

# On the Barremian-Early Albian biogeography (by ammonites) of Colombia

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On the basis of new and published palaeontological and stratigraphical data, the qualitative and quantitative variations in the Barremian-early Albian ammonite fauna of Colombia have been documented and analyzed. The position adopted here is that in the early Barremian the Andean Province became replaced by the Caribbean Subprovince in Colombia. The Caribbean Subprovince became separated as an independent unit from the Andean Province on the generic level (*Buergliceras*, *Pedioceras*), but especially on the species level. In the middle/upper Aptian many new endemic genera and subgenera appeared; *Juandurhamiceras*, *Neodeshayesites*, *Laqueoceras*, *Zambranoites*, *Riedelites* and *Pseudoptychoceras*. Besides, many endemic middle Aptian species of other, non-endemic genera appeared. Beginning from the middle Aptian the Caribbean area was a separate biogeographic entity with the rank of Province; the Colombian region is considered to be the core area of the Caribbean Province.

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## Introduction

The Early Cretaceous ammonite biogeography of the northern part of South America and the southern part of North America (i.e., the so-called Caribbean province), and its interrelation with the North American, North Pacific and Andean provinces, as well as with the Mediterranean and North European provinces, is still imperfectly understood. The first palaeontologist to write about the faunal province of the Caribbean region and Middle America was Kauffman (1973), who introduced a Caribbean Province as a part of the Tethyan Realm. He subdivided the Tethyan Realm into an Indo-Mediterranean Region and a second region without a name in which the Caribbean Province is the main province. He based the Caribbean Province on Cretaceous Bivalvia. He distinguished a Caribbean Province only from the Santonian

onward, whereas from the Aptian onward he could distinguish only a Caribbean Subprovince. The Caribbean (Sub)province includes all Antillean islands, Mexico, Baja California, Colombia, Ecuador and the northern tip of Peru. Texas and the Gulf Coast of the United States belong to the North American Province. He included Venezuela in the South Atlantic Subprovince. The boundary between the Indo-Mediterranean Region and the unnamed western region is situated in the western part of the Atlantic Ocean. Kauffman did not distinguish any province for the Berriasian up to the Barremian for the Bivalvia. South of the Caribbean (Sub)province he distinguished an Andean Subprovince (= part of the South Temperate Realm); north of the Caribbean Province he distinguished a Northeast Pacific Subprovince being a part of the North Pacific Province. Antarctica is part of an Austral Province together with Western Australia. Kauffman repeated his scheme of faunal provinces in 1979, but then he based the Caribbean (Sub)province also on ammonites; he mentioned only species of the genera *Dufrenoyia* and *Hypacanthoplites*. Kauffman still could not discern a Caribbean Subprovince in the Berriasian to Barremian.

Khudoleyi (*in* Khudoleyi & Rjonsnitskaia, 1979) reconstructed the palaeobiogeographical schemes of the Pacific Ocean area for the Berriasian, Valanginian and Albian interval, as well as for the Late Cretaceous, on the basis of ammonites. In the Berriasian and Valanginian of the west Pacific area, however, this author recognized two provinces; a North Pacific Province and an East Asiatic Province. On the other hand, within the Americas he distinguished a North American Province, a Mexican-Colombian (Caribbean) Province and an Argentinian-Chilean Province for Berriasian and Valanginian times; the Caribbean Province was included in the so-called Pacific Region. The biogeography of the Barremian and Aptian time interval was not studied by this author, but in the Albian all above-mentioned provinces, except the Argentinian-Chilean one, were still recognized by Khudoleyi.

Rawson (1981) based his biogeographic units on ammonites and distinguished for the Berriasian to earliest Barremian a Tethyan Realm, which he subdivided into a Mediterranean-Himalayan Province (which is equivalent to the Indo-Mediterranean Region of Kauffman) and an Andean Province, in which he included Peru, Argentina and Patagonia. In the Andean Province grooved berriasellids dominate, whereas phylloceratids and lycoceratids are absent. The faunas from California, Mexico and Cuba are of the "Mediterranean" type, and most generic names are synonyms of well-known Mediterranean ones. He included these areas in his Mediterranean-Himalayan Province. For the Barremian to Albian times he did not subdivide the Tethyan Realm, because evidence for such subdivision was scant.

Hoedemaeker's (1990) biogeographic subdivision was also based on ammonites and was recognized for the Berriasian to Barremian time interval (this author recognized only formal faunal regions and mentioned provinces only in an informal way). The entire Caribbean area was included in the East Pacific Region, which can be recognized from the Berriasian up to the Hauterivian. During this time interval most East Pacific genera were different from those of the Mediterranean and the Indo-Malagasian Provinces. The East Pacific Faunal Region was subdivided into Andean and North Pacific Provinces. Colombia was included in the Andean Province.

The last review about ammonite biogeographic provinces including Colombia was written by Page (1996), who recognized an Andean Province, which can be

distinguished from the Berriasian up to the Barremian. It included the Caribbean, Mexico, Central America, Colombia, Venezuela, Ecuador, Peru, central Argentina and Patagonia (for the Aptian, unfortunately, there is no indication which of these areas belonged to any province). He included the entire Andean Province in the Tethyan Realm, as he distinguished only Boreal and Tethyan Realms. He also distinguished a new Northeast Pacific Province for the Valanginian, Hauterivian and Albian, not for the Barremian and Aptian. For the Albian and younger time intervals, Central America, including Mexico, the Caribbean, Colombia, Venezuela and Peru were included in his newly introduced Afro-Atlantic Province.

Thus, as to the Early Cretaceous of Colombia, there is no consensus in biogeographical interpretations among the researchers: Kauffman (1973, 1979) – Caribbean Province in the Aptian-Albian; Khudoleyi (*in* Khudoleyi & Rjonsnitskaia, 1979) – Pacific Region, Mexican-Colombian (Caribbean) Province in the Berriasian-Valanginian and Albian; Rawson (1981) – Mediterranean-Himalayan Province in the Berriasian-Hauterivian, Tethyan Realm in the Barremian-Albian; Hoedemaeker (1990) – East Pacific Region, Andean province in the Berriasian-Hauterivian, and East Pacific Province in the Barremian; Page (1996) – Tethyan Realm, Andean Province in the Berriasian-Barremian, no province in Aptian, and Afro-Atlantic Province in Albian.

Additional study of the very rich ammonite collection of Creutzberg from Colombia somewhat facilitates the investigation of this problem. As it was noted (Kakabadze & Hoedemaeker, 1997), Creutzberg did not know the precise stratigraphy of the localities from which he collected the fossils; on the specimens' labels only stages and substages are indicated. Though in his field catalogue there are more detailed stratigraphical indications (enumerated stratigraphical levels) of fossil occurrence in sections. It is clear that this collection cannot be used to improve the zonal subdivision of the Lower Cretaceous deposits of Colombia. Nevertheless, it appears that in this collection stage-guide, substage-guide genera and zonal guide-species are present. If we take into account the data presented in early (Etayo-Serna, 1964, 1968, 1983) and recent (Patarroyo, 1997, 1999, 2000; Hoedemaeker, 2004) publications on the Early Cretaceous biostratigraphy of Colombia, Creutzberg's collection undoubtedly gives a great amount of additional data for creating multitaxial palaeobiogeographic schemes and may therefore be very important for reconstructing an Early Cretaceous palaeobiogeography. The biogeographical interpretation of the Early Cretaceous ammonites of Colombia given below is not based on the study of the rich palaeontological collection of Creutzberg only, but also on analyses of the palaeontological and stratigraphical data in published literature (Forbes, 1845; Karsten, 1858, 1886; Gerhardt, 1897; Douvillé, 1906; Basse, 1928, 1949; Riedel, 1938; Royo y Gomez, 1945; Bürgl, 1954, 1957; Haas, 1960; Etayo-Serna, 1964, 1966, 1968, 1979, 1983; Kakabadze & Thieuloy, 1991; Kakabadze & Hoedemaeker, 1997; Patarroyo, 1994, 1997, 1998, 2000, 2001). Moreover, the most important data (Gabb, 1864; Anderson, 1938; Khudoleyi & Rjonsnitskaia, 1979; Renz, 1982; Kauffman, 1973, 1979, 1984; Murphy, 1975; Myczynski & Triff, 1986; Drushchits & Smirnova, 1979; Hoedemaeker, 1990; Rodda & Murphy, 1992; Page, 1996; Dias-Brito, 2000) on Early Cretaceous palaeontology, stratigraphy and palaeobiogeography of Colombia and its adjacent South and North American territory, as well as other eastern areas of the Tethyan, Boreal and 'Austral' Realms, are taken into account.

We acknowledge that criteria for distinguishing biogeographical units (biochores) should be based on differences in both qualitative (taxonomic composition, phylo-

genetic relationships) and quantitative (relative abundance, taxonomic diversity) parameters in the distribution pattern of various groups of organisms of the area under study (Kauffman, 1973, 1979; Makridin, 1973; Bengtson & Kakabadze, 1999; Westermann, 2000).

In order to carry out a biogeographical investigation of the Colombian Early Cretaceous ammonites, it is first of all necessary to group all known ammonite taxa on the basis of the following distribution patterns (Bengtson & Kakabadze, 1999); (1) Tethyan genera, (2) Boreal (North Temperate) genera, (3) 'Austral (South Temperate)' genera, (4) cosmopolitan genera, (5) endemic genera (distributed only in Colombia), (6) genera that are distributed in Colombia and/or its southern and/or northern adjacent area, (7) genera that are characteristic in the Tethyan Realm, but with some species penetrating into the Boreal (North Temperate) Realm, (8) genera that are distributed in the Tethyan Realm, but with some species penetrating into the 'Austral (South Temperate)' Realm, (9) genera that are characteristic of Boreal (North Temperate) Realm, but with some species penetrating into the adjacent area of the Tethyan Realm, and (10) genera that are characteristic of 'Austral (South Temperate)' Realm, but with some species penetrating into the adjacent area of the Tethyan Realm.

Among marine organisms the benthic (rather than nektonic) fauna has prime significance for the palaeobiogeographical subdivision of Cretaceous oceanic (marine) areas. It is, therefore, clear that the global biogeographic scheme of Cretaceous marine basins based on the study of benthic molluscs (Kauffman, 1973) was on the whole accepted by biogeographers as the basic scheme for the Cretaceous. We conditionally accept the general point of view of Kauffman (1973, 1979, 1984), Drushchits & Smirnova (1979) and Rawson (1981), who, on the basis of the distribution pattern of benthic and nektonic organisms, acknowledged the hypothesis of the existence of a South Temperate ('Austral') Realm in the Early Cretaceous inherited from the Jurassic. But the question where the boundary between the Tethyan and 'Austral' Realms should be drawn in the Barremian and Aptian is still unclear. Should the central and southern areas of South America and Africa (together with Madagascar) be regarded as parts of the 'Austral' Realm, or only the southern parts of South America (Patagonia) and South Africa (without Madagascar), Australia and New Zealand? Why is there no testimony of a typical Early Cretaceous, antiboreal fauna or flora in the southern part of the southern hemisphere? As to these questions the idea of Shulgina (1985) that such southernmost antiboreal province may have existed, but is still not discovered (under Antarctic ice-cap?), should be taken into account. If the latter is true, then the latitude of Patagonia, Antarctic Peninsula, South Africa and Australia should be regarded as the southern marginal strip of the Tethyan Realm in the Early Cretaceous (Kauffman, 1973, 1984). However, lack of sufficient material does not permit the satisfactory solution of this problem. Therefore, in this paper the term 'Austral Realm' is referred to with inverted commas.

During the Cretaceous Period the boundaries between the Tethyan and Boreal Realms shifted with time, and the principal causes of these shifts were the global changes of temperature, global transgressions and regressions, and plate-tectonic movements (Kauffman, 1973; Rawson, 1981; Hallam, 1994; Bengtson & Kakabadze, 1999). Shifts of boundaries, not only between realms, but also between provinces and subprovinces, are clear. The shifts of the boundaries of minor units were associated

with changes in climate, as well as with changes in salinity and oxygen content of the water. Such environmental changes were in turn attended by changes in the composition of marine biota in space and in time, and could, therefore, sufficiently influence the spatial and temporal distribution of the marine organisms as a whole. In connection with this it should be noted that the cause of the absence, or the scanty presence, of representatives of phylloceratids, lycoceratids and belemnites in the Barremian to lower Albian deposits of Colombia still remains problematic (Renz, 1982); this phenomenon should in all probability be expanded by the possibly environmental (facial) peculiarities in the Colombian basin during the Barremian-early Albian. The composition of the Colombian ammonite faunas and the distribution patterns of the various ammonite species varies rather considerably through the Barremian-early Albian time interval, and, therefore, the data of the ammonite biogeographic analysis of Colombia are separately given in the present paper; for the early Barremian, late Barremian, early Aptian, middle/late Aptian, and early Albian time-intervals respectively.

## Discussion

### Early Barremian

During the early Barremian the Colombian basin abounded in members of the families Ancyloceratidae and Pulchelliidae, while the Desmoceratidae and Holcodiscidae were only scantily present. The data on the distribution patterns of all characteristic early Barremian genera and species in Colombia are given below.

#### Family Ancyloceratidae Gill, 1871

1. *Crioceratites* (*Crioceratites*) Léveillé, 1837 – Upper Valanginian-lower Barremian of southeastern France, north Germany, England, Spain, Zululand; Hauterivian in west Carpathians, Azerbaijan, Egypt, Madagascar, Mozambique, Mexico, California, Japan, Chile, Patagonia, Antarctic; Hauterivian-lower Barremian in Bulgaria, Spain; Barremian of Cuba, lower? Barremian of Colombia.
  - C. (*C.*) *emerici* Léveillé, 1837 – Lower Barremian of southeastern France, Caucasus, Crimea, Bulgaria, Hungary, Spain, Italy, Jugoslavia, Austria, Switzerland, Cuba, Colombia.
  - C. (*C.*) aff. *emerici* Léveillé, 1837 – Lower? Barremian of Colombia.
  - C. (*C.*) cf. *tener* Kakabadze & Thieuloy, 1991 – Lower? Barremian of Colombia.
  - C. (*C.*) *thiollierei* (Astier, 1851) – Lower Barremian of southeastern France, Caucasus, Bulgaria, Roumania, Italy, Switzerland, Spain, Colombia.
2. *Crioceratites* (*Paracrioceras*) Spath, 1924 – Barremian in England, Germany, France, Bulgaria, Roumania, Italy, north Caucasus, Georgia, Turkey, Morocco, South Africa, Colombia.
  - C. (*P.*) *cabreraense* Kakabadze & Hoedemaeker, 2004 – Lower? Barremian of Colombia (together with *Nicklesia* sp.).
  - C. (*P.*) *leivaensis* Kakabadze & Hoedemaeker, 1997 – Lower? Barremian of Colombia.
3. *Karsteniceras* Royo y Gomez, 1945 – Barremian in southern Spain, Austria, Bulgaria, west Carpathians, Cuba, Colombia.
  - K. beyrichi* (Karsten, 1858) – Barremian of southern Spain, Austria, Bulgaria. Lower

- Barremian (Zone of *Nicklesia pulchella* after Patarroyo, 2000) of Colombia.  
*K. multicosatum* Kakabadze & Hoedemaeker, 1997 – Lower? Barremian of Colombia.
4. *Orbignyiceras* Royo y Gomez, 1945 – Lower? Barremian of Colombia, Czechia.  
*O. veleziensis* Royo y Gomez, 1945 – Lower? Barremian of Colombia, Czechia.
  5. *Pedioceras* Gerhardt, 1897 – Lower? Barremian in Mexico, California, Colombia.  
*P. caquesense* (Karsten, 1858) – Lower Barremian of Colombia.  
*P. asymmetricum* Kakabadze & Hoedemaeker, 1997 – Lower? Barremian of Colombia.  
*P. multicosatum* Kakabadze & Hoedemaeker, 1997 – Lower? Barremian of Colombia.
  6. *Acrioceras* Hyatt, 1900 – Upper Hauterivian-lower Aptian. Western and central Europe, Crimea, Caucasus, Turkmenistan, Mangyshlak(?), Australia, California, Japan, Antarctica.  
*A. julivertii* (Etayo-Sernana, 1968) – Lower Barremian of Colombia.
  7. *Acanthoptychoceras* Manolov, 1962 – Lower Barremian of southeastern France, Austria (Tyrol), Bulgaria, Colombia.  
*A. trumpyi* (Breistroffer, in coll.) (Kakabadze & Thieuloy, 1991) – Lower Barremian of Colombia.
  8. *Moutoniceras* Sarkar, 1955 – Lower-upper? Barremian of southeastern France, Spain, Austria, Italy, Crimea, Madagascar, California?, Cuba, Colombia.  
*M. cf. moutonianum* (d'Orbigny, 1850) – Lower Barremian of southeastern France, Spain, Colombia.

#### Family Hamulinidae Gill, 1871

1. *Anahamulina* Hyatt, 1900 – Barremian of southern and central Europe, Japan, California, Cuba, Colombia.  
*Anahamulina* sp. – Lower Barremian of Colombia.

#### Family Pulchelliidae H. Douvillé, 1890

1. *Buergliceras* Etayo-Serna, 1968 – Lower Barremian in Colombia.  
*B. buerglii* Etayo-Serna, 1968 – Lower Barremian (Zone of *Nicklesia pulchella* after Patarroyo, 2000) of Colombia.
2. *Nicklesia* Hyatt, 1903 – Lower Barremian of France, Switzerland, Italy, Spain, west Carpathians, north Caucasus (Tshechenia), Georgia, Marokko, Mexico, Cuba, Trinidad, Colombia.  
*N. pulchella* (d'Orbigny, 1840-1842) – Lower Barremian of southeastern France (Zone of *Nicklesia pulchella*), Spain, west Carpathians, Bulgaria, north Caucasus (Tshechenia), Georgia, Marokko, Mexico, Cuba, Spain; Lower Barremian (zone *Nicklesia pulchella* after Patarroyo, 2000) of Colombia.  
*N. nodosa* Bürgl, 1956 – Lower Barremian of Colombia.  
*N. communis* (Bürgl, 1956) – Lower Barremian of France and Colombia.  
*N. didayana didayana* Bürgl, 1956 – Lower Barremian of Colombia.  
*N. didayana multifida* Bürgl, 1956 – Lower Barremian of Colombia.  
*N. nolani* (Nickles, 1890-1894) – Lower Barremian of Colombia.  
*N. cf. alicantensis* Hyatt, 1900 – Lower Barremian of Colombia.  
*N. cf. lenticulata* Hyatt, 1900 – Lower Barremian of Colombia.
3. *Pulchellia* Uhlig, 1883, emend. Gignoux, 1921 – Lower Barremian of France, Switzerland, Spain, Bulgaria, Rumania, Trinidad, Chile, California, northern Africa, Crimea,

Georgia, Armenia, Himalaya (Tibet), Japan, Venezuela, Cuba, Colombia.

*P. galeata galeata* (von Buch, 1839) – Lower Barremian of southeastern France, Carpathians, Colombia, Trinidad.

*P. hettneri* Gerhardt, 1897 – Lower Barremian of Italy?, Colombia.

*P. fasciata* Gerhardt, 1897 – Lower Barremian of Trinidad?, Colombia.

*P. selecta* Gerhardt, 1897 – Lower Barremian of Colombia.

*P. radians* Bürgl, 1956 – Lower Barremian of Colombia.

*P. compressissima* (d'Orbigny, 1840-1842) – Lower Barremian of southeastern France, Spain, Bulgaria(?), Armenia, Georgia, Rumania, Italy, Colombia.

4. *Psilotissotia* Hyatt, 1900 – Lower Barremian of France, Switzerland, Italy, Spain, Czechia, Algeria, Crimea, Georgia, Colombia.

*P. colombiana* (d'Orbigny, 1842b) – Lower Barremian of southeastern France, Colombia.

*P. malladae* (Nickles, 1890-1894) – Lower Barremian of southeastern France, Spain, Colombia.

*P. chalmasi* (Nickles, 1890-1894) – Lower Barremian of Colombia.

#### Family Desmoceratidae Zittel, 1895

##### Subfamily Puzosiinae Spath, 1922b

1. *Valdedorsella* Breistroffer, 1947 – Hauterivian-Barremian of Crimea; Hauterivian-Aptian of north Caucasus; lower Barremian of Bulgaria; upper Barremian of west Carpathians; upper Aptian of southeastern France, Spain, Georgia, minor Caucasus, central Asia (Transcaspian area), Mozambique, Venezuela, Madagascar; lower Barremian-upper Aptian of Colombia.

*Valdedorsella* ex gr. *getulina* (Coquand, 1880) – Barremian of Colombia.

*Valdedorsella inca* (Forbes, 1845) – Lower Barremian of Bulgaria and Colombia.

2. *Pseudohaploceras* Hyatt, 1900 – Barremian-Aptian of Colombia, Venezuela?; upper Barremian-lower Aptian of Bulgaria, west Carpathians, Tunisia?; lower Aptian of north Germany, Austria, north Caucasus, minor Caucasus, Turkmenistan, Tanzania; Barremian-Aptian of Spain; Barremian-lower Aptian of Barremian-Aptian of France, Mexico, Egypt (Sinai), Japan; Barremian-Aptian? of Algeria.

*P. douvillei* (Fallot, 1920) – Barremian of Egypt (Sinai), lower Aptian of north Caucasus, Carpathians, middle Aptian (Gargasian) of southeastern France; Barremian-Aptian of Colombia.

*P. leivaense* Etayo-Serna, 1979 – Barremian-Aptian of Colombia.

*P. incertum* Riedel, 1938 – Lower Barremian (Zone of *Nicklesia pulchella* after Patarroyo, 2000) of Colombia.

*P. yucaense* Bogdanova & Hoedemaeker, 2004 – Barremian-lower? Aptian of Colombia.

*P. simile* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

*P.?* *yeseaense* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

#### Family Holcodiscidae Spath, 1923b

1. *Holcodiscus* Uhlig, 1883 – Hauterivian(?)–Barremian in Bulgaria, Crimea; lower Barremian in France, Austria, Hungary, Armenia, Spain, Czechia, north Caucasus, Georgia, California, Mexico, Cuba, Colombia.

- H. cf. camelinus* (d'Orbigny, 1850) – Lower Barremian of France, Colombia (one unpublished specimen).
2. *Parasaynoceras* Breistroffer, 1947 – Barremian of Mexico, Japan?, Colombia  
*P. horridum* (d'Orbigny, 1850) – Lower Barremian of France, Colombia.

The early Barremian ammonite fauna in the Colombian basin was represented by five families; Ancyloceratidae, Hamulinidae, Pulchelliidae, Holcodiscidae and Desmoceratidae. The Ancyloceratidae is represented by eight genera (*Crioceratites*, *Karsteniceras*, *Orbignyceras*, *Pedioceras*, *Acrioceras*, *Acanthoptychoceras*, *Moutoniceras*, *Anahamulina*). The genus *Crioceratites* is characterized by a world-wide distribution; subgenus *C.* (*Crioceratites*) is widely distributed in the Tethyan Realm (Mediterranean, Caribbean), several species penetrated into the southern marginal area of the Boreal Realm and in the northern part of the 'Austral Realm'. Subgenus *C.* (*Paracrioceras*) is distributed in the Boreal, Tethyan and 'Austral' Realms. Among the other seven genera, *Pedioceras* is distributed only in Caribbean Subprovince (Colombia, Mexico, California), *Anahamulina* in the Tethyan and Boreal Realms, and *Acrioceras* in Tethyan, Boreal and 'Austral Realms'. However, four genera (*Karsteniceras*, *Orbignyceras*, *Acanthoptychoceras*, *Moutoniceras*) are typically Tethyan. As to the distribution pattern of the species of the Ancyloceratidae in the lower Barremian of Colombia, there are altogether 13 species, among which nine are endemic and four characteristic for the Mediterranean Province. The family Pulchelliidae is a typical Tethyan family, and most of its species and genera abound especially in the Caribbean and Mediterranean regions. There are four genera in the early Barremian of Colombia, of which *Buergliceras* is endemic and three genera (*Nicklesia*, *Psilotissotia*, and *Pulchellia*) are widely distributed in the Tethyan Realm. Remarkable is the northernmost occurrence of *Pulchellia* in north California (*P. cf. compressissima* d'Orbigny) (Murphy, 1975) and in Japan (*P. ishidoensis* Yabe & Shimizu). Moreover, a representative was found in the Tibet (Liu Guifang & Wang Sien, 1987). The family Hamulinidae is represented by the genus *Anahamulina*, which is distributed in the Tethyan Realm and in the southern Boreal area. The family Holcodiscidae is represented by Tethyan genera *Holcodiscus* and *Parasaynoceras*. Among two genera of the family Desmoceratidae, the genus *Valdedorsella* is widely distributed in the Tethyan Realm. As to genus *Pseudohaploceras*, it also widely occurs in the Tethyan Realm and a few species penetrated into the southern marginal area (north Germany) of the Boreal Realm.

#### Late Barremian

In the late Barremian Colombian basin the families Ancyloceratidae, Heteroceratidae and Pulchelliidae were represented by rather numerous genera and species, whereas Desmoceratidae was rather scantily represented.

#### Family Ancyloceratidae Gill, 1871

1. *Crioceratites* (*Paracrioceras*) Spath, 1924 – Barremian of England, Germany, France, Bulgaria, Rumania, Italy, north Caucasus, Georgia, Turkey, Marocco, South Africa, Colombia.  
*C. (P.) ex gr. barremense* (Kilian in Kilian & Leenhardt, 1895) – Species of the groupe



*barremense* are known from the upper Barremian of southeastern France, Spain, Italy, Georgia; upper? Barremian of Colombia.

*C. (P.) royogomezii* Kakabadze & Hoedemaeker, 2004 – Upper? Barremian of Colombia.

2. *Pseudocrioceras* Spath, 1924 – Upper Barremian-lower Aptian of the Caucasus, western Europe, Morocco, California, Colombia.

*P. anthulai* (Eristavi, 1955) – Uppermost Barremian-lowermost Aptian of north Caucasus (Daghestan), Georgia; uppermost? Barremian of Colombia.

*P. simitiense* (Breistroffer in coll.) (Kakabadze & Thieuloy, 1991) – Uppermost? Barremian of Colombia.

*P. guanense* Kakabadze & Hoedemaeker, 2004 – Uppermost? Barremian in Colombia.

3. *Hemihoplites* Spath, 1924 – Upper Barremian-lower? Aptian of France, Mallorca, Balearic Islands, north Germany, west Carpathians, Bulgaria, Yugoslavia, north Caucasus, Daghestan, Georgia, Turkmenistan, Indonesia, Mangyshlak (Kazakhstan), Mexico?, Canada?, Cuba, Colombia (the reported presence of this genus in Mexico and Canada rest on erroneous identifications).

*H. (Matheronites) ridzewskiyi sachicaensis* Kakabadze & Hoedemaeker, 2004 – Uppermost Barremian of Daghestan. Uppermost? Barremian of Colombia.

4. *Kutatissites* Kakabadze, 1970 – Upper Barremian-lower Aptian. Georgia, north Caucasus, Daghestan, Turkey, Bulgaria, Rumania, France, Spain, Colombia.

*K. simionescui* (Avram, 1976) – Lower? Aptian of Bulgaria. Uppermost? Barremian of Colombia.

*K. creutzbergi* Kakabadze & Hoedemaeker, 2004 – Uppermost? Barremian of Colombia.

*K. densecostatus compactus* Kakabadze & Hoedemaeker, 2004 – Uppermost? Barremian of Colombia.

*K. etayoSei* Kakabadze & Hoedemaeker, 2004 – Uppermost? Barremian of Colombia.

*K. grandis* Kakabadze & Hoedemaeker, 2004 – Uppermost? Barremian of Colombia.

?*K. galanensis* Kakabadze & Hoedemaeker, 2004 – Uppermost? Barremian of Colombia.

#### Subfamily Leptoceratoidinae Thieuloy, 1966

1. *Hamulinites* Paquier, 1900 – Barremian in France, Spain, Austria, west Carpathians, Italy?, Rumania, Cuba, Colombia.

*H. munieri* (Nickles, 1894) – Barremian of Spain, France. Upper? Barremian of Colombia.

#### Family Heteroceratidae Spath, 1922a

1. *Heteroceras* (*Heteroceras*) d'Orbigny, 1849 – Lower and upper Barremian of Bulgaria and Serbia; upper Barremian of Caucasus, Crimea, Turkey, Kopet-Dag, Bolshoi Balkhan, Tuarkyr (Turkmenistan), Hungary, southeastern France, Algeria, Tunisia, Tanzania, Zululand, Madagascar, Mexico, California, Canada, Patagonia, Japan, Colombia.

*H. (H.) astieri* d'Orbigny, 1851 – Upper Barremian of southeastern France, Bulgaria, Caucasus, Colombia.

- H. (H.) heliceroides* (Karsten, 1858) – Upper Barremian of southeastern France, Canada, Colombia.
- Heteroceras* (*Argoethites*) Rouchadzé, 1933 – Upper Barremian of Georgia, Armenia, north Caucasus, Bolshoi Balkhan and Kopetdag (Turkmenistan), southeastern France, England, South Africa, California?, Colombia?  
*Heteroceras?* (*Argoethites*) sp. – Upper? Barremian of Colombia.
  - Colchidites* Djanelidzé, 1926 – Upper Barremian in north Caucasus, Transcaucasus (Georgia, Armenia), Turkey, Turkmenistan, Iran, France, South Africa (Zululand), Patagonia, Cuba, Colombia.  
*C. apolinari* (Royo y Gomez, 1945) – Upper Barremian of Colombia.  
*C. breistrofferi* Kakabadze & Thieuloy, 1991 – Upper Barremian of Colombia.  
*C. riosuarezi* Kakabadze & Hoedemaeker, 2004 – Upper Barremian of Colombia.  
*C. pseudovulanensis* Kakabadze & Hoedemaeker, 2004 – Upper Barremian of Colombia.  
*C. guanensis* Kakabadze & Hoedemaeker, 2004 – Upper Barremian of Colombia.  
*C. striatocostatus* Kakabadze & Hoedemaeker, 2004 – Upper Barremian of Colombia.

#### Family Pulchelliidae Douvillé, 1890

- Heinzia* (*Gerhardtia*) Hyatt, 1903 – Upper Barremian in Algeria, France, Spain, Georgia, Peru?, Colombia.  
*H. (G.) veleziensis* (Hyatt, 1903) – Upper Barremian of France, Georgia, Peru, Colombia.  
*H. (G.) galeatoides* (Karsten, 1858) – Upper Barremian of Colombia.
- Heinzia* (*Heinzia*) Bürgl, 1956 – Upper Barremian of southeastern France, Italy, Spain, Slovakia, Bulgaria, Georgia, Algeria, China?, Trinidad, Colombia.  
*H. (H.) colleti* Bürgl, 1956 – Upper Barremian of Colombia.  
*H. (H.) provincialis* (d'Orbigny, 1850) – Upper Barremian of southeastern France, Italy, Spain, Slovakia, Bulgaria, Algeria, Georgia, Colombia.  
*H. (H.) aff. provincialis* (d'Orbigny, 1850) – Upper Barremian of Colombia.
- Carstenia* Hyatt, 1903 – Upper Barremian in Italy, Spain, Georgia, Bulgaria, west Carpathians, Trinidad, Colombia.  
*C. lindigii* (Karsten, 1858) – Upper Barremian of Italy, Georgia, west Carpathians, Trinidad, Colombia.

#### Family Desmoceratidae Zittel, 1895

##### Subfamily Puzosiinae Spath, 1922b

- Pseudohaploceras* Hyatt, 1900 – Barremian-Aptian in Colombia, Venezuela?; upper Barremian-lower Aptian of Bulgaria, west Carpathians, Tunisia?; lower Aptian in north Germany, Austria, north Caucasus, minor Caucasus, Turkmenistan, Tanzania; Barremian-Aptian of Spain; Barremian-Aptian of France, Mexico, Egypt (Sinai), Japan; Barremian-Aptian? in Algeria.  
*P. cf. liptoviense* (Zeuschner, 1846) – Upper? Barremian of Silesia and Colombia.  
*P. douvillei* (Fallot, 1920) – Gargasian of southeastern France; Barremian of Egypt, Bulgaria; lower Aptian of Caucasus; Barremian-Aptian of Colombia.  
*P. leivaense* Etayo-Serna, 1979 – Barremian-Aptian of Colombia.  
*P. yucaense* Bogdanova & Hoedemaeker, 2004 – Barremian-lower? Aptian of Colombia.

- P. gerhardti* Bogdanova & Hoedemaeker, 2004 – Barremian?-Aptian of Colombia.  
*P.?* *yeseraense* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.  
*P. simile* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.
2. *Valdedorsella* Breistroffer, 1947 – Hauterivian-Barremian of Crimea; Hauterivian-Aptian of north Caucasus; lower Barremian of Bulgaria; upper Barremian of west Carpathians; upper Aptian of southeastern France, Spain, Georgia, minor Caucasus, central Asia (Transcaspian area), Mosambique, Venezuela, Madagascar; lower Barremian-upper Aptian of Colombia.  
*Valdedorsella* ex gr. *getulina* (Coquand, 1880) – Barremian of Colombia.
  3. *Melchiorites* Spath, 1923b – Barremian of Crimea; lower Barremian of Czechia; upper Barremian of Spain and Rumania; Barremian-middle Aptian (Gargasian) of France; Barremian-Aptian of Austria, Tunisia; Aptian of Georgia, Minor Caucasus; lower Aptian of Tansania; middle Aptian (Gargasian)-lower Albian of Madagascar; Venezuela, upper Barremian-Aptian of Colombia.  
*M. colombianus* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

#### Subfamily Beudanticeratinae Breistroffer, 1953

1. *Zuercherella* Casey, 1954 – Upper Aptian of Spain, France, north Germany, north Caucasus, minor Caucasus, Tunisia, Venezuela; middle (Gargasian) and upper (Clansayesian) Aptian of Turkmenistan; upper Barremian-upper? Aptian of Colombia.  
*Z. etayosernai* Bogdanova & Hoedemaeker, 2004 – Upper Barremian-Aptian of Colombia.

On the basis of the above data, the late Barremian basin of Colombia was populated by four families; Ancyloceratidae, Heteroceratidae, Pulchelliidae and Desmoceratidae (Creutzberg's indication of the presence of *Neodeshayesites* aff. *cingularis* Etayo-Serna in the upper Barremian of Colombia is undoubtedly wrong). The family Ancyloceratidae is represented by five genera/subgenera; *Crioceratites* (*Paracrioceras*), *Pseudocrioceras*, *Hemihoplites*, *Kutatissites*, *Hamulinites*. The subgenus *Paracrioceras* is widely distributed in the Tethyan (Mediterranean Province and Caribbean Subprovince) and Boreal (North European Province) Realms, with a penetration into 'Austral Realm' (South Africa). The three species of *Paracrioceras* identified from Colombia, are endemic. The genus *Hemihoplites* is widely distributed in the Tethyan and Boreal Realms. In Colombia only one species (*H. Matheronites*) *ridzewskyi sachicaensis* Kakabadze & Hoedemaeker, 2004) occurs; a similar specimen was described also from Daghestan (Mediterranean Province). *Pseudocrioceras* is a typical late Barremian-early Aptian Tethyan genus (Mediterranean Province and Caribbean Subprovince). Among the three Colombian upper Barremian species of this genus only one occurs also in the Mediterranean Province; the other two are endemic. *Kutatissites* occurs only in the Tethyan Realm (Mediterranean Province and Caribbean Subprovince). Among the six species of this genus known from Colombia, one also occurs in the Mediterranean Province, whereas the other five are endemic. The genus *Hamulinites* is characteristic of the Tethyan Realm (Mediterranean and Caribbean regions). *Hamulinites munieri* (Nickles) noted from the upper Barremian of Colombia also occurs in the Mediterranean Province. The family Heteroceratidae is distributed in the Tethyan (Mediterranean,

Caribbean), the 'Austral' (South Africa, Patagonia) and the Boreal (Canada, England) Realms. In Colombia this family is represented by two genera, *Colchidites* and *Heteroceras*. *Colchidites* is widely distributed in the Tethyan (Mediterranean and Caribbean regions) and 'Austral' (Patagonia, South Africa) Realms, whereas representatives of *Heteroceras* (*Heteroceras*) abundantly occur in the Tethyan, less numerous in the 'Austral' and scantily in the Boreal (Canada) Realms. In the upper Barremian of Colombia only two species of *H.* (*Heteroceras*) are known; one (*H. astieri*) also occurs in the Mediterranean Province, and the other (*H. heliceroides*) is known from the Tethyan (Mediterranean and Caribbean regions) and Boreal (North Pacific Province) Realms. As to subgenus *H.* (*Argvethites*), it is distributed in the Mediterranean Province and only one specimen is found in the North European Province (England, Speeton). In Colombia only one specimen of *Heteroceras* (*Argvethites*) sp. is known. The family Pulchelliidae in the upper Barremian of Colombia is represented by three genera/subgenera; *Carstenia*, *Heinzia* (*Heinzia*) and *H.* (*Gerhardtia*). They were widely distributed in the Tethyan Realm (Mediterranean and Caribbean regions). Among the listed six species of the genus *Heinzia*, three are distributed in the Mediterranean Province and Caribbean Subprovince, but other three are endemic. The family Desmoceratidae in the upper Barremian of Colombia is represented by four genera; *Pseudohaploceras* (abundantly), *Zuercherella* (scantily), *Valdedorsella* and *Melchiorites* (very scantily). The genera *Pseudohaploceras* and *Zuercherella* are characterized by wide distribution in the Tethyan Realm; however, some species penetrated into the Boreal Realm. Among the above listed eight species of genus *Pseudohaploceras*, two also occur in the Mediterranean Province, whereas the other six are endemic. As to *Zuercherella*, noted from upper Barremian of Colombia, *Z. etayo-sernai* is endemic. *Valdedorsella* and *Melchiorites* in the Barremian are characteristic of the Tethyan Realm (Mediterranean and Caribbean regions).

#### Early Aptian

During the early Aptian the family Douvilleiceratidae had a leading position (diversity and frequency) in the Colombian basin, while families Ancyloceratidae and Desmoceratidae were in a second position. As to the families Macroscaphitidae and Oppeliidae, they were very scantily represented.

#### Family Oppeliidae Douvillé, 1890

##### Subfamily Aconeceratinae Spath, 1923b

1. *Aconecerases* Hyatt, 1903 – Upper Barremian-lower Albian of Europe, Greenland, Algeria, South Africa, Madagascar, Australia (Queensland), Western Australia, Argentina, Nepal, Colombia.  
*A. nisoides* (Sarasin, 1893) – Lower Aptian of southern England, north Germany, southeastern France, Bulgaria, Volga region (Povoljje, Russia), Transcaspian area, South Africa, Colombia.

#### Family Macroscaphitidae Hyatt, 1900

1. *Macroscaphites* Meek, 1876 – Upper Barremian-lower Aptian of southern and central Europe, northern Africa, Egypt (Sinai), Mexico, Cuba, Venezuela, Colombia.  
*M. yvani disjuncticostatus* Kakabadze & Thieuloy, 1991 – Upper? Barremian-lower Aptian of Colombia.

*M. recticostatus* (d'Orbigny, 1840-1842) – Upper Barremian-lower Aptian of France, Spain, Italy, Austria, Bulgaria, central Europe, northern Africa, Egypt (Sinai), Mexico, Colombia (one small, unfigured specimen).

#### Family Ancyloceratidae Gill, 1871

1. *Ancyloceras* d'Orbigny, 1840-1842 – Barremian-lower Aptian of France, Bulgaria, England, Spain, Italy, Georgia, Azerbaijan, Volga region, Turkmenistan, Japan, California, Colombia. Middle? Aptian of Venezuela.  
*A. cf. matheronianum* d'Orbigny, 1840-1842 – Upper? Barremian-lower Aptian of southeastern France, north Caucasus, Crimea? At the Barremian/Aptian boundary (probably lower Aptian) in Colombia.  
*A. cf. mantelli* Casey, 1960 – Lower Aptian of England and Colombia.
2. *Tonohamites* Spath, 1924 – Lower Aptian of France, southern England, north Germany, minor Caucasus, Colombia. Middle Aptian of Georgia, Madagascar and South Africa (Zululand).  
*T. ex gr. koeneni* Casey, 1961 – Lower? Aptian of Colombia.
3. *Toxoceratoides* Spath, 1924 – Lower Barremian-upper Aptian of France, Spain, Italy, England, Germany, Rumania, west Carpathians, Crimea, Caucasus, Australia?, Mozambique, Zululand, Patagonia, Antarctica, California, Canada, Mexico, Colombia.  
*T. aff. nagarai* (Leanza, 1970) – At the Barremian/Aptian boundary of Colombia.
4. *Monsalveiceras* Kakabadze & Hoedemaeker, 1997 – Lower? Aptian of Colombia.  
*M. monsaloense* Kakabadze & Hoedemaeker, 1997 – Lower? Aptian of Colombia.
5. *Australiceras* (*Proaustraliceras*) Kakabadze, 1977 – Lower Aptian of southern England, southeastern France, Georgia, Volga-region (Povoljje), northern Koryakia (Siberia) and Japan. Aptian (lower? Aptian) in Colombia. There are no reliable records of this subgenus from the southern hemisphere.  
*A.? (P.) bolivari* Royo y Gomez, 1945 – Lower? Aptian of Colombia.

#### Family Deshayesitidae Stoyanov, 1949

1. *Dufrenoyia* Kilian & Reboul, 1915 – Lower Aptian of southeastern France, Mexico, Texas, Arizona, Equador, Venezuela, England, Russian platform, north Caucasus, Georgia, Turkmenistan, western Kasakhstan, Nigeria, Japan, Somali, Colombia; lower? Aptian of Mexico.  
*D. coddaziana* (Karsten, 1858) – Uppermost lower Aptian of Venezuela, Equador, Colombia. Middle? Aptian in Mexico.  
*D. aff. coddaziana* (Karsten, 1858) – Uppermost lower Aptian of Colombia.  
*D. ex gr. lurensis* (Kilian, 1888) – Uppermost lower Aptian of Colombia.  
*D. justinae* (Hill, 1893) – Uppermost? lower Aptian in Texas, Mexico, Venezuela, Arizona, Colombia.  
*D. sanctorum* Bürgl, 1956 – Uppermost lower Aptian of Colombia.  
*D. ex gr. bösei* Humphrey, 1949 – Uppermost lower Aptian of Colombia.  
*D. ex gr. scalata* Casey, 1964 – Uppermost lower Aptian of Colombia.  
*D. boteroi* Etayo-Serna, 1979 – Uppermost lower Aptian of Colombia.  
*D. renzi* Bogdanova & Hoedemaeker, 2004 – Uppermost lower Aptian of Colombia and Venezuela.

Family Douvilleiceratidae Parona & Bonarelli, 1897

Subfamily Cheloniceratinae Spath, 1923b

1. *Prochelonicerias* Spath, 1923b – Lower Aptian of southern England, north Germany, Austria, southeastern France, Switzerland, Hungary, west Carpathians, Bulgaria, Poland, north Caucasus, Georgia, Armenia, Azerbaijan, Mangyshlak (Kazakhstan), South Africa, northern Africa, California, Mexico, Colombia; uppermost? Barremian-lower Aptian of France.
 

*P. albrechtiaustriae* (Hohenegger *in* Uhlig, 1883) – Lower Aptian of southeastern France, Bulgaria, Poland, Czechia, north Caucasus, Georgia, Armenia, Mangyshlak (Kazakhstan) and Colombia.

*P. aff. dechauxi* (Kilian & Reboul, 1915) – Lower Aptian of Colombia.
2. *Chelonicerias* Hyatt, 1903 – Lower Aptian (perhaps also lowermost middle Aptian) of southeastern France, Austria, southern England, north Germany, west Carpathians, Bulgaria, Crimea, north Caucasus, Daghestan, Georgia, Armenia, Azerbaijan, Mangyshlak (Kazakhstan), Turkmenistan, Volga region (Povoljje), Mozambique, South Africa, Madagascar, Egypt, Iran, Japan, California, Texas, Mexico, Cuba?, Venezuela, Colombia.
 

*Ch. gottschei* (Kilian, 1902) – Uppermost lower Aptian/lowermost upper Aptian of south Tanzania, Zululand, Madagascar(?); lower Aptian, *Deshayesites deshayesi* and *Tropaeum bowerbanki* zones of southern England; lower Aptian of Colombia.

*Ch. disparile* Casey, 1961 – Lower Aptian, Zone of *Tropaeum bowerbanki* of southern England; lower Aptian, Zone of *Dufrenoyia furcata* of Georgia; lower Aptian of Colombia.

*Ch. cornuelianum* (d'Orbigny, 1840-1842) – Lower Aptian of west Europe, Georgia, north Caucasus, Daghestan, Mangyshlak (Kazakhstan), Turkmenistan; lower Aptian of Colombia.

*Ch. seminodosum* Sinzow (1906) – Lower Aptian of southeastern France, north Germany, west Carpathians, Bulgaria, north Caucasus, Daghestan, Mangyshlak (Kazakhstan), Tuarkyr, Minor Balkhan (Turkmenistan), Armenia; lower Aptian (Zone of *Deshayesites deshayesi*) of Georgia; lower Aptian of Colombia.

*Ch. meyendorffi* (d'Orbigny, 1845) – Lower Aptian, Zone of *Tropaeum bowerbanki*, Subzone of *Chelonicerias meyendorffi* of southern England; lower Aptian, Zone of *Deshayesites deshayesi* of France, Georgia and north Caucasus; lower Aptian of Volga region, Colombia.

*Ch. kiliani kiliani* (Koenen, 1902) – Lower Aptian, Zones of *Deshayesites deshayesi* (Subzone of *Deshayesites grandis*) and *Tropaeum bowerbanki* (Subzone of *Chelonicerias meyendorffi*) in southern England; lower Aptian of Germany, Colombia.

*Ch. kiliani obesum* Casey, 1961 – Lower Aptian, Zone of *Tropaeum bowerbanki*, Subzone of *Chelonicerias meyendorffi* of southern England; lower Aptian of Colombia.

*Ch. aff. kiliani* (Koenen, 1902) – Lower Aptian of Colombia.

*Ch. parinodum* Casey, 1962 – Lower Aptian, Zone of *Deshayesites deshayesi* (Subzone of *Chelonicerias parinodum*) in southern England; lower Aptian of Colombia.

*Ch. crassum crassum* Spath, 1930 – Lower Aptian, Zones of *Deshayesites deshayesi* (Subzone of *Deshayesites grandis*) and Zone of *Tropaeum bowerbanki* in southern England; lower Aptian, Zone of *Dufrenoyia furcata* in Georgia; lower Aptian of Bulgaria, Colombia

*Ch. crassum impar* Casey, 1961 – Lower Aptian, Zones of *Deshayesites deshayesi* (Subzone of *Deshayesites grandis*) and *Tropaeum bowerbanki* of southern England; lower Aptian of Colombia.

*Ch. quadrarium quadrarium* Casey, 1962 – Lower Aptian, Zones of *Deshayesites deshayesi* (Subzone of *Deshayesites grandis*) and *Tropaeum bowerbanki* of southern England; lower Aptian of Colombia.

*Ch. delagoense* (Krenkel, 1910) – Upper part of lower Aptian and lower part(?) of middle Aptian of Mozambique; lower Aptian of Colombia.

*Ch. mackesoni* Casey, 1962 – Lower Aptian of England and Colombia.

*Ch. rectangulatum* Sharikadze, Kakabadze & Hoedemaeker, 2004 – Lower Aptian of Colombia.

*Ch. guanense* Sharikadze, Kakabadze & Hoedemaeker, 2004 – Lower Aptian of Colombia.

#### Subfamily Roloboceratinae Casey, 1961

1. *Roloboceras* Casey, 1954 – Lower Aptian of southern England, France, Spain, Colombia, Venezuela.

*R. saxbyi* Casey, 1961 – Lower Aptian, Zone of *Deshayesites forbesi* (subzones of *Deshayesites kiliani* and *Deshayesites callidiscus*) of southern England; upper part of the lower Aptian of Venezuela; lower Aptian of Colombia.

*R. cf. regale* Casey, 1961 – Lower Aptian of southern England and Colombia.

#### Family Desmoceratidae Zittel, 1895

##### Subfamily Pseudosaynellinae Casey, 1961

1. *Pseudosaynella* Spath, 1923a – Lower Aptian of Spain, France, England, north Caucasus, Transcaspian area (Turkmenistan, Tuarkyr, Great Balkhan); Aptian of Austria, Colombia, Japan?, Russian platform?; Aptian (middle? Aptian) of Arkansas.

*P. bicurvata* (Michelin, 1838) – Lower Aptian of Spain, France, England, north Caucasus, Transcaspian area (Turkmenistan, Tuarkyr, Great Balkhan), Colombia; Aptian of Austria, Russian platform?; Aptian (middle? Aptian) of Arkansas.

*P. ex gr. undulata* (Sarasin, 1893) – Lower Aptian of Colombia.

##### Subfamily Puzosiinae Spath, 1922b

1. *Pseudohaploceras* Hyatt, 1900 – Barremian-Aptian of France, Mexico, Egypt (Sinai), Japan Colombia, Venezuela?; upper Barremian-lower Aptian of Bulgaria, west Carpathians, Spain, Tunisia; lower Aptian of north Germany, Austria, north Caucasus, minor Caucasus, Turkmenistan, Tanzania; Barremian-Aptian? of Algeria.

*P. aff. ramosum* Bogdanova, 1991 – Aptian of Colombia.

*P. douvillei* (Fallot, 1920) – Barremian of Egypt (Sinai), lower Aptian of north Caucasus, Roumenian Carpathians, middle Aptian (Gargasian) of southeastern France; Barremian-Aptian of Colombia.

*P. leivaense* Etayo-Serna, 1979 – Barremian-Aptian of Colombia.

*P. hopkinsi* (Forbes, 1845) – Upper Aptian of Colombia.

*P. yucaense* Bogdanova & Hoedemaeker, 2004 – Barremian-lower? Aptian of Colombia.

*P. gerhardti* Bogdanova & Hoedemaeker, 2004 – Barremian?-Aptian of Colombia.

*P.? yeseraense* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

*P. simile* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

2. *Melchiorites* Spath, 1923b – Barremian of Crimea; lower Barremian of Czechia; upper Barremian of Spain; Barremian-middle Aptian (Gargasian) of France; Barremian-Aptian of Austria; Barremian/Aptian of Tunisia; Aptian of Georgia, minor Caucasus; lower Aptian of Tansania; middle Aptian (Gargasian)-lower Albian of Madagascar; upper Barremian-Aptian of California, Venezuela, Colombia.

*M. colombianus* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

#### Subfamily Beudanticeratinae Breistroffer, 1953

1. *Zuercherella* Casey, 1954 (= *Cortezicerias* Etayo-Serna, 1979) – Upper Barremian-Upper Aptian of Spain, France, north Germany, north Caucasus, minor Caucasus, Tunisia, Venezuela; middle (Gargasian) and upper (Clansayesian) Aptian in Turkmenistan; upper Barremian-Aptian of Colombia.

*Z. etayosernai* Bogdanova & Hoedemaeker, 2004 – Upper Barremian-Aptian of Colombia.

Widely represented families in the early Aptian strata of Colombia are Ancyloceratidae, Douvilleiceratidae, Deshayesitidae and Desmoceratidae; comparatively poorly represented are Macroscaphitidae and Oppeliidae. The family Oppeliidae is represented by the world-wide distributed genus *Aconecerias* in the lower Aptian strata of Colombia; *A. nisoides* (Sarasin) is a cosmopolitan species. The family Macroscaphitidae is represented only by one endemic species of the genus *Macroscaphites*; this genus is characteristic of the Tethyan Realm (Mediterranean and Caribbean Provinces). The family Ancyloceratidae is represented by five genera/subgenera; *Ancyloceras*, *Tonohamites*, *Toxoceratoides*, *Australicerias* (*Proaustralicerias*) and *Monsalveicerias*. The genus *Ancyloceras* was distributed in the Tethyan (Mediterranean Province and Caribbean Subprovince) and Boreal (North European and North Pacific provinces) Realms. One of the two species listed above from Colombia is distributed in the Mediterranean Province, but the other is known from the North European Province. *Tonohamites* is characteristic of the Tethyan (Mediterranean and Caribbean regions) and Boreal (North European Province) Realms. Only one endemic species of this genus is known from Colombia. The genus *Toxoceratoides* has world-wide distribution; it is known from Boreal, Tethyan and 'Austral' Realms. The subgenus *Australicerias* (*Proaustralicerias*) is distributed in the Tethyan Realm and in the southern area of the Boreal Realm. There are no reliable records of this subgenus from the southern hemisphere and, accordingly, it can be regarded as characteristic of the Tethyan Realm and the adjacent part of the Boreal Realm. Only one endemic species of this genus is known from Colombia. The genus *Monsalveicerias* is known only from Colombia. The family Douvilleiceratidae is represented by three genera in the lower Aptian of Colombia; *Procheloniceras*, *Cheloniceras* and *Roloboceras*. The genus *Procheloniceras* is characteristic of the Tethyan Realm (Mediterranean and Caribbean provinces) and of the southern area of the Boreal Realm (North European Province). The species from Colombia is common in the Tethyan Realm and rare in the Boreal Realms. *Cheloniceras* is widely distributed in the Tethyan (Mediterranean and Caribbean regions), Boreal (North and East European regions) and 'Austral' (South Africa) Realms. Among the 17 species of this genus identified in Colombia, five are distributed in the Tethyan



(Mediterranean and Caribbean regions) and Boreal (North European Province) Realms, six occur in the Boreal Realm (North European Province), one is distributed in the Tethyan, Boreal and 'Austral' Realms, two in the Tethyan Realm and three species are endemic. The genus *Roloboceras* is distributed in the Tethyan (Mediterranean and Caribbean regions) and southern area of the Boreal (North European Province) Realms. The two listed species of this genus occur in the North European and Caribbean provinces. The lower Aptian representatives of *Dufrenoyia* are distributed in the Tethyan (Mediterranean and Caribbean provinces) and Boreal (North European and North Pacific provinces) Realms. In the lower Aptian of Colombia there are nine species, from which one species is distributed in the Caribbean and North Pacific (Texas) provinces, two species in the Caribbean Province, while the other six species are endemic. The family Desmoceratidae is represented in the lower Aptian of Colombia by four genera; *Pseudosaynella*, *Pseudohaploceras*, *Melchiorites* and *Zuercherella*. *Pseudosaynella* is characteristic of the Tethyan Realm and the southern part of the Boreal Realm. One of the two species listed from Colombia is common in the Mediterranean Province, but rare in the North European and North American provinces; the other species is endemic. *Pseudohaploceras* and *Zuercherella* are widely distributed in the Tethyan (Mediterranean and Caribbean regions) Realm, but rare in the southern part of the Boreal Realm. *Melchiorites* is characteristic of the early Aptian of the Tethyan Realm.

#### Middle/late Aptian

Hitherto, the middle (= Gargasian) and upper (= Clansayesian) Aptian substages in Colombia are not studied separately; they are considered together under the name upper Aptian (e.g., Etayo-Serna, 1979) and accordingly detailed stratigraphical ranges of many ammonite species are not established. Hence, in the present paper, the middle and upper Aptian substages are treated together.

The dominant ammonites in Colombia during the middle and late Aptian were the families Douvilleiceratidae, Ancyloceratidae, Parahoplitidae, Acanthohoplitidae and Deshayesitidae, whereas the families Desmoceratidae, Ptychoceratidae, Oppeliidae, Gaudryceratidae and Silesitidae were represented scantily.

#### Family Oppeliidae Douvillé, 1890

##### Subfamily Aconeceratinae Spath, 1923b

1. *Aconecerases* Hyatt, 1903 – Upper Barremian-lower Albian. Europe, Greenland, Algeria, South Africa, Madagascar, Australia (Queensland), Western Australia, Argentina, Nepal, Colombia.  
*A. gutierrezpalmae* Etayo-Serna, 1979 – Middle/upper Aptian of Colombia.

#### Family Gaudryceratidae Spath, 1927

1. *Eogaudrycerases* (*Eogaudrycerases*) Spath, 1927 – Barremian-upper Albian. France, Spain, England, Bulgaria, Caucasus, Italy, Switzerland, Algeria, South Africa (Zululand), Madagascar, Egypt (Sinai), California, Antarctica (Alexander Island), Colombia.  
*E. (E.) helmsi* Etayo-Serna, 1979 – Upper Aptian of Colombia.
2. *Eogaudrycerases* (*Eotetragonites*) Breistroffer, 1947 – Upper Aptian-middle Albian.

France, Spain, Switzerland, Bulgaria, Caucasus, South Africa (Zululand), Madagascar, Egypt (Sinai), California, Antarctica (Alexander Island), Colombia.

*E. (Eotetragonites) cabaricoi* Etayo-Serna, 1979 – Upper Aptian of Colombia.

#### Family Ancyloceratidae Gill, 1871

1. *Ammonitoceras* Dumas, 1876 – Lower Aptian-Upper Aptian of France; middle Aptian-upper? Aptian of England, north Germany, Mangyshlak (Kazakhstan), Turkmenistan, north Caucasus, Georgia, Turkey, Bulgaria, Zululand, Mozambique, Mexico, Colombia.

*A. giganteum* Kakabadze & Hoedemaeker, 2004 – Middle? Aptian of Colombia.

*A. galanensis* Kakabadze & Hoedemaeker, 2004 – Middle? Aptian of Colombia.

2. *Pseudoaustraliceras* Kakabadze, 1981 – Middle-upper Aptian of Mangyshlak (Kazakhstan), Kopetdag, Bolshoy Balchan and Tuarkir (Turkmenistan), Georgia, Armenia, Azerbaijan, north Caucasus, Volga region (Russia), Bulgaria, Hungary, Switzerland, Germany, Madagascar, Angola, India, Colombia.

*P. colombiae* (Basse, 1928) – Middle? Aptian of Colombia.

*P. pavlovi* (Wassiliewskyi, 1908) – Middle Aptian of north Caucasus, Mangyshlak (Kazakhstan), Great Balkhan (Turkmenistan), west Europe; middle? Aptian of Colombia.

*P. ex gr. ramososeptatum* (Anthula, 1899) – Middle? Aptian of Colombia.

4. *Laqueoceras* Kakabadze & Hoedemaeker, 2004 – Middle? Aptian of Colombia.  
*Laqueoceras laqueus* Kakabadze & Hoedemaeker, 2004 – Middle? Aptian of Colombia.
5. *Hamiticeras* Anderson, 1938 – Aptian of California, Oregon, Caucasus, , Colombia.  
*H. pilsbryi* Anderson, 1938 – Middle Aptian of California, Oregon, Caucasus, Colombia.

*H. chipatai* Kakabadze & Hoedemaeker, 1997 – Middle? Aptian of Colombia.

*H. ventrotuberculatum* Kakabadze & Hoedemaeker, 2004 – Middle? Aptian of Colombia.

*H. longum* Kakabadze & Hoedemaeker, 2004 – Middle? Aptian of Colombia.

6. *Helicancylus* Gabb, 1869 (emend. Aguire-Urreta, 1986) – Upper Hauterivian of southeastern France. Middle and upper Aptian of California, Oregon, Argentina (Patagonia). Aptian (middle? Aptian) of Colombia.

*H. cf. philadelphium* Anderson, 1938 – Middle Aptian of California, Oregon, Colombia.

7. *Tonohamites* Spath, 1924 – Lower Aptian of France, southern England, north Germany, minor Caucasus. Middle Aptian of Georgia, Madagascar, South Africa (Zululand). Middle Aptian of Colombia.

*T.? renzoni* Etayo-Serna, 1979 – Middle? Aptian of Colombia.

#### Family Ptychoceratidae Meek, 1876

1. *Ptychoceras* d'Orbigny, 1840-1842 – Hauterivian-upper Albian; England, France, Spain, Italy, Austria, west Carpathians, Caucasus, Madagascar, southern India, Australia? (Queensland), New Zealand, Alaska, British Colombia, California, Cuba; middle/upper Aptian of Colombia.

*P. aff. puzosianum* d'Orbigny, 1840-1842 – Middle/upper Aptian of Colombia.

2. *Pseudoptychoceras* Etayo-Serna, 1979 – Middle? Aptian of Colombia.

*P. gilberti* Etayo-Serna, 1979 – Middle? Aptian of Colombia.

## Family Deshayesitidae Stoyanov, 1949

1. *Juandurhamiceras* Etayo-Serna, 1979 – Middle/upper Aptian in Colombia.
  - J. juandurhami* Etayo-Serna, 1979 – Middle/upper Aptian in Colombia.
  - J. joepecki* Etayo-Serna, 1979 – Middle/upper Aptian in Colombia.
  - J. giraldoi* Etayo-Serna, 1979 – Middle/upper Aptian in Colombia.
2. *Neodeshayesites* Casey, 1964 – Uppermost Aptian-lower Albian in Colombia; Aptian in Venezuela.
  - N. ex gr. nodosus* (Riedel, 1938) – Uppermost Aptian of Colombia.
  - N. ex gr. albertoalvarezi* Etayo-Serna, 1979 – Uppermost Aptian-lower Albian of Colombia.
  - N. longicostatus* Bogdanova & Hoedemaeker, 2004 – Uppermost Aptian of Colombia.
  - N. buergli* Bogdanova & Hoedemaeker, 2004 – Uppermost Aptian of Colombia.
  - N. stutzeri* (Riedel, 1938) – Uppermost Aptian-lower Albian of Colombia; Aptian (middle? Aptian) of Venezuela.
  - N.? euglyphoides* Bogdanova & Hoedemaeker, 2004 – Uppermost Aptian of Colombia.
  - N. multicostatus* Bogdanova & Hoedemaeker, 2004 – Uppermost Aptian of Colombia.
  - N.? tuberculatus* Bogdanova & Hoedemaeker, 2004 – Uppermost Aptian of Colombia.
  - N. contracta* (Riedel, 1938) – Uppermost Aptian of Colombia; upper? part of lower Aptian of Venezuela.
  - N. nodosus* (Riedel, 1938) – Uppermost Aptian of Colombia; upper? part of lower Aptian of Venezuela.
  - N. rotundus* (Riedel, 1938) – Uppermost Aptian of Colombia; upper? part of lower Aptian of Venezuela.
  - N. biplicatus* Bogdanova & Hoedemaeker, 2004 – Uppermost Aptian-lower Albian of Colombia.
  - N. columbianus* (Riedel, 1938) – Uppermost Aptian-lower Albian of Colombia.
  - N. aff. cingulatus* Etayo-Serna, 1979 – Uppermost Aptian-lower Albian of Colombia.

## Family Douvilleiceratidae Parona &amp; Bonarelli, 1897

## Subfamily Cheloniceratinae Spath, 1923b

1. *Epicheloniceras* Casey, 1954 – Middle Aptian, rarely upper Aptian, of southern England, north Germany, France, Austria, Bulgaria, Switzerland, Hungary, north Caucasus, Daghestan, Georgia, Azerbaijan, Armenia, Mangyshlak (Kazakhstan), Turkmenistan, Volga region (Povoljje), eastern and southern Africa, Madagascar, Iran, California, Mexico, Colombia.
  - E. tschernyschewi* (Sinow, 1906) – Middle Aptian of southern England, northwestern Germany, Bulgaria, north Caucasus, Mangyshlak (Kazakhstan); middle Aptian, Zone of *Epicheloniceras subnodosocostatum* of Daghestan, Georgia, southeastern Caucasus, Turkmenistan; middle Aptian of Hungary and Colombia.
  - E. buxtorfi* (Jacob & Tobler, 1906) – Middle Aptian of Switzerland; middle Aptian, Zone of *Epicheloniceras subnodosocostatum* of north Caucasus, Turkmenistan; middle Aptian, Zone of *Epicheloniceras martinioides* (Subzone of *E. buxtorfi*) of southern England; middle Aptian of Colombia.
  - E. stoliczkanum* (Gabb, 1869) – Middle? Aptian (Zone? of *Epicheloniceras bradleyi*) of California; middle Aptian of Colombia.
  - E. santafecinum* (Burckhardt, 1925) – Middle Aptian of Colombia.

- E. aff. santafecinum* (Burckhardt, 1925) – Middle Aptian of Colombia.  
*E. pusillum* (Sinzow, 1906) – Middle Aptian of north Caucasus, Switzerland, Austria, Colombia.  
*E. aff. clansayense* (Jacob, 1905) – Middle Aptian of Colombia.  
*E. wiedmanni* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*E. dognaelvirae* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. camachoi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. carlosacostai* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. jimenoii* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. barreroi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. pardoi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. leonhardtiedeli* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. huertasi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*E. bambucaense* Etayo-Serna *et al.*, 1994 – Middle Aptian of Colombia.  
*E.? amazonarum* (Burckhardt, 1925) – Middle Aptian of Colombia.  
*E. douvillei* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*E. bradleyiformis* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*E. stoliczkanum* (Gabb, 1869) – Middle Aptian of California, Colombia.  
*E. cf. subnodosocostatum* (Sinzow, 1907) – Middle Aptian of north Caucasus, Georgia, southeastern France, Switzerland, southern England, Colombia.  
*E. clansayense* (Jacob, 1905) – Middle Aptian of France, north Caucasus, Georgia, Colombia.  
*E. martini occidentalis* (Jacob, 1905) – Middle Aptian of Switzerland, Colombia.  
*E. aff. nazacense* Burckhardt, 1925 – Middle Aptian of Colombia.  
*E. debile* Casey, 1962 – Middle Aptian, Zone of *Epicheloniceras martinoides* (Subzone of *E. debile*) of southern England; middle Aptian of Colombia.  
*E. waageni* (Anthula, 1899) – Middle Aptian of the north Caucasus, Mangyshlak (Kazakhstan), southeastern Iran, Colombia.
2. *Vectisites* (*Zambranoites*) Etayo-Serna, 1979 – Middle Aptian of Colombia, north-eastern Brazil.  
*V. (Z.) nodosus* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*V. (Z.) etayosernai* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*V. (Z.) obscurus* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*V. (Z.) grandis* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*V. (Z.) zambranoi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*V. (Z.) cruzi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*V. (Z.) mateusi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*V. (Z.) cadenai* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*V. (Z.) duquesi* Etayo-Serna, 1979 – Middle Aptian of Colombia.

Subfamily *Douvilleiceratinae* Parona & Bonarelli, 1897

1. *Eodouvilleiceratas* Casey, 1961 – Upper Aptian (Clansayesian)-lower? Albian of France, Georgia, northwest Caucasus, Daghestan, Turkmenistan, California, Venezuela; middle/upper Aptian-lower? Albian of Colombia.  
*E. horridum* (Riedel, 1938) – Upper Aptian of Colombia.  
*E. aff. planum* Rouchadzé, 1933 – Upper Aptian of Colombia.  
*E.? tequendamai* Etayo-Serna, 1979 – Upper Aptian of Colombia.

## Family Parahoplitidae Spath, 1922a

1. *Parahoplites* Anthula, 1899 – Middle Aptian (rarely? upper Aptian) of north Caucasus, Daghestan, Mangyshlak, Turkmenistan, England, France, Mexico, California, Arizona, Colombia, Chile, Peru, Iran, Algeria, Madagascar, Zululand.  
*P. maximus* Sinzow, 1907 – Middle Aptian of Daghestan, Mangyshlak, England, Colombia.  
*P. macfarlandi* Anderson, 1938 – Middle Aptian of California, Colombia.  
*P. triston* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*P.?* *hubachi* Etayo-Serna, 1979 – Middle Aptian of Colombia.  
*P.?* *inconstans* (Riedel, 1938) – Middle Aptian of Colombia.  
*P. cf. nutfieldi*ensis (Sowerby *in* Sowerby & Sowerby, 1815) – Middle Aptian of England and Colombia.  
*P. treffryanus* (Karsten, 1858) – Middle Aptian of Colombia.  
*P. cinctatum* (Etayo-Serna, 1979) – Middle Aptian of Colombia.  
*P. cf. shupi* Anderson, 1938 – Middle Aptian of California and Colombia.  
*P. cf. stantoni* Anderson, 1938 – Middle Aptian of California and Colombia.  
*P. cf. umbilicostatus* Scott, 1940 – Middle Aptian of Texas and Colombia.  
*P. sjögreni* Anthula, 1899 – Middle Aptian of California and Colombia.

## Family Acanthohoplitidae Stoyanow, 1949

## Subfamily Colombiceratinae Tovbina, 1979

1. *Gargasicerias* Casey, 1954 – Middle Aptian (Gargasian) of France, Daghestan, Turkmenistan, Mexico, Colombia, Venezuela, Peru.  
*G. attenuatum* (Kilian, 1913) – Middle Aptian (Gargasian) of southeastern France, Colombia.  
*G. aptiense* (Roch, 1926) – Middle Aptian (Gargasian) of southeastern France, Venezuela (Vale Grande Formation), Colombia.  
*G. recticostatum* (Kilian, 1913) – Middle Aptian (Gargasian) of southeastern France, Colombia, Venezuela?  
*G. aff. recticostatum* (Roch, 1926) – Middle Aptian of Colombia.  
*G. aff. interiectum* (Riedel, 1938) – Middle Aptian of Colombia.  
*G. acutecostum* (Riedel, 1938) – Middle Aptian of Venezuela, Colombia.  
*G. subpulcher* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.  
*G. cf. gargasense* (d'Orbigny, 1841) – Middle Aptian of southeastern France, Colombia.  
*G. interiectum* (Riedel, 1938) – Middle Aptian of Colombia.  
*G. pulcher* (Riedel, 1938) – Middle Aptian of Colombia.  
*G.?* *juanwoyatti* Etayo-Serna, 1979 – Middle Aptian of Colombia.
2. *Colombicerias* Spath, 1923b – Middle Aptian (and perhaps upper Aptian) of France, England, north Germany, Austria, Bulgaria, Switzerland, Bulgaria, Rumania, Sardinia, Crimea, Ukrainian Carpathians, north Caucasus, Daghestan, Georgia, Mangyshlak (Kazakhstan), Turkmenistan, north Africa, Madagascar, India, California?, Arizona, Texas, Venezuela, Mexico, Colombia.  
*C. tobleri* (Jacob & Tobler, 1906) – Middle Aptian of north Caucasus, Daghestan, Mangyshlak (Kazakhstan), Georgia, France, Switzerland, Austria and Colombia.  
*C. subpeltocerooides* (Sinzow, 1907) – Middle Aptian of Bulgaria, north Caucasus, Daghestan, Georgia, Crimea, Colombia. Upper Aptian? of Ukrainian Carpathians.

- C. caucasicum* Luppov *et al.*, 1949 – Middle Aptian, Zone of *Epicheloniceras subnodosocostatum* of the north Caucasus, Daghestan, Georgia, Turkmenistan; middle Aptian of Bulgaria; middle Aptian of Colombia.
- C. aff. crassicosatum* (d'Orbigny, 1841) – Middle Aptian of Colombia.
- C. cf. angulatum* Egoian, 1969 – Middle Aptian (Gargasian) of the north Caucasus, Colombia; upper part of the middle Aptian of eastern Carpathians.
- C. cf. sinzowi* (Kazansky, 1914) – Middle Aptian of north Caucasus, Daghestan, Georgia, Colombia.
- C.? foreroi* Etayo-Serna, 1979 – Middle Aptian of Colombia.
- C.? sarmientoi* Etayo-Serna, 1979 – Middle Aptian of Colombia.
- C. formosum* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.
3. *Protacanthoplites* Tovbina, 1970 – Middle Aptian-lowermost? upper Aptian of Bulgaria, north Caucasus, Daghestan, Georgia, Armenia, Mangyshlak (Kazakhstan), Turkmenistan, Colombia.
- P. abichi* (Anthula, 1899) – Upper part of middle Aptian of the north Caucasus, Daghestan, Mangyshlak (Kazakhstan), Turkmenistan, Georgia; upper Aptian of Bulgaria; middle Aptian of Colombia.
- P. cf. allanovi* Tovbina, 1970 – Middle Aptian of Turkmenistan, Colombia.
- P.? originalis* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.
4. *Riedelites* Etayo-Serna, 1979 – Middle Aptian of Colombia.
- R. latecostatus* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.
- R. esthersee* Etayo-Serna, 1979 – Middle Aptian of Colombia.
- R.? quebradanegra* Etayo-Serna, 1979 – Middle Aptian of Colombia.
- R. obliquum* (Riedel, 1938) – Middle Aptian of Colombia.
- R. filosum* Etayo-Serna, 1979 – Middle Aptian of Colombia.
- R. cf. inconstans* (Riedel, 1938) – Middle Aptian of Colombia.
- R. latecostatus* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.
- R. microtuberculatus* Sharikadze *et al.*, 2004 – Middle Aptian of Colombia.

#### Subfamily Acanthohoplitinae Stoyanow, 1949

1. *Acanthohoplites* Sinzow, 1907 – Middle Aptian (Gargasian)-upper Aptian (Clansayesian). England, north Germany, France, west Carpathians, Rumania, Bulgaria, Sardinia, Crimea, north Caucasus, Daghestan, Georgia, Armenia, Azerbaijan, Mangyshlak, Turkmenistan, Iran, Algeria, Tunis?, Madagascar, Mozambique, Japan, California, Arizona, Mexico, Venezuela, Colombia.
- A. nolani* (Seunes, 1887) – southeastern France, England, north Germany, Crimea, north Caucasus, Daghestan, Georgia Mangyshlak, Kopetdag (Turkmenistan), Madagascar, Sardinia, Venezuela; lower part of Upper Aptian (Clansayesian); upper Aptian of Colombia. This species is also noted from upper part of the Clansayesian (Zone of *Hypacanthoplites jacobi*) in the northwest Caucasus.
- A. cf. teres* Stoyanow, 1949 – Upper Aptian of Arizona (Zone of *Acanthohoplites nolani*); upper Aptian of Colombia.
- A. bigoti* (Seunes, 1887) – Upper Aptian (Clansayesian) of southeastern France, Georgia, north Caucasus, Daghestan, Mangyshlak, Turkmenistan and Colombia.
- A. bigouretiforme* Etayo-Serna, 1979 – Upper Aptian of Colombia.
- A. ex gr. ashiltaensis* (Anthula, 1899) – Upper Aptian of Colombia.

- A. seunesiforme* Etayo-Serna, 1979 – Upper Aptian of Colombia.  
*A. quitasuegno* Etayo-Serna, 1979 – Upper Aptian of Colombia.  
*A. odiosus* Etayo-Serna, 1979 – Upper Aptian of Colombia.  
*A. pluricostatum* Etayo-Serna, 1979 – Upper Aptian of Colombia.  
*A. eleganteante* Etayo-Serna, 1979 – Upper Aptian of Colombia.  
*A. luisperezi* Etayo-Serna, 1979 – Upper Aptian of Colombia.  
*A.? leptoceratiforme* Etayo-Serna, 1979 – Upper Aptian of Colombia.  
*A.? serpentiforme* Etayo-Serna, 1979 – Upper Aptian of Colombia.
2. *Hypacanthoplites* Spath, 1923b – Uppermost upper Aptian-lowermost lower Albian. England, north Germany, France, Hungary, Bulgaria, Crimea, north Caucasus, Daghestan, Georgia, Mangyshlak, Turkmenia, Tadjikstan, Algeria, Tunis?, Iran, Madagascar, California, Texas, Mexico, Venezuela, Colombia.  
*H. sigmoidalis* Casey, 1965 – Upper Aptian (Clansayesian) of southern England, Daghestan, Colombia.  
*H. milletoides* Casey, 1965 – Upper Aptian (Clansayesian, Zone of *Hypacanthoplites jacobi*) of southern England. Upper Aptian of Colombia.  
*H.? dognaliciae* Etayo-Serna, 1979 – Upper Aptian of Colombia.

#### Family Desmoceratidae Zittel, 1895

##### Subfamily Puzosiinae Spath, 1922b

1. *Valdedorsella* Breistroffer, 1947 – Hauterivian-Barremian of Crimea; Hauterivian-Aptian of north Caucasus; lower Barremian of Bulgaria; upper Barremian of west Carpathians; upper Aptian of southeastern France, Spain, Georgia, minor Caucasus, central Asia (Transcaspien area), Mozambique, Venezuela, Madagascar; lower Barremian-upper Aptian of Colombia.  
*V. ex gr. akuschaensis* (Anthula, 1899) – Middle/upper Aptian of Colombia.  
*V. colombiana* Etayo-Serna, 1979 – Middle/upper Aptian of Colombia.
2. *Melchiorites* Spath, 1923b – Barremian of Crimea; lower Barremian of Czechia; upper Barremian of Spain and Roumania; Barremian-middle Aptian (Gargasian) of France; Barremian-Aptian of Austria; Barremian/Aptian of Tunisia; Aptian of Georgia, Minor Caucasus; lower Aptian of Tanzania; middle Aptian (Gargasian)-lower Albian of Madagascar; upper Aptian of Venezuela, Colombia.  
*M. media* Riedel, 1938 – Middle/upper Aptian of Colombia.  
*M. palmeri* Etayo-Serna, 1979 – Middle/upper Aptian of Colombia.  
*M. colombianus* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.
3. *Pseudosaynella* Spath, 1923b – Lower Aptian of Spain, France, England, north Caucasus, Transcaspien area (Turkmenistan, Tuarkyr, Great Balkhan); Aptian of Austria, Colombia, Japan?; Aptian of Russian platform?; middle? Aptian of Arkansas.  
*P. ralphimlayi* Etayo-Serna, 1979 – Middle/upper Aptian of Colombia.  
*P. ex gr. undulate* (Sarasin, 1893) – Lower Aptian of Colombia.
4. *Pseudohaploceras* Hyatt, 1900 – Barremian-Aptian of Colombia, Venezuela?; upper Barremian-lower Aptian of Bulgaria, west Carpathians, Tunisia?; lower Aptian of north Germany, Austria, north Caucasus, minor Caucasus, Turkmenistan, Tanzania; Aptian of Spain; Barremian-Aptian of France, Mexico, Egypt (Sinai), Japan; Barremian-Aptian? of Algeria.

*P. leivaense* Etayo-Serna, 1979 – Barremian-Aptian of Colombia.

*P. douvillei* (Fallot, 1920) – Upper Barremian of southeastern France; Barremian of Egypt, Bulgaria; lower Aptian of Caucasus; Barremian-Aptian of Colombia.

*P. hopkinsi* (Forbes, 1845) – Aptian of Colombia.

*P. gerhardti* Bogdanova & Hoedemaeker, 2004 – Barremian?-Aptian of Colombia.

*P.?* *yeseaense* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

*P. simile* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

#### Subfamily Beudanticeratinae Breistroffer, 1953

1. *Zuercherella* Casey, 1954 (= *Corteziceras* Etayo-Serna, 1979) – Upper Barremian-upper Aptian of Spain, France, north Germany, north Caucasus, Minor Caucasus, Tunisia, Venezuela; middle (Gargasian) and upper (Clansayesian) Aptian of Turkmenistan; upper Barremian-Aptian of Colombia.

*Z. zuercheri* (Jacob & Tobler, 1906) – Upper Aptian of France, north Germany, Spain, Tunisia, north Caucasus, Venezuela, Colombia.

*Z. etayoserai* Bogdanova & Hoedemaeker, 2004 – Barremian-Aptian of Colombia.

*Z. cortezi* (Etayo-Serna, 1979) – Middle/upper Aptian of Colombia.

*Z. latecostata* (Riedel, 1938) – Middle/upper Aptian of Colombia, Spain?

#### Family Silesitidae Hyatt, 1900

1. *Miyakoceras* Obata, 1967 – Upper Aptian of Japan; middle/upper Aptian of Colombia.

*M. ex gr. tanohatense* Obata, 1967 – Middle/upper Aptian of Colombia.

On the basis of above the middle/late Aptian basin of Colombia was characterized by the following ten ammonite families; Oppeliidae, Gaudryceratidae, Deshayesitidae, Ancyloceratidae, Ptychoceratidae, Douvilleiceratidae, Parahoplitidae, Acanthohoplitidae, Desmoceratidae and Silesitidae. The family Oppeliidae is represented by genus *Aconeceras* Hyatt, 1903, which is widespread in the 'Austral' (southernmost Argentina, South Africa, Australia), Tethyan (Mediterranean and Caribbean Provinces), and in the Boreal (North European and North Pacific Provinces) Realms. Only one endemic species of this genus is known from the upper Aptian of Colombia. The family Gaudryceratidae in Colombia is represented by subgenera *Eogaudryceras* (*Eogaudryceras*) Spath and *E. (Eotetragonites)* Breistroffer. The first subgenus is widely distributed in the Tethyan (Mediterranean and Caribbean Provinces) and 'Austral' (Alexander Island, South Africa) Realms, but rarely occurs in the southern area of the Boreal Realm (England). Only one endemic species, *E. (Eogaudryceras) helmsi* Etayo-Serna, of this subgenus is recorded from the upper Aptian of Colombia. Subgenus *E. (Eotetragonites)* is characteristic of the 'Austral' (Alexander Island, South Africa) and Tethyan (Mediterranean and Caribbean Provinces) Realms. From Colombia only one endemic species is known, *E. (Eotetragonites) cabaricoi* Etayo-Serna. The family Ancyloceratidae is represented by six genera (*Ammonitoceras*, *Pseudoaustraliceras*, *Laqueoceras*, *Hamiticeras*, *Helican cylus* and *Tonohamites*). The genus *Ammonitoceras* is widely distributed in the Tethyan, 'Austral' and Boreal (its southern marginal area) Realms. The two species of this genus, found in Colombia, are endemic. *Pseudoaustraliceras* is characteristic of the Tethyan and Boreal Realms. In Colombia there are three endemic species of this



genus. The genus *Laqueoceras* (with its two species) is endemic. Representatives of the genus *Hamiticeras* are known from the Tethyan (Mediterranean and Caribbean Provinces) and Boreal Realms (North Pacific Province). Among the four species known in the middle/upper Aptian of Colombia, one species (*H. pilsbryi* Anderson) is widely distributed, whereas the other three are endemic. The genus *Helicancyclus* is common in the middle/upper Aptian of California and Oregon, but also in the middle and upper Aptian of Argentina (Patagonia). The single species *H. cf. philadelphium* Anderson is distributed in the middle Aptian of the marginal area of the Caribbean (California) and North Pacific Province (Oregon). The middle Aptian genus *Tonomamites* was distributed in the Tethyan (Mediterranean and Caribbean Provinces) and 'Austral' (South Africa) Realms. In the middle/upper Aptian of Colombia only one endemic species, *T.? renzoni*, is known. The family Ptychoceratidae in the middle/upper Aptian of Colombia is represented by two genera (*Ptychoceras*, *Pseudoptychoceras*). *Ptychoceras* is widely distributed in the Boreal (North American, North Pacific and North European Provinces), Tethyan (Mediterranean and Caribbean Provinces) and 'Austral' Realms (Australia, Queensland). Only *P. aff. puzosianum* d'Orbigny is known from the middle/upper Aptian of Colombia. The genus *Pseudoptychoceras* (with its only species *P. gilberti* Etayo-Serna from middle/upper Aptian of Colombia) is endemic. The family Deshayesitidae is represented by two genera (*Neodeshayesites* and *Juandurhamiceras*). *Neodeshayesites* is known only from Colombia and Venezuela. Among the above listed 14 species recorded from Colombia, ten are endemic, but four are found also in Venezuela (Caribbean Province). The genus *Juandurhamiceras* (with its three species) is endemic. The family Douvilleiceratidae from the middle Aptian of Colombia is represented by two genera (*Epicheloniceras*, *Vectisites*). *Epicheloniceras* is widely distributed in the Tethyan (Mediterranean and Caribbean Provinces) and Boreal Realms (North European Province). Among 27 species listed above from the middle/upper Aptian of Colombia, two species are characteristic of the Boreal Realm (North European Province), six species occur in the Boreal (North European Province) and Tethyan (Mediterranean Province) Realms, two species are known from Caribbean (California) Province, and 17 species are endemic. Subgenus *Vectisites* (*Zambranoites*) is common only in the middle/upper Aptian of Colombia, but there are several findings of *V. (Zambranoites)* sp. from the middle/upper Aptian of Brazilia (P. Bengtson, personal communication). All eight species of this subgenus listed above are endemic. In the Upper Aptian of Colombia the family Douvilleiceratidae is represented by the genus *Eodouvilleiceras*, of which the distribution pattern is restricted to the Tethyan (Mediterranean and Caribbean Provinces) Realm. The family Parahoplitidae is represented by one genus, *Parahoplites*, which is characteristic of the Tethyan Realm (Mediterranean and Caribbean Provinces) with penetrations into southern area of the Boreal Realm (North American and North European provinces). Among the ten species listed above from Colombia, four are known from other localities (California) of Caribbean Province, one from the southern area of the North Pacific Province (Texas), one is found in North European Province (England), one in both the Mediterranean and North European provinces, and three species are endemic. The family Acanthohoplitidae in the middle Aptian of Colombia is represented by four genera (*Gargasiceras*, *Colombiceras*, *Protacanthoplites*, *Riedelites*) and in the upper Aptian

by two genera (*Hypacanthoplites*, *Acanthohiplites*). The genus *Gargasicerias* was widely distributed in the Tethyan (Mediterranean and Caribbean Provinces) Realm during the middle Aptian. Among the eleven species found in the middle? Aptian of Colombia, three species are characteristic of the Mediterranean Province, one species is known from Caribbean Province (Venezuela), whereas the other seven species are endemic. The genus *Colombicerias* was widely spread in the Tethyan (Mediterranean and Caribbean Provinces) Realm and in the southern area of the Boreal (North American and North European provinces) Realm during the middle Aptian. Among the ten species of *Colombicerias* listed above, one species is distributed in the Tethyan (Mediterranean Province) and Boreal Realms (North European Province), four species are characteristic only of the Tethyan Realm (Mediterranean Province) and four species are endemic. *Protacanthoplites* is characteristic of the Tethyan (Mediterranean Province) Realm. Among the five species of this genus noted above, two species also occur in the Tethyan (Mediterranean Province) Realm, while the other three species are endemic. *Riedelites* is widely distributed in the middle? Aptian of Colombia and all eight species listed above are endemic. *Hypacanthoplites* is characteristic of the Tethyan Realm (Mediterranean and Caribbean Provinces) and of the southern area of the Boreal Realm (England, north Germany, Texas). Among the three species noted above from the uppermost Aptian of Colombia, one also occurs in the Mediterranean and North European provinces, one species also in the North European Province (England), while the third one is endemic. *Acanthohiplites* is widely spread in many regions of the Tethyan and Boreal Realms. Among the noted 13 species of this genus from Colombia, two are distributed in the Mediterranean Province, one species in North Pacific (Arizona) Province and the other eight are endemic. The family Desmoceratidae in the middle/upper Aptian of Colombia is represented by five genera (*Valdedorsella*, *Melchiorites*, *Zuercherella*, *Pseudosaynella*, *Pseudohaploceras*). *Valdedorsella* was widely spread in the Tethyan (Mediterranean and Caribbean Provinces) Realm. The ten species listed above are endemic. The genus *Pseudosaynella* is known from the Tethyan (Mediterranean and Caribbean Provinces) Realm, and from the southern part of the Boreal Realm. Only two endemic species, *viz.* *P. ralphimleyi* Etayo-Serna and *P. ex gr. undulate* (Sarasin), are noted from the Aptian (middle/upper Aptian) of Colombia. *Pseudohaploceras* is distributed in the Tethyan Realm (Mediterranean and Caribbean Provinces) and in the southern marginal part of the Boreal Realm. One of the species noted above (*P. douvillei* Fallot) is widely distributed in the Tethyan Realm, but the other seven species are endemic. *Melchiorites* is widely distributed in the Mediterranean and Caribbean Provinces. Both species noted above are endemic. *Valdedorsella* is characteristic of the Mediterranean and Caribbean Provinces. All species noted above from Colombia are endemic. *Zuercherella* is characteristic of the Tethyan Realm (Mediterranean and Caribbean), but rarely occurs also in the southernmost area of the Boreal Realm (north Germany). Among four species of this genus listed above, one is spread in the Mediterranean, Caribbean and North European Provinces, whereas the other three are endemic. The family Silesitidae in the middle/upper Aptian of Colombia is represented by the genus *Miyacoceras*, which is known from the upper Aptian of Japan. *Miyacoceras tanohatense* Obata was first reported from Japan (Japanese-East Asian Subprovince), but is now recorded from the middle/upper Aptian of Colombia.

## Early Albian

In the early Albian there were, besides the Douvilleiceratidae and Desmocerotidae, a few representatives of Phylloceratidae, Deshayesitidae and Anisoceratidae in the Colombian area.

## Family Phylloceratidae Zittel, 1884

1. *Phylloceras* Suess, 1865 – Jurassic-Lower Cretaceous of western Europe, Crimea, Caucasus, Colombia.  
*P.?* (*P.*) *buchianum* (Forbes, 1845) – Lower Albian of Colombia.
2. *Hypophylloceras* Salfeld, 1924 – Lower Cretaceous (Valanginian)-Upper Cretaceous (Cenomanian) of western Europe, Crimea, Caucasus, Colombia.  
*H. wiedmanni* Etayo-Serna, 1979 – Upper Aptian-lower Albian of Colombia.
3. *Holcophylloceras* Spath, 1927 – Lower Cretaceous (Barremian-Aptian-lower? Albian) of western Europe, Crimea, Caucasus, Colombia.  
*H. hernandezii* Etayo-Serna, 1979 – Lower? Albian of Colombia.

## Family Anisoceratidae Hyatt, 1900

1. *Protanisoceras* Spath, 1923c – Upper Aptian-middle Albian of western and central Europe, Madagascar, India, Peru (Wright *et al.*, 1996), Colombia.  
*P.* (*Protanisoceras*) *creutzbergi* Kakabadze & Hoedemaeker, 1997 – Lower? Albian of Colombia.

## Family Deshayesitidae Stoyanow, 1949

1. *Neodeshayesites* Casey, 1964 – Uppermost Aptian-lower Albian of Colombia; Aptian of Venezuela.  
*N. albertoalvarezii* Etayo-Serna, 1979 – Uppermost Aptian-lower Albian of Colombia.  
*N. striatus* Bogdanova & Hoedemaeker, 2004 – Lower Albian of Colombia.  
*N. karsteni* (Marcou, 1875) – Lower Albian of Colombia.  
*N. columbianus* (Riedel, 1938) – Uppermost Aptian-lower Albian of Colombia.  
*N. stutzeri* (Riedel, 1938) – Uppermost Aptian-Albian of Colombia; Aptian of Venezuela.  
*N. aff. cingulatus* Etayo-Serna, 1979 – Uppermost Aptian-lower Albian of Colombia.

## Family Douvilleiceratidae Parona &amp; Bonarelli, 1897

## Subfamily Douvilleiceratinae Parona &amp; Bonarelli, 1897

1. *Eodouvilleiceratas* Casey, 1961 – Upper Aptian (Clansayesian)-lower? Albian of southeastern France, Georgia, northwest Caucasus, Dagestan, Turkmenistan, California, Colombia.  
*E. pedrocarvajali* Etayo-Serna, 1979 – Lower Albian of Colombia.
2. *Douvilleiceratas* de Grossouvre, 1894 – Lower Albian, rarely in the lower part of the middle Albian of southern England, northern Germany, France, Bulgaria, Poland, Switzerland, Sardinia, Crimea, west Carpathians, Ukrainian Carpathians, north Caucasus, Georgia, Mangyshlak (Kazakhstan), Turkmenistan, Egypt, Angola, Madagascar, India, Pakistan, Texas, Mexico, California, Venezuela, Colombia, Peru, northeastern Brazil.

- D. orbignyi* Hyatt, 1903 – Lower Albian of southern England, France, Poland, Angola, Madagascar, Georgia, Colombia.
- D. magnodosum* Casey, 1962 – Lower Albian, Zone of *Douvilleiceras mammillatum*, Subzone of *Cleoniceras floridum* of southern England; lower Albian of Colombia.
- D. cf. pustulosum* Casey, 1962 – Lower Albian of southern England, Colombia.
- D. solitae* (d'Orbigny, 1853) – Lower Albian of Colombia.
- D. tarapacaense* Etayo-Serna, 1979 – Lower Albian of Colombia.
- D. abozogloi* Etayo-Serna, 1979 – Lower Albian of Colombia.
- D. monile* (Sowerby *in* Sowerby & Sowerby, 1816) – Lower Albian of England, Caucasus, Colombia.
- D. mammillatum* Schlotheim, 1913 – Lower Albian of France, west Carpathians, Georgia, California, Venezuela, Mexico, northeastern Brazil, Colombia.

#### Family Trochleiceratidae Breistroffer, 1951

1. *Trochleiceras* Fallot & Termier, 1923 – Upper Aptian-lower Albian of the Balearic Islands, Madagascar; lower Albian of Colombia.  
*T. (Trochleiceras) juliverti* Etayo-Serna, 1979 – Lower Albian of Colombia.  
*T. (Jaumaportaiceras) hoffstetteri* Etayo-Serna, 1979 – Lower Albian of Colombia.

#### Family Desmoceratidae Zittel, 1895

##### Subfamily Puzosiinae Spath, 1922b

1. *Puzosia* Bayle, 1878 – Lower Cretaceous (upper? Aptian-lower Albian)-Upper Cretaceous (upper Campanian) of Europe, Asia, Africa, North and South America; Albian in Colombia.  
*P. quenstedti* (Parona & Bonarelli, 1897) – Albian of Spain, France, Austria, Crimea, Angola, Madagascar, Venezuela, Colombia.
2. *Carloscaceresiceras* Etayo-Serna, 1979 – Lower and middle? Albian of Colombia.  
*C. caceresi* Etayo-Serna, 1979 – Lower Albian of Colombia.  
*C. monteroi* Etayo-Serna, 1979 – Lower Albian of Colombia.

On the basis of the above given data we can conclude that the early Albian basin of Colombia was characterized by six ammonite families; Douvilleiceratidae, Anizoceratidae, Trochleiceratidae, Desmoceratidae, Phylloceratidae and Deshayesitidae. The family Phylloceratidae is represented by *Phylloceras*, *Hypophylloceras* and *Holcophylloceras*. These genera are distributed in the Tethyan Realm and in the southern part of the Boreal Realm. In the lower Albian of Colombia each of these is represented by one endemic species. The family Anisoceratidae is represented by *Protanisoceras*, which is characteristic of the Tethyan (Mediterranean and Caribbean Provinces) and Boreal (North European Province) Realms. Only one endemic species is known from the lower Albian of Colombia. The family Trochleiceratidae is represented by the Tethyan genus *Trochleiceras*; both mentioned species of this genus are endemic. *Neodeshayesites* of the family Deshayesitidae is known only from the Aptian-lower Albian of the Caribbean Province (Colombia, Venezuela). The family Douvilleiceratidae in the lower Albian of Colombia is represented by two genera, *Eodouvilleiceras* and *Douvilleiceras*. *Eodouvilleiceras* is widespread in the Mediterranean and Caribbean Provinces. Only one endemic species (*E. pedrocarvajali* Etayo-Serna) is known from lower Albian of

Colombia. *Douvilleiceras* is widely distributed in the Tethyan Realm (Mediterranean and Caribbean Provinces) and also in southern marginal area of the Boreal Realm (North Pacific and North American provinces). Among the eight species identified from the lower Albian of Colombia, two also occur in the North European Province, one is known from the Mediterranean and North European provinces, and only three are endemic. The family Desmoceratidae in the lower Albian of Colombia is represented by the genera *Carloscaceresiceras* and *Puzosia*. *Carloscaceresiceras* is endemic, while *Puzosia* is widely distributed in the Tethyan Realm. One species, listed above from the lower Albian of Colombia, is distributed in the Mediterranean and Caribbean Provinces.

### Conclusion

Before passing on to palaeobiogeographical characterization of the five subages here distinguished within the Barremian-early Albian time interval, it is necessary to note that the East Pacific faunal 'Region', recognized for Berriasian to Hauterivian times, consisted of Andean and Northern Pacific provinces, and that the Colombian area was a part of the Andean Province (Hoedemaeker, 1990). At the end of the Hauterivian the endemicity of the East Pacific 'Region' became rather low and altered into the East Pacific Province of the Tethyan Realm.

#### *Early Barremian*

In the early Barremian the tropical fauna of Colombia reached down to the northern part of Peru. During this time Colombia, Ecuador and Peru constituted a distinct tropical area with abundant endemicity. The distribution of the early Barremian genera *Hatchericeras* and *Pseudohatchericeras* seems to have been restricted to Patagonia, South Africa (Zululand) and Australia? (Queensland). These genera may define a true Austral Province. Though they have not been reported from Alexander Island (Thomson, 1974), the composition of the ammonite fauna reveals that this part of Antarctica also belongs to the Austral Province. As the Andean Cordillera lacks ammonite-bearing Barremian deposits between northern Peru and Patagonia, the boundary between the Tethyan and 'Austral' Realms cannot be drawn precisely and may be situated not far south of the southernmost occurrence of *Pulchellia* in Peru. As to the boundary between the early Barremian Boreal (North American Province) and Tethyan (Caribbean Subprovince) domains, the data on the distribution of early Barremian ammonites for these purposes is scanty. Nevertheless, the boundary between Boreal and Tethyan Realms can conveniently be defined on the basis of the presence or absence of pulchelliids and barremitids (Hoedemaeker, 1990). According to the distribution pattern of early Barremian pulchelliids (Murphy, 1975) and the genus *Pedioceras* (which are characteristic of the Tethyan Realm), their northernmost occurrence in northern California gives ground to conclude that the northern boundary of the Caribbean Subprovince in the Early Barremian, was probably situated there. On the other hand, in north California representatives of *Shasticioceras* occur, which are widely distributed in the Boreal provinces of North America, but also genera that are characteristic for both the Tethyan and the southern margin of the Boreal Realm. Therefore, California represented a transitional interrealmal area during the early Barremian and the above traced boundary is gradational.

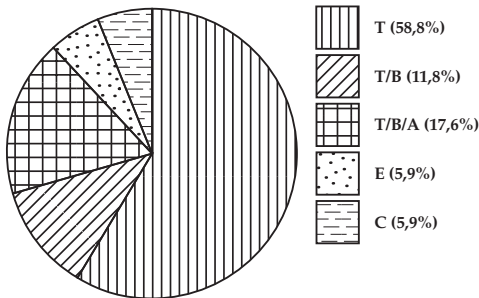


Fig. 1. Qualitative and quantitative ratio of distribution patterns of genera of the families Ancyloceratidae, Pulchelliidae, Desmoceratidae and Holcodiscidae, found in the lower Barremian of Colombia. Key: T = Tethyan; B = Boreal; A = Austral; C = Caribbean; E = Endemic. This key applies to all figures unless stated otherwise.

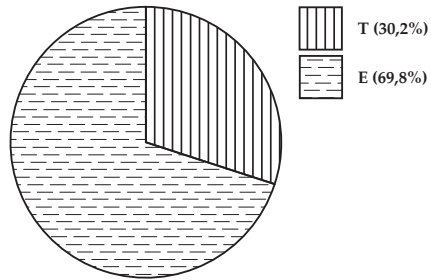


Fig. 2. Qualitative and quantitative ratio of distribution patterns of species of the families Ancyloceratidae, Pulchelliidae, Desmoceratidae and Holcodiscidae found in the lower Barremian of Colombia.

The analysis of early Barremian ammonites indicates that the early Barremian Colombian basin abounded with 17 genera/subgenera. Among them ten (58.8%) are Tethyan (*Karsteniceras*, *Orbignyceras*, *Acanthoptychoceras*, *Moutoniceras*, *Nicklesia*, *Pulchellia*, *Psilotissotia*, *Valdedorsella*, *Holcodiscus*, *Parasaynoceras*); two (11.8%) (*Pseudohaploceras*, *Anahamulina*) occur in the Tethyan and the adjacent regions of the Boreal Realm. There are three (17.6%) (*Crioceratites*, *Paracrioceras*, *Acriceras*) which are distributed in the Tethyan (Mediterranean Province), Boreal (North European Province) and 'Austral' Realms. Moreover, there is one (5.9%) endemic genus (*Buergliceras*) and one genus (*Pedioceras*) that was restricted to the Caribbean area (Fig. 1). Three genera, which are common in the Mediterranean Province, seem to be absent in Colombia; *Barremites*, *Torcapella*, *Aoramidiscus*.

With respect to the species composition, there are 43 species of the above noted five early Barremian families noted above from the lower Barremian of Colombia. Among them, 30 species (69.8%) are endemic (only in Colombia) and 13 species (30.2%) are characteristic of the Tethyan Realm (Mediterranean, Caribbean) (Fig. 2).

On the basis of these data we may conclude that during the early Barremian the Colombian area already undoubtedly belonged to the Tethyan Realm. On the other hand, based on the existence of two endemic genera (*Buergliceras*, *Pedioceras*) and on the abundance of the endemic species (of other genera, too), this area, together with its adjacent southern (Ecuador, Peru) and northern (Mexico, California) regions, has to be considered of subprovincial rank, i.e., the Caribbean Subprovince (Fig. 3).

#### Late Barremian

From the beginning of the middle of the late Barremian, an equalization of the conditions in the Boreal, Tethyan and 'Austral' Realms started (Kakabadze, 1992, 1996). This process was associated with a rise of the sea level and an increase in temperature. Accordingly, especially at the end of the Barremian (during the biochrons of *Colchidites sarasini* and *Pseudocrioceras waagenoides*), the tendency of the disappearance of ammonite provincialism at the generic level becomes noticeable. This process con-

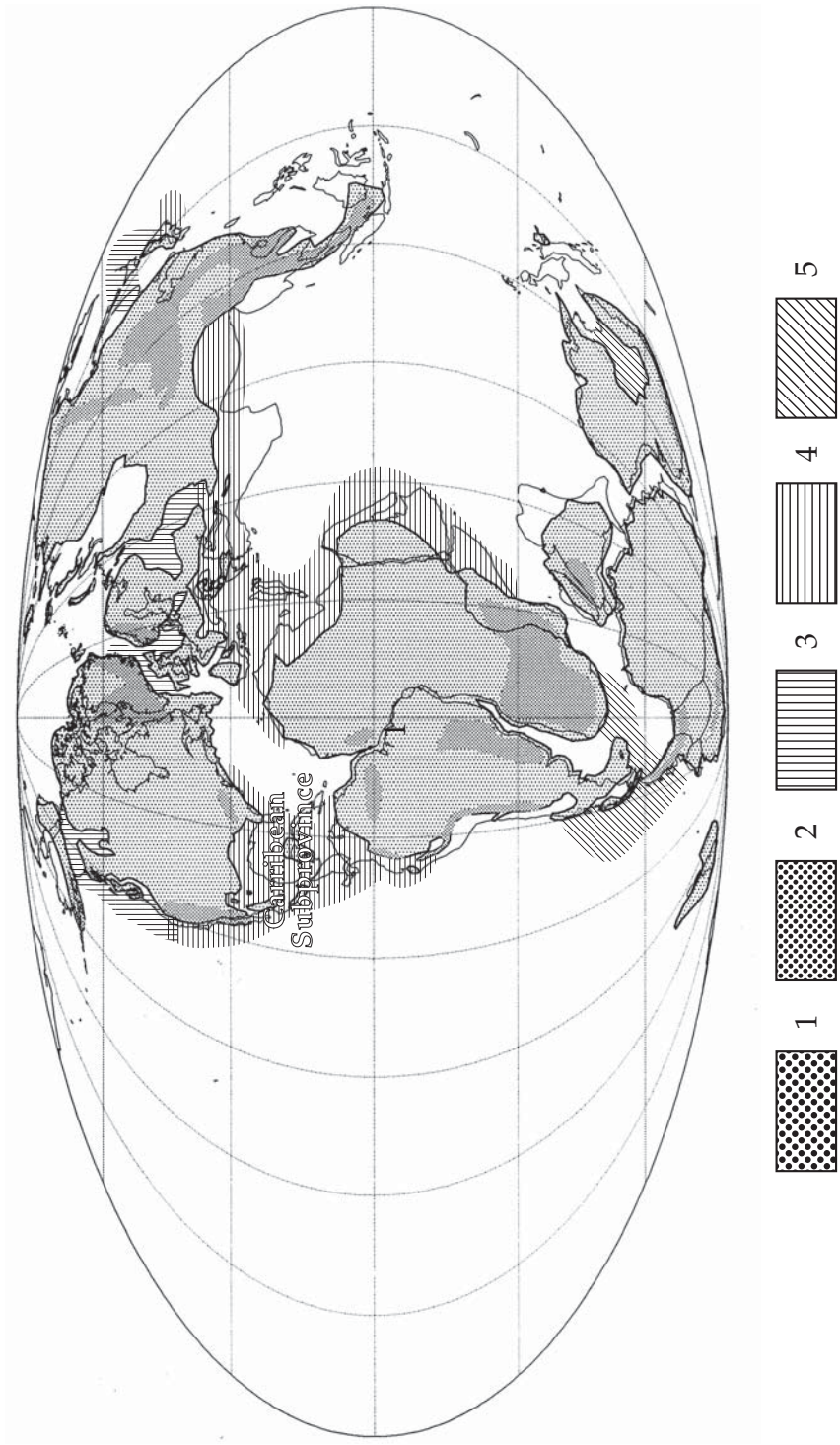


Fig. 3. Ammonite palaeobiogeography of the early Barremian.  
Key: 1 = land; 2 = Boreal Realm; 3 = Tethyan Realm; 4 = "Austral Realm"; 5 = "highlands" (background from Smith *et al.*, 1994).

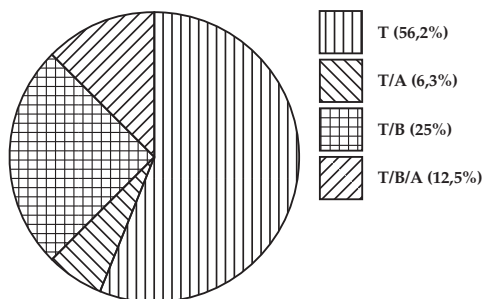


Fig. 4. Qualitative and quantitative ratio of distribution patterns of genera of the families Ancyloceratidae, Heteroceratidae, Pulchelliidae and Desmooceratidae found in the upper Barremian of Colombia. Legend see Fig. 1.

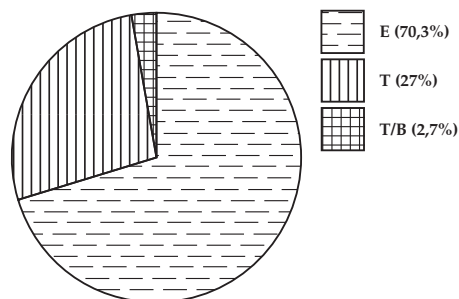


Fig. 5. Qualitative and quantitative ratio of distribution patterns of species of the families Ancyloceratidae, Heteroceratidae, Pulchelliidae and Desmooceratidae found in the upper Barremian of Colombia.

tinued into the early Aptian, when simultaneously with the next global transgression, the dispersion of Tethyan ammonites into the Boreal and 'Austral' areas increased (see below).

The biogeographic analysis of genera and species shows that among the 15 genera/subgenera documented in the upper Barremian of Colombia, eight (56.2%) are Tethyan (*Pseudocrioceras*, *Kutatissites*, *Hamulinites*, *Carstenia*, *Heinzia*, *Gerhardtia*, *Valdedorsella*, *Melchiorites*), and four (25%) are characteristic of the Tethyan Realm and the southern part of the Boreal Realm (*Hemihoplites*, *Pseudohaploceras*, *Zuercherella*, *Argvethites*). There is also one genus (*Colchidites*) (6.3%) that was distributed in the Tethyan and 'Austral' Realms, and two subgenera (12.5%) that were distributed in the Tethyan, Boreal and 'Austral' Realms (*Heteroceras*, *Paracrioceras*). The following genera, common in the Mediterranean Province, seem to be absent in Colombia; *Silesites*, *Barremites*, *Macroscephalites*. As for the species composition, among the listed 37 species from the upper Barremian of Colombia, 26 (70.3%) are endemic, ten (27.0%) occurred only in the Tethyan Realm, and only one species (2.7%) was distributed in the Tethyan and Boreal Realms (Figs. 4, 5).

During the late Barremian the North Pacific Province was characterized by *Shastrioceras* in North America and Japan. The degree of endemism in the Tethyan and Boreal faunas, however, decreased to the level of province around the Barremian-Aptian boundary. Many heteromorphic genera and aconoceratids have a wide distribution and spread into many regions of the Tethyan Realm and adjacent marginal areas of the Boreal Realm. A separate Indo-Malagasian Province cannot be recognized any longer and merged into the East Mediterranean subprovince.

The faunal interrelation between the Mediterranean province and the southernmost basins of the southern hemisphere became intensive. The data on the distribution pattern of the late Barremian family Heteroceratidae clearly proves equalization of conditions between Tethyan and 'Austral' Realms. The faunal similarity between the Mediterranean regions (e.g., Caucasus), southern Africa and Patagonia is too striking to be merely coincidental (Klinger *et al.*, 1984). The migration route of heteroceratids from the Mediterranean Province to the Patagonia can be traced along the east coast



of Africa (around the southern part of Africa) (in more detail see Klinger *et al.*, 1984, p. 49). The global dispersion of heteroceratids from the Mediterranean basin also went along three other different directions (Kakabadze, 1994, p. 207): from the Caucasian area to the east, *viz.* to the Middle Asia (*Heteroceras*, *Paraimerites*, *Colchidites*); from the west Mediterranean to the north (*Paraimerites*), *viz.* to the Volga region and to the England (*Argoethites*); and from the Mediterranean region to the west, *viz.* to the Caribbean region (*Heteroceras*, *Colchidites*), and (*Heteroceras*) from there to the north (along the west coast of North America) up to Canada and Japan (for more detail see Klinger *et al.*, 1984; Kakabadze, 1994). There are no data on the interrelation of heteroceratids between the Colombian (Caribbean) and Patagonian basins. The existence of species of the typical Tethyan genera *Kutatissites*, *Pseudocrioceras* and *Hemihoplites* in Colombia also proves the direct interrelation between the Mediterranean and the Caribbean basins in the late Barremian. The Colombian and Patagonian basins have no species in common, whilst each of these regions separately reveals a similarity in generic and species composition with the late Barremian ammonite fauna of the Mediterranean basins.

Besides the rise of the sea level, the Cretaceous climate should be taken into account as a cause for the nearly global distribution of the family Heteroceratidae, *i.e.*, the tendency to global warming is well noticeable after Neocomian times and the temperature gradient from equator to pole was not as steep as it is today (*e.g.*, Saks *et al.*, 1964; Frakes, 1979). It becomes obvious that in the late Barremian there is no principal difference in ammonite composition between the Mediterranean and Patagonia-South African regions. Judged by the late Barremian ammonite composition, the Patagonian and South African regions can even be regarded as the Austral Province of the Tethyan Realm. Another acceptable variant may be to consider the region comprising Patagonia, Alexander Island and South Africa as the northern marginal area of the 'Austral' Realm, which has transitional interrealmal (Tethyan-'Austral') features. In that case we assume that the geographic position of a typical 'Austral' Province is farther to the south and possible witnesses of this province are buried under the Antarctic ice-cap.

#### *Early Aptian*

The tendency of the equalization of conditions and, as a result, the rather close faunal similarity between the adjacent marginal areas of the Tethyan and Boreal Realms continued in the early Aptian (Förster, 1975; Klinger & Kennedy, 1977; Kakabadze, 1981). Simultaneously with the early Aptian global transgression, the biogeographic pattern with clearly differentiated Boreal and Tethyan Realms broke down rapidly (Rawson, 1981).

The significant northward migration of the Temperate-Subtropical and Subtropical-Tropical biogeographic boundaries across Mexico and Texas during Aptian-Albian times was associated with a rise of the sea level (Kauffman, 1973, 1984). We cannot identify the precise northern boundary of the Caribbean Subprovince for the early Aptian. Remarkable is the presence of early Aptian Tethyan genera; *Deshayesites* in Arizona, *Ancyloceras*, *Procheloniceras* and *Cheloniceras* in California and Mexico. Similar conditions are traced in west and east Europe, when the limits of the Mediterranean Province had significantly expanded (Kotetishvili, 1988; Baraboshkin, 1997).

On the other hand, the close faunal interrelation of the Mediterranean basin with the South Africa-Patagonian basins (Austral Province), which started in the late Barremian (see above), continued well into the Aptian (Förster, 1975; Klinger & Kennedy, 1977). The migration of *Chelonicer*s, *Costidiscus*, *Proaustralicer*s, *etc.* occurred via the same way as in the late Barremian; along the east coast of Africa and South Africa down to Patagonia. There are no reliable data on a direct faunal interrelation between the Colombian and Patagonian basins in the early Aptian.

Analysis of the early Aptian ammonite fauna of Colombia shows that among the 15 genera/subgenera there are eight (53.3%) (*Ancyloceras*, *Tonohamites*, *Proaustralicer*s, *Dufrenoyia*, *Roloboceras*, *Pseudosaynella*, *Zuercherella*, *Pseudohaploceras*) which were widely distributed in the Tethyan Realm, but also penetrated into the southern area of the Boreal Realm. There are four genera (26.7%) (*Aconeceras*, *Toxoceratoides*, *Prochelonicer*s, *Chelonicer*s) which were distributed in all Tethyan, Boreal and "Austral" Realms, two (13.3%) (*Macroscaphites*, *Melchiorites*) which are typical Tethyan and one (6.7%) (*Mon-salveicer*s) which is endemic (Fig. 6). The following genera, which are common in the Mediterranean Province, seem to be absent in Colombia; *Deshayesites* and *Audouliceras*.

As for species analysis, among 49 species/subspecies listed from the lower Aptian of Colombia, 25 species were endemic (51.0%), nine (18.4%) were characteristic of the Tethyan and Boreal Realms, two (4.1%) were spread over the Tethyan Realm, eight (16.3%) in the Boreal Realm, two (4.1%) were distributed in the Tethyan, Boreal and "Austral" Realms, two (4.1%) in the Caribbean Province, and one species (2.0%) in the "Austral Realm" (Fig. 7). So, in terms of the interrelation between the Tethyan and Boreal Realms, twelve genera/subgenera (80.0%) (out of 15) are common for both the Tethyan and Boreal Realms. As for the species/subspecies composition, endemism in Colombian basin was rather high (51.0%), though the number of common Tethyan/Boreal species was far less (22.5%).

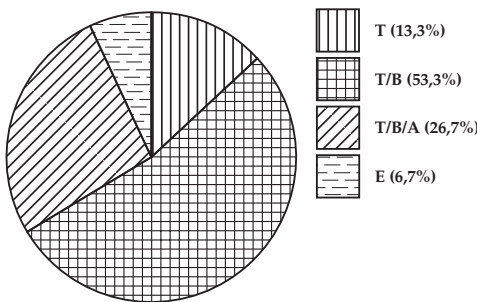


Fig. 6. Quantitative and qualitative ratio of distribution patterns of genera of the families Ancyloceratidae, Douvilleiceratidae, Desmoceratidae, Opeleliidae and Macroscaphitidae found in the lower Aptian of Colombia.

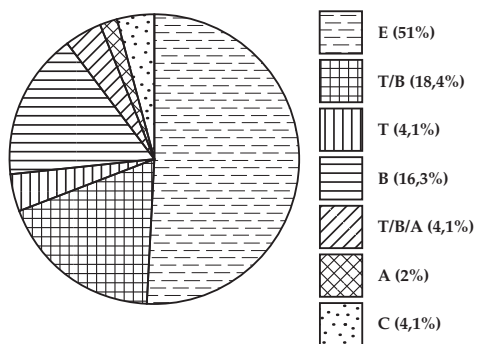


Fig. 7. Quantitative and qualitative ratio of distribution patterns of species of the families Ancyloceratidae, Douvilleiceratidae, Desmoceratidae, Opeleliidae and Macroscaphitidae found in the lower Aptian of Colombia.

*Middle/Upper Aptian*

During the middle and late Aptian, continuing change of the global environment (such as higher temperature, sea-level changes) influenced the composition of faunas. Analysis of the middle and late Aptian ammonite fauna of Colombia indicates that among the 29 genera known, six genera (20.7%) (*Gargasicerias*, *Protacanthoplites*, *Valdedorsella*, *Eodouvilleicerias*, *Melchiorites*, *Miyakoceras*) are characteristic of the Tethyan Realm, whereas eight (27.6%) (*Pseudoaustralicerias*, *Hamiticeras*, *Colombicerias*, *Acanthohoplites*, *Zuercherella*, *Hypacanthoplites*, *Pseudosaynella*, *Pseudohaploceras*) were distributed in the Tethyan Realm and in the southern part of the Boreal Realm. Moreover, eight (27.6%) genera/subgenera (*Aconecerias*, *Eogaudrycerias*, *Ammonitoceras*, *Helican-cylus*, *Tonohamites*, *Ptychoceras*, *Epicheloniceras*, *Parahoplites*) were distributed in the Boreal, Tethyan and 'Austral' Realms, one (3.4%) (*Eotetragonites*) was spread in the Tethyan and Austral Realms, two (6.9%) (*Neodeshayesites*, *Zambranoites*) were found only in the Caribbean Province and four (13.8%) (*Juandurhamiceras*, *Laqueoceras*, *Ridelites*, *Pseudoptychoceras*) were endemic (Fig. 8). Among 151 species from the middle and upper Aptian of Colombia, twelve (8.0%) were characteristic of the Tethyan Realm, 13 (8.6%) were distributed in the Tethyan and Boreal Realms, four (2.6%) in the Boreal Realm, twelve (8.0%) were distributed in the Caribbean Province, and 115 species (72.8%) were endemic (Fig. 9).

On the basis of the analysis of the distribution patterns of the Barremian and Aptian ammonite faunas in Colombia and adjacent regions, we conclude that the tendency of progressive ammonite endemism in this area lasted through the late Barremian-early Aptian and had its culmination in the middle Aptian. From the middle Aptian onwards this area, together with the other areas of the Caribbean Subprovince, became an independent Province of the Tethyan Realm. It was characterized by a distinct ammonite fauna, with numerous endemic genera/subgenera (*Juandurhamiceras*,

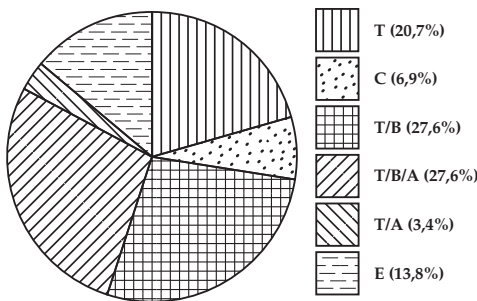


Fig. 8. Quantitative and qualitative ratio of distribution patterns of genera of the families Ancyloceratidae, Ptychoceratidae, Douvilleiceratidae, Parahoplitidae, Acanthohoplitidae, Desmoceratidae, Oppeliidae, Gaudryceratidae, Deshayesitidae and Silesitidae found in the middle and upper Aptian of Colombia.

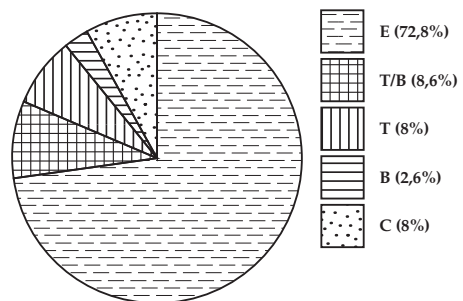


Fig. 9. Quantitative and qualitative ratio of distribution patterns of species of the families Ancyloceratidae, Ptychoceratidae, Douvilleiceratidae, Parahoplitidae, Acanthohoplitidae, Desmoceratidae, Oppeliidae, Gaudryceratidae, Deshayesitidae and Silesitidae found in the middle and upper Aptian of Colombia.

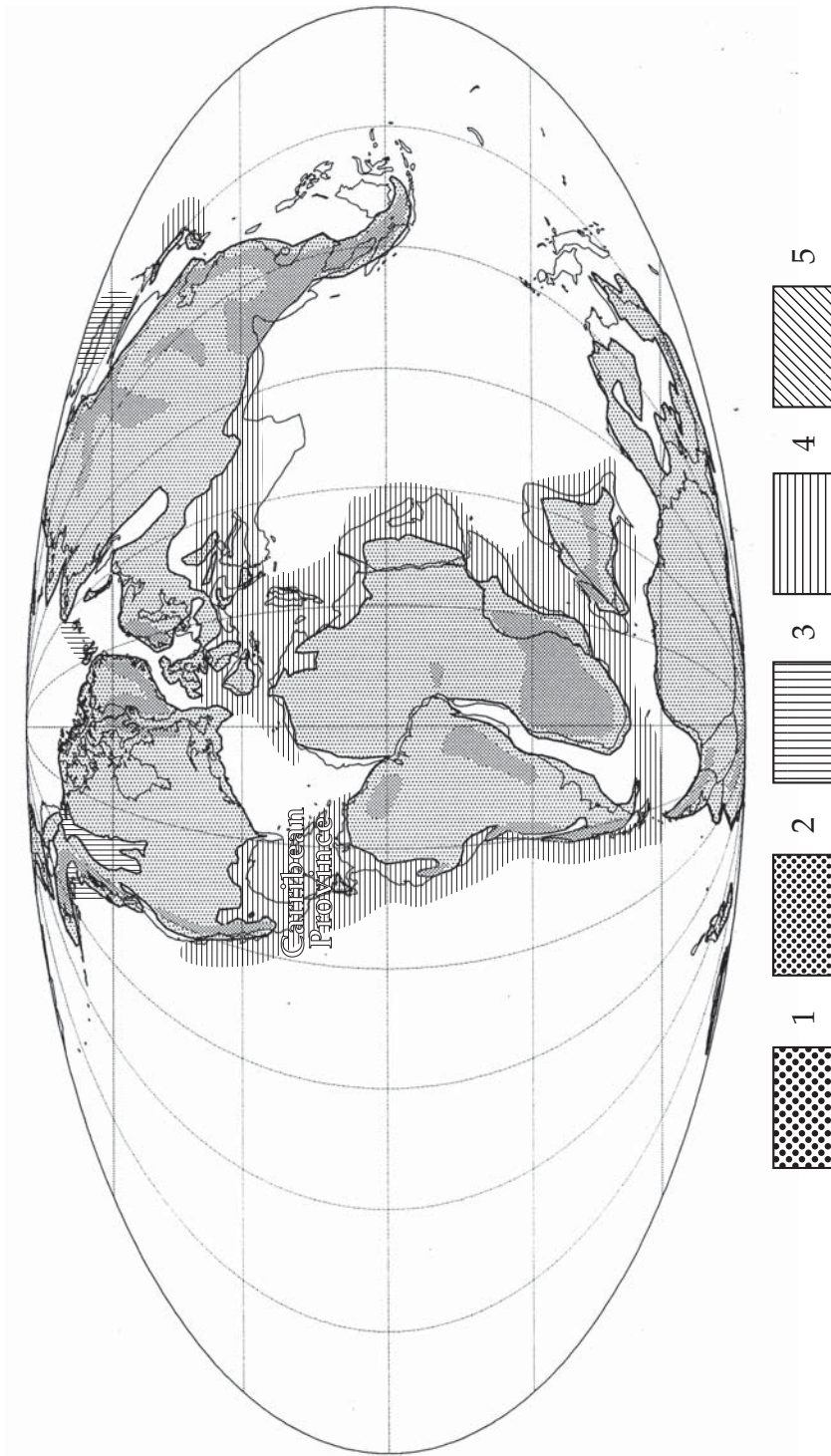


Fig. 10. Ammonite palaeobiogeography of the late Aptian. Key as in Fig. 3.

*Neodeshayesites*, *Laqueoceras*, *Zambranoites*, *Riedelites*, *Pseudoptychoceras*) and by numerous endemic species of other genera. This picture is especially distinct in Colombia, considered the core area of the Caribbean Province (Fig. 10).

*Early Albian*

In comparison with the middle/late Aptian, the early Albian strata of Colombia are characterized by a reduced number of genera, and especially species, within five families (Douvilleiceratidae, Anisoceratidae, Desmocerotidae, Phylloceratidae, Deshayesitidae). The early Albian ammonite fauna of Colombia consists of ten genera; among them three (27.3%) (*Eodouvilleiceras*, *Trochleiceras*, *Puzosia*) are characteristic of the Tethyan Realm (Mediterranean and Caribbean Provinces), five (54.5%) (*Phylloceras*, *Hypophylloceras*, *Holcophylloceras*, *Protanisoceras*, *Douvilleiceras*) have a Tethyan/Boreal distribution, one (9.1%) (*Neodeshayesites*) is known only in the Caribbean Province and another (*Carloscaceresiceras*) is endemic (Fig. 11).

There is a high percentage of endemic species in the early Albian. Among the 24 listed species, 17 (71.0%) are endemic, two (8.3%) are distributed in the Tethyan Realm, one (4.1%) only in the Caribbean Province, two (8.3%) in the Boreal Realm, and two (8.3%) are known from the lower Albian of Tethyan (Mediterranean and Caribbean Provinces) and Boreal (North European Province) Realms (Fig. 12).

The progressive northward migration of Tethyan and marginal Tethyan biotas during middle Aptian-early Albian times is obvious. In this respect the data from the Colombian area are remarkable, i.e., the occurrence of middle Aptian (*Helicancylus philadelphium* Anderson, *Hamiticeras pilsbryi* Anderson, *etc.*), late Aptian (*Acanthohoplites teres* Stoyanow) and early Albian (*Douvilleiceras mammillatum* (Schlotheim)) ammonite species in Colombia and in the southern regions of the North Pacific Province (Arizona, Oregon, Arkansas). In connection with the northward migration of the ammonite fauna in the early Albian, Young (1972) showed the episodic migration of Tethyan ammonites into central Texas. Rodda & Murphy (1992) noted that the occurrence of early Albian *D. mammillatum* Schlotheim in northeastern Brazil and north California (also *Douvilleiceras* sp. in Venezuela) suggested that this connection

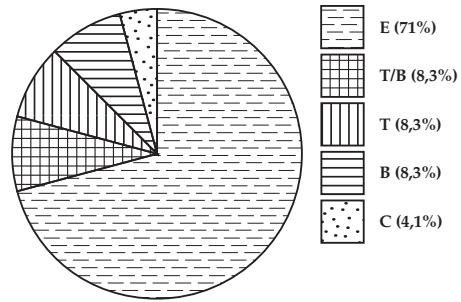
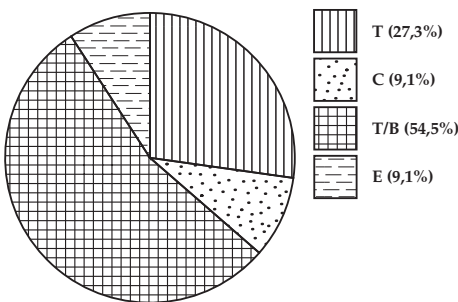


Fig. 11. Quantitative and qualitative ratio of distribution patterns of genera of the families Douvilleiceratidae, Anisoceratidae, Desmocerotidae, Phylloceratidae and Deshayesitidae found in the lower Albian of Colombia.

Fig. 12. Quantitative and qualitative ratio of distribution patterns of species of the families Douvilleiceratidae, Anisoceratidae, Desmocerotidae, Phylloceratidae and Deshayesitidae found in the lower Albian of Colombia.

may have been directly along the latitude between southern France and the west coast of America.

Besides of the ammonites, the data on the distribution pattern of some other groups (bivalves, corals) of marine organisms are even more notable; on the whole, the northward migration of the Tethyan biotas culminated in development of rudist-coral frameworks throughout central Texas by the early middle Albian (Kauffman, 1984). Thus, the Caribbean Province in the middle Aptian-early Albian time-interval embraced all Antillean Islands, California, southern and central Texas, Mexico, Trinidad, Venezuela, Colombia, Ecuador, northern Peru and the northeastern tip of Brazil (with Caribbean endemic middle/upper Aptian *Zambranoites* sp. and early Albian *Douvilleicerias mammillatum*).

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