

Intraspecific and intrageneric variabilities and their implication for the systematics of Cretaceous heteromorph ammonites; a review

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The variability in the dimensions of the shell, and some changes in suture line, sculpture, whorl section and mode of coiling in the late ontogenetic stages, have in some cases no taxonomic significance for the recognition of genera and higher taxa of Cretaceous heteromorph ammonites. In many cases, such phenomena are due to intraspecific variation or variation within a genus. The intrageneric variations of some Cretaceous heteromorphs are discussed in detail in the light of new, rich Colombian material. In relation to these problems in systematics, some questions on the systematics of the superfamily Ancyloceratoidea Gill are considered.

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Introduction

Heteromorphic ammonites, compared to monomorphic taxa, are characterized by a much greater variability in shell construction and, as a rule, by a wider range of intraspecific, as well as intrageneric variations. Many investigators (e.g., Wiedmann, 1962; Rawson, 1975a, b; Kakabadze, 1981, 2000; Egojan, 1969; Delanoy, 1997; Delanoy *et al.*, 1995) have pointed out this property, though, in practice, this phenomenon is not always properly taken into account. Apparently, this is one of the reasons why, even in Wright *et al.* (1996), the questions of systematics of the various heteromorph groups, in comparison with the monomorphic ones, are still insufficiently worked out.

Theoretically, two main types of the intraspecific variation are possible among the Cretaceous heteromorph ammonites:

1. *Intraspecific variation related to sexual dimorphism.* This variation is expressed by the existence of microconchs and macroconchs. In the case of equal sizes of the shells, dimorphs may differ from one another in the type of ribbing or in the mode of coiling in a late growth stage, or both, and in some cases in the shape of the apertural region. Alternately, sexual dimorphism may be expressed by different sizes of the shell and at the same time by different types of ribbing and/or mode of coiling in the late ontogenetic stages.

2. *Intraspecific variations not related to sexual dimorphism (i.e., polymorphy independent of sexual dimorphism)*. Commonly, such variations are comparatively small and they may be expressed differently (not similarly) among putative male and female representatives. For example, among macroconchs morphological variability is expressed by different modes of coiling or ribbing, *etc.*, while the morphological variation among the microconchs is of another kind (Davis *et al.*, 1996; Melendez & Fontana, 1993).

The investigation of both categories of variations depends on the availability of abundant and well preserved material, and on precise stratigraphical data. Unfortunately, often due to the absence of well preserved and well dated material, the nature of the various kinds of morphological variability (within a taxon) is still poorly investigated and therefore many questions remain problematic. On the other hand, various investigations of intraspecific variations are undoubtedly of considerable importance for the systematics of the Cretaceous heteromorph ammonites. Besides the rich palaeontological material of early Cretaceous heteromorph ammonites from Colombia described in the present volume, various heteromorphs have been studied from the Caucasus and the Crimea (Kakabadze, 1967a, b, 1970, 1971a, b, 1977, 1981; Sharikadze *et al.*, 1989; Wiedmann *et al.*, 1990; Wiedmann & Kakabadze, 1993), from Middle Asia (Kakabadze, 1971a, 1981; Bogdanova & Kakabadze, 1976; Kakabadze *et al.*, 1978), South Africa (Klinger *et al.*, 1984) and Colombia (Kakabadze & Thieuloy, 1991; Kakabadze & Hoedemaeker, 1997). Additionally, examination of the collections in palaeontological museums in France, The Netherlands, Germany, Spain, Bulgaria, Slovakia, Czechia, England, Middle Asia, Russia, Ukraine, Azerbaijan, *etc.*, have allowed an analysis of the existing literature, permitted a detailed investigations of intraspecific variations and variations within the genus, and reconsideration of principles (problems) of the identification of various taxa (species, genera and family) of early Cretaceous heteromorph ammonites.

Discussion

In heteromorph ammonites, intraspecific and intrageneric variations are expressed by the morphological variability in elements of the suture line, sculpture, shell size, whorl section and mode of coiling during ontogeny.

Suture line – The prime significance of suture lines in relation to the identification of higher taxa (superfamily, suborder, *etc.*) of ammonoids has been recognised by many authors. However, the question of using the suture line for the identification of families and lower taxa is still disputed. Some families and genera (especially of monomorphic ammonites) are characterized by their own particular features of the suture line (its shape, and process of origin and arrangement of suture elements in ontogeny). However, in other families and genera (especially among heteromorphs) there are no principal differences in the features of the suture line. For example, the type of suture line of the families Ancyloceratidae Gill, 1871, and Heteroceratidae Spath, 1922, do not differ (with rare exceptions) from each other. In conclusion, it appears that, for example, among the principal elements (*ELUI*) of Ancyloceratidae or Ptychoceratidae Gill, 1871, the umbilical (*U*) and (rarely) lateral (*L*) lobes are unstable;

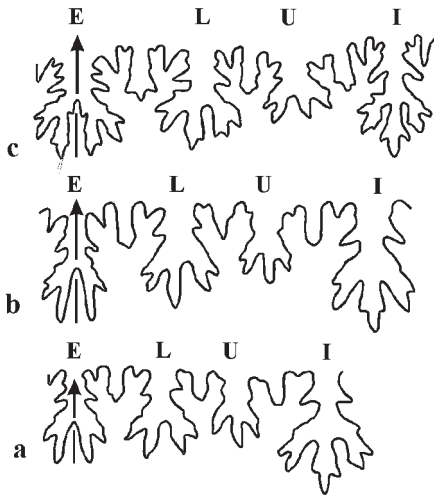


Fig. 1. Variation in the pattern of adult suture lines of different representatives of the genus *Ptychoceras* d'Orbigny: a - *P. cf. levoigatum* Egojan, $\times 1.5$; specimen 8-66/2; b - *P. cf. parvum* Egojan, $\times 2$, specimen 8-66/1; c - *P. cf. renngartenii* Egojan, $\times 1.25$; specimen 8-66/4 (from Wiedmann *et al.*, 1990).

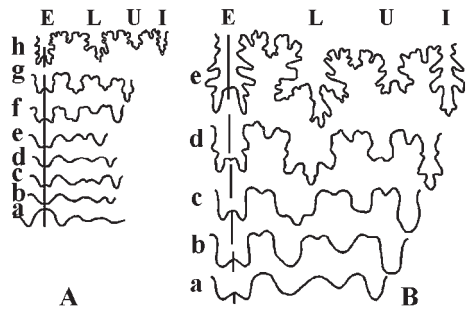


Fig. 2. Variation in the pattern of adult suture lines of the genus *Luppovia* Bogdanova, Kakabadze & Michailova: A - *L. dostshanensis* Bogdanova, Kakabadze & Michailova, specimen 1/97; a-e ($\times 18$); f-h ($\times 6$). Mangishlak, Doshchan, Middle Aptian, Zone *E. subnodosocostatum*. B - *L. adjiderensis* Bogdanova, Kakabadze & Michailova, specimen 9/97; a - $\times 20$; b - $\times 16.5$; c - $\times 9$; d - 6.7; e - $\times 3.3$. Tuarkir, Mansu, middle Aptian, Zone of *E. subnodosocostatum* (from Kakabadze *et al.*, 1978).

they can be bifid, trifid or not clearly divided. If the adult suture lines of different species of *Ptychoceras* are compared, there is no constancy on the shape of *L* and *U*; both elements can be bifid or trifid. *L* can be bifid while *U* is trifid and *vice versa* (Fig. 1). There can even be variance in shape of suture line within the same specimen of *Ptychoceras minimum* Rouchadze (Sharikadze, 1986; Wiedmann *et al.*, 1990).

Similar observations apply to two species of *Luppovia* Bogdanova, Kakabadze & Michailova in Kakabadze *et al.*, 1978 (family Ancyloceratidae). In particular (Fig. 2), lobe *U* of *Luppovia dostshanensis* Bogdanova *et al.* is trifid, but in *L. adjiderensis* Bogdanova *et al.* it is bifid. There is also no constancy in the shape of the suture line elements of *Hemihoplites* Spath, 1924. In particular, in most of the specimens of *H. ridzewskyi* Karakasch I have studied from the Upper Barremian of the north Caucasus, the lobe *U* is trifid, but sometimes bifid. Moreover, there are specimens (Fig. 3) which have a bifid *U* on one side of the whorl, but a trifid *U* on the other side. It is also remarkable that some of the specimens of *H. ridzewskyi* have an inner central saddle (I_1/I_1), whereas in most specimens such a saddle is absent (Fig. 4). Similar variations in the pattern of the suture line are rather widespread among heteromorphs and have, for instance, been documented from anisoceratids (Wiedmann & Dieni, 1968, fig. 85).

These examples clearly demonstrate intraspecific and intrageneric variations in different heteromorphic families, expressed by various morphological combinations of the *L*, *U* and, rarely, *I* lobes. This means that the shape of the lateral (*L*), as well as the umbilical (*U*) and inner (*I*), lobes are not so stable as expected. Hence, the suture line in heteromorphic ammonites should not be used independently from other morphological features for separating new genera or families, as it has been done by

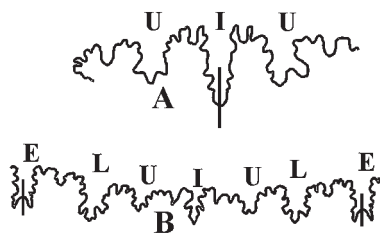


Fig. 3. Variation in pattern of the suture line on the different flanks of one and the same specimen of genus *Hemihoplites*: A - *H. (Matheronites) cf. ridzewskyi* Karakasch, specimen 253/90, $\times 2$, Daghestan, beds with mixed late Barremian-early Aptian fauna; B - *Hemihoplites* sp., specimen 252/90, $\times 2.5$, North Caucasus, to the south from Nalchik, riv. Belaia rechka, beds with mixed Barremian-early Aptian fauna.

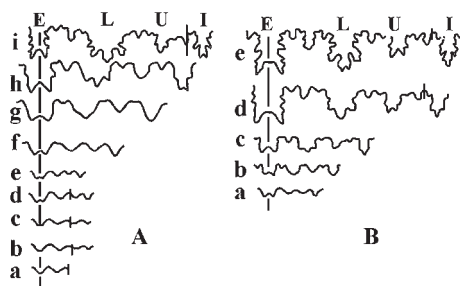


Fig. 4. Two different variants of ontogeny of the suture line of *Hemihoplites (Matheronites) ridzewskyi* Karakasch: A - specimen 8 (108/4); a-g - $\times 12.5$; h - $\times 7$; i - $\times 2$. B - specimen 8 (108); a - $\times 16$; b-d - $\times 5$; e - $\times 3.2$, Daghestan, village Kasumkent, upper Barremian (from Sharikadze *et al.*, 1989).

some authors. For example, the introduction of *Pseudocrioceratites* Egojan, 1969, and *Epacrioceratidae* Egojan, 1974, has no reasonable basis and is considered unnecessary (Wiedmann & Kakabadze, 1993; Wright *et al.*, 1996).

The causes of the intraspecific variation of the suture lines in various groups of heteromorph ammonites still remain unclear. It is possible that dimorphism also has its expression in the shape of the smooth body of the ammonites. Hence, it is surmised that some of the intraspecific variability in suture lines is perhaps connected with sexual dimorphism. However, it is impossible to prove this idea because of the lack of sufficiently well preserved palaeontological material and I refrain from further discussion of this question.

Sculpture – Peculiarities in the ontogenetic development of the sculpture are important when one tries to identify species and genera among Cretaceous heteromorph ammonites. Intraspecific variability of the sculpture finds its expression, for instance, by different densities of ribbing, unstable disposition of the primary and secondary (*sensu lato*) ribs, and uneven strength of the ribs and/or tubercles at a corresponding growth stage. Taxonomic validity of many species of heteromorph ammonites has been revised on the basis of such observations. In these cases, similar specimens formerly described as independent species were united into one species (e.g., Casey, 1961; Wiedmann, 1962; Kakabadze, 1971a; Rawson, 1975a, b; Klinger & Kennedy, 1977; Kakabadze & Thieuloy, 1991; Ropolo, 1995; Hoedemaeker, 1994; Kakabadze & Hoedemaeker, 1997). My first attempt to study the intraspecific variability of the shell morphology of heteromorphs was on material of the genera *Colchidites* Djanelidze, 1926, and *Paraimerites* Kakabadze, 1967b (family *Heteroceratidae* Spath, 1924) (Kakabadze, 1971a). Before this study, the number of species in these genera was about forty. On the basis of additional material it was established that the intraspecific variation was greater in some species than was supposed earlier. Individuals of a given species may differ from each other in not having a similar disposition of main

and intermediate ribs, in the density of ribbing, and in the shape and measurements of whorl section. On the basis of such data I united *Colchidites ellipticus* Rouchadze and *C. horeshaensis* Rouchadze; *C. costatus* Rouchadze and *C. aff. costatus* Egojan, 1965; *C. ratshensis* Rouchadze and *C. nicortsmindensis* Rouchadze; *C. rionensis* Simonovich *et al.* and *C. lachepaensis* Rouchadze; *C. shaoriensis* Djanelidze and *C. aff. shaoriensis* Tovbina, 1963. Although it seems paradoxical, eleven new species of *Colchidites* were described at the same time (Kakabadze, 1971a), all characterized by their own morphological peculiarities. The existence of such a great number of species of *Colchidites* in the Caucasus and adjacent regions (Rouchadze, 1933; Kakabadze, 1971a) arouses doubt on the validity of many of them (Kakabadze & Thieuloy, 1991), but there is still not enough well preserved material at our disposal to solve the problems of variability. Analysis of various ways in which the ribbing developed is of prime importance in the determination of species. Variables are the type of curvature of the ribs, the presence or absence of intermediate ribs, and the presence of constrictions. In the case of the tuberculate forms, the arrangement and shape of the tubercles or spines, the peculiarities of their appearance and disappearance, and the ways in which the tuberculate (simple or forked, *etc.*) and non-tuberculate ribs are distributed in the different growth stages are important.

The prime significance of the type of sculpture in the identification of ammonoid genera and subgenera is clear. The type of sculpture is one of the leading arguments for determining the systematic position of the generic groups in Ancyloceratoidea. For example, the genus *Kutatissites* Kakabadze, 1970, is characterized by a similar mode of coiling to *Colchidites* Djanelidze, 1926. The juvenile parts of the shells of both genera have the shape of a helicoidal spiral, then coiling becomes planispiral and some of the species of both genera stop their growth in this planispiral ontogenetic stage. After this planispiral stage, however, some species are characterized by an adult uncoiled stage (shaft, hook). However, the sculpture of *Colchidites* is of the heteroceratid type, whereas *Kutatissites* is clearly characterized by an ancyloceratid sculpture, and by its shell morphology on the planispiral and uncoiled stages. The ancyloceratid type of sculpture and the shape of the cross section of the whorls in the planispiral and uncoiled stages were the main features used by many authors to place the genus *Kutatissites* in the family Ancyloceratidae Gill (Kakabadze, 1970; Avram, 1976; Etayo-Serna, 1983; Stoykova, 1992; Delanoy & Ebbo, 1997). The decision of Wright *et al.* (1996) to include this genus in the family Heteroceratidae Spath, 1924, without any remarks, seems somewhat surprising. In this case the similarity in the mode of coiling (helicoidal, planispiral or helicoidal, planispiral and uncoiled) is not important for identifying the systematic position as to family. For example, there are late Cretaceous ammonites of the family Nostoceratidae Hyatt, 1894 (e.g., *Jouaniceras* Basse, 1939) with similar helicoidal and planispiral coiling, but otherwise with different morphological features; their position in the superfamily Turrilitoidea is accepted without doubt.

The type of sculpture is one of the principal properties by which the genera in the family Heteroceratidae can be distinguished. For example, the general characteristic feature of the *Imerites* (*Imerites*) Rouchadze, 1933, is the existence of two pairs of tubercles (ventral and ventro-lateral) on the planispiral whorl (sometimes also on the last helicoidal whorl). The representatives of the subgenus *Imerites* (*Eristavia*) Kakabadze, 1971a, also bear ventral and ventro-lateral tubercles on the first planispiral whorl, but

they differ from *Imerites* (*Imerites*) in the following features; from the ventrolateral tubercles arise two branches, which, in the same manner as intercalatory ribs, pass over the internal side, but not over the external side (Fig. 5). Phylogenetically, *Imerites* and *Eristavia* represent two parallel lineages probably arising from the tuberculate subgenus *Heteroceras* (*Argvethites*) Rouchadze, 1933 (Kakabadze, 1967b, 1982). Taking into account all the above, these two groups are supposed to be subgenera of the genus *Imerites* Rouchadze, 1933.

On account of phylogenetic arguments (Kakabadze, 1971b), it seems logical to suppose that the group of "*Imerites*" *densecostatus* Renngarten, 1926, with only one pair of ventral tubercles, may not be phylogenetically related to the genus *Imerites*. However, the existence of intermediate forms between *Colchidites* and the group of "*I.*" *densecostatus*, and chronostratigraphical data (*Colchidites* appears earlier than the group of *densecostatus*), point to a direct phylogenetic connection between them. Therefore, the *densecostatus* group was removed from the genus *Imerites* and regarded as an independent genus, *Paraimerites* Kakabadze (Kakabadze, 1967b, 1971a). Revision of the available material shows that one of the most important properties for the classification of Ancyloceratidae or Heteroceratidae is the course of ontogenetic development and formation of the sculpture. Many genera of these families are characterized by a peculiar mode of coiling and sculpture, but there are also genera which have been established solely on the basis of peculiarities of their sculpture (e.g., *Ancyloceras* d'Orbigny, 1842; *Audouliceras* Thomel, 1964; *Pseudocrioceras* Spath 1924; *Australiceras* Whitehouse, 1926; *Caspianites* Casey, 1961). There are many examples (e.g., *Kutatissites*, *Pseudocrioceras*, *Colchidites*) showing that, among the species of one and the same genus, the sculpture is more conservative than the mode of coiling. Thus, the type of sculpture is one of the leading properties (together with the type of whorl coiling in some cases) in the systematics of the families Ancyloceratidae and Heteroceratidae, and tuberculate or non-tuberculate features are supposed to be significant taxonomic features in identification of genera in many cases.

Size and mode of coiling – In the earliest ontogenetic stage of most of Cretaceous heteromorph ammonites the mode of coiling is probably similar. The embryonic shell is planispirally coiled and fixed by the nepionic constriction at the end of the whorl. After the nepionic constriction the second whorl is uncoiled, has the shape of a wide-arc and approaches (or even is in contact with) the embryonic whorl from the inner side (Fig. 6). In symmetrical heteromorphs the second uncoiled whorl is oriented in the same plane as in the embryonic whorl, but in most of asymmetric heteromorphs it is declined from its plane of symmetry. Consequently, in this growth stage, the shell is characterized by the presence of an umbilical hiatus inside the second whorl (Kakabadze *et al.*, 1978, pp. 85-86, text-fig 3v, g, pl. 1, figs. 1, 4, 6). The various kinds of coiling (e.g., crioconic, ancyloconic, colchiconic, ptychoconic) begin from the third whorl (in the asymmetrical heteromorphs sometimes earlier) and fundament

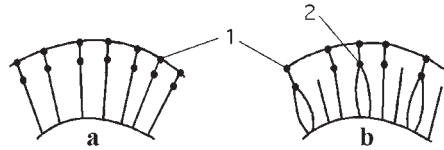


Fig. 5. Different types of the sculpture: a - *Imerites* (*Imerites*); b - *Imerites* (*Eristavia*); 1 - ventral (external) tubercles and 2 - ventro-lateral tubercles.

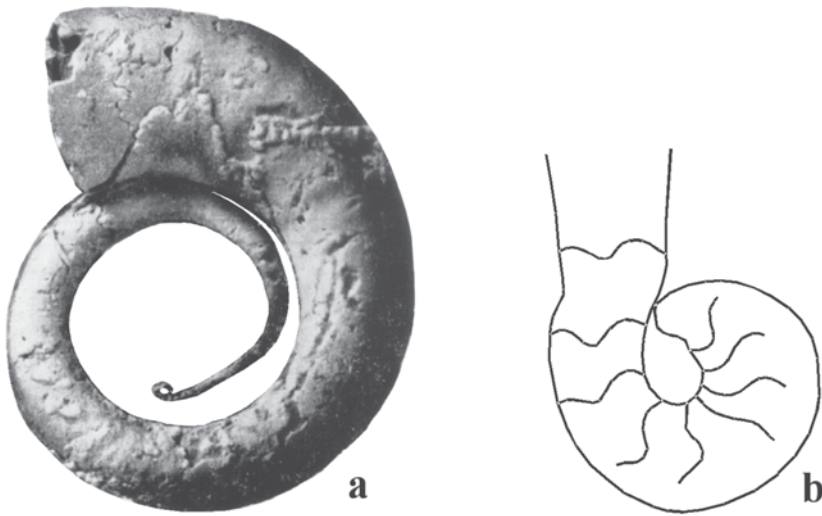


Fig. 6. The early ontogenetic stage of *Luppovia dostshanensis* Bogdanova et al.: a – mode of coiling of 1-3 whorls. Specimen 8/97 ($\times 12$), Great Balchan, Kirov, middle Aptian, Zone of *E. subnodosocostatum*; b – first whorl and initial part of the uncoiled second whorl. Specimen 7/97 ($\times 43$), Great Balchan, Bardjakli, middle Aptian, Zone of *E. subnodosocostatum*.

for the formation of the various shell types is laid in this stage (Kakabadze, 1988).

The type and size of the shell have in some cases a great taxonomic value among heteromorphic ammonites. Although there are also many examples of intraspecific variation in the sizes of the shell (e.g., *Crioceratites*, *Heteroceras*, *Colchidites*), some genera, such as *Karsteniceras*, *Tonohamites* and the subfamily Leptoceratoidinae Thieuloy, 1966, do not show any polymorphism in shell size. Therefore, in Leptoceratoidinae, the small size of the shells is, besides the simplified suture line, supposed to be of great taxonomic value (Vašiček & Wiedmann, 1994). However, such a conclusion does not hold for the Helicancyliinae Hyatt, 1894. The validity of this subfamily was suspect for a long time and discussion continued when Casey (1961) included it in the family Ancyloceratidae. According to Casey (1961), the Helicancyliinae is characterized by small shell size and simplified sculpture on the gerontic growth stage; by these features it differs from Ancyloceratidae. The species of the latter have a large shell and coarse sculpture on the gerontic growth stage. Their separation as a subfamily within the Ancyloceratidae was not accepted by many authors. For instance, it was pointed out (Kakabadze, 1981, pp. 74-76) that simplification of sculpture in the gerontic stage is observed not only in species with small shells, but also in genera with large shells (e.g., *Tropaeum*, *Ammonitoceras*, *Australiceras*). Furthermore, there are genera (such as in the families Ancyloceratidae and Heteroceratidae) which have both large and small sized species.

The various modes of coiling also exhibit great intraspecific and intrageneric variation. In some cases the shape of the shell in the mature growth stage of species may not be similar (especially in the gerontic stage). They may also be dissimilar among species of one and the same genus, as among individuals of one and the same species. For example, the principal diagnostic features of *Acrioceras* Hyatt, 1900, are

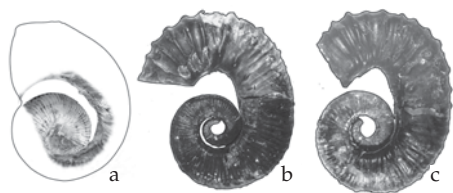


Fig. 7. Variation in the pattern of mode of uncoiling in *Pseudocrioceras anthulai* (Rouchadze). a - RGM 353 631, $\times 0.1$, Colombia, Guane, lowermost Aptian (?). Nationaal Natuurhistorisch Museum, Leiden. b - specimen ID 3013, $\times 0.1$ and c - specimen ID 3015, $\times 0.1$, Colombia, Simiti, upper Barremian (?). University of Grenoble, France.

small-sized ancyloconic shells, ornamented with main (with one to three tubercles) and intermediate (generally non-tuberculate) ribs on the planispiral whorls, and on the first part of the shaft. In a later stage, especially at the end of the hook, the tubercles may partially or wholly disappear. Nevertheless, Sarkar (1954) divided *Acrioceras* into two subgenera, *A. (Acrioceras)* Hyatt, 1900, and *A. (Protacrioceras)* Sarkar, 1954. He pointed out that *A. (Protacrioceras)* differs from *A. (Acrioceras)* in having a hoplocrioconic shell shape. Kakabadze (1981, p. 96) noted that *A. (Acrioceras)* and *A. (Protacrioceras)* are mainly characterized by similar morphological features on the planispiral stage, and that the above mentioned differences in the mode of uncoiling should not be accepted as a ground for the separation of a new subgenus (i.e., *Protacrioceras*). On the basis of a similar analysis *A. (Aspinoceras)* Anderson, 1938, was considered a junior synonym of *A. (Hoplocrioceras)* Spath, 1924.

Intraspecific variations in the morphology of the uncoiled part of the shell were observed also among the species of the genus *Pseudocrioceras* Spath, 1924. Among the material from the uppermost Barremian? of Colombia ('lower concretion horizon' at the Aptian/Barremian boundary according to unpublished data of P. Creutzberg) and Georgia, various specimens of *Pseudocrioceras* have an ancyloconic or hoplocrioconic type of uncoiling in the late ontogenetic stage. Figure 7 shows the variation in the pattern of uncoiling of three mature specimens that have the same characteristic sculpture of *Pseudocrioceras anthulai* (Rouchadze, 1933), and the characteristic shape and parameters of the planispiral whorl. In my opinion these three specimens all belong to *Pseudocrioceras anthulai*, because of their identical ornamentation during ontogeny and the similar mode of coiling of the early whorls.

Intraspecific variability in the mode of uncoiling and shell size is clearly present

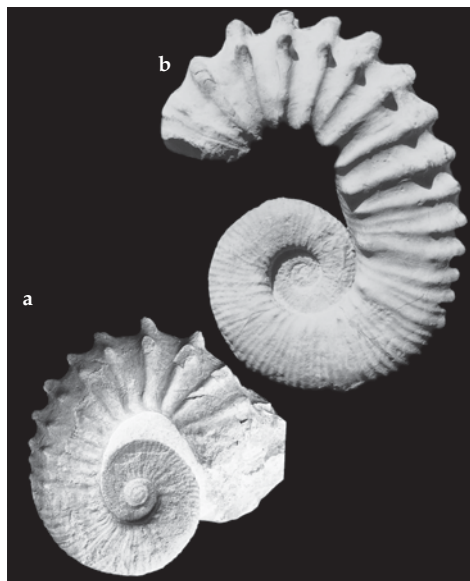


Fig. 8. Variation in the pattern of mode of uncoiling in *Pseudocrioceras coquandi* (Matheron): a - microconch, $\times 0.1$, France, La Bedoule, Le Bigadon section (bed 79), uppermost Barremian; b - macroconch, $\times 0.1$, France, La Bedoule, Les Camerlots section (bed 75), uppermost Barremian (after Ropolo *et al.*, 1999).



Fig. 9. Variation in the morphology and parameters of the shell in *Crioceratites shibaniae* Sarkar: a, b - macroconchs, c, d - microconchs, $\times 0.25$, France, Ravin du Cave de Dion section (bed 92), upper Hauterivian, Zone of *S. sayni* (after Ropolo, 1995).

Africa, were considered by these authors to be conspecific and may be regarded as a dimorphic pair. Klinger & Kennedy (1992) also raised a question about the orthodoxy of the unification of Crioceratitinae and Ancyloceratitinae into one subfamily, but, because of the lack of additional material at that time, this question remained unsolved. Later, Ropolo (1995) studied a very rich collection of heteromorphic ammonites from the Hauterivian of France and demonstrated that the species *Crioceratites shibaniae* Sarkar, 1955, is characterized by a wide spectrum of intraspecific variability, expressed in the parameters of the shell. In particular, its representatives may have a crioconic, hoplocrioconic or ancyloconic shell shape of different sizes (Fig. 9), while their other morphological features (type of sculpture, suture line) are very similar to each other. These representatives were found together in one stratigraphical level. Great intraspecific variation was also revealed in *C. curnieri* Ropolo, 1991, *C. duvali* Léveillé, 1837, and *C. majoricensis* Nolan, 1894 (Ropolo, 1995, pl. 3, figs. 1-5, pl. 4, figs. 1-3, pl. 6, figs. 1-5). In conclusion, Ropolo noted (1995, p. 139) that "if we accept dimorphic pairs, we have to unite the subfamilies Crioceratitinae and Ancyloceratitinae and regard *Crioceratites*, *Aspinoceras* and *Acriceras* as synonyms, the oldest name, *Crioceratites* (Léveillé, 1837) having priority".

Ropolo's (1995) work undoubtedly has great significance for the study of the phylogeny and systematics of the heteromorphic ammonites. Nevertheless, the many

(Fig. 8) in *Pseudocriocereras coquandi* Matheron, 1878 (e.g., Ropolo *et al.*, 1999, pl. 10, figs. 1,2). Interspecific variability of the shell shape and size is well expressed in *Crioceratites* Léveillé, 1837. Until recently, one of the principal diagnostic features of the genus *Crioceratites* was the crioconic shell type. Rawson (1975b) was the first to suggest that some small heteromorph ammonites with aspinoceratid/ancyloceratid coiling may be dimorphs of larger crioconic forms. Later, Klinger & Kennedy (1992) described a specimen from Zululand that has an ancyloconic shell type, but with the type of sculpture on the crioconic whorls that is characteristic of *Crioceratites thiollieri* Astier, 1851. Based on these data Klinger & Kennedy (1992) also called into question the 'old' diagnosis of the genus *Crioceratites*. Moreover, on the basis of the great morphological similarity of the early whorls, the species *Acriceras* (A.) *zulu* Klinger & Kennedy, 1992, and *Crioceratites* (C.) *yrigoyeni* (Leanza, 1970), found associated in the Upper Barremian of South

instances in which true dimorphic pairs could be established should still be regarded with great care. In conclusion, these data point out convincingly that the unification of those species, in the family Ancyloceratidae and into one genus, that have similar types of sculpture, suture line, *etc.*, but that have more or less different shell shapes, has to be accepted. Such an interpretation is confirmed by the variability in shell shape that is not related to sexual dimorphism. I not only refer to those phenotypic variations that are revealed within synchronous populations, but also the changes in shell shape (transition from crioconic shell to a shell shape with contiguous whorls) that occur in the phylogeny (in Hauterivian-Barremian) of *Crioceratites* Léveillé or the changes expressed by gradual reduction (during the Aptian) of the uncoiled part of the shell (Casey, 1961; Wiedmann, 1962; Thieuloy, 1964; Kakabadze, 1994) of the genera *Tropaeum* J. de C. Sowerby, 1837, *Australiceras* Whitehouse, 1926, and *Ammonitoceras* Dumas, 1876.

Among the asymmetrically or partly asymmetrically coiled ancyloceratids are genera with a rather great variability of shell size and shape. For example, the genus *Kutatissites* Kakabadze, 1970, unites species with various shell shapes and sizes, such as imeriticones, *i.e.*, the combination of a helicoidal and a planispiral part, or colchicones, *i.e.*, the combination of a helicoidal, a planispiral and an uncoiled part. However, the different shell shapes have a similar type of sculpture, suture line and whorl section.

Kakabadze (1970) united species in the genus *Kutatissites* that are characterized by an ancyloceratid trituberculate type of sculpture and initial helicoidal coiling, followed only by planispiral coiling. Avram (1976), who was not acquainted with Kakabadze's paper, independently created a new genus, *Simionescites*, representatives of which are characterized by the same type of sculpture and mode of coiling. Thieuloy (1976) was the first to consider *Simionescites* Avram as junior synonym of *Kutatissites* Kakabadze. Later, Kakabadze (1981) enlarged the diagnostic features of *Kutatissites* on the basis of additional material from Georgia and included in it species, such as *Kutatissites chreithiensis* Kakabadze, 1981, that are characterized by helicoidal, planispiral and additional uncoiled (shaft, hook) growth stages.

Stoykova (1992) did not accept Kakabadze's diagnostic emendation and proposed to create a new genus, which she did not name, on the basis of species *K. chreithiensis* Kakabadze, 1981. This was not accepted by Wright *et al.* (1996) and Delanoy & Ebbo (1997). The latter studied several species of *Kutatissites* with uncoiled (shaft, hook) part of the shell (*K. paquieri* (Kilian & Rebul), *K. niongalense* (Krenkel), *K.?* aff. *edwardsi* (Reynes) and *K. aff. chreithiensis* Kakabadze). These authors noted the existence of two morphological groups in *Kutatissites*, helicoidal-planispiral forms and helicoidal-planispiral-uncoiled forms; the type of sculpture and the whorl section of the representatives of both groups are typical for genus *Kutatissites*. They also indicated that there are several species with insufficiently known adult shells. Most interesting are the three possible ways in which these authors interpreted the existence of the uncoiled and non-uncoiled groups in *Kutatissites*.

1. It could be the expression of strong polymorphism, but there are no convincing arguments for this; only *K. paquieri* may be interpreted as having an intermediate morphology between the uncoiled and non-uncoiled forms.
2. It could be the expression of sexual dimorphism. This hypothesis is less convincing because of the lack of sufficient palaeontological material.

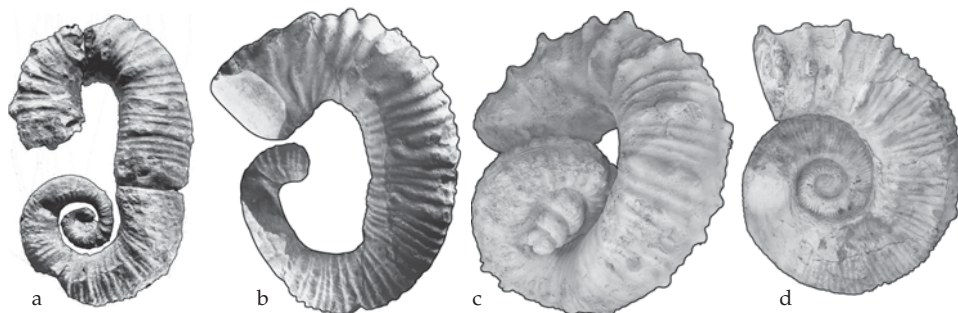


Fig. 10. Variation in pattern of mode of coiling in *Kutatissites*: a - *K. chreithiensis* Kakab., holotype, $\times 0.17$, western Georgia, Khreithi, lowermost Aptian; b - *K. paquieri* (Kilian & Reboul), spec. ID 81, $\times 0.17$. Coll. Paquir, lower Aptian (?), Les Combes, Gigors, (Drome) (after Delanoy & Ebbo, 1997); c - *K. creutzbergi* Kakab. & Hoed., holotype, $\times 0.17$. Colombia, Galan, lowermost Aptian? d - *K. denscostatus compactus* Kakabadze & Hoedemaeker, holotype, lowermost Aptian (?), $\times 0.1$, Colombia, Galan, left bank of Río Suarez.

3. It could also be the expression of phylogenetic evolution, but the absence of sufficient data on the stratigraphical distribution of many species of the genus *Kutatissites* does not permit satisfactory solution of this question.

The study of rich new material of *Kutatissites* from Colombia has revealed additional data on the existence of a third group with a variable shell morphology among its representatives. This group includes species that are characterized by a poorly developed planispiral coiling; for example, after the helical spire in *K. creutzbergi* Kakabadze & Hoedemaeker, 2004, there follows a short portion with an irregular planispiral coiling which passes into a more or less straight shaft that ends in a hook (Fig. 10). As to its type of sculpture and its whorl section, *K. creutzbergi* is typical for the genus *Kutatissites*. It should be mentioned that, together with this species, there are also species of the helicoidal-planispiral group of *Kutatissites* (according to Creutzberg's unpublished data, they are registered from the same stratigraphical level, but one can not be sure that they are from the same bed). Data on stratigraphic distribution of the uncoiled and non-uncoiled species of *Kutatissites* show that there are localities in which the uncoiled species *K. chreithiensis* Kakabadze occurs in the lowermost? Aptian in western Georgia. However, in France the uncoiled species *K. paquieri* was found in the lower Aptian?, *K. aff. chreithiensis* around the Barremian-Aptian boundary, whereas uncoiled and non-uncoiled species, *K. aff. edwardsii* and *K. aff. simionescui* Avram, 1976, are found together in the uppermost Barremian (Delanoy & Ebbo, 1997), and in the lowermost Aptian? in Georgia (Kakabadze, 1981). These occurrences make it difficult to accept the assumption of a definite phylogenetic trend in the mode of coiling (from uncoiled to planispiral or the reverse) or in the shell size of *Kutatissites* during the latest Barremian and earliest Aptian. In some cases such variability may be an expression of strong polymorphism, in others sexual dimorphism may be accepted, but this is still difficult to prove from the available material. However, the type of sculpture and the whorl section are similar in all species of these groups and there is no fundamental ground to split *Kutatissites* into two or three separate genera or subgenera.

The given examples point out that some genera of the family Ancyloceratidae are

characterized by appreciable, intrageneric morphological variability, i.e., when one and the same genus may consist of species with various shell sizes and different modes of coiling (e.g., ancyloconic, aspiniconic, crioconic and even forms with planispirally coiled contiguous whorls in the late growth stage). However, as indicated above, there are also good examples of intraspecific variations expressed by shell size or the mode of coiling in late stages. All these data give fundamental ground for unification of Ancyloceratinae Gill, 1871, Crioceratitinae Gill, 1871, and Helicancylinae Hyatt, 1894, into one subfamily; Ancyloceratinae Gill has priority.

Well-documented examples of a wide range of intraspecific and intrageneric variations also exist in the genus *Colchidites* Djanelidze, 1926 (Heteroceratidae). Rich collections of *Colchidites* have been described (Rouchadzé, 1933; Eristavi, 1955; Kakabadze, 1971a; Klinger *et al.*, 1984; Aguirre Urreta & Klinger, 1986; Kakabadze & Thieuloy, 1991; Delanoy, 1997; Kakabadze & Hoedemaeker, 2004) from different regions of the world (Caucasus, western Europe, South Africa, Patagonia, Colombia). It becomes obvious that this genus shows a considerable amount of intrageneric variability in shell shape and size, while the type of sculpture and suture line remain comparatively stable. As to intraspecific variation, in many species of *Colchidites* it is expressed by the variability in the mode of coiling, in the size of the shell, and in the normally minor variability in ornamentation, suture-line elements and whorl section.

In the diagnosis of *Colchidites* (Djanelidze, 1926; Rouchadzé, 1933), it was emphasized that one of the principal characteristics is the existence of two, helicoidal and planispiral, ontogenetic stages, whereas the presence of an uncoiled stage (shaft with hook) is not primarily characteristic. In some cases there is great similarity in ornament, whorl section and suture line among the representatives of the 'uncoiled' and 'not uncoiled' *Colchidites*. Consequently, three morphological groups were separated in *Colchidites*, of *C. intermedius* Djanelidze, 1926, *C. colchicus* Djanelidze, 1926, and *C. shaoriensis* Djanelidze, 1926. The group of *C. intermedius* (which is morphologically intermediate between *Heteroceras* and *Colchidites*) is characterized by a well-developed helical spiral (of 5-8 whorls, sometimes more) and a poorly developed planar spire (not more than one whorl) with the same plane of symmetry as the following well-developed uncoiled part (shaft and hook). The group of *C. colchicus* has rather well-developed helical (of 4-7 whorl, sometimes more) and planispiral (1-2 whorls, possibly more) whorls, and a relatively well-developed shaft and hook. The third group of *C. shaoriensis* is characterized by having helical whorls (2-7 whorls, possible more) and well-developed planispiral whorls (usually more than two whorls, but some individuals of this group have only one whorl); the absence of an uncoiled stage is characteristic for this group. If we accept the hypothesis of Aguirre Urreta & Klinger (1986) about the existence of sexual dimorphism in the group of *C. shaoriensis* (see below), then the first antidimorph may have more than two planispiral whorls, whereas the second antidimorph may have only one planispiral whorl. With respect to sexual dimorphism, if dimorphic pairs may be established in the groups of *C. intermedius* and *C. colchicus*, then the diagnosis of all three groups will undergo considerable changes. However, at the present state of knowledge one is forced to accept the diagnosis given by Rouchadzé (1933), and closer definitions and additions indicated there.

In all three groups there are species with large and small shells, but occasional differences in shell size are observed within the individuals of one and the same

species (e.g., Aguirre Urreta & Klinger, 1986; Kakabadze & Thieuloy, 1991). The plane of symmetry of the planispiral and uncoiled whorls is the same, but the axis of coiling of the helix is oblique to it with an angle that is different for each species and may vary intraspecifically; it is only rarely parallel with it. It should be mentioned that in some cases intraspecific variation is also expressed by dextral and sinistral coiling of the helicoidal spire (Kakabadze, 1971a; Aguirre-Urreta & Klinger, 1986).

According to Djanelidzé (1926), the ancestor of *Colchidites* is *Heteroceras* d'Orbigny, 1850, and there are some intermediate forms between *Heteroceras* and the group of *Colchidites intermedius*. Moreover, Djanelidzé predicted that more intermediate forms may be found and this was fulfilled by Rouchadzé (1933). Today, there are unmistakable indications of a close phylogenetic relation between these two genera. Occasionally, it is difficult to determine the taxonomic position of some of the intermediate species; do they belong to *Heteroceras* or to *Colchidites* (Kakabadze, 1971a, pp. 24-25; Kakabadze & Thieuloy, 1991, p. 96)?

However, the different interpretation of these intermediate forms has led to different conclusions. The existence of such intermediate forms caused Delanoy (1994, 1997) to include the groups of *C. intermedius* and *C. colchicus* in the genus *Heteroceras*, whereas the third group of *C. shaoriensis* Djanelidze should be included in *Martelites* Conte, 1989. So, according to Delanoy the genus *Colchidites* Djanelidze has to be abolished. The remark of Delanoy (1997) that the group of *C. shaoriensis* occurs stratigraphically higher than the representatives of the group *C. colchicus* is incorrect. Representatives of the *C. shaoriensis* group appear in the *Colchidites securiformis* Zone and occur together with the representatives of the group *C. colchicus* in rather deep marine deposits of Georgia (Kotetishvili, 1970, 1986; Kakabadze, 1971a). The fact that these two groups do not occur together in France may have an ecological cause (Kakabadze, 1967a, 1971a).

Though by Wright *et al.* (1996) and Bogdanova & Michailova (1999), Djanelidzé's point of view has been accepted without discussion, I am of the opinion that it is necessary to give a fuller explanation. Djanelidzé (1926) pointed out that, unlike *Heteroceras*, *Colchidites* shows planispiral coiling that starts immediately after the helicoidal coiling of the early whorls. In the intermediate group of *C. intermedius* the planispiral coiling is poorly developed, though the acquisition of the planispiral ontogenetic stage, a new trait, is already fixed in the genotype. This planispiral stage, which appeared and developed in *Colchidites*, was actually considered to be a new progressive structure by Djanelidzé (1926). The origin of planispiral coiling probably initiated a new function, which gave the animal the ability to pass into a more active mode of swimming (Kakabadze, 1971a; Kakabadze & Sharikadze, 1993). This new planispiral stage gradually became dominant and it is this development that became the general trend in the progressive evolution of *Colchidites* (Tovbina, 1963; Kakabadze, 1967b; Bogdanova, 1971; Michailova, 1983). This was probably the reason why Djanelidzé (1926) and Rouchadzé (1933) stressed that the principal diagnostic feature of *Colchidites* is the presence of a helicoidal and a planispiral stage, whereas the uncoiled stage (with shaft and hook) is not fundamentally characteristic.

The group of *C. intermedius* is essentially intermediate between *Heteroceras* and *Colchidites*, and some species are only conditionally assigned to *Colchidites*. Here we have almost a whole continuous phylogenetic succession from *Heteroceras* to *Colchidites*. Such a picture cannot often be observed in palaeontology. According to

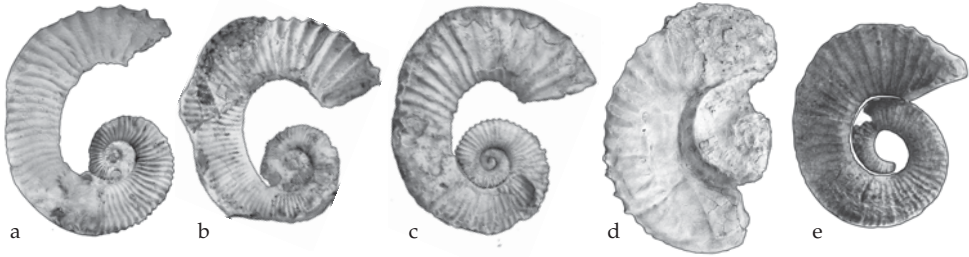


Fig. 11. Variation in the pattern of the whorl coiling/uncoiling in the gerontic stage of *Colchidites* Djanelidze: a - *C. apolinari* Royo y Gomez, RGM 353692, $\times 0.15$, Colombia, Galan, upper Barremian; b - *C. apolinari* Royo y Gomez, RGM 353696, $\times 0.15$, Colombia, Guane, upper Barremian; c - *C. rio-suarezi* Kakabadze & Hoedemaeker, RGM 353682, $\times 0.15$, Colombia, Galan, upper Barremian; d - *C. cf. breistrofferi* Kakabadze & Thieuloy, RGM 353698, $\times 0.15$, Colombia, Guane, upper Barremian; e - *C. djanelidzei* Rouchadze, holotype, $\times 0.2$, western Georgia, Kutaisi, upper Barremian.

Mayr (1970, pp. 360-361), "Our delimitation of higher taxon and its ranking in the hierarchy have a large arbitrary component ... A new taxon does not arise as an order, class, or phylum. It arises as a new species and eventually becomes a new genus that we assign to a new order only because its subsequent descendants show the degree of distinctness and of discontinuity (after much extinction) that by convention is considered to signify ordinal rank ... Where a new group is the result of a broad and varied adaptation, it may arise cryptically and its distinguishing characters may not become apparent until some time after the group has branched off. In other cases, the origin of a new group is very closely correlated with, and even sometimes preceded by, a structural invention, the origin of an evolutionary novelty." Thus, the suggestion of Delaney (1994) that the genus *Colchidites* Djanelidze has to be abolished is unacceptable. The intrageneric and intraspecific variability of the mode of coiling/uncoiling in *Colchidites* is discussed below.

On the basis of additional material from the Upper Barremian of Colombia and Georgia, it is apparent that some species of *Colchidites* show a considerable variation in the mode of coiling or uncoiling in the mature ontogenetic stage. For example, *Colchidites breistrofferi* Kakabadze & Thieuloy, 1991, is characterized by repeated slight uncoiling and recoiling during the planispiral stage (Kakabadze & Thieuloy, 1991, pl. 5, 6). *Colchidites djanelidzei* Rouchadze, 1933, however, is not uncoiled in the mature stage, but, as shown in Figure 11e, the sculpture and the shape of the almost contiguous last whorl (which includes a part of the living-chamber) is very similar to that of the uncoiled part of some other species of *Colchidites* (see Fig. 11). Moreover, some species of *Colchidites* consist of individuals that either have ancyloconic or hoplocricconic shells (shaft and hook). It should also be mentioned that among *Colchidites* found in the same stratigraphical level, it is possible to select pairs in which the pattern of growth of the helicoidal and planispiral whorls, and the sculpture are almost identical to each other until the onset of the mature stage (Fig. 12) in which some specimens become uncoiled, whereas others remain coiled. These specimens are so closely similar that, if one breaks off their living chambers, it would be impossible to distinguish them from one another. In this case we may assume that these specimens belong to

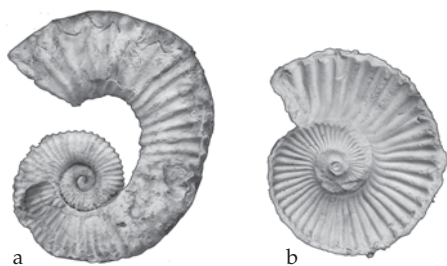


Fig. 12. a - *Colochidites riosuarezi* Kakabadze & Hoedemaeker, RGM 353682, $\times 0.25$. Colombia, Guane, upper Barremian; b - *Colchidites guanensis* Kakabadze & Hoedemaeker, RGM 353 683 (cast), $\times 0.25$. Colombia, Guane, upper Barremian.

The groups of *Heteroceras emerici* d'Orbigny, 1842 (with large shells), and *Heteroceras heliceroides* Rouchadze, 1933 (with small shells), differ from each other only in shell size, and it is plausible to look for dimorphic pairs among the representatives of these groups. Further, on the basis of rich palaeontological material of *Colchidites* from the upper Barremian of South Africa and Patagonia, they came to conclusion that among the specimens of *Colchidites vulanensis australis* Klinger *et al.* (1984), it is possible to distinguish micro- and macroconchs with a similar sculpture on the helicoidal whorls and on the first planispiral whorl. In Patagonia (section of Loma Pelada) they were found in the upper Barremian *Colchidites* beds, but unfortunately it was not indicated whether they were fixed together in the same bed. It is remarkable that adult microconchs have only one planispiral whorl (at $D=50$ mm) and have distinct apertural modifications consisting of strong, prominent, widely spaced ribs. As to the macroconchs, they must have had more than two planispiral whorls (at $D = 300$ mm) and do not show signs of uncoiling (Aguirre-Urreta & Klinger, 1986, pp. 326-331).

Delanoy *et al.* (1995) discussed the problems of dimorphism in Heteroceratidae. According to these authors the species of the group of *Heteroceras baylei*, which have small longiheteroconic shells, may form dimorphic pairs either with the species of the group *Heteroceras couletti/emeric*i (large shells with helicoidal, planispiral and uncoiled stages) or with the species of the group of *Colchidites sarasini* Rouchadze, 1933 (= '*Martelites*' *sarasini*), which also have large shells with helicoidal and planispiral whorls, but without uncoiled (shaft, hook) parts.

The first hypothesis (*H. baylei* - *H. couletti/emeric*i) might be possible, but the second hypothesis (*H. baylei* - *C. sarasini*) cannot be accepted even on the level of assumption. The morphological features (such as the shell parameters, mode of coiling and sculpture) of the species of the two latter groups and their stratigraphical ranges markedly differ from each other. The species of the group of *H. baylei* appears markedly earlier (in the top of the Zone *Hemihoplites feraudianus*), and also occur in the following two zones of *Imerites giraudi* and *Colchidites sarasini*. As to stratigraphical range of *C. sarasini*, it is known only in the *C. sarasini* Zone. These data prevent the species of *H. baylei* and *C. sarasini* forming dimorphic pairs.

closely related species of one and the same genus; they may even be sexual dimorphs. Thus, morphological similarities between 'uncoiled' and 'recoiled' representatives of *Colchidites* have to be interpreted as variation within the genus or as intraspecific variations. As to the latter example (Fig. 12), it may be interpreted hypothetically as an expression of sexual dimorphism.

Very interesting opinions about sexual dimorphism in Heteroceratidae have appeared recently. Aguirre Urreta & Klinger (1986) have studied some representatives of late Barremian *Heteroceras* from South Africa and Patagonia.

Preference is given here to the hypothesis of the existence of micro- and macroconchs in *C. vulanensis australis*, but this is not yet clear. In order to prove this hypothesis with more confidence, it is necessary to study the character of the disposition and the changes in complexity of the ultimate sutures in both micro- and macroconchs. It has to be mentioned that the probable presence of sexual dimorphism in Heteroceratidae will undoubtedly stimulate palaeontologists and will call for additional research of dimorphic pairs among the other species of Heteroceratidae. However, I realize that this problem will be difficult to solve because of the scarcity of well-preserved specimens.

Taking into account everything written here as to the intraspecific variability in heteroceratids, I cannot agree with Egojan (1976) who divided the group of *C. intermedius* into two new genera, *Epiheteroceras* and *Eocolchidites*, on the basis of the different orientation of axis of helicoidal coiling and on the basis of the degree of planispiral coiling. Moreover, he restricted the genus *Colchidites* to the group of *C. colchicus*, whereas he united the species of the group *C. shaoriensis* into a new genus *Epicolchidites* (Egojan, 1977). I have already noted (Kakabadze, 1982) that such taxonomical splitting of *Colchidites* evidently rests on shaky grounds and is not acceptable. Both of Egojan's papers (1976, 1977) are unpublished and his taxa are thus *nomina nuda*; nevertheless, I believe that the classification of Heteroceratidae suggested by this author in his doctoral thesis is necessarily considered here.

The separation of *Martelites* Conte, 1989 (emend. Delanoy, 1994) on the basis of the group *C. shaoriensis* is unacceptable; in fact, *Martelites* unites all representatives of this group and should therefore be regarded as a junior synonym of the *Epicolchidites nom. nud.* All presently existing material shows that the variability in the orientation of the axis of the early helicoidal whorls, and the variability in the mode of planispiral coiling in the middle and late ontogenetic stages, are clearly discerned in all three groups of *Colchidites*. This kind of variability should be regarded as intrageneric, but sometimes it can also be intraspecific (Kakabadze, 1971a; Aguirre Urreta & Klinger, 1986). Thus, the above-mentioned suggestions of Egojan (1976, 1977), Conte (1989) and Delanoy (1994, 1997) to split *Colchidites* into several new genera lack any weighty arguments.

The act of splitting 'Linnean' genera and families is undoubtedly a progressive tendency in the study of the systematics of the whole organic world. However, at times perpetrators of an excessive splitting of 'old' genera have appeared (and still appear); they introduce not only too many new genera, but also new families without justification. In this respect the systematics of the family Heteroceratidae Spath, 1922, is no exception. For example, Kakabadze (1967b) subdivided Heteroceratidae into two subfamilies, Heteroceratinae Spath and Colchiditinae Kakabadze. It was considered that they differ from each other in the absence (Heteroceratinae) or in the presence (Colchiditinae) of a planispiral ontogenetic stage. Later, the separation of a third subfamily Epicolchiditinae was suggested by Egojan (1977), in which he included all those heteroceratid genera that are characterized by having only helicoidal and planispiral ontogenetic stages.

With the accumulation of additional material, and by reconsidering existing phylogenetic data of heteroceratids, I came to the conclusion (Kakabadze, 1982) that there are insufficient arguments to separate the subfamily Colchiditinae Kakabadze, 1967b, and it should therefore be considered invalid. Also, the subfamily Epicolchiditinae

nomen nudum should be considered an artificial unification of morphotypes, merely based only on shell modification on the late ontogenetic stage. So, as noted by Kakabadze (1982), the taxonomic subdivision of the family Heteroceratidae Spath, 1922, into the subfamilies Heteroceratinae, Colchiditinae and Epicolchiditinae has no evident basis, and should be abandoned.

Conclusions

The data discussed in this paper indicate that intraspecific variations and variations within the genus are very common and variable in Cretaceous heteromorphic ammonites, and are expressed by dimensional changes of the shell and changes in the mode of whorl coiling, sculpture, whorl section and suture line. With regard to the systematics of heteromorphs, it is clear that emphasis should be put on the degree of the taxonomic implication shown by certain shell morphological features (sculpture, mode of coiling, suture line, etc.). Combinations of these morphological features are supposed to be different for each taxon (genus, family), but it becomes obvious that special attention has to be paid to intraspecific variation, expressed by morphological peculiarities, especially in mature ontogenetic stages. Detailed studies of such morphological features of heteromorphic species, together with data on their evolutionary tendencies in time and space, are expected to result in more reliable phylogenetic pictures and more precise systematics.

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