

Towards a phylogenetic classification of the Cretaceous ammonites V. Euomphaloceratidae

By

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With 5 figures in the text

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Abstract: Phylogenetic analysis of Euomphaloceratinae COOPER, 1978, a group within highly diversified and heterogeneous Acanthocerataceae, indicates a fundamental dichotomy which suggests promotion of this taxon to family rank with recognition of two subfamilies. Nominat Euomphaloceratinae comprise *E. (Euomphaloceras)*, *E. (Kanabicerias)*, *Burroceras*, *Paraburroceras*, *P. (Pseudaspidoceras)*, *P. (Ampakabites)*, and *Morrowites*, and Romaniceratinae subfam. nov. is made up of *Schindewolfites*, *Kamerunoceras*, *Codazziceras*, *Proromaniceras (Proromaniceras)*, *P. (Obiraceras)*, *Neomphaloceras*, *Yubariceras* and *Romaniceras* (?with *Shuparoceras* as a subgenus).

Zusammenfassung: Die phylogenetische Analyse der Euomphaloceratinae COOPER, 1978, einer Gruppe der hoch diversifizierten und heterogenen Acanthocerataceae, weist auf eine fundamentale Dichotomie innerhalb der Unterfamilie hin. Der Gruppe wird daher Familienrang verliehen und zwei Unterfamilien abgegrenzt. Die Nominat-Unterfamilie Euomphaloceratinae umfaßt *E. (Euomphaloceras)*, *E. (Kanabicerias)*, *Burroceras*, *Paraburroceras*, *P. (Pseudaspidoceras)*, *P. (Ampakabites)* und *Morrowites*. Zur zweiten Unterfamilie Romaniceratinae subfam. nov. gehören *Schindewolfites*, *Kamerunoceras*, *Codazziceras*, *Proromaniceras (Proromaniceras)*, *P. (Obiraceras)*, *Neomphaloceras*, *Yubariceras* und *Romaniceras* (? mit *Shuparoceras* als Untergattung).

This paper continues the writer's phylogenetic analysis of Cretaceous ammonites and concerns Euomphaloceratinae COOPER (1978), a distinctive group within diversified and heterogeneous Acanthoceratidae. Ammonites of this subfamily first appeared in the Upper Cenomanian and rose to dominance in the Turonian. They have noteworthy biostratigraphical value in the Middle Turonian (DE GROSSOUVRE 1901, HANCOCK et al. 1993) and the lineage may have survived into the Coniacian. Knowledge of the group comes mainly from T. MATSUMOTO, who in many publications over 40 years has made an invaluable contribution, the late J. WIEDMANN, and most-recently

W. J. KENNEDY (with C. W. WRIGHT) and W. A. COBBAN who have provided a wealth of information on European and North American representatives; KENNEDY and WRIGHT have attempted to rationalise nomenclature. This paper critically re-examines the data accumulated by these and other workers.

Typically, euomphaloceratines are derived acanthoceratids with a wide umbilicus, generally depressed whorls, frequently flattened flanks, broadly arched to flattened venter, constricted early whorls which are commonly smooth, and usually at least 7 rows of tubercles (umbilical, inner and outer ventrolateral, and siphonal). Primitively ribbing is irregular, with additional ribs intercalated high on the flank and across the venter. Normally ventral ribs are ornamented with 3 rows of tubercles (outer ventrolateral and siphonal) and, as a result, primitively there is a multiplicity of ventral tubercles. With evolution the rows of tubercles increase to 11 (as lateral rows are added) and the number of siphonal tubercles comes to match the inner ventrolaterals. There are two contrasting sutural patterns (Figs. 1-3) (cf. MATSUMOTO et al. 1989): a romaniceratid suture with large, broad, asymmetrically bifid E/L and relatively deep narrow L, and a euomphaloceratid suture with fairly narrow, not obviously rectangular E/L and very broad bifid L.

Although at the time included in the synonymy of *Euomphaloceras*, COOPER (1978) regarded *Cunningtoniceras* COLLIGNON (1937) the most primitive euomphaloceratine. Typically, *Cunningtoniceras* is a large, evolute, Middle Cenomanian acanthoceratid with depressed subquadrate whorls, flattened subparallel flanks, and a broad weakly-convex venter. There are periodic constrictions in early growth (cf. MATSUMOTO et al. 1989) and the juvenile whorls are ornamented with simple distant ribs carrying 7 rows of tubercles (umbilical bullae, laterally-directed inner ventrolateral spines, outer ventrolateral clavi and siphonal tubercles). Ribs loop across the venter from the inner ventrolaterals, and are joined by occasional intercalatories all with outer ventrolateral and siphonal tubercles, leading to a multiplicity of ventral tubercles. In maturity the umbilical bullae strengthen markedly, the ventrolaterals coalesce to form laterally-directed horns, and the siphonal tubercles are effaced to leave a smooth slightly-depressed venter, i. e. the shell homeomorphs *Mammites*. At the end of the adult body chamber tuberculation declines markedly, sometimes leaving prominent almost annular ribs. The suture (Fig. 1D, F) has a very deep E, broad bifid E/L, relatively narrow bifid L, and rather narrow L/U2; it resembles that of *Acanthoceras* (Fig. 1G).

Few workers dispute the *Acanthoceras* ancestry of *Cunningtoniceras* s. s. (cf. KENNEDY 1971, COOPER 1978, WRIGHT & KENNEDY 1987, MATSUMOTO et al. 1989), although *Cunningtoniceras* auctorum may be polyphyletic (COBBAN et al. 1989).

According to WRIGHT & KENNEDY (1990), however, the origins of Euomphaloceratinae lie in *Lotzeites* WIEDMANN (1960). The latter taxon was introduced as a subgenus of *Calycoceras* for low Upper Cenomanian homeomorphs of *Chelonicerases*, and is based on immature material. It comprises

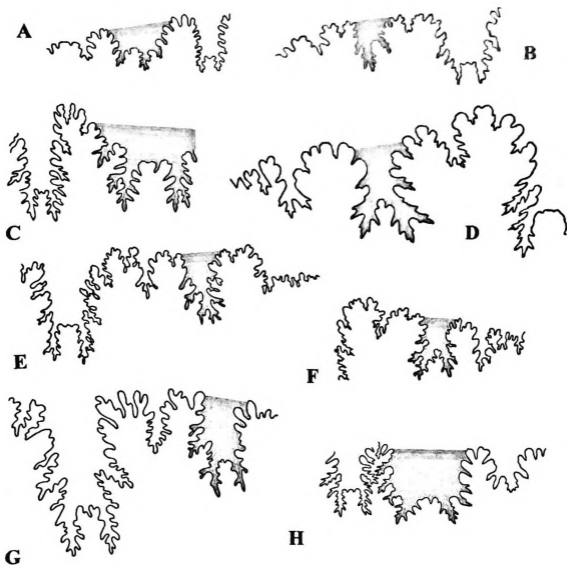


Fig. 1. Suture lines of **A** - *Burroceras clydense* COBBAN, HOOK & KENNEDY, **B** - *Yubari-ceras ornatissimum* (STOLICZKA), **C** - *Euomphaloceras (Euomphaloceras) euomphalum* (SHARPE), **D** - *Cunningtoniceras cornutum* (KOSSMAT), **E** - *Romaniceras (Romaniceras) deverianum* (D'ORBIGNY), **F** - *Cunningtoniceras inerme* (PERVINQUIÈRE), **G** - *Acanthoceras rhotomagenese* (BRONGNIART), **H** - *Pseudaspidoceras pseudonodosoides* (CHOFFAT). Not to scale and from various sources; the first lateral lobe (L) is shaded.

ammonites with a very depressed coronate whorl section, rapidly expanding whorls and a fairly wide umbilicus ($U = 33-36\%$) with broad steep umbilical walls. The flanks are flattened and the wide venter is broadly arched to nearly flat. Ornament comprises strong but irregular main ribs ornamented with conspicuous umbilical tubercles and exaggerated, laterally-directed ventrolateral spines (= inner ventrolaterals). Ribs maintain their strength across the venter, looping between ventrolaterals, and there are occasional intercalatories. Ventral ribs are adorally convex and show slight but distinct

strictions and invariable siphonal tubercles when young". However, MATSUMOTO et al. (1989) reported constricted early whorls to *Cunningtoniceras meridionale* (STOLICZKA). Since, ultimately, the euomphaloceratid suture had to derive from the acanthoceratid suture, the sutural differences do not preclude *Cunningtoniceras* as an ancestor, nor does the stage at which siphonal tubercles appear. Interestingly, KENNEDY & JUIGNET (1993, figs. 1g, 25) figure an example of *Cunningtoniceras lonsdalei* (ADKINS) with typical euomphaloceratid suture (Fig. 2B), quite unlike that of *Cunningtoniceras*; presumably its malformed E affected the shape of L.

Stratigraphically *Cunningtoniceras* s. l. is well placed as a possible ancestor for *Euomphaloceras*, and the presence of constricted early whorls and a multiplicity of ventral tubercles are derived characters which link it to Euomphaloceratinae. The type species of *Lotzeitites*, on the other hand, co-exists with morphologically-dissimilar *Euomphaloceras euomphalum* (SHARPE) in Bed C of the south Devon coast (KENNEDY 1971, WRIGHT & KENNEDY 1990) and, at best, they are sister taxa sharing a common ancestor.

Kanabicer REESIDE & WEYMOUTH (1931) was introduced for rather small ammonites with a wide shallow umbilicus, inflated whorls which vary from subquadrate to rounded and strongly depressed, and a broadly-arched venter. There are 7 rows of tubercles (umbilical, inner and outer ventrolateral, and siphonal) and, typically, ribbing is highly variable and irregular. Ribs project forward across the venter where they are joined by intercalatories, so that there are far more outer ventrolateral (typically obliquely clavate) and siphonal tubercles than inner ventrolateral spines. There is a tendency for the siphonal tubercles to form a prominently-nodate siphonal keel in middle growth, flanked by deep sulci, although this may not be evident on internal moulds and the keel breaks up on adult whorls (cf. HOWARTH 1985, figs. 26-29), when the umbilical tubercles may migrate up the flank. The suture (Fig. 2C) is euomphaloceratid, with a deep E, broad-based symmetrically bifid E/L, and wide L (cf. MATSUMOTO 1959; KENNEDY et al. 1989).

KENNEDY (1971) commented on the close relationship between *Kanabicer* and *Euomphaloceras* and recorded passage forms; MATSUMOTO (1975) sought derivation of the former in the latter. This phylogeny was accepted by COOPER (1978) who relegated *Kanabicer* to a subgenus of *Euomphaloceras*, distinguished by its continuous finely nodate siphonal keel and obliquely clavate outer ventrolaterals. However, WRIGHT & KENNEDY (1981, 1990) considered these subgenera unnecessary, including *Kanabicer* in the synonymy of *Euomphaloceras*; this synonymy has gained widespread acceptance.

The earliest *Kanabicer* co-exists with *Euomphaloceras euomphalum* (SHARPE) in the Upper Cenomanian *Metoiceras mosbyense* Zone of south-western New Mexico (COBBAN et al. 1989) and, therefore, they are sister taxa; it is distinguished by its well-defined, continuous siphonal keel flanked by deep and obliquely clavate outer ventrolaterals. Since these derived characters are found also in younger *E. septemseriatum* (CRAGIN) and *E. costatum*

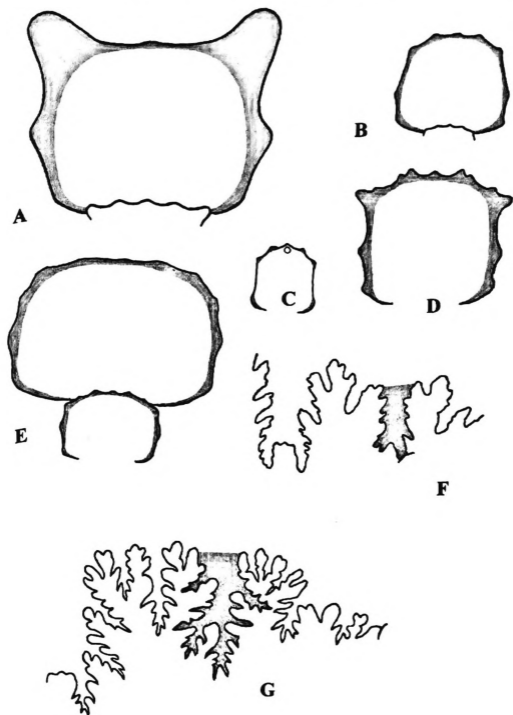


Fig. 3. Whorl sections of (A) *Euomphaloceras euomphalum* (SHARPE), (B) *Neomphaloceras japonicum* (MATSUMOTO, SAITO & FUKADA), (C) *Codazziceras ospinae* (KARSTEN), (D) *Proromaniceras (Obitraceras) ornatum* MATSUMOTO, (E) *Yubariceras ornatissimum* (STOLICZKA), and sutures of (F) *Kamerunoceras eschii* (SOLGER) and (G) *Romaniceras (Shuparoceras) yagii* MATSUMOTO with the first lateral lobe (L) shaded. Not to scale and from various sources.

COBBAN, HOOK & KENNEDY they have phylogenetic significance and warrant recognition; here *Kanabicerias* is retained as a valid taxon currently treated as a subgenus of *Euomphaloceras*. According to MATSUMOTO (1959), *Kanabicerias* is also smaller than *Euomphaloceras* and does not develop the adult ventrolateral horns (Fig. 3A) of the latter.

Burroceras COBBAN, HOOK & KENNEDY (1989) is an uppermost Cenomanian taxon introduced for slightly to moderately evolute ($U = 37\%$) euomphaloceratines with robust whorls, flattened flanks and weak to strong ribs with umbilical and inner and outer ventrolateral tubercles. The outer ventrolaterals outnumber the larger inner ventrolaterals and, at some growth stages, there may be siphonal tubercles. The earliest whorls are smooth with only periodic tuberculate ribs which may back constrictions. The suture (Fig. 1A) has a deep E, relatively narrow E/L, and very broad bifid L (COBBAN et al. 1989).

According to COBBAN et al. (1989: 37) "... *Burroceras* combines the shell form and suture of *Pseudaspidoceras pseudonodosoides* (CHOFFAT, 1899), of which it is the direct ancestor, with the tuberculation of its ancestor *Euomphaloceras*".

Paraburroceras COBBAN, HOOK & KENNEDY (1989: 40) was introduced for small moderately evolute ($U = 33\%$) euomphaloceratines with broadly rounded flanks and venter and a slightly depressed whorl section. Most of the phragmocone is smooth; only the last part of the phragmocone and the body chamber are ornamented with prorsiradiate ribs that are asymmetrically convex over the venter. On the phragmocone ribs have equal inner and outer ventrolateral and siphonal tubercles but, on the body chamber, the inner ventrolaterals are stronger and fewer in number.

According to COBBAN et al. (1989), the smooth early stage, style of tuberculation, and curious asymmetry of ventral ribs ally *Paraburroceras* with *Burroceras*; they regard the former as a progenic dwarf offshoot of the latter.

Pseudaspidoceras HYATT (1903) was introduced for large evolute shells ($U = 38\%$) with broad flat subparallel flanks, a broad gently arched venter which is flattened to shallowly concave across the siphonal line, and a somewhat depressed subquadrate whorl section. Weak long ribs arise from distinct umbilical bullae and pass to prominent ventrolateral tubercles (= inner ventrolaterals) before arching weakly across the venter and developing faint ventral (= outer ventrolaterals) nodes on either side of the siphonal line; siphonal tubercles are lacking. Weak irregular ribs are intercalated on the flank in the wide interspaces between long ribs and cross onto the venter where they are ornamented with ventral tubercles; as a result the latter (= outer ventrolaterals) outnumber the ventrolaterals (= inner ventrolaterals). Some flank ribs appear to be looped. The suture (Fig. 1H, 2E) is euomphaloceratid, with a deep E, rather narrow asymmetrically bifid E/L with broad stem, a very broad bifid L, and a very broad asymmetrically bifid L/U2 (STOLICZKA 1865).

For many years *Pseudaspidoceras* was included in Mammitinae (WRIGHT 1957), derived from *Mammites* itself (KENNEDY et al. 1980); it fell to KENNEDY et al. (1987) to recognize its true affinities and reassign it to Euomphaloceratinae. As shown by COBBAN et al. (1989), *Pseudaspidoceras* is descended from *Burroceras* in the uppermost Cenomanian; it still retains the multiplicity of outer ventrolaterals (= ventral tubercles) and the juvenile figured by KENNEDY et al. (1987, text-fig. 6E-F) shows the ghost-like remnant of closely-spaced siphonal nodes. COOPER (1978, fig. 19K-L) figured a pathological *E. (K.) septemseriatum* (CRAGIN) in which there is an abrupt change to *Pseudaspidoceras*-type ornament.

Ampakabites COLLIGNON (1965) was introduced as a subgenus of *Kamerunoceras* for material from the "Middle" Turonian of Madagascar; the type material (based on internal moulds) was refigured by KENNEDY et al. (1987). It shows a moderately evolute ($U = 30\%$) shell with broad flat subparallel flanks and a wide gently convex venter. Umbilical bullae of irregular strength give rise to weak, distant, adorally-convex ribs which frequently loop to enlarged, conspicuously clavate inner ventrolateral tubercles. There is a multiplicity of bubble-like outer ventrolateral nodes close to the siphonal line. Two to three weak irregular ribs are intercalated between main ribs on the flank and occasionally form weak folds on the phragmocone. A groove on the paralectotype may represent a constriction. The suture (Figs. 1F-G) is intricately subdivided with a deep E, narrow-stemmed asymmetrically bifid E/L, very deep rather narrow trifid L (deeper than E), and narrow-stemmed asymmetrically bifid L/U2.

COLLIGNON (in COBBAN & SCOTT 1972: 81) himself was one of the first to recognize that the affinities of *Ampakabites* lay with *Pseudaspidoceras* rather than *Kamerunoceras*; COBBAN & SCOTT (1972) elevated it to generic rank. However, KENNEDY et al.'s (1987: 38) study of *Pseudaspidoceras flexuosum* POWELL from the Lower Turonian of Texas led them to suggest "... considerable variation in adults of this species, sufficient to encompass the types of *Kamerunoceras (Ampakabites) auriculatum* COLLIGNON 1965 ... and perhaps *Ampakabites collignoni* COBBAN & SCOTT"; they placed *Ampakabites* in synonymy with *Pseudaspidoceras*, as had KENNEDY & WRIGHT (1979) before them. KENNEDY et al. (1987: 38) commented on the "... Euomphaloceras-like appearance" of one of their juvenile *P. flexuosum* (POWELL). MATSUMOTO & OBATA (1982: 77) felt that the distinctive suture of *Ampakabites* merited recognition, and suggested retaining this taxon as a valid subgenus of *Pseudaspidoceras*. The persistence of the euomphaloceratid suture in younger more-derived taxa, e. g. *Morrowites*, suggests this character is consistent and meaningful; therefore, the writer follows MATSUMOTO & OBATA (1982) in treating *Ampakabites* as a derived subgenus of *Pseudaspidoceras* with distinctive suture.

Morrowites COBBAN & HOOK (1983) was introduced for medium-sized to large, evolute ($U = 30\%$) Turonian acanthoceratids which homeomorph

Mammites. It has quadrangular to very depressed whorls, broadly rounded to depressed venter, and smooth and constricted innermost whorls. Ornament comprises robust distant simple ribs with 6 rows of prominent tubercles (umbilical bullae, nodate inner ventrolateral and clavate outer ventrolateral). In maturity the outer ventrolaterals weaken and become obsolete, whereas the inner ventrolateral strengthen and, in derived species, form exaggerated ventrolateral horns. The suture is euomphaloceratid, with a deep E, narrow E/L, very broad bifid L and small L/U2 (COBBAN & HOOK 1983).

Morrowites occurs in strata above *Pseudaspidoceras*, with which it shares the derived characters (among euomphaloceratids) of large size and obsolete siphonal tubercles. It is assumed, therefore, to be descended from *Pseudaspidoceras* by the development of *Mammites*-like characters such as a square to strongly depressed whorl section, coarse robust ribs and ventrolateral horns. *Pseudaspidoceras mocamedense* (HOWARTH), which has typical *Pseudaspidoceras* inner whorls and horned *Mammites*-like outer whorls is close to the ancestry of *Morrowites*.

Schindewolfites WIEDMANN (1960) was introduced for a small, very evolute Turonian acanthoceratid with strong but irregular rursiradiate ribs ornamented with 7 row of tubercles (umbilical, inner and outer ventrolateral, and siphonal), the siphonal row being weakly clavate. WIEDMANN (1960) claimed addition of an extra lateral row high on the flank (close to the inner ventrolaterals) in maturity although KENNEDY & WRIGHT (1979) could not detect it on a cast of the holotype. Its suture (Fig. 2A) is euomphaloceratid with a relatively narrow E/L and a deep, very broad bifid L.

THOMEL (1972) sought the ancestry of *Schindewolfites* in "*Acanthoceras*" *vergonense* THOMEL (a *Cunningtoniceras*), whereas COOPER (1978) linked it to *Kanabicerias*. KENNEDY & WRIGHT (1979) and KENNEDY et al. (1980) included *Schindewolfites* in the synonym of *Kamerunoceras*, even considering the possibility it was the sexual dimorph of *Kamerunoceras*. For reasons outlined later, this synonymy is not supported here and the writer follows MATSUMOTO et al. (1989) in resurrecting *Schindewolfites*.

In the writer's opinion, *Kanabicerias puebloense* COBBAN & SCOTT (which may be a synonym of *S. isovokyense* COLLIGNON), and *Kamerunoceras calvertense* (POWELL), are good *Schindewolfites* (they have distinct umbilical tubercles and lack the low-lateral tubercles of superficially similar *Kamerunoceras*). The raised nodate keel of *Schindewolfites jacobsoni* (REYMENT) (which may be a senior synonym of *S. inaequicostatum* WIEDMANN), flanked in early growth by shallow sulci (cf. REYMENT 1955), point to an origin in *Euomphaloceras* s. l.

Schindewolfites differs from *Euomphaloceras* s. l. in its squarer whorls, stronger more-regular well-spaced ribbing, shorter inner ventrolateral spines which may strengthen on the adult body chamber (cf. REYMENT 1955: 59), less-obvious multiplicity of ventral tubercles, and tendency (in more-derived species) for the siphonal tubercles to be clavate. *Schindewolfites* is easily

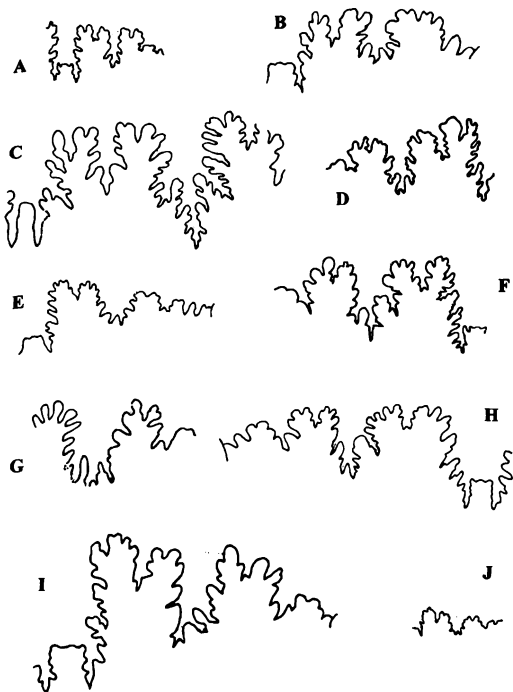


Fig. 4. Suture lines of **A** - *Tunesites salambo* PERVINQUIÈRE, **B** - *Proromaniceras* (*Proromaniceras*) *otatumei* (MATSUMOTO), **C** - *Neomphaloceras mexicanum* (JONES), **D** - *Kamerunoceras tyroniense* (D'ORBIGNY), **E-F** - *Yubariceras yubarensis* MATSUMOTO, SAITO & FUKADA, **G** - *Proromaniceras* (*Obiraceras*) *ornatum* MATSUMOTO, **H** - *Yubariceras deverioide* (De GROSSOUVRE), **I** - *Neomphaloceras pseudomphalum* (MATSUMOTO), **J** - *Codazziceras ospinae* (KARSTEN). Not to scale and from various sources; the first lateral lobe (L) is shaded.

distinguished from *Kamerunoceras* by its suture and the retention of well-developed umbilical bullae throughout ontogeny, and the absence of low-lateral tubercles. If it develops lateral tubercles, which is by no means certain, these are added high on the flank in later growth; they are not homologous to the low lateral tubercles in *Kamerunoceras* which are achieved by migration of the umbilical bullae.

Kamerunoceras REYMENT (1954) was introduced for a Lower Turonian acanthoceratid. As diagnosed by KENNEDY & WRIGHT (1979), Upper Cenomanian to Lower Turonian *Kamerunoceras* is a small to medium-sized evolute ammonite ($U = 35-45\%$) with a rounded to quadrate whorl section and smooth constricted early whorls. Ornament comprises long ribs initially with 7, later sometimes 9, rows of tubercles. The lateral row of tubercles is achieved by migration of the umbilical bullae to a low-lateral position (cf. SOLGER 1904), sometimes with development of new umbilical bullae (to produce 9 rows). The suture (Figs. 3F, 4D) is relatively simple with a deep E, broad asymmetrically bifid E/L, narrower asymmetrically bifid L, and a small bifid L/U2.

Initially REYMENT (1954) treated *Kamerunoceras* as an offshoot of *Collignoniceras* but later regarded it a probable derivative of the *Protacanthoceras* stock which gave rise to *Mammites* (REYMENT 1955). WRIGHT (1957) placed it in Mammitinae and WIEDMANN (1960) regarded it a probable synonym of *Pseudaspidoceras*. COOPER (1978) sought derivation in E. (*Kanabicerias*), independent of *Schindewolfites*, but according to KENNEDY & WRIGHT (1979: 1176) "... there are early Turonian *Kamerunoceras* which link *Kanabicerias* to the more typical late *K. eschii* and *K. turoniense*". Although KENNEDY et al. (1989: 69) claimed "... passage forms between *Kamerunoceras* and *Pseudaspidoceras pseudonodosoides* in New Mexico", it seems unlikely that siphonal tubercles would be regained immediately after having been lost.

Kamerunoceras is closest to *Schindewolfites*, differing in being larger, having a suture with narrow L, and developing low-lateral tubercles by early migration of the umbilical bullae (with or without the development of new but weaker umbilical tubercles).

Tunesites PERVINQUIÈRE (1907) was introduced for smooth nuclei from the "Cenomanian" of Tunisia. COOPER (1978: 105) considered it stratigraphically misplaced and "...with advanced morphological features which are not compatible with an Upper Albian-Lower Cenomanian age". The type material was refigured and discussed at length by KENNEDY et al. (1980); they concluded that the type species could be a stratigraphically-misplaced nucleus of any of *Kamerunoceras*, *Hourcquiceras*, *Romaniceras* or *Yubariceras*, and recommended it be regarded generically indeterminate, a *nomen dubium*. The characters of the *Tunesites* suture (Fig. 4A) most closely approach those of *Proromaniceras* and *Kamerunoceras*.

Proromaniceras WIEDMANN (1960) was introduced for *Acanthoceras pseudodeverianum* JIMBO, a Turonian acanthoceratid resembling *Romaniceras*

but with evolute coiling ($U = 35\%$), a low expansion rate to the whorls, generally compressed adult whorls, tuberculation subordinate to ribbing on outer whorls, and umbilical and lateral tubercles close together. WIEDMANN (1960) considered *Proromaniceras* intermediate between *Calycoceras* and *Romaniceras*, its name implying an ancestral relationship to *Romaniceras*. KENNEDY et al. (1980: 340) discussed the type species and, although admitting "... the lateral tubercle appears to remain low on the flank throughout growth" concluded that these "... differences seem to be no more than of individual significance"; they included it in the synonymy of *Romaniceras* s. s., as had MATSUMOTO (1975) before them. Unfortunately, they overlooked the fact that there is a whole group of nominal species, centered around *R. pseudodeverianum* (JIMBO), with exactly this character, i. e. a low-lateral tubercle; indeed; it includes *R. kallesi* ZAZVORKA which KENNEDY et al. (1980: 340) regarded a "... distinct early species". This relationship was re-examined by MATSUMOTO & UCHIDA (1985) who concluded that *R. pseudodeverianum* (JIMBO) is specifically distinct and may include *R. kallesi* ZAZVORKA in its synonymy.

Since a low-lateral tubercle is phylogenetically significant (it occurs in primitive *Kamerunoceras* and also derived *Obiraceras*), there is a group of nominal species centred around *R. pseudodeverianum* (JIMBO) which suggest that *Proromaniceras* is a valid taxon: besides the type species, these include *P. kallesi* (ZAZVORKA), *P. hispanicum* (WIEDMANN), and *P. otatumiei* (MATSUMOTO, SAITO & FUKADA) (Fig. 4B). Treatment of *Proromaniceras* as a subgenus of *Romaniceras* is inappropriate since it emphasises primitive characters. *Kossmatia* YABE (1927) was introduced to include *Acanthoceras pseudodeverianum* JIMBO (the only valid species listed, cf. WRIGHT & MATSUMOTO 1954); it is pre-occupied by *Kossmatia* UHLIG (1907), an Upper Jurassic perisphinctid, and has the same type species as *Proromaniceras* of which it is thus a synonym.

According to KENNEDY & WRIGHT (1979: 1177), *Proromaniceras kallesi* (ZAZVORKA) "... is morphologically intermediate between *Kamerunoceras* and the later *Romaniceras* species". This claim was reiterated by HANCOCK et al. (1993: 455) who stated "...*Kamerunoceras turoniense* (D'ORBIGNY) is the ancestor of *Romaniceras kallesi* ZAZVORKA". It is not difficult to derive *Proromaniceras* from *Kamerunoceras*; it differs only in its more regular ornament, lack of a low siphonal ridge, and the persistent development of prominent umbilical and low-lateral tubercles, i. e. 9 rows of tubercles. It differs from *Romaniceras* in retaining a low-lateral tubercle to large size.

Codazziceras ETAYO-SERNA (1979) was introduced for homeomorphs of *Lyelliceras*, allegedly from the Lower Coniacian, characterized by small adult size, serpenticone coiling ($U = 44\%$), smooth constricted inner whorls, strong bifurcating or simple ribs and 7-9 rows of tubercles (the umbilical tubercles may be doubled) (Fig. 3C). All tubercles and ribs weaken on the adult body chamber. The suture (Fig. 4J) shows a deep E, broad asymmetrically

bifid E/L, fairly wide L, and broad L/U2 (ETAYO-SERNA 1979, WRIGHT et al. 1983); it closely resembles that of juvenile *Yubariceras* (cf. MATSUMOTO 1975, fig. 11).

WRIGHT et al. (1983) recognized that the smooth constricted early whorls of *Codazziceras* placed it in Euomphaloceratinae and interpreted it as a paedomorphic offshoot of *Romaniceras*. According to WRIGHT et al. (1983), the umbilical tubercles in *Codazziceras* are doubled and it seems to show the same condition as in *Kamerunoceras*, i. e. shifting of the umbilical tubercle to a low-lateral position with development of a new (weaker) umbilical tubercle. *Codazziceras* differs from *Kamerunoceras*, from which it is presumed to derive, only in being serpenticone, with more regular ornament, ribs which are uninterrupted and broaden across the venter, and in lacking a low siphonal ridge.

Obiraceras MATSUMOTO (1975) was introduced for moderately evolute ($U = 33\%$) medium-sized ammonites with slightly compressed subrectangular whorls, flat parallel flanks and a gently arched venter. Rectiradiate main ribs are ornamented with 9 rows of tubercles (umbilical, low lateral, inner and outer ventrolateral and siphonal) (Fig. 3D); shorter intercalated ribs carry only the 5 ventral rows of tubercles. In middle growth, the inner and outer ventrolaterals are doubled to produce 13 rows of tubercles. The suture (Fig. 4G) is romaniceratid, with a narrow L.

MATSUMOTO (1975) considered *Obiraceras* most closely allied to *Schindewolfites*, but the latter lacks a low-lateral row of tubercles and has a very different suture. But for the doubled ventrolaterals, KENNEDY et al. (1980: 328) considered *Obiraceras* "... otherwise identical to *Yubariceras*"; they treated *Obiraceras* as a subgenus of *Romaniceras*. Significantly, however, KENNEDY et al. (1980, pl. 47, figs. 3-4) figure a specimen of *Romaniceras* aff. *kallei* (ZAZVORKA) "... with incipient doubling of outer ventrolateral tubercles, suggesting affinities with *R. (Obiraceras)*" (p. 350). In possessing low-lateral tubercles, *Obiraceras* is closest to *Proromaniceras* from which it differs in being smaller, more-conspicuously tuberculate, and with doubled ventrolateral tubercles.

In recent years *Romaniceras* SPATH (1923b) has been discussed at length (KENNEDY et al. 1980; KENNEDY & COBBAN 1988, KENNEDY 1991). The type species, *R. deverianum* (D'ORBIGNY) is moderately evolute ($U = 37-31\%$), high whorled, with rapidly-expanding whorls and a subquadrate depressed whorl section. Primary ribs are ornamented with 9 rows of tubercles (umbilical, lateral, inner and outer ventrolateral and siphonal), the outer ventrolateral and siphonal tubercles generally clavate. Initially the lateral tubercle is low on the flank (cf. KENNEDY et al. 1980, fig. 6), but it migrates upward during ontogeny to a mid-lateral position. Some ribs branch at the mid-lateral tubercle and there may be intercalatories high on the flank. Umbilical bullae tend to protrude into the umbilicus and ribbing coarsens markedly in maturity (without developing ventrolateral horns). The suture (Fig. 1E) has a

very deep E, very broad asymmetrically bifid E/L, narrow L, and fairly broad bipartite L/U2.

Although COOPER (1978) sought derivation of *Romaniceras* from *Yubariceras*, subsequent workers have favoured *Kamerunoceras* as the ancestor (cf. KENNEDY et al. 1980). However, with resurrection of *Proromaniceras* the ancestry of *Romaniceras* lies here (as implied by WIEDMANN 1960). It is derived from *Proromaniceras* by becoming higher whorled and more involute, with tuberculation strengthening, umbilical bullae protruding into the umbilicus, and the lateral tubercles shifting to midflank in maturity.

Shuparoceras MATSUMOTO (1975) was introduced for fairly involute forms ($U = 24-32\%$) with compressed high whorls, flattened flanks and a narrow rather flat venter. Ribbing is rather dense and projected across the venter. Long ribs arise from distinct umbilical bullae and either branch or are separated by a shorter intercalatory. In early growth there are 9 rows of tubercles, but the inner ventrolaterals evanesce at about 60 mm diameter. Although the outer ventrolaterals and siphonal clavi are better developed and more persistent, they too weaken in maturity when the ribs become broad and flat topped. Constrictions persist to maturity and the suture (Fig. 3G) is romaniceratid.

KENNEDY & COBBAN (1988: 25) included *Shuparoceras* in the synonymy of *Romaniceras*, concluding that it "... is no more than a feebly ribbed variant". Support for this view is provided by similar weakly-ornamented variants within *Neomphaloceras mexicanum* (JONES), but more material is required.

Neomphaloceras MATSUMOTO & OBATA (1982) was introduced for *Yubariceras pseudomphalum* MATSUMOTO, a moderately evolute ($U = 29\%$) low Middle Turonian euomphaloceratine with depressed, subquadrate whorls (Fig. 3B), gently inflated parallel flanks, and a broadly arched venter. Rectiradial to gently flexuous main ribs are ornamented with 9 rows of tubercles and, due to intercalated ribs across the venter, there is a multiplicity of ventral tubercles. The lateral tubercle is positioned midway between the umbilical and inner ventrolateral tubercles in maturity. Ribs coarsen and become distant in maturity when ventrolateral horns develop and the shell resembles *Cunningtoniceras*. The suture (Fig. 4C, I) is romaniceratid, with very deep E, rectangular bipartite E/L, deep narrow L, and narrow L/U2.

MATSUMOTO & OBATA (1982) assigned *Yubariceras fujishimai* MATSUMOTO, *Y. japonicum* MATSUMOTO, SAITO & FUKADA, and the *Y. aff. japonicum* of MATSUMOTO (1975) to *Neomphaloceras*. This is significant, because these species all show a low-lateral tubercle in early growth and WIEDMANN (1960) had questionably included *Y. japonicum* in *Proromaniceras*. *Neomphaloceras* is undoubtedly very close to *Proromaniceras* but migration of the lateral tubercle to midflank during ontogeny is a derived character shared with *Romaniceras*. Typically, however, the latter taxon does not develop coarse adult ornament with prominent ventrolateral horns and has more compressed whorls; the best-known species which belongs here is "*Romaniceras*" *mexicanum* JONES (cf. KENNEDY & COBBAN 1988).

Subfamily Euomphaloceratinae COOPER, 1978

Diagnosis: Primitive euomphaloceratids with a narrow E/L and very wide L to the suture (except in *Ampakabites*). Primitively with irregular ribbing, 7 rows of tubercles (umbilical, inner and outer ventrolateral, and siphonal); later with only 6 (siphonal row becoming obsolete) or 4 rows (siphonal row obsolete and inner and outer ventrolaterals coalescing to form horns). Siphonal tubercles mostly bullate to nodate (clavate in derived forms), sometimes forming a serrated siphonal keel in middle growth (in *Kanabicer*). Age: Upper Cenomanian to Middle Turonian.

Discussion: As interpreted here, this taxon comprises *E. (Euomphaloceras)*, *E. (Kanabicer)*, *Burrocer*, *Paraburrocer*, *P. (Pseudaspidoceras)*, *P. (Ampakabites)*, and *Morrowites*. The ancestry of the taxon lies in Middle Cenomanian Acanthoceratidae, probably *Cunningtonicer*. For those who regard *Lotzeites* closely related, it should be placed here.

Subfamily Romaniceratinae nov.

Diagnosis: Derived euomphaloceratids mostly with a broad bipartite E/L and narrow L to the suture (except in primitive *Schindewolfites*). Generally medium-sized to large, with strong regular ribbing, and outer ventrolateral and siphonal clavi equal in number to the lower ventrolaterals. Primitively with 7 rows of tubercles; later 9 (by splitting and migration of the umbilicals) or 11 (by splitting of lateral row). Age: U.Cenomanian - U. Turonian (?L. Coniacian).

Remarks: This taxon comprises *Schindewolfites*, *Kamerunoceras*, *Codazzicer*, *Proromanicer* (*Proromanicer*), *P. (Obiraceras)*, *Romanicer* (and for those who choose to recognize it, *R. (Shuparoceras)*), *Neomphaloceras*, and *Yubariceras*. Although the suture of this subfamily is seemingly primitive, i. e. acanthoceratid, morphological and stratigraphical considerations such it is derived, i. e. convergent towards the condition in *Acanthoceras*. The origins of the subfamily lie in Euomphaloceratinae, probably *Euomphaloceras* itself.

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