Variation and ontogeny in *Bauchioceras* and *Gombeoceras*

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Bauchioceras and *Gombeoceras* are closely allied coeval genera which produced a range of species with ecophenotypic variants adapted to life in the Cenomano-Turonian trans-Saharan epicontinental sea. *Pseudotissotia*, a genus occurring in the Middle Turonian, is shown to have evolved from *Bauchioceras* through paedomorphosis by neoteny. The systematic position of *Gombeoceras* and *Bauchioceras* straddles Vascoceratidae and Pseudotissotiidae. Both of these genera have similar earlier ontogenies. *Gombeoceras* may be tricarinate during part of growth, *Bauchioceras* is always tricarinate at some stage of growth. The multivariate statistical analysis of the morphological variation in *Gombeoceras*, *Wrightoceras*, *Pseudotissotia* and *Bauchioceras*, shows *Pseudotissotia* to lie well apart from the *Gombeoceras-Bauchioceras* complex.

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Introduction

Kennedy, Cooper & Wright (1979) have given an illuminating and valuable account of some features of the ornamental development of *Pseudotissotia*. For the first time since the genus was erected (Peron, 1897), we now have a reasonable idea of the intermediate and adult ontogeny of the ornament of the type species of the genus. Owing to the poor preservation of all available material of *Pseudotissotia galliennei* (d'Orbigny), the sutural development remains incompletely known, although we now have a fair concept of the properties of mature sutures.

Kennedy et al. (op. cit.) came to the conclusion that *Bauchioceras* (Reyment, 1954) is best regarded as a synonym of *Pseudotissotia* (Peron, 1897), while *Wrightoceras* (Reyment, 1954) should be considered as being generically distinct from *Pseudotissotia*.

Reyment (1978) analyzed morphological variation in keeled vascoceratids and pseudotissotiids (*Bauchioceras*, *Gombeoceras*, *Wrightoceras*, *Discovascoceras* and *Gombeoceras*) using measures of shell shape and sutural characteristics. This analysis showed the suture line of *Bauchioceras* to be more akin to that of *Gombeoceras* than that of *Pseudotissotia* and that the variational modes of the former two genera are close. It also indicated that *Wrightoceras* may have a diphyletic origin. In the same paper, it was demonstrated that *Discovascoceras* (Collignon, 1957) belongs to the bauchioceratid group of species.

The aim of the present note is to outline the ontogeny of *Gombeoceras* and *Bauchioceras*, using recently acquired, well preserved material and to show how closely related the ontogenies of the two genera are.

All of the material used for the dissections comes from the Akahana locality, Benue State, Nigeria, described by Offodile & Reyment (1977).

Preservation

For the identification, recognition and interpretation of the essential taxonomic features of vascoceratids and pseudotissotiids, the shell substance must be preserved. One layer of shell at least is needed for the ornamental details to be correctly interpreted. The state of the Akahana specimens is such that detailed study of the inner whorls can be undertaken. Although no longer aragonitic, the ammonite shells are not recrystallized and several layers of shell are usually preserved.

Methods

The specimens were carefully cut back by development a quarter of a whorl at a time. The fossil was then photographed stereographically. Special care was taken to ensure that as little shell material as possible was damaged in the process of dissection. I am grateful to Mrs. S. Bengtson for the careful dissections and to Mr. G. Andersson for the stereophotography.

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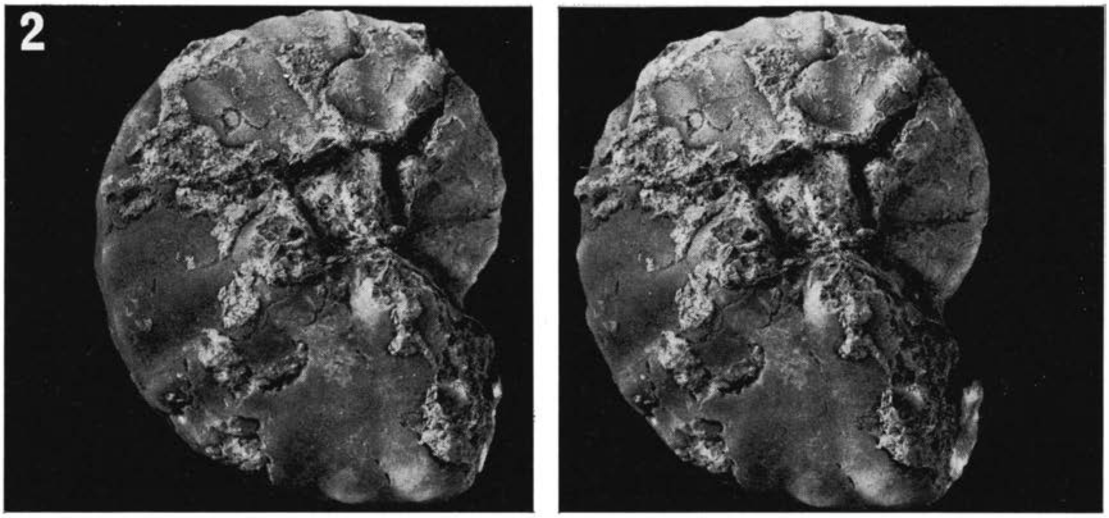

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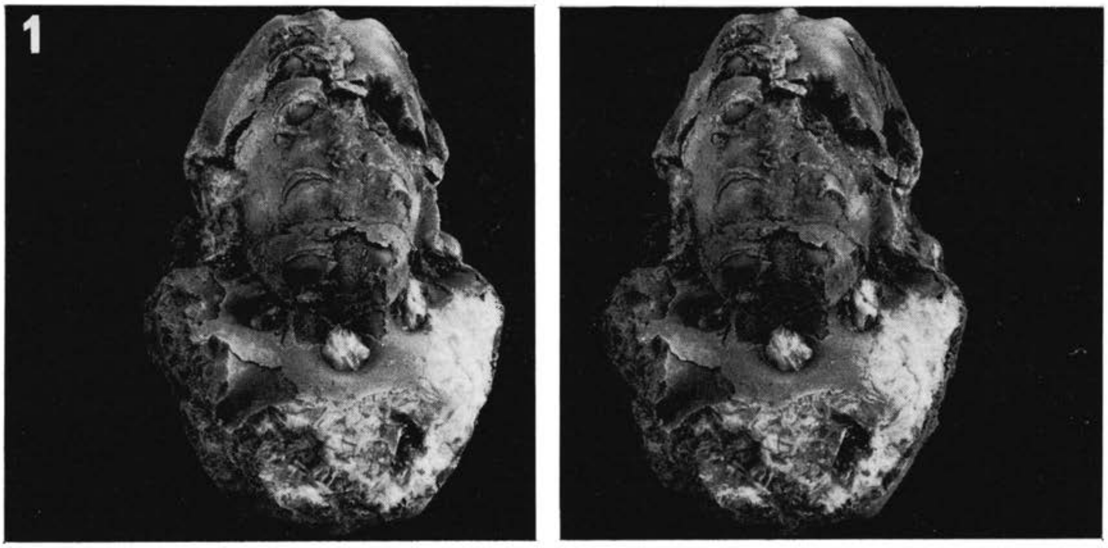


Ontogeny of Gombeoceras

1. *Gombeoceras gongilense* (Woods). Variant close to the holotype of the species.

The set of observations summarized below begins at a whorl diameter of 40 mm and continues to a diameter of 106 mm.

(a) Diameter of 40 mm. There is a median keel and ventrolateral tubercles (Fig. 1), which are slightly elongated at right angles to the direction of coiling. There is approximately one strong, bullate umbilical tubercle to three ventrolateral tubercles. The ribs are club-shaped folds, some of which rise in pairs from the umbilical tubercles (Fig. 2).

(b) Diameter of 52 mm. The median keel is relatively less pronounced and shows a tendency towards weak crenulation (Fig. 3).

(c) Diameter of 63 mm. The median keel is now clearly serrate and the ventrolateral tubercles have fused with the ribs. The umbilical tubercles are weaker. Intercalated ribs, starting around mid-flank, appear (Figs. 4, 5, 7).

(d) Diameter of 80 mm. Ridges begin to appear between the ventrolateral tubercles. The median keel is serrate (Fig. 6).

(e) Diameter of 86 mm. The median keel is now strong and sharp and only vestigially serrate. The ridges uniting the ventrolateral tubercles strengthen, the tubercles weaken. The ribbing is now feeble and the club-shape of the inner whorls has been lost (Fig. 8).

(f) Diameter of 90 mm. The median keel has reached full development. The ventrolateral tubercles have been absorbed into the ventrolateral ridges to form low ventrolateral keels. The ribbing has now totally disappeared. This stage of development resembles some mature *Bauchioceras* (Fig. 9).

(g) Diameter of 106 mm. All ornament becomes greatly reduced on the body chamber. The ventrolateral and median keels although weak can be discerned on shell-bearing parts of the body chamber (Fig. 10).

2. *Gombeoceras gongilense* (Woods). A somewhat more compressed variant than P.I. Af 456. This specimen bears the number P.I. Af 455: it comes from the Gongila area of northeastern Nigeria.

(a) Diameter of 8,5 mm. Faint, bullate ventrolateral tubercles flank a shallowly sulcate median keel. There are straight ribs, every second of which rises at a bullate umbilical tubercle (Figs. 11, 12).

(b) Diameter of 36 mm. The median keel is well developed and the ribs terminate at sharp ventrolateral tubercles (Fig. 13).

Ontogeny of *Bauchioceras*

1. *Bauchioceras nigeriense* (Woods). A variant close to the holotype. P.I. Af 457.

(a) Diameter of 8 mm. The whorls are almost completely smooth, apart from feebly defined bulges, which herald the ribbing (Fig. 17). There are no keels at this stage.

(b) Diameter of 10 mm. Flat ribs with subtuberculate ventrolateral terminations. Some ribs cross the broadly rounded venter. There are no keels at this stage (Figs. 18, 19).

(c) Diameter of 19 mm. The lateral ornament fades before the completion of this whorl. The remnants of the ribs swing forward on the venter. There are ventrolateral tubercles and the median keel is weakly developed (Figs. 20, 21, 22).

(d) Diameter of 27 mm. The lateral surface bears only growth striae. All three keels have by now appeared on the final part of the whorl. In anterior aspect, only the median keel is entire, while the outer keels can be seen to develop by coalescing of the ventrolateral tubercles through weak linking ridges. This phase is analogous to early *Gombeoceras* as regards the formation of the outer keels (cf. Fig. 8). (Figs. 23, 24, 25.)

(e) Diameter of 36 mm. All keels are now equally strong, although the ventrolateral keels still display occasional serrations (Fig. 26).

2. *Bauchioceras nigeriense* (Woods). Variant with strongly developed median keel. P.I. Af 458.

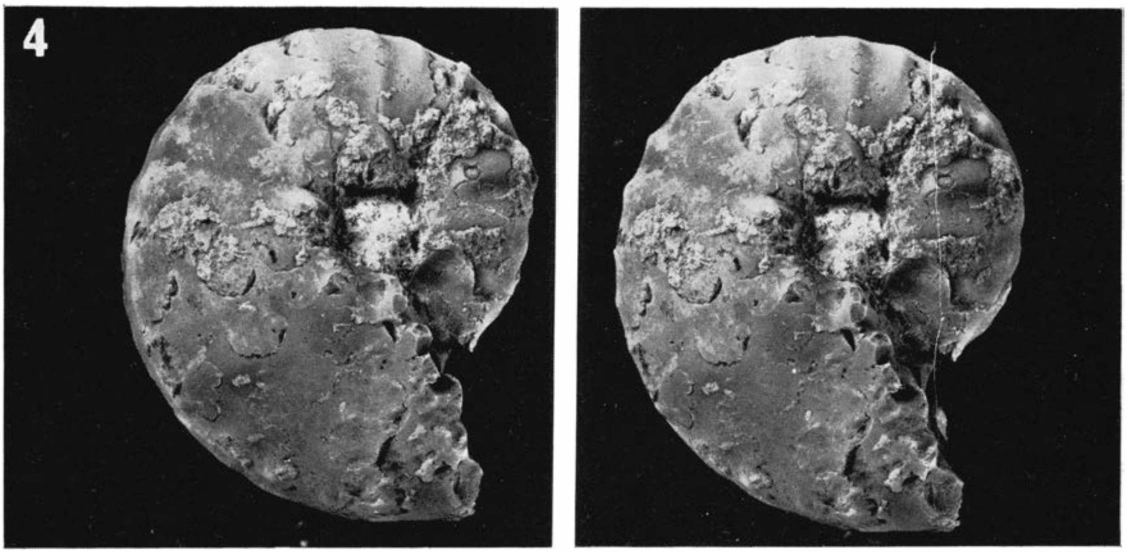
(a) Diameter of 19,5 mm. A weak median keel exists at this stage of growth; it is flanked by ventrolateral tubercles. At this diameter, there is a close resemblance to *Gombeoceras gongilense*. The ribbing disappears on this whorl (Figs. 27, 28, 30).

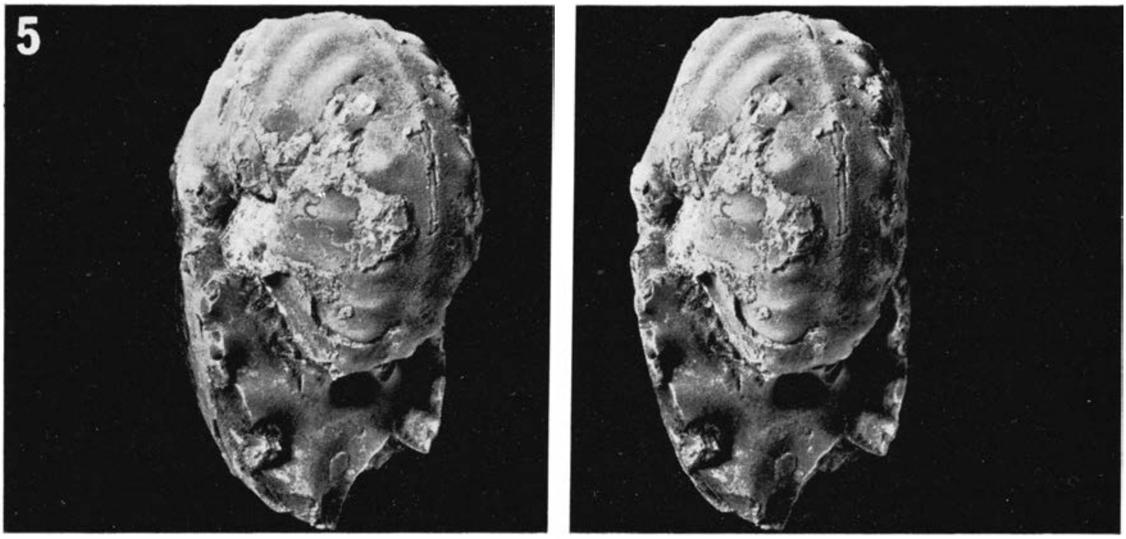
(b) Diameter of 37 mm. There is no lateral ornament. The median keel is now strong. The ventrolateral keels are just beginning to form by coalescence of the ventrolateral tubercles. By the end of this whorl, the outer keels have become fully developed (Figs. 29, 31, 32).

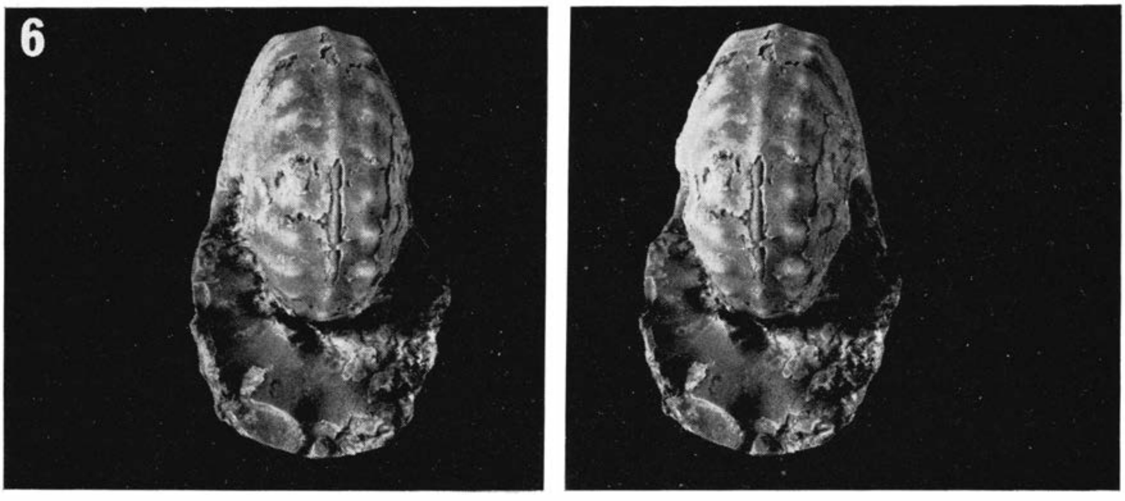
Gombeoceras gongilense (Woods). P.I. Af 456.

Fig. 1. Anteroventral aspect. Diameter = 40 mm.
Fig. 2. Lateral aspect. Diameter = 40 mm.
Fig. 3. Posteroventral aspect. Diameter = 52 mm.

(N.B. Here, and in almost all subsequent figures, each orientation is represented by a stereo-pair. These are not numbered independently.)





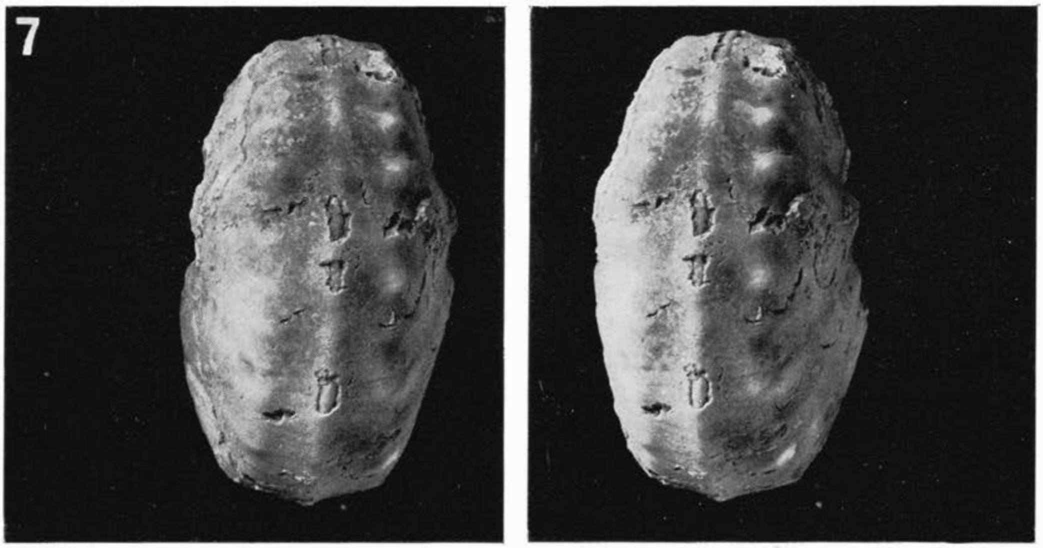


Gombeoceras gongilense (Woods). P.I. Af 456.

Fig. 4. Lateral aspect. Diameter = 63 mm.

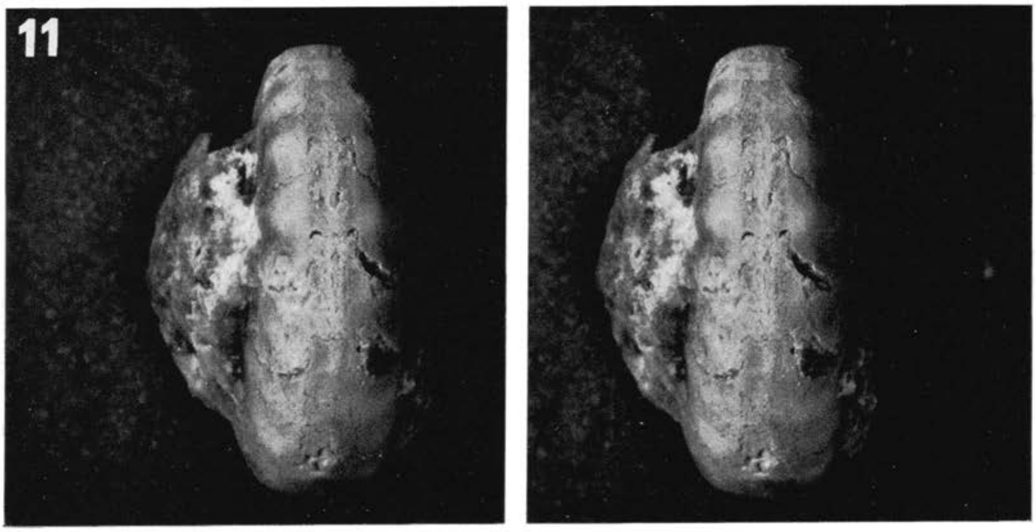
Fig. 5. Oblique view of the anteroventral aspect. Diameter = 63 mm.

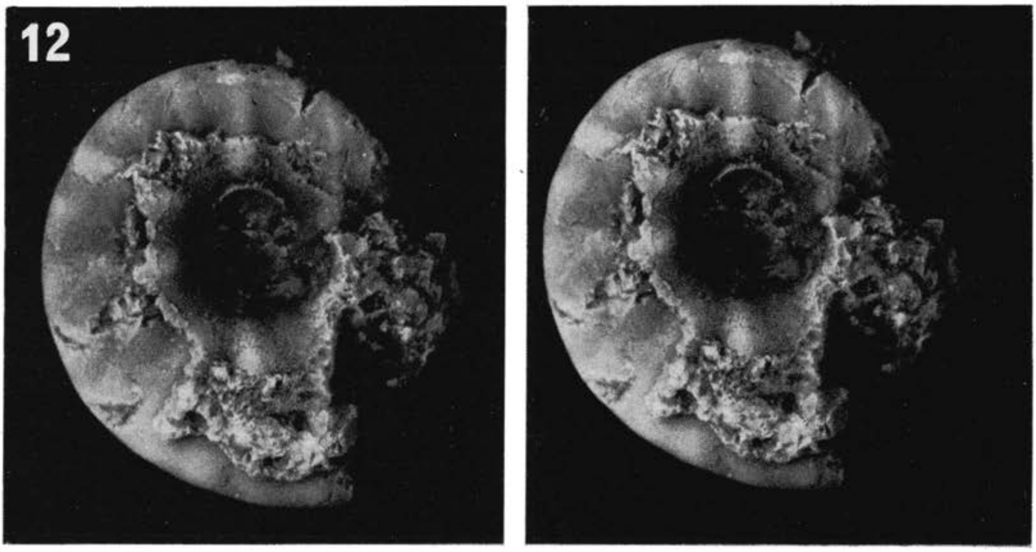
Fig. 6. Anterior aspect. Diameter = 80 mm.



Gombeoceras gongilense (Woods). P.I. Af 456.
Fig. 7. Posteroventral view. Diameter = 63 mm.

Fig. 8. Anteroventral aspect. Diameter = 86 mm.
Fig. 9. Anteroventral aspect. Diameter = 90 mm.

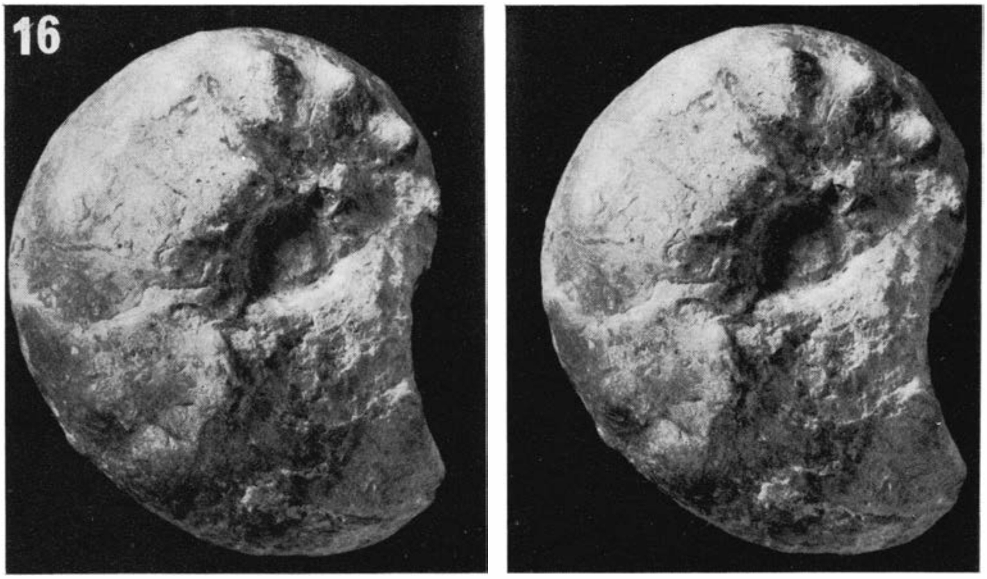


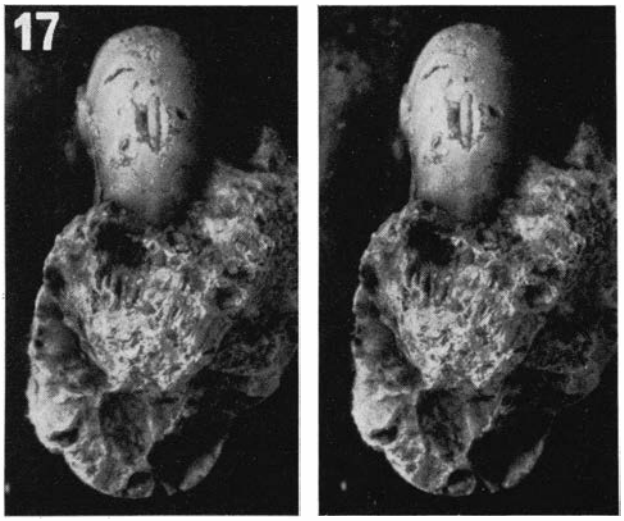


Gombeoceras gongilense (Woods). P.I. Af 456.
Fig. 10. Posteroventral view. Diameter = 106 mm.

Gombeoceras gongilense (Woods). P.I. Af 455.
Fig. 11. Lateral aspect at a diameter of 8,5 mm.
Fig. 12. Posteroventral aspect at a diameter of 8,5 mm.

Fig. 13. *Gombeoceras gongilense* (Woods). P.I. Af 455. Oblique posteroventral view at a diameter of 36 mm.
Fig. 14. *Thomasites* sp. P.I. MÖ 1. Anteroventral aspect of a specimen from Israel (Geol. Surv. Israel No. HU 21123), shown at a diameter of 98 mm. There is no shell and the interior is coarsely recrystallized.
Fig. 15. *Thomasites* sp. Specimen from Israel. Diameter = 120 mm. P.I. MÖ 2.





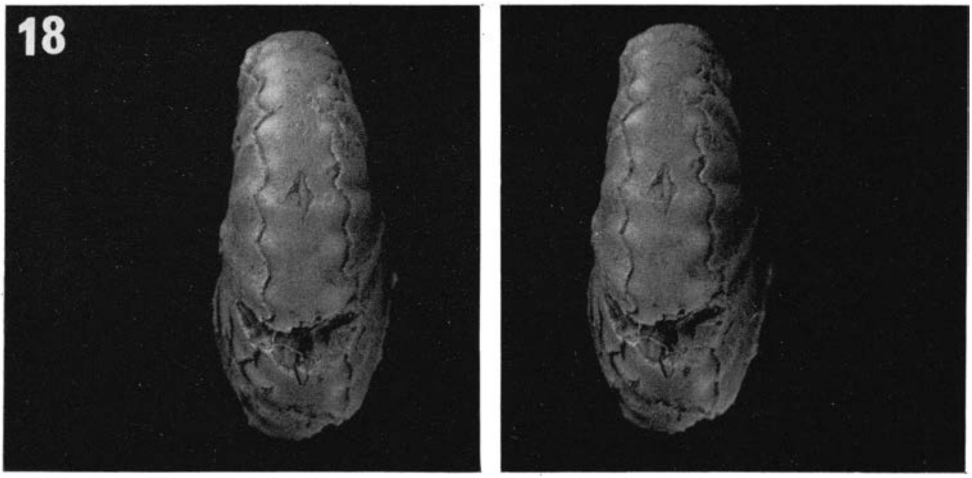
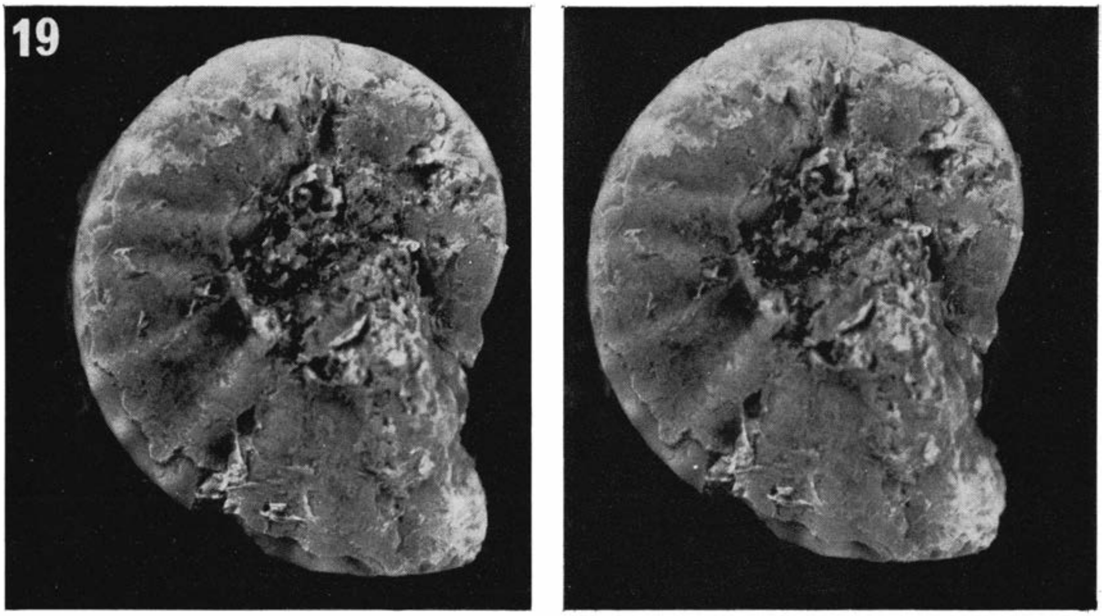
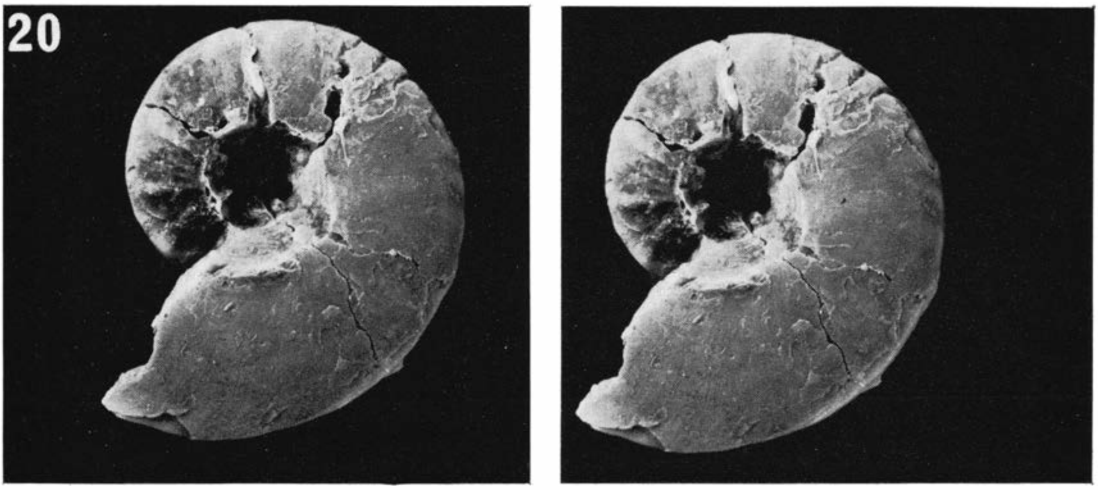
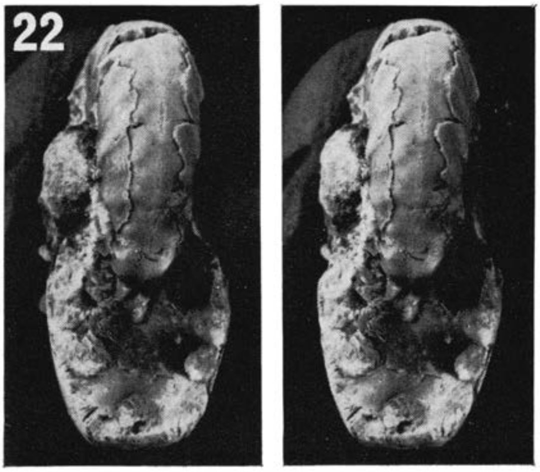


Fig. 16. *Thomasites* sp. P.I. MÖ 3. A crushed specimen from Israel. Diameter = 75 mm.
Fig. 17. *Bauchioceras nigeriense* (Woods). P.I. Af 457. Anteroventral view at a diameter of 8 mm.
Fig. 18. Posteroventral view of Af 457 at a diameter of 10 mm.

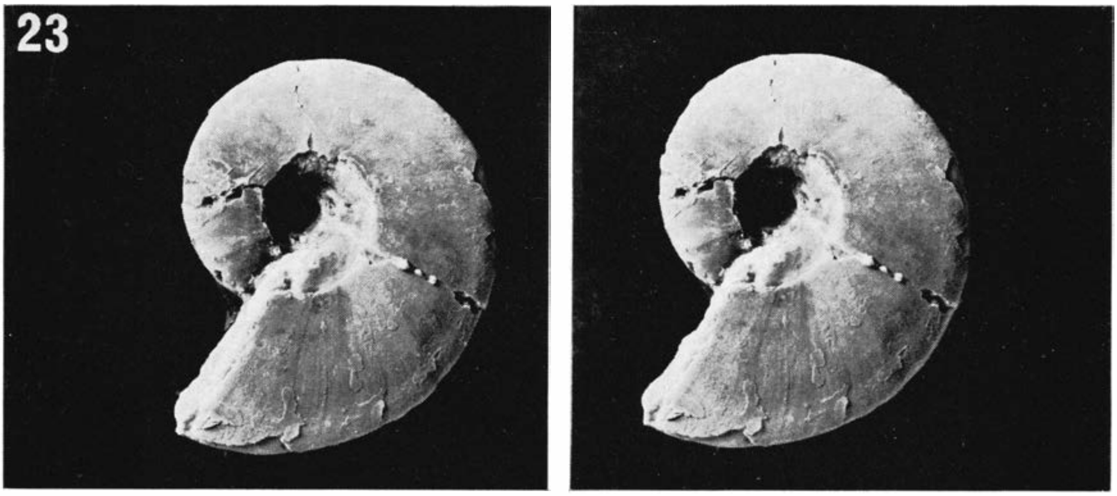


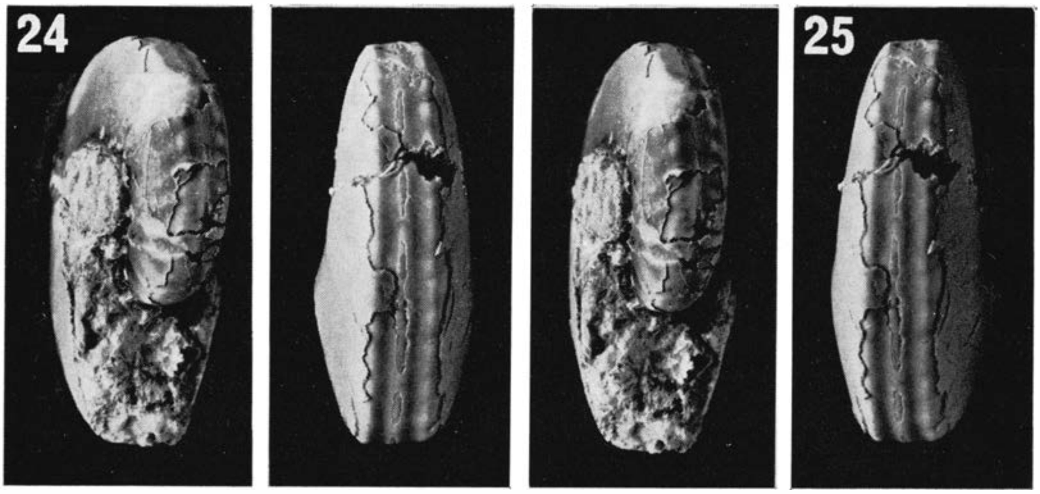


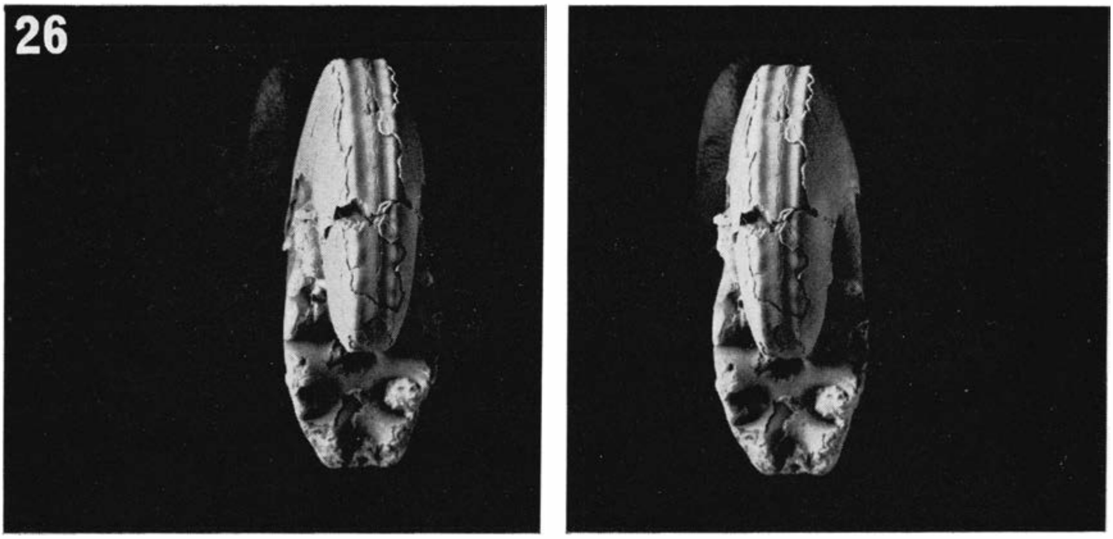


Bauchioceras nigeriense (Woods). P.I. Af 457.

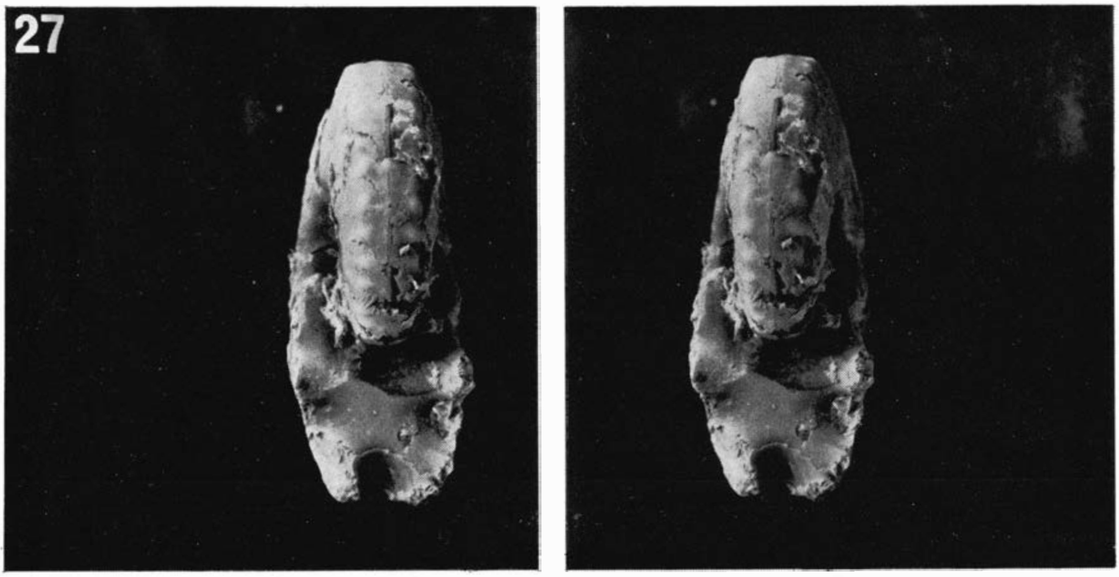
Fig. 19. Lateral aspect at a diameter of 10 mm.
Fig. 20. Lateral aspect at a diameter of 19 mm.
Fig. 21. Posteroventral aspect at a diameter of 19 mm.
Fig. 22. Anteroventral view at a diameter of 19 mm.







Bauchioceras nigeriense (Woods). P.I. Af 457.
Fig. 23. Lateral aspect at a diameter of 27 mm.
Fig. 24. Posterior aspect at a diameter of 27 mm.
Fig. 25. Anterior view at a diameter of 27 mm.
Fig. 26. Anterior view at a diameter of 36 mm.



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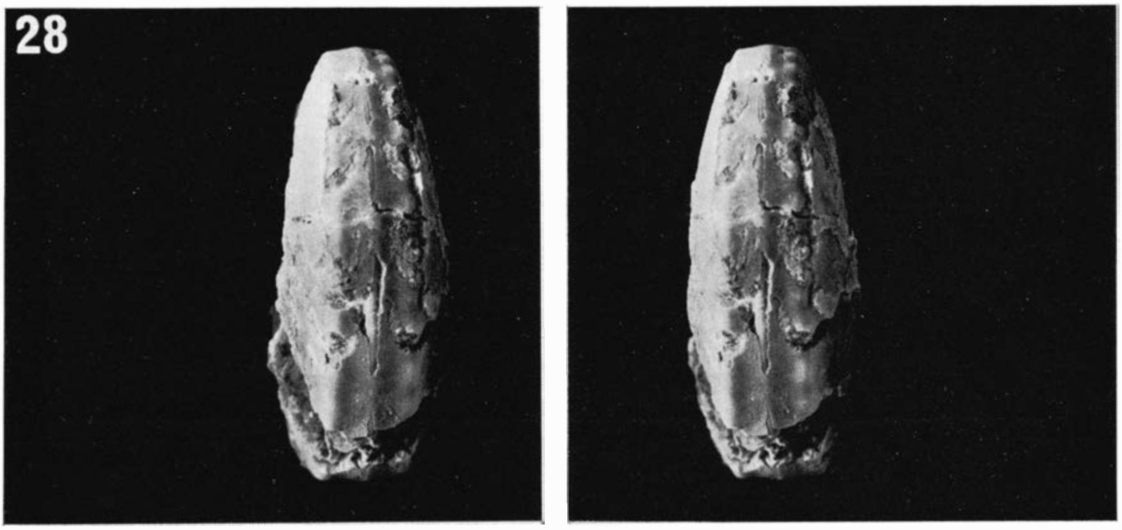

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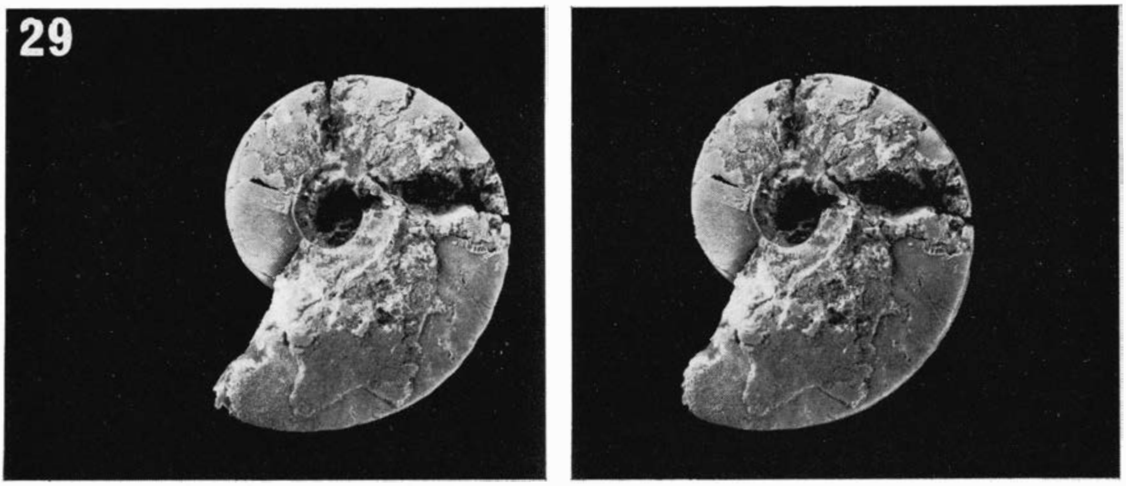

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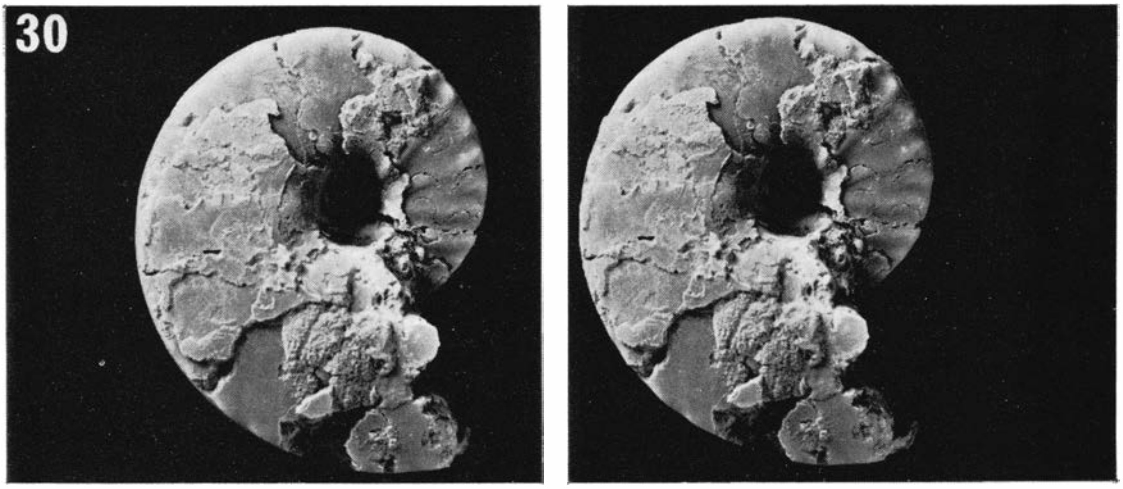
Bauchioceras nigeriense (Woods). P.I. Af 458.
Fig. 27. Anterior view at a diameter of 19,5 mm.
Fig. 28. Posterior aspect at a diameter of 19,5 mm.
Fig. 29. Lateral view at a diameter of 37 mm.



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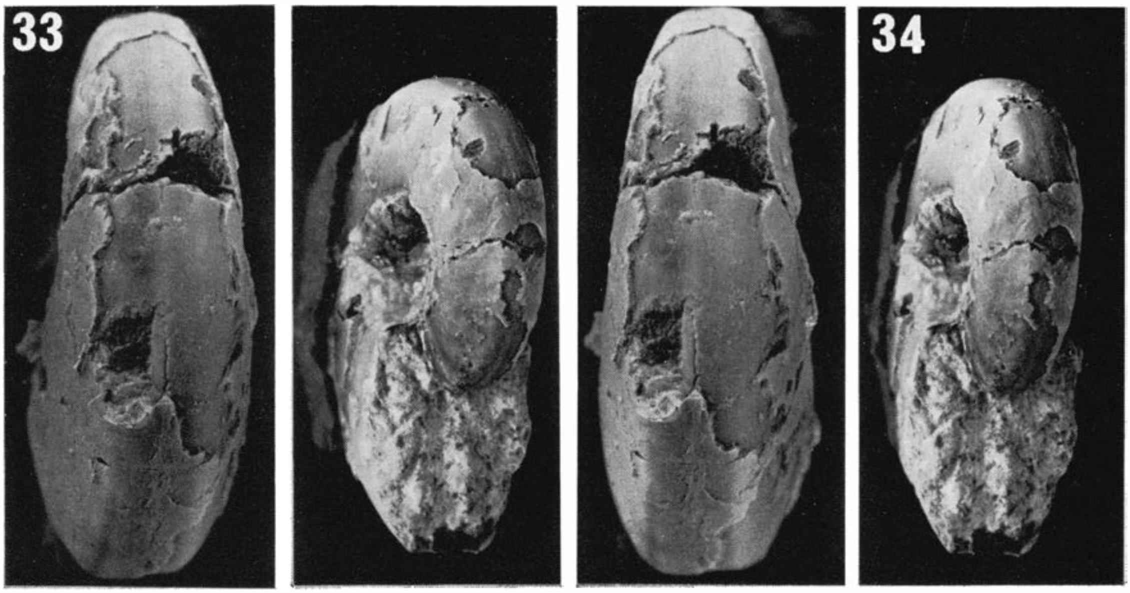

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Variations in the ornamental development of *Bauchioceras*

The examples just described present what can be said to be a normal mode of development of the species *B. nigeriense.* There are, however, important deviations, the most significant of which are reviewed below.

1. Suppressed development of the ventrolateral and median rows of tubercles.

This type of variation is marked by the early appearance of the median and ventrolateral keels. The example figured is numbered P.I. Af 464.

(a) At a diameter of 16 mm, all three keels are well developed and the lateral ornament has already been lost (Fig. 33). At a diameter of 37 mm, the keels have increased only slightly in strength, the median one now being relatively broad (Fig. 34).

2. Suppressed developed of the median keel. Another common ornamental variant is characterized by the accentuated development of the ventrolateral keels and the loss of the median keel at a relatively mature stage of growth. The following observations were made on specimen P.I. Af 460.

(a) At a diameter of 31 mm, this specimen displays well developed ventrolateral keels and a broad, low median keel (Fig. 35). There are a few, faint ribs on the first part of this whorl, but these have disappeared before reaching half way on the volution.

(b) At a diameter of 101 mm, the median keel has been completely lost (Fig. 36). There is no lateral ornament. The sulcate form of the venter on inner whorls of this specimen can be studied in Fig. 37, a polished surface of P.I. Af 460. This specimen is of the "*bicarinatum*" type.

3. Loss of the lateral ornament of *Bauchioceras.*

The Akahana collection is noteworthy in that all the individuals of *B. nigeriense* lose their lateral ornament before whorl diameters of 30—35 mm, whereas some of the specimens found in northeastern Nigeria retain the ribbing until about 50—60 mm.

Bauchioceras nigeriense (Woods). P.I. Af 454.

Fig. 30. Lateral aspect at a diameter of 19,5 mm.
Fig. 31. Anterior aspect at a diameter of 37 mm.
Fig. 32. Posterior aspect at a diameter of 37 mm.

Bauchioceras nigeriense (Woods). P.I. Af 464.

Fig. 33. Posterior view of carination at a diameter of 16 mm.
Fig. 34. Anterior view of the same specimen as shown in Fig. 33 at a diameter of 37 mm.

Ontogeny of *Bauchioceras tabulatum* (Barber)

B. tabulatum was erected by Barber (1957) on poor material, a fact which has distorted subsequent interpretations of the species. The innermost whorls, at a diameter of 15 mm, show a well developed median keel and sharp ventrolateral angles without ventrolateral tubercles (Fig. 43). At a diameter of 42 mm all traces of the faint lateral ribs have disappeared (Fig. 41) and there is a weak median keel, flanked by weak ventrolateral tubercles (Fig. 42). At a diameter of 60 mm, all keels have disappeared (Figs. 38, 39, 40).

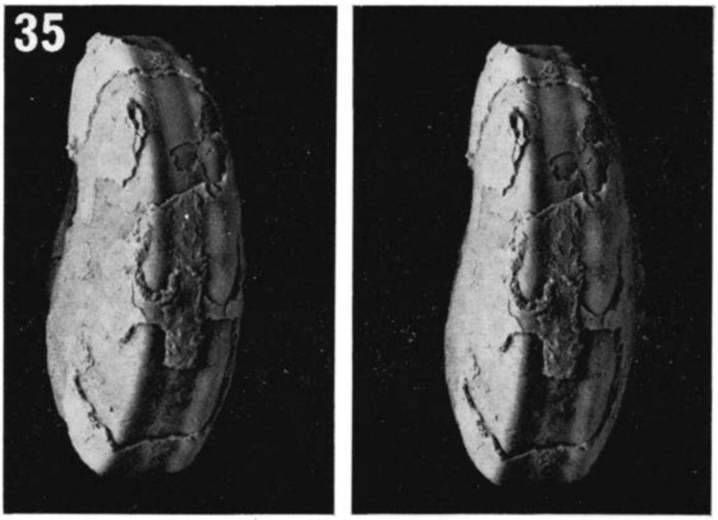
Relationships between Gombeoceras and Bauchioceras

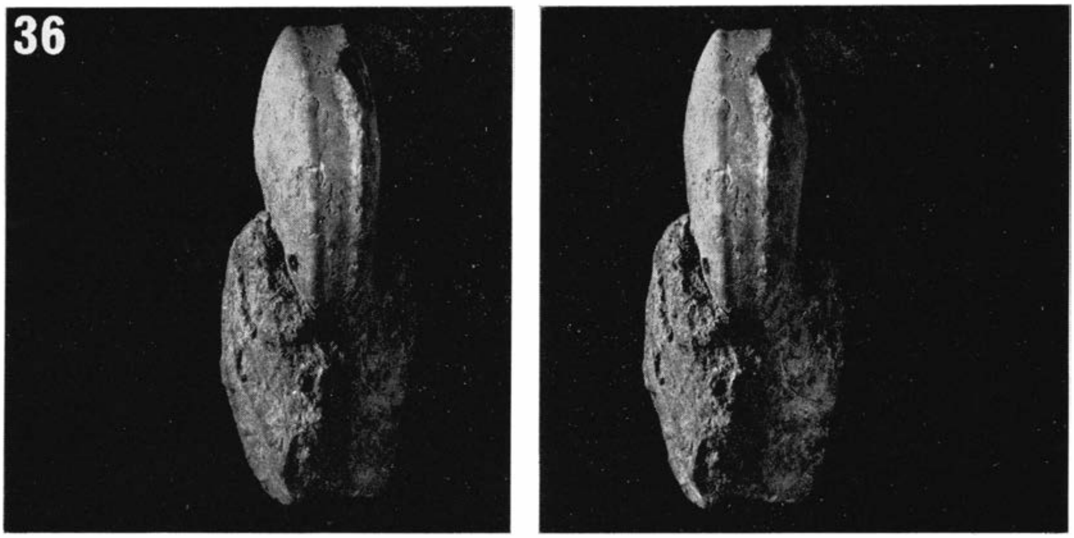
Reyment (1978) pointed out the close agreements in the morphological modes of variation of the two genera. In that study, it was found that the multivariate statistical analysis of the species *Bauchioceras nigeriense* (Woods), *B. tricarinatum* Reyment, *B. bicarinatum* Barber, *B. planum* Barber, *B. tabulatum* Barber, *Gombeoceras gongilense* (Woods), *G. compressum* Barber, *G. lautum* Barber, *G. tectiforme* Barber, *G. crassicostatum* Barber and *Wrightoceras wallsi* Reyment show identical variational modes with respect to the shapes of the shells. This agreement even extends to the ornamental features.

The present analysis has disclosed close parallels in the ontogenetic development of the two type species. The earliest whorls bear lateral ribs and there are three rows of ventral tubercles which fuse to form keels. The lateral ornament is lost at an early stage of growth, usually before a diameter of 40 mm. Adult whorls have smooth flanks. The ventral ornament of *Gombeoceras* is greatly weakened on the body chamber, although on well preserved specimens retaining shell substance, traces of the keels can often be observed. The ventral ornament of *Bauchioceras* is usually retained on the final whorl, although in compressed variants, it tends to weaken and even to be lacking in one species. The greatest affinities in the morphologies of the two groups occur during the initial ontogeny in which it may be difficult to identify the generic status of individual specimens. At more advanced growth stages, *Gombeoceras* usually has squarer whorls and is more evolute than *Bauchioceras.*

Relationships between *Bauchioceras* and *Pseudotissotia*

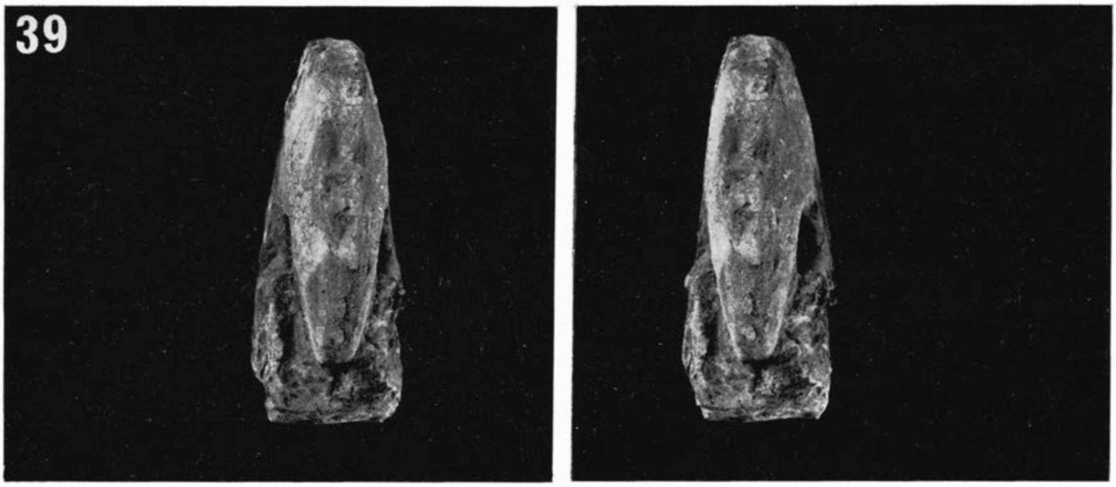
As pointed out by Kennedy et al. (1979), middle-sized *Bauchioceras* and *Pseudotissotia* may be





Bauchioceras nigeriense (Woods). P.I. Af 460. Specimen from Gulani, northeastern Nigeria.

Fig. 35. Posterior aspect at a diameter of 31 mm.
Fig. 36. Posterior view at a diameter of 101 mm.
Fig. 37. Polished section through Af 460 at a diameter of 31 mm to show the sulcate ventral development of the inner whorls.
Fig. 38. *Bauchioceras tabulatum* Barber. P.I. Af 459. Lateral view at a diameter of 60 mm (the inflation of the shell is distorted by the stereophotographs).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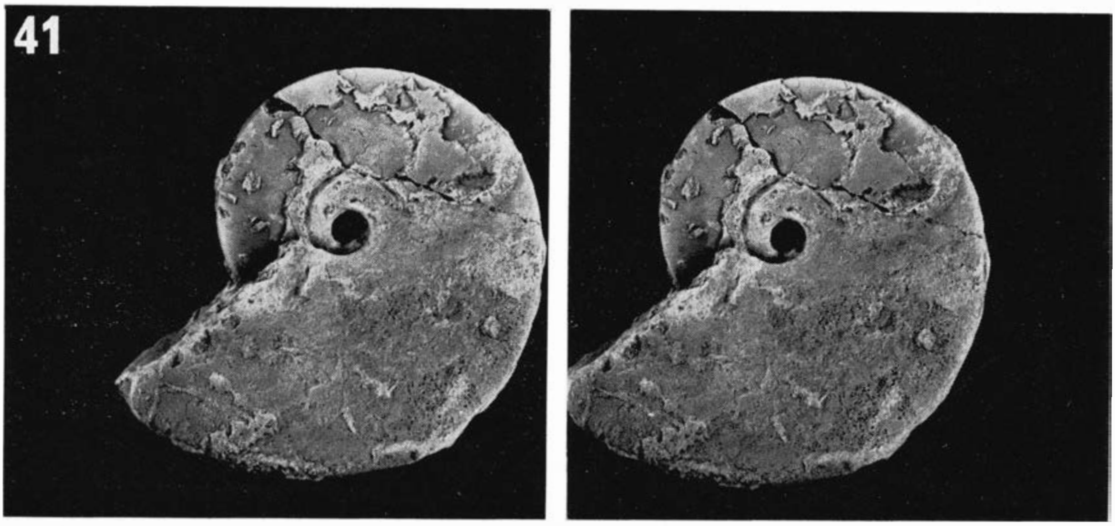
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Bauchioceras tabulatum Barber. P.I. Af 459.
Fig. 39. Anterior view at a diameter of 60 mm.
Fig. 40. Posterior aspect at a diameter of 60 mm.
Fig. 41. Lateral aspect at a diameter of 42 mm.

Bauchioceras tabulatum Barber. P.I. Af 420.
Fig. 42. Posterior view at a diameter of 42 mm.

Fig. 43. View of innermost whorls for a maximum diameter of 42 mm of the specimen.

identical in general appearance. For this reason, Kennedy et al. (op. cit.) have suggested that *Bauchioceras* should be included within *Pseudotissotia.* I do not believe this to be a phylogenetically acceptable solution although, on morphological grounds, it has an undeniable intuitive appeal. The genus *Pseudotissotia* is clearly younger than *Bauchioceras*, as observed by Kennedy et al. (op. cit.). Its type species, *P. galliennei* (d'Orbigny), is known only from Poncé in the Sarthe area, France, where its stratigraphical position is high in the Turonian to which attests its co-occurrence with *Collignoceras woollgari* and *Romaniceras ornatissimum. Bauchioceras* appears immediately above the Cenomanian-Turonian transition in Nigeria — beds dated by fossils of the *gracile* zone. The range of *Bauchioceras* coincides with the existence of the shallow epicontinental sea across north and west Africa and it became extinct simultaneously with the close of the epicontinental episode.

It is therefore not unreasonable to consider *Bauchioceras* as being post-dated by *Pseudotissotia.* The ontogeny of the ornament of *Pseudotissotia* proceeds from smooth whorls to a ribbed median growth stage. There are three ventral keels but their ontogeny has not been described. Mature shells bear strong, club-shaped ribs which stretch from the umbilical tubercles to the ventrolateral margin, where they may cause the keels to become sub-nodate. Usually, the keels of mature specimens are nodate to some extent. The ontogeny for *Bauchioceras* is the opposite to the above-described. The innermost whorls are ornamented, but all ornament, apart from the three ventral keels, is lost well before mid-growth. In fact, few *Bauchioceras* are ornamented beyond a whorl diameter of 45 mm, whereas *Pseudotissotia* does not begin to develop lateral ornament until a diameter of around 50 mm.

Paedomorphosis and Bauchioceras. — I shall now summarize the evidence supporting my belief that *Pseudotissotia* may have evolved from *Bauchioceras* as a result of paedomorphosis. Gould (1977, p. 214) points out that if a feature appearing at a standardized point of ancestral ontogeny arises earlier and earlier in descendants, we have evolution by recapitulation. The reverse situation, in which an originally ancestral feature arises later and later in descendants, is known as paedomorphosis. For a meaningful analysis of such evolutionary relationships it is necessary to have a standardization point in the ontogenetic sequences. Inasmuch as both type species reach analogous sizes, a diameter of 50 mm makes a good point of reference.

The Akahana material is somewhat older than the well known occurrences of northeastern Nigeria. It is therefore significant that the latter tend to retain the lateral ornament to a more advanced growth stage (cf. Barber, 1957) than the Akahana specimens (cf. this paper and Offodile & Reyment, 1977). Evolution by displacement is not uncommon in the fossil record. It seems to offer a reasonable explanation of the ornamental relationships between the two genera since it concerns, basically, a change of timing for developmental stages already present in ancestors, the genetic basis for which lies with the regulatory system. The ornamental features present in *Pseudotissotia* appear at a later stage of ontogeny by retardation. The descendant has the ornamental characteristics of juvenile *Bauchioceras*, including the crenulated keels and the initial smooth stage of one whorl in *Bauchioceras* stretches to 5—6 whorls in *Pseudotissotia.* We note that there has been no size increase. In rather general terms, adult *Pseudotissotia* are scaled-up versions of the early ontogeny of *Bauchioceras.* Evolution of the type described here is sometimes said to occur by neoteny, that is ,the adults of the descendant form retain the characteristics of juveniles of the ancestor.

Ecophenotypic variation

Developmental flexibility produces different environmental phenotypes under different environmental conditions (Thoday, 1953). The ammonites of the Cenomanian-Turonian epicontinental sea are polymorphic variants (there are numerous "morphs"). Although little is known about ecophenotypic variation in cephalopods, and we have no analogous situation today to that prevailing in northwestern Africa in the Cenomanian-Turonian, a considerable amount of information has been amassed for the gastropod genus *Cepaea.* Species of this genus produce a variety of morphs which display different tolerances and preferences with respect to environmental conditions. The epicontinental sea inhabited by the vascoceratids and pseudotissotiids during the basal Turonian constituted an unsafe and changeable environment.

Species inhabiting a uniform and stable environment will not be subject to selection in favour of genetic or phenotypic flexibility, whereas those living in a heterogeneous environment, such as the Cenomanian-Turonian trans-Saharan sea, will come under the influence of strong selection for phenotypic, thence environmental, flexibility (Mayr, 1963, p. 414). The wide range of morphological expression of *Gombeoceras* and *Bauchioceras* seems to be compatible with an interpreta-

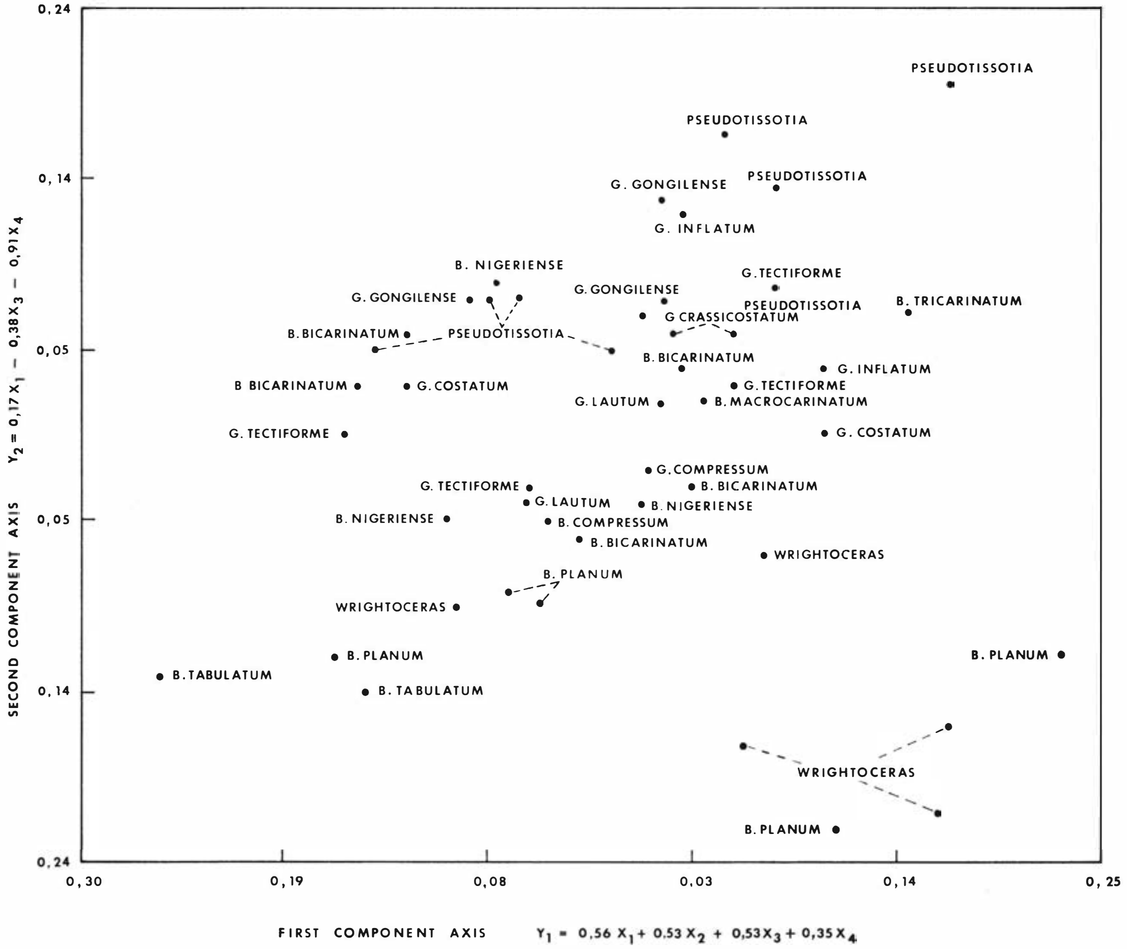

Fig. 44. All specimens projected onto the plane of the first two principal components. G = *Gombeoceras*, B = *Bauchioceras*.

tion of there being just a few species, each of which could produce a number of non-genetic ecophenotypes; this is a characteristic feature of molluscs (cf. Mayr, 1969, p. 152). A well known example that may be cited here as an illustration is that provided by the banded Florida land-snail *Liguus fasciatus*.

Note on Thomasites

Thomasites, an Early Turonian vascoceratid, is not unlike some *Gombeoceras*, if comparisons are made on poorly preserved material. There are, however, important differences between the two genera. *Thomasites* is never keeled. The general shape is very like *Neoptychites* (Figs. 14, 15). The venter is often sharply rounded and may still bear tubercules on the body chamber. The specimen illustrated in Fig. 16 displays strong ventrolateral tuberculation and prominent umbilical tubercules.

Thus, *Thomasites*, as we know the genus at present, differs from *Gombeoceras* in lacking median and, or, ventrolateral keels at any stage. The whorl section is usually different and the ornament more spaced and coarser. Dr. Z. Lewy (Geological Survey of Israel) kindly provided this material.

Morphometric Analysis

A useful means for studying the variational morphology of the shell of related ammonites and homeomorphs is offered by the multivariate statistical method of principal component analysis. The four most commonly measured dimensions of ammonite shells, to wit, x_1 = maximum dia-

Table 1. Summary of the principal component analysis.

Covariance (upper triangle) and correlation (lower triangle) matrices

Variable	1	2	3	4
1	0,0152	0,0139	0,0152	0,0094
2	0,8125	0,0194	0,0140	0,0108
3	0,9590	0,7801	0,0165	0,0063
4	0,4814	0,4890	0,3071	0,0251
	1	2	3	4
Eigenvalues	2,978	0,763	0,237	0,022
Percentage of trace	74,45	19,06	5,92	0,56
Eigenvectors				
diameter	0,561	−0,167	0,361	−0,726
breadth	0,527	−0,035	−0,849	−0,007
height	0,534	−0,384	0,343	0,671
umbilicus	0,350	0,907	0,179	0,150

meter of the conch, x_2 = breadth of the last preserved whorl, x_3 = maximum height of the last preserved whorl and x_4 = maximum diameter of the umbilicus were analyzed for *Gombeoceras gongilense* (Woods) (N = 5), *G. lautum* Barber (N = 2), *G. tectiforme* Barber (N = 4), *G. compressum* Barber (N = 2), *G. costatum* Barber (N = 3), *G. inflatum* Barber (N = 2), *G. crassicostatum* Barber (N = 3), *Bauchioceras nigeriense* (Woods) (N = 3), *B. tricarinatum* Reyment (N = 1), *B. macrocarinatum* Barber (N = 1), *B. planum* Barber (N = 5), *B. bicarinatum* Barber (N = 5), *B. tabulatum* Barber (N = 2), *Wrightoceras wallsi* Reyment (N = 5) and *Pseudotissotia galliennei* (d'Orbigny) (N = 8).

In order to stabilize the analysis with respect to size differences, the logarithms of the observations were used and the computations made on the correlation matrix. The results of the principal component analysis are summarized in Table 1.

Table 1 shows that variable 4 has a somewhat greater variance than the other three variables. An indication of the overall close morphological similarity in the whole material is given by the very high correlations for r_{12}, r_{13} and r_{23}. The variability of the umbilical diameter leads to rather low values for r_{14}, r_{24} and r_{34}.

The results of the principal component analysis are very informative (cf. Jöreskog et al., 1976, Chapters 3 and 4 for a description of this multivariate statistical method). The first principal component is isometric with respect to x_1, x_2 and x_3, these variables being locked in an allometric relationship with x_4.

The plot of the first and second transformed observations, shown in Fig. 44, contrasts general morphological variation in all four variables (the first component axis) with a whorl-height and umbilical diameter relationship (the second component axis). Several significant patterns are shown in this figure:

1. The morphological closeness of *Wrightoceras* and *Bauchioceras* through *B. planum* and *B. tabulatum*; in fact, all specimens of these forms are concentrated to the lower third of the figure.
2. The specimens of *Pseudotissotia galliennei* (Kennedy et al., 1979, p. 7) lie in the upper third of the diagram. Some of them compare with *Gombeoceras* but eventual affinities with *B. nigeriense* are not observable in this projection.
3. The locations of the individuals in Fig. 44 suggest several possibilities of simplification in the taxonomy of *Bauchioceras* and *Gombeoceras*. The use of sub-specific names for various morphological entities is indefensible (there are neither time nor space differences). We have seen how an hypothesis of ecophenotypic variation provides an adequate explanation of some of the morphological instability manifested by ammonites inhabiting an epicontinental environment. There are, however, groupings in the patterns of variation such as would be consistent with the existence of several species inhabiting the same environment. Thus, *G. gongilense* and *G. tectiforme* seem to build a natural entity, as do also *G. inflatum* and *G. costatum*. The nearest affinities of *G. lautum* remain unresolved. *Bauchioceras nigeriense*, *B. tricarinatum* and *B. bicarinatum* form a natural unit.

Strong support for the above interpretations is offered by the projection of the data points into the space of the second and third principal component axes, shown in Fig. 45. The isolated position of all specimens of *Pseudotissotia galliennei* is clearly apparent as is also the close liaison between most *Bauchioceras* and all *Gombeoceras*.

Wrightoceras and the highly compressed, weakly ornamented forms of *Bauchioceras*, to wit, *B. planum* and *B. tabulatum*, occupy a field characterized by an identical inverse relationship between variation in the umbilical diameter and the maximum whorl height.

Analysis of taxonomic groups. — The objective information yielded by the principal component analysis was used as a basis for constructing taxonomically realistic groupings of the morphological types given subspecific status by Barber (1957) in his attempt to bring order into the wide variety of ornamental categories displayed by the Nigerian material. The principal component analysis points to a logical condensation of the "subspecies" into a

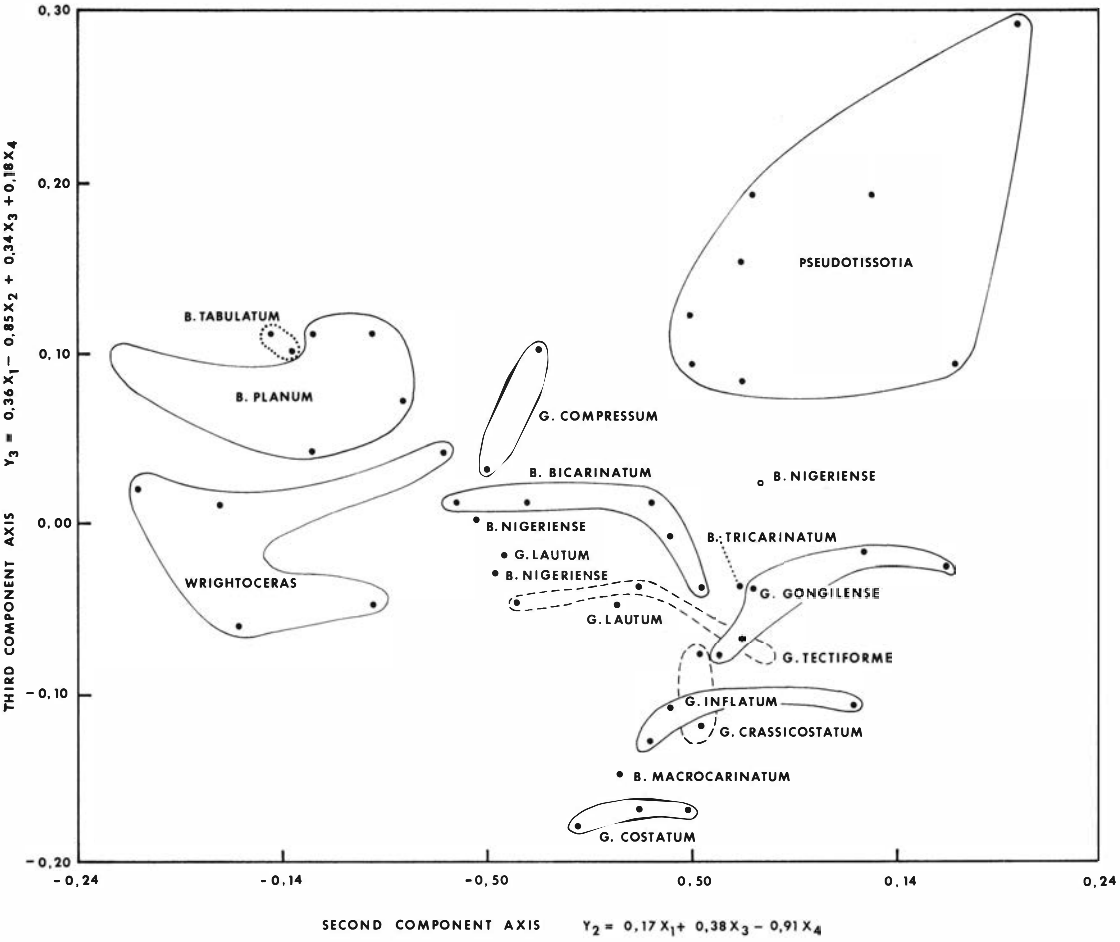

Fig. 45. All specimens projected onto the plane of the second and third principal components. G = *Gombeoceras*, B = *Bauchioceras*.

number of morphologically and biologically acceptable species. Consequently, the following species would appear to be recognizable:

1. *Gombeoceras gongilense* (Woods), which includes *G. tectiforme* Barber.
2. *Gombeoceras inflatum* Barber, which includes *G. crassicostatum* Barber.
3. *Bauchioceras nigeriense* (Woods), including *B. tricarinatum* Reyment, and *B. bicarinatum* Barber.
4. *Bauchioceras planum* Barber.
5. *Bauchioceras tabulatum* Barber.
6. *Wrightoceras wallsi* Reyment.

Analysis of the species groups. — The reliability of the analytically determined species groups can be tested objectively by a within- and between-groups contrasting technique. A suitable multivariate statistical procedure is that of canonical variate analysis (Blackith & Reyment, 1971). The basic statistical information from the analysis of the six groups *G. gongilense*, *G. inflatum*, *B. nigeriense*, *B. planum*, *W. wallsi* and *P. galliennei* is listed in Table 2. As in the case of the principal component analysis, logarithmically transformed observations were employed.

The first canonical vector represents an equally balanced "shape" relationship between the shell diameter and the maximum breadth. The second canonical vector is dominated by a similar relationship between the maximum height of the last whorl and the umbilical diameter.

The plot of the first and second canonical variates, shown in Fig. 46, is informative. In this projection, *B. nigeriense*, *G. gongilense* and *G. inflatum* are located in close morphological proximity

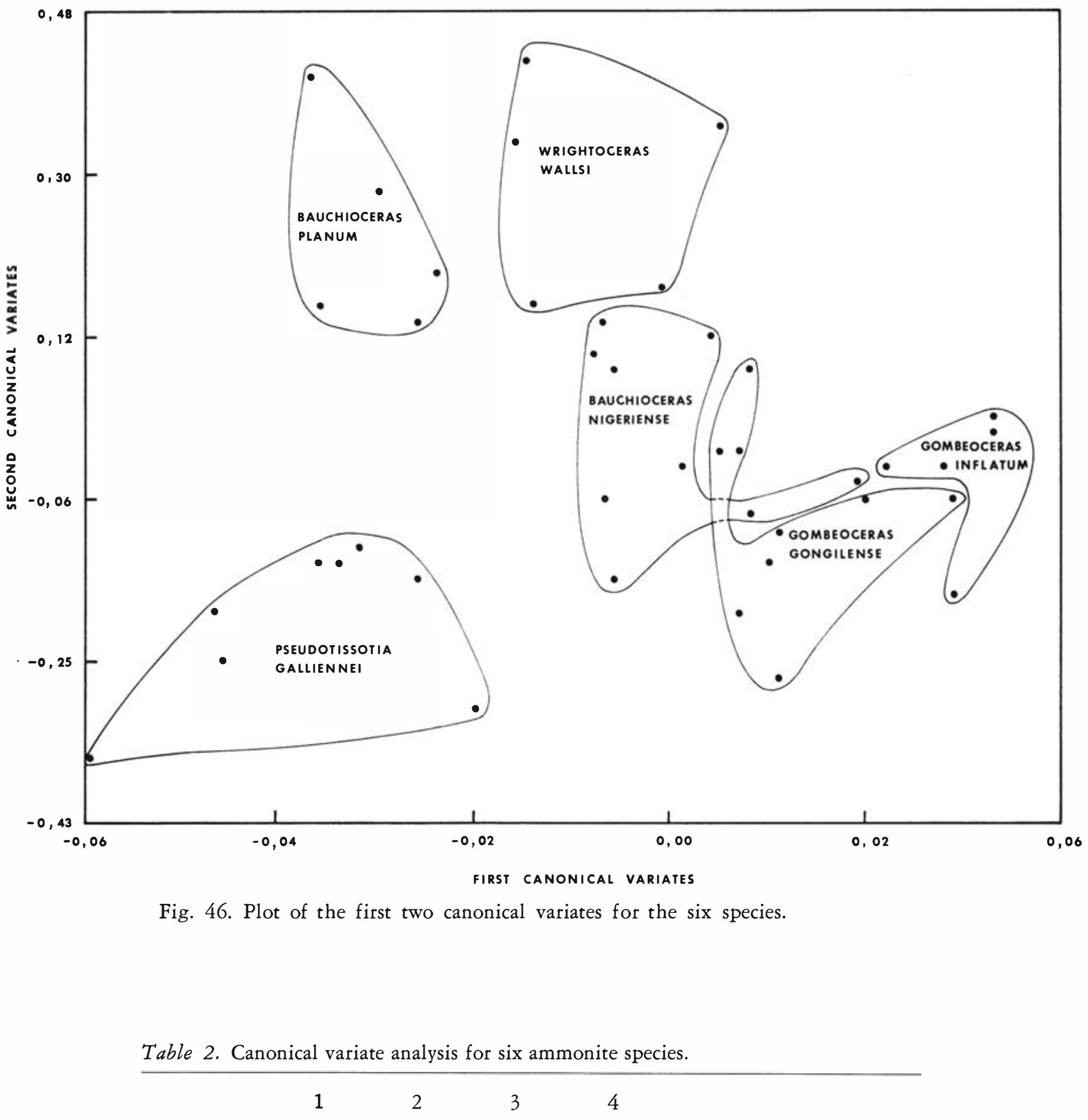

Fig. 46. Plot of the first two canonical variates for the six species.

Table 2. Canonical variate analysis for six ammonite species.

	1	2	3	4
Canonical roots	7,100	3,097	0,256	0,031
Canonical vectors				
diameter	−0,721	−0,230	−0,727	0,662
breadth	0,692	0,272	−0,108	0,056
height	0,022	0,638	0,667	−0,722
umbilicus	0,020	−0,683	0,127	−0,196

Squared generalized distances (above diagonal) and probabilities (below diagonal)

	1	2	3	4	5	6
1 = *G. gongilense*	0	3,96	3,51	32,44	18,77	31,76
2 = *G. inflatum*	0,038	0	11,47	51,00	27,84	56,84
3 = *B. nigeriense*	0,016	0,000	0	16,62	10,83	22,29
4 = *B. planum*	0,000	0,000	0,000	0	7,52	20,21
5 = *W. wallsi*	0,000	0,000	0,000	0,007	0	34,86
6 = *P. galliennei*	0,000	0,000	0,000	0,000	0,000	0

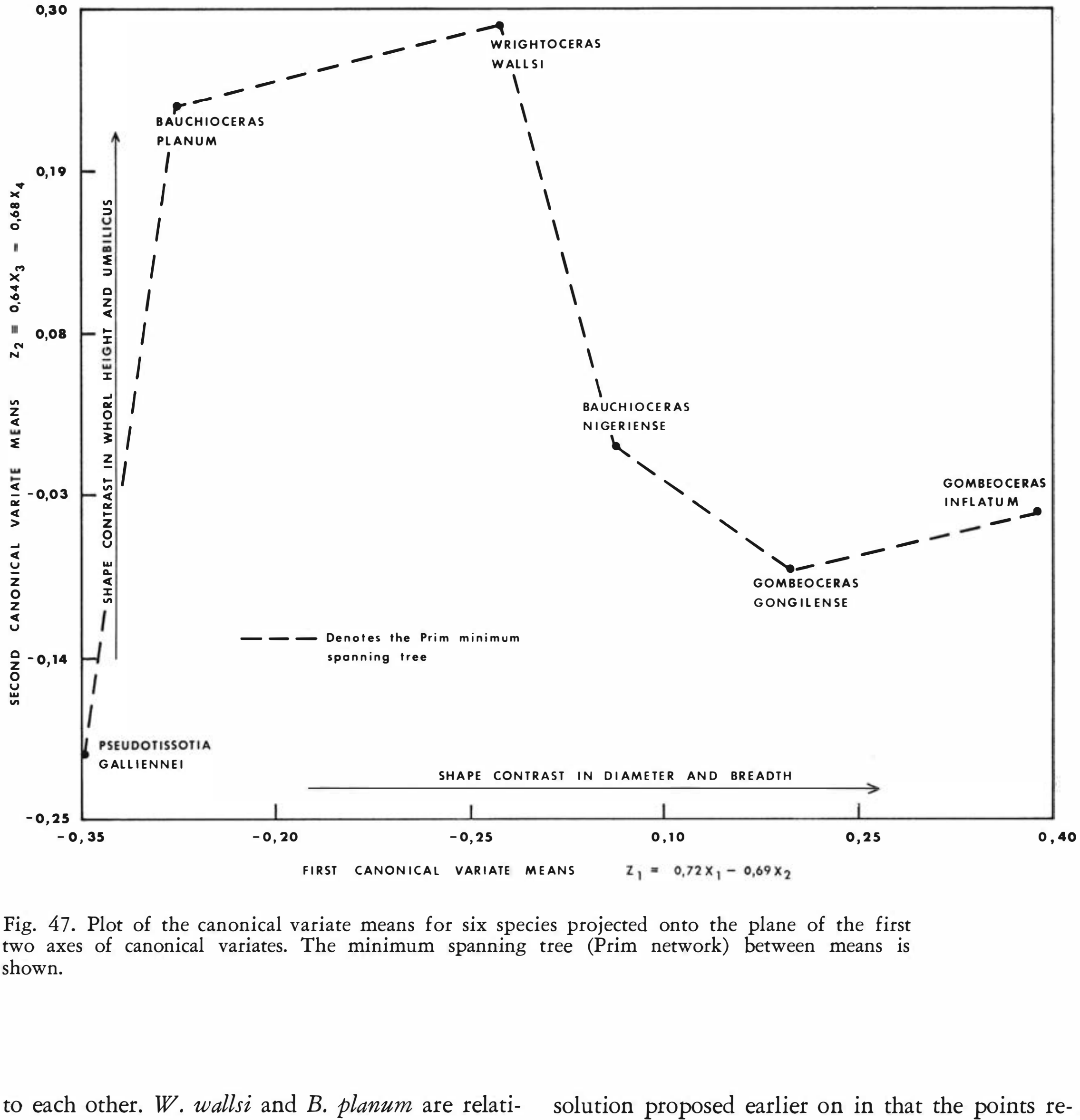

Fig. 47. Plot of the canonical variate means for six species projected onto the plane of the first two axes of canonical variates. The minimum spanning tree (Prim network) between means is shown.

to each other. *W. wallsi* and *B. planum* are relatively near to each other but *P. galliennei* is widely separated from all of the Nigerian species. This impression is confirmed by the minimum spanning tree (Prim network) shown in Fig. 47 for the six pairs of first and second canonical variate means. The close morphological relationships between the two species of *Gombeoceras* and *B. nigeriense* are clearly manifested. Particularly informative is the link with *P. galliennei*, which lies right at the end of the tree, much further from *B. nigeriense* than suggested by the relative locations in the projection onto the plane formed by the first and second axes.

A further point of significance arising from Fig. 46 is the support given to the taxonomical solution proposed earlier on in that the points representing the specimens have a convincingly low dispersion. The intimate clustering of the individuals of *G. gongilense*, *G. inflatum* and *B. nigeriense* points to close morphological affinities in these species. The Akahana occurrence suggests *Gombeoceras* and *Bauchioceras* to have appeared at the same time (Offodile and Reyment, 1977), support for which is yielded by the close shape relationships disclosed by Fig. 46.

Referring to Table 2 again, we see that the generalized distances are small (though all are statistically significant) for contrasts between the two *Gombeoceras* and *B. nigeriense*. *P. galliennei* lies far from all, including *B. planum*, the Nigerian species most similar to it in general aspect.

Comments on classification

The conclusions of Kennedy et al. (1979) imply that *Gombeoceras*, *Bauchioceras*, and *Wrightoceras* should be grouped with Pseudotissotiidae, which they regard as being well separated from Tissotiidae. The idea that *Gombeoceras*, *Bauchioceras* and *Wrightoceras* are specialized vascoceratids is not upheld by their work.

On the whole, I am inclined to agree with the above interpretation of the affinities of the genera mentioned. This would group all keeled Early Turonian acanthoceratid derivatives together in a natural manner. The classification of the Vascoceratidae now becomes somewhat less artificial, although the status of *Spathites* and *Paramammites* is still problematic.

Concluding remarks

The present analysis demonstrates the close relationships between species of *Gombeoceras* and *Bauchioceras* at both the ontogenetic and general morphological levels. The fact that the ontogeny of all species of *Bauchioceras* is the reverse of that shown by *Pseudotissotia* would appear to argue against the union of the two categories within the same genus. In fact, a convincing case can be made for *Pseudotissotia* having evolved from *Bauchioceras* by paedomorphosis.

There does not, however, seem to be much doubt that the systematic position of *Gombeoceras* and *Bauchioceras* straddles Vascoceratidae and Pseudotissotiidae.

Further details of the development of the venter in *Gombeoceras* are provided by the material examined here. The median keel is prominent during part of the ontogeny and, at a fairly advanced stage of growth, subdued ventrolateral keels appear. The properties of the ventral ornament and the ontogeny of the lateral costation in *Gombeoceras* and *Bauchioceras* indicates their having shared a common origin. Previously held opinions concerning the phyletic relationships between the two genera have been replaced by the information deriving from the Akahana material, which occurs, demonstrably, immediately above beds containing fossils of the *gracile* zone.

The remarkable variability of species of *Gombeoceras* and *Bauchioceras* (similar variability has yet to be documented for *Pseudotissotia*) would seem to be an outcome of the epicontinental environment and the unstable conditions prevailing in it. Vascoceratids that lived in the same milieu display an analogous range of morphological types. This has produced an analogous range of morphs in what now seem to be only distantly related genera; it is this expression of ecophenotypic variation that has persuaded workers to group a number of ammonites of the epicontinental environment into a single family, rather than genuine phyletic affinity.

Contribution to IGCP project 58
"Mid-Cretaceous Events".

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