *P.* (*K.*) *mortilleti*; they remain relatively fine up to the adult stage. The distribution of main and intermediate ribs is characteristically irregular. The differentiation in main and intermediate ribs begins early (D = 12 mm) in the ontogeny. Effacement of intermediate ribs around the umbilicus especially in late ontogenetic stages is a normal, characteristic feature and gives the species quite a different appearance than *P.* (*K.*) *mortilleti*. In *P.* (*K.*) *mortilleti* the intermediate ribs are long and usually reach the umbilical rim, or nearly so, whereas in the effaced parts of *P.* (*K.*) *caravacaensis* the intermediate ribs are short and only some of them may reach the umbilical rim. Characteristic for *P.* (*K.*) *caravacaensis* is that the ribs are often bundled in twos or threes, or split into two at midflank. Umbilical bullae are present on the main ribs and are provided with a pointed tip. The distance between the bullae and between the main ribs is irregular and may be rather great, especially in the largest specimens and in the variety *gracilis*. The venter is mod-

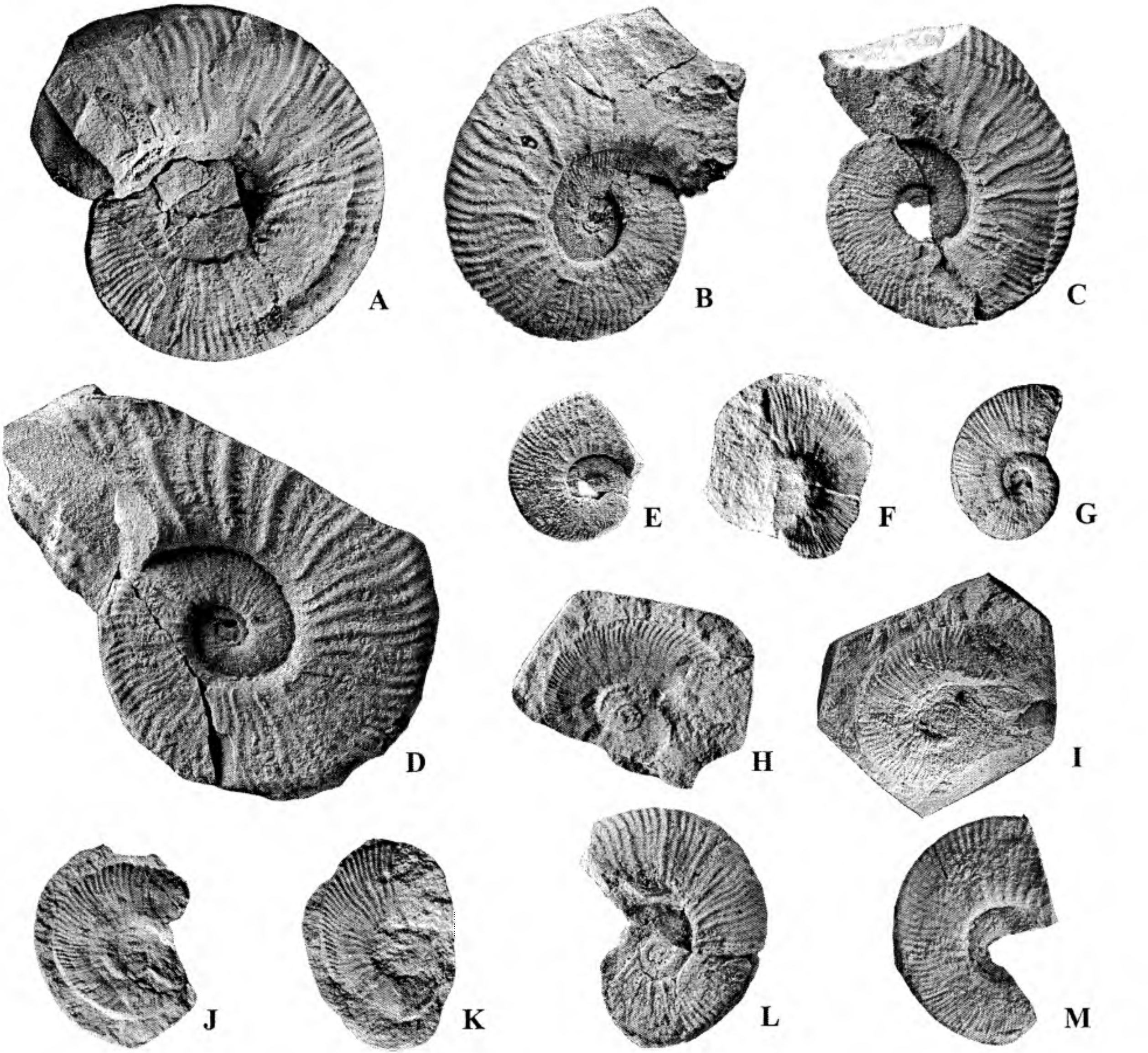


Fig. 16: A-D, *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., syntypes. A, RGM 387907, locality 1W, loose from W34-36; ×1. B, RGM 387884 in loose block B from bed W35-46; ×1. C, RGM 541931, locality 1W, in loose block b from beds W35-46; ×1. D, RGM 541930, locality 1W, bed W38, macroconch with suture line; ×1.
E-M, *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., young specimens. E, RGM 541983, locality 1W, bed W35; ×1. F, RGM 387953, locality 1W, in loose block M from beds W35-46; ×1. G, RGM 541922, locality 1W, in loose block B from beds W35-46; ×1. H, RGM 541924, locality 1W, in loose block L from bed W35-46, mark the wide-spaced main ribs; ×1. I, RGM 541985, locality 1W; ×1. J, RGM 541923A, locality 1W, in loose block L from beds W35-46; ×1. K, RGM 541923B, locality 1W, in loose block F from beds W35-46; ×1. L, RGM 542669, locality 1W, bed W35; ×1. M, RGM 541961, locality 1W, loose from bed 35; ×1.

erately rounded; the shoulders are adorned with rows of uniform clavi. The egression of the whorls begins earlier in the ontogeny (at a diameter of c. 30-40 mm) than in *P.* (*K.*) *mortilleti*.

This species is sexually dimorphic. The microconchs have thick, distant, sigmoid ribs on the living chamber beginning at the approximate diameter of 30 mm. The largest microconch sampled measures 65 mm. The macroconch presumably reaches a large diameter as in *P.* (*K.*) *mortilleti* and *P.* (*K.*) *catulloi*.

Description: Planulate shells with compressed whorls, flat to slightly rounded flanks and a truncated though moderately rounded ventral side. Rather narrow umbilicus. The whorls are slightly thicker. The first whorl is almost smooth and leaves open a perforated umbilicus. The ribbing is preserved from a diameter of 4 mm. At first, the ribs are distant, simple, and uniform, and are highest on the flanks; later, the ribs are less distant and fine, and the main ribs are separated by intermediate ribs. The differentiation of ribs begins at a diameter of 12 mm.

All the ribs are fine, originate at the umbilical seam and show small clavi on the ventrolateral shoulder. The ribs do not cross the ventral side; the mid-ventral line remains smooth. Many ribs split on the flanks, also fasciculation occurs. Weak umbilical bullae already may appear at a diameter of 15 mm.

At a diameter of 20 mm, umbilical bullae become prominent and mark off the main ribs. The bullae are long and look like slightly raised main ribs; they are rursiradiate on the umbilical wall and are concave towards the aperture on the umbilical rim; on the rim they are raised into a small pointed tip. There are generally 1-2, but also 3-4, and in some cases even 6-7 intermediate ribs between two main ribs. Most intermediate ribs start at midflank. The distribution of main and intermediate ribs may vary from very regular to very irregular. In some cases the main ribs even differ in thickness. Bundling and splitting of ribs is frequent. On the upper half of the flanks all ribs are equally strong. All ribs are S-shaped and cross the slightly rounded venter almost straight. The ventrolateral shoulders are adorned with rows of uniform clavi.

The continuation of the ornamentation is not the same for all specimens. Two different forms can be distinguished, which differ in the size and ribbing of the adult. The author interprets them as sexual dimorphs, because they occur in the same beds, in the same section W, and have the same ornamentation on the inner whorls.

Suture line: The suture line depicted by Sornay (1968, fig. 1) is from *P.* (*K.*) *caravacaensis* instead of *P.* (*K.*) *mortilleti*. The present author could draw only a part of the suture line (Fig. 17). It shows the incomplete E/L and L/U saddles; the L/U saddle is appreciably higher than the E/L saddle. The lateral lobe is very deep and trifid with two long side arms that cause the saddles to be narrow-necked. The lobe has a narrower throat than that of *P.* (*K.*) *mortilleti*. The deep incisions at the top of the saddles leave two asymmetric parts; the external part of saddle E/L could not be studied well, and only one branch could be drawn (Sornay, 1968 depicted three branches); the inner part consists of four branches. The external part of saddle L/U consists of three branches, whereas only two branches of the inner part could be studied (Sornay, 1968 depicted three branches for the inner part of saddle L/U).

Macroconchs: From about 40 mm diameter the whorls begin to egress and the umbilicus rapidly widens. The ribs remain fine, but the distance between the ribs increases and may exceed the thickness of the ribs; this gives the ribs an attenuated appearance. The main ribs generally become more prominent and the distance between them becomes irregular, but averagely increases. The umbilical bullae also become more prominent and may even become pointed. The main ribs are rursiradiate on the umbilical wall, slightly prorsiradiate and slightly sigmoidal on the flanks. The lower parts of the intermediate ribs become effaced, but remain well marked near the venter; they generally start at midflank, but also may continue faintly down to the umbilical rim where they may form bundles; they may exceed the main ribs in thickness. The number of intermediate ribs to one main rib is very irregular and commonly varies from 1-6. The lower parts of the flanks between the bullae and main ribs are commonly smooth with growth lines or occupied by a weak undulation from which the intermediate ribs bundle, but the intermediate ribs may also continue down to the umbilical rim. The ribs pass the ventral side uninterrupted with a slight adoral convexity; the small ventrolateral clavi remain faintly visible. The venter is only a little arched. The largest macroconch collected reaches a diameter of 80 mm, but a whorl fragment of a macroconch of 105 mm in diameter was sampled (Figs. 20E-F). The last whorl of the macroconchs shows very wide-spaced main ribs with up to six short intermediate ribs.

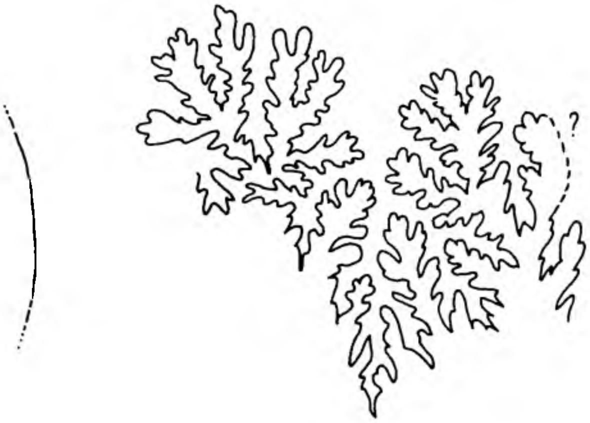


Fig. 17: Suture line of *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* nov. sp., RGM 541930, syntype, Wh 20 mm; ×4.

Microconchs: Fig. 18. The inner whorls are similar to those of the macroconchs, but from a diameter of 40 mm the ribbing becomes very coarse and irregular. From this diameter egression begins and the living chamber only slowly increases in height. The ribs become thick, more prominent, broader, irregularly distributed, sigmoidal and more separated; forking also occurs. The distance between the ribs becomes larger than the thickness of the ribs and their thicknesses become unequal. The main ribs are swollen in the lower part of the flanks. The intermediate ribs are about as thick as the main ones and vary in length. All the ribs pass the truncated venter without interruption and with a marked adoral curve. The ventrolateral clavi remain visible on both sides of the venter.

Variety *fissicostulata*: Among the macroconchs there are specimens in which the ribbing remains very dense and fine (Fig. 19); they hardly become coarser and more separated in later ontogenetic stages. These specimens are united in the variety *fissicostulata*. The number of intermediate ribs is very irregular and varies from 1-7,

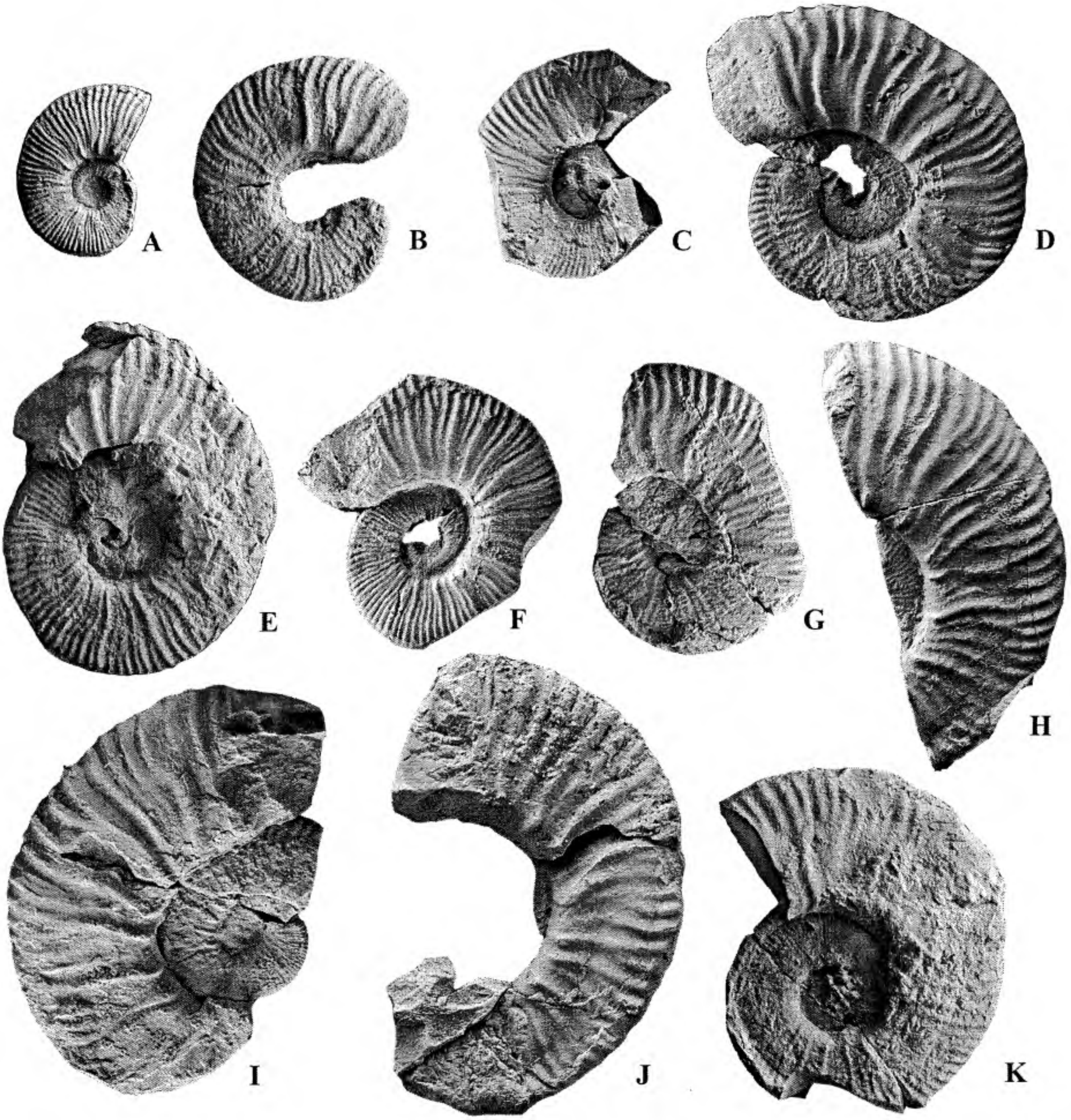


Fig. 18: A-K, *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., microconchs. A, RGM 541981, locality 1W, from one of the beds W35-46; ×1. B, RGM 541964, locality 1W, in loose block C from beds W35-46; ×1. C. RGM 541975, locality 1W, in loose block D from beds W35-46; ×1. D, RGM 387905, locality 1W, in loose block B from beds W35-46; ×1. E, RGM 541982, locality 1W, in loose block A from beds W35-46; ×1. F, RGM 541979, locality 1W, bed W41; ×1. G, RGM 541973, locality 1W, in loose block C from beds W35-46; ×1. H, RGM 541977, locality 1W, in loose block B from beds W35-46; ×1. I, RGM 541980, locality 1W, bed W35; ×1. J, RGM 541974, locality W, from one of the beds W35-46; ×1. K, RGM 541970, locality 1W, bed W38; ×1.

in one case even amounting to eight and nine. There are several intermediate forms between these specimens and those that do show some coarsening and increment of the rib distance. Therefore, they were considered to represent fine-ribbed morphotypes, var. *fissicostulata* of *P.* (*K.*) *caravacaensis,* and not to represent a separate species.

Variety *gracilis*: In some specimens the effacement is extreme (Figs. 20A-D), and the intermediate ribs are only visible in the upper third or quarter of the flanks. Similar specimens were identified as *Pseudothurmannia belimelensis* Dimitrova by Hoedemaeker (1995) and as *Pseudothurmannia sarasini* variety *belimelensis* Dimitrova by Cecca *et al.* (1998). These macroconch specimens are here included as variety *gracilis* in *P.* (*K.*) *caravacaensis* sp. nov. because of the presence of specimens with a transitional ornamentation. They are

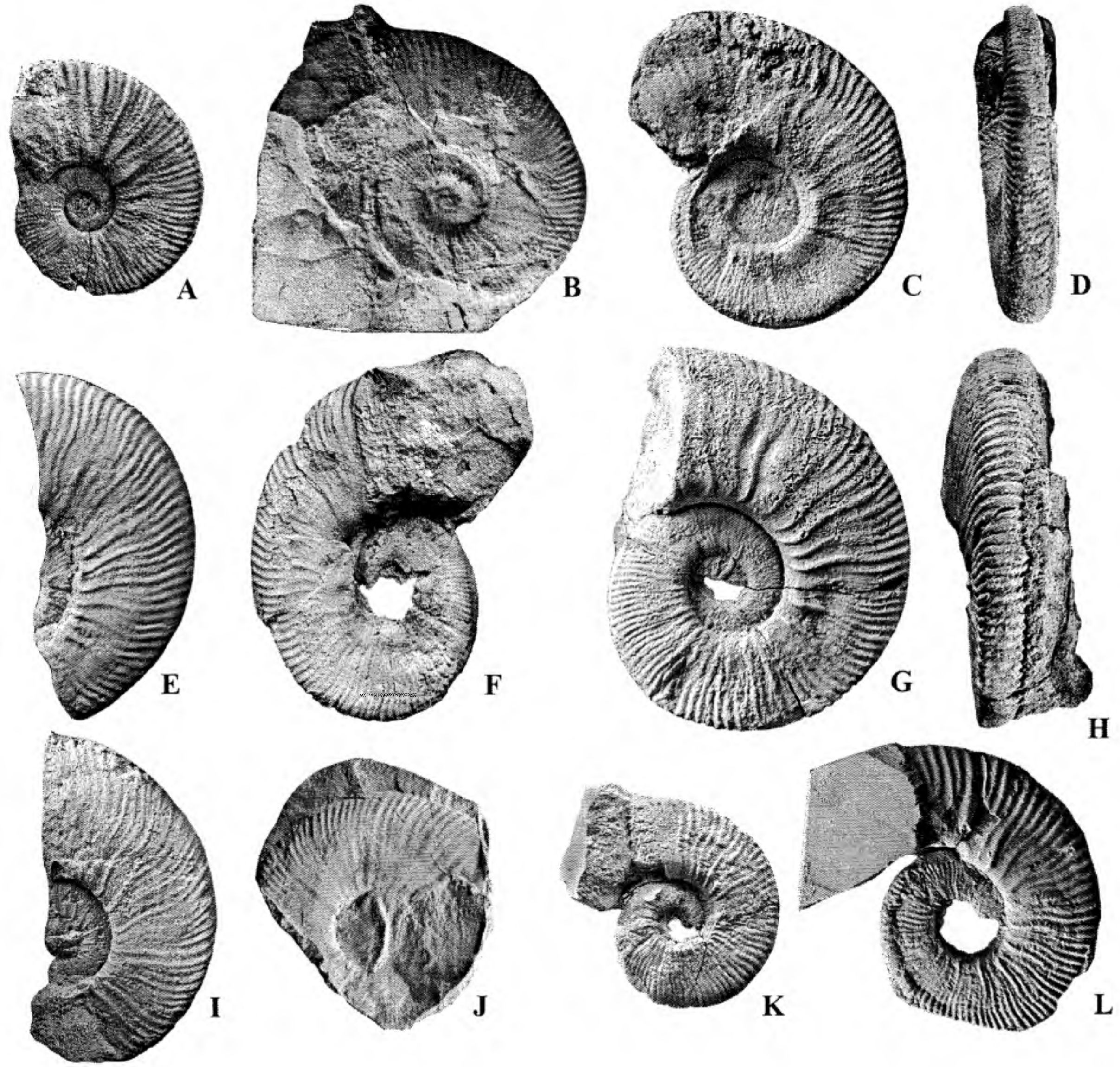


Fig. 19: A-L, *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov. var. *fissicostulata*. A, RGM 541929, locality 2; ×1. B, RGM 541920, locality 1W, loose from one of the beds W46-56; ×1. C, RGM 541928, locality 2, lateral view; ×1. D, same specimen, ventral view; ×1. E, RGM 541919, locality 1W, from one of the beds W35-46; ×1. F, RGM 541917, locality 1W, in loose block N from beds W35-46; ×1. G, RGM 541927, locality 2, lateral view; ×1. H, same specimen, ventral view; ×1. I, RGM 387881, locality 1W, bed W36; ×1. J, RGM 541921, locality 1W, loose from one of the beds W35-46; ×1. K, RGM 541976, locality 1W, in loose block A from beds W35-46; ×1. L, RGM 541978, locality 1W, in loose block E from beds W35-46; ×1.

characterized by the great separation of the elegant, S-shaped main ribs and by having 4-5 shorter intermediate ribs, which efface towards the umbilicus.

The great distance between the main ribs has already developed at a diameter of 11-12 mm, where the number of intermediate ribs changes from two to four and the first umbilical bulla appears. From a diameter of 22 mm the ornamentation consists of radial, prominent, S-shaped main ribs with small pointed umbilical tubercles, and 7-9 thinner S-shaped intermediate ribs without umbilical tubercles. Most intermediate ribs originate at the rounded umbilical rim, but many others are intercalated and originate at midflank. Every rib is provided with a small ventrolateral clavus. All the ribs cross the venter without interruption; the main ribs remain slightly more prominent than the intermediate ribs on the venter. Between diameters 30 and 45 mm, the number of long intermediate ribs diminishes until all intermediate ribs originate at midflank. Also their number diminishes to 4-5.

From a diameter of 45 mm, the number of short intermediate ribs becomes still smaller, viz. three (Fig. 20D). Most of them are restricted to the upper half of the flanks, but some are longer and may reach down

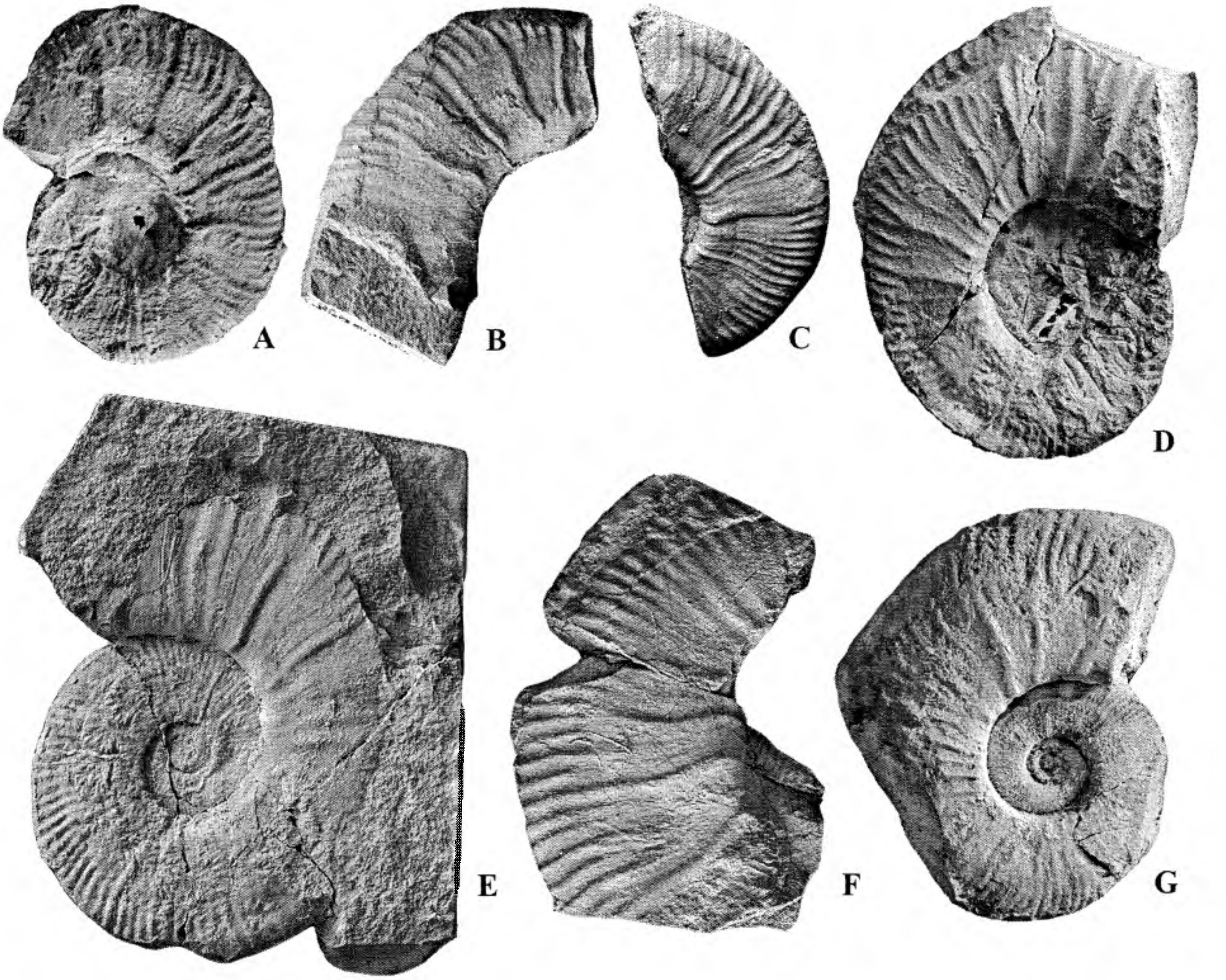


Fig. 20: A-D, *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov. var. *gracilis*. A, RGM 387980, locality 1W, in loose block E from beds W35-46, early disappearance of intermediate ribs from the lower part of the flanks; ×1. B, RGM 541989, locality 1W, in loose block E from beds W35-46; ×1. C, RGM 541960, locality 1W, loose from one of the beds W35-46; ×1. D, RGM 541988, locality 1W, bed W36; ×1.
E-G, *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov. largest macroconchs. E, RGM 541949 (GIA P113), locality 1W, loose from one of the beds W35-46; ×1. F, RGM 541958, locality 1W, bed W45; ×1. G, RGM 542666, locality 2; ×1.

to the umbilical rim again. Forking may occur. The ribs cross the venter without interruption and all are provided with a small uniform ventrolateral tubercle. The main ribs become more pronounced; some of them are flanked by shallow constrictions.

Variety *gracilis* lacks any affinity with *Pseudothurmannia belimelensis* Dimitrova, 1967, because it has a much smaller umbilicus, a much more rapid growth in whorl height, and, starting at least at a diameter of 11 mm, commonly more intermediate ribs between the main ribs. Furthermore, the ribs are almost radial, whereas those of *P.* (*K.*) *belimelensis* are prorsiradiate.

Remarks: In the Río Argos succession this species occurs almost exclusively in section W in the Los Miravetes area (101 specimens); only three specimens occur in the Las Oicas area (one in section K, two from section F). All 13 specimens of *Pseudothurmannia mortilleti* described and figured by Cecca *et al.* (1998) belong to *P.* (*K.*) *caravacaensis*; those of figs. 3-4 are microconchs. Four specimens of *P. mortilleti* described and figured by Hoedemaeker (1995, pl. 2, figs. 2, 3, 5, 6) also belong to *P.* (*K.*) *caravacaensis*; they were regarded as a variety or chronosubspecies of *P.* (*K.*) *mortilleti* (Hoedemaeker, 1995, p. 229). That is the reason why Cecca *in* Baudin *et al.* (1999) figured a specimen of *P.* (*K.*) *caravacaensis* under the name of '*Pseudothurmannia mortilleti sensu* Hoedemaeker.' Small specimens of *P.* (*K.*) *caravacaensis* closely resemble small specimens of *mortilleti*, but differ from the latter in the slightly thicker whorls, the greater projection of the ribs in the upper part of the flanks, the greater irregularity of the distribution of main and intermediate ribs and the gradual effacement of its ribbing in adult stages, the greater frequency of fasciculating and splitting ribs, and the early start of egression of the whorls. The microconchs differ in the early start of coarser and more distant ribbing at a diameter of about 25 mm (see also diagnosis). The author now considers *P. (K.) caravacaensis* to be a genuine species, because of its consistent differences from *P. (K.) mortilleti* in its suture line and ornamentation. It replaces *P. (K.) mortilleti* in the Catulloi Zone.

Pseudothurmannia (*Kakabadziella*) *catulloi* differs from *P* (*K.*) *caravacaensis* in developing coarser, blunter and more flexuous ribbing in middle and adult growth stages, in exhibiting a regular distribution of ribs with mainly 1-2, rarely three, intermediate ribs to one main rib, in the absence of fasciculating or splitting of ribs (except in a very early transitional stage), in the absence of umbilical bullae (except in some adult macroconchs) and in the absence of rib effacement.

Pseudothurmannia (*Kakabadziella*) *caravacaensis* is considered the ancestor of *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955. They look like each other because of the great distance of the main ribs on the young whorls of both species, but in *P.* (*Pa.*) *sarasini* this feature begins at a diameter of 10 mm, in *P.* (*K.*) *caravacaensis* at a diameter of 25 mm. In fact, all specimens of *Pseudothurmannia sarasini* Sarkar, 1955, described and depicted by Cecca *et al.* (1998) belong to *P. (K.) caravacaensis*. Cecca *et al.* (1998) showed the great variability of this species, which includes the variety *gracilis*. The ornamentation of the latter variety differs from that of *P.* (*Pa.*) *sarasini* (1) in the main ribs being still widely spaced at the diameter in which they already are closely spaced in *P.* (*Pa.*) *sarasini*, (2) in the bullae in *P.* (*Pa.*) *sarasini* being comma-shaped, and (3) in the intermediate ribs of *P.* (*Pa.*) *sarasini* originating in the lower quarter of the flanks instead of in the upper third. The largest specimen of this variety has a diameter of 62 mm.

Range: Restricted to the Catulloi Zone (beds W 35 to W46).

Geographical distribution: Spain [Río Argos (Caravaca), Arroyo de Gillico (Cehegin), La Guardia (Jaen), Ibiza, Casas Les Fontanelles (Biar, Alicante)], France (Vergons, Les Voirons), Italy [Bertigo, Mount Belloca, Bosco Chiesdanuova, Umbria-Marche Apennines (Mt. Petrano, Stirpeto), La Stua], Switzerland [La Veveyse (Châtel-St.-Denis)], Austria (Lackbach, 25 km WSW of Unken, Salzburg), Bulgaria (Gragoman, Prevala, Salash), Hungary (Városlöd).

7.1.3. *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)

Figs. 21-31; Pls. III-XIV; Tab. III

* 1897. *Hoplites Catulloi* n.f.– Parona, p. 141, pl. 1 (17), fig. 5a-c.

pars 1901. *Hoplites angulicostatus* d'Orbigny.– Sarasin & Schöndelmayer, p. 81, pl. 9, fig. 8 (= macroconch), *non* pl. 10, fig. 3 [= holotype of *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955].

pars 1907. *Crioceras angulicostatum* d'Orbigny.– Karakasch, p. 134, pl. 16, only fig. 7a-b, *non* fig. 4a-b [= *B.* (*K.*) *ohmi valbonnettensis* subsp. nov.], *non* pl. 15, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov., macroconch].

non 1949. *Hoplites Catulloi* Parona.– Petkovic & Miletic, p. 133, pl. 2, figs. 7-9 (Parahoplitidae?).

1960. *Pseudothurmannia picteti* Sarkar.– Drushchits & Kudrjavtsev, p. 288, pl. 30, fig. 6.

1962. *Crioceratites* (*Pseudothurmannia*) *mortilleti catulloi* (Parona).– Wiedmann, p. 136, pl. 7, fig. 4.

pars 1964. *Pseudothurmannia* [ex. gr. *P. angulicostata* (d'Orbigny)].– Fülöp, only pl. 18, fig. 5, *non* pl. 27, fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* Winkler, 1868].

? 1965. *Pseudothurmannia angulicostata* (d'Orbigny).– Dimitrova, p. 217, pl. 1, fig. 2, *non* fig. 1 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955], *non* fig. 3 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* nov. subsp. (microconch)].

non 1967. *Crioceratites* (*Pseudothurmannia*) *mortilleti catulloi* Parona.– Bacelle & Lucchi Garavello, p. 137, pl. 3, fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

1967. *Pseudothurmannia uhligi* (Weerth).– Dimitrova, p. 73, pl. 34, fig. 1 (= macroconch).

pars 1968. *Pseudothurmannia catulloi* (Parona).– Sornay, p. 5, pl. 1, fig. 3, *non* fig. 5 [= *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955].

1976. *Pseudothurmannia catulloi* (Parona).– Mandov, p. 65, pl. 9, fig. 2.

non 1976. *Pseudothurmannia* aff. *catulloi* (Parona).– Mandov, p. 66, pl. 9, fig. 3 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

pars 1976. *Pseudothurmannia biassalensis* Dimitrova.– Mandov, p. 66, pl. 9, only fig. 5, *non* fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

1981. *Pseudothurmannia* (*Pseudothurmannia*) *isocostata* sp. nov.– Kakabadze, p. 91, pl. 3, fig. 2.

1988. *Crioceratites* (*Pseudothurmannia*) *provencalis* Wiedmann.– Wilke, p. 20, pl. 2, fig. 28.

pars 1990. *Pseudothurmannia angulicostata* (d'Orbigny).– Thomel, pl. 6, figs. 8-9, *non* figs. 1-7 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* figs. 10-12 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].

non 1994. *Pseudothurmannia mortilleti* morphotype *catulloi* (Parona).– Cecca *et al.*, p. 560, fig. 5c [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* nov. sp.].

1995b. *Pseudothurmannia catulloi* (Parona).– Hoedemaeker, p. 227, pl. 1, figs. 1a-b, 3.

non 1995. *Pseudothurmannia mortilleti catulloi* (Parona).– Cecca & Pallini, p. 212, pl. 1, figs. 9-10 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1995. *Pseudothurmannia mortilleti catulloi* (Parona).– Cecca *et al.*, pl. 1, figs. 3-4 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

pars 1995. *Pseudothurmannia picteti* Sarkar.– Avram, p. 119, pl. 8, figs. 5-6, *non* fig. 7 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].

pars 1995. *Pseudothurmannia biassalensis* Dimitrova.– Avram, p. 120, pl. 8, fig. 10, *non* fig. 9 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

pars 1996. *Pseudothurmannia catulloi* (Parona).– Faraoni *et al.*, p. 253, pl. 2, figs. 6, 8, *non* 4, 5, 7 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

1998. *Pseudothurmannia* cf. *catulloi* (Parona).– Arnaud *et al.*, p. 15, pl. 1, fig. 4.

non 1998. *Pseudothurmannia* sp. cf. *catulloi?* (Parona).– Cecca *et al.*, p. 94, pl. 5, fig. 14 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

? 2002. *Pseudothurmannia* cf. *ohmi* Winkler.– Bodrogi & Fogarasi, p. 304, pl. 2, fig. 3.

pars 2003. *Parathurmannia mortilleti* (Pictet & De Loriol).– Busnardo, p. 69, pl. 16, fig. 1 (microconch), fig. 2 (macroconch), *non* pl. 32, fig. 2 [= paralectotype of *Pseudothurmannia* (*Kakabadziella*) *mortilleti*], fig. 4 [= lectotype of *Pseudothurmannia* (*Kakabadziella*) *mortilleti*].

pars 2003. *Parathurmannia* gr. *sarasini* (Sarkar).– Busnardo, p. 69, pl.12, fig. 1, *non* pl. 9, fig. 2 [= *Crioceratites* (*Binelliceras*) *rotundata* Sarkar, 1955]; *non* pl. 12, figs. 2, 9 (= *Crioceratites* sp. indet); pl. 15, fig. 1 [= probably *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], *non* pl. 32, figs. 3, 5-6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

pars 2003. *Pseudothurmannia picteti* Sarkar.– Company *et al.*, fig. 6.7., *non* 6.6. [= *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* sp. nov.].

2003. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Company *et al.*, p. 691, fig. 6.4. (microconch).

2004. *Pseudothurmannia* (*Pseudothurmannia*) cf. *catulloi* (Parona, 1897).– Kakabadze, p. 386, pl. 2, fig. 1.

? 2004. *Pseudothurmannia* (*Balearites*) cf. *balearis* (Nolan).– Kakabadze, p. 387, pl. 2, figs. 4, 6 (inner whorls).

pars 2004. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Kakabadze, p. 384, pl. 2, fig. 7, *non* figs. 2-3 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

2005. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Company *et al.*, p. 188, fig. 4D (microconch).

Holotype by monotypy: The young specimen from Breonio in the Province of Venice described by Parona [1897, p. 141, pl. 17 (1), fig. 5a-c]. Deposited in the Geological Museum in Pisa. Repeated urgent requests for a plaster cast were not replied to.

Material: Two hundred and twelve specimens in total: 107 specimens from the Río Argos succession (Caravaca), 105 specimens from the Sierra de la Muela (Moratalla).

Emended diagnosis: The species *catulloi* belongs to *Pseudothurmannia* (*Kakabadziella*), has a narrow umbilicus in pre-adult growth stages [appreciably narrower (75%-80%) than the whorl height] and a rapid growth of the whorl height. The adult whorls are egressing, so that in adult growth stages the umbilicus is larger than the whorl height; the macroconchs start egressing at a diameter of 110 mm and the microconchs at a diameter of 60 mm. The whorl section is compressed, high trapezoidal with almost flat sides and weakly arched venter; the species lacks umbilical bullae that protrude above the main ribs (except on the outer whorl of large macroconchs). The shoulders are marked with rows of fine, uniform clavi on every rib. The inner whorls are finely ribbed and look like *P.* (*K.*) *mortilleti*. There is a marked coarsening of the ribs in the adult stage; the main ribs are blunt and sigmoidal. In the coarse-ribbed part there are generally only one or two short intermediate ribs between two main ribs. Macroconchs may reach a diameter of more than 300 mm, the microconchs c. 85-90 mm. In microconchs, the ribs become vigorous, blunt, radial or inclined backward instead of projected, and fasciculating from weak bullae.

Description: Compressed planulates with almost flat flanks and rounded venter. The whorl section is high trapezoidal and the greatest thickness is at the umbilical rim. The whorls are slightly overlapping each other. The shallow umbilicus is narrower than the whorl height. The umbilical walls are vertical and the rim rounded. In young specimens the flanks are slightly rounded and the venter rounded, but show distinct shoulders. In adult specimens the venter is rounded.

The ornamentation is visible from a diameter of 3 mm. The first whorl shows wide-spaced ribs which are highest at midflank (Fig. 21I and RGM 387873). The first whorl is loosely coiled and leaves an umbilical perforation of about 2.5 mm wide. Rapidly, intermediate ribs become intercalated between the main ones. From a diameter of 7.5 mm (RGM 387822) the ribbing is fine, dense and slightly flexuous, and consists of main and intermediate ribs. At first only one intermediate rib is present between each pair of main ribs, but later there are 1-2. The main ribs originate on the umbilical wall, where they are inclined backward. The intermediate ribs originate on the umbilical rim or higher on the flank, and have the same thickness as the main ribs. All ribs are extremely weakened when crossing the venter. Every rib is provided with a small ventrolateral clavus forming delicate rows of small uniform clavi on the shoulders.

At a diameter of 13 mm, the main ribs heighten and thicken at the umbilical rim, and form long comma-shaped 'bullae' from which in addition one or two adjacent intermediate ribs originate. In this transient ontogenetic stage the ribs are bundled. At first, the elevated and thickened 'bullae' of the main ribs are restricted to the umbilical rim, but they rapidly grow in length up to one third of the flank. Higher on the flanks all ribs are fine and equal in height. Two or three intermediate ribs are generally present between each pair of main ribs; they originate above the umbilical rim. Between the bullae at the umbilical rim there are no ribs. The ribs are slightly sigmoidal.

From a diameter of 20 mm the ribs become coarser and

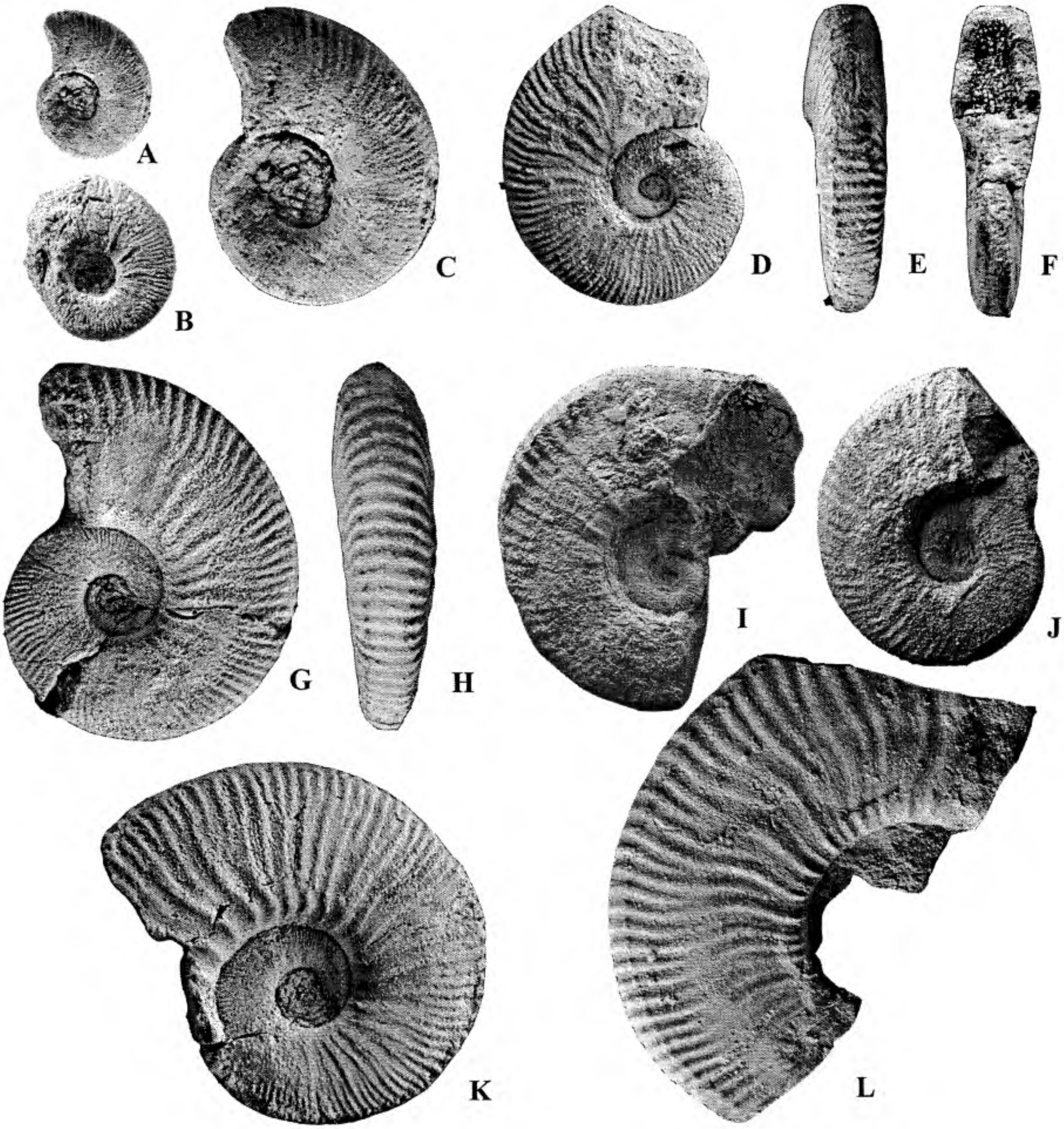


Fig. 21: A-C, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), juveniles. A, RGM 387820, locality 2; ×1. B, RGM 387821, locality 2; ×1. C, same specimen as in Fig. 21A; ×2.
D-L, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), fine-ribbed variety. D, RGM 542651, locality 2; ×1. E, same specimen, ventral view; ×1. F, same specimen, apertural view; ×1. G, RGM 542654, locality 2, lateral view; ×1. H, same specimen, ventral view; ×1. I, RGM 542178, locality 1W, in loose block B from beds W35-46; ×1. J, RGM 542175, locality 1K, bed K175; ×1. K, RGM 542657, locality 2; ×1. L, RGM 542176, locality 1W, loose from one of the beds W46-W56; this specimen closely resembles *Hoplites angulicostatus* (d'Orbigny) in Sarasin & Schöndelmayer, 1901, pl. 9, fig. 8; ×1.

sigmoidal; the elevated part of the main ribs begins on the umbilical wall, but the rib stays elevated and thick over its entire length. This is the reason why from this diameter bullae are not protruding anymore. The number of intermediate ribs between each pair of main ribs diminishes to one or two; they generally originate at midflank and, when approaching the venter, they obtain the same thickness as the main ribs. Sometimes there are three intermediate ribs of which the middle one may reach down to the umbilical rim; sometimes the second intermediate rib is longer than the other; rarely, an intermediate rib may split off from the middle part of a main rib. The lower half of the flank is commonly occupied only by main ribs with smooth interspaces. The

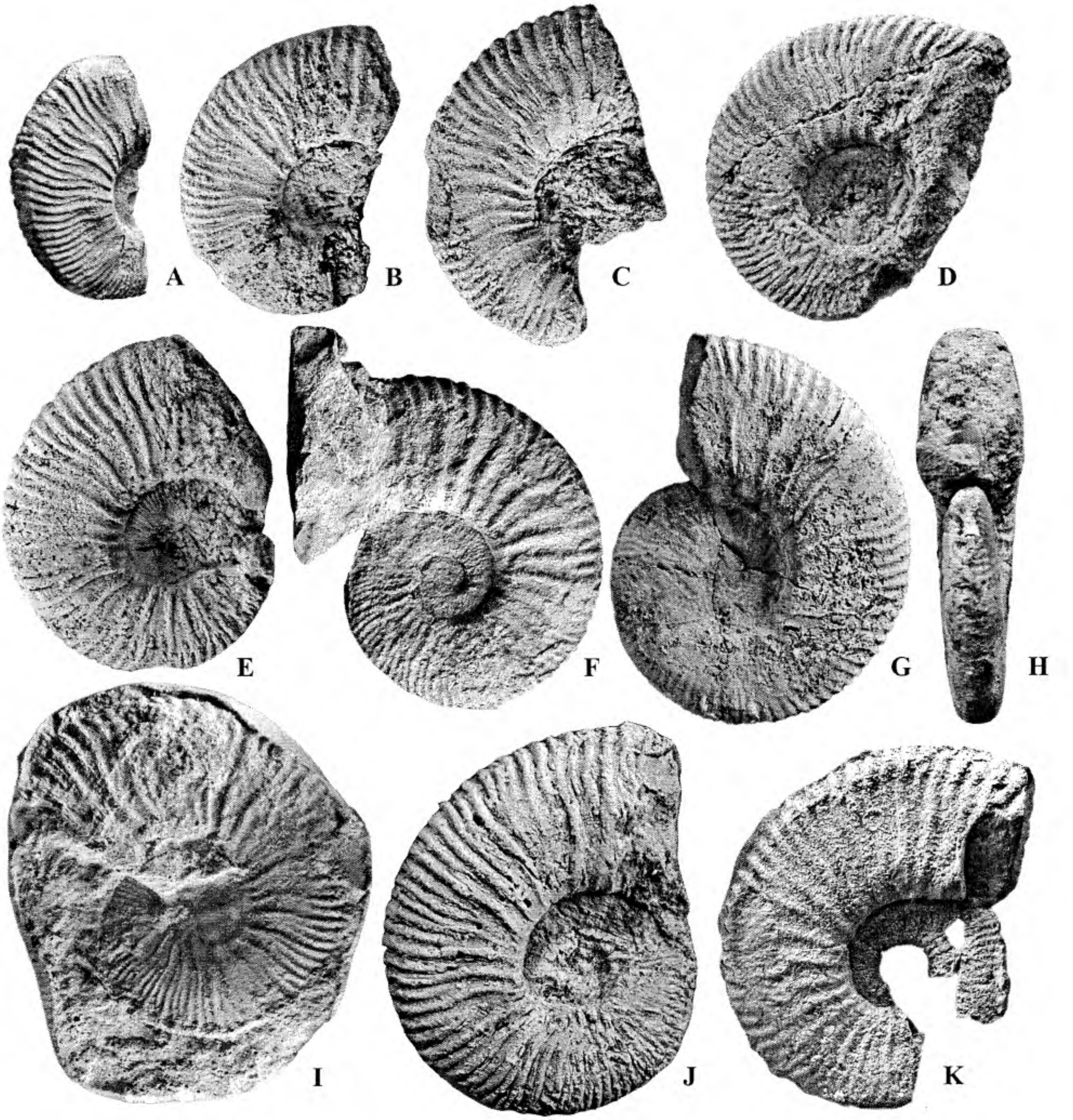


Fig. 22: A-J, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), typical variety. A, GIA P 100A, locality 2; ×1. B, RGM 387813, locality 2; ×1. C, RGM 387817, locality 2; ×1. D, RGM 387812, locality 2; ×1. E, RGM 387814, locality 2; ×1. F, RGM 542172, locality 1A, bed A153; ×1. G, GIA P 100B, locality 2, lateral view; ×1. H, same specimen, apertural view; ×1. I, RGM 387787, locality 2, plaster cast; ×1. J, RGM 387811, locality 2; ×1. K, RGM 387908, locality 1A, loose from one of the beds A149-195; ×1.

ribs cross the venter without any weakening and every rib is provided with a tiny clavus forming two ventrolateral rows of fine uniform clavi. They tend to disappear with only slight a wear. The venter is arched, but show distinct shoulders. The ribs describe a weak forward curve on the venter. The holotype is in this ontogenetic stage.

Suture line: Fig. 23-24. The lateral lobe is narrow and much deeper than the external lobe and the narrow umbilical lobe; the external lobe has a rather broad and high median saddle. Both lateral and umbilical lobes have two long side arms, which cause the saddles in between them to be thin-necked. Saddles E/L and L/U are broad and rounded in outline, their crests being symmetrically split into two parts by a deep narrow incision. Both halves of the E/L saddle consist of four branches. Saddle L/U is a little higher than saddle E/L and both halves consist of

Fig. 23: A-B, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), suture lines. A, RGM 542631, Wh 55 mm; ×2.4. B, RGM 542637, Wh 45 mm; ×2.8.

three branches. Saddle U/I is low, but also split into two halves. The inner lobe is not visible.

Varieties: In some large species the main ribs are rather wide-spaced, and the intermediate ribs originate at the upper third or upper quarter of the flanks. This gives the specimen a different appearance. The author refers to these specimens as var. *externicostata* (Fig. 25; Pls. IV-V). In this variety the main ribs are slightly adorally convex, but in the upper third or upper quarter of the flank all ribs become strongly projected and cross the rounded venter with an adoral curve. On the lower two thirds of the flanks the rib interspaces are smooth, whereas the on

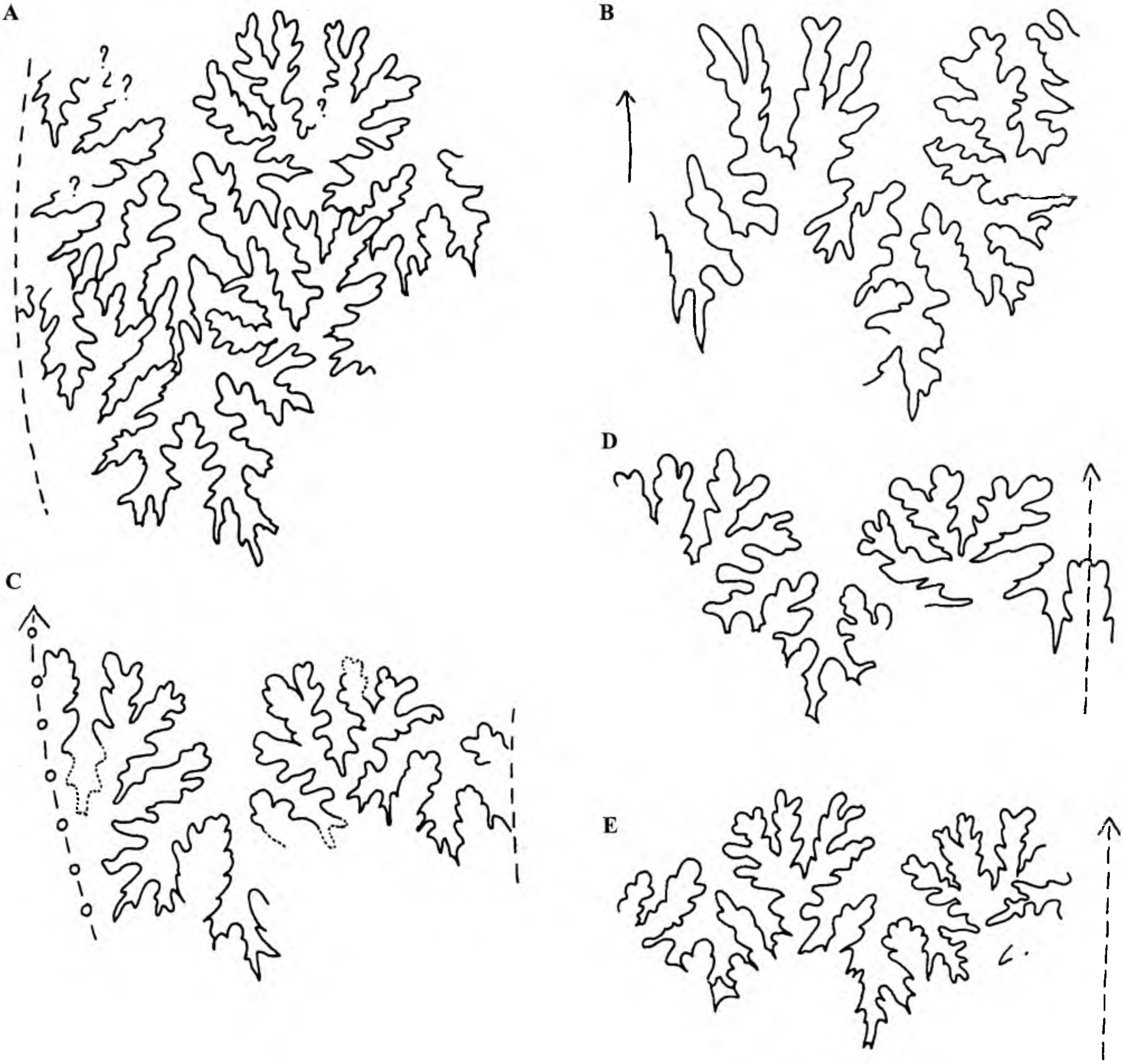


Fig. 24: A-E, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), suture lines. A, RGM 542651, Wh 15 mm; ×3. B, RGM 542178, Wh 14 mm; ×6. C, GIA P100A, Wh 10 mm; × 7. D. GIA P100B, Wh 13 mm; ×6. E, same specimen, Wh 18 mm; ×3.9.

the upper quarter there is a row of equally thick, strongly projected, regularly spaced ribs. The specimens figured by Avram (1995, pl. 8, figs. 5-6) belong to this variety.

There are also fine-ribbed (Figs. 21D-L; Pl. X) and coarse-ribbed varieties. Among the latter are forms with closely spaced ribs (Figs. 26-28; Pls. VI-IX) and others with widely spaced ribs (Pl. VIII). The coarse-ribbed forms differ widely from those of the fine-ribbed specimens, but all transitions exist with the specimens of the typical variety (Figs. 29-30; Pls. XI-XIII).

Macroconchs: In the basal condensed bed of the Barremian Bolos Formation in the Sierra de La Muela the author collected more than 100 specimens of *P.* (*K.*) *catulloi* from small to large dimensions; so the development with growth could be followed in detail. Among the small specimens there are a few with appreciably coarser and blunter ribs on the last whorl. These specimens already begin to egress from a diameter of approximately 60 mm; the umbilical width equals the whorl height at a diameter of 75-85 mm. The whorls of the large specimens begin to egress much later at a diameter of approximately 110 mm; the umbilical width equals the whorl height at a diameter of 123 mm. This convinced the author that the large specimens are macroconchs

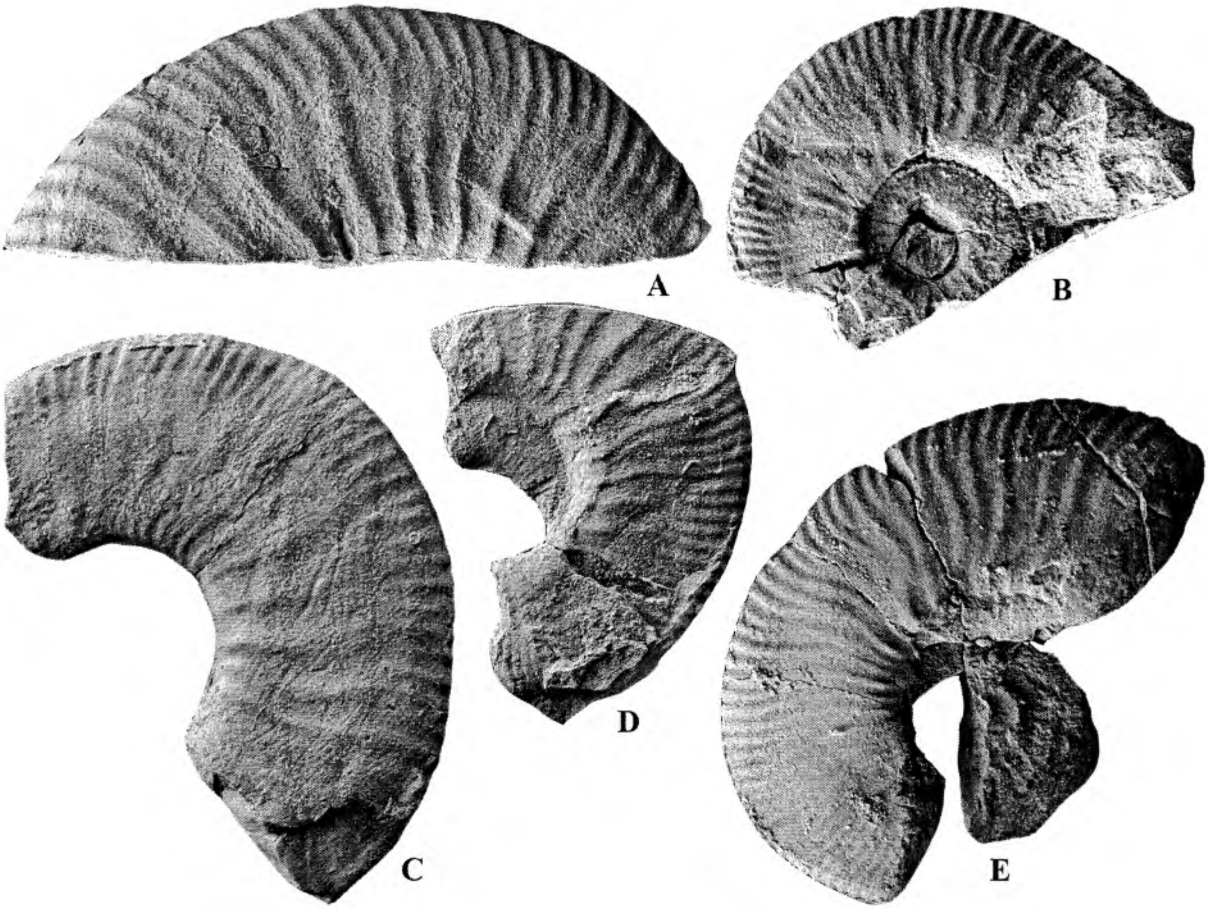


Fig. 25: A-E, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897) var. *externicostata*, small macroconchs. A, RGM 542173, locality 1A, loose from beds A153-195; ×1. B. RGM 387653, locality 1C, bed C160; ×1. C, RGM 542177, locality 1W, bed W45; ×1. D, RGM 542179, locality 1A, loose from beds A166-170; ×1. E, GIA P105, locality 1W; ×1.

and most small specimens young macroconchs; only the few blunt-ribbed ones among the small specimens were interpreted as microconchs.

In macroconchs, the ornamentation of the rather coarse ribbing of the holotype continues up to a diameter of around 130-140 mm. At this diameter the adult ornamentation sets in, viz. besides the long and short ribs, a third type of rib appears at great, but variable, distances from each other. They are separated by on the average 4-5 main (= long) ribs between every two of which 0-1 short rib is intercalated. This third type of rib is extra thick and high, may be bordered by an inconspicuous constriction, and is provided with a slightly protruding umbilical bulla. From this diameter the other main ribs may also show small umbilical bullae. At a diameter of 140 mm the ribs of the third type are still weak, but gradually gain in strength. They may even have more prominence on the highly arched venter. These extra thick ribs do not have the same prominence on all specimens; on some conchs they are hardly discernible, whereas on others they are very prominent and even show weak lateral swellings. In one occasion the constrictions are more developed than the bordering ribs. The largest macroconch collected has a diameter of more than 300 mm.

Two fine-ribbed specimens from the Río Argos succession (Figs. 21L and 25E) closely resemble the specimen from Les Pleiades figured by Sarasin & Schöndelmayer (1901, pl. 9, fig. 8) under the name *Hoplites angulicostatus* d'Orbigny. This specimen is a well preserved young macroconch of *P.* (*K.*) *catulloi* and is refigured by Busnardo (2003, pl. 16, fig. 2).

Microconchs: Pl. XIV; Fig. 31. At a diameter of approximately 40-50 mm the ornamentation gradually coarsens, and the ribs become more vigorous and blunter than those of the strong-ribbed variety. The ribbing becomes irregular and the upper parts of the ribs are generally radial or inclined backward instead of projected forward. Most microconchs have a few ribs that fasciculate by two from the umbilical rim; the point of fasciculation may be slightly raised into a weak bulla. The whorls begin to egress at a diameter of 60 mm and the umbilicus becomes wider than the whorl height. The height of the last whorl grows only slowly, much slower than the whorl of the macroconchs at the same diameter.

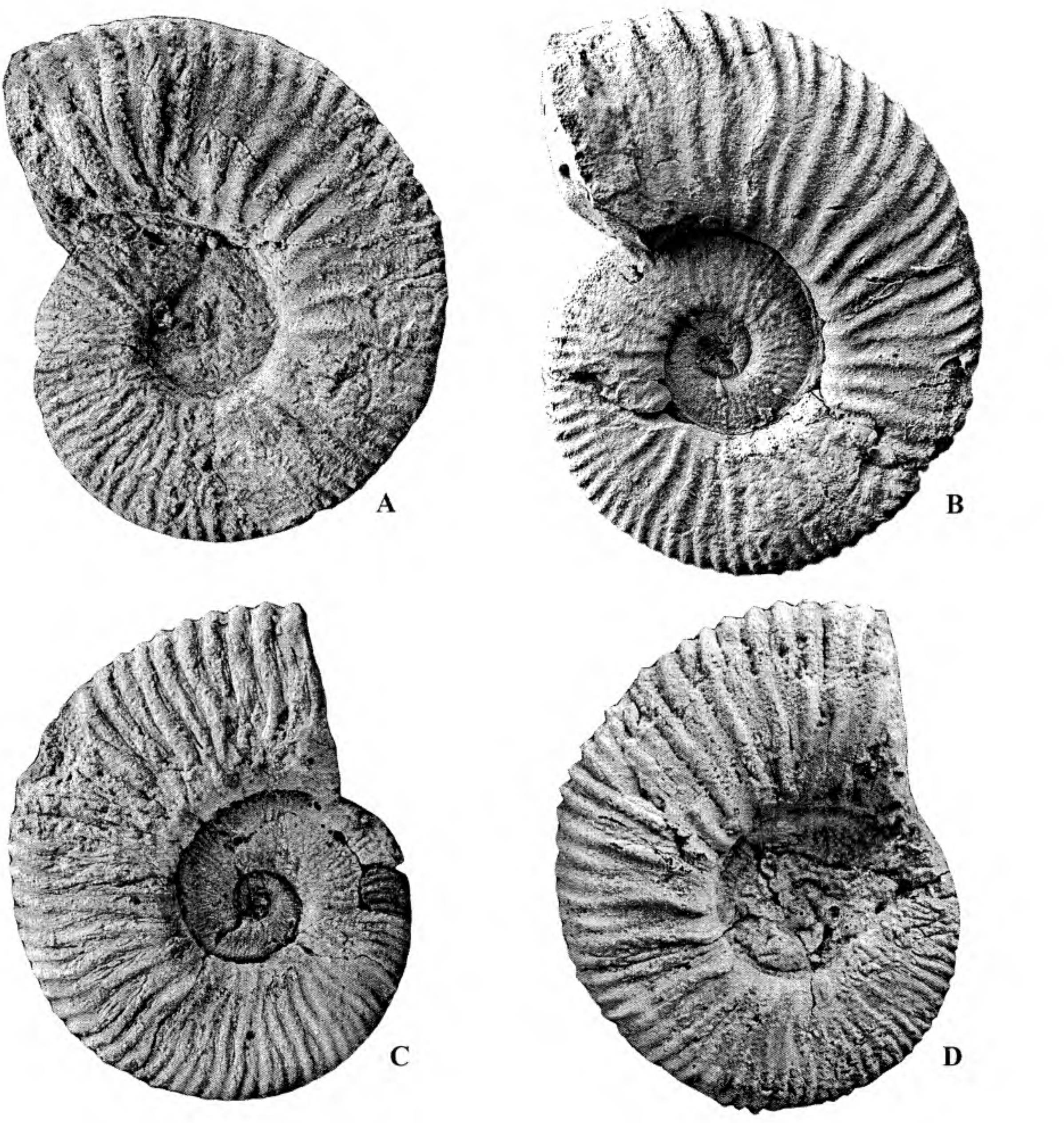


Fig. 26: A-D, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), coarse ribbed variety, small macroconchs. A, RGM 387855, locality 2; ×1. B, RGM 387909, locality 1A, bed A153; ×1. C, RGM 387799, locality 2; ×1. D, RGM 387808, locality 2; ×1.

The largest microconch the author found measures 90 mm.

Remarks: The inner whorls and young specimens of *P.* (*K.*) *catulloi* closely resemble *P.* (*K.*) *mortilleti*, but differ in the absence of umbilical bullae, and in the thicker whorls with slightly rounded flanks and arched venter. The whorl section is high trapezoidal. The ribs of *catulloi* are more sigmoidal than those of *P.* (*K.*) *mortilleti*, and the main ribs are generally thicker and blunter. The main ribs are generally separated by one or two intermediate ribs, which are generally shorter than in *P.* (*K.*) *mortilleti*. Young specimens of *P.* (*K.*) *mortilleti* have flat parallel flanks and more truncated venters; their whorl section is high and almost rectangular (looks like a coin). Large specimens of *P.* (*K.*) *catulloi* have coarser ribs with only one or two intermediate ribs between each pair of main ribs, whereas *P.* (*K.*) *mortilleti* remains fine-ribbed and has generally three or four intermediate ribs between each pair of main ribs.

Vermeulen *et al.* (2002) and Company *et al.* (2003) considered *P.* (*K.*) *catulloi* a junior synonym of *P.* (*K.*) *mortilleti*. This is incorrect because of the consistent

Fig. 27: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), coarse ribbed variety, large macroconch, RGM 387792, locality 2; ×1.

differences in whorl section, ornamentation and suture line, which has narrow-throated lobes and narrow-necked saddles. The author agrees that the young whorls resemble each other, but the inner whorls of *P.* (*K.*) *ohmi*, *P.*. (*K.*) *ohmi valbonnettensis* and *P.* (*K.*) *caravacaensis* also closely resemble those of *P.* (*K.*) *mortilleti* (interpreted here as a case of peramorphosis).

Pseudothurmannia (*Kakabadziella*) *catulloi* and *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* are both derived from *P.* (*K.*) *mortilleti* at the same time. Young *P.* (*K.*) *catulloi* differs from *P.* (*K.*) *caravacaensis* in the regular distribution and the greater thickness of ribs, and in having only one or two intermediate ribs, rarely three, to one main rib. Moreover, *P.* (*K.*) *catulloi* has thicker S-shaped ribs. Young *P.* (*K.*) *caravacaensis* has irregularly distributed thinner ribs and has 3-7 intermediate ribs to one main rib. *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* shows small sharp umbilical tubercles on the main ribs, whereas *P.* (*K.*) *catulloi* lacks umbilical bullae. There are no intermediate forms between these two species.

According to Bogdanova & Mikhailova (2004, pp. 198, 200), *P.* (*K.*) *catulloi* would be a species of genus *Turkmeniceras* Tovbina, 1963. The ornamentations of *Turkmeniceras turkmenicum* Tovbina, 1962, and *P.* (*K.*) *catulloi* are indeed reminiscent of each other. The differences between the two species are, however, the fine dense ribbing and the great overlap of the youngest whorls in *P.* (*K.*) *catulloi*, which contrast with the coarser ribs and the advolute whorls of *Turkmeniceras*. Moreover, the fine, dense ribbing on the inner whorls of *P.* (*K.*) *catulloi* differs markedly from their coarseness and

Fig. 28: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), coarse ribbed variety, large macroconch, RGM 387794, locality 2; 92%.

greater distance on its outer whorls, while this difference is very small in *Turkmeniceras* in which only the distance between the ribs evenly increases with growth. Finally, adult *P.* (*K.*) *catulloi* reach much larger dimensions than *Turkmeniceras*.

Range: Catulloi Zone and basal Hugii Zone. Lowest bed A153 (= W35), highest bed A176 (= W60), which is above the appearance of *Taveraidiscus hugii*.

Geographical distribution: Italy (Breonio, Bosco Chiesdanuova), Spain [Río Argos (Caravaca), La Guardia (Jaen), Arroyo Gillico (Cehegín), Barranco de Cavila (Caravaca), Ibiza, Majorca (Selva)], Switzerland (La Veveyse, Les Pleiades), Austria (Lackbach?), France (Nice, Vergons, Pas de l'Essaure), Roumania (Vodiniciki valley), Hungary (Hárskút-Rendkö), Bulgaria (Salash, Brestak, Beli Mel, Varnensko), The Crimea (Biassala, Verkhoreche, Kacha), Georgia (River Ritseula).

Fig. 29: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), typical variety, large macroconch, RGM 542636, locality 2; extra thick ribs appear lined by weak constrictions; 91%.

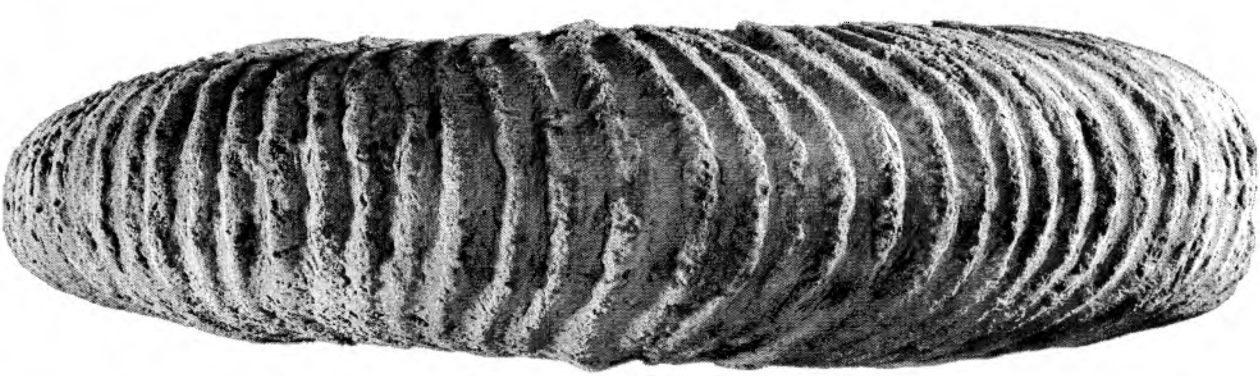


Fig. 30: A, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), ventral side of the same specimen as on Plate XII; 80%.

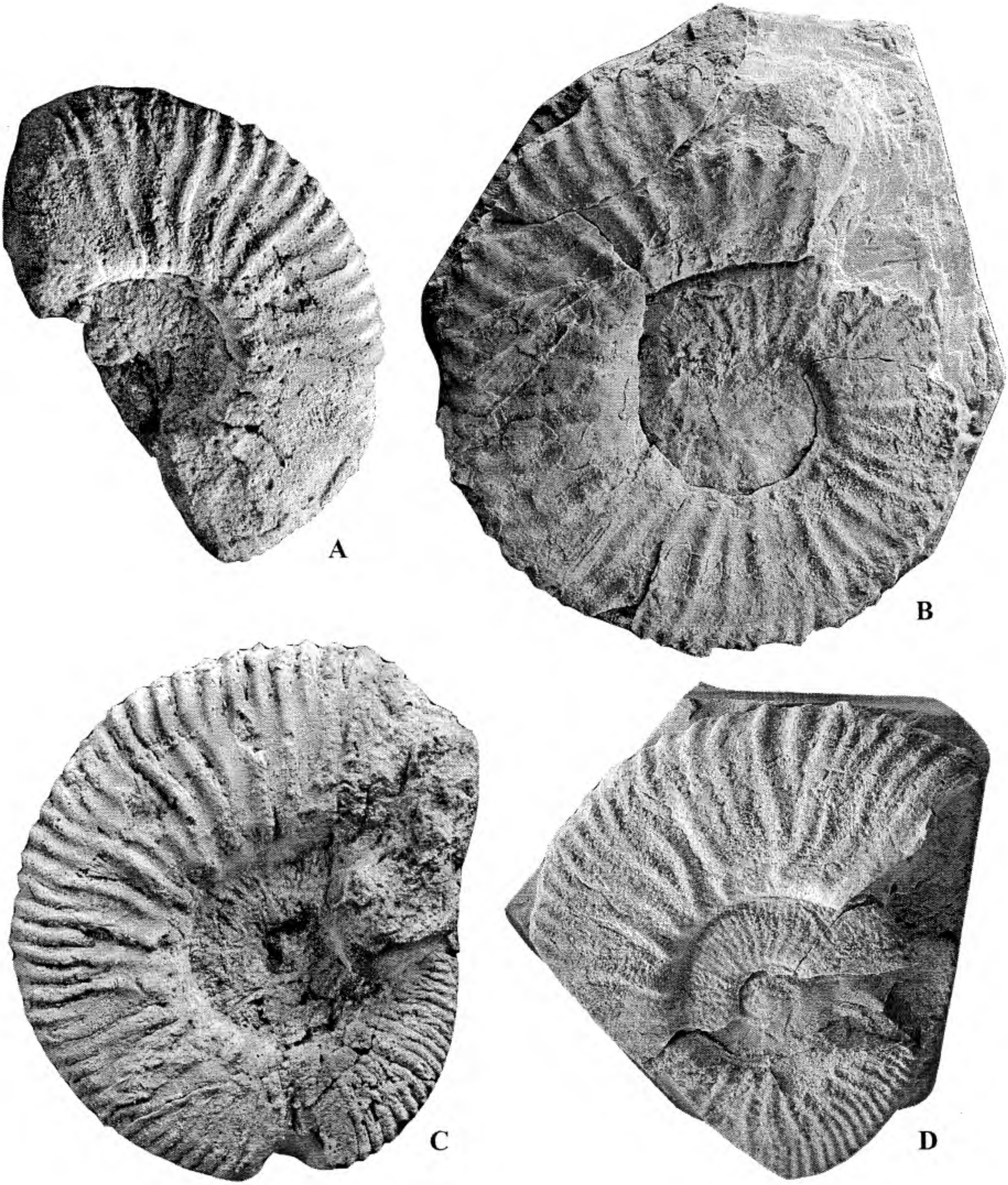


Fig. 31: A-D, *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), large microconchs. A, RGM 387802, locality 2; ×1. B, RGM 542171, locality 1A, bed A153; ×1. C, RGM 387797, locality 2; ×1. D, RGM 542174, locality 2; ×1.

7.1.4. *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)

Figs. 32-33; Pls. XV-XIX; Tab. IV

pars 1860. *Ammonites angulicostatus* d'Orbigny.– Ooster, p. 114, pl. 23, fig. 1 (microconch), non figs. 2-3 [= *Pseudothurmannia* (*Kakabadziella*) *tornajensis* sp. nov.], non fig. 4 (= *Crioceratites* sp. indet).

v* 1868. *Ammonites Ohmi* Winkler, p. 6, pl. 1, fig. 8.

1955. *Pseudothurmannia angulicostata* Hyatt (= printers error, should be d'Orbigny).– Eristavi, p. 94, pl. 3, fig. 7.

1958. *Pseudothurmannia angulicostata* (d'Orbigny).– Luppov & Drushchits, pl. 46, fig. 5.

1961. *Pseudothurmannia angulicostata* d'Orbigny.– Eristavi, p. 97, pl. 4, fig. 4.

1964. *Pseudothurmannia* sp. [ex gr. *P. angulicostata*] (d'Orbigny).– Fülöp, pl. 27, fig. 6; *non* pl. 18, fig. 5 [= *P.* (*K.*) *catulloi* (Parona, 1897)].

pars 1965. *Pseudothurmannia angulicostata* (d'Orbigny).– Dimitrova, p. 217, pl. 1, only fig. 3 (microconch), *non* fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* fig. 2 (= unidentifiable ammonite).

1967. *Pseudothurmannia angulicostata* (d'Orbigny).– Dimitrova, p. 72, pl. 31, fig. 1 (microconch).

v* 1967. *Pseudothurmannia biassalensis* sp. n.– Dimitrova, p. 74, 221, pl. 33, fig. 1-2 (macroconchs).

v* 1967. *Balearites lorioli* sp. n.– Dimitrova, p. 77, pl. 36, fig. 7.

1976. *Pseudothurmannia* sp. 1.– Mandov, p. 67, pl. 9, fig. 4 (microconch).

1976. *Pseudothurmannia* aff. *catulloi* (Parona).– Mandov, p. 66, pl. 9, fig. 3.

1983. *Crioceratites* (*Pseudothurmannia*) *belimelensis* Dimitrova.– Adamíková *et al.*, p. 608, pl. 2, fig. 4.

v* 1987. *Crioceratites* (*Pseudothurmannia*) *provencalis* Wiedmann.– Immel, p. 118, pl. 12, fig. 2 [= holotype of *P* (*K.*) *ohmi ohmi* (Winkler, 1868)].

? 1988. *Crioceratites* (*Pseudothurmannia*) *angulicostatus* (d'Orbigny).– Wilke, p. 20, pl. 2, fig. 27-28 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi*? (Winkler, 1868)].

1989. *Pseudothurmannia angulicostata* (d'Orbigny).– Vašíček, p. 118, pl. 1, fig. 4.

1989. *Pseudothurmannia shankariae* Sarkar.– Vašíček, p. 118, pl. 1, fig. 5 (= inner whorls).

1994. *Pseudothurmannia angulicostata* (d'Orbigny).– Vašíček *et al.*, p. 65, pl. 20, fig. 3.

1995. *Pseudothurmannia* (*Pseudothurmannia*) *angulicostata* (d'Orbigny).– Vašíček, p. 176, pl. 5, fig. 2.

pars 1995b. *Pseudothurmannia* (*Pseudothurmannia*) *ohmi* (Winkler).– Hoedemaeker, p. 228, pl. 1, only fig. 5, *non* fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* fig. 6 [= possibly *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

non 1995. *Pseudothurmannia angulicostata* (d'Orbigny).– Cecca *et al.*, pl. 1, fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1995. *Pseudothurmannia angulicostata* (d'Orbigny).– Cecca & Pallini, pl. 1, fig. 11 [= *P* (*K.*) *caravacaensis* sp. nov.].

non 1996. *Pseudothurmannia ohmi* (Winkler).– Faraoni *et al.*, pl. 2, figs. 9-10 (= *Crioceratites* sp. indet.).

1997. *Pseudothurmannia picteti* (Sarcar) (sic).– Atabekian *et al.*, p. 128, pl. 36, fig. 5-6 (macroconch).

? 2000. *Pseudothumannia* (*Pseudothurmannia*) aff. *ohmi* (Winkler).– Vašíček & Faupl, p. 604, pl. 6, fig. 6.

non 2002. *Pseudothurmannia ohmi* Winkler.– Bodrogi & Forgarasi, p. 304, pl. 1, fig. 4 (= *Crioceratites* sp.).

non 2002. *Pseudothurmannia* cf. *ohmi* Winkler.– Bodrogi & Forgarasi, p. 304, pl. 1, fig. 3 [= possibly *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], pl. 2, fig. 3 [= possibly *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

pars 2003. *Pseudothurmannia ohmi* (Winkler).– Company *et al.*, p. 691, only fig. 6.2., *non* fig. 6.1 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov?].

pars 2003. *Crioceratites angulicostatus* (d'Orbigny).– Company *et al.*, p. 689, fig. 5.9., *non* fig. 5.10. (= *Crioceratites* (*Binelliceras*) *seitzi* Sarkar, 1955).

2005. *Crioceratites angulicostatus* (d'Orbigny).– Company *et al.*, p. 188, fig. 4C.

2006. *Parathurmannia macilenta* (d'Orbigny), neotype.– Busnardo, p. 46, pl. 16, fig. 4.

Holotype by monotypy: Specimen no 1873 III E 7 of the Bayerische Staatssammlung für Paläontologie und historische Geologie, München. Derived from the Upper Hauterivian beds of the Sulzbachgraben near Ruhpolding (Pl. XV, fig. 1), kindly sent to the author by Dr Max Wippich.

Material: One hundred and sixty-three specimens. Cast of the holotype from the Sulzbachgraben in Germany, cast of holotype of *Pseudothurmannia biassalensis* Dimitrova, 1967 (collection of the University of Sofia, no. Cr$_1$ 1537, kindly sent to the author by Prof. Dr T. G. Nikolov) from the Krivo River in Bulgaria (Pl. XVI, fig. 1), cast of holotype of *Balearites lorioli* Dimitrova, 1967 (collection of the University of Sofia, no. Cr$_1$ 1541, kindly sent to the author by Prof. Dr T. G. Nikolov) from Ruzhentsi (Belogradchishko, Bulgaria) (Pl. XVII, fig. 1), three specimens from bed 42 and 45 of the section along the route d'Angles (St.-André-les-Alpes, Alpes-de-Haute-Provence, France), seven specimens (from beds 313, 314 2x, 317, 320 3x) from the section near Chamaloc along the road to the Col de Rousset (Die, Drôme, France), 96 specimens from the Río Argos succession (Caravaca, Murcia, Spain), two specimens from Ermita de la Virgin de Cuadros near Bédmar (Jaén, Spain), and 53 specimens from the Cretaceous outcrop at the northwest end of the Tornajo Mountain (Lorca, Murcia, Spain).

Diagnosis: Evolute *Pseudothurmannia* (*Kakabadziella*) with fine-ribbed, *mortilleti*-like inner whorls and rather coarse, slightly flexuous, characteristically irregularly distributed main and intermediate ribs on the last whorl. At diameters larger than 42 mm, the umbilicus of the subspecies *P.* (*K.*) *ohmi ohmi* is wider than the whorl height, the whorl height grows only slowly, the whorl section is thick and umbilical bullae are absent, that is,

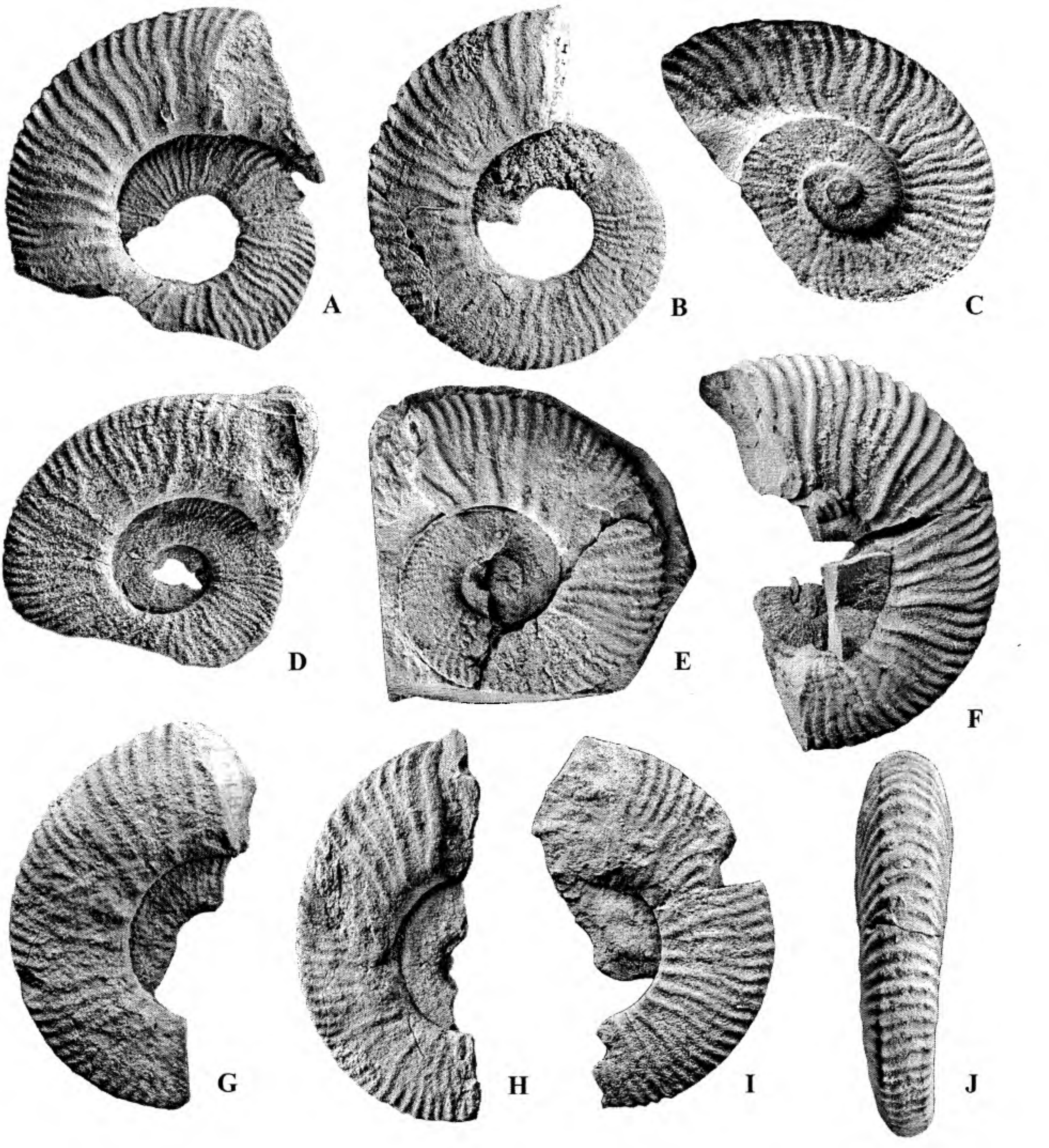


Fig. 32: A-J, *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868), young macroconchs. A, RGM 387903, locality 1A, loose from beds A139-151; ×1. B, RGM 387656, locality 1J; ×1. C, RGM 541862, locality 3T, bed T3; ×1. D, RGM 541864, locality 3B, bed B200; ×1. E, RGM 541912 locality 1A, bed A144; ×1. F, RGM 542262, locality 5, lateral view; ×1. G, RGM 387621, locality 1A, bed A144; ×1. H, RGM 387622, locality 1A, bed A144; ×1. I, RGM 387633, locality 1A, bed A144; ×1. J, RGM 542262, locality 5, ventral view; ×1.

the height of the main ribs on the umbilical edge is the same as on the flanks.

Description: Evolute planulate shells with a rather thick whorl section. The flanks are almost parallel and nearly flat. The venter is only slightly arched, separated from the flanks by two marked shoulders. The whorl section is thickest at one third of the flank height. The inner whorls are like *P.* (*K.*) *mortilleti*, i.e. finely ribbed with a narrow umbilicus; the umbilicus is three quarters of the whorl height. In specimens larger than about 42 mm the umbilicus becomes wider than the whorl height, but the whorls remain overlapping a little.

The ornamentation of the innermost whorls can be studied from a diameter of 9 mm and consists of fine uniform

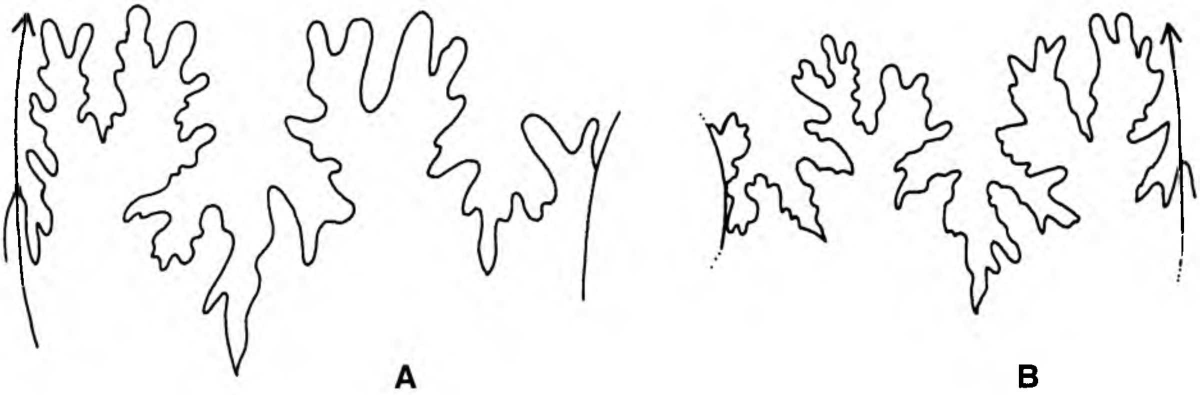


Fig. 33: A-B, *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868), suture lines. A, RGM 387606, Wh 8 mm; ×10.8. B, RGM 387615, Wh 10 mm; ×6.

ribs, which are almost straight. At a diameter of 11 mm, the differentiation in main and intermediate ribs sets in. The main ribs start at the umbilical seam and are slightly elevated on the umbilical rim, whereas the intermediate ribs originate at the umbilical rim or higher on the flanks. All the ribs become slightly sigmoidal and remain so up to the aperture. On the shoulders all ribs have a tiny clavus forming two delicate ventrolateral rows. All the ribs cross the venter with a slight forward curvature. The main and intermediate ribs are irregularly distributed; there are generally 0-4 intermediate ribs to one main rib, but most specimens also show trajectories with only one short rib to one main rib. The absence of umbilical bullae is diagnostic. The main ribs are retroradiate on the umbilical wall and curve sharply forward at the umbilical rim, where they already have the prominence that they keep up to the venter; the weakness of the intermediate ribs at the umbilical rim gives the impression as if the main ribs have umbilical bullae.

Macroconchs: Pl. XVI-XVIII. The holotype of *Pseudothurmannia biassalensis* Dimitrova, 1967, with rather wide-spaced ribs, is here interpreted as a macroconch of *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi*. Also the holotype of *Balearites lorioli* Dimitrova, 1967, with rather dense ribbing, is interpreted as a macroconch of *P.* (*K.*) *ohmi ohmi*. In the Rio Argos succession bed A144 yielded a population of 58 specimens of *P.* (*K.*) *ohmi ohmi* consisting of many ornamental transitions between *P. biassalensis*, *B. lorioli*, and *P.* (*K.*) *ohmi ohmi*. In literature, the ornamentation of *P.* (*K.*) *ohmi ohmi* has erroneously been compared with the ornamentation of the holotype of *Ammonites angulicostatus* d'Orbigny, owing to the faulty reconstructed drawing of the latter. Most specimens of *P.* (*K.*) *ohmi ohmi* have been identified as *angulicostatus* d'Orbigny in literature.

The rib pattern of the large macroconchs of the *P. biassalensis* type is a continuation of the pattern of the younger whorls, but the ribbing becomes less prominent. The ribs are irregularly distributed; between every two flexuous main ribs are 0-5 intermediate ribs, of which some reach the umbilical rim, whereas others originate at midflank. So, the succession of main and intermediate ribs is irregular, but the mutual distance of the ribs remains the same as well as their curvature. All the ribs cross the venter without interruption and with a forward curvature.

Occasionally there are shallow constrictions lined by extra thick ribs, which are broader than the other main ribs and remain broader on the venter. From a diameter of about 105 mm these extra thick ribs become more frequent and occur at regular distances; they are provided with small pointed umbilical bullae and are separated by 6-8 ribs. Apart from these extra thick ribs, the main ribs keep starting at the umbilical seam, whereas the intermediate ribs originate at, or at various distances above, the umbilical rim. The largest macroconch specimen found along the Río Argos has a diameter of c. 150 mm, the one from the Angles section c. 165 mm, but the macroconchs of *P.* (*K.*) *ohmi ohmi* can certainly reach larger dimensions. The whorls remain overlapping a little.

Microconchs: Pl. XV. The holotype of *P.* (*K.*) *ohmi ohmi* is interpreted as a microconch. The largest microconch specimen measures only 83 mm in diameter. The ribs on the living chambers are wide apart, S-shaped and prominent in contrast to the non-prominent ribbing of the macroconch. The ribs on the entire last whorl show a similar prominence. The length of the living chamber is slightly more than half a whorl; the whorl height of the living chamber hardly increases over this length. The main and intermediate ribs are irregularly distributed and there are 1-5 intermediate ribs to one main rib. In a few occasions there is a true forking of ribs. The ribs cross the venter with a slight forward curvature and show small clavi on the shoulders.

Suture line: Only two suture lines of the inner whorls could be drawn (Fig. 33). They show a deep lateral lobe with a wide throat and a wide umbilical lobe. The lateral lobe is much deeper than the external lobe. The lateral and umbilical lobes have short side arms, which leave broad necked saddles; the latter has a small siphonal saddle. All saddles are asymmetrically split into two parts by a deep incision. The external part of saddle E/L has three branches and the internal part four. Both parts of saddle L/U have three branches. The suture line is similar to that of *P.* (*K.*) *mortilleti*, but that may be due to fact that the suture lines were drawn from young whorls.

Remarks: The specimens of *P.* (*K.*) *ohmi ohmi* have commonly been identified as *Pseudothurmannia angulicostata* (d'Orbigny), because it is evolute, and because its ornamentation resembles that of the holotype of *Ammonites angulicostatus* d'Orbigny, owing to the faultily reconstructed drawing of the latter.

As the holotype of *Ammonites macilentus* d'Orbigny, 1841 (p. 138, pl. 42, figs. 3-4) is lost, Busnardo (2006, p. 46, pl. 16, fig. 4) designated a specimen from the d'Orbigny collection as 'neotype.' Busnardo rightly identified this 'neotype' as a representative of genus *Parathurmannia sensu* Busnardo, 2003, which in this paper is called *Pseudothurmannia* (*Kakabadziella*). However, this neotype of *A. macilentus* can easily be identified as *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* Winkler, for it shows the narrow-umbilicated fine-ribbed inner whorls, the typical irregular ribbing and the large umbilicus of *P.* (*K.*) *ohmi ohmi*, which are quite different from the original figure of *A. macilentus* in the *Paléontologie française*. According to Busnardo's investigations (2006, p. 47), the lappets of *A. macilentus* have erroneously been added to the original figure in the *Paléontologie française*; for the rest the lithographic drawing can be considered correct. The specimen figured in d'Orbigny (1841) (lappets omitted) strikingly resembles *Turkmeniceras multicostatum* Tovbina, 1963. Representatives of the genus *Turkmeniceras* occur in France and have been figured by Autran & Delanoy (1987, pl. 1, figs. 1-2) under the name *Deshayesites* sp. Delanoy (pers. comm., 2005, Cretaceous Symposium, Neuchâtel) found several more specimens of *Turkmeniceras* in the section along the route d'Angles (St.-André-les-Alpes, Alpes-de-Haute-Provence, France).

Pseudothurmannia (*Kakabadziella*) *ohmi ohmi* gave rise to *P.* (*K.*) *ohmi valbonnettensis* subsp. nov. A specimen of this subspecies was proposed by Lapeyre (1974) as the neotype of *Pseudothurmannia angulicostata* (d'Orbigny), but was in 1995 identified by the author as *Pseudothurmannia ohmi* Winkler, 1868, and herein as *P.* (*K.*) *ohmi valbonnettensis* subsp. nov. It differs from subspecies *P.* (*K.*) *ohmi ohmi* mainly in the slightly, but consistently, smaller umbilicus, in the finer and denser ribbing especially on the inner whorls, and in the presence of rather prominent umbilical bullae in middle and late growth stages. The differences in ornamentation between typical *P.* (*K.*) *ohmi ohmi* and this direct descendant are small. Therefore, and because *P.* (*K.*) *ohmi ohmi* and *P.* (*K.*) *ohmi valbonnettensis* occur in two different zones, the author prefers to consider them to be two successive subspecies of one lineage, chronosubspecies, instead of species.

Range: Restricted to the Ohmi Zone. Range along the Río Argos from bed A142 to A152.

Geographical distribution: France (Voirons), Spain [Casas Les Fontanelles (Biar), Arroyo Gilico (Cehegin), Rio Argos (Caravaca)], Slovakia (Sekaniny, Polomec quarry, Belichina), Bulgaria (Salash, Ruzhentsi, Belogradchishko, Kriva reka, Karapelit), Germany (Sulzbachgraben), Italy, Georgia [Kvatskhuti (Racha)], The Crimea (Biassala), Hungary (Zirc), Austria [Reschen (Groszraming)], Germany [Sulzbachgraben (Bayern)].

7.1.5. *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* nov. subsp.

Figs. 34-35; Pls. XX-XXII; Tab. V

pars 1901. *Hoplites Mortilleti* Pictet & De Loriol.– Sarasin & Schöndelmayer, p. 84, pl. 11, only fig. 3-4 (microconch), *non* fig. 5 [= lectotype of *Pseudothurmannia* (*Kakabadziella*) *mortilleti* Pictet & De Loriol, 1858].

pars 1907. *Crioceras angulicostatum* (d'Orbigny).– Karakasch, p. 134, pl. 15, fig. 1 (macroconch), pl. 16, fig. 4, *non* pl. 16, fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

pars 1919. *Parahoplites angulicostatus* (d'Orbigny).– Rodighiero, p. 103, pl. 11, fig. 2, *non* fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* subsp. nov.].

1955. *Balearites* cf. *balearis* Nolan sp. (forme no 2).– Sarkar, p. 143, pl. 11, fig. 2, text-fig. 21B.

1958. *Pseudothurmannia angulicostata* (d'Orbigny).– Luppov & Drushchits, p. 101, pl. 46, fig. 5.

pars 1965. *Pseudothurmannia angulicostata* (d'Orbigny).– Dimitrova, pl. 1, fig. 1 (macroconch), fig. 3 (microconch), *non* fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi*? (Parona, 1897)].

* 1974. *Pseudothurmannia angulicostata* (d'Orbigny).– Lapeyre, p. 82, pl. 1, figs. 1-9 (macroconchs).

1976. *Pseudothurmannia* aff. *catulloi* (Parona).– Mandov, p. 66, pl. 9, fig. 3.

1976. *Pseudothurmannia* sp. 1.– Mandov, p. 67, pl. 9, fig. 4.

pars 1976. *Pseudothurmannia biassalensis* Dimitrova.– Mandov, p. 66, pl. 9, fig. 6, *non* fig. 5 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

1980. *Pseudothurmannia angulicostata* (d'Orbigny).– Thomel, p. 53, fig. 91. [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

pars 1981. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol) .– Kakabadze, p. 91, pl. 1 only fig. 8, *non* fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

pars 1990. *Pseudothurmannia angulicostata* (d'Orbigny).– Thomel, pl. 6, figs, 1-7, *non* figs. 8-9 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], *non* figs. 10-12 [= *Pseudothurmannia* (*Kakabadziella*) *picteti* Sarkar].

1993. *Pseudothurmannia angulicostata* (d'Orbigny).– Autran, p. 114, pl. 13, fig. 6.

1995. *Pseudothurmannia* aff. *mortilleti* (Pictet & De Loriol).– Ambrosi *et al.*, p. 63, pl. 3, fig. 2.

pars 1995. *Pseudothurmannia biassalensis* Dimitrova.– Avram, p. 120, pl. 8, only fig. 9. (macroconch), *non* fig. 10 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona)].

1995. *Pseudothurmannia* cf. *angulicostata* (d'Orbigny).– Avram, p. 119, pl. 9, figs. 1a-b, 2 (microconchs).

1995. *Pseudothurmannia* cf. *belimelensis* Dimitrova.– Avram, p. 119, pl. 8, fig. 2.

pars 1995. *Pseudothurmannia ohmi* (Winkler).– Hoedemaeker, p. 228, pl. 1, only fig. 2, *non* fig. 5 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)], *non* fig. 6 [= *Crioceratites* (*Binelliceras*) *rotundatus*? (Sarkar, 1955)].

1996. *Pseudothurmannia angulicostata* (d'Orbigny).– Wright *et al.*, p. 214, fig. 163, fig. 4a-b.

pars 2002. *Pseudothurmannia sarasini* Sarkar.– Bodrogi & Forgarasi, p. 304, pl. 1, fig. 2, pl. 2.

non 2002. *Pseudothurmannia* cf. *ohmi* Winkler.– Bodrogi & Forgarasi, p. 304, pl. 2, fig. 3.

pars 2003. *Parathurmannia* cf. *biassalensis* (Dimitrova).– Busnardo, p. 69, pl. 15, figs. 3, 8, *non* fig. 2 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].

pars? 2003. *Parathurmannia* gr. *sarasini* (Sarkar).– Busnardo, p. 69, probably pl. 15, fig. 1, *non* pl. 9, fig. 2 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955]; *non* pl. 12, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], *non* pl. 12, figs. 2, 9 (= *Crioceratites* sp. indet); *non* pl. 15, fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], *non* pl. 32, figs. 3, 5-6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

2003. *Pseudothurmannia pseudomalbosi* (Sarasin & Schöndelmayer.– Company *et al.*, p. 691, fig. 6.5.

2004. *Pseudothurmannia (Balearites) balearis* (Nolan, 1894).– Kakabadze, p. 387, pl. 2, fig. 5 (inner whorls).

Holotype and locus typicus: The specimen depicted in Lapeyre (1974) on figs. 1-4, in Thomel (1980) on fig. 91, and in Thomel (1990) on pl. 6, figs. 1-4 from bed 210 of the lower Barremian section along the Valbonnette Valley near Barrême (Alpes-de-Haute-Provence, France) under the name *Pseudothurmannia angulicostata* (d'Orbigny) deposited in the Muséum d'Histoire Naturelle de Nice, Collection Centre d'Etudes Méditerranéennes, échantillon nr. 14107.

Diagnosis: The inner whorls are fine-ribbed. From a diameter of c. 56 mm weak umbilical bullae appear on the main ribs and gradually become more prominent. The ribbing of the middle growth stages is similar to the ribbing in *P.* (*K.*) *ohmi ohmi*, but denser. This produces a morphological aspect that only slightly differs from *P.* (*K.*) *ohmi ohmi*; its recognition helps to differentiate the populations occurring in the Ohmi Zone from those in the Catulloi Zone.

Derivation of name: From the valley of the Valbonnette Brook, a tributary of the Asse River, 1.5 km west of Barrême (Alpes-de-Haute-Provence, France), from which the two macroconch specimens from Valbonnette (bed 210, Catulloi Zone) are derived. One of them was described and introduced by Lapeyre (1974, pl. 1, figs. 1-4) as a paratype of the ex-neotype of "*Pseudothurmannia angulicostata* (d'Orbigny)." These macroconch specimens and the ex-neotype are here considered to represent the subspecies *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.

Material: One hundred and fourteen specimens. Three specimens from the Chamaloc section along the road to the Col de Rousset (Die, Drôme, France), 31 specimens from the Río Argos succession (from bed A153 to A 162), at least 79 specimens (mainly whorl fragments) from the Chamateuil section near Castellane (Alpes-de-Haute-Provence, France), and one specimen from Morocco (Aftas Imsouane, bed 254, Wiedenroth collection).

Description: The whorl section is compressed with slightly curved parallel flanks. The venter is moderately arched and separated from the flanks by distinct shoulders in the adult. The sigmoidal main ribs start at the umbilical seam and every two are separated by 1-7 intermediate ribs, but mainly 1-4, which start at various heights on the flank; the distribution of the main and intermediate ribs is irregular. The ribbing is finer and denser than in *P. (K.) ohmi ohmi*. In some specimens the ribbing of the inner whorls is very fine, dense and hardly differentiated (Pl. XX, figs. 11-14, 16-18). The main ribs are provided with umbilical bullae, which at first are very weak, but become prominent from a diameter of c. 55-60 mm. The bullae are situated on the umbilical rim. On the rim, the umbilical part of the main ribs curves from a retroradiate direction to a prorsiradiate direction. The bullae become crested and are provided with an apically directed point. In well-preserved specimens it can be seen that tiny ventrolateral clavi are present on every rib up to the aperture. The ribs cross the venter with a convex forward curve. From a diameter of 56 mm the umbilicus becomes wider than the whorl height.

Macroconchs: Three macroconch specimens (Pl. XXI) display the continuation of the same type of ornamentation, that is, sigmoid main ribs, which start at the umbilical seam and are irregularly distributed; every two of them are separated by 1-6 intermediate ribs starting at various heights on the flank. The umbilical bullae are very prominent which gives the species an aspect that is quite different from that of the smaller immature specimens. From a diameter of 98 mm the main ribs become extra thick and broad, and ventrolateral clavi can at least be discerned up to a diameter of 116 mm. The macroconch of *P.* (*K.*) *ohmi valbonnettensis* reached a diameter of about 140 mm at least, but may have been appreciably larger.

In section K of the Río Argos succession a large macroconch of *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* was found (Pl. XXI, fig. 2), which

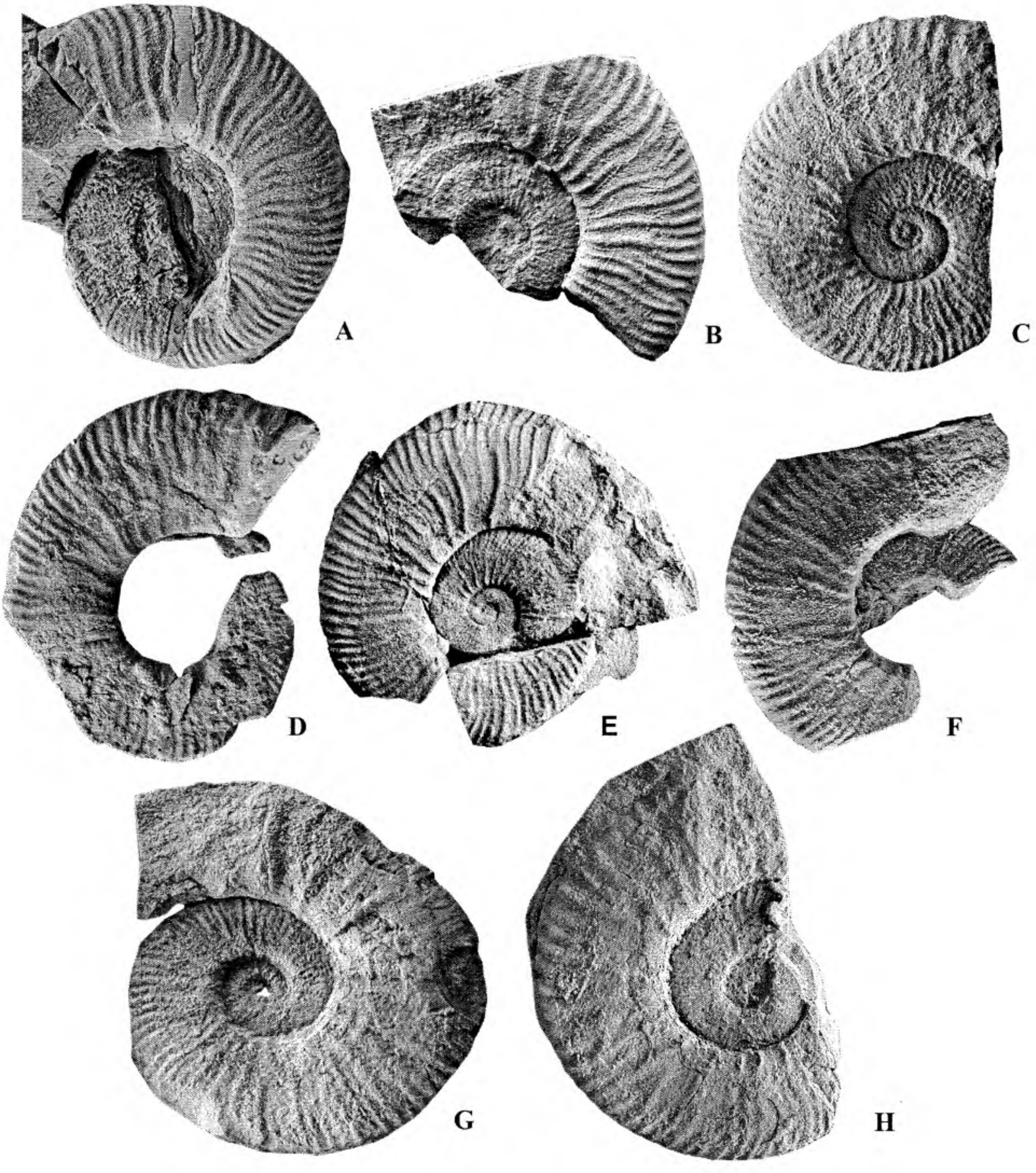


Fig. 34: A-H, *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov., small macroconchs. A, RGM 387646, locality 1W, loose from bed W35; ×1. B, RGM 387651, locality1K, bed K154; ×1. C, RGM 387642, locality 1F, loose from beds F147-153; ×1. D, RGM 387601, locality 1C, bed C162; ×1. E, RGM 542419, locality 6, bed CR321; ×1. F, RGM 542154, locality 1W, loose from beds W35-36; ×1. G, RGM 387645, locality 1E, bed E154; ×1. H, RGM 387649, locality 1A, bed A154; ×1.

closely resembles the specimen from Biassala (The Crimea) figured by Karakasch (1907, pl. 15, fig. 1) under the name of *Crioceras angulicostatum* d'Orbigny. The identification of this specimen has hitherto been a problem. Drushchits & Kudrjavtsev (1960) identified it as *Pseudothurmannia picteti* Sarkar, 1955. Wiedmann (1962) thought that it perhaps could be *Balearites crimensis* Wiedmann, 1962. Manolov (1962) called it *Pseudothurmannia karakaschi* sp. nov., but chose as holotype an imprint of an unidentifiable ammonite. At first Hoedemaeker (1995) followed Manolov, but now he regards the specimen of Manolov as unidentifiable.

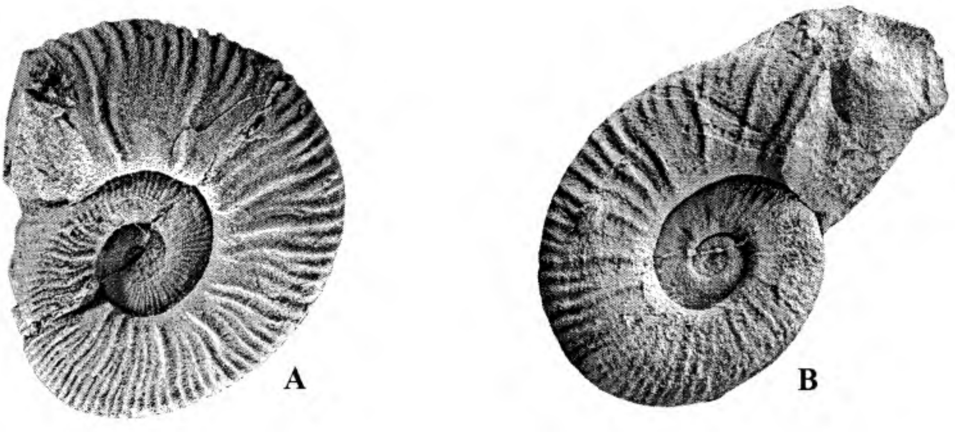


Fig. 35: A-B, *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov., small macroconchs. A, RGM 542667, locality 3A, bed 4; ×1. B, RGM 541861, locality 3A, bed 4; ×1.

Dimitrova (1967) called it *Pseudothurmannia biassalensis* sp. nov., but designated a specimen from the Hauterivian of Kriva Reka, near Chumensko, Bulgaria as holotype; the latter holotype is a macroconch of *Pseudothurmannia ohmi ohmi* Winkler, 1868.

The specimen of *Crioceras angulicostatum* d'Orbigny in Karakasch (1907, pl. 15, fig. 1) is here considered a macroconch of *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov. because it displays all the characteristics of this species. The width of the umbilicus is equal to the whorl height. The ribbing is very fine on the inner whorls and remains rather fine up to the aperture. The prorsiradiate main and intermediate ribs are irregularly distributed; there are 1-6 intermediate ribs to one main rib and they markedly vary in length. On the last whorl the lower three quarters of the main ribs are thicker and higher than the main ribs on the penultimate whorl, but they remain strongly prorsiradiate and are still provided with pointed umbilical tubercles. The phragmocone ends at a diameter of 70 mm.

Microconchs: The microconchs (Pl. XXII) have an almost rectangular whorl section with slightly curved flanks and a slightly arched venter. The egression of the whorls already begins at a diameter of c. 50 mm. The microconchs can be recognized by having distant, prominent, sigmoidal ribs; the interspaces are wider than the thickness of the ribs. The intermediate ribs are not always parallel to the main ribs; the latter are irregularly distributed and separated by 1-4 intermediate ribs. The tiny ventrolateral clavi can be discerned up to the most adoral rib. The main ribs on the living chamber show weak umbilical bullae.

Remarks: *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* closely resembles *P.* (*K.*) *ohmi ohmi*. In 1995b the author regarded these two subspecies as varieties, but as the differences are consistent, there are no transitional specimens, and they occur in different ammonite zones, the author considers them to be subspecies. The first occurs exclusively in the Catulloi Zone, whereas the latter is restricted to the Ohmi Zone. *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* differs from *P.* (*K.*) *ohmi ohmi* in the slightly smaller umbilicus being approximately as wide as the whorl height, in the appearance of umbilical bullae from a diameter of 55 mm, and in the denser ribbing, especially on the inner whorls.

Range: Restricted to the Catulloi Zone. Range along the Río Argos from bed A153 to A162.

Geographical distribution: Spain [Rio Argos (Caravaca)], France [Chamateuil (Castellane), Valbonnette (Barrême), Chamaloc (Die), Barrême], The Crimea (Biassala), Bulgaria (Brestak, Pali Lula, Salash), Georgia (Rioni river), Italy (Asiago), Switzerland [Veveyse river (Châtel-St.-Denis)], Roumenia [Vodiniciki valley (Svinita)], Georgia [River Rioni (Tesnina Khidikari)].

7.1.6. *Pseudothurmannia* (*Kakabadziella*) *tornajensis* n. sp.

Fig. 36; Tab. VI

? 1861. *Ammonites angulicostatus* d'Orbigny.– Ooster, p. 114, pl. 23, figs. 2-3

? 1905. *Hoplites angulicostatus* d'Orbigny.– Richarz, p. 346, pl. 9, fig. 4.

pars 1986. *Crioceras* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Darga & Weidich, p. 103, pl. 3, fig. 5, *non* fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

? 1987. *Crioceratites* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Immel, p. 117, pl. 12, fig. 1.

Syntypes: Three syntypes (Figs. 36A-E): RGM 542390 (Tornajo Mountain, section 2A; moderately large, well-preserved specimen); RGM 542391 (Tornajo Mountain, section 2A bed 3; well preserved ventral side); RGM 542392 (Tornajo mountain, section 2A, bed 3; large well-preserved specimen). Deposited in the Naturalis Diversity Center, Leiden, The Netherlands.

Locus typicus: Bed 3 (Catulloi Zone) of section 2A of the Cretaceous outcrops in the northern slope of the Tornajo Mountain (communality of Lorca, Prov. of Murcia).
Derivation of name: Named after the Tornajo Mountain near the northern border of the communal district of Lorca (Province of Murcia, Spain) where the author found this species in great numbers.
Material: Fifty-six specimens in total: 44 specimens from the Tornajo Mountain (Ohmi Zone) and 11 specimens from the Río Argos succession (7 specimens from the Ohmi Zone, viz. two *in situ* from beds A142 D and K147, two loose from bed A145 and beds W30-W30E, three loose specimens from beds W32-W33, and four specimens from the Catulloi Zone in loose block K from beds W35-46); one specimen from bed 45 of the Angles section near Angles (St.-André-les-Alpes, Alpes-

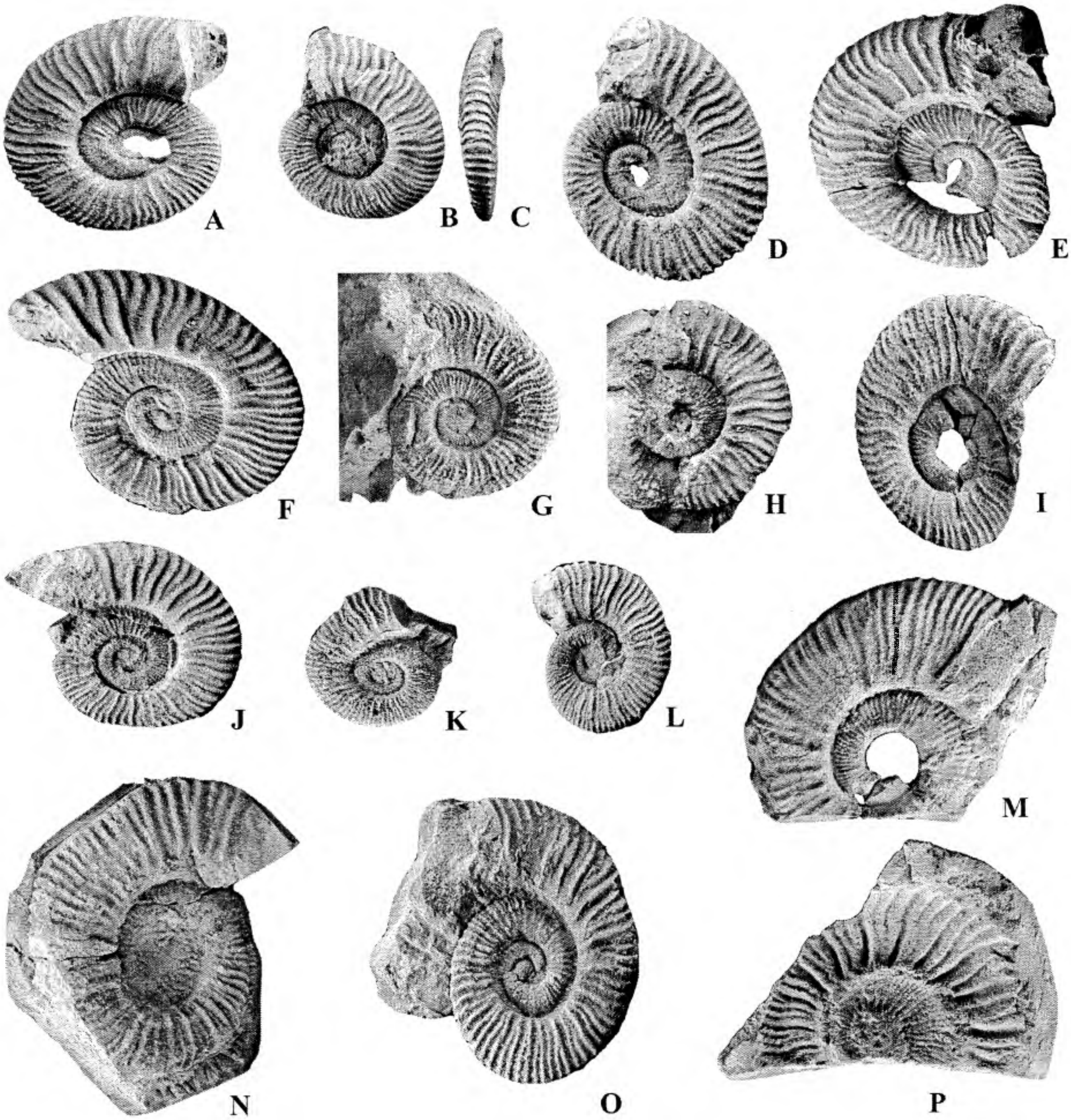


Fig. 36: A-N, *Pseudothurmannia* (*Kakabadziella*) *tornajensis* sp. nov. A, RGM 542390, locality 3A, syntype; ×1. B, RGM 542391, locality 3A, bed 3, lateral view of syntype; ×1. C, same syntype, ventral view; ×1. D, RGM 542392, locality 3A, bed 3, syntype; ×1. E, RGM 342380, locality 3A, bed 1; ×1. F, RGM 542383, locality 3A, bed 3; ×1. G, RGM 542381, locality 3A; ×1. H, RGM 542347, locality 1W, loose from beds W30-W30E; ×1. I, RGM 542378, locality 3A, bed 3; ×1. J, RGM 542376, locality 3A, bed 1; ×1. K, RGM 542384, locality 3A; ×1. L, RGM 542387, locality 3A; ×1. M, RGM 542389, locality 1W, in loose block K from beds W35-46, syntype; ×1. N, RGM 542348, locality 1K, bed K147; ×1. O, RGM 542385, locality 3A, bed 1; ×1. P, RGM 542865, locality 1A, bed A142D; ×1.

de-Haute-Provence, France). The specimens from the Tornajo Mountain are steinkerns (internal casts), those of the Río Argos succession are external casts.

Diagnosis: Small, advolute to slightly crioconic shells with an oval whorl section and sharp distant sigmoidal ribs; only one or two intermediate ribs to one main rib. On each side of the venter a row of small uniform ventrolateral clavi, on every rib one clavus. If the shell had been preserved, the whorls would probably have touched each other everywhere. The height of the whorls grows slowly (Wh:wh = 3:2). The innermost whorls are finely ribbed, but advolute; the species lacks the fine-ribbed involute *mortilleti*-like whorls.

Description: Small shells with advolute whorls, which have an oval whorl section, a slightly truncated venter and slightly flattened flanks. The steinkerns (or internal casts) of the whorls are within certain intervals just touching and the dorsal side shows the shallow impression of the foregoing whorl; in other intervals they are not touching and show a gap of 0.5 mm. If the shell had been preserved, the whorls would probably have touched each other everywhere. The umbilical rim is rounded. The whorl height increases only slowly and grows with a ratio of 3/2 to half a whorl. The umbilicus is perforated.

The ornamentation can be studied from a diameter of 4 mm. At this diameter it consists of equal, distant, sharp, straight ribs, which are highest at midflank. At a diameter of 5 mm the ribs become more approximated. From this diameter they gradually become differentiated in main and intermediate ribs. The main ribs start just below the umbilical rim and are slightly crested upon this rim, whereas the intermediate ribs start at the rim without a crest. One or two intermediate ribs separate the main ribs. The ribs do not cross the venter and are all provided with equal, tiny ventrolateral clavi, which form two rows on both sides of the venter.

From a diameter of 13 mm most main ribs are provided with marked umbilical bullae, and the ribs become sigmoidal and gradually more distant. In a later growth stage, the umbilical bullae gradually decrease in prominence again. All ribs cross the venter without interruption. Each rib still has a small ventrolateral clavus, which form two rows of uniform tubercles on the shoulders. When the whorls are not touching, the dorsal sides are smooth with adorally convex growth lines.

The ornamentation of the living chamber consists of sharp, distant, sigmoidal main ribs separated by only one or two, rarely three, sigmoidal intermediate ribs, which start at one third of the flank height or at midflank. The interspaces are twice as broad as the ribs. On each shoulder a row of small clavi, on each rib one clavus. There is one specimen of which a part of the aperture is preserved. The living chamber occupies half a whorl and the two or three ribs closest to the aperture are still more distant from each other and slightly more prominent.

Suture lines are not preserved

Remarks: All the species of subgenus *Pseudothurmannia* (*Kakabadziella*) show *mortilleti*-like inner whorls, with a moderately small umbilicus and a rapidly increasing whorl height, except *P.* (*K.*) *tornajensis* and *P.* (*K.*) *belimelensis*. In *P.* (*K.*) *tornajensis* the whorls increase slowly in height and are just touching each other. As to the ornamentation, this species has the characteristic ribbing of *Kakabadziella*, that is, long main ribs separated by a few shorter intermediate ribs, with ventrolateral clavi on every rib, but without lateral tubercles. It mostly looks like *P.* (*K.*) *ohmi ohmi*, but the inner whorls are advolute instead of moderately involute. Moreover, *P.* (*K.*) *ohmi ohmi* has a highly irregular number of intermediate ribs between every two main ribs. Finally, *P.* (*K.*) *tornajensis* is small in comparison to other specimens of *Kakabadziella*; the largest specimen found has a diameter of about 65 mm.

Range: Ohmi Zone to lower part of Catulloi Zone. Range along the Río Argos is from bed A142D to bed A147 and from bed W30 to bed W33; four specimens were collected in block K, a loose block from one of the beds W35-46 (lower Catulloi Zone).

Geographical distribution: Spain (Tornajo Mountain, Río Argos), France (section along the route d'Angles, Alpes-de-Haute-Provence), Austria (Section along the Lackbach, 25 km WSW of Unken, Salzburg; Groszer Flössel near Kaltenleutgeben, Wienerwald), Switzerland (River Veveyse, Châtel-St.-Denis, Fribourg).

7.1.7. *Pseudothurmannia* (*Kakabadziella*) *belimelensis* Dimitrova, 1967
Fig. 37; Tab. VII

v* 1967. *Pseudothurmannia belimelensis* sp. n.– Dimitrova, p. 75, pl. 31, fig. 2.

non 1976. *Pseudothurmannia belimelensis* Dimitrova.– Mandov, p. 66, pl. 9, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1984. *Crioceratites* (*Pseudothurmannia*) *belimelensis* Dimitrova.– Adamíková *et al.*, p. 608, pl. 2, fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* Winkler, 1868].

non 1994. *Pseudothurmannia belimelensis* Dimitrova.– Cecca *et al.*, p. 560, fig. 5a [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1995. *Pseudothurmannia* cf. *belimelensis* Dimitrova.– Avram, p. 119, pl. 8, fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

non 1995b. *Pseudothurmannia belimelensis* Dimitrova.– Hoedemaeker, p. 230, pl. 2, *non* fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* var. *gracilis* nov.)], *non* fig. 9 [= *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* (Torcapel, 1884)].

non 1995. *Pseudothurmannia belimelensis* Dimitrova.– Cecca *et al.*, p. 198, pl. 1, fig. 5 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., macroconch].

non 1995. *Pseudothurmannia belimelensis* Dimitrova.– Cecca & Pallini, p. 212, pl. 1, fig. 13 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov. macroconch].

non 1998. *Pseudothurmannia sarasini* Sarkar var. *belimelensis* Dimitrova.– Cecca *et al.*, p. 93, pl. 5, fig. 17, 18 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1998. *Pseudothurmannia* aff. *belimelensis* Dimitrova.– Witam, p. 51, pl. 4, fig. 1a-b [= *Pseudothurmannia* (*Pseudothurmannia*) *ohmi ohmi* (Winkler, 1868) macroconch].

Holotype: By original desination. The specimen figured by Dimitrova (1967, pl. 31, fig. 2) from the upper Hauterivian Salash Formation near village Beli Mel (Mikhailovgrad, Bulgaria) deposited in the Geological Museum in the State University Collection, nr. $Cr_1$1540. A plaster cast was kindly sent to the author by Prof. Dr. T. G. Nikolov (University of Sofia, Bulgaria).

Diagnosis: The whorls of the holotype of *Pseudothurmannia* (*Kakabadziella*) *belimelensis* Dimitrova, are advolute, and grow slowly in height. The ornamentation is fairly regular, and consists of almost straight, prorsiradiate main ribs of which every two are separated by a few shorter intermediate ribs mainly originating just below midflank. The number of intermediate ribs to one main rib on the inner whorls is two, rarely three, and increases gradually to 3-5 on the last whorl. Lateral tubercles are absent on the innermost whorls, only umbilical bullae are present. Ventrolateral tubercles are only visible in a small part of the outer margin, because the specimen is largely embedded in the rock. *Pseudothurmannia* (*Kakabadziella*) *belimelensis* lacks the fine-ribbed, involute *mortilleti*-like inner whorls.

Material: A plaster cast of the holotype.

Description of the holotype: The whorls of the holotype of *Pseudothurmannia belimelensis* Dimitrova are just in contact and grow slowly in height (wh:Wh = 2:3). Only one side of the holotype is visible; the other side is still embedded in sediment.

The ornamentation of the holotype of *P* (*K.*) *belimelensis* is fairly uniform, typically *Pseudothurmannia*-like, and consists of flexuous, prorsiradiate main ribs at regular distances from each other, and a few shorter intermediate ribs to one main rib; the intermediate ribs mainly originate just below midflank. The number of intermediate ribs to one main rib on the inner whorls is two, rarely three, and increases gradually to 3-5 on the last whorl. Near the venter, the thicknesses of the main ribs are equal to those of the intermediate ribs. All ribs are straight and the upper thirds are projected. The great regularity of the distance between the main ribs, and the equality of the curvature of the ribs gives the specimen a special appearance.

The whorls are visible down to a diameter of 3.5 mm. Lateral tubercles are lacking on the innermost whorls of the plaster cast, only umbilical bullae can be seen from a diameter of 5 mm. Ventrolateral tubercles are visible only between diameters of 20 and 25 mm. They are difficult to discern, because they are partly embedded in the rock, but they are undoubtedly present, although not mentioned in the description of the holotype. *Pseudothurmannia* (*Kakabadziella*) *belimelensis* lacks the fine-ribbed *mortilleti*-like inner whorls, and in this respect looks like *P.* (*K.*) *tornajensis* sp. nov.; the inner whorls are as evolute as the outer whorls.

Remarks: *P* (*K.*) *tornajensis* differs from *P.* (*K.*) *belimelensis* in the more sigmoidal and more irregular ribbing, the smaller whorl height, and the wider umbilicus.

The author considers the species *P* (*K.*) *belimelensis* a representative of *Pseudothurmannia* (*Kakabadziella*) because of the typical *Pseudothurmannia*-like ornamentation, because of the presence of ventrolateral rows of uniform tubercles, and because of the absence of lateral tubercles on the first whorl.

Pseudothurmannia (*Kakabadziella*) *belimelensis* and *P.* (*K.*) *tornajensis* are considered to form a separate lineage, because both species differ from all other species of *Pseudothurmannia* (*Kakabadziella*) in the lack of *mortilleti*-like inner whorls that characterizes all other species of *Pseudothurmannia* (*Kakabadziella*). Both species have advolute inner whorls, which only grow slowly in height. As the ornamentation of *P.* (*K.*) *belimelensis* is closest to that of *P.* (*K.*) *ohmi ohmi*, the latter is the only species of *Pseudothurmannia* that could be considered ancestral to this lineage, and *P.* (*K.*) *belimelensis* ancestral to *P.* (*K.*) *tornajensis*, a progenetic dwarf. It would be justified to unite the two species *P.* (*K.*) *tornajensis* and *P.* (*K.*) *belimelensis* into a separate subgenus within *Pseudothurmannia*, but the author refrains from unnecessarily splitting up the genus *Pseudothurmannia* into too many subgenera.

Range: *P.* (*K.*) *belimelensis* probably occurs in the Ohmi Zone, because *P.* (*K.*) *ohmi ohmi* is considered to be its ancestor. As *P* (*K.*) *tornajensis*, its descendant, starts its

Fig. 37: *Pseudothurmannia* (*Kakabadziella*) *belimelensis* Dimitrova, 1967, plaster cast of the holotype from the upper Hauterivian Salash Formation near village Beli Mel (Mikhailovgrad, Bulgaria).

range in the lower Ohmi Zone, *P.* (*K.*) *belimelensis* must have appeared in the lowest Ohmi Zone.

Geographical distribution: Hitherto only found in the upper Hauterivian Salash Formation near the village Beli Mel (Mikhailovgrad, Bulgaria). Vermeulen, 2005 (p. 149) mentioned, but not figured, *Pseudothurmannia* aff. *belimelensis* from the Angles section from bed 38-39; these beds are very close to the beginning of the range of *P.* (*K.*) *ohmi ohmi*.

7.2. Subgenus *Pseudothurmannia* (*Parathurmannia*) Busnardo, 2003

Type species: *Pseudothurmannia sarasini* Sarkar, 1955 (by original designation).

Diagnosis: The inner whorls of the species within the subgenus *P.* (*Parathurmannia*) are overlapping and the umbilicus is small. The outer whorls egress, but remain slightly overlapping except for *edouardi*, which has slightly crioconic whorls. The fine-ribbed inner whorls have fine, wide-spaced main ribs every two of which are separated by generally 4-5, but uncommonly 3-6, intermediate ribs. This is followed by a stage with more closely spaced main ribs every two of which are separated by 1-3 intermediate ribs to one main rib, in some species followed by an adult stage with distantly spaced main ribs with 3-6 intermediate ribs. Here the main ribs are high and broad in lower part of the flanks, and originate from prominent umbilical bullae; the upper parts are thin and low like the intermediate ribs. Rows of prominent uniform ventrolateral clavi are present. The species of *P.* (*Parathurmannia*) have no lateral tubercles on the inner whorls. Lateral tubercles appear in the middle growth stage and may disappear again before the adult aperture.

Remarks: *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955, has generally been misinterpreted, because the holotype is a juvenile specimen, which does not show the adult ornamentation. The large specimen of *sarasini* from the Río Argos has a small umbilicus and a transient phase with lateral tubercles in middle growth stages. However, the ontogenetic development of the ornamentation of *P.* (*P*) *sarasini* is so different from that of the species of *Pseudothurmannia* (*Pseudothurmannia*) that the author had to conclude that *sarasini*, together with *dissiticostata* and *edouardi*, should have had a different ancestor than the species of *Pseudothurmannia* (*Pseudothurmannia*). This small group of species should be separated as an independent subgenus within *Pseudothurmannia* for which the name *Parathurmannia* is available. The subgenus *Pseudothurmannia* (*Parathurmannia*) is supposedly descended from *P.* (*K.*) *caravacaensis* and *Pseudothurmannia* (*Pseudothurmannia*) from *P.* (*K.*) *catulloi*.

Pseudothurmannia (*Parathurmannia*) differs from *P.* (*Pseudothurmannia*) in the finer, more wide-spaced main ribs with 3-6 intermediate ribs on the inner whorls instead of the strong, less wide-spaced main ribs with 2-3 intermediate ribs on the inner whorls of the latter subgenus. The species of both subgenera lack the dense *mortilleti*-like ribbing on the inner whorls.

7.2.1. *Pseudothurmannia* (*Parathurmannia*) *sarasini* (Sarkar, 1955)

Fig. 38; Tab. VII

1901. *Hoplites angulicostatus* (d'Orbigny).– Sarasin & Schöndelmayer, p. 81, pl. 10, fig. 3 (holotype).
* 1955. *Pseudothurmannia sarasini* n. sp.– Sarkar, p. 155.
pars 1967. *Balearites mortilleti* (Pictet & De Loriol).– Dimitrova, p. 76, pl. 36, only fig. 5, *non* fig. 6 [=*Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858)].
pars 1968. *Pseudothurmannia catulloi* (Parona).– Sornay, p. 5, pl.1, fig. 5, *non* fig. 3 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].
1976. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Mandov, p. 64, pl. 8, fig. 3.
1995b. *Pseudothurmannia sarasini* Sarkar.– Hoedemaeker, p. 230, pl. 2, fig. 10.
non 1995. *Pseudothurmannia sarasini* Sarkar.– Cecca *et al.*, p. 198, pl. 1, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].
non 1995. *Pseudothurmannia sarasini* Sarkar.– Cecca & Pallini, p, 212, pl. 1, fig. 12 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].
non 1996. *Pseudothurmannia sarasini* Sarkar.– Cecca *et al.*, p. 418, fig. 3. [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].
non 1998. *Pseudothurmannia sarasini* Sarkar.– Cecca *et al.*, p. 92, pl. 5, fig. 15-25 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., figs. 15, 22-25 microconchs, figs. 17-18 var. *gracilis*, figs. 19-21 macroconchs].
? 1999. *Pseudothurmannia* aff. *sarasini* Sarkar.– Baudin *et al.*, fig. 3c. [= *Pseudothurmannia* (*Pseudothurmannia*) sp.?].
1999. *Pseudothurmannia sarasini* Sarkar.– Baudin *et al.*, fig. 3d.
non 2002. *Pseudothurmannia* aff. *sarasini* Sarkar.– Vermeulen *et al.*, p. 77, pl. 3, fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858)].
non 2002. *Pseudothurmannia sarasini* Sarkar.– Bodrogi & Forgarasi, p. 304, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], fig. 2 [= probably *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].
non 2003. *Parathurmannia* gr. *sarasini* (Sarkar).– Busnardo, p. 69, pl. 9, fig. 2 [= *Crioceratites* (*Binelliceras*) *rotundatus* (Sarkar, 1955)]; *non* pl.12, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], *non* figs. 2, 9 (= *Crioceratites* sp. indet) ; pl. 15, fig. 1 [= probably *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.)], *non* fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], *non* pl. 32, figs. 3, 5, 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

pars 2003. *Parathurmannia renevieri* (Sarasin & Schöndelmayer).– Busnardo, p. 70, only pl. 9, fig. 8, *non* pl. 17, fig. 1 and pl. 18, fig. 2. [= both *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858) macroconchs].

2003. *Pseudothurmannia* (*l.s.*) sp. D.– Busnardo, p. 68, pl. 19, fig. 1.

non 2004. *Pseudothurmannia* (*Pseudothurmannia*) *sarasini* Sarkar.– Kakabadze, p. 385, pl. 2, fig. 8 [= *Crioceratites* (*Binelliceras*) *rotundatus* (Sarkar, 1955)].

non 2005. *Pseudothurmannia* (*Pseudothurmannia*) *sarasini* Sarkar.– Kakabadze, p. 350, pl. 72, fig. 5 [= *Crioceratites* (*Binelliceras*) *rotundatus* (Sarkar, 1955)].

Holotype: The specimen from Châtel St.-Denis, Switzerland, depicted by Sarasin & Schöndelmayer 1901 (pl. 10, fig. 3), Ooster Collection, Naturhistorisches Museum, Bern.

Material: Four specimens; the largest is rather well preserved; the other three are less well preserved. All from Section W, 250 m west of the Casa de Alguacil along the Río Argos west of Caravaca (Murcia, Spain).

Emended diagnosis: Compressed, flat-sided *Pseudothurmannia* with a rather small umbilicus and a truncated venter. On the inner whorls fine flexuous ribs are differentiated into widely separated main ribs of which each pair is separated by 4-6 intermediate ribs. The intermediate ribs are long and almost reach the umbilical border; they attenuate in the direction of the umbilicus. The main ribs are provided with comma-shaped umbilical bullae. At a diameter of 40 mm the ribbing becomes more prominent and wider spaced, and the number of intermediate ribs diminishes to 2-3. At this diameter begins a transient stage (a quarter of a whorl) in which the main ribs are adorned with small pointed lateral tubercles. The ventral parts of the main ribs are slightly thicker than the intermediate ribs. On the lower part of the flanks the main ribs are slightly more elevated than on the upper part. Rows of small uniform clavi mark the rather angular ventrolateral shoulders at both sides of the truncated venter; the clavi on the main ribs are slightly more prominent than those on the intermediate ribs. On the adult living chamber, ribbing is somewhat effaced and irregular; the main ribs are provided with small pointed umbilical tubercles and are bordered by weak constrictions; lateral tubercles are absent. The truncated venter is still provided with ventrolateral rows of clavi.

Description: The problem with the identification of this species is that the holotype is a small immature specimen. The author has three small specimens that are identical to the holotype, and one large specimen of which the inner whorls exactly fit the holotype. Here, only the large specimen is described, because the other specimens are incomplete and not well preserved, even though well identifiable. The large specimen has a compressed conch with high whorls and a truncated venter. The flanks are only slightly convex; the whorl section is high trapezoidal with the thickest part near the umbilical border.

The umbilicus of the inner whorls is smaller than the whorl height and the whorls are overlapping. The umbilical wall is steep, the umbilical border rounded, but prominent. The ornamentation of the innermost whorl is visible from a diameter of 4 mm (Wh 2 mm) where the main ribs, which have their highest elevation on the flanks, are separated by two intermediate ribs. All ribs rapidly acquire the same thickness; the ornamentation thus consists of uniform, fine sigmoidal ribs.

At a diameter of 10 mm the main ribs distinguish themselves at first only by being provided with prominent umbilical bullae. The main ribs originate at the umbilical seam, have a rursiradiate direction on the umbilical wall and make a forward curve at the umbilical border, where they are heightened into long, curved bullae. They resume a radial direction at midflank, but are projected again near the venter. With growth, the main ribs gradually become more prominent than the intermediate ribs, first in the lower part of the flanks, but gradually also in the upper part. The distance between the main ribs is great, which is characteristic for the subgenus *Parathurmannia*. Each pair of main ribs is separated by 4-5, rarely six, long flexuous intermediate ribs, which originate at the umbilical border, rarely on the umbilical wall. The truncated venter is separated from the flanks by angular shoulders, each adorned with a row of uniform clavi. The ribs are less prominent on the venter and cross it in a straight line.

The whorls start to egress at a diameter of 40 mm. At this diameter the ribbing rather suddenly becomes coarse, less flexuous, and more elevated; the distance between the main ribs diminishes and each pair is separated by only two, rarely three, intermediate ribs. The main ribs are, over their total length, thicker and higher than the intermediate ribs. They still originate at the umbilical seam and are rursiradiate on the umbilical wall. The main ribs are markedly prominent on the lower flank and clearly less prominent on the upper flanks, but remain slightly thicker than the intermediate ribs even on the venter. In this ontogenetic stage the main ribs are adorned with small pointed lateral tubercles over a quarter of a whorl (Fig. 38A). The intermediate ribs originate at the umbilical border, rarely on the umbilical wall. The ribs cross the truncated venter in a nearly straight line. The ventrolateral clavi on the thicker main ribs are more prominent than those on the thinner intermediate ribs.

At a diameter of 68 mm the ornamentation changes again. The lateral tubercles disappear, the distance between the main ribs increases, and between each pair 3-4 intermediate ribs are present. The ribs become less flexuous.

On the living chamber, which begins at a diameter of 83 mm, the ribs are almost straight and radial on the lower two thirds of the flank, but projected near the venter. The

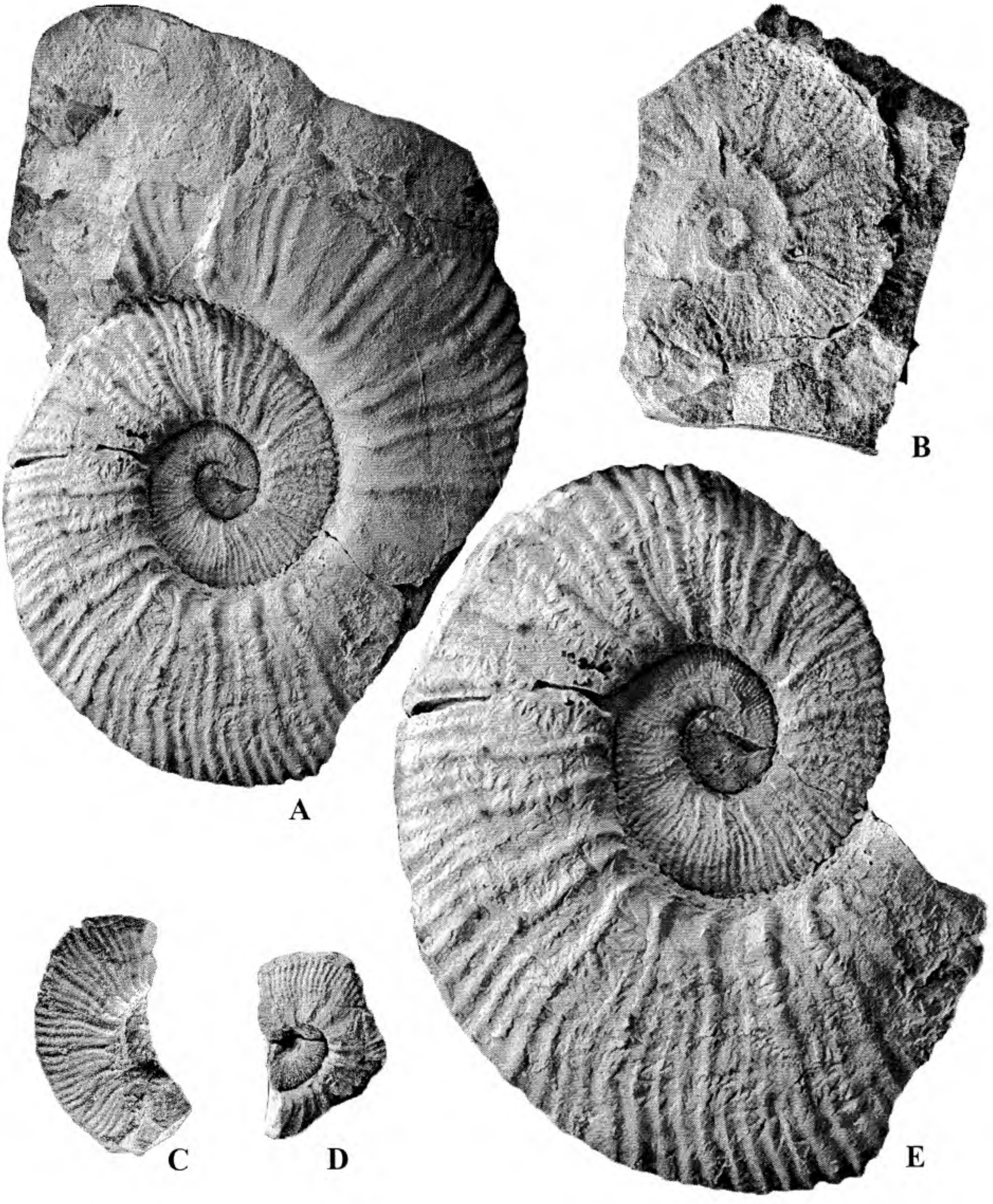


Fig. 38: A-D, *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955. A, RGM 387877, locality 1W, bed 39, large macroconch showing small lateral tubercles over a quarter of a whorl; ×1. B, RGM 542143, locality 1A, loose from beds A145-160, impression of the size if the holotype; ×1. C, RGM 542146, locality 1W, bed W36; ×1. D, RGM 542145, localty 1W, bed W55; ×1. E, RGM 387877 detail of specimen A, displaying lateral tubercles; × 1.5.

intermediate ribs become more or less effaced below the middle of the flanks, like in *P.* (*K.*) *caravacaensis*. Moreover, the main ribs become still more distant, are bordered by inconspicuous constrictions, and every two are separated by 3-5 intermediate ribs. The amount of overlap of the living chamber over the foregoing whorl is almost zero.

Remarks: The holotype of *P.* (*Pa.*) *sarasini* is a young specimen, which does not show the adult part with lateral tubercles on the main ribs. This is the reason why Busnardo (2003) designated this species as the type species of his new genus *Parathurmannia,* which was supposed to unite all the species without lateral tubercles in any stage. He was unaware of the fact that this species develops lateral tubercles in an adult ontogenetic stage, firstly mentioned by Hoedemaeker (1995b). Busnardo united all species with lateral tubercles in the adult stage in genus *Sornayites* Wiedmann, 1962.

Although *P.* (*Pa.*) *sarasini* and *P.* (*Pa.*) *dissiticostata* are here considered distinct species, it is possible that the two constitute a dimorphic pair, because they have the same range, and the ornamentation of the latter only developed more slowly than that of the former. But the author hesitates to consider them a dimorphic pair because of the effacement of intermediate ribs in *P.* (*Pa.*) *sarasini*, which is a strange feature in a microconch, and because of the absence of strong egression.

Cecca *et al.* (1998) unjustly regarded *Pseudothurmannia belimelensis* Dimitrova as a variety and junior synonym of *P.* (*Pa.*) *sarasini* Sarkar. The inner whorls of *Pseudothurmannia* (*Kakabadziella*) *belimelensis* differ from those of *P.* (*Pa.*) *sarasini* mainly in the appreciably larger umbilicus and in the rather straight ribs separated only by 2 or 3 intermediate ribs. Moreover, the whorls of the holotype of *P.* (*K.*) *belimelensis* are constantly advolute instead of overlapping as in young *P.* (*Pa.*) *sarasini.* The specimens figured by Cecca *et al.* (1998) under the name *Pseudothurmannia sarasini* variety *belimelensis* Dimitrova, and the specimen figured by the author under the name *Pseudothurmannia belimelensis* (Hoedemaeker, 1995, pl. 2, fig. 7), are assigned here to *P* (*K.*) *caravacaensis* sp. nov. var. *gracilis,* whereas the other specimen figured by the author under the same name (Hoedemaeker, 1995, pl. 2, fig. 9) is now regarded as a possible microconch of *Pseudothurmannia* (*Parathurmannia*) *crioceroides* (Torcapel, 1884).

In fact all the specimens identified as *Pseudothurmannia sarasini* by Cecca *et al.* (1998) are here included in *P.* (*Kakabadziella*) *caravacaensis* sp. nov., because the fine, dense, uniform ribbing of these specimens continues up to a diameter 25-30 mm, whereas in *P* (*Pa.*) *sarasini* the characteristic ornamentation of 4-5 intermediate ribs to one main rib has already set in at this diameter.

Cecca's variety *tuberculata* Sarkar, 1955, is also incorporated by the present author in *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., while Sarkar's *Pseudothurmannia angulicostata* variety *tuberculata* represents the inner whorls of *P* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884.

Range: Base Catulloi Zone and basal Hugii Zone (that is from bed W36 up to bed W55)

Geographical distribution: Spain (Río Argos), Bulgaria (Komshchitsa), Switzerland (Châtel-St.-Denis), France (Vergons).

7.2.2. *Pseudothurmannia* (*Parathurmannia*) *dissiticostata* nov. sp.
Fig. 39; Tab. IX

2003. *Pseudothurmannia* (*l.s.*) sp. E.– Busnardo, p. 68, pl. 19, fig. 6.

Syntypes: Three incomplete specimens from the Río Argos succession: RGM 542149 from block A derived from one of the beds W35-46 (half a whorl); RGM 542150 from one of the beds W35-36 (small whorl fragment); and RGM 542151 from bed C153 (imprint of the inner whorls); Catulloi Zone, Miravetes Formation, Río Argos, Caravaca (Murcia, Spain) (Fig. 39B-D). Deposited in the Naturalis Diversity Center, Leiden, The Netherlands

Loci typici: Along the Río Argos in section W, 250 m west of the Casa de Alguacil, and in section C, 500 m east of the Molino de las Oicas de Abajo.

Material: Ten specimens: three syntypes and two additional specimens from the Río Argos succession (Caravaca, Murcia), two fragments from the Cretaceous outcrops northwest of the Tornajo Mountain (Lorca, Murcia), and three fragments from the basal part of the lower Barremian Bolos Formation (Sierra de la Muela, Moratalla, Murcia).

Derivation of name: Latin *dissitus* = 'at a distance from each other;' *costatus* = ribbed. The species is named so because of the great distance between the main ribs.

Diagnosis: This species of the subgenus *Pseudothurmannia* (*Parathurmannia*) has a close affinity to *P* (*Pa.*) *sarasini.* Its ornamental stages are similar to those of *P.* (*Pa.*) *sarasini*, but appreciable longer. In *P.* (*Pa.*) *sarasini* the main ribs become coarser and get closer together at a diameter of about 40 mm, whereas in *P.* (*Pa.*) *dissiticostata* they continue to be distantly spaced at least up to a diameter of c. 70 mm. At diameters smaller than 70 mm, the distantly spaced, slightly flexuous main ribs are separated by 3-6 intermediate ribs (mostly 4-5), which generally appear between the umbilical rim and midflank, and taper towards the umbilicus. The main ribs are provided with small umbilical tubercles and there are two ventrolateral rows of tiny clavi. Small lateral tubercles appear on the main ribs at a diameter of c. 70 mm. From this diameter every two main ribs are separated by 3-4 intermediate ribs. The lateral tubercles continue at least to a diameter of 115 mm. At a diameter of 150 mm the lateral tubercles have disappeared, and between every pair of main ribs are 2-4 flexuous intermediate ribs.

Description: The shell is rather involute and the width of the umbilicus is equal to the whorl height at a diameter of about 70 mm. At this diameter the involution is about one third. The whorls moderately grow in height and the ratio wh:Wh = 2:3. The whorl section is rather compressed subrectangular with slightly curved flanks and a slightly curved truncated venter.

The first, innermost whorl curves around a perforated umbilicus. Its ribs are distantly spaced and highest at

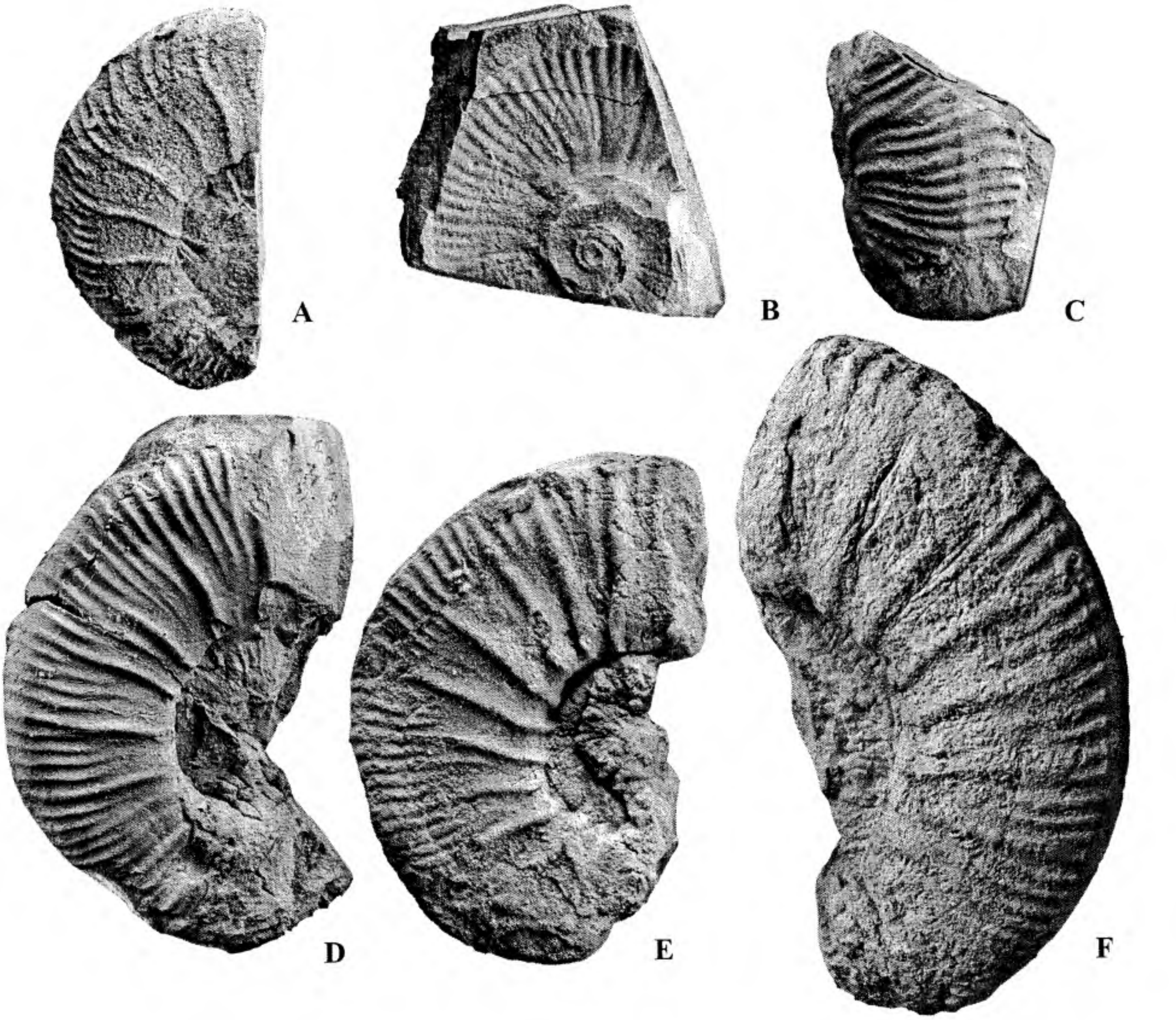


Fig. 39: A-F, *Pseudothurmannia* (*Parathurmannia*) *dissiticostata* sp. nov. A. RGM 542331, locality 3C; ×1. B, RGM 542151, locality 1C, bed C153, syntype; ×1. C, RGM 542150, locality 1W, loose from bed W35-36, syntype; ×1. D, RGM 542149, locality 1W, in loose block A from beds W35-46, syntype; ×1. E, RGM 542327, locality 2; ×1. F, RGM 387838, locality 2, with small lateral tubercles on the main ribs; ×1.

midflank. At a diameter of 8 mm there are already main ribs that can be distinguished from the intermediate ribs by the presence of umbilical bullae. They are separated by 3-6 intermediate ribs, which originate at the umbilical rim.

At a diameter of 17 mm, however, the umbilical rim between every pair of main ribs is smooth, as only a few intermediate ribs originate at the umbilical rim. The ribbing is slightly flexuous. The main ribs become more prominent than the intermediate ribs and are provided with small pointed umbilical tubercles. There are mainly 4-6, rarely two or three, intermediate ribs to one main rib; most of them originate above the umbilical rim, several originate at midflank. A few seem to split off from a main rib, but in reality they originate very close to the main rib at midflank or at the umbilical rim. All intermediate ribs taper towards the umbilicus and only one bifurcates at midflank. This type of ribbing persists up to a diameter of c. 70 mm. The lower parts of the main ribs are more prominent than the upper parts, which in turn are still broader and more rounded than the fine and sharp intermediate ribs. The distance between the intermediate ribs is constant and slightly greater than their thickness; the distance between the main ribs is irregular and depends on the number of intermediate ribs between them.

On the ventral side the main ribs are still slightly broader than the intermediate ribs and pass over the venter in a straight or slightly forward curve. Each rib is provided with a very small clavus; they form two ventrolateral rows at both sides of the venter; the clavi on the main ribs are longer than those on the intermediate ribs.

Three specimens were sampled from the Sierra de la Muela. One has the same diameter as the larger syntype (Fig. 39E); the second consists of half a whorl with tubercle-like lateral knobs slightly above the middle of the main ribs (Fig. 39F); the third is a large whorl fragment without lateral knobs belonging to a specimen with a diameter of c. 150 mm. This implies that *dissiticostata* also shows tubercle-like knobs between a diameter of c. 70 mm and a diameter of at least 115 mm, but not at a diameter of 150 mm.

Remarks: It is not clear what the precise relation is between *P.* (*Pa.*) *sarasini* and *P.* (*Pa.*) *dissiticostata*. The author still considers the latter as a separate species, but it is possible that both species are the components of a dimorphic pair in which *P.* (*Pa.*) *dissiticostata* would be the macroconch. Much more and better material is needed to solve this uncertainty.

Most specimens figured by Busnardo (2003) under the name *Parathurmannia* gr. *sarasini* do not exhibit rows of ventrolateral clavi and do not belong to the genus *Pseudothurmannia*.

Range: Catulloi Zone and basal Hugii Zone (that is from bed W35-W53).

Geographical distribution: Spain [Río Argos (Caravaca, Prov. of Murcia), Tornajo Mountain (Lorca, Prov. of Murcia), Sierra de la Muela (Moratalla, Prov. of Murcia)], Switzerland [River Veveyse (Châtel-St.-Denis)]).

7.2.3. *Pseudothurmannia* (*Parathurmannia*) *edouardi* (Honnorat-Bastide, 1889)
Pl. XXIII; Tab. X

v* 1889. *Crioceras Edouardi* nov. sp.– Honnorat-Bastide, p. 462, pl. 11, fig. 1, 2.
1965b. *Crioceratites* (*Crioceratites*) *edouardi* Honnorat-Bastide.– Thomel, p. 417, pl. 9.
1993. *Pseudothurmannia simionescui* Sarkar.– Autran, p. 115, pl. 13, fig. 5.
2003. *Sornayites edouardi* Honnorat-Bastide.– Busnardo, p. 73, pl. 28, fig. 4a-b (= holotype).
2009. *Pseudothurmannia edouardi* (Honnorat-Bastide) .– Vermeulen, pl. 3, fig. 1 (= holotype).

Holotype by monotypy: *Crioceras Edouardi* Honorat-Bastide, from le Cheiron near Castellane (Alpes-de-Haute-Provence, France), deposited in the University Pierre et Marie Curie, Place Jussieu, Paris, Collection Honnorat-Bastide, nr. 3933 (Pl. XXIII), kindly sent to me by Dr. Max Wippich.

Material: Plaster cast of the holotype.

Description of the holotype: Slightly crioconic outer whorl with a gap between them of about 1 mm. The inner whorls are touching each other. At a diameter of 52 mm, the whorl height equals the umbilical width. The whorl section is oval with rounded flanks and a rather broad rounded venter, which is only slightly truncated. The umbilical rim is rounded and the umbilical wall rounded and steep. The whorls grow slowly in height (wh:Wh = 4:5).

The inner whorls, visible from a diameter of 20 mm, are finely ribbed with 5-7 almost straight intermediate ribs to one main rib. From the prominent umbilical bullae often arise two ribs, one main rib and one intermediate rib. Among the intermediate ribs fasciculation occurs. Faint lateral tubercles are already present on the main ribs and gradually increase in prominence. At a diameter of 40 mm this ornamentation is replaced by a coarse-ribbed ornamentation in which the strong, straight, trituberculate main ribs are broader and higher than the intermediate ones. From a diameter of 45 mm only two intermediate ribs, one short and one long, are present between every two main ribs, and this pattern remains so at least up to a diameter of 113 mm. This gives the specimen a very regular appearance. Only in three intervals were three intermediate ribs counted, but the third rib seems to fork from the lateral tubercle. The main ribs originate at the dorsal side and are rursiradiate on the umbilical wall. On the flanks they are straight, slightly prorsiradiate, and much broader and higher than the thin, straight intermediate ribs. Towards the venter they diminish in strength and become equal to the intermediate ribs. They are provided with umbilical tubercles and lateral ones just above midflank. The intermediate ribs taper in the direction of the umbilicus, and at diameters smaller than 80 mm they do not reach farther than the umbilical rim. At greater diameters the long intermediate rib originates on the dorsal side. The distance between the main ribs does not change. All the ribs are equal when crossing the venter. Each rib has a small ventrolateral clavus, which form two rows of clavi at both sides of the venter. In the large specimen described by Thomel (1965b) there are three intermediate ribs to one main rib from a diameter of 130 mm.

Remarks: The species *edouardi* Honnorat-Bastide is included in subgenus *Pseudothurmannia* (*Parathurmannia*) because it has the same ornamental ontogeny as *P.* (*Pa*) *sarasini*. It has fine-ribbed inner whorls with 5-6 long intermediate ribs to one main rib. At a diameter of 40 mm this fine-ribbed inner part is, like *P.* (*Pa.*) *sarasini*, followed by a coarse-ribbed part in which each pair of trituberculate main ribs is regularly separated by only 2-3 intermediate ribs. However, *P.* (*Pa.*) *edouardi* differs from *P.* (*Pa.*) *sarasini* in having straight main ribs on the inner whorls instead of sigmoidal ones, in having slightly crioconic whorls instead of overlapping whorls, in having a large umbilicus instead of a small umbilicus, and in having a long, coarse-ribbed part with trituberculate ribs, which extends over more than one whorl instead of over a quarter of a whorl.

Pseudothurmannia (*Parathurmannia*) *edouardi* differs from the species of subgenus *Pseudothurmannia* (*Pseudothurmannia*), with which it is generally united, in the large distance between the main ribs on the inner whorls with 5-6 intermediate ribs to one main rib. The species of *Pseudothurmannia* (*Pseudothurmannia*) have normally 2-3, rarely four intermediate ribs to one main rib.

Nevertheless, *P.* (*Pa.*) *edouardi* is reminiscent of *P.* (*P.*) *simionescui*, because its whorls are just not in contact as the last whorl of *P (P) simionescui*, and the overall ornamentation also consists of 2-3 intermediate ribs to one main rib. The latter species has been synonymized with *P* (*Pa.*) *edouardi* by Wiedmann (1962). However, the inner whorls of *P.* (*P.*) *simionescui* are more compressed with flatter flanks, have a higher whorl section, a more truncated venter, and only three intermediate ribs to one main rib, rarely two or four. This is in contrast with the 5-6 intermediate ribs on the inner whorls of *P (Pa.) edouardi.* The regularity of only two, rarely three, intermediate ribs to one main rib in *P.* (*Pa.*) *edouardi* differs from the irregularity in *P.* (*P.*) *simionescui*, which also has mainly two intermediate ribs to one main rib, but often three or one.

Range and distribution: The only three known specimens, from Honnorat-Bastide, Thomel and Autran respectively, were all collected in, what Thomel called 'lowest Barremian' and Autran the uppermost Hauterivian 'Pseudothurmannia angulicostata Zone' (probably in the Catulloi Zone) in the valley of Le Cheiron near La Baume (Castellane, Alpes-de-Haute-Provence, France) and in the valley of the Riou.

7.3. Subgenus *Pseudothurmannia* (*Pseudothurmannia*) Spath, 1923

Type species: *Pseudothurmannia picteti* Sarkar, 1955. Invalidly designated by Spath (1923), but validly redesignated by Company *et al.* (2002, 2003). These authors again designated *Pseudothurmannia picteti* Sarkar as type species of the genus *Pseudothurmannia* Spath, but this time in accordance with the new rules of the ICZN (1999 article 70.3.2). The species *Ammonites angulicostatus* d'Orbigny, 1841 has lost its status of type species and can, without violating the rules, be considered to belong to the genus *Crioceratites*.

Diagnosis: Diagnostic for subgenus *Pseudothurmannia* (*Pseudothurmannia*) are the wide-spaced main ribs with only 2-3, rarely four, intermediate ribs to one main rib in young ontogenetic stages instead of the 4-6 intermediate ribs in the young stages of subgenus *Pseudothurmannia* (*Parathurmannia*). These two subgenera lack the fine, dense *mortilleti*-like ribbing of the inner whorls of subgenus *Pseudothurmannia* (*Kakabadziella*). The lower parts of the main ribs are distinctly thicker and higher than the upper parts, and are provided with prominent umbilical tubercles. All the ribs have the same thickness on the venter, but in a few species the main ribs may remain slightly thicker than the intermediate ones in the upper part of the flanks and on the venter. Lateral tubercles appear in middle to late ontogenetic stages in all the species of *P* (*Pseudothurmannia*), a feature that they have in common with *P.* (*Parathurmannia*), but are absent in the early growth stages. They are situated at the abrupt transitions from the prominent lower parts of the main ribs to the less prominent upper parts. The uniform ventrolateral clavi are more prominent than in *P. (Kakabadziella)* and remain visible up to the aperture. Sexual dimorphism has not been established among the species of this subgenus, except perhaps for *P.* (*P.*) *crioceroides* and *P* (*P.*) *picteti*.

Remarks: Wiedmann (1962, p. 140, footnote) and Busnardo (2003, p. 72) included all the species with lateral tubercles in middle to late ontogenetic stages, which are here united under the subgeneric names *Pseudothurmannia* (*Parathurmannia*) and *Pseudothurmannia* (*Pseudothurmannia*), in the genus *Sornayites* Wiedmann, 1962. They did not include *P.* (*Pa.*) *sarasini*, *P.* (*P.*) *picteti* and *P.* (*P.*) *pseudomalbosi* in *Sornayites*, because these species do not have lateral tubercles on the inner whorls. This exception is incomprehensible, because none of the species included in *Pseudothurmannia* have lateral tubercles on the inner whorls. The author does not consider *Sornayites* (type species *Sornayites paronai* Sarkar, 1955) congeneric with any of the species that he includes in subgenera *P.* (*Pseudothurmannia*) and *P.* (*Parathurmannia*).

Vermeulen (2004) introduced the generic name *Prieuriceras* with the same type species as the genus *Pseudothurmannia*, viz. *Pseudothurmannia picteti* Sarkar, 1955. *Prieuriceras* is, therefore, a junior objective synonym of *Pseudothurmannia*. Vermeulen united in *Prieuriceras* all the species that are here included in subgenera *Pseudothurmannia* (*Pseudothurmannia*) and *Pseudothurmannia* (*Parathurmannia*).

7.3.1. *Pseudothurmannia* (*Pseudothurmannia*) *picteti* (Sarkar, 1955)

Figs. 40-46; Pls. XXIV-XXVII; Tab. XI

v *pars* 1863. *Ammonites angulicostatus* d'Orbigny, forme à tours emboités.– Pictet, p. 13, pl. 1bis, fig. 1a-b, *non* fig. 2a-b [= *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955], *non* fig. 3a-b (= *Crioceratites angulicostatiformis* nom. nov.).

pars 1910. *Hoplites* (*Neocomites*) *angulicostatus* d'Orbigny.– Kilian, p. 222, pl. 5, fig. 6a *non* fig. 6b [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* n. sp.].

1923. *«Parahoplites »* (*Thurmannites?*) *angulicostatus* (d'Orbigny) in Pictet.– Spath, p. 66, footnote 1 (designation of type species of *Pseudothurmannia*).

v *pars* 1939. *Parahoplites* (*Pseudothurmannia*) *angulicostatus* (d'Orbigny) in Pictet.– Roman, p. 347, pl. 34, fig. 328a-b, *non* fig. 329 [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.].

v 1952. *Pseudothurmannia angulicostata* (d'Orbigny).– Basse, pl. 19, fig. 11.

v* 1955. *Pseudothurmannia picteti* nom. nov.– Sarkar, p. 155-156.

1958. *Pseudothurmannia picteti* Sarkar.– Luppov & Drushchits, pl. 46, fig. 4.

non 1960. *Pseudothurmannia picteti* Sarkar.– Drushchits & Kudrjavtsev, p. 228, pl. 30, fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

1961. *Pseudothurmannia* cf. *pseudomalbosi* (Sarasin & Schöndelmayer).– Eristavi, p. 98, pl. 5, fig. 1.

v 1962. *Crioceratites* (*Pseudothurmannia*) *provencalis* nov. nom.– Wiedmann, p. 141.

1962. *Crioceratites* (*Pseudothurmannia*) aff. *angulicostatus* (d'Orbigny).– Wiedmann, p. 138, pl. 10, fig. 1a, b.

pars 1965. *Pseudothurmannia angulicostata* (d'Orbigny).– Dimitrova, p. 217, pl. 1, fig. 1, *non* fig, 2 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi*? (Parona, 1897)], *non* fig. 3 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov. (microconch)].

1966. *Pseudothurmannia picteti* Sarkar.– Breskovski, p. 81, pl. 2, figs. 5-6.

1967. *Pseudothurmannia pseudomalbosi* (Sarasin & Schöndelmayer).– Dimitrova p. 72, pl. 31, fig. 3.

1967. *Pseudothurmannia picteti* Sarkar.– Dimitrova, p. 74, pl. 35, fig. 1.

1970. *Pseudothurmannia grandis* n. sp.– Busnardo, p. 140, pl. 1, fig. 1, fig. 3.

1970. *Pseudothurmannia* sp. A.– Busnardo, p. 140, pl. 1, fig. 2.

1970. *Pseudothurmannia lurensis* n. sp.– Busnardo, p. 137, pl. 1, fig. 4.

pars 1990. *Pseudothurmannia angulicostata* (d'Orbigny).– Thomel, pl. 6, figs. 10-12, *non* figs. 1-7 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* figs. 8-9 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

pars 1995. *Pseudothurmannia picteti* Sarkar.– Avram, p. 119, pl. 8, fig. 7, *non* figs. 5-6 [= both *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

1995. *Pseudothurmannia* aff. *picteti* Sarkar.– Avram, p. 119, pl. 8, fig. 8.

non 1997. *Pseudothurmannia picteti* (Sarcar) (sic).– Atabekian *et al.*, p. 128, pl. 36, figs. 5-6 [= ambo *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (macroconch)].

? 2002. *Pseudothurmannia sarasini* Sarkar.– Bodrogi & Fogarasi, p. 304, pl. 1, fig. 2.

2002. *Pseudothurmannia picteti* (Sarkar).– Vermeulen, p. 33, pl. 57, fig. 4.

2002. *Pseudothurmannia picteti* (Sarkar).– Vermeulen *et al.*, p. 73, pl. 2, fig. 1.

non 2003. *Pseudothurmannia picteti* Sarkar.– Company *et al.*, p. 688, fig. 6.6. [= *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* sp. nov.], *non* fig. 6.7. [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

v 2003. *Pseudothurmannia picteti* Sarkar.– Busnardo, p. 67, pl. 29, fig. 4 (= holotype).

non 2003. *Pseudothurmannia* cf. *picteti* Sarkar.– Busnardo, p. 67, pl. 29, fig. 1 [= *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955].

pars 2003. *Parathurmannia* cf. *biassalensis* (Dimitrova).– Busnardo, p. 69, pl. 15, fig. 2, *non* figs. 3, 8 [= ambo *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

Holotype Specimen depicted by Pictet (1863, pl. 1bis, fig. 1a-b) under the name '*Ammonites angulicostatus*, forme à tours emboités,' derived from the section near Angles (St.-André-les-Alpes, Alpes-de Haute-Provence, France) deposited in the Muséum d'Histoire naturelle de Genève (Switzerland), Collection Pictet, nr. 16849.

Material: Nineteen specimens in total. Eleven specimens and whorl fragments from the lower Barremian (Catulloi Zone) of the Sierra de la Muela, (Moratalla, Murcia, Spain). Plaster cast of the holotype kindly sent to the author by Dr. D. Decrouez from the Muséum d'Histoire naturelle de Genève, and a plaster cast of the cotype of the d'Orbigny collection (Muséum National d'Histoire Naturelle in Paris, Nr. 5366A) described and figured by Wiedmann (1962, pl. 10, fig. 1a-b) under the name *Crioceratites* (*Pseudothurmannia*) aff. *angulicostatus*, and kindly sent to the author by Dr. Max Wippich. Five specimens from the Río Argos succession. One specimen from The Crimea.

Locus typicus: Angles section, probably in the Catulloi Zone from one of the beds 64-72.

Description of the holotype: Since the holotype of *Pseudothurmannia picteti* Sarkar (Pl. XXIV, figs. 7-8) has legitimately been proposed by Company *et al.* (2002, 2003) as the type species of the genus *Pseudothurmannia* Spath, it is necessary to describe the species precisely, which has never been done before.

The whorls are compressed with parallel, slightly rounded flanks and a broad truncated venter; the umbilical shoulders are prominent. The shell is rather involute; the overlap is one third of the whorl height at a diameter of 97 mm, the maximum diameter of the holotype, but among the specimens from the Sierra de la Muela the overlap diminishes to one quarter at diameter 200 mm and to one sixth at diameter 240 mm. The umbilicus is deep and small, somewhat smaller than the whorl height. At a diameter of c. 150 mm the umbilicus has the same width as the whorl height; at larger diameters it is greater. The umbilical wall is perpendicular; the umbilical rim rounded. The venter is broad and almost flat. The ventrolateral shoulders are angular. The whorls grow moderately in height. At a diameter of 97 mm the ratio wh:Wh = 2:3. The growth in whorl height diminishes with the growth of the shell, for the ratio wh:Wh = 3:4 at diameter 225 mm.

On the plaster cast of the holotype, the innermost whorls are visible from a diameter of 13 mm and exhibit already strong sigmoidal main ribs at some distance from each other; they originate at the umbilical seam, are slightly inclined backward on the umbilical wall,

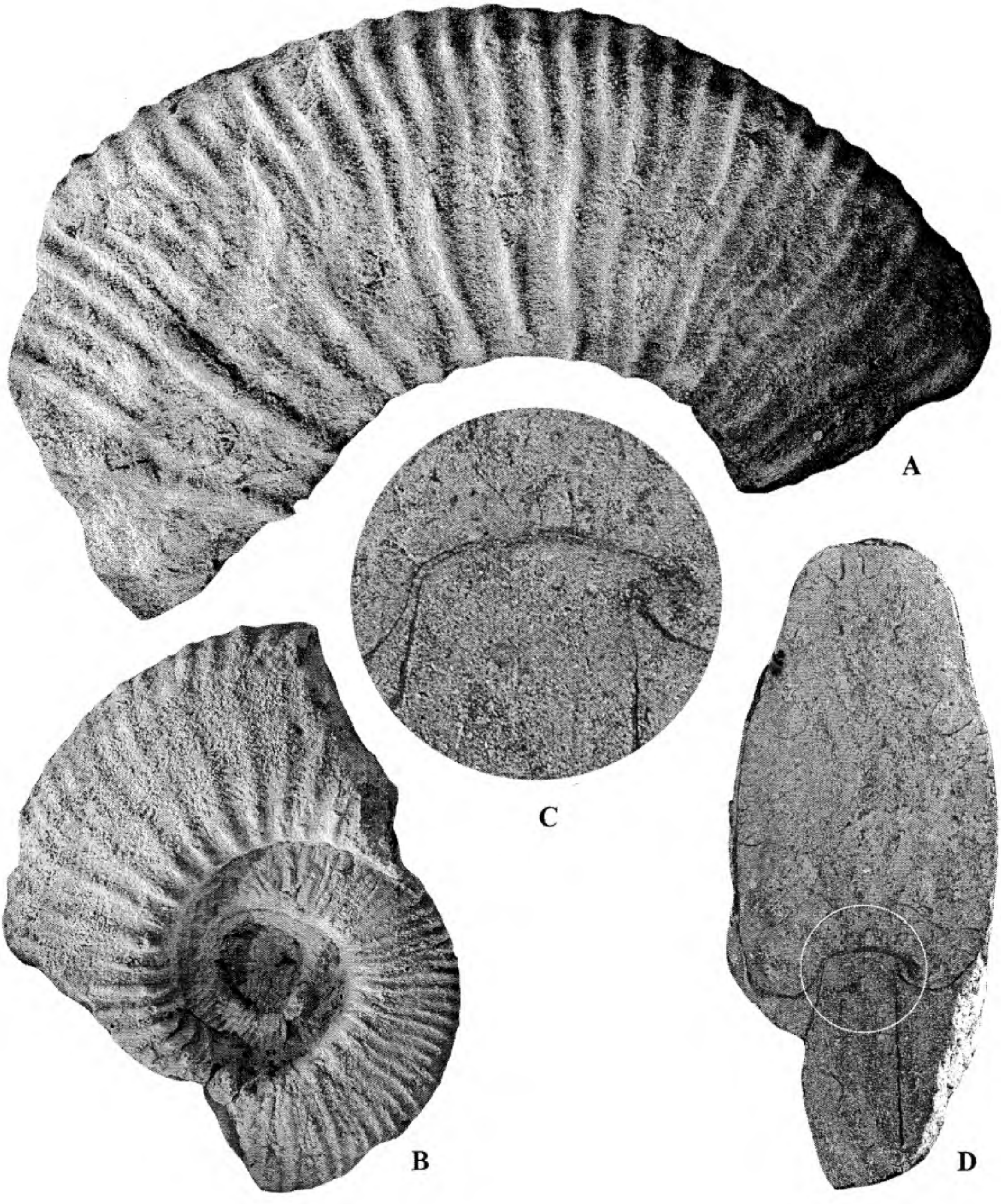


Fig. 40: A-C, *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955. A, RGM 542640, locality 2; ×1. B, RGM 387836, locality 2; ×1. C, magnification of a part of the whorl section of Text-figure 35 D, showing the doubling of the shell at the contact between the dorsal side and the ventral side of the foregoing whorl; ×3. D, RGM 542648, locality 2, whorl section; ×1.

and are provided with pointed umbilical tubercles when passing the umbilical rim. Between every two main ribs, 1-3, rarely four, weaker sigmoidal intermediate ribs are visible, which may reach down to the umbilical wall, but also may be shorter. The number of intermediate ribs gradually diminishes with growth.

From a diameter of about 35 mm, the middle one of the intermediate ribs between two main ribs originates from the umbilical seam, but is not provided with an umbilical tubercle. They are separated from the main ribs by one or two intermediate ribs that originate at midflank, or slightly lower; some intermediate ribs may be a little longer. The sigmoidal main ribs are provided with umbilical tubercles, and on the lower part of the flank they are much higher and broader than on the upper part. All the ribs are adorned with small, uniform ventrolateral

Fig. 41: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955, RGM 542649, locality 2, specimen with long intermediate ribs; ×1.

clavi, which form delicate rows at both sides of the flat venter. On the venter all the ribs are equal and pass straight over the venter.

Between a diameter of 47 and 63 mm, the ornamentation of the holotype is not visible except for umbilical tubercles.

On the last half a whorl of the holotype, that is, from a diameter of 63 to 97 mm, the main ribs are almost straight, only slightly flexuous, originate at the umbilical seam, are slightly inclined backward on the umbilical wall and are provided with pointed umbilical tubercles. Every two main ribs are separated by one or two intermediate ribs, which originate at, or slightly below, midflank. In only two instances an intermediate rib does reach the umbilical seam. The lower parts of the main ribs are high and strong, but suddenly reduce in height a little above midflank to become as low and thin as the intermediate ribs. The upper ends of the strong lower parts do not protrude, but from a diameter of 75 mm these upper ends do protrude forming blunt, tubercle-like knobs just above midflank. All the ribs are equal when they pass straight over the flat venter. All ribs have uniform ventrolateral clavi at the shoulders. Till so far the description of the holotype.

Small specimens: Small specimens (Pl. XXIV, figs. 1-8), that is, smaller than 60 mm (four from the Rio Argos, one from the Sierra de la Muela and one from the Crimea), are reminiscent of *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897) because of the small umbilicus and the greater distance of the ribs in comparison with *P.* (*K.*) *mortilleti*. However, these specimens can readily be distinguished from *P.* (*K.*) *catulloi*, because they lack the fine-ribbed *balearis*-like inner whorls of *P.* (*K.*) *catulloi* and have a truncated venter. The innermost whorls of *P.* (*P.*) *picteti* show rather distant sigmoidal ribs; the main ribs have umbilical tubercles and are separated by one or two, rarely three or four short intermediate ribs. If there are three or four intermediate ribs, the middle one looks like a main rib without umbilical tubercle. In slightly larger specimens, with a diameter greater than 25 mm, all main ribs have prominent umbilical tubercles and become rather straight, but remain separated by only one

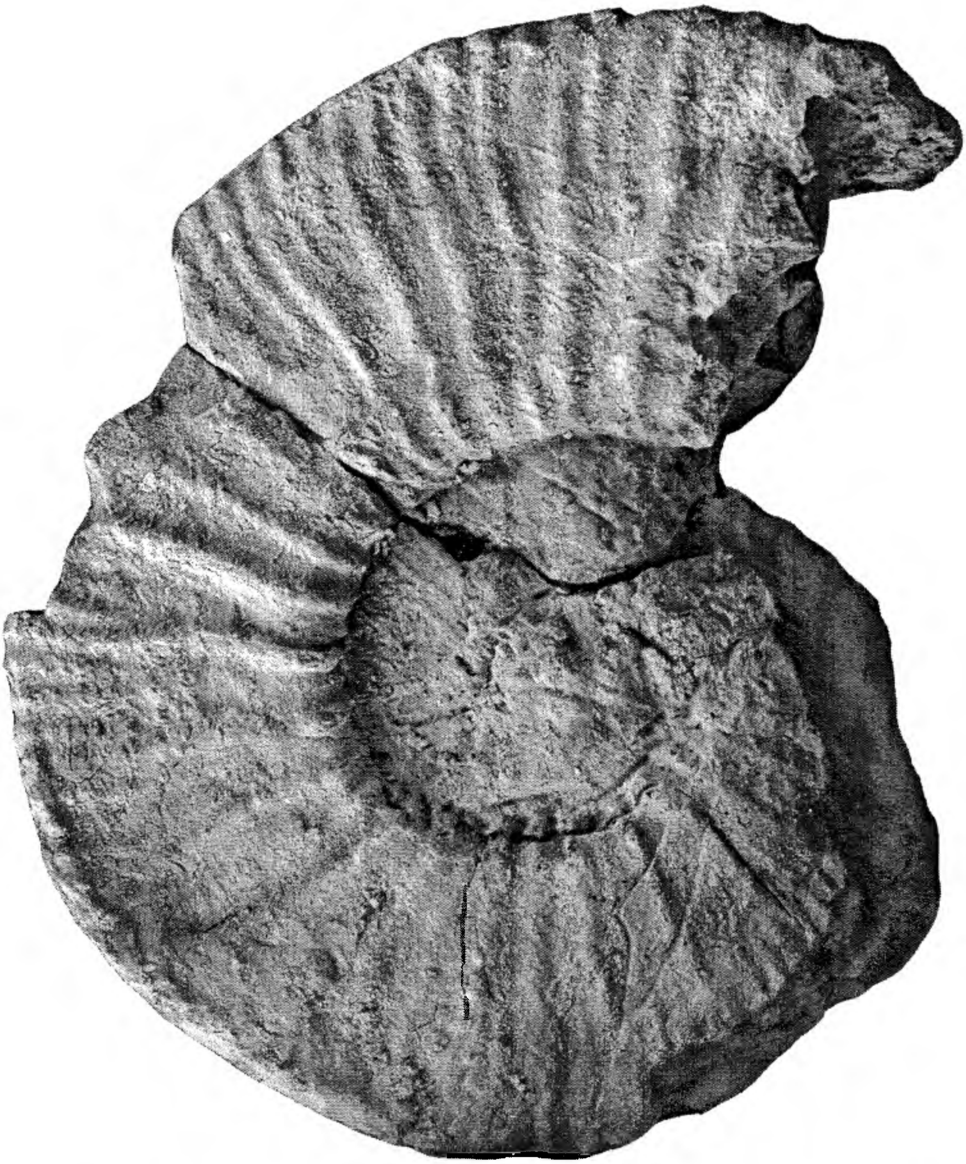


Fig. 42: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955. RGM 542647, locality 2, specimen with short intermediate ribs; ×1.

or two intermediate ribs. This regularity is striking and remains so in adult specimens. The venter of the small specimens is truncated, and the flanks are slightly curved and parallel. All the ribs cross the venter in a rectilinear manner and have the same strength. Ventrolateral uniform clavi are visible on every rib.

Large specimens from the Sierra de la Muela: (Pl. XXIV, fig. 9, Pls. XXV-XXVII, Figs. 40-45). The main ribs of the smallest but one specimen from the Sierra de la Muela (Pl. XXIV, fig. 9), which has a diameter of about 120 mm, reach their highest elevation just above midflank and merely form blunt round swellings; in none of the intervals does an intermediate rib reach the umbilical seam.

The tubercle-like knobs gradually disappear with growth and do not exist anymore at diameters greater than 130-140 mm. So, the lateral knobs exist only over c. three quarters of a whorl; they can be pronounced or practically invisible. On the large specimens from the Sierra de la Muela, the lower parts of the main ribs remain high and thick, and abruptly become lower and thinner just above midflank. The number of intermediate ribs to one main rib remains one or two, less commonly three. On the truncated venter all the ribs are equally strong and straight. Ventrolateral clavi occur on every rib. The whorl section is compressed rectangular with nearly flat flanks and nearly flat venter.

Variability: In the adult specimens there is variability in the number of intermediate ribs that reach the umbilical seam. There are six specimens from the Sierra de la Muela in which the intermediate ribs are generally short, or a little longer (Figs. 40B, 42, 44- 45; Pl. XXVII), but

Fig. 43: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955. RGM 542641, locality 2, specimen with long intermediate ribs; ×1.

uncommonly reach the umbilical seam. In the holotype and in the specimen figured by Dimitrova (1967), there are only two intermediate ribs that reach the umbilical seam; in the small specimen from the Sierra de la Muela there are none. Five specimens with short intermediate ribs have only one interval in which two long intermediate ribs originate at the umbilical seam, and the sixth specimen has only four such intervals. There are, however, five other specimens from the Sierra de la Muela in which most or nearly all long intermediate ribs originate at the umbilical seam (Figs. 40A, 41, 43; Pls. XXV-XXVI). These specimens have the same ribbing as *Pseudothurmannia grandis* Busnardo. This difference in the general length of the ribs is regarded as an expression of variability and not important enough to distinguish species.

Fig. 44: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955. RGM 542642, locality 2, specimen with short intermediate ribs; 82%.

Secondly, there are specimens on which the lateral knobs seem to be absent, but only the rather abrupt transition from the high and broad lower part into a low and narrow upper part remains. In one specimen even the difference in strongness between the lower and upper parts of the main ribs is hardly discernable.

Finally, there are coarse-ribbed and fine-ribbed varieties. The smallest but one specimen from the Sierra de la Muela (Pl. XXIV, fig. 9) has coarser ribs than the holotype. However, the specimen from Ravin de Valbonnette (Vermeulen, 2002), the specimen figured by Dimitrova (1967) and the inner whorls of specimen RGM 542645 (Pl. XXV) from the Sierra de la Muela have finer and denser ribbing than the holotype.

Fig. 45: *Pseudothurmannia (Pseudothurmannia) picteti* Sarkar, 1955. RGM 542833, locality 2, specimen with short intermediate ribs; ×1.

It is quite possible that the coarse-ribbed specimens such as the holotype (Pl. XXIV, fig. 7), the specimen from the d'Orbigny collection (Pl. XXIV, fig. 6), the specimen of section F (Pl. XXIV, figs. 4, 5) and the smallest but one specimen from the Sierra de la Muela described above (Pl. XXIV, fig. 9) are microconchs.

Suture line: Fig. 46. Only the saddle U/L and the lateral lobe L were visible on specimen RGM 387836. The trifid lateral lobe has a rather narrow throat, but is widely branched and every branch has a trifid ending. The saddles are narrow-necked and divided into two parts by a deep incision. The internal part of saddle E/L and both parts of saddle L/U consist of four branches.

Remarks: The drawing of the holotype of *P.* (*P.*) *picteti* in Pictet (1863) is very unlike the real specimen and looks like *P.* (*K.*) *catulloi*, because it does not show the lateral tubercles. Therefore, many specimens of *P.* (*K.*) *catulloi* have been called *P. picteti* in the literature (see synonymy). The drawing is so unlike the real specimen that other specimens of *P.* (*P*) *picteti* have not been recognized as such, and were identified by Dimitrova (1967) as *P. pseudomalbosi* (Sarasin & Schöndelmayer),

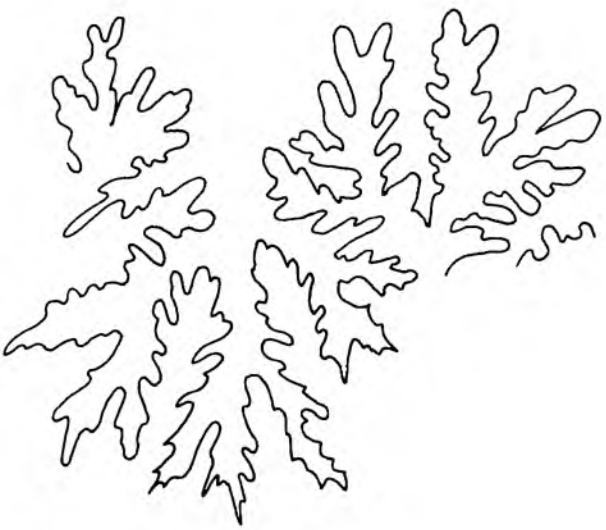


Fig. 46: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955, suture line. RGM 387836, Wh 18 mm; ×6.

or were given a new name, for instance, *P. lurensis* Busnardo (1970) and *P. grandis* Busnardo (1970). Wiedmann (1962) depicted a cotype of *Ammonites angulicostatus* d'Orbigny (National Museum of Natural History in Paris, d'Orbigny Collection, no 5366 A) from Barrême (Pl. XXIV, fig. 6), which he identified as *Crioceratites* (*Pseudothurmannia*) aff. *angulicostatus*, but which is a small specimen of *P.* (*P.*) *picteti*.

The main differences between *P.* (*P.*) *picteti* and *P.* (*K.*) *catulloi* are the rather wide-spaced main ribs on the innermost whorls of *P.* (*P.*) *picteti* in contrast to the fine, dense, uniform ribbing on the innermost whorls of *P.* (*K.*) *catulloi*. The macroconchs of *P..* (*K.*) *catulloi* obtain a third additional type of ribs in late ontogenetic stages, which are a thick, prominent, very wide-spaced and lined by weak constrictions, whereas *P.* (*P.*) *picteti* has no such ribs or constrictions. *Pseudothurmannia* (*Pseudothurmannia*) *picteti* has prominent pointed umbilical bullae, whereas *P.* (*K.*) *catulloi* lacks them. Finely, *P.* (*P.*) *picteti* has a nearly flat truncated venter, whereas *P.* (*K.*) *catulloi* has an arched venter.

The main difference between *P.* (*P.*) *picteti* Sarkar and *P.* (*P.*) *simionescui* Sarkar is the degree of involution. *P.* (*P.*) *picteti* has rather involute whorls, which become evolute in the adult. The inner whorls of *P.* (*P.*) *simionescui* are already evolute, and the later whorls easily disengage from each other. The whorl height is growing faster in *P.* (*P.*) *picteti* than in *P.* (*P.*) *simionescui*. In *P.* (*P.*) *picteti* the flanks are flat, especially in the adult specimens; in *P.* (*P.*) *simionescui* they are curved. In *P.* (*P.*) *picteti* the lateral tubercles are rounded, blunt and disappear at a diameter of 130-140 mm; in *P.* (*P.*) *simionescui* they are prominent, pointed and remain prominent presumably up to the aperture.

Pseudothurmannia (*Pseudothurmannia*) *picteti* differs from *P.* (*P.*) *arundicostata* and *P.* (*P.*) *crioceroides* mainly in its small umbilicus, in the transient presence of lateral tubercles, in the small number (1-2, rarely three) of intermediate ribs in the adult ontogenetic stage and in the compressed rectangular whorl section.

Range: Lower Catulloi Zone.

Geographical distribution: Switzerland (River Veveyse near Châtel-St.-Denis), France (Angles, Montagne de Lure, Barrême, Valbonnette valley), Spain (Río Argos near Caravaca, Sierra de la Muela north of Moratalla), Rumania (Orşova-Moldova), Bulgaria (Brestak, Senedair, Beli Mel), The Crimea.

7.3.2. *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955

Figs. 47-48; Pls. XXVIII-XXIX; Tab. XII

pars 1863. *Ammonites angulicostatus* d'Orbigny.– Pictet, p. 13, pl. 1bis, fig. 2a-b (forme à tours en contact), *non* fig. 1a-b [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar], *non* fig. 3a-b [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nov. nom.].

1898. *Crioceras angulicostatum* d'Orbigny.– Simionescu, p. 86, pl. 6, fig. 2.

* 1955. *Pseudothurmannia simionescui* n. sp.– Sarkar, p. 157, pl. 11, fig. 1.

non 1966. *Pseudothurmannia simionescui* Sarkar.– Breskovski, p. 80, pl. 2, fig. 3 (= '*Emericiceras*' *paramahansai* Sarkar, 1955).

1967. *Pseudothurmannia simionescui* Sarkar.– Dimitrova, p. 73, pl. 34, fig. 2.

1969. *Pseudothurmannia edouardi* (Honnorat-Bastide).– Patrulius, pl. 5, fig. 5

non 1976. *Pseudothurmannia simionescui* Sarkar.– Mandov, p, 67, pl. 8, fig. 1 [= *Pseudothurmannia* (*Pseudothurmannia*) *perevoluta* sp. nov.].

non 1993. *Pseudothurmannia simionescui* Sarkar.– Autran, pl. 13, fig. 5 [= *Pseudothurmannia* (*Parathurmannia*) *edouardi* (Honnorat-Bastide, 1889)].

non 1995b. *Pseudothurmannia simionescui* Sarkar.– Hoedemaeker, p. 231, pl. 2, fig. 8 [= *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* (Torcapel, 1884)].

non 2002. *Pseudothurmannia* ex gr. *simionescui* Honnorat-Bastide.– Bodrogi & Fogarasi, p. 304, pl. 2, fig. 2 (= *Emericiceras* gr. *emerici* Léveillé, 1837).

2003. *Sornayites simionescui* (Sarkar) .– Busnardo, p. 72, pl. 29, fig. 5.

non 2005. *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Honnorat-Bastide.– Kakabadze, p. 351, pl. 72, fig. 8 [= *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* (Torcapel) or *P.* (*P.*) *monasteriensis* (Simionescu, 1899)].

Holotype: *Pseudothurmannia simionescui* Sarkar, 1955, deposited in the Muséum National d'Histoire Naturelle de Paris, no. 4872.

Material: Ten specimens in total: one well preserved specimen and six whorl fragments from the condensed bed at the base of the lower Barremian Bolos Sandstone Formation (Hoedemaeker, 1973) in the Sierra de la Muela (Moratalla, Murcia, Spain); two specimens from Chamaloc (Die, Drôme, France); and a plaster cast of the specimen from Angles (France) described by Pictet by the name of *Ammonites angulicostatus* d'Orbigny, 'forme à tours en contact' (Pictet collection no. 16848), kindly sent to the author by Dr. D. Decrouez of the Muséum d'histoire naturelle de Genève.

Description: The well-preserved specimen from the Sierra de la Muela (Pl. XXVIII) is described herein, because it is better preserved than the holotype. The outer whorls are just not touching each other, but the external side of the preceding whorl is bedded in the dorsal concavity of the next whorl. However, the inner whorls are overlapping each other. The whorls grow moderately in height (wh:Wh = 2:3). From a diameter of about 113 mm, the umbilicus becomes larger than the whorl height. From this diameter the last whorl becomes slightly crioconic. The whorl section is oval with a broad, truncated venter. The large umbilicus has vertical walls and a rounded umbilical rim. The flanks and venter are slightly rounded.

The general ornamentation consists of main ribs, which originate at the umbilical seam, and intermediate ribs, which show considerable difference in length. The longest intermediate ribs start from the umbilical seam, the shorter from the upper third of the flank. The presence of many long intermediate ribs originating at the umbilical seam is characteristic for the species.

The ribbing is fine at the smallest visible diameter (8 mm in the specimen from Chamaloc, Fig. 47) and consists of 1-2, rarely three, flexuous intermediate ribs to one main rib. At a diameter of 25 mm, the number of intermediate ribs augments to 3-4; the flexuous main ribs are provided with small pointed umbilical tubercles. From this diameter, the ornamentation of the well-preserved specimen from the Sierra de la Muela can be studied. From a diameter of 55 mm the main ribs become gradually thicker and higher below midflank than above midflank, and all the main ribs are provided with a short, but sharp, lateral tubercle at midflank. At the same diameter the umbilical bullae develop into small sharp spines, pointing obliquely downward. Sharp ventrolateral clavi are present at least from a diameter of 25 mm, but probably already exist at much smaller diameters.

From a diameter of c. 65 mm the ribbing becomes strong and radial with a slight forward curve when approaching the venter. The number of thin intermediate ribs to one thick main ribs changes abruptly to two (c. 60%) or one (c. 30%), rarely three (c. 10%). On the last whorl, c. 35% (n = 23) of the intermediate ribs start at the umbilical seam, c. 10% (n = 6) at the umbilical rim, whereas more than 50% (n = 32) of the intermediate ribs do not reach further down than midflank. The intermediate ribs uncommonly bifurcate at midflank. Two rows of small, uniform, sharp, ventrolateral clavi are pointing obliquely upward and are prominent up to the aperture. On the venter main and intermediate ribs are equal in strength and pass the venter in a straight line. The general appearance of the ribbing is irregular.

Fig. 47: *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955. RGM 542627, locality 6, bed CR 324; 83%.

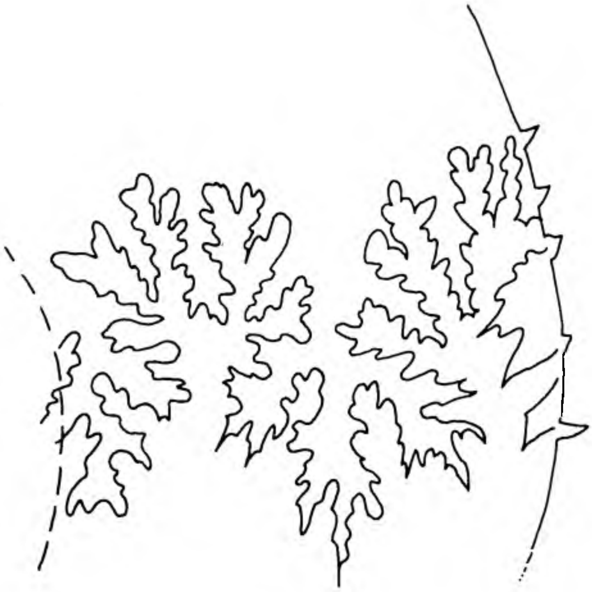


Fig. 48: *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955, suture line. RGM 542660, Wh 11 mm; ×6.

The tubercles are not always as prominent as on the well-preserved Muela specimen. On a few fragments from the Sierra de la Muela, lateral tubercles are absent or nearly absent. On the specimen depicted by Simionescu (1898, pl. 6, fig. 2), lateral tubercles are also absent on some main ribs.

Suture line: Only one suture line could be drawn, which show the saddles E/L and L/U with the lateral lobe in the middle with a narrow throat. The saddle L/U is higher than saddle E/L. The lateral lobe has long side arms which cause the saddles to be thin-necked. The saddles are asymmetrically divided into two parts by an incision. The external part of saddle E/L has three branches, whereas the internal part of this saddle and both parts of saddle L/U have four branches. The trifid umbilical lobe is shallower than the lateral lobe

Remarks: Busnardo (2003) proposed *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* to be the type species of the genus *Sornayites* Wiedmann, 1962, because the original type species *Emericiceras paronai* Sarkar, 1955 could not be retrieved. However, the differences between *P.* (*P.*) *simionescui* and *E. paronai* are so great that they could not be considered congeneric. It is against the rules (International Commission of Zoological Nomenclature, 1999) to use as type species of a genus a species that is not congeneric with the lost type species of the same genus.

The ornamentation of *P.* (*P.*) *simionescui* Sarkar and *P.* (*P.*) *picteti* Sarkar are very similar; the ribbing of *P.* (*P.*) *simionescui* is generally more irregular than in *P.* (*P.*) *picteti*. The main difference between *P.* (*P.*) *picteti* and *P.* (*P.*) *simionescui* is the degree of involution: *P.* (*P.*) *picteti* is rather involute, whereas in adult *P.* (*P.*) *simionescui* the whorls are just not in contact; the whorl height is growing faster in *P.* (*P.*) *picteti* than in *P.* (*P.*) *simionescui*. The whorl section of *P.* (*P.*) *picteti* is more elongate and subrectangular, and the flanks are flatter than the broad oval whorl section and rounded flanks of *P.* (*P.*) *simionescui*. In *P.* (*P.*) *picteti* the lateral tubercles disappear at a diameter of 130-140 mm, whereas those of *P.* (*P.*) *simionescui* persist up to the aperture.

Pseudothurmannia (*Pseudothurmannia*) *simionescui* differs from *P.* (*P.*) *arundicostata* sp. nov. in having 2-4 intermediate ribs between every two main ribs on the inner whorls instead of only two in *P.* (*P.*) *arundicostata*, and in having generally two, less frequently one or three, intermediate ribs to one main rib up to a diameter of 108 mm, instead of not more than 1-2 intermediate ribs between more closely spaced main ribs in *P.* (*P.*) *arundicostata*. *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* may have the same *crioceratites*-like ornamentation as in *P.* (*P.*) *arundicostata*, *P.* (*P.*) *crioceroides*, and *P.* (*P.*) *perevoluta*, that is, three or more long intermediate ribs between each pair of trituberculate main ribs.

Range: Catulloi Zone

Geographical distribution: Roumania (Dimboviciora), Bulgaria (Brestak), France (Angles, Chamaloc), Spain (Sierra de la Muela, north of Moratalla).

7.3.3. *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884
Figs. 49-50; Pls. XXX-XXXIV; Tab. XIII

* 1884. *Ammonites crioceroides* Torcapel.– Torcapel, p. 189, pl. 8, fig. 1.

1901. *Hoplites pseudo-Malbosi* nov. sp.– Sarasin & Schöndelmayer, p. 79, pl. 10, figs. 1, 2.

non 1949. *Pseudothurmannia pseudomalbosi* Sarasin & Schöndelmayer.– Luppov, p. 223, pl. 63, figs. 5-6 (= possibly deshayesitoideans with forking ribs).

non 1952. *Pseudothurmannia pseudo-malbosi* Sarasin & Schöndelmayer.– Luppov, p. 199, pl. 5, figs. 2-3 (= possibly deshayesitoideans with forking ribs).

1955 *Pseudothurmannia angulicostata* d'Orbigny var. *tuberculata*.– Sarkar, p. 155, pl. 6, fig. 13.

1957. *Pseudothurmannia angulicostata* d'Orbigny var.– Almela & De La Revilla, pl. 11, fig. 2, 2a, b.

non 1961. *Pseudothurmannia* cf. *pseudomalbosi* Sarasin & Schöndelmayer.– Eristavi, p. 98, pl. 5, fig. 1 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar].

non 1966. *Pseudothurmannia pseudomalbosi* (Sarasin & Schöndelmayer) .– Breskovsky, p. 80, pl. 2, fig. 4 (= *Binelliceras* sp.?).

non 1967. *Pseudothurmannia pseudomalbosi* Sarasin & Schöndelmayer.– Dimitrova, p. 72, pl. 31, fig. 3 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar].

1995b. *Pseudothurmannia simionescui* Sarkar.– Hoedemaeker, pl. 2, fig. 8.

pars 1995b. *Pseudothurmannia belimelensis* Dimitrova.– Hoedemaeker, pl. 2, fig. 9, *non* fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov. var. *gracilis* nov.].

1995. *Pseudothurmannia* cf. *pseudomalbosi* Sarasin & Schöndelmayer.– Avram, p. 119, pl. 8, fig. 3-4.

2003. *Parathurmannia pseudomalbosi* (Sarasin & Schöndelmayer).– Busnardo, p. 71, pl. 18, fig. 4.

non 2003. *Pseudothurmannia pseudomalbosi* (Sarasin & Schöndelmayer).– Company *et al.*, p. 691, fig. 6.5. [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

? 2005. *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar.– Kakabadze, p. 351, pl. 72, fig. 8 [may be *P.* (*P.*) *monasteriensis* (Simionescu)].

Holotype by monotypy: *Ammonites crioceroides* Torcapel, 1884, (pl. 8, fig. 1) from the Cruasien or Barutelien (= upper Hauterivian or lower Barremian), probably Catulloi Zone, of the Languedoc (near Beaucaires, Lussan or Nîmes, France) in the fossil collection of the Musée de Nîmes. Lectotype (designated by Busnardo, 1970) of a conspecific species: *Hoplites pseudo-Malbosi* Sarasin & Schöndelmayer, 1901 (pl. 10, fig. 1), deposited in the Muséum d'histoire naturelle de Genève, Collection Pictet, no. 17085, from a bed along the River Veveyse near Châtel-St.-Denis (Switzerland, Canton Fribourg).

Material: Fifty-two specimens: 36 specimens and whorl fragments from the *Pseudothurmannia* beds of Chamateuil (near Castellane, Alpes-de-Haute-Provence, France); 14 specimens and whorl fragments from the Río Argos (Caravaca, Murcia, Spain) all from section W and found loose between W35-W46 (in situ only in bed W38); two specimens from the Tornajo Mountain (Lorca, Murcia, Spain).

Fig. 49: *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884. RGM 387732, typical specimen, deformed, locality 7, *Pseudothurmannia* beds; 89%.

Description: The shell is very evolute, but the whorls are in touch with each other. The early whorls are overlapping and leave a rather small umbilicus free. From a diameter of about 74 mm, the umbilicus becomes wider than the whorl height. The whorl section is compressed oval and thickest at a quarter of the flank height; the flanks are curved and the costal section is hexagonal. The venter is narrow, arched, but slightly truncated. Ventrolateral shoulders are present, but not prominent. The umbilicus is rather shallow, the umbilical wall short and perpendicular, and the umbilical rim rounded. The dorsal side is concave and the dorsolateral sides slightly overhang the preceding whorl.

The ornamentation of the earliest whorl consists of equal, rather distant ribs; shorter ribs are intercalated from a diameter of 6 mm. From that diameter the ribbing consists of main and intermediate ribs. The main ribs have the same thickness as the intermediate ribs and distinguish themselves from the latter only in having weak umbilical bullae. From a diameter of 6 mm the main ribs become gradually more prominent than the intermediate ribs and the latter efface towards the umbilical rim. The distance between the main ribs becomes great, and the number of intermediate ribs between every two main ribs is 3-4.

At a diameter of 12 mm the main ribs are provided with prominent umbilical bullae, which develop into pointed tubercles at a diameter of about 50 mm. Below midflank the main ribs are slightly more prominent than above midflank. The ribs are strong, straight and only the upper part is slightly projected. The ribs are widely spaced. On the umbilical wall they are inclined backward. In most intervals the number of intermediate ribs has decreased to 2-3, rarely one or four. Generally, the anterior of the two intermediate ribs is short, originates close to the adjacent main rib as if it is forking from it (in a few occasions it really forks from it) and diverges from it in an upward direction; it may originate at three quarters of the flank height, at midflank or at the umbilical rim close to the umbilical bulla. The posterior intermediate rib is long, originates at the umbilical seam and runs parallel to the posteriorly adjacent main rib. This pattern implies that with every main rib the ribbing changes direction and resumes a radial direction. This pattern proceeds up to a diameter of 90 mm. There could be some irregularities in this pattern; for instance, there could be a third intermediate rib parallel with the posterior main rib, which may be long or short, or there could be only one intermediate rib, which converges to the anterior main rib. The ribs pass the venter with equal strength and with a slight forward curve. All the ribs have a tiny clavus at the ventrolateral shoulders, forming two ventrolateral rows of uniform clavi.

From a variable diameter of 50-80 mm, the main ribs become provided with lateral tubercles just above midflank, at first hardly visible, but gradually growing in strength, and becoming sharp and equal in strength to the umbilical tubercles. Up to a diameter of 90 mm (in two specimens 60 mm), all the ribs have the same thickness on the venter, but at larger diameters the main ribs become broader and higher than the intermediate ribs over their entire length and on the venter; their ventrolateral clavi are as long as the breadth of the ribs. All the ribs pass the venter with a forward curve. At the umbilical rim the main ribs are provided with pointed umbilical tubercles.

At a variable diameter of 60-90 mm the number of intermediate ribs increases again to 3-4, but may vary from one to five. All the intermediate ribs are long and originate at the umbilical rim or seam except the anteriormost intermediate rib, which is still the shortest and originates as if it is splitting off from the anteriorly adjacent main rib (the intermediate ribs of the supposed microconchs markedly vary in length and only one or two reach the umbilical rim). The main ribs are broad and rounded, and are provided with pointed umbilical tubercles; the intermediate ribs are thin and distantly spaced, the interspaces being wider than the ribs. All ribs are slightly curved forward and are slightly more prominent at the venter.

Until so far our description matches the lectotype of *P. pseudomalbosi*. However, the author collected several specimens from Chamateuil (near Castellane, Alpes-de-Haute-Provence, France) that are much larger than the lectotype of *P. pseudomalbosi*. The outer whorls of these specimens cannot be distinguished from the outer whorls of *P* (*P.*) *crioceroides*. They exhibit the same *crioceratites*-like ornamentation, the same whorl section, and the same measurements as the outer whorls of *P.* (*P.*) *crioceroides*. The author did not examine the holotype of *P.* (*P.*) *crioceroides*, but Torcapel (1884) explicitly described only the ornamentation of the outer whorl, which means that the inner whorls are not well preserved. There is no impediment to consider *P. pseudomalbosi* and *P.* (*P.*) *crioceroides* as conspecific.

From a diameter of about 100 mm all the intermediate ribs originate at the umbilical seam, just as the main ribs. The latter are radial, and stand out as strong straight ridges each with a prominent lateral tubercle just above midflank and a prominent umbilical tubercle. The ventrolateral tubercles are still visible.

From a diameter of 145 mm the number of intermediate ribs increases to six or seven and from a diameter of 220 mm decrease again to four. Above midflank the ribs curve a little forward. The ribs are prorsiradiate and slightly projected near the venter.

Probable microconchs: It is quite possible that the specimens from the Río Argos (Pl. XXX, figs. 1, 3-4, 6) could be microconchs of *P.* (*P.*) *crioceroides*, because (1) the ontogenetic stage with two, rarely one or three, intermediate ribs between each pair of main ribs is short and does not exceed diameter of c. 60 mm; (2) the ribbing with three or more intermediate ribs between each pair of main ribs begins earlier, viz. at a diameter c. 60 mm instead of 90 mm; and (3) at diameters larger than 60 mm most intermediate ribs originate on the flank, have a variable length, attenuate and become effaced toward the umbilical rim, are not parallel or may fork. The ribbing gives an irregular impression and may represent the variocostate ribbing of microconchs. The differences between the supposed micro- and macroconchs are consistent, but too small to warrant the introduction of separate species. The ornamentation of the inner whorls is quite similar and the main difference is the earlier appearance of certain adult characteristics. The microconchs are smaller and show more irregular ribbing in the adult growth stage. The supposed microconchs all occur in deep water environment, whereas all macroconchs occur in platform deposits. These are the only arguments to support the possibility of sexual dimorphism.

Fig. 50: A-B, *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884. A, medium large typical specimen, RGM 542333, locality 3T, bed 3; ×1. B, RGM 387737, whorl fragment of thick-ribbed specimen, locality 7; ×1.

Variability: There are some varieties of *P* (*P.*) *crioceroides* that look different at first sight, but that appear to differ only in one aspect, for instance, the strange, monotonous persistence of two intermediate ribs, rarely one or three, between each pair of main ribs from the earliest visible ribbing at diameter 32 mm up to diameter 88 mm (Fig. 50A); or the greater distance of the ribs, which gives the specimen a peculiar aspect; or the early appearance of strong trituberculate ribs from a diameter of c. 50 mm (RGM 387724, 387725, and 387746; Pl. XXXIII). The latter variety may be the younger whorls of *Pseudothurmannia* (*Pseudothurmannia*) *monasteriensis* Simionescu, 1899, but they differ from *P.* (*P.*) *monasteriensis* in the compressed whorl section and the truncated venter.

Remarks: The main difference between *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* and *P.* (*P.*) *arundicostata* is that in the latter the number of intermediate ribs to one main ribs remains two up to a diameter of 140-150 mm, and that only from this diameter the number of intermediate ribs becomes three or more. However, in *crioceroides* the number of intermediate ribs to one main rib becomes three or more from a diameter of 80-90 mm, and the interval with only two intermediate ribs to one main rib is short and normally not more than a quarter of a whorl except on the specimen on Fig. 50A, in which it is more than half a whorl.

Company *et al.* (2003) considered *Pseudothurmannia* (*Pseudothurmannia*) *pseudomalbosi* (Sarasin & Schöndelmayer, 1901) a senior synonym of *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955, but the inner whorls of the former species exhibit straight, distantly spaced, radial ribs, with a mainly 2-3 intermediate ribs between the main ribs, whereas the latter has thin, sigmoid, prorsiradiate ribs with 4-6 intermediate ribs between each pair of main ribs. *Pseudomalbosi* has a rather thick, oval whorl section, whereas *sarasini* has a higher and more compressed whorl section with flat flanks. The differences of the adult stages are more striking; the thick, straight, slightly projected ribs of *pseudomalbosi* are in strong contrast to the thin, attenuated ribs of *sarasini.*

Range: At least in the lower half of the Catulloi zone.

Geographical distribution: France (Chamateuil near Castellane, Languedoc), Spain (Río Argos, Tornajo Mountain), Switzerland (River Veveyse near Châtel-St-Denis).

7.3.4. *Pseudothurmannia* (*Pseudothurmannia*) *monasteriensis* Simionescu, 1899
Fig. 51; Tab. XIV

1895. *Hoplites monasteriensis*.– Kilian & Leenhardt, p. 975 (not described nor figured).

* 1899. *Hoplites monasteriensis* Kilian in coll.– Simionescu, p. 483, pl. 1, fig. 3.

Holotype by monotypy: *Hoplites monasteriensis* Simionescu, 1899, from the Hauterivian (probably Catulloi Zone) in the neighbourhood of Moustiers-Sainte-Marie (Alpes-de-Haute-Provence, France) deposited in the collection of the 'Faculté des Sciences' of the University of Grenoble (inaccessible at present).

Remarks: This species is discussed here only for completeness. There is only one photographic figure of *P.* (*P.*) *monasteriensis* reduced to half its natural size (Simionescu, 1899, pl. 1, fig. 3). The author magnified the photograph two times to its natural magnitude, so that he could better judge its real appearance. Looking at the description and figure, this species is close to *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884. It differs from the latter species only in its subrounded whorl section (ratio Wh /Wt of *P.* (*P.*) *monasteriensis* is 1.03, the ratio Wh/Wt of *P.* (*P.*) *crioceroides* is 1.21), in its thicker sturdier ribs and in the early appearance of strong trituberculate ribs from a diameter of c. 50 mm. At first the author considered *P.* (*P.*) *monasteriensis* a variation of *P.* (*P.*) *crioceroides*, but the rounded whorl section cannot be explained thus. More and well-preserved material is needed to decide whether *P.* (*P.*) *monasteriensis* is a separate species or a variety of *P.* (*P.*) *crioceroides*. In the *Pseudothurmannia* beds of Chamateuil the author collected a large, thick-ribbed variety of *P.* (*P.*) *crioceroides* (Pl. XXXIV), and three specimens (Pl. XXXIII) in which the main ribs become thick and trituberculate at a diameter of 50 mm exactly like the figure of the holotype of *P.* (*P.*) *monasteriensis*, but the whorl sections are compressed like *P.* (*P.*) *crioceroides* instead of rounded and show a truncated venter. These specimens are here provisionally regarded as varieties of *P.* (*P.*) *crioceroides*, in which thick trituberculated ribs appear earlier, but they may represent diagenetically compressed *P.* (*P.*) *monasteriensis*.

Pseudothurmannia (*Pseudothurmannia*) *monasteriensis* differs from *P.* (*P.*) *arundicostata* in having a rounded whorl section, and thicker and more distant ribs. Moreover, the ribbing of *P.* (*P.*) *arundicostata* is quite different, that is, straight main ribs with generally only 1-2 intermediate ribs on the inner whorls up to a diameter of 140 mm.

Range: Presumably Catulloi Zone.

Geographical distribution: Hitherto found only in southeastern France (Moustier-Ste-Marie, Alpes-de-Haute-Provence).

7.3.5. *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* sp. nov.
Figs. 52-53; Pl. XXXV; Tab. XV

pars 2003. *Pseudothurmannia picteti* Sarkar.– Company *et al.*, p. 691, only fig. 6.6, *non* fig. 6.7 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

Holotype: RGM 387730 (Pl. XXXV) from the *Pseudothurmannia* beds (Catulloi Zone) of Chamateuil

Fig. 51: Holotype of *Pseudothurmannia* (*Pseudothurmannia*) *monasteriensis* (Simionescu, 1899). Copy of the photography *in* Simionescu (1899) of the holotype from Moustier-Sainte-Marie; ×1.

near Castellane (Alpes-de-Haute-Provence, France). Paratype: RGM 387728 (Fig. 53) from the same beds and the same locality. Deposited in the Naturalis Biodiversity Centre, Leiden, The Netherlands.

Derivation of name: *Arundicostata* = latin for 'with cane-like ribs', because of the radial, long, straight, tapering, closely spaced, trituberculate ribs, which makes the impression of a dense bush of bamboo canes.

Material: Five specimens from Chamateuil near Castellane (Alpes-de-Haute-Provence, France) (RGM

387727, 387726, 387728, 387730, 387749) and one (RGM 542862) from section W of the Río Argos succession (Caravaca, Murcia, Spain).

Diagnosis. Large, slightly crioconic species of the subgenus *Pseudothurmannia* (*Pseudothurmannia*) with outer whorls like *P.* (*P.*) *crioceroides* (= with three or more long intermediate ribs to one trituberculate main rib), with inner whorls like *P.* (*P.*) *simionescui* (= with only one or two intermediate ribs between every two trituberculate main ribs) up to a diameter of 140 mm. The innermost whorls have main ribs with umbilical tubercles, but without lateral tubercles; the latter appear at a diameter of 58 mm. Every two main ribs are separated by two intermediate ribs, one short and one long. The inner whorls are touching each other. The whorls are more rounded and thicker than those of *crioceroides* and *simionescui*.

Description: The inner whorls of *P.* (*P.*) *arundicostata* are touching each other. The later whorls are just not in contact; it is difficult to find the point where the whorls become detached. The whorl section of the inner whorls is subrectangular with rather flat, but weakly rounded, flanks and a narrow, truncated, but slightly arched, venter with distinct shoulders; in the adult growth stage the whorl section is more oval with a narrow, arched venter, slightly rounded flanks and a broad, slightly concave dorsum. From a diameter of c. 85 mm the umbilicus becomes wider than the whorl height. The whorls rather slowly grow in height (wh:Wh = 5:7).

On the inner whorls, visible from a diameter of 25 mm, the main ribs are straight, their lower parts stronger and higher than the straight intermediate ribs, and their upper parts equally strong as the intermediate ribs. The main ribs are close together, slightly prorsiradiate and provided with rather sharp umbilical tubercles; each pair is separated by two intermediate ribs, of which the posterior one is long and the anterior one short. The long rib may reach the umbilical rim and runs parallel to the posterior main rib, the short one originates at two thirds or a half of the flank height close to the anterior main rib, as if splitting off from it. This pattern implies that with every main rib the ribbing changes direction and resumes a radial direction.

At a diameter of 58 mm the main ribs develop lateral tubercles just above midflank, at first hardly visible, but gradually growing in strength. This is the beginning of the characteristic ribbing with thick trituberculate main ribs and long thin, tapering intermediate ribs. The main ribs are still closely spaced. Approximately from this diameter the upper parts and ventral parts of the main ribs gradually become coarser than the intermediate ribs; the long intermediate rib reaches the mid-dorsal side. There may also be intervals with only one intermediate rib to one main rib. This single intermediate rib either seems to split off from the umbilical tubercle of the anteriorly adjacent main rib or originate from the mid-dorsal side. This type of ribbing, with one or two intermediate ribs parallel to the posterior main rib and making an angle with the anterior main rib, continues to a diameter of c.140 mm. Before this diameter is reached, the thick main ribs are closely spaced, radial, straight and have a rounded outline, whereas the thin, closely spaced, straight intermediate ribs are regularly tapering towards the umbilicus and rather sharp. The ribbing makes the impression of a dense bush of bamboo canes, the umbilical and lateral tubercles the impression of segmented bamboo. All ribs pass the venter in a straight line and are equally thick, but from a diameter of about 90 mm the main ribs on the venter gradually become thicker than the intermediate ribs.

From a diameter of about 140 mm, the number of intermediate ribs to one main rib increases to three; the anterior one is still the shortest, whereas the long ones reach the umbilical seam. On the arched venter all the ribs reach their greatest height and thickness, and markedly stand out with their anterior side being less steep than the

Fig. 52: A-C, *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* sp. nov., young specimens. A, RGM 542862, locality 1W, bed W35; ×1. B, RGM 387727, locality 7; ×1. C, RGM 387726, locality 7, oblique stand showing flank as well as venter; ×1.

Fig. 53: *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* sp. nov., paratype, RGM 387728, locality 7; ×1.

posterior side. The ventrolateral clavi on the intermediate ribs are small and may not be preserved; those on the main ribs are more stretched and may remain visible up to large diameters. The tapering shape and the sharpness of the intermediate ribs are conspicuous and gave the species its name. At a diameter of 205 mm, the anterior intermediate rib ceases to become shorter than the others and also reaches the umbilical seam. However, the space between the anterior intermediate rib and the main rib increases towards the venter; this space is rarely filled with a short rib. The maximum number of intermediate ribs between two main ribs may reach six. At a diameter of about 180 mm the straight ribs begin to curve slightly forward. The largest specimen collected from Chamateuil has a diameter of 320 mm and, at the latest ontogenetic stage visible, the number of intermediate ribs between each pair of main ribs is still three or four.

Remarks: The specimen that Company *et al.* (2003, fig. 6.6.) identified as *Pseudothurmannia picteti* should be included in *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata*, which is the only species that shows the combination of strong main ribs separated by one long and one short intermediate rib, and the presence of lateral tubercles in this early ontogenetic stage. A similar specimen is figured here on Fig. 52A. In *picteti*, the lateral knobs are far less prominent and do not start before a diameter of 65 mm.

Pseudothurmannia (*Pseudothurmannia*) *arundicostata* differs from *P.* (*P.*) *picteti* in being very evolute, in the sharpness of its ribs and tubercles, and in the general length of the intermediate ribs. *Pseudothurmannia* (*Pseudothurmannia*) *picteti* keeps a low number of one or two intermediates to one main rib up to the aperture (330 mm) and loses its lateral knobs at a diameter of 150 mm or earlier.

Pseudothurmannia (*Pseudothurmannia*) *arundicostata* shows the same ribbing as *P.* (*P.*) *crioceroides* at diameters larger than 140 mm and has the same measurements. *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* differs, however, from *P.* (*P.*) *crioceroides* in the persistence up to a diameter of 140 mm of a peculiar cane-like ribbing on the inner whorls consisting of closely spaced, straight, trituberculate main ribs separated by 1-2 long, tapering intermediate ribs. *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* also differs from *P.* (*P.*) *crioceroides* in the thicker whorl section and in the earlier appearance of lateral tubercles, viz. at a diameter of 58 mm instead of 80 mm.

Pseudothurmannia (*Pseudothurmannia*) *simionescui* also has many similarities with *P.* (*P.*) *arundicostata*, but, instead of 1-2 intermediate ribs to one main rib, *P.* (*P.*) *simionescui* has 1-3 intermediate ribs, and the distribution of the intervals with one, two or three intermediate ribs is irregular. In *simionescui* this type of ribbing continues up to a diameter of at least 180 mm instead of 140 mm.

Range: Catulloi Zone.

Geographical distribution: France (Chamateuil near Castellane, Alpes-de-Haute-Provence), Spain (Arroyo Gillico, Cehegín, Murcia; Río Argos, Caravaca, Murcia).

7.3.6. *Pseudothurmannia* (*Pseudothurmannia*) *perevoluta* sp. nov.
Figs. 54-55; Tab. XVI

1967. *Pseudothurmannia renevieri* (Sarasin & Schöndelmayer).– Dimitrova, p. 75, pl. 35, fig. 2.

? 1976. *Pseudothurmannia simionescui* Sarkar.– Mandov, p. 67, pl. 8, fig. 1.

Holotype: Specimen GIA J.9981, from the Hauterivian-Barremian boundary beds at the site called Escaramujo (01° 57' W. long., 38° 09' N. lat., a small mountain range directly west of the Buitre Mountain, Moratalla, Murcia, Spain); deposited in the Naturalis Biodiversity Center, Leiden, the Netherlands.

Derivation of name: *Perevoluta* (Latin) means very evolute.

Material: Two specimens: the holotype from Escaramujo and another, badly preserved whorl fragment from bed 2 (= Catulloi Zone) of the Chamateuil section near Castellane (Alpes-de-Haute-Provence, France).

Diagnosis: The shell is weakly crioconic. *Pseudothurmannia* (*Pseudothurmannia*) *perevoluta* is the only species in the subgenus that has such a large umbilicus at small diameters, for already at a diameter of 23 mm the umbilicus is equal to the whorl height. The whorls grow very slowly in height; this is the main characteristic of the species. The main ribs are provided with prominent umbilical tubercles and are provided with prominent lateral tubercles from a diameter of 37 mm. There are two rows of uniform clavi at both sides of the venter. The ribbing is fine, dense and slightly flexuous. The lower parts of the main ribs are more prominent than their upper parts. Every two main ribs are separated by three to five intermediate ribs of variable length, of which generally the one in the middle mimics a main rib. However, this mimicking rib lacks the umbilical tubercle and the prominence of its lower part. In the adult stage, exemplified by the specimen figured by Dimitrova (1967, pl. 35, fig. 2), it has a *crioceratites*-like ornamentation of trituberculate main ribs and 4-5 intermediate ribs to one main rib. The largest known *P.* (*P*) *perevoluta* has a diameter of 290 mm, but may reach a diameter of more than 300 mm.

Fig. 54: *Pseudothurmannia* (*Pseudothurmannia*) *perevoluta* sp. nov., holotype, GIA J9981, locality Escaramujo, a mountainous part just west of the Buitre Mountain, south of Moratalla (Prov, of Murcia, Spain); ×1.

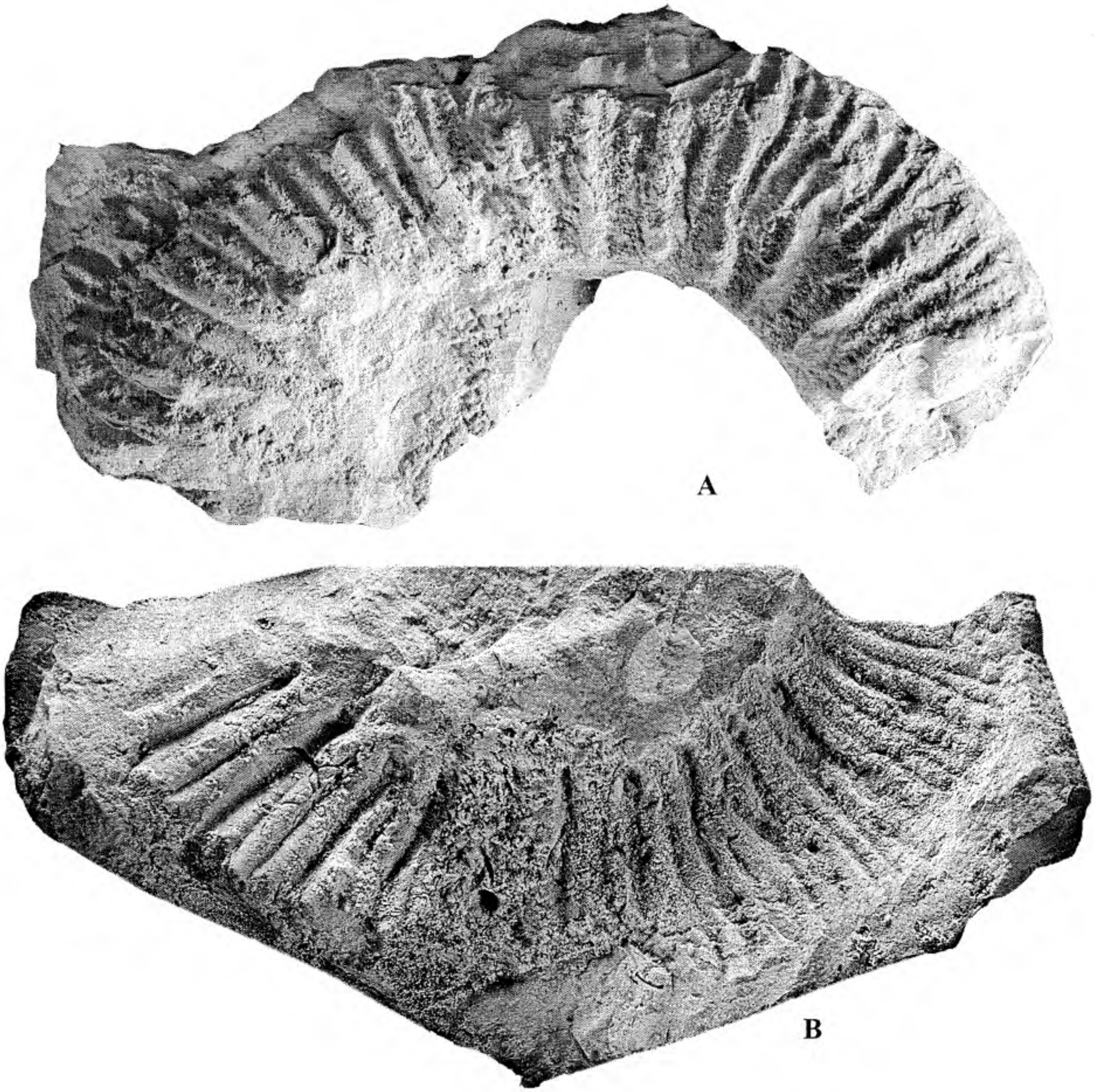


Fig. 55: A-B, *Pseudothurmannia* (*Pseudothurmannia*) *perevoluta* sp. nov. A, RGM 387747, badly preserved whorl fragment, locality 7; ×1. B, imprint of the sames specimen, shows the ribbing better; ×1.

Description: The shell is weakly crioconic. The distance between the whorls is 1 mm. The whorls grow very slowly in height (Wh:wh = 3:2) and have an oval whorl section with its maximum thickness at one third of the flank height; the flanks are slightly rounded and the venter is rounded. The umbilicus is very wide, and nearly one and a half times wider than the whorl height at a diameter of 75 mm. The umbilical width is equal to the whorl height at a diameter of 23 mm. The umbilical wall is vertical and the umbilical rim rounded. Only the innermost whorls are probably touching each other.

The ribbing, which is visible from a diameter of 12 mm, is fine and dense, and consists of main and intermediate ribs. The main ribs are provided with prominent umbilical tubercles. From this diameter the main ribs are separated by 3-4 intermediate ribs, which do not have umbilical tubercles and weaken near the umbilical rim. All ribs have the same strength higher on the flanks and on the venter.

From a diameter of 29 mm the distance between the main ribs diminishes; they are separated only by one or two intermediate ribs. This interval with closely spaced main ribs extends over one quarter of a whorl.

The type of ribbing that continues at least up to a diameter of 75 mm begins at a diameter of 33 mm. From this diameter the main ribs are flexuous, rather widely spaced and separated by 3-5 intermediate ribs. The main ribs are provided with pointed umbilical tubercles, and their lower parts are higher and thicker than their upper parts. The transition of the lower and upper part is abrupt. The flexuous intermediate ribs vary in length and originate either at the umbilical rim or higher on the flank; some are very short and originate at the upper quarter of the flank. Many of the intermediate ribs seem to split from the neighbouring rib, but at closer inspection it appears that they are merely converging. In many intervals between two main ribs there is one intermediate rib, rarely two, that originate low on the umbilical wall. These mimic the main ribs, but lack umbilical tubercles and also the prominence of their lower parts. These pseudo-main ribs and the variable lengths of the intermediate ribs give the ribbing an irregular appearance.

All main ribs are adorned with lateral tubercles from a diameter of 53 mm, but on the imprint the main ribs already show faint lateral thickenings from a diameter of 37 mm. The latter are interpreted as pimples on the outside of the shell without markings on the steinkern. All ribs have small ventrolateral clavi of equal size; these uniform clavi form two rows at both sides of the rounded venter. On the venter all ribs are equally strong and pass the venter with a forward curve.

The badly preserved whorl fragment from Chamateuil (Fig. 55A-B) represents a later growth stage. It shows the same unique slow increment in whorl height and a similar ornamentation as just described, viz. closely spaced main ribs with two or three intermediate ribs of which at least one reaches the dorsal side, one reaches down to one third flank height and one is very short. The main ribs are trituberculate and their lower parts are the most prominent. All ribs cross the venter almost in a straight line. Ventrolateral clavi cannot be observed.

The only *Pseudothurmannia* with a similar large umbilicus, a similar unique slow increment in whorl height, and a similar ribbing and tuberculation on its penultimate whorl as the Chamateuil specimen, is the large specimen figured by Dimitrova (1967) under the name *Pseudothurmannia renevieri*. The ribbing of the inner whorls of Dimitrova's specimen is badly preserved, but fine and dense. The similarities with the *P.* (*P.*) *perevoluta* are so great that the author cannot find any impediment to include this specimen in *P.* (*P.*) *perevoluta*. The last half a whorl of this specimen has, like *P.* (*P.*) *arundicostata*, 4-5, rarely three, long, radial, straight intermediate ribs to one main rib; only a few ribs are short. It has umbilical and lateral tubercles on the main ribs, and small clavi on all ribs.

Range: Catulloi Zone.

Geographical distribution: Spain (Escaramujo: mountain range south-west of the Buitre Mountain south-west of Moratalla, Murcia), France (Chamateuil near Castellane, Alpes-de-Haute-Provence), Bulgaria (Beli Mel; Odrintsi, Varnensko).

8. Genus *Crioceratites* Léveillé, 1837

8.1. Subgenus *Crioceratites* (*Balearites*) Sarkar, 1954

Type species: *Crioceras baleare* Nolan, 1894, by original designation (Sarkar, 1954).

Diagnosis: *Crioceratites* with their whorls in contact and with fine dense ribbing. Widely spaced thick ribs along constrictions provided with umbilical and ventrolateral tubercles appear only in the adult growth stage. Two rows of very fine, uniform ventrolateral tubercles are present on the inner whorls adapical of the first thick rib along a constriction; fibulation is absent. Umbilical bullae absent or present. Innermost whorls provided with trituberculate ribs up to a diameter of 7-11 mm; umbilicus perforated.

8.1.1. *Crioceratites* (*Balearites*) *balearis* Nolan, 1894

Figs. 56-57; Tab. XVII

1861. *Ancyloceras hillsi* d'Orbigny (= error, Sowerby was meant).– Ooster, p. 62, pl. 52, only fig. 1.

* 1894. *Crioceras baleare* n. sp.– Nolan, p. 193, pl. 10, fig. 2a-b.

1901. *Hoplites balearis* Nolan.– Sarasin & Schöndelmayer, p. 87, pl. 10, fig. 4.

non 1948. *Crioceras* ex gr. *balearis* Nolan.– Slavin, p. 72, fig. 1 (= *Lytoceras* sp.).

1954. *Crioceras baleare* Nolan.– Sarkar, p. 97.

pars 1955. *Crioceras binelli* Astier.– Sarkar, p. 57, pl. 2, only fig. 6 (var. *shankariae*), *non* fig. 5 [= *Crioceratites* (*Binelliceras*) *binelli* Astier, 1851, lectotype].

non 1955. *Balearites* cf. *balearis* Nolan sp. (forme no 1).– Sarkar, p. 142, pl. 6, fig. 14 (= *Crioceratites loryi?* Sarkar, 1955).

non 1955. *Balearites* cf. *balearis* Nolan sp. (forme no 2).– Sarkar, p. 143, pl. 11, fig. 2, [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

non 1955. *Balearites* cf. *balearis* Nolan sp. (forme no 3).– Sarkar, p. 144, pl. 10, fig. 12 (= *Crioceratites* indet.).

1955. *Balearites shankariae* n. sp.– Sarkar, p. 146, pl. 11, fig. 12.

1955. *Balearites* sp., forme incertae sedis.– Sarkar, p. 147, pl. 6, fig. 10.

1957. *Balearites balearensis* (*sic*) (Nolan).– Arkell *et al.*, p. L208, fig. 238, 1a-b (holotype).

1958. *Balearites balearis* (Nolan).– Luppov & Drushchits, p. 102, pl. 46, fig. 8a-b.

pars? 1960. *Crioceratites honnoratii* Léveillé.– Drushchits & Kudrjavtsev, p. 289, pl. 31, fig. 3?, *non* fig. 2 [= *Crioceratites* (*Binelliceras*) *binelli* Astier, 1851].

non 1960. *Balearites balearis* (Nolan).– Drushchits & Kudrjavtsev, p. 291, pl. 33, figs. 2-3 [renamed in *Pseudothurmannia* (*Pseudothurmannia*) *crimensis* (Wiedmann, 1962) (= probably *Eleniceras* sp.)].

1962. *Crioceratites* (*Pseudothurmannia*) *balearis balearis* (Nolan).– Wiedmann, p. 128, pl. 8, fig. 5, pl. 9, fig. 1.

non 1964. *Balearites balearis* (Nolan).– Fülöp, pl. 27, fig. 7 [= *Crioceratites* (*Binelliceras*) *binelli*? Astier, 1851].

pars 1965a. *Crioceratites* (*Crioceratites*) *binelli* (Astier) échantillon 1.– Thomel, p. 28, pl. 3, fig. 3 (= variety *shankariae*), *non* fig. 2 [échantillon 3 = *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.].

non 1967. *Balearites shankariae* Sarkar.– Dimitrova, p. 76, pl. 36, fig. 2.

non 1967. cfr. *Crioceratites* (*Pseudothurmannia*) *balearis* Nolan.– Baccelle & Lucchi Garavello, p. 138, pl. 3, fig. 3 [= *Avramidiscus hugii* (Ooster, 1861)].

1979b. *Crioceratites* (*Crioceratites*) ex gr. *balearis* (Nolan).– Immel, p. 46, pl. 2, fig. 2.

? 1981. *Crioceratites* (*Pseudothurmannia*) *balearis* (Nolan).– Nagy, p. 73, pl. 1, fig. 5.

non 1981. *Pseudothurmannia* (*Balearites*) *balearis* (Nolan).– Kakabadze, p. 91, pl. 19, figs. 3-5 [= *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.]

non 1989. *Pseudothurmannia shankariae* Sarkar.– Vašíček, p. 118, pl. 1, fig. 5 [= *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.].

non 1993. *Balearites balearis* (Nolan).– Autran, pl. 13, fig. 4 [= *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.]

pars 1994. *Pseudothurmannia balearis* (Nolan).– Vašíček *et al.*, p. 66, pl. 19, fig. 3, *non* fig. 4 [= *Crioceratites* (*Balearites*) *oicasensis* sp. nov.].

non 1994. *Pseudothurmannia shankariae* (Sarkar).– Vašíček *et al.*, p. 66, pl. 19, fig. 5. [= *Crioceratites* (*Balearites*) sp. indet.].

1995. *Pseudothurmannia balearis* (Nolan).– Vašíček, p. 174, pl. 3, fig. 3.

non 1995. *Pseudothurmannia* (*Pseudothurmannia*) *shankariae* (Sarkar).– Vašíček, pl. 4, fig. 1 [= *Crioceratites* (*Balearites*) sp. indet.].

non 1995. *Pseudothurmannia* (*Balearites*) *balearis* (Nolan).– Vašíček, p.174, pl. 4, fig. 5 [= *Crioceratites* (*Balearites*) *oicasensis* sp. nov.].

? 1995. *Crioceratites balearis* (Nolan).– Avram, pl. 6, fig. 4.

1995b. *Pseudothurmannia* (*Balearites*) *shankariae* (Sarkar).– Hoedemaeker, p. 231, pl. 3, figs. 1, 3 (= typical variety), and 2 (= var. *shankariae*).

1996. *Pseudothurmannia baleare* (Nolan).– Wright, p. 214, fig. 163, 4c, d. (holotype)

1997. *Pseudothurmannia balearis* (Nolan).– Vašíček, p. 237, pl. 2, fig. 2.

2002. *Balearites balearis* (Nolan).– Vermeulen *et al.*, pl. 1, fig. 3 (holotype).

pars 2003. *Crioceratites balearis* (Nolan).– Company *et al.*, p. 689, fig. 5.3. (= var. *shankariae*), *non* figs. 5.1. [= *Crioceratites* (*Balearites*) *oicasensis* sp. nov.], *non* fig. 5.2. (= inner whorls of *Crioceratites binelli* Astier, 1851?).

non 2004. *Pseudothurmannia* (*Balearites*) *balearis* (Pictet & De Loriol).– Kakabadze, p. 387, pl. 2 fig. 5 [= inner whorls of *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

non 2004. *Pseudothurmannia* (*Balearites*) cf. *balearis* (Pictet & De Loriol).– Kakabadze, p. 387, pl. 2 figs. 4, 6 [= probably inner whorls of *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)].

non 2005. *Pseudothurmannia* (*Balearites*) *balearis* (Nolan).– Kakabadze, p. 351, pl. 72, fig. 2 [= inner whorls of *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

Holotype by monotypy: The specimen from Mallorca figured by Nolan (1894, pl. 10, fig. 2a-b), deposited in the Geological Institute Dolomieu in Grenoble (inaccessible at present), no. ID 131. Plaster cast (M 110) refigured by Vermeulen *et al.* (2002, pl. 1, fig. 3). At this moment the holotype appears to be mislaid (Jean Vermeulen, pers. comm., 2005). It should be noted that the holotype has a diameter of c. 40 mm and that Nolan's figure of the holotype is 1.6 times enlarged. The holotype of *Balearites shankariae* Sarkar is the specimen depicted by Sarkar (1955, pl. 11, fig. 12), deposited in the 'Laboratoire de Géologie' of the Université de Sorbonne, Paris. *B. shankariae* is herein considered a variety of *C.* (*B.*) *balearis*.

Material: Twenty imperfectly preserved specimens; four specimens from the section along the road to Angles (Alpes-de-Haute-Provence, France) (Klein Collection); 16 specimens from beds D124-D133 and W16-W27 along the Río Argos.

Description: Described here is the whorl fragment of a young specimen of 40 mm diameter from the Angles section, which is morphologically closest to the holotype (RGM 542276, Coll. Klein, Fig. 56C-E). This specimen is compressed and has parallel, slightly curved flanks; the whorl section is high rectangular; the umbilical rim is rounded and smooth, except for a few weak ribs reaching the umbilical seam; the umbilical wall is steep. The ventral side is rounded, but shows two indistinct shoulders. The umbilicus is slightly narrower than, or equal to, the whorl height. The growth in height over half a whorl is 2:3. The innermost whorls are not present. At a diameter of 50 mm the umbilical width equals the whorl height.

The ornamentation consists of fine, dense, uniform, prorsiradiate, straight to slightly flexuous ribs, which originate at the umbilical rim and pass over the rounded venter. The ribs become thinner towards the umbilicus. Some ribs split off from the neighbouring one, whereas some others are intercalated and originate somewhat higher on the flank. The first thick rib bordered by a constriction, characteristic for the subgenus *Balearites*, occurs at a diameter of 40 mm. These prominent thick ribs are slightly flexuous, and provided with umbilical bullae and ventrolateral tubercles. Directly adapical of this constriction, a few ribs originate at the umbilical seam instead of at the umbilical rim. Two weak umbilical bullae occur before the first thick rib/constriction pair. In earlier growth stages, the ribs crossing the venter are weakened at mid-venter, which leaves a practically smooth midventral band; ribs do not lose their strength when crossing the venter in more adult growth stages. The venter clearly shows two rows of tiny uniform tubercles, one on every rib, on the ventrolateral shoulders up to a diameter of 30 mm. Perhaps because of their

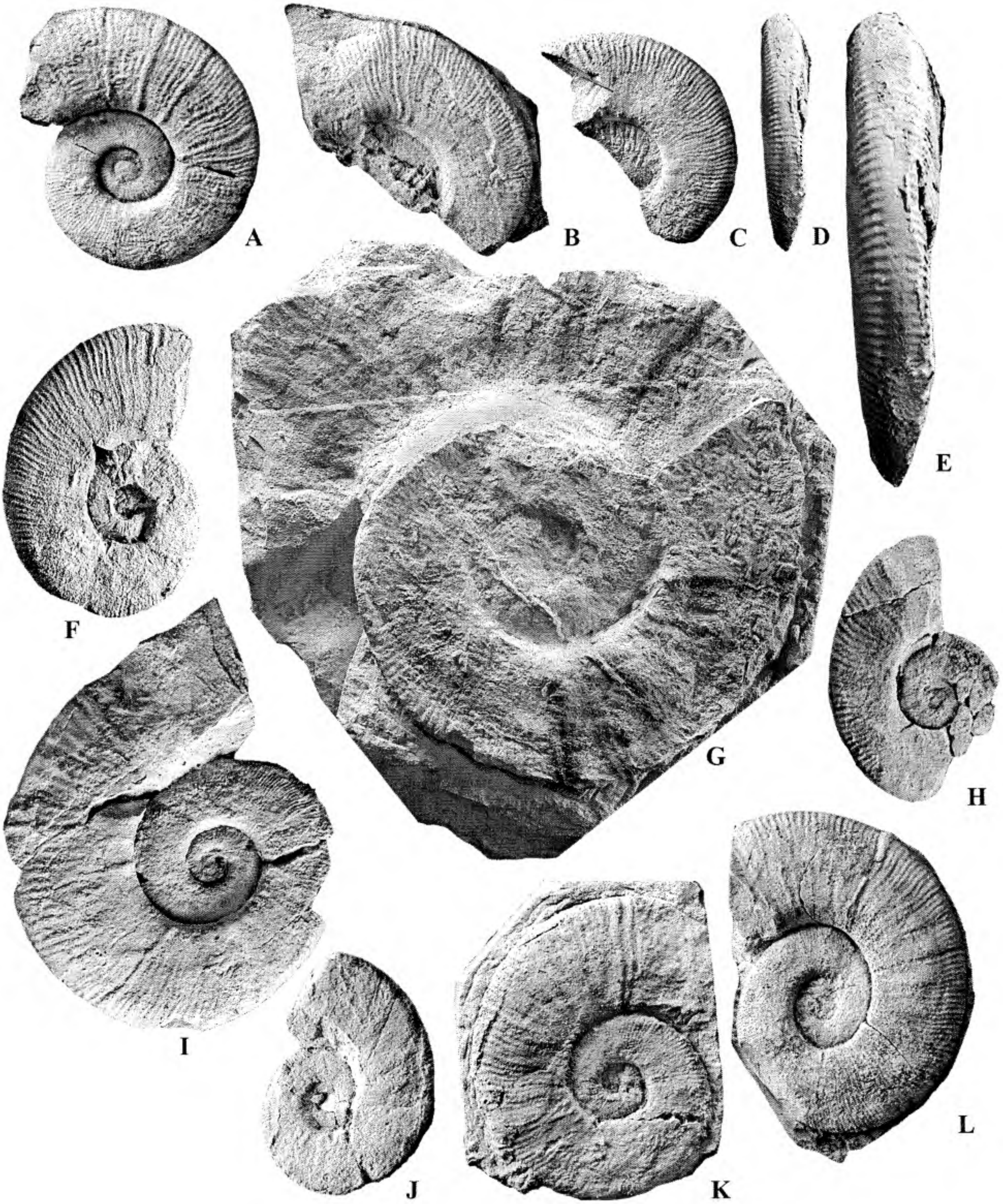


Fig. 56: A-L, *Crioceratites* (*Balearites*) *balearis* Nolan, 1894. A, RGM 542275, variety *shankariae* locality 5; ×1. B, RGM 542276B, specimen closely resembling the holotype with faint ventrolateral rows of small uniform tubercles, locality 5; ×1. C, RGM 542276A, specimen closely resembling the holotype with clear ventrolateral rows of small uniform tubercles, lateral view; ×1. D, same specimen, ventral view; ×1. E, same specimen, ventral view; ×2. F, RGM 542118, variety *shankariae*, locality 1W, bed W20; ×1. G, RGM 542120, variety *shankariae*, locality 1W, bed W27; ×1. H, RGM 387910, resembling the specimen figured by Wiedmann, 1962, pl. 8, fig. 5, locality 1W, bed W20; ×1. I, RGM 542121, possible adult specimen, locality 1D, bed D131; ×1. J, RGM 387956, typical specimen with small ventrolateral tubercles at the beginning of the last whorl, locality 1W, bed W18; ×1. K, RGM 387887, variety *shankariae*, locality 1F, loose from beds F127-158; ×1. L, RGM 542277, resembling the specimen figured by Wiedmann, 1962, pl. 8, fig. 5, locality 5; ×1.

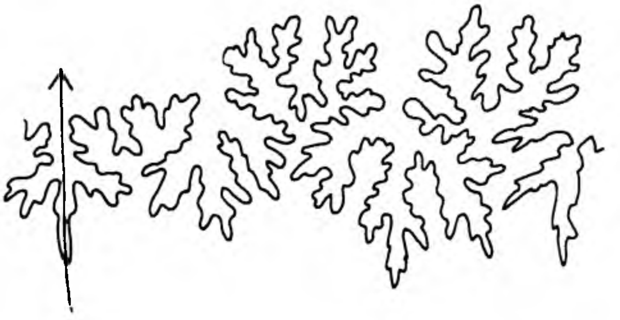


Fig. 57: *Crioceratites* (*Balearites*) *balearis* Nolan, 1894, suture line. RGM 542117, Wh 8.7 mm; ×6.

smallness, they have not been mentioned from the holotype. Fibulation does not occur. The inner whorls are not uncovered.

Ventrolateral tubercles have been described from only one other specimen figured by Sarkar (1955, pl. 6, fig. 10). Because of their presence, Sarkar identified this specimen as *Balearites* sp. (forme *incertae sedis*), as the holotype of *C.* (*B.*) *balearis* was described by Nolan as totally non-tuberculate. The author identified Sarkar's specimen as *Crioceratites* (*Balearites*) *balearis*, mainly because of the fineness of the ribs, the similarity of the measurements and the near absence of umbilical bullae.

Suture line: A limonitic young specimen from the Río Argos succession exhibits a complete suture line that shows all characteristics of the suture of *Crioceratites* (Fig. 57); it has four trifid lobes. The lateral lobe is the deepest and has a narrow throat. The saddle U/L is the highest, saddle I/U the shortest. The ventral saddle is high and narrow. All saddles are divided into two parts by deep incisions. The external part of saddle E/L has three branches, the internal part four; both parts of saddle L/U have three branches. The external part of saddle U/I has two branches and the internal part consists of one branch.

Variety *shankariae*: The shape and ornamentation of *Balearites shankariae* Sarkar, 1955, and *C.* (*B.*) *balearis* are quite similar. However, the holotype of *B. shankariae* is supposed to differ from the holotype of *C.* (*B.*) *balearis* in the presence of ventrolateral rows of fine uniform tubercles on the inner whorls visible up to a diameter of about 30 mm (without fibulation) and in the presence of regularly and widely spaced umbilical bullae separated by 5-7 non-bullate ribs (Figs. 56A, F, K, I). According to Nolan (1894) *C.* (*B.*) *balearis* would totally lack tubercles.

However, all the specimens of the *balearis/shankariae* group studied by the author, exhibit one or a few small weak umbilical bullae on the smooth umbilical rim adapical of the first thick rib/constriction pair. Besides, most specimens of *C.* (*B.*) *balearis* figured in literature also show one or a few weak, irregularly spaced umbilical bullae at diameters smaller than the first thick rib. As for the number of umbilical bullae that are present adapically of the thick ribs, all transitions exist from one bulla to several weak umbilical bullae. It would be plausible to identify all these specimens as *B. shankariae* as the author did earlier (Hoedemaeker, 1995b), but it would equally be possible to identify those specimens with a smooth umbilical rim with only one or a few weak, irregularly spaced umbilical bullae as *C.* (*B.*) *balearis*, and those with a larger number of regularly and widely spaced bullae as *B. shankariae*.

In the seven young specimens that show a partially well-preserved venter, two ventrolateral rows of weak, uniform tubercles are visible up to c. 30 mm diameter. The ventrolateral tubercles are rounded and probably the bases of small spines that wear off easily; fibulation has not been determined. These ventrolateral tubercles were found on specimens having a smooth umbilical rim with only one or two weak umbilical bulla as well as on specimens with several umbilical bullae. So, they are present, irrespective of the number of umbilical bullae preserved. Hoedemaeker (1995b) identified all these specimens as *P.* (*B.*) *shankariae*, but it is quite possible that the holotype of *C.* (*B.*) *balearis* also have such rows of ventrolateral tubercles, which have escaped the attention of Nolan because of their weakness or defective preservation. Unfortunately, the venter of the recently re-figured plaster cast of the holotype of *C.* (*B.*) *balearis* (Vermeulen *et al.*, 2002) has not been studied and may not show the small tubercles clearly.

The four specimens from the Río Argos succession that expose parts of the innermost whorls, show lateral tubercles on every rib up to a diameter of 7 mm. At least one of these specimens also has several regularly spaced umbilical bullae and ventrolateral tubercles, which means that at least *B. shankariae*, has lateral tubercles on the ribs of the innermost whorls [Thomel, 1965a, pl. 3, fig. 3, described lateral tubercles from the specimen of *B. shankariae* that he figured under the name *Crioceratites* (*Crioceratites*) *binelli* échantillon 1]. As *Crioceratites* (*Balearites*) *theodomirensis*, which has the closest affinities to *C.* (*B.*) *balearis*, also exhibits lateral tubercles on the innermost whorls, it is plausible to presume that *C.* (*B.*) *balearis* also has lateral tubercles on the innermost whorls, but, as these whorls are not preserved on the holotype, this cannot be confirmed. Therefore, and because none of the specimens are totally devoid of tubercles, *balearis* could be discarded as a *nomen dubium*, and all specimens from the Río Argos succession and from the Angles section named as *Balearites shankariae* Sarkar, 1955, as the author did earlier (Hoedemaeker, 1995b).

However, the author does not want to discard *C.* (*B.*) *balearis* as a *nomen dubium* merely because the inner whorls are not preserved, for in that case more holotypes of the species of *Pseudothurmannia* and *Binelliceras* should be discarded. Besides, both *C.* (*B.*) *balearis* (with one or a few weak irregularly spaced umbilical bullae) and *B. shankariae* (with several regularly spaced umbilical bullae) have the same fine, slightly flexuous, uniform ribbing up to the aperture; the same distantly spaced thick ribs alongside constrictions in the adult stage; a similar shape and measurements; a similar stratigraphic range; two ventrolateral rows of fine uniform tubercles on the inner whorls; a few irregularly spaced to several regularly spaced umbilical bullae; and presumably lateral tubercles on the innermost whorl.

In conclusion, the species *C.* (*B.*) *balearis* and *B. shankariae* resemble each other so strongly that for the present the author considers them to be the end members of a continuous variability series of *Crioceratites* (*Balearites*) *balearis* Nolan, 1894 (see also Hoedemaeker, 1995b); they vary only in the number of umbilical bullae. However, more and better preserved material should confirm this opinion.

Other variabilities within *C.* (*B.*) *balearis*: The diameter at which the thick constriction-lined ribs appear is variable. On the holotype and two specimens before the author, this diameter is about 35 mm. However, on other specimens, for instance those figured by Wiedmann (1962) and Immel (1979b), only weak, hardly discernible, irregularly spaced main ribs appear at this diameter, whereas the thick constriction-lined main ribs appear at much greater diameters, and are more widely and more irregularly spaced than on the holotype (Figs. 56F, 56L).

Adult *C.* (*B.*) *balearis*? The author interpreted the large (101 mm diameter) specimen from bed D132 (Fig. 56H) as representing the adult of *C.* (*B.*) *balearis*. It is badly preserved and heavily compressed. It shows eleven thick ribs alongside constrictions at irregular distances. Some of the thick ribs are provided with prominent umbilical tubercles. It has the same proportional relations as *C.* (*B.*) *balearis* and the same fine ribbing. *C.* (*B.*) *balearis* is only known as young immature specimens.

Remarks: *Crioceratites* (*Balearites*) *crimensis* Wiedmann, 1962 (= nov nom. for *Balearites balearis* Drushchits & Kudrjavtsev, 1960, *non* Nolan) is probably a species of the genus *Eleniceras* because of the presence of thick trituberculate ribs in the adult, at first with about five intermediate ribs, which become effaced on the last whorl. The inner whorls have many, close-spaced main and intermediate ribs. The main ribs are provided with umbilical bullae. The inner whorls are overlapping and rather involute. Also *Balearites tauricus* Drushchits & Kudrjavtsev, 1960 (pl. 33, fig. 1), *non* Eichwald, 1868, has rightly been synonymized by Breskovsky (1967) with *Eleniceras tcheshitevi* Breskovsky and has nothing to do with *Balearites*.

Crioceratites (*Binelliceras*) *binelli* Astier, 1851, is morphologically close to *C.* (*Balearites*) *balearis*, but differs from it in its whorls not being in contact, in the presence of trituberculate main ribs up to a diameter of 15 mm and in the main ribs of the inner whorls being provided with small, but prominent, umbilical bullae.

Crioceratites (*Binelliceras*) *oicasensis* differs from the presumed adult *C.* (*B.*) *balearis* by the main ribs starting earlier and being more closely and more regularly spaced. The specimen described and figured by Dimitrova (1967) as *Balearites shankariae* is too small to be identified properly. Besides, it shows some coarser ribs near the aperture, which are not present at this diameter in the variety *shankariae*.

Pseudothurmannia (*Pseudothurmannia*) *shankariae* Vašíček, 1995, *non* Sarkar, 1955, exhibits a ribbing showing close-spaced, fine main ribs separated by one or two equally fine intermediate ribs, which originate at midflank. This kind of ribbing is not present in the variety *shankariae*. Vašíček's specimen is identical to the inner whorls of *Pseudothurmanni* (*Kakabadziella*) *ohmi ohmi* Winkler.

Range: Restricted to the lower part of the Balearis Zone. Occurring in beds D124-D133 and W16-W27.

Geographical distribution: Spain (Majorca, Caravaca, La Guardia), Switzerland (Châtel St.-Denis, Veveyse), France (La Motte-Chalençon, Angles, La Charce, Barrême, Alpes-de-Haute-Provence, Hautes-Alpes), Roumania (Vodiniciki valley) and Slovakia (Polomec Quarry).

8.1.2. *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.
Fig. 58; Pl. XXXVI; Tab. XVIII

1955. *Balearites* sp. (nov. sp.?).– Sarkar, p. 148, pl. 11, fig. 10.

pars 1964. *Balearites* sp.– Fülöp, pl. 16, fig. 6, *non* pl. 9, fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.)].

pars 1965a. *Crioceratites* (*Crioceratites*) *binelli* (Astier).– Thomel, p. 28, pl. 3, fig. 2, *non* fig. 3 [= *Crioceratites* (*Balearites*) *balearis* var. *shankariae* Sarkar, 1955].

1981. *Pseudothurmannia* (*Balearites*) *balearis* (Nolan).– Kakabadze, p. 91, pl. 19, figs. 3-5.

1982. *Crioceratites* (*Crioceratites*) *binelli* (Astier).– Braga *et al.*, p. 684, pl. 1, fig. 2.

1989. *Pseudothurmannia mortilleti* (Pictet & Loriol).– Michalík & Vašíček, p. 518, pl. 2, fig. 5.

1993. *Balearites balearis* (Nolan).– Autran, pl. 13, fig. 4.

1995. *Pseudothurmannia* (*Pseudothurmannia*) *mortilleti* (Pictet & De Loriol).– Vašíček, pl. 4, fig. 6.

1995b. *Pseudothurmannia* (*Balearites*) *"binelli"* Thomel, *non* Astier.– Hoedemaeker, p. 232, pl. 3, figs. 5-9.

1996. *Crioceratites* (*Crioceratites*) *binelli* Astier.– Wright, p. 211, fig. 164, 5e.

1997. *Pseudothurmannia mortilleti* (Pictet & De Loriol).– Vašíček, p. 237, pl. 2, fig. 3.

pars 2003. *Crioceratites krenkeli* Sarkar.– Company *et al.*, p. 688, fig. 5.6., *non* figs. 5.7., 5.8. [= both *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

Syntypes: Three syntypes (Pl. XXXVI, figs. 1-3): RGM 387919 is from one of the beds W20-W26 (best preserved specimen) from section W; RGM 387930 is from bed W26 (specimen showing adult features) also from section W; and RGM 542088 from bed A142D (specimen with suture line) from section A.

Derivation of name: *Theodomira* is the name of the ancient Greek settlement at the site where is now the town Caravaca (Province of Murcia, Spain).

Loci typici: Section W of the Río Argos succession, 250 m west of Casa de Alguacil (the site is now changed into a fruit orchard), and Section A along the Rio Argos, 100 m south of the Molina de Las Oicas de Abajo (now Hospederia "El Molino del Río Argos"). Sections A and W are seven km apart.

Material: Forty-two specimens in total. Thirty specimens from section W, where they occur *in situ* in beds W24-W32. Only seven specimens were collected in parallel sections A, C, D and K, from beds D142-153. Four specimens were collected in the *Pseudothurmannia* beds of the Tornajo Mountain (north of Lorca, Murcia, Spain). One specimen is from the section along the road to Angles (St. André-les-Alpes, Alpes-de-Haut-Provence, France).

Diagnosis: *Crioceratites* (*Balearites*) with many distinct and prominent umbilical bullae, and with fine, only slightly flexuous ribs. The innermost whorls adorned with lateral tubercles. The ribs are less uniform than in *C.* (*B.*) *balearis* and show a weak, but distinct, differentiation in main and intermediate ribs. The main ribs, which are provided with umbilical bullae, are separated by 2-5 intermediate ribs. Small, uniform ventrolateral tubercles are visible up to the aperture. Fibulation is not observed. In the adult the main ribs are thick, widely separated and lined by constrictions; there are commonly 5-7 intermediate ribs to one main rib.

Description: The first whorl forms an open spire, leaving a hole in the centre. All prorsiradiate ribs are provided with lateral and ventrolateral tubercles up to a diameter of seven mm, at first without, but later accompanied by umbilical bullae. From a diameter of seven mm all ribs are fine, slightly flexuous and of equal strength, each with a fine, sharp ventrolateral tubercle. Fibulation is absent. The ribs do not cross the venter, which remains smooth up to a diameter of 30 mm. The ribs with prominent umbilical bullae are the main ribs between every two of which 2-5 long intermediate ribs are inserted. From the umbilical bullae bundles of two or three ribs may originate.

The umbilicus is smaller than the whorl height. At a diameter of c. 36 mm the phragmocone ends. From this point the umbilical seam starts to egress and the whorl thickness increases more than its height. From this point the main ribs rapidly increase in thickness and the spaces between them increase considerably; they are separated by 5-7 intermediate ribs, rarely 1-3. The thick ribs are accompanied by constrictions, which are commonly on their adoral side. In this part the intermediate ribs are irregular in length and some may begin above the middle of the flanks. The thick ribs are provided with prominent ventrolateral tubercles and prominent umbilical bullae; they cross the venter without loosing in strength.

At a diameter of 50 mm the umbilical width equals the whorl height. The specimens of *C.* (*B.*) *theodomirensis* may reach a diameter of 60-65 mm. All whorls are just touching each other.

Suture line: The suture line (Fig. 58) is very similar to that of *C.* (*B.*) *balearis* and exhibits the characteristic four lobes of the suture of *Crioceratites*. It has a trifid lateral and umbilical lobe; the internal lobe was not visible. The lateral lobe is the deepest and has a narrow throat. The Umbilical lobe is more slender and deeper than the umbilical lobe of *C.* (*B.*) *balearis*. Saddle U/L is the highest, saddle I/U the shortest. The ventral saddle is high and narrow.

Remarks: The presence of constriction-lined thick ribs is a diagnostic feature of adult *Crioceratites* (*Balearites*) and therefore *C.* (*B.*) *theodomirensis* is considered a species of that subgenus. As *C.* (*B.*) *theodomirensis* is

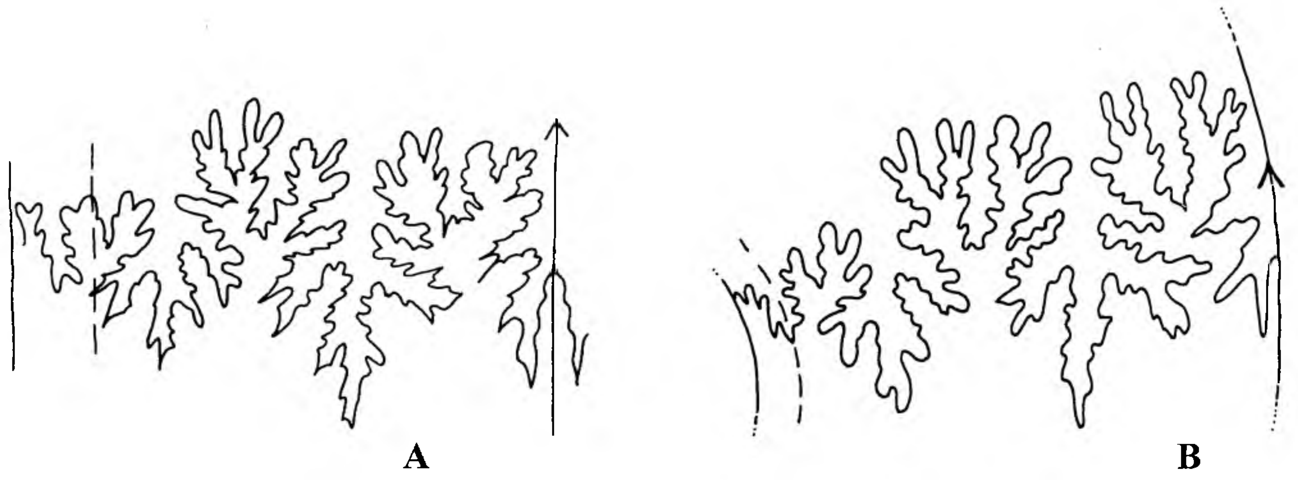


Fig. 58: A-C, *Crioceratites* (*Balearites*) *theodomirensis* sp. nov., suture lines. A, RGM 542088, Wh 13 mm; ×5.3. B, RGM 542088, Wh 14 mm; ×4.8.

morphologically intermediate between *C.* (*B.*) *balearis* and *P.* (*K.*) *mortilleti*, the author holds the view that *C.* (*B.*) *balearis* is immediately ancestral to *C.* (*B.*) *theodomirensis* and the latter the immediate ancestor of *P.* (*Kakabadziella*) *mortilleti*.

Crioceratites (*Balearites*) *theodomirensis* has many closely spaced umbilical bullae by which it can be distinguished from *C.* (*B.*) *balearis* var. *shankariae*; the rows of ventrolateral tubercles are persistent to the aperture and more conspicuous in *C.* (*B.*) *theodomirensis* than in *balearis*; in the latter species they are hardly visible. Although the differences are not always sharp, *C.* (*B.*) *theodomirensis* cannot be considered an extreme variety of the *balearis-shankariae* variability series, because it has a different range; it appears halfway up the Balearis Zone and continues its range high into the Ohmi Zone.

It cannot be decided whether *Balearites paramhansi* Sarkar, 1955, is conspecific with *P.* (*B.*) *theodomirensis*, because in Sarkar's description of the holotype, the presence of rows of small uniform ventrolateral tubercles is not mentioned, neither the presence of lateral tubercles on the first whorl.

C. (*B.*) *theodomirensis* mimics *P.* (*K.*) *mortilleti*, but differs from the latter mainly in its greater umbilicus and in the presence of thickened ribs alongside constrictions in the adult stage. The whorls of *mortilleti* grow faster in height than those of *C.* (*B.*) *theodomirensis*. The umbilical bullae of *C.* (*B.*) *theodomirensis* are smaller and more pointed, whereas those of *P.* (*K.*) *mortilleti* are long, curved and crested. *Pseudothurmannia* (*Kakabadziella*) *mortilleti* lacks the lateral tubercles on the innermost whorls.

Crioceratites (*Balearites*) *theodomirensis* differs from *Crioceratites* (*Binelliceras*) *binelli* in the whorls being in contact, the closer spacing of the umbilical bullae and the smaller number of intermediate ribs between two bullae. The ribs of *C.* (*B.*) *theodomirensis* are less uniform than those of young *C.* (*Bi.*) *binelli*.

Crioceratites (*Balearites*) *theodomirensis* resembles *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, which has approximately the same range. The latter species differs from *C.* (*B.*) *theodomirensis* in the whorls not being in contact, the frequent fibulation of the ribs towards relatively prominent ventrolateral tubercles, the persistence of trituberculation up to a diameter of 15 mm and the ventrolateral tubercles on the main ribs being greater than those on the intermediate ribs.

Range: Balearis and Ohmi Zones.

Geographical distribution: France (Barrême, Castellane, Angles), Spain (Río Argos, La Guardia, Tornajo Mountain), Slovakia (Polomec Quarry), Hungary (Hárskút).

8.1.3. *Crioceratites* (*Balearites*) *pseudothurmannii* (Dimitrova, 1967)
Fig. 59; Pl. XXXVII; Tab. XIX

v* 1967. *Balearites pseudothurmannii* sp. nov.– Dimitrova, p. 77 + 222, pl. 36, figs. 3 (paratype), 4-4a (holotype).

1995b. *Crioceratites pseudothurmannii* (Dimitrova).– Hoedemaeker, p. 234, pl. 4, figs. 8-9.

1995b. *Crioceratites* sp. n. A.– Hoedemaeker, p. 235, pl. 7, fig. 7.

Holotype: By original designation. Specimen $Cr_1$1543 from the State University Collection (Sofia, Bulgaria), figured by Dimitrova (1967, pl. 36, fig. 4, 4a) from the upper Hauterivian marly limestones near Beli Mel (Mikhailovgrad, Bulgaria) (pl. 37, fig. 4). Paratype (pl. 37, fig. 9): specimen $Cr_1$1544 from the State University Collection (Sofia, Bulgaria) (Dimitrova, 1967, pl. 36, fig. 3) from upper Hauterivian of Balgarski izvor (Loveshko, Bulgaria), kindly sent to the author by Prof. Dr. T. G. Nikolov (Sofia).

Material: Nineteen specimens, consisting of six impressions, 11 whorl fragments and two plaster casts (holotype and paratype). The specimens are not well preserved, but clearly identifiable. All specimens derived from beds W23-W31 (= range).

Description: The evolute whorls of *C.* (*B.*) *pseudothurmannii* are in contact. Whorl section with flat flanks, concave dorsum and rounded venter. Umbilicus approximately as wide as the whorl height. Umbilical rim rounded.

The ornamentation is visible from a diameter of 10 mm. A possible earlier stage with lateral tubercles was not revealed in the author's material. From this diameter the ribs originate in pairs from weak umbilical bullae at the umbilical rim. At regular distances larger umbilical bullae give rise to thicker main ribs. The ribs are

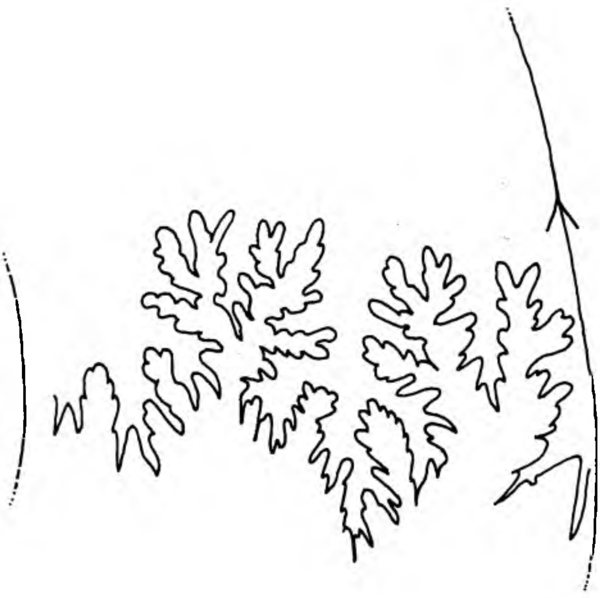


Fig. 59: *Crioceratites* (*Balearites*) *pseudothurmannii* Dimitrova, 1967, suture line. RGM 542395, at diameter 17.5 mm, ×4.

prorsiradiate and slightly flexuous. The main ribs cross the venter without interruption, but the intermediate ones are weakened at mid-venter. Every rib has a pointed ventrolateral tubercle, which is clearly larger on the thick main ribs than on the intermediate ones.

The smaller umbilical bullae on the intermediate ribs commonly disappear at a diameter of 18 mm, in some specimens somewhat earlier or later. Only rarely are the intermediate ribs raised at the umbilical rim. The distant umbilical tubercles on the main ribs become more prominent. The intermediate ribs have different lengths; some of them arise on the umbilical wall, some at, or just above, the umbilical rim and some around midflank or even higher. The number of intermediate ribs between every two main ribs varies from 3-6, but may rarely be two or seven. They are slightly flexuous to sigmoidal and have small, weak, ventrolateral tubercles. The ventrolateral tubercles are larger on the main ribs than on the intermediate ones. At larger diameters the ventrolateral tubercles on the intermediate ribs become smaller and finally virtually disappear. The intermediate ribs pass over the venter without interruption. One main rib on the adult most part of the holotype shows a weak lateral tubercle; lateral tubercles are not present in the material from the Río Argos succession.

The main ribs start on the umbilical wall and are provided with prominent curved bullae at the umbilical rim. They may be rather thin as on the holotype or relatively thick and prominent as on the paratype; their prominence depends on the thickness of the main ribs. Also the ventrolateral tubercles are extra prominent on the main ribs, and may clearly be elongated in the direction of coiling (clavi). The main ribs pass the venter without interruption and are lined by constrictions which pass over the venter. In a few occasions both sides of a constriction are lined by thick ribs. Some constrictions are narrow and shallow, and hardly visible.

On the specimens that look quite similar to the holotype, the ribs are generally finer, radial, and slightly flexuous with relatively small tubercles (Pl. XXXVII, figs. 1, 3-4). On the specimens that look quite similar to the paratype (Pl. XXXVII, figs. 7-10), the ribs are less fine, sigmoidal, and more prorsiradiate; the constrictions are deeper and the ventrolateral tubercles on the main ribs are clearly elongated in the direction of coiling. Hoedemaeker (1995b) separated the paratype from the holotype as a separate species. However, these two 'species' closely resemble each other, have the same range, and there are intermediate specimens (Pl. XXXVII, figs. 2, 5-6) that are difficult to assign to either of the 'end members' defined by the types.

Suture line: One incomplete suture line could be drawn (Fig. 59); the lateral lobe (L) and the two adjacent saddles. The external (E) and umbilical (U) lobes are incomplete. The trifid lateral lobe is deeper than the external lobe, has a rather narrow throat, and the side arms are wide-spread. The bifid saddles have narrow necks and are subdivided into two parts by deep incisions. The external part of saddle E/L has three branches, the internal part four. The saddle L/U is the highest saddle; its external part has four arms and the internal part three. The trifid umbilical lobe (U) is the shallowest lobe and has wide-spread side arms.

Remarks: The species *C.* (*B.*) *pseudothurmannii* is here interpreted to belong to *Crioceratites* (*Balearites*), because of the combined presence of fine ventrolateral tubercles without fibulation, of constrictions alongside main ribs, and of main ribs that broaden towards the venter. On the other hand, this species may not belong to *Crioceratites* (*Balearites*), because of the inequality of the ventrolateral tubercles.

Range: Balearis Zone.

Geographical distribution: Bulgaria (Belimel, Bulgarski Isvor), Spain (Río Argos).

8.1.4. *Crioceratites* (*Balearites*) *oicasensis* nov. sp.
Fig. 60; Tab. XX

? 1955. *Balearites paramhansi* n. sp.– Sarkar, p. 145, pl. 11, fig. 6.

1993. *Binelliceras krenkeli* (Sarkar).– Autran, pl. 13, fig. 13.

pars 1994. *Pseudothurmannia balearis* (Nolan).– Vašíček *et al.*, p. 66, pl. 19, fig. 4, *non* fig. 3 [= *Crioceratites* (*Balearites*) *balearis* Nolan].

1995. *Pseudothurmannia* (*Balearites*) *balearis* (Nolan).– Vašíček, p. 174, pl. 4, fig. 5.

1995b. *Pseudothurmannia* (*Balearites*) nov. sp. A.– Hoedemaeker, p. 231, pl. 3, fig. 4a-b.

pars 2002. ?*Pseudothurmannia "binelli"* Thomel, 1964, *non* Astier, 1851.– Vašíček, p. 194, pl. 2, fig. 7, *non* fig. 6 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar].

pars 2003. *Crioceratites balearis* Nolan.– Company *et al.*, p. 688, 689, only fig. 5.1, *non* fig. 5.2. [= inner whorls of *Crioceratites* (*Binelliceras*) *binelli* Astier, 1851], *non* fig. 5.3. [= *Crioceratites* (*Balearites*) *balearis* Nolan var. *shankariae*].

Syntypes: Three syntypes (Figs. 60A-C) from the Río Argos succession: RGM 387925, loose upon bed A139 near Molino de Las Oicas de Abajo; specimen RGM 542344 from bed C128, c. 500 m east of Molino de Las Oicas de Abajo; and RGM 542343 from bed D129, c. 150 m east of Molino de Las Oicas de Abajo.

Material: Three syntypes occurring between C128-139.

Derivation of name: Called after a restricted area along the southern border of the Río Argos, Las Oicas. The Molina de Las Oicas de Abajo and the Cortijo de las Oicas de Abajo are in the close neighbourhood. Cortijo de Las Oicas de Enmedio and Cortijo de Las Oicas de Ariba are farther to the west.

Diagnosis: Very evolute *Balearites* with fine ribs throughout the conch and lateral tubercles on the innermost whorls up to a diameter of 10 mm. From this diameter all ribs are equally fine and closely spaced. Thicker main ribs appear at regular distances from a

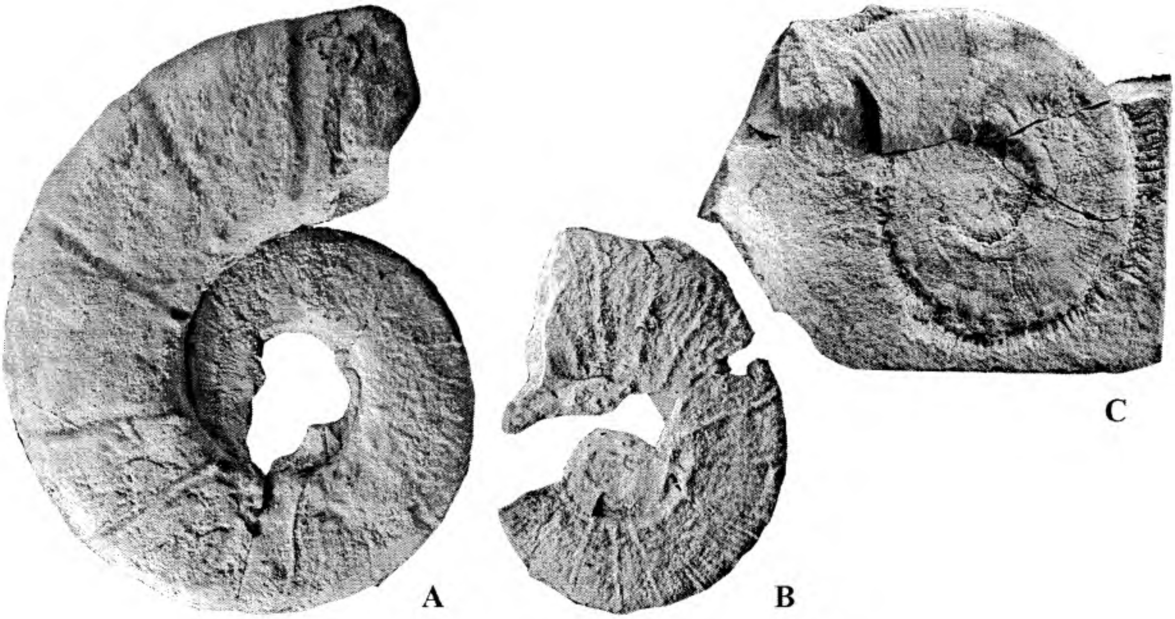


Fig. 60: A-C, *Crioceratites* (*Balearites*) *oicasensis* sp. nov. A, RGM 387925, syntype, locality 1A, loose from beds A139-151; ×1. B, RGM 542343, syntype, locality 1D, bed D129; ×1. C, RGM 542344, syntype, locality 1C, bed C128; ×1.

diameter of about 20 mm; the first of these ribs is hardly thicker than the fine intermediate ribs. All ribs exhibit tiny ventrolateral tubercles, which on our material is only visible up to a diameter of about 30 mm. The regularly spaced main ribs gradually grow in strength and from a diameter of about 30 mm become flanked by shallow constrictions. The thick ribs are provided with umbilical bullae and ventrolateral tubercles. At larger diameters all ribs cross the venter.

Description: The innermost whorl is not preserved. The whorls are compressed and touch each other. On the smallest specimen the ornamentation is visible from a diameter of 6 mm and all the ribs are provided with lateral tubercles. One or two intermediate ribs separate the laterally tuberculated ribs in a later growth stage. The venter cannot be observed. The lateral tubercles disappear at a diameter of 10 mm. From that diameter the ribs are all equally fine and closely spaced. The first main rib that becomes slightly thicker than the intermediate ribs appears at a diameter of 20 mm.

From this diameter, the ornamentation of the largest specimen is visible. The whorls are just in contact and ornamented with closely spaced, fine, flexuous ribs of equal thickness. The widely spaced umbilical tubercles mark the slightly more prominent main ribs, which are separated by 6-8 intermediate ribs. All the ribs are sigmoid. Two or three ribs may originate from each umbilical tubercle. Only on the first part of the last whorl (that is, from a diameter of 31 mm to 32 mm), where the ribs still do not cross the venter, tiny ventrolateral tubercles are visible on every rib. The remainder of the venter is too badly preserved to show these ventrolateral tubercles.

At a diameter of 31 mm the first ventrolateral tubercle occurs that is distinctly larger than the other ventrolateral tubercles. Only the main rib on which it sits crosses the venter, the intermediate ribs do not; this main rib is situated alongside a constriction, which is distinct on the venter as well as on the flanks. On the flanks this rib is slightly, but hardly, thicker than the adjacent ribs, is provided with prominent, sharp umbilical tubercle and is sigmoidal. The constrictions and main ribs gradually grow in strength towards the aperture and are regularly distributed. They are separated by 5-9 thin intermediate ribs, which tend to efface near the umbilical edge. The larger ventrolateral tubercles cannot be discerned because of the badly preserved ventral side, but they are presumably still present. The living chamber begins at a diameter of 54.5 mm. The last part of the living chamber is just not in contact with the penultimate whorl.

Remarks: *Crioceratites* (*Balearites*) *oicasensis* differs from *Crioceratites* (*Balearites*) *balearis* in the early presence of main ribs from a diameter of 20 mm, which gradually grow in strength and are disposed at regular distances from each other, and in having pronounced umbilical bullae at regular distances. It belongs to the subgenus *Balearites* because of the presence of lateral tubercles only on the innermost whorl, the very fine ribbing of the inner whorls, the whorls being in contact, the presence of ventrolateral tubercles on every rib on the early whorls, and the presence of constrictions alongside the thick ribs from a diameter of 31 mm.

Crioceratites (*Balearites*) *oicasensis* differs from *Crioceratites* (*Binelliceras*) *binelli* in the main ribs being more pronounced than the intermediate ribs from a diameter of c. 20-30 mm instead of c. 50 mm as in *C.* (*B.*) *binelli*, the lateral tubercles disappearing at a diameter of 10 mm instead of 15 mm as in *C.* (*B.*) *binelli*, the whorls being in contact, the regular distance of the main ribs, and the prominence and sharpness of the umbilical tubercles. In *C.* (*B.*) *binelli*, the disposition of the main ribs is irregular, the umbilical bullae weak and the whorls not in contact.

The inner whorls of *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955, may resemble those of *oicasensis*, but the main ribs are stronger, and the number of intermediate ribs is much smaller than in *oicasensis*.

The differences between *C.* (*B.*) *oicasensis* and *C.* (*B.*) *pseudothurmannii* are the larger umbilicus, the finer ribbing and the thinner, more delicate main ribs of the former species.

Specimen SNM (Slovak National Museum) Z 23020 from the uppermost Hauterivian of the Podbranč Quarry in Slovakia figured by Vašíček (2002, pl. 2, fig. 7) seems to be the best preserved young specimen figured in literature.

Range: Balearis Zone.

Geographical distribution: Spain (Río Argos, La Guardia), Slovakia (Polomec quarry, Podbranč quarry), perhaps France (Angles).

8.2. Subgenus *Crioceratites* (*Binelliceras*) Sarkar, 1977

Type species: *Ancyloceras Binelli* Astier, 1851.

Emended diagnosis: A subgenus of *Crioceratites* closely related to *Crioceratites* (*Balearites*). Whorls are slightly crioconic. Ribbing consists of usually strong main ribs, which are commonly provided with umbilical bullae, and separated by a rather small number of weaker and generally shorter intermediate ribs. Ribs may be fine and uniform on the inner whorls. Trituberculate main ribs are characteristically present up to a diameter of 11-23 mm. Ventrolateral tubercles are present on inner whorls, but in some species continue up to the aperture. On the inner whorls the ventrolateral tubercles are wider apart than the ribs and frequent fibulation occurs. Fibulation becomes less frequent with growth, and almost all the ribs are provided with a ventrolateral tubercle. The ventrolateral tubercles on the intermediate ribs become weaker in adoral direction and may disappear.

Remarks: The main differences with *Crioceratites* (*Balearites*) are that the whorls are slightly crioconic in *Binelliceras* and in contact in *Balearites*, that lateral tubercles are present up to diameters of 11-23 mm in *Binelliceras* instead of up to diameters smaller than 11 mm in *Balearites*, and that fibulation in *Binelliceras* in is very frequent in contrast to the absence of it in *Balearites*. The subgenus *Binelliceras* is herein subdivided into two groups, viz. the *binelli* group, and the *angulicostatus* group. Both have a comparable ontogenetic development of the ornamentation.

8.3. *Binelli* group

Diagnostic features: All the species of this group have compressed whorls, an arched to flattened venter and a concave dorsum. The earliest whorls have lateral tubercles up to a diameter of 11-16 mm. The early part of the conch has characteristically fine uniform flexuous ribs up to a diameter of 25-50 mm; this ribbing is followed by more differentiated ribbing. The adult part is characterized by an irregular distribution or irregular curvature of main and intermediate ribs.

8.3.1. *Crioceratites* (*Binelliceras*) *binelli* (Astier, 1851)
Fig. 61; Tab. XXI

* 1851. *Ancyloceras Binelli*.– Astier, p. 444, pl. 16, fig. 2.

pars 1894. *Crioceras Picteti* var. *majoricensis* nobis.– Nolan, p. 192, pl. 10, only fig. 1c, *non* figs. 1a and 1b (= *Crioceratites majoricensis* Nolan, 1894), *non* 1d [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955?].

pars?1907. *Crioceras duvali* Léveillé.– Karakasch, p. 131, probably only pl. 16, fig. 3a-b, *non* fig. 6a-b (*Crioceratites* sp.).

non 1927. *Ancyloceras Binelli* Astier.– Roch, p. 29, pl. 4, fig. 2. (= *Ancyloceras rochi* Sarkar, 1955).

1955. *Crioceras nowaki* n. sp.– Sarkar, p. 49, pl. 4, fig. 11, text-fig. 8b.

pars 1955. *Crioceras binelli* Astier.– Sarkar, p. 57, pl. 2, fig. 4 (lectotype), *non* fig. 6 [= *Crioceratites* (*Balearites*) *balearis* var. *shankariae*].

pars 1960. *Crioceratites honnoratii* Léveillé.– Drushchits & Kudrjavtsev, p. 289, pl. 31, fig. 2, *non* fig. 3 [= *Crioceratites* (*Balearites*) *balearis*? Nolan, 1894].

1964. *Balearites balearis* (Nolan).– Fülöp, pl. 27, fig. 7.

non 1965a. *Crioceratites* (*Crioceratites*) *binelli* (Astier).– Thomel, p. 28, pl. 3, fig. 2 [= *Balearites* (*Balearites*) *theodomirensis* n. sp.], *non* fig. 3 [= *Crioceratites* (*Balearites*) *balearis* var. *shankariae*].

non 1966. *Crioceratites* (*Crioceratites*) *binelli* (Astier).– Linares & Vera, p. 69, pl. 8, fig. 1 (= *Crioceratites* gr. *villiersianus* d'Orbigny, 1842).

1977. *Binelliceras binelli* Astier.– Sarkar, p. 258.

1981. *Crioceratites honnorati* Léveillé.– Kakabadze, p. 86, pl. 1, fig. 4a-b.

non 1982. *Crioceratites* (*Crioceratites*) *binelli* (Astier).– Braga *et al.*, p. 684, pl. 1, fig. 2 [= *Pseudothurmannia* (*Balearites*) *theodomirensis* n. sp.].

non 1989. *Crioceratites binelli* (Astier).– Vašíček, p. 118, pl. 1, fig. 3 [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar].

non 1989. *Crioceratites binelli* (Astier).– Michalík & Vašíček, pl. 1, fig. 3. [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955].

1993. *Binelliceras binelli* (Astier).– Autran, pl. 13, fig. 2.

1993. *Binelliceras krenkeli* (Sarkar).– Autran, pl. 13, fig. 13.

non 1994. *Crioceratites binelli* (Astier).– Vašíček *et al.*, p. 64, pl. 20, figs. 1-2 [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955].

? 1995. *Crioceratites* cf. *binelli* (Astier).– Avram, pl. 7, fig. 4.

non 1995. *Crioceratites binelli* (Astier).– Vašíček, pl. 4, fig. 2 [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955], *non* fig. 3 [= *C.* (*Binelliceras*) *rotundatus* Sarkar, 1955].

1995b. *Crioceratites binelli* (Astier).– Hoedemaeker, p. 234, pl. 4, fig. 7.

non 1996. *Crioceratites* (*Crioceratites*) *binelli* Astier.– Wright, p. 211, fig. 164, 5e [= *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.].

non 1999. *Crioceratites binelli sensu* Thomel, *non* Astier.– Vašíček & Michalík, p. 254, fig. 7.5. [= *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, 1962].

non 2000. *Pseudothurmannia* (*?Balearites*) *"binelli"* Thomel, 1964, *non* Astier, 1851.– Vašíček & Faupl, p. 605, pl. 6, fig. 7 [= *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, 1962].

non 2002. *?Pseudothurmannia "binelli"* Thomel, 1964, *non* Astier.– Vašíček, p. 194, pl. 2, fig. 6 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955], *non* fig. 7 [= *Crioceratites* (*Balearites*) *oicasensis* sp. nov.].

pars?2003. *Crioceratites balearis* (Nolan).– Company *et al.*, pp. 688, 689, fig. 5.2?, *non* fig. 5.1. [= *Crioceratites* (*Binelliceras*) *oicasensis* sp. nov.], *non* fig. 5.3. [= *Crioceratites* (*Balearites*) *balearis* var. *shankariae*].

2003. *Crioceratites binelli* (Sarkar) .– Company *et al.*, p. 689, fig. 5.4.

non 2003. *Binelliceras* gr. *binelli* (Astier).– Busnardo, p. 65, pl. 8, fig. 7 [= *Crioceratites* (*Balearites*) *rotundatus* Sarkar, 1955?], *non* fig. 8 [= *Crioceratites* (*Balearites*) *rotundatus* Sarkar, 1955], *non* fig. 9 [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955], *non* pl. 9, fig. 6 (= *Crioceratites* sp. indet.), *non* pl. 17, fig. 2 [= *Crioceratites nolani*, Kilian, 1910 (p. 224)], *non* fig. 3 (= *Crioceratites* sp. indet.), *non* fig. 4 (= *Crioceratites majoricensis* Thomel, 1965a, *non* Nolan).

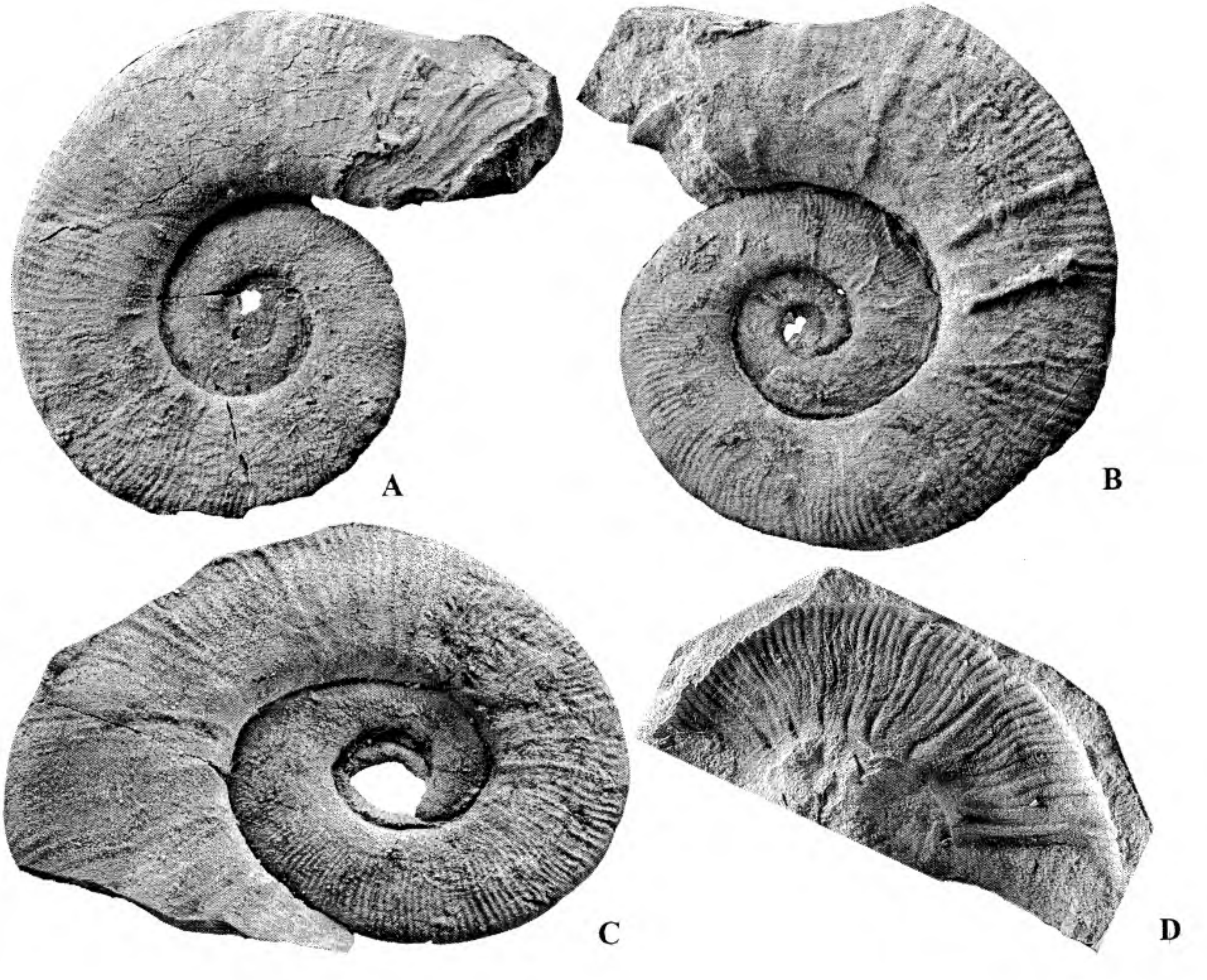


Fig. 61: A-D, *Crioceratites* (*Binelliceras*) *binelli* Astier, 1851. A, RGM 19423, locality Barrême (France); ×1. B, RGM 542337, locality 5; ×1. C, RGM 542338, locality 5; ×1. D, RGM 542850, locality 5; ×1.

Lectotype: The specimen depicted by Astier (1851, pl. 16, fig. 2) under the name *Ancyloceras Binelli* and refigured by Sarkar (1955, pl. 2, fig. 4); this is one of the six specimens with the same name in the Astier collection. Designated by Sarkar (1955, p. 57).

Material: Seven specimens in total. Five from southeast France, that is, one from an unknown locality in the department of Alpes-de-Haute-Provence (RGM 19423) and four from the Angles section, viz. from bed 20 (RGM 542339), loose upon bed 12 (RGM 542850) and two from unknown beds (RGM 542338, RGM 542337). Two badly preserved specimens from the Río Argos succession (Caravaca, Murcia, Spain), viz. one from bed D133 (RGM 542335), and one *C.* (*Bi.*) cf. *binelli* from bed A127 (RGM 542336).

Description: The whorls are not in contact, growing slowly in height (wh:Wh = 2:3). The whorl section is compressed with slightly convex flanks and arched venter. The dorsal side is flat to slightly depressed, and smooth.

The first whorl is not visible, but the second whorl has trituberculate main ribs separated at first by two, and slightly later, by 5-6 intermediate ribs of which the one in the middle also has a ventrolateral tubercle. The main ribs are slightly thicker than the intermediate ones. The lateral tubercles disappear at a diameter of 15 mm.

From this diameter only umbilical and ventrolateral tubercles are present. All the ribs are thin, of equal strength and flexuous. The umbilical tubercles are at great, regular distance from each other and are separated by 6-8 (rarely four) intermediate ribs. Two or, occasionally, three ribs may originate from the umbilical tubercles (fasciculation). Most ribs are provided with small ventrolateral tubercles; often two ribs converge to one tubercle (fibulation), while some ribs lack them. The intermediate ribs weaken towards the umbilical border and do not cross the venter; from a diameter of 35 mm, however, they do cross the venter and the ventrolateral tubercles disappear.

From a diameter of about 45-50 mm the shell attains its adult ornamentation; the main ribs become slightly thicker than the intermediate ones, are adorally bordered by shallow constrictions (a *Balearites*-like feature), and provided with umbilical bullae and ventrolateral tubercles. All ribs now cross the venter. The main ribs are irregularly spaced and separated by 3-16 intermediate ribs; the latter make a small angle with the thick rib at the adapical side of the constriction. The constrictions and the bordering main ribs become more prominent towards the aperture. The largest phragmocone measured by the author has a diameter of 70 m

Remarks: *Crioceratites* (*Binelliceras*) *krenkeli* differs from *C.* (*Bi.*) *binelli* in the presence of large ventrolateral clavi up to 27 mm diameter, in the shorter fine-ribbed portion of the shell up to a diameter of 35 mm [45-50 mm in *C.* (*Bi.*) *binelli*], and in the coarser ribbing with regularly spaced main ribs with at first 2-3 and later 4-6 intermediate ribs to one main rib.

Range: Balearis Zone. Range from bed D127-A133.

Geographical distribution: Spain (Río Argos, Majorca, La Guardia?), France (Castellane, Cheiron, Angles, Ravin du Riou), Hungary (Zirc), Roumania (Vodiniciki valley), The Crimea (River Kacha, Verkhoreche, Biassala).

8.3.2. *Crioceratites* (*Binelliceras*) *krenkeli*
Sarkar, 1955
Fig. 62; Tab. XXII

pars 1894. *Crioceras Picteti* var. *majoricensis* nobis.– Nolan, p. 186, pl. 10, only fig. 1d, *non* figs.1a-b (= *Crioceratites majoricensis* Nolan, 1894), *non* fig. 1c [= *Crioceratites* (*Binelliceras*) *binelli* (Astier, 1851)].

* 1955. *Crioceras krenkeli* n. sp.– Sarkar, p. 37, pl. 5, fig. 5, text-fig. 4C.

? 1965a. *Crioceratites* (*Crioceratites*) *krenkeli* (Sarkar).– Thomel, p. 23, pl. 2 (40), figs. 2-3.

? 1979b. *Crioceratites* (*Crioceratites*) *krenkeli* Sarkar, 1955; Immel, p. 45, fig. 5c.

non 1982. *Crioceratites krenkeli* Sarkar.– Braga *et al.*, pl. 1, fig. 3 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

1984. *Crioceratites* (*Crioceratites*) *quenstedti* (Ooster).– Adamiková *et al.*, p. 604, pl. 1, fig. 2.

1989. *Crioceratites binelli* (Astier).– Michalík & Vašíček, pl. 1, fig. 3.

1989. *Crioceratites binelli* (Astier).– Vašíček, p. 118, pl. 1, fig. 3.

non 1993. *Binelliceras krenkeli* (Sarkar).– Autran, pl. 13, fig. 13 [= *Crioceratites* (*Binelliceras*) *binelli* (Astier, 1851)].

pars 1994. *Crioceratites binelli* (Astier).– Vašíček *et al.*, p. 64, pl. 20, fig. 1, *non* fig. 2 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

pars 1995. *Crioceratites binelli* (Astier).– Vašíček, p. 176, pl. 4, fig. 2, *non* fig. 3 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

non 1995b. *Crioceratites krenkeli* Sarkar.– Hoedemaeker, p. 235, pl. 7, figs. 4-6 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

non 1995b. *Crioceratites "krenkeli"* Braga *et al.*, *non* Sarkar.– Hoedemaeker, p. 234, pl. 4, figs. 1-4 [= *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955].

non 2003. *Crioceratites krenkeli* Sarkar.– Company, p. 688, fig. 5.7 - 5.8 [= ambo *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955], fig. 5.6 [= *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.].

pars 2003. *Binelliceras* gr. *binelli* (Astier).– Busnardo, p. 65, only pl. 8, fig. 9, *non* fig. 7 [= *Crioceratites* (*Balearites*) *rotundatus*? Sarkar, 1955], *non* fig. 8 [= *Crioceratites* (*Balearites*) *rotundatus* Sarkar, 1955], *non* pl. 9, fig. 6 (= *Crioceratites* sp. indet.), *non* pl. 17, fig. 2 (= *Crioceratites nolani* Kilian, 1910, p. 224), *non* fig. 3 (= *Crioceratites* sp. indet.), *non* fig. 4 (= *C. majoricensis* Thomel 1965a, *non* Nolan).

Lectotype: The specimen figured by Sarkar [1955, pl. 5, fig. 5 (×0.5)] from the Neocomian of Castellane (Alpes-de-Haute-Provence, France) deposited in the Laboratoire de Paléontologie du Museum National d'Histoire Naturelle, Paris. Desinated by Immel (1979b)

Material: Nine specimens, viz. two specimens from bed 33 (Balearis Zone) of the Route d'Angles section [Alpes-de-Haut-Provence, France (Balearis Zone)] and six specimens from the Río Argos succession (Caravaca, Murcia, Spain), and a loose specimen from section W.

Description: The whorls of the specimen that most resembles the lectotype, are just not in contact, and are flat-sided with rounded venter and concave dorsum. The gap between the whorls is about 2 mm.

The ornamentation of the innermost whorls is visible only for a small part (RGM 542342 and RGM 542274); this part shows lateral and ventrolateral tubercles on every rib; intermediate ribs are absent. This ornamentation continues up to a diameter of 7 mm. From that diameter the tuberculated main ribs are separated by 1-3 intermediate ribs. Umbilical tubercles are already present at a diameter of 8 mm. The lateral tubercles disappear at a diameter of 15-16 mm. The inner whorls of *Crioceratites* (*Binelliceras*) *krenkeli* have a similar ribbing as the innermost whorls of *C.* (*Bi.*) *binelli.* The inner whorls of *C.* (*Bi.*) *krenkeli* have large ventrolateral tubercles at regular distances from each other, first only on the ribs with lateral tubercles (main ribs), but from a diameter of 9 mm also on the intermediate ribs, one per interval, later two per interval. The ventrolateral tubercles transform into ventrolateral clavi with growth.

At a diameter of 16 mm the trituberculate ornamentation is substituted by fine uniform flexuous ribbing, which occupies about the first half of the penultimate whorl. The distant umbilical bullae give rise to 2-3 ribs. Between these fascicules c. seven ribs may originate at

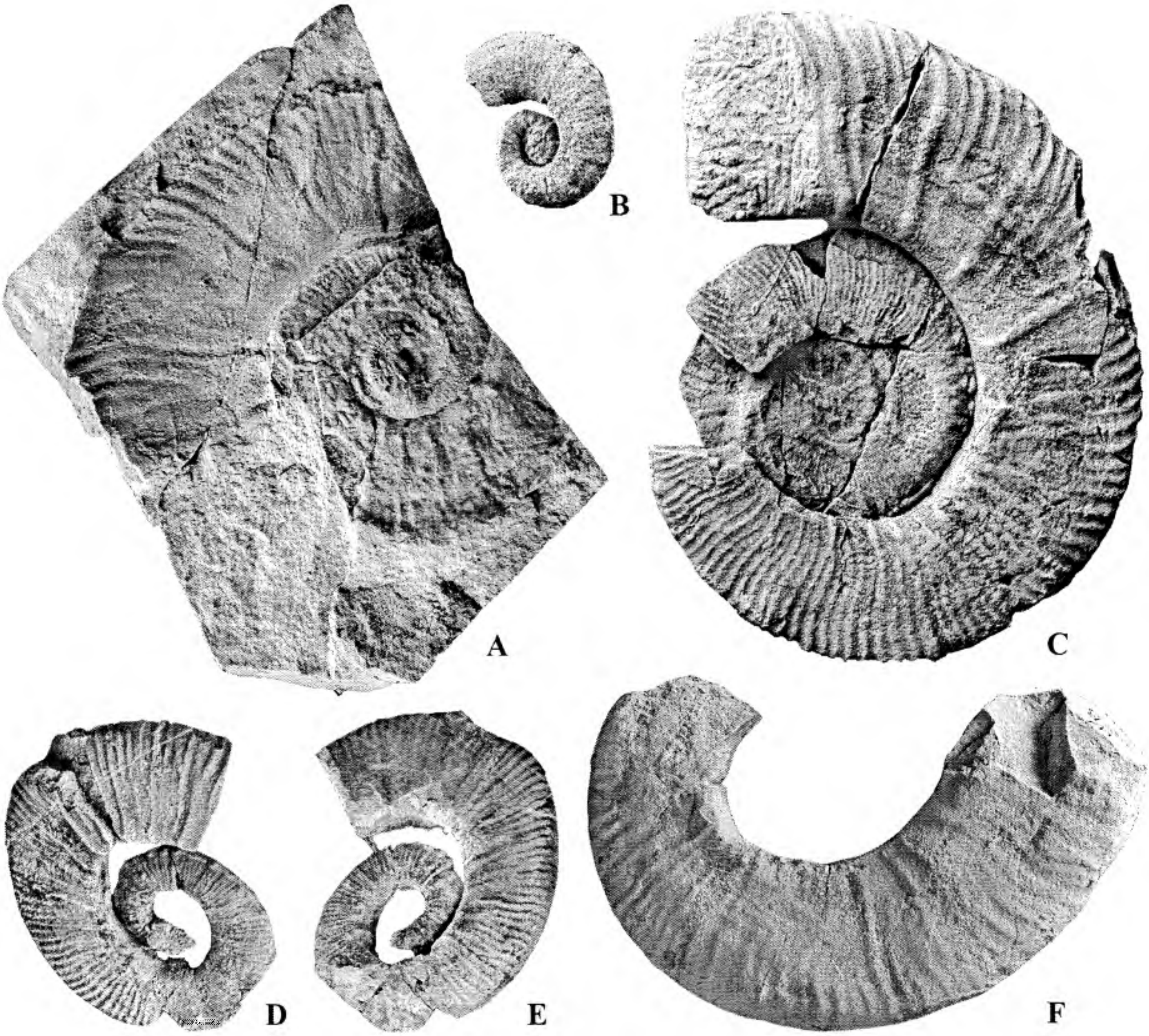


Fig. 62: A-F, *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955. A, RGM 542342, locality 1W, bed W30C; ×1. B, RGM 541916, young specimen showing large clavi, locality 1A, bed A142A; ×1. C, RGM 542273, locality 5, bed 33; ×1. D, RGM 542274 young specimen showing large clavi, right side, locality 5, bed 33; ×1. E, same specimen, left side; ×1. F, RGM 542854, half a whorl, locality 1W, bed W30B; ×1.

the umbilical edge. The umbilical bullae become more closely spaced and are only separated by 2-3 intermediate ribs from a diameter of 42 mm.

There are still many large ventrolateral clavi at regular distance of 2.5 mm sitting on more than one rib (fibulation) up to a diameter of 27 mm. From this diameter the strong distant tuberculation gradually transforms into rows of small, almost uniform clavi on every rib; the main ribs, however, are still provided with longer clavi up to a diameter of 63 mm. The small clavi on the intermediate ribs also disappear at D = 63 mm.

From a diameter of 35 mm one of the ribs of a fascicule becomes slightly thicker than the ribs between the fascicules; they become the main ribs. They are flexuous and rather regularly distributed. The number of intermediate ribs between two main ribs gradually diminishes from 6 to 2-3. The main ribs are provided with ventrolateral clavi and cross the venter as broad blunt undulations. The intermediate ribs weaken on the venter and are provided with fine ventrolateral tubercles. From a diameter of 62 mm all ribs cross the venter without interruption, and ventrolateral tubercles could not be discerned anymore.

The adult living chamber begins at 62 mm. From a diameter of 54 mm a coarser and more widely spaced flexuous ribbing becomes gradually installed. The coarse main ribs are regularly and widely spaced and separated by 4-6 intermediate ribs. The main ribs have umbilical bullae. The intermediate ribs originate either at the umbilical rim or at midflank. All the ribs cross the venter. On the ventral side the main ribs remain thicker than the intermediate ones and are still provided with ventrolateral tubercles; the latter are absent on the intermediate ribs. The intermediate ribs tend to become effaced on the lower half of the flanks.

Remarks: There is no species that has been as consequently misinterpreted as *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, not least by the author. The main reason for this is the bad, reduced figure and the short, insufficient description of Sarkar (1955). *Crioceratites* (*Binelliceras*) *krenkeli* may be circumscribed as a coarse-ribbed *C.* (*Bi.*) *binelli*. The specimens described by Braga *et al.* (1982), Hoedemaeker (1995b) and Company *et al.* (2003) under the name *Crioceratites krenkeli*, all belong to *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955, and not to *C.* (*Bi.*) *krenkeli*. The specimen described by Thomel (1965a) questionably belongs to the species; it differs in some aspects from our specimens and from the holotype.

Crioceratites (*Binelliceras*) *krenkeli* looks as if it is a coarse-ribbed variety of *C.* (*Bi.*) *binelli*. However, *C.* (*Bi.*) *krenkeli* occurs in the lower part of the Ohmi Zone instead of the Balearis Zone and differs from *C.* (*Bi.*) *binelli* in the regularly spaced, coarse main ribs on the living chamber; in the 4-6 intermediate ribs which only partly reach the umbilical rim; in the smaller number of prominent ventrolateral tubercles on, and between, the main ribs of the inner whorls; and in the presence of clavi on the main ribs of the last whorl. These ventrolateral clavi were not described by Sarkar (1955), Thomel (1965a), or Busnardo (2003).

Crioceratites (*Binelliceras*) *krenkeli* differs in several aspects from *C.* (*Bi.*) *rotundatus*; for instance in the longer fine-ribbed part (up to a diameter of 35 mm), in the wider spacing of the ventrolateral tubercles on the inner whorls, in the venter being rounded, in the more irregularly distributed ribbing in the adult, and in the less prominent ribbing.

Range: Lower part of Ohmi Zone. In beds W30B-D and A142A, A142B.

Geographical distribution: France (Noyers-le-Vieux, Castellane, Angles), Slovakia (Polomec quarry), Spain (Rio Argos), Switzerland (River Veveyse near Châtel-St.-Denis).

8.3.3. *Crioceratites* (*Binelliceras*) *ibizensis* (Wiedmann, 1962)
Figs. 63-64; Pl. XXXVIII; Tab. XXIII

pars 1894. *Crioceras angulicostatum* d'Orbigny.– Nolan, p. 195, pl. 10, only fig. 3a, *non* fig. 3b [= *Crioceratites* (*Balearites*) *rotundatus* Sarkar], *non* fig. 3c (= *Crioceratites remanei* Wiedmann).

* 1962. *Crioceratites* (*Pseudothurmannia*) *balearis ibizensis* n. ssp. Wiedmann, p. 130.

? 1967. *Balearites ibizensis* (Wiedmann).– Dimitrova, p. 78, pl. 36, fig. 1.

pars?1967. *Balearites mortilleti* (Pictet & De Loriol).– Dimitrova, possibly pl. 36, fig. 5, *non* fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858)].

1995b *Crioceratites ibizensis* Wiedmann.– Hoedemaeker, p. 233, pl. 5, figs. 1-7, 10.

1999. *Crioceratites binelli* sensu Thomel, *non* Astier.– Vašíček & Michalík, p. 254, fig. 7.5.

? 2000. *Crioceratites* sp. (?ex gr. *ibizensis* Wiedmann).– Vašíček & Faupl, pl. 6, fig. 5.

2000. *Pseudothurmannia* (*?Balearites*) *"binelli"* Thomel, 1964, *non* Astier, 1851.– Vašíček & Faupl, p. 605, pl. 6, fig. 7.

Holotype: *Crioceras angulicostatum* d'Orbigny *in* Nolan (1894, pl. 10, fig. 3a). Collection of Nolan deposited in the Geological Institute Dolomieu in Grenoble (inaccessible now). Designated by Wiedmann (1962, p. 130).

Material: Forty-one specimens, viz. six from sections 2A and T3 of the Tornajo Mountain (Communality of Lorca, Murcia, Spain), three from the Angles section in beds 33, 36, 39 (Alpes-de-Haute-Provence, France), and 32 from the Río Argos succession (Caravaca, Murcia, Spain).

Description: Because of the large number of specimens collected in the Río Argos succession, the author was able to recognize the great variability of this species. The whorls of *C.* (*Bi.*) *ibizensis* are nearly in contact, and, in some specimens, they probably are actually in contact at some places. However, the coiling is slightly irregular, not strictly spiral; the distance between the whorls is widest (1 to 3 mm) at the beginning of the last whorl and diminishes towards the aperture and in apical direction; this produces a slight deviation from the strictly spiral curvature of the whorls. The whorls are compressed, but, owing to diagenetic compression, the true thickness is uncertain.

This species is not the large ammonite that Wiedmann (1962) thought it was; the figure of the holotype is *reduced to* four fifths and therefore *reduced by* one fifth. It is not five times larger than the figure of Nolan. The diameter of largest specimen from the Río Argos does not exceed 63 mm.

The inner whorls are not preserved in the holotype. The first whorl forms an open spire and leaves a perforated umbilicus; its cross section is round. The first ribs are widely spaced, prorsiradiate and do not have lateral tubercles. The latter appear a little later on every rib; ventrolateral tubercles could not be seen on the innermost whorls of the Río Argos specimens. At a diameter of 4 mm the uniform, distant ribs assume a radial direction and are provided with ventrolateral tubercles. Umbilical

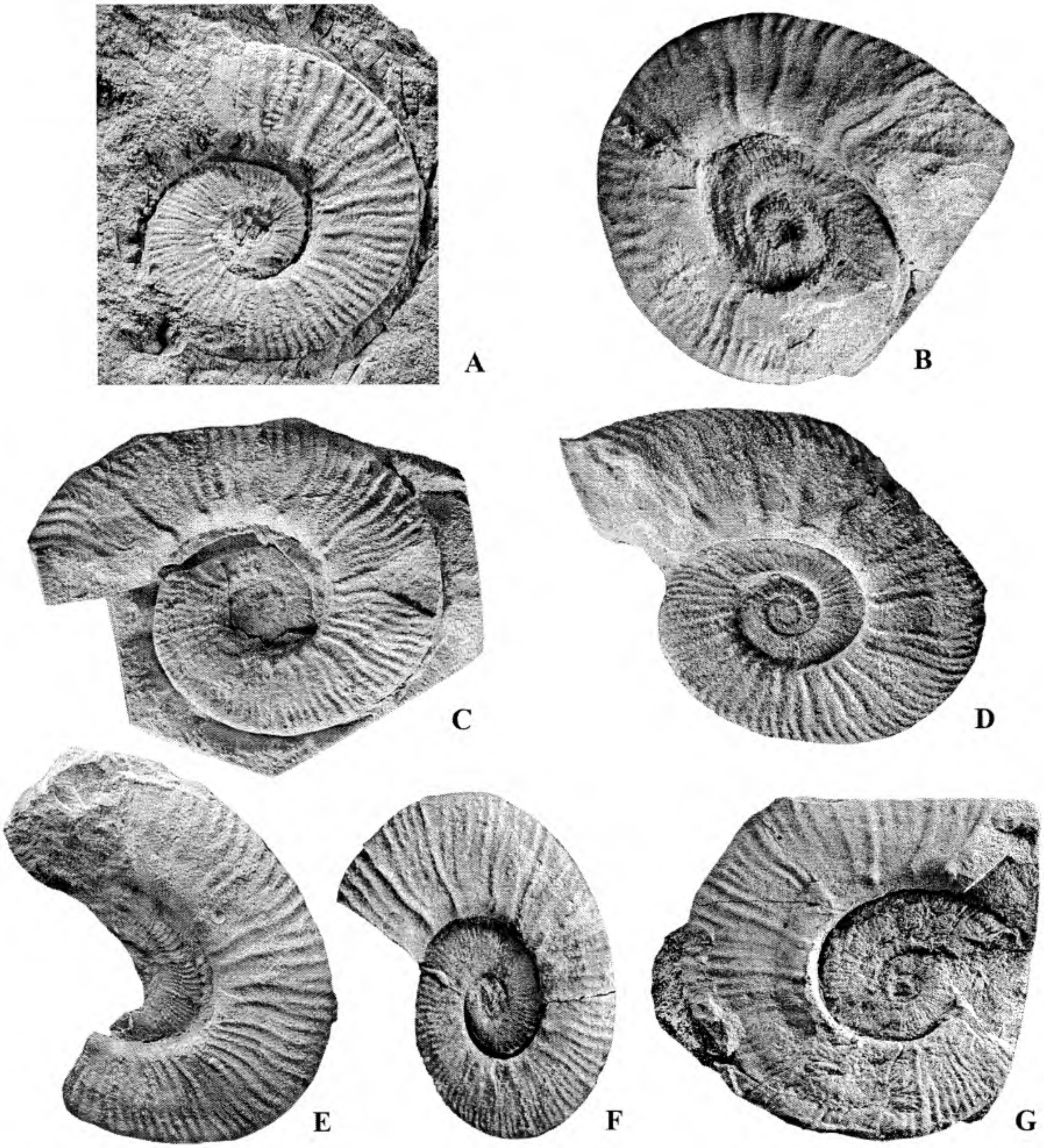


Fig. 63: A-G, *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, 1962, large specimens. A, RGM 542668, locality 1W, loose from beds W20-30; ×1. B, RGM 542320, locality 3A; ×1. C, RGM 387938, locality 1W, bed W30; ×1. D, RGM 542318, locality 3T, bed T3; ×1. E, RGM 542319, locality 3A; ×1. F, RGM 542317, locality 3A, bed 1; ×1. G, RGM 387879, locality 1W, loose from beds W20-30; ×1.

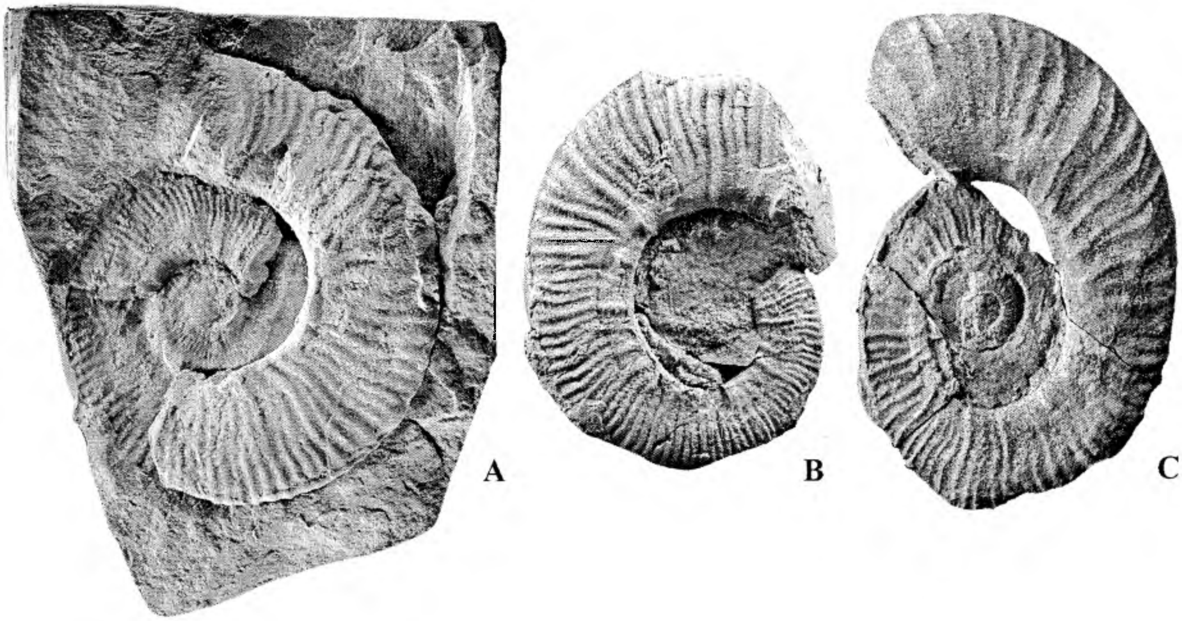


Fig. 64: A-C, *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, 1962, large specimens. A, RGM 387935, locality 1W, bed W30B; ×1. B, RGM 387937, locality 1W, bed W30B; ×1. C, RGM 542321, locality 3A; ×1.

tubercles appear slightly later on every second to fourth rib, which differentiate themselves as main ribs. The intermediate ribs lose their lateral tubercles and may split from the main rib at the umbilical tubercle; they may converge to one ventrolateral tubercle (fibulation). The whorl section is sexangular with convex flanks and truncated venter. The greatest thickness is at midflank.

From a diameter of 10 mm the number of intermediate ribs between two main ribs augments to 3-6 and all the ribs become flexuous. At first the middle intermediate rib between two main ribs still has a small lateral and umbilical tubercle, but after one or two intervals this feature disappears. The lateral tubercles on the main ribs may be visible up to a diameter of 15 mm. Generally, bundles of two or three ribs originate from one umbilical tubercle; the intermediate ribs may not reach the umbilical rim. Near the venter the thickness of the main ribs hardly exceeds that of the intermediate ones. The latter do not cross the venter of the phragmocone; the main ribs do, but are weak on the venter. However, prominent ventrolateral tubercles remain present at the same mutual distance as on the earlier whorls. Often two ribs may converge to one ventrolateral tubercle. This fibulation is more or less frequent in some young specimens, but almost disappears with growth.

From a diameter of 20 mm every rib has a small ventrolateral tubercle; those on the main ribs are slightly greater than those on the intermediate ribs; fibulation has stopped. The venter remains smooth except for the main ribs, which cross the venter without interruption. The uniformly ribbed part ends at a diameter of 23-25 mm. The ribs remain flexuous, gradually gain in prominence and the number of intermediate ribs to one main rib varies between two and six. The whorl section is compressed, has flat parallel flanks and a truncated venter.

On the adult living chamber, which begins at a diameter of 40 mm, the ribbing becomes irregular; the ribs do not always have the same parallel curvature, forking of ribs at midflank occurs as well as fasciculation, and intermediate ribs originate low and high on the flanks, and vary in prominence or even are effaced. On the whole, ribbing remains rather fine. The main ribs may, or may not, differ in thickness from the intermediate ribs and they may be bordered by weak constrictions. The umbilical tubercles are less prominent than on earlier whorls. Only on the adult living chamber do the intermediate ribs cross the venter with an adoral convexity; at the beginning of the living chamber they are still weakened on the venter. Two rows of small ventrolateral tubercles can still be observed. The whorl section is still compressed with flat parallel flanks, but the truncated venter is more arched.

Remarks: *C.* (*Bi.*) *ibizensis* shows some resemblance to *Crioceratites* (*Balearites*) *theodomirensis*, which occurs in the same beds as *C.* (*Bi.*) *ibizensis*. The latter differs from *C.* (*B.*) *theodomirensis* in the whorls not being in contact, in the high frequency of fibulation of the ribs, in the persistence of trituberculation of the main ribs up to a diameter of 15 mm, and lastly in the ventrolateral tubercles on the main ribs of the last whorl being greater than those on the intermediate ribs.

C. (*Bi.*) *ibizensis* differs from *P.* (*Kakabadziella*) *mortilleti* in the whorls not being in contact, the wider umbilicus, the more pointed umbilical tubercles, and in the occasional presence of weak constrictions in the adult and in the presence of lateral tubercles up to a diameter of 15 mm.

C. (*Bi.*) *ibizensis* shows great resemblance to *C.* (*Bi.*) *rotundatus*, but remains smaller (64 mm) than the latter (127 mm), has a marked irregular ornamentation on the living chamber contrasting with the regular main-intermediate rib distribution in *C.* (*Bi.*) *rotundatus*, has an irregular type of coiling, and has lateral tubercles up to a diameter of 15 mm instead of 10 mm.

Range: Upper Hauterivian Balearis and Ohmi Zones. From beds W21-W31.

Geographical distribution: Spain (Ibiza, Río Argos, Tornajo Mountain), Austria (Reschen near Groszraming), Slovakia (Podbranč), Bulgaria? (Sredno selo), France (Angles).

8.3.4. *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955
Pls. XXXIX-XL; Tab. XXIV

pars 1894. *Crioceras angulicostatum* d'Orbigny.– Nolan, p. 195, pl. 10, only fig. 3b, *non* fig. 3a [= *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, 1962], *non* fig. 3c (= *Crioceratites remanei* Wiedmann, 1962).

1919. *Crioceras Quenstedti* Ooster.– Rodighiero, p. 113, pl. 12, fig. 2.

* 1955. *Pseudothurmannia mortilleti* Pictet & De Loriol var. *rotundata* nov.– Sarkar, p. 156, pl. 6, fig. 12.

1981. *Crioceratites* (*Pseudothurmannia*) aff. *mortilleti* (Pictet & De Loriol).– Nagy, p. 73, pl. 2, fig. 2.

1982. *Crioceratites krenkeli* Sarkar.– Braga *et al.*, p. 684, pl. 1, fig. 3.

pars 1994. *Crioceratites binelli* (Astier).– Vašíček *et al.*, pl. 20, fig. 2, *non* fig. 1 [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955].

pars 1995. *Crioceratites binelli* (Astier).– Vašíček, pl. 4, fig. 3, *non* fig. 2 [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955].

1995b. *Pseudothurmannia ohmi* (Winkler).– Hoedemaeker, p. 228, pl. 1, fig. 6.

1995b. *Crioceratites "krenkeli"* Braga *et al.*, *non* Sarkar.– Hoedemaeker, p. 234, pl. 4, figs. 1-4.

1995b. *Crioceratites krenkeli* Sarkar.– Hoedemaeker, p. 235, pl. 7, figs. 4-6.

pars 2002. *?Pseudothurmannia "binelli"* Thomel, 1964, *non* Astier, 1851.– Vašíček, p. 194, pl. 2, fig. 6, *non* fig. 7 [= *Crioceratites* (*Balearites*) *oicasensis* sp. nov.].

pars 2003. *Binelliceras* gr. *binelli* Astier.– Busnardo, p. 65, pl. 8, figs. 7-8, *non* fig. 9 [= *Crioceratites* (*Binelliceras*) *krenkeli* Sarkar, 1955], *non*, pl. 9, fig. 6 (= *Crioceratites* sp, indet.), *non* pl. 17, fig. 2 (*Crioceratites nolani* Kilian, 1910), *non* fig. 3 (= *Crioceratites* sp. indet.), *non* fig. 4 (= *Crioceratites majoricensis* Thomel, 1965a, *non* Nolan).

pars 2003. *Parathurmannia* gr. *sarasini* (Sarkar).– Busnardo, p. 69, pl. 9, fig. 2, *non* pl. 12, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], *non* figs. 2, 9 (= *Crioceratites* sp. indet); *non* pl. 15, fig. 1 [= probably *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.], *non* pl. 32, figs. 3, 5, 6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

pars 2003. *Crioceratites krenkeli* Sarkar.– Company *et al.*, p. 688, figs. 5.7., 5.8., *non* fig. 5.6. [= *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.].

2004. *Pseudothurmannia* (*Pseudothurmannia*) *sarasini* Sarkar.– Kakabadze, p. 385, pl. 2, fig. 8.

2005. *Pseudothurmannia* (*Pseudothurmannia*) *sarasini* Sarkar.– Kakabadze, p. 350, pl. 72, fig. 5.

Holotype: Specimen from Cheiron figured by Sarkar (1955, pl. 6, fig. 12) under the name *Pseudothurmannia mortilleti* Pictet & De Loriol sp. var. *rotundata* nov., deposited in the Collection of the Geological Institute Dolomieu in Grenoble (inaccessible at present). The holotype is a very young specimen (diameter 36.5 mm) and is hardly adequate to be a holotype, because the innermost whorls and the adult whorls are not preserved. Nevertheless, it is retained as holotype because of the priority of the name, and because it could clearly be identified as a young specimen of the species. Designated herein.

Material: Forty-eight specimens in total: 46 from the Balearis Zone and basal Ohmi Zone of the Río Argos succession (Caravaca, Murcia, Spain); one specimen from the lower Cretaceous outcrops northeast of the Tornajo Mountain (Lorca, Murcia, Spain); one specimen from bed 36 of the Angles section near Angles (St. André-les-Alpes, Alpes-de-Haute-Provence, France).

Diagnosis: A species of the subgenus *Crioceratites* (*Binelliceras*) with crioconic whorls that almost touch each other and trituberculate main ribs up to a diameter of 10-11 mm. Ornamentation reminiscent of *Pseudothurmannia ohmi*, that is, strong main ribs separated by a few shorter intermediate ribs, most of them having ventrolateral tubercles. On the inner whorls the intermediate ribs do not cross the ventral side and the ventrolateral tubercles may sit on two ribs (fibulation). The ventrolateral tubercles probably represent the bases of small spines. In the adult stage the main ribs are strong, radial, regularly spaced, and provided with prominent umbilical bullae and ventrolateral tubercles; the latter are stronger than those on the thinner intermediate ribs and discernable up to the aperture. All intermediate ribs, 2-6 per interval, have smaller ventrolateral tubercles, which also remain visible up to the aperture.

Description: The whorls are just not in contact and the distance between them is 0-0.5 mm. The whorl section is compressed oval and the broadest part is at the umbilical rim. The venter is rounded, but slightly truncated and the flanks are slightly convex. The dorsal side is slightly concave and in some specimens the venter of the penultimate whorl disappears in this concavity.

The ornamentation of the innermost whorls could not be examined. At a diameter of 6 mm (whorl height 2 mm) the ornamentation consists of distant prorsiradiate ribs adorned with ventrolateral and lateral tubercles. The first small umbilical tubercle appears at a diameter of 7.5 mm. From this diameter intermediate ribs become inserted between the tuberculated main ribs, first only one or two, but rapidly augmenting to five, increasing the distance between the main ribs. However, the ventrolateral tubercles keep the same mutual distance and, therefore, their number between two main ribs increases gradually, though not as quickly as the number of intermediate ribs. This means that there are intermediate ribs with or without a ventrolateral tubercle, or two intermediate ribs converging to one tubercle (fibulation). From a diameter of 9 mm, two or three ribs may originate from one umbilical bulla. At first, the main ribs are almost straight to slightly flexuous, have the same thickness as the intermediate ones, and distinguish themselves only by their trituberculation. The inner whorls of the holotype are not preserved up to a diameter of 10 mm.

At a diameter of approximately 10-11 mm, lateral tubercles disappear (in two specimens they disappear at a diameter of 20 mm) and the main ribs gradually thicken, though the difference between the main and intermediate ribs remains small, which gives the impression of fine, uniform ribs up to a diameter of 25-30 mm. The main ribs are nearly straight, only slightly flexuous; every two of them are irregularly separated by 2-6 intermediate ribs, but normally they are regularly separated by 3-4 intermediate ribs, and are bituberculate. The umbilical bullae become prominent and pointed at their upper end. As to the ventrolateral tubercles, fibulation gradually diminishes and almost every rib has one ventrolateral tubercle; those on the main ribs are larger than those on the intermediate ribs. The ventrolateral tubercles can be traced up to the aperture and are very small. The intermediate ribs only exceptionally reach the umbilical rim. The main ribs cross the ventral side. The intermediate ribs do not cross the ventral side at diameters smaller than c. 30 mm. The largest specimen found is about 127 mm in diameter, and the living chamber begins at a diameter of 80 mm. The holotype is a young specimen of less than 40 mm, and only the small specimens can be compared with the holotype.

Remarks: *Crioceratites* (*Binelliceras*) *rotundatus* is reminiscent of *P.* (*K.*) *ohmi ohmi,* from which it differs in the presence of lateral tubercles on the inner whorls, in the ventrolateral tubercles on the main ribs being notably larger than the fine ventrolateral clavi of *P.* (*K.*) *ohmi ohmi*, in the presence of fibulation of the ribs on the inner whorls, the main ribs being regularly spaced and thicker than the intermediate ribs on the outer part of the flanks and on the venter, and in the main ribs having larger ventrolateral tubercles than the intermediate ribs.

Crioceratites (*Binelliceras*) *rotundatus* is closely related to *C.* (*Bi.*) *ibizensis* Wiedmann, and differs from the latter in its whorls being almost in contact, the diameter of a full-grown specimen being far greater (127 mm) than in *C.* (*Bi.*) *ibizensis* (64 mm), the near lack of differentiation in the ribs up to a diameter of 25-30 mm, the intermediate ribs on the last whorl rarely reaching the umbilical edge and the main ribs of the last whorls being thick and straight, the ribbing being coarser in general and, on the living chamber, regular in distribution and direction instead of the great irregularity in *C.* (*Bi.*) *ibizensis*, and finally in the regular curvature of the whorls, which does not show the irregularity shown by *C.* (*Bi.*) *ibizensis*.

Crioceratites (*Binelliceras*) *rotundatus* is very similar to *C.* (*Bi.*) *krenkeli*, from which it differs in the early disappearance of the lateral tubercles at a diameter of 10 mm, the more robust main ribs at moderately regular distances, the lack of large clavi on the inner whorls, the presence of ventrolateral tubercles on every rib up to the aperture, and in the shortness of the part with fine uniform ribs (up to a diameter of 25 mm).

Wiedmann (1962, p. 116) considered *Crioceras angulicostatum* d'Orbigny *in* Nolan (1894, pl. 10, fig. 3a), identified herein as *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, to be conspecific with *Crioceratites majoricensis* Nolan, 1894. This is partly because Wiedmann did not consider the measure of uncoiling to be of significance among crioceratids. Besides, the ontogenetic developments of the ornamentations of *C. majoricensis* and of *C.* (*Bi.*) *rotundatus* are quite different. The trituberculate ribs disappear much earlier in *C.* (*Bi.*) *rotundatus*.

The differences between *C.* (*Bi.*) *rotundatus* and *C. angulicostatus* d'Orbigny are rather great. The latter has a thicker whorl section, coarser ribs and trituberculate ribs up to a diameter of 17 mm instead of 11 mm.

Range: Upper Balearis Zone and Ohmi Zone. From beds W23-W32 and beds A129-A149.

Geographical distribution: Spain (Majorca, Río Argos near Caravaca, La Guardia), Slovakia (Podbranč quarry, Polomec quarry), Italy (Monte Sisemol, Monte Malago), France (Cheiron), Switzerland (River Veveyse near Châtel-St.-Denis), Hungary (Marble quarry near Zirc), Georgia (Khidikari gorge of River Rioni).

8.4. *Angulicostatus* group

Diagnosis: The diagnosis of the *angulicostata* group may be worded as follows: all species of this group have their whorls not in contact, have flattened parallel flanks, and a subquadrate to subrectangular whorl section. They lack the fine, dense, uniformly ribbed part on the inner whorls, which is characteristic for the species of the *binelli* group. The species of the *angulicostatus* group have rather strong trituberculate main ribs up to the penultimate whorl at a diameter of 16-23 mm. They diagnostically have ventrolateral tubercles on every rib up to the aperture; in places two ribs may unite in one ventrolateral tubercle (fibulation); and in the early trituberculate part the ventrolateral tubercles of the main ribs are stronger than those of the thinner intermediate ones. The outer whorls have a typical pseudothurmannian ornamentation consisting of flexuous main ribs, which arise from the umbilical wall, and are provided (or not) with prominent umbilical bullae between which only a few shorter flexuous intermediate ribs are intercalated; the latter have the same thickness as the main ribs near the venter. The intermediate ribs may originate at the base or at the middle of the flanks. All ribs cross the venter without interruption.

Remarks: The species of the *angulicostatus* group were incorporated in the subgenus *Crioceratites* (*Binelliceras*) because of the similarity of the characteristics with the *binelli* group and because of the similarity of the ontogeny of these characteristics. They have, however, features that are considered more primitive than those of the *binelli* group, such as the coarseness of the ribbing and the presence of trituberculate ribs up to a large diameter. Their phylogenetic derivation is obscure and may be different from that of the *binelli* group.

8.4.1. *Crioceratites* (*Binelliceras*) *angulicostatus* (d'Orbigny, 1841)
Fig. 65; Tab. XXV

v* 1841. *Ammonites angulicostatus* d'Orbigny, p. 146, pl. 46, figs. 3-4.

non 1858. *Ammonites angulicostatus* d'Orbigny. – Pictet & De Loriol, pl. 4, figs, 3, 5-6 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1860. *Ammonites angulicostatus* d'Orbigny.– Ooster, p. 114, pl. 23, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)], *non* figs. 2-3 [probably *Pseudothurmannia (Kakabadziella) tornajensis* sp. nov.], *non* fig. 4 (*Crioceratites* sp. indet).

v *non* 1863. *Ammonites angulicostatus* d'Orbigny.– Pictet, p. 11, pl. 1bis, fig. 1, [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955], *non* fig. 2 [= *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955], *non* fig. 3 [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.].

non 1868. *Ammonites angulicostatus* d'Orbigny.– Winkler, p. 5, fig. 7, 7a-b [= *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858)].

v *non* 1888. *Crioceras angulicostatum* Pictet, *sensu* Kilian.– Kilian, p. 212 (= nom. nov. for *Ammonites angulicostatus* d'Orbigny *in* Pictet, 1863, pl. 1 bis, fig. 3 = *Crioceratites angulicostatiformis* nom. nov.).

non 1894. *Crioceras angulicostatum* d'Orbigny sp.– Nolan, p. 195, pl. 10, *non* fig. 3a [= holotype of *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, 1962], *non* fig. 3b [= *Crioceratites* (*Balearites*) *rotundatus* Sarkar, 1955], *non* fig. 3c (= *Crioceratites remanei* Wiedmann, 1962).

non 1898. *Crioceras angulicostatum* d'Orbigny.– Simionescu, p. 86, pl. 6, fig. 2 [= *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955].

non 1901. *Hoplites angulicostatus* d'Orbigny.– Sarasin & Schöndelmayer, p. 81, pl. 10, fig. 3 [= *Pseudothurmannia* (*Parathurmannia*) *sarasini* Sarkar, 1955, holotype], *non* pl. 9, fig. 8 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), macroconch].

non 1905. *Hoplites angulicostatus* d'Orbigny.– Richards, p. 346 (4), pl. 9, fig. 4 [= possibly *Pseudothurmannia* (*Kakabadziella*) *tornajensis* sp. nov.].

non 1907. *Crioceras angulicostatum* d'Orbigny.– Karakasch, p. 134, pl. 16, fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], *non* pl. 15, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov. macroconch].

v *non* 1910. *Hoplites* (*Neocomites*) *angulicostatus* d'Orbigny.– Kilian, p. 222, pl. 5, fig. 6a [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955], *non* fig. 6b (= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.).

v *non* 1910. *Crioceras angulicostatum* (d'Orbigny, Pictet) Kilian.– Kilian, p. 224, pl. 5, fig. 6a [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955], *non* fig. 6b [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.].

non 1919. *Parahoplites angulicostatus* d'Orbigny.– Rodighiero, p. 103, pl. 25(11), fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1923. *"Parahoplites"* (*Thurmannites?*) *angulicostatus* (d'Orbigny) *in* Pictet.– Spath, p. 66, footnote 1 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].

v *non* 1939. *Parahoplites* (*Pseudothurmannia*) *angulicostatus* (d'Orbigny) *in* Pictet.– Roman, p. 347, pl. 34, fig. 328a-b [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955], *non* fig. 329 [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.].

non 1939. *Parahoplites angulicostatus* (d'Orbigny).– Ramaccioni, p. 207, pl. 14, figs. 13-14 (= unidentifiable ammonite).

non 1949. *Crioceras angulicostatum* d'Orbigny.– Petkovic & Miletic, p. 134, pl. 2, figs. 11-12 (= *Dufrenoyia*).

non 1949. *Pseudothurmannia angulicostata* d'Orbigny.– Luppov *et al.*, p. 223, pl. 63, fig. 4 [= *Pseudothurmannia (Kakabadziella) ohmi valbonnettensis* subsp. nov. (macroconch)].

non 1955. *Pseudothurmannia angulicostata* Hyatt (error: should be by d'Orbigny).– Eristavi, p. 94, pl. 3, fig. 7 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)].

non 1955. *Pseudothurmannia angulicostata* var. *tuberculata* nov.– Sarkar, p. 155, pl. 6, fig. 13 [= *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* (Torcapel, 1884)].

non 1957. *Pseudothurmannia angulicostata* d'Orbigny var.– Almela & De La Revilla, pl. 11, fig. 1 [= *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* (Torcapel, 1884)].

v 1957. *Pseudothurmannia angulicostatus* d'Orbigny.– Arkell *et al.*, p. L212, fig. 241, fig. 1a-b.

non 1958. *Parahoplites angulicostatus* d'Orbigny.– Fülöp, p. 78, pl. 7, fig. 6 (= *Crioceratites* sp. indet.).

non 1958. *Pseudothurmannia angulicostata* (d'Orbigny).–

Luppov & Drushchits, p. 101, pl. 46, fig. 5 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

non 1960. *Pseudothurmannia angulicostata* d'Orbigny.– Drushchits & Kudrjavtsev, p. 288, pl. 30, fig. 5a-b (= unidenfiable ammonite, perhaps a douvilleiceratoidean).

non 1961. *Pseudothurmannia angulicostata* d'Orbigny.– Eristavi, p. 97, pl. 4, fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)].

v *non* 1962. *Crioceratites* (*Pseudothurmannia*) aff. *angulicostatus* (d'Orb.) (cotype).– Wiedmann, p. 138, pl. 10, fig. 1a-b. [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].

non 1964. *Pseudothurmannia* [ex gr. *angulicostata* (d'Orb.)].– Fülöp, pl. 18, fig. 5 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], pl. 27, fig. 6 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)].

non 1965. *Pseudothurmannia angulicostata* (d'Orbigny).– Dimitrova, p. 217, pl. 1, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *picteti* Sarkar, 1955], *non* fig. 2 [= probably *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], *non* fig. 3 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

non 1967. *Pseudothurmannia angulicostata* (d'Orbigny).– Dimitrova, p. 72, pl. 31, fig. 1 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.].

non 1969. *Pseudothurmannia angulicostata* (d'Orbigny).– Pasternak & Lozynyak, p. 42, pl.1, fig. 4 (unidentifiable ancyloceratacean).

non 1974. *Pseudothurmannia angulicostata* (d'Orbigny).– Lapeyre, p. 82, pl. 1, figs. 1-9 [*Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov. macroconchs].

non 1975. *Pseudothurmannia angulicostata* d'Orbigny.– Leshchukh, p. 103, pl. 1, figs. 5-6. (= *Pseudothurmannia*? indet.).

non 1980. *Pseudothurmannia angulicostata* (d'Orbigny).– Thomel, p. 53, fig. 91 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.]

non 1988. *Crioceratites* (*Pseudothurmannia*) *angulicostatus* (d'Orbigny) .– Wilke, p. 20, pl. 2, figs. 27-28 [= ambo *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi*? (Winkler, 1868)].

non 1989. *Pseudothurmannia angulicostata*.– Vašíček, p. 118 pl. 1, fig. 4 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)].

non 1990. *Pseudothurmannia angulicostata* (d'Orbigny).– Thomel, pl. 6, figs. 1-7 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.], *non* figs. 8-9 [= *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897)], *non* figs. 10-12 [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].

non 1993. *Pseudothurmannia angulicostata* (d'Orbigny).– Autran, p. 114, pl. 13, fig. 6 [= *Pseudothurmannia* (*Pseudothurmannia*) *ohmi valbonnettensis* subsp. nov.].

non 1994. *Pseudothurmannia angulicostata* (d'Orbigny).– Vašíček *et al.*, p. 65, pl. 20, fig. 3 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)].

non 1995. *Pseudothurmannia* cf. *angulicostata* (d'Orbigny).– Avram, p. 119, pl. 9, figs. 1-2 [= both *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* n. sp. (microconchs)].

non 1995. *Pseudothurmannia* (*Pseudothurmannia*) *angulicostata* (d'Orbigny).– Vašíček, p. 176, pl. 5, fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)].

non 1995. *Pseudothurmannia angulicostata* (d'Orbigny).– Cecca & Pallini, p. 212, pl. 1, fig. 11 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

v 1995b. *Crioceratites angulicostatus* d'Orbigny, *non* Kilian.– Hoedemaeker, p. 232, pl. 4, fig. 5a-c (holotype with uncovered penultimate whorl).

non 1995. *Pseudothurmannia angulicostata Auctt.*– Faraoni *et al.*, p. 230, pl. 2, fig. 11 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., microconch].

non 1995. *Pseudothurmannia angulicostata* (d'Orbigny).– Cecca *et al.*, p. 199, pl. 1, fig. 2 [= *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov.].

non 1996. *Pseudothurmannia angulicostata* (d'Orbigny).– Wright, p. 214, fig. 163, fig. 4a-b [= *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov.]

v 2002. *Pseudothurmannia angulicostata* (d'Orbigny) – Vermeulen, p. 28-29, pl. 57, fig. 3 (holotype).

non 2002. *Spathicrioceras angulicostatum* (Kilian).– Vermeulen, p. 29, pl. 57, fig. 1 [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.].

v 2002. *Pseudothurmannia angulicostata* (d'Orbigny).– Vermeulen *et al.*, p. 73, pl. 2, fig. 2 (holotype).

non 2002. *Spathicrioceras angulicostatum* (Kilian).– Vermeulen *et al.*, p. 73, pl. 1, fig. 1 [= *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.].

non 2002. *Spathicrioceras* aff. *angulicostatum* (Kilian).– Vermeulen *et al.*, p. 73, pl. 2, fig. 3 [= *Crioceratites* (*Binelliceras*) *seitzi* ? Sarkar, 1955].

v *pars* 2003. *Pseudothurmannia angulicostata* (d'Orbigny).– Busnardo, p. 66, pl. 29, figs. 2-3. (holotype with uncovered penultimate whorl), possibly pl. 31, fig. 1, *non* pl. 14, fig. 3 (= *Crioceratites* sp. indet.).

v *non* 2003. *Pseudothurmannia angulicostata* (d'Orbigny) Pictet.– Busnardo, p. 67, pl. 29, fig. 6 (= *Crioceratites angulicostatiformis* nom. nov.).

non 2003. *Crioceratites angulicostatus* (d'Orbigny).– Company *et al.*, p. 688, fig. 5.9. [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)], *non* fig. 5.10. [= *Crioceratites* (*Binelliceras*) *seitzi* Sarkar, 1955].

v 2004. *Pseudothurmannia angulicostata* (d'Orbigny).– Vermeulen, p. 73, pl. 1, fig. 2 (holotype).

non 2005. *Crioceratites angulicostatus* (d'Orbigny).– Company *et al.*, p. 188, fig. 4C [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi*].

v 2006. *Pseudothurmannia angulicostata* (d'Orbigny).– Busnardo & Gauthier, p. 50, pl. 16, fig. 5a-b (holotype).

v 2009. *Spathicrioceras angulicostatum* (d'Orbigny, 1841).– Vermeulen, p. 71, pl. 2, fig. 2.

Holotype by monotypy: *Ammonites angulicostatus* d'Orbigny, 1841 (p. 146, pl. 46, figs. 3-4), from the Neocomian of the site called Chamateuil near Castellane (Alpes-de-Haute-Provence); deposited in Muséum National d'Histoire Naturelle de Paris, nr LPMP-R4272 (Emeric collection nr 7.A.51).

Material: Two specimens: (1) two different plaster casts of the holotype of *Ammonites angulicostatus* d'Orbigny, one showing the penultimate whorl, being stripped of the surrounding stone by Busnardo (kindly sent to the author by Dr. L. G. Bulot), and one from which the surrounding stone was not yet stripped off (kindly sent to the author by Dr. Max Wippich; (2) a second specimen from the Tornajo Mountain (Lorca, Spain). Additionally, two small whorl fragments from the Tornajo Mountain identified as *P.* (*Bi.*) cf. *angulicostatus* (d'Orbigny).

Description of the plaster cast of the holotype: Figs. 60A-C. The specimen consists of one half of the outer whorl and the penultimate whorl. The whorl section is subquadrate and considerably thicker than any known *Pseudothurmannia* (*Kakabadziella*); Wh 18 mm, Wt 15 mm, Wt/Wh = 0.83. The flanks of the ultimate half whorl are slightly curved and the venter is slightly arched creating a subrectangular shoulder. The steep and high umbilical wall is smooth. The main ribs are thin and sharp, and originate closely below the rounded umbilical rim; they are prorsiradiate and slightly heightened when passing the rim. The main ribs are rather close together and every two of them commonly separated by one short intermediate rib, occasionally by two. One of them is forked. The intermediate ribs have the same thickness as the main ribs and generally originate around midflank.

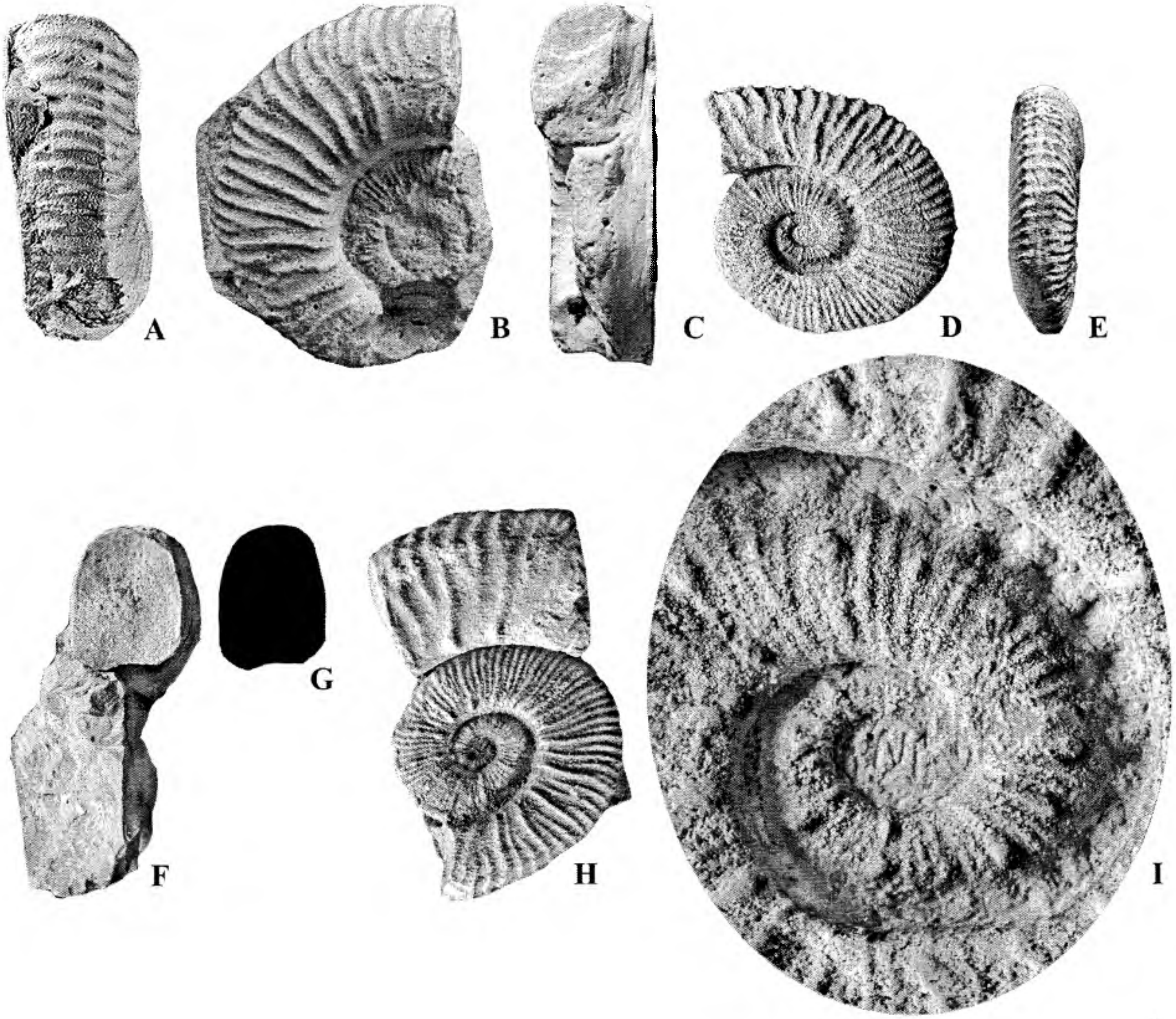


Fig. 65: A-H, *Crioceratites* (*Binelliceras*) *angulicostatus* (d'Orbigny, 1841), A, plaster cast of holotype, lateral view, locality 7; ×1. B, same specimen, apertural view; ×1. C, same specimen, ventral view; ×1. D, RGM 542863, only certain second specimen of this species, left lateral view of inner whorls, locality 3B, loose from beds B200-208; ×1. E, inner whorls of same specimen, ventral view, showing uniform ventrolateral tubercles on every rib; ×1. F, same specimen, apertural view, whorl section comparable with holotype; ×1. G, same specimen, outline of whorl section; ×1. H, same specimen, right lateral view of whole specimen; ×1. I, same specimen, left lateral view of innermost whorls showing the large distance of ventrolateral tubercles; ×4.

Near the oral side, the main ribs become flexuous, have somewhat stronger umbilical crests and in one instance are separated by four intermediate ribs. All ribs pass the venter equal in strength with a weak adoral convexity. On each shoulder every rib exhibits a tiny ventrolateral tubercle (on the plaster cast they are hardly visible, but become apparent when the light is falling in with a small angle).

The penultimate whorl, uncovered by Prof. Dr. Robert Busnardo, exhibits a quite different ribbing. The cleaned portion of the penultimate whorl shows 14 straight main ribs with prominent umbilical tubercles; seven of them have lateral tubercles. The lateral tubercles are slightly above the middle of the whorl. The thick main ribs are straight and rather wide apart. They are separated by 2-3 thinner non-tuberculate intermediate ribs, which are also straight and rather wide apart. The ventral side cannot be studied. The lateral tubercles disappear in adoral direction at a diameter of 17 mm and the main ribs become less thick. The last two main ribs visible on the cleaned half penultimate whorl become slightly flexuous and the number of intermediate ribs between the last two main ribs augments to four (D= 20 mm).

The last half a whorl shows the well-known ribbing consisting of main ribs with 1-2 long and short intermediate ribs. The main ribs are raised a little at the umbilical rim; this raising differentiates them from the long intermediate ribs, which appear at the rim without such raising. These raisings are degenerated umbilical bullae. Near the aperture the number intermediate ribs between every two main ribs increases to three or four. Weak ventrolateral tubercles remain discernable.

The whorls are separated by a narrow gap of about 1 mm Diameter of the plaster cast: 49 mm; Umbilical width: c. 22 mm (44.0)

Comment: This specimen that d'Orbigny had before him (Dr. Max Wippich, Bochum, Germany, kindly sent the author the plastercast) was in fact inadequate to function as holotype, because it consisted only of one third of a whorl, was visible from one side only, and the inner whorls were not preserved. There are so many parts that cannot be studied that it had better be considered a *nomen dubium*. However, since Busnardo (pers. comm. 1990, during the first meeting of the Lower Cretaceous Cephalopod Team in Digne, see Hoedemaeker & Bulot, 1990) freed the penultimate whorl of the holotype from its surrounding stone and detected the lateral tubercles, its systematic position became clear. It is the merit of Nolan (1894) to have produced arguments that *angulicostatus* probably belongs to *Crioceratites*, but only after 1990 did this become certain, and it then became possible to search for a second specimen. The search for a neotype in the *locus typicus* by Lapeyre (1974) and later independently by the author was doomed to failure, because neither of them was searching for a crioconic ammonite with lateral tubercles on the inner whorls. In 1972 and 1973, the author collected a lot of specimens from Chamateuil near Castellane (Alpes-de-Haute-Provence), the locus typicus of *Ammonites angulicostatus* d'Orbigny; he has a drawer full of fragments. He selected a 'neotype' of *A. angulicostatus*, but Lapeyre (1974) published his neotype first, and the present author gave up publishing it. However, after having obtained the plaster cast of the holotype of *A. angulicostatus* with the uncovered penultimate whorl (kindly sent to the author by Dr. Luc Bulot, Marseille), none of the ammonites found near Chamateuil could be matched with the holotype and the neotype proved to be identical to *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov. Therefore, it was a surprise to find an incomplete specimen that shows all characteristics of *A. angulicostatus* among the material collected from the Tornajo Mountain (Lorca, Murcia, Spain). This specimen will be described here. *Crioceratites* (*Binelliceras*) *angulicostatus* (d'Orbigny) is no longer the type species of the genus *Pseudothurmannia*.

Description of the specimen from the Tornajo Mountain. Figs. 60D-I. RGM 542863. The whorls slightly crioconic and leave a gap of 1 mm. They can be studied from a diameter of 4 mm (whorl height of 1 mm). Here thick main ribs with lateral and ventrolateral tubercles are wide apart, and separated by two thinner intermediate ribs. Every second main rib is provided with an umbilical bulla from a diameter of 6 mm and every second main rib becomes weak. The latter still has a weak lateral tubercle, but loses its umbilical bulla with growth. Not only the main ribs, but also the intermediate ribs are provided with small ventrolateral spines. The two intermediate ribs between the main ribs unite into one ventrolateral spine (fibulation).

From a diameter of 15 mm the main ribs are at a regular distance from each other and separated by four intermediate ribs. All ribs originate on the steep and high umbilical wall just below the rounded rim. The four intermediate ribs correspond with three ventrolateral spines, because two of them unite into one spine (fibulation).

From a diameter of about 20 mm the lateral tubercles disappear and the main ribs, which are separated by a diminishing number of intermediate ribs, become finer and slightly flexuous (this corresponds to the last part of the uncovered penultimate whorl of the holotype). In this trajectory the number of intermediate ribs gradually diminishes from four to two. The umbilical bullae become less prominent and more elongated. The ventral side is smooth and is traversed only by the main ribs. The ventrolateral spines on the main ribs have a broad base, which straddles the main rib and the adjacent adoral rib; the latter is shorter than the other intermediate ribs and starts at one third flank height. Every second intermediate rib has now its own small spine.

From a diameter of 33 mm the number of intermediate ribs to one main rib diminishes to two (this corresponds to the beginning of the preserved part of the last whorl of the holotype). Most intermediate ribs originate at about one third of the flank height. The umbilical bullae are reduced to weak elevations. All ribs are of equal size, markedly prorsiradiate and cross the venter in an almost straight line. The shoulders exhibit rows of small equal tubercles.

One third of the last whorl is missing.

The adoral part of the outer whorl (which corresponds to the aperture of the holotype) shows prominent main ribs, which are a little higher at the umbilical rim, and 2-3 intermediate ribs which bifurcate or not; the point of forking is at midflank. One of the main ribs also forks at midflank. The whorl section is subquadrate and at the place that corresponds to the aperture of the holotype it measures Wh 19.4 mm, Wt 16.4 mm, Wt/Wh = 0.84. The ribs cross the venter with a weak adoral convexity and each of them is provided with a small ventrolateral tubercle, probably the preserved base of a small spine.

Remarks: The missing one third of the whorl of the Tornajo specimen is equivalent to the middle portion of the preserved outer half whorl of the holotype of *Crioceratites* (*Binelliceras*) *angulicostatus* (d'Orbigny). Only the ornamentation at the beginning and the end of the preserved outer whorl of the holotype can be compared with the ornamentation at both sides of the missing part in the Tornajo specimen. The ornamentations on the parts that can be compared are very alike. The ornamentation of the penultimate whorl of the holotype is the same as that of the equivalent part of the Tornajo specimen; the trituberculate part of the Tornajo specimen ends at approximately the same diameter as in the holotype. So, the ornamentation as well as the ontogenetic development of both specimens is the same as far as it can be compared. However, the most compelling reason why the author thinks that the two specimens are conspecific is the subquadrate whorl section at the aperture. There is no species among the whole group of *Crioceratites* of the *angulicostata* group that has a subquadrate whorl section in which Wt/Wh = 0.84, except for *Crioceratites* (*Binelliceras*) *angulicostatus* (d'Orbigny). The Tornajo specimen is hitherto the only other sure specimen of *C.* (*B.*) *angulicostatus* (d'Orbigny).

The Tornajo specimen has a similar ornamentation and a similar ontogenetic development of ornamentation as *Crioceratites* (*Binelliceras*) *seitzi* Sarkar, 1955. However, *C.* (*Bi.*) *seitzi* has a rounded venter, whereas *C.* (*Bi.*) *angulicostatus* has a flattened venter; *C.* (*Bi.*) *seitzi* has a much more compressed whorl section than *C.* (*Bi.*) *angulicostatus*. The two known specimens of *C.* (*Bi.*) *angulicostatus* were found in the Tornajo Mountain and in Chamateuil near Castellane in neritic facies, whereas the specimens of *C.* (*Bi.*) *seitzi* were found only in deep water environments (deep shelf or upper bathyal environments) in Angles and in the Río Argos succession. Perhaps the two species have the same stratigraphic range, but have a different biotope.

Range: The second specimen from the Tornajo Mountain was found in one of the beds B200 to 208, which form part of the upper Hauterivian Ohmi Zone.

Geographic distribution: France (Chamateuil near Castellane; Les Voirons), Spain (Tornajo Mountain in the municipality of Lorca),

8.4.2. *Crioceratites* (*Binelliceras*) *seitzi* Sarkar, 1955
Fig. 66; Tab. XXVI

* 1955 *Crioceras seitzi* n. sp.– Sarkar, p. 70, pl. 3, fig. 3.
1982 *Crioceratites* (*Pseudothurmannia*) *provencalis* (Wiedmann).– Braga *et al.*, p. 687, pl. 1, fig. 6.
1995b *Crioceratites "provencalis"* Braga *et al.*, *non* Wiedmann.– Hoedemaeker, p. 236, pl. 5, figs. 8, 9.
2000 *Crioceratites "provencalis"* Braga *et al.*, *non* Wiedmann.– Vašiček & Faupl, p. 603, pl. 6, fig. 8.
? 2002 *Spathicrioceras* aff. *angulicostatum* (Kilian, 1888).– Vermeulen *et al.*, p. 74, pl. 2, fig. 3.
2003 *Crioceratites angulicostatus* (d'Orbigny).– Company *et al.*, p. 688, fig. 5.10, *non* fig. 5.9. [= *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868)].
? 2004 *Pseudothurmannia seitzi* (Sarkar).– Vermeulen, p. 73, pl. 1, fig. 3.
2009 *Spathicrioceras seitzi* (Sarkar).– Vermeulen, p. 71, pl. 2, fig. 3.

Holotype by monotypy: The specimen from the Angles section depicted by Sarkar (1955, pl. 3, fig. 3), which is deposited in the Geological Institute Dolomieu in Grenoble (inaccessible at present).

Material: Ten specimens. Eight from the Río Argos succession (Caravaca): one well preserved specimen (GIA J9963) from an unknown bed of section W, c. 250 m west of the Cortijo de Alguacil; four fragments and three imprints from beds W28-W30, and from A142-A144 along the Río Argos (Caravaca). Two gypsum casts from bed 26 (ED.84.26.3) and bed 27 (ED.84.27.1) from the section of the Ermita de Cuadros (near Bédmar, Province of Jaen) kindly sent to the author by Prof. Dr. M. Company (Granada).

Description of specimen GIA J9963 from the Río Argos succession (Fig. 66D). The whorls of this well preserved specimen are just not in contact. The gap between the whorls is about 1 mm. Two whorls are preserved. Whorls compressed with a high-oval section, which is thickest at one third of the flank height. Venter rounded; flanks slightly curved; umbilical wall rounded.

The ornamentation is visible from a diameter of 9 mm. The inner whorls show lateral tubercles on the main ribs. Ventrolateral tubercles are not visible. The main ribs are generally separated by two thinner intermediate ribs without tubercles. Ribs become flexuous and originate from the umbilical wall at a diameter of 12 mm. From this diameter the first three intervals between the main ribs have five flexuous intermediate ribs of which the middle one is still provided with a weak lateral tubercle and is a degenerated main rib. From a diameter of 14 mm, the number of intermediate ribs varies from three to four, rarely two. The lateral tubercles disappear at a diameter of 16 mm. The intermediate ribs become thinner towards the umbilicus and originate at or just above the umbilical rim except one, which originates on the umbilical wall. Every rib has a ventrolateral tubercle, forming two rows of uniform tubercles, which are visible from a diameter of 16 mm.

On a large part of the penultimate whorl, the ribbing remains less differentiated than in more adult parts, that is, the main ribs do not differ much in strength from the intermediate ribs up to a diameter of 24 mm. The ribbing of the adult stage begins at this diameter. The main ribs are distant from each other, are provided with pointed umbilical tubercles, become more prominent than the intermediate ribs and remain so on the outer part of the flanks. There are three intermediate ribs between every pair of main ribs. The intermediate rib at the apical side of the main rib is generally the shortest and may converge to, or in a few cases split from, the main rib near the umbilical bulla or at midflank.

The ribs become coarse and are more distantly spaced from a diameter of 37 mm. From this diameter there are only 1-2 intermediate ribs between each pair of main ribs. On the rounded venter the ribs are approximately equal and cross it with an adoral convexity. Rounded ventrolateral tubercles (remnants of small spines) are present on every rib on the inner whorls and remain present up to the aperture.

Near the aperture the number of intermediate ribs to one main rib increases to 3-4.

Remarks: *Crioceratites* (*Binelliceras*) *seitzi* clearly belongs to the *angulicostatus* group; the ornamentation closely resembles that of *Crioceratites* (*Binelliceras*) *angulicostatus* (d'Orbigny). The only difference is that the latter has thicker whorls, a flattened venter, and Wt/Wh ratio of 0.84. According to the measurements of Sarkar on the holotype of *C.* (*Bi.*) *seitzi*, the ratio Wt/Wh = 0.58; in our specimen, which is flattened by compaction, the ratio Wt/Wh = 0.55. The gap between the whorls on the photograph in Sarkar, 1955, of the holotype *C.* (*Bi.*) *seitzi* is clearly wider than in *C.* (*Bi.*) *angulicostatus*, although Sarkar (1955, p. 70) describes it as 'faiblement disjoint' ('weakly uncoiled'). Sarkar (1955) regards this species as a transitional form between *Crioceratites* and *Pseudothurmannia* because of the presence of two ventrolateral rows of very small tubercles on every rib. It was not known in Sarkar's time that the holotype of

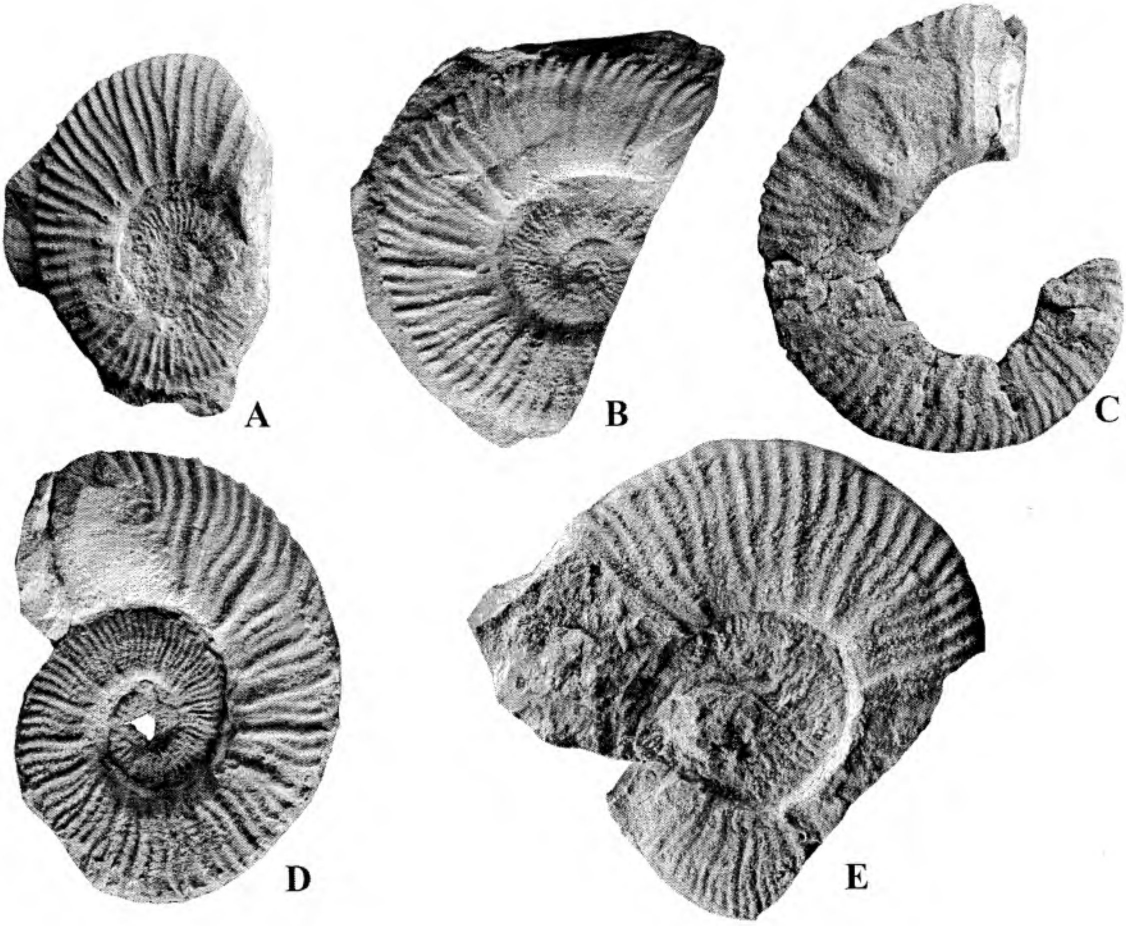


Fig. 66: A-E, *Crioceratites* (*Binelliceras*) *seitzi* Sarkar, 1955. A, ED.84.27.1, locality 4, bed 26; ×1. B, ED.84.27.3, locality 4, bed 27; ×1. C, RGM 387979, locality 1A, bed A144; ×1. D, GIA J9963, locality 1W; ×1. E, RGM 542315, locality 1W, bed W30; ×1.

C. (*P.*) *angulicostatus* has a similar ornamentation on the penultimate whorl.

A second specimen of *C.* (*Bi.*) *seitzi* from the Angles section has been figured by Vermeulen (2004, pl. 1, fig. 3) and was collected from the same bed (bed 37) in which he found his *'Spathicrioceras' angulicostatum* (Kilian) [here renamed in *Crioceratites* (*Binelliceras*) *angulicostatiformis* nov. nom.]. Vermeulen (2004) considered *C.* (*Bi.*) *seitzi* the transitional species between *'Spathicrioceras' angulicostatum* (Kilian, 1888) and *Ammonites angulicostatus* d'Orbigny, 1841. Two years earlier Vermeulen *et al.* (2002) identified the same specimen as *Spathicrioceras* aff. *angulicostatum* (Kilian, 1888).

Crioceratites (*Binelliceras*) *seitzi* shows a great likeliness to *Pseudothurmannia karakaschi* Manolov, 1962, in the coarseness of the ribs, the prominence of the distantly spaced main ribs, the flexuosity of the ribs, the length of the intermediate ribs and the large umbilicus. However, the holotype of *P. karakaschi* is so badly preserved that it cannot be used as a holotype of a new species. The inner whorls are not preserved, and the presence or absence of lateral and ventrolateral tubercles remains unknown.

Range: Upper Hauterivian, upper Balearis and lower Ohmi zones. W30 and from A142-A144.

Geographical distribution: France (Angles), Spain (Río Argos near Caravaca, La Guardia near Jaen, Arroyo Gilico near Cehegin), Austria (Reschen near Groszraming).

8.4.3. *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov.

Figs. 67-69; Tab. XXVII

v* *pars* 1863. *Ammonites angulicostatus* d'Orbigny.– Pictet, p. 13, pl. 1 bis, only fig. 3a-b, *non* fig. 1a-b [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955], *non* fig. 2a-b [= *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955].
1888. *Crioceras angulicostatum* Pictet sp.– Kilian, p. 212 (see note 3).
v *pars* 1910. *Crioceras angulicostatum* Pictet.– Kilian, p. 222, 270, pl. 5, fig. 6b, *non* fig. 6a [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].
v *pars* 1910. *Crioceras angulicostatum* [d'Orbigny, Pictet] Kilian.– Kilian, pp. 224, 236, pl. 5, figs. 6b, *non* 6a [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].
v *pars* 1939. *Parahoplites* (*Pseudothurmannia*) *angulicostatus* (d'Orbigny) in Pictet.– Roman, p. 347, pl. 34, fig. 329, *non* fig. 328a-b [= *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955].
2002. *Spathicrioceras angulicostatum* (Kilian).– Vermeulen, pl. 57, fig. 1.
2002. *Spathicrioceras angulicostatum* (Kilian).– Vermeulen *et al.*, p. 74, pl. 1, fig. 1.
v 2003. *Pseudothurmannia angulicostata* (d'Orbigny) Pictet, 1863.– Busnardo, p. 67, pl. 29, fig. 6.

Holotype by monotypy: The specimen from the Angles section (Alpes-de-Haute-Provence, France) figured by Pictet (1863, pl. 1 bis, fig. 3a, b) under the name *Ammonites angulicostatus* d'Orbigny, deposited in the Museum d'histoire naturelle de Genève, Switzerland, Pictet collection, No. 16850, kindly sent to the author by Dr. D. Decrouez.

Material: A plaster cast of the specimen depicted by Pictet (1863, pl. 1 bis, fig. 3a, b) from the section near Angles.

Derivation of name: *Angulicostatiformis* means 'having the shape of *angulicostatus*.' As both *Ammonites angulicostatus* (d'Orbigny, 1841) and *Crioceras angulicostatum* (Kilian, 1888) are different species of the same genus *Crioceratites* and the same subgenus *Binelliceras*, this change of name for the latter species is necessary. The solution of Vermeulen (2002, 2009) to call both species with the same name, but with different author's names, viz."*Spathicriocras angulicostatum* (d'Orbigny)" and "*Spathicrioceras angulicostatum* (Kilian)" is not acceptable.

Description of the plaster cast of the holotype: The holotype of this specimen will be described here, especially since the drawing in 'Mélanges paléontologiques' is wrong and Vermeulen did not describe the second specimen he found.

The whorls of this species are just not in contact. The gap between the whorls is c.1 mm. The umbilicus is

Fig. 67: A-B, *Crioceratites* (*Binelliceras*) *angulicostatiformis* nom. nov. A, plaster cast of holotype, ventral view, locality 5; ×1. B, same specimen, lateral view; ×1.

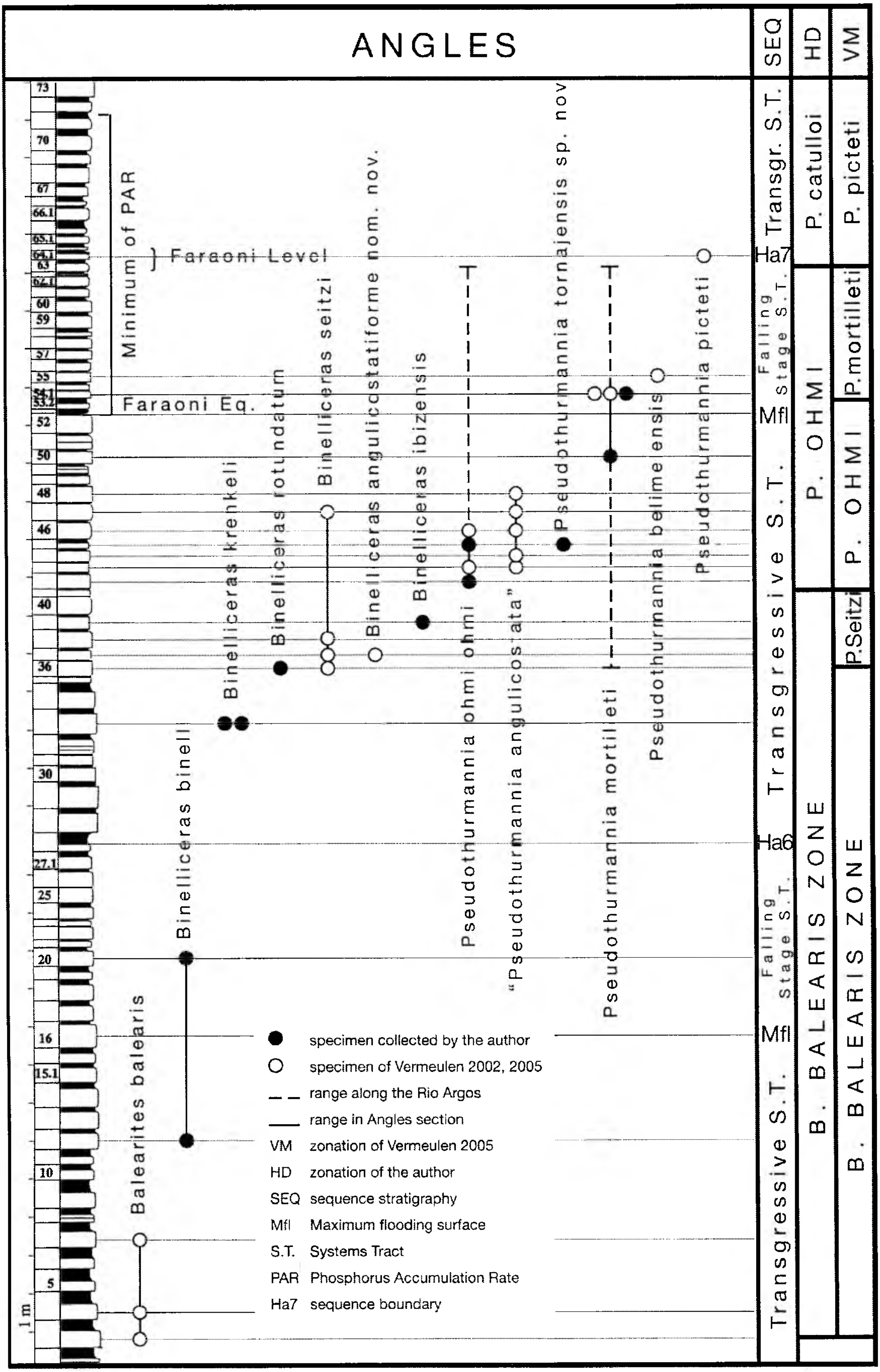


Fig. 68: Ranges of species of *Pseudothurmannia*, *Binelliceras* and *Balearites* in the Angles section (Alpes-de-Haute-Provence, France) according to Vermeulen (2005) and the author, and the probable stratigraphic position of the Faraoni Level.

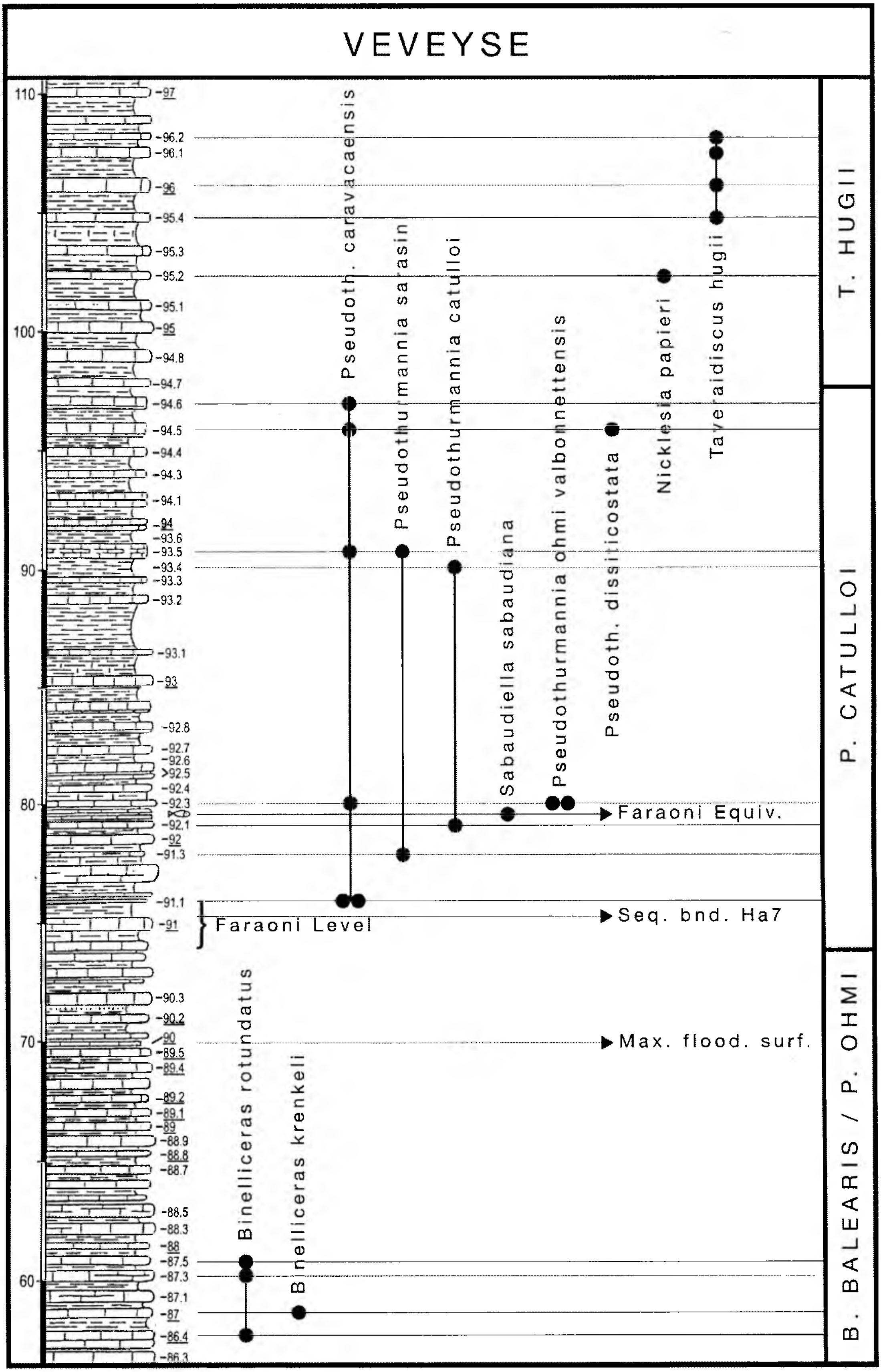


Fig. 69: Ranges of *Pseudothurmannia* and *Binelliceras* in the section along the River Veveyse near Châtel-St.-Denis (Fribourg, Switzerland) according to the samples collected and figured by Busnardo *et al.* (2003), and the probable stratigraphic position of the Faraoni Level.

perforated, and two and one third whorls are preserved. Whorls compressed with a high-oval section. Venter flattened, only slightly arched; flanks slightly curved; whorls thickest just above the umbilical rim; umbilical wall rounded; and dorsal side flat or slightly concave.

The ornamentation can be studied from a diameter of 6 mm and a whorl height of 2 mm. The inner whorls are ornamented by thick main ribs with lateral tubercles and thinner, non-tuberculate intermediate ribs. Between every two main ribs is only one intermediate rib [*C.* (*Bi.*) *seitzi* GIA J9963 and *C.* (*Bi.*) *angulicostatus*, RGM 542863, have two intermediate ribs]. Every second main rib is thick, and has, apart from the lateral tubercle, an umbilical tubercle. Every other main rib is thinner and lacks an umbilical tubercle, but still has a lateral tubercle. The latter type of rib can be referred to as degenerated main ribs. All ribs originate on the umbilical wall.

From a diameter of 18 mm the thinner main ribs lose their lateral tubercles and can be referred to as intermediate ribs, but remain long, whereas the other intermediate ribs originate at one third flank height. Between every two main ribs there are now three to four intermediate ribs. The intermediate ribs become thinner towards the umbilicus and originate at, or just above, the umbilical rim except one, which originates on the umbilical wall. On the flanks the main ribs are thicker than the intermediate ribs and remain so near the venter.

At a diameter of 23 mm the main ribs lose their lateral tubercles too, and the ornamentation consists of long and short ribs. There are two kinds of long ribs, that is, long ribs either without or with umbilical tubercles; the latter look like main ribs. Every two long ribs are separated by one shorter and thinner intermediate rib. From a diameter of 28 mm the number of thin intermediate ribs between every two long ones augments to two, of which one originates on the umbilical wall, and the other at one third flank height.

There are three intermediate ribs at a diameter of 43 mm, of which the middle one is the longest (immature main rib). At a diameter of 50 mm the immature main ribs become real main ribs by strengthening and obtaining umbilical tubercles; they are generally separated by one short intermediate rib, rarely two, which originate from the neighbourhood of the adapical main rib or actually may split off from it at midflank or at the umbilical bulla. The umbilical bullae become slightly more pronounced and are pointed.

At this diameter begins the living chamber. Close to the aperture the main ribs are farther apart and markedly thicker; they are separated by two or three intermediate ribs; forking at three quarters of the flank height is frequent.

The ventral side can be studied from a diameter of 33 mm. The venter is flattened, only slightly arched, and all ribs cross the venter without interruption and are almost equal in thickness. On the venter the ribs are convex towards the aperture. The shoulders exhibit two rows of equal, very fine tubercles, one on every rib.

Remarks: Vermeulen (2002) classified this species into the genus *Spathicrioceras*, which characteristically has very loosely coiled whorls with a very wide gap between them instead of the very small gap between the whorls of the species of the *angulicostatus* and *binelli* goups. Further *Spathicrioceras* lacks the ventrolateral rows of uniform tubercles which are characteristic for the *angulicostatus* group. He collected the second specimen known of this species in bed 37 of the Angles section.

Crioceratites (*Binelliceras*) *angulicostatiformis* mimics *Crioceratites* (*Binelliceras*) *angulicostatus* (d'Orbigny). These two species mainly differ in the whorls being more compressed, the ribbing on penultimate whorl less closely spaced than in *C.* (*Bi.*) *angulicostatus*, a greater prominence of the main ribs than in *C.* (*Bi.*) *angulicostatus*, the presence of lateral tubercles up to a diameter of 23 mm instead of 17 mm, and most intermediate ribs originating at the umbilical rim instead of at midflank. The resemblance of the ornamentation and ontogenetic development of the two species is striking, but they are definitely not conspecific.

Crioceratites (Binelliceras) angulicostatiformis differs from the *Crioceratites* (*Binelliceras*) *seitzi* in the longer trituberculate stage (up to a diameter of 23 mm instead of 16 mm) and in the more slender ribs. *Crioceratites* (*Binelliceras*) *angulicostatiformis* has generally only one or two intermediate ribs between two main ribs.

Range and geographical distribution: The holotype is derived from the upper Hauterivian of Angles (Alpes-de-Haute-Provence, France). Vermeulen's specimen is derived from bed 37 of the Angles section (in Vermeulen's Seitzi Zone).

9. KEY TO THE SPECIES OF *PSEUDOTHURMANNIA*, *BALEARITES* AND *BINELLICERAS*

I. *Pseudothurmannia* (*Pseudothurmannia*) Spath, 1923 (= *Sornayites* Wiedmann, 1962 *pro parte* = *Prieuriceras* Vermeulen, 2003 *pro parte*). Catulloi Zone

Lacks the fine-ribbed *mortilleti*-like stage, but ribs moderately wide-spaced on inner whorls. Main ribs with 2-3, rarely four intermediate ribs in young ontogenetic stages, in most species [except in *P.* (*P.*) *picteti*] followed by a *Crioceratites*-like adult stage with distantly spaced trituberculate main ribs and 3-7 intermediate ribs. The lower parts of the main ribs are broad and high starting from prominent umbilical tubercles; in young ontogenetic stages the upper and ventral parts of the main ribs are narrow and low. Lateral tubercles are absent on inner whorls, but appear on the main ribs in middle or middle to late growth stages. Rows of uniform ventrolateral clavi are present on both sides of the venter up to the aperture.

A. Early whorls overlapping.

1. *picteti* Sarkar, 1955 (= type species) (= *provincalis* Wiedmann, 1962, = *grandis* Busnardo, 1970, = *lurensis* Busnardo, 1970, = sp. A Busnardo, 1970).
Inner whorls have relatively wide-spaced ribbing with 1-4 intermediate ribs between every two main ribs, followed by a stage with 1-2, rarely three intermediate ribs, by a transient interval with blunt lateral knobs between D 65 and D 140 mm, and by an adult stage with 1-3 intermediate ribs without lateral knobs up to diameter 300 mm. Whorls overlapping up to the aperture. Venter truncated and nearly flat.

2. *simionescui* Sarkar, 1955. Early whorls with widely spaced main ribs with 3-4 intermediate ribs. At D 60 mm followed by 1-3 irregularly distributed intermediate ribs to one trituberculated main rib; this ornamentation continues at least to D 180 mm (= largest specimen known). Venter slightly rounded. Outer whorls just not in contact. Adult stage with *crioceratites*-like ornamentation consisting of 3-5 intermediate ribs to one trituberculate main rib may probable be present.

3. *crioceroides* Torcapel, 1884. (= *pseudomalbosi* Sarasin & Schöndelmayer, 1901; = *angulicostata* var. *tuberculata* Sarkar, 1955). Whorls in contact up to the aperture. On inner whorls coarse, widely spaced main ribs with 2-3 intermediate ribs. Very short stage with closely spaced main ribs with 1-2 intermediate ribs, followed at D 80-90 mm by a long adult *crioceratites*-like stage with 3-6 intermediate ribs to one trituberculate main rib. Ribs generally widely spaced and thin.

B. Early whorls evolute, in contact. Late whorls not in contact.

4. *monasteriensis* Simionescu, 1899. Similar to *crioceroides*, but whorl section subrounded instead of oval/truncated; ribs sturdier; trituberculate ribs from a diameter of 50 mm. Late whorls just not in contact. Inner whorls unknown.

5. *arundicostata* sp. nov. Sharp and straight ribs very close to each other. Long, early stage with 1-2 tapering intermediate ribs between every two closely spaced trituberculate main ribs at least from D 25 mm up to D 140 mm, followed by an adult crioceratitic stage with 3-6 intermediate ribs between every two trituberculate main ribs. Lateral tubercles appear at D 58 mm. Late whorls just not in contact.

6. *perevoluta* sp. nov. Whorls growing very slowly in height leaving an extremely wide umbilicus. Lateral tubercles in middle to late growth stages. Early whorls with fine dense ribbing and umbilical tubercles on the main ribs; 3-5 intermediate ribs to one main rib. In many intervals the middle intermediate rib originates low on the umbilical wall mimicking the main ribs, but lacking the umbilical tubercle and the prominence of its lower part. Late whorls with crioceratitic ornamentation of 4-5 intermediate ribs to one trituberculated main rib. Whorls just not touching except inner whorls.

II. *Pseudothurmannia* (*Parathurmannia*) Busnardo, 2003 (= *Sornayites* Wiedmann, 1962 *pro parte;* = *Prieuriceras* Vermeulen, 2003 *pro parte;* = *Parathurmannia* Busnardo *pro parte*). Catulloi Zone

Inner whorls overlapping with small umbilicus. Inner whorls with fine and dense ribbing consisting of widely separated main ribs and 3-6 intermediate ribs to one main rib, followed by a stage with more closely spaced strong main ribs with 1-3 intermediate ribs to one main rib, followed by an adult stage with 3-5 intermediate ribs between every two distantly spaced main ribs. The lower parts of the main ribs are high and broad starting from prominent umbilical bullae; their upper parts are thin and low like the intermediate ribs. Rows of prominent uniform ventrolateral clavi remain visible up to the aperture. Lateral tubercles are absent on the inner whorls, but present in middle growth stages or in middle to late stages.

A. With narrow umbilicus and overlapping whorls and a transient trituberculate stage.

1. *sarasini* Sarkar, 1955. (= type species)
Fine, dense, sigmoidal ribs with 3-6 long intermediate ribs between every two main ones on inner whorls; main ribs with strong comma-shaped umbilical bullae. Transient stage of half a whorl with only two, rarely three, intermediate ribs between the pairs of main ones, and with lateral tubercles on the main ribs over a quarter of a whorl, followed by adult stage without lateral tubercles with 3-5 intermediates, which efface towards the umbilicus. All whorls are overlapping.

2. *dissiticostata* sp. n. Continuation of the *sarasini*-like ribbing of the inner whorls to late growth stages, i.e. widely spaced main ribs with small umbilical tubercles and 3-6 intermediate ribs to one main rib, at first long, later short, followed by a stage with 2-3 intermediate ribs, followed by a stage with 3-5 intermediates. Lateral tubercles present in middle growth stage. Whorls are overlapping or in contact.

B. With wide umbilicus, slightly crioconic whorls, and lateral tubercles up to the aperture.

3. *edouardi* Honnorat-Bastide, 1889.
Early stage with widely spaced main ribs separated by 5-6 fine intermediate ribs visible from 25 mm diameter. Very weak lateral tubercles appear in this stage, which gradually become stronger. Probably innermost whorls in contact without lateral tubercles. Later whorls just not in contact. Later stage with only two, rarely three intermediate ribs at least to diameter 113 mm. Main and intermediate ribs more regularly distributed than in *simionescui*.

III. *Pseudothurmannia* (*Kakabadziella*) subgen. nov. (= *Parathurmannia* Busnardo, 2003, *pro parte*). Ohmi and Catulloi zones

Without lateral tubercles in any growth stage. Rows of fine uniform ventrolateral clavi. Inner whorls with fine, dense *balearis*-like ribbing and narrow umbilicus like *mortilleti*, except in *tornajensis* and *belimelensis*, which are advolute from the start. Main ribs closely spaced in middle ontogenetic stages with 1-3 intermediate ribs. In later stages ribs regularly or irregularly distributed.

A. Umbilicus smaller than whorl height.
1. *mortilleti* Pictet & De Loriol, 1858. ♀+♂ (= type species) (= *renevieri* Sarasin & Schöndelmayer, 1901 = macroconch). With prominent umbilical bullae, most compressed flat-sided species of *Kakabadziella*. Venter truncated. Ribbing remains fine and regularly distributed up to the aperture. Splitting rare. In large macroconchs generally 2-4 intermediate ribs between two ribs. Probably small microconchs.
2. *caravacaensis* sp. nov. ♀+♂ [= *Parathurmannia* sp. A *in* Busnardo, 2003 (macroconch); = *rugosa* Busnardo, 2003 (microconch)]. With prominent umbilical bullae. Ribs very fine. Distribution of ribs very irregular, splitting frequent. In small specimens there may be 7 intermediate ribs between two main ribs. Strong early egression of the whorls.
3. *catulloi* Parona, 1897. ♀+♂ (= *isocostata* Kakabadze, 1981). In middle to late growth stages ribs become slightly more distant, thicker, blunter and more sigmoidal than in *P.* (*K.*) *mortilleti*; in middle to late growth stages there are generally only 1-2 rarely three, commonly short intermediate ribs to one main rib. Umbilical bullae absent.

B. Umbilicus equal or larger than whorl height; with mortilleti-like inner whorls.
4. *ohmi ohmi* Winkler, 1868. ♀+♂ (= *biassalensis* Dimitrova, 1967, macroconch; = *lorioli* Dimitrova, 1967, macroconch). Umbilical bullae absent, only present in late growth stages of macroconchs. Irregular disposition of ribs. Umbilicus larger than whorl height.
5. *ohmi valbonnettensis* subsp. nov. ♀+♂ [= *angulicostata* Karakasch, 1907, pl. 15, fig. 1, macroconch; = ex-lectotype of *Pseudothurmannia angulicostata* (d'Orbigny) *in* Lapeyre 1974]. With prominent umbilical bullae in middle to late ontogenetic stages. Umbilicus has the same width as the whorl height, and is consistently smaller than in *P.* (*K.*) *ohmi ohmi*. Ribbing of inner whorls finer and more uniform than in *P.* (*K.*) *ohmi ohmi*

C. Umbilicus wider than whorl height; without *mortilleti*-like inner whorls.
6. *belimelensis* Dimitrova, 1967. With larger whorl height and narrower umbilicus than in *P.* (*K.*) *tornajensis*. Ribs almost straight, only slightly projected near the venter. Main ribs regularly distributed. On inner whorls two intermediate ribs to one main rib, later increasing to 3-5. Umbilical bullae on main ribs and ventrolateral clavi on all the ribs.
7. *tornajensis* sp. nov. Small conches with advolute whorls. Umbilicus larger than in *P.* (*K.*) *belimelensis*. Whorls of steinkerns are not touching, whorls with preserved shell probably touching. Main ribs regularly distributed with mostly two intermediate ribs to one main rib; later increasing to 3-4. Ribs irregularly curved. Umbilical bullae on main ribs and ventrolateral clavi on all the ribs.

IV. *Crioceratites* mimicking *Pseudothurmannia*

With ventrolateral tubercles on every rib over a part of, or the entire conch, but with lateral tubercles in earliest growth stages. Considered to be ancestral to *Pseudothurmannia*.

A. *Crioceratites* (*Balearites*) Sarkar, 1954, has closest affinity to *Pseudothurmannia*. Balearis and Ohmi zones. Whorls in contact. Fine dense ribbing. In the adult growth stage, thick ribs appear along constrictions provided by umbilical and ventrolateral tubercles. Two rows of very fine, uniform ventrolateral tubercles present on the inner whorls; fibulation absent or rare. Innermost whorls with trituberculate ribs up to D = 6-10 mm.
1. *balearis* Nolan, 1894 (= type species) (= *Balearites shankariae* Sarkar, 1955). Ribbing very fine, uniform, dense and slightly flexuous. Without umbilical bullae, or with weak umbilical bullae at irregular distances. With weak rows of ventrolateral tubercles. Transitions exist with variety *shankariae* Sarkar with regularly

Plate I

Fig. 1-5: *Pseudothurmannia* (*Kakabadziella*) *mortilleti* (Pictet & De Loriol, 1858), macroconchs identical to *Hoplites renevieri* Sarasin & Schöndelmayer, 1901.
1, RGM 542022, locality 1A, bed A145; ×1. 2, RGM 387640, locality 1A, bed A149; ×1. 3, RGM 541824, locality 3A, bed 1 or 2; ×1. 4, RGM 541821, locality 3B, bed B200; ×1. 5, RGM 541820, locality 3B, bed B200; ×1.

Plate I

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spaced umbilical bullae and laterally tuberculate ribs on innermost whorls up to D = 7 mm.

2. *theodomirensis* sp. nov. Mimics *P.* (*K.*) *mortilleti*. Ribs fine, but with growth distinctly coarser and less uniform than in *C.* (*B.*) *balearis*, with differentiation in main and intermediate ribs. Umbilical bullae and ventrolateral tubercles present up to adult stage.

3. *pseudothurmannii* Dimitrova, 1967 (= *Crioceratites* sp. n. A *in* Hoedemaeker, 1995b). Trituberculate innermost whorls not determined, but probably present. Ribbing much coarser than in *C.* (*B.*) *balearis*. Strong prorsiradiate main ribs with strong ventrolateral clavi or tubercles with transitions to small ventrolateral tubercles on less strong intermediate ribs.

4. *oicasensis* sp. nov. [= *Pseudothurmannia* (*Balearites*) n. sp. A *in* Hoedemaeker, 1995b; = possibly *Balearites paramhansi* Sarkar, 1955?]. Trituberculate ribs up to D = 10 mm. Ribbing very fine and dense; with weak main ribs appearing as early as at D = 20 mm at regular distances; main ribs gradually grow in strength and are provided with ventrolateral tubercles and pointed umbilical tubercles and are alongside constrictions.

B. *Crioceratites* (*Binelliceras*) Sarkar, 1977. Balearis and Ohmi zone. Closely related to *Balearites*. Whorls just not in contact. With trituberculate ribs up to a diameter of 10-17 mm. Ventrolateral tubercles on inner whorls or up to the aperture; fibulation frequent on inner whorls, becoming less frequent with growth.

α. *Binelli* group; Balearis and Ohmi zones. Long early ontogenetic stage with fine uniform ribs.

1. *binelli* Astier, 1851. (= type species) (= *nowaki* Sarkar, 1955). Trituberculate main ribs up to D = 15 mm. Fine, uniform and flexuous ribs with fasciculation up to D = 50 mm. Ventrolateral tubercles up to D = 35 mm with frequent fibulation. On outer whorl ribbing remains rather fine, is irregularly distributed, and weakly differentiated in main and 3-16 intermediate ribs with a few additional constrictions.

2. *krenkeli* Sarkar, 1955. Coarse ribbed issue of *C.* (*Bi.*) *binelli*. Trituberculate ribs up to D = 16 mm and strong, large, distantly spaced ribs with large ventrolateral tubercles up to D = 27 mm; from this diameter the strong distant tuberculation transforms into rows of small, uniform tubercles on every rib, which disappear at D = 63 mm; on the main ribs they are slightly greater and persist to the aperture. Fine, uniform, flexuous ribs with fasciculation and fibulation on inner whorls up D = 35 mm. Here begins a differentiation into regularly distributed main and intermediate ribs (4-6 per interval); differentiation becomes more pronounced in adult stage.

3. *ibizensis* Wiedmann, 1962. Trituberculate ribs up to D = 15 mm, followed by a stage with hardly differentiated ribbing with 6-8 intermediate ribs to one main rib; fasciculation and fibulation occurs. From D = 25 mm ribbing well-differentiated an irregularly distributed with 2-6 intermediate ribs to one main rib. Irregular ornamentation on the outer whorl. Ventrolateral tubercles on every rib up to the aperture.

4. *rotundatus* Sarkar, 1955 (= *P. mortilleti* var. *rotundata* Sarkar, 1955). Mimics *P.* (*K.*) *ohmi*. Trituberculate ribs up to D = 10-11 mm. Slightly differentiated ribbing up to D = 30 mm. Fibulation frequent. Strong main ribs with strong ventrolateral tubercles up to the aperture, regularly separated by generally 3-4 less strong intermediate ribs, which become very weak on the venter and have very small ventrolateral tubercles on every rib up to the aperture.

β. *Angulicostatus* group. Balearis and Ohmi zones. Whorls not in contact. Inner whorls coarse-ribbed with thick trituberculate main ribs up to a diameter of 16 to 23 mm. In this respect, the *angulicostatus* group is more primitive than the *binelli* group. Ventrolateral tubercles on every rib; on inner whorls tubercles on main ribs larger than on intermediate ribs. On inner whorls frequent fibulation.

5. *angulicostatus* d'Orbigny, 1841. Coarse-ribbed inner whorls. Trituberculate main ribs up to D = 17-20 mm. Thick, subquadrate adult whorl section. Ventrolateral tubercles on inner whorls rather widely spaced, later closely spaced with frequent fibulation and larger tubercles on main ribs, finally very weak tubercles on every rib. On inner whorls main ribs separated by about 3-4 intermediate ribs, on outer whorl only by two and near aperture by 3-4 again.

6. *seitzi* Sarkar, 1955. Trituberculate main ribs up to D = 16 mm. Its ornamentation is very similar to that of *C.* (*Bi.*) *angulicostatus*, but whorl section is less thick.

Plate II

Fig. 1-11: *Pseudothurmannia* (*Kakabadziella*) *caravacaensis* sp. nov., typical variety.
1, RGM 542522, locality 9; ×1. 2. RGM 541963, locality 1W, bed W35; ×1. 3, RGM 541953, locality 1W, in loose block B from beds W35-46; ×1. 4, RGM 541957, locality 1W, bed W39; ×1. 5, RGM 541926, locality 2; ×1. 6, RGM 541950, locality 1W, in loose block A from beds W35-46; ×1. 7, RGM 541918, locality 1W, in loose block B from beds W35-46; ×1. 8, RGM 541954, locality 1W, from one of the beds W35-46; ×1. 9, RGM 541951, locality 1W, bed W38; ×1. 10, RGM 541925, locality 1F, bed F154; ×1. 11, RGM 541956, locality 1W, bed W35; ×1.

Plate II

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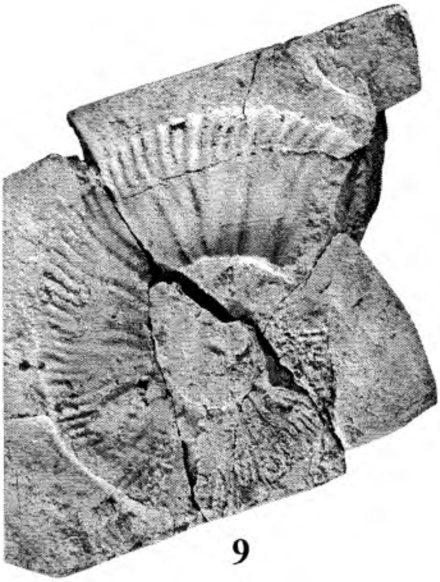

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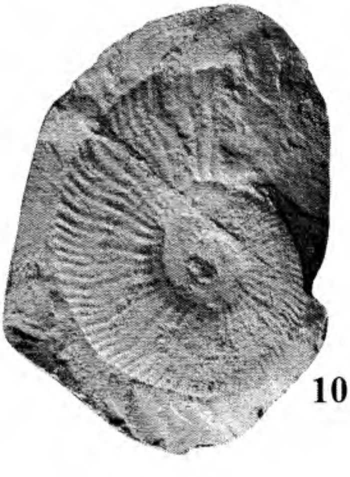

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7. *angulicostatiformis* nov. nom. (= *Crioceras angulicostatum* Kilian, 1888, *non* d'Orbigny). Resembles *C.* (*Bi.*) *angulicostatus*. Trituberculate main ribs up to D = 23 mm. Coarse-ribbed inner whorls. Outer whorl mainly adorned with close-spaced main ribs separated by one intermediate rib. Short sections with 2-3 intermediate ribs.

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Plate III

Fig. 1-6: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), typical variety, small macroconchs.
1, RGM 387859, locality 2; ×1. 2, RGM 387815, locality 2; ×1. 3, RGM 387822, locality 2; ×1. 4, RGM 387816, locality 2; ×1. 5, RGM 387800, locality 2; ×1. 6, RGM 387809, locality 2; ×1.

Plate III


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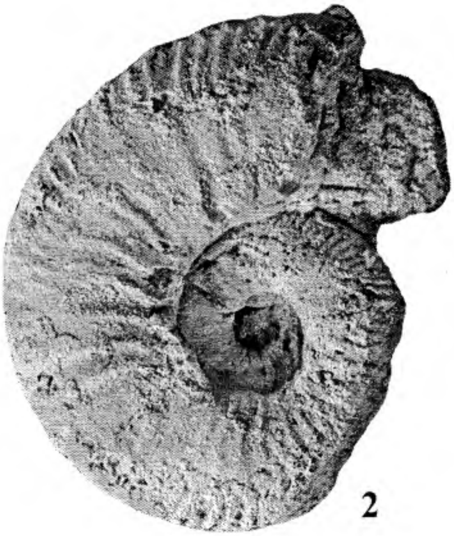
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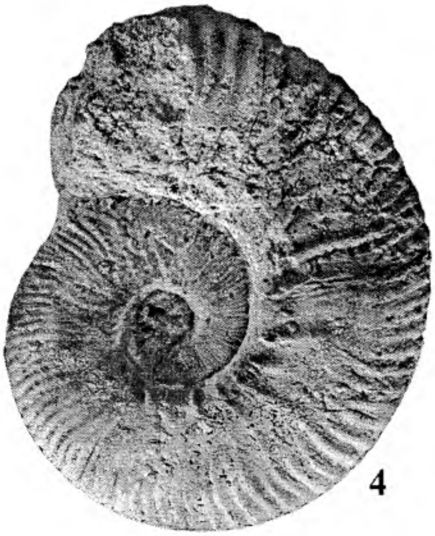
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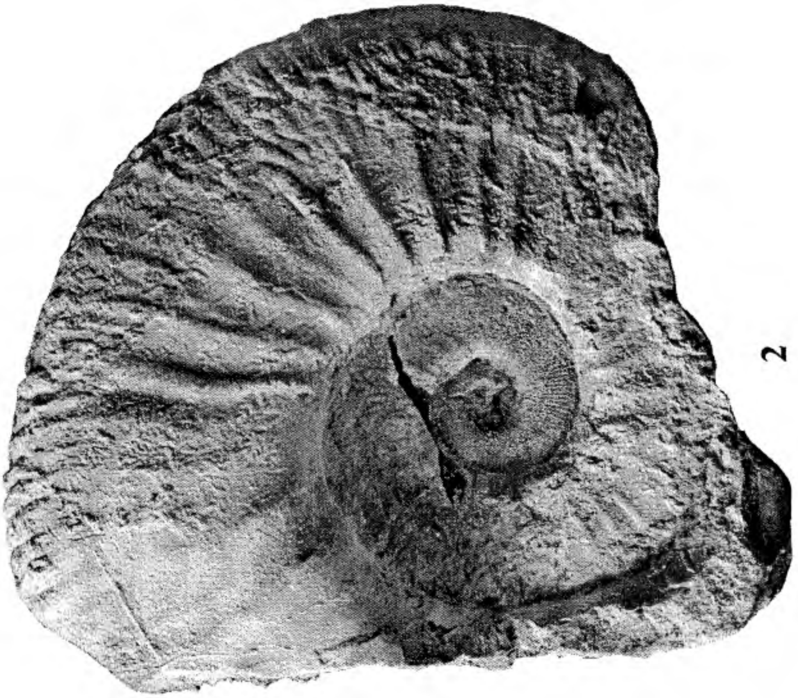
Plate IV

Fig. 1-2: *Pseudothurmannia (Kakabadziella) catulloi* (Parona, 1897) var. *externicostata*, medium large macroconchs. 1, RGM 542630, locality 2; ×1. 2, RGM 387804, locality 2; ×1.

Plate IV



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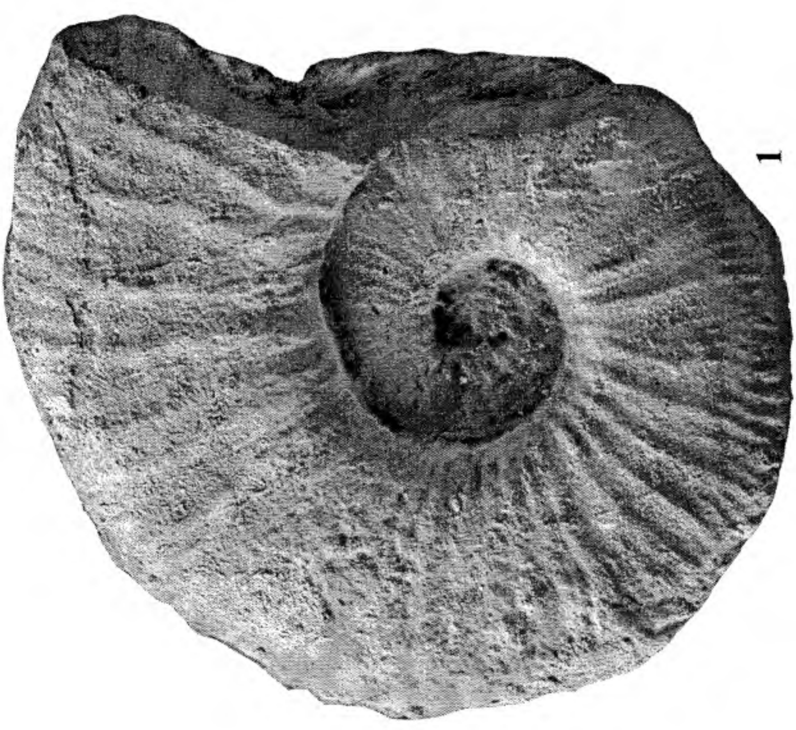

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Plate V

Fig. 1-2: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897) var *externicostata*, medium large macroconchs. 1, RGM 387807, locality 2; ×1. 2, RGM 387806, locality 2; ×1.

Plate V

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Plate VI

Fig. 1-2: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), coarse ribbed variety, medium large macroconchs. 1, RGM 387871, locality 1A, loose from beds A142-A195; ×1. 2, RGM 387805, locality 2; ×1.

Plate VI


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Plate VII

Fig. 1-2: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), coarse ribbed variety, medium large macroconchs. 1, RGM 387803, locality 2; ×1. 2, RGM 387795, locality 2; ×1.

Plate VII

2

1

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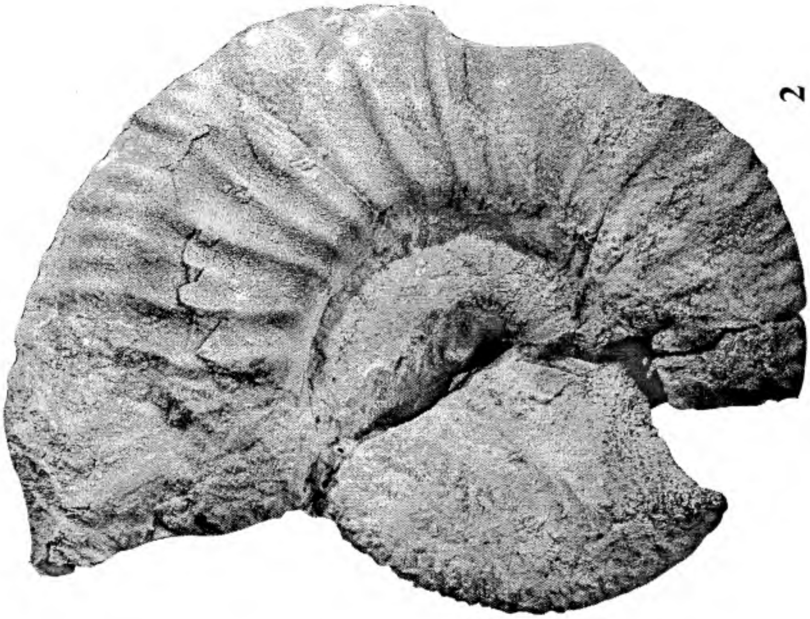
Plate VIII

Fig. 1-2: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), coarse ribbed variety with wide spaced ribs, medium large macroconchs.
1, RGM 542643, locality 2; ×1. 2, RGM 387796, locality 2; ×1.

Plate VIII



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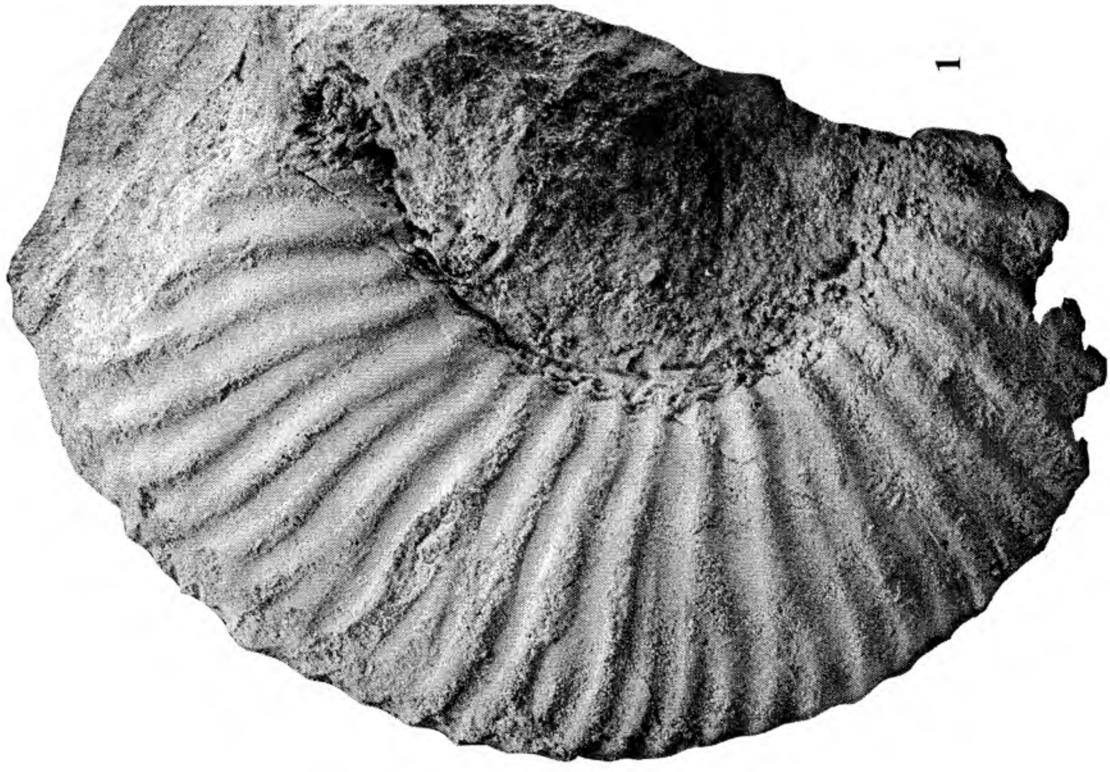

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Plate IX

Fig. 1-2: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), coarse ribbed variety, medium large macroconchs. 1, RGM 387793, locality 2; ×1. 2, RGM 387835, locality 2; ×1.

1

2

Table I: Measurements of *P.* (*K.*) *mortilleti*

RGM 541831	D 21.2	Wh 9.4	(44.3)	U 6.6	(31.1)	Wt 5.9	(27.8)
RGM 542261	D 22.2	Wh 9.2	(41.4)	U 8.0	(36.0)		
RGM 542026	D 23.7	Wh 10.2	(43.0)	U 7.9	(33.3)	Wt 5.0	(21.1)
RGM 542260	D 25.1	Wh 10.3	(41.0)	U 8.0	(31.9)		
RGM 541828	D 25.6	Wh 11.2	(43.7)	U 7.8	(30.5)	Wt 6.6	(25.8)
RGM 541850	D 28.8	Wh 11.0	(38.2)	U 10.0	(34.7)		
RGM 387962	D 29.7	Wh 12.3	(41.4)	U 9.0	(30.3)		
RGM 541842	D 32.7	Wh 12.5	(38.2)	U 11.3	(34.6)	Wt 7.4	(22.6)
RGM 541834	D 33.8	Wh 13.9	(41.1)	U 11.2	(33.1)		
RGM 542076	D 33.9	Wh 13.6	(40.1)	U 11.2	(33.0)	Wt 6.8	(20.0)
RGM 541827	D 34.8	Wh 13.9	(39.9)	U 11.1	(31.9)	Wt 7.5	(21.6)
RGM 542079	D 34.8	Wh 14.0	(40.2)	U 11.7	(33.6)	Wt 8.3	(23.9)
RGM 541848	D 35.4	Wh 14.4	(40.7)	U 11.8	(33.3)		
RGM 542023	D 35.8	Wh 14.3	(40.0)	U 12.2	(34.1)	Wt 7.4	(20.7)
RGM 542068	D 36.0	Wh 15.1	(42.0)	U 12.4	(34.0)	Wt 7.3	(20.2)
RGM 541833	D 38.4	Wh 15.4	(40.1)	U 12.6	(32.9)	Wt 10.6	(27.6)
RGM 541837	D 38.4	Wh 16.2	(42.3)	U 12.0	(31.2)		
RGM 541829	D 40.2	Wh 15.4	(38.4)	U 13.6	(33.8)		
Lectotype cast	D 40.4	Wh 16.3	(40.3)	U 13.6	(33.7)	Wt 9.3	(23.0)
RGM 542030	D 40.7	Wh 17.5	(43.0)	U 12.4	(30.5)		
RGM 542059	D 40.7	Wh 17.5	(43.0)	U 13.0	(32.0)		
RGM 542050	D 41.0	Wh 17.5	(42.7)	U 13.0	(31.7)	Wt 9.0	(22.0)
RGM 541836	D 42.1	Wh 17.9	(42.5)	U 14.7	(34.9)		
RGM 541835	D 43.9	Wh 16.8	(38.3)	U 14.0	(31.9)		
RGM 542066	D 44.4	Wh 19.2	(43.2)	U 16.0	(36.0)		
RGM 542064	D 44.6	Wh 17.6	(39.5)	U 15.9	(35.7)		
RGM 542078	D 46.2	Wh 18.8	(40.7)	U 17.2	(37.2)		
RGM 542038	D 47.6	Wh 18.0	(38.6)	U 16.2	(34.8)	Wt 9.0	(19.3)
RGM 542025	D 49.0	Wh 20.0	(40.8)	U 17.5	(35.7)		
RGM 542027	D 49.2	Wh 18.2	(37.0)	U 17.8	(36.2)		
RGM 542032	D 49.0	Wh 19.8	(40.4)	U 15.0	(30.6)	Wt 11.6	(23.7)
RGM 542043	D 50.9	Wh 20.9	(41.1)	U 17.0	(33.4)		
RGM 541832	D 51	Wh 21	(41.2)	U 17	(33.3)		
RGM 542047	D 51.9	Wh 21.9	(42.2)	U 16.9	(32.6)	Wt 10.0	(19.2)
RGM 541823	D 53.5	Wh 21.6	(41.1)	U 17.2	(32.8)	Wt 8.6	(16.1)
RGM 541823	D 56	Wh 23.3	(41.6)	U 19.2	(34.3)	Wt 9.5	(17.0)
RGM 541824	D 71	Wh 29	(40.8)	U 24	(33.8)	Wt 15	(21.1)
RGM 542022	D 71.6	Wh 27.3	(38.1)	U 25.4	(35.5)		
RGM 542049	D 78.6	Wh 31.4	(40.0)	U 27.0	(34.3)		
RGM 541821	D 93	Wh 36	(38.7)	U 32	(34.4)	Wt 17	(18.3)
RGM 541820	D 109	Wh 40.2	(36.8)	U 42.7	(39.2)	Wt 22.6	(20.7)
♂ RGM 541852	D 25.0	Wh 10.0	(40.0)	U 7.0	(28.0)	Wt 6.0	(24.0)
♂ RGM 541826	D 27.8	Wh 11.2	(40.3)	U 9.0	(32.4)	Wt 6.6	(23.7)
♂ RGM 541853	D 33.1	Wh 14.0	(42.3)	U 12	(36.3)	Wt 7.3	(22.0)

Plate X

Fig. 1: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), fine-ribbed variety, large macroconch. RGM 542635, locality 2; 95%.

Table II: Measurements of *P.* (*K.*) *caravacaensis* (s is syntype)

RGM 541936	D 20.0	Wh 8.7	(43.5)	U 5.8	(29.0)		
RGM 541923A	D 22.25	Wh 8.85	(39.8)	U 6.1	(27.4)		
RGM 542424	D 22.4	Wh 9.0	(40.2)	U 7.4	(33.0)		
RGM 541922	D 22.7	Wh 9.75	(42.9)	U 6.7	(29.5)		
RGM 541935	D 24.7	Wh 10.8	(43.7)	U 6.4	(25.9)		
RGM 541923B	D 25.4	Wh 12.4	(48.8)	U 8.5	(33.5)		
RGM 54192	D 30.5	Wh 12.7	(51.6)	U 8.0	(26.2)	Wt 5.0	(16.4)
RGM 541943	D 30.85	Wh 13.3	(43.1)	U 10.2	(33.1)		
RGM 541961	D 33	Wh 14.4	(43.6)	U 10.5	(31.8)		
RGM 541929	D 34.8	Wh 15.1	(43.4)	U 9.3	(26.7)	Wt 7.4	(21.3)
RGM 542669	D 35.0	Wh 13.9	(39.7)	U 11.3	(32.3)		
RGM 541963	D 40	Wh 17.2	(43)	U 12.8	(32)		
RGM 541920	D 40.2	Wh 17.8	(44.3)	U 11	(37.4)		
RGM 541952	D 41.6	Wh 16.4	(39.4)	U 13.1	(31.5)		
RGM 541973	D 41.9	Wh 15.8	(37.7)	U 14.0	(33.4)		
RGM 541962	D 41.5	Wh 15.85	(37.5)	U 12.9	(31.1)	Wt 8.7	(21)
RGM 541926	D 41.8	Wh 18.5	(44.3)	U 11.2	(26.8)	Wt 9.4	(22.6)
RGM 541928	D 43.0	Wh 18.9	(44.0)	U 11.8	(27.4)	Wt ± 9	(20.9)
RGM 541986	D 43.6	Wh 16.0	(36.7)	U 15.6	(35.8)		
RGM 541931s	D 44.3	Wh 18.6	(42.0)	U 14.1	(31.8)		
RGM 387884s	D 44.2	Wh 17.6	(39.8)	U 15.0	(33.9)	Wt 8.6	(19.5)
RGM 541925	D 45	Wh 16	(33.5)	U 15	(33.3)		
RGM 541950	D 46.4	Wh 17.6	(37.9)	U 15.0	(32.3)	Wt 9.3	(20.0)
RGM 387881	D 46.7	Wh 18.1	(38.8)	U 15.5	(33.2)	Wt 9.3	(19.9)
RGM 38788	D 47.0	Wh 18.7	(39.8)	U 15.7	(33.4)	Wt 9.0	(19.1)
RGM 387980	D 47.8	Wh 19.6	(41.0)	U 16.6	(34.7)		
RGM 541953	D 48.5	Wh 18.4	(37.9)	U 17.2	(35.5)		
RGM 542178	D 48.7	Wh 19.0	(39.0)	U 16.0	(32.9)		
RGM 541954	D 49.4	Wh 19.0	(38.5)	U 17.2	(34.8)	Wt 10.5	(21.3)
RGM 541970	D 57	Wh 22.5	(39.5)	U 19.3	(33.9)	Wt 9.8	
RGM 541957	D 58.2	Wh 22.3	(38.3)	U 20.0	(34.4)		
RGM 541988	D 60	Wh 21.8	(36.3)	U 21	(35.0)		
G.I.A. P.113	D 62	Wh 22	(35.5)	U 22	(35.5)		
RGM 541930s	D 68.1	Wh 26.4	(38.8)	U 23.6	(34.7)	Wt 12.3	(18.1)
♂ RGM 541981	D 26.2	Wh 12.2	(46.6)	U 8.6	(32.8)	Wt 5.7	(22.5)
♂ RGM 541976	D 30	Wh 11	(36.7)	U 9	(30.0)		
♂ RGM 541972	D 33.0	Wh 14.9	(45.2)	U 11.5	(34.8)	Wt 12.3	(37.3)
♂ RGM 541964	D 36.1	Wh 14.0	(38.8)	U 12.4	(34.3)		
♂ RGM 541962	D 36.3	Wh 14.4	(39.7)	U 12.7	(35.0)		
♂ RGM 541979	D 39.5	Wh 15.4	(39.0)	U 13.7	(34.7)		
♂ RGM 541973	D 42	Wh 16.3	(36.4)	U 15.2	(33.9)		
♂ RGM 387905	D 48	Wh 17.5	(36.5)	U 18.7	(39.0)		
♂ RGM 541982	D 50.8	Wh 18.2	(35.8)	U 18	(35.4)		
♂ RGM 541971	D 51.9	Wh 19.5	(37.6)	U 19.3	(37.2)		
♂ RGM 541974	D 65.7	Wh 23	(35.0				

Plate XI

Fig. 1: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), typical variety, large macroconch, RGM 387791, locality 2; 80%.

Table III: Measurements of *P.* (*K.*) *catulloi*

RGM 387820	D 20.7	Wh 8.5	(41.1)	U 6.7	(32.4)	Wt 5.5	(26.6)
RGM 387821	D 24.0	Wh 10.4	(43.3)	U 6.3	(26.2)	Wt 7.0	(29.2)
GIA. P100A	D 38.0	Wh 16.8	(44.2)	U 11.0	(28.9)		
RGM 542175	D 42.8	Wh 17.3	(40.4)	U 12.9	(30.1)	Wt 8.5	(19.9)
RGM 387816	D 44.8	Wh 21.0	(46.9)	U 15.4	(34.4)	Wt 14	(29.2)
RGM 387813	D 45.7	Wh 17.5	(38.3)	U 14.7	(32.2)		
RGM 542232	D 46.8	Wh 19.3	(41.2)	U 14.9	(31.8)		
Holotype	D 47		(38)		(34)		(24)
RGM 387814	D 48.3	Wh 19.8	(41.0)	U 15.5	(32.1)	Wt 11.5	(23.8)
RGM 387787	D 50	Wh 21	(42)	U 16	(32)	(gypsum)	
RGM 387815	D 50.5	Wh 21.3	(42.2)	U 17.2	(34.1)	Wt 13.7	(27.1)
RGM 387812	D 52.4	Wh 21.0	(40.1)	U 17.0	(32.4)		
RGM 542172	D 53.0	Wh 21.5	(40.6)	U 16.9	(31.9)	Wt 9.5	(17.9)
RGM 542181	D 53.4	Wh 23.0	(43.1)	U 17.9	(33.5)		
RGM 542652	D 53.7	Wh 21.3	(39.7)	U 17.9	(33.3)		
RGM 542191	D 53.8	Wh 21.8	(40.5)	U 16.6	(30.9)		
RGM 387653	D ±55	Wh 21.0	(38.2)	U 17.0	(30.9)		
RGM 387811	D 58.3	Wh 23.8	(40.8)	U 18.2	(31.2)	Wt 14	(24.0)
RGM 387799	D 58.8	Wh 24.0	(40.8)	U 18.3	(31.1)	Wt 14.9	(25.3)
GIA. P100 B	D 59.0	Wh 23.2	(39.3)	U 18.8	(31.9)	Wt 14.8	(25.1)
RGM 387808	D 60.2	Wh 23.0	(38.2)	U 21.6	(35.9)	Wt 14.5	(24.1)
RGM 387908	D 61.4	Wh 24.9	(40.6)	U 19.6	(31.9)		
RGM 387809	D 64.2	Wh 25.7	(40.0)	U 22.1	(34.4)	Wt 15.5	(24.1)
RGM 387822	D 64.4	Wh 25.6	(39.8)	U 21.7	(33.7)	Wb15.7	(24.4)
RGM 387816	D 65.5	Wh 27.0	(41.2)	U 20.4	(31.4)	Wt 14.9	(22.7)
RGM 387815	D 66.4	Wh 26.5	(39.9)	U 21.9	(33.0)	Wt 17.7	(26.7)
RGM 542195	D 71.9	Wh 28.0	(38.9)	U 24.6	(34.2)		
RGM 387800	D 72.0	Wh 27.9	(38.7)	U 25.2	(35.0)	Wt 14.7	(20.4)
RGM 387799	D 73.6	Wh 27.1	(36.8)	U 25.5	(34.6)	Wt 16.1	
RGM 387808	D 75.2	Wh 31.0	(38.8)	U 26.6	(33.3)	Wt 21	(26.3)
RGM 387909	D 87.4	Wh 30.2	(34.6)	U 34.0	(38.9)		
RGM 387804	D 93.2	Wh 35.7	(38.3)	U 32	(34.3)	Wt 24.7	(26.5)
RGM 387807	D 95.9	Wh 39.2	(40.9)	U 29.5	(30.8)	Wt 22.5	(23.5)
RGM 387871	D 97.2	Wh 33.5	(34.5)	U 32.5	(33.4)		
RGM 387805	D 100	Wh 38.7	(38.7)	U 35.0	(35.0)	Wt 20	(20.0)
RGM 387803	D 105	Wh 38	(36.2)	U 41	(39.0)		
RGM 387806	D 110	Wh 42	(38.2)	U 36.5	(33.2)	Wt 25	(22.7)
RGM 387795	D 112.4	Wh 40.6	(36.1)	U 40.0	(35.6)	Wt 26.1	(23.2)
RGM 387793	D 128.3	Wh 46.4	(36.2)	U 50.0	(39.0)	Wt 28	(21.8)
RGM 387792	D 131	Wh 48.3	(36.9)	U 48.3	(36.9)	Wt 30.5	(23.3)
RGM 387794	D 175	Wh 60	(34.3)	U 69	(39.4)		
RGM 542636	D 180	Wh 61.7	(34.3)	U 74.3	(41.3)		
RGM 542635	D 210	Wh 70	(33.3)	U 90	(42.8)	Wt 50	(23.8)
RGM 542659	D 214	Wh 71.5	(33.4)	U 87	(40.7)	Wt 54	(25.2)
RGM 387791	D 243.5	Wh 82.5	(33.9)	U 99.3	(40.8)	Wt 54.5	(22.4)
RGM 542659	D 258	Wh 89	(34.5)	U 115	(44.6)	Wt 64	(24.8)
RGM 542635	D 275	Wh 92	(33.5)	U 119	(43.3)	Wt 60	(21.8)
♂ RGM 387810	D 49	Wh 21.6	(44.1)	U 14.4	(29.4)	Wt 13.9	(28.4)
♂ RGM 387872	D 54.7	Wh 22.5	(41.1)	U 16.7	(30.5)	Wt 10.6	(19.4)
♂ RGM 387801	D 58.8	Wh 22.3	(37.9)	U 20.5	(34.9)	Wt 12.5	(21.3)
♂ RGM 387810	D 64.5	Wh 24	(37.2)	U 20.8	(32.2)		
♂ RGM 387823	D 65.6	Wh 26.6	(40.5)	U 21.2	(32.3)	Wt 15.5	(23.6)
♂ RGM 387801	D 69.8	Wh 23.0	(33.0)	U 26.6	(38.1)	Wt 15.7	(22.5)
♂ RGM 387802	D 76.3	Wh 28.3	(37.1)	U 25.0	(32.8)	Wt 15.6	(20.4)
♂ RGM 387797	D 77.9	Wh 29.0	(37.2)	U 29.0	(37.2)	Wt 15.5	(19.9)
♂ RGM 387789	D 82.3	Wh 28.8	(35.0)	U 30.0	(36.5)	Wt 15.6	(19.0)

Plate XII

Fig. 1: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), typical variety, large macroconch, RGM 542659, locality 2; extra thick ribs well developed and lined by weak constrictions; note the appearance of small umbilical tubercles on the last whorl; 77%.

Plate XII

Table IV: Measurements *P.* (*K.*) *ohmi ohmi*

RGM 542269	D 27.5	Wh 10.0	(36.4)	U 9.4	(34.2)		
RGM 541825	D 32	Wh 12.7	(39.7)	U 11.6	(36.2)	Wt 7.5	(23.4)
RGM 541856	D 32.9	Wh 14.1	(42.9)	U 12.1	(36.8)	Wt 8.1	(24.6)
RGM 387606	D 34.7	Wh 12.95	(37.3)	U 12.9	(37.2)		
RGM 387660	D 37.6	Wh 15	(39.9)	U 13.7	(36.4)		
RGM 541899	D 37.6	Wh 14.2	(37.8)	U 13.9	(37.0)	Wt 9.6	(25.5)
RGM 387614	D 42.3	Wh 16	(37.8)	U 15	(35.5)		
RGM 541864	D 43.3	Wh 15.8	(36.5)	U 16.3	(37.6)	Wt 8.0	(18.5)
RGM 387616	D 44.1	Wh 15.9	(36.0)	U 17.5	(39.7)		
RGM 541861	D 45.4	Wh 16	(35.2)	U 17.4	(38.3)	Wt 10.5	(23.1)
RGM 387615	D 46	Wh 17	(36.9)	U 17	(36.9)		
RGM 541901	D 53.0	Wh 19.3	(36.4)	U 22.4	(42.3)	Wt 10.4	(19.6)
RGM 387903	D 53.9	Wh 18.4	(34.1)	U 22	(40.8)		
RGM 541862	D 56.8	Wh 19.9	(35.0)	U 23.5	(41.4)		
RGM 387656	D 56.85	Wh 19.65	(34.6)	U 23.2	(40.8)		
RGM 387644	D 57	Wh 20	(35.1)	U 22	(38.6)		
RGM 541860	D 57.4	Wh 20.4	(35.5)	U 23.8	(41.5)	Wt 11.7	(20.4)
RGM 542263	D 61.8	Wh 23.9	(38.7)	U 22.9	(37.1)		
RGM 542268	D 61.2	Wh 22.3	(36.4)	U 22.2	(36.3)	Wt 12.6	(20.6)
RGM 542262	D 65.2	Wh 23.0	(35.3)	U 25.7	(39.4)	Wt 15.4	(23.6)
RGM 387655	D 66.2	Wh 24.1	(36.4)	U 27.4	(41.4)		
RGM 387643	D 68.3	Wh 21.8	(31.9)	U 29.1	(42.6)		
♀ Holot. *lorioli*	D 69	Wh 25	(36.2)	U 27	(39.1)	(young macroconch, cast)	
RGM 541865	D 73.8	Wh 25.0	(33.9)	U 31.2	(42.3)		
♀ Holot. *ohmi*	D 74	Wh 25.8	(34.9)	U 30.3	(40.9)	(young macroconch, cast)	
RGM 387629	D 75.5	Wh 21.75	(28.8)	U 30	(39.7)		
♀ Hol. *biassal.*	D 80	Wh 27.5	(34.4)	U 32.9	(41.1)	(young macroconch, cast)	
RGM 387640	D 80.8	Wh 32.0	(39.6)	U 32	(39.6)		
♂ RGM 541854	D 43.3	Wh 15.7	(36.3)	U 18.5	(42.7)	Wt 9.3	(21.5)
♂ RGM 541863	D 51.65	Wh 18.3	(35.4)	U 20.7	(40.0)		
♂ RGM 541913	D 73	Wh 25.3	(34.7)	U 30.4	(41.6)		

Table V: Measurements *P.* (*K.*) *ohmi valbonettensis*

RGM 542519	D 28.8	Wh 11.6	(40.3)	U 9.8	(34.0)	Wt 7.3	(25.4)
RGM 387677	D 34.0	Wh 13.1	(38.5	U 13.1	(38.5)	Wt 7.8	(27.1)
RGM 542156	D 35.9	Wh 13.2	(36.8)	U 13.2	(36.8)		
RGM 387888	D 40.75	Wh 14.9	(36.6)	U 14.9	(36.6)		
RGM 387647	D 49.75	Wh 19.2	(38.6)	U 18.35	(36.9)	Wt 8.65	(17.4)
RGM 387645	D 55.2	Wh 23.8	(43.1)	U 18.3	(33.2)	Wt 10.8	(19.6)
RGM 542415	D 56	Wh 21	(37.5)	U 20	(35.7)		
RGM 387642	D 56.5	Wh 21.1	(37.3)	U 21.1	(37.3)		
RGM 387646	D 58.7	Wh 21	(35.8)	U 23	(39.2)	Wt 12	(20.4)
RGM 387601	D 58.8	Wh 21.4	(36.4)	U 22.5	(38.3)		
RGM 387646	D 59	Wh 21.3	(36.1)	U 22.5	(38.1)	Wt 11.65	(19.7)
♀ RGM 542417	D 66.6	Wh 24.6	(36.9)	U 25	(37.5)		
♀ RGM 542155	D 106.9	Wh 41.4	(39)	U 40.7	(38.0)	Wt 19.0	(18)
♀ RGM 387662	D 116	Wh 41	(35.3)	U 48.8	(42.1)	Wt 24.4	(21.1)
♂ RGM 387716	D 48.6	Wh 17	(35)	U 19	(39.1)		
♂ RGM 387649	D 60.4	Wh 21	(34.8)	U 23.5	(38.9)		
♂ RGM 387721	D 68	Wh 23	(33.8)	U 28.2	(41.5)	Wt 13	(19.1)
♂ RGM 387723	D 72	Wh 23.2	(32.2)	U 33	(45.9)	Wt 15.7	(21.8)
♂ RGM 542152	D 73.4	Wh 24.7	(33.7)	U 28.6	(39.0)		

Plate XIII

Fig. 1: ***Pseudothurmannia*** **(*Kakabadziella*) *catulloi*** (Parona, 1897), large whorl fragment of macroconch of typical variety with extra strong ribs and extra pronounced contrictions, RGM 542629, locality 2; ×1.

Table VI: Measurements *P.* (*K.*) *tornajensis* (s is syntype)

RGM 541876	D 18.4	Wh 6.9	(37.5)	U 7.3	(39.7)	Wt 4.1	(22.3)
RGM 542384	D 20.2	Wh 7.4	(36.6)	U 8.6	(42.6)		
RGM 542387	D 25.2	Wh 8.8	(34.9)	U 10.0	(39.7)	Wt 5.4	(21.4)
RGM 542382	D 25.3	Wh 9.0	(35.6)	U 10.0	(39.5)	Wt 6.5	(25.7)
RGM 542355	D 26.8	Wh 9.6	(35.0)	U 11.9	(44.4)	Wt 5.4	(20.1)
RGM 542391s	D 27.2	Wh 9.4	(34.6)	U 12.2	(44.9)	Wt 6.0	(22.1)
RGM 542361	D 28.3	Wh 10.0	(35.3)	U 13.3	(47.0)	Wt 6.0	(21.2)
RGM 542381	D 29.1	Wh 10.1	(34.7)	U 12.4	(42.6)		
RGM 542347	D 31.3	Wh 10.2	(32.6)	U 14.0	(44.7)		
RGM 542390s	D 32.8	Wh 10.6	(32.3)	U 14.6	(44.5)	Wt 8.7	(26.5)
RGM 542378	D 34.0	Wh 13.0	(38.2)	U 14.5	(42.6)	Wt 7.7	(22.6)
RGM 542380	D 36.7	Wh 13.0	(35.4)	U 16.6	(45.2)	Wt 9.5	(25.9)
RGM 542392s	D 37.9	Wh 11.8	(31.1)	U 16.6	(43.8)	Wt 7.8	(20.6)
RGM 542385	D 41.8	Wh 13.2	(31.6)	U 19.7	(47.1)	Wt 9.6	(23.0)
RGM 542865	D 43.0	Wh 13.5	(31.4)	U 19.5	(45.0)		
RGM 542383	D 43.5	Wh 13.4	(30.8)	U 19.1	(43.9)	Wt 8.3	(19.1)
RGM 542348	D 43.6	Wh 13.4	(30.7)	U 20.0	(45.9)		
RGM 541881	D 50.7	Wh 17.5	(34.5)	U 22.5	(44.4)		

Table VII: Measurements of holotype *P.* (*K.*) *belimelensis*

D 42	Wh 15.5	(36.9)	U16.6	(39.5)

(Dimitrova's diameter is presumably not the largest diameter)

D 47	Wh 17	(36.2)	U 17	(40.4)

(authors measurements of the plaster cast)

Table VIII: Measurements *P.* (*P.*) *sarasini*

RGM 387 877	D 95.3	Wh 35.0	(36.7)	U 35.0	(36.7)	Wt 20.0	(21.0)
same specimen	D 80.4	Wh 31.0	(38.6)	U 30.0	(37.3)	Wt 15.9	(19.8)
RGM 542143	D 49.2	Wh 20.4	(41.5)	U 17.9	(36.4)		(impression)
Holotype	D 48.4	Wh 19.4	(40)	U 15.8	(32.6)		(photo)

Table IX: Measurements of *P.* (*Pa.*) *dissiticostata*

RGM 542149 s	D 68	Wh 26.5	(39.0)	U 26.3	(38.7)
Same specimen s	D 51.5	Wh 19.8	(38.4)	U 18.8	(36.5)
RGM 542327	D 69	Wh 27	(39.1)	U 25	(36.2)

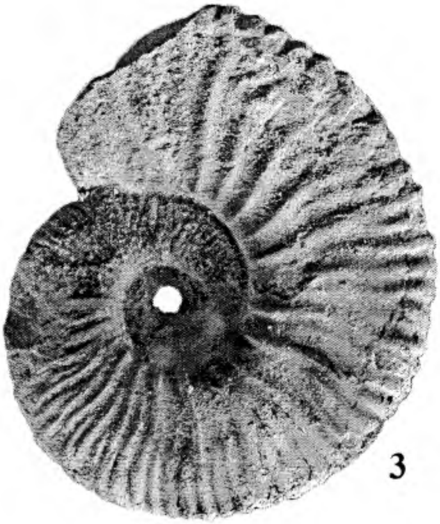
Plate XIV

Fig. 1-7: *Pseudothurmannia* (*Kakabadziella*) *catulloi* (Parona, 1897), small to large microconchs.
1, RGM 542652, locality 2; ×1. 2, RGM 387872, locality 1W, in loose block M from beds W35-46; ×1. 3, RGM 387810, locality 2; ×1.4, RGM 387789, locality 2; ×1. 5, RGM 387801, locality 2; ×1. 6, GIA P100, locality 2; ×1. 7, RGM 387823, locality 2; ×1.

Plate XIV


1


2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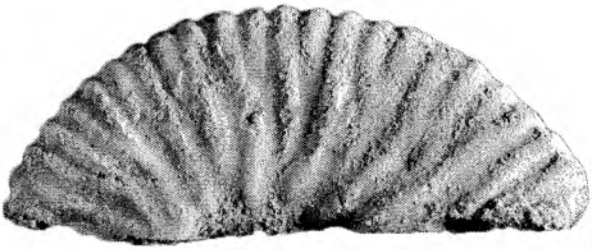
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Table X: Measurements *P.* (*P.*) *edouardi*

Specimen of Thomel (1965b):	D 187	Wh 57	(30.5)			Wt 52	(27.8)
Photograph Thomel (1965b):	D 177	Wh 52	(29.4)	U 85	(48.0)		
Plaster cast of the Holotype:	D 108	Wh 38.3	(35.5)	U 46	(42.6)	Wt 30	(27.7)

Venter between ventrolateral tubercles 13.5

Table XI: Measurements *P.* (*P.*) *picteti* (bv = breadth of the venter)

RGM 542520	D 33.8	Wh13.1	(38.8)	U 12.2	(36.1)			
RGM 542650	D 40	Wh 17.0	(42.5)	U 11.0	(27.5)			
RGM 542848	D 43.5	Wh 15.8	(36.3)	U 14.7	(33.9)			
RGM 542847	D 66.3	Wh 24.0	(36.2)	U 25.0	(37.7)			
Figure of the specimen from Ravin de Valbonnette (Vermeulen, 2002):	D 87.5	Wh 35	(40.0)	U 27	(30.8)	Wt 24.5	(28.0)	breadth venter 15
Measurements of the plaster cast of the holotype:	D 97	Wh 37	(38.1)	U 31.8	(32.8)	Wt 26.5	(27.3)	breadth venter 15
Pseudothurmannia 'lurensis' Busnardo, 1970:	D 98	Wh 39	(39.8)	U 32	(32.7)	Wt 16	(16.3)	
Specimen figured by Dimitrova, 1967:	D 120	Wh 47	(39.2)	U 40	(33.3)			
RGM 542647	D 159	Wh 57	(35.8)	U 60	(37.7)			
RGM 542641	D 190	Wh 67.8	(35.7)	U 77	(40.5)			
RGM 542639	D 222	Wh 79	(35.6)	U 85	(38.3)	Wt 40	(17.8)	breadth venter 25
RGM 542642	D 224	Wh 74	(33.0)	U 88	(39.3)	Wt 40	(17.6)	breadth venter 25
RGM 542645	D 227	Wh 79	(34.8)	U 90	(39.6)	Wt 41	(18.0)	breadth venter 25
Pseudothurmannia grandis Busnardo, 1970:	D 230	Wh 84	(36.5)	U 98	(42.6)			
RGM 542646	D 250	Wh 80	(32.0)	U 109	(43.6)	Wt 45	(18.0)	breadth venter 27

large whorl fragment determined as *picteti* has a whorl height of 105 mm (Fig. 45) and should have belonged to a specimen with a diameter of c. 320 mm.

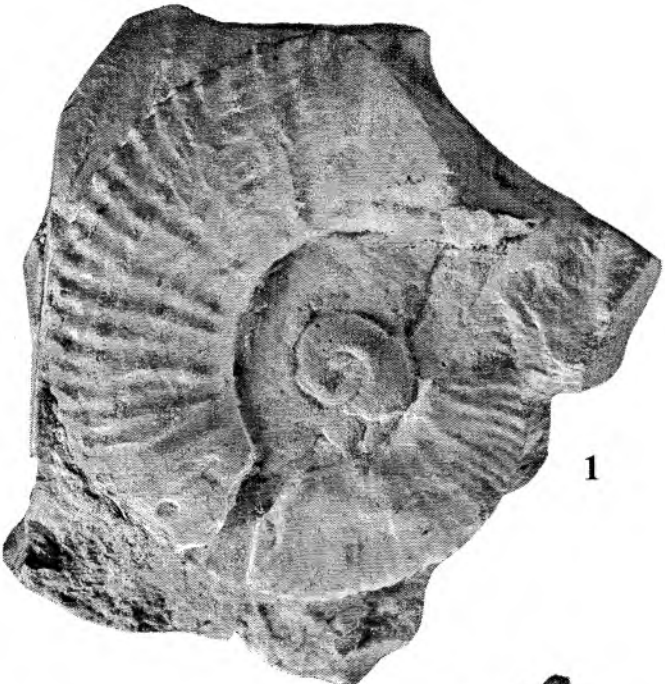
Table XII: Measurements *P* (*P.*) *simionescui*

Well-preserved specimen of the Sierra de la Muela:								
RGM 542660	D 176	Wh 58	(32.9)	U 80	(45.4)	Wt 40.4	(23.0)	Venter 20
idem	D 103	Wh 37	(35.9)	U 43	(41.7)	Wt 27.2	(26.4)	Venter 11.5
A.angulicostatus d'Orbigny, forme à tours en contact in Pictet, pl. 1bis, fig. 2 (plaster cast):	D 125	Wh 45	(36.0)	U 49	(39.2)	Wt 34.5	(27.6)	Venter 15
Holotype of P. (P.) *simionescui* measured by Busnardo, 2003:	D 130	Wh 41	(31.5)	U 47	(36.2)	Wt >28	(> 21.5)	
Holotype of P. (P.) *simionescui* measured by Sarkar, 1955:	D 123	Wh 44	(35.8)	Wt 28.5	(23.1)			

Plate XV

Fig. 1-6: *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868), microconchs.
1, plaster cast of holotype, Sulzbachgraben (Germany); ×1. 2. RGM 541863, locality 3B, bed B201; ×1. 3. RGM 387648, locality 1A, bed A144; ×1. 4. RGM 541858, locality 3A; ×1. 5. RGM 541913, locality 4, loose from beds 28-30; ×1. 6. RGM 541859, locality 3B, bed B202.

Plate XV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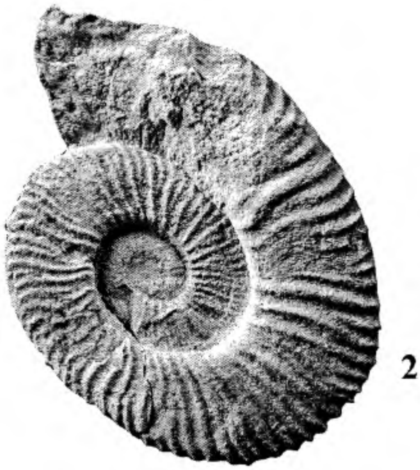
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Table XIII: Measurements *P.* (*P.*) *crioceroides*

Holotype:	D 365	Wh 110	(30.1)	U 160	(43.8)	Wt 77	(21.1)	(Wh:Wt = 1.43)
RGM 387729	D c. 315	Wh 93	(29.5)	U 155	(49.2)	Wt >56	(17.8)	
RGM 387729	D c. 300	Wh 92.2	(30.7)	U 150.2	(50.0)	Wt 57.3	(19.1)	(Wh:Wt = 1.60)
RGM 387767	D 265	Wh 72	(27.2)	U 131.5	(49.6)	Wt >46		
RGM 542205	D 132.7	Wh 42.8	(32.3)	U 57.9	(43.6)	Wt >22		
RGM 387725	D 115.4	Wh 35.5	(30.8)	U c.47	(40.7)	Wt 20.8	(18.0)	
Holotype of *Hoplites pseudo-malbosi* Sarasin & Schöndelmayer (fig. in Busnardo, 2003):								
	D 112	Wh 38	(33.9)	U 46	(41.1)			
RGM 387724	D 111	Wh 40.8	(36.8)	U 46.3	(41.7)	Wt 21.1	(19.0)	
RGM 387725	D 97.2	Wh 33.6	(34.6)	U 42.4	(43.6)	Wt 20.8	(21.4)	(Wh:Wt = 1.61)
♂RGM 542129	D c. 90	Wh c. 32	(35.6)	U 34.3	(38.1)			
♂RGM 387984	D 71.5	Wh 29.0	(40.6)	U 25.5	(35.7)	Wt >14.8		
♂RGM 542136	D 42.8	Wh 17.9	(41.8)	U 8.3	(19.4)	Wt >7.5		

RGM 387719: Wh:Wt = 1.21 (seems to be the least compressed specimen)

Table XIV: Measurements *P.* (*P.*) *monasteriensis*

Holotype	D 210	Wh 62	(29.5)	U 100	(47. 6)	Wt 60	(28. 6)

Table XV: Measurements *P.* (*P.*) *arundicostata*

RGM 387730	D c. 320	Wh c. 87.7	(27.4)	U c. 158	(49.4)	Wt c. 60	(18.7)	Wh:Wt = 1.45
Same specim.	D 185	Wh 57	(30.8)	U 85	(45.9)	Wt 45	(24.3)	
RGM 387728	D 177	Wh 58.8	(33.2)	U 80	(45.2)	Wt 38.6	(21.8)	Wh:Wt = 1.52
Same specim.	D c. 224	Wh c. 68	(30.4)	U c. 105	(46.9)	Wt c. 43	(19.2)	
RGM 387727	D 89	Wh 35.6	(40.0)	U 35.5	(39.9)			

Table XVI: Measurements *P.* (*P.*) *perevoluta*

GIA J9981	D 74.2	Wh 24.6	(33.2)	U 34	(45.8)	Wt 13.3	(17.9)
(Diagenetically compressed)							
RGM 387747	D c.110	Wh c. 40	(36.4)				
Dimitrova's specimen:							
	D 290	Wh 86 (30)		U 151	(52)		

Plate XVI

Fig. 1-4: *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868), macroconchs looking like *'Pseudothurmannia biassalensis'*.

1, plaster cast of holotype of *'Pseudothurmannia biassalensis'* Dimitrova, 1967, from Kriva reka (Bulgaria); ×1. 2, RGM 541911, locality 1A, bed A145; ×1. 3, RGM 387600, locality 1A, loose from beds A139-151; ×1. 4, RGM 387659, locality 1A, bed A144; ×1.

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Table XVII: Measurements *C.* (*B.*) *balearis*

RGM 387957	D 30.0	Wh 12.2	(40.7)	U 11.5	(38.3)	Wt 5.7	(19.0)
RGM 387956	D 39.5	Wh 15.3	(38.7)	U 13.1	(33.2)	Wt 7.7	(19.5)
RGM 542275	D 43.6	Wh 16.0	(36.7)	U 15.3	(35.1)	Wt 9.4	(21.6)
RGM 542120	D 43.7	Wh 16.4	(37.5)	U 15.8	(36.2)		
RGM 387887	D 49.6	Wh 18.5	(37.3)	U 17.1	(34.5)		
RGM 542277	D 54.6	Wh 19.3	(35.3)	U 21.1	(38.6)		
RGM 387910	D 55.5	Wh 21.1	(38.0)	U 21.4	(38.6)	Wt 12.4	(22.3)
RGM 542121	D 101	Wh 35	(34.7)	U 42.5	(42.1)		

Table XVIII: Measurements *C.* (*P.*) *theodomirensis* (s = syntype)

RGM 542115	D 20.5	Wh 8.1	(39.5)	U 7.0	(34.1)	Wt 4.2	(20.5)
RGM 387914	D 22.8	Wh 9.2	(40.4)	U 8.0	(35.1)	Wt 4.1	(17.9)
RGM 542093	D 22.8	Wh 8.7	(38.2)	U 7.0	(30.7)	Wt 4.8	(21.1)
RGM 542092	D 25.2	Wh 10.0	(39.7)	U 7.5	(29.8)		
RGM 542094	D 33.2	Wh 13.3	(40.1)	U 11.0	(33.1)		
RGM 542108	D 35.0	Wh 13.5	(38.6)	U 12.5	(35.7)		
RGM 542087	D 35.1	Wh 13.7	(39.0)	U 12.6	(35.9)	Wt 5.2	(14.8)
RGM 542105	D 35.2	Wh 15.0	(42.6)	U 11.4	(32.4)	Wt 6.0	(17.0)
RGM 542110	D 36.4	Wh 14.8	(40.7)	U 13.1	(36.0)	Wt 6.0	(16.5)
RGM 387919s	D 37.8	Wh 15.0	(39.7)	U 13.3	(35.2)	Wt 6.3	(16.7)
RGM 542086	D 39.0	Wh 15.9	(40.8)	U 13.3	(34.1)	Wt 6.3	(16.2)
GIA J 9959	D 40.5	Wh 15.3	(37.8)	U 14.6	(36.0)		
RGM 387928	D 40.8	Wh 16.0	(39.2)	U 15.4	(37.7)		
RGM 542088s	D 41.5	Wh 16.0	(38.5)	U 14.7	(35.4)		
RGM 542096	D 45.5	Wh 17.7	(38.9)	U 15.2	(33.4)		
RGM 542090	D 45.6	Wh 17.0	(37.3)	U 15.8	(34.6)	Wt 6.0	(13.2)
RGM 542278	D 48.8	Wh 19.6	(40.2)	U 19.4	(39.8)	Wt 7.5	(15.4)
RGM 387930s	D 52.4	Wh 19.2	(36.6)	U 19.2	(36.6)		

Table XIX: Measurements *C.* (*P.*) *pseudothurmannii*

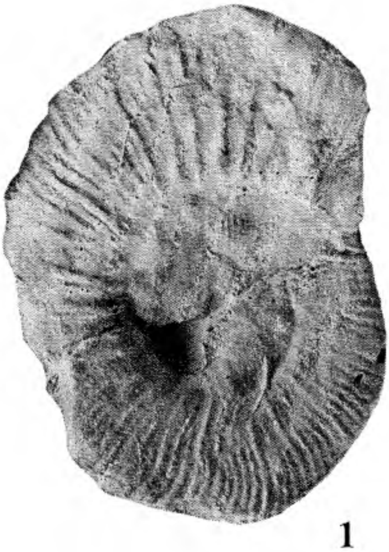
Paratype	D 45.0	Wh 18.1	(40.2)	U 17.0	(37.8)
RGM 542397	D 49.5	Wh 18.3	(37.0)	U 19.0	(38.4)
RGM 542395	D 50.0	Wh 18.1	(36.2)	U 19.1	(38.2)
RGM 542395	D 50.2	Wh 18.3	(36.5)	U 19.2	(38.2)
RGM 542394	D 52.5	Wh 20.0	(38.1)	U 19.5	(37.1)
RGM 387974	D 53.0	Wh 19.8	(37.4)	U 19.4	(36.6)
RGM 387882	D 51.8	Wh 20.0	(38.6)	U 19.1	(36.9)

Plate XVII

Fig. 1-8: *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868), small macroconchs looking like *'Balearites lorioli'*.

1, plaster cast of holotype of *'Balearites lorioli"* Dimitrova, 1967, from Belogradchishko (Bulgaria); ×1. 2, 387655, locality 1J, bed J142; ×1. 3, RGM 387644, locality 1K, bed K144; ×1. 4, RGM 542269, locality 3C; ×1. 5, RGM 387632, locality 1A, bed A144; ×1. 6, RGM 541860, locality 3A; ×1. 7, RGM 542263, locality 3C; ×1. 8, RGM 387643, locality 1K, bed K143; ×1.

Plate XVII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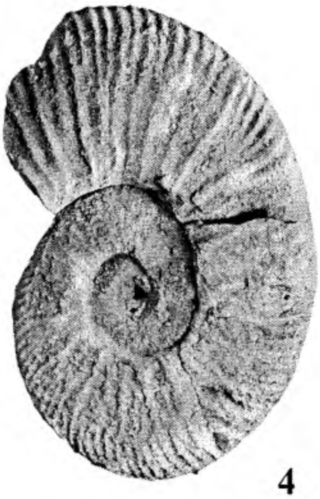
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Table XX: Measurements *C.* (*B.*) *oicasensis*

RGM 387925	D 74.5	Wh 26.0	(34.9)	U 29.5	(39.6)	Wt 13	(17.4)
Same specimen	D 50.2	Wh 18.0	(35.8)	U 18.8	(37.4)		
RGM 542343	D 49.5	Wh 17.2	(34.7)	U 20.0	(40.4)		
RGM 542344	D 43.9	Wh 17.4	(39.6)	U 15.1	(34.4)		

Table XXI: Measurements *C.* (*B.*) *binelli* (D phragm. = diameter at the end of the phragmocone)

RGM 19423	D 71.7	Wh 25.0	(34.9)	U 28.4	(39.6)	Wt 10.5	(14.6)	D phragm. 53
RGM 542337	D 74.0	Wh 27.3	(36.9)	U 30.5	(41.2)	Wt 10.3	(13.9)	D phragm. 70
RGM 542338	D 81.2	Wh 30.0	(36.9)	U 34.7	(42.7)			D phragm. 51

Table XXII: Measurements *C.* (*B.*) *krenkeli*

RGM 542852	D 62.4	Wh 24.5	(39.3)	U + narrow gap 27	(43.3)
RGM 542273	D 87.2	Wh 26.5	(30.4)	U + narrow gap 40.0	(45.9)
RGM 542854	D 76.8	Wh 28.3		U + narrow gap 29.6	(38.5)

Table XXIII: Measurements *C.* (*P.*) *ibizensis*

RGM 542321	D + gap 64.0	Wh 23.0	(35.9)	U + gap 29.5	(46.1)		
RGM 542318	D + gap 60.8	Wh 23.0	(37.8)	U + gap 23.0	(37.8)		
RGM 387938	D + gap 59.8	Wh 19.3	(32.3)	U + gap 25.3	(42.3)		
RGM 387935	D + gap 57.5	Wh 17.8	(31.0)	U = gap 24.4	(42.4)		
RGM 541765	D + gap 53.7	Wh 18.8	(35.0)	U + gap 22.0	(41.0)		
RGM 541775	D + gap 52.9	Wh 17.4	(32.9)	U + gap 21.8	(41.2)		
RGM 387879	D + gap 52.4	Wh 18.0	(34.4)	U + gap 20.8	(39.7)		
RGM 542320	D + gap 53.3	Wh 20.2	(37.9)	U + gap 21.0	(39.4)		
RGM 387937	D + gap 51.4	Wh 19.8	(38.5)	U + gap 22.5	(43.8)		
RGM 387880	D + gap 50.0	Wh 17.1	(34.2)	U + gap 20.7	(41.4)	Wt 10.9	(21.8)
RGM 542319	D + gap 48.6	Wh 15.7	(32.3)	U + gap 20.0	(41.2)		
RGM 541761	D + gap 47.1	Wh 16.3	(34.6)	U + gap 18.5	(39.3)	Wt 9.9	(21.0)
RGM 387892	D + gap 49.1	Wh 15.9	(32.4)	U + gap 18.6	(37.9)		
RGM 387891	D + gap 47.3	Wh 17.9	(37.8)	U + gap 18.5	(39.1)		
RGM 542317	D + gap 46.2	Wh 15.7	(34.0)	U + gap 20.0	(43.3)		
RGM 387894	D + gap 44.5	Wh 15.9	(35.7)	U + gap 16.7	(37.5)		
RGM 541760	D + gap 43.3	Wh 16.7	(38.6)	U + gap 15.9	(36.7)		
RGM 541941	D + gap 40.6	Wh 16.0	(39.4)	U + gap 14.0	(34.5)		
RGM 542316	D + gap 42.7	Wh 17.0	(39.8)	U + gap 17.1	(40.0)		
RGM 542668	D + gap 35.1	Wh 12.9	(36.8)	U + gap 13.8	(39.3)		
RGM 541762	D + gap 34.6	Wh 13.0	(37.6)	U + gap 14.0	(40.5)		
RGM 387942	D + gap 33.9	Wh 13.0	(38.3)	U + gap 12.0	(35.4)		
RGM 541764	D + gap 26.3	Wh 10.0	(38.0)	U + gap 10.0	(38.0)		
RGM 541763	D + gap 24.9	Wh 10.5	(42.3)	U + gap 9.5	(38.2)		

Plate XVIII

Fig. 1-7: *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868), small macroconchs.
1, RGM 541865, locality 3A; ×1. 2, RGM 387630, locality 1A, bed A144; ×1. 3, RGM 387625, locality 1A, bed A144; ×1. 4, RGM 541901, locality 3B, bed B200; ×1. 5, RGM 387627, locality 1A, bed A144; ×1. 6, RGM 387631, locality 1C, bed C144; ×1. 7, Q (R)26-30, locality 4, loose from beds 26-30; ×1.

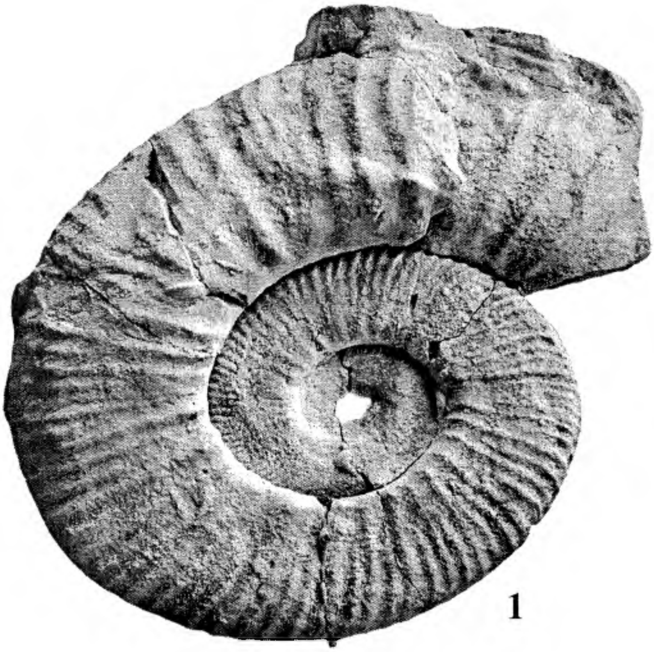
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Table XXIV: Measurements of *C.* (*Bi.*) *rotundatus*

RGM 541819	D + gap 102.8	Wh 32.9	(32.0)	U + gap 48.0	(46.7)		
RGM 542855	D + gap 82.3	Wh 28.4	(34.5)	U + gap 32.4	(39.4)		
RGM 541807	D + gap 70.3	Wh 23.9	(34.0)	U + gap 29.4	(41.8)	Wt 11	
RGM 387936	D + gap 71.2	Wh 25.5	(35.8)	U + gap 29.1	(40.9)		
RGM 387921	D + gap 70.2	Wh 26.0	(37.0)	U + gap 27.6	(39.3)	Wt 12.9	
RGM 541818	D + gap 70.0	Wh 25.0	(35.7)	U + gap 29.6	(42.3)		
RGM 387939	D + gap 66.5	Wh 25.4	(38.2)	U + gap 25.3	(38.0)		
RGM 341798	D + gap 64.6	Wh 22.5	(34.8)	U + gap 26.6	(41.2)		
RGM 541747	D + gap 63.0	Wh 21.2	(33.7)	U + gap 26	(41.3)		
RGM 541808	D + gap 59.3	Wh 21.3	(35.9)	U + gap 25.7	(43.3)		
RGM 541809	D + gap 56.8	Wh 18.3	(32.9)	U + gap 24.0	(42.9)		
RGM 541795	D + gap 51	Wh 17.0	(33.3)	U + gap 20.2	(39.6)		
RGM 541796	D + gap 51.3	Wh 16.3	(31.8)	U + gap 20.9	(40.7)		
RGM 541804	D + gap 45.1	Wh 16.1	(35.7)	U + gap 18.2	(40.4)		
G.I.A. P 231	D + gap 45	Wh 15.7	(34.9)	U + gap 16.8	(37.3)	Wt 9.3	(20.7)
RGM 541800	D + gap 40.4	Wh 15.1	(36.4)	U + gap 14.5	(35.9)		
RGM 541802	D + gap 35.8	Wh 15.0	(41.9)	U + gap 11.8	(33.0)		
RGM 541799	D + gap 28.5	Wh 12.6	(44.2)	U + gap 8.6	(30.2)		

Table XXV: Measurements of *C.* (*B*) *angulicostatus*

RGM 542863	D + gap 59	Wh 19.3	(32.7)	U + gap 26.8	(45.4)	Wt 18	(30.5) Gap 1
Holotype:	D + gap 49	Wh 18	(36.7)	U + gap 22	(44.9)	Wt 15	(30.6) Gap 1

Table XXVI: Measurements of *C.* (*B.*) *seitzi*

GIA J9963	D + gap 57.3	Wh 18.65	(32.5)	U + gap 25.9	(45.2)	Wt 10
RGM 387979	D + gap 57.9	Wh 20.2	(34.9)	U + gap 25.3	(43.7)	

Table XXVII: Measurements of *C.* (*B.*) *angulicostatiformis*

Plaster cast of holotype 16850:

D + gap 75	Wh 25	(33.3)	U + gap 31.3	(41.7)	Wt 18.8	(25.1)	Wt/Wh 0.75

Plate XIX

Fig. 1-18: *Pseudothurmannia* (*Kakabadziella*) *ohmi ohmi* (Winkler, 1868), young specimens.

1, RGM 542264, locality 3C; ×1. 2, same specimen; ×2. 3, RGM 541856, locality 3T, bed 3; ×1. 4, RGM 541825, locality 3B; ×1. 5, RGM 542261, locality 5; ×1. 6, RGM 387609, locality 1A, bed A144; ×1. 7, RGM 542864, locality 1A, bed A144; ×1. 8, RGM 541855, locality 3B, bed 201; ×1. 9, RGM 542266, locality 3T, bed T3; ×1. 10, RGM 387610, locality 1A, bed A144; ×1. 11, RGM 387606, locality 1A, bed A144; ×1. 12, RGM 387615, locality 1A, bed A144; ×1. 13, RGM 387616, locality 1A, bed A144; ×1. 14, RGM 387658, locality 1J, bed J142; ×1. 15, RGM 542267, locality 3; ×1. 16, 387620, locality 1A, bed A144; ×1. 17, RGM 387608, locality 1A, bed A144; ×1. 18, RGM 542029, locality 1A, bed A149; ×1.

Plate XIX


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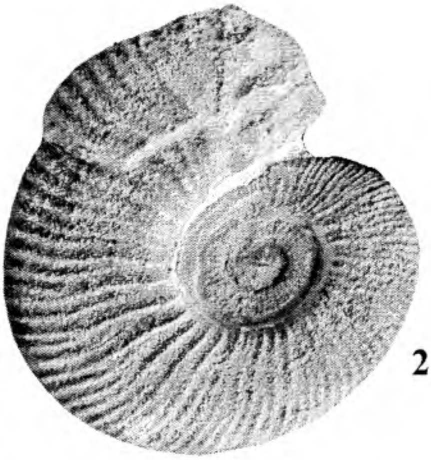
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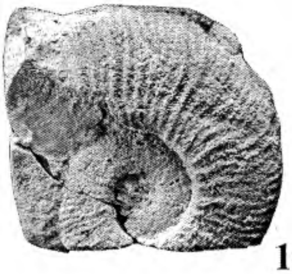
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Plate XX

Fig. 1-18: *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov., young specimens.

1, RGM 542519, locality 7, *Pseudothurmannia* beds; ×1. 2, RGM 387652, locality 1K, bed K153; ×1. 3, RGM 387677, locality 7, bed 83; ×1. 4, RGM 387650, locality 1F, bed F154; ×1. 5, RGM 387888, locality 1A, bed A160; ×1. 6, RGM 542156, locality, 1C, bed C153; ×1. 7, RGM 387694, locality 7, *Pseudothurmannia* beds, apertural view; ×1. 8, same specimen, lateral view; ×1. 9, same specimen, ventral view; ×1. 10, RGM 387711, locality 7, bed 83; ×1. 11, RGM 542084, locality 8, lateral view; ×1. 12, same specimen, apertural view; ×1. 13, 542158, locality 8; ×1. 14, 387853, locality 10, bed 5/254; ×1. 15, RGM 387647, locality 1F, bed F154; ×1. 16, 542157, locality 2, lateral view; ×1. 17, same specimen, ventral view; ×1. 18, same specimen, apertural view; ×1.

Plate XX


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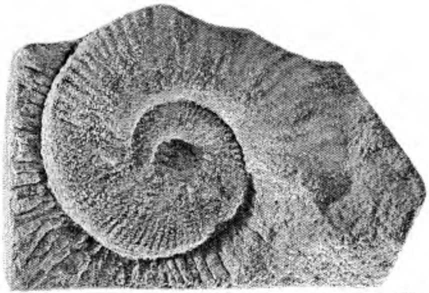
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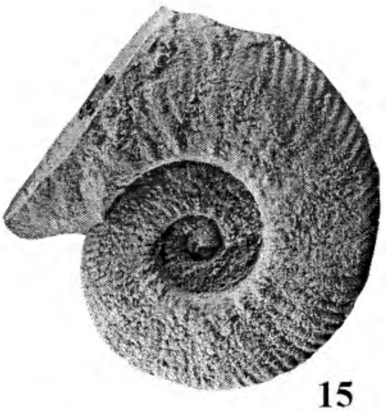
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Plate XXI

Fig. 1-3: *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov., macroconchs.
1, RGM 542153, locality 1C, bed C158; ×1. 2, RGM 542155, locality 1K, loose from beds K143-163, closely resembles *Crioceras angulicostatum* (d'Orbigny) in Karakasch (1907, pl. 15, fig. 1); ×1. 3, RGM 387662, locality 7, bed 2'; ×1.

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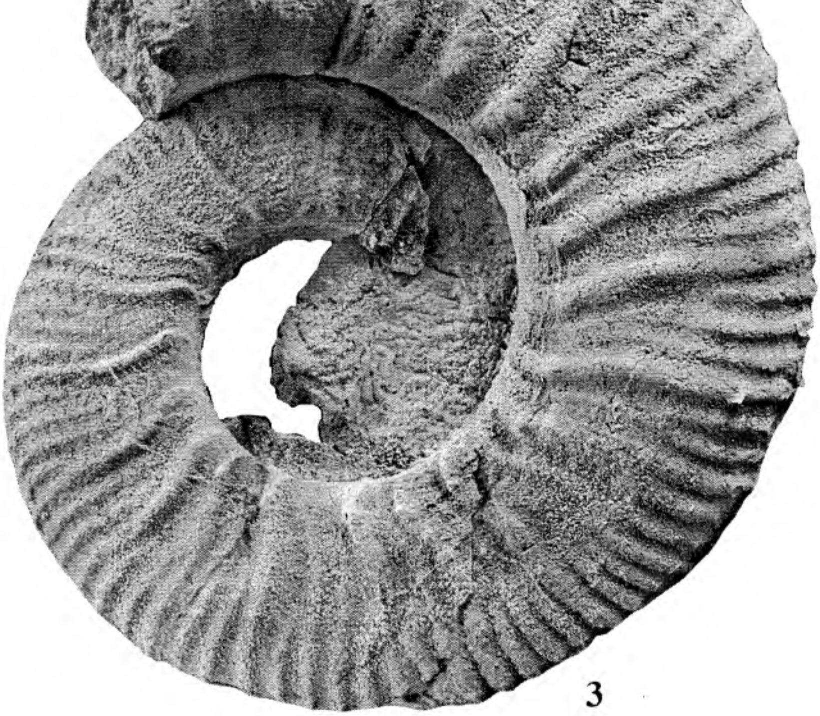

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Plate XXII

Fig. 1-8: *Pseudothurmannia* (*Kakabadziella*) *ohmi valbonnettensis* subsp. nov., microconchs.
1, RGM 542152, locality 1K, bed K162; ×1. 2, RGM 387723, locality 7, bed 83; ×1. 3. RGM 387721, locality 7, bed 2; ×1. 4, RGM 387720, locality 7, bed 83; ×1. 5, RGM 387668, locality 7, bed 3'; ×1. 6, RGM 387716, locality 7, bed 83, young microconch (?) closely resembling the drawing of *Ammonites angulicostatus* d'Orbigny (pl. 46, figs 3, 4). 7, RGM 542417, locality 6, bed CR327, small microconch; ×1. 8, RGM 542521, locality 7, bed 83; ×1. 9, RGM 542521 locality 7, bed 83; ×1.

Plate XXII


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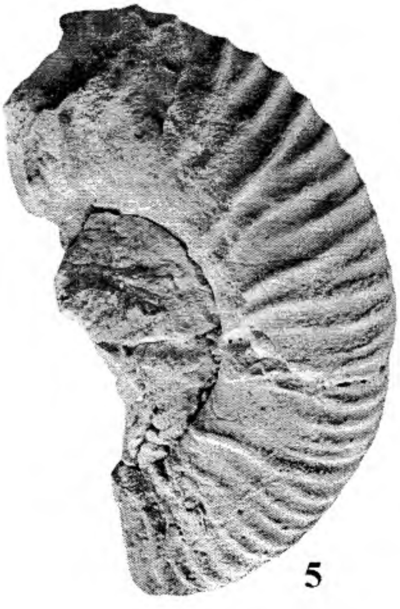
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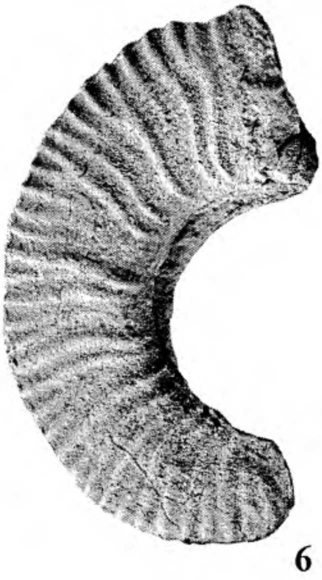
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Plate XXIII

Fig. 1-3: *Pseudothurmannia* (*Parathurmannia*) *edouardi* (Honnorat-Bastide, 1889).
1, plaster cast of holotype, left lateral view, same side as the drawing of the holotype; ×1. 2, same specimen, ventral view, suture of the mold clearly visible; ×1. 3, same specimen right lateral view, shown for the first time; ×1.

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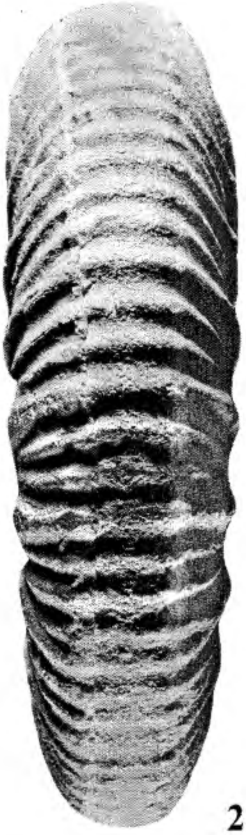

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Plate XXIV

Fig. 1-9: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955. Holotype and young specimens.
1, RGM 542520, locality 8; ×1. 2, RGM 542650, locality 2; ×1. 3, RGM 542848, locality 1W, bed W35; ×1. 4, RGM 542847, locality 1F, bed F153; ×1. 5, same specimen, plaster cast; ×1. 6, plaster cast of specimen figured by Wiedmann (1962) under the name *Crioceratites* aff. *angulicostatus* (d'Orbigny), locality Barrême (Alpes-de-Haute-Provence, France); ×1. 7, plaster cast of holotype, lateral view; ×1. 8, same specimen, apertural view; ×1. 9, RGM 642644, locality 2; ×1.

Plate XXIV


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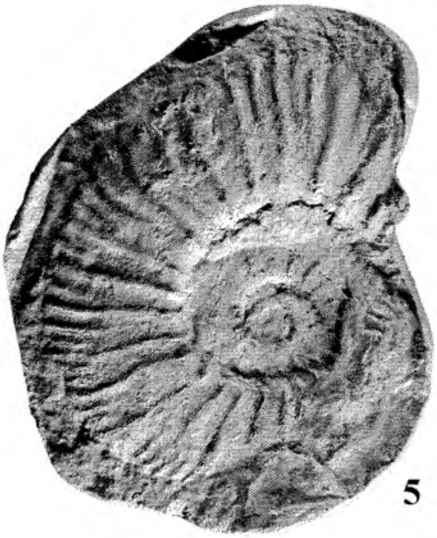
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Plate XXV

Fig. 1: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955. RGM 542645, locality 2, specimen with long intermediate ribs; 84%.

Plate XXVI

Fig. 1-2: *Pseudothurmannia (Pseudothurmannia) picteti* Sarkar, 1955.
1, RGM 542639, locality 2, specimen with long intermediate ribs, lateral view; 82%. 2, same specimen, ventral view; 72%.

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Plate XXVII

Fig. 1: *Pseudothurmannia* (*Pseudothurmannia*) *picteti* Sarkar, 1955. RGM 542646, locality 2, specimen with short intermediate ribs; 90%.

Plate XXVIII

Fig. 1-2: *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955.
1, RGM 542660, locality 2, apertural view; 91%. 2, same specimen, lateral view; ×1.

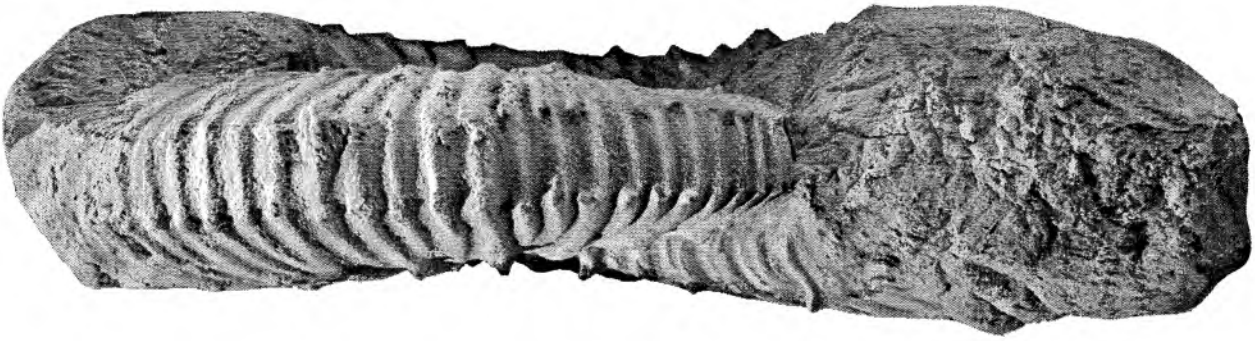

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Plate XXIX

Fig. 1-3: *Pseudothurmannia* (*Pseudothurmannia*) *simionescui* Sarkar, 1955.

1, plaster cast of specimen figured by Pictet (1863) pl. 1bis, fig. 2a, b under the name of *Ammonites angulicostatus* d'Orbigny, 'forme a tours en contact' (Pictet collection number 16848) ; ×1. 2, RGM 542665, locality 2; ×1. 3, RGM 387834, locality 2, note the near absence of lateral tubercles; ×1.


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Plate XXX

Fig. 1-6: *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884, young specimens.
1, RGM 542129, locality 1W, bed W38; ×1. 2, RGM 542130, Locality 1W, bed W38; ×1. 3, RGM 542132, locality 1W, in loose block from beds W35-46; ×1. 4, RGM 542134, locality 1W, in loose block C from beds W35-46; ×1. 5, RGM 542136, locality 1K, bed K154, looks closely like type of '*Pseudothurmannia angulicostata* var. *tuberculata* Sarkar, 1955; ×1. 6, RGM 387984, locality 1W, in loose block A from beds W35-46; ×1.

Plate XXX


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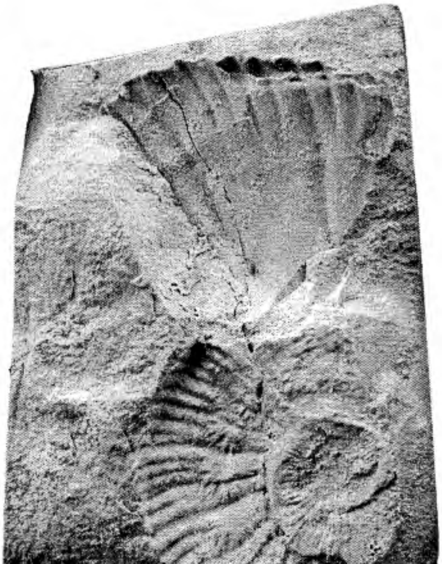
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Plate XXXI

Fig. 1: *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884. RGM 387767, specimen closely resembling the holotype, locality 7, *Pseudothurmannia* beds; 73%.

Plate XXXII

Fig. 1-2: *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884.
1, RGM 542205, specimen closely resembling the holotype of *Hoplites pseudomalbosi* Sarasin & Schöndelmayer, 1901, locality 7; ×1. 2, RGM 387745, large whorl fragment of typical specimen, locality 7; ×1.


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Plate XXXIII

Fig. 1-3: *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884, medium large specimens of the variety with an early start of trituberculate ribs.
1, RGM 387725, locality 7; ×1. 2, RGM 387746, locality 7; ×1. 3, RGM 387724, locality 7; ×1.

Plate XXXIII


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Plate XXXIV

Fig. 1: *Pseudothurmannia* (*Pseudothurmannia*) *crioceroides* Torcapel, 1884. RGM 387729, thick-ribbed specimen, locality 7; 66%.

Plate XXXV

Fig. 1: *Pseudothurmannia* (*Pseudothurmannia*) *arundicostata* sp. nov., holotype, RGM 387730, locality 7; 73%.

Plate XXXV

Plate XXXVI

Fig. 1-17: *Crioceratites* (*Balearites*) *theodomirensis* sp. nov.

1, RGM 387919, syntype, locality 1W, loose from beds W20-26; ×1. 2, RGM 542088, syntype with suture line, locality 1A, bed A142D; ×1. 3, RGM 387930, syntype, locality 1W, bed W26; ×1. 4, RGM 397914, young specimen, locality 1W, loose from beds W28-29; ×1. 5, RGM 542093, young specimen, locality loose from beds W30-30E; ×1. 6, RGM 387912, clearly shows the lateral tubercles on the innermost whorls, locality 1W, loose from beds W20-30; ×1. 7, RGM 542096, locality 1W; ×1. 8, RGM 542324, locality 3B, bed B202; ×1. 9, RGM 542086, locality 1W, bed W29; ×1. 10, RGM 542094, locality 1W, bed W31; ×1. 11, RGM 542087, locality 1A, bed A142C; ×1. 12, RGM 542090, locality 1W, loose from beds W20-26; ×1. 13, RGM 387928, locality 1W, loose from beds W24-30; ×1. 14, RGM 542095, locality 1W; ×1. 15, RGM 542325, locality 3B, bed B200; ×1. 16, RGM 542278, locality 5; ×1. 17, RGM 542091, locality 1W, loose from beds W30-30E; ×1.


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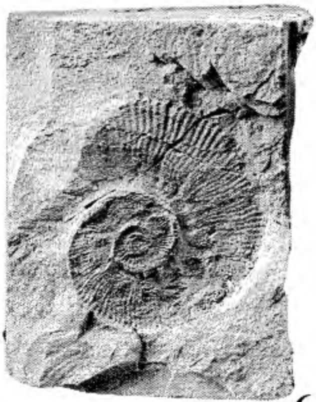
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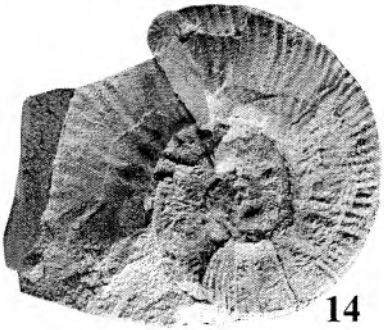
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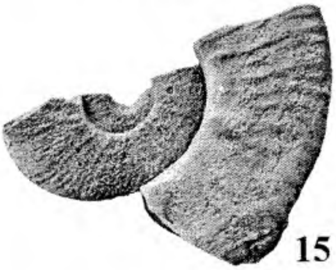
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Plate XXXVII

Fig. 1-10: *Crioceratites* (*Balearites*) *pseudothurmannii* Dimitrova, 1967.

1, RGM 387882, similar to holotype, locality 1W, bed W26; ×1. 2, RGM 542396, similar to holotype, locality 1F, bed F142C; ×1. 3, RGM 542394, similar to holotype, locality 1W, bed W24; ×1. 4, plaster cast of holotype, locality Beli Mel, Bulgaria; ×1. 5, RGM 387893, intermediate between holotype and paratype, locality 1W, loose from beds W24-27; ×1. 6, RGM 542395, intermediate between holotype and paratype, locality 1W, bed W27; ×1. 7, GIA J9967, similar to paratype, locality 1W; ×1. 8, RGM 542397, similar to paratype, locality 1W, bed W30; ×1. 9, plaster cast of paratype, locality Bulgarski izvor (Bulgaria) ; ×1. 10, RGM 387974, similar to paratype, locality 1W, loose from beds W28-30; ×1.

Plate XXXVII


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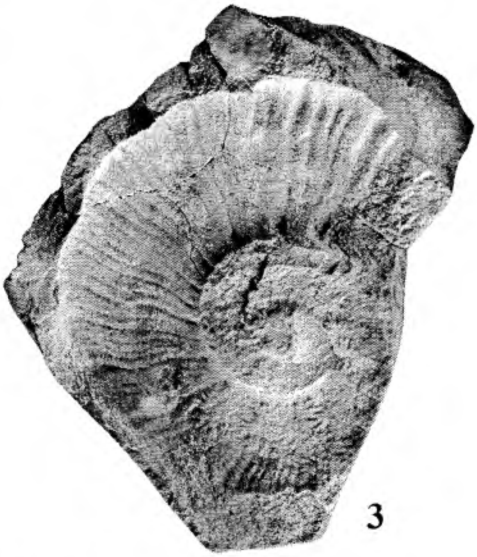
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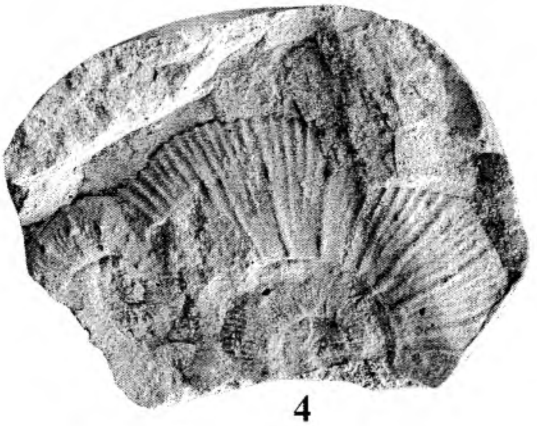
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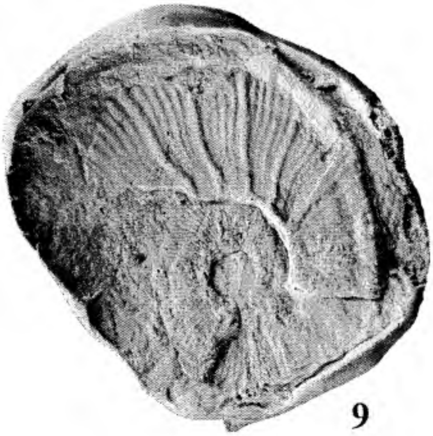
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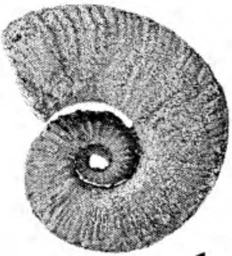
Plate XXXVIII

Fig. 1-14: *Crioceratites* (*Binelliceras*) *ibizensis* Wiedmann, 1962, small specimens.
1, RGM 387942, locality 1W, loose from beds W27-30; ×1. 2, RGM 541764, locality 1W, bed W23; ×1. 3, RGM 541762, locality 1W, bed W23; ×1. 4, 541767 locality 1W, bed W30B; ×1. 5, RGM 542272, locality 5, bed 39; ×1. 6, RGM 387894, locality 1W, bed W30B; ×1. 7, RGM 387891, locality 1W, bed W31; ×1. 8, RGM 541760, locality 1W, bed W31×1. 9, RGM 541768, locality 1W, bed W30; ×1. 10, RGM 541766, locality 1W, loose from beds W28-29; ×1. 11, RGM 387892, locality 1W, bed W30B; ×1. 12, RGM 542316, locality 3; ×1. 13, RGM 387880, locality 1W, bed W24; ×1. 14, RGM 541765, locality 1W, bed W30A; ×1.

Plate XXXVIII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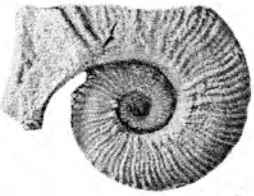
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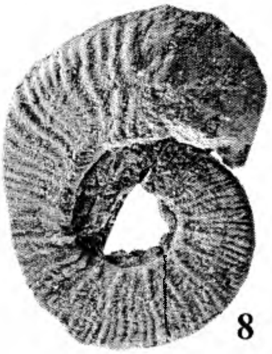
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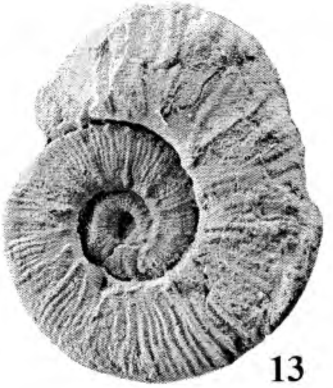
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Plate XXXIX

Fig. 1-13: *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955, small specimens.
1, GIA J9960, locality 1W; ×1. 2, RGM 541803, locality 1W, bed W26; ×1. 3, RGM 541802, locality 1W loose from beds W24-27; ×1. 4, RGM 387890, locality 1W, bed W30; ×1. 5, RGM 541800, locality 1W, bed W30B; ×1. 6, GIA P23, in a loose block from the Campo de Bejar (Moratalla, Prov. of Murcia, Spain); ×1. 7, RGM 542271, locality 5, bed 36; ×1. 8, RGM 541804, locality 1W, bed W30B; ×1. 9, RGM 542265, locality 1A, bed A144; ×1. 10, GIA P115, locality 1; ×1. 11, RGM 541809, locality 1A, bed A142; ×1. 12, RGM 542326, locality 3A, bed 1; ×1. 13, RGM 541808, locality 1A, bed A142; ×1.

Plate XXXIX


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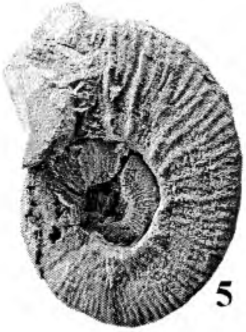
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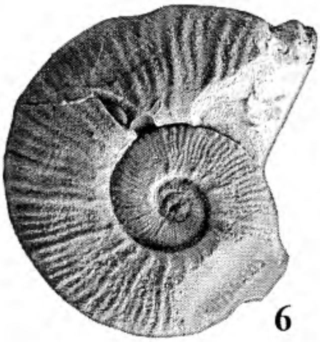
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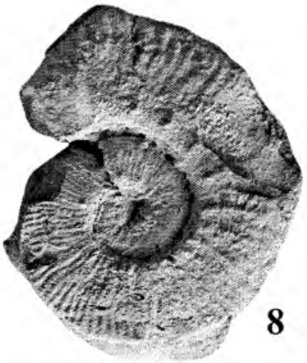
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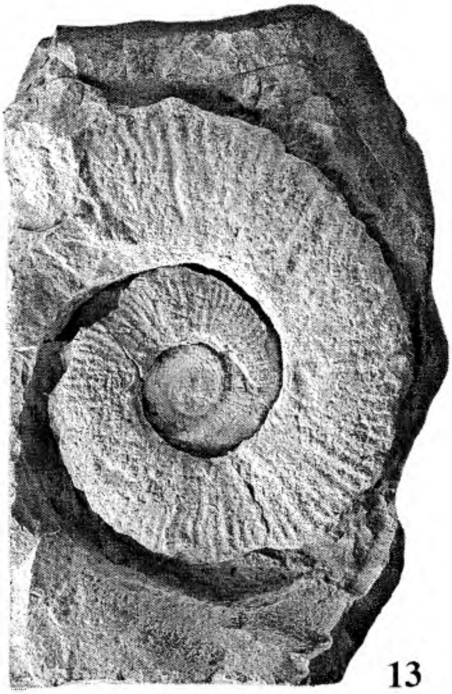
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Plate XL

Fig. 1-7: *Crioceratites* (*Binelliceras*) *rotundatus* Sarkar, 1955, large specimens.
1, RGM 387927, locality 1W, bed W30D; ×1. 2, RGM 541807, lateral view, locality 1A, bed A142; ×1. 3, same specimen, apertural view; ×1. 4, RGM 387936, locality 1W, loose from beds W30B-30E; ×1. 5, RGM 387939, locality 1W, bed W32; ×1. 6, RGM 541796, locality 1W, bed W30B; ×1. 7, RGM 541819, locality 1A, bed A142; ×1.

Plate XL


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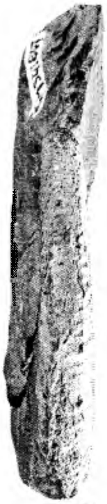
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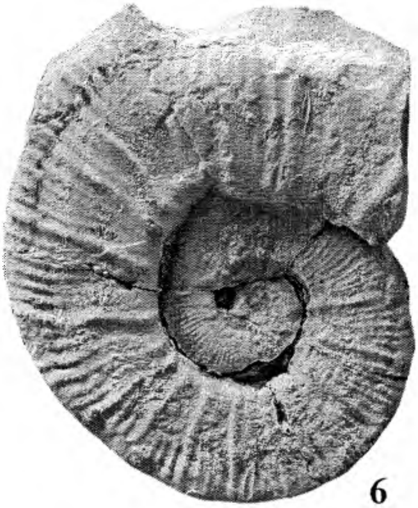
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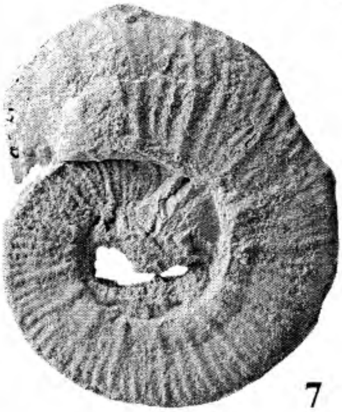
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