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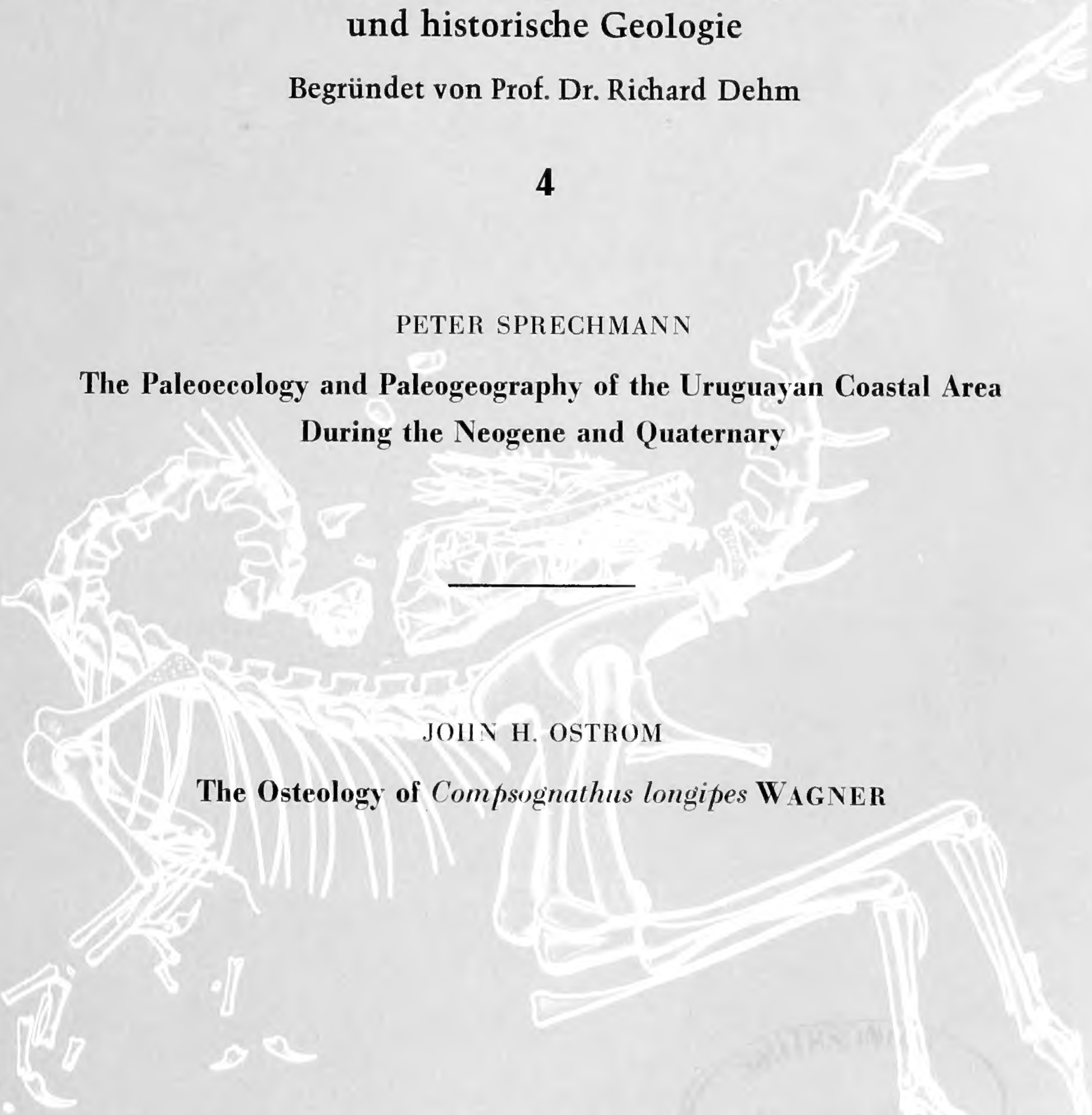

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The Paleoecology and Paleogeography of the Uruguayan Coastal Area During the Neogene and Quaternary[1]

BY

PETER SPRECHMANN[2])

With 16 text figures and plates 1—6

ABSTRACT

Miocene, Pleistocene and Holocene foraminiferal and molluscan assemblages found in water wells and outcrops distributed along nearly 700 km of the coastal plain of Uruguay were analyzed. Marine Miocene faunas were found only in the Chuy No. 364 well. Faunal associations using well data were correlated by ecostratigraphic unit. Depositional environments of Neogene and Quaternary foraminiferids and molluscan bearing strata were reconstructed. The distributional pattern of the various faunas that today populate the Río de la Plata are analyzed in reference to the salinity gradient of the estuary. As a tool the Curve of REMANE for foraminiferids and bivalves is used, as well as the distributional pattern of gastropods. Various criteria for the recognition of ancient estuaries are proposed. The early Holocene paleogeography in the Río de la Plata was reconstructed. A reconstruction of the Miocene and Quaternary geological evolution in the southernmost part of the Pelotas Basin (area of Chuy) since the Miocene is attempted. This is characterized by the alternation of marine (or marginal marine) and terrestrial depositional environments. The distribution of the paleozoogeographical littoral provinces of the eastern coast of South America during the Miocene and lower Holocene is elucidated.

KURZFASSUNG

Es werden Foraminiferen- und Mollusken-Vergesellschaftungen aus dem Miozän, Pleistozän und Holozän untersucht, die aus hydrogeologischen Bohrungen und Aufschlüssen entlang einer Strecke von ca. 700 km der Uruguayischen Küstenregion stammen. Die Assoziationen aus dem Miozän kommen aus einer einzigen Bohrung (Chuy Nr. 364). Die Fauna der Bohrungen wird ökostratigraphisch gegliedert; daraus werden die Ablagerungsräume im Neogen und Quartär rekonstruiert. Die gegenwärtige Zonierung verschiedener Faunen auf Grund von Salinitätsgradienten im La-Plata-Ästuar wird untersucht. Hierzu dient die REMANE-Kurve für die Foraminiferen und die Muscheln, sowie die Verbreitung der Schnecken. Daraus ergeben sich Kriterien für die Erkennung ehemaiger Ästuare. Die Paläogeographie des Gebietes des La-Plata-Ästuars während des unteren Holozäns wurde rekonstruiert. Die geologische Entwicklung im südlichen Teil des Pelotas-Beckens (Chuy-Gebiet) während des Miozäns und Quartärs wird rekonstruiert. Es ist gekennzeichnet durch ein Ineinandergreifen mariner (oder marginal mariner) und kontinentaler Verhältnisse.

Abschließend wird ein Überblick über die litoralen paläozoogeographischen Provinzen an der Ostküste Südamerikas während des Miozäns und Holozäns gegeben.

RESUMEN

Se estudian asociaciones de foraminíferos y de moluscos del Mioceno, Pleistoceno y Holoceno halladas en perforaciones hidrogeológicas y en afloramientos situados a lo largo de casi 700 km de la planicie costera del Uruguay. Unicamente se hallaron asociaciones Miocénicas en la Perf. Chuy N° 364. La fauna de las perforaciones se correlaciona ecoestratigráficamente. Se reconstruyen los ambientes de deposición de las secuencias del Neógeno y Cuartario portadoras de foraminíferos y de moluscos. Asimismo se analiza el padrón de distribución de la fauna

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[1]) Fossil-Vergesellschaftungen No. 76. — No. 75: BECKER, G., Clausthaler Abh., 1979.

[2]) DR. PETER SPRECHMANN, Institut und Museum für Geologie und Paläontologie, Sigwartstr. 10, D-7400 Tübingen, West-Germany.

que puebla actualmente el Río de la Plata en base al gradiente de salinidad, utilizándose la Curva de Remane de los foraminíferos y los bivalvos, y la distribución de los gastrópodos en el estuario. Se proponen varios criterios para la identificación de ambientes estuariales antiguos. Se reconstruye la paleogeografía de la región del Río de la Plata durante el Holoceno inferior. Por otra parte se describe la evolución geológica acaecida en el extremo sur de la Cuenca de Pelotas (área del Chuy) desde el Mioceno, caracterizada por la alternancia de depósitos marinos (o marginal marinos) y continentales. Finalmente se analiza la distribución de las provincias paleozoogeográficas litorales de la costa oriental de América del Sur durante el Mioceno y Holoceno inferior.

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I. PREFACE

This study was a research program for the development of micropaleontology and paleoecology in Uruguay with the support of Dr. R. Méndez-Alzola.

The Alexander von Humboldt Foundation supported the realization of this study by a research fellowship which was carried out in the Institut und Museum für Geologie und Paläontologie der Universität Tübingen. Dr. D. Herm acted as academic supervisor and coordinator and Dr. J. Wendt as referee. The publication of the results has been possible due to a financial support to the printing costs by the Alexander von Humboldt Foundation.

In this thesis J. da Silva helped with the preparation of bore-hole samples and evaluating lithological and stratigraphic data, A. Figueiras with the taxonomic determination of macro- and micromolluscs, V. Scarabino with the taxonomic determination of macromolluscs, H. Goso with the stratigraphic interpretation of Chuy N° 364, S. C. Bender Kotzian with the taxonomic determination of ostracods, and Dr. M. Scherer in the X-ray diffraction analysis. Valuable SEM work and photos were made with the expert help of Ms. R. Klett and Mr. W. Wetzel respectively.

Productive and beneficial suggestions, discussions and criticism were also made by Drs. A. Seilacher, F. Frölicher, F. Fürsich, Ch. Hemleben, W. v. Koenigswald, A. Liebau, W. Reif and D. Hilgemann.

For the taxonomic determination of the foraminiferids, comparisons were made with the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires) and Departamento de Paleontologia y Estratigrafia-Instituto de Geociências (Porto Alegre) with the assistence of Drs. E. Boltovskoy, A. Bertels and M. Madeira-Falcetta. The bore-hole samples were provided by the Instituto Geológico del Uruguay.

To all the above institutions and persons many thanks are due.

The largest helping of thanks are due to my wife Ana María who typed the manuscript and also my entire family and friends who kept me going and alive through these years of work.

II. INTRODUCTION: GEOLOGICAL SETTING

During the Cenozoic, sedimentation in Uruguay was predominately continental. Marine fossils were only found in exposures from the Camacho Formation (= Entrerriana) and Vizcaíno Formation (= Querandina); and in some subsurface (well) sequences attributed to the Chuy Formation.

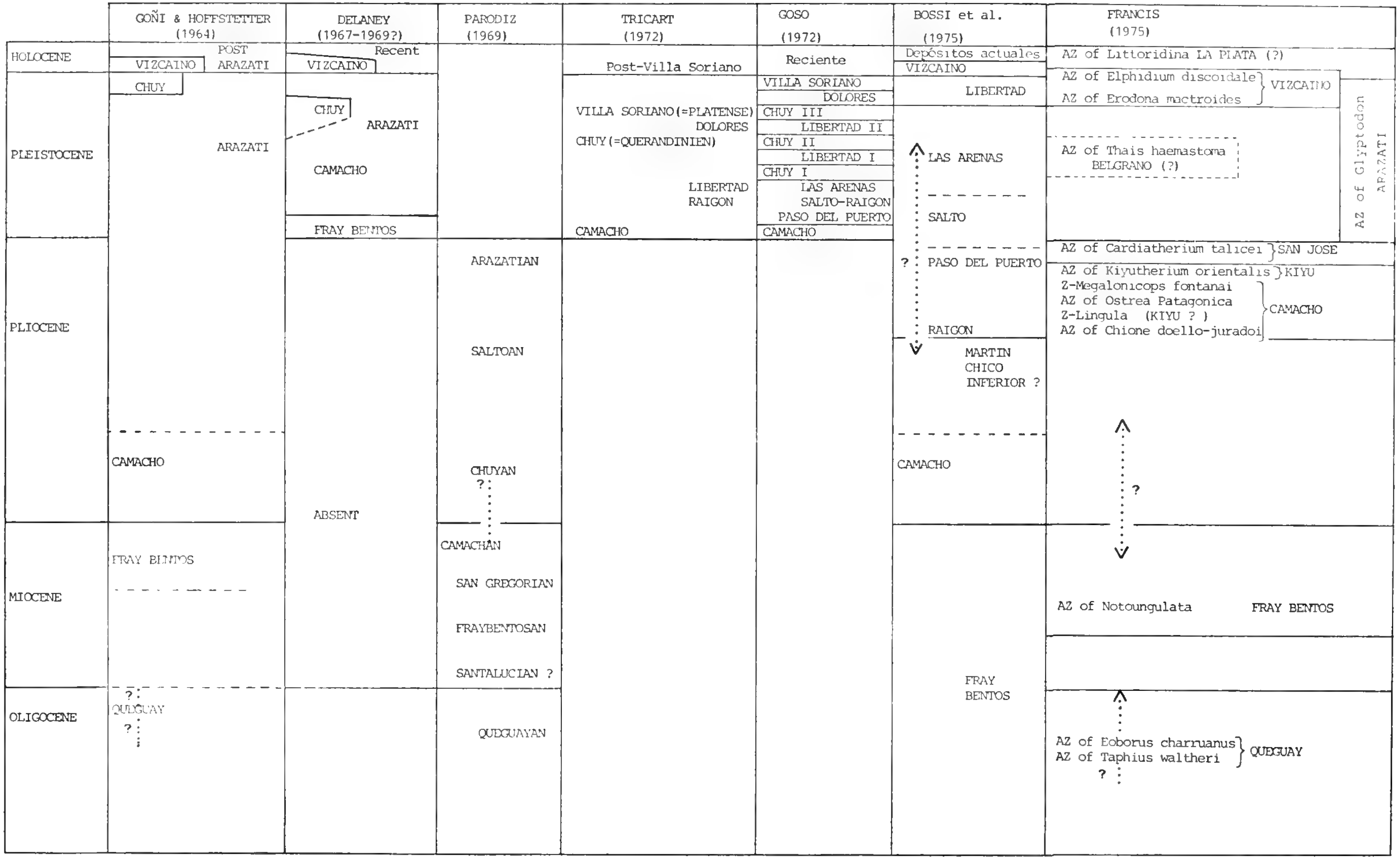
Features of regional geology in the area of study were summarized by BOSSI (1966), BOSSI et al. (1975) and DELANEY (1967, 1969 ?).

In the course of the last twenty years several schemes were presented in an attempt to explain the geological evolution of Uruguay during the Tertiary and / or Quaternary (BOSSI, 1966, 1969; BOSSI et al. 1975; CAORSI & GOÑI, 1958; DELANEY, 1967, 1969?; FRANCIS, 1975; GOÑI & HOFFSTETTER, 1964; GOSO, 1965, 1972; HARRINGTON, 1956; PARODIZ, 1969; TRICART, 1972). Some of these schemes are summarized in Table I. The analysis of these research publications shows a progressive increase in knowledge of the Uruguayan Cenozoic, although their conclusions were repeatedly contradictory. Furthermore extended regions were not even mapped in detail. No precise biostratigraphical studies have been made.

The greatest amount of disagreement is present in reference to relationships existing between stratigraphical units and their age (table I). The Camacho Formation is a good example of this situation. Two points of view have been given of its age: a) The Camacho Formation is ancient, belonging to the Miocene or lower Pliocene. This was the first opinion and was DARWIN's, and traditionally was shared by MENDEZ-ALZOLA, FRENGUELLI, SERRA, LAMBERT, FIGUEIRAS & BROGGI, PARODIZ, among others; b) The Camacho Formation is modern, being placed within upper Pliocene (FRANCIS, 1975; MONES, 1975) or into the lower Quaternary (BERTELS & MADEIRA-FALCETTA, 1977; CLOSS, 1966a; DELANEY, 1967, 1969?; ECOCHARD, 1970; GOSO, 1972; TRICART, 1972). The age given to this marker horizon has direct implications in the reconstruction of this area, as will be shown.

III. GEOGRAPHICAL POSITION AND CHARACTERISTICS OF THE BORE-HOLES

The paleontological material analysed in this work was obtained from drillings made during a search for drinking water, and from an outcrop located in Parque Lecocq. The wells were made by the "Instituto Geológico del Uruguay". The samples are deposited in the "Sección Hidrología y Servicio de Perforaciones" of the above mentioned institution. Almost all of the wells were drilled by the cable-tool method. There were no continuous cores available, and the samples came from drill cuttings which were in chip and/or powder form. As TOOMEY & WINLAND (1973) have shown, the information for an identifi-



	GOÑI & HOFFSTETTER (1964)	DELANEY (1967-1969?)	PARODIZ (1969)	TRICART (1972)	GOSO (1972)	BOSSI et al. (1975)	FRANCIS (1975)
HOLOCENE	VIZCAINO POST ARAZATI	VIZCAINO Recent		Post-Villa Soriano	Reciente	Depósitos actuales VIZCAINO	AZ of Littoridina LA PLATA (?)
PLEISTOCENE	CHUY ARAZATI	CHUY ARAZATI CAMACHO FRAY BENTOS		VILLA SORIANO (=PLATENSE) DOLORES CHUY (=QUERANDINIEN) LIBERTAD RAIGON CAMACHO	VILLA SORIANO DOLORES CHUY III LIBERTAD II CHUY II LIBERTAD I CHUY I LAS ARENAS SALTO-RAIGON PASO DEL PUERTO CAMACHO	LIBERTAD LAS ARENAS SALTO	AZ of Elphidium discoidale } VIZCAINO AZ of Erodona mactroides } AZ of Thais haemastoma BELGRANO (?) AZ of Glyptodon ARAZATI
PLIOCENE	CAMACHO	ABSENT	ARAZATIAN SALTOAN CHUYAN ?			? PASO DEL PUERTO RAIGON MARTIN CHICO INFERIOR ? CAMACHO	AZ of Cardiatherium talicei } SAN JOSE AZ of Kiyutherium orientalis } KIYU Z-Megalonicops fontanai AZ of Ostrea Patagonica Z-Lingula (KIYU ?) AZ of Chione doello-juradoi } CAMACHO ?
MIOCENE	FRAY BENTOS		CAMACHAN SAN GREGORIAN FRAYBENTOSAN SANTALUCIAN ?			FRAY BENTOS	AZ of Notoungulata FRAY BENTOS
OLIGOCENE	? QUEGUAY ?		QUEGUAYAN				AZ of Eoborus charruanus } QUEGUAY AZ of Taphius waltheri } ?

TABLE I:

Comparison of stratigraphic interpretations cation of facies and microfaunas can be obtained from examination of drill cuttings. Nevertheless, this fact reduces part of the available information, because the sedimentary structures are not preserved, and a portion of the macrofossils were broken.

The location of the bore-holes are shown in Fig. 1. They are located on the Uruguayan coastal plain area. The geographic inner limit of the coastal plain usually forms the contact with the underlying crystalline rocks. This contact is usually marked by a low sloping topographic escarpment which occurs between the 20 and 40 meter contour lines on the topographic maps (Delaney, 1967, 1969?).

For each well the geographic coordinates are given according to the "Carta del Uruguay al Millonésimo", edited in 1971 by the "Servicio Geográfico y Militar".

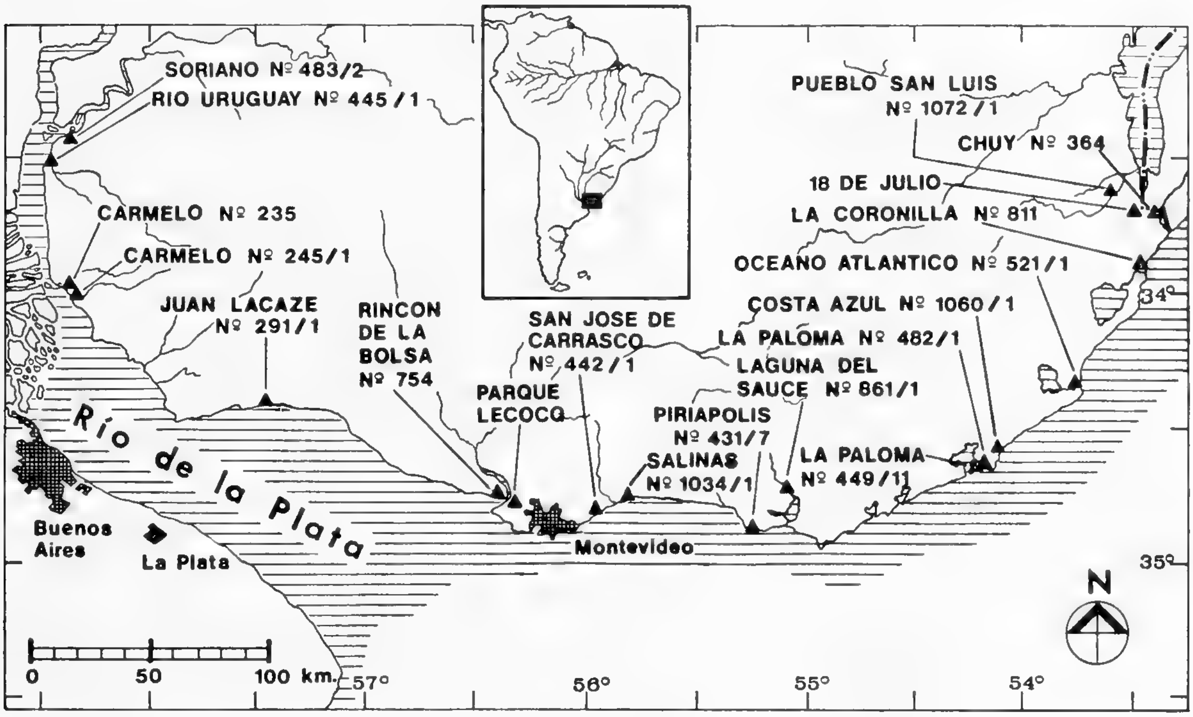


Fig. 1: Bore-hole locations dealt with in the text.

IV. METHODS AND MATERIAL

140—150 cm³ of sediment from each sample of drill cutting was picked clean of all megafauna (molluscs and barnacle plates). 35—40 cm³ of the above 140—150 cm³ was then inspected for microfauna. This is equivalent to a core sample 4—5 mm high and 10 cm in diameter.

Samples were prepared in 15 % H_2O_2, washed, sieved (0,063 mm mesh net), and dried. In a smaller number of samples, so marked in Chapter VI-B, the tests were separated out by flotation in carbontetrachloride. The samples were then sieved as above. The rest of the sediment was inspected under the binocular microscope to check for any remaining microfossils in the residue. All tests were removed, taxonomically identified and counted. The photographs were made with a Cambridge Stereoscan electron microscope Type Mark 2 A.

The illustrated and photographed foraminiferids are deposited in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, N°. 1978 VIII. The bore-hole samples, the molluscs of the wells, and remaining microfossils are deposited in the Instituto Geológico del Uruguay and the Departamento de Paleontología, Facultad de Humanidades y Ciencias, Uruguay.

V. MARINE MIOCENE

Marine Miocene faunas were found only in one well: Chuy N° 364.

A. Location of Chuy N° 364

City of Chuy, Rocha County (Lat. 33°42'S, Long. 53°26'W) (fig. 1). Geomorphologically this region belongs to the coastal plain of southen Brazil and tectonically to the Pelotas Basin (Delaney, 1965, 1966).

B. Previous paleontological, geological and stratigraphical studies

This well has been the object of repeated studies, as it presently gives the most complete information about the evolution of the upper Tertiary and Quaternary of Uruguay (Antón & Armstrong, 1973; Bertels & Madeira-Falcetta, 1977; Bossi, 1966; Closs, 1966a, 1970; Closs & Madeira, 1968a; Ecochard, 1970; Figueiras & Broggi, 1971, 1972/73; Francis, 1975; Goso, 1972; Malumian, 1970, 1972; Medina, 1962).

The following publications provide taxonomic descriptons of the macro- and microfossils previously found in Chuy N° 364: 1) Medina (1962) studied the macrofauna of a single fossil level, at depth of 124 m, 2) Closs & Madeira (1968a) studied the microfauans of this well and described three fominiferid bearing beds, and 3) Figueiras & Broggi (1971, 1972/73) compiled a review of the molluscan fauna of the Camacho Formation. They include in this study the Chuy well. They also reviewed systematically the species previously described by Medina (1962), and proposed a modified taxonomy, henceforth used in this work.

C. Distribution of the micro- and macrofaunas

The distribution of the Miocene micro- and macrofaunas is shown in Table II. Remarks:

1) Mollusca: The species which were described by Medina (1962) are marked with "M" in Table II. The species described by Figueiras & Broggi (1971, 1972/73) are marked with "FB" in the same Table. The disintegration of the drill cuttings with H_2O_2 for micropaleontological porposes gave additional material not previously cited. In Table II these fossils are marked with "x".

Some remarks are made about the systematics of molluscs in Table II: a) *Semele* sp., was described as *Semele bravardiana* (in litt.) by Figueiras & Broggi (1972/73), b) *Ostrea* sp., was previously cited as *Ostrea patagonica* by Figueiras & Broggi (1972/73), and c) *Americuna* sp.: is a form that probably represents a new species. The genus *Americuna* was described on the basis of a single living species, *Americuna besnardi* (Cox, Newell, Boyd et al., 1969; Klappenbach, 1962).

2) Brachiopoda: Medina (1962) shows the presence of *Bouchardia transplatina* Ihering, 1907, at a depth of 124 m.

3) Bryozoa: The presence of the bryozoans *Cellaria* and *Discoporella* between 124—125 m was previously indicated by Closs (1966a) and Closs & Madeira (1968a).

TABLE II
Faunal distribution in Chuy Nº 364

Depth/m	122 124	124 125	125 128	128 130	130 133
FORAMINIFERA					
Ammonia beccarii var. *parkinsoniana*	•		•	•	
Amphistegina gibbosa	———	———	———	□□□	— —
Buccella peruviana, s. l.	—	•	••		
Cancris sagra		••			
Cassidulina curvata			•		
Cassidulina laevigata	———	— —	—	•	
Cassidulina subglobosa	•				
Cibicides aknerianus	▭	□□□	□□□	••	
Cibicides "pseudoungerianus"	□□□	□□□	— —		
Cibicides sp.?	•				
Discorbinella? bertheloti f. *boueana*	— —	••	—	•	
Elphidium depressulum	•	•			
Elphidium discoidale	••	••		••	
Elphidium gunteri	•				
Elphidium aff. *sagrum*	— —			•	
Elphidium cf. *tuberculatum*	———	—	— —	••	•
Elphidium sp. A	•				
Elphidium sp.			•		
Fursenkoina sp.		•			
Lagena laevis f. *perlucida*		•			
Lagena sp.	•				
Lenticulina rotulata	••				
Marginulina gr. *tenuis*	•				
Massilina secans	•				
Miliammina fusca	•				
Miliolinella subrotunda		••			
Nonionella atlantica	••	••	•	—	
Nonionella auricula			•		
Nonion grateloupii	•	••	•		
Nonion sp. A	•				
Nonion sp. B				•	
Oolina melo	•		•		
Poroeponides lateralis	••				
Pyrgo nasuta	•		•		
Quinqueloculina agglutinata	•				
Quinqueloculina patagonica	•		•		
Quinqueloculina seminulum	••	••	••		
Quinqueloculina vulgaris	••				
Quinqueloculina sp. A		•	•		
Quinqueloculina sp. B		•			
Quinqueloculina sp. C	•				
Quinqueloculina div. spp. indet.	••	••	•	•	
Rotorbinella rosea	••				
Textularia gramen		•			
Textularia sp. A	•				

References: Numbers of foraminiferids:

• (1)
•• (2—5)
— (6—10)
— — (11—20)
——— (21—40)
□□□ (41—80)
▭ (81—160)

TABLE II (continued)
Faunal distribution in Chuy N° 364

Depth/m	113	115	117	120	122	124	125	128	130
	115	117	120	122	124	125	128	130	133
BIVALVIA									
Adrana sp.					x		x	x	
Americuna sp.					x				
Amiantis purpurata		FB	FB		x	FB			
Anadara sp.		FB			x	M			
Cardita sp.						FB		x	
Chione doello-juradoi		FB	x			M			x
Chione meridionalis burmeisteri			FB		x	M	FB		FB
Chione sp.					x	x			x
Codakia sp.		x							
Corbula caribaea						x			
Corbula pulchella						M	FB		
Cyrtopleura lanceolata ornata								FB	
Diplodonta vilardeboana						M			
Diplodonta sp.								x	
Glycymeris sp.									FB
Laevicardium sp.?						x			
Lucina sp.					x		x		
Mactra bonariensis					x	M			
Mactra sp.		x							
Mactrellona sp.		x							
Nucula sp.		x		x	x				
Nuculana sp.				x				x	
Ostrea sp.				FB	x		FB		
Plicatula sp.					x				
Semele sp.						FB			
Solen sp.?					FB				
Tagelus plebeius entrerianus							FB		
Tellina sp.					x				
Tivela (Eutivela) isabelleana						FB		x	FB
Tivela sp.						x			x
debris	x	x		x	x	x	x	x	x
GASTROPODA									
Anachis sp.		FB							
Caecum (Micranellum) sp.					x				
Calliostoma sp.					x	FB			
Epitonium sp.					FB	FB			
Halistylus columna					x	FB			
Iselica anomala						FB			
"*Marginella*" sp.				FB					
Odostomia sp.		x							
Olivancillaria urceus						M			
Olivella (O.) puelcha				FB					
Olivella sp.							x		
Polinices entrerriana						M			
Tegula sp.						x			
Turbonilla (Pyrgiscus) sp.		FB			FB	x			
Turritella sp.						M			
debris			x	x	x	x	x		
POLYPLACOPHORA									
Chaetopleura sp.						FB			
SCAPHOPODA									
Dentalium sp.						FB			

TABLE II (continued)
Faunal distribution in Chuy N° 364

Depth/m	113 115	115 117	117 120	120 122	122 124	124 125	125 128	128 130	130 133
BRACHIOPODA									
Bouchardia transplatina						M			
OSTRACODA[3])									
Bairdia								x	
Buntonia					x				
Caudites					x				
Callistocythere					x				
Cytherelloidea					x				
Cytheretta							x		
Cytheropteron					x				
Krithe					x				
Loxoconcha					x		x		
Mutilus					x				
Paradoxostoma					x				
Procytheropteron					x				
div. ssp. indet.					x	x			
BALANOMORPHA									
Balanus sp. (barnacle plates)	x	x		x	x	x	x	x	x
BRYOZOA									
Cellaria sp.					x	x	x	x	x
Discoporella sp.					x	x	x	x	x
ECHINOIDEA-REGULARIA									
spines					x	x	x	x	
plates						x			
CHONDRICHTHYES									
teeths					x		x		
OSTEICHTHYES									
debris							x		
OTOLITHS					x	x		x	

D. Microfaunal age

No planktonic foraminiferal associations are contained in the 122.10—133.00 m sequences in Chuy N° 364. Age dating was based on benthic species, which generally are not adequate for these purposes.

The microfauna of the 124—125 m sample is considered to be of Miocene age (Closs, 1966a, 1966b, 1970, 1971; Closs & Madeira, 1968a). The malacological associations of this well were included in the upper Miocene (Figueiras & Broggi, 1971, 1972/73). On the other hand Bertels & Madeira-Falcetta (1977) states that only Pleistocene foraminiferids are present in this well.

It must be pointed out, that the subdivision of the marine Miocene on the South American atlantic borderland is very controversial.

In Argentina the known assemblages are characteristic of shallow environments. Malumian & Masiuk (1973) distinguish between: 1) lower and middle Miocene assemblages; and 2) upper Miocene-Pliocene? assemblages. Bertels (1975) also distinguishes between two units: 1) the Superpatagonian, which is correlated with the Aquitanian; and 2) the Entrerrian, which is tentatively considered to belong to the Tortonian.

In southern Brazil the Miocene associations found in the Pelotas Basin contain numerous planktonic fo-

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[3]) Additional abundant ostracods were found in the 122.10—124.00 m level sample, and scarce specimens from the 124.00—125.40 m level. This material was also given to Prof. Kotzian for taxonomic identification.

raminiferal species, which are situated near the boundary of the *Globigerinatella insueta* and *Globorotalia foshi barisanensis*-Zones of the Trinidad sequences (CLOSS, 1966a, 1967, 1970). The *Globorotalia foshi barisanensis*-Zone is equivalent to the *Globorotalia foshi peripheroronda*-Zone (NOGUTI, 1975).

Species in the phylogenetic line *Globigerinoides bisphericus*-*Orbulina suturalis* are also found. They belong to the „*Orbulina*-Surface" (CLOSS, 1966a, 1966b, 1967). *Globigerinoides bisphericus* TODD, 1954 is considered by NOGUTI (1975) to be a synonym of *Globigerinoides sicanus* DE STEFANI, 1951.

The ages attributed to these zones is very controversial. Some authors place them in the Aquitanian/Burdigalian boundary; others in the Tortonian (CLOSS, 1966a, 1966b, 1967, 1970, 1971; CLOSS & MADEIRA, 1968a). NOGUTI (1975) believes that the planktonic foraminiferids found in the Pelotas Basin indicate a lower Miocene age. TROELSEN & QUADROS (1971) analysed the calcareous nanoplankton found at a depth of 716 m in the well N° 2-MO-1-RS, located in the Pelotas Basin. They indicate a probable lower Miocene age. BERTELS & MADEIRA-FALCETTA (1977, p. 446) indicated that the transgression in the Pelotas Basin took place in late Miocene times, i. e., approximately at Zone N 14 of BLOW. This is supported by the presence of *Globorotalia acostaensis*, *Globigerina nepenthes* and other planktonic species. They also state that the series described by CLOSS (1966a, 1970), as well as other lower Miocene assemblages, were probably reworked from adjacent areas.

Elphidium cf. *tuberculatum* was found in Chuy N° 364 between 122.10—133.00 m. The first reference of the existence of this species in South America was given by MALUMIAN (1970), who makes several remarks about the chronological worth of *Elphidium tuberculatum*. This species indicates an upper Miocene-Pliocene? age.

The associations found in Chuy N° 364 between 122.10—133.00 m certainly belong to the Miocene for three reasons:

1) They are related with the faunas of the Pelotas Basin, and those of the Entrerrian Stage (= Entrerriense) of Argentina;

2) Paleoclimatologically the associations of foraminiferids, gastropods and bivalves indicate warm waters. The existence of these warm temperatures in the area point out a Miocene age (see Chapter VIII); and

3) Marine Pliocene sediments seem to be absent in the South American atlantic borderland (BARTELS, 1975; BERTELS & MADEIRA-FALCETTA, 1977).

There are no objective facts that permit the assigning of these assembleges of Chuy N° 364 to a certain stage or epoch within the Miocene.

E. Correlations

The microfauna found in the 124—125 m sample has been correlated with the Miocene sequences belonging to the "*Orbulina*-Surface" from different wells of the Pelotas Basin (CLOSS, 1966a, 1970; CLOSS & MADEIRA, 1968a). On the other hand, the Miocene sequences belonging to the wells drilled in the Pelotas Basin were separated into four subdivisions, named Mio 1, 2, 3 and 4 (CLOSS, 1970). The Miocene foraminiferal associations belonging to Chuy N° 364 are similar to those of Mio 1.

The time-stratigraphic correlation between the Las Flores N° 24 and Monte Veloz N° 1 wells (Buenos Aires County, Argentina) is clear. The faunal sequences found in Chuy N° 364 between 122.10—133.00 m belong to the "*Protelphidium*" *tuberculatum-zone*. This local informal zone ("hemerozona") was proposed by MALUMIAN (1970) and represents the "Paranense-Entrerriense Transgression".

F. Paleoecology

1. GENERAL CHARACTERISTICS OF THE FORAMINIFERAL ASSOCIATIONS

Only benthic species were found, whereas the planktonic foraminifera were completely absent.

For the most part the species found still exist today. This offers an excellent opportunity to establish paleoecological conclusions supported by present conditions. It allows the utilization and evaluation of ecological and biogeographical data that are available from the living fauna today.

In analyzing the Miocene associations, data pertaining to the present time foraminiferal fauna of Brazilian oceanic coasts will be used repeatedly (BOLTOVSKOY, 1959a, 1961, 1970a, 1976; BOLTOVSKOY & LENA, 1966; CARVALHO & CHERMONT, 1952; CLOSS & BARBERENA, 1960a, 1960b, 1962; CUSHMAN & PARKER, 1931; MADEIRA-FALCETTA, 1974; NARCHI, 1956; PEREIRA, 1969; RODRIGUES, 1968, 1971, 1972;

Roettger, 1970, 1973; Ribas, 1971; Tinoco; 1955, 1965/66, 1971, 1972). Almost all available information is contained in papers based on the study of empty tests.

Unfortunately only a few studies have differentiated between foraminiferids bearing protoplasm at collection time, and those which belong to the thanatocoenosis.

Murray (1968, 1973, 1976) proposed two criteria which are useful for characterizing foraminiferal associations:

a. Diversity. In order to determine they diversity the Fischer α index was used. Only samples with more than 100 specimens were evaluated. The following index values were obtained (fig. 2): α = 6 (128.00—125.40 m), α = 5 (125.40—124.00 m) and α = 8 (124.00—122.10 m).

b. Triangular plot of suborders. In plotting this diagram the occurence of the suborders Rotaliina-Miliolina-Textulariina is presented in percentile figures (fig. 2). This diagram although not a triangle, is similar in information presented (Murray, 1973, fig. 103).

2. ANALYSIS OF MICROFAUNAL MIXING

The distribution of the microfauna in shallow waters is affected to a large extent by displacement and mixing (Herm, 1969; Liebau, 1975). The forms found in a certain fossil assemblage do not exactly represent an ancient biotope. They do not automatically identify an ancient biocoenosis, neither in its qualitative or quantitative spectrum. The fossil fauna is a post mortum association resulting in the interaction of sedimentological factors such as transport; and fossil diagenesis. Through this mechanism a vertically mixed condensate is formed which incorporates epi- and endobenthic elements mixing those forms originating from the phytal with those of the pelagic environments. Studies made in one and the same region, in which living foraminiferids and empty tests were examined separately, demonstrate this phenomena clearly. Examples with special reference to foraminiferids are summarized by Boltovskoy (1965), Boltovskoy & Wright (1976), Grabert (1971), Pujos (1971) and Murray (1973, 1976). The transport originated by the current and the wave action can cause a selection or separation which is characteristic for the fossil microfauna. In contrast, submarine displacements or slumps can produce unmodified unmixed allochthonous faunal spectra.

The analysis of mixed microfaunal assemblages must be identified as to the autochthonous and allochthonous components which generally are contained in microfossil assemblages.

First it is necessary to establish the type of sediments in which the foraminiferids were found, and the type of preservation of its tests.

The sediment lithofacies were described by Antón & Armstrong (1973). Between 133.00—130.00 m loose quartz in size from coarse sand to granules was found. They contain pebbles of the "San Miguel" granophyre. The few foraminiferal tests that were found show evident abrasion signs and are size sorted. The sediments of the 130.00—128.00 m level of the core sample was made up of coarse quartz sands to granules sized particles. They also contain gravels of the "San Miguel" granophyre, which indicates the proximity of the sediment source.

Grain size decreases gradually, whereas the number of foraminiferal tests increases gradually. Between 128.00—125.40 m loose coarse quartz sand to granule deposites were found. Among 125.40—124.00 m fine quartz sand to granule deposits were found. Between 124.00 and 122.10 m level the sample shows fine quartzose sands. It is subangular and well sorted.

Preservation of the foraminiferal tests: The difference between autochthonous and allochthonous elements is primarily established with the help of *Amphistegina gibbosa* as this species is an excellent indicator for salinity, temperature and bathymetry (see pages 15—16).

The tests from the adult specimens of this species are found:

a) well preserved, frequently showing small fractures.

b) with polished exterior wall.

c) poorly preserved with large fractures.

This preservation observed from the tests of *Amphistegina gibbosa* can be explained by the following: 1) The tests come from a high energy biotope, where they are exposed to rolling in the substrate while still alive. 2) In high energy environments the tests are affected by postmortem transport. Only tests with thick and resistent walls are preserved, the rest is destroyed. 3) The effect of selective postmortem transport, that is governed by sedimentological laws, and consequently a size sorting.

At 122.10—125.40 m the tests of *Amphistegina gibbosa* constitute 12 % of the foraminiferal assemblages. The type a) and b) of preservation could be explained with the concept of the "rolled-abraded" foraminiferids (in German "Abroll" Foraminiferen) introduced by Liebau (1975, p. 375) who specially applied it to *Amphistegina*. The "rolled-abraded" foraminiferids are forms adapted to live in the sediment and are subject to rolling during life. These are adapted in life to a high energy biotope, where active sediment transport takes place. Generally the tests of the "rolled-abraded" foraminiferids are found in great numbers, and almost always evidence of rolling and abrasion is found. Therefore this preservation

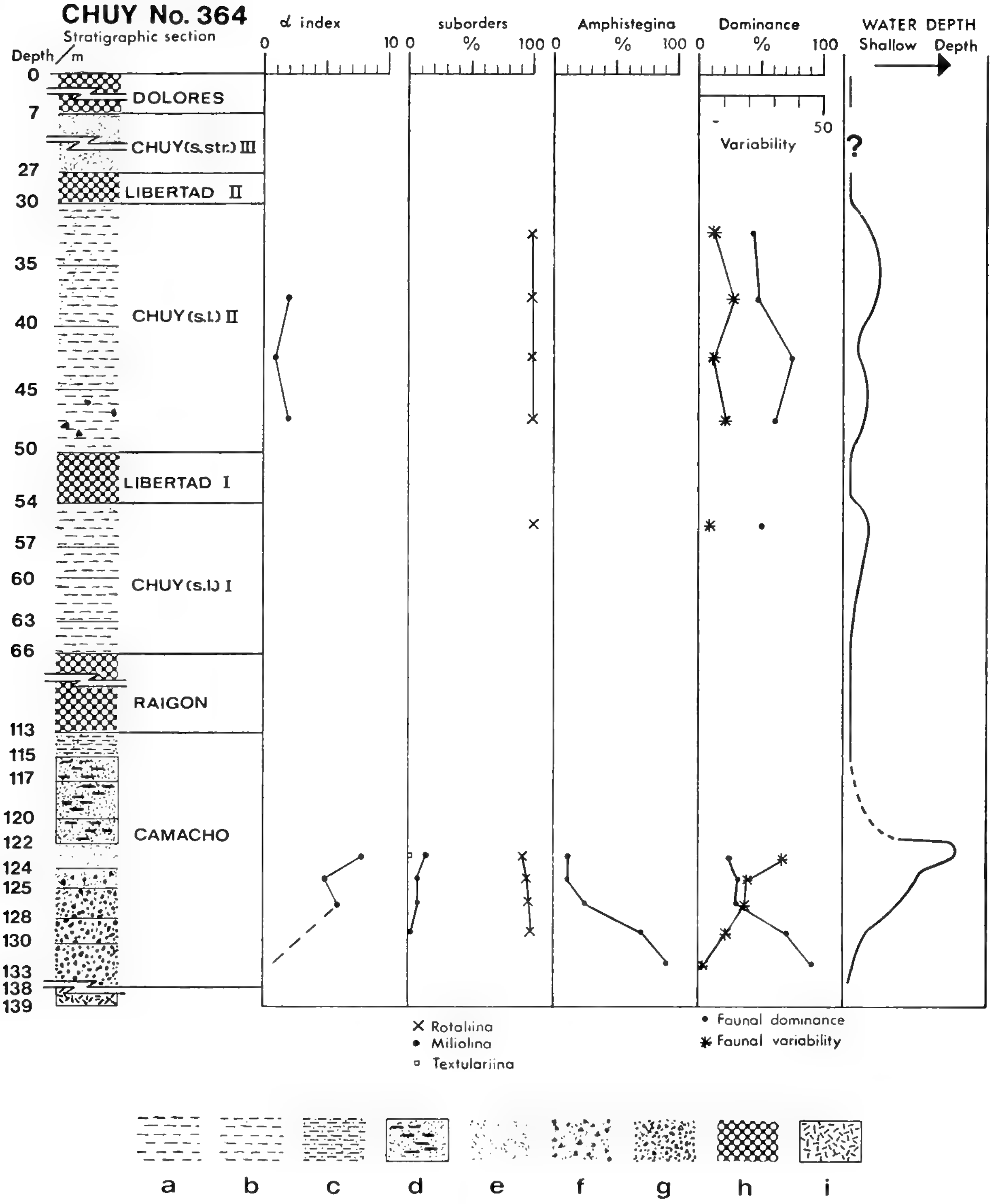


Fig. 2: Chuy N° 364 stratigraphic section. Different paramenters used in the text are plotted against the water depth. Key: a = mud, b = sandy silty mud, c = sandy mud, d = muddy sandstone, e = very fine to fine sands, f = poorly sorted sands of fine to granule quartz sand, g = coarse to granule sized quartz sand, h = terrestrial environments, i = bedrock. [Lithological section based on ANTON & ARMSTRONG's (1973) rock descriptions].

speakes for the fact that *Amphistegina gibbosa* is par-authochthonous. The term *par-authochtonous* is used according to Herm's (1969, p. 83) definition.

With the adult tests, juvenile specimens of *Amphistegina gibbosa* were also found. This fact confirms that this species is a par-autochthonous form. The presence of poorly preserved tests of *Amphistegina gibbosa* with large fractures and abrasions also points to the same cause as in 2) above.

The increase of the per cent fraction occurence of *Amphistegina gibbosa* between 125.40—133.00 m is directly proportional to the size of the sediments grains (fig. 2). That means that a selection takes place after death in connection with the fossil diagenesis, conserving the large and resistant tests, destroying the small and fragile ones. A size sorting effect also takes place.

Glauconitization of foraminiferids is frequent, and is confirmed by X-ray diffraction analysis. Glauconite fills the chambers and pores. Only rare specimens are filled with pyrite.

On the basis of these facts, the major part of the species are considered to be par-autochthonous. On the other hand, it is thought that *Miliammina fusca, Oolina melo, Lagena laevis* f. *perlucida* and *Lagena* sp. probably are allochthonous. This will be discussed later (see pages 17).

The relationship between numbers of species and per cent dominance gives additional criteria for the analysis of microfaunal mixing. It shows the relationship found, in each sample, between faunal variability and faunal dominance. In the Miocene associations found at 122.10—128.00 m stay within the normal variation range of the curve established by Walton (1964, fig. 26), which is typical for autochthonous assemblages.

3. POSSIBLE DEPOSITIONAL ENVIRONMENTS

In order to reduce the range of environmental possibilities the method proposed by Murray (1973) is applied, taking also into consideration the limitations indicated by Murray (1976). The summary diagram for the α index and the summary triangular plot are used (Murray, 1973, figs. 32, 101 and 102). The α index is very useful because it clearly restricts the environmental posibilities. The triangular plot, however, is not so obvious because the samples examined lie near the Rotaliina corner.

Synthesising both criteria, the environmental possibilities are reduced to: normal marine shelf seas, normal marine lagoons, and hypersaline lagoons.

In order to specify the environment the data given by the microfauna is used, in relation to the following factors:

a) Salinity. The α index values from 5 to 8 eliminate hypersaline environments.

The presence of the genus *Amphistegina* is most important. All finds known from the Present come from waters of normal marine salinity, or slight hypersality (Larsen, 1976; Murray, 1973). The species *Amphistegina lessonii* (and/or *Amphistegina radiata)* was also found on the atlantic South American coast in normal marine environments (Boltovskoy & Lena, 1966; Closs & Barberena, 1960b; Tinoco, 1965/66).

According to Murray (1973) the following genera contained in the analysed microfauna are characteristic for normal marine environments: *Amphistegina, Cassidulina, Cibicides, Buccella, Nonionella,* and *Textularia.* The fauna also includes the genera *Quinqueloculina* and *Miliolinella* (Miliolidae) which are characteristic for salinities above 32 per mil. The per cent incidence of these genera are:

Depth/m	122 124	124 125	125 128
Normal marine genera	75 %	88 %	84 %
Miliolidae	7 %	5 %	4 %
	82 %	93 %	88 %

The remaining genera can be found in normal marine conditions and also in hyper and hyposaline waters.

The presence of the bryozoan *Discoporella* gives an additional argument for the existence of a normal marine environment. Today this genus is virtually restricted to sands of the continental shelf (Driscoll, Gibson & Mitchell, 1971).

In summary, the faunas studied indicate normal marine salinities. Therefore *Miliammina fusca* is considered probably to be an allochthonous species, because it proliferated in hyper and hyposaline environments.

b) Temperature. *Amphistegina* is also important for determination of ancient temperatures during the Miocene, as was shown by Hornibrook (1968) and Todd (1976).

There are two points of view concerning the tolerance of *Amphistegina* to water temperature:

Murray (1973, p. 183—185) shows that *Amphistegina* is a stenothermal genus. All occurences in the oceans are encompassed by the 25°C surface-water isotherms for the southern and northern summers. The available information indicates that the critical temperature needed by *Amphistegina* for its reproduction seems to be close to 25°C. This genus can colonize areas where the water temperature is lower, but as it cannot reproduce, its colonization is temporary.

Larsen (1976, p. 18, 24) considers *Amphistegina* to be a tropical to warm subtropical genus. Its distribution can be limited by the 14° C winter isotherm of surface-water.

Murray and Larsen used different criteria for their interpretation of the range of geographical distribution of *Amphistegina*. Murray considers the capacity of reproduction as the basic criterion. Larsen cited laboratory experiments about the capacity of movement of different species of *Amphistegina* to suport his view.

At the present time, distribution of *Amphistegina* along the South American atlantic area confirms Murray's point of view. Today *Amphistegina* is only found north of 23° S latitude (Boltovskoy, 1961, 1965, 1976; Boltovskoy & Lena, 1966; Boltovskoy & Wright, 1976; Closs & Barberena, 1960b; Ribas, 1971; Rodrigues, 1968, 1971, 1972; Tinoco, 1965/66, 1971, 1972). It is a region of tropical warm waters, with mean annual temperatures higher than 24° C (Balech, 1954). The surface-water temperatures range between 24° C in February and 21° C in August (Boltovskoy, 1976, fig. 2).

Furthermore, adult and juvenile tests of *Amphistegina gibbosa* have been found in Chuy N° 364. This indicates the existence of high enough temperatures that the whole reproductive cycle of this species could be completed.

Cibicides aknerianus and *Cibicides "pseudoungerianus"* are the dominant species between 122.10 to 128.00 m. *Cibicides aknerianus* is a cosmopolitan species (Boltovskoy, 1970a). The present geographical range covers warm and cold water bodies. This species is frequent along the coasts of the State of Pernambuco (Boltovskoy & Lena, 1966) and in the Malvin or Falkland Islands area (Boltovskoy, 1965, 1970a; Boltovskoy & Wright, 1976). *Cibicides "pseudoungerianus"* is considered to be actually a common form on the South Brazilian and Uruguayan shelf seas, between 21—35° S latitudes. It is also frequent in the littoral zone of Pernambuco (Boltovskoy & Lena, 1966).

If we exclude the extinct forms, and the living ones such as *Miliammina fusca* and *Cassidulina subglobosa,* the remaining species belong to the present warm water faunas of the South American atlantic shelf areas. Most of them also live south of this parallel.

Rare specimens of *Buccella peruviana,* s. l. were found in the Miocene assemblages. The highest per cent occurence is 1,5 % in the 125.40—128.00 m level. This species is a characteristic living form in cold water bodies. Today its northermost occurence lies at 21°46'S latitude (Boltovskoy, 1961, p. 257, 338). This species was also found in the Cabo Frio area (Tinoco, 1955). *Cassidulina subglobosa* is considered to be an indicator of the Malvinian current (Pereira, 1969).

It must be concluded that the analized microfaunas indicate warm water temperatures equivalent to those existing today in the Cabo Frio area. It must also be pointed out that during the Miocene the world mean annual temperatures were undoubtedly higher than today (Brasier, 1975b; Schwarzbach, 1974).

c) Bathymetry. *Amphistegina* is also useful for bathymetric zonation. Different opinions are given in reference to its depth range. According to Murray (1973) *Amphistegina* possesses excellent reliability as a bathymetric indicator. All reported finds of this genus came from shallow waters (5—20 m, inner shelf). Boltovskoy & Lena (1966) and Boltovskoy & Wright (1976) agreed with this point of view. In contrast other evidence is given that indicates that *Amphistegina* lived at somewhat greater depth (Bandy, 1956, 1964; Brasier, 1975a; Poag & Sidner, 1976; Tinoco, 1972). Additional data from the literature is summarized by Larsen (1976, p. 18).

These apparent contradictions have been recently explained. Todd (1976) concluded that different species of *Amphistegina* have their major concentrations in different environments and different depths. Furthermore, there is a relationship between the shape of the tests of *Amphistegina* and the environment where it lives. Probably fragile and complanate tests imply deeper water more distant from shore, than the thick, heavy walled tests that would be more suitable to withstand the turbulence. Larsen (1976, fig. 3) found that different species of *Amphistegina* live within distinct depth intervals. Shallow water species are thick shelled (small diameter/thickness ratio) while the deeper species are thin shelled. Generalizing, there is a variation from almost globular shallow species to almost plate-like depth species. This means that there is a general tendency towards increasing shape index with increasing depth (Larsen, 1976, table 1). It is suggested that this is the consequence of a relationship between the surface area to the amount of incoming light, because this genus is dependant on symbionts.

The adult tests of *Amphistegina* found in Chuy N° 364 are thick or globular shaped and heavy walled. That means that they belong to the shallow water species, i. e. a shallow environment.

Other genera which are useful for bathymetric zonation are *Elphidium* and *Quinqueloculina.* Several *Elphidium* species are characteristic for shallow environments, particularly *Elphidium discoidale. Quinqueloculina* is regularly found on the inner shelf (Bandy, 1964; Boltovskoy, 1965; Boltovskoy & Wright, 1976; Murray, 1973; Walton, 1964). The remaining genera and/or species have a low reliability as far as depth zonation goes.

Moreover the foraminiferal fauna is different from that of the outer shelf. In the Miocene assemblages planktonic foraminiferids are absent. The benthic genera which are typically found in greater depths, such as *Nodosaria, Uvigerina, Fissurina, Gyroidina, Lenticulina, Lagena,* are nearly completely absent. In their diversity the investigated associations are also different from those of the outer continental shelf.

Summarizing, the assemblages indicate nearshore shelf environments.

d) Substrate. The facies found between 122.10—133.00 m are made up of sandy deposits that were accumulated during a progressive overlap.

Lists were made that established relationships between the substrate type and the distributional pattern of certain genera and/or species of benthic foraminiferids (Boltovskoy, 1965; Boltovskoy & Wright, 1976; Murray, 1973). Sometimes the data offered are contradictory. This is also valid for *Amphistegina* (Larsen, 1976, p. 17, 18; Murray, p. 185, 248). This difference originates in the fact that many genera and/or species do not possess a strict dependence on a certain facies type. Deposits formed by unconsolided sands are characterized by a lack of or low vegetation growth. This fact could partially explain the absence of *Peneroplis, Marginopora, Amphisorus,* and other common genera that actually develop in the warm water zone of the South American atlantic coast. These genera grow on sea flora, especially seagrasses (Brasier, 1975b; Murray, 1973). This fact could also explain the low abundance of other Miliolids. It must be noted that sea grasses are today, significantly, absent from the major part of the South American coasts, except the tropical Atlantic region and a few finds from Chile and Argentina. This fact is related to the evolution of the seagrass communities in this region (Brasier, 1975b; Hartog, 1970).

According to Murray (1973) the genera *Oolina* and *Lagena* live on muddy sediments. Therefore *Oolina melo, Lagena laevis* f. *perlucida* and *Lagena* sp. could be considered as allochthonous forms.

4. PALEOECOLOGICAL RESULTS SUPPORTED BY FORAMINIFERAL ASSOCIATIONS

The foraminiferids indicate a normal marine shallow environment with warm waters. The substrate probably had no sea flora cover.

No studies have been made of living foraminiferids from normal marine lagoons in the South American tropical region that could be used to establish relationships. Using available information, a normal marine lagoon as a possible depositional environment is rejected. The present living foraminiferal assemblages found in this type of lagoon differ clearly from the associations found in the Chuy drilling (see Murray, 1973, table 12).

The characteristics of the foraminiferal assemblages of Chuy N° 364 are similar to the idealized depth zonation on a continental shelf gived by Murray (1973, p. 168). This shows a nearshore shelf environment, particularly within the turbulence zone. The foraminiferal assemblage possess a low diversity ($\alpha = 5—8$) and the triangular plot show an evident predominance of Rotaliina (fig. 2). The values are typical for this idealized depth zone. The value number of the faunal variability and the faunal dominance also indicates the same environment, according to Walton's (1964) method.

This environment is related to a nearshore sedimentation zone. The assemblages are par-autochthonous and distinctive for high energy moving waters. A rolling of the microfossils during life is evident. The empty tests can also be worn down by rolling after death. Subsequently glauconitization took place. This type of fossilization can be explained at least in the following ways:

a) A fraction of the test were transported to an adjacent area, where somewhat lower energy conditions exist. The test accumulated in a basin or a pan situated on the shelf sea. This acted as a trap, where a great number of tests, larger fossil debris, and organic matter was accumulated. This process was described by Whatley & Wall (1969). In this situation slight reduction conditions appear, which produce the glauconitization.

b) Weak influence of hyposaline waters or fluviatile sediments led to slight anaerobic conditions. In this situation glauconitization took place as described by Seigle (1970) in the Yabucoa Bay. Large fluviatile influences prevent glauconitization. Selley (1976, p. 78) points out that glauconite occurs in ancient sediments of marine origin.

In high energy waters a reworking of the foraminiferids took place. These reworked tests are mostly glauconitized and subsequently rolled. This foraminiferal preservation is typical for this kind of depositional environment.

The following events occured during a transgression. Information found at the 133.00—130.00 m level of the sample indicate the beginning of the transgression. The greatest water depth was reached at the 124.00—122.10 m level of core sample. Here the foraminiferal assemblage has its major diversity and abundance. The sandy deposits contain the finest grain sizes, and are well sorted.

The foraminiferal assemblages also indicate the existence of a transgressive sequence. This is shown by an increase in the faunal variability, and a decrease in the faunal dominance (fig. 2). Both concepts are used according to Walton's (1964) criteria.

The fossil assemblages found between 122.10—113.00 m contain only molluscan fragments and barnacle plates. No microfossils are present. This sequence may have been deposited during a regression.

VI. QUATERNARY

A. General considerations and previous works on foraminiferal microfaunas

During the Quaternary only local transgressions took place in the South American atlantic borderland. This fact explains the low number of papers referring to Quaternary foraminiferids in this zone.

In Uruguay studies were made only by Closs (1966a) and Closs & Madeira (1968a). Brief references are also given by Bertels & Madeira-Falcetta (1977) and Closs (1970).

The present knowledge of the Quaternary foraminiferal associations found in Brazil is summarized by Bertels & Madeira-Falcetta (1977). Quaternary sequences of bore-holes drilled in the Pelotas Basin contain foraminiferal associations characterized by low diversities. Only 15 benthic and a single planktonic species were found (Closs, 1970).

In Argentina the exposures show littoral deposits, lying subparallel to the shore, from Buenos Aires to the southernpart of the country. The foraminiferal assemblages also have low diversities (Bertels, 1975; Bertels & Madeira-Falcetta, 1977; Boltovskoy, 1959b; de Carli & Farinati, 1975; Malumian, 1970).

B. Distribution of the microfossils and macrofossils

The distribution of the associations found in each bore-hole and outcrop is given in Tables III—XVII. The geographic location of the wells and exposures, and the identified stratigraphic units, are also presented. Complete lithological profiles of the bore-holes are not given for the following reasons: 1) previous publication, 2) no autorization was obtained for the publication of the remaining geological sections.

PUEBLO SAN LUIS (WELL) N° 1072/1

Well location: Pueblo San Luis, Rocha County (Lat. 33°36' S, Long. 53°43' W). Length of drill column: 42 m.

Paleontology: Distribution of fossils is shown in Table III.

TABLE III
Faunal distribution in San Luis N° 1072/1

Depth/m	21 25	25 28	28 29	29 30	30 32	32 35	35 36
FORAMINIFERA							
Ammonia beccarii var. *parkinsoniana*	•		•	——			
Elphidium discoidale			•	—			
Elphidium gr. *excavatum*				•			
Elphidium galvestonense				•			
Elphidium gunteri				••			
Elphidium div. spp. indet.	••	••	••	——			
BIVALVIA							
Pitar (P.) rostrata							x
debris	x	x	x	x	x	x	x
GASTROPODA							
Littoridina sp.				x			
debris				x			
OSTRACODA	x		x	x			x
BALANOMORPHA							
barnacle plates					x		
PLANTAE							
debris					x		

References: Numbers of foraminiferids: • (1) •• (2—5) — (6—10) —— (11—20)

Lithostratigraphic units: These are established using the criteria indicated in Chapter VII. The following units were identified: Raigón Formation (42—36 m), Chuy (sensu lato) I (36—21 m), Libertad I (21—17 m), Chuy (sensu lato) II (17—6 m), and Libertad II (6—0 m).

CHUY (WELL) N° 364

Well location and previous studies: See Chapter V—A and V—B.

Distribution of Quaternary micro- and macrofauna: is indicated in Table IV.

TABLE IV
Faunal distribution in Chuy N° 364

Depth/m	2 7	30 35	35 40	40 45	45 50	54 57	57 60	60 63	63 66
FORAMINIFERA									
Ammonia beccarii var. *parkinsoniana*		———	▬	▭	▭	— —			
Bolivina striatula			—		••				
Bolivina sp.			—	••					
Buccella peruviana, s. l.		••	•		—				
Bulimina cf. *affinis*					•				
Buliminella elegantissima		—	▭	—	••				
Cibicides "pseudoungarianus"					•				
Discorbis sp.?					•				
Elphidium discoidale		••	———	—	— —	••			
Elphidium gr. *excavatum*		••	———	••	— —	••			
Elphidium gunteri			••		— —				
Elphidium sp. B			•						
Elphidium div. spp. indet.		— —	— —	— —	———	—			
Fissurina laevigata			•						
Fissurina sp.			•						
Quinqueloculina sp.			•						
(+)									
BIVALVIA									
Erodona mactroides						x	x	x	x
debris					x	x	x	x	x
OSTRACODA									
Argilloecia			x						
Bensonia			x						
Callistocythere			x		x				
Cyprideis			x	x	x	x			
Cytherella					x				
Cytheropteron				x	x				
Harmanites?				x					
BALANOMORPHA									
Balanus sp. (barnacle plates)		x	x	x		x			
ECHINOIDEA-IRREGULARIA									
spines			x						
PLANTAE									
pollen	x	x							

(+) Closs & Madeira (1968a) also recorded the presence of *Elphidium galvestonense* between 54.20—57.60 m.

References: Numbers of foraminiferids:

•	(1)	••	(2—5)
—	(6—10)	— —	(11—20)
———	(21—40)		
▭	(81—160)	▬	(> 160)

Stratigraphy: See Chapter VII.

COSTA AZUL (WELL) N° 1060/1

Well location and previous studies: This bore-hole was drilled in Balneario Costa Azul, in the property of O.S.E., Rocha County (Lat. 34°37' S, Long. 54°09' W) and attained the depth of 66 m. The lithofacies of this well were described by Da Silva (1975).

Paleontology: The distribution of the micro- and macrofauna is shown in Table V.

TABLE V
Faunal distribution in Costa Azul N° 1060/1

Depth/m	19 21	21 25	25 28	28 32
FORAMINIFERA				
Ammonia beccarii var. *parkinsoniana*	□□□	••	•	•
Buccella peruviana, s. l.	▬	———	•	••
Buliminella elegantissima	—			
Cibicides aknerianus	•			
Discorbis peruvianus	•	•		
Discorbis gr. *vilardeboanus*	••			
Discorbis williamsoni f. *praegeri*	— —			•
Discorbis gr. sp. "A"	•			
Discorbis div. spp. indet.	•	••		••
Elphidium discoidale	———	••	•	
Elphidium gr. *excavatum*	—			
Elphidium gunteri	••			
Elphidium div. spp. indet.	••	•		•
Guttulina problema	•			
Oolina melo	•			
Poroeponides lateralis	•	•		
Pyrgo nasuta	•			
Pyrgo ringens patagonica	•			
Quinqueloculina seminulum	•			
Quinqueloculina sp.	•			
Rosalina sp. ?	•			
Textularia sp.	•			
BIVALVIA				
Amiantis purpurata	x	x	x	
Brachidontes (B.) rodriguezi	x	x		
Corbula caribaea	x			
Corbula lyoni		x		
Corbula sp.	x		x	
Crassinella cf. *maldonadoensis*	x			
Mactra patagonica	x	x		
Mactra sp.	x	x	x	
Mytilus sp.	x			
Ostrea sp.	x			
Plicatula cf. *gibbosa*			x	

TABLE V (continued)
Faunal distribution in Costa Azul N° 1060/1

Depth/m	19 21	21 25	25 28	28 32
GASTROPODA				
Caecum sp.	x			
Crepidula aculeata	x			
Epitonium aff. *unifasciatum*		x		
Halistylus cf. *columna*	x		x	
Ocenebra cala		x		
Olivella (O.) cf. *tehuelcha*	x			
OSTRACODA	x	x		x
BALANOMORPHA				
Balanus sp. (barnacle plates	x	x	x	
MALACOSTRACA				
cheliped	x			
BRYOZOA	x			
ECHINOIDEA-CLYPEASTEROIDEA				
Mellita sp.		x		
ECHINOIDEA-IRREGULARIA				
spines	x	x		

References: Numbers of foraminiferids:

•	(1)	••	(2—5)
—	(6—10)	— —	(11—20)
———	(21—40)	□□□	(41—80)
▬	(> 160)		

LA PALOMA (WELL) N° 482/1

Well location and previous studies: La Paloma City, Rocha County (Lat. 34°39′ S, Long. 54°09′ W), in the Parque Andrecito. Length of drill column: 73.30 m. The lithofacies were described by DA SILVA (1975) and SCARABINO (1974).

Paleontology: The first paleontological approach of the well was given by SCARABINO (1974), who mainly studied the macro-molluscs, which are marked with "S" in Table VI. The disintegration of the drill cuttings with H_2O_2 for micropaleontological porposes gave scarce foraminiferids. Small and juvenile molluscs were also found, which are marked with "x" in Table VI. The fossils are mostly abraded and transported.

TABLE VI
Faunal distribution in La Paloma N° 482/1

Depth/m	3.9 5.8	5.8 7.8	7.8 9.0	9.0 10.0	10.0 10.9	10.9 12.9	12.9 13.9	13.9 18.0
FORAMINIFERA								
Ammonia beccarii var. *parkinsoniana*	●							
Buccella peruviana, s. l.	●●							
Discorbis williamsoni f. *praegeri*	●							
Poroeponides lateralis					●●			
Quinqueloculina sp.	●							
BIVALVIA								
Abra uruguayensis			x					
Amiantis purpurata			S					
Brachidontes (B.) rodriguezi	x		x		x			
Cardita (C.) plata			x		x			
Chlamys tehuelcha			S		S			
Crassinella cf. *guadalupensis*					x			
Crassinella maldonadoensis			x					
Glycymeris longior		S	S				x	x
Mactra isabelleana	x		S	S	S		x	
Mactra cf. *marplatensis*		x						
Mytilus platensis			S		x			x
Ostrea equestris			S		S	S		x
Ostrea puelchana			S		S			
Ostrea sp.				x	x	x	x	
Sphenia hatcheri			x					
Strigilla (R.) cf. *rombergii*	x							
GASTROPODA								
Anachis isabellei			x				x	
Anachis moleculina							x	
Caecum (Caecum) sp.			x					
Calliostoma sp.?			x					
Crepidula aculeata			S		x			
Crepidula protea			x		S			
Halistylus columna	x		S		S		x	
Odostomia (C.) aff. *jadisi*			x					
Odostomia sp.?			x					
Olivella (O.) tehuelcha			x					
Tegula (A.) cf. *patagonica*			x					x
Turbonilla (Bartschella) sp.			x					
Turbonilla (Strioturbonilla) sp.			x					
Turbonilla sp.					x			
Urosalpinx rushi			x		x			
Vitrinellidae?			x					
OSTRACODA	x				x			
BALANOMORPHA								
Balanus sp. (barnacle plates)	x			x	x		x	x
BRYOZOA	S		S					
SERPULIDAE			x					
PLANTAE								
debris					x			

References: Numbers of foraminiferids: ● (1) ●● (2—5)

PUERTO LA PALOMA (WELL) N° 449/11

Well location and previous studies: La Paloma, Rocha County (Lat. 34°39′ S, Long. 54°09′ W). The bore-hole was drilled in the Puerto Nuevo area. Length of drill column: 8.50 m. DA SILVA (1975) and SCARABINO (1974) described the lithofacies.

Paleontology: The macro-molluscs were described by SCARABINO (1974), and mare marked with "S" in Table VII. Micropaleontological study allowed identification of foraminiferids and micro-molluscs. The latter are marked in Table VII with "x". The microfossils of the 7.50—8.00 m drill cutting level were found in 140 cm³ of sediment. The tests were separated out by flotation in CCl_4. In this way more information about diversity and faunal spectrum is obtained. The microfauna of the remaining drill cutting was prepared in H_2O_2 using 35—40 cm³ of sediment.

TABLE VII
Faunal distribution in Puerto La Paloma N° 449/11

Depth/m	0.0 0.5	0.5 2.5	2.5 3.5	3.5 4.5	4.5 5.0	5.0 6.5	6.5 7.5	7.5 8.0	8.0 8.5
FORAMINIFERA									
Ammonia beccarii var. *parkinsoniana*			••		••		•	—	
Baggina sp.?								•	
Buccella peruviana, s. l.	———	••	— —	—	— —	———	— —	▬	••
Cibicides aknerianus								••	
Dentalina communis								•	
Discorbis peruvianus		•	••					•	
Discorbis williamsoni f. *praegeri*					•			— —	
Discorbis sp.								•	
Elphidium discoidale	••		••	•	••	•	••	———	•
Elphidium gr. *excavatum*								••	
Elphidium galvestonense								•	
Elphidium gunteri	•				•	•		••	
Elphidium div. spp. indet.	••	•	••	••			•		
Flintinella sp.								•	
Guttulina plancii						•			
Miliolinella subrotunda	••		•	•		•	•	———	
Miliolinella sp.			••					••	
Oolina melo								•	
Poroeponides lateralis	— —		••	—	— —	— —	— —	▭	••
Pyrgo nasuta								•	
Pyrgo ringens patagonica		•			•		••	••	•
Pyrgo sp.							••		
Quinqueloculina angulata f. *typica*								•	
Quinqueloculina atlantica							•	••	
Quinqueloculina aff. *frigida*					•				
Quinqueloculina intricata								•	
Quinqueloculina seminulum	••	•	•	••	••	•	••	— —	•
Quinqueloculina sp. D								•	
Quinqueloculina sp. E								—	
Quinqueloculina div. spp. indet.	••			••	—	•	••	— —	•
Textularia gramen							•		
Textularia sp. B								•	

References: Numbers of foraminiferids:

• (1)
•• (2—5)
— (6—10)
— — (11—20)
——— (21—40)
▭ (81—160)
▬ (> 160)

TABLE VII
Faunal distribution in Puerto La Paloma N° 449/11
(continued)

Depth/m	0.0 0.5	0.5 2.5	2.5 3.5	3.5 4.5	4.5 5.0	5.0 6.5	6.5 7.5	7.5 8.0	8.0 8.5
BIVALVIA									
Brachidontes (B.) rodriguezi	S	S	S	S	x	S	x	S	x
Cardita (C.) plata			x			x		S	
Crassinella guadalupensis						x			
Crassinella maldonadoensis	x			x	S	x	x	x	
Diplodonta vilardeboana				S					
Glycymeris longior		S	x	S	S	S	S	S	x
Mactra isabelleana	S	S	S		S		S	S	
Mactra marplatensis			x			x			
Mactra sp.	x		x				x		x
Mytilus platensis				S				S	
Ostrea equestris?	S								
Ostrea puelchana		S		S			S	S	
Ostrea sp.	x								
Petricola sp.				x					
Pleuromeris sanmartini				x					
Sphenia hatcheri				x					
GASTROPODA									
Acmaea subrugosa		S		S			S	S	
Buccinanops sp.			x						
Caecum (Brochina) sp.						x		x	
Caecum sp.	x			x					
Crepidula aculeata		S	x	S	S	S		S	
Crepidula protea					S				
Diodora patagonica						S	S		
Epitonium sp.					S				
Halistylus columna	S		x	x	x	S	S	x	
Littoridina australis	S								
Ocenebra cala	x		x	S			x		
Olivella (O.) puelcha		S			S		S		
Olivella (O.) tehuelcha				S					
Tegula (A.) patagonica							S	S	
Triphora sp.			x			S			
Turbonilla sp.	x								
Urosalpinx rushi		S			S	x	S		
POLYPLACOPHORA									
Chaetopleura isabellei							S		
Chaetopleura sp.			x						
OSTRACODA	x	x	x	x	x	x	x	x	x
BALANOMORPHA									
Balanus sp. (barnacle plates)	x	x	x	x	x	x	x	x	
BRYOZOA	x		x	x	x	x	x	x	x
ECHINOIDEA-IRREGULARIA									
spines	x				x				
ALGAE	x	x	x	x	x	x	x	x	x

LA CORONILLA (WELL) N° 811

(Lat. 33°54′ S, Long. 53°31′ W). Unfossiliferous.

OCÉANO ATLÁNTICO (WELL) N° 521/1

(Lat. 34°20′ S, Long. 53°48′ W). Unfossiliferous.

18 DE JULIO (WELL) N° 801/1

(Lat. 33°41′ S, Long. 53°33′ W). Unfossiliferous.

LAGUNA DEL SAUCE (WELL) N° 861/1

Located in the property of I.G.G.A.M. Uruguay; 8 km north of the km. 119.5 of the national road N° 5, in Maldonado County. Unfossiliferous.

PIRIÁPOLIS (WELL) N° 431/7

Well location and previous studies: Piriápolis City, Maldonado County (Lat. 34°53′ S, Long. 55°16′ W), in the Jardín de los Angeles district. Length of drill column: 23 m. Maytía de Scarabino (1974) described the lithofacies and molluscs of this bore-hole (Table VIII). *Littoridina australis* was shown to be the dominant species between 5.50—7.00 m.

Paleontology: No foraminiferids were found.

TABLE VIII

Faunal distribution in Piriápolis N° 431/7

Depth/m	5.5 7.0	7.0 9.0
BIVALVIA		
Anomalocardia brasiliana	x	x
Ostrea puelchana	x	
GASTROPODA		
Littoridina australis	x	x
OSTRACODA	x	

SALINAS (WELL) N° 1034/1

Well location and previous studies: Salinas, Canelones County (Lat. 34°46′ S, Long. 55°49′ W), in the place of the O.S.E. reservoir tank. Length of drill column: 72.70 m. The lithofacies of this bore-hole were studied by Da Silva (1975).

Paleontology: The distribution of the fossils found is shown in Table IX.

TABLE IX

Faunal distribution in Salinas N° 1034/1

Depth/m	28 31	31 32	32 34	34 37	37 39
FORAMINIFERA					
Ammonia beccarii var. *parkinsoniana*		••	—	••	•
Bolivina striatula		•	— —		•
Bolivina div. spp. indet.	•	••	—		
Buccella peruviana, s. l.			—	••	
Buliminella elegantissima	••	••	□□□	—	••
Cibicides aknerianus			••		
Discorbis sp.			•		
Elphidium discoidale	••	••	□□□	••	••
Elphidium gunteri			•		
Elphidium div. spp. indet.	••	••	— —	—	••
Fissurina laevigata			••		
Lagena laevis f. *perlucida*			•		
Lenticulina limbosa			•		
Nonionella atlantica			••		
Nonion tisburyensis			••		
Pyrgo nasuta			••		
Pyrgo sp.			•	•	
Reophax artica			•		
BIVALVIA					
debris	x	x	x	x	x
OSTRACODA	x		x	x	x
BALANOMORPHA					
Balanus sp. (barnacle plates)			x		
ECHINOIDEA-IRREGULARIA					
spines			x		

References: Numbers of foraminiferids:
• (1) •• (2—5)
— (6—10) — — (11—20)
□□□ (41—80)

SAN JOSÉ DE CARRASCO (WELL) N° 442/1

Well location and previous studies: San José de Carrasco, Canelones County (Lat. 34°51′ S, Long. 55°58′ W). Length of drill column: 73 m. Maytía de Scarabino (1974) described the lithofacies and the molluscs belonging to the macrofauna. These are marked on Table X with "MS". The micropaleontological study allow the identification of foraminiferids; juvenile and micro-molluscs. They are marked in Table X with "x".

TABLE X
Faunal distribution in San José de Carrasco N° 442/1

Depth/m	11 13	13 17	17 18	18 19	19 21	21 23
FORAMINIFERA						
Ammonia beccarii var. *parkinsoniana*	•	••	— —			
Bolivina striatula			•			
Bolivina sp.		•	••			
Buccella peruviana, s. l.	••	———	□□□			
Buliminella elegantissima		•	••			
Discorbis williamsoni f. *praegeri*			•			
Discorbis sp.			•			
Elphidium discoidale	••	—	— —			
Elphidium cf. *discoidale*			•			
Elphidium galvestonense			••			
Elphidium div. spp. indet	•	••	—			
Miliolinella sp.			•			
Poroeponides lateralis	•	•	••			
Quinqueloculina div. spp. indet.	••	—	———			
Triloculina sp.			••			
BIVALVIA						
Chlamys cf. *tehuelcha*			MS			
Chlamys sp.			x			
Mactra isabelleana	MS	MS		MS	MS	
Mactra marplatensis		x			x	
Mactra sp.		x	x			
Ostrea equestris	MS	MS	MS			
Ostrea puelchana		MS	MS			
Ostrea sp.			x			
Pitar (P.) cf. *rostrata*			MS			
debris	MS	MS	MS	MS	MS	
GASTROPODA						
Anachis sp.?			x			
Buccinanops gradatum		MS				
Crepidula aculeata	MS					
debris	x		x	x	x	
OSTRACODA			x			
BALANOMORPHA						
Balanus sp. (barnacle plates)	x	x	x	x		x
BRYOZOA	x	x	x			
PLANTAE						
debris				x		

References: Numbers of foraminiferids:
• (1)
•• (2—5)
— — (6—10)
— — (11—20)
——— (21—40)
□□□ (41—80)

ARENERAS CALCAGNO

Location and previous studies: This exposure is situated in Avenida Calcagno, 600 m, SE of the Camino Carrasco, near Arroyo Carrasco, Canelones County (Lat. 34°52′ S, Long. 56°03′ W). The molluscs of this outcrop were described by FIGUEIRAS (1962, 1967, 1973) and DE MATA (1947), and were assigned to the Vizcaíno Formation. The foraminiferids of this outcrop were studied by SICARDI (1969), as shown in Table XI.

TABLE XI

Faunal distribution in Areneras Calcagno

Dominant species: *Elphidium discoidale*, *Buccella peruviana*, s. l.

Frequent species: *Ammonia beccarii* var. *parkinsoniana*, *Discorbis williamsoni* f. *praegeri*,

In decreasing frequency were also reported: *Buliminella elegantissima*, *Bolivina striatula*, *Poroeponides lateralis*, *Quinqueloculina seminulum*, *Oolina costata*, *Pyrgo nasuta*, *Pyrgo ringens*, *Lagena laevis* and *Nonionella* sp. Fragmentary tests of Miliolidae and Nonionidae were also reported.

PARQUE LECOCQ

Location and previous studies: This outcrop is situated in the Zoológico Municipal, in Parque Lecocq, Montevideo County (Lat. 34°47′ S, Long. 56°10′ W). DA SILVA (1975) described the lithofacies and stratigraphy of this locality. Exposures of similar characteristics were described in the same area by CARDELLINO & FERRANDO (1965, 1969). The microfaunas found in 80 cm^3 of sediment from each sample are shown in Table XII. The tests were separated in CCl_4.

TABLE XII

Faunal destribution in Parque Lecocq

Depth/m below surface scooped out by shovel	0.3	0.5	0.6	0.7	0.9	1.0	1.1	1.2
FORAMINIFERA								
Ammonia beccarii var. *parkinsoniana*	•	•	— —	———	••	□□□	———	———
Bolivina compacta						••		••
Bolivina cf. *lomitensis*			•			—		••
Bolivina cf. *variabilis*						••		
Bolivina sp.			••					••
Discorbis peruvianus			•					
Discorbis gr. *vilardeboanus*			•					
Discorbis sp.						•		•
Elphidium discoidale		••	••	••		—	— —	— —
Elphidium galvestonense			—	— —	••	□□□	••	— —
Elphidium gunteri		•				—	••	•
Elphidium div. spp. indet.				••		••	••	••
OSTRACODA		x		x	x	x		x
BALANOMORPHA								
Balanus sp. (barnacle plates)			x					

References: Numbers of foraminiferids:
• (1) •• (2—5)
— (6—10) — — (11—20)
——— (21—40) □□□ (41—80)

The faunal spectrum of the molluscs is as follows:

BIVALVIA: *Anomalocardia brasiliana*, *Brachidontes (H.) darwinianus mulleri*, *Corbula caribaea*, *Corbula patagonica*, *Erodona mactroides*, *Mactra isabelleana*, *Mytilus platensis*, *Ostrea* cf. *equestris*, *Ostrea puelchana*, *Ostrea* sp., *Tagelus plebeius*.

GASTROPODA: *Acmaea subrugosa*, *Acteocina* sp., *Anachis isabellei*, *Anachis paessleri*, *Austroborus lutescens*, *Buccinanops globulosum*, *Crepidula aculeata*, *Crepidula protea*, *Littoridina australis*, *Littoridina charruana*, *Odostomia* sp., *Parodizia uruguayensis*, *Rissoa* sp.?, *Scolodonta* sp., *Siphonaria (P.) lessoni*, *Triphora medinae*.

Lithostratigraphic unit: Vizcaíno Formation.

RINCÓN DE LA BOLSA (WELL) N° 754

Well location and previous studies: This well was drilled in the Delta del Tigre disctrict, 193 m to the south of the water reservoir tank, San José County. Length of the drill column: 810 m. The lithofacies and stratigraphy were described by Bossi (1966), Cardellino & Ferrando (1969) and Goso (1965). The following lithostratigraphic units were identified: Vizcaíno Formation (0—4 m); Raigón Formation (4—6 m); Fray Bentos Formation (6—95 m); Miguez Formation (95—801 m); Precambrian (801—810 m).

Paleontology: The disintegration of samples of drill cuttings using H_2O_2 only allowed the identification of fossil assemblages in the strata belonging to the Vizcaíno Formation (Table XIII).

TABLE XIII
Faunal distribution in Rincón de la Bolsa N° 754

Depth/m	1.5 2.8	2.8 4.0
FORAMINIFERA		
Ammonia beccarii var. *parkinsoniana*	▬	—
Elphidium discoidale	□□□	••
Elphidium cf. *discoidale*	•	
Elphidium gr. *excavatum*	———	
Elphidium galvestonense	—	
Elphidium gunteri	— —	•
Elphidium div. spp. indet	— —	••
BIVALVIA		
Corbula caribaea	x	
Ostrea sp.	x	
debris	x	x
GASTROPODA		
Littoridina sp.?	x	
debris	x	
OSTRACODA	x	x
BALANOMORPHA		
Balanus sp. (barnacle plates)	x	

References: Numbers of foraminiferids:

• (1)	•• (2—5)
— (6—10)	— — (11—20)
——— (21—40)	□□□ (41—80)
▬ (> 160)	

JUAN LACAZE (WELL) N° 291/1

Well location and previous studies: Juan Lacaze City, Colonia County (Lat. 34°26′ S, Long. 57°26′W). Length of drill column: 118 m. The lithofacies and stratigraphy were described by Da Silva (1975) and Serra (1943). Only shark teeth were identified between 20.70 and 21.70 m.

CARMELO (WELL) N° 245/1

Well location and previous studies: Carmelo City, Colonia County, in the property of the Usina de Filtración y Bombeo, O.S.E. (Lat. 33°59′ S, 58°17′ W). Length of drill column: 45.30 m. The lithofacies and stratigraphy of the bore-hole were described by Da Silva (1975) and Serra (1943). The strata of the Vizcaíno Formation are found between 0 and 19 m, and those of the Fray Bentos Formation between 19 and 37 m.

Paleontology: Only molluscs were found, whose distribution is shown in Table XIV. The presence of *Erodona mactroides* in the 9 to 17 m drill cutting is given according to Serra (1943).

TABLE XIV
Faunal distribution in Carmelo N° 245/1

Depth/m	0.0	7.5	9.0
	7.5	9.0	17.0
BIVALVIA			
Brachidontes (H.) cf. *darwinianus mulleri*	x		
Chione sp.		x	
Erodona mactroides	x	x	x
Mactra isabelleana	x		
Ostrea sp.		x	
Pitar (P.) rostrata	x		
Tagelus cf. *plebeius*	x		
GASTROPODA			
Littoridina australis	x	x	
Littoridina charruana	x	x	
BALANOMORPHA			
Balanus sp. (barnacle plates)	x	x	

CARMELO (WELL) N° 235

Well location and previous studies: Carmelo City, 300 m north of Carmelo N° 245/1, Colonia County. The lithofacies and stratigraphy were described by Serra (1943).

Paleontology: Fossils were found in strata of the Vizcaíno Formation, as indicated in Table XV.

TABLE XV
Faunal distribution in Carmelo N° 235

Depth/m	1	3	7	11	15	18	23	31
	3	7	11	15	18	23	26	37
BIVALVIA								
Erodona mactroides		x	x	x	x	x	x	x
Mytilus sp.?		x						
Ostrea sp.		x						
Tagelus cf. *plebeius*			x	x	x			
GASTROPODA								
Littoridina australis		x	x	x	x			
Littoridina sp.?	x							
MOLLUSCA								
debris	x		x		x			x
PLANTAE								
debris								x

RIO URUGUAY (WELL) N° 445/1

Well location and previous studies: In the nearness of the Río Uruguay and Río San Salvador confluence, Soriano County. Length of drill column: 31.20 m. The lithofacies were studied by Da Silva (1975).

Paleontology: The assemblages found are shown in Table XVI.

TABLE XVI
Faunal distribution in Río Uruguay N° 445/1

Depth/m	10.0 20.0	20.0 25.0	25.0 31.2
BIVALVIA			
Brachidontes (H.) cf. *darwinianus mulleri*	x		
Erodona mactroides	x	x	x
GASTROPODA			
Littoridina australis	x	x	
OSTRACODA			x

SORIANO (WELL) N° 483/2

Well location and previous studies: Soriano City, Soriano County (Lat. 33°24′ S, Long. 58°19′ W). Length of drill column: 78 m. The lithofacies of this bore-hole were studied by Da Silva (1975).

Paleontology: See Table XVII.

TABLE XVII
Faunal distribution in Soriano N° 483/2

Depth/m	14.0 17.0	26.0 26.7	43.0 48.0	48.0 51.0	51.0 51.5
BIVALVIA					
Erodona mactroides		x	x	x	x
debris	x	x	x		

C. Ages of the fossil assemblages

1) FORAMINIFERIDS:

Large differences were found between the microfaunas of the Miocene and the Quaternary in regard to:

a) the faunal spectrum. Whereas the Miocene assemblages indicate warm climate, the Quaternary ones are typical of cold temperate waters, being similar with the biocoenosis of this area.

b) their diversities. The Miocene assemblages are more diversified than the Quaternary ones. During the Quaternary sedimentation took place in estuarine and marginal marine environments, whereas in the Miocene generally deeper water is indicated.

c) the preservation and coloration of the tests (Closs, 1970 p. 35).

2) MOLLUSCS:

The faunal spectrum of the Quaternary associations are analogous with the living ones.

In reference to age the fossil assemblages do not allow for a more precise fine-stratigraphy within the Quaternary strata.

3) THE AGE OF QUATERNARY FORMATIONS WITH MARINE FOSSILS:

Chuy Formation: According to Delaney (1963, 1965, 1966, 1967, 1969?) the Chuy Formation was deposited as a beach or bar deposit during the last Pleistocene interglacial. Bertels & Madeira-Falcetta (1977), Goñi & Hoffstetter (1964), Goso (1972) and Tricart (1972) also considers the Chuy Formation as belonging to the Pleistocene. Antón (1975) also placed this formation in the Pleistocene, particularly in the Belgranense Stage. Closs (1970) indicated a Pleistocene age, but considered a Holocene age as possible. Holocene age is proposed by Closs & Forti (1971). Jost, Pinto & Loss (1972) considered the top of the formation to probably be of lower Holocene age, whereas Jost (1972) included this unit in the upper Pleistocene, lower and middle Holocene.

There is a general agreement between previous workers that the Chuy Formation was deposited during a time of high sea level. The regional geologic history during the upper Pleistocene and Holocene (Chapter VI-E) shows: a) the existence of Holocene high sea levels, b) the presence of previous transgressive events. The age and extension of these Pleistocene high sea level events is very controversial. On the other hand new data shows that in many parts of the world a widespread occurence of active sand dunes can be observed between 18,000—16,000 y. BP in coincidence with the peak of last glacial intensity. New research is necessary to solve contradictions data by C 14 datings. Taking into consideration the available information, an upper Pleistocene age seems to be probable for the Chuy Formation.

Vizcaíno Formation (= Querandina): This unit belongs to the Holocene, as is indicated by geological and paleontological approaches (Bordas, 1957; Bossi et al. 1975; Calcaterra, 1971; Cardellino & Ferrando, 1969; de Mata, 1947; Figueiras, 1961, 1962, 1967; Forti, 1968, 1969; Goñi & Hoffstetter, 1964), and by radiometric datings (Auer, 1974; Delaney, 1967, 1969?; Urien & Ewing, 1974; Vogel & Lerman, 1969).

The above is dealt more extensively by Sprechmann (1978a).

D. Stratigraphy

In order to establish lithostratigraphic correlations, the identification of stratigraphic units is indispensable. Several handicaps are apparent in identifying these units:

1) The cable-tool method used to drill the cores.

2) The lack of informations in establishing the exact altitude of some bore-holes.

3) The imprecision with which some of the Tertiary and Quaternary superficial stratigraphic units were defined and described by their lithology.

4) In addition rapid facies changes are observed.

5) The lack of geological maps with appropiate scales and cross sections for the greater part of the well region.

Classically, it is considered that the greater part of the molluscan and foraminiferal faunas, found in the Uruguayan Quaternary, were deposited in the Holocene during a single transgressive event, the so called "Querandina Transgression", which was assigned to the Vizcaíno Formation. In this way a tacit time-stratigraphic correlaction was established between different exposures bearing fossils from the Querandinense. Only few exceptions were marked: a) The molluscan assemblages found in the ex-cementerio de Nueva Palmira. The prevailing point of view is that these molluscan assemblages belong to the Vizcaíno Formation. Some authors, however, have attributed them to the Belgranense Transgression; b) the associations from the Arroyo La Palma outcrop, tentatively attributed to the Belgranense by Figueiras (1974); and c) the foraminiferids found in the Quaternary strata of Chuy N° 364 (Chapter VII). Closs (1970) proposed a time-stratigraphic correlation of these strata of Chuy N° 364 with bore-holes PJst-1-RS (Ponta do Juncal), Cast-1-RS (Curral Alto), and Cist-1-RS (Cassino) from the Pelotas Basin.

For the solution of some of these questions of Quaternary stratigraphy it would be very useful tool to review the geological history of this region (Chapter VI-E). Secondly it is indispensable to recognize and use certain marker horizons as marker beds, to clarify the chaotic situation existing in this area. With this aim new ecostratigraphic correlations are proposed in Chapter VI-G.

E. Upper Pleistocene and Holocene history of the Río de la Plata region

An understanding of geological evolution and development of the Río de la Plata area in the modern Quaternary is necessary for biostratigraphical and paleogeographical studies. Only data based on C 14 age dating are used.

35,000 years ago, during middle Wisconsin time (Porter, 1971), the shore line was situated not less than 120 m below the present level. The most probable level has been estimated to be approximately 150 m below present (Boltovskoy, 1973; Closs, 1970; Delaney, 1966, 1967; Fray & Ewing, 1963; Richards, 1966; Richards & Broecker, 1963; Richards & Craig, 1963).

15,300 y. BP the shore line was situated between 55 and 73 m lower than present (Auer, 1970, 1974; Boltovskoy, 1973; Fray & Ewing, 1963; Richards & Craig, 1963; Urien, 1967).

12,000 to 11,000 y. BP sea level was 110 to 140 m below present. (Auer, 1970, 1974; Boltovskoy, 1973; Fray & Ewing, 1963; Richards, 1966; Richards & Craig, 1963; Urien, 1967; Urien & Ottmann, 1971).

Between 11,000 and 7,000 y. BP a transgressive phase commenced, raising the sea level from minus 110 to 140 m to somewhat higher than the present.

The shore of 8,620 ± 100 years ago can be found 18 m below ground surface. This was confirmed by radiocarbon dating made on peats underlying sediments of the Querandina Formation from Boring 2, in Delta of Río Paraná near Campana, Buenos Aires County, Argentina (Auer, 1970, 1974; Vogel & Lerman, 1969).

According to Urien & Ottmann (1971), the delineation of the following episodes in the Río de la Plata area are possible:

1) During the culmination of the early Holocene transgression, the waters flooded into the estuary, penetrating to the site of the city Rosario (Argentina), reaching a level 7 to 8 m higher than the present sea shore.

2) Between 7,000 and 3,000 y. BP the advance of the sea seems to have stabilized itself, showing only small oscillations. About 6,000 years ago the sea retreated to approximately 30 m below present, and a barrier complex formed, obstructing the estuary. These waters then formed an enormous lagoon.

3) Afterwards the sea advanced once again back into the Río de la Plata estuary, but the climatic conditions were more humid, therefore showed increasing runoff. The marine phase was restricted to the outer part of the estuary.

4) About 3,000 y. BP until present the sea level tends progressively to regress, exposing the coastal plains of today which border on the estuary.

Only few radiocarbon dates have been made for this part of the South American atlantic coastal region. According to Auer (1974) and Vogel & Lerman (1969) some of them probably were carried out on allochthonous shells. There is no guarantee that in every case the dates were corrected in relation to contaminations, as were those of Erlenkeuser (in: Einsele, Herm & Schwarz, 1974).

Urien & Ewing (1974) stated that only the following evidence seems to hold: 1) The Holocene transgression began at 11,000 ± 500 y. BP, raising the sea level from minus 139 m to its present level; and 2) between 9,000 and 2,000 y. BP sea level oscillated, and then stabilized.

Nevertheless the Holocene sea level fluctuations described by Urien & Ottmann (1971) show clearly the existence of the following events:

1) The first transgressive phase was reached and the highest vertical rise attained i. e. penetration of marine facies into the inner estuary.

2) A regression follows, and a barrier complex was formed.

3) A second less extensive transgressive stage took place.

In the inner estuary only fluvial facies existed.

4) The sea level reached its actual stand.

These succesive transgressive and regressive events, and their amplitude are similar to the oscillation of sea level curves reported by Auer (1974, Appendix), Einsele, Herm & Schwarz (1974, fig. 5), and Einsele et al. (1977). These curves are similar to other Holocene sea level oscillations recorded from different world regions. This is also true for the South American atlantic coasts, as reported in papers which based their conclusions on radiocarbon dates (Bigarella, 1964; Delibrias & Laborel, 1971).

The most adequate explanation for sea level changes, which occur during the late Quaternary in the Río de la Plata region, is eustasy. This explanation does not reject the incidence of hydro-isostasy or local epeirogenic movements.

At present it is not possible to correlate these Holocene transgressive events in the Río de la Plata, with those reported in other regions. Reliable conclusions about this topic can be made only with radiocarbon datings and field work on the Quaternary terraces, together with an analysis of the cores from this area. Nonetheless it is very significant that the presence of two chronostratigraphic sequences, designated as Vizcaíno 1 and Vizcaíno 2 were recognized by Goso (1965) and Bossi (1966).

F. Paleoecology

A paleoecological approach based on actualistic method of Schäfer (1962) has to be supported by recent researches, particularly those made in the same geographical area. The studied area is related to the Río de la Plata estuary and its zone of influence, and also with the Uruguayan and South Brazilian Atlantic coasts.

1. THE RIO DE LA PLATA ESTUARY

a) Physical characteristics

In the Río de la Plata estuary, the tides are of low amplitude. On the Uruguayan shore they may reach 60 cm, being somewhat greater on the Argentine coast, with a 1 m mean average (Ottmann & Urien, 1967, 1972). The current systems in the estuary are reported by Urien (1967, 1972).

Records of the annual and daily water temperature changes are given by Boltovskoy & Lena (1974a). The highest summer mean water temperature was 27.5° C. The lowest mean water temperature for the winter was 7° C. The daily change of the water temperatures fluctuated between 0.3° C and 7° C.

The value of salinities in the estuary show a net longitudinal change, this was verified by measurements made on surface and bottom waters. In the inner estuary fresh water conditions are always present, however in the outer zone marine salinities are encountered. In the middle of the estuary great fluctuation of the salinities are found. This longitudinal zonation in salinity value is typical for positive or normal estuaries. A vertical stratification also occurs, i. e. higher the salinities are found in bottom waters than in surface waters (OTTMANN & URIEN, 1965a, 1965b; URIEN, 1967, 1972).

A considerable amount of suspended sediments is carried by the estuarine waters, with average values of 150—300 mg/l. Frequently they exceed 600 mg/l (OTTMANN & URIEN, 1965a, 1966; URIEN, 1966, 1967).

The sediment distribution and bathymetry in the estuary and in the adjacent shelf, were much analysed in the past few years. Diverse physiographic charts were also made (BISCAYE, 1972; OTTMANN & URIEN, 1965b, 1966; URIEN, 1966, 1967, 1972; URIEN & EWING, 1974; URIEN & OTTMANN, 1971). URIEN (1972) described the sediment distribution and the depositional environments. The actual sedimentary pattern is mostly controlled by the estuarine environments, and correlated in a broad way with zones of water salinities.

b. Previous work on living foraminiferids and thecamoebians.

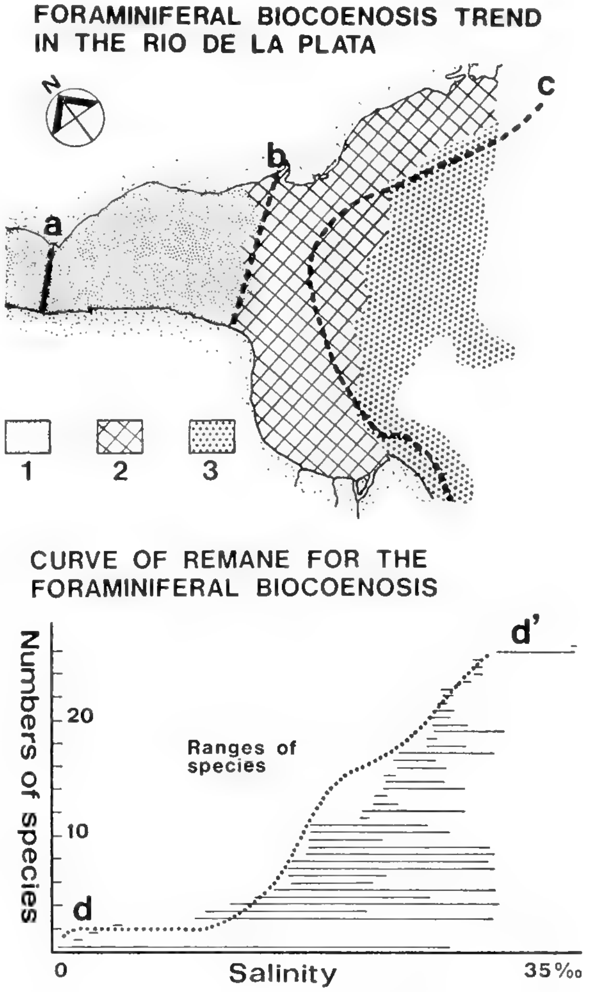
A study of the thecamoebians in this estuary was made by BOLTOVSKOY (1957b) and BOLTOVSKOY & LENA (1974a). The foraminiferids of the Río de la Plata and its zone of influence were described by BOLTOVSKOY (1957a, 1958, 1970a), and BOLTOVSKOY & LENA (1971, 1974b). Additional references were also given by BOLTOVSKOY (1954, 1959a, 1961, 1976) and BOLTOVSKOY & WRIGHT (1976). The fauna from the Arroyo Chuy was described by CLOSS & MADEIRA (1962) and MADEIRA-FALCETTA (1974), and of the mouth of the Río Santa Lucía by SCARABINO (1967).

c) Characteristics of the foraminiferal biocoenosis.

The salinity is the controlling factor in the distributional pattern of the living foraminiferids in the Río de la Plata. The distribution of the foraminiferids is correlated as well with the depositional environments found in the estuary.

BOLTOVSKOY & LENA (1974b) defined three biofacies for the living foraminiferal fauna of the Río de la Plata estuary (fig. 3):

1. Biofacies of *Nonion tisburyensis*. This biofacies overlaps with: a) the inner-fluvial environment, which corresponds to the upper river delta front platform, and is characterized by the presence of limnic conditions, and b) the outer-fluvial environment, also called the intermediate river (URIEN, 1972). In this area fresh water conditions are mostly found. At times of stormy winds, water bodies from the east can be pushed into this area, raising the salinities. Measurements indicate fluctuation in salinities ranging between 0.5 and 25 ‰. The most characteristic species of this biofacies is *Nonion tisburyensis*. Thecamoebians were also reported living (BOLTOVSKOY & LENA, 1971, 1974a, 1974b).


FORAMINIFERAL BIOCOENOSIS TREND IN THE RIO DE LA PLATA

CURVE OF REMANE FOR THE FORAMINIFERAL BIOCOENOSIS

Fig. 3: Foraminiferal biocoenosis trend in the Río de la Plata (after BOLTOVSKOY & LENA, 1974b). Key: 1 = Biofacies of *Nonion tisburyensis*, 2 = Biofacies of *"Rotalia beccarii parkinsoniana"*, 3 = Biofacies of *Buliminella elegantissima*. These biofacies overlap with the following environments defined by URIEN (1972): inner-fluvial environment from line **a** to the west; intermediate-fluvial environment between lines **a** and **b**; fluvio-marine environment between lines **b** and **c**; and marine zone from line **c** to the east. Curve of REMANE for the foraminiferal biocoenosis of the Río de la Plata (**d** — **d'**). Parallel lines indicate the distributional range of living species (after BOLTOVSKOY & LENA, 1974b).

2. Biofacies of *"Rotalia beccarii parkinsoniana"*. This corresponds to the fluvio-marine environment, or "Río exterior" (Urien, 1967, 1972). The dominant species are *Ammonia beccarii* var. *parkinsoniana*, which is distributed within the whole biofacies; and *Elphidium discoidale*, which prevails in the northern and southern coasts. *Miliammina fusca* is present in smaller amounts.

3. Biofacies of *Buliminella elegantissima*. This biofacies has boundaries which are similar with those of the Río de la Plata marine zone. *Buliminella elegantissima* is the most frequent and typical species, followed by *Bolivina striatula*.

Boltovskoy & Wright (1976, fig. 113) showed the distributional patterns of the species which are characteristic for these biofacies in the Río de la Plata estuary. *Epistominella exigua* is the dominant species in the shelf sea adjacent to the Biofacies of *Buliminella elegantissima*.

Boltovskoy & Lena (1974b) indicated that the salinity has an additional effect on the distribution of the living foraminiferids. The per cent fraction occurence of the agglutinated species in the estuary increases with the decrease of salinity. A zonation of similar characteristics was observed in different marginal marine environments and estuaries (Bandy, 1964; Boltovskoy & Boltovskoy, 1968; Closs, 1963; Closs & Medeiros, 1965; Ellison & Nichols, 1970; Murray, 1968, 1973; Walton, 1964).

d. Remane's curve for the foraminiferal biocoenosis of the Río de la Plata.

Remane (1934, 1940, 1963, 1971) formulated another criterion to reveal the relationship existing between the water salinity and the number of species. The most important characteristics of the curve are present in Chapter VI-F-4.

Remane's curve for foraminiferal biocoenosis of the Río de la Plata estuary (fig. 3, d—d') was plotted using the distributional ranges of living species illustrated by Boltovskoy & Lena (1974b, map. 17).

In Fig. 3 Remane's curve here presented was correlated with the pattern of salinity zonation of this estuary proposed by Urien (1972), and with the foraminiferal biofacies reported by Boltovskoy & Lena (1974b).

Remane's curve for living foraminiferids in the Río de la Plata shows clearly, that the number of species decreases with reduction in water salinities. This is similar with Remane's curve of the living foraminiferal faunas in the Balthic Sea (Lutze, 1965, fig. 28).

2. PALEOECOLOGICAL INTERPRETATION BASED ON FORAMINIFERIDS.

The Uruguayan Quaternary foraminiferal assemblages provide information of the following environmental factors:

a. Bathymetry: The foraminiferids encounted in the drill samples and outcrops are characteristic of shallow environments (estuaries, bays, lagoons, beaches, etc.). The water depth does not exceed 20 m (Bandy, 1964; Boltovskoy, 1965, 1970a, 1976; Boltovskoy & Wright, 1976; Murray, 1968, 1973; Walton, 1964). The absence of *Epistominella exigua* seems to confirm this point of view. At the Present this is the dominant species in the open shelf areas beyond the Río de la Plata estuary (Boltovskoy, 1957a; Boltovskoy & Wright, 1976, fig. 113).

b. Temperatures: The foraminiferal associations are typical of cold-temperate water masses. The species which indicate the influence of warm water masses are *Ammonia beccarii* var. *parkinsoniana*, *Elphidium discoidale*, *Bolivina striatula* and *Poroeponides lateralis*. The cold water influence is shown chiefly by *Buccella peruviana*, s. l. (Boltovskoy, 1954, 1965, 1970a, 1976; Boltovskoy & Wright, 1976). This faunal spectrum is representative of the Argentina Biogeographic Province, also called the "kingdom" of *Buccella peruviana*, s. l., defined for living foraminiferal faunas. Most precisely they belong to the northern sub-area of this biogeographical unit, which is denoted as the North-patagonian subprovince (Boltovskoy, 1970a, 1976; Boltovskoy & Wright, 1976). Other species which are frequent in the drill cuttings, and that are characteristic of living assemblages of the North-patagonian subprovince are *Buliminella elegantissima* and *Miliolinella subrotunda*.

c. Substrates: No correlations were postulated in the Río de la Plata region between the distributional pattern of living foraminiferids and the type of substrates. Material from the wells is inappropriate for this kind of study because the number of drill cuttings where tests were found is not large enough to establish a relationship of any kind. Besides, changes in biotope are frequently found in estuarine inhabitants. Their main biotope in brackish water thus differs from that in the sea. This is particularly true for their substrate dependence (Remane, 1971).

d. Salinities: In nearly all the estuaries the salinity is the most important factor in determining the extent of the foraminiferal biocoenosis. Only in those environments, such as in the Baltic Sea (Lutze, 1965), in which a thermohaline stratification occurs salinity *and* temperature are the main factors that control the foraminiferal distribution.

In an attempt to establish the Quaternary depositional environments, paleoecologic analysis is primarly based on the identification of the tolerance of each foraminiferal assemblage in relation with salinity. Different criteria were described for recognizing brackish foraminiferal assemblages (Hiltermann, 1963a, 1963b; Lutze, 1965; Murray, 1968, 1973; Walton, 1964).

The foraminiferal biocoenosis of the Río de la Plata and Río Quequén Grande were used to determine the range of the salinity tolerance for each species found in the Quaternary well boring sequences (Boltovskoy, 1958, 1976; Boltovskoy & Boltovskoy, 1968; Boltovskoy & Lena, 1971, 1974b; Wright, 1968). In addition data from different biocoenosis and biotopes of the South American atlantic area was also evaluated to establish the salinity tolerance of various species (Closs, 1963, 1964; Closs & Madeira, 1962, 1967, 1968b; Closs & Medeiros, 1965, 1967; Lena & L'Hoste, 1975). Likewise, the available information about the distribution of foraminiferids from different estuaries was used (Boltovskoy, 1965; Boltovskoy & Wright, 1976; Ellison & Nichols, 1970; Kane, 1967; Lutze, 1965; Madeira-Falcetta, 1974; Murray, 1968, 1973; Pujos, 1973).

Only those species found and recorded in the Uruguayan Pleistocene and Holocene were classified with reference to their salinity tolerance within three Quaternary biofacies:

1. Quaternary Biofacies of *Buliminella elegantissima:* In this ecozone salinities are close to marine. Those species which are capable of tolerating small fluctuations in salinities, as well as some euryhaline species, were included in this biofacies: *Buliminella elegantissima, Buccella peruviana,* s. l., *Poroeponides lateralis, Bolivina compacta, Bolivina striatula, Bolivina* cf. *lomitensis, Cibicides aknerianus, Dentalina communis, Discorbis peruvianus, Discorbis williamsoni* f. *praegeri, Fissurina laevigata, Guttulina problema, Lagena laevis* f. *perlucida, Lenticulina limbosa, Miliolinella subrotunda, Nonionella atlantica, Oolina melo, Pyrgo nasuta, Pyrgo ringens patagonica, Quinqueloculina angulata* f. *typica, Quinqueloculina atlantica, Quinqueloculina* aff. *frigida, Quinqueloculina intricata, Quinqueloculina seminulum, Reophax artica* and *Textularia gramen.*

2. Quaternary Biofacies of *Ammonia beccarii* var. *parkinsoniana:* This overlaps the fluviomarine environment, and includes high and intermediate euryhaline species: *Ammonia beccarii* var. *parkinsoniana, Elphidium discoidale, Elphidium* gr. *excavatum, Elphidium galvestonense, Bolivina compacta, Discorbis peruvianus, Lagena laevis* f. *perlucida, Nonion tisburyensis, Oolina melo* and *Reophax artica.*

3. Quaternary Biofacies of *Nonion tisburyensis:* This biofacies contains species which are able to dwell permanently or temporarily in fresh waters: *Nonion tisburyensis* and *Reophax artica.*

This classification is based on studies made of the biocoenosis and indicates the lowest salinity needed by the species to survive, but does not indicate the lowest allowable salinity needed for reproduction.

The most abundant species found in the drill cuttings which characterize the Quaternary biofacies, are cosmopolitan. They are typical for these environments even if in different geographical areas.

The depositional environments are determinated chiefly on the basis of the percentile occurence of the dominant species for each biofacies, but not exclusively indicative of a single association.

A second method is also used to evaluate the salinity tolerance shown by the Quaternary associations. It is based on the evaluation of the capacity of the genera to withstand changes in salinities. The information given by Murray (1973) is used (table XVIII).

In the wells and exposures shown in Table XVIII foraminiferal assemblages were found that allow one to make paleoecological interpretations. In each locality the sample with the greatest diversity was used.

3. PALEOECOLOGICAL CONCLUSIONS OF DEPOSITIONAL ENVIRONMENTS BASED ON BENTHIC FORAMINIFERIDS.

The analized foraminiferal assemblages indicate shallow and cold temperate waters. Their salinity tolerance was the greatest difference found between assemblages.

In almost all the estuaries salinities, and other physical characteristics (bathymetry, substrate, etc.) gradually change in direction of its longitudinal axis. The water salinities decrease in a gradational way and a zonation is produced, which is particularly evident in the channels. This type of zonation is herewith called "estuarine front".

A second latitudinal zonation is also present in the estuarine environment, which is reflected as well in its physical and biological characteristics. Shorewards the limnic influence increases, as a consequence of rivers, rivulets, marshes, lagoons and other marginal environments. This latitudinal or lateral zonation is herewith designated the "lateral-marginal zone of influence".

Along the longitudinal estuarine axis, the boundaries between facies and biofacies are gradual. In contrast, along latitude these lateral changes are sudden, and therefore the environmental and faunal limits are sharp (Ellison & Nichols, 1970). The presence of this double zonation makes paleoecological reconstruction difficult.

TABLE XVIII
Salinity tolerance of foraminiferal associations

Locality	α	Rotaliina	Miliolina	Genera	Salinity
Chuy N° 364 (40—35 m level, drill cutting)	2	100 %		*Ammonia* 48 % *Bolivina* 4 % *Buliminella* 27 % *Elphidium* 20 %	hyposaline
Costa Azul N° 1060/1 (21—19 m level, drill cutting)	4.5	99 %	1 %	*Buccella* 60 % *Discorbis* 6 % *Ammonia* 14 % *Elphidium* 12 %	slightly hyposaline
Puerto La Paloma N° 449/11 (8.00—7.50 m level, drill cutting)	6	82 %	16 %	*Buccella* 46 % *Discorbis* 3 % *Elphidium* 7 % *Poroeponides* 23 % *Miliolinella* 5 % *Quinqueloculina* 10 %	normal marine
Salinas N° 1034/1 (34—32 m level, drill cutting)	4	99 %	1 %	*Ammonia* 4 % *Bolivina* 8 % *Buccella* 4 % *Buliminella* 32 % *Elphidium* 44 %	moderately hyposaline
Areneras Calcagno[4])					slightly hyposaline
San José de Carrasco N° 442/1 (18—17 m level, drill cutting)	3	81 %	19 %	*Ammonia* 11 % *Buccella* 37 % *Elphidium* 21 % *Quinqueloculina* 10 % other Miliolidae 9 %	slightly hyposaline
Parque Lecocq (1 m below surface, scooped out)	2	100 %		*Ammonia* 51 % *Bolivina* 6 % *Elphidium* 40 %	hyposaline
Rincón de la Bolsa N° 754 (2.80—1.50 m level, drill cutting)	1	100 %		*Ammonia* 59 % *Elphidium* 41 %	hyposaline

The Quaternary foraminiferal assemblages are included in the following biofacies:

a. Quaternary Biofacies of *Buliminella elegantissima:* Well La Paloma N° 449/11. Perhaps Costa Azul N° 1060/1.

b. Transitional area between the Quaternary Biofacies of *Buliminella elegantissima* and *Ammonia beccarii* var. *parkinsoniana:* Salinas N° 1034/1, San José de Carrasco N° 442/1, and Areneras Carrasco.

c. Quaternary Biofacies of *Ammonia beccarii* var. *parkinsoniana:* Parque Lecocq, Rincón de la Bolsa N° 754 and Chuy N° 364.

In each well or exposure only those samples carrying the highest species diversity were considered. *Nonion tisburyensis* was nearly completely absent in foraminiferal assemblages originating from drill cuttings. This species characterizes a biofacies of living foraminiferids in the Río de la Plata. Today this biofacies overlaps with the inner and intermediate-fluvial environments. Furthermore, this biofacies presents the highest standing crop for the estuarine biocoenosis (Boltovskoy & Lena, 1974b). *Miliammina fusca* was not found, although it is frequent today in this biofacies.

The same authors have analysed the longitudinal

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[4]) The information given by Sicardi (1969) about foraminiferids from this exposure is not sufficient to establish the α index as well as the percentile occurence of the genera. However, the available data of the species composition shows that the salinity was slightly hyposaline.

distribution in each environment of the calcareous and arenaceous foraminiferids in the Río de la Plata. The per cent occurence of the arenaceous species increases with a decrease in salinity. In the Quaternary foraminiferal assemblages only scarce specimenes of Textulariina were found. This absence is interpreted to mean that the depositional environments were not related with the inner and intermediate-fluvial estuarine zone, at least in the drill samples that have supplied foraminiferids. Nevertheless it must be pointed out, that the "arenaceous pattern" does not always offer total reliability, and can lead to errors in paleoecological interpretations (LUTZE, 1965, p. 133).

The Quaternary foraminiferal assemblages indicate an estuarine or lagoonal environment. Hyposaline, normal marine and hypersaline marshes are rejected on the basis of the absence of Textulariina in the studied assemblages; and in the species composition, because no "typical" marsch species were found (MURRAY, 1973, p. 26—27, table 5).

MURRAY (1968, 1973, 1976) also pointed out the difficulties that exist in distinguishing between estuaries and lagunes and other marginal marine environments, using foraminiferal associations. It is thought that almost all the foraminiferal associations were deposited in an estuarine environment, because they indicate a longitudinal distributional pattern. They reveal a decrease of water salinities toward the head of the estuary. The foraminiferal assemblages from, La Paloma N° 449/11, Salinas N° 1034/1, San José de Carrasco N° 442/1, Areneras Calcagno and Lecocq correspond to the "estuarine front". In contrast, the foraminiferal assemblages from Chuy N° 364 could indicate an environment belonging to the "lateral-marginal zone of influence". Probably to a lesser extent this is also valid for Costa Azul N° 1060/1 and Rincón de la Bolsa N° 754.

In Fig. 4 the paleoecological results are shown by the foraminiferids and are schematically illustrated. The percentile occurence of each species is plotted in a cumulative histogram. For every well only the sample carrying the greatest foraminiferal diversity is considered. Those species illustrated with dotted signature indicate the marine influence and belong to

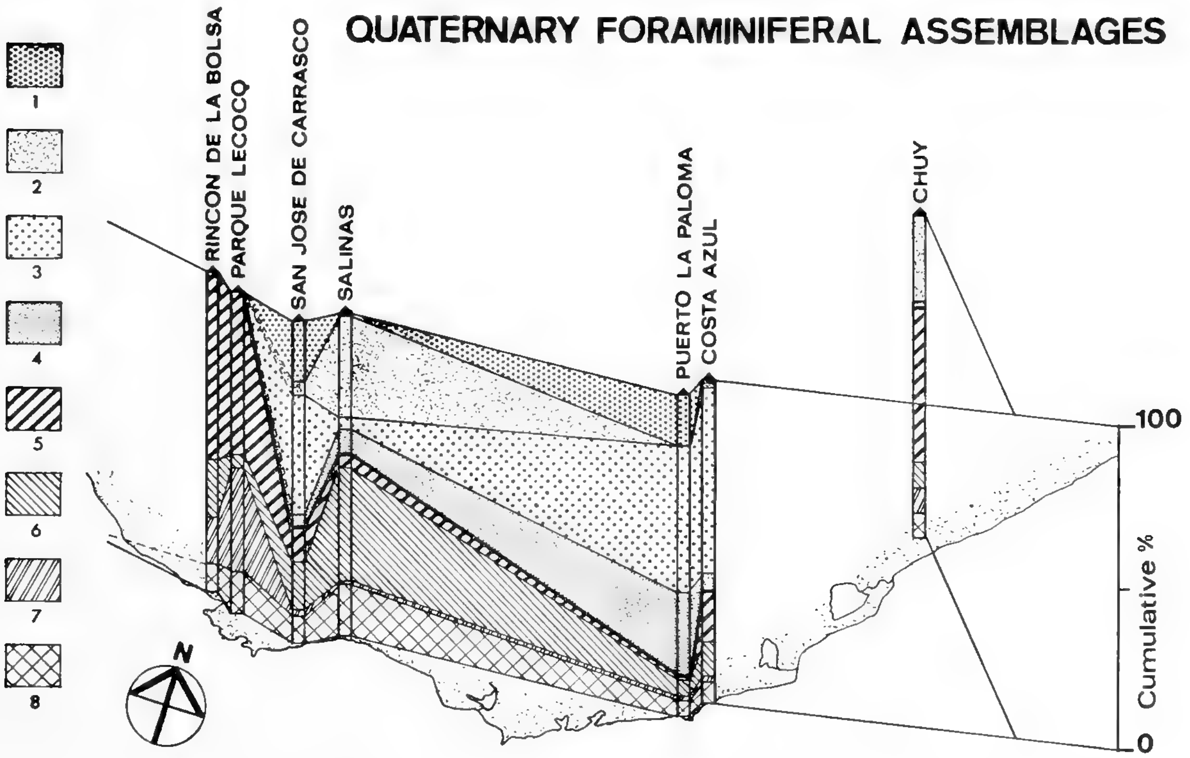

Fig. 4: Longitudinal distribution pattern of the Quaternary foraminiferal assemblages. The percentile occurence of species is shown in a cumulative histogram. Species illustrated with dotted signature indicate the marine influence. Slanting lines represent areas chiefly fluvio-marine. Key: **1** = Miliolidae, **2** = *Buliminella elegantissima,* **3** = *Buccella peruviana,* s. l., **4** = other species characteristic for the Quaternary Biofacies of *Buliminella elegantissima,* **5** = *Ammonia beccarii* var. *parkinsoniana,* **6** = *Elphidium discoidale,* **7** = other species indicating the Quaternary Biofacies of *Ammonia beccarii* var. *parkisoniana,* **8** = Non indicative species.

the Quaternary Biofacies of *Buliminella elegantissima.* Slanting lines represent areas chiefly fluvio-marine, and are typical for the Quaternary Biofacies of *Ammonia beccarii* var. *parkinsoniana.* The cumulative histogram clearly shows the longitudinal zonation which is characteristic for this estuarine environment. Towards the head of the estuary, the Quaternary Biofacies of *Ammonia beccarii* var. *parkinsoniana* gradually replaces the *Buliminella elegantissima* one.

The depositional environment of Puerto La Paloma N° 449/11 (8.00—7.50 m level, drill sample) probably was an open sandy beach. This is supported by the lithofacies, and the fact that the foraminiferal assiciation is similar to living ones in this biotope (Closs & Barberena, 1962; Madeira-Falcetta, 1974; Murray, 1973).

In San José de Carrasco N° 442/1 (18—17 m level, drill cutting) many abraded tests were found due to the characteristics of the lithofacies which is an angular quartzose sand. The environment was probably a sand beach exposed to waves and located on the estuarine shore. This environment is a difficult biotope for many animal groups, because it is mobile and unstable. The only permanent residents from the benthic macrofauna belong to the infauna (Hedgpeth, 1957; Herm, 1969; Perkins 1974; Seilacher, 1953). Destruction of foraminiferids and molluscs due to abrasion is usual in this environment (Einsele et al., 1977; Murray, 1973).

The distribution of the foraminiferids in Chuy N° 364 does not agree with the trend that is normal in estuarine longitudinal zonation. This fact can be explained in two ways: a) deposition took place in a marginal marine environment, revealing estuarine latitudinal or lateral zonation; b) the foraminiferids were deposited during a different transgressive event, being older or younger.

The wells which are located in Colonia and Soriano Counties, do not contain foraminiferids. These boreholes are located in the innermost estuarine region. The sequences of these bore-holes, that were considered as belonging to the Vizcaíno Formation, probably were deposited in a hyposaline environment. Foraminiferids usually are not adequate for paleoecological reconstruction of these biotopes, because only few species are able to survive there. This is also valid for living foraminiferids of the Río de la Plata, and is clearly illustrated by Remane's curve of this estuary (fig. 3, d-d'). Post mortal diagenetical effects as i.e post depositional dissolutions, also could have affected the microfaunas.

It is necessary to evaluate other fossil assemblages to reconstruct the depositional environments of the sequences which are attributed to the Vizcaíno Formation, namely the wells located in Colonia and Soriano Counties. Mollusca are used for this purposes.

4. PALEOECOLOGICAL INTERPRETATION OF MOLLUSCAN ASSEMBLAGES.

a. Methods.

The Quaternary malacological associations found in the wells can be evaluated for paleoecological and paleogeographical information. On one hand it allows one to compare and check the paleoecological conclusions that were given, by foraminiferal assemblages. On the other hand they offer a valuable additional information, particularly for those environments that are not suitable to foraminiferal life or preservation.

The bivalves and gastropods in the wells are mainly used to delineate the boundaries between the Quater-

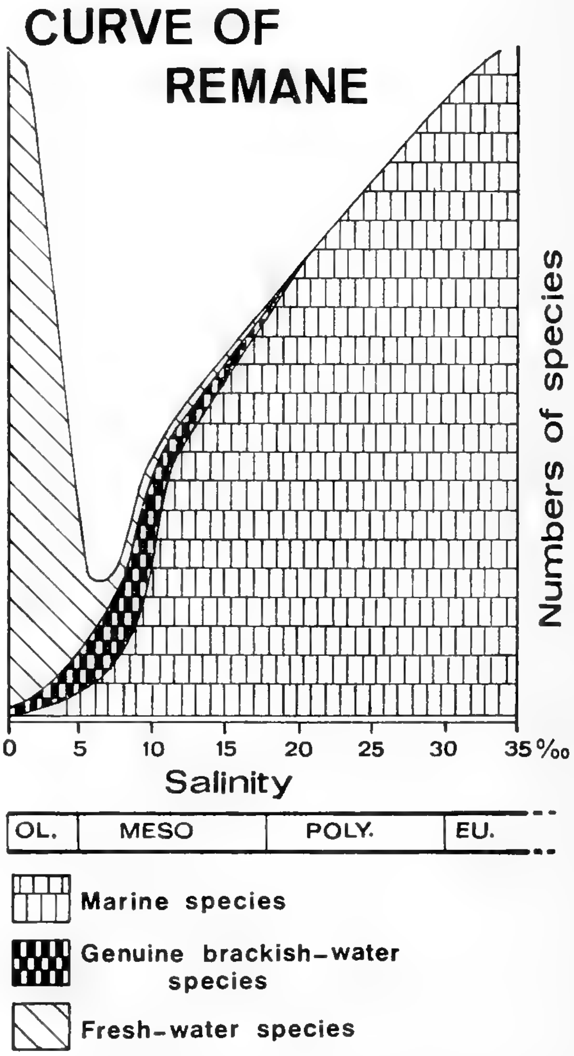

Fig. 5: Graph of numbers of marine, fresh-water, and genuine brackish-water species in different salinities [after Remane (1934, 1940, 1963, 1971)].

nary biofacies and/or environments. They also offer information that allows one to verify and define the range of the biofacies during the Querandina Transgression.

For this purpose it was particularly useful to use criteria that allow a discrimination between marine and limnic organisms:

1. Marine and limnic environments have been colonized by different species.

2. The curve that establishes a relationship between the species number and the water salinities was made by REMANE (1934, 1940, 1963, 1971) (fig. 5). Towards the head of the estuary (inwards the estuary) — with decreasing salinities — the number of species decreases. With salinity of 18 ‰ approximately half of the marine species survive. Limnic organisms are already very scarce at a salinity of 3 ‰. The species minimum is near the boundary of fresh water environments, with salinities in the range of 5—8 ‰ (REMANE, 1934), 5—7 ‰ (REMANE, 1963, 1971), 4—6 ‰ (HILTERMANN, 1963b) or by 5 ‰ (McLUSKY, 1971; PERKINS, 1974). The asymmetry on REMANE's curve originates by the fact that fresh water species react with much greater mortality with the increase of water salinities than the marine faunas do with increase of fresh water. Therefore marine environments are separated from the limnic ones by a zone characterized by a low species diversity, with salinities ranging between 5—8 ‰.

3. Brackish waters are characterized by the presence of some species which reach their highest abundance in this environment, and which have been designated "genuine brackish-water species" or "true estuarine species" (HILTERMANN, 1963b; REMANE, 1934, 1940, 1963, 1971). Generally these species belong to genera which are present in marine environments, with a few belonging to limnic environments.

4. An additional useful way is to evaluate the vicariad species, i. e. closely related species whose distribution is allopatric.

b. Curve of REMANE for living bivalves from the Río de la Plata estuary.

To use the actualistic principle the first step is to reconstruct REMANE's curve for the living malacological assemblages of the intertidal and sublittoral zones of the Uruguayan part of the estuary. With this aim a review of the available literature about the living molluscan faunas at the Uruguayan coasts was made.

Some limitations of the reconstruction of the curve that relates the species number to salinities are given:

1. Generally the available information is imprecise in reference to the species range of dispersion.

2. Usually no discrimination is made between the information based on living species, and those obtained on the thanatocoenosis.

3. The presence of some species previously refered to this area must be considered as fortuitous, or are questionable.

4. The nonexistence in the literature of precise data about the salinities that existed at the moment in which the molluscs were capturated.

Notwithstanding these limitations, it was possible to plot the curve of REMANE for the living bivalves of intertidal and sublittoral zones of the Uruguayan coast, within a very acceptable approximation (fig. 6). For this purpose the number of bivalve species reported from the following areas were counted:

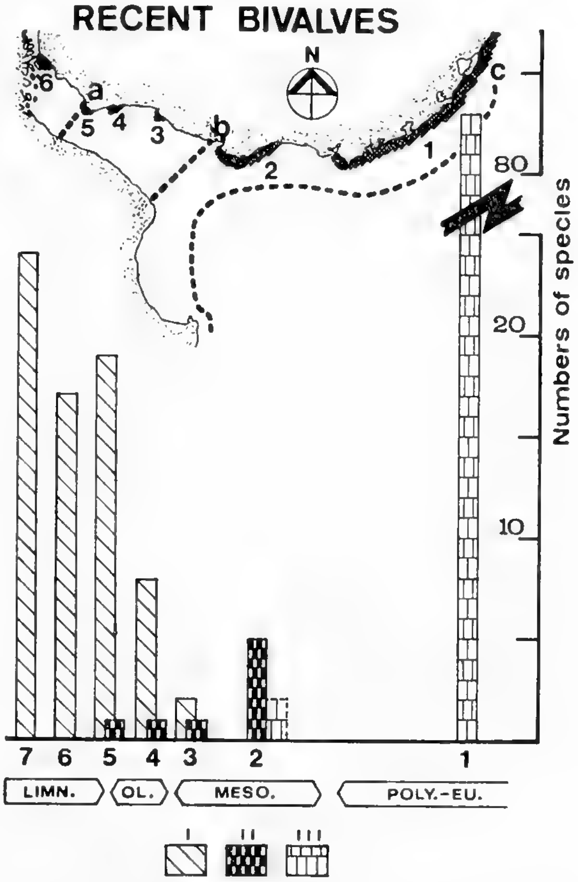

Fig. 6: Curve of REMANE for living bivalves from the Río de la Plata estuary. Key: I = fresh-water species, II = genuine brackish-water species, III = marine species. Geographical setting of areas 1—6, as well as references of column 7 of histogram are shown in pages 40. Lines **a**, **b** and **c** are the boundaries between estuarine environments, as shown in Fig. 3.

Uruguayan oceanic region (fig. 6, area 1): This covers the coasts of Rocha County in all its extension, and those of County Maldonado, from Portezuelo to the east. The characteristics of the living communities of the sandy beaches in this area were reported by SCARABINO, MAYTÍA & FAEDO (1973).

The rocky substrates of this region are characterized by the presence of the *Mytilus platensis-Brachidontes rodriguezi-Perna perna* Community (SCARABINO, MAYTÍA & CACHÉS, 1975).

To establish the number of bivalvian species of this area, the information provided by the "Catálogo de los moluscos marinos del Uruguay" was used (FIGUEIRAS & SICARDI, 1968b, 1969, 1970a, 1970b), as well as additional data by BARATTINI & URETA (1960) and FIGUEIRAS (1975). A total of 109 species of pelecypods belonging to the biocoenosis and thanatocoenosis were reported. They are tentatively classified as:

1. marine species, of the intertidial and upper sublittoral zones: 83(?)
2. middle and lower sublittoral marine species: 17 (?)
3. genuine brackish-water species: 5
4. not classified and doubtfull species: 4

This data is approximate, because the available information about the distribution and ecology of many species is insufficient. *Petricola pholadiformis* can be used to illustrate the point. According to FREY, VOORHIES & HOWARD (1975) this species is one of the best indicators for estuarine environments. Nevertheless, in the Río de la Plata area, its distributional range is reported as being only along oceanic coasts.

Area of Montevideo (fig. 6, area 2): The bivalve species living in this zone are described by SCARABINO, MAYTÍA & CACHÉS (1975). In the "sandy beach" physiographic unit, characterized by sandy substrates with high organic matter the following bivalve species were found: *Erodona mactroides, Mactra isabelleana* and *Tagelus plebeius.* These species live in the intertidal and upper sublittoral zones. In rocky substrates the *Brachidontes darwinianus* Community is dominant, being frequently associated with *Mytella charruana.* Both species are also dwellers of the littoral sensu stricto and upper sublittoral zones. TEISSEIRE (1927, 1928) has reported already the presence of these five species for the coasts of the Montevideo County. FIGUEIRAS & SICARDI (1968b, 1969, 1970a, 1970b) also recorded along coasts of Counties Montevideo and Canelones the presence of the same five species, which were described as euryhaline forms. They also reported the presence of *Macoma uruguayensis* and *Mactra petiti* in the same area. Therefore the Area of Montevideo also includes the coasts of Canelones County, mainly in its western region.

It must be pointed out, that the *Brachidontes darwinianus-Mytella charruana* Community, which lives in the area of Montevideo, is substituted in the oceanic region by another community, integrated by the vicariad species *Mytilus platensis-Brachidontes rodriguezi-Perna perna* (SCARABINO, MAYTÍA & CACHÉS, 1975). This latter species invaded the Atlantic Uruguayan coasts only recently (FIGUEIRAS & SICARDI, 1968b, p. 265).

Coasts of the Colonia County: To obtain the distributional range of the bivalve species of this estuarine zone, the information detailed by OLAZARRI (1966) was used. This autor described the bivalves of Colonia County. For each analyzed species a list of the localities in which it was found is presented. In using REMANE's curve only those localities were considered which were located on, or near the Río de la Plata, and also those situated on the Río Uruguay, between Punta Gorda and Arroyo Sauce. The localities in the inner part of the County were excluded, because they could not provide any information about salinity zonation. The localities in question were grouped into four zones, along the coasts of Colonia County:

Mouth of Arroyo Cufré area (fig. 6, area 3)

Artilleros area (fig. 6, area 4): localities of Arroyo Artilleros, Balneario Santa Ana y Puerto Platero.

Area of Colonia City (fig. 6, area 5): localities of Playa Ferrando, Bahía de Colonia, Playa La Arenisca, Barrancas San Pedro e Isla San Gabriel.

Area of Carmelo and Nueva Palmira (fig. 6, area 6): localities of Punta Piedras, Playa Seré, Balneario Zagarzazú, Punta Gorda, Nueva Palmira and Brisas del Uruguay.

According to OLAZARRI (1966) the total number of limnic bivalve species found in Colonia County is 24 (fig. 6, column 7). FIGUEIRAS (1965a, 1965c) presented a review of freshwater pelecypods of the Uruguayan territory. He described 29 species. No precise distributional data is offered for many species. The total number of species is close to that given by OLAZARRI (1966), especially if it is considered that OLAZARRI restricted his observations to Colonia County. The total number of species previously referred to do not include various subspecies which were reported by both authors, because in some cases their allopatric distribution are not evident.

The resultant histogram and curve (fig. 6) reveals a very similar distribution as in REMANE's curve (fig. 5). They also are similar to that REMANE's curve which was exclusively plotted for molluscan faunas (Hiltermann, 1963b; Remane, 1934, 1940, 1963, 1971).

For ecological reconstruction, the salinities of each area previously referred to must be estimated. For this purposes the zonation of the salinities in the Río de la Plata reported by Urien (1972) is used. This allows one to establish the relationship existing between the inner-fluvial, intermediate-fluvial, fluviomarine and marine environments of the estuary, i. e. areas 1 to 6, of the histogram of Fig. 6. The boundaries between these environments are graphically illustrated in the same figure. They also overlap with the biofacies limits, which were defined using living foraminiferids.

The histogram and curve of Fig. 6 indicate the following conclusion:

In the oceanic region the species diversity is very high (area 1). According to Remane's curve it must have a relationship with euhaline and polyhaline salinities.

In the inner-fluvial environment, where limnic conditions are always present, the fauna of fresh water bivalves is also diversified (areas 5 and 6).

In the intermediate-fluvial environment the increasing salinities causes a quick decrease of the number of limnic bivalve species. In the Artilleros area eight fresh water species were reported (area 4), and in the mouth of Arroyo Cufré only two (area 3). These limnic bivalves coexist with *Erodona mactroides.* Remane (1963) and Hiltermann (1963b) reported that the dominant fauna in oligohaline waters is a limnic one, but with an evident decrease in species diversity. The lowest diversity is reached in the miomesohaline (= ß mesohaline). According to Remane (1971) fresh-water bivalves are rather intolerant of brackish water. Only a few reach the 5 ‰ boundary, none transgress the 8 ‰ salinity limit. Based on these data it can be concluded that the bivalves of the Astilleros area indicates an approximate oligohaline environment; and those of the Arroyo Cufré shows a miomesohaline one.

In the fluvio-marine environment only seven bivalve species were reported of marine origin. This faunal spectrum indicates mesohaline salinities.

An examination of the range of distribution of the genuine brackish-water species shows clearly that their optimum lies in the mesohaline. The salinity ranges from about 3 ‰ to 18 ‰ and is the habitat of over 90 % of the genuine brackish-water organisms (Remane, 1971).

The genuine brackish-water species are here defined according to Remane's (1934) wider definition: "Genuine brackish-water species are those which abound in brackish water and occur only occasionally in the sea or fresh water". Often great practical difficulties exist in establishing if a species belongs to this category, or if it is a euryhaline form. A classical example is the case of *Mytilus.*

Erodona mactroides, Brachidontes darwinianus, Mytella charruana and *Tagelus plebeius* are considered to be genuine brackish-water species. Scarabino, Maytía & Cachés (1975) included these species within the "estuarine association".

Probably *Mactra isabelleana* must also be considered a genuine brackish-water species. This species is dominant in several exposures of the Querandinense which are characterized by very low saline depositional environments. Calcaterra (1971) reported that *Mactra isabelleana* constitutes about the 60 % of the fossil assemblage in Cantera Ferrando. This species is also dominant in Punta Francesa constituting 40 % of the molluscan fauna, and in the ex cementerio de Nueva Palmira, where its occurence goes to 90 %. Bordas (1957) also considered *Mactra isabelleana* as being an "estuarine species". Klappenbach & Scarabino (1969, p. 54) reported that this species prefers waters of low salinity. It must be pointed out that Teisseire (1927, 1928) was the first who recognized the paleoecological value of these five genuine brackish-water species.

Macoma uruguayensis and *Mactra petiti* are considered as euryhaline marine species. Their range of distribution goes from Montevideo toward the east, but they do not constitute dominant forms in this environment.

Among these five genuine brackish-water species there is one, *Erodona mactroides,* that has been repeatedly mentioned as being useful for ecological and paleoecological interpretations (Carcelles, 1941; Closs, 1963; Costa, 1971; Figueiras, 1965a; Olazarri, 1966; Teisseire, 1927, 1928).

Closs (1963) offers precise information about the distributional pattern of *Erodona mactroides,* and its direct correlation with water salinities. In Laguna de los Patos this species is scarce in areas with relatively high salinities (polyhaline), and is completely absent in fresh water zones. It is frequent in salinities ranging between 15—8 ‰, and can be very abundant in waters whose salinities fluctuate between 9—3 ‰.

In reference to the westernmost penetration of *Erodona mactroides* in the Río de la Plata, the most accurate information is given by Teisseire (1927) and Olazarri (1966). The former author indicated that this species was found near Colonia City. Olazarri (1966) described the presence of some big specimens in the harbour of Colonia City, together with nayades, emphasizing that *Erodona mactroides* never was found living at the NW of this geographical area, on the Uruguayan coast.

These biological data are in total agreement with the physical parameters of water salinities, which were described by Urien (1972). The limnic sensu stricto environment begins somewhat to the NW of Colonia City, on the Uruguayan coast. There *Erodona mactroides* disappears in living assemblages. That means that the maximum headward estuarine penetration of *Erodona mactroides* indicates the nearness of the boundary between the inner-fluvial and intermediate-fluvial environments.

The remaining genuine brackish-water species were not found living on the Colonia County coasts (Olazarri, 1966), not even in San José County. Towards the head of the estuary the maximum penetration was observed along the coasts of the area of Montevideo (fig. 6, area 2), as was described by Figueiras & Sicardi (1968b, 1969, 1970a, 1970b) and Teisseire (1927, 1928).

Life habits of the dominant genuine brackish-water species.

The life habits of *Tagelus plebeius* were extensively described by Stanley (1970) as being a suspension-feeder of the deep infauna.

No detailed biological studies have been made of *Erodona mactroides* and *Mactra isabelleana* life habits. However they have been tentatively established using criteria formulated by Cox, Nuttall & Trueman (1969), Kauffman (1969) and Stanley (1970).

Erodona mactroides is considered to be a suspension-feeder of the upper infauna, based on the functional morphology of its test, i. e., absence of a pallial sinus and its taxonomic position within the Myacea.

Mactra isabelleana is a suspension-feeder of the intermediate infauna.

Apparently no genuine brackish-water bivalve detritus feeders exist in the Río de la Plata. In almost all estuaries the detritus-feeders are present as characteristic forms. Suspension-feeding bivalves are, however, generally rare in estuaries (Barnes, 1974).

c. Distribution of the living gastropods in the Río de la Plata estuary, and its zone of influence.

The distributional pattern of the gastropod species is as follows (fig. 7):

In the oceanic Uruguayan region the presence of about 183 species of gastropods from the biocoenosis and/or thanatocoenosis were reported (Figueiras & Sicardi, 1970c, 1971, 1972, 1973, 1974; Sicardi, 1975). The taxonomic status and/or the ecology of many of these species are little or not at all known. These species were tentatively, and in an approximate form, grouped as:

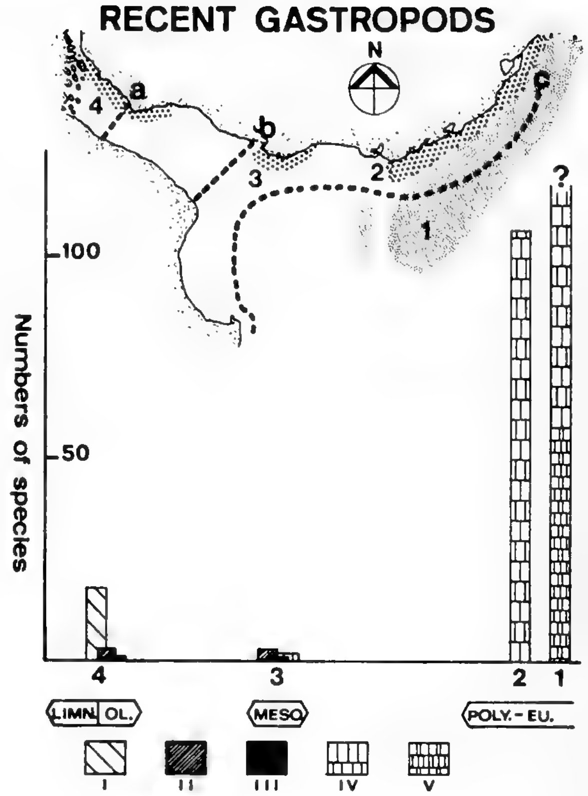

Fig. 7: Distribution of living gastropods in the Río de la Plata estuary, and its zone of influence. Key: I = freshwater gastropods, II = genuine brackish-water and/or euryhaline limnic species, III = genuine brackish-water species, IV = marine intertidal and upper sublittoral species, V = middle and lower sublittoral marine species, and pelagic forms. Location of areas 1—4 and their features are given in pages 42, 43. Lines a, b and c are the boundaries between estuarine environments, as shown in Fig. 3.

1. marine species which are typically from the middle and lower sublittoral zones; and pelagic forms: 58(?) (fig. 7, area 1). They live together with many species of the next area.
2. marine intertidal and upper sublittoral species: 102 (?) (fig. 7, area 2)
3. genuine brackish-water and euryhaline species: 2.
4. unclassified and doubtful species: 21.

According to Figueiras (1964) and Figueiras & Sicardi (1971, 1972, 1974) the following species were recorded from the littoral sensu lato of Montevideo County (fig. 7, area 3): *Littoridina australis, Littoridina charruana, Littoridina isabelleana, Parodizia uruguayensis, Buccinanops deformis, Cylichna (Cylichnella) bidentata, Caecum capitanum* and *Meioceras tumidissimum.* The presence of the last two species in this region must still be confirmed (KLAPPENBACH, 1964). *Buccinanops deformis* is a marine stenohaline species (FIGUEIRAS & SICARDI, 1968a, p. 237). *Cylichna (Cylichnella) bidentata* is not abundant.

Littoridina australis is the unique dominant gastropod in this region, and is considered as an "estuarine species" by BORDAS (1957), OLIVER et al. (1972) and SCARABINO, MAYTÍA & CACHÉS (1975). According to the latter authors, this genuine brackish-water species is found on sandy substrates with high a content of organic matter, in the intertidal and upper sublittoral zones; and also in the "marshland" i. e. in muddy sediments.

No precise data were published about the tolerance of *Littoridina australis* in relation to decreasing water salinities. PARODIZ (1962) indicates that its habitat is always "brackish". BARATTINI & URETA (1960) considered that it is a typical species in "brackish" and "limnic" environments. This point of view is also supported by FIGUEIRAS (1964), who writes that the normal biotope of *Littoridina australis* lies in "brackish waters". CAMACHO (1966) considered this species as an euryhaline form. CASTELLANOS (1965) has described *Littoridina australis* in Punta Lara (Buenos Aires County), as being very abundant and coexisting with numerous limnic species. Punta Lara is located in the region were the boundary between the inner-fluvial and intermediate-fluvial environments is found.

Littoridina charruana, Littoridina isabelleana, and *Parodizia uruguayensis* were also reported from the coasts of the Montevideo County (BARATTINI & URETA, 1960; FIGUEIRAS, 1964; PEREIRA DE MEDINA, 1959). The available information about these species is mainly based on the thanatocoenosis. The lack of ecological data of the biocoenosis makes it difficult to decide if they are genuine brackish-water species or euryhaline limnic ones.

Besides, it must be remembered that a more marked tolerance of changes in salinity is found in the limnic gastropods than in bivalves (REMANE, 1971).

Along the coasts of Colonia County (fig. 7, area 4) the existence of 17 to 19 stenohaline freshwater gastropod species were reported (FIGUEIRAS, 1964, 1965c). This number must be considered as an approximation due limitations previously cited. Moreover, *Littoridina australis, Littoridina charruana, Littoridina isabelleana* and *Parodizia uruguayensis* are also present.

The distributional pattern of gastropod species from the intertidal and upper sublittoral zones of the Uruguayan estuarine and oceanic regions, shows an evident similarity with those of the bivalve fauna:

1. in the oceanic region a high species diversity is present, indicating an euhaline and polyphaline environment.
2. the fluvio-marine environment is characterized by a low species diversity. The genuine brackish-water species *Littoridina australis* is here dominant. Besides, in this environment were found limnic euryhaline and marine species.
3. in the inner-fluvial environment high species diversity is present.
4. no precise data are available for the intermediate-fluvial environment, which could be fitted graphically into REMANE's curve. It can be inferred that the species diversity decreases, if the highs of columns 3 and 4 on the histogram in Fig. 7 are interpolated.

Some facts about the distribution of the living molluscs in the Río de la Plata region must be given. The salinity is the main environmental factor which determines the distribution of the bivalves and gastropods. This result is the same as that given for the molluscan faunas in different estuaries (DAVIES, 1972; DÖRJES & HOWARD, 1975; HEDGPETH, 1957; HILTERMANN, 1963b; MCLUSKY, 1971; REMANE, 1934, 1940, 1963, 1971). Therefore they are valid correlations, between the molluscan assemblages and environments, based fundamentaly on the salinity tolerance of the bivalve and gastropod species. Nevertheless, it must be remembered that the distributional pattern of the molluscan faunas is also subjected to other environmental factors, as temperatures, type of sediment, currents and tides, bathymetry, water turbidity, food availability, oxygen concentration, ionic concentration, flocculation of silt particles, etc. (DAVIES, 1972; DÖRJES & HOWARD, 1975; EMERY & STEVENSON, 1957; GREEN, 1968; HEDGPETH, 1957; MCLUSKY, 1971; PARKER, 1955, 1959, 1975). In an estuarine environment a faunal dislocation, like te one illustrated by EMERY & STEVENSON (1957, fig. 2) can also occur, as well as sediment and faunal mixings.

The fine sediments deposited in the estuarine environment display another particularly important feature. Their interstitial water is more constant in its salinity than the overlying water body. Although the interstitial salinity reflects the salinity of the overlying water, changes in the interstitial salinity take place at a much slower rate. Many species utilize this ameliorating effect of the substrate to survive in this unstable environment (BARNES, 1974; MCLUSKY, 1971). This ameliorating effect also favours the paleoecological reconstruction because it has a stabilizing result on the biocoenosis, and therefore on the thanatocoenosis.

In short, the present day distributional pattern of the molluscs in the Río de la Plata estuary show very evident trends, which will be used for the paleoecological and paleogeographical interpretation.

d. Reconstruction of Quaternary depositional environments

The molluscan faunas deposited in Uruguay during the Querandina Transgression have been referred to in many publications. The most important are those of Bordas (1957), Broggi (1967, 1970, 1973), Calcaterra (1971), de Mata (1947), Figueiras (1961, 1962, 1967, 1973), Francis (1975), Frenguelli (1930), Goñi & Hoffstetter (1964), Ihering (1907, 1923, 1930), Kraglievich (1928, 1932), Parodiz (1962) and Teisseire (1927, 1928). Recently Closs & Forti (1971) and Forti (1969) described molluscan faunas of the same age from southern Brazil. The largest part of this research concerns itself with taxonomy and stratigraphy, whereas the paleoecological and paleogeographical interpretation were somewhat downgraded. The work of Teisseire (1928) was the exception in which the paleoecological data is still of great use today.

QUATERNARY MOLLUSCS

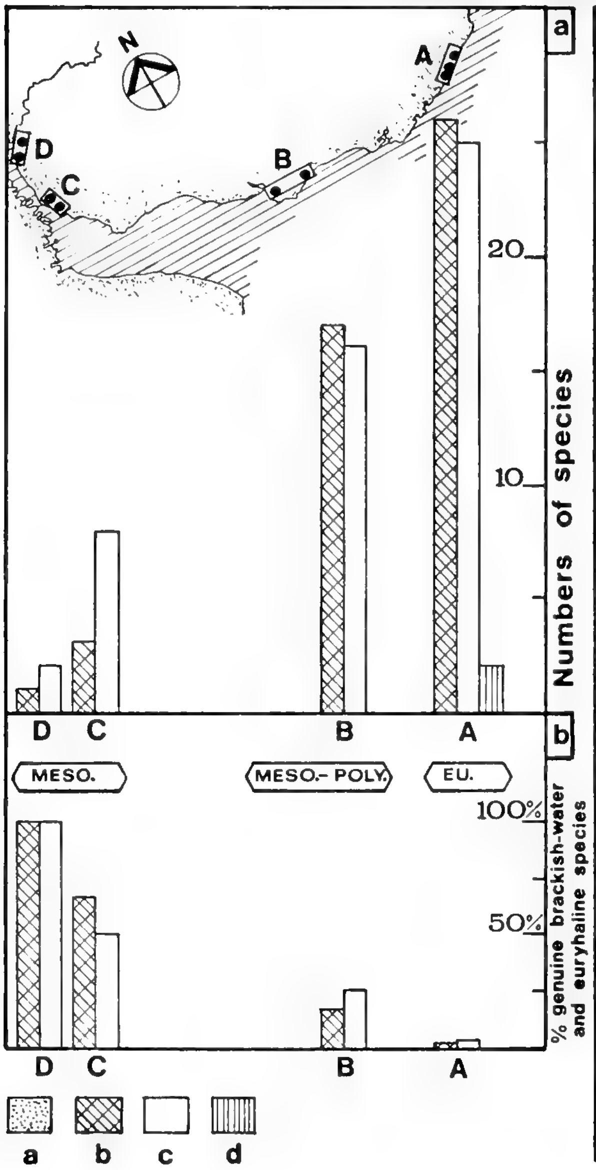

Fig. 8a: Distribution of Quaternary molluscs found in bore-holes and Lecocq. The bore-holes are grouped in areas A to D, as is explained in pages 45. Fig. 8b: Shows the percentile occurence of genuine brackish-water and euryhaline species in each area. Key: b = gastropods, c = bivalves, d = polyplacophorids.

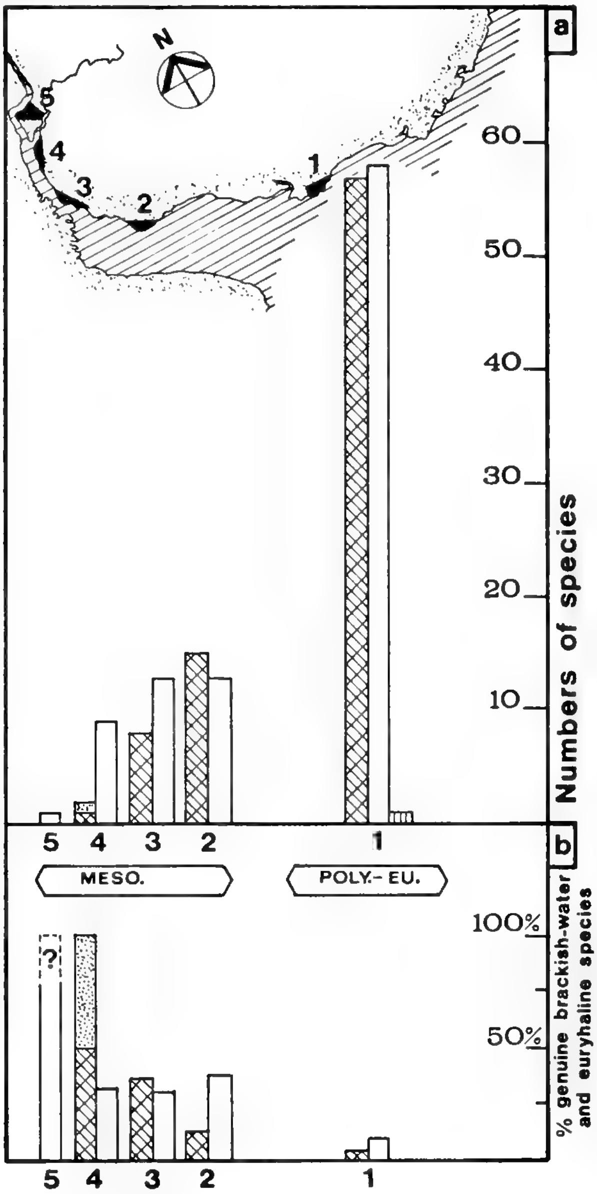

Fig. 9a: Distribution of molluscs recorded at exporsures of Vizcaíno Formation. These outcrops are located in areas 1 to 5. Their geographic location are given in page 45. Fig. 9b: Percentile occurence of genuine brackish-water and euryhaline species. Key: a = Chilina sp.?, b = gastropods, c = bivalves, d = polyplacophorids.

To establish the tolerance of certain species of water salinity, the work of Frey, Voorhies & Howard (1975), Parker (1955, 1956, 1959, 1975) and Stanley (1970) were also taken into consideration.

The study of Quaternary malacological assemblages begins with faunas recorded from wells and in Parque Lecocq. The histogram of Fig. 8a is designed to study the distribution of Quaternary molluscs, and their relationship to Remane's curve. Only those assemblages which allow one to identify the "estuarine front" of the transgression were used. The malacological faunas which were deposited in the "lateral-marginal zone of influence" were excluded. The bivalve and gastropod associations are grouped as follows:

Area A : species found in Costa Azul N° 1060/1, La Paloma N° 482/1 and La Paloma N° 449/11.

Area B : San José de Carrasco N° 442/1 and Parque Lecocq.

Area C : Carmelo N° 235 and Carmelo N° 245/1.

Area D : Bore-holes Río Uruguay N° 445/1 and Soriano N° 483/2.

The distribution of the bivalve and gastropod species is similar to those illustrated in the right half of Remane's curve.

The species spectrum of area A is similar to that reported for living assemblages of the oceanic region of Uruguay. *Brachidontes rodriguezi* and *Mytilus platensis* are also present. Both species make up a living community, which was defined for the living malacological faunas of the oceanic region of Uruguay. The area A assemblage indicate the prevalence of marine conditions.

In area B the species diversity decreases. In San José de Carrasco N° 442/1 the faunal spectrum indicates a polyhaline environment. In Lecocq it suggests a greater fall of water salinity, which was partially determinated by Río Santa Lucía runoff.

The diversity and faunal spectrum in area C corresponds predominately to a miomesohaline (= β mesohaline) environment, with a certain influence of pliomesohaline (= α mesohaline) waters. According to Remane (1963) and Hiltermann (1963b) the pliomesohaline is characterized by the dominance of a marine fauna, represented by few species. They coexist with genuine brackish-water species, and with some very tolerant limnic euryhaline ones. The miomesohaline is the most optimum environment for the genuine brackish-water species development, scarce euryhaline and limnic forms also being present. The associations in area D indicate miomesohaline salinities.

The *Brachidontes darwinianus* Community is present from Lecocq towards the inner part of estuary. This species is also recorded at Carmelo N° 245/1 and at Río Uruguay N° 445/1. Today this community lives in the fluvio-marine environment.

The percentile occurence of genuine brackhish-water and euryhaline species in areas A - D is illustrated in Fig. 8b. It is minimal at area A. At San José de Carrasco N° 442/1 it reaches 11 % for bivalves. From Lecocq towards the estuarine head or to the NW, it is evident that there is an increase in the percentile occurence of these species, which are excellent indicators for reduction in water salinity.

The given data are almost exclusively based on the malacological assemblages found in the wells. This fact may imply some limitations:

1. the number of specimens recorded from each drill cutting is low, and could introduce a bias in reference to species diversity,

2. the localities in which the wells are situated, are not always the most appropriate in analyzing faunas of the Querandina Transgression. The study of the molluscan assemblages recorded from wells also can bring adventages, because the drill samples generally contain those species which are dominant in their associations.

To verify the authenticity and validity of any given conclusions, a review of the available literature about molluscan faunas recorded from the Vizcaíno Formation exposures will be made. The re-examination of these faunas is offered, in an attept to adjust the information in reference to species diversity, and obtain additional data that are not available through the wells.

A faunal study made with this method presents several handicaps. The most relevant one is the multiplicity of criteria and methods used in faunal descriptions by different researchers. All the consulted work was not written with an aim towards paleoecological results. It is not possible in many situations to decide if the assemblages are autochthonous or allochthonous. Besides, faunas collected in different facies are related.

A histogram is given that indicates species diversity, in the following areas (fig. 9a):

Montevideo and Areneras de Carrasco (area 1).
Colonia City (area 2).
Carmelo and Nueva Palmira (area 3).
Soriano (area 4).
Fray Bentos and Mercedes (area 5).

The geographic extension of these areas, the implicated exposures, and the bivalve and gastropod species that they contain, are contained in Sprechmann (1978b).

The resulting histogram (fig. 9a) possess a similar configuration with the one prepared for the malacological faunas recorded from the wells (fig. 8a).

The following conclusions are established on the molluscan assemblages recorded from the Vizcaíno Formation exposures:

The area 1 (Montevideo and Areneras Carrasco) is characterized by:

1. a high species diversity (fig. 9a),

2. the per cent occurence of the genuine brackish-water species is small (fig. 9b); and

3. these associations possess predominantely a marine species spectrum, indicating an euhaline-polyhaline environment.

Area 2 shows:

1. an evident decrease of the diversity (fig. 9a);

2. the per cent occurence of the euryhaline and genuine brackish-water species increases greatly;

3. these associations possess predominantely a marine species coexist. This association is attributed to a pliomesohaline environment.

The assemblage of area 3 is also included within the mesohaline environment, but having lower salinity than area 2.

In area 4 a definite difference between the bivalve and gastropod diversity is present. The former are represented by eight species, whereas the latter only possess two. The diversity, faunal spectrum and per cent occurence of the genuine brackish and euryhaline bivalve species, indicate pliomesohaline salinities (fig. 9a—b). In contrast the gastropods reveal a miomesohaline environment. They are only represented by *Littoridina australis*, a genuine brackish-water species, and *Chilina* sp.?, probably a fresh water snail.

For area 5 only *Erodona mactroides* was reported, but the faunal content of the exposures in this region are little known as yet. They are considered as belonging to the miomesohaline environment.

The Archaeogastropoda (excluding the Neritacea) are the most intolerant gastropods as far as brackish environments is concerned (REMANE, 1963). In area 1, which is considered a euhaline-polyhaline environment, five Archaeogastropod species were reported, whereas in the remaining areas, only one was found.

These results, carried out on the molluscan faunas from different exposures could be affected by some built in errors. The weakest aspect is the overevaluation of the incidence and value of uncommon and rare species. In the case of the histogram in Fig. 9a this risk is grater, because the majority of the authors that have described the molluscan faunas of the Vizcaíno Formation put a special emphasis on the description of rare species. They gave special importance to reporting even greater numbers of molluscan species in each different exposure. This could even be enlarged by taxonomic and nomenclatural disagreements.

To counteract this as much as possible, the percentile occurence of genuine brackish-water species must be evaluated. These data are not obtainable from assemblages in drill cuttings. Data as to percentile occurence of the recorded species in each fossiliferous locality are not found in the literature. The unique exception is a paper of CALCATERRA (1971). This worker studied several exposures of the Vizcaíno Formation which are located in Colonia and Soriano Counties. For each outcrop the percentile occurence of found specimens belonging to each species is presented. Only those species that constitute more than 1 % of the assemblages in each outcrop were considered. Fig. 10 was plotted by using CALCATERRA's data. There the per cent occurence of genuine brackish-water species in the following exposures is offered: Cantera Ferrando (area i), Bahía de Colonia (area ii), Arroyo San Pedro (area iii), Punta Francesa (area iv), ex-cementerio de Nueva Palmira (area v), Colonia Concordia (in Rincón del Catalán) (area vi), and Pueblo Soriano (area vii). From an analysis of fig. 10, the fact stands out that the genuine brackish-water species constitute more than 90 % of the assemblages located between Bahía de Colonia and Pueblo Soriano. They make up the trophic nucleus of their assemblages. Somewhat to the east, in Cantera Ferrando, they constitute 65 % of the assemblages. This evidence shows the value of genuine brackish-water species, and this fact must be taken into consideration for paleoecological and paleozoogeographical reconstructions.

Fig. 11 is designed with this aim in mind, based also on data of CALCATERRA (1971). For each locality the percentile occurence is illustrated by the following:

1. marine species,

2. the recorded genuine brackish-water species: *Tagelus plebeius*, *Mactra isabelleana* and *Erodona mactroides*,

3. limnic species.

The assemblages plotted in Fig. 11 can be grouped as follows:

Brackish assemblage, with a moderate marine influence: locality i.

Brackish "polyspecific" assemblages. They have three dominant genuine brackish-water species: localities ii and iv.

Brackish "monospecific" assemblages. A single genuine brackish-water species is dominant: localities iii, v, vi and vii.

One of the greatest difficulties for paleoecological reconstruction of an estuarine region, is to discriminate between the "estuarine front" and the "lateral-marginal zone of influence".

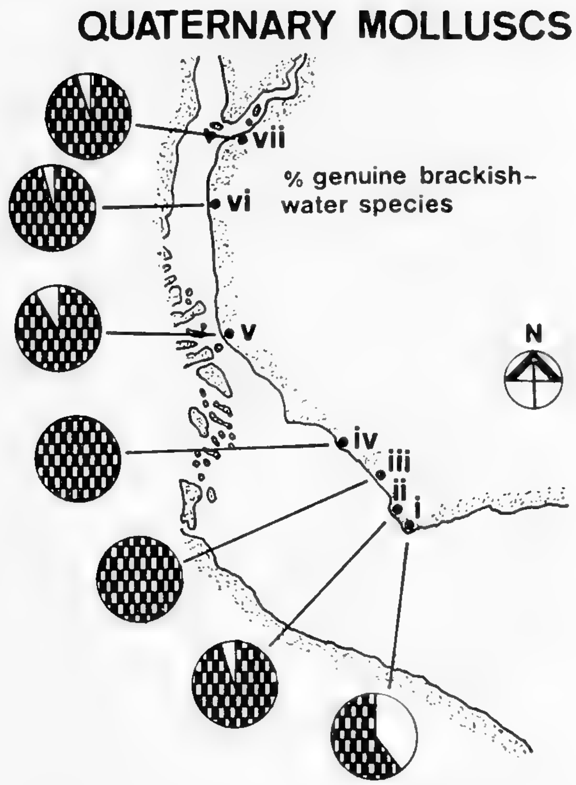

Fig. 10: Percentile occurence of genuine brackish-water species from several exposures from the Vizcaíno Formation in Colonia and Soriano Counties (after Calcaterra, 1971). Exposure location is indicated on page 46.

On Fig. 11 criteria for the identification of the associations deposited in the "estuarine front" are given. It allows to select the representative assemblages for reconstruction of saline zonation during the Querandina Transgression.

The assemblages ii and iv are comparable with the living ones on the shores of Montevideo County. Hence, they belong to the fluvio-marine environment, and indicate mesohaline salinity. According to Scarabino, Maytía & Cachés (1975) their faunal spectrum is typical for sandy muddy sediments. The absence of *Brachidontes darwinianus mulleri* and/or of *Mytella charruana* is a consequence of the absence of hard grounds in this area.

The brackish "monospecific" assemblages are considered as indicative of intermediate-fluvial environments (oligohaline-mesohaline). Only two brackish "monospecific"assemblages identify the "estuarine front": the associations found in the exposures of the ex-cementerio de Nueva Palmira (fig. 11, area v), and in Pueblo Soriano (fig. 11, area vii). On the contrary, the fauna recorded from localities iii and vi were deposited in the "lateral-marginal zone of influence".

Detailed evidences allows one to establish, with reasonable certainty the geographical setting of the Transitional-area between fluvio-marine and intermediate-fluvial environments during the Querandina Transgression. It was located approximately between Punta Francesa and Nuava Palmira. The term "Transitional-area" is used to underscore the fact that the changes between the environments are gradual. The faunal association of a "Transitional-area" is constituted by a combination of those species from adjacent environments.

The analysis of depositional environments provided by malacological assemblages of bore-holes Carmelo N° 245/1 and Carmelo N° 235 (fig. 13) permits one to define even more closely the location of the Transitional-area between fluvio-marine and inter-

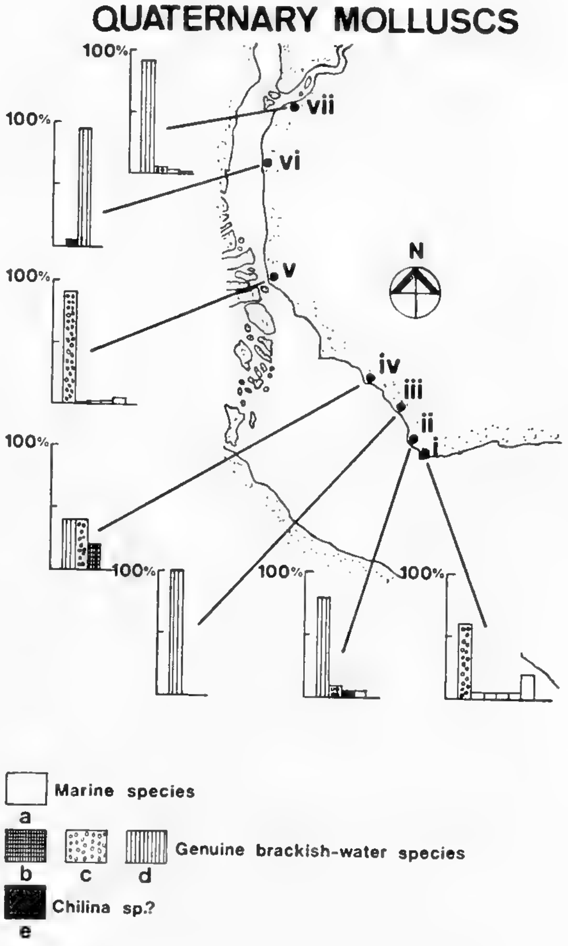

Fig. 11: Faunal composition in the various exposures from the Vizcaíno Formation in Colonia and Soriano Counties (after Calcaterra, 1971). Key: a = marine species, b = *Tagelus plebeius*, c = *Mactra isabelleana*, d = *Erodona mactroides*, e = *Chilina* sp.?. Location of exposures i — vii is shown on page 46.

mediate-fluvial environments. It allows one to deduce that it was situated between Carmelo and Nueva Palmira (fig. 12).

During the Querandina Transgression, the Transitional-area between intermediate-fluvial and inner-fluvial environments was located somewhat to the north of Fray Bentos, and a little east from Mercedes (fig. 12).

Identification of euryhaline bivalve and gastropod species

Several molluscan species found in the Río de la Plata estuary were defined as genuine brackish-water species and marine euryhaline ones by the malacologists that studied the living faunas of the region (Chapter VI. F. 4. b—c). The analysis of the range of distribution from the species found in the Querandina Transgression allows one to infer that the following species must be considered as marine euryhaline forms: *Anomalocardia brasiliana, Ostrea equestris, Pitar rostratum, Acmaea subrugosa, Thais (S.) haemastoma* and *Siphonaria (P.) lessoni.*

e) Paleoecological reconstruction on molluscs from additional localities of the Querandina Transgression.

The depositional environments of the strata of various outcrops which were assigned to the Querandina Transgression, are established on the basis of their molluscan assemblages. For this purpose a method of analysis is used, which defines following parameters:

1. the faunal spectrum,
2. the number of present stenohaline-marine, euryhaline-marine, genuine brackish-water, euryhaline-limnic and stenohaline-limnic species, and their per cent occurence.
3. determination of the number of dominant species in each assemblage.

These data are compared with ones used for living assemblages, and also for those plotted on Figs. 8, 9, 10 and 11.

This method is applied on the molluscan assemblages described by the named authors in localities from:

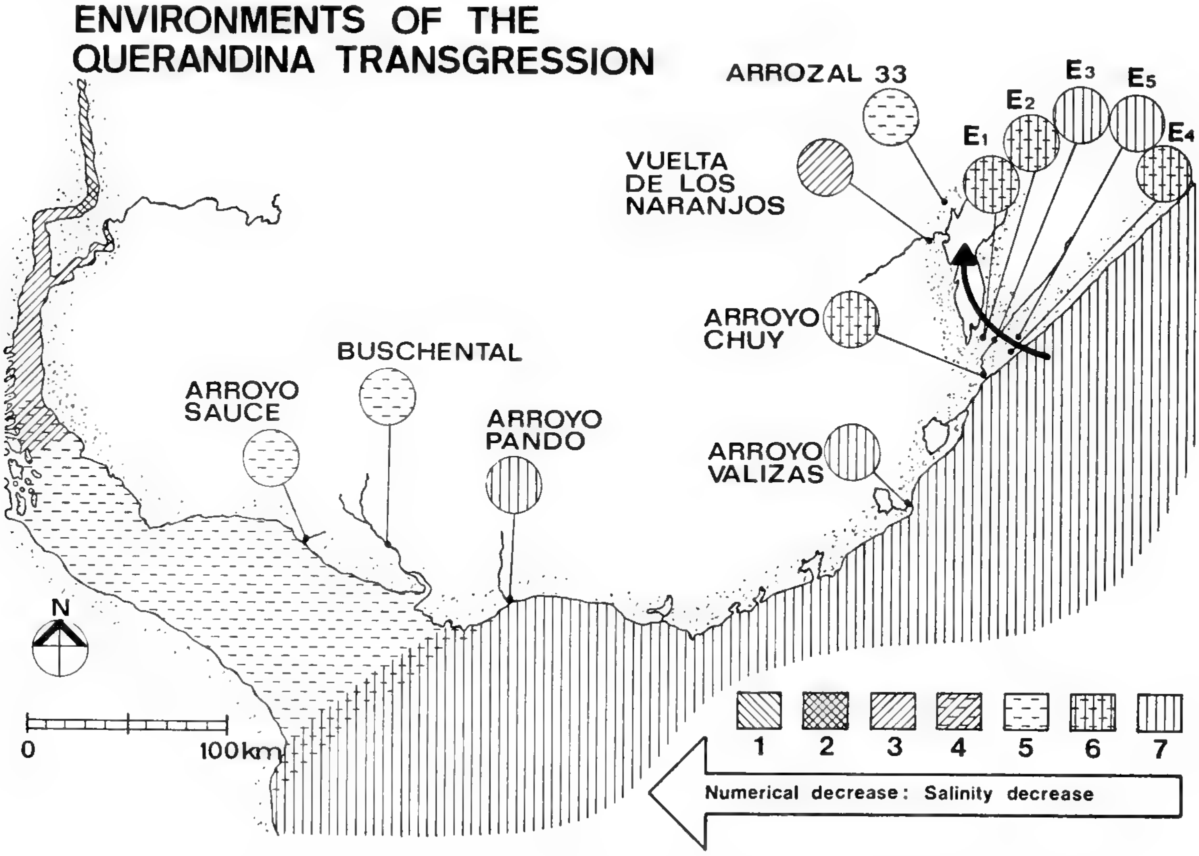

Fig. 12: Paleoecological reconstruction of estuarine environments as well as on additional localities of the Querandina Transgression. The following environments were identified: 1 = inner-fluvial environment, 2 = Transitional-area between intermediate-fluvial and inner-fluvial environments, 3 = intermediate-fluvial environment, 4 = Transitional-area between fluvio-marine and intermediate-fluvial environments, 5 = fluvio-marine environment, 6 = Transitional area between marine and fluvio-marine environments, 7 = marine environment. See pages 49 for information about indicated localities.

Rio Grande do Sul (southernmost Brazil): malacological associations from exposures E_1, E_2, E_3, E_4 and E_5, located in the Santa Vitória do Palmar County (CLOSS & FORTI, 1971).

Uruguay: Arrozal 33 (SERRA, 1944), Vuelta de los Naranjos, section II (SERRA, 1944), Arroyo Chuy (FIGUEIRAS, 1967), Arroyo Valizas (BROGGI, 1970), Arroyo Pando (BROGGI, 1967), Buschental (KRAGLIEVICH, 1932), Arroyo Sauce-Boca de los Ceibos (TEISSEIRE, 1928).

Using the proposed criteria corresponding environments were established, as is illustrated in Fig. 12. These environments are related with the shown estuarine zonation during the Querandina Transgression. It must be remembered that the reconstruction was approximate in determined environments. The degree of correctness in this approach depends on the realiability and accuracy with which faunal records were made in each fossiliferous locality.

The depositional environments show the following relationships with the estuarine ecozones (fig 12):

1. The assemblages from the exposures E_3, E_5, Arroyo Valizas, Arroyo Pando and Sauce-Boca de los Ceibos belong to the marine and "estuarine front" depending on their geographic setting.

2. The molluscs of localities Arroyo Chuy, E_1, E_2, E_4, Arrozal 33 and Vuelta de los Naranjos were deposited in the "lateral-marginal zone of influence".

3. During the Querandina Transgression the Laguna Merín was inhabited (settled), in the Arrozal 33 region, by a molluscan fauna which is characteristic for the fluvio-marine environment. In contrast, today in the inner part of the Laguna Merín the salinities do not exceed values of 0.2 ‰, reaching exceptionally up to 1 ‰ (CLOSS & MEDEIROS, 1967; MADEIRA-FALCETTA, 1974).

4. Throughout the course of the lower Holocene Transgression, the Laguna Merín was directly open to the ocean in its southernmost part. The molluscan assemblages from Santa Vitória do Palmar County and Laguna Merín display a zonation beginning with marine environments that range to fluvio-marine, and

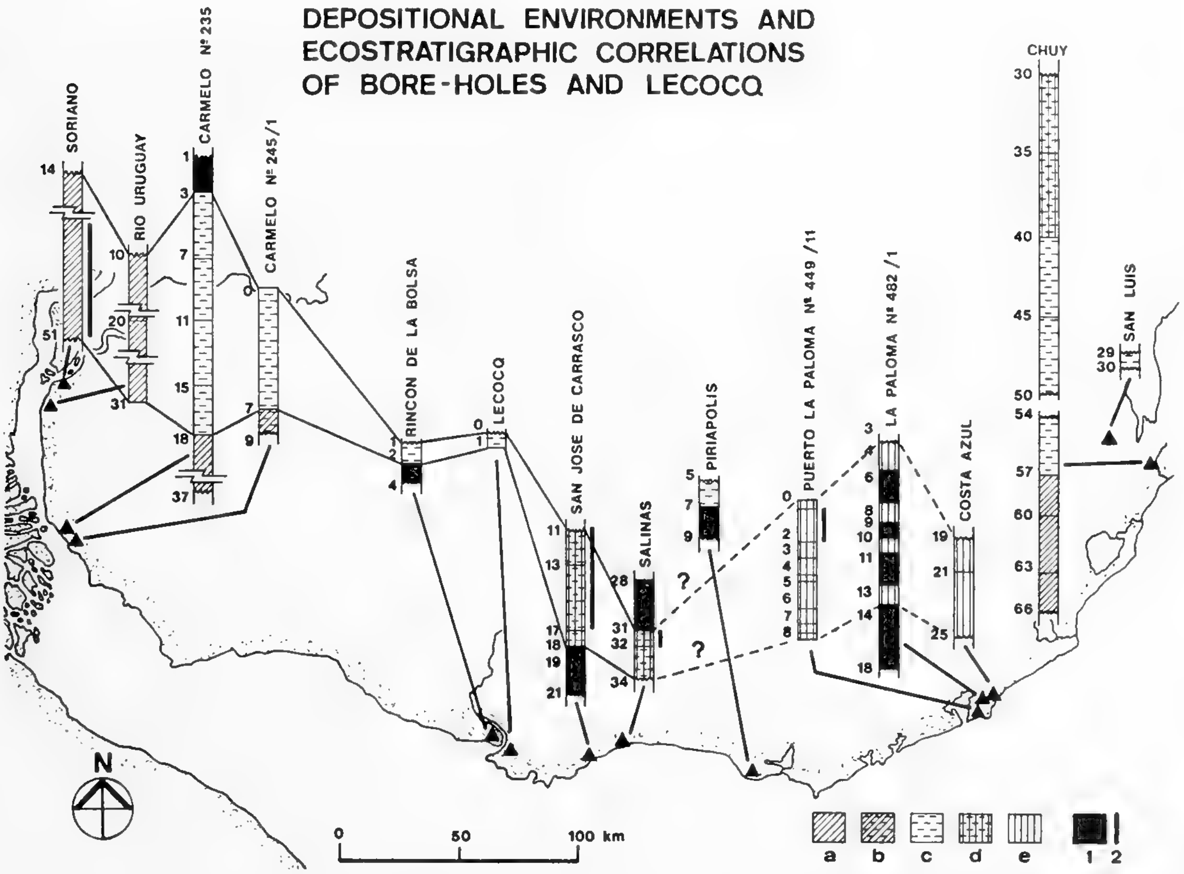

Fig. 13: Depositional environments of bore-holes and Lecocq, and ecostratigraphic correlations. Key: **a** = intermediate-fluvial environment, **b** = Transitional-area between fluvio-marine and intermediate-fluvial environments, **c** = fluvio-marine environment, **d** = Transitional-area between marine and fluvio-marine environments, **e** = marine environment. — **1** = environment not identified, material lacking, **2** = environment tentatively established.

somewhat to the north into those of the intermediate-fluvial environment (fig. 12). It is not the purpose of this paper to make a detailed reconstruction of the facies and paleogeography of the Laguna Merín during the Querandina Transgression, or to determine its relation with the coastal plain evolution. JOST, SOLIANI Jr. & GODOLPHIN (1975) studied the paleogeographical evolution of this region during the Quaternary. They described the existence during the Flandrian Transgression of an inlet between the sea and Laguna Merín, located in the proximity of the locality of Taim, which was designated as "Vertedouro do Taim". However, they did not mention the presence of any Holocene connexion between Laguna Merín and the ocean, which was situated to the south of "Vertedouro do Taim".

5. DEPOSITIONAL ENVIRONMENTS DETERMINED BY WELL DRILLING AND IN PARQUE LECOCQ

The ancient environment of each Quaternary fossiliferous drill cutting from bore-holes, and from Lecocq, is represented on the basis of the evaluation of foraminiferal and molluscan associations (fig. 13). The conclusions which were established on those drill cuttings carrying scarce fossiliferous material must be considered as approximate.

G. Biostratigraphy

The paleoecological and paleogeographical reconstructions previously presented have several different biostratigraphic consequences:

1. ECOSTRATIGRAPHIC CORRELATIONS

It is not possible to make time-biostratigraphic correlations using index fossils. This is the usual situation working with Quaternary benthic assemblages. Besides, there are no climatic fluctuations of great enough extent to be used for time-stratigraphic correlations.

The only way to establish biostratigraphic correlation is by using ecostratigraphic units or ecozones. These ecozones are correlated by their place in the cycle of greatest salinity. A similar technique was used by ISRAELSKI (1949) and KRUMBEIN & SLOSS (1963, fig. 10—18), who made their correlations using the method of position in the bathymetric cycle.

The ecostratigraphic correlations that are proposed are illustrated on Fig. 13. The presented time-stratigraphic horizon contain fossil associations carrying different faunal spectra. For these correlations only those assemblages are taken into consideration which were deposited in the "estuarine front". Only the assemblages that indicate environments with the greatest salinity for each estuarine region are used. This stratigraphic position then may be considered to be time equivalent at each well.

The fossil associations of San Luis N° 1072/1, Chuy N° 364 and Piriápolis N° 431/7 show environments that are not in agreement with the cycle of the greatest salinity for their geographical setting. They could have been deposited in:

a) the "lateral-marginal zone of influence" being in this case isochronous.

b) the course of an earlier or latter transgressive event. For Chuy N° 364 it is shown that the fossil assemblages were more ancient, being deposited during the Pleistocene (Chapter VII).

The reliability of the provided correlations increases towards the head of the estuary. From Salinas to the NW net differences between the contemporaneous depositional environments are present, as a consequence of displacements of depositional environments during the Querandina Transgression. On the contrary, the depositional environments found in Costa Azul N° 1060/1, La Paloma N° 482/1, and La Paloma N° 449/11 correspond to a marine environment, being coincident with the ones existing today in these localities. Hence, a correlation supported on the environmental displacement is not possible, due to the absence of differentiated depositional environments. The indicated correlation between these wells must be considered as tentative.

The ecostratigraphic correlations illustrated in Fig. 13 must be confirmed and verified by C 14 dating.

The above is dealt more extensively by SPRECHMANN (1978a).

2. DATA SHOWING THAT THE ASSEMBLAGE ZONES DESCRIBED FOR THE URUGUAYAN QUATERNARY ARE INVALID

The age of malacological associations found in the region of Nueva Palmira and southern Fray Bentos have given origin to some controversy. The prevailing opinion has assigned them to the Querandinense, but some workers included them within the Belgranense (CASTELLANOS, 1948; FRANCIS, 1975; FRENGUELLI, 1930; GOÑI & HOFFSTETTER, 1964; KRAGLIEVICH, 1928, 1932). A paleontological argument was used supported on the presence or absence of certain species, which were considered typical for each stage. *Mactra isabelleana* and *Thais haemastoma* were mentioned as characteristic fossils for the identification of the Belgranense. The faunal assemblages deposited during the Querandinense may be recognized by the dominance of *Erodona mactroides*. Nevertheless, FORTI (1969) correctly considered that *Mactra isabelleana* is a typical form in the Querandinense.

The time-stratigraphic interpretation supported on the presence or absence of these species are incorrect. They are isochronous. Their presence or absence in a certain time equivalent assemblage is due to environmental factors, one being the salinity. Moreover, the benthic molluscs have a patchy distributional pattern (Parker, 1975).

Francis (1975) defined the following biostratigraphic units:

a. *Thais haemastoma* Assemblage Zone (middle Pleistocene?), which is tentatively correlated with the Belgranense;

b. *Erodona mactroides* Assemblage Zone (Vizcaíno Formation: upper Pleistocene-Holocene);

c. *Elphidium discoidale* Assemblage Zone (Chuy Formation and Vizcaíno Formation: upper Pleistocene-Holocene); and

d. *Littoridina australis* Assemblage Zone (La Plata Formation?: Holocene).

The results proposed by Francis are the consequence of a mistake. As is indicated in the present work, the species that identify the assemblage zones are essentially time-parallel. Therefore they can not be used as time-stratigraphic indicators, because their presence or absence in an association is determined by facial and ecological changes.

H. Results of the Holocene paleogeography in the Río de la Plata region

The available data of the history of the Río de la Plata supported on C 14 datings (Chapter VI-E), and the proposed ecostratigraphic correlations (Chapter VI-G-1), allow one to conclude that the major part of the foraminiferal and molluscan assemblages were deposited during the first transgresive phase of the Holocene Transgression.

According to Urien & Ottmann (1971) during the early Holocene the waters transgressed penetrating deep into the estuary. Sea level reached as far as + 8 m above present stand.

The paleoecological reconstruction corroborated the existence of displacement of the estuarine depositional environments simultaneously with the first transgresive phase of the Holocene Transgression. The geographic range covered by each depositional environments was evidently different from the prevailing today (fig. 14).

The assemblages of foraminiferids are most suited to reveal the location (situation) of the Transitional-area between marine and fluvio-marine environments during the earlier phase of the Holocene Transgression. It formed an arch along the Uruguayan coast, extending from Salinas as fas as San José de Carrasco, Areneras de Carrasco, and the eastern coastal region of Montevideo County. In contrast, the foraminiferids are not useful in the reconstruction of the location of the remaining transitional-areas. By evaluating molluscan assemblages, reconstruction of the geographical setting of fluvio-marine and intermediate-fluvial environments was possible. The Transitional-area between fluvio-marine and intermediate-fluvial environ-

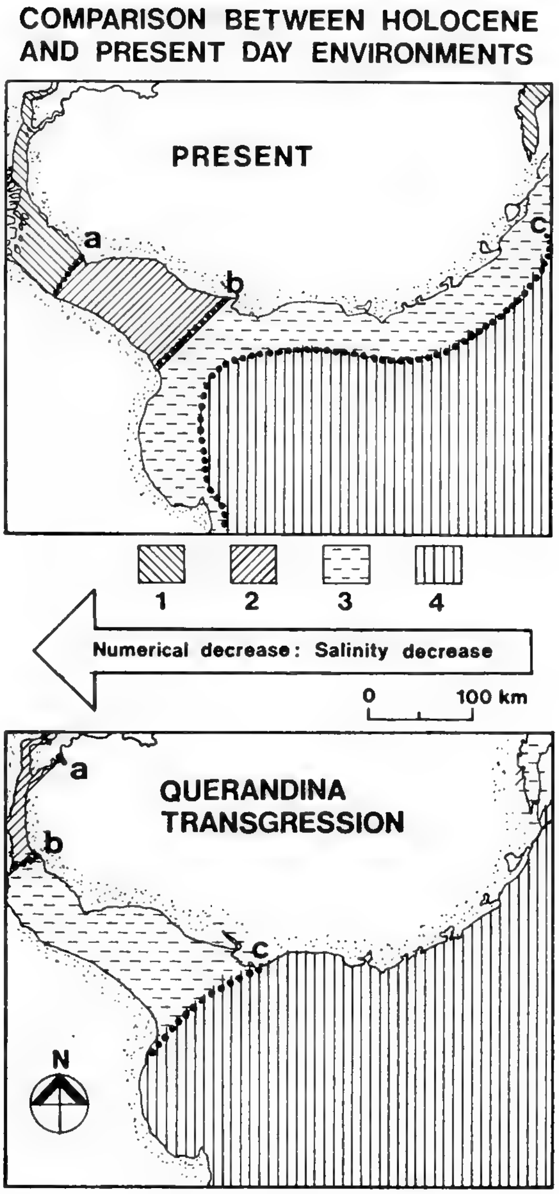

Fig. 14: Comparison between depositional environments from the first transgressive phase of the Holocene Transgression, and those of the present day, showing environmental displacements. Key: **1** = inner-fluvial environment, **2** = intermediate-fluvial environment, **3** = fluvio-marine environment, **4** = marine environment. **a**, **b** and **c** location of transitional-areas (also see figs. 3 and 12).

ments was located between Carmelo and Nueva Palmira. The transitional-area between intermediate-fluvial and inner-fluvial environments was localized in the Río Uruguay somewhat to the north of Fray Bentos; and a little east from Mercedes on the Río Negro (fig. 12).

The depositional environments and transitional-areas were reconstructed using foraminiferal and molluscan assemblages found on the Uruguayan coast of the Río de la Plata. Their projection towards the central and southern estuarine region is tentatively outlined.

The great extent of the movement of the depositional environments shown in Fig. 14 shows that they could not had occured as a consequence of a saline stratification.

Paleogeographical reconstruction has confirmed the validity and authenticity of the argument that the foraminiferal and molluscan associations were deposited during the earlier Holocene transgressive events. Urien & Ottmann (1971) wrote that the transgressive events during the upper Holocene had less vertical amplitude and smaller superficial extent. Furthermore, the marine influence remains restricted to the outer part of the estuary.

These results are also in agreement with those of Urien (1972), who by using sedimentological methods showed the existence of:

1. an onlap of marine sandy facies during the Querandina Transgression, which was followed by,
2. an offlap of fluvial sitly muddy facies.

The sea also invaded the Laguna Merín area simultaneously to the Querandina Transgression. It was connected with the ocean by it southernmost part. Jost, Soliani Jr. & Godolphin (1975) previously described the existence of a second connecting body designated the "Vertedouro do Taim". The molluscan assemblages of the Querandina Transgression reveal in the Laguna Merín region the existence of zonation, beginning in the south with marine environments, that gradually change north into fluvio-marine and intermediate-fluvial environments.

VII. CONCLUSIONS ABOUT THE NEOGEN-QUATERNARY EVOLUTION IN THE CHUY AREA

Chuy well N° 364 is located in the western region of the Pelotas Basin. This well presents the most complete known sedimentary sequences for the study of the Uruguayan Neogene and Quaternary. This fact explains the repeated studies made about this bore-hole, and justifies the inclusion of a special review of this well. Several stratigraphic interpretations were made for the well (see Chapter V-B). Only the interpretation proposed by Goso (1972) shows good parallelism with the distribution of fossil assemblages. For this reason it is used as a basic reference for the stratigraphic interpretation.

The drill cuttings situated between 133.00—113.00 m (fig. 2) had been assigned to the Camacho Formation (Ecochard, 1970; Figueiras & Broggi, 1971, 1972/73; Goso, 1972; Medina, 1962). The depositional environments corresponding to these drill samples are analysed in Chapter V-F-4. The assemblages show a Miocene age.

Between 113.00—66.00 m continental sedimentation took place that lithostratigraphically corresponds to the Raigón Formation (Goso, 1972). Probably it was deposited during the Pliocene.

The Quaternary sequences of Chuy N° 364 which contain foraminiferids and molluscs are analyzed in Chapter VI. Its distribution shows that between 66.00—57.60 m only the bivalve *Erodona mactroides* occured. This species is also present between 57.60—54.20 m associated with foraminiferids, ostracods and barnacle plates. The whole assemblages found between 66.00—54.20 m shows a shallow, cold temperate, and hyposaline (oligohaline, mesohaline) depositional environment.

Between 50.00—30.00 m assemblages made up of foraminiferids, ostracods, barnacle plates and bivalve fragments are present. Their faunal spectrum indicate shallow, cold temperate, and hyposaline (polyhaline-mesohaline) waters.

Goso (1972) points out that these transgressive episodes correspond lithostratigraphically to the Chuy Formation. He also refers to the same formation the drill samples which lie between 27.40—7.10 m. These three sequences which are part of the entire lithostratigraphic Chuy Formation, were named Chuy I, Chuy II and Chuy III.

The Chuy Formation was defined by Delaney (1963, 1965). Only the sediments lying between 27.40—7.10 m are the same of those found in the type locality of the Chuy Formation. The lithofacies of the Chuy Formation were described by DELANEY (1963, 1965, 1966, 1967, 1969?) and JOST (1972). The sequence situated between 27.40—7.10 m, whose lithofacies is equivalent with that of the Chuy Formation, is here named Chuy (sensu stricto) III (fig. 2). Probably it belongs to the upper Pleistocene (see Chapter VI-C-3).

The drill cuttings found between 66.00—54.20 m, and 50.00—30.00 m, lithologically are not similar to the facies of the Chuy Formation sensu stricto. For their identification the names Chuy (sensu lato) I, and Chuy (sensu lato) II are used (fig. 2). Its position in the section indicates that they were deposited probably during the Pleistocene.

According to Goso (1972), the continental strata that were deposited after each one of the chronostratigraphic events Chuy (sensu lato) I, Chuy (sensu lato) II, and Chuy (sensu stricto) III, belong lithostratigraphically to the Libertad Formation. Each of these continental events are chronostratigraphically named Libertad I, Libertad II, and Libertad III. Libertad III ist considered to be a synonym for Dolores Formation (fig. 2).

Goso (1972) correlated the Chuy I, Chuy II and Chuy III events with the first, second and third Quaternary interglaciations, respectively. Libertad I, Libertad II and Dolores were considered as being time equivalent with the second, third and fourth glaciation, whereas Raigón is considered to have been deposited during the first glaciation. ECOCHARD (1970) also established time-stratigraphic correlations between the sedimentary sequences of Chuy N° 364, and the Quaternary glaciations and interglaciations. TRICART (1972) also provided time-stratigraphic correlations between the Quaternary glaciations and interglaciations and the Uruguayan formations. But the correlations proposed by these authors do not in themselves agree.

In this work none of these criteria has been adopted. There is no objective evidence for dating, even less to verify time-stratigraphic correlations with certain glaciations or interglaciations.

VIII. DISTRIBUTION OF THE PALEOZOOGEOGRAPHICAL LITTORAL PROVINCES

The paleozoogeographical evolution of the region in study, since the Miocene up to the Holocene, is very controversial.

One of the most polemic aspects was postulated by IHERING (1927). He theorized that the Gulf of Mexico-Caribbean area was connected with the South Atlantic by an arm of the Tethys crossing through the continent and providing tropical waters. This hypothesis has been examined from different points of view. In reference to foraminiferids it has been discussed by BOLTOVSKOY (1958, 1973, 1976), BOLTOVSKOY & LENA (1971, 1974b), CLOSS (1963) and MALUMIAN (1970).

In this chapter an attempt is made to make a paleozoogeographical contribution with a different point of view. The relationships between the distribution of the marine currents and the paleozoogeographical littoral provinces that they determine are analyzed from the Miocene to Holocene. This paleozoogeographical zonation must be considered the first approach to this subject for this region. It must be completed and adjusted on the basis of new fossiliferous findings and the use of other phyla.

The evaluated data have been provided by:

a. the fossil assemblages found in Uruguayan boreholes; and

b. the interpretation of available information contained in previous literature.

This analysis presents difficulties as a consequence of the low number of known fossil localities. In addition, great disagreement exist in reference to the time-stratigraphic relations of the Miocene assemblages recorded from the South American atlantic region. This fact has been documented by BERTELS (1975), BERTELS & MADEIRA-FALCETTA (1977), BOLTOVSKOY (1973), CLOSS (1967, 1970), MALUMIAN (1970), MALUMIAN & MASIUK (1973), NOGUTI (1975) and STAINFORTH (1975). This problem is even more acute in the Quaternary.

The distributional pattern of the littoral foraminiferids from the atlantic coasts of South America since the Miocene, can be explained by the existence of two marine currents; one flowing from north to south carrying warm masses, and another that flowing in the opposite direction, transporting cold water bodies. It is assumed and hypothesized that these currents are the Brazilian and the Malvin respectively. Therefore, the information offered by the foraminiferal associations of the wells, can be related to the present-day distribution of the littoral zoogeographical provinces in this region. The term littoral is used in the broad sense. It includes the intertidal zone and the upper part of the sublittoral zone (upper sublittoral zone).

The present distribution of the West Indian Province (= Caribbean or Antillean Province) in South America, and its division into subprovinces is described by BOLTOVSKOY (1964, 1965, 1976), BOLTOVSKOY & WRIGHT (1976), and TINOCO (1971), (fig. 15c). The features of the Argentine Province (= "kingdom" of *Buccella peruviana*, s. l. or South American Atlantic Province) were given by BOLTOVSKOY (1970a, 1976) and BOLTOVSKOY & WRIGHT (1976), (fig. 15c).

A. Miocene

Studies on the paleogeography of the Entrerriana Transgression are provided by HARRINGTON (1962) and CAMACHO (1967).

The Miocene foraminiferal assemblages found in Chuy N° 364 (133.00—122.10 m) are characterized by the presence of *Amphistegina gibbosa*. At the present time, *Amphistegina radiata* (and/or *Amphistegina lessonii*) is the most characteristic foraminiferid from the littoral and upper sublittoral warm waters of nordeast Brazil. Its present range of distribution is situated between the 23° S and 4° N parallels. This species disappears north of Cabo Orange, and south of Cabo Frio, and defines the North-brazilian Subprovince (TINOCO, 1971). In this subprovince tropical waters of the Brazilian current are found and the cold Malvin stream has no influence. It is a region of tropical warm waters, with mean annual temperatures higher than 24° C (BALECH, 1954). The surface-water temperatures range between 24° C in february and 21° C in august (BOLTOVSKOY, 1976, fig. 2).

The presence of *Amphistegina gibbosa* in the Chuy area during the Miocene, indicates that the North-brazilian Subprovince possessed a geographical distribution which extended further south, reaching al least 34° S latitude (fig. 15 a).

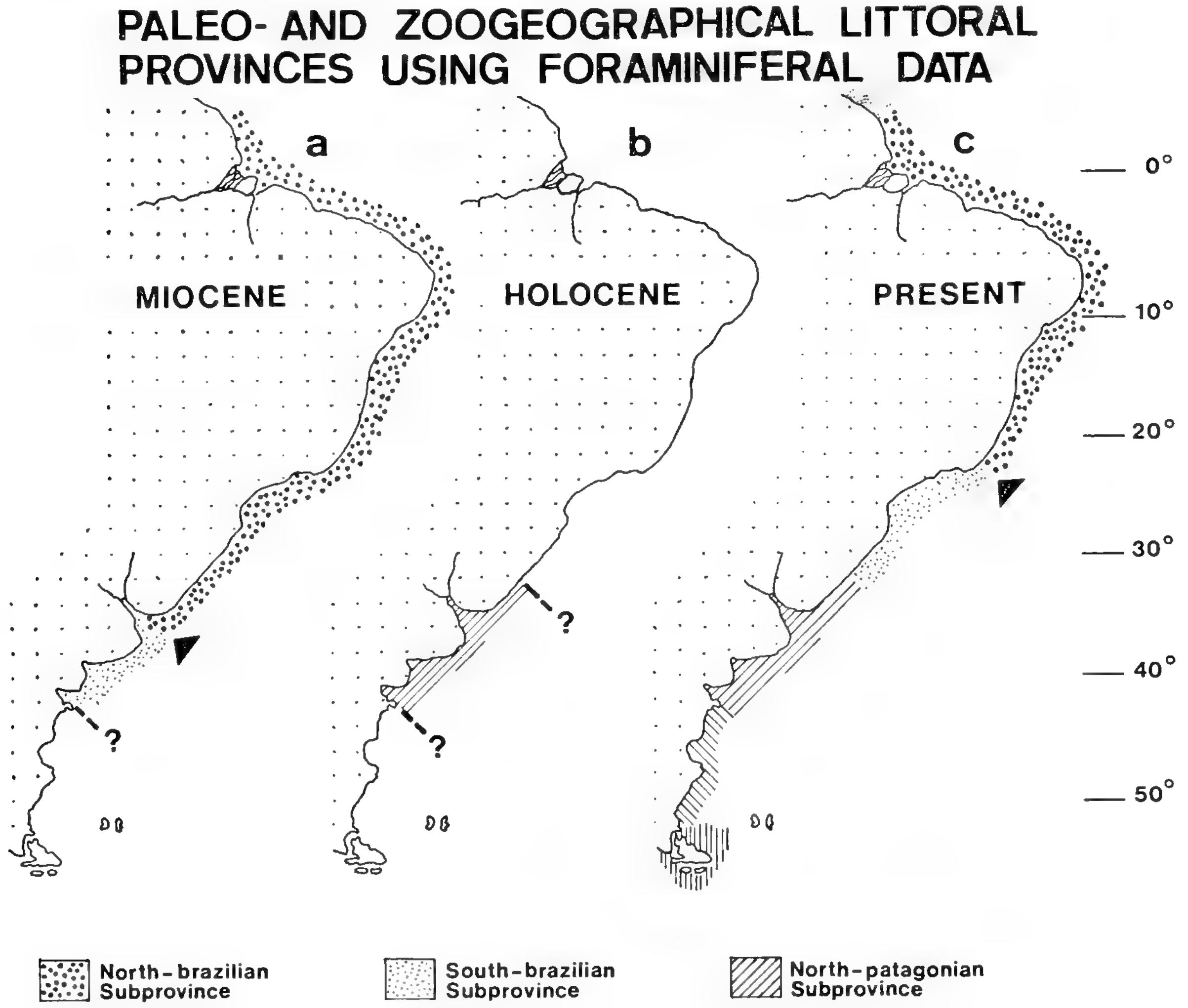

Fig. 15: Distribution of paleozoogeographical littoral provinces from Miocene to Holocene, based on foraminiferids.

Todd (1976, p. 388) also said that during the Eocene and Miocene *Amphistegina* significantly reach a greater geographic area than in modern seas. This may be related in part to the warmer climates during those times, and in part to the possibility of different positions of the continents to the equator and to the influence of oceanic currents.

These data are coincident with a pantropical expansion of certain shallow-water foraminiferids, specially seagrass-dwelling forms, that took place during the lower and middle Miocene. This is correlated with a climatic amelioration of 5—8° C that occured in higher latitudes of the southern hemisphere during early and middle Miocene times (Brasier, 1975b, p. 693—695).

The existence of warm water bodies in the Brazilian Miocene has also been shown for the Pelotas Basin (Closs, 1966a, 1967, 1970), the Marajó Basin (Petri, 1954) and the Pirabas Basin (Petri, 1957). In these fossiliferous localities *Amphistegina* is also present. Therefore all these regions must be included in one paleozoogeographic unit, which is designated as North-brazilian Miocene Subprovince (fig. 15a). The concept "paleozoogeographic province" is used to signify a climatic unit. This is a consequence of the fact that temperature is the most important factor limiting the geographic range of the species distribution (Boltovskoy, 1965; Boltovskoy & Wright, 1976; Valentine, 1963).

In Argentina, the microfaunas from the Entrerriense and/or Paranense (upper Miocene-lower Pliocene?) of the Salado Basin, indicate somewhat higher temperatures than exist today in this region (Malumian, 1970; Malumian & Masiuk, 1973). *Amphistegina* is absent. Bertels (1975) considered that the ostracods from the Argentinian Entrerrian Stage (= Entrerriense) indicated warm temperate waters. Based on these evidences, it is thought that warm temperate waters from the Entrerriense of Argentina correspond with those of the South-brazilian Subprovince. Today this subprovince is characterized by the presence of warm temperate water bodies, the influence of the Brazilian current prevailing on the Malvin. For this unit the name South-brazilian Miocene Subprovince is proposed. These results complement those of Groot et al. (1967, p. 215). They indicated that the subtropical zone of convergence was situated, at least during the lower and middle Tertiary, somewhat further south than today.

These results obtained for the marine faunas agree with the paleoclimatological reconstructions made for continental areas. Meléndez (1971) showed that in the Miocene tropical floras prevail at this latitude. Volkheimer (1971) indicated that in the Pampas region during the Miocene a very warm climate existed, and in Patagonia temperate temperatures.

The existence of warm water bodies in the Uruguay nearshore shelf during the Miocene must have had consequences for the distribution of the gastropods and bivalves. For the analysis of Miocene malacological assemblages from Uruguay, a comparison is made with their present range of distribution.

The influence of the marine currents on the distribution of the present day molluscs from Uruguay was studied by Sicardi (1967), who described the distributional range of 81 gastropod species, and 73 bivalves species. These are classified into:

1. species reaching this region by influence of the Malvin Current;
2. species belonging to the Brazilian current;
3. autochthonous ones.

There is a direct relationship between both mentioned currents and the zoogeographical provinces defined on the basis of the molluscan assemblages (Balech, 1954; Carcelles, 1944; Castellanos, 1967; Forti, 1969; Sicardi, 1967). The Magellanic Province is related to the influence of the cold Malvin current; the Caribbean or Antillean is characterized by the presence of the warm Brazilian current; and the autochthonous species correspond with the Argentinian or Patagonian Province. The boundary between the Caribbean and Argentinian Provinces lies approximately in the 28° S latitude. The boundary between the latter and the Magellanic Province is situated at the 43° S latitude (fig. 16a).

Carcelles (1944) found that bathymetric zonation is also present in the distributional pattern of molluscs. The species from the Caribbean or Antillean Province possess for the most part a more superficial distribution. In middle depths the autochthonous species are most frequently represented, whereas in deeper water the number of species belonging to the Magellanic Province increases. Evidently this bathymetric zonation is determined by the distribution of the marine currents. The water that is carried by the Brazilian current lies in a more superficial position than those transported by the Malvin current. Similar results were obtained and supported by the study of foraminiferids. On the coastal areas the Brazilian and autochthonous species are dominant, whereas outside of the 80 m isobath the typical species of the Malvin current prevail (Boltovskoy, 1965, 1973, 1976; Boltovskoy & Wright, 1976). This is interesting because they allow errors to be avoided in paleogeographical interpretation. In each association from the different zoogeographical provinces the percentile occurence of the individual species is determined not only by the latitude, but also by the bathymetry.

The zoogeographical littoral provinces, defined on the basis of foraminiferids and molluscs, disagree somewhat in their conventional boundaries. But the criteria used for their definition are the same, since they are based on the interaction between the Malvin and Brazilian currents. Hence the comparisons that follow are legitimate.

Based on the data of Sicardi (1967, 1975) the per cent occurence of the species given for the present day Uruguayan gastropod and bivalve faunas is determined. The gastropod fauna is composed of 37 % of the species related to the Brazilian-Antillean influence, and therefore brought by the Brazilian current; 17 % are related to the Malvin current; 46 % are autochthonous (fig. 16b). The bivalve fauna consists of 44 % of the species attributed to the Brazilian current, 20 % of a Magellanic origin, having been carried by the Malvin current, and the remaining 35 % are autochthonous (fig. 16c).

For the paleozoogeographical interpretation the Miocene molluscs found in Chuy N° 364 are evaluated in relation to their present distributional range. Only the surviving Miocene species are taken into consideration; the extinct ones have been rejected, because their paleozoogeographical distributional pattern is controversial. The analyzed species are classified in reference to their present zoogeographical distribution (table XIX).

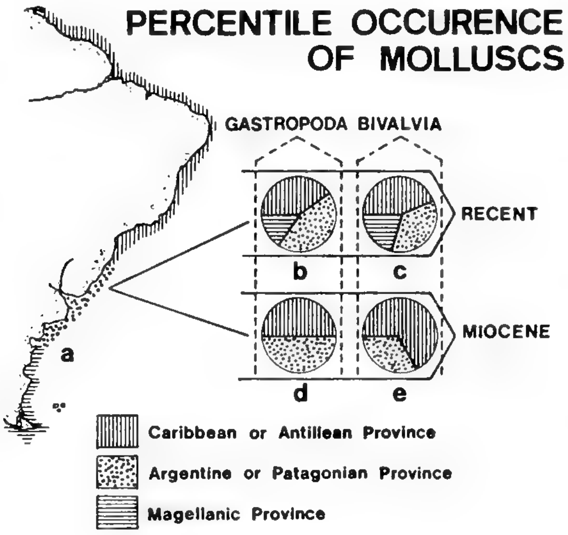

Fig. 16: Percentile occurence of Uruguayan Miocene and Recent molluscs belonging to the Caribbean, Argentinian and Magellanic Provinces.

TABLE XIX
Paleozoogeography of molluscs from Chuy N° 364

Caribbean or Antillean Province	Argentinian or Patagonian Province
GASTROPODA	
Halistylus columna	*Olivella puelcha*
Iselica anomala (+)	
Olivancillaria urceus	
BIVALVIA	
Amiantis purpurata	*Mactra bonariensis*
Corbula caribaea	*Tivela (Eutivela) isabelleana*
Diplodonta vilardeboana	
(Cyrtopleura lanceolata ornata)	
(Tagelus plebeius entrerianus)	

Cyrtopleura lanceolata ornata and *Tagelus plebeius entrerianus* constitute extinct subspecies of species that today live in the Caribbean Province. In Table XIX they are placed between parenthesis to indicate that their paleozoogeographical distribution is tentatively established.

The number of Miocene molluscan species of Chuy N° 364 which can be evaluated is relatively low. This could introduce a bias in the paleozoogeographical interpretation. Therefore Table XX was plotted — using the same criteria — with the Miocene molluscs found at Chuy N° 364 as well as additional species of the Camacho Formation found in exposures of the Colonia and San José Counties (Figueiras & Broggi, 1971, 1972/73). The percentile occurence of the Miocene molluscs from the entire Camacho Formation belonging to the different provinces in shown in Fig. 16d-e.

TABLE XX
Paleozoogeography of molluscs from the Camacho Formation

Caribbean or Antillean Province		Argentinian or Patagonian Province
	GASTROPODA	
Halistylus columna		*Olivella puelcha*
Iselica anomala (+)		*Buccinanops gradatum*
Olivancillaria urceus		*Buccinanops uruguayensis*
Epitonium aff. *unifasciatum* (+)		*Buccinanops duartei*
Dorsanum moniliferum		*Adelomelon brasiliana*
	BIVALVIA	
Amiantis purpurata		*Mactra bonariensis*
Corbula caribaea		*Tivela (Eutivela) isabelleana*
Diplodonta vilardeboana		*Nucula puelcha*
Adrana electa		*Lithophaga patagonica* (+)
Plicatula gibbosa		*Tellina (Angulus)* gibber
Crassostrea rizophorae (+)		
Dinocardium robustum (+)		
Labiosa (Raeta) plicatella (+)		
(Cyrtopleura lanceolata ornata)		
(Tagelus plebeius entrerianus)		

The species are assigned to their provinces primarly using the data of Sicardi (1967). The zoogeographical classification of species identified in Tables XIX and XX with a plus (+) is supported by the data of their present distribution as stated by Figueiras & Broggi (1971, 1972/73).

From the analysis in Tables XIX and XX and from Fig. 16d-e a total and significant absence of Miocene species belonging to the Magellanic Province is seen. The gastropod and bivalve associations are exclusively made up of species from the Caribbean and Argentinian Provinces. They indicate a predominance of warm water bodies transported by the Brazilian current, in latitudes located between the 34°—35° south parallels.

The comparison between the percentile occurence of the Miocene and Recent gastropod and bivalve species shows that:

1. The percentile occurence of species belonging to the Argentinian or Patagonian Province remains very similar.
2. The incidence of Magellanic species in present day Uruguayan faunas was a consequence of substitution for the Miocene Caribbean or Antillean forms.

These paleozoogeographical results agree and confirm those given by the foraminiferids. Furthermore they offer an explanation for a reiterated observation. Several mollusc species from the Entrerriense sea still exist in the Caribbean region. The explanation for this is that both regions were integrated during the Miocene in the same paleozoogeographical province, characterized by tropical waters.

B. Pliocene

In Uruguay marine Pliocene fossil faunas have not been found. According to Bertels (1975) and Bertels & Madeira-Falcetta (1977) no marine Pliocene sediments were found on the atlantic borderland of South America.

Camacho (1967) reported that Pliocene molluscs from Patagonia indicate the prevalence of species from temperate waters. They show a greater influence of the Brazilian current in comparison to the situation existing today in this region. The substitution of species of the Brazilian current by others of polar origin began in the Pliocene, and have increased primarily since the Pleistocene. In contrast BOLTOVSKOY (1973) considers that the Pliocene climate was colder than today. The characteristics and distribution of the Pliocene floras are very similar to the present (MELÉNDEZ, 1971).

C. Quaternary

Two different points of view exist with regard to the Quaternary paleotemperatures which existed in the temperate South American atlantic region.

BORDAS (1957) and PARODIZ (1962) reject categorically the existence of changes in the molluscan faunas which could be related to climatic cycles during the Quaternary.

In contrast, RICHARDS & CRAIG (1963) and RICHARDS (1966) consider that the climate was colder than the present one during Pleistocene glaciations, particularly during the last glacial (Wisconsin). Their conclusions are based on molluscs from the Argentinian shelf. Similar results are given by GROOT et al. (1967), supported by palynological studies, and by diatoms; as well as by evaluation of foraminiferids (BOLTOVSKOY, 1973).

The foraminiferal assemblages from the lower Holocene of Uruguay, typically indicate cold temperate waters, similar to the biocoenosis of this area (Chapter VI-F-2). They belong to the Argentinian Province, or "kingdom" of *Buccella peruviana*, s. l., and particularly to the North-patagonian Subprovince. This zoogeographical unit is delineated by 32°—41° S latitudes, and is characterized by the abundance of *Elphidium discoidale* (BOLTOVSKOY, 1970a, 1976; BOLTOVSKOY & WRIGHT, 1976). In this subprovince the Malvin current is dominant, but subtropical influences still exist, determined by the Brazilian current. Other studies made on Quaternary microfaunas of foraminiferids and ostracods from this region agree with these results, showing that the temperature was similar to the present day (BERTELS, 1975; BOLTOVSKOY, 1959b; CLOSS, 1966a, 1970).

In contrast, the analyzed malacological assemblages from the lower Holocene indicate mean annual temperatures somewhat higher than those that exist today. This conclusion arises from the analysis of the percentile occurence of those species whose distribution is considered to be determined: 1. by the Brazilian current; 2. by the Malvin Current; and 3. are autochthonous forms.

The comparison between the present day assemblages of molluscs (gastropods, bivalves and polyplacophorids) and those of the wells and Lecocq shows, that those from the Querandinense have a lower occurence of species considered to belong to the Malvin current, therefore from the Magellanic Province (table XXI.). Similar results were reported by FORTI (1968, 1969) studying malacological associations from the coastal plain from southern Brazil, which are considered to probably be from the lower Holocene. The data given by FORTI are expressed in percentages in Table XXI. FIGUEIRAS (1962) reported that all molluscan species of the Querandinense from Uruguay are still found in the present assemblages. They are classified in species correspoinding to the Caribbean, Magellanic and Argentinian Provinces. Their percentile occurence is shown on Table XXI. Further, this author indicates that the distributional range of some species has changed. Several species, which lived or were abundant during the Querandinense in the Uruguayan region, are very rare today, or else are found living somewhat farther north.

To what extent the percentages given in Table XXI can be considered significant, depends on the following features:

1. First of all on the accuracy of knowledge of the distributional pattern of living molluscan species. RICHARDS & CRAIG (1963) and RICHARDS (1966) point out that for many species the available information is inadequate.
2. The malacological assemblages from the lower Holocene were deposited in shallow water environments. As has been indicated, the species from the Brazilian current today have a more superficial distributional range than the autochthonous and Malvin ones. It is very difficult to establish to what degree the given percentages are determined by the paleotemperatures, or whether they are only the consequence of a bathymetric selection.
3. The malacological assemblages found in the wells allow only the study of faunal diversity, and are not appropriate in analyzing the species dominance.
4. The risks formulated by HERM (1969, p. 87) are inherent if a comparison is to be made between faunas from different biotopes.

The results provided by molluscs and foraminiferids found in the wells and Lecocq, are in disagreement concerning the paleotemperatures which existed during the Querandina Transgression. A possible explanation for this discrepancy is that the bivalves, and the majority of marine gastropods, have a free-swimming trochophore and veliger larvae. On the contrary, the benthic foraminiferids do not possess true pelagic stages during their ontogenethic development. This enables a greater potential speed in the migration rate of bivalves and the majority of marine gastropods.

This difference is most evident during short-term environmental changes, as those occuring during the Holocene.

Taking all evidence into consideration the interpretation that follows has to be considered tentative. Probably during the Querandina Transgression, the warm Brazilian current, in the Río de la Plata region, had a greater influence than today, with mean annual water temperatures somewhat higher than at present. Hence, the existence of warm climatic cycles during the Holocene was repeatedly postulated (Schwarzbach, 1974). This slight increase in the water paleotemperatures did not appreciably modify the distribution of the littoral paleogeographical provinces. The faunas from Querandina Transgression, as well as the present ones, belong to the North-patagonian Subprovince (fig. 15b).

TABLE XXI
Percentile occurence of molluscs belonging to zoogeographic provinces

	Caribbean or Antillean Province	Argentinian or Patagonian Province	Magellanic Province
PRESENT DAY FAUNAS			
Puerto Quequén (Carcelles, 1944)	29 %	44 %	25 %
Uruguay (Sicardi, 1967)	39 %	41 %	19 %
QUERANDINA TRANSGRESSION			
Uruguay (present study)	34 %	55 %	10 %
Uruguay (Figueiras, 1962)	38 %	57 %	4 %
Southermost Brazil (Forti, 1969)	55 %	37 %	6 %

The shown percentages in Table XXI include the faunas of gastropods, bivalves and polyplacophorids. No corrections were made for the number of species attributed to each province by the authors listed. The only exception is the zoogeographical classification of the genus *Anachis*. The *Anachis* species referred to by Figueiras (1962), Sicardi (1967) and in the present study, are grouped according to Sicardi's (1975) criterion.

IX. FAUNAL REFERENCE LIST

A. Foraminiferids

The Foraminiferids found in the wells and Lecocq are listed alphabetically below citing the original description. Additional references are often given for each of the species. Where changes in classification have been made, the reasons for these are discussed briefly.

Ammonia beccarii (Linnaeus) var. *parkinsoniana* d'Orbigny: *Nautilus beccarii* Linnaeus, 1758, Systema naturae. Ed. 10. Holmiae, impensis L. Salvii, tomus 1, p. 710, pl. 1, fig. 1a—c, pl. 19, figs. h—h, i—i.

Ammonia beccarii (Linné), Schnitker, 1974, Journ. Foram. Res. v. 4, no. 4 : 217—223, pl. 1. The variety *parkinsoniana* is morphologically used according to the criterion of Boltovskoy (1957a, p. 58).

Amphistegina gibbosa d'Orbigny: *Amphistegina gibbosa* d'Orbigny, 1839. In: Ramón de la Sagra, Histoire physique et naturelle de l'Ile de Cuba. A. Bertrand, Paris, p. 120; pl. 8, figs. 1—3 (in Ibid., vol. 8). — *Amphistegina gibbosa* d.'Orbigny, Hofker, Sr., 1969. Studies fauna Curaçao other Caribbean islands, vol. 31, no. 115, p. 81, figs. 235—237.
See also: Larsen, 1976, p. 151.

Baggina sp.?

Bolivina compacta Sidebottom: *Bolivina robusta* Brady var. *compacta* Sidebottom, 1905, Manchester Lit. Philos, Soc., Mem., Proc., vol. 49, no. 5, p. 15, pl. 3, fig. 7a, b.

Bolivina cf *lomitensis* Galloway & Wissler: *Bolivina lomitensis* Galloway & Wissler, 1927, Journ. Paleont. vol. 1, no. 1, p. 71, pl. 11, fig. 7a, b. — *Bolivina* cf. *lomitensis* Galloway & Wissler, Boltovskoy, 1954, Rev. Inst. Nac. Invest. Cienc. Nat. y Mus. Argentino Cienc. Nat. "B. Rivadavia", Cienc. Geol., tomo 3, no. 4, p. 281, pl. 26, figs. 3a, b, 4.

Bolivina striatula Cushman: *Bolivina striatula* Cushman, 1922, Carnegie Inst., Publ. no. 311 (Dept. Marine Biol., Papers, vol. 17) Washington, D. C., p. 27, pl. 3, fig. 10. — *Bolivina Striatula* Cushman, Boltovskoy, 1954, p. 190, pl. 13, fig. 12a, b, 13a, b, 14a, b, 15a, b, 16a, b.

Bolivina cf. *variabilis* (Williamson): *Textularia variabilis* Williamson, 1858, On the Recent foraminifera of Great Britain. Ray Soc., London, p. 76, pl. 6, figs. 162—163. — *Bolivina variabilis* (Williamson), Boltovskoy, 1954, p. 187, pl. 12, fig. 13a—c.

Buccella peruviana (d'Orbigny), sensu lato: *Rosalina peruviana* d'Orbigny, 1839, Voyage dans l'Amérique Méridionale; Foraminifères, tome 5, pt. 5, p. 41, pl. 1, figs. 12—14. — Boltovskoy, 1970a, p. 342.

Bulimina cf. *affinis* d'Orbigny: *Bulimina affinis* d'Orbigny, 1839, Foraminifères. In: Ramón de la Sagra, Histoire physique et naturelle de l'Ile de Cuba. A. Bertrand, Paris, p. 105; pl. 2, figs. 25—26 (in: Ibid., vol 8). — *Bolivina affinis* d'Orbigny (?), Boltovskoy, 1954, p. 179, pl. 10, fig. 18.

Buliminella elegantissima (d'Orbigny): *Bulimina elegantissima* d'Orbigny 1839, Voyage dans l'Amérique Méridionale; Foraminifères tome 5, pt. 5, p. 51, pl. 7, figs. 13—14. — *Buliminella elegantissima* (d'Orbigny), Boltovskoy, 1954, p. 173, pl. 8, figs. 9—10.

Cancris sagra (d'Orbigny): *Rotalina (Rotalina) sagra* d'Orbigny, 1839, Foraminifères. In: Ramón de la Sagra, Histoire physique et naturelle de l'Ile de Cuba. A. Bertrand, Paris, p. 77; pl. 5, figs. 13—15 (in Ibid., vol. 8). — *Cancris sagra* (d'Orbigny), Boltovskoy, 1957a, p. 59, pl. 11, figs. 1a, b, 2a—c.

Cassidulina curvata Phleger & Parker: *Cassidulina curvata* Phleger & Parker, 1951, Geol. Soc. Amer., Mem. no. 46, pt. 2, p. 26, pl. 14, fig. 5a, b.

Cassidulina laevigata d'Orbigny: *Cassidulina laevigata* d'Orbigny, 1826, Ann. Sci. Nat., Paris, sér. 1, tome 7, p. 282, pl. 15, figs. 4—5, 5 bis.

Cassidulina subglobosa Brady: *Cassidulina subglobosa* Brady, 1881, Quart. Jour. Micr. Sci., London, n. s., vol. 21, p. 60; pl. 54, fig. 17a—c (in Brady 1884, Rept. Voy. Challenger, Zool., vol. 9).

Cibicides aknerianus (d'Orbigny): *Rotalina akneriana* d'Orbigny, 1846, Foraminifères fossiles du bassin tertiaire de Vienne (Autriche), p. 156, pl. 8, figs. 13—15. — *Cibicides aknerianus* (d'Orbigny), Boltovskoy, 1954, p. 213, pl. 15, fig. 6a, b, pl. 18, fig. 8.

Cibicides "pseudoungerianus" (Cushman): *Truncatulina pseudoungeriana* Cushman, 1922, U. S. Geol. Suv., Prof. Pap., no. 129—E, p. 97, pl. 20, fig. 9. — *Cibicides "pseudoungarianus"* (Cushman), Boltovskoy & Lena, 1966, p. 291, pl. 2, fig. 4.

Dentalina communis d'Orbigny: *Nodosaria (Dentaline) communis* d'Orbigny, 1826, Ann. Sci. Nat., Paris, sér. 1, tome 7, p. 254. — *Dentalina communis* d'Orbigny, Boltovskoy, 1959a, p. 63, pl. 9, fig. 1.

Discorbinella? bertheloti, forma *boueana* (d'Orbigny): *Truncatulina boueana* d'Orbigny, 1846, Foraminifères fossiles du bassin tertiaire de Vienne (Autriche), p. 169, pl. 9, figs. 24—26. — *Cibicides bertheloti* (d'Orbigny), forma *boueana* (d'Orbigny), Boltovskoy, 1959a, p. 106, pl. 17, figs. 5a, b, 6.

Discorbis peruvianus (d'Orbigny): *Rosalina peruviana* d'Orbigny, 1839, Voyage dans l'Amérique Méridionale; Foraminifères, tome 5, pt. 5, p. 41, pl. 1, figs. 12—14. — *Discorbis peruvianus* (d'Orbigny), Boltovskoy & Lena, 1966, p. 297, pl. 3, figs. 4—7.

Discorbis gr. *vilardeboanus* (d'Orbigny): *Rosalina vilardeboana* d'Orbigny, 1839, Voyage dans l'Amérique Méridionale; Foraminifères. Strasbourg, Levrault, tome 5, pt. 5, p. 44, pl. 6, figs. 13—15. — *Discorbis vilardeboanus* (d'Orbigny), Boltovskoy, 1954, p. 201, pl. 14, fig. 9a—c.

Discorbis williamsoni (Chapman & Parr), forma *praegeri* Heron-Allen & Earland: *Rotalina nitida* Williamson, 1858, On the Recent foraminifera of Great Britain, Ray Soc., London, p. 54, pl. 4, figs. 106—108. — *Discorbina praegeri* Heron-Allen & Earland, 1913, Proc. Roy. Irish. Acad. vol. 31, no. 64, p. 122, pl. 10, figs. 8—10. — *Discorbis nitidus* (Williamson), Boltovskoy, 1957a, p. 55, pl. 9, figs. 1a—c, 2a—c, 3a—c, 4a—c, 5a-c, 6a-c. — *Discorbis williamsoni* (Chapman & Parr), forma *praegeri* Heron-Allen & Earland, Boltovskoy, 1959a, p. 89. According to Loeblich & Tappan (1964, p. C578) this species belongs to the genus *Gavelinopsis* Hofker being its type-species.

Discorbis gr. sp. "A" Boltovskoy: *Discorbis* sp. "A", Boltovskoy, 1954, p. 203, pl. 15, fig. 4a, b.

Elphidium depressulum Cushman: *Elphidium advenum* (Cushman) var. *depressulum,* Cushman, 1933, U. S. Nat. Mus. Bull. 161, p. 51, pl. 12, fig. 4. — *Elphidium depressulum* Cushman, Boltovskoy, 1954, Rev. Inst. Nac. Inv. Cienc. Nat. y Mus. Argentino Cienc. Nat. "B. Rivadavia", Cienc. Geol., tomo 3, no. 4, p. 276, pl. 25, figs. 3a, b, 4a, b. — *Elphidium advenum depressulum* Cushman, Boltovskoy, 1959a, p. 96, pl. 15, fig. 4. — *Elphidium depressulum* Cushman, Boltovskoy, 1976, p. 223.

Elphidium discoidale (d'Orbigny): *Polystomella discoidalis* d'Orbigny, 1839. In: Ramón de la Sagra, Histoire physique et naturelle de l'Ile de Cuba. A. Bertrand, Paris, p. 56; pl. 6, figs. 23—24 (in Ibid., vol. 8). — *Elphidium discoidale* (d'Orbigny), Boltovskoy, 1957a, p. 43, pl. 8, figs. 1a, b, 2a, b, 3a, b, 4a, b, 5a, b.

Elphidium gr. *excavatum* (Terquem): *Polystomella excavata* Terquem, 1875, Soc. Dunkerquoise, Mém., Dunkerque, 1876, vol. 19 (1874—1875), p. 429, pl. 2, fig. 2a, b. — *Elphidium excavatum* (Terquem), Closs, 1963, p. 56, pl. 4, fig. 4, 7.

Elphidium galvestonense Kornfeld: *Elphidium gunteri* Cole var. *galvestonensis* Kornfeld, 1931, Stanford Univ. Dept. Geol., Contr., vol. 1, no. 3, p. 87, pl. 15, figs. 1a, b, 2a, b, 3a, b. — *Elphidium galvestonense* Kornfeld, Closs, 1963, p. 57, pl. 4, fig. 6, pl. 6, fig. 28a, b.

Elphidium gunteri Cole [sensu Closs, 1963]: *Elphidium gunteri* Cole, 1931, Florida State Geol. Surv., Bull., no. 6, p. 34, pl. 4, figs. 9—10. — *Elphidium gunteri* Cole, Closs, 1963, p. 55, pl. 4, figs. 1—3, 5, 8, pl. 6, fig. 29a, b. non: *Elphidium günteri* Cole, Rosset-Moulinier, 1976, Revue Micropaléont., vol 19, no. 2, p. 92, pl. 1, figs. 10—11, pl. 2, figs. 1—4. In Rosset-Moulinier a different species from the Bretagne coast is described under the same species designation. As Rosset-Moulinier does not give references about the holotype, the concept of Closs is adopted. — *Elphidium guntheri* Cole, Hansen & Lykke-Andersen, 1976, p. 12, pl. 8, figs. 10—12, pl. 9, figs. 1—3.

Elphidium aff. *sagrum* (d'Orbigny): *Polystomella sagra* d'Orbigny, 1839, In: Ramón de la Sagra, Histoire physique et naturelle de l'Ile de Cuba. A. Bertrand, Paris, p. 55; pl. 6, figs. 19—20 (in Ibid., vol. 8).

Elphidium cf. *tuberculatum* (d'Orbigny): *Nonionina tuberculata* d'Orbigny, 1846, Foraminifères fossiles du bassin tertiaire de Vienne (Autriche) p. 108, pl. 5, figs. 13—14. — *Protelphidium tuberculatum* (d'Orbigny), Malumian, 1972, p. 116, pl. 4, fig. 4a, b. — *Elphidium tuberculatum* (d'Orbigny), Hansen & Lykke-Andersen, 1976, p. 14, pl. 12, figs. 1—4.

Elphidium sp. A

Elphidium sp. B

Fissurina laevigata Reuss: *Fissurina laevigata* Reuss, 1850, K. Akad. Wiss. Wien, Math.-Nat. Cl. Bd. 1, p. 366, pl. 46, fig. 1a, b. — Boltovskoy, 1954, p. 157, pl. 11, fig. 5a, b.

Flintinella sp.

Fursenkoina sp.

Guttulina plancii d'Orbigny: *Guttulina (Guttulina) plancii* d'Orbigny, 1839, Voyage dans l'Amérique Méridionale; Foraminifères, tome 5, pt. 5, p. 60, pl. 1, fig. 5. — *Guttulina plancii,* d'Orbigny, Boltovskoy, 1954, Rev. Inst. Nac. Invest. Cienc. Nat. y Mus. Argentino Cienc. Nat. "B. Rivadavia", Cienc. Geol., tomo 3, no. 4, p. 270, pl. 23, fig. 5a—c.

Guttulina problema d'Orbigny: *Guttulina problema* d'Orbigny, 1826, Ann. Sci. Nat., Paris, sér. 1, tome 7, p. 266, no. 14. — *Guttulina problema* d'Orbigny, Closs & Barberena, 1962, p. 31, pl. 2, fig. 8, pl. 6, fig. 8.

Lagena laevis (Montagu), forma *perlucida* (Montagu): *Vermiculum perlucidum* Montagu, 1803, Testacea Britannica, or natural history of British shells, marine, land and fresh-water, including the most minute. Romsey, England, p. 525, pl. 14, fig. 3. — *Lagena laevis* (Montagu), *forma perlucida* (Montagu), Boltovskoy, 1959a, p. 67, pl. 9, fig. 8.

Lagena sp.

Lenticulina limbosa (Reuss): *Robulina limbosa* Reuss, 1863, Sitzber. kaiserl. Akad. Wissensch., math.-naturw. Cl., Wien, vol. 46, pt. 1, p. 55, pl. 6, fig. 69. — *Robulus limbosus* (Reuss) s. l., Boltovskoy, 1959a, p. 61, pl. 7, figs. 6, 7.

Lenticulina rotulata (Lamarck): *Lenticulites (rotulata)* Lamarck, 1804, Mus. National Hist. Nat., Ann., Paris (An 13), tome 5, p. 188; pl. 62 (14), fig. 11 (in Ibid., vol. 8, 1806). — *Lenticulina rotulata* Lamarck, Malumian, 1972, p. 111, pl. 3, fig. 8.

Massilina secans (d'Orbigny): *Quinqueloculina secans* d'Orbigny, 1826, Ann. Sci. Nat., Paris, sér. 1, tome 7, p. 303. — *Massilina secans* (d'Orbigny), Boltovskoy, 1957a, p. 26, pl. 6, fig. 1a, b, 2a, b, 3a, b, 4a, b, 5a, b.

Marginulina gr. *tenuis* Bornemann: *Marginulina tenuis* Bornemann, 1855, Z. Deutsch. geol. Ges., Berlin, vol. 7, p. 326, pl. 13, fig. 14a, b.

Miliammina fusca (Brady): *Quinqueloculina fusca* Brady, 1870, Ann. Mag. Nat. Hist., London, ser. 4, vol. 6, p. 286, pl. 11, figs. 2a—c, 3a, b. — *Miliammina fusca* (Brady), 1963, Closs, p. 27, pl. 1, figs. 8—10, pl. 6, figs. 1a—c, 6—16.

Miliolinella subrotunda (Montagu): *Vermiculum subrotundum* Montagu, 1803, Testacea Britannica, or natural history of British shells, marine, land and fresh-water, including the most minute. Romsey, England, J. S. Hollis, p. 521. — *Miliolinella subrotunda* (Montagu), Ponder, 1974, Micropaleontology, vol. 20, no. 2, p. 201, pl. 1, figs. 1a, b, 2a, b, pl. 2, fig. 6a—c, 7, 8a, b, 9a—i, 10, 11.

Nonion grateloupii (d'Orbigny): *Nonionina grateloupii* d'Orbigny, 1839, Foraminifères. In: Ramón de la Sagra, Histoire physique et naturelle de l'Ile de Cuba. A. Bertrand, Paris, p. 46; pl. 6, figs. 6—7 (in Ibid., vol. 8). — *Nonion grateloupi* (d'Orbigny), Boltovskoy & Lena, 1966, p. 315, pl. 5, fig. 7. — *Florilus grateloupi* (d'Orbigny), Andersen, 1975, Tulane Stud. Geol. Paleont., vol. 11, no. 4, p. 298, pl. 10, fig. 10. The genus *Nonion* is used according to Hansen & Lykke-Andersen (1976) point of view.

Nonion tisburyensis Butcher [sensu Boltovskoy, 1958]: *Nonion tisburyensis* Butcher, 1948, Cushman Lab. Foram. Res., Contr., vol. 24, p. 21, p. 22, tfs. 1—3. — *Nonion tisburyensis* Butcher, Boltovskoy, 1958, p. 18, pl. 6, figs. 1a, b, 2—4, 5a, b, 6. The genus *Nonion* is used according to Hansen & Lykke-Andersen (1976) criterion.

Nonion sp. A.

Nonion sp. B.

Nonionella atlantica Cushman: *Nonionella atlantica* Cushman, 1947, Cushman Lab. Foram. Res., Contr., vol. 23, p. 90, pl. 20, figs. 4a—c, 5. — *Nonionella atlantica* Cushman, Boltovskoy, 1959a, p. 76, pl. 10, fig. 14a—c. — *Nonionella atlantica* Cushman, Hansen & Lykke-Andersen, 1976, p. 23, pl. 21, figs. 9—12.

Nonionella auricula Heron-Allen & Earland: *Nonionella auricula* Heron-Allen & Earland, 1830, Roy. Micr. Soc., Jour., London, ser. 3, vol. 50, p. 192, pl. 5, figs. 68—70. — *Nonionella auricula* Heron-Allen & Earland, Boltovskoy, 1954, p. 167, pl. 7, fig. 9a—c.

Oolina melo d'Orbigny: *Oolina melo* d'Orbigny, 1839, Voyage dans l'Amérique Méridionale, Foraminifères, Strasbourg, Levrault, tome 5, pt. 5, p. 20, pl. 5, fig. 9.

Poroeponides lateralis (Terquem): *Rosalina lateralis* Terquem, 1878, Soc. Géol. France, Mém., sér. 3, tome 1, no. 3, p. 25, pl. 2, fig. 11a—c. — *Poroeponides lateralis* (Terquem), Boltovskoy, 1957a, p. 59, pl. 10, fig. 5a—c.

Pyrgo nasuta Cushman: *Pyrgo nasutus* Cushman, 1935, Smithsonian Inst. Misc. Coll. vol. 91, no. 21 (publ. 3327), p. 7, pl. 3, figs. 1a, b, 2—4. — *Pyrgo nasuta* Cushman, Boltovskoy, 1957a, p. 30, pl. 4, fig. 9a—c.

Pyrgo ringens patagonica (d'Orbigny): pars? *Miliolites (ringens) subglobosa* Lamarck, 1804, Mus. National Hist. Nat., Ann., Paris, (An 13), tome 5, p. 351; pl. 17 (15), fig. 1 (in Ibid., vol. 9, 1807). — *Biloculina patagonica* d'Orbigny, 1839, Voyage dans l'Amérique Méridionale; Foraminifères, tome 5, pt. 5, p. 65, pl. 3, figs. 15—17. — *Pyrgo patagonica* (d'Orbigny), Boltovskoy, 1954, p. 133, pl. 3, fig. 3a—c, pl. 19, fig. 7a, b. — [pars] *Pyrgo ringens patagonica* d'Orbigny, Boltovskoy & Lena, 1966, p. 326.

Quinqueloculina cf. *agglutinata* Cushman: *Quinqueloculina agglutinata* Cushman, 1917, U. S. Nat. Mus., Bull., no. 71, p. 43, pl. 9, fig. 2a—c. — *Quinqueloculina* cf. *agglutinata* Cushman, Boltovskoy, 1957a, p. 24, pl. 4, figs. 1, 2, 3a—c, 4.

Quinqueloculina angulata (Williamson), forma *typica: Miliolina bicornis* (Walker) var. *angulata* Williamson, 1858, On the Recent foraminifera of Great Britain. Ray Soc., London, p. 88, pl. 7, fig. 196. — *Quinqueloculina angulata* (Williamson), Boltovskoy, 1954, p. 123, pl. 2, fig. 1a—c. — *Quinqueloculina angulata* (Williamson), forma *typica,* Boltovskoy & Lena, 1966, p. 327.

Quinqueloculina atlantica Boltovskoy: *Quinqueloculina atlantica* Boltovskoy, 1957, Rev. Inst. Nac. Invest. Cienc., Nat. y Mus. Argentino Cienc. Nat. "B. Rivadavia", Cienc. Geol., tomo 6, no. 1, p. 25, pl. 5, fig. 2a—c, 3, 4a—c, 5, 6a—c.

Quinqueloculina aff. *frigida* Parker: *Quinqueloculina frigida* Parker, 1952, Mus. Comp. Zool., Bull., Cambridge, vol. 106 (1951—1952), no. 9, p. 406, pl. 3, fig. 20a, b. — *Quinqueloculina* aff. *frigida* Parker, Boltovskoy, 1957a, p. 24, pl. 4, fig. 7a—c.

Quinqueloculina intricata Terquem: *Quinqueloculina intricata* Terquem, 1878, Soc. Géol. France, Mém., sér. 3, tome 1, no. 3, p. 73, pl. 8, figs. 16a, b, 17a, b, 18a—c, 19a—c, 20a—c, 21a, b. — *Quinqueloculina intricata* Terquem, Wright, 1968, p. 250, pl. 2, figs. 1—4.

Quinqueloculina patagonica d'Orbigny: *Quinqueloculina patagonica* d'Orbigny, 1839, Voyage dans l'Amérique Méridionale; Foraminifères, Strasbourg, Levrault, tome 5, pt. 5, p. 74, pl. 4, figs. 14—16. *Quinqueloculina pata-*

gonica d'Orbigny, Boltovskoy, 1954, p. 122, pl. 1, figs. 4a—c, 5a, b.

Quinqueloculina seminulum (Linnaeus): *Serpula seminulum* Linnaeus, 1758, Systema naturae. Ed. 10. Holmiae, impensis L. Salvii, tomus 1, p. 786, pl. 2, fig. 1a—c. — *Quinqueloculina seminulum* (Linnaeus), Boltovskoy, 1954, p. 120, pl. 1, figs. 1a—c, 2, 3a—c.

Quinqueloculina vulgaris d'Orbigny: *Quinqueloculina vulgaris* d'Orbigny, 1826, Tableau méthodique de la classe des Céphalopodes. Ann. Sci. Nat., Paris, sér. 1, tome 7, p. 302. — *Quinqueloculina vulgaris* d'Orbigny, Cushman, 1929, U. S. Nat. Mus. Bull. 104, pt. 6, p. 25, pl. 2, fig. 3a—c.

Quinqueloculina sp. A

Quinqueloculina sp. B

Quinqueloculina sp. C

Quinqueloculina sp. D

Quinqueloculina sp. E

Reophax artica Brady: *Reophax artica* Brady, 1881, K. Akad. Wiss. Wien, math.-naturw. Cl., Bd. 43, Abth. 2, p. 99, pl. 2, fig. 2a, b.

Rosalina sp.?

Rotorbinella rosea (d'Orbigny): *Rotalia (Rotalie) rosea* d'Orbigny, 1826, Ann. Sci. Nat., Paris, sér. 1, tome 7, p. 272. Type fig.: Modeles, no. 35, 2me livraison. [Parker, Jones & Brady, 1865, Ann. Mag. Nat. Hist., London, vol. 16, ser. 3, pl. 3, fig. 79], d'Orbigny, 1939, Foraminifères. In: Ramón de la Sagra, Hist. Phys. Pol. Nat. Ile Cuba, p. 72, pl. 3, figs. 9—11. *Rotorbinella rosea* (d'Orbigny), Hofker, Sr., 1969, Studies Fauna Curaçao other Caribbean islands, vol. 31, no. 115, p. 85, figs. 247—250.

Textularia gramen d'Orbigny: *Textularia gramen* d'Orbigny, 1846, Foraminifères fossiles du bassin tertiaire de Vienne (Autriche), p. 248, pl. 15, figs. 4—6. — *Textularia gramen* d'Orbigny, Boltovskoy, 1957a, p. 19, pl. 2, figs. 1a, b, 2a, b, 3a, b, 4a, b, 5a, b, 6a, b, 7a, b, 8a, b, 9a, b.

Textularia sp. A

Textularia sp. B

Triloculina sp.

B. Molluscs

An alphabetical list of species of bivalves, gastropods and polyplacophorids found in the bore-holes and Lecocq is given. In recent years several reviews of the systematics of Neogene, Quaternary and living molluscs in this area were published. Figueiras & Broggi have a paper in preparation of taxonomic descriptions of species found in the Vizcaíno Formation, and include data from the wells and Lecocq outrop. For this reason only the original and present names of the recorded species are given, as well as a reference to help in researching original bibliographic sources.

1. BIVALVIA

Abra uruguayensis: Semele (Abra) uruguayensis Pilsbry, 1897; Figueiras & Sicardi, 1969, p. 372, pl. 4, fig. 65.

Amiantis purpurata: Cytherea purpurata Lamarck, 1818; Figueiras & Broggi, 1972/73, p. 226.

Anomalocardia brasiliana: Venus brasiliana Gmelin, 1791; Figueiras & Sicardi, 1969, p. 363, pl. 4, fig. 49.

Brachidontes (Hormomya) darwinianus mulleri: Mytilus mulleri Dunker, 1875; Figueiras & Sicardi, 1968b, p. 265, pl. 2, fig. 19.

Brachidontes (Brachidontes) rodriguezi: Mytilus rodriguezi d'Orbigny, 1846; Figueiras & Sicardi, 1968b, p. 266, pl. 2, fig. 20.

Cardita (Carditamera) plata: Cardita plata Ihering, 1907; Forti, 1969, p. 78, pl. 3, fig. 3a, b.

Chione doello-juradoi: Chione doello-juradoi Medina, 1962, pl. 1, fig. 1—2.

Chione meridionalis burmeisteri: Venus burmeisteri Borchert, 1901; Figueiras & Broggi, 1972/73, p. 228.

Chlamys tehuelcha: Pecten tehuelchus d'Orbigny, 1846, Figueiras & Sicardi, 1968b, p. 269, pl. 2, fig. 26.

Corbula caribaea: Corbula caribaea d'Orbigny, 1845; Figueiras & Sicardi, 1970a, p. 409, pl. 5, fig. 75.

Corbula lyoni: Corbula lyoni Pilsbry, 1897; Figueiras & Sicardi, 1970a, p. 410, pl. 5, fig. 77.

Corbula patagonica: Corbula patagonica d'Orbigny, 1846; Figueiras & Sicardi, 1970a, p. 410, pl. 5, fig. 76.

Corbula pulchella: Corbula pulchella Philippi, 1893; Figueiras & Broggi, 1972/73, p. 232.

Crassinella guadalupensis: Crassatella guadalupensis d'Orbigny, 1842. In: Ramón de la Sagra, Histoire physique, politique et naturelle de l'Ile de Cuba, p. 288, pl. 27, fig. 21—23.

Crassinella maldonadoensis: Crassatella (Eriphyla) maldonadoensis Pilsbry, 1897; Forti, 1969, p. 77, pl. 3, fig. 2a, b.

Cyrtopleura lanceolata ornata: Pholas ornata Borchert, 1901, Figueiras & Broggi, 1972/73, p. 234.

Diplodonta vilardeboana: Lucina vilardeboana d'Orbigny, 1846; Castellanos, 1967, p. 243, pl. 18, fig. 7—9.

Erodona mactroides: Erodona mactroides Daudin, 1801; Costa, 1971, p. 4, fig. 1—27.

Glycymeris longior: Pectunculus longior Sowerby, 1832; Forti, 1969, p. 70, pl. 2, fig. 2a, b.

Mactra bonariensis: Mactra bonariensis Philippi, 1893; Figueiras & Broggi, 1972/73, p. 220.

Mactra isabelleana: Mactra isabelleana d'Orbigny, 1846; Castellanos, 1967, p. 237, pl. 21, fig. 9, 10.

Mactra marplatensis: Mactra marplatensis Doello-Jurado, 1949; Castellanos, 1967, p. 234, pl. 21, fig. 11—13.

Mactra patagonica: Mactra patagonica d'Orbigny, 1846; Castellanos, 1967, p. 235, pl. 21, fig. 1—3.

Mytilus platensis: Mytilus platensis d'Orbigny, 1846; Castellanos, 1967, p. 210, pl. 17, fig. 3, 4.

Ostrea equestris: Ostrea equestris Say, 1834; Figueiras & Sicardi, 1968b, p. 272, pl. 2, fig. 33.

Ostrea puelchana: Ostrea puelchana d'Orbigny, 1842; Figueiras & Sicardi, 1968b, p. 271, pl. 2, fig. 32.

Pitar (Pitar) rostrata: Cytherea rostrata Koch, 1844; Camacho, 1966, p. 81, pl. 18, fig. 1a—c.

Pleuromeris sanmartini: Pleuromeris sanmartini, Klappenbach, 1970, p. 36, fig. 1—5.

Plicatula cf. *gibbosa: Plicatula gibbosa* Lamarck, 1801; Figueiras & Broggi, 1972/73, p. 209.

Sphenia hatcheri: Sphenia hatcheri Pilsbry, 1899; Figueiras & Sicardi, 1970b, p. 22, pl. 7, fig. 103.

Strigilla (Rombergia) cf. *rombergii: Strigilla rombergii* Mörch, 1853; Cox, Newell & Boyd et al., 1969, p. N 622; *Strigilla rombergi* Mörch, Figueiras & Sicardi, 1969, p. 375, pl. 4, fig. 71.

Tagelus plebeius: Solen plebeius Solander, 1786; Figueiras & Sicardi, 1969, p. 369, pl. 4, fig. 60.

Tagelus plebeius entrerianus: Tagelus gibbus entrerianus Ihering, 1907; Figueiras & Broggi, 1972/73, p. 224.

Tivela (Eutivela) isabelleana: Venus isabelleana d'Orbigny, 1846; Figueiras & Broggi, 1972/73, p. 225.

2. GASTROPODA

Acmaea subrugosa: Acmaea subrugosa d'Orbigny, 1841; Figueiras & Sicardi, 1970c, p. 28, pl. 8, fig. 110.

Anachis isabellei: Nassa isabellei, d'Orbigny, 1841; Sicardi, 1975, p. 106.

Anachis moleculina: Columbella moleculina Duclos, 1840; Sicardi, 1975, p. 104.

Anachis paessleri: Columbella (Seminella) paessleri Strebel, 1905; Sicardi, 1975, p. 107.

Austroborus lutescens: Bulinus lutescens King & Broderip, 1832; Figueiras & Broggi, 1969, p. 349.

Buccinanops globulosum: Buccinum globulosum Kiener, 1834; Castellanos, 1967, p. 90, pl. 7, fig. 5.

Buccinanops gradatum: Buccinum gradatum Deshayes, 1844; Castellanos, 1967, p. 92, pl. 7, fig. 6.

Crepidula aculeata: Patella aculeata Gmelin, 1791; Figueiras & Sicardi, 1971, p. 116, pl. 10, fig. 145.

Crepidula protea: Crepidula protea d'Orbigny, 1835; Figueiras & Sicardi, 1971, p. 116, pl. 10, fig. 146.

Diodora patagonica: Fissurella patagonica d'Orbigny, 1841; Castellanos, 1967, p. 20, pl. 1, fig. 8.

Epitonium aff. *unifasciatum: Scalaria unifasciata* Sowerby, 1844; Figueiras & Sicardi, 1971, p. 109, pl. 9, fig. 132.

Halistylus columna: Halistylus columna Dall, 1889; Castellanos, 1967, p. 38, pl. 4, fig. 1.

Iselica anomala: Narica (?) anomala Adams, 1850; Figueiras & Broggi, 1971, p. 140.

Littoridina australis: Paludina australis d'Orbigny, 1835; Castellanos, 1967, p. 47, pl. 4, fig. 3.

Littoridina charruana: Paludestrina charruana d'Orbigny, 1835; Figueiras, 1964, p. 175.

Ocenebra cala: Ocinebra cala Pilsbry, 1897; Figueiras & Sicardi, 1972, p. 173, pl. 12, fig. 167.

Odostomia (Chrysallida) aff. *jadisi: Odostomia (Chrysallida) jadisi* Olsson & Mc Ginty, 1958; Figueiras & Sicardi, 1974, p. 334, pl. 19, fig. 242.

Olivancillaria urceus: Porphyria urceus Roding, 1798; Figueiras & Broggi, 1971, p. 149.

Olivella (Olivina) puelcha: Oliva puelcha, d'Orbigny, 1840; Figueiras & Sicardi, 1973, p. 265, pl. 15, fig. 194.

Olivella (Olivina) tehuelcha: Oliva tehuelcha d'Orbigny 1840; Figueiras & Sicardi, 1973, p. 265, pl. 15, fig. 195.

Parodizia uruguayensis: Parodizia uruguayensis Nieves de Medina, 1959, p. 53, 1 fig.

Polinices entrerriana: Natica entrerriana Borchert, 1901; Figueira & Broggi, 1971, p. 142.

Siphonaria (Pachysiphonaria) lessoni: Patella lessoni Blainville, 1824; Camacho, 1966, p. 146, pl. 17, fig. 12a, b.

Tegula (Agathistoma) patagonica: Trochus patagonicus, d'Orbigny, 1840; Forti, 1969, p. 100, pl. 7, fig. 3a, b.

Triphora medinae: Triphora medinae Parodiz, 1955; Figueiras & Sicardi, 1971, p. 107, pl. 9, fig. 128.

Urosalpinx rushi: Urosalphinx rushi Pilsbry, 1897; Castellanos, p. 77, pl. 5, fig. 8.

3. POLYPLACOPHORA

Chaetopleura isabellei: Chiton isabellei d'Orbigny, 1841; Castellanos, 1967, p. 161, pl. 1, fig. 11.

X. SUMMARY AND CONCLUSIONS

The ecology and paleoecology of the Uruguayan coastal area was studied by Miocene, Pleistocene, Holocene and present-day micro- and macrofaunal assemblages. They are:

Miocene assemblages. Marine Miocene faunas were only found in well Chuy N° 364 between 133.00—113.00 m. The associations are make up of benthonic foraminiferids, molluscs, brachiopods, ostracods, bryozoans, barnacle plates and additional microfossil remains, all which are listed on Table II. They are considered to be of Miocene age, using mainly paleoclimatological data. This fact is supported mainly by the distribution of *Amphistegina gibbosa,* as well as by foraminiferal and molluscan associations. Time-stratigraphic correlations with bore-holes from the Pelotas Basin and Salado Basin were establisched and/

or confirmed. The depositional environments of these strata were reconstructed using foraminiferids, and indicate a normal marine nearshore environment, with high energy warm waters. The substrate probably had no sea flora cover. They were deposited during a pregressive overlap. An analysis of microfaunal mixing was made to find allochthonous foraminiferids. The preservation of the foraminiferal tests is related to the environmental parameters of the depositional environments where they were found.

New data are given of the ecological distribution of the present-day faunas of the Río de la Plata estuary and its zone of influence. They include:

Foraminiferids: The curve of REMANE for the estuarine biocoenosis was plotted.

Bivalves: The curve of REMANE was reconstructed evaluating data from living and dead assemblages.

Gastropods: Their distributional pattern was reconstructed.

The genuine brackish-water and euryhaline molluscan species were identified, and the life habits of the dominant genuine brackish-water species were established.

Quaternary assemblages. The foraminiferal and molluscan assemblages found mainly in the bore-holes were widely distributed along nearly 700 km of coast line of the Río de la Plata and Río Uruguay, and these are analyzed. The depositional environments of strata bearing foraminiferids and molluscs were reconstructed. Faunal associations indicate shallow and cold temparate-waters. The depositional environments show great differences in salinity. The study of the foraminiferids allowed one to be able to distinguish between the Quaternary Biofacies of *Buliminella elegantissima* and the Quaternay Biofacies of *Ammonia beccarii* var. *parkinsoniana*. This was made on the basis of the percentile occurence of the dominant species, as well as evaluating the capacity of the genera to withstand changes in salinities. The foraminiferal associations show an estuarine environment because they indicate a longitudinal distributional pattern. Towards the head of the estuary the Quaternary Biofacies of *Ammonia beccarii* var. *parkinsoniana* replaces the *Buliminella elegantissima* one. The environments of the innermost estuarine region were reconstructed using bivalves and gastropods, using the Curve of REMANE, the identification of genuine brackish-water species, the faunal composition and the existence of vicariad species. Various criteria are given for the identification of ancient estuarine environments, and how they differ from other marginal marine environments. Paleontological criteria are also given in order to be able to distinguish between the estuarine zonation existing along a longitudinal axis, and its latitude.

The early Holocene paleogeography in the Río de la Plata and its zone of influence was reconstructed. It shows the existence of a displacement of the estuarine depositional environments simultaneous to the Querandina Transgression. On the Uruguayan coastal area, the marine environments penetrated inwards towards the head of the estuary, being found as far west as Arroyo Pando. The Transitional-area between marine and fluvio-marine environments formed an arch along the Uruguayan coast, extending from Salinas to San José de Carrasco, Areneras de Carrasco, and the eastern coastal region of Montevideo County. The Transitional-area between fluvio-marine and intermediate-fluvial environments was located between Carmelo and Nueva Palmira. The Transitional-area between intermediate-fluvial and inner-fluvial environments was localized in the Río Uruguay somewhat to the north of Fray Bentos; and a little east from Mercedes on the Río Negro. Throughout the course of the lower Holocene Transgression, the Laguna Merín was directly open to the ocean at its southernmost part. The molluscan associations display a zonation from marine environments, to fluvio-marine to intermediate-fluvial environments.

Biostratigraphic correlations were made using a new method, i. e. ecostratigraphic units. These are correlated by their place within the cycle of greatest salinity. Several assemblage zones previously described for the Uruguayan Quaternary are invalidated.

The Neogene and Quaternary geological evolution of the southernmost part of the Pelotas Basin was analyzed. It is characterized by the alternation of marine (or marginal marine) and terrestrial (continental) depositions. The following stratigraphic units were recognized: Camacho, Raigón, Chuy (sensu lato) I, Libertad I, Chuy (sensu lato) II, Libertad II, Chuy (sensu stricto) III and Dolores.

The distribution and boundaries of the paleozoogeographical littoral provinces of the atlantic region of South America since the Miocene were reconstructed using foraminiferids and molluscs. Two Miocene littoral units were identified, which are designated as: 1) North-brazilian Miocene Subprovince. This is characterized by the existence of tropical water bodies, extending at least from 34°—35° south latitude to the north; 2) South-brazilian Miocene Subprovince, characterized by warm temperate water bodies, which extended south of the 34°—35° south latitude. Therefore there is proof that tropical waters reached 1800 km further south along the eastern South American coast line during the Miocene than they do at the present time. This is supported by the faunal composition of the Miocene foraminiferids of Chuy N° 364, specially by the presence of *Amphistegina gibbosa*. It is also confirmed by the study of bivalves and gastropods from the entire Camacho Formation.

The gastropod and bivalve associations are exclusively made up of species of the Caribbean and Argentinian Provinces, the Magellanic forms being completely absent.

The foraminiferal faunas of the Querandina Transgression indicate cold temperate climes, similar to those prevailing today. In contrast, the malacological assemblages indicate mean annual temperatures somewhat higher than those existing today in this region. This is shown by the lower percentile occurence of cold species carried by the Malvin current in the malacological associations from the Querandina Transgression. This difference is explained by the greater potential speed in the migration rate of bivalve larvae and the majority of marine gastropod larvae. It is concluded that the faunas from the Querandina Transgression, as well as the present ones belong to the North-patagonian Subprovince. Probably the mean annual water temperature was somewhat higher than today.

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The Osteology of *Compsognathus longipes* WAGNER

by

JOHN H. OSTROM*)

With 16 text figures and plates 7—14

ABSTRACT

Detailed analysis of the holotype specimen of *Compsognathus longipes* — the classic or archtypical "coelurosaurian" theropod, does not substantiate the traditional carnosaur — coelurosaur subdivision of the Theropoda. Only in its diminutive size, is *Compsognathus* a typical coelurosaurian. The smallest of all known theropods, *Compsognathus* possesses a carnosaur-like large skull (perhaps a juvenile condition); a neck that is intermediate between the long cervical series of coelurosaurs and the short neck of carnosaurs; and forelimbs that are robust, but of intermediate length and bear carnosaur-like two-fingered hands. The hands, however, are unique among theropods, with a peculiar phalangeal formula of 2-2-0 for digits I, II and III. That condition excludes *Compsognathus* from an ancestral relationship with any known later theropod, as well as separating it from other presently known Late Jurassic theropods. The so-called impressions of integument and supposed skin armor are judged to be nothing more than solution-etched surfaces. The tiny skeleton preserved within the body cavity of *Compsognathus* is identifiable, and proves to be a small individual of the lacertilian *Bavarisaurus* (cf. *macrodactylus*), and not an embryo. Analysis of those stomach contents indicates a very long-tailed species, probably a highly cursorial ground-dwelling variety. This remarkable evidence establishes beyond any doubt that *Compsognathus* was a very agile and fleet-footed predator. On the basis of the unique construction of the hand, *Compsognathus* appears to belong to a dead-end lineage among theropods. On the same grounds, it is judged to be somewhat removed from the theropod line that earlier gave rise to *Archaeopteryx*, and ultimately to later birds.

KURZFASSUNG

Eine eingehende Analyse des Holotyps von *Compsognathus longipes*, dem klassischen und archaetypischen „coelurosauriden“ Theropoden, stützt nicht die traditionelle Gliederung der Theropoda in Carnosauria und Coelurosauria. Nur hinsichtlich seiner geringen Größe ist *Compsognathus* ein typischer Coelurosaurier. Als kleinster bekannter Theropode besitzt *Compsognathus* einen carnosaurierartigen, großen Schädel (vielleicht ein juveniles Merkmal), einen Hals, dessen Länge zwischen der langen Cervicalreihe der Coelurosaurier und dem kurzen Hals der Carnosaurier liegt und Vordergliedmaßen, die kräftig, aber von intermediärer Länge sind, mit carnosaurierartigen, zweifingerigen Händen. Das Handskelett ist jedoch einzigartig unter den Theropoden und besitzt die eigenartige Phalangenformel 2-2-0 für die Finger I, II, und III. Diese Verhältnisse schließen *Compsognathus* von einer Verwandtschaft mit irgendeinem bekannten, späteren Theropoden aus; ebenso trennen sie ihn von anderen bis jetzt bekannten Oberjura-Theropoden.

Die sogenannten Hautabdrücke und der vermutete Hautpanzer werden für nichts anderes als angelöste Oberflächen gehalten. Das winzige, in der Leibeshöhle von *Compsognathus* erhaltene Skelett ist mit Sicherheit als ein kleines Individuum des Lacertiliers *Bavarisaurus* (cf. *macrodactylus*) zu bestimmen. Es ist kein Embryo. Die Analyse dieses Mageninhaltes deutet auf eine sehr langschwänzige Art hin, wahrscheinlich eine sehr schnelle, bodenlebende Form. Dies erlaubt die bemerkenswerte Feststellung, daß *Compsognathus* zweifellos ein sehr agiler und schnellfüßiger Räuber war. Aufgrund der einzigartigen Konstruktion der Hand, scheint *Compsognathus* im Hinblick auf die Phylogenie der Theropoden zu einer blind endenden Seitenlinie zu gehören. Es wird deshalb angenommen, daß seine stammesgeschichtliche Position etwas abseits von der Theropodenlinie lag, die früher zum Ursprung von *Archaeopteryx* und letztlich zu den späteren Vögeln führte.

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*) Prof. Dr. J. H. OSTROM, Dept. of Geology and Geophysics, and Peabody Museum of Natural History, Yale University, New Haven, Conn., U.S.A.

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INTRODUCTION

For more than a century, *Compsognathus* has been one of the better-known dinosaurs — partly, for exactly the opposite reason that some other dinosaur kinds are well-known: *Compsognathus* is the smallest of all known dinosaurs. In life, it measured no more than 70 to 75 cm from snout tip to tail tip. In texts and popular writings, it has repeatedly been compared in size with the common chicken. *Compsognathus* also acquired fame because it was one of the first dinosaurian specimens discovered that was virtually complete, although, curiously enough, it was not originally identified as dinosaurian in the first report by Andreas Wagner (1861) — perhaps because it was so small, or because no one at that time really knew what dinosaur anatomy should be like. But perhaps more than anything else, the fame of *Compsognathus* was caused by Thomas Huxley's reference to it as a "bird-like reptile" in his speculations (1868, 1870) on the relationship between birds and dinosaurs.

Since Wagner's original description, this now classic specimen has been studied by many prominent scholars, including Huxley, Zittel, Marsh, Baur, Gegenbaur, von Huene and others, and has been the subject of several intriguing questions: the possibility of viviparity in dinosaurs, and the evolutionary relationship between dinosaurs and birds.

Until 1972, when a second very similar but larger specimen was reported (Bidar, Demay and Thomel) from southern France, the Munich specimen was unique. Except for three isolated "metatarsals" and an associated phalanx (Dames, 1884) sometimes referred to *Compsognathus*, no other specimens have been recovered from the Solnhofen Limestones, or elsewhere. (But see page 101—102).

The present study is a consequence of several factors: my persistent interest in dinosaurian biology and evolution; the recently re-recognized (and now reinforced) evidence of a probable dinosaurian origin of birds; the often-cited bird-like nature of *Compsognathus;* and finally, the need for a comprehensive detailed study of this classic specimen.

In the pages that follow, references are made to specimens that are housed in various paleontological collections. In those references, institutional names are abbreviated as follows:

A.M.N.H. — American Museum of Natural History, New York.
B.S.P. — Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.
G.I.M. — Geological Institute of Mongolia, Ulan Bator.
S.M.N.S. — Staatliches Museum für Naturkunde Stuttgart.
U.S.N.M. — United States National Museum, Washington, D.C.

Y.P.M. — Peabody Museum of Natural History, Yale University, New Haven.
Z.P.W. — Zaklad Palaeobiologii, Warsaw.

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SYSTEMATICS

Class Reptilia
Order Saurischia Seeley, 1887
Suborder Theropoda Marsh, 1881
Family Compsognathidae Marsh, 1882

Definition: Small theropods with elongated hindlimbs, medium length forelimbs and large skull. Vertebral formula: 10 cervicals, 13 dorsals, 4 sacrals and more than 20 caudals. Cervical vertebrae opisthocoelous and pleurocoelous. Dorsal vertebrae amphyplatyan or platycoelous. Cervicals not elongated, rather approximating dorsal vertebral length. Pelvis of normal triradiate (propubic) organization. Pubis markedly longer than ischium and expanded distally. Ilium long and low. Tibia significantly longer than femur and metatarsals elongated. Tarsus and pes of normal theropod construction with I reduced and reverted and V vestigial. Pes digital formula: 2-3-4-5-0. Manus reduced to two functional digits, I and II, and vestigial metacarpal III. Digital formula: 2-2-0- - . Skull relatively very large, equal to or longer than femur. Two antorbital fenestrae and very large orbit. Mandible very slender. Dental count high: $\frac{3 + 15 \text{ or } 16.}{18}$ Anterior teeth with distinctly "bent", fang-like crowns.

Distribution: Malm of Europe: Solnhofen Lithographic Limestones of Bavaria and the lithographic Portlandian limestone of "Petit Plan", Canjuers, France.

Included taxa: *Compsognathus longipes* Wagner, 1861, holotype specimen: B. S. P. A. S. I 563; and *Compsognathus "corallestris"* Bidar, Demay and Thomel, 1972.

Discussion: The systematic history of *Compsognathus* is rather interesting, especially as it relates to the early development of dinosaurian systematics. Although now widely viewed as the archtypical "coelurosaurian" dinosaur, curiously enough, Wagner (1861) gave no opinion on its systematic placement other than to refer to it as "einen Saurier". Huxley (1868) was the first to recognize that *Compsognathus* should be "placed among, or close to, the Dinosauria". As is well-known, the term Dinosauria was coined by Richard Owen (1842) as a reptilian order to encompass various extinct giant reptiles that had been unearthed in Britain. In 1887 and 1888, Seeley demonstrated that the "dinosaurs" then-known did not constitute a natural group, and proposed two distinctly different orders of dinosaurs — the Saurischia and Ornithischia — orders that are still generally accepted today. As a result, the term "Dinosauria" dropped from use as a formal taxon in classifications. Between the proposals by Owen and Seeley, a number of other schemes were proposed by various scholars. The more important of these classifications are summarized below:

Cope, 1866	Huxley, 1870	Marsh, 1878—84	Cope, 1883	Seeley, 1887
Orders	Suborders	Orders	Orders	Orders
		Stegosauria		
			Orthopoda	Ornithischia
Orthopoda		Ornithopoda		
	Dinosauria	Sauropoda	Opisthocoela	
Goniopoda		Theropoda	Goniopoda	Saurischia
Symphopoda	Compsognatha			
			Hallopoda	

Of special interest here is Huxley's classification, which established a new order, Ornithoscelida, containing two suborders, Dinosauria and Compsognatha. His suborder Dinosauria included all then known dinosaurs (Megalosauridae, Scelidosauridae, Iguanodontidae), including the Cetiosaurs (sauropods). The suborder Compsognatha was proposed by Huxley to include only *Compsognathus,* which he considered close to the Dinosauria in its "ornithic modifications", but different from them in the relatively greater length of the cervicals and a femur shorter than the tibia. The taxon Compsognatha persisted as a higher category of "dinosaurs" as late as 1896, when Marsh last listed it as a suborder of his order Theropoda. Marsh's classification of 1896 was as follows:

- Class Reptilia
  - Subclass Dinosauria
    - Order Theropoda
      - Suborder Coeluria
        - Family Coeluridae
      - Suborder Compsognatha
        - Family Compsognathidae[1]
      - Suborder Ceratosauria
        - Family Ceratosauridae
        - Family Ornithomimidae
      - Suborder Hallopoda
        - Family Hallopidae
    - Order Theropoda (No sub-ordinal assignments)
      - Family Megalosauridae
      - Family Dryptosauridae
      - Family Labrosauridae
      - Family Plateosauridae
      - Family Anchisauridae
    - Order Sauropoda (Six families)
    - Order Predentata (Equals Ornithischia)
      - Suborder Stegosauria (Three families)
      - Suborder Ceratopsia (One family)
      - Suborder Ornithopoda (Seven families)

Current traditional classifications subdivide the suborder Theropoda into two infraorders, Carnosauria and Coelurosauria, the former including the large carnivorous forms (Families Megalosauridae and Tyrannosauridae) and the latter all of the smaller and medium-sized theropods (Podokesauridae, Segisauridae, Coeluridae, Compsognathidae, Ornithomimidae and Oviraptoridae). *Compsognathus* has always been allied with the Coelurosauria, ever since its inception by von Huene in 1914. However, the general relationships among theropods have never been clear, and this is reflected in the numerous classification schemes and revisions of the Theropoda that have been proposed over the years (see Huene, 1909, 1914, 1920, 1921 b, 1926, 1928; Osborn, 1917; Gilmore, 1920; Matthew and Brown, 1922; Colbert, 1964; Charig, Attridge and Crompton, 1965; and Colbert and Russell, 1969).

In recent years, doubt has been expressed by some, as to the validity of this two-fold subdivision of the Theropoda. The discovery of *Deinonychus* (Ostrom, 1969a, 1969b), demonstrated once again that it is not always a simple matter to assign a particular taxon to one or the other of these infraorders. *Deinonychus* possesses anatomical features that are usually considered exclusively carnosaurian or coelurosaurian, but not common to both. Colbert and Russell (1969) resolved this problem by placing the Dromaeosauridae (including *Deinonychus*) in a third infraorder, Deinonychosauria. But the question remains: are the categories Coelurosauria and Carnosauria real and valid categories? For example, if the size factor is disregarded, can we justify them on purely anatomical grounds? *Deinocheirus* (Osmolska and Roniewicz, 1970), on anatomical grounds is an ornithomimid —

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[1] Coincidentally, Marsh (1882) authored the family Compsognathidae.

the classic coelurosaurian family —, but an ornithomimid of enormous size. Because of its huge size, Osmolska and Roniewicz placed it in its own family, Deinocheiridae, and assigned it to the Carnosauria. In 1972, I suggested that *Deinocheirus* was an overblown ornithomimid, but how could I justify placing it in the Coelurosauria? I could not, and therefore repeated the position I had taken earlier with *Deinonychus;* the infraordinal categories were omitted.

Most recently, Barsbold (1976) followed the same principle, but with a different twist. He proposed yet another revision of the Theropoda, wherein he recognizes six infraorders: Coelurosauria, Deinonychosauria, Oviraptorosauria, Ornithomimosauria, Carnosauria and Deinocheirosauria. This is comparable to the systematics implicit in my 1969 and 1972 papers, except that it is at a higher taxonomic level. Although I am not comfortable with the elevated rank, this arrangement, like my following "neutral" classification, simplifies some taxonomic assigments. At least as presently known, there are no difficulties in recognizing deinonychosaurs, oviraptorosaurs, ornithomimosaurs and deinocheirosaurs — if diagnostic remains are preserved. But if only non-diagnostic elements of these are available, we would be hard-pressed to assign them to any one of these categories. But even here with Barsbold's "neutral" classification, the Carnosauria and Coelurosauria still remain "mixed bags", with the implication that the carnosaurian Megalosauridae and Tyrannosauridae are more closely related to each other than either is to any other theropod group, and that all remaining small theropods (Segisauridae, Compsognathidae, Podokesauridae, Coeluridae, etc.) are likewise more closely related to each other. I prefer not to make that systematic judgement at this time, explicitly or implicitly. The data presented here on *Compsognathus* may provide new insight, but at the moment I believe that present evidence is inadequate for final conclusions. For these reasons, the following study is presented in the context of a conservative classification as follows:

Class Reptilia
  Subclass Archosauria
    Order Saurischia[2])
      Suborder Theropoda
        Family Podokesauridae
        Family Compsognathidae
        Family Segisauridae
        Family Coeluridae
        Family Dromaeosauridae
        Family Ornithomimidae
        Family Oviraptoridae
        Family Megalosauridae
        Family Tyrannosauridae

Missing from this classification is the Family Hallopidae. The fragmentary (and only) specimen of *Hallopus* (Marsh, 1881, 1882), long considered as possibly closely related to *Compsognathus* and other "coelurosaurs", has been shown by Walker (1970) to be an early crocodilian. Thus, it is not considered further here.

Although not directly pertinent to the systematic placement of *Compsognathus*, two radical proposals have been published recently, that do involve the systematic assignment of the Theropoda. In 1974, Bakker and Galton reviewed certain anatomical evidence which led them to the conclusion that the Ornithischia and Saurischia were of monophyletic — common — ancestry, resurrecting Owen's "Dinosauria". Largely on their belief that all dinosaurs were endothermic and capable of high aerobic exercise metabolism (a popular, but unestablished hypothesis), they concluded that the "Dinosauria" deserved class rank. In their Class Dinosauria, the Theropoda is elevated to ordinal rank (thus returning to Marsh's classification of 1884), within the subclass Saurischia. Their most radical departure from conventional systematics, however, is their inclusion of birds as a subclass of the Dinosauria. This move was prompted by my studies (Ostrom, 1973 and work then in progress — 1976b) showing that *Archaeopteryx* probably was derived from a small theropod ancestor. Charig (1976), in a thorough review of the Bakker and Galton paper, correctly concludes that "until the case for endothermy in dinosaurs is proven (which is unlikely), there are no grounds for separating those reptiles into a different class from all others". As for the inclusion of birds as a subclass of Dinosauria, the possibility that *Archaeopteryx* evolved from a theropod ancestry (a theory that is not accepted by everyone), does not justify such radical departure from conventional classification. Moreover, their proposal fails to enhance the usefulness of the classification on either practical or theoretical grounds, and therefore should be rejected.

Of greater relevance here, is a paper by Thulborn (1975), which was generated by the Bakker — Galton paper. Thulborn argues persuasively (as did Charig, 1976), that existing evidence does not establish monophyly of the dinosaurs. He further rejects the speculation that dinosaurs were endothermic, but he does accept the theory that birds arose from theropods. This last conclusion prompts Thulborn to re-assign the Theropoda to the Class Aves, in order to put "full emphasis on the dinosaurian origin of birds". Desirable though that rationale may (or may not) be, classifying theropods such as *Tyrannosaurus* and *Allosau-*

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[2]) The suborder Sauropodomorpha is included, but not listed here.

rus as birds, will not add to the utility of vertebrate classification either, and therefore will not be accepted by the ornithological community or other systematists — even if the therapod-avian evolutionary relationships should achieve general acceptance. The conventional classification of the higher tetrapod classes Reptilia, Aves and Mammalia is adequate and flexible enough to accommodate these views, and I prefer to use the conservative subdivision of the Theropoda presented above, in the traditional Class Reptilia.

STRATIGRAPHIC AND LOCALITY DATA

Unfortunately, considerable doubt exists about the exact locality of *Compsognathus longipes*, with no apparent way to resolve it. The oldest surviving documentary record of the existence of this specimen, is Wagner's (1861) original description, which describes it as coming from the lithographic shales near Kelheim. A hand-written label glued to the underside of the *Compsognathus* case reads: "Compsognathus longipes Wagner — keine Eidechsen species — aus dem lithographischen Schiefer — im Altmühlthal bei Kelheim". The author of this label is unknown, but in all probability, it was the original owner, a Dr. Oberndorfer, a physician in Kelheim. However, another, more recent printed label gives different information. It reads: "Compsognathus longipes Wagn. — (Orig. Ex. z. Wagn. Abh. Bd. IX T. 3) — Lithograph. Schiefer. — Jachenhausen. Oberpfalz". Jachenhausen is a small village 15 km northwest of Kelheim.

No other records exist in the archives of the Bayerische Staatssammlung to explain these conflicting locality data, or why or by whom the locality Jachenhausen was first used. According to Professor Dehm, the printed label dates from before 1900, possibly during Zittel's time, but the author is unknown. The Oberndorfer collection was obtained by the Bayerische Staatssammlung in 1866, five years after Wagner described *Compsognathus*. Besides the specimen of *Compsognathus*, two other specimens of the Oberndorfer collection have labels with the same handwriting; a turtle *Eurysternum crassipes* and a pterosaur *Pterodactylus kochi*. This suggests that Oberndorfer probably authored these labels. The label for *Eurysternum* also reads "Kelheim".

It is presumed that Dr. Oberndorfer, as an amateur collector, obtained his specimens from a number of different Solnhofen quarries. It may be, that in order to protect his sources from other collectors, he concealed the precise localities under the general description "bei Kelheim", and that the more specific locality of Jachenhausen is the correct locality of *Compsognathus*. But that is not supported by known stratigraphic evidence. Professor Dehm informed me that he attempted to identify the quarry site in the Jachenhausen area from which this specimen might have come. He was unsuccessful on two separate attempts, and reported to me that he was unable to find exposures of Solnhofen strata anywhere in the Jachenhausen area that corresponded with the lithology of the *Compsognathus* slab. Dr. Wellnhofer and I also attempted to re-establish the source of the *Compsognathus* specimen, and checked the large quarries north of the town of Jachenhausen. We also failed to discover any stratum that matched the lithology of the *Compsognathus* slab. Most important, is the fact that we failed to find a single specimen of the ubiquitous crinoid *Saccocoma* (half a dozen specimens of which are preserved on the *Compsognathus* slab) anywhere in the Jachenhausen area. Thus, neither the locality, or the stratigraphic provenance of *Compsognathus* can be determined now. All that can be said is that it came from lithographic facies of the Solnhofen Limestone — probably from somewhere in the Riedenburg — Kelheim area.

In order that this report be as complete as possible, it must be noted that both Marsh (1896) and von Huene (1923, 1925, 1932 and 1956) published that *Compsognathus* came from Solnhofen, but these seem to have been general references to the area in which the Solnhofen strata occur, rather than to the immediate vicinity of the town of Solnhofen. At least there is no surviving original record to substantiate a Solnhofen locality, and it is assumed here to be incorrect. Steel (1970) is the only author to publish the "Jachenhausen locality" as the source of *Compsognathus*, presumably having obtained this information from the printed label with the specimen.

GENERAL DESCRIPTION

The classic specimen of *Compsognathus longipes* is well known, having been repeatedly illustrated and cited in numerous texts, technical papers and popular articles as the smallest dinosaur. Aside from its diminutive size (about that of a small partridge), it is remarkable for the completeness and quality of preservation. Although some regions are crushed, fractured or disarticulated, most of the skeleton is present,

Figure 1: Camera lucida drawing of the specimen of *Compsognathus longipes,* showing preserved bone and bone impressions, together with my identifications. The parenthetic identifications of the hand elements are von Huene's (1925, 1926) interpretations for comparison with my interpretations of the same objects. The original drawing was made by me with a Wild binocular microscope and camera lucida at a magnification of 3.3. *Abbreviations:* Ac. — acromion; An. Cer. Ri. — anterior cervical rib; Ang. — angular; Art. — articular; Ast. — astragalus; At. Int. — atlas intercentrum; At. L. Ne. — atlas left neural arch; At. R. Ne. — atlas right neural arch; Ax. — axis; Ax. N. S. — axis neural spine; Br. C. — braincase; Ca. 1, 2, etc. — caudal vertebrae; Ca. n. S. — caudal neural spine; Cal. — calcaneum; Car. — carpal; Ce. 3, 4, etc. — Cervical vertebrae; Cer. Ri. 4. — cervical rib 4; Co. — coracoid; De. — dentary; Do. 1, 2, etc. — dorsal vertebrae; Do. Ri. 1, 2, etc. — dorsal ribs; Ep. — epipterygoid; Fe. — femur; Fib. — fibula; Fr. — frontal; Ga. — gastralia; Hu. — humerus; Hy. — hyoid; Il — ilium; In. Den. — inter dental plates; Is. — ischium; Jaw — mandible; La. — lachrymal L. — left; Max. — maxilla; Mt. — metatarsal; Mtc. — metacarpal; Na. — nasal; Pa. — parietal; Pal. — palatine; Pm. — premaxilla; Po. — postorbital; Po. Cer. Ri. — posterior cervical rib; Pt. — pterygoid; Pu. — pubis; Q. — quadrate; Qj. — quadratojugal; R. — right; Rad. — radius; Sa. 3, 4, etc. — sacral vertebrae; Sca. — scapula; Sp. — splenial; Sur. — surangular; Ta. — tarsal; Tib. — tibia; Ul. — ulna; Vo. — vomer; I, II, III, IV, V. — digit number; 1, 2, 3, 4, 5. — phalangeal number.

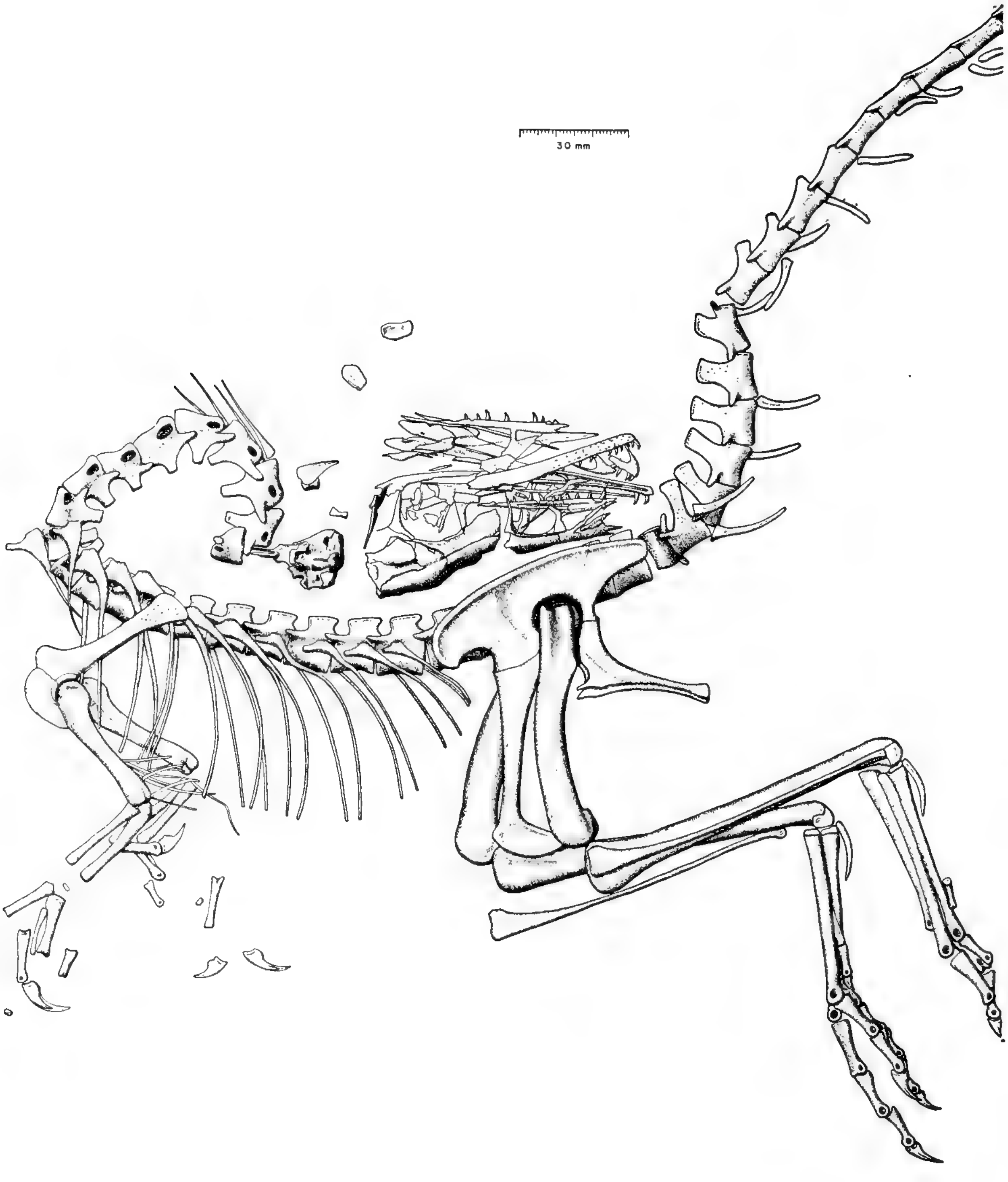

Figure 2: Restoration of the skeleton of *Compsognathus* based on the camera lucida drawing of Figure 1.

either as actual bony elements or as impressions. A few areas have been obliterated by calcite crystals, especially in the lower part of the body cavity and the pelvis, or removed by solution. Apparently, the slab was situated close to the surface and subject to solution by sub-surface runoff: the importance of this will be discussed later. In spite of solution and crystallization, most of the bones are finely preserved, apparently completely replaced by calcite with no recrystallization and consequent distortion and loss of detail (see Plate 7.).

The specimen is preserved on its right side almost completely articulated. The only regions that have suffered some disarticulation are the hands, the skull, some of the cervical ribs and the posterior gastralia.

Why these particular regions have been disarranged is difficult to understand, although in the case of the gastralia there is some evidence that the stomach and body cavity were breached — perhaps due to build-up of gases generated within the rotting carcass. The posterior cervical ribs, the slightly displaced right fibula and the scattered phalanges of the hands may have been scattered by scavengers, but more likely they simply were drifted away from their original sites by gentle currents after connective tissues had decomposed.

The most peculiar aspect is its "death pose" — the highly contorted arrangement of the cervical series and the respective positions of the axis, braincase and dermal skull. The cervical column is looped back on itself almost a full 360 degree arc. This opisthotonic condition is not unusual, having been recorded in numerous pterosaur specimens (especially pterodactyloids), small theropods (see, for example, *Struthiomimus altus*, A. M. N. H. 5339, reported in Osborn, 1917, which is preserved in almost exactly the same pose as *Compsognathus*) and modern birds. It seems to be a common occurrence in carcasses of long-necked animals; notice, for example, that it is much less common in rhamphorhynchoid pterosaurs (than in pterodactyloids) and short-necked theropods. The most frequently invoked explanation of this backward distortion of the neck is shrinkage (due to drying) of the dorsal neck muscles and ligaments, particularly the ligamentum nuchae. However, that presumably requires that the carcass initially was exposed to subaerial conditions and perhaps even mummified, before being submersed, circumstances that are rejected by Rietschel (1976) for the several specimens of *Archaeopteryx* that are similarly contorted.

Whether or not desiccation is involved, contraction of dorsal muscles and/or ligaments appears to be the most probable explanation of this opisthotonic state. But in the case of *Compsognathus*, we are faced with a curious anomaly: the braincase and skull, to which these ligaments and muscles were firmly attached, are completely separated from the cervical column and each other. The braincase has been displaced backward, by more than its length, from the anterior end of the axis (and rotated 90 degrees about its longitudinal axis), while the dermal skull components have been displaced even further backward, and turned completely around (the braincase faces forward, but the skull faces backward). As one of the largest and strongest ligaments in the body, it seems unlikely that the connection of the ligamentum nuchae to the skull would have disintegrated before most other connective tissues. Yet that appears to be exactly what happened. The entire axial skeleton, except for the atlas and the skull, are preserved in close articulation. How this happened is unknown. There is no evidence that the head was severed by scavenger action and currents strong enough to displace it surely would have disarranged the skeleton as well.

As for the skeleton itself, it is well formed and gives the impression of a fully developed individual (however, see later comments on this). The skull is relatively very large, a possible indication of immaturity. The neck is slightly shorter than the trunk. The caudal series extend off the end of the slab, so tail length is unknown. But from the very gradual reduction along the proximal caudals, the original tail length must have been more than twice as long as the preserved caudal series. The hind limbs are extraordinarily long and robust, while the forelimbs are of only medium length. *Compsognathus* clearly was an obligate biped and probably highly cursorial.

Cranial Skeleton

Skull.

Most of the skull and mandibles (see Plate 8) are present, but somewhat disarticulated. Certain regions are crushed and sufficiently damaged so as to make reconstruction difficult and uncertain. The fact that so many skull and jaw elements are separated from adjacent bones, while there was relatively little disarticulation in the post-cranium, suggests that either the skull was highly kinetic and very loosely bound together, or that this is a young individual in which the cranial elements had not yet become firmly united. The very small size of the specimen, the seemingly disproportionately long hind legs, and the relatively large orbit, support the juvenile explanation. But the fact that there are no textural differences, or differences in the degree of ossification between dermal and endochondral bones, plus the fact that all vertebral sutures apparently were closed, suggest that we are dealing with a mature individual.

The skull, as I have reconstructed it, is quite long (70—75 mm), very low and with a sharply tapered snout. The orbit was very large and nearly circular. Two antorbital fenestrae are present, one quite large about half the size of the orbit, and the other small. Both are sub-triangular in shape. The external nares were narrow, elliptical, and somewhat elongated. The temporal fenestrae have been obliterated by displacement of some bones and loss of others, but the lateral fenestra appears to have been quite high and narrow from front to back. In general appearance, the skull is most similar to that of *Archaeopteryx*. My reconstruction of the skull is given in Figure 3.

A convenient index of head size is the ratio of skull length to the length of the presacral vertebral column. Using a skull length of 72 mm and a presacral length of 235 mm, the ratio for *Compsognathus* is .30, somewhat higher than most "coelurosaurs", but not

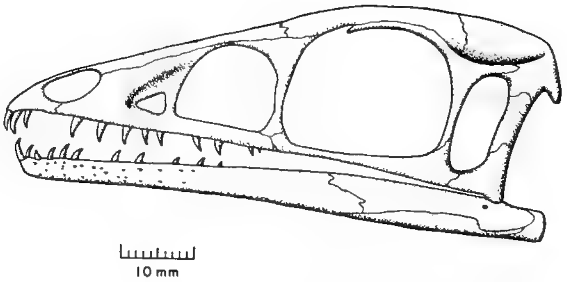

Figure 3: Reconstruction of the skull and jaws of *Compsognathus longipes.* The temporal region is largely hypothetical, as are the sutural details between the maxilla, jugal and lachrymal, the jugal and post-orbital, and the quadratojugal, quadrate and squamosal. The number of teeth shown is the absolute minimum, recording only those that are preserved in place or are indicated by tooth impressions. Empty alveoli due to tooth replacement or post mortem loss cannot be distinguished. The diastema at the premaxilla — maxilla suture is real.

significantly so. This higher ratio might be taken as further evidence that this specimen was immature. On the other hand, it might indicate a close affinity to the larger-headed "carnosaurs". A comparison of skull / presacral ratios in several other theropods with that of *Compsognathus,* is as follows:

Ornithomimus altus (A.M.N.H. 5339) . .	.15
Gallimimus bullatus (ZPW-MgD-194 & GIM-DSP 100/11)	.16
Coelophysis longicollis (A.M.N.H. 7224)	.23
Ornitholestes hermanni (A.M.N.H. 619) .	.24
Allosaurus fragilis (U.S.N.M. 4734) . .	.28
Compsognathus longipes (B.S.P. AS I 563)	.30
Deinonychus antirrhopus (Reconstruction, various Y.P.M.)	.35 - .40
Tyrannosaurus rex (A.M.N.H. 5027) . .	.41

Not surprisingly, there seems to be an uninterrupted gradation between so-called "coelurosaurs" and "carnosaurs". Notice that *Compsognathus* has a ratio slightly greater than *Allosaurus.*

Premaxilla: Both premaxillae are present, displaced and lying between the extremities of the two dentaries. The lateral surface is exposed in both. The premaxilla is roughly triangular in shape, deeply emarginated posteriorly by the large external naris. The nasal process is long and very slender and does not appear to have been overlapped laterally or ventrally by the nasal. The maxillary process (missing in the right premaxilla) is much deeper and more robust. The end of this process is concealed beneath the left dentary, so the nature of the junction with the maxilla cannot be determined. The external premaxillary surfaces are smooth and devoid of even tiny foramina. Premaxillary teeth number three, with the middle tooth the largest. Two teeth are preserved in place in the right premaxilla and a third lies slightly removed from the empty posterior alveolus. Only the middle tooth is preserved in place in the left premaxilla. A long diastema occurs behind these teeth, the entire maxillary process below the naris being devoid of alveoli. Preserved as they are, lying on their medial surfaces, little can be said about the nature of their mid-line articulation except that it must have been a flexible union.

Maxilla: The nearly complete left maxilla is displaced and lies below the rest of the skull and the mandibles. This exposes the inner surface of the less complete right maxilla situated close to its normal position. The maxilla is a rather delicate and thin bone with a surprisingly shallow tooth-bearing ramus. The jugal process seems to have tapered gradually to a very slender process less than 1 mm in depth, for what must have been an extremely weak (or flexible) junction with the jugal. Anteriorly, the maxilla is more robust, indicating a more extensive — and presumably stronger articulation with the premaxilla. The tapered anterior process of the maxilla, like the posterior maxillary process of the premaxilla, seems to have lacked teeth, although neither maxilla is well enough preserved to establish the absence of alveoli. However, it does appear that the upper diastema extended several mm behind the premaxillary-maxillary suture. The entire lower external surface, like that of the premaxilla, is free of foramina.

A thin sheet of bone extends upward from the premaxillary process, apparently forming most or all of the inferior-posterior margin of the external naris, although this region is not clearly preserved here. A small, triangular subsidiary antorbital fenestra is partly preserved here, separated by a robust vertical bony bar from the large sub-triangular antorbital fenestra behind.

The dentition extends over approximately two thirds of the maxilla length, reaching to a position just behind the main antorbital fenestra. The left maxilla still bears 6 teeth, plus 9 or 10 empty alveoli or tooth imprints. The right maxilla contains 5 teeth in situ, plus 6 clear tooth impressions or empty alveoli and 5 possible alveoli. Accordingly, the maxillary tooth count appears to have been 15, and possibly 16. The anterior extremity of the left maxilla shows several small triangular bony plates between some of the empty alveoli: these are interpreted as inter-dental plates.

Nasal: The nasal bones are represented by several thin fragments and a long impression. The precise shape cannot be determined from these, but the paired nasals appear to have formed a straight, rather broad and perhaps wedge-shaped, smooth-surfaced plate of bone extending between the premaxillae and the frontals. The contact with the frontals appears to have been squamous. The nasal contribution to the narial posterior border is not known, but it appears to have been small.

Frontal: Much of the dorsal surface of the frontals is well-exposed, these bones having been rotated to lie almost parallel with the bedding plane. This permits an accurate measure of inter-orbital skull width (9.1 mm, minimum). It also shows that the frontals were firmly united, but not fused, along a very straight sagittal suture. The frontal plate is almost flat with only slight longitudinal convexities on either side of the midline, and of moderate thickness, as is shown along the posterior broken edge. The articulation with the parietals is not certain.

One interesting feature of the frontals is the presence of a short forward projection along the lateral margin, forming a unique feature of the superior orbital margin. It is faintly reminiscent of a palpebral or supra-orbital bone, but it projects forward rather than backward, and seems to be in contact with the main body of the frontal. It is well preserved on the right side, but is largely broken away on the left side. On both sides, it seems to have been continuous with the post-orbital, and may have been an anterior expansion of that element into the supraorbital region. No comparable feature is known to me in other theropods.

Parietal: The parietals are represented by crushed, thin sheets of bone lying behind the frontals on both sides of the midline, and extensive impressions of their internal surfaces. The latter indicate that the sagittal suture persisted into the parietal area. Although not certified as such, the fronto-parietal union appears to have been positioned just behind the orbit. A slightly raised narrow ridge extends transversely in an irregular line across the large convex fragment of the left side that lies just behind the orbit. This appears to extend from a bone that I have interpreted as the left post-orbital. A corresponding linear feature shows faintly in the matrix impression of the internal surface of the right fronto-parietal. If these indeed are the fronto-parietal suture, it seems to reflect a very firm, solid union of these bones, a condition that is substantiated by the fact that they are preserved together with no apparent displacement and little distortion. That is in contrast to the disarticulated and displaced occurrence of most other cranial elements.

Lachrymal: Both lachrymals are preserved close to their natural positions, but both are damaged sufficiently to preclude full description. The lachrymal appears to have been I-shaped, with a stout vertical shaft forming a narrow pre-orbital bar between the orbit and the antorbital fenestra. The upper and lower extremities seem to have been expanded, probably for firm union with the maxilla (and jugal?) and the nasal-frontal complex. Some or most of the upper expansion may have been composed of the pre-frontal, but this cannot be established. There is a distinct sutural facet on the inferior anterior edge of the left frontal, which I interpret as the articular facet for the pre-frontal.

Postorbital: This bone is easily recognized by its T-shape. Only the left has been identified here, forming the posterior margin of the orbit, slightly separated from the fronto-parietal. It appears to be a relatively thin sheet of bone with wedge-shaped anterior (frontal) and posterior (squamosal) processes above. The inferior process tapers gradually to an indeterminate articulation with the jugal.

Jugal and Quadratojugal: Neither of these bones has been identified with certainty, and apparently are lost, concealed beneath other bones, or so damaged as to be unrecognizable.

Squamosal: In all probability, the fragments overlying the postero-lateral region of the left parietal, represent what remains of the left squamosal. That is far from certain, though, as these fragments are so severely damaged that no details are discernible.

Quadrate: At the rear of the skull is a thin vertical lamina of bone which I interpret as the posterior part of the internal half of the left quadrate. The external half is missing. The upper extremity of this lamina ends in a broken surface and the lower part is concealed by the adjacent left pterygoid. If correctly identified, this portion of the quadrate is surprisingly slender and delicate, but the external part of the quadrate shaft must have been much more robust. Situated in the anterior part of the left orbit is an L-shaped fragment which may be part of this missing half of the quadrate, and perhaps part of the quadratojugal. The "ascending" shaft of this L-shaped fragment is quite stout and appears to have been either L, or C-shaped in cross section. The lower part is overlapped by a very thin sheet of bone (with broken edges), which may be the left quadratojugal.

Pterygoid: The left pterygoid is conspicuous below the orbital and temporal regions, extending, forward from the quadrate to pass beneath the left dentary. The distinctive feature is the deeply concave cotylus of the basipterygoid articulation. Forward of this, the palatine ramus is straight and quite narrow, with a broadly convex ventral surface. Further anteriorly, this appears to expand in a broad, slightly concave bony sheet, but the lateral margin is not preserved. The medial margin is intact, though, showing that an interpterygoidal vacuity existed over most or all of the length of the pterygoids. Behind the basipterygoid articulation, the quadrate ramus extended postero-laterally as a relatively high thin lamina at an angle of about 30 degrees to the palatine ramus. Unfortunately, the posterior extremity is missing.

The right pterygoid is not identifiable with certainty, but the several fragments in front of the quadrate-quadratojugal fragment, and in the orbit itself, probably represent remains of that element.

Ectopterygoid: Not recognized.

Epipterygoid: This element has rarely been reported in theropods, and its presence in *Compsognathus* is open to serious question. It is mentioned here only because one small bone closely associated with the skull and braincase, resembles the epipterygoids reported by Madsen (1976) in *Allosaurus.* It must be emphasized that this is an extremely tenuous identification. The bone in question is preserved between the cervicals and the left quadrate, just above the braincase. The preserved portion flares slightly to a gently convex oval surface which apparently was an articular surface. The opposite end, preserved as impression in the matrix, flares into a broad (thin ?) sheet of bone which terminates in a nearly straight edge. If this is indeed an epipterygoid, the latter must be the pterygoid process and the oval articular surface is for articulation with the laterosphenoid.

Palatine: Indeterminate.

Vomer: Not recognized, with certainty.

Braincase: The braincase is situated between the dermal skull on one side and the anterior cervical vertebrae on the other, completely separated from both. This peculiar circumstance has been noted by others, especially by Nopcsa (1903). It suggests a possible violent severing of the head from the neck, except for the fact that all components are preserved very close together.

Certain features of the braincase are clearly recognizable, but in other places it has been severely damaged and some bones are missing. Thus, the endocranium is not easily or fully interpreted. In addition, those regions that are recognizable, for the most part do not correspond closely with those of other theropods. Again, it is difficult to establish whether these differences are real, or due to damage and missing parts. (See Plate 9:1.)

In general, the endocranium is widely triangular in its ventral aspect, very broad behind at the occiput and tapering abruptly forward. The original width across the paraoccipital processes exceeded 16 mm and the basioccipital-basisphenoid length is about the same. Total preserved length of the basioccipital-basisphenoid-parasphenoid complex is 24.5 mm. Aside from the broad triangular form, the other distinctive aspect of this braincase is the nearly perpendicular relation between the ventral surfaces and the occiput.

The occipital condyle and the foramen magnum are the most obvious features. The condyle, however, is distinctly not theropod-like, being kidney-shaped rather than nearly spherical. The transverse width of the condyle is more than twice the sagittal dimension. Sutures clearly show that the lateral portions are formed of the exoccipitals, but the largest part is basioccipital. The exoccipitals do not meet in the mid-line, thus the basioccipital forms the ventral floor of the foramen magnum, as usual. The original shape and size of the foramen magnum are uncertain because of possible crushing and broken bone edges adjacent to the foramen, but it appears that it was much larger than the condyle, and perhaps oval in shape, with the transverse dimension the larger. If correct, these also are not typical of theropods, where the foramen is usually nearly circular and much smaller than the condyle. The dorsal margin of the foramen is formed by a smooth, transversely convex, sheet of bone that must be the supraoccipital. The upper part is concealed in matrix, but the height of this bone above the foramen magnum is at least 5 mm, which indicates that the foramen and condyle were positioned quite low on the occipital surface. The supraoccipital is oriented almost perpendicular to the basioccipital — basisphenoid surface.

Lateral to the condyle, several fragments of bone represent portions of the paraoccipital processes. No suture is evident separating the exoccipital and opisthotic. Although Nopcsa (1903) described this region as pierced by many foramina, as in birds, it is so fractured and damaged that only one doubtful foramen can now be recognized. I agree with Nopcsa, however, that this region is bird-like in its position and orientation. It lies almost entirely in the plane of the basioccipital-basisphenoid complex, although there is a dorsal expansion of unknown dimension more or less in the plane of the foramen magnum.

Anterior to the condyle, much of the basioccipital and basisphenoid have been lost, leaving only impressions of their internal surfaces. The impression shows that the floor of the endocranial cavity, at least in the region of the basioccipital, was traversed by a low sagittal ridge extending forward from the foramen magnum. A similar feature is present in some birds, but I am not aware of such a feature in other theropods, or in reptiles in general. In fact, very often there is a slight mid-line groove in the basioccipital and basisphenoid, which marks the position of the basal artery.

Anterior to this region are paired, but no longer symmetrical, lateral flanges that appear to have been crushed down onto the ventral surface of the braincase. These are quite prominent and apparently projected well below the endocranium. The most likely interpretation of these structures is basipterygoid process of the basisphenoid. Nopcsa (1903), interpreted much smaller lateral projections further forward as the "pterygoid apophyses", but their position at the posterior end of the cultriform process of the parasphenoid, makes that interpretation unlikely.

Nopcsa (1903) puzzled over the paired, near-vertical longitudinal laminae at the anterior extremity of the braincase, postulating that they might be the pterygoids, palatines or the vomer. He finally decided, with some reservations, that they were the palatines. However, these laminae are unquestionably continuous with the other ventral elements of the braincase, and therefore cannot be any of the bones Nopcsa considered. Because of its double condition, Nopcsa was correct when he ruled out the presphenoid (which is rare in reptiles anyway). But it is quite obvious to me that these two lamina, which join in the mid-line, form the cultriform process of the parasphenoid, which normally is a double structure with an inverted V-shaped section.

Portions of the lateral wall of the braincase are present, and have been well-prepared (undoubtedly with great difficulty because of the narrow space between the braincase and other nearby elements). On the left side, there are two distinct foramina, piercing a slightly concave bone which I interpret to be the prootic. The larger foramen probably is the fenestra ovalis, and immediately anterior to it, a similar-sized foramen I take to be the trigeminal foramen. If correctly identified, the latter foramen must mark the approximate junction between the prootic and the laterosphenoid, but no suture is evident.

Mandible.

Both lower jaws are present, but disarticulated and slightly displaced. The most distinctive aspect of the mandible is its extremely slender form with nearly parallel upper and lower margins. No evidence has been recognized to indicate the presence of a coronoid process or of an external mandibular fenestra. Since all three of the lateral mandibular elements are nearly complete, I conclude that this fenestra probably was not present in *Compsognathus*, as is the case in *Ornitholestes*. However, the matter is beyond proof.

Dentary: The dentary is long and surprisingly slender, with nearly parallel upper and lower margins. It deepens slightly toward the rear. Externally, it appears to have been slightly convex dorso-ventrally. In its anterior part, the external surface is pierced by a large number of very fine pores, many of which are arranged in two parallel rows, an upper row just beneath the alveolar margin and a lower row close to the inferior margin. Other foramina are scattered in between. The upper foramina do not seem to coincide with tooth alveoli, either in number or position. The medial surface of the right dentary reveals a deep and very prominent Meckelian canal, bordered above and below by stout ridges. Much or all of this canal presumably was covered by the splenial, but there are no distinct articular scars for this bone, except posteriorly near the end of the dentary. Thus, it is possible that the Meckelian canal was open anteriorly. The symphysis is quite short, and appears to have formed a relatively loose or flexible union between the two mandibles. Tiny interdental plates are present between alveoli along the entire inner side of the tooth row. These occur as separate wedges of bone at each interalveolar position.

The tooth row, as measured on the left dentary, is quite long (26.2 mm), perhaps slightly longer than the maxillary row. There are 11 teeth preserved in place (or slightly dislocated) in the left dentary and seven empty alveoli. The right dentary has 16 empty sockets, plus two anterior teeth in place. Thus, the dentary tooth count is 18, which is one of the higher counts among theropods, exceeded only by that of *Coelophysis* (25) among theropod taxa known to me.

Splenial: These elements are questionably identified here (see Fig. 1), largely on the basis of their location and shape. They are preserved as thin sheets of bone or impressions which indicate a rather long and narrowly tapered bone. The shape and dimensions correspond approximately with those of the posterior part of the Meckelian canal. Both elements are located close to the dentaries — apparently lying in between them. One (the left ?) overlies the upper ramus of the left maxilla and the other (the right ?) seems to lie beneath that maxilla.

Surangular: Both surangulars are easily recognized lying side by side next to the left maxilla. Both bones show the external surface, the right surangular having been turned over. The surangular foramen is evident in both. Also clearly preserved in the right surangular is the articular cotylus for the distal end of the quadrate. The position of this cotylus clearly establishes that the retroarticular process was quite long (more than 5 mm) and the articular may have extended beyond the surangular extremity.

The external surface appears to have been almost planar. Dorsally, a stout angulation separates the lateral and dorsal surfaces, as in most other theropods, so they are oriented nearly perpendicular to each other. A faint antero-posterior ridge parallels the lower margin, marking the upper boundary of the articulation surface for the angular.

Angular: The left angular, incomplete, lies immediately adjacent and parallel to the left surangular, only slightly removed from its articulation with that bone. Most of the lateral lamella is missing, but part of its original shape can be determined from the articulation scar on the surangular. Extending back from this is a very slender, slightly tapered process which articulated with the lower edge of the surangular all the way to its posterior extremity. Thus the retroarticular process was constructed of at least three elements, the surangular and angular in addition to the articular. The right angular possibly is represented by two fragmentary sheets of bone that overlie the right surangular, but no distinctive features are preserved. The form of the anterior end of the angular is not known, but presumably it overlapped the posterior end of the dentary in a squamous articulation.

Prearticular: Not recognized.

Articular?: Two sub-rectangular bones, which at first glance look like dermal scutes, lie one to two cm away from the two surangulars. Their identity cannot be verified, but I believe them to be the two articulars. My belief stems from their preserved location close to the surangulars, their size and shape, and the fact that there are two of them and they are paired. Although they seem to have slightly different shapes, perhaps due to differential crushing and somewhat different positions in the matrix, the exposed surfaces clearly are mirror images of each other. If my identification is correct, the exposed surface is the surangular or external surface. Each bone shows a prominent ridge which bifurcates into two lesser ridges at one end. This feature divides the exposed surface into two unequal areas, the larger of which I interpret as the articular surface for the surangular. The smaller surface is probably for the posterior process of the angular (see Plate 10:3).

Dentition.

Stromer (1934), presented a detailed description of the dentition of *Compsognathus*, together with a summary comparison with the teeth of selected other theropods. There is little that can be added to Stromer's study and what follows here is in part taken from his work, in order that this study of *Compsognathus* be complete.

As noted elsewhere in this report, the tooth count for *Compsognathus* is $\frac{3+15 \text{ or } 16}{18}$. Stromer (1934) gave it as $\frac{3+15+}{18}$, but it looks to me as though there might have been 16 tooth positions in the maxilla. Upper and lower teeth are quite similar at equivalent positions in the tooth rows, but there is gradational change in tooth morphology and size along the tooth rows.

The premaxillary teeth, and the anterior teeth in the dentary, are long and slender, tapering gradually to sharp points. The lower two thirds of the crown is straight, but the tip is bent sharply backward at an angle of 30 to 40 degrees. The crown is nearly circular or slightly oval in section, with the transverse diameter slightly greater than the longitudinal dimension. The crown is completely devoid of serrations or carina. The first premaxillary tooth appears to have been slightly procumbent, but probably not as sharply as Stromer (1934) illustrated.

The first two or three dentary teeth (Plate 9:2) are almost exactly the same as the premaxillary teeth, both in size and shape, and the first is slightly procumbent like its counterpart above. The next three or four teeth are similar, but instead of the sharply bent tip, the entire crown curves backward in a continuous curve. These teeth also lack a serrated edge, but where the forward-most dentary teeth are slightly compressed in their anterior and posterior surfaces, these are slightly compressed latero-medially, so that the greatest crown diameter is longitudinal. There is slight variation in size among these teeth as well. The remaining posterior dentary teeth become progressively smaller (shorter) and more compressed transversely, toward the rear of the tooth row. These posterior dentary teeth also become progressively less curved toward the back, becoming more nearly triangular in lateral profile, the rear edge being almost straight and perpendicular to the dentary with the anterior surface curving, gently back to meet it at the apex.

With only a few maxillary teeth well preserved, it is difficult to reconstruct the complete nature of the upper dentition. However, those that are present seem to parallel the posterior dentary teeth in form and size, becoming progressively shorter and less curved toward the back. And like their dentary counterparts, they are also laterally compressed and oval in section, with short serrated posterior carinae.

It is not possible to say very much about tooth replacement because so many teeth are missing. There are at least eight loose teeth scattered around the jaw elements, and numerous impressions of now missing teeth occur along all tooth rows. The left dentary perhaps gives the best evidence of the replacement pattern. Eleven teeth are present, six of which are crowded together in the anterior -most region (7 mm). The remaining five teeth are somewhat irregularly spaced over the next 18 mm of the tooth row. No indisputable tooth impressions are present at the now empty alveoli of the left dentary, so the existing eleven teeth still in situ represent the minimum number of functional dentary teeth when this specimen was buried. There could have been more. The overall distribution of these eleven remaining teeth is as follows: × × × × × × O O × O × O O × O × O × (where "O" is an empty socket and "×" a tooth in place). As we might have expected, this pattern suggests tooth replacement at alternating positions.

Hyoid Apparatus.

Hyoid elements have been recovered in a number of dinosaurs, but in most instances these have been ornithischians. Marsh (1896) and Gilmore (1920), reported the presence of possible ossified hyoid bones in *Ceratosaurus nasicornus* (U. S. N. M. No. 4735), and I recall seeing what appeared to me to be possible hyoid elements in some of the American Museum specimens of *Coelophysis longicollis.* With these exceptions, the hyoid apparatus appears to be unknown in theropods. For that reason, the identification of possible hyoid bones in *Compsognathus* must be considered as very tentative. But the two bones in question do not fit any other alternative skull element.

In so far as can be seen from their shapes, size and lengths, they are the same, and thus appear to have been paired. Both are very long, slender and straight bones nearly 30 mm long. One is located between the right dentary and maxilla, extending parallel to those two tooth rows. Imprints of maxillary teeth are pressed into it, indicating that it lies beneath (external to) the maxilla. The second one overlaps (lies external to) the left maxilla at a slight angle to its tooth row. Both of these objects are parallel-edged, flat ribbon-like bones, as preserved, but they may have been rod-like and only flattened after burial by sediment compaction. I doubt this, though, because similar-sized ribs in this specimen do not show a comparable degree of flattening. The fact that both bones seem to lie external to the maxillae is troublesome, since the hyoid apparatus in life is situated between the mandibles, and thus lies inside, or medial to, the maxillae. How they both could have been displaced to lie outside of the maxillae, is the critical question against their being hyoid elements. But, in view of the disarticulation and dislocation of many other skull elements, that identification is not precluded, and on morphological grounds it seems most probably correct.

Axial Skeleton

Vertebral Column.

The vertebral column is complete, except for an unknown number of caudals distal to the fifteenth, and two segments in the dorso-sacral region that are represented only by impressions. The pre-sacral count totals 23, and the pre-sacral length approximates 23.6 cm, of which less than half (10.5 cm) is cervical length. There are 10 cervicals, 13 dorsals, 4 sacrals and more than 15 (probably more than 30) caudals.

Cervical vertebrae: The cervical series consists of 10 segments, including the atlas, and is complete, although not all of the atlas has been recognized. Von Huene (1908) reported 12 cervicals and 11 dorsals, without giving any detailed explanation, but later (1925) he specified 10 cervicals and 13 dorsals[3]). As noted previously, the neck is highly arched backward, with the atlas and skull separated from the cervicals. Only the intercentrum of the atlas has been (questionably) recognized here, together with two thin fragments that I suspect might be the atlas neurapophyses, (see Fig. 1). No sign of the odontoid has been detected. The atlas intercentrum is situated in the area between the skull, braincase and anterior cervicals, with its posterior and ventral surfaces exposed. The posterior surface is gently convex transversely, and strongly convex dorso-ventrally. The ventral surface is also convex transversely, but slightly concave longitudinally. Its upper part is concealed by a thin triangular sheet of bone (the right atlas neurapophysis ?), so that part of the intercentrum cannot be determined, but presumably it was strongly concave so as to fit beneath the odontoid. The transverse width of the intercentrum (4.45 mm) is the largest dimension and is close to that of the occipital condyle (4.6 mm). Little can be said about the questionable neurapophyseal fragments, except that they are very thin, concavo-convex, triangular sheets of bone with original lengths of something more than 10 mm.

The axis is situated just to the left of the braincase and slightly removed from the third cervical. I am not certain, but there appears to be a very thin axis intercentrum fused to its anterior end. The axis centrum is distinctly shorter than those of succeeding cervicals, but like all the following cervicals, it is marked by a conspicuous small oval pleurocoel in its anterior lateral surface. The axis centrum also is slightly opisthocoelous. The neural arch is damaged, but appears to have been long and of moderate height.

Although the quality of preservation varies from one segment to another, the remaining eight cervicals appear to have been quite similar to each other. The centra incerease in length to a maximum of 12.7 mm for the sixth and seventh segments, then length diminishes progressively to 10.9 mm for the ninth and tenth. All cervicals are strongly opisthocoelous and centra are narrow-waisted with laterally facing, anteriorly placed pleurocoels. The neural arches are all severely damaged and difficult to interpret, but they appear to have been relatively low, long and massive, with stout zygapophyses. No diapophyses could be identified, although the double-headed design of the cervical ribs clearly establishes their original existence. Similarly, no cervical neural spines have been recognized.

Dorsal vertebrae: In many instances, it is difficult to select a distinctive point of separation between the cervical and dorsal vertebrae, and in most cases it is decided on the basis of arbitrary features.

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[3]) Von Huene's thirteenth dorsal, in fact, turns out to be the twelfth, a point that is discussed later.

The present specimen is no exception. I selected the point between the tenth and eleventh presacrals as the most appropriate place because there is a distinct change in the morphology of the ribs here and, although the preservation does not permit an absolute statement, there appears to be a change in vertebral morphology here as well. Although badly crushed and fractured, the eleventh presacral is much shorter (9.9 mm) than the tenth (10.9 mm). Also, the eleventh presacral seems to be the first in the series that lacks pleurocoels, although the crushed state of the centrum does not allow an unqualified statement on this. Most of the succeeding presacrals clearly are without pleurocoels. Finally, the rib (impression) adjacent to the eleventh presacral is more robust, although not much longer, than the preceeding cervical ribs and bears a well-defined, long-shafted capitular process like those of the succeeding thoracic ribs. On these criteria, there are 13 dorsal vertebrae, the last two of which are indicated only by impressions.

The second dorsal vertebra has a length of 9.4 mm, slightly shorter than the first, perhaps the result of distortion, whereas the rest have lengths very close to 10 mm. The centra appear to have been elongated, slightly narrow-waisted, spool-shaped structures. They are either amphiplatyan or slightly platycoelous. Because of the crushed state of many vertebrae, and the superimposed dorsal ribs, no sign of parapophyses or facets for the capituli are discernible. Even more surprising, in view of the widely separated capitulum and tuberculum of the dorsal ribs, is the apparent absence of prominent transverse processes.

The neural arches are all long and low, with stout zygapophyses. The neural spines also are low, rising less than 3 mm above the arches, but long — ranging from 7 to 9 mm in longitudinal dimension. These spines are situated at the rear of each segment, and in most instances overhang the anterior part of the succeeding vertebra. Anterior neural spines are nearly rectangular in shape, but posteriorly they become somewhat fan-shaped. All the dorsal spines have slightly thickened anterior margins (suggestive of well-developed interspinous ligaments), as well as lateral surfaces with distinctly sculptured texture. The latter may reflect muscular attachment, presumably slips of the M. lattisimus dorsi.

The zygapophyses are short, but stout and situated well above the centra. The postzygapophyses are positioned directly below the posterior margin of the neural spine, whereas the prezygapophyses project far forward of the neural spine. Because all zygapophyses are poorly preserved but still in close articulation, it is not possible to determine the attitude of the articular facets. Most probably, though, they were slightly inclined toward the mid-line.

A curious and inexplicable problem exists concerning Huene's (1925 & 1926) tally of the dorsal vertebrae. After concluding that there were ten cervical vertebrae, he then noted that these are followed by 12 dorsal vertebrae in front of the ilium and the neural process of the 13th is still to be seen above the anterior tip of the ilium. He then stated that five sacral vertebrae must follow this last. In other words, according to von Huene, the "neural process above the tip of the ilium" is the 23rd presacral segment, including an undetected atlas. According to my count, that same neural spine is the 22nd presacral vertebra. I count the impression behind that "neural spine above the tip of the ilium" as the 13th dorsal, largely on the grounds that it (like its predecessor) is missing, and not preserved co-ossified with the sacrals behind. This last segment, von Huene obviously counted as one of his "five" sacrals, but that in no way explains how he counted 23 segments in front of this segment.

The relatively long and slender centra of the dorsal vertebrae, and the fan-shaped neural spines are unique among theropods, although a variety of "coelurosaurs" (i. e., *Coelophysis*, *Aristosuchus*, *Coelurus*, and to a lesser extent, ornithomimids) have moderately elongated dorsal vertebrae.

Sacral vertebrae: The sacrum, unfortunately, is entirely obscured by solution, overlying portions of the ilium and femur, and growth of secondary calcite crystals. Consequently, nothing can be said about the morphology of the sacrum, or the sacral number with absolute certainty. However, using the lengths of the last dorsal, of about 12 mm (for the thirteenth dorsal by my count) and the first complete caudal preserved (the second caudal by my interpretation) of 11 mm, as indices, the sacrum probably consisted of only four segments, rather than five as von Huene (1908, 1925, 1926, 1932) and subsequent authors have cited. Unless the sacral segments of *Compsognathus* were much shorter than adjacent vertebrae in front and behind, the space available (41 mm) in this specimen simply is too short to have contained five sacral vertebrae. Yet, I cannot prove that the sacral number was four rather than five. Two vertebrae are missing (although preserved poorly as impressions) at the dorsal — sacral "junction", as was noted above. Their absence suggests that they were not co-ossified with the segments behind, and therefore are best considered as the 12th and 13th dorsals. Two co-ossified centra are partly visible behind the acetabulum. These are interpreted here as the 3rd and 4th sacrals (on the dimensional grounds listed above). The next vertebra behind is displaced, turned almost 90 degrees to the sacral and caudal series, and thus clearly not co-ossified with the sacrum. I assume this to be the first of the caudal vertebrae.

Caudal vertebrae: The caudal series is represented by 16 segments, the last seven of which are only impressions. The centra of the proximal caudals are strikingly similar to the dorsal centra; long, slender, slightly narrow-waisted, spool-shaped elements. There are no pleurocoels, and no transverse processes — not even on the most anterior segments. This last feature, is a most unusual condition, and raises questions about the organization of the tail musculature and the function of the tail. It is not certain, but the preserved centra all appear to be amphiplatyan. The centra become progressively longer distally, with the last preserved vertebra (the tenth), the longest. This suggests a very long tail.

All neural arches have been destroyed by a large fracture which follows the course of the caudal series. The neural spines on the first few caudals are taller and narrower (shorter in the anterior-posterior dimension) than those of the dorsal vertebrae, but still are fan-shaped and erect. At the seventh caudal, the neural spine is inclined slightly backward, and succeeding spines slope progressively further backward and are successively shorter until at the tenth caudal only a low nubbin remains.

Chevrons: Chevrons are present throughout the preserved portion of the caudal series. The first is preserved in place between the second and third caudals. All are similar in form and size, with very little apparent progressive diminution distally. They are slender, parallel-edged and slightly curved bones that taper only very slightly toward their extremities. The fact that the most distal chevron preserved (the tenth) is not much shorter than the first, suggests that the tail was unusually long and that the preserved part represents only a small fraction — perhaps less than a third — of the original tail length. This is supported by the relative sizes and lengths of the last preserved caudals and the proximal elements. On the other hand, the complete absence of transverse processes on the caudals could be interpreted as evidence of a relatively short tail, but I consider that unlikely.

Dorsal Ribs.

Cervical ribs: A total of 14 cervical ribs can be identified about the slab. Four of these clearly are paired and situated adjacent to the ventral surfaces of the fifth and sixth cervical vertebrae, presumably close to their natural positions. These seem best interpreted as the ribs of the fourth and fifth cervicals, in view of the fact that there are no ribs closely associated with the next five vertebrae and there are ten similar ribs scattered about in the area of the neck (see Fig. 1). From this scattered occurrence, it is obvious that the cervical ribs were free. All cervical ribs feature broad, triangular proximal portions with widely separated capitular and tubercular heads. Posteriorly, they taper abruptly into long (up to 30 mm or more), hair-like filaments (diameter, 0.2 mm or less). The anterior-most ribs are less delicate and are straight, whereas those that are scattered about (and have been attributed to the posterior cervical segments) are very delicate and distinctly curved. Presumably, this curvature reflects a degree of "permanent" natural curvature of that part of the neck.

Thoracic ribs: One or both members of eleven pairs of thoracic ribs are discernible, either as fragments of bone, or as impressions. In most instances, only the proximal third or half is present, the distal portions having been broken away or obscured by crystal masses in the lower regions of the body cavity. A few fragments of distal portions (fourth and fifth ribs of the left side) indicate the approximate complete length of some. All were double headed, with the tuberculum and capitulum widely separated, the latter at the end of a long narrow process. The rib shafts are slightly curved, tapering abruptly proximally to a nearly uniform thickness over half or two thirds of rib length. The distal third tapers very slightly. The shafts appear to have been oval in cross section and perhaps hollow, since nearly all preserved ribs have collapsed due to compaction into a figure 8 cross section.

Gastralia.

A number of small rod-like bones adjacent to the humerus represent part of the gastralia cuirasse, and marks the position of the ventral surface of the body. Additional displaced gastralia are scattered close to the knee. These last suggest that the ventral body wall ruptured, perhaps due to decomposition gases built up within the body cavity. Further evidence of that is the isolated tiny lower jaw preserved together with these displaced gastralia elements, that presumably belongs to the small skeleton within the body cavity of *Compsognathus*. None of these elements are complete, so original shapes and lengths are indeterminate. Some of them are more than 15 mm long, most are cylindrical or slightly compressed and nearly all are curved, either uniformly or variably. Most elements seem not to have been symmetrical, suggesting that most were lateral (but not necessarily paired) components of a two (or three) rowed structure, perhaps similar to the arrangement illustrated by Lambe (1917) and Gilmore (1920). A few fragments look as though they might have been symmetrical, and thus components of a median row of gastralia. The ventral body wall region has been disturbed by solution and crystal growth, so it is not possible to reconstruct accurately the original arrangement or dimensions of the gastralia cuirasse. It is presumed to have extended from near the sternal region close to the pectoral girdle back close to the distal extremity of the pubis, but there seem to be far too few elements preserved here to form such a long structure. The gastralia close to the humerus seem to be little disturbed, showing that this region was sheathed ventrally by these dermal bones. The displaced gastralia back close to the pubis suggest, but certainly do not prove, that they may have extended this far back.

Appendicular Skeleton:
Pectoral Girdle and Forelimb

Both forelimbs and the pectoral girdle are incompletely represented by impressions and partial or complete elements. Despite being incomplete, most of the important features are discernible. In contrast to the hindlimb, the forelimb total length is quite short, little more than one third (approximately .37) the hindlimb length, unusually short for a "coelurosaur". The forelimb is moderately robust, though.

Pectoral girdle.

As with the pelvis, portions of the pectoral girdle are completely missing or concealed and other parts are represented only by impressions. Only the upper portions of the scapulae and the anterior margins of the coracoids are preserved. Consequently, the morphology of the complete shoulder girdle cannot be reconstructed.

Scapula: The scapular blade was a very thin, narrow sheet of bone slightly expanded at its dorsal extremity. In the lower part, the blade was somewhat thicker and parallel-edged. An impression of the lower part of the right scapula shows a distinct convex dorsal margin which, from its shape and location, is interpreted here as the acromion. If that is correct, *Compsognathus* possessed an unusually large acromion for a theropod. Presumably, this reflects the one time existence of relatively large deltoideus musculature, which would correlate with the robust construction of the forelimb.

Coracoid: Situated at the upper end of the humerus, and lying beneath it, are two very thin, sheet-like fragments of bone. The anterior margins of both are alike and uniformly convex. The margin of the underlying right fragment appears to be continuous with a curved impression margin that extends dorsally and meets the anterior extremity of the acromion mentioned above. This junction presumably marks the position of the coracoid — scapula suture, as in most theropods. Unfortunately, nothing can be determined about the posterior or lateral portions of the coracoid, but what is preserved indicates a relatively large semi-circular anterior portion. The glenoid is completely unknown.

Forelimb.

Humerus: Only the left humerus is present, the right being represented only by an incomplete impression. Unfortunately, the proximal 10 to 20 per cent of the humerus is missing, so no information is available about the nature of the proximal articulation, the deltopectoral crest, or humeral length. I estimate the original length to have been 38 to 40 mm, but it might have been as great as 45 mm. Von Huene (1932) estimated a maximum length of 52 mm, but that seems excessive. In non-tyrannosaurid theropods, the radius ranges from two thirds to three fourths of humeral length. On the basis of the radius length in *Compsognathus* (24.7 mm), the humerus should have been between 32.8 and 36.9 mm long. I suspect it may have been slightly longer. The shaft was hollow (it is now crushed almost flat), straight and probably nearly cylindrical. No details pertaining to the distal condyles, which face down into the matrix, can be determined, but the preserved conformation of the crushed posterior surface suggests that the radial condyle (as usual) was larger than the ulnar condyle. Contrary to von Huene's (1925) remark that the processus lateralis extends two thirds of the length of the humerus[4]), the deltopectoral crest seems to have been quite short. Its preserved length is less than 8 mm (out of a preserved humeral length of 33 mm). This is relatively short compared with other theropods where the deltopectoral crest usually approximates one third of humeral length (much less in ornithomimids), but in no instance that I am aware of, does it reach two thirds. However, in the absence of the proximal end of the humerus, it is quite possible that the deltopectoral crest of *Compsognathus* was of normal proportions.

Radius and Ulna: The radius and ulna are straight, slender bones with slightly expanded proximal and distal extremities — especially the proximal end of the ulna which bears a prominent olecranon. Both bones were hollow and seem to have been nearly circular in cross section. No details of the articulations can be seen. As shown in the table of dimensions, the radius is significantly shorter than the ulna, underscoring the prominence of the olecranon. In fact, relatively speaking, I am not aware of such an elongate olecranon in any other theropod. This must have provided unusual leverage for the M. triceps brachii for quick or powerful extension of the forearm, but it is not clear what adaptive significance this might have had.

Carpus: Curiously, the left manus is preserved separated from the radius and ulna by a gap of more than 6 mm, within which there is no evidence of any carpals. At first glance, this gap might be interpreted

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[4]) Von Huene's statement is here attributed to the possibility that he misinterpreted the anterior portion of the right coracoid (see Fig. 1) as the left deltopectoral crest, but this thin sheet of bone is clearly separate from the humeral shaft, which in fact, overlies it.

TABLE 1

Measurements (in mm) of *Compsognathus longipes.*

Skull length	70—75 est.
Skull width	20 est.
Skull height	30 est.
Orbit length	19 est.
Orbit height	15 est.
Antorbital fenestra	11.8

	Left	Right
Dentary length	42.9	
Surangular length	29.9 +	29.8 +
Scapula length	38 est.	
Humerus length	38—40 est.	
Radius length	24.7	
Ulna length	28.5	
Mtc. I length	17.6	
Mtc. II length	13.95	
Mtc. III length	13.1	
Phalanx I—1 length	7.7	7.8
Phalanx I—2 length	9.6	9.7
Phalanx II—1 length	14.5	14.45
Phalanx II—2 length	10.4	10.4
Femur length		67 est
Tibia length	87.7	87.6
Fibula length		82.1
Pubis length	60 est.	
Ischium length	40 est.	
Mtt. I length		9.7
Mtt. II length	48.8 ?	50.4
Mtt. III length	56.0	55.95
Mtt. IV length	51.8	
Mtt. V length	16.0	15.9
Phalanx I—1 length	8.7	8.8
Phalanx I—2 length		4.5 +
Phalanx II—1 length	14.2	14.3
Phalanx II—2 length	13.7	13.65
Phalanx II—3 length		12.35
Phalanx III—1 length	17 est.	16.9
Phalanx III—2 length		13.65
Phalanx III—3 length		11.5
Phalanx III—4 length		10.2
Phalanx IV—1 length	10.5 est.	
Phalanx IV—2 length		10.6
Phalanx IV—3 length		9.1
Phalanx IV—4 length		10.5 est.
Phalanx IV—5 length		7.1

Vertebral lengths

Vertebral Number

Cervical 1 — —
Cervical 2 — 8.7
Cervical 3 — 9.5
Cervical 4 — 11.0
Cervical 5 — 12.3
Cervical 6 — 12.7
Cervical 7 — 12.7
Cervical 8 — 11.3
Cervical 9 — 10.9
Cervical 10 — 10.9
Dorsal 1 — 9.9
Dorsal 2 — 9.4

Dorsal 3 — 9.8 est.
Dorsal 4 — 9.1 est.
Dorsal 5 — 9.7 est.
Dorsal 6 — 9.9
Dorsal 7 — 10.5
Dorsal 8 — 10.2
Dorsal 9 — 12.2 ?
Dorsal 10 — 10.75
Dorsal 11 — 11.4
Dorsal 12 — 11.5 est
Dorsal 13 — 12 est.
Total sacral length 41.1

Sacral 4 — 8.6
Caudal 1 — —
Caudal 2 — 10.9
Caudal 3 — 11.2
Caudal 4 — 11.5
Caudal 5 — 11.8
Caudal 6 — 12.1
Caudal 7 — 12.6
Caudal 8 — 12.9
Caudal 9 — 13.2
Caudal 10 — 13.3

as evidence of a cartilagenous state of the carpals, but considering the highly ossified nature of the adjacent elements, that seems most unlikely. The right carpal area is concealed. It is certain that carpals were present during life, but whether they are preserved here and can be recognized is another matter. Three objects are present and seem to be of proper size. These are: first, a roughly rectangular impression 3.5 mm in maximum dimension is situated between the impressions of the left radius and ulna; second, there are two equal-sized and similarly shaped objects, one close to the prominent claw at the end of the left hand and the other, an impression, just to the right of the right hand next to the isolated long phalanx impression (see Fig. 1). The location of these three objects in the immediate vicinity of the two disarticulated hands, their size and shape, and the gap at the left wrist, all lead me to the conclusion that they are the missing carpals.

Recognizing the uncertainty of negative evidence, nevertheless, I suggest that the carpus of *Compsognathus* probably consisted of only two carpals because of the presence of only two distinct types among these three objects, and the absence of any other obvious carpal-like objects anywhere else on the slab. Such a wrist condition seems unlikely in view of the carpus construction in other theropods: four carpals in *Ornitholestes* and *Coelophysis* and five in *Allosaurus, Gorgosaurus* and *Ornithomimus.* But *Deinonychus* apparently had only two separate carpals, and *Velociraptor* also may have had only two wrist elements. Not much can be said about the morphology of these supposed carpals in *Compsognathus,* except that they are more or less rectangular, and apparently were relatively thin plates with at least one surface slightly concave.

Manus: In his original description of *Compsognathus,* Wagner (1861) was very careful not to specify the number of digits in the manus, but nearly everyone else who has since written about this unique specimen (Marsh, 1895, 1896; Zittel, 1895, 1911, 1918; von Huene, 1932, 1956; Romer, 1956; Steel, 1970) has specified three functional digits in the hand. I disagree. Both hands are partly disarticulated, but the elements are not widely scattered over the slab. Close inspection reveals that only 14 elements are present, including four claws of two kinds. These are preserved either as impressions or actual bones. Further inspection shows that there are only seven different kinds of elements represented — each of which is duplicated. There are no extra or unmatched bones. In the left hand, there are three relatively long bones, one quite robust, another slightly less robust, and a third that is very slender. On the bases of their location, sizes and proximal articular surfaces, these appear to be metacarpals. They are preserved in the proximal region in both hands. In addition, the left

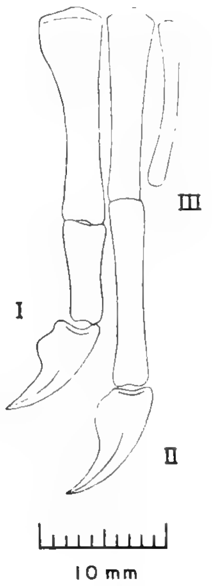


Figure 4: Reconstruction of the left hand of *Compsognathus longipes* in dorsal aspect, according to my interpretation of the hand elements as registered in Figure 1. As explained in the text, it is highly improbable that additional phalanges were originally present, but then lost in the specimen. The reduced formula of II (two phalanges instead of three) is unique, clearly separating *Compsognathus* from all other two-fingered theropods.

hand contains two phalanges of quite disparate lengths and one claw very close to the longer of the two phalanges. These same three elements of the right hand are preserved displaced and separated to the right of the forelimbs. Among the four claws, only two sizes and shapes are present, as is shown in Figure 1 and Plate 9:3 and 9:4.

I interpret the most robust metacarpal as the first, largely because of the basal expansion on one side, which clearly did not adjoin an adjacent metacarpal and therefore must have been either an external or internal surface of the metacarpus. This expansion is quite similar to the basal internal expansion of metacarpal I in *Deinonychus, Velociraptor, Ornitholestes, Struthiomimus* and other theropods, hence I conclude this must be metacarpal I. The very slender element is interpreted as metacarpal III, and apparently was vestigial. That leaves the remaining element as metacarpal II. On the basis of their relative widths proximally, I believe the short phalanx to be the proximal phalanx of the first digit and the long phalanx to be the proximal phalanx of II. Because of the preserved relation in the left hand, I interpret the longer of the two claw types to belong to the second digit. Since there are no unmatched extra phalanges or claws, and it seems highly improbable that only corresponding elements would be missing from both hands, I conclude that there could only have been two functional digits in the hand of *Compsognathus,* plus a remnant (metacarpal) of a third, non-functional digit.

Von Huene (1926) interpreted the hand elements preserved here somewhat differently, apparently believing that some phalanges were missing. In the left hand, he interpreted the long phalanx as the proximal phalanx of digit I, but in the right hand, the impression of the long phalanx, which has exactly the same length and shaft width, he interpreted as the second phalanx of digit II. I consider these to be the same bone (II-1) from opposite hands. He also interpreted the massive broken bone adjacent to the ulna, which has a claw impression apparently articulated with it, as I-1, but its size and position adjacent to the other metacarpals indicate it is metacarpal I. Von Huene's interpretation of the hand has been included in Figure 1, together with mine, because of the importance of evaluating his and my reconstructions of the hand. In my opinion, the organization of the hand, perhaps is the most critical evidence available for judging the proper systematic placement of *Compsognathus.*

I recognize that there may well be several phalanges missing, but this seems highly unlikely since all seven kinds that are preserved are matched by a mate. If any elements are missing, then the same bones would have to be missing from both hands. Thus, the digital formulae appear to have been 2—2—0, with digits IV and V completely lost. The position and very slender construction of the bone that I interpret as metacarpal III, seems to eliminate the possibility of a functional third digit. (It is also possible that this slender metacarpal is the first, rather than the third, but this would be contrary to patterns in all other theropods.)

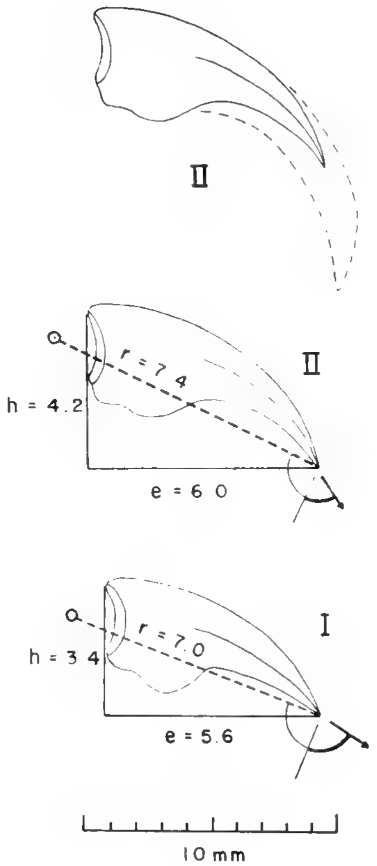


Figure 5: Profile of the first and second unguals of the hand of *Compsognathus* for comparison with the ungual form of other theropods (see Fig. 77, Ostrom, 1969b). The orientation is standard, with the chord of the articular facet arc oriented vertically. This chord has been extended (h = height) to meet a perpendicular (e = extension) from the ungual extremity. The ratios of height to extension (.61 and .70) are relatively low, and the radius (r = heavy dashed line) of ungual rotation has a low inclination similar to that of *Ornitholestes* and *Ornithomimus.* The arrows indicate the projected traces of the inner cutting edges of each ungual compared with the tangents to the arcs of ungual rotation (see Figure 6). — The upper figure shows the bony ungual of the second digit with the outline (dashed line) of the horny sheath (see also Plate 9:5).

If my reconstruction is correct, the hand of *Compsognathus* is unique among theropods, although it is somewhat similar to that of *Albertosaurus (Gorgosaurus), Tyrannosaurus* and *Tarbosaurus.* But unlike these larger theropods with two fingered hands, a complete third metacarpal is present, the second digit is shortened, and the forelimb is not so extremely

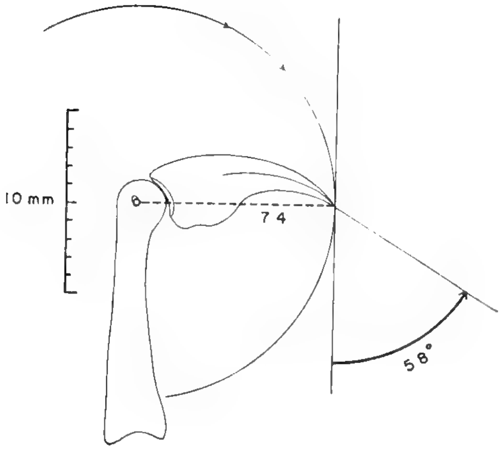


Figure 6: Mechanics of the ungual and penultimate phalanx of the second digit of the manus in *Compsognathus,* showing the angular relationship of the "cutting edge" of the bony ungual to the arc of ungual rotation. This angle is a very large 58 degrees, which compares with the 60 degree angle of the third ungual of *Ornitholestes.* (The "cutting edge" of the horny claw would be much smaller, and thus more efficient, as can be judged from the upper figure of Figure 5, but since the horny claw is so rarely preserved, I apply this technique to the bony ungual for comparsion with other theropods.) The large "cutting angle" in *Compsognathus* suggests that the hand claws were less suited for cutting or piercing than were those of *Deinonychus,* or even *Allosaurus* (see Fig. 78, Ostrom, 1969b).

shortened in *Compsognathus.* In another respect, the hand of *Compsognathus* resembles that of ornithomimids (and *Deinocheirus*), with its three similar lengthed metacarpals. In all other theropods, the first metacarpal is much shorter than the second.

Another interesting aspect of the hand is the design of the terminal phalanges. The claw of the second left finger is particularly well preserved (see Plate 9:5), including parts of the horny sheath that covered the bony ungual. The latter was about 50 per cent longer than the supporting ungual. In my *Deinonychus* study (Ostrom, 1969 b), I utilized a number of parameters by which claw shapes could be compared and described. Applying these parameters to the bony unguals of *Compsognathus,* reveals that they are not strongly curved as compared with some other theropod manual unguals. They have only a moderately high ratio of height to extension and a short height relative to the radius. This suggests to me that the manual claws were not purely raptorial or grasping, and certainly not piercing or cutting structures. This interpretation seems to be substantiated by the angular relationship between the ventral "cutting" edge of the ungual tip and a tangent to the arc through which the ungual tip passed during flexion against the proximal phalanx (Fig. 6). This angle is a large 58 degrees. In all these parameters, the bony claws of *Compsognathus* most closely resemble that of digit III of *Ornitholestes hermanni* (A. M. N. H. 587). Compare these features of *Compsognathus* (Fig. 5 and 6) with those of Figures 77 and 78 in Ostrom, 1969 b.

Appendicular Skeleton: Pelvis and Hindlimb

Although neither one is completely preserved, the hindlimbs are one of the most distinctive features of *Compsognathus,* being very robust and surprisingly long. With a total length of more than 27 cm, the hindlimb is much more than twice the length of the forelimb, and is at least 10 per cent longer than the presacral vertebral length. *Compsognathus* was a very long-legged creature. The pelvis is less complete, but what is preserved is of typical theropod organization.

Pelvis.

The pelvis has suffered extensive post-preservational damage, particularly to the ilia. All elements were originally present in natural articulation, but now most of the left ilium is missing and only the impression of the upper border of the right ilium remains, the shaft of the left pubis is broken away and only the ischia are still nearly intact. The pelvis was of normal theropod design with the ischia projecting down and to the rear and the pubes extending antero-ventrally.

In past years, no special attention to pubic — ischiadic orientations would have been considered necessary in describing a theropod pelvis. But several recent discoveries have changed all that. The Harvard specimen of *Deinonychus* (Ostrom, 1976 a) clearly shows that in that taxon (at least), the pubes projected downward and slightly — or perhaps sharply — backward, perhaps even parallel to the ischium. Barsbold (pers. com.) has reported that in *Velociraptor* the pubes project backward parallel and immediately adjacent to the ischia. A similar, bird-like pubic arrangement also appears to have been present in *Oviraptor* (Barsbold, pers. com.). No such ornithic pelvic traits are evident in the *Compsognathus* remains.

Ilium: From the fragmentary evidence pertaining to the ilia, these bones appear to have been quite long (between 5 and 6 cm)., shallow in height, and positioned quite close to the mid-line. The impression of the upper border of the right ilium gives the best evidence of length and shape. It shows a nearly straight, but gently convex upward profile, the highest point of which occurs above the level of the sacral neural spines. The original length of the ilium is indeterminate, but the anterior process appears to have been slightly longer than the posterior iliac process. The original shapes of these processes are unknown.

Pubis: The pubes have been slightly displaced from each other, with the left pubic shaft represented only by an incomplete impression, and the right shaft by several massive fragments. The incomplete proximal portion (of the left pubis) is massive in its construction, presumably for robust articulation with the ilium. Distally, the pubes narrow abruptly into slender, oval-in-section shafts, which join each other just above mid-length in a very narrow symphysis. The fused, distal extremities, are expanded longitudinally into the typical foot-like structure of all theropods. Due to breakage, the exact size and shape of this pubic "foot" is not determinate, but the preserved portion of the anterior part suggests that there was very little (if any) projection of this expansion anterior to the pubic shaft, as there is in most theropods (see *Struthiomimus, Deinonychus, Tyrannosaurus, Allosaurus,* for example).

Ischium: The two ischia are preserved together, one overlying the other. They are the best preserved elements of the pelvis. Compared with the long pubes, the ischia are surprisingly short — reminiscent of the condition in *Deinonychus* (Ostrom, 1976 a), although not so extreme. The proximal region is expanded dorsally and anteriorly for union with the ilium and pubis. Below this, the body of the ischium narrows markedly, with the anterior and upper margins distinctly concave. The anterior margin then expands forward into a delicate, sharply pointed obturator process, which is much more delicate and sharply tapered than in any other presently known theropod. From this process, the ischium tapers sharply backward into a narrow cylinder with a slight distal expansion. Because they are slightly displaced (as preserved), the underlying right ischium clearly reveals the symphysial suture surface extending over the ventral ischial length from the obturator process to the posterior extremity. The overall shape of the ischium — plate-like proximally and rod-like distally — most closely resembles that of *Tyrannosaurus,* differing only in the longer taper of the obturator process, the slighter distal expansion, and of course, in size.

Hindlimb.

Femur: Neither femur is complete, so few anatomical features can be reported. Fragments of the proximal end of the left femur (and the dorsal rim of the acetabulum) mark the upper extremity and the impression of the proximal end of the left tibia permit a reasonable length estimate (75 mm) for the femur. This estimate is corroborated by the preserved location of the distal end of the right femur, approximately 70 mm distant from the acetabulum. The clear impression of the left femur shows a rather thick, cylindrical shaft with slight antero-posterior curvature. No clear imprint or other evidence of a fourth trochanter is discernible in this impression. The splintered and incomplete shaft of the right femur shows that the femora were hollow, and nearly circular in section. The most distinctive aspect of the femur, though, is its surprisingly stout or robust proportions.

Tibia: The tibia is slightly less robust, but much longer than the femur. It too is hollow and circular in section (as evidenced by the shaft impressions). The proximal ends of both are missing or incomplete, so the nature of the articular surfaces and the cnemial crest cannot be determined. But the distal end of the left tibia, and a good impression of that of the right, show some of the details of the tibia-tarsal construction. In contrast to the femur, the tibia is straight-shafted.

Fibula: The right fibula has separated completely from the tibia, showing that these elements were not fused at any point along their lengths. The fibula is an extremely slender long bone with a strongly concave medial shaft surface for close apposition against the tibia, and an equally convex external surface. The left tibia shaft shows a very narrow, faintly flattened strip along its antero-external surface, marking the area of fibular contact. Proximally, the fibula flares into a very broad (antero-posteriorly) head for articulation against the femur, while distally it is only slightly enlarged into a short rounded articular surface for union with the calcaneum. The most distinctive thing about the fibula, is its extremely slender shaft, which is in sharp contrast to the robust shaft of the tibia.

Tarsus: The tarsus clearly was of mesotarsal design, but unfortunately the exact details are no longer determinable. The distal extremity of the left tibia is present, more or less intact, showing its external aspect, including the extremity of the fibula next to it and a "proximal tarsal" in natural articulation closely appressed against the end of the tibia. The surprising feature of this left tarsus is the large anterior-posterior dimension of the "proximal tarsal", which is almost twice as broad as the fibular extremity. The impression in the matrix of the external surface of of the right tibia extremity seems to show the same condition — a very large (antero-posteriorly) "proximal tarsal" with a strongly rounded distal profile. The only difference here is that the right fibula is displaced, thereby revealing an underlying "ledge and shelf" articulation of this tarsal with the distal surface of the tibia (see Fig. 1). Unfortunately the anterior surface of the right tibia is poorly exposed, but what can be seen does not show an ascending process of the astragalus — this large "proximal tarsal".

Wagner (1861) made no mention of the tarsus, except to say that it was short, and Marsh (1895, 1896) gave no detailed description or illustration, but Baur (1882) described and figured a fragment of the distal end of the right tibia which he removed from the specimen. Most unfortunately, this fragment, apparently with tarsal elements attached, no longer exists. Thus we are forced to rely on Baur's interpretations and illustrations, with no means of checking them. Furthermore, these illustrations (1882: Figs. 42 and 43) and descriptions are not as clear as we might like. For example, the lateral surface of Baur's fragment does not correspond with the impression left in the matrix, nor does it match the exposed lateral (equivalent) surface of the left tibia and tarsus, which are still present. The large, rounded "proximal tarsal" is not present in Baur's illustration, nor does he show any scar or articular facet for this element — which is most conspicuous on the left side. But perhaps the most important detail of Baur's paper is his interpretation of a narrow ridge-like feature that extends along his "anterior" surface of this now-lost tibial fragment. He identified this as the "Tibiale-aufsteigende Fortsatz" — the ascending process of the astragalus. I would accept this interpretation except for the fact, noted above, that Baur's figures do not match the preserved parts of the left leg, or the impression of the right — from which the missing fragment purportedly was removed.

Only two options are open to us. We either accept Baur's interpretations on faith, for they cannot be verified now, or we conclude that the construction of the tarsus in *Compsognathus* cannot be established in this specimen. It must be noted, however, that Baur's reconstruction of the astragalus is consistent with those known in other theropods.

But a nagging question remains: What is the large proximal tarsal? Is it the calcaneum, which it appears to be? If so, it is unusually large. Moreover, its relationship to the tibia is unusual for a theropod in that it clearly articulates with the distal surface of the tibia and not just its lateral surface, as in most theropods. This is quite evident in the impression of the left tarsus. But, on the other hand, it also clearly articulated with the fibula. If Baur (and Marsh) was correct in his interpretation, then it probably is the calcaneum. But at this point, I am not sure whether it is the calcaneum, the astragalus, or the lateral part of a fused astragalo-calcaneum. One thing is certain, though: the mesotarsal condyle of this proximal tarsal extends far in front of the anterior surface of the tibial shaft, much more than in any other theropod known to me. This would seem to indicate an unusually high degree of extension was possible at the ankle.

Baur (1882) detected three distal tarsals, which he labeled tarsals 2, 3 and 4—5. The latter is clearly recognizable as a flat disc closely articulated with the proximal end of the left metatarsal IV (see Pl. 10:1). It does not appear to have been co-ossified with the metatarsal, but it may have been. The other two tarsals identified by Baur, are preserved as impressions and are not so unequivocal. As noted by Baur, the impression of the right metatarsus seems to show two convex cap-like elements at the upper extremities of metatarsals II and III. But in the left metatarsus, these same features appear to be just the proximal convex extremities of the two metatarsals. No clear suture or physical discontinuity separates these ends from the metatarsal shafts, but then the tarsals and metatarsals might have been fully co-ossified. Molds made of the impressions of the right metatarsus show the same condition, hence, if these two features are in fact distal tarsals, they were completely co-ossified with metatarsals II and III. Since at least two distal tarsals, and usually three, are found in all other adequately known theropods, I strongly suspect that this last condition is the correct interpretation, but it must be pointed out that the present specimen does not permit certification.

Pes: The pes is greatly elongated, with the metatarsal length somewhat greater than the median toe

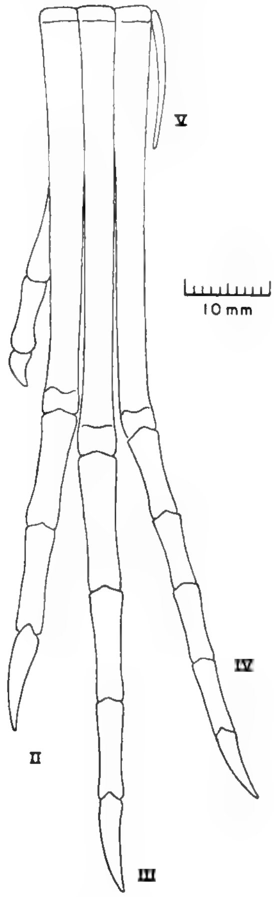


Figure 7: Reconstruction of the left foot of *Compsognathus longipes* in dorsal or anterior aspect. Notice the great length and very slender design, reminiscent of *Archaeopteryx* and later birds, and suggestive of high cursorial ability.

length. The central metatarsals (II, III, and IV) are stout and closely appressed together. Their respective lengths, where determinable, are given in the table of dimensions. Metatarsal I consists of a stout wedge-shaped bone fixed against the posterior surface of the shaft of metatarsal II just below mid-length. Its upper end fails to reach the tarsus by more than 20 mm, and there is no sign of a proximal portion, as has been found in *Allosaurus* (Gilmore, 1920; Madsen, 1976). The fifth metatarsal is a slender curved splint-like bone extending some 15 mm from the tarsus down the postero-lateral aspect of metatarsal IV. There are no distal elements of digit V. All of the first four metatarsals have well-developed distal ginglymoid facets and deep collateral ligament fossae, indicative of strong, precise toe actions, and perhaps cursorial habits (Plate 10:1).

The foot digits have the normal theropod formulae (2-3-4-5-0) and show the usual proportions, with the third toe the longest and II and IV somewhat shorter and nearly equal in length, and the first toe extremely short (it does not even reach the lower end of metatarsal II), and reverted to the back. The hallux ungual is preserved oriented like those of the other toes. However, this seems to be an artifact, as the proximal phalanx and the ungual obviously have been rotated about their long axes by more than 90 degrees, as is evidenced by the disparate orientations of the collateral ligament fossae on metatarsal I and the proximal phalanx of the first digit. (The penultimate phalanx of digit III has been similarly rotated about its long axis by about 180 degrees, without separation from adjacent phalanges: see Plate 10:2.) All pedal phalanges are quite robust, with pronounced collateral ligament fossae and strongly ginglymoid distal articulations. Where observable, the proximal phalanx always is the longest element in each toe. The unguals are obviously straighter than those of the manus, and broader, with a more triangular cross-section and less pronounced flexor tubercles. The ungual of digit I is very short and stubby, suggesting an almost vestigial state.

Mystery Bone.

There are a number of bone fragments, especially in the area around the skull, that I have not been able to identify with certainty. Most of these are too fragmentary, or contain no diagnostic features. One bone, however, appears to be complete, and does have distinctive features. Yet, I have not been able to identify it. This mystery bone (Plate 10:4) lies quite isolated, well above the skull and close to two cervical ribs. It is roughly quadrangular in shape, with a rounded articular process at one end. At first glance, it resembles the proximal end of a dicocephalous rib, with the articular process the capitulum and the adjacent "shoulder" the tuberculum. However, the other end, which is only 4.5 mm distant, is not a broken end, but rather is a distinct articular surface. The total length of this object is 5.85 mm, and its maximum and minimum widths are 3.8 and 2.4 mm, and it is complete. Its form does not match any bone that I am familiar with, and I have no suggestions other than that it may be a cranial element — perhaps the ectopterygoid.

SUPPOSED SKIN-ARMOR OF *COMPSOGNATHUS*

Von Huene (1901) made much of a series of surface irregularities, which he described as polygons, in the prominent depressions along the ventral regions of the trunk and abdomen. In the circular depression between the scapula and the left humerus, he claimed that 15 "polygons" could be seen, most of which were six-sided. In the oval depression just behind this, he saw impressions of 10 more similar but larger polygons arranged in rows. Because of their shape, and what he termed their regularity of arrangement, he concluded that these surface impressions were evidence of horny skin armor in *Compsognathus*. Von Huene acknowledged that no such plates are preserved along the back, where we would most expect skin armor, but he did claim that the neural spines of the trunk and tail are elongated lengthwise and strongly thickened transversely in their upper edges, forming a row of broadened platform-supports for the (missing) dorsal scutes. In support of this inaccurate description (the dorsal neural spines are not thickened distally) and supposed dorsal armor plates, Huene alluded to the dozen or so irregularly shaped bony ossicles found associated with some of the caudal neural spines in *Ceratosaurus* (U. S. N. M. 4735), reported by Gilmore (1920), as evidence of dermal armor in theropods. Nopcsa (1903) rejected both of these interpretations of Huene's, but interpreted other features as evidence of skin and muscle impressions.

I have examined the areas on the *Compsognathus* slab specified by von Huene under high magnification and various lighting conditions and have concluded that his evidence is very doubtful. As I have attempted to show in Plate 11:1, the surface configuration in these areas is unusual and different from that of other areas on the slab. But I do not see any consistent regularity of form or arrangement in any of the sites mentioned by von Huene. It is evident, though, that the regions concerned with von Huene's "polygons" have been subjected to a very different history of solution and precipitation than other regions of the specimen. First of all, there are the peculiar depressions along the ventral part of the body of *Compsognathus,* with their irregular "hummocky" surfaces that appear to have been etched into the matrix. This is in sharp contrast to the usual, very smooth, planar, and sometimes almost glassy surfaces characteristic of other parts of the slab. Secondly, throughout these "etched depressions", there are irregular masses of very fine druzy crystals, mostly of calcite, but also (surprisingly) some of quartz. In some places it can be seen that these masses of druzy crystals coincide with the borders of the so-called "polygons", suggesting that these polygonal patterns reflect some aspect of crystal growth rather than impressions of skin armor. The general appearance of the ventral part of the body region and the area anterior to the sacrum, is that of a series solution cavities — vugs — dissolved into this slab along the bedding plane containing the skeleton of *Compsognathus.* This solution must have occurred long before the slab was excavated. Following formation of these solution cavities, masses of druzy calcite and occasional quartz crystals formed along the walls of these vugs, as they did within the hollow limb bones. In short, the hummocky "polygon" surfaces are the result of differential solution.

Further evidence in support of this explanation is the fact that the *Compsognathus* slab is traversed by a number of fractures. One prominent fracture extends the length of the trunk and abdomen of *Compsognathus* (see Plate 7), directly through the series of "etched" depressions or solution cavities, then follows along the trace of the tibia and across the left foot. A second fracture branches off this first one in the abdominal region and extends up through the "solution" cavity at the anterior part of the sacrum and then follows along the course of the caudal vertebrae. Throughout almost the entire courses of these fractures, the fracture edges are rounded — clear evidence of solution. This is especially evident in the trunk and abdominal regions and along much of the caudal series. Several other fractures present on the slab are characterized by sharp edges, and apparently are of more recent origin, not having been subjected to solution.

I suggest that prior to its excavation, the *Compsognathus* slab was situated quite close to the surface where it was subjected to solution by periodic ground water percolations through these fractures. Solution and subsequent crystalization resulted along parts of these fracture traces, resulting in crystal-lined vug-like cavities on this slab, and thus von Huene's "skin armor" is nothing more than the etched walls of these solution cavities. That these "polygon"-lined cavities are secondary in origin (contrary to von Huene's interpretation) is clearly established by the unexpected presence of tiny, well-formed quartz crystals scattered about on these vug walls. Hückel (1974) reported the quartz content of the Solnhofen limestones varies up to a maximum of 0.4% of total matrix, the quartz occurring in the form of sponge spicules, tiny well-rounded grains and rare perfect crystals. Barthel (1976) found the rounded quartz grains (usually less than 10 microns) to be widespread in the Solnhofen deposits and concluded that they were eolian in origin. The unabraded crystals, however, must be autogenic, and most probably post-diagenic crystallization derived from sources external to the Solnhofen matrix and introduced via bedding planes and fractures, such as described above (see Plate 10:6).

Nopcsa (1903) dismissed von Huene's "skin-armor" for much the same reasons, but maintained that skin impressions and traces of muscle fibers were preserved in several areas around the skeleton of *Compsognathus.* His "skin impressions" are curious, finely granular textured areas, and his "muscle fibers" occur as faint traces of "parallel irregular fibers" at several locations (but not every where he mentioned). Nopcsa illustrated both of these features in a drawing of *Compsognathus* (1903, Plate XVIII).

The granular texture is very evident throughout most of the rib cage (except within the polygon-lined depressions discussed earlier), between the femora, around the skull and especially close to the left humerus (see Plate 11:3). The contrast between this granular-textured surface and the more normal surface texture typical of other areas on the slab, is shown in Plate 11:4. Nopcsa may have been correct in his interpretation of this feature, but I have serious doubts. First of all, this granular texture occurs over much of the orbit! — as well as within the open jaws, areas that I would hardly expect to find scaly integument. Moreover, this same texture is present, perhaps less distinctly, surrounding all scattered and isolated bones and is not confined to the general region of the body. For example, it is quite clear in the areas surrounding the several scattered phalanges of the hands, as well as around the displaced cervical ribs. Obviously, this is not consistent with the integument explanation, but suggests that the bones themselves are the controlling factor in the distribution of this curious textural pattern. I suspect that this texture is also the result of solution etching along the bedding plane and is localized around three-dimensional objects lying on that plane. Evidence for that is the presence of what appears to be the same texture surrounding some of the specimens of the small crinoid *Saccocoma.* Notice that this granular texture is most prominently developed around the skeletal remains and *Saccocoma* specimens that are situated closest to the fractures that served as solution channels. Also notice that this texture seems to grade imperceptibly into normal surface textures, rather than an abrupt transition at well-defined boundaries. The organic objects on this slab appear to have acted as centers of solution and / or chemical activity, resulting in this granular-textured surface. Whatever its origin, though, the integument theory of Nopcsa does not explain its occurrence around the specimens of *Saccocoma.*

Concerning the "parallel and irregular fibers" seen by Nopcsa, I must admit that I was unable to see most of the examples he cited (Nopcsa listed seven specific areas in which these were present). The "fibers" between the femur and ischium, and between the femur and tibia, and those along the base of the tail, simply are not there! Nor are "fibers" evident above the dorsal vertebrae, near the cervicals, or distally along the tail. A striated or linear textural pattern does occur proximally at the lower edge of the ischium, and also between the right radius and ulna (see Plate 11:2). In both of these sites, the striations are parallel to the adjacent bone edges. There also appears to be a very faint lineation along the dorsal region of the proximal caudals close to the tip of the right dentary. Nopcsa's "fibers" may well represent impressions of soft tissues, including muscle fibers. Such occurrences are not uncommon in Solnhofen specimens. Most notable are the feather impressions in the several specimens of *Archaeopteryx* and wing membrane impressions in numerous pterosaur specimens (but see also Reis, 1893). However, I am inclined to think that these striations are merely lineated granular texture etched into these surfaces, with the lineations being due to the local influence of the adjacent parallel bone margins.

COMPARISON WITH OTHER SPECIMENS REFERRED TO *COMPSOGNATHUS*

At the present time, only two other specimens have been recorded in the literature as possibly referrable to *Compsognathus.* The first of these consists of three metatarsals and a single phalanx, now in the Humboldt Museum für Naturkunde, East Berlin. The second is a nearly complete skeleton, *Compsognathus corallestris,* from Portlandian limestones of southern France. This specimen is in the Muséum d'Histoire Naturelle of Nice, France.

The Humboldt Specimen.

This specimen was first reported by Dames (1884) and has been cited subsequently by von Huene (1925, 1926 and 1932) as questionably referrable to *Compsognathus.* As shown in Plate 10:5, the specimen consists of four bones, three of which appear to be metatarsals and the fourth a proximal phalanx. These are preserved on counterpart slabs. First of all, it is important to mention that it is impossible to determine from these remains the exact nature of the complete metatarsus — whether it was composed of three, four or five metatarsals. So it is not possible to say which metatarsals are preserved here (and indeed whether these are metatarsals rather than metacarpals). The specimen is preserved with the shortest bone in the middle, a condition not known in the metapodials of any tetrapod, but Dames concluded (correctly, I think) that the longest element had been displaced and interpreted the three as follows: mtt. I = 54 mm; mtt. II = 60 mm; mtt III = 68 mm. This configuration does not correspond with the metatarsus of *C. longipes,* and on the basis of other tetrapod metatarsal construction, implies that a fourth, and perhaps a fifth metatarsal are missing. In *C. longipes,* metatarsal I is incompletely formed, and metatarsals II, III and IV have lengths respectively of 50.4, 56.0 and 51.8 mm.

If we assume that the three long bones of the Humboldt specimen are metatarsals II, III and IV, and that the longest element is metatarsal III (as in *Compsognathus),* the relative lengths do not compare closely with those of either *C. longipes* or the Nice specimen (both of which are close in these proportions. A comparison of metatarsal ratios in the three specimens is as follows:

	C. longipes	*Nice specimen*	*Humboldt specimen*
Mtt III / Mtt II	— 1.11	1.14	1.27
Mtt III / Mtt IV	— 1.08	1.12	1.13
Mtt IV/ Mtt II	— 1.03	1.02	1.11

Considering the fact that the Humboldt specimen is intermediate in size between the Nice specimen and *C. longipes,* these ratios suggest that the Humboldt specimen is not referrable to *Compsognathus,* the same conclusion reached by Dames. The longest bone is too long relative to the others. This conclusion seems to be reinforced by the single phalanx that appears to be articulated with the shortest of the three metatarsals (II ?). If that articulation is correct, then its length (20 mm) is much greater relatively than that of the proximal phalanx of the second toe in *C. longipes.* Consequently, my conclusion is that the Humboldt specimen is not assignable to *Compsognathus longipes.*

TABLE 2

Comparative Anatomical Dimensions of *Compsognathus longipes*
(Dimensions in mm.)

	Type specimen	Nice specimen (C. "*corallestris*")	C. c. / C. l.*
Skull length	70—75 est.	110 est.	1.42
Orbit length	19 est.	27 est.	1.52
Humerus length	38—40 est.	67 est.	1.76
Radius length	24.7	42	1.70
Ulna length	28.5	45	1.57
Scapula length	38 est.		
Femur length	67 est.	110	1.49
Tibia + astragalus	87.7	135.5	1.54
Fibula length	82.1		
Mtt. II length	50.4	70.5	1.39
Mtt. III length	56.0	81.0	1.44
Mtt. IV length	51.8	72.0	1.39
Pubis length	60 est.	95 est.	1.58
Ischium length	40 est.	70 est.	1.75
Hindlimb length	264	377	1.42
Forelimb length	102	?	
Hand length	39	?	
Presacral column	236	310 + two = 342	1 44
	Anatomical Proportions		
Femur / Tibia	.76	.81	
Mtt. III / Tibia	.64	.59	
Humerus / Femur	.56	.61	
Humerus / Tibia	.43	.50	
Forelimb / Hindlimb	.38		
Skull / Presacral	.30	.32	
Forelimb / Presacral	.43		
Hindlimb / Presacral	1.11	1.10	
Skull-Orbital-Length Index	26	24	

* Ratio of *Compsognathus "corallestris"* / *Compsognathus longipes.*

The Nice Specimen.

In 1972, Bidar, Demay and Thomel reported the discovery of a nearly complete skeleton of a small theropod from Portlandian lithographic limestones (Petit Plan) at Canjuers, some 60 km west of Nice, which they assigned to a new species, *Compsognathus corallestris.* This new specimen (see Plate 12) is extremely similar anatomically to *C. longipes,* but is approximately 50% larger. It also is preserved in a pose that is astonishingly similar to that of the Munich specimen, including the parallel flexed hind legs, the upswept tail, the 360 degree opisthotonic arc of the cervical series, the severed head in an upside down position pointing backward, and even the presence of stomach contents within the rib cage. So remarkably similar are the positions of the two skeletons, one cannot help wondering if this represents some obscure clue about the living habits of these specimens.

I was fortunate to be able to examine the Nice specimen in some detail in 1973, thanks to the kindness of Dr. Demay. It is not my intention here to give a full analysis of this specimen, the original authors have provided that. However, I think it is necessary to examine the criteria they adopted in establishing a new species.

In their diagnosis of *C. corallestris,* the authors emphasized the larger size of this specimen and cited varying size differences between corresponding elements as rationale for the establishment of a new species. Another key factor was their interpretation of the forelimb as a flipper-like appendage. In Table 2, I have listed a number of dimensions that are available from both specimens, together with some estimated dimensions, and calculated the ratios of *C. longipes* to *C. corallestris.* The dimensions given are mine, and in a few instances they differ from those given by Bidar, Demay and Thomel. All measurements given in this report were made by me (unless otherwise indicated), with a Helios dial caliper with scale divisions to 0.05 mm. The data in Table 2 show that the various skeletal elements of *C. corallestris* range from about 40 % to 75 % larger than the corresponding element of *C. longipes*. Apparently, it was this varying difference that led the authors to conclude that the Nice specimen was distinct from *C. longipes* (together with the flipper forelimb). But these varying differences might simply reflect differing allometric growth of different parts of the skeleton, and thus are not reliable criteria for establishing a new taxon — especially since there are only two specimens available for comparison.

Unfortunately, their interpretation of the forelimb as a flipper-like structure is also highly questionable. The forelimb of the Nice specimen is very poorly preserved. In fact, it is so poorly preserved that it is extremely difficult — indeed impossible — to decipher the various components with absolute certainty. Most of the forelimb elements are represented by impressions only, many of which are indistinct, and their identities doubtful. The construction of the metatarsus and manus are entirely unknown. Finally, their evidence for a flipper consists of several "wrinkle-like" linear undulations paralleling the forelimb along its anterior margin. These surface features might represent the impression of soft parts, but it certainly does not look that way to me. Moreover, similar "wrinkle-like" surface irregularities occur further up on the slab which *continue the same exact trace* as their "flipper imprint". These can be seen extending away from the loop of cervical vertebrae, to the left and almost parallel to the lower jaw. This "wrinkle" along side the forearm, thus seems to be part of a much longer linear trace that extends well beyond the skeleton and therefore cannot be part of the specimen at all. I consider the flipper interpretation of the forelimb by Bidar, Demay and Thomel to be poorly founded and highly improbable. (See Plate 12.)

Beyond the size differences and the questionable flipper like forelimb, a considerable volume of anatomical evidence raises serious question about the validity of *Compsognathus corallestris*. In short, the two specimens are nearly identical, within the limits of imperfect preservation. In the skull, corresponding available elements, such as the premaxillae, maxillae, lacrymal, are the same. The dentaries also are alike, being long, very narrow and parallel-sided. The chief difference between the tooth-bearing elements of the two specimens is the greater number of teeth that are preserved in place in the Nice specimen, but I have already remarked about the numerous displaced teeth in the Munich specimen. Concerning the teeth, of particular importance is the "bent" shape of the anterior teeth of the premaxilla and dentary that is so distinctive of *C. longipes*. The same tooth form is present in the Nice specimen.

Because of the poor preservation of the forelimb in the Nice specimen, no comparison with *C. longipes* is possible. But the hind limbs are comparable, and the striking similarities are most obvious, down to the detailed construction of the pes and even the identical form of the metatarsus — including the shape of the vestigial fifth metatarsal. In the pelvis, the ischium is exactly the same in both (the authors clearly misinterpreted the lower ischial margin, placing it much too low), with a narrow, slightly club-ended posterior extremity and an anteriorly placed, delicate, triangular obturator process. The pubis, contrary to their statement, is not much longer relatively than it is in the genotype specimen. As in the Munich specimen, the pubis is about the same length as the femur (notice that the distal extremities of the pubis and femur coincide in both specimens). Furthermore, although Bidar, Demay and Thomel reconstruct a much longer distal pubic "foot" than I believe is warranted by the specimen, the overall shape is very much like that in *C. longipes*, with long narrow cylindrical shafts and a large distal expansion. The ilium too, was long and low, as in *C. longipes* although no further comparisons can be made since only the upper margin is preserved in the type specimen. Finally, there are no distinctions preserved in the cervical or dorsal vertebral column that justify specific separation of these specimens, whereas the proximal caudals are virtually identical, with low neural spines and an absence of transverse processes. Even the chevrons are the same in both specimens.

On the bases of all these striking anatomical similarities, I see no justification for placing the Nice specimen in a separate species, especially considering the very doubtful nature of the criteria cited by the authors as their rationale. Accordingly, I consider the binomial *C. corallestris* to be a junior synonym of *Compsognathus longipes*, and refer the Nice specimen to that taxon.

Casamiquela (1975), described a very fragmentary specimen from the Middle Jurassic Lotena Formation (Callovian) of Neuquen Province, Argentina, which he referred to the Family Compsognathidae and assigned to a new genus and species, *Herbstosaurus pygmaeus*. The specimen consists of impressions or fragments of a sacrum, the right ilium and ischium, both femora a phalanx, and other unidentified fragments. Unfortunately, it is difficult to identify with certainty the several elements that are illustrated in the two unlabeled photographs of Casamiquela's report. However, if the lowermost long bone on those two photographs is a femur (as I believe the author interpreted it to be), then this specimen almost certainly can not be referred to any presently known theropod species because the "shaft" of that bone curves in the transverse plane of the medially directed "femoral head", rather than in a para-sagittal plane as in all theropods. On that basis alone, I consider it highly unlikely that *Herbstosaurus pygmaeus* is closely allied with *Compsognathus*, or with any other theropod. (I suspect that this specimen may actually be pterosaurian, because of this unusual design of the "femur", plus the long and unusually shallow form of the ilium — an opinion that is shared by J. F. Bonaparte [personal communication]).

THE SUPPOSED EMBRYO WITHIN *COMPSOGNATHUS*

The Munich specimen of *Compsognathus* is remarkable in a number of features — its small size, completeness, quality of preservation and certain bird-like characters —, but perhaps the most remarkable feature is the tiny skeleton of a small reptile well-preserved within the rib cage of *Compsognathus.* In some ways, this tiny skeleton is one of the most important features of this specimen, for it either demonstrates viviparity in theropods (as Marsh claimed), or it provides direct evidence of feeding habits. Marsh (1881, 1883, 1895, 1896) was the first to notice the presence of this small skeleton and promptly concluded that "This unique fossil affords the only conclusive evidence that dinosaurs were viviparous." (My emphasis.) A few years later, Nopcsa (1903) discussed these important "gastronomic" remains at some length and provided the first illustration (1903, Plate XVII). He concluded that this small skeleton probably was not an embryo on the following grounds:

1) The estimated length of 8 cm was too large for the body cavity of *Compsognathus* which could not have been more than 11 cm in length.
2) The proportions of femur to tibia.
3) The proportions of humerus to lower jaw.
4) The position of the tail and hind foot.
5) The shapes of the upper and lower jaws.
6) The shape of the pelvis.
7) Single headed ribs.
8) The strongly ossified and well-formed articulations. Nopcsa concluded that this specimen probably was lacertilian.

I arrived at the same conclusions prior to reading Nopcsa's paper, for most of the same reasons, plus a number of others. I did not arrive at a definite identification until somewhat later, but at this point it can be stated quite categorically that the small skeleton within the rib cage of *Compsognathus* is positively not an embryo, or even a young individual of *Compsognathus.* In addition to Nopcsa's points (with the exception of # 3, which cannot be determined precisely in *Compsognathus*, and # 4, which is of no significance), the following features preclude this specimen being an embryo:

1) The large astragalo-calcaneum.
2) Long transverse processes on the proximal caudals.
3) Lepidosaurian design of the distal end of the humerus, with pronounced entepi- and ectepicondyles.
4) The very robust fibula.
5) Only two sacral vertebrae.
6) Autotomous caudal vertebrae.

In Figure 8, I have recorded the distribution of these remains, together with my identifications. The only important differences between Nopcsa's interpretations and mine, are his failure to recognize some elements of the left foot, fragments of the right tibia and fibula, the right astragalo-calcaneum, and his mistaking the right metatarsus for a metacarpus.

The prey object lies on its left side, with its head-end pointing toward the rear of *Compsognathus.* That it actually lies within the rib cage of *Compsognathus* is certain, as can be seen in Plate 13, which shows it overlying the right ribs of *Compsognathus* and overlain by the left ribs. Included are at least nine dorsal vertebrae, 11 pairs of dorsal ribs, the left humerus, parts of the pelvis, the entire left hindlimb and parts of the right, plus an extremely long caudal series including at least 50 segments. Lying out side of the body cavity of *Compsognathus,* is a left mandible which also probably belongs to this specimen. Nopcsa also identified a triangular impression just above this jaw and anterior to the right femur of *Compsognathus,* as a maxilla, but I am very doubtful of this identification — at least as the specimen now exists. The dimensions of the various elements of this tiny skeleton are given in Table 3.

The rib cage and dorsal vertebrae are little disturbed, although details of the vertebrae are difficult to interpret. The ribs themselves are robust, surprisingly so for such a small individual, but most distinctive is their single-headed articulation with the vertebrae. The sacrum consists of two, apparently co-ossified segments clearly discernible between the last rib-bearing vertebra and the first vertebra behind with elongated transverse processes. The proximal caudals

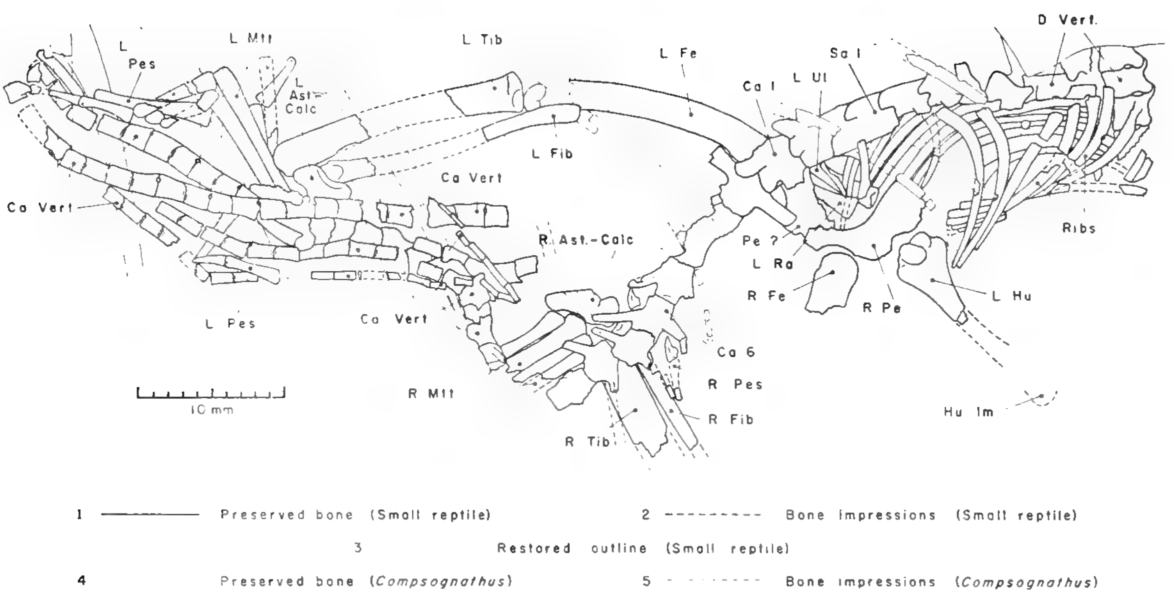


Figure 8: Camera lucida drawing of the small reptile skeleton inside the body cavity of *Compsognathus.* The original drawing was made by me at a magnification of 6.6, with a Wild binocular microscope and camera lucida. *Abbreviations:* Ast.—Calc. — astragalo-calcaneum; C. 1, 6, etc. — caudal vertebrae; Ca. Vert. — caudal vertebrae; D. Vert. — dorsal vertebrae; Fe. — femur; Fib. — fibula; Hu. — humerus; Hu. Im. — Imprint of the distal end of the humerus; L. — left; Mtt. — metatarsals; Pe. — pelvis; R. — right; Ra. — radius; Sa. 1. — first sacral vertebra; Tib. — tibia; Ul. — ulna.

TABLE 3

Comparative Measurements (in mm) of the small skeleton within *Compsognathus,* and the type specimen of *Bavarisaurus macrodactylus**.

	"stomach" contents	*Bavarisaurus macrodactylus**
Humerus length	14.0	15.3
Femur length	16.8—18.0	21.15
Tibia length	16.9	19.2
Fibula length	17.2	18.8
Mtt. I length	6.8—8.1	5.5 ?
Mtt. II length	9.2—10.4	9.2 ?
Mtt. III length	10.4—11.4	11.2
Mtt. IV length	8.9—10.1	11.15
Body length	47 est.	52
Tail length	190 +	

extend down toward the solution cavities described earlier, then cross over the right tarsus. At this point, the series is interrupted.

My initial attempts to decipher these stomach contents were frustrated by the presence of several long rows of bony elements in the posterior regions adjacent to the left foot. At first, these appeared to be rows of vertebrae, giving the impression that there were several small skeletons present within the body cavity of *Compsognathus.* Then, because of their flat form, and what appeared to be sculptured surfaces and paired arrangements, I concluded that they were

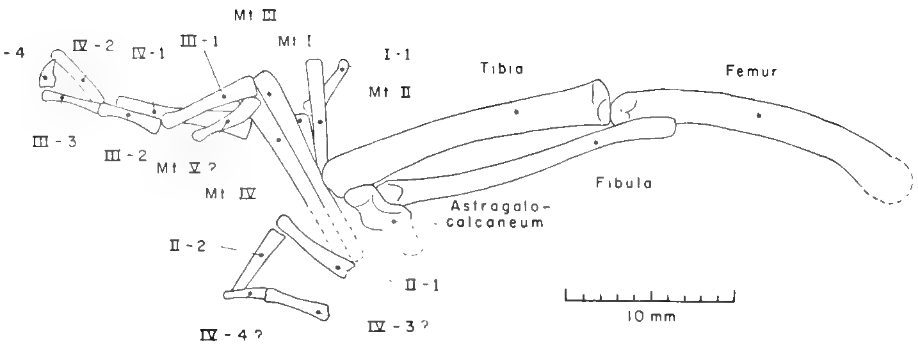


Figure 9: Camera lucida outline drawing of the restored left hindlimb of the small reptile shown in Figure 8, preserved within the body cavity of *Compsognathus*, together with my interpretations of the various elements.

rows of dermal scutes. The objects are very small, and preservation is not perfect, all of which complicates the matter. But now I am absolutely certain that these are rows of caudal vertebrae. Zygapophyseal processes are detectable at several places, but they are rarely distinct. The most distinctive features are the autotomy sutures dividing each centrum into subequal anterior and posterior halves. These are well-defined throughout most of the caudal series and appear to have been present on all caudals, except perhaps the first 8 or 10 segments. The caudal series appears to be nearly complete, with only a few elements missing in the vicinity of the tenth caudal, and perhaps a few others at several points. The tail is preserved folded back and forth on itself in four subparallel rows. At least 50 segments can be identified, with the total length exceeding 19 cm. That is extremely long, when compared with the hindlimb length (femur plus tibia equals 3.4 cm, approximately).

Adjacent to the sacrum, a large L-shaped plate of bone represents parts of the right pelvis, with the proximal end of the right femur still in almost full articulation with the acetabulum. Details are not clear, but there can be no question that the L-shaped bone is the right ilium, with perhaps a portion of the pubis. Next to the pelvic bones, is a well-preserved distal end of a left humerus. This, together with the autotomous caudal structure, is perhaps the most important clue to the identification of these remains. Very distinct here is a large radial condyle and a much smaller trochlea for the ulna. Also evident is a large and pronounced ventral supratrochlear fossa. But most important are the very large entepicondyle and somewhat less prominent ectepicondyle, which clearly show that this is not an archosaurian humerus (Plate 14:4).

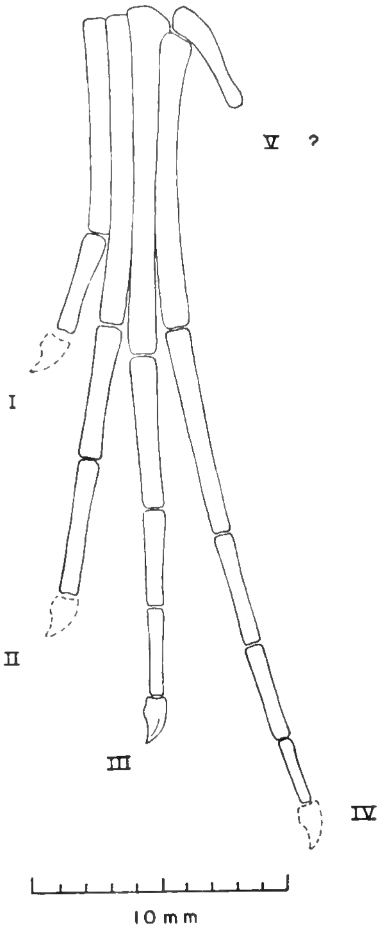


Figure 10: Reconstruction of the left foot (in dorsal aspect) of the small reptile, according to my identifications recorded in Figure 9. Although my identifications cannot be certified, this foot is readily distinguished from that of *Compsognathus* in the completely formed metatarsal I, the relatively more massive metatarsus, the stout and curved metatarsal V (?), the relatively longer toes, and the unusual length of the proximal (?) phalanx of the fourth digit.

The left hindlimb is nearly intact, although the foot bones are disarrayed. The femur and tibia are both stout and very nearly the same length. The tibia is straight, the femur slightly curved. The fibula is surprisingly robust. Articulated with the latter is an irregular-shaped bone which I interpret as a fused astragalo-calcaneum. Two articular facets are evident, which appear to have been for the two epipodials. The medial part, unfortunately, is concealed beneath some of the caudal vertebrae, but in the right ankle this region is exposed, showing what appears to be a stout expansion or process. This does not correspond to the calcaneal tuber of the crocodilian or pseudosuchian tarsus, either in form or position. No other tarsals are discernible in either ankle. The large size of this element, together with its proximal position articulated with the tibia and fibula, leave little doubt that it is the co-ossified astragalus and calcaneum. Important here is the fact that this bone is quite unlike the proximal tarsals of known theropods (see Welles and Long, 1974).

Closely associated with this tarsal bone are the somewhat disarrayed bones of the left foot. My identification of these foot bones is given in Figure 9. The respective positions of the main metatarsals, and the normal (expected) serial arrangement of the four phalanges associated with the middle metatarsal, leave little doubt that this is the third digit. The very long proximal phalanx beneath, and the shorter phalanx at its extremity, seem best linked with the fourth metatarsal. Other identifications are less certain. Figure 10 is my reconstruction of the foot according to the interpretations given in Figure 9. If correctly reconstructed, this foot is very distinct from that of *Compsognathus*, but it is surprisingly similar to that of another Solnhofen taxon.

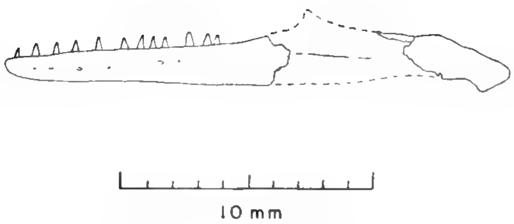


Figure 11: The isolated left mandible that is preserved outside of the body cavity of *Compsognathus*. As is shown in Figure 1, it is closely associated with a number of displaced gastralia of *Compsognathus*. Presumably, it belongs to the small reptile within *Compsognathus*. Notice that it bears a distinct coronoid process and that it is relatively less slender than that of *Compsognathus*. See also Plate 14: 3.

The tiny jaw lying outside of *Compsognathus*' body cavity, most probably also belongs to this specimen, although that cannot be certified. In support of this, there are no other remains of small vertebrates on the *Compsognathus* slab, and the mandible is of appropriate size. Two features of this mandible distinguish it from that of *Compsognathus:* the presence of a well-developed coronoid process, and the greater degree of forward taper of the dentary. Tiny sharp, symmetrical, conical teeth are present, apparently with thecodont (or possibly pleurodont) implantation. No evidence of the "bent" tooth form of *Compsognathes* is visible. (See Plate 14:3.)

Now that I have emphatically rejected the "conclusive" evidence of Marsh, and his embryonic iden-

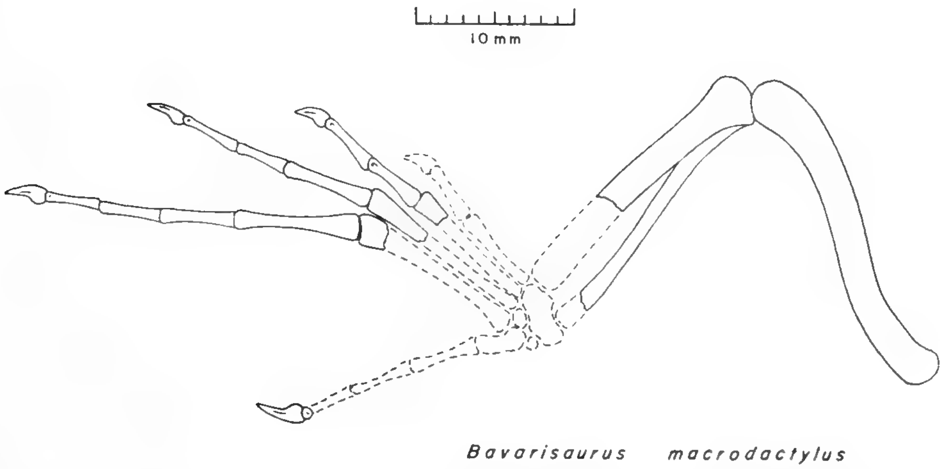


Figure 12: Camera lucida drawing of the left hindlimb of the type specimen of *Bavarisaurus macrodactylus*, for comparison with the hindlimb elements of the small reptile illustrated in Figures 8, 9 and 10. The slight differences in pedal proportions may be due to erroneous interpretations of the foot elements in the *Compsognathus* stomach contents, or to ontogenetic differences, or, most likely, to taxonomic differences.

TABLE 4

Some Available Skeletal Proportions of the Small Reptile Skeleton Inside *Compsognathus*, Compared With Other Solnhofen Lower Tetrapods.

	Femur / Tibia	Femur / Humerus	Tibia / Mtt. III
"Stomach contents" of *Compsognathus*	1.00 — 1.06	1.20 — 1.28	1.48 — 1.66
Bavarisaurus macrodactylus (B. S. P. 1873 III 501)	1.10	1.38	1.76
Homaeosaurus brevipes (B. S. P. 1887 VI 2)	1.25	1.39	1.48
Homaeosaurus maximiliani (B. S. P. AS I 565)	1.06	1.19	1.39
Kallimodon pulchellus (B. S. P. 1887 VI 1)	1.24	1.30	1.43
Eichstaettisaurus schroederi (B. S. P. 1937 I 1)	1.40	1.32	1.46
Ardeosaurus digitatellus (B. S. P. 1923 I 501)	1.68	1.33	1.46
Palaeolacerta bavarica Mus. Maxberg	1.12 est.	1.32 est.	—
Alligatorellus beaumonti (B. S. P. 1937 I 26)	1.03	1.17	2.0
Atoposaurus oberndorferi (B. S. P. 1901 I 12)	1.03	1.13	1.97

tity of this skeleton, the question remains: What is it? Can it be identified? I believe that it is identifiable. After examining various other Solnhofen specimens, and reviewing the literature on other small tetrapods from the Solnhofen beds, I am convinced that these remains are those of a small individual of the lacertilian, *Bavarisaurus.* Recognizing that the small size of this specimen may be due to immaturity, comparison of limb proportions and other size factors must be viewed with skepticism. Nevertheless, the ratios of femur to tibia, femur to humerus and tibia to metatarsus (Table 4) agree quite closely with those of the type specimen of *Bavarisaurus macrodactylus* (Hoffstetter, 1953), and several species of *Homoeosaurus.* Reference of these remains to any species of *Homoeosaurus* is precluded by the thecodont (or perhaps pleurodont), rather than acrodont, dentition.

In addition to this dimensional evidence, further support for identifying these remains as *Bavarisaurus* is found in the several distinctive parts of the skeleton preserved. The foot, as I have reconstructed it in Figure 10, corresponds quite closely with that of *Bavarisaurus macrodactylus* (see Fig. 12), except for the unknown state of the fifth toe in the present specimen. In addition, *Bavarisaurus* possesses a large, irregular-shaped astragalo-calcaneum (see Fig. 40C of Cocude-Michel, 1963), although preservation does not permit recognition of close morphological similarities. These elements are illustrated in Plates 13 & 14. Also important here is the distal end of the humerus, which is very similar to that of *Bavarisaurus* (see Fig. 2B, Hoffstetter, 1964), as I have attempted to show in Plate 14: 4 & 5. Finally, the construction of the numerous caudal vertebrae seem to provide the most compelling evidence of all for identifying these remains as *Bavarisaurus* cf. *macrodactylus.*

As shown in Figures 8 and 13, an extremely long series of caudal vertebrae are folded back and forth on itself into four sub-parallel rows. Microscopic examination of these vertebrae reveals that all except the most proximal centra are marked by complete and well-defined autotomy sutures. Each suture traverses the middle of the centrum in a nearly vertical course, then bends sharply forward in its upper part (Plate 14:1). This identical structure (see Plate 14:2), and what appears to be the same vertebral morphology, are found in all preserved caudal vertebrae of the type specimen of *Bavarisaurus macrodactylus* (see Fig. 1b, Hoffstetter, 1964). Furthermore, the morphology and disposition of the long transverse processes of the proximal caudals in the small specimen are like those of *Bavarisaurus.* The only apparent difference between the two specimens is the extremely long tail of the small individual and the apparently relatively short tail in the type of *Bavarisaurus.* The latter, however, looks as though it might have been shortened as a result of tail autotomy: the last distinct vertebra is still quite large, causing the tail extremity to have a somewhat "stubby" appearance. Also, there is a faint impression distal to the last recognizable caudal which

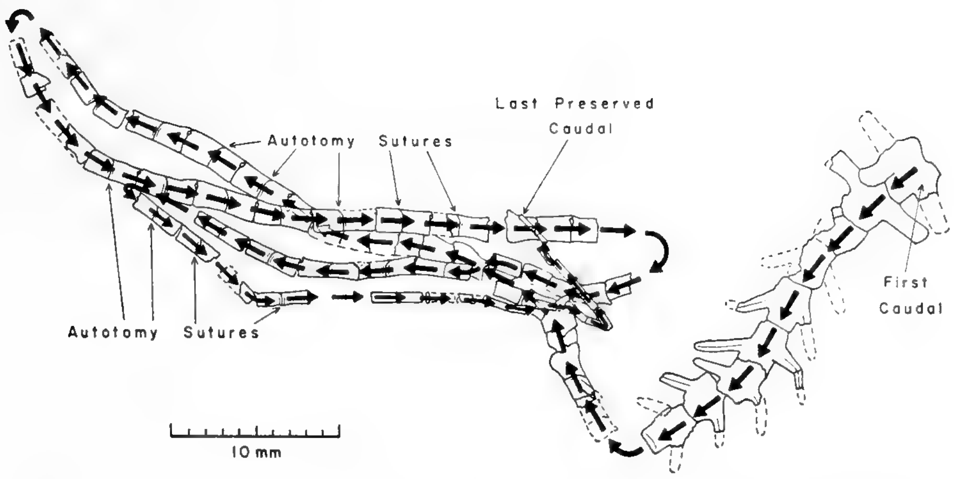


Figure 13: Outline drawing of the folded caudal series of the small reptile, taken from Figure 8. Missing segments are restored by dashed outline. The heavy arrows register my reconstruction of the caudal sequence, progressing from the first caudal to the extremity. Notice the forward flexure of the autotomy sutures.

looks to be that of a fleshy stump-like tail extremity, reminiscent of regenerated tail stumps that are commonly found in modern autotomous lizards. Another aspect of the caudal anatomy preserved in these two specimens that may be important is that all caudal centra, except the most proximal segments, seem to be autotomous. In most modern autotomous lizards, autotomy fracture planes occur throughout the caudal series (except for a few proximal segments), but functional autotomy may be confined to a limited region of the tail by progressive ontogenetic fusion at the autotomy cartilage septa throughout the other parts of the tail (Etheridge, 1967).

The extraordinary length of the tail in the specimen within *Compsognathus* appears highly improbable at first glance, but all I can do is to present the evidence as I see it. In Figure 13, I have traced the sequence of caudals (line of heavy arrows) as I interpret it, from the sacrum through four 180 degree bends, to the delicate tail extremity. A minimum of 50 segments can be discerned, and the total length of this folded series is not less than 19 cm. That is more than four times the probable body length of 46 mm (estimated from the proportions of the larger-sized type specimen of *Bavarisaurus*). Improbable though such an extreme tail length seems, I am convinced that it is correct. The only other possible explanation is that more than one caudal series is present among these stomach contents. Against that interpretation, I offer the following evidence: 1) There is no other evidence that more than one individual is preserved within the the body cavity of *Compsognathus;* 2) Notice that the complete sequence as interpreted in Figure 13 consists of progressively smaller vertebrae proceeding toward the tail tip; 3) Notice also, that the dorsal flexure of the autotomy sutures consistently bend in a forward direction — toward the sacrum — showing that two of the four rows are oriented in one direction (with the anterior end toward the rib cage) and the other two rows are oriented in the opposite direction (with the anterior end pointing away from the rib cage). This verifies my interpretation that the "ends" of the vertebral rows actually are "folds" — 180 degree bends, as illustrated in Figure 13; 4) And finally, there is a physical break at an autotomy fracture plane at each of the three proximals folds in the tail. From these facts, I conclude that these parallel rows of vertebrae represent a folded, but nearly continuous caudal series of a single individual. Thus the extraordinary tail length is correct.

Other parts of the so-called *Compsognathus* embryo skeleton are much too fragmentary to be of reliable value in support of this identification, but the pelvic bone does seem to resemble the L-shaped ilium of the type specimen of *Bavarisaurus.* Also, the ribs of *Bavarisaurus* are quite robust in construction (but not pachyostostic), and are single-headed, as in the small specimen. A very small fragment of the anterior tip of the left dentary of *Bavarisaurus* preserves small, sharp, conical pleurodont teeth, which are very similar to the teeth in the tiny jaw on the *Compsognathus* slab. The latter, however, appear to be thecodont, although this mandible lies on its medial surface and a pleurodont implantation cannot be ruled out.

In summary, a surprising amount of anatomical and proportional evidence establishes the identity of *Compsognathus*' last meal as a young individual of *Bavarisaurus* (cf. *macrodactylus*).

COMPSOGNATHUS THE ANIMAL

The Munich Specimen: Adult or Juvenile?

Curiously enough, the small size of the type specimen of *Compsognathus* has never provoked published inquiry about the maturity of this individual, although the question has often been debated in classroom discussions. In fact, the literature on *Compsognathus* seems to meticulously avoid the subject, tacitly treating the matter as though there could be no question, and accepting the Munich specimen as an adult individual. That conclusion is far from established, as the discovery of the Nice specimen clearly demonstrates.

As was mentioned earlier, the Munich specimen gives the appearance of being a mature individual, at least in the texture and completeness of the bones of the skeleton and the apparently closed sutures of the vertebral column. However, other factors (besides its small size) suggest that it may not be a fully mature specimen. But with only two specimens available for comparison, no definitive statement can be made.

Three distinctive features of *C. longipes* suggest, but do not prove, that this is not a fully adult individual: 1) The relatively large skull; 2) The disproportionately large orbit; 3) The relatively long hindlimbs. As is well-known, the head is disproportionately large in all hatchling or new-born amniotes, but in some theropods (Megalosauridae, Tyrannosauridae) the skull remained disproportionately very large in the adult stage. A comparison of skull and post-cranial proportions of *Compsognathus* and various other theropods (given on page 82), unfortunately proves to be inconclusive as regards the relative ontogenetic age of the Munich specimen.

Even though the occipital and posterior portions of the temporal region are not preserved, the orbit can be seen to be relatively enormous compared with the estimated length of the skull (70 to 75 mm). Using Kälin's (1933) skull — orbital — length index $\frac{(19\ \text{mm} \times 100)}{72\ \text{mm}}$ gives a relatively high value of 26, which by comparison with Kälin's numbers suggests a juvenile state. Skull — orbital — length indices for other theropods are given in Table 5, but again, comparisons with *Compsognathus* are not conclusive, because we are comparing different taxa rather than individuals known to be of differing ages, but belonging to the same species. Yet, the type specimen of *Compsognathus* does have one of the highest skull — orbital — length indexes among theropod specimens.

Finally, as was noted earlier, the hindlimb length of *Compsognathus* is relatively long (but not excessively for theropods) and is reminiscent of precocial limb proportions in the young of certain cursorial animals (horse, deer, antelope, etc.). Yet, for the simple reason that the hindlimb is not unusually long for a theropod (of any size) clearly indicates that we should not consider long limb length per se as evidence of immaturity. Comparison with the only other specimen certifiably referrable to *Compsognathus* (the French specimen, "*C. corallestris*") offers little additional evidence in this regard. For example, the ratio of total hindlimb length to presacral length is approximately the same in "*C. corallestris*" and *C. longipes* (1.10 vs 1.11), even though the French specimen is 50% larger. (I obtained a different presacral length than the authors of "*C. corallestris*", measuring 31 cm, with two cervicals missing or unmeasurable. Adding an average vertebral length of 16 mm for each of the two missing segments, I estimated the total presacral length to be 34.2 cm.) Assuming my vertebral length estimate to be reasonably close, there is no difference in the relative hindlimb lengths of these two specimens. If these two specimens belong to the same species, as I believe, this indicates that either there was

TABLE 5

Skull — Orbital — Length Indexes of Some Theropods.

Compsognathus longipes (Holotype)	26
Compsognathus longipes (Nice specimen)	24
Ornithomimus altus	26
Ornitholestes hermanni	25
Gallimimus bullatus	24
Velociraptor mongoliensis	23
Saurornithoides mongoliensis	22
Allosaurus fragilis	14
Tyrannosaurus rex	10

little allometric change in hindlimb length during growth, or both specimens are essentially mature. Thus, on the basis of just these two specimens, it is not possible to decide whether long hindlimb length is a juvenile condition or an adult cursorial adaptation.

Returning to skull size, on the basis of my estimates of skull length and presacral column length, the skull of "*C. corallestris*" appears to have been relatively larger (.35 of presacral length) than that of *C. longipes* (.30 of presacral length), even though the latter is smaller. The difference could well be due to errors in my estimates, rather than to an unlikely positive allometric skull growth. With regard to skull — orbit — length index, *C. longipes* and "*C. corallestris*" have fairly close indexes (26 and 24). The slightly lower index for the larger French specimen suggests more advanced maturity.

With such a limited sample, none of these parameters can be considered as conclusive evidence of relative age, but I am inclined to believe that the Munich specimen of *Compsognathus* is an immature, although probably not a juvenile, individual. That belief is based primarily on the enormous size of the orbit, the larger size of the Nice specimen, and the texture and fully ossified state of the skeleton.

Reconstruction and Life Habits

Attempts to reconstruct posture and life habits of extinct animals are educated guesses at best, and must always be viewed as such. The present effort is no exception. Speculations about the functional significance of particular skeletal features are even more suspect, unless one can point to a nearly identical modern analogue. Because of its chicken-size, (estimated live weight, 3-3.5 kg), and certain bird-like features in its skeleton (foot, hind leg, skull ?), there is a natural tendency to turn to modern ground-dwelling birds for our analogues in reconstructing life style and posture in *Compsognathus*. Certainly, that seems reasonable grounds for claiming bipedal carriage in this creature. But, as Figure 14 shows, there is much else about *Compsognathus* that is not bird-like, and this is where my reconstruction falters. Whether my reconstruction in Figure 14 is any closer to the truth than the earlier reconstuctions by Huxley in 1876 (see Marsh, 1895), Marsh (1895, 1896) and von Huene (1925) can never be known, but I offer it as my best estimate of the posture and skeletal organization of *Compsognathus longipes*.

The osteology of the hind and fore limbs establish conclusively that *Compsognathus* was a biped, and in all probability, an obligate biped. The length of the forelimb, although not as shortened as has been generally held (.43 of presacral column length), when considered against the greater length of the hindlimbs, makes a four-legged stance rather awkward, but perhaps not impossible. However, the reduced two-finger construction of the manus, while not short in the absolute sense, appears to be a specialized adaptation incompatible with quadrupedal locomotion. On the other hand, we can be quite certain that the forelimbs were used to some extent in raising the animal from a resting pose, as well as in predatory activities.

At first glance, the hindlimbs appear to be unusually long, but when compared with the length of the presacral column, they are comparable to those of other theropods. The relative proportions of femur to tibia and tibia to metatarsus suggest that *Compsognathus* may have been only a moderately fast cursorial biped. That interpretation, however, is strongly contradicted by the stomach contents, which are discussed later. Using my estimate of femur length of 67 mm, the femur / tibia ratio is a moderately low .76, which is less than that of *Ornithomimus* (= *Struthiomimus*) at .88, but still much greater than that of fleet-footed struthious birds such as *Struthio* (.46) and *Casuarius* (.57). The metatarsus / tibia ratio, the commonly accepted index of cursorial ability, is a moderate .63, close to that of *Ornithomimus* (.68) and *Ornitholestes* (.73), but well below that of *Struthio* (.95) and *Casuarius* (.85). So, contrary to earlier suppositions, *Compsognathus* appears not to have been as fleet-of-foot as some other "coelurosaurian" theropods. In fact, this last ratio is surprisingly close to that of graviportal "carnosaurian" theropods like *Albertosaurus* (= *Gorgosaurus*), although *Compsognathus* obviously cannot be categorized as graviportal. Perhaps this "graviportal" index, and the stomach contents of *Compsognathus*, are important reasons for us to re-examine the theoretical basis of designating certain limb element ratios as "graviportal" and others as "cursorial".

Compared with the hindlimb, the forelimb definitely is reduced, measuring only 38 % of hindlimb length and 43 % of presacral vertebral length. This compares with typical non-tyrannosaurid forelimb / presacral ratios that range from .50 to .60. Despite its somewhat reduced length, though, the forelimb elements of *Compsognathus* are quite robust and the hand equals almost 40 % of the total forelimb length. All of this suggests an active and powerful role for the anterior appendage. This interpretation is reinforced by the relatively large coracoids, the very prominent acromion and the stout scapula. The acromion and coracoids especially, suggest the presence of a powerful pectoral and deltoideus musculature, which in turn implies powerful antero-ventral adduction and flexion of the forelimb and hand, and strong elevation of the humerus. Presumably, these actions were critical in the prey-catching process, but exactly how is not clear.

The unique design of the manus — long, but reduced to just two functional fingers (one of which has

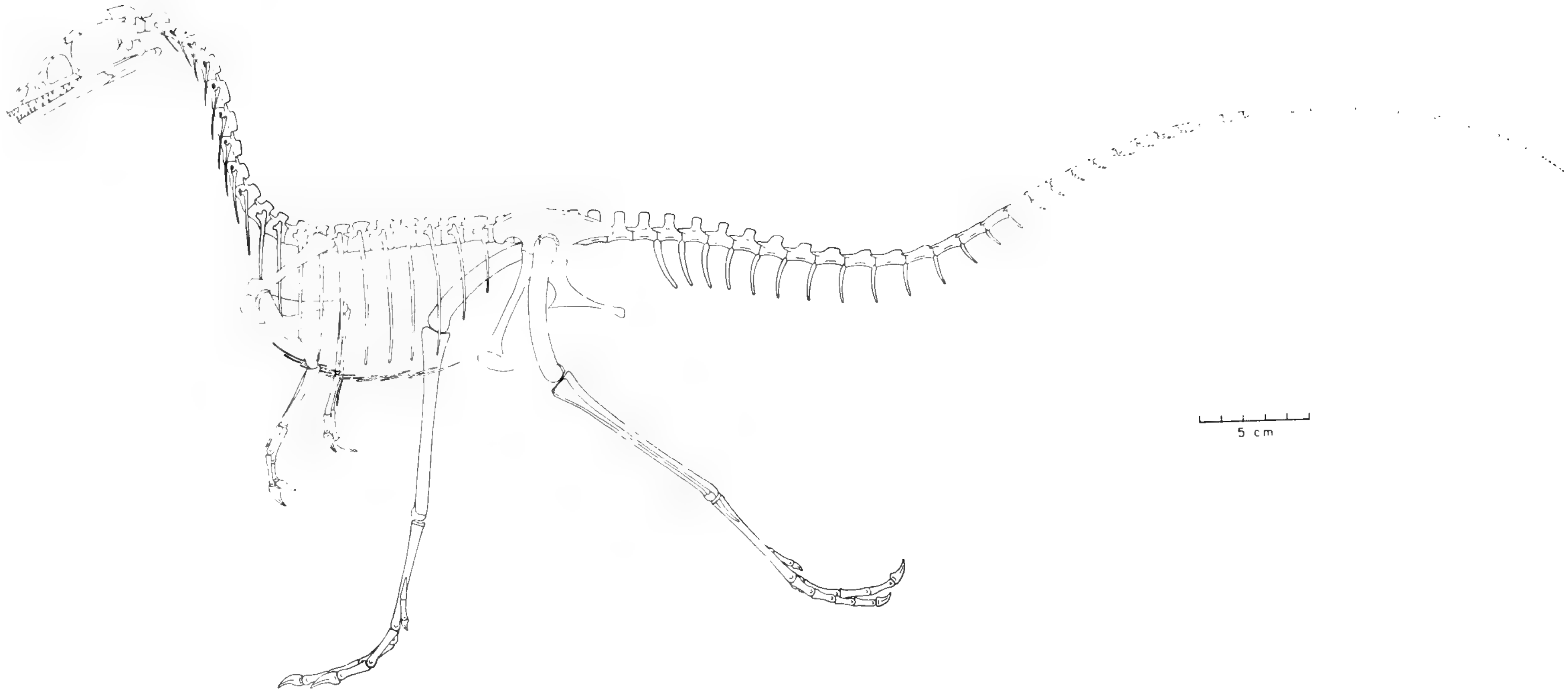


Figure 14: Skeletal reconstruction of *Compsognathus longipes.* The distal parts of the tail are hypothetical, as is the exact form of the ilium and the posterior part of the skull. Notice the large size of the head, the long hands, and the great length of the foot and metatarsus.

a reduced phalangeal formula) — is difficult to understand, especially when considered in terms of the more usual three-fingered hands of most other theropods, or the more primitive five digit manus. First thoughts are that the manus of *Compsognathus* was not suited for raptorial activities, and this seems to be substantiated by the rather straight and short form of the unguals (see Figs. 5 and 6), and the reduced phalangeal count of digit II, as compared with the ungual form of other theropods. However, that interpretation seems to be in conflict with the robust construction of the arm and hand, and the prominent elements of the shoulder girdle. My conclusion is that the hand was specialized for some role, but probably not the usual prey-catching action usually envisioned for most theropods. But what kind of activity requires a long, stout, two-fingered hand? Is it possible that it served as a digging structure — to tear apart insect nests, ant hills or termite mounds? That seems unlikely in view of the stomach contents.

That *Compsognathus* was a predator, there can be no doubt. The dentition alone indicates that. Since virtually all modern flesh-eating vertebrates are opportunistic feeders, we can be certain that *Compsognathus* ate whatever small creatures it could find and catch. For that reason, and because of its small size, we should conclude that *Compsognathus* probably was insectivorous, at least in part. But in addition, the tiny skeleton preserved within *Compsognathus* is dramatic and indisputable evidence that *Compsognathus* preyed on small vertebrates as well. Identification of these stomach contents as *Bavarisaurus* (cf. *macrodactylus*) provides specific critical evidence about the food-seeking habits and skills and the food preferences of *Compsognathus* that go far beyond any previous intuitive deductions about the predatory habits of any other theropod *(Deinonychus* included). Dinosaur remains that contain recognizable stomach contents, let alone identifiable food items or prey remains, are extremely rare. So whatever can be deduced about the adaptations and live nature of *Bavarisaurus* provides unusual specific insight into the hunting skills and behavior of *Compsognathus.*

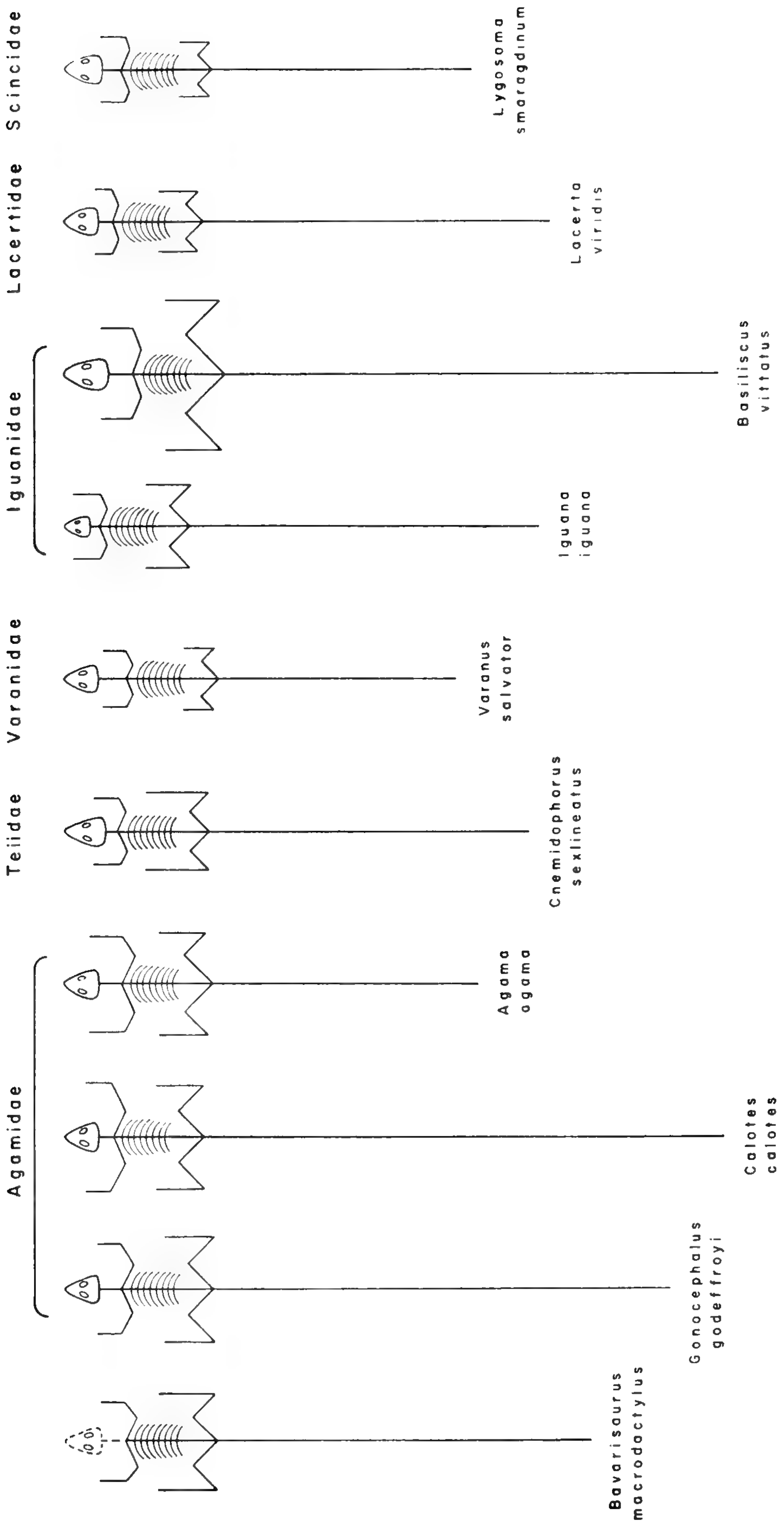
Overall, the relative proportions of the tail, the limbs and feet of *Bavarisaurus* are quite similar to those of modern lizards that are noted for their speed and/or agility, such as certain teiids, iguanids, lacertids and agamids. The type specimen of *Bavarisaurus macrodactylus* (B. S. P. 1873 III 501) displays the usual lacertilian disparity of hindlimb vs. forelimb length. But more important, is the fact that the pes is markedly longer than the manus. Most important of all, though, is the extremely long tail of *Bavarisaurus*, as can be seen in the remains preserved within *Compsognathus* (see Fig. 8 and Plate 13). Romer (1956) observed that long tails are most common among arboreal lizards. While that is true, long tails are also typical of many of the fastest-running ground-dwelling species, such as some teiids and iguanids.

In Figure 15, I have plotted the major body parameters of some of the longest-tailed living lacertilian species for comparison with those of *Bavarisaurus* (taken from both the type specimen and the remains within *Compsognathus).* Of interest here are the several species (and there must be others) in which the tail is relatively longer than in *Bavarisaurus.* For example, the agamids *Gonocephalus godeffroyi* and *Calotes calotes*, among the longest-tailed lizards known, are very active climbing and leaping forms. *Agama agama* also is an active climber, but perhaps not as quick as *Gonocephalus* and *Calotes. Iguana iguana* and *Lacerta viridis* also are long-tailed, although not to the extent of the two agamids included above, but the iguanid, *Basiliscus vittatus* has a tail length comparable to that of *Calotes calotes. Iguana iguana* is a good climber, but also is a fast runner. *Lacerta viridis* is predominantly a running form, as is the teiid *Cnemidophorus.* Mertens (1960) recorded that *Cnemidophorus limniscatus* was capable of speeds up to 15 miles (23 km) per hour over short distances. *Basiliscus* also is noted for its high running speed, and its ability at maximum velocity to run on its hind legs (notice [Fig. 15] the extreme disparity of hindlimb vs. forelimb length, as compared with another fast-running form, *Cnemidophorus sexlineatus*). From these data, I conclude that long tails from 3 to 5 times the body length, are found in both highly cursorial and active climbing lizards.

The question of interest here, is, can we determine whether *Bavarisaurus* was predominantly a fast-running ground-dweller, or an agile climber? I think we can.

Notice in Figure 15 that the hands and feet of climbing forms (the agamids and *Iguana)* are not so disproportionate, and in *Agama* they are of nearly equal length. Presumably, this is a reflection of the need for enhanced (enlarged) grasping powers of the manus in climbing species. In the highly cursorial species, on the other hand, the manus is conspicuously shorter than the pes — extremely so in *Cnemidophorus*, and somewhat less so in *Basiliscus* and *Lacerta.* On this basis, the elongated foot and relatively short hand of *Bavarisaurus* suggest that it probably was a fast-running ground lizard, rather than a habitual tree-dwelling or climbing species.

While the data of Figure 15 represent only a small sampling of the Lacertilia, and may be viewed as merely suggestive but not conclusive as regards the living habits of *Bavarisaurus*, one additional piece of evidence preserved in the "consumed" specimen strongly supports the cursorial interpretation. That evidence is the autotomy fracture septa of the caudal


Agamidae
Teiidae
Varanidae
Iguanidae
Lacertidae
Scincidae
Bavarisaurus macrodactylus
Gonocephalus godeffroyi
Calotes calotes
Agama agama
Cnemidophorus sexlineatus
Varanus salvator
Iguana iguana
Basiliscus vittatus
Lacerta viridis
Lygosoma smaragdinum

vertebrae. Autotomy is far from rare in modern lizards, but it does seem to occur most commonly in ground -dwelling species.

On the basis of the autotomous and very long tail, and the hand and foot proportions, the picture that emerges of *Bavarisaurus* is one of a very fast-running, predominantly ground-dwelling lizard, perhaps similar to the living species of *Cnemidophorus.* From this unusual evidence, it is clear that *Compsognathus* was equipped to pursue and catch very fast-running and agile prey. If you have ever attempted to run down and catch specimens of *Cnemidophorus* (as I have) or *Basiliscus,* you can appreciate what that involves — keen sight, rapid acceleration, high speed and quick reaction and maneuverability.

AFFINITIES OF *COMPSOGNATHUS*

Early attempts, especially those by Huxley (1870), to decipher the affinities of *Compsognathus,* were confounded by the facts that the tibia was significantly longer than the femur and the cervical vertebrae were viewed as "elongated", conditions that were unknown in other then-known dinosaurs. These conditions led Huxley to propose his higher taxon, Compsognatha, which he ranked equally with the Dinosauria. The problem was that almost no other remains of small dinosaurs, let alone what we would now identify as "coelurosaurian" theropods, were known at the time. Not until the 1880's did fragmentary remains of small theropods begin to surface: *Coelurosaurus,* 1865; *Coelurus,* 1879; *Hallopus,* 1881; *Thecospondylus,* 1882; *Aristosuchus,* 1887; *Coelophysis,* 1889; *Ornithomimus,* 1890; *Agrosaurus* and *Calamospondylus,* 1891. But none of these finds were anywhere near as complete as the specimen of *Compsognathus.* Most consisted of only a few vertebrae, or teeth, or limb fragments. Only the specimens of *Hallopus* and *Coelurus* preserved sufficient parts to permit meaningful comparisons. Thus, it is not surprising that early works often allied *Compsognathus* with *Hallopus,* and somewhat less frequently with *Coelurus.* But, it is important here that proper credit be given to Huxley. Despite these facts, and its diminutive size, as early as 1868 Huxley perceived that the affinities of *Compsognathus* were among or close to the giant dinosaurs.

Walker (1970) established conclusively that *Hallopus* has nothing whatever to do with theropods, but is an early crocodilian. This leaves *Coelurus* and a relatively small number of adequately founded theropod taxa for comparison with *Compsognathus,* out of a total of 40-odd genera listed by Steel (1970) under the "Coelurosauria". These other taxa are: *Coelophysis, Coelurus, Halticosaurus, Ornitholestes, Procompsognathus* and *Segisaurus.* While the type specimens of other small theropods may be adequate bases for establishing the respective taxa, I consider the types of *Avipes, Velocipes, Agrosaurus, Aristosuchus, Calamospondylus, Caudocoelus, Coelurosaurus, Thecocoelurus* and *Thecospondylus* to be quite inadequate for assessing the affinities of *Compsognathus.* And for obvious reasons, there can be no close relationship between *Compsognathus* and oviraptorids, ornithomimids or dromaeosaurids, so these will not be reviewed here.

Figure 15: Diagramatic comparison of the main skeletal components of *Bavarisaurus* cf. *macrodactylus* (the stomach contents of *Compsognathus)* with those of selected modern, long-tailed lizards. All skeletons are represented with equal body lengths to facilitate comparison of relative tail lengths. Data on *Bavarisaurus* are derived from the type specimen (B. S. P. 1873 III 501) and the remains preserved within the rib cage of *Compsognathus.* Data on the recent lizard species were obtained from specimens in the Bayerische Zoologische Staatssammlung, through the courtesy of Dr. U. Gruber. The long-tailed agamids, *Gonocephalus* and *Calotes,* are extremely active and agile climbers. *Iguana* also is a good climber, but is a speedy ground runner as well. The other species illustrated are predominantly ground-dwelling forms, all of which are fast over short distances. Fastest of all, are the teiid *Cnemidophorus* and especially the iguanid *Basiliscus.* Long tails seem to be typical of highly active lacertilians and not distinctive per se of either predominantly climbing species, or highly cursorial forms. However, there is other evidence in the data plotted here that is suggestive: there appears to be less disparity of fore and hind foot length in the climbing forms (agamids, *Iguana)* than there is in the fast-running ground dwelling kinds *(Cnemidophorus* and *Basiliscus).*

Compsognathus is distinct from each of six previously mentioned genera as follows:

1) *Coelophysis* (Late Triassic): High tooth count ($\frac{23}{12}$), deep mandible, four-fingered manus, femur and tibia sub-equal, no distal pubic expansion or expansion is very small, dorsal vertebrae are pleurocoelous.
2) *Halticosaurus* (Late Triassic): Deep mandible, five-fingered manus, femur longer than tibia, dorsal vertebrae possibly pleurocoelous.
3) *Procompsognathus* (Late Triassic): Broad apron-like pubic plates as in pseudosuchians, with a long mid-line symphysis and lacking a distal expansion.
4) *Segisaurus* (Late Triassic): Presence of clavicles and an interclavicle (?), three-fingered manus, and what appears to be a prominent calcaneal tuber.
5) *Coelurus* (Late Jurassic): Cavernously pleurocoelous dorsal vertebrae, and extremely elongated metatarsals.
6) *Ornitholestes* (Late Jurassic): Three-fingered manus, and femur longer than tibia.

The distinctive features of *Compsognathus* are: The very slender or shallow mandible, "bent" form of the anterior teeth, "sub-equal" length of cervical and dorsal vertebrae, pleurocoelus cervicals and non-pleurocoelous dorsals, very short ischium (relative to pubic length) and two-fingered construction of the hand. The most important of these, in my opinion, is the specialized design of the manus, and on that basis alone I place *Compsognathus* in its own separate family, Compsognathidae. My rationale for this is first, no other theropod is presently known which posesses this unique manus morphology, and second, this construction of the manus precludes *Compsognathus* being ancestral to any other known theropod. I have no doubt that some critics will point out that the exact design of the manus in *Compsognathus* is open to question, but I think it has been demonstrated above that the hand could not have consisted of more than two fingers, both of which apparently were constructed of two phalanges. Contrary to the view of some, that the phyletic loss of structures should not be considered as specialized or advanced conditions, I believe the two-fingered hand of *Compsognathus* does represent a specialized adaptation. But more important, the unique phalangeal formulae (2-2-0) establish that this is unrelated to the digital reduction characteristic of later deinodonts *(Albertosaurus, Tarbosaurus* and *Tyrannosaurus),* where the formulae are 2-3-0.

If the evidence for close relationship between *Compsognathus* and known "contemporaneous", or later theropods is preclusive, as I believe it is, then evidence for close affinity with earlier taxa is less conclusive, although suggestive. The presence of a two-fingered manus precludes "close" relationship with later three-fingered forms, but it does not negate proximity to preceding three-(or more)-fingered kinds. Among the pre-*Compsognathus* theropods mentioned above, *Procompsognathus triassicus* is the most interesting. The type specimen (S. M. N. S. 12 591), named but not described by Fraas (1913), consists of a dorso-ventrally crushed incomplete skull and mandibles, a complete right hindlimb and foot, left femur, both pubes, the left scapulo-coracoid, a radius and ulna, ten dorsal vertebrae plus ribs, five or six cervicals and eight or nine caudals. Additional material (S. M. N. S. 12 352) found later, consisting of an incomplete manus and pre-orbital parts of a somewhat larger skull, were referred to this species by von Huene (1921 a), but his referral must be viewed with skepticism.

In several respects, the type remains are quite similar to those of *Compsognathus longipes*, most notably in the construction and proportions of the foot and dorsal vertebrae, and to a lesser extent, the hindlimb. The chief differences lie in the distinctly primitive design of the pubes (broad transverse plates meeting in a long mid-line symphysis with no distal expansion) and the long transverse processes of the proximal caudal vertebrae. The femur to tibia ratio also differs slightly (.83 in *Procompsognathus* to .76 in *Compsognathus*). Although the pubis is relatively much longer than in most pseudosuchians, approaching the length of the femur as in theropods, its broad transverse, apron-like form is reminiscent of the pseudosuchian condition. This primitive design of the pubis contrasts with the advanced design of the foot, which is remarkably similar to that of *Compsognathus* (see Fig. 16).

The type skull of *Procompsognathus* is moderately crushed dorso-ventrally, making comparison with the laterally crushed skull of *Compsognathus* somewhat difficult. The nares are indistinct, a large triangular antorbital fossa is present containing what appears to be two disparate sized fenestrae, and the orbit is quite large. The mandibles appear to be very shallow, as in *Compsognathus*, but the teeth are of typical theropod form, with no sign of the "bent" shape characteristic of the anterior teeth of *Compsognathus*.

Von Huene (1921 a), considered *Procompsognathus* to be a "coelurosaur" — presumably close to *Compsognathus* — and over the ensuing years it has consistently been placed with other small or lightly-built Triassic theropods (or presumed theropods, such as *Hallopus*). That would seem to be a reasonable assignment in view of the distinctly theropod-like design of the pes. But the apparently pseudosuchian-like construction of the pubis, together with the indeterminate condition of the acetabulum and the absence of

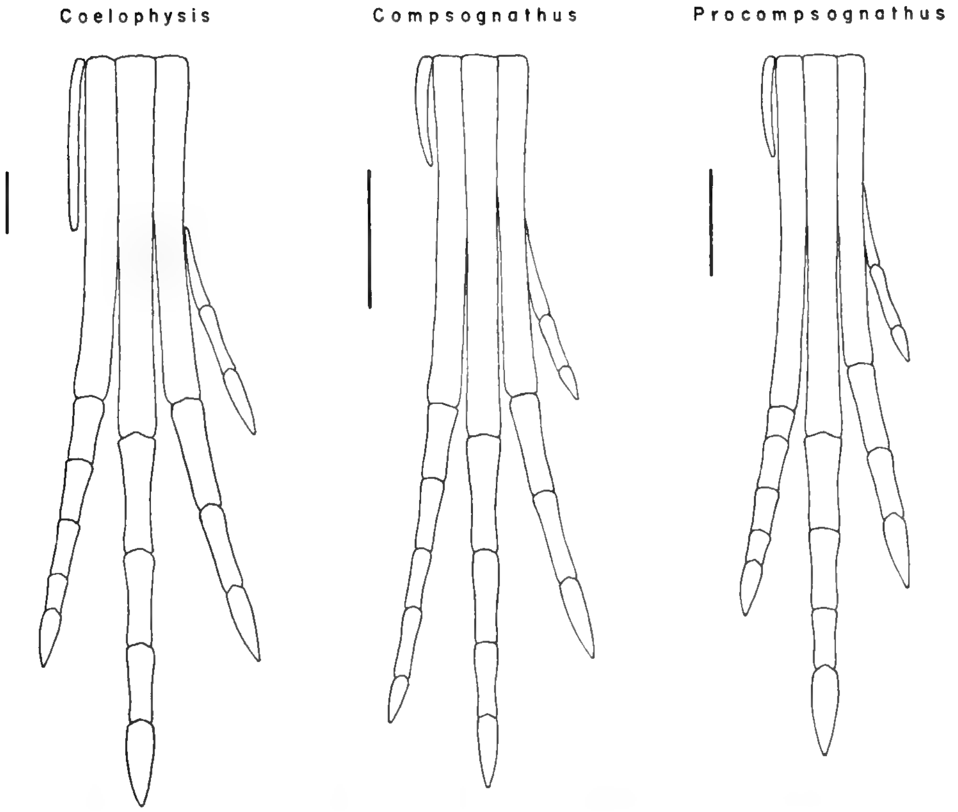


Figure 16: Comparison of foot morphology in *Compsognathus longipes, Procompsognathus triassicus* (S. M. N. S. 12 591) and *Coelophysis longicollis* (A. M. N. H. 7223). All three are drawn with the third metatarsals equal in length to eliminate size differences and to show the relative proportions of the digits to the metatarsus. The similarities are obvious. The foot of *Compsognathus* might have been derived from either *Procompsognathus* or *Coelophysis* — or a common ancestor of these Triassic forms. The vertical lines equal 20 mm for all three specimens, to show relative sizes.

other pelvic bones, raises the question as to whether this specimen is truely theropodan, or perhaps thecodontian. That question takes on added significance in the light of recent discoveries of the small pseudosuchians (?) *Lagosuchus* and *Lagerpeton* (Romer, 1971, 1972) from the Middle Triassic of Argentina. Both of these taxa possess an elongated foot with reduced digits I and V, and what appears to be near meso-tarsal grade ankle joints.

Until a very much needed, new and detailed analysis of *Procompsognathus* is available, little can be said about its placement, or its possible relationship to *Compsognathus*. However, I suspect that these remains represent those of a late, but advanced (in foot structure) pseudosuchian not ancestral to any theropod. *Compsognathus* appears to represent a dead-end theropod line derived from the primitive podokesaurids (*Coelophysis, Halticosaurus).* The foot of podokesaurs is typical theropod in its construction and comparable to that of *Procompsognathus* (see Fig. 16), but the pelvis is more advanced than that of *Procompsognathus*, at least in the form of the pubis. This last point, together with overall primitive theropodan anatomy of *Coelophysis* (as the best-known podokesaurid), qualify podokesaurids as possibly ancestral to *Compsognathus*, coelurids and perhaps other theropods.

One final observation concerning the possible affinities of *Compsognathus*, is required here. Elsewhere (Ostrom, 1973, 1976b), I have argued that *Archaeopteryx* and later birds evolved from a "coelurosaurian" ancestry, and I raised a speculative question (1974) "whether some small theropod dinosaurs might have had feathers". As a small theropod, *Compsognathus* cannot be very far removed from the theropod line that gave rise to birds, but its reduced manus, as well as its contemporaneous occurrence with *Archaeopteryx*, exclude it from direct ancestry of *Archaeopteryx* and later birds.

If the speculative question about feathered "coelurosaurs" can ever be answered, the Munich specimen of *Compsognathus* is the critical specimen to examine. It is the smallest of known theropods and it comes from the same Solnhofen limestones (but not exactly the same facies) as the specimens of *Archaeopteryx* with their distinct feather impressions. There are no feather impressions — nor any evidence whatever that is suggestive of feathers — anywhere on the *Compsognathus* slab. The reader can be sure that I made an exhaustive examination, under various lighting conditions, in search of evidence for feathers, but to no avail. If feathers had been present in *Compsognathus,* it is inconceivable to me that no evidence of them would be preserved, considering the complete and almost undisturbed manner in which the skeleton is preserved, the fine details of the skeleton, and the presence of portions of one horny claw. But the fine-grained matrix shows nothing. Thus, I conclude that *Compsognathus* almost certainly was not feathered.

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TAFELN

Plate 1

Fig. 1: *Miliammina fusca* (Brady). — a, side view: X 130; b, apertural detail: X 226 [Chuy N° 364: 122.10—124.00 m].

Fig. 2: *Textularia gramen* d'Orbigny. — a, side view: X 130; b, detail of apertural region: X 289 [Puerto La Paloma N° 449/11: 6.50—7.50 m].

Fig. 3: *Textularia* sp. A. — X 191 [Chuy N° 364: 122.10—124.00 m].

Fig. 4: *Textularia* sp. B. — X 125 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 5: *Reophax artica* Brady. — X 100 [Salinas N° 1034/1: 32—34 m].

Fig. 6: *Quinqueloculina* cf. *agglutinata* Cushman. — a, side view: X 115; b, apertural view: X 100 [Chuy N° 364: 122.10—124.00 m].

Fig. 7: *Quinqueloculina patagonica* d'Orbigny. — X 100 [Chuy N° 364: 122.10—124.00 m].

Fig. 8: *Quinqueloculina vulgaris* d'Orbigny. — X 75 [Chuy N° 364: 122.10—124.00 m].

Fig. 9: *Quinqueloculina intricata* Terquem. — X 38 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

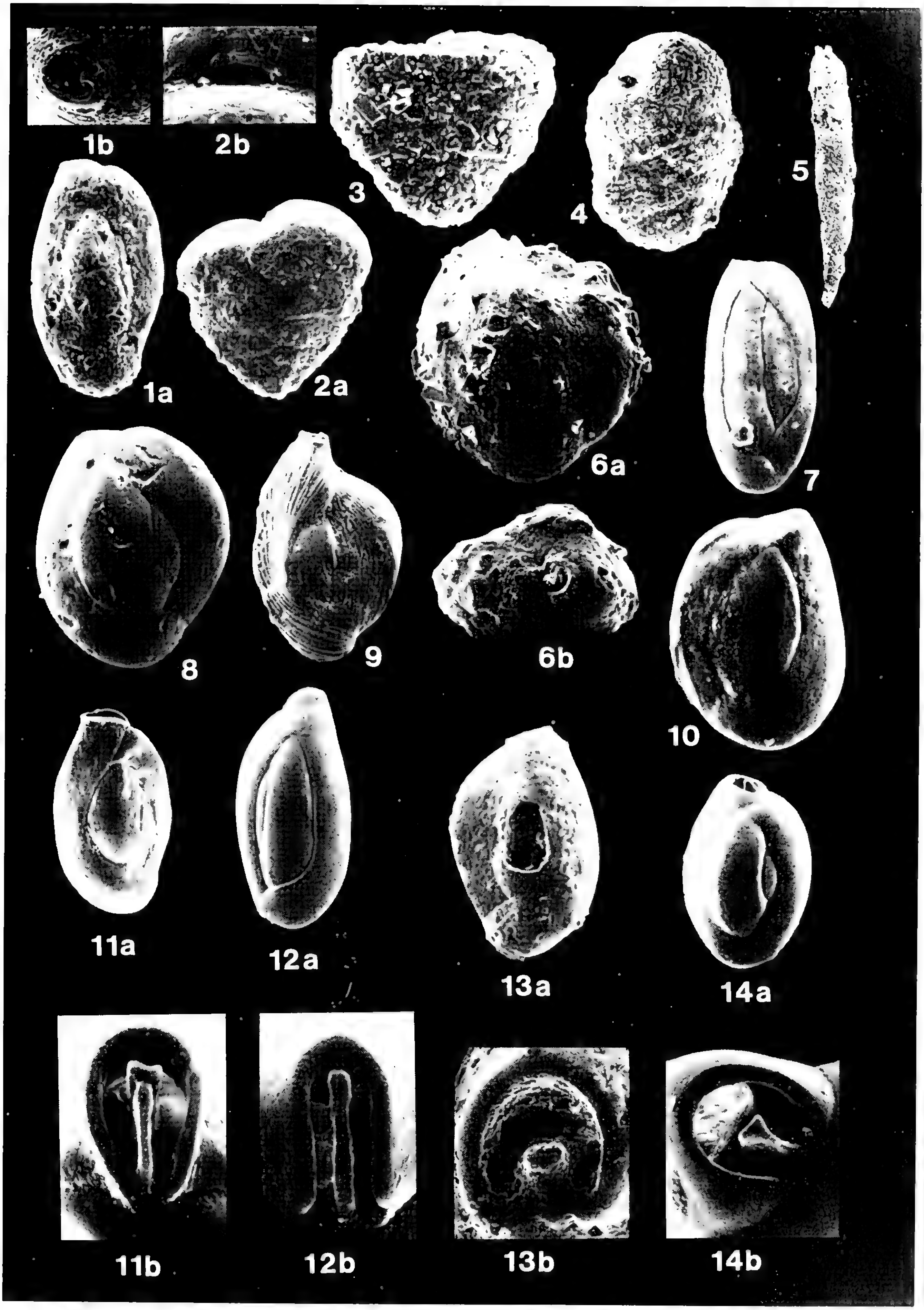
Fig. 10: *Quinqueloculina* sp. A. — X 170 [Chuy N° 364: 124.00—125.40 m].

Fig. 11: *Quinqueloculina angulata* (Williamson), forma typica. — a, side view: X 98; b, detail of apertural region: X 351 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 12: *Quinqueloculina atlantica* Boltovskoy. — a, side view: X 85; b, apertural detail: X 351 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 13: *Quinqueloculina* aff. *frigida* Parker. — a, side view: X 100; b, detail of apertural region: X 412 [Puerto La Paloma N° 449/11: 4.50—5.00 m].

Fig. 14: *Quinqueloculina seminulum* (Linnaeus). — a, side view: X 65; b, apertural detail X 226 [Puerto La Paloma N° 449/11: 7.50—8.00 m].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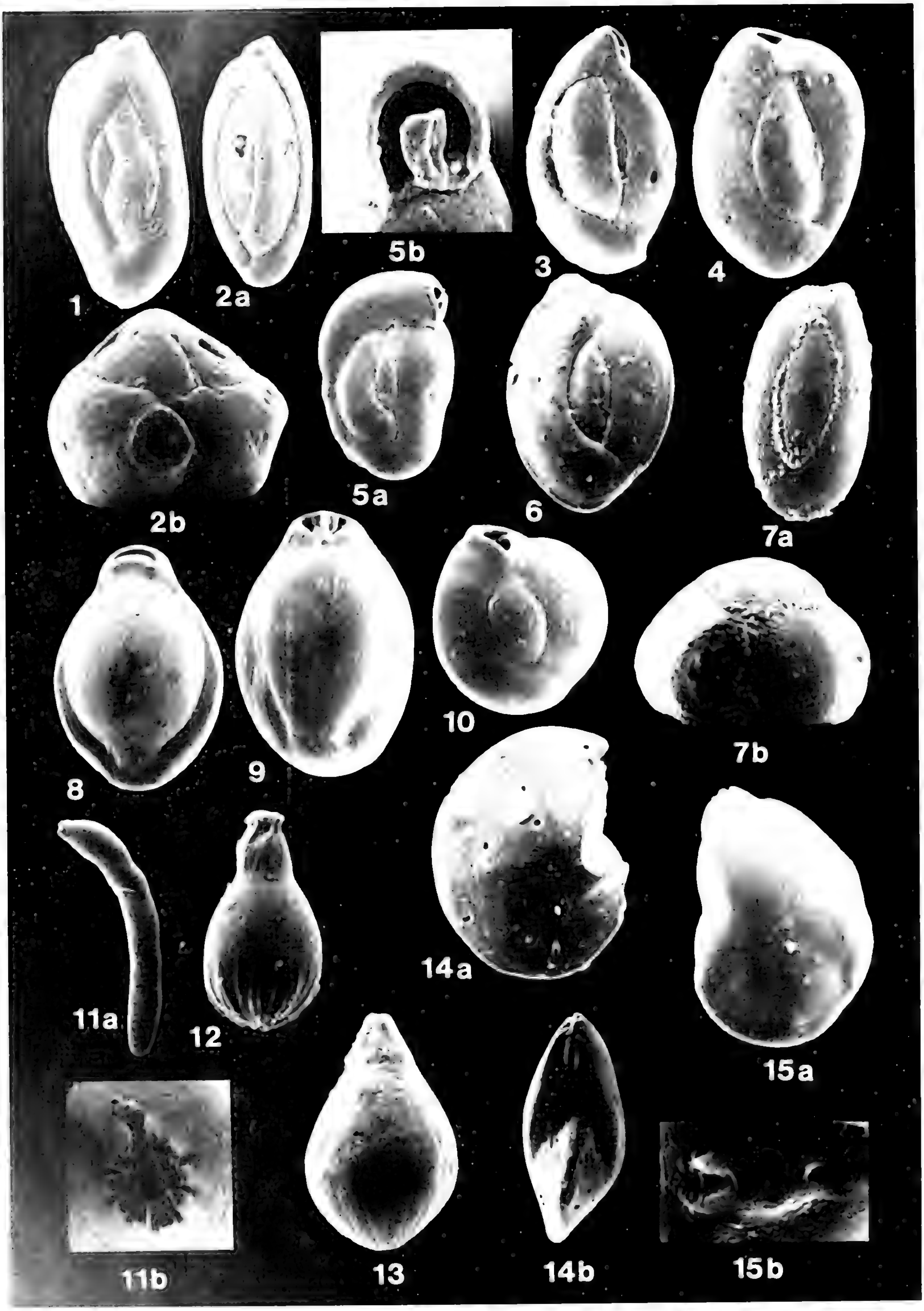
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Plate 2

Fig. 1: *Quinqueloculina* sp. B. — X 125 [Chuy N° 364: 124.00—125.40 m].

Fig. 2: *Quinqueloculina* sp. C. — a, side view: X 110; b, apertural view: X 226 [Chuy N° 364: 122.10—124.00 m].

Fig. 3: *Quinqueloculina* sp. D. — X 100 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 4: *Quinqueloculina* sp. E. — X 130 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 5: *Flintinella* sp. — a, side view: X 80; b, apertural detail: X 238 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 6: *Massilina secans* (d'Orbigny). — X 80 [Chuy N° 364: 122.10—124.00 m].

Fig. 7: *Triloculina* sp. — a, side view: X 160; b, apertural view: X 286 [San José de Carrasco N° 442/1: 17—18 m].

Fig. 8: *Pyrgo nasuta* Cushman. — X 115 [Chuy N° 364: 125.40—128.00 m].

Fig. 9: *Pyrgo ringens patagonica* (d'Orbigny). — X 100 [Puerto La Paloma N° 449/11: 6.50—7.50 m].

Fig. 10: *Miliolinella subrotunda* (Montagu). — X 120 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 11: *Dentalina communis* d'Orbigny. — a, side view: X 20; b, detail of apertural region: X 135 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 12: *Lagena laevis* (Montagu), forma perlucida (Montagu). — X 150 [Chuy N° 364: 124.00—125.40 m].

Fig. 13: *Lagena* sp. — X 160 [Chuy N° 364: 122.10—124.00 m].

Fig. 14: *Lenticulina rotulata* (Lamarck). — a, side view: X 140; b, edge view: X 175. — 14a and 14b are different specimens [Chuy N° 364: 122.10—124.00 m].

Fig. 15: *Lenticulina limbosa* (Reuss). — a, side view: X 326; b, detail of apertural region: X 653 [Salinas N° 1034/1: 32—34 m].

Plate 3

Fig. 1: *Guttulina plancii* d'ORBIGNY. — a, side view: X 110; b, apertural detail: X 226 [Puerto La Paloma N° 449/11: 5.00—6.50 m].

Fig. 2: *Guttulina problema* d'ORBIGNY. — a, side view: X 90; b, detail of apertural region: X 226 [Costa Azul N° 1060/1: 19—21 m].

Fig. 3: *Oolina melo* d'ORBIGNY. — X 251 [Costa Azul N° 1060/1: 19—21 m].

Fig. 4: *Buliminella elegantissima* (d'ORBIGNY). — X 201 [Salinas N° 1034/1: 32—34 m].

Fig. 5: *Bolivina striatula* CUSHMAN. — X 140 [Chuy N° 364: 35—40 m].

Fig. 6: *Fissurina laevigata* RFUSS. — a, side view: X 201; b, apertural detail: X 362 [Salinas N° 1034/1: 32—34 m].

Fig. 7: *Bolivina compacta* SIDEBOTTOM. — X 251 [Lecocq: 1.20 m].

Fig. 8: *Bolivina* cf. *lomitensis* GALLOWAY & WISSLER. — X 191 [Lecocq: 1.00 m].

Fig. 9: *Bolivina* cf. *variabilis* (WILLIAMSON). — X 201 [Lecocq: 1.00 m].

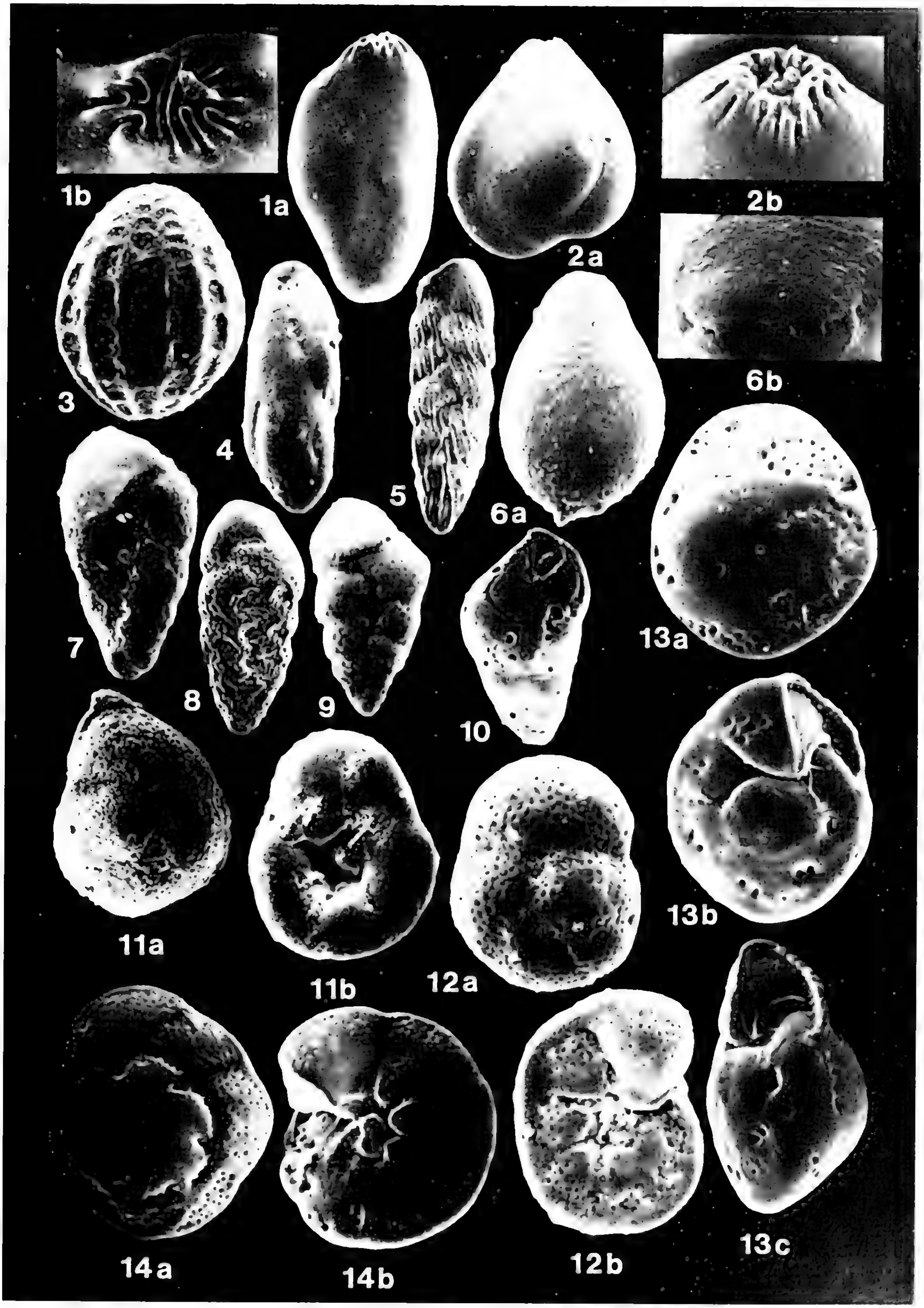
Fig. 10: *Bulimina* cf. *affinis* d'ORBIGNY. — X 160 [Chuy N° 364: 45—50 m].

Fig. 11: *Discorbis peruvianus* (d'ORBIGNY). — a, spiral view: X 145 [Costa Azul N° 1060/1: 19—21 m]; b, umbilical side: X 201 [Lecocq: 0.60 m].

Fig. 12: *Discorbis* gr. *vilardeboanus* (d'ORBIGNY). — a, spiral side: X 238 [Lecocq: 0.60 m]; b, umbilical side: X 201 [Costa Azul N° 1060/1: 19—21 m].

Fig. 13: *Rotorbinella rosea* (d'ORBIGNY). — Test from three sides. a: X 201; b: X 201; c: X 226. — 13b and 13c two views of same specimen [Chuy N° 364: 122.10—124.00 m].

Fig. 14: *Discorbis williamsoni* (CHAPMAN & PARR), forma *praegeri* HERON-ALLEN & EARLAND. — a, spiral side: X 191; b, umbilical side: X 251. 14a and 14b are different specimens [Puerto La Paloma N° 449/11: 7.50—8.00 m].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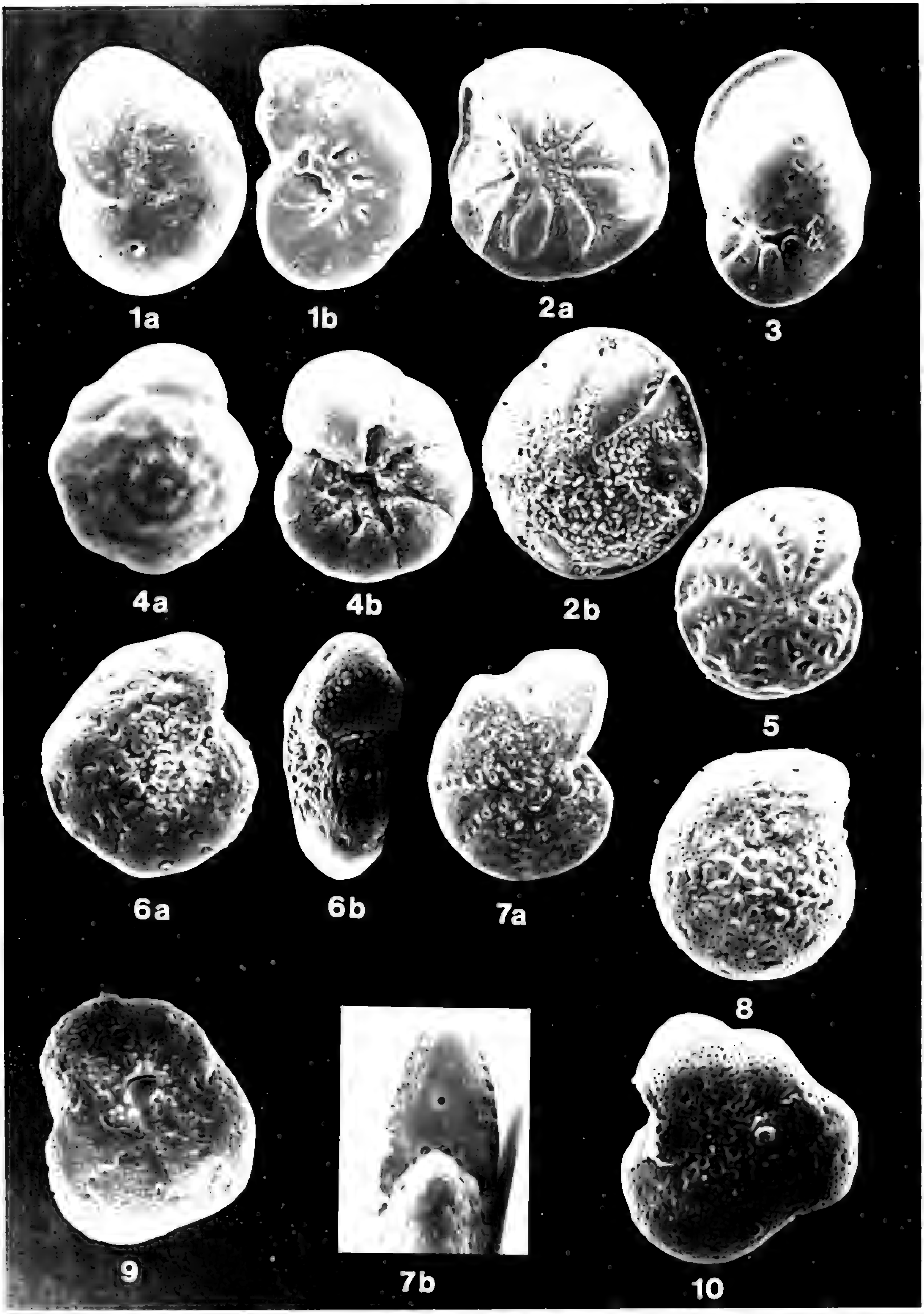

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Plate 4

Fig. 1: *Discorbinella? bertheloti*, forma *boueana* (d'ORBIGNY). — a, spiral side: X 191 [Chuy N° 364: 125.40—128.00 m]; b, umbilical side: X 150 [Chuy N° 364: 122.10—124.00 m].

Fig. 2: *Buccella peruviana* (d'ORBIGNY), s. l. — a: X 160 [Puerto La Paloma N° 449/11: 7.50—8.00 m]; b: X 160 [Chuy N° 364: 122.10—124.00 m].

Fig. 3: *Cancris sagra* (d'ORBIGNY). — X 110 [Chuy N° 364: 124.00—125.40 m].

Fig. 4: *Ammonia beccarii* (LINNAEUS) var. *parkinsoniana* (d'ORBIGNY). — a, spiral side: X 130; b, umbilical side: X 170. — 4a and 4b are different specimens [Rincón de la Bolsa N° 754: 1.50—2.80 m].

Fig. 5: *Elphidium depressulum* CUSHMAN. — X 150 [Chuy N° 364: 124.00—125.40 m].

Fig. 6: *Elphidium* gr. *excavatum* (TERQUEM). — a, side view: X 130; b, apertural view: X 130 [Chuy N° 364: 35—40 m].

Fig. 7: *Elphidium discoidale* (d'ORBIGNY). — a, side view: X 130; b, apertural view: X 191 [Puerto La Paloma N° 449/11: 7.50—8.00 m].

Fig. 8: *Elphidium gunteri* COLE. — X 130 [San Luis N° 1072/1: 29—30 m].

Fig. 9—10: *Elphidium* cf. *discoidale* (d'ORBIGNY). — 9: X 130 [Rincón de la Bolsa N° 754: 1.50—2.80]; 10: X 145 [San José de Carrasco N° 442/1: 17—18 m].

Plate 5

Fig. 1—2: *Elphidium galvestonense* KORNFELD. — 1a, side view: X 150; 1b, appertural view, aperture apparently closed: X 130 [Lecocq: 1.00 m]; 2a, side view: X 140; 2b, detail of apertural region, showing slitlike interiomarginal aperture: X 301 [Lecocq: 0.70 m].

Fig. 3: *Elphidium* aff. *sagrum* (d'ORBIGNY). — X 135 [Chuy N° 364: 122.10—124.00 m].

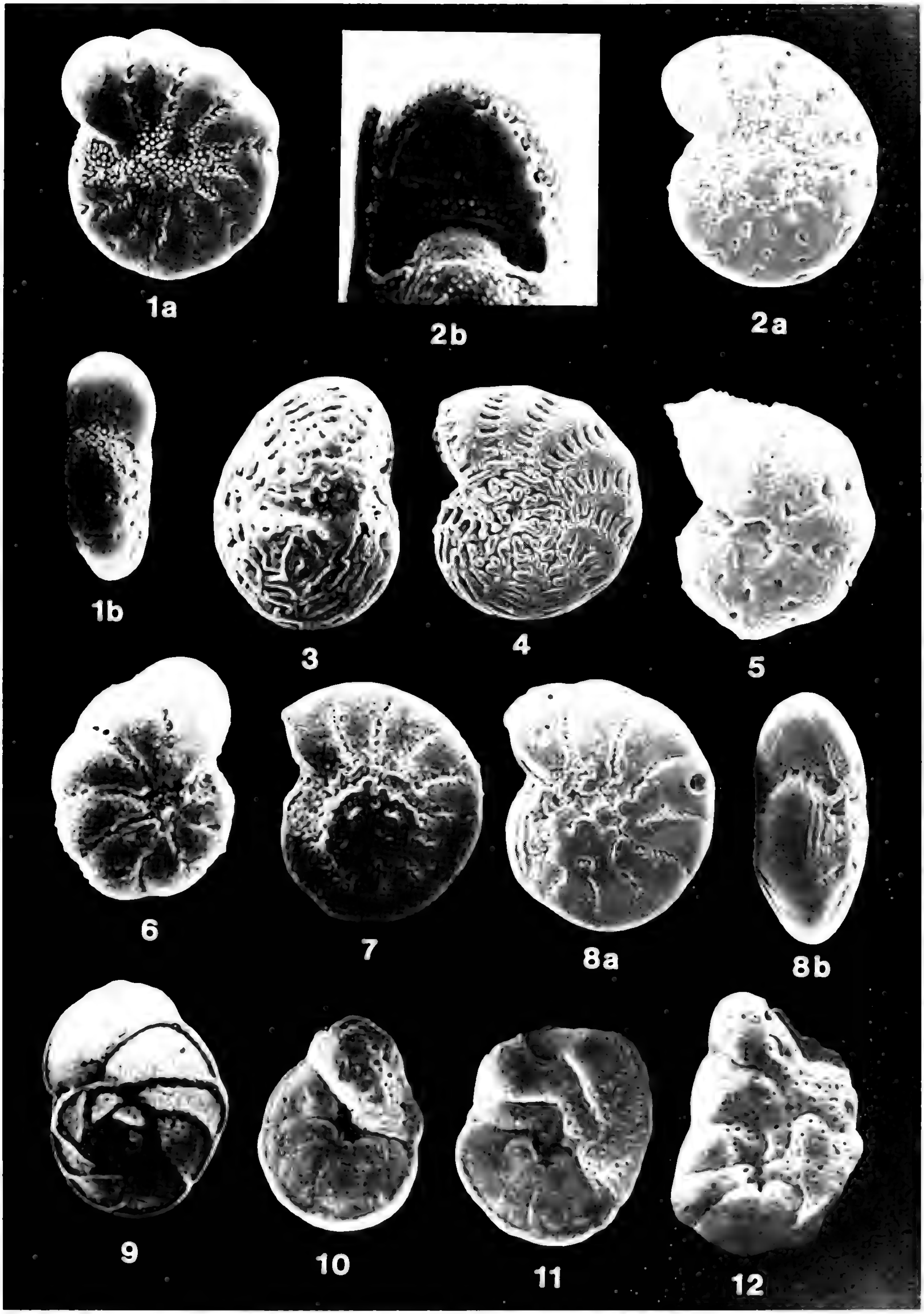
Fig. 4: *Elphidium* sp. A. — X 115 [Chuy N° 364: 122.10—124.00 m].

Fig. 5: *Elphidium* sp. B. — X 251 [Chuy N° 364: 35—40 m].

Fig. 6: *Nonion tisburyensis* BUTCHER. — X 181 [Salinas N° 1034/1: 32—34 m].

Fig. 7—8: *Elphidium* cf. *tuberculatum* (d'ORBIGNY). — 7: X 125 [Chuy N° 364: 122.10—124.00 m]; 8a: X 120; 8b: X 110 [Chuy N° 364: 125.40—128.00 m].

Fig. 9—12: *Poroeponides lateralis* (TERQUEM). — 9, spiral side: X 65; 10, umbilical side: X 50; 11: X 50; 12: X 43. — 9—12 are different specimens [Puerto La Paloma N°449/11: 7.50—8.00 m].



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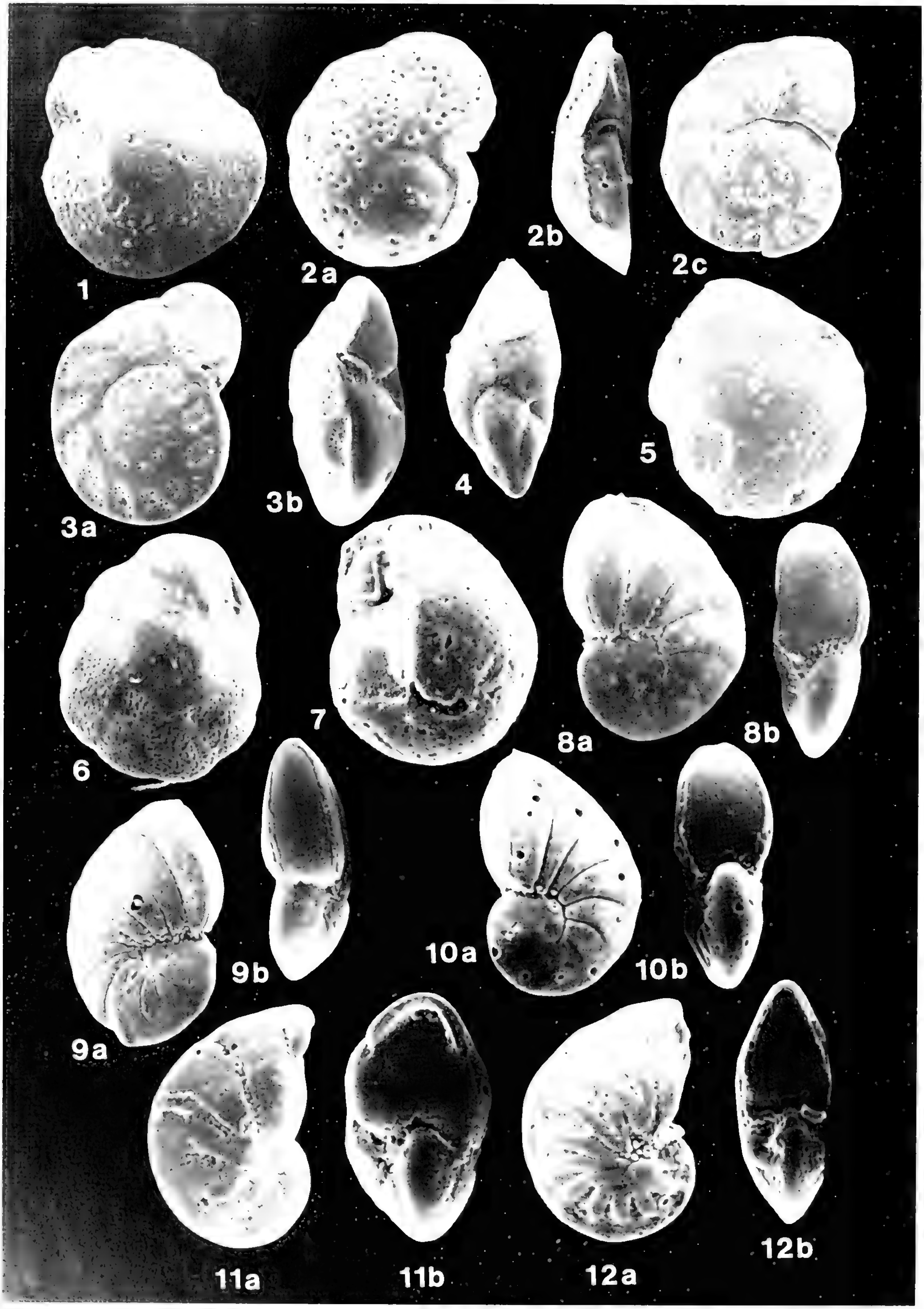
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Plate 6

Fig. 1: *Amphistegina gibbosa* d'ORBIGNY. — X 60 [Chuy N° 364: 128.00—130.00 m].

Fig. 2: *Cibicides aknerianus* (d'ORBIGNY). — Test from three sides. a: X 160; b: X 160; c: X 140. — 2a and 2b two views of same specimen [Chuy N° 364: 122.10—124.00 m].

Fig. 3: *Cibicides "pseudoungerianus"* (CUSHMAN). — a: ventral view: X 140; b: edge view: X 145 [Chuy N° 364: 122.10—124.00 m].

Fig. 4: *Fursenkoina* sp. — X 160 [Chuy N° 364: 124.00—125.40 m].

Fig. 5: *Cassidulina curvata* PHLEGER & PARKER. — X 201 [Chuy N° 364: 125.40—128.00 m].

Fig. 6: *Cassidulina laevigata* d'ORBIGNY. — X 150 [Chuy N° 364: 122.10—124.00 m].

Fig. 7: *Cassidulina subglobosa* BRADY. — X 251 [Chuy N° 364: 122.10—124.00 m].

Fig. 8: *Nonionella atlantica* CUSHMAN. — a, side view: X 140; b, edge view: X 130 [Chuy N° 364: 122.10—124.00 m].

Fig. 9: *Nonionella auricula* HERON-ALLEN & EARLAND. — a, side view: X 85; b, edge view: X 88 [Chuy N° 364: 125.40—128.00 m].

Fig. 10: *Nonion grateloupii* (d'ORBIGNY). — a, side view: X 145; b, edge view: X 150 [Chuy N° 364: 124.00—125.40 m].

Fig. 11: *Nonion* sp. A. — a, side view: X 150; b, edge view: X 156 [Chuy N° 364: 122.10—124.00 m].

Fig. 12: *Nonion* sp. B. — a, side view: X 150; b, edge view: X 150 [Chuy N° 364: 128.00—130.00 m].

Plate 7

Holotype specimen of *Compsognathus longipes* Wagner, 1861 (B. S. P. A. S. I 563).
The scale is 100 mm long.

Ostrom, J. H.: The Osteology of *Compsognathus longipes* Wagner.

Ostrom, J. H.: The Osteology of *Compsognathus longipes* Wagner.

Plate 8

Skull of the holotype specimen of *Compsognathus longipes.* Scale divisions equal 1.0 mm. For identification of the various skull bones and fragments, see Figure 1.

Plate 9

Compsognathus longipes (B. S. P. A. S. I 563).

Fig. 1: Braincase, in ventral aspect. The occipital condyle is conspicuous at the right. The two-pronged structure at the left represents the ventral margins of the cultriform process of the parasphenoid. Scale units equal 1.0 mm.

Fig. 2: Rostral extremity of the left dentary to show the "bent" form of anterior teeth. Succeeding teeth are less "bent", becoming uniformly curved. The horizontal line equals 5 mm.

Fig. 3: The disarticulated hands; left hand to the left and right manus to the right. Scale divisions equal 1.0 mm.

Fig. 4: Example of the two different sized manual unguals preserved. On the left is an impression which is interpreted here as the ungual of digit I, left hand. That on the right includes the bony ungual and parts of the horny sheath of digit II, right hand. Scale divisions equal 1.0 mm.

Fig. 5: Bony ungual and parts of the horny claw (arrows) of digit II of the left manus. Compare with the upper illustration of text figure 5. Scale divisions equal 1.0 mm.


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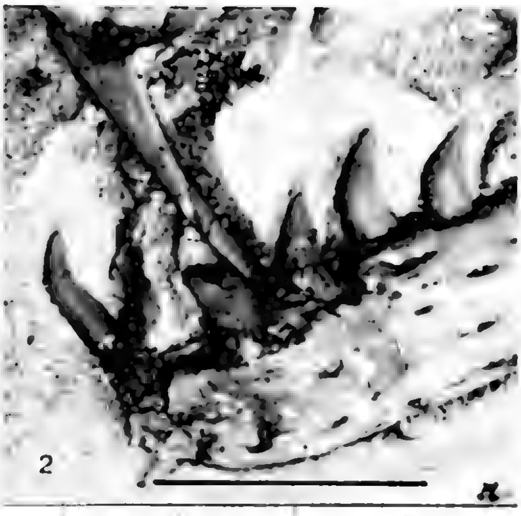
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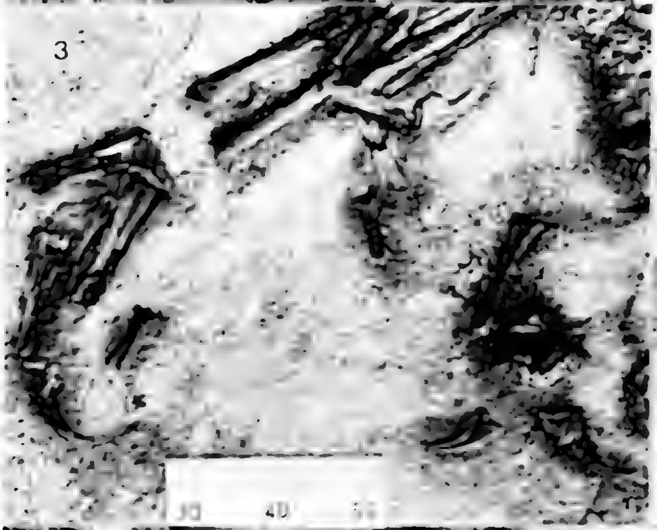
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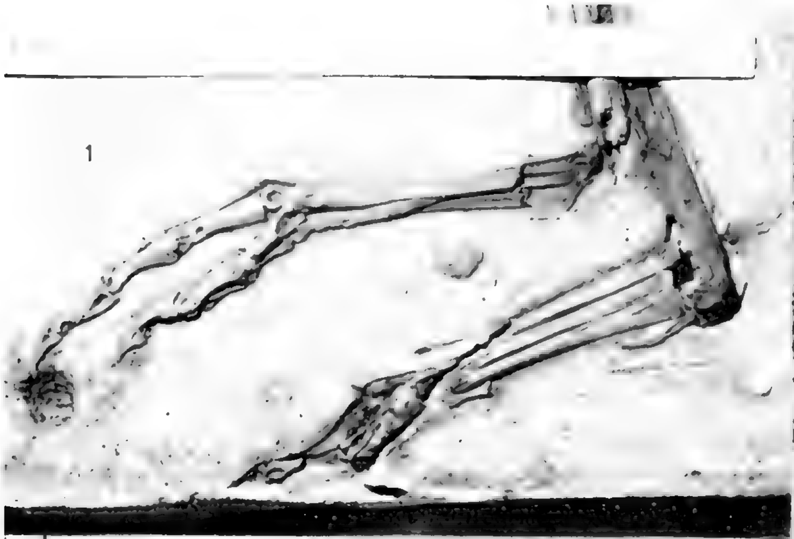
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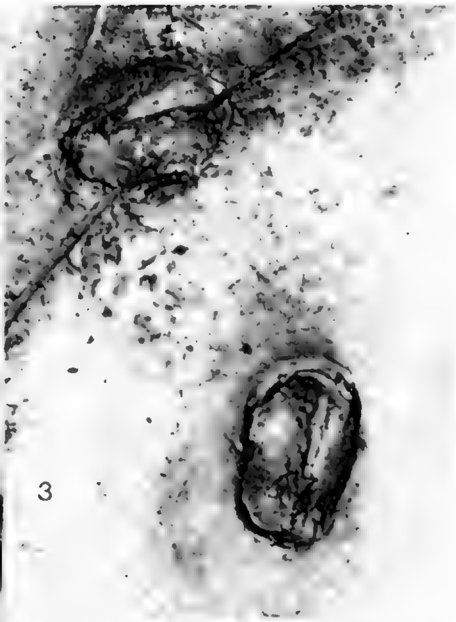
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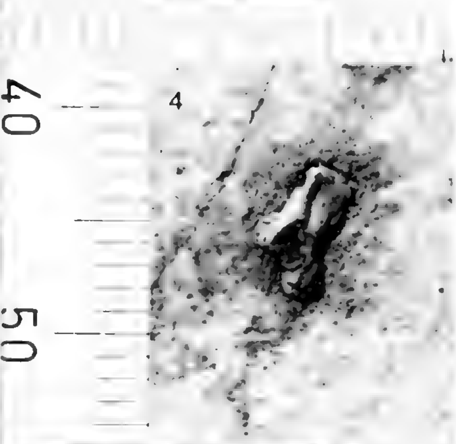
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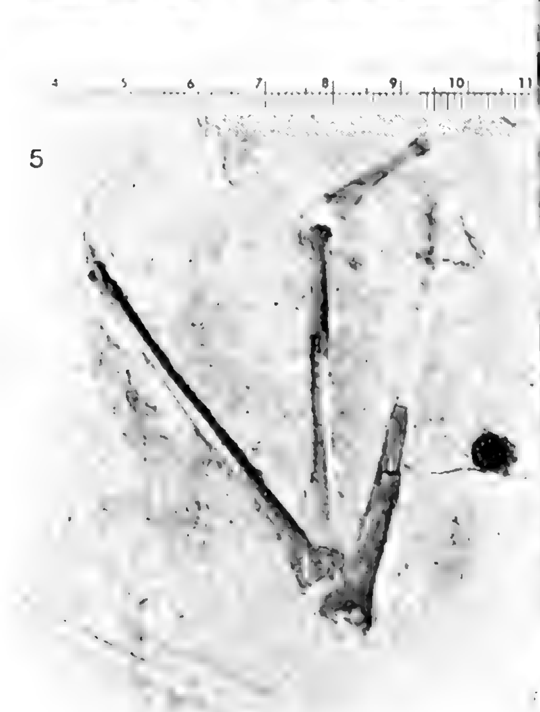
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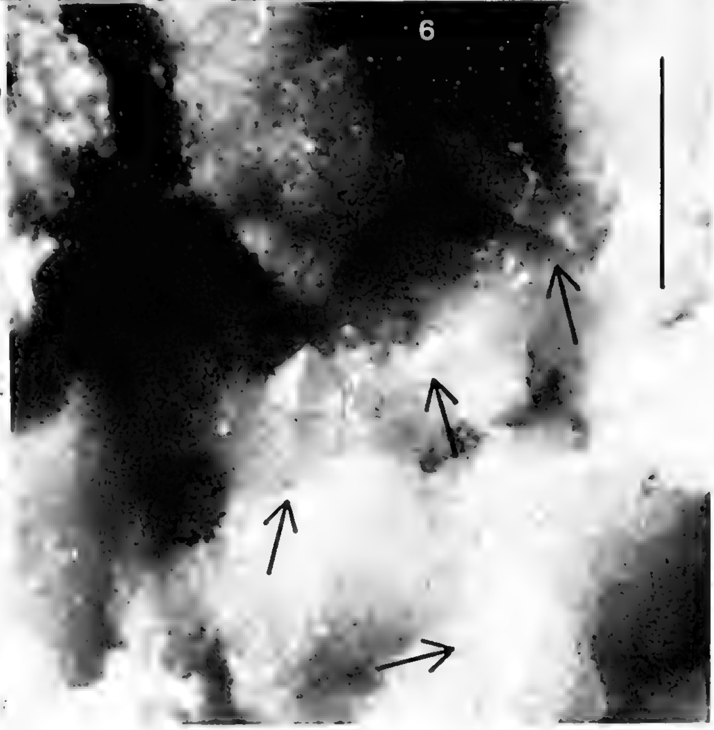
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Ostrom, J. H.: The Osteology of *Compsognathus longipes* Wagner.

Plate 10

Compsognathus longipes (B. S. P. A. S. I 563).

Fig. 1: Right (uppermost) and left hind feet. Scale equals 100 mm.

Fig. 2: Distal phalanges of digit III of the right pes. The penultimate phalanx appears to have been rotated about its long axis and preserved up-side-down. Scale divisions at left equal 1.0 mm.

Fig. 3: Two similar, isolated bones which are believed to be the left and right articulars. They are preserved just above the left maxilla (see Figure 1 and Plate 7.). Scale units equal 1.0 mm.

Fig. 4: Unidentified mystery bone. Scale units at left equal 1.0 mm.

Fig. 5: The Humboldt specimen described by Dames (1884), that sometimes has been referred to *Compsognathus.* These bones appear to represent (from left to right) metatarsals IV, II and III, plus a solitary proximal phalanx. It is concluded here that this specimen is not referrable to *Compsognathus.* Scale Units equal 1.0 mm.

Fig. 6: Rare, minute crystals of quartz (arrows) occurring within calcite crystal-lined vug-like cavities in the body region of *Compsognathus.* These are vidence of solution and secondary crystallization. The vertical line equals 1.0 mm.

Plate 11

Compsognathus longipes (B. S. P. A. S. I 563); so-called dermal armor and soft-tissue impressions.

Fig. 1: The so-called impressions of "skin armor", described by von Huene (1901). This is the site (the depression just below the scapula) in which Huene saw "15 polygons" (arrows ?), which he interpreted as evidence of bony skin plates. Scale divisions equal 1.0 mm.

Fig. 2: Nopsca (1903) interpreted these parallel striations (arrow) between the right radius and ulna of *Compsognathus* as "muscle fibers". Magnification, approximately 15 X.

Fig. 3: This "dimpled texture" was interpreted by Nopcsa (1903) as integument impressions, but it seems much more likely to be a solution-etched surface. Magnification is approximately 15 X.

Fig. 4: Normal, un-etched surface of the *Compsognathus* slab, for comparison with the "skin imprint" of Fig. 3. The curved line is a human hair, to provide scale. Magnification, approximately 15 X.

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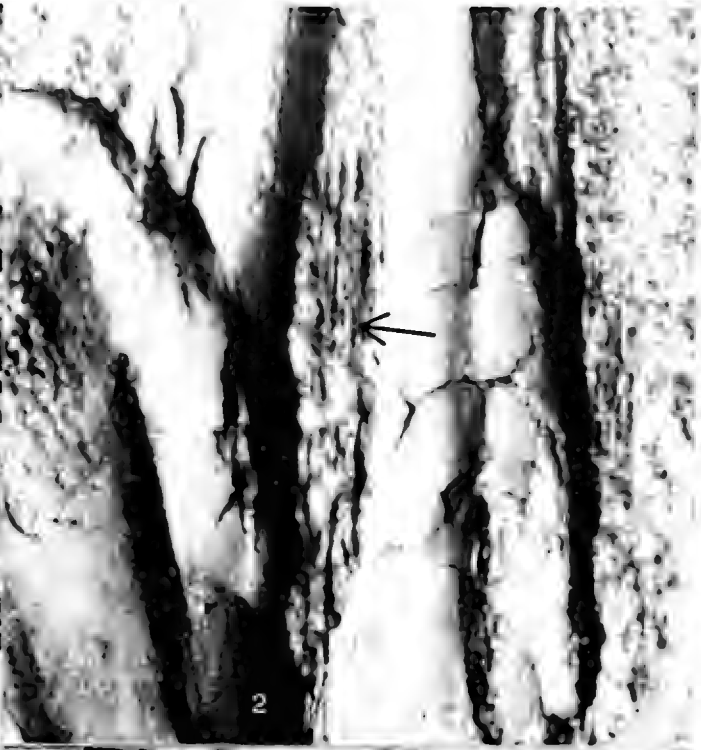

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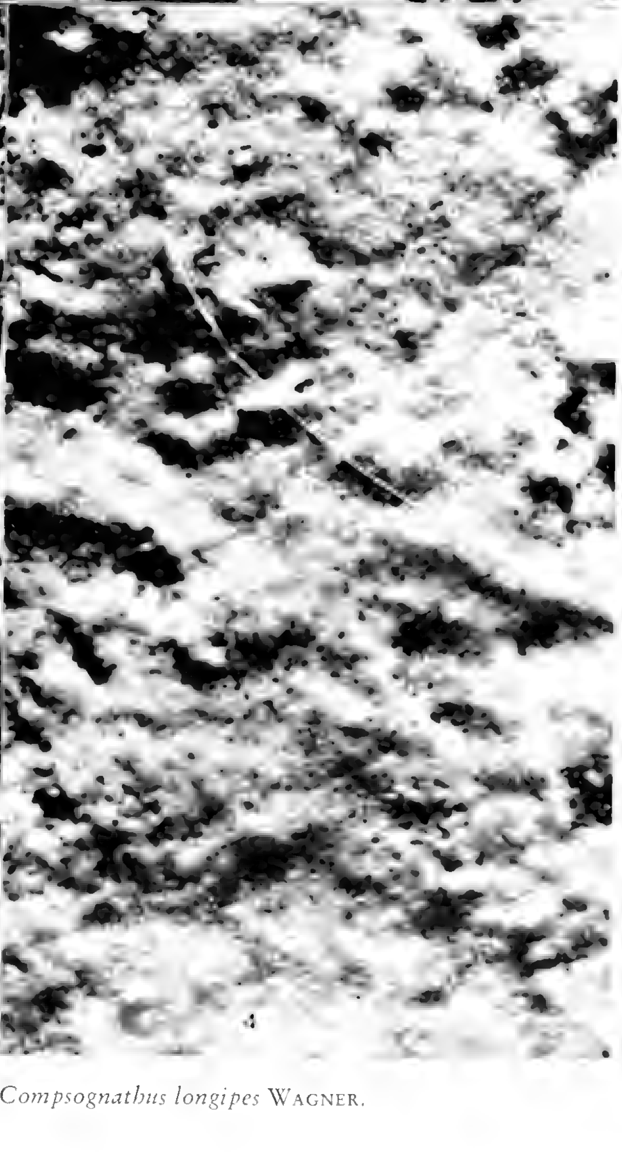

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Ostrom, J. H.: The Osteology of *Compsognathus longipes* Wagner.

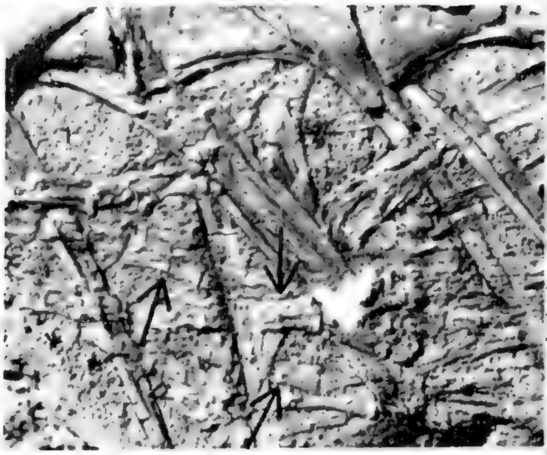
Plate 12

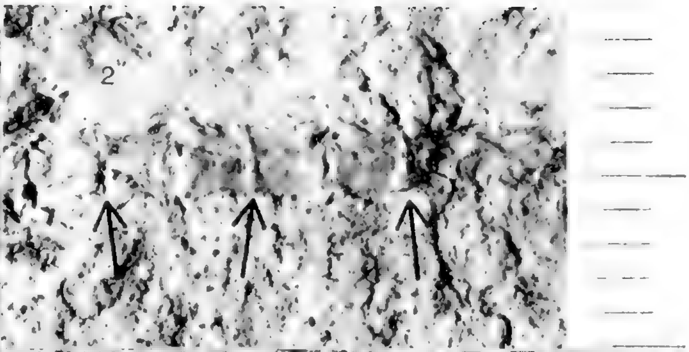
The Nice specimen of *Compsognathus longipes.* Originally, this specimen was assigned to a new species, *C. corallestris,* by Bidar, Demay and Thomel (1972). It is here considered to be indistinct from *C. longipes.*

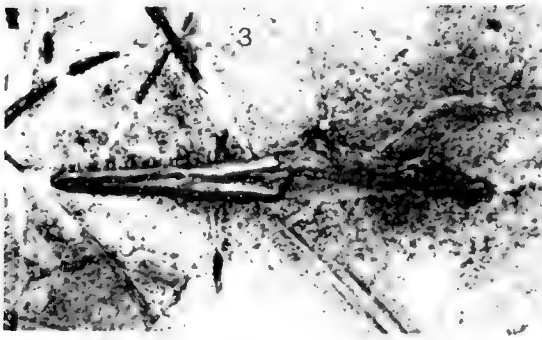
Plate 13

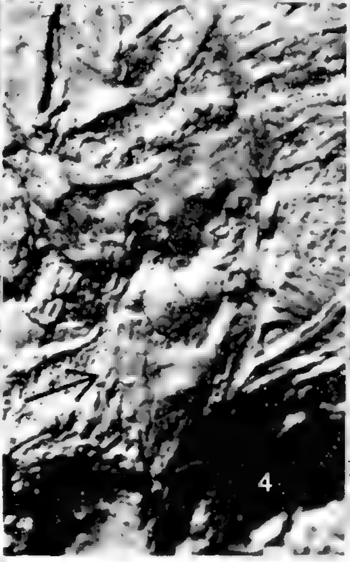
The stomach contents preserved within the rib cage of the Munich specimen of *Compsognathus longipes* — a small lizard skeleton. For identification of these remains, refer to Figures 8 and 9 in the text. Scale is in mm.

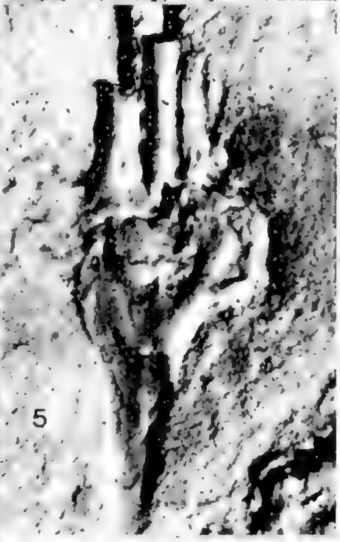
Ostrom, J. H.: The Osteology of *Compsognathus longipes* Wagner.











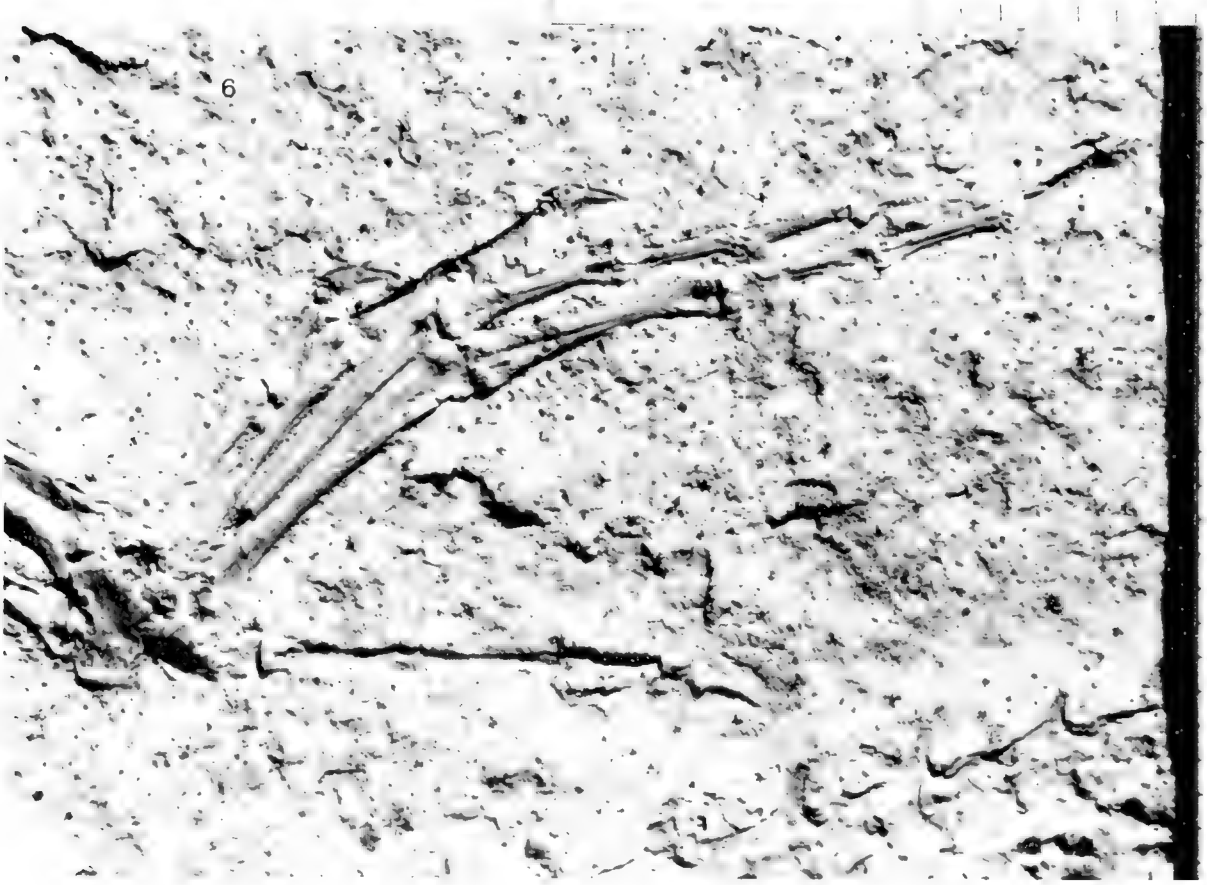


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Plate 14

Bavarisaurus cf. *macrodactylus.*

Fig. 1: Autotomous tail vertebrae of the "stomach contents", for comparison with Fig. 2, at the right. The arrows indicate the autotomy sutures. Scale divisions equal 1.0 mm.

Fig. 2: Autotomous caudal vertebrae of the holotype specimen (B. S. P. 1873 III 501) of *Bavarisaurus macrodactylus.* The arrows point to the autotomy sutures of three contiguous vertebrae. Scale units equal 1.0 mm.

Fig. 3: Isolated left lower jaw preserved outside of the body cavity of *Compsognathus.* Presumably, it belongs to the small skeleton preserved within *Compsognathus.* Scale units equal 1.0 mm.

Fig. 4: The distal end of the left humerus (arrow) of the "consumed" little reptile. Compare this with the humerus illustrated in Fig. 5, to the right. Scale units equal 1.0 mm.

Fig. 5: The distal end of the left humerus of the holotype specimen (B. S. P. 1873 III 501) of *Bavarisaurus macrodactylus.* Compare this with Fig. 4, to the left. The scale divisions equal 1.0 mm.

Fig. 6: The left pes of the holotype specimen of *Bavarisaurus macrodactylus* (B. S. P. 1873 III 501). Compare this with text Figure 10, the reconstructed foot of the "stomach contents" of *Compsognathus.* The scale units at the right equal 1.0 mm.

Lithograph of the type specimen of *Compsognathus longipes* Wagner 1861, in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich. Coincidentally, the stone from which this print was made, was discovered by the author in 1961 in the Vertebrate Paleontology collections of the Peabody Museum of Natural History, Yale University, New Haven, Connecticut. How and when this stone was obtained by Yale are not known, but it probably was acquired by O. C. Marsh sometime after his visit to Munich in 1881. The art work apparently was completed after 1882, because the right tarsal fragment described by Baur (1882) is missing in the lithograph. The artist is unknown, but this work may be the "careful drawing of the original made by Krapf in 1887" (Marsh, 1895, p. 409; 1896, p. 228) mentioned by Marsh as part of the basis for his restoration of *Compsognathus*. The print reproduced here was made from the original stone by Heddi Seibel of the Yale University School of Art.

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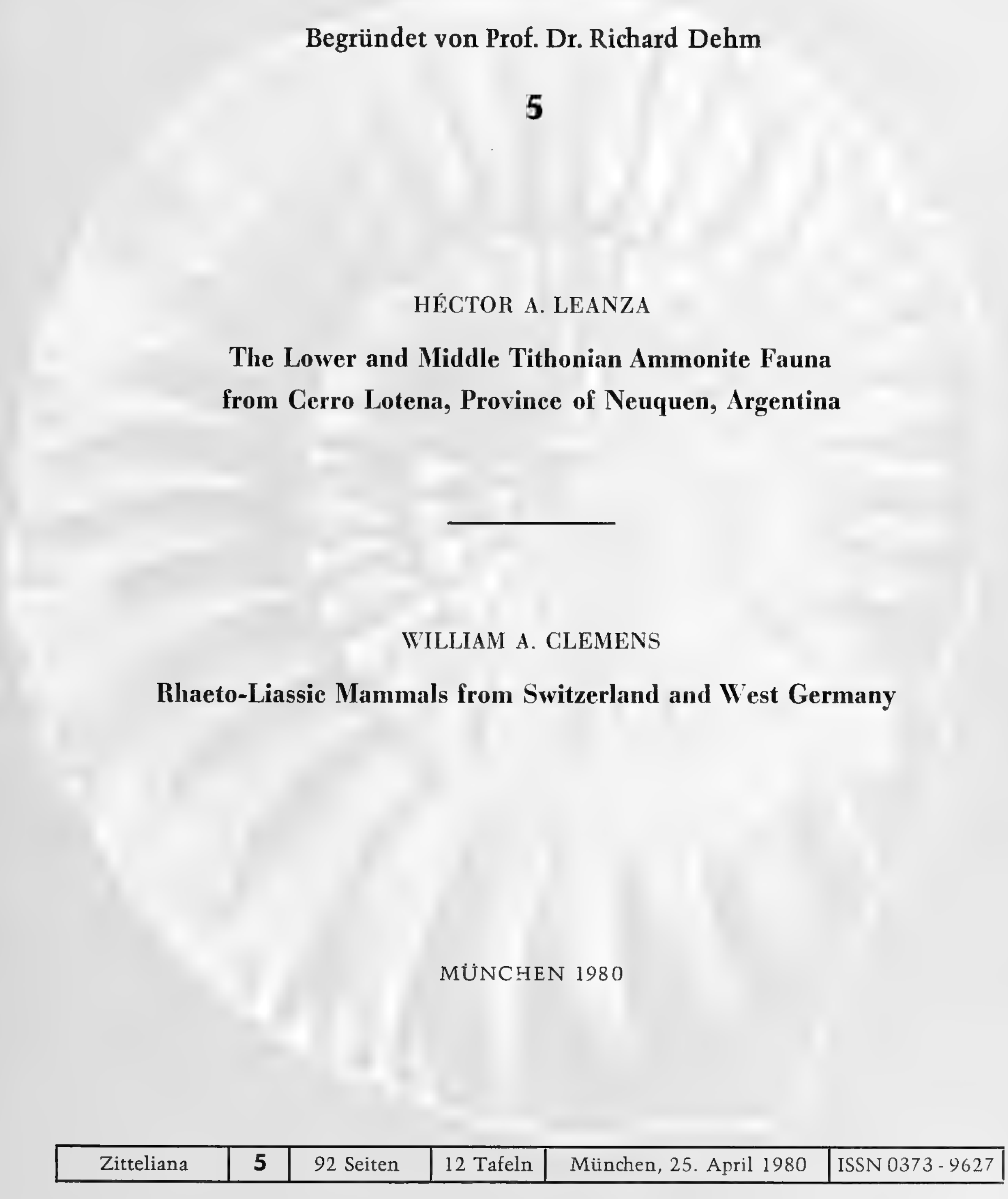

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The Lower and Middle Tithonian Ammonite Fauna from Cerro Lotena, Province of Neuquen, Argentina.

BY

HÉCTOR A. LEANZA*)

With 10 text figures and plates 1—9

ABSTRACT

The present monograph deals with the description of the ammonite fauna from Cerro Lotena, located in the south central part of the Neuquén province, Argentine Republic. The stratigraphic section investigated occurs on the southern slope of Cerro Lotena. In this section the following formations were distinguished in ascending order: the Vaca Muerta Formation (129 m), the Picún Leufú Formation (57 m) and the Mulichinco Formation (101 m) *pars.* The entire ammonite fauna described here is from the Vaca Muerta Formation. The Picún Leufú Formation, characterized by a coastal facies of bivalves contains ammonites only sporadically. The Vaca Muerta Formation is attributed to the Lower and Middle Tithonian, the Picún Leufú Formation to the Upper Tithonian and the Mulichinco Formation to the Berriasian.

The fauna consists of 5 families, 16 genera, 30 species and 2 subspecies. Of these, one genus, 6 species and one subspecies are new, as follows: *Choicensisphinctes* gen. nov., *Glochiceras steueri* n. sp., *Hildoglochiceras wiedmanni* n. sp., *Parastreblites comahuensis* n. sp., *Subdichotomoceras araucanense* n. sp., *Pachysphinctes americanensis* n. sp., *Virgatosphinctes evolutus* n. sp. and *Choicensisphinctes choicensis sutilis* n. ssp. The genera *Hildoglochiceras, Parastreblites, Pachysphinctes* and *Parapallasiceras* are cited for the first time from the Andean Tithonian.

The fauna can be grouped in 4 associations that basically correspond to ammonite zones previously established by others authors, as follows: *Virgatosphinctes mendozanus* Zone, *Pseudolissoceras zitteli* Zone, *Aulacosphinctes proximus* Zone and *Windhauseniceras internispinosum* Zone. Considering the tripartite division of the Tithonian adopted here, the first zone corresponds to the uppermost Lower Tithonian and the remaining three to the Middle Tithonian. The age and other features of these zones are considered, and suggestions are made toward improving their definition.

The described fauna shows close affinities principally with those of Mexico, Madagascar and India, and to a lesser extent with those of the Mediterranean Realm. No true Boreal elements have been found.

KURZFASSUNG

Es wird die Ammonitenfauna des Cerro Lotena beschrieben, der im Süden des zentralen Teils der Provinz Neuquén (Argentinien) liegt. Das hier beschriebene Profil ist am Südhang des Cerro Lotena aufgeschlossen. Von unten nach oben werden folgende Formationen unterschieden: Vaca Muerta-Formation (129 m), Picún Leufú-Formation (57 m) und Mulichinco-Formation (101 m) *pars.* Die hier beschriebene Ammonitenfauna stammt aus der Vaca Muerta-Formation, die Unterem und Mittlerem Tithon entspricht. Die dem Oberen Tithon entsprechende Picún Leufú-Formation ist in Litoralfazies mit Bivalven und nur sporadischen Ammoniten entwickelt. Die Mulichinco-Formation entspricht dem Berrias.

Die hier beschriebene Fauna besteht aus 5 Familien, 16 Gattungen, 30 Arten und 2 Unterarten. Davon sind 1 Gattung, 6 Arten und 1 Unterart neu, und zwar *Choicensisphinctes* n. g., *Glochiceras steueri* n. sp., *Hildoglochiceras wiedmanni* n. sp., *Parastreblites comahuensis* n. sp., *Subdichotomoceras araucanense* n. sp., *Pachysphinctes americanensis* n. sp., *Virgatosphinctes ecolutus* n. sp. und *Choicensisphinctes choicensis sutilis* n. ssp. Die Gattungen *Hildoglochiceras,*

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*) Secretaría de Minería, Av. Santa Fe 1548, 1060 Capital Federal, Argentina. Temporarily at Institut und Museum für Geologie und Paläontologie, Sigwartstr. 10, 7400 Tübingen, West Germany.

Parastreblites, Pachysphinctes und *Parapallasiceras* werden zum ersten Mal aus dem andinen Tithon beschrieben.

Die Fauna kann in vier Associationen gruppiert werden, die im wesentlichen bereits bestehenden Ammonitenzonen entsprechen. Es sind dies die Zone des *Virgatosphinctes mendozanus,* die Zone des *Pseudolissoceras zitteli,* die Zone des *Aulacosphinctes proximus* und die Zone des *Windhauseniceras internispinosum.* Da hier der Dreigliederung des Tithon gefolgt wird, entspricht die erstgenannte Zone dem höchsten Untertithon, die drei übrigen Zonen dem Mitteltithon. Die Zonengliederung wird ausführlich diskutiert.

In paläogeographischer Hinsicht zeigt die Fauna enge Beziehungen zu Mexico, Madagascar und Indien, dagegen geringere Verbindungen zur mediterranen Faunenprovinz. Boreale Faunenelemente sind demgegenüber nicht nachweisbar.

RESUMEN

La presente monografía trata acera de la descripción de la fauna de ammonites del Cerro Lotena, situado en la parte sud central de la provincia del Neuquén, República Argentina. Se ofrece la sección estratigráfica levantada en el faldeo sur del Cerro Lotena, donde se distinguen en orden ascendente las Formaciones Vaca Muerta (129 m), Picún Leufú (57 m) y Mulichinco (101 m) *pars.* La totalidad de la fauna de ammonites estudiada procede de la Formación Vaca Muerta. La Formación Picún Leufú, caracterizada por una facies costera de bivalvos, posee ammonites sólo muy esporádicamente. Según los resultados alcanzados, la Formación Vaca Muerta se atribuye al Tithoniano inferior y medio, la Formación Picún Leufú al Tithoniano superior y la Formación Mulichinco al Berriasiano.

El estudio de la fauna permitió individualizar 5 familias, 16 géneros, 30 especies y 2 subespecies. De ellos, un género, 6 especies y una subespecie son nuevos, a saber: *Choicensisphinctes* gen. nov., *Glochiceras steueri* n. sp., *Hildoglochiceras wiedmanni* n. sp., *Parastreblites comahuensis* n. sp., *Subdichotomoceras araucanense* n. sp., *Pachysphinctes americanensis* n. sp., *Virgatosphinctes evolutus* n. sp. y *Choicensisphinctes choicensis sutilis* n. ssp. Los géneros *Hildoglochiceras, Parastreblites, Pachysphinctes* y *Parapallasiceras* se citan por primera vez en el Tithoniano andino.

La fauna estudiada puede agruparse en 4 asociaciones que básicamente responden a zonas de ammonites previamente establecidas por otros autores, a saber: Zona de *Virgatosphinctes mendozanus,* Zona de *Pseudolissoceras zitteli,* Zona de *Aulacosphinctes proximus* y Zona de *Windhauseniceras internispinosum.* Según la división tripartita del Tithoniano aquí adoptada, la primera zona corresponde al más alto Tithoniano inferior, mientras que las tres restantes indican el Tithoniano medio. Se efectuan consideraciones y aportes que permiten ampliar el conocimiento de cada una de ellas, así como precisar su edad con mayor exactitud.

La fauna descripta presenta estrechas afinidades principalmente con aquéllas de México, Madagascar e India y, en menor grado, con aquéllas del dominio mediterráneo. No se hallaron elementos boreales en la fauna estudiada.

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I. INTRODUCTION

The description of the ammonite fauna from Cerro Lotena, which is the basis of this monograph, was necessary in order to advance our knowledge of the Andean Tithonian. Although important progress related to the Upper Jurassic and Lower Cretaceous was made by A. F. LEANZA (1945), who described the ammonite fauna from Sierra Azul, the Lower and Middle Tithonian faunas have not been sufficiently investigated. The Sierra Azul was a topographically elevated area during most of the Jurassic period and, therefore, the Tithonian transgression begins in this area with the *Windhauseniceras internispinosum* Zone, which is poorly documented and contains only *Wichmanniceras mirum* in association with the index species. Above this zone the ammonites become abundant up to the late Valanginian, including the transition from the Jurassic to the Cretaceous.

Knowledge concerning the Lower and Middle Tithonian, however, has not appreciably improved since the classic monographs of BURCKHARDT (1900a, 1900b, 1903), HAUPT (1907), KRANTZ (1926, 1928) and WEAVER (1931). The work of INDANS (1954), although referred to the Lower Tithonian, deals exclusively with the Virgatosphinctinae Beds at the base of the Tithonian transgression in southern Mendoza, and therefore does not allow zonation of the Tithonian.

As anticipated by GROEBER (in A. F. LEANZA, 1945, p. 85), knowledge of the Andean Tithonian could be improved by the study of the Cerro Lotena fauna. Since this fauna extends downwards from the *W. internispinosum* Zone, it provides important information on the earlier part of the Tithonian.

The collection of ammonites described here was made by Dr. Anselmo WINDHAUSEN during the summer of 1912. It was archieved in the repository of the Museo de la Secretaría de Minería of the Argentine Republic. Part of this collection was temporarily sent to Tübingen in order to carry out the present study. The specimens were numbered according to the outlines of the stratigraphic section made by WINDHAUSEN (1914, table VIII), and they were subdivided in correspondence with WINDHAUSEN's profiles I to III, which he later respectively identified as "Kimmeridge-Portland", "Lower Tithonian" and "Upper Tithonian".

The death of A. F. LEANZA in 1975 prevented his intended description of the WINDHAUSEN collection. The present author, however, has had several opportunities, beginning in 1970, to visit the Cerro Lotena area in association with a phosphate exploration programme carried out by the Secretaría de Minería of the Argentine Republic. As a result, revision of WINDHAUSEN's section and relocation of his collected samples has been carried out.

A visitor to the Cerro Lotena area today will surely not find specimens of quality comparable to those figured here from the WINDHAUSEN collection. The fact that this area is relatively accessible, and close to oil fields and kaolin and bentonite mines, has led to invasions of tourists and collectors who over the years have removed a large amount of scientifically valuable material.

Acknowledgements

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I am particularly grateful to Prof. Dr. Jost WIEDMANN, who acted as academic supervisor and coordinator, for his kind assistance and stimulating discussions during my stay in Tübingen. Special thanks are due to Dr. Peter SPRECHMANN for valuable help and critiscism, and to Dr. T. J. BARRETT, who improved the English text. The photographs of this monograph were made with the expert help of Mr. W. WETZEL (Tübingen), and the illustrations were prepared by K. MICHAEL.

This monograph is dedicated to the memory of my father, Prof. Dr. Armando F. LEANZA.

II. PREVIOUS WORK

In the year 1907, Oscar HAUPT described a fossil assemblage composed of cephalopods, pelecypods, brachiopods, echinoderms, worms and fishes from Cerro Lotena. The material on which HAUPT based his study was collected by Gustav STEINMANN during his study trip to the Andes in the years 1902 and 1903. A few years later, R. DOUVILLÉ (1910) published the results of his paleontological investigations on cephalopods collected by M. RECOPE. Though DOUVILLÉ (1910, p. 5) stated that the fossils came from a region between the Agrio river and the Picún Leufú creek, it is likely that most of them are from the Cerro Lotena area since at this time RECOPE was working as inspector at the oil concession at Cerro Lotena.

The ammonites studied by Haupt and Douvillé became rapidly known in the scientific world because the latter author favoured the presence of Boreal elements in this region of the Andes. This was just at the time when the legendary discussion between the great ammonitologists Charles Burckhardt (1911a, 1911b) and Victor Uhlig (1910, 1911a, 1911b) regarding the presence or absence of ammonites with Boreal affinities in the Andean domain, reached its most intense point.

It was at this time, with an interest in both the presence of oil and the supposed presence of Boreal ammonite faunas in this region, that Windhausen visited Cerro Lotena in 1912. There, with the help of A. Flossdorf, he collected the ammonites described in this monograph. Two years later, Windhausen (1914) gave a summary of his results, illustrating for the first time and with particular detail the Cerro Lotena section.

New geological descriptions of the area were later made, as a result of its petroliferous potential by J. Keidel (1925). One year later F. Krantz (1926) published an important paper on Middle and Upper Tithonian ammonites, describing some species from Cerro Lotena. A translation of this work into Spanish appeared two years later (F. Krantz, 1928). Ch. Weaver (1931) also presented very important biostratigraphical data for the Cerro Lotena, including its stratigraphical section.

Regional mapping of the area was carried out by T. Suero (1942, 1951), who mapped the Hoja 36c, Cerro Lotena, at a 1:200 000 scale.

More recently, detailed studies of the stratigraphy of this area have been made (H. Leanza, 1973; H. Leanza, H. Marchese & J. C. Riggi, 1977; H. Leanza & C. Hugo, 1977). Z. Gasparini & D. Dellape (1976) also have presented stratigraphic data relating to the occurrence of fossil crocodiles in the Vaca Muerta Formation.

It is also important to mention the classic monographs of O. Behrendsen (1891—1892; 1922, transl.), A. Steuer (1897; 1921, transl.), H. Gerth (1925, 1926), A. F. Leanza (1945) and J. Indans (1954), in which a great number of cephalopods were described from the Neuquén and Mendoza basin; these are directly or indirectly related to the fauna described here.

III. STRATIGRAPHY

The Cerro Lotena is located 70 km south east of Zapala, in the southern part of the Neuquén province, Argentina (see Fig. 1).

The stratigraphic section described below was measured on the southern slope of Cerro Lotena, and consists of the following Formations: Vaca Muerta (Weaver, 1931, *emend.* H. Leanza, 1972, 1973), Picún Leufú (H. Leanza, 1973) and Mulichinco (Weaver, 1931). All these Formations constitute part of the Mendoza Group. The stratigraphy of the area can be summarized as follows:

Campanian-Santonian	Candeleros Formation	Neuquén Group *pars*
	Unconformity	
Lower Berriasian	Mulichinco Formation	Mendoza Group *pars*
Upper Tithonian	Picún Leufú Formation	
Middle Tithonian Lower Tithonian	Vaca Muerta Formation	
	Unconformity	
Calovian	Lotena Formation	

The ammonite faunas studied in this monograph are entirely from the Vaca Muerta Formation. The beds of this formation strike nearly east-west and dip about 20° to the south, a value which decreases slightly upsection. The Vaca Muerta Formation rests unconformably upon the Lotena Formation by means of a basal conglomerate termed the Quebrada del Sapo Formation by some authors (cf. Digregorio, 1972), and is conformably overlain by the Picún Leufú Formation, which is characterized by a coastal facies of bivalves. Ammonites are rare in this latter formation but sufficient to postulate an Upper Tithonian age (cf. H. Leanza & C. Hugo, 1977, p. 253).

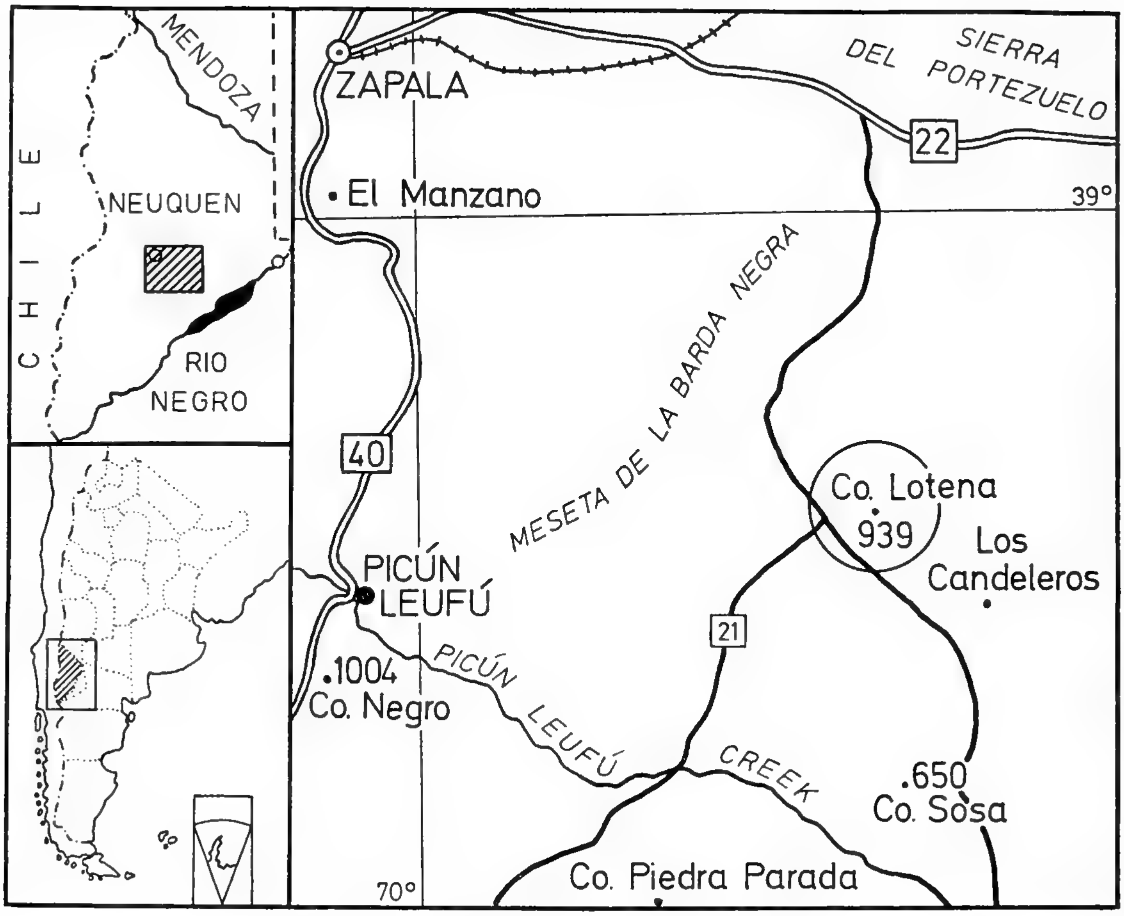

Figure 1: Sketch map of the Cerro Lotena area.

Description of the Cerro Lotena Section

The lithological characteristics of the sediments of the stratigraphic section, as well as its paleontological contents, are as follow (from top to base):

Top: base of the Mulichinco Formation

Picún Leufú Formation H. Leanza, 1973. Total thickness: 57 m

Bed 36: 0.80 m fine grained calcarenite, yellowish white, hard.

Bed 35: 4.20 m brownish calcarenite, with *Pholadomya gigantea* Sow., *Lucina leufuensis* Weav. and *Panope dupiniana* d'Orb.

Bed 34: 4.00 m fine grained calcarenite, yellowish. At the base are quartz geodes In the more calcareous portion are *Myoconcha transatlantica* Burck. and *Lucina leufuensis* Weav.

Bed 33: 2.00 m fine banded calcareous sandstone, yellowish brown.

Bed 32: 2.00 m yellowish white coquina, with *Lucina neuquensis* Haupt, *Pholadomya gigantea* Sow. and *Panope dupiniana* d'Orb.

Bed 31: 5.00 m fine grained calcareous sandstone, brownish, fissile.

Bed 30: 0.70 m yellowish white coquina, with *Pholadomya gigantea* Sow., *Lucina leufuensis* Weav. and *Panope* sp.

Bed 29: 6.30 m fine grained calcarenite, brownish.

Bed 28: 0.80 m yellowish white coquina, with *Ostrea minos* Coq., *Panope dupiniana* d'Orb. and *Lucina leufuensis* Weav.

Bed 27: 7.20 m dark green shales.

Bed 26: 8.00 m yellowish white coquina, which constitutes an excellent guide horizon. *Ostrea minos* Coq., *Ostrea lotenoensis* Weav., *Megatrigonia eximia* (Phil.), *Panope dupiniana* d'Orb. and *Substeueroceras* sp. indet.

Bed 25: 14.00 m fine grained calcareous sandststone, fissile, with some aragonitic horizons. *Ostrea lotenoensis* Weav., *Exogyra couloni* (Defr.) d'Orb. and *Lucina neuquensis* Haupt.

Bed 24: 2.00 m brownish coquina, with *Exogyra couloni* (Defr) d'Orb. sp. juv., *Lucina neuquensis* Haupt and *Serpula* sp.

Vaca Muerta Formation WEAVER, 1931, *emend.* H. LEANZA, 1972. Total thickness: 129 m.

Bed 23: 25.00 m dark olive-green shales, with some bentonitic levels. *Ostrea lotenoensis* WEAV. and *Serpula antiquata* SOW.

Bed 22: 0.40 m pinkish-gray limestone, with *Windhauseniceras internispinosum* (KRANTZ) and *Pachysphinctes americanensis* n. sp.

Bed 21: 1.60 m olive-green and dark gray marls.

Bed 20: 0.20 m pinkish-gray massive limestone, with *Hemispiticeras* aff. *H. steinmanni* (STEUER).

Bed 19: 0.80 m dark olive-green marls.

Bed 18: 0.50 m pinkish-gray massive limestone, with *Parapallasiceras* sp. indet.

Bed 17: 4.00 m olive-green marls and shales.

Bed 16: 0.30 m yellowish-white massive limestone, with *Subdichotomoceras windhauseni* (WEAV.), *W. internispinosum* (KRANTZ), *Corongoceras lotenoense* SPATH and *Parapallasiceras* aff. *P. pseudocolubrinoides* OLORIZ.

Bed 15: 3.20 m yellowish-green marls.

Bed 14: 0.40 m yellowish-grey massive limestone, with *W. internispinosum* (KRANTZ) and *Aulacosphinctoides* aff. *A. hundesianus* (UHLIG).

Bed 13: 3.00 m yellowish-grey marls.

Bed 12: 0.80 m yellowish-grey massive limestone, with *Subdichotomoceras araucanense* n. sp. and *Aulacosphinctoides* sp. indet.

Bed 11: 2.00 m yellowish-brown marls.

Bed 10: 0.80 m greyish-white limestone, with *Parapallasiceras* aff. *recticosta* OLORIZ, and *A. euomphalum* STEUER.

Bed 9: 4.00 m dark brownish-grey shales. *W. internispinosum*

Bed 8: 10.00 m greenish marls and shales.

Bed 7: 21.00 m greenish and dark brownish shales, with many nodules and calcareous concretions. Abundant *Aulacosphinctes proximus* (STEUER) and *Laevaptychus crassissimus* (HAUPT), and rare *Subdichotomoceras* sp. juv. indet.

Bed 6: 10.00 m dark brown shales, with *Pseudolissoceras zitteli* (BURCK.) and *P. pseudooolithicum* (HAUPT). Remains of fish scales and *Ichthyosaurus* bones.

Bed 5: 0.70 m dark grey limestone, with some quartz veins. *P. zitteli* (BURCK.) and *Parastreblites comahuensis* n. sp.

Bed 4: 14.30 m dark brown shales, with *P. zitteli* (BURCK.).

Bed 3: 1.00 m grey brownish limestone with *P. zitteli* (BURCK.) and rare *Glochiceras steueri* n. sp. and *Hildoglochiceras wiedmanni* n. sp.

Bed 2: 25.00 m brown, yellowish-brown and dark green bituminous shales (Virgatosphinctinae Beds). At the top are remains of *Geosaurus araucanensis* (Crocodilia). Ammonites: *Pseudinvoluticeras douvillei* SPATH, *P. windhauseni* (WEAV.), *P. (?) wilfridi* (DOUV.), *Virgatosphinctes andesensis* (DOUV.), *V. mexicanus* (BURCK.), *V. burckhardti* (DOUV.), *V. denseplicatus rotundus* SPATH, *V. evolutus* n. sp., *Choicensisphinctes choicensis* (BURCK.), *Ch. choicensis sutilis* n. ssp. and *Ch. erinoides* (BURCK.).

Bed 1: 0.50 m to 5.00 m basal conglomerate with rounded clasts of quartz, porphirites and pre-Tithonian sedimentary rocks, up to 4 cm of diameter. Several strongly eroded Virgatosphinctinae fragments also present. The conglomerate constitutes the Quebrada del Sapo Formation of some authors (cf. DIGREGORIO, 1972).

Unconformity

Base: Lotena Formation WEAVER, 1931, Calovian.

IV. ANALYSIS OF THE FAUNA

The Cerro Lotena ammonite fauna described here comprises 156 specimens, which are distributed amongst 5 families, 16 genera, 30 species and 2 subspecies. Of these, one genus, 6 species and one subspecies are new. The family Perisphinctidae constitutes 66 % of the fauna, followed by the families Berriasellidae and Haploceratidae with 13 % each. The remaining 8 % is represented by the families Oppeliidae and Aspidoceratitidae. The systematic descriptions follow the order proposed by ARKELL *et al.* (1957) in the Treatise of Invertebrate Paleontology.

The family Haploceratidae is represented by the genera *Pseudolissoceras, Glochiceras* and *Hildoglochiceras*. The genus *Pseudolissoceras* is very important because it is a cosmopolitan form, known not only from the Andean Tithonian of South America (BURCKHARDT, 1903; HAUPT, 1907; KRANTZ, 1926, 1928; WEAVER, 1931), Cuba (IMLAY, 1942) and Mexico (BURCKHARDT, 1906; VERMA & WESTERMANN, 1973), but also in such distant regions as Tunisia (ARNOULD-SAGET, 1951, 1951a), Iraq (SPATH, 1950), Spain (OLORIZ, 1978), southeast France (DONZE & ENAY, 1961), south Germany (BARTHEL, 1962), the Carpathians (ZITTEL, 1870), Rumania (AVRAM, 1976) and Italy (*fide* ENAY, 1972). In Cerro Lotena 2 species of this genus were found and identified as *P. zitteli* (BURCK.) and *P. pseudooolithicum* (HAUPT). The first species is particularly abundant, and gives the name to the *P. zitteli* Zone, which belongs to the Lower or Middle Tithonian depending on whether the bi- or tripartite division of the Tithonian is used.

The genus *Glochiceras* is abundant in the European White Jura (cf. ZIEGLER, 1958) and has also been reported from the Tithonian and/or Kimmeridigian of Mexico (CASTILLO & AGUILERA, 1895; BURCKHARDT, 1906; IMLAY, 1939) and Argentina (KRANTZ, 1926, 1928; STEUER, 1897, 1921) as well as from Russia (ZONOV, 1937), Madagascar (COLLIGNON, 1960), Somaliland (SPATH, 1925), Tanganyika (DIETRICH, 1933), Iraq (SPATH, 1950), India (SPATH, 1927—33), Rumania (AVRAM, 1976) and Japan (YOKOYAMA, 1904, revised by ARKELL, 1956). The species from Cerro Lotena is new and is named *G. steueri* n. sp., with *Oppelia nimbata* STEUER (*non* OPPEL) as the type species. It was found in strata belonging to the P. zitteli Zone.

The genus *Hildoglochiceras* also has a world wide distribution, and is known from beds of generally Lower Tithonian age from the Himalayas (UHLIG, 1903—10), India (SPATH, 1927—33), Tanganyika (ZWIERZYCKI, 1914), Madagascar (COLLIGNON, 1960), Mexico (IMLAY, 1939) and Cuba (IMLAY, 1942). The only species found in Cerro Lotena is new and is named *H. wiedmanni* n. sp.. It also belongs to the *P. zitteli* Zone.

The family Oppeliidae is represented by a new species of the genus *Parastreblites*, which was originally described as a subgenus of *Taramelliceras* from Lower Tithonian beds at Saint Concors, southeast France (DONZE & ENAY, 1961). The species from Cerro Lotena is closely related to *P. waageni* (OPPEL), formerly included by SPATH (1925) in *Neochetoceras*, and is named *P. comahuensis* n. sp.

The family Perisphinctidae constitutes 66 % of the studied fauna, but most of its representatives belong to the subfamily Virgatosphinctinae, with the following genera present: *Subdichotomoceras*, *Pachysphinctes*, *Aulacosphinctoides*, *Parapallasiceras*, *Virgatosphinctes*, *Pseudinvoluticeras* and *Choicensisphinctes* gen. nov.

The genus *Subdichotomoceras*, which can only be distinguished from *Pavlovia* by the less densely-ribbed internal whorls, is represented in Cerro Lotena, by three species, one of them new: *S. windhauseni* (WEAV.), *S. araucanense* n. sp., and *S.* sp. juv. indet. This genus has also been recorded in England (SPATH, 1925), Spain (OLORIZ, 1978), Somaliland (SPATH, 1925), Kenya (SPATH, 1930), Tanganyika (DIETRICH, 1933), Madagascar (COLLIGNON, 1960), India (SPATH, 1927—33), Greenland ? (SPATH, 1936) and Mexico (VERMA & WESTERMANN, 1973). The Cerro Lotena specimens occur in the *A. proximus* and *W. internispinosum* Zones of the Middle Tithonian. Though the presence of *Subdichotomoceras* is known in Argentina, the specimens illustrated here are the first to be originally described under this name.

The genus *Pachysphinctes* is reported here for the first time from the Andes of South America, under the name of *P. americanensis* n. sp. This genus is a common form in the Middle Katrol Beds of Cutch, India, where its occurs in association with *Subdichotomoceras* (cf. SPATH, 1927—33). The same association is also present in the Tendaguru Group in the east of Africa (cf. SPATH, 1930; DIETRICH, 1925, 1933), and in southern Spain (OLORIZ, 1978). In Cerro Lotena it also occurs in association with *Subdichotomoceras*, in the *W. internispinosum* Zone.

The genus *Aulacosphinctoides* is represented in Cerro Lotena by a form very similar to *A. hundesianus* (UHLIG) from the Spiti Shales, and by another form whose poor preservation prevents specific classification. *Aulacosphinctoides* is another typical Tithonian genus of world wide distribution, very common in New Zealand (SPATH, 1923; STEVENS, 1968), the Himalayas (UHLIG, 1903—10), India (SPATH, 1927—33), Somaliland (SPATH, 1925), Japan (cf. ARKELL, 1956) and Mexico (VERMA & WESTERMANN, 1973). In Argentina, its presence was suggested by ARKELL (1956, p. 583) on the basis of examination of the ammonite fauna illustrated by INDANS (1954) from south Mendoza; however the forms described here are the first from Argentina originally referred to by this name.

Within the genus *Parapallasiceras*, typical of the Lower and Middle Tithonian (cf. ZEISS, 1968), three species have been distinguished: *P.* aff. *P. pseudocolubrinoides* OLORIZ, *P.* aff. *P. recticosta* OLORIZ, and *P.* sp. indet. All three species are from the *W. internispinosum* Zone at Cerro Lotena.

The genus *Virgatosphinctes* has a world wide distribution and is known from Europe (cf. ARKELL, 1956), north Africa (ROMAN, 1936), Somaliland (SPATH, 1925), Abyssinia (CRICK, 1897, revised by SPATH, 1925), Tanganyika (ARKELL, 1956), Madagascar (COLLIGNON, 1960; BESAIRIE, 1936; LEMOINE, 1911), Persia (CLAPP, 1940), Cutch (SPATH, 1927—33), Baluchistan (ARKELL, 1956), the Himalayas (UHLIG, 1903 bis 1910), Pakistan (FATMI, 1972), Australia (BRUNNSCHWEILER, 1954), Mexico (IMLAY, 1939; VERMA & WESTERMANN, 1973), Cuba (IMLAY, 1942), Trinidad (HUTCHINSON, 1938), Chile (CORVALÁN & PEREZ, 1958) and Argentina (WEAVER, 1931; INDANS, 1954). This genus is common in the Lower Tithonian as well as in the Upper Tithonian. Though the presence of *Virgatosphinctes* in the Andean domain has been questioned in some cases, it is well documented from the Cerro Lotena section, and is represented by the following species: *V. andesensis* (DOUV.), *V. mexicanus* (BURCK.), *V. denseplicatus rotundus* SPATH, *V. burckhardti* (DOUV.), and *V. evolutus* n. sp.

The genus *Pseudinvoluticeras*, typical of the Lower Tithonian, has been reported from Somaliland (SPATH, 1925), Madagascar (COLLIGNON, 1960), Anatolia (*fide* ENAY, 1972), Mexico (VERMA & WESTERMANN, 1973) and Argentina (SPATH, 1925, 1950). In Cerro Lotena two, or possibly three species, have been found, named *P. douvillei* SPATH, *P. windhauseni* (WEAV.), and *P.* (?) *wilfridi* (DOUV.). The identification of this last species is questionable because it is based on internal whorls of a single specimen which could also belong to *Aulacosphinctoides*. *P.* "*decipiens*" SPATH is considered synonymous with the first species.

The genus *Choicensisphinctes* is here proposed in order to group together certain ammonites having inflated shells of olcostephanid aspect, and ornamentation composed of fascicules with 4 to 10 ribs.

These ammonites constitute a homogeneous stock which includes the following species of BURCKHARDT: "*P.*" *choicensis* (type species), "*P.*" *erinoides* and possibly "*P.*" aff. *erinus*. The proposal of this genus follows the original suggestion by UHLIG (1911a, p. 542) that these species could belong to a particular group of ammonites. It should be noted that *Ch. choicensis* is the most common species in the basal beds of the Vaca Muerta Formation within the Neuquén and Mendoza basin, and has been found by the author, in addition to Cerro Lotena, at Mallín de los Caballos, Mallín Quemado, Cajón de Almaza and Bardas Blancas (cf. H. LEANZA & C. HUGO, 1977). *Virgatosphinctes* cf. *raja* INDANS (*non* UHLIG) is included in the synonymic list of *Ch. choicensis*. In Cerro Lotena the genus *Choicensisphinctes* is represented by two species and one subspecies, as follows: *Ch. choicensis*, *Ch. choicensis sutilis* n. ssp. and *Ch. erinoides*. These species are common in the *V. mendozanus* Zone at the base of the Tithonian transgression.

Finally, it should be remarked that the genus *Torquatisphinctes*, although it is not represented in the fauna described here, it has been found by the author at Cerro Lotena in the mandibles of a crocodile — *Geosaurus araucanensis* — (cf. GASPARINI & DELLAPE, 1976) in the lower part of the Vaca Muerta Formation, as well as in other parts of the Neuquén and Mendoza basin (cf. H. LEANZA & C. HUGO, 1977).

The genera *Virgatosphinctes*, *Pseudinvoluticeras* and *Choicensisphinctes*, as well as *Torquatisphinctes*, occur together at the base of the Vaca Muerta Formation, within the *V. mendozanus* Zone (= Virgatosphinctinae Beds).

The family Aspidoceratidae is represented by only one genus and one species: *Aspidoceras euomphalum* STEUER. In the Cerro Lotena area, however, *A. haupti* KRANTZ (1926) and *A. neuquensis* WEAVER (1931) as well as *A. steinmanni* HAUPT, the type species of the genus *Pseudhimalayites* SPATH (1925) have also been reported. The genus *Aspidoceras* is very cosmopolitan and is common in sediments of Tithonian age.

The family Berriasellidae is represented exclusively in the described fauna by the subfamily Himalayitinae, containing the genera *Windhauseniceras*, *Hemispiticeras*, *Aulacosphinctes and Corongoceras*.

The genus *Windhauseniceras*, which is apparently endemic, is very well represented by its type species *W. internispinosum*. This species is very abundant and next to *P. zitteli*, is the commonest form in Cerro Lotena. It gives the name to the *W. internispinosum* Zone, which in this monograph is placed in the upper part of the Middle Tithonian.

The genus *Hemispiticeras* is represented by a single specimen that closely resembles its type species "*R.*" *steinmanni* STEUER, differing only by having a less obvious lateroventral row of tubercules. It is therefore regarded as *H.* aff. *H. steinmanni* (STEUER).

The genus *Aulacosphinctes* is well represented in Cerro Lotena by a single species identified as *A. proximus* (STEUER). This typical Tithonian genus is known from Algeria (ROMAN, 1936), Somaliland (SPATH, 1925), Abyssinia (CRICK, 1897, revised by SPATH, 1925), Madagascar (COLLIGNON, 1960), Cutch (SPATH, 1927—33), the Himalayas (UHLIG, 1903—10), Pakistan (FATMI, 1972), California ? (IMLAY, 1952), Argentina (STEUER, 1897, 1921; WEAVER, 1931; A. F. LEANZA, 1945; INDANS, 1954) and in Chile (CORVALÁN, 1959). The described species is particularly abundant in the Cerro Lotena section in the beds occurring between the *P. zitteli* and *W. internispinosum* Zones.

The genus *Corongoceras* is represented in Cerro Lotena by its type species *C. lotenoense*. This genus is widely distributed in the Andean Tithonian. Apart from the type species referred to by SPATH (1925, p. 144) from Corongo, Perú, 5 further species are known in South America, as follows: *C. mendozanum* (BEHR.), *C. alternans* (GERTH), *C. duraznense* KRANTZ, *C. submendozanum* KRANTZ and *C. rigali* LEANZA. In Cuba *C. filicostatum* IMLAY (1942) and in Mexico *C. mendozanum* and *C. cordobai* VERMA & WESTERMANN (1973) have been recorded. Elsewhere in the world the genus is known from Madagascar (COLLIGNON, 1960), Algeria (ROMAN, 1936), Nepal (HELMSTEADT, 1969) and Spain (OLORIZ, 1978). The species from Cerro Lotena occurs in the beds of the *W. internispinosum* Zone. Field observations indicate that it is not common in the overlying *C. alternans* Zone of the Upper Tithonian (cf. A. F. LEANZA, 1945).

No true Boreal elements have been recorded in the fauna from Cerro Lotena. It should also be remarked that no representatives of the genera *Lytoceras* or *Phylloceras* have been found. This feature, considering the paleogeographical and paleoenvironmental conditions under which the Vaca Muerta Formation was deposited, favours the suggestion of SPATH (1932, p. 151, 152) that these were pelagic organisms which were not adapted to living in shallow epicontinental seas.

Preservation of the ammonite fauna

The degree of preservation of the fossils depends upon their stratigraphic position. In the lower part of the Vaca Muerta Formation (*V. mendozanus* and *P. zitteli* Zones), most of the specimens have been affected by diagenetic compaction and usually one side is better preserved than the other. All the fossils are calcified, with calcite crystals commonly present in the camerae. Oysters are attached to some specimens, particularly to the umbilicus and appear to be true epizoans. Specimens are generally dark grey in colour and the suture line can be observed in most cases.

In the upper part of the Vaca Muerta Formation *(A. proximus* and *W. internispinosum* Zones) the ammonites shells are commonly occuring as recrystallized to white yellowish-white, granular, calcium carbonate. Both the fossils and the matrix consists of the same material, and the test of the shell is usually preserved. The suture lines are not preserved in any specimens, a fact which creates a serious problem in the determination of taxonomic position.

V. TAXONOMIC REVISION

The classification used here at the generic level is in accordance with the Treatise of Invertebrate Paleontology (Arkell *et al.*, 1957). *Parastreblites* Donze & Enay (1961) is regarded as a genus and not a subgenus of *Taramelliceras* as originally described. In Table I the suggested taxonomic changes are summarized. The reasons for these changes are given in the discussions of the respective genera and species in the systematic descriptions.

TABLE I
Revision of Ammonite Species

Previous classification	New classification
Pseudolissoceras zitteli (Burck.) Arnould-Saget, 1951, p. 9, Pl. I, figs. 12a-c, 13a-c, 14, 16a-c	? *Pseudolissoceras pseudooolithicum* (Haupt)
Oppelia nimbata Steuer (*non* Oppel) 1897, p. 74, pl. VII, figs. 16, 17.	*Glochiceras steueri* n. sp.
Pseudinvoluticeras decipiens Spath 1925, p. 124 = *S. payeri* Douv. (*non* Toula) 1910, p. 18, pl. III, figs. 3a-b	*Pseudinvoluticeras douvillei* Spath
Virgatosphinctes lotenoensis Weaver, 1931, p. 423, pl. 48, figs. 322, 323	*Pseudinvoluticeras douvillei* Spath
Virgatosphinctes erinoides Indans (*non* Burck.) 1954, p. 109, pl. 15, fig. 1	*Pseudinvoluticeras douvillei* Spath
Virgatosphinctes windhauseni Weaver, 1931, p. 425, pl. 48, figs. 324, 325	*Pseudinvoluticeras windhauseni* (Weav.) n. comb.
Holcodiscus wilfridi Douv., 1910, p. 12, pl. II, fig. 6	*Pseudinvoluticeras* (?) *wilfridi* (Douv.)
Perisphinctes aff. *transitorius* Burck. (*non* Oppel), 1903, p. 40, pl. V, figs. 4-9	*Virgatosphinctes evolutus* n. sp.
Aulacosphinctes cf. *A. transitorius* Weaver (*non* Oppel), 1931, p. 415, pl. 45, fig. 306	*Virgatosphinctes evolutus* n. sp.
Perisphinctes contiguus Burck. (*non* Catullo), 1903, p. 38, pl. IV, figs. 7-10	*Virgatosphinctes evolutus* n. sp.
Perisphinctes choicensis Burck., 1903, p. 50, pl. VI, figs. 10-12, pl. VIII, fig. 6	*Choicensisphinctes choicensis* (Burck.) gen. nov.
Virgatosphinctes cf. *raja* Indans (*non* Uhlig), 1954, p. 110, pl. 14, figs. 1-3	*Choicensisphinctes choicensis* (Burck.)
Perisphinctes erinoides Burck. 1903, p.	*Choicensisphinctes erinoides* (Burck.) n. comb.
Perisphinctes aff. *erinus* Burck. (*non* d'Orb.), 1900a, p. 42, pl. XXV, fig. 1	*Choicensisphinctes erinoides* (Burck.)
Aulacosphinctes windhauseni Weaver 1931, p. 412, pl. 44, fig. 300	*Subdichotomoceras windhauseni* (Weav.) n. comb.
Oppelia (Neochetoceras) waageni Krantz (*non* Zittel), p. 434	? *Parastreblites comahuensis* n. sp.
Oppelia (Neoochetoceras) waageni Weaver (*non* Zittel), 1931, p. 399	? *Parastreblites comahuensis* n. sp.

VI. AMMONITE ZONES AND CORRELATIONS

The ammonite fauna of the Vaca Muerta Formation can be grouped into 4 associations which basically correspond to ammonite zones previously established for the Andean Tithonian by other authors (BURCKHARDT, 1900a, 1900b, 1903; WEAVER, 1931; A. F. LEANZA, 1945, 1947; GROEBER, 1946; GROEBER *et al.*, 1952; STIPANTICIC, 1969; H. LEANZA, 1973; H. LEANZA & C. HUGO, 1977). These are the *V. mendozanus* Zone, the *P. zitteli* Zone, the *A. proximus* Zone and the *W. internispinosum* Zone. The first zone is located in the uppermost Lower Tithonian while the remaining three constitute the Middle Tithonian. Upper Tithonian sediments are present in the overlying Picún Leufú Formation, but their coastal facies prevented the establishment of an ammonite fauna. In Cerro Lotena, only *Substeueroceras* has been recorded from this formation (H. LEANZA, 1973).

Data from this and previous studies indicate that the *V. mendozanus* Zone is not a completely satisfactory one. This is because this species is present only in very small numbers within the Neuquén and Mendoza basin, and, moreover, its systematic position is still rather uncertain. Progress has been made, however, in the *W. internispinosum* Zone, where genera which previously were unknown or poorly documented have now been identified and described. In Table II, correlations between Cerro Lotena (Neuquén) and Sierra Azul (Mendoza) are given.

The *Virgatosphinctes mendozanus*[1]) Zone

This zone was originally established by BURCKHARDT (1900a, p. 82; 1903, p. 106) as those sediments containing numerous Virgatosphinctinae in the basal portion of the Vaca Muerta Formation, at the beginning of the Tithonian transgression in the Neuquén and Mendoza basin. The type locality is situated in the region between Cajón del Burro and the Choica River valley at the beginning of the Río Grande, Mendoza province, Argentina. This zone, which is characterized by a notable uniformity throughout the basin, consists of bituminous black shales with common, variably sized calcareous nodules and concretions, which usually contain Virgatosphinctinae.

On the basis of studies of several sections of the Vaca Muerta Formation in the Neuquén and Mendoza basin, LEANZA & HUGO (1977, p. 250) suggested that the *V. mendozanus* Zone could be revised. This zone, which occurs at the base of the Tithonian transgressive sequence across hundreds of kilometers, frequently lacks *V. mendozanus* itself. In its place, *Choicensisphinctes choicensis* is often present. This species has been recorded in the sections of Cerro Lotena, Picún Leufú, Mallín de los Caballos, Mallín Quemado, Cajón de Almaza, Bardas Blancas and Arroyo Cieneguitas. *V. mendozanus* was found only in the Puerta Curaco section. It is worth noting that although WEAVER (1931) stated that specimens of *V. mendozanus*, particularly in central and southern Neuquén, constituted up to 75 % of this assemblage, he neither illustrated nor described this species. Nevertheless, on the basis of priority, together with the fact that *Ch. choicensis* is an endemic form, the present author favours retention of the original name, though noting the rarity of the species and its somewhat uncertain systematic position.

In Cerro Lotena, the *V. mendozanus* Zone is 25 m thick and contains the following ammonites: *Pseudinvoluticeras douvillei* SPATH, *P. windhauseni* (WEAV.) n. comb., *P.* (?) *wilfridi* (DOUV.), *Virgatosphinctes andesensis* (DOUV.), *V. mexicanus* (BURCK.), *V. denseplicatus rotundus* SPATH, *V. evolutus* n. sp., *V. burckhardti* (DOUV.) *Choicensisphinctes choicensis* (BURCK.),

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[1]) The history of this species begins with BURCKHARDT (1900a, p. 41, pl. 25, figs. 6-8), who figured some specimens from Portezuelo Montañés as *Perisphinctes* aff. *lothari* CHOFFAT. Three years later, the same author referred to the same specimens as *Virgatites scythicus* VISCHNIAKOFF (BURCKHARDT, 1903, p. 45, pl. VII, figs. 1-8) a determination which in this case was supported by PAVLOW. This latter classification was questioned by DOUVILLÉ (1910, p. 7) who, when establishing *Virgatites andesensis* DOUVILLÉ on the basis of material from Neuquén, included *Virgatites scythicus* BURCK. (*non* VISCHNIAKOFF) in this species. BURCKHARDT himself (1911a, foot note; 1911b, p. 772) partly accepted the opinion of DOUVILLÉ in the sense that the specimens from Portezuelo Montañés did not correspond to the cited Russian species, but also stated that his *Virgatites scythicus* could be included in the synonymic list of *V. andesensis* DOUVILLÉ. Consequently, BURCKHARDT (1911a, p. 482, foot note) proposed a new name for the specimens of Paso Mantanés — *Virgatites mendozanus* — retaining the name *V. andesensis* only for the specimens figured by DOUVILLÉ in 1910. A few years later, STEIGER (1914, p. 502) included BURCKHARDT's species in the genus *Perisphinctes*. SPATH (1927-33, p. 527) also commented on this problem, and included the *mendozanus* species of BURCKHARDT in the genus *Dorsoplanites*. However, five years later, after studying it in more detail he stated that the similarity with *Dorsoplanites* is "probably entirely superficial" (SPATH, 1936, p. 72) and "could equally well be included in *Virgatosphinctes*" (SPATH, op. cit., p. 29). Recently, R. ENAY (1964, p. 365) included the same species in *Subplanites*. However, the identification of BURCKHARDT's species as belonging to the genus *Virgatosphinctes*, as made by WEAVER (1931) SPATH (1936), INDANS (1954) and many others, has gained more widespread popularity. Considering the shortage of material which could throw light on the taxonomic filiation of this enigmatic species, the present author prefers to place it in *Virgatosphinctes* retaining in this way the more widely known name.

TABLE II
Ammonite Zones in Cerro Lotena and Sierra Azul

Age		Ammonites Zones	Cerro Lotena (Neuquén)	Sierra Azul (Mendoza)
VALANGINIAN	U	*O. curacoensis*	▥	+
	L	*N. wichmanni*	▥	+
BERRIASIAN	U	*S. damesi*	▥	+
	L	*A. noduliferum*	▥	+
TITHONIAN	U	*Ss. koeneni*	▥	+
		C. alternans	▥	+
	M	*W. internispinosum*	+	+
		Au. proximus	+	▥
		P. zitteli	+	▥
	L	*V. mendozanus*	+	▥

Abbreviations: O = *Olcostephanus*, N = *Neocomites*, S = *Spiticeras*, A = *Argentiniceras*, Ss = *Substeueroceras*, C = *Corongoceras*, W = *Windhauseniceras*, Au = *Aulacosphinctes*, P = *Pseudolissoceras*, V = *Virgatosphinctes*, L = Lower, M = Middle, U = Upper.

Ch. choicensis sutilis n. ssp. and *Ch. erinoides* (Burck.). *V. mendozanus* is absent.

On the basis of the studies of Burckhardt (1900a, 1900b, 1903), Haupt (1907), Krantz (1926, 1928), Weaver (1931) and Indans (1954) this zone is placed in the Lower Tithonian. This assignment is confirmed in the case of Cerro Lotena by the presence of the genus *Pseudinvoluticeras*, common in sediments of Lower Tithonian age in Somaliland (Spath, 1925), Madagascar (Collignon, 1960) and Mexico (Verma & Westermann, 1973). Zeiss (1968) has correlated this zone with the uppermost Lower Tithonian *Parapallasiceras palatinum* Zone of the Franconia region.

The *Pseudolissoceras zitteli* Zone

This zone, which overlies the *V. mendozanus* Zone in the region situated between Cajón del Burro and the Choica River valley, was proposed by Burckhardt (1900a, p. 83; 1903, p. 107). It has a wide distribution throughout the whole Neuquén and Mendoza basin (cf. Leanza & Hugo, 1977). In Cerro Lotena, the *P. zitteli* Zone is 26 m thick and contains numerous variably sized specimens of *P. zitteli*, in association with limited numbers of *P. pseudooolithicum* (Haupt), *Glochiceras steueri* n. sp., *Hildoglochiceras wiedmanni* n. sp. and *Parastreblites comahuensis* n. sp. Also present are abundant *Laevaptychus* (cf. Closs, 1961a, b) and vertebrate bones and fish scales (see Windhausen, 1914).

In the chapters dealing with faunal analysis and systematics descriptions, data are given on the distribution of the genus *Pseudolissoceras* and its species. On the basis of the studies by Haupt (1907), Krantz (1926, 1928), Weaver (1931), H. Gerth (1935), Groeber (1946), Groeber *et al.* (1952), Stipanicic (1969), H. Leanza (1973), and Leanza & Hugo (1977), the age of the *P. zitteli* Zone can be taken as the lowermost Middle Tithonian, although the presence of the new haploceratids described in this report suggests a slightly older age. Considering the uppermost Lower Tithonian age of the underlying ammonite zone, the *P. zitteli* Zone is placed in the lowermost Middle Tithonian. The same age for the genus *Pseudolissoceras* had been suggested by Barthel (1962) and Zeiss (1968). The record of *P. zitteli* by Arnould-Saget (1951, 1951a) in the Upper Tithonian of Tunisia does not seem to be concordant with its known stratigraphic distribution. If the bipartite division of the Tithonian stage is used, the *P. zitteli* Zone would fall into the Lower Tithonian (cf. R. Enay, 1964, 1972, 1973; J. Wiedmann, 1968; Verma & Westermann, 1973).

The *Aulacosphinctes proximus* Zone

This zone is equivalent to the *Aulacosphinctes colubrinoides* Zone proposed by Burckhardt (1900a, p. 84; 1903, p. 108), and overlies the *P. zitteli* Zone. Following the works from Groeber (1946) and Groeber *et al.* (1952), the *A. colubrinoides* Zone was renamed as the *A. proximus* Zone, a name which was later accepted by Stipanicic (1969), H. Leanza (1973) and Leanza & Hugo (1977). This is the most poorly defined zone in the Andean Tithonian because, excluding *Subdichotomoceras, Aspidoceras* and *Pseudhimalayites* it contains no other ammonite genera. Moreover, many species of *Aulacosphinctes* range throughout almost the whole Tithonian Stage. However, the vertical extent of the *A. proximus* Zone can be defined if it is considered as the interval that has as its base the last representatives of *P. zitteli*, and as its top the first occurrence of the species *W. internispinosum*. So defined, this zone at Cerro Lotena is 21 m thick, and in addition to numerous specimens of *A. proximus*, contains *Subdichotomoceras* sp. juv. indet, *Laevaptychus crassissimus* (Haupt), *Aspidoceras andinum* (Steuer), *A. neuquensis* (Weav.), and *Pseudhimalayites steinmanni* (Steuer).

The *A. proximus* Zone has also been identified in the Chilean part of the Andean geosyncline (Corvalán & Perez, 1958; Corvalán, 1959). As it occurs between the *P. zitteli* and *W. internispinosum* Zones, its age accordingly falls into the middle part of the Middle Tithonian.

The *Windhauseniceras internispinosum* Zone

This zone was originally proposed by Weaver (1931, p. 46), who placed it in the Upper Tithonian *sensu lato*. Later, A. F. Leanza (1945, table *hors de text)* placed this zone in the lowermost Upper Tithonian, noting that only *Wichmanniceras mirum* occurred in association with the index species. Arkell (1956, p. 582), who considered this zone uncorrelatable with those of the European Upper Tithonian, placed it in the Middle Tithonian.

Though *W. internispinosum* is an entirely endemic form, it is very abundant at Cerro Lotena in the upper part of the Vaca Muerta Formation. In this zone, ammonites have been found which were previously unknown or poorly documented in the Andean domain, but which now allow its age to be more precisely determined. The zone is 38 m thick and contains the following ammonites: *Windhauseniceras internispinosum* (Krantz), *Hemispiticeras* aff. H. *steinmani* (Steuer), *Pachysphinctes americanensis* n. sp., *Corongoceras lotenoense* Spath, *Subdichotomoceras windhauseni* (Weav.), *S. araucanense* n. sp., *Aulacosphinctoides* aff. *A. hundesianus* (Uhlig), *A.* sp. indet., *Parapallasiceras* aff. *P. pseudocolubrinoides* Oloriz, *P.* aff. *recticosta* Oloriz, *P.* sp. indet. and *Aspidoceras euomphalum* Steuer.

Assemblages containing *Subdichotomoceras, Pachysphinctes, Aulacosphinctoides* and *Aspidoceras* have been reported from the Middle Katrol beds of Cutch, which Arkell (1956, p. 388) refers to the Middle Kimmeridgian with interrogant. In the Tendaguru Group of east Africa, *Subdichotomoceras* and *Pachysphinctes* have also been found together, and were referred by Arkell (1956, p. 335) to the uppermost Kimmeridgian. Considering the equivalence of the Middle and Upper Kimmeridgian to the Lower and Middle Tithonian, and taking into account the stratigraphic position of the *W. internispinosum* Zone, it is accordingly placed more properly in the Middle Tithonian than in the Upper Tithonian. Moreover, the genus *Parapallasiceras,* which is also present in Cerro Lotena, apparently never crosses into levels younger than the Middle Tithonian (cf. Zeiss, 1968). Although the genus *Corongoceras* is common in the Andean Upper Tithonian (cf. A. F. Leanza, 1945), *C. lotenoense* Spath appears to occur in the Neuquén basin at somewhat lower levels (cf. H. Leanza, 1973, p. 116; 1975, p. 583). On the basis of these reasons, the *W. internispinosum* Zone is placed in the uppermost Middle Tithonian, and is probably equivalent to the *Burckhardticeras* Zone in the Betic ranges of southern Spain (cf. Oloriz, 1978).

The Upper Tithonian of the Andean domain therefore is entirely represented by the *Corongoceras alternans* and *Substeueroceras koeneni* Zones. The first zone, proposed by A. F. Leanza (1945), appears inmediately above the *W. internispinosum* Zone and probably is equivalent to the *Berriasella delphinensis* Zone of southeast France, and to the lower part of the *"Virgatosphinctes" transitorius* Zone of the Alpine region (cf. Enay, 1964). The *Substeueroceras koeneni* Zone is equivalent to the *Berriasella chaperi* Zone of southeast France and to the upper part of the *„Virgatosphinctes“ transitorius* Zone of the Alpine region. Therefore, the *C. alternans* and *S. koeneni* Zones can easily be correlated with the European Ardescian.

As noted above, the Upper Tithonian is represented at Cerro Lotena in the overlying Picún Leufú Formation. However, this formation lacks the ammonites so common in more pelagic facies, such as in the Sierra Azul in the southern part of Mendoza. In Table III the ammonite zonation of the Andean Tithonian is given.

TABLE III
Ammonite Zonation of the Andean Tithonian

Age		Ammonite Zones	Fossils
TITHONIAN	UPPER	SUBSTEUEROCERAS KOENENI	*Aulacosphinctes azulensis* Leanza, *A. mangaensis* (Steuer), *Pectinatites* (?) *striolatus* (Steuer), *Berriasella fraudans inflata* Leanza, *B. inaequicostata* Gerth, *Parodontoceras calistoides* (Behr.), *Aspidoceras longaevum* Leanza, *Substeueroceras exstans* Leanza, *Blanfordiceras vetustum* (Steuer), *Himalayites andinus* H. Leanza, *Spiticeras acutum* Gerth.
		CORONGOCERAS ALTERNANS	*Micrancanthoceras tapiai* Leanza, *M. lamberti* Leanza, *B. pastorei* Leanza, *B. australis* Leanza, *B. krantzi* Leanza, *B. bardensis* Krantz, *B.* (?) *delhaesi* Leanza.
	MIDDLE	WINDHAUSENICERAS INTERNISPINOSUM	*Pachysphinctes americanensis* H. Leanza, *Hemispiticeras* aff. *H. steinmanni* (Steuer), *Subdichotomoceras araucanense* H. Leanza, *S. windhauseni* (Weav.), *Parapallasiceras* aff. *pseudocolubrinoides* Oloriz, *P.* aff. *P. recticosta* Oloriz, *P.* sp. indet., *Aulacosphinctoides* aff. *A. hundesianus* (Uhlig), *Aspidoceras euomphalum* Steuer, *Corongoceras lotenoense* Spath.
		AULACOSPHINCTES PROXIMUS	*Subdichotomoceras* sp. juv. indet. *Pseudhimalayites steinmanni* (Steuer), *Aspidoceras andinum* Steuer, *A. neuquensis* Weav., *Laevaptychus crassissimus* (Haupt).
		PSEUDOLISSOCERAS ZITTELI	*Pseudolissoceras pseudooolithicum* (Haupt), *Glochiceras steueri* H. Leanza, *Hildoglochiceras wiedmanni* H. Leanza, *Parastreblites comahuensis* H. Leanza.
	LOWER	VIRGATOSPHINCTES MENDOZANUS	*Pseudinvoluticeras douvillei* Spath, *P. windhauseni* (Weav.), *P.* (?) *wilfridi* (Douv.), *Choicensisphinctes choicensis* (Burck.), *Ch. choicensis sutilis* H. Leanza, *Ch. erinoides* (Burck.), *Virgatosphinctes andesensis* (Douv.), *V. mexicanus* (Burck.), *V. burckhardti* (Douv.), *V. denseplicatus rotundus* Spath, *V. evolutus* H. Leanza, *Subplanites malargüensis* Spath.

VII. SYSTEMATIC DESCRIPTIONS

Measurements and abbreviations

All measurements are in millimeters and include the ornament. With rare exceptions they are taken on the internal mold. The abbreviations employed in the systematic descriptions are as follows:

D = maximum diameter at a given growth stage
U = diameter of umbilicus measured at seam
H = height of the whorl measured in the plane of coiling
W = maximum width of whorl at right angles to the plane of coiling

In most cases, measurements are given only for the figured and better preserved specimens.

The suture line abbreviations are the following:

E = external lobe
L = lateral lobe
U = umbilical lobe

Repositories

All specimens studied in this report are deposited at the Geological Survey of Argentina (Servicio Geológico Nacional, República Argentina), with the exception of 3 specimens from the F. von Huene collection at the University of Tübingen, Germany.

The following abbreviation are employed:

S.G.N. = Servicio Geológico Nacional, República Argentina.
G.P.I.T. = Institut und Museum für Geologie und Paläontologie Tübingen, Germany.

Gypsum copies of the specimens figured in this report are also deposited at the Tübingen Institute.

Order AMMONOIDEA Zittel, 1884
Suborder AMMONITINA Hyatt, 1889
Superfamily HAPLOCERATACEAE Zittel, 1884
Family HAPLOCERATIDAE Zittel, 1884
Genus PSEUDOLISSOCERAS Spath, 1925

Type species. — *Neumayria zitteli* Burckhardt, 1903, p. 55, pl. 10, figs. 1, 2. SD Roman, 1938, p. 176.

In the genus *Pseudolissoceras* two groups with distinctive characteristics can be clearly distinguished: the *Pseudolissoceras zitteli* group and the *Pseudolissoceras rasile* group.

Both groups have in common a characteristic suture line, with E and L wide but not deep; both the width and depth of the E/U saddle equivalent to almost half of the E/L saddle. The second lateral saddle (E/U) is diagnostic and clearly differs from that of the genus *Haploceras* Zittel, 1870 (type species: *Ammonites elimatus* Oppel, in Zittel, 1868, pl. 13, (figs. 1a—c, SD Spath, 1923) which displays an E/U saddle larger and higher than the E/L saddle (cf. Schindewolf, 1963, p. 379, text fig. 208).

The group of *P. zitteli* (Burckhardt, 1903, p. 55, pl. 10, figs. 1—8) is characterized by very involute shells (U/D = 0.18 to 0.26), ornamentation with fine falcoidal striae, whorl sections higher than wide, and sharp umbilical borders. The following species have been placed in this group: *P. zitteli* (Haupt, 1907, pl. 7, figs. 3a, b; 4a, c), *P. zitteli* (Krantz, 1928, pl. 1, fig. 6), *P. zitteli* (Weaver, 1931, pl. 43, fig. 291), *P.* cf. *zitteli* (Imlay, 1942, pl. 4, figs. 1, 3, 4, 7, 8, 11, 12), *P. zitteli* (Oloriz, 1978, pl. 2, fig. 12, text fig. 43), *P. advena* (Spath, 1950, pl. 6, figs. 9—10), *P. concorsi* (Donze & Enay, 1961, pl. 1, fig. 1, text fig. 4), *P. bavaricum* (Barthel, 1962, pl. 2, figs. 7—9) and *P. zitteli* (Verma & Westermann, 1973, pl. 26, figs. 3—5, text figs. 12—13).

The group of *P. rasile* (Oppel, 1865, p. 549; in Zittel, 1870, p. 55, pl. 4, figs, 2, 3) is characterized by more evolute whorls (U/D = 0.22 to 0.36), smooth tests, somewhat inflated shells, whorl sections almost as wide as high, and the absence of sharp umbilical borders. This group differs from *Haploceras* only in its suture line (cf. *supra*); the morphology of the shells is almost identical. The following species have been placed in this group: *P. rasile inflatum* (Zittel, 1870, pl. 4, figs. 2), *P. rasile planiusculum* (Zittel, 1870, pl. 4, figs. 3a—c) which was reported by Behrendsen (1892, p. 388) from Rodeo Viejo and Malargüe (Mendoza, Argentina), *P. planiusculum* (Zittel) (Avram, 1976, pl. 7, figs. 5a, b; pl. 8, figs. 2a, b, text fig. 10a—c), *P. subrasile* (Burckhardt, 1906, pl. 34, figs. 8—11) and *P. pseudooolithicum* (Haupt, 1907, pl. 8, figs. 2a—c). It is possible that *P. zitteli* of Arnould-Saget (1951, pl. 1, figs. 12—14, 16) also belongs to this group (see Barthel, 1962, p. 14).

In the Cerro Lotena section, 55 specimens attributed to *P. zitteli* have been found; only 3 specimens have been identified as *P. pseudooolithicum.*

Pseudolissoceras zitteli (Burckhardt, 1903)

Pl. 1, Figs. 1a—b, 2a—b, Text-Figs. 2a and 3.

1903 *Neumayria Zitteli* Burckhardt, p. 55, pl. 10, figs. 1-8.
1907 *Neumayria Zitteli* Burckhardt — Haupt, p. 200. pl. 7, figs. 3a-b, 4a-c.
1925 *Pseudolissoceras zitteli* (Burckhardt) — Spath, p 113 (Gen. nov.).
1926 *Haploceras (Pseudolissoceras)* Zitteli (Burckhardt) — Krantz, p. 436, pl. 17, figs. 4, 5.

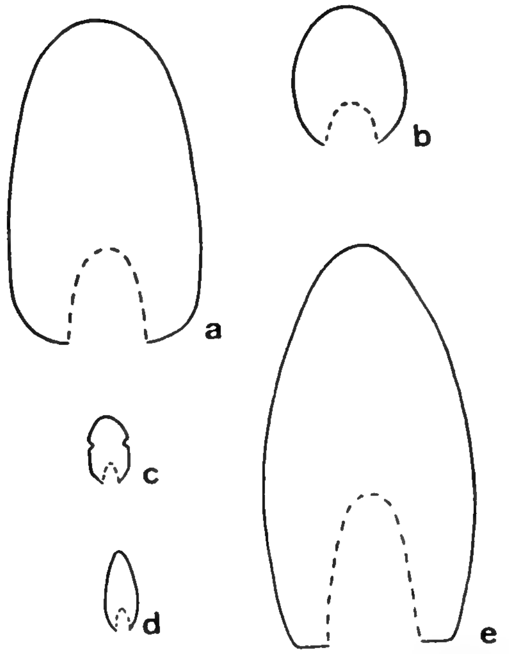

Figure 2: Whorl sections of Haploceratidae and Oppeliidae. **a**: *Pseudolissoceras zitteli*, S.G.N. 8887/1; **b**: *P. pseudooolithicum*, S.G.N. 7327/1; **c**: *Hildoglochiceras wiedmanni* n. sp., G.P.I.T. 1545/1 (Holotype); **d**: *Glochiceras steueri* n. sp., S.G.N. 7333/5 (Paratype); **e**: *Parastreblites comahuensis* n. sp., S.G.N. 7326. (Holotype). Natural size.

1928 *Haploceras (Pseudolissoceras) Zitteli* (Burckhardt) — Krantz, p. 18, pl. 1, fig. 6.
1931 *Pseudolissoceras zitteli* (Burckhardt) — Weaver, p. 401, pl. 43, fig. 291.
1938 *Haploceras (Pseudolissoceras) Zitteli* (Burckhardt) — Roman, p. 176, pl. 16, fig. 170 (Reproduction of Burckhardt's original: pl. 10, figs. 1, 2; 1903).
1942 *Pseudolissoceras* cf. *P. zitteli* (Burckhardt) — Imlay, p. 1443, pl. 4, figs. 1, 3, 4, 7, 8, 11, 12.
1950 *Pseudolissoceras zitteli* (Burckhardt) — Spath, p. 101, pl. 6, figs. 8a-c.
1973 *Pseudolissoceras zitteli* (Burckhardt) — Verma & Westermann, p. 168, pl. 26, figs. 3-5, text figs. 12-13.
1978 *Pseudolissoceras zitteli* (Burckhardt) — Oloriz, p. 34, pl. 2, fig. 12, text fig. 43.

Material. — 55 specimens, mostly well preserved. S.G.N. 7325/1—2; S. G. N. 7331/1—4, 6; S.G.N. 7333/1—4; S.G.N. 7334/1—4; S.G.N. 8887/1—2; S.G.N. 8897/1; S.G.N. 8920/1—4; S.G.N. 8938/1—3; S.G.N. 8925/1—21; S.G.N. 8926/1—9. The specimens illustrated in plate 1, figs. 1a—b and 2a—b, correspond respectively to numbers S.G.N. 7325/1 and S.G.N. 7333/1.

Description. — The largest specimen has a diameter of 124 mm (S.G.N. 7334/1) and the smallest a diameter of only 12.8 mm (S. G. N. 1925/14). The diameters of the remaining samples transitionally cover the range between these extremes. The shell is involute. On the average, the umbilicus of the smaller specimens occupies 18 % of the shell diameter, and up to 26 % in the larger specimens. The most extreme ratios were measured in specimens S.G.N. 7333/1 (U/D = 0.13) and S.G.N. 7334/1 (U/D = 0.27). This latter ratio belongs to the specimen of maximum size (diameter = 124 mm). These data clearly show the tendency for the shell to become more evolute with age.

Whorl sections are higher than wide (text-fig. 2a). Umbilical borders become sharper with increase in shell size: smaller specimens show rounded umbilical borders, while larger ones exhibit an umbilical slope which is strongly inclined and sometimes almost vertical. The flanks are gently convex and the periphery sligthly rounded. In some specimens whose tests have been preserved it is possible to observe very fine somewhat falcoidal striae.

The suture line (text-fig. 3) coincides exactly with that originally described by Burckhardt (1903, p. 55). The E/L saddle is wide and is divided by an accessory lobe in two asymmetrical parts. The L lobe is very shallow and somewhat less wide than E/L. The E/U saddle has a width almost equivalent to half the E/L saddle, and also is divided by a small lobe into two asymmetrical parts. There are also two U lobes (U_2 and U_3) which are not very elaborate.

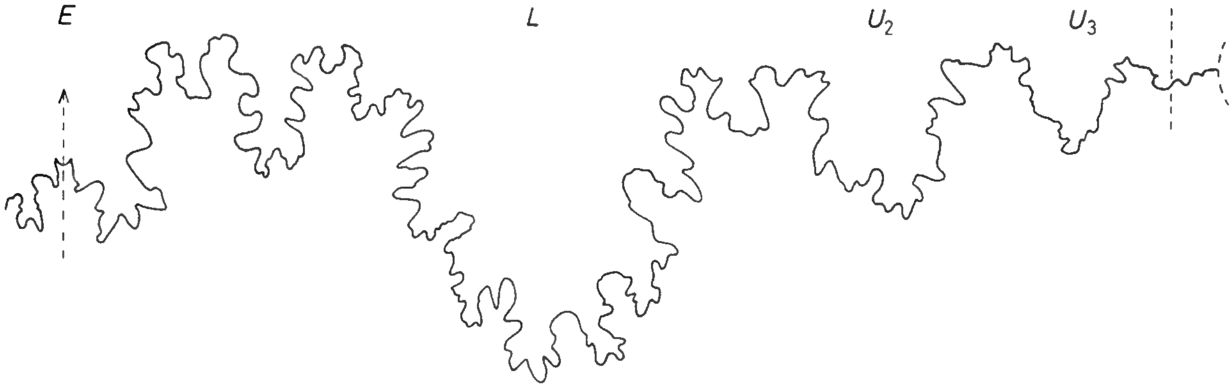

Figure 3: Suture line of *Pseudolissoceras zitteli* (Burck.), S.G.N. 7325/1. ×3.

Measurements (better-preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	7325/1	94	25	0.26	40	26	1.53
S.G.N.	7325/2	51	12	0.23	23	14	1.64
S.G.N.	7331/1	117	29	0.24	42	27	1.55
S.G.N.	7331/2	69	12	0.17	33	19	1.73
S.G.N.	7331/3	46	8	0.17	24	12	2.00
S.G.N.	7331/4	81	17	0.20	37	24	1.54
S.G.N.	7331/6	14	3	0.21	7	5	1.40
S.G.N.	7333/1	51	7	0.13	28	15	1.86
S.G.N.	7333/2	41	9	0.21	22	12	1.83
S.G.N.	7333/3	32	8	0.25	19	12	1.58
S.G.N.	7333/4	38	10	0.26	20	12	1.66
S.G.N.	7334/1	124	34	0.27	51	35	1.45
S.G.N.	7334/2	53	9	0.16	29	15	1.93
S.G.N.	7334/3	58	10	0.17	29	14	2.07
S.G.N.	8920/1	53	10	0.18	29	16	1.81
S.G.N.	8920/2	44	7	0.15	23	13	1.76
S.G.N.	8920/4	45	10	0.22	21	15	1.40
S.G.N.	8887/1	97	23	0.23	42	25	1.68
S.G.N.	8897/3	33	7	0.21	18	12	1.50
S.G.N.	8926/1	43	9	0.20	26	15	1.73
S.G.N.	8926/2	37	8	0.21	18	12	1.50
S.G.N.	8926/3	31	7	0.22	17	11	1.54
S.G.N.	8926/4	31	6	0.19	17	10	1.70
S.G.N.	8926/5	25	5	0.20	14	10	1.40
S.G.N.	8926/6	28	5	0.17	16	10	1.60
S.G.N.	8926/7	23	4	0.17	13	9	1.44
S.G.N.	8926/8	21	3.5	0.16	11.5	7.5	1.53
S.G.N.	8926/9	17	4	0.23	7	5.5	1.27
S.G.N.	8925/2	37	7	0.18	20	12	1.66
S.G.N.	8925/3	34	7	0.20	18	10	1.80
S.G.N.	8925/4	26	6	0.23	13	9	1.44
S.G.N.	8925/5	23	5.5	0.23	12	9	1.33
S.G.N.	8925/6	19	4	0.21	11	7.5	1.46
S.G.N.	8925/7	18	3.5	0.19	10	7	1.42
S.G.N.	8925/8	17.5	3	0.17	10	6.5	1.53
S.G.N.	8925/9	16	4	0.25	8	5.5	1.45
S.G.N.	8925/10	17.5	3.5	0.20	8	5.5	1.45
S.G.N.	8925/11	15.5	3	0.19	8	5	1.60
S.G.N.	8925/12	15	3	0.20	9	6	1.50
S.G.N.	8925/13	17	3.1	0.18	8	5	1.60
S.G.N.	8925/14	12.8	2.5	0.19	7	4.8	1.45

Remarks. — The described specimens can be readily placed in the genus *Pseudolissoceras* Spath (1925, p. 113); specifically they correspond to *P. zitteli* (Burckhardt, 1903). The specimens illustrated by Haupt (1907), Krantz (1926, 1928) and Weaver (1931) were also found in Cerro Lotena. Some authors have suggested that this species displays sexual dimorphism (cf. Verma & Westermann, 1973, p. 145), but the present study reveals that most of the smaller specimens (up to 23 mm diameter) belong to immature specimens which could have attained a greater size.

No specimens have been found with the whorl section as figured by Haupt (1907, pl. 7, fig. 4b). It is possible that this whorl section is from an unusually crushed specimen and does not constitute a variety of *P. zitteli,* as was suggested by Barthel (1962, p. 13, 15). It does, however, resemble the whorl section of *P. concorsi* Donze & Enay (1961, p. 46).

The inclusion of *"Neumayria" subrasilis* Burckhardt (1906, p. 127, pl. 34, figs. 8—11) in the synonymic list of *P. zitteli* by Verma & Westermann (1973, p. 168) appears to be inadequate because the umbilicus occupies 36 % of the diameter of the shell (U/D = 0.36) and the whorls are only slightly higher than wide (H/W = 1.14). These features suggest that Burckhardt's species is related to the *P. rasile* group (cf. supra). The cited ratios are much more anomalous for the *P. zitteli* group because *"N." subrasilis* has only an 18 mm diameter; for this size, the average U/D ratio of the *P. zitteli* group does not exceed 26 % of the shell diameter.

Occurrence. — *P. zitteli* occurs in beds 3, 4, 5 and 6 of the Cerro Lotena section, in association with *P. pseudooolithicum, Glochiceras steueri* n. sp., *Parastreblites comahuensis* n. sp. and *Hildoglochiceras wiedmanni* n. sp. The first specimens of *P. zitteli* occur 25 m above the basal conglomerate of the Vaca Muerta Formation.

Age. — Lowermost Middle Tithonian. *P. zitteli* Zone.

Pseudolissoceras pseudooolithicum (Haupt, 1907)

Pl. 1, Figs. 5a—b; Text-Figs. 2b and 4.

1903 *Neumayria pseudooolithica* Haupt, p. 200, pl. 8, figs. 2a-c.
1926 *Pseudolissoceras pseudooolithicum* (Haupt) — Krantz, p. 435 (n. comb.)
1931 *Pseudolissoceras pseudoolithica* (Haupt) — Weaver, p. 400.
? 1951 *Pseudolissoceras zitteli* (Burck.) — Arnould-Saget, p. 9, pl. 1, figs. 12a-c, 13a-c, 14 and 16a-c.

Material. — Three well-preserved specimens. S.G.N. 7328/1 (Figured in Pl. 1, Figs. 5a—b); S.G.N. 7328/2 and S.G.N. 7331/5.

Description. — Small shell, moderately evolute, with suboval whorl section, only very slightly higher than wide (text-fig. 2b). U/D = 0.26 to 0.27. The umbilical slope is strongly inclined but passes transitionally into the flanks forming an rounded umbilical border. In contrast to *P. zitteli* an umbilical edge never exists. The flanks are clearly convex and the periphery is rounded. The suture line (text-fig. 4) strongly resembles that of *P. zitteli,* and is characterized by a wide E/L saddle divided by a small accessory lobe in two asymmetrical parts. The L lobe is wide and shallow and the E/U saddle has a width equivalent to half of E/L. The U lobes are very simple and not oblique.

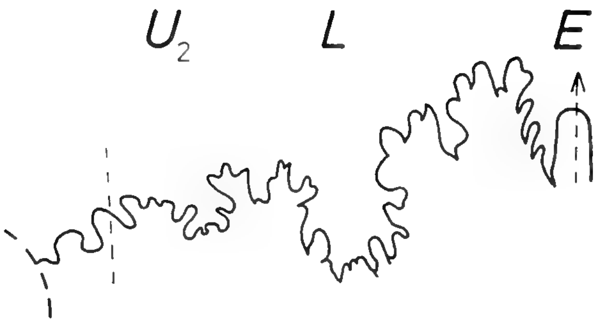

Figure 4: Suture line of *Pseudolissoceras pseudooolithicum* (Haupt), S.G.N. 7328/2. ×6.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	7328/1	38	10	0.26	18.5	16	1.15
S.G.N.	7328/2	22	6	0.27	12	11	1.09
S.G.N.	7331/5	21	5.5	0.26	11	10	1.10

Remarks. — The described specimens closely resemble *P. pseudooolithicum* (Haupt, 1907, p. 200, pl. 8, figs. 2a—c) which, as previously mentioned, is included in the *P. rasile* group. The shell morphology of *P. pseudooolithicum* strongly resembles that of *Haploceras elimatum* (Oppel, 1865, Zittel, 1870), which is the type species of *Haploceras* by the subsequent designation of Spath (1923); however, it differs in having a suture line with a E/U saddle as wide as the E/L saddle and also clearly more elevated. By contrast, Haupt's species displays a smaller and more depressed E/U, similar to that of *P. zitteli*. For this reason the present author retains Haupt's species in the genus *Pseudolissoceras*. Acquisition of better material may, however, eventually allow establishment of a new genus.

It is very probable that "*P. zitteli*" of Arnould-Saget (1951, p. 9, pl. 1, figs. 12a—c, 13a—c, 14 and 16a—c) from Tunisia, on the basis of whorl shape, dimensions and suture, could also belong to the species here described.

It is worth remarking that Haupt (1907, p. 200) gives an umbilicus diameter of 13.5 mm for the specimen figured in pl. 8, fig. 2a. This specimen, as can be seen, is only 8 mm in diameter, with the other dimensions as stated by Haupt. Consequently, the U/D ratio for this specimen is 0.25 and not 0.43, which agrees very well with the described material.

Occurence. — Bed 6 of the Cerro Lotena section, in association with *P. zitteli*.

Age. — Lowermost Middle Tithonian. *P. zitteli* Zone.

Genus GLOCHICERAS Hyatt, 1900

Type species. — *Ammonites nimbatus* Oppel, 1863, p. 191, pl. 52, figs. 5a, b.

Glochiceras steueri n. sp.
Pl. 1, Figs. 3a—b, Text-Fig. 2d.

Holotype. — *Oppelia nimbata* Steuer (*non* Oppel), 1897, p. 74, pl. 7, fig. 17.

Paratypes. — *Oppelia nimbata* Steuer (*non* Oppel), 1897, p. 74, pl. 7, fig. 16 and specimen S.G.N. 7333/5, illustrated in Pl. 1, Figs. 3a—b of this paper.

Locus typicus. — Arroyo Cieneguitas, near its junction with the Salado river, southern Mendoza, Argentina.

Stratum typicum. — Lower part of the Vaca Muerta Formation, in the *P. zitteli* Zone.

Derivatio nominis. — In honour of Doctor Alfred Steuer, who described this species.

Diagnosis. — Small shell, involute and compressed. Ornamentation characterized by fine striae which form, in the internal part of the flanks, a lateral linguiform band projecting towards the aperture. This band is narrow and crenulate, and does not constitute a true sulcus.

Material. — Only one specimen, complete, but with aperture not preserved and umbilicus not very clear. S.G.N. 7333/5. The shell is somewhat crushed.

Description. — Small involute shell, with a U/D ratio = 0.26. Whorl section somewhat subelliptical, higher than wide (text-fig. 2d). Umbilical border gently rounded. Surface of the flanks slightly convex. Periphery gently rounded. Ornamentation characterized by fine striae which commence in the umbilical slope and form a biconvex parabola over the flanks. In the internal portion of the flanks, near the umbilical border, the striae form a small and narrow linguiform band, which is strongly directed towards the aperture. Contiguous bundles of weak striae produce depressions, while bundles of strong striae form elevated folds. As a result, in the lateral linguiform band, folds and depressions alternate throughout the test. Neither the aperture nor the suture line could be observed.

Measurements. — (in mm)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	7333/5	23	6	0.26	11	5?	2.2?

Remarks. — Though the lappets of the specimen are not preserved, it is nevertheless possible, on the basis of whorl shape and ornamentation, to include it in the genus *Glochiceras* Hyatt, 1900 (type species:

Ammonites nimbatus OPPEL, 1863, p. 191, pl. 52, figs. 5a, b). The genus *Hildoglochiceras* SPATH, 1924 (type species: *Hecticoceras latistrigatum* UHLIG, 1903, p. 27, pl. 2, figs. 4a, c; pl. 3, fig. 5) is much more evolute and exhibits a deep lateral groove and, as well, subplanate flanks. "*Paraglochiceras*" COLLIGNON, 1960 (type species not designated) does not have a deep lateral groove, but has a whorl shape more evolute and inflated than the true *Glochiceras.*

Specifically, the specimen appears to be identical to *Oppelia nimbata* STEUER (*non* OPPEL) (1897, p. 74, pl. 7, figs. 16 and 17) from Arroyo Cieneguitas, Mendoza, Argentina. However, this species differs from the genotype, *G. nimbatum* (OPPEL, op. cit.), as it shell is much more compressed, and the strongly crenulate lateral bands is in a position nearer to the umbilical border. For these reasons, it is proposed to designate the specimen as *G. steueri* n. sp., with *Oppelia nimbata* STEUER, 1897, *non* OPPEL, 1863, as type species.

G. steueri n. sp. has closer affinities with the group of *G. fialar* BURCKHARDT (*non* OPPEL) (1906, p. 77, pl. 19, figs. 1—19; pl. 20, figs. 6, 12, 14, 15) from Mazapil, Mexico, but differs from these forms in having a more compressed and involute shell. The authentic *G. fialar* (OPPEL, 1863, p. 205, pl. 53, figs. 6a—c) differs from *G. steueri* in being more evolute and in displaying small crenulations around the periphery. *G. angustiumbilicatum* IMLAY (1939, p. 26, pl. 7, figs. 4—6), although bearing some similarities, clearly differs in having a distinct umbilical border and a strongly inclined umbilical slope. *G. somalicum* SPATH (1925, p. 114, pl. 16, fig. 7) is also more evolute and has a distinct umbilical border and wider lateral band. Finally, *G. parabolistriatum* KRANTZ (1926, p. 434, pl. 15, figs. 3, 4) from Arroyo Loncoche, Mendoza, Argentina, has a more inflated shell, with whorls wider than high, and also a much wider lateral band.

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 3 of the Cerro Lotena section, in association with *P. zitteli* and *H. wiedmanni.*

Age. — Lowermost Middle Tithonian. *P. zitteli* Zone.

Genus HILDOGLOCHICERAS SPATH, 1924

Type species. — *Hecticoceras latistrigatum* UHLIG, 1903, p. 27, pl. 2, fig. 4a—e; pl. 3, fig. 5.

Hildoglochiceras wiedmanni n. sp.
Pl. 1, Figs. 4a—b; Text-Figs. 2c and 5.

Holotype. — *H. wiedmanni* H. LEANZA n. sp., figured in Pl. 1, Figs. 4a—b. G.P.I.T. 1545/1.

Locus typicus. — Cerro Lotena, Neuquén province, Argentina.

Stratum typicum. — Lower part of the Vaca Muerta Formation.

Derivatio nominis. — In honour to the outstanding ammonitologist, Prof. Dr. Jost WIEDMANN, University of Tübingen, Germany.

Diagnosis. — Small shell, strongly evolute. Whorl section somewhat compressed. Subplanate flanks. Rounded umbilical border and convex periphery. Ornamentation smooth, with the presence of a lateral groove in the upper third of the flanks. Somewhat below the groove there is a linguiform parabola directed towards the aperture. Suture line simple, with the E/L saddle very wide and the L lobe narrow and deep.

Material. — One complete specimen, very well preserved. Almost half of the last whorl belongs to the body chamber. G.P.I.T. 1545/1.

Description. — Small evolute shell, with umbilicus wide and shallow. U/D ratio = 0.40. Whorl section somewhat compressed, subrectangular in shape, with rounded borders (text-fig. 2c). Umbilical slope gently inclined. Subplanate flanks and rounded periphery. Ornamentation characterized by a nitid and narrow groove in the upper third of the flanks. In addition, very fine striae form a biconvex parabola, producing in the middle part of the flank, just below the groove, a linguiform process which projects towards the aperture.

The suture line (text.-fig. 5) is very simple, with the E/L saddle very wide and the L lobe narrow and deep; very poorly-developed accessory elements.

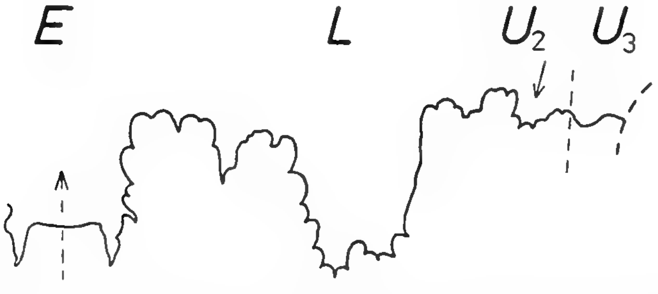

Figure 5: Suture line of *Hildoglochiceras wiedmanni* n. sp., G.P.I.T. 1545/1. ×6.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
G.P.I.T.	1545/1	22	9	0.40	9	6	1.5

Remarks. — The evolute shell with subplanate flanks and the presence of the characteristic lateral groove allow assignment of the specimen to the genus *Hildoglochiceras* SPATH, 1924 (type species: *Hecticoceras latistrigatum* UHLIG, 1903, p. 27, pl. 2, figs. 4a—e; pl. 3, fig. 5). Originally, the specimen was catalogued in the collections of the University of Tübingen as *Haploceras* n. sp. aff. *tenuifalcatum*, a species described more than 100 years ago by NEUMAYR (1873, p. 162, pl. 31, figs. 6a—b) from the *Aspidoceras acanthicum* Zone. However, this classification does not appear to be correct as NEUMAYR's species does not have the lateral groove on the flanks. Instead, the specimen is more similar to *Haploceras* cf. *tenuifalcatum* HAUPT (*non* NEUMAYR) (1907, p. 201) from Cerro Lotena, which bears lateral grooves. HAUPT compared his material with *Ammonites lingulatus* QUENSTEDT (1858), which is actually included in *Glochiceras* (cf. ZIEGLER, 1958). However, the classification of this ammonite in either *Glochiceras* or *Haploceras* does not appear to be correct because the first genus has a completely smooth test, without ornamentation, while the second one is always much more involute. For these reasons, the specimen is placed in *Hildoglochiceras*. Specifically, the closest form is *H. tenuicostulatum* COLLIGNON (1960, pl. 145, fig. 568, 569) from Madagascar, but this species is more involute and shows some ribbing in the upper part of the flanks. With respect to the other known species of *Hildoglochiceras*, the differences are still more obvious. For this reason, the specimen is considered as a new species named *H. wiedmanni* n. sp.

Occurence. — Lower part of the Vaca Muerta Formation. Bed 3 of the Cerro Lotena section, in association with *P. zitteli* and *G. steueri*.

Age. — Lowermost Middle Tithonian. *P. zitteli* Zone.

Family OPPELIIDAE BONARELLI, 1884
Subfamily TARAMELLICERATINAE SPATH, 1928
Genus PARASTREBLITES DONZE & ENAY, 1961

Type species. — *Oppelia tenuilobata* (OPPEL) var. *circumnodosa* FONTANNES, 1879, p. 23, pl. 3, fig. 6.

Parastreblites comahuensis n. sp.
Pl. 1, Figs. 6a—c; Text-Figs. 2e and 6

? 1926 *Oppelia (Neochetoceras) Waageni* ZITTEL — KRANTZ, p. 434.

? 1931 *Oppelia (Neoochetoceras) waageni* ZITTEL — WEAVER, p. 399.

Holotype. — *Parastreblites comahuensis* H. LEANZA n. sp., figured in Pl. 1, Figs. 6a—c. S.G.N. 7326.

Locus typicus. — Southern slope of Cerro Lotena, province of Neuquén, Argentina.

Stratum typicum. — Lower part of the Vaca Muerta Formation. *P. zitteli* Zone.

Derivatio nominis. — From Comahue, an araucan name for the region lying between the Colorado and Limay-Negro Rivers, and occupying the province of Neuquén and part of the provinces of La Pampa and Río Negro.

Diagnosis. — Shell strongly involute, compressed, with whorl section higher than wide. Umbilicus narrow and very deep. Venter rather acute but rounded. Ornamentation characterized by fine striae which describe a falcoidal trajectory over the flanks. Suture line with L lobe narrow and much deeper than the E lobe, and 3 accessory lobes (U_2, U_3 and $U_4 = S$).

Material. — One specimen. S.G.N. 7326: phragmocone very well preserved.

Description. — Because only one specimen was found, little can be added to the diagnosis. The most distinctive features are its suture line (text-fig. 6), similar to that of the genus *Parastreblites*, and its very narrow and deep umbilicus, which represents only 11 % of the shell diameter. The umbilical slope is vertical. The maximum width is in the upper part of the internal third of the flanks (text-fig. 2e). The periphery is narrowly rounded. The test is smooth except for some weak striae which cross the flanks fal-

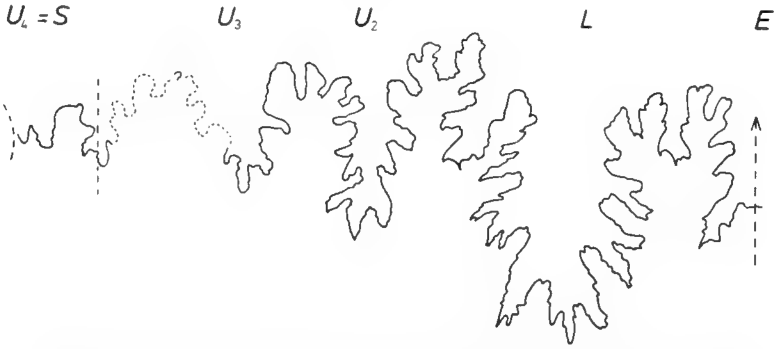

Figure 6: Suture line of *Parastreblites comahuensis* n. sp., S.G.N. 7326/1. ×2.

coidally. The suture line (text-fig. 6) shows an narrow L lobe and 3 accessory lobes (U_2, U_3 and $U_4 = S$).

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	7326	90	10	0.11	53	28	1.89

Remarks. — The specimen resembles "*Oppelia*" *waageni* ZITTEL (1870, pl. 19, fig. 1) in its lack of ornamentation and in its whorl section, which has a rather narrowly rounded venter. In addition the suture line of both displays three accessory elements. However, the specimen from Cerro Lotena clearly differs in having a deeper and narrower umbilicus. The species *waageni* of ZITTEL was included by SPATH (1925, p. 117, footnote) in the genus *Neochetoceras* (type species: *Ammonites steraspis* OPPEL, 1863, p. 251, pl. 69, figs. 1—9). This author implicitly considered *Neochetoceras* to include not only forms with an acute venter, but also those with a rounded venter. Later, DONZE & ENAY (1961, p. 52) transferred "*Oppelia*" *waageni* to *Parastreblites,* originally created by this authors as a subgenus of *Taramelliceras,* considering *Oppelia tenuilobata* (OPPEL) var. *circumnodosa* FONTANNES (1879, p. 23, fig. 6) as type species. DONZE & ENAY stated that its suture line was intermediary between *Taramelliceras* (type species: *Ammonites trachynotus* OPPEL, 1863, pl. 56, fig. 4) and *Metahaploceras* SPATH, 1925 (type species: *Ammonites lingulatus nudus* QUENSTEDT, 1887, p. 852, pl. 92, fig. 55) (cf. HOLDER, 1955, p. 59).

Specifically, the specimen closely resembles *P. waageni* (ZITTEL), and, to a lesser extent, *P. similis* (SPATH, 1925, p. 116, pl. 15, figs. 4a, b). However, the specimen clearly differs in its deeper and narrower umbilicus and in its almost smooth test. *P. hölderi* DONZE & ENAY (1961, p. 55, pl. 4, fig. 1, text-fig. 8) also differs by having a somewhat more sculpturated test with falcoidal ribbing. For these reasons, the specimen is proposed as the type of a new species named *P. comahuensis* n. sp., its essential features being a shell shape and suture line similar to those of *Parastreblites,* and a smooth test with deep and narrow umbilicus.

WEAVER (1931, p. 399) as well as KRANTZ (1926, p. 434) have described but not figured some specimens from Cerro Lotena referred to as *Oppelia (Neochetoceras) waageni.* However, judging by their descriptions, these forms probably belong to *P. comahuensis* n. sp.

Occurence. — Lower part of the Vaca Muerta Formation. Bed 5 of the Cerro Lotena section, in association with *P. zitteli.*

Age. — Lowermost Middle Tithonian. *P. zitteli* Zone.

Superfamily PERISPHINCTACEAE STEINMANN, 1880
Family PERISPHINCTIDAE STEINMANN, 1890
Subfamily VIRGATOSPHINCTINAE SPATH, 1925
Genus PSEUDINVOLUTICERAS SPATH, 1925

Type species. — *Pseudinvoluticeras somalicum* SPATH, 1925, p. 141, pl. 15, figs. 7a—c, text-fig. 10.

The genus *Pseudinvoluticeras* is characterized by an involute shell, vertical umbilical slope and groups of fine ribs which commence in periumbilical swellings which with the age show a tendency to become smooth and distant. The following originally described or subsequently transferred species are known: *P. somalicum* SPATH (1925, p. 141, pl. 15, figs. 7a—c, text-fig. 10), *P. douvillei* SPATH, 1925 (= *Simbirskites barbotanus* DOUVILLÉ *non* LAHUSEN, 1910, p. 17, pl. 3, figs. 4a, b), *P. mozambicum* COLLIGNON (1960, pl. 159, fig. 631) and *P.* cf. *P. mozambicum* COLLIGNON (VERMA & WESTERMANN, 1973, p. 182, pl. 29, fig. 1).

The species found in Cerro Lotena, named *P. windhauseni* (WEAVER) n. comb., can now be added to this list.

"*P. decipiens*" SPATH (1925, p. 134; 1950, p. 115), originally based on *Simbirskites payeri* DOUVILLÉ *non* TOULA (1910, p. 18, pl. 3, figs. 3a, b), is considered for reasons given below as synonymous with *P. douvillei* SPATH. In the same species is also included "*Virgatosphinctes lotenoensis*" WEAVER (1931, p. 423, pl. 48, figs. 322, 323) and "*Virgatosphinctes erinoides*" INDANS *non* BURCKHARDT (1954, p. 109, pl. 15, fig. 1).

Pseudinvoluticeras douvillei SPATH, 1925
Pl. 3, Figs. 3a—b, 5a—b; Pl. 4, Figs. 2a—b,
Text-Figs. 7a and 8.

1910 *Simbirskites barbotanus* DOUVILLÉ (*non* LAHUSEN), p. 17, pl. 3, fig. 4a-b.
Simbirskites payeri DOUVILLÉ (*non* TOULA), p. 18, pl. 3, figs. 3a-b.
1925 *Pseudinvoluticeras douvillei* SPATH, p. 134 (sp. nov.) (= *S. barbotanus* DOUV. *non* LAHUSEN).
Pseudinvoluticeras decipiens SPATH, p. 134, (sp. nov.) (= *S. payeri* DOUV. *non* TOULA).
1931 *Virgatosphinctes lotenoensis* WEAVER, p. 423, pl. 48, figs. 322, 323.
1954 *Virgatosphinctes erinoides* INDANS (*non* BURCKHARDT), p. 109, pl. 15, fig. 1.

Material. — 14 specimens in general well preserved. S.G.N. 8904/1—3: three well preserved phragmocones without body chamber. S.G.N. 8885/1: fragment of body chamber. S.G.N. 8894/1: phragmocone not well preserved, without body chamber. S.G.N. 8903/1—3: three small phragmocones, well preserved. S.G.N. 8912/3: small phragmocone fragment. S.G.N. 8899/1—4: four phragmocones, poorly

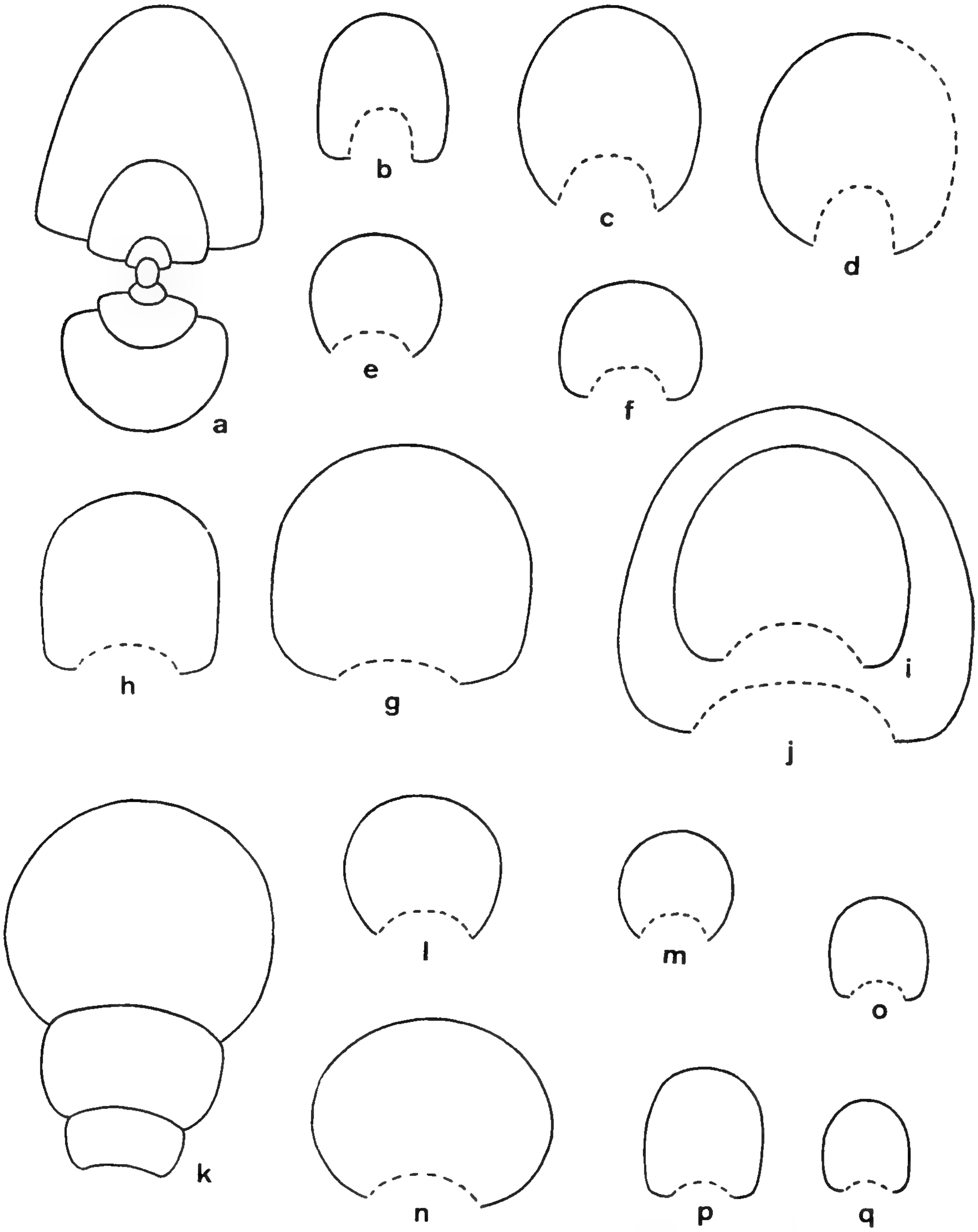

Figure 7: Whorl sections of Virgatosphinctinae. **a**: *Pseudoinvoluticeras douvillei*, S.G.N. 8904/1; **b**: *P. windhauseni*, S.G.N. 8900/2; **c**: *Virgatosphinctes mexicanus*, S.G.N. 8883; **d**: *V. andesensis*, S.G.N. 8894/2; **e**: *V. denseplicatus rotundus*, G.P.I.T. 1545/2; **f**: *Pseudinvoluticeras* (?) *wilfridi*, S.G.N. 8898/1; **g**: *V. evolutus* n. sp., S.G.N. 8901/1 (Holotype); **h**: *Choicensisphinctes choicensis sutilis* n. ssp., S.G.N. 8902/1 (Holotype); **i**: *Ch. choicensis*, S.G.N. 8905/3; **j**: *Ch. erinoides*, S.G.N. 8885/2; **k**: *Pachysphinctes americanensis* n. sp., S.G.N. 8952/1 (Holotype); **l**: *Subdichotomoceras araucanense* n. sp., S.G.N. 8935/1 (Holotype); **m**: *S. windhauseni*, S.G.N. 8940/2; **n**: *Aulacosphinctoides* aff. *A. hundesianus*, S.G.N. 8934/1; **o**: *Parapallasiceras* sp. indet., S.G.N. 8942/2; **p**: *P.* aff. *pseudocolubrinoides*, S.G.N. 8947/1; **q**: *P.* aff. *recticosta*, S.G.N. 8942/5. Natural size.

preserved. S.G.N. 8884/3: phragmocone fragment, poorly preserved.

Description. — Medium size shell, inflated and involute, with a whorl overlap ranging from 28 % to 30 % with regard to the diameter of the shell. The whorls are regularly higher than wide, with a H/W ratio ranging from 1.06 to 1.10. The whorl section is subtrapezoidal, but with rounded periphery (text-fig. 7a). The maximum width is at the umbilical border. The umbilicus is narrow and very deep, and the umbilical slope, of diagnostic value, is high and almost vertical. The flanks and the umbilical slope form a rect angle with rounded border, and they are slightly convex, converging to a gently rounded periphery.

The internal whorls are somewhat depressed, and therefore wider than high. Ornamentation is characterized by fine, mostly biplicate ribs and to a lesser proportion virgate ribs. Projected constrictions are also present.

In the last whorl, particularly in the body chamber, the ornamentation changes its aspect due to the formation of periumbilical swellings. In the last whorl there is an average of 30 periumbilical primary ribs, from which originate bundles containing 3 to 4 fine ribs, the more anteriorly-situated being more prorsiradiate, with the posteriorly-situated somewhat rursiradiate. Between these bundles are intercalated secondary ribs which reach the middle of the flank; the shape of these ribs is similar to that of the primary ribs. Both types of ribs cross the venter without interruption. The ribbing in the last part of the body chamber becomes gradually smooth, until only the umbilical swellings remain. In the last whorl there is a total of about 110 primary and secondary ribs.

The suture line (text-fig. 8) is very elaborate; the L lobe is slightly deeper than the E lobe. The E/L saddle is higher and wider than the E/U saddle, and both are asymmetrically divided by two accessory lobes. There are also three elaborate U lobes (U_2, U_3 and U_4).

Figure 8: Suture line of *Pseudinvoluticeras douvillei* Spath, S.G.N. 8904/2. ×3.

Measurements. — (better-preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
"*S. barbotanus*" Douv.		89	25	0.28	—	—	—
"*S. payeri*" Douv.		84	25	0.29	—	—	—
S.G.N.	8904/1	83	24	0.28	37	34	1.08
S.G.N.	8904/2	68	21	0.30	32	30	1.06
S.G.N.	8904/3	67	20	0.29	30	28	1.07
S.G.N.	8905/1	94	29	0.30	38	36	1.05
S.G.N.	8894/1	72	21	0.29	31	29	1.06
S.G.N.	8885/1	97	28	0.28	45	42	1.07
S.G.N.	8903/1	58	17	0.29	24	22	1.09
S.G.N.	8903/2	42	12	0.28	22	20	1.10
S.G.N.	8903/3	49	15	0.30	24	21	1.10
S.G.N.	8899/1	52	15	0.28	20	?	—
S.G.N.	8899/4	37	11	0.29	15	14	1.07

Remarks. — The material described here can be included in the genus *Pseudinvoluticeras* Spath, 1925 (type species: *P. somalicum* Spath, 1925, pl. 15, figs. 7a—c, text-fig. 10), but differs from the genotype in being slightly less involute and also less densely ribbed. On the other hand, it strongly resembles *P. douvillei* Spath, 1925 (= *Simbirskites barbotanus*

Douvillé *non* Lahusen, 1910, p. 17, pl. 3, figs. 4a, b) in all at its morphologic characteristics.

"P. decipiens" Spath (1925, p. 134), based on *"Simbirskites payeri"* Douvillé *non* Toula (1910, p. 18, pl. 3, figs. 3a, b) is apparently cospecific with the species *douvillei* of Spath. In the original description of *"S. payeri"*, Douvillé (1910, p. 18) stated that "La forme générale, le profil de la coquille, la dimension de l'ombilic, les dimensions et disposition des côtes ombilicales et externes chez l'adulte son tout à fait comparables aux éléments correspondants de l'espèce que nous venons de rapporter à *S. barbotanus*". The essential difference which influenced Douvillé to separate this "species" appears to be "... la ornamentation très caractéristique de la partie jeune" (op. cit., p. 18). As can be seen in the specimens figured by Douvillé, the only ones he had available for study, the internal whorls are impossible to compare, because in the specimen of pl. 3, fig. 4a they are entirely covered. Furthermore, *"S. payeri"* has the test preserved only in the first fourth of the last whorl, while *"S. barbotanus"* has it entirely preserved. This would explain the very slight differences in the ornamentation of both specimens. The different U/D ratios (0.28 for *"S. barbotanus* and 0.29 for *"S. payeri")* fall within the range of variation of the species described here. It is for these reasons that these two "species" are considered here to be cospecific.

As mentioned above, Spath (1925, p. 134 and 142) considered *"S. barbotanus"* Douvillé (*non* Lahusen) as the type species of *P. douvillei,* and *"S. payeri"* Douvillé (*non* Toula) as the type species of *P. decipiens.* On the basis of the analysis made above, and retaining the name of *P. douvillei* because it is better known and has priority in the paper by Spath (op. cit., p. 134), it is clear that *"S. payeri"* falls into the synonymic list of *P. douvillei.*

Another specimen that can also be included in *P. douvillei,* as already suggested by Spath (1950, p. 115), is *"Virgatosphinctes lotenoensis"* Weaver (1931, p. 423, pl. 48, figs. 322, 323), found by Weaver 6.5 km to the west of Cerro Lotena.

"Virgatosphinctes erinoides" Indans *non* Burckhardt (1954, p. 109, pl. 15, fig. 1), from Portezuelo del Burro, Mendoza, Argentina, can also be included in *P. douvillei* Spath. Indans herself noted the strong analogy between this form and *"S. payeri"* Douvillé and, in fact, it resembles much more *P. douvillei* than the true *"Perisphinctes" erinoides* of Burckhardt (1903, p. 51, pl. 8, fig. 1), a form much more evolute that is included in this study in the new genus *Choicensisphinctes.*

P. mozambicum Collignon (1960, pl. 159, fig. 631) differs from *P. douvillei* in being more involute and in having weaker periumbilical swellings. Finally, *P. windhauseni* (Weaver) has a more compressed shell and is much more densely ribbed.

Occurence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section. Virgatosphinctinae Beds. Occurs in association with *Virgatosphinctes andesensis, V. mexicanus, V. burckhardti, V. evolutus* n. sp., *V. denseplicatus rotundus, P. windhauseni, P.* (?) *wilfridi, Choicensisphinctes choicensis, Ch. choicensis sutilis* and *Ch. erinoides.*

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Pseudinvoluticeras windhauseni (Weaver, 1931)
n. comb.

Pl. 3, Fig. 2, 4a—b; Text-Fig. 7b.

1931 *Virgatosphinctes windhauseni* Weaver, p. 425, pl. 48, figs. 324, 325.

Material. — 15 specimens, mostly fragments, not very well preserved. S.G.N. 8900/1—10: phragmocone fragments, poorly preserved. S.G.N. 8912/1—2: two phragmocone fragments. S.G.N. 8884/2: phragmocone fragment. S.G.N. 8893/1—2: incomplete phragmocone, badly preserved.

Description. — Shell of medium size, slightly inflated and involute. The diameter of umbilicus ranges from 23 % to 26 % of the whorl overlap. The umbilicus is narrow and deep, and the umbilical wall almost vertical; the flanks and the umbilical wall form a rect angle with rounded border. The whorl section is elliptical, with somewhat convex flanks converging rapidly to a widely convex periphery (cf. text-fig. 7b). The maximum width is at the umbilical border. In the internal whorl the ornamentation is characterized by very fine, regularly spaced ribs, which begin in the umbilical wall, crossing it in a somewhat rursiradiate direction. At the umbilical border, they gradually turn towards the aperture; on the flanks they clearly project and cross the venter without interruption. Near the base of the middle third of the flank, the ribs begin to bi- or triplicate, but maintain the same prominence.

In the last part of the body chamber there is a tendency towards formation of periumbilical swellings, and also a gradual decrease in the prominence of the ribbing, leading to the formation of smoother surfaces.

Because of the fragmentary preservation of the material, the number of ribs could not be established exactly; it is estimated as consisting of 50 primaries and 130 secondaries. The poor preservation also precluded determination of the suture line.

Measurements. — (better preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
“V. ”windhauseni							
WEAV., spec. n° 1		85	20	0.23	19	18.5	1.02
S.G.N.	8900/2	49	11	0.22	22	20	1.10
S.G.N.	8900/3	50	12	0.24	22	20	1.10
S.G.N.	8900/4	57	14	0.24	25	19	1.31
S.G.N.	8900/5	51	12	0.23	22	20	1.10
S.G.N.	8900/6	30	7	0.23	13	13	1.00

Remarks. — The coiling of the shell, narrow and deep umbilicus, almost vertical umbilical slope, and ribbing with a tendency to form periumbilical swellings and smooth surfaces in the body chamber, together suggest that the material can be included in the genus *Pseudinvoluticeras*.

Specifically, it shows very close correspondence to *“Virgatosphinctes” windhauseni* WEAVER (1931, p. 425, pl. 48, figs. 324, 325), which was also found by WEAVER in the Cerro Lotena area. Therefore, the name *P. windhauseni* (WEAVER) n. comb. is proposed.

None of the species of *Pseudinvoluticeras* known to date shows such fine and dense ribbing as the described material. This characteristic is therefore considered to be of diagnostic value.

“Virgatosphinctes” (Lithacoceras) tenuilineatus INDANS (1954, p. 103, pl. 13, figs. 1, 2), contrary to the view of DONZE & ENAY (1961, p. 70), falls more properly in *Pseudinvoluticeras* than in *Lithacoceras*, and appears to be closely related to *P. windhauseni*.

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *Virgatosphinctes andesensis, V. mexicanus, V. burckhardti, V. evolutus, V. denseplicatus rotundus, Pseudinvoluticeras douvillei, P.* (?) *wildfridi, Choicensisphinctes choicensis, Ch. choicensis sutilis* and *Ch. erinoides*.

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Pseudinvoluticeras (?) *wilfridi* (DOUVILLÉ, 1910)
Pl. 5, Figs. 3a—b; Text-Fig. 7f.

1910 *Holcodiscus wilfridi* DOUVILLÉ, p. 12, pl. 2, fig. 6.
1954 *Virgatosphinctes wilfridi* (DOUVILLÉ) — INDANS, p. 107, pl. 13, fig. 3.

Material. — One specimen. S.G.N. 8898/1: phragmocone well preserved, but internal whorls not very apparent.

Description. — The shell is discoidal, small and relatively involute. The umbilicus is narrow and deep. The U/D ratio = 0.31. The whorls are somewhat inflated and wider than high. The umbilical wall is strongly inclined, almost vertical. The umbilical wall and the flanks form a rectangle with rounded edge. The flanks are subplanate and rapidly converge to a widely-rounded periphery. The ornamentation is characterized by fine and dense ribbing. The ribs commence in the umbilical slope, where they are somewhat rursiradiate. At the umbilical border they bend forward, describing a sigmoidal trajectory over the flanks. The ribbing is characterized by dicotomic or virgatotomic branching at different heights on the flanks. The branched ribs maintain the same prominence as the primaries, and cross the venter without interruption. In the last volution there are three rather unclear constrictions, anteriorly bordered by a simple rib and posteriorly by virgate bundles. The suture line could not be detected.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8898/1	45	14	0.31	17	21	0.80

Remarks. — The specimen, which consists of the internal whorls of the phragmocone, is surprisingly similar to that figured as *“Holcodiscus” wilfridi* by DOUVILLÉ (1910, p. 12, pl. 2, fig. 6). This species, coincidently, is also based on an incomplete phragmocone which only shows the internal whorls. The specimen figured by INDANS (1954, p. 107, pl. 13, fig. 3) is also very similar. A problem arises as to where this species should be generically placed, because its attribution to the genus *Virgatosphinctes* UHLIG, as made by INDANS (1954) — perhaps influenced by the words of UHLIG (1911a, p. 542) — does not appears to be acceptable. Although this species resembles *Virgatosphinctes* of the *denseplicatus* group, the similarity is only superficial because its whorl section is somewhat more inflated, the umbilical slope is almost vertical and the shell is more involute, all features which are absent in *Virgatosphinctes*. The enigmatic species *wilfridi* of DOUVILLÉ could also be included either in the genus *Aulacosphinctoides* or *Pseudinvoluticeras*. UHLIG himself, in discussing the inclusion of DOUVILLÉ's species in his genus *Virgatosphinctes*, stated with regard to *“V.” wilfridi* that “Vielleicht bildet diese Art das Jugendstadium des *Simbirskites payeri* R. Douv.” UHLIG, 1911a, p. 542). As mentioned above, *“S. payeri”* is actually included in *Pseudinvoluticeras*.

In view of the lack of material, the specimen described here is provisionally attributed to the genus *Pseudinvoluticeras* with interrogant, though bearing in mind the problem outlined above.

Perisphinctes (Aulacosphinctes) wilfridi BURCKHARDT *non* DOUVILLÉ (1921, p. 51, pl. 17, figs. 1—3) has no relation to the form described here and is probably an *Aulacosphinctoides* (cf. SPATH, 1927—33, p. 533).

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. andesensis, V. mexicanus, V. burckhardti, V. evolutus, V. denseplicatus rotundus, P. douvillei, P. windhauseni, Ch. choicensis, Ch. choicensis sutilis* and *Ch. erinoides*.

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Genus VIRGATOSPHINCTES Uhlig, 1910

Type species. — *Perisphinctes (Virgatosphinctes) broilii* Uhlig, 1910, p. 336, pl. 91, figs. 1a—d. SD R. Douvillé, 1910a, p. 737.

The controversial and variable genus *Virgatosphinctes*, which was originally described by Uhlig (1910) from the Spiti Shales of India, has been the subject of much discussion, and, until recently, its presence in the Andean domain has not been fully accepted (cf. R. Enay, 1972, p. 374).

Before beginning any analysis of the problem, it is worthwhile to recall the words of Uhlig himself in the introduction of his subgenus *Virgatosphinctes*, stating that "... In no other group is the variability so great as in the present one; every character undergoes an almost incredible degree of fluctuation. Hardly a single specimen resembles another one in every detail ..." (Uhlig, 1910, p. 308). Although *Virgatosphinctes* was immediately typified by R. Douvillé (1910a, p. 737), who designated *V. broilii* Uhlig as the type species, the words of Uhlig did not lost their import to those dealing with this polifacetic genus, and were reiterated by Spath (1927—33, p. 532 and followings) in his description of the Jurassic cephalopod fauna of Cutch.

It should be noted that Uhlig himself (1910, p. 312, 1911a, 1911b) had suggested that many of the forms previously figured as *Virgatites* by Burckhardt (1903) could be included in the genus *Virgatosphinctes*, though this point of view was strongly rejected by Burckhardt (1911a, 1911b, 1930).

Although the Andean *Virgatosphinctes* appears to be a group with variable characteristics (cf. Steiger, 1914, p. 497 and following), most specimens clearly display the diagnostic features of this genus. In any case, it is not reasonable to refute the presence of *Virgatosphinctes* in the Andean Tithonian if such Himalayan forms as *Aulacosphinctoides, Torquatisphinctes, Aulacosphinctes, Himalayites* and *Subdichotomoceras* are accepted without reservation. The Cerro Lotena section ha yielded several examples of *Virgatosphinctes*, represented by the species *V. andesensis, V. mexicanus, V. burckhardti, V. denseplicatus rotundus* and *V. evolutus* n. sp., which are described below.

It is also worth noting that affinities exist between *Virgatosphinctes* and *Subplanites*. As stated by the author who defined the latter genus "the resemblances of this group with the true *Virgatosphinctes* is often close" (Spath, 1925, p. 120). However, when Spath established the genus *Subplanites* (type species: *Virgatosphinctes reisi* Schneid, 1914, p. 163, pl. 6, fig. 2), he did not give an adequate diagnosis and therefore it was the subject of much misinterpretation among later authors. Spath himself, while describing the Jurassic fauna of Cutch, stated that the forms described under *Subplanites* (v. gr. *S. elegans, S. adeloides, S. ? flexuosus*) "are more closely allied to *Perisphinctes contiguus* (Zittel) Uhlig" (Spath, 1927—33, p. 468) than to the typical *reisi-schlosseri-subdanubiensis* group of Neuburg, "... but the frequent confusion of *contiguus*-like species of *Subplanites* with the true *Virgatosphinctes* shows that the two genera are closely similar at certain stages".

More recently, Hölder (in Berckhemer & Hölder, 1959, p. 51) placed *Virgatosphinctes reisi* Schneid, the type species of *Subplanites*, in the synonymic list of *Perisphinctes (Virgatosphinctes) rupellianus*. The cited examples clearly show that the two genera are closely related.

Although many specimens from Cerro Lotena resemble *Subplanites*, it appears more reasonable to include them in *Virgatosphinctes* on the basis of (1): whorl section, which is subcircular and somewhat depressed in most cases, a feature atypical of *Subplanites*, and (2): suture line, which is relatively simple in contrast to that of *Subplanites*, where the accessory lobe dividing the E/U saddle is strongly oblique and the U lobes are much more elaborate.

For the above reasons, the present author includes some specimens from Cerro Lotena in the genus *Virgatosphinctes*, though bearing in mind its close affinities with the genus *Subplanites*.

Virgatosphinctes mexicanus (Burckhardt, 1906)

Pl. 2, Figs. 1a—b; Text-Fig. 7c.

1906 *Virgatites mexicanus* Burckhardt, p. 115, pl. 31, figs. 5-9.
1910 *Virgatites mexicanus* Burckhardt — Douvillé, p. 8, pl. 1, figs. 1-2.
1954 *Virgatosphinctes mexicanus* (Burckhardt) — Indans, p. 113, pl. 18, fig. 1.

Material. — One specimen. S.G.N. 8883: phragmocone fragment with remains of body chamber.

Description. — Discoidal shell, rather evolute, with the whorls overlapping the external third of the flanks of the precedents. U/D ratio = 0.44. Whorl section subelliptical, somewhat higher than wide (text-fig. 7c). Umbilical slope inclined, umbilical border rounded, with slightly convex flanks converging to a rounded periphery. The umbilicus is wide and relatively deep. Ribbing on the internal whorls, with probable bifurcation at the external third of the flank. In the last whorl the ribbing becomes virgatomous. The virgate ribs commence at different heights on a projected primary rib; a further division occurs at a level somewhat higher on the flanks. Constrictions are also present, and are prorsiradiate, and anteriorly-bordered by a stronger rib. The suture line could not be observed.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8883	95	42	0.44	31	28	1.10

Remarks. — All of the described morphological characteristics agree with those of the genus *Virgatosphinctes* Uhlig (1910). Specifically the specimen strongly resembles *Virgatosphinctes mexicanus* (Burckhardt, 1906, p. 115, pl. 31, figs. 5—9).

The specimens figured by Douvillé (1910, p. 8, pl. 1, figs. 1, 2) and Indans (1954, p. 113, pl. 18, fig. 1) from the provinces of Neuquén and Mendoza, respectively, belong without doubt to Burckhardt's species, though the specimens from Neuquén are somewhat more densely ribbed in the internal whorls.

Occurence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. andesensis, V. burckhardti, V. evolutus, V. denseplicatus rotundus, P. douvillei, P. windhauseni, P.* (?) *wilfridi, Ch. choicensis, Ch. choicensis sutilis* and *Ch. erinoides.*

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Virgatosphinctes andesensis (Douvillé, 1910)

Pl. 2, Figs. 5a—b; Text-Figs. 7d and 9.

1910 *Virgatites andesensis* Douvillé, p. 17, pl. 1, figs. 3a-b, 4a-f.
1931 *Virgatosphinctes andesensis* (Douvillé) — Weaver, p. 422, pl. 47, figs. 313, 314; pl. 48, figs. 318—321.
1954 *Virgatosphinctes andesensis* (Douvillé) — Indans, p. 111, pl. 13, fig. 9; pl. 16, figs. 1—5.
1958 *Virgatosphinctes andesensis* (Douvillé) — Corvalán, p. 43, pl. 8, figs. 18a, b.

Material. — One specimen. S.G.N. 8894/2: phragmocone well preserved, with two thirds of the last whorl belonging to the body chamber. One side somewhat deteriorated and crushed.

Description. — Discoidal shell, evolute. U/D ratio = 0.41. Whorl section suboval, somewhat higher than wide (text-fig. 7d). Umbilical slope strongly inclined, umbilical border rounded with slightly convex flanks converging to a rounded periphery. The body chamber occupies two thirds of the last whorl. The ornamentation is well defined, and composed of prominent primary ribs that commence near the base of the umbilical slope, where they are somewhat rursiradiate. At the umbilical border they become narrow and more prominent, crossing the internal part of the flank prorsiradiately and the external part radially. The ribs display a slight inflection in the middle part of the flank. There is also a virgatotomic branching of the ribs at different heights on the flanks. A given rib can be divided into two in the lower part of the flank. A further division occurs at a level somewhat higher on the flanks, as was described by Uhlig (1910, p. 306) in his diagnosis of *Virgatosphinctes.* This type of division becomes more evident towards the aperture of the shell, particularly at the body chamber. In the phragmocone, it is more common to find bi- or trifurcate ribs. The virgate ribs situated anteriorly project strongly, while the posterior ones are radial or somewhat rursiradiate. There are also intercalatory ribs which disappear on the internal third of the flank. The virgate and intercalatory ribs cross the venter without interruption. In the last whorl there are 42 primary ribs and 107 secondary ribs on the periphery. In the body chamber a nitid constriction is present which is first projected and then radial, and which is anteriorly bordered by a fine, prominent rib.

The suture line (text-fig. 9) has E and L lobes of the same depth, the E/L saddle is wider than the E/U saddle and there are two somewhat oblique U lobes of decreasing depth.

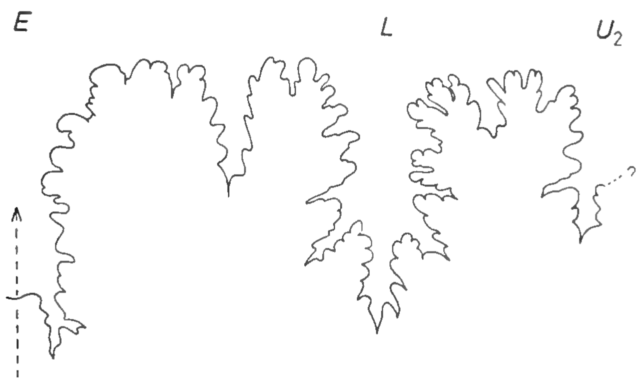

Figure 9: Suture line of *Virgatosphinctes andesensis* (Douv.), S.G.N. 8894/2. ×3.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8894/2	96	40	0.41	33	31	1.06

Remarks. — On the basis of the diagnosis of *Virgatosphinctes* (cf. Douvillé, 1910a, p. 737; Arkell *et al.*, 1957, p. L 330), the specimen can be assumed to belong to this genus. The whorl section, rate of whorl overlap, umbilical slope, and the ribbing characterized in the internal whorls by bi- or tricotomic branching and in the external ones by virgatotomic branching as described by Uhlig, indicate that the specimen can unquestionably be included in the genus *Virgatosphinctes.*

Specifically, it closely resembles *V. andesensis* (Douvillé, 1910, p. 17, pl. 1, figs. 3a—b; 4a—f), but it resembles even more the specimens attributed to the same species by Weaver (1931) and Indans (1954), in whose respective illustrations a rather notable variability in the ornamentation can be observed. In the described specimen, as well as in those figured by the above authors, the umbilicus is somewhat narrower than that of the larger specimen of Douvillé (1910, pl. 1, fig. 3a), though this difference may be only an apparent one because the umbilical border of the Douvillé species is partially covered by matrix which prevents observation of the line of coiling. The specimen of this study is almost identical to that figured by Weaver (1931, pl. 47, figs. 313 and 314), which also comes from Cerro Lotena.

"Virgatosphinctes" sanchezi Verma & Westermann (1973, p. 185, pl. 32, pl. 33, pl. 34, fig. 2, text-fig. 15) from the Tithonian of Sierra Catorce, Mexico, has an inverted ontogeny with regard to *Virgatosphinctes,* showing transposed stages of ornamentation, that is, virgate ribs occur in the young stage while simple and bipartite ribs are present in the adult stage.

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. mexicanus, V. burckhardti, V. evolutus, V. denseplicatus rotundus, P. douvillei, P. windhauseni, P.* (?) *wilfridi, Ch. choicensis, Ch. choicensis sutilis* and *Ch. erinoides.*

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Virgatosphinctes burckhardti (Douvillé 1910)

Pl. 5, Figs. 2a—b.

1903 *Virgatites* aff. *Quenstedti* Burckhardt (*non* Rouill), p. 42, pl. 6, figs. 104.
1910 *Virgatites Burckhardti* Douvillé, p. 10 (sp. nov.).
1910 *non Perisphinctes (Virgatosphinctes) Burckhardti* Uhlig, p. 332, pl. 62, figs. 3a-c.
1954 *Virgatosphinctes (Lithacoceras ?) burckhardti* (Douvillé) — Indans, p. 103, pl. 13, figs. 4—5.

Material. — One specimen. S.G.N. 8896/1: well-preserved incomplete phragmocone, with remains of body chamber.

Description. — Medium size shell, moderately evolute. U/D ratio = 0.35. Whorl section depressed, with the maximum width at the umbilical border. Umbilical slope strongly inclined, umbilical border rounded and flanks slightly convex, converging to a widely rounded periphery. The ornamentation is fine, densely ribbed and typically virgate. The primary ribs commence at the umbilical seam, and cross the umbilical slope rursiradiately. At the umbilical border they become stronger, and on the flanks they are prorsiradiate. In the internal third of the flank, the ribs shows virgatotomic branching, resulting in new divisions in the upper third of the flanks. In the last half of the last whorl there are 21 primary ribs at the umbilical border and 72 secondaries on the periphery. All the ribs cross the venter without interruption. Constrictions are usually present, following the direction of the ribbing. They are generally anteriorly bordered by a single rib. The suture line could not be observed.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8896/1	57	20	0.35	21	25	0.84

Remarks. — The specimen coincides in its morphological characteristics with the genus *Virgatosphinctes* Uhlig. Specifically, it shows close affinities with *V. burckhardti* (Douvillé, 1910, p. 10), which is based on "*Virgatites* aff. *quenstedti*" Burckhardt *non* Rouill (1903, p. 42, pl. 6, figs. 1—4). The specimen figured by Indans as *Virgatosphinctes (Lithacoceras ?) burckhardti* (see synonymic list) also coincides with the described specimen.

V. densistriatus (Steuer, 1897, p. 62, pl. 15, figs. 8 to 10) differs in its less evolute shell and more distant primaries. Also *V. denseplicatus* (Waagen, 1875, p. 201, pl. 45, figs. 3a—b; pl. 55, figs. 1a—b) is also a closely similar form, but differs in its larger evolution and denser, less prominent ribbing. *V. haughtoni* Spath (1927—33, p. 534, pl. 77, fig. 6) from Madagascar and *"Perisphinctes" aguilari* Burckhardt (1906, p. 110, pl. 27, figs. 6—9) from Mexico are also close species, but they differ from *V. burckhardti* in its less vigorous primaries, which are more distant and less projected.

It is worth noting that *"Perisphinctes" (Virgatosphinctes) burckhardti* Uhlig (1910, p. 332, pl. 62, figs. 3a-c) is a species which is more closely allied to *Subplanites,* and does not belong to the Douvillé species described here.

Occurence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section

(Virgatosphinctinae Beds), in association with *V. mexicanus*, *V. andesensis*, *V. evolutus*, *V. denseplicatus rotundus*, *P. douvillei*, *P. windhauseni*, *P.* (?) *wilfridi*, *Ch. choicensis*, *Ch. choicensis sutilis* and *Ch. erinoides*.

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Virgatosphinctes denseplicatus rotundus Spath, 1931
Pl. 2, Figs. 2 and 3; Text-Fig. 7e.

1931 *Virgatosphinctes denseplicatus* (Waagen) var. *rotunda* Spath — in Spath, 1927-33, p. 532, pl. 96, figs. 3a-b; pl. 102, fig. 4.

1954 *Virgatosphinctes* cf. *denseplicatus* (Waagen) var. *rotunda* Spath — Indans, p. 106, pl. 21, fig. 1.

Material. — Two specimens. S.G.N. 8905/1: well preserved phragmocone, with the last part of the last whorl somewhat crushed. G.P.I.T, 1545/2: very well preserved phragmocone.

Description. — The shell is discoidal and rather small. Umbilicus relatively narrow but not deep. U/D ratio = 0.35 to 0.39. Umbilical slope strongly inclined, umbilical border rounded, and flanks gently convex, gradually converging to a rounded periphery. Whorl section subelliptical and somewhat wider than high (text-fig. 7e). Ornamentation dense and formed of fine ribs that commence in the middle of the umbilical slope; in the flank they are somewhat prorsiradiate and they cross the periphery without interruption. Virgatotomic and dicotomic branching of the ribs occurs in the last whorl. Constrictions are also present, and are anteriorly bordered by a rib of similar prominence to the others. The suture line could not be observed.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8905/1	57	20	0.35	24	?	—
G.P.I.T.	1545/2	46	18	0.39	19	21	0.90

Remarks. — In shape the described specimen closely resembles *V. denseplicatus* (Waagen, 1875, p. 201, pl. 46, figs. 3a, b; pl. 55, figs. 1a, b), and corresponds exactly to the variety *rotundus* of Spath (1931, p. 532, pl. 96, figs. 3a, b; pl. 102, fig. 4). Spath stated that "It is possible that this variety also includes the inmature form figured in Pl. 102, fig. 4, although its umbilicus is somewhat too narrow" (Spath, 1927 to 33, p. 533). The specimen described in this study appears to be identical to this inmature form referred to by Spath.

V. denseplicatus (Waagen) from west Pakistan, figured by Fatmi (1972, p. 346, pl. 9, figs. 1a—b), also closely resembles the described material.

V. densistriatus (Steuer, 1897, p. 63, pl. 15, figs. 8 to 10) also resembles this variety, although it was suggested by Spath (1927—33, p. 534) to be a Pseudovirgatitid.

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. mexicanus*, *V. andesensis*, *V. burckhardti*, *V. evolutus*, *P. douvillei*, *P. windhauseni*, *P.* (?) *wilfridi*, *Ch. choicensis*, *Ch. choicensis sutilis* and *Ch. erinoides*.

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Virgatosphinctes evolutus n. sp.
Pl. 5, Figs. 4a—c; Text-Fig. 7g.

1903 *Perisphinctes* aff. *transitorius* Burckhardt (*non* Oppel), p. 40, pl. 5, figs. 4-9.
Perisphinctes contiguus Burckhardt (*non* Catullo), p. 38, pl. 4, figs. 7—10.

1931 *Aulacosphinctes* cf. *A. transitorius* (Oppel) — Weaver, p. 415, pl. 45, fig. 306.

Holotype. — *Virgatosphinctes evolutus* H. Leanza n. sp., figured in Pl. 5, Figs. 4a—c, Text-Fig. 7g of this paper. S.G.N. 8901/1.

Locus typicus. — Southern slope of Cerro Lotena, province of Neuquén, Argentina.

Stratum typicum. — Lower part of the Vaca Muerta Formation. *V. mendozanus* Zone.

Derivatio nominis. — From the evolute character of the shell.

Diagnosis. — Shell strongly evolute, with whorl section subcircular, somewhat depressed. Ornamentation in the internal whorls consists of elevated and narrow biplicate ribs; in the outer whorls these become gradually triplicate and virgatotomic. Constrictions are present. Suture line with trifid L lobe of almost the same depth as the E lobe. The E/L and E/U saddles are not very elaborate and are separated by small lobes into two asymmetrical saddles. There are also two U lobes which are somewhat oblique and not very elaborate.

Material. — One specimen. S.G.N. 8901/1: well preserved phragmocone with body chamber, which occupies almost half of the last volution.

Description. — The shell is discoidal and evolute. U/D ratio = 0.43. The last whorl section is subcircular and somewhat depressed (cf. text-fig. 7g). The periphery is slightly convex, the flanks are very gently convex, the umbilical border is very well rounded, and the umbilical slope is modertely inclined. Almost half of the last whorl belongs to the body chamber. The phragmocone is composed entirely of calcite which has eliminated all traces of the suture line except that limiting with the body chamber, which is fossilized in limestone. The last volution contains 49 primary ribs which commence at the umbilical slope, where they are rursiradiate. They bend forward on the umbilical border, and are prorsiradiate on the flanks. In the portion of the last whorl corresponding to the phragmocone, almost all the primary ribs are divided in two branches, both of the same prominence. In this portion, two or three intercalatory ribs are also preserved, which extend from the external part of the shell to the middle of the flanks.

There are also two examples of virgatotomic branching which are limited anteriorly by constrictions. In the portion of the whorl belonging to the body chamber, numerous virgate and triplicate examples of ribbing are observed, but only one case of bifurcation is present, located at the beginning of the body chamber. Three nitid constrictions are also present in this portion of the volution; they are limited anteriorly by a single rib and posteriorly by trifurcate or virgate ribs.

The suture line, preserved in a septum linking with the body chamber, shows a trifid L lobe of almost the same depth as the E lobe. The E/L and E/U saddles are not very elaborate and are separated by small lobes into two asymmetrical saddles. There are also two U lobes which are somewhat oblique and not very elaborate.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8901/1	106	46	0.43	35	38	0.92

Remarks. — This new species is closely related to *Perisphinctes* aff. *transitorius* Burckhardt (*non* Oppel) (1903, p. 40, pl. 5, figs. 4—9) and *Perisphinctes contiguus* Burckhardt (*non* Catullo) (1903, p. 38, p. 4, figs. 7—10), both from Casa Pincheira, southern Mendoza, Argentina. It differs only in its more depressed whorl sections, perhaps because they represent younger ontogenetic stages. Therefore, these two species are included in the synonymic list.

It is possible that "*Aulacosphinctes*" cf. *transitorius* Weaver (*non* Oppel) (1931, p. 415, pl. 45, fig. 306) also belongs to the newly-described species.

"*Perisphinctes* aff. *pseudolictor*" Choffat (Burckhardt, 1903, p. 36, pl. 5, figs. 1—6), later renamed by Spath as *Subplanites malargüensis*, is a form superficially similar to *V. evolutus* n. sp. differing only in its more compressed whorls and its more elaborate suture line.

With regard to the evolute *Virgatosphinctes* described by Uhlig from the Spiti Shales, *V. evolutus* n. sp. strongly resembles *V. haydeni* Uhlig (1910, p. 334, pl. 61, figs. 2a, d). With respect to the species from Madagascar, *V. rouselli* Collignon (1960, pl. 157, fig. 630) it is the closer related species.

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. andesensis*, *V. mexicanus*, *V. burckhardti*, *V. denseplicatus rotundus*, *P. douvillei*, *P. windhauseni*, *P.* (?) *wilfridi*, *Ch. choicensis*, *Ch. choicensis sutilis* and *Ch. erinoides*.

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Genus CHOICENSISPHINCTES nov.

Type species. — *Perisphinctes choicensis* Burckhardt, 1903, p. 50, pl. 6, figs. 10—12; pl. 8, fig. 6.

Diagnosis. — Discoidal, somewhat inflated and rather evolute shell. Whorl section subtrapezoidal, with rounded borders, wider than high. Ornamentation of the internal whorls regularly biplicate. Outer whorls display strong, prominent and projected primary ribs. Periumbilical swellings originate from bundles of 4 to 10 fine equally spaced, somewhat projected secondary ribs which cross the venter without interruption. No virgatotomic branching occurs. Constrictions are present. Suture line has trifid L lobe as deep as E, and E/L saddle wider and higher than E/U saddle. Two U lobes are present which are very simple and not oblique.

Locus typicus. — Area between Cajón del Burro and the Choica-River valley, at the beginning of the Rio Grande river, Mendoza province, Argentina.

Stratum typicum. — Lower part of the Vaca Muerta Formation. *V. mendozanus* Zone.

Derivatio nominis. — After the species of Burckhardt, *P. choicensis*, which is itself named after the Choica River, its locus typicus.

Discussion. — *Choicensisphinctes* gen. nov. is here proposed to include those ammonites having an inflated and rather evolute shell of olcostephanid aspect, and ornamentation characterized by bundles of 4 to 10 ribs. These forms constitute an homogeneous stock including the species "*P.*" *choicensis*, "*P.*" *erinoides* and "*P.*" aff. *erinus* of Burckhardt (1903). It is worth recalling that Uhlig himself (1911a, p. 542) had already suggested that the cited species of Burckhardt could be grouped as a determinate group of ammonites.

With regard to "*P.*" *choicensis*, Douvillé (1910a, p. 738) stated that it could not be placed in the so-called Andean *Virgatites*, which was later transferred to *Virgatosphinctes.* Moreover, Uhlig (1910, p. 336) pointed out that Burckhardt's species could be differentiated from his genus *Virgatosphinctes* (v. gr. *V. krafti* Uhlig) "by its narrower umbilicus, trapezoid cross section, simpler suture and much more numerous branch ribs".

The species *erinoides* of Burckhardt (1903, p. 51, pl. 8, figs. 1—4) was included successively in the genera *Olcostephanus* (Burckhardt, 1930, p. 111, 112), *Aulacosphinctes* (Weaver, 1931, p. 417), *Pararasenia ?* (Spath, 1927—33, p. 469) and *Virgatosphinctes* (Indans, 1954, p. 109), but none of these generic attributions appears to be plausible. However, as shown below, it can probably be included in *Choicensisphinctes.*

Finally, *P.* aff. *erinus* (D'Orb.) Burckhardt (1903, p. 52, pl. 9, figs. 1—2; pl. 8, fig. 5), which was later renamed by Burckhardt himself (1930, p. 110) as *Craspedites limitis,* probably incorrectly, can also be included more properly in *Choicensisphinctes.*

Choicensisphinctes gen. nov. differs from *Virgatosphinctes* Uhlig, 1910 (type species: *V. broilii* Uhlig, Sd Douvillé, 1910a), in addition to the differences already pointed out by Uhlig, in its more inflated shell, its strongly inclined umbilical wall, and the absence of virgatotomic branching.

The genus *Pseudinvoluticeras* Spath, 1925 (type species: *P. somalicum* Spath, 1925) in some cases shows a similar ornamentation, but it is always more involute.

Choicensisphinctes therefore represents a transitional form between *Virgatosphinctes* and *Pseudinvoluticeras:* it exhibits the coiling of the former, but an ornamentation more similar to the latter.

Other genera which show close affinities with *Choicensisphinctes* gen. nov. are *Sublithacoceras, Phanerostephanus* and *Usseliceras. Sublithacoceras* Spath, 1925 (type species: *Perisphinctes penicillatus* Schneid, 1915) is much more compressed and shows a tendency towards smooth surfaces in the body chamber. The suture line is also much more elaborate. *Phanerostephanus* Spath, 1950 (type species: *P. subsenex* Spath, 1950) is more involute and displays periumbilical swellings without ribbing in the last whorls. Finally, *Usseliceras* Zeiss, 1968 (type species: *U. franconicum* Zeiss, 1968), from south Franconia area, is very similar with regard to the ornamentation, but differs in being much more compressed, with whorls higher than wide.

Occurrence. — Very common in the basal beds of the Vaca Muerta Formation within the Neuquén and Mendoza basin. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds).

Age. — Lower Tithonian. *V. mendozanus* Zone.

Choicensisphinctes choicensis (Burckhardt, 1903)
Pl. 2, Figs. 4a—b; Text-Fig. 7i.

1903 *Perisphinctes choicensis* Burckhardt, p. 50, pl. 6, figs. 10-12; pl. 8, fig. 6.
1931 *Aulacosphinctes* cf. *A choicensis* (Burckhardt) — Weaver, p. 414.
1954 *Virgatosphinctes* cf. *raja* Uhlig — Indans, p. 110, pl. 14, fig. 1-3.

Material. — One specimen. S.G.N. 8905/3: phragmocone with remains of body chamber, very well preserved.

Description. — Discoidal shell of medium size, moderately inflated and rather evolute. U/D ratio = 0.36. Whorl section subtrapezoidal with rounded borders, a little wider than high (text fig. 7i). The maximum width occurs at the umbilical border. The umbilical slope is strongly inclined, the umbilicus wide and rather deep.

The flanks are gently convex and rapidly converge to a rounded periphery. The ornamentation is characterized by strong and projected primary ribs that show small radial periumbilical swellings which are more pronounced near the aperture. In the last volution there are 28 to 32 primaries, each of which gives rise to bundles of 4 to 7 secondary ribs, all having the same prominence and an equal spacing. The ribs are somewhat prorsiradiate, especially those more anteriorly situated, and cross the periphery without interruption. In the last whorl there are constrictions, two of which are very clear; these are anteriorly bordered by a more prominent and projected simple rib, and posteriorly bordered by the more anterior of the secondary ribs. The suture line has a trifid L lobe as deep as E, with an E/L saddle wider and higher than the E/U saddle. There are also two U lobes which are very simple and not oblique (see Burckhardt, 1903, pl. 6, fig. 12).

Measurements. —

Specimen n°	D	U	U/D	H	W	H/W
Ch. choicensis						
(Burck., 1903)	78	29	0.37	32	34	0.94
S.G.N. 8905/3	66	24	0.36	24	26	0.92

Remarks. — The described specimen corresponds exactly to "*Perisphinctes*" *choicensis* Burckhardt (1903, p. 50, pl. 6, figs. 10—12; pl. 8, fig. 6), which is the type species of *Choicensisphinctes* gen. nov. It is very probable that "*Aulacosphinctes*" cf. "*A.*" *choicensis,* described by Weaver (1931, p. 414) belongs to the species described here. This form also comes from Cerro Lotena (Weaver, op. cit., p. 415). On the other hand, "*Virgatosphinctes*" cf. *raja* Indans *non* Uhlig (Indans, 1954, p. 110, pl. 14, figs. 1—3), from southern Mendoza, Argentina, shows the morphological characteristics of *Choicensisphinctes* in terms of ornamentation and whorl shape.

Parapallasiceras ? *Danubisphinctes* ? n. sp., *lydistratiforme* Zeiss (1968, p. 110, pl. 20, fig. 1), compared by Zeiss (Op. cit., p. 115) to *Virgatosphinctes* cf. *raja* Indans (*non* Uhlig), appears to be very closely related to *Choicensisphinctes*.

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. andesensis*, *V. mexicanus*, *V. burckhardti*, *V. denseplicatus rotundus*, *V. evolutus*, *P. douvillei*, *P. windhauseni*, *P.* (?) *wilfridi*, *Ch. choicensis sutilis* and *Ch. erinoides*. *Ch. choicensis* is the commonest species found at the base of the Tithonian transgression within the Neuquén and Mendoza basin. It had been found by the author in the sections of Cerro Lotena, Picún Leufú, Mallín de los Caballos, Mallín Quemado, Cajón de Almaza (Neuquén province), Bardas Blancas and Arroyo Cieneguitas (Mendoza province).

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Choicensisphinctes choicensis sutilis n. ssp.

Pl. 3, Figs. 1a—b, Pl. 4, Fig. 3; Text-Fig. 7h.

Holotype. — *Choicensisphinctes choicensis sutilis* H. Leanza n. ssp., figured in Pl. 3, Figs. 1a—b of this paper. S.G.N. 8902/1.

Paratype. — *Choicensisphinctes choicensis sutilis* H. Leanza n. sp., figured in Pl. 4, Fig. 3 of this paper. S.G.N. 8902/2.

Locus typicus. — Southern slope of Cerro Lotena, province of Neuquén, Argentina.

Stratum typicum. — Lower part of the Vaca Muerta Formation. *V. mendozanus* Zone.

Derivatio nominis. — After the fine and elegant ribbing.

Diagnosis. — Shell discoidal, somewhat evolute, with wide umbilicus and strongly inclined umbilical slope. Whorl section subquadrangular, and as high as wide. Ornamentation in the internal whorls composed of very fine and dense ribbing, mostly with dicotomic branching. In the outer whorls are strong and somewhat irregularly-spaced and projected primary ribs, with periumbilical swellings which arise from bundles of 5 to 9 fine and projected secondary ribs. Constrictions are present.

Material. — Two specimens. S.G.N. 8902/1: phragmocone with remains of body chamber, very well preserved, but lacking the test (Holotype). S.G.N. 8902/2: phragmocone fragment and body chamber, laterally crushed (Paratype).

Description. — Discoidal and somewhat evolute shell. U/D ratio = 0.36. The umbilicus is wide and rather deep. The whorl section (text-fig. 7h) is subquadrangular, and as high as wide. The umbilical slope is strongly inclined. The internal whorls are ornamented by fine and elevated ribs which are very densely spaced, most of them with dicotomic branching. In the last whorl the ribs commence in the middle of the umbilical wall, where they are rursiradiate. At the umbilical border they bend forward, producing periumbilical swellings. In this whorl there are an average of 40 primary ribs. In the internal third of the flank there is a branching into bundles composed of 5 to 9 secondary ribs, all of which have the same prominence, being more projected the more anteriorly situated ribs. All the ribs cross the periphery without interruption. Between two contiguous bundles of ribs are intercalatory ribs which, except where they disappear in the upper third of the flank, have the same prominence as the rest of the ribbing. Three constrictions occur in the last whorl; they are prorsiradiate and limited anteriorly by a single prominent rib and posteriorly by the more anterior of the secondary ribs. The body chamber occupies more than half the last whorl, and the aperture shows a projected lappet at the height of the middle third of the flank. The suture line could not be detected.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8902/1	71	26	0.36	28	28	1.00
S.G.N.	8902/2	92	33	0.35	36	?	—

Remarks. — The material agrees in its morphological characteristics with the genus *Choicensisphinctes*, but differs from its type species *Ch. choicensis* (Burckhardt, 1903, p. 50, pl. 6, figs. 10—12; pl. 8, fig. 6) in being more densely ribbed and in having a whorl section as high as wide. These differences, although small are nevertheless clear and easy to identify. Consequently, the new subspecies of *Ch. choicensis* is proposed.

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. andesensis*, *V. mexicanus*, *V. burckhardti*, *V. denseplicatus rotundus*, *V. evolutus*, *P. douvillei*, *P. windhauseni*, *P.* (?) *wilfridi*, *Ch. choicensis* and *Ch. erinoides*.

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Choicensisphinctes erinoides (Burckhardt, 1903)

Pl. 4, Figs. 1a—b; Text-Fig. 7j.

1900a *Perisphinctes* aff. *erinus* D'Orbigny — Burckhardt, p. 42, pl. 25, fig. 1.
1903 *Perisphinctes erinoides* Burckhardt, p. 51, pl. 8, figs. 1-4.

1907 *Perisphinctes erinoides* BURCKHARDT — HAUPT, p. 197.
1931 *Perisphinctes erinoides* BURCKHARDT — WEAVER, p. 417.
1954 *non Virgatosphinctes erinoides* (BURCKHARDT) — INDANS, p. 109, pl. 15, fig. 1 (= *Pseudinvoluticeras douvillei).*

Material. — One specimen. S.G.N. 8885/2; relatively well preserved phragmocone with remains of body chamber.

Description. — Large shell, inflated and somewhat evolute. U/D ratio = 0.34. Umbilical slope very high, almost vertical. Rounded umbilical border. Flanks slightly convex, converging gradually to a widely rounded periphery. The maximum width occurs at the umbilical border. The ornamentation is of low relief, and consists of primary ribs with periumbilical swellings which disappear near the middle of the flank, giving way to bundles of 5 to 7 secondary ribs. They are equally spaced and of very low relief, and cross the venter without interruption. The suture line could not be detected.

Measurements. —

Specimen n°	D	U	U/D	H	W	H/W
S.G.N. 8885/2	120	41	0.34	47	51	0.92
"P." erinoides (BURCK., 1903)	160	55	0.34	61	60	1.01

Remarks. — The specimen displays specific characteristics in agreement with *"P." erinoides* BURCKHARDT (1903, p. 51, pl. 8, figs. 1—4). It differs only in having somewhat less dense and sharper ribbing, possibly due to the greater weathering of the BURCKHARDT's specimen. In this latter specimen, the higher whorl section is only present in an advanced ontogenetic stage, while the younger volutions are wider than high (Pl. 8, fig. 3, BURCKHARDT, 1903). This is also characteristic of the specimen described in this study.

The enigmatic species *erinoides* of BURCKHARDT was attributed by different authors to distinct genera such as *Aulacosphinctes* (WEAVER, 1931, p. 417), *Pararasenia* ? (SPATH, 1927—33, p. 469), *Virgatosphinctes* (INDANS, 1954, p. 109) and *Olcostephanus* (BURCKHARDT, 1930, p. 111, 112). In the opinion of the writer, none of these generic attributions are acceptable. In *Pararasenia* SPATH, 1925 (type species: *Aulacostephanus zacatecanus* BURCKHARDT, 1906, p. 67, pl. 16, figs. 1—4), there is a tendency towards interruption of the ribs over the venter, resulting in the presence of a smooth band. This feature is completely absent in *"P." erinoides.* With respect to INDANS' classification, reasons were given above for the transferral of *"Virgatosphinctes erinoides"* to *Pseudinvoluticeras douvillei.* The attributions of this species by WEAVER to *Aulacosphinctes*, and by BURCKHARDT firstly to *Perisphinctes* and secondly to *Olcostephanus*, appear also to be inadequate, because of the considerable morphological differences with regard to the diagnostic features of these genera.

"P." erinoides appear to resemble the genus *Choicensisphinctes* more closely than any other. The similarities of the internal whorl section and ornamentation of *"P." erinoides* with *Choicensisphinctes choicensis* (BURCKHARDT, 1903, p. 50, pl. 6, figs. 10—12; pl. 8, fig. 6) are very clear. A noticeable difference between the two species is however, the suture line, which is more elaborate in *"P." erinoides.*

It is also possible that *"P."* aff. *erinus* (D'Orb.) BURCKHARDT (1903, p. 52, pl. 9, figs. 1—2; pl. 8, fig. 5) belongs to *Choicensisphinctes*, although it shows a smoother ornamentation, a somewhat more involute shell and a more subtrapezoidal whorl section. *P.* aff. *erinus* was formerly renamed by BURCKHARDT himself (1930, p. 110) as *Craspedites limitis*, but as can clearly be seen, this attribution appears inadequate because of the much different morphologic features of the Boreal genus *Craspedites.*

Occurrence. — Lower part of the Vaca Muerta Formation. Bed 2 of the Cerro Lotena section (Virgatosphinctinae Beds), in association with *V. andesensis, V. mexicanus, V. burckhardti, V. denseplicatus rotundus, V. evolutus, P. douvillei, P. windhauseni, P.* (?) *wilfridi, Ch. choicensis sutilis* and *Ch. choicensis.*

Age. — Uppermost Lower Tithonian. *V. mendozanus* Zone.

Genus AULACOSPHINCTOIDES SPATH, 1923

Type species. — *Aulacosphinctes infundibulus* UHLIG, 1910, p. 371, pl. 72, figs. 1a—c.

Aulacosphinctoides aff. *A. hundesianus* (UHLIG, 1910)
Pl. 5, Figs. 1a—b; Text-Fig. 7n.

? 1910 *Aulacosphinctoides hundesianus* UHLIG, p. 374, pl. 71, figs. 3a-c; pl. 73, figs. 2a-c.
? 1923 *Aulacosphinctoides hundesianus* (UHLIG) — SPATH, p. 299.
? 1960 *Aulacosphinctoides hundesianus* (UHLIG) — COLLIGNON, pl. 151, figs. 605, 606.

Material. — One specimen. S.G.N. 8934/1: phragmocone and body chamber, relatively well preserved.

Description. — Medium size shell, discoidal and rather evolute. U/D ratio = 0.47. Whorl section subelliptical, somewhat depressed, wider than high (see text-fig. 7n). Umbilical wall strongly inclined, umbilical border rounded with slightly convex flanks, converging gradually to a widely rounded periphery. The internal whorls are ornamented by narrow and elevate simple ribs, with mostly dicotomic branching in the upper third of the flanks. In the outer whorls, the ribs describe a sigmoidal curve, and in the upper third of the flank they bifurcate or trifurcate, this being more common near the aperture. In the last volution there are 52 primary ribs and 107 secondaries. There are also sharp constrictions anteriorly bordered by a single rib which is more prominent than the other ribs, and which also describes a sigmoidal curve. The calcifized nature of the specimen prevented detection of the suture line.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8934/1	84	40	0.47	28	34	0.82

Remarks. — The specimen coincides exactly with the genus *Aulacosphinctoides* SPATH, 1923 (type species: *Aulacosphinctoides infundibulus* UHLIG, 1910, p. 371, pl. 72, figs. 1a, b). It also shows close affinities with *Torquatisphonctes* SPATH, 1924 (type species: *Ammonites torquatus* J. C. de SOWERBY, 1840, pl. 61, fig. 12). However, *Aulacosphinctoides* differs from this latter genus in having more depressed whorls, sigmoidal ribbing over the flanks, and frequent triplicate branching in the body chamber.

Specifically, the specimen has closer affinities with *A. hundesianus* (UHLIG, 1910, p. 374, pl. 71, figs. 3a—c; pl. 73, figs. 2a—c), included in *Aulacosphinctoides* by SPATH (1923, p. 299), but the specimen from Neuquén differs only in having somewhat narrower ribs, and branching at a level rather higher on the flanks.

A. chidamensis (UHLIG, 1910, p. 376, pl. 74, figs. 1a—d) is also a closely related species, but differs in its wider whorls and much more numerous trifurcate ribs. *A. brownei* (MARSHALL) SPATH (1923, p. 289, pl. 17, figs. 1a—d), from the Tithonian of New Zealand, is very similar to *A. hundesianus*, differing only in its less densely ribbed internal and external whorls.

With regard to the Argentine species, it should be noted that "*Aulacosphinctes*" *colubrinus* WEAVER (*non* BURCKHARDT) (WEAVER, 1931, *partim*, p. 413, pl. 44, fig. 301, *non* pl. 44, figs. 302, 303) probably belongs to *Aulacosphinctoides*. "*Aulacosphinctes*" cf. *bangei* INDANS (*non* BURCKHARDT) (INDANS, 1954, p. 122, pl. 18, fig. 2), as suggested by ARKELL (1956, p. 583), could also be included in SPATH's genus.

Occurrence. — Vaca Muerta Formation. Bed 14 of the Cerro Lotena section, in association with *W. internispinosum*.

Age. — Middle Tithonian. *W. internispinosum* Zone.

Aulacosphinctoides sp. indet.

Material. — One specimen. S.G.N. 8927/1: phragmocone poorly preserved, with internal whorls just discernible and external whorls without test.

Description. — Shell discoidal, strongly evolute. Whorl section not determinable because of crushing of the specimen. Umbilical slope slightly inclined, umbilical border rounded, and flanks gently convex. In the internal whorls the ornamentation is composed of elevated, narrow, irregularly spaced and apparently bifurcate ribs. In the outer whorls, where they can be observed, the ribs are mostly triplicate but some are also biplicate. These ribs describe a gently sigmoidal curve over the flanks. There are also constrictions anteriorly bordered by rather elevated ribs.

Remarks. — The morphological characteristics of this ammonite in general resemble the genus *Aulacosphinctoides*. Althoguh quite similar to the *hundesianus-chidamensis* group, the fragmentary preservation of the specimen does not permit a specific classification.

Occurrence. — Vaca Muerta Formation. Bed 12 of the Cerro Lotena section, in association with *Subdichotomoceras araucanense* n. sp.

Age. — Middle Tithonian. *W. internispinosum* Zone.

Genus SUBDICHOTOMOCERAS SPATH, 1925

Type species. — *Subdichotomoceras lamplughi* SPATH, 1925 (= *Perisphinctes lacertosus* PAVLOW (*non* FONTANNES), in: PAVLOW & LAMPLUGH, 1892, p. 110, fig. on text, p. 111).

Subdichotomoceras windhauseni (WEAVER, 1931)

Pl. 8, Figs. 2a—b; Text-Fig. 7m.

1931 *Aulacosphinctes windhauseni* WEAVER, p. 412, pl. 44, fig. 300.

Material. — One specimen. S.G.N. 8940/2: complete specimen with aperture, moderately preserved.

Description. — Medium size shell, strongly evolute. Whorl section subcircular, as high as wide (see text-fig. 7m). U/D ratio = 0.48. Ornamentation composed of narrow, prominent and rather widely spaced ribs. In the upper third of the flank, each rib bifurcates into two branches which cross the venter without interruption. Both primary and secondary ribs have the same prominence. The aperture is simple and is bordered by a single, much more elevated rib which describes a sigmoidal curve.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8940/2	47	23	0.48	17	17	1.00

Remarks. — All morphological features of the specimen agree with *"Aulacosphinctes" windhauseni* WEAVER (1931, p. 412, pl. 44, fig. 300). Although WEAVER did not figure the ventral view, he stated in his very accurate description that the ribs cross the venter without interruption. For this reason, WEAVER's attribution to the genus *Aulacosphinctes* UHLIG can not be accepted. SPATH (1936, p. 26) and ARKELL (1956, p. 582) have both suggested that *"A." windhauseni* could belong to the genus *Pavlovia* ILOVAISKY, 1917 (type species: *P. iatriensis* var. *primaria* ILOVAISKY, 1917, pl. 9, figs. 3a, b). This view has also been accepted by the present author (H. LEANZA, 1973, p. 127, foot note). However, although the described specimen strongly resembles *Pavlovia,* its attribution to the genus *Subdichotomoceras* appears to be more reasonable, because of the more widely spaced ribs in the internal whorls. Indeed, this feature (cf. ARKELL *et al.,* 1957, p. L328) is the only one that can be considered to differentiate the genera *Pavlovia* and *Subdichotomoceras.* The densely ribbed internal whorls of *Pavlovia* are well illustrated in the species from the Kimmeridge Clay of Dorset figured by NEAVERSON (1925) and COPE (1978) (see *P. rotunda* = *Pallasiceras rotundum* (SOW.) NEAVERSON, 1925, p. 18, pl. 1, fig. 6).

For the above reasons, the new combination *Subdichotomoceras windhauseni* (WEAVER) is therefore proposed. The specimen figured by WEAVER is also from Cerro Lotena, and has the same stratigraphic position as the specimen described here. A species formerly referred to as *Pavlovia* sp. indet., found in Picún Leufú and Mallín Quemado in Neuquén (H. LEANZA, 1973, p. 127), can also be definitely assigned to *Subdichotomoceras* (H. LEANZA & C. HUGO, 1977, p. 253).

These considerations indicate that the genus *Subdichotomoceras* has an areal distribution in the Andean-Madagascan-Himalayan domains during the Lower and Middle Tithonian, while *Pavlovia* is restricted to the Boreal realm in the Upper Kimmeridgian. It is for this reason that the origin of *Pavlovia* from *(via) Pectinatites,* as suggested by COPE (1978, p. 527), appears to be more suitable than an origin from *Subdichotomoceras,* as was formerly postulated by ARKELL *et al.* (1957, p. L332).

Occurrence. — Vaca Muerta Formation. Bed 16 of the Cerro Lotena section, in association with *W. internispinosum, Corongoceras lotenoense* and *Parapallasiceras* aff. *P. pseudocolubrinoides.*

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Subdichotomoceras araucanense n. sp.

Pl. 6, Figs. 1a—b, 3a—b; Text-Fig. 7 l.

Holotype. — *S. araucanense* H. LEANZA n. sp., figured in Pl. 6, figs. 3a—b. S.G.N. 8935/1.

Paratype. — *S. araucanense* H. LEANZA n. sp., figured in Pl. 6, figs. 1a—b. S.G.N. 8906/1.

Locus typicus. — Cerro Lotena, Neuquén province, Argentina.

Stratum typicum. — Middle part of the Vaca Muerta Formation in the Cerro Lotena area.

Derivatio nominis. — From Araucanos, the name given to the Indians from Chile who lived in the area of Neuquén, Rio Negro and Chubut.

Diagnosis. — Shell planulate, strongly evolute. Whorl section subquadrangular with rounded borders. Ribbing strong, sharp, regularly biplicate to the aperture, and without interruption on the venter. Aperture simple, somewhat projected, and without lappets. Constrictions bordered by simple and strong ribs.

Material. — 10 specimens. S.G.N. 8935/1: complete specimen, with phragmocone, body chamber and aperture, very well preserved (Holotype). S.G.N. 8906/1: phragmocone and damaged body chamber (Paratype). S.G.N. 8935/2: phragmocone, moderately preserved. S.G.N. 8935/3: incomplete phragmocone, somewhat deteriorated. S.G.N. 8931/9—13: five specimens, poorly preserved. S.G.N. 8942/8: complete specimen, rather well preserved.

Description. — Shell planulate and strongly evolute. U/D ratio = 0.48 to 0.51. Whorl section subquadrangular, with rounded borders, as wide as high (text-fig. 7 l) or slightly depressed. Umbilical slope gently inclined, umbilical border rounded, and flanks subplanate, gradually converging to a widely rounded periphery. Ornamentation composed of simple, elevated and narrow ribs, which are separated by spaces equal to three times the rib width. In the upper third of the flank each rib bifurcates into two branches which cross the venter without interruption.

The pairs of secondary ribs are somewhat less separated. In the last whorl of the holotype, there are 38 primary ribs and 72 secondaries. There are also constrictions bordered by elevated, strong, and somewhat projected single ribs. The suture line could not be detected.

Measurements. — (better preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8935/1 (Holotype)	78	39	0.50	22	22	1.00
S.G.N.	8906/1 (Paratype)	62	32	0.50	16	16	1.00
S.G.N.	8935/2	83	40	0.48	27	27	1.00
S.G.N.	8931/11	84	43	0.51	32	33	0.96

Remarks. — The morphological features of the material described here, undoubtedly resemble those of the genus *Subdichotomoceras* Spath (1925). Although the material shows close affinities with species from speeton (Pavlow & Lamplugh, 1892), Cutch (Spath, 1927—33) and Madagascar (Collignon, 1960), it does, however, differ in some aspects from each of them. Therefore a new species is proposed, named *S. araucanense*.

This new species differs from *S. lamplughi* (Pavlow, in: Pavlow & Lamplugh, 1892, p. 110, text-fig. on p. 111, SD Spath, 1925, p. 120), which is the type species of *Subdichotomoceras*, in having more elevated, projected and denser ribbing.

Of the species from Cutch figured by Spath (1927 to 33, p. 521 to p. 526), close resemblances are shown by *S. inversum* Spath (1927—33, p. 521, pl. 84, figs. 7a, b; pl. 85, fig. 4) and *S. simplex* Spath (op. cit., p. 522, pl. 83, figs. 8a, b), but these differ in having a lower density of ribs, with the bifurcation at a level somewhat lower on the flanks.

S. n. sp. aff. *S. inversum* Spath of Verma & Westermann (1973, p. 183, pl. 30, figs. 1—2; pl. 31, figs. 1—2, text-fig. 14B) from Mexico, has a much more depressed whorl section. The Madagascan species figured by Collignon, v. gr. *S. mandarenense* Collignon (1960, pl. 149, figs. 597—599), differs in being more involute and in having a more depressed whorl section.

Finally, *S. windhauseni* (Weaver) differs from *S. araucanense* n. sp. in having a lower density of ribs, and a clearly greater angle of divergence of the secondary ribs.

Occurrence. — Vaca Muerta Formation. Bed 12 of the Cerro Lotena section, in association with *Aulacosphinctoides* sp. indet.

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Subdichotomoceras sp. juv. indet.
Pl. 8, Figs. 5a—b.

Material. — One specimen. S. G. N. 8942/2: well preserved phragmocone of a young specimen.

Description. — Moderate size shell, relatively evolute. U/D ratio = 0.39. Whorl section suboval, somewhat depressed. Umbilical slope strongly inclined, and the umbilical border, flanks and periphery widely rounded. Ornamentation characterized by elevated and acute ribs, with dichotomic branching throughout the phragmocone. The outer whorl as well as the body chamber is not preserved. Bifurcation occurs in the upper third of the flank, and the secondary ribs cross the venter without interruption. In the internal whorls, the ribs are not densely spaced. Constrictions are present, bordered anteriorly by a single rib.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8942/2	46	18	0.39	15	17	0.88

Remarks. — The regular dichotomic branching of the ribs throughout the shell, as well as its whorl section, allow inclusion of this specimen in the genus *Subdichotomoceras*. Because only the inner whorls are preserved, with the evolution of the outer whorls unknown, it is not possible to make a specific classification. The specimen does, however, show some affinities with *S. rebillyi* Collignon (1960, pl. 148, figs. 594—596) from the Lower Tithonian of Madagascar. The latter species differs, however, in having somewhat more depressed whorls.

Occurrence. — Vaca Muerta Formation. Bed 7 of the Cerro Lotena section, in association with *A. proximus*.

Age. — Middle Tithonian. *A. proximus* Zone.

Genus PARAPALLASICERAS Spath, 1925

Type species. — *Berriasella (Aulacosphinctes ?) praecox* Schneid, 1915, p. 64, pl. 3, fig. 5.

Parapallasiceras aff. *P. pseudocolubrinoides* Oloriz, 1978
Pl. 8, Fig. 3; Text-Fig. 7p.

? 1978 *Parapallasiceras pseudocolubrinoides* Oloriz, p. 555, pl. 55, fig. 3, text-fig. on p. 565.

Material. — Three specimens. S.G.N. 8947/1: fragment of phragmocone with body chamber; one side only preserved. S.G.N. 8935/5: complete specimen, but with the inner whorls not well preserved. S.G.N. 8940/5: complete specimen not very well preserved.

Description. — Shell evolute, with wide and shallow umbilicus. U/D ratio = 0.41 to 0.45. Whorl section suboval, a little higher than wide (text-fig. 7p). Umbilical border rounded and flanks slightly convex, gradually converging to a rounded periphery. Ornamentation composed of elevated, acute, narrow ribs. The ribs normally biplicate or triplicate at a level somewhat above the middle of the flanks, and in a few cases also show poligyrate branching. They commence in the umbilical seam, and are somewhat rursiradiate on the umbilical slope. On the umbilical border they bend forward and cross the flanks radially or a little prorsiradiately, without any inflection. Over the venter the ribs, which display no interruption, describe a small adoral projection. In the inner whorls, however, they become weaker, leading to the formation of a very gentle ventral groove. In specimen S.G.N. 8935/5, there are numerous examples of poligyrate branching. Lappets in the aperture were not observed, but this is probably due to the somewhat incomplete preservation of the body chamber. Constrictions are present in the last whorl. The suture line could not be detected.

Measurements. — (better preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8947/1	65	27	0.41	20	?	—
S.G.N.	8940/5	58	25	0.43	17	?	—
S.G.N.	8935/5	75	34	0.45	21	20	1.05

Remarks. — This material, in terms of general shape, most strongly resembles the genus *Parapallasiceras* SPATH, 1925. Although similar to *Torquatisphinctes,* its whorl section is more compressed; furthermore, poligyrate branching is not present in the latter genus. There are even more notable differences with *Berriasella,* which is characterized by a more involute shell, and a somewhat more compressed whorl section and flattened venter, generally with a persistent groove. In addition, branching of the ribs in *Berriasella* occurs on a level rather lower on the flanks.

Although *Parapallasiceras* was originally proposed by SPATH (1925, p. 133), but without an adequate diagnosis, however, it has been recently redefined by ZEISS (1968, p. 105). On the basis of this definition, the described material can be readily included in *Parapallasiceras.*

MAZENOT (1939, p. 41) and DONZE & ENAY (1961, p. 185) considered that *Berriasella praecox* SCHNEID, which is the type species of *Parapallasiceras,* could be included in *Berriasella,* which they considered synonymus with the genus of SPATH. On the other hand, ARKELL *et al.* (1957, p. L329) and ZEISS (1968, p. 105) stated that *Parapallasiceras* has sufficient distinctive features to be considered an independent genus, an opinion which is also accepted here.

Specifically, the closest affinities of the material are with *P. pseudocolubrinoides* OLORIZ (1978, p. 555, pl. 55, fig. 3, text-fig. in p. 565), from the Lower Tithonian of Southern Spain; this species differs only in having somewhat less dense ribbing. Another species which appears similar to the described material is *P. spurium* (SCHNEID, 1915, p. 81, pl. 10, figs. 5, 5b; pl. 11, figs. 5, 5a), from Neuburg, Germany. This species, however, differs from the Cerro Lotena specimens in having more projected ribbing in the inner whorls and more involute shell.

Occurrence. — Vaca Muerta Formation. Bed 16 of the Cerro Lotena section, in association with *S. windhauseni, W. internispinosum* and *C. lotenoense.*

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Parapallasiceras aff. *P. recticosta* OLORIZ, 1978
Pl. 8, Figs. 6a—b; Text-Fig. 7q.

? 1978 *Parapallasiceras recticosta* OLORIZ, p. 553, pl. 55, fig. 5, text-fig. on p. 565.

Material. — One specimen. S.G.N. 8942/5: well preserved phragmocone, wigh remains of somewhat damaged body chamber.

Description. — Shell small, evolute, with rather shallow umbilicus. U/D ratio = 0.35. Whorl section suboval, a little higher than wide. Umbilical slope strongly inclined. Umbilical border gently rounded, passing upwards to short flanks which rapidly converge to a rounded periphery (text-fig. 7q). Ornamentation strong, with dichotomic branching throughout the phragmocone. Ribs of the inner whorls are fine, elevated and densely arranged. They are somewhat projected and show dicotomic branching at a level a little above the middle of the flanks. This type of ribbing is essentially the same in the last whorl, but somewhat more widely spaced. The ribs cross the venter with a slight adapertural convexity, but without interruption. Pairs of secondary ribs are less separated than contiguous pairs, a feature which is clearer in the last part of the last whorl. The angle of divergence of the secondaries is very small. No tuberculation at the point of branching has been observed. The illustration of the ventral view (pl. 8, fig. 6b) represents the undamaged part of the last whorl. In the figured specimen there are 36 primary ribs and 69 secondaries, as well as two clear and deep constrictions. The suture line was not detected.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8942/5	39	14	0.35	16	15	1.06

Note: The diameter of the umbilicus was measured on the unillustrated side, where the coiling is more regularly preserved. The height and width of the last whorl were measured immediately before the deformed portion.

Remarks. — This relatively small, constricted, *Pavlovia*-like specimen can tentatively be included in the genus *Parapallasiceras* Spath, 1925. Although at first view it resembles *Berriasella nitida* Schneid (1915, p. 70, pl. 5, figs. 4, 4b), it does not have simple ribs, the ribbing is less flexuous, and the secondary ribs show less divergence and cross the venter without interruption. Although Donze & Enay (1961, p. 188) included this species in the genus *Berriasella* Uhlig, 1905, Oloriz (1978, p. 608, 609) has recently stated that it belongs to the genus *Lemencia* Donze & Enay (1961). Another similarity, although perhaps only superficial, is with the subgenus *Epipallasiceras* Spath (1936), and in particular with the variety *superba* (Spath, 1936, p. 57, pl. 39, figs. 2a, b) from the Glauconitic Series of Cape Leslie.

Specifically, the strong nature of the ribbing, the entirely dicotomic branching of the ribs at a level slightly above the middle of the flanks, and the fact that these ribs cross the venter without interruption, relate the specimen to *P. recticosta* Oloriz (1978, p. 553, pl. 55, fig. 5, text-fig. on p. 565) from the Betic ranges of Southern Spain. The latter species differs from the Cerro Lotena specimen in its more compressed whorls and its denser ribbing in the inner whorls. As only one specimen exists, more detailed comparisions can not be made and it is therefore regarded as *Parapallasiceras* aff. *P. recticosta* Oloriz.

Occurrence. — Vaca Muerta Formation. Bed 10 of the Cerro Lotena section, in association with *A. euomphalum.*

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Parapallasiceras sp. indet.

Pl. 7, Figs. 2a—b; Text-Fig. 7 o.

Material. — Five specimens. S.G.N. 8942/4: complete specimen, but with last part of body chamber somewhat damaged. S.G.N. 8942/6—7: two incomplete specimens, poorly preserved. S.G.N. 8942/10: small specimen, moderately preserved. S.G.N. 8944/2: well preserved whorl fragment.

Description. — Shell strongly evolute, with umbilicus very wide and shallow. U/D ratio = 0.45 to 0.49. Whorl section subcircular, as high as wide. Umbilical slope strongly inclined, umbilical border gently rounded, flanks somewhat convex and the periphery slightly rounded (text-fig. 7 o). Ornamentation of inner whorls characterized by simple, acute and elevated ribs, regularly disposed and with bifurcation at a level somewhat below the line of coiling. In the last whorls, ribbing remains essentially the same up to the body chamber. The ribs commence in the umbilical slope, where they are slightly rursiradiate, but at the umbilical border they bend forward and become clearly prorsiradiate. In the upper third of the flanks the ribs bifurcate, crossing the venter with a somewhat convex form, but without interruption. There are also some sharp constrictions bordered anteriorly by a simple rib which occasionally interrupts the regularity of the rest of the ribbing. The suture line was not detected.

Measurements. — (better preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8942/4	55	27	0.49	16	16	1.00
S.G.N.	8942/10	35	16	0.45	12	12	1.00

Remarks. — This rather poorly preserved material is included in the genus *Parapallasiceras* Spath, 1925 (type species: *Berriasella praecox* Schneid, 1915, p. 64, pl. 3, fig. 5) on the basis of its evolute shell, whorl section and mainly biplicate ribbing from the phragmocone to the body chamber. Although it also strongly resembles *Torquatisphinctes* Spath, 1924 (type species: *Ammonites torquatus* J. C. de Sowerby, 1840, p. 719, pl. 61, fig. 12), this latter genus has a subquadrangular whorl section, and is more regularly ribbed and lacks poligyrate branching. Although the specimen described here shows some similarities with *T. regularis* Zeiss (1968, p. 51, pl. 7, fig. 2) with regard to its projected ribbing, the latter species shows a very compressed whorl section (cf. Zeiss, 1968, text-fig. 5 on p. 61), a feature that appears to be completely atypical of the true *Torquatisphinctes* from India (cf. Spath, 1927—33, p. 475 and following), which in general has a subquadrangular whorl section. It is therefore probable that the attribution of Zeiss could be revised.

Considering the lack of better preserved material, the specimens described here are regarded as *Parapallasiceras* sp. indet.

Occurrence. — Vaca Muerta Formation. Bed 18 of the Cerro Lotena section.

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Genus PACHYSPHINCTES Dietrich, 1925

Type species. — *P. africogermanus* Dietrich, 1925, p. 12, pl. 1, fig. 2; pl. 3, fig. 1. SD Spath, 1927—33.

Pachysphinctes americanensis n. sp.
Pl. 7, Figs. 1a—d; Text-Fig. 7k.

Holotype. — *P. americanensis* H. Leanza n. sp., figured in pl. 7, figs. 1a—d, text-fig. 7k. S.G.N. 8952/1.

Locus typicus. — Southern slope of Cerro Lotena, province of Neuquén, Argentina.

Stratum typicum. — Upper part of the Vaca Muerta Formation in the Cerro Lotena area.

Derivatio nominis. — From South America, continent were this species was found.

Diagnosis. — Very large shell, strongly evolute. Whorl section depressed. Internal whorls have regularly biplicate ribbing. Outer whorls display strong, irregularly spaced ribs, with bi- or trichotomic branching. Intercalatory ribs also present. In the body chamber the ribing becomes simple, elevated and distant.

Material. — Two specimens. S.G.N. 8952/1: very well preserved phragmocone fragment with remains of body chamber (Holotype). S.G.N. 8933/2: phragmocone fragment with poorly preserved internal whorls.

Description. — Very large, strongly evolute shell. U/D ratio = 0.51. Umbilicus wide and relatively deep. Internal whorls very depressed, with ornamentation composed of simple, regularly spaced, elevated and somewhat projected primary ribs that at the coiling line bifurcate into two branches. No spines occur at the point of bifurcation. In the last whorl, and particularly in the body chamber, the shape of the shell clearly changes. The whorl section is not as depressed, the umbilical slope is more elevated and strongly inclined, and the umbilical borders is more gently rounded. With regard to the ornamentation, the ribbing becomes stronger and more separated. The ribs commence in the umbilical slope in the areas where the test is preserved. They are initially rursiradiate, but then bend forward and over the middle of the flank they are clearly projected, crossing the periphery without interruption. In the first half of the last volution the ribs bifurcate or trifurcate; also present are simple ribs which disappear near the middle of the flanks. Towards the end of the last whorl, the ribs are simple and become stronger and much more widely spaced. The suture line is not preserved.

Measurements. — (better preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8952/1	196	101	0.51	58	69	0.84

Remarks. — The morphological features of the described material resemble those of the genus *Pachysphinctes* Dietrich, 1925 (type species: *P. africogermanus* Dietrich, op. cit., p. 12, pl. 1, fig. 2; pl. 3, fig. 1), which was later well illustrated by Spath (1927—33). Eleven species of this genus occur in the Middle Katrol Beds of Cutch. In these beds, *Pachysphinctes* is therefore the most common genus (cf. Arkell, 1956, p. 388). As noted by Spath (1927—33, p. 469), *Pachysphinctes* is an intermediate genus between *Katroliceras* and *Torquatisphinctes*. In adopting the name proposed by Dietrich for this group, Spath was influenced not only by the illustration of the genotype, but also by Dietrich's inclusion in this genus of *P. mülleri* Burckhardt (1921, p. 33 = *P. elizabethae* Müller, 1900, p. 529, pl. 15, fig. 4).

The described material undoubtedly belongs to the genus *Pachysphinctes*, and strongly resembles several forms figured by Spath from Cutch. There is a close resemblance, for example, with *P. bathyplocus* (Waagen), reillustrated by Spath (1927—33, p. 493, pl. 77, figs. 1a—b; pl. 93, figs. 5, 9; pl. 94, fig. 4). However, the specimens from Cerro Lotena differ from the latter species in having more widely spaced ribbing in the last whorl, especially in the body chamber. *P. crassus* Spath (1927—33, p. 492, pl. 85, figs. 3a—b) is also a closely related species but differs in having distinct periumbilical swellings, stronger ribs, and a more depressed whorl section. Accordingly, it is proposed that the described material be designated as a new species of *Pachysphinctes*, named *P. americanensis* n. sp.

Occurrence. — Vaca Muerta Formation. Bed 22 of the Cerro Lotena section, in association with *W. internispinosum*.

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Family ASPIDOCERATIDAE Zittel, 1895
Subfamily ASPIDOCERATINAE Zittel, 1895
Genus ASPIDOCERAS Zittel, 1868

Type species. — *Ammonites rogoznicensis* Zeuschner, 1846, in Zittel, 1868, p. 117, pl. 24, figs. 4—5.

Aspidoceras euomphalum Steuer, 1897
Pl. 8, Figs. 1a—b; Text-Fig. 10e.

1897 *Aspidoceras euomphalum* Steuer, p. 69, pl. 5, figs. 1-4 (= 1921, trans., pl. 5, figs. 1—4).
1907 *Aspidoceras euomphalum* Steuer — Haupt, p. 191.
1926 *Aspidoceras euomphalum* Steuer — Krantz, p. 432.
1928 *Aspidoceras euomphalum* Steuer — Krantz, p. 12.
1931 *Aspidoceras euomphalum* Steuer — Weaver, p. 436.

Material. — One specimen. S.G.N. 8931/15: well preserved phragmocone with remains of body chamber.

Description. — Medium size shell, inflated, moderately involute, with deep umbilicus. Whorl section suboval, depressed and wider than high. U/D ratio = 0.30. Umbilical slope high and strongly inclined. Umbilical border rounded, with convex flanks, converging strongly to a widely rounded periphery. The maximum width occurs in the middle part of the flanks. Ornamentation consists of two rows of spines, of which the stronger and more prominent are those situated in the middle of the flanks at the maximum width of the whorls. The other row, located at the umbilical border, is characterized by smaller spines which are only half as numerous as those situated in the middle of the flanks. The remainder of the ornamentation consists of striae which are rursiradiate on the umbilical slope and prorsiradiate over the rest of the shell. On the umbilical slope these striae form some folds which tend to disappear in the flank. The suture line could not be detected.

Measurements. —

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8931/15	82	25	0.30	40	50	0.80

Remarks. — The described specimen closely resembles *Aspidoceras euomphalum* Steuer (1897, p. 69, pl. 5, figs. 1—4), particularly with regard to the internal whorls. It differs from *A. andinum* Steuer (1897, p. 70, pl. 5, figs. 5—7) in being more involute and in having a deeper umbilicus, more fine and large spines, and more numerous spines in the interior row. *A. euomphaloides* Burckhardt (1906, p. 37, pl. 6, figs. 5—8) is very similar to the described specimen and, as was suggested by Krantz (1926, p. 432), could be cospecific with it. On the other hand, *A. quemadense* Burckhardt (1906, p. 31, pl. 6, figs. 1—4) undoubtedly belongs to the species *andinum* of Steuer, as was expressed by Verma & Westermann (1973, p. 192). On the basis of illustrations, *A. neuquensis* Weaver (1931, p. 435, pl. 52, figs. 341, 342) could also belong to *A. euomphalum*, but Weaver (op. cit.) has noted in his description that it has more elevated whorls and a more elaborate suture line. *A. longaevum* Leanza (1945, p. 26, pl. 2, figs. 1,15), although having a shell of somewhat similar shape, has stronger and less dense spines.

Finally, it should be noted that *A. euomphalum* Steuer (pl. 5, fig. 1) was incorrectly figured in the Treatise of Invertebrate Paleontology (cf. Arkell *et al.*, 1957, p. L346, fig. 454, 3a—b) as "*Spiticeras (Kilianiceras) damesi*" (Steuer, 1897).

Occurrence. — Vaca Muerta Formation. Bed 10 of the Cerro Lotena section, in association with *P.* aff. *recticosta.*

Age. — Upper Middle Tithonian. *W. internispinosum* Zone

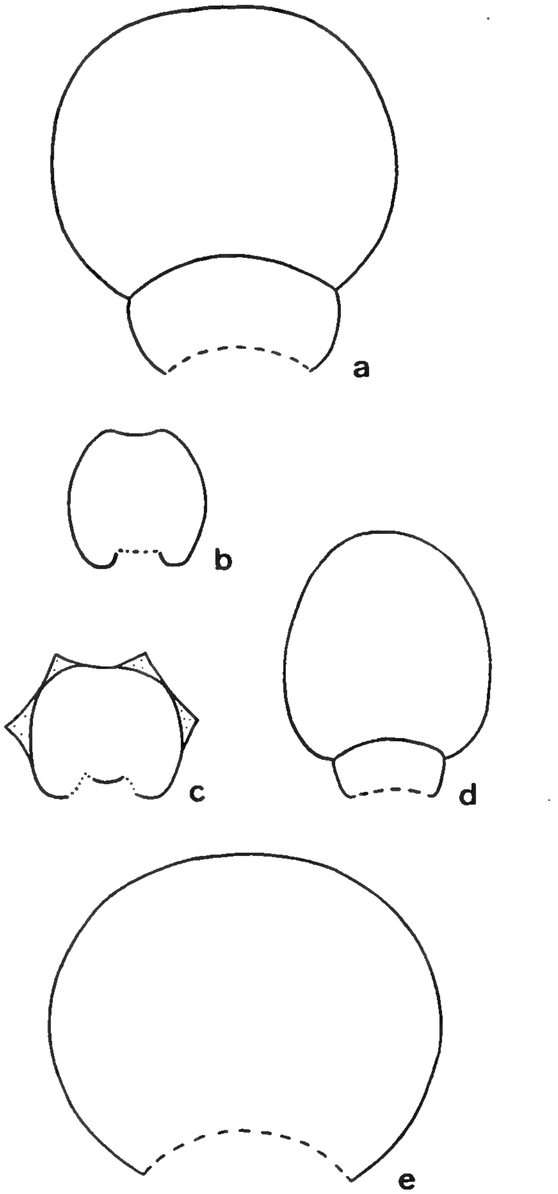

Fig. 10: Whorl sections of Berriasellidae and Aspidoceratidae. **a:** *Hemispiticeras* aff. *H. steinmanni,* S.G.N. 8950/1; **b:** *Aulacosphinctes proximus,* S.G.N. 8944/1; **c:** *Corongoceras lotenoense,* S.G.N. 8940/1; **d:** *Windhauseniceras internispinosum,* S.G.N. 8941/1; **e:** *Aspidoceras euomphalum,* S.G.N. 8931/15. Natural size.

Family BERRIASELLIDAE SPATH, 1922
Subfamily HIMALAYITINAE SPATH, 1923
Genus WINDHAUSENICERAS A. F. LEANZA, 1945

Type species. — *Perisphinctes internispinosus* KRANTZ, 1926, p. 453, pl. 14, figs. 1, 2; pl. 15, figs. 5, 6 (= 1928, transl., p. 39, pl. 2, figs. 3a, b and 4a, b).

Windhauseniceras internispinosum (KRANTZ, 1926)

Pl. 8, Figs. 4a—b; Pl. 9, Figs. 1a—b; Text-Fig. 10d.

Material. — This species is, next to *P. zitteli*, the most abundant in Cerro Lotena. The studied collection contains twenty specimens, which are in general well preserved. S.G.N. 8931/1—8: eight moderately well preserved phragmocones. S.G.N. 8933/1: well preserved phragmocone with remains of body chamber. S.G.N. 8934/1—2: very well preserved phragmocone, with remains of body chamber, somewhat distorted. S.G.N. 8935/4: whorl fragments. S.G.N. 8940/3: complete specimen, with internal whorls rather distorted. S.G.N. 8940/4: very well preserved phragmocone (Pl. 8, figs. 4a—b). S.G.N. 8941/1: phragmocone and body chamber, very well preserved (Pl. 9, figs. 1a—b). S.G.N. 8942:1: very distorted specimen. S.G.N. 8948/1: somewhat distorted phragmocone. S.G.N. 8949/1: somewhat crushed but well preserved specimen. S.G.N. 8951/1—2: poorly preserved specimens.

Description. — Shell discoidal, with greater or lesser evolution depending upon whether it represents adult or young stages of growth. U/D ratio ranges between 0.41 and 0.52. Young whorls are wider than high, with very wide and rounded periphery. Flanks strongly convex, gradually converging to a gently inclined umbilical slope. Ornamentation consists of strong, radial and prominent ribs. At the lateroventral border they show a narrow and elevated spine, enlarged radially. From this spine commence two or sometimes three ribs of less prominence than the primary rib; these cross the periphery without interruption. The line of spines can be clearly observed immediately below the line of coiling (see pl. 8, figs. 4a—b).

Outer whorls are higher than wide, with suboval whorl section. The periphery tends to become more acute, and the umbilical slope more strongly inclined. Ornamentation is characterized by rectiradiate or somewhat prorsiradiate, simple or biplicate ribs. The bifurcation takes place in the middle part of the flanks; spines or tubercules are absent. The resulting secondary ribs retain the same prominence as the primaries, crossing the periphery transversally without interruption. Simple ribs extending from the periphery to different levels on the flanks are also present. The aperture is simple, describing only a somewhat sigmoidal curve.

The calcitized nature of the specimens prevented detection of the suture line.

Measurements. — (better preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8930/1	93	47	0.50	29	27	1.07
S.G.N.	8931/1	71	37	0.52	22	23	0.95
S.G.N.	8933/1	97	51	0.52	29	28	1.03
S.G.N.	8934/2	108	47	0.43	36	35	1.02
S.G.N.	8940/3	70	32	0.45	24	25	0.96
S.G.N.	8941/1	93	42	0.45	30	?	—
S.G.N.	8948/1	152	74	0.48	54	52	1.03
S.G.N.	8949/1	140	58	0.41	58	56	1.03

Remarks. — The described material is identical to the genus *Windhauseniceras* LEANZA (1945), and coincides specifically with its type species, that is, *Perisphinctes internispinosus* KRANTZ (1926, p. 453, pl. 14, figs. 1, 2; pl. 15, figs. 5, 6 = 1928, transl. p. 39, pl. 2, figs. 3a, b and 4a, b). The type species was also found in the Cerro Lotena area (cf. KRANTZ, 1926, p. 454).

W. internispinosum is very variable depending on its ontogenetic stage, particularly with regard to the ornamentation of the body chamber. It is, in fact, very difficult to find identical specimens. On the other hand, the diagnostic features of the genus always remain the same. Therefore, it was not considered advisory to propose new varieties for the described material. It should be noted, however, that virgatotomic branching has not been observed, as it has in *W. humphreyi* LEANZA (1949, p. 240, pl. 1, figs. 1, 1a, 2, 2a) from the Tithonian of Arroyo Los Molles, Neuquén, Argentina.

Occurrence. — Vaca Muerta Formation. Beds 9, 14, 16 and 22 of the Cerro Lotena section.

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Genus HEMISPITICERAS SPATH, 1925

Type species. — *Reineckeia steinmanni* STEUER, 1897, p. 28, pl. 8, figs. 1—4.

Hemispiticeras aff. *H. steinmanni* (STEUER, 1897)

Pl. 9, Figs. 2a—b; Text-Fig. 10a.

? 1897 *Reineckeia steinmanni* STEUER, p. 28, pl. 8, figs. 1-4.
? 1921 *Reineckeia steinmanni* STEUER, pl. 8, figs. 1-4.
? 1925 *Hemispiticeras steinmanni* (STEUER) — SPATH, p. 144 (Gen. nov.).

Material. — One specimen. S.G.N. 8950/1: well preserved phragmocone.

Description. — Discoidal shell, strongly evolute. U/D ratio = 0.49. Inner whorls coronate, similar to those of *Windhauseniceras* or *Stephanoce-*

ras. Outer whorl section is, by contrast, slightly higher than wide. Umbilical slope gently inclined, umbilical border rounded, but in the inner whorls slightly flattened. Ornamentation characterized by strong, elevated and acute ribs that divide at the line of coiling into two or three branches which are less prominent and wider than the primaries. At the point of furcation are radially elongate tubercules, sometimes poorly preserved. This type of ribbing remains the same in the inner and outer whorls, in contrast to the genus *Windhauseniceras*. In the last whorl there are 35 primary ribs and 76 secondaries, which cross the venter without interruption, and display a somewhat adapertural convexity. Calcitization prevented detection of the suture line.

Measurements. — (in mm)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8950/1	140	69	0.49	37	46	0.80

Remarks. — The general shape of the shell of this specimen closely resembles that of the genus *Hemispiticeras* Spath, 1925 (type species: *Reineckeia steinmanni* Steuer, 1897, p. 28, pl. 8, figs. 1—4), differing only in having smaller and rounded tubercules at the point of the rib furcation. Therefore, the specimen is considered here as *H.* aff. *H. steinmanni* (Steuer).

Although the inner whorls ornamentation is almost identical to that of *Windhauseniceras* Leanza, 1945 (type species: *P. internispinosus* Krantz, 1926, p. 453, pl. 14, figs. 1, 2; pl. 15, figs. 5, 6 = 1928, transl., p. 39, pl. 2, figs. 3a, b and 4a, b). However, in the described material this ornamentation continues in the outer whorls, while in the Leanza's genus the ribbing loses tubercules, closes together and reverts to a typical *Perisphinctes* style.

Another genus which shows affinities with the described specimen is *Paskentites* Imlay & Jones, 1970 (type species: *P. paskentaensis* Imlay & Jones, 1970, p. B47, pl. 13, figs. 11—17), from the Middle Valanginian of the *Buchia pacifica* Zone, in northwestern California and southern Gregon, U.S.A. This genus "... is represented by eight specimens of which most are fragmentary and crushed laterally" (Imlay & Jones, op. cit., p. B47). Judging from the illustrations, the apparent projection of the ribs — which forms chevrons over the venter — is essentially the only difference from the species described here.

Occurrence. — Vaca Muerta Formation. Bed 20 of the Cerro Lotena section.

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

Genus AULACOSPHINCTES Uhlig, 1910

Type species. — *Ammonites mörickeanus* Oppel, 1863, p. 281, pl. 80, figs. 2a, b. SD Spath, 1924, p. 16.

Aulacosphinctes proximus (Steuer, 1897)

Pl. 6, Figs. 2a—b, 4a—b and 5a—b; Text-Fig. 10b.

1897 *Reineckeia proxima* Steuer, p. 34, pl. 8, figs. 7-11. (= 1921, transl., pl. 8, figs. 7-11).
1907 *Perisphinctes proximus* (Steuer) — Haupt, p. 192.
? 1931 *Aulacosphinctes proximus* (Steuer) — Weaver, p. 411, pl. 44, figs. 298 and 299.

Material. — Ten specimens which are particularly suitable for the study of this genus, are present in the collection. S.G.N. 8922/1: very well preserved phragmocone of young specimen (pl. 6, figs. 4a—b). S.G.N. 8922/2: phragmocone with remains of body chamber. S.G.N. 8944/1: very well preserved phragmocone with remains of body chamber (pl. 6, figs. 2a—b). S.G.N. 8937/1—6: six small specimens, mostly fragmentary and not very well preserved. G.P.I.T. 1545/3: internal mold of phragmocone and body chamber, very well preserved (pl. 6, figs. 5a—b).

Description. — Shell of moderate size, planulate, and strongly evolute. U/D ratio ranges between 0.46 and 0.50. Umbilicus very wide and shallow. Internal whorl section subtrapezoidal, higher than wide. Outer whorl sections somewhat depressed and of subcircular shape (text-fig. 10b). Umbilical slope gently inclined, umbilical border rounded, flanks gently convex and the periphery somewhat flattened. Ornamentation characterized by simple, sharp, acute and fine ribs. They commence in the umbilical seam, cross the umbilical slope in a somewhat rursiradiate manner, bend forward at the umbilical border, and cross the flanks in a recti- or prorsiradiate fashion. Just above the middle of the flanks, most of the ribs bifurcate into two branches of the same shape as the primaries. The more anteriorly situated are prorsiradiate, while those located posteriorly are somewhat rursiradiate. All the ribs are interrupted over the venter, where a shallow groove is developed, which is more pronounced in the inner whorls. Interruption of the ribbing also occurs in the body chamber, although not as clearly (see Pl. 6, Fig. 5b). The number of ribs increases with age. For example, for a diameter of 40 mm there are about 30 primaries, while for one of 60 mm there are about 40. The suture line, observed in the septa limiting with the body chamber, is very simple, displaying an E lobe slightly larger than L, but of the same width. The L/U saddle is two thirds the size of the L lobe.

Measurements. — (better preserved specimens only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8922/2	61	31	0.50	17	18	0.94
S.G.N.	8944/1	60	30	0.50	17	18	0.94
S.G.N.	8922/1	43	21	0.48	13	13	1.00
S.G.N.	8937/1	36	17	0.47	12	12	1.00
S.G.N.	8937/6	30	14	0.46	11	10	1.10
G.P.I.T.	1545/3	58	29	0.50	18	19	0.94

Remarks. — The morphological features of the described specimens closely resemble those of the genus *Aulacosphinctes* UHLIG, 1910 (type species: *Ammonites mörickeanus* OPPEL, 1863, p. 281, pl. 80, figs. 2a, b). Although UHLIG stated with regard to the ventral groove that ... "As is well known, its development is restricted to the chambered nucleus, and does not extend to the body chamber" (UHLIG, 1910, p. 345), in the Cerro Lotena species the ventral groove is apparently also present in the body chamber.

Specifically, the material closely agrees with "*Reineckeia*" *proxima* STEUER (1897, p. 34, pl. 8, figs. 7 to 11) which was transferred in 1910 to the genus *Aulacosphinctes* by UHLIG himself (op. cit., p. 347). Although at first view the material also resembles *Aulacosphinctes colubrinoides* (BURCKHARDT, 1903, p. 57, pl. 10, figs. 9—11), this similarity appears superficial because in this latter species, as indicated by BURCKHARDT's description (op. cit., p. 57), the ribs cross the venter without interruption, a feature which is considered diagnostic to the identification of this genus. It is worth noting that *A. colubrinoides* was transferred by SPATH (1925, p. 145) to the genus "*Crendonites*" BUCKMAN (1923) (= *Glaucolithites* BUCK., 1922), although the same author later stated that it ... "probably does not belong to this genus, contrary to my previous view" (SPATH, 1936, p. 31). With regard to *A. mörickeanus* (OPPEL), the described species differs in having somewhat rounded flanks, wider whorls, more rapid range of growth, and absence of ribs with tricotomic branching (cf. UHLIG, 1910, p. 351). Another species rather similar to *A. proximus* is *A. parvulus* UHLIG (1910, p. 364, pl. 32, figs. 4a—d) from the Spiti Shales; however, this latter species has a deeper ventral groove and simpler ribbing. With regard to the Madagascan forms, the material described here resembles *A. proximus* (STEUER) var. *angusta* COLLIGNON (1960, pl. 172, fig. 731). The *A. proximus* figured by WEAVER (1931, p. 411, pl. 44, figs. 298, 299) does not display the interruption of the ribs over the venter and therefore its attribution to *Aulacosphinctes* is doubtful. Finally, it can noted that *A. occultefurcatus* (WAAGEN, 1875, p. 195, pl. 1, figs. 4a, b) from Cutch, India, and *A. wanneri* KRANTZ (1928, p. 42, pl. 2, figs. 6a—b) from Arroyo de la Manga, Mendoza, Argentina, are also closely related species.

Occurrence. — Vaca Muerta Formation. Bed 7 of the Cerro Lotena section, in association with *Subdichotomoceras* sp. juv indet. and *Laevaptychus crassissimus*.

Age. — Middle part of the Middle Tithonian. A. proximus Zone.

Genus CORONGOCERAS SPATH, 1925

Type species. — *Corongoceras lotenoense* SPATH, 1925, p. 144 (= "*Hoplites köllickeri*" HAUPT, 1907 (*non* OPPEL), p. 201, pl. 9, figs. 7a—e).

Corongoceras lotenoense SPATH, 1925
Pl. 6, Figs. 6a—b; Text-Fig. 10c.

1907 *Hoplites köllickeri* HAUPT (*non* OPPEL), p. 201, pl. 9, figs. 7a-e.
1925 *Corongoceras lotenoense* SPATH, p. 144 (Gen. nov., type species).
1926 *Berriasella (Corongoceras) lotenoensis* SPATH — KRANTZ, p. 444 (= 1928, transl., p. 28).
1931 *Berriasella* cf. *koellickeri* (OPPEL) STEUER — WEAVER, p. 444.
? 1969 *Corongoceras* cf. *lotenoense* SPATH — HELMSTAEDT, p. 78.

Material. — Two specimens. S.G.N. 8932/1: whorl fragment with remains of body chamber, very well preserved. S.G.N. 8940/1: phragmocone and body chamber, moderately preserved (pl. 6, figs. 6a—b).

Description. — Discoidal shell of medium size, strongly evolute. U/D ratio = 0.50. Umbilical slope gently inclined, with slightly convex flanks and somewhat flat venter (as in *Berriasella*). Whorl section as high as wide (text-fig. 10c). Ornamentation strong, formed by very acute ribs. All ribs bifurcate on the middle of the flanks. At the point of branching an acute tubercule, rather radially elongate, is developed. At the lateroventral border, all secondary ribs show a new row of tubercules elongated transversely to the shell venter; they tend to disappear in the siphuncle. In the last whorl are 24 primary ribs and 40 secondaries. The suture line was not detected.

Measurements. — (better preserved specimen only)

Specimen	n°	D	U	U/D	H	W	H/W
S.G.N.	8940/1	54	27	0.50	18	18	1.00

Remarks. — The whorl section, evolution, number of ribs and general shape of the ornamentation are identical to *Hoplites köllickeri* HAUPT (*non* OPPEL) (1907, p. 201. pl. 9, figs. 7a—e), also from Cerro Lotena. This species was proposed by SPATH (1925, p. 144) as the type species of *Corongoceras lo-*

tenoense. Therefore, the described material is attributed to this species. *"Reineckeia koellickeri"* Steuer (*non* Oppel, *non* Haupt) (1897, p. 31, pl. 8, figs. 5, 6), which was found by Bodenbender (1892) in Loncoche creek, Mendoza, Argentina, undoubtedly belongs to the genus *Corongoceras,* but differs from the type species in having a more disordered ribbing as well as a larger umbilical diameter. Weaver (1931, p. 444), stated that *Berriasella* cf. *koellickeri* (Oppel) Steuer " . . . occurs in the lower part of the Upper Tithonian strata at Cerro Loteno . . . ", that is, in a similar stratigraphic position to the described material. Weaver did not illustrate this species, but in view of his description and the fact that it appears in the same stratigraphic position, it can be included in *Corongoceras lotenoense.* The specimens referred to by Krantz as *Berriasella (Corongoceras) lotenoensis* (Krantz, 1926, p. 444 = 1928, p. 28) are also from Cerro Lotena.

Recently, another record of *Corongoceras,* which probably belongs to the *lotenoense* species of Spath, was cited from Nepal (Helmstaedt, 1969, p. 78).

Corongoceras loetonense (sic) var. *fortior* Collignon (1960, pl. 167, fig. 687), judging by the illustrations, does not appear to belong to the species of Spath, as it displays greater involution and less divergent secondary ribs. The species referred to as *C. cordobai* by Verma & Westermann (1973, p. 248, pl. 52, figs. 4, 5; pl. 54, fig. 1, text-fig. 28 B) should not be assigned to *Corongoceras* because of the lack of bifurcation of the ribs, a feature which is considered diagnostic to the identification of this genus.

Occurence. — Vaca Muerta Formation. Bed 16 of the Cerro Lotena section, in association with *S. windhauseni, W. internispinosum* and *P.* aff. *P. pseudocolubrinoides.*

Age. — Uppermost Middle Tithonian. *W. internispinosum* Zone.

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Rhaeto-Liassic Mammals from Switzerland and West Germany

BY

WILLIAM A. CLEMENS*)

With 5 text figures and plates 10—12

ABSTRACT

European mammals and advanced mammal-like reptiles of Rhaeto-Liassic (Late Triassic-Early Jurassic) age are now known from localities in Switzerland, West Germany (BRD), France, and Great Britain. The Rhaetic bonebeds at Hallau, Switzerland, and in Baden-Württemberg, southwestern West Germany, contain samples of the animals that lived on the deltas and other coastal regions along the northwestern flank of the Vindelizian High, a continental area covering parts of northern Switzerland and southern West Germany. During the Rhaetian and early Liassic large parts of northwestern Europe were inundated by marine transgressions from the west and south creating an ephemeral archipelago that was largely submerged later in the Jurassic. Differences in known representation of mammals in Rhaeto-Liassic local faunas of northwestern Europe probably reflect: 1) small sample sizes of some local faunas, 2) differences in age within the Rhaeto-Liassic interval, and 3) the evolutionary diversification of insular faunas.

Rhaetic bonebed local faunas of Hallau and Baden-Württemberg are known to include haramiyids, vertebrates of uncertain but probably mammalian affinities. *Morganucodon* (Mammalia, Triconodonta) is represented at Hallau by a new species. Two other new mammalian species in the Hallau local fauna are referable to new genera. One is provisionally allocated to the Morganucodontidae; the other is not referable to any previously known family or order. *Tricuspes* (?Mammalia) is recorded from Rhaetic bonebeds at Hallau and in Baden-Württemberg. Tritylodontids (Reptilia, Synapsida), present in several Rhaetic bonebed local faunas of Baden-Württemberg, are not part of the Hallau local fauna.

The taxonomic diversity of mammals now known from a very few samples of Rhaetian and Liassic age strongly suggests the time of origin of the Mammalia was significantly earlier in the Triassic.

KURZFASSUNG

Europäische Säugetiere und fortschrittliche säugetierähnliche Reptilien des Räto-Lias (Obertrias — Unterjura) sind jetzt von Lokalitäten in der Schweiz, Westdeutschland (BRD), Frankreich und Großbritannien bekannt. Die Rät-Bonebeds von Hallau (Schweiz) und Baden-Württemberg (Südwest-Deutschland) enthalten Reste von Wirbeltieren, die in Delta- oder anderen Küstengebieten entlang der Nordwest-Flanke des Vindelizischen Landes, eines kontinentalen Gebietes im Bereich der heutigen Nordschweiz und des südlichen Westdeutschland lebten. Während des Rät und tieferen Lias waren weite Teile von Nordwesteuropa durch marine Transgressionen von Westen und Süden überflutet. Sie schufen einen vorübergehenden Archipel, der im höheren Jura weitgehend wieder versank. Unterschiede innerhalb der bisher bekannten Vorkommen von Säugetieren in den rätoliassischen Lokalfaunen von Nordwest-Europa spiegeln wahrscheinlich wider: 1. kleine Probengröße einiger Lokalfaunen, 2. Altersunterschiede innerhalb der Zeitspanne des Rätolias und 3. eine stammesgeschichtliche Differenzierung in Inselfaunen.

Lokalfaunen aus den Rät-Bonebeds von Hallau und Baden-Württemberg enthielten nach bisheriger Kenntnis Haramiyiden und Wirbeltiere von unsicherer, aber wahrscheinlicher Säugetierzugehörigkeit. *Morganucodon* (Mammalia, Triconodonta) ist in Hallau durch eine neue Art vertreten. Zwei weitere neue Säugetierarten werden auf neue Gattungen bezogen. Eine wird

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*) Prof. Dr. W. A. CLEMENS, Dept. of Paleontology and Museum of Paleontology, University of California Berkeley, Berkeley, Calif. 94720, U.S.A.

vorläufig zu den Morganucondontidae gestellt; die andere ist mit keiner anderen bisher bekannten Familie oder Ordnung vergleichbar. *Tricuspes* (?Mammalia) wird aus den Rät-Bonebeds von Hallau und Baden-Württemberg nachgewiesen. Tritylodontiden (Reptilia, Synapsida), die in einigen Lokalfaunen der Rät-Bonebeds Baden-Württembergs vorkommen, fehlen in Hallau. Die taxonomische Vielfalt von Säugetieren, die bis jetzt von sehr wenigen Proben des Rät und Lias bekannt sind, spricht sehr dafür, daß die Entstehungszeit der Säugetiere auf jeden Fall in einen deutlich früheren Abschnitt der Trias fällt.

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INTRODUCTION

Mesozoic mammals were for the most part minute creatures in comparison to the dinosaurs and their other reptilian contemporaries. Even under the best of conditions their tiny bones and teeth are rarely seen as they weather out of the entombing sediments. About the middle of the 19th Century two vertebrate paleontologists, Prof. T. Plieninger of Stuttgart and Charles Moore of Bath, undertook research on natural concentrations of fragmentary small bones thought to be of Late Triassic age. Each of them washed the fossiliferous sediments in screens to remove as much of the associated sand and mud as possible. This separated the fossils and produced an even richer concentrate for sorting. Thus the screen washing technique of collecting fossil vertebrates got its start.

With rare exceptions, in the following years of the 19th and early 20th centuries collectors focused their attention on the mighty and gigantic vertebrates of the past. Remains of smaller, mouse-sized animals were found, but frequently these were almost accidental by-products of the search for larger animals. Almost a century later Profs. W. KÜHNE, C. W. HIBBARD, and a few others championed the inclusion of screen washing in the basic repertoire of collecting techniques. Modern modifications of these techniques and improvement of equipment now permit recovery of minute fossils even when they occur in very low densities in the sediments.

After Plieninger's work many years elapsed before additional specimens of mammals and advanced mammal-like reptiles were recovered from the Rhaetic bonebeds of Baden-Württemberg. The next collecting programs were those carried out by E. VON HUENE and, later, Prof. O. H. SCHINDEWOLF. The entire collection of mammalian fossils from Hallau was obtained by Prof. B. PEYER who devoted many years to the processing of screen washing concentrates obtained from rock collected in 1942.

In 1956 Prof. PEYER published a monograph on mammals and reptiles from the Rhaetic bonebed at Hallau. This was an interim report based on the collection available in 1951. Sorting of the screen washing concentrates from Hallau was continued and, ultimately, almost doubled the size of the sample.

My involvement in research on the mammals from Hallau began in 1961. A postdoctoral fellowship from the National Science Foundation made it possible for me to visit Zürich where Prof. PEYER introduced me to his work. Unfortunately Prof. PEYER died in 1963 before he could complete his projected study. In 1974-75, thanks to a fellowship from the JOHN SIMON GUGGENHEIM MEMORIAL FOUNDATION, I was able to return to Europe. Prof. E. KUHN-SCHNYDER graciously made the collections from Hallau available for my study. Also it was possible to review the pertinent collections of Rhaetic mammals and advanced mammal-like reptiles from sites in adjacent parts of Baden-Württemberg. These, like the collections from Hallau, had yet to be analyzed in light of the flood of new data coming from research on the Rhaeto-Liassic local faunas of southern Wales. An award from the ALEXANDER-VON-HUMBOLDT-STIFTUNG, the hospitality of the Institut für Paläontologie und historische Geologie, Universität München, and a leave of absence from the University of California Berkeley made it possible for me to return to Europe in 1978-79 and provided the freedom and support necessary to finish my research.

Designation of specimens

The fossils considered here are elements of several different collections and, over the years of the past century, some have been left without specific museum catalogue designations; others have been given several different catalogue numbers. The following are utilized in this paper:

Fossils in the Charles Moore collection, Bath Geology Museum, Bath, England, are identified by a three digit number with the letter C or M as a prefix.

Elements of the collections of the Institut und Museum für Geologie und Paläontologie, Universität Tübingen, have the prefix G. I. T.

In his monograph PEYER (1956) identified fossils from Hallau in the collections of the Paläontologisches Institut und Museum der Universität Zürich with Roman numerals. The same numerical designations, although written in arabic numerals, were used to identify the figures in the plates of his monograph. Fossils collected after the completion of the monograph were numbered separately and sequentially with arabic numerals. These designations are recorded here as NC (= new collection) 1, 2, etc. Subsequently the entire collection was recurated and the fossils given sequential numbers, in arabic numerals, with the prefix AIII.

In the descriptions of the fossils from Hallau these catalogue data are summarized at least in the lists of referred material. In parentheses after the current catalogue number the reader will find either PEYER's designation of the specimen in Roman numerals followed by a reference to the Tafel in his monograph (PEYER, 1956) on which it is illustrated, or its NC number in the new, hitherto unpublished collection.

Abbreviations

The following abbreviations have been used:
CV = coefficient of variation
M = mean
N = number
OR = observed range of variation
S = standard deviation

Acknowledgements

My involvement in studies of European Mesozoic mammals began in the academic year 1960-61 when, supported by a National Science Foundation postdoctoral fellowship, I was able to work with Dr. Kenneth KERMACK at University College London. In following years I have been fortunate in being able to return to Europe and continue my research and education. Many colleagues and institutions have contributed to this and to all those named here and many others I am deeply grateful.

This paper is focused on the collections of mammalian fossils from northern Switzerland and Baden-Württemberg. For permission to study the collection from Hallau, information and advice, and provision of excellent research facilities during my visits, I wish to thank Prof. Drs. B. PEYER, E. KUHN-SCHNYDER, and H. RIEBER, and Dr. K. A. HÜNERMANN of the Paläontologisches Institut und Museum der Universität Zürich. Dr. R. SCHLATTER, Museum zur Allerheiligen, provided considerable information concerning the geological setting of the Hallau bonebed.

At the Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Drs. F. WESTPHAL and W.-E. REIF assisted me in my review of the collections. Dr. C. HEMLEBEN arranged for preparation of scanning electron microscope pictures of several fossils. Dr. R. WILD, Staatliches Museum für Naturkunde, Stuttgart, helped me in both recapitulating the history of the type of *Thomasia antiqua* and exploring the possibility that some of the minute teeth found in Rhaetic bonebeds might be from the dentitions of pterosaurs. Also, my sincere thanks go to Dr. DENISE SIGOGNEAU-RUSSELL, Institut de Paléontologie, Paris for discussions and the opportunity to review her recent discoveries at Saint-Nicolas-du-Port.

Many British colleagues have helped me, in particular I would acknowledge Drs. K. A. and D. M. KERMACK, Frances MUSSETT, and Patricia M. LEES not only for the opportunity to study material in the collections of University College London, but also for the many days spent with them at fossil localities in southern Wales and southwestern Britain. Drs. R. PARRINGTON and K. JOYSEY gave me access to collections in the Zoology Museum, Cambridge University. Prof. P. M. BUTLER, Royal Holloway College — my host during a year spent in England on a JOHN SIMON GUGGENHEIM FELLOWSHIP — and Dr. R. J. G. SAVAGE, University of Bristol, gave me access to collections and provided stimulating discussions. Mr. R. F. PICKFORD, Bath Geological Museum, helped in my review of the Charles Moore collection.

The shaded drawings in the plates are the work of Mr. A. J. LEE. Their preparation was made possible by a grant from the ANNIE M. ALEXANDER ENDOWMENT, Museum of Paleontology, University of California Berkeley.

It is a great pleasure to acknowledge my hosts who made it possible for me to work at the Institut für Paläontologie und historische Geologie, Universität München during the 1978-79 acadmic year. Prof. Drs. Volker FAHLBUSCH and Richard DEHM invited me to work at the institute. I am deeply greatful to them and to Prof. Dr. Dietrich HERM and Dr. Peter WELLNHOFER not only for professional assistance that greatly advanced my studies, but also the warm hospitality they extended to me and my family making it a memorable stay. Finally, I wish to express my sincere thanks and deep appreciation to the Alexander von Humboldt-Stiftung for both providing me with a "Senior U. S. Scientist Award" and their continuing interest that added highlights to our year in Germany.

GEOLOGY AND PALEOGEOGRAPHY

In a recent review of the Mesozoic records of mammalian evolution (CLEMENS et al., 1979) several fossil localities in northwestern and central Europe that have yielded the remains of primitive mammals and advanced mammal-like reptiles were grouped under the heading of sites of Late Triassic or Early Jurassic age. These included the Rhaetic bonebeds at Hallau, Switzerland, and in the Tübingen-Stuttgart area of West Germany (BRD), a locality in the vicinity of Nancy, France, and fossiliferous fissure fillings in western England and Wales. Goals of the research project reported here included reevaluation of the data available in the literature concerning the German and Swiss localities in order: 1) to arrive at a more precise determination of their relative ages and their temporal relationships to the French and British sites; 2) to summarize what is known of their taphonomy; and 3) to place these local faunas in the context of the major and rapid changes that occurred in the paleogeography of Europe during the Late Triassic and Early Jurassic. In following sections of this chapter these data on the Swiss and German sites are summarized and followed by a brief resumé of information concerning the French and British localities. For various reasons it was not possible to reopen and restudy the geological settings of the localities in Switzerland and Germany.

The results of this review were far from satisfactory. Clearly the period of earth history under consideration is of short duration. The fossiliferous deposits of interest are within the so-called Germanic geological province (e. g., see BRINKMAN, 1960) that during the Late Triassic was a largely continental area and primarily a site of erosion or deposition of terrestrial or shallow-water marine sediments. Contemporaneously, to the south in Tethys, considerable thicknesses of marine sediments accumulated. The Rhaetian was typified in this Tethyian (or Alpine) province.

Development of understanding of the evolution of the Germanic province and its faunas has been impeded by several obstacles. Possibly the most basic is the proclivity of many workers to avoid distinguishing between lithologic, biostratigraphic, chronostratigraphic, and chronologic units (see AGER, 1970). Thus Mittlerer Keuper, or Middle Keuper, for example, can be a designation for a very specific sequence of deposits in the Keuper basin of southwestern Germany (BRD), a chronostratigraphic designation for rocks deposited during the middle of the Late Triassic, a designation for middle Late Triassic time, or some mixture of these concepts (note PEARSON, 1970). Currently many workers utilize a sequence of stages/ages based upon studies of the Tethyian Triassic sequence as a standard scale of reference (note papers in ZAPFE, 1974a, for example). However there are uncertainties and disagreements concerning the definition of Rhaetian and Norian in the Tethyian province and utilization of these units in the Germanic province (note PEARSON, 1970, TOZER, 1974, ZAPFE, 1974a, and references cited). Palynological studies (note SCHUURMAN, 1979) and research on ostracods (note WILL, 1969) offer promise of surmounting correlation problems, but their resolution remains a goal for future research. Without precise correlations it is impossible to closely interrelate the evolution of the terrestrial fauna with the physical changes in the Germanic province, which was largely submerged during the Rhaeto-Liassic transgression. What has emerged from this work is a cloudy, hypothetical picture of their coevolution.

For the purposes of this paper the following concepts and units will be utilized with limited meanings. These choices reflect a geographic bias. The Swiss and German bonebed sites, which are the focus of this report, were formed as the Keuper basin of southwestern Germany and northern Switzerland was being filled and then flooded during the close of the Triassic and beginning of the Jurassic. Definitions of these concepts and units currently utilized by some workers in this part of central Europe are favored with the recognition that they can have significantly different meanings in other areas and for other workers.

Hettangian: The base of the Hettangian (frequently equated with the beginnings of the Liassic and Jurassic) will be taken as the beginning of the *Psiloceras planorbis* Zone. In this and in choice of subsequent, younger units of the Liassic the scale presented by ULRICHS (1977) for use in southwestern Germany is followed. This definition of the base of the Hettangian (or Lias) differs from that used by other workers in northwestern Germany (e. g., WILL, 1969) and suggested for international adoption (e. g., PEARSON, 1970) in which a Pre-*planorbis* Zone or Beds is recognized as the basal unit of the Hettangian.

Rhaetian: The complex history of the concept of the Rhaetian has been reviewed by PEARSON (1970, also see TOZER, 1974, WIEDMANN, 1974, ZAPFE, 1974b, and SCHUURMAN, 1979). Currently there is an unresolved debate over whether the Rhaetian is properly recognized as an age between the older Norian and the Hettangian or is simply coeval with part of the Norian.

Correlations have been attempted between the type region of the Rhaetian in the Tethyian province and sections containing shallow water to brackish marine deposits formed in a different faunal realm in northwestern Germany (see WILL, 1969, and SCHUURMAN, 1979). In Baden-Württemberg Rhaetic, Rät, or Upper Keuper, appear to have been used most frequently to designate the sediments, contained faunas, and/or an interval of time between the termination of deposition of the Middle Keuper and the lowest stratigraphic occurrence of beds containing a Liassic marine fauna. GEYER and GWINNER (1968) present a generalized Rät section for Baden-Württemberg dividing it into an Oberrät or *Triletes*-Schichten and an Unterrät or *contorta*-Schichten. On lithologic grounds the bonebeds of the Tübingen-Stuttgart area might be included in the Unterrät (AEPLER, 1974). How the times of formation of the Rhaetic bonebeds in the Tübingen region relate to the times of deposition of the Hallau bonebed, the Lower Rhaetic of the Nancy region, and the Rhaetian sections of northern Germany, Britain, and the Tethyian province remain open questions.

Rhaetic: This term is used here in the limited sense of a lithostratigraphic name. As will be argued below, the time of formation of some Rhaetic bonebeds might not be Rhaetian.

Middle Keuper: The uppermost lithostratigraphic unit of this sequence in Baden-Württemberg is the Knollenmergel. BRENNER (1973) argued that it can be considered as an essentially isochronous unit of Norian age. How the time(s) of termination of deposition of the Knollenmergel relate to the Rhaetian-Norian boundary (or the Hettangian-Norian boundary for those who reject the Rhaetian Age) is not yet determined.

Rhaetic local faunas of the Tübingen-Stuttgart area

Although varying in thickness and sporatic in occurrence Rhaetic bonebeds are common elements of the Rhaetic Sandstone (Rhätsandstein) in the vicinity of Tübingen and Stuttgart and as far southwest as the region of Täbingen and Balingen (Fig. 1). Within this area the Rhaetic Sandstone is not a continuous unit but consists of a group of usually thin, lenticular bodies of sandstone separated by areas of Rhaetic Clay (Rhätton) or regions where Rhaetic deposits are lacking. Formation of the Rhaetic Sandstone has been attributed to the development of prograding deltas modified by longshore currents (Aepler, 1974).

In 1847, after a painstaking search of minute fossils concentrated by washing bonebed samples from exposures south of Stuttgart at Degerloch and Steinenbronn, Plieninger announced his discovery of two mammal-like teeth. One is now the type of the haramiyid *Thomasia antiqua*; the other is a fragment of a tritylodont cheek tooth. For the following 86 years, until 1931, discoveries of specimens of Rhaetic mammals or advanced mammal-like reptiles in bonebeds of Baden-Württemberg appear to have been limited to the recovery of fragmentary teeth of tritylodontid therapsid reptiles. *Tritylodon fraasi* Lydekker, 1887, was typified on a tooth from Schlößlesmühle bei Steinenbronn; the type of *Chaleopotherium plieningeri* Ameghino 1903, might have come from the same site. Hennig (1922) used a tooth from either Schlößlesmühle or Olgahain as the basis of his concept of *Oligokyphus triserialis* and a second specimen, certainly from Olgahain, was informally named *O. biserialis* (see Kühne, 1956). Branca (1915), Hennig (1922) and Schmidt (1928) reviewed various aspects of the vertebrate fauna of the bonebeds. Finally, Simpson (1928) presented a thorough analysis of the small, pertinent sample in his monographic study of the Mesozoic mammals of Europe.

During the summer of 1931 E. von Huene prospected a series of natural and man-made exposures of Rhaetic bonebeds. Apparently she limited herself to those that could be easily disaggregated and utilized a binocular microscope to search through the material. Rhaetic bonebeds at Sonnenberg bei Degerloch, Gais-

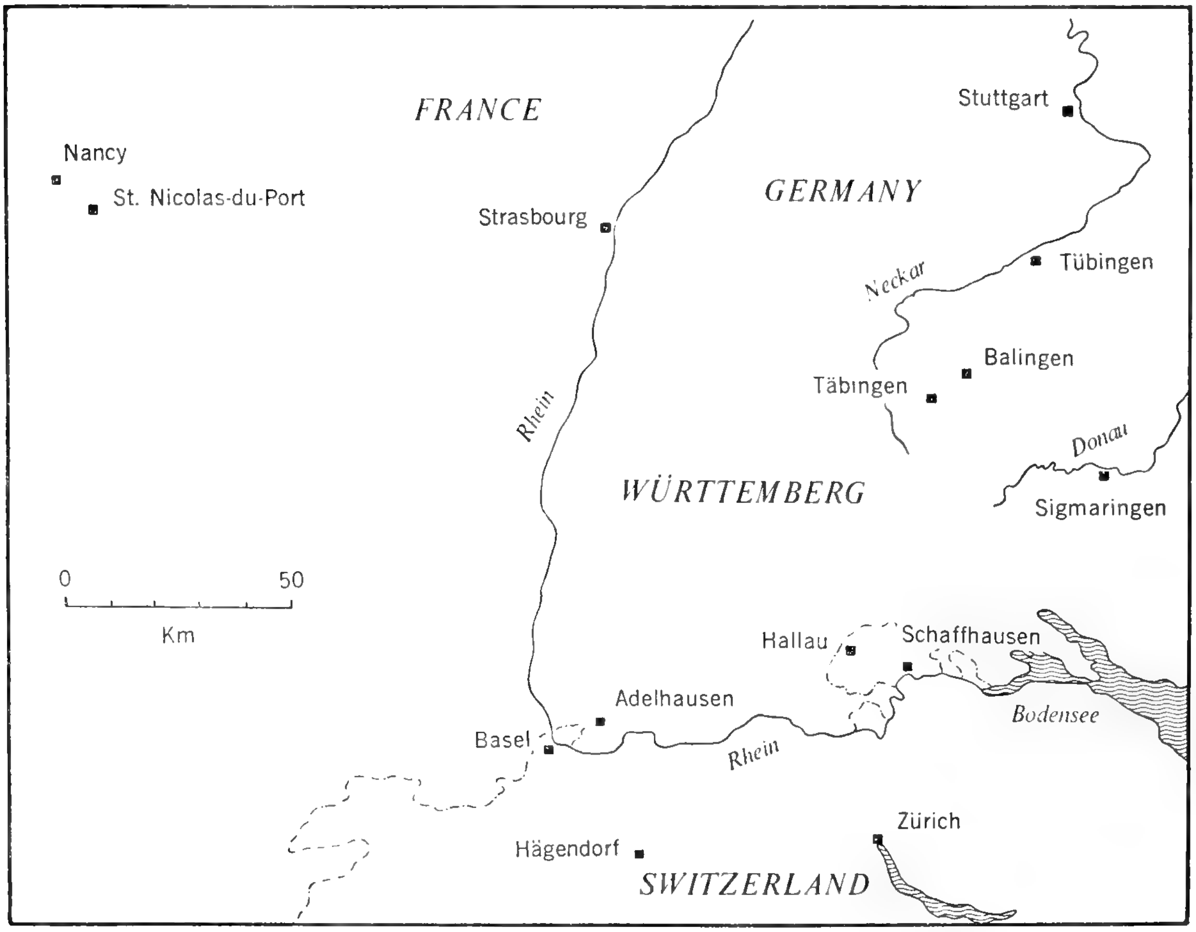

Figure 1: Sketch map of parts of northern Switzerland, southwestern Germany, and eastern France.

brunnen, and Olgahain proved to be the most productive. The results of her research were published two years later (E. VON HUENE, 1933).

Subsequently, the only major attempt to sample the microvertebrates of the Rhaetic bonebeds in the Tübingen-Stuttgart area appears to have been that undertaken by Prof. O. H. SCHINDEWOLF of Tübingen. Bonebed material was collected at Gaisbrunnen in 1947 and at Olgahain in 1948. Material from Olgahain was disaggregated and a fossiliferous fraction concentrated by use of heavy liquid flotation. This concentrate was subdivided by use of a series of screens; the smallest was 0.5 mm mesh. Only part of these concentrates have been sorted.

Since 1933 a few publications have dealt with the mammals or advanced mammal-like reptiles from the Rhaetic bonebeds of Baden-Württemberg. BUTLER (1939) and KÜHNE (note particularly 1950, 1956) considered the morphology and taxonomy of European tritylodonts. KÜHNE (1950) concluded that *Mucrotherium cingulatum* E. VON HUENE and *Uniserium enigmaticum* E. VON HUENE were based on fragmentary teeth of a tritylodont, probably *Oligokyphus*. Currently the specimens from the Rhaetic bonebeds of Baden-Württemberg appear to document the presence of no more than one species for which the name *Oligokyphus triserialis* is appropriate. It should be noted that KÜHNE (1956) justified recognition of two new species of *Oligokyphus*, *O. major* and *O. minor*, members of the Windsor Hill local fauna of England, on apparent differences in the geological ages of the English and German sites and absence of sufficient data demonstrating identity. HAHN (1973), in his review of the haramiyids found in Germany (BRD and DDR), described two teeth found in the collections made under the direction of Prof. SCHINDEWOLF.

As discussed in the following section on haramiyids, Schlößlesmühle bei Steinenbronn, once thought to be the type locality of *Thomasia antiqua*, can no longer be listed among the Rhaetic bonebed sites of Baden-Württemberg yielding remains of mammals or advanced mammal-like reptiles other than tritylodonts. HENNIG (1922, Section D) reported additional discoveries of "mammalian teeth" from various localities, some known e. g., Hohenheim and the valley of Goldersbach near Bebenhausen, and others not recorded. For various reasons — the specimens were not described in sufficient detail and now are lost or were shown to be referable to other kinds of vertebrates — these will not be considered further. However, they, other lost fossils (e. g., ZAHN G_2, E. VON HUENE, 1933), and the small number of specimens of mammals and mammal-like reptiles now available for study suggest that the current sample surely does not document the diversity of these animals in the Rhaetic bonebed fauna. These rare fossils of mammals and mammal-like reptiles (excluding teeth of tritylodonts) are now known certainly from just three localities in Baden-Württemberg:

Gaisbrunnen: The collecting locality was in a quarry in the Rhaetic Sandstone lying between Bebenhausen and Waldhausen, approximately 3.5 km north of Tübingen. Although giving a description of the lithology of the Rhaetic Sandstone, E. VON HUENE (1933) did not pay equal attention to the subjacent and superjacent strata. She noted the occurrence of four pelycepods *(Pecten acutauritis, ?Myoconcha beyrichi, Modiola minima,* and *Cardita praecursor)* and two ammonites, both represented by specimens of juvenile individuals *(Psiloceras [Waehneroceras]* sp. and *?Psilophyllites* sp.) in the bonebed. The lithology of the Rhaetic Sandstone was analyzed by AEPLER (1974).

The Geologische Karte von Tübingen und Umgebung (1969, 1:50,000, Geol. Landesamt Baden-Württemberg) shows that in the immediate vicinity of Gaisbrunnen the Rhaetic Sandstone lies on the Knollenmergel and is overlain by Lias α_{1+2}. ALTMAN (1965) described two nearby sections. In one (Section 35) approximately 2 km southsoutheast of Gaisbrunnen, a limestone directly above the Rheatic Sandstone yielded a fragment of *Psiloceras (Curviceras)* aff. *subangulare.* In a second (Section 37) approximately 1 km northwest of Gaisbrunnen the Rhaetic Sandstone is overlain by 2—5 cm of unfossiliferous marl. On top of the marl is a limestone. Altman (ibid.) reported the occurrence of *Psiloceras planorbis* and *Psiloceras plicatulum* in the lower part of the limestone. At higher levels he found *Psiloceras (Caloceras) johnstoni* and *Psiloceras (Curviceras?).*

Olgahain: E. VON HUENE (1933) noted that her collections came from part of the Rhaetic bonebed exposed by the toppling of a large tree on the slopes of Kirnberg above Olgahain, approximately 1 km east of Gaisbrunnen. Again, although discussing the lithology of the bonebed and Rhaetic Sandstone, she did not review its geological setting. Probably it is similar to that of Gaisbrunnen. Shells of two kinds of pelecypods *(Modiola minima* and *Leda deffneri)* were identified but she did not recover any remains of ammonites.

Sonnenberg bei Degerloch: This collecting area is approximately 25 km northnortheast of Tübingen in the suburbs of Stuttgart. HAAG (1928) relocated the site where PLIENINGER presumably discovered the type of *Thomasia antiqua* and described a second section exposed about 500 m to the southsouthwest near Sonnenberg. A few years later E. VON HUENE (1933) noted that this second section was covered over but the overburden was removed in order to collect a sample. Thus the type of *Thomasia antiqua* and the fragment of a tooth collected by E. von Huene and here very tentatively referred to *Tricuspes tubingensis* probably came from different localities in the region of Degerloch.

E. von Huene (1933) gives a geological section that, though less detailed, can be reasonably correlated with Haag's (1928). Haag noted that the lowest unit exposed in the section was the Knollenmergel. The bonebed is shown to be overlain by: 1) a thin (1 cm) red-brown to yellow-brown earthy mass, 2) Liasmergel (up to 1 m) and, finally, 3) the first limestone of the Lias α. E. von Huene (ibid.) reported the discovery of a pelecypod, *Pecten actauritis*, and a juvenile individual of the ammonite *Psilophyllites* at Sonnenberg bei Degerloch.

At these three bonebed localities the Rhaetic Sandstone rests on the Knollenmergel, the stratigraphically highest unit of the Middle Keuper. The upper Middle Keuper was studied recently and intensively by Brenner (1973, 1978a, 1978b) from whose publications the following summary is drawn.

During deposition of the upper Middle Keuper, in the late Carnian and Norian, Baden-Württemberg and Kanton Schaffhausen lay in the southern part of the slowly but irregularly sinking German Keuper Basin (note Brenner, 1973, Abb. 19). One area of relatively greater subsidence within this basin was centered in the region just north of Sigmaringen (Fig. 1). The sites of the fossil localities in the Tübingen-Stuttgart area considered here lay in the northern part of this area of subsidence; Hallau (Kt. Schaffhausen) in the southern part. Sheet floods transported sediments to the most rapidly sinking parts of the basin, which apparently was quickly leveled. Brenner (1978a) suggested annual precipitation increased during the deposition of the Knollenmergel and the climate became semiarid to subhumid (annual precipitation 250 to 450 mm). Also, he (Brenner, 1973, note Tab. 2) treated the Knollenmergel as an essentially isochronous unit within the basin.

The genesis of bonebeds was studied in detail by Reif (see 1976), Aepler (see 1974), and their colleagues. These studies based on thorough sedimentological analyses, include a wide range of taphonomic considerations. In this work bonebeds were simply and generally defined as sediments with high concentrations of greatly fragmented and, usually, heavily rolled bones. Frequently the fragments of bone are well sorted and lie in the range of fine to coarse pebbles. Three categories of bonebeds were differentiated on the basis of their place and mode of origin:

Condensation bonebeds formed in shelf areas where the rate of sedimentation was low and fine sediments were winnowed away from the bones.

Placer bonebeds deposited in deltas and other sites of prograding sedimentation (e. g., channels).

Transgression bonebeds developed as lag deposits during marine transgressions.

Of the German and Swiss bonebeds considered in this report Gaisbrunnen and Sonnenberg bei Degerloch (Aepler, 1974) and, probably, Olgahain are placer bonebeds. Most likely the Hallau bonebed is a combination of a placer bonebed in part reworked during a marine transgression, but its genesis needs further analysis. Aepler's (ibid. and reports in preparation) studies focus on the genesis of the Rhaetic Sandstone and its bonebeds in the Tübingen area. The following points directly pertinent to this analysis were extracted from his work.

As already noted, the Rhaetic Sandstone occurs in lenticular bodies, each probably the deposit of a prograding delta modified by coastal longshore currents. The Rhaetic Sandstone delta in the vicinity of Tübingen is reconstructed as having had a low relief with its terrestrial area broken up by many channels and shallow lagoons. The streams forming these deltas are thought to have had their headwaters in low source areas to the south and/or east and carried a relatively small load of sediment, even in times of flood. They flowed generally northward emptying into the shallow sea that covered northwestern Germany during the Rhaetian. During development of this and other deltas sea level appears to have remained relatively constant.

Aepler (ibid., p. 147, also see Brenner, 1978a) summarized evidence suggesting that after the intensive aridity characteristic of most of Middle Keuper times annual precipitation increased and the climate became characterized by seasonal periods of intense rainfall resulting in occasional flooding. Although dune sands formed immediately along the coast, most of the delta surface and coastal area was well vegetated with major forests occurring upstream.

Formation of the placer bonebeds appears to have been a two-stage process. As the animals living in and around the streams and lagoons on the delta died their skeletons settled in or were brought into these water bodies. Initial fragmentation was primarily the result of the activities of carnivores and scavengers. Once submerged, the bones and teeth permineralized by uptake of phosphates provided by decay of organic material. The water in streams and lagoons on the delta usually was either calm or slow moving. Only the finest particles were winnowed away and a relatively low amount of sediment was brought in from source areas. Condensation bonebeds formed on the delta surface. At times of flooding the permineralized bones and teeth were transported and further fragmented, hydrodynamically sorted, and then deposited as placer bonebeds in the channels or on the delta front. Possibly the process of reworking on the delta surface occurred several times before the bones and teeth were entombed in the foreset beds of the prograding delta.

This reconstruction of the sedimentary regime indicates the fossils concentrated in the placer bonebeds are a thanatocenose of the remains of aquatic (both freshwater and, possibly, marine) and terrestrial organisms.

Although the possibility that some of the heavily abraided fossils might be parts of mammals or mammal-like reptiles that lived along the upper reaches of the tributary streams and were washed down at times of flood cannot be entirely ruled out, it seems more likely they are parts of the inhabitants of the delta.

Determination of the geological age of the mammals and mammal-like reptiles whose remains are preserved in the bonebeds of the Rhaetic Sandstone in terms of the standard European time scale remains an unattained goal. This is not simply the result of problems of correlation between the Tethyian and Germanic provinces already noted, although these are major contributing factors. AEPLER (1974) argued that the development of a Rhaetic Sandstone delta was a slow, complex process; probably one encompassing tens if not hundreds of thousands of years. In this multistaged process many years might have passed between the time an animal died and parts of its skeleton were finally entombed in a bonebed. Thus, determination of the age of a bonebed only sets a minimum age for the time of existence of the animals represented in the deposit.

On the basis of data currently available maximum and minimum ages of the bonebeds at Gaisbrunnen, Olgahain, and Sonnenberg bei Degerloch can be established within a limited range. All three bonebeds are parts of deposits laid down upon the Knollenmergel. This is the uppermost unit of the Middle Keuper and, following BRENNER (1973), can be assigned a Norian age.

At the other extreme, the Tübingen-Stuttgart area was largely if not fully submerged by marine waters during the Hettangian. Although his geological sections do not include those of the Gaisbrunnen and Olgahain localities, ALTMAN (1965) reports *Psiloceras planorbis* and, slightly higher stratigraphically, *P. johnstoni*, from a nearby section. HAAG (1928) did not record what, if any, ammonites were recovered in the section at Sonnenberg bei Degerloch, but reported the bonebed was capped by strata of Lias α, i. e., early Hettangian.

AEPLER (1974) considered the implications of the discovery of fragments of juvenile ammonites in some bonebeds (e. g., those reported by E. VON HUENE (1933) from Gaisbrunnen and Sonnenberg bei Degerloch), and suggested that the time of formation of these bonebeds might be correlative with the Pre-*planorbis* Zone as recognized by WILL (1969) in the Liassic section of northwestern Germany.

Restudy of the Rhaetic bonebeds, particularly investigations focused on recovery of ostracods and palynological samples, might permit more refined correlations. However, currently available data only warrant delimitation of a range of possible ages. The mammals and advanced mammal-like reptiles represented in the bonebeds at Gaisbrunnen, Olgahain, and Sonnenberg bei Degerloch most likely are no younger than Hettangian. They might be of earliest Hettangian (Pre-*planorbis* or *Psiloceras planorbis* Zone), Rhaetian, or latest Norian age. Probably they are no older than Norian.

Hallau local fauna

The mammals and mammal-like reptiles of the Hallau local fauna are known from fossils found at a single locality in the Klettgau region of northern Switzerland to the west of Lake Constance (Fig. 1). The site, sometimes called Breitelen, is near the crest of the Hallauerberg immediately to the northwest of the town of Hallau (formerly designated Unter-Hallau), in the western part of Kanton Schaffhausen. Here the Rhaetic bonebed is not now exposed at the surface, but probably occurs over an area of at least 1 kilometer's length in a southwest to northeast direction above the vineyards of Hallau. Apparently this bonebed has only been seen in man-made excavations.

Knowledge of the geology of the Hallau and adjacent areas stems from and in many respects still is directly based upon results of the research of Bergrat Dr. Ferdinand SCHALCH. SCHALCH's interest in strata adjacent to the boundary between the Keuper and Lias is illustrated in his dissertation (SCHALCH, 1873). Then and for many years thereafter it was commonly held that Rhaetic bonebeds, or other Rhaetian deposits, were absent from geological sections in a large part of southwestern Germany (Baden-Württemberg) and northern Switzerland. However, to the northeast of a line drawn through Täbingen and Balingen in Baden-Württemberg (Fig. 1) deposits of Rhaetian age, including the Rhaetic bonebeds of the Tübingen-Stuttgart area, were known to be well developed. To the southwest of a line through Adelhausen in Baden-Württemberg and Hägendorf bei Solothurn in Switzerland Rhaetian deposits were also known to be present in the geological sections.

SCHALCH was attracted to the section on Hallauerberg by a paper by Prof. MERKLEIN (1809), a professor of natural history in the gymnasium in Schaffhausen, who noted that a Herr HENSLER reported a Keuper bonebed was encountered during construction of a road below the poor houses of Unter-Hallau (now the site of a Bürgerheim, a home for the aged). In 1915 this site had long been covered over but the widening of a farm road opened new exposures of Liassic deposits less than a kilometer from the spot where HENSLER reported the bonebed. SCHALCH had a shaft sunk to a depth of approximately 3 m and exposed the geological section down to the Upper Triassic deposits. Part of this section included the following units (from PEYER, 1956, with emendations):

SCHALCH's alphabetic designations	Thickness (meters)	Unit
m	2.5	Arietenkalk
l	0.23	Angulatusbank
k	5.35	Schwaichel (an ugly colored, dark gray to brownish green, irregularly stratified, marly shale with many finely dispersed, calcareous, sandy inclusions
i	0.20	Upper Psilonotenbank
h	0.70	marly shale, resembling the Posidonienschiefer
g	0.14—0.17	Lower Psilonotenbank
f	0.04—0.05	black, impure marl with abundant Liassic fossils
e	1.00	loose marl bonebed with the same (vertebrate) fossils as unit d
d	0.25	compact Zanclodonmergel breccia with bonebed
c	0.80	Zanclodonmergel resembling unit a
b	0.20	beds with loaf-like calcareous nodules
a	2.00+?	ordinary, green and red-spotted Zanclodonmergel

At SCHALCH's invitation PEYER undertook analysis of the vertebrate fossils found in the bonebeds (units d and e). The blocks of compact bonebed (unit d) were broken mechanically for inspection. Portions of the friable sediment of unit e were spread out on tables, carefully sprayed with water, and then sorted with the aid of an eight or ten-power magnifying glass. Not surprisingly fragments of very small mammals or mammal-like reptiles were not discovered during this project, although the remains of many larger vertebrates were recovered (see SCHALCH and PEYER, 1919, and PEYER, 1944a, 1944b, 1956).

In the autumn of 1942 a second shaft was sunk in the vicinity of the earlier excavation. Over eight metric tons of bonebed (probably this weight is for material from unit e and excludes blocks of unit d [PEYER, 1944 b, p. 306]) was collected and taken to Zürich for preparation. The friable bonebed (unit e) was dried, washed through screens (the smallest with a 1 mm mesh [ibid.]) and the concentrates divided according to grain size prior to sorting. Samples of the material that passed through the smallest screen were checked without the discovery of indentifiable fragments of bones or teeth. The compact bonebed (unit d) was left outdoors over winter to break down and then processed and sorted. Sorting was carried out with a binocular microscope and, in later phases of the work, heavy liquids were employed to further concentrate the bone fragments. The first report on the mammalian and mammal-like reptile remains (PEYER, 1956) was based on material found up to 1951, prior to completion of sorting of the concentrates. PEYER began preparation of a second report dealing with materials collected subsequently, but unfortunately this study was not completed before his death. Except for a small amount of material preserved as lithological samples in the Paläontologisches Institut und Museum der Universität Zürich, all the rock collected by PEYER has now been broken down, processed and the concentrates sorted.

SCHALCH and PEYER (1919) present the most thorough, available analysis of the geological section exposed in the Hallau excavations. PEYER (1944b) added observations made during the 1942 excavation. The basal units (a through c) were first referred to the Zanclodonmergel, which is now considered an alternative name for the Knollenmergel (see SCHALCH, 1916, PEYER 1944 b, BRENNER, 1973). This allocation was made on the basis of: 1) the position of the strata at the top of the extensive Middle Keuper section, which except for the Jurassic strata at the crest, forms most of the Hallauerberg, and 2) their lithology. Other than a small fragment of bone and another scrap of carbonaceous material (jet) no fossils were encountered in these units during the 1915 excavation. However, during the 1942 excavation bones of *Gresslyosaurus* were found in unit c of the Zanclodonmergel (PEYER, 1944 b). The Zanclodonmergel is interpreted as a unit deposited in nonmarine conditions and no evidence from the Hallau site is contradictory.

The bonebed (units d and e) lies directly on the Zanclodonmergel. SCHALCH and PEYER's (1919) initial basis for separating the two units was difference in the degree of cementation, the particles of unit d being bound together with a calcite or, rarely, barite cement while those of unit e were not cemented. Dominant particles of the bonebed are fragments of limestone and marl (usually small, 1 to 2 mm in diameter, but some were reported to reach a diameter of 16 mm). Almost all these appeared to be derived from the Zanclodonmergel. Only a few were lithologically distinct, but these could have been derived locally from lower units in the Middle Keuper. The absence of quartz was noteworthy.

In addition to fragments of limestones and marls Schalch and Peyer (ibid.) noted the bonebeds contain abundant carbonaceous fragments, pieces of bone, fish and reptilian vertebrae, teeth, and coprolites. Peyer (ibid.) provided the following list of genera and species identified from the collections made in 1915 (many fragments were not identifiable at the generic or specific levels):

Ceratodus parvus
Sargodon tomicus
Hybodus sp.
Hybodonchus sp. ?
Gresslyosaurus sp.
Termatosaurus albertii
Megalosaurus sp.

Also recovered were scales of ganoid fishes and bones of nothosaurids and labyrinthodonts.

Later work by Peyer (1956) demonstrated that the bonebed units (d and e) do not differ solely in hardness but also in faunal content. Unit d, the compact bonebed, lacks fragments of marine invertebrates and probably was formed in a freshwater or brackish environment prior to the time of the marine transgression of the Hallau area. In contrast, in addition to the vertebrate fossils, during the sorting of the concentrates obtained from the upper unit (e) fragments of shells of mollusks, parts of crinoid stems, and various skeletal elements of echinoderms were found. Peyer (ibid.) concluded these fossils represent animals that were part of a typical lower Liassic marine fauna. Unfortunately the presence of these fossils was not recognized during collection of the rock. Some of the invertebrates found in the concentrate might be contaminants, fossils that fell or were washed down from exposures of unit f within the shaft. Although aware of this possiblity, Peyer (1944 b) suggested that many if not most of them were derived from unit e.

Unit e now appears to be the product of partial reworking of unit d with addition of more material from the Zanclodonmergel during the transgression of the sea. Reworking of the Keuper deposits and bonebed continued in other regions providing sediment to the Hallau area until the beginning of deposition of the Upper Psilonotenbank (Schalch and Peyer, 1919, and Peyer, 1944 b).

I could not find any record distinguishing the fossils of mammals or mammal-like reptiles that came from unit d from those derived from unit e. Because rock from both units was processed by Peyer, it is reasonable to assume the rare teeth of these animals occurred or appeared to occur in both. If the simplifying, but not particularly justified assumption is made that these teeth occurred in a random distribution throughout units d and e, then probably the majority of the fossils collected came from unit e for a much greater volume of this unit was available and processed.

The structure and composition of the bonebeds give ample testimony to transport of material from other areas and reworking of the fragments of rock and vertebrate fossils. Schalch and Peyer (1919) and Peyer (1944 b) tried to assess the degree to which these process might have mixed materials from different geological or biological sources. In the first paper they note that some fragments of limestone and marl show heavy abrasion suggesting considerable movement in transportation or at the site of deposition, others do not. There is equal diversity in the preservation of the fossils. Stromer and Peyer (1917, p. 18) commented that material of *Ceratodus* from Hallau showed greater morphological detail and was more complete than the heavily water-worn specimens found in British Rhaetic deposits, e. g., Aust Cliff near Bristol, or bonebeds in the Tübingen-Stuttgart area.

In this study of the mammals and mammal-like reptiles from Hallau no consistent differences in mode of preservation or postmortem wear suggested a heterogeneous sample derived from two or more sources of distinctly different ages or distances from the site of deposition. Lacking evidence to the contrary it is tentatively assumed that these fossils can be treated as representing members of a single local fauna (sensu Tedford, 1970).

Although not a substitute for a thorough taphonomic analysis, which definitly is needed, the following scenario is suggested. The formation of the Hallau bonebed started with reworking of the uppermost Zanclodonmergel by fresh or brackish water. Remains of terrestrial and aquatic vertebrates, probably parts of the local riparian and aquatic fauna, were concentrated in a bonebed. What is left of this deposit is now designated unit d. During the transgression of the sea the upper part of the bonebed was reworked. Fragments of marine invertebrates and, possibly, freshwater or terrestrial organisms were introduced to produce unit e.

Expression of the time of deposition of the Hallau bonebed in terms of the units of a standard European chronological scale cannot be made directly or with great precision. Schalch and Peyer's (1919) assignment of a Rhaetian age sparked considerable debate (see Peyer, 1944 b). The second excavation at Hallau provided some new information, but still did not permit precise correlation. The currently available data pertinent to this question can be outlined as follows:

The Knollenmergel, traditionally termed the Zanclodonmergel in reports on the Hallau bonebed, is the uppermost unit of the Middle Keuper and thought to have been deposited in the Norian (BRENNER, 1973). The discovery of bones of *Gresslyosaurus* in unit c is in accord with this view. Thus the age of the Hallau bonebeds appears to be no greater than Middle Keuper (Norian).

The compact, lower bonebed (unit d) lacks large invertebrates that could be the basis for a correlation. Fragmentary invertebrate fossils found in unit e included no specimens that have been identified as representing species of sufficient biostratigraphic utility for the refined correlations needed. Also, they might well represent organisms that lived after most or all of the vertebrates represented in the bonebed.

PEYER (1956) suggested the ganoid fish *Sargodon tomicus*, the dipnoan *Ceratodus parvus*, and haramiyids might serve as Rhaetian index fossils. Haramiyids are now known to have existed from the Middle Keuper (HAHN, 1973) into the Jurassic, possibly as late as Bathonian (see CLEMENS and KIELAN-JAWOROWSKA, 1979). Considering the kind of data on the biostratigraphic ranges of the fishes available to PEYER, their utility as index fossils must be regarded as warranting further testing. To the best of my knowledge studies of ostracods, other microinvertebrates, or paleobotanical material from the Hallau bonebeds have not yet been attempted and the results published.

The bonebed is overlain by a black, impure marl containing many fossils of Liassic marine invertebrates (fide PEYER, 1956). Shells of ammonites identifiable at the specific level were not discovered. However, in the overlying Lower Psilonotenbank (unit g) an ammonite referable to *Psiloceras* was discovered during the 1915 excavation. Prof. POMPECKJ (quoted in SCHALCH and PEYER, 1919) identified it as an Laqueolusform of the *Psiloceras johnstoni* group. Allocation to *Psiloceras johnstoni* (or *P. [Caloceras] johnstoni)* apparently has not been subsequently modified.

URLICHS (1977) in his review of the Lower Jurassic of southwestern Germany recognized the *Psiloceras planorbis* Zone as the lowest zone of the Jurassic. In stratigraphic sequence it is followed by the *Psiloceras (Caloceras) johnstoni*, *Psilophyllites hagenowi*, and *Alsatites laquens* zones. These four zones comprise the Lower Hettangian. The Lower Psilonotenbank (unit g) is the lowest unit in the Hallau bonebed section whose age of deposition can be correlated with this sequence. The occurrence of *Psiloceras johnstoni* indicates an early but not earliest Hettangian age.

In summary, on the basis of the data currently available all that can be said is that the Hallau bonebed local fauna might be of Rhaetian age. It is probably no older than Middle Keuper (Norian) and no younger than the *Psiloceras johnstoni* Zone, early but not earliest Hettangian.

Saint-Nicolas-du-Port local fauna, France

The occurrence of vertebrate fossils in Triassic and Liassic deposits of northeastern France has been known for many years, but until recently none of these fossils documented the presence of mammals or advanced mammal-like reptiles. It should be noted that instead of including it within the Triassic most French stratigraphers usually classify the Rhétien as the initial stage of the Jurassic arguing that it is the time of the beginning of the major marine transgressions of Europe that characterize the Liassic (note RICOUR, 1961, PEARSON, 1970).

In 1975 G. WOUTERS, screening sands in an old quarry at Saint-Nicolas-du-Port, discovered a curious, two-rooted tooth that might be an element of the dentition of an advanced mammal-like reptile (RUSSELL et al., 1976). Prompted by this discovery D. SIGOGNEAU-RUSSELL (1978) undertook screen washing of a large quantity of the fossiliferous sand. This unit is part of a thick sequence of sandstones locally designated as Rhétien inférieur (note geological section given by LAUGIER, 1961). HOWEVER, as SCHUURMAN (1977) cautioned such stratigraphic assignments have been made on the basis of local lithostratigraphy and might not have chronostratigraphic significance.

In a preliminary report SIGOGNEAU-RUSSELL (1978) announced the discovery of isolated teeth of morganucodontids, possibly a docodont, kuehneotheriids, and haramiyids. This work is being continued and gives promise of providing the first large sample of a Rhaetic mammalian fauna from continental western Europe.

The systematic affinities of some of the mammals reported to date will be discussed after description of the materials from the Tübingen-Stuttgart area and the Hallau local fauna. However, it is appropriate to point out here that the only genera in common to two or all three of the French, Swiss, and German faunas are the haramiyids *Thomasia* and *Haramiya*. These haramiyid "genera" are probably loosely defined typological units for different kinds of teeth and might bear little relationship to the genera of animals represented. Thus, at our present state of knowledge, it is only at the family or higher levels that common occurrences of taxa in two or all three of these faunas are recorded with some degree of certainty. Most likely these differences in faunal composition reflect both differences in age and the evolution of insular faunas as the European continent was subdivided by epicontinental seas during the Rhaetian and early Liassic.

Late Triassic - Early Jurassic local faunas from fissure fillings, western Great Britain

In recent years most of our knowledge of Late Triassic-Early Jurassic mammals has come from fossils found in remarkable abundance in fissure fillings in Wales and southwestern England. Three groups of fissure fillings have yielded mammalian and advanced mammal-like reptile remains that are of concern here. First, the fissure fillings near the town of Bridgend in Glamorgan, South Wales, include deposits that are the source of immense samples of *Morganucodon* and *Kuehneotherium*. These were exposed during operation of commercial quarries in Carboniferous limestones. During the Rhaeto-Liassic this limestone plateau is thought to have been an island, which ROBINSON (note 1971) dubbed St. Brides Island. Most of the field research has been carried out by Dr. K. A. KERMACK and his associates at University College London (see KERMACK et al., 1973, for a history of research).

A second group of fissure fillings are those exposed in Holwell Quarry near Frome in Somerset, England. In 1858 a fossiliferous fissure filling was discovered in the quarry and Charles MOORE had over 3 tons of the matrix transported to his home in Bath. Sorting this matrix required over three years and yielded a wealth of vertebrate material including a few isolated teeth of haramiyids (note DUFFIN, 1978, and PICKFORD, 1971). Subsequently fissures at Holwell were worked by KÜHNE (1946) and SAVAGE and WALDMAN (1966, also see SAVAGE, 1971). Finally, another fissure filling in Somerset, "Mendip 14", at Windsor Hill Quarry near Shepton Mallet has yielded an extensive sample of *Oligokyphus* that was collected and studied by KÜHNE (1956).

As is the case with bonebeds, establishment of the time of deposition of a fissure filling only sets a minimum age for the contained fossils. Many of the processes that have led to the concentration of bones in fissure deposits are still poorly understood (note KERMACK et al., 1973). There is evidence suggesting that some of the fissure deposits just cited might have had developmental histories as long and complex as the placer bonebeds (REIF, 1976).

The age of the fissure fillings and contained fossils found near Bridgend, Wales, has been discussed recently by ROBINSON (1971) and KERMACK et al. (1973). ROBINSON dealt primarily with age determinations based upon a reconstruction of the physical evolution of the Bristol Channel region. During a later part of the Late Triassic (Norian), St. Brides Island and several other areas composed largely of Carboniferous limestones deformed by Hercynian folding still rose as plateaus above extensive piedmonts (note TUCKER and BURCHETTE, 1977). At this time the plateaus could have been ecological islands supporting faunas and floras different from those of the surrounding piedmont.

Starting in the Rhaetian and continuing in the Liassic seas flooded the area and, apparently, during the Sinemurian (*Arietes bucklandi* Zone) fully inundated St. Brides Island. When during the period Norian to Sinemurian the fissure fillings were formed remains an unresolved question. ROBINSON (1971) argued that the narrow, slot fissures containing the vertebrate fossils appear to be elements of a relatively immature system of underground water courses. She suggested this fissure system was cut after the seas had isolated the island, raised the base level, and promoted the evolution of new drainage patterns. "Just before submergence sedimentation, rather than solution, became the dominant process in these fissures (ibid., p. 136)". She concluded that the fauna of the fissures is largely of Liassic age.

KERMACK et al. (1973) present a broader discussion of the problem of age determination. They note that the local faunas including *Morganucodon* and *Kuehneotherium* occur in deposits containing other vertebrates, occasionally invertebrates, and plants, particularly remains of the conifer *Hirmeriella (Cheirolepis) muensteri*. To date this assemblage of organisms, the *Hirmeriella* association, is only known from fossil localities on St. Brides Island. Although little help in precise correlations with other mammal-bearing deposits, the distinctive composition of this association supports the hypothesis that beginning with ecological islands formed by highlands in arid to semiarid environments and later isolated by Rhaeto-Liassic seas many different insular faunas evolved.

KERMACK et al. (1973) cite evidence suggesting the fissure-filling local faunas are not as old as "Keuper", *i. e.*, pre-Rhaetian. They conclude, "the age of the *Hirmeriella* association in these fissures must be either the Lower Lias (Hettangian and Lower Sinemurian) or the Rhaetic. There is insufficient evidence to decide between them." To this can only be added the observation that differences in composition of individual concentrations of bone within various fissures might not be just a product of variations in taphonomy but also reflect differences in age. The chronological duration of the *Hirmeriella* association could encompass a significant fraction of the Rhaetian to Lower Sinemurian interval.

The specimens of haramiyids and *Eozostrodon* found at Holwell Quarry were discovered in at least two fissure fillings. These deposits are thought to be neptunian dikes, submarine fillings of fissures opening beneath the sea and, in some instances, close to shore (KÜHNE, 1956, ROBINSON, 1957, SAVAGE and WALDMAN, 1966). KÜHNE (1946) reviewed faunal and geological evidence and came to the conclusion that the fissure fillings could have been formed sometime in the interval from Rhaetian to Bajocian but favored a Rhaetian age for the haramiyids and *Eozostrodon.*

In his monograph on *Oligokyphus* Kühne (1956) presented thorough studies of the taphonomy and age of the fossiliferous fissure filling in the Windsor Hill Quarry, "Mendip 14". Although a year or two might have elapsed between the time of death of the individuals of *Oligokyphus* and the burial of their remains in the submarine fissure, there is strong evidence this interval was not significantly greater. Kühne (ibid.) concluded that the age of the fissure filling and the specimens of *Oligokyphus* was Charmouthian (Lias γ or Pliensbachian).

In summary, except for "Mendip 14", currently available data only warrant estimations of age ranges of the fissure fillings and their faunas. (Both D. Pacey and C. Duffin, University College London, have undertaken studies of different aspects of the problems of determination of the ages of these and other British Rhaeto-Liassic vertebrate localities). In the cases of both the fissure fillings of St. Brides Island and Holwell, the minimum ages of the vertebrate fossils are well within the Liassic. If, following Robinson's interpretation that sedimentation became the dominant process in the development of the fissures late in their history, then there is a possibility that their local faunas are younger than the Rhaetic bonebed local faunas of Switzerland, Baden-Württemberg, and France. The sample of *Oligokyphus* from "Mendip 14" appears to be distinctly younger than the genotypic species from Baden-Württemberg.

Paleogeography

During the early Mesozoic northwestern Europe was of approximately triangular outline (see Ziegler, 1978). The base of the triangle was formed by extension movements leading to the development of a complex graben system flooded by the Triassic, Tethyian seas. Contemporaneously, to the west, the active rift zones that would later produce the basin of the North Atlantic Ocean and link it to the Arctic Ocean formed the other side. The third side of the triangle was delimited by the edge of the stable Russian platform (Fig. 2).

In the Triassic the system of Permian basins within northwestern Europe was modified by the development of a new trough and graben complex. It was an area largely characterized by erosion and, except for the geographically limited transgression of the Middle Triassic seas, deposition of terrestrial sediments. Toward the close of the Triassic most of northwestern Europe had been reduced to an area of relatively low relief, extensive flood plains, tidal flats, and shallow basins separated by low hills and pla-

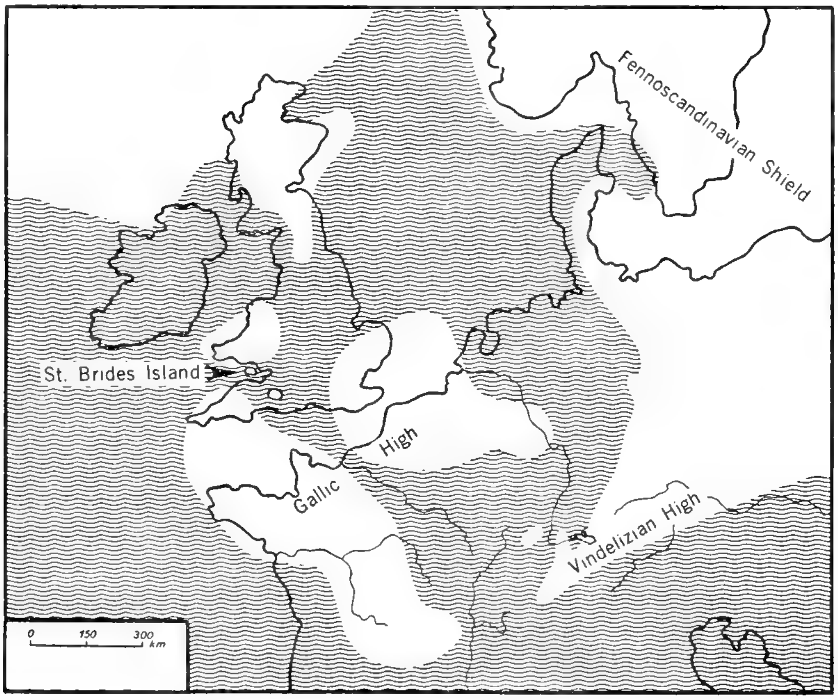

Figure 2: Schematic reconstruction of northwestern Europe showing areas covered by seas during the Rhaetian transgression (Based on data from Will, 1969, Ziegler, 1978, Muller, 1974, and T. R. Owen, 1976).

teaus. The arid climatic conditions characteristic of most of the Late Triassic (note Robinson, 1973) were ameliorated by increasing amounts of rainfall during the Norian and Rhaetian.

At the beginning of the Rhaetian marked regional extension movements, the Early Kimmerian tectonic pulse, affected not only the North Atlantic to Arctic and Tethyian rift systems but also northwestern Europe (Ziegler, 1978). This period of extension was the prelude to the Rhaeto-Liassic marine transgression that ultimately covered most of northwestern Europe.

Among the three areas of interest possibly the first to be affected by marine transgressions were the parts of Wales and southwestern England bordering the Bristol Channel. Although the range of variation in elevation was not great, the British Isles was an area of relatively varied relief that waters from the proto-North Atlantic probably quickly transformed into an archipelago (note Audley-Charles, 1970 a und 1970 b, Donovan et al., 1979, and summary in T. R. Owen, 1976). By early Hettangian (*Psiloceras planorbis* Zone), if not earlier, St. Brides Island could have been fully encircled by marine waters (Robinson, 1971). Its fossiliferous fissure fillings were formed sometime after the beginning of the Rhaetian but before final submergence of the island in the Lower Sinemurian. The fissure fillings at Holwell might also have been formed during this interval, but the "Mendip 14" fissure filling is younger (Pliensbachian).

During the Rhaeto-Liassic transgression what are now the continental parts of northwestern Europe were characterized by three major areas of erosion (note Will, 1969, Figs. 47—49, Ziegler, 1978, Figs. 3 and 5, and Fig. 2). The Gallic High included, in varying combinations, parts of southeastern England, Belgium, and northwestern France (i. e., London-Brabant Massif, Ardennes High, Armorican High, and adjacent areas). To the northeast was the stable area of the Russian Platform (including the Fennoscandinavian Shield). Finally, in the southeast the Vindelizian High occupied parts of what are now northwestern Switzerland and southern West Germany. To the northeast it was linked to the Bohemian Massif.

Marine waters flooding the basins of northwestern Europe came primarily from the proto-North Atlantic Ocean. They transgressed in a generally eastward direction from the area of the British Isles flooding the basins between the Gallic High and the Russian Platform. A lobe of this sea expanded from the northeast toward the west and south into the Paris Basin. Early in the Rhaetian it breached the Gallic High in the vicinity of the modern Seine River valley and established a connection with seas in southern England (Muller, 1974). Farther to the south a connection with Tethys was established (Will, 1969).

The transgression of northern Germany came to a halt or slowed toward the end of the Rhaetian providing a stable sea level, one condition thought to be requisite for the development of the Rhaetic Sandstone deltas of the Tübingen-Stuttgart area (Aepler, 1974). The streams forming these deltas had their headwaters in the Vindelizian High. Surface outcrops of the Rhaetic Sandstone containing bonebeds are known from the region of Stuttgart southwest to the Täbingen-Balingen area. Wells drilled in the vicinity of Lake Constance have encountered Rhaetic sediments that thin westward (Büchi et al., 1965). An approximately north-south trending high from the Aar Massif in the south, through the region of Zürich and into the Schwarzwald of southwestern Baden-Württemberg formed a peninsula into the Rhaetic sea. On the western side of this peninsula, *i. e.*, west of the Adelhausen-Hägendorf line (Fig. 1), sediments including bonebeds were also deposited during the Rhaetian (note Tanner, 1978).

Aepler (1974) developed two working hypotheses concerning the chronology of development of the Rhaetic Sandstone deltas in Baden-Württemberg. One (note ibid., Abb. 12) suggests that the deltas were deposited in sequence as the seas transgressed, and, therefore, from the oldest in the Stuttgart area the Rhaetic deposits become progressively younger southwestward. The Rhaetic Sandstone in the Tübingen area is overlain by sediments of the *Psiloceras planorbis* Zone. However, the first Liassic ammonite found above the Hallau bonebed is *P. johnstoni*. It is tempting to hypothesize the bonebeds of the Tübingen-Stuttgart area are somewhat older than the Hallau bonebed. This might be the case. But, as Aepler (ibid.) noted, the available data from Baden-Württemberg are also in accord with a hypothesis that the Rhaetic Sandstone deltas developed at about the same time throughout this area.

How the time of deposition of the bonebeds at Saint-Nicolas-du-Port relates to that of the Swiss and German bonebeds remains unclear. If the assignment of a Lower Rhaetian age proves correct and Will's paleogeographic map of the area for the time of the *contorta*-Schichten (Will, 1969, Fig. 49) is reasonably accurate, the bonebeds of Saint-Nicolas-du-Port were formed on the eastern margin of the Gallic High. This area was then separated by a marine strait from the shores of the Vindelizian High.

In summary, a review of biostratigraphic studies of Rhaeto-Liassic stratigraphy of northwestern Europe does not result in a marked increase in precision of correlation of the vertebrate localities. In recent years detailed palynological research and studies of ostracods have added to development of a biostratigraphic framework. However these research techniques have yet to be applied in renewed investigations of the vertebrate fossil localities and the results published. The fissure fillings of St. Brides Island and Holwell Quarry, and the Rhaetic bonebeds of Saint-Nicolas-du-Port, the Tübingen-Stuttgart area and Hallau can be correlated with no more precision than to say that they all are of Rhaeto-Liassic age.

To speculate, making use of the probabilities and educated guesses of specialists, it can be argued that the oldest occurrence of a haramiyid is that from the probably Norian, *Plateosaurus* beds of Halberstadt (Hahn, 1973). If the assignment of Rhétien inférieur has more than local significance, the Saint-Nicolas-du-Port local fauna would be the oldest assemblage of mammals yet found in Europe, and possibly the world. The mammals from the bonebeds of Germany and Switzerland might be slightly younger but no younger than early Hettangian. Heavily weighting Robinson's (1971) argument that the filling of the fissures at St. Brides Island occurred close to the time of the island's final inundation in the Sinemurian, these local faunas could have a Hettangian-Sinemurian age. The Holwell local fauna might fall in this interval. The differences in faunal composition distinguishing it from those on St. Brides Island could be a product of insular evolution rather than differences in age. Probably both factors are involved. Finally, the rich accumulation of bones of *Oligokyphus* at the "Mendip 14", Windsor Hill quarry appears to be even younger, Pliensbachian.

FOSSILS FROM THE TÜBINGEN-STUTTGART AREA BADEN-WÜRTTEMBERG, WEST GERMANY

Introduction

Unlike the sample of the Hallau local fauna that was collected at one site, the fossils described here come from various exposures of the Rhaetic bonebeds in the Tübingen-Stuttgart area. Currently available data, reviewed in a preceding section, suggest they are derived from approximately contemporaneous sites formed under similar depositional regimes. For these reasons, and convenience, the systematic analyses of these few fossils are grouped in the following section. Whether they actually document members of one faunal unit remains to be determined.

Systematics

Class ?Mammalia
Order and Family incertae sedis
Tricuspes E. von Huene, 1933

Type species: *Tricuspes tubingensis* E. von Huene, 1933

Revised diagnosis: In comparison to the approximately contemporaneous morganucodontids, cheek teeth are of larger size and simpler morphology consisting of only three main cusps. The median or principal cusp is larger than the anterior and posterior accessory cusps. These cusps are not aligned directly behind one another, but the apex of the principal cusp is slightly buccal(?) to a line drawn through the apices of the anterior and posterior accessory cusps. A small cusp may be present on the presumed posterobuccal side of the crown. Directly below the crown the root is bilobed in cross section and might have been fully subdivided farther from the crown.

Distribution: Type locality: Gaisbrunnen, Baden-Württemberg, West Germany. Referred material from the following localities: Sonnenberg bei Degerloch, Baden-Württemberg; Hallau, Kanton Schaffhausen, Switzerland; and Saint-Nicolas-du-Port district of Meurthe-et-Moselle, France (pers. comm., D. Sigogneau-Russel).

Tricuspes tubingensis E. von Huene, 1933

Revised diagnosis: As for the genus until additional species are recognized.

Type specimen: An isolated tooth tentatively identified as a right lower molariform now in the collections of the Geologisch-Paläontologischen Institut der Universität Tübingen (see E. von Huene, 1933, Taf. I, Fig. 7, and Pl. 1:1—2).

Orientation: On the basis of several tenuous assumptions the type specimen is identified as a lower right molariform tooth (Pl. 1:1—2). A survey of teeth of the known Triassic and Jurassic mammals shows that usually, but not always, the lower molariform teeth have crowns higher (maximum cusp height relative to crown height) than those of the uppers. In many species cingula or cusps lateral to the main cusps are found on only one side of the lowers but on both sides of the uppers. These criteria, assumed to be applicable to *Tricuspes*, are the basis for identification of the type specimen as an element of the lower dentition.

In many molariform teeth of triconodont-type and known orientation, the anterior accessory cusp is lower than the posterior. Also, the anterior slopes of the main cusps tend to be more gradual and slightly convex in lateral outline. These two lines of evidence are the basis for the designation of the anterior end of the crown.

Identification of the type specimen as a right, rather than a left lower cheek tooth is almost an arbitrary choice. Two criteria are available for consideration, the angulation of the row of main cusps and the orientation of the small lateral cuspule. On lower molariform teeth of a tribosphenic or pre-tribosphenic pattern and some triconodont-like teeth (note *Amphilestes,* see Mills, 1971, p. 53-4), the apex of the principal cusp lies labial to the anterior and posterior accessory cusps. Second, lateral cingula or cusps are usually on the lingual side of the crown of lower molars. Thus, by the first criterion, the type of *Tricuspes tubingensis* is probably from the right dentition, by the second it is a left molariform. The first criterion is slightly favored because it might prove to be a more stable feature. A very similar tooth in the collection from Hallau lacks the lateral cusp, but shows the angulation of the main cusps.

Description: The root(s) are broken away leaving a fracture surface with a figure-eight outline showing subdivision of the pulp cavity. The crown appears to be well preserved and lacks evidence of wear facets of post-mortem abrasion (Pl. 1:1—2). A high principal cusp dominates the relatively simple crown. The anterior accessory cusp is lower than the posterior and both are separated from the principal cusp by distinct notches. A slight bulge at the base of the crown extends from the posterior end of the tooth around the presumed lingual side of the posterior accessory cusp. This swelling does not appear to have been the base of a distinct cingulum nor did it support cingular cusps. The fourth cusp on the crown is a small but distinct cuspule on the posterobuccal slope of the principal cusp. If the assumed orientation is correct, this is not a kühnecone, a cusp on the lingual margin of the crown.

Dimensions of the type specimen are as follows: crown length = 2.64 mm, width = 1.12 mm.

Discussion: A fragment of tooth described and illustrated by E. von Huene (1933, p. 84—5, Taf. I Fig. 9), found in the Rhaetic bonebed at Sonnenberg bei Degerloch, might be referable to *Tricuspes tubingensis.* The fossil appears to be less than half of a two-rooted tooth slightly larger than the type. Although having suffered some further damage since its original description, what little remains of the crown is not strikingly different from the posterior part of the crown of the type of *T. tubingensis.* If this identification is correct, then the specimen shows that some teeth of *T. tubingensis* were supported by two separate roots.

In her study E. von Huene (1933, Taf. III, Figs, 40, 41, 42, 44, 48) figured five fossils and described several more from the collections of Charles Moore, now housed in the Bath Geology Museum, Bath, England (see Pickford, 1971, Duffin, 1978). The figured specimens — a tooth, three vertebrae, and a phalanx — were identified as coming from the Rhaetic site "Vallis bei Frome" and not from the fissure fillings in Holwell Quarry. Of these fossils E. von Huene referred the tooth to *Tricuspes*; the bones were tentatively allocated to an undescribed, primitive crocodilian. Catalogue numbers were not recorded and, because of the turbulent history of the collection during and after World War II (see Pickford, 1971), these bones cannot now be certainly identified.

The illustration (E. von Huene, 1933, Taf. III, Fig. 40) of the tooth referred to *Tricuspes* shows a three-cusped crown supported by a single, blunted root. Crown length, measured from the illustration, is on the order of 1.4 mm. The accuracy of this drawing cannot be directly assessed, but clearly its shading is not rendered with the same care and detail used in the drawings of the type of *Tricuspes* or teeth of *Oligokyphus.*

Search of the Moore collection in 1975 resulted in discovery of only one tooth that could possibly have been the model for E. von Huene's illustration. It (C108) is a single-rooted tooth with a transversely flattened crown of 1.6 mm anteroposterior length. On either side of the principal cusp are small anterior and posterior accessory cusps. Below each accessory cusp, at the level of maximum length of the crown, are minute cusps, only easily visible with magnification. This fossil is identified as coming from Holwell Quarry. It resembles those from Hallau described by Peyer (1956, p. 56—59) as, "Zähne von wahrscheinlich Synapsiden Reptilien, Gruppe a".

Thus, the tooth from "Vallis bei Frome" allocated to *Tricuspes* by E. von Huene cannot be certainly relocated. The only fossil in what remains of the Moore collection that might have served as the model for her drawing is C108, which is recorded as coming from Holwell Quarry, not from the site at Vallis. It differs from the type of *Tricuspes* in its smaller size, morphology of cusps, proportions of the crown and undivided root. If found at Hallau, C108 would be included in "Gruppe a" of the teeth tentatively allocated to synapsid reptiles by Peyer (1956). However, the possibility that C108 was not the model for her drawing and the illustrated tooth was lost when the Moore collection was rapidly packed for storage cannot be dismissed. In summary, there is no unequivocal evidence that *Tricuspes* was part of the British Mesozoic fauna.

Family Haramiyidae

In addition to being represented in local faunas of the Tübingen-Stuttgart area and the Hallau local fauna, haramiyids are members of other continental European and British local faunas. Most of these records of haramiyids come from sites of Rhaetic or Liassic age, but a tooth is known from a locality in the Late Triassic, Keuper (Norian), *Plateosaurus*-Schichten (Hahn, 1973). Freeman (1976) reported the occurrence of an isolated tooth in Bathonian (mid-Jurassic) deposits in England that might have been part of the dentition of a late haramiyid or an early multituberculate. In spite of their widespread geographic and stratigraphic distribution in Europe, at no site yet discovered has a large sample of haramiyids been recovered. The group remains known from only isolated, usually fragmentary teeth. If only complete teeth or major fragments are counted, the total haramiyid sample consists of approximately fifty specimens (see Clemens and Kielan Jaworowska, 1979, for review).

The currently utilized classification of haramiyid genera and species has not changed greatly from that proposed by Simpson (1928). Two genera are recognized, *Haramiya* (= *Microlestes, Microcleptes*) and *Thomasia*, which are distinguished on the basis of number and relative size of cusps. In addition to the four species formally recognized by Simpson (1928) — *Haramiya moorei, H. fissurae, Thomasia antiqua*, and *T. anglica* — several unnamed "taxa" have been noted (see Hahn, 1973) or morphological variants described (Parrington, 1947). Currently there is no basis for determining whether these formal and informal groupings represent collections of teeth of different species or are simply associations of morphologically similar teeth. Prof. P. M. Butler and Dr. Giles MacIntyre (pers. comm.) are now engaged in research on occlusal patterns of haramiyid dentitions that might contribute to the resolution of some problems of classification. For the limited purposes of this analysis the "taxa" of haramiyids are treated as though they are based on collections of morphologically similar teeth that might be samples of different biological species. The difficulties encountered in assignment of some fossils strongly suggest they are not, but do not clearly offer the basis for an alternative classification.

In the following descriptions the terminology suggested by Hahn (1973) is employed. Briefly, Row A is the row of cusps of higher average height, which usually are three in number. Row B, usually consists of four or more cusps most of which are smaller than the cusps in Row A. The "U-shaped rim" is the low ridge connecting the two rows of cusps at one end of the central basin. At the other end of the crown, the higher cusps of Rows A and B are frequently linked by a saddle marking a terminus of the central basin. *As a convenience in preparing descriptions*, the "U-shaped rim" is assumed to be at the posterior end of the crown.

Thomasia Poche, 1908

The diagnosis of this genus currently utilized is that proposed by Simpson (1928, p. 63):

> "Microcleptidae [= Haramiyidae] with one rim of basined molar teeth [Row A] with three tubercules of which the anterior is markedly the largest and the posterior one may be much reduced. The anterior cusp of the other side [Row B] is not as high as that just mentioned, and is followed by four or more smaller cusps, the most posterior of which forms part of the posterior closure of the basin ["U-shaped rim"].

Currently two species of *Thomasia, T. antiqua* (Plieninger, 1847) and *T. anglica* Simpson (1928), are formally recognized, but Hahn (1973) also described teeth under the rubrics of *Thomasia* sp. 1 and sp. 2. As the name suggests, *T. anglica* is typified on and was known only from specimens found at Holwell Quarry, England.

Thomasia antiqua (Plieninger, 1847)

Simpson (1928) reviewed the confused history of the fossils originally referred to *Thomasia antiqua* by Plieninger (1847). In 1979, with the assistance of Dr. Rupert Wild, I reviewed the Rhaetic bonebed material in the collections of the Staatliches Museum für Naturkunde, Stuttgart. The original descriptions of the two teeth allocated to what is now *Thomasia antiqua* are in a paper (Plieninger, 1847) dealing with fossils from the bonebeds at Degerloch and Steinenbronn. Plieninger did not record which of the localities yielded the specimens of *Thomasia*. Henning (1922) argued that the type specimen probably came from Schlößlesmühle bei Steinenbronn and was followed in this by Simpson (1928), Hahn (1973), and Clemens et al. (1979). However a note now with the fossils that apparently was written by Prof. Dr. F. Berckhemer, the former curator of the Stuttgart paleontological collections, indicates that this is not the case. Berckhemer cites the autobiography of Herr Eser, a contemporary and friend of Plieninger, in which it is stated that the type was found at Degerloch. Also, in his study of *Belodon* Plieninger (1852, p. 428, footnote) notes that the fossils came from the Grenzbreccia (= Rhaetic bonebed) at Degerloch. As pointed out in the section on Geology and Paleogeography, Plieninger's locality is approximately 0.5 km away from Sonnenberg bei Degerloch a site worked by E. von Huene.

In addition to the type PLIENINGER (1847) described a second, similar, but somewhat larger tooth. Currently the collection contains several small pieces of bonebed that are labled, "*Microlestes antiquus* Plien., verletztes Orig. z-PLIENINGER, Jahresb. 1847, Taf. I, fig. 4". A cusp and part of the base of a tooth are preserved in one of the fragments. The size and configuration of the cusp suggests it is part of the second specimen and part of a tooth of *Oligokyphus.*

The hypodigm of *Thomasia antiqua*, as revised by HAHN (1973), consists of two isolated teeth, the type specimen and GIT 1430/1. Their dimensions are as follows:

	Length (anteroposterior)	Width
Type	2.1	1.3
GIT 1430/1	1.7	1.0

E. VON HUENE (1933) referred two teeth found at Gaisbrunnen to "*Microcleptes?*" One (see ibid., Taf. I, Fig. 6) now is lost. The illustrations of this specimen suggest some similarities to teeth that have been tentatively identified as haramiyid incisors. The second specimen, which she identified as "*Microcleptes* (?) sp.", is a heavily worn haramiyid molariform (see ibid., Taf. I, Fig. 4) that is designated ?*Thomasia* sp. and described below.

Collections from the Rhaetic bonebed exposed at Olgahain, made in 1948 under the direction of Prof. O. H. SCHINDEWOLF, contain three teeth of haramiyids. Two were described by HAHN (1973) and identified, respectively, as *Thomasia antiqua* (GIT 1430/1) and *Thomasia* sp. 2 (GIT 1430/2). The third specimen (GIT 1541/1), described below, is another heavily worn molariform that can be tentatively referred to *Thomasia.*

Thomasia sp. 1 is based on a single molariform found in the *Plateosaurus*-Schichten of the upper middle Keuper near Halberstadt (HAHN, 1973). At the moment this fossil provides the oldest record of the Haramiyidae, and possibly the Mammalia.

? *Thomasia* sp.

Description: The crown of the haramiyid found at Gaisbrunnen and described by E. VON HUENE (1933, Taf. I, Fig. 4) is heavily abraided (Pl. 1:4). Except for the lining of its basin and small parts of the margin of the crown, most of the enamel has been removed. However, large parts of the two roots are preserved. The almost complete root under the basin is transversly broader than the other. Starting at about the vertical midpoint of the broader (?posterior) root and continuing to the base of the crown, a bony septum links the roots. Dimensions of the crown are as follows: length = 1.17 mm, width = .99 mm.

The enamel-lined basin occupies less than half of the occlusal surface of the tooth. Its rim is not complete but interrupted by a notch near the end of the crown over the broader root. The cusps have been worn away. What remains of their bases suggests the basin was closed at the other end of the crown by a major cusp or cusps. It can be argued, but not forcefully, that the basin was situated toward the posterior end of the tooth, its "U-shaped rim" was breached by wear, and the mound at the other end of the crown was formed by the bases of the anterior cusps of Rows A and B. This orientation would place the smaller root at the anterior end of the crown.

The third haramiyid specimen (GIT 1541/1, Pl. 1:3) collected under the direction of Prof. SCHINDEWOLF at Olgahain is more heavily worn than the others. Dimensions of its crown are as follows: length = 1.63 mm, width = 1.35 mm.

Large, apical wear facets mark the positions of the anterior two cusps of Row A. Unlike typical molariform teeth of *Thomasia* the first cusp of this row was about the same basal diameter and not significantly larger than the second, and these cusps are well separated. The third cusp of Row A appears to have been much smaller, a character of some teeth referred to *Thomasia* (SIMPSON, 1928).

The cusps of Row B are almost completely obliterated by a wear facet that slopes laterally at a low angle and is likely the result of greater development of facets of the kind illustrated by HAHN (1973, Fig. 1d). A small shelf at the front of the crown could be what remains of an anterior cusp. The enamel has been removed from the anterior end of the median valley. This appears to have been initiated by a wear facet that did not breach the "U-shaped rim". Only their bases are preserved, but these suggest the tooth was supported by a larger, broader, anterior and a smaller, posterior root.

Discussion: In summary, the current record of haramiyids from the Tübingen-Stuttgart area includes fossils from the Degerloch, Gaisbrunnen, and Olgahain localities. The taxa, or morphologically defined units, recognized are: *Thomasia antiqua, Thomasia* sp. 2 (HAHN, 1973), and ?*Thomasia* sp. The small collection contains no evidence of the presence of *Haramiya*, but this could easily be an artifact of the small sample size.

HALLAU LOCAL FAUNA, KANTON SCHAFFHAUSEN SWITZERLAND

All the fossils from the Rhaetic bonebed at Hallau discussed here are in the collection of the Paläontologischen Institut der Universität Zürich, and are part of the material obtained in a project carried out under the direction of Prof. Bernhard PEYER. To the best of my knowledge this is the only collection of small vertebrate fossils to be assembled from this locality. Descriptions of more than half the fragments of teeth of mammals or mammal-like reptiles in the collection were presented in a major monograph by PEYER (1965); the remainder is described here.

Systematics

Class Reptilia

No attempt has been made to thoroughly review the records of reptiles in the sample of the Hallau local fauna. However in going through the collections two points worthy of note became apparent.

Order Pterosauria

The teeth of most known pterosaurs are simple, conical structures that probably are only certainly identifiable when found in association with larger elements of the skull (see WELLNHOFER, 1978). In contrast, the dentitions of the few pterosaurs discovered in strata of Late Triassic (Norian) age include multicusped cheek teeth. Some of the cheek teeth of the Norian pterosaur *Eudimorphodon* Zambelli, 1973 (and see WILD, 1979) have crowns made up of as many as five cusps aligned anteroposteriorly and on first inspection resemble teeth of members of the mammalian order Triconodonta.

Dr. Rupert WILD, who has just completed a detailed study of *Eudimorphodon*, reviewed the illustrations of triconodont-like teeth in PEYER's (1956) monograph. He noted (pers. comm.) that some of the teeth PEYER designated "wahrscheinlich synapside Reptilien, Gruppe b" showed striking resemblances to cheek teeth of *Eudimorphodon* [for example: AIII-301 (PEYER, 1956, Taf. 12, Fig. 47), AIII-312 (ibid., Taf. 2, Fig. 58), and AIII-321 (ibid., Taf. 10, Fig. 67)]. Other teeth from Hallau that PEYER included in "wahrscheinlich synapside Reptilien, Gruppe a" resemble cheek teeth of a new, second genus of Norian pterosaur (WILD, 1979) and the Hettangian genus *Dimorphodon* [for example: AIII-272 (ibid., Taf. 9, Fig. 18), AIII-288 (ibid., Taf. 9, Fig. 34), AIII-320 (ibid., Taf. 5, Fig. 66), and AIII-322 (ibid., Taf. 10, Fig. 68)].

These teeth from Hallau share several morphological differences from the primitive conical pattern. In lateral view their crowns are relatively high (height of central cusp relative to anteroposterior basal length) and generally triangular in outline. Two, four, or possibly six (AIII-321, PEYER, 1956, Taf. 10, Fig. 67) cusps are symmetrically arranged on the anterior and posterior edges of the main cusp. On some teeth ridges on the lateral slopes of the cusps extend toward, but do not reach the base of the crown. No basal cingula are present. In occlusal view the teeth exhibit relatively little lateral expansion. As far as known all were supported by a large, single root (for example, AIII-320, ibid., Taf. 5, Fig. 66).

Dr. WILD's notations of morphological resemblance should not be interpreted as positive identifications of different genera of pterosaurs in the Hallau local fauna. Much more detailed research on the morphology and patterns of variation (both ontogenetic and individual) must be completed before identification of different pterosaur genera on the basis of isolated teeth can be attempted. PEYER (1956) is not alone among vertebrate paleontologists faced with the problem of identifying isolated, somewhat triconodont-like teeth of Late Triassic or Early Jurassic age who asked the question, are they teeth of primitive mammals or advanced mammal-like reptiles? Dr. WILD's observations require that the question now be phrased, are they teeth of primitive mammals, advanced mammal-like reptiles, or pterosaurs?

Order Therapsida

Family Tritylodontidae

The absence of identifiable remains, particularly fragments of teeth, of tritylodonts in the sample of the Hallau local fauna warrants special emphasis. These advanced mammal-like reptiles are common members of several Late Triassic and Early Jurassic local faunas. The possibility that their absence is the result of post-mortem sorting of skeletal elements according to size, either during deposition of the bonebed or collection, probably can be dismissed. A survey of part of the collection of bone fragments picked from the washing concentrates obtained at Hallau and samples of the original bonebed matrix revealed pieces of bone much larger than the cheek teeth of any known tritylodont. At the other end of the size range, isolated, individual cusps of teeth of morganucodontids and haramiyids, much smaller than the major cusps of tritylodontid cheek teeth were recovered. No fragments of teeth preserving the easily recognizable, selenodont-like cusps of tritylodonts are present in the collection. Thus, it seems most likely that the absence of tritylodontids is the result of biogeographic or ecological factors rather than postmortem sorting of the bone.

Class ?Mammalia
Order and Family incertae sedis
Tricuspes E. von Huene, 1933
Tricuspes cf. *tubingensis*

Referred material:

AIII-351 (NC 23), crown lacking root(s).

Description: One isolated tooth in the collection from Hallau closely resembles the type of *Tricuspes tubingensis*, but is slightly larger: crown length = 2.82 mm, crown width = 1.47 mm. Like the type, the central cusp is by far the largest and the three main cusps are not directly aligned one behind the other. Comparsion of occlusal views (Pl. 1:2a & 1:5a illustrates the more bulbous outline of the Hallau specimen and the absence of a cusp near the base of the presumed posterolabial side of the principal cusp. On the anterior base of the anterior accessory cusp, at the level of the maximum length of the crown, is a minute but distinct conule.

The apex of the anterior accessory cusp was lost by breakage, the apices of the other two main cusps appear to have been blunted by wear. No other wear facets can be unequivocally identified. Comparison of the lateral views of the two fossils (Pl. 1:2 b—c & 1:5 b—c) suggests the crown of the tooth from Hallau has a slightly more prominent basal constriction. Particularly on the lingual side of the tooth, what remains of its root shows a deep indentation indicative of at least the beginnings of subdivision.

Discussion: Reference of AIII-351 from Hallau to *Tricuspes* is based on similarities to the type in size and gross morphology; there are no unique, shared derived characters indicative of special phylogenetic relationship. Features distinguishing the two teeth would easily fall within the range of dental variation of a polyphyodont, advanced mammal-like reptile or of the diphyodont or monophyodont cheek teeth of an early mammal. Tentative allocation of *Tricuspes* to the Mammalia is also made on inconclusive evidence. The complexity of the morphology of the crown, particularly the slight angulation in alignment of the main cusps, and evidence suggesting the crown was supported by a partially divided root suggest, but do not demonstrate, mammalian affinity.

Family Haramiyidae

To date all fragmentary teeth of haramiyids found in the Tübingen-Stuttgart area that preserve enough of the crown to warrant identification at the generic level are referable to *Thomasia* with some degree of certainty. None show characters diagnostic of *Haramiya*. In contrast the larger sample from Hallau includes some teeth referable to *Thomasia* and *Haramiya* as well as a large collection of fragments that can only be identified as haramiyid. Again it should be stressed that as used here, *Haramiya* and *Thomasia* are names for different types of teeth that are assumed, primarily for the sake of convenience of description, to represent biological taxa. The conventions for orientation and terminology employed are those proposed by Hahn (1973).

Thomasia Poche, 1908
cf. *Thomasia antiqua* (Plieninger, 1847)

Referred material:

AIII-371 (NC 43), anterior end of Row B.
AIII-372 (NC 44), anterior end of Row B.
AIII-377 (NC 49), anterior end of Row B.
AIII-436 (NC 106), anterior end of Row B.

Revised diagnosis of *Thomasia antiqua:* Following Simpson (1928, p. 63—64), but recast in the terminology of Hahn (1973):

> The posterior cusp of Row A is small but distinct (minute to indistinct in *T. anglica*). Anterior cusp of Row B preceded by a well marked basal cuspule (a slight anterior cingulum not forming a distinct cusp in *T. anglica*). Anterior cusp of Row B followed by three well-differentiated, small cusps and then by a fourth, which is obscurely bifid (in *T. anglica* followed by 4 to 6 cusps, the last of which are posteromedial).

Description: The referred specimens include one or more cusps posterior to the largest cusp of Row B, but in none is the entire row preserved. Of the three AIII-371 is the most inclusive preserving what appears to be most of the basin-like depression anterior to the saddle, as well as the two cusps on either side of the largest cusp of Row B, which are of approximately the same size. Only part of the basin anterior to the saddle is preserved in AIII-372 and the cusp anterior to the largest cusp of Row B is distinctly smaller than that immediately behind this cusp. AIII-377 is smaller but otherwise very similar to this tooth.

AIII-436 requires special notice. It differs from the specimens just described in the smaller difference in size between the largest cusp of Row B and the two immediately adjacent to it. Discrete, in echelon wear facets are present on the lateral sides of the largest cusp of Row B and the cusp behind it. These facets are not in the same plane so could not have been produced by propalinal wear.

Discussion: Designation of these four specimens as cf. *Thomasia antiqua* rests solely on the basis that this is the only one of the four recognized haramiyid "species" in which a basal cuspule is thought to constantly occur anterior to the highest cusp of Row. B. A cusp in this position is usually not developed on teeth allocated to the other three "species". However, note that on AIII-309+314, described below and designated *Haramiya* sp., the anterior cingulum has a cusp-like terminus in front of Row B. The projection is admittedly much smaller than the cusps on the four specimens referred to cf. *Thomasia antiqua*. Also PARRINGTON (1947, p. 712—713) noted that a small cusp was present anterior to the largest cusp of Row B on the lectoholotype of *Haramiya moorei* (M211), but apparently is not a constant feature of the crowns of the other eight teeth referred to this species by SIMPSON (1928). The difficulty in taxonomic assignment of these four specimens from Hallau not only reflects their fragmentary condition but also stems from the typological nature of the named taxa of haramiyids. It underscores our lack of understanding of even the basic morphology and ranges of variation of haramiyid dentitions.

Thomasia anglica SIMPSON, 1928

Referred material:

AIII-295 (XLI, Taf. 1), anterior end of crown.

Description: AIII-295 (PEYER, 1956, Taf. 1, Fig. 41) appears to be the anterior end of the crown of a haramiyid molariform. The largest cusps of both rows are at the preserved end of the crown, those posterior to them are of lesser height. The highest cusp is taken to be the anterior cusp of Row A. It and the second cusp of Row A are larger and more widely spaced than their counterparts in Row B. Low but distinct, irregular ridges are present on the medial sides of the cusps of Row A and the posterior sides of cusps of Row B.

Anterior to the largest cusp of Row B is a narrow cingular ledge that is abruptly terminated laterally producing a small conule. This cingulum continues across the crown onto the anterior slope of the first cusp of Row A where there is a cusp-like irregularity in the crest. Unfortunately the posterior end of the crown of this tooth is missing and the number of cusps in the two rows cannot be determined. Maximum width of the crown is 1.72 mm.

Discussion: Reference of this tooth to *Thomasia* is based on the distinctly smaller size of the second cusp in Row A relative to the first. Allocation to *T. anglica* recognizes the absence of a distinct basal or cingular cusp at the anterior end of Row B. In PEYER's (1956, Taf. 1) Figure 41 b of the anterior end of the crown, the end of the anterior cingulum in front of Row B is given an unwarranted cusp-like appearance. Figures 41a and 41c (ibid.) are more accurate representations of its morphology. The other two characters in the diagnosis of *T. anglica* require knowledge of the total number of cusps in each row and the morphology of the posterior end of the crown. Neither can be determined because of damage to the specimen. Thus, the reference of this tooth to a "species" otherwise known only from England rests solely on the absence of a distinct basal cusp anterior to Row B. The presence or absence of such a cusp could easily be a matter of individual variation.

The small, irregular ridges in the enamel on the medial slopes of cusps of Row A and posterior slopes of cusps of Row B of AIII-295 are a minor exception to a criterion for distinguishing the teeth of haramiyids from those of multituberculates noted by HAHN (1973). Prior to this study ridges in the enamel had not been observed on teeth of haramiyids. Whether or not this occurrence should be interpreted as the first indication of a derived character better developed in members of the Multituberculata and evidence of an ancestor-descendant relationship of these groups remains to be determined.

?*Thomasia* sp.

Referred material:

AIII-308 (LIV, Taf. 2), posterior end of crown.

Discussion: AIII-308 (PEYER, 1956, Taf. 2, Fig. 54) is a fragment of the posterior end of a molariform possibly slightly smaller than AIII-295, which is allocated to *Thomasia anglica*. Identification beyond the level of haramiyid is based on the following tenuous interpretations. As oriented in Figure 54 a (ibid.) the cusps of the upper (in the figure) row are identified as part of Row A, which extends almost to the posterior end of the crown. If this identification is correct, the posterior cusp of Row A appears to have been much smaller than the middle cusp, a characteristic distinguishing *Thomasia* from *Haramiya*.

cf. *Thomasia* sp.

Referred material:

AIII-323 (LXIX, Taf. 12), posterior end of crown.

Description: Probably AIII-323 (PEYER, 1956, Taf. 12, Fig. 69) consists of at least half of the posterior end of the crown of a molariform. A row of one complete and half of another cusp (to the left in

Fig. 69, ibid.) appears to be what remains of Row A. Row B is represented by four cusps of approximately the same basal diameter and individual height but increasing anteriorly in elevation on the crown. At the preserved end of the crown a small basal cusp is present on the slope of the terminal cusp of Row A. It is linked to a small central cusp and that to the terminal cusp of Row B by low crests. Maximum width of the preserved part of the crown, measured perpendicular to the central basin is 2.12 mm.

Discussion: The absence of a low crest or higher saddle directly linking the terminal cusps of the two rows, the consequent absence of any indication of an anterior cingulum or basin and, in occlusal view, the sinuous outline of the crown all support Peyer's view that the fragment preserves the posterior end of the crown. Comparison of the specimen to *Thomasia* is suggested because of the apparent decrease in size of the last two cusps in Row A and closure of the central basin by two small cusps.

The tooth is large for a haramiyid molariform and its sides are not parallel. On the outside of Row A the crown had prominent lateral bulges around the slopes of the last two cusps. In contrast, on the outside slope of Row B there is a noticeable bulge around the base of only one cusp. This irregularity in occlusal outline broadly resembles that of the type of *Haramiya fissurae*, but on detailed comparison many differences become apparent.

Haramiya Simpson, 1947

Teeth allocated to this genus differ from those of *Thomasia* in the following respects (a formal diagnosis is given by Simpson, 1928, p. 55): The three cusps of Row A are of approximately equal size or the presumed anterior cusp is smaller than the other two. Row B consists of a single, large anterior cusp followed by three or four progressively smaller cusps.

Haramiya moorei (R. Owen, 1871)

Referred material:

AIII-269 (XV, Taf. 1), anterior end of crown.

AIII-309+314 (LV & LX, Taf. 1, Fig. 3), crown of molariform.

Two fragments of a haramiyid molariform were described separately by Peyer (1956): AIII-314 (ibid., Taf. 1, Fig. 60) is the anterior end, AIII-309 (ibid., Taf. 1, Fig. 55) is the posterior end. The fragments are now glued together and form the most complete haramiyid tooth in the Hallau sample.

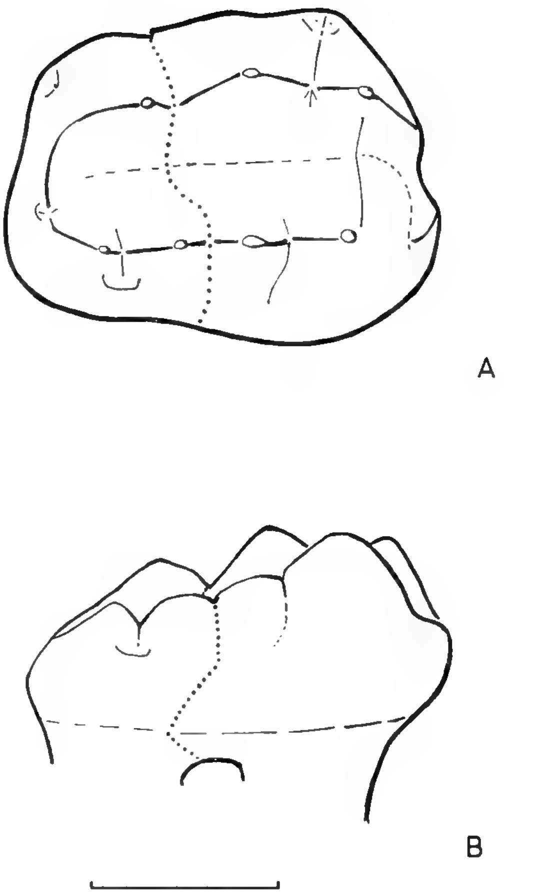

Figure 3: Outline drawing of AIII-309+314, *Haramiya moorei,* Hallau local fauna, Switzerland. Regularly dotted line marks the trace of the fracture. A. occlusal view, B. lateral view. Scale equals 1 mm.

Description: Row A of AIII-309+314 consists of three cusps of approximately equal height; the anterior is only slightly lower in height than the other two. This row of cusps is not fully aligned, the apex of the middle cusp is slightly lateral to those of the terminal cusps (Fig. 3). In occlusal view the edge of the crown lateral to Row A is bowed outward. Below and posterior to the anterior cusp of Row A is a distinct expansion of the crown forming an almost cusp-like basal cingulum (note Peyer, 1956, Taf. 1, Figs. 60a & 60c). Row B consists of four cusps of which the first is distinctly higher and larger than the other three. The lateral side of Row B is expanded and bulbous except for the groove separating the third and fourth cusps, which is deep and forms a cup-like depression.

The central valley is straight from the relatively low saddle linking the anterior cusps of Rows A and B to the "U-shaped rim". Anterior to the saddle is a small basin limited anteriorly and laterally by crests but extending without interruption to the edge of the crown (ibid., Fig. 60a). In front of Row B the crest is expanded but a distinct cusp does not appear to have been present. The anterior basin appears to be larger and better defined, at least laterally, than that of the molar of *H. moorei* illustrated by Simpson (1928, Fig. 14), but the morphology of this area of the crown differs among the teeth in Simpson's hypodigm (ibid., p. 58). At the posterior end of the crown a crest extends from the base of the last cusp of Row A posteriorly then medially to meet the base of the last cusp of Row B. At the posterior end of Row A the side of the crown has lost some chips of enamel, but clear evidence of a small basal cusp posterior to the last cusp of Row A (Peyer, 1956, Taf. 1, Fig. 55a) is present.

In occlusal view the tooth has an irregularly rectangular outline (Fig. 3). Crown dimensions are as follows: length = 2.23 mm, maximum width of crown across anterior cusps of Rows A and B = 1.83 mm, width at posterior end of Row A = 1.58 mm. The crown was supported by two transversely expanded roots. Just below the crown the broken surfaces of the roots have figure-eight outlines suggesting that at a greater distance from the crown both would have bifurcated.

Discussion: The relative proportions of the cusps of both Rows A and B clearly justify reference of AIII-309+314 to *Haramiya*. Morphologically the specimen appears to be easily encompassed within the range of variation of *H. moorei*.

Bases for reference of AIII-269 (Peyer, 1956, Taf. 1, Fig. 15) to *H. moorei* are very tenuous. If the complete cusp and the partial cusp shown above and to the right in Peyer's Figure 15 a (ibid.) are taken to be cusps of Row A and the other partial cusp identified as the first cusp of Row B, comparison of AIII-269 to the slightly smaller AIII-309+314 reveals some similarities. The first cusps of the two rows are linked by a saddle that is only slightly higher than the saddle of AIII-309+314. On AIII-269, anterior to the first cusp of Row A, what is preserved of a small basal cingulum could be part of the margin of an anterior basin. Resembling AIII-309+314 lateral to the presumed cusps of Row A are several small basal cusp-like expansions.

Haramiyid ?gen. et sp.

Referred material:

AIII-307 (LIII, Taf. 2), fragment of crown with Row A.

AIII-370 (NC 42, Fig. 4), fragment of crown with Row B.

Description: AIII-307 (Peyer, 1956, Taf. 2, Fig. 53) has been damaged since it was illustrated. It appears to have consisted of an entire Row A of a small molariform, crown length = 1.3 mm (measurement from figure). The three cusps of Row ?A were not well separated and of strikingly similar size and height. One cusp of Row ?B appears to have been preserved. It is illustrated as being linked to a terminal cusp of Row ?A by a low crest, possibly the anterior saddle.

AIII-370 consists of one row of cusps of another small haramiyid molar (Fig. 4), crown length = 1.98 mm. Apparently it was part of a relatively wide tooth. The maximum width of the fragment measured from the midline of the central valley to the edge of the crown is approximately 0.8 mm. One terminal cusp is decidedly higher than the other three cusps suggesting Row B is preserved. A saddle linking the anterior cusps of Rows A and B, if present, must have been small. A small fragment of a shelf-like cingulum suggests the anterior basin was also small.

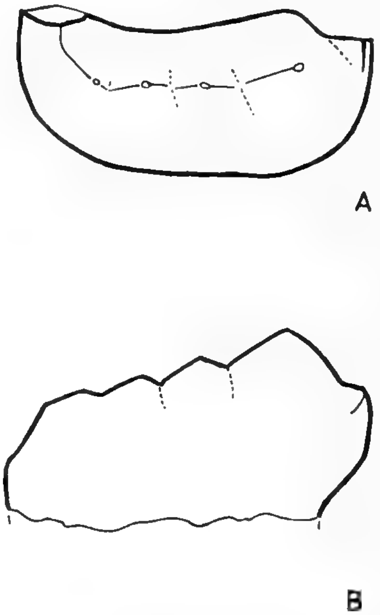

Figure 4: Outline drawing of AIII-370, haramiyid ?gen. et sp., Hallau local fauna, Switzerland. A. occlusal view, B. lateral view. Scale equals 1 mm.

Discussion: These two fragments are parts of relatively small haramiyid molariforms. If AIII-307 is correctly identified as preserving Row A, the cusps show the morphology characteristic of *Haramiya*, but the tooth was smaller than the smallest molariform referred to *H. moorei* by Simpson (1928; M217, crown length = 1.7 mm). If AIII-370 preserves Row B it preserves no characters allowing a choice in allocation to either *Thomasia* or *Haramiya*. The two specimens are grouped here simply to recognize their similar, relatively small size.

Other fossils possibly representing haramiyids: For the sake of completeness the following, slightly annotated list of fragments of haramiyid or haramiyid-like molariforms is included:

AIII-256 (II, Taf. 12), several cusps. PEYER (1956, p. 9) thought this was not a fragment of a mammalian or mammal-like reptile tooth. The cusps resemble those of some haramiyid or morganucodontid teeth. The morphology of the base of the crown is now obscured by glue.

AIII-257 (III, Taf. 12), a cusp. Possibly this is part of a large haramiyid molariform.

AIII-285 (XXXI, Taf. 7), possibly a side of a haramiyid molariform.

AIII-299 (XLV, Taf. 2), two small cusps, probably haramiyid.

AIII-306 (LII, Taf. 2), a large cusp and parts of two others that might be a fragment of a large haramiyid molariform.

AIII-315 (LXI, Taf. 2), a row of two complete and two fragments of cusps, possibly the posterior end of Row B of a tooth the size of AIII-309+314, *Haramiya moorei.*

AIII-374 (NC 46), part of a row of large cusps from a haramiyid molariform.

AIII-388 (NC 58), one and a half cusps, possibly haramiyid.

AIII-417 (NC 87), one and a half cusps, possibly haramiyid.

AIII-429 (NC 99), a large cusp, possibly haramiyid.

AIII-461 (NC 131), heavily abraided crown of a haramiyid molariform. Probably the posterior end is preserved. The root is transversely broad and has a figure-eight cross section.

AIII-491 (NC 161) probably preserves part of Row B. The cusps are large, inflated, closely approximated, and separted by deep, narrow clefts. The longitudinal crest connecting the apices of the cusps is sharp and forms carnassial notches where it passes from one cusp to another.

Isolated teeth that might include incisors or canines of haramiyids are noted below in the section on *Helvetiodon schutzi,* sp. et gen. nov.

Class Mammalia
Order Triconodonta
Family Morganucodontidae

The taxonomy and nomenclature of the Morganucodontidae has been reviewed elsewhere (CLEMENS, 1979). The conclusions of this review are that the known morganucodontids can be allocated to four genera of which the following three are monotypic: *Eozostrodon parvus* from Somerset, England, and *Erythrotherium parringtoni* and *Megazostrodon rudnerae* from Lesotho. *Morganucodon* includes three named species: *M. watsoni,* the common but possibly not the only species represented in the fissure fillings in Wales, Great Britain, and *M. oehleri* and *M. heikuopengensis* from China. A molariform of a morganucodontid from the Bathonian (mid-Jurassic) Forest Marble of England was illustrated by FREEMAN (1976, Fig. 1 g) and later allocated to a new genus and species, *Wareolestes rex* (Freeman, 1979).

Among the vertebrates in the Hallau local fauna currently only the morganucodontids and morganucodontid-like species can be classified as members of the Mammalia with reasonable confidence. For the most part this is not based upon the evidence provided by the fossils from Hallau, but on the close resemblances of these isolated teeth to those of morganucodontids from other areas that are known from much more complete material.

Morganucodon KÜHNE, 1949
Morganucodon peyeri, sp. nov.

Etymology: Dedicated to the late Prof. Bernhard PEYER.

Type specimen: AIII-329 (NC 1, Pl. 2:1), slightly damaged, probably left, lower molariform preserved in a fragment of dentary.

Type locality: Hallau bonebed, Kanton Schaffhausen, Switzerland.

Diagnosis: A small morganucodontid with molariform teeth smaller than those of *Morganucodon oehleri* but approximately the same size as those of *M. watsoni,* however, their crowns appear to be relatively narrower than those of the latter species. Buccal and lingual cingula of upper molariforms tend to be more weakly developed than those of *M. watsoni* and *M. oehleri* and the buccal more frequently interrupted across the base of the principal cusp. Resembling *M. watsoni,* but not *M. oehleri,* the lingual cingulum of the lower molars of *M. peyeri* is relatively well developed. Possibly the presence of a large, anterolingual cingular cusp, almost as large as the anterior accessory cusp, might separate *M. peyeri* from the other species. No evidence of buccal cingula, present on a very few lower molars of *M. watsoni* (PARRINGTON, 1971) and on some of the few described molars of *M. oehleri* (MILLS, 1971), has been found in the small sample of *M. peyeri.*

Referred material:

Upper molariform teeth

AIII-255 (I, Taf. 3), principal and posterior accessory cusp, left.

AIII-264 (X, Taf. 4), anterior accessory cusp, left.

AIII-267 (XIII, Taf. 4), posterior accessory cusp and part of principal cusp, right.

AIII-279 (XXV, Taf. 4), fragment of last molariform, left.
AIII-283 (XXIX, Taf. 4), posterior accessory cusp, left.
AIII-292 (XXXVIII, Taf. 4), anterior accessory cusp, right.
AIII-310 (LVI, Taf. 3), principal and posterior accessory cusp in fragment of maxilla, left.
AIII-324 (LXX, Taf. 12), principal and posterior accessory cusp, left.
AIII-428 (NC 98), posterior accessory cusp?

Lower molariform teeth

AIII-266 (XII, Taf. 4), principal cusp and kühnecone, left.
AIII-273 (XIX, Taf. 4), posterior accessory cusp and kühnecone, right.
AIII-280 (XXVI, Taf. 4), fragment with kühnecone, left.
AIII-284 (XXX, Taf. 4), possibly fragment of anterior end of crown, right.
AIII-296 (XLII, Taf. 4), anterior accessory cusp, right.
AIII-319 (LXV, Taf. 5), principal cusp, kühnecone, and posterior accessory cusp, left.
AIII-380 (NC 50), principal cusp, kühnecone, and posterior accessory cusp, left.
AIII-480 (NC 150), anterior accessory cusp and part of principal cusp, left.

Premolariforms

AIII-258 (IV, Taf. 6), posterior lower premolariform, left.
AIII-261 (VII, Taf. 2), posterior lower premolariform, left.
AIII-263 (IX, Taf. 6), upper premolariform, right.
AIII-277 (XXIII, Taf. 6), premolariform.
AIII-278 (XXIV, Taf. 6), premolariform.
AIII-282 (XXVIII, Taf. 6), premolariform.
AIII-335 (NC 7), posterior lower premolariform, left.
AIII-336 (NC 8), upper premolariform, left.
AIII-350 (NC 22), premolariform.
AIII-368 (NC 40), upper premolariform, left.
AIII-423 (NC 93), premolariform.
AIII-441 (NC 111), premolariform.
AIII-460 (NC 130), upper premolariform.
AIII-509, upper premolariform.

Upper molariforms: The available sample from Hallau lacks examples of complete upper molariform teeth, and the problems of identification and orientation of the fossils are challenging. Criteria developed for orientation of isolated teeth of *Morganucodon watsoni* (see, for example, Mills, 1971) stem from studies of teeth found in maxillary fragments, but unfortunately do not always go into the detail necessary for analysis of isolated teeth. In the following paragraphs the criteria for orientation of the upper molariform teeth are evaluated in a description of the dental morphology. The position in the dentition and orientation of many of the fragments proposed here (see list of referred specimens) differ from those suggested by Peyer (1956). Although usually in agreement on identification of specimens as upper and lower molariforms and on determination of their bucco-lingual orientation, we frequently differ on identification of the anterior and posterior ends of the crowns.

Resembling *M. watsoni,* teeth identified as upper molars of *M. peyeri* have three main cusps aligned mesiodistally with the principal (central) cusp larger and higher than either the anterior or posterior accessory cusp. Differences in their height are not as great as those distinguishing the main cusps of the lower molars. A second criterion applied in identification of upper molars is the presence of both buccal and lingual basal cingula. Mills (1971, p. 37) noted, "although the cingulum is continuous around the unworn tooth [upper molars of *M. watsoni*], it rapidly wears away on the lingual side". Upper molars of *Erythrotherium* and *Megazostrodon* are also characterized by the presence of both cingula but they show greater variation in development. A central break or gap interrupts the buccal cingula of M^{1-2} of *Megazostrodon* and M^1 of *Erythrotherium.* Fragments of molariform teeth allocated to *M. peyeri* with both buccal and lingual cingula (structures more extensive than simply cusps on the sides of the anterior and posterior ends of the crown) have been identified as upper molariforms. Apparently unlike *M. watsoni,* but similar to *Megazostrodon* and *Erythrotherium,* the buccal, and less frequently lingual cingula of unworn upper molariforms of *M. peyeri* are not always continuous along the total length of the crown. In the few instances where the principal and one accessory cusp are preserved and their relative size and height can be determined, the teeth having the cusp proportions taken as characteristic of upper molariforms always have both lingual and buccal cingula.

Parrington (1973, 1978) noted another criterion for differentiating upper from lower molars of *M. watsoni;* this is a feature of the morphology of their roots. The anterior root of an upper molar of *M. watsoni* tends to be oval in cross section with its long axis oriented anteroposteriorly while the posterior root has the long axis of its oval cross section oriented transversely. The long axes of cross sections of both roots of lower molars are oriented anteroposteriorly. This criterion does not appear to be fully applicable to upper molariforms of *M. peyeri.* On some (e. g., AIII-310) the posterior root, identified on criteria of crown morphology, is transversely expanded, but on others (e. g., AIII-283 and the posterior root of the tooth preceding the molar preserved in AIII-310 [Peyer, 1956, Taf. 3, Fig. 56 e]) it is not. These dissimilarities might reflect differences in ontogenetic stage, transverse expansions being a characteristic of older animals; position in the dentition; or perhaps the expansion is a derived morphology that did not characterize all members of *M. peyeri.*

On the basis of the morphology of AIII-310 (Peyer, 1956, Taf. 3, Fig. 56), the only fragment of an upper molariform preserved in a bit of the maxillary bone and, where applicable, comparisons with *M. watsoni, Erythrotherium,* and *Megazostrodon,* several criteria appear to be available for distinguishing the buccal and lingual sides of the crown. First, the buccal cingulum is usually wider than the lingual and surmounted by more and larger cusps. The degree of difference in these features, if any, varies between teeth. Mills (1971) noted that in *M. watsoni* development of the buccal cingulum varies along the tooth row being proportionately widest on the anterior molars. The few available fossils of *M. peyeri* suggest its buccal cingulum is more frequently interrupted across the slope of the principal cusp than the lingual.

Secondly, when viewed in transverse section, the apices of the principal and accessory cusps are not situated over the midpoint of the crown but are displaced lingually. Likewise the lingual slope of these cusps rises more steeply and is less convex than the buccal. Particularly on the slopes of the principal cusp, the labial cingulum is situated higher (nearer the apex of the cusp) than the buccal.

Finally, the general occlusal pattern of therapsids and mammals suggests that wear facets might be found on the lingual side of the upper molars, produced by contact with the labial sides of the lowers. Unfortunately, there is clear evidence that the bones concentrated in the Hallau bonebed underwent considerable post-mortem abrasion. Although some teeth show apical facets on the cusps that were most likely formed by abrasion with food, I have not been able to unequivocally identify wear facets on sides of any molariform upper teeth. The only possible exceptions are AIII-267 (Peyer, 1956, Taf. 4, Fig. 13) where one side of the crown is heavily abraided, and possibly AIII-310 (ibid., Taf. 3, Fig. 56), where cusps of the lingual cingulum might be blunted by wear.

Criteria utilized for identification of the anterior and posterior ends of the crown are even more uncertain for the fragment of maxillary preserved with AIII-310 does not give any information about its anteroposterior orientation. Usually in cheek teeth of early mammals the anterior edges of the main cusps do not rise as steeply, are more convex, and are longer than the posterior. This criterion usually appears to be applicable to at least the principal and anterior accessory cusps.

Mills (1971) noted that the anterior accessory cusp is lower than the posterior on M^{1-2}, almost equal on M^3, and quite equal on M^4 and presumed M^5 of *M. watsoni.* Unfortunately none of the fragments of teeth from Hallau preserve both accessory cusps. However the relative depths of the notches separating the main and accessory cusps can be determined. Like upper molars of *Morganucodon watsoni* the notch separating the anterior accessory cusp from the principal cusp appears to have been slightly deeper than that separating the principal and posterior accessory cusp.

In triconodontids the cheek teeth are interlocked by a projecting cusp on the posterior end of one tooth and a groove or basin, usually bounded by buccal and lingual cusps, on the anterior end of the following tooth. This mechanism is weakly developed in *M. watsoni* (Mills, 1971) where the anterior end of a molariform can slightly overlap the buccal side of the preceding tooth. On some upper molariforms of *M. peyeri* (e. g., AIII-310) the end of the crown with a projecting cingular cusp is supported by a transversely wide root; in others (e. g., AIII-283) the root at this end of the crown is elongated in an anteroposterior direction.

In his attempts to distinguish the anterior and posterior ends of the crown Peyer (1956) considered the position of the edge of the crown relative to the underlying root. He thought that characteristically the "anterior" end of the crown juts forward, balcony-like, in advance of the "anterior" face of the root, while the "posterior" accessory cusp is more directly situated over the "posterior" root and the back of the crown is almost in line with the back of the root. On the basis of the other criteria adopted here some of the anteroposterior orientations proposed by Peyer must be reversed and the balcony-like projections of the crowns of some teeth (e. g., AIII-255) are considered to be at the posterior end of the crown. However, the projections of the crown on what are thought to be posterior ends of other teeth are not as extreme and match those of fragments of the anterior end of the crown (e. g., AIII-292). As is the case with orientation of the maximum diameter of the root, the relationship of the margins of the root to the crown in *M. peyeri* might be diagnostic in some instances, but the morphology of the roots could be more variable than morphology of the cusps, and might require information on ontogenetic stage of the tooth before being applied.

In summary, most of the smaller fragments appear to pertain to molariform teeth similar to AIII-255 and AIII-310. A composite upper molariform can be briefly characterized as being dominated by three main cusps, of which the principal is higher than either the anterior or posterior accessory cusps. Probably on any tooth the posterior accessory cusp is as large as, if not larger than, the anterior and separated from the principal cusp by a shallower notch. The apices of these cusps are displaced toward the lingual side of the crown. Cusp development on the broad buccal cingulum varies, but usually the cusps are larger and more numerous than those on the narrower lingual cingulum. Apparently, the larger buccal cingular cusps are situated on the posterior part of the cingulum. When viewed in a transverse section, the lingual cingulum is higher (closer to the apices of the main cusps) than the buccal and the lingual slopes of the cusps are steeper than the buccal. At the posterior end of the crown a cingular cusp projects distally to form a weak interlocking mechanism with the depression in the anterior end of the next (posterior) molariform tooth. Two well separated, slightly diverging roots support the crown. In at least a few specimens the anterior root is anteroposteriorly elongated while the posterior is transversely widened.

One fragmentary tooth differs from this generalized pattern. AIII-279 (Peyer, 1956, Taf. 4, Fig. 25) is heavily damaged and beyond the presence of a large central cusp and anterior and posterior accessory cusps, little can be said about the morphology of its crown. However, the crown appears to have been supported by two closely approximated roots. As Peyer (1956, p. 26—27) suggested, what remains of the tooth is not unlike the posterior upper molars of triconodonts and, in a general way, resembles last upper molariform teeth of *M. watsoni*.

Lower molariforms: A fossil consisting of a damaged molariform and fragment of a mandible (AIII-329, Pl. 2:1) is the most complete mammalian specimen in the collections made by Prof. Peyer after he prepared his 1956 monograph and has been chosen as the type specimen of *Morganucodon peyeri*. This and AIII-319 (Peyer, 1956, Taf. 5, Fig. 65), a fragment consisting of the principal cusp and posterior end of the crown, are the basis for reconstructing the morphology of the lower molariform teeth. Fortunately the bone associated with AIII-329 is clearly a fragment of dentary and both these molariforms preserve the kühnecone, which identifies both the lingual and posterior sides of the crown. Unlike upper molariforms referred to *M. peyeri*, there appears to be little question concerning the anteroposterior and lateral orientation of the lowers.

Resembling the upper molariform teeth, the crown of the lowers consists of three main cusps essentially aligned anteroposteriorly with the principal (central) cusp distinctly larger and higher than the anterior and posterior accessory cusps. Of the two accessory cusps the posterior is the larger. In one fragment (AIII-380) the notch separating the principal and posterior accessory cusps ends in a deep cleft similar to the carnassial notch of therian carnivores. AIII-319 demonstrates the presence of a posterior cingular cusp behind and in line with the posterior accessory cusp; AIII-329 (Pl. 2:1) is damaged in this region but almost certainly had a distinct posterior cingular cusp. The posterior cingular cusp of AIII-273 (Peyer, 1956, Taf. 4, Fig. 19) is slightly more prominent than that of AIII-319.

The buccal side of the crown lacks any indication of basal cusps or cingula. In contrast, on the anterolingual side of the crown there are two cusps on AIII-329. The anterior is the larger of the two and is situated beside but slightly in advance of the only somewhat larger anterior accessory cusp. In occlusal view the anterolingual cingular cusp and anterior accessory cusp bound a shallow concavity in the anterior end of the crown, which probably received the posterior cingular cusp of the preceding molar. If correctly referred to *M. peyeri*, AIII-296 (Peyer, 1956, Taf. 4, Fig. 42) demonstrates the development of an interdentinal wear facet on the front of the crown below and between the anterolingual cingular cusp and anterior accessory cusp.

On both AIII-319 and AIII-329 part of the lingual slope of the principal cusp extends to the base of the crown without interruption by a cingulum. The kühnecone of AIII-329 is relatively larger than that of AIII-319, but both are distinct cusps separated by a cleft from the posterolingual side of the principal cusp.

Behind the kühnecone of AIII-319 are four cingular cusps generally increasing in height and size posteriorly. The most posterior of these lies lingual to the largest posterior cingular cusp, which is situated behind the posterior accessory cusp. The area of the crown between the kühnecone and the posterior cingular cusp shows considerable variation in the development of small cingular cusps. AIII-319 has a high number of cusps while, at the other extreme, on AIII-380, although a cingulum links the kühnecone with the posterior cingular cusp, no individual cusps are present between them.

The crown is supported by two roots but AIII-319 and AIII-329 give little information concerning their morphology. Peyer (1956) identified AIII-280 (ibid., Taf. 4, Fig. 26) as a last upper molariform but more likely it is a fragment of a lower molariform. His figures of the root of this specimen show the suggestion of a blunderbuss-like expansion of the tip of the root.

As was the case with the upper molars, the only unambiguous traces of dental wear are facets on the apices of some cusps (e. g., AIII-266, Peyer, 1956, Taf. 4, Fig. 12). The fragment of dentary of AIII-329 is heavily damaged. A groove along its ventrolingual edge might be what remains of a trough for accessory mandibular bones or, with equal uncertainty, it might be simply an artifact of postdepositional crushing.

Dimensions of molariforms: An accurate assessment of the size of the upper molariforms cannot be made on the basis of the present sample because of the lack of complete teeth. Several specimens are made up of the principal cusp, one accessory cusp, and, infrequently, part of the base of the missing accessory cusp. The range of variation in length of the preserved parts of their crowns is from approximately 1.2 to 1.5 mm. The longest fragment of crown is that of AIII-310, which is the least damaged tooth. Probably it had a maximum crown length of approximately 1.6 to 1.7 mm.

Width of the crown of the upper molars of *M. watsoni* varies according to the relative development of the buccal and lingual cingula and the amount of wear on the lingual side of the crown. The same sources of variation could influence measurements of the width of molars of *M. peyeri*. In order to get an approximation of average crown width of the upper molariforms of the latter species, the maximum widths of the fragments were measured with the following results: N = 7, OR = .48—.70 mm, M = .58 mm.

Only slightly more data on the dimensions of the lower molariforms of *M. peyeri* are available. The perimeter of the crown of one lower molariform, AIII-329, is intact and its dimensions are: length = 1.65 mm, width = .62 mm. Maximum widths of the fragments of lower molariforms were measured with the following results: N = 6, OR = .59—.66 mm, M = .64 mm.

While making comparisons of the fragmentary teeth of *M. peyeri* with a small reference collection of teeth of *M. watsoni* it appeared that the teeth of *M. peyeri* were longer (anteroposteriorly) and relatively narrower (transversely). With so little data available on the dimensions of the teeth of *M. peyeri* it is, of course, impossible to make any rigorous comparisons. However, to see if there was any basis for this impression of differences in proportions, a series of teeth of *M. watsoni* were measured. These teeth are all from Pontalun Quarry, Wales (see KERMACK et al., 1973) and are preserved in mandibles so that their position in the dental arcade could be determined on criteria other than the individual morphology of their crowns. These specimens are in the collections of the British Museum (Natural History); Department of Zoology, University College London; and Museum of Zoology, Cambridge University. My analysis was focused on the question, to what extent, if any, do the teeth of the species of *Morganucodon* represented at Hallau differ in coronal dimensions from those of the sample of *M. watsoni* recovered from Pontalun Quarry? It is not a substitute for a still needed, thorough taxonomic study of the species of *Morganucodon* represented in the collections from Pontalun and other fossil localities in southern Wales.

As has been recognized by others (e. g., see MILLS, 1971, PARRINGTON, 1971) the longest molariform teeth of *M. watsoni* are M^2 and M_2. The data on the dimensions of these teeth obtained from a study of the Pontalun sample are given in Table 1. Their coefficients of variation are high. This could reflect taxonomic heterogeneity, the mechanical difficulties of obtaining precise measurements of such small teeth, or both.

Table 1

Comparisons of dimensions of molariform teeth of *Morganucodon watsoni*, Pontalun Quarry, and *M. peyeri*, Hallau local fauna.

	N	OR	M	S	CV
Morganucodon watsoni					
M^2					
Length	16	1.10-1.61	1.37	.15	10.7
Width	11	.55- .84	.68	.09	13.8
M_2					
Length	14	1.17-1.65	1.43	.13	9.1
Width	14	.59- .81	.69	.07	10.1
Morganucodon peyeri					
Lower molariform, AIII-329					
Length	1.65				
Width	.62				

Comparison of the dimensions of AIII-329 with the data on M_2 of *M. watsoni* (Table 1) shows that its crown is as long as the longest M_2 in this sample from Pontalun, but its transverse width, 0.62 mm, is less than the mean value. The mean breadths of the fragments of molariforms of *M. peyeri*, 0.58 mm for the upper and 0.64 mm for the lower, are smaller than the means of M^2, M^3, M_2 and M_3, but larger than means of M^1 and M_1 of *M. watsoni*. However, the first molariforms of *M. watsoni* are short (anteroposteriorly) with mean lengths of only 1.13 mm and 1.20 mm respectively.

Visual comparisons of apparently homologous parts of fragments of teeth of *M. peyeri* and *M. watsoni* suggest the molariform teeth of *M. peyeri* tend to be longer and relatively narrower than those of *M. watsoni*. When compared to a sample of *M. watsoni* from Pontalun, Wales, the few dimensions that can be obtained from the fossils from Hallau appear to substantiate this impression.

Premolariform teeth possibly referable to *Morganucodon peyeri*: Considering the relative abundance of its molariform teeth, most likely premolariform teeth of *M. peyeri* are included in the collection from Hallau. The small premolariform teeth described in this section are all of the simple, trenchant morphology that would be expected in the dentition of a morganucodontid. However, *M. peyeri,* is not the only morganucodontid present in the sample from Hallau and there are several other kinds of animals, be they mammal-like reptiles or mammals, represented that might also have had such simple, premolariforms in their dentitions. Grouping the descriptions of these teeth in this section is primarily a literary convenience and only secondarily a suggestion of possible zoological affinities.

AIII-258 (Peyer, 1956, Taf. 6, Fig. 4), AIII-261 (ibid., Taf. 2, Fig. 7), and AIII-335: Assuming the pattern of variation in length of the postcanines of *M. peyeri* is similar to that of *M. watsoni,* these premolariforms are of a size appropriate for posterior lower premolariforms of *M. peyeri* (OR length = 1.15—1.25 mm). The principal cusp of each tooth has a high trenchant crown suggesting it is part of the lower dentition. Two of the three specimens had a low anterior basal cusp. Basal cingula are lacking on the buccal and lingual side of the crown. Two low posterior cusps are present, one directly behind the principal cusp, the other more posterior and lingual in position. To this extent these premolariforms resemble P_4's of *M. watsoni,* but the premolars of *M. watsoni* usually (Mills, 1971) have two anterior basal cusps, a short anterolingual cingulum, and a small kühnecone. No premolariforms resembling P_4's of *M. watsoni* in these details have yet been discovered at Hallau. Whether the absence of additional anterior basal cusps and a kühnecone on P_4 of *M. peyeri* is a characteristic of this species or whether the lower posterior premolariform of *M. peyeri* has not been discovered, of course, cannot yet be determined.

One of the premolariforms, AIII-258 (Peyer, 1956, Taf. 6, Fig. 4) lacks enamel on the buccal side of the posterior accessory cusp. This might be the result of occlusion with an upper tooth.

Five premolariform teeth, AIII-263 (Peyer, 1956, Taf. 6, Fig. 9), AIII-336, AIII-368 (Pl. 2:2), AIII-460, and AIII-509 could be upper premolariforms of *M. peyeri.* Principal cusps of all these teeth are relatively low in comparison to those of the group of premolariforms just described. Similar differences in proportions distinguish upper and lower premolars of *M. watsoni.* Among these premolariforms from Hallau there is variation in development of the basal cingula from absence to presence of an almost complete lingual and a posterior buccal cingulum (Pl. 2:2), a range of variation like that found in *M. watsoni.* Dimensions of the crowns of these premolariforms are as follows: OR length = 0.70—0.95 mm, OR width = 0.44—0.55 mm. Major sections of the roots of AIII-368 (Pl. 2:2) are preserved and show that the posterior was slightly larger and transversely wider than the anterior.

Other premolariforms exhibit some differences in proportions but all have simple, trenchant crowns and might also be referred to *M. peyeri.* Three, AIII-277 (Peyer, 1956, Taf. 6, Fig. 23), AIII-278 (ibid., Taf. 6, Fig. 24) and AIII-423 are of small size (OR length = 0.77—1.03 mm). Their crowns are simple consisting of a principal cusp, a small posterior basal cusp and, on one, an anterior basal cusp. The crowns of AIII-277 and AIII-278 are supported by two, well separated roots; the roots of AIII-423 are missing. Two other small premolariforms, AIII-350 and AIII-441 (OR length = 0.82—1.00 mm) have similar crown morphologies but the roots are not fully divided. Finally, AIII-282 (Peyer, 1956, Taf. 6, Fig. 28) is a single-rooted premolariform with a large principal cusp and a small posterior accessory cusp.

Discussion: The systematic relationships of *Morganucodon peyeri* are considered in a later section following the descriptions of the other morganucodontid and morganucodontid-like mammals of the Hallau local fauna.

?*Morganucodon* sp.

Referred material:

AIII-305 (LI, Taf. 7), fragment of upper molariform, left.

AIII-333 (NC 5, Pl. 2:3) fragment of upper molariform, left.

AIII-340 (NC 12, Pl. 2:4) fragment of lower molariform, left.

Description: These three teeth are approximately the same size as the molariforms of *Morganucodon peyeri* and resemble them in general configuration. However, they are easily distinguished by the absence or relatively weak development of buccal and lingual cingula, and symmetry in length and curvature of the anterior and posterior slopes of the main cusps. Also, if the projecting cingular cusp is at the posterior end of the crown then the posterior roots of these teeth do not show the distinct transverse broadening typical of posterior roots of the upper molars of *M. watsoni* and some teeth from Hallau referred to *M. peyeri* (e. g., AIII-255 and AIII-310).

Of the three, AIII-340 (Pl. 2:4) is the most complete preserving most of the crown and part of one root. Its smallest cusp is assumed to be at the posterior end of the crown. This cusp is slightly offset in what is taken to be a lingual direction from the line of the three main cusps. The other end of the crown is damaged and the presence of an anterior basal cusp cannot be excluded. Except for a minor cingulum bordering a basin between the posterior basal and posterior accessory cusp, no other cingula are present on the crown. This essential absence of cingula and relative size of the cusps suggests AIII-340 is a lower molariform. Other than apical blunting of the main cusps there is no indication of wear facets. The crown was supported by two, well separated roots. The anterior root appears to have been longer anteroposteriorly than the posterior. The posterior probably was slightly wider than the anterior, but the difference might not have been great. A curious rugose area on the presumed buccal side of the posterior root probably is a growth on the root and not a thickening of its wall. A color change on the broken end of the root appears to demark the "normal" wall of the root from the exostosis. Dimensions of the crown of AIII-340 are as follows: length = 1.54 mm, width = 0.48 mm.

The relatively smaller difference in height of their main cusps and presence of basal cingula on one or both sides of their crowns suggest AIII-305 (PEYER, 1956, Taf. 7, Fig. 51) and AIII-333 (NC 5, Pl. 2:3) are upper molariforms. Neither specimen is complete. Both have lost one accessory cusp, which on both teeth appears to have been the anterior. The degree of cingular development on the two teeth differs but, in transverse section, the apices of the main cusps of both are set to one side of the midlines of the crowns. Their steeper slopes are assumed to be on the lingual side of the crown. If so oriented the buccal cingulum of AIII-305 would be relatively better developed and more continuous than the lingual. AIII-333 lacks a lingual cingulum and the buccal is not continuous. Both teeth were supported by two, well separated roots. The widths of the crowns are as follows: 0.37 mm (AIII-333); 0.66 mm (AIII-305).

Discussion: Several interpretations of taxonomic affinity of these teeth are immediately apparent. First, they are teeth of a small morganucodontid that retain a primitive condition in only modest development of basal cingula. Or that the simplicity of their crowns indicates they are posterior premolariforms, deciduous premolariforms, or posterior molariforms of *Morganucodon peyeri.* Finally, and with equal uncertainty, it might be argued that these teeth document the presence of an early representative of the triconodontine triconodontids. Thus designation of these teeth as *?Morganucodon* sp. is no more than a device to highlight their distinctive morphology. It is recognized that most of the similarities of these fossils to teeth of species of *Morganucodon* probably are the result of shared plesiomorphous characters.

Order ?Triconodonta
Family ?Morganucodontidae
Helvetiodon gen. nov.

Etymology: Helvetia, Switzerland; Odontos, Greek, tooth.

Type species: *Helvetiodon schutzi* sp. nov.

Diagnosis: As for the type and only species.

Helvetiodon schutzi sp. nov.

Etymology: Named for Herr Emil SCHUTZ of Neunkirch who assisted Prof. PEYER in his research in the Hallau area.

Type: AIII-348 (NC 20, Pl. 3:1), a damaged molariform, tentatively identified as a right, upper molariform.

Type locality: Hallau bonebed, Kanton Schaffhausen, Switzerland.

Diagnosis: Based on isolated teeth thought to be upper molariforms. Premolariforms probably are present in the sample, but lower molariforms are either missing or are unrecognized. Molariforms are large, approximately one and a half times the size of those of *Morganucodon, Megazostrodon,* and *Erythrotherium,* and in the size range of *Tricuspes* and *Wareolestes.* They differ from molariforms of *Tricuspes* in more complex morphology of the crown with extensive development of labial and lingual cingula and cusps. Presumed upper molariforms of *Helvetiodon* differ from those of *Megazostrodon* in absence of an anterior accessory cusp, more massive and bulbous morphology, and different pattern of development of cingular cusps. *Wareolestes* is known from a tooth that in number and disposition of cusps is little more than an enlarged edition of a lower molar of *Morganucodon.* In contrast, the presumed upper molariforms of *Helvetiodon schutzi* are not as close in their morphological resemblance to the upper molars of any known species of *Morganucodon.*

Referred materials:

Molariforms

AIII-268 (XIV, Taf. 4), fragment of posterior end of upper molariform.
AIII-270 (XVI, Taf. 4), fragment of posterior end of upper molariform.
AIII-303 (XLIX, Taf. 7), fragment of posterior end of upper molariform.
AIII-354 (NC 26, Pl. 3:2), crushed crown lacking posterior end, upper right.
AIII-390 (NC 60), fragment of posterior end of upper molariform.
AIII-437 (NC 107), fragment of an end of a molariform.

Premolariforms (reference to *Helvetiodon schutzi* tentative, see text)

AIII-259 (V, Taf. 11), anterior premolariform or incisiform.
AIII-265 (XI, Taf. 7), principal and anterior basal cusp.
AIII-291 (XXXVII, Taf. 8), anterior premolariform.
AIII-302 (XLVIII, Taf. 7), principal and accessory cusp.
AIII-325 (LXXI, Taf. 12), principal cusp.
AIII-334 (NC 6), principal and accessory cusp.
AIII-359 (NC 31), slightly damaged, principal and accessory cusp.
AIII-360 (NC 32), fragment with principal and accessory cusp.
AIII-393 (NC 63), fragment of crown.
AIII-402 (NC 72), principal and small, ?anterior basal cusp.
AIII-424 (NC 94, Pl. 3:3), anterior premolar.
AIII-439 (NC 109), anterior premolar.
AIII-458 (NC 128, Pl. 3:4), principal and accessory cusp.
AIII-459 (NC 129), principal and small, ?anterior basal cusp.

Incisiforms and caniniforms (reference to *Helvetiodon schutzi* tentative, see text).

AIII-260 (VI, Taf. 6)
AIII-271 (XVII, Taf. 6)
AIII-274 (XX, Taf. 8)
AIII-294 (XL, Taf. 6)
AIII-304 (L, Taf. 11)
AIII-311 (LVII, Taf. 11)
AIII-316 (LXII, Taf. 8)
AIII-326 (LXXII, Taf. 12)
AIII-330 (NC 2)
AIII-341 (NC 13)
AIII-345 (NC 17)
AIII-347 (NC 19)
AIII-349 (NC 21)
AIII-365 (NC 37)
AIII-416 (NC 86)
AIII-477 (NC 147)

The hypodigm of this taxon consists of two nearly complete molariforms and several fragments. None are of typical haramiyid morphology, and they show some resemblance to teeth of morganucodontids. The teeth are large, about one and a half times the size of teeth of similar morphology referred to *Morganucodon peyeri*, and lie in the estimated size range of *Tricuspes tubingensis*. A number of premolariforms ranging from essentially complete teeth to fragments of crowns, as well as incisiforms and caniniforms are also described here. These are the large premolariforms, incisiforms, and caniniforms found at Hallau and for the sake of convenience are described as a unit. Some could well be elements of the dentition of *Helvetiodon*, but the possibility that others are parts of dentitions of *Tricuspes*, haramiyids, or other mammals or mammal-like reptiles cannot be excluded.

Description: Both the type specimen of *Helvetiodon schutzi* and the complete referred molariform (AIII-354) are elements of the new collection assembled after 1956. The two fossils preserve a large part but not all of the crown. As a result of abrasion and/or chemical attack the type (AIII-348) has lost large segments of its enamel cap (in Pl. 3:1 enamel-covered areas are rendered in darker tones). More of the crown of AIII-354 (Pl. 3:2) is preserved, but the tooth has been crushed laterally (buccolingually) and distorted. The crowns of both teeth are dominated by a large principal cusp. When viewed laterally, the longer, slightly steeper slope of the principal cusp is assumed to be its anterior slope, and the accessory cusp a posterior accessory cusp.

In comparison to known morganucodontids and triconodontids the relative height of the principal cusp of these two teeth would be extreme but not inappropriate for an upper molariform (e. g., note the M^2 of *Morganucodon oehleri* [Mills, 1971, Pl. 5A]) or the last, upper premolariform (note *M. watsoni* [ibid., Pl. 1D; Parrington, 1971, Fig. 16f] or *M. oehleri* [Mills, 1971, Pl. 5A]). However, the relative proportions of height of principal cusp to length of crown more frequently would be matched by lower molars of *Morganucodon*. This characteristic suggesting the two teeth are lower molariforms is contradicted by the presence of both lingual and buccal cingula on the type and, probably, the referred specimen. With few exceptions (e. g., note *Hallautherium* gen. nov., described below) development of basal cingula on both sides of the crown is a definitive characteristic of upper molariform teeth of advanced mammal-like reptiles and early mammals. Provisionally, this character is given greater weight. But it must be stressed that both teeth are isolated and their tentative identification as upper molariforms is not substantiated by association with recognizable fragments of the maxillary bone.

Finally, and again essentially arbitrarily, degrees of completeness and complexity of the basal cingula are used to distinguish buccal and lingual sides of the crown. In morganucodontids, if there is any difference in complexity or completeness of the basal cingula of upper molars, usually the buccal cingulum is not as completely developed as the lingual, but it can be wider and carry larger cusps.

In summary, all the molariforms and fragments of molariforms allocated to *Helvetiodon schutzi* are isolated specimens lacking associated segments of maxillary or dentary bones. Their identification as elements of the upper dentition and determination of anteroposterior as well as lateral orientations are based primarily on comparison with molariform teeth of morganucodontids, to which they show some resemblance. All these determinations of position and orientation must be regarded as tentative.

Posterior to the dominant, principal cusp of the type (Pl. 3:1) is a small, low accessory cusp, which is now missing most of its enamel cap. An anterior accessory cusp, similar to those found on molars of *Morganucodon* was not present. The two major cusps at the anterior end of the crown are set laterally; the anterolingual is larger and positioned more anteriorly than the buccal. Configuration of the dentine core of the anterobuccal cusp suggests a ridge connected its apex with the crest along the anterior edge of the principal cusp.

On the lingual side of the preserved part of the crown the basal cingulum becomes lower from both ends toward the midpoint where it is interrupted for a short distance. The anterior segment carries two small cusps behind the large anterior cusp. On the posterior segment a large cingular cusp is present lingual to the notch separating the principal and posterior accessory cusps. What remains of the rest of the posterior end of the crown has been stripped of most of its enamel covering. There appears to have been a small, posterolingual basin enclosed by the posterior accessory cusp, large posterolingual cingular cusp, and the rising posterior end of the crown. The posterior crest of the posterior accessory cusp could have interrupted the cingulum across the posterior end of the crown.

Except around the apex of the principal cusp, most of the enamel is missing from the buccal side of the crown. The configuration of the remaining dentine indicates the presence of at least two, distinct posterior cingular cusps. There is no evidence of a buccal cingulum connecting the posterior and anterior cingular cusps. Dimensions of what remains of the crown of AIII-348 are as follows: length = 2.67 mm; width = 1.39 mm. The crown was supported by two, large but well divided roots.

Although somewhat crushed and distorted, AIII-354 (Pl. 3:2) also appears to be a right, upper molariform that in most respects is a duplicate of the type. The few morphological differences most likely reflect individual variation or difference in positions in the dentition. Like the type, the anterobuccal cingular cusp apparently was smaller than the lingual, but in AIII-354 it is clearly a terminus of the midline crest of the principal cusp.

The posterior slope of the principal cusp is transversely narrower than the body of the cusp and demarked from it by symmetrical vertical, buccal and lingual depressions. These might be the result of postmortem distortion, but more likely are original features of the tooth. Another possible difference from AIII-348 is the apparent absence of posterobuccal cingular cusps. The enamel is preserved over the buccal side of the principal cusp, and a cingulum is not present. Probably the two roots supporting the crown were well separated.

Dimensions of the crushed crown of AIII-348 are now: length = 2.85 mm; width = 1.09 mm. This tooth and the type of *Helvetiodon* are larger than would be expected for elements of the dentition of *Morganucodon peyeri*, *M. watsoni*, or *Hallautherium* (gen. nov., described below) and are in the predicted size range of *Tricuspes*.

In his description of the fossils from Hallau Peyer (1956) noted the presence of several fragments of large, molariform, triconodont-like teeth. These, and a specimen in the new collection appear to be too large to be parts of teeth of *Morganucodon peyeri* and *Hallautherium* (gen. nov., described below), but have a more complex morphology than would be expected in teeth of *Tricuspes tubingensis*. Comparisons with the more complete molariforms just described suggest that AIII-268 (Peyer, 1956, Taf. 4, Fig. 14) and AIII-303 (ibid., Taf. 7, Fig. 49) could be fragments of the posterior ends of crowns of molariforms of *Helvetiodon schutzi*. AIII-390 (NC 60) and AIII-437 (NC 204) might have had a similar origin.

AIII-270 (Peyer, 1956, Taf. 4, Fig. 16) preserves part of the slope of what probably was the principal cusp, posterior accessory cusp, and a cingular cusp. On one side of the crown a crenulated cingulum extends at least part way around the base of the accessory cusp; the full extent of this cingulum and morphology of the base of the other side of the crown are unknown. Peyer (ibid., p. 43) noted the "symmetrodont-like" disposition of the cusps of this fragment. If what remains of the posterior crest of the principal cusp is assumed to have extended directly to its apex, then the cingular cusp does not lie on a line defined by the apices of the principal and accessory cusps. The angulation is not as great as that at the junction of the anterior crest of the principal cusp and the crest of the anterobuccal cusp of AIII-354 and, probably, AIII-348. AIII-270 (Peyer, 1956, Taf. 4, Fig. 16) might be part of either an upper molariform or an otherwise unknown (or unrecognized) lower molariform of this species.

Premolariforms tentatively referred to *Helvetiodon schutzi:* The collection from Hallau contains several large premolariform teeth, probably too large to have been parts of the dentition of *Morganucodon peyeri.*

Some of these have accessory and basal cingular cusps suggesting they are elements of the dentition of *Helvetiodon schutzi;* others lacking such cusps might be parts of the presumably morphologically simpler dentition of *Tricuspes tubingensis.* For the sake of convenience all are briefly considered here.

Many of the large premolariform teeth resemble AIII-458 (Pl. 3:4). The principal cusp is not at the center of the crown, but is offset toward the assumed anterior end. Strong anterior and posterior crests from the edges of the principal cusp whose relatively great height suggests the tooth might be a lower premolariform. Near the base of the crown the anterior crest is deflected laterally to join a basal cingulum, which is truncated by a fracture. Probably the tooth lacked an anterior basal cusp. From comparisons with premolars of *Morganucodon watsoni* it appears likely that the basal cingulum is on the lingual side of the crown. The notch between principal and posterior accessory cusps is not particularly deep. On either side of this notch depressions extend basally; the lingual depression is larger. Buccal and smaller, lingual basal cusps are linked by a distinct, low crest. The crown was supported by two, well separated roots. Its dimensions are as follows: length = 1.47 mm, width = 0.77 mm.

The distal end of the crown of AIII-359 (NC 31) is damaged but the tooth appears to be essentially a duplicate of AIII-458 (width of crown = 0.84 mm). AIII-334 (NC 6) is similar to but smaller (length of crown = 0.99 mm, width = 0.48 mm) than the two teeth just described and its posterior basal cusps are not as large. It was supported by two distinct roots.

Proportions of the crown of AIII-302 (Peyer, 1956, Taf. 7, Fig. 48) are slightly different from those of AIII-458, but easily could be encompassed within the range of individual variation of homologous teeth. The apex of the principal cusp of AIII-302 has been blunted; apparently by contact with foodstuffs and not post-mortem abrasion. Dimensions of the crown are as follows: length = 1.42 mm; width = 0.77 mm.

Peyer (1956) thought AIII-265 (ibid., Taf. 7, Fig. 11) was part of the posterior end of a premolariform. The fragment is in the same size range as most of those premolariforms just described (crown width = 0.84 mm). Configuration of what is preserved of the crown suggests it is a fragment of the anterior end of a premolariform differing from AIII-458 in the presence of a anterior basal cusp. A weakly developed lateral cingulum extending to the apex of this basal cusp might be on the lingual side of the crown.

AIII-402 (NC 72) and AIII-459 (NC 129) appear to be fragments of large, two-rooted premolariforms each having a small, ?anterior basal cusp but lacking lateral basal cingula. A large segment of the root of AIII-459 is preserved and exhibits a slight but distinct curvature toward the midpoint of the crown. There is no evidence of expansion of the root but part of its tip is missing.

Although what little is preserved of its crown does not closely resemble those of any of the other large premolariforms, one of the roots of AIII-393 (NC 63) is preserved. It is curved, strongly diverging from the presumed vertical axis. Again, the tip is broken, but there is no sign of expansion.

AIII-325 (Peyer, 1956, Taf. 12, Fig. 71) is a small fragment of what appears to have been a large premolariform. One side of the crown (the side not illustrated by Peyer, ibid.) is heavily damaged. The width of the remaining part of the crown is 0.73 mm. If the preserved basal region of the crown is its anterior end, which seems more likely, then AIII-325 differs from AIII-458 in the greater complexity of cingular development. If it is part of the posterior end of the crown, it is of much simpler construction than AIII-458.

AIII-360 (NC 32) is a complete premolariform but is sligthly smaller than most of those described above (crown length = 1.06 mm; width = 0.62 mm). Its crown consists essentially of the principal cusp. A small basal cusp is present at the posterior end of the crest of the posterior ridge of the principal cusp. Just lateral to this basal cusp on the slightly more bulbous, convex side of the crown is a short basal cingulum. Most of the root(s) of the tooth is missing. What remains shows some indication of subdivision but does not clearly demonstrate whether the tooth was double or single rooted.

AIII-424 (NC 94, Pl. 3:3) is a small premolariform that, except for its large size (crown length = 0.73 mm; width = 0.40 mm) is similar to P_1 or P_2 of *Morganucodon watsoni.* The crown is simple consisting of an anteriorly canted principal cusp, two cusps on the lower part of the posterior crest of the principal cusp, and a simple cingulum along the anterobasal (?lingual) side of the crown. Although there is a vertically oriented depression on the ?buccal side of the root, a similar depression is lacking from the opposite side. The crown of AIII-439 (NC 109) is similar to that of AIII-424 but slightly larger (crown length = 0.92 mm, width = 0.44 mm). A depression on one side of the root of this tooth, which also is probably an anterior premolar, separates it into two lobes. The crown of AIII-291 (Peyer, 1956, Taf. 8, Fig. 37) is similar to those of the two premolariforms just described but it is significantly larger (length = 1.47 mm; width = 0.73 mm). AIII-259 (ibid., Taf. 11, Fig. 5) might be the crown of an anterior premolariform or an incisor.

Incisiforms and caniniforms: Finally, and primarily for the sake of completeness, teeth that might be incisiforms or caniniforms of *Tricuspes* or *Helvetio-*

don are noted in the list of referred material. All appear to be too large to be referable to either *Morganucodon* or *Hallautherium* (gen. nov. described below). If haramiyids were not multituberculate-like in the morphology of the anterior part of their dentitions (a common working assumption based on no conclusive evidence), the derivation of some of the teeth from dentitions of these animals is also possible.

Discussion: The possibility that teeth allocated to *Helvetiodon* might be parts of the dentition of *Tricuspes* was considered. It can be suggested that *Tricuspes* is based on lower molariforms and *Helvetiodon* on upper molariforms of the same taxon. However, the difference in degree of development of their basal cingula and of the separation of their roots argue against this possibility. Another hypothesis is that *Tricuspes* is typified on premolars of *Helvetiodon,* which could explain the differences in cingular structure. Again the differences in morphology of the roots (those of *Tricuspes* being only incipiently divided while the molariforms of *Helvetiodon* were supported by two well-divided roots) and the presence in the sample of several large, two-rooted premolariforms more likely referable to *Helvetiodon* argue against this hypothesis. On the limited data available a third hypothesis, that *Tricuspes* and *Helvetiodon* are distinct taxa, appears to be slightly more probable.

Order and Family incertae sedis
Hallautherium gen. nov.

Etymology: Hallau; Ther, Greek, beast.
Type species: *Hallautherium schalchi* sp. nov.
Diagnosis: As for the type and only species.

Hallautherium schalchi sp. nov.

Etymology: Named for Ferdinand Schalch whose studies of the Triassic-Jurassic boundary resulted in the discovery of the fossil locality near Hallau.

Type specimen: AIII-318 (Peyer, 1956, LXIV, Taf. 5, Fig. 64 & Text-figs. 2a—b; Fig. 5), left lower molariform preserved in a fragment of dentary.

Diagnosis: Only known from lower molariforms with a main row of four cusps and one or more anterior and posterior lingual cusps. These molariforms lack a basal, lingual cingulum or kühnecone. Unlike any known morganucodontids a large, posterior buccal basin is present on the type (a small depression on the referred specimen). Teeth are in the size range of *Morganucodon watsoni* and *M. peyeri,* but are smaller than those of *Tricuspes* and *Helvetiodon.*

Referred material:

AIII-337 (NC 9, Pl. 3:5), isolated lower molariform, right.

Description: The orientation of the type specimen (Fig. 5) suggested here differs from that proposed by Peyer (1956) and utilized by Hopson and Crompton (1969) and Parrington (1978). That the tooth is a lower molariform is clearly demonstrated by the fragment of dentary in which it is implanted. The principal cusp is anterior to the midpoint of the crown length (anteroposteriorly).

Two lines of evidence suggest the tooth is a left rather than a right lower molariform. The fragment of dentary of AIII-318 preserves essentially a full cross section of this bone (see Peyer, 1956, Taf. 5,

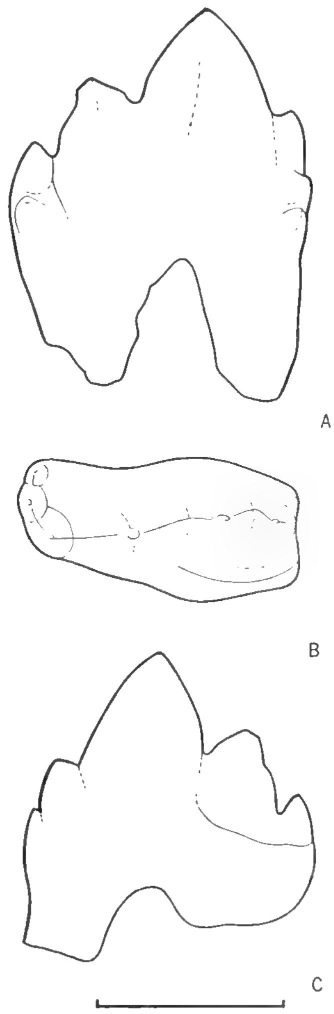

Figure 5: Outline drawing of AIII-318, *Hallautherium schalchi,* Hallau local fauna, Switzerland. A. lingual view, B. occlusal view, C. buccal view. Scale equals 1 mm.

Fig. 64, and Text-figs 2a—b). Directly behind the molariform there is a deep depression in the dentary. If this is part of the wall of a dental crypt, it suggests that at time of death the preserved molariform was near the posterior end of the horizontal ramus of the dentary. In support of this interpretation, a low ridge along the posterior part of the top of the dentary lateral to the molariform appears to be the anterior end of the coronoid process. As far as known the coronoid process of the dentary of advanced mammal-like reptiles and early mammals lies either in line with or, usually, buccal to the posterior teeth. A second line of evidence is the apparent development of buccal wear facets on AIII-318 and presence of a large wear facet on the referred specimen (AIII-337, Pl. 3:5).

If identification of AIII-318 as a posterior molariform is correct, the absence of indications of a lingual groove to house the splenial and, possibly, the prearticular and angular, as well as "Crompton's groove" (see PARRINGTON, 1971) is of some significance. In a homologous section of a dentary of a young individual of *Morganucodon watsoni* both grooves, particularly the former would be expected to be present (note PARRINGTON, ibid., fig. 10e—f). Enough of the surface of the dentary of AIII-318 is preserved to suggest the apparent absence of these grooves is not a result of post-mortem abrasion. Thus, possibly the mandible of *Hallautherium schalchi* was more mammal-like in construction than that of *Morganucodon watsoni* and other approximately contemporaneous morganucodontids.

The crowns of the lower molariforms are dominated by the relatively high principal cusp, situated anterior to the midpoint of the crown. Of the two accessory cusps the posterior is distinctly larger. The central row of cusps is completed by a small, posterior cusp set slightly buccal to the line formed by the other three. On AIII-318 there are two cusps lingual to the anterior accessory cusp. Of these the cusp in the most lingual position is the smaller. On AIII-337 only one major cusp is present lingual to the anterior accessory cusp, but a small cuspule is developed on its posterior slope (Pl. 3:5). Both teeth have a small posterolingual cusp lingual to the last cusp of the main row. There is no evidence of even slight development of either a cingulum between the anterior and posterior lingual cusps or a kühnecone.

Although closely similar in all characters described so far, AIII-318 and AIII-337 differ in structure of the buccal side of their crowns. On AIII-318 a distinct basin is present low and buccal to the posterior accessory cusp and the last (posterior) cusp of the main row. The buccal rim of this basin is smooth, but in comparison to adjacent parts of the crown differences in the texture of the rim and internal surface of the suggest the presence of wear facets. The degree to which attrition could have modified the configuration of the basin and its buccal rim cannot be assessed. Anterior to this basin the buccal surface of the crown is not interrupted by a cingulum or cusps. In contrast, AIII-337 lacks a distinct posterior buccal basin. A well-defined elongate wear facet lies along the buccal surface of its posterior accessory cusp. Posterior to it is a small basin-like depression.

Both teeth appear to have been supported by two, well separated roots. Of the two fossils, AIII-318 is distinctly the larger, length = 1.39 mm, width = 0.66 mm. Dimensions of AIII-337 are length = 1.08 mm, width = 0.44 mm. As long as the positions of these teeth in the dental arcade remain unknown, it is impossible to directly compare the size of *Hallautherium schalchi* with the known species of morganucodontids. However, assuming that AIII-337 is not the most posterior of the lower molariforms their dimensions suggest the dentition of *H. schalchi* was approximately in the size range of that of *Morganucodon watsoni* and *M. peyeri* but smaller than *Tricuspes*.

Discussion: Several paleontologists (e. g., PARRINGTON, 1978) have noted the differences between the type specimen of *Hallautherium schalchi* and the large samples of teeth of *Morganucodon watsoni* from localities in Wales. Size and/or configuration of cusps also clearly distinguish *Hallautherium* from *Megazostrodon* and *Erythrotherium*. However, there is a basic similarity in the overall configuration of their crowns, which are dominated by a central row of three or more cusps. This similarity is interpreted to be a common trait of many advanced mammal-like reptiles and early mammals in which increased complexity of the crown was achieved simply by multiplication of cusps along an anteroposterior (mesiodistal) axis.

The key difference between *Hallautherium* and known morganucodontids is the extreme development of the posterobuccal basin on at least one of the lower molariforms. Posterobuccal cusps occur on a few lower molars of *M. watsoni* (PARRINGTON, 1978), and MILLS (1971) noted the presence of a "suggestion of a cingulum on the buccal surface" of M_3 of *M. oehleri*. However, the presence of such a large buccal basin, which appears to have occluded with a cusp(s) of an upper molariform, is unknown in any species of *Morganucodon*, *Erythrotherium*, *Megazostrodon* or *Eozostrodon*. By the admittedly subjective standards employed in the taxonomy of early mammals, recognition of a new genus and species appears warranted. Whether the differences are indicative of a degree of phylogenetic separation that might be recognized through establishment of a new family is an assessment that should await collection of additional material.

SYSTEMATIC RELATIONSHIPS

The data currently available suggest that during the Middle and Late Triassic a number of lineages of cynodont therapsid reptiles diversified and independently underwent selection for decrease in body size, reduction in relative size of many elements of the lower jaw, increased complexity of dental morphology and occlusal pattern, and other characters of the mammalian grade of organization (see CROMPTON and JENKINS, 1979). If better known evolutionary radiations of other groups of vertebrates can be used as models, probably many characters now taken as diagnostic of mammals evolved in parallel in distinct lineages. Also the models would suggest that most of these lineages became extinct and were not represented by descendants in Middle or Late Jurassic faunas. Finally, if these assumptions are correct, the occurrence of species with a mosaic of a primitive grades of mammalian dental morphology and function but reptilian grades in other skeletal traits must be expected. Proper taxonomic allocation of such species has to await discovery of specimens yielding more than just information on dental morphology.

The class and ordinal affinities of many of the vertebrates in the local faunas of the Tübingen-Stuttgart area and Hallau that are known only from mammal-like teeth cannot be established on the meager data available. *Tricuspes* is an excellent case in point. The genus is now represented by isolated, fragmentary teeth found at Gaisbrunnen, Hallau, and, possibly, Sonnenberg bei Degerloch (D. SIGOGNEAU-RUSSELL, pers. comm., has found teeth referable to *Tricuspes* at Saint-Nicolas-du-Port). These teeth have some mammal-like features: presence of three cusps that are not aligned anteroposteriorly; development of a fourth, ?postero-buccal cusp; and at least incipient, if not full subdivision of the root. However, beyond these there is nothing suggesting mammalian affinity of the animal that bore these teeth. Among the few known Middle or Late Jurassic mammals or cynodonts none appear to be descendants of *Tricuspes*. However, the available samples of Jurassic faunas probably give us only limited documentation of their diversity. Though descendants might be identified in the future, most likely *Tricuspes* is a member of an advanced cynodont or cynodont-derived mammalian lineage. Querried allocation of *Tricuspes* to the Mammalia recognizes the few mammal-like features of its teeth.

Although ranging from the Middle Keuper (Norian) to possibly the Bathonian (see (CLEMENS and KIELAN-JAWOROWSKA, 1979), the Haramiyidae remains a poorly represented group in the fossil record. Haramiyids are known only from isolated teeth found at localities in Great Britain, France, West Germany, and Switzerland. A jaw fragment containing two or more teeth, an edentulous jaw, or any other skeletal material of a haramiyid have yet to be discovered or recognized. Current hypotheses concerning the systematic relationships of haramiyids were reviewed by (CLEMENS and KIELAN-JAWOROWSKA (1979) but can be summarized here as follows: Many workers, emphasizing the mammal-like complexity of cusp morphology and root structure, tentatively include the Haramiyidae in the Mammalia. Some argue that haramiyids might be ancestral or closely related to the ancestors of multituberculates, but there is division of opinion on these hypotheses. Most likely the formally named taxa and informal taxonomic groupings are based simply on associations of morphologically similar teeth, and the current intrafamilial classification primarily reflects degrees of morphological similarity.

Review of the haramiyid teeth in the samples of local faunas of the Tübingen-Stuttgart area and Hallau revealed considerable morphological diversity. *Thomasia antiqua*, *Thomasia* sp. 2 (HAHN, 1973), and ?*Thomasia* sp. were identified in the collections from the German localities. Specimens referable to *Haramiya* have yet to be found, but this could easily be a product of the small sample sizes. Both form genera are represented in the Hallau local fauna. Isolated teeth of cf. *Thomasia antiqua*, *T. anglica*, ?*Thomasia* sp., cf. *Thomasia* sp., *Haramiya moorei*, as well as fragments of haramiyid teeth of uncertain specific or generic affinity are present in this sample. Unfortunately these fossils do not provide a key to understanding the composition of the haramiyid dentition or the systematic affinities of the group, but only document greater diversity in dental morphology.

Since publication of PEYER's (1956) monograph many workers have recognized that at least one species of morganucodontid was present in the Hallau local fauna. Detailed analyses of the material supports this view revealing the presence of a species closely resembling *Morganucodon watsoni*, *M. oehleri*, and *Erythrotherium parringtoni*. In order to distinguish specimens of *Morganucodon* and *Erythrotherium* data on the relative proportions and sequential morphologic differences of the cheek teeth are required (CROMPTON, 1974). These are not available for the Swiss species. Its allocation to *Morganucodon*, known from localities in Europe and Asia, rather than *Erythrotherium*, known only from South Africa, is based solely on the biogeographic probabilities.

The known molariforms of *Morganucodon peyeri* do not show particularly close resemblances to the morganucodontid recently described by SIGOGNEAU-RUSSELL (1978) in her preliminary report on the mammals found at Saint-Nicolas-du-Port. Full evaluation of the relationships of this animal must await further study of the new material from France.

Molariforms of *Morganucodon peyeri* differ from those of *M. watsoni* and *M. oehleri* in several morphological details that warrant recognition of a new species. The possibility that the Hallau local fauna is older than the local faunas from Rhaeto-Liassic fissures in Wales invited testing the hypothesis that *M. peyeri* was either ancestral to *M. watsoni* or documented a more primitive grade of evolution. Some features tend to support these speculations. The buccal and lingual cingula of the upper molariforms of *M. peyeri* are not as large as those of *M. watsoni.* Possibly the lower frequency in development of expansions of the roots of the molariforms of *M. peyeri* is a primitive trait. Also, the relative rarity of wear facets might be interpreted as indicating a more primitive grade in evolution of precise occlusal patterns

Although suggestive, none of these observations strongly supports the hypothesis and all can be interpreted in other ways. The geological evolution of western Europe during the Rhaeto-Liassic involved reduction in size and subdivision of land areas. The fossil record suggests *Morganucodon* or its ancestors were wide spread over what is now Eurasia. During the marine transgressions populations of terrestrial vertebrates were subdivided and isolated. They appear to have evolved independently to produce a series of distinct insular faunas. *Morganucodon watsoni* and *M. peyeri* probably represent different lineages formed during this radiation.

Three isolated teeth from Hallau are identified as ?*Morganucodon* sp. Although illustrating some features also found in morganucodontids, for example the presence of three principal cusps aligned anteroposteriorly, their crowns lack others, such as distinct cuspidate lateral cingula and kühnecones. The teeth are of the proper size to have been elements of the dentition of *M. peyeri,* perhaps posterior premolariforms, deciduous premolariforms, or posterior molariforms. Also, it is quite possible that they are molariform teeth of a primitive triconodontid or a hitherto unknown family of mammals.

Two new genera and species of vertebrates, probably mammals, are recognized in the Hallau local fauna. The teeth used to typify *Helvetiodon schutzi* are relatively large and bulbous for elements of the dentition of a Rhaeto-Liassic mammal. Although in approximately the same range of size as *Tricuspes,* the possibility that they are elements of the dentition of this or a closely related genus appears unlikely at the moment. As currently known, the molariforms of *Helvetiodon* had two, large principal cusps, the central being the larger. An anterior accessory cusp similar to those found on molars of *Morganucodon* is not present on the available teeth. Like *Morganucodon* upper molars, the molariforms of *Helvetiodon* had buccal and lingual cingula, but the morphology of the cingular cusps differs.

Recently FREEMAN (1979) described *Wareolestes rex* from a single tooth found in deposits of Bathonian age (Middle Jurassic) in the Forest Marble of Oxfordshire, England. The type is a large tooth (crown length = 2.31 mm; width = 1.24 mm, ibid.) comparable in size to the type and referred molariform of *Helvetiodon schutzi.* However, the type of *Wareolestes* appears to be an "enlarged" or "inflated" version of a lower molar of *Morganucodon watsoni.* As pointed out by FREEMAN (ibid.), the points of resemblance include occurrence of a principal row of four cusps and, although positioned somewhat anteriorly opposite the principal cusp, presence of an apparent homologue of the kühnecone. However, unlike most molars of *Morganucodon,* a subdued, noncuspidate cingulum is present on the buccal side of the crown. In contrast, although exhibiting some similarities, the molariforms of *Helvetiodon* are not so closely comparable to the upper molars of *Morganucodon.*

Hallautherium schalchi, the second new genus of mammals recognized in the Hallau local fauna, is based on lower molariform teeth smaller than the molariforms of *Helvetiodon.* The type specimen, AIII-318, was described by PEYER (1956). As has been argued above, the data suggest that PEYER's identification of the buccal and lingual sides of the tooth was in error. At least one of the lower molariforms of *Hallautherium* had a distinct posterior buccal basin that might well have received and been worn by a cusp of an upper molariform. Also, both the type and referred specimens, apparently also a lower molariform, lack kühnecones. Finally, the morphology of the small fragment of dentary preserved in the type suggests it was more mammal-like in construction than that of *Morganucodon watsoni.* These characters set *Hallautherium* well apart from any known morganucodontid or other Rhaeto-Liassic mammal.

Although following PEYER (1956) in orientation of AIII-318, HOPSON and CROMPTON's (1969) comments on this fossil are still pertinent to the problem of unraveling the ancestry of the multituberculates. Among the known, non-therian mammals of the Rhaeto-Liassic the general pattern of dental morphology is one of molariform teeth dominated by an anteroposteriorly oriented row of three or more cusps. The buccal side of the lower molariforms occluded against the lingual side of the uppers. Basal cusps or cingula normally occur on both sides of the upper molariforms, but only on the lingual side of the lowers.

Multituberculates first certainly appear in the fossil record in the Kimmeridgian (Late Jurassic), but might be recorded by a specimen of Bathonian age (Middle Jurassic, FREEMAN, 1976) from Britain or an Early Jurassic fossil found in India (DATTA et al., 1978). Like other non-therians the cusps of the molars of multituberculates are arranged in anteroposteriorly oriented rows. Although yet to be documented, it appears most likely that their molar pattern originated through the addition of basal cingula, which evolved into rows of cusps lateral to the main row of cusps. Evidence provided by the structure of their premolars and relative development of cusp rows on their molars suggests that multituberculate lower molars and M^1 evolved through addition of a buccal row of cusps to the primitive row while M^2 appears to have originated by the addition of a lingual row of cusps (see CLEMENS and KIELAN-JAWOROWSKA, 1979). Currently this presumed pattern of addition of cusp rows stands as the key apomorphy of the Multituberculata.

The importance of the dental morphology of *Hallautherium* in considerations of the ancestry of multituberculates is not that these teeth exhibit apomorphies hitherto only known in multituberculates. They do not. However, in being an exception to what has been regarded as the standard pattern of cingular development on molariform teeth of non-therians, they add to the documented range of morphological variation among these mammals. Thus they strengthen the plausibility of the hypothesis calling for origin of molars of multituberculates through a unique pattern of cingular development. Unless there were major reversals in the evolutionary trend in development of these additional cingula and rows of cusps, a correlary of this hypothesis is that the common ancestors of multituberculates and other non-therian mammals would be animals whose molariform teeth lacked basal cingula. Clearly such a grade in dental evolution would be appropriate for very early non-therian mammals or cynodont reptiles.

In summary, the available collections of Rhaeto-Liassic mammals from Switzerland and West Germany add to the documented diversity of mammalian lineages at this time. These collections, and that being assembled by SIGOGNEAU-RUSSELL from a locality in eastern France, clearly show that Rhaeto-Liassic mammals can no longer be easily classified in just three families, Morganucodontidae, Kuehneotheriidae, and Haramiyidae. Distinctly different mammalian lineages were present during this interval. Their diversity tends to support the view that the first members of the Mammalia are to be sought in older, Late Triassic or possibly Middle Triassic faunas.

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TAFELN

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All figures natural size

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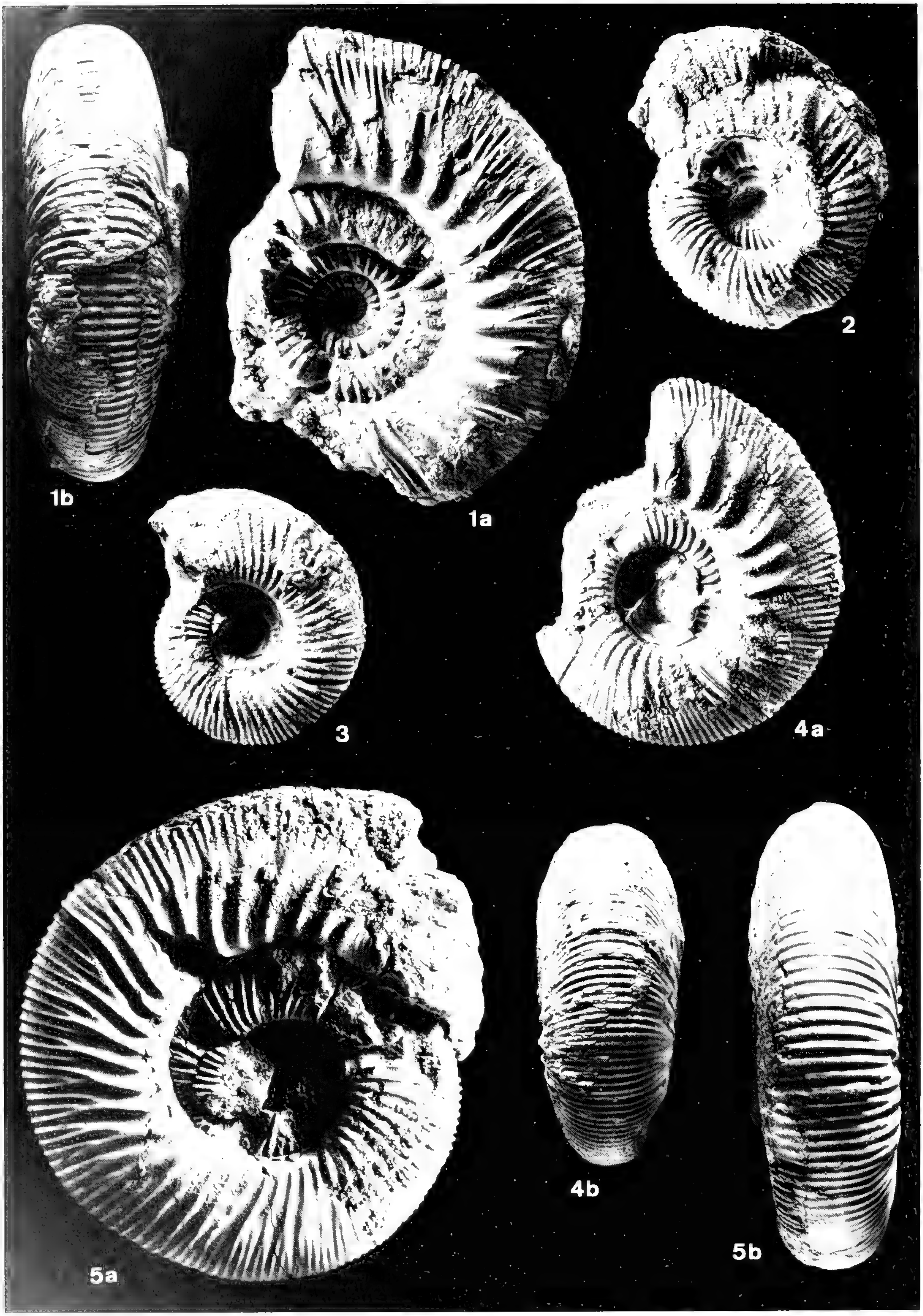

I [illegible], H. A.: Lower and Middle Tithonian Ammonite Fauna.

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All figures natural size

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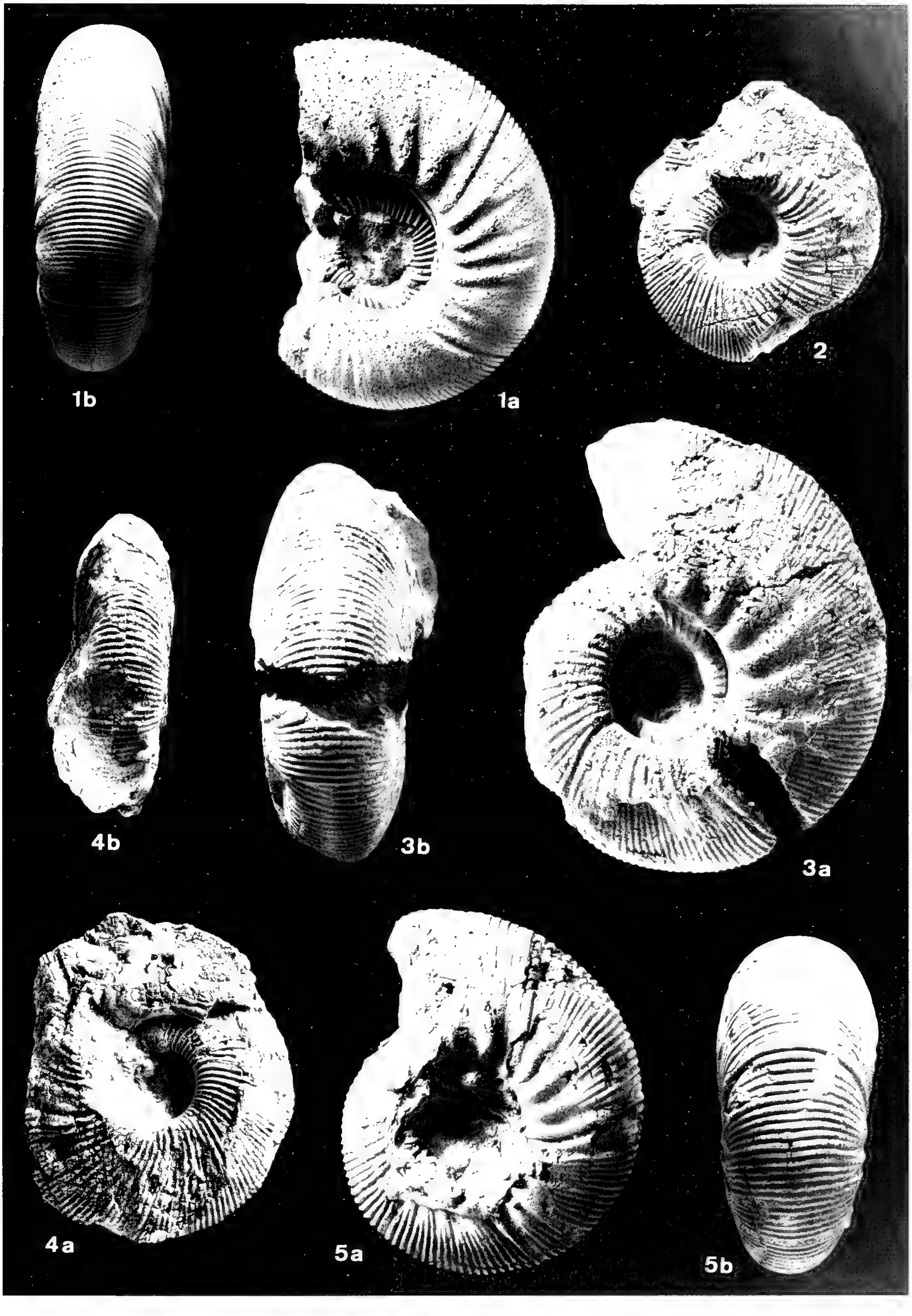
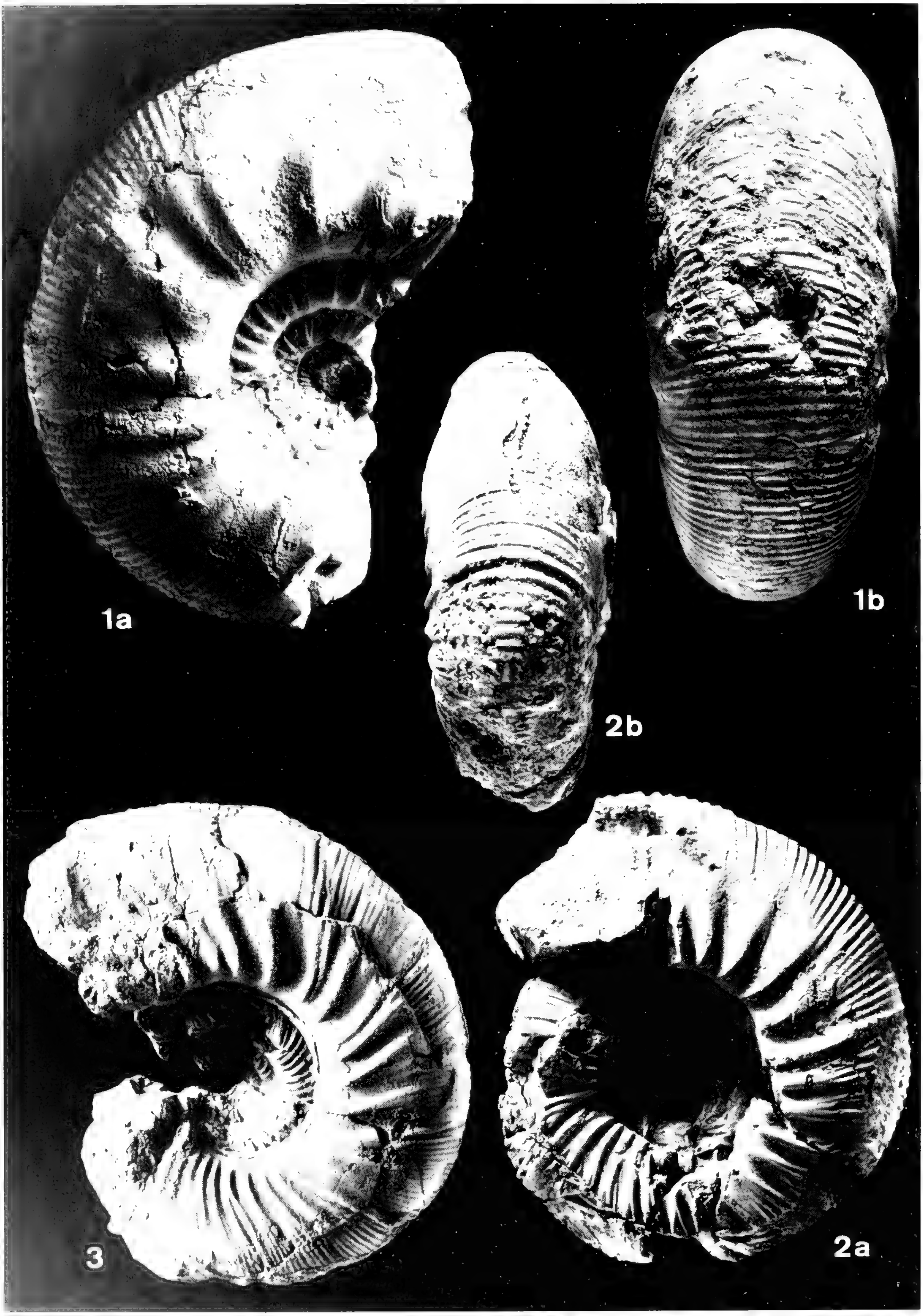


LEANZA, H. A.: Lower and Middle Tithonian Ammonite Fauna.



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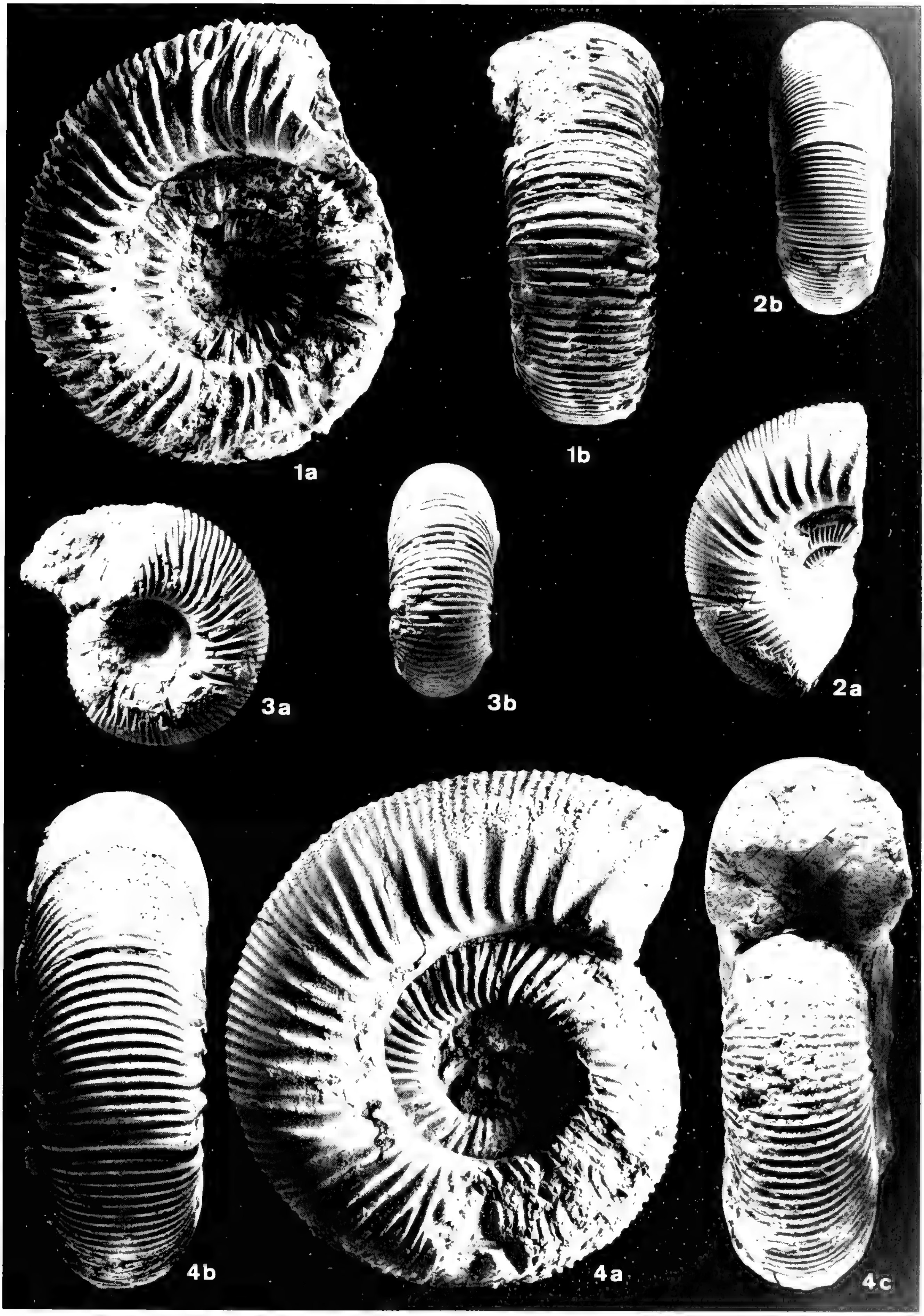
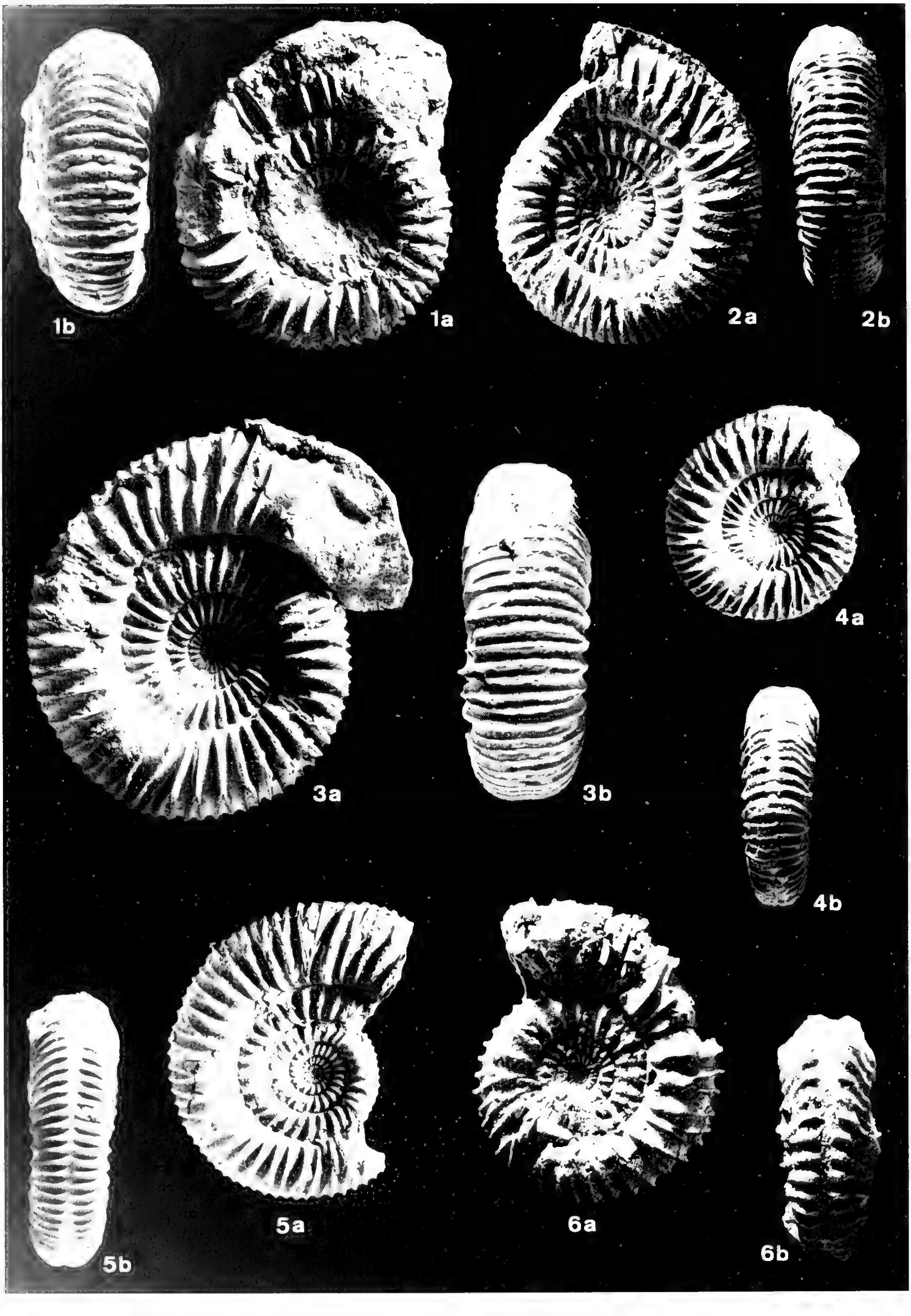


LEANZA, H. A.: Lower and Middle Tithonian Ammonite Fauna.



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1b


2a


1c


1a


1d


2b


1e

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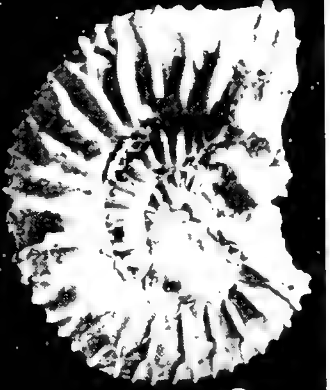
1a


1b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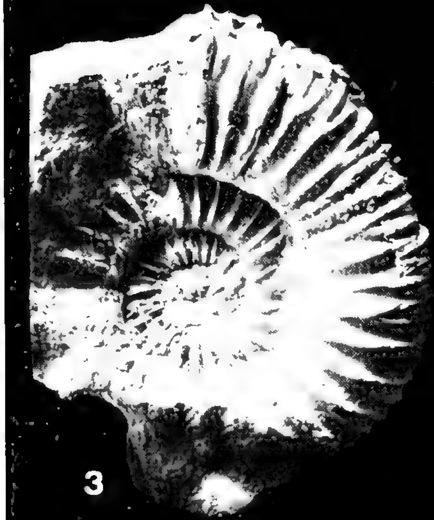
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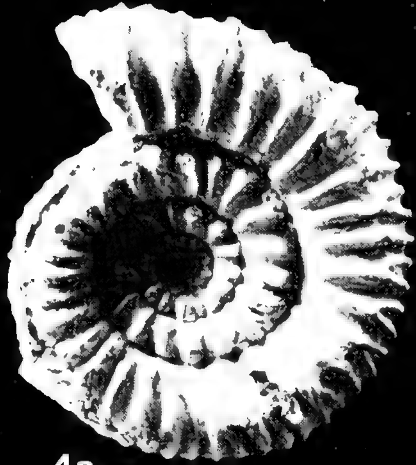
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4b


5b


5a


6a


6b

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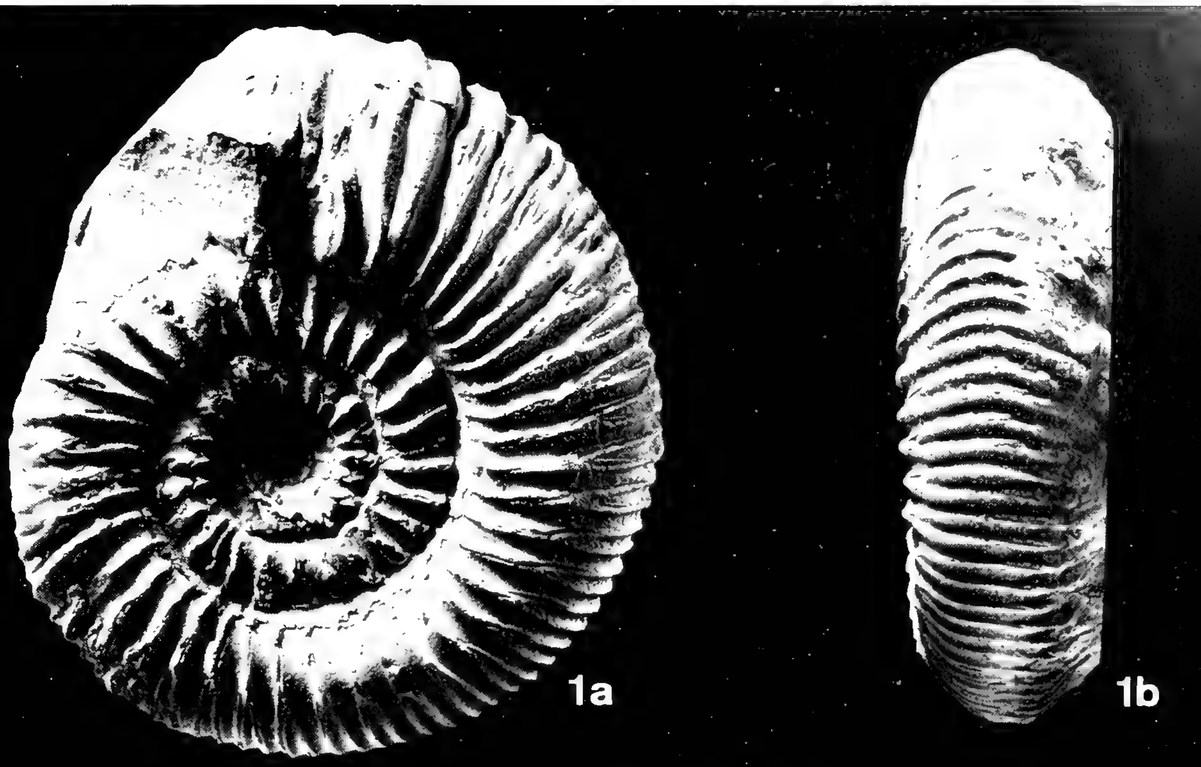

LEANZA, H. A.: Lower and Middle Tithonian Ammonite Fauna.

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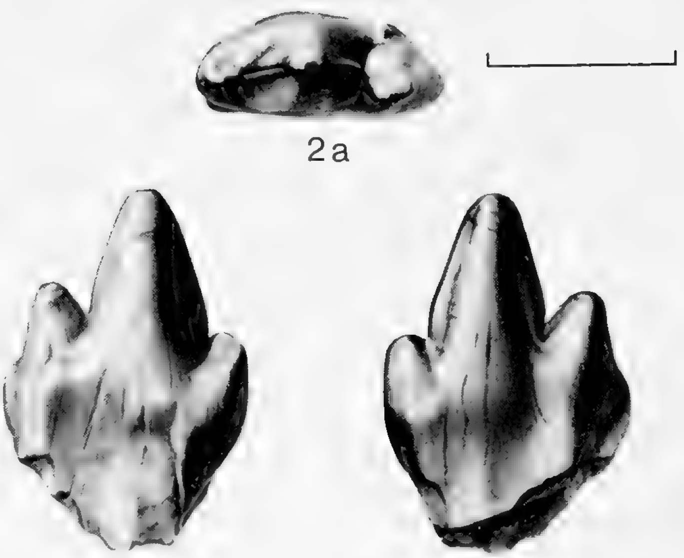

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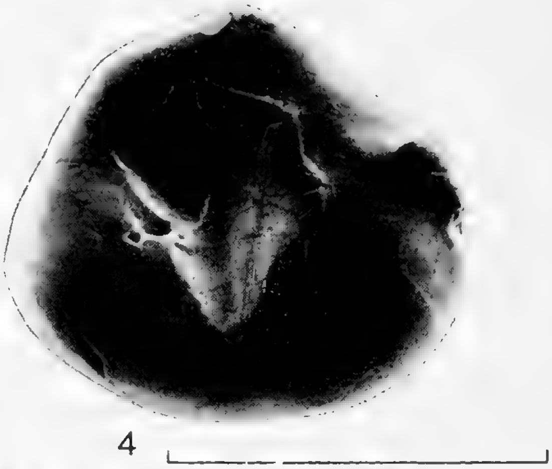

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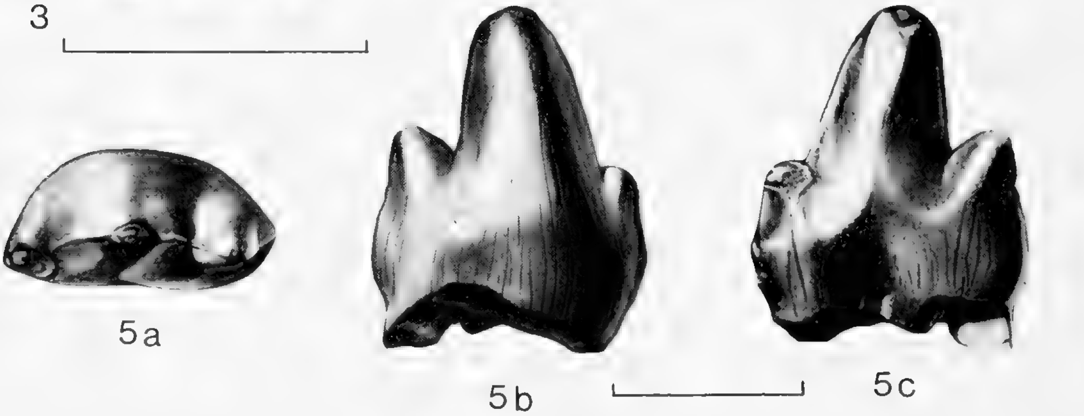

5a

5b

5c

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Fig. 1: *Tricuspes tubingensis,* type specimen, tentatively identified as a right lower molariform, slightly retouched scanning-electron microscope photograph of lateral, probably buccal side. Also, see E. von Huene, 1933, Taf. 1, Fig. 7. Scale below photograph equals 1 mm.

Fig. 2: *Tricuspes tubingensis,* type specimen, tentatively identified as a right lower molariform: a, occlusal view, tentative orientation anterior to left, buccal upwards; b, lateral, probably buccal view, anterior to right, and c, lateral, probably lingual view, anterior to left. Scale above Fig. 2c equals 1 mm.

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All figures drawn same scale. Scale below Fig. 4a equals 1 mm.

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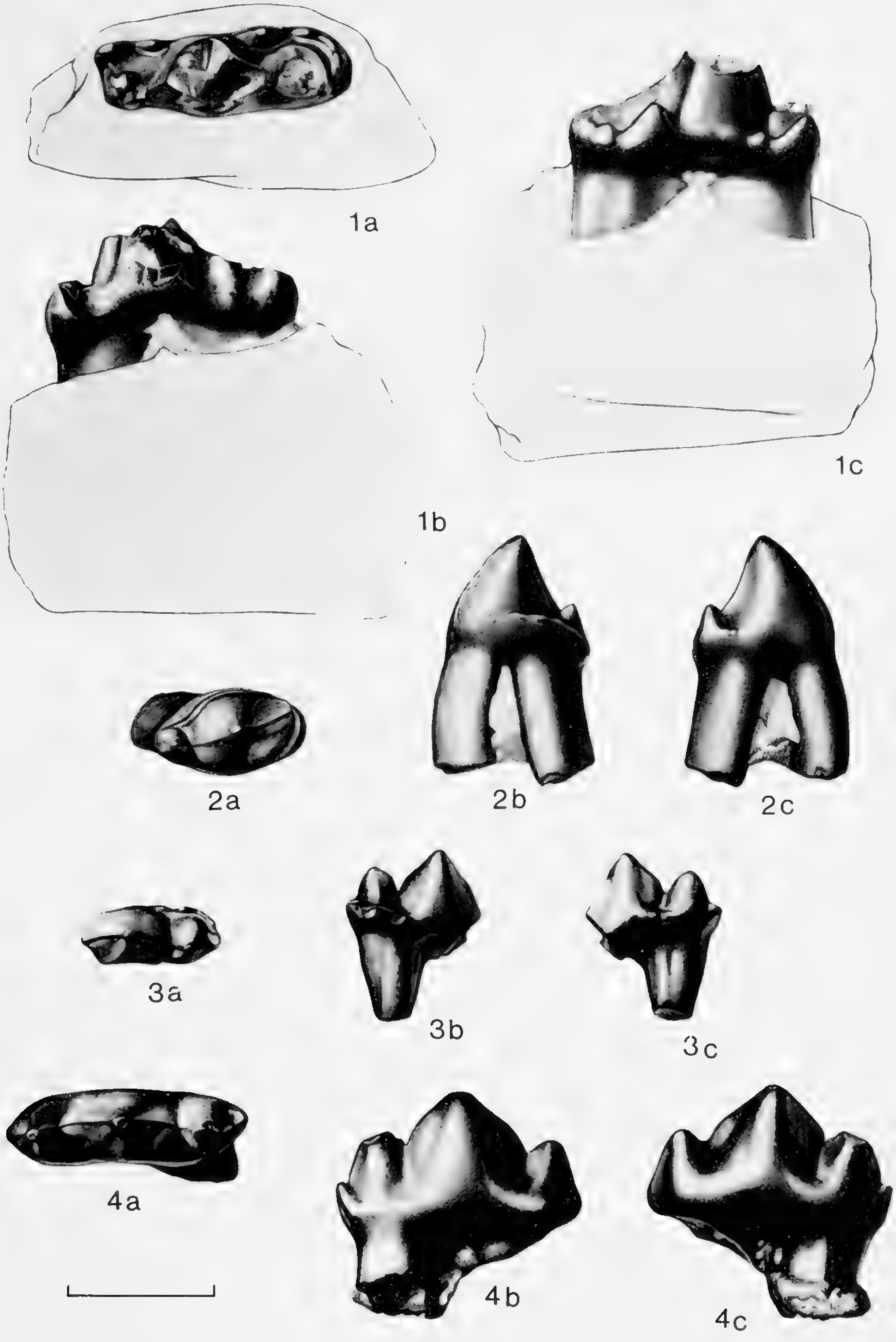

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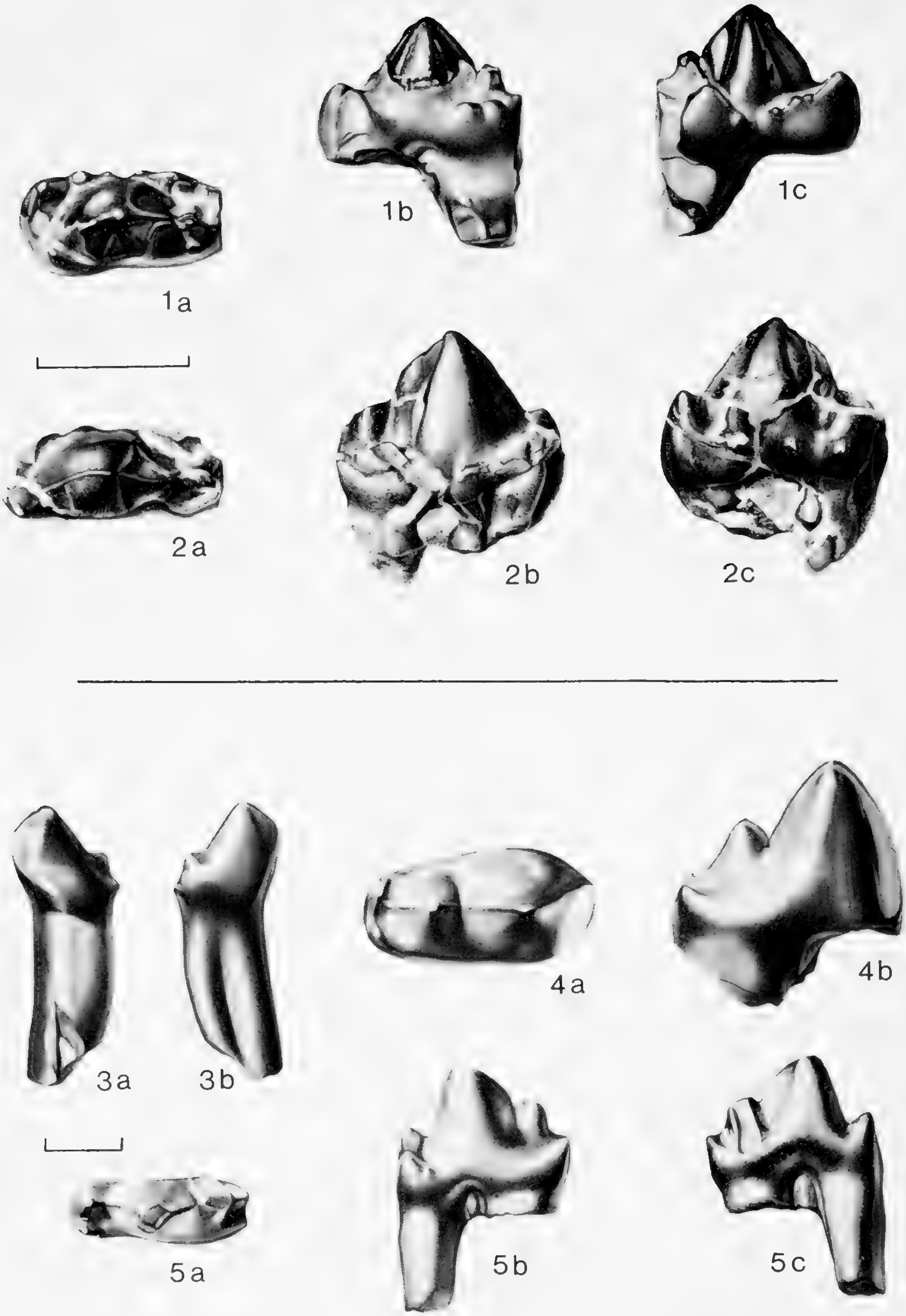

CLEMENS, W. A.: Rhaeto-Liassic Mammals from Switzerland and West Germany.

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Figures 1 and 2 drawn to same scale. Scale below Fig. 1a equals 1 mm. Figures 3 to 5 drawn to a different scale. Scale below Fig. 3a equals 1 mm.

Fig. 1: *Helvetiodon schutzi*, type, Hallau local fauna, AIII-348 (NC 20), tentatively identified as a right, upper molariform, enamel-covered areas rendered in darker tones: a, occlusal view, tentative orientation anterior to left, lingual upwards; b, lateral, probaly buccal view, anterior to left; and c, lateral, probably lingual view, anterior to right.

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Die Arten der Gattungen *Dactylioceras, Nodicoeloceras,*
Peronoceras und *Collina*

MÜNCHEN 1981

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von

A. von HILLEBRANDT* & R. SCHMIDT-EFFING**

mit 8 Tafeln und 26 Abbildungen

Aufteilung:

1. Einleitung: v. Hillebrandt
2. Fundpunkte (Profile): v. Hillebrandt
3. Paläontologischer Teil:
   Dactylioceras und *Nodicoeloceras:* Schmidt-Effing
   Peronoceras und *Collina:* v. Hillebrandt
4. Biostratigraphische Folgerungen: v. Hillebrandt und Schmidt-Effing

KURZFASSUNG

Aus 23 Juraprofilen der Hochkordillere Nordchiles werden aus dem unteren und mittleren Toarcium, die dort vorkommenden Arten der Gattungen *Dactylioceras (Eodactylites)*, *Dactylioceras (Orthodactylites)*, *Nodicoeloceras, Peronoceras* und *Collina* beschrieben. Insgesamt werden 24 Arten bzw. Unterarten bekannt gemacht, von denen 7 Arten bzw. Unterarten neu sind. Mit Hilfe der Dactylioceratidae läßt sich in Chile das untere und mittlere Toarcium biostratigrapisch in 6 Zonen bzw. Subzonen unterteilen, die sich z. T. sehr gut mit gleichaltrigen Zonen in Europa vergleichen lassen.

Die *tenuicostatum*-Zone ist in 2 Subzonen gegliedert, wobei die tiefere Subzone durch *Dactylioceras (Eodactylites) simplex* charakterisiert wird, eine Art und Untergattung des Mediterran-Bereichs. Die Leitform der höheren Subzone ist *Dactylioceras (Orthodactylites) tenuicostatum,* das in Chile durch eine neue Unterart vertreten wird. Das Zeitäquivalent der *falcifer*-Zone in Europa ist die *hoelderi*-Zone, die durch *Dactylioceras (Orthodactylites) hoelderi* n. sp. und *Dactylioceras (Orthodactylites) helianthoides* gekennzeichnet wird. Letztere Art ist für den pazifischen Raum (Japan, Kanada, Chile) typisch. Wie im Mediterran-Gebiet tritt *Peronoceras* bereits in der basalen *bifrons*-Zone auf und nicht erst in der mittleren *bifrons*-Zone wie in NW-Europa. Die *bifrons*-Zone kann durch neue Arten der Gattungen *Peronoceras* und *Collina* untergliedert werden, die mit europäischen Artgruppen nahe verwandt sind und einen biostratigraphischen Vergleich ermöglichen. Es werden die Subzone des *Peronoceras largaense*, die Subzone des *Peronoceras pacificum* und die Subzone der *Collina chilensis* unterschieden. Im oberen Horizont der *chilensis*-Subzone treten mit einem Durchmesser von 16 cm die größten bisher bekannten Vertreter der Gattung *Peronoceras* auf.

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* Prof. Dr. A. von HILLEBRANDT, Institut für Geologie und Paläontologie der Technischen Universität Berlin, Hardenbergstraße 42, D-1000 Berlin 12.

** Doz. Dr. R. SCHMIDT-EFFING, Geologisch-Paläontologisches Institut der Universität Münster, Gievenbecker Weg 61, D-4400 Münster.

ABSTRACT

From 23 Jurassic profiles of the Northern Chilian high Cordilleras species of the genera *Dactylioceras (Eodactylites), Dactylioceras (Orthodactylites), Nodicoeloceras, Peronoceras* and *Collina* are described which occur here in the Lower and Middle Toarcian strata. Altogether 24 species, respectively subspecies are made known, 7 of which are new. The Chilian Lower and Middle Toarcian may be subdivided biostratigraphically by means of Dactylioceratidae into 6 zones or subzones that partly may well be compared with European zones of the same age.

The *tenuicostatum* zone is divided into 2 subzones, whereby the lower subzone is characterized by *Dactylioceras (Eodactylites) simplex* being a species and subgenus of the mediterranean region. *Dactylioceras (Orthodactylites) tenuicostatum,* represented in Chile by a new subspecies, is the index fossil of the upper subzone. Chronologically the European *falcifer* zone is equivalent to the *hoelderi* zone which is characterized by *Dactylioceras (Orthodactylites) hoelderi* n. sp. and *Dactylioceras (Orthodactylites) helianthoides.* The latter species is typical for the Pacific region (Japan, Canada and Chile). Similar to the mediterranean, *Peronoceras* already appears at the basis of the *bifrons* zone and by no means within the *bifrons* zone as known from northwestern Europe. The *bifrons* zone may be subdivided by new species of the genera *Peronoceras* and *Collina* which show close relationship with European species groups and which render possible biostratigraphical comparison. Three subzones as there are the subzone of *Peronoceras largaense,* the subzone of *Peronoceras pacificum* and the subzone of *Collina chilensis* are differantiated. With a diameter of 16 cm, the largest represantatives of the genus *Peronoceras*, so far known, do appear in the upper horizon of the *chilensis* subzone.

RESUMEN

De los géneros *Dactylioceras (Eodactylites), Dactylioceras (Orthodactylites), Nodicoeloceras, Peronoceras* y *Collina* se describe todas las especies encontradas en las capas del Toarciano Inferior y Medio de 23 secciones del Jurásico de la Cordillera Alta de Chile septentrional. En total 24 especies respectivamente subespecies están estudiadas, de las cuales 7 son nuevas. A base de los representantes de la familia Dactylioceratidae se clasifica bioestratigráficamente el Toarciano Inferior y Medio de Chile en 6 zonas respectivamente subzonas las que permiten en general una buena comparación con las zonas correspondientes de Europa.

La zona de *tenuicostatum* se divide en dos subzonas: La subzona inferior está caracterizada por *Dactylioceras (Eodactylites) simplex,* un elemento muy mediterráneo, la superior por *Dactylioceras tenuicostatum chilense* que es una forma noroccidental europea por su especie, un elemento endémico en Chile por su subespecie. A la zona de *falcifer* de Europa corresponde en Chile la zona de *hoelderi* caracterizada por *Dactylioceras (Orthodactylites) hoelderi* n. sp. y *Dactylioceras (? Orthodactylites) helianthoides.* Esta especie es un elemento faunistico del área Pacifica (Japón, Canadá, Chile). *Peronoceras* ya aparece en la base de la zona de *bifrons* como en el área mediterránea y no en la parte media de la zona de *bifrons* como en Europa noroccidental. Nuevas especies de los géneros *Peronoceras* y *Collina* facilitan la subdivisión de la zona de *bifrons*, las cuales corresponden con grupos de especies europeas por su filogenia y permiten así una comparación bioestratigráfica. Se distingue la subzona de *Peronoceras largaense*, la subzona de *Peronoceras pacificum* y la subzona de *Collina chilensis*. En el horizonte superior de la subzona de *chilensis* se encuentra con un diámetro de 16 cm los representantes más grandes del género *Peronoceras* conocido hasta ahora.

INHALTSVERZEICHNIS

Prof. Dr. Helmut Hölder
zum 65. Geburtstag gewidmet.

1. EINLEITUNG

Die Aufnahme der Profile, aus denen die Dactylioceratidae stammen, erfolgte durch den ersten der beiden Autoren in den Jahren 1966 bis 1968 während eines Aufenthaltes als Gastdozent am Departamento de Geología der Universidad de Chile in Santiago de Chile und im Südsommer 1971/72 im Rahmen einer von der Deutschen Forschungsgemeinschaft unterstützten Forschungsreise nach Argentinien und Chile (v. Hillebrandt 1970, 1971, 1973 a, b). Die bisher in Chile gefundenen Dactylioceratidae stammen sämtlich aus Juraprofilen der Hochkordillere zwischen der Cordillera de la Punilla im Süden (29°30′ südl. Br.) und der Cordillera Domeyko im Norden (25° südl. Br.). Artlich bestimmbare Dactylioceratidae wurden zwischen der Quebrada Chanchoquin (28°50′ südl. Br.) und dem Salar de Pedernales (26°13′ südl. Br.) gefunden (Abb. 1). Dactylioceratidae sind im chilenischen Unter- und Mittel-Toarcium (*tenuicostatum-* bis *bifrons*-Zone) verhältnismäßig häufig, zumeist häufiger als die mit ihnen zusammen vorkommenden Hildoceratidae. Die verschiedenen Gattungen und Arten der Dactylioceratidae ermöglichen eine detaillierte biostratigraphische Unterteilung des Unter- und Mittel-Toarcium in Zonen, Subzonen und Horizonte, die gut mit gleichaltrigen biostratigraphischen Einheiten in Europa verglichen werden können. Aus diesem Grund erschien eine monographische Bearbeitung dieser Ammoniten-Familie besonders wichtig und lohnend, besonders auch deswegen, weil bisher aus dem südamerikanischen Jura nur eine einzige Art der Dactylioceratidae beschrieben und abgebildet wurde (Rigal 1930).

Allen Kollegen, Freunden und Institutionen, die diese Aufsammlungen unterstützten und bei der Auswertung behilflich waren, sei an dieser Stelle gedankt.

Zum Studium von Originalen und Vergleichsmaterial wurden folgende Sammlungen aufgesucht: Bayerische Staatssammlung für Paläontologie und historische Geologie in München, Staatliches Museum für Naturkunde in Stuttgart, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Geologisch-Paläontoligisches Institut der Universität Freiburg i. Br., Naturhistorisches Museum Basel, Museum für Naturkunde der Humboldt Universität in Berlin.

Das Belegmaterial zu dieser Arbeit wird in der Bayerischen Staatssammlung für Paläontologie und historische Geologie in München unter der Inventarnummer 1978 II aufbewahrt.

2. FUNDPUNKTE (PROFILE)

Es werden nur diejenigen Fundpunkte aufgeführt, die bei der Beschreibung der verschiedenen Arten berücksichtigt wurden. Daneben gibt es weitere Profile mit Dactylioceraten, die jedoch bei der monographischen Bearbeitung nicht ausgewertet wurden, da sie zu schlecht erhalten waren und zumeist artlich nicht bestimmt werden konnten.

Bei den meisten Fundpunkten wird das gesamte oder zumindest ein Teil des Profils beschrieben, aus dem die Dactylioceraten stammen, um einen besseren Überblick über die Stratigraphie und Lage der Fossilhorizonte zu ermöglichen.

Bei den Abbildungen der Profile wurden schichtparallele, postjurassische Porphyritintrusionen weggelassen.

In den Fossillisten bedeutet ss = sehr selten, s = selten, h = häufig und sh = sehr häufig.

2.1 SALAR DE PEDERNALES
(Abb. 1, Profil 1)

Das Juraprofil, aus dem mehrere Bruchstücke von *Peronoceras* cf. *moerickei* n. sp. stammen, liegt am Westrand des Salars, etwa in der Mitte zwischen den Punkten 3351 im Salar und 3610 westlich des Salars (Karte 1:100000, Blatt Potrerillos).

Die Mächtigkeit des Jura bis zum mittleren Bajocium beträgt 350 bis 400 m.

Das Liegende bilden grünliche Tuffe der ? Trias. Der Jura beginnt mit 12 bis 15 m mächtigen Sandsteinen, die konglomeratische Lagen an der Basis enthalten. Etwa 8 bis 10 m über der Basis sind Fossilien häufig:

Montlivaltia sp. s
Modiolus sp. s
Entolium
Chlamys sp. s
Weyla sp. h
Myophorella catenifera (Hupé) s
Pleuromya sp. s
Homomya neuquena Leanza s
Radstockiceras sp. 1 s

Die Fauna gleicht der der Basisschichten des Portezuelo de Pedernales und der oberen Quebrada El Asiento, die dort in den oberen Teil des unteren Pliensbachium (± davoei-Zone) zu stellen sind. Ungefähr 2 m über dieser Fossilschicht folgt ein Horizont mit *Atractites* sp.

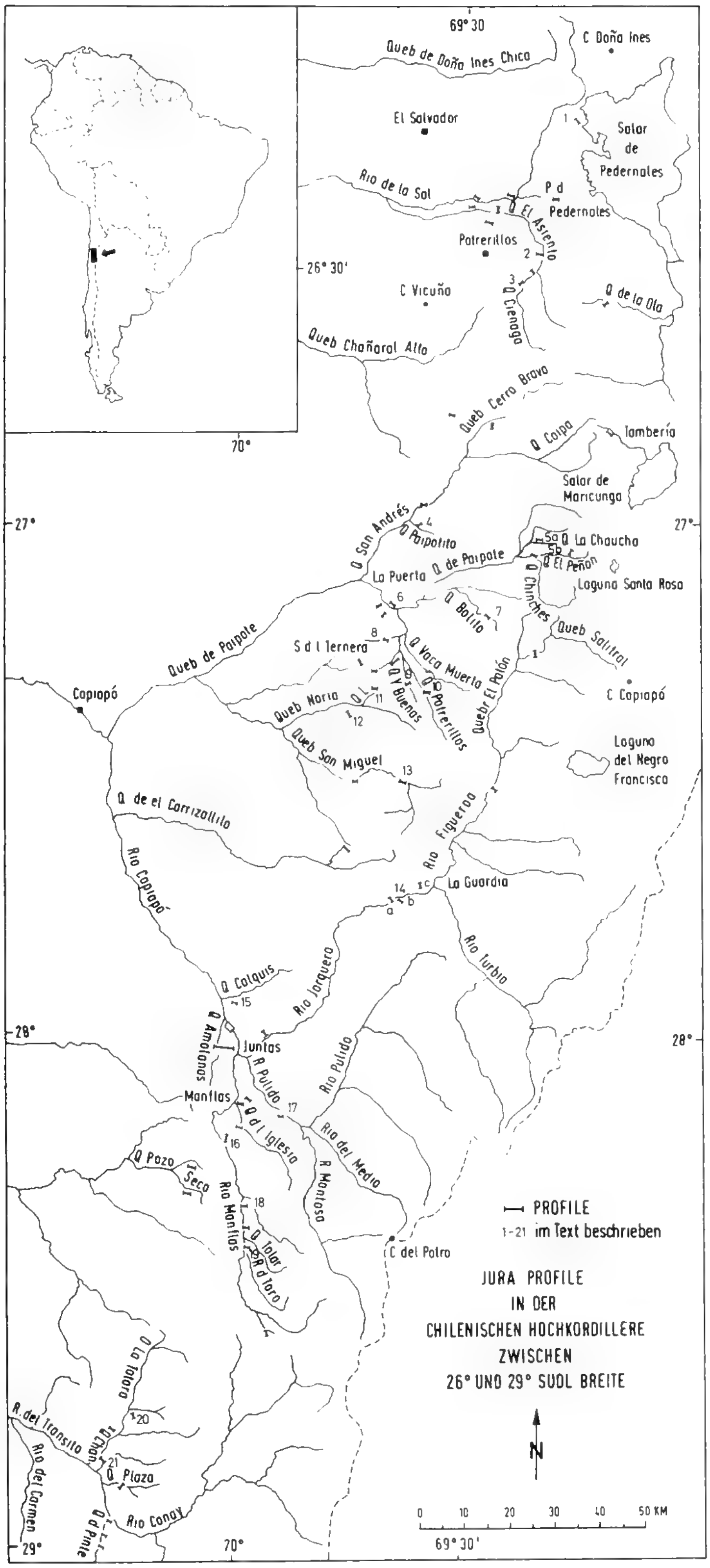

Abb. 1: Übersichtskarte mit Juraprofilen in der chilenischen Hochkordillere zwischen 26° und 29° südl. Breite und Angabe der im Text beschriebenen Profile mit Dactylioceraten (1 bis 21).

Nach dem Hangenden zu wird die Schichtfolge kalkiger und geht in dunkle, gut gebankte Kalke mit schiefrigen Zwischenlagen über. Aus diesen Kalken (ewa 100 m über der Basis) stammt *Peronoceras moerickei* n. sp., zusammen mit *Harpoceras* cf. *subexaratum*, *Maconiceras* sp. und einer neu zu beschreibenden Gattung und Art der Hildoceratidae. Diese Fossilschicht ist in den obersten Teil des unteren Toarcium zu stellen *(chilensis* -Subzone).

Knapp 200 m über der Basis enthalten die Bankkalke *Phymatoceras* div. sp. und verkieselte Pelecypoden *(Nuculana, Grammatodon, Myophorella, Mesomiltha, Rollierella)* .

Hangend folgen Schichten reich an Brachiopoden („*Rhynchonella*", „*Terebratula*"), weniger häufig sind Pelecypoden, selten Ammoniten (*Pleydellia* cf. *fluitans*, *Bredyia* sp.). Diese Schichten gehören dem Grenzbereich Toarcium/Aalenium an.

Es folgen weiterhin Bank- bis Knollenkalke, bei 270 m über der Basis mit großwüchsigen *Entolium* und *Modiolus*.

In den hangendsten dunklen, bituminösen Bankkalken kommen vor (v. HILLEBRANDT 1970, S. 189; WESTERMANN & RICCARDI 1972, S. 20):

Dorsetensia romani (OPPEL)
Dorsetensia liostraca BUCKMAN forma tecta BUCKMAN
Stephanoceras cf. *humphriesianum* (SOW.)

Die Fauna ist in das mittlere Bajocium *(humphriesianum*-Zone) zu stellen.

Aus den bituminösen Kalken gehen Kalke mit zunehmendem Feinsandgehalt hervor, die ihrerseits in zunächst Feinsandsteine, dann mittel- bis grobkörnige Sandsteine der Asientos-Formation des Callovium übergehen.

2.2 QUEBRADA EL ASIENTO UND PORTEZUELO DE PEDERNALES

Im Bereich der oberen Quebrada El Asiento wurden in mehreren Horizonten Dactylioceraten gefunden. Auf der Übersichtskarte (Abb. 2) sind sämtliche im Bereich des Rio de la Sal, Portezuelo de Pedernales, Quebrada El Jardin, Quebrada El Asiento und Quebrada El Hueso aufgenommenen Profile angegeben. Die beschriebenen Dactylioceraten stammen aus den Profilen 1, 3 und 4 (Abb. 2). Das abgebildete Profil (Abb. 3) der oberen Quebrada El Asiento entspricht Profil 3 (Abb. 2). Die Fossilangaben (Abb. 3) beziehen sich auf die Profile 3 bis 7, sowie 16.

Im Bereich der Profile 3 bis 6 (Abb. 2) transgrediert der Jura auf Granit oder Porphyrit. An einigen Stellen greift er taschenförmig mit einer Mächtigkeit bis ca. 5 m in den Untergrund. Die Taschenfüllungen beginnen mit einer groben Brekzie, die hauptsächlich aus dem aufgearbeite-

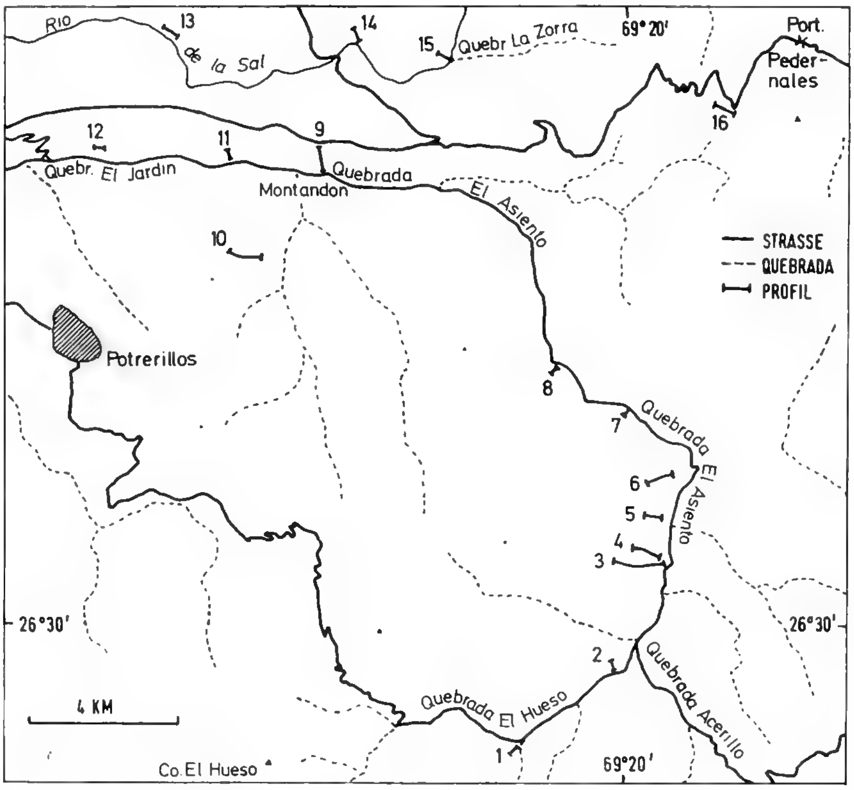

Abb. 2: Übersichtskarte über die im Bereich des Rio de la Sal, Portezuelo de Pedernales, Quebrada El Jardin, Quebrada El Asiento und Quebrada El Hueso aufgenommenen Profile. Profile 1, 3 und 4 mit im Text beschriebenen Dactylioceraten.

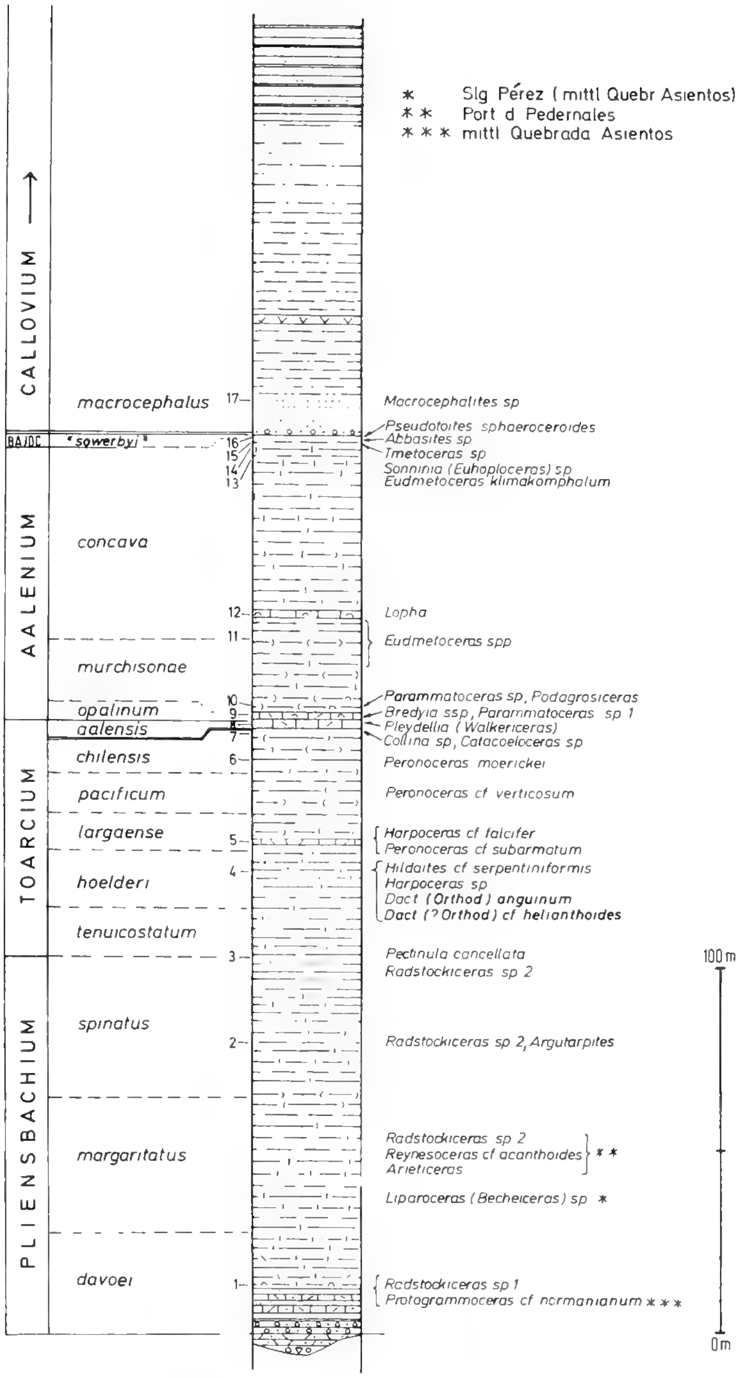

Abb. 3: Juraprofile (Lias bis Basis Callovium) der Quebrada El Asiento (Abb. 2, Profil 3); intrusive, ± schichtparallele Porphyrite nicht berücksichtigt; Fossilangaben ohne Stern(e) aus den Profilen 3 bis 6 (Abb. 2), * Sammlung Pérez (mittlere Quebrada El Asiento bei Profil 7, Abb. 2), ** Portezuelo de Pedernales (Profil 16, Abb. 2), *** mittlere Quebrada El Asiento (Profil 7, Abb. 2); Legende zur Gesteinsausbildung Abb. 10.

ten Untergrund besteht. Es folgen Sandsteine, die zum Hangenden hin kreuzgeschichtet sind. Fossilschutt tritt bereits in der basalsten Schicht auf.

Über diesen Taschenfüllungen oder direkt über dem Porphyrit bzw. Granit liegt eine konglomeratische Brekzie, die ebenfalls fehlen kann. Es folgen sandige Fossilschuttbänke mit einzelnen Geröllen und umgelagerten Korallenstöcken.

Etwa 10 bis 15 m über der Basis (je nach Mächtigkeit der Basalschichten) liegt zwischen zwei sandigen Fossilschuttkalkbänken eine um 50 cm mächtige, fossilreiche Schicht (Schicht 1, Abb. 3). Am häufigsten sind Muscheln, die vorwiegend doppelklappig erhalten sind, Einzelklappen stecken ohne Orientierung im Sediment. Korallen und Brachiopoden sind seltener, Ammoniten und Gastropoden sind sehr selten.

Andenipora liasica Gerth s
Montlivaltia sp. h
,,*Rhynchonella*" sp. s
,,*Terebratula*" sp. s bis h
Gryphaea sp. (kleinwüchsig) s
Lopha sp. ss
Modiolus cf. scalprus (Sow.) s
Modiolus cf. baylei (Philippi) h
Oxytoma sp. ss
Entolium demissum (Philipps) h
Weyla sp. h
Myophorigonia neuquensis (Groeber) ss
Myophorigonia sp. h
Jaworskiella burckhardti (Jaw.) s
Quadratojaworskiella pustulata (Reyes & Perez) ss
Myophorella catenifera (Hupé) h
Mesomiltha huayquimili (Leanza) h
Astartidae gen. et sp. indet h
Protocardia (?) sp. (= Gen. et sp. indet. in Leanza) ss
Sphaeriola liasica (Carral Tolosa) h
Pholadomya corrugata Koch & Dunker in Leanza s
Pholadomya cf. *plagemanni* Möricke in Leanza s
Bucardiomya sp. ss
Homomya rotundocaudata (Leanza) s
Pleuromya sp. s
Actaeon sp. s
Radstockiceras sp. 1 s

Bei den Profilen 7 und 16 (Abb. 2) kommt in dem gleichen Fossilhorizont zusätzlich *Protogrammoceras* cf. *normanianum* (d'Orb.) vor. Eine sehr ähnliche Fauna wurde aus annähernd gleichaltrigen Schichten von Piedra Pintada (Provinz Neuquen, Argentinien) (Leanza 1942) beschrieben.

Hangend folgen nochmals einige Fossilschuttkalkbänke. Diese Serie geht allmählich über in dunkle, gut gebankte, dichte Kalke, die mit Kalkmergeln wechsellagern. In diesen Schichten kommen *Radstockiceras* sp. 2 und *Argutarpites* sp. vor. Herr Perez (Santiago de Chile) fand in diesen Schichten bei Profil 7 ein *Liparoceras (Becheiceras)* sp. Am Portezuelo de Pedernales ist im basalen Teil dieser Schichtfolge ein fossilreicher Horizont ausgebildet:

,,*Rhynchonella*" sp. (2 Arten) h
,,*Terebratula*" sp. s
Modiolus sp. ss
Oxytoma sp. ss
Frenguelliella tapiai Lambert h
Mesomiltha huayquimili (Leanza) sh
Cardinia sp. ss
Omphaloptycha sp. h
Cenoceras sp. ss
Phylloceras sp. s
Lytoceras sp. ss
Radstockiceras sp. 2 h
Arieticeras sp. s
Reynesoceras cf. *acanthoides* (Reynès) s
Atractites sp. s

Im Bereich der oberen Quebrada El Asiento (Profile 2 bis 6, Abb. 2) ist in diese Kalkbankserie des oberen Pliensbachium ein bis über 40 m mächtiger Porphyrit intrudiert, weitgehend schichtparallel (auf Abb. 3 weggelassen).

Die Kalkbankserie wird im hangenden Teil dünnbankiger und schiefrig. Einzelne Lagen bestehen aus Vollpflastern von *Pectinula cancellata* Leanza (Schicht 3, Abb. 3).

Hangend folgen zunächst wieder dunkle Bankkalke und dann eine etwa 6 m mächtige Serie rostbraun anwitternder Kalke mit geringmächtigen Mergelzwischenlagen und folgender Fauna (Schicht 4, Abb. 3):

,,*Rhynchonella*" sp. h
,,*Terebratula*" sp. h
Propeamussium sp. h
Dactylioceras (Orthodactylites) anguinum (Reinecke) s
Dactylioceras (? *Orthodactylites*) cf. *helianthoides* Yokoyama s
Nodicoeloceras cf. *crassoides* (Simpson) Form B ss
Nodicoeloceras cf. *crassoides* (Simpson) Form C ss
Hildaites cf. *serpentiniformis* (Buckman) ss
Harpoceratoides cf. *alternatus* (Simpson) ss

Über diesen rostbraun anwitternden Kalken liegen knollige Kalke mit *Peronoceras* cf. *subarmatum* und *Harpoceras* cf. *falcifer* im liegenden Teil (Schicht 5), *Peronoceras* cf. *verticosum* im mittleren Teil, *Peronoceras moerickei* n. sp. im oberen Teil (Schicht 6) und *Collina* sp. und *Catacoeloceras* sp. im hangendsten Abschnitt (Schicht 7).

Bei Profil 1 (Abb. 2) (= Profil 3, Abb. 1) tritt im hangendsten Teil dieser Knollenkalke *Peronoceras* cf. *vortex* auf. Über diesen Kalken des unteren Toarcium liegt ein 4 bis 6 m mächtiger, besonders an der Basis sandiger Fossilschuttkalk, der in sich 0,3 bis 1,0 m gebankt ist. Dieser Fossilschuttkalk greift mit kleinen Taschen und Bohrgängen (∅ 1 bis 3 cm) bis 30 cm tief in die liegenden Bankkalke. Im unteren Teil dieses Fossilschuttkalkes (Schicht 8) kommt *Pleydellia (Walkericeras)* cf. *fluitans* und im oberen Teil (Schicht 9) *Bredyia* sp. und ,,*Parammatoceras*" sp. 1 vor.

Zwischen den Knollenkalken und dem Fossilschuttkalk ist eine Schichtlücke vorhanden, die den größten Teil des oberen Toarcium umfaßt.

Besonders in der hangendsten Bank ist bei allen Profilen eine großwüchsige ,,*Terebratula*" häufig. Bei Profil 6 kommt auch eine Lage mit ,,*Rhynchonella*" sp. vor. Muscheln sind weniger häufig, bei diesen ist am häufigsten

Lopha, selten *Chlamys, Modiolus, Pholadomya* cf. *plagemanni* und *Pleuromya.* Sehr selten sind reguläre Seeigel. Die Fossilien liegen nicht orientiert im Sediment. Die Muscheln sind häufig doppelklappig.

Über dem Fossilschuttkalk folgen 4 bis 5 m mächtige, fossilschuttreiche, knollige Kalke, in denen ein großwüchsiges *Entolium* (z. T. doppelklappig) häufig ist. Etwa 2,5 bis 3 m über dem Fossilschuttkalk kommt *„Parammatoceras“* sp. 2 und *Podagrosiceras* cf. *athleticum* vor (Schicht 10, Abb. 3).

Die Schichtfolge geht mit knolligen bis gut gebankten, vorwiegend dichten Kalken mit mehreren Arten der Gattung *Eudmetoceras* weiter. Eine 1,5 m mächtige Bank (Schicht 12) setzt sich fast ausschließlich aus *Lopha* (vorwiegend doppelklappig) zusammen.

Hangend folgen wieder gut gebankte, seltener knollige Kalke mit häufig desmodonten Muscheln *(Pleuromya)* im hangenden Teil. Im hangendsten Abschnitt (Schicht 13) kommen *Eudmetoceras klimakomphalum* und *Sonninia (Euhoploceras)* vor. In Schicht 14 ist *Tmetoceras* häufig. Schicht 15 enthält *Abbasites* und Schicht 16 *Pseudotoites sphaeroceroides.*

Auf diese Serie transgrediert mit einem geringmächtigen Konglomerat das Callovium. Das mittlere und obere Bajocium, sowie Bathonium fehlen.

2.3 QUEBRADA PAIPOTITO

(Abb. 1, Profil 4)

Die Quebrada Paipotito ist eine linke Seitenquebrada der Quebrada San Andrés. Im Jura dieser Quebrada wurde 1966 ein Profil, 2 km oberhalb der Quebrada San Andrés, auf der rechten Talseite aufgenommen. Das gleiche Profil beschrieben Cisternas & Vicente (1976).

Das aus diesem Profil abgebildete *Peronoceras* cf. *vortex* (Taf. 6, Fig. 1) stammt aus den basalen, 2 bis 3 m mächtigen, dunkelgrauen bis schwärzlichen, 5 bis 20 cm gebankten Plattenkalken, die mit intrusivem Kontakt an graue Porphyrite grenzen. Aus der folgenden, mergeligkalkigen Serie mit Sandsteinen geben Cisternas & Vicente (1976) *Phymatoceras* (ob. Toarcium) an. Die bei diesen Autoren als a4 bezeichneten Schichten enthalten *Gryphaea* cf. *bilobata* Sow., die im Aalenium der chilenischen Hochkordillere in mehreren Profilen vorkommt. Die vorwiegend sandige Schichtfolge (a5 bei Cisternas & Vicente) im Hangenden muß zumindest im oberen Teil dem Callovien zugerechnet werden, da in dieser *Gryphaea* cf. *santiagensis* Hupé (in Gottsche 1878) vorkommt. Es ist dies eine im Callovium von Chile und Argentinien weit verbreitete Art.

2.4 QUEBRADA LA CHAUCHA UND QUEBRADA EL PEÑON

(Abb. 1, Profile 5 a u. b; Abb. 3 a)

Die Quebrada La Chaucha ist eine östliche Seitenquebrada der Quebrada Vizcachas, die ihrerseits in die oberste Quebrada de Paipote mündet. Das in der Quebrada La Chaucha aufgeschlossene Juraprofil ist überkippt. Das Liegende des Jura wird von Tonen und Sandsteinen gebildet, die Pflanzenreste der oberen Trias enthalten.

Der Jura beginnt mit einer 10 bis 15 m mächtigen Sandsteinserie. Die obersten 1 bis 2 m sind als Fossilschuttsandstein mit *Weyla* entwickelt.

Die hangenden Schichten sind schlecht aufgeschlossen und vorwiegend kalkig-mergelig ausgebildet. Aus dieser Schichtfolge (etwa 20 m mächtig) stammen nicht aus dem Anstehenden entnommene Dactylioceraten: *Dactylioceras (Orthodactylites) tenuicostatum chilense, Dact. (Orthod.)* cf. *directum, Dactylioceras* sp., *Peronoceras* cf. *renzi, Peronoceras* sp. Die *Dactylioceras*-Arten stammen aus der *tenuicostatum*-Subzone, *Peronoceras* aus jüngeren Schichten *(largaense*-Subzone).

Es folgt ein 2 m mächtiger Fossilkalk mit *Bredyia* sp., *„Parammatoceras“* sp. 1, *Lopha,* Isognomonidae nov. gen. nov. sp. (cf. *Gervilleioperna), Ctenostreon* cf. *pectiniformis* (v. Schloth.), *Trigonia, Mesomiltha, Neocrassina andium* (Gottsche), *Trigonastarte* (?) *steinmanni* (Möricke), *Pleuromya* und *„Terebratula“.* Dieser Fossilkalk ist in das basale Aalenium zu stellen. Er wird von ammonitenreichen Kalkmergeln mit *Eudmetoceras* und *Tmetoceras* des mittleren Aalenium überlagert.

Etwa 35 m im Hangenden dieses Fossilkalkes enthält ein 20 cm mächtiger Fossilkalk *Sonninia (Papilliceras) espinazitensis* Tornquist und *Pseudotoites sphaeroceroides* (Tornquist) des unteren Bajocium (Grenzbereich *„sowerbyi“/sauzei*-Zone). Etwa 8 bis 10 m im Hangenden folgt ein 4 m mächtiger Sandstein, der von 35 bis 40 m mächtigen Mergeln überlagert wird.

Die hangende, etwa 200 m mächtige, kalkig-sandige Serie ist in das Callovium zu stellen.

Auf das Juraprofil der Quebrada El Peñon machte mich Herr J. Davidson (Departamento de Geología, Universidad de Chile, Santiago de Chile) aufmerksam. Zusammen mit ihm nahm ich im Januar 1979 dieses Profil auf. Der Profilausschnitt (Abb. 3 a) wurde etwa 400 m unterhalb der Lokalität El Peñon (topographische Karte 1 : 100 000, Blatt Laguna del Negro Francisco) auf der rechten Talseite aufgenommen.

Die Transgression des marinen Jura auf eine mächtige Serie von vorwiegend Sandsteinen der ? Trias ist auf der rechten Talseite ca. 800 m unterhalb der Lokalität El Peñon aufgeschlossen.

Der Jura beginnt mit einer oolithischen Bank, es folgen Kalksandsteine (z. T. mit Fossilschutt), die in Mürbsandsteine übergehen. Diese Schichtfolge ist etwa 7 m mäch-

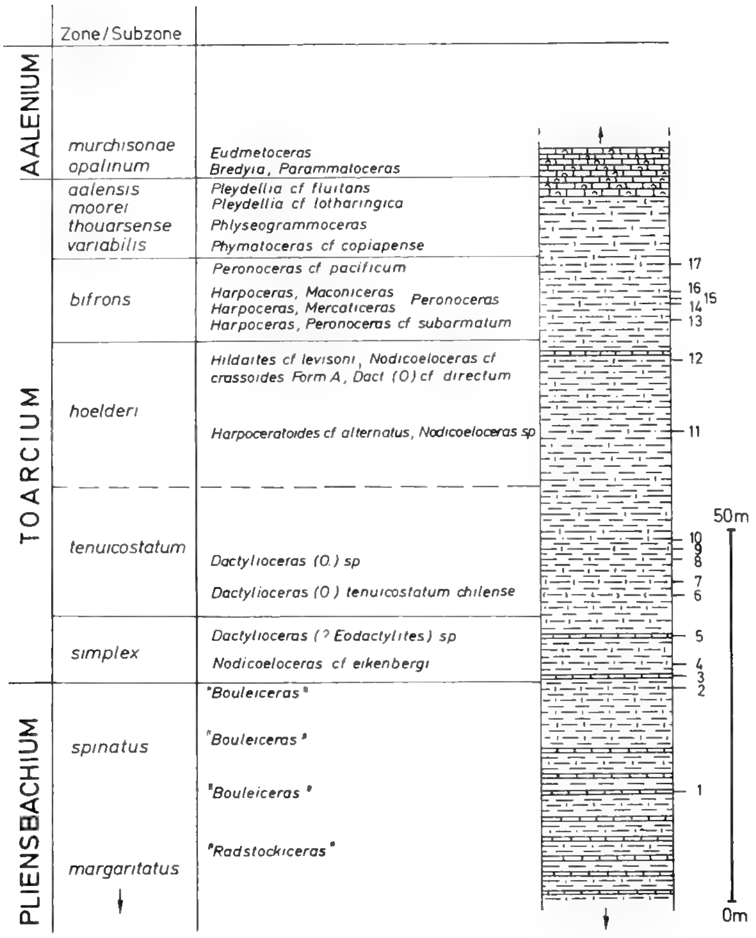

Abb. 3a: Teilprofil des Jura der Quebrada El Peñon (Abb. 1, Profil 5b); Legende zur Gesteinsausbildung Abb. 10.

tig, und über ihr liegt die erste Fossilschicht mit *Andenipora liasica*, ,,*Rhynchonella*", ,,*Terebratula*", *Gryphaea*, *Pseudolimea*, *Mesomiltha* und *Pleuromya*. Es folgen ca. 1 m mächtige, mürbe Fossilschichten mit härteren Kalkbänken, dann dickbankige (bis 1 m ∅) Fossilschuttkalke mit mergeligen Zwischenlagen und z. T. großwüchsigen *Weyla*. Häufig ist ,,*Rhynchonella*". In der drittletzten Bank kommt *Pinna* in Lebensstellung vor, und in der obersten Bank ist *Pholadomya* häufig. Diese Schichten sind insgesamt ca. 10 m mächtig und enthalten folgende Fauna:

,,*Rhynchonella*" sp.
,,*Terebratula*" sp.
Bryozoa gen. et sp. indet.
Gryphaea sp.
Lopha sp.
Modiolus sp.
Gervilleioperna turgida LEANZA
Pinna sp.
Camptonectes sp.
Chlamys cf. *textoria* (SCHLOTH.)
Weyla sp.
Pseudolimea sp.
Mesomiltha sp.
Pholadomya corrugata KOCH & DUNKER in LEANZA
Pholadomya sp.
Actaeon sp.

Ammoniten wurden keine gefunden, jedoch läßt sich die Fauna bei Vergleich mit anderen Lokalitäten in das untere Pliensbachium einstufen.

Über diesen fossilreichen Schichten liegt eine etwa 8 m mächtige Serie gut gebankter Fossilschuttkalke, die in ebenfalls gut gebankte Kalke mit weniger Fossilschutt übergehen. Im basalen Teil enthalten diese Kalke *Radstockiceras* und *Protogrammoceras* und im höheren Teil *Radstockiceras* und *Argutarpites*.

Die Schichtfolge des detailliert aufgenommenen Profilabschnittes (Abb. 3 a) beginnt in den Kalken mit *Radstokkiceras* und selten *Pectinula cancellata*. Das oberste Pliensbachium und tiefere Toarcium besteht aus einer Wechsellagerung von mehr oder minder mergeligen, z. T. knolligen Kalkbänken mit dunklen, z. T. bituminösen Mergeln. Die Ammoniten dieser Serie lassen sich am besten aus dem Grenzbereich der Kalkbänke zu den Mergeln gewinnen. *Pectinula cancellata* tritt in dieser Serie wiederholt auf, daneben ist seltener *Mesomiltha* und *Pleuromya* vorhanden.

Bei Schicht 1 (Abb. 3 a) ist eine 60 cm mächtige Kalkbank aufgeschlossen, in der schlecht erhaltene ,,*Bouleiceras*" sp. (v. HILLEBRANDT 1973 a, S. 359) häufig sind.

Herr WIEDENMAYER (Naturhistorisches Museum Basel) machte mich darauf aufmerksam, daß die von mir (V. HILLEBRANDT 1973 a) aus Argentinien beschriebenen *Bouleiceras* sp. nicht zu dieser Gattung zu rechnen sind, sondern große Ähnlichkeit mit Ammoniten aufweisen, die von FUCINI (1931) aus dem obersten Pliensbachium von Sizilien beschrieben wurden. Nach GUEX (1974) ist *Taurومeniceras* ein unmittelbarer Vorläufer von *Bouleiceras*. Diese Gattung kommt auch im obersten Pliensbachium von Portugal (MOUTERDE 1967) und Südspanien (MOUTERDE et al. 1971) vor.

Auch in den folgenden Schichten treten Querschnitte von „*Bouleiceras*“ sp. auf. Zwischen Schicht 2 (20 cm Kalkbank mit Fossilschutt an der Basis und „*Bouleiceras*“ sp.) und 3 treten die letzten Querschnitte von „*Bouleiceras*“ sp. auf. Etwa 1,5 m hangend Schicht 2 wurden in einer bräunlich anwitternden, ca. 20 cm mächtigen Kalkbank (Schicht 3) die ersten nicht näher bestimmbaren und unvollständigen Exemplare von *Dactylioceras* gefunden.

Die Schichten mit „*Bouleiceras*“ sp. sind in das oberste Pliensbachium zu stellen. Das Toarcium beginnt mit Schicht 3. Schicht 4 (20 cm Kalkbank) enthält eine Reihe untereinander sehr ähnlicher Dactylioceraten, die nicht direkt zu *Dactylioceras (Eodactylites)* gestellt werden können, obwohl sie sicherlich nicht weit davon entfernt sind. Es sind Formen die *Nodicoeloceras* cf. *eikenbergi* entsprechen. Diese Art kommt in England im tieferen Teil der *tenuicostatum*-Zone vor.

In Schicht 5 (30 cm Bank) treten Querschnitte kräftig berippter Formen auf, die vielleicht zu *Dactylioceras (Eodactylites)* zu stellen sind.

In Schicht 6 (10 bis 20 cm Bank) und 7 sind *Dactylioceras (Orthodactylites) tenuicostatum chilense* häufig, in Schicht 6 kommt zusätzlich selten *Nodicoeloceras* sp. und *Dactylioceras (Orthodactylites) helianthoides* vor.

Schicht 8 enthält Bruchstücke eines großwüchsigen *Dactylioceras (Orthodactylites)* sp.. Etwa 1 m hangend (Schicht 9) tritt ein schiefriger Kalk auf mit *Weyla*, *Mesomiltha*, *Pleuromya* und nicht näher bestimmbaren Fragmenten von *Dactylioceras*.

Ungefähr 1 m im Hangenden (Schicht 10) folgen feinsandige Kalke mit einer kleinwüchsigen „*Terebratula*“ und *Propeamussium* sp. Die hangende Schichtfolge besteht hauptsächlich aus Mergeln, die zu Beginn noch geringmächtige Kalkbänke und sehr häufig „*Terebratula*“ (kleinwüchsig) enthalten. Dann beginnt eine Serie aus dm-gebankten (bis 30 cm Ø), bräunlich anwitternden Kalkbänken. Etwa 1,5 m über Beginn dieser Serie enthält eine Bank (Schicht 11) häufig *Harpoceratoides* cf. *alternatus* und selten *Nodicoeloceras* sp. Diese Ammonitenbank kann bereits der *hoelderi*-Zone zugeordnet werden.

Im Folgenden treten wieder Bänke mit „*Terebratula*“ auf, denen Mergel zwischengelagert sind.

Schicht 12 ist eine 20 cm mächtige Kalkbank, an der Basis mit *Nodicoeloceras* cf. *crassoides* Form A und *Dactylioceras (Orthodactylites) directum* und im oberen Teil mit großwüchsigen *Hildaites* cf. *levisoni*. Direkt im Hangenden schließt eine 1 m mächtige Kalkbank mit „*Terebratula*“ an.

In den folgenden ruppigen Kalken (Schicht 13) tritt *Harpoceras* sp. und *Peronoceras* cf. *subarmatum*, sowie „*Rhynchonella*“, „*Terebratula*“, *Eopecten* und *Pholadomya* auf. Dieser Fossilhorizont kann bereits in den tieferen Teil der *bifrons*-Zone (*largaense*-Subzone) gestellt werden.

In den folgenden Schichten ist „*Rhynchonella*“ häufig, Ammoniten sind selten, und es wurden zumeist nur Bruchstücke gefunden. In Schicht 14 kommt *Harpoceras* sp. und *Mercaticeras* sp. vor, in Schicht 15 *Peronoceras* sp. und in Schicht 16 *Harpoceras* sp. und *Maconiceras* sp., Schicht 18 ist die letzte bräunlich anwitternde Kalkbank. In dieser Bank tritt „*Rhynchonella*“ nicht auf und es wurde ein *Peronoceras* cf. *pacificum* gefunden.

Es folgt eine ca. 8 m mächtige Serie aus mikritischen, grauen Kalken und Mergeln, in der „*Rhynchonella*“ z. T. häufig ist. Aus dieser Serie stammen *Phymatoceras* cf. *copiapense*, *Phlyseogrammoceras* und *Pleydellia* cf. *lotharingica*. Die letzten Bänke dieser Serie sind etwas feinsandig und dm-gebankt. Sie werden von einer Fossilschuttbrekzie überlagert, die 50 cm über ihrer Basis häufig *Pleydellia* cf. *fluitans* enthält. Außerdem kommen „*Terebratula*“, *Lopha*, *Entolium*, *Chlamys* und *Trigonia* vor. Etwa 1,5 m über der Basis tritt eine für diesen stratigraphischen Horizont typische, neue Gattung und Art der Isognomonidae (cf. *Gervilleioperna*) auf. *Pleydellia* cf. *fluitans* kommt in mehreren Horizonten vor.

Darüber liegen petrographisch ähnlich ausgebildete Schichten mit *Bredyia* sp. und *Parammatoceras* sp. und über diesen Fossilschuttkalke mit *Lopha* und *Eudmetoceras* sp.

Auf der linken Talseite sind die Schichten mit *Eudmetoceras* zumindest 30 m mächtig. Einige Bänke sind reich an *Gryphaea* und auch *Entolium* tritt in mehreren Bänken auf. Über den Fossilbänken mit *Eudmetoceras* liegen Bänke mit großwüchsigen *Gryphaea*.

Die folgende Serie (ca. 40 m mächtig) besteht aus schlecht aufgeschlossenen Lutiten, denen im mittleren Teil eine 15 cm mächtige Kalkbank mit schlecht erhaltenen *Sonninia (Papilliceras)* sp. eingeschaltet ist. Diese Serie ist bereits in das Bajocium zu stellen. Über ihr folgen kalkige Sandsteine mit selten Belemniten.

Nach einer Aufschlußlücke (ca. 5 bis 10 m Mächtigkeit entsprechend) steht eine ca. 1 m mächtige Oolithbank an. Darüber liegen sandige Kalkbänke mit „*Terebratula*“ (kleinwüchsig) und *Nerinea*. Es folgen grüne Tuffe, rote Sandsteine und rote Tuffe, die ca. 5 bis 10 m mächtig sind.

Darüber ist eine mächtige Serie aus dickbankigen Kalken aufgeschlossen, in denen Korallenstöcke und Ostreiden häufig sind. Den dickbankigen Kalken sind gelblich verwitternde Sandsteine mit einer großwüchsigen *Mesomiltha* zwischengelagert. Im mittleren Teil treten auch

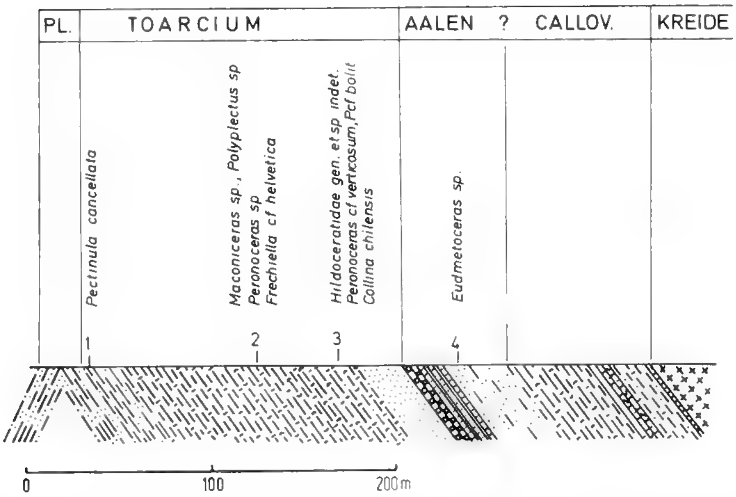

Abb. 4: Juraprofil der Quebrada Paipote bei Redonda (Abb. 1, Profil 6), Südflügel des Sattels auf der rechten Talseite; Legende zur Gesteinsausbildung Abb. 10.

dichte Kalke auf. In der hangendsten Bank wurden *Vaugonia* sp., *Mesomiltha* (großwüchsig) und ein Abdruck einer ? *Reineckeia* gefunden. Darüber liegen einige Meter mächtige Bänke mit z. T. maßenhaft *Gryphaea* (kleinwüchsig). Diese Dickbankserie ist etwa 200 m mächtig und ist wahrscheinlich in das Callovium zu stellen.

Im Hangenden folgen Vulkanite und über diesen sind noch gelbliche, sandige Kalke und graue Kalke mit schlecht erhaltenen ,,Trigonien" aufgeschlossen. Diese Serie läßt sich lithologisch gut mit den von v. Hillebrandt (1973 b, S. 179) in der Quebrada Cerros Bravos und Vicuñita gefundenen Schichten der tieferen Unterkreide vergleichen.

2.5 QUEBRADA DE PAIPOTE BEI REDONDA
(Abb. 1, Profil 6, Abb. 4)

In der Quebrada de Paipote ist bei Redonda auf der rechten Talseite ein Jurasattel aufgeschlossen. Das Profil des Südflügels wurde aufgenommen (Abb. 4).

Der Sattelkern wird durch gebankte Feinsandsteine mit Tonschieferzwischenlagen gebildet, die z. T. *Pectinula cancellata* Leanza enthalten. Über einer 50 cm mächtigen Feinsandsteinbank liegen ca. 12 m mächtige, feinschichtige, schiefrige Kalke (mit Feinsandsteinbänken bis 10 cm ∅) mit Vollpflastern aus *Pectinula cancellata* (Schicht 1, Abb. 4). Die Pectinulaschiefer gehen in grünlichgraue Feinsandsteine über und werden von 30 bis 40 m mächtigen, dünnbankigen Mergelkalken überlagert, die schlecht aufgeschlossen sind. Es folgen knollige Kalke mit zum Hangenden hin an Mächtigkeit abnehmenden, tonig-mergeligen Zwischenlagen. Aus diesen Knollenkalken (Schicht 2, Abb. 4) stammen *Peronoceras*, *Maconiceras*, *Polyplectus* und *Frechiella* cf. *helvetica* (v. Hillebrandt 1973a, Taf. 2, Fig. 8).

Die Knollenkalke gehen in sandige z. T. Fossilschutt führende, z. T. knollige Kalke (Schicht 3, Abb. 4) über mit *Peronoceras* cf. *verticosum*, *P.* cf. *bolitoense*, *Collina chilensis* und einer neu zu beschreibenden Gattung und Art der Hildoceratidae. Aus dieser Serie geht eine Sandsteinserie hervor, die ihrerseits von z. T. dickbankigen Konglomeraten (Gerölle bis 20 cm ∅) und Sandsteinen überlagert wird. Zum Hangenden hin werden die Sandsteine allmählich wieder feinkörniger und feinschichtig. Fossilien (Schicht 4, Abb. 4) sind selten: *Entolium* sp. (großwüchsig), *Eudmetoceras* sp. Der hangendste Teil des Profils kann in das Callovium gestellt werden, wobei allerdings die Grenze zum Aalenium nicht genau festzulegen ist. Über dem Callovium folgen Andesite.

2.6 QUEBRADA EL BOLITO
(Abb. 1, Profil 7; Abb. 5)

(= Quebrada La Tola bei v. Hillebrandt 1973b, Abb. 1) Die Quebrada El Bolito (Karte 1:100000, Blatt Laguna del Negro Francisco) ist eine Seitenquebrada der Quebrada del Hielo, die ihrerseits in die Quebrada de Paipote mündet. Der Anfang der Quebrada El Bolito wird auf dem Blatt Carrera Pinto als Quebrada La Tola und als Quebrada El Bolito eine weiter westlich liegende Quebrada bezeichnet. Auf dem Blatt Laguna del Negro Francisco liegt eine als Quebrada La Tola bezeichnete Quebrada 4 km östlich der Quebrada El Bolito. Die Quebrada El Bolito teilt sich bei der gleichnamigen Vega in einen westlichen (Quebrada Animitas) und östlichen Ast. Etwa 1,5 km südöstlich der Vega El Bolito ist in dem östlichen Ast ein steilstehendes Juraprofil (Abb. 5) gut aufgeschlossen.

Das Liegende des Jura bildet eine mächtige, konglomeratische, rote Brekzie mit kantengerundeten Blöcken bis über 1 m Durchmesser. In den obersten 50 m sind die

Komponenten weniger groß, und diese Schichtfolge endet mit einem ca. 2 m mächtigen, roten Konglomerat (Gerölle bis 50 cm Ø).

Es folgen konglomeratische Sandsteine, Brekzien und Sandsteine mit Bruchstücken von *Weyla* und schließlich gebankte Sandsteine (Schicht 1) mit viel Fossilschutt, einzelnen Geröllen, sowie „*Rhynchonella*", „*Terebratula*", *Liostrea* und *Entolium*.

Die Sandsteine gehen über in sandige bis mergelig-kalkige Schichten (Schichten 2), in denen doppelklappige Pelecypoden (*Weyla, Pholadomya, Pleuromya, Pholadomyocardia*) häufig sind. Aus diesen Schichten gehen knollig-mergelige Kalke (Schichten 3) hervor, in denen ebenfalls doppelklappige Pelecypoden (*Weyla, Modiolus* cf. *baylei, Pholadomya corrugata, Homomya rotundocaudata, Pleuromya*) häufig sind. Im hangenden Teil dieser knolligen Kalke kommen *Cenoceras, Lytoceras* und *Radstockiceras* vor. Es folgen gut gebankte, vorwiegend dichte Kalke, in denen *Radstockiceras* sp. 2 und *Atractites* (Schicht 4) auftreten.

Schicht 5 ist eine rostig anwitternde, etwas sandige Fossilkalkbank mit großwüchsigen *Weyla* sp. und *Dact. (Orthodactylites) tenuicostatum chilense*. Schicht 6 ist petrographisch ähnlich ausgebildet und enthält *Peronoceras* cf. *subarmatum, P. largaense, Harpoceras* cf. *chrysanthemum* (Yokoyama) und *Mercaticeras* (?) sp. Anschließend folgen mergelig-kalkige Schichten (Schichten 7), im basalen Teil mit häufig Brachiopoden, *Modiolus, Gryphaea*, sowie *Peronoceras pacificum, Harpoceras* sp. und *Polyplectus* sp. Schicht 8 ist ein 1 Meter mächtiger, in sich 10 bis 20 cm gebankter Knollenkalk mit *Peronoceras bolitoense* n. sp., *Collina chilensis* n. sp., *Harpoceras* sp., *Maconiceras* sp., *Phymatoceras* sp., sowie einer neuen Gattung und Art der Hildoceratidae. An der Basis ist eine

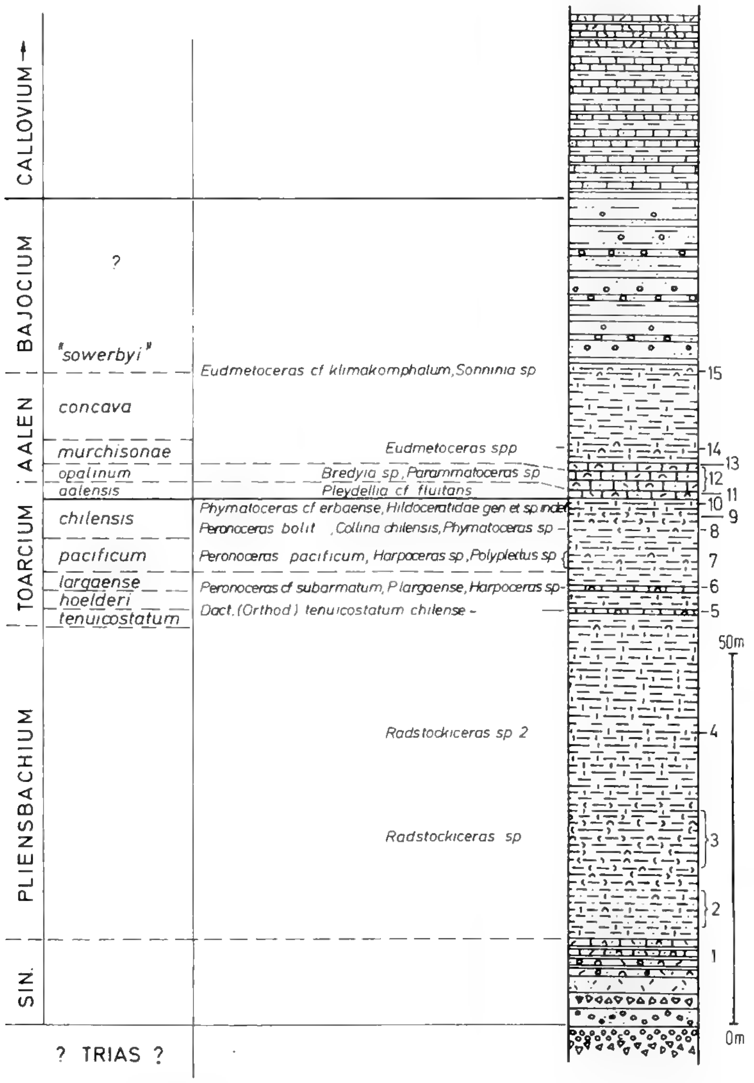

Abb. 5: Juraprofil der Quebrada El Bolito (Abb. 1, Profil 7), Callovium nicht vollständig dargestellt; Legende zur Gesteinsausbildung Abb. 10.

knollige, kalkig-mergelige, rötliche Schicht mit gut erhaltenen Exemplaren von *Peronoceras* und *Collina* entwickelt. Schicht 9 besteht aus 10 bis 20 cm gebankten Kalken mit *Phymatoceras* cf. *erbaense* und 2 Arten mit retroklinen Rippen einer neu zu beschreibenden Gattung der Hildoceratidae.

Die Kalkbank von Schicht 10 enthält eine weitnabelige, glatte Art dieser neu zu beschreibenden Gattung der Hildoceratidae. Über dieser Bank liegt ein fossilreicher, sandiger, dickbankiger Kalk mit *Pleydellia* cf. *fluitans* im liegenden Teil (Schicht 11) und *Bredyia* sp. und „*Parammatoceras*" sp. 1 im hangenden Teil (Schicht 12). Neben Ammoniten kommen in diesem Fossilkalk vor:

„*Terebratula*" sp. h
Grammatodon sp. (großwüchsig) s
Isognomonidae nov. gen. nov. sp. (cf. *Gervilleioperna)* s
Trigonia sp. h
Myophorella sp. 1 h
Myophorella sp. 2 h
Mesomiltha cf. *bellona* (D' ORB.) s
Mesomiltha sp. (großwüchsig) s
Neocrassina andium (GOTTSCHE) h
Trigonastarte (?) *steinmanni* (MÖRICKE) h
Pleuromya sp. s

Zwischen den Schichten 10 und 11 besteht eine Schichtlücke, die wie in der Quebrada El Asiento fast das gesamte obere Toarcium umfaßt.

Schicht 13 enthält großwüchsige *Entolium* cf. *demissum* (PHILIPPS). Bei Schicht 14 sind ca. vier 10 bis 30 cm mächtige, rötliche Kalkbänke aufgeschlossen, in denen *Eudmetoceras* div. sp. und *Fontannesia austroamericana* JAW. häufig sind.

Es folgt eine mergelig-kalkige Serie, im hangenden Teil mit drei 10 bis 20 cm mächtigen, grauen bis rötlichen Kalkbänken, die *Eudmetoceras* cf. *klimakomphalum* und *Sonninia (Euhoploceras)* führen. Die anschließende Serie rötlicher und bräunlicher, mittel- bis grobkörniger Sandsteine mit Geröllen (bis 0,5 cm ∅) ist fossilleer. Darüber beginnt eine mächtige Serie mit dickbankigen Sandsteinen im tieferen Teil und ebenfalls dickbankigen Kalken mit viel Fossilschutt im höheren Teil. Diese Serie kann dem Callovium zugerechnet werden.

2.7 QUEBRADA CORTADERITA
(Abb. 1, Profil 8)

Am westlichen Beginn der Quebrada Cortaderita, auf dem Bergrücken zwischen dieser und der nördlich anschließenden, unbenannten Quebrada (ebenfalls eine Seitenquebrada der Quebrada Cortadera) ist ein Juraprofil aufgeschlossen. In einem topogr. Sattel nordwestlich Punkt 2819 grenzt eine Serie von Kalkschiefern und Kalken, die einen Sattel bilden, an Intrusivgesteine. In den Kalken kommt *Radstockiceras* vor.

In der westlichen Fortsetzung ist nach intrusiven Porphyriten eine Serie sandiger Mergel mit sandigen Kalkbänken aufgeschlossen, die z. T. rostbraun anwittern und schlecht erhaltene Dactylioceraten und *Harpoceras* sp. führen (± *hoelderi*-Zone des unterenToarcium).

Es folgt eine etwa 20 m mächtige Serie dickbankiger (bis über 1 m ∅), sandiger Fossilschuttkalke. Diese Serie endet an einer Kuppe, an der die oberste Bank dieser Serie aufgeschlossen ist.

Diese Bank ist stärker verwittert und enthält folgende Fauna:

„*Terebratula*" sp. h
Ctenostreon sp. s
Entolium cf. *demissum* (PHILIPPS) h
Trigonia sp. s
Neocrassina cf. *andium* (GOTTSCHE) h
Cenoceras sp. s
Peronoceras cf. *vortex* (SIMPSON)
Peronoceras cf. *bolitoense* n. sp.
Collina chilensis n. sp.
Harpoceras cf. *subexaratum* BONARELLI
Phymatoceras sp. ex gr. *P. erbaense* (v. HAUER)
Hildoceratidae gen. et sp. indet.

Die Fauna gehört dem Horizont mit *Peronoceras bolitoense* der *chilensis*-Subzone an.

Über dieser Fossilschicht liegt eine etwa 5 m mächtige Serie gebankter (5 bis 10 cm ∅), bräunlich verwitternder Sandsteine mit *Phymatoceras* sp. des basalen oberen Toarcium. Es folgt ein 0,3 bis 1,0 m mächtiges Konglomerat (Gerölle bis 5 cm ∅). Die hangende Serie (60 bis 70 m mächtig) ist auf der linken Talseite der unbenannten Quebrada nördlich der Quebrada Cortaderita aufgeschlossen. Diese Serie besteht aus vorwiegend dickbankigen Sandsteinen mit einzelnen Konglomeratbänken (Gerölle bis 15 cm ∅) und sandigen Mergellagen. Im hangenden Teil kommen auch dickbankige Fossilschuttkalke mit *Gryphaea*, *Pholadomya* und *Pleuromya*, sowie in einem sandigen, mürben Fossilschuttkalksandstein *Gryphaea*, *Trigonia*, *Pleuromya* und *Eudmetoceras* vor. Zumindest dieser Teil der Serie kann in das Aalenium gestellt werden. Das Juraprofil endet mit etwa 35 m mächtigen Mürbsandsteinen (z. T. mit Geröllen), die an Vulkanite grenzen.

2.8 QUEBRADA YERBAS BUENAS
(Abb. 1, Profil 9; Abb. 6)

Das Gesamtprofil wurde von v. HILLEBRANDT (1973b, Abb. 1, S. 175) dargestellt. Das Teilprofil (Abb. 6) wurde auf der rechten Seite der Quebrada Yerbas Buenas aufgenommen.

Schicht 1 ist eine etwa 2 m mächtige Kalkbank (nimmt nach Norden sehr stark an Mächtigkeit zu) mit häufig, kleinwüchsigen Gryphaeen und selten einem großwüchsigen *Coeloceras* cf. *pinguecostatum* (BREMER) und einem *Eoderoceras* aus der Gruppe des *E. armatum* (SOW.). Schicht 2 besteht aus mergeligen Kalken und Kalkmergeln mit zumindest 2 Arten der Gattung *Uptonia*.

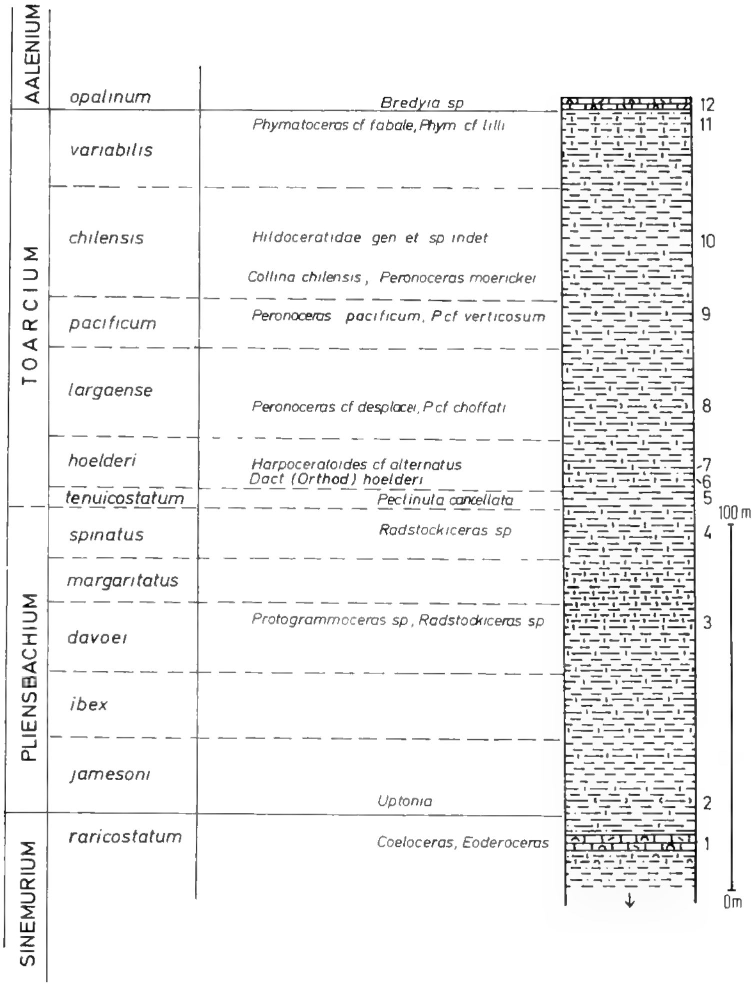

Abb. 6: Teilprofil des Jura der Quebrada Yerbas Buenas (Abb. 1, Profil 9); intrusive, ± schichtparallele Porphyrite nicht berücksichtigt; Legende zur Gesteinsausbildung Abb. 10.

Es folgen Mergel mit einzelnen Kalkbänken. Die Kalkbänke werden zum Hangenden hin mächtiger und die Mergel geringermächtig. Bei Schicht 3 sind die Kalkbänke bis 40 cm mächtig und enthalten häufig *Protogrammoceras* und *Radstockiceras.*

Bei Schicht 4 sind die Kalkbänke wieder weniger mächtig, und es kommt ebenfalls *Radstockiceras* vor.

Schicht 5 besteht aus etwa 10 m mächtigen, feinschichtig-schiefrigen Kalken mit *Pectinula cancellata* LEANZA.

Schicht 6 folgt direkt im Hangenden, ist etwa 1 m mächtig und setzt sich aus bis 20 cm mächtigen Kalkbänken zusammen, die *Dactylioceras (Orthodactylites) hoelderi, D. (O.) directum* und *D. (O.)* cf. *directum* enthalten. Darüber liegen 2 bis 3 m mächtige, rostig anwitternde Kalke (10 cm gebankt) mit Mergelzwischenlagen. Die oberste (oder vorletzte) Bank (Schicht 7) ist reich an Ammoniten:

Nodicoeloceras cf. *crassoides* (SIMPSON) Form A
Hildaites cf. *serpentiniformis* (BUCKMAN)
Hildaites cf. *serpentinus* (REINECKE)
Harpoceratoides cf. *alternatus* (SIMP.)
Polyplectus sp.

Anschließend folgen wieder Mergel mit Kalkbänken, bei Schicht 8 mit *Peronoceras* cf. *desplacei, P.* cf. *choffati, P.* sp. ex gr. *P. subarmatum* und *Harpoceras* cf. *chrysanthemum.*

Schicht 9 enthält *Peronoceras pacificum, P.* cf. *verticosum, Maconiceras* sp. und *Polyplectus* sp.

Ein *Peronoceras* cf. *bolitoense* (Taf. 7, Fig. 3), zusammen mit *Collina chilensis, Maconiceras* sp. und einer neuen Art (glatt) und Gattung der Hildoceratidae wurde in etwas jüngeren Schichten gefunden.

Ein äußeres Windungsbruchstück von *Peronoceras moerickei* (Taf. 7, Fig. 2) dürfte aus etwa gleichalten Schichten stammen.

In mehr mergeligen Schichten kommen bei Schicht 10 Bruchstücke einer neuen Art und Gattung der Hildoceratidae vor, die weitnabelig ist und retrokline Rippen besitzt.

Bei Schicht 11 sind Kalkbänke mit sandig-mergeligen Zwischenlagen aufgeschlossen. Es wurden *Phymatoceras* cf. *fabale* und *Phym.* cf. *lilli* gefunden.

Diese Schichten werden von mit ca. 2 bis 3 m Mächtigkeit aufgeschlossenen Fossilschuttkalken (Schicht 12) überlagert, die in einem Muldenkern die jüngsten Schichten bilden. Sie enthalten *Bredyia* sp., *Ctenostreon* cf. *pectiniformis* (v. Schloth.) (großwüchsig), *Myophorella, Mesomiltha* cf. *bellona* (d'Orb.), *Mesomiltha* (großwüchsig), *Myoconcha steinmanni* (Jaw.), *Pholadomya* cf. *plagemanni* und *Pleuromya*.

Zwischen den Schichten 11 und 12 ist eine Schichtlücke vorhanden, die den oberen Teil des oberen Toarcium umfaßt.

2.9 QUEBRADA POTRERILLOS

(Abb. 1, Profil 10)

Von der Quebrada Vaca Muerta erstreckt sich ein Juragebiet nach Süden bis in die Quebrada Potrerillos. Das Gesamtprofil wurde bei v. Hillebrandt (1973b, Abb. 1) dargestellt. Der tiefere Teil des Profils ist sehr gut in der Quebrada Vaca Muerta aufgeschlossen. Das obere Sinemurium ist vorwiegend sandig-konglomeratisch ausgebildet. Über einer 4 m mächtigen Grobsandsteinbank mit einzelnen Geröllen beginnt eine sehr fossilreiche Serie (hauptsächlich Brachiopoden) von sandig-mergelig-kalkigen Schichten mit einzelnen, dickbankigen, kalkigen Sandsteinen bis sandigen Kalken. Die Oberfläche einiger Bänke besteht aus Pflastern von *Weyla*. Diese Serie beginnt im obersten Sinemurium *(Epideroceras* (Pseuduptonia ?), *Coeloceras)* und reicht bis in das unterste Pliensbachium *(Uptonia)*. Das mittlere und obere Pliensbachium besteht aus etwa 50 m mächtigen, 10 bis 20 cm gebankten, dichten Kalken mit Kalkmergelzwischenlagen. In dieser Serie kommt *Radstockiceras* vor. Die Serie endet mit mehrere Meter mächtigen, feinschichtigen Mergelkalken, in denen *Pectinula cancellata* Schalenpflaster bildet. Hangend folgen wieder gebankte Kalke mit *Peronoceras* und *Harpoceras*.

In der Quebrada Potrerillos sind die Schichten sehr viel stärker gestört und gefaltet als in der Quebrada Vaca Muerta. Die Schichtfolge ist jedoch im hangenden Teil vollständiger. Großtektonisch besteht die Schichtfolge des Jura von Osten nach Westen aus einer Mulde und einem anschließenden Sattel. Im Osten grenzt der Jura mit tektonischem Kontakt an Granit. Die basale Sandsteinserie und auch die darauffolgenden, fossilreichen Schichten sind tektonisch stark verdünnt. Dem oberen Teil des unteren Toarcium *(pacificum-*Subzone) gehört ein Fossilhorizont mit *Peronoceras pacificum, P.* cf. *verticosum, Harpoceras* sp. und *Maconiceras* sp. an, der in den gebankten Kalken über den *Pectinula-*Schiefern liegt.

Hangend folgen weiterhin vorwiegend dichte, gut gebankte Kalke mit schiefrigen Zwischenlagen. Im obersten Teil treten wenige Meter mächtige, mehr knollige Kalke mit *Phymatoceras* (z. T. großwüchsig) auf.

Überlagert werden diese Schichten von ca. 4 m mächtigen Fossilkalken mit häufig *Bredyia* sp. (bis 0,5 m Ø), *Myophorella, Neocrassina* cf. *andium* (Gottsche) und *Trigonastarte* (?) *steinmanni* (Mör.) des unteren Aalenium.

Wie in der Quebrada Yerbas Buenas fehlt der obere Teil des oberen Toarcium.

Die hangende, vorwiegend sandige Schichtfolge gehört wahrscheinlich zum größten Teil dem Callovium an, die den Muldenkern bildet. Der westlich anschließende Sattelkern wird von der basalen Sandsteinserie gebildet. Die Basis wird jedoch nicht erreicht. Die Kalkserie des oberen Pliensbachium und Toarcium ist stark spezialgefaltet, und der Jura grenzt mit einer Ruschelzone an eine mächtige, rote Sandsteinserie.

2.10 QUEBRADA LARGA

(Abb. 1, Profil 11; Abb. 7)

Der Jura der Quebrada Larga gehört zu einem Jurastreifen, der sich von der Quebrada Larga im Süden bis zu einer unmittelbar westlich der Quebrada San Pedrito und mit dieser im Oberlauf parallel verlaufenden Quebrada im Norden erstreckt. Profile wurden in dieser Quebrada und in der Quebrada Larga aufgenommen. Das Gesamtprofil der Quebrada Larga wurde bei v. Hillebrandt (1973b, Abb. 1) abgebildet. Auf Abbildung 7 ist nur der obere Teil dieses Juraprofils berücksichtigt.

Der basale Jura besteht aus einer 70 bis 100 m mächtigen Sandsteinserie, im Liegendteil schlecht gebankt, im Hangendteil zunehmend kalkiger. Fossilien sind selten und schlecht erhalten (Bruchstücke von *Weyla, Frenguelliella, Myophorigonia*). Es folgen mehrere, 20 bis 30 cm mächtige, graue Kalkbänke mit *Lithotrochus humboldti* (v. Buch), *Spiriferina*, „*Rhynchonella*", *Gryphaea darwini* Forbes und *Epophioceras* sp. (1 Windungsbruchstück) (*obtusum*-Zone, Basis des oberen Sinemurium). Über ihnen liegen wieder gebankte Sandsteine und eine ca. 15 m mächtige Serie von mehr oder minder kalkigen Mergeln mit einer 15 cm mächtigen Fossilschuttkalkbank. In einzelnen Lagen ist *Gryphaea tricarinata* Philippi sehr häufig, daneben kommen vor *Spiriferina*, „*Rhynchonella*", *Chlamys, Weyla, Pseudolimea, Plicatula* und *Lithotrochus humboldti*.

Diese Serie wird zum Hangenden hin wieder sandiger und der obere Teil des oberen Sinemuriums wird von einer mächtigen Konglomeratserie gebildet, die von Sandsteinen überlagert wird.

Bei Schicht 1 (Abb. 7) sind diesen Sandsteinen gebankte Kalke mit sehr häufig „*Terebratula*" eingelagert.

Schicht 2 sind fossilreiche Kalksandsteine mit folgender Fauna:

Andenipora liasica Gerth h
Montlivaltia sp. s

Abb. 7: Teilprofil des Jura der Quebrada Larga (Abb. 1, Profil 11); Legende zur Gesteinsausbildung Abb. 10.

Actinastrea sp. h
„*Rhynchonella*“ sp. sh
„*Terebratula*“ sp. h
Entolium cf. *demissum* (PHILIPPS) h
Camptonectes sp. s
Chlamys cf. *textoria* (SCHLOTH.) h
Weyla sp. sh
Pseudolimea sp. s
Frenguelliella sp. s
Pholadomya sp. s
Pleuromya sp. h
Lithotrochus andinus (MÖRICKE) h
Uptonia sp. h

Über einer 1 m mächtigen Fossilschuttkalkbank folgen nochmals sandige Schichten (Schicht 3) mit sehr häufig *Weyla*, häufig „*Rhynchonella*“, sowie „*Terebratula*“, *Entolium*, *Pseudolimea*, *Pholadomya* und *Radstockiceras*.

Bei Schicht 4 sind mehr oder minder gut gebankte Kalke mit *Mesomiltha huayquimili* (LEANZA), *Cenoceras*, *Radstockiceras* sp. 2 und *Atractites* aufgeschlossen.

In Schicht 5 kommen in petrographisch ähnlichen Kalken *Radstockiceras* sp. 2 und *Argutarpites* vor.

Im Bereich von Schicht 6 und 7 sind feinschichtige bis schiefrige Kalke mit *Pectinula cancellata* LEANZA aufgeschlossen, bei Schicht 6 mit einer 10 cm mächtigen Kalkbank in der neben *P. cancellata Radstockiceras* sp. 2 auftritt. In den sandigen Kalkschiefern von Schicht 7 wurde ein schlecht erhaltenes, weitnabeliges *Bouleiceras* gefunden, das große Ähnlichkeit mit *Bouleiceras* sp. bei v. HILLEBRANDT (1973b, S. 359) besitzt (s. S. 13).

Es folgt eine Serie aus Mergeln mit sandigen Kalkbänken, in den Schichten 8 mit *Peronoceras* cf. *subarmatum*, *Peronoceras largaense*, *Harpoceras* sp., *Hildaites* sp. und *Mercaticeras* sp. Diese Serie endet mit ca. 5 m mächtigen, in sich 40 cm gebankten, sandigen Fossilschuttkalken mit sandigen Kalkschieferlagen. Unmittelbar im Hangenden enthalten mergelige Kalke eine reiche Ammonitenfauna (Schicht 9):

Peronoceras cf. *planiventer* (GUEX)
Peronoceras cf. *crassicostatum* (GUEX)
Collina sp.
Polyplectus sp.
Osperlioceras sp.
Phymatoceras sp. ex gr. *P. erbaense* (v. HAUER)
Hildoceratidae gen. et sp. indet. (3 Arten)

Direkt im Hangenden dieser Ammonitenfauna folgt Schicht 10 mit *Phymatoceras* cf. *fabale* und *Phym.* cf. *lilli*.

In den hangenden Sandsteinbänken (10 bis 20 cm ∅), die mit sandigen Mergeln wechsellagern, kommt *Phymatoceras copiapense* (MÖRICKE) vor (Schicht 11).

Es folgt eine kleine Steilstufe aus dickbankigen Sandsteinen mit Geröllen (2 bis 4 mm ∅), die von weicheren, mürben Sandsteinen überlagert werden, im hangenden Teil mit *Gryphaea* und *Lopha*. In der nördlichen Fortsetzung der Quebrada Larga (Quebrada unmittelbar westlich der Quebrada San Pedrito) ist diesen Mürbsandsteinen ein ca. 3 m mächtiger Fossilkalk eingeschaltet, mit sehr häufig *Lopha*, seltener *Entolium* und sehr selten *Eudmetoceras*. Hangend folgt eine 1 m mächtige Bank mit häufig

Eudmetoceras, sowie *Gryphaea* cf. *bilobata* (Sow.), *Lopha, Chlamys* cf. *textoria* (Schloth.), *Eopecten* cf. *tuberculosus* (Goldf.) und *Pleuromya* sp.

Diese Sandsteinserie wird von grünen Tuffen, Vulkaniten und einer Serie aus roten Sandsteinen und Konglomeraten überlagert.

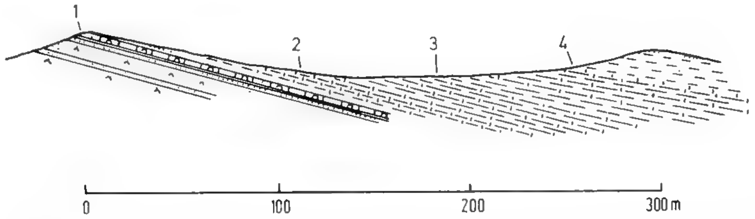

Abb. 8: Oberster Abschnitt des Juraprofils der Quebrada Noria südlich Salto de la Muerte (700 m SSW Punkt 3132) (Abb. 1, Profil 12); Legende zur Gesteinsausbildung Abb. 10.

2.11 QUEBRADA NORIA

(Abb. 1, Profil 12; Abb. 8)

Auf der Höhe von Agua del Medio und Salto de la Muerte (Karte 1 : 100 000, Blatt Carrera Pinto) beginnt südlich der Quebrada Noria bei 2600 m ein Juraprofil, das über den Punkt 3132 bis 700 m SSW dieses Punktes reicht. Das Gesamtprofil wurde bei v. Hillebrandt (1973 b, Abb. 1) dargestellt. Abbildung 8 umfaßt nur den hangenden Teil des Profils.

Das Liegende des Jura bilden mächtige Konglomerate, die von ebenfalls mächtigen Vulkaniten überlagert werden, die z. T. auch als Mandelsteinlaven ausgebildet sind.

Der tiefste Teil des Juraprofils mit Sandsteinen und Konglomeraten kann in das untere Sinemurium gestellt werden. Nach einer 50 cm mächtigen Kalkbank kommen in den Sandsteinen vereinzelt *Weyla, Gryphaea darwini* Forbes und eine Gattung und Art der Eotomariinae (Gastropoda) vor, die für den tiefsten Teil des oberen Sinemurium in Chile typisch ist.

Über der Sandsteinserie folgen mergelige Schichten, in denen *Gryphaea tricarinata* Philippi häufig, Brachiopoden *(Spiriferina, „Rhynchonella“, „Terebratula“)* und *Lithotrochus humboldti* (v. Buch) selten sind.

Der größte Teil des oberen Sinemurium ist als eine mächtige Serie aus Sandsteinen und Konglomeraten entwickelt, die wenig Fossilien enthält.

Die Grenze zum unteren Pliensbachium verläuft durch den obersten Abschnitt dieser Serie, hier fehlen Konglomerate. In den Sandsteinbänken sind Steinkerne von *Weyla* häufig. Diese Schichten reichen bis Punkt 3132.

Der höchste Teil des Profils ist 700 m SSW Punkt 3132 aufgeschlossen (Abb. 8). Über den Sandsteinen mit Abdrücken von *Weyla* liegt ein 1 m mächtiger, kalkiger Sandstein mit Schalenexemplaren von *Weyla* (Schicht 1, Abb. 8) und darüber nochmals ca. 2 m Sandstein. Es folgen mehr oder minder sandige und fossilschuttreiche Kalke mit Brachiopoden und *Atractites* (Schicht 2). Ungefähr in der Mitte zur folgenden kleinen Kuppe beginnen dünnbankige, schiefrige Kalke mit *Radstockiceras* sp. 2 (Schicht 3). Die Kalkschiefer reichen noch etwas den folgenden Hügel hinauf. Im hangendsten Teil der Kalkschiefer treten die ersten, schlecht erhaltenen Dactylioceraten auf. Über ihnen liegt eine Serie aus 10 bis 25 cm mächtigen, kalkigen Sandsteinbänken, die mit Mergeln gleicher Mächtigkeit wechsellagern. Im liegendsten Teil dieser Serie (Schicht 4) sind gut erhaltene Dactylioceraten häufig, Harpoceraten selten:

Dactylioceras (Orthodactylites) hoelderi n. sp.
Dactylioceras (Orthodactylites) directum (Buckman)
Dactylioceras (? Orthodactylites) helianthoides Yokoyama
Eleganticeras cf. *elegantulum* (Young & Bird)

2.12 QUEBRADA LLARETA

(Abb. 1, Profil 13)

Die Quebrada Llareta ist eine Seitenquebrada der Quebrada Tolar, die ihrerseits von der Quebrada San Miguel abzweigt.

Ein Profil wurde auf der linken Talseite, beginnend bei der Abzweigung von der Quebrada Tolar, aufgenommen. Der Jura grenzt mit unscharfem Kontakt an Granodiorit. Im Randbereich treten dunkle Intrusiva auf. Die stark gestörten Juraschichten sind zunächst marmorisiert oder in Hornfels umgewandelt. Porphyritintrusionen sind häufig. Schlecht erhaltene *Weyla* treten auf. Es folgen dunkle, geschieferte Kalke bis Kalkschiefer mit selten *Radstockiceras.* Darüber liegen hellere Mergel- und Kalkschiefer mit *Peronoceras* sp. ex gr. *P. subarmatum* und *Harpoceras.* In der Profilfortsetzung (nach Osten) sind in einem Sattelkern nochmals dunkle Kalkschiefer mit *Radstockiceras* aufgeschlossen und wieder die helleren Mergel- und Kalkschiefer. Über ihnen liegt eine Kalkbank mit *Peronoceras* cf. *P.* cf. *vortex, Maconiceras* sp., *Polyplectus* sp. und *Phymatoceras* sp. Der Jura grenzt im Osten an Porphyrite.

Bei Cueva de Mendez ist in der Quebrada San Miguel auf der linken Talseite zwischen 2 kleinen Seitenquebradas ein durch Intrusiva begrenztes Juraprofil aufgeschlossen. Der Jura beginnt mit grauen und grünlichen Feinsandsteinen, die zum Hangenden hin etwas kalkiger werden und nach ca. 50 bis 70 m Mächtigkeit häufig, schlecht erhaltene *Phymatoceras* des oberen Toarcium enthalten. Darüber liegen mittel- bis grobkörnige Sandsteine mit häufig, einer neu zu beschreibenden Gattung und Art der Isognomonidae (cf. *Gervilleioperna)*, selten *Lopha* und *Pholadomya*, sehr selten *Bredyia* sp. (unteres Aalenium). Die obersten 10 m der Sandsteine sind wieder etwas feinkörniger.

2.13 RIO JORQUERA

(Abb. 1, Profil 14a–c; Abb. 9)

9 km vor La Guardia ist auf der linken Seite des Rio Jorquera, bei der Mündung der Quebrada del Carrizo (Majada del Carrizo) in den Fluß, ein Juraprofil aufgeschlossen, das Schichten des Pliensbachium und unteren Toarcium umfaßt.

Der Jura transgrediert mit einer 60 bis 70 cm mächtigen, sandig-konglomeratischen Kalkbank (Gerölle bis 4 cm ∅) auf rote, schlecht gebankte Tuffe der ? Trias. An der Unterseite der Kalkbank wurde eine *Uptonia* gefunden. Es folgen 10 bis 40 cm gebankte, knollige, kalkige Fein- bis Grobsandsteine mit vereinzelt *Weyla* (Bruchstücke), konglomeratische Lagen sind selten. Viele Bänke werden von Bohrgängen durchzogen, die vorwiegend mit rotem Sediment ausgefüllt sind. Zum Hangenden hin werden die Bänke feinkörniger (10 bis 20 cm gebankt). Die Oberflächen sind häufig von *Weyla* bedeckt. Im oberen Drittel dieser Serie wurden Bruchstücke von *Uptonia* gefunden. Die hangendsten Bänke dieser Serie (Schicht 1) enthalten häufig *Chlamys* cf. *textoria, Weyla, Plagiostoma,* Bryozoen, *Andenipora liasica* und selten „*Terebratula*".

Über dieser vorwiegend sandigen Serie liegen 10 bis 20 cm gebankte, mehr oder minder knollige, fossilschutt-

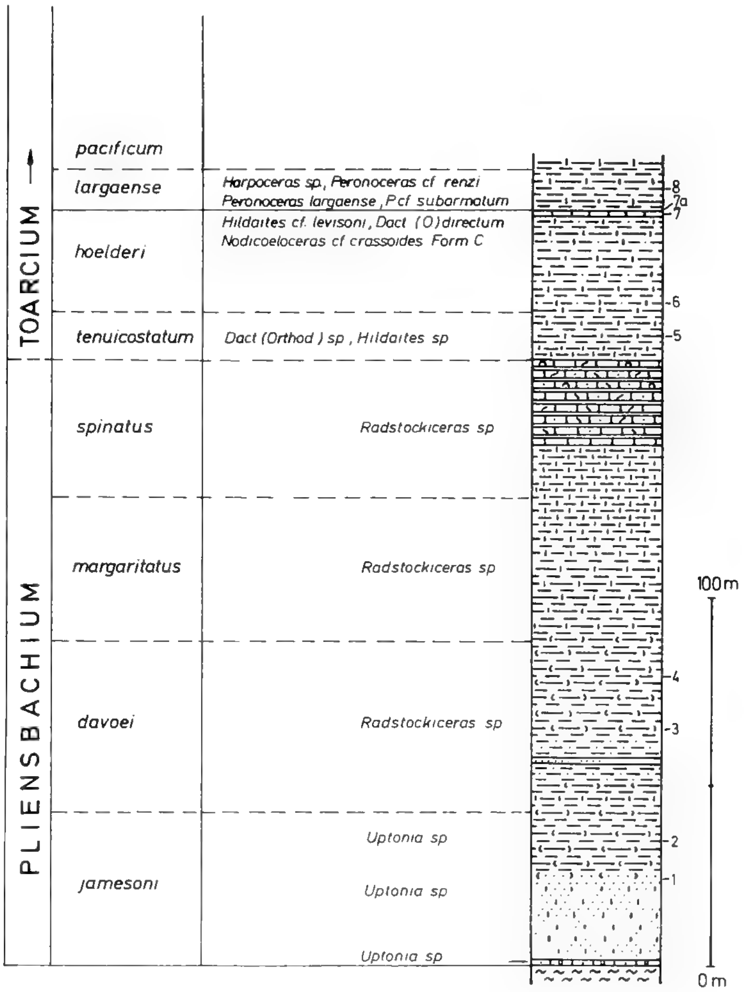

Abb. 9: Juraprofil bei Majada del Carrizo (Rio Jorquera) (Abb. 1, Profil 14b); Legende zur Gesteinsausbildung Abb. 10.

reiche Kalke, die mit kalkig-mergeligen Schichten wechsellagern.

Schicht 2 ist ein Horizont mit häufig „*Rhynchonella*“ und „*Terebratula*“, sowie selten *Modiolus, Cardinia, Pholadomya* cf. *corrugata, Lithotrochus andinus* und *Uptonia*.

Die folgende Bank ist reich an „*Rhynchonella*“, „*Terebratula*“, Ostreiden, *Chlamys, Weyla* und viel Fossilschutt. Im Hangenden dieser Bank werden die mergelig-kalkigen Lagen etwas mächtiger, ihnen sind noch 3 Bänke (15 bis 30 cm ∅) mit reichlich Fossilien eingelagert. In einer Bank ist eine flache Einzelkoralle *(Montlivaltia)*, an der Oberfläche einer weiteren Bank *Weyla* häufig. Es folgen schiefrig-sandige Mergel bis Sandsteine und eine 60 cm mächtige Sandsteinbank, die von ebenfalls stark sandigen Mergeln mit „*Rhynchonella*“, „*Terebratula*“ und *Weyla* überlagert wird. Diese gehen wieder in kalkige Mergel mit knolligen Kalkbänken über. Bei Schicht 3 sind diese sehr fossilreich und enthalten:

Montlivaltia sp. h
„*Rhynchonella*“ sp. h
„*Terebratula*“ sp. sh
Modiolus sp.
Gervilleioperna turgida LEANZA ss
Weyla sp.
Plagiostoma sp. s
Cardinia cf. *andium* GIEBEL s
Neocrassina sp. ss
Pholadomya cf. *corrugata* K. & DUNKER h
Homomya rotundocaudata (LEANZA) ss
Radstockiceras sp. ss

Die Schichtfolge geht mit petrographisch ähnlichen Sedimenten weiter, die z. T. ebenfalls sehr fossilreich sind.

Bei Schicht 4 wurden gefunden:

Actinastrea sp. ss
„*Rhynchonella*“ sp. h
„*Terebratula*“ sp. h
Modiolus sp. ss
Entolium cf. *demissum* (PHILIPPS) ss
Mesomiltha huayquimili (LEANZA) s
Pholadomya cf. *plagemanni* MÖRICKE s
Pholadomya cf. *corrugata* K. & DUNKER s

Es folgt eine Wechsellagerung von Mergeln mit gut gebankten, weniger fossilschuttreichen Kalken (10 bis 20 cm ∅), die Querschnitte von Radstockiceras enthalten. Sie werden von zunächst bis 40 cm mächtigen, mehr oder minder feinsandigen und gut gebankten Kalken überlagert, in denen selten Querschnitte von *Radstockiceras* vorkommen. Einzelne Bänke sind reich an Fossilschutt. Zum Hangenden hin enthalten die Bänke zunehmend Sandsteinschnüre und Sandsteinlinsen, sind zum Teil knollig ausgebildet, und die Oberflächen der Bänke können wellig sein. Im hangenden Teil werden die Bänke bis 60 cm mächtig, sind zumeist reich an Fossilschutt und in manchen Bänken kommt *Weyla* häufig vor.

In der Profilfortsetzung werden die Bänke wieder geringermächtig, und sie werden von einer Serie aus Mergeln mit gut gebankten Kalken (bis 20 cm ∅) mit wenig Fossilschutt überlagert. Schicht 5 enthält die ersten, sehr schlecht erhaltenen *Dactylioceras (Orthodactylites)* und *Hildaites*.

Schicht 6 ist die erste rostbraun anwitternde Kalkbank einer Serie petrographisch ähnlich ausgebildeter Kalke (Bänke bis 30 cm mächtig), die mit Mergeln wechsellagern. Die letzte dieser Kalkbänke (40 cm ∅) (Schicht 7) ist reich an *Propeamussium* und es kommen *Dactylioceras (Orthodactylites) directum, Dact. (O.)* cf. *directum, Nodicoeloceras* cf. *crassum* Form C, *Polyplectus* sp., *Harpoceras* cf. *falcifer* (stark involut) und ein großwüchsiges (bis über 30 cm ∅) *Hildaites* vor, das mit dem von SCHLEGELMILCH (1976; Taf. 44, Fig. 3) abgebildeten *Hildaites* cf. *levisoni* große Ähnlichkeit aufweist.

Es folgt eine Wechsellagerung von knolligen Kalken mit Mergeln. Etwa 25 cm über der Bank mit *Dactylioceras (O.) directum* kommen *Peronoceras* cf. *subarmatum, P. largaense* (Bruchstücke) und *Harpoceras* sp. vor (Schicht 7a).

Das Hangende bilden Mergel mit geringmächtigen Kalkbänken.

In Schicht 8 kommen sehr häufig „*Rhynchonella*“ und „*Terebratula*“ vor, sehr selten sind *Peronoceras* cf. *renzi* und *Harpoceras* sp. Mit diesen Schichten endet das Profil Majada del Carrizo am Rio Jorquera.

1,3 km talabwärts der Quebrada del Carrizo wurde auf der rechten Talseite des Rio Jorquera bei Vegas de Chañar ein weiteres Profil aufgenommen. Der Jurastreifen dieses Profils quert weitere 700 m talabwärts das Tal und ist nun auf der linken Talseite aufgeschlossen.

Der Jura transgrediert bei diesem Jurastreifen auf dunkle Mandelsteinlaven. Die basalen Sandsteine enthalten keine Bohrgänge. Das Pliensbachium (+ ? obere Sinemurium) ist mächtiger (ca. 200 m) als bei der Quebrada del Carrizo (ca. 160 m), die Schichtfolge sonst ähnlich ausgebildet. Auch das Toarcium liegt in der gleichen Fazies vor, im tiefsten Toarcium mit schlecht erhaltenen, flachgepreßten Dactylioceraten und Harpoceraten, hangend die rostbraun anwitternden Kalke und die diese Serie abschließende Kalkbank mit *Propeamussium* und selten *Peronoceras* und *Harpoceras* (schlecht erhalten). Es folgen die mehr mergeligen Schichten mit „*Rhynchonella*“ und „*Terebratula*“ (= Schicht 8 der Quebrada del Carrizo). Das untere Toarcium schließt mit sandig-knolligen Fossilschuttkalkbänken ab. Besonders eine der hangendsten Bänke ist reich an Ammoniten. Diese Bank ist auf der linken Talseite, 500 m westlich der Basis des Jura, aufgeschlossen und enthält:

„*Terebratula*“ sp. h
Plagiostoma sp. s
Myophorella sp. s
Pholadomya cf. *corrugata* K. & DUNKER h
Pholadomya cf. *plagemanni* MÖRICKE h
Peronoceras sp. cf. *P.* cf. *vortex* (SIMPSON)
Peronoceras cf. *bolitoense* n. sp.
Collina chilensis n. sp.
Harpoceras cf. *subexaratum* (BON.)
Hildoceratidae gen. et sp. indet (glatte Art)

Über diesen Fossilschuttkalken liegen gut gebankte Kalke (bis 30 cm Ø) mit *Phymatoceras*, die in Kalke mit zunehmendem Gehalt an Fossilschutt übergehen und auf der linken Talseite tektonisch stark verdrückte *Pleydellia (Walkericeras)* enthalten. Von der rechten Talseite stammt eine relativ gut erhaltene *Pleydellia (Walkericeras)* cf. *lotharingica* und *Hammatoceras* sp.

Es folgt eine Serie dickbankiger (bis 2 m Ø), zunächst stark sandiger Kalke, die auf der linken Talseite stark gestört sind. Diese z. T. fossilschuttreichen Kalke werden auf der rechten Talseite ca. 50 m mächtig, und sie sind in das Aalenium zu stellen.

Über einem bis 3 m mächtigen Andesit liegt mit sedimentärem Kontakt eine Serie (ca. 25 m mächtig) von roten, grünlichen und grauen Mürbsandsteinen und darüber sandigen Kalken und Fossilkalken mit Ostreiden. Diese Serie gehört wahrscheinlich bereits dem Callovium an. Das Callovium wird von einer mächtigen, roten Sandsteinserie überlagert.

2,5 km westlich La Guardia wurde oberhalb Las Banderitas (Rio Jorquera), zwischen 3290 m (Jurabasis) und 3450 m Gipfel, ein weiteres Profil aufgenommen.

Das untere Pliensbachium ist sehr viel geringer mächtig (ca. 20 m) als bei Majada del Carrizo. Den vorwiegend sandigen Schichten sind im mittleren Teil nach einem 2 m mächtigen Konglomerat auch Fossilschuttkalke eingeschaltet.

Die dickbankigen, sandigen Kalke des oberen Pliensbachium sind etwa 40 m mächtig, stärker sandig als bei Majada del Carrizo, enthalten großwüchsige „*Terebratula*" im mittleren Teil und *Weyla* in den obersten, dickbankigen Kalksandsteinen. Es folgen 10 bis 50 cm gebankte Kalke (ca. 10 m mächtig) mit Querschnitten von *Radstokkiceras,* die in 10 bis 20 cm gebankte, knollige Kalke übergehen. Über ihnen liegen die braun anwitternden, feinsandigen Kalke mit *Weyla* sp., *Dactylioceras (Orthodactylites)* und *Hildaites* (oder *Harpoceratoides).* Das Toarcium ist in ähnlicher Mächtigkeit und Fazies wie bei Majada del Carrizo ausgebildet. Die bräunlich anwitternden Kalke enden mit einer kleinen, 3 m hohen Steilstufe, die von bis 1 m mächtigen Fossilschuttkalkbänken gebildet wird, in denen *Propeamussium* häufig und *Chlamys* selten sind. Außerdem kommen *Peronoceras* sp. ex gr. *P. subarmatum* und *Harpoceras* vor. Hangend folgen Mergel mit geringmächtigen Kalkbänken, im oberen Teil mit häufig „*Rhynchonella*" und „*Terebratula*", selten *Modiolus* und *Harpoceras* (entspricht Schicht 8 bei Majada del Carrizo).

Diese mergelige Serie wird von dickbankigen, fossilschuttreichen Knollenkalken (ca. 5 m mächtig) überlagert, die eine kleine Steilstufe bilden. In den unteren 2 m sind schlecht erhaltene *Peronoceras* cf. *bolitoense* und *Harpoceras* sp. vorhanden. Aus der gleichen Schicht stammt ein großwüchsiges Exemplar einer *Leukadiella* cf. *gallitellii* Pinna. Es ist dies der erste Nachweis dieser Gattung in Südamerika. Aus diesem Schichtbereich (oder nächsten Fossilschicht) muß das von Möricke (1894, Taf. 2, Fig. 6) beschriebene „*Deroceras* aff. *Davoei* Sow." (= *Peronoceras moerickei* n. sp.) von La Guardia stammen.

Etwa 1 m hangend der Knollenkalke liegt eine 20 cm mächtige, brüchige, bituminöse Kalkbank mit *Peronoceras* sp. (Bruchstück), *Catacoeloceras* sp. und Hildoceratidae gen. et sp. indet. (3 Arten). Direkt hangend folgt eine weitere, 10 cm mächtige, brüchige Kalkbank mit *Phymatoceras* cf. *fabale.*

Die weitere Schichtfolge besteht aus 10 bis 20 cm gebankten, splittrigen Kalken mit schlecht erhaltenen Ammoniten, zuerst noch mit *Phymatoceras*, dann *Phlyseogrammoceras*. Unterhalb des Grates bei 3435 m stehen dickbankige Fossilkalke mit *Gryphaea* und selten *Lopha* an. Am Grat ist eine 10 cm mächtige Schicht mit häufig *Neocrassina* cf. *andium* (Gottsche), sowie *Lopha*, *Myophorella* und *Pleydellia (Walkericeras)* cf. *lotharingica* des obersten Toarcium aufgeschlossen.

Die hangenden, ca. 2 m mächtigen, knollig-kalkig-sandigen Schichten enthalten noch schlecht erhaltene *Pleydellia (Walkericeras).* In dem folgenden 2 m mächtigen Fossilkalk tritt *Bredyia* sp. des basalen Aalenium auf. In diesem Fossilkalk ist eine neue Gattung und Art der Isognomonidae (cf. *Gervilleioperna*) häufig, daneben kommen *Chlamys, Ctenostreon* und „*Terebratula*" vor.

In den anschließenden Kalken (ca. 2 m mächtig) sind ein großwüchsiges *Entolium* und *Chlamys* häufig, *Bredyia* sehr selten. Darüber liegen 3 bis 1 m mächtige Kalkbänke mit *Gryphaea* und sehr selten Bruchstücken von ? *Eudmetoceras.*

Über diesen Kalken des Aalenium folgen noch geringmächtige, sandige und kalkige, z. T. rötliche Schichten des Callovium und über diesen eine mächtige, rote Sandsteinserie.

2.14 QUEBRADA CALQUIS
(Abb. 1, Profil 15)

Die Quebrada Calquis mündet 3 km nördlich der Hacienda Amolanas in den Rio Copiapó. Auf dem Bergrükken, der die untere Quebrada Calquis südlich begrenzt, wurde ein Juraprofil aufgenommen. Die Schichten fallen vorwiegend steil nach Westen ein. Mehrere durch Störungen und enge Falten bedingte Schichtverdoppelungen sind vorhanden.

Mergelige Kalke mit häufig Weyla, selten *Radstockiceras behrendseni* und *Atractites* können in den oberen Teil des unteren Pliensbachium (± ibex-Zone) gestellt werden. Graue Mergel mit häufig *Nuculana* (doppelklappig) und plattige, mehr oder minder mergelige Sandsteine mit flachgepreßten *Radstockiceras* gehören dem oberen Pliensbachium an. Im Hangenden folgen kalkreiche

Schichten. Über ihnen liegt eine etwa 100 m mächtige Serie, die aus einer Wechsellagerung von roten Mergeln mit mehr oder minder sandigen Mergelkalken besteht. Im hangenden Teil enthalten die rotbraunen Sandsteine häufig *Propeamussium,* weniger häufig ,,*Rhynchonella*", selten *Modiolus, Plagiostoma, Mesomiltha,* sowie *Dactylioceras (Orthodactylites)* cf. *hoelderi, Nodicoeloceras* cf. *crassoides* Form A, *Hildaites* und *Polyplectus.* Diese Serie muß dem tieferen Teil des unteren Toarcium (*hoelderi*-zone) zugeordnet werden.

Am NW-Fuß des Bergrückens grenzen mit einer Störung Sandsteine an Rotschichten mit ebenfalls rötlichen Fein- bis Grobsandsteinen, in denen schlecht erhaltene Bruchstücke von *Peronoceras* ex gr. *P. subarmatum* und *Harpoceras* vorkommen. Diese Fauna ist etwas jünger als die mit *Dactylioceras (Orthod.)* cf. *hoelderi.*

2.15 RIO MANFLAS, PROFIL ZWISCHEN DEM FLUSS UND DEM PORTEZUELO EL PADRE

(Abb. 1, Profil 16)

Vom Rio Manflas (Basis) wurde zum Portezuelo El Padre (Übergang zur Quebrada de la Iglesia) ein Juraprofil aufgenommen, das eine Mächtigkeit von 1700 m erreicht. Die Profilaufnahme wurde dort begonnen, wo die Basisschichten des Jura den Fluß kreuzen. Das Liegende des Jura bilden grünliche Tuffe. Der Jura beginnt mit 4 bis 5 m mächtigen, 30 bis 60 cm gebankten Fossilschuttkalken, die in mehr oder weniger kalkige, 20 bis 40 cm gebankte Sandsteine (z. T. mit Fossilschutt) übergehen. Etwa 60 m über der Basis beginnt eine ca. 5 m mächtige Serie von Kalken mit mergelig-kalkigen Zwischenlagen, in denen *Gryphaea darwini* FORBES und *Lithotrochus humboldti* (v. BUCH) häufig sind. Selten kommen vor ,,*Rhynchonella*", *Weyla, Entolium* (mehr in den Kalkbänken) und eine für den tiefsten Teil des oberen Sinemurium typische Gattung und Art der Eotomariinae. Es folgen Mergel mit kalkigen, z. T. sandigen Bänken und Fossilschutt, etwa 130 m über der Basis mit einer weiteren Fossilschicht: *Spiriferina,* ,,*Rhynchonella*", *Gryphaea tricarinata, Plicatula, Jaworskiella gryphitica, Cardinia, Lithotrochus humboldti* u. *L. andinus.* Diese sandig-mergeligen Schichten gehen über in eine sehr mächtige Serie (über 600 m) aus dunkelgrauen, dm-gebankten Kalken, die mit dunkelgrauen Mergeln wechsellagern. Abschnittsweise überwiegen die Kalkbänke, dann wieder die Mergel. Fossilien sind selten *(Plagiostoma, Mesomiltha, Cardinia).* Im hangendsten Abschnitt wurde ein *Dactylioceras (Orthodactylites) tenuicostatum chilense* gefunden. Diese kalkig-mergelige Serie umfaßt also zumindest einen Teil des oberen Sinemurium, das Pliensbachium und reicht bis in das basale Toarcium. Sie geht in eine 50 bis 60 m mächtige, vorwiegend bräunlich verwitternde, kalkige Sandsteinserie über mit selten kalkigen Bänken. Vereinzelt kommen ,,*Rhynchonella*" und ,,*Terebratula*" vor. In den obersten Bänken ist *Liostrea* häufig. Außerdem wurden in dieser Serie ein kleines Bruchstück eines *Dactylioceras (Orthodactylites)* und *Plagiostoma* gefunden.

Es folgen 60 bis 70 m mächtige, gelblich-braun verwitternde, z. T. kalkige Mergel und anschließend wieder 70 bis 80 m mächtige, dm-gebankte, kalkige Sandsteine, die im tieferen Teil mit sandig-mergeligen Schichten wechsellagern, in denen vereinzelt ,,*Terebratula*" und *Weyla* vorkommen. Den Abschluß dieser Serie bildet eine ca. 10 m hohe Steilstufe aus Kalksandsteinen.

Über dieser Steilstufe liegen wieder gelblich-braun verwitternde, z. T. kalkige Mergel mit *Peronoceras bolitoense, P.* sp., *Collina* cf. *chilensis, Polyplectus* sp. und Hildoceratidae gen. et sp. indet. (glatte Art) im basalen Teil. Nach etwa 100 m Mächtigkeit werden die Kalkmergel rötlich und enthalten *Phymatoceras copiapense.* Zum Hangenden hin nimmt allmählich der Sandgehalt der Mergel zu. Aus diesen Schichten stammt ein *Phlyseogrammoceras tenuicostatum.* Diese mergelig-sandige Serie endet mit einer ca. 5 m mächtigen, roten Grobsandsteinbank mit einzelnen Geröllen (bis 0,5 cm ∅) und sehr selten *Bredyia* (basales Aalenium). Es folgen etwa 4 m mächtige graue Kalke mit *Eudmetoceras,* die in feinschichtige, etwa 4 m mächtige, z. T. rötliche Mergel übergehen. Über ihnen liegen rote Mergelkalke, die zum Hangenden hin sandiger werden und Sonninien und Stephanoceraten der ,,*sowerbyi*"- und der *sauzei*-Zone (unteres Bajocium) enthalten. Es sind dies die jüngsten im Bereich des Portezuelo El Padre aufgeschlossenen Schichten.

2.16 RIO PULIDO

(Abb. 1, Profil 17; Abb. 10)

Bei Iglesia Colorada wurde auf der linken Talseite des Rio Pulido in einer kleinen Seitenquebrada ein Profil aufgenommen. Der Jura grenzt mit einer schlecht aufgeschlossenen Störung an Granit. Der Jura beginnt mit dickbankigen, mehr oder minder sandigen Kalken, die an Fossilien *Weyla* und Einzelkorallen enthalten (Schichten 1). Es folgen stark gestörte, dickbankige Sandsteine. Darüber liegen dickbankige Kalke mit massenhaft *Gryphaea* (kleinwüchsig) (Schichten 2) und gebankte Fossilschuttkalke mit geringmächtigen Kalkmergelzwischenlagen und *Weyla* (Schichten 3). Diese Schichten gehen über in eine Serie 5 bis 20 cm gebankter, vorwiegend dichter Kalke mit ebensomächtigen (oder mehr) Kalkmergelzwischenlagen. Vereinzelt tritt *Weyla* auf. Über dieser Serie liegen feinschichtige, mergelig-sandig-schiefrige Schichten mit flachgepreßten *Radstockiceras.* Es folgen graue Mergel mit selten Kalkbänken, dann vorwiegend 10 bis 20 cm gebankte, rostbraun anwitternde, feinsandige Kalke mit sandigen Mergelzwischenlagen. Sie gehen in dünnbankige Kalke (5 bis 15 cm ∅) über, die mit Mergeln wechsellagern. *Propeamussium* ist in diesen Schichten häufig.

Anschließend ist eine Serie mehr oder minder sandiger und fossilschuttreicher Kalke mit *Gryphaea* und „*Rhynchonella*" aufgeschlossen. Die Bänke sind 20 bis 50 cm mächtig. Im mittleren Teil sind die sandig-mergeligen Zwischenlagen mächtiger als die Kalkbänke. In der hangendsten Bank sind Ammoniten häufig: *Peronoceras* cf. *bolitoense* n.sp., *Collina chilensis* n.sp., *Harpoceras* cf. *subexaratum*, Hildoceratidae gen. et sp. indet. (glatte Art).

Die Fortsetzung des Profils ist schlecht aufgeschlossen. Es wiegen Mergel vor. Nach ca. 80 m Mächtigkeit kommen in einer 30 bis 50 cm mächtigen Kalkbank *Pleydellia (Walkericeras)* cf. *lotharingica* (Branco) und *Dumortieria pusilla* Jaw. vor. Über dieser Bank werden die den Mergeln eingelagerten Kalkbänke zunehmend mächtiger und die Bänke allmählich knollig. Die Serie endet mit gebankten Kalken, in denen vereinzelt Brachiopoden und Pelcypoden vorkommen. Aus diesen Schichten stammt ein *Hammatoceras* sp.

Den Abschluß des Juraprofils bildet eine Serie häufig dickbankiger und fossilschuttreicher, z. T. sandiger Kalke, die mit weicheren, sandig-mergelig-kalkigen Schichten wechsellagern, die z. T. ebenfalls sehr fossilreich sind. An der Basis kommt *Bredyia* vor, im mittleren Teil *Spaerocoeloceras* und im hangenden Abschnitt *Eudmetoceras*.

Außerdem wurden in dieser Serie gefunden:

„*Rhynchonella*" sp.
„*Terebratula*" sp. (großwüchsig)
Gryphaea sp.
Lopha sp.
Modiolus sp.
Isognomonidae nov. gen. nov. sp. (cf. *Gervilleioperna*)
Entolium cf. *demissum* (Philipps)
Chlamys cf. *textoria* (Schloth.)
Eopecten cf. *tuberculosus* (Goldf.)
Trigonia sp.
Mesomiltha cf. *bellona* (d'Orb.)
Mesomiltha sp. (großwüchsig)
Neocrassina andium (Gottsche)
Trigonastarte (?) *steinmanni* (Möricke)
Pleuromya sp.
Cercomya sp.

Der Jura grenzt an einen Andesit, und über diesem liegt eine Serie roter Sandsteine und Konglomerate.

2.17 RIO MANFLAS
(Abb. 1, Profile 18 und 19; Abb. 10)

Zwischen der Quebrada del Medio und der Quebrada Berrocal beginnt am Rio Manflas ein Jurastreifen, der 15 km lang ist und bis Juntas del Toro reicht. Südlich Los Graneros befinden sich die Juraschichten vollständig auf der rechten Talseite. In diesem Jurastreifen wurden 3 Profile aufgenommen. Das nördlichste Profil liegt 2,5 km südlich Los Graneros, zwischen dem Rio Manflas und dem Cerro Salto del Toro. Das zweite Profil wurde 2 km nördlich Juntas del Tolar und das dritte Profil bei Juntas del Toro, am Beginn des Rio del Toro, vermessen. Von Norden nach Süden nimmt die Mächtigkeit des Jura allmählich ab (Abb. 10). Bestimmbare Dactylioceraten wurden in den Profilen Cerro Salto del Toro und Juntas del Toro gefunden.

2.17.1 Profil Salto del Toro
(Abb. 1, Profil 18)

Auf feinschichtige Tuffe transgrediert eine 1,0 bis 1,3 m mächtige Aufarbeitungslage mit Porphyritgeröllen (bis 30 cm ∅). Darüber liegt eine 40 bis 50 cm mächtige Kalkbank, die sich fast vollständig aus einer kleinwüchsigen *Gryphaea* zusammensetzt. Bruchstücke von *Weyla* sind selten. Direkt hangend folgt eine 20 bis 30 cm mächtige Kalkbank mit „*Rhynchonella*" an der Basis. Darüber liegen Kalke mit vereinzelt *Gryphaea*, die zum Hangenden hin seltener wird. Aus diesem Bereich (Schicht 2, Abb. 10) stammt ein *Epideroceras* des obersten Sinemurium. Die Kalke werden knollig und bei Schicht 3 fehlen auf 2 bis 3 m mergelige Zwischenlagen. In diesen schlecht gebankten Kalken tritt *Uptonia* und selten *Weyla* auf. Nach einem schichtparallel intrudierten Porphyrit sind wieder gut gebankte (15 bis 30 cm ∅) Kalke mit selten *Weyla* vorhanden. Bei Schicht 4 treten Fossilschuttkalke mit *Gryphaea* (kleinwüchsig), *Weyla*, *Pholadomya* cf. *corrugata* und *Pleuromya* auf. In den gut gebankten Kalken der Schichten 4a und 5 wurden *Cenoceras* und *Radstockiceras* gefunden. Bei Schicht 6 sind 2 bis 3 m mächtige, feinschichtig-schiefrige, kalkige Sandsteine bis feinsandige Kalke mit Fossilschutt, *Pectinula cancellata* und *Radstockiceras* aufgeschlossen.

Über diesen Pectinulaschiefern liegen wieder Mergel (bis 1,5 m mächtig) mit einzelnen, dichten, 10 bis 30 cm gebankten Kalken. Zum Hangenden hin werden die Mergellagen geringermächtig und die Kalkbänke häufiger. In dieser Serie wurde im Bereich von Schicht 7 *Dactylioceras (Orthodactylites) tenuicostatum chilense*, *Dactylioceras* (? *Orthodactylites*) cf. *helianthoides* und Bruchstücke nicht näher bestimmbarer Hildoceratidae gefunden. Ammoniten sind selten und zumeist schlecht erhalten. Das *Dact. (Orthod.) tenuicostatum chilense* stammt wahrscheinlich aus etwas tieferen Schichten als die übrigen Ammoniten. Die Serie geht in gut gebankte Sandsteine mit Mergellagen über, die „*Rhynchonella*", „*Terebratula*" und *Weyla* enthalten (Schicht 8). Es folgt eine Steilstufe aus bräunlich verwitternden Sandsteinen. Im mittleren Teil ist ein 2 m mächtiger Horizont vorhanden, in dem Querschnitte von *Weyla* häufig sind. Auf der Oberfläche der obersten Bank dieser Sandsteinserie kommen großwüchsige *Peronoceras* cf. *bolitoense* vor (Schicht 9). In den unmittelbar hangenden, feinschichtigen, sandigen Kalken treten schlecht erhaltene *Phymatoceras* auf.

Es folgen vorwiegend dunkle Mergel mit einzelnen Kalkbänken. Bruchstücke von *Phymatoceras copiapense*

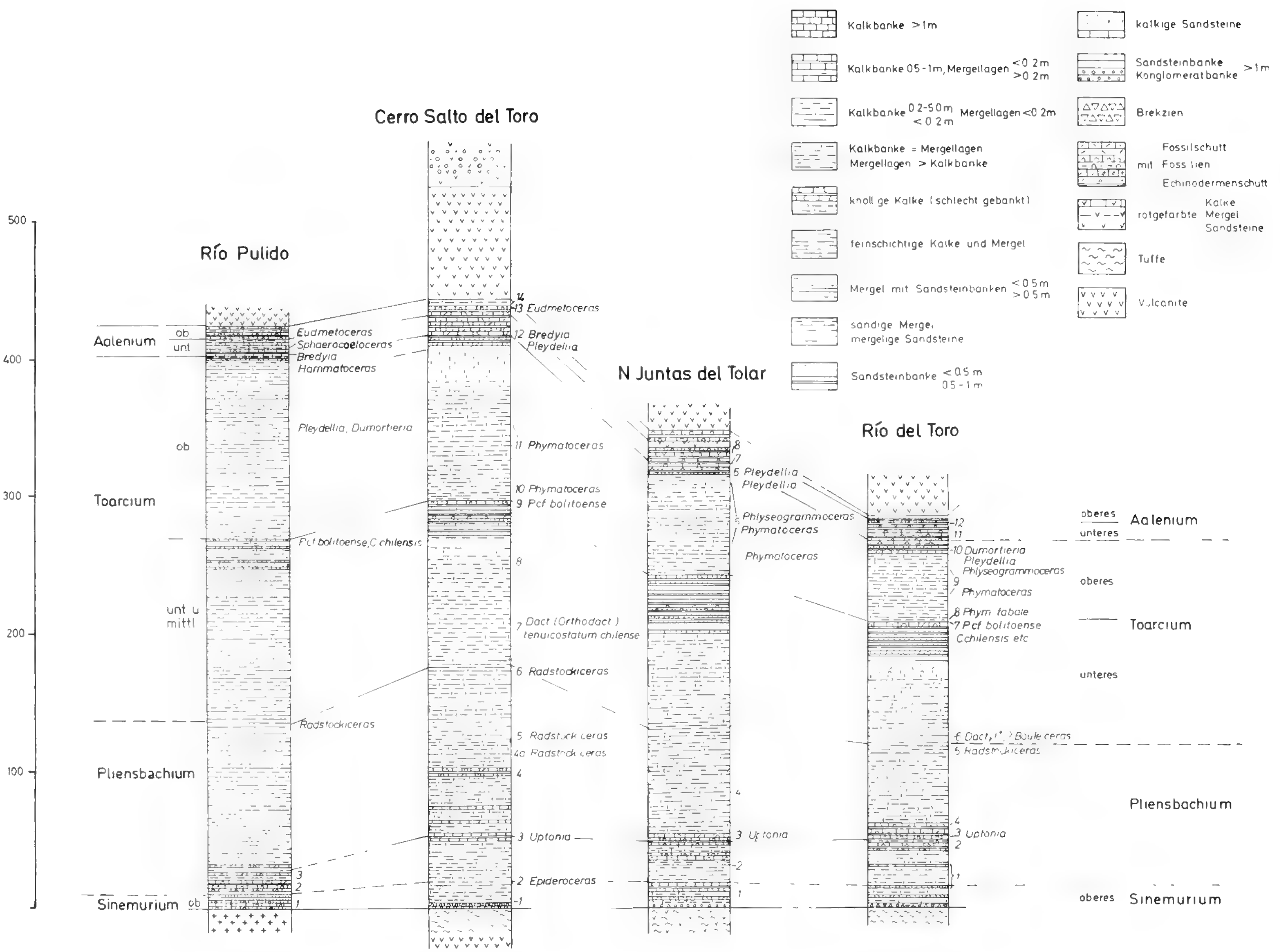

Abb. 10: Juraprofile Rio Pulido (Abb. 1, Profil 17) und Cerro Salto del Toro bis Rio del Toro am Rio Manflas (Abb. 1, Profile 18 und 19).

und „*Terebratula*" sind häufig, *Modiolus* und *Pleuromya* selten. Zum Hangenden hin werden die Kalke zunehmend sandig. In den Bänken sind wulstige Sandsteinlagen vorhanden. Es schließt eine Serie dickbankiger, grob- bis mittelkörniger, kalkiger Sandsteine mit viel Fossilschutt an. Im tiefsten Teil kommt *Pleydellia*, etwas höher *Bredyia* vor. Pelecypoden sind häufig. In den Schichten 12 kommen neben (selten) Ammoniten vor:

„*Terebratula*" sp.
Gryphaea sp.
Grammatodon sp. (großwüchsig)
Eopecten cf. *tuberculosus* (GOLDF.)
Plagiostoma sp.
Trigonia sp.
Isognomonidae nov. gen. nov. sp. (cf. *Gervilleioperna*)
Stomechinus andinus (PHILIPPI)

Die hangendste Bank (1 m mächtig) (Schicht 13) dieser Sandsteinserie ist erfüllt von *Gryphaea*, außerdem kommen „*Rhynchonella*", „*Terebratula*" und *Lopha* vor. Direkt im Liegenden dieser Bank tritt *Eudmetoceras* auf. 1 bis 2 m mächtige, dunkle, dichte Kalke mit *Bositra* bilden den Abschluß des Jura und grenzen gegen einen Andesit, der mit stratigraphischem Kontakt von roten Sandsteinen und Konglomeraten überlagert wird.

2.17.2 Profil Juntas del Toro (Rio del Toro)
(Abb. 1, Profil 19)

Das Profil bei Juntas del Toro stimmt petrographisch weitgehend mit dem 2 km nördlich Juntas del Tolar überein.

Der Jura transgrediert mit einer Brekzie oder Konglomerat auf Tuffe der ? Trias. Darüber liegen mehr oder minder sandige, knollige Kalke (bis 1 m ∅) mit *Weyla* und doppelklappigen, desmodonten Muscheln *(Pholadomya, Homomya)* (Schicht 1, Profil N Juntas del Tolar). Es folgen mergelige Kalke bis Kalkmergel im Rhythmus von 5 bis 20 cm mit häufig „*Rhynchonella*", „*Terebratula*" und *Gryphaea*, weniger häufig *Weyla* (Schicht 2, Profil N Juntas del Tolar; Schichten 1 Rio del Toro). Diese fossilreichen Schichten enden mit einer zweigeteilten, kleinen Steilstufe aus 50 cm bis 1 m gebankten Kalken mit „*Terebratula*", *Gryphaea* und *Weyla* im liegenden Teil, mergeligen Kalken mit häufig „*Terebratula*", seltener „*Rhynchonella*" im mittleren Teil (Schicht 2 Rio del Toro) und mehrere Meter mächtigen, z. T. etwas sandigen, häufig schlecht gebankten Kalken mit geringmächtigen Mergelfugen im hangenden Teil. In diesen knolligen Kalken sind Bohrgänge und *Weyla* häufig. *Uptonia* kommt in mehreren Bänken vor, außerdem „*Terebratula*", *Pholadomya* cf. *corrugata* und *Pleuromya* (Schicht 3, Profil N Juntas del Tolar; Schicht 3 Rio del Toro). Am Ende der Steilstufe wurde in Schicht 4 (Rio del Toro) „*Rhynchonella*", „*Terebratula*", *Lopha longistriata* (JAW.), *Myoconcha neuquena* LEANZA und *Homomya neuquena* LEANZA gefunden. Über der Steilstufe folgt eine Wechsellagerung von Fossilschuttkalken mit Mergellagen und häufig *Weyla*. Die Fossilschuttkalke werden zum Hangenden hin durch gut gebankte, dichte Kalke (10 bis 30 cm ∅) ersetzt. Diese Serie endet mit 1,5 bis 2 m mächtigen, feinschichtig-schiefrigen, z. T. sandigen Kalkmergeln, in denen *Pectinula cancellata* sehr häufig ist. Beim Profil Rio del Toro ist in diese Pectinulaschiefer schichtparallel ein Porphyrit intrudiert. Im Liegenden des Porphyrit (Schicht 5) kommt *Radstokkiceras* vor und über ihm (Schicht 6) stark verdrückte *Dactylioceras (Orthodactylites)* und ein schlecht erhaltener, weitnabeliger Ammonit, der sich noch am ehesten mit *Bouleiceras* sp. bei v. HILLEBRANDT (1973a) vergleichen läßt (s. S. 13).

Über den Pectinulaschiefern liegen wieder gut gebankte (10 bis 20 cm ∅) Kalke, die mit Mergeln wechsellagern. Zum Hangenden hin werden die Bänke allmählich sandig und mächtiger, die Mergellagen geringermächtig und die Serie geht in dickbankige Kalksandsteine über, denen im mittleren Teil einige Bänke mit sehr häufig *Weyla* und Brachiopoden eingeschaltet sind. Die hangendste Bank dieser Serie ist bei Profil Rio del Toro (Schicht 7) sehr fossilreich und enthält folgende Fauna:

„*Rhynchonella*" sp. h
„*Terebratula*" sp. h
Gryphaea sp. s
Entolium cf. *demissum* (PHILIPPS) s
Myophorella sp. s
Neocrassina cf. *aureliae* FERUGLIO h
Neocrassina sp. s
Pholadomya cf. *fidicula* SOW. s
Eucyclus sp. ss
Zygopleura cf. *quinetta* (PIETTE) s
Peronoceras cf. *bolitoense* n. sp.
Collina chilensis n. sp.
Harpoceras cf. *subexaratum* (BON.)
Phymatoceras sp.
Hildoceratidae gen. et sp. indet. (2 Arten)

Direkt hangend folgen eine Bank (Schicht 8) mit *Phymatoceras* cf. *fabale* und 1,0 bis 1,5 m mächtige, gelbliche Mergel mit dünnbankigen, kalkigen Feinsandsteinen.

In der anschließenden Mergelserie werden im Hangendteil die Kalkbänke häufiger, und die Serie endet mit sandigen, knolligen Kalken mit geringmächtigen Mergelzwischenlagen, die reich an desmodonten Muscheln *(Pholadomya* cf. *fidicula)* sind. Im hangenden Teil der Mergelserie ist *Phymatoceras copiapense* häufig, darüber tritt *Phlyseogrammoceras* auf, und in den sandigen, knolligen Kalken kommt *Pleydellia (Walkericeras)* cf. *lotharingica*, *P. (W.)* cf. *fluitans* und *Dumortieria* cf. *pusilla* vor.

Die folgende Steilstufe besteht aus dickbankigen Sandsteinen mit viel Fossilschutt. An der Basis kommen noch *Pleydellia (Walkericeras)* und *Dumortieria* vor (Schicht 6 N Juntas del Tolar; Schicht 10 Rio del Toro). Dann werden die kalkigen Sandsteine allmählich rötlich. Pelecypoden *(Eopecten* cf. *tuberculosus, Ctenostreon pectiniformis, Pholadomya* cf. *plagemanni, Pleuromya* sp.) sind häufig, Querschnitte von großen Ammoniten (? *Eudme-*

toceras) selten (Schichten 8 N Juntas del Tolar; Schicht 12 Rio del Toro). Der Jura endet mit nochmals grauen Grobsandsteinen, die an Andesit grenzen.

2.18 EL TRÁNSITO

(Abb. 1, Profil 20 und 21; Abb. 11)

Nördlich (Quebrada Chanchoquin/La Totora), östlich (Quebrada Plaza) und südlich El Tránsito (Quebrada Pinte) wurden mehrere Juraprofile aufgenommen und bei v. Hillebrandt (1973b, Abb. 2) dargestellt. Artlich bestimmbare Dactylioceratidae wurden bei den abgebildeten Profilen nur in dem zweiten (geringermächtigen) mit Quebrada La Totora bezeichneten Profil (Abb. 1, Profil 20) gefunden. Das mächtigere, der beiden mit Quebrada La Totora bezeichneten Profile bei v. Hillebrandt (1973b, Abb. 2), wurde in dem Jurastreifen zwischen der Quebrada Chanchoquin und der Quebrada Acevedo (Blatt El Tránsito) vermessen.

Weitere Dactylioceratidae stammen aus Schichten, die im Liegenden des Steinbruchs *(Plicatostylus*-Kalke) an der Vereinigung der Quebrada Chanchoquin mit der Quebrada Paitepén aufgeschlossen sind. Das Profil wurde bei v. Hillebrandt (1973a, S. 353) beschrieben.

2.18.1 Profil südlich Quebrada El Corral

(Abb. 1, Profil 20)

Südlich der Quebrada El Corral (Seitenquebrada der Quebrada La Totora) (Karte 1:50000, Blatt Lagunillas), zwischen dieser und Punkt 2360 (Blatt Conay) wurde ein Juraprofil aufgenommen.

Die Transgression des Jura erfolgt mit einem 20 cm mächtigen Fossilschuttsandstein auf Vulkanite der ? Trias. Die anschließenden Feinsandsteine enthalten selten ,,*Terebratula*" (einklappig) und gehen über in Mürbsandsteine mit sandigen Mergeln. Die obersten Bänke sind kalkig und führen neben Fossilschutt schlecht erhaltene ,,*Terebratula*" und *Weyla*. In der Quebrada Chanchoquin kommen in diesen basalen Sandsteinen vor:

Entolium sp. h
Jaworskiella gryphitica (Mör.) h
Pholadomya cf. *plagemanni* Möricke h
Pleuromya sp. h
Eotomariinae gen. et sp. indet. s
Epophioceras sp. ss

Die Fauna kann in das untere Ober-Sinemurium eingestuft werden. Über dieser basalen Sandsteinserie folgt eine mehr oder minder sandige Mergelserie, der im mittleren Teil zwei 30 und 60 cm mächtige Fossilschuttkalksandsteine mit *Gryphaea tricarinata* Philippi, *Weyla* und ,,*Terebratula*" eingeschaltet sind. Im oberen Teil treten einzelne, 20 bis 50 cm mächtige Kalk- und Sandsteinbänke auf.

Die Mergelserie wird von einer Serie dickbankiger Kalke überlagert. Sie beginnt mit einem 60 cm mächtigen Fossilschuttkalk, der hauptsächlich aus Echinodermenschutt besteht. 2,5 m hangend enthält ein 1 m mächtiger, knolliger Kalk *Weyla* und häufig desmodonte Muscheln. Selten kommen ,,*Rhynchonella*", *Lopha longistriata*, *Modiolus*, *Plagiostoma* und *Lithotrochus andinus* vor. Über diesem Knollenkalk liegt ein 1 m mächtiger Fossilschuttkalk mit viel Echinodermenschutt (u. a. Seeigelstachel). Es folgen weiterhin dickbankige Fossilschuttkalke (bis 1,5 m ∅) mit geringmächtigen Mergelzwischenlagen. Im hangenden Abschnitt ist dieser Kalkbankserie ein 20 m mächtiger, intrusiver Porphyrit eingeschaltet. Über ihm werden die Kalke allmählich dünnbankiger und gehen in eine Wechsellagerung von 20 bis 40 cm gebankten Fossilschuttkalken mit bis 1 m mächtigen Mergelzwischenlagen über. Etwa 10 m im Hangenden des Porphyrit ist *Spiriferina* sehr häufig, wenig oberhalb dieses Horizontes kommt *Montlivaltia* und in beiden Schichten ,,*Rhynchonella*" und ,,*Terebratula*" häufig vor. In diesem Schichtbereich wurde in der Quebrada Chanchoquin ein *Eoderoceras* ex gr. *E. armatum* gefunden, was für eine Einstufung dieser Schichten in das höhere Ober-Sinemurium spricht.

Im obersten Abschnitt dieser Kalk-Mergel-Serie werden die Mergellagen wieder geringermächtig, bis 1 m mächtige Fossilschuttkalkbänke kommen vor.

Es folgt eine Steilstufe aus dickbankigen, z. T. feinsandigen und fossilschuttreichen Kalken. In einzelnen Bänken sind ,,*Rhynchonella*" und ,,*Terebratula*" häufig. Im mittleren Teil tritt eine Schicht mit *Gryphaea* auf. Im oberen Teil ist *Weyla* nicht selten, und in den hangendsten Bänken sind sehr häufig Bryozoen vorhanden.

Die von Zeil (1960, S. 653) aus der Quebrada Pinte angegebene *Uptonia* cf. *jamesoni* (Sow.) stammt aus der Kalk-Mergel-Serie oder den basalen Fossilschuttkalken der folgenden Serie.

Oberhalb der Quebrada Chanchoquin bilden die dickbankigen Kalke ebenfalls eine kleine Steilstufe. An der Basis wurde das Bruchstück eines zu den Polymorphitinae zu stellenden Ammoniten gefunden (s. a. v. Hillebrandt 1973b, S. 197), im mittleren Teil ein mäßig erhaltenes *Radstockiceras* cf. *behrendseni* (Jaw.). Beide Ammoniten sprechen für eine Einstufung dieser Schichten in das untere Pliensbachium (± ibex-Zone).

Über dieser Steilstufe liegen Mürbsandsteine, die mit Mergeln wechsellagern und *Radtstockiceras* sp. 1 enthalten. Es folgen vorwiegend gelbliche Mergel, schiefrige Kalke und dünnbankige Kalke. In diesen Schichten wurde 2,2 km SW Punkt 2360 *Radstockiceras* sp., *Protogrammoceras* cf. *normanianum* (d'Orb.) und *Atractites* gefunden (± davoei-Zone).

Die dünnbankigen Kalke gehen über in eine Wechsellagerung von rötlichen, feinsandigen, gut gebankten (10 bis 40 m ∅) Kalken mit 10 bis 50 cm mächtigen, rötlichen

Mergeln. Diese Schichtfolge wird von einem 2 bis 3 m mächtigen, rötlichen, in sich gebankten, knolligen Sandstein mit Fossilschutt überlagert, in dem *Weyla, Mesomiltha, Pleuromya* und *Cenoceras* vorkommen. Im hangendsten Teil ist der Sandstein mürb, enthält zahlreiche Bohrgänge, reichlich Fossilschutt und 2,2 km SW Punkt 2360 wurde ein *Radstockiceras* sp. 2 mit 25 cm Durchmesser gefunden.

Anschließend folgen wieder graue, feinsandige, gut gebankte (10 bis 40 cm) Kalke, die mit Mergeln (20 bis 50 cm Ø) wechsellagern. Bis etwa 10 m über der rötlichen Sandsteinbank wurde *Radstockiceras* gefunden. In der Quebrada Chanchoquin fehlt diese rötliche Sandsteinbank, und in diesem Schichtbereich tritt zusätzlich zu *Radstokkiceras Argutarpites* und *Lytoceras* auf (± spinatus-Zone).

Im Hangendteil sind die Schichten wieder rötlich gefärbt und sie werden von roten, feinkörnigen Sandsteinen (20 bis 40 cm gebankt) überlagert, die z. T. Echinodermenschutt enthalten. Nach ca. 3 m Mächtigkeit ist den Sandsteinen ein 40 cm mächtiger Fossilschuttkalk mit „*Terebratula*" und *Weyla* eingeschaltet. Diese Kalkbank geht nach SW in eine zunächst 1 m mächtige, dann 3 m mächtige (350 m SW Punkt 2360), in sich gebankte Lumachelle bis Fossilschuttkalk über, der auch hier von etwa 3 m mächtigen, roten Sandsteinen unterlagert wird. Über dieser Lumachelle/Fossilschuttkalk liegt eine aus 2 Bänken bestehende, insgesamt 2 m mächtige Lumachelle, die sich aus den Bruchstücken von *Plicatostylus* zusammensetzt.

Im Bereich des Normalprofils (ca. 250 m östl. Punkt 2360) folgen über der 40 cm Kalkbank nochmals ca. 20 m mächtige, fein- bis mittelkörnige, rote Sandsteine. Etwa 4 m unterhalb der Hangendgrenze ist eine etwa 1 m mächtige Zone mit häufig *Pholadomya* cf. *fidicula* Sow. und *Pleuromya*, selten *Myophorella*, *Cercomya* und Gastropodensteinkernen, sowie schlecht erhaltenen Bruchstücken eines großwüchsigen *Peronoceras* eingeschaltet.

Den Abschluß der Sandsteine bildet ein 50 cm mächtiger, grauer Fossilschuttkalk, der im Hangendteil reich an Fossilien ist:

„*Rhynchonella*" sp. h
„*Terebratula*" sp. h
Liostrea sp. h
Lopha sp. s
Modiolus cf. *baylei* (PHILIPPI) h
Pseudolimea sp. ss
Plagiostoma sp. ss
Trigonia sp. s
Myophorella sp. s
Pholadomya cf. *fidicula* SOW. h
Pleuromya sp. h
Zygopleura sp. s
Catacoeloceras (?) sp. s
Collina chilensis n. sp. h
Harpoceras cf. *subexaratum* (BON.) s
Phymatoceras ex gr. *P. erbaense* (HAUER) h
Hildoceratidae gen. et sp. indet (3 Arten) h

Über dieser Fossilbank liegen ca. 10 m mächtige Mergel mit knolligen Fossilschuttkalkbänken. Die Schichten sind fossilreich und es kommen vor:

„*Rhynchonella*" sp. h
„*Terebratula*" sp. h
Liostrea sp. s
Grammatodon sp. s
Modiolus cf. *scalprum* SOW. h
Entolium sp. s
Pseudolimea sp. s
Myophorella sp. h
Mesomiltha sp. s
Pleuromya sp. sh
Phymatoceras cf. *fabale* (SIMPSON) h
Phymatoceras ex gr. *P. lilli* (HAUER) h

In den hangenden Mergeln werden Kalkbänke wieder häufiger. Im oberen Teil kommen Fossilschuttkalke vor. Die Fauna setzt sich zusammen aus:

„*Rhynchonella*" sp. s
„*Terebratula*" sp. sh
Lopha sp. s
Modiolus sp. s
Eopecten cf. *tuberculosus* (GOLDF.) s
Ctenostreon sp. s
Plagiostoma cf. *gigantea* (SOW.) s
Pseudolimea sp. s
Trigonia sp. s
Phymatoceras copiapense (MÖRICKE) h
Phlyseogrammoceras cf. *tenuicostatum* (JAW.) s
Pleydellia (Walkericeras) sp. s

Die Fauna umfaßt mehrere Zonen (Subzonen) des oberen Toarcium.

Die Mergelserie wird von einem ca. 3 m mächtigen, sandigen Fossilschuttkalk überlagert, in dessen hangendem Teil folgende Fossilien vorkommen:

„*Rhynchonella*" sp. s
Costigervillia sp. ss
Trigonia sp. h
Pleuromya sp. s
Seeigelstachel

Zwischen der Quebrada Chanchoquin und der Quebrada Acevedo ist dieser sandige Fossilschuttkalk sehr fossilreich und enthält:

Actinastrea sp. h
„*Rhynchonella*" sp. s
„*Terebratula*" sp. h
Lopha sp. s
Grammatodon sp. (großwüchsig) h
Entolium cf. *demissum* (PHILIPPS) s
Eopecten cf. *tuberculosus* (GOLDF.) s
Trigonia sp. h
Myophorella sp. s
Vaugonia sp. s
Mesomiltha cf. *bellona* (D'ORB.) h
Mesomiltha sp. (großwüchsig) s
Neocrassina cf. *andium* (GOTTSCHE) s
Protocardia sp. s
Pholadomya cf. *plagemanni* MÖRICKE h
Pleuromya sp. h
Cercomya iglesiae MÖRICKE h
Bredyia sp. s

Über dem Fossilschuttkalk liegen 6 bis 8 m mächtige, rote, mürbe Sandsteine mit Geröllen (bis 5 cm Ø). In diesen Sandsteinen kommt im Profil der Quebrada Canchoquin eine großwüchsige *Ceratomya* (?) und *Bredyia* vor (unteres Aalenium).

Hangend folgt ein ca. 2 m mächtiger Grobsandstein mit Fossilschutt und Geröllen (bis 5 cm ∅). Dieser Horizont ist südlich der Quebrada Acevedo (r. Seitenquebrada der Qu. Chanchoquin) als Konglomerat ausgebildet, das z. T. taschenförmig und in Spalten bis 25 cm tief in den liegenden Sandstein greift. Im Hangendteil des Konglomerats ist *Trigonia* häufig und es wurde eine *Fontannesia* (?) *austroamericana* Jaw. gefunden (oberes Aalenium).

Den Abschluß des Juraprofils bilden graue, dichte, gut gebankte Kalke mit häufig *Mesomiltha intumescens* (Gottsche) und Bruchstücken von *Sonninia (Papilliceras) espinazitensis* Tornquist (unt. Bajocium, *sauzei*-Zone).

In der Quebrada Acevedo kommen im sandigen, liegenden Teil der Kalke *Pseudotoites sphaeroceroides* (Tornquist) und *Sonninia (Papilliceras) altecostata* (Tornquist) vor (unt. Bajocium, „*sowerbyi*“/*sauzei*-Zone).

Über dem Jura liegen Porphyrite.

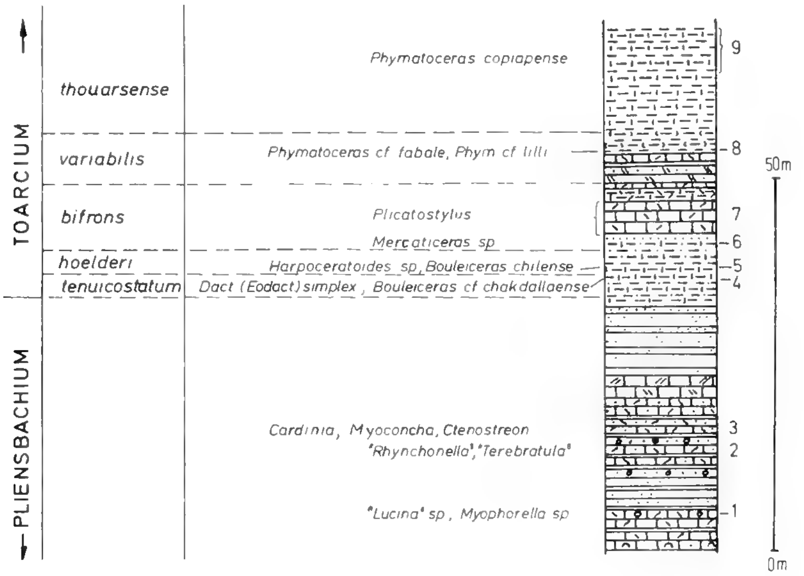

Abb. 11: Teilprofil des Jura bei der Vereinigung der Quebrada Chanchoquin mit der Quebrada La Totora („Steinbruch-Profil“); Legende zur Gesteinsausbildung Abb. 10.

2.18.2 Profil Quebrada Chanchoquin/Paitepén (Abb. 1, Profil 21; Abb. 11)

Das Profil an der Vereinigung der Quebrada Chanchoquin mit der Quebrada Paitepén wurde bei v. Hillebrandt (1973a, S. 353, 354) beschrieben. Im Liegenden der *Plicatostylus*-Kalke (Abb. 11) ist eine Serie gut gebankter Kalke aufgeschlossen, die im Abstand von 2 bis 3 m 2 Ammoniten-Horizonte enthält. Im tieferen Horizont kommen sehr häufig Dactylioceratidae vor. Die ursprüngliche Bestimmung bei v. Hillebrandt (1973a) muß korrigiert werden. Der tiefere Horizont enthält nunmehr folgende Arten:

Dactylioceras (Eodactylites) simplex Fucini h
Dactylioceras (Orthodactylites) directum (Buckman) h
Dactylioceras (Orthodactylites) anguinum (Reinecke) s
Nodicoeloceras cf. *eikenbergi* (Hoffmann) ss
Nodicoeloceras cf. *pseudosemicelatum* (Maubeuge) h
Radstockiceras sp. ss
Bouleiceras cf. *chakdallaense* Fatmi ss

Die Fauna des höheren Horizontes setzt sich zusammen aus:

Vaugonia n. sp. (cf. *V. oregonensis* Poulton) h
Mesomiltha huayquimili (Leanza) h
Discohelix sp. h
Cenoceras sp. ss
Harpoceratoides sp. ss
Hildaites sp. ss
Bouleiceras chilense v. Hillebrandt h
Bouleiceras cf. *chilense* v. Hillebrandt h

3. PALÄONTOLOGISCHER TEIL

3.1 GENUS: *DACTYLIOCERAS* HYATT, 1867

Typus-Art: *Ammonites communis* Sowerby, 1815

Diagnose: (ausführliche Charakteristik siehe Schmidt-Effing 1972: 54–55): Evolute, flach-scheibige, serpentikone Gehäuse, die selten 10 cm Durchmesser überschreiten. Ontogenetische Merkmalsänderungen sind in der Regel wenig ausgeprägt. Der Windungsquerschnitt ist hochoval bis rundlich. Die Skulptur wird aus geraden, nur selten leicht geschwungenen Flankenrippen, die sich am Außenbug in 2 bis 3 Externrippen teilen und ununterbrochen die Externseite queren, gebildet. Außerdem können Schaltrippen und ungeteilt durchlaufende Einfachrippen auftreten, seltener, und dann immer an bestimmte Windungsabschnitte gebunden, werden Dornen bzw. Knoten an den Rippenspaltpunkten, auch fibulate Rippen beobachtet.

Bemerkungen: In der Terminologie und Morphologie des Dactylioceraten-Gehäuses folge ich Schmidt-Effing (1972: 21–30), in der Taxonomie entsprechend (1972: 54–62). Von Guex (1973b) abgesehen sind zu diesen Gebieten inzwischen keine neuen Beiträge erfolgt (Schmidt-Effing 1975). Howarth (1973: 247) weist auf die große Variabilität der *Dactylioceras*-Arten hin. Rocha (1976: 96–97) gibt einen historischen Überblick, Krymgolz (1974b) eine Artenliste.

Verbreitung: Höchstes Domerium bis Mittel-Toarcium (*bifrons*-Zone); weltweit.

3.1.1 Subgenus: *Dactylioceras (Eodactylites)* Schmidt-Effing, 1972

Typus-Art: *Dactylioceras pseudocommune* Fucini, 1935

Diagnose: Ein Subgenus von *Dactylioceras*, das sich durch kräftige Rippen, wobei die Externrippen häufig gespreizt sind und zu den Flankenrippen abgewinkelt stehen, und häufig auch durch eine im Querschnitt keilförmig zugespitzte Externfläche auszeichnet. Der Windungsquerschnitt ist im Alter immer hoch oval, im Bereich der jüngeren Windungen jedoch rundlich bis breit oval.

Bemerkungen: Gerade durch die ausgeprägteren ontogenetischen Merkmalsänderungen springt das Subgenus etwas aus dem Rahmen der allgemeinen Gattungsdiagnose. Seine Arten sind von dem stratigraphisch folgenden *Dactylioceras (Orthodactylites)* sehr verschieden, von dem erst viel höher folgenden *D. (Dactylioceras)* weniger verschieden (Howarth 1978: 252). Doch sind auch diese beiden Subgenera in allen Eigenschaften, nicht nur morphologisch, so verschieden, daß ihre Unterscheidung gerechtfertigt ist. So sind sie stratigraphisch durch große Teile des gesamten Unter-Toarciums getrennt. Biogeographisch ist *Eodactylites* auf die mediterrane Faunenprovinz beschränkt, wobei sein Auftreten in Chile als starker mediterraner Einfluß zu werten ist. *Dactylioceras* ist zwar weltweit verbreitet, doch im Mediterran allgemein selten. Für die mediterrane Stratigraphie und Paläontologie hat sich die Aufstellung des Subgenus als praktisch erwiesen (z. B. Elmi, Atrops & Mangold 1974: 54).

Verbreitung: Höchstes Domerium und tieferes Unter-Toarcium des Mediterrans (*mirabile*-Subzone) und Chiles (*simplex*-Subzone).

3.1.1.1 *Dactylioceras (Eodactylites) simplex* Fucini, 1935

Taf. 1, Fig. 1–4; Abb. 12, 16a, b

1935 *Dactylioceras simplex n. sp.* – Fucini: 86–87, Taf. 9, Fig. 4–5.
?1935 *Dactylioceras polymorphum n. sp.* – Fucini: 88 (pars), Taf. 9, Fig. 13.
1935 *Coeloceras ? cfr. Sellae* (Gemm.) – Fucini: 92, Taf. 8, Fig. 11–12.
1966 *Dactylioceras simplex* Fucini – Fischer: 23, Taf. 1, Fig. 2, Taf. 3, Fig. 5–6, Taf. 4, Fig. 7.
1968 *Dactylioceras polymorphum* Fuc. – Cantaluppi & Savi: 231, (pars), Taf. 20, Fig. 2, 3.
1971 *Dactylioceras (Dactylioceras) simplex* Fucini, 1935. – Pinna & Levi-Setti: Taf. 1, Fig. 9.
1972 *Dactylioceras simplex* Fucini, 1935 – Ferretti: 108, Taf. 18, Fig. 1.
1973a „*Catacoeloceras*“ *simplex* (Fuc.) – Guex: 509, Taf. 12, Fig. 11.

Material: Quebrada Chanchoquin (Abb. 1, Profil 21; Abb. 10, Schicht 4), topographische Karte 1:50000, Blatt El Tránsito: x = 375,1 km, y = 6811,05 km. Profilbeschreibung siehe v. Hillebrandt (1973a: 353–354). Die Dactylioceraten stammen aus dem tieferen Horizont, zusammen mit sehr seltenen *Radstockiceras* sp. und *Bouleiceras* cf. *chakdallaense* Fatmi. Sieben Exemplare (B. St. M. 1978 II 1–7) und zwei weitere Bruchstücke (B. St. M. 1978 II 8–9).

Erhaltung: Steinkernerhaltung, wobei die Schalen verkieselt sind. Besonders günstig sind erhalten: Nr. 7 (Teile von 5 Umgängen des Phragmokons), Nr. 4 (4 Umgänge des Phragmokons und ein Stück der Wohnkammer) und Nr. 5 ($3^1/_2$ Umgänge des Phragmokons). Bei den restlichen Exemplaren sind 2 bis 5 Umgänge jeweils erhalten, wobei diese teilweise verdrückt sind.

Maße (in mm):

Nr.	DM	WH	WB	NW	WB/WH
4	ursprünglicher Gesamtdurchmesser mindestens 70 mm				
6	46,0	12,5 (0,27)	14,0 (0,30)	22,5 (0,49)	(1,12)
4	45,5	14,0 (0,31)	18,0 (0,40)	22,2 (0,49)	(1,29)
1	35,0	—	—	18,0 (0,51)	—
5	ca. 35	10,0 (0,29)	13,5 (0,39)	ca. 17 (0,49)	(1,35)
3	34,5	10,0 (0,29)	ca. 12 (0,35)	16,5 (0,48)	(1,2)
2	34,5	10,0 (0,29)	—	16,0 (0,46)	—
7	—	13,5 —	16,5 —	—	(1,22)
7	—	9,1 —	11,5 —	—	(1,26)
7	—	4,0 —	6,0 —	—	(1,50)

Beschreibung: Die Gehäuse sind weit genabelt und gedrungen, der Nabel ist napfförmig eingesenkt. Der Windungsquerschnitt der frühen Umgänge ist sehr breit oval, der letzten Umgänge, besonders des letzten, breitrundlich, wobei die Flanken auf dem letzten Umgang (Wohnkammer) stärker abgeflacht sind. Die Flanken knicken scharf an der Nabelkante in eine senkrechte, hohe Nabelfläche um. Die Externfläche ist sehr breit gerundet; die Flanken sind schmal. Die konkave Windungszone der inneren Umgänge beträgt etwa $^1/_4$, des äußeren Umganges jedoch nur $^1/_5$.

Die Rippen setzen auf der Nabelfläche ein, erreichen ihre volle Stärke an der Nabelkante, verlaufen rectoradiat, auf den innersten Umgängen teils proradiat, über die Flanke und gabeln sich am Außenbug in 2 bis 3 gleichwertige Externrippen auf. Die Flankenrippen sind breit und kräftig. Die Rippenspaltpunkte liegen auf einer geraden Linie, wobei sie auf den inneren Umgängen Dornen tragen. Die Interkostalräume sind relativ breit. Die Externrippen sind fein (Ausnahme Exemplar 7 mit scharfen Externrippen) und stehen dicht. Nr. 14 besitzt bei einem Durchmesser von 46 mm auf dem letzten Umgang (Phragmokon) 37 Flanken- und ca. 90 Externrippen, auf dem vorletzten Umgang 24 und auf dem drittletzten Umgang ca. 19 Flankenrippen. Die Externrippen verlaufen leicht asymmetrisch, da sie leicht proximal ausgebaucht sind, über die Externfläche.

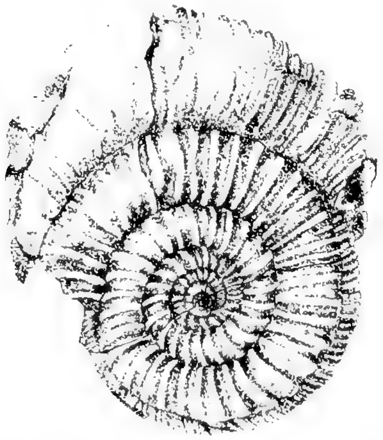

Abb. 12: *Dactylioceras (Eodactylites) simplex* Fucini, 1935; Quebrada Chanchoquin; B. St. M. 1978 II 4; nat. Gr.

Das Exemplar 4 ist wohl das Fragment eines adulten Gehäuses. Denn die hier teilweise erhaltene Wohnkammer zeigt deutliche Wachstumsunterschiede gegenüber den inneren Umgängen: sie ist im Verhältnis höher, besitzt eine schmalere konkave Windungszone und zeigt eine andersartige Skulptur, nämlich die Rippen stehen wesentlich dichter, sind schärfer und verlaufen auf der Nabelfläche proklin (Externrippen sind nicht günstig beobachtbar).

Die Exemplare Nr. 5 und Nr. 7 lassen an freien Septalflächen auch die Lobenlinie erkennen. Diese stimmt im wesentlichen mit der Abb. 15 (Schindewolf 1962: 589) für *Dactylioceras commune* überein: Soweit erkennbar, sind drei U vorhanden. U_1 scheint gespalten zu sein. Der Externsattel ist hier breiter als bei *Dactylioceras commune*.

Vergleich: Alle neun Exemplare bzw. Bruchstücke stimmen in den beschriebenen Merkmalen gut miteinander überein. Lediglich Exemplar Nr. 2 besitzt auf den beiden erhaltenen Windungsfragmenten (Durchmesser maximal 35 mm) ausgeprägt proradiate Rippen. Es herrscht gute Übereinstimmung mit den Angaben in der Literatur (vgl. Synonymieliste). Besonders wertvoll für einen Vergleich ist die Beschreibung von Fischer (1966: 23). Eine deutliche Variabilität ist nur in der Dichte der Flankenrippen erkennbar.

Bemerkungen: *Dactylioceras (Eodactylites) simplex* zeigt in beispielhafter Weise einen palingenetischen Merkmalswechsel von einem charakteristischen Dactylioceraten *(Coeloderoceras)* des Pliensbachium im Bereich der Innenwindungen zu einem *Dactylioceras,* wie er für das Toarcium so typisch ist, im Bereich der äußeren Windungen und besonders der Wohnkammer. Die gehäusemorphologische Trennung von *Coeloderoceras* und *Dactylioceras* ist in einem solchen Übergangsbereich schwierig und nur durch Übereinkunft zu lösen (Schmidt-Effing 1975: 94). Das Auftreten neuer Merkmale rechtfertigt jedoch die Zuordnung dieser Formen zu *Dactylioceras,* was für die biostratigraphische Definition der Pliensbachium/Toarcium-Grenze auch einen hohen praktischen stratigraphischen Wert besitzt (Elmi et al. 1974: 54). Daher möchte ich diese Formen von *Coeloderoceras,* welchem ich sie 1972 (Schmidt-Effing: 88) zunächst zugeordnet hatte, trennen.

Die Merkmale wechseln zu verschiedenen Zeitpunkten der Ontogenese: als erstes setzt die Bedornung der Rippenspaltpunkte aus, dann erniedrigt sich die Zahl der Externrippen von 3 auf 2 pro Flankenrippe, später verändert sich der Windungsquerschnitt von breit oval in hoch oval, und mit diesem Merkmal kombiniert werden die Flankenrippen wesentlich länger und stehen dichter.

Von einem ähnlichen Fall bei *Coeloderoceras* cf. *ponticum* habe ich 1972 (Schmidt-Effing: 90) berichtet. Unter Berücksichtigung der hier angeführten Gesichtspunkte stelle ich heute diese Form zu *Dactylioceras (Eodactylites)* cf. *polymorphum*.

Verbreitung: *Dactylioceras (Eodactylites) simplex*, wie auch die anderen Arten dieser Untergattung, sind auf die mediterrane Faunenprovinz beschränkt. Nur sehr vereinzelt werden sie auch in der nordwesteuropäischen Provinz gefunden (Schmidt-Effing 1972: 143; Howarth 1973: 253). Die Häufigkeit dieser, neben anderen Arten, in Chile weist damit eindeutig auf mediterranen Einfluß hin, also eine zoogeographische Beziehung, die im älteren Unterjura Chiles weniger deutlich zu beobachten ist (Schmidt-Effing 1976: 215).

Stratigraphisch tritt *Eodactylites* immer im Liegenden der Schichten auf, die reichlich *D. (Orthodactylites)* und besonders die Leitarten *D. tenuicostatum* und *D. semicelatum* führen. Daher haben Elmi et al. (1974: 55) im Rahmen ihrer mediterranen Zonengliederung im Liegenden der *semicelatum*-Subzone die Subzone des *D. (Eodactylites) mirabile* ausgeschieden. Zeit-stratigraphisch entspricht diese Subzone im wesentlichen dem tieferen Abschnitt der nordwesteuropäischen *tenuicostatum*-Zone – hier gebraucht als abstrahierende Zone im Sinn von Howarth (1978), denn *D. tenuicostatum* tritt in diesen Schichten überhaupt nicht auf –; sie reicht jedoch eindeutig auch noch in die höchsten Schichten mit *Pleuroceras* (Schmidt-Effing 1972: viele Beispiele; Howarth 1973: 255; 1978: 252).

3.1.2 Subgenus: *Dactylioceras (Orthodactylites)* Buckman, 1926

Typus-Art: *Orthodactylites directus* Buckman, 1926.

Diagnose: Ein Subgenus von *Dactylioceras* mit rundlichem bis hoch ovalem Windungsquerschnitt, der sich während der Ontogenese wenig verändert, mit relativ undifferenzierten Rippen, wobei die annularen Flanken- und Externrippen ähnlich entwickelt sind und rectoradiat bis proradiat verlaufen. Gabelrippen wechseln häufig mit Einfach- und Schaltrippen ab. Die Skulptur ist weniger kräftig und unregelmäßiger als bei beiden anderen Subgenera ausgebildet. Bei verschiedenen Arten treten manchmal, besonders auf den Innenwindungen, Dornen bzw. Knoten an den Rippenspaltpunkten auf; auch fibulate Rippen werden vereinzelt beobachtet.

Verbreitung: *Orthodactylites* ist ein ausgesprochener Kosmopolit mit Verbreitung- und Artenmaxima in der nordwesteuropäischen und der borealen Provinz (Schmidt-Effing 1972: 57). Stratigraphisch ist er an die *tenuicostatum*- und die *falcifer*-Zone gebunden und tritt damit später als der dickrippige *Eodactylites* auf.

3.1.2.1 *Dactylioceras (Orthodactylites) anguinum* (Reinecke, 1818)

Taf. 1, Fig. 5–7; Abb. 16c, d

1818 *Argonauta anguinus* – Reinecke: 83, Taf. 12, Fig. 73.
1885 *Ammonites anguinus* – Quenstedt: Taf. 46, Fig. 9 (von Schmidt-Effing 1972: 183 als Neotyp für den verlorenen Holotyp vorgeschlagen).
?1898 *Coeloceras (Dactylioceras) anguinum* Reinecke sp. – Hug: 23, Taf. 6, Fig. 2.
1927 *Coeloceras (Dactylioceras) anguinum* Reinecke – Schröder: 101, Taf. 4 (11), Fig. 2.
1928 *Anguidactylites anguiformis* S. Buckman – Buckman: Taf. 763.
1965 *Dactylioceras anguinum* (Reinecke) – Pannkoke: 22, Taf. 2, Fig. 1.
1966 *Dactylioceras anguinum* (Reinecke) – Fischer: 22, Taf. 3, Fig. 9.
1972 *Dactylioceras (Orthodactylites) anguinum* (Reinecke) – Schmidt-Effing: 57 u. 183, Taf. 7, Fig. 5a, b.
?1973a *Nodicoeloceras* cf. *spicatum* (Buck.) – Guex: 509, Taf. 13, Fig. 3.
1976 *Dactylioceras anguinum* (Reinecke, sensu Quenstedt 1885) – Schlegelmilch: 77, Taf. 38, Fig. 8 (Abbildung des Neotyps.).

Material: a) Quebrada El Asiento (Abb. 2, Profil 3; Abb. 3, Schicht 4), topographische Karte 1:100000, Blatt Potrerillos: x = 467,5 km, y = 7070,45 km. Zwei Exemplare (B. St. M. 1978 II 10–11) als Steinkerne teilweise mit Schale, zusammen mit *Hildaites* cf. *serpentiniformis* (Buckman) und *Harpoceratoides* cf. *alternatus* (Simpson).

b) Quebrada Chanchoquin (Abb. 1, Profil 21; Abb. 10, Schicht 4), topographische Karte 1:50000, Blatt El Tránsito: x = 375,1 km, y = 6811,05 km. Profilbeschreibung siehe v. Hillebrandt (1973a: 353–354). Die Dactylioceraten stammen aus dem tieferen Horizont, zusammen mit sehr seltenen *Radstockiceras* sp. und *Bouleiceras* cf. *chakdallaense* Fatmi. Zwei Exemplare (B. St. M. 1978 II 12: Teil des Phragmokons; B. St. M. 1978 II 13: Phragmokon und halber Umgang der Wohnkammer), Steinkerne mit verkieselter Schale.

Maße (in mm):

Expl.	DM	WH	WB	NW	WB/WH
Neotyp	41,4	12,0 (0,29)	11,0 (0,27)	20,5 (0,50)	(0,92)
13	41,0	ca. 12,0 (0,29)	13,5 (0,33)	18,5 (0,45)	(1,12)
11	35,2	11,0 (0,31)	12,0 (0,34)	19,5 (0,55)	(1,09)
12	22,0	7,2 (0,33)	9,8 (0,45)	9,2 (0,42)	(1,36)

Beschreibung: Evolute Gehäuse, die breit ovale Innenwindungen und rundliche äußere Umgänge besitzen. Weder Nabel- noch Externkante sind ausgebildet.

Die Rippen stehen sehr dicht, besitzen eine relativ breite Rippenbasis, wie sie bei Steinkernerhaltung sichtbar wird, bilden jedoch scharfe Rippengrate, wie es bei Schalenerhaltung zu beobachten ist. Exemplar Nr. 10 hat auf dem letzten Umgang etwa 60, Exemplar Nr. 12 etwa 45 Flankenrippen. Flanken- und Externrippen verlaufen rectoradiat und sind sehr gleichmäßig ausgebildet (annulat). Die Rippenspaltpunkte sind völlig unverdickt und liegen etwas unregelmäßig am Außenbug der Flanken. Die Flankenrippen spalten in sehr spitzem Winkel in zwei gleichartige Externrippen. Auch Schaltrippen treten auf, besonders häufig in der letzten Windung. Rippen und Interkostalräume sind etwa von gleicher Breite.

Vergleich: Untereinander stimmen die vorliegenden vier Exemplare gut überein. Sie unterscheiden sich jedoch in zwei Merkmalen vom Neotyp: Dieser besitzt nämlich einen nicht so ausgeprägten breit ovalen Windungsquerschnitt (diagenetische Ursache?), außerdem zeigt er auf den innersten Windungen, bis etwa 2 cm Durchmesser, noch feinere Rippen, die z. T. fibulat sind. Während der Windungsquerschnitt generell variabler sein mag, ist dieser auffallende Unterschied in der Berippung in seiner Bedeutung nicht einwandfrei bewertbar. Ihm scheint jedoch kaum eine arttrennende, allenfalls subspezifische Bedeutung zuzukommen, wie das auch für die Skulpturvariationen von *Dactylioceras (Orthodactylites) directum* gilt (Schmidt-Effing 1975: 80).

Bemerkungen: In der Literatur und zwar besonders in den Fossillisten der älteren Arbeiten, werden sehr verschiedene Formen als *Dactylioceras anguinum* aufgeführt. Dies dürfte auf der mehrdeutigen Abbildung und der ungenügenden Beschreibung des Holotyps beruhen, der außerdem verloren ist (Zeiss 1972: 38). In der letzten Zeit gaben Pannkoke (1965) und besonders Fischer (1966) sehr treffende Beschreibungen. Schmidt-Effing (1972: 183) bestimmte das Exemplar von Quenstedt (1885: Taf. 46, Fig. 9) als Neotyp. Wegen der darstellerischen Mängel und der Seltenheit des Werkes von Reinecke, sind die meisten früheren Bestimmungen ohnehin nach diesem Stück vorgenommen worden. Wie schon Fischer feststellt, gehört *Dactylioceras anguinum* in die nähere Verwandtschaft von *Dactylioceras (Orthodactylites) tenuicostatum*. Es unterscheidet sich von diesem jedoch deutlich durch dichter stehende und feinere Rippen und durch breitere Umgänge.

Dactylioceras (Orthodactylites) anguinum wurde bisher aus der mediterranen Provinz zwar nur gelegentlich gemeldet, doch wie ein Vergleich mit zahlreichen Formen in Pinna & Levi-Setti (1972) zeigt, tritt diese Art bzw. außerordentlich nah verwandte Formen hier sogar häufiger auf als in NW-Europa. Die verschiedenen Erhaltungen – hier kalkige, reine Steinkernerhaltung, dort diagenetisch mehr oder weniger komprimierte Kalkmergel-Steinkerne, häufig mit Schale – verursachen scheinbare Unterschiede. Das *Dactylioceras (Orthodactylites) anguinum*, das auf Taf. 3., Fig. 1 (Pinna & Levi-Setti 1972) abgebildet ist, gehört allerdings einer anderen Art an. Doch stehen viele Formen, die zu *Mesodactylites merlai* (z. B. Taf. 3, Fig. 8a, b, 11), zu *M. mediterraneus, M. ghinii, M. sapphicus* und zu *Nodicoeloceras* gestellt werden, dem echten *Dactylioceras (Orthodactylites) anguinum* sehr nahe.

Verbreitung: Unter-Toarcium der nordwesteuropäischen und der mediterranen Provinz und Chile.

3.1.2.2 *Dactylioceras (Orthodactylites) directum* (Buckman, 1926)

Taf. 1, Fig. 8–11; Abb. 13, 16f

1926 *Orthodactylites directum*, nov. – Buckman: pl. 564.
1927 *Orthodactylites mitis*, nov. – Buckman: pl. 738.
1957 *Dactylioceras directus* S. Buckman – Maubeuge: 216, Taf. 26, Fig. 52–56.
?1971 *Rakusites pruddeni* n. sp. – Guex: 238, Taf. 1, Fig. 1a–c, Taf. 3, Fig. 5 (vgl. Schmidt-Effing 1975: 80).
1972 *Dactylioceras (Orthodactylites) directum* (Buckman, 1926) – Schmidt-Effing: 107–109, Taf. 7, Fig. 4a, b, Taf. 18, Fig. 14.

Material: a) Quebrada Chanchoquin (Abb. 1, Profil 21; Abb. 10, Schicht 4), topographische Karte 1:50000, Blatt El Tránsito: x = 375,1 km, y = 6811,05 km. Profilbeschreibung siehe v. Hillebrandt (1973a: 353–354). Die Dactylioceraten stammen aus dem tieferen Horizont, zusammen mit sehr seltenen *Radstokkiceras* sp. und *Bouleiceras* cf. *chakdallaense* Fatmi. Die Schalen sind verkieselt, die Hohlräume als Steinkerne erhalten, wobei die Wohnkammer von einem feinsandigen Kalk, der Phragmokon vorzugsweise von Kalzit ausgefüllt ist. Das besonders günstig erhaltene Exemplar Nr. 14 besitzt $2^1/_2$ Umgänge des Phragmokons, ein weiterer äußerer Umgang ist durch ein Nabelband angedeutet, die innersten Windungen, bis etwa 7 mm, sind nicht erhalten.

b) Quebrada Noria, 700 m SSW Punkt 3132 (südlich Salto de la Muerte), (Abb. 1, Profil 12; Abb. 8, Schicht 4), topographische Karte 1:100000, Blatt Carrera Pinto: x = 426,5 km, y = 6970,6 km. Vier Exemplare

(B. St. M. 1978 II 20–23), Steinkerne teilweise mit Schale. Zusammen mit *Dactylioceras (Orthodactylites) hoelderi* n. sp., *Dactylioceras (?Orthodactylites) helianthoides* und *Elegenticeras* cf. *elegantulum* (YOUNG & BIRD).

c) Quebrada Yerbas Buenas (Abb. 1, Profil 9; Abb. 6, Schicht 6), topographische Karte 1 : 100 000, Blatt Carrera Pinto: x = 439,4 km, y = 6979,3 km. Ein Exemplar (B. St. M. 1978 II 24) und drei weitere Bruchstücke, die wahrscheinlich zu *D. (O.) directum* zu stellen sind (B. St. M. 1978 II 25–27), Steinkerne; zusammen mit *Dactylioceras (Orthodactylites) hoelderi* n. sp.

d) Río Jorquera (Majada del Carrizo), (Abb. 1, Profil 14), topographische Karte 1 :100 000, Blatt La Guardia: x = 437,4 km, y = 6931,7 km. 4 Exemplare (B. St. M. 1978 II 28, 229–231), Steinkern, zusammen mit *Nodicoeloceras* cf. *Crassoides* FORM C, *Hildaites* cf. *levisoni* (großwüchsig) und *Harpoceras* cf. *falcifer*.

Maße (in mm):

Nr.	DM	WH	WB	NW	WB/WH
17	51,0	—	—	—	—
14	45,0	12,3 (0,27)	11,0 (0,24)	23,3 (0,52)	(0,89)
19	29,8	7,5 (0,25)	ca. 7,5 (0,25)	17,4 (0,58)	(1,0)
22	32,5	9,0 (0,28)	9,0 (0,28)	16,5 (0,51)	(1,0)
20	55,0	16,0 (0,29)	15,0 (0,27)	27,0 (0,49)	(0,94)
23	21,3	6,5 (0,31)	6,5 (0,31)	10,0 (0,47)	(1,0)
21	18,2	6,5 (0,36)	6,5 (0,36)	8,5 (0,47)	(1,0)
24	39,5	12,0 (0,30)	11,5 (0,29)	20,0 (0,51)	(0,96)
28	36,0	—	10,5 (0,29)	18,0 (0,50)	(0,96)

Beschreibung: Die Gehäuse sind flach-scheibenförmig, evolut und von serpentikoner Gestalt. Der Windungsquerschnitt ist rund bis leicht oval, wobei die konkave Windungszone nicht ganz ein Viertel der Windungshöhe ausmacht. Die Flanken sind deutlich abgeflacht, knicken an der Nabelkante in steile Nabelflächen um. Die Externfläche ist breitgerundet.

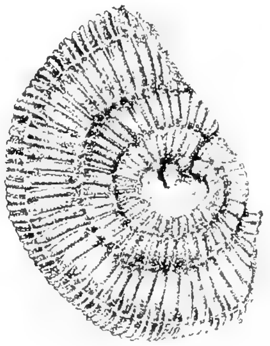

Abb. 13: *Dactylioceras (Orthodactylites) directum* (BUCKMANN, 1926); Quebrada Chanchoquin; B. St. M. 1978 II 14; nat. Gr.

Die Rippen setzen schon auf der Nabelfläche ein, erreichen ihre volle Stärke erst oberhalb der Nabelkante und verlaufen rectoradiat bis leicht proradiat über Flanken und Externfläche. Die Rippen sind sehr scharf und stehen relativ dicht (Exemplar Nr. 14 besitzt auf dem letzten Umgang ca. 30 Flanken- und ca. 60 Externrippen, auf dem vorletzten halben Umgang 25 Flankenrippen; Nr. 19 auf dem letzten Umgang 40 Flanken-, auf dem vorletzten Umgang ca. 31 Flankenrippen). Die Interkostalräume sind etwa doppelt so breit wie die Rippen. Die Externrippen sind nur wenig schwächer als die Flankenrippen ausgebildet. An den Rippenspaltpunkten lassen sich keine Verdickungen, nur manchmal schwache Knötchen beobachten. Die Rippenspaltpunkte liegen auf einer Linie, und zwar noch auf der Flanke. Das Nabelband der äußeren, nicht erhaltenen Windung (Exemplar Nr. 14) liegt auf den Externrippen und läßt daher Rippenspaltpunkte wie Flankenrippen frei. Die Art der Rippengabelung ist etwas unregelmäßig, wobei jedoch die dichotome Rippengabelung (d. h. die Aufteilung in zwei gleichwertige Externrippen) überwiegt. Untergeordnet treten auch Einfachrippen auf, die mit zwei Schaltrippen gekoppelt sind. Deutliche ontogenetische Merkmalsänderungen sind weder im Gehäusebau noch in der Skulptur zu erkennen.

Lobenlinien sind nicht sichtbar. Bei einer Windungshöhe von 12,1 mm besitzt der Sipho einen Durchmesser von 1,1 mm.

Vergleich: Obwohl die Exemplare der vier verschiedenen Lokalitäten sehr unterschiedlich erhalten sind, bereitet ihre artliche Zuordnung zu *Dactylioceras (Orthodactylites) directum* keine Schwierigkeiten. Dies liegt wohl daran, daß diese Art während der Ontogenese kaum Wachstumsänderungen aufweist und auch, daß es sich um eine überhaupt wenig variable Art handelt. Das Exemplar Nr. 14, Durchmesser ursprünglich mindestens 55 bis 60 mm, stimmt besonders gut mit dem Holotypus (Durchmesser 66 mm) überein. Doch treten auch beim übrigen Material nur wenige Abweichungen auf. Subspezifische Unterschiede sind jedoch nicht zu erkennen.

Bemerkungen: Da *Dactylioceras (Orthodactylites) directum* – der auch stratigraphisch älteste *Orthodactylites* – morphologische Übergänge zu *Dactylioceras (Eodactylites) simplex* erkennen läßt, ist eine phylogenetische

Ableitung von ähnlichen *Eodactylites*-Formen wahrscheinlich (SCHMIDT-EFFING 1972: 172). Daß bis heute keine angemessene Beschreibung dieser so wichtigen Art aus dem englischen Typusgebiet vorliegt, nur eine eigenartige BUCKMANsche Kurzbeschreibung (1926) und Abbildung, ist sehr bedauerlich.

Verbreitung: *Dactylioceras (Orthodactylites) directum* ist ein charakteristisches Element des nordwesteuropäischen Unter-Toarciums, das hiermit zum ersten Mal aus Südamerika, wie überhaupt aus der pazifischen Provinz (SCHMIDT-EFFING 1972: 162–163), beschrieben wird. Doch scheint diese Art auch in der mediterranen Provinz nicht selten zu sein. Unter Beachtung der unterschiedlichen, die Morphologie beeinflussenden Fossilisationsarten (vgl. Abschnitt „Bemerkungen" bei *Dactylioceras anguinum)* dürfte *Dactylioceras annulatiforme* mit zahlreichen Subspezies (z. B. KOTTEK 1966: 127–130) und zahlreiche Formen, die PINNA & LEVI-SETTI (1972) zu *Mesodactylites* und *Nodicoeloceras* stellen, mit *Dactylioceras directum* synonym sein oder doch wenigstens sehr nahe stehen.

3.1.2.3 *Dactylioceras (?Orthodactylites) helianthoides* YOKOYAMA, 1904

Taf. 1, Fig. 12–18, Taf. 2, Fig. 4; Abb. 14, 16e

1904 *Dactylioceras helianthoides* YOKOYAMA – YOKOYAMA: 16–17, Taf. 4, Fig. 4–6.
1964 *Dactylioceras* sp. – FREBOLD: 11, Taf. 5, Fig. 7–8.
1971 *Dactylioceras (Dactylioceras) helianthoides* YOKOYAMA – HIRANO: 104–108, Taf. 14, Fig. 1–10.
?1971 *Nodicoeloceras* sp. – PINNA & LEVI-SETTI: Taf. 5, Fig. 3.

Material: a) Quebrada Noria, 700 m SSW Punkt 3132 (südlich Salto de la Muerte), (Abb. 1, Profil 12; Abb. 8, Schicht 4), topographische Karte 1 : 100000, Blatta Carrera Pinto: x = 426,5 km, y = 6970,6 km. Zwanzig Exemplare (B. St. M. 1978 II 29–48) in ziemlich vollständiger Erhaltung als teilweise frühdiagenetisch verdrückte Steinkerne großteils mit erhaltener Schale. Exemplare Nr. 30 und Nr. 38 mit im wesentlichen vollständiger Wohnkammer, Nr. 37 schließt mit 40,5 mm Durchmesser noch im Bereich des Phragmokons ab.

b) Quebrada El Asiento (Abb. 2, Profil 3; Abb. 3, Schicht 4), topographische Karte 1 : 100000, Blatt Potrerillos: x = 467,5 km, y = 7070,45 km. Drei Exemplare (B. St. M. 1978 II 49–51) von Steinkernfragmenten.

c) Río Manflas, Profil 2,5 km südlich Los Graneros, zwischen dem Fluß und dem Cerro Salto del Toro (Abb. 1, Profil 18; Abb. 9), (69°58,5' Länge, 28°19,7' Breite). Ein Exemplar (B. St. M. 1978 II 52) eines sehr unvollständigen Steinkerns. Im Liegenden tritt *Dactylioceras (Orthodactylites) tenuicostatum chilense* auf.

d) Quebrada El. Peñon (Abb. 1, Profil 5b; Abb. 3a), topographische Karte 1 : 100000, Blatt Laguna del Negro Francisco: x = 473,7 km, y = 7007,5 km. 1 Steinkernexemplar (B. St. M. 1978 II 232) zusammen mit häufig *Dact. (Orthodactylites) tenuicostatum chilense*.

Maße (in mm):

Nr.	DM	WH	WB	NW	WB/WH
38	60,0	ca. 18,0 (0,28)	—	27,5 (0,46)	—
30	46,0	16,0 (0,35)	ca. 17,0 (0,37)	20,5 (0,45)	(1,06)
37	40,5	13,5 (0,33)	13,5 (0,33)	17,5 (0,43)	(1,0)
32	34,0	10,5 (0,31)	ca. 12,0 (0,35)	16,5 (0,49)	(1,14)
31	ca. 31	—	13,5 (0,44)	12,0 (0,39)	—
33	30,0	10,5 (0,35)	14,0 (0,47)	12,0 (0,4)	(1,33)
47	29,0	9,0 (0,31)	8,0 (0,28)	12,5 (0,26)	(0,89)
34	29,5	9,5 (0,32)	11,0 (0,37)	12,0 (0,41)	(1,16)
41	27,0	9,0 (0,33)	11,0 (0,41)	11,5 (0,43)	(1,22)
42	22,5	7,0 (0,31)	—	11,0 (0,49)	—
43	21,5	8,0 (0,37)	10,0 (0,47)	9,0 (0,42)	(1,25)

Beschreibung: Recht weitgenabelte Formen mit rundlichem bis quer ovalem Windungsquerschnitt, wobei sich die Windungen etwa $^1/_4$ übergreifen. Die Externseite ist breit gerundet und geht ebenfalls in gerundete, bei manchen Exemplaren auch etwas abgeflachte Flanken über. Eine Nabelkante ist bei einigen Exemplaren überhaupt nicht, bei manchen nur schwach ausgebildet. Die Nabelfläche fällt steil gerundet zur Naht ab.

Die Rippen verlaufen von der Naht über Flanken und Externseite rectoradiat, sind sehr scharf und hoch (bei Exemplar Nr. 38 bis über 1 mm), was jedoch nur bei Schalenerhaltung deutlich zu beobachten ist. Es sind Vollrippen. Sie sind massiv und lassen nach Ablösen auf dem Steinkern nur eine reliefarme, breit-rundliche Rippenspur zurück. Die Externrippen sind kaum weniger kräftig als die Flankenrippen ausgebildet. Die Rippendichte ist an den einzelnen Exemplaren verschieden (z. B. besitzt Exemplar 38 bei 60 mm Durchmesser 41 Flankenrippen auf dem letzten Umgang, Exemplar 30 dagegen bei 46 mm Durchmesser 55 Flankenrippen). Die Rippenspaltpunkte sind sehr unregelmäßig ausgebildet, was sowohl die Lage, die Form und die Art der Rippenspaltung betrifft. Meist gabeln die Flankenrippen in zwei, nicht selten auch in drei Externrippen. Auch treten Einfachrippen auf, neben die sich auf der Externseite Schaltrippen gesellen können, ohne daß überhaupt ein Rippenspaltpunkt ausgebildet ist.

In Abständen von 4 bis 10 Flankenrippen können die Rippenspaltpunkte zu kräftigen Dornen ausgebildet sein, die die Rippen um bis zu 2 mm überragen. An solchen Stellen treten manchmal auch fibulate Flankenrippen, wie auch Aufspaltung in drei Externrippen auf. Die Rippenspaltpunkte der Innenwindungen liegen meist frei, sind also nicht von der nächstfolgenden Windung überdeckt.

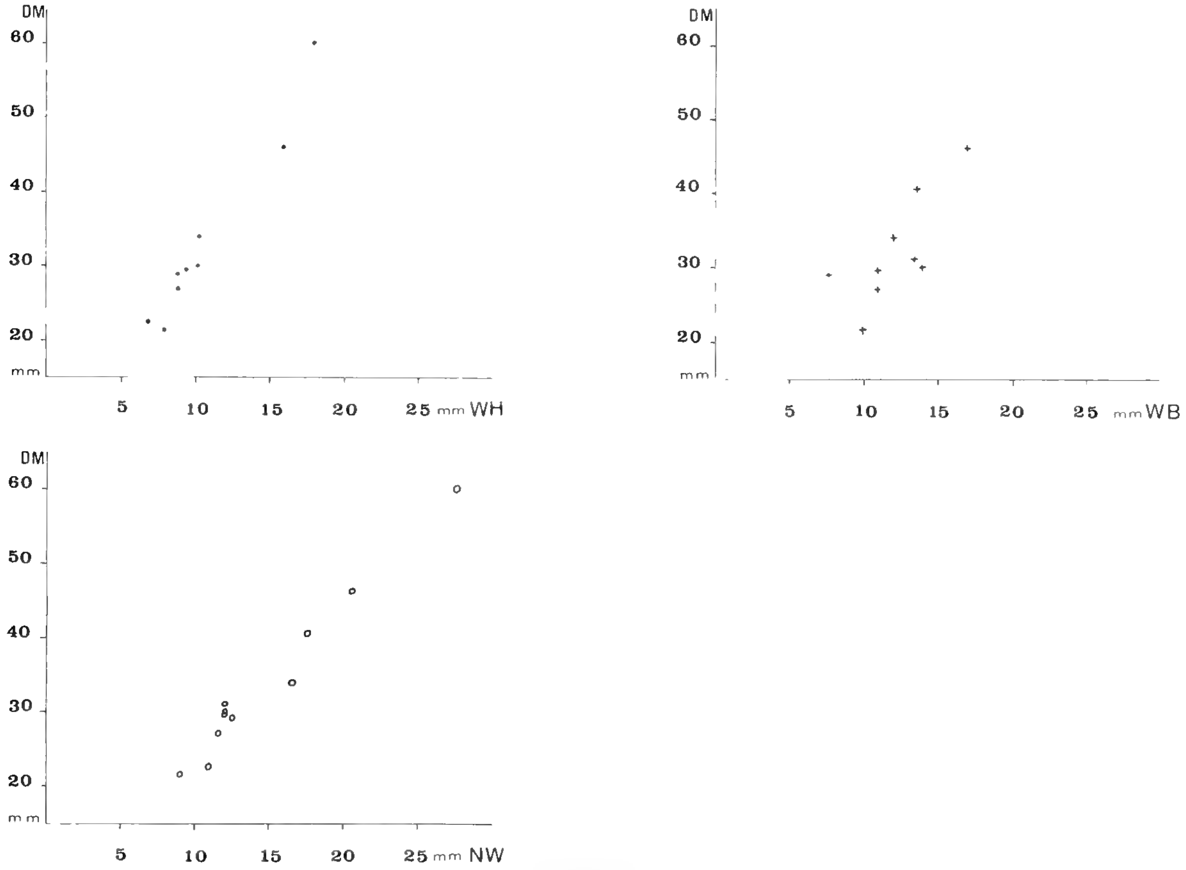

Abb. 14: *Dactylioceras (?Orthodactylites) helianthoides* YOKOYAMA, 1904; Werte der Windungshöhe, der Windungsbreite und der Nabelweite im Verhältnis zum Durchmesser (vgl. Tabelle).

Analysierbare Lobenlinien treten nicht auf.

Während der Ontogenese machen sich, abgesehen von der allgemeinen großen Variabilität, keine besonderen Entwicklungstendenzen bemerkbar.

Vergleich: Trotz dieser ausgeprägten Variabilität im einzelnen, erscheint diese Formengruppe eine gute Art zu bilden. Möglicherweise handelt es sich bei den großen Exemplaren (z. B. bei Nr. 38, 37, 30 und 35) um Makrokonche, bei den kleinen um Mikrokonche. Die Übereinstimmung der Formen von Quebrada Noria mit der Beschreibung und den Abbildungen von *Dactylioceras helianthoides* bei HIRANO (1971) ist bemerkenswert gut. Das Material von Río Manflas und Quebrada El Asiento läßt sich wegen ungenügender Erhaltung nur als *Dactylioceras* cf. *helianthoides* bestimmen.

Bemerkungen: Aufgrund der älteren Literatur war die richtige Bestimmung dieser Art nicht möglich. Erst HIRANO (1971) hat eine präzise und ausführliche Beschreibung und Bearbeitung geliefert. Dabei hat sich gezeigt, daß sämtliche aus Europa stammenden Exemplare, die zu dieser Art gestellt worden waren und mit Abbildungen veröffentlicht sind, nicht dieser Art angehören (SCHMIDT-EFFING 1972: 110). Nur in PINNA & LEVI-SETTI (1971: Taf. 5, Fig. 3) ist ein Exemplar als *Nodicoeloceras* sp. abgebildet, das dieser Art zugeordnet werden könnte (vgl. z. B. HIRANO 1971: Taf. 14, Fig. 6).

Nach dem Gesamtbild zu urteilen, gehört *Dactylioceras helianthoides* sicherlich zu *Orthodactylites*. Besonders rundliche und bedornte Exemplare ließen jedoch auch an eine Zuordnung zu *Nodicoeloceras* denken. Warum HIRANO (1971 : 104) diese Art der Untergattung *Dactylioceras* zuordnet, was nicht nur der morphologischen, sondern auch der stratigraphischen Stellung widerspricht, bleibt unklar.

Verbreitung: Es handelt sich um eine, besonders für den pazifischen Raum (Japan, Kanada und Chile) charakteristische Art – in Japan ist es sogar die einzige bekannte *Dactylioceras*-Art –, wobei besonders erstaunlich ist, daß sie aus dem relativ nahen Ostsibirien trotz des guten Bearbeitungszustandes (z. B. Dagis 1968 und Krymgolz 1974 a) nicht bekannt ist. Nach Hirano (1973: 55 u. 58) ist *Dactylioceras helianthoides* in Japan vom Domerium (zusammen mit *Amaltheus* cf. *stokesi*) bis in die untere *falcifer*-Zone (zusammen mit *Harpoceras* aff. *exaratum)* verbreitet. Die chilenischen Funde sind aufgrund der Begleitfauna in das höhere Unter-Toarcium *(hoelderi*-Zone) zu stellen.

3.1.2.4 *Dactylioceras (Orthodactylites) hoelderi* n. sp.

Taf. 2, Fig. 1–3, 5; Abb. 15, 16 h, i

Holotyp: Taf. 2, Fig. 1 a, b (B. St. M. 1978 II 53). Ziemlich vollständiger Steinkern mit erhaltener Schale.

Derivatio nominis: Zu Ehren von Herrn Prof. Dr. H. Hölder, Münster/Westfalen, der sich um die internationale Jura-Forschung sehr verdient gemacht hat.

Locus typicus: a) Quebrada Yerbas Buenas (Chile, Provinz Atacama), (Abb. 1, Profil 9; Abb. 6, Schicht 6), topographische Karte 1 : 100000, Blatt Carrera Pinto: x = 439,4 km; y = 6979,3 km.

Stratum typicum: Etwa 1 m mächtige Schichtfolge mit bis 20 cm mächtigen Kalkbänken, die auch *Dactylioceras (Orthodactylites) directum* enthalten. Im Liegenden Kalkschiefer mit *Pectinula cancellata* Leanza und Kalke mit *Radstockiceras* sp. 2. Direkt im Hangenden 2 bis 3 m mächtige, ca. 10 cm gebankte, rostig anwitternde Kalke mit Mergelzwischenlagen. Oberste (oder vorletzte) Bank mit *Nodicoeloceras* cf. *crassoides* (Simpson) Form A, *Hildaites* cf. *serpentiniformis* (Buckman), *H.* cf. *serpentinus* (Reinecke), *Harpoceratoides* cf. *alternatus* (Simpson) und *Polyplectus* sp. Höheres Unter-Toarcium, *hoelderi*-Zone.

Diagnose: Es handelt sich um eine neue Art von *Dactylioceras (Orthodactylites)* mit hochovalem Windungsquerschnitt, wobei die Windungsbreite an der Nabelkante am größten ist und mit Rippen, die an der Naht in voller Stärke einsetzen und hoch auf den Flanken in zwei bis drei Externrippen gabeln. Die Rippen sind leicht geschwungen und gabeln an etwas unregelmäßig gelegenen Rippenspaltpunkten auf. Auf den inneren Windungen, bis etwa 25 mm Durchmesser, treten gelegentlich auch fibulate Rippen auf, wobei die Rippenspaltpunkte Knötchen tragen und 3 bis 4 Externrippen von diesen abspalten.

Material: a) Locus typicus: Holotypus und vier weitere Exemplare (Nr. 54: Erhaltung nur der inneren Windungen, von Serpeln überwachsen; Exemplar Nr. 55: Fragment der inneren Windungen; B. St. M. 1978 II 56–57). Erhaltung wie Holotypus.

b) Quebrada Calquis (Abb. 1, Profil 15), topographische Karte 1 : 100000, Blatt La Guardia: x = 402,5 km, y = 6909,5 km. Zwei Exemplare (B. St. M. 1978 II 58–59), zusammen mit *Nodicoeloceras* cf. *crassoides* (Simpson) Form A, *Hildaites* sp. und *Polyplectus* sp.

c) Quebrada Noria, 700 m SSW Punkt 3132 (südlich Salto de la Muerte), (Abb. 1, Profil 12; Abb. 8, Schicht 4), topographische Karte 1 : 100 000, Blatt Carrera Pinto: x = 426,5 km, y = 6970,6 km. Ein Exemplar (B. St. M. 1978 II 60) *Dactylioceras (? Orthodactylites) helianthoides* aufsitzend.

Maße (in mm):

Nr.	DM	WH	WB	NW	WB/WH
53	49,3	15,5 (0,31)	13,5 (0,27)	22,2 (0,45)	(0,87)
53	ca. 40	13,7 (0,34)	ca. 12,5 (0,31)	16,5 (0,41)	(0,90)
54	27,6	10,1 (0,36)	9,3 (0,33)	10,5 (0,38)	(0,92)
56	26,0	10,0 (0,38)	ca. 8,5 (0,33)	9,0 (0,35)	(0,85)

Beschreibung des Holotypus: Flachscheibiges, mäßig evolutes, hochmündiges Gehäuse mit flach eingesenktem Nabel, wobei mindestens 5 Umgänge zu erkennen sind. Der äußere Umgang entspricht im wesentlichen der Wohnkammer, wobei nur etwa 1 cm der Wohnkammerlänge im Mündungsbereich zu fehlen scheint.

Der Windungsquerschnitt ist ausgeprägt hochoval im Wohnkammerbereich, innen etwas rundlicher. Die größte Windungsbreite wird in der unmittelbaren Nähe der Nabelkante erreicht. Die flachen, breiten Flanken fallen daher leicht zur Externseite hin ein. Eine Externkante fehlt, die Nabelkante ist scharf ausgebildet. Die Nabelfläche ist steil, die Externfläche schmal. Die konkave Windungszone beträgt etwa $^{1}/_{4}$ des Umganges. Die Windungszunahme (WH, WB und NW) während der Ontogenese erfolgt sehr gleichmäßig.

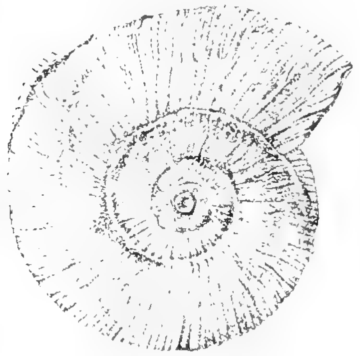

Abb. 15: *Dactylioceras (Orthodactylites) hoelderi* n. sp., Holotypus, Quebrada Yerbas Buenas; B. St. M. 1978 II 53; nat. Gr.

Die Flankenrippen beginnen unmittelbar an der Naht und verlaufen proradiat und etwas geschwungen über Nabelfläche und inneren Flankenbereich, wobei sie von Anfang an in voller Stärke ausgebildet sind. Die Flankenrippen sind scharf, relativ fein und stehen dicht (letzter Umgang mit 60, vorletzter Umgang mit etwa 43 Flankenrippen). Die Rippenspaltpunkte sind unverdickt, befinden sich ungewöhnlich hoch auf den Flanken und liegen unregelmäßig, also nicht auf einer geraden Linie. Unter sehr spitzem Winkel spalten an den Rippenspaltpunkten 2 bis 3 Externrippen, im einzelnen etwas unregelmäßig ab. Die Externrippen sind in ihrer Ausbildung und in ihrem Verlauf den Flankenrippen ähnlich.

Lobenlinien sind nicht sichtbar.

Vergleich: Die Paratypen stimmen bis auf Exemplar Nr. 57, das in Querschnitt und Rippengabelung etwas abweicht, gut mit dem Holotyp überein. Bei ihnen sind die inneren Windungsbereiche jedoch günstiger sichtbar als beim Holotyp, weshalb einige wichtige Beobachtungen ergänzt werden können: Auf den inneren Windungen, bis zu einem Durchmesser von etwa 25 mm, treten neben den vorherrschenden einfachen Flankenrippen gelegentlich auch fibulate Rippen auf (bei Exemplar Nr. 56 entfallen auf etwa 8 Flankenrippen jeweils 2, die fibulat im Rippenspaltpunkt zusammenlaufen). Diese tragen Knötchen und spalten in 3 bis 4 Externrippen auf.

Die beiden Exemplare von der Quebrada Calquis sind nicht so gut erhalten, daß ihre Zuordnung völlig gesichert wäre.

Vergleich mit ähnlichen Arten: *Dactylioceras hoelderi* läßt morphologische Beziehungen zu *Dactylioceras semicelatum* (Schmidt-Effing 1972: 95), zu *Dactylioceras hispanum* (Schmidt-Effing 1972: 102) und zu *Dactylioceras helianthoides* (vgl. S. 36) erkennen. Die neue Art ist jedoch dichter berippt, zeigt unregelmäßigere Rippengabelung und besitzt durch die Art der Rippengabelung wesentlich mehr Externrippen als *Dactylioceras semicelatum*. Auch sind die Rippen leicht geschwungen. *Dactylioceras hispanum* ist wesentlich lockerer berippt und besitzt außerdem gerade Rippen. *Dactylioceras helianthoides* weicht durch einen rundlicheren Windungsquerschnitt und eine in vielen Merkmalen wesentlich unregelmäßigere Berippung ab.

Bemerkungen: Da Formen, die zu *Dactylioceras hoelderi* zu stellen wären, bisher aus der Literatur nicht bekannt sind, wird angenommen, daß es sich um eine Art handelt, die in Chile und den umgebenden Räumen des südöstlichen Pazifiks und Südamerikas endemisch ist.

Verbreitung: Höheres Unter-Toarcium *(hoelderi-*Zone) von Chile.

3.1.2.5 *Dactylioceras (Orthodactylites) tenuicostatum chilense* n. ssp.

Taf. 2, Fig. 6–8; Abb. 16g

Holotypus: Taf. 2, Fig. 6a, b (B. St. M. 1978 II 61) Steinkern der Wohnkammer, Innenwindungen weitgehend verdeckt.

Derivatio nominis: Nach dem Vorkommen in Chile.

Locus typicus: Río Manflas (Departamento Copiapó, Provinz Atacama), Profil 2,5 km südlich Los Graneros, zwischen dem Fluß und dem Cerro Salto del Toro (69°58,5′ Länge, 28°19,7′ Breite), (Abb. 1, Profil 18, Abb. 9).

Stratum typicum: Aus dem hangenden Teil einer Serie 10 bis 30 cm mächtiger, gut gebankter, dichter Kalke, die mit bis zu 1,5 m mächtigen Mergellagen wechsellagern. Zum Hangenden hin Mergel geringermächtig und mehr Kalkbänke. Ammoniten sehr selten. Übergehend in eine Serie gebankter Sandsteine, die zunächst noch mit Mergeln wechsellagern (Brachiopoden und *Weyla* sp. häufig).

Etwa 30 m im Liegenden 2 bis 3 m mächtige, feinschichtige bis schiefrige, sandige Kalke mit *Pectinula cancellata* Leanza und *Radstockiceras* sp.

Unter-Toarcium, *tenuicostatum*-Zone, sehr wahrscheinlich höherer Abschnitt dieser Zone.

Diagnose: Die neue Unterart unterscheidet sich von der Typus-Art durch den Besitz von Knötchen, die im Bereich der Rippenspaltpunkte in Abständen auftreten. Besonders deutlich sind diese Knötchen auf den Innenwindungen ausgebildet; sie sind jedoch auch noch auf dem letztem Umgang (Wohnkammer) zu beobachten.

Material: a) Locus typicus: Ein Exemplar (Holotypus): Steinkern aus tonreichem, dunklem Kalk, der diagenetisch teilweise verdrückt ist. Erhalten ist der äußere Umgang, der wohl der Wohnkammer eines adulten Gehäuses entspricht.

b) Río Manflas, Profil zwischen dem Río Manflas und dem Portezuelo El Padre (70°0,9′ Länge, 28°11,8′ Breite), (Abb. 1, Profil 16). Ein schlecht erhaltenes Windungsfragment (B. St. M. 1978 II 62).

c) Quebrada El Bolito (Abb. 1, Profil 7; Abb. 5, Schicht 5), topographische Karte 1 : 100000, Blatt Laguna del Negro Francisco: x = 458,4 km, y = 6995,5 km. Vier kalkige, z. T. limonitisierte Steinkern-Fragmente z. T. mit Schalenerhaltung verschiedener Windungsabschnitte (B. St. M. 1978 II 63–66).

d) Quebrada La Chaucha (Abb. 1., Profil 5a), topographische Karte 1 : 100000, Blatt Laguna del Negro Francisco: x = 468 km, y = 7011 km. Zwei kalkig-mergelige Steinkern-Fragmente (B. St. M. 1978 II 67–68), nicht aus dem Anstehenden entnommen, wahrscheinlich zusammen mit einem Fragment von *Dactylioceras (Orthodacty-*

lites) cf. *directum* (Exemplar Nr. 69) und *Dactylioceras (Orthodactylites)* sp. (Exemplar Nr. 70, juvenil, Durchmesser 12 mm).

e) Quebrada El Peñon (Abb. 1, Profil 5 b; Abb. 3 a), topographische Karte 1 : 100000, Blatt Laguna del Negro Francisco: x = 473,7 km y = 7007,5 km. Schicht 6 7 Steinkerne (B. St. M. 1978 II 212–218 zusammen mit sehr selten *Dact. (Orthodactylites) helianthoides* und Schicht 7 3 Steinkernexemplare (B. St. M. 1978 II 219–221).

Maße: Der Holotyp besitzt einen Durchmesser (= Enddurchmesser) von etwa 125 mm, Exemplar Nr. 63 etwa 86 mm, Exemplar Nr. 64 mindestens 90 mm, Exemplar Nr. 65 etwa 41 mm und Exemplar Nr. 68 = 67 mm Durchmesser.

Beschreibung: Sehr evolutes, serpentikones, flachscheibiges Gehäuse, das durch eine besonders langsame und konstante Windungszunahme auffällt. Die Zahl der Umgänge ist am vorliegenden Material nicht feststellbar. Der Windungsquerschnitt ist hoch oval bis rundlich, die Nabelfläche steil; die konkave Windungszone ist nur gering ausgebildet.

Die Rippen sind fein und stehen dicht – der Holotypus besitzt etwa 120 Flankenrippen auf dem letzten Umgang –; sie entspringen auf der Nabelfläche, verlaufen leicht proradiat über die Flanken, spalten teilweise am Außenbug auf und verlaufen in ähnlicher Stärke und Richtung über die Externfläche. Die Form der Gabelung ist unregelmäßig, am vorliegenden Material im einzelnen nicht gut zu beobachten. Auf den Innenwindungen (z. B. Exemplar von Quebrada El Bolito) ist die Skulptur kräftiger als auf der Wohnkammer. Im Mündungsbereich, z. B. beim Holotypus, fällt die große Zahl der Einfachrippen auf, die außerdem leicht geschwungen und nach vorne etwas ausgezogen sind. Der Schalenbau, wie auch die Verteilung der verschiedenen Rippentypen (normale Vollrippen auf den Innenwindungen, von Schalensubstanz erfüllte Rippen auf dem hinteren Teil der Wohnkammer, wieder normale Vollrippen auf dem vorderen Teil der Wohnkammer) entspricht im wesentlichen den Beobachtungen von Schmidt-Effing (1972: 27) und Lehmann (1975).

Als besonderes Merkmal ist jedoch hervorzuheben, daß auf allen Windungsabschnitten im Bereich der Rippenspaltpunkte in Abständen von 3 bis 10 Flankenrippen, auf den Innenwindungen dichter, auf den äußeren Windungen in größeren Abständen, Knötchen auftreten. Ein direkter Zusammenhang von Berippungsmuster/Rippenspaltpunkt und Knötchen ist nicht immer feststellbar, d. h., die Knötchen können auch neben den Rippenspaltpunkten sitzen. Auf den Steinkern-Innenwindungen zeigen die Knötchen Relief (z. B. Exemplar Nr. 63), sind also Voll-Knötchen, auf den Außenwindungen nur flache Erhebungen, die möglicherweise als Basis von Hohl-Knötchen zu deuten sind.

Lobenlinien sind nicht erhalten.

Vergleich: Die vorliegenden Formen stimmen untereinander gut überein. Lediglich Exemplar Nr. 68 weicht insofern etwas ab, als hier die Knötchen kräftiger ausgebildet sind und außerdem Rippenbündel auftreten, wie sie etwa von *Prodactylioceras* bekannt sind.

Vergleich mit der Typus-Art: Von den Knötchen abgesehen, stimmt das vorliegende Material gut mit dem Neotypus der Typusart aus Yorkshire überein. Der Holotyp der Unterart fällt durch seine besondere Größe – *Dactylioceras tenuicostatum* ist nur selten größer als 10 cm – auf. Sehr bemerkenswert sind die Knötchen, ein Merkmal, das bisher noch nicht von dieser Art beschrieben wurde und das eine subspezifische Abtrennung rechtfertigt.

Bemerkungen: Die beschriebene Unterart unterscheidet sich von *Dactylioceras tenuicostatum* nur durch den Besitz von Knötchen (Schmidt-Effing 1975: 80). Dieses Merkmal läßt taxonomisch, je nach dem Gewicht, das man ihm zubilligt, verschiedene Interpretationen zu. Folgt man den Arbeiten von Guex (1971, 1973 b), so wären diese Formen als neue Art der von ihm aufgestellten Gattung *Rakusites* oder, da Knötchen auch untergeordnet auf den Altersstadien auftreten, zu einer neuen Art von *Porpoceras* zu stellen. Das Merkmal „Knötchen" („épines") ist in der Dactylioceraten-Systematik von Guex von übergeordneter Bedeutung (vgl. Schmidt-Effing 1975).

Da es sich bei den beknoteten Orthodactyliten der *tenuicostatum*-Zone bisher meist um Einzelfunde gehandelt hat, wobei ihre morphologische Beziehung zu bekannten Arten immer offenkundig war, sehe ich darin eher eine Parallelität zu dem Phänomen der fastigaten Ceratiten des germanischen Muschelkalkes (Wenger 1957, Rothe 1955). Auch diese lassen sich einwandfrei bei bekannten Ceratiten-Arten einordnen, unterscheiden sich jedoch von diesen in einem markanten Merkmal, nämlich den die Externfläche ohne Unterbrechung querenden Ringrippen.

So wie im Fall der fastigaten Muschelkalk-Ceratiten neue Merkmale zeitlich verfrüht in Einzelindividuen, in Populationen oder Rassenkreisen ihren Ausdruck finden können, mag auch das Auftreten von beknoteten Orthodactyliten in der *tenuicostatum*-Zone zu erklären sein. Im Fall der Muschelkalk-Formen kam das neue Merkmal aus paläogeographischen Gründen nicht zum Durchbruch, entspricht aber vollkommen der üblichen morphogenetischen Reihenfolge im Sinne von Wedekind. Im Fall der weltweit verbreiteten Dactylioceraten kam dieses Merkmal im höheren Unter-Toarcium jedoch zur Entfaltung.

In diesem Zusammenhang kann angeführt werden, daß Pinna & Levi-Setti (1971) aus Formen der *Dactylioceras (Orthodactylites)*-Gruppe in der *falcifer*-Zone die durch Knötchen charakterisierte und im Mediterran weit verbreitete Gattung *Mesodactylites* ableiten. Ähnliche Knötchen sind es auch, die bei *Dactylioceras tenuicostatum chilense* auftreten. Auch das durch Knötchen charakterisierte *Nodicoeloceras* wird von verschiedenen Bearbeitern (Howarth 1962, Pinna & Levi-Setti 1971, Schmidt-Effing 1972) aus der Gruppe des *Dactylioceras (Orthodactylites)* abgeleitet.

Diesen Sachverhalt möchte ich in folgender Weise interpretieren: In der *tenuicostatum*-Zone deutet sich bei verschiedenen Arten von *Dactylioceras (Orthodactylites)* eine Entwicklung neuer Merkmale an – im Fall der beschriebenen chilenischen Form dürfte es sich um eine geographische Rasse handeln –, die dann bei weiteren Veränderungen eine Aufspaltung in verschiedene Arten und Gattungen zuläßt. Im Artbereich sollte jedoch eine taxonomische Abtrennung von der Mutterart erst dann erfolgen, wenn sich beide durch wenigstens zwei markante und gut definierbare artspezifische Merkmale unterscheiden (Schmidt-Effing 1972: 32). Die Knötchen stellen zunächst nur ein markantes Merkmal dar, das eine artliche Abtrennung bei verantwortlicher Anwendung des Art-Begriffes (Mayr 1967) nicht erlauben kann, so einfach es zweifellos wäre, die Dactylioceraten-Gattungen schematisch in solche mit und solche ohne Knötchen einzuteilen. Aus diesem Grund ist die beschriebene Form nur als Unterart von *Dactylioceras tenuicostatum* klassifiziert. Entsprechend könnte auch *Rakusites pruddeni,* um auf das eingangs gewählte Beispiel zurückzukommen, als *Dactylioceras (Orthodactylites) directum pruddeni* eingestuft werden.

Verbreitung: Durch Vergleich mit dem stratigraphischen Auftreten der Typus-Art in NW-Europa und der chilenischen Gesamtfauna gehört *Dactylioceras (Orthodactylites) tenuicostatum chilense* dem höheren Abschnitt der *tenuicostatum*-Zone *(tenuicostatum*-Subzone) an.

3.1.2.6 *Dactylioceras (Orthodactylites)* sp.

Aus dem Profil vom Río Manflas liegen zwei kleine Fragmente vor (B. St. M. 1978 II 71–72), die wegen zu unvollständiger Erhaltung artlich nicht bestimmbar sind.

3.1.3 Subgenus: *Dactylioceras (Dactylioceras)* Hyatt, 1867

Typus-Art: *Dactylioceras communis* (J. Sowerby, 1815)

Diagnose: vgl. Schmidt-Effing 1972: 59.

Verbreitung: Vertreter dieser Untergattung sind aus Chile und auch aus dem restlichen Südamerika bis jetzt unbekannt. Ihr Hauptverbreitungsgebiet ist die nordwesteuropäische und die boreale Faunenprovinz. Im Mediterran werden Formen dieser Untergattung relativ selten und nur in wenigen Arten angetroffen.

Selten im höheren Unter-Toarcium, häufig im Mittel-Toarcium *(commune*-Subzone).

3.2 GENUS: *NODICOELOCERAS* BUCKMAN, 1926

Typus-Art: *Ammonites crassoides* Simpson, 1855

Diagnose: (ausführliche Charakteristik und Synonymie des Genus und seiner Arten in Schmidt-Effing 1972: 63–66): Dickscheibige Vertreter der Familie Dactylioceratidae mit breit ovalem, im Bereich der Innenwindungen sehr breit ovalem bis kadikonem Windungsquerschnitt. Kräftige annulare Rippenskulptur, ähnlich wie bei *Orthodactylites.* Die Rippenspaltpunkte sind oft mit Dörnchen oder Knötchen besetzt; auch fibulate Rippen treten gelegentlich auf. In vielen Merkmalen werden während der Ontogenese ausgeprägte Wachstumsallometrien beobachtet.

Bemerkungen: Auch Howarth (1978: 256) gab jüngst eine Diagnose dieser Gattung, die mit der hier vorgelegten in allen wichtigen Punkten zwar übereinstimmt, in der Praxis sich jedoch darin unterscheidet, daß er die von Schmidt-Effing (1972) und anderen Autoren erkannten *Nodicoeloceras*-Formen der *tenuicostatum*-Zone zu *Dactylioceras (Orthodactylites)* stellt. Beide Wege sind zwar gangbar, doch halte ich die Zuordnung auch der älteren Formen mit breit ovalem Windungsquerschnitt und ausgeprägten Wachstumsallometrien, schon wegen ihrer leichten Unterscheidbarkeit von *Orthodactylites,* für natürlicher und besser anwendbar.

Nodicoeloceras ist zwar eine sehr charakteristische und daher leicht erkennbare Gattung; große Schwierigkeiten bereiten dagegen, wegen des ausgeprägten ontogenetischen Merkmalswechsels, die artliche Zuordnung nur fragmentär erhaltener Exemplare. Auch durch die unterschiedlichen Erhaltungsweisen der hier stärker differenzierten Skulpturelemente und -strukturen (z. B. Schmidt-Effing 1972: 28) werden starke Unsicherheiten in der artlichen Zuordnung verursacht.

Nach dem Versuch (Schmidt-Effing 1972: 63–66) über die Taxonomie von *Nodicoeloceras* mehr Klarheit zu gewinnen, sind von Howarth (1973, 1978) mehrere Stellungnahmen zu den englischen Vertretern dieser Gattung – die meisten ihrer Arten haben englische Typen – erschienen, die schwerwiegend sind. Howarth synonymiert zahlreiche in England aufgestellte und dann in anderen Ländern ebenfalls erkannte *Nodicoeloceras*-Arten, wobei er, was sehr verwirrend ist, in seinen beiden Arbeiten auch durchaus unterschiedliche Standpunkte bezieht. Das betrifft z. B. seine Stellungnahmen zu *Nodicoeloceras annulatum* und die stark überkreuzenden Synonymierungen von *Nodicoeloceras crosbeyi* (Howarth 1973: 255) und *Nodicoeloceras crassoides* (Howarth 1978: 256).

Wie heißen die außerhalb Englands gefundenen Arten, die nach englischen Typen bestimmt sind, jetzt, nachdem diese synonymiert wurden? Das erscheint als eine groteske Frage, doch sind diese Formen in den meisten Fällen durchaus nicht wie die englischen zu behandeln. Die Ur-

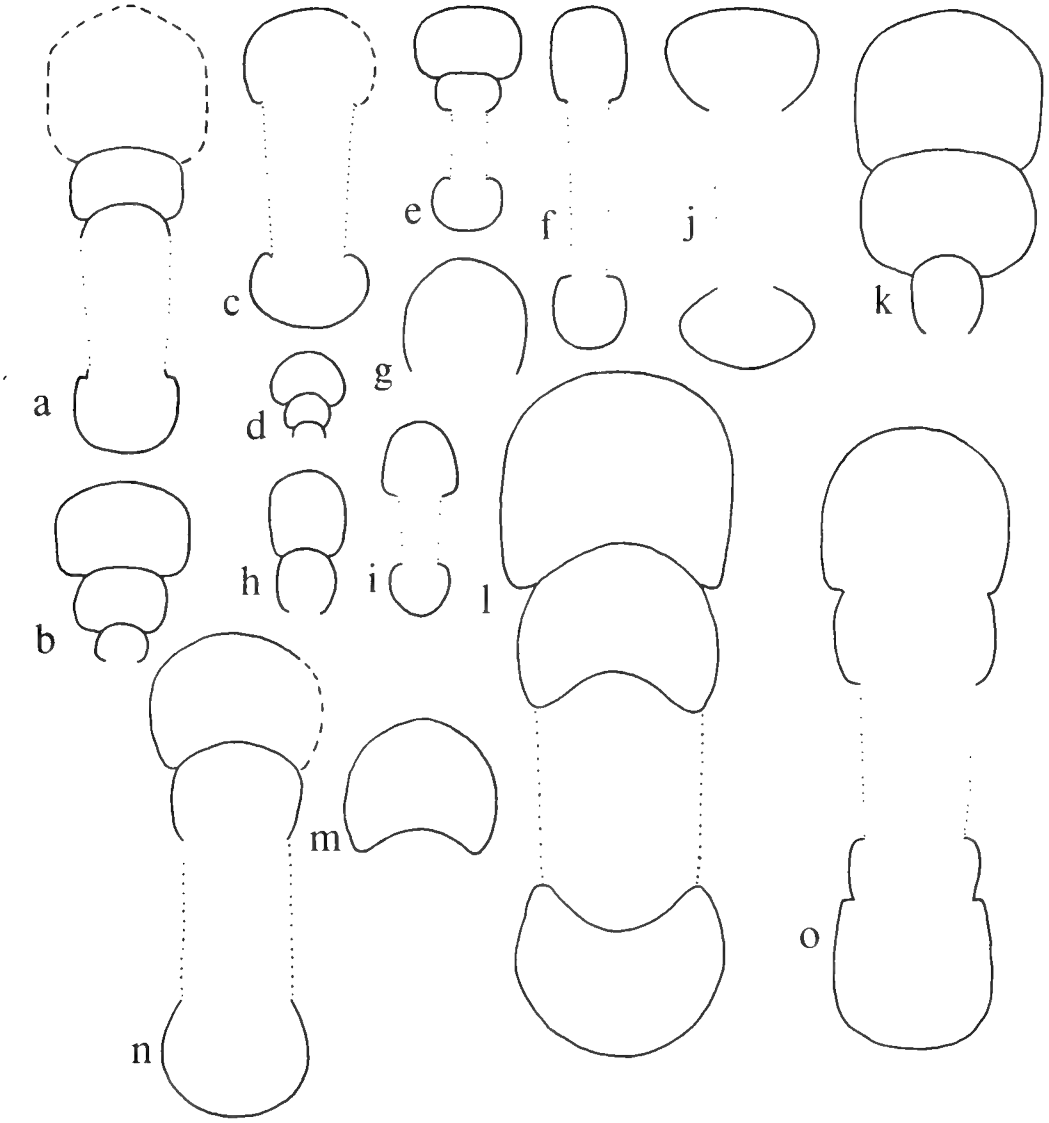

Abb. 16: Windungsquerschnitte, nat. Gr. a: *Dactylioceras (Eodactylites) simplex* FUCINI, 1935; Quebrada Chanchoquin; B. St. M. 1978 II 4. b: *Dactylioceras (Eodactylites) simplex* FUCINI, 1935; Quebrada Chanchoquin; B. St. M. 1978 II 7. c: *Dactylioceras (Orthodactylites) anguinum* (REINECKE, 1818); Quebrada Chanchoquin; B. St. M. 1978 II 12. d: *Dactylioceras (Orthodactylites) anguinum* (REINECKE, 1818); Quebrada Chanchoquin; B. St. M. 1978 II 13. e: *Dactylioceras (?Orthodactylites) helianthoides* YOKOYAMA 1904; Quebrada Noria; B. St. M. 1978 II 33. f: *Dactylioceras (Orthodactylites) directum* (BUCKMAN, 1926); Quebrada Chanchoquin; B. St. M. 1978 II 14. g: *Dactylioceras (Orthodactylites) tenuicostatum chilense* n. sp.; Quebrada La Chaucha; B. St. M. 1978 II 68. h: *Dactylioceras (Orthodactylites) hoelderi* n. sp.; Quebrada Yerbas Buenas; B. St. M. 1978 II 57. i: *Dactylioceras (Orthodactylites) hoelderi* n. sp.; Quebrada Yerbas Buenas; B. St. M. 1978 II 56. j: *Nodicoeloceras* cf. *pseudosemicelatum* (MAUBEUGE, 1957); Quebrada Chanchoquin; B. St. M. 1978 II 77. k: *Nodicoeloceras* cf. *eikenbergi* (HOFFMANN, 1968); Quebrada Chanchoquin; B. St. M. 1978 II 78. l: *Nodicoeloceras* cf. *crassoides* (SIMPSON, 1855) Form A; Quebrada Yerbas Buenas; B. St. M. 1978 II 79. m: *Nodicoeloceras* cf. *crassoides* (SIMPSON, 1855) Form A; Quebrada Yerbas Buenas; B. St. M. 1978 II 82. n: *Nodicoeloceras* cf. *crassoides* (SIMPSON, 1855) Form B; Quebrada El Asiento; B. St. M. 1978 II 84. o: *Nodicoeloceras* cf. *crassoides* (SIMPSON, 1855) Form C; Quebrada El Asiento; B. St. M. 1978 II 85.

sache ist in der sehr frühen Aufstellung der englischen Arten bei ungenügender Abbildung und Beschreibung zu suchen, wobei offenbar dort von Anfang an „splitters“ am Werke waren, wie jetzt Howarth entlarvt. Die Bearbeiter nicht-englischen Materials erkannten unter Verwendung dieser Namen in vielen Fällen gute Arten, die in die Literatur nun schon seit langem eingeführt sind, wenn sie auch den englischen Typen nicht entsprechen. *Nodicoeloceras annulatum* ist da ein ganz besonders klassisches Beispiel. Es ist seit Oppel (1856) eine gute Art von großer Bedeutung, doch kann Howarth (1973: 257) zeigen, daß der völlig ungenügend abgebildete Lectotyp zu *Nodicoeloceras crassoides* zu stellen ist.

Diese Arten müßten jetzt neu benannt werden. Um jedoch weitere Verwirrungen zu vermeiden, kann dies nur an einem umfangreichen Material von adulten Exemplaren bei guter und möglichst vollständiger Erhaltung geschehen. Das chilenische Material ist viel zu unvollständig und außerdem so weit von den klassischen Lokalitäten entfernt, daß eine Neubearbeitung in diesem Rahmen sehr wenig sinnvoll erscheinen würde.

Da über die Zuordnung der *Nodicoeloceras*-Arten so grundsätzliche Unklarheiten herrschen, können die hier beschriebenen chilenischen Formen nur in offener Nomenklatur behandelt werden.

3.2.1 *Nodicoeloceras* cf. *pseudosemicelatum* (Maubeuge, 1957)

Taf. 2, Fig. 9; Abb. 16j

cf. 1957 *Dactylioceras pseudosemicelatum* nov. spec. – Maubeuge 1957: 193, Taf. 3, Fig. 6

Material: Quebrada Chanchoquin (Abb. 1, Profil 21; Abb. 10, Schicht 4), topographische Karte 1:100000, Blatt El Tránsito: x = 375,1 km, y = 6811,05 km. Profilbeschreibung: siehe v. Hillebrandt (1973: 353–354). Die Dactylioceraten stammen aus dem tieferen Horizont, zusammen mit sehr selten *Radstockiceras* sp. und *Bouleiceras* cf. *chakdallaense* Fatmi. Fünf teilweise etwas verdrückte Exemplare (B. St. M. 1978 II 73–76) als Fragmente und B. St. M. 1978 II 77 als relativ komplettes Stück. Die Schalenhohlräume sind teils von Sediment, teils auch von Kalzit erfüllt, wobei die Schale verkieselt ist. Der Sipho ist teilweise sichtbar.

Maße: Exemplar Nr. 77 besitzt 60 mm, Exemplar Nr. 73 46 mm und Exemplar Nr. 75 etwa 62 mm Durchmesser.

Beschreibung: Weitgenabeltes, gedrungenes Gehäuse mit napfförmig eingesenktem Nabel. Der Windungsquerschnitt ist ausgeprägt breit oval, gerundet. Daher fehlen Nabel- und Externkante, weshalb Nabel-, Flanken- und Externfläche ohne deutliche Grenze ineinander übergehen.

Die Rippen verlaufen auf den Flanken annähernd rectoradiat, auf der Externfläche stärker proklin. Sie sind auf den inneren Windungen kräftiger ausgebildet als auf den äußeren. Die Rippen sind relativ fein, teils auch etwas kräftiger, schmal und stehen dicht – bei Exemplar Nr. 77 etwa 60 Flankenrippen auf dem letzten Umgang. Die Externrippen sind meist etwas feiner als die Flankenrippen ausgebildet. Die Rippenspaltpunkte sind auf den inneren Windungen wenig, auf den äußeren nicht verdickt und liegen auf einer Linie. Meist gabeln sich die Flankenrippen in zwei Externrippen.

Die Lobenlinie ist nicht analysierbar.

Vergleich: Die Formen sind *Dactylioceras pseudosemicelatum* Maubeuge, 1957 sehr ähnlich, welche Howarth (1973: 255) mit *Dactylioceras (Orthodactylites) crosbeyi* (Simpson) vergleicht.

Verbreitung: *Tenuicostatum*-Zone (*simplex*-Subzone von Chile). Nach Howarth (1973: 255) sind solche Formen in England besonders für die tiefere *tenuicostatum*-Zone (*clevelandicum*-Subzone) bezeichnend.

3.2.2 *Nodicoeloceras* cf. *eikenbergi* (Hoffmann, 1968)

Taf. 3, Fig. 1; Abb. 16k

cf. 1968 *Dactylioceras (? Orthodactylites) eikenbergi* nov. spec. – Hoffmann: 8, Taf. 1, Fig. 2a–c.

cf. 1972 *Nodicoeloceras eikenbergi* (Hoffmann, 1968) – Schmidt-Effing: 126, Taf. 14, Fig. 3a, b, Taf. 15, Fig. 2a, b, Taf. 16, Fig. 1a, b, Taf. 19, Fig. 1.

cf. 1973 *Dactylioceras (Orthodactylites) clevelandicum* sp. nov. – Howarth: 257, Taf. 3, Fig. 1–3, Taf. 4, Fig. 1, 2, Taf. 5, Fig. 3.

Material: Ein Fragment eines soweit erkennbar adulten Exemplars (Abschnitte von drei Windungen) von Quebrada Chanchoquin (B. St. M. 1978 II 78; Steinkern mit verkieselter Schale).

Weitere Exemplare (Steinkerne) liegen von der Quebrada El Peñon (Abb. 3a, Schicht 4) (B. St. M. 1978 II 233–239) vor.

Maße: Ursprünglicher Durchmesser etwa 90 mm.

Beschreibung: Gehäuse scheibenförmig, im Bereich der inneren Windungen wenig evolut, der letzten Windung sehr evolut. Der Windungsquerschnitt ist breit oval. Externkante nicht ausgebildet, Nabelkante abgerundet, Externfläche breit-gerundet. Zur Mündung flachen die Flanken ab und der Windungsquerschnitt wird rundlicher (WB/WH etwa 1,2).

Die Rippen sind relativ fein, stehen dicht und spalten an einem meist leicht verdickten Rippenspaltpunkt in sehr spitzem Winkel in zwei Externrippen. Sie verlaufen proradiat, teils auch proklin.

Eine Lobenlinie ist nicht zu beobachten.

Vergleich: Das beschriebene Fragment stimmt gut mit den Beschreibungen von Hoffmann (1968), Schmidt-Effing (1972) und Howarth (1973) überein. Wie Howarth und Schmidt-Effing feststellen, ist diese Art recht variabel. Als wichtiger Unterschied ist festzuhalten, daß das chilenische Exemplar keinen solch ausgeprägten Skulpturwechsel von den inneren zur äußeren Windungen zeigt (ähnlich auch das Exemplar auf Taf. 3, Fig. 1 a, in: Howarth 1973).

Bemerkungen: Howarth (1973: 257–258) beschreibt als neue Art „*Dactylioceras clevelandicum*", das nur aus Yorkshire bekannt sein soll. Ich halte diese Art jedoch, da ich keinen wesentlichen Unterschied feststellen kann, für ein Synonym von *Nodicoeloceras eikenbergi*.

Verbreitung: Tiefere *tenuicostatum*-Zone („*clevelandicum*-Subzone") von England, Norddeutschland, Spanien und Chile (*simplex*-Subzone).

3.2.3 *Nodicoeloceras* cf. *crassoides* (Simpson, 1855)
Form A

Taf. 3, Fig. 2–4; Abb. 16 l, m

Synonymie: vgl. die umfangreiche Synonymieliste in Schmidt-Effing (1972: 122).

Material: a) Quebrada Yerbas Buenas (Abb. 1, Profil 9, Abb. 6, Schicht 7), topographische Karte 1 : 100 000, Blatt Carrera Pinto: x = 439,4 km, y = 6979,3 km. Vier Fragmente jeweils etwa eines halben Umgangs als Steinkerne, teils auch mit Schale (B. St. M. 1978 II 79–82), zusammen mit *Hildaites* cf. *serpentiniformis* (Buckman), *Hildaites* cf. *serpentinus* (Reinecke), *Harpoceratoides* cf. *alternatus* (Simpson) und *Polyplectus* sp.

b) Quebrada Calquis (Abb. 1, Profil 15), topographische Karte 1 : 100 000, Blatt La Guardia: x = 402,7 km, y = 6909,5 km. Ein ungünstig erhaltener Steinkern einer äußeren Windung (B. St. M. 1978 II 83, ursprünglicher Durchmesser mindestens 65 mm), zusammen mit *Dactylioceras (Orthodactilites) hoelderi* n. sp.

Maße (in mm):

Nr.	DM	WH	WB	WB/WH
79	etwa 89 mm	26	27,5	(1,06)
		24	27	(1,13)
		20,5	25	(1,22)
82	mind. 57 mm	13	16,5	(1,27)
81	mind. 30 mm	11	12	(1,09)
80	mind. 30 mm	—	—	—

Beschreibung: Breit ovaler, weitgehend zugerundeter, im adulten Stadium rundlicher Windungsquerschnitt, bei leicht abgeflachten Flanken. Lediglich die Nabelkante ist leicht angedeutet. Die konkave Windungszone ist sehr gering (etwa $^1/_6$ der Windungshöhe).

Die Rippen verlaufen rectoradiat über Flanken und Externfläche, auf der Nabelfläche allerdings teilweise auch retroklin. Neben dichotomer Rippengabelung treten auch viele Einfach- und Schaltrippen auf. Auf den Steinkernen erscheinen die Rippen breitrundlich, bei Schalenerhaltung sind sie jedoch breit und hoch, entsprechend sind die Interkostalräume bei Schalenerhaltung breiter. Die Rippen stehen mäßig dicht.

Vergleich: Das Material von Quebrada Yerbas Buenas ist sehr einheitlich. Das Exemplar von Quebrada Calquis ist zu ungünstig erhalten, daß seine Zuordnung völlig gesichert wäre.

Mit *Nodicoeloceras crassoides* im Sinne von Schmidt-Effing (1972: 122) stimmen diese Formen recht gut überein. Doch hat Howarth (1978: 258) diese, abgesehen von einigen englischen Formen, nicht in seine Synonymieliste von *Nodicoeloceras crassoides* aufgenommen, obwohl er auf der anderen Seite diese Art außerordentlich weit faßt. So synonymiert er mit *Nodicoeloceras crassoides* auch so wichtige Arten wie *Nodicoeloceras annulatum*, offensichtlich auch *Nodicoeloceras crosbeyi*, das Howarth (1973) mit diesem synonymiert hat, obwohl diese Formen 1978 nicht in der Synonymieliste erscheinen, und *Nodicoeloceras pingue*. Da es sich in allen Fällen um englische Typen handelt, soll hier keine weitere Stellungnahme dazu bezogen werden.

Verbreitung: Höheres Unter-Toarcium (*hoelderi*-Zone) von Chile.

3.2.4 *Nodicoeloceras* cf. *crassoides* (Simpson, 1855)
Form B

Taf. 3, Fig. 5; Abb. 16n

Material: Quebrada El Asiento (Abb. 2, Profil 6), topographische Karte 1 : 100 000, Blatt Potrerillos: x = 467,9 km, y = 7072,85 km. Ein Schale-tragender Steinkern (B. St. M. 1978 II 84) aus den rostbraun anwitternden Kalken (Abb. 3, Schicht 4).

Maße: DM = 65 mm; WH = 19,5 (0,3); WB = ca. 23 (0,35); NW = 31 (0,48); WB/WH = (1,18).

Kurzbeschreibung: Ähnlich *Nodicoeloceras* cf. *crassoides* Form A, doch ist der Windungsquerschnitt noch rundlicher ausgebildet, da auch keine Nabelkante angedeutet ist. Ebenfalls in der Skulptur herrscht Übereinstimmung, doch abweichend sind auf den Innenwindungen in Abständen von 2 bis 3 Flankenrippen ausgeprägte Knötchen entwickelt, ein Merkmal, das häufig bei *Nodicoeloceras crassoides* beobachtet wird.

Verbreitung: höheres Unter-Toarcium (*hoelderi*-Zone) von Chile.

3.2.5 *Nodicoeloceras* cf. *crassoides* (Simpson, 1855)
Form C

Taf. 3, Fig. 6; Abb. 16o

Material: a) Quebrada El Asiento (Abb. 2, Profil 4), topographische Karte 1 : 100 000, Blatt Potrerillos: x = 467,6 km, y = 7070,7 km. Ein Steinkern mit Schalenresten, besonders der Rippen (B. St. M. 1978 II 85), aus den rostbraun anwitternden Kalken (Abb. 3, Schicht 4).

b) Río Jorquera (Majada del Carrizo) (Abb. 9, Schicht 7): 7 Steinkerne (B. St. M. 1978 II 222–228), zusammen mit *Dactylioceras (Orth.) directum*, *Polyplectus* sp., *Harpoceras* cf. *falcifer*, *Hildaites* cf. *levisoni* (großwüchsig).

Maße: Maximaler Durchmesser etwa 83 mm; DM = 75 mm; WH = 20,5 (0,27); WB = 22,5 (0,3: Wert vielleicht aus diagenetischen Gründen zu gering); NW = 35 (0,47); WB/WH = (1,1).

Beschreibung: Scheibenförmiges Gehäuse, wobei die Windungszunahme (WH, WB) im Bereich der Innenwindungen groß, auf dem letzten Umgang (wahrscheinlich die Wohnkammer) aber gering ist. Der Windungsquerschnitt ist breit oval, wobei die Flanken abgeflacht sind. Eine Nabelkante ist angedeutet, eine Externkante fehlt.

Die Skulptur wird durch sehr kräftige, dicht stehende Vollrippen gebildet, die auf dem Steinkern nur eine relativ schwache Rippenspur zurücklassen. Hohlrippen sind nicht zu beobachten. Auf dem letzten Umgang dominieren Einfachrippen gegenüber Spaltrippen. Auf den Innenwindungen scheinen Knötchen an den Rippenspaltpunkten aufzutreten, doch ist durch die weitgehende Überdeckung der folgenden Windungen keine sichere Aussage möglich. Die Rippen verlaufen rectoriat über Flanken und Externseite, auf der Nabelfläche aber retroklin, weshalb als Gesamteindruck die Rippen etwas geschwungen erscheinen.

Vergleich: Das beschriebene Stück ist am besten mit *Nodicoeloceras annulatum* vergleichbar (vgl. Synonymieliste und Beschreibung in Schmidt-Effing 1972: 124–126). Doch stellt Howarth (1978: 256) den Lectotypus dieser Art, der nur in der unklaren Abbildung von Sowerby (1819: Taf. 222, Fig. 5) in der Literatur zugänglich ist, zu *Nodicoeloceras crassoides*. Diese von Howarth (1978) vollzogene Synonymierung mag für die englischen Formen gelten, nicht notwendigerweise für die nicht-englischen (vgl. S.52). Die Entscheidung, ob es sich hier um ein echtes *Nodicoeloceras crassoides* handelt, was eine besonders große Variabilität dieser Art voraussetzen würde, oder eine noch nicht benannte Art, kann nur an einem umfangreicheren Material getroffen werden.

Verbreitung: Nach Howarth (1973, 1978) *tenuicostatum*- und *falcifer*-Zone. In Chile in der *hoelderi*-Zone des höheren Unter-Toarciums.

Nodicoeloceras sp.

Aus dem Profil Quebrada Yerbas Buenas liegt ein Fragment (B. St. M. 1978 II 86) vor, das wegen zu unvollständiger Erhaltung artlich nicht bestimmbar ist.

3.3 GENUS: *PERONOCERAS* HYATT, 1867

Typus-Art: *Ammonites fibulatus* Sowerby, 1823

Diagnose: Gehäuse evolut, scheiben- bis napfförmig. Windungsquerschnitt wenig bis stark abgerundet, trapezförmig oder rechteckig bis quadratisch. Windungsbreite im allgemeinen größer als Windungshöhe. Skulptur kräftig, charakteristisch das fibulate Berippungsmuster, kann zu einfacher Flankenberippung reduziert sein. Rippenspaltpunkte mit Dornen oder Knoten versehen. Flankenrippen in 2 bis 3 Externrippen aufgespalten.

Bemerkungen: Wie Fischer (1966) und Schmidt-Effing (1972, 1975) halte ich *Porpoceras* Buckman, 1911 (Typus-Art: *Ammonites vortex* Simpson, 1855) für ein Synonym von *Peronoceras*. Auch *Telodactylites* Pinna & Levi-Setti, 1971 (Typus-Art: *Ammonites desplacei* d'Orbigny, 1844) muß als Synonym von *Peronoceras* betrachtet werden. Die Abgrenzung einiger Arten gegenüber *Nodicoeloceras* Buckman, 1926 ist schwierig, vor allem dann, wenn die Wohnkammer nicht vorhanden ist. Die typischen Arten von *Nodicoeloceras* besitzen ausgeprägte Wachstumsallometrien (Schmidt-Effing 1972, S. 63). Die Abgrenzung gegenüber *Collina* Bonarelli, 1893 (Typus-Art: *Collina gemma* Bonarelli, 1893) ist bei Arten, die auf der Externfläche keine kielartige Erhöhung besitzen, ebenfalls schwierig. Diese Arten unterscheiden sich dann von *Peronoceras* vor allem durch das sehr evolute, flachscheibenförmige Gehäuse mit mehr oder minder quadratischem Windungsquerschnitt.

Bei den stratigraphisch älteren Arten der Gattung *Peronoceras* tritt das fibulate Berippungsmuster vorwiegend in bereits älteren Stadien auf und kann in jüngeren Stadien wieder fehlen. Bei den stratigraphisch jüngeren Arten fehlt zumeist das fibulate Berippungsmuster bei den älteren Stadien und ist wie bei *Collina* (Pinna & Levi-Setti 1971, S. 112) deutlicher bei den jüngeren Stadien ausgeprägt. Es besteht also die phylogenetische Tendenz während der Ontogenese, das fibulate Berippungsmuster auf immer jüngere Stadien zu verlegen.

Nach Schmidt-Effing (1972, S. 176) sind die Ahnen von *Peronoceras* wahrscheinlich bei *Dactylioceras (Dactylioceras)* des Unter-Toarcium zu suchen (s. a. Howarth 1962b, Guex 1971). Kottek (1966) leitet *Peronoceras* von *Nodicoeloceras* ab. Pinna & Levi-Setti (1971, Fig. 16) unterscheiden zwischen einer phylogenetischen Entwicklung in der zentraleuropäischen und der mediterranen Faunenprovinz, wobei *Peronoceras* von *Dactylioceras (Dactylioceras)*, *Nodicoeloceras* und *Collina* von *Dactylioceras (Orthodactylites)* und *Telodactylites* von *Mesodactylites* abgeleitet werden. Zu *Nodicoeloceras* werden von Pinna & Levi-Setti auch Arten *(P. verticosum, P. vorticellum, P. choffati)* gerechnet, die bisher von den meisten Autoren *Peronoceras* zugeordnet wurden.

Eine Darstellung der Verwandtschaftsverhältnisse einiger Arten von *Peronoceras* wurde von Fischer (1966,

Tab. 3) gegeben. Sie stimmt nicht überein mit der phylogenetischen Entwicklung, die von Pinna & Levi-Setti (1971) angenommen wird. So werden bei Fischer *Peronoceras verticosum, P. vorticellum* und *P. vortex* von *P. fibulatum* über *P. acanthopsis* und *P. desplacei* abgeleitet. Pinna & Levi-setti hingegen stellen *P. verticosum* und *P. vorticellum* zur Gattung *Nodicoeloceras* und leiten beide Arten von Nodicoeloceraten der *falcifer*-Zone ab. *Peronoceras vortex* wird bei dieser Gattung belassen, während *P. acanthopsis* (= *P. renzi* [Pinna & Levi-Setti]) und *P. desplacei* zur Gattung *Telodactylites* gerechnet werden.

Howarth (1973, S. 248) hingegen stellte fest, daß es alle Übergänge zwischen *Peronoceras vortex, P. verticosum* und *P. vorticellum* gibt und auch bei *Dactylioceras (Orthodactylites)* die Variationsbreite sehr groß ist. So lange noch derartig unterschiedliche Meinungen zur Phylogenie der Peronoceraten bestehen, erscheint es nicht angebracht, diese in mehrere Gattungen aufzuspalten.

Das vorliegende Material reicht leider für variationsstatistische Untersuchungen nicht aus, sowohl was die Anzahl der vorhandenen Exemplare als auch den Erhaltungszustand anbelangt.

Aus diesen Gründen war ein eindeutiger Vergleich mit europäischen Formen bei keiner Art möglich, was in den cf.-Bestimmungen zum Ausdruck kommt. Neue Arten wurden nur dann aufgestellt, wenn einerseits keine Übereinstimmung zu bereits bekannten Formen bestand und andrerseits das Material nach Anzahl der Exemplare und Erhaltungszustand die Aufstellung einer neuen Art zuließ.

3.3.1 *Peronoceras* cf. *subarmatum* (Young & Bird, 1822)

Taf. 3, Fig. 7–10; Abb. 17d, f, 18a

cf. 1962 *Peronoceras subarmatum* (Young and Bird). – Howarth, S. 117, Taf. 17, Fig. 5a, b (Neotypus).
cf. 1978 *Peronoceras subarmatum* (Young & Bird 1822). – Howarth, S. 262, Taf. 4, Fig. 4, 5, 7.

Bemerkungen: Howarth (1962) stellte für *Peronoceras subarmatum* einen Neotypus auf, der möglicherweise dem Holotypus entspricht.

Aus dem Mediterranbereich wurde in den letzten Jahren mehrfach *P. subarmatum* beschrieben und abgebildet (Zanzucchi 1963, Pinna 1966, Kottek 1966, Fischer 1966, Gallitelli Wendt 1969, Pinna & Levi-Setti 1971, Dezi & Ridolfi 1975). Der Erhaltungszustand der meisten abgebildeten Exemplare erlaubt es nicht, diese eindeutig *P. subarmatum* zuzuweisen.

Die von Zanzucchi (1963) und Fischer (1966) unter *P. subarmatum* abgebildeten Exemplare werden von Pinna & Levi-Setti (1971) *Peronoceras vortex* (Simpson) zugeordnet. Sicherlich handelt es sich jedoch zumindest bei den von Fischer (1966) abgebildeten Exemplaren um eine mit *P. subarmatum* sehr nahe verwandte Form und nicht um *P. vortex*.

Material: a) Quebrada El Bolito (Abb. 5), topogr. Karte 1 : 100 000, Blatt Laguna del Negro Francisco: x = 456,5 km, y = 6994,5 km. Ein Steinkernexemplar (B. St. M. 1978 II 87) (Taf. 3, Fig. 7; Abb. 17d, 18a), sowie ein weiteres Exemplar aus wahrscheinlich etwas jüngeren Schichten (B. St. M. 1978 II 88). Zwei weitere Exemplare gehören wahrscheinlich ebenfalls zu dieser Art (B. St. M. 1978 II 89 u. 90). Zusammen mit *Peronoceras largaense* n. sp., *Harpoceras* cf. *chrysanthemum* (Yokoyama) und *Mercaticeras* sp.

b) Quebrada Larga (Abb. 7), topogr. Karte 1 : 100000, Blatt Carrera Pinto: x = 432,7 km, y = 6978,7 km. Ein Exemplar (Abb. 17f) (B. St. M. 1978 II 91), sowie weitere Exemplare, die wahrscheinlich zu dieser Art gehören (B. St. M. 1978 II 92, 93, 94).

c) Rio Jorquera (Majada del Carrizo) (Abb. 9), topogr. Karte 1 : 100000, Blatt La Guardia: x = 437,4 km, y = 6931,7 km, 2 Steinkernexemplare (B. St. M. 1978 II 95 u. 96) (Taf. 3, Fig. 8), 2 Windungsbruchstücke (B. St. M. 1978 II 97 u. 98) (Taf. 3, Fig. 9, 10) zusammen mit *Peronoceras largaense* und *Harpoceras* sp.

d) Quebrada El Asiento, topogr. Karte 1 : 100000, Blatt Potrerillos, Profil 4 (Abb. 2): x = 467,6 km, y = 7070,7 km, 2 Steinkernexemplare (innere Windungen schlecht erhalten) (B. St. M. 1978 II 99 u. 100), 1 Steinkernexemplar (1 cm ∅, innere Windungen) B. St. M. 1978 II 101), 1 Windungsbruckstück (B. St. M. 1978 II 102). Zusammen mit *Harpoceras* cf. *falcifer*. Profil 3 (Abb. 2): x = 467,5 km, y = 7070,45 km, 3 Exemplare von unvollständigen, inneren Windungen (B. St. M. 1978 II 103 bis 105).

Maße:

	d	N	H	Q	Z
B. St. M. 1978 II 87	1,25 cm			0,55	
	3,65	47	30	0,73	42
B. St. M. 1978 II 89	6,0 cm	47	30	0,84	
B. St. M. 1978 II 88	3,1	46	30,5	0,7	
B. St. M. 1978 II 91	4,7	47	30	0,78	
B. St. M. 1978 II 95	6,0 cm	45	31,5	0,9	
	4,3	44	32,5	0,8	

Beschreibung: Die vorliegenden Exemplare können nur mit Vorbehalt zu *P. subarmatum* gestellt werden, da sie für einen genauen Vergleich nicht ausreichend erhalten sind. Zumindest sind sie jedoch mit *P. subarmatum* nahe verwandt.

Sämtliche Exemplare liegen als Steinkerne vor. Bei den Innenwindungen der weitgenabelten Gehäuse ist der Windungsquerschnitt breit trapezförmig und wird dann allmählich breit rechteckig, wobei der Q-Wert größer wird. Am Ende des Phragmokon wird die vorher deutliche Externkante abgerundet.

Fibulate Flankenrippen mit Knoten herrschen vor allem auf dem Phragmokon vor, während auf der Wohnkammer zunehmend diesen zwischengeschaltete einfache Flankenrippen häufiger werden, die zumeist gegabelt, selten ungegabelt sind und vorwiegend am Spaltpunkt keinen Knoten besitzen. Selten vereinigen sich auch 3 Rippen zu einem Knoten. Von den Knoten gehen 2 bis 3 Spaltrippen aus. Die äußere Lobenlinie wurde bei einem Exemplar gezeichnet (Abb. 18a). Extern- und Laterallobus sind gleich tief, der U_2 ist wesentlich kleiner.

Verbreitung: *Peronoceras subarmatum* kommt nach Howarth (1978) in Europa in der *fibulatum*-Subzone vor.

3.3.2 *Peronoceras largaense* n. sp.

Taf. 4, Fig. 1–4, Abb. 17i

Holotypus (B. St. M. 1978 II 106): Schalenexemplar mit ? Teil der Wohnkammer (Taf. 4, Fig. 1; Abb. 17i).

Derivatio nominis: Nach dem Vorkommen in der Quebrada Larga.

Locus typicus: Quebrada Larga (Provinz Atacama) (Abb. 1, Profil 11), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 432,7 km, y = 6978,7 km.

Stratum typicum: Wechsellagerung von sandigen Kalkbänken mit Kalkmergeln, die Ammoniten (*P.* cf. *subarmatum*, *P. largaense* n. sp., *Harpoceras* sp., *Mercaticeras* sp.) enthalten.

Mittleres Toarcium, Zone des *Hildoceras bifrons*, Subzone des *Peronoceras largaense* (= *commune* – bzw. *sublevisoni*-Subzone in Europa).

Diagnose: Gehäuse stark evolut, scheibenförmig, Windungsquerschnitt annähernd quadratisch, fibulate Flankenrippen mit langen Stacheln oder Knoten, von denen 2 bis 3 nach vorn gebogene Externrippen ausgehen. Einfache Schaltrippen selten.

Material: a) Am locus typicus wurde außer dem Holotypus ein weiteres, kleines Steinkern-Exemplar (B. St. M. 1978 II 107) (Taf. 4, Fig. 2), sowie ein Steinkern-Windungsbruchstück gefunden (B. St. M. 1978 II 108) (Taf. 4, Fig. 4).

b) Quebrada El Bolito (Abb. 5), topogr. Karte 1:100000, Blatt Laguna del Negro Francisco: x = 456,5 km, y = 6994,5 km.

3 Steinkernexemplare (B. St. M. 1978 II 109 bis 111) (Taf. 4, Fig. 3), sowie Steinkern-Windungsbruchstücke (B. St. M. 1978 II 112, 113). Zusammen mit *P.* cf. *subarmatum*, *Harpoceras* cf. *chrysanthemum*, *Mercaticeras* sp.

Maße:	d	N	H	Q	Z
Holotypus	4,9 cm	57	23,5	0,9	50 FR ca. 72ER
	4,2	55	ca. 22	ca. 0,8	40 FR
Paratypen					
B. St. M. 1978 II 107	3,5	52,5	26,5	0,97	
B. St. M. 1978 II 109	3,5	ca. 50	28–29	0,85	51 FR (Anfang letzter Umgang)

Beschreibung des Holotypus: Der Holotypus liegt in Schalenerhaltung vor und wurde auf einer Seite aus der kalkig-mergeligen Matrix herauspräpariert. Zumindest ein Teil der letzten Windung dürfte bereits der Wohnkammer angehören.

Das Gehäuse ist stark evolut. Die Windungen umfassen sich nur wenig. Der Nabel ist wenig eingesenkt, da die Windungsbreite im Verhältnis zur Windungshöhe während der Ontogenese allmählich abnimmt. Der Windungsquerschnitt ist am Ende des letzten Umgangs fast quadratisch (Q = 0,9), zu Beginn des letzten Umgangs etwas breiter als hoch (Q = 0,8). Die Externseite ist wenig gewölbt.

Bis zu einem Nabeldurchmesser von ca. 3 mm sind auf Grund der ungenügenden Erhaltung die Rippen schlecht zu erkennen, dann sind Einzelrippen zu erkennen, ab einem Nabeldurchmesser von ca. 4 mm treten fibulate Rippenpaare auf. Der externe Vereinigungspunkt ist zu einem langen Dorn verlängert, der bis zur Mitte des nächsten Umgangs reichen kann. Auf dem vorletzten Umgang tritt das fibulate Berippungsmuster zurück, da sich jede zweite Flankenrippe nur wenig an die dorntragende Rippe anlehnt oder als Schaltrippe ausgebildet ist. Bedingt, zumindest verstärkt, wird dies wahrscheinlich durch die Schalenerhaltung. Auf dem letzten Umgang treten wieder häufiger fibulate Rippen auf, die auf der Externkante einen kräftigen Knoten tragen (der ursprünglich sicherlich auch hier vorhandene Dorn ist nicht erhalten).

Die fibulaten Flankenrippen spalten in 2 bis 3 Externrippen auf. Den fibulaten Flankenrippen sind am Ende des letzten Umgangs einige Einfachrippen zwischengeschaltet, die nicht in Gabelrippen aufspalten. Auf 50 Flankenrippen kommen im letzten Umgang ca. 72 Externrippen.

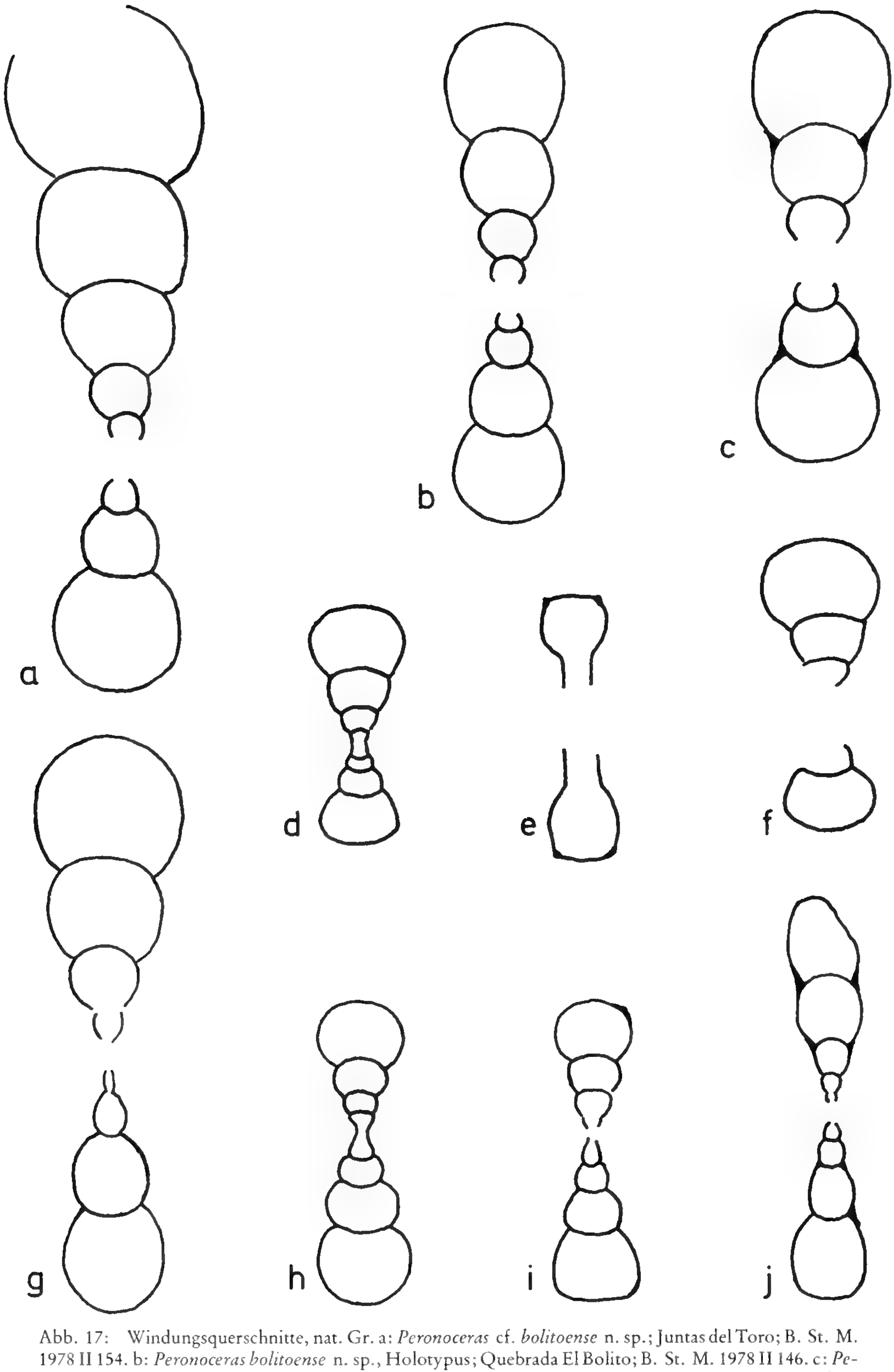

Abb. 17: Windungsquerschnitte, nat. Gr. a: *Peronoceras* cf. *bolitoense* n. sp.; Juntas del Toro; B. St. M. 1978 II 154. b: *Peronoceras bolitoense* n. sp., Holotypus; Quebrada El Bolito; B. St. M. 1978 II 146. c: *Peronoceras* cf. *bolitoense* n. sp.; Quebrada Yerbas Buenas; B. St. M. 1978 II 153. d: *Peronoceras* cf. *subarmatum* (YOUNG & BIRD, 1822); Quebrada El Bolito; B. St. M. 1978 II 87. e: *Peronoceras pacificum* n. sp.; Quebrada Yerbas Buenas; B. St. M. 1978 II 123. f: *Peronoceras* cf. *subarmatum* (YOUNG & BIRD, 1822); Quebrada Larga; B. St. M. 1978 II 91. g: *Peronoceras bolitoense* n. sp.; Quebrada El Bolito; B. St. M. 1978 II 147. h: *Peronoceras* sp. cf. *P.* cf. *verticosum* (BUCKMAN, 1914); Quebrada Yerbas Buenas; B. St. M. 1978 II 136. i: *Peronoceras largaense* n. sp., Holotypus; Quebrada Larga; B. St. M. 1978 II 106. k: *Collina chilensis* n. sp., Holotypus; Quebrada El Bolito; B. St. M. 1978 II 176.

Die Flankenrippen stehen vorwiegend rectoradiat, selten leicht retroradiat. Spaltet ein fibulates Rippenpaar in 3 Externrippen auf, so ist der Verlauf der ersten Externrippe gerade, die zweite Externrippe ist etwas und die dritte kräftig nach vorn gebogen. Ein Zick-Zack-Muster tritt selten auf, da die Externrippen, die von dem Knoten der einen Seite ausgehen, sich auf der anderen Seite auch wieder in einem Knoten vereinigen.

Beschreibung der Paratypen: Bei den Paratypen handelt es sich um Steinkerne. Die Lobenlinie ist jedoch an keinem Exemplar zu erkennen, da vorwiegend die Wohnkammer erhalten ist.

Die Nabelweite und der Windungsquerschnitt entsprechen denen des Holotypus.

Fibulate Flankenrippen herrschen bei sämtlichen Paratypen vor. Manchmal sind auch 3 Flankenrippen extern zu einem Knoten vereinigt (nicht abgebildete Seite B. St. M. 1978 II 107 [Taf. 4, Fig. 2]). Bei Exemplar B. St. M. 1978 II 109 (Taf. 4, Fig. 3) ist nur die Wohnkammer in der Länge von einem Umgang erhalten. Die letzte Hälfte der Wohnkammer ist zunehmend Richtung Mündung verdrückt. Auf der ersten Hälfte herrschen fibulate Flankenrippen vor, auf der zweiten Hälfte sind diesen zunehmend Gabel- und Einzelrippen zwischengeschaltet und die Flankenrippen nehmen einen retroradiaten Verlauf an. Die Knoten der fibulaten Rippen entsenden 2 bis 3 Externrippen. Teilweise tritt bei den Externrippen ein Zick-Zack-Muster auf.

Vergleiche: Peronoceras subarmatum und P. cf. subarmatum besitzen einen breiteren Windungsquerschnitt. Peronoceras fibulatum (Sow.) weist eine stark gewölbte Externseite auf.

3.3.3 *Peronoceras* cf. *desplacei* (d'Orbigny, 1844)

Taf. 4, Fig. 7, 10

cf. 1844 *Ammonites Desplacei* d'Orb. – d'Orbigny, S. 334, Taf. 107, Fig. 1–4.
cf. 1971 *Telodactylites desplacei* (d'Orbigny, 1844). – Pinna & Levi-Setti, S. 117, Taf. 10, Fig. 10–14, Taf. 11, Fig. 9; Fig. 21/12.
cf. 1976 *P. desplacei* (d'Orb. 1844). – Schlegelmilch, S. 79, Taf. 40, Fig. 1.
Weitere Literatur bei Pinna & Levi-Setti (1971).

Material: Quebrada Yerbas Buenas (Abb. 6), topogr. Karte 1 : 100 000, Blatt Carrera Pinto: x = 439,45 km, y = 6979,3 km. 1 kleines, unvollständiges Exemplar (B. St. M. 1978 II 114) (Taf. 4, Fig. 10), 1 halbes Exemplar (B. St. M. 1978 II 115) (Taf. 4, Fig. 7) mit angeschliffenem Querschnitt, dessen Flanken schlecht sichtbar sind. Außenwindungsbruchstücke von Exemplaren mit einem Durchmesser von ca. 6 cm können nur mit Vorbehalt zu dieser Art gestellt werden. Zusammen mit *Peronoceras* cf. *choffati*, *P.* sp. ex gr. *P. subarmatum* und *Harpoceras* cf. *chrysanthemum*.

Maße:	D	N	H	Q
B. St. M. 1978 II 115	4,2 cm	43	33	0,7
B. St. M. 1978 II 114	2,5	48	30	0,69

Beschreibung: Die beiden vorliegenden Exemplare sind nicht ausreichend erhalten, um eindeutig *Peronoceras desplacei* zugeordnet werden zu können. Die Gehäuse sind mäßig evolut, die Umgänge umfassen sich zu einem Drittel. Der Nabel ist schüsselförmig eingesenkt. Der rundlich querovale Windungsquerschnitt ändert sich nur wenig während der Ontogenese. Die Externseite und die Flanken sind stark gewölbt. Bei dem kleinsten Exemplar trägt jede zweite rectoradiate Flankenrippe einen Knoten, von dem 2 bis 3 Externrippen ausgehen. Die Rippen ohne Knoten sind Einfach- oder Gabelrippen. Deutlich fibulate Rippen kommen nicht vor.

Auch bei den größeren Exemplaren, die nur mit Vorbehalt zu *P.* cf. *desplacei* gestellt werden können, ist jede zweite rectoradiate Flankenrippe mit einem Knoten versehen, von dem jedoch vorwiegend 3 Externrippen ausgehen. Die Schalrippen bleiben einfach oder sind bifurkat aufgespalten. Fibulate Rippen sind etwas häufiger.

Vergleiche: Der Windungsquerschnitt ist etwas weniger breit als bei *Peronoceras desplacei.* Die Art der Berippung stimmt weitgehend mit der dieser Art überein.

Verbreitung: *Peronoceras desplacei* ist nach Fischer (1966) in Europa aus der *fibulatum*- und *braunianum*-Subzone bekannt.

3.3.4 *Peronoceras* cf. *renzi* (Pinna & Levi-Setti, 1971)

Taf. 4, Fig. 8; Abb. 18c, d, e

non 1912 *Coeloceras Desplacei* d'Orb. – Renz, S. 61, Taf. 6, Fig. 6
cf. 1971 *Telodactylites renzi* n. sp. – Pinna & Levi-Setti, S. 117, Taf. 10, Fig. 1–5; Fig. 14 B; Fig. 21/7.

Bemerkungen: Pinna & Levi-Setti (1971) benannten die Art nach C. Renz, der eine ähnliche Art unter *Coeloceras desplacei* d'Orb. abbildete. Das Original zu dem von Renz (1912) abgebildeten Exemplar befindet sich im Naturhistorischen Museum in Basel. Einen Gipsabguß dieses Originals erhielt ich freundlicherweise von Herrn Dr. F. Wiedenmayer. Die Maße sind:

d	N	H	Q	Z
3,7 cm	46	30	ca. 0,8	54

Der wenig breitovale, rundliche Querschnitt gleicht mehr dem von *Peronoceras desplacei*, stimmt jedoch auf keinen Fall mit dem Querschnitt von *Peronoceras renzi* (Q = 0,5 bis 0,65) bei Pinna & Levi-Setti überein. Nach diesen Autoren unterscheidet sich *Peronoceras renzi* von *P. desplacei* hauptsächlich dadurch, daß bei *P. renzi* die fibulate Berippung ontogenetisch früher erscheint.

Material: a) Rio Jorquera (Majada del Carrizo) (Abb. 9), topogr. Karte 1 : 100 000, Blatt La Guardia: x = 437,35 km, y = 6931,75 km: 2 Windungsbruchstücke (B. St. M. 1978 II 116 u. 117), zusammen mit nicht näher bestimmbaren Windungsbruchstücken von *Peronoceras* sp. und *Harpoceras* sp.

b) Quebrada La Chaucha (Abb. 1, Profil 6), topogr. Karte 1 : 100 000, Blatt Laguna del Negro Francisco: x = 468 km, y = 7011 km. Ein nicht horizontiert entnommener Steinkern (B. St. M. 1978 II 118) (Taf. 4, Fig. 8).

Maße:

	d	N	H	Q
B. St. M. 1978 II 118	3,5 cm	48,5	28,5	0,61
116				0,57

Beschreibung: Der Erhaltungszustand der vorliegenden Exemplare reicht für eine eindeutige Zuordnung nicht aus.

Die Gehäuse sind mäßig evolut. Die Umgänge umfassen sich nur wenig. Der Nabel ist schüsselförmig eingesenkt. Der Windungsquerschnitt ist breit rechteckig, die Externkante nur wenig abgerundet. Die Externseite und die Flanken sind wenig gewölbt.

Vor allem bei dem Exemplar von der Quebrada La Chaucha sind – so weit erkennbar – fibulate Rippen vorhanden, die an einem deutlichen Knoten in vorwiegend 3 Externrippen aufspalten. Den fibulaten Rippen können

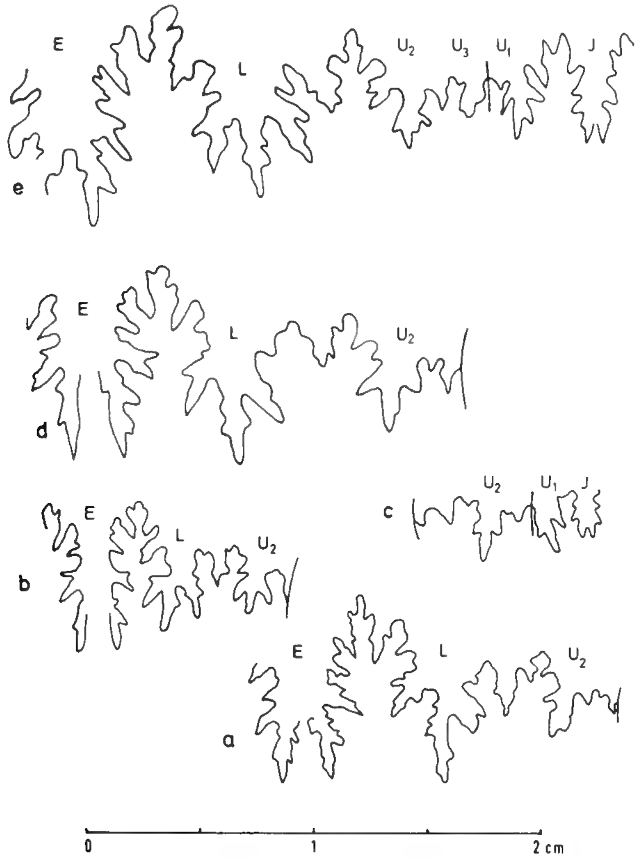

Abb. 18: Lobenlinien a: *Peronoceras* cf. *subarmatum* (Young & Bird, 1822); Quebrada El Bolito; B. St. M. 1978 II 87. b: *Peronoceras* sp. ex gr. *P. bolitoense* n. sp.; Quebrada Cortaderita; B. St. M. 1978 II 152. c: *Peronoceras* cf. *renzi* (Pinna & Levi-Setti, 1971); Rio Jorquera; B. St. M. 1978 II 116. d: *Peronoceras* cf. *renzi* (Pinna & Levi-Setti, 1971); Rio Jorquera; B. St. M. 1978 II 116. e: *Peronoceras* cf. *renzi* (Pinna & Levi-Setti, 1971); Rio Jorquera; B. St. M. 1978 II 117.

einfache Rippen zwischengeschaltet sein, die sich ohne Knoten bifurkat teilen. Die Windungsbruchstücke von der Majada del Carrizo zeigen die fibulate Berippung weniger deutlich (bedingt auch durch den Erhaltungszustand).

Bei Exemplar B. St. M. 1978 II 116 ließ sich bei der vorletzten Windung die innere und bis zur Externkante die äußere Lobenlinie, sowie auf dem äußeren Umgang die vollständige äußere Lobenlinie zeichnen (Abb. 18c, d). Bei Exemplar B. St. M. 1978 II 117 konnte die vollständige Lobenlinie gezeichnet werden (Abb. 18e). Laterallobus und Externlobus sind nahezu gleich groß. Der Umbilikallobus U_2 ist bedeutend kleiner als der Laterallobus. U_2 und U_1 sind dreispitzig. Die von Pinna & Levi-Setti (1971) abgebildete äußere Lobenlinie von *Peronoceras renzi* ist sehr ähnlich.

Verbreitung: *Peronoceras renzi* kommt nach Pinna & Levi-Setti in der *bifrons*-Zone vor.

3.3.5 *Peronoceras* cf. *choffati* (Renz, 1912)

Taf. 4, Fig. 5, 6

cf. 1912 *Coeloceras Choffati* n. sp. – Renz, S. 86, Taf. 6, Fig. 5

Bemerkungen: Durch Herrn Dr. F. Wiedenmayer erhielt ich einen Gipsabguß des Holotypus von *Peronoceras choffati*, der sich im Naturhistorischen Museum in Basel befindet. Seine Maße sind:

d	N	H	Q	Z
3,35	47	29	0,5	48
ca. 2,1	45	33	0,47	38

Die von Pinna & Levi-Setti (1971, S. 100, Taf. 4, Fig. 3–7, 10, 13) als *Nodicoeloceras choffati* bezeichneten und abgebildeten Exemplare, sowie die in deren Synonymieliste angeführten Exemplare, können nicht zu *Peronoceras choffati* gestellt werden, da sie sämtlich eine weit geringere Windungsbreite (bei Pinna & Levi-Setti Q = 0,53 bis 0,73) besitzen. Das bei Pinna & Levi-Setti in der Synonymieliste genannte Exemplar von Monestier (1931, Taf. 1, Fig. 28) wurde von Guex (1972, S. 623) als *Porpoceras* cf. *crassicostatum* Guex bezeichnet und läßt sich noch am besten mit *P. choffati* vergleichen. *Peronoceras crassicostatum* ist allerdings etwas weniger weitnabelig (weniger Umgänge) und besitzt in den Innenwindungen keine fibulaten Rippen.

Material: Quebrada Yerbas Buenas (Abb. 6), topogr. Karte 1 : 100000, Blatt Carrera Pinto: x = 439,45 km, y = 6979,3 km. Zwei unvollständige Exemplare (B. St. M. 1978 II 119 u. 120), zusammen mit *Peronoceras* cf. *desplacei*, *P.* sp. ex gr. *P. subarmatum* und *Harpoceras* cf. *chrysanthemum*.

Maße:

	d	N	H	Q
B. St. M. 1978 II 119	3,22	45	29,5	0,51
120				ca. 0,55

Beschreibung: Beide Exemplare sind unvollständig und können deshalb nur mit Vorbehalt *P. choffati* zugeordnet werden. Bei Exemplar B. St. M. 1978 II 119 (Taf. 4, Fig. 5) ist nur die äußere Windung erhalten, die den für *P. choffati* typischen Windungsquerschnitt zeigt. Das zweite Exemplar B. St. M. 1978 II 120 ist mit ca. 125° der Windungen (ohne die innersten) erhalten. Der Querschnitt wurde poliert (Taf. 4, Fig. 6), die Flanken konnten jedoch nicht gut präpariert werden. Der Wert von Q liegt mit ca. 0,55 etwas höher als bei *P. choffati*. Soweit erkennbar, zeigen beide Exemplare fibulate Berippung. Die Flanken- und Externrippenzahl ist kleiner als bei *P. choffati*. Die fibulaten Rippenpaare endigen in einem deutlichen Knoten (bzw. Stachel bei dem angeschliffenen Exemplar), und von diesem gehen 3 bis 4 Externrippen aus. Den fibulaten Rippen können einfache oder gegabelte Rippen (ohne Knoten) zwischengeschaltet sein. Bei Exemplar B. St. M. 1978 II 119 muß es sich um einen Teil der Wohnkammer handeln, da keine Lobenlinie erkennbar ist. Das zweite Exemplar ist bis zu seinem Ende gekammert.

Verbreitung: Aus der Faunenliste von Renz (1912) ist schwer zu ermitteln, welcher Faunenzone der Holotypus von *P. choffati* entstammt. Mouterde (1967) und Gabilly et al. (1971) geben *P. choffati* aus der *serpentinus*-Zone von Portugal an, die der *falcifer*-Zone entspricht. *Peronoceras crassicostatum* kommt nach Guex (1972) im oberen Teil der *bifrons*-Subzone vor.

3.3.6 *Peronoceras pacificum* n. sp.

Taf. 4, Fig. 9, 11–16, Taf. 5, Fig. 1, 2; Abb. 17e, 19a

1966 *Peronoceras vorticellum* (Simpson) 1855. – Fischer, S. 41, Taf. 2, Fig. 2, Taf. 6, Fig. 8.

Holotypus (B. St. M. 1978 II 125): Leicht verdrückter Phragmokon (vorwiegend Schalenerhaltung) mit $^3/_4$ Windung Wohnkammer (Taf. 4, Fig. 13).

Derivatio nominis: Nach dem Vorkommen im Bereich des Pazifik.

Locus typicus: Quebrada Potrerillos (Abb. 1, Profil 10); topogr. Karte 1 : 100000, Blatt Carrera Pinto: x = 444,25 km, y = 6976,4 km.

Stratum typicum: Fossilschicht in gebankten Kalken mit schiefrigen Mergellagen.

Fauna: *Peronoceras pacificum*, *P.* cf. *verticosum*, *Harpoceras* sp., *Maconiceras* sp.

Der nächste Fossilhorizont im Liegenden feinschichtige Kalke mit *Pectinula cancellata.* Im Hangenden weiterhin gut gebankte Kalke mit schiefrigen Zwischenlagen. Oberster Abschnitt der Serie mit wenige Meter mächtigen, mehr knolligen Kalken und *Phymatoceras.*

Altersstellung: Mittleres Toarcium, Zone des *Hildoceras bifrons,* Subzone des *Peronoceras pacificum* (= tieferer Teil der *bifrons-* bzw. *fibulatum*-Subzone in Europa).

Diagnose: Gehäuse mittelwüchsig, weitnabelig und scheibenförmig. Windungsquerschnitt subquadratisch. Flankenrippen dichtstehend, vorwiegend rectoradiat. Phragmokon und erste Hälfte der Wohnkammer jede zweite Flankenrippe mit Stachel (bzw. Knoten). Fibulate Flankenrippen z. T. auf Wohnkammer vorhanden, am Ende vorwiegend Einzelrippen. Knoten (bzw. Stachel) Spaltpunkt für 2 bis 3 Externrippen, selten Zick-Zack-Muster.

Material: a) Am Locus typicus wurden außer dem Holotypus ein unvollständiges Exemplar (B. St. M. 1978 II 126) (Abb. 19a, Taf. 4, Fig. 16) (parallel zur Windungsachse halbiert, äußerer Umgang Wohnkammer), ein weiteres unvollständiges Exemplar (B. St. M. 1978 II 127) (Taf. 4, Fig. 12) (Außenskulptur der Wohnkammer nicht erhalten) und Windungsbruchstücke gefunden.

b) Quebrada Yerbas Buenas (Abb. 6), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 439,55 km, y = 6979,3 km. 3 Wohnkammerexemplare (B. St. M. 1978 II 121 bis 123) (Taf. 4, Fig. 9, 11, 15), z. T. mit Resten der Schale, Phragmokon mit Kalzit ausgefüllt und unregelmäßig gespalten; ein kleines Exemplar (nur Externseite freipräpariert) (B. St. M. 1978 II 124) (Taf. 4, Fig. 14), Windungsbruchstücke. Zusammen mit *Peronoceras* cf. *verticosum, Maconiceras* sp. und *Polyplectus* sp.

c) Quebrada El Bolito (Abb. 5), topogr. Karte 1:100000, Blatt Laguna del Negro Francisco: x = 458,4 km, y = 6995,5 km. 2 Wohnkammersteinkerne (B. St. M. 1978 II 128 und 129) (Taf. 5, Fig. 1, 2), letzte Windung des Phragmokons mit Kalzitresten, sonst flachgepreßt. Zusammen mit *Harpoceras* sp., *Maconiceras* sp., *Polyplectus* sp.

Maße:

	d	N	H	Q	Z
B. St. M. 1978 II 121	3,85 cm	52	26		
122	4,4	55	25	0,9	
123	4,15	53	26,5	1,0	
	3,6	50	27,8	0,9	
126	4,93	57,5	23,3	1,1	
	3,95	52,5	25,3	ca. 1,1	
	3,0	50,0	ca. 29	1,05	
128	4,8	55,5	24	ca. 0,9	59
129	5,2	53	26,5	0,92	60

Beschreibung: Die scheibenförmigen Gehäuse sind stark evolut, und die Windungen umfassen sich nur wenig. Der Windungsquerschnitt ist wenig breiter als hoch bis wenig höher als breit. Die Externseite ist etwas gewölbt. Während der Ontogenie wird der Q-Wert größer. Die innersten Windungen sind glatt. Als erstes erscheinen am Außenrand der Flanken kleine Stacheln, ab einer Nabelweite von ca. 1 mm allmählich Flankenrippen (Taf. 4, Fig. 16, c).

Die Flankenrippen stehen vorwiegend rectoradiat, am Ende der Wohnkammer leicht retroradiat. Auf dem Phragmokon (ab n 2,5 mm) und ersten Hälfte der Wohnkammer trägt jede zweite Flankenrippe einen Knoten (Steinkern) oder langen Stachel (Schale). Fibulate Flankenrippen können am Ende der ersten Hälfte der Wohnkammer auftreten. Auf der zweiten Hälfte der Wohnkammer werden Rippen ohne Knoten zunehmend häufiger. Von den Knoten gehen zwei, selten drei Spaltrippen aus, die auf der Externseite leicht nach vorn gebogen sind. Ein Zick-Zack-Muster ist nur selten vorhanden. Die Rippen ohne Knoten spalten zumeist nicht auf.

Die Lobenlinie konnte bei keinem der Exemplare gezeichnet werden.

Vergleiche: *Peronoceras vorticellum* (Simpson) ist sehr ähnlich, besitzt jedoch einen etwas breiteren Windungsquerschnitt, und die Windungshöhe ist im Verhältnis zum Durchmesser kleiner. Bei *Peronoceras krumbecki* (Monestier) beträgt das Verhältnis von Windungshöhe zu Windungsbreite 1,5 bis 1,6 und ist somit größer als bei *P. pacificum.*

Gute Übereinstimmung besteht zu dem von Fischer (1966) unter *P. vorticellum* abgebildeten Exemplar, das einen ähnlichen Windungsquerschnitt (Taf. 2, Fig. 2) wie die im chilenischen Lias gefundenen Exemplare besitzt.

Bemerkungen: *Peronoceras pacificum* gehört in den Formenkreis von *P. vorticellum.* Nach Fischer (1966) steht *Peronoceras vorticellum* am Anfang einer morphologischen Reihe, die von dieser Art über *P. verticosum* zu *P. vortex* führt. Pinna & Levi-Setti (1971) stellen *P. verticosum* und *P. vorticellum* zur Gattung *Nodicoeloceras* und halten die Unterschiede zwischen beiden Arten für gering, während *P. vortex* unter der Gattung *Peronoceras* aufgeführt wird. Howarth (1973) beobachtete in der *braunianus*-Zone von Yorkshire eine kontinuierliche Variation zwischen *P. vorticellum, P. verticosum* und *P. vortex.* Die Holotypen von *P. vorticellum* und *P. verticosum* unterscheiden sich hauptsächlich durch die verschiedene Gehäusegröße, was durch Dimorphismus bedingt sein könnte.

Guex (1973) hält die von ihm als *Collina* gr. *gemma* und *Porpoceras* gr. *verticosum* bezeichneten Exemplare für ein dimorphes Paar. Schmidt-Effing (1975) wies darauf hin, daß zwischen beiden ,,Arten" keine morphologischen Unterschiede bestehen, abgesehen vom Größenunterschied. Beide ,,Arten" müßten also zumindest der gleichen Gattung, wenn nicht auch der gleichen Art zugeordnet werden. Die von Guex (1972) als *Collina gemma* und Guex (1973) als *C.* gr. *gemma* bezeichneten Exemplare stimmen nicht mit *Collina gemma* Bonarelli (Holotypus neu abgebildet bei Gallitelli Wendt 1969, Taf. 6, Fig. 3 a–c) überein. Es fehlt ihnen vor allem die für diese Gattung und Art typische, kielartige Erhöhung auf der Externseite. Die von Guex (1972, 1973) abgebildeten Exemplare sind zu *Peronoceras* zu stellen und gehören in die Gruppe *vorticellum-verticosum-vortex* dieser Gattung.

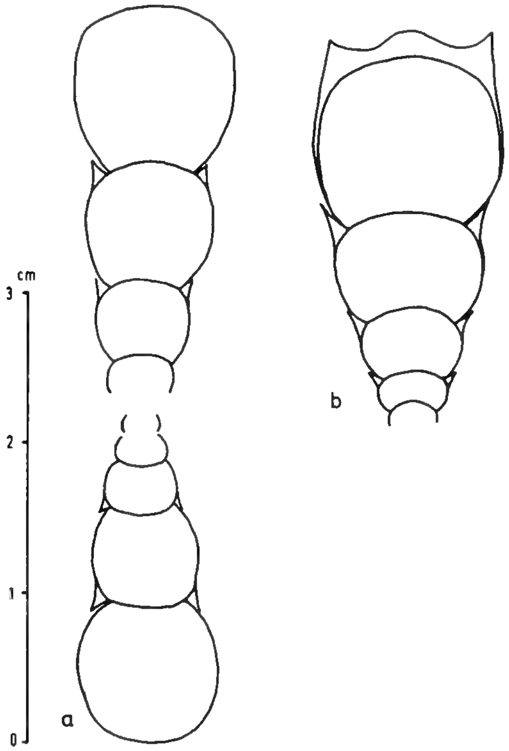

Abb. 19: Windungsquerschnitte a: *Peronoceras pacificum* n. sp.; Quebrada Potrerillos; B. St. M. 1978 II 126. b: *Collina* sp.; Quebrada Larga; B. St. M. 1978 II 209.

3.3.7 *Peronoceras* cf. *verticosum* (Buckman, 1914)

Taf. 5, Fig. 3, 5

cf. 1914 *Porpoceras verticosum,* nov. – Buckman, Taf. 91 (Holotypus).

Bemerkungen siehe *Peronoceras pacificum.*

Material: a) Quebrada Yerbas Buenas (Abb. 6), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 439,55 km, y = 6979,3 km. Ein Wohnkammersteinkern (Phragmokon mit Kalzit ausgefüllt und unregelmäßig gespalten) (B. St. M. 1978 II 130 [Taf. 5, Fig. 5]); ein Windungsbruchstück. Faunenvergesellschaftung siehe bei *P. pacificum.*

b) Quebrada Potrerillos (Abb. 1, Profil 10), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 444,25 km, y = 6976,4 km. Ein stark verdrücktes Exemplar mit Teilen der Wohnkammer und teilweise erhaltenem Phragmokon (B. St. M. 1978 II 131); Windungsbruchstücke. Faunenvergesellschaftung wie bei *P. pacificum.*

c) Quebrada Paipote bei Redonda (Abb. 4), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 436,3 km, y = 6996,55 km. Ein Wohnkammersteinkern (Phragmokon nicht erhalten), der nur mit Vorbehalt zu dieser Art gestellt werden kann (B. St. M. 1978 II 132) (Taf. 5, Fig. 3) und auch zu *Peronoceras* cf. *vortex* gehören könnte. Zusammen mit *Peronoceras* cf. *bolitoense* n. sp. und *Collina* cf. *chilensis* n. sp. Aus annähernd gleichaltem Horizont im Streichen des gleichen Profils *Collina chilensis* n. sp., Hildoceratidae gen. et sp. indet. (2 Arten).

d) Quebrada El Asiento (Abb. 2, Profil 3), topogr. Karte 1:100000, Blatt Potrerillos: x = 467,5 km, y = 7070,45 km. 2 Wohnkammersteinkerne (Phragmokon nicht erhalten) (B. St. M. 1978 II 133 u. 134). Beide Exemplare wurden aus etwa 15 m mächtigen Knollenkalken gesammelt, die auch *Peronoceras* cf. *subarmatum* sowie *Harpoceras* sp. enthalten.

Die gleichen Schichten treten durch eine tektonisch bedingte Verdoppelung in dem gleichen Profil zweimal auf. Von x = 467,4 km und y = 7070,4 km stammt deshalb ein weiterer Wohnkammersteinkern (B. St. M. 1978 II 135).

Maße:

	d	N	H	Q	Z
B. St. M. 1978 II 130	8,55 cm	56	24,5		
	7,0	54	25,7	0,88	ca. 70
132	8,5	59	27	0,8	

Beschreibung: Die flachen Gehäuse sind weitnabelig. Nur bei dem verdrückten Exemplar von der Quebrada Potrerillos ist ein Teil des Phragmokons vorhanden, bei allen übrigen Exemplaren ist nur die Wohnkammer erhalten, die bei dem Exemplar aus der Quebrada Yerbas Buenas eine Länge von zumindest 420° besitzt. Der abgerundet-rechteckige Windungsquerschnitt ist etwas breiter als hoch. Die Externseite und die Flanken sind etwas gewölbt. Auf dem Phragmokon (innerste Umgänge bei keinem Exemplar erhalten) und zu Beginn der Wohnkammer trägt jede zweite der rectoradiaten Flankenrippen einen Knoten (Steinkern) oder Stachel (Schale). Fibulate Rippen sind auf den ersten 90° der Wohnkammer zumeist selten, treten dann regelmäßig auf und verschwinden wieder am Ende der Wohnkammer. Zwischen den fibulaten Rippenpaaren liegen 1 bis 2 Flankenrippen ohne Knoten. Von den Einfachrippen mit Knoten gehen zwei, von den fibulaten Rippen zwei bis drei Spaltrippen aus. Besonders die jeweils vorderste Spaltrippe ist auf der Externseite leicht nach vorn gebogen. Die Flankenrippen ohne Knoten bleiben zumeist einfach, manchmal spalten sie auch in zwei Externrippen auf. Zumindest nach 390° Wohnkammer (B. St. M. 1978 II 130) treten vorwiegend Einfachrippen auf, die nicht mehr aufspalten. Ein Zick-Zack-Muster ist auf der Externseite nur selten vorhanden.

Die Lobenlinie konnte bei keinem der untersuchten Exemplare beobachtet werden.

Vergleiche: Das Verhältnis von Nabelweite zu Gehäusedurchmesser (N) ist bei *Peronoceras verticosum* etwas größer, bedingt durch die weniger schnell anwachsende Windungshöhe. Der Windungsquerschnitt ist sehr ähnlich.

Verbreitung: Die Verbreitung in Europa ist die gleiche wie bei *Peronoceras vorticellum.*

3.3.8 *Peronoceras* sp. cf. *P.* cf. *verticosum* BUCKMAN, 1914)

Taf. 5, Fig. 6; Abb. 17h

Material: Quebrada Yerbas Buenas (Abb. 6), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 439,55 km, y = 6979,3 km. Ein Exemplar (B. St. M. 1978 II 136).

Maße:

d	N	H	Q	Z
4,9	54	25,5	0,8	60
4,55	52,5	26,5	0,76	58
4,1	49	27	0,76	51

Beschreibung: Von der gleichen Fundschicht, in der *Peronoceras* cf. *verticosum* gefunden wurde, liegt ein Exemplar vor, das sich von dieser Art durch die geringere Größe, den etwas breiteren Windungsquerschnitt und das Fehlen von fibulaten Rippen auch auf der Wohnkammer unterscheidet.

Der mit Kalzit ausgefüllte Phragmokon endet wahrscheinlich etwas vor Beginn des letzten Umgangs, der als Steinkern mit Schalenresten vorliegt und mit Sediment ausgefüllt ist. Soweit erkennbar, ist ab einer Nabelweite von ca. 4 mm auf dem Phragmokon und zu Beginn der Wohnkammer jede zweite rectoradiate Flankenrippe mit einem Stachel oder Knoten versehen. Auf der zweiten Hälfte des letzten Umgangs liegen zwischen den leicht rectoradiaten Flankenrippen zuerst 2, dann 3 und am Ende 4 Rippen ohne Knoten. Die Rippen mit Knoten oder jede zweite Flankenrippe spaltet in 2, selten 3 Externrippen auf, die vordere leicht nach vorn gebogen. Auf der zweiten Hälfte des letzten Umgangs bleiben zunehmend 2, am Ende auch 3 aufeinander folgende Flankenrippen einfach.

3.3.9 *Peronoceras* cf. *vortex* (Simpson, 1855)

Taf. 5, Fig. 4, 7, 8; Taf. 6, Fig. 1

cf. 1911 *Porpoceras vortex*, Simpson sp. – Buckman, Taf. 29 A (Holotypus) 29 B.
cf. 1930 *Deroceras subarmatum* Y. et B. – Rigal, S. 7, Taf. 2, Fig. 4.
cf. 1976 *Peronoceras vortex* (Simpson 1855). – Schlegelmilch, S. 79, Taf. 40, Fig. 2 (Holotypus).
Bemerkungen siehe bei *Peronoceras pacificum*.

Material: a) Quebrada Cortaderita (Abb. 1, Profil 8), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 435,05 km, y = 6988,2 km. Ein Steinkernexemplar (B. St. M. 1978 II 137) (Taf. 5, Fig. 7) mit Schalenresten auf dem teilweise angebrochenen und mit Kalzit ausgefüllten Phragmokon; ein Steinkernexemplar (B. St. M. 1978 II 138) (Taf. 5, Fig. 8) mit zwei unvollständig erhaltenen äußeren Windungen. Zusammen mit *Peronoceras* cf. *bolitoense* n. sp., *Collina chilensis* n. sp., *Harpoceras* cf. *subexaratum*, *Phymatoceras* ex gr. *P. erbaense*, Hildoceratidae gen. et sp. indet.

b) Quebrada Llareta (Abb. 1, Profil 13), topogr. Karte 1:100000, Blatt La Guardia: x = 438,6 km, y = 6957,5 km. Ein senkrecht zur Aufrollungsachse verdrückter Steinkern (B. St. M. 1978 II 139) (∅ ca. 8 cm) mit etwas mehr als ein Umgang langer Wohnkammer, ein Phragmokonsteinkern (B. St. M. 1978 II 140) (Taf. 5, Fig. 4) von 2,5 cm Durchmesser und weitere, unvollständige, verdrückte Exemplare (B. St. M. 1978 II 141 und 142) können nur mit Vorbehalt zu dieser Art gestellt werden. Zusammen mit *Maconiceras* sp., *Polyplectus* sp., *Phymatoceras* sp.

c) Quebrada Paipotito (Abb. 1, Profil 4), topogr. Karte 1:100000, Blatt Inca de Oro: x = 441,2 km, y = 7013,65 km. Ein Wohnkammerexemplar mit etwas mehr als 1¼ Umgängen, seitlich vermutlich stark komprimiert, aber nur mit Vorbehalt zu dieser Art zu stellen (B. St. M. 1978 II 143) (Taf. 6, Fig. 1).

d) Quebrada El Hueso/Quebrada Cienaga (Abb. 2, Profil 1), topogr. Karte 1:100000, Blatt Salar de Maricunga: x = 463,9 km, y = 7065,6 km. Ein Steinkernexemplar (B. St. M. 1978 II 144) (ca. 7,8 cm ∅) kann nur mit Vorbehalt zu dieser Art gestellt werden. Die inneren Umgänge sind nicht erhalten. Fibulate Rippen treten besonders am Ende des letzten Umgangs auf. Der Windungsquerschnitt ist weniger breit als bei *P.* cf. *vortex*.

e) Rio Jorquera (Vegas de Chañar) (Abb. 1, Profil 14a), topogr. Karte 1:100000, Blatt La Guardia: x = 435,1 km, y = 6931,1 km. Ein Steinkernexemplar (B. St. M. 1978 II 145) (8,4 cm ∅), dessen äußerer Umgang nicht gekammert ist. Die inneren Umgänge sind nicht erhalten. Fibulate Rippen treten am Ende des letzten Umgangs auf. Das Exemplar kann nur mit Vorbehalt zu dieser Art gestellt werden, da der Windungsquerschnitt weniger breit ist. Die Flankenrippenzahl gleicht jedoch weitgehend der von *P.* cf. *vortex*.

Maße:

	d	N	H	Q	Z
B. St. M. 1978 II 137	7,75	55	23	0,72	ca. 59
B. St. M. 1978 II 138	11,25	58	20,5	0,76	
	9,75	57,5	22,0	0,72	
B. St. M. 1978 II 140	2,5	48	28	0,78	33
B. St. M. 1978 II 143	12,0	60	21		
B. St. M. 1978 II 144	7,8	52	25	0,82	65
B. St. M. 1978 II 145	8,4	52,5	25	0,89	

Beschreibung: Das flache Gehäuse ist weitgenabelt. Der Windungsquerschnitt ist breiter als hoch. Die Externseite und die Flanken sind gewölbt. Das kleine Exemplar von der Quebrada Llareta (B. St. M. 1978 II 140) besitzt erst ab einem Nabeldurchmesser von ca. 1 mm Flankenrippen, vorher sind kleine Stacheln zu beobachten, die sich am Außenrand der Flanken befinden. Ab einem Nabeldurchmesser von ca. 2,5 mm ist nur noch jede zweite Rippe mit einem Stachel versehen. Bei dem kleineren Exemplar aus der Quebrada Cortaderita trägt – soweit sichtbar – jede zweite der recto- bis leicht retroradiaten Flankenrippen einen Knoten, von dem 2, selten 3 Externrippen ausgehen, die gerade (selten leicht nach vorn gebogen) die Externseite überqueren. Die Rippen zwischen den Knotenrippen spalten zumeist nicht auf. Bei dem größeren Exemplar aus der Quebrada Cortaderita und dem Exemplar aus der Quebrada Paipotito sind besonders auf dem letzten Umgang zahlreiche fibulate Rippen vorhanden. Bei dem kleineren Exemplar aus der Quebrada Cortaderita ist der letzte Umgang mit Sediment ausgefüllt, und es ist keine Kammerung mehr zu erkennen. Wahrscheinlich handelt es sich um den ersten Umgang der Wohnkammer. Bei dem größeren Exemplar endet die Kammerung zu Beginn des erhaltenen, vorletzten Umgangs. Die Wohnkammer würde demnach bei diesem Exemplar eine Länge von mehr als 1½ Windungen besitzen.

Die Lobenlinie konnte bei keinem Exemplar beobachtet werden.

Vergleiche: *Peronoceras vortex* ist noch etwas weitnabeliger und das Verhältnis von Windungshöhe zu Windungsbreite etwas kleiner. Die Flanken der in Chile gefundenen Exemplare sind stärker gewölbt. Auch bei *P. vortex* erscheinen die fibulaten Rippen sehr spät.

Verbreitung: Die Verbreitung von *P. vortex* in Europa ist die gleiche wie von *P. vorticellum* und *P. verticosum*.

3.3.10 *Peronoceras bolitoense* n. sp.
Taf. 6, Fig. 2, 4–6; Abb. 17b, g, 18b, 20, 21

Holotypus (B. St. M. 1978 II 146): Teils als Steinkern, teils als Schalenexemplar erhalten, letzter Umgang Wohnkammer, diese am Ende etwas seitlich verdrückt (Taf. 6, Fig. 5; Abb. 17b).

Derivatio nominis: Nach dem Vorkommen in der Quebrada El Bolito.

Locus typicus: Quebrada El Bolito (Prov. Atacama) (Abb. 5); topogr. Karte 1:100000, Blatt Laguna del Negro Francisco: x = 456,5 km, y = 6994,5 km.

Stratum typicum: Etwa 1 m mächtige, in sich 10 bis 20 cm gebankte Knollenkalke mit großwüchsigen Peronoceraten (zumeist nur Wohnkammer erhalten, Phragmokon hohl), zwischen den Bänken weichere Lagen mit verdrückten Peronoceraten. An der Basis der Knollenkalke eine knollige, kalkig-mergelige Schicht (rötlich) mit zum Teil sehr gut erhaltenen Ammoniten (vorwiegend *Peronoceras* und *Collina*).

Fauna: *Peronoceras bolitoense* n. sp., *Collina chilensis* n. sp., *Harpoceras* sp., *Maconiceras* sp., *Phymatoceras* sp., Hildoceratidae gen. et sp. indet. (glatte Art).

Im Liegenden der Knollenkalke Mergel mit *Peronoceras* cf. *vorticellum*, *Harpoceras* sp., *Maconiceras* sp., *Polyplectus* sp. Im Hangenden 10 bis 20 cm gebankte Kalke mit *Phymatoceras* cf. *erbaense* (Hauer), Hildoceratidae gen. et sp. indet. (2 Arten mit retroklinen Rippen).

Altersstellung: Mittleres Toarcium, Zone des *Hildoceras bifrons*, Subzone der *Collina chilensis*, Horizont mit *Peronoceras bolitoense*.

Die Fauna mit *P. bolitoense* n. sp. ist gleichaltrig mit dem oberen Teil der Subzone des *Hildoceras bifrons* oder tieferen Teil der Subzone des *Hildoceras semipolitum* (Zone des *Hildoceras bifrons*) (Gabilly et al. 1971) in Europa.

Diagnose: Gehäuse großwüchsig, weitnabelig und scheibenförmig. Windungsquerschnitt rundlich bis subquadratisch, dicht berippt, besonders auf der Wohnkammer. Rippenzahl pro Umgang während der Ontogenie stark zunehmend. Auf dem Phragmokon jede zweite Flankenrippe mit Stachel versehen. Fibulate Rippen nur auf der Wohnkammer, ihnen 2 bis 4 Einzelrippen ohne Knoten zwischengeschaltet. Am Ende der Wohnkammer ungespaltene Einzelrippen vorherrschend.

Material: a) Am locus typicus wurden außer dem Holotypus 3 weitere Exemplare sowie ein Windungsbruchstück gefunden. Exemplar B. St. M. 1978 II 147 (Taf. 6, Fig. 4; Abb. 17g) ist nur halb erhalten und wurde zur Ermittlung des Windungsquerschnittes angeschliffen. Exemplar B. St. M. 1978 II 148 (∅ 11 cm) ist seitlich komprimiert, und die inneren Umgänge sind nur als Abdruck erhalten. Bei Exemplar B. St. M. 1978 II 149 sind nur 2 Umgänge des Phragmokons und diese unvollständig erhalten. Das Windungsbruchstück (ca. $^1/_3$ Windung) (B. St. M. 1978 II 150) besteht aus zwei äußeren, ungekammerten Windungen.

b) Rio Manflas (Department Copiapó, Prov. Atacama), Profil zwischen dem Rio Manflas und dem Portezuelo El Padre (70°0,9′ Länge, 28°11,8′ Breite) (Abb. 1, Profil 16): Ein kleines Exemplar (∅ 3 cm) mit gut erhaltenen Innenwindungen (B. St. M. 1978 II 151) (Taf. 6, Fig. 6), zusammen mit Windungsbruchstücken von *Peronoceras* sp., *Collina* cf. *chilensis* n. sp., *Polyplectus* sp., Hildoceratidae gen. et sp. indet. (glatte Art).

c) Quebrada Cortaderita (Abb. 1, Profil 8), topogr. Karte 1 : 100000, Blatt Carrera Pinto : x = 435,05 km, y = 6988,2 km. Ein unvollständig erhaltener Steinkern mit Resten der Wohnkammer B. St. M. 1978 II 152 (Taf. 6, Fig. 2; Abb. 18b) kann nur mit Vorbehalt zu der neuen Art gestellt werden.

Zusammen mit *Peronoceras* cf. *vortex*, *Collina* cf. *chilensis* n. sp., *Harpoceras* cf. *subexaratum*, *Phymatoceras* ex gr. *P. erbaense*, Hildoceratidae gen. et sp. indet.

Maße:

	d	N	H	Q	Z
Holotypus B. St. M. 1978 II 146	8,6 cm	58	—	—	109
	7,7	55	23,5	ca. 0,95	93
	6,0	52,5	25	0,9	63
	5,5	51,5	26,5	0,9	57
Paratypus B. St. M. 1978 II 147	8,9 cm	58	23,5	0,95	
	7,1	55	24,5		
	5,6	50,5	27,7	0,86	
	4,2	48	28,5	1,0	
Paratypus 148	ca. 6,5	54	27		
Paratypus 151	3,0	48	29,5	0,8–0,85	40
	2,65	47,5	31,0	ca. 0,9	38
	2,3	46	30,5	0,83	37
	ca. 1,65	43	31,5	0,71	35
Paratypus 152	ca. 5,6	53,5	25,0	0,78–0,75	
	ca. 3,2	47,0	31	0,73	37
	ca. 2,35	45,0	ca. 32	0,73	33

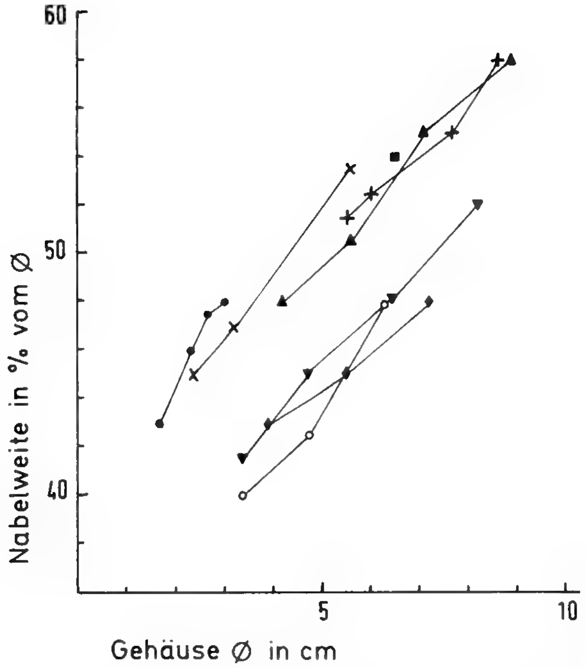

Abb. 20: Änderung der relativen Nabelweite im Verlauf der Ontogenie bei *Peronoceras bolitoense* n. sp. und *Peronoceras* cf. *bolitoense* n. sp. *Peronoceras bolitoense* n. sp.: × B. St. M. 1978 II 152, ● B. St. M. 1978 II 151, ■ B. St. M. 1978 II 149, + B. St. M. 1978 II 146, ▲ B. St. M. 1978 II 147. *Peronoceras* cf. *bolitoense* n. sp.: ▼ B. St. M. 1978 II 154, ♦ B. St. M. 1978 II 153, ○ B. St. M. 1978 II 155.

Beschreibung des Holotypus: Die innersten Windungen sind nicht erhalten. Die abgebildete Seite des Phragmokons (Taf. 6, Fig. 5) liegt in Schalenerhaltung vor und ist mit Kalzit ausgefüllt. Die mit einem Umgang vorhandene Wohnkammer ist ein Steinkern mit Schalenresten. Besonders die letzten 110° der Wohnkammer sind seitlich etwas verdrückt. Das Gehäuse ist weitnabelig und scheibenförmig, der Nabel wenig eingesenkt. Der Windungsquerschnitt ist rundlich, am Ende der erhaltenen Wohnkammer subquadratisch.
Das Gehäuse, besonders die Wohnkammer, ist dicht berippt. Die Anzahl der rectoradiaten Flankenrippen pro Umgang nimmt während der Ontogenese stark zu (Abb. 21). Auf dem Phragmokon (soweit sichtbar) ist jede zweite Flankenrippe mit einem Stachel versehen, der sich an den folgenden Umgang anlehnt. Die Stachellänge kann bis $^1/_3$ der Flankenhöhe betragen. Auf der ersten Hälfte der Wohnkammer sind die Rippen schlecht zu erkennen, auf der zweiten Hälfte sind fibulate Rippenpaare mit Knoten vorhanden. Kurz vor Erreichen der Naht sind die sonst rectoradiaten Flankenrippen nach vorn gebogen. Zwischen den fibulaten Rippen stehen 2 bis 4 Einzelrippen. Die fibulaten Rippenpaare spalten in 2 bis 3 Externrippen auf. Die Einzelrippen bleiben einfach, soweit erkennbar. Der Verlauf der Externrippen ist gerade.

Die Lobenlinie konnte nicht ermittelt werden.

Beschreibung der Paratypen: Die relative Nabelweite (N) wird während der Ontogenese allmählich größer (Abb. 20) und die relative Windungshöhe (H) allmählich kleiner.

Der Windungsquerschnitt ist bei den ersten Windungen des Phragmokons etwas breiter als hoch, wird dann rundlich und ist auf der zweiten Hälfte der Wohnkammer subquadratisch, da hier die Flanken weniger stark gewölbt sind. Die Externseite ist jedoch weiterhin stark gewölbt (Abb. 17b, g).

Auf dem Phragmokon sind Vollrippen vorhanden. Zumindest am Ende der Wohnkammer liegen Hohlrippen vor. Die ersten Umgänge sind glatt. Bei einer Nabelweite von 1,5 mm erscheinen dicht unterhalb der Naht kleine, spitze Knoten, die erst ab einer Nabelweite von 2 mm mit retroradiaten Flankenrippen verbunden sind. Jede der Flankenrippen trägt zunächst einen Stachel. Allmählich wird jedoch jeder zweite Stachel kleiner, und ab einer Nabelweite von 5,5 mm ist nur noch jede zweite, nunmehr rectoradiate Flankenrippe mit einem kräftigen Stachel versehen. Am Ende des vorletzten Umgangs des Phragmokons sind bei Exemplar B. St. M. 1978 II 149 die Stacheln (Schalenerhaltung) wieder kleiner (Länge ca. 2 mm). Auf Steinkernexemplaren können die entsprechenden Knoten, besonders am Ende des Phragmokons und zu Beginn der Wohnkammer, schwach entwickelt sein. Bei Exemplar B. St. M. 1978 II 148 treten einzelne fibulate Rippen etwa 90° nach Beginn der Wohnkammer auf, und die fibulate Berippung reicht bis kurz vor das Ende des 1. Umgangs der Wohnkammer. Zwischen den fibulaten Rippen liegt zu-

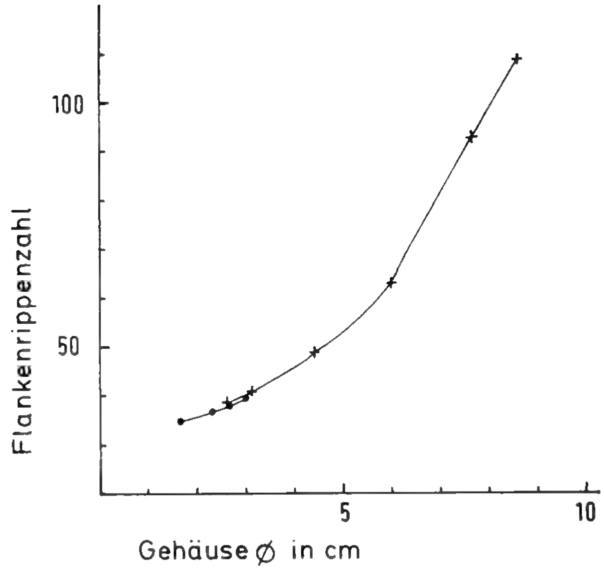

Abb. 21: Änderung der Flankenrippenzahl im Verlauf der Ontogenie bei *Peronoceras bolitoense* n. sp.: + B. St. M. 1978 II 146 (Holotypus), ● B. St. M. 1978 II 151.

erst eine Flankenrippe ohne Knoten, dann sind es 2, 3 und am Ende bis zu 4 Einfachrippen. Zumindest ab Ende des 1. Umgangs der Wohnkammer sind keine Knoten mehr ausgebildet und Gabelrippen treten gegenüber Einzelrippen zunehmend zurück. Bei Exemplar B. St. M. 1978 II 147 (Taf. 6, Fig. 4) kommen auf 25 Flankenrippen 28 Externrippen (1. Hälfte des zu 120° erhaltenen äußeren Umgangs). Die Flankenrippen nehmen dann eine rectoradiate bis leicht retroradiate Richtung ein. In Höhe des Spaltpunktes können sie etwas retroklin werden. Auf der Externseite verlaufen die Rippen auf dem größten Teil des Phragmokons und der Wohnkammer vorwiegend gerade. Bei Exemplar B. St. M. 1978 II 151 (3 cm ∅) (Taf. 6, Fig. 6) gehen von einem Knoten oder Stachel 2 bis 3 Externrippen aus, wobei die vorderste Externrippe nach vorn gebogen sein kann. Die zwischen den Stachelrippen gelegenen Rippen bleiben einfach oder sie sind bifurkat gespalten. Ein ausgeprägtes Zick-Zack-Muster besteht nicht.

Exemplar B. St. M. 1978 II 152 (Taf. 6, Fig. 2) unterscheidet sich von den Exemplaren der Quebrada El Bolito durch eine etwas größere Windungsbreite, die zwischen der von *Peronoceras bolitoense* n. sp. und der von *P.* cf. *vortex* liegt.

Bei diesem Exemplar konnte die äußere Lobenlinie gezeichnet werden (Abb. 18b). Der Laterallobus ist etwas kürzer als der Externlobus. Der Umbilikallobus U_2 ist dreispitzig.

Vergleiche: *Peronoceras bolitoense* n. sp. unterscheidet sich von *P. vortex* und *P. verticosum* vor allem durch die dichtere Berippung auf der Wohnkammer. Die Windungsbreite ist bei *P. vortex* größer und die Gehäusegröße bei *P. verticosum* kleiner. Die Windungshöhe nimmt bei *P. bolitoense* n. sp. schneller zu als bei den genannten Arten. *Catacoeloceras (? = Peronoceras) tuberculatum* Kottek (nach Pinna & Levi-Setti 1971 = *Nodicoeloceras (? = Peronoceras) angelonii* (Ramaccioni) ist ebenfalls ähnlich. Diese Art ist jedoch ebenfalls kleinwüchsiger, besitzt einen breiteren Windungsquerschnitt und eine geringere Rippenzahl pro Umgang.

3.3.11 *Peronoceras* cf. *bolitoense* n. sp.

Taf. 6, Fig. 3, Taf. 7, Fig. 3, 4; Abb. 17a, c

Material: a) Quebrada Yerbas Buenas (Abb. 6), topogr. Karte 1 : 100000, Blatt Carrera Pinto: x = 439,4 km, y = 6979,35 km. Phragmokon (teils Steinkern, teils Schalenexemplar) mit Beginn und verdrücktem Ende des 1. Umgangs der Wohnkammer B. St. M. 1978 II 153 (Taf. 7, Fig. 3; Abb. 17c). Zusammen mit *Collina chilensis* n. sp., *Peronoceras* sp. indet., *Maconiceras* sp., Hildoceratidae gen. et sp. indet. (glatte Art).

b) Juntas del Toro (Department Copiapó, Provinz Atacama), Profil auf der rechten Talseite, kurz unterhalb der Vereinigung von Rio Manflas und Rio del Toro (Abb. 10) (69°58,3′ Länge, 28°24,5′ Breite). Ein Phragmokon mit Resten der Wohnkammer (B. St. M. 1978 II 154) (Taf. 7, Fig. 4; Abb. 17a), ein zur Hälfte erhaltener Phragmokon (B. St. M. 1978 II 155) (Taf. 6, Fig. 3), sowie Windungsbruchstücke. Zusammen mit *Collina chilensis* n. sp., *Harpoceras* cf. *subexaratum*, *Phymatoceras* sp., Hildoceratidae gen. et sp. indet. (glatte Art und weitnabelige Art mit retroklinen Rippen).

c) Rio Manflas (Department Copiapó, Provinz Atacama), Profil 2,5 km südlich Los Graneros, zwischen dem

Fluß und dem Cerro Salto del Toro (Abb. 10) (69°58,5′ Länge, 28°19,7′ Breite). Ein weniger als zur Hälfte erhaltenes Exemplar (Ø 14 cm) mit verdrückten Innenwindungen (B. St. M. 1978 II 156). Gleicher lithostratigraphischer Horizont wie Profil Juntas del Toro.

d) Rio Pulido (Department Copiapó, Provinz Atacama), Profil südlich Iglesia Colorada auf der linken Talseite (Abb. 10) (69°53,2′ Länge, 28°9,8′ Breite). Mehrere Windungsbruchstücke (B. St. M. 1978 II 157 bis 159), die wahrscheinlich zu dieser Art gehören. Zusammen mit *Collina chilensis* n. sp., *Harpoceras* cf. *subexaratum*, Hildoceratidae gen. et sp. indet. (glatte Art).

e) Rio Jorquera (Vegas de Chañar) (Abb. 1, Profil 14a), topogr. Karte 1 : 100000, Blatt La Guardia: x = 435,1 km, y = 6931,1 km. 1 Windungsbruchstück (B. St. M. 1978 II 160), das wahrscheinlich zu dieser Art gehört. Zusammen mit *Peronoceras* cf. *P.* cf. *vortex*, *Collina chilensis*, *Harpoceras* cf. *subexaratum* und Hildoceratidae gen. et sp. indet. (glatte Art).

Maße:

	d	N	H	Q	Z
B. St. M. 1978 II 153	7,2 cm	48	27	0,85	68
	5,5	45	31	0,88	53
	3,9	43	32	ca. 0,8	
154	8,2 cm	52	24,4	0,87	ca. 70
	6,4	48	29,0	0,92	ca. 61
	4,7	45	32,0	0,88	ca. 58
	3,35	41,5	33,0	0,92	
B. St. M. 1978 II 155	6,35 cm	48	28	0,86	
	4,75	42,5	31,5	0,88	
	3,4	ca. 40	ca. 35	ca. 0,85	

Beschreibung: Die Gehäuse sind mäßig weitnabelig. Der Nabel ist wenig eingesenkt. Der rundliche bis subquadratische Windungsquerschnitt ist wenig breiter als hoch. Der Q-Wert verändert sich während der Ontogenese nur wenig. Das Exemplar von der Quebrada Yerbas Buenas zeigt bei einem Teil der Innenwindungen (Schalenerhaltung) kräftig ausgebildete Flankenrippen-Stachel, wobei jede zweite, manchmal jede dritte Flankenrippe einen Stachel trägt. Soweit erkennbar spalten die recto- bis leicht retrocostaten Flankenrippen mit Knoten (bzw. Stacheln) in vorwiegend 2 Externrippen auf. Die Flankenrippen ohne Knoten bleiben zumeist einfach. Die Externrippen überqueren die Externseite gerade. Fibulate Rippenpaare sind bei diesem Exemplar nicht zu erkennen. Es fehlt allerdings der größte Teil der Wohnkammer, und die Rippen sind nur auf dem kurzen, erhaltenen Anfangsteil der Wohnkammer gut zu beobachten. Am Ende des 1. Umgangs der Wohnkammer stehen die Flankenrippen sehr dicht.

Die beiden Exemplare von Juntas del Toro sind etwas weniger engnabelig als das Exemplar von der Quebrada Yerbas Buenas. Der Windungsquerschnitt ist ähnlich und etwas weniger breit. Bei dem größeren Exemplar ist ein Teil der Wohnkammer erhalten. Die Rippen sind nur bei dem kleineren Exemplar gut zu erkennen (Taf. 6, Fig. 3). Vorwiegend jede zweite Flankenrippe trägt einen Stachel und spaltet in 2, manchmal 3 Externrippen auf. Die Schaltrippen bleiben einfach, oder sie sind ebenfalls als Gabelrippen ausgebildet. Auf dem erhaltenen Teil des letzten Umgangs stehen die Flankenrippen dicht und biegen von der abgerundeten Nabelkante nach vorn zur Naht hin um.

Das Exemplar (B. St. M. 1978 II 156) vom Profil südlich Los Graneros muß einen Durchmesser von mehr als 14 cm besessen haben. Der Windungsquerschnitt ist rundlich (Wohnkammer Q = 0,85 bis 0,9). Auf dem letzten Umgang (Wohnkammer) stehen die etwas retroradiaten Flankenrippen ebenfalls dichter als auf der vorhergehenden Windung. Einfachrippen sind häufiger als Gabelrippen (auf 30 Flankenrippen kommen 37 Externrippen). Fibulate Rippenpaare treten nicht auf.

Vergleiche: *Peronoceras* cf. *bolitoense* unterscheidet sich von *P. bolitoense* n. sp. durch die kleinere relative Nabelweite (Abb. 20), das größere Gehäuse und die geringere Zahl von Flankenrippen bei einem Gehäusedurchmesser von 6 bis 8 cm.

Die Exemplare vom Rio Manflas und Rio Pulido besitzen auch Ähnlichkeit mit *Peronoceras moerickei* n. sp., das jedoch auf der Wohnkammer fibulate Rippen besitzt und bei dem der Rippenabstand auf der Wohnkammer größer ist.

Verbreitung: Die Exemplare vom Rio Manflas und Rio Pulido kommen in etwas jüngeren Schichten als *Peronoceras bolitoense* vor.

3.3.12 *Peronoceras moerickei* n. sp.

Taf. 7, Fig. 1, 2

1894 Deroceras aff. Davoei Sow.–Möricke, S. 11, Taf. 2, Fig. 6.–

Holotypus (B. St. M. 1978 II 161): Steinkern der Wohnkammer (500° lang) und Reste der letzten Windung des Phragmokons (Taf. 7, Fig. 1).

Derivatio nominis: Nach W. Möricke, der als erster ein dem Holotypus ähnliches Exemplar aus Chile abbildete.

Locus typicus: Quebrada El Asiento (Provinz Atacama) (Abb. 2, Profil 4), topogr. Karte 1:100000, Blatt Potrerillos: x = 467,55 km, y = 7070,7 km.

Stratum typicum: Dichte, graue, knollige Kalke mit wenig Fossilschutt und Gastropoden (vorwiegend kleinwüchsig).

Etwa 10 m im Liegenden *Harpoceras* sp. und *Peronoceras* sp. in lithologisch ähnlichen Kalken, z. T. mit mehr Fossilschutt und häufiger Ammoniten.

Etwa 10 m im Hangenden Grenze der knolligen bis mehr oder minder gut gebankten Kalke (mit *Catacoeloceras* sp., *Collina* sp.) gegen einen ca. 4 m mächtigen, in sich gebankten, groben Fossilschuttkalk mit Brachiopoden und Pelecypoden, sowie *Pleydellia* cf. *fluitans* im liegenden und *Bredyia* spp. im hangenden Teil. Der Fossilschuttkalk greift mit Täschchen und Grabgängen in die liegenden Knollenkalke.

Altersstellung: Mittleres Toarcium, Zone des *Hildoceras bifrons*, Subzone der *Collina chilensis*, Horizont mit *Peronoceras moerickei*. Die Fundschicht mit *Peronoceras moerickei* n. sp. ist gleichaltrig mit dem oberen Teil der Subzone des *Hildoceras semipolitum* (Zone des *Hildoceras bifrons*) in Europa.

Diagnose: Sehr großwüchsige, weitnabelige Art mit rundlichem Windungsquerschnitt. Mäßig dicht berippt, Rippenabstand sich während der Ontogenese wenig verändernd. Fibulate Flankenrippen nur auf der Wohnkammer. Rippen gerade die Externseite überquerend. Am Ende der Wohnkammer ungegabelte Einzelrippen vorherrschend.

Material: a) Am locus typicus wurde nur der Holotypus gefunden.

b) Salar de Pedernales, NW-Seite (Abb. 1, Profil 1), topogr. Karte 1:100000, Blatt Potrerillos: x = 475,05 km, y = 7199,8 km und x = 475,75 km, y = 7100,75 km (zwei Fundpunkte aus der gleichen Schicht im Streichen). Windungsbruchstücke (Phragmokon und Wohnkammer) (B. St. M. 1978 II 162–168). Zusammen mit *Harpoceras* cf. *subexaratum, Maconiceras* sp., Hildoceratidae gen. et sp. indet. (Innenwindungen berippt, äußere glatt).

c) Das von Möricke (1894) abgebildete Exemplar (Taf. 2, Fig. 6) ist nicht mehr vorhanden. Es wurde bei La Guardia gefunden (topogr. Karte 1:100000, Blatt La Guardia: x = 445,3 km, y = 6935,5 km).

d) Quebrada Yerbas Buenas (Abb. 6), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 439,4 km, y = 6979,3 km. Ein nicht im Anstehenden gefundenes Windungsbruchstück der Wohnkammer (B. St. M. 1978 II 169) (Taf. 7, Fig. 2).

Maße:

	d	N	H	Q	Z
Holotypus B. St. M. 1978 II 161	16,0 cm	62			
	14,0	60	22	0,95	107
Möricke (1894, Taf. 2, Fig. 6)	13,3 cm	58			

Beschreibung des Holotypus: Vom Phragmokon sind nur Reste der letzten Windung erhalten. Die Wohnkammer besitzt eine Länge von 500° und ist am Ende seitlich verdrückt. Die Rippen sind nur auf der abgebildeten Seite gut zu erkennen. Der Windungsquerschnitt ist rundlich (Q = 0,9 bis 0,95) und besonders die Externseite stark gewölbt. Die Flanken sind auf dem Phragmokon ebenfalls stark gewölbt und flachen auf der Wohnkammer allmählich ab. Die Flankenrippen stehen auf dem Phragmokon rectoradiat, besonders auf der 2. Hälfte der Wohnkammer können sie auch eine retrocostate Richtung einnehmen. Auf dem letzten Umgang sind zahlreiche fibulate Rippen zu erkennen, zwischen denen auf der 2. Hälfte des letzten Umgangs 2 bis 3 Einzelrippen stehen. Von den fibulaten Knoten gehen 2 bis 3 Externrippen aus. Die Einzelrippen spalten bifurkat auf oder bleiben einfach. Die Rippen überqueren die Externseite gerade.

Beschreibung der Paratypen: Das von Möricke (1894) als *Deroceras* aff. *davoei* bezeichnete Exemplar ist auf keinen Fall mit *Prodactylioceras davoei* näher verwandt, sondern muß zur Gattung *Peronoceras* gerechnet werden. Am meisten Ähnlichkeit besitzt das von Möricke abgebildete Exemplar mit *Peronoceras moerickei* n. sp. Nach Möricke besaßen die von diesem Autor beschriebenen Exemplare (2 Stück) ebenfalls einen rundlichen Windungsquerschnitt, etwas breiter als hoch. Fibulate Flankenrippen sind bei dem abgebildeten Exemplar wie beim Holotypus auf der Wohnkammer vorhanden. Die zwischen den fibulaten Rippen liegenden Einzelrippen scheinen jedoch zahlreicher zu sein und somit auch der Abstand der Knoten größer. Die Flankenberippung insgesamt ist dichter. Am Ende der (erhaltenen) Wohnkammer herrschen Einzelrippen vor, und die Flankenrippen stehen immer stärker retroradiat.

Vom Salar de Pedernales liegen Windungsbruchstücke des Phragmokons und der Wohnkammer vor, die sehr große Ähnlichkeit mit dem Holotypus aufweisen. Bis zu einer Windungshöhe von ca. 10 mm ist der Windungsquerschnitt sehr viel breiter als hoch (Q = 0,65 bis 0,7), wird dann zunehmend rundlicher und der Q-Wert beträgt am ? Ende des Phragmokons bei einer Windungshöhe von 2,1 cm 0,9. Auf der Wohnkammer liegt der Q-Wert bei 0,95 (Wh 2,8 bis 2,9 cm). Die Flanken und die Externseite sind auf dem Phragmokon stark gewölbt, auf der Wohnkammer flachen die Flanken ab. Bei den Innenwindungen des Phragmokons trägt jede zweite rectoradiate Flankenrippe einen Stachel (Schale) oder Knoten (Steinkern), von dem 2 bis 3 Externrippen ausgehen, die leicht nach vorn gebogen sind. Die Schaltrippen bleiben einfach oder sind bifurkat aufgespalten. Auf der letzten Windung des Phragmokons sind die Knoten auf dem Steinkern stark abgeschwächt. Auf eine bifurkate Rippe folgt zumeist eine Einfachrippe, die gerade die Externseite überquert. Zwei Wohnkammerbruchstücke zeichnen sich durch fibulate Rippenpaare aus. Zwischen den beknoteten, fibulaten Rippen liegen 1 bis 3 Einfachrippen oder unbeknotete Spaltrippen. Ein drittes Wohnkammerbruchstück weist eine dichtere Berippung als der Holotypus auf, die fibulaten Rippen stehen in großem Abstand, Einfach- und Spaltrippen herrschen vor. Die Berippung gleicht mehr der des von Möricke abgebildeten Exemplars.

Das 8 cm lange Wohnkammer-Windungsbruchstück (leicht seitlich verdrückter Steinkern) von der Quebrada Yerbas Buenas (Taf. 7, Fig. 2) weist ebenfalls eine dichtere Berippung auf. Zwischen den fibulaten Rippen liegen 2 bis 4 einfache oder bifurkat aufgespaltene Schaltrippen. Von den fibulaten Rippen gehen vorwiegend 3, manchmal auch nur 2 Externrippen aus. Auf 35 Flankenrippen kommen 47 Externrippen. Auch dieses Exemplar stimmt gut mit dem von Möricke abgebildeten Exemplar überein.

Die Lobenlinie konnte bei keinem der Exemplare gezeichnet werden.

Vergleiche: *Peronoceras moerickei* n. sp. unterscheidet sich von sämtlichen bisher bekannten Arten durch die Großwüchsigkeit. Die Art der Berippung gleicht der von *Peronoceras bolitoense* n. sp., das jedoch feinrippiger ist (vor allem auf der Wohnkammer). *Peronoceras* cf. *vortex* besitzt einen breiteren Windungsquerschnitt. Auf den Vergleich mit *Peronoceras* cf. *bolitoense* n. sp. wurde bei der Beschreibung dieser Art hingewiesen.

3.3.13 *Peronoceras* cf. *planiventer* (Guex, 1972)
Taf. 8, Fig. 1

cf. 1972 *Porpoceras planiventer* sp. n. – Guex, S. 633, Taf. 8, Fig. 10, 14; Taf. 12, Fig. 7.

Material: Quebrada Larga (Abb. 7); topogr. Karte 1:100000, Blatt Carrera Pinto: x = 432,75 km, y = 6978,7 km. 1 Exemplar (B. St. M. 1978 II 170) zusammen mit *Peronoceras* cf. *crassicostatum*, *Collina* sp., *Polyplectus* sp., *Osperlioceras* sp., *Phymatoceras* ex gr. *P. erbaense*, Hildoceratidae gen. et sp. indet. (3 Arten).

Maße:

d	N	H	Q	Z
2,8 cm	48	29,5	0,6	27
2,4	48	ca. 30	0,6	23
			0,56	(Beginn letzter Umgang)

Beschreibung: Es handelt sich um einen gekammerten Steinkern mit Schalenresten (besonders bei den inneren Umgängen). Das Gehäuse ist mäßig evolut, der Nabel tief. Der Windungsquerschnitt ist breiter als hoch. Die Flanken und die Externseite sind wenig gewölbt, und es ist eine deutliche Externkante ausgebildet. Die Flankenrippen stehen nicht sehr dicht. In den Innenwindungen ist jede der recto- bis leicht proradiaten Flankenrippen mit einem Knoten (Steinkern) oder Stachel (Schale) versehen. Auf der letzten Windung können den Flankenrippen auch Einzelrippen ohne Knoten zwischengeschaltet sein. Deutlich fibulate Rippen fehlen. Die Rippen mit Knoten spalten in 3, selten 2 Externrippen auf. Die Einfachrippen sind selten bifurkat gespalten.

Vergleich: *Peronoceras planiventer* besitzt große Ähnlichkeit, ist jedoch etwas weitnabeliger. Bei dieser Art ist außerdem nur jede zweite Flankenrippe mit einem Knoten versehen. Bei dem von Guex auf Taf. 8, Fig. 10 abgebildeten Exemplar scheinen jedoch bei den Innenwindungen auch sämtliche Flankenrippen bedornt zu sein. *Peronoceras planiventer* besitzt zusätzlich eine deutlich fibulate Berippung. Im Gegensatz zu sämtlichen anderen chilenischen Arten der Gattung *Peronoceras* (außer *P.* cf. *crassicostatum*) sind bis zu einem Durchmesser von 2,5 cm sämtliche Flankenrippen mit einem Knoten bzw. Stachel versehen.

Altersstellung: *Peronoceras planiventer* wurde von Guex aus dem oberen Teil der Subzone des *Hildoceras bifrons* beschrieben.

3.3.14 *Peronoceras* cf. *crassicostatum* (Guex, 1972)
Taf. 8, Fig. 2; Abb. 22

cf. 1972 *Porpoceras crassicostatum* sp. n. – Guex, S. 633, Taf. 8, Fig. 11, 17; Taf. 12, Fig. 9.

Material: Quebrada Larga (Abb. 7), topogr. Karte 1:100000, Blatt Carrera Pinto: x = 432,75 km, y = 6978,7 km. 5 unvollständig erhaltene Exemplare (B. St. M. 1978 II 171–175) zusammen mit *Peronoceras* cf. *planiventer* (Guex), *Collina* sp., *Polyplectus* sp., *Osperlioceras* sp., *Phymatoceras* ex gr. *P. erbaense*, Hildoceratidae gen. et sp. indet. (3 Arten).

Maße:

	d	N	H	Q
B. St. M. 1978 II 171	3,7 cm	40	38	0,6
172	2,6 cm	44	33	0,5

Beschreibung: Sämtliche Exemplare sind gekammert. Das Gehäuse ist engnabelig und der Nabel tief eingesenkt. Der rechteckige Windungsquerschnitt ist bis doppelt so breit wie hoch. Die Flanken und die Externseite sind wenig gewölbt. Es ist eine deutliche Externkante ausgebildet. Die recto- bis leicht proradiaten Flankenrippen enden in einem Stachel oder Knoten. Fibulate Flankenrippen sind selten, treten jedoch bei einem Exemplar bereits bei einer Windungshöhe von 6 mm auf. Von den Knoten gehen 2 oder 3 Externrippen aus, die etwas nach vorn gebogen sind.

Vergleiche: *Peronoceras crassicostatum* ist etwas weitnabeliger und fibulate Flankenrippen treten regelmäßiger auf. Auch *Nodicoeloceras fontis* GUEX ist ähnlich. Bei dieser Art trägt jedoch nur jede zweite Flankenrippe einen Knoten und fibulate Rippen fehlen. Das zusammen mit *P.* cf. *crassicostatum* gefundene *P.* cf. *planiventer* besitzt eine sehr ähnliche Berippung, ist jedoch weitnabeliger, und der Windungsquerschnitt ist weniger breit. *Peronoceras choffati* ist bereits in den Innenwindungen regelmäßig mit fibulaten Rippen versehen. *Transicoeloceras viallii* PINNA ist noch engnabeliger.

Altersstellung: *Peronoceras crassicostatum* wurde von GUEX aus dem oberen Teil der Subzone des *Hildoceras bifrons* beschrieben, *Nodicoeloceras fontis* vom gleichen Autor aus der Zone der *Haugia variabilis*.

Peronoceras cf. *planiventer* und *P.* cf. *crassicostatum* sind die beiden jüngsten Vertreter der Gattung *Peronoceras*, die im chilenischen Lias gefunden wurden.

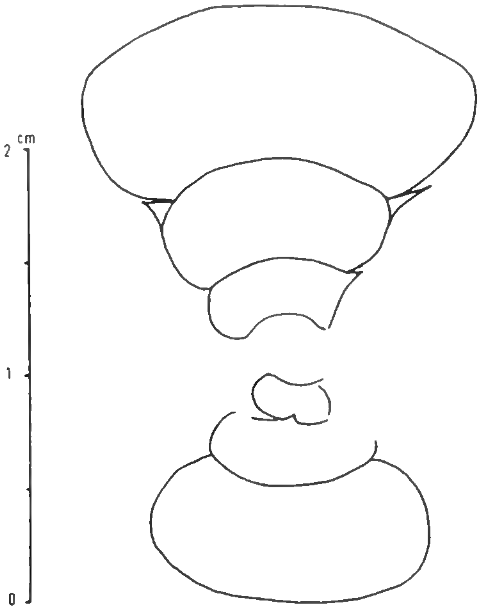

Abb. 22: Windungsquerschnitt von *Peronoceras* cf. *crassicostatum* (GUEX, 1972); Quebrada Larga; B. St. M. 1978 II 172.

3.4 GENUS: *COLLINA* BONARELLI, 1893

Typus-Art: *Collina gemma* BONARELLI, 1893

Diagnose: Gehäuse flach-scheibenförmig und stark evolut, Umgänge locker aufeinander liegend, Windungsquerschnitt zumindest in den Außenwindungen subquadratisch bis höher als breit. Skulptur kräftig, Flankenrippen regelmäßig mit Dornen oder Knoten versehen. Fibulate Rippenpaare und kielartige Erhöhung – wenn überhaupt vorhanden – vor allem auf der Wohnkammer ausgebildet. Die Externrippen queren die kielartige Erhöhung.

Laterallobus (nach GALLITELLI WENDT 1969) bifid und genauso tief wie der Externlobus. Internlobus ebenfalls bifid, 3 Umbilikalloben, U_1 tiefer als I und U_2.

Bemerkungen: *Collina* unterscheidet sich von *Peronoceras* durch das stark evolute Gehäuse, den überwiegend weniger breiten Windungsquerschnitt und die kielartige Erhöhung auf der Externseite. Nach PINNA & LEVI-SETTI (1971) kann die kielartige Erhöhung auf der Externseite auch fehlen, was dann eine Unterscheidung von *Peronoceras* erschwert.

ATROPS (1972) unterscheidet nach dem Dimorphismus zwei Untergattungen. Die microconchen Gehäuse werden zur Untergattung *Collina* und die macroconchen Gehäuse zur Untergattung *Collinites* ATROPS, 1972 (Typus-Art: *Collina meneghinii* BONARELLI, 1899) gerechnet. Nach ATROPS unterscheidet sich *Collinites* von *Collina* vor allem durch das Fehlen einer kielartigen Erhöhung auf der Externseite. Auch sollen fibulate Rippen nicht vorhanden sein, die jedoch sowohl bei der Typus-Art (Pinna 1969, Taf. 4, Fig. 7), als auch bei *Collina kampemorpha* Kottek bei Pinna & Levi-Setti (1971, Taf. 9, Fig. 14) auf der Wohnkammer zu erkennen sind.

Nach Calloman (1969) und anderen Autoren ist es ratsam, dimorphe Arten zumindest der gleichen Gattung oder Untergattung zuzuweisen.

Pinna & Levi-Setti (1971) stellen in die Synonymie von *Collina gemma* 8 weitere Arten.

3.4.1 *Collina chilensis* n. sp.

Taf. 8, Fig. 3, 4, 6–12; Abb. 17b, 23, 24

Holotypus (B. St. M. 1978 II 176): Phragmokon (z. T. in Kalzit erhalten), letzter Umgang Wohnkammer (Steinkern), seitlich komprimiert (Taf. 8, Fig. 4; Abb. 17k).

Derivatio nominis: Nach dem Vorkommen in Chile.

Locus typicus und Stratum typicum wie bei *Peronoceras bolitoense* Hillebrandt, n. sp. (S. 56).

Diagnose: Gehäuse flach-scheibenförmig und sehr weitnabelig, Windungsquerschnitt bei den Innenwindungen etwas breiter als hoch, bei der Wohnkammer subquadratisch bis etwas höher als breit. Flankenrippenzahl niedrig, jede zweite Flankenrippe mit einem Dorn oder Knoten versehen. Fibulate Rippen auf dem letzten Viertel des ersten Wohnkammer-Umgangs. Flankenrippen mit Knoten bifurkat in Externrippen aufspaltend, Schaltrippen überwiegend einfach. Externseite häufig mit Zick-Zack-Muster.

Material: a) Am locus typicus (Quebrada El Bolito) wurden außer dem Holotypus 7 weitere, unvollständig erhaltene Exemplare gefunden (B. St. M. 1978 II 177 bis 183) (Taf. 8, Fig. 8–10).

b) Quebrada Cortaderita (Abb. 1, Profil 8); topogr. Karte 1 : 100000, Blatt Carrera Pinto : x = 435,05 km, y = 6988,2 km. 4 Windungsbruchstücke (B. St. M. 1978 II 184–187), die nur mit Vorbehalt zu dieser Art gestellt werden können. Zusammen mit *Peronoceras* cf. *vortex*, *P.* cf. *bolitoense* n. sp., *Harpoceras* cf. *subexaratum*,

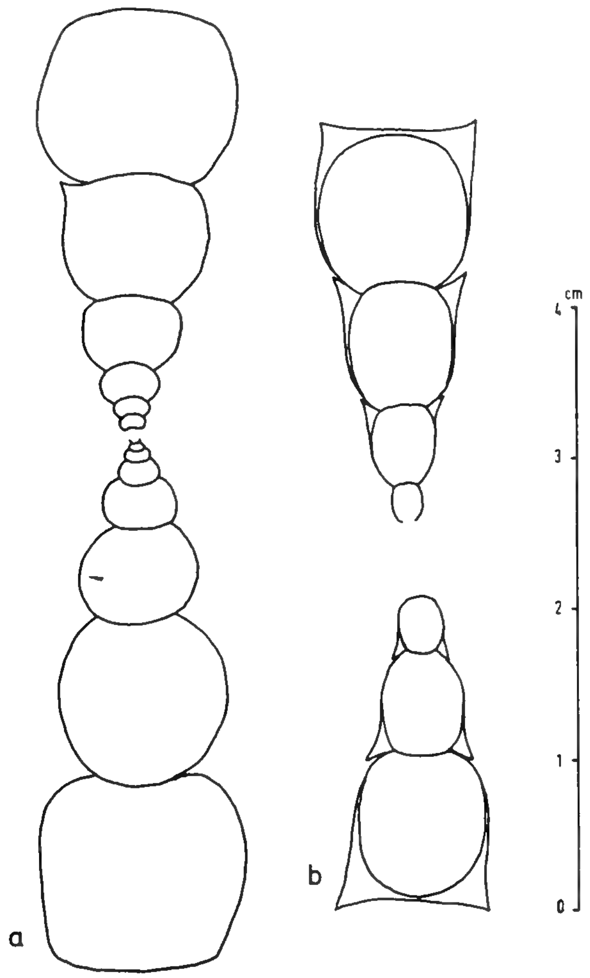

Abb. 23: Windungsquerschnitte von *Collina chilensis* n. sp. a: Rio Pulido; B. St. M. 1978 II 190. b: Quebrada El Bolito; B. St. M. 1978 II 178.

Phymatoceras ex gr. *P. erbaense,* Hildoceratidae gen. et sp. indet.

c) Quebrada Paipote bei Redonda (Abb. 4); topogr. Karte 1 : 100000, Blatt Carrera Pinto : x = 436,3 km, y = 6996,55 km und x = 436,0 km, y = 6996,3 km. Aus annähernd gleichalten Horizonten im Streichen 2 unvollständig und mäßig erhaltene Exemplare (B. St. M. 1978 II 188 u. 189), die nur mit Vorbehalt zu *Collina chilensis* n. sp. gestellt werden können. Aus dem gleichen Horizont *Peronoceras* sp. cf. *P.* cf. *verticosum, P.* cf. *bolitoense* n. sp., Hildoceratidae gen. et sp. indet. (2 Arten).

d) Rio Pulido (Department Copiapó, Prov. Atacama), Profil südlich Iglesia Colorada auf der linken Talseite (Abb. 10) (69°53,2′ Länge, 28°9,8′ Breite). Zwei unvollständig erhaltene Exemplare (B. St. M. 1978 II 190 u. 191) (Taf. 8, Fig. 6, 7), 7 Fragmente bzw. Windungsbruchstücke (B. St. M. 1978 II 192 bis 198) (Taf. 8, Fig. 3). Zusammen mit *Peronoceras* cf. *bolitoense* n. sp., *Harpoceras* cf. *subexaratum,* Hildoceratidae gen. et sp. indet. (glatte Art).

e) Juntas del Toro (Department Copiapó, Prov. Atacama), Profil auf der rechten Talseite, kurz unterhalb der Vereinigung von Rio Manflas und Rio del Toro (Abb. 10) (69°58,3′ Länge, 28°24,5′ Breite). Ein Windungsbruchstück (Steinkern) (B. St. M. 1978 II 199) der Wohnkammer zusammen mit *Peronoceras* cf. *bolitoense* n. sp., *Harpoceras* cf. *subexaratum, Phymatoceras* sp., Hildoceratidae gen. et sp. indet. (2 Arten).

f) Quebrada Yerbas Buenas (Abb. 6); topogr. Karte 1 : 100000, Blatt Carrera Pinto : x = 439,4 km, y = 6979,35 km. Ein kleines Exemplar (B. St. M. 1978 II 200) mit schlecht erhaltenem Phragmokon und $^3/_4$ Umgang der Wohnkammer (Taf. 8, Fig. 12). Zusammen mit *Peronoceras* cf. *bolitoense* n. sp., *Peronoceras* sp. indet., *Maconiceras* sp., Hildoceratidae gen. et sp. indet. (glatte Art).

g) Profil südlich Quebrada El Corral (östliche Seitenquebrada der Quebrada La Totora) (Abb. 1, Profil 20); topogr. Karte 1 : 50000, Blatt Conay : x = 381,3 km, y = 6818,9 km. Ein Wohnkammerexemplar (Phragmokon nicht erhalten) (B. St. M. 1978 II 201) (Taf. 8, Fig. 11), Windungsbruchstücke (B. St. M. 1978 II 202 bis 205). Zusammen mit *Catacoeloceras* (?) sp., *Harpoceras* cf. *subexaratum*, Hildoceratidae gen. et sp. indet. (2 Arten mit retroklinen Rippen).

h) Río Jorquera (Vegas de Chañar) (Abb. 1, Profil 14a), topogr. Karte 1 : 100000, Blatt La Guardia : x = 435,1 km, y = 6931,1 km. Ein unvollständiges Exemplar (2 äußere Windungen zu $^2/_5$ erhalten) (B. St. M. 1978 II 206), sowie 2 Windungsbruchstücke (B. St. M. 1978 II 207 u. 208) zusammen mit *Peronoceras* cf. *P.* cf. *vortex, P.* cf. *bolitoense, Harpoceras* cf. *subexaratum*, Hildoceratidae gen. et sp. indet. (glatte Art).

Maße:

		d	N	H	Q	Z
Holotypus B. St. M. 1978 II	176	6,3 cm	59,5	21	—	52
		5,64	59,5	22	1,03	46
		5,2	56,0	22	0,9	42
Paratypus	181	6,15	59	22	0,96	
Paratypus	179	4,5	60			52
Paratypus	178	5,3	60	20,5	1,05	
Paratypus		4,3	56	23,5	1,1	
Paratypus	180	ca. 4,7	54	25	1,075	
Paratypus	177	7,2	59	21,5	1,13	(Schale)
					1,03	(Steinkern)
Paratypus	190	6,5	61	20,8	0,98	
		5,2	55	22,5	0,88	
		4,1	51	28,0	1,0	
Paratypus	191	3,5	51,5	26,0		30
Paratypus	200	3,85	55	24	0,85 bis 0,9	
Paratypus	201	4,2	56	21,5		

Beschreibung des Holotypus: Besonders die inneren Windungen sind seitlich komprimiert und mit Kalzit ausgefüllt, auf der linken Seite besser als auf der rechten Seite erhalten. Der letzte Umgang gehört der Wohnkammer an. Die relative Nabelweite nimmt während der Ontogenese zu und ist beim letzten Umgang sehr groß. Die Windungen überdecken sich nur wenig. Der Windungsquerschnitt des letzten Umgangs ist subquadratisch.

Die Rippenzahl pro Umgang ist relativ klein. Jede zweite der rectoradiaten Flankenrippen trägt einen Stachel (Schale) oder Knoten (Steinkern). Von den Stacheln oder Knoten gehen je 2 Externrippen aus, von denen jedoch häufig eine auf der anderen Seite auf eine Schaltrippe trifft, die nicht aufspaltet. Dadurch entsteht ein Zick-Zack-Muster. Auf dem letzten Viertel des Wohnkammer-Umgangs treten etwas retroradiate, fibulate Rippenpaare auf, und die Rippen stehen etwas dichter.

Die Lobenlinie konnte nicht gezeichnet werden.

Beschreibung der Paratypen: Die Paratypen der Quebrada El Bolito sind bis auf Exemplar B. St. M. 1978 II 177 seitlich etwas komprimiert (Taf. 8, Fig. 10), ob-

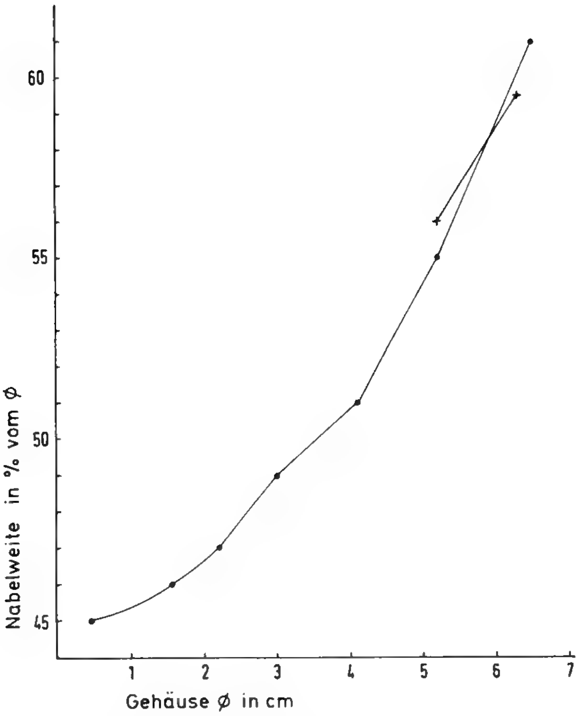

Abb. 24: Änderung der relativen Nabelweite im Verlauf der Ontogenie bei *Collina chilensis* n. sp.: ● B. St. M. 1978 II 176 (Holotypus); + B. St. M. 1978 II 190.

wohl der Phragmokon häufig mit Kalzit ausgefüllt ist. Die Kompression macht sich bei den innersten Umgängen am stärksten bemerkbar.

Offensichtlich erfolgte zunächst ein Ausfüllung der Wohnkammer mit Sediment, dann eine seitliche Kompression mit Verkleinerung des Phragmokon-Hohlraumes und erst anschließend eine Ausfüllung dieses Hohlraumes mit Kalzit. Die Wohnkammern der Exemplare von der Quebrada El Bolito besitzen einen subquadratischen Querschnitt.

Die Exemplare vom Río Pulido sind nur zum Teil seitlich komprimiert. Das zur Hälfte erhaltene Exemplar B. St. M. 1978 II 190 wurde angeschliffen und gezeichnet (Abb. 23a). Wie bei den Exemplaren der Quebrada El Bolito nimmt während der Ontogenie die relative Nabelweite zu (Abb. 24) und ist beim letzten Umgang sehr groß. Auch der Windungsquerschnitt verändert sich während der Ontogenese. Bis zu einem Durchmesser von 1,5 cm ist der Querschnitt sehr viel breiter als hoch und wird dann allmählich subquadratisch.

Exemplar B. St. M. 1978 II 179 (Taf. 8, Fig. 9) von der Quebrada El Bolito ist bei gleichem Durchmesser weitnabeliger als die übrigen Exemplare. Zumindest ein Teil des letzten Umgangs gehört bereits der Wohnkammer an, und es treten auch fibulate Rippen auf. Es dürfte sich um ein ausgewachsenes Exemplar mit kleinerem Enddurchmesser handeln.

Die innersten Umgänge sind bei keinem Exemplar erhalten. Jede zweite der vorwiegend rectoradiaten, manchmal etwas retroradiaten und nicht dicht stehenden Flankenrippen trägt einen Stachel oder Knoten. Die Schaltrippen bleiben einfach, während die Stachel bzw. Knoten tragenden Rippen bifurkat aufspalten. Ein Zick-Zack-Muster ist bei einigen Exemplaren vorhanden. Besonders die vorderen durch Bifurkation entstandenen Externrippen können nach vorn gebogen sein. Nach einer halben Windung Wohnkammer können die ersten fibulaten Flankenrippen auftreten, die dichter als die vorhergehenden Rippen stehen. Die fibulaten Rippenpaare spalten bifurkat auf, zwischen ihnen können Schaltrippen liegen, die nicht aufspalten.

Exemplar B. St. M. 1978 II 177 (Taf. 8, Fig. 10) ist mit einem Durchmesser von 7,2 cm größer als die übrigen Exemplare. Die zweite Hälfte des erhaltenen Umgangs weist fibulate Berippung auf. Bei Schalenerhaltung werden hier die Rippen auf der Mitte der Externseite doppelt so hoch wie auf den Flanken. Die fibulaten Rippen spalten ebenfalls in je 2 Externrippen auf. Auch auf Phragmokonen mit Schale sind die kräftigen Rippen auf der Externseite zumindest ebenso hoch wie auf den Flanken.

Das Wohnkammerexemplar (280° erhalten) von der Quebrada El Corral (B. St. M. 1978 II 201) (Taf. 8, Fig. 11) ist kleinwüchsig. Zu Beginn der Wohnkammer beträgt der Q-Wert 0,9. Auch bei den Windungsbruchstücken handelt es sich ausschließlich um Teile der Wohnkammer.

Der Windungsquerschnitt ist subquadratisch oder wenig breiter als hoch. Die flachen Flanken tragen mehr oder minder rectoradiate Rippen, die häufig in einem Knoten zu fibulaten Rippenpaaren vereinigt sind und zwischen denen Schaltrippen stehen können. Bei Einfachrippen trägt – soweit erkennbar – jede zweite Flankenrippe einen Knoten. Von den Knoten gehen zwei Externrippen aus, manchmal ist auch nur eine Externrippe wie bei den Schaltrippen vorhanden. Bei dem Exemplar von der Quebrada Yerbas Buenas (B. St. M. 1978 II 200, Taf. 8, Fig. 12) ist ebenfalls nur die Wohnkammer (ca. $^3/_4$ Umgang) gut erhalten. Es treten jedoch keine fibulaten Rippenpaare auf. Die Knotenrippen spalten in 2, selten 3 Externrippen auf. Die Schaltrippen bleiben zumeist einfach.

Die Lobenlinie konnte bei keinem Exemplar gezeichnet werden.

Vergleiche: Zu *Collina gemma* besteht große Ähnlichkeit. *Collina chilensis* n. sp. fehlt jedoch die kielartige Erhöhung auf der Externseite. *Collina kampemorpha* Kottek ist in der Seitenansicht ebenfalls ähnlich.

Diese Art besitzt aber einen etwas breiteren Windungsquerschnitt, und von den Knoten der Flankenrippen gehen 3 bis 4 Externrippen aus. Die Externseite ist also sehr viel dichter berippt.

Peronoceras pacificum besitzt einen ähnlichen Windungsquerschnitt, jedoch ist die Externseite stärker gewölbt und bei dieser Art ist bei gleichem Durchmesser die Flankenrippenzahl pro Umgang größer.

3.4.2 *Collina* sp.

Taf. 8, Fig. 5; Abb. 19

Material: Quebrada Larga (Abb. 7); topogr. Karte 1:100000, Blatt Carrera Pinto: x = 432,75 km, y = 6978,7 km. Ein unvollständig erhaltenes Exemplar (z. T. beschalt) (B. St. M. 1978 II 209) (Taf. 8, Fig. 5; Abb. 19b), 2 Windungsbruchstücke (B. St. M. 1978 II 210 u. 211). Zusammen mit *Peronoceras* cf. *planiventer*, *P.* cf. *crassicostatum*, *Polyplectus* sp., *Osperlioceras* sp., *Phymatoceras* ex gr. *P. erbaense*, Hildoceratidae gen. et sp. indet. (3 Arten).

Beschreibung: Das Exemplar B. St. M. 1978 II 209 ist bis zu einem Durchmesser von 8 mm vollständig erhalten, dann nur noch ca. $^1/_4$ der Windungen. Der Windungsquerschnitt ist in den inneren Windungen sehr viel breiter als hoch, bei der letzten Windung subquadratisch. Ab einem Durchmesser von ca. 5 mm sind die Flankenrippen zu erkennen, von denen jede in einem Stachel endet. Auch in den folgenden Windungen ist jede Flankenrippe mit einem Stachel oder Knoten versehen. Die letzte Windung (110° erhalten) gehört der Wohnkammer an. Die Flankenrippen spalten bifurkat auf oder bleiben einfach (unregelmäßig jede zweite). Wie bei Collina chilensis sind bei Schalenerhaltung die Externrippen der Wohnkammer in der Mitte höher als an den Seiten und etwas nach vorn gebogen.

Vergleiche: *Collina* sp. unterscheidet sich von *C. chilensis* durch die geringere Größe, die kleinere relative Nabelweite und die größere Windungsbreite am Ende des Phragmokons. Außerdem ist bei *Collina* sp. wie bei *Peronoceras* cf. *planiventer* und *P.* cf. *crassicostatum* (gleicher Fundpunkt!) jede Flankenrippe mit einem Stachel versehen.

4. BIOSTRATIGRAPHISCHE FOLGERUNGEN

Unter-Toarcium (Schmidt-Effing), vgl. Abb. 25

v. Hillebrandt legte, zuletzt 1973b (Tab. 1), eine detaillierte biostratigraphische Gliederung vom Hettangium bis Aalenium der chilenisch-argentinischen Hochkordillere vor, die durch die hier vorgelegte monographische Bearbeitung der Arten von *Dactylioceras* und *Nodicoeloceras* für das Unter-Toarcium ergänzt und verfeinert wird. Da bisher keine Bearbeitung der Ammoniten des Unter-Toarciums Südamerikas vorliegt und auch das hier untersuchte Material vorwiegend nur Einzelfaunen aus neun teilweise weit auseinander liegenden Profilen repräsentiert, ist eine Zonengliederung zunächst nur indirekt durch Vergleich mit den klassischen stratigraphischen Abfolgen außerhalb Südamerikas, besonders von Europa, erschließbar. Doch läßt sich mit Hilfe der vorliegenden Faunen für das Unter-Toarcium, in Anlehnung an die internationale Gliederung, folgende biostratigraphische Zonierung durchführen:

4.1 Zone des *DACTYLIOCERAS (ORTHODACTYLITES) TENUICOSTATUM*

Diese weltweit angewandte erste Zone des Toarciums ist eine Zone sensu abstracto (vgl. Hölder 1964: 27). Sie wird auch Standardzone genannt und ist mit der Oppel-Zone vergleichbar (Hölder & Zeiss 1972: 389), d. h., die Zonen-Art tritt nur in einem Teil der nach ihr benannten Zone auf. Definitionsgemäß fällt der Beginn dieser Zone mit der Grenze Pliensbachium/Toarcium zusammen (Elmi et al. 1974; Howarth 1973, 1978). In Chile ist diese Zone in zwei Subzonen (= Zonen sensu concreto, Hölder 1964) gliederbar:

4.1.1 Subzone des *Dactylioceras (Eodactylites) simplex*

Diese Subzone ist von der Quebrada Chanchoquin und Quebrada El Peñon bekannt:

a) Quebrada Chanchoquin:

Dactylioceras (Eodactylites) simplex (9 Exemplare),
Dactylioceras (Orthodactylites) directum (6 Exemplare),
Dactylioceras (Orthodactylites) anguinum (2 Exemplare),
Nodicoeloceras cf. *eikenbergi* (1 Exemplar),
Nodicoeloceras cf. *pseudosemicelatum* (5 Exemplare),

b) Quebrada El Peñon:

Dactylioceras (? *Eodactylites*) sp.
Nodicoeloceras cf. *eikenbergi*

Von diesen Arten treten *D. anguinum* und *D. directum* im gesamten Unter-Toarcium auf, während die restlichen drei das tiefste Unter-Toarcium charakterisieren, wobei *D. (Eodactylites)* grundsätzlich auch schon im höchsten Domerium vorhanden ist. Nach Howarth (1973, 1978) treten Formen, die mit den beiden hier gefundenen *Nodicoeloceras*-Arten ident oder doch sehr nahe stehen, als Leitformen in der „*clevelandicum*"-Subzone der *tenuicostatum*-Zone in Yorkshire auf, indem sie dort die ältesten Dactylioceraten überhaupt stellen. Nach Hoffmann (1968: 9) tritt *N. eikenbergi* in der tieferen *tenuicostatum*-Zone (*siemensis*-Subzone) auf, ebenfalls *N. pseudosemicelatum* innerhalb eines ähnlichen stratigraphischen Bereichs (Maubeuge 1957: 193).

Das Vorkommen von *D. (Eodactylites)* zeigt tiefstes Unter-Toarcium aber auch höchstes Domerium an (Howarth 1978: 252; Schmidt-Effing 1972: 180); hier ist jedoch durch das gemeinsame Auftreten mit den genannten Arten von *Dactylioceras (Orthodactylites)* und *Nodicoeloceras* Untertoarcium-Alter sichergestellt.

Elmi, Atrops & Mangold (1974: 55), ähnlich auch Guex (1973 a: 512), scheiden als tiefsten Abschnitt der *tenuicostatum*-Zone in der mediterranen Provinz eine Subzone des *D. (E.) mirabile* aus. Da im gesamten Abschnitt der *mirabile*-Subzone, wie auch in dem zeitlich äquivalenten Bereich der tieferen *tenuicostatum*-Zone der nordwest-europäischen Provinz noch nie ein *D. tenuicostatum* gefunden wurde, ist es wenig sinnvoll, diese Subzone zur *tenuicostatum*-Zone zu stellen. Vielmehr wäre dieser Abschnitt im Mediterran als *mirabile*-Zone – im Hangenden folgt die *semicelatum*-Zone, da *D. tenuicostatum* hier auch in der höheren „*tenuicostatum*-Zone" kaum auftritt (Elmi et al. 1974) – auszuscheiden. Die *tenuicostatum*-Zone, so wie sie in Yorkshire ausgeschieden wurde (Howarth 1973), widerspricht den stratigraphischen Richtlinien (1977: 135) wie auch dem stratigraphischen Verständnis. Die Basis einer Zone wird durch das Erstauftreten der Zonen-Leitart definiert, doch die Leitart tritt in den Yorkshire-Profilen nur zu Anfang des obersten Drittels der Gesamtzone auf. Die internationale Zonengliederung des Unter-Toarciums ist also noch wenig ausgereift.

Da in Chile bis jetzt nur *Dactylioceras (Eodactylites) simplex*, nicht aber *D. (E.) mirabile* bekannt ist, schlage ich vor, diesen Abschnitt *simplex*-Subzone zu benennen. Sie dürfte ziemlich exakt der *mirabile*-Zone des mediterranen Bereiches entsprechen.

<table>
<tr><th colspan="2">HOWARTH 1978</th><th colspan="3">ELMI, ATROPS & MANGOLD 1974</th><th colspan="2">CHILE</th></tr>
<tr><td rowspan="3"><i>falcifer</i> - Zone</td><td><i>falcifer</i> - Subzone</td><td rowspan="3"><i>serpentinus</i>-Z.</td><td colspan="2">(<i>mulgravium</i> - Subzone)</td><td colspan="2" rowspan="3"><i>hoelderi</i> - Zone</td></tr>
<tr><td rowspan="2"><i>exaratum</i> - Subzone</td><td rowspan="2">(<i>strangewaysi</i>-Sz.)</td><td><i>serpentinif.</i>-H.</td></tr>
<tr><td><i>elegantulum</i>-H.</td></tr>
<tr><td rowspan="4"><i>tenuicostatum</i> - Zone</td><td><i>semicelatum</i> - Subzone</td><td rowspan="4"><i>tenuicostatum</i> - Zone</td><td colspan="2" rowspan="2"><i>semicelatum</i> - Horizont</td><td rowspan="4"><i>tenuicostatum</i> - Zone</td><td rowspan="2"><i>tenuicostatum</i> - Subzone</td></tr>
<tr><td><i>tenuicostatum</i> - Subzone</td></tr>
<tr><td><i>clevelandicum</i> - Subzone</td><td colspan="2" rowspan="2"><i>mirabile</i> - Horizont</td><td rowspan="2"><i>simplex</i> - Subzone</td></tr>
<tr><td><i>paltum</i> - Subzone</td></tr>
</table>

Abb. 25: Biostratigraphische Gliederung des Unter-Toarciums.

4.1.2 Subzone des *Dactylioceras (Orthodactylites) tenuicostatum*

Diese Subzone ist aus fünf verschiedenen chilenischen Profilen bekannt und zwar mit folgender Fauna:

a) Quebrada El Bolito:

Dactylioceras (Orthodactylites) tenuicostatum chilense (4 Exemplare),

b) Río Manflas (bei Los Graneros):

Dact. (Orthodactylites) tenuicostatum chilense (1 Exemplar),
Dact. (? Orthodactylites) cf. *helianthoides* (1 Exemplar),
Dact. (Orthodactylites) sp. (2 Exemplare);

Die drei letzten Exemplare stammen aus etwas jüngeren Schichten als das aufgeführte *D. (O.) tenuicostatum chilense*.

c) Río Manflas (bei Portezuelo El Padre):

Dact. (Orthodactylites) tenuicostatum chilense (1 Exemplar),

d) Quebrada La Chaucha:

Dact. (Orthodactylites) tenuicostatum chilense (2 Exemplare),
Dact. (Orthodactylites) cf. *directum* (1 Exemplar),
Dact. sp. juvenil (1 Exemplar).

e) Quebrada El Peñon:

Dact. (Orthodactylites) tenuicostatum chilense (10 Exemplare),
Dact. (? *Orthodactylites) helianthoides* (1 Exemplar),
Nodicoeloceras sp. (1 Exemplar).

Das Alter dieser Fauna ist durch das Vorkommen von *Dactylioceras tenuicostatum,* das hier durch eine besondere Unterart vertreten wird, mit den klassischen europäischen Profilen direkt korrelierbar. Es entspricht der *tenuicostatum*-Subzone der *tenuicostatum*-Zone von Howarth (1973: 241). Entsprechend den Stratigraphischen Richtlinien (1977: 135, § 3.2.9) sollte dieser Abschnitt, in welchem die Leitart tatsächlich auftritt, entgegen der bisherigen internationalen Gepflogenheit *tenuicostatum*-Zone genannt werden.

4.2 Zone des *DACTYLIOCERAS (ORTHODACTYLITES) HOELDERI*

Diese Zone ist aus fünf chilenischen Profilen bekannt und zwar mit folgender Fauna:

a) Quebrada Yerbas Buenas:

Dactylioceras (Orthodactylites) hoelderi (5 Exemplare),
Dact. (Orthodactylites) directum (1 Exemplar),
Dact. (Orthodactylites) cf. *directum* (4 Exemplare),
Nodicoeloceras cf. *crassoides* Form A (4 Exemplare);

b) Quebrada El Asiento:

Dact. (Orthodactylites) anguinum (2 Exemplare),
Dact. (? Orthodactylites) cf. *helianthoides* (3 Exemplare),
Nodicoeloceras cf. *crassoides* Form B (1 Exemplar),
Nodicoeloceras cf. *crassoides* Form C (1 Exemplar);

c) Rio Jorquera (Majada del Carrizo):

Dact. (Orthodactylites) directum (4 Exemplare),
Dact. (Orthodactylites) cf. *directum* (3 Exemplare),
Nodicoeloceras cf. *crassoides* Form C (7 Exemplare);

d) Quebrada Noria:

Dact. (Orthodactylites) hoelderi (1 Exemplar),
Dact. (Orthodactylites) directum (4 Exemplare),
Dact. (? Orthodactylites) helianthoides (20 Exemplare);

e) Quebrada Calquis:

Dact. (Orthodactylites) cf. *hoelderi* (2 Exemplare),
Nodicoeloceras cf. *crassoides* Form A (1 Exemplar);

Dactylioceras directum und *Dact. anguinum* treten im gesamten Unter-Toarcium auf, während die übrige Fauna innerhalb dieses Zeitabschnittes zeitspezifischen Charakter besitzt. *Nodicoeloceras* cf. *crassoides* charakterisiert vorwiegend das höhere Unter-Toarcium, in England besonders die *falcifer*-Zone. *Dact. (? Orthodactylites) helianthoides* ist für diese Zone in Chile sehr bezeichnend, doch tritt es in Japan im gesamten Unter-Toarcium und auch schon im höheren Domerium auf, so daß bei biostratigraphischer Datierung mit dieser Art, wenn sie alleine auftritt, Vorsicht geboten sein sollte. Mit Hilfe der endemischen Art *Dact. (Orthodactylites) hoelderi* ist jedoch eine gute Biozone ausgliederbar. Zeitlich entspricht diese Zone im wesentlichen dem höheren Abschnitt der *semicelatum*-Subzone der *tenuicostatum*-Zone und der *falcifer*-Zone Europas und des Mediterrans.

Eine Zonenbenennung nach *Harpoceras* oder ähnlichen Formen, wie das besonders in NW-Europa praktiziert wird, sollte vermieden werden, da diese weltweit nicht nur sehr unterschiedlich, sondern vor allen Dingen auch stratigraphisch noch viel höher und tiefer häufig auftreten (vgl. Schmidt-Effing 1972: 181; Elmi, Atrops & Mangold 1974). Mit der *hoelderi*-Zone schließt das chilenische Unter-Toarcium ab.

Mittel-Toarcium (von HILLEBRANDT), vgl. Abb. 26.

4.3 ZONE DES *HILDOCERAS BIFRONS*

In den letzten Jahren hat es mehrere Versuche gegeben, die Zone des *Hildoceras bifrons* in Subzonen zu unterteilen, sowohl im NW-europäischen Bereich, als auch im Mediterrangebiet.

DEAN, DONOVAN & HOWARTH (1961) stellten eine Zonengliederung für die NW-europäische Provinz auf und unterteilten die *bifrons*-Zone in die Subzonen des *Dactylioceras commune, Peronoceras fibulatum* und *Zugodactylites braunianum.* Diese Gliederung wurde für diesen Bereich auch von späteren Autoren übernommen.

DONOVAN (1958) gab für die Südalpen und den Apennin eine Zonengliederung. Seine Zone des *Mercaticeras mercati* entspricht der *bifrons*-Zone. Die *mercati*-Zone unterteilte er in die Subzonen des *Hildoceras sublevisoni* und *Hildoceras semipolitum.*

GABILLY et al. (1971) stellten für den Stratotyp des Toarcium (Thouars) und die benachbarten Gebiete eine Zonengliederung auf. Die *bifrons*-Zone wird von Ihnen unterteilt in die Subzonen des *Hildoceras sublevisoni, Hildoceras bifrons* und *Hildoceras semipolitum.* Die *sublevisoni*-Subzone wird zusätzlich unterteilt in die Horizonte des *Hildoceras sublevisoni, Dactylioceras commune* und *Hildoceras lusitanicum.*

ELMI, ATROPS & MANGOLD (1974) unterscheiden innerhalb der *bifrons*-Zone 4 Subzonen; die Subzonen des *Hildoceras sublevisioni, H. lusitanicum, H. bifrons* und *H. semipolitum.*

HOWARTH (1978) stellte fest, daß in England (Northhamptonshire und Yorkshire) *Peronoceras fibulatum* und *Zugodactylites braunianum* zusammen vorkommen. Er untergliedert deshalb die *bifrons*-Zone in die Subzonen des *Dactylioceras commune, Peronoceras fibulatum* und *Catacoeloceras crassum.*

Die Subzone des *Dactylioceras commune* ist gleichaltrig mit der Subzone des *Hildoceras sublevisioni* (bzw. *H. sublevisioni* und *H. lusitanicum* bei ELMI, ATROPS & MANGOLD), die Subzone des *Peronoceras fibulatum* entspricht der Subzone des *Hildoceras bifrons* und die Subzone des *Catacoeloceras crassum* kann mit der Subzone des *Hildoceras semipolitum* verglichen werden.

Zur Untergliederung der *bifrons*-Zone werden also in Europa Arten der Gattung *Hildoceras* oder Arten verschiedener Gattungen der Dactylioceratidae herangezogen. Bei einem Vergleich mit Südamerika ergibt sich die Schwierigkeit, daß die Gattung *Hildoceras* bisher in Südamerika nicht nachgewiesen wurde, ebenso die Gattungen *Dactylioceras* s. str. und *Zugodactylites* fehlen. Die Gattung *Catacoeloceras* ist selten und es liegen bisher keine artlich bestimmbaren Exemplare vor. Arten der Gattungen *Peronoceras* (+ *Porpoceras*) und *Collina* sind hingegen weit verbreitet und mit ihnen ist eine Unterscheidung mehrerer Faunenzonen möglich.

In England (HOWARTH 1978) erscheint die Gattung *Peronoceras* an der Basis der *fibulatum*-Subzone. In Frankreich (GABILLY 1976) tritt diese Gattung bereits ab der Basis der *sublevisoni*-Subzone auf. In Portugal (MOUTERDE 1967), Algerien (ELMI, ATROPS & MANGOLD 1974) und Marokko (GUEX 1973) treten die ersten zur Gattung *Peronoceras* zu rechnenden Arten bereits in der *serpentinus*- bzw. *levisoni*-Zone auf. Beide Zonen sind mit der *falcifer*-Zone gleichaltrig. Im Mediterranbereich erscheint also die Gattung *Peronoceras* früher als in der NW-europäischen Provinz.

In den Schichten, die altersmäßig denen der *bifrons*-Zone in Europa entsprechen, lassen sich in Chile mit Hilfe von Arten der Gattungen *Peronoceras* und *Collina* 3 Subzonen unterscheiden.

4.3.1 Subzone des *Peronoceras largaense*

Diese Subzone ist aus 6 chilenischen Profilen bekannt und zwar mit folgender Fauna:

a) Quebrada Larga (Abb. 7, Schicht 8)
Peronoceras largaense (Holotypus)
Peronoceras cf. *subarmatum*
Harpoceras sp.
Mercaticeras sp.

b) Quebrada El Bolito (Abb. 5, Schicht 6)
Peronoceras largaense
Peronoceras cf. *subarmatum*
Harpoceras cf. *chrysanthemum*
Mercaticeras sp.

c) Rio Jorquera (Majada del Carrizo) (Abb. 9)

Schicht 7a:
Peronoceras largaense
Peronoceras cf. *subarmatum*
Harpoceras sp.

Schicht 8:
Peronoceras cf. *renzi*
Peronoceras sp.
Harpoceras sp.

d) Quebrada Yerbas Buenas (Abb. 6, Schicht 8)
Peronoceras cf. *desplacei*
Peronoceras cf. *choffati*
Peronoceras sp. ex gr. *P. subarmatum*
Harpoceras cf. *chrysanthemum*

e) Quebrada El Asiento (Abb. 3, Schicht 5)
Peronoceras cf. *subarmatum*
Harpoceras cf. *falcifer*

f) Quebrada La Chaucha
Peronoceras cf. *renzi*

HOWARTH 1978	GUEX 1972	GABILLY et al. 1971		ELMY, ATROPS & MANGOLD 1974	CHILE	
		Subzonen	Horizont		Subzonen	Horizont
crassum	*semipolitum*	*semipolitum*		*semipolitum*	*chilensis*	*moerickei*
						bolitoense
fibulatum	*bifrons*	*bifrons*		*bifrons*		
					pacificum	
commune	*sublevisoni*	*sublevisoni*	*lusitanicum*	*lusitanicum*	*largaense*	
			commune			
			sublevisoni	*sublevisoni*		

Abb. 26: Biostratigraphische Gliederung des Mittel-Toarciums.

Der biostratigraphische Vergleich der *largaense*-Zone mit gleichaltrigen Schichten in Europa ist schwierig, da der tiefere Teil der *bifrons*-Zone dort durch Arten charakterisiert wird, die in Südamerika nicht auftreten und von denen auch keine nahe verwandten Formen vorhanden sind. *Peronoceras* cf. *subarmatum* ist zwar nahe verwandt mit *P. subarmatum*, das jedoch in England nach Howarth (1978) nur im unteren Teil der *fibulatum*-Subzone vorkommt. *Peronoceras choffati* tritt nach Mouterde (1967) bereits in der *serpentinus*-Zone auf. *Peronoceras desplacei* ist in Europa eine Art der *bifrons*- bzw. *fibulatum*-Subzone. Der genaue Faunenhorizont von *Peronoceras renzi* innerhalb der *bifrons*-Zone ist nicht bekannt. *Harpoceras chrysanthemum* kommt nach Dagis (1974) in der *commune*-Zone vor.

Das *Harpoceras* cf. *falcifer* aus der Quebrada El Asiento ist eine engnabelige Varietät dieser Art, die in Frankreich nach Gabilly (1976) in der *sublevisoni*-Subzone auftritt.

Am Rio Jorquera, in der Quebrada Yerbas Buenas und in der Quebrada El Asiento wird die *largaense*-Subzone von Schichten mit einer Fauna der *hoelderi*-Zone unterlagert und in der Quebrada El Bolito, Quebrada Yerbas Buenas und Quebrada El Asiento von Schichten mit einer Fauna der *pacificum*-Subzone überlagert.

4.3.2 Subzone des *Peronoceras pacificum*

Diese Subzone ist aus 4 Profilen in Chile bekannt, die folgende Fauna enthalten:

a) Quebrada Yerbas Buenas (Abb. 6, Schicht 9)
Peronoceras pacificum
Peronoceras cf. *verticosum*
Peronoceras cf. *P.* cf. *verticosum*
Maconiceras sp.
Polyplectus sp.

b) Quebrada Potrerillos (Abb. 1, Profil 10)
Peronoceras pacificum (Holotypus)
Peronoceras cf. *verticosum*
Harpoceras sp.
Maconiceras sp.

c) Quebrada El Bolito (Abb. 5, Schicht 7)
Peronoceras pacificum
Harpoceras sp.
Maconiceras sp.
Polyplectus sp.

d) Quebrada El Asiento
Peronoceras cf. *verticosum*
Harpoceras sp.

Peronoceras pacificum ist nahe verwandt mit *Peronoceras vorticellum*. *Peronoceras vorticellum* und *P. verticosum* kommen nach Howarth (1978) in England und S-Frankreich (nach Guex 1972) im oberen Teil der *fibulatum*-Subzone vor. Die Gattung *Phymatoceras* ist in der *pacificum*-Subzone noch nicht vorhanden, tritt jedoch in England und S-Frankreich bereits im oberen Teil der *fibulatum*-Subzone auf. Die *pacificum*-Subzone umfaßt daher wahrscheinlich nur den tieferen Teil der *fibulatum*- bzw. *bifrons*-Subzone.

4.3.3 Subzone der *Collina chilensis*

Nach Fischer (1966), Pinna & Levi-Setti (1971) und Guex (1972) beginnt die Gattung *Collina* in der obersten Subzone der *bifrons*-Zone und reicht bis in die *variabilis*-Zone. Gallitelli Wendt (1969), Atrops & Elmi (1971) und Elmi, Atrops & Mangold (1974) stellten eine Subzone der *Collina gemma* auf. Elmi, Atrops & Mangold vergleichen diese Zone mit dem tiefsten Teil der *variabilis*-Zone in England und Frankreich. Gallitelli Wendt gibt jedoch zusammen mit *Collina gemma* verschiedene Arten der Gattung *Peronoceras* an. Elmi, Atrops & Mangold fanden in den Schichten der *semipolitum*-Subzone keine Dactylioceratidae. Da es sich bei *Collina chilensis* wahrscheinlich um einen frühen Vertreter dieser Gattung handelt, dem noch die kielartige Erhöhung auf der Externseite fehlt, und da *C. chilensis* zusammen mit Vertretern der Gattung *Peronoceras* vorkommt, ist ein Vergleich der *chilensis*-Subzone mit der *crassum*-Subzone im Sinne von Howarth (1978) wahrscheinlicher als ein Vergleich mit dem tieferen Teil der *variabilis*-Zone. Innerhalb der *chilensis*-Subzone können zwei Faunenhorizonte unterschieden werden. In beiden Horizonten kommt *C. chilensis* vor. Der tiefere Horizont wird durch *Peronoceras bolitoense* und *P.* cf. *vortex* und der höhere Horizont durch *Peronoceras moerickei* und *P.* cf. *bolitoense* charakterisiert. Die *Peronoceras*-Exemplare im höheren Horizont sind großwüchsiger als im tieferen Horizont. *Peronoceras moerickei* und *P.* cf. *bolitoense* sind sehr viel großwüchsiger als alle bisher bekannten Arten dieser Gattung.

4.3.3.1 Horizont mit Peronoceras bolitoense

Dieser Horizont kommt bei folgenden chilenischen Profilen vor:

a) Quebrada El Bolito (Abb. 5, Schicht 8)
Peronoceras bolitoense (Holotypus)
Collina chilensis (Holotypus)
Harpoceras sp.
Maconiceras sp.
Phymatoceras sp.
Hildoceratidae gen. et sp. indet. (glatte Art)

b) Quebrada Cortaderita (Abb. 1, Profil 8)
Peronoceras cf. *vortex*
Peronoceras sp. ex gr. *P. bolitoense*
Collina chilensis
Harpoceras cf. *subexaratum*
Phymatoceras ex gr. *P. erbaense*
Hildoceratidae gen. et sp. indet. (glatte Art)

c) Rio Manflas (Profil zum Portezuelo El Padre) (Abb. 1, Profil 16)

Peronoceras bolitoense
Peronoceras sp.
Collina cf. *chilensis*
Polyplectus sp.
Hildoceratidae gen. et sp. indet. (glatte Art)

d) Quebrada Llareta (Abb. 1 Profil 13)

Peronoceras cf. *vortex*
Maconiceras sp.
Polyplectus sp.
Phymatoceras sp.

e) Rio Jorquera (Vegas de Chañar) (Abb. 1, Profil 14a)

Peronoceras cf. *bolitoense*
Peronoceras cf. *P.* cf. *vortex*
Collina chilensis
Harpoceras cf. *subexaratum*
Hildoceratidae gen. et sp. indet. (glatte Art)

f) Quebrada Paipote bei Redonda (Abb. 4, Schicht 3)

Peronoceras sp. ex gr. *P.* cf. *verticosum*
Peronoceras cf. *bolitoense*
Collina chilensis
Hildoceratidae gen. et sp. indet. (2 Arten)

g) Quebrada Yerbas Buenas (Abb. 6)

Peronoceras cf. *bolitoense*
Collina chilensis
Maconiceras sp.
Hildoceratidae gen. et sp. indet. (glatte Art)

Der Horizont mit *Peronoceras bolitoense* kann mit dem oberen Teil der *fibulatum*-Subzone und dem tieferen Teil der *crassum*-Subzone in Europa verglichen werden, da in diesem Horizont erstmals die Gattung *Phymatoceras* auftritt.

4.3.3.2 Horizont mit *Peronoceras moerickei*

Dieser Horizont wurde bei folgenden Profilen gefunden:

a) Juntas del Toro (Abb. 10, Schicht 7)

Peronoceras cf. *bolitoense*
Collina chilensis
Harpoceras cf. *subexaratum*
Phymatoceras sp.
Hildoceratidae gen. et sp. indet. (2 Arten)

b) Salto del Toro (Abb. 10, Schicht 9)

Peronoceras cf. *bolitoense*

c) Rio Pulido (Abb. 10)

Peronoceras cf. *bolitoense*
Collina chilensis
Harpoceras cf. *subexaratum*
Hildoceratidae gen. et sp. indet. (glatte Art)

d) Quebrada El Asiento (Abb. 3, Schicht 6 u. 7)

Peronoceras moerickei (Holotypus)
Collina sp.
Catacoeloceras sp.

e) Salar de Pedernales (Abb. 1, Profil 1)

Peronoceras moerickei
Harpoceras cf. *subexaratum*
Maconiceras sp.
Hildoceratidae gen. et sp. indet. (2 Arten)

f) Quebrada Yerbas Buenas (Abb. 6)

Peronoceras moerickei

g) La Guardia

Peronoceras moerickei

h) Quebrada El Corral (Quebr. La Totora) (Abb. 1, Profil 20)

Collina chilensis
Catacoeloceras (?) sp.
Harpoceras cf. *subexaratum*
Hildoceratidae gen. et sp. indet. (2 Arten)

i) Quebrada El Bolito (Abb. 5, Schicht 9 u. 10)

Phymatoceras cf. *erbaense*
Hildoceratidae gen. et sp. indet. (3 Arten)

k) Quebrada Larga (Abb. 7, Schicht 9)

Peronoceras cf. *planiventer*
Peronoceras cf. *crassicostatum*
Collina sp.
Polyplectus sp.
Osperlioceras sp.
Phymatoceras ex gr. *P. erbaense*
Hildoceratidae gen. et sp. indet. (3 Arten)

Der Horizont mit *Peronoceras moerickei* kann mit dem oberen Teil der *crassum*-Subzone in Europa verglichen werden.

Die Fauna der Schicht 9 von der Quebrada Larga unterscheidet sich von der der übrigen Lokalitäten. Sie gehört möglicherweise bereits der *variabilis*-Zone an.

Bei den Profilen Juntas del Toro, Quebrada Larga, Quebrada El Corral und La Guardia liegen unmittelbar über dem letzten Horizont mit Dactylioceraten Schichten mit *Phymatoceras* cf. *fabale* und *Phymatoceras* cf. *lilli*. Diese Schichten können nicht mehr zur *bifrons*-Zone gerechnet werden und dürften gleichaltrig mit denen der *variabilis*-Zone in Europa sein.

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TAFELN

Tafel 1

Fig. 1–4: *Dactylioceras (Eodactylites) simplex* FUCINI, 1935

1 a, b: Phragmokon und Teil der Wohnkammer in Schalenerhaltung; Quebrada Chanchoquin; B. St. M. 1978 II 4; a: Lateral-, b: Frontalansicht; nat. Gr.

2 a, b: Phragmokon in Schalenerhaltung; Quebrada Chanchoquin; B.St.M. 1978 II 5; a: Lateral-, b: Ventralansicht; nat. Gr.

3: Teile von 5 Umgängen des Phragmokons in Schalenerhaltung; Quebrada Chanchoquin; B. St. M. 1978 II 7; Lateralansicht; nat. Gr.

4: Phragmokon in Schalenerhaltung; Quebrada Chanchoquin; B. St. M. 1978 II 6; Lateralansicht; nat. Gr.

Fig. 5–7: *Dactylioceras (Orthodactylites) anguinum* (REINECKE, 1818).

5: Steinkern z. T. mit Schale; Quebrada El Asiento; B. St. M. 1978 II 10; Lateralansicht; nat. Gr.

6 a, b: unvollständiger Steinkern mit Schale des Phragmokons und Teilen der Wohnkammer; Quebrada Chanchoquin; B. St. M. 1978 II 13; a: Lateral-, b: Ventralansicht; nat. Gr.

7 a, b: Teil des Phragmokons in Schalenerhaltung; Quebrada Chanchoquin; a: Lateral-, b: Ventralansicht; 1,5-fach vergr.

Fig. 8–11: *Dactylioceras (Orthodactylites) directum* (BUCKMAN, 1926).

8 a, b: Phragmokon weitgehend in Schalenerhaltung; Quebrada Chanchoquin; B. St. M. 1978 II 14; a: Lateral-, b: Ventralansicht; (teils Sipho sichtbar); nat. Gr.

9: Steinkern teilweise mit Schale; Quebrada Noria; B. St. M. 1978 II 21; Lateralansicht; 2-fach vergr.

10: Steinkern teilweise mit Schale; Quebrada Noria; B. St. M. 1978 II 22; Lateralansicht; nat. Gr.

11: Steinkern; Quebrada Yerbas Buenas; B. St. M. 1978 II 24; Lateralansicht; nat. Gr.

Fig. 12–18: *Dactylioceras (?Orthodactylites) helianthoides* YOKOYAMA, 1904.

12: Phragmokon und Wohnkammer in Schalenerhaltung; Quebrada Noria; B. St. M. 1978 II 30; Lateralansicht; nat. Gr.

13: Steinkern teilweise mit Schale; Quebrada Noria; B. St. M. 1978 II 31; Lateralansicht; nat. Gr.

14 a, b: Schalenerhaltung; Quebrada Noria; B. St. M. 1978 II 33; a: Lateral-, b: Ventralansicht; nat. Gr.

15: Schalenerhaltung; Quebrada Noria; B. St. M. 1978 II 34; Lateralansicht; nat. Gr.

16 a, b: Schalenerhaltung; Quebrada Noria; B. St. M. 1978 II 43; a: Lateral-, b: Ventralansicht; nat. Gr.

17: Schalen- und Steinkernerhaltung; Quebrada Noria; B. St. M. 1978 II 38 und 39 (aufsitzendes weiteres Fragment); Lateralansicht; nat. Gr.

18: Schalenerhaltung; Quebrada Noria; B. St. M. 1978 II 47; Lateralansicht; nat. Gr.

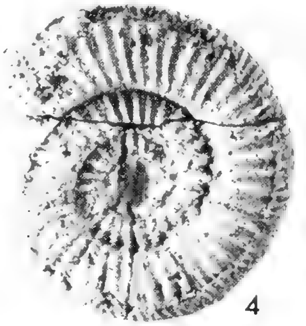
1a

1b

2a

2b

3



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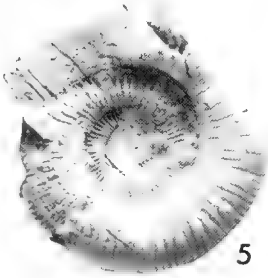

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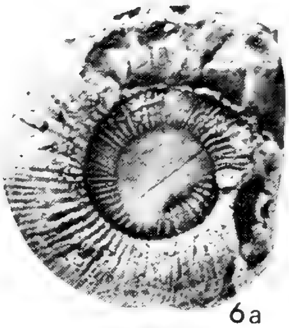

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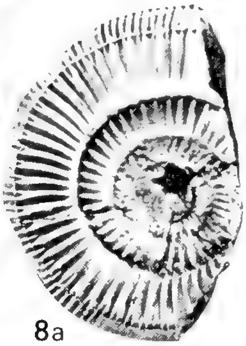

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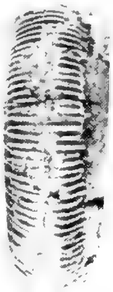

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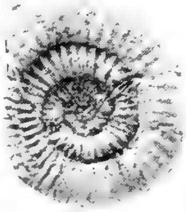

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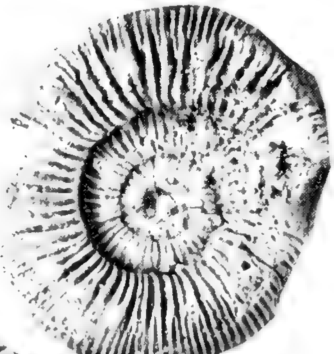

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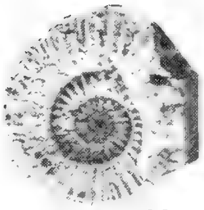

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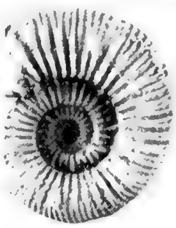

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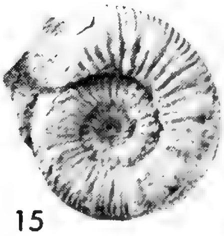

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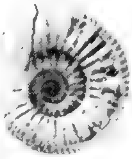

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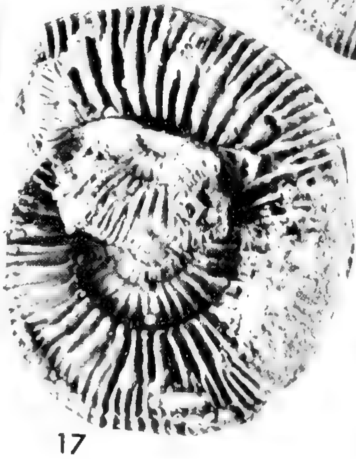

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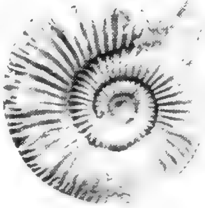

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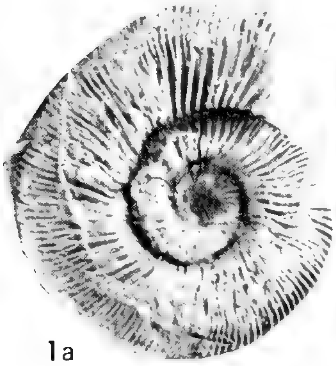

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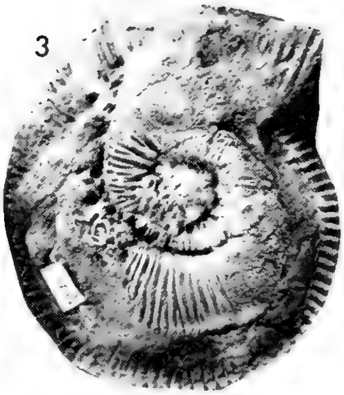

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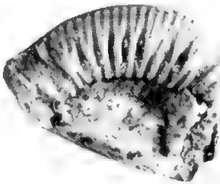

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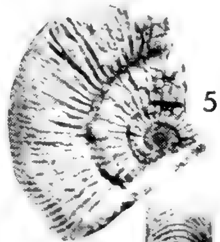

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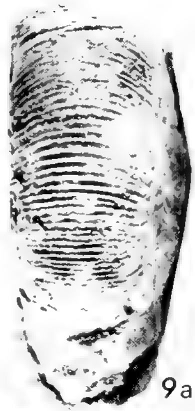

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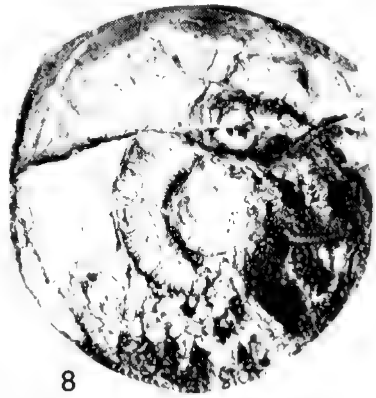

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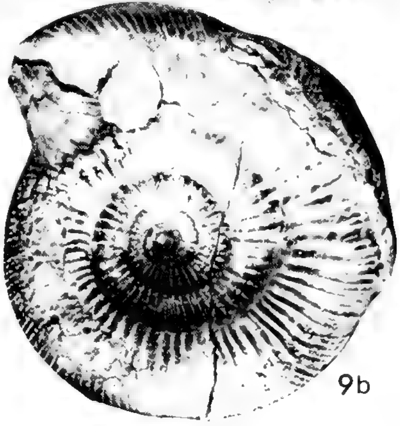

9b

Tafel 2

Fig. 1–3 u. 5: *Dactylioceras (Orthodactylites) hoelderi* nov. spec.

1 a, b: Holotypus; Phragmokon und Wohnkammer in Schalenerhaltung; Quebrada Yerbas Buenas; B. St. M. 1978 II 53; a: Lateral-, b: Frontalansicht; nat. Gr.

2 a, b: Teil des Phragmokons in Schalenerhaltung; Quebrada Yerbas Buena; B. St. M. 1978 II 56; a: Lateral-, b: Ventralansicht; nat. Gr.

3: Teile des Phragmokons und der Wohnkammer in Schalenerhaltung, auf einem Expl. von *Dactylioceras (?Orthodactylites) helianthoides;* Quebrada Noria; B. St. M. 1978 II 60; Lateralansicht; nat. Gr.

4: *Dactylioceras (?Orthodactylites)* cf. *helianthoides* YOKOYAMA, 1904; Steinkern; Rio Manflas; B. St. M. 1978 II 52; Lateralansicht; nat. Gr.

5 a, b: Schalenerhaltung; Quebrada Yerbas Buenas; B. St. M. 1978 II 57; a: Lateral-, b: Ventralansicht; nat. Gr.

Fig. 6–8: *Dactylioceras (Orthodactylites) tenuicostatum chilense* nov. subspec.

6 a, b: Holotypus; Steinkern der Wohnkammer; Rio Manflas; B. St. M. 1978 II 61; a: Ventral-, b: Lateralansicht; nat. Gr.

7: Steinkern-Fragment; Quebrada La Chaucha; B. St. M. 1978 II 68; Lateralansicht; nat. Gr.

8: Teils limonitiertes Steinkern-Fragment; Quebrada El Bolito; B. St. M. 1978 II 63; Lateralansicht; nat. Gr.

Fig. 9 a, b: *Nodicoeloceras* cf. *pseudosemicelatum* (MAUBEUGE, 1957), Schalenerhaltung; Quebrada Chanchoquin; B. St. M. 1978 II 77; a: Ventral-, b: Lateralansicht; nat. Gr.

Tafel 3

Fig. 1 a, b: *Nodicoeloceras* cf. *eikenbergi* (HOFFMANN, 1968), Schalenerhaltung; Quebrada Chanchoquin; B. St. M. 1978 II 78; a: Lateral-, b: Ventralansicht; nat. Gr.

Fig. 2–4: *Nodicoeloceras* cf. *crassoides* (SIMPSON, 1855) Form A.

2 a, b: Steinkern teils mit Schale; Quebrada Yerbas Buenas; B. St. M. 1978 II 79; a: Lateral-, b: Ventralansicht; nat. Gr.

3 a, b: Steinkern teils mit Schale; Quebrada Yerbas Buenas; B. St. M. 1978 II 82; a: Ventral-, b: Lateralansicht; nat. Gr.

4: Steinkern teils mit Schale; Quebrada Yerbas Buenas; B. St. M. 1978 II 81; Lateralansicht; nat. Gr.

Fig. 5: *Nodicoeloceras* cf. *crassoides* (SIMPSON, 1855) Form B; Schalenerhaltung; Quebrada El Asiento; B. St. M. 1978 II 84; Lateralansicht; nat. Gr.

Fig. 6: *Nodicoeloceras* cf. *crassoides* (SIMPSON, 1855) Form C; Steinkern mit Schalenresten; Quebrada El Asiento; B. St. M. 1978 II 85; Lateralansicht; nat. Gr.

Fig. 7–10: *Peronoceras* cf. *subarmatum* (YOUNG & BIRD, 1822)

7 a, b, c: Phragmokon-Steinkern mit Beginn (↑) der Wohnkammer; Quebrada El Bolito; B. St. M. 1978 II 87; a: Lateral-, b: Sagittal-, c: Ventralansicht; nat. Gr.

8: Wohnkammer-Steinkern; Majada del Carrizo; B. St. M. 1978 II 95; nat. Gr.

9: Wohnkammer-Steinkern; Majada del Carrizo; B. St. M. 1978 II 97; nat. Gr.

10: ? Wohnkammer-Steinkern; Majada del Carrizo; B. St. M. 1978 II 98; nat. Gr.


1a


1b


2a


2b


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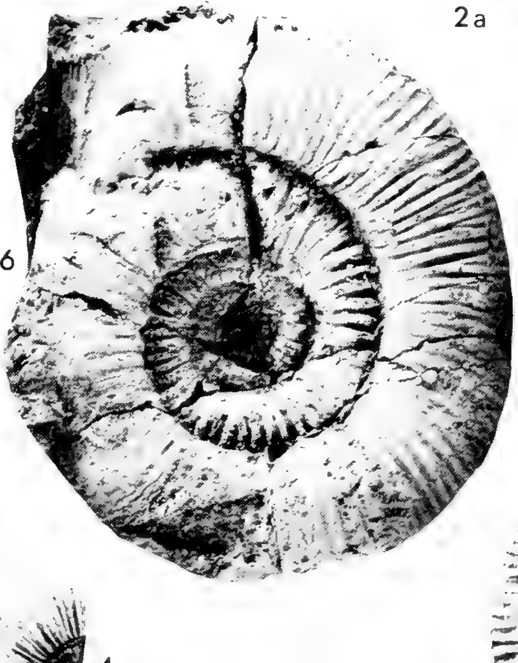
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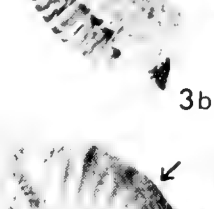
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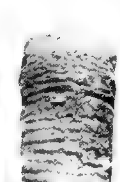
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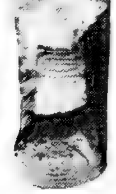
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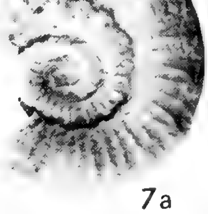
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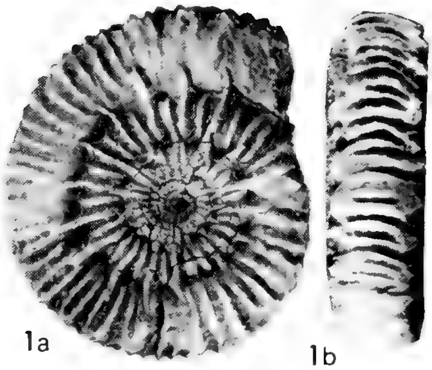

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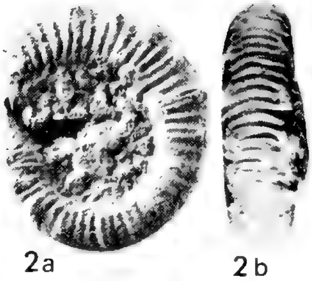

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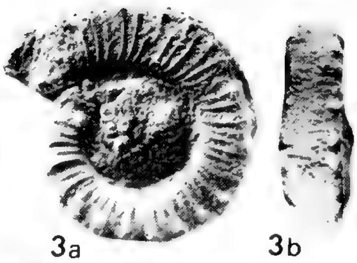

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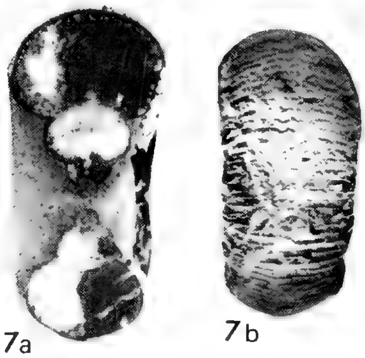

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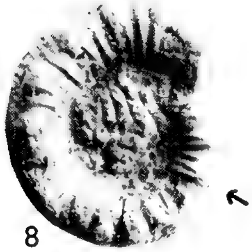

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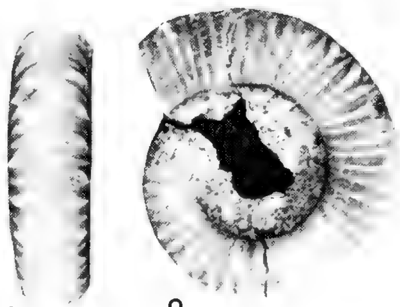

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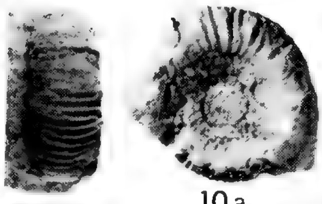

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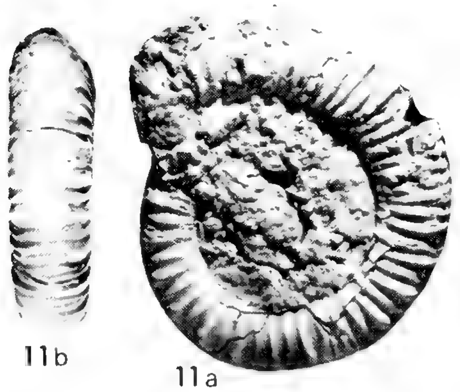

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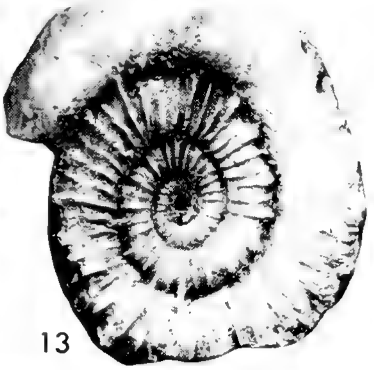

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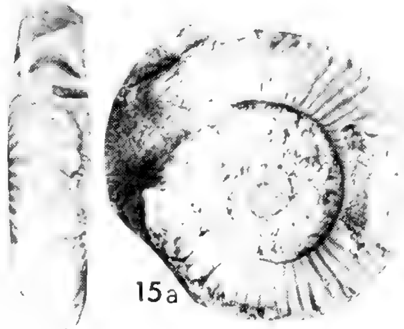


15b 15a

16c 16b 16a

Tafel 4

Fig. 1–4: *Peronoceras largaense* n. sp.

1 a, b: Holotypus; Phragmokon und Teil der Wohnkammer in Schalenerhaltung; Quebrada Larga; B. St. M. 1978 II 106; a: Lateral-, b: Ventralansicht; nat. Gr.

2 a, b: Wohnkammer-Steinkern; Quebrada Larga; B. St. M. 1978 II 107; a: Lateral-, b: Ventralansicht; nat. Gr.

3 a, b: Wohnkammer-Steinkern; Quebrada El Bolito; B. St. M. 1978 II 109; a: Lateral-, b: Ventralansicht; nat. Gr.

4: Wohnkammer-Steinkern (äußerer Umgang); Quebrada Larga; B. St. M. 1978 II 108; nat. Gr.

Fig. 5, 6: *Peronoceras* cf. *choffati* (RENZ, 1912)

5: Wohnkammer-Steinkern; Quebrada Yerbas Buenas; B. St. M. 1978 II 119; nat. Gr.

6: Phragmokon (125° der Umgänge erhalten), angeschliffene Querschnitte; Quebrada Yerbas Buenas; B. St. M. 1978 II 120; nat. Gr.

Fig. 7, 10: *Peronoceras* cf. *desplacei* (D'ORBIGNY, 1844)

7 a, b: Phragmokon in Schalenerhaltung; Quebrada Yerbas Buenas; B. St. M. 1978 II 115; a: angeschliffener Querschnitt; b: Ventralansicht; nat. Gr.

10 a, b: Äußerer Umgang Steinkern mit z. T. Schale (? Wohnkammer), innere Umgänge mit Kalzit ausgefüllter Phragmokon; Quebrada Yerbas Buenas; B. St. M. 1978 II 114; a: Lateral-, b: Ventralansicht; nat. Gr.

Fig. 8: *Peronoceras* cf. *renzi* (PINNA & LEVI SETTI, 1971)
Wohnkammer-Steinkern (↑ Beginn der Wohnkammer); Quebrada La Chaucha; B. St. M. 1978 II 118; nat. Gr.

Fig. 9, 11–16: *Peronoceras pacificum* n. sp.

9 a, b: Wohnkammer-Steinkern, Phragmokon mit Kalzit ausgefüllt (Oberfläche nicht erhalten); Quebrada Yerbas Buenas; B. St. M. 1978 II 123; a: Lateral-, b: Ventralansicht; nat. Gr.

11 a, b: Erhaltung wie Fig. 9; Quebrada Yerbas Buenas; B. St. M. 1978 II 122; a: Lateral-, b: Ventralansicht; nat. Gr.

12: Phragmokon, z. T. in Schalenerhaltung, Oberfläche der Wohnkammer nicht erhalten; Quebrada Potrerillos; B. St. M. 1978 II 127; nat. Gr.

13: Holotypus; Phragmokon (z. T. in Schalenerhaltung) und Wohnkammer (vorwiegend als Steinkern); Quebrada Potrerillos; B. St. M. 1978 II 125; nat. Gr.

14: Steinkern mit Schale (nur Ventralseite freipräpariert); Quebrada Yerbas Buenas; B. St. M. 1978 II 124; nat. Gr.

15 a, b: Erhaltung wie Fig. 9; Quebrada Yerbas Buenas; B. St. M. 1978 II 121; a: Lateral-, b: Ventralansicht; nat. Gr.

16 a–c: Innenwindungen Phragmokon (in Schalenerhaltung), Außenwindungen Wohnkammer-Steinkern; Quebrada Potrerillos; B. St. M. 1978 II 126; a, c: Lateral-, b: Sagittalansicht; a, b: nat. Gr., c 2:1.

Tafel 5

Fig. 1, 2: *Peronoceras pacificum* n. sp.

1 a, b: Wohnkammer-Steinkern, Phragmokon als Abdruck (letzte Windung z. T. mit Kalzit ausgefüllt); Quebrada El Bolito; B. St. M. 1978 II 129; a: Lateral-, b: Frontalansicht; nat. Gr.

2 a, b: Erhaltung wie Fig. 1; Quebrada El Bolito; B. St. M. 1978 II 128; a: Lateral-, b: Ventralansicht; nat. Gr.

Fig. 3 a, b: *Peronoceras* sp. ex gr. *P.* cf. *verticosum* (BUCKMAN, 1914); Wohnkammer-Steinkern (lateral etwas verdrückt); Quebrada Paipote bei Redonda; B. St. M. 1978 II 132; a: Lateral-, b: Frontalansicht; nat. Gr.

Fig. 4: *Peronoceras* sp. ex gr. *P.* cf. *vortex* (SIMPSON, 1855); Phragmokon-Innenwindungen (Steinkern mit Schalenresten); Quebrada Llareta; B. St. M. 1978 II 140; nat. Gr.

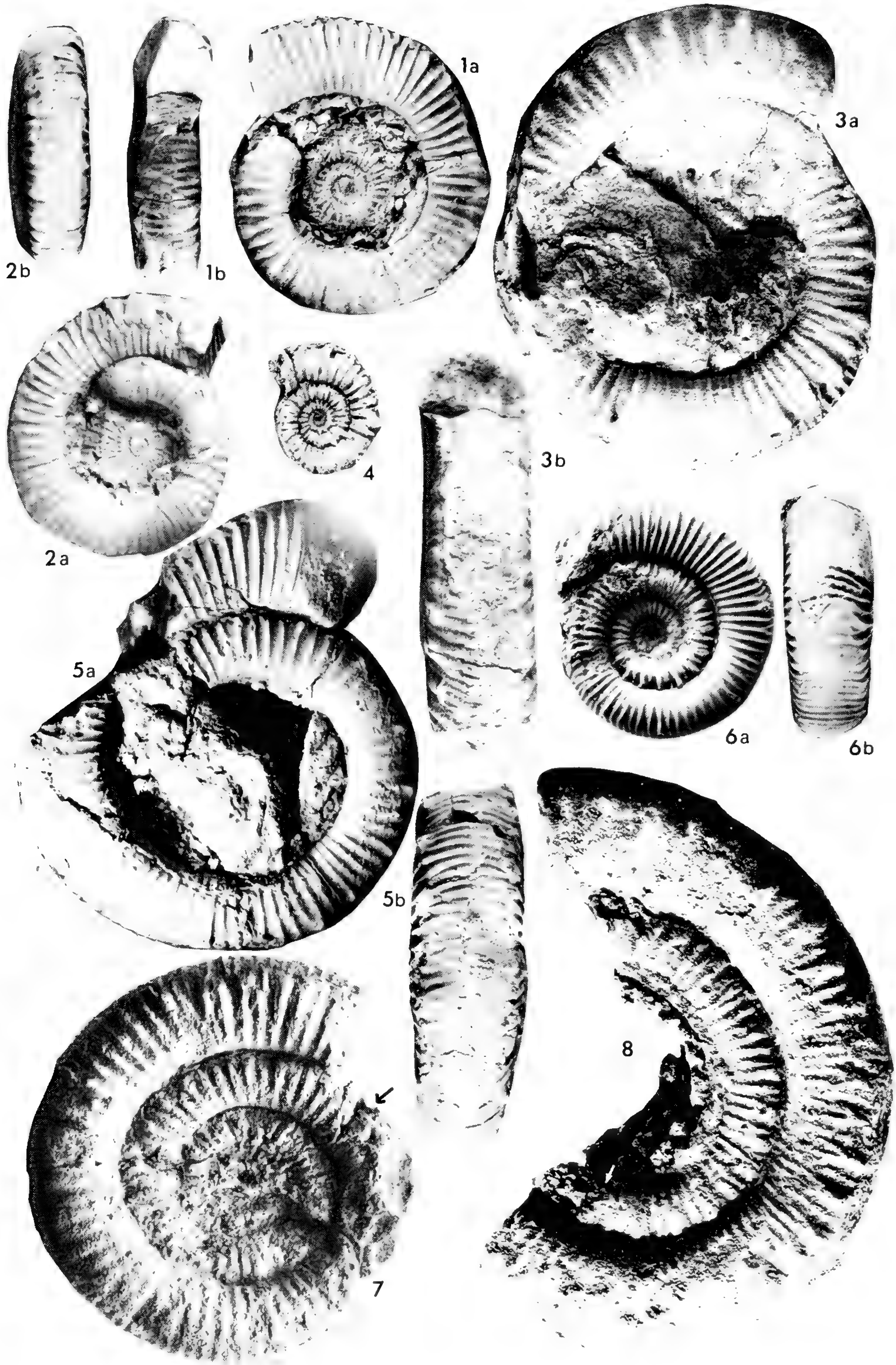
Fig. 5 a, b: *Peronoceras* cf. *verticosum* (BUCKMAN, 1914); Wohnkammer-Steinkern, Phragmokon mit Kalzit ausgefüllt (Oberfläche nicht erhalten); Quebrada Yerbas Buenas; B. St. M. 1978 II 130; a: Lateral-, b: Ventralansicht; nat. Gr.

Fig. 6 a, b: *Peronoceras* sp. cf. *P.* cf. *verticosum* (BUCKMAN, 1914); Phragmokon mit Schale, Wohnkammer als Steinkern mit Schalenresten; Quebrada Yerbas Buenas; B. St. M. 1978 II 136; a: Lateral-, b: Ventralansicht; nat. Gr.

Fig. 7, 8: *Peronoceras* cf. *vortex* (SIMPSON, 1855)

7: Phragmokon mit Kalzit ausgefüllt (Oberfläche nur z. T. erhalten), (↑ Beginn der Wohnkammer); Quebrada Cortaderita; B. St. M. 1978 II 137; nat. Gr.

8: Wohnkammer Steinkern (↑ Beginn der Wohnkammer) mit Resten des Phragmokons; Quebrada Cortaderita; B. St. M. 1978 II 138; nat. Gr.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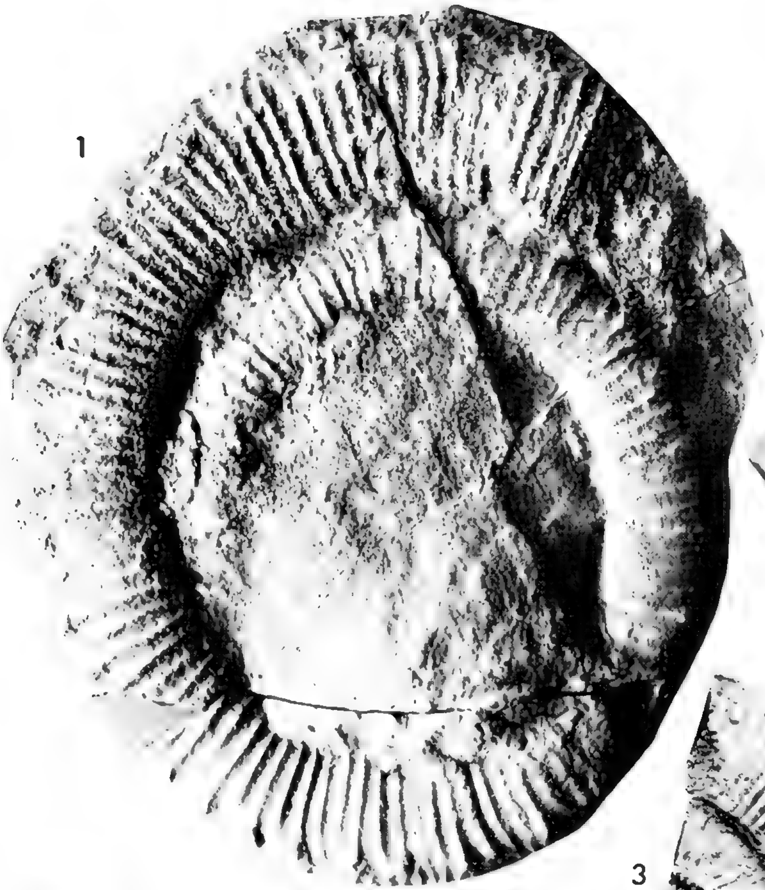

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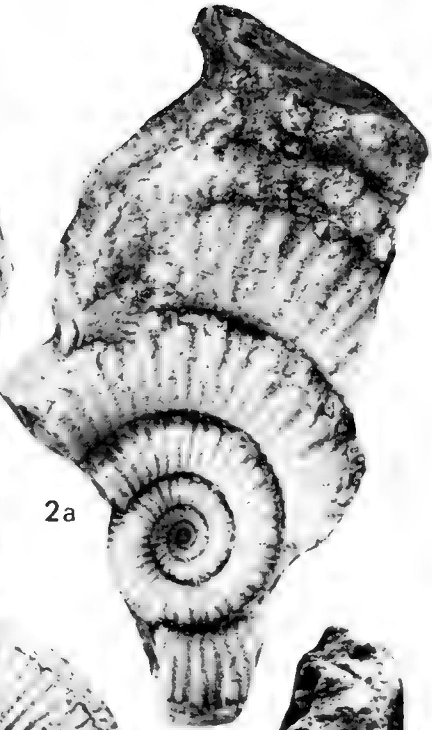

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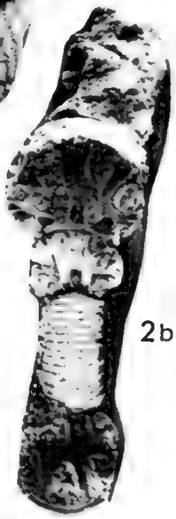

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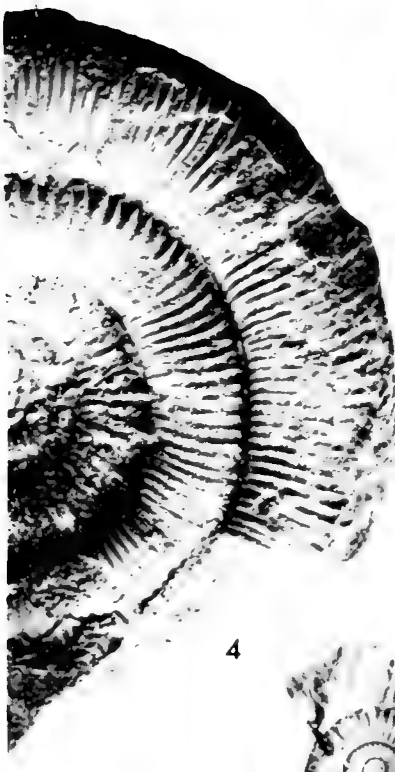

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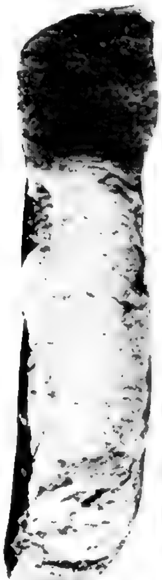

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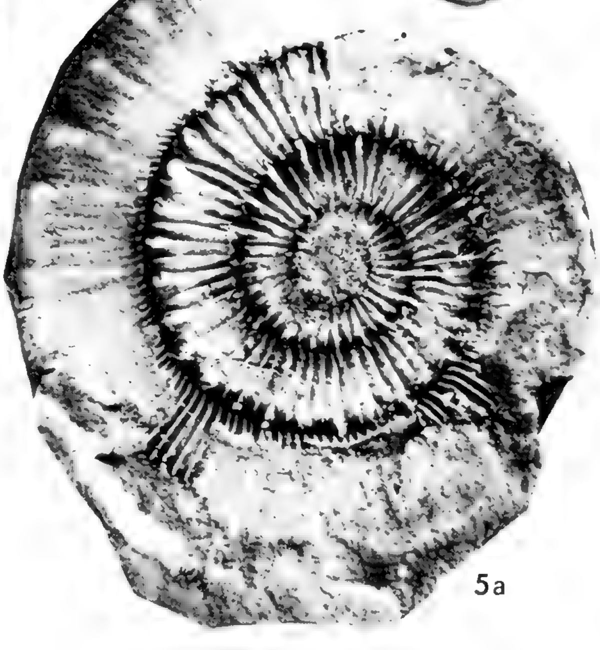

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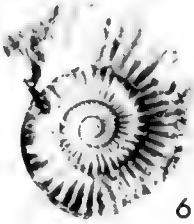

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Tafel 6

Fig. 1: *Peronoceras* cf. *vortex* (Simpson, 1855); Wohnkammer-Steinkern; Quebrada Paipotito; B. St. M. 1978 II 143; nat. Gr.

Fig. 2 a, b: *Peronoceras* sp. ex gr. *P. bolitoense* n. sp.; Steinkern-Phragmokon mit Rest der Wohnkammer; Quebrada Cortaderita; B. St. M. 1978 II 152; a: Lateral-, b: Sagittalansicht; nat. Gr.

Fig. 3: *Peronoceras* cf. *bolitoense* n. sp.
Phragmokon mit Schalenresten; Juntas del Toro; B. St. M. 1978 II 155; nat. Gr.

Fig. 4–6: *Peronoceras bolitoense* n. sp.

4: Wohnkammer-Steinkern (die beiden letzten Windungen), Phragmokon mit Schalenresten und Kalzit ausgefüllt; Quebrada El Bolito; B. St. M. 1978 II 147; nat. Gr.

5 a, b: Holotypus; Phragmokon in Schalenerhaltung (mit Kalzit ausgefüllt), letzter Umgang Wohnkammer-Steinkern; Quebrada El Bolito; B. St. M. 1978 II 146; a: Lateral-, b: Frontalansicht; nat. Gr.

6: Phragmokon-Innenwindung (vorw. in Schalenerhaltung); Rio Manflas (Profil zum Portezuelo El Padre); B. St. M. 1978 II 151; nat. Gr.

Tafel 7

Fig. 1, 2: *Peronoceras moerickei* n. sp.

1: Holotypus; Wohnkammer-Steinkern mit Resten des Phragmokons; Quebrada El Asiento; B. St. M. 1978 II 161; nat. Gr.

2: Wohnkammer-Steinkern; Quebrada Yerbas Buenas; B. St. M. 1978 II 169; nat. Gr.

Fig. 3, 4: *Peronoceras* cf. *bolitoense* n. sp.

3 a, b: Phragmokon (innere Windungen in Schalenerhaltung, letzte als Steinkern), ↑ Beginn der Wohnkammer (am Ende lateral verdrückt); Quebrada Yerbas Buenas; B. St. M. 1978 II 153; a: Lateral , b: Frontalansicht; nat. Gr.

4: Phragmokon (in Kalziterhaltung) mit Resten der Wohnkammer; Juntas del Toro; B. St. M. 1978 II 154; nat. Gr.

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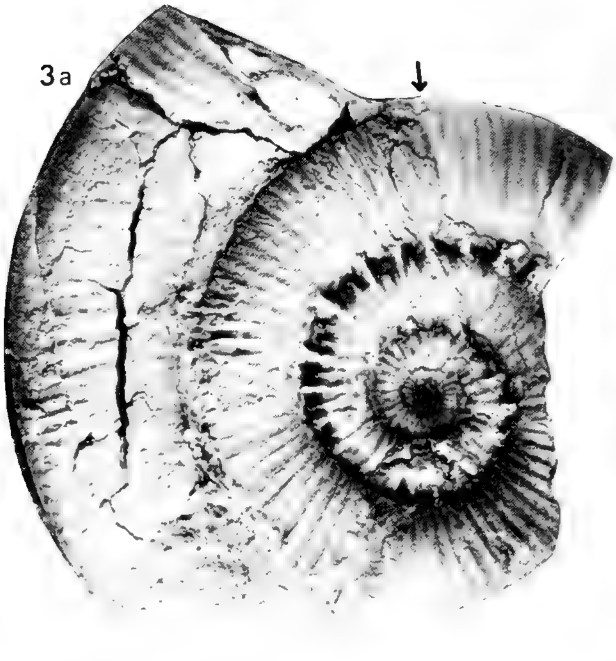

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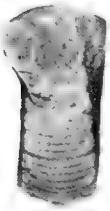

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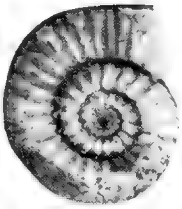

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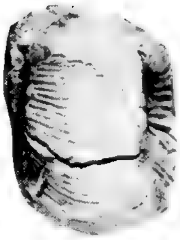

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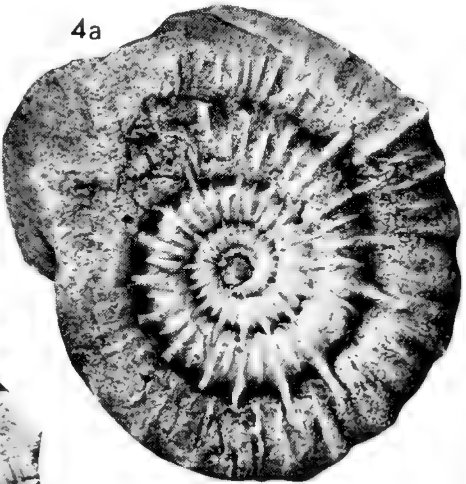

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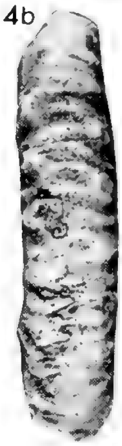

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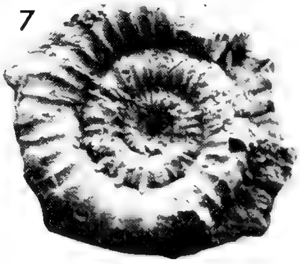

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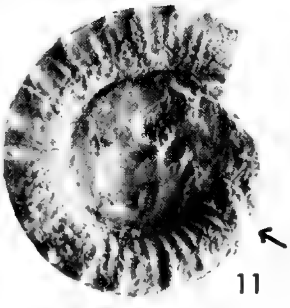

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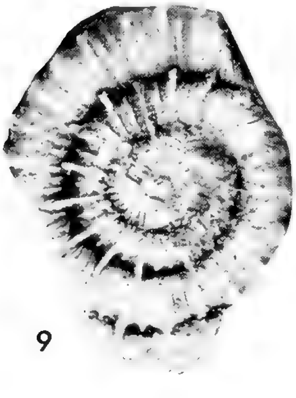

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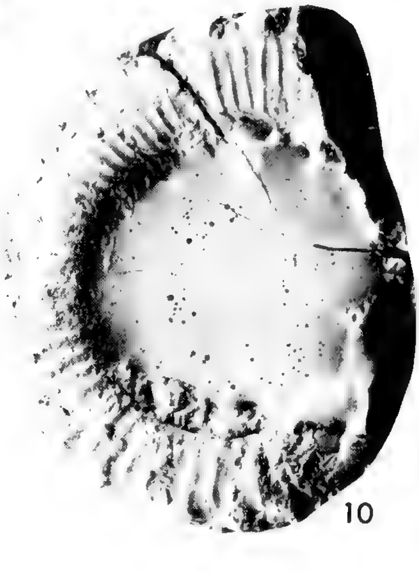

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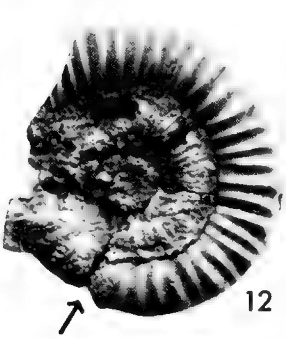

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Tafel 8

Fig. 1 a, b: *Peronoceras* cf. *planiventer* (GUEX, 1972)
Phragmokon-Steinkern mit Schalenresten; Quebrada Larga; B. St. M. 1978 II 170; a: Lateral-, b: Frontalansicht; nat. Gr.

Fig. 2 a, b: *Peronoceras* cf. *crassicostatum* (GUEX, 1972)
Phragmokon-Steinkern mit Schalenresten; Quebrada Larga; B. St. M. 1978 II 171; a: Lateral-, b: Frontalansicht; nat. Gr.

Fig. 3, 4, 6–12: *Collina chilensis* n. sp.

3: Ventralseite der Wohnkammer (Steinkern mit Schalenresten, ↑ Beginn der Wohnkammer); Rio Pulido; B. St. M. 1978 II 192; nat. Gr.

4 a–c: Holotypus; Phragmokon (z. T. in Kalzit erhalten und mit Schale), letzter Umgang Wohnkammer-Steinkern; Quebrada El Bolito; B. St. M. 1978 II 176; a, c: Lateral-, b: Ventralansicht; nat. Gr.

6: Phragmokon z. T. mit Schale, letzter Umgang Wohnkammer-Steinkern; Rio Pulido; B. St. M. 1978 II 190; nat.Gr.

7: Phragmokon mit Schalenresten; Rio Pulido; B. St. M. 1978 II 191; nat. Gr.

8 a, b: Phragmokon als Kalzitsteinkern und mit Schale (lateral etwas verdrückt); Quebrada El Bolito; B. St. M. 1978 II 180; a: Lateral-, b: Sagittalansicht; nat. Gr.

9: Phragmokon mit Schalenresten, letzter Umgang zumindest z. T. Wohnkammer; Quebrada El Bolito; B. St. M. 1978 II 179; nat. Gr.

10: Wohnkammer-Steinkern, Phragmokon mit Kalzit ausgefullt (Oberfläche nicht erhalten); Quebrada El Bolito; B. St. M. 1978 II 177; nat. Gr.

11: Wohnkammer-Steinkern (↑ Beginn der Wohnkammer), Quebrada El Corral; B. St. M. 1978 II 201; nat. Gr.

12: Wohnkammer-Steinkern (↑ Beginn der Wohnkammer), Phragmokon mit Kalzit ausgefüllt (Oberfläche nur z. T. erhalten); Quebrada Yerbas Buenas; B. St. M. 1978 II 200; nat. Gr.

Fig. 5: *Collina* sp.
Äußere Windung Wohnkammer-Steinkern (z. T. mit Schale), Phragmokon mit Kalzit ausgefüllt (z. T. Schalenoberfläche erhalten); Quebrada Larga; B. St. M. 1978 II 209; nat. Gr.

14