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Towards a phylogenetic classification of the Cretaceous ammonites. VI. Mammitinae

M. R. Cooper, Durban

With 3 figures

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Abstract: Phylogenetic analysis of the subfamily Mammitinae HYATT indicates derivation from acanthoceratid stock. The taxon (which includes Metoicoceratinae HYATT, Buchiceratinae HYATT and Fallotitinae WIEDMANN) arose in the Middle Cenomanian of North America, became cosmopolitan in the Upper Cenomanian, attained dominance in the Lower Turonian, and became extinct in the Coniacian. The "acanthoceratids" *Dunveganoceras* WARREN & STELCK, *Plesiacanthoceras* HAAS and *Paracompsoceras* COBBAN are included here as primitive representatives, as also are *Texacanthoceras* n. g., *Praemetoicoceras* n. g., *Dunveganoceras* (*Ottohaasites*) n. subg. and *Parabuchiceras* n. g.

Zusammenfassung: Die Subfamilie Mammitinae HYATT kann phylogenetisch von den Acanthoceratiden abgeleitet werden. Das Taxon (das die Metoicoceratinae HYATT, Buchiceratinae HYATT und Fallotitinae WIEDMANN einschließt), entstand im Mittelcenoman von Nordamerika, wurde kosmopolitisch im Obercenoman, dominierte im unteren Turon und starb im Coniac aus. Die „Acanthoceratiden" *Dunveganoceras* WARREN & STELCK, *Plesiacanthoceras* HAAS und *Paracompsoceras* COBBAN werden hier als primitive Vertreter mit eingeschlossen, genau wie *Texacanthoceras* n. g., *Praemetoicoceras* n. g, *Dunveganoceras* (*Ottohaasites*) n. subg. und *Parabuchiceras* n. g.

This paper continues the writer's phylogenetic analysis of the Cretaceous Ammonoidea (COOPER 1990, 1992, 1994a, b, 1997) and concerns the subfamily Mammitinae HYATT (1903), comprising derived representatives of mid-Cretaceous Acanthoceratidae (ROMAN 1938). Typically mammites are medium-sized to large ammonites, though micromorphs are represented, with distinct umbilical bullae and inner and outer ventrolateral tubercles, the

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latter typically clavate; primitively there are siphonal clavi which are lost early in ontogeny and several forms develop ventrolateral horns in maturity. Usually the venter is tabulate to shallowly sulcate, occasionally rounded in maturity, the ribs are strong but may weaken at midflank, and the whorls vary from compressed and very involute to inflated and evolute. Mammites are a very important group of mid-Cretaceous ammonites which arose in the Middle Cenomanian, from *Acanthoceras* itself, and persisted into the Coniacian. Throughout their range they have considerable biostratigraphical significance and many species have been the basis of local and even international zonations, e. g. *Metoicoceras geslinianum* and *Mammites nodosoides*. The phylogeny of Metoicoceratinae was discussed by COOPER (1978) and KENNEDY et al. (1980) dealt with Mammitinae (including Metoicoceratinae). WRIGHT & KENNEDY (in JUIGNET et al. 1973) introduced *Thomelites* WRIGHT & KENNEDY as the most primitive representative of Metoicoceratinae, and ancestor of *Metoicoceras*; now, however, it is clear this phylogeny (cf. KENNEDY et al. 1980) is untenable and the similarities are due to convergence. Here cladistic methodology is used in an attempt to address the main problems of mammite evolution, namely origin and content. This paper is dedicated to Dr. WILLIAM A. COBBAN (Denver) who, over 45 years, has made a lasting contribution to Cretaceous stratigraphy and ammonite systematics in general, and an understanding of the mammites in particular.

The earliest mammite is Middle Cenomanian *Texacanthoceras* n. g. (type species *Acanthoceras amphibolum* MORROW), a largely North American group characterized by early loss of siphonal tubercles (at 40-60 mm diameter), the inner ventrolateral tubercles developing into laterally-projecting ventrolateral horns and the exaggerated umbilical bullae shifting up the flank in maturity, having the siphonal clavi situated on a blunt siphonal ridge, the tendency for the clavate tubercles to be asymmetric, and with intercalated siphonal clavi at some stage in early growth; also some early representatives, e. g. "*Acanthoceras alvaradoense*" MOREMAN, have constricted earliest whorls (COBBAN 1977).

As noted by KIRKLAND & COBBAN (1986), the group of "*Acanthoceras*" centred around *T. amphibolum* includes *T. bellense* (ADKINS), *T. muldoonense* (COBBAN & SCOTT), and perhaps Japanese *A. takahashii* MATSUMOTO. *Texacanthoceras* n. g. differs from true *Acanthoceras* in being more involute, higher whorled, having fewer rectiradiate ribs, stronger umbilical and inner ventrolateral tubercles, ribs that cross the venter, early loss of siphonal clavi which at some stage exceed the ventrolateral tubercles in number, a low siphonal ridge, and in developing ventrolateral horns in maturity, thereby homoeomorphing *Cunningtoniceras* (COBBAN et al. 1989), and its suture (Fig. 1) has L as deep as, or deeper than E; some also have asymmetric clavi which are steepest adorally. *Texacanthoceras* n. g. differs from *Cunningtoniceras* in early loss of inner ventrolateral and siphonal tubercles, possessing very clavate outer ventrolateral tubercles (which may be asymmetric) and a blunt siphonal ridge, and its distant flank costae (KENNEDY et al. 1988).

As recognized by COBBAN & SCOTT (1972), ultimately the ancestry of *Texacanthoceras* n. g. lies with *Acanthoceras* s. s., to which genus it has always been assigned (on the basis of primitive characters). *Acanthoceras granerosense* COBBAN & SCOTT, which occurs in beds underlying those with *T. amphibolum,* differs from *A. rhotomagense* in just those characters that anticipate the *Texacanthoceras* n. g. condition, viz. it is more involute, has stronger umbilical and inner ventrolateral tubercles, the inner ventrolateral tubercles strengthen on the body chamber, and it looses its siphonal clavi earlier (COBBAN & SCOTT 1972). Here, therefore, *A. granerosense* is regarded the most primitive *Texacanthoceras* n. g., one that does not develop ventrolateral horns in maturity. It is perhaps worth mentioning that the blunt siphonal ridge ("keel") of *Texacanthoceras* n. g. is present in several later mammites also, including *Jeanrogericeras,* the inner whorls of *Mammites*, and *Buchiceras*.

ADKINS (1928: 244) noted that the venter and suture of *Acanthoceras wintoni* ADKINS, a synonom of *Conlinoceras tarrantense* (ADKINS)"... are in many ways strikingly suggestive of *Mammites*"; *Conlinoceras* COBBAN & SCOTT (1972) occurs in beds underlying those with *Texacanthoceras* g. n. (COBBAN 1984, HANCOCK et al. 1993) and, although the relationship warrants closer scrutiny, here the similarities are believed to be the result of convergence.

Paracompsoceras COBBAN (1972) has always been assigned to Acanthoceratinae, of which it is regarded an aberrant member; KENNEDY et al. (1979) considered it a probable synonym of *Acompsoceras*. However, the inner whorls of *Paracampsoceras* (cf. KENNEDY et al. 1988), are like those of *Texacanthocercas* n. g. in being relatively involute, having a low siphonal ridge with weak siphonal clavi which become obsolete in midgrowth. *Paracompsoceras* is characterized by developing distinctive outer whorls in which the ribs are reduced to low bulges of the flank and ventral tuberculation is lost completely; at this stage it homoeomorphs *Acompsoceras*. Here *Paracompsoceras* is regarded an offshoot of *Texacanthoceras* n. g. in- dependent of *Plesiacanthoceras*, and treated as an early member of Mammitinae. COOPER (1979) sought derivation of *Kennediella* COOPER from *Para- compsoceras* but their geographic distributions are different and WRIGHT & KENNEDY (1987: 188) link it to *Acanthoceras* s. s.

Plesiacanthoceras (HAAS 1964 = *Paracanthoceras* HAAS 1963, non FURON 1935) first appears high in the zone of *Texacanthoceras amphibolum* (COBBAN & HOOK 1983), represented by the type species *P. wyomingense*

(REAGAN). However, the latter species is more abundant higher in the stratigraphy where it constitutes the zonal index for the overlying zone (COBBAN 1984). Although, traditionally, *Plesiacanthoceras* is assigned to Acanthoceratinae (HAAS 1964), and even has been included in the synonymy of *Acanthoceras* (cf. MATSUMOTO & OBATA 1966, KENNEDY & HANCOCK 1970), HAAS (1949) recognized its affinities with *Texacanthoceras* n. g. It is of some significance, therefore, that the type species was introduced (REAGAN 1924) as a species of *Metoicoceras* characterized by involute early whorls, early loss of siphonal tubercles, retention of strong inner and outer ventrolateral tubercles to the body chamber where they merge to form ventrolateral horns, and loss of ribs on the adult whorls (MEREWETHER et al. 1979). The suture has a very wide E/L and a wide mostly bifid L (HAAS 1964).

HAAS (1963, 1964) assigned *Texacanthoceras amphibolum* (MORROW) to *Plesiacanthoceras* because of its horned body chamber. However, COBBAN & SCOTT (1972: 67) noted that the inner whorls are very different, being "... considerably more involute for *P. wyomingense*, the siphonal tubercles are never so strong as the ventrolateral ones and disappear at a very small diameter, and the ribs are of alternate lengths out to a large diameter". These differences, although noteworthy, are not sufficient to preclude a phyletic relationship and present evidence leans toward derivation of *Plesiacanthoceras* from *Texacanthoceras* n. g.; *Plesiacanthoceras* differs from *Texacanthoceras* n. g. in being more involute, more compressed, and loosing its siphonal clavi earlier, trends which anticipates the *Metoicoceras* condition, and with a more complex suture (Fig. 1).

Strata immediately overlying the *Plesiacanthoceras wyomingense* Zone, assigned to the low Upper Cenomanian *Dunveganoceras pondi* Zone (COBBAN 1984), have yielded two genera of early mammites; these are primitive species of *Dunveganoceras* (WARREN & STELCK 1940) and *Metoicoceras* (HYATT 1903). The most primitive *Dunveganoceras, D. pondi* HAAS, displays a subquadrate adult body chamber with broad venter and blunt ventrolateral horns, this is reminiscent of ancestral *Plesiacanthoceras* (COBBAN, in WRIGHT & KENNEDY 1987: 153) but very different from the lanceolate whorl section of the younger type species, *D. albertense* WARREN & STELCK, which lacks ventrolateral horns and, in the subspecies *D. a. regale* COBBAN, develops backwardly-arching siphonal swellings. In fact HAAS (1949: 20) was led to regard the type species as "... a somewhat aberrant representative of the genus"! Here *D. pondi* HAAS is made type species of *Dunveganoceras* (*Ottohaasites*) n. subg., it is transitional between *Plesiacanthoceras* and *D.* (*Dunveganoceras*), differing from the former in the persistence of strong ribs and its less well-developed horns, and from the latter in having inflated, subquadrate adult whorls with blunt ventrolateral

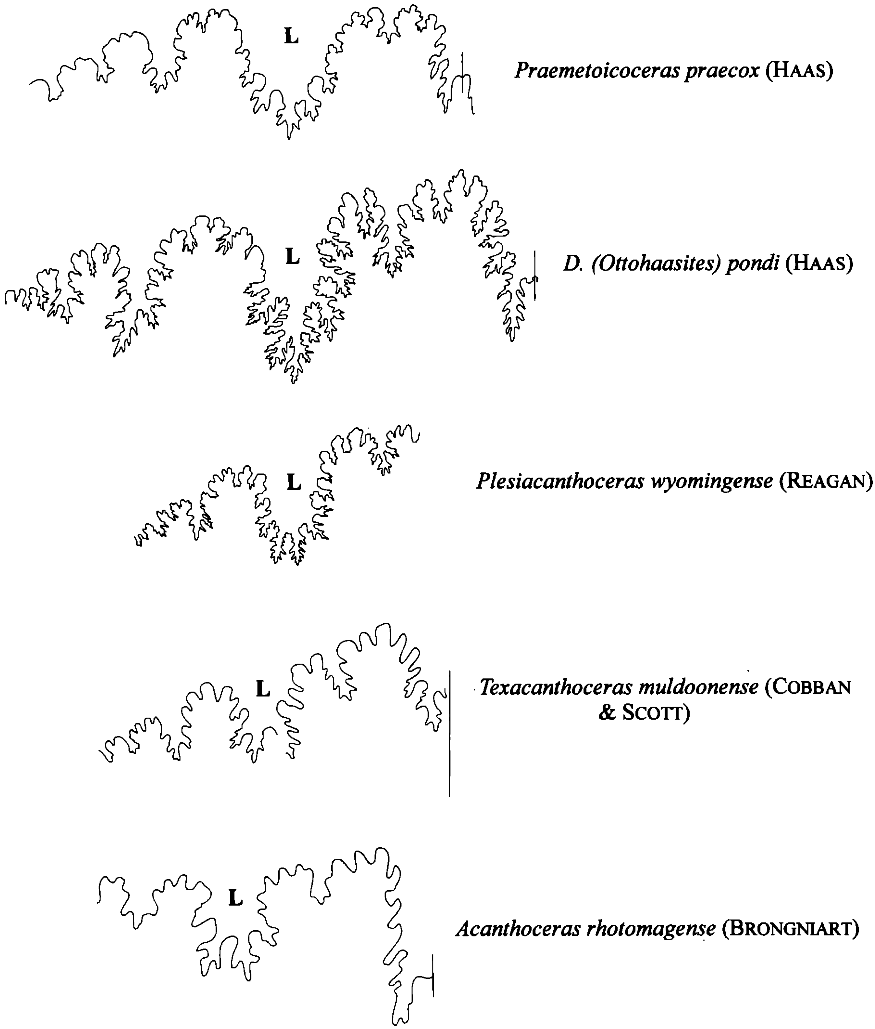

Fig. 1. Suture lines of various mammites, **L** = first lateral lobe. Not to scale and from various sources.

horns. Like *Plesiacanthoceras, Dunveganoceras* has always been assigned to Acanthoceratinae (HAAS 1964, COBBAN 1988b) but, as shown by COBBAN (1988b), it has *Metoicoceras*-like inner whorls and, rather than being intermediate between *Mantelliceras* and *Acanthoceras* (cf. WARREN & STELCK 1940), it is a primitive mammite.

Praemetoicoceras n. g., (type species *Metoicoceras whitei praecox* HAAS) has inner whorls like *Dunveganoceras* but its outer whorls are more involute and strongly compressed, with a narrow venter and weak to absent tuberculation; in addition, it attains maturity at a much smaller adult size and has a broader L to the suture (Fig. 1). Besides the type species, others to be included here are *P. frontierense* (COBBAN) and *P. latoventer* (STEPHENSON).

Metoicoceras HYATT (1903) (type species *Ammonites swallovi* SHUMARD) differs from ancestral *Praemetoicoceras* n. g. in lacking siphonal tubercles at all growth stages and in being more involute. *Nannometoicoceras* (KENNEDY 1988) is a very involute dwarf derivative of *Metoicoceras* with rectangular whorl section and simple suture.

Late in the Cenomanian, *Metoicoceras* gave rise to *Jeanrogericeras* WIEDMANN (1960) (cf. COOPER 1978, KENNEDY et al. 1980, COBBAN 1988a), of which *Fallotites* WIEDMANN (1960) is a subjective junior synonym based on inflated variants (cf. KENNEDY et al. 1980). *Jeanrogericeras* differs from ancestral *Metoicoceras* in being more inflated, commonly with a trapezoidal to subquadrate whorl section, with a broader venter and different suture with narrow L.

KENNEDY et al. (1980) relegated *Fallotites* (*Ingridella*) WIEDMANN (1960) to a subgenus of *Jeanrogericeras*, distinguished by subdued inner and outer ventrolateral tubercles to the early whorls, sparse exaggerated umbilical tubercles which persist to maturity, feeble ribs, and loss of ornament on the outer whorls so as to homoeomorph *Vascoceras*. WIEDMANN's (1960) taxon is so poorly known that little further can be added, though KENNEDY (1994) pointed to the similarity of the body-chamber ornament of *F.* (*Ingridella*) to *S.* (*Jeanrogericeras*) *combesi* (SORNAY). Here the writer follows KENNEDY et al. (1980) in regarding it an offshoot of *Jeanrogericeras*, independent of *Spathites*; it is treated as a distinct genus.

Mammites LAUBE & BRUDER (1887), of which *Schlueterіceras* HYATT (1903) is an objective synonym, is a fairly large, flat-sided, high-whorled, upper Lower Turonian taxon with prominent umbilical tubercles; in early growth the venter is quadrituberculate but tubercles coalesce in maturity to form ventrolateral horns. As noted by KENNEDY et al. (1980), its inner whorls are virtually indistinguishable from inflated *Jeanrogericeras* (i. e. *Fallotites*) and it is here that its ancestry should be sought. Like the latter genus, *Mammites* has a narrow L to the suture (Fig. 2).

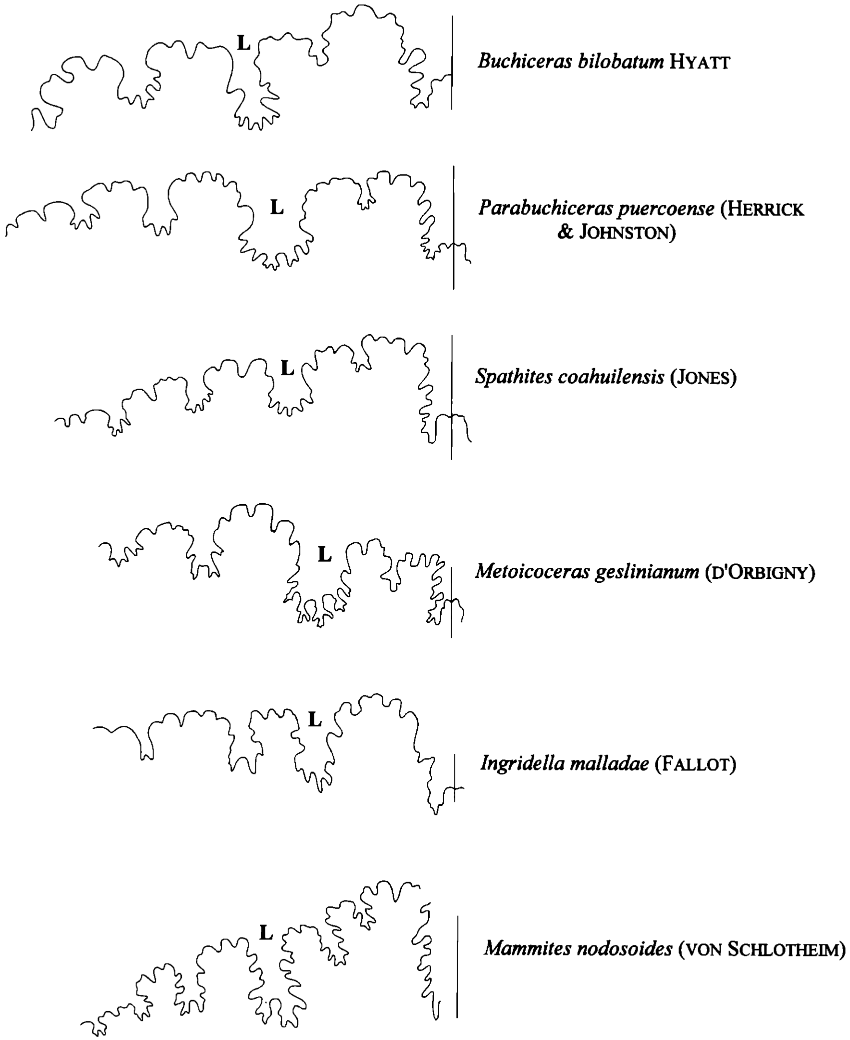

Fig. 2. Suture lines of various mammites, **L** = first lateral lob. Not to scale and from various sources.

Metasigaloceras HYATT (1903) is a large Lower Turonian genus with wide umbilicus, trapezoidal whorl section, very large blunt umbilical tubercles which have shifted to midflank, low ventrolateral clavi which are twice as numerous as the flank tubercles, and a smooth flat venter. It is still not well known and the suggestion (KENNEDY et al. 1980) that it is derived from (or the sister taxon of) *Mammites* is followed here.

Middle Turonian *Spathites* KUMMEL & DECKER (1954) is easily derived from earlier *Jeanrogericeras*, independent of *Mammites* and *Ingridella*, by loss of ornament on the adult body chamber which becomes smooth with sharp ventrolateral shoulders and broadening of the venter which, sometimes, is shallowly concave (COOPER 1978). *Spathitoides* WIEDMANN (1960), introduced as a subgenus of *Neoptychites*, is widely regarded a subjective junior synonym of *Spathites*, based on an individual with unusually sulcate venter (KENNEDY et al. 1980, COBBAN 1988a).

COBBAN (1988a, cited also in KENNEDY et al. 1980) showed that *Buchiceras puercoensis* HERRICK & JOHNSTON (1900), usually assigned to *Spathites*, retains ribbing to maturity and thus resembles ancestral *Jeanrogericeras* from which it differs, however, in having a pseudoceratitic suture (Fig. 2). Here it is made type species of *Parabuchiceras* n. g. intermediate between *Jeanrogericeras* and *Buchiceras* and, on the basis of derived characters (pseudoceratitic suture), it is closest to Coniacian *Buchiceras*.

Fig. 3. Hypothesized relationships within Mammitinae. **1**: Evolute (inner whorls > 22 %, increasing to 35-45 %), whorls quadrate depressed, 5 rows of tubercles across venter, outer ventrolaterals and siphonals clavate, siphonal clavi often persist to large diameter, inner whorls with strong prorsiradiate ribs alternating long and short, becoming long in maturity, umbilical bullae prominent in early growth, tending to weakening in maturity but remaining on the umbilical shoulder, suture with a square asymmetrically-bifid L/U, narrow L and E deeper than L. **2**: Relatively involute (inner whorls = 17-18 %, increasing to 25-26 %), umbilical and inner ventrolateral tubercles strong, ribs rectiradiate and relatively sparse (generally about 18 per whorl) particularly in later growth, early whorls of primitive forms with constrictions, there may be a multiplicity of siphonal clavi at some stage during early growth, siphonal clavi lost in midgrowth (at about 60 mm diameter), siphonal and outer ventrolateral clavi asymmetrical, derived species develop ventrolateral horns and homoeomorph *Cunningtoniceras*, suture with L almost as deep as, or deeper than, E; **3**: Outer whorls compressed, with convergent flanks, sharp ventrolateral shoulders, shallowly concave venter, weak ribbing and obsolete ventrolateral tubercles; **4**: Inner whorls involute and compressed, siphonal clavi lost early, outer whorls evolute with exaggerated ventrolateral horns exaggerated in maturity, suture

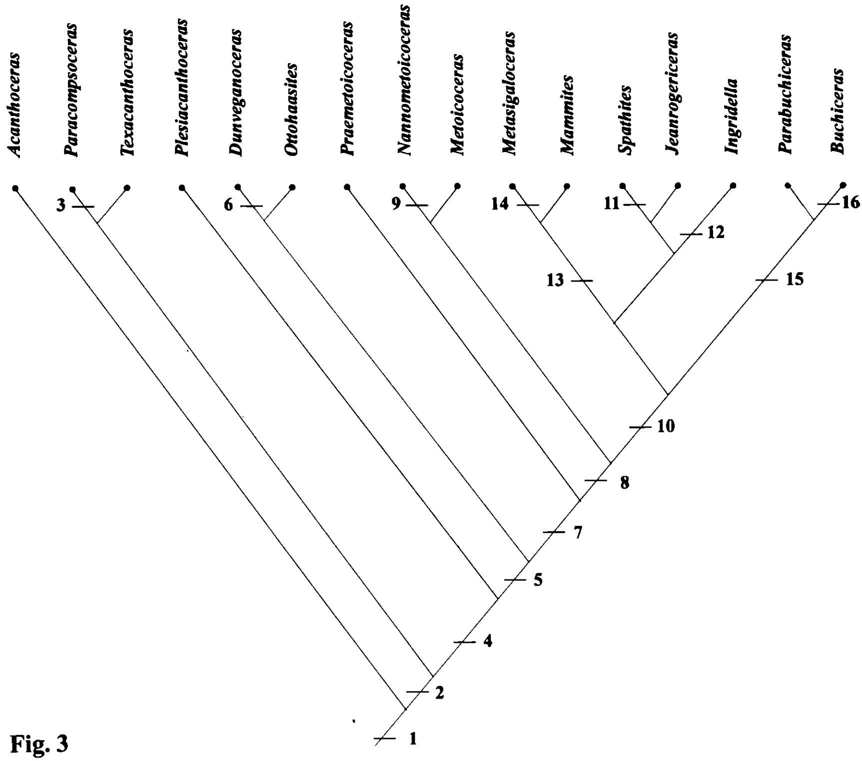

Fig. 3

relatively complex; **5**: Ribs persist to maturity, adult body chamber subquadrate with blunt ventrolateral horns; **6**: Adult body chamber fastigiate to lanceolate, without ventrolateral horns but with siphonal tubercles; **7**: Relatively small, outer whorls comparatively involute (U < 26 %) and strongly compressed, venter flattened to narrowly rounded, ribs relatively broad and flattened, tuberculation moderately weak to absent in maturity, suture with broad digitate L; **8**: Inner whorls very involute, siphonal clavi absent at all growth stages; **9**: Micromorph with rectangular cross section and simple suture; **10**: Inflated, whorls trapezoidal to subquadrate, suture with relatively narrow L; **11**: Outer whorls smooth, with sharp ventrolateral shoulders and weakly concave venter; **12**: Umbilical bullae prominent but ribs and tubercles lost on outer whorls, venter rounded, homoeomorph of *Vascoceras*; **13**: Large, relatively evolute, flat-sided, with quadrate outer whorls which develop ventrolateral horns; **14**: Whorl section very depressed, trapezoidal, with massive umbilical tubercles moving to midflank, ventrolateral tubercles do not form horns in maturity; **15**: Suture pseudoceratitic; **16**: Adult whorls quadrate, prominent ribs, umbilical and ventrolateral tubercles retained to maturity, broad venter with a siphonal ridge, suture with narrow L.

Buchiceras (HYATT 1875) (type species *B. bilobatum* HYATT) differs from *Parabuchiceras* n. g. in having squarer adult whorls, stronger tuberculation, a blunt siphonal ridge, and a narrow L to the suture (Fig. 2). Although both HYATT (1903) and DOUVILLÉ (1890, 1928) emphasized that similarities between the sutures of *Buchiceras* and *Tissotia* were superficial, WRIGHT (1957) erred in assigning *Buchiceras* to Tissotiidae; subsequently he rectified this error (in COOPER 1978, KENNEDY et al. 1980).

Roemeroceras HYATT (1903: 30) was introduced for forms similar to *Buchiceras* but with a narrower umbilicus, more compressed whorls, broader flanks, and a "quite distinct" suture; the original material was from an unknown stratigraphical level ("Upper Cretaceous") in Peru. Most subsequent workers, however, have emphasized the wide intraspecific variability of *Buchiceras* and have regarded *Roemeroceras* a synonym (LISSÓN 1908, BRÜGGEN 1910, LÜTHY 1918, BENAVIDES-CÀCERES 1956, WRIGHT 1957). PARNES (1964), on the other hand, referred material from the Upper Coniacian of the Negev (Israel) to *Roemericeras,* considering it a valid taxon which differed from *Buchiceras* not only in the characters mentioned by HYATT (1903) but, also, in the adult whorls becoming subquadrate to elliptical. As figured by HYATT (1903, pl. 2, figs. 1-3), *Roemericeras* differs from the Israeli material in being more evolute, stronger ornamented and with much wider whorls; it remains to be determined if the Israeli material does not represent a convergent development of some other stock.

A number of genera have, over the years, been assigned to Mammitinae but appear to belong elsewhere. Both *Watinoceras* WARREN (1930) and *Pseudaspidoceras* HYATT (1903) were long included in Mammitinae but, now, the former is assigned to Acanthoceratinae (COBBAN 1983, COBBAN et al. 1989), probably with an ancestry in *Neocardioceras* (WRIGHT 1957, KENNEDY et al. 1996), and the latter to Euomphaloceratinae (KENNEDY et al. 1987). COOPER (1978) treated *Benueites* REYMENT (1954) as a derived subgenus of *Watinoceras* but RENZ (1982: 91) claimed intermediates between *Mammites* and *Benueites* and suggested derivation of the latter from the former. Forms such as *B. trinidadensis* RENZ, which have inner whorls like *Benueites* and outer whorls like *Mammites* are not transitional to *Mammites* but are convergent (cf. WRIGHT 1957). The genus *Mitonia* RENZ & ALVAREZ (1979) was introduced for evolute micromorphs of uncertain affinity, but provisionally placed in Mammitinae, with prominent bullae just below mid-flank and at the ventrolateral shoulders, and a slightly concave venter; some species added subsequently (RENZ 1982) have paired ventrolateral tubercles. At present the relationships of *Mitonia* are obscure but, more likely, they lie with *Watinoceras* and *Benueites* in Acanthoceratinae.

The above relationships, when translated into a cladogram (Fig. 3), support the view (KENNEDY et al. 1980) that the subfamilies Buchiceratinae HYATT, Metoicoceratinae HYATT and Fallotitinae WIEDMANN are unnecessary; they indicate that a number of "acanthoceratids" should be included here also, as primitive representatives. As interpreted here, the subfamily Mammitinae ranges from Middle Cenomanian to Coniacian and comprises *Texacanthoceras* n. g., *Paracompsoceras, Plesiacanthoceras, D.* (*Dunveganoceras*), *D.* (*Ottohaasites*) n. subgen., *Praemetoicoceras* n. g., *Metoicoceras, Nannometoicoceras, Ingridella, Jeanrogericercas* (including *Fallotites*), *Spathites* (including *Spathitoides*), *Mammites, Metasigaloceras, Parabuchiceras* n. g. and *Buchiceras* (including *Roemeroceras*). Five of the first six taxa are endemic to North America, where the group originated.

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Anschrift des Verfassers:

Prof. Dr. M. R. COOPER, University of Durban-Westville, Dept. Geology, Private Bag X54001, 4000 Durban, Südafrika.