

Cretaceous cephalopods of the Tethyan Himalaya of southern Tibet

Von

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ABSTRACT

Following a short review of the regional and stratigraphic distribution of Cretaceous cephalopods (Neocomian – Maastrichtian, especially Aptian to Cenomanian) from the Tethyan Himalaya of southern Tibet 29 taxa are described, including three new species: *Pleuroboplites (Pleuroboplites) robusticostatus*, *Lemuroceras tibeticum*, and *Tonohamites multituberculatus*.

In conclusion some palaeobiogeographic aspects are discussed. The ammonite fauna of the Middle Cretaceous shows some influence from the southern temperate realm but indicates a closer relationship to the hoplitenid faunal province of the northern temperate (boreal) realm. This suggests that during the Middle Cretaceous the Tethyan Himalaya of southern Tibet might have occupied a geographic position farther to the north, with an open marine connection to the south.

KURZFASSUNG

Ausgehend von der regionalen und stratigraphischen Verbreitung kretazischer Cephalopoden (Neokom - Maastricht) des Tethys-Himalaya von Südtibet werden 29 Gattungen und Arten beschrieben, vor allem aus dem Apt - Cenoman. Dabei werden drei neue Arten aufgestellt: *Pleuroboplites (Pleuroboplites) robusticostatus*, *Lemuroceras tibeticum* und *Tonohamites multituberculatus*.

Abschließend werden einige paläobiogeographische Zusammenhänge diskutiert. Die mittelkretazische Ammonitenfauna zeigt neben Einflüssen aus dem südlichen gemäßigten Bereich vor allem enge Beziehungen zur Hopliten-Provinz des nördlichen gemäßigten (borealen) Raumes. Insofern muß für den Tethys-Himalaya Südtibets zur Zeit der mittleren Kreide eine paläogeographische Position weiter im Norden angenommen werden, allerdings auch eine offene Verbindung nach Süden.

1. INTRODUCTION

An ammonite fauna from two localities in southern Tibet is described. Field work was carried out in 1983 and 1986, and preliminary results have been discussed at the Third Meeting of the European Union of Geosciences (EUG III) at Strasbourg in April 1985 (see HE & IMMEL 1985). For several reasons the paper could not be published earlier, although other studies have been, for example on lithostratigraphy (e.g. WILLEMS & ZANG 1993), bio- and ichnofacies (ZHOU et al. 1997), the bivalve fauna (WEN 2000), and also the palaeomagnetic results (e.g. PATZELT et al. 1996).

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2. LOCALITIES AND STRATIGRAPHY

Previous works: The first Cretaceous cephalopods (ammonites only) of southern Tibet - especially from the Gamba region - were announced by DOUVILLE (1916) who described and figured the ammonoids sampled by the British expedition to Tibet in 1903. The stratigraphic data have been published by HAYDIN (1907). In modern terms all ammonoids originate from parts of the Gamba Group (see the correlation in WFN 1987: 144). The updated systematic and stratigraphic results of DOUVILLE (1916) are presented in fig. 1. A second suite of Cretaceous ammonites was collected by the Chinese Scientific Expedition to the Mount Jolmo Lungma region (1966-1968) described and figured by ZHAO (1976). Beside these two papers only a few notes or lists of Cretaceous ammonites exist but without any description or figures, for example in MU et al. (1973: 107ff.). A recent listing of ammonoids from the Gamba Group in southern Tibet is given by WFN (1987: 133ff.) who named also some ammonoids from the Cretaceous of the more northern Gyangze area (op. cit.: 148ff.). From the younger Zongshan Formation no cephalopods are reported except a short mention in WAN (1988: 114, tab. 3).

New results: The new cephalopods described below originate from two areas in southern Tibet: Gamba and Duela. The topographic and geologic position of the two localities are shown in fig. 2. It follows a short overview of the cephalopod fauna as far as it was determinable, with its stratigraphic and tectonic implications.

2.1 GAMBA AREA

In the Gamba area cephalopods have been found in eight sections, respectively sampling points. Fig. 3 schematically shows seven of them yielding ammonites with their geographic position and age.

Section K

Several dozen fragments of specimens of ammonoids have been found. All are extremely broken, crushed and badly preserved.

Identified ammonites: A precise generic or specific assignment is not possible. Most ammonoids belong to the subfamily Neocomitinae but a few fragments could also be assigned to the family Haploceratidae, probably to *Neolissoceras* SPATH, 1923.

Age: lower Lower Cretaceous.

Section A

This section is by far the most important one, not only with respect to its duration but also to the ammonites of the Gamba Group. The great number of samples will be summarized in 11 ammonite 'levels' (figured representatives are indicated with sample numbers in brackets). The same applies to the following sections).

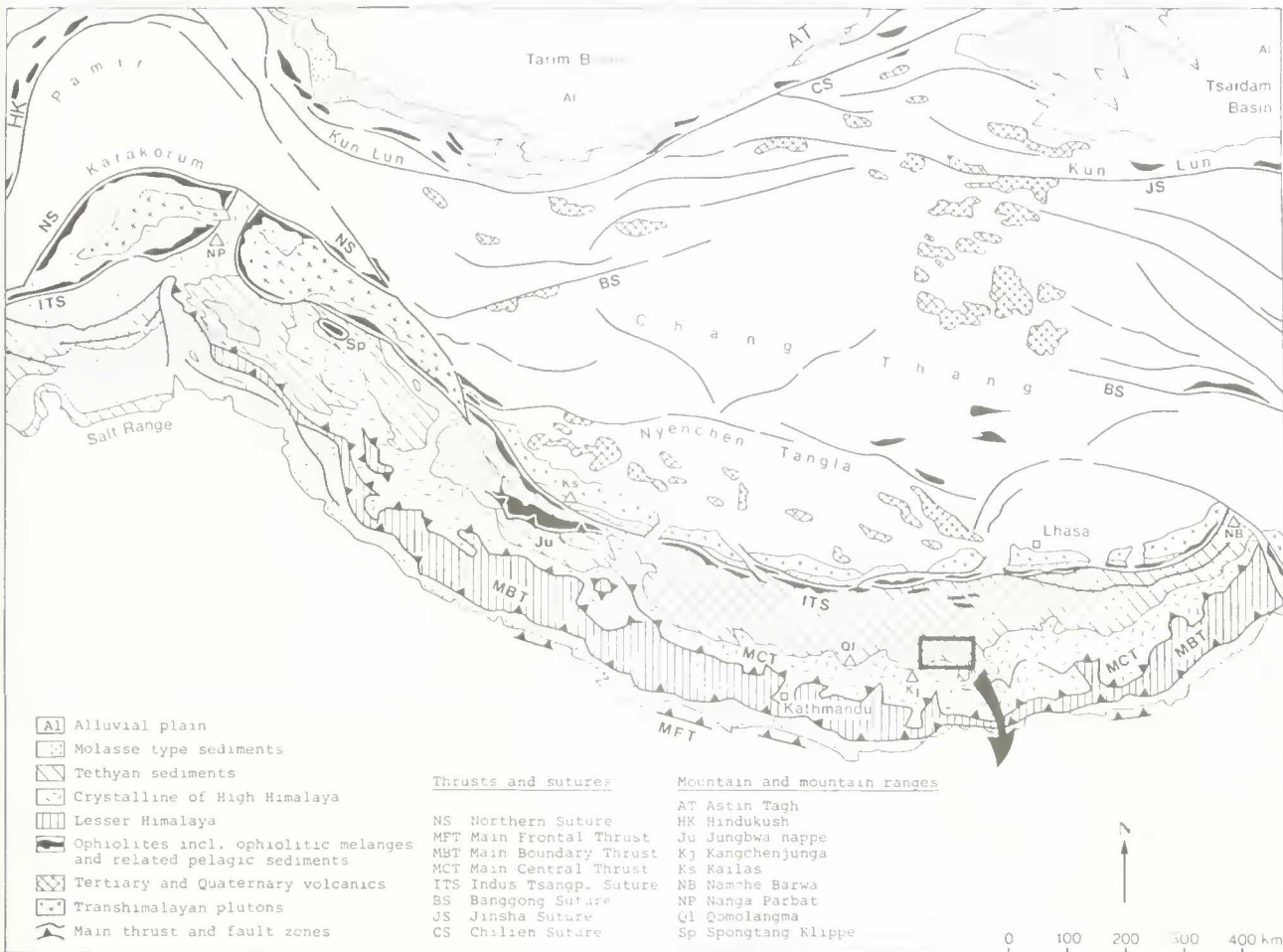
Identified ammonites:

(top)

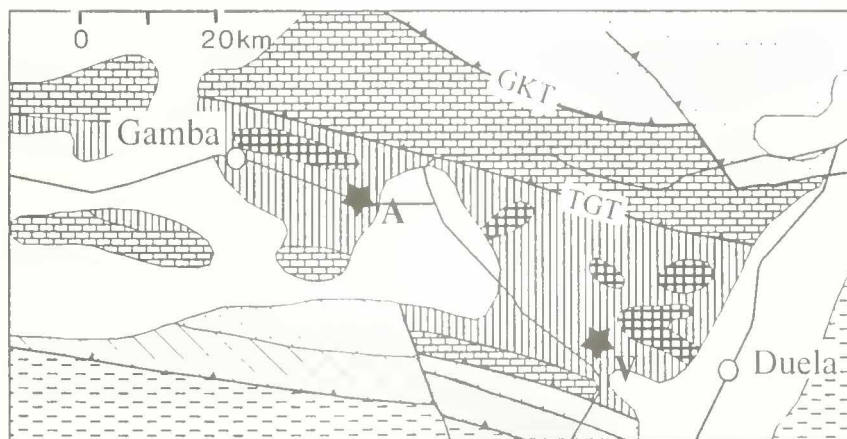
- level 11: *Hysterocheras semileve* (e.g. Af 84/1, see pl. 1, fig. 5)
Mortonoceras (?*Mortonoceras*) sp.
 undeterminable Anisoceratidae
- level 10: *Mortonoceras* (*Mortonoceras*) sp.
Goodhallites cf. *gracillimum* (e.g. Af 150/1, see pl. 3, fig. 7)
- level 9: *Cymbabophites* sp. (Af 76A/2, see pl. 1, fig. 4)
Douvillicerias sp.
- level 8: *Douvillicerias pustulosum* (e.g. Af 73A/1, see pl. 4, fig. 7)
- level 7: *Helicancylus* sp. (Af 71/6, see pl. 4, fig. 5)
Toxoceratoides aff. *royerianum* (Af 71/7, see pl. 4, fig. 6)
Tonobamutes multituberculatus (Af 71/8 and Af 71/5, see pl. 4, fig. 3, 4)
Chelonoceras (*Chelonoceras*) aff. *buxtoni* (e.g. Af 71/1, see pl. 4, fig. 8)
Colombiceras (*Colombiceras*) cf. *subpeltoceroideis* (e.g. Af 71/4, see pl. 4, fig. 2)
Parabophites trautscholdi (e.g. Af 71/10 and Af 71/11, see pl. 4, fig. 11, 12)
- level 6: *Aconoceras* (*Aconoceras*) sp. (Af 65/1, see pl. 1, fig. 3)
Chelonoceras (*Chelonoceras*) sp.

Original determination	Modern nomenclature	Cenomanian		
		L	M	U
<i>Acanthoceras Newboldi</i> (p.3;pl.1,fig.1,2,3,4)	<i>Calycoceras</i> (<i>Newboldiceras</i>) <i>newboldi</i>		—	
<i>Mantelliceras laticlavium</i> (p.4;pl.1,fig.5;pl.2,fig.1-2)	<i>Sharpoiceras laticlavium</i>	—		
<i>Mantelliceras discoideale</i> (p.4;pl.3,fig.1)	<i>Acanthoceras discoideale</i>		—	
<i>Turrilites costatus</i> (p.5;pl.3,fig.3)	<i>Turrilites costatus</i>		—	—
<i>Turrilites Wiestii</i> (p.5;pl.3,fig.2)	<i>Turrilites acutus</i>		—	—
<i>Turrilites Desnoyersi</i> (p.6;pl.3,fig.4-5)	<i>Turrilites scheuchzerianus</i>		—	—

Fig. 1: Ammonites described and figured from the Gamba Group of southern Tibet by H. DOUVILLE (1916) and their names in modern nomenclature.



a



b

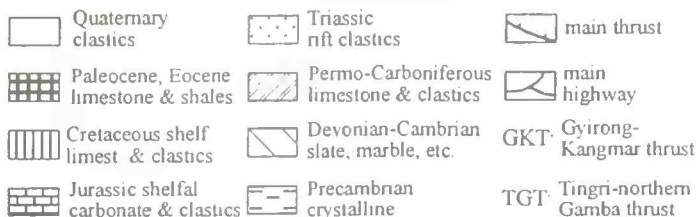


Fig. 2 a: Simplified geological map of Tibet and the Himalayas (modified after GANSSER 1983; fig. 3)
 2 b: geological map of the investigation area with the location of the sections A and V (after PAVETTI et al. 1996; fig. 1b). For the location of all other sections and sampling points of the Gamba area see fig. 3.

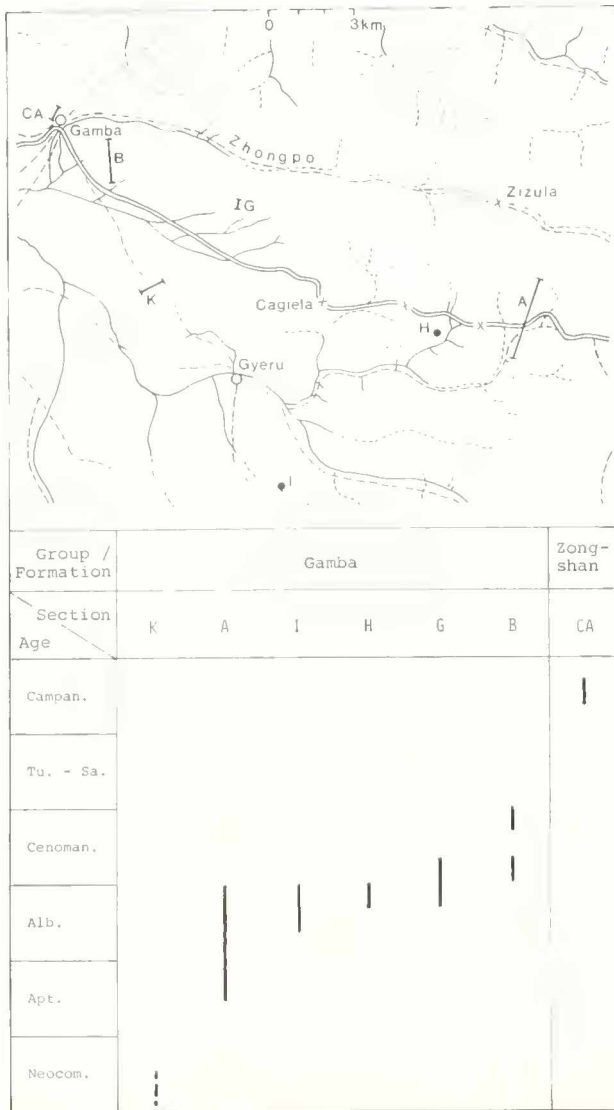


Fig. 3: Topographic map of the Gamba area with the location of the sections and sampling points. The stratigraphic ages are that provided by the ammonite fauna. Nearly all ammonites are from the Gamba Group, with only few exceptions, which are from the younger Zongshan Formation.

- level 5: *Calliboplites tetragonus*
 level 4: *Calliboplites tetragonus*
Calliboplites cf. glossonotus (e.g. Af 39/1, see pl. 1, fig. 7)
 level 3: *Calliboplites tetragonus* (e.g. Af 172/1, see pl. 1, fig. 6)
 level 2: *Lemuroceras tibeticum* (Af 18/1, see pl. 1, fig. 10)
 level 1: *Lemuroceras tibeticum* (Af 184/1, see pl. 1, fig. 11)
 (bottom)

Age: The stratigraphic position of these ammonite horizons is given in fig. 4. They range, including some gaps, from the Upper Aptian to the uppermost Albian. However, there is clearly a thrust between level 5 and 6 where the stratigraphic age is shifted back by one stage. Also some imbrication structures are likely, for example between levels 1 and 2 and also between levels 8 and 9.

Section I

This section was not measured, so it is regarded here as a single sampling point.

Identified ammonites:

Calliboplites cf. tetragonus

Pleuroboplites (Pleuroboplites) robusticostatus (Hf 1/1 and Hf 1/3, see pl. 1, fig. 8, 9)

Proturritoides sp. (Hf 2/1, see pl. 4, fig. 13)

Age: Middle - Upper Albian.

Section H

This section was not measured, so it is regarded here as a single sampling point.

Identified ammonites:

Calliboplites sp.

Pleuroboplites (Pleuroboplites) sp.

Age: Upper Albian.

Section G

Several meters above the measured section some isolated ammonites have been found.

Identified ammonites:

Mortonoceras (Durnovantes) kilian (Gf 16/1, see pl. 3, fig. 1)

Mantelliceras sp.

Age: Upper Albian - Lower Cenomanian.

Section B

There are three horizons from which ammonites have been determined.

Identified ammonites:

(top)

Eucalycoceras colligom (e.g. Bf 74/1, see pl. 3, fig. 3)

Mantelliceras cf. mantelli (Bf 35/1, see pl. 3, fig. 6)

Mantelliceras lymense (Bf. 31/1, see pl. 3, fig. 5)

(bottom)

Age: Lower and Upper Cenomanian.

Section CA

The two ammonites out of one horizon of this section are the only ones found in the Zongshan Formation.

Identified ammonite:

Submortonoceras tenuicostulatum (e.g. CAf 74/1, see pl. 4, fig. 1)

Age: Middle Campanian.

Section D

Two nautilids originate from this section.

Identified cephalopod:

Pseudococeras aff. largilliertianum (e.g. Df 147/1, see pl. 1, fig. 1)

Age: Maastrichtian according to benthonic foraminifera.

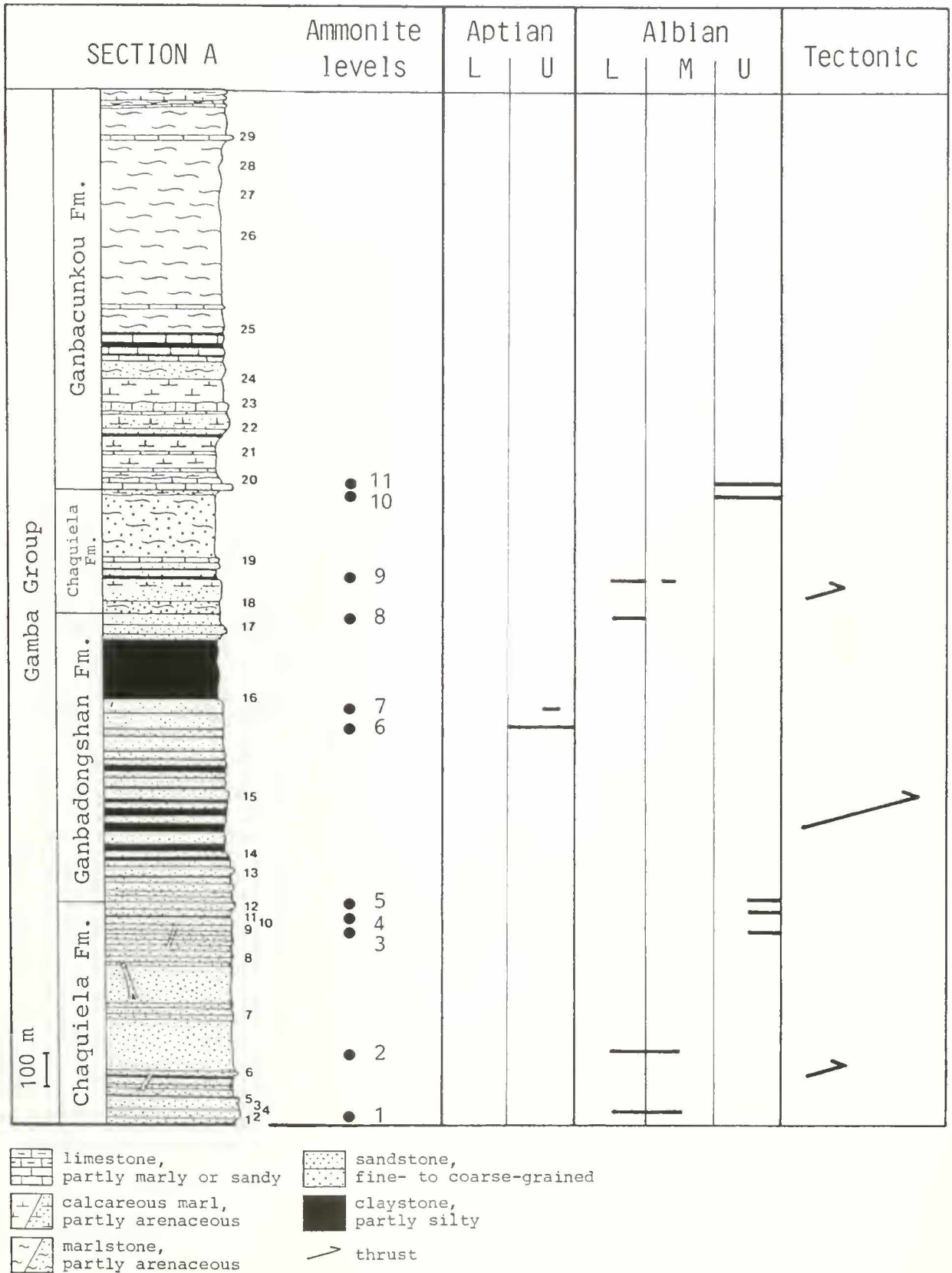


Fig. 4: Section A (Gamba area, for location see figure 2 and 3) with eleven ammonite 'levels', their stratigraphic age and tectonic implication (the sample numbers correspond with those by WILLEMS & ZHANG 1993: fig 3). The Gamba Group is divided into three formations. In ascending order these are the Ganbadongshan Formation (Fm. I), the Chaquiela Formation (Fm. II) and the Ganbacunkou Formation (Fm. III) (see ZHOU et al. 1997: 5, for different spelling see WEN 2000: 2).

In fig. 5 the ammonite taxa of the Gamba Group and their stratigraphic ages are summarized. Comparison with previous studies (see especially fig. 1) shows a wider systematic and stratigraphic spectrum, but also a poor documentation for the Cenomanian. In part, however, this could be due to the fact that some material, especially a small collection of turrilitids, got lost at the transport from Nanjing to Munich.

2.2 DUEL AREA

In the only measured section at the Zala valley of Duela area (Section V) all cephalopods originate from the lower part, from a series of thick layers of limestone, with a total thickness of three and a half meters. This series is composed of a calcareous facies within the Gamba Group that can not be compared directly with any sequence of the Gamba Group at the type locality.

Identified cephalopods:

Cymatoceras kaycanus (Vf 16/2, see pl. 1, fig. 2)

Mortonoceras (*Mortonoceras*) *intermedium* (Vf 17/1, see pl. 2, fig. 4)

Mortonoceras (*Mortonoceras*) *pricei* (Vf 15/1, see pl. 2, fig. 2)

Mortonoceras (*Mortonoceras*) *rostratum* (e.g. Vf 16/1, see pl. 2, fig. 3)

Mortonoceras (*Deiradoceras*) *bispinosum* (Vf 16/3, see pl. 2, fig. 1)

Mortonoceras (*Deiradoceras*) *devonense* (e.g. Vf 17/3, see pl. 3, fig. 4)

Goodhallites procerum (Vf 17/2, see pl. 3, fig. 2)

It should be noted that all ammonites belong to the subfamily Mortoniceratinae which is rare in the Gamba area, indicating that this subfamily preferred a calcareous facies rather than the mud-dominated siliciclastic facies of the typical Gamba Group.

Age: Upper Albian.

Ammonites (Gamba Group)	Aptian		Albian			Cenomanian		
	L	U	L	M	U	L	M	U
<i>Aconeceras</i> (<i>Aconeceras</i>) sp.			-					
<i>Cymatoceras</i> sp.								
<i>Lemuroceras tibeticum</i> n.sp.								
<i>Pleurohoplites</i> (<i>Pleurohoplites</i>) <i>robusticostatus</i> n.sp.								
<i>Callihoplites tetragonus</i>								
<i>Callihoplites</i> cf. <i>glossonotus</i>								
<i>Hysteroceras semileve</i>								
<i>Mortonoceras</i> (<i>Mortonoceras</i>) <i>intermedium</i>								
<i>Mortonoceras</i> (<i>Mortonoceras</i>) <i>pricei</i>								
<i>Mortonoceras</i> (<i>Mortonoceras</i>) <i>rostratum</i>								
<i>Mortonoceras</i> (<i>Deiradoceras</i>) <i>bispinosum</i>								
<i>Mortonoceras</i> (<i>Deiradoceras</i>) <i>devonense</i>								
<i>Mortonoceras</i> (<i>Durnovarites</i>) <i>kiliani</i>								
<i>Goodhallites procerum</i>								
<i>Goodhallites</i> cf. <i>gracillimum</i>								
<i>Mantelliceras</i> cf. <i>mantelli</i>								
<i>Mantelliceras lymense</i>								
<i>Eucalycoceras collignoni</i>								
<i>Toxoceratoides</i> aff. <i>royerianum</i>								
<i>Tonohamites multituberculatus</i> n.sp.								
<i>Helicancylus</i> sp.								
<i>Proturrilitoides</i> sp.								
<i>Chelonoceras</i> (<i>Chelonoceras</i>) aff. <i>buxtorfi</i>								
<i>Douvilleiceras pustulosum</i>								
<i>Colombiceras</i> (<i>Colombiceras</i>) cf. <i>subpeltocerooides</i>								
<i>Parahoplites trautscholdi</i>								

Fig. 5: The ammonites of the Gamba Group at Gamba and Duela area and their stratigraphic distribution.

3. SYSTEMATIC DESCRIPTION

The classification of the ammonoids follows the outline of WRIGHT (1996) in Part L of the Treatise on Invertebrate Paleontology (Mollusca 4, revised: Cretaceous Ammonoidea). All originals are provisionally deposited in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

The measurements of specimens are given in millimeters. The abbreviations are as follows:

D = diameter

Wh = whorl height

Wb = whorl breadth

Wh/Wb = ratio of whorl height to whorl breadth

U = umbilical diameter

Figures in parentheses are measurements as a percentage of total diameter.

The suture terminology is following KUFFMANN & WILDMANN (1970):

I = Internal lobe

U = Umbilical lobe

L = Lateral lobe

E = External lobe

Class Cephalopoda CUVIER, 1797

Subclass Nautiloidea AGASSIZ, 1847

Order Nautilida AGASSIZ, 1847

Superfamily Nautilaceae DE BLAINVILLE, 1825

Family Nautilidae DE BLAINVILLE, 1825

Genus *Pseudocnoceras* SPATH, 1927

Type species: *Pseudocnoceras largilliertianum* (D'ORBIGNY, 1840)

Pseudocnoceras aff. *largilliertianum* (D'ORBIGNY, 1840)
(Pl. 1, Fig. 1)

Material: Two isolated fragments from the higher part of the Zongshan Formation (Section D).

Description: The specimens are incomplete, no exact measurements can be given. The maximum diameter will be approximately 140 mm, the whorl section is broad and well rounded. The umbilicus is open, the umbilical wall nearly vertical. The diameter of the umbilicus may be nearly 15% of the total diameter. No sculpture is visible. The suture shows a broad and shallow lateral lobe and is more or less straight across the venter.

Discussion: The smooth shell, the open and steep umbilicus, and the simple suture line show clearly that the genus is *Pseudocnoceras*. This genus has only few species, eight are listed in KUMMEL (1956: 384f.). The fragments best correspond with the type species, *C. largilliertianum*. But in contrast to examples of this species, the Tibetan specimens seem to have a broader cross-section and the flanks are less flattened.

Occurrence: The genus *Pseudocnoceras* has been described in Europe from the Cretaceous of England to the

Crimea and also from the upper Cretaceous of Libya and the southern USA. According to WILDMANN & SCHNEIDER (1979: 654) *P. largilliertianum* is a species of the West-European Cenomanian, but since then it has been reported also from New Mexico (COBBAN & KENNEDY 1994). The isolated fragments of the Gamba area have been sampled in sediments of Maastrichtian age.

Family Cymatoceratidae SPATH, 1927

Genus *Cymatoceras* HYATT, 1884

Type species: *Cymatoceras pseudoelegans* (D'ORBIGNY, 1840)

Cymatoceras kayeanus (BLAINFORD, 1861)

(Pl. 1, Fig. 2)

1951 *Cymatoceras kayei* BLAINF. = COLLIGNON: 13 (with synonymy).

Material: One isolated fragment from Duela (Section V).

Description: The incomplete but nearly not deformed specimen contains half a whorl of the phragmocon. The measurements will be compared with those of a specimen of comparable size, described by SPENGLER (1910: 127f., specimen b) from the Cretaceous of South India.

	D	Wh	Wb	Wh/Wb	U
Vf 16/2	82	46(0.56)	49(0.60)	0.94	8(0.10)
SPENGLER (1910) 78	44.4(0.57)	44.5(0.57)	1.00	8.4(0.11)	

The coiling is moderately involute, the external side broadly rounded, the flanks are slightly flattened, the umbilical shoulders narrowly rounded. Nearly no sculpture is visible, only nearby the umbilical shoulder there exist first signs of relatively broad ribs. The suture lines are slightly curved, they show a wide and shallow lateral lobe, but cross the external side more or less straight. The half whorl shows approximately 9-10 suture lines.

Discussion: The tight coiling and the first signs of ribbing indicate that the genus is *Cymatoceras*. The typical ribs are not visible, but according to SPENGLER (1910: 128) they produce 'erst in einem vorgeschrittenen Wachstumsstadium auch Eindrücke auf dem Steinkern'.

Within the genus *Cymatoceras* there exists an excellent correspondence with the species *C. kayeanus* concerning the measurements as well as the number and curvature of the suture lines. *C. kayeanus* differs from the closely related species *C. radiatus* (J. SOWERBY, 1822) and *C. albensis* (D'ORBIGNY, 1850) especially in having more septa per whorl and contrary to the species *C. virgatus* (SPENGLER, 1910) the suture lines run straight across the venter.

Occurrence: *C. kayeanus* has been described from the middle and upper Albian of India and Madagascar. According to BASSE (1931: 9) the species has been found also in the lower Turonian of Madagascar. The Tibetan specimen comes from sediments of Upper Albian age.

Subclass Ammonoidea ZITTEL, 1884

Order Ammonitida AGASSIZ, 1847

Suborder Ammonitina HYATT, 1889

Superfamily Haplocerataceae ZITTEL, 1884

Family Oppeliidae H. DOUVILLÉ, 1890

Subfamily Aconeceratinae SPATH, 1923

Genus *Aconecerus* HYATT, 1903

Subgenus *Aconecerus* (*Aconecerus*) HYATT, 1903

Type species: *A. (Aconecerus) nisus* (D'ORBIGNY, 1841)

Aconecerus (*Aconecerus*) sp.

(Pl. 1, fig. 3, Text-fig. 6)

Material: One crushed and corroded specimen from the Ganbadongshan Formation of the Gamba Group (Section A).

Description: The crushed specimen probably had a diameter of less than 45 mm, but no exact measurements can be given. The coiling is very involute with a small steep-sided umbilicus. The whorl section is high and strongly compressed, the flanks are distinctly flattened and the venter is fastigate. There exist dense weak striae on the flanks, which are sigmoidal to slightly falcoid on the outer part. The suture line is highly differentiated with deep narrow trifid lobes (fig. 6).

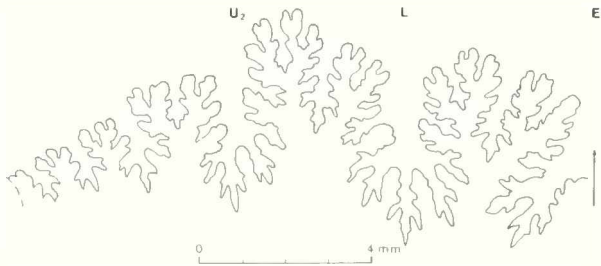


Fig. 6: Suture line of *Aconecerus* (*Aconecerus*) sp. (specimen Af 65/1, see also pl. 1, fig. 3).

Discussion: Because of the incompleteness and the bad preservation of the specimen it seems somewhat uncertain if the subgenus is *A. (Aconecerus)* or *A. (Sanmartinoceras)* BONARELLI, 1921. But the feeble ornament and the highly differentiated suture line correspond better with *A. (Aconecerus)*. KENNEDY & KLINGER (1979: 117) give a list of species referred to this subgenus, but the poor preservation of the Tibetan specimen will not allow an exact identification with one of them.

Occurrence: *A. (Aconecerus)* has been described widely from the Aptian and also the Lower Albian of western Europe, the former USSR, Nepal, northern Africa, Madagascar, South Africa and Australia. The specimen of southern Tibet is from the Upper Aptian.

Superfamily Desmocerataceae ZITTEL, 1895

Family Cleoniceratidae WHITEHOUSE, 1926

Genus *Cymaboplites* SPATH, 1922

Type species: *Cymaboplites kerenskianus* (BOGOSLOWSKY, 1902)

Cymaboplites sp.

(Pl. 1, Fig. 4, Text-fig. 7)

Material: One single specimen from the basis of the Chaquiela Formation of Gamba Group (Section A).

Description: The somewhat corroded specimen has a diameter of 50 mm. The coiling is rather evolute, the umbilicus nearly 20 mm (0.40). The cross section is compressed, with flat flanks, a rounded umbilical edge and also a rounded and somewhat flattened outer side.

The dense and thin ribs are projected forward on the lower part of the flank, they are sinuous and also slightly projected forward on the external side. The ribs start with weak and radially elongated nodes and branch often at the flanks. Also some intercalatories exist. Passing to the outer side the ribs are slightly thickening but weaker again on the external side.

Plate 1

Fig. 1: *Pseudocnoceras* aff. *largillertianum* (D'ORBIGNY); Section D (Zongshan Formation, Df 147/1); x 2/3.

Fig. 2: *Cymatoceras kayeanus* (BLANEFORD); Section V (Gamba Group at Duola, Vf 16/2); a: lateral view, b: frontal view; x 1.

Fig. 3: *Aconecerus* (*Aconecerus*) sp.; Section A (Ganbadongshan Formation of Gamba Group, Af 65/1); x 1.

Fig. 4: *Cymaboplites* sp.; Section A (Chaquiela Formation of Gamba Group, Af 76A/2); x 1.

Fig. 5: *Hysterocherus senileve* HAAS; Section A (Chaquiela Formation of Gamba Group, Af 84/1); x 2.

Fig. 6: *Calliboplites tetragonus* (SEELY); Section A (Chaquiela Formation of Gamba Group, Af 172/1); x 1.

Fig. 7: *Calliboplites* cf. *glossomotus* (SEELY); Section A (Chaquiela Formation of Gamba Group, Af 39/1); x 1.

Fig. 8: *Pleuroboplites* (*Pleuroboplites*) *robusticostatus* n. sp.; Holotype (H 1/1); Section I (Chaquiela Formation of Gamba Group); x 1.

Fig. 9: *Pleuroboplites* (*Pleuroboplites*) *robusticostatus* n. sp.; Paratype (Pf 1/3); Section I (Chaquiela Formation of Gamba Group); x 1.

Fig. 10: *Lemiroceras tibeticum* n. sp.; Holotype (Af 18/1); Section A (Chaquiela Formation of Gamba Group); a: lateral view, b: ventral view; x 1.

Fig. 11: *Lemiroceras tibeticum* n. sp.; Paratype (Af 184/1); Section A (Chaquiela Formation of Gamba Group); x 1.

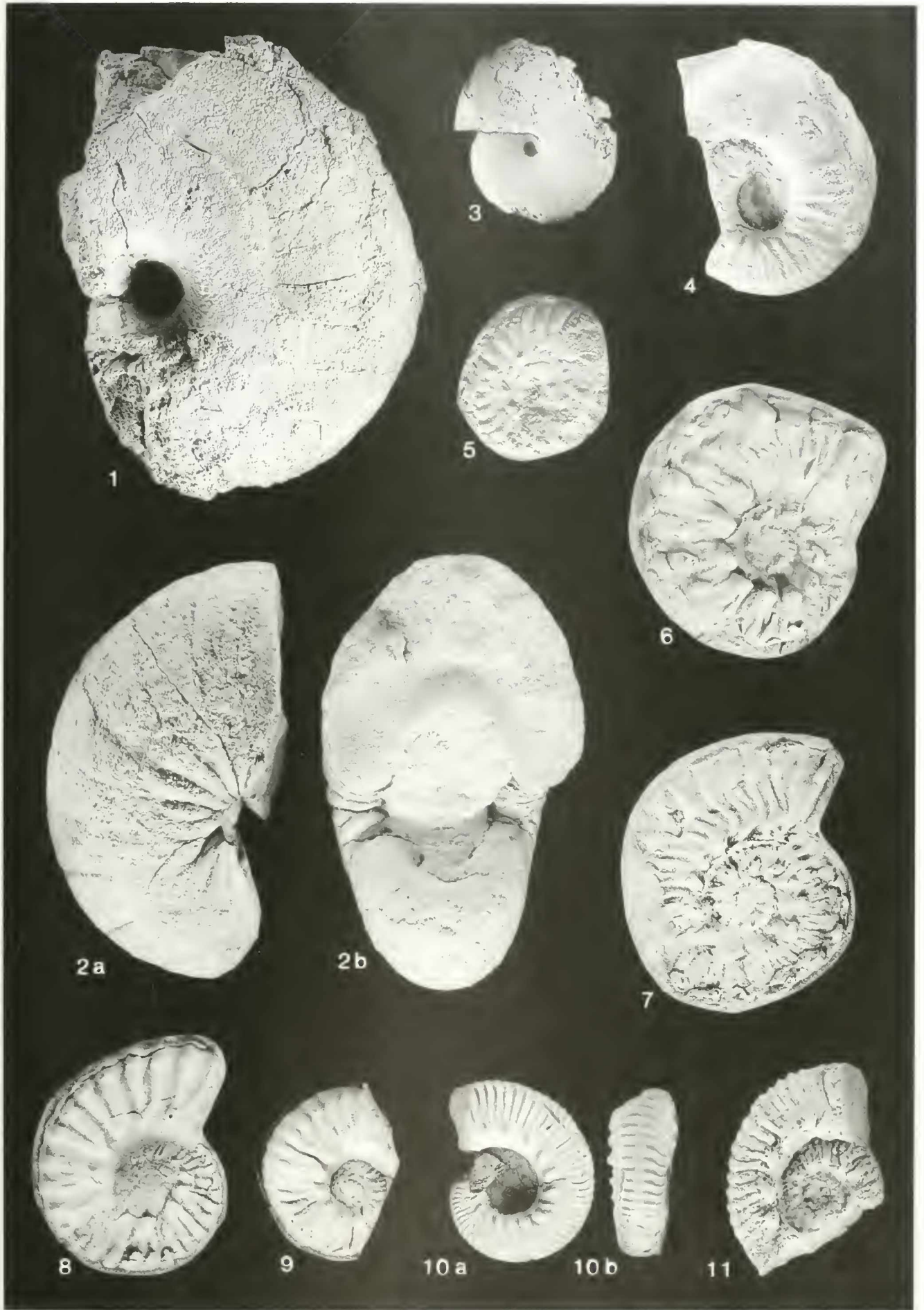




Fig. 7: Suture line of *Cymabophites* sp. (specimen Af 76A/2, see also pl. 1, fig. 4).

The suture line shows some details (fig. 7), especially the broad external lobe, the likewise broad trifold lateral lobe and the much smaller and simpler umbilical lobes.

Discussion: The specimen is a typical *Cymabophites* in size, coiling, shape and especially in the sculpture. This genus is very close to *Lemuroceras* SPATH, 1942, which is according to JELIŹKY (1964: 80) 'a junior synonym of *Cymabophites*'. But already CASEY (1961: 167) has pointed out some morphological differences between the two genera. So in *Cymabophites* the ribs are weaker and the primary ribs are directed more radially and not so oblique in the lower part of the flanks.

The Tibetan species differs from all known species of *Cymabophites*. For example, in contrast to the type species, *C. kerenskianus*, the coiling is more evolute, the ribbing on the outer part of the whorl is more dense, and the ribs are commonly bifurcating at the lower flank while in *C. kerenskianus* the ribs are often singles. Probably the Tibetan specimen is a new species, but because of its poor preservation it seems better to describe it in open nomenclature.

Occurrence: Originally the genus was thought to be of Lower Albian or Middle Albian age (WRIGHT 1957: L400), but in a short revision by CASEY (1966: 551) 'the Lower Albian dating of *Cymabophites*' is confirmed. Especially there is an association with *Leymeriella tardefurcata* (LEYMERIE, in D'ORBIGNY 1841), the index species for the lower Lower Albian. The genus is best known from the former central (type) and southern USSR. Furthermore a 'septate fragment' (CASEY 1961: 168) from England and some small, mostly fragmented specimens from Canada (JELIŹKY 1964: pl. 24, fig. 10; pl. 26, fig. 6, 10) have been described.

Genus *Lemuroceras* SPATH, 1942

Type species: *Lemuroceras aburense* (SPATH, 1933)

Lemuroceras tibeticum n. sp.

(Pl. 1, Fig. 10, 11, Text-fig. 8)

Holotype: Af 18/1.

Derivatio nominis: The name refers to the region where the species was found.

Locus typicus: South Tibet, area of Gamba, lower part of section A.

Stratum typicum: Gamba Group, basal part of the Chaquiela Formation, probably within the range of upper Lower Albian to lower Middle Albian.

Diagnosis: *Lemuroceras* with evolute coiling, subquadrate, only slightly compressed whorl section and dense ribbing.

Material: One good preserved and only a little corroded specimen from the basal Chaquiela Formation of the Gamba Group (Section A). Another broken and somewhat crushed specimen, probably the same species, is from the same section and formation, from a level 150 m deeper in the Chaquiela Formation.

Description: The holotype (pl. 1, fig. 10) consists of almost one whorl. The following measurements can be given:

	D	Wh	Wb	Wh/Wb	U
Af 18/1	36	12.5 (0.35)	12 (0.33)	1.05	13 (0.36)

The coiling is rather evolute, the whorl height increases slowly. The whorl section is subquadrate, slightly compressed with flat and somewhat converging flanks and a tabulate external side. The greatest thickness of the whorl is at the distinct and slightly elongated umbilical tubercles. There exist nine at the last half whorl.

At each umbilical tubercle three, sometimes only two, ribs are bundled. Somewhat irregularly between two bundles a further rib is intercalated, starting at the lower part of the flank. All ribs are slightly sinuous on the flanks and straight across the external side. There are approximately 35 ribs on the last half whorl. The suture line shows a prominent broad and deep bifid lateral lobe (fig. 8).

The second specimen (pl. 1, fig. 11) is less well preserved. The maximum diameter was approximately 50 mm but no exact measurements can be given. Coiling, whorl section and type of ornamentation seem to be identical with the holotype. Only the umbilical tubercles and also the ribs are somewhat stronger. But this ought to be because of its later ontogenetic stage.

Discussion: The specimens belong to *Lemuroceras*, which has close relationships with the genus *Cymabophites* SPATH, 1922 (see there). Characteristics for *Lemuroceras* are the strong ribbing and the obliquity of the elongated umbilical nodes. Also the slow increase of whorl height is a feature of *Lemuroceras* rather than of *Cymabophites*.

Within the genus *Lemuroceras* the Tibetan material can not be identified with one of the known species. The combination of evolute coiling, subquadrate whorl section and dense ribbing is unique and may be reason enough to establish a new species.

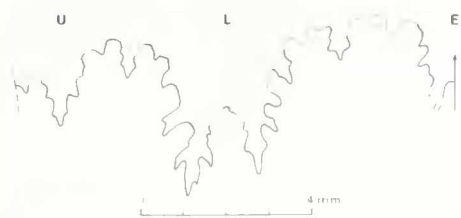


Fig. 8: Suture line of *Lemuroceras tibeticum* n. sp. holotype, specimen Af 18/1, see also pl. 1, fig. 10).

The closest affinities exist to *L. spathi* COLLIGNON, 1949 and *L. umbilicatum* COLLIGNON, 1963. The latter has been regarded by its author as a variation (subspecies?) of *L. spathi* (see COLLIGNON 1963: 97). *L. spathi* has a comparable dense ribbing but a more involute coiling and a clearly more compressed whorl section (see the measurements in COLLIGNON 1949: 67). In *L. umbilicatum* the coiling is comparable to *L. tibeticum* ($U = 0.34$) but also the ribbing is less dense. Only in *L. dubium* COLLIGNON, 1949 the whorl section ($Wh/Wb = 1.0$) is comparable but this species has also a closer coiling and the ribbing is much coarser.

Occurrence: From *L. tibeticum* only isolated specimens exist from southern Tibet. The stratigraphic position is presumably within the upper Lower Albian to lower Middle Albian interval - in accordance with the known stratigraphic range of the genus.

Superfamily Hoplitaceae H. DOUVILLE, 1890

Family Hoplitidae H. DOUVILLE, 1890

Subfamily Anahoplitinae BRISTROFFER, 1947

Genus *Pleuroboplites* SPATH, 1921

Subgenus *Pleuroboplites* (*Pleuroboplites*) SPATH, 1921

Type species: *P. (Pleuroboplites) renauxianus* (D'ORBIGNY, 1840)

Pleuroboplites (*Pleuroboplites*) *robusticostatus* n. sp.

(Pl. 1, Fig. 8, 9)

Holotype: If 1/1.

Derivatio nominis: The name refers to the strong ribs which are unusual in the subgenus.

Locus typicus: South Tibet, area of Gamba, section I.

Stratum typicum: Chaquiela Formation of Gamba Group, probably Upper Albian.

Diagnosis: *P. (Pleuroboplites)* with a relatively dense ribbing. Ribs strong and rounded, crossing the external side without interruption.

Material: From the Gamba Group section I (not measured) four specimens belong to the subgenus *P. (Pleuroboplites)*. Two of them can be identified as belonging to a new species. Both of these are preserved as external moulds of which casts have been made.

Description: The holotype (pl. 1, fig. 8) has a maximum diameter of 46 mm. The coiling is rather evolute, the umbilicus is 16 mm (0.35) wide. The cross section is compressed with flattened flanks. The greatest thickness is at the umbilical tubercles, the external side is fastigate. Due to poor preservation no exact measurements can be given.

At the umbilical edge of the last whorl arise 13 somewhat elongated umbilical tubercles running oblique to the umbilical edge. At each two strong and rounded ribs start, the one cross the flank straight, the other is convex at the inner flank and straight on the outer flank. On the innermost part single ribs without umbilical tubercles are sometimes intercalated. All ribs bear strong tubercles which have a tendency to be clavi. The ribs are weakened at the external side but are not interrupted. From the suture line nothing is visible.

The second specimen (pl. 1, fig. 9) probably is an inner whorl of the same species, with a diameter of 32 mm. At this earlier stage the coiling is the same, the umbilicus 11 mm (0.34). The external side seems to be more rounded but is also subcarinate, the ribbing is somewhat denser with more intermediate ribs. The ribs are less straight and more flexuous and are also weakened at the external side.

Discussion: The specimens have characteristics of both subgenera of *Pleuroboplites*, *P. (Pleuroboplites)* and *P. (Arrhaphoceras)* WHITEHOUSE, 1927. The compressed whorl section and the persistence of the external tubercles are typical of *P. (Pleuroboplites)* but the ribs which cross the external side without interruption are more a feature of *P. (Arrhaphoceras)*. This shows the close relationship between both forms which are regarded here as subgenera following WRIGHT (1957: L398 and 1996: 117) rather than two separated genera as listed by KENNEDY & HANCOCK (1978: V10).

Within *P. (Pleuroboplites)* the ornamentation with strong and rounded ribs, which cross straight the flanks and also the external side without interruption, is quite different to all known species. In the type species, *P. (P.) renauxianus*, the ribs are finer, concave and interrupted on the external side. *P. (P.) epigonus* SPATH, 1928 has also strong ribs. But this hardly known species has a wider ribbing and a subtabulate external side where the ribs also are interrupted.

Occurrence: *P. (P.) robusticostatus* is known only from the Upper Albian of southern Tibet. The stratigraphic range is suggested only because this subgenus is constricted to this period of time.

Subfamily Hoplitinae H. DOUVILLE, 1910

Genus *Calliboplites* SPATH, 1925

Type species: *Calliboplites catillus* (J. DE C. SOWERBY, 1827)

In the lower part of the Gamba Group of section A more than a dozen specimens of the genus *Calliboplites* are preserved as crushed external moulds of which rubber casts have been made. They are concentrated near the top of the Chaquiela Formation of Gamba Group (Section A).

Calliboplites tetragonus (SEELFY, 1865)

(Pl. 1, Fig. 6)

1928 *Calliboplites tetragonus* (SEELFY) - SPATH: 210; pl. 22, fig. 1-2, 9-10; pl. 23, fig. 11(?); text-fig. 66 (with synonymy).

Material: More than half a dozen of the mentioned specimens of *Calliboplites* belong to this species.

Description: Exact measurements can not be given. The maximum diameter was almost 50 mm. The coiling is moderately evolute, the external side seems to be rounded. There are strong umbilical tubercles, 12-13 per half whorl. From each tubercle arise 2-3 ribs, which cross straight or slightly flexuous the flanks. Often two are looped and end at ventrolateral tubercles, which are somewhat clavi. Of the suture line nothing is visible.

Discussion: Size, coiling and sculpture are typical for the genus *Calliboplites*, which is very similar to *Dimorphoplites* SPATH, 1925 but can be distinguished by means of its slightly rounded external side. Within *Calliboplites* a complete correspondence is seen to *C. tetragonus*, especially to *C. tetragonus* var. *vulgaris* SPATH, 1928 (p. 212; pl. 22, fig. 1). Characteristic is the throughout coarse ornamentation, the short and only very slightly falcoid ribs and the prominent inner and outer tubercles. Also *C. auritus* (J. SOWERBY, 1816) has a coarse ornamentation, but the costation of this species seems to be more regular and the outer tubercles are all 'clavi parallel to the ventral edges' (SPATH 1928: 212).

Occurrence: *C. tetragonus* has been described from the Upper Albian (*dispar* Zone) of southern England.

Calliboplites cf. *glossonotus* (SEELLY, 1865)

(Pl. 1, Fig. 7)

Material: Nearly half a dozen of the referred specimens of *Calliboplites* are closely related to *C. glossonotus*.

Description: The diameter is approximately 50 mm, the coiling rather evolute. An exact reconstruction of the cross section and exact measurements are not possible. The sculpture consists of dense and somewhat sigmoidal ribs, strong umbilical nodes, 13-14 per half whorl and smaller outer tubercles. Nothing is visible of the suture line.

Discussion: The specimens can be compared best with *C. glossonotus* (see SPATH 1928: 223; pl. 23, fig. 2; text-fig. 72, with synonymy), but this species is poorly known. Contrary to the specimen figured by SPATH, the Tibetan material seems to be more evolute, the whorl height is increasing slower and the costation is somewhat more irregular. As nothing is known about the variability of the species the identification is

uncertain. However, these specimens are different from *C. tetragonus*, described above, in its relatively fine and dense ribbing as well as in the smaller outer tubercles.

Occurrence: The species *C. glossonotus* is known from the Upper Albian of southern England. A taxon called '*Calliboplites* cf. *glossonotus* (SEELLY) SPATH' is mentioned also from the Kirchrode I borehole, northern Germany (WIEDMANN & OWEN 2001: 167).

Superfamily Acanthocerataceae GROSSOUVRE, 1894

Family Brancoceratidae SPATH, 1934

Subfamily Brancoceratinae SPATH, 1934

Genus *Hysterocheras* HYATT, 1900

Type species: *Hysterocheras varicosum* (J. DE C. SOWERBY, 1824)

Hysterocheras semileve HAAS, 1942

(Pl. 1, Fig. 5)

1942 *Hysterocheras semileve*, forma typica - HAAS: 42; pl. 5, fig. 19; pl. 7, fig. 8-11; text-fig. 5c, 5h.

1942 *Hysterocheras semileve* var. *sparsicostata* - HAAS: 44; pl. 5, fig. 22; pl. 7, fig. 13; text-fig. 5g-h.

1968 *Hysterocheras semileve* HAAS - RINZ: 63; pl. 11, fig. 6; text-fig. 22g-h.

Material: More than a dozen specimens of the genus have been found in one level at the top of the Chaquiela Formation of Gamba Group (Section A), some of which can be identified at species level.

Description: All the specimens are small (diameter maximal 20 mm) and crushed, therefore no exact measurements can be given. The coiling is rather involute with a shallow umbilical and steep umbilical walls. The flanks are flattened and the outer side is keeled. There exist broad flattened ribs, starting out almost in pairs, rarely as single ribs at small umbilical nodes. The ribs are very weak at the lower flank but strong at the outer side where they are projected somewhat forward. Per half whorl there are 14-15 ribs between which the intercostals are somewhat smaller. Of the suture line nothing is visible.

Discussion: The micromorph specimens are clearly related to the genus *Hysterocheras* from which *Spathiceras* WHITEHOUSE 1927 can be regarded as a junior synonym (COOPER & KENNEDY 1979: 267). The rather involute coiling, the number of broad ribs and their projection at the outer flank have the best correspondence with *H. semileve* and its

Plate 2

Fig. 1: *Mortoniceras* (*Detradoceras*) *bispinosum* (SPATH); Section V (Gamba Group at Duela, Vf 16/3); a-b: lateral views, c: ventral view; x 2/3.

Fig. 2: *Mortoniceras* (*Mortoniceras*) *prucei* (SPATH); Section V (Gamba Group at Duela, Vf 15/1); x 2/3.

Fig. 3: *Mortoniceras* (*Mortoniceras*) *rostratum* (J. SOWERBY); Section V (Gamba Group at Duela, Vf 16/1); x 2/3.

Fig. 4: *Mortoniceras* (*Mortoniceras*) *intermedium* SPATH; Section V (Gamba Group at Duela, Vf 17/1); x 2/3.



var. *sparstostata*. The most closely related species, *H. propinquum* HAAS, 1942, may be distinguished by its weaker ribs which are also straight and not distinctly sigmoidal.

Occurrence: *H. semileve* (including several 'varieties') has been described from the Upper Albian of Madagascar and Switzerland.

Subfamily Mortoniceratinae H. DOUVILLE, 1912

Genus *Mortoniceras* MEFF, 1876

Subgenus *Mortoniceras* (*Mortoniceras*) MEFF, 1876

Type species: *M. (Mortoniceras) vespertinum* (MORTON, 1834)

Mortoniceras (*Mortoniceras*) *intermedium* SPATH, 1932

(Pl. 2, Fig. 4)

1971 *Mortoniceras* (*Mortoniceras*) *pricei* aff. *intermedium* SPATH – RINZ: 596; pl. 6, fig. 1, 2(?); pl. 7, fig. 2; text-fig. 5i, 7f (with synonymy).

1995 *Mortoniceras* (*Mortoniceras*) *pricei intermedium* SPATH – WILDMANN & DURR: 21, figs. 3 B-C, 4 A (with synonymy).

Material: One specimen from the calcareous facies within the Gamba Group at Duela (section V).

Description: The well preserved specimen is somewhat broken and flattened. The diameter was approximately 180 mm. The coiling is very evolute and the whorl section compressed but no exact measurement is possible.

On the inner whorl there is a somewhat irregular alternation of the dense ribs, bifurcating at umbilical nodes or intercalating on the lower part of the flank. All ribs have small lateral tubercles and bigger ventrolateral ones. On the outer whorls the simple straight ribs are more distant, mostly beginning at umbilical nodes or starting at the lower flank, always with small lateral and heavy ventral tubercles. No details of the suture line are visible.

Discussion: The best agreement exists with *M. (Mortoniceras) intermedium* in size, coiling and the sculpture with straight tuberculate ribs, closer at the inner whorls and more distant at the later stages (see number and direction of ribs by SPATH 1932; pl. 38, fig. 5 for a smaller specimen and RINZ 1971; pl. 6, fig. 1a for a larger one).

In the interpretation of SPATH (1932: 392) and later authors, *M. (M.) intermedium* is only a subspecies of *M. (Mortoniceras) pricei* SPATH, 1922 and a transitional form to *M. (Dumovartites) kiliani* (EASSWITZ, 1904). But from the first it could be distinguished for example by the presence of weak lateral tubercles (see also discussion there), whereas the latter is not consistent with the definition of the subgenus treated here, especially because of its quadrituberculation.

Occurrence: *M. (M.) intermedium* has been described from the Upper Albian of South England, Madagascar, Venezuela and also from the Xigaze Group of South Tibet. The species may be restricted to the *inflatum* Zone.

Mortoniceras (*Mortoniceras*) *pricei* (SPATH, 1922)

(Pl. 2, Fig. 2)

1999 *Mortoniceras* (*Mortoniceras*) *pricei* (SPATH, 1922) – KENNEDY et al.: 1109, fig. 8-9, 10.6 (with synonymy).

Material: One specimen of nearly half a whorl from the calcareous facies within the Gamba Group at Duela (Section V).

Description: The maximum diameter has been approximately 180 mm, the exact whorl section can not be reconstructed. The strong ribs are most simple, somewhat irregularly alternating long and shorter ones, or rarely also bifurcating at umbilical nodes. The long ribs start all at radially elongated umbilical tubercles. All ribs are very slightly falcoid on the flank but stronger projected forward at the outer shoulder. They all bear ventral nodes. Only some details of the suture line are visible.

Discussion: The specimen agrees well with *M. (Mortoniceras) pricei* as described by SPATH (1932: 391ff.) and others. *M. (M.) pricei* is closely related to *M. (Mortoniceras) intermedium* SPATH, 1932 (see discussion there). But in contrast to this species *M. (M.) pricei* has a denser ribbing on the outer whorl and more sinuous ribs. Also it lacks lateral tubercles and the umbilical tubercles are ontogenetically longer prominent.

Occurrence: *M. (M.) pricei* is widely distributed and known from western Europe, Poland and the former USSR, as well as from northern Africa, Nigeria, Madagascar, Texas and Venezuela. The species is restricted to the lower Upper Albian (*inflatum* Zone).

Mortoniceras (*Mortoniceras*) *rostratum* (J. SOWERBY, 1817)

(Pl. 2, Fig. 3)

1985 *Mortoniceras* (*Subschloenbachia*) *rostratum* (J. SOWERBY 1817) – IMMEH & SIYED-EMAMI: 96; pl. 3, fig. 2 (with synonymy).

1998 *Mortoniceras* (*Subschloenbachia*) *rostratum* (J. SOWERBY, 1817) – KENNEDY et al.: 17, figs. 9-11, 13-18 (with synonymy).

1998 *Mortoniceras* (*Mortoniceras*) *rostratum* (SOWERBY, 1817) – MATSUMOTO et al.: 176, figs. 4-7 (with synonymy).

Material: Two isolated specimens from the calcareous facies within the Gamba Group at Duela (Section V).

Description: The better preserved specimen has a diameter of 115 mm. The coiling is evolute, the umbilical diameter 43 mm (0.37), the whorl section can not be measured because of secondary flattening. The ribs are first close, simple or branching at the umbilical edge. After a diameter of nearly 60 mm the ribs become stronger and distant, finally there are 11 ribs per half whorl. All ribs are tuberculate, on the inner whorl they may be quadrituberculate, later on they are clearly trituberculate, with small umbilical and lateral and prominent ventral nodes, the latter developing to be clavate. Only few details of the suture line are visible.

Discussion: There is good correspondence with *M. (M.) rostratum* in measurements (see SPATH 1932: 401) and development of the sculpture. Especially the rapid formation

of distant single ribs is characteristic and the best argument to distinguish the specimens from *Mortoniceras* (*Mortoniceras*) *inflatum* (J. SOWERBY, 1818).

Occurrence: *M. (M.) rostratum* has been described from the Anglo-Paris basin, Hungary, former southern USSR, and central Iran as well as Angola, Madagascar, Japan and Texas. The species is restricted to the uppermost Albian (*dispar* Zone).

Subgenus *Mortoniceras* (*Deiradoceras*) VAN HOEPEN, 1931

Type species: *M. (Deiradoceras) prerostratum* SPATH, 1921

Mortoniceras (*Deiradoceras*) *bispinosum* (SPATH, 1921)

(Pl. 2, Fig. 1)

1975 *Mortoniceras* (*Deiradoceras*) *bispinosum* (SPATH, 1921) – FORSTER: 228; pl. 12, fig. 2, 5; text-fig. 73 (with synonymy).

Material: One specimen from the calcareous facies within the Gamba Group at Duela (Section V).

Description: The specimen consists of more than half a whorl and is nearly not crushed, so that some measurements can be given. These are compared with those of the type species (SPATH 1921: 285) as following:

	D	Wh	Wb	U
SPATH 1921	148	(0.32)	(0.30)	(0.44)
Vf 16/3	134	42(0.31)	39(0.29)	61(0.46)

The coiling is evolute, the whorl section subquadrate. The ribs are strong, more or less alternate simple or bifurcating at strong umbilical nodes. All ribs bear external tubercles. On the outer side there are 19 ribs at a half whorl. This is somewhat more than in the two complete specimens figured by FORSTER (1975: pl. 12, fig. 2, 5), but these are of a smaller size. Only some details of the suture line are visible.

Discussion: Coiling, measurements and sculpture agree very well with the data given by SPATH (1921) for a specimen of Zululand and two specimens of southern Mozambique, described by FORSTER (1975). *M. (D.) bispinosum* is most similar to the type species *M. (D.) prerostratum* (SPATH, 1921). This species is distinguished from *M. (D.) bispinosum* by the coarser ribs and the umbilical nodes being situated higher on the flanks. But one should note that according to FORSTER (1975: 229) there exist transitional specimens between the two species.

Occurrence: *M. (D.) bispinosum* has been described so far from the lower Upper Albian of South Africa, southern Mozambique and Madagascar.

Mortoniceras (*Deiradoceras*) *devonense* SPATH, 1933

(Pl. 3, Fig. 4)

1971 *Mortoniceras* (*Deiradoceras*) *devonense* SPATH – RENZ: 605; pl. 10, fig. 1; pl. 11, fig. 2; text-fig. 6a, 6b, 7d, 7k (with synonymy).

Material: Three specimens from the calcareous facies within the Gamba Group at Duela (Section V), in one of which the identification is somewhat uncertain.

Description: The specimens are incomplete and somewhat crushed, therefore no exact measurements can be given. The best preserved specimen (pl. 3, fig. 4) had a diameter of approximately 140 mm and a subquadrate whorl section, a little higher than wide. At first nearly all ribs are bifurcating at the umbilical nodes which are somewhat elongated radially. Later on single ribs are sometimes intercalated. All ribs bear external nodes, slightly projected tangentially. The suture line is nearly invisible.

Discussion: The specimen is matching *M. (D.) devonense* in coiling, whorl section and sculpture. Especially there is some similarity with the variety *compressa* described from southern England (SPATH 1932-33: 420; pl. 39, fig. 1). *M. (D.) devonense* can be distinguished from the closely allied species *M. (D.) bispinosum* (SPATH, 1921) by the whorl height which is increasing faster, and the projection of the external nodes.

Occurrence: *M. (D.) devonense* is known from the Upper Albian of western Europe, South Africa and Venezuela. In England and France the species is restricted to the lower Upper Albian (*inflatum* Zone).

Subgenus *Mortoniceras* (*Durnovarites*) SPATH, 1932

Type species: *Mortoniceras* (*Durnovarites*) *perinflatum* (SPATH, 1922)

Mortoniceras (*Durnovarites*) *kiliani* (LASSWITZ, 1904)

(Pl. 3, Fig. 1)

1932 *Mortoniceras* (*Pervinqueria*) *kiliani* (LASSWITZ) – SPATH: 408; pl. 38, fig. 1, 2; pl. 42, fig. 1; pl. 47, fig. 1; text-fig. 140 (with synonymy).

Material: One isolated specimen, found several meters out of section G in the same facies of the Chaquiela Formation of the Gamba Group.

Description: The diameter was something less than 100 mm, the coiling is rather evolute. No exact measurements can be given because the specimen is somewhat crushed. The section is subrectangular with parallel flanks, broad and keeled external sides and a deep umbilicus. The ribs are mostly bifurcating at the umbilical edge. They bear four tubercles: umbilical, lateral, marginal and external. At a diameter of approximately 65 mm there exist 21 ribs and 11 umbilical nodes per half whorl. The suture line is not visible.

Discussion: In coiling, cross section and sculpture the specimen is a typical *M. (D.) kiliani*. The holotype of this species has the same number of ribs and umbilical nodes at a comparable size (see SPATH 1932: text-fig. 140). According to SPATH (op. cit.: 408) *M. (D.) kiliani* may 'be somewhat transitional' to *Mortoniceras* (*Durnovarites*) *pachys* (SEELEY, 1865). But from this species *M. (D.) kiliani* can be distinguished because it is less densely ribbed and has a more inflated cross section.

Occurrence: *M. (D.) kiliani* has been described from the Upper Albian of Texas and Southern England. It is also mentioned from Poland (see MARCINIOWSKI & WIEDMANN 1990: 88).

Genus *Goodballites* SPATH, 1932Type species: *Goodballites goodballi* (J. SOWERBY, 1820)*Goodballites procerum* (VAN HOEPEN, 1942)

(Pl. 3, Fig. 2)

1942 *Letheceras procerum* n. sp. – VAN HOEPEN: 146; text-fig. 162-163.

Material: One fragmentary specimen from the calcareous facies within the Gamba Group at Duela (Section V).

Description: The broken and crushed specimen has a diameter of approximately 80 mm, the whorl section cannot be reconstructed exactly. The coiling is relatively involute (umbilical diameter approximately 25 mm). The ribs are straight to slightly sinuous. They start at small umbilical tubercles or are intercalated on the flanks. They get wider to the outer side and terminate before reaching the keel in heavy nodes. Only some relics of the suture line can be seen.

Discussion: Size, coiling and presumed whorl section, with a little bit convergent flanks, and sculpture are typical of *Letheceras* VAN HOEPEN, 1942, which is regarded as a junior synonym of *Goodballites* by WRIGHT (1996: 142).Within this genus the best match is found with *G. procerum* in size, involution and number of ribs per half whorl (15-16). There are some species very similar to *G. procerum*, especially *G. densicostatum* VAN HOEPEN, 1942 and *G. proximum* VAN HOEPEN, 1942. The first can be distinguished from *G. procerum* by the greater number of ribs per half whorl (20), the latter by the slender ribs and the smaller external nodes which become more clavate.Occurrence: *G. procerum* has been described only from the lower Upper Albian of Zululand (South Africa).*Goodballites* cf. *gracillimum* (KOSSMAT, 1895)

(Pl. 3, Fig. 7)

Material: Four specimens from the uppermost part of the Chaquiela Formation of Gamba Group (Section A).

Description: All specimens are crushed and mostly incomplete, so that exact measurements can not be given. The maximum diameter has been approximately 55 mm. The coiling is rather evolute, the whorl height increases rapidly. The flanks are flattened, the outer side is keeled. Most of the ribs are starting in pairs or as single ribs from distinctive umbilical

tubercles, but also some secondary ribs begin higher on the flanks. All ribs are widening at the outer flank and end in broad ventrolateral nodes. At first the ribs are straight and nearly interrupted on the midflank, but later on they are falcoid and externally projected forward. Of the suture line no details are visible.

Discussion: The best correspondence is found with *G. gracillimum*, a form which was compared by SPATH (1934: 472) with the inner whorls of the subgenus *Mortoniceris* (*Deinadoceras*) VAN HOEPEN, 1931, but belongs to *Goodballites* according to FORSTER (1975: 240). He regarded this genus as a subgenus of *Probysteroceras* SPATH, 1921 as WRIGHT (1957: L 406) has done previously.Because of the crushed and incomplete preservation the species identification seems not quite sure. Especially the closely related species *G. besakatrense* COLLIGNON, 1963 can be distinguished only due to its more compressed cross section and the more straight and slightly broader ribs.Occurrence: The species *G. gracillimum* is known from the Upper Albian of southern India, southern Mozambique, and somewhat questionable from South Africa.

Family Acanthoceratidae DE GROSSOUVRE, 1894

Subfamily Mantelliceratinae HYATT, 1903

Genus *Mantelliceras* HYATT, 1900Type species: *Mantelliceras mantelli* (J. SOWERBY, 1814)

Of this genus exist four specimens, two each of sections B and G of the Ganbacunkou Formation of the Gamba Group, but only the two specimens of section B can be identified on species level.

Mantelliceras cf. *mantelli* (J. SOWERBY, 1814)

(Pl. 3, Fig. 6)

Material: One isolated fragment of nearly half a whorl of the phragmocone from section B (Ganbacunkou Formation of Gamba Group).

Description: The slightly distorted specimen had a diameter of approximately 45 mm. The coiling is moderately involute, the whorl section somewhat depressed with flattened flanks and ventral sides. The sculpture consists of 16 alternating long and short ribs with umbilical, lower and upper

Plate 3

Fig. 1: *Mortoniceris* (*Dumocartes*) *kiliani* (LASSWITZ); Section G (Chaquiela Formation of Gamba Group, Gf 16/1); a: frontal view, b: lateral view; x 1.Fig. 2: *Goodballites procerum* VAN HOEPEN; Section V (Gamba Group at Duela, Vf 17/2); x 1.Fig. 3: *Fucalycoceras collignoni* (FABRI); Section B (Ganbacunkou Formation of Gamba Group, Bf 74/1); x 1.Fig. 4: *Mortoniceris* (*Deinadoceras*) *devonense* SPATH; Section V (Gamba Group at Duela, Vf 17/3); x 1.Fig. 5: *Mantelliceras lymense* (SPATH); Section B (Ganbacunkou Formation of Gamba Group, Bf 31/1); a: ventral view, b: lateral view; x 1.Fig. 6: *Mantelliceras* cf. *mantelli* (J. SOWERBY); Section B (Ganbacunkou Formation of Gamba Group, Bf 35/1); a: ventral view, b: lateral view; x 1.Fig. 7: *Goodballites* cf. *gracillimum* (KOSSMAT); Section A (Chaquiela Formation of Gamba Group, Af 150/1); x 1.



ventrolateral tubercles. No lateral tubercles are visible, perhaps due to corrosion. The suture lines are well preserved.

Discussion: The specimen is clearly a *Mantelliceras*. The closest similarity is found with the type species *M. mantelli* because of its small size and coiling, the slightly depressed whorl section and the density of the ribs. But there is a little difference in tuberculation (lacking of lateral tubercles) and the preservation is too poor; so the determination can not be sure.

Occurrence: *M. mantelli* is the index species for the lowermost standard zone of the Cenomanian and has a widespread distribution in Europe, Africa and Asia as stated by IMMEL & SEYED-EMAMI (1985: 99), KENNEDY et al. (1986: 27), and IMMEL (1987: 103).

Mantelliceras lymense (SPATH, 1926)

(Pl. 3, Fig. 5)

1986 *Mantelliceras lymense* (SPATH) - KENNEDY, JUIGNET & WRIGHT: 27; fig. 5a-f; fig. 6d-e; fig. 16e-f (with synonymy).

Material: One moderately preserved fragment, a quarter of a whorl of a phragmocone from section B (Ganbacunkou Formation of Gamba Group).

Description: The diameter of the specimen was approximately 100 mm. Exact measurements are not possible. The whorl section is subrectangular, slightly wider than high, with flattened flanks and a tabulate venter. The umbilical wall is vertical. The ribs, regularly long and short, are coarse and straight. There are only strong elongated umbilical nodes and rather weak upper ventrolateral tubercles. Parts of the suture are preserved.

Discussion: The specimen can best be compared with *M. lymense*, a synonym of *Mantelliceras costatum* (MANTELL, 1822) (which is invalid due to homonymy) according to WRIGHT & KENNEDY (1984: 102). The whorl section, the straight and coarse ribs and especially the rare tuberculation are important points for this identification.

Occurrence: *M. lymense* is widespread in the Lower Cenomanian of western Europe, the Central Iran and Tunisia.

Subfamily Acanthoceratinae DE GROSSOUVRE, 1894

Genus *Eucalycoceras* SPATH, 1923

Type species: *Eucalycoceras pentagonum* (JUKES-BROWNE, 1896)

Eucalycoceras collignoni (FABRE, 1940)

(Pl. 3, Fig. 3)

1972 *Eucalycoceras (Eucalycoceras) collignoni* (FABRE) - THOMAS: 85; pl. 27, fig. 7 (with synonymy).

Material: Four specimens from the genus are from the upper part of the Ganbacunkou Formation of Gamba Group (Section B), but only two crushed fragments can be identified at the species level and belong to here.

Description: The better preserved specimen has a diameter of approximately 75 mm, but no exact measurements can be given. The coiling is moderately involute, about half of the previous whorl being covered. The whorl section can not be reconstructed exactly but was probably compressed with flattened flanks.

There are long ribs, seven on the last quarter of the whorl, which arise from sometimes elongated umbilical tubercles and pass across the flank with gentle flexing. They are separated by one or almost two intercalated ribs of quite irregular length starting from below mid-flank. At first all ribs are bearing distinct lower and upper ventrolateral tubercles, which will be lost at the end of the whorl. Sometimes there are indications of siphonal tubercles. The sutures are not visible even at the better preserved specimens.

Discussion: Coiling and sculpture are typical for the genus *Eucalycoceras*. The density of the ribs and the clavate form of the ventrolateral tubercles are most similar to *E. collignoni*. From this species the rather similar type species *E. pentagonum* is separated in having more flattened ribs with smaller interspaces. Also there is some similarity to *E. gothicum* (KOSSMAT, 1895), but this species can be distinguished from *E. collignoni* by the strong projection of the umbilical tubercles into the umbilicus.

Occurrence: *E. collignoni* has been described previously only from the Upper Cenomanian of SE-France.

Family Collignoniceratinae WRIGHT & WRIGHT, 1951

Subfamily Texanitinae COLLIGNON, 1948

Genus *Submortoniceras* SPATH, 1926

Type species: *Submortoniceras woodsi* (SPATH, 1921)

Submortoniceras tenuicostulatum COLLIGNON, 1948

(Pl. 4, Fig. 1)

1970 *Submortoniceras tenuicostulatum* COLL. - COLLIGNON: 44; pl. 176, fig. 2317 (with synonymy).

Material: Two isolated specimens from the upper part of section CA (middle Zongshan Formation), one of which is poorly preserved and corroded, the other is a well preserved phragmocone.

Description: From the better preserved specimen the following measurements can be given:

	D	Wh	Wb	Wh/Wb	U
CAf 74/1	112	46(0.41)	37(0.33)	1.25	35(0.31)

The coiling is moderately evolute, the whorl height increases rapidly. The whorl section is compressed with flattened flanks and external side, and an overhanging umbilical wall. The pentatuberculate ribs are dense, starting simple or bifurcating at strong umbilical tubercles. They pass across the flank slightly prorsiradiate and end on clavate external tubercles. Additionally weak lateral, submarginal and marginal tubercles exist. The ornament seems to be attenuated on the outer whorl. The sutures are not distinct but appear to be of normal texanid type.

Discussion: The tight coiling and ornamentation, especially the attenuation of the latter on the outer whorl, show that the specimens belong to *Submortonicerus*. The compressed whorl section and the fairly narrow umbilicus is most similar to *S. tenuicostulatum*. As discussed broadly by KENNEDY & KLINGER (in KENNEDY, KAUFFMAN & KLINGER 1973: 103) and KLINGER & KENNEDY (1980: 253ff.) this species may be included as a junior synonym in the type species *S. woodsii*, but till now this is an unresolved problem.

Occurrence: *S. tenuicostulatum* has been described from the middle Campanian (Zone of *Pachydiscus grossouvrei*) of Madagascar.

Suborder Ancyloceratina WIEDMANN, 1966

Superfamily Ancylocerataceae GILL, 1871

Family Ancyloceratidae GILL, 1871

Subfamily Helicancylineae HYATT, 1894

Genus *Toxoceratoides* SPATH, 1924

Type species: *Toxoceratoides royerianum* (D'ORBIGNY, 1842)

Toxoceratoides aff. *royerianum* (D'ORBIGNY, 1842)

(Pl. 4, Fig. 6)

Material: One fragment from the middle part of the Ganbadongshan Formation of Gamba Group (Section A). For the most part it is only a cavity in a concretion from which a cast was made.

Description: The fragment consists of a part of the nearly straight shaft and the beginning of the hook. The whorl section of the shaft is subcircular, the hook is somewhat compressed and subrectangular. On the shaft the prorsiradiate ribs are alternatively primaries, with weak umbilical, and stronger lateral and external nodes, and weaker nontuberculate intercalatories. Between the umbilical and lateral tubercles and also between the latter and the external ones, the primary ribs may be looped. On the hook the tuberculation of the ribs disappears, the external tubercles at last. Of the suture line nothing is visible.

Discussion: The alternation of strong tuberculate and fine nontuberculate ribs is typical for *Toxoceratoides*, contrasting the closely allied *Helicancyclus* GABB, 1869 and *Tonohamites* SPATH, 1924 (see there).

A list of species belonging to *Toxoceratoides* is given by KLINGER & KENNEDY (1977: 307) and AGUIRRE URRETA (1986: 296f.). The best correspondence is seen in the type species *T. royerianum*, especially the very regular alternation of primaries and intercalatories, the looping of the primary ribs on the shaft and the rapid expansion of the whorl on the final hook. But contrary to the French type species, the whorl section is compressed in the Tibetan specimen and not depressed and also on the final hook the umbilical tubercles disappear (see the neotype of *T. royerianum* in CASEY 1961: 79f. and text-fig. 30a-c).

Occurrence: The genus *Toxoceratoides* ranges from the Upper Barremian to the Upper Aptian and is known from Europe, California, Mozambique, South Africa and Patagonia. The Tibetan specimen is from the Upper Aptian.

Genus *Tonohamites* SPATH, 1924

Type species: *Tonohamites decurrens* SPATH, 1924

Tonohamites multituberculatus n. sp.

(Pl. 4, Fig. 3, 4)

Holotype: Af 71/8.

Derivatio nominis: The name refers to the numerous and long persisting nodes, which are unusual for the genus.

Locus typicus: South Tibet, area of Gamba, section A.

Stratum typicum: Gamba Group, middle level of the Ganbadongshan Formation, Upper Aptian.

Diagnosis: *Tonohamites* with regular trituberculate ribs on the whole shaft.

Material: Two specimens from a middle level of the Ganbadongshan Formation of Gamba Group (Section A).

Description: The holotype (pl. 4, fig. 3) is a nearly complete and only slightly crushed specimen, existing as a cavity in a concretion, from which a cast was made. The second specimen (pl. 4, fig. 4), also a cast, is less complete and somewhat more crushed.

The coiling is toxoceratid in the sense of AGUIRRE URRETA (1986: 282, fig.7). The holotype has a maximum height of 47.5 mm. The whorl section of the shaft is somewhat ovoid, on the hook becomes subcircular. The broadly rounded ribs are straight on the initial spiral and slightly prorsiradiate on the shaft. There are 5-6 ribs within a distance equal to the whorl height.

On the early spiral and on the shaft all ribs bear small and rounded umbilical and lateral tubercles. Where the external side can be seen, there exist also a row of external tubercles, so the species is - at least at times - trituberculate. At the beginning of the hook the lateral and external tubercles disappear and only some ribs still bear weak umbilical nodes. Of the suture line nothing is visible.

Discussion: The generic allocation of the specimens is somewhat difficult as they share characteristics of *Tonohamites* and *Helicancyclus* GABB, 1869. The presence of trituberculate ribs on the shaft would be characteristic for *Helicancyclus*, but contrary to this genus the tubercles are always very weak. Also the broad and rounded ribs which are flattened on the final hook are features of *Tonohamites* rather than of *Helicancyclus*.

Within the genus *Tonohamites* the frequent and regular tubercles are unusual and can not be compared with any known species.

A species of some similarity is *T. acquicingulatus* (VON KOENEN, 1902), some of its ribs 'in the early stage ... bear siphonal, lateral and umbilical tubercles' (AGUIRRE URRETA 1986: 310). But this tubercles also disappear earlier than in the

Tibetan species. Also the interspaces between the ribs are wider in *T. acquicingulatus* which has only 4 ribs within a distance equal to the whorl diameter contrary to 5-6 in *T. multituberculatus*.

Occurrence: *T. multituberculatus* is known only from the Upper Aptian of southern Tibet. The stratigraphic position is fixed because the species is associated with *C.* (*Cheloniceras*) aff. *buxtorfi* (JACOB, in JACOB & TOBLER 1906), *Colombiceras* cf. *subpeltoceroide*s SINZOW, 1907, and *Paraboplites trautscholdi* (SIMONOVITSH, BATSIVITSH & SOROKIN, 1876).

Genus *Helicancylus* GABB, 1869

Type species: *Helicancylus acquicostatus* (GABB, 1864)

Helicancylus sp.

(Pl. 4, Fig. 5)

Material: One fragment from the middle part of the Ganbadongshan Formation of Gamba Group (Section A). It is preserved as a cavity in a concretion from which a cast was made.

Description: The fragment is a 34 mm long part of a slightly curved shaft. The whorl section is subcircular. There exist 15 prorsiradial ribs of equal size, approximately six ribs are present per whorl height. All ribs bear umbilical, lateral and ventral tubercles of variable strength. Of the suture line nothing is visible.

Discussion: The specimen is clearly a *Helicancylus*. It can be distinguished from the closely allied *Toxoceratoides* SPATH, 1924 by the total lack of nontuberculate intermediate ribs and from *Tonobamutes* SPATH, 1924 by the presence of strong tubercles on every rib. A recent list of species attributed to *Helicancylus* is given by AGUIRRE URRETA (1986: 284). But due to its fragmentary preservation the Tibetan specimen can not be assigned to one of them.

Occurrence: The genus *Helicancylus* has been described from the Aptian of southern England, northern Germany and Switzerland as well as from California (type species), Patagonia and - somewhat questionable - Antarctica.

Superfamily Turrilitaceae GILL, 1871

Family Turrilitidae GILL, 1871

Genus *Proturrilitoides* BREISTROFFER, 1940

Type species: *Proturrilitoides asticerianus* (D'ORBIGNY, 1842)

Proturrilitoides sp.

(Pl. 4, Fig. 13)

Material: One incomplete specimen, an external mould from the Chaquiela Formation of Gamba Group (Section I).

Description: The fragment is 15 mm high, the coiling loose, the apical angle is large (nearly 55°), the whorl section can not be reconstructed exactly. The oblique and non tuberculate ribs are strong, simple and flexuous. There exist approximately 12 ribs per half whorl. Of the suture line nothing is visible.

Discussion: Because of the poor preservation even the identification of the genus is somewhat uncertain. According to WIEDMANN (1962: 189) and RENZ (1968: 83) *Proturrilitoides* is regarded only as a subgenus of *Turrilitoides* SPATH 1923, but WRIGHT (1996: 241) confirms its status as a separate genus as he did before (WRIGHT 1957: L 220). Differences between the two genera are listed in KLINGER & KENNEDY (1978: 35), but only the apical angle can be taken into account here. It is large, which is a characteristic feature of *Proturrilitoides* (see also COOPFER 1999: 3f.). Only the type species is listed in KLINGER & KENNEDY (1978: 39), from which the Tibetan specimen differs clearly in its coarser costulation. Probably it is a new species but too poorly preserved to be described as such.

Plate 4

- Fig. 1: *Submortoniceras tenuicostulatum* COLLIGNON; Section CA (Zongshan Formation, CAf 74/1); a: lateral view, b: ventral view; x 2/3.
 Fig. 2: *Colombiceras* (*Colombiceras*) cf. *subpeltoceroide*s SINZOW; Section A (Ganbadongshan Formation of Gamba Group, Af 71/4); a: lateral view, b: ventral view; x 1.
 Fig. 3: *Tonobamutes multituberculatus* n. sp.; Holotype (Af 71/8); Section A (Ganbadongshan Formation of Gamba Group); a-b: lateral views; x 1.
 Fig. 4: *Tonobamutes multituberculatus* n. sp.; Paratype (Af 71/5); Section A (Ganbadongshan Formation of Gamba Group), x 1.
 Fig. 5: *Helicancylus* sp.; Section A (Ganbadongshan Formation of Gamba Group, Af 71/6); a: ventral view, b: lateral view; x 1.
 Fig. 6: *Toxoceratoides* aff. *royerianum* (D'ORBIGNY); Section A (Ganbadongshan Formation of Gamba Group, Af 71/7); a: lateral view, b: ventral view; x 1.
 Fig. 7: *Douvillericeras pustulosum* CASIY; Section A (Chaquiela Formation of Gamba Group, Af 73A/1); a: ventral view, b: lateral view; x 1.
 Fig. 8: *Cheloniceras* (*Cheloniceras*) aff. *buxtorfi* (JACOB, in JACOB & TOBLER); Section A (Ganbadongshan Formation of Gamba Group, Af 71/1), x 1.
 Fig. 9: *Paraboplites trautscholdi* (SIMONOVICH, BATSIVICH & SOROKIN); Section A (Ganbadongshan Formation of Gamba Group, Af 71/12); a: ventral view, b: lateral view; x 1.
 Fig. 10: *Cheloniceras* (*Cheloniceras*) aff. *buxtorfi* (JACOB, in JACOB & TOBLER); Section A (Ganbadongshan Formation of Gamba Group, Af 63/1); a: ventral view, b: lateral view; x 1.
 Fig. 11: *Paraboplites trautscholdi* (SIMONOVICH, BATSIVICH & SOROKIN); Section A (Ganbadongshan Formation of Gamba Group, Af 71/10); a and c: lateral views, b: ventral view; x 1.
 Fig. 12: *Paraboplites trautscholdi* (SIMONOVICH, BATSIVICH & SOROKIN); Section A (Ganbadongshan Formation of Gamba Group, Af 71/11), x 1.
 Fig. 13: *Proturrilitoides* sp.; Section I (Chaquiela Formation of Gamba Group, If 2/1), x 2.



Occurrence: The genus *Proturritoides* is known from the Middle Albian of France and Poland.

Superfamily Douvilleicerataceae
PARONA & BONARELLI, 1897

Family Douvilleiceratidae PARONA & BONARELLI, 1897

Subfamily Cheloniceratinae SPATH, 1923

Genus *Cheloniceras* HYATT, 1903

Subgenus *Cheloniceras* (*Cheloniceras*) HYATT, 1903

Type species: *Ch. (Cheloniceras) cornuclanum* (D'ORBIGNY, 1841)

Cheloniceras (*Cheloniceras*) aff. *buxtorfi*
(JACOB, in JACOB & TOBLER 1906)

(Pl. 4, Fig. 8, 10)

Material: Half a dozen specimens from a middle part of the Ganbadongshan Formation of Gamba Group (Section A). The most specimens are cavities in concretions from which casts can be made.

Description: For several specimens exact measurements can be given:

	D	Wh	Wb	Wh/Wb	U
Af 63/1	35.5	13.5(0.38)	20.5(0.58)	0.66	8.5(0.24)
Af 71/1	29	12(0.41)	17(0.59)	0.71	8(0.28)
Af 71/2	26.5	10(0.38)	15(0.57)	0.67	7(0.26)
Af 71/3	23.5	9(0.38)	13(0.55)	0.69	7(0.30)

The coiling is rather involute, the depressed whorl section is at first coronate and subquadrate in a later stage. The simple ribs are primaries and alternate with one or two intermediaries. There are approximately twenty ribs per half whorl. The primaries bear umbilical and lateral tubercles. The lateral tubercles, in early stages more pronounced, will be reduced later on. Of the suture line nothing is visible.

Discussion: The specimens belong clearly to the subgenus *Ch. (Cheloniceras)* due to coiling, cross section and sculpture, which lacks ventral tubercles, typical for the subgenus *Ch. (Epicbeloniceras)* CASEY, 1954.

Within the subgenus there is a perfect correspondence in measurements with *Ch. (Cheloniceras) buxtorfi*. The lectotype of this species - described by JACOB & TOBLER (1906: 15; pl. 1, fig. 9) and selected by CASEY (1962: 253) - has the following measurements: D = 35, Wh = 14(0.40), Wb = 20(0.57), Wh/Wb = 0.70, U = 10(0.28). But in the sculpture there is a distinct difference because in the Tibetan material the ribs are more dense (20 contrary to 14-15 per half whorl), and the difference between primaries and intermediaries is more pronounced.

Probably the Tibetan material will belong to a new species. But we have only inner whorls and these stages are not well known in some *Cheloniceras*. So it seems better to describe the specimens in open nomenclature.

Occurrence: The subgenus *Ch. (Cheloniceras)* is a typical Upper Aptian form. The Tibetan material is of the same age.

Subfamily Douvilleiceratinae PARONA & BONARELLI, 1897

Genus *Douvilleiceras* DE GROSSOUVRE, 1894

Type species: *Douvilleiceras mammillatum* (SCHLOTHEIM, 1813)

Douvilleiceras pustulosum CASEY, 1962

(Pl. 4, Fig. 7)

1962 *Douvilleiceras pustulosum* - CASEY: 288; pl. 42, fig. 11; text-fig. 102 g, 103 c, d (with synonymy).

Material: One crushed specimen and three small fragments from the base of the Chaquiela Formation of Gamba Group (Section A).

Description: The maximum diameter of the most complete specimen was less than 33 mm, no exact measurements can be given. The coiling was moderately involute, the cross section is somewhat depressed with a wide shallow external sulcus. The sharp single ribs bear five nodes to a row on each side. From the suture line is nothing visible.

Discussion: The specimens are clearly representatives of the genus *Douvilleiceras* because of their shape and tuberculation. This genus has been splitted extremely. The best correspondence is found with *D. pustulosum* due to the shallow sulcus and the number of nodes on each rib.

It should be noted, that GEBHARD (1983: 126ff.) has proposed to reduce the number of species drastically. Instead of 24 species two species should be realistic: *D. mammillatum* (SCHLOTHEIM, 1813) with all ribs and nodes of the same shape and *D. maequodum* QUENSTEDT, 1849 with variable sculpture. An equivalent differentiation between this two groups has already been made by DESTOMBES (1979: 69). In such an extremely reduced system the Tibetan material would belong to *D. mammillatum*.

Occurrence: *D. pustulosum* has been described from the Lower Albian (*mammillatum* Zone) of southern England.

Superfamily Deshayesitaceae STOYANOW, 1949

Family Parahoplitidae SPATH, 1922

Subfamily Acanthohoplitinae STOYANOW, 1949

Genus *Colombiceras* SPATH, 1923

Subgenus *Colombiceras* (*Colombiceras*) SPATH, 1923

Type species: *C. (Colombiceras) crassicostatum* (D'ORBIGNY, 1841)

Colombiceras (*Colombiceras*) cf. *subpeltoceroideus*
SINZOW, 1907

(Pl. 4, Fig. 2)

Material: Two specimens from the Ganbadongshan Formation of Gamba Group (Section A).

Description: The maximum diameter is nearly 55 mm, the coiling moderately evolute, the flanks flattened and the external side well rounded. From the better preserved specimen

the measurements will be compared with '*Paraboplites treffrianus*' (ANTHULA 1899: 115; pl. 8, Fig. 6) from the former southern USSR (Caucasus), which is a *C. (Colombiceras) subpeltocerooides* according to DRUSHCHITS & KUDRYAVTSEV (1960: 329):

	D	Wh	Wb	Wh/Wb	U
Af 71/4	53	20(0.38)	18.5(0.35)	1.08	18.5(0.35)
"USSR"	45	19(0.42)	19(0.42)	1.12	15(0.33)

The strong ribs, which are very rapidly widening, start at the umbilical edge simple or branching at elongated swellings. They cross the flank slightly prorsiradiate or curved and run straight across the external side. Of the suture line nothing is visible.

Discussion: The broad accentuate ribs and the umbilical swellings are characteristics of the subgenus *C. (Colombiceras)*, the distinguishing feature to the subgenus *Colombiceras (Egoianiceras)* AVRAM, 1974 is the presence of tubercles, also contrasting to *Paraboplites* ANTHULA, 1899, which is a very closely allied genus (see there).

Within *C. (Colombiceras)* the best correspondence is with *C. (C.) subpeltocerooides*, although there are some minor differences in measurements (see above) and ribbing. But as nearly nothing is known about the variability of *C. (C.) subpeltocerooides*, only an approximative identification of the Tibetan material seems possible.

Occurrence: The species *C. (C.) subpeltocerooides* is known from the Upper Aptian of the former southern USSR.

Subfamily Paraboplitinae SPATH, 1922

Genus *Paraboplites* ANTHULA, 1899

Type species: *Paraboplites melchioris* ANTHULA, 1899

Paraboplites is one of the most common genera. Although there is a broad variability presumably all specimens can be assigned to one species.

The greatest problem is the determination of the genus, because there is no general agreement about the diagnosis of *Paraboplites*, *Acanthoboplites* SINZOV, 1907 or *Colombiceras* SPATH, 1923. The type species of all this genera were united by ANTHULA (1899: 110) in his new genus *Paraboplites*. So it is necessary to clarify the diagnostic features of the genera:

Paraboplites is characterized - as the whole subfamily - 'by the absence of tubercles at all stages of growth' (CASEY 1965: 400).

Acanthoboplites is distinguished from *Paraboplites* due to its prominent lateral tubercles, where the ribs are branching on the inner whorls.

C. (Colombiceras) is even more similar to *Paraboplites* but may be distinguished by its sculpture with more heavy, accentuate and straight ribs, and also by the appearance of strong and elongated umbilical swellings.

Paraboplites trautscholdi

(SIMONOVICH, BATSEVICH & SOROKIN, 1876)

(Pl. 4, Fig. 9, 11, 12)

1960 *Acanthoboplites trautscholdi* SIM., BATS., SOR. - DRUSHCHITS & KUDRYAVTSEV: 322; pl. 10, fig. 1-3 (with synonymy).

Material: Several dozen specimens and fragments can be found, especially as cavities in concretions in the Ganbadongshan Formation of Gamba Group (Section A).

Description: The coiling is quite involute, the whorl height increases moderately rapid. The section is compressed with slightly convergent sides and broadly arched venter. From the most complete specimens the following measurements can be given. They will be compared with a specimen from the former southern USSR, described by GLAZUNOVA (1953: 45, see also pl. 8, fig. 5):

	D	Wh	Wb	Wh/Wb	U
'USSR'	51	22.2(0.43)	18.7(0.36)	1.19	13.2(0.26)
Af 71/11	38	15.5(0.41)	~13(0.34)	1.19	11.5(0.30)
Af 71/12	38	14.5(0.35)	12.5(0.33)	1.16	11(0.29)
Af 71/10	35	14(0.40)	12(0.34)	1.17	9.5(0.27)
Af 71/9	34	14(0.41)	12(0.35)	1.17	9.5(0.28)
Af 70/1	26	10(0.39)	8.5(0.32)	1.18	7(0.27)

The ribs, first branching near the umbilical wall later alternatively longer and shorter ones, are somewhat sinuous on the flanks. They thicken rapidly and cross straight the venter without building any tubercles. Of the suture line mostly nothing is visible.

Discussion: Coiling and cross section as well as the complete absence of any tubercles show that the specimens belong to the genus *Paraboplites*. Within this genus the rapid thickening of the ribs as well as their straight crossing of the external side is unusual. But exact in this details and also in the measurements, there is a perfect correspondence with *P. trautscholdi*, described and figured from the former southern USSR by GLAZUNOVA (1953). GLAZUNOVA assigned this species to *Acanthoboplites*, as DRUSHCHITS & KUDRYAVTSEV (1960: 322) did it later. But *P. trautscholdi* lacks any tubercles, as already described by SIMONOVICH et al. (1876: 101), so it can not be an *Acanthoboplites*.

Occurrence: *P. trautscholdi* has been described till now only from the lower Upper Aptian of the former southern USSR (*nolani* Zone).

4. PALAEOBIOGEOGRAPHIC ASPECTS

The palaeobiogeographic situation of Central and South Asia during the Cretaceous has been discussed highly controversial for a long time. For example, as far as India is concerned, there is much disagreement as to when it has rifted off Gondwana and collided with Asia. Generally, a late separation in a southern position is assumed and also a late collision in the early Eocene (e.g. GOMBOS *et al.* 1995: Fig. 3). This view has recently been confirmed by BARDHAN *et al.* (2002) based on an ammonite fauna from Coniacian horizons in Bagh, central India, indicating close affinities to coeval horizons of Madagascar and Zululand, South Africa. Contrary to this view, however, JAEGER *et al.* (1989) proposed a more northern position of India and an earlier contact with Asia according to

the late Cretaceous vertebrate fauna of India. This fauna can be compared with Eurasian forms and is lacking endemisms. This would be inconsistent with a long isolation of the Indian plate (see also CHATTERJEE 1985).

With regard to South Tibet, the Tethyan Himalaya is generally considered to represent the northern shelf of the Indian plate. Therefore the same debate is going on. For example, the bivalve fauna of the Gamba Group clearly indicates a southern position during the Aptian and Albian and remained in 'relation and exchange with that of Antarctica-Australia in spite of its strong local colour' (WEN 2000: 5). Contrary, the Cretaceous corals of Tibet, analysed by LOSER

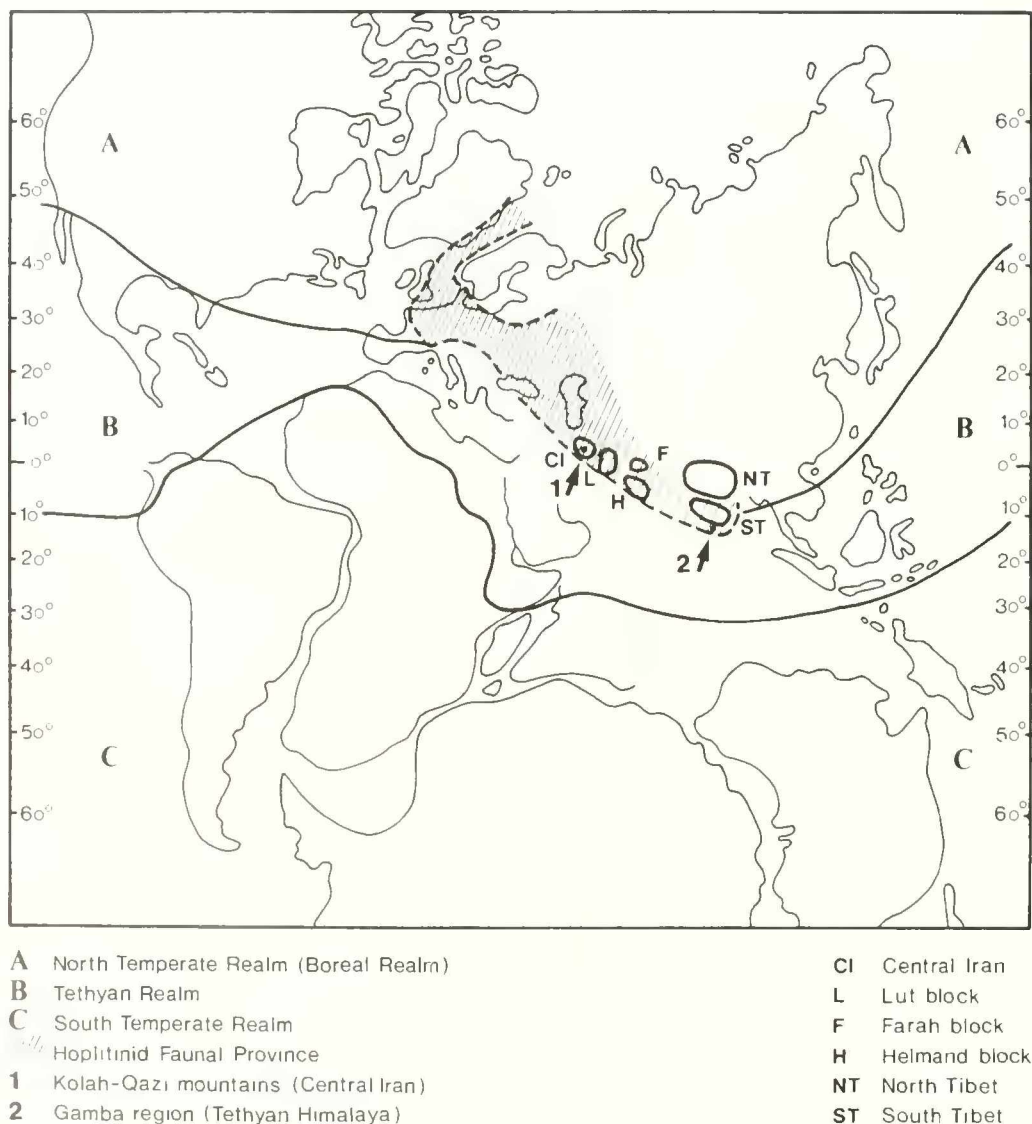


Fig. 9: Simplified middle Cretaceous palaeogeography (modified after SMITH *et al.* 1981: map 25) and palaeobiogeographic realms (after KAUFFMAN 1973: fig. 2). Also shown are some microplates of the Middle and Far East and the outline of an extended hoplitinid faunal province.

& LIAO (2001) have their closest relationships with Tethyan faunas from Western Europe to Asia, despite of a great number of endemisms.

On one side, the ammonites described in this paper show some affinities to those of southern India, Madagascar, and South Africa – i.e. to the southern temperate realm as defined by KAUFFMAN (1973). This is confirmed by several genera and species from the Gamba area (*Lemuroceras*, *Goodhallites* cf. *gracillimum*) and from the Zala valley of the Duela area [*Mortoniceras* (*Deiradoceras*) *bispinosum*, *Goodhallites procerum*].

On the other side, however, the ammonoid fauna has also a strong affinity to the northern temperate realm (boreal realm), especially to the hoplitinid faunal province, first introduced by OWEN (1971) and later on cited and refigured by JUIGNET & KENNEDY (1976: fig. 20). According to these authors this faunal province ranges from southwestern England to the eastern border of the Caspian Sea. Significant ammonoids of this province, the Upper Albian genera *Calliboplites*, *Pleuroboplites* and *Cymboplites*, all occur in the Gamba Group. A boreal influence is also documented in the Upper Aptian by *Paraboplites*, one of the most common genera in the Gamba

Group. This genus is restricted to the boreal realm too. In more detail, *Paraboplites trautscholdi*, hitherto known only from the former southern USSR was found now in Gamba.

In conclusion the hoplitinid faunal province is considered to expand as far to the southeast as to include the Gamba area (see figure 9, point 2). This result complements the extension first suggested by IMMIL & SIYED-EMAMI (1985). They documented that the ammonite fauna of the glauconitic limestone of the Kolah-Qazi-mountains (Central Iran) also belonged to the boreal hoplitinid province in middle Cretaceous times (see figure 9, point 1).

However, there is a considerable difficulty if these two regions were added to the hoplitinid faunal province. The Kolah-Qazi-mountains are situated on a well defined microplate, Central Iran. In contrast, the Tethyan Himalaya, including the Gamba area, is generally considered to be part of the northern edge of the Indian plate (see above), which is usually taken to be situated far more to the south in middle Cretaceous times (see Figure 9). One possibility to solve this problem would be to postulate that the Tethyan Himalaya was part of a separate microplate as well, as suggested by SINHA-ROY (1976) or SRIKANTIA (1987).

5. SUMMARY

This paper deals with the Cretaceous cephalopods from the Tethyan Himalaya of southern Tibet (Gamba and Duela area). Following a short review of previous studies the authors discuss three aspects in more detail.

5.1 GEOLOGY

The cephalopod fauna of eight sections and sampling points, respectively, is listed and their stratigraphic age is indicated. It ranges from Neocomian to Maastrichtian, with a concentration in the middle Cretaceous (Aptian - Cenomanian).

At one section (A) the stratigraphic results are used to reconstruct the tectonic disruption of the Gamba Group.

5.2 SYSTEMATICS

Twenty-nine cephalopod genera and species are described in detail and are figured. Two taxa belong to the nautilids, all

others are ammonites. Among the ammonites three new species are established: *Pleuroboplites* (*Pleuroboplites*) *robusticostatus*, *Lemuroceras tibeticum*, and *Tomohamites multituberculatus*.

5.3 PALAEOBIOGEOGRAPHY

The ammonites of the middle Cretaceous of the Tethyan Himalaya display a mixed biogeographic pattern. Some genera and species – as for example *Lemuroceras* – are known only from the southern temperate realm. But more genera exist that are characteristic for the hoplitinid faunal province of the northern temperate (boreal) realm: in the Upper Aptian *Paraboplites*, in the Lower Albian *Cymboplites*, and in the Upper Albian *Calliboplites* as well as *Pleuroboplites*. Therefore it is suggested that the Gamba area of southern Tibet was part of an extended hoplitinid faunal province and that in middle Cretaceous times the geographic position of the Tethyan Himalaya of southern Tibet was far more to the north.

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