

THE DEVELOPMENT OF
GLOBIGERINOIDES RUBER (D'ORBIGNY 1839)
FROM THE MIOCENE TO RECENT

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ABSTRACT. Previous workers considered that *Globigerinoides ruber* d'Orbigny 1839 ranged, with no appreciable morphological change, from early Miocene (*Globigerinita dissimilis* zone) to Recent. The present study, based on material from various parts of the world, suggests that the early to Middle Miocene forms can be distinguished from the Uppermost Miocene to Recent forms on the basis of ontogeny and phylogeny. The early to Middle Miocene forms are referred to *Globigerinoides subquadratus* Bronnimann 1954, which is redefined, the younger forms (Uppermost Miocene to Recent) to *G. ruber*. The ancestral form of *G. subquadratus* was *G. quadrilobatus altiapertura* (Bolli 1957), and *G. subquadratus* s.s. (*G. ruber* of previous workers, e.g. Bolli 1957) first appears in the *stainforthi* and not in the *G. dissimilis* zone. Evidence from Jamaica suggests that a form broadly similar to *G. obliquus* Bolli 1957 is the ancestral form of *G. ruber* (here defined). An examination of the wall structure of the group reveals considerable variation, but there appears to be no fundamental differences between the earlier and later occurrences.

THIS study is an attempt to trace the development of *Globigerinoides ruber* d'Orbigny 1839, which first appears in widely separated areas at about the level of *Globigerinita dissimilis*, *G. stainforthi*, or *Globigerinatella insueta* zones and ranges through to Recent. There is a distinct break in the range of *ruber* in both the Caribbean area and in the East Indies (Bolli, *personal communication*), where it disappears at about the top of the *Globorotalia fohsi robusta* zone (slightly higher in the East Indies) only to reappear at about the Uppermost Miocene or Basal Pliocene. It was suggested by J. B. Saunders (and partly by Dr. H. Bolli) that a comparative study of these two main occurrences might reveal differences between them which would be interesting, mainly from the phylogenetic point of view. There appeared to be no differences in external morphology between the two populations (cf. Bolli 1957, p. 114) and the investigation commenced with a study of the wall structure.

However the examination of over 100 thin sections from various levels failed to reveal any significant differences between the Miocene and younger material. Variations in wall structure were observed which compared with certain of the sections shown by Bé (1965) in the test of *Globigerinoides sacculifer* (Brady). It would appear that the wall structure of *G. ruber* could be affected by depth, as suggested by Bé (1965) in the case of *G. sacculifer* (and also *Globorotalia truncatulinoides* Bé 1963). Parker (1962) showed that thickening of the test can also be affected by changes in latitude.

However, in the process of thin-sectioning, differences were observed between the Miocene and younger forms and these are described in detail. For purposes of this discussion the Oligocene–Miocene boundary is taken at the base of the *Globigerina ampliapertura* zone (see Eames *et al.* 1962).

The material used in this study came from:

(a) The type localities of the *Globigerinita dissimilis*, *G. stainforthi*, *Globigerinatella*

insueta, and *Globorotalia fohsi robusta* zones of the Cipero Formation of Trinidad (collected by the author);

(b) Bodjonegoro No. 1, Java, ranging in age from *G. insueta* zone to the Pliocene.

(c) Jamaica, ranging in age from the *G. insueta* zone to the Pleistocene.

(d) A late Tertiary to Quaternary mid Pacific core CAP 38 BP.

In addition, two samples of late Pleistocene age from the Niger Delta, and also some Recent material, were examined.

The specimens are deposited at the British Museum (Natural History), whose registered numbers are quoted, prefixed BMNH.

SYSTEMATICS AND MORPHOLOGY

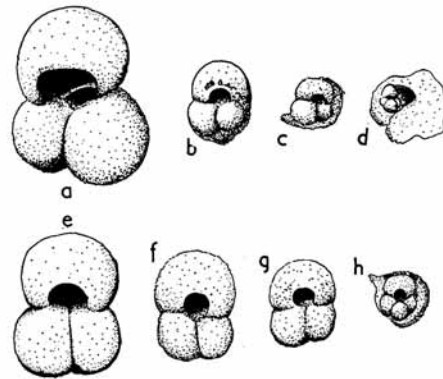
G. ruber is a very common and easily identified planktonic species. Fossil material was described by Bolli (1957) and Banner and Blow (1960), while the ecology and morphology of the living form was discussed in some detail by Bradshaw (1959), Bé (1959), Parker (1962), and Cifelli (1965). It is restricted in Recent seas to tropical and temperate waters. Banner and Blow (1960, p. 21), in their discussion of the species, considered that *Globigerinoides subquadratus* Bronnimann 1954 was at least subspecifically distinct. The writer regards Bronnimann's species as quite distinct from *G. ruber*, as discussed more fully below. The high spired forms encountered in this study differ from *Globigerina pyramidalis* (Van den Broeck 1876) with respect to the supplementary apertures. The type figure of *G. pyramidalis* shows two supplementary apertures on each chamber but they are not placed symmetrically over the dorsal intercameral sutures as in *G. ruber*.

Although variation in morphology is observed in *G. ruber*, the character which appears to vary least is the primary aperture. This is usually a broad arch placed symmetrically with respect to the penultimate and antepenultimate chamber suture. The shape of the aperture appears to be fairly constant (text-fig. 1). It is a useful character in distinguishing *G. ruber* s.l. from forms which bear a gross morphological similarity to it, e.g. *Globigerinoides elongatus* d'Orbigny 1826, which has a more consistently ovate primary aperture (Banner and Blow 1960, pl. 3, fig. 10c).

One considerable difficulty experienced was to determine the exact number of chambers in the tests of individuals at various stratigraphic levels; this is because of test thickening over the apical area, obscuring the detail of the initial whorl. In Pleistocene and Recent material it was possible to remove successively older chambers, and obtain an accurate count. The maximum number of chambers observed was twelve, excluding the proloculus. This differs somewhat from Parker's (1962) observations, which gave a maximum number of seventeen. Infilling of the chamber lumen, in the early to Middle Miocene material (*robusta* zone and older), prevented study by successive chamber removal. Particularly well-preserved material from the Cipero Formation at about the *Globorotalia fohsi lobata*/*G. fohsi robusta* zone transition, showed the test, in dorsal view, to have as many as twelve chambers.

G. ruber has hitherto been regarded as a single species ranging from the early to Middle Miocene to Recent (Bolli 1957, p. 114). Bronnimann (*in Todd et al.* 1954) described a

new species, *G. subquadratus*, from Saipan and the Cipero Formation, Trinidad. It is not clear from this work whether or not Bronnimann considered that both *G. subquadratus* and forms later described by Bolli (1957) as *G. ruber* could be recognized in the Cipero. Bronnimann made no comparison between his species and *G. ruber* but Bolli (1957) considered *G. subquadratus* from the Cipero a junior synonym. The present paper demonstrates morphological differences between early to Middle Miocene forms (described from Trinidad as either *G. subquadratus* or *G. ruber* (Bronnimann 1954; Bolli 1957) and those from the Pliocene and younger deposits, generally referred to as *G. ruber*. Therefore it is proposed that the name *G. subquadratus* be used for the early to



TEXT-FIG. 1. Series of specimens illustrating the ontogeny of *G. ruber* and *G. subquadratus*. *a-d*, *G. ruber*; *a*, No chambers removed; *b*, Four chambers removed; *c*, Five chambers removed; *d*, Six chambers removed and showing four chambers in ventral view; late Pleistocene, Niger Delta, $\times 140$. *e-h*, *G. subquadratus*; *e*, No chambers removed; *f*, One chamber removed; *g*, Two chambers removed; *h*, Penultimate whorl, the final whorl of three chambers removed; from type locality of *G. insueta* zone, Trinidad. All $\times 60$, BMNH P46606-15.

Middle Miocene forms. This species is redefined on the basis of observations more fully discussed below. The use of the name *G. ruber* is restricted to the Pliocene to Recent forms. Where a discussion of the gross morphology of both these species is concerned (and particularly with reference to the chamber arrangement in the final whorl) the term '*G. ruber* s.l.' is used.

Banner and Blow (1960) distinguished *G. ruber ruber* and *G. ruber subquadratus*, the latter being the ancestral form. However, the writer regards these morphological differences as constituting ordinary variation. Their lectotype (of *G. ruber*) is therefore considered to apply only to the Uppermost Miocene to Recent forms. The type figures (Banner and Blow 1960, pl. 3, figs. 8*a*, *b*) clearly show the three-chambered penultimate whorl typical of many of these younger forms. The proloculus appears abnormally large (pl. 3, fig. 8*a*) and probably additional initial chambers occur, but could not be observed due to thickening of the test over the apical area.

SYSTEMATIC DESCRIPTION

Globigerinoides subquadratus Bronnimann

Plate 103, figs. 2-4

1954 *Globigerinoides subquadratus* Bronnimann in Todd *et al.*, p. 680, pl. 1, figs. 5, 8.1957 *Globigerinoides rubra* d'Orbigny; Bolli, p. 113, pl. 25, figs. 12a-13b, text-fig. 21, no. 6.

Description. Test moderately large, consisting of proloculus followed by whorl of four or possibly five chambers, a second (or penultimate) whorl of four chambers, gradually and uniformly increasing in size, and a final whorl of three chambers. Periphery varies from lobulate to quadrate in outline. Primary aperture usually large, interiomarginal, umbilical, and situated symmetrically with respect to the penultimate and antepenultimate chambers. Two dorsal supplementary apertures are present at the base of the final chamber, and one at the junction of the basal suture and the intercameral suture of the preceding whorl. Umbilicus shallow. Wall radiate calcareous, frequently thickened, with a slightly rugose surface.

Remarks. The essential difference between *G. subquadratus* and *G. ruber* is in their ontogeny. The former has a penultimate whorl of four chambers (Pl. 103, figs. 2a, 3, 4), while the latter consists of a penultimate whorl of three chambers, with the final chamber of the initial whorl to a greater or lesser extent forming part of it (cf. Pl. 103, figs. 2a, 3, 4

EXPLANATION OF PLATE 103

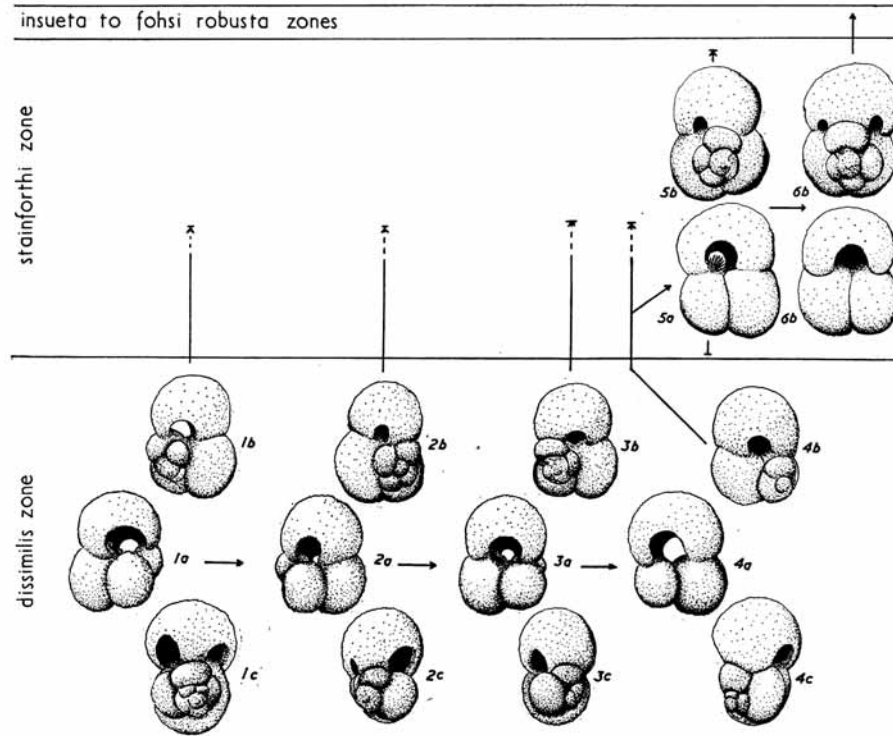
- Fig. 1 *a, b.* *Globigerinoides subquadratus* s.l. *a*, dorsal view; *b*, ventral view. From type locality of *G. stainforthi* zone, Ciperó Coast, Trinidad. BMNH P46593, $\times 113$.
- Figs. 2 *a, b-4.* *Globigerinoides subquadratus* Bronnimann 1954. *a*, Dorsal view; *b*, Ventral view; Sample ER 577, *G. insueta/bisphericus* zone, type section Montpelier Formation, St. James, Jamaica; BMNH P46594, $\times 117$. 3, Dorsal view; type locality of *G. fohsi robusta* zone, Ciperó Coast, Trinidad; BMNH P46595, $\times 110$. 4, Dorsal view; Bodjonegoro No. 1, 1,270-m. level, *Globigerinoides ruber* zone, Java; BMNH P46596, $\times 112$.
- Fig. 5 *a, b.* *Globigerina* sp. or ?*Globigerinoides* sp. *a*, Dorsal view; *b*, Ventral view; specimen pseudomorphing the *subquadratus/ruber* type morphology in ventral view, supplementary aperture indistinct; Sample ER 146/37, higher part of Buff Bay Formation, Jamaica; BMNH P46597, $\times 114$.
- Fig. 6 *a, b.* *Globigerinoides* sp. *a*, Dorsal view; *b*, Ventral view; specimen showing general similarity to the *subquadratus/ruber* type morphology; Sample ER 143/37, higher part of Buff Bay Formation, Jamaica; BMNH P46598, $\times 114$.
- Figs. 7-10. *Globigerinoides ruber* (d'Orbigny 1839.) 7*a*, Ventral view; 7*b*, Dorsal view, specimen showing fourth chamber in the penultimate whorl; Bodjonegoro No. 1, 308-m. level, Pliocene, Java; BMNH P46599, $\times 102$. 8, Dorsal view; specimen showing fourth chamber only just entering penultimate whorl; Bodjonegoro No. 1, 308-m. level, Pliocene, Java; BMNH P46600, $\times 121$. 9*a*, Ventral view; 9*b*, Dorsal view; Pacific Core CAP 38 BP at 460-463 cm., Pliocene; BMNH P46601, $\times 110$. 10*a*, Dorsal view; 10*b*, Ventral view; showing three-chambered penultimate whorl, details of the initial whorl not seen; late Pleistocene, Niger Delta; BMNH P46602, $\times 110$.
- Figs. 11-13, 15. *Globigerinoides ruber*, dissected specimens with the last three chambers (i.e. final whorl) removed. 11, 12, Showing four chambers ventrally; 13, 15, only three; Bodjonegoro No. 1, 308-m. level, Pliocene, Java. 11, BMNH P46603; 12, BMNH P46604; 13, BMNH P46605; 15, BMNH P46837. All approx. $\times 100$.
- Fig. 14. Dissected specimen of *G. ruber* with three chambers removed; Pacific Core CAP 38 BP at 460-463 cm., Pliocene; BMNH P46606; $\times 80$.

with Pl. 103, figs. 7a, 8, 9b); in the following discussion this is termed a whorl of $3\frac{1}{2}$ chambers. However, this fourth chamber is invariably much smaller than the remainder of the chambers in this whorl and thus differs from the relative size of each chamber in the penultimate whorl of *G. subquadratus*. This appears to be a character useful in distinguishing the two species. The other chamber arrangement in *G. ruber* is one in which there are only three chambers in the penultimate whorl (Pl. 103, fig. 10a). Therefore in *G. subquadratus* removal of three chambers invariably produces a form with four chambers present (Pl. 103, fig. 11; text-fig. 1h). However, in *G. ruber* upward of four chambers (frequently six) can be removed before four chambers are seen in ventral view (Pl. 103, fig. 14; text-fig. 1g). Many of the specimens in which there is a fourth chamber in the penultimate whorl in dorsal view, when dissected still show the three-chambered whorl (Pl. 103, fig. 15). However, exceptions occur (Pl. 103, figs. 12, 13) but this fourth chamber is only just visible (cf. Pl. 103, fig. 11 with figs. 12, 13). These latter forms are discussed further in the section on Bodjonegoro below.

Globigerinoides subquadratus in *Trinidad*. Bolli (1957) recorded *G. ruber* (i.e. *G. subquadratus* here defined) from the *Globigerinita dissimilis* to the *G. fohsi robusta* zones. Specimens from the type locality of the *G. dissimilis* zone show a chamber arrangement consisting of a proloculus followed by four or five chambers, and a second whorl of four chambers, all of which show a gradual and uniform increase in size as in a typical *Globigerina*. This is followed by a final whorl of three chambers, arranged in the typical tricamerate mode (Pl. 103, figs. 1a, b). The primary aperture, however, was never seen to be absolutely symmetrically placed with respect to the penultimate and antepenultimate chambers (text-fig. 2, 4a) as in a typical *G. subquadratus*. Examination of the dorsal side showed a single large supplementary aperture at the base of the final chamber, and above the third chamber of the penultimate whorl (text-fig. 2, 1-4). Approximately 70% of the forms were coiled dextrally.

There appears to be continuous variation between these specimens (i.e. *G. ruber* of Bolli 1957) and forms referable to *Globigerinoides quadrilobatus altiaperturae* (Bolli 1957), and the former are evidently extreme variants of the latter, which are far more numerous. This development is the result of the coiling becoming looser, so that the final chamber is in contact with penultimate and antepenultimate chambers as in typical *G. ruber* s.l. (text-fig. 2). A marked change in the morphology is seen in the succeeding zone of *G. stainforthi*. The extreme variants of *G. quadrilobatus altiaperturae* described from the *G. dissimilis* zone are still present, but the primary aperture is now truly symmetrically placed with respect to the penultimate and antepenultimate chambers (text-fig. 2, 5a). These forms were not observed above the *G. stainforthi* zone. There are, in addition, forms which differ from the extreme variants of *G. quadrilobatus altiaperturae* in several ways. They possess two supplementary apertures, instead of one, at the base of the final chamber (text-fig. 2, 6b). Additional supplementary apertures on earlier chambers are present, but an exact count is rendered difficult by poor preservation. These are regarded as *G. subquadratus* s.s. The proloculus is followed by whorls of five, four, and finally three chambers, i.e. as seen in the previous zone (Pl. 103, figs. 2a, b). The proportions of forms with a single supplementary aperture and those with two is about equal, with sinistrally coiled forms dominating in the former, and dextral in the latter. The same transition from *G. quadrilobatus altiaperturae* was also seen.

The succeeding zone of *Globigerinatella insueta* is characterized by a predominance of *G. subquadratus* with two supplementary apertures, while those with only one now constitute only a very small percentage (about 2%) of the fauna, and sinistrally coiled forms dominate. Occasionally the final chamber of the penultimate whorl shows a



TEXT-FIG. 2. Diagram to illustrate the variation of the *G. quadrilobatus altiapertura*-*G. subquadratus* series in the type localities of the *G. dissimilis* and *G. stainforthi* zones of Trinidad. 1a-c, 2a-c, *G. quadrilobatus altiapertura*; 3a-c, Intermediate forms; 4a-c, 5a-c, *Globigerinoides subquadratus* s.l.; 6a-c, *Globigerinoides subquadratus* s.s. All $\times 50$. BMNH P46616-21.

marked increase in size over the one before, but the majority of specimens have a penultimate whorl of four chambers gradually and uniformly increasing in size.

In the succeeding zones of *G. fohsi barisanensis*, *fohsi fohsi*, *fohsi lobata*, and *fohsi robusta*, *G. subquadratus* is in all respects identical to the *insueta* forms, the penultimate whorl consisting of four chambers. There is not such a gradual increase in chamber size as previously observed in the penultimate whorl, and the final chamber is often markedly larger than the preceding one.

The lack of specimens in the younger deposits considerably handicapped the study. However, the group reappears in the Upper Miocene Melajo Formation, but the

specimens (now regarded as *G. ruber*) are often small. They appear to be juveniles since they are exactly equivalent in size to the first and second whorls of much larger specimens. The chamber arrangement appears to be an initial whorl of five chambers followed by three.

Occasional specimens of *G. ruber* (as here defined) are seen in the Pliocene Talparo Formation. The test most probably consists of an initial whorl of five chambers, but thickening, and the lack of sufficient numbers of specimens, prevent an accurate count. This is followed by two whorls of three chambers each.

Therefore, it appears that *G. subquadratus* arises from *G. quadrilobatus altiaperturae*, the first indication occurring in the *dissimilis* zone, where it is very much an extreme variant of the latter species. *G. subquadratus* s.s. first appears in the *stainforthi* zone, being characterized by the presence of two supplementary apertures at the base of the final chamber. The precise limits of *G. quadrilobatus altiaperturae* are subjective, and it is a matter of choice whether the extreme variants of this species (text-fig. 2) are regarded as a distinct species or subspecies. The writer refers those forms with three chambers visible in ventral view, and having a single supplementary aperture, to *Globigerinoides subquadratus* s.l. (text-figs. 2, 4, 5). It is considered that the range of *G. subquadratus* s.s. in Trinidad is *G. stainforthi* zone to the *G. fohsi robusta* zone, and not *G. dissimilis* to *G. fohsi robusta* zone as given by Bolli (1957).

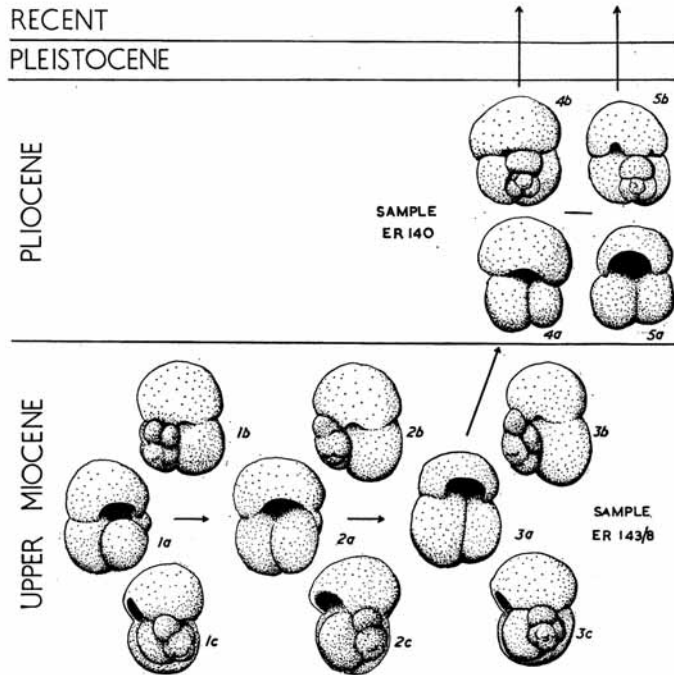
Blow and Banner (in Eames *et al.* 1962) suggest that *G. subquadratus* (i.e. *G. ruber*) could develop from *Globigerina woodi* Jenkins 1965. In the writer's opinion this may be correct only in that *G. woodi* could have given rise to *G. quadrilobatus altiaperturae*. In terms of morphology the latter is considered the closest ancestral form to *G. subquadratus* (see Jenkins 1965).

G. subquadratus in *Jamaica*. Samples were examined from several levels ranging in age from the Miocene *insueta* zone to the Pleistocene. A few specimens of *G. subquadratus* were obtained from a sample (ER 518) thought to be low in the *insueta* zone. Preservation was poor, and the initial chamber arrangement could not be determined. However, two specimens were obtained, which had only a single supplementary aperture and therefore were similar to specimens obtained from the *dissimilis* and *stainforthi* zones of Trinidad. One specimen with two supplementary apertures was found.

A sample (ER 577) from the type section of the Montpelier Formation, north of Montpelier, of *G. insueta/bispherica* zone age was examined. This showed a chamber arrangement identical with material from the *insueta* zone of Trinidad described above. The coiling was equally divided between dextral and sinistral. A sample from near the top of the Montpelier Formation, Buff Bay section, in the zone of *G. fohsi robusta*, yielded a few specimens of *G. subquadratus* which were identical with specimens described above from Trinidad.

A sample (ER 146/33A) low in the Buff Bay Formation yielded no specimens of the group. Another sample (ER 146/37) higher in this formation yielded a few specimens which had a morphology similar to the *ruber* group (Pl. 103, figs. 5, 6). These specimens are not considered to belong to *G. ruber*, but are regarded as either abnormal forms, or possibly extreme variants of some other species. Similar forms have occasionally been observed in the Lengua Formation of Trinidad. An Upper Miocene sample (ER 143/8) from the lower part of the San San Member, Bowden Formation, yielded a number of

specimens which possessed a primary aperture, varying from a symmetrical to a slightly asymmetrical position. Only one supplementary aperture was present, four chambers in the penultimate whorl, and three in the final one (details of the initial whorl could not be determined owing to thickening of the test). Furthermore, there appears to be a



TEXT-FIG. 3. Diagram to illustrate the suggested development of *G. ruber* from a form similar to *G. obliquus* Bolli 1957 (fig. 1 a-c) in Jamaica. 2 a-c, Intermediate form; 3 a-c, *G. ruber* s.l.; 4 a, b, 5 a, b, *G. ruber* s.s. Note the single supplementary aperture in 3b and the two apertures in 4b, 5b. Figs. 1-3 from the lower part of the San San Clay Member, Bowden Formation, San San Bay, Jamaica; BMNH P46622-5. Figs. 4, 5 from the type locality, Bowden Mollusc Bed, Jamaica; BMNH P46626-7. All approx. $\times 50$.

gradational series varying in morphology from forms similar to *Globigerinoides obliquus* Bolli 1957 to those close to *G. ruber* (text-fig. 3, 1a-3a).

This variation is interesting as it parallels (in terms of gross morphology) the variations seen in the Middle Miocene *G. dissimilis* zone of Trinidad. Here, the ancestral form appeared to be *G. quadrilobatus altiapertura*. Both series can be distinguished in terms of detailed morphology, the *altiapertura/subquadratus* series having the high inflated final chamber, while the '*obliquus/ruber*' series is characterized by the more depressed final chamber (text-fig. 3, 1a-3a).

Another sample (ER 143/21A) from the highest exposed part of the San San Clay, considered to be approximately at the level of the Miocene-Pliocene boundary, yielded

only two specimens of *G. ruber*. One possessed a single primary aperture, the other had two such apertures. The latter appeared to have an initial whorl of five chambers followed by $3\frac{1}{2}$ and finally 3 chambers.

A Pliocene sample (ER 140) from the type locality of the Bowden Mollusc Bed yielded a number of specimens. The details of the initial chamber arrangement could not be determined owing to poor preservation. The penultimate whorl was comprised of 3 or $3\frac{1}{2}$ chambers. However, it would appear that in the case of specimens with a penultimate whorl of $3\frac{1}{2}$ chambers in dorsal view, only 3 are visible ventrally, as in a typical specimen of *ruber*. This differs from the Middle Miocene material, from both Trinidad and Jamaica, where specimens with a 4-chambered penultimate whorl, when dissected and examined ventrally, clearly showed 4 chambers (text-fig. 1h) and not 3 with a fourth just visible as in the case of the younger material (cf. Pl. 103, figs. 11, 12). All specimens possessed two supplementary apertures in the final chamber.

This same morphology was seen in a younger sample (ER 536) from the Bowden Formation, Folly Point section. The number of specimens with 3 or $3\frac{1}{2}$ chambers in the penultimate whorl was about equal, and the proportion of dextrally and sinistrally coiled specimens was also equal.

Finally a series of specimens were examined in a Pleistocene sample (ER 150) from the Navy Island Member of the Manchioneal Formation, exposed in San San Bay. All specimens possessed 2 supplementary apertures in the final chambers, and 27 out of 30 specimens had a penultimate whorl of 3 chambers only, followed by a final whorl of 3.

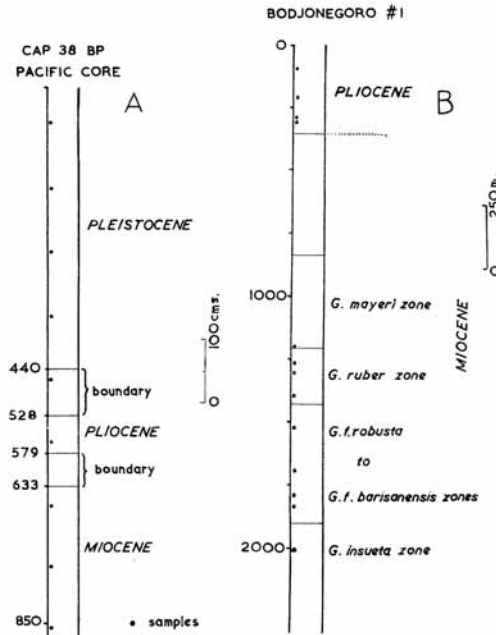
Java, Bodjonegoro No. 1. The benthonic foraminifera have been described by Boomgaard (1949), and the planktonics by Bolli (1966). Material was examined from thirteen levels, a total of about eighty specimens in varying states of preservation. The stratigraphic details are given in text-fig. 4b.

The range of *G. subquadratus* in Java is thus slightly greater than in Trinidad, since according to Bolli (1966) the *G. ruber* zone lies above the *G. fohsi robusta* zone, the former zone being absent in Trinidad.

The Middle Miocene specimens (i.e. *Globigerinatella insueta* to *Globigerinoides ruber* zone) all possessed five chambers in the initial whorl, followed by four chambers in the penultimate whorl. All specimens possessed two supplementary apertures in the final chamber.

The species, as in Trinidad, and apparently the Caribbean area generally, is absent in the remainder of the Miocene, reappearing in the Pliocene. These Pliocene forms all show either $3\frac{1}{2}$ and less frequently 3 chambers in the penultimate whorl, and 2 supplementary apertures. Specimens from the 308-m. level were dissected, and removal of the final whorl showed the typical *G. ruber* s.l. type of chamber arrangement. However, the removal of the final whorl of some specimens showed a four-chamber arrangement (Pl. 103, figs. 12, 13, 15). These forms, therefore, have an ontogeny similar to that described for *G. subquadratus*. However, it is suggested that *G. ruber* arose from an ancestral form similar in gross morphology to *G. obliquus* Bolli 1957 and it is reasonable to expect that such forms would persist for a time. With these forms were specimens in which up to 6 chambers were removed before a 4-chambered whorl was observed (Pl. 103, fig. 14). These were never observed in the Middle Miocene *G. subquadratus* Bronnimann 1954 described above.

Pacific Core, CAP 38 BP. 14° 16' S., 119° 11' W. (water depth 3,400 m.). Samples from this core, representing sediments of Upper Miocene to Pleistocene age, were examined at eight levels (text-fig. 4). The greatest numbers of specimens were obtained in samples from the 460- and 360-cm. levels. All specimens of *ruber* had two supplementary apertures on the final chamber, and no ancestral forms were observed.



TEXT-FIG. 4. A, Stratigraphic details of Pacific Core CAP 38 BP (after F. L. Parker). B, Stratigraphic details of Bodjonegoro No. 1 (after H. M. Bolli).

Although fewer specimens were obtained from samples below the 460-cm. level, there is a fairly even distribution of forms with $3\frac{1}{2}$ and 3 chambers in the penultimate whorl. However, in samples at 460 cm. and 360 cm. there is an appreciable change in the proportions, the three-chambered forms being dominant. Whether or not this trend becomes firmly established could not be definitely determined, owing to lack of specimens at the highest levels. Two samples supplied by Dr. W. H. Blow from the Niger Delta, and considered by him to be late Pleistocene, showed that three-chambered forms were dominant (text-fig. 1 a-d). A few Recent samples were examined, and these also indicated the dominance of three-chambered forms. The coiling ratios in the Pacific Core material were equally divided between dextrally and sinistrally coiled forms, with the exception of the 261-cm. level, where dextrally coiled specimens dominated. However, only thirteen specimens were obtained and this is a possible explanation for the change.

The evidence from the Upper Miocene to Recent material examined suggests the following conclusions. Initially, forms with 3 and $3\frac{1}{2}$ chambers in the penultimate whorl occur. Certain of the latter on removal of the final whorl show four chambers present in ventral view (Pl. 103, figs. 12, 13, 15). At successively higher levels, the three-chambered forms become more dominant, with the accompanying change in the ontogeny described above. This appears to take place in the late Pliocene or early Pleistocene. Therefore, the separation of the species *G. ruber* from *G. subquadratus* (as here defined) is not based on the morphology of any single specimen of the former, but rather on the morphological development of an assemblage of specimens.

The writer considers that the forms here referred to as *G. subquadratus* and *G. ruber* constitute two separate and unrelated lineages, since:

- (a) There is a break in the range of the *subquadratus/ruber* group in widely separated parts of the world. This is more suitably explained by regarding the forms as constituting two lineages, rather than postulating unfavourable environment as an explanation for the break (cf. Bolli 1957).
- (b) *G. subquadratus* in the *G. fohsi robusta* zone in Trinidad and Jamaica, and in the *G. ruber* zone in Java, possesses two supplementary apertures at the base of the final chamber. When forms with a similar morphology reappear in late Miocene times, they at first possess a single supplementary aperture (text-fig. 3, 1a-3a). This parallels a similar development in the ancestral form of *G. subquadratus*, here considered to be *G. quadrilobatus altiaperturae*.
- (c) There is evidence to suggest that *G. ruber* in the Uppermost Miocene of Jamaica was derived from a form similar to *G. obliquus* in gross morphology. *G. subquadratus* is thought to have developed from *G. quadrilobatus altiaperturae* (Bolli 1957).
- (d) Details of ontogeny are, with few exceptions, quite different in the two lineages.

CONCLUSIONS

An examination of forms previously regarded as belonging to the single species *Globigerinoides ruber* d'Orbigny from widely separated localities, representing its entire stratigraphic range, indicates the following:

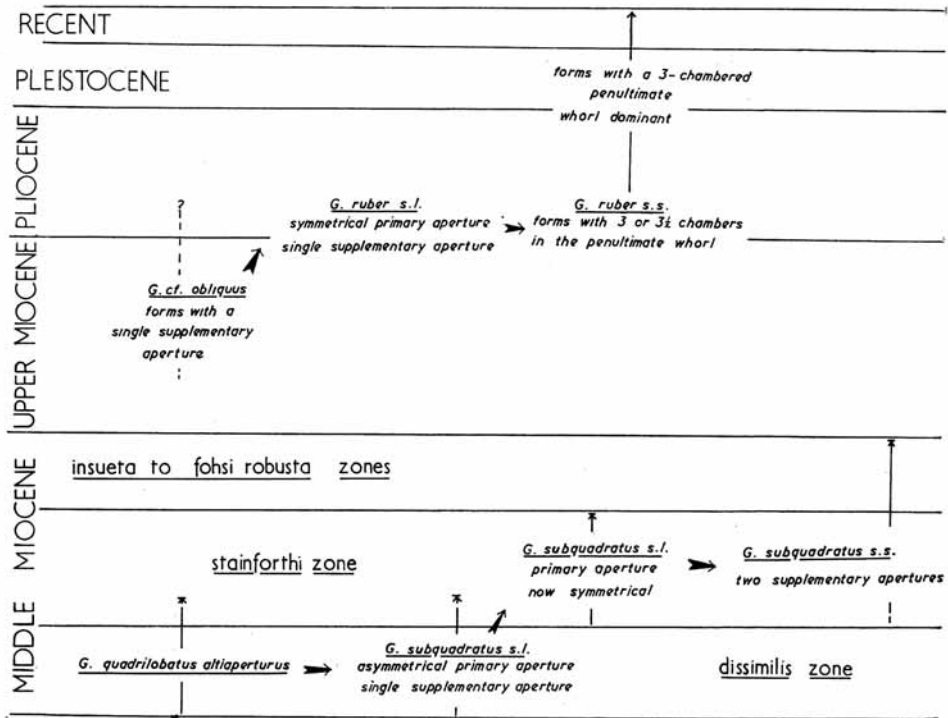
1. The existence of two unrelated lineages, one in the early to Middle Miocene, the other in the Uppermost Miocene (or basal Pliocene) to Recent.

2. Evidence from the *G. dissimilis* zone in Trinidad suggests that the ancestor of the early to Middle Miocene forms is *Globigerinoides quadrilobatus altiaperturae*, *G. subquadratus* s.s. occurring first in the succeeding zone of *G. stainforthi*. Specimens from the Uppermost Miocene San San Member, Bowden Formation, Jamaica, suggest that the younger lineage could have arisen from an ancestor similar in gross morphology to *Globigerinoides obliquus*. This is therefore an example of heterochronous homeomorphy.

3. It is proposed that the species name *Globigerinoides subquadratus* Bronnimann 1954 be used for the early to Middle Miocene forms and *Globigerinoides ruber* (d'Orbigny 1839) for the Uppermost Miocene (or Pliocene) to Recent forms.

4. An examination of the wall reveals a variation in structure, but this was not considered to be of stratigraphic importance, and there appears to be no significant difference in this respect between the two lineages.

5. Insufficient numbers of specimens at many levels prevent any definite statement as to the value of coiling ratios in the group as a whole. In specimens from the Cipero



TEXT-FIG. 5. Suggested phylogeny of *G. subquadratus* and *G. ruber*.

Formation the ratio of dextral to sinistral is not constant, whereas in the Pliocene–Pleistocene material from Jamaica and the Pacific Core CAP BP 38, the ratios were generally equally divided between the two directions of coiling.

6. *G. subquadratus* s.s. is considered to have its first occurrence in the *stainforthi* zone (cf. Bolli 1957), the *subquadratus*-like variants are included in *G. subquadratus* s.l., and these forms do not range above the *insueta* zone in Trinidad.

7. The forms described above have previously been regarded as a single long-ranging species, but it is suggested that this morphological group can be subdivided, and certain developmental trends have been noted. An alternative explanation to Bolli's (1957,

1966) view that these forms represent a single species (*G. ruber*) which is absent in the Middle–Upper Miocene owing primarily to environmental factors, is also put forward.

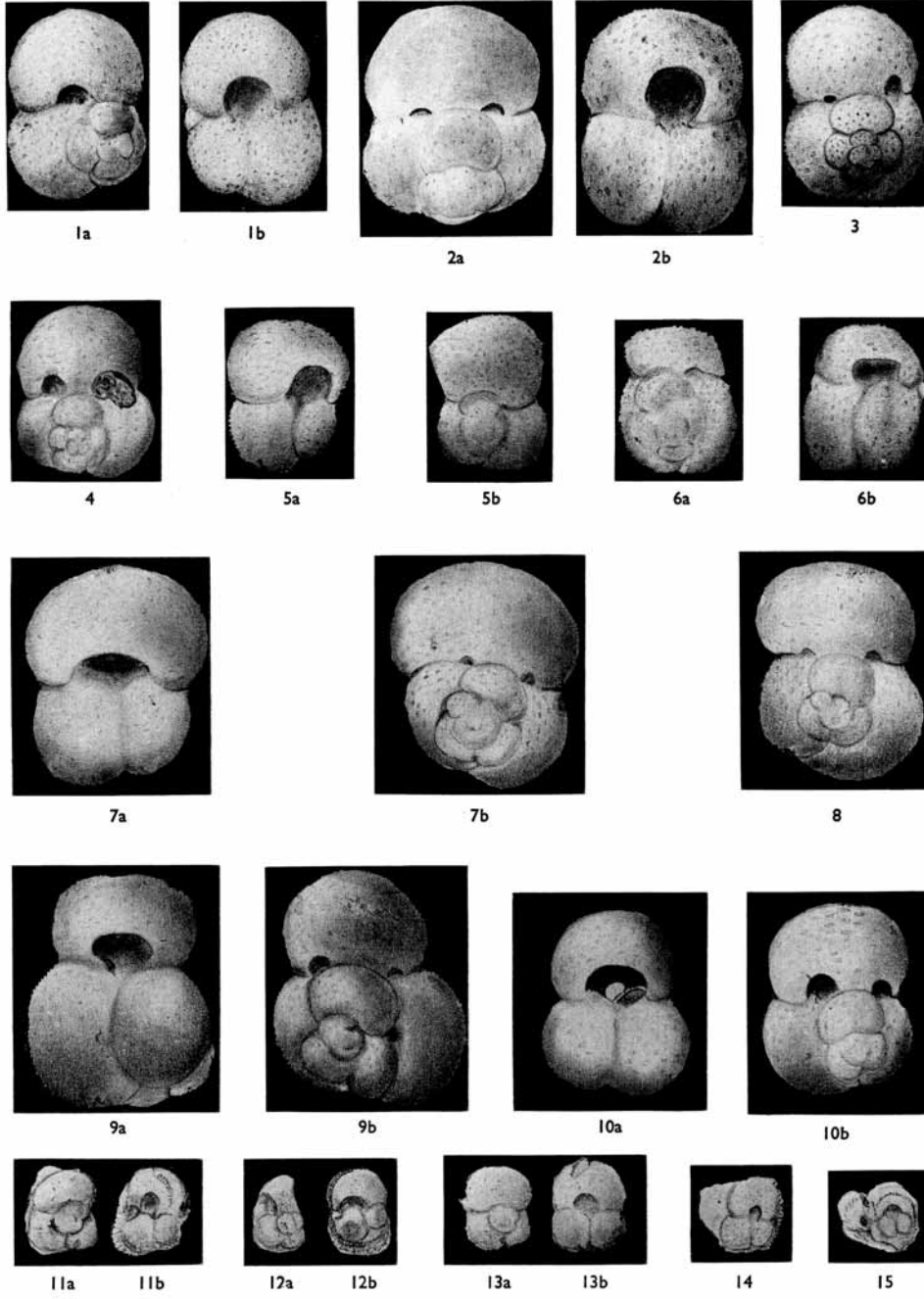
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