

Zeitschrift: Eclogae Geologicae Helvetiae
Herausgeber: Schweizerische Geologische Gesellschaft
Band: 96 (2003)
Heft: 2

Artikel: Palaeobiogeography of the Middle Jurassic protoglobigerinids (Foraminifera)
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DOI: <https://doi.org/10.5169/seals-169018>

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Palaeobiogeography of the Middle Jurassic protoglobigerinids (Foraminifera)

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Key words: Palaeobiogeography, Middle Jurassic, planktonic foraminifera, protoglobigerinids, Tethys.

Mots clés: Paléobiogéographie, Jurassique moyen, foraminifères planctoniques, protoglobigérines, Téthys.

ABSTRACT

The palaeogeographical distribution of the Middle Jurassic protoglobigerinids is discussed using three maps, which correspond to the Aaleno–Bajocian, Bathonian and Callovian intervals. During these intervals small, thin-walled species are found in epicontinental areas, as well as in the Tethys, while the large, occasionally thick-walled taxa were restricted to the Tethyan area. In the Callovian large forms could migrate into the deeper basins of the epicontinental area. In the Aaleno–Bajocian the thick wall of some tests may represent a crust (late stage calcification) because protoglobigerinids with the same external morphology, but different wall thickness, can be found in the Bajocian and the Bathonian. This phenomenon is generally interpreted as a deep water character in planktonic foraminifera. Some taxonomic problems related to morphology are also discussed.

RESUME

La distribution paléogéographique des protoglobigérines au Jurassique moyen est donnée sur trois cartes, correspondant à l'Aaléno-Bajocien, au Bathonien et au Callovien. Durant cette période, les petites espèces à paroi mince se trouvent en domaine épicontinental, aussi bien qu'en Téthys, alors que les grandes espèces, quelquefois à paroi épaisse, sont restreintes à la Téthys. Au Callovien les grandes formes migrent dans les bassins plus profonds du domaine épicontinental. A l'Aaléno-Bajocien l'épaississement des parois de certains test pourrait correspondre à une croûte car on retrouve dans le Bathonien des espèces de même morphologie générale mais avec des parois plus minces. Ce phénomène est interprétée généralement comme un caractère d'eau profonde chez les foraminifères planctoniques. Quelques problèmes taxonomiques en relation avec la morphologie sont aussi discutés.

I. Introduction

The Jurassic protoglobigerinids and other *Globigerina*-like foraminifera have been known for a long time as isolated specimens or in rock thin sections, but they still raise several morphological and taxonomic problems. They are interesting as they assist in the understanding of the phyletic evolution of the Cretaceous plankton but there is also a need to identify the origin of the first planktonic foraminifera and study the morphological changes associated with the benthic-planktonic transition.

Reports of isolated forms are relatively scarce and the taxa are often poorly illustrated. Banner & Desai (1988) proposed a systematics and Simmons et al. (1997) have reviewed and re-illustrated, by means of SEM, many of the species described in the literature. Gorbachik & Kuznetsova (1998) have also reviewed the systematics and nomenclature of the early planktonic taxa. While recognising the value of these compilations, we do not want to sit in judgement of these systematic schemes because we consider that the palaeontological record is still too limited.

The record and illustrations of protoglobigerinids in rock thin sections are much more common, particularly in the Middle and Late Jurassic. These individuals can be particularly abundant in “ammonitico rosso” facies, where they appear as blooms, but unfortunately their identification remains very difficult. Giovagnoli & Schiavinotto (1986, 1987a, b, 1991) and Wernli (1988), comparing Bajocian and Kimmeridgian associations of undetermined sections, showed that large tests characterise the Bajocian and smaller-sized tests the Kimmeridgian. However, the occurrence of giant species in the Aaleno–Bathonian (Giovagnoli & Schiavinotto 1986, 1987a, b, 1991; Wernli 1987; Wernli & Görög 1999, 2000) so early in the stratigraphic record is difficult to integrate into a classical evolutionary trend, where small forms generally precede large ones. Moreover, some of these large species have a characteristic thick wall in the Aaleno–Bajocian. We have extracted tests from samples of hard “ammonitico rosso” limestones by means of acetolysis, and so determined the species (Wernli & Görög 1999; Görög & Wernli 2002). We have also made oriented thin sections of these isolated tests and presented a cor-

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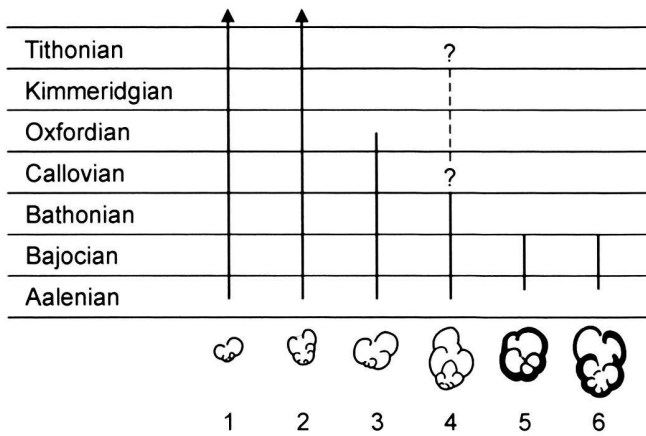


Fig. 1. Stratigraphical distribution of protoglobigerinid morphotypes. 1. Small, thin-walled, low trochospired; 2. Small, thin-walled, high trochospired; 3. Large, thin-walled, low trochospired; 4. Large, thin-walled, high trochospired; 5. Large, thick-walled, low trochospired; 6. Large, thick-walled, high trochospired.

pus of these, in order that they can be used for the identification of protoglobigerinids in rock thin sections (Wernli & Görög 2000). On the basis of the external morphology we have found a very similar protoglobigerinid association in the Bajocian (Wernli & Görög 1999) and in the Bathonian (Görög & Wernli 2002). However, the thin sections reveal that the same large species have a thick-walled test in the Bajocian and a thin-walled test in the Bathonian. This is summarised in figure 1. We have recently (Görög & Wernli 2002) discussed this problem and suggest that it could indicate a palaeoceanographical control. The aim of this paper is to support this issue and comment on some of the taxonomic implications of this interpretation that can serve as a guide for further research.

II. Taxonomic problems

The tests of the Jurassic protoglobigerinids have a rather simple morphology with few discriminating characters. The intra- and inter-specific variability is great. In this respect these foraminifera pose the same problems as the simple Tertiary “*Globigerina*” (*Subbotina*), about which we know that few of them are good stratigraphic markers. A good illustration of this problem can be found, for example, in the discussion of the “*Globigerina*” *linaperta* group of the Late Eocene-Oligocene presented in Stainforth et al. (1975).

The principal morphological characters of the Jurassic protoglobigerinids are:

- 1) The wall (mineralogy, texture, etc.);
- 2) The sculpture of the test surface;
- 3) The construction of the test (consecutive versus concurrent);
- 4) The number of chambers in each of the whorls (problem of bulla);

- 5) The form and the position of the primary aperture; and
- 6) The juvenile stage and ontogeny.

For the majority of the species described in the literature (apart from *Globuligerina oxfordiana* (GRIGELIS) and *G. bathoniana* (PAZDROWA)) the characters listed above are not adequately covered.

1). The wall of the Jurassic protoglobigerinids was almost certainly aragonitic (Premoli Silva 1966; Gorbachik & Kuznetsova 1986; Gorbachik & Kozłowa 1987; BouDagher-Fadel et al. 1997), but it is almost always altered through diagenesis to sparry calcite. In rock thin sections it always appears the same as the other well-known aragonitic fossils such as ammonites, gastropods, epistominids and involutinids (Wernli 1987). The fine perforations of the original wall have been clearly demonstrated (see, for example, Pazdrowa 1969; Brönnimann & Wernli 1971, Gorbachik 1983; Riegraf 1987b). Following the classification of Loeblich & Tappan (1964, 1987) the mineralogy and crystallography of the wall is of considerable taxonomic value. The aragonitic protoglobigerinids (Favusellidae) should, therefore, be totally separated from the Suborder Globigerinina, which is defined as having a calcitic wall. For the moment it might be better to emend the definition of this suborder to include both calcitic and aragonitic walls as proposed by BouDagher-Fadel et al. (1997). In that case this suborder would be monophyletic.

2). The sculpture of the test surface appears to be one of the best taxonomic characters. It is now widely recognised as a fundamental criterion for the Late Cretaceous and the Tertiary Globigerinina at a supra-generic level. Alekseeva & Gorbachik (1981) have proposed an evolutionary lineage of Jurassic-Early Cretaceous protoglobigerinids based on this character. This lineage starts with irregular, rounded or worm-like pseudomuricae in *G. bathoniana*. Later the worm-like muricae fuse into a small irregular meshwork i.e. at *Conoglobigerina gulekshensis* (GORBACHIK & POROSHINA) and finally evolves into a honey-comb meshwork in *Favusella washitensis* (CARSEY), the end-member of the lineage. In our opinion the most representative species of this lineage are, respectively, *G. oxfordiana*, *F. hoterivica* (SUBBOTINA) and *F. washitensis*, because we lack convincing illustrations of the other protoglobigerinids. Let us recall that the first, complete, honey-comb stage appeared in *F. hoterivica* which is already in the Berriasian (Wernli et al. 1995).

3). The construction of the test is a fundamental taxonomic criterion at the suborder level in the systematics of Loeblich & Tappan (1988). The Suborder Globigerinina is defined as having “secondary laminations due to addition of shell material during formation of new chamber” (Loeblich & Tappan 1988, p. 452).

There is very little information on the construction of the test in Jurassic protoglobigerinids. Pazdrowa (1969, p. 45, pl. 2,

Fig. 9) shows that *G. bathoniana* has a concurrently built test. Gorbachik (1983), in a study of *G. oxfordiana*, established that “the wall is primarily double layered, secondarily multi-layered”. Despite the addition of these layers, the wall remains relatively thin and does not exceed 11µm (see Premoli Silva 1966; Pazdrowa 1969; Brönnimann & Wernli 1971). However, the study of Jurassic protoglobigerinids in sections clearly shows that some species have a thick-walled test, where the septa remains thin, but the thickness of the external wall on the juvenile whorls attains 40µm (Giovagnoli & Schiavinotto 1986, 1987a, b, 1991; Wernli 1988; Wernli & Görög 2000).

In our previous work (Görög & Wernli 2002) we compared the protoglobigerinids of the Bathonian Gyenespuszta section and of the Bajocian Som Hill section, Bakony Mts, Hungary. Both assemblages are from similar indurated “ammonitico rosso” limestones. On the basis of this comparison and of an unpublished study of the Bajocian part of the Gyenespuszta section, we have established that the large thick-walled species are restricted to the Aaleno-Bajocian, as we previously suggested (Wernli & Görög 2000). This observation appears to be confirmed by the inventory of the literature presented in Table 1.

By means of acetolysis we have isolated specimens and confirmed that *Conoglobigerina? avariformis* KASIMOVA has a thick wall in the Bajocian (Wernli & Görög 1999) and a thin wall in the Bathonian (Görög & Wernli 2002). We previously indicated (Wernli & Görög 2000, Görög & Wernli 2002) that this was the result of the construction of the test (consecutive versus concurrent *sensu* Blow 1979). In the light of our new results, mentioned above, it is most probable that all Middle Jurassic species have a concurrently built test and the over-thickening of some specimens is the result of the presence of a crust (“late stage calcification” of Blow 1979). This feature is well known in Recent planktonic species and links to the deep-water mode of life (e.g., Bé & Lott 1964). From this it would appear logical that the Bajocian *C.? avariformis* lived in deeper water than those in the Bathonian.

4). The number of chambers by whorls is a relatively objective character, but it is mostly used in connection with the final whorl. As a large number of protoglobigerinids have a final senile chamber or a bulla-like chamber (more or less shifted into an umbilical position and difficult to differentiate from a true chamber), this character sometimes remains ambiguous (Wernli *et al.* 1995; Wernli & Görög 1999). The number of chambers in the first whorl will be discussed later.

5). The form and the position of the aperture are clear only in *Globuligerina oxfordiana* and *G. bathoniana*. This type of aperture, sometimes called “bulimine”, “virguline” or, correctly speaking, “globuligerine”, is an asymmetrical, higher than wide arch with an anterior (distal) out-going lip and a re-entering posterior (proximal) lip. Its position is not strictly umbilical, but slightly shifted distally, giving place to a dimple (fossa) in an umbilical position. This kind of aperture resem-

bles, at least seen from the exterior, that of the Late Cretaceous *Guembeltria cretacea* CUSHMAN, or *Chiloguembelina*, *Streptochilus* and *Woodringina* of the Palaeogene (for example). This opening defines the genus *Globuligerina* BIGNOT & GUYADER. The genus *Conoglobigerina* MOROZOVA is distinguished by a small, low arched and umbilically positioned aperture. This last criterion is still not clear, because this type of aperture has never been well illustrated, and possibly could be an infralaminar aperture of a bulla (Görög & Wernli 2002).

6). Juvenile stage and ontogeny. The importance of the number of chambers in the first whorl has been identified by Morozova & Moskalenko (1961). They described a feature known as “generational dimorphism”, with microspheric forms differing from the megalospheric forms in having a larger test and a rounded blunt juvenile stage. However, the juvenile ontogeny is difficult to decipher, because of the small size of the tests. Making oriented thin sections is technically difficult and SEM examination is not always conclusive. On the other hand, generational dimorphs have never been detected in Cretaceous and Cenozoic planktonic foraminifera. Because of these facts we attempt to use the trochospira of U versus V types, which is an easily discernible character on the external gross morphology (Görög & Wernli 2002). In the V type the trochospira follows a regular cone of α angle giving a pointed test, whereas in the U type it begins with large α angle followed by more acute β angle, giving a rounded test apex. The U versus V types, therefore, are determined by the shape of the juvenile stage. We found that there is a link between the U or V type trochospira and low or high trochospira. A better knowledge of the juvenile stage can also provide information about possible ancestors.

III. Palaeogeographical distribution of Middle Jurassic protoglobigerinids

In order to discuss the palaeogeographical distribution of the Middle Jurassic protoglobigerinid assemblages the records from adopted publications are listed in Table 1 and the data used to construct the three maps shown in figures 2-4.

We only used papers with acceptable illustrations of protoglobigerinids or where there were adequate descriptions of the species. For example, Tamajo (1960) was one of the first to illustrate protoglobigerinids in thin section, but his figures from the Middle Jurassic are not suitable for the purpose of our research. As the majority of records concern specimens in thin section the characters selected are those which can be recognised both on isolated forms and in thin section. In the thin sections approximate determinations have been made with the help of our previous work (Wernli & Görög 2000). We have used objective characters, such as the size of the test, wall thickness and abundance, which can characterise the average features of faunas, without detailed species composition, and without becoming involved with taxonomic problems.

Tab. 1. List of data numbered on the palaeogeographical maps (Figures 2-4). For explanation of symbols see text.

	Locality	Reference	Thin section (T) or isolated (I)	Size: small (S), middle (M), large (L)	Wall thickness, thick=TK, thin=TN	Abundance	Age	Tethyan association=TA
1	Scotian Shelf, Canada	Ascoli 1976	I	S-M	?	2	Bathonian-Callovian	
2	Canada, Grand Banks	Gradstein 1976, 1978, 1979	I	S	?	2	Bajocian-Callovian	
2	Canada, Grand Banks	Stam 1986	I	S	?	2	Bajocian-Oxfordian	
3	Rif, Morocco	Wernli 1987	T	L+M	TK	3	Late Bajocian	TA
4	Mid Atlas, Morocco	Brun 1969	T, not figured	?	?	?	Bajocian	
5	Brenha, Mareta Beach, Trojeira and Montejunto, Portugal	Stam 1986	I	S	?	1	Bajocian-Oxfordian	
6	Mallorca, Spain	Colom 1967	T	S	TK	2	Bajocian	
6	Mallorca, Spain	Colom 1975	T	S	TK?	3	Bathonian	
7	Cantabrian Mts, Spain	Perconig 1968	T	S	TN	2	Bathonian	
8	Ebro Basin, Iberian Range	Perconig 1968	T	S	TN	2	Bajocian	
9	Calvados, France	Bignot & Janin 1984	T+I	S	TN	1	Bajocian	
10	Jura Mts, France	Brönnimann & Wernli 1971	T+I	S	TN	1	Bajocian-Bathonian	
10	Jura Mts, France	Ecoffey 1994	T+I	L	TN	2	Callovian	
11	North Tunisia	Bismuth et al. 1967	T, not figured	L?	TN	1	Late Bathonian- Callovian	
12	NE Sicily	Sirna 1962	T	L	TN	3	Callovian	
12	Kumeta Mts, Sicily	Görög unpublished	T+I	L	TK, TN	3	Bajocian, Bathonian	TA
13	NE Sicily	Gianotti 1958	T, not figured	S	TN	3	Bajocian? -Bathonian	
14	Trento Plateau, Italy	Cita 1965; Martire 1996	T	L	TK	3	Bajocian-Bathonian	TA
14	Western Feltrino, Trento Plateau, Italy	Bosellini & Dal Cin 1968	T	L	TK	3	Bajocian-Bathonian	TA
14	M. Verzegnis-Colle dei Larici-M., North-eastern Italy	Gnaccolini & Martinis 1974	T	L	TK	3	Bajocian? fissure infilling	TA
14	Brescia, Italy	Zanmatti Scarpa 1957	T	S	TN	1	Dogger?	
14	Romagna, Marche, Italy	AGIP Mineraria 1959; Sartorio & Venturini 1988	T	L	TN	3	Callovian-Oxfordian	
15	Umbrian-Marchean Appenines, Italy	Giovagnoli & Schiavinotto 1986, 1987a, b, 1991	T	L+M	TK	3	Bajocian	TA
16	Thören and Hildesheim, NW Germany	Bartenstein & Brand 1937	I	L	?	1	Callovian	
17	Frankonian Alb, Germany	Munk 1978, 1997	I, moulds	L	?	1, 3	Callovian	
18	SW Germany	Riegraf 1987a, b, 1988	I	L	?	3	Callovian	
19	Wolin, NW Poland	Bielecka & Styk 1981	I	S-M	?	1	Late Bathonian, Callovian	
20	Ogrodzieniec, Czestochowa region, Extra Carpathians, middle Poland	Pazdrowa 1969; Alekseeva & Gorbachik 1981; Stam 1986; Bielecka et al. 1988	T+I	S	TN	3	Bathonian	
20	Ogrodzieniec, Czestochowa region, Extra Carpathians, middle Poland	Fuchs 1973; Alekseeva & Gorbachik 1981	I, moulds	L	?	3	Late Callovian	
21	Tatra Mts, S Poland	Szulczewski 1963	T	S	TN	2	Bathonian	

Tab. 1 (contin.). List of data numbered on the palaeogeographical maps (Figures 2-4). For explanation of symbols see text.

	Locality	Reference	Thin section (T) or isolated (I)	Size: small (S), middle (M), large (L)	Wall thickness, thick=TK, thin=TN	Abundance	Age	Tethyan association=TA
22	Osternhorn Block, SE of Salzburg, Austria	Böhm 1992	T	S	TN	3	Callovian	
23	Close to Kufstein, Bavaria, SE Germany	Wendt 1969; Ebli 1997	T	L	?	3	Aalenian-Callovian	TA
24	Manin, Porazská Bystrica, Klippen Zone, western Carpathians, Slovakia	Borza 1969	T	S	TN	?	Callovian-Oxfordian	
25	Bakony Mts, Hungary	Wernli & Görög 1999, 2000	T+I	L+M	TK	3	Bajocian	TA
25	Bakony Mts, Hungary	Görög & Wernli 2000	T+I	L	TN	3	Bathonian	TA
25	Gerecse Mts, Hungary	Fülöp, 1975	T	L	TK	3	Bajocian	TA
26	Betlanovce, Vernár Belt; Geravy Strantenská hornatina Mts, Silicium, Slovakia	Rakús & Šykora 2001	T	L	TN	3	Callovian-Oxfordian	
27	Durmitor Basin, Dinarides, North Herzegovina	Radoičić 1966, 1996	T, mat. Wernli	L+M	TK	3	Late Bajocian	TA
28	Bucegi Mts, Romania	Neagu 1996	I	L+M	?	3	Callovian	
29	Turgovishte, Moesian Platform and Prebalkan, NE Bulgaria	Mihailova-Yovcheva & Trifonova 1967	I	S	?	3	Callovian	
30	NE Sinai, Egypt	Abd-Elshafy & Sallam 1994	I	?	?	1	Bathonian, Callovian	
31	Domuz Dag, Turkey	Wernli 1988	T	L	TK	3	Aalenian	TA
32	SE Crimea, Ukraine	Hofman 1958	I	S+M	?	?	Bathonian-Early Callovian	
33	Meganom, E Crimea, Ukraine	Kuznetsova & Uspenskaja 1980; Kuznetsova & Gorbachik 1985; Gorbachik 1986	I	S	?	?	Early Callovian	
34	Barakaevskaja area, NW Caucasus	Gorbachik 1986	I	S	?	?	Late Bajocian	
35	Near the villages Chokh and Gunib, Central Dagestan	Morozova & Moskalenko 1961; Gorbachik 1986	I	S	?	2	Bajocian-Bathonian	
36	Negramskoye gorge, Aras, River, Nakhichevan, Azerbaijan	Kasimova & Aliyeva 1984	I	L	?	?	Late Bajocian	
37	Gaurdak district, Turkmenia	Morozova & Moskalenko 1961	I	S	?	2	Bajocian, Callovian	
38	Arneh, Anti Lebanon; Coastal Mts; Bab Janneh, Syria	Kuznetsova et al. 1996	I	L	?	1	Bathonian	
38	Wadi al Karn and Jebel Shekif, Anti Lebanon; Bchili, Coastal Mts, Syria	Kuznetsova et al. 1996	I	L?	?	1	Callovian	
39	Saharian Atlas, Algeria	Sebane et al. 2002	I	S	?	2	Bajocian	

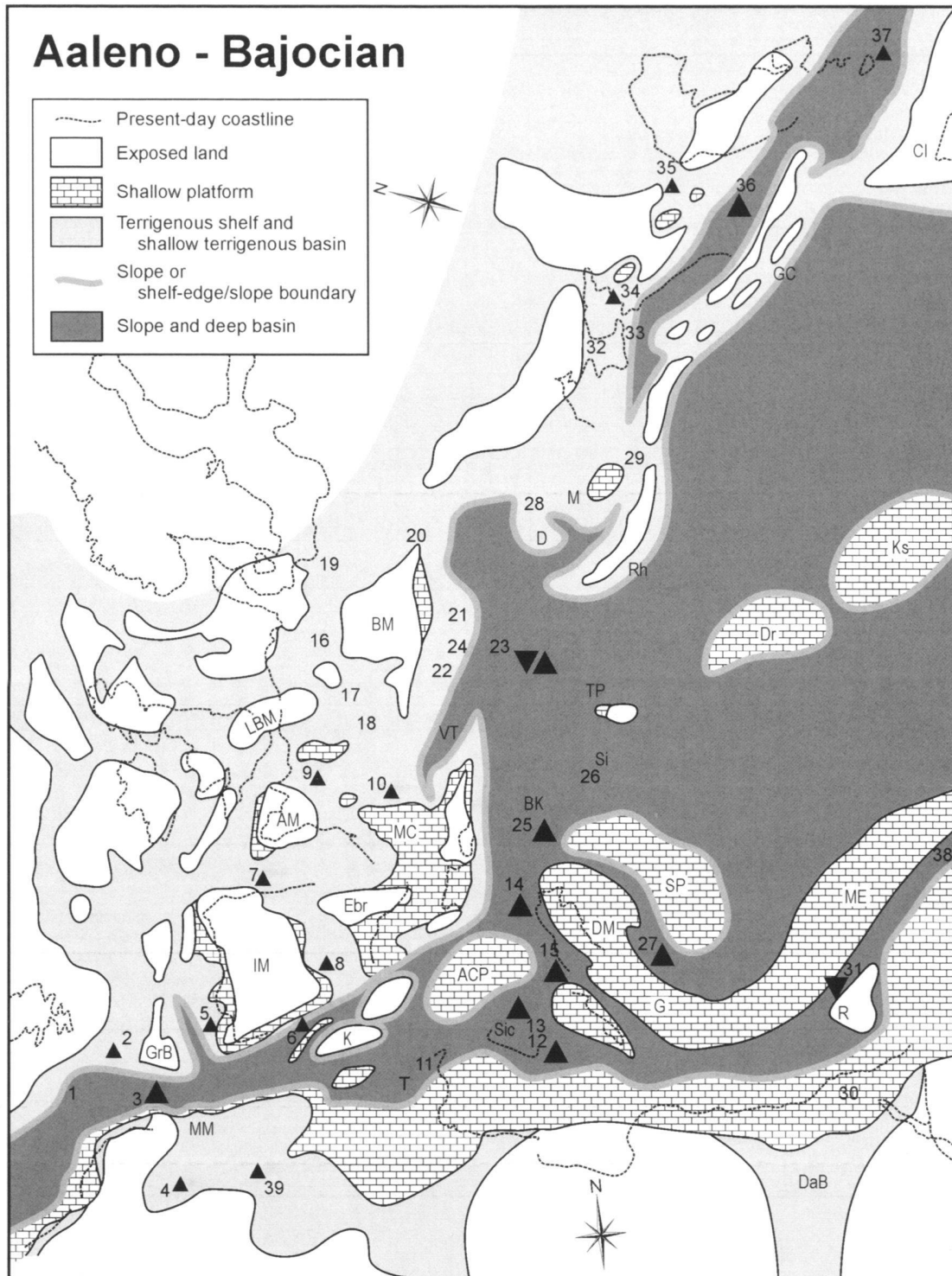


Fig. 2. Palaeogeographical distribution of the protoglobigerinids in the Aaleno-Bajocian. The numbers refer to the localities listed in Table 1.

ACP Apennine Carbonate Platform / AM Armorican Massif / BK Bakony / BM Bohemian Massif / CI Central Iran / D Danubian Zone / DaB Dakhla Basin / DM Dalmatia / Dr Drama / EM Ebro Massif / G Gavrovo / GC Greater Caucasus / GrB Great Bank / IM Iberian Meseta / K Kabylia / Ks Kirsehir / LBM London Brabant Massif / M Moesia / MC Massif Central / ME Menderes / MM Moroccan Meseta / R Rhodos / Rh Rhodope / Si Silicium / Sic Sicily / SP Serbo Pelagonian / T Tunisia / TP Tisza Plate / VT Valais Trough

▼ Occurrence of large protoglobigerinids with thin and thick wall in the Aalenian.

▲ Occurrence of large protoglobigerinids with thin and thick wall in the Bajocian.

▲ Protoglobigerinid association of small species with thin wall.

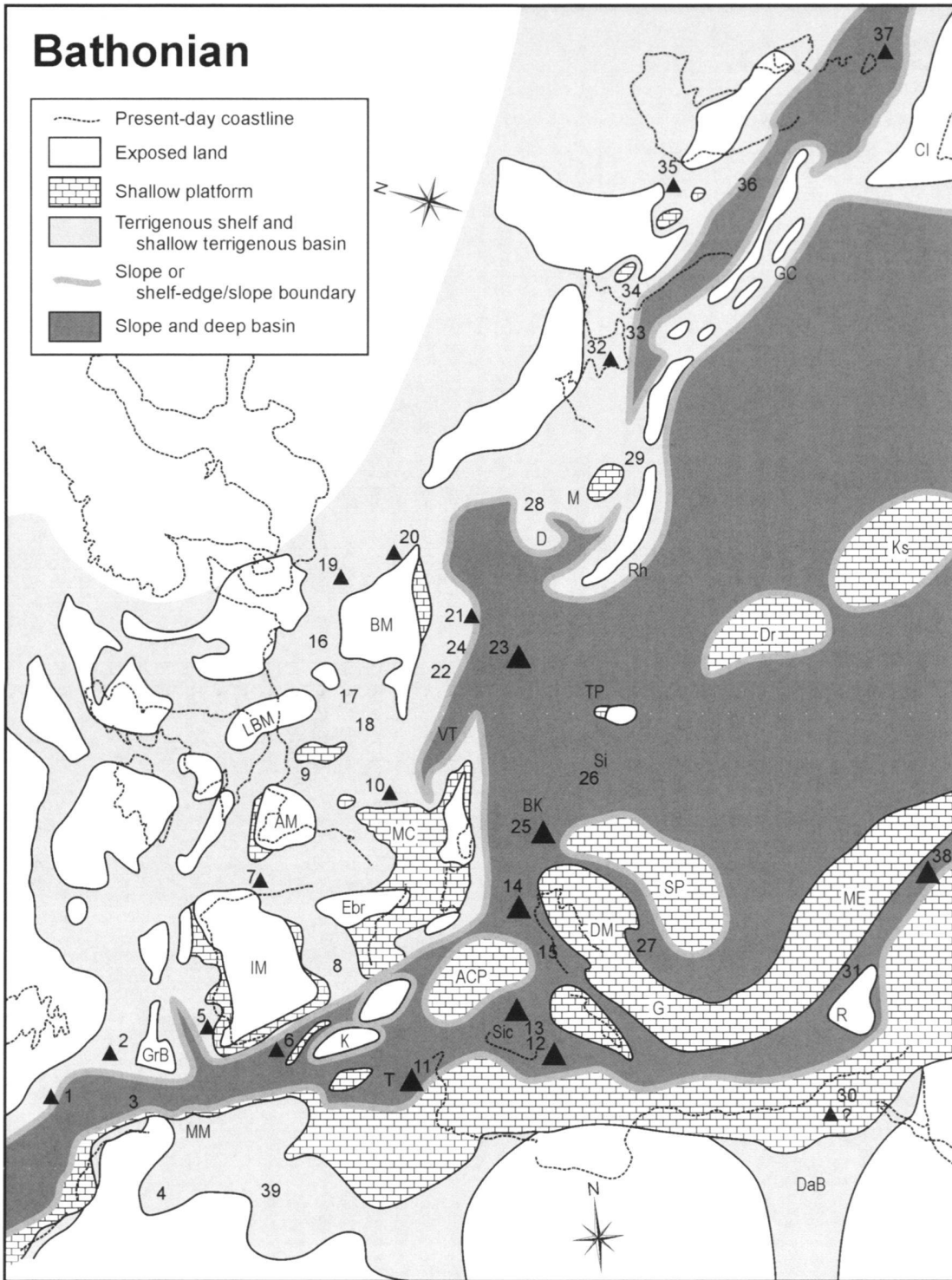


Fig. 3. Palaeogeographical distribution of the protoglobigerinids in the Bathonian. Legend see Figure 2 and Table 1.

- ▲ Occurrence of large protoglobigerinids with thin wall in the Bathonian.
- ▲ Protoglobigerinid association of small species with thin wall.

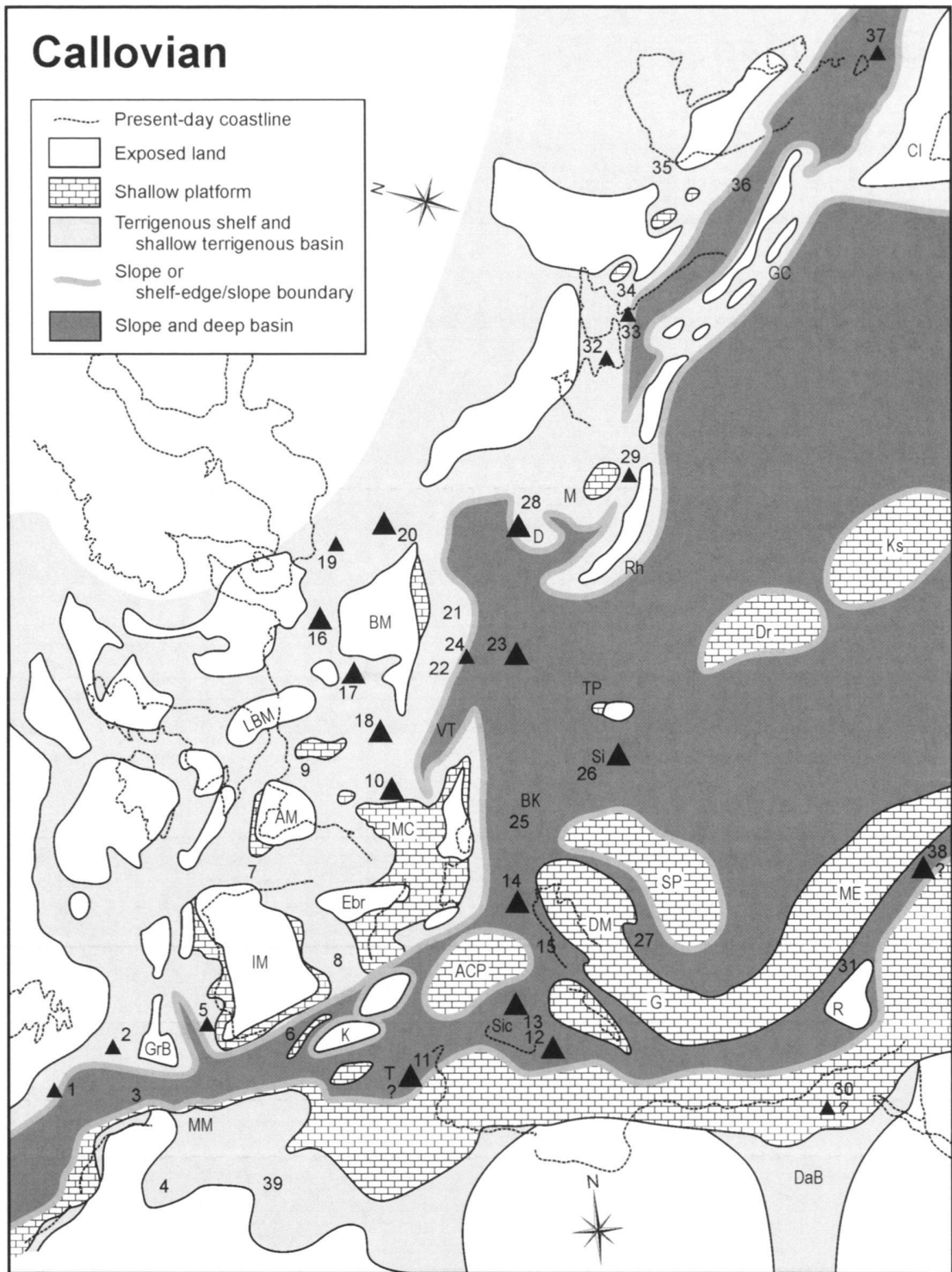


Fig. 4. Palaeogeographical distribution of the protoglobigerinids in the Callovian. Legend see Figure 2 and Table 1.

▲ Occurrence of large protoglobigerinids with thin wall in the Callovian.

▲ Protoglobigerinid association of small species with thin wall.

The size refers to the largest diameter of the test.

-small: fauna contains only small specimens approx. 60-150µm; e.g., *Conoglobigerina balakhmatovae* (MOROZOVA), *Globuligerina bathoniana*.

-middle: fauna also contains middle sized specimens, approx. 150-220µm; e.g., *C. avarica* MOROZOVA, *C. dagestanica* MOROZOVA, *G. oxfordiana* medium, *G. aff. bathoniana* (PAZDROWA) in Wernli & Görög (1999).

-large: fauna also contains large sized specimens, up to 400µm; e.g., *C.? avariformis* s. l., *G. bathoniana gigantea* WERNLI & GÖRÖG.

The wall is characterized as '**thin**', if the fauna consists only of thin-walled specimens. When it also contains thick-walled specimens as we identify it as '**thick**'.

-TA indicates a Tethyan Association, which will be defined later.

Several authors have presented the distribution of the Middle Jurassic protoglobigerinids on geographical maps (e.g., Gorbachik & Kuznetsova 1983; Gradstein 1986), while others have used palaeogeographic maps (e.g., Bignot & Janin 1984; Riegraf 1987a, b), but without a compositional analysis of the fauna, or even its relationship to the facies. The maps on which we have plotted our data are simplified versions of those in the *Atlas Tethys Palaeoenvironmental Maps* of Dercourt et al. (1993), because they show the different palaeoenvironments and palaeogeographical situation. For our purpose it seems best to select the Callovian map of Enay et al. (1993) from this atlas, as a base map for all the studied Middle Jurassic stages. It is an acceptable solution, because only minor palaeogeographical changes took place during this interval (Cariou et al. 1985).

The Aaleno-Bajocian map (Fig. 2)

Because we have only two sites (Bavaria, Turkey) for the Aalenian stage, they are included on the same map as that used for the Bajocian. The map shows that over the epicontinental area only a small-sized fauna with a thin wall is recorded (Figs 1, 2). On the basis of the literature (Table 1) there is a relatively low abundance and a low diversity fauna that rarely numbers three species.

In the Tethyan realm large-sized protoglobigerinids occur and some of them have a thick wall. They are normally abundant and the specific diversity is relatively high.

The Bathonian map (Fig. 3)

During the Bathonian the protoglobigerinid associations of the epicontinental areas are very similar to those of the Aaleno-Bajocian. It is a similar situation in the Tethyan area, except that the thick-walled species have disappeared (Figs 1, 3).

The Callovian map (Fig. 4)

In the Callovian, the faunal composition changes and the diversity are reduced in both areas. The larger-sized forms are

only represented by *G. oxfordiana* type forms (up to 310µm) with a thin wall (Figs 1, 4). These large forms are not restricted to the Tethyan area, but migrate north-westwards into the epicontinental basin, which has been identified as the Central European Basin by Grigelis & Norling (1999).

On the basis of the palaeogeographical maps and the adopted literature (Table 1) we propose two types of protoglobigerinid associations that are related to the different palaeoenvironments during Middle Jurassic:

a) Tethyan association

The majority of the data come from rock thin section. Some have been studied as isolated specimens, by means of acetolysis (Wernli & Görög 1999; Görög & Wernli 2002).

This association is characterised by large-sized species (e.g., *C.? avariformis*), frequently reaching 400µm in diameter, sometimes with a thick-walled test, and by middle-sized and small-sized species. In the thanatocoenosis the protoglobigerinids often represent more than 70% of the foraminiferal fauna. The diversity is relatively high and the following species have been identified in the literature:

Conoglobigerina? avariformis KASIMOVA s.l. (forma *alta* and forma *sphaerica*)

C. aff. dagestanica MOROZOVA (large form)

Globuligerina bathoniana (PAZDROWA)

G. aff. bathoniana (large form)

G. bathoniana gigantea WERNLI & GÖRÖG

G. oxfordiana (GRIGELIS) (small, medium large and giant forms)

G. hungarica WERNLI & GÖRÖG.

b) Epicontinental association

Almost all the data come from isolated specimens. The few recorded oriented sections or preparations always show thin-walled tests (Premoli Silva 1966; Pazdrowa 1969; Brönnimann & Wernli 1971; Gorbachik 1983; Riegraf 1987b; BouDagher-Fadel *et al.* 1997). This epicontinental association is characterised by small-sized species rarely reaching 220µm in maximum diameter. Their abundance in the foraminiferal association is lower than that recorded in the Tethyan association. Locally the diversity is low. The following species have been described by different authors:

Conoglobigerina avarica MOROZOVA

C. balakhmatovae (MOROZOVA)

C. dagestanica MOROZOVA s.s.

C. jurassica (HOFMAN)

C. meganomica (KUZNETSOVA)

Globuligerina bathoniana (PAZDROWA) s.s.

G. calloviensis KUZNETSOVA

G. oxfordiana (GRIGELIS) (small-sized and middle-sized forms)

Compactogenerina gaurdakensis (BALAKHMATOVA & MOROZOVA).

IV. Conclusions

In our previous papers (Wernli & Görög 1999, 2000; Görög & Wernli 2002) we sought an explanation of how to explain the occurrence of giant species so early in the evolution of the protoglobigerinids. Our study of the literature and the plotting of the various faunas onto different palaeogeographical maps show a relatively coherent distribution.

During the Middle Jurassic small, thin-walled taxa are recorded in epicontinental areas, while the large, sometimes thick-walled specimens were restricted to the Tethyan area. The only exception was during the Callovian, when large forms could migrate to the deeper basins of the epicontinental area. A similar phenomenon was described by Cariou *et al.* (1985) concerning the ammonites. In the Bajocian and the Bathonian the Boreal and Tethyan bio-provinces appear to have been entirely separate, while a faunal exchange begun in the Callovian. We, therefore, distinguish a Tethyan association and an epicontinental association.

We have followed the models of Hart & Bailey (1979), Hart (1980) and Caron & Homewood (1983), who have presented suggestions on the palaeoceanographical distribution of the Middle Jurassic-Late Cretaceous morphogroups of planktonic foraminifera. Generally speaking the small, less specialised taxa appear to have lived in surface waters and reproduce on the shallow epicontinental platforms. The large-sized, morphologically more structured taxa appear to have colonised the open basins with reproduction cycles that involved a migration into deeper water. Following these authors, in the Middle Jurassic, there are only small taxa restricted to the neritic area. In the Late Jurassic and in the Early Cretaceous they follow a similar pattern, perhaps because the open sea was occupied by the calpionnellids.

Our data suggest that, in the Middle Jurassic, small protoglobigerinids are not restricted to the epicontinental area but can also be found in the Tethyan realm. In this area they are accompanied by large, sometimes thick-walled species.

We suppose that the small forms were surface-dwellers, while the large ones were inhabited the deeper-water environments.

In the Aalen-Bajocian the thick-walled tests could represent the external 'crust', that is generally interpreted as a deep-water characteristic of some Recent planktonic foraminifera. Their disappearance in the studied area could be connected with the reported regression in the Bathonian (Cariou *et al.* 1985). As a result of this, the occurrence of the giant species so early in the Aalen-Bajocian can be explained by palaeoceanographical reasons.

Acknowledgements

We thank J. Metzger (cartographer) for having drafted the figures. Prof. W. Wildi (Univ. Geneva), Prof. Poisson (Univ. Orsay) and Prof. András Galácz (Eötvös Univ.) provided information about the palaeogeography. Prof. R. Radoičić (Belgrade) kindly sent us some samples from Yugoslavia while L. Giusberti provided some references for our review of the literature. Sincere

thanks are due to Dr. J.-M. Jaquet for valuable suggestion and to Prof. M. B. Hart (Univ. Plymouth) who greatly improved our original text. This work was supported by the Foundation Dr. Joachim de Giacomi of the Académie Suisse des Sciences naturelles and by the Hungarian OTKA foundation (contract nr. T37538).

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Manuscript received August 29, 2002
Revision accepted February 28, 2003