Phenotypic variation in *Gyroidinoides altiformis* (Stewart & Stewart) and *Gyroidinoides subangulatus* (Plummer) (Foraminifera).

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ABSTRACT - The morphological variation of two benthic foraminiferal species, *Gyroidinoides altiformis* (Stewart & Stewart) and *Gyroidinoides subangulatus* (Plummer), are described from Late Neogene - Quaternary, and Palaeogene sequences from northern Italy and Greece. A number of morphotypes, two for each species, are thought to be ecophenotypes. The inferred ecological (bathymetric) conditioning derives from: 1) comparable shape variations occur in species of very different ages; 2) both species exhibit the same morphological changes as a result of a comparable environmental trend.

INTRODUCTION

Foraminifera generally have excellent potential in environmental reconstructions. Palaeobathymetric estimates based on the preferential depths of selected taxa are commonly inferred from benthic foraminiferal populations and, less controllably, from planktonic foraminifera. The latter group is mainly used in the plankton/benthos ratio, allowing the assumption that there is a correspondence between the abundance of plankton and the depth of the water, as widely documented since Grimsdale & van Morkhoven (1955). Recently greater knowledge of major environmental changes allows the stratigraphical use (Ecostratigraphy) of isochronous environmentally defined units (Martinsson, 1973; Hoffman, 1980).

The bathymetric significance of selected fossil taxa is generally obtained by analogy with the ecological preferences of living cospecific populations. The method becomes increasingly unreliable as the age of the sediment increases. With relatively old sediments it is necessary to use fossil groups of higher taxonomic rank such as genera or, when possible, species having long stratigraphic ranges. According to Douglas (1979) distributional data on present-day populations should be adopted with caution in sediments older than the Oligocene. Bathymetric migration caused by general increase or decrease of sea floor temperatures may cast doubt on the validity of using depthrestricted taxa (Douglas 1973).

Considerable importance is attached to understanding morphological variation within bathymetric index taxa originating in depth changes (origin of clines and ecophenotypes).

The present paper takes into consideration the ecologically controlled morphotypes developed in different time intervals and different geographical areas by two *Gyroidinoides* species: the Neogene - Quaternary *G. altiformis* (Stewart & Stewart) and the Palaeogene *G. subangulatus* (Plummer). These two species show morphological affinities with each other and both develop depth-related morphotypes. The purpose of this study is to document the convergence towards similar morphologies by both species as a result of comparable palaeobathymetric variations.

MATERIAL STUDIED

The provenance of the material studied (Fig. 1) is from one Palaeogene and six Late Neogene - Quaternary sequences of the eastern part of the subsurface Po Valley, in northern Italy. Two surface sections of the Oligocene Eptahorion Formation of northern Greece have also been examined, one located on the northern side of the Thessalia Plain (Meteora region), the second in the type area of the formation, close to the village of Eptahorion.

Neogene-Quaternary

The large number of gas wells drilled in the eastern Po Valley



Fig. 1. Location of the sequences studied: 1. Vicenza 1 well, Veneto Plain, northern Italy; 2. gas wells of the eastern Po Plain, northern Italy; 3. Eptahorion area, and 4. Meteora area, northern Greece.

provides a considerable number of thick and highly fossiliferous Pliocene and Pleistocene sequences (the youngest foredeep sequence of the Appenine orogenic belt). The Pleistocene marine interval represents a depositional cycle (Ricci Lucchi *et al.*, 1982), ending with a significant shallowing. The presence of such a widespread regressive sequence allows the possibility of using the disappearance of selected benthic foraminiferal taxa (Fig. 2) to calibrate the palaeobathymetric position of the *Gyroidinoides altiformis* group with respect to other significant taxa. Most of the samples used come from ditch cuttings, with minor amounts from bottom hole and side wall cores. The six boreholes considered in the present study have the following coordinates:

LatitudeLongitude

12° 00.50' E44° 29.10' N 11° 56.47' E44° 25.11' N 11° 54.16' E44° 26.01' N 11° 51.24' E44° 25.26' N 10° 13.19' E44° 55.53' N 10° 11.22' E44° 53.05' N

Palaeogene

The Late Eocene sequence, mainly marls and sandy shales of the geothermic Vicenza 1 well (latitude 11° 33.12'E, longitude 45° 33.53' N) is located in the subsurface of the Veneto Plain, northern Italy. This sequence is the stratigraphical equivalent of the Priabonian marls cropping out in Lessini and in the Colli Berici (Vincentin, northern Italy), where they are well known for their abundant microfaunal content (Setiawan, 1983). The Greek material comes from the type area of the Early Oligocene Eptahorion Marls (Brunn, 1956), a lithostratigraphic unit which consists mainly of laminated shales with a few sandstone interbeds. This unit occurs widely in northern Greece. In the Meteora area (Kalampaka) only the uppermost part of the sequence, lithologically and chronologically equivalent with the Eptahorian Marls, has been considered; it is overlain by the thick deltaic deposits of the Meteora conglomerates (Ori & Roveri, 1987). In both the Italian and Greek Late Palaeogene sequences, comparisons were made between their faunal content and the distribution of the Gyroidinoides subangulatus morphotypes.

GYROIDINOIDES ALTIFORMIS GROUP

Gyroidinoides altiformis is defined as an isobathyal species. Bandy & Chierici (1966) indicated the same upper depth limits in the Mediterranean, off southern California and in the Gulf of Mexico. The taxon provides a reliable bathymetric control to identify the upper limit of the epibathyal zone. Fig.2 shows the last occurrences of the *G. altiformis* group and of several other taxa from the boreholes of the eastern Po Plain. These benthic foraminiferal species and genera were chosen because of the relative stability in their known water-depth distribution. For the Po Plain and northern Adriatic area at least, they seem to exhibit valid upper depth limits. Because of the possibility of



Fig. 2. Ecologic last occurrences of selected benthic foraminiferal taxa during the Late Neogene-Quaternary final regressive cycle of the eastern Po Basin subsurface, northern Italy. Data from six gas wells. Bathymetric zones are according to Wright (1978).

included dirupta and mediterranea.

** Included stellatus and umbonatus ..

contamination, which may add to the masking effect of originally displaced faunas, the upper depth limits are particularly useful in the micropalaeontologic analyses of wells, i.e. using first appearances down-hole. General bathymetric subdivisions may be difficult to determine for faunas studied only through well cuttings because of the effects of biofacies mixtures. In order to have more reliable data, the upper depth limits of many species have not been taken into consideration when they are represented by only one or scattered specimens. Taxa listed in Fig. 2 appear useful because of their relative abundance and continuous records. Supplementary bathymetric information from species frequently reported by workers, such as the epibathyal buliminids (Bulimina buchiana and B. striata) were taken into account but not listed due to their sporadic occurrence. The G. altiformis group exhibits the characteristics of all useful bathymetric index species: 1) it has a wide stratigraphic range; 2) it frequently occurs in living and fossil assemblages; 3) it is easily identifiable; 4) it is isobathyal.

The environmentally related shape variation in the G. altiformis group leads to the development of two ecophenotypes: G. altiformis acutus and G. altiformis altiformis. Pflum & Frerichs (1976) described the cline and the bathymetric meaning of the group in the Gulf of Mexico. G. altiformis acutus has a narrower umbilicus than the commoner G. altiformis altiformis and lacks the radially arranged shell material deposits on the umbilical shoulders. Moreover, the umbilical side exhibits a more sharply conical development (Pl.1, figs 1-2). The subsurface sequences studied here from the Po Valley provide populations with an absolute predominance of *G. altiformis altiformis*. The *acutus* morphotype is restricted to the lower part of the sequence representing the lower epibathyal zone, corresponding on a regional level to the time of the deepest environments developed in the Po Basin during the Late Neogene and Quaternary.

There are no intermediate morphologies between the *altiformis* and *acutus* morphotypes. Records of G. *altiformis acutus* hardly exist in previous works on recent and fossil material; this may be due to its rare occurrence, so it is probably best placed under the heading of G. *altiformis sensu lato*.

The Late Pliocene and Pleistocene palaeoenvironmental history of the Po Basin seems to exhibit a stable bathymetric evolution. The major changes in the distribution of the benthic foraminiferal faunas are correlated with decreasing depth during the regressive phase of the Early Pleistocene. This is the reason, furthermore, for the numerical abundance of *G. altiformis*, which is a frequent but never abundant taxon, as it seems to appear in water depths greater than 800m (Wright, 1978). No special facies characteristics are involved; *G. altiformis* is as frequent with clastic substrates as it is with carbonate ones (Pflum & Frerichs, 1976), and the Po Basin lithofacies was always siliciclastic.

GYROIDINOIDES SUBANGULATUS GROUP

This taxon exhibits a wide stratigraphic range and a cosmopolitan distribution, being reported from uppermost Maastrichtian, Palaeocene, Eocene and Oligocene assemblages worldwide (northern Sinai, Said & Kenawy, 1956; New Jersey Coast Plain, Ollson, 1960; Midway-type faunas, worldwide, Berggren & Aubert, 1975 and Aubert & Berggren, 1976; southern Atlantic, Proto Decima & Bolli, 1978; northern Tunisia, Keller, 1988). This is to be expected, taking into account the widespread palaeogeographic distribution of benthic and planktonic foraminiferal populations during the Palaeogene, particularly between the Tethyan and Atlantic regions. According to Berggren & Aubert (1975), this was due to the North Equatorial current and Gulf Stream.

From the literature quoted above the species seems to have preferred epibathyal to neritic conditions, with a relatively wide distribution within this palaeobathymetric interval. There does not appear to be any latitudinal differentiation. There is some connection between facies and species occurrence; the taxon is typical of shaly-marl lithofacies and when the ecology and the age are correct, as in the case of the Palaeocene Midway Group in the Gulf Coastal Plain, it forms a typical and persistent faunal element. On the other hand *G. subangulatus* is absent, for instance, in the calcareous Apollonia Formation, a richly fossiliferous unit outcropping in Cyrenaica (Libya). This is Late Palaeocene to Eocene in age (Barr & Berggren, 1980; Bellini & Duronio, 1984), but the epibathyal to outer neritic water depth of this formation of carbonate facies seems to have been unsuitable for this species.

It is possible to separate two distinct groups of specimens within the population of G. subangulatus, named here G. subangulatus Form 1 and Form 2 (Pl 1, figs 5-7 and 8-10 respectively), each of them easily identifiable. G. subangulatus Form 1 strictly corresponds to the type figures of Plummer's species; it differs from Form 2 in having a wider umbilicus and less umbilical convexity, associated with a considerably more conico-truncate shape. The ecological control on the morphotypes (ecophenotypes) is documented by their distribution in the studied sediments. In the middle-upper part of the Eptahorion Formation, a dominantly upper epibathyal sequence, G. subangulatus Form 2 constantly occurs with a considerable number of specimens per sample. The morphotype typifies the foraminiferal assemblage in this interval, together with other epibathyal taxa such as costate uvigerinids, Bulimina rostrata and several species of Melonis. In contrast, high relative abundances and persistent recordings of Form 1 have been noted in the regressive Meteora sediments. Within these deposits taxa which frequently occur suggest inner shelf conditions; taxa include abundant arenaceous foraminifera and several miliolids. Typical specimens of Form 1 also characterize the upper Eocene marls of well Vicenza 1, where a diverse assemblage with high frequencies of Almaena epistominoides and other relatively shallow water taxa has been identified (Fig. 3). G. subangultus Form 1 is the dominant gyroidinoid species. The lack of any evident mixture of the two morphotypes in the overall faunal composition is ascribed to the sharp difference between the relatively deep and shallow water associations recovered in the studied material.



Fig. 3. Comparison of characteristic foraminiferal taxa and estimated water depth of deposition in the Palaeogene sequences.

DISCUSSION AND CONCLUSIONS

The studied material provides further support for the origin of the G. altiformis cline and the distribution of the ecophenotypes in the palaeobathymetric zones. This has already been described elsewhere, as mentioned previously. One outstanding difference separates the faunas of the Gulf of Mexico from those of northern Italy. The upper depth limit of G. altiformis acutus in the former area is around 1000m (top of upper mezobathyal), while in Italy it appears to be 500-700m (top of lower epibathyal). This can probably be accounted for by differences in water circulation and temperature. If the records are explained by palaeoenvironmental changes the phenomenon of bathymetric migration could be expected. It is widely agreed that a significant cooling trend took place in the Mediterranean starting in the Late Pliocene (c. 2.5 MYBP) (Thunell & Williams, 1983, cum. bibl.). During such an event a gradual bathymetric shift of the benthic populations into shallower conditions could have been a reasonable response to changing bottom conditions. If the most frequently reported convergences of similar morphologies between two foraminiferal plexus have been documented as evolutionary, it is plausible to assume an ecological control when it occurs: 1) at different times; 2) in different geographical areas; 3) is correlated with the same environmental trends; 4) involves unrelated taxa.

Some morphological tendencies, recurring in time, have been reported. Grunig (1984) clearly documented the general trend of some species of carinate Spiroplectammina to develop noncarinate morphovariants with decreasing water depth. The ecological dependence of this trend is proved by its reiterative occurrence in diachronous taxonomic groups, from Middle Eocene to Miocene, in both regressive and transgressive sequences, involving geographical areas considerably distant from each other. Another example comes from the costate uvigerinids which are an excellent depth indicator group. Grunig (1984) and Sztrakos (1983) provided reliable documentation from Eocene (Uvigerina eocaena) and Oligocene (Uvigerina cocoaensis and U. gallowayi) species exhibiting surface sculpture consisting of strong costae. All these species seem to develop unribbed morphovariants with decreasing depth.

Comparison of depth/distribution-morphology of the investigated *Gyroidinoides* reveals that their morphovarieties are independent of species level taxonomy. Some morphological trends, namely the development of a wider umbilical area provided with thicker shell material deposits and a less conical ventral side (G. altiformis altiformis and G. subangulatus Form 1), tend to correlate with shallowing water depths (neritic). In contrast, the morphotypes developing a more tightly coiled and conical ventral side (G. altiformis acutus and G.subangulatus Form 2) are discovered in deeper water (epibathyal). Both observations satisfy the four conditions previously related, which suggest an ecological control.

SYSTEMATICS

Gyroidinoides altiformis acutus (Boomgaart), 1949 (Plate 1, figs 1-2)

1949 Gyroidina neosoldanii Brotzen var. acuta Boomgaart: 125, pl.14, figs 1a-c (fide Ellis & Messina, 1940 et seq.).

1976 Gyroidina altiformis acuta Boomgart, Pflum & Frerichs: pl.4, figs 8, 9, pl.5, fig. 1.

1984 Gyroidina altiformis Stewart & Stewart, Ross & Kennett: pl.3, fig.11.

Gyroidinoides altiformis altiformis (Stewart & Stewart), 1930 (Plate 1, figs 3-4)

1930 Gyroidina soldanii d'Orbigny var. altiformis Stewart & Stewart: 67, pl.9, figs 2a-c.

1949 Gyroidina cushmani Boomgaart: 124, pl.9, figs 9a-c (fide Ellis & Messina, 1940 et seq.).

1957 Gyroidina longispira Tedeschi & Zanmatti var. miocenica Tedeschi & Zanmatti: 254, figs 8a-c.

1976 Gyroidina altiformis cushmani Boomgaart, Pflum & Frerichs: pl.5, figs 2, 3, 4.

1984 Gyroidina altiformis Stewart & Stewart, Ross & Kennett: pl.3, figs 12-13.

Gyroidinoides subangulatus (Plummer), 1927 Form 1 (Plate 1, figs 5-7)

1927 Rotalia soldanii (d'Orbigny) var. subangulatus Plummer: 154, pl.12, fig.1.

1960 Gyroidinoides subangulata (Plummer), Ollson: 36, pl.5, figs 24, 25.

1975 Gyroidinoides subangulata (Plummer), Berggren & Aubert: 148-149, pl.3, figs 2a-c, pl.9, fig.7, pl.10, fig.3, pl.11, fig.5.

Explanation of Plate 1

All Fig.s are X112

Figs 1-2 Gyroidinoides altiformis acutus (Boomgaart). Ventral and peripheral views. Pleistocene, eastern Po Basin subsurface (northern Italy). Figs 3-4 Gyroidinoides altiformis altiformis (Stewart & Stewart). Ventral and peripheral views. Pleistocene, eastern Po Basin subsuface (northern Italy). Italy).

Figs 5-7 *Gyroidinoides subangulatus* (Plummer) Form 1. Dorsal, peripheral and ventral views. Early Oligocene, uppermost Eptahorion Marls equivalent, Kalampaka, Meteora region (northern Greece).

Figs 8-10 Gyroidinoides subangulatus (Plummer) Form 2. Dorsal, peripheral and ventral views. Early Oligocene, Eptahorion Marls, type area (northern Greece).



Gyroidinoides subangulatus (Plummer), 1927 Form 2 (Plate 1, figs 8-10)

1954 *Gyroidinoides altiformis* (Stewart & Stewart), Beckmann: 381-382, pl.23, fig.22.

1956 Gyroidina subangulata (Plummer), Said & Kenawy: 149, pl.5, figs 9a-c.

1978 Gyroidinoides subangulatus (Plummer), Proto Decima & Bolli: 794, pl.4, fig.12.

1988 Gyroidinoides subangulatus (Plummer), Keller: pl.2, figs 1-4.

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