Cenomanian—Turonian ammonites from Coahuila, Mexico

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The ammonite fauna from Loma el Macho, Coahuila, Mexico, originally monographed by Böse (1920), is restudied in the light of recent work on the Cenomanian—Turonian ammonites of Texas and northeast Mexico. A description of Loma el Macho is given and it is shown that the collections available must be treated as a stratigraphically mixed assemblage. The less well known locality of Piedra de Lumbre and its ammonite fauna is also reviewed in relation to Loma el Macho. The Loma el Macho ammonites are described and discussed in detail, revising Böse's results where necessary. The species are *Metoicoceras* cf. *geslinianum* (d'Orbigny), *Metoicoceras*? sp., *Mammites* cf. *nodosoides* (Schlüter), *M.* cf. *mutabilis* Reyment, *Pseudaspidoceras* cf. *flexuosum* Powell, *P. footeanum* (Stoliczka), *Vascoceras* cf. *gamai* Choffat *Paravascoceras hartti* (Hyatt), *P.* aff. *hartti* (Hyatt), *P. carteri* (Barber), *P. angermanni* (Böse), *P. compressum* (Powell not Barber?) *Fagesia haarmanni* Böse, *F? pervinquieri* Böse, *Paramammites? mohovanensis* (Böse), *Neoptychites* sp., *Pseudotissotia* cf. *nigeriensis* (Woods), *P. adkinsi* (Kummel & Decker), and *Wrightoceras* cf. *munieri* (Pervinquière), These are predominantly lower Turonian ammonites, with the exception of *Metoicoceras* from the uppermost Cenomanian and, in terms of the Old-World sequences, several genera which range into the middle Turonian. The Loma el Macho association has close biogeographical relationships with regions throughout the mid-Cretaceous low and middle latitudes, including Europe, Turkestan, the Middle East, north and west Africa, Madagascar, India, Japan, California, western Interior U.S.A., the Caribbean, and the Pacific and Atlantic coasts of South America.

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Introduction

This work is a study of some Cenomanian—Turonian ammonites from Coahuila, Mexico, and consists mainly of a revision of an association monographed by Emil Böse in 1920. Preliminary results have been published in an earlier volume of this Bulletin (Chancellor et al. 1977) and a basic stratigraphical orientation will be found therein. By way of introduction, a brief summary is given here.

Much of Coahuila, now occupying a large area of the desert of northeast Mexico, is thought to have been a region of comparatively high elevation throughout the Cretaceous, known as the Coahuila Platform (see map, fig. 1). While surrounding areas were under deep water, the Coahuila Platform extended south from the North American continent and acted as a shallow-water reef-fringed block, perhaps comparable to the modern Bahamas or Florida (for a useful review of the mid-Cretaceous palaeogeography of Mexico see Wilson 1975).

The rocks which yielded the ammonites treated below are laterally continuous, although not necessarily of the same facies, with sediments in the United States which today outcrop over a vast area, even at zonal level (Koch 1980). The main localities concerned here are Loma el Macho and Piedra de Lumbre, both on the Coahuila Platform, and the rock unit is the Indidura Formation. For an excellent synopsis of what is currently known about this formation and its immediate correlatives the reader is referred to Young (1977) and Young & Powell (1978).

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The Loma el Macho locality

In 1920 Emil Böse published a monograph on the first sizeable collection of mammitine and vascoceratid ammonites from the North American continent. The fossils had been given to Böse

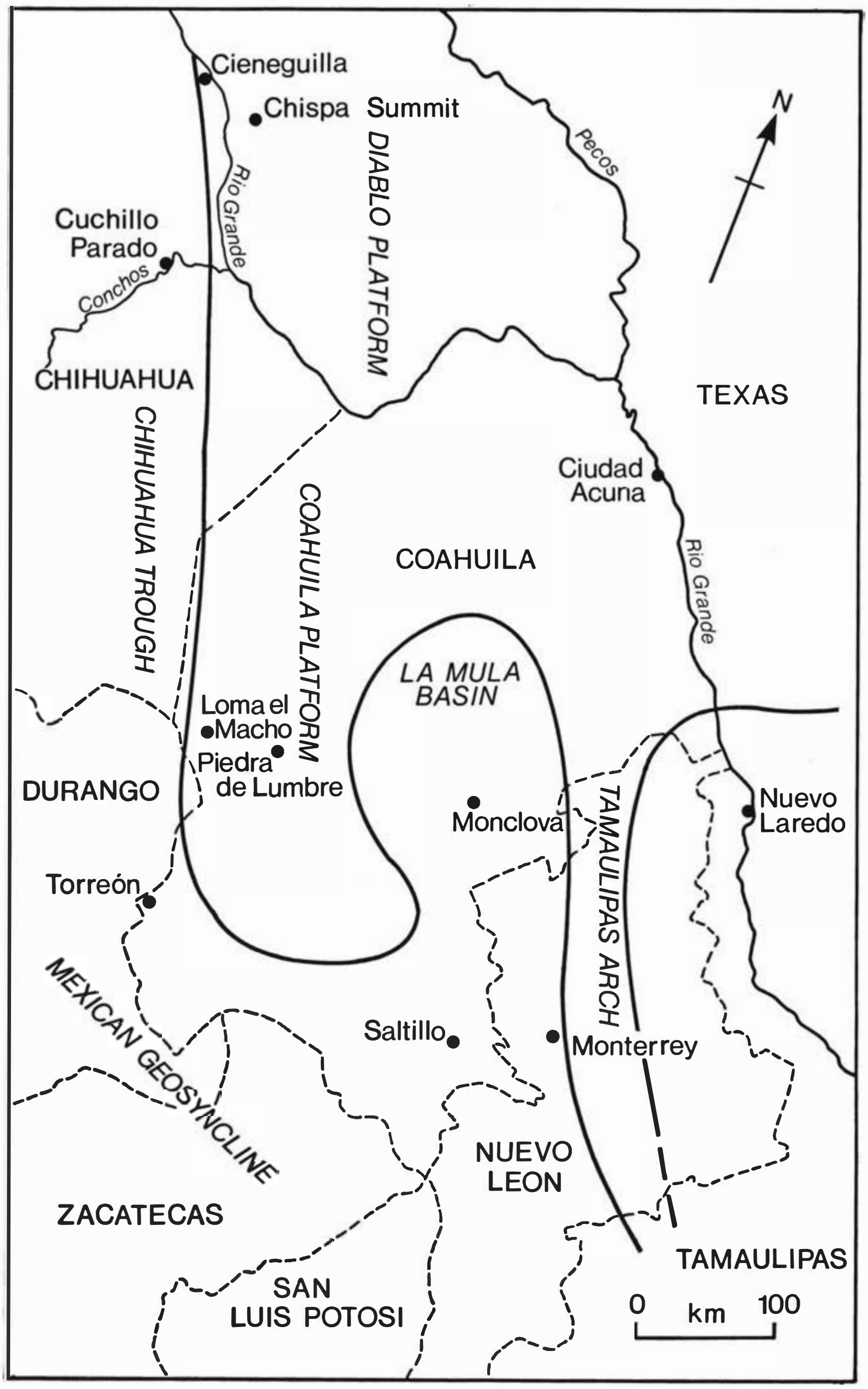


Fig. 1. Map of northeast Mexico and southwest Texas showing states, rivers, major towns and important localities mentioned in the text. Also shown are the principal elements of mid-Cretaceous palaeogeography (mainly after Young 1977).

on different occasions by Dr. E. Angermann and Dr. E. Haarmann, and had been found at a locality in the Mexican desert known to them as Cerro del Macho. This locality was located by Böse in an area approximately 30 km northwest of the Sierra del Tlahualilo (see Kellum & Robinson 1963) and was described as being on the Hacienda del Mohóvano, in the Municipality of San Pedro, District of Parras in the State of Coahuila.

Table 1. Böse's original (1913) list of ammonites from Cerro del Macho. The numbers on the right are the catalogue numbers of the Museum für Naturkunde, East Berlin, where the fossils are now kept. The roman numerals to the left indicate the stratigraphic horizons Böse believed his specimens to have come from (see Table 2).

I	*Metoicoceras* aff. *whitei* Hyatt C560.
I	*M. boesei* Jones [= *M.* n. sp. Böse; group *M. geslinianum* (Petrascheck not d'Orbigny)] C561.
II	*Mammites mohovanensis* Böse [group *M. nodosoides* (Schlüter)] C562.
II	*Pseudaspidoceras* aff. *footeanum* (Petrascheck not Stoliczka) C557.
II	*P.* aff. *pedroanum* (White) C556.
III	*Vascoceras angermanni* Böse [group *V. kossmati* Choffat] C568, C569, C570.
II	*V.* aff. *adonense* Choffat C571.
III	*V.* aff. *gamai* Choffat ("juv.") C567.
III	*V. mohovanense* Böse [group *V. polymorphum* Pervinquière] C574.
III	*Vascoceras*? sp. [group *'Ammonites' arnesensis* Choffat] C572.
II	*Fagesia haarmanni* Böse [group *F. superstes* (Kossmat)] C566.
II	*F. pervinquieri* Böse [group *F. tevesthensis* (Peron)] C565.
III	*Neoptychites* aff. *xetriformis* Pervinquière C576.
III	*N.* aff. *cephalotus* (Courtiller) C577.
III	*Hoplitoides* aff. *mirabilis* Pervinquière C558, C559.

Böse's (1920) monograph contains, besides a detailed description of the ammonites and their associated fauna of bivalves, including *'Inoceramus labiatus* Schlotheim', gastropods and echinoids, a full discussion of their biostratigraphical and palaeobiogeographical relations, as far as they could be deduced at that time.

Böse (1913, footnote on p. 13) had published some years before a preliminary list of identifications of the Cerro del Macho ammonites, and this is given here in modern taxonomic order, with spellings, etc., brought up to date (Table 1). Böse (1913) considered the ammonites to be an uppermost Cenomanian? (horizon I) and lower Turonian (horizon II and III) assemblage, displaying strong affinites with those known from North Africa and Portugal (see Table 2). The only changes made to this earlier (1913) list in Böse's (1920) monograph were a removal of the ? from *Vascoceras* sp. and a noting of the *V.* aff. *adonense* as a new species. (For a short history of what subsequently became of Böse's ammonites, so far as I have been able to reconstruct it, see the Appendix herein.)

Böse explained that Haarmann in making his collection had obtained the fossils from the three different horizons present at Cerro del Macho. Haarmann had drawn a section of the locality showing these horizons, which Böse reproduced (1920, p. 183).

There seems to have been uncertainty as to the exact horizon of some of the fossils; Böse expressed doubt about the levels of *V.* aff. *gamai* and *M.*

Table 2. The complete fauna from Cerro del Macho, tabulated according to Böse (1920, p. 192) but with the ammonite names revised (see text for details).

Lower Turonian	Horizon III	5—6 m of grey limestones with: *Paravascoceras hartti*? (C570), *P. carteri* (C569), *P. angermanni* (C568, C572, C573), *P. compressum* (C577), *Paramammites*? *mohovanensis* (C574), *Neoptychites* sp. (C576), *Wrightoceras* cf. *munieri* (C558, C559), *Inoceramus labiatus*, *Avicula* sp., *Trigonia* sp., *Crassatella* sp., *Tylostoma* sp. (bivalves and gastropods extremely abundant).
	Horizon II	2,5 m of grey-bluish marls with: *Mammites* cf. *nodosoides* (C563, C564), *M. mohovanensis* (C562, C575), *Pseudaspidoceras* cf. *flexuosum* (C557), *P. footeanum* (C556), *Paravascoceras* aff. *hartti* (C571), *Fagesia haarmanni* (C566), *F.*? *pervinquieri* (C565).
Upper Cenomanian	Horizon I	2 m of yellow and reddish marls and limestones with: *Metoicoceras* cf. *geslinianum* (C560, C561), *Exogyra* spp., *Hemiaster* sp.

The following forms were not recorded by Böse: *Metoicoceras*? sp. (PMMA1), *Mammites* cf. *mutabilis* (PMMA19), *Pseudotissotia* cf. *nigeriensis* (PMMA11), *P. adkinsi* (PMMA12, PMMA31, PMMA34).

boesei and he contradicts himself concerning the horizons of *V. mohovanense* and *N.* aff. *xetriformis.* Some of the handwritten labels with the specimens today in Berlin include stratigraphical data (e.g. "Unterturon, Ob. Horiz" with *N.* aff. *xetriformis*); where dated, however, these labels seem to have been written by Haarmann in 1926, and I have for this reason chosen to ignore them.

There are some differences in lithology among Böse's ammonites; the rather coarse, marly texture of C564, for example, contrasting with the fine, micritic limestone of C566. Unfortunately, I doubt very much if these differences can be used today to separate the fossils into their various horizons, as Haarmann did. In my experience the fossils change colour when a fresh surface is exposed and the specimens in the older collections always seem to be darker than more recently collected material.

The result of all this uncertainty, plus the fact that there no longer appears to be a recognisable section at Loma el Macho (today the official name of Cerro del Macho; see below) leads me to believe that Haarmann's "horizons" must be treated with caution.

In connection with the work of Reyment & Tait (1972) on the distribution of Cretaceous organisms around the formative Atlantic Ocean, these authors visited Haarmann's and Angermann's locality in 1975. Some new material was collected and I was subsequently engaged as a research student to study this material. Our preliminary joint results appeared in 1977 in which year Reyment and Tait, this time accompanied by me, made a second visit to the locality to collect more specimens. The results of my study of the collections made in 1975 and 1977, combined with Böse's original collection, are presented in this paper.

Böse's locality is apparently today mapped as a hill at 103° 32′ 30″ W, 26° 47′ 30″ N called Loma el Macho (1:50,000 scale map, El Cinco sheet, no. G-13-B-55 published by DETENAL: Dirección de Estudios del Territorio Nacional). There is a wet-season dam on the northwest side of Loma el Macho, named "El Macho" on the map. Since Haarmann's geological section for Cerro del Macho (Böse 1920, p. 183) also shows a "tank" (anglicization of the Spanish "estanque") or wet-season dam, there seems little doubt that Cerro del Macho is the same place as Loma el Macho. It should, however, be noted that Haarmann's section shows the "tank" on the south side of Cerro del Macho, rather than the north.

Unfortunately Chancellor et al. (1977) did not make clear that the exact points at which their collections were made (and which are shown in their fig. 4 photographs) are not on the hill mapped on the El Cinco sheet as Loma el Macho, but are in fact small hillocks on the northwest side of the dam. It should be noted that these hillocks were indicated to be "la loma llamada el Macho" by the local guide, Mr. Juan Chispasa, employed by Reyment and Tait in 1975. Chancellor et al.'s (1977) fig. 4a looks towards one of these hillocks in a northeasterly direction, with the dam extending off the photograph to the right. The track shown leading to the dam in fig. 4a is marked as a pecked line on the map, running northeastwards past the dam on the northern side of Loma el Macho. Professor Reyment informs me (personal communication) that some of the material he collected in 1975 was found in situ in an arroyo east of the "tank", but none of the specimens collected in 1977 could be so well localised.

I now believe it almost certain, notwithstanding the probably erroneous explanation of fig. 4a given by Chancellor et al., that this hillock is the one shown in Haarmann's section. That is to say, the precise locality from which the fossils have been collected is not Loma el Macho as it appears today on the map. In 1975 and 1977 fossils were also picked up loose on some of the other hillocks west of the dam; none is shown on the map as more than an irregularity in the contours. I found no fossils nor exposed section on the hill now named Loma el Macho.

Böse (1920, p. 184) quoted the total thickness of Haarmann's outcrop as "about 10 metres". This figure would approximate to the height of the fossiliferous hillock shown in Chancellor et al.'s fig. 4a, whereas the hill mapped as Loma el Macho is a much larger feature. It also seems likely that a true section may have been available near the dam in Haarmann's day, perhaps in connection with its construction. For the present it seems sensible to regard Cerro del Macho and Loma el Macho as synonymous, but until a far more rigorous geological study of the area is undertaken, there can be no certainty on this point.

Young & Powell (1978, footnote 1) relied heavily on Böse's Loma el Macho monograph in compiling their lists of species from the upper Cenomanian—lower Turonian of Mexico. Their zonation based on these lists is given here (Table 3); the *S. gracile* Zone corresponds to Haarmann's horizon I, the *M. nodosoides* Zone to horizon II, and the *V. mohovanense*(?) Zone to horizon III. Apart from the difficulty of using "*Vascoceras mohovanense*" as an index species (the holotype

Table 3. Young's & Powell's (1978, p. 24) ammonite zonation for the Cenomanian—Turonian of Mexico.

CONIACIAN	*Prionocyclus hazzardi*
TURONIAN	? ? *Prionocyclus hyatti* *Vascoceras mohovanense* (?) *Mammites nodosoides*
CENOMANIAN	*Sciponoceras gracile*

is the only certain specimen; see p. 112), Haarmann's horizons are clearly a weak foundation for recognition of two zones in the early Turonian. It is probably advisable, however, to retain the *S. gracile* and *M. nodosoides* Zones for use in Mexico, since they have been widely recognised throughout North America and Europe.

The Piedra de Lumbre locality

A measureable section is known to exist at Piedra de Lumbre, some 70 km east-northeast of Loma el Macho (Böse & Cavins 1928). Facies are probably alike at both localities — the few known ammonites from Piedra de Lumbre have a matrix similar to that of specimens in the Loma el Macho collection.

No stratigraphical study of Piedra de Lumbre seems to have been published since Böse & Cavins (1928, p. 29) listed the following species (Böse's determinations are retained here): *Austiniceras* aff. *austeni* (Sharpe), *Vascoceras angermanni* Böse, *V.* aff. *adonense* Choffat, *V.* cf. *mohovanense* Böse, *Vascoceras* (undescribed new species), *Fagesia haarmanni* Böse, *F.* aff. *haarmanni* (undescribed new species), *Fagesia* (undescribed new species), *Neoptychites* (undescribed new species), *Hoplitoides* aff. *mirabilis* Pervinquière, *Hoplitoides* (undescribed new species), [? = '*H.*' *adkinsi* Kummel & Decker; see below], *Acanthoceras?* sp., *Metoicoceras* cf. *whitei* Hyatt, *Metoicoceras* sp.

These determinations were left provisional by Böse's accidental death while his paper was in press (see Böse & Cavins 1928, p. 6). I quote here part of a letter dated June 28th., 1925 written by Böse to W. S. Adkins, almost certainly referring to Piedra de Lumbre: "Among other things I have found a new locality of Salmurian [= lower Turonian] with relatively better material than the Cerro del Macho on the Mohovano [= Loma el Macho] but with a number of new species and perhaps genera ... please keep these things I tell you in my letters and especially this one entirely to yourself until I publish...". All my attempts to locate the original fossils have so far been fruitless.

The only specimens from Piedra de Lumbre I have seen are those at the Bureau of Economic Geology in Austin, Texas. These were collected, apparently, in 1928 by Messrs. Wellings and Tappolet for the El Aguila Oil Company (La Compañía Shell de México) for whom Adkins worked from early 1921 until 1924 (see Adkins 1931; Young 1979). There is one specimen from Piedra de Lumbre in the University of Texas, Geology Department Collections in Austin (WSA 1318/1319). It is a half body whorl of *F. haarmanni* which I have reconstructed from two fragments. It is in a much better state of preservation than the equivalent part of the holotype (C566) from Loma el Macho.

Kummel & Decker (1954) reviewed the then known lower Turonian ammonites of Texas and Mexico kept at the Bureau of Economic Geology. They described the Piedra de Lumbre material under the names *F. haarmanni* (one specimen, WSA 2080; one fragment, BEG 20828), *Fagesia* sp. (one specimen, BEG 20826) and "*Hoplitoides*" *adkinsi* (the holotype, BEG 20832, first described by Adkins (1931, p. 59, pl. 4, fig. 2) together with five topotypes: BEG 20827; 20830; 20831; 20833; 20834), discussed below.

Systematic palaeontology

Location of specimens. — The following abbreviations are used to indicate the repositores of specimens studied:

BMNH	British Museum (Natural History), London.
UT	University of Texas at Austin, Geology Department Collections.
WSA	University of Texas at Austin, Geology Department Collections, W. S. Adkins Collection.
BEG	Texas Memorial Museum, Bureau of Economic Geology, Austin.
PM	Paleontologiska museet, University of Uppsala. (MA designates Middle America.)
USNM	United States National Museum, Washington DC.
C	Museum für Naturkunde, East Berlin.
OUM	Oxford University Museum.

Dimensions. — All dimensions are given in millimetres; figures in parentheses are dimensions ex-

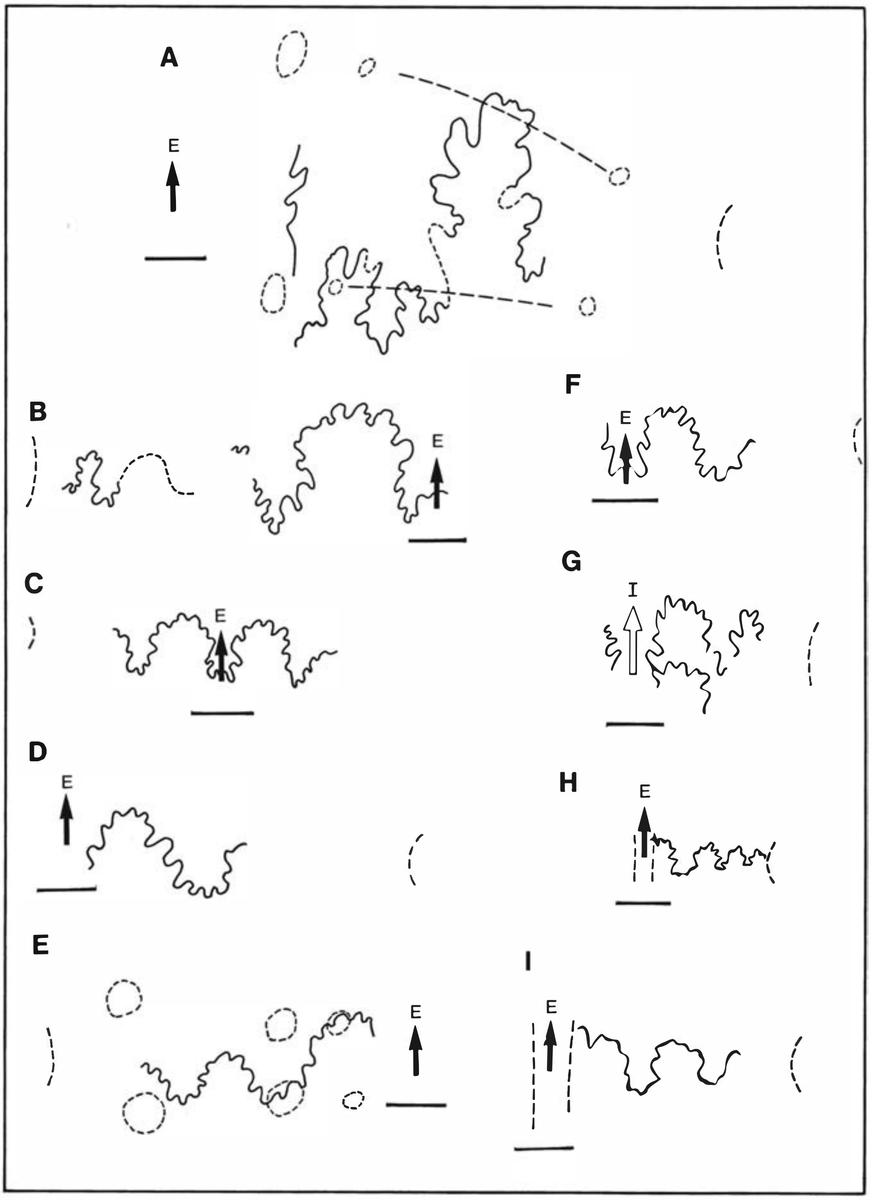


Fig. 2. Sutures of ammonites from Loma el Macho. E = External lobe, I = Internal lobe. Bar scales are 1 cm. A, *Pseudaspidoceras footeanum* (Stoliczka), from PMMA38; B, *Paravascoceras hartti* (Hyatt), from PMMA9; C, *Paravascoceras hartti* (Hyatt), from PMMA20; D, *Paravascoceras angermanni* (Böse), from PMMA8; E, *Mammites mohovanensis* (Böse), from PMMA2; F, *Fagesia? pervinquieri* Böse from PMMA5; G, *Fagesia? pervinquieri* Böse, from PMMA29; H, *Wrightoceras* cf. *munieri* (Pervinquière), from PMMA37; I, *Pseudotissotia adkinsi* (Kummel & Decker), from PMMA12.

pressed as a percentage of the diameter. D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus.

Techniques. — Specimens were whitened and photographed by Dr. W. J. Kennedy on Kodak Pan F35 mm film, ASA rating 50, using a Pentax reflex camera with a 1:2/55 Super Takumar lens.

Order AMMONOIDEA Zittel 1884

Suborder AMMONITINA Hyatt 1889

Superfamily ACANTHOCERATACEAE de Grossouvre 1894

Family ACANTHOCERATIDAE de Grossouvre 1894

Subfamily MAMMITINAE Hyatt 1900 (= Metoicoceratidae Hyatt 1903; Fallotitinae Wiedmann 1960)

REMARKS: Kennedy et al. (1980) provide a detailed discussion of this subfamily.

Genus METOICOCERAS Hyatt 1903

TYPE SPECIES: *Ammonites swallovi* Shumard 1859 by subsequent designation of Shimer & Shrock 1944.

REMARKS: *Metoicoceras* is discussed in full by Kennedy et al. (1981). In addition to the geographical range mapped by Cooper (1978, text-fig. 39) and Matsumoto (1973, text-fig. 4) there are reports of this genus from Colombia (Petters 1955), Iran (James & Wynd 1965) and Turkestan (Khakimov 1971).

Metoicoceras cf. *geslinianum* (d'Orbigny)
Figs. 3, 4

Metoecoceras aff. *whitei* Hyatt; Böse, p. 203, pl. 12, figs. 4, 7; text-fig. 1.

Metoecoceras sp. nov. [= *M. boesei* Jones]; Böse, p. 205, pl. 12, figs. 1—3.

COMPARE:
Metoicoceras geslinianum (d'Orbigny); Wright & Kennedy 1981, p. 62, pl. 17, fig. 2; pl. 18, figs. 1, 2; pl. 19, figs. 1, 2; pl. 20, figs. 1—3; pl. 21, figs. 1, 2; text-figs. 19C—E, 20, 21A—D (with full synonymy).

MATERIAL: C560, C561, from Loma el Macho.

REMARKS: Kennedy et al. (1981) give a complete synonymy for *M. geslinianum*, including within it Böse's *M.* aff. *whitei* and *M. boesei* Jones (1938, p. 127, pl. 10, figs. 1—3).

DISCUSSION: I have examined Böse's two poorly preserved extant specimens of *Metoicoceras*, casts of which are figured here. In my opinion neither can with certainty be referred to *M. geslinianum.* One might note that in reality the flexuous ribs of C561 are more impressive than they appear in Böse's illustrations (1920, pl. 12, figs. 1—3).

Metoicoceras? sp.
Figs. 5, 6

1977 *Metoicoceras* aff. *whitei* Hyatt; Chancellor et al., p. 91, fig. 5.

MATERIAL: Fragment PMMA1, length 28 mm, found in the matrix of PMMA7 (see below), from Loma el Macho.

DESCRIPTION: It is impossible to reconstruct the original whorl section of PMMA1, since only one flank is preserved. If the ventral area is assumed to be complete, however, the ammonite seems to have been compressed and discoidal with high, subparallel flanks which converge rather sharply just below the narrow, arched venter. Along each ventrolateral shoulder is a row of sharp, slightly oblique clavi, which number about 18 per half whorl at this projected diameter. There is a faint suggestion of a double row of minute clavate swellings on the venter. The ventrolateral clavi are connected by very low folds, which extend down the flanks as markedly alternating strong and weak ribs which inflect (probably forwards, although the direction of growth is uncertain) at the point on the flank where the whorl section becomes convergent.

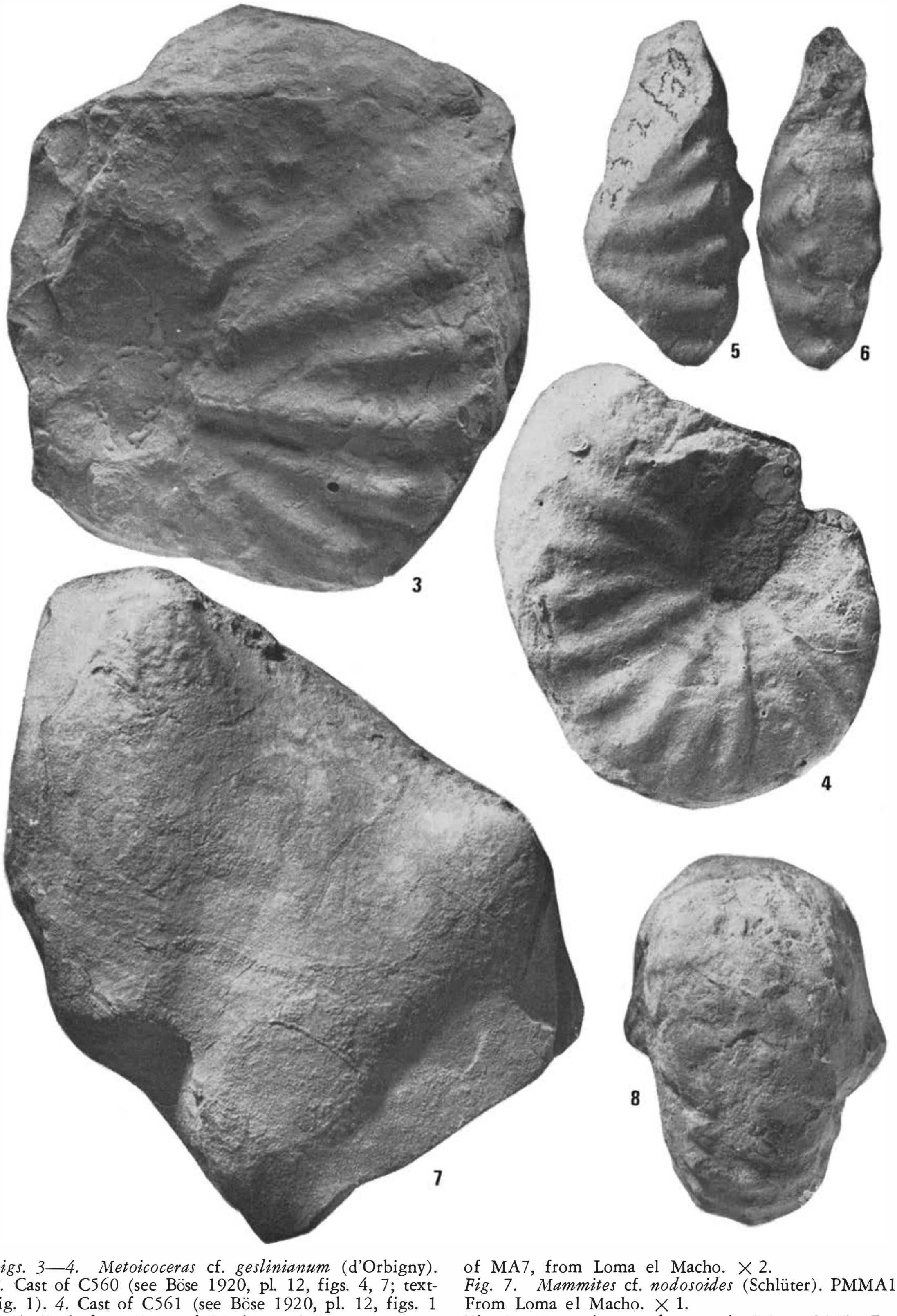
DISCUSSION: Previously Chancellor et al. (1977, p. 91) determined PMMA1 as *M.* aff. *whitei*, but I now believe it is too fragmentary for any certain identification. It may, as Cooper (1979, p. 124) thought, be a *Quitmaniceras* Powell. I have compared PMMA1 with numerous specimens and fragments of *Quitmaniceras* from Calvert Canyon, Texas (Oxford University Museum Collections) and find a particularly strong resemblance to OUM KT547.

Genus MAMMITES Laube & Bruder 1887 (= *Schlueterіceras* Hyatt 1903)

TYPE SPECIES: *Ammonites nodosoides* Schlüter 1871 by monotypy. De Grossouvre (1894) was the first to state *nodosoides* as the type of *Mammites.*

REMARKS: See Wright & Kennedy (1981, p. 75) for a diagnosis and remarks on this genus.

DISCUSSION: I have encountered particular difficulties in establishing a clear distinction between this genus and *Pseudaspidoceras* Hyatt (see below)

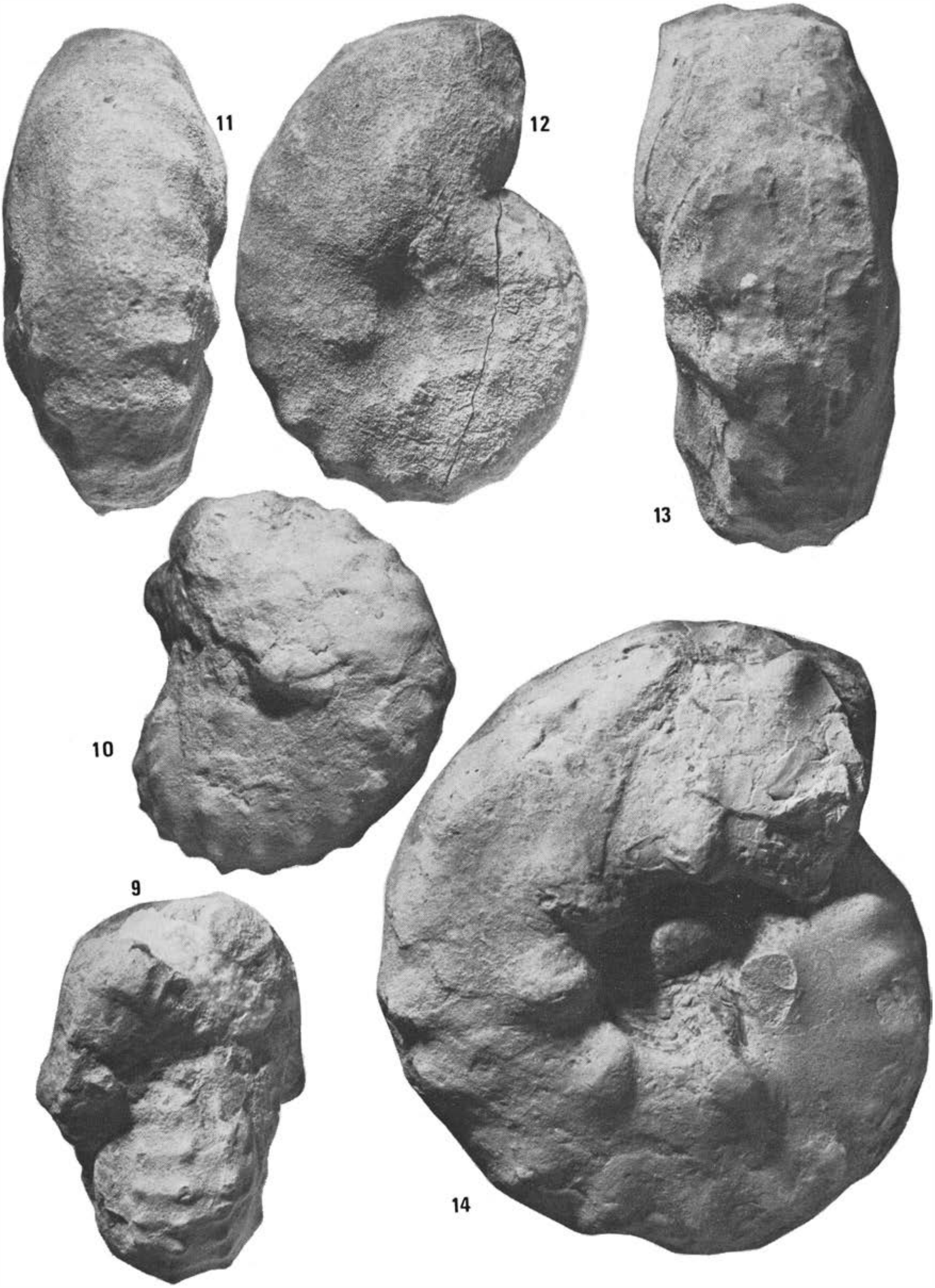


Figs. 3—4. Metoicoceras cf. *geslinianum* (d'Orbigny). *3.* Cast of C560 (see Böse 1920, pl. 12, figs. 4, 7; text-fig. 1). *4.* Cast of C561 (see Böse 1920, pl. 12, figs. 1—3). Both from Loma el Macho. × 1.

Figs. 5—6. Metoicoceras? sp. PMMA1. From the matrix of MA7, from Loma el Macho. × 2.

Fig. 7. Mammites cf. *nodosoides* (Schlüter). PMMA18. From Loma el Macho. × 1.

Fig. 8. Mammites mohovanensis Böse. C575. From Loma el Macho. × 1. See also Figs. 9—10.



Figs. 9—10. *Mammites mohovanensis* Böse. C575. From Loma el Macho. × 1. See also Fig. 8.
Figs. 11—12. *Mammites* cf. *nodosoides* (Schlüter). C 563. From Loma el Macho. × 1.

Fig. 13. *Mammites* cf. *nodosoides* (Schlüter). C564 (see Böse 1920, text-fig. 4). From Loma el Macho. × 1. See also Fig. 15.
Fig. 14. *Mammites mohovanensis* Böse. PMMA2. From Loma el Macho. × 1. See also Figs. 2E, 16.

although the type species are distinct enough. I follow Matsumoto et al. (1978) in referring *Ammonites conciliatus* Stoliczka to *Mammites*, whereas some authors (notably Collignon 1965b) consider it a *Pseudaspidoceras*. In my opinion, the essential differences between *Mammites* and *Pseudaspidoceras* resides in the greater involution of the former. As Dr. P. Bengtson has indicated to me, however, the exaggerated development of ventrolateral horns often seen in mature *Mammites* rarely occurs in undoubted *Pseudaspidoceras*, although a possible exception is *P. vincentinii* Collignon (1966, pl. 23).

Mammites cf. *nodosoides* (Schlüter)
Figs. 7, 11—13, 15

COMPARE:
Mammites nodosoides (Schlüter); Wright & Kennedy 1981, p. 75, pl. 17, fig. 3; pl. 19, fig. 3; pl. 20, fig. 4; pl. 22, fig. 4; pl. 23, figs. 2, 3, ?1; pl. 24, figs. 2, 3; text-figs. 19B, 23, 24 (with full synonymy).

MATERIAL: Three poorly preserved but more or less complete juvenile specimens, C563, C564 and PMMA16, with one fragment PMMA18 consisting of one side of about 60° of a large body chamber, all from Loma el Macho.

DIMENSIONS (approximate):

	D	Wb	Wh	Wb:Wh	U
C563	70(100)	30(43)	30(43)	1,00	12(17)
C564	90(100)	43(48)	43(48)	1,00	15(16)
PMMA16	70(100)	30(43)	30(43)	1,00	—
PMMA18	?200 —	?70 —	—	—	—

DESCRIPTION: C563, C564 and PMMA16 appear to belong to a single species, although all the material is very poorly preserved. The suture of C564 was erroneously described by Böse (1920, p. 207, text-fig. 4) as that of *M. mohovanensis*. The whorl section is a high trapezoid, with flat convergent flanks and a broadly arching venter. The umbilical shoulder appears to be smoothly rounded. The better preserved of the two smaller specimens, C563, has four moderately prominent, slightly bullate umbilical nodes per half whorl, slightly narrower than the interspaces between them. C564 has about five much less prominent umbilical nodes per half whorl, which bifurcate irregularly into low rectiradiate ribs which end at a row of 10 sharp clavate inner ventrolateral tubercles high on the shoulder. An equal number of outer ventrolateral tubercles are set slightly behind the inner tubercles and are joined to them by prominent but narrow ridges which weakly extend across the venter. The ventrolateral tubercles of the smaller specimens are approximately equal in number to those of C564 but have the outer row set somewhat forward of the inner row. During growth the outer row of tubercles on C564 gradually weakened and moved outwards from the siphonal area.

PMMA18 is a mere fragment and no whorl section can be reconstructed from it. It may, however, be stated that the rather steep umbilical wall appears to curve into a generally flat flank which rapidly declines towards the venter so that the ventrolateral shoulder is well rounded. Prominent ventrolateral horns project sharply away from this shoulder and terminate in clavate ridges or arêtes. There must have been about 5—6 ventrolateral tubercles per half whorl when PMMA 18 was complete. The two remaining tubercles are linked to the umbilical shoulder by fold-like ribs across the flanks. One of these is rectiradiate while the other is offset by about 20° from the vertical. Probably this indicates that PMMA18 is part of a mature body whorl, near the aperture. On the internal part of PMMA18 is the impression of the previous whorl; from this it is possible to say that involution was about 25 %. This previous whorl had about 9—10 prominent ventrolateral clavi per half whorl, from which strong fold-like ribs extended down the flanks.

DISCUSSION: C563 and C564 are the "several fragments" Böse (1920, p. 206) referred to *M. mohovanensis*, except that one of these, C575, is described below as belonging to the latter species (see Appendix). Since the suture described from *M. mohovanensis* cannot be made visible on the holotype of that species (C562), but has instead been painted in on C564 and figured by Böse, one must assume that the suture he described belongs here and not to *M. mohovanensis*. Moreover, C562 has a broader whorl section (Wb:Wh = 1,27) than the present material. PMMA18 can only be compared with difficulty to other specimens, but when all together are compared with the lectotype of *M. nodosoides* (C555, see Wright & Kennedy 1981 for a full description) good agreement is found, within the limits of preservation. It is worth noting that C564 is comparable with some of the more widely umbilicated specimens of *Spathites*, a genus apparently absent from Loma el Macho but well-known from elsewhere in Mexico (see below in discussion of *M. mohovanensis*).

Mammites mohovanensis Böse
Figs. 2E, 8—10, 14, 16—21

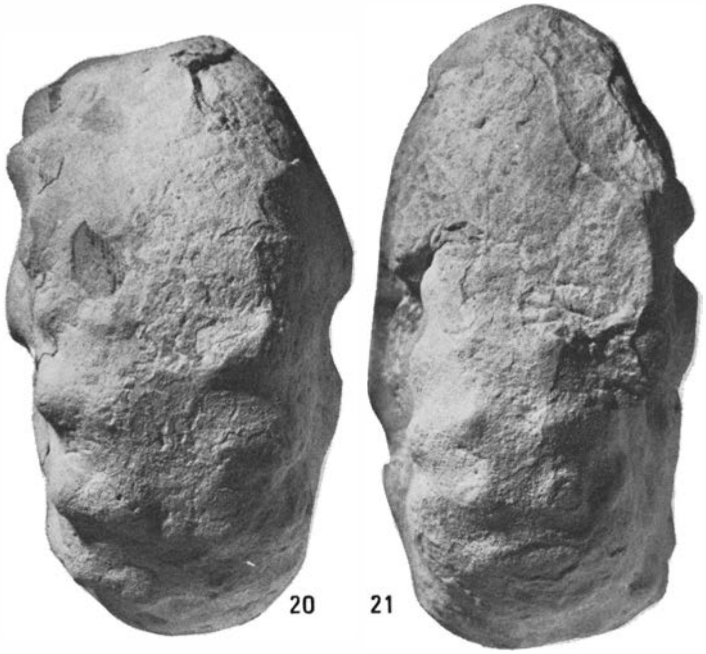
1920 *Mammites mohovanensis* Böse, p. 206, pl. 12, figs. 6, 8; not text-fig. 4.

1977 *Mammites mohovanensis* Böse; Chancellor et al., p. 91, figs. 6, 7.

Fig. 15. *Mammites* cf. *nodosoides* (Schlüter). C564 (see Böse 1920, text-fig. 4). From Loma el Macho. × 1. See also Fig. 13.

Fig. 16. *Mammites mohovanensis* Böse. PMMA2. From Loma el Macho. × 1. See also Figs. 2E, 14.

Figs. 17—19. *Mammites mohovanensis* Böse. Holotype C562 (see Böse 1920, pl. 12, figs. 6—8). From Loma el Macho. × 1.



Figs. 20—21. Mammites mohovanensis Böse. PMMA14. From Loma el Macho. × 1.

MATERIAL: Böse's holotype C562 and one of his presumed paratypes C575. The latter, figured here (Figs. 8—10), is a distorted juvenile, showing well the ventral ornament. The other material Böse grouped under this name is described above as *M.* cf. *nodosoides*. Further material is PMMA2, preserved more completely than C562 and apparently retaining a little over half a whorl of body chamber. PMMA14 shows well the earlier whorls but without the body chamber. PMMA15, also without body chamber and badly corroded on one side. PMMA2 and C562 are encrusted in places by oysters. All are from Loma el Macho.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
C575	? 50(100)	?35(70)	?30(60)	?1,16	? 6(12)
PMMA2	101(100)	51(51)	39(39)	1,31	29(29)
PMMA14	? 80(100)	38(48)	33(41)	1,15	?10(13)

DESCRIPTION: Böse (1920) provided an adequate description of *M. mohovanensis* apparently based almost entirely on the holotype, but the juvenile C575 and the new collections allow a more thorough account. Unfortunately, the partial suture of PMMA2 is all we know of this character of the species: it is apparently very simple and close to that of typical *Vascoceras* (see Fig. 2E).

C575 shows the following features: rapidly expanding very involute whorls with a very small umbilicus showing one or two prominent nodules per half whorl. The section is a little wider than high, with smooth convergent flanks meeting a flat, bevelled ventrolateral shoulder ornamented with about 11 small but prominent round or slightly bullate inner and outer ventrolateral tubercles per half whorl. These tubercles are linked by slightly prorsiradiate narrow ridges which in turn extend feebly over the slightly concave midventer and fade below the inner ventrolateral tubercles high on the flanks.

A distinctive feature of PMMA2 is the bullate tubercles, the earliest of which appear twisted, such that their adoral faces slope more gently than their adapical faces. The ribbing described by Böse for his material is poorly developed on PMMA2, presumably because the latter shows later growth stages; the ratio of about 16—17 ventrolateral tubercle pairs to 6—7 umbilical tubercles is, however, retained on the outer whorl of PMMA2. The umbilical tubercles are much larger and project much further than the inner ventrolateral tubercles, giving a flared costal whorl section with strongly convergent, concave flanks.

The intermediate growth stages are shown by PMMA14 (see Figs. 20, 21). On this specimen, at a point equivalent to about 70° behind the earliest visible section of PMMA2, the whorl is roughly square with vertical flanks and more pronouncedly bevelled ventrolateral shoulders, inclined at about 45° to the flanks. In this respect PMMA14 stands out from the rest of the material since we know that in both smaller and larger specimens the whorl section is more trapezoidal.

As Böse predicted for larger specimens than he had seen, the outer ventrolateral tubercles of PMMA2 become somewhat less prominent in later growth stages. They also move out from the siphonal area, which thus becomes flatter and smoother and eventually broadly arched. The outer ventrolateral tubercles tend to be set a little further forward than the inner row. Since a single row of ventrolateral horns such as occur in mature *M. nodosoides* is not seen in the present material, the possibility remains that only immature material has been seen in *M. mohovanensis.*

DISCUSSION: *M. mohovanensis* appears to be quite distinctive, if we accept that the present specimens are not merely juveniles of some species better known at larger sizes. *M. mohovanensis* is a highly involute *Mammites* with exceptionally prominent umbilical tubercles and broad whorl section.

M. nodosoides (see above) is distinct from *M. mohovanensis* in its more compressed section at comparable diameters. The specimen figured as *M. michelobensis* [= *nodosoides*] from Saxony by Petrascheck (1902, pl. 9, figs. 2a, b) has prominent umbilical tubercles and a squarish whorl section and may represent a transition to *M. mohovanensis.* The small Tunisian specimen figured by Pervinquière (1907, pl. 18, fig. 1) appears to be close in whorl section to the Mexican species.

Many reports of *M. nodosoides* refer only to early whorls, but species can usually only be compared at later stages of ontogeny. The specimens of intermediate size figured from Turkestan by Arkhanguelskij (1916, pl. 8, figs. 4, 6) have a broad trapezoidal section and thus resemble *M. mohovanensis.* The *M. nodosoides* figured by Powell (1963a, pl. 33, figs. 1, 3, 4, 6, 10, 11; text-figs. 3m—o, t, u) from Chihuahua are also similar to *M. mohovanensis* in their involution and low whorl section with prominent umbilical tubercles, and the fragment of *M. nodosoides* from New Mexico figured by Cobban & Hook (1979, pl. 9, figs. 6, 7) is very close to the Mexican species.

Ammonites conciliatus Stoliczka (1864, p. 99, pl. 50, fig. 4, 4a, pl. 51, fig. 1, 1a), which as stated above I take to be a *Mammites*, was represented in the original illustrations by the inner whorls of a "very large" syntype (pl. 50) and the "large" lectotype (pl. 51) both from Mungilpadi, India. As Spath (1935, p. 416) observed, following Kossmat (1897, p. 21), this species is "a near relation" of *M. nodosoides.* Böse (1920, p. 186) noted that *M. conciliatus* is "still more similar" to *M. mohovanensis* than is *M. nodosoides*, the main difference consisting "in its more evolute form" (one-third as against two-thirds embracing) and in "some details of ornamentation", i.e. denser ventrolateral tubercles in the Indian species. Böse considered that the specimen figured from Bohemia as *Ammonites conciliatus* by Fritsch & Schlönbach (1872, pl. 7, figs. 1, 2) in being more involute than Stoliczka's specimens resembled *M. mohovanensis* more closely. In my opinion, the Bohemian specimen is too compressed to be considered as close to *M. mohovanensis* as is Stoliczka's small specimen, which is almost identical to PMMA2, except for its involution and less prominent umbilical tubercles.

M. conciliatus is well-known from Madagascar, where it is the index ammonite for the middle Turonian (Collignon 1977). Besairie (1930, pl. 18, figs. 1, 1a, 2) figured two specimens from Betioky and Maintirano Provinces, which I have examinated at the Université Pierre et Marie Curie in Paris, and Basse (1931, pl. 13, fig. 4) figured the suture of one of these specimens (although it is impossible to determine which one); Cobban & Scott (1972, p. 82) stated that this suture "has a wide lateral lobe that is deeply bifid and asymmetric like *Ampakabites*". Collignon (1965b, p. 34, pl. 390, figs. 1666, 1667, 1668; pl. 391, fig. 1669) figured four specimens, to three of which he appended the subspecific names *inflata*, *perinflata* and *ampakabensis* (he referred the species to *Pseudaspidoceras*, following Hyatt 1903, p. 107). There are strong resemblances between *M. mohovanensis* and the material figured by Collignon, that between his fig. 1666 and PMMA2 being especially marked, although the Madagascan individual is a little more compressed. On the other hand, his fig. 1668 is more depressed than PMMA2 and the possibility remains that the variation seen in the Madagascan and Mexican specimens does not warrant specific separation. In no specimen figured from Madagascar, however, are umbilical tubercles as strongly developed as in *M. mohovanensis.*

M. wingi Morrow (1935, p. 467, pl. 51, fig. 2; pl. 52, fig. 2a—c; text-fig. 2; see also Wright & Kennedy, 1981) is a large species with a section at least as broad as high. It seems to differ from *M. mohovanensis* in its weaker umbilical tubercles and squarer whorl section. Cobban & Scott (1972, p. 79, pl. 26, figs. 1—4, 9, 10) figured several early whorls as *M. wingi*, treating it as a subspecies of *M. nodosoides.* At comparable sizes some of their material is almost indistinguishable from

M. mohovanensis. The *Mammites* sp. from Kansas of Morrow (1935, p. 468), with its nodate umbilical tubercles, is even closer to the Mexican form.

Two species described by Collignon (1939) from Madagascar appear to show an unusually simple suture; this was remarked upon by Collignon (1939, p. 97) and may indicate a close relationship with *M. mohovanensis*. *M. menabensis* (Collignon (1939, p. 80, pl. 6, figs. 2, 2a, 2b; text-fig. E) is rather more evolute than the Mexican form, with a narrower whorl section. *M. hourcqi* (Collignon (1939, p. 82, pl. 7, figs. 1, 1a, 2, 2a; text-fig. F), like *M. depressus* Powell (see Cobban & Hook, 1979, p. 15), is an evolute species with a deeply depressed whorl section. Collignon (1939, p. 83) drew attention to the similarity between *M. hourcqi* and *M. mohovanensis*, but noted that the latter is far more involute than the Madagascar form.

The Nigerian ammonites *M. dixeyi dixeyi* Reyment (1955, p. 50, pl. 9, fig. 4; pl. 11, fig. 2a, b; text-figs. 20, 21) and *M. dixeyi laevis* Reyment (1955, p. 51, pl. 10, fig. 3) seem to be adult at small diameters like *M. mohovanensis*, from which they differ in being more evolute, with squarer whorl section and less massive umbilical tubercles, and in the presence of more outer ventrolateral tubercles than inner ones. *M. mutabilis mutabilis* Reyment (1955, p. 51, pl. 10, fig. 1a, b) and the variable *M. mutabilis benueensis* Reyment (1955, p. 53, pl. 10, fig. 2a, b; text-figs. 22, 23) are also small forms, with umbilical tubercles matching more closely the Mexican species. An especially strong resemblance is noted for Reyment's (1955) pl. 10, fig. 1a, b (BMNH C47394). Professor R. Reyment believes that the two subspecies of each of these species are best interpretable as sexual dimorphs (personal communication).

Having examined the Nigerian material in the British Museum (Natural History), I feel inclined to regard *M. dixeyi* and *M. mutabilis* as possibly conspecific. Like *M. mohovanensis* they have a tendency for the outer ventrolateral tubercles to be located forward of the inner row. This characteristic is also seen in the *Mammites* spp. described by Reyment (1972, p. 365, fig. 8 (2—4)), from Trinidad and Colombia (see also Etayo-Serna, 1979, p. 85, pl. 13, fig. 1), but sharply clavate ventrolateral tubercles seem to set this material apart from *M. mohovanensis*.

Spathites (*Jeanrogericeras*) Wiedmann includes certain forms described from Iberia and Turkestan under the synonym *Fallotites* Wiedmann (see Kennedy et al. 1980, for a full review of *Spathites*) which bear a striking resemblance to *M. mohovanensis*. Karrenberg (1935; see appendix herein) first recognised the similarity of C575 to some *S.* (*J.*) *subconciliatus* (Choffat). Examination of substantial collections of *Spathites* (*Jeamrogericeras*) from France and Spain, however, has not convinced me of a similarity close enough to warrant removal of *M. mohovanensis* from *Mammites sensu stricto*. As is obvious from Kennedy et al.'s (1980) text-fig. 9, *S.* (*Jeanrogericeras*) and *Mammites* are intimately related, and perhaps suggests that *M. mohovanensis* is an early representative of its genus.

Mammites cf. *mutabilis* Reyment
Figs. 22, 23

COMPARE:
Mammites mutabilis Reyment 1955, p. 51, pl. 10, fig. 1a, b.

MATERIAL: One specimen PMMA19, from Loma el Macho.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA19	105(100)	33(32)	48(46)	0,69	38(36)

DESCRIPTION: Moderately evolute, with a rather wide umbilicus, and a square (intercostal) to trapezoidal (costal) whorl section. The last whorl only is exposed and at least half of this is apparently a body chamber, which becomes smooth and tubular towards the aperture. This may be partly due to abrasion, but encrusting oyster fragments near the aperture support the view that the body chamber is moderately well preserved. Ornamnt of 5—6 bullate umbilical tubercles projected outwards, giving rise to strong ribs which fade rapidly but just persist to the ventrolateral shoulder where they each meet a prominent, clavate inner tubercle, between which are intercalated an equal number of tubercles from which irregular ribs descend to fade on the flank. Each inner ventrolateral tubercle is linked to a less prominent outer ventrolateral tubercle by a coarse ridge directed obliquely forwards, but apparently not extending over the mid-venter. There seem to be at least 13—14 pairs of ventrolateral tubercles per whorl.

DISCUSSION: PMMA19 is less inflated and more evolute than the material described above as *M. mohovanensis*, but ornament is very similar in the two forms. *M. mutabilis* apparently only differs from *M. mohovanensis* in its more evolute shell, so a tentative reference of PMMA19 to the Nigerian species seems reasonable. There are also some specimens in the Oxford University Museum Collections from Calvert Canyon (see p. 104) closely comparable to PMMA19.

Figs. 22—23. Mammites cf. *mutabilis* Reyment. PMMA19. From Loma el Macho. × 1.

Genus PSEUDASPIDOCERAS Hyatt 1903

TYPE SPECIES: *Ammonites footeanus* Stoliczka 1864 by original designation.

REMARKS: See Wright & Kennedy (1981, p. 81) for a diagnosis and remarks on this genus.

DISCUSSION: *Pseudaspidoceras* is the most abundantly represented genus at Loma el Macho, and presents proportionately large taxonomical problems. In addition to the difficulty of differentiating *Pseudaspidoceras* from *Mammites* (see above), Kennedy & Wright (1979b) have drawn attention to the similarities between *Pseudaspidoceras flexuosum* Powell and forms described as *Ampakabites* Collignon 1965b.

Pseudaspidoceras cf. *flexuosum* Powell

1920 *Pseudaspidoceras* aff. *footeanum* (Petrascheck not Stoliczka); Böse, p. 208.

COMPARE:

Mammites footeanus (Stoliczka); Petrascheck 1902, p. 144, pl. 9, fig. 1a, b.

Pseudaspidoceras flexuosum Powell 1963a, p. 318, pl. 32, figs. 1, 9, 10; text-fig. 2a—c, f. g.

Pseudaspidoceras flexuosum Powell; Young & Powell 1978, pl. 2, figs. 7, 8.

MATERIAL: C557, an incomplete poorly preserved specimen, from Loma el Macho.

DISCUSSION: C557 is almost certainly the specimen described by Böse (1920, p. 208). Böse provisionally identified his specimen with *P. footeanum* as figured from Saxony by Petrascheck (1902) but specifically not with Stoliczka's type for the species (1864, p. 101, pl. 52, figs. 1, 2) from Odium, southern India. Böse stressed the distinction between Petrascheck's and Stoliczka's specimens, namely the higher whorl section of the former (approximate Wb:Wh = 0,62 as against 1,05).

Powell (1963a) described a large collection of *Pseudaspidoceras* from Kelsey's Crossing, Chihuahua, which was very similar to Petrascheck's material, and he named *P. flexuosum* to include both (Wb:Wh of the holotype, UT 30842, approximately 0,84). It seems logical, therefore, to identify C557 as *P.* cf. *flexuosum*; it has already been listed as such by Cooper (1978, p. 140). Somewhat contrary to Böse's description, the ribs of C557 follow exactly the pattern described by Powell (op. cit.) for *P. flexuosum*, i.e. "flexuous, concave at the umbilical shoulder, convex at mid-flank, concave at the ventrolateral margin, and convex again on the venter". (1963a, p. 318).

Böse had thought that the difference in whorl section between C557 and Stoliczka's *P. footeanum* might be due to the large size of C557. This is unlikely, since several large specimens of the *footeanum-pedroanum* group (see below) show no signs of becoming more compressed with maturity. This applies to Stoliczka's largest figured specimen (1864, pl. 52, fig. 1, 1a—c) of which Dr. C. W. Wright has very kindly shown me a cast, which has a maximum diameter of 260 mm.

Some of the high-whorled Texan material described by Adkins (1931, p. 54) as *P.* aff. *footeanum* may belong here, as may *P. footei grecoi* Collignon (1965a, p. 14, pl. E, fig. 1a, b) from the Sahara, although the latter appears distinctive in possessing very strong ventrolateral tubercles. The extent to which high-whorled forms with straight ribs should be admitted here is uncertain; thus the *P.* cf. *footeanum* (Petrascheck not Stoliczka) figured by Young & Powell (1978, pl. 3, fig. 16) may belong here if, as its identification suggests, its whorl section is much higher than wide.

P. paganum as figured by Barber (1957, p. 9, pl. 1, figs. 1a, b, 2a, b; pl. 25, figs. 5—7) but not the low-whorled holotype of Reyment (1954b, p. 253, pl. 4, fig. 1; text-figs. 3h, 4), have high whorls and somewhat flexuous ribs. The same applies to *P. curvicostatum* Reyment (1955, p. 55, pl. 11, fig. 1; pl. 12, text-fig. 24) a species only doubtfully separable from *P. paganum* as figured by Barber (1957). All these Nigerian forms are closely related to *P. flexuosum*; they are discussed further below.

Pseudaspidoceras footeanum (Stoliczka)
Figs. 2A, 24, 25

1864 *Ammonites footeanus* Stoliczka, p. 101, pl. 52, figs. 1a—c, 2a, b.
1887 *Ammonites pedroanus* White, p. 212, pl. 22, figs. 1, 2 (pl. 20, fig. 3 is mislabelled; it is *Paravascoceras hartti* (Hyatt)).
1920 *Pseudaspidoceras* aff. *pedroanum* (White); Böse, p. 209, pl. 13, fig. 1; pl. 15, fig. 1.
?1931 *Pseudaspidoceras* sp. aff. *footeanum* (Stoliczka); Adkins, p. 54 *pars.*
?1954b *Pseudaspidoceras paganum* Reyment, p. 253, pl. 4, fig. 1; text-figs. 3h, 4.
1977 *Pseudaspidoceras* aff. *pedroanum* (White); Chancellor et al., p. 91, figs. 8—10.

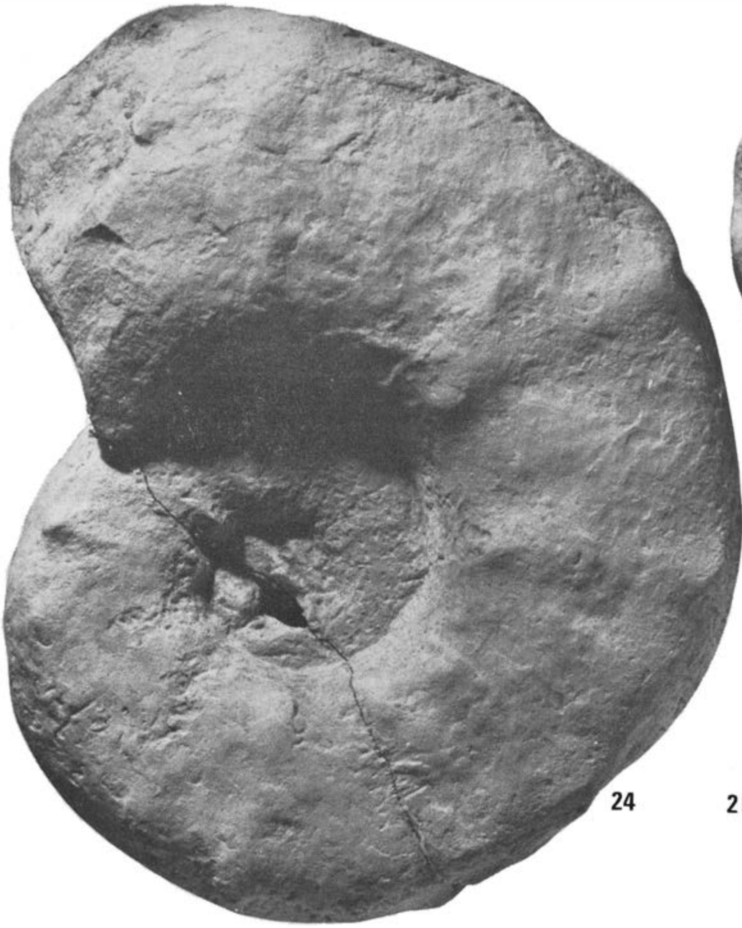
MATERIAL: C556, plus three measureable new specimens of which the smallest but most complete (PMMA3) is figured here. PMMA4 is the largest complete new specimen, but its phragmacone is badly crushed (see Chancellor et al. 1977, fig. 10). PMMA17 is complete but for about one seventh of its last whorl. There are about 20 other specimens, mostly fragments of about one-quarter whorl each (e.g.PMMA38). Much of the material is encrusted by oysters. All of it is from Loma el Macho.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA3	122(100)	49(40)	50(41)	0,98	40(32)
PMMA4	211(100)	81(38)	85(41)	0,95	73(34)
PMMA17	142(100)	63(44)	60(42)	1,05	58(41)

DESCRIPTION: See Böse (1920, p. 209) for a description of his single large specimen (C556). The new material displays considerable variation, which I attempt to summarise here: extremely evolute with subrectangular whorl section, never much higher than wide, but highly variable; umbilicus very wide, with walls varying from steep to gently curving but with generally a distinct shoulder. Venter broadly arched and almost always more curved than the flanks, but on some specimens rather flat or slightly concave. The earliest whorl seen (on PMMA3) is rather compressed, with flat, slightly divergent flanks, but almost invariably larger whorls are more depressed with slightly convergent flanks or a trapezoidal section (e.g. PMMA4). Some specimens have an almost round, tubular section. Involution never sufficient to cover the ventrolateral shoulder of the preceding whorl.

Generally about 11 bullae per whorl of variable strength arise on the umbilical shoulder, this number increasing to about 13 on the largest whorls. These bullae are linked across the flanks to an approximately equal number of inner ventrolateral tubercles by ribs which vary from flat to coarse and fold-like. The inner ventrolateral tubercles may be located anywhere from high on the shoulder to high on the flanks, where they appear as swellings on the ribs. They are in some cases linked across the venter by a low ridge which may bear a weak outer ventrolateral tubercle set at a variable separation either side of mid-



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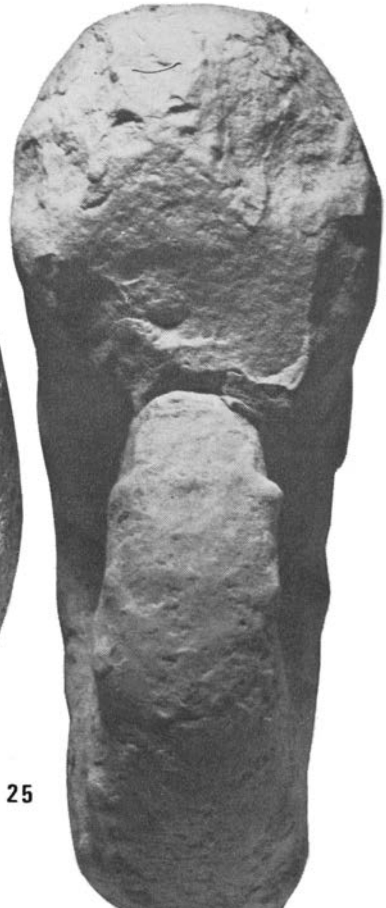

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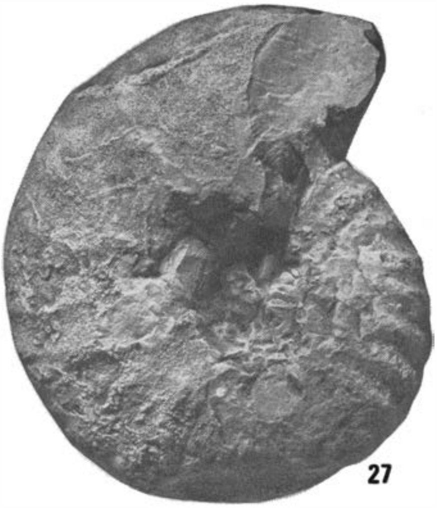

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Figs. 24—25. Pseudaspidoceras footeanum (Stoliczka). PMMA3. From Loma el Macho. × 1.

Figs. 26—28. Vascoceras cf. *gamai* Choffat. C567 (see Böse 1920, pl. 15, figs. 3—5; text-fig. 3). From Loma el Macho. × 1.

venter, these apparently being confined to smaller specimens (e.g. PMMA3). Regrettably the suture can rarely be made out, but a few specimens (e.g. PMMA38, Fig. 2A) show rather tall and complex saddles with a wide first lateral lobe.

On some specimens (e.g. PMMA4) striae are observed on the flanks. These follow the pattern of the ribs of *P. flexuosum* (see above); where these striae are present the ribs tend to be exactly parallel to them and indeed the two features seem to intergrade. The striae presumably indicate the successive positions of the aperture.

DISCUSSION: Agreement between the new material and Böse's specimen is good and I have been able to compare the collection with casts of Stoliczka's species, kindly supplied by Dr. C. W. Wright. PMMA3 is identical to the specimen in Stoliczka's pl. 52, fig. 2a, b, and C556 is virtually identical to Stoliczka's pl. 52, fig. 1, 1a—c. I feel confident that all four specimens are conspecific.

Dr. P. Bengtson has shown me photographs of the specimen figured by White (1887) from Sergipe, Brazil, and these suggest that *P. pedroanum* is a synonym of *P. footeanum*. White's figures have been reproduced by, e.g. Maury (1936, p. 230, pl. 21, figs. 1, 2) and by Magalhães & Mezzalira (1953, p. 240, pl. 67).

Of the other specimens described from Sergripe as *P. pedroanum*, Reyment & Tait's (1972, pl. 3, fig. 12a—f) specimen PMSA3 (Uppsala Collections) agrees closely with PMMA3, except in being more strongly tuberculate. Beurlen's (1970, pl. 1, figs. 4, 5) specimens seem to differ little from White's, but those described by Oliveira & Brito (1969, p. 219, pl. 1, figs. 1, 2; text-fig. 2) are probably *Dunveganoceras* Warren & Stelck (see Bengtson 1982) or an allied form. Through the kindness of Dr. Bengtson, I have examined the original of Oliveira & Brito's pl. 1, fig. 1 and also Dr Bengtson's own extensive collections of *Pseudaspidoceras* from Sergipe. I may here note that a specimen in the Uppsala Collections from Sidi Hajaj, Morocco, (PMAf531) is also identical with PMMA3.

The two specimens figured by Choffat (1898, pl. 16, figs. 9a—c, 10; pl. 22, fig. 34) as *Acanthoceras*? cf. *footeanus*, though apparently more coarsely ornamented than the typical material from Loma el Macho, otherwise differ only in possessing a broader venter with more divergent flanks. Choffat's doubtful specimen (1898, pl. 6, fig. 5a—c) with rather sparse, flexuous ribs, remains enigmatic.

The Egyptian specimen figured by Eck (1915, pl. 17, figs. 1, 2; Berlin Collections) is indistinguishable from PMMA3, within the limits of its poor preservation. The specimen figured by Greco (1915, pl. 17, fig. 5a, b), also from Egypt, differs from the Mexican material again only in possessing a wider venter. Greco's specimen has been referred to the Portuguese species *P. pseudonodosoides* by Freund & Raab (1969, p. 14) who, on the same page, described some fragmentary *P. footeanum* from Israel. In the latter case, however, as with the Syrian specimen of Basse (1937, p. 184), the material was not figured. I have examined Madame Basse's specimen at the Musée National d'Histoire Naturelle in Paris, and it is certainly conspecific with the Mexican material.

P. pseudonodosoides (Choffat 1898, p. 65, pl. 16, figs. 5—8; pl. 22, figs. 32, 33) is itself closely comparable with the Mexican material, but presents a special problem since, although its extreme evoluteness identifies it as a *Pseudaspidoceras* (as Freund & Raab 1969, p. 15, pointed out) it displays the nodate ornament of a *Mammites*; Barber (1957, p. 33) even considered it close to his *Paramammites tuberculatus*, a vascoceratid. It has most recently been cited as a *Mammites* (Wright & Kennedy 1981, p. 79).

Although Choffat himself thought *P. pseudonodosoides* differed from typical *Mammites* in details of suture and whorl section, both Roman (1912, p. 12, pl. 2, fig. 2; pl. 3, fig. 2) and Collignon (1957, p. 121, pl. 2, fig. 1) have described it as a *Mammites*. Roman's French specimen differs from any specimen figured by Choffat in being more evolute. Collignon's Saharan specimen is poorly preserved and cannot be determined with certainty; indeed, Freund & Raab (1969, p. 18) considered it closely resembled material they described as *Paramammites*. There is, however, a specimen from Sidi Hajaj, Morocco (Uppsala Collections, PMAf534) in a more complete condition which agrees well with Choffat's figures, except in being a little more compressed. Rolland (1924, p. 249) recorded this species from Sidi Hajaj, while Karrenberg (1935, p. 136) and Wiedmann (1964, p. 111) have reported it from Spain.

Barber (1957, p. 11, pl. 25, fig. 8) described a specimen from Nigeria he called *Pseudaspidoceras* sp., which seems very close to *P. pseudonodosoides*. Freund & Raab (1969, p. 14, pl. 1, figs. 10, 11; text-fig. 4j, k) provide the most complete account of this species, on the basis of a large collection from Israel. I agree that their photographed specimen (M3450—4) is conspecific with *P. footeanum* as figured by Greco (1915); it is also probably conspecific with a fragment in the Uppsala Collections from Sidi Hajaj (PMAf535) and is very close to the English specimen (OUM

K10481) described by Wright & Kennedy (1981, p. 82, pl. 21, fig. 3).

Although Freund & Raab (1969) place greater stress on ventral ornament in their treatment than I do, it is nevertheless clear that there exist some striking parallels between the Israeli *P. pseudonodosoides* and the *Pseudaspidoceras* from Loma el Macho. Perhaps most significantly, Freund & Raab have been able to divide their material into two reasonably distinct groups, on the basis of covarying differences in juvenile whorl section, umbilicus width, whorl expansion rate and ornamental density, pattern and persistence. I have grouped the Loma el Macho material between two taxa (*P.* cf. *flexuosum* and *P. footeanum*) differentiated mainly by whorl section, but to a lesser extent by ornament. It is tempting to ask whether the two taxa may not in fact represent intraspecific dimorphs (sexual dimorphism?), as appears to be the case in Israel. Unfortunately, we do not have enough juvenile material in the Mexican case to decide the question.

P. paganum Reyment (1954b; see my discussion of *P.* cf. *flexuosum*, p. 92 above) is based on a Nigerian holotype (BMNH C47422; Wb:Wh = 0,98) which I have examined. It is probably a *P. footeanum.* I have also examined the Nigerian *Mammites* (*Pseudaspidoceras*) sp. of Woods (1911, p. 283, pl. 23, figs. 1, 2; Sedgwick Museum, Cambridge) and feel confident that it is conspecific with C47422, allowing for ontogenetic and preservational differences (see Barber 1957, p. 11). I am not so convinced that all the Nigerian specimens described by Barber (1957, p. 9, pl. 1, figs. 1a, b, 2a, b; pl. 25, fig. 5—7) as *P. paganum* are likely to be referable to *P. footeanum.* As Freund & Raab (1969, p. 16) have already noted in their remarks on a fragment of *P.* cf. *paganum* from Israel, there are substantial differences between Barber's material and the holotype.

The Moroccan species *P. vicentinii* Collignon (1966, p. 43, pl. 23) has a square whorl section with flexuous striae after the pattern of *P. flexuosum.* It is perhaps within the range *P. footeanum* but differs from any Mexican specimen I have seen in its extraordinary horn-like ventrolateral tubercles and its complete absence of umbilical tubercles. I may also mention that there are some specimens in the British Museum (Natural History) from Angola which may belong here (BMNH C80168—74). The fragment figured from Japan by Matsumoto et al. (1978, p. 14, pl. 6, fig. 2; text-fig. 6) as *Ampakabites*? sp., although with a deep suture, appears almost identical to several fragments described here from Loma el Macho.

Family VASCOCERATIDAE H. Douvillé 1912 (name corrected and translated by Spath, 1925 from Vascoceratinés H. Douvillé, 1912).

REMARKS: For a diagnosis and remarks on this family see Wright & Kennedy (1981, p. 84).

DISCUSSION: Since the detailed synopsis of the Vascoceratidae which appeared in the *Treatise on Invertebrate Paleontology* (Wright 1957), many new vascoceratid faunas have been recorded from around the world (e.g. from England, France, Spain, Texas, Mexico, Brazil, Peru, Columbia, Venezuela, Turkestan, Israel, the Sahara, Morocco, Colorado, Angola, Japan and Madagascar). Several of these faunas have included forms which have forced revisions of the Vascoceratidae; here I briefly summarise the changes which have been made.

Wright (1957, p. L418) included within this family the following genera: *Nigericeras* Schneegans, 1943; *Spathites* Kummel & Decker, 1954; *Gombeoceras* Reyment, 1954a; *Ezilloella* Reyment, 1954b; *Paravascoceras* Furon, 1935; *Pachyvascoceras* Furon, 1935; *Vascoceras* Choffat, 1898; *Paramammites* Furon, 1935; *Plesiovascoceras* Spath, 1925; *Fagesia* Pervinquière, 1907; *Thomasites* Pervinquière, 1907; *Neoptychites* Kossmat, 1895.

Spathites (of which *Fallotites* Wiedmann, 1960 and *Spathitoides* Wiedmann, 1960 are synonyms) has been transferred to the Mammitinae (see Kennedy et al. 1980). The subfamily Fallotitinae Wiedmann, 1960 is therefore a synonym (Cooper 1978, p. 128) as is probably the subfamily Neoptychitinae Collignon, 1965b for which *Masiaposites* Collignon, 1965b was proposed as type genus (he should have employed *Neoptychites* for this purpose, since the family-group name is derived from it). Collignon (1965b) added another new genus, *Hourcquia*, which seems to have been accepted as a vascoceratid. Kennedy & Wright (1979a) believed *Betiokyites* Collignon, 1965b to be best regarded a subgenus of *Neoptychites*, of which they considered *Pseudoneoptychites* Leanza, 1967 a synonym. I choose rather to keep these two genera distinct on account of the umbilical tubercles present in *Pseudoneoptychites.*

Gombeoceras and its subgenus *Ferganites* Stankevich & Poyarkova 1969 (including *Koulabiceras* Atabekyan 1966) are syonyms of *Thomasites* (see Freund & Raab 1969; Reyment 1979; Wright & Kennedy 1981), which is referred to the vascoceratid subfamily Pseudotissotiinae (Wright & Kennedy 1981) (see, however, Reyment 1979). *Discovascoceras* Collignon, 1957 and *Imlayiceras*

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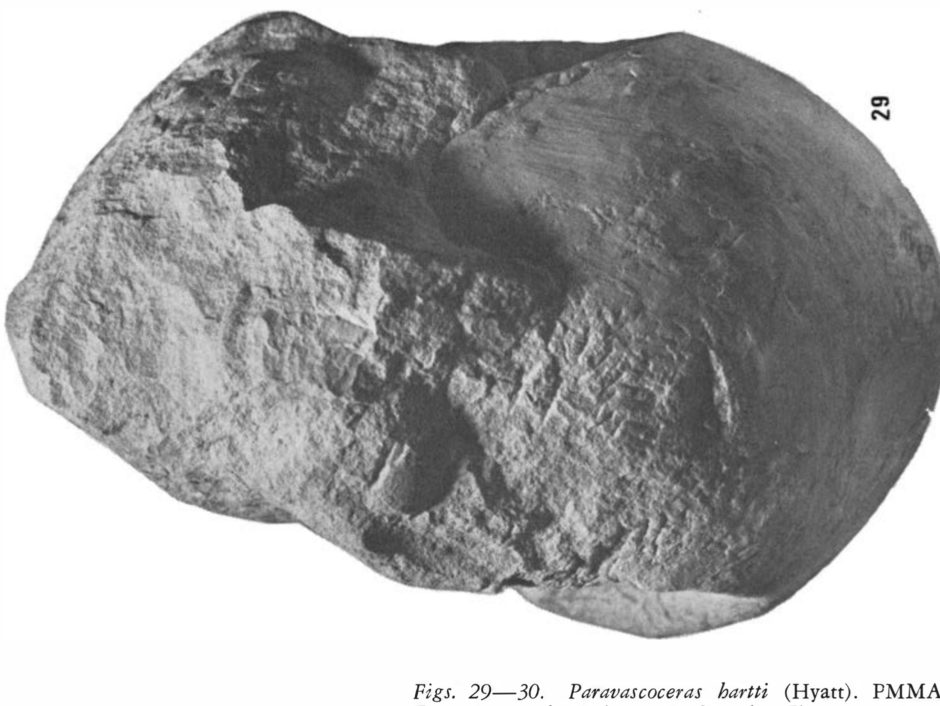

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Figs. 29—30. Paravascoceras hartti (Hyatt). PMMA9. From Loma el Macho. × 1. See also Figs. 2B, 31.

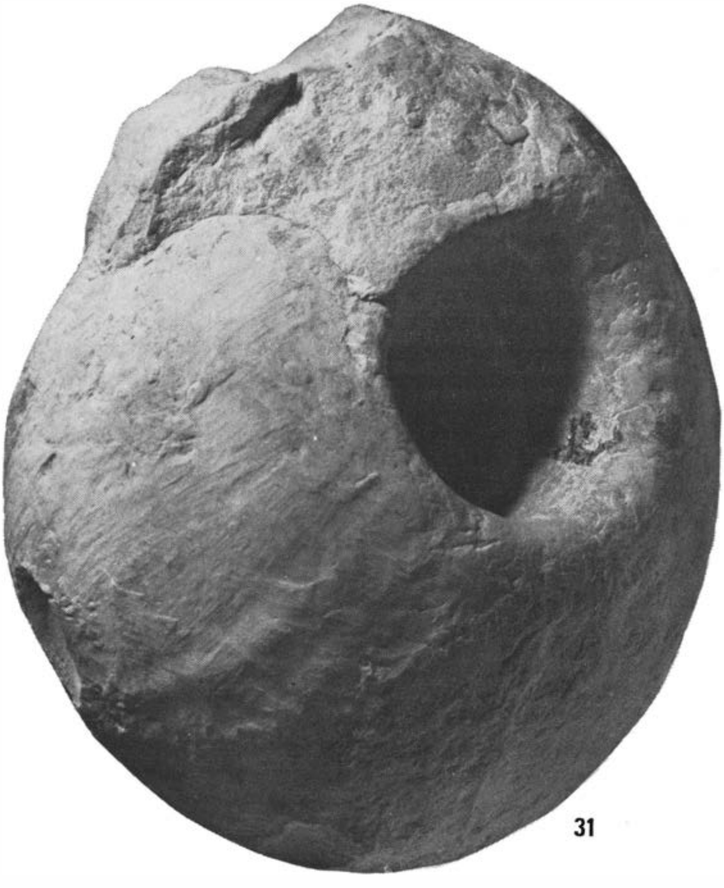

Fig. 31. *Paravascoceras hartti* (Hyatt). PMMA9. From Loma el Macho. × 1. See also Figs. 2B, 29—30.

Leanza 1967 will be discussed below under the latter subfamily.

Pachyvascoceras and *Broggiiceras* Benavides-Caceres, 1956 are synonyms of *Paravascoceras* (see Freund & Raab 1969, p. 19). Cooper (1979) named *Provascoceras* but this is regarded as a synonym of *Vascoceras* by Wright & Kennedy (1981). Cooper (1979) believed *Ezilloella* to be a synonym of *Nigericeras*, and Wright & Kennedy (1981) show that *Plesiovascoceras* is a synonym of *Fagesia. Franciscoites* Etayo-Serna, 1979 and *Nannovascoceras* Renz & Alvarez, 1979 are little-known vascoceratids from South America; *Greenhornoceras* Cobban & Scott, 1972 is a subgenus of *Vascoceras*, from the United States.

Subfamily VASCOCERATINAE H. Douvillé 1912

Genus VASCOCERAS Choffat 1898
(= *Provascoceras* Cooper 1979)

TYPE SPECIES: *Vascoceras gamai* Choffat 1898 by original designation.

REMARKS: Cooper (1978, p. 128) and Wright & Kennedy (1981, p. 86) discuss this genus. I differ from Cooper in treating *Paravascoceras* as a distinct genus, not a subgenus of *Vascoceras.* Kennedy & Juignet (1977, p. 587) provide useful remarks on some of the species referred to *Vascoceras.*

Vascoceras cf. *gamai* Choffat
Figs. 26—28

1920 *Vascoceras* aff. *gamai* Choffat; Böse, p. 216, pl. 15, figs. 3—5; text-fig. 3.

COMPARE:
Vascoceras gamai Choffat 1898, p. 54, pl. 7, figs. 1—4; pl. 8, fig. 1; pl. 10, fig. 2; pl. 21, figs. 1—5.

MATERIAL: C567, a complete specimen, with apparently about one-quarter of a body whorl preserved. From Loma el Macho.

DISCUSSION: Böse (1920) described C567, the single known specimen of *Vascoceras* from Loma el Macho. I can add nothing to Böse's description and his illustrations are good. C567 is poorly preserved, but apart from being comparable with Choffat's species is also reminiscent of some of the *'Fallotites'* [= *Spathites* (*Jeanrogericeras*)] described by Wiedmann (1964) from Spain and by Khakimov (1972) from Turkestan, and of *Vascoceras* (*Greenhornoceras*) *birchbyi* Cobban & Scott (1972, p. 85, especially pl. 23, figs. 4—6, 9, 10, 11—13).

Genus PARAVASCOCERAS Furon 1935

(= *Paracanthoceras* Furon 1935 = *Pachyvascoceras* Furon 1935 = *Broggiiceras* Benavides-Caceres 1956)

TYPE SPECIES: *Vascoceras cauvini* Chudeau 1909 by original designation.

Paravascoceras hartti (Hyatt)
Figs. 28C, 29—33

1870 *Ceratites harttii* Hyatt, p. 386.

1875 *Buchiceras harttii* Hyatt, p. 370.

1887 *Ammonites* (*Buchiceras*) *harttii* Hyatt; White, p. 226, pl. 19, figs. 1, 2; pl. 20, fig. 3 (mislabelled *Ammonites pedroanus* White).

1903 *Vascoceras hartti* (Hyatt); Hyatt, p. 103, pl. 14, fig. 16. (Refigured by Faraud, 1940, pl. 9, fig. 2).

?1920 *Vascoceras angermanni* Böse, p. 217, pl. 17, fig. 1 only; text-fig. 2 upper.

1925 *Vascoceras hartti* (Hyatt); Maury, p. 594.

1930 *Vascoceras hartti* (Hyatt); Maury, p. 281.

1936 *Vascoceras hartti* (Hyatt); Maury, p. 247, pl. 22, figs. 1, 2 (copy White 1887).

?1940 *Vascoceras* (*Pachyvascoceras*) cf. *hartti* (Hyatt); Faraud, p. 48, pl. 4, fig. 2; pl. 5, fig. 2; pl. 9, fig. 1.

?1960 *Vascoceras* (*Pachyvascoceras*) cf. *hartii* (Hyatt); Wiedmann, p. 712.

non 1966 *Vascoceras hartii* (Hyatt)?; Willard, pl. 41, fig. 2; pl. 42, fig. 1.

?1969 *Pachyvascoceras harttii* (Hyatt); Oliveira & Brito, p. 220, pl. 2, frigs. 1—3; text-fig. 3.

1972 *Pachyvascoceras hartii* (Hyatt); Reyment & Tait, pl. 5, fig. 26a—c. (Also figured by Beurlen 1970, pl. 1, fig. 9).

?1972 *Vascoceras* cf. *globosum* (Reyment); Reyment & Tait, pl. 5, fig. 25a—c. (Also figured by Beurlen 1970, pl. 1, figs. 10, 11).

?1972 *Vascoceras* cf. *compressum* (Barber); Reyment & Tait, pl. 5, fig. 27. (Also figured by Beurlen 1970, pl. 1, figs. 12, 13).

1977 *Paravascoceras hartti* (Hyatt); Chancellor et al., p. 96, fig. 20.

REMARKS: Choffat (1898, p. 62, pl. 13, fig. 7) refigured White's (1887, pl. 20, fig. 3) whorl section diagram and also (1898, pl. 21, fig. 25) gave the suture, taken from White's (1887, pl. 19) illustrations. Magalhães & Mezzalira (1953, p. 238, pl. 68) have reproduced White's figure of the species in lateral view only. Hyatt's (1903) spelling of *hartti* is used here, simply for convenience; Article 33a of the draft for comment of the 3rd edition of the *International Code of Zoological Nomenclature* (*I.C.Z.N.*) reads: "the terminations *-i* and *-ii* ... are permissible alternatives and the use of either for the other does not constitute an emendation or an incorrect subsequent spelling." All the material in the synonymy above is from Mexico (the material described here), Spain (Wiedmann 1960, 1964), France (Faraud 1940), or Sergipe (all other records). There are two specimens labelled as this species in the British Museum (Natural History) from "loc. 1007, 5,5 km south of Novo Redondo [Angola]" (BMNH C80175—6).

MATERIAL: C570, figured in lateral view only by Böse (1920) and described as *Vascoceras angermanni*, only doubtfully referred here on account of its poor state of preservation. PMMA9, complete except for the body chamber; this is a well-preserved specimen, previously figured only in lateral view by Chancellor et al. (1977). C570, PMMA9 and PMMA20, a juvenile probably belonging here, all show partial sutures. All are from Loma el Macho.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA9	113(100)	82(73)	46(41)	1,78	27(24)
PMMA20	54(100)	52(96)	21(39)	2,48	15(27)

DESCRIPTION: Very globose, involute cadicone, with tightly embracing whorls leaving exposed only the smoothly rounded umbilical shoulders of previous whorls. Section semilunar, but slightly triangular in the juvenile; thickness almost constant across the section. Umbilicus very deep and funnel-shaped, with flat, very steep walls. There is no ornament, except low folds which cross the venter of MA9 in the region where the suture is exposed. Although scarcely perceptible, these folds are slightly prorsiradiate and seem to number about 5 over the space of a quarter-whorl. Weak growth striae cross the juvenile shell. The suture seen on PMMA9 (Fig. 2B) consists of four large, rounded saddles of the typical *Vascoceras* pattern. The suture of C570 was described by Böse under *Vascoceras angermanni* (1920, p. 217; see below). The suture of PMMA20 (see Fig. 2c) shows simple, rounded elements, again of the typical *Vascoceras* pattern.

DISCUSSION: Identity of PMMA9 with Hyatt's *'Vascoceras hartti'* is confirmed by comparison

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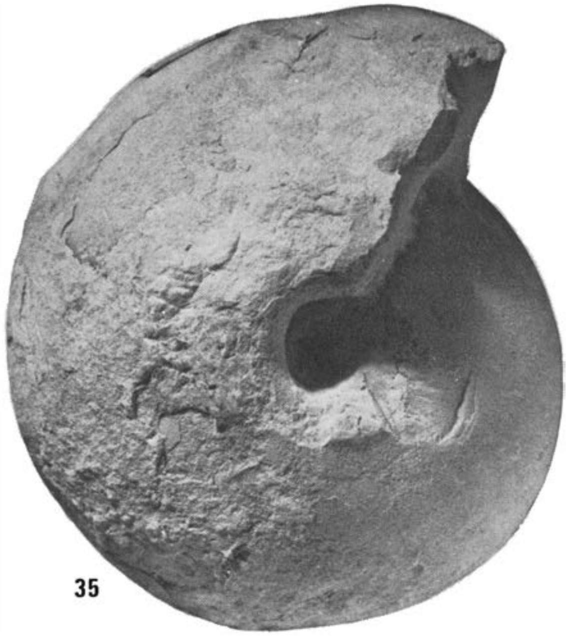

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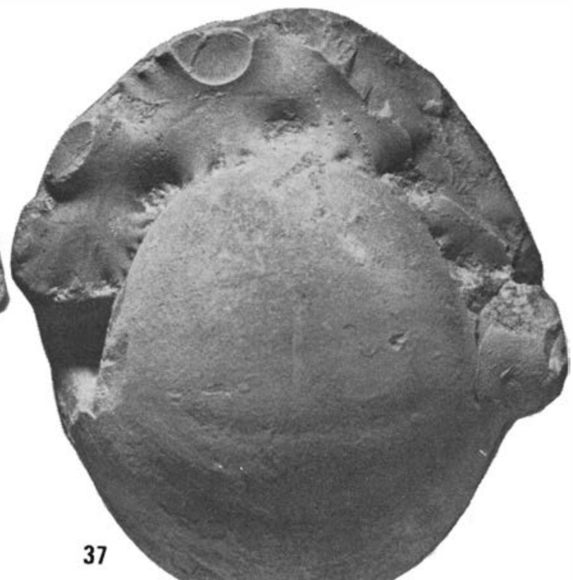

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Figs. 32—33. Paravascoceras hartti (Hyatt). PMMA20. From Loma el Macho. × 1. See also Fig. 2C.

Figs. 35—37. Paravascoceras carteri (Hyatt). PMMA7. From Loma el Macho. × 1.

with the Uppsala Collections from Sergipe. These collections contain some specimens scarcely distinguishable from PMMA9, and indicate that White's (1887) figured specimen is a typical example of the species; there is considerable variation, however, particularly in regard to umbilical width.

The Uppsala Collections also confirm the generic assignment of *Paravascoceras* for *hartti.* Most authors since Faraud (1940) have referred Hyatt's species to *Pachyvascoceras*, but this genus has been shown to be a synonym of *Paravascoceras* (see Schöbel 1975). The latter is distinguished by "the absence of umbilical tubercles at early stages" and also includes "the forms which are entirely devoid of ornament throughout their development" (Freund & Raab 1969, p. 20). I have seen no ornament on any of the Uppsala specimens, although the earliest growth stages have not been examined. Folds on the venter of mature shells, as are seen on PMMA9, are common in *Paravascoceras.*

A general conclusion to be drawn from the Uppsala Collections is that there is no clear distinction between *P. hartti* with narrow umbilici and *P. angermanni* with wide umbilici (see below). Likewise, there is no clear distinction between *P. angermanni* and *P. carteri* in regard to umbilical width. There thus appears to be a more or less continuous range of variation in this character linking the globose *Paravascoceras* species. Inflation of the shell is also highly variable in these forms, so it will be appreciated that my use of the word 'species' here may have little biological meaning.

Böse (1920, p. 217) included C570 within his *Vascoceras angermanni.* Comparison with the Uppsala Collections has shown, however, that C570 lies within the range of variation seen in the Uppsala *P. hartti,* although it is too poorly preserved to be certain. C570 has several partial sutures, including that shown painted in on Böse's pl. 17, fig. 1 and drawn as his upper text-fig. 2. Böse's (1920, p. 217) description of the suture is probably based largely on a more complete example about 180° behind the aperture of the specimen. It should be noted, however, that Böse's smallest specimen of *V. angermanni* (C569) also shows some suture (it was figured by Karrenberg 1935, text-fig. 3 right) which may also have contributed to Böse's description. C569 is referred below with a full discussion to *P. carteri.*

Choffat (1898) noted that the whorl section figured by White (pl. 20, fig. 3) is more triangular than that of the specimen on his pl. 19. Only in the explanation to his pl. 13, fig. 7 did Choffat (1898) tentatively refer *hartti* to his genus *Vascoceras*, but this referral was accepted by Hyatt (1903, p. 103).

Although Böse (1920) did not identify Hyatt's species in his collection, he summarised what was known then of its affinities. Kossmat (1895, p. 53) had indicated that Hyatt's '*Buchiceras*' was not related to that genus (see Kennedy et al. 1980), but that *hartti* was a close relative of the Indian *Fagesia rudra* (Stoliczka) (see Kennedy & Wright 1979b). In fact, Hyatt's (1903) figure of the suture of *hartti* confirmed that it was better referred to *Vascoceras*, and related to the Portuguese species *V. harttiforme*, *V. amieirense* and *V. kossmati.* (According to Berthou et al. 1975, the Portuguese species are not actually known to possess umbilical tubercles. They recommend considering *V. harttiforme* a synonym of *V. kossmati*).

I have examined the Peruvian specimen figured by Willard (1966) as *V. hartii?* and do not think it belongs here, but ought perhaps to be united with Lisson's (1908, pl. 9A—C) *V. amieirense* Lisson not Choffat. *V.* aff. *harttiforme* has been described from Spain (Karrenberg 1935, pl. 33, fig. 11), while *V.* gr. *harttiforme* has been reported from southern Mexico (Burckhardt & Müllerried 1936, p. 321), although no other information was given.

Pervinquière (1907, p. 332) described a form from Tunisia he referred to *V. durandi* (Thomas & Peron; see below), which he also considered to include *V. douvillei* Choffat. Pervinquière (1907) thought *V. durandi* similar to '*V. hartti*' but different in the possession of tubercles and a somewhat more complex suture. There is a specimen in the Oxford University Museum from Ain Sfaia, 18 km south of Thala, Tunisia which is almost identical with PMMA9, (OUM KX207, maximum diameter approximately 140 mm).

Furon (1935, p. 58) described a form similar to *P. hartti* from the Niger Republic which he named *Vascoceras* (*Pachyvascoceras*) *crassus* and which Schneegans (1943, p. 131) included within *Paravascoceras.* Faraud (1940, p. 48) described a form from France comparable with *P. hartti* and showed that the latter was related to his *Vascoceras triangulare crassum.*

Ammonites which apparently differ from *P. hartti* in being more compressed include the Tunisian *V. durandi* (Thomas & Peron 1889, p. 27, pl. 18, figs. 5—8; see below under *P. angermanni*), *V. ellipticum* Barber from Nigeria (e.g. Offodile & Reyment 1977, p. 54, fig. 25), *Vascoceras* sp. in Douvillé (1928, p. 15, pl. 1, fig. 6) from Sinai, *Vascoceras* sp. in Cobban & Scott (1972, p. 83, pl. 36, figs. 3, 4; text-fig. 41A only) — only the

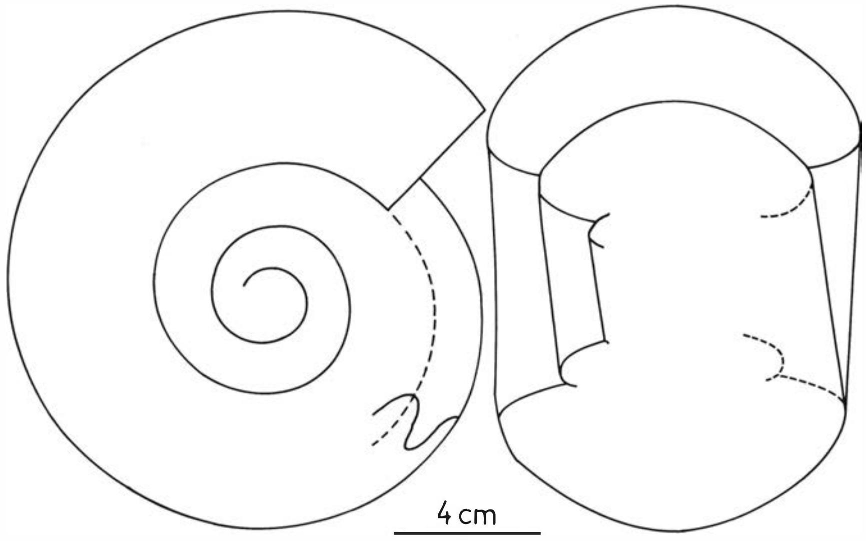


Fig. 34. Paravascoceras aff. *hartti* (Hyatt). Outline diagram of PMMA21 from Loma el Macho, restored and corrected for distortion.

last two seem to be free of umbilical tubercles — and *P. angermanni* (Böse). All the material figured by Reyment & Tait (1972; see synonymy above) is close to the Mexican *P. hartti*.

Paravascoceras aff. *hartti* (Hyatt)
Fig. 34

1920 *Vascoceras* sp. nov. ex. aff. *adonense* Choffat; Böse, p. 214, pl. 14, fig. 4; pl. 17, fig. 2; text-fig. 2 lower.

?1928 *Vascoceras* aff. *adonense* Choffat; Böse & Cavins, p. 29.

MATERIAL: C571 described by Böse (1920); the body chamber, shown in place on Böse's pl. 17, fig. 2 is lost. Also PMMA21, reconstructed from fragments, but lacking the body chamber. The accompanying diagram (Fig. 34) portrays PMMA39 as it would appear if complete and undistorted. Both specimens from Loma el Macho.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA21	140(100)	100(71)	30(21)	3,33	80(57)

DESCRIPTION: PMMA21 and C571 are identical, even in mode of preservation and distortion. The following description is complementary to that given by Böse(1920) for C571: Rather evolute cadicone with very wide, deep umbilicus. Whorl section extremely depressed, semilunar, only slightly higher at mid-section than near the umbilicus. Each successive whorl leaves exposed only the umbilical shoulder of the preceding whorl. Umbilical walls high and very steep (almost vertical at the umbilical seam), with curvature decreasing near the umbilical shoulders. The latter become progressively more angular, although this may be due to crushing. The only perceptible ornament seen were low folds on a part of the earliest preserved whorl, now concealed. Suture apparently of the simple *Vascoceras* type (see Böse's (1920) text-fig. 2 lower).

DISCUSSION: The two specimens are identical with *P. hartti* in all respects except umbilical width. They both have an umbilicus wider than that of any specimen I have seen in the Uppsala Collections, and White's figured specimen differs from PMMA21 in this character only (U = 45 % of diameter as against 57 %).

Böse considered that C571 resembled the Portuguese *Vascoceras adonense* Choffat (1898, p. 59, pl. 9, fig. 3; pl. 21, fig. 12) but noted "this latter species shows nodules on its umbilical border, while these are entirely missing [on C571]", (1920, p. 215). The present form may, therefore, be referred to *Paravascoceras*. As Böse noted, C571 is much more evolute than *V. adonense*, and there are apparently differences in the sutures. Böse concluded that C571 represented a new form, with suture similar to that of *V. gamai* Choffat (1898, p. 54, pl. 21, figs. 1, 2; Choffat's figured specimen of *V. adonense* has itself been referred to *V. gamai* by Berthou et al.

1975). Since most of the Portuguese *Vascoceras* possess umbilical tubercles (although see note above concerning *V. amieirense*, *V. harttiforme*, and *V. kossmati*), I think it more likely that the closest relatives of the Mexican form will be found elsewhere.

Fagesia catinus (Mantell) shares the same overall shape and wide umbilicus with PMMA21 and C571, but differs in being more strongly ornamented. An English example mentioned by Spath (1925, p. 198) and figured by Wright & Kennedy (1981, text-fig. 32; BMNH C8316, see p. 110 herein) is strikingly similar to the Mexican form. Some specimens of *F. haarmanni* Böse (see below) are smooth at sizes comparable with PMMA21 and some (e.g. Powell 1963a, pl. 33, fig. 2) also agree in the possession of an angular umbilical shoulder.

The Israeli *V. durandi*, *V. harttiforme* and *V.* cf. *amieirense* described but not photographed by Freund & Raab (1969, p. 29—32) are probably similar to the specimens treated here. I have examined one of their specimens of *V. durandi* (USNM 23672) and find that this is confirmed, although it does possess umbilical tubercles, as described. Freund & Raab's *V.* cf. *adonense* (p. 32, pl. 5, fig. 1; text-fig. 7a, b) was stated as showing "no significant difference" from C571, but it was added that "the latter is so badly preserved that any comparison would be uncertain".

Paravascoceras carteri (Barber)
Figs. 35—37

1920 *Vascoceras angermanni* Böse, p. 217, pl. 16, figs. 1, 3 only.

1935 *Vascoceras angermanni* Böse; Karrenberg, p. 140, text-fig. 3 right not left?

1957 *Vascoceras globosum carteri* Barber, p. 25, pl. 8, fig. 2; pl. 28, figs. 8, 9.

?1963a *Pachyvascoceras globosum* Reyment; Powell, p. 321, pl. 34, figs. 7, 11; text-fig. 3s.

1977 *Paravascoceras carteri* (Barber); Offodile & Reyment, p. 55, figs. 27a, b, 28.

1977 *Paravascoceras carteri* (Barber); Chancellor et al., p. 92, figs. 15—17.

MATERIAL: Böse's specimen C569, plus one other well-preserved specimen, PMMA7. Also PMMA22, badly crushed, plus PMMA23, which is half of an ammonite split across the whorls, and PMMA24. The fragment PMMA1, described above as *Metoicoceras*? sp., was found in the body chamber of PMMA7. All from Loma el Macho.

DIMENSIONS:

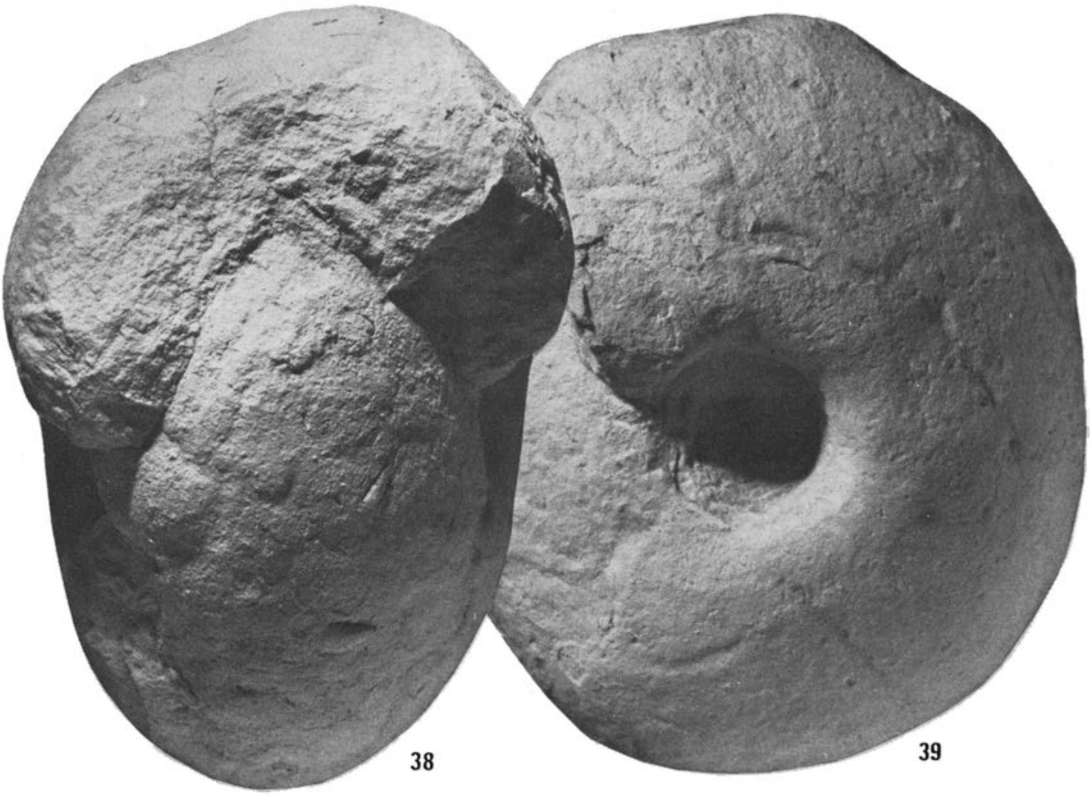
	D	Wb	Wh	Wb:Wh	U
PMMA7	94(100)	82(87)	25(27)	3,28	15(16)
PMMA22	66(100)	66(100)	14(21)	4,71	12(18)
PMMA23	74(100)	62(84)	—	—	12(16)
PMMA24	54(100)	52(96)	14(26)	3,71	7(13)

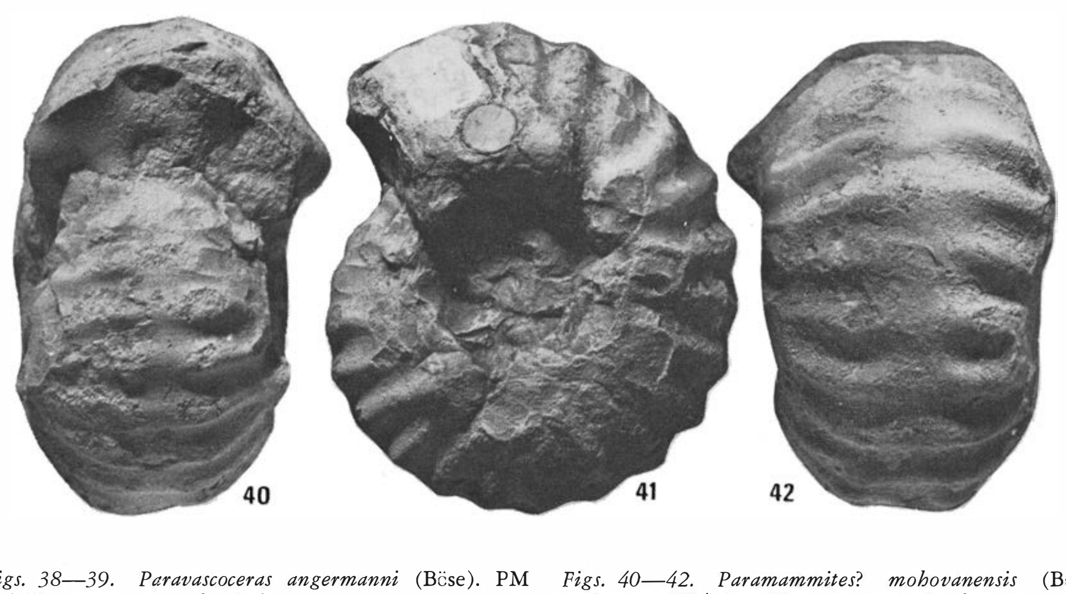
DESCRIPTION: Extremely inflated, globose and involute; whorls almost completely embracing; early shell subspherical but sometimes slightly triangular. Whorl section semilunar, about five times as broad as high. Umbilicus very small and deep, with nearly vertical walls and subangular shoulder. Low folds can be discerned crossing the venter at middle growth stages on PMMA7; these number about 5 per quarter whorl. No other ornament is visible. A poorly preserved suture occurs about 180° behind the aperture of C569 and was figured by Karrenberg (1935, p. 140, text-fig. 3 right). This is a simple *Vascoceras* suture, and may have been partly the basis for Böse's (1920, p. 217) description of the suture of *V. angermanni*.

DISCUSSION: Böse (1920, pl. 16, figs. 1, 3) figured C569 as *V. angermanni*. Chancellor et al. (1977, p. 92) selected C568 (Böse's pl. 16, figs. 2, 4) as lectotype of *V.* [= *Paravascoceras*] *angermanni*, and referred C569 to *P. carteri*. Unfortunately, both judgements were made before the actual specimens were seen, and it must be admitted that C568 was a poor choice for lectotype since it is in a very poor state of preservation. On the basis of the total collection from Loma el Macho, however, it still seems reasonable to distinguish C568 and C569 at the specific level, as understood here. Likewise I refer C570, Böse's third specimen of *V. angermanni*, to *P. hartti*, mainly on the basis of comparison with the Uppsala collections from Sergipe.

The variation seen in the Loma el Macho material, however, shows that *P. carteri* grades into *P. angermanni* which in turn grades into *P. hartti*, principally by an increase in umbilical width, and I must stress again my use here of the species category may not reflect biological reality.

I have compared the present material with the Nigerian holotype BMNH C47630 of Barber's (1957) *V. globosum carteri* and find that although the latter is crushed, it is almost certainly conspecific with the Mexican specimens. The species *V. globosum*, however, bears umbilical tubercles at early stages whereas *carteri* apparently does not, so more logically (according to Offodile & Reyment 1977, p. 55) *carteri* should be elevated to species rank and referred to *Paravascoceras*. There is good agreement between the Mexican speci-





Figs. 38—39. Paravascoceras angermanni (Böse). PM MA28. From Loma el Macho. × 1.

Figs. 40—42. Paramammites? mohovanensis (Böse). Holotype C574 (see Böse 1920, pl. 18, figs. 1, 2; text-fig. 4 upper). From Loma el Macho. × 1.

mens and the *P. carteri* described by Offodile & Reyment (1977) from Nigeria.

Karrenberg (1935, p. 140) described a specimen of *V. angermanni* from Spain, but only figured its suture (text-fig. 3 left) alongside that of C569 (see above). Judging from the dimensions and description of Karrenberg's specimen, it would certainly seem close to *P. carteri.* The small specimen WSA230 figured by Powell (1963a, p. 321, pl. 34, figs. 7, 11; text-fig. 3s) from Texas may belong here, and a specimen in the Oxford University Museum Collections from Calvert Canyon (OUM KT378) is identical with Barber's species (Kennedy et al., in preparation).

Paravascoceras angermanni (Böse)
Figs. 2D, 38, 39

1920 *Vascoceras angermanni* Böse, p. 217, pl. 16, figs. 2, 4 only.
1920 *Vascoceras* sp.; Böse, p. 216, pl. 18, fig. 12.
?1972 *Vascoceras* sp.; Cobban & Scott, p. 83, pl. 36, figs. 1, 2; text-fig. 41B.
1977 *Paravascoceras angermanni* (Böse); Chancellor et al., p. 96, figs. 18, 19.

MATERIAL: The lectotype C568, plus Böse's figured specimen referred by him to *Vascoceras* sp., C572, plus C573, which is almost certainly his unfigured specimen referred to *Vascoceras* sp. (see Appendix), which shows the inner whorls. Also PMMA8, previously figured by Chancellor et al. (1977), and PMMA25—28, all somewhat crushed and poorly preserved and all from Loma el Macho.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA8	112(100)	76(67)	50(45)	1,52	19(17)
PMMA25	79(100)	50(63)	39(49)	1,28	12(15)
PMMA26	112(100)	85(76)	50(45)	1,70	21(18)
PMMA27	97(100)	74(76)	46(47)	1,61	19(19)
PMMA28	99(100)	72(73)	41(41)	1,76	18(18)

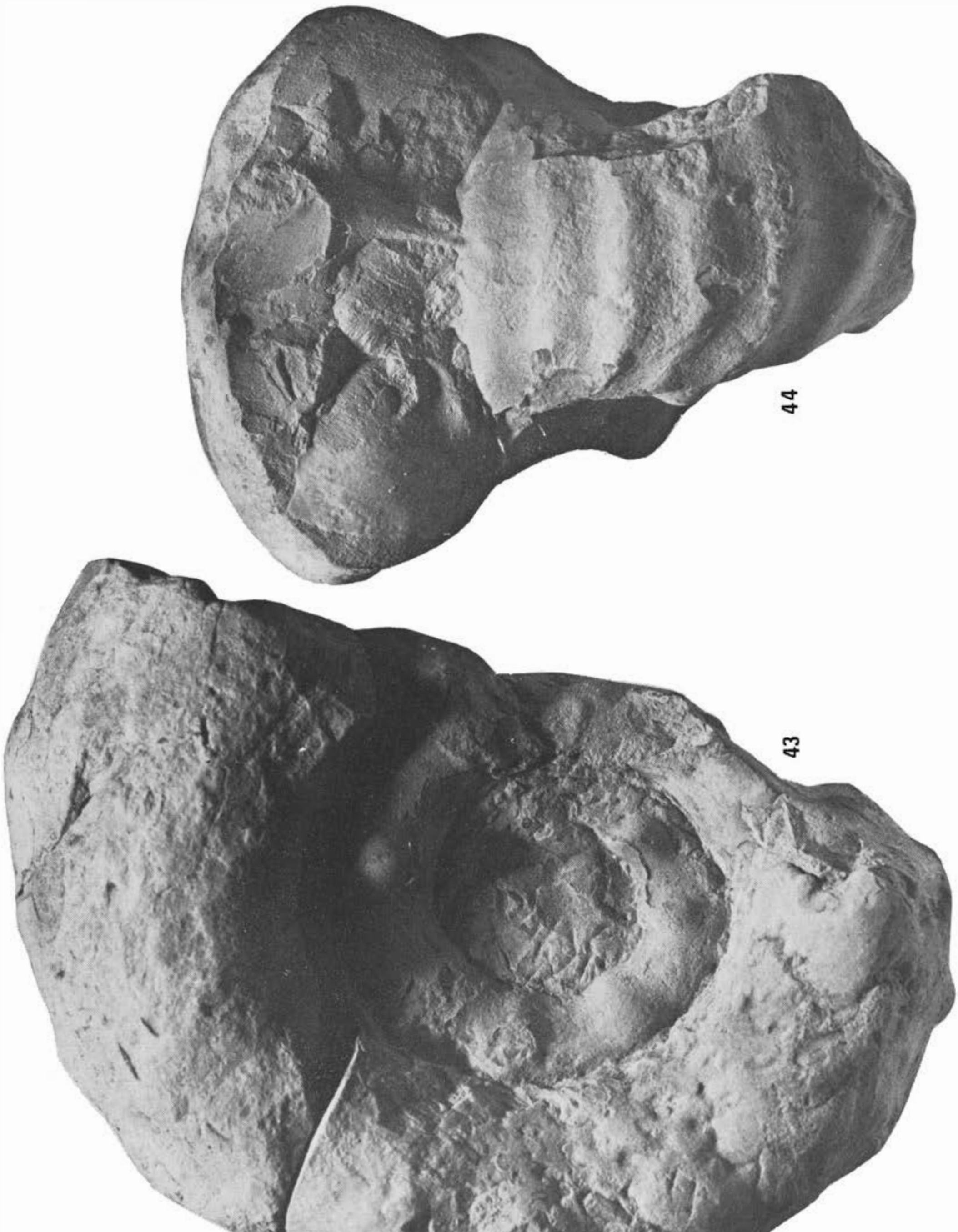
DESCRIPTION: Globose, but highly variable; some shells somewhat compressed (e.g. PMMA28) but generally very inflated, with whorls almost completely embracing. Whorl section semilunar, only slightly thicker at mid-section than near umbilicus, which is variable but generally rather narrow and deep, with almost vertical walls and smoothly rounded shoulder. There appears to be a tendency to uncoiling in some large specimens (e.g. PMMA8). Suture of the simple *Vascoceras* type, although incompletely known (see Fig. 2D).

DISCUSSION: This species apparently does not possess umbilical tubercles and is therefore here referred to *Paravascoceras.* As such it grades into *P. carteri* and *P. hartti*, as discussed above. Böse originally included three specimens in *P. angermanni*, C568, C569 and C570. I have referred C569 to *P. carteri* and C570 (somewhat doubtfully) to *P. hartti*, and selected C568 as lectotype of *P. angermanni.* I also include in *P. angermanni* Böse's *Vascoceras* sp. since, in terms of overall shape and umbilical width, they are indistinguishable from C568.

It seems likely that Böse (1920, p. 218) had C570 in mind when he compared *P. angermanni* with *Vascoceras kossmati* Choffat (1898, p. 63, pl. 13, figs. 8, 9; pl. 14, figs. 1, 2; pl. 21, figs. 26, 27; the comparison was reiterated by Karrenberg 1935, p. 140). I have compared C570 directly with a cast of Choffat's pl. 13, fig. 8; pl. 14, fig. 1 kindly lent to me by Dr. C. W. Wright, and with Eck's (1915, p. 202) Egyptian specimen (Berlin Collections) which is apparently identical with the Portuguese species. Although both specimens are closest in size to C569 (*P. carteri*) and closest in umbilical width to C568 (*P. angermanni*) in overall shape they are closest to C570 (*P. hartti*). Böse cited as the main difference between *P. angermanni* and *V. kossmati* the less tightly rounded inner whorls of the former (by which he must have meant C569). The suture "is also different, the saddles of [*P. angermanni*] being relatively higher and the lobes deeper" and "one might add that [*P. angermanni*] grows to a larger size than the Portuguese species" (p. 218). These latter comparisons were presumably based on specimen C570.

Böse (1920, p. 219) compared his *Vascoceras* sp. with *Ammonites arnesensis* Choffat (1898, p. 68, pl. 13, fig. 10; pl. 14, fig. 3; pl. 22, fig. 39); indeed, on p. 214 Böse refers to his material as '*V.* aff. *arnesense*'. He also noted the similarity between his *Vascoceras* sp. and *P. angermanni*, but felt that the latter was too globose; this objection is removed if comparison is made only with the lectotype, C568. *Ammonites arnesensis* itself is a singular form. Photographs of Choffat's holotype (specimen no. 836, Geological Survey of Portugal), which as far as I can tell is the only specimen known, confirm Böse's observation that i s suture is quite different from that of typical *Vascoceras.* Faraud (1940, p. 48, pl. 3, fig. 3) compared '*V. arnesense*' with his own *V. triangulare* and refigured Choffat's diagram of its whorl section.

Vascoceras sp. of Cobban & Scott (1972, p. 83, pl. 36, figs. 1, 2; text-fig. 41B) from Colorado (USNM 164020), although crushed, is very similar to some of the more compressed specimens of *P. angermanni.* The Tunisian species *V. durandi* (see under *P. hartti* above) is also close to *P. anger-*



Figs. 43—44. Fagesia haarmanni Böse. Holotype C566 (see Böse 1920, pl. 14, figs. 1, 2; pl. 15, fig. 2). From Loma el Macho. × 1.

manni; I hope to publish a full revision of *V. durandi* elsewhere.

It remains a question whether Karrenberg's (1935) Spanish specimen of '*V. angermanni*' (see under *P. carteri* above) should be included here, since it was not figured.

Paravascoceras compressum (Powell not Barber)
Figs. 49, 50

1920 *Neoptychites* aff. *cephalotus* (Courtiller); Böse, p. 221, pl. 18, figs. 3, 10, 13; text-figs. 5, 6.
1931 *Thomasites* sp.; Adkins, p. 56, pl. 2, figs. 16, 17.
?1957 *Vascoceras globosum compressum* Barber, p. 25, pl. 7, fig. 4a, b; pl. 9, fig. 1a, b; pl. 28, figs. 10, 11.
1963a *Pachyvascoceras compressum* (Barber); Powell p. 321, pl. 32, figs. 2—4, 7; pl. 34, figs. 8, 10; text-figs. 3b—d, f.

MATERIAL: C577, a juvenile, plus PMMA30, a larger specimen with some body chamber preserved. Both from Loma el Macho.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA30	71(100)	37(52)	36(51)	1,0	5(7)

DISCUSSION: As noted in the Appendix, the specimen C577 described by Böse (1920) as *Neoptychites* aff. *cephalotus* now lacks the body chamber which was shown in position in Böse's pl. 18, figs. 3, 13 and is now indistinguishable from the '*Pachyvascoceras compressum* (Barber)' figured by Powell (1963a) from Chihuahua, especially Powell's pl. 32, fig. 4. The larger Loma el Macho specimen, PMMA30, though poorly preserved, is very close in shape to abundant specimens from Chihuahua and west Texas I have seen and is clearly conspecific with Powell's material. I am rather less certain that these forms are identical with Barber's Nigerian subspecies, elevated to species rank by Powell. Barber (1957, p. 25) specifically refers to "ornament on early whorls of umbilical tubercles" and if this is the case his material cannot be *Paravascoceras* (cf. Reyment 1978, p. 58). In none of the Texan or Mexican material, however, do there seem to be any such umbilical tubercles.

Genus FAGESIA Pervinquière 1907
(= *Plesiovascoceras* Spath 1925)

TYPE SPECIES: *Olcostephanus superstes* Kossmat 1897 by original designation.

REMARKS: See Wright & Kennedy (1981, p. 87) for a diagnosis of and remarks on *Fagesia*, under which they synonymise *Plesiovascoceras* Spath. A comprehensive account of the occurrence of this genus is given by Cobban & Scott (1972, p. 87).

Fagesia haarmanni Böse
Figs. 43—48

1920 *Fagesia haarmanni* Böse, p. 211, pl. 14, figs. 1, 2; pl. 15, fig. 2.
1923 *Vascoceras thomi* Reeside, p. 29, pl. 11, figs. 1, 2; pl. 12, figs. 1, 2; pl. 13, figs. 1, 2; pl. 14, figs. 1, 2; pl. 15, figs. 1—7; pl. 16, figs. 1—6.
1923 *Vascoceras moultoni* Reeside, p. 30, pl. 17, figs. 1, 2; pl. 18, figs. 1, 2.
1923 *Vascoceras stantoni* Reeside, p. 30, pl. 19, figs. 1, 2; pl. 20, figs. 1—3; pl. 21, figs. 1—3.
?1923 *Vascoceras* sp.; Reeside, p. 30, pl. 20, fig. 4.
?1928 *Fagesia haarmanni* Böse; Böse & Cavins, p. 29.
?1928 *Fagesia* aff. *haarmanni* Böse; Böse & Cavins, p. 29.
?1931 *Fagesia* cf. *haarmanni* Böse; Adkins, p. 29.
1954 *Fagesia haarmanni* Böse; Kummel & Decker, p. 313, text-fig. 3.
1963a *Fagesia haarmanni* Böse; Powell, p. 320, pl. 33, fig. 2; pl. 34, figs. 1—5; text-fig. 2h—k.
1971 *Fagesia haarmanni* Böse; Brito, fig. 13 (copy Kummel & Decker 1954).
?1972 *Fagesia* sp.; Cobban & Scott, p. 88, pl. 34, figs. 1, 2; pl. 38, fig. 4.
1978 *Fagesia haarmanni* Böse; Young & Powell, pl. 2, fig. 1 (copy Powell 1963a, pl. 34, fig. 1).
non 1977 *Fagesia haarmanni* Böse; Chancellor et al., p. 91.

MATERIAL: Böse's holotype C566 is the only surviving specimen of this species definitely known from Loma el Macho and is reillustrated here (Figs. 43, 44). The specimen PMMA13 referred here by Chancellor et al. (1977) is more probably part of a large pseudotissotiine. To C566 may be added from Piedra de Lumbre: WSA 1318/1319, WSA 2080 and BEG 20828, which is probably the material reported by Böse & Cavins (1928). These specimens are discussed below.

DISCUSSION: Reeside (1923) knew of Böse's fossils from Loma el Macho, but believed that "none of the species seem to be identical with those from Montana" which he was describing as *Vascoceras*. This remark may be partly the reason why Böse & Cavins (1928, p. 94) thought Reeside's fauna contained "different species of *Vascoceras*", even though Böse must surely have seen Reeside's illustrations. Reeside's material consisted of abundant large ammonites which he divided among three new species, *V. thomi*, *V. moultoni* and *V. stantoni*. His taxonomic discussion was limited to comparison with some of Choffat's (1898) Portuguese *Vascoceras*, none of which are really similar to the Montanan forms.

By his listing of '*Plesiovascoceras*' from Mexico and Montana, Wright (1957, p. L419) seems to have been the first to note in print the similarity between Böse's and Reeside's specimens (although see Appendix herein concerning the label of a cast of *haarmanni*). I have examined a large body of material from Montana in the United States National Museum (including Reeside's specimens) and from the University of Wisconsin (the latter collected by Young (1951) and kindly loaned to me by Dr. K. Westphal). In my opinion this material displays a continuous range of variation, that is, I do not believe more than one species should be recognised.

Kummel & Decker (1954) described a poorly preserved specimen (WSA 2080) and a fragment (BEG 20828) from Piedra de Lumbre, both of which they referred to *F. haarmanni.* Kummel & Decker (1954) figured the suture of BEG 20828 (1954, text-fig. 3). WSA 2080 is figured here (Figs. 46—48). A third specimen (WSA 1318/1319) from Piedra de Lumbre seems to have escaped Kummel's and Decker's attention; it is half of a well preserved body whorl, constructed from two fragments (Wb = 95 mm; Wh = 51 mm, intercostal) and is obviously identical to the outermost whorl of C566. It is illustrated here (Fig. 45) to show the venter.

Adkins (1931) described a poorly preserved fragment, perhaps referable to *F. haarmanni*, from Texas. Powell (1963a) described a substantial collection under the same name from Chihuahua, and observed that the ventral ornament of the species is gradually lost during ontogeny, generally at diameters of about 150—200 mm. Some specimens are strongly ornamented while other are completely smooth at equivalent diameters, and there seems to be a continuous sequence of specimens representing all variations between these extremes. WSA 1318/1319 is the most strongly ornamented individual I have seen however,, among any of the specimens which I refer here. It shows no sign of loosing its very strong ribs at a maximum diameter of about 165 mm.

Powell's material also shows a more or less continuous variation of whorl sections, in fact identical, in my view, with that seen in the collections from Montana. Bearing in mind that there are differences in preservation between the two areas, I do not regard as more than, at most, a subspecific difference the fact that "the juvenile ribbing is interrupted over the venter in *P. stantoni* and continuous on the venter of *F. haarmanni*" (Powell 1963a, p. 321). In this regard it is interesting that the two juvenile fragments described by Cobban & Scott (1972, pl. 34, figs. 1, 2; pl. 3, fig. 4) as *Fagesia* sp. from Colorado have ribbing more like that seen in *F. haarmanni* from Mexico, than from Montana.

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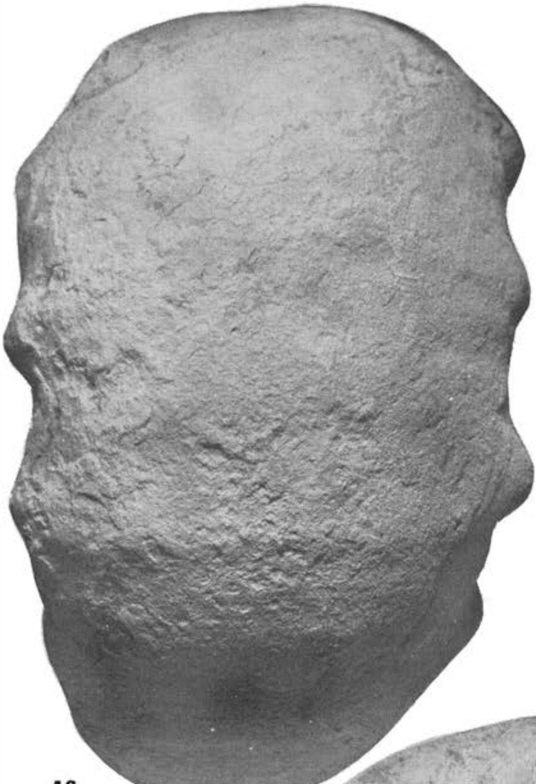
Fig. 45. Fagesia haarmanni Böse. WSA 1318/1319. From Piedra de Lumbre. × 1.

Böse (1920) described *F. haarmanni* as belonging to the group of *F. superstes* (Kossmat), but differing from that species, known principally from India and Tunisia, in being more evolute, with sparser but stronger ornament.

Unfortunately, Böse seems to have relied for knowledge of the English Turonian ammonites on Solger (1904, p. 207) who omitted to list '*Ammonites catinus* Mantell' (1822, p. 198, pl. 22, fig. 10). '*A. catinus*' of Mantell is based on the holotype BMNH C3379, and is now referred to *Fagesia.* '*A. catinus*' as figured by Sharpe (1855, p. 29, pl. 13, fig. 1a, b) is based on BMNH 88583 and is now referred to *Fagesia pachydiscoides* (Spath). BMNH C3379 is refigured by Wright & Kennedy (1981, text-fig. 31). BMNH 88583 is refigured by Wright & Kennedy (1981, text-fig. 37). Wright & Kennedy (op. cit.) include *F. haarmanni* in their



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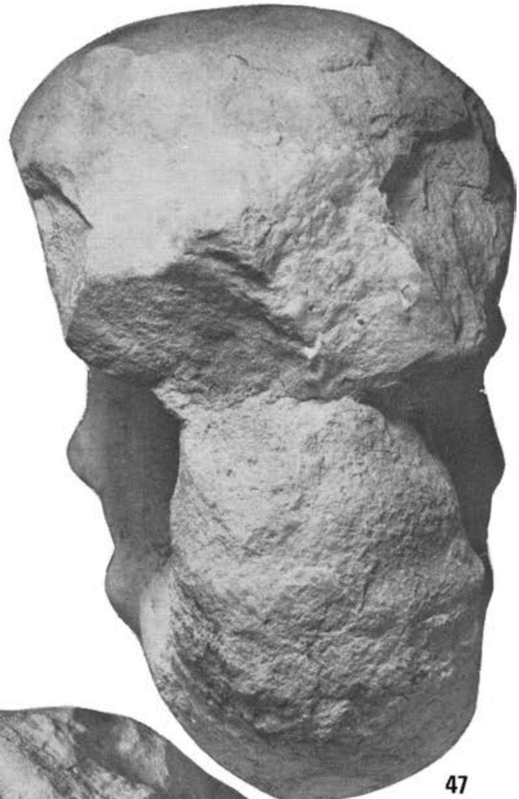

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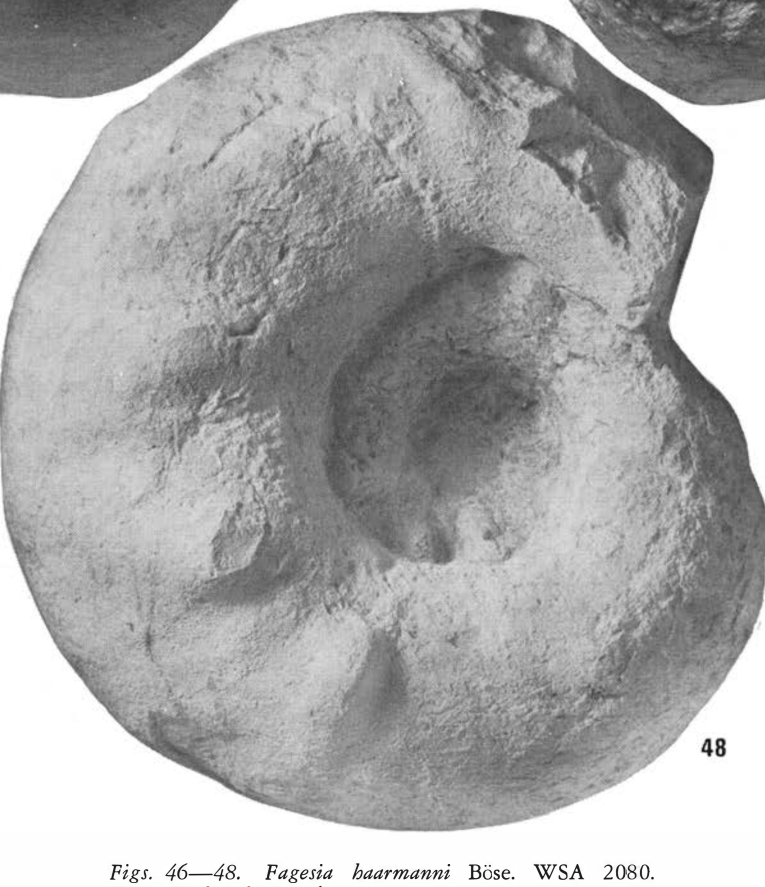

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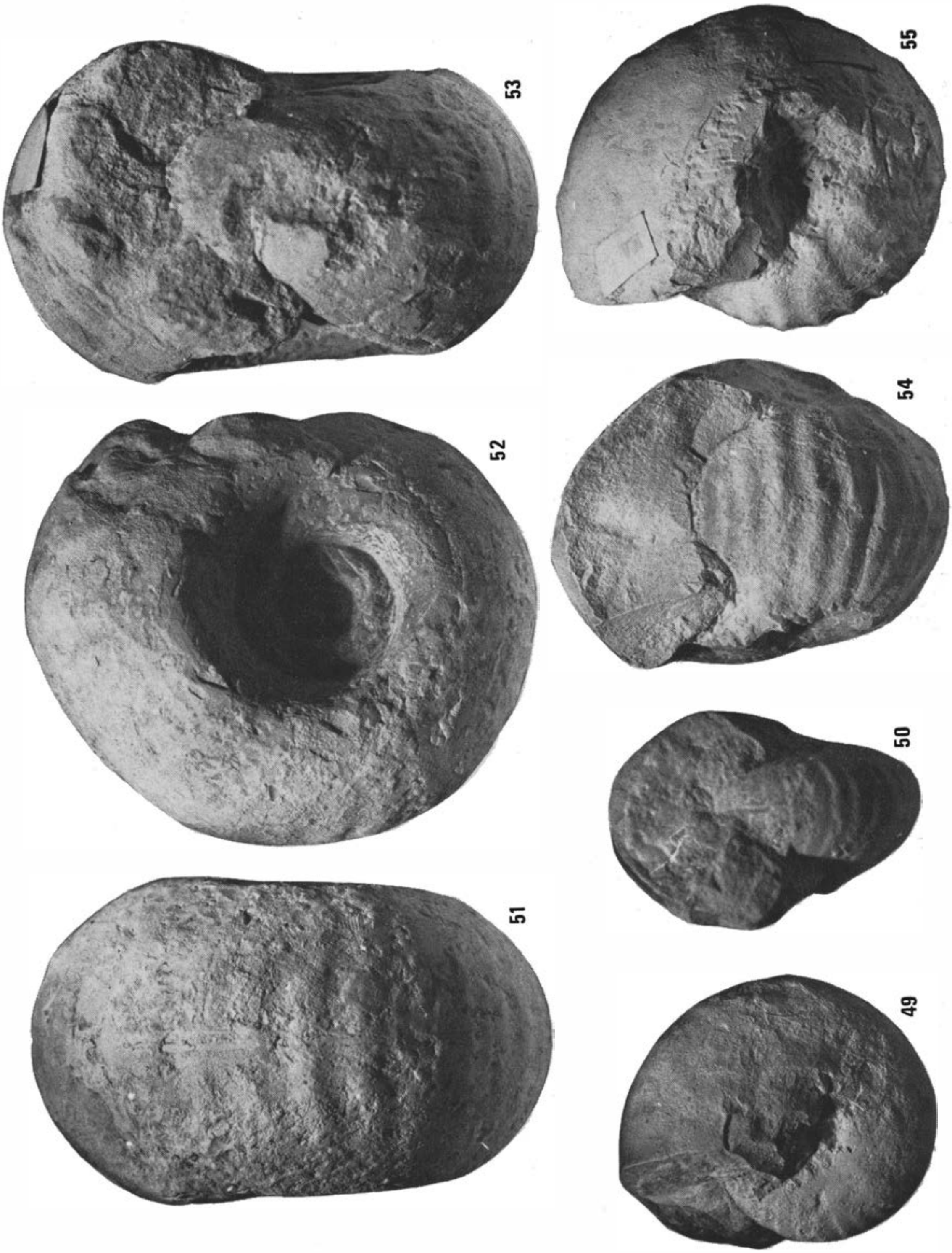
Figs. 46—48. Fagesia haarmanni Böse. WSA 2080.
From Piedra de Lumbre. × 1.



Figs. 49—50. Paravascoceras compressum (Powell not Barber?). C577 (see Böse 1920, pl. 18, figs. 3, 10, 13; text-figs. 5, 6). From Loma el Macho. × 1.

Figs. 51—53. Fagesia? pervinquieri Böse. PMMA5. From Loma el Macho. × 1. See also Fig. 2F.

Figs. 54—55. Fagesia? pervinquieri Böse. PMMA6. From Loma el Macho. × 1.

synonymy for *F. catinus*, but I prefer to regard the two species as distinct. In my experience, the largest specimens of *F. haarmanni* from the New World are almost always more involute than BMNH C3379 and become more depressed, with flatter, broader venters, at equivalent diameters. Reeside's pl. 13 specimen (USNM 32536) is a possible exception, however, and post-mortem effects must always be remembered when dealing with these large vascoceratids. BMNH C3379 is also considerably larger (approaching 400 mm) than any *F. haarmanni* I have seen, so other English specimens must be used for making the comparison.

The specimen BMNH C8316 mentioned by Spath (1925, p. 198, see p. 102 herein) as "another new species of *Fagesia*" has a diameter of about 350 mm and is figured by Wright & Kennedy (1981, text-fig. 32) as *F. catinus*. BMNH C8316 has already been mentioned above in connection with *Paravascoceras* aff. *hartti* and differs from both BMNH C3379 and BMNH 88583 chiefly in its more depressed section and flatter venter. Ornament consists of about 12 circular tubercles cresting the angular umbilical shoulder on the last whorl, which become increasingly low, clavate and irregular towards the aperture. The expansion rate of the last whorl is very low and as such, BMNH C8316 strongly resembles some of the largest *F. haarmanni* (cf. Reeside's pl. 21, USNM 32533; also WSA 1298).

Other specimens figured as *F. catinus* by Wright & Kennedy (1981) are BMNH C79352 (text-fig. 33), OUM K1763 (text-fig. 34) and the innermost whorls of OUM K10480 (pl. 26, fig. 2). Of the two complete figured specimens BMNH C79352 is only distinguishable from the holotype and only figured specimen of *F. pachydiscoides* (BMNH 88583) by being a little more globose, while OUM K1763 is very similar in all respects to BMNH C3379.

Confining attention to specimens more directly comparable in size with *F. haarmanni*, one may note that BMNH 88583 is slightly more involute than C566, with a more rounded, arched venter, less angular umbilical shoulder, rather weaker tubercles and no ventral ribs on the outer whorl. Some specimens of *F. haarmanni* (e.g. Reeside's p. 11, USNM 32535) approach more closely the round inflated shape of BMNH 88583, but these seem to represent an extreme of variation in the American species. BMNH C79352 is closer in this regard to such specimens of *F. haarmanni*.

According to these observations, therefore, the holotype of *F. pachydiscoides* is apparently very similar to one end of the variation seen in *F. haarmanni*, and as such recalls the latter species more than does *F. catinus*, with the exception of specimens BMNH C8316 and BMNH C79352. Until more material is figured from Europe I prefer to maintain the distinction between *F. haarmanni* and *F. catinus*. It seems to me perhaps harder to maintain the distinction between *F. catinus* and *F. pachydiscoides*.

French specimens comparable with *F. haarmanni* include those figured by Destombes & Sornay (1959, pl. 14), by Faraud (1940, pl. 7, fig. 1; pl. 9, fig. 3; photographs on p. 59), and by Thomel (1969, pl. E, figs. 1, 2; pl. D, figs. 1, 2), all of which are included by Wright & Kennedy (1981, p. 88) in their synonymy for *F. catinus*. Destombes & Sornay's specimen is distorted, but Faraud's photographed specimen seems very similar to some of the larger *F. haarmanni*. Thomel's (op. cit.) pl. E specimen is closely comparable to Reeside's (1923) pl. 17, USNM 32537 and Powell's (1963a) pl. 33, fig. 2, text-fig. 2k, UT 30895.

Anderson (1931) described three American species of '*Fagesia*': *californica* (p. 123, pl. 15, fig. 1; pl. 16, figs. 1, 2; pl. 17, fig. 1; text-fig. 1a, b), *shastensis* (p. 124, pl. 16, fig. 3; text-fig. 2) and *siskiyouensis* (p. 125, pl. 17, figs. 2, 3). He later (Anderson 1958) redescribed *californica* (p. 248, pl. 39, figs. 1, 2) and *siskiyouensis* (p. 248, pl. 28, figs. 1, 2), adding a fourth species *klamathensis* (p. 248, pl. 28, figs. 3, 3a). Without stating his reason, he redescribed *shastensis* as a *Vascoveras* (p. 248). Matsumoto (1958, p. 653) referred *californica* to *Plesiovascoceras* [= *Fagesia*] and included *shastensis* in synonymy with it. He referred *klamathensis* to *Eupachydiscus periplicatus* (Whiteaves) and *siskiyouensis* to *Anapachydiscus*.

Matsumoto (1959, p. 102, pl. 36, fig. 1a—c; text-fig. 54a, b), having seen Anderson's material, described some additional specimens of *F. californica*, including a figured specimen of which I have seen a cast (BEG 35231). He also (Matsumoto 1959, p. 35) showed *klamanthensis* to be a *Eupachydiscus haradai haradai* (Jimbo). We are therefore left with *F. californica*, of which Brito (1971, fig. 12) refigured the suture, and there can be little doubt that this species is closely related to *F. haarmanni*.

The holotype of *F. californica* is larger and more evolute than C566, with more rounded umbilical shoulders and weaker ribs, but smaller specimens seem to resemble the Mexican specimen more strongly. Matsumoto (1959, p. 104) indicated the essential differences between *F. californica* and Reeside's (1923) material, and I might note that I have never seen a specimen of *F. haarmanni* identical with any of the figured *F. californica.* In my view, the two species are best regarded as distinct at present.

Fagesia? pervinquieri Böse
Figs. 2F, G, 51—55

1920 *Fagesia pervinquieri* Böse, p. 212, pl. 12, fig. 5; pl. 14, fig. 3.
?1975 *Fagesia pervinquieri* Böse; Brundrette in Frush & Eicher, p. 285.
1977 *Fagesia? pervinquierei* Böse; Chancellor et al., p. 92, figs. 11—14.

MATERIAL: In addition to the holotype C565, there are four other specimens of this species from Loma el Macho. PMMA5 is well preserved but lacks the body chamber; it shows several partial sutures (Figs. 2F, 51—53). The outer whorl of PMMA6 is badly corroded but the inner whorls are well preserved, as is shown here (Figs. 54, 55) and in Chancellor et al.'s (1977) figs. 13, 14, where the specimen is developed back to a diameter of 58 mm (not 70 mm as stated by Chancellor et al.). PMMA29 is a fragment of about one-sixth of a relatively large whorl which shows some internal sutures (Fig. 2G).

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA5	72(100)	46(63)	30(42)	1,53	21(29)
PMMA6	70(100)	47(67)	33(47)	1,42	20(28)
PMMA29	?100(100)	61(61)	37(37)	1,64	?40(40)

DESCRIPTION: Subglobose, very involute, with semilunar whorl section. Umbilicus deep, rather narrow, with steep walls. Inner whorls with about 8 umbilical nodes per whorl at approximately D = 45 mm, which disappear at an undetermined diameter on later whorls and from each of which about three rectiradiate ribs extend across the venter, gaining their maximum development at mid-venter. These ribs weaken somewhat on later whorls and become slightly prorsiradiate, while increasing in frequency to about 35 per whorl at D = 70 mm. They may disappear completely on larger specimens, but the present material is too poorly preserved to show this. The suture is of the simple *Vascoceras* pattern with weakly indented elements.

DISCUSSION: The most complete specimen described here, PMMA5, is immediately recognisable as identical with C565, inasmuch as the latter is a little larger (D = 94 mm). The only other record of this species is that of Brundrette in Frush & Eicher (1975, p. 285) from west Texas. Unfortunately, I have not seen the fossil in question and it is at least possible that Brundrette had in fact found *F. texana* Adkins (1931, p. 55, pl. 2, figs. 4, 10, 15; see also Kummel & Decker, 1954, p. 313, pl. 32, figs. 1, 2; text-fig. 2), because Frush & Eicher (op. cit., p. 287) refer to Kummel & Decker's (1954) specimen of '*F. pervinquieri*', which must be the holotype of *F. texana* (see below).

Böse (1920, p. 212) gave a full description of C565 and recognised it as a near relative of *F. tevesthensis* (Peron 1897, p. 23, pl. 7, figs. 2, 3) and "especially the large specimen figured by Pervinquière" (1907, pl. 20, fig. 6). (The name was misspelt by Pervinquière 1907, p. 325, who described Tunisian material as *F. thevestensis.*) Böse simply stated that his species "belongs to *Fagesia* ... on account of its general form and ornamentation ... although the suture could not be made visible". Chancellor et al. (1977, p. 92) reported misleadingly from the evidence of the new material that the suture of *F.? pervinquieri* is "more suggestive of *Vascoceras* or *Plesiovascoceras* than of *Fagesia*". It has now been established that *Plesiovascoceras* is a synonym of *Fagesia*, and where forms previously referred to *Plesiovascoceras* show well preserved sutures, they are quite similar at equivalent diameters to that of *F.? pervinquieri.* Furthermore, as Reeside (1923, p. 29) himself pointed out, two Montanan specimens of *F. haarmanni* of comparable size to PMMA5 (cf. Reeside's pl. 15, fig. 6; pl. 16, fig. 6) may display rather different sutures, even though their overall shapes are similar (the specimen on pl. 16 is USNM 32536; pl. 15 is apparently mislabelled).

Considering that ontogenetic stage and style of preservation can have such a profound effect on the suture, I prefer here to follow Barber (1957) who, according to Freund & Raab (1969, p. 33) "emphasised the importance of the shape of the shell and of the ornament". Barber (1957, p. 15, 27, 29) stressed that the umbilical tubercles of *pervinquieri*, being lost at an early ontogenetic stage, indicated a *Vascoceras*-affinity for the species. Freund & Raab (1969, p. 31) considered C565 "almost identical" with *V. durandi.* I am therefore forced to leave the generic placement of *pervinquieri* open to question.

I know of no figured ammonite in the literature which is exactly comparable with *F.? pervinquieri.* All the following are obviously similar but differ for one reason or another: *V. douvillei* Choffat (1898, pl. 10, figs. 3, 6; pl. 11, figs. 2—5); *F. tevesthensis* (Peron) in Pervinquière (1907, pl. 20, figs. 5a, b, 6a, b); *Thomasites rollandi globosa* Pervinquière (1907, pl. 22, figs. 3, 4) although this has a much smaller umbilicus anyway; *F.?*

fleuryi Pervinquière (1907, pl. 20, fig. 9a, b) which, like the Mexican species at comparable diameters, has an apparently simple suture; *F. rudra* (Stoliczka) in Kennedy & Wright (1979a, p. 666, pl. 82, figs. 1, 2).

It is of especial interest to compare *F.? pervinquieri* with *F. texana* (see above). The only figured specimen of the Texas species is the holotype, which differs from *F.? pervinquieri* in its undoubted true *Fagesia*-suture, more globose shell and early loss of ribbing. I think it quite possible, however, that *F. texana* is some sort of variant of *F.? pervinquieri*, but I leave this subject for future research.

Genus PARAMAMMITES Furon 1935

TYPE SPECIES: *Vascoceras polymorphum* Pervinquière 1907 by subsequent designation of Reyment (1954a).

REMARKS: Wright (1957, p. L419) gave the following diagnosis of *Paramammites*: "Variable, more or less evolute; prominent coarse ribs bear strong and blunt umbilical, ventrolateral and one or more lateral tubercles." Wright (op. cit.) gave the geographical distribution of the genus as Tunisia, Portugal and Mexico. The Mexican reference is presumably to the species discussed here, which was assigned to *Paramammites* by Barber (1957, p. 33). *Paramammites* is also known from Nigeria (Barber 1957), Colombia and Venezuela (Leanza 1967; Etayo-Serna 1979), the Sahara (Collignon 1965a), Spain (Wiedmann 1964), France (Thomel 1969), Turkestan (Stankevich & Poyarkova 1969) and Israel (Freuid & Raab 1969), although as I shall outline below, some of these may not be *Paramammites* s.str. The map given by Matsumoto & Muramoto (1978, text-fig. 4) showing the distribution of this genus must therefore be used with caution.

Paramammites? mohovanensis (Böse)

Figs. 40—42

1920 *Vascoceras mohovanense* Böse, p. 219, pl. 18, figs. 1, 2; text-fig. 4 upper.

?1928 *Vascoceras* cf. *mohovanense* Böse; Böse & Cavins, p. 29.

?1954 *Fagesia* sp.; Kummel & Decker, p. 314, pl. 33, figs. 4, 5; text-fig. 4.

1957 *Paramammites mohovanensis* (Böse); Barber, p. 33.

MATERIAL: The holotype C574, from Loma el Macho. Perhaps also BEG 20826, from Piedra de Lumbre.

DISCUSSION: Böse (1920) gave a description of this species based on C574, still the only definitely known specimen and therefore not an adequate choice as a zonal index fossil (cf. Young & Powell 1978; see p. 81). There is, however, reason to believe that specimen BEG 20826 figured as *Fagesia* sp. from Piedra de Lumbre by Kummel & Decker (1954) may have been the material listed from that locality as '*V.* cf. *mohovanense*' by Böse & Cavins (1928), since there are some strong points of similarity between C574 and BEG 20826. The absence of a mid-ventral sulcus on BEG 20826, such as is formed by the gap between the angulate ventrolateral rib swellings on C574, could be an ontogenetic difference. On C574 itself it is noticeable that the sulcus becomes steadily less obvious with growth; C574 and BEG 20826 could therefore be conspecific.

As for the generic placement of '*V. mohovanense*', there is here a considerable problem. As noted above, Barber (1957) referred the species to the multituberculate genus *Paramammites*, which resulted in unfortunate nomenclatorial confusion with *Mammites mohovanensis*. This confusion can only be avoided with difficul y in view of the obvious resemblance between '*V. mohovanense*' and '*V. polymorphum* Pervinquière' (1907, p. 337, pl. 21, figs. 2—6), as stressed by Böse. As Böse (1920) pointed out, however, C574 lacks lateral tubercles (mentioned in Wright's diagnosis of *Paramammites*) and for this reason *mohovanense* can only with doubt be referred to *Paramammites*.

C574 shows a limited similarity to some *Fagesia haarmanni*. A specimen in Dr. C. W. Wright's collection from Reeside's Montanan locality is figured by Wright & Kennedy (1981, text-fig. 36A, B); it shows at a diameter of about 40 mm an exceptionally strong development of the ventrolateral rib-swellings (discussed under *F. haarmanni* above) and at that stage is very similar to the earliest visible portions of C574. The ribs of Dr. Wright's specimen rapidly become subdued, however, and are relatively insignificant at a diameter equivalent to the maximum size of C574.

There is no published description, as far as I am aware, of any other ammonite which bears more than a passing resemblance to '*V. mohovanense*'. A few forms are comparable to BEG 20826, however, which all share with that specimen the absence of a distinct lateral tubercle, at least at the adult stage. They have also all been figured as *Paramammites*, although some with a?.

Pervinquière's own large specimen (D = 103 mm) of *P. polymorphus* (1907, p. 336, pl. 21, fig. 3a—c) is similar to BEG 20826 (D = 86 mm), but has a depressed subtrapezoidal rather than a semicircular whorl section. The Spanish *P.?*

saenzi Wiedmann (1964, p. 137, figs. 24a, b, 25; 1975a, fig. 3a, b), a cast of the holotype of which I have before me, clearly possesses four rows of ventrolateral tubercles at its earliest visible stage, and is therefore unlikely to be conspecific with C574. The outermost whorl of the holotype (D = 100 mm) is septate throughout, however, and seems to be losing its lateral tubercles. Its body chamber might then resemble BEG 20826, but would be considerably larger with a narrower umbilicus. *P.? postsaenzi* Weidmann (1964, p. 138, fig. 26a, b; 1975a, fig. 7a, b) shows partly this later stage of growth (D = 114 mm) at which it starts to uncoil. In its wider umbilicus, strongly prorsiradiate ribs and apparent absence of lateral tubercles this Spanish species is closer to BEG 20826; it differs from the latter, however, apart from being larger, in possessing a deep mid-ventral sulcus.

P. saenzi cassissianum Thomel (1969, p. 115, pl. C) from France, which I have examined at the United States National Museum, is larger (D = 145 mm) than BEG 20826 and is more involute and inflated, with weaker, sparser ribs (20 per whorl as against 30). The French specimen also lacks the regularly alternating, very strong umbilical tubercles and intercalated ribs of BEG 20826 and has a distinct mid-ventral sulcus.

Genus NEOPTYCHITES Kossmat 1895

TYPE SPECIES: *Ammonites telinga* Stoliczka 1865 [= *Ammonites cephalotus* Courtiller 1860] by original designation.

REMARKS: Kennedy & Wright (1979a) have provided a thorough revision of this genus (although see p. 95 herein).

Neoptychites sp.
Figs. 56—59

1920 *Neoptychites* aff. *xetriformis* Pervinquière; Böse, p. 223, pl. 18, figs. 9, 11; text-fig. 7 lower left.

1931 *Neoptychites* aff. *gourguechoni* Pervinquière; Adkins, p. 57, pl. 2, figs. 18—20.

1954 *Neoptychites* cf. *xetriformis* Pervinquière; Kummel & Decker, p. 315, pl. 32, fig. 3; text-figs. 5, 6.

?1963b *Neoptychites xetriformis* Pervinquière; Powell, p. 1229, pl. 171, figs. 2—4; text-fig. 5b.

1977 *Neoptychites* aff. *xetriformis* Pervinquière; Chancellor et al., p. 96, figs. 21, 22.

MATERIAL: Two poorly preserved specimens from Loma el Macho, PMMA10 and Böse's (1920) specimen, C576. In both specimens the last visible suture is at approximately Wh = 35 mm.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA10	85(100)	39(46)	45(53)	0,86	5(6)

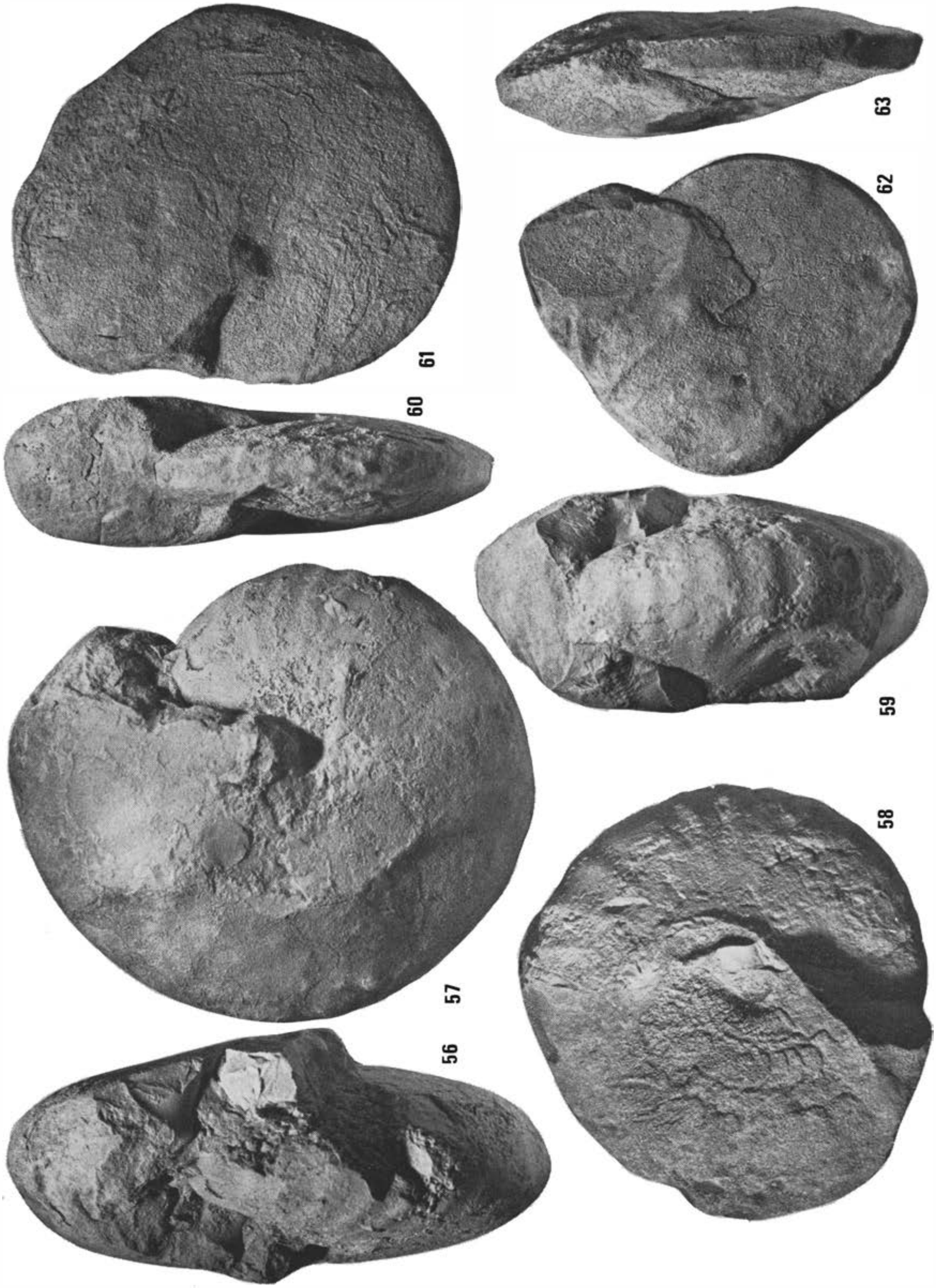
NOTE: The diameter for PMMA10 quoted by Chancellor et al. (1977, p. 97) as 113 mm is for the specimen complete with its outer whorl.

DESCRIPTION: Shell discoidal, very involute. Whorl section higher than wide, although this is variable. Flanks slightly convex and venter parabolically rounded, giving a fusiform whorl section with widest point near umbilicus. The penultimate whorl shows about 30 broad, low ribs which originate near mid-flank and pass over the venter where they become strongest or (as described by Böse 1920, p. 223—4) become "very low and scarcely discernible" but nevertheless "do not completely disappear". The suture of C576 was adequately figured and described by Böse (1920).

DISCUSSION: The material described here is identical with the specimen (now in the Bureau of Economic Geology, Austin) described by Adkins (1931) and redescribed and refigured from the opposite flank by Kummel & Decker (1954). This specimen is from Culbertson County, Texas. The material from Chihuahua described by Powell (1963b) may also belong here, but neither of the Loma el Macho specimens preserves any apertural modification and it is therefore impossible to judge to what stage of growth they attain. Powell (1963b, p. 1231) noted that Adkins's (1931) specimen differed somewhat from his material in apparently lacking strong ribs and having a simpler suture.

Kennedy & Wright (1979a, p. 679) included Powell's material in their synonymy for *N. xetriformis*, but only with doubt listed the material treated here. Differences from *N. xetriformis* are, firstly, the fact that the ribs extend over the venter on Böse's and Adkins' specimens, whereas they are limited to the flanks in Pervinquière's species (1907, p. 398, pl. 27, figs. 5—7; text-figs. 153, 154). Secondly, Böse (1920, p. 224) noted that the ribs of C576 are "much more numerous" than in the Tunisian form, which observation links C576 with *N. cephalotus* (Courtiller) (see Kennedy & Wright 1979a, p. 670, for a revision of this species) and the specimen of *N. xetriformis* from Colorado described by Cobban & Scott (1972, p. 89, pl. 30, figs. 2—6; text-fig. 48; USNM 164046).

Kennedy & Wright (1979a) have shown how, at comparable diameters, *N. cephalotus* may develop ribs and whorl sections not unlike those of

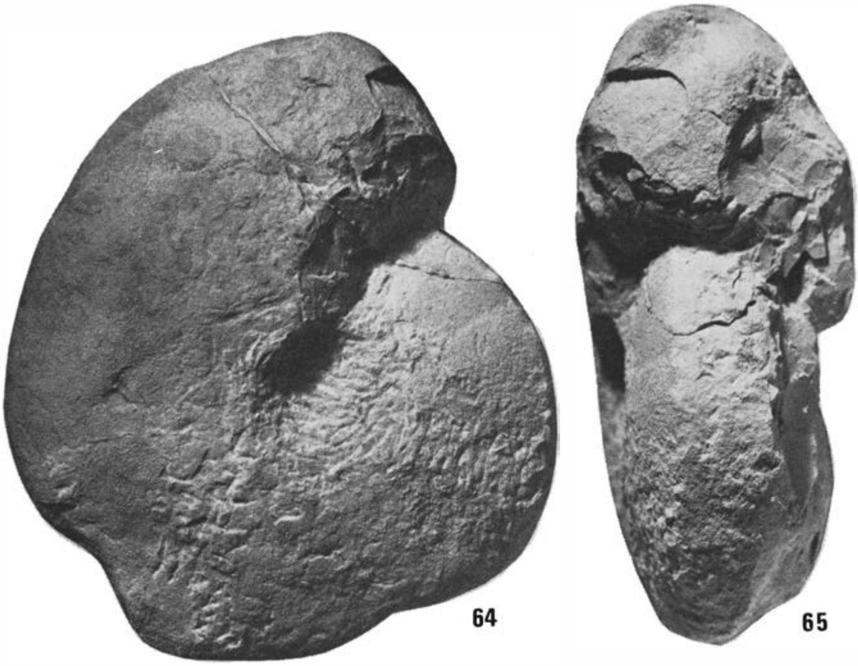


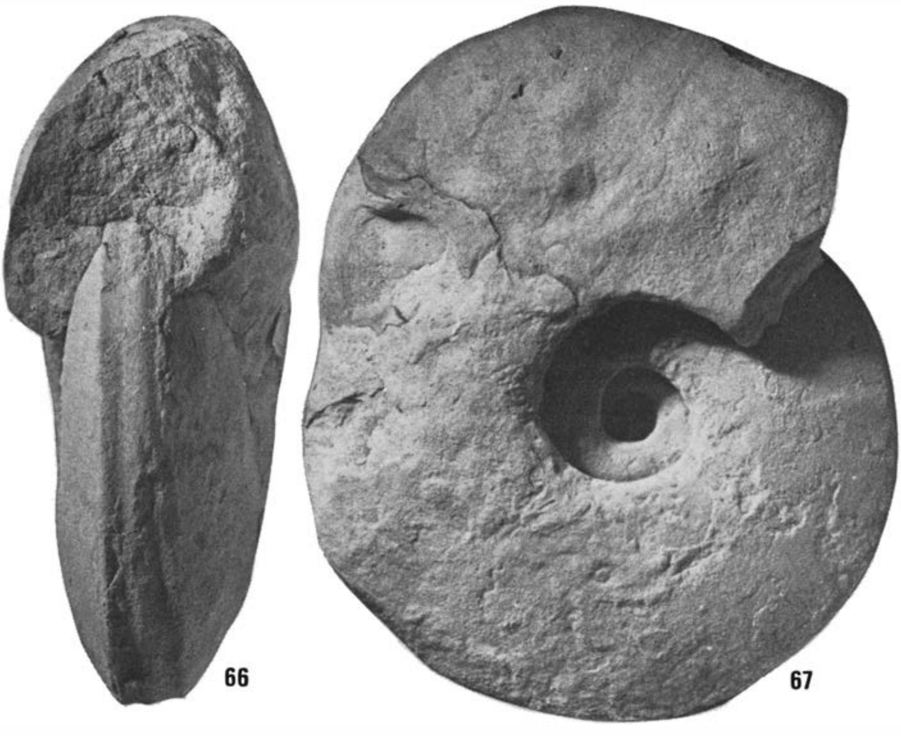
Figs. 56—57. *Neoptychites* sp. C576 (see Böse 1920, pl. 18, figs. 9, 11; text-fig. 7 lower left). From Loma el Macho. × 1.

Figs. 58—59. *Neoptychites* sp. PMMA10. From Loma el Macho. × 1.

Figs. 60—61. *Wrightoceras* cf. *munieri* (Pervinquière). PMMA36. From Loma el Macho. × 1.

Figs. 62—63. *Wrightoceras* cf. *munieri* (Pervinquière). PMMA37. From Loma el Macho. × 1. See also Fig. 2H.





Figs. 64—65. Pseudotissotia cf. *nigeriensis* (Woods). PMMA11. From Loma el Macho. × 1.

Figs. 66—67. Pseudotissotia adkinsi (Kummel & Decker). FMMA12. From Loma el Macho. × 1. See also Fig. 2I.

the material treated here (cf. their pl. 85, figs. 4, 5). Unfortunately, the poor preservation of this material does not allow detailed comparison to extend to development of the suture, but one might note that Böse (1920, p. 224) saw a similarity between C576 and Stoliczka's juvenile *N. xetra* (1865, p. 124, pl. 61, fig. 2) from India, which is now considered a synonym of *N. cephalotus* (Kennedy & Wright 1979a).

The precise identity of the specimens described here cannot be determined at present. It is nevertheless intriguing to speculate on what Böse & Cavins (1928, p. 29) may have had in mind when they reported '*Neoptychites* n. sp.' from Piedra de Lumbre.

Subfamily PSEUDOTISSOTIINAE Hyatt 1903

REMARKS: Wright & Kennedy (1981, p. 98) discuss this subfamily and assign is to the Vascoceratidae, as Wiedmann (1960, p. 758) recommended (see also Reyment (1978, p. 57) and (1979 p. 111)). The Pseudotissotinae includes *Pseudotissotia* Peron 1897; *Hemitissotia* Peron 1897; *Wrightoceras* Reyment 1954a (of which *Imlayiceras* Leanza 1967 appears to be a synonym; see below); *Thomasites* Pervinquière 1907; *Choffaticeras* Hyatt 1903; *Donenriquoceras* Wiedmann 1960, and perhaps *Eotissotia* Barber 1957. *Plesiotissotia* Peron 1897 is probably a synonym of *Hemitissotia.*

Genus PSEUDOTISSOTIA Peron 1897

TYPE SPECIES: *Ammonites galliennei* d'Orbigny 1850 by original designation.

REMARKS: For a diagnosis and revision of this genus see Kennedy et al. (1979).

DISCUSSION: Kennedy et al. (1979, p. 6) have shown to my satisfaction that "separation of *Bauchioceras* and *Pseudotissotia* at generic or subgeneric level is inappropriate in terms of the scope of genera and subgenera of Pseudotissotinae [*sic*] as currently conceived". The revision of Kennedy et al. does not, however, take account of the reversed ontogeny of Nigerian as against European species of *Pseudotissotia* (Reyment 1979). Kennedy et al. (1979) accord generic status to *Wrightoceras*, originally a subgenus of *Bachioceras* and later (Reyment 1955) of *Pseudotissotia.* *Wrightoceras* and *Discovascoceras* Collignon 1957 are discussed below.

Pseudotissotia cf. *nigeriensis* (Woods)

Figs. 64, 65

1977 *Bauchioceras* cf. *nigeriense* (Woods); Chancellor et al., p. 96, figs. 23, 24.

COMPARE:
Pseudotissotia nigeriensis (Woods); Kennedy et al., 1979, p. 12, figs. 21, 22, 25—27.
Bauchioceras nigeriense (Woods); Reyment, 1979, figs. 17—37.

MATERIAL: One specimen, PMMA11, from Loma el Macho. It is not certain whether or not this specimen is entirely septate, but traces of suture can be made out on the flanks of one side, at approximately Wh = 20 mm and 30 mm.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA11	77(100)	29(37)	36(46)	0,81	?10(12)

DESCRIPTION: Very involute, compressed. Venter truncate, apparently tricarinate, at least on the earliest section of the venter seen, where the outer keels bear weak traces of minute clavi. Umbilicus small, steep-walled. Flanks saucer-shaped. Suture apparently as in *P. nigeriensis* (e.g. Barber 1957, pl. 34, figs. 8, 12, 14), but deeply corroded.

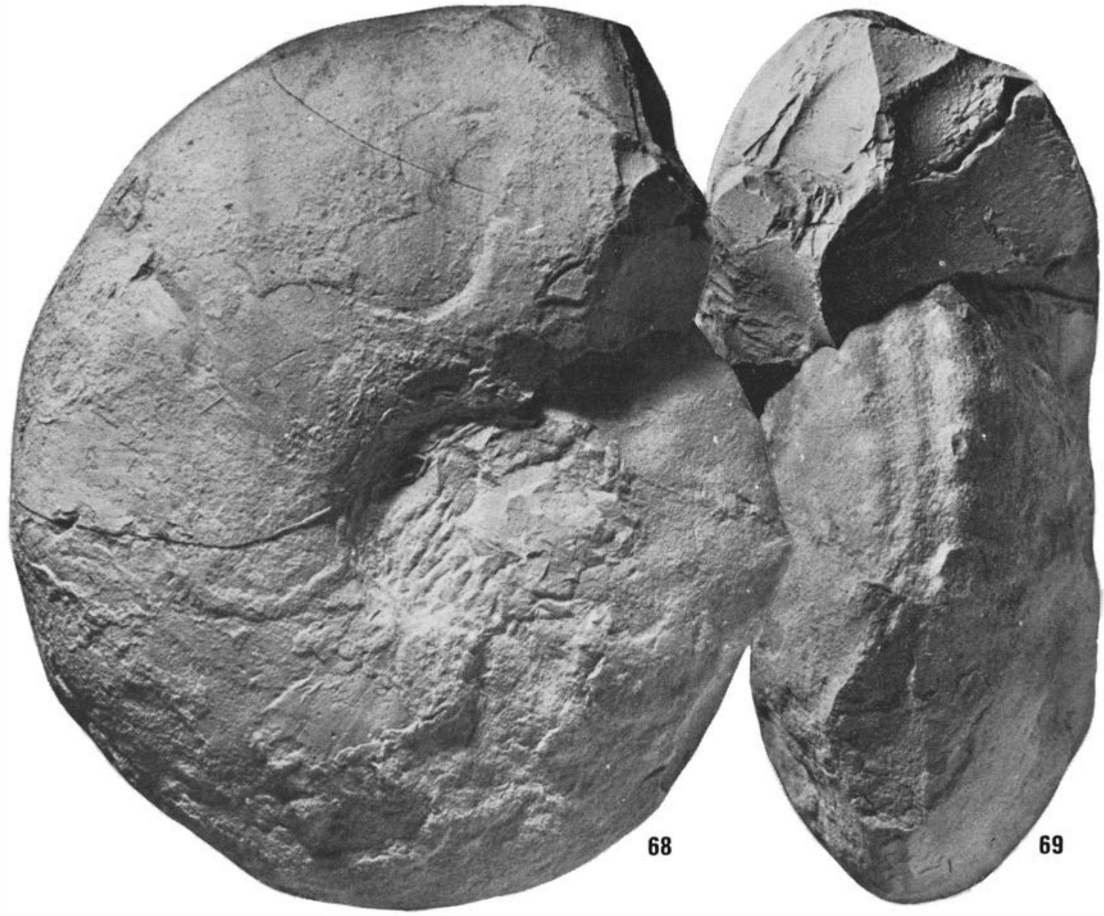
DISCUSSION: Although PMMA11 is very poorly preserved, it seems to agree closely with Woods's species, of which I have examined many specimens. PMMA11 is probably, therefore, the first example of the Nigerian species from North America. Brito (1971, p. 427, text-figs. 4, 9) has figured *Pseudotissotia* from Brazil, and Gonzales-Arreola (1977, p. 168, fig. 2a) has figured a fragment referred to *P. galliennei* from Guerrero in southern Mexico; Kennedy et al. (1979) and Reyment (1979) have analysed the differences between this latter species and *P. nigeriensis.*

Pseudotissotia adkinsi (Kummel & Decker)

Figs. 2I, 66—69

?1928 *Hoplitoides* n. sp.; Böse & Cavins, p. 29.
1931 *Hoplitoides*? *mirabilis* Böse not Pervinquière; Adkins, p. 59, pl. 4, fig. 2.
1954 '*Hoplitoides*' *adkinsi* Kummel & Decker, p. 316, pl. 32, fig. 6; pl. 33, fig. 3; text-figs. 7, 8.
1955 *Pseudotissotia* (*Bauchioceras*) *adkinsi* (Kummel & Decker); Reyment, footnote p. 70.
1977 *Bauchioceras* (*Discovascoceras*) *adkinsi* (Kummel & Decker); Chancellor et al., p. 96, figs. 25, 26.

MATERIAL: Three complete specimens have been found at Loma el Macho: PMMA12, PMMA31 and PMMA34, although none were in Böse's collection. It is also possible that a fragment (PMMA 13) recorded as *Fagesia haarmanni* by Chancellor et al. (1977, p. 91) may belong here. PMMA12 is



Figs. 68—69. Pseudotissotia adkinsi (Kummel & Decker). PMMA34. From Loma el Macho. × 1.

the smallest specimen and seems to be entirely septate but for perhaps 20°—30° of body chamber. Part of the outer whorl is crushed where it is encrusted by an oyster, but the early phragmocone is well preserved (see Fig. 66, 67) and shows the details of several sutures (Fig. 2I). PMMA31 is a little larger than PMMA12 and also shows several partial sutures; the body chamber has been broken back to reveal a moderately well preserved venter. PMMA34 shows no suture, but an almost completely intact body whorl, part of which has been removed to reveal a well preserved venter (see Figs. 68—69 and note to d mensions). Growth striae are visible on the body whorl of PMMA34.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA12	92(100)	36(38)	37(40)	1,05	22(24)
PMMA31	112(100)	41(37)	46(41)	0 89	24(21)
PMMA34	113(100)	47(42)	48(42)	0,98	22(19)

NOTE: The diameter of PMMA12 was erroneously stated by Chancellor et al. (1978, explanation to figs. 25, 26) to be 62 mm. The dimensions quoted here for PMMA34 are taken at least one quarter whorl behind the aperture, although the aperture itself is not preserved.

DISCUSSION: The present material conforms with the type series of *'Hoplitoides' adkinsi* from Piedra de Lumbre, except in a few points of departure noted here. Firstly, the proportional widths of the umbilici of PMMA31 and PMMA34 are slightly smaller than in the type series and in PMMA12, while PMMA34 is more inflated than any of the Piedra de Lumbre (type) specimens. Secondly, according to Kummel & Decker (1954, p. 316), the umbilical wall of *'H.' adkinsi* is "almost vertical and high". While this is a reasonable description applied to the type series, the umbilical wall of PMMA12 is distinctly undercut and overhangs the vertical. Thirdly, the ventral carinae of PMMA34 exposed by removal of part of the body chamber bear clavate swellings not observed on any of the other specimens. Unfortunately it has not proved possible to develop the specimen any further back, but on the small part of the venter where the swellings are exposed they occur at approximately 10° intervals and are much stronger on the outer carinae than on the siphonal one. From alternate swellings arise weak, rather narrow rectiradiate ribs which efface at about mid-flank. Although the details of these ribs are not well known, they seem to conform to those described by Kummel & Decker (1954).

The material from Loma el Macho adds significantly to our understanding of *P. adkinsi*, a species only known from here and Piedra de Lumbre, although Adkins (1931, p. 59) and Kummel & Decker (1954, p. 317) referred to material I have not seen from west Texas. Adkins made the confusing comparison of *P. adkinsi* with Böse's specimens of '*Hoplitoides* aff. *mirabilis*' from Loma el Macho, which are in fact almost certainly very poorly preserved *Wrightoceras* (see below). Adkins's comparison gave the impression that he considered the two forms congeneric, and this has misled subsequent workers (e.g. Young 1958, p. 171; Collignon 1965a, p. 181). The present material, combined with the type series, totals nine specimens, all of which I have studied. Reyment (1978) included three specimens of *P. adkinsi* in his biometrical analysis of "keeled vascoceratids", presumably those tabulated by Kummel & Decker (1954, p. 316).

Kummel & Decker (1954) noted the resemblance between *P. adkinsi* and *P. nigeriensis* (see above). The new specimen PMMA12 shows a suture at about 90 mm better preserved than any shown by Kummel & Decker's (1954) material at an equivalent diameter (see Fig. 21). This suture is apparently identical with that of *P. nigeriensis* (cf. Barber 1957, pl. 34, all suture figures) and supports the view that the two species are congeneric. This is a critical point, because the tubercles on the outer keels of PMMA34 are highly suggestive of some Nigerian forms referred to '*Gombeoceras*' [= *Thomasites*] (cf. Reyment 1979).

A further problem that will be treated is that the umbilici of the Loma el Macho specimens are narrower than those from Piedra de Lumbre, as noted above. PMMA34 has the narrowest umbilicus of all, is also the most inflated, and the only specimen showing the '*Gombeoceras*' ornament. Further collections might show that PMMA 34 should be referred to another species. Regrettably, the specimen does not show a suture.

P. adkinsi is said (Kennedy et al. 1979, p. 12) to differ from *P. galliennei* "in lacking flank ornament when adult and being more evolute, as in other forms referred to '*Discovascoceras*' ". Collignon (1965a, p. 181) noticed the strong similarity between *P. adkinsi* and the type species *tesselitense* of his genus *Discovascoceras*, and suggested that they might be conspecific. He made particular reference to the identity of the last sutures of BEG 20832 (at about D = 100 mm) with the last sutures of *D. tesselitense* (e.g. 1965a, pl. G, fig. 1a, b), both of which are 'vascoceratine' in general outline. Approximately one whorl behind the last suture of *D. tesselitense* the sutures were said to be closely comparable with that of Nigerian '*Bauchioceras*' [= *Pseudotissotia*], just as we have seen is the case with *P. adkinsi*. Chancellor et al. (1977) therefore followed Collignon's suggestion that *adkinsi* be referred to *Discovascoceras*.

Although the Mexican material at my disposal is too meagre to permit any deeper analysis of the problematical status of *Discovascoceras*, I here follow the suggestion of Kennedy et al. (1979, p. 6) that this genus should possibly "be treated as a synonym of *Pseudotissotia*".

As already noted by Kummel & Decker (1954, p. 317) *P. adkinsi* bears some resemblance to *Vascoceras barcoicense* Choffat (1898, p. 67, pl. 17, fig. 1a—c; pl. 22, fig. 35; *non* pl. 16, fig. 11; pl. 22, fig. 36 which Berthou et al. (1975, p. 81) referred to *V. gamai*).

Genus WRIGHTOCERAS Reyment 1954
(? = *Imlayiceras* Leanza 1967)

TYPE SPECIES: *Bauchioceras* (*Wrightoceras*) *wallsi* Reyment 1954, by original designation.

REMARKS: For a diagnosis of *Wrightoceras* see Wright (1957, p. L423). There are a number of problems associated with *Wrightoceras*, a form to which (as noted above) Kennedy et al. (1979) accord generic status. These authors consider *Wrightoceras* (p. 6) "clearly separable from *Pseudotissotia* at all growth stages".

DISCUSSION: Besides the type species from Nigeria and Gabon, Reyment (1954a, 1955) referred the following species to *Wrightoceras*: *Hoplitoides munieri* Pervinquière and *H. mirabilis* Pervinquière, reported from Spain, North Africa, the Middle East and Mexico (see below); *Pseudotissotia llarenai* Karrenberg from Spain, and *P. gagnierei* Faraud from France. Leanza (1967) described a species from Colombia, which as

I discuss below is almost certainly a *Wrightoceras*, under the name *Imlayiceras washbournei*. Etayo-Serna (1979) described a new species *ralphimlayi* which he doubtfully assigned to *Imlayiceras* and which also appears to be a *Wrightoceras*. Freund & Raab (1969, p. 65) suggested that it might "be reasonable to include" in *Wrightoceras* the Peruvian *Hoplitoides inca* Benavides-Caceres (1956), since its suture lacks the characteristics of a true coilopoceratid. Amard et al. (1974) cited without description a new species from Algeria, and Wiedmann (1975) has described a new species from Spain, *W. submunieri* (found above *W. munieri*!). Reyment & Tait (1972) have recorded the genus from Sergipe, Brazil.

Freund & Raab (1969, p. 65) were inclined to reverse Reyment's original assignation of *H. mirabilis* to *Wrightoceras*, because specimens they described from Israel as similar to Pervinquière's (1907) type material of that species seemed to possess a true coilopoceratid suture. Freund & Raab preferred to retain Pervinquière's original generic assignment of *H. mirabilis*, although they pointed out that by contrast, Pervinquière's *H. munieri*, like Benavides-Caceres's *H. inca* mentioned above, lacked the suture of a true coilopoceratid. I suggest, on this evidence, that *H. mirabilis* might be better referred to the coilopoceratid genus *Herrickiceras* Cobban & Hook (1980). Reyment (1978, p. 57, 60) now believes that the Spanish and north African "*Hoplitoides*" have a different phylogenetic origin from true *Wrightoceras*.

Leanza (1967, p. 196) erected the genus *Imlayiceras* to include the type species *I. washbournei*, and what he considered a natural group comprising Pervinquière's two species, together with the Mexican material described by Böse (1920) and Kummel & Decker (1954) as *H.* aff. *mirabilis* and *'H.'* cf. *munieri* respectively. Although Leanza thought his genus showed constrictions in the juvenile stages (1967, pl. 4, figs. 3, 4), this was hardly justification for a new genus since all other observable characters of *washbournei* agree with *Wrightoceras* (cf., however, Reyment 1978). The suture of Leanza's pl. 6, fig. 1 specimen (USNM 132558) is unrecognisable, so *Imlayiceras* is treated here as a probable synonym of *Wrightoceras*, although as Cobban & Hook (1980) point out, it may be a precursor of *Herrickiceras*.

Wrightoceras cf. *munieri* (Pervinquière)
Figs. 2H, 60—63

1920 *Hoplitoides* aff. *mirabilis* Pervinquière; Böse, p. 225, pl. 19, figs. 1—3.

1920 *Hoplitoides* sp.; Böse, text-fig. 7 (pars).

?1928 *Hoplitoides* aff. *mirabilis* Pervinquière; Böse & Cavins, p. 29.

non 1931 *Hoplitoides*? *mirabilis* Böse not Pervinquière; Adkins, p. 59, pl. 4, fig. 2.

1954 *'Hoplitoides'* cf. *munieri* Pervinquière; Kummel & Decker, p. 317, pl. 33, figs. 1, 2; text-figs. 7, 10.

COMPARE:
Hoplitoides munieri Pervinquière, p. 217, pl. 10, figs. 1a, b, 2a, b; text-fig. 83.

MATERIAL: Three specimens from Loma el Macho in the Berlin collections are referable here: the two specimens figured by Böse (1920, pl. 19, fig. 1, C558; figs. 2, 3, C559) plus part of an outer whorl similar to C559, comprising two fragments. The four fragments referred to by Böse (1920) appear to be lost. New Material from Loma el Macho includes "two very poorly preserved specimens of *Wrightoceras*" (PMMA32, PMMA33) referred to by Chancellor et al. (1977, p. 96), as well as PMMA35, PMMA36 and PMMA 37, described here.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
PMMA35	95(100)	30(31)	37(39)	0,81	8(8)
PMMA36	67(100)	20(30)	32(48)	0,62	5(7)
PMMA37	60(100)	16(27)	30(50)	0,53	5(8)

DESCRIPTION: Discoidal, very involute. Whorl section strongly compressed, lanceolate, generally thickest near the narrow umbilicus which has steep walls and smoothly curved shoulders. Flanks broadly convex at the thickest part of the section, tapering smoothly to become convergent, flat, or (in the case of PMMA37 slightly concave just below a narrow, truncated venter which, where sufficiently well preserved, shows a pair of sharp ventrolateral carinae. The suture is badly corroded, but shows a general outline like that of *W. munieri* (Pervinquière). The suture of PMMA37 at Wh = 20 mm is figured here (Fig. 2H).

DISCUSSION: I have examined the two specimens described by Kummel & Decker (1954) from near Cuchillo Parado, Chihuahua, and believe them conspecific with the Loma el Macho specimens. The Cuchillo Parado specimens show ribs which cross the venter, but in all other respects agree with the material described here. I cannot see that the suture figured by Kummel & Decker (1954, text-fig. 10) is close enough to that of *Herrickiceras costatum* (Herrick & Johnson) figured by Cobban & Hook (1980, text-fig. 16A—C) to warrant listing the former in synonymy with the latter, as Cobban & Hook do (1980, p. 22). *H. costatum* is a Middle Turonian species from

New Mexico, but the exact stratigraphical horizon of Kummel's & Decker's (1954) specimens is unknown.

Böse recognised his material to be closely similar to the 'bicarinate *Hoplitoides*' of Pervinquière (1907) which he realised might not be true *Hoplitoides*. Böse felt his material was closest to Pervinquière's '*H.*' *mirabilis*, probably on account of the larger size of that species as compared with '*H.*' *munieri*, although he pointed out, perhaps significantly, that '*H.*' *mirabilis* seems to have the relatively smaller umbilicus of the two species. I am inclined to agree with Freund & Raab (1969), as discussed above, that '*H.*' *mirabilis* may be a coilopoceratid homeomorph of '*H.*' *munieri*. The view of several authors (e.g. Reyment 1954a, footnote on p. 157) that '*H.*' *mirabilis* and '*H.*' *munieri* might be conspecific, although Pervinquière had separated them on sutural details, is untenable.

Adkins (1931, p. 59) was aware that Böse's '*H.* aff. *mirabilis*' were not true *Hoplitoides*, and (as I have discussed already) he made the misleading comparison of Böse's specimens with the eventual holotype of *P. adkinsi* which he was describing, seeming to imply that he thought the two forms congeneric. In a brief notice on the faunas of Chispa Summit and Cuchillo Parado, Adkins (1933) noted, however, the presence of "a new genus also known, by L. F. Spath from Nigeria but still unpublished" (i.e. *Bauchioceras* Reyment), which he apparently thought generically distinct from Böse's material, because he added there was also "another new genus called '*Hoplitoides mirabilis*' by Böse". The second genus was *Wrightoceras*, and the Cuchillo Parado material included the two specimens of '*H.*' cf. *munieri* later described by Kummel & Decker (1954). These latter authors, as Reyment (1955, footnote on p. 70) indicated, were fully aware of the necessity for a new genus for their material, as Böse had tacitly suggested for his.

Barber (1957, p. 53) stated that Kummel's & Decker's (1954) specimens were originally in the material described as '*H.? mirabilis* Böse' [= *P. adkinsi*] by Adkins (1931), but I can find no independent support for this claim. Kummel & Decker (1954, p. 310) specified that their '*H.*' cf. *munieri* formed part of the King & Adkins (1946) Mexican collection, whereas Adkin's (1931, p. 40) material was apparently collected in west Texas by Charles Baker in 1922.

The specimens of both Böse (1920) and Kummel & Decker (1954) were referred to *Imlayiceras* by Leanza (1967). As discussed above, however, *Imlayiceras* is probably a synonym of *Wrightoceras* and in fact '*I. washbournei* Leanza' is quite similar to the Mexican material (e.g. cf. Leanza 1967, pl. 4, fig. 1; Kummel & Decker 1954, text-fig. 7A). However, Reyment (1978, 1979) now believes that Nigerian *Wrightoceras* are distinct from the group of "*Hoplitoides*" *munieri*.

As noted by Kummel & Decker (1954, p. 312) one of the paratypes described as '*Pseudotissotia?* [= *Spathites*] *kellyi?* Jones' (1938, pl. 8, fig. 3) from Tanque Toribio, Coahuila "has a compressed conch with a narrow tabulate and bicarinate venter". This poorly preserved specimen is said to show "very close similarities with the group of '*Hoplitoides*' *munieri* Pervinquière and is not a *Spathites*". Jones's specimen seems likely to be a *Wrightoceras*.

There are several well preserved specimens and fragments from Calvert Canyon in the Oxford University Museum identified as *Wrightoceras munieri* (e.g. OUM KT396; KT399), as well as new material from Tunisia which I am currently comparing with Pervinquière's original specimens.

Biostratigraphy

As was pointed out in the introduction to this paper, there is little reliable evidence that the Loma el Macho ammonites can today be treated as anything but a mixed assemblage. When I visited the locality myself I found no section, just a rocky hillock, with fossils lying loose in the surface scree. No clear segregation of the collections by lithology seems possible, and the stratigraphical data given by Böse are in some points uncertain and contradictory.

Throughout the systematic section of this paper, in view of the above difficulties, I have omitted discussion of the age of the Loma el Macho ammonites. The subject is now summarised here, and the approach I have followed is to compare the Mexican fauna with well-dated sections from other regions of the world.

In terms of geographical proximity the fauna from Bed B at Cieneguilla, Chihuahua, documented by Powell (1963a, 1965), is the most important for comparison with Loma el Macho. Unfortunately, however, Bed B is an isolated ammonitiferous horizon sandwiched between thick sequences of undated shales and is therefore of limited use for providing stratigraphical control. The meticulous records of Cobban & Scott (1972) for the Rock Canyon reference section in Colorado provide the best standard in North America for dating the Loma el Macho fauna, while for the

Old World sequences I have relied heavily on the work in Israel of Freund & Raab (1969), in England of Wright & Kennedy (1981) and in Spain of Wiedmann (1964). I should add, however, that although I use the original numbers given by Wiedmann (1964) for his Turonian zones, I follow Wiedmann & Kauffman (1978) in transferring Turonian Zone I to Cenomanian VII, and I follow Hancock & Kennedy (1981) in transferring Turonian Zone II to Cenomanian VIII.

The ammonites from Loma el Macho apparently represent several zones by comparison with the sequences mentioned above. Only further research will show whether this is a case of condensation or is in fact a genuine faunule spanning a very short time interval, say, a few tens of thousands of years. If the latter, we have a demonstration that the time ranges of different species do not everywhere coincide.

In terms of the northwest European standard, Loma el Macho shows elements from the uppermost Cenomanian to at least the highest lower Turonian. *Metoicoceras* cf. *geslinianum* links Loma el Macho with the *Metoicoceras geslinianum* Zone in England and France, while *Mammites* cf. *nodosoides* allows correlation with all but the lowest part of the lower Turonian. There is some suggestion, however, that *M. nodosoides* ranges into the lowest middle Turonian (Cobban & Scott (1972) record it from the same horizon as *Collignoniceras woollgari* (Mantell)). *Fagesia haarmanni* from Loma el Macho and Piedra de Lumbre are comparable if not conspecific with *Fagesia* from the *M. nodosoides* Zone of England and France (Wright & Kennedy 1981; Amedro et al. 1978).

Wright & Kennedy (1981) have erected a new ammonite zonation to apply to the English succession, with a Zone of *Neocardioceras juddii* above the *Metoicoceras geslinianum* Zone and below the *Watinoceras coloradoense* Zone of the lowest Turonian. Wright & Kennedy regard the *Neocardioceras juddii* Zone as Cenomanian, but as mentioned below the same zone is treated as Turonian in the United States.

Metoicoceras and *Vascoceras gamai* occur in Wiedmann's (1964) topmost Cenomanian Zone VIII in the sense used here (see above), while *M. nodosoides* seems to characterise Spanish Turonian Zones V—VI and possibly VII, i.e. high early Turonian and middle Turonian. The doubtful *V. gamai* from Loma el Macho may thus strengthen correlation with the European uppermost Cenomanian and provide a link with the Portuguese *V. gamai* Zone (see Amard et al. 1977). Globose vascoceratines seem to occur most often in the high lower Turonian and middle Turonian of the Iberian Peninsula and help to date the Loma el Macho *Paravascoceras*, as do the Iberian *Fagesia* from roughly the same levels. Spanish records of '*Plesiovascoceras*' from the *V. gamai* Zone (Wiedmann 1964) clearly need confirming in this respect. A further link with Spanish Turonian VI is provided by the *Wrightoceras* cf. *munieri* from Loma el Macho. Wiedmann (1964, p. 111) records *Pseudaspidoceras* (as *Mammites pseudonodosoides*) from Zone IV, although Zone V is given in his stratigraphical summary.

Still outside North America, we may note *Paravascoceras hartti* occurring with *Pseudaspidoceras footeanum* at the Bom Jesus locality in Brazil (White 1887), an association which, as Böse (1920) noted, also occurs at Loma el Macho. Most Middle Eastern records are not useful for dating, but Freund & Raab (1969) have introduced order into the Israeli sequences; *Pseudaspidoceras footeanum* is found very low in the Israeli lower Turonian, whereas globose vascoceratines seem to occur most prolifically rather high. The specimen of *Pseudotissotia* cf. *nigeriensis* allows one to correlate Loma el Macho with Barber's (1957) highest early Turonian zone at Pindiga, Nigeria, which is, however, not above suspicion (Offodile & Reyment 1977).

In terms of the Rock Canyon section in Colorado we may state with some confidence that the presence at Loma el Macho of *Metoicoceras* proves the existence of the *Sciponoceras gracile* Zone. Less certainly, some of the *Paravascoceras*, *Fagesia* and *Neoptychites* at Loma el Macho may be conspecific with Rock Canyon forms which would partly indicate the presence of the *Watinoceras coloradoense* Zone (see Cobban & Scott 1972, Table 3). Most of the range of the vascoceratids at Rock Canyon (i.e. Beds 90—105) overlaps the lower part of the range of *Mammites*, however, and since *Mammites* is a conspicuous genus at Loma el Macho it seems safer to rely on a correlation with the Rock Canyon *M. nodosoides* Zone. As Kennedy & Wright (1979a) point out, some at least of the vascoceratids in the western interior seem to make their first appearance anomalously low in terms of the European standard. In this connection it is worth noting that Cobban & Hook (1979, p. 6, text-fig. 1) report a Zone of *Pseudaspidoceras* (apparently much like *P. pseudonodosoides* according to Dr. Cobban, personal communication, 1981) from the United States which occurs below a Zone of *Nigericeras scotti* Cobban which is itself just below the *W. coloradoense* Zone! In their most recent paper Hook & Cobban (1981, p. 9, text-fig. 1) redesignate this *Pseudaspidoceras* Zone as the *Neocardioceras juddii* Zone.

Although *Neocardioceras* has not been found at Loma el Macho I suppose the *N. juddii* Zone may prove to be of very simlar age to the Loma el Macho fauna.

Matsumoto (1960, p. 139) has recorded *Fagesia californica* from California in association with *Mammites?* sp. and *Euomphaloceras septemseriatum* (Cragin). I mention this not because it helps to date the Mexican *Fagesia*, but because Matsumoto (1973) has described a Japanese *Fagesia* (from a unit which has yielded *Inoceramus labiatus*) which he has stated elsewhere (Matsumoto et al. 1969, p. 289) as being associated with *E.* cf. *septemseriatum.* If confirmed, both records would represent a strange mixture in terms of the European standard, in which Wright & Kennedy (1981) categorically place *E. septemseriatum* in the upper Cenomanian.

Powell's (1963a) Bed B fauna at Cieneguilla includes in common with Loma el Macho (allowing for open determinations) *Paravascoceras compressum* sensu Powell, *Fagesia haarmanni*, "*Mammites nodosoides*" and *Pseudaspidoceras flexuosum*, as well as several other forms probably conspecific (see also Powell 1967). Powell assigned Bed B to his early Turonian *P. flexuosum* Zone. As we have seen, the genera *Paravascoceras*, *Fagesia* and *Mammites* are probably also common to Loma el Macho and Beds 90 to 105 at Rock Canyon. One is tempted to speculate that these three faunas, plus perhaps the *Fagesia haarmanni* from Montana which we know are from one horizon (Young 1951), are all exactly contemporaneous. Dr. Cobban (personal communication, 1981) has, however, informed me that on the evidence available at present the *P. flexuosum* fauna is perhaps a little older than the *Vascoceras birchbyi*—*Watinoceras coloradoense* bed at Pueblo.

Palaeobiogeography

In this section I consider what, if anything, we can learn from the Loma el Macho ammonites regarding their biogeographical relations. For the purposes of discussion I have used a world map with continents repositioned as they would probably have been 90 million years ago (Ma). The map (Fig. 70) is a composite based on the reconstructions of Smith & Briden (1977) for 80 Ma and 100 Ma; according to Koch (1980) Cenomanian—Turonian bentonites from the western interior have yielded radiometric dates of about 90 Ma.

There are many uncertainties and difficulties involved in producing these palaeocontinental reconstructions but it is beyond the scope of the present contribution to elaborate further on the subject. Instead, the reader is referred to the excellent recent review by Lillegraven et al. (1979) of Mesozoic world palaeogeography, and particularly to their treatment (p. 289 et seq.) of the "Middle" and Late Cretaceous. The following references deal more especially with the marine environment: Berggren & Hollister (1977) on palaeocirculation; Arthur & Schlanger (1979) on oceanic anoxic events; Hancock & Kauffman (1979) and Pitman (1978) on transgressions; Kauffman (1977) on the North American Cretaceous western interior seaway; papers in Pilger (1980) on the early history of the Gulf of Mexico—Caribbean and Atlantic basins. Relevant papers on biogeography not reviewed by Lillegraven et al. (1979) are: Brett-Surnam (1979), Buffetaut & Taquet (1979), Ferrusquía-Villafranca (1978), Förster (1978), Gordon (1976) and Sues (1980). It is also worth briefly reviewing here the evidence from marine invertebrates on the question of marine communication between the Gulf of Mexico—Caribbean and the Pacific during the mid-Cretaceous.

There is clear evidence for the restriction of certain groups of marine invertebrates to a distinct Tethyan realm during the mid-Cretaceous (for references see Kennedy & Cobban 1976, p. 54). This implies that certain dispersal routes, such as between the Caribbean and Northeast Asia via the North Pacific (through the north temperate realm of Kauffman 1973) were rather unlikely. The presense of "corals, rudists and gastropods of Aptian to Cenomanian age with Tethyan relationships on guyots in an area 950—1750 km west of Hawaii (Hamilton 1956)" is, however, good evidence for "a westward set of ocean currents from the Caribbean area" (Gordon 1973, p. 275).

A close similarity exists between the non-rudist bivalves of Peru and the Greater Antilles during the Upper Cretaceous (Kauffman 1973), but there otherwise seems to have been rather limited exchange of Cretaceous bivalves between the eastern and western sides of Central America. Indeed, Kauffman (1973) thought that in the Cenomanian—Turonian a distinct sub-province was recognisable in the west, and referring to the Pacific Coast of North America, Popenoe (in Sohl 1971, p. 1621) recognised marked endemism in the molluscan faunas "by Turonian times".

The ammonite fauna of the Pacific coast of North America has long been known to have more in common with that of Japan than with regions flanking the Tethys (Freund & Raab 1969, p. 79). To what extent this is due to differences

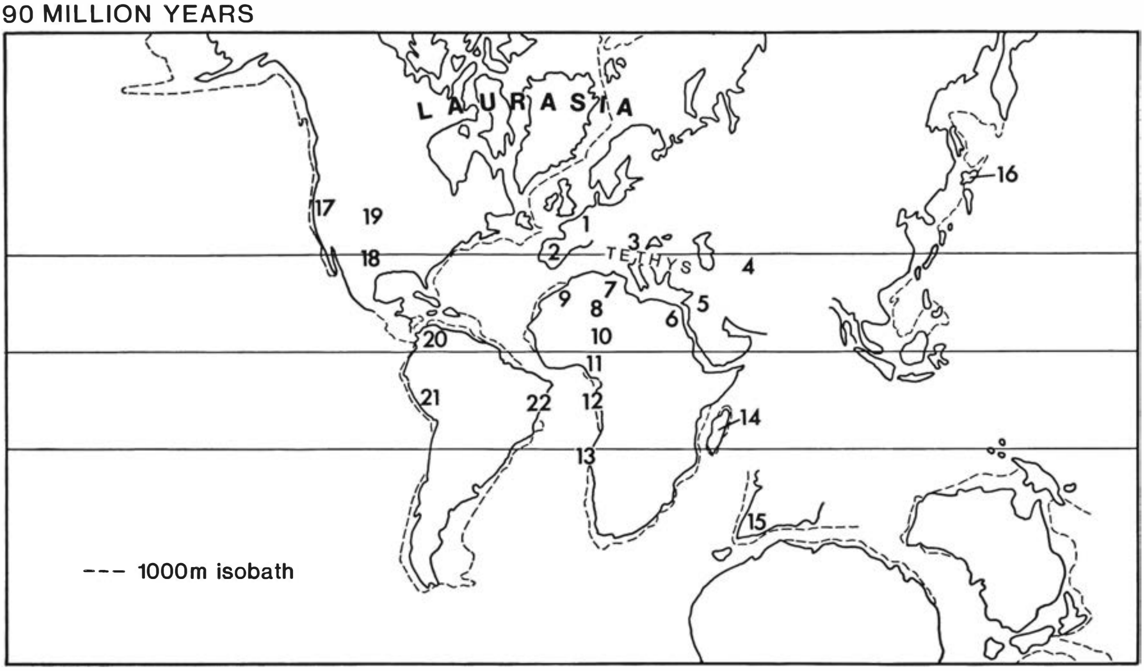


Fig. 70. Palaeocontinental reconstruction for 90 Ma (Mercator projection) interpolated from 100 Ma and 80 Ma reconstructions of Smith & Briden (1977). Horizontal lines are the equator and latitudes 30° N. and S. Numbers are regions, as given below, from which ammonite faunas comparable with the fauna described in this paper are known.
1 England—France—Germany; 2 Spain—Portugal; 3 Czechoslovakia—Rumania—Yugoslavia; 4 Turkestan; 5 Syria—Lebanon—Israel; 6 Egypt—Libya; 7 Tunisia—northern Algeria; 8 southern Algeria (the Sahara); 9 Morocco; 10 Niger; 11 Nigeria—Cameroon; 12 Gabon; 13 Angola; 14 Madagascar; 15 southern India; 16 Japan—Saghalien; 17 California; 18 Texas—Mexico; 19 western interior U.S.A.; 20 Trinidad—Venezuela—Colombia; 21 Peru; 22 Sergipe (Brazil).

in facies and preservation rather than to true faunal similarity is uncertain, however. According to Matsumoto (1960, p. 171) "the species common to California and the Gulf Coastal province are few and those common to California and the Western Interior province are very few". On the other hand, we have the testimony of Benavides-Caceres (1956) to whom the Cretaceous ammonites of Peru seemed to belong to a faunal province which includes Columbia, Venezuela, and Brazil. The faunas of this province "are closely comparable and parallel with those of Mexico, the Gulf Coast, southern Europe, northern Africa, Madagascar, the Middle East, India and Borneo" (Benavides-Caceres 1956, p. 434). We shall now turn to a consideration of the Loma el Macho fauna, to see how it fits into this picture.

Reyment & Tait (1972) realised the significance of the lower Turonian ammonites from Mexico which appeared to show 'South Atlantic' affinities, but "thought that the few species involved could have been introduced via the western coast of South America" (Chancellor et al. 1977, p. 98). There was, however, a seaway connecting the Central and South Atlantic basins by late Albian times, so there is no need to invoke a western South America migration route to explain the Mexican fauna (see Förster 1978).

In 1920 Böse recognised that the Loma el Macho fauna, at that time unique in North America, belonged to a distinctive 'Mediterranean facies', typified by vascoceratid ammonites and the genus *Pseudaspidoceras*. Böse (1920) thought that this facies occurred throughout northern and central Africa and in Portugal, but had not then been proved in the Middle or Near East; it was, however, present, if somewhat impoverished, in southern France. Böse (1920) saw *Mammites* as linking Loma el Macho with Germany, Czechoslovakia, France, Peru, Japan and India, and he was aware of the link with Brazil.

What has the present analysis revealed that was not known to Böse? Firstly, we now know that *Metoicoceras* is very widely distributed in all but the Pacific area, although it can only be said to be well known from the Atlantic realm. Notable is the link which this genus establishes between Mexico and Turkestan, a link strengthened by the occurrence in both regions of *Mammites* of the *nodosoides* group.

Böse was of course unaware of the diverse mammitines and tuberculate vascoceratids which have since been described from Turkestan, which Bobkova and Luppov (1964) took as evidence of a connection with the Mediterranean via Iran and Syria, at peak transgression. (Bobkova & Luppov (op. cit.) stressed that the Late Cretaceous invertebrate fauna of Central Asia as a whole constituted a separate province, somewhat analogous to the North American western interior).

Secondly, we now have good data for Spain and Morocco, mainly through the labours of Wiedmann (1964) and Collignon (1966) respectively, which have augmented the links between Mexico and the western Tethys. These links apply especially to *Mammites*, *Pseudaspidoceras*, *Neoptychites* and *Spathites*. It must be said, however, that the abundance of the smooth vascoceratine *Paravascoceras* at Loma el Macho somewhat reduces the faunal similarity between Mexico and Portugal, where the genus, as now interpreted, may be very rare.

We also now have much more complete data from southern France, amplifying the connections between that region and Mexico. Recently described vascoceratids from Japan (Matsumoto & Muramoto 1978) have proved the link suggested by Böse (1920), and it might be added that the Japanese fauna seems to share with Mexico the elements in common with India and France (*Neoptychites* and *Fagesia*). The *Mammites* of northwest Europe were well known to Böse, but the recent reappraisal of vascoceratid faunas from England and northern France may point to stronger links with Mexico.

Mammites is only known from the areas indicated on Fig. 70, and thus shows a fairly strong latitudinal restriction; it is curious, then, that several authors have expressed the view that *Mammites* is more widespread than the 'typically Tethyan' vascoceratids (e.g. Matsumoto 1973). With the exception of a record from Burma (Spath 1935) the genus *Pseudaspidoceras* is also restricted to the areas indicated on the map.

Probably the largest single factor in the reinterpretation of the Mexican fauna has been the description since Böse's time of the ammonites from Madagascar, which include many genera common to Mexico. Broadly speaking, the similarities between Mexico and Madagascar seem to be of the same order of closeness as those between Mexico and India, and essentially the same forms are involved (*Mammites*, *Pseudaspidoceras*, *Fagesia* and *Neoptychites*). We may speak, therefore, of faunal links between Mexico and a united Indo-Malgache province, but at present there is no way to decide if the faunal communication was via the Tethys or around the southern tip of Africa. The lack of lower Turonian ammonites from South Africa can be explained by the absence there of lower Turonian strata (Kennedy & Cooper 1975). A warm current deflected south from the westward-lowing circum-global current (Gordon 1973), perhaps by 'proto-Indonesia', could account for the otherwise anomalously high southern latitude of the Indian fauna. A similar current deflected north could explain the Tethyan ammonites in Japan.

In northwest Europe and North America the most 'northerly' vascoceratids encountered are the forms closely comparable with the Mexican *Fagesia.* The European forms probably reflect a general shift northwards in that region of the boundaries of the Tethys due both to deflection of the circum-global current and to the palaeo-Gulf Stream (Gordon 1973). When Böse was writing there were no other vascoceratids known from North America, but we now know that *Fagesia* spread northwards through the western interior and up the Pacific coast to what is now almost the Canadian border. Gordon (1973, p. 279) provides a possible explanation for the western interior occurrence in the "powerful flow of Tethyan water" northwards via the Gulf coast which is thought to have flowed in the latest Cenomanian. The Californian occurrence might support the "northward flow of water along the Pacific coast" postulated by Gordon (1973, p. 279) to explain the records there of rudists and warm-water foraminifers. It should be remembered, however, that a relatively cold Californian palaeocurrent was probably already flowing southwards down that coast.

The strong faunal connections between Mexico and the South Atlantic in some respects are evidence against the cold current postulated by Gordon (1973) to have flowed northwards up the Atlantic coast of Africa, mainly to explain the absence there of rudists. The genera *Mammites*, *Pseudaspidoceras*, *Paravascoceras*, *Neoptychites*, *Pseudotissotia* and *Wrightoceras* all point to connections between Mexico and Nigeria, Brazil, Angola and the Congo. Many faunas not known to Böse have also been described from the Sahara and from North Africa and the Middle East; these have strengthened the faunal unity of his 'Mediterranean facies', while supporting the hypothesis of Furon (1935) and others of a trans-Saharan seaway in the early Turonian.

All the above genera, with the exception of *Neoptychites*, are also known from the Pacific coast of South America (Benavides-Caceres 1956; Etayo-Serna 1979). This supports a direct connection between Mexico and the Pacific via the Caribbean during the mid-Cretaceous, but does not require anything more than a narrow gap through the Straits of Panama.

Appendix: A short account of the Böse (1920) collection of ammonites

The Böse (1920) collection of ammonites from Loma el Macho is now preserved at the Museum für Naturkunde, East Berlin. Through the helpful agency of its curator, Dr. Jochen Helms, I was able in May 1978 to examine the collection and subsequently to borrow some of the smaller specimens.

All the specimens are in a poor state of preservation as was shown in Böse's illustrations of most of them. The total collection comprises 22 specimens and some fragments (the catalogue numbers of the complete specimens are C556—C577 inclusive, some of which are figured in this paper). Böse (1920) figured all the material except (according to the numbers of specimens he cites):

1. one specimen of '*Metoicoceras* aff. *whitei* Hyatt', now lost;
2. three specimens of *Mammites*, two of which (C563, C564) are today labelled "*Mammites* sp. ex. gr. *nodosoides* Schlt. nach Haarmann", whilst the third (C575) bears the label "Vergl. *Mammites subconciliatus* var. *lata* nov. var." written by Herbert Karrenberg in 1933. (I consider this specimen a juvenile *M. mohovanensis* Böse);
3. the specimen (C557) of '*Pseudaspidoceras* aff. *footeanum* Petrascheck not Stoliczka' [= *P.* cf. *flexuosum* Powell];
4. probably Böse's unfigured specimen of '*Vascoceras* sp.' (C573), although its label simply reads "Macho" (this specimen has been broken open to reveal the inner whorls; I have referred it to *Paravascoceras angermanni* (Böse));
5. the second specimen of *Fagesia haarmanni* Böse; now lost;
6. various fragments.

C563, C564 and C575 are figured for the first time in the present work. As far as I know, the only published restudy of any of the Böse ammonites is that of Karrenberg (1935) who mentioned C575 in his discussion of '*Mammites subconciliatum* Choffat' (see Karrenberg 1935, p. 135; Collignon 1957, p. 121) and also discussed and figured (p. 140) the suture of Böse's small specimen of '*Vascoceras angermanni* Böse' (C569). Karrenberg's citation of the Böse collection in the Museum für Naturkunde, Berlin, led me to the fossils, which have generally been assumed lost.

Judging from the labels, the collection went to Berlin in 1926, presumably because Dr. Haarmann was based there at the time as a consultant, but also perhaps because of Böse's connection with Berlin University, of which the Museum für Naturkunde forms a part (for a brief biography of Böse, see Burckhardt & Waitz 1928). During the Second World War some of the specimens went to Leningrad, others to the local salt mines for safe keeping, where many of the labels rotted. The collection was reassembled in the 1950's, but now lacks, in addition to the items noted above:

1. the body chamber of C577, which is thus now indistinguishable from '*Pachyvascoceras compressum* (Barber)' *in* Powell (1963a);
2. the body chamber of C571, which I have referred to *Paravascoceras* aff. *hartti* (Hyatt);
3. the fragments of '*V. angermanni*' mentioned by Böse, although a large, flat section of unlabelled vascoceratine body chamber is present;
4. the four fragments of '*Hoplitoides* aff. *mirabilis* Pervinquière' mentioned by Böse, although I believe two connected fragments comprising about one-half of an outer whorl similar to that of Böse's pl. 19, figs. 2, 3, (C559) are present.

I know of only one, incomplete, set of casts, namely those at the Texas Memorial Museum (Bureau of Economic Geology, Austin). This set may have been brought back to Texas by W. S. Adkins after a trip to Europe (for example see Adkins 1931, p. 72) but there are today no documents in Berlin to prove this. Adkins helped Böse prepare his monograph and it seems likely that he saw the original fossils. The casts bear German labels, that for *Fagesia haarmanni* reading *Plesiovascoceras*, which must, therefore, post-date Spath's (1925) erection of that genus. That the casts were made in Berlin is also deducible from the fact that they show the specimens already bore the markers used in Berlin to identify figured material. Dr. Helms has pointed out to me that these markers could have been applied at any time after 1926. The casts are of specimens C560

—1, C566, C570—2 and C576—7, of which the casts of C560—1 are figured here (Figs. 3, 4).

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A contribution to
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