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Cape Town Kaapstad

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(With 26 figures)

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ABSTRACT

Representatives of the ammonite subfamily Heteroceratinae from the province of Santa Cruz, Patagonia, Argentina, include *Heteroceras (H.) elegans* Rouchadzé and *Colchidites vulanensis* Egojan *australis* Klinger, Kakabadze & Kennedy. Examination of this material and that of Zululand casts doubt on the current systematic concepts applied within the subfamily, shows distinct size-related dimorphism in *Colchidites*, and further illustrates the scope of intraspecific variation.

CONTENTS

INTRODUCTION

The Upper Barremian ammonite subfamily Heteroceratinae Spath, 1922, is best known from the south-western part of the U.S.S.R. Recent description of abundant representatives of this heteromorph group from Zululand, South Africa (Klinger 1976; Klinger *et al.* 1984) has shown distinct faunal similarities with the Caucasus; a trend that continues well into the Aptian, as indicated by other heteromorph ammonite groups (Förster 1975*a*, 1975*b*; Klinger & Kennedy 1977). Blasco *et al.* (1980) recorded the first occurrence of the heteroceratine genus *Colchidites* from Tucu Tucu in the province of Santa Cruz, Patagonia, Argentina. Since then, more material was collected by Aguirre Urreta in Patagonia for comparison with the Zululand and Caucasian material. Also, additional material from Zululand became available.

This material casts doubt on the current systematic concepts applied in the subfamily and displays the extensive range of intraspecific variation within the group. In addition, size-related dimorphism is demonstrated in the group for the first time.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repository of material:

SAM = South African Museum, Cape Town
BMNH = British Museum (Natural History), London
GIAS = Geological Institute, Academy of Science, Georgian S.S.R., Tbilisi
CPBA = Cátedra de Paleontología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires
UP = Geology Department, University of Pretoria (Boshoff collection)
SAS = Geological Survey, Pretoria, South Africa

FIELD LOCALITIES

Patagonia

Most of the Patagonian material was collected at two localities: Chorrillo del Medio and Loma Pelada, situated in the central-western province of Santa Cruz, approximately 48°25′S 72°00′W (Fig. 1). These were described by Aguirre Urreta (1983) and details of the sections are shown in Figure 2. Only one specimen was collected at locality Cerro Cornillos, situated south of the former, 10 km north of Lake San Martín, approximately 48°47′S 72°23′W.

Zululand

All the Zululand material was collected at locality 170 of Kennedy & Klinger (1975: 302, fig. 11), cliff and gully sections 2 km north-west of Mlambongwenya Trading Store on the north side of the Mlambongwenya Stream, 27°10′10″S 32°10′13″E. Details of the section are shown in Figure 3, which is a composite for this locality and extends over several hundred metres. It corresponds to Haughton's (1936: 293) localities L_7–L_{13}.

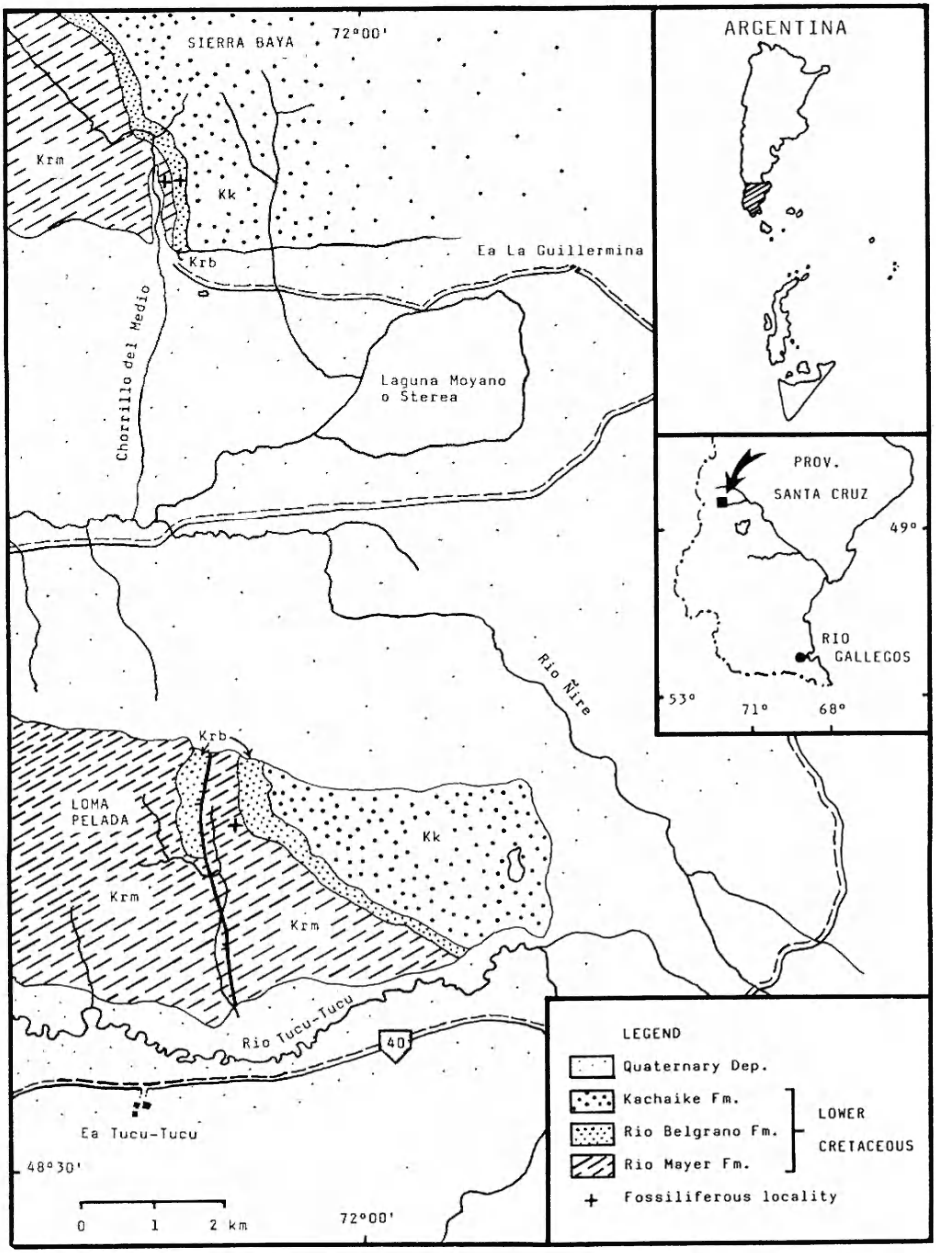

Fig. 1. Locality map of Patagonian exposures.

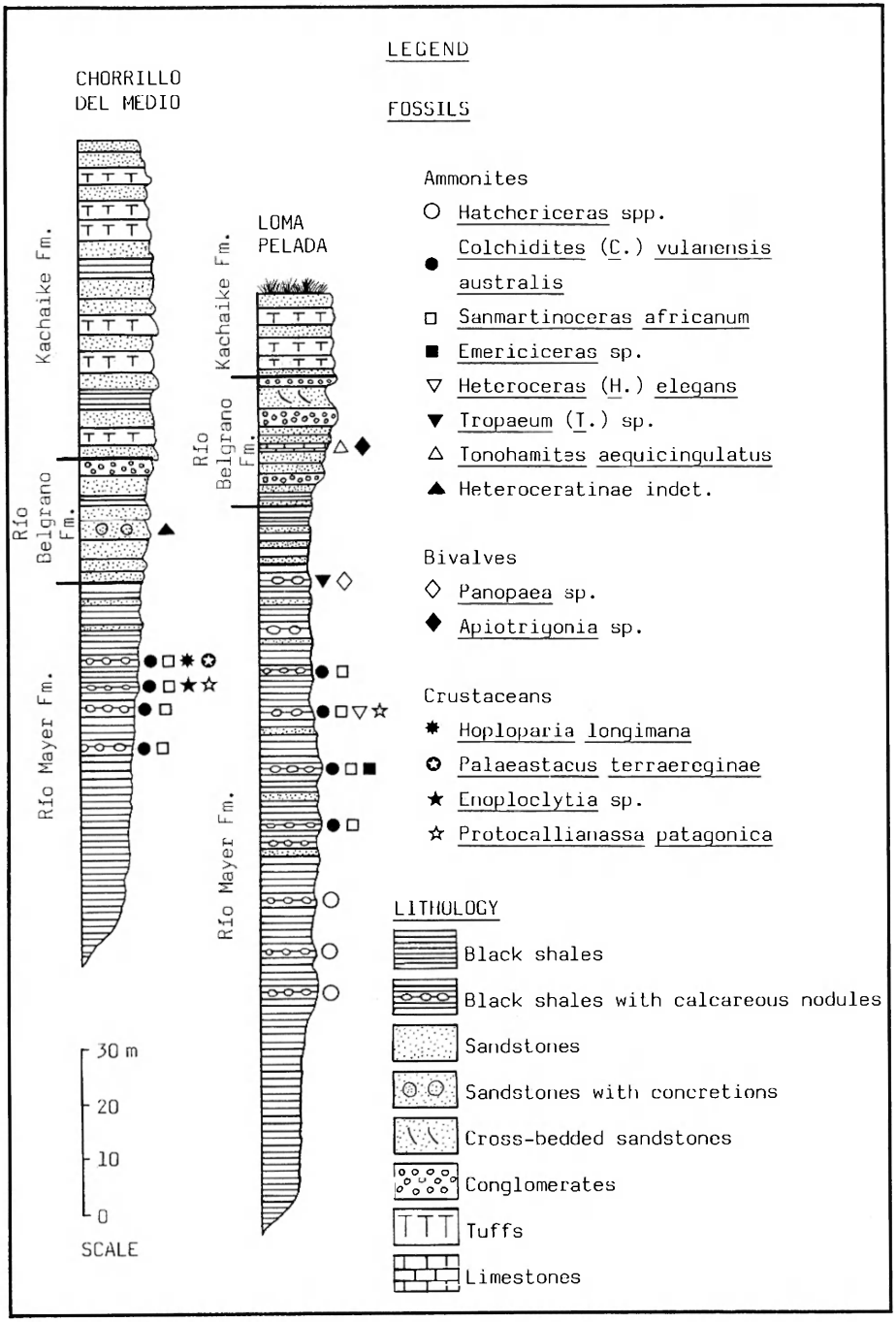

Fig. 2. Stratigraphic section at Loma Pelada and Chorrillo del Medio, Patagonia.

Fig. 3. Stratigraphic section at locality 170, Mlambongwenya Creek, Zululand. Reproduced with permission of British Museum (Natural History), London.

Note should be taken of the different lithologies. In Zululand the fauna occurs in a near-shore facies of silts and sandstones with abundant plant material, including well-preserved impressions of *Zamites recta* and *Cladophlebis dundrodiensis*. In Patagonia the dominant lithologies are anoxic black shales, with several levels of calcareous nodules in which the fossils are preserved.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916; see Kullmann & Wiedmann 1970 for a recent review) is followed in the present work.

I = internal lobe; U = umbilical lobe; L = lateral lobe; E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Phylum **MOLLUSCA** Cuvier, 1797
Class CEPHALOPODA Zittel, 1884
Order AMMONOIDEA Zittel, 1884
Suborder ANCYLOCERATINA Wiedmann, 1966
Superfamily ANCYLOCERATACEAE Gill, 1871
Family **Heteroceratidae** Spath, 1922
Subfamily Heteroceratinae Spath, 1922

The subfamily Heteroceratinae Spath, 1922, has a virtually world-wide distribution (see e.g. pp. 322, 325) but is best known from the south-western part of the U.S.S.R. (Georgia, Caucasus and Turkmenia) through the monographical studies of Djanélidzé (1926), Rouchadzé (1933), Eristavi (1955), Egojan (1965), Kotetishvili (1970) and Kakabadze (1967, 1971*a*, 1975); especially the latter. The systematics of the subfamily are based mainly on the work of Rouchadzé (1933), and subsequently elaborated by Kakabadze (1967, 1971*a*, 1975). According to Kakabadze (1967, 1971*a*, 1971*b*, 1975) the group is elevated to familial level, and consists of two subfamilies that are further subdivided as follows:

Heteroceratinae Spath, 1922	Colchiditinae Kakabadze, 1967
Heteroceras (Heteroceras) d'Orbigny, 1850	*Imerites* Rouchadzé, 1933
Heteroceras (Argvethites) Rouchadzé, 1933	*Eristavia* Kakabadze, 1967
Hemibaculites Hyatt, 1900	*Colchidites* Djanélidzé, 1926
	Paraimerites Kakabadze, 1967

With the exception of *Hemibaculites*, which is an enigmatic genus and of uncertain affinities, all the above genera are closely related, both morphologically and phylogenetically.

Division at subfamilial level is based on coiling. In Heteroceratinae an initial helix is immediately followed by an uncoiled section, which may either be a straight shaft or a broadly curved section, ending in a recurved hook of which the

shafts may be parallel or divergent. In the Colchiditinae an initial helix is followed by a planispirally coiled section of variable duration, which embraces the initial helix, finally uncoiling into a shaft and recurved hook. In some forms an uncoiled section has not yet been recorded, and it is suspected that they may reach maturity in the planispirally coiled stage.

As discussed earlier (Klinger 1976: 8) division into separate subfamilies as advocated by Kakabadze is considered superfluous.

Differentiation at generic or subgeneric level is based mainly on the presence or absence of tuberculation. *Heteroceras* s.s. is non-tuberculate throughout, whereas *H. (Argvethites)* has a pair of ventral tubercles on the shaft. *Colchidites* is non-tuberculate throughout; *Paraimerites* has a pair of variably developed ventral tubercles on part of the planispiral section and *Eristavia* and *Imerites* are both quadri-tuberculate on part of the planispiral whorls. *Eristavia* differs from *Imerites* in having intercalatory and bifurcating ribs; the latter originate at the ventrolateral tubercles and continue over the dorsum.

Within the genera *Heteroceras* and *Colchidites*, several species groups have been recognized. These were already identified by Rouchadze (1933) and subsequently either retained or elevated in rank by Kakabadze (1967, 1971*a*, 1975). Within *Heteroceras* s.s. Rouchadzé (1933) recognized two species groups: *Heteroceras astieri* d'Orbigny and *Heteroceras helicoceroides* Karsten (misspelled *heliceroides*). The group of *H. astieri* includes large forms with a high helix, and axis of coiling oblique to the dorso-ventral symmetry of the shell. The shaft is long and curved, with a recurved crozier. The group of *H. helicoceroides* includes small forms with the axis of coiling of the helix oblique to the plane of symmetry of the shell, with a slender, straight shaft and relatively long recurved crozier. *Heteroceras (Argvethites)* is similar in size to the latter species group, but differs by the possession of a row of ventral tubercles on the shaft, and often a siphonal depression on the crozier.

In *Colchidites*, Rouchadze (1933) identified three species groups:

(1) *Colchidites* gr. ex *intermedius* Djanélidzé, with a well-developed helical stage consisting of 5–8 whorls, a poorly developed planispiral part not exceeding one whorl, and a well-developed shaft and hook.

(2) *Colchidites* gr. ex *colchicus* Djanélidzé, with 4–7 whorls in the helical stage, one or two planispiral whorls, and a relatively well-developed uncoiled part.

(3) *Colchidites* gr. ex *shaoriensis* Djanélidzé with a low helix consisting of 2–3 whorls and a well-developed planispiral section with two or more whorls. An uncoiled part has as yet not been found in this species group.

According to Kakabadze (1975) these three species groups of *Colchidites* form a phylogenetic sequence, demonstrating yet another trend towards recoiling amongst heteromorphs (cf. Wiedmann 1969)—starting with *Heteroceras* at the one end, and ending at the other with a near-ammonitic coiled, streamlined form, *C.* gr. ex *shaoriensis*, which in turn may have given rise to the 'normally' coiled Deshayesitidae. It is unknown whether similar species groups and trends are

present in *Paraimerites*, as only one, monotypical uncoiled species, *P. brevihelicoides* Kakabadze, is known. No uncoiled forms are known in either *Imerites* or *Eristavia*. Both genera appear stratigraphically before *Paraimerites* and *Colchidites* from a common ancestor with *Heteroceras*, but range into the uppermost Barremian with *Paraimerites* and *Colchidites*.

The validity of this classification will be discussed below on the basis of the Patagonian and Zululand material.

Fig. 4. Lumachelle with *Colchidites* from locality 170, Mlambongwenya Creek, Zululand. Note the co-occurrence of fine and coarsely ribbed forms. SAM–PCZ6393. × 0,65.

Genus *Heteroceras* s.s. d'Orbigny, 1850

Type-species. *Turrilites emerici* d'Orbigny, 1842, from the Upper Barremian of south-western France.

Diagnosis

Open-coiled heteromorphs with an initial helix followed by a straight or curved shaft and recurved crozier. Coiling in helix dextral or sinistral, with whorls tightly coiled or scarcely in contact. Ornament on helix consists of sinusoidal, single ribs. On the shaft and on the bend of the crozier, there are single, bifurcating and intercalatory ribs. These cross the dorsum with a slight forward curvature, sometimes duplicating there, and straight over the venter. In some, a slight siphonal depression may interrupt ribbing over the venter on part of the shaft and/or crozier. Suture line rather simple with low elements.

Occurrence

Heteroceras s.s. occurs in south-western U.S.S.R. (Georgia, Caucasus, Turkmenia) (Rouchadzé 1933; Eristavi 1955; Egojan 1965; Kotetishvili 1970; Kakabadze 1975), Bulgaria (Nikolov 1964; Dimitrova 1967), Hungary (Fülöp 1964), Czechoslovakia (Silesia) (Uhlig 1883), France (d'Orbigny 1842, 1850, 1851; Kilian 1888*a*, 1888*b*), California (Murphy 1975), Colombia (Karsten 1858, 1886; Royo y Gómez 1945), Canada (Jeletzky 1970), Japan (Obata & Ogawa 1976; Obata *et al.* 1976), Zululand (Klinger 1976; Klinger *et al.* 1984; herein), Patagonia (herein).

It has also been listed in Algeria (Blayac 1905; Simionescu 1905), Morocco (Roch 1930), Tunisia (Burollet *et al.* 1983), Tanzania (Spath 1930), Spain (Simionescu 1905) and Romania (Simionescu 1905). Reference to this genus in Peru seems to be due to geographic misinterpretation of Karsten's (1856, 1886) works.

Many unsubstantiated references to *Heteroceras* are probably misidentifications of Upper Cretaceous nostoceratids.

Heteroceras (Heteroceras) elegans Rouchadzé, 1933

Figs 5, 10E–I

Heteroceras elegans Rouchadzé, 1933: 232, pl. 13 (fig. 4), text-fig. 36. Eristavi, 1955: 118. Kakabadze, 1975: 89, pl. 3 (figs 1, 3–5), pl. 8 (fig. 5).
Heteroceras astierianum d'Orb.: Drushchits & Eristavi, 1958, pl. 49 (fig. 3).
Heteroceras (H.) sp. aff. *H. (H.) astieranum* d'Orbigny: Klinger, 1976: 11, pl. 1 (figs 1–2), text-figs 5a–c, 6a.
Heteroceras (Heteroceras) elegans Rouchadzé: Klinger, Kakabadze & Kennedy, 1984: 44, figs 2A–F, 3A–G, 4A–C.

Type

Lectotype by subsequent designation (as holotype) by Kakabadze (1975) is the specimen figured by Rouchadzé (1933, pl. 13 (fig. 4)) from western Georgia, Goresha, Upper Barremian zone of *Colchidites securiformis*, housed in the

collections of the Geological Institute of the Academy of Science, Georgian S.S.R., cat. no. GIAS 350/1016.

Material

CPBA 11898–11900 from Loma Pelada, Tucu Tucu, CPBA 11121 from Cerro Cornillos, Lake San Martín, Patagonia, Río Mayer Formation, Upper Barremian, and SAS H54/29hi, BMNH C80025a–c, 80026a–b, 80028–9 from locality 170, Mlambongwenya Creek, northern Zululand, Makatini Formation, Upper Barremian.

Description

The helix consists of 4–5 contiguous whorls, coiled either dextrally or sinistrally. The last helical whorl passes directly into the straight to slightly curved shaft. The recurved crozier is relatively long, and nearly parallel to the shaft.

The whorl section in the helix is subcircular; on the shaft it varies from slightly compressed to depressed, and on the crozier it becomes equidimensional to subquadrate.

Ornament on the helix consists of fine, single, sinusoidal ribs. Ribbing on the shaft is usually single and slightly prorsiradiate, but at the end of the shaft and in the bend of the crozier bifurcating ribs are common. On the final part of the crozier the ribs are single, slightly curved and separated by interspaces wider than themselves.

A siphonal depression is present in some, but not all of the Zululand and Patagonian specimens (cf. Fig. 5A). It may already occur on the shaft, or only on the crozier, or on both. Ribs may be slightly thickened here, but no distinct tubercles develop.

Comparison

The Patagonian and Zululand material compares favourably with the specimens of *H. (H.) elegans* figured from western Georgia (Rouchadzé 1933; Kakabadze 1975; Klinger *et al.* 1984). According to Kakabadze (1975: 66) a siphonal depression occurs in the majority of tuberculate heteroceratids, i.e., *H. (Argvethites)*. Our material shows that this feature also occurs at random in non-tuberculate forms, and seems to be of very low taxonomic value.

The specimens here described also resemble the single helix and shaft fragment referred to *Heteroceras* aff. *astieri* by Obata & Ogawa (1976, pl. 4 (fig. 5)).

Heteroceras (H.) elegans differs from *H. (H.) helicoceroides* (Karsten) by the presence of chevron-like ornament on the venter of the latter—a rather *Hemibaculites*-like feature.

In *H. (H.) eristavii* the helix does not pass directly into the shaft; the latter is shorter and the recurved crozier forms a very tight bend (Kakabadze 1975: 90, pl. 4 (figs 1, 3), pl. 5 (fig. 5), pl. 8 (fig. 7)).

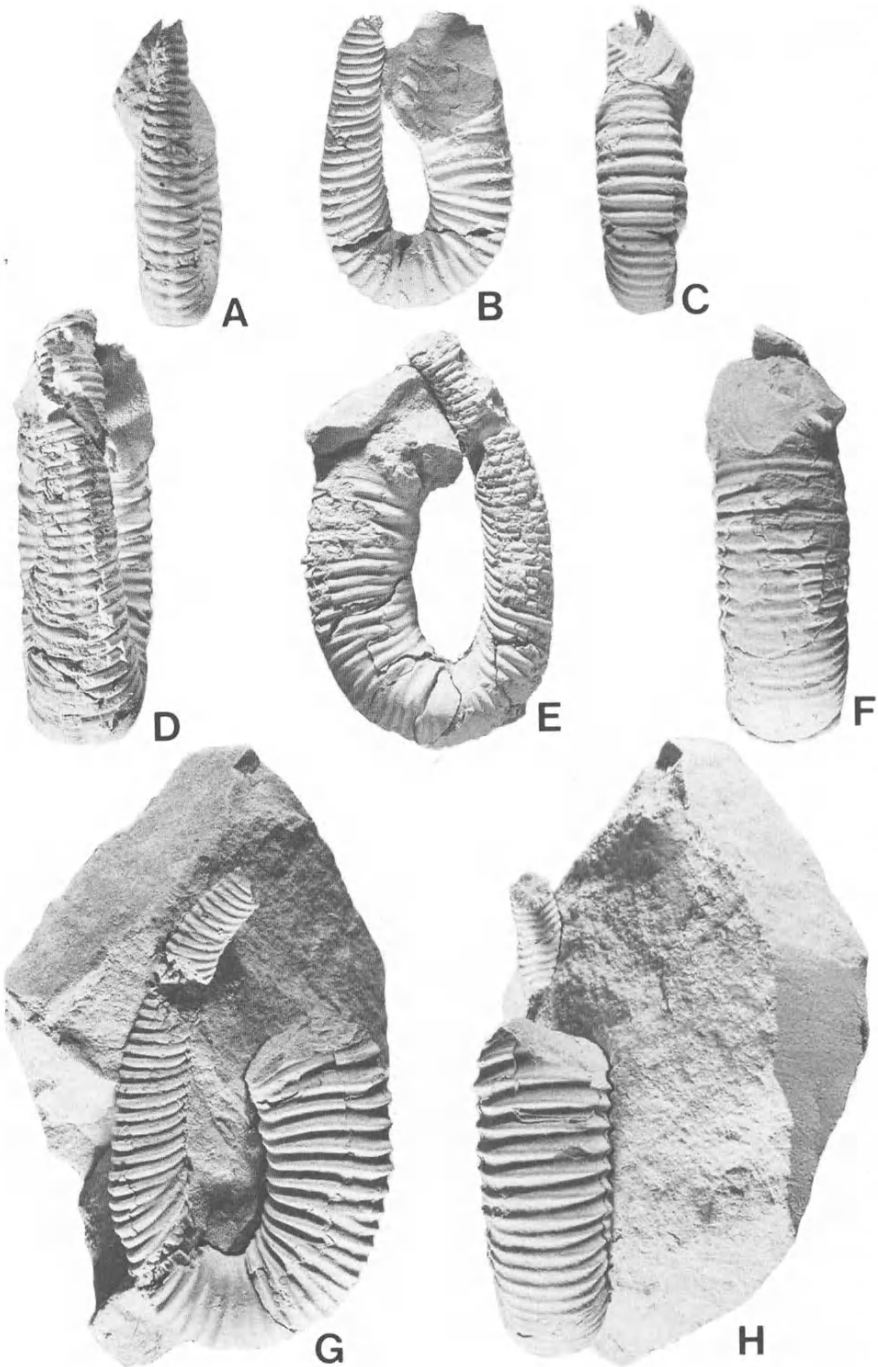

Fig. 5. *Heteroceras (Heteroceras) elegans* Rouchadzé, 1933. A–C.CPBA 11898. D–F. CPBA 11121. G–H. SAS H54/29hi. All × 1.

Heteroceras (H.) vermiforme Rouchadzé is only known from fragments. It is a very small species, with fine ribbing and an open, recurved crozier (Rouchadzé 1933, pl. 13 (fig. 5); Kakabadze 1975, pl. 3 (figs 6–8), pl. 4 (fig. 2)).

According to Kakabadze (1975: 92), *H. (H.) isocostata* Kakabadze is related to *H. (H.) elegans*, but differs in its greater size, stronger ornament on the helical part and the presence of bifurcating ribbing at the beginning of the shaft.

Occurrence

Upper Barremian of northern Caucasus, western Georgia, Zululand and Patagonia.

Genus *Colchidites* Djanélidzé, 1926

Type-species. *Colchidites colchicus* Djanélidzé, 1926, from the Upper Barremian of Georgia.

Diagnosis

Three distinct coiling modes occur during ontogeny—an initial helical spire consisting of between two and eight whorls, followed by a planispiral, discoidal section coiled more or less at right angles to the spire, which in turn may or may not end in a straight shaft with recurved crozier. Ornament consists of non-tuberculate, single, dichotomizing or intercalatory ribs.

Occurrence

Colchidites occurs in south-western U.S.S.R. (Turkmenia, Caucasus, Georgia) (Djanélidzé 1926; Rouchadzé 1933; Eristavi 1955; Drushchits & Kudryavtsev 1960; Kotetishvili 1970; Kakabadze 1971*a*), France (Kilian 1888*a*, 1888*b*), Turkey (Pelin & Thieuloy 1975), Colombia (Royo y Gómez 1945; Etayo Serna 1964), Patagonia (Blasco *et al.* 1980; herein); Zululand (Klinger 1976; Klinger *et al.* 1984). Myczynski's (1977) record of *Colchidites* sp. aff. *C. colchicus* from Cuba is accepted with reservation. The illustrated specimen is a poorly preserved, very small open-coiled heteromorph with no initial helix.

Colchidites vulanensis Egojan *australis* Klinger, Kakabadze & Kennedy, 1984

Figs 4, 6–9; 10A–D, J; 11–25, 26A–D

Colchidites sp. A Klinger, 1976: 16, pl. 1 (figs 6–7), pl. 3 (fig. 1), text-figs 5g, 6f–g.
Colchidites sp. B Klinger, 1976: 17, pl. 3 (fig. 2), text-fig. 5h.
Colchidites aff. *C. colchicus* Djanélidzé: Blasco, Nullo & Ploszkiewicz, 1980: 45, pl. 1 (figs 1–8).
Colchidites vulanensis Egojan *australis* Klinger, Kakabadze & Kennedy, 1984: 45, figs 6A–F, 7A–F, 8A–L, 9A–N.

Type

Holotype is SAS 3304/L54 from locality 170, Mlambongwenya Creek, northern Zululand, Makatini Formation, Upper Barremian.

Material

CPBA 11784, 11786, 11789, 11791, 11797–11803, 11805–6, 11809–11, 11814–18, 11821–23, 11829–30, 11839–47, 11849, 11851, 11856–61, 11863, 11865–67, 11874, 11876, 11878, 11884–5, 11888, 11901–2, all from Loma Pelada, Tucu Tucu (Bald Mountain of Hatcher 1903: 139) and CPBA 11828, 11838, 11848, 11852, 11894–6, all from Chorrillo del Medio, Tucu Tucu, Province of Santa Cruz, Patagonia, Río Mayer Formation, Upper Barremian; SAS L54/36h, L54/3288, BMNH C80013, 80015–20, 80022–25, SAM–PCZ6388–92, and more than 50 uncatalogued specimens, including blocks of colchiditid lumachelle, all from locality 170, Mlambongwenya Creek, northern Zululand, Makatini Formation, Upper Barremian.

Description

Dimorphic colchiditid with an initial helix consisting of at least five whorls, surrounded by one or two or more planispiral whorls. No uncoiled section is present.

The whorls of the helix are tightly coiled and impressed; they are either dextral or sinistral. Of 57 specimens, 30 are dextral and 27 sinistral. The most complete specimen (Fig. 6E) shows five whorls in the helix, thus the actual number may be as high as six or seven. The apical angle of the helix varies between 42 and 64 degrees. The axis of coiling of the helix is oblique to the plane of coiling of the planispiral section, forming an acute angle of between 31 and 42 degrees. The apex of the helix rests on the umbilical edge of the planispiral section. The whorl section in the helix is slightly depressed, subquadrate with rounded edges.

Ornament on the helix consists of sharp, narrow, sinusoidal ribs, which coalesce in twos or threes at the umbilical edge. Density varies between 24 and 32 per whorl.

Coiling in the first half of the planispiral whorl is irregular, with lateral deviations, but then becomes regular. In most specimens the planispiral whorl embraces the helix tightly, leaving no openings. The first planispiral whorl is higher than wide (Wb:Wh = 0,97–0,83), but the whorl section varies considerably from subrectangular to subcircular in different specimens. The ornament also shows a wide range of variation. In some specimens the ribs are high and sharp, slightly sinusoidal, usually simple, separated by wide interspaces, with rib density between 20 and 22. In others, the ornament consists of dense, rounded, sinusoidal ribs, which are simple or bifurcate from midflank. Bifurcations are asymmetrical on either side of the flanks, and are not arranged in a regular pattern. Rib density varies between 32 and 36. However, between these extremes there is a complete series of intermediate forms, so that separation on these grounds alone is impossible.

Some specimens are adult after one planispiral whorl at a diameter of about 50 mm. There are distinct apertural modifications consisting of strong, widely spaced prominent ribs. These are here interpreted as microconchs. Other

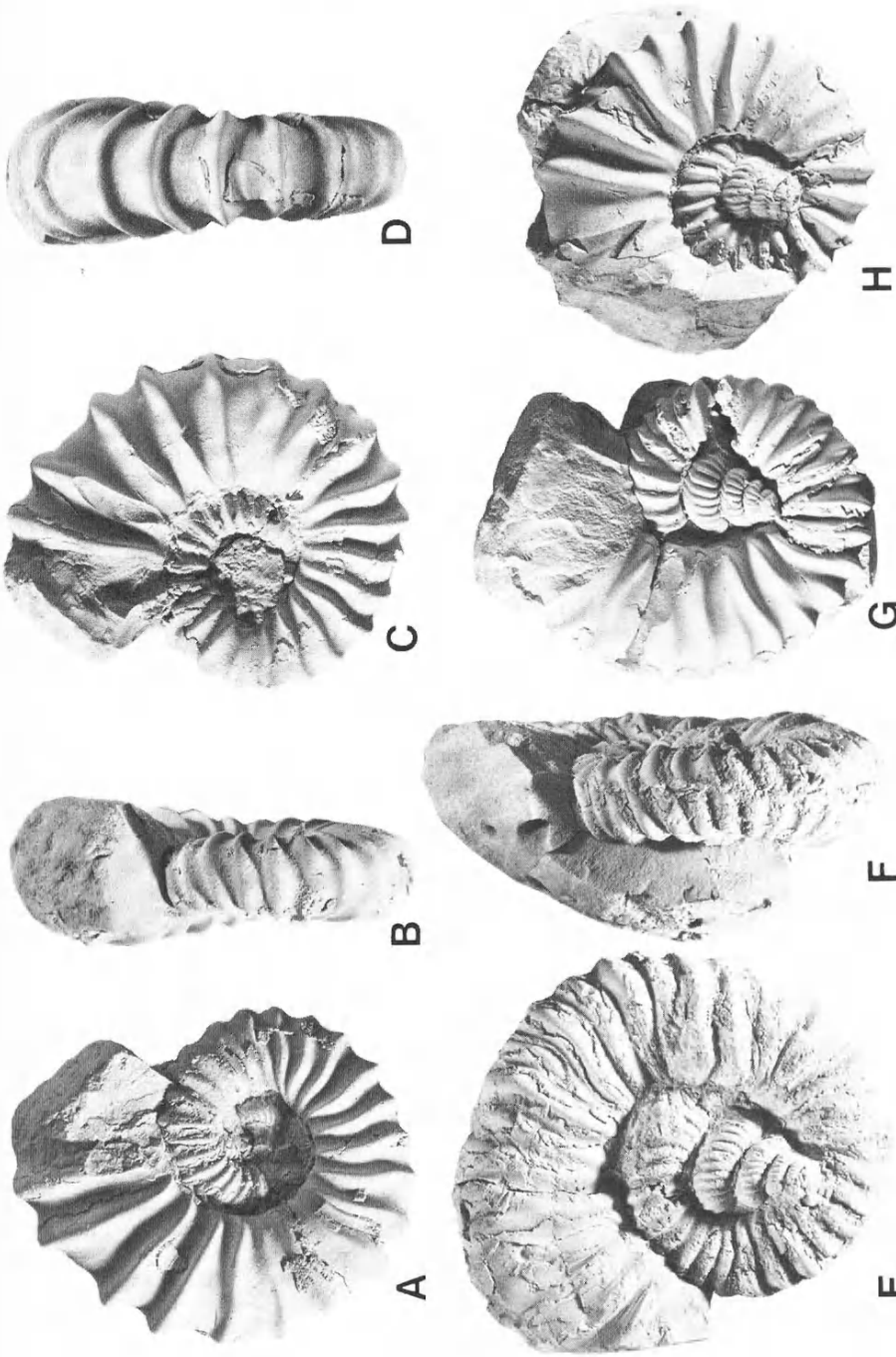

Fig. 6. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch with apertural modification. CPBA 11876. E–F. Microconch. CPBA 11842. G–H. Microconch with apertural modification. CPBA 11823. All × 1.

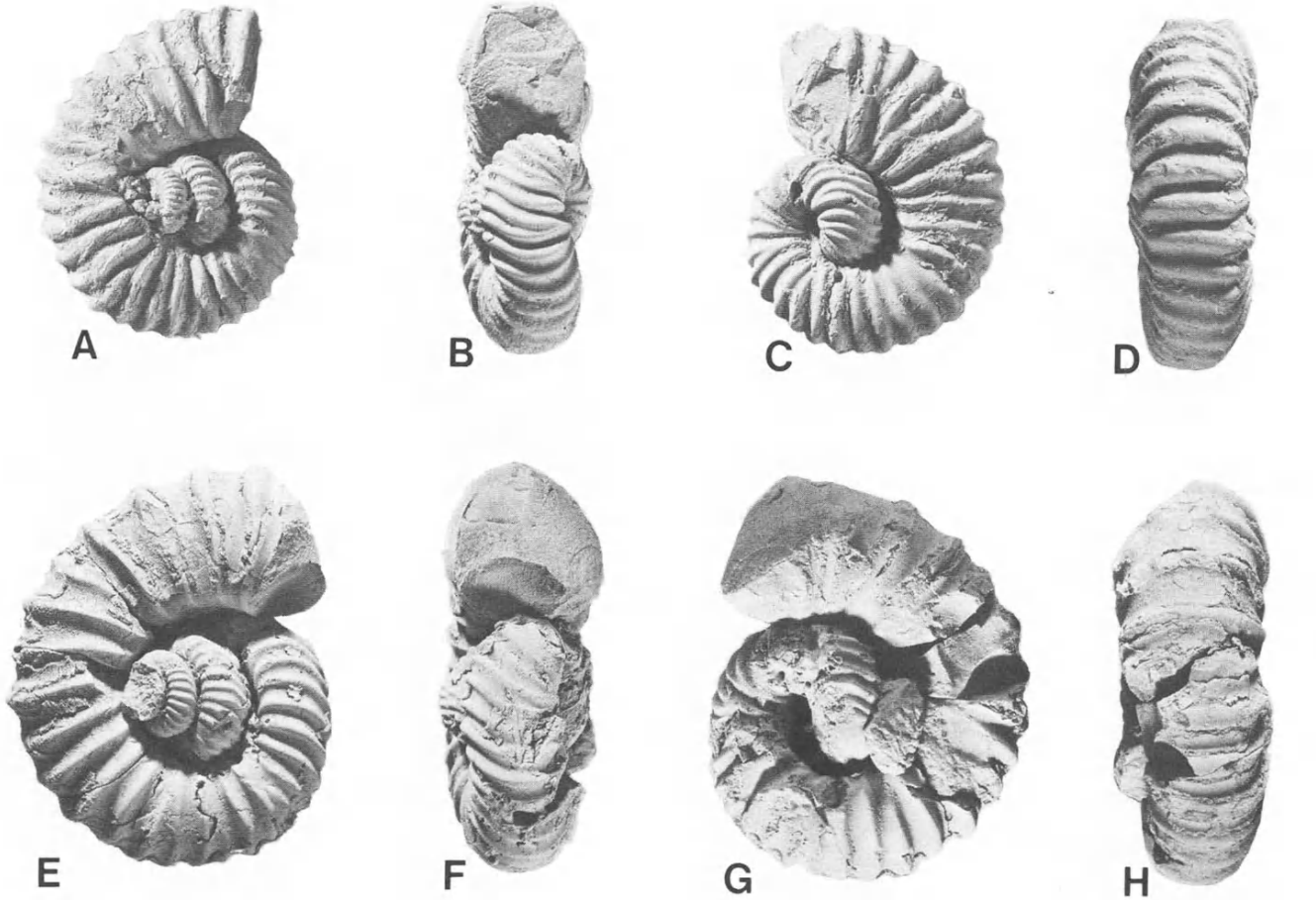

Fig. 7. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch. CPBA 11815. E–H. Microconch. CPBA 11863. All × 1.

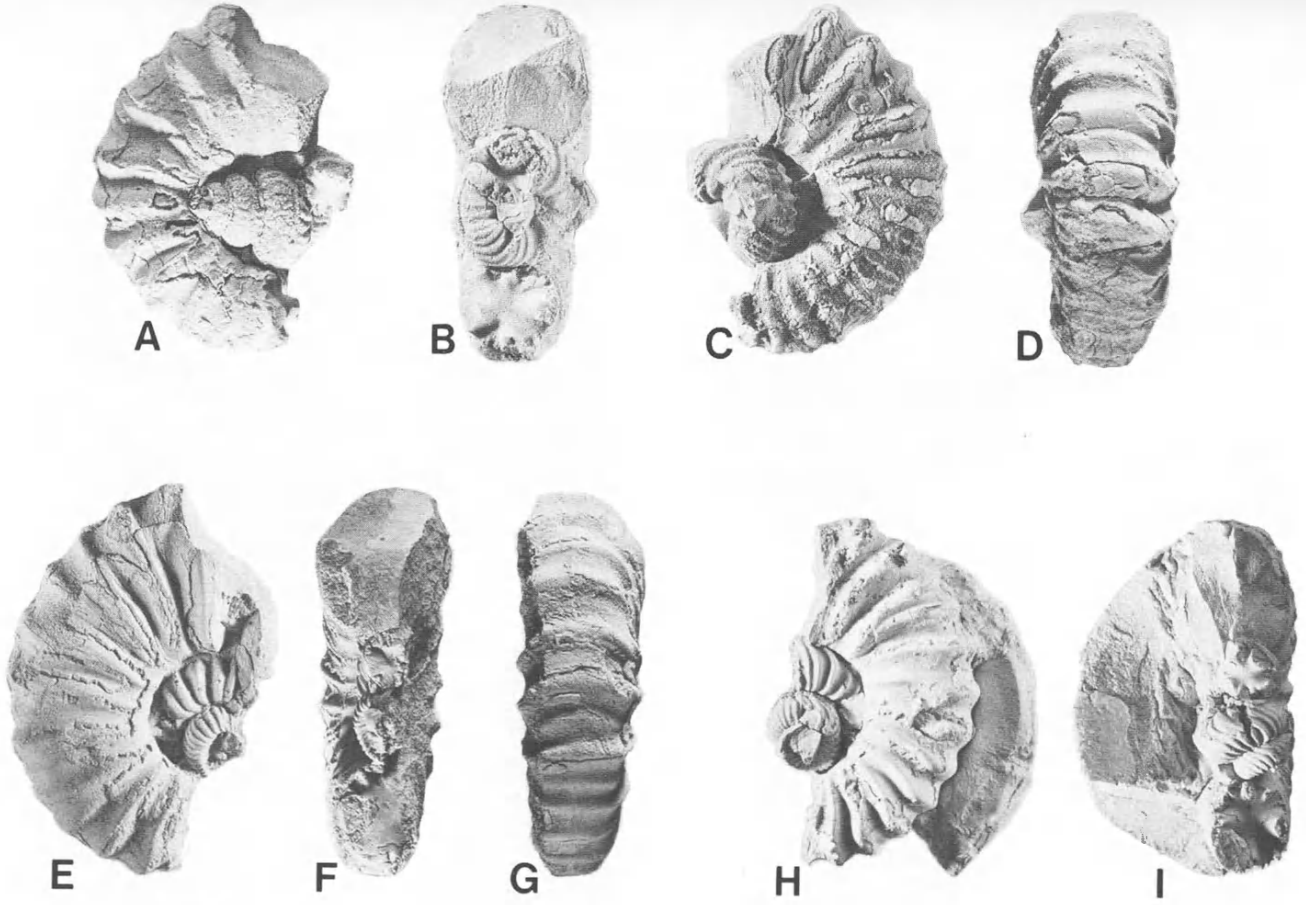

Fig. 8. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch. CPBA 11861. E–G. Microconch. CPBA 11816. H–I. Microconch. CPBA 11789. All × 1.

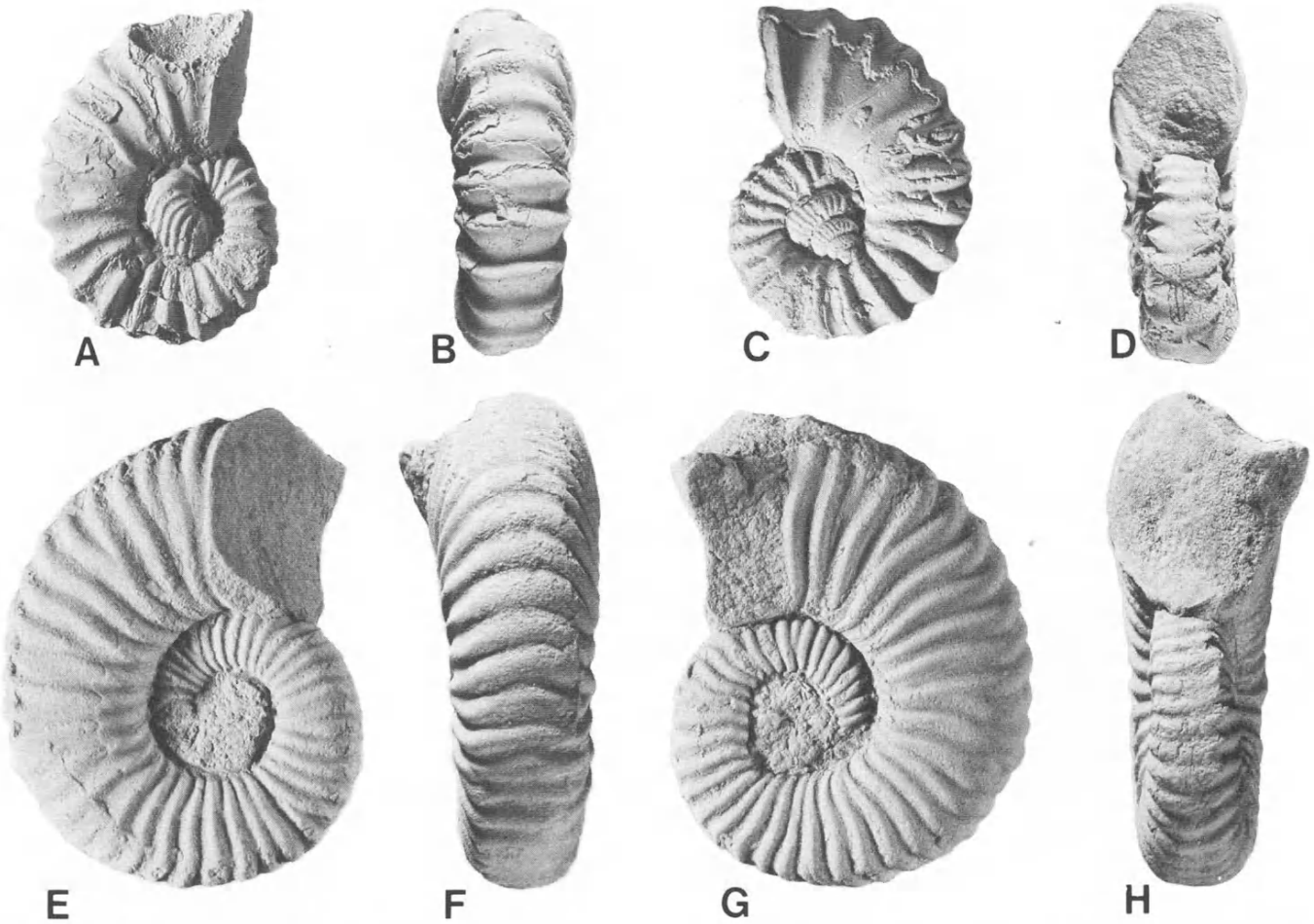

Fig. 9. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch. CPBA 11846. E–H. Immature macroconch? CPBA 11894. All × 1.

specimens have more than two planispiral, still septate whorls. It is estimated that fully grown specimens must have had at least two and a half to three planispiral whorls at a diameter of 300 mm. No signs of uncoiling or uncoiled fragments are known.

Ornament on the planispiral section is very variable, but generally tends to weaken on the outer whorls, becoming nearly smooth in some specimens.

Dimensions

Specimen	D	W_h	W_b	W_h/W_b	U
Holotype	44,2	18,0 (0,40)	17,0 (0,38)	1,06	15,5 (0,35)
L54/36h	91,0	38,0 (0,42)	31,0 (0,34)	1,22	31,0 (0,34)
C80022	37,0	16,5 (0,44)	15,0 (0,40)	1,10	12,0 (0,32)
C80016	51,5	21,0 (0,41)	21,0 (0,41)	1,00	19,0 (0,37)
C80018	54,0	25,0 (0,46)	21,5 (0,40)	1,16	20,0 (0,37)
C80015	50,0	23,0 (0,46)	23,0 (0,46)	1,00	18,0 (0,36)
C80017	53,0	22,0 (0,41)	21,0 (0,40)	1,05	18,0 (0,34)
PCZ6389	112,0	46,0 (0,41)	34,0 (0,31)	1,35	— —
CPBA 11848	37,0	15,0 (0,41)	12,5 (0,34)	1,20	12,0 (0,32)
CPBA 11828	35,0	16,5 (0,46)	16,0 (0,44)	1,03	12,0 (0,33)
CPBA 11821	36,5	14,5 (0,40)	13,5 (0,37)	1,07	12,0 (0,33)
CPBA 11817	41,0	17,0 (0,41)	16,5 (0,40)	1,03	12,0 (0,29)
CPBA 11809	45,5	18,5 (0,41)	16,0 (0,35)	1,15	— —
CPBA 11815	45,0	18,0 (0,40)	16,0 (0,36)	1,13	14,0 (0,31)
CPBA 11851	47,5	19,5 (0,41)	16,0 (0,37)	1,22	15,0 (0,32)
CPBA 11839	40,0	15,0 (0,38)	15,0 (0,38)	1,00	12,5 (0,31)
CPBA 11800	39,0	16,5 (0,42)	15,0 (0,38)	1,10	13,0 (0,33)
CPBA 11791	53,5	21,0 (0,39)	19,0 (0,36)	1,11	22,0 (0,41)
CPBA 11830	54,0	20,5 (0,38)	20,0 (0,37)	1,03	21,0 (0,39)
CPBA 11867	48,5	20,0 (0,41)	20,0 (0,41)	1,00	14,5 (0,30)
CPBA 11894	60,0	25,0 (0,42)	22,0 (0,37)	1,14	21,0 (0,35)
CPBA 11797	160,0	65,0 (0,41)	48,0 (0,30)	1,35	50,0 (0,31)

Comparison

Most of our material compares favourably with Egojan's (1965) original figured specimens, especially as far as the large size of the macroconchs is concerned. The Zululand material was separated from the Caucasian material at subspecific level by Klinger *et al.* (1984) on account of the broader and flatter venter of the planispiral section, but on the basis of the present material we doubt if even this is necessary.

Egojan (1965: 120) compared *C. vulanensis* to *C. djanelidzei* Rouchadzé but the two species differ on account of the disparate number of whorls in the helical section; *C. djanelidzei* only has 2–3 as compared to 6–7 in *C. vulanensis australis*.

Occurrence

Colchidites vulanensis s.l. occurs in the Upper Barremian of the Caucasus, Zululand and Patagonia.

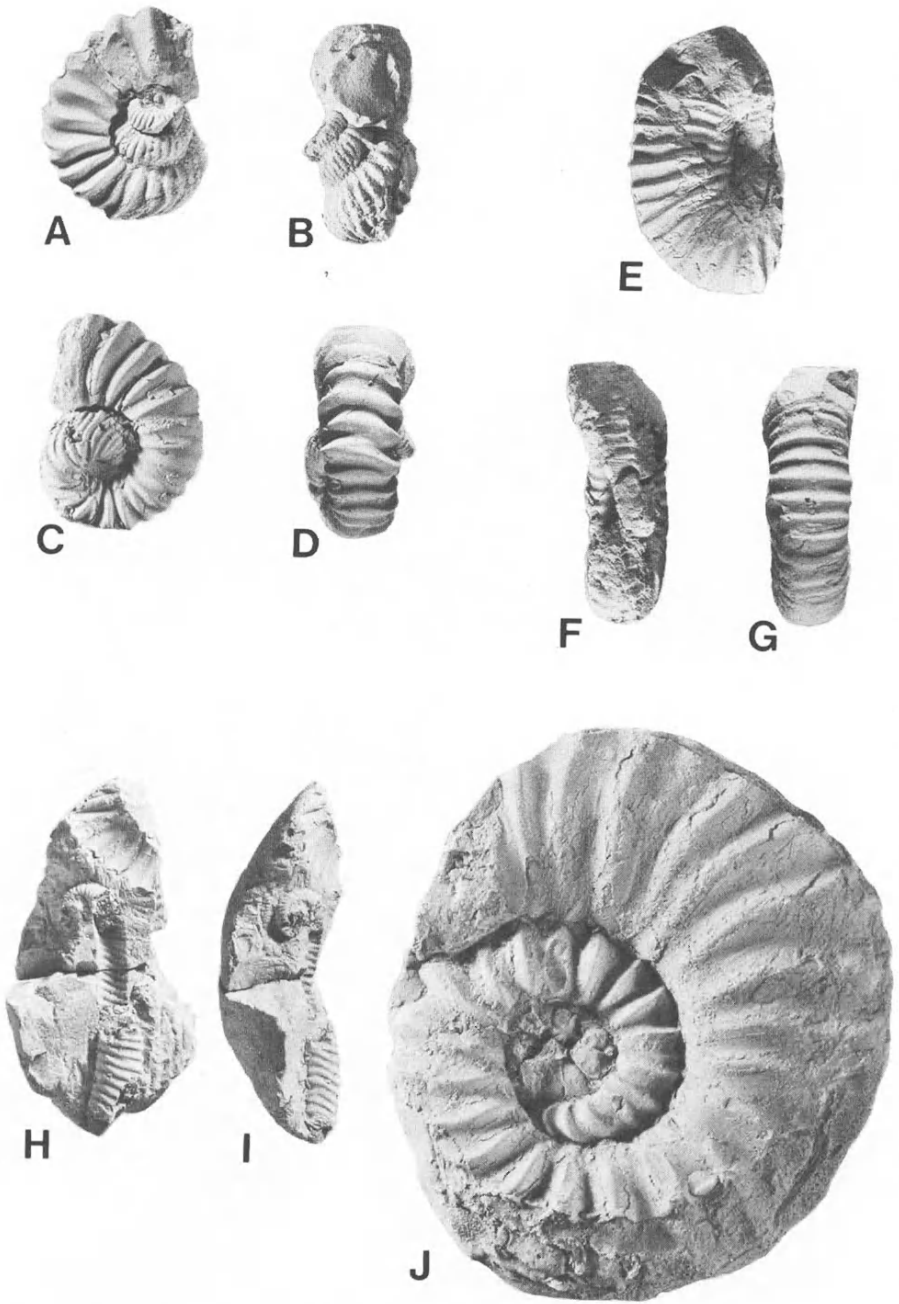

Fig. 10. A–D. *Colchidites vulanensis australis*. Coarsely ribbed microconch. CPBA 11821. E–G. *Heteroceras (H.) elegans* Rouchadze, 1933. CPBA 11900. H–I. *Heteroceras (H.) elegans* Rouchadze, 1933. CPBA 11899. J. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Immature macroconch? CPBA 11784. All × 1.

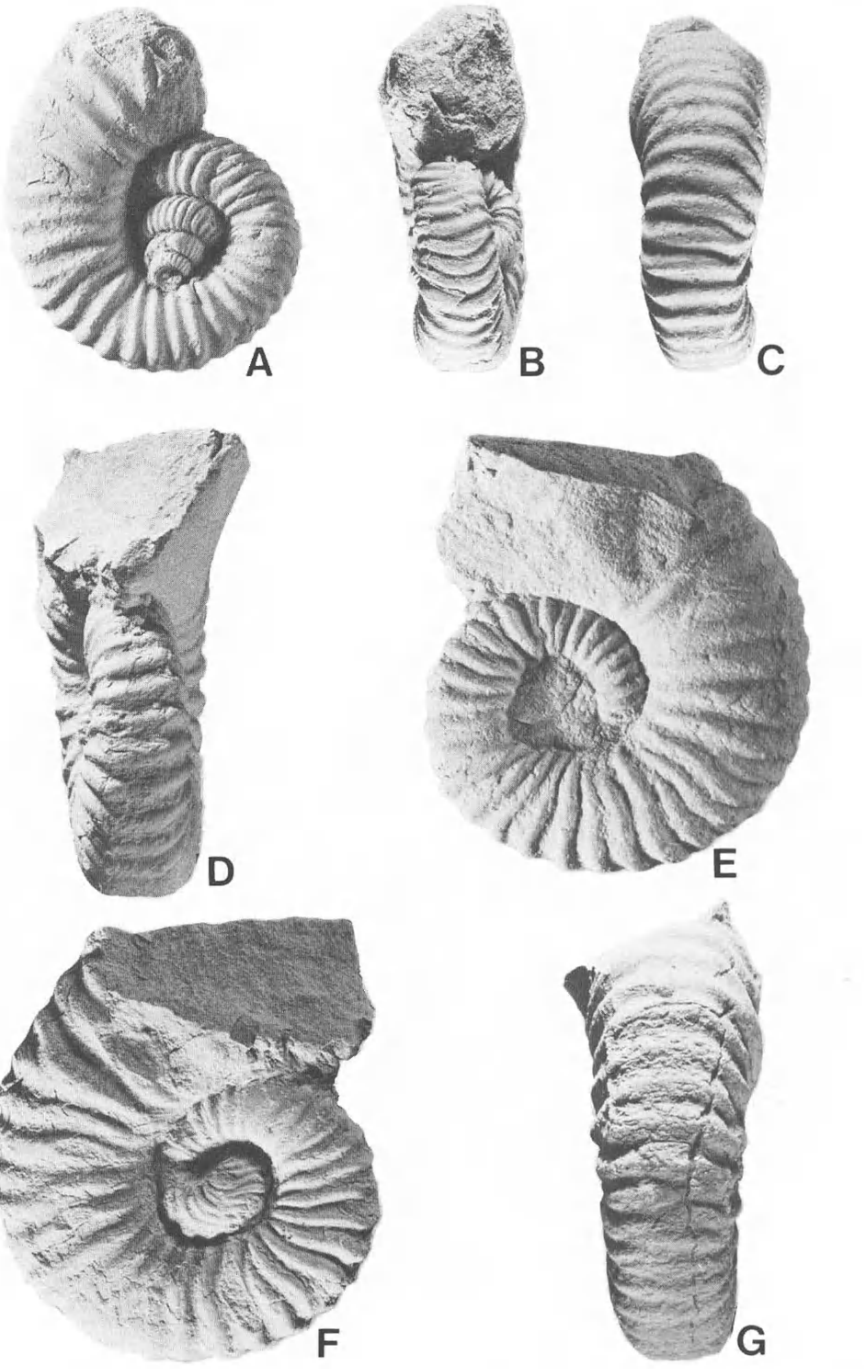

Fig. 11. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–C. Holotype. SAS 3044/L54. D–G. Immature macroconch? CPBA 11838. All × 1.

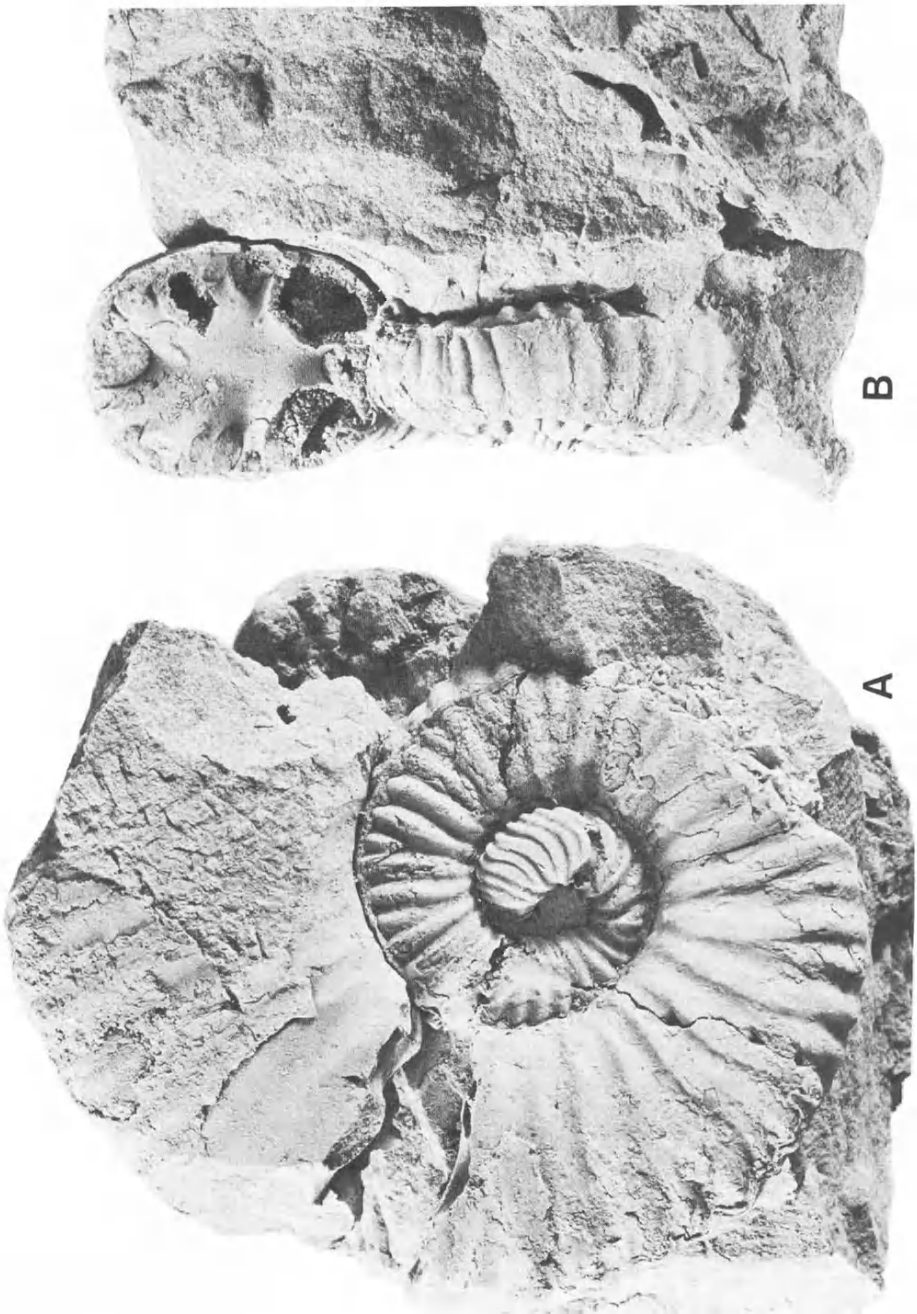

Fig. 12. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAS L54/36h. × 1.

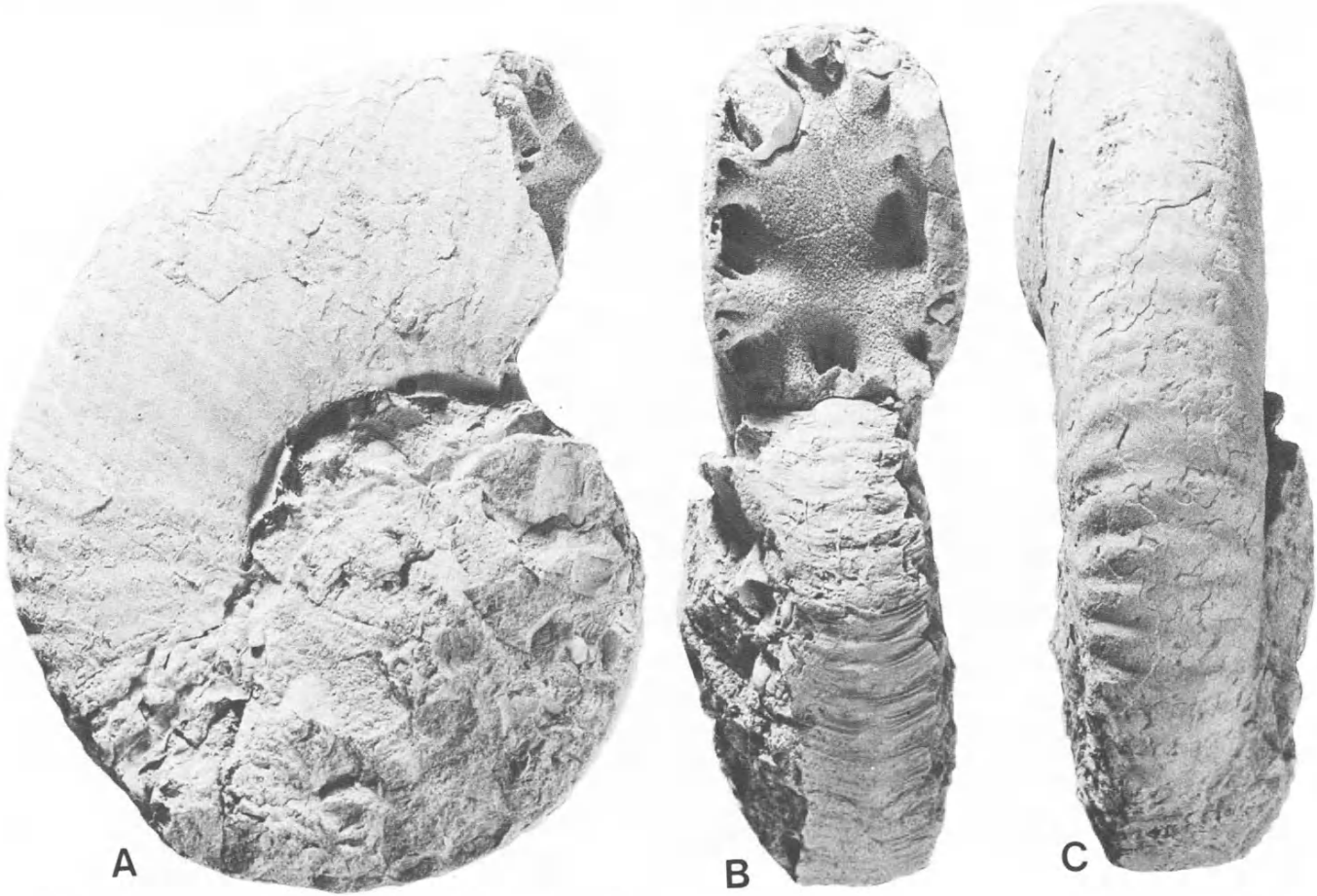

Fig. 13. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM–PCZ6389. × 1.

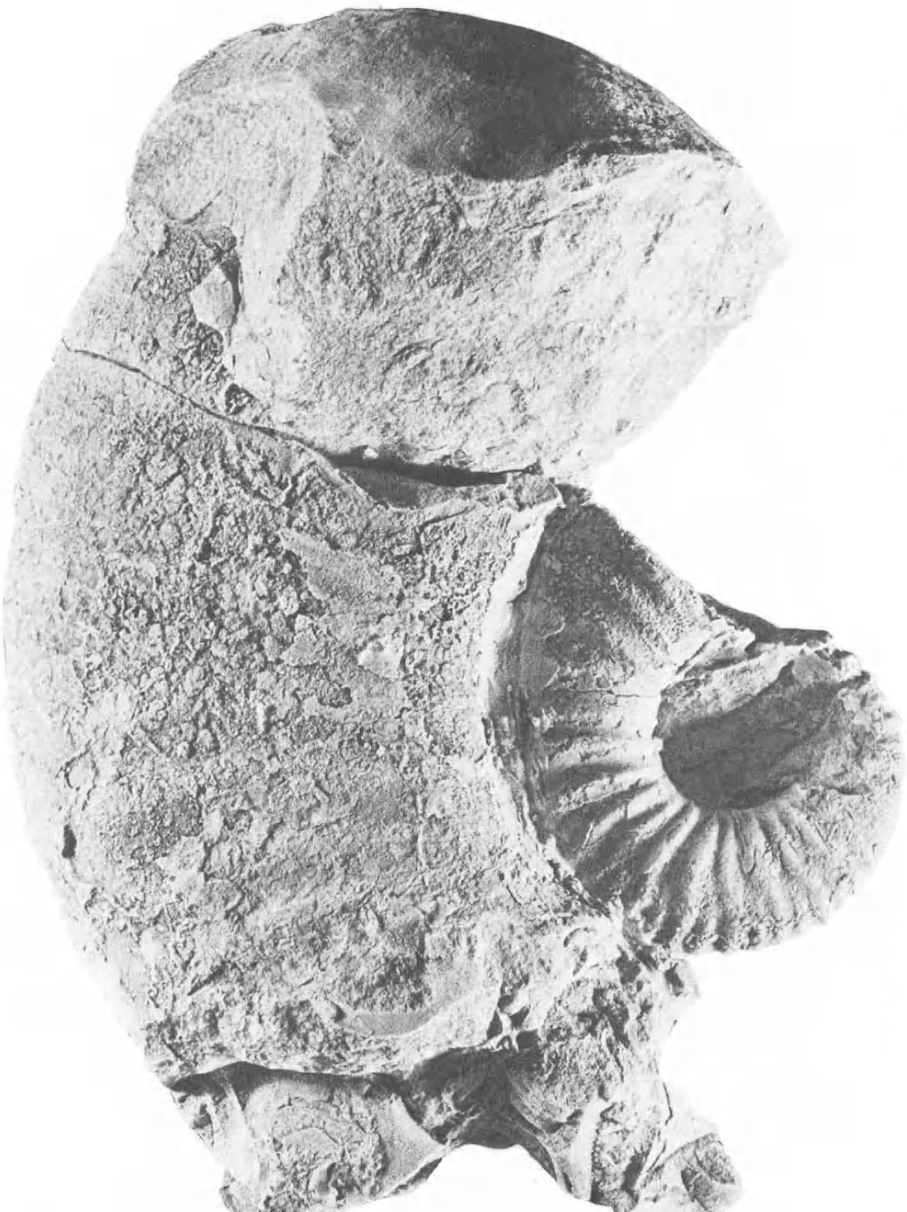

Fig. 14. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM–PCZ6388. × 0,65.

Fig. 15. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM–PCZ6388. × 0,65.

Fig. 16. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM–PCZ6388. × 0,65.

Fig. 17. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11896. × 1.

Fig. 18. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11896. × 1.

Fig. 19. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11797 × 1.

Fig. 20. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11797 × 1.

Fig. 21. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. CPBA 11799. × 1.

DISCUSSION

Validity of genera and species groups

Description of the Patagonian and Zululand material raises a number of questions that cast doubt on the current systematic concepts employed within the Heteroceratinae, and these merit discussion.

The first concerns the tripartite division of *Colchidites* into species groups *C. intermedius*, *C. colchicus* and *C. shaoriensis*. This was originally conceived by

Rouchadze (1933) and retained by Kakabadze (1971*a*). Egojan (1965), however, had already cast doubts on the correct allocation of *C. vulanensis*. The well-developed planispiral part places it in the group of *C. shaoriensis*, whereas the well-developed helix places it more suitably in *C. colchicus*. These same doubts were raised by Klinger (1976) and Klinger *et al.* (1984) and two alternatives were proposed: either an uncoiled section was never developed; or, the Zululand assemblage was an ontogenetically segregated population, with the representatives of the discoidal stage inhabiting the shallow, near-shore water, and the uncoiled ancyloceratid forms inhabiting the deeper parts of the basin. The discovery of microconchs with complete apertures, however, clearly rules out the

Fig. 22. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. CPBA 11799. × 1.

Fig. 23. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11829. × 1.

presence of an uncoiled section in *C. vulanensis australis*. Thus, as far as the number of whorls in the helix and planispiral sections are concerned, *C. vulanensis australis* fits none of the three recognized species groups. Instead, it more closely resembles representatives of *Paraimerites* or *Imerites*. With the exception of *Paraimerites brevihelicoides* Kakabadze, a monotypical species, none of the

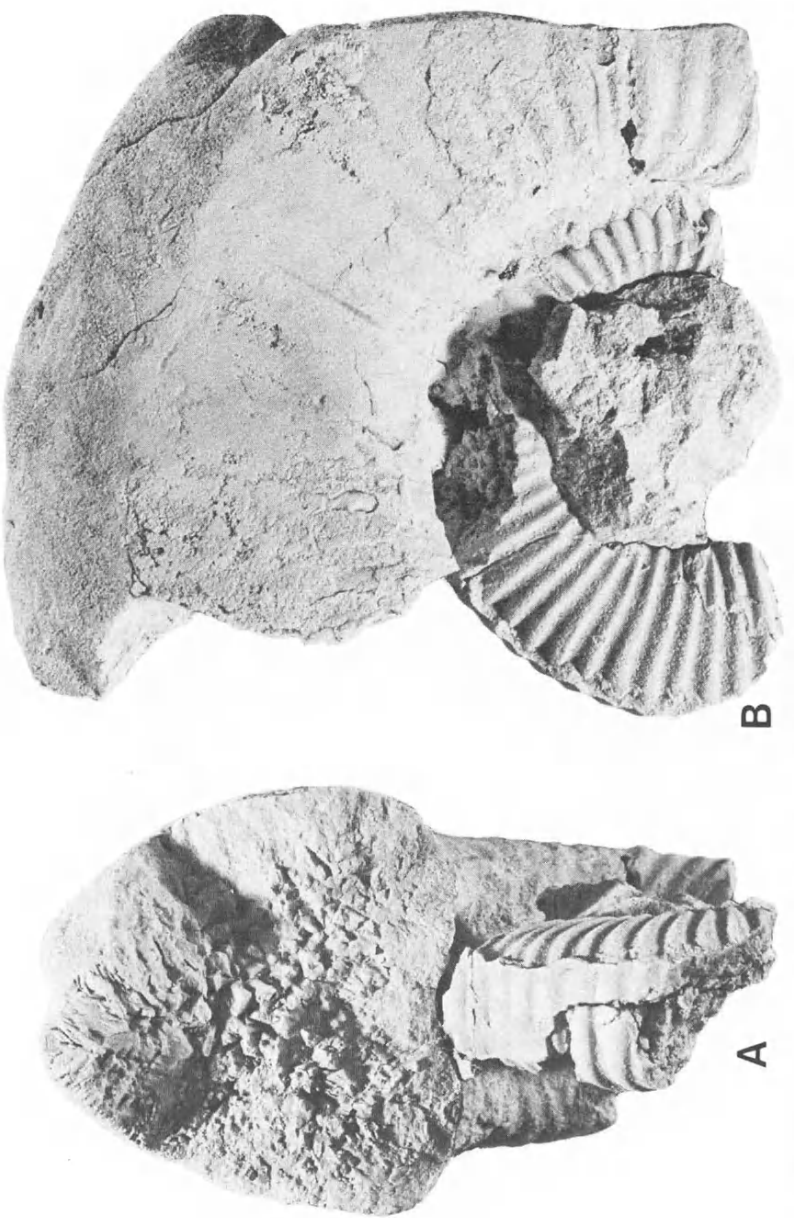

Fig. 24. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch with subtrigonal whorl section. SAM-PCZ6390. × 1.

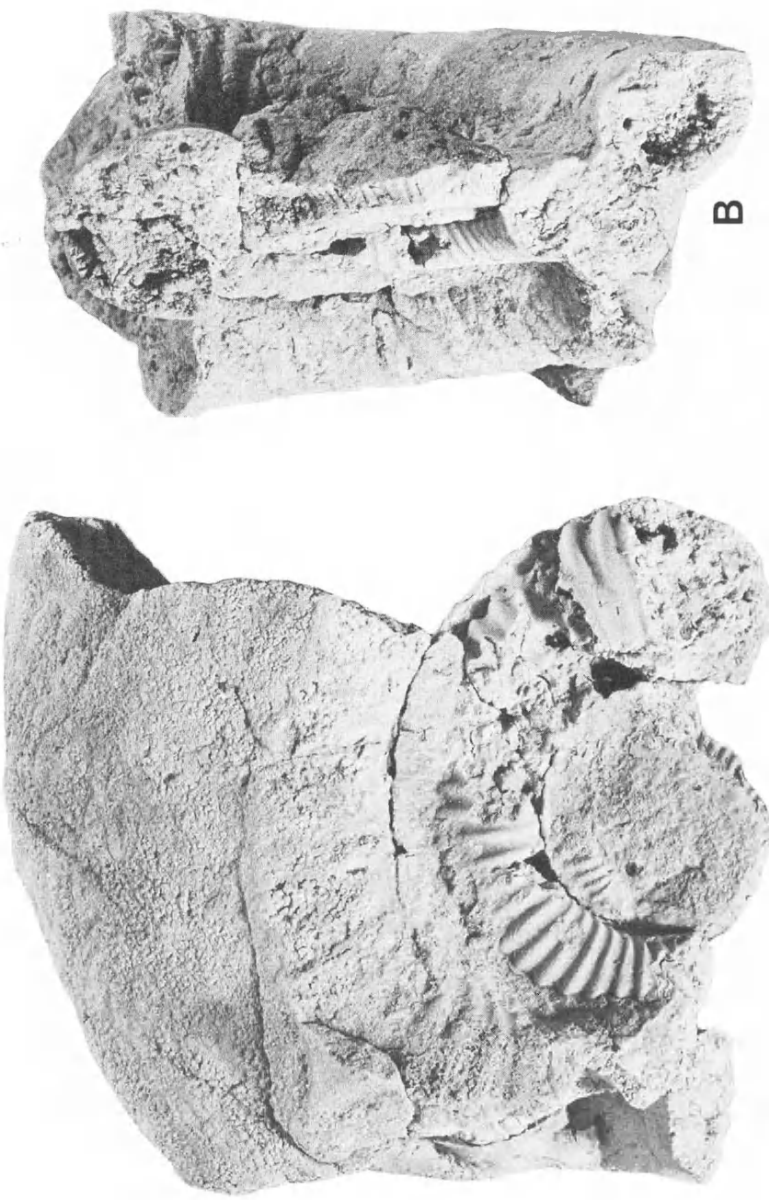

Fig. 25. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch with subtrigonal whorl section. SAM-PCZ6390. × 1.

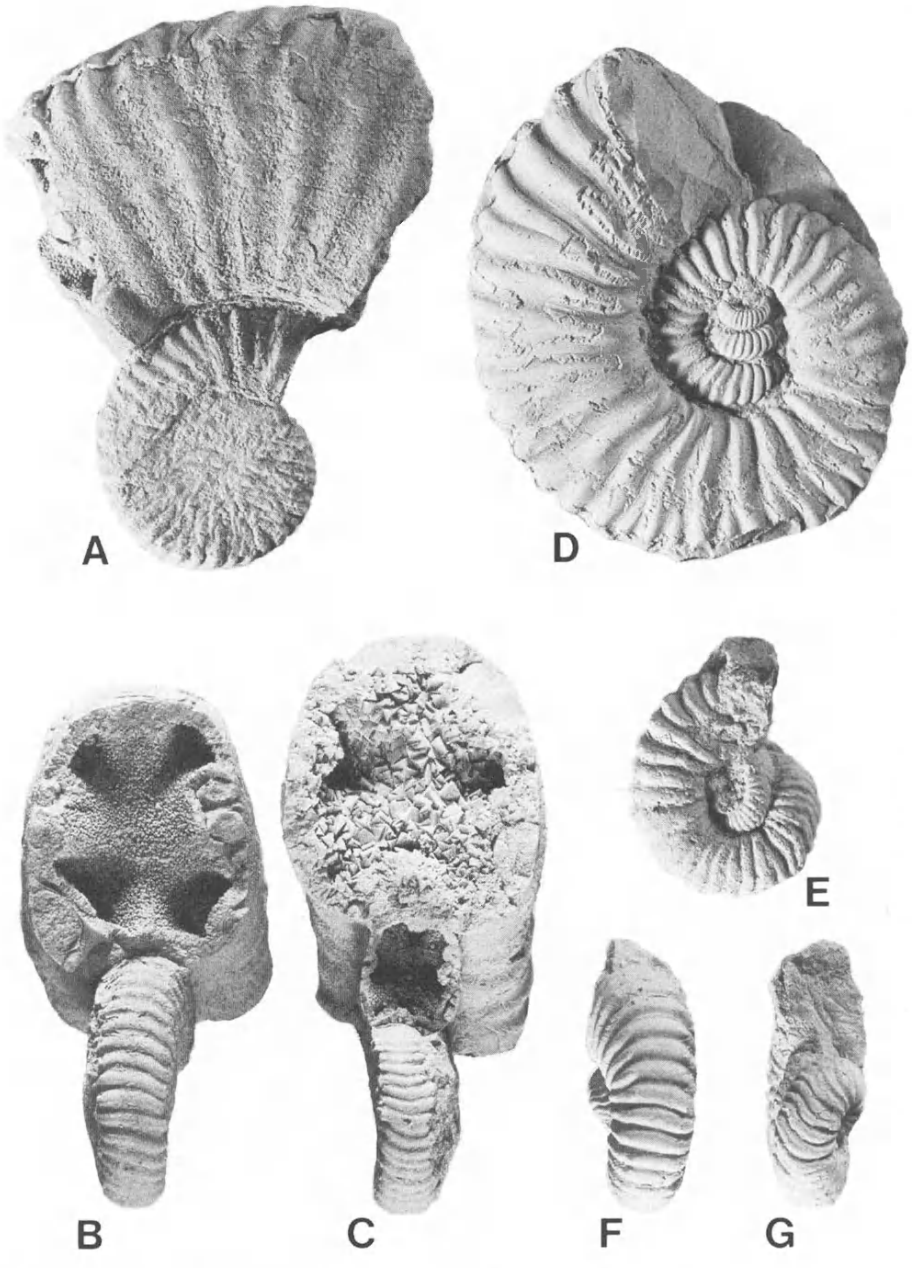

Fig. 26. A–C. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. SAS L54/3288. D. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. CPBA 11805. E–G. *Paraimerites haughtoni* Klinger, Kakabadze & Kennedy, 1984. SAS L54/D5. All × 1.

other species referable to either *Paraimerites* or *Imerites* has an uncoiled section. Affinities of *C. vulanensis australis* with *Paraimerites* or even *Imerites* become more obvious in specimens with distinct quadrate to rectangular whorl section. Here the ribs are slightly flared near the venter, and the ventrolateral edges of these may easily be interpreted as tubercles. Also, there is a slight thickening of the ribs on the ventrolateral flanks that coincides with a slight forward flexure and/or bifurcation of the ribs. This could be interpreted as incipient *Imerites* ornament.

Having established that *Colchidites vulanensis australis* does not fit the traditionally accepted tripartite division of genus *Colchidites*, but instead shows more affinities toward *Paraimerites* and *Imerites*, division at generic level may be scrutinized.

Differentiation within the subfamily Heteroceratinae at generic or subgeneric level is based mainly on the presence or absence of tubercles, as outlined above (p. 320). The presence or absence of tubercles has been used extensively in the classification of other heteromorph taxa. In most cases this is an objective, unambiguous criterion and easy to apply, and forms the mainstay of heteromorph taxonomy. Recent work on various heteromorph groups, especially the *Hamites–Protanisoceras–Anisoceras* plexus (Casey 1961; Wiedmann 1962; Wiedmann & Dieni 1968; Scholz 1979), the Turrilitinae (Klinger & Kennedy 1978; Scholz 1979), Baculitidae (Cooper & Kennedy 1977; Scholz 1979), etc., has made it painfully obvious how divided workers are in assessing the importance of tuberculation. Thus the tuberculate forms of the baculitid genus *Lechites* are accorded subgeneric rank by Cooper & Kennedy (1977) while the same are merely regarded as subspecific variants of the non-tuberculate species by Scholz (1979). Indeed, Scholz (1979) has shown that in some heteromorph groups (*Lechites*), tubercles may appear iteratively, and that the proportion or absence of tuberculate to non-tuberculate forms may differ in different geographic regions. In addition, transitions occur between tuberculate and non-tuberculate forms, e.g. *Hamites praegibbosus* Spath and *Protanisoceras* gr. ex *blancheti* (cf. Casey 1961: 94) where allocation to one genus or another becomes subjective and a matter of opinion.

Bearing these data in mind, we provisionally accept the criterion of presence or absence of tubercles in the systematics of the subfamily Heteroceratinae. Thus those colchiditid specimens without distinct tubercles are referred to genus *Colchidites*, and those with a pair of siphonal rows, to *Paraimerites*, even though the coiling strategies do not fit the diagnoses as applied to the material from south-western U.S.S.R.

These same criteria are applied to differentiating between *Heteroceras* s.s. and *H. (Argvethites)*. According to Kakabadze (1975: 66) a siphonal furrow on the shaft occurs mainly in tuberculate forms, i.e., *H. (Argvethites)*. However, a siphonal furrow occurs in two of the non-tuberculate specimens of *H. (H.) elegans* from Argentina. In addition, siphonal furrows are known from other unrelated heteromorph groups, e.g. *Toxoceratoides* (Aguirre Urreta 1986),

Hamites (Stomohamites) virgulatus (see Wiedmann & Dieni 1968, pl. 5 (fig. 2), text-figs 21–22) and thus seem to be of no or little taxonomic significance.

Sexual dimorphism

Dimorphism has not been discussed previously in Heteroceratinae. In other groups of ammonites it has been well documented over the past two decades (see e.g. Makowski 1963; Westermann 1969; Kennedy & Cobban 1976; Callomon 1981; Donovan *et al.* 1981; Wright 1981 for discussions), but evidence has come mainly from Jurassic forms—the notable Cretaceous exception being some scaphitids (see Cobban 1969). Callomon (1981) mentioned that sexual dimorphism in the Cretaceous remains largely to be explored, especially amongst the Ancyloceratina. Unfortunately, apart from the above-mentioned scaphitids, data here are still very scant. Dimorphism has been demonstrated in the baculitid genus *Sciponoceras* (see Kennedy & Juignet 1983: 17 for summary) and *Lechites* (Cooper & Kennedy 1977) and suggested in *Hamites* by Cooper (unpublished data, see Kennedy & Juignet 1983: 12).

Dimorphism in Heteroceratinae was only found in the austral representatives of *Colchidites vulanensis*, but we suspect that it may also be present in *Heteroceras*. The two species groups recognized within *Heteroceras*, *H.* gr. ex. *helicoceroides* and *H.* gr. ex. *astieri* may possibly be dimorphic pairs.

Intraspecific variation

Finally, the Patagonian and Zululand material illustrates the extent of intraspecific variation magnificently. Admittedly, coarsely and finely ornamented forms can be identified, as can forms with quadrate whorl sections approaching *Paraimerites* ornament; but these are all connected by transitions, so that it would be futile to separate these at any formal level. This variation also casts doubt on the validity of the great number of species referred to the genera *Heteroceras* and *Colchidites*, as listed below. Egojan (1965) had already commented on the disparate number of species to specimens in the Georgian collections but, without direct access to this material, we have to refrain from definite comments on the synonymies.

SUMMARY

The ammonite subfamily Heteroceratinae is represented in Patagonia by *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy and *Heteroceras (H.) elegans* Rouchadzé, both species also known from Zululand and the Caucasus. The representatives of *Colchidites vulanensis australis* demonstrate dimorphism in the genus: microconchs mature at diameters of about 50 mm and one planispiral whorl; and macroconchs with more than two planispiral whorls still septate at diameters exceeding 150 mm. The microconchs show apertural modifications in the planispiral section, clearly ruling out the possibility of an uncoiled section. The ratio of helical to planispiral coils, plus the absence of an uncoiled section in *C. vulanensis australis* fits none of the three species groups

traditionally accepted within the genus *Colchidites*, but instead shows greater affinity with *Paraimerites* or *Imerites*. Comparison with other heteromorph groups shows that the presence or absence of tubercles may be of very little taxonomic significance, and in cases, be ambiguous. Siphonal depressions occur in various unrelated heteromorph groups, and seem to be of no taxonomic significance. The wide range of intraspecific variation as seen in the Patagonian and Zululand material casts severe doubt on the validity of the multitude of species erected for the material from the south-western U.S.S.R., and suggests that systematics can be greatly simplified.

LIST OF SPECIES OF *HETEROCERAS (HETEROCERAS)* AND *COLCHIDITES*

Species described in open nomenclature are omitted. Most of the references listed below provide descriptions and/or figures of the species concerned.

Genus and subgenus *Heteroceras* d'Orbigny, 1850 (= *Lindigia* Karsten, 1858)

Type-species. *Turrilites emericianus* d'Orbigny, 1842, by subsequent designation Meek (1876: 477).

Heteroceras emericianum (d'Orbigny) (1842: 580, pl. 141 (figs 3–6); 1851: 220, pl. 3 (fig. 1); Kakabadze 1971*a*: 48, pl. 3 (fig. 2)). Upper Barremian of France.

Heteroceras emericianum (d'Orbigny) var. *costata* Rouchadzé (1933: 242, pl. 15 (fig. 3); Kakabadze 1971*a*: 49, pl. 3 (fig. 1)). Upper Barremian of western Georgia and northern Caucasus.

Heteroceras astierianum d'Orbigny (1851: 219, pl. 4 (fig. 1); Kilian 1888*a*: 430, pl. 3 (fig. 2); 1888*b*: 687, pl. 21 (fig. 1a–b); Dimitrova 1967: 65, pl. 37 (fig. 2); Kakabadze 1975: 86, pl. 1 (fig. 1a–b), pl. 2 (fig. 1), pl. 8 (fig. 2)). [= *Heteroceras imericum* Rouchadzé (1933: 230, pl. 13 (figs 1–2), text-fig. 34).] Upper Barremian of Bulgaria, Caucasus, France and western Georgia.

Heteroceras bifurcatum d'Orbigny (1851: 221, pl. 3 (figs 2–3); Kilian 1888*a*: 432, pl. 3 (fig. 3); Nikolov, 1964: 124, pl. 4 (figs 1–2), pl. 5 (fig. 5a–b); Dimitrova 1967: 64, pl. 39 (fig. 2)). Upper Barremian of Bulgaria and France.

Heteroceras bifurcatum d'Orbigny var. *trifurcata* Kilian (1888*a*: 432). Upper Barremian of France.

Heteroceras devii Rouchadzé (1933: 231, pl. 13 (fig. 3), text-fig. 35; Kakabadze 1975: 87, pl. 1 (fig. 2), pl. 2 (fig. 3), pl. 8 (fig. 1)). Upper Barremian of western Georgia.

Heteroceras elegans Rouchadzé (1933: 232, pl. 13 (fig. 4), text-fig. 36; Kakabadze 1975: 89, pl. 3 (figs 1a–b, 3–5), pl. 8 (fig. 5); Klinger *et al.* 1984: 44, figs 2A–F, 3A–G, 4A–C). Upper Barremian of western Georgia, northern Caucasus, Zululand and Patagonia.

Heteroceras eristavii Kakabadze (1975: 90, pl. 4 (figs 1a–b, 3), pl. 5 (fig. 5), pl. 8 (fig. 7)). Upper Barremian of western Georgia.

Heteroceras haugi Karakasch (1907: 144, pl. 26 (fig. 2)). Upper Barremian of Crimea.

Heteroceras helicoceroides (Karsten) (1858: 103, pl. 1 (fig. 5a–c); 1886: 27, pl. 1 (fig. 5a–c); Royo y Gómez 1945: 466, text-fig. 3). Upper Barremian of Colombia.

Heteroceras isocostata Kakabadze (1975: 91, pl. 4 (fig. 5a–b)). Upper Barremian of western Georgia.

Heteroceras jeletzkyi Murphy (1975: 36, pl. 7 (fig. 4)). Upper Barremian of California.

Heteroceras kotetishviliae Kakabadze (1975: 88, pl. 1 (fig. 4)). Upper Barremian of western Georgia.

Heteroceras tardieui Kilian (1888*a*: 433, pl. 4). Upper Barremian of France.

Heteroceras tskaltuboensis Kakabadze (1975: 87, pl. 2 (fig. 2), pl. 8 (fig. 3)). Upper Barremian of western Georgia.

Heteroceras vermiforme Rouchadzé (1933: 233, pl. 13 (fig. 5); Kakabadze 1975: 90, pl. 3 (figs 6–8), pl. 4 (fig. 2a–b). Upper Barremian of western Georgia.

Genus *Colchidites* Djanélidzé, 1926
(= *Heteroceras (Santandericeras)* Royo y Gómez, 1945)

Type-species. *Colchidites colchicus* Djanélidzé, 1926.

Colchidites colchicus Djanélidzé (1926: 256, pl. 1 (fig. 1); Kakabadze 1971*a*: 54, pl. 6 (figs 1–2)). Upper Barremian of western Georgia.

Colchidites colchicus Djanélidzé var. *phasiensis* Rouchadzé (1938: 169, pl. 5 (figs 5–6), text-fig. 21; Kakabadze 1971*a*: 56, pl. 8 (fig. 1)). Upper Barremian of western Georgia.

Colchidites colchicus Djanélidzé var. *renngarteni* Rouchadzé (1938: 169, pl. 5 (fig. 4), text-fig. 20; Kakabadze 1971*a*: 55, pl. 7 (fig. 1), text-fig. 23). Upper Barremian of western Georgia.

Colchidites apolinarii (Royo y Gómez) (1945: 468, pl. 74 (fig. 1a–b), pl. 75 (fig. 1), text-figs 4–5; Etayo Serna 1968: 59, pl. 1 (figs 4, 6), pl. 2 (figs 1–2), text-figs 3B, 4,4; Kakabadze 1971*a*: 59, pl. 9 (fig. 2a–c)). Upper Barremian of Colombia.

Colchidites atsharensis Rouchadze (1933: 246, pl. 17 (fig. 2), text-fig. 16; Kakabadze 1971*a*: 76, pl. 9 (fig. 4), pl. 18 (fig. 2a–b), text-fig. 46). Upper Barremian of western Georgia and western Turkmenia.

Colchidites belaiaensis Kakabadze (1971*a*: 66, pl. 15 (fig. 2a–c)). Upper Barremian of northern Caucasus.

Colchidites bethleviensis Kakabadze (1971*a*: 56, pl. 5 (fig. 4a–c), text-figs 24–25). Upper Barremian of western Georgia.

Colchidites colleti Rouchadzé (1933: 249, pl. 18 (fig. 2), text-fig. 48; Kakabadze 1971*a*: 69, pl. 14 (fig. 1), text-fig. 39). Upper Barremian of western Georgia.

Colchidites colleti Rouchadzé var. *shaoriensis* Rouchadzé (1938: 170, pl. 6 (fig. 3)). Upper Barremian of western Georgia.

Colchidites cuneicostatus Kakabadze (1971*a*: 57, pl. 8 (fig. 2a–c), text-figs 26–27). Upper Barremian of western Georgia.

Colchidites djanelidzei Rouchadzé (1933: 247, pl. 17 (fig. 1), text-fig. 47; Kakabadze 1971*a*: 77, pl. 18 (fig. 1a–b), text-fig. 47). Upper Barremian of western Georgia.

Colchidites elissoae Kakabadze (1971*a*: 60, pl. 5 (fig. 3), text-figs 28–29). Upper Barremian of western Georgia.

Colchidites ellipticus Rouchadzé (1933: 252, pl. 20 (fig. 1); Drushchits & Kudryavtsev 1960: 296, pl. 40 (fig. 5a–b); Kakabadze 1971*a*: 64, pl. 11 (fig. 2a–b), pl. 12 (fig. 1a–b), text-fig. 35). Upper Barremian of western Georgia and northern Caucasus.

Colchidites ellipticus kvadaurensis Rouchadzé (1933: 253, pl. 20 (figs 33–34); Kakabadze 1971*a*: 65, pl. 5 (fig. 2), text-fig. 36). Upper Barremian of western Georgia.

Colchidites eristavii Kotetishvili (1970: 80, pl. 12 (fig. 3a–c); Kakabadze 1971*a*: 59, pl. 9 (fig. 2a–c)). Upper Barremian of western Georgia.

Colchidites gamkrelidzei Rouchadzé (1933: 251, pl. 19 (fig. 2), text-fig. 50; Kakabadze 1971*a*: 63, pl. 10 (fig. 2a–b), text-figs 33–34). Upper Barremian of western Georgia.

Colchidites intermedius Djanélidzé (1926, fig. 14; Kakabadze 1971*a*: 51, pl. 4 (fig. 3)). (Non *Colchidites intermedius* in Rouchadzé 1933: 239, pl. 14 (fig. 6), text-fig. 40.) Upper Barremian of western Georgia.

Colchidites kakabadzei Kotetishvili (1970: 81, pl. 13 (fig. 3); Kakabadze 1971*a*: 75, pl. 17 (fig. 1a–c)). Upper Barremian of western Georgia.

Colchidites kakhadzei Rouchadzé (1938: 170, pl. 6 (fig. 4), text-fig. 23; Kakabadze 1971*a*: 61, pl. 10 (fig. 1a–b), text-fig. 30). Upper Barremian of western Georgia and south-eastern France.

Colchidites kutatissiensis Kakabadze (1971*a*: 53, pl. 5 (fig. 1), text-figs 21–22). Upper Barremian of western Georgia.

Colchidites latecostatus Rouchadzé (1933: 246, pl. 16 (fig. 3), text-fig. 45); Kotetishvili 1970: 83, pl. 14 (fig. 1a–b); Kakabadze 1971*a*: 75, pl. 16 (fig. 1a–b)). Upper Barremian of western Georgia.

Colchidites leenhardti (Kilian) (1888*b*: 688, pl. 20 (fig. 3), pl. 21 (fig. 2); Kakabadze 1971*a*: 52, pl. 3 (fig. 3)). Upper Barremian of south-eastern France and western Georgia.

Colchidites longicostatus Kakabadze (1971*a*: 71, pl. 19 (fig. 6), text-fig. 42). Upper Barremian of western Georgia.

Colchidites longus Rouchadzé (1933: 240, pl. 14 (fig. 7), pl. 15 (fig. 1), text-fig. 41; Kakabadze 1971*a*: 50, pl. 4 (fig. 4)). Upper Barremian of western Georgia.

Colchidites multicostatus Kakabadze (1971*a*: 67, pl. 12 (fig. 3a–c), text-fig. 38). Upper Barremian of western Georgia.

Colchidites ratshensis Rouchadzé (1933: 254, pl. 20 (fig. 6); 1938: 170, pl. 4 (fig. 6); Kakabadze 1971*a*: 72, pl. 12 (fig. 5a–b), pl. 14 (figs 2, 4–5), text-figs 43–44). [= *Colchidites nicortsmindensis* Rouchadzé (1933: 255, pl. 20 (fig. 7); Tovbina 1963: 110, pl. 3 (fig. 5)).] Upper Barremian of western Georgia and Turkmenia.

Colchidites ratshensis Rouchadzé var. *kopetdaghensis* Tovbina (1963: 111, pl. 3 (fig. 6); Kakabadze 1971*a*: 73, pl. 12 (fig. 2)). Upper Barremian of Turkmenia.

Colchidites rionensis (Simonovich, Batsevich & Sorokin) (1875: 173, pl. 6 (fig. 1a–b); Rouchadzé 1933: 243, pl. 15 (figs 4–5), text-fig. 43; Kakabadze 1971*a*: 74, pl. 13 (fig. 1), text-fig. 45). Upper Barremian of western Georgia.

Colchidites rotundus Rouchadzé (1933: 241, pl. 15 (fig. 2), text-fig. 42; Drushchits & Kudryavtsev 1960: 296, pl. 37 (fig. 2a–b); Kakabadze 1971*a*: 49, pl. 3 (fig. 4), text-fig. 19). Upper Barremian of western Georgia and northern Caucasus.

Colchidites rouchadzei Eristavi (1955: 121; Kakabadze 1971*a*: 51, pl. 4 (fig. 1)). Upper Barremian of western Georgia.

Colchidites sarasini Rouchadzé (1933: 250, pl. 18 (fig. 3), pl. 19 (fig. 1), text-fig. 49; Kakabadze 1971*a*: 62, pl. 11 (fig. 1a–c), text-figs 31–32). Upper Barremian of western Georgia and Lower Aptian? of north-western Caucasus.

Colchidites securiformis (Simonovich, Batsevich & Sorokin) (1875: 166, pl. 4 (fig. 3a–b); Rouchadzé 1938: 168, pl. 4 (fig. 5); Kotetishvili 1970: 84, pl. 10 (fig. 4); Kakabadze 1971*a*: 81, pl. 17 (fig. 4), pl. 19 (fig. 2), text-fig. 53). Upper Barremian of western Georgia.

Colchidites shaoriensis Djanélidzé (1926, pl. 1 (fig. 2); Kakabadze 1971*a*: 79, pl. 14 (fig. 3), pl. 19 (fig. 3), text-fig. 50). Upper Barremian of western Georgia and western Turkmenia.

Colchidites tenuicostatus Kakabadze (1971*a*: 82, pl. 17 (fig. 2), pl. 19 (fig. 4), text-fig. 54). Upper Barremian of western Georgia.

Colchidites tinae Eristavi (1955: 121, pl. 4 (fig. 11); Kakabadze 1971*a*: 52, pl. 4 (fig. 2)). Upper Barremian of western Georgia.

Colchidites tovbinae Kakabadze (1971*a*: 80, pl. 17 (fig. 3), text-fig. 51). Upper Barremian of western Georgia.

Colchidites trifurcatus Kakabadze (1971*a*: 66, pl. 12 (fig. 4a–b), text-fig. 37). Upper Barremian of northern Caucasus.

Colchidites tzotnei Rouchadzé (1933: 254, pl. 20 (fig. 5), text-fig. 51; Kakabadze 1971*a*: 68, pl. 13 (fig. 2a–c)). (Non *Colchidites tzotnei* in Dimitrova 1967: 65, pl. 26 (fig. 2)). Upper Barremian of western Georgia.

Colchidites veleurensis Kakabadze (1971*a*: 83, pl. 19 (fig. 5), text-fig. 55). Upper Barremian of western Georgia.

Colchidites vulanensis Egojan (1965: 119, pl. 1 (figs 1a–b, 3), pl. 2 (figs 1–2); Kakabadze 1971*a*: 70, pl. 15 (fig. 1), text-fig. 41). Upper Barremian of north-western Caucasus.

Colchidites vulanensis Egojan *australis* Klinger, Kakabadze & Kennedy (1984: 45, figs 6A–F, 7A–F, 8A–L, 9A–N). Upper Barremian of Zululand and Patagonia.

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