

PHYLOGENETIC RELATIONSHIPS AND EVOLUTIONARY HISTORY OF THE PALEOGENE GENUS *IGORINA* THROUGH PARSIMONY ANALYSIS

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ABSTRACT

The evolution of planktic foraminifera in the Paleocene–Eocene time interval is characterized by a high rate of diversification after the major extinction event observed at the Cretaceous/Paleogene boundary. An accelerated speciation rate resulted in the appearance of several new genera. Phylogenetic relationships among many of genera are still poorly understood. This study investigates the origin and phylogeny of the genus *Igorina*, which is characterized by a thick, nonspinose and incrustated wall. *Igorina* appears in Subzone P3a (early late Paleocene) and disappears in Zone P11 (middle Eocene). To date, nine species have been assigned to the genus *Igorina* (*I. pusilla*, *I. trichotrocha*, *I. tadjikistanensis*, *I. convexa*, *I. albeari*, *I. laevigata*, *I. lodoensis*, *I. broedermanni*, and *I. anapetes*) based on both wall texture and morphologic similarities. However, the taxonomic identification at species level is affected by several problems, mainly those resulting from poor descriptions and illustrations of the primary type specimens of several species. This study reconstructs the phylogeny and evolution of the igorinids through cladistic analysis by applying the method of parsimony.

Phylogenetic relationships of the species assigned to *Igorina* are determined through stratocladistic analysis by using a data matrix of 23 taxa (including key species of *Acarinina*), 31 morphological characters (unordered), and a stratigraphic character (ordered) mapping the first occurrence of the taxa under investigation. The matrix (Appendix 1) was processed with PAUP* 4.0b10 software by using the heuristic search option to discover the most parsimonious trees. Results suggest that *I. pusilla* is the first representative of the *Igorina* lineage, and it is followed by *I. laevigata*, *I. convexa*, and *I. albeari*. Morphotypes of uncertain taxonomic identification have been coded and analyzed separately as morphotypes A–F to determine their ancestor-descendant relationships and to evaluate their validity as discrete species. As the result of our analysis, two new species are formally described as *I. praecarinata* (= morphotype A) and *I. paraspinalis* (= morphotypes C, E, and F). Finally, our analysis provides evidence that *I. lodoensis*, *I. broedermanni*, and *I. anapetes* are more closely related to *Acarinina* than to *Igorina* and clearly belong to a different lineage.

INTRODUCTION

Planktic foraminifera are marine protists with a calcium carbonate (calcite) shell and that have an excellent geological record characterized by high rates of morphological diversification and speciation. For these reasons,

planktic foraminifera have been widely used in biostratigraphic and paleoceanographic studies of marine deposits ranging from their first major radiation in the Early Cretaceous to the Quaternary.

At the end of the Cretaceous (~65.5 Ma), planktic foraminifera experienced an almost complete extinction. Thus far, only three species are known to have survived into the Paleocene, including one of the serial genus *Guembelitra* Cushman 1933 and two of the trochospiral hedbergellids.

Nowadays, the primary criterion for classifying Cenozoic planktic foraminifera at genus level is the wall structure as described for modern taxa from detailed examination using the scanning electron microscope, or SEM (i.e., Cifelli, 1982; Spiegler and Bijvank, 1986; Hemleben and others, 1989, 1991). Subsequently, Olsson and others (1992) classified the earliest Paleocene planktic foraminifera into four groups based on surface wall texture: 1) microperforate (pore size <1 µm); 2) normal (pore size >1–8 µm) perforate smooth-walled; 3) normal perforate cancellate non-spinose; and 4) normal perforate cancellate spinose (spines are planted in the wall).

According to Olsson and others (1992), among the Cretaceous genera that survived the extinction, the triserial *Guembelitra* gave rise to the microperforate group, and the trochospiral *Hedbergella* Brönnimann and Brown (1958) gave rise first to the normal perforate smooth-walled group *Globanomalina* Haque (1956), emend. Olsson and others (1992), and soon afterward to both the cancellate-spinose group (*Eoglobigerina* Morozova 1959 and *Parasubbotina* Olsson, Hemleben, Berggren and Liu 1992, then *Subbotina* Brotzen and Pozaryska 1961) and the cancellate non-spinose group (*Praemurica* Olsson, Hemleben, Berggren and Liu 1992). The spinose-cancellate type of wall structure is characterized by regular ridges similar to, for instance, the extant genus *Globigerinoides* Cushman 1927, where the cancellate-type wall structure devoid of spines is characterized by subparallel longer ridges connected by shorter ridges that originate from coalescing pustules. This irregularly cancellate type occurs in the genera *Praemurica* Olsson and others 1992 and *Igorina* Davidzon 1976, and has an analogue in the extant neogloboquadrinids that, to avoid confusion, was referred to as the praemuricate type (Olsson and others, 1999).

A new type of wall texture developed in the mid Paleocene, namely the muricate non-spinose wall, which is characterized by short pointed pustules (muricae or pseudospinae, layered structures forming during ontogeny as part of the wall) located over part or all of the test and often concentrated around the umbilicus (Olsson and others, 1999). This wall texture is typical of some Paleocene–Eocene taxa: muricae cover the entire test of *Acarinina* Subbotina 1953, while they are confined to the peripheral margin of the test forming a keel (muricocarina)

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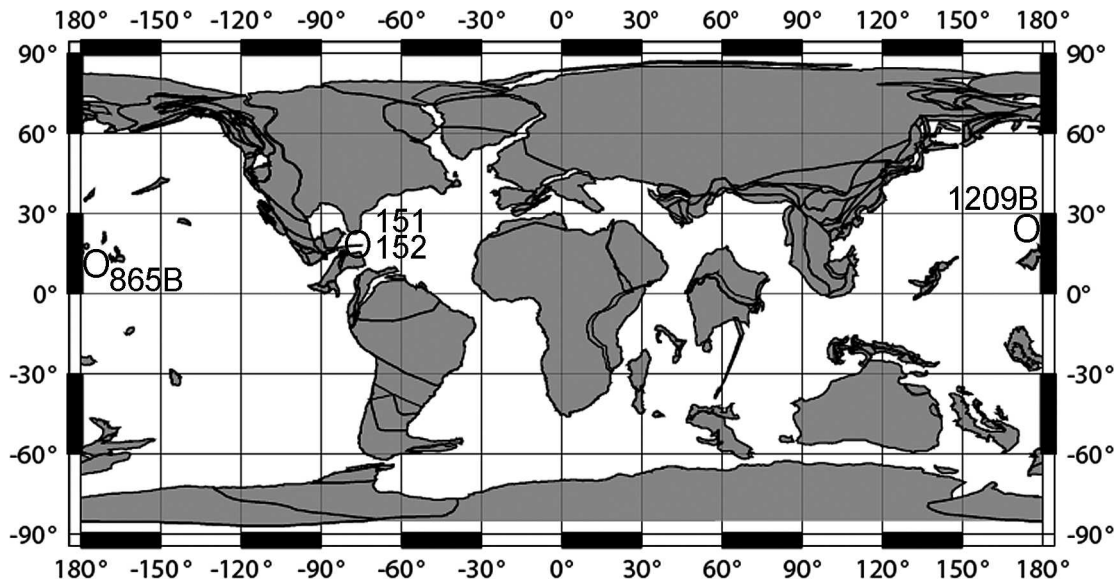


FIGURE 1. Map showing the locations of Hole 1209B (ODP Leg 198, Shatsky Rise), Hole 865B (ODP Leg 143, Allison Guyot), and Sites 151 and 152 (DSDP Leg 15, Caribbean Sea), (Hay and others, 1999).

in *Morozovella* McGowran 1964 and *Morozovelloides* Pearson and Berggren 2006. Moreover, Olsson and others (1999) interpreted the praemuricate wall structure as intermediate between the cancellate-type without spines and the muricate-type. In addition, the pustules on *Igorina* Davidzon 1976 may further coalesce to form a characteristic crust on the inner spire.

Based on the different types of wall structure/texture, accompanied by an overall marked, rapid increase in the mean sizes of the assemblages, planktic foraminifera experienced a high rate of diversification through the Paleocene and continuing into the Eocene. The speciation rate accelerated especially in the mid-Paleocene as a result of the appearance of the new genera *Igorina*, *Morozovella*, and *Acarinina*, each of them characterized by distinctive wall texture of the shell as noted above.

Despite the very large literature concerning Paleocene planktic foraminifera, the taxonomy of this group is still affected by several problems of identification at species level due to the poor descriptions and illustrations (mainly only drawings, inadequate to modern standard) of the original material. As a consequence, the morphological characteristics proper of each taxon were frequently misinterpreted by various authors according to their subjective approach. Another strong bias is related to the poor communications in the 1950–60s between specialists from the former Soviet Union and those operating in western countries especially in the Caribbean area (Bolli, 1957). When the monograph by Subbotina (1953), which also summarizes previous works, became available to western specialists in the early 1960s, it became clear that several of the same species were described twice under different names. The first attempts to overcome this taxonomic dualism were those of Berggren (1960, 1968) and Luterbacher (1964), both having visited the Soviet Union in the early 1960s, where they discussed taxonomic problems with prominent Soviet specialists and examined Russian collections (see Luterbacher, 1964).

From a phylogenetic point of view, the first attempts at reconstructing Paleocene lineages were made by Bolli (1957), for at least some globorotaliids (i.e., morozovellids), and by McGowran (1968), whose taxonomy was still in a preliminary stage. A major contribution to phylogenetic reconstructions came from the Paleogene Planktonic Foraminifera Working Group, notably the publications by Olsson and others (1992, 1999) and Berggren and Norris (1997) for the Paleocene, and by Pearson and others (2006) for the Eocene.

The aim of this paper is to investigate the taxonomy, phylogenetic relationships, and evolution of the genus *Igorina* by using a parsimony analysis.

MATERIALS AND METHODS

To perform this study we analyzed 120 samples from Ocean Drilling Program (ODP) sites namely Leg 198 Hole 1209B (Shatsky Rise, northwestern Pacific Ocean), Leg 143 Hole 865B (Allison Guyot, Central Pacific Ocean), and DSDP Leg 15 Sites 151 and 152 (Caribbean Sea) (Fig. 1). A complete Paleocene–Eocene stratigraphic section was recovered at ODP Holes 1209B and 865B, whereas only the lower Paleocene and lower Eocene are complete at DSDP Sites 151 and 152. We chose these localities because they contain abundant *Igorina* that show different degrees of preservation and provide broad geographic coverage.

Samples were washed, dried, and sieved following standard procedure (Petrizzo and others, 2005), and the three size-fractions ($>250\ \mu\text{m}$, $>150\ \mu\text{m}$, $>38\ \mu\text{m}$) obtained for each sample were stored in glass vials. These residues were examined under a stereomicroscope and picked for planktic foraminifera to obtain a complete record of their igorinid content. Preservation of planktic foraminifera is generally good, except for the presence of sporadic fragmented tests (Petrizzo and others, 2008) that were excluded from our analysis. Several specimens were cleaned

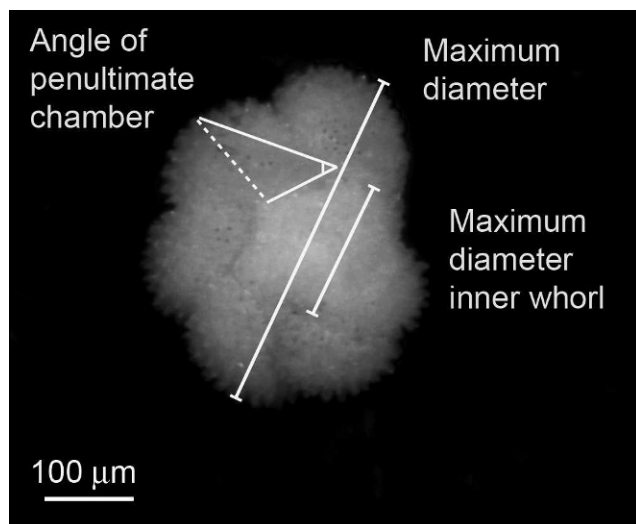


FIGURE 2. Example of image taken with the digital camera and analyzed with Image J software (measurement of morphometric characters in spiral view).

in an ultrasonic bath to remove residual micrite prior to being examined with the Scanning Electron Microscope (SEM).

Morphometric measurements were performed on digital images of the spiral, umbilical, and edge views for each specimen using the open source software Image J (<http://RSD.INFAnIH.GOV/13/INDEX.html>) (Fig. 2). Digital images of single specimens were obtained using a digital camera connected to a stereomicroscope. We also took morphometric measurements of the igorinid holotypes and related species for which SEM images were included in Olsson and others (1999) and Pearson and others (2006).

THE GENUS *IGORINA*

OVERVIEW OF THE GENUS CONCEPT

The concept of *Igorina* Davidzon (1976) has been ignored for sometime as this globorotaliiform group of Paleocene planktic foraminifera had been included within the morozovellids. However, several authors (i.e., Boersma and Premoli Silva, 1983; Toumarkine and Luterbacher, 1985; Premoli Silva and Boersma, 1988) considered the small globorotaliid forms with pustules (*pusilla-laevigata* and *convexa-broedermanni* groups) as a separate group distinct from both *Acarinina* and the mainstream morozovellids. Subsequently, Loeblich and Tappan (1987) included in the genus *Igorina* the globorotaliid forms with muricate wall texture, biconvex test, curved spiral sutures, and low curving aperture. On the other hand, Pearson (1993) believed that even though *Igorina* should be distinguished from *Acarinina*, he invalidated the genus by interpreting *Globorotalia tadjikistanensis* Bykova 1953, the type species of *Igorina*, as a morozovellid probably related to *Morozovella conicotruncata*. Subsequently, observations of new SEMs of the holotype of *Globorotalia tadjikistanensis* led Berggren and Norris (1997) to conclude that it is not related to *M. conicotruncata*. Finally, Olsson and others (1999), in agreement with the results obtained by Berggren and Norris

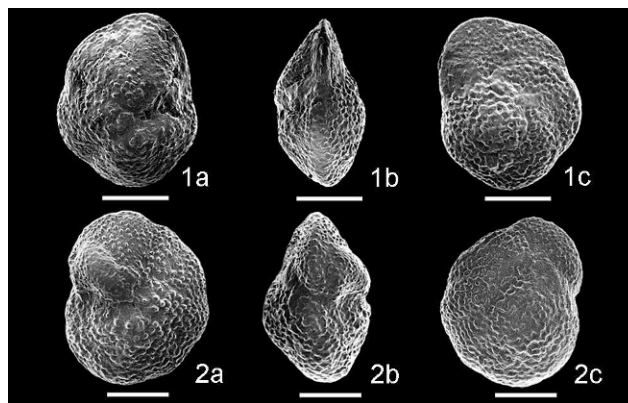


FIGURE 3. 1 *Igorina laevigata* (Bolli) (= *Globorotalia pusilla laevigata* Bolli, 1957), holotype, *Globorotalia pseudomenardii* Zone, Lizard Spring Formation, Trinidad. 2 *Igorina albeari* (Cushman and Bermúdez) (= *Globorotalia albeari* Cushman and Bermúdez, 1949), holotype, *Globorotalia pseudomenardii* Zone, Madruga Formation, Cuba. Scale bar = 100 μ m.

(1997), and on the basis of new observations of the praemuricate wall structure, considered *Igorina* as a valid genus.

According to Loeblich and Tappan's (1987) definition, the species known in the literature that appear to fall, or have been included, in the genus *Igorina* are the Paleocene species *Globorotalia albeari* Cushman and Bermúdez 1949, *Globorotalia tadjikistanensis* Bykova 1953, *Globorotalia convexa* Subbotina 1953, *Globorotalia pusilla pusilla* Bolli 1957, *Globorotalia pusilla laevigata* Bolli 1957, and *Globorotalia trichotrocha* Loeblich and Tappan 1957, and the mainly Eocene species *Globorotalia* (*Truncorotalia*) *broedermanni* Cushman and Bermúdez 1949, *Globorotalia broedermanni lodoensis* Mallory 1959, and *Globorotalia* (*Acarinina*) *broedermanni anapetes* Blow 1979.

SYNONYMS AND MORPHOTYPES

In their revision of Paleocene planktic foraminifera, Olsson and others (1999) studied and re-illustrated several holotypes, and provided a list of synonyms for each species they ascribed to *Igorina*. Specifically, these authors included *I. laevigata*, characterized by 5–6 chambers in the last whorl and the presence of a weak muricocarina along the entire margin, in the concept of *I. albeari*, which typically has 9–10 chambers in the last whorl and, according to the original description, a somewhat rounded peripheral margin. In addition, Sprong and others (2009) included in the variability of *I. albeari* specimens with only 5 chambers and a slight muricocarena. In our opinion, *I. laevigata* differs from *I. albeari*, specifically by displaying compressed chambers and developing a keel around the acute peripheral margin. The holotype of *I. albeari* shows a very thin keel on the last chamber that looks very different from the well-developed keel of *I. laevigata*. *Igorina albeari* also differs from *I. laevigata* by having less-compressed chambers and less-curved sutures on the spiral side (Fig. 3). In agreement with Blow (1979), Arenillas and Molina (1997), and Orué-Etxebarria and others (2006), we include in the concept of *I. albeari* the specimens with a subcircular test, more than 7 chambers in last whorl, a medium-high spiral

side, and occasionally a weak muricocarina on the last chamber. Besides, we follow the interpretation of Oru  -Etzebarria and others (2007) that the specimen with 5 chambers in the final whorl described by Sprong and others (2009) could be included in the variability of *I. laevigata*.

Olsson and others (1999) and Berggren and others (2006) included *I. convexa* (Subbotina, 1953) in the variability of *I. tadjikistanensis*. In our view, this synonymy does not stand, as the holotype of *I. convexa* is very different from *Igorina tadjikistanensis*, particularly in its equally biconvex profile, crescentic to petaloid chambers in the last whorl, and more compressed test.

To date, the nine species assigned to *Igorina*, based on both wall texture and morphological similarities (Fig. 4, 5), can be grouped as follows: 1) the “keeled” group that includes *I. pusilla* (Bolli 1957), *I. laevigata* (Bolli 1957), and *I. albeari* (Cushman and Berm  dez 1949); 2) the non-keeled group that includes *I. tadjikistanensis* (Bykova 1953), *I. convexa* (Subbotina 1953), and *I. trichotrocha* (Loeblich and Tappan 1957); and 3) the *I. broedermanni* group that includes *I. lodoensis* (Mallory 1959), *I. broedermanni* (Cushman and Berm  dez 1949), and *I. anapetes* (Blow 1979). Junior synonyms of these species are listed in Berggren and Norris (1997), Olsson and others (1999), and Berggren and others (2006). It is worth mentioning that *I. trichotrocha* (= *Globorotalia trichotrocha* Loeblich and Tappan 1957) was first included in *Acarinina* (Shutskaya, 1970) and later assigned to *Igorina* (Olsson and others, 1999). Moreover, this species has been seldom mentioned in the literature probably because is a very rare component of the mid-Paleocene assemblages and, according to Berggren (communication, 2009), the original figures of the holotype resemble a benthic foraminifera. In our planktic foraminiferal assemblages, we recognized few specimens that strictly match the original description of *I. trichotrocha*. It is of small size like *I. pusilla*, but differs from the latter by having a planoconvex test, less-elongated chambers in the last whorl, and weakly curved sutures on the spiral side (see Systematic Taxonomy section). In addition, we also observed numerous morphotypes displaying similarities to some forms of *Igorina* cited above (Fig. 6). These morphotypes, here annotated as *Igorina* morphotypes A–F, occur in the Paleocene assemblages of the Pacific Ocean (Hole 1209B and Hole 865B), and have been observed previously by Petrizzo (2005) in Shatsky Rise planktic foraminiferal assemblages. The main morphological features of identified species and annotated morphotypes are summarized in Table 1.

PHYLOGENETIC ANALYSIS

INTRODUCTION

In this study, the phylogenetic relationships of *Igorina* is based on the analysis of cladograms obtained with the analytical technique of maximum parsimony. Maximum parsimony is a nonparametric statistical method commonly used for grouping taxa and estimating phylogenetic relationships. It involves the construction of a matrix describing the character states for each examined taxon. This cladistic analysis is not frequently used in phylogenetic studies of planktic foraminifera because the morphocharacters are

often variations of the same feature. Different genera include similar morphologies that may confuse data in a parsimony analysis and thus lead to incorrect conclusions. In planktic foraminifera, the recognizable discrete characters are few and often present in several taxa. Therefore some character states may overlap. Another problem studying planktic foraminifera with the parsimony method is species polymorphism. For example, in *Igorina tadjikistanensis* we observed specimens with six chambers on the umbilical and spiral sides, while other specimens showed nine chambers on the spiral side and eight on the umbilical side. This polymorphism can produce ambiguity in definition of character states, as well as numerous unresolved polytomies in phylogenetic trees. However, if the characters are well recognizable and their states are correctly defined, we maintain that it is possible to reconstruct the lineages within a genus (i.e., at the species level).

Berggren and Norris (1997) were the first to apply applied parsimony analysis to study interrelationships between Paleocene trochospiral planktic foraminifera. They used 73 morphologic characters, including four characters based on positive/negative carbon and oxygen isotope ratios.

Our cladistic analysis is based on 22 descriptive (qualitative) and nine numerical (quantitative) characters. Descriptive characters correspond to the morphological features, whereas numerical characters include morphometric values based on shell measurements. The character states are defined and described in Appendix 2, and ordered and illustrated according to the edge, umbilical and spiral views of the test in Figures 7–9.

The list of characters was created without any reference to published lists (i.e., Berggren and Norris, 1997) to avoid bias of phylogenetic results toward those previously obtained. Within each character, character states were defined as mutually exclusive, non-overlapping conditions. Besides the characters observed and measured on the specimens picked in the studied samples, we included in our analysis those characters observed in SEM images of type specimens and on illustrations of species by previous authors (Subbotina, 1953; Blow, 1979; Olsson and others, 1999; Berggren and others, 2006). Only adult specimens were examined.

In the character lists we have included stratigraphic data. Stratigraphic information has often occupied a privileged position in studies aimed at understanding planktic foraminifera evolutionary relationships because of high-resolution sampling. In our opinion stratigraphic data are important in any cladistic study on the evolution of planktic foraminifera because their stratigraphic distribution is usually well known and calibrated against the time scale (i.e., Olsson and others, 1999; Pearson and others, 2006).

In some studies on other fossil groups, such as those on ammonoids by Moyne and Neige (2004) and Jana and others (2005), morphological characters were believed to be, and therefore treated as, independent of stratigraphic distribution. On the contrary, Pardo and others (2008) demonstrated that “stratocladistics” is a helpful tool for elucidating the extent of anagenesis and cladogenesis in extinct lineages, owing to its capacity to reconstruct phylograms in their temporal framework. In agreement with the latter authors, we have used the stratigraphic character inasmuch as the first occurrence of the most

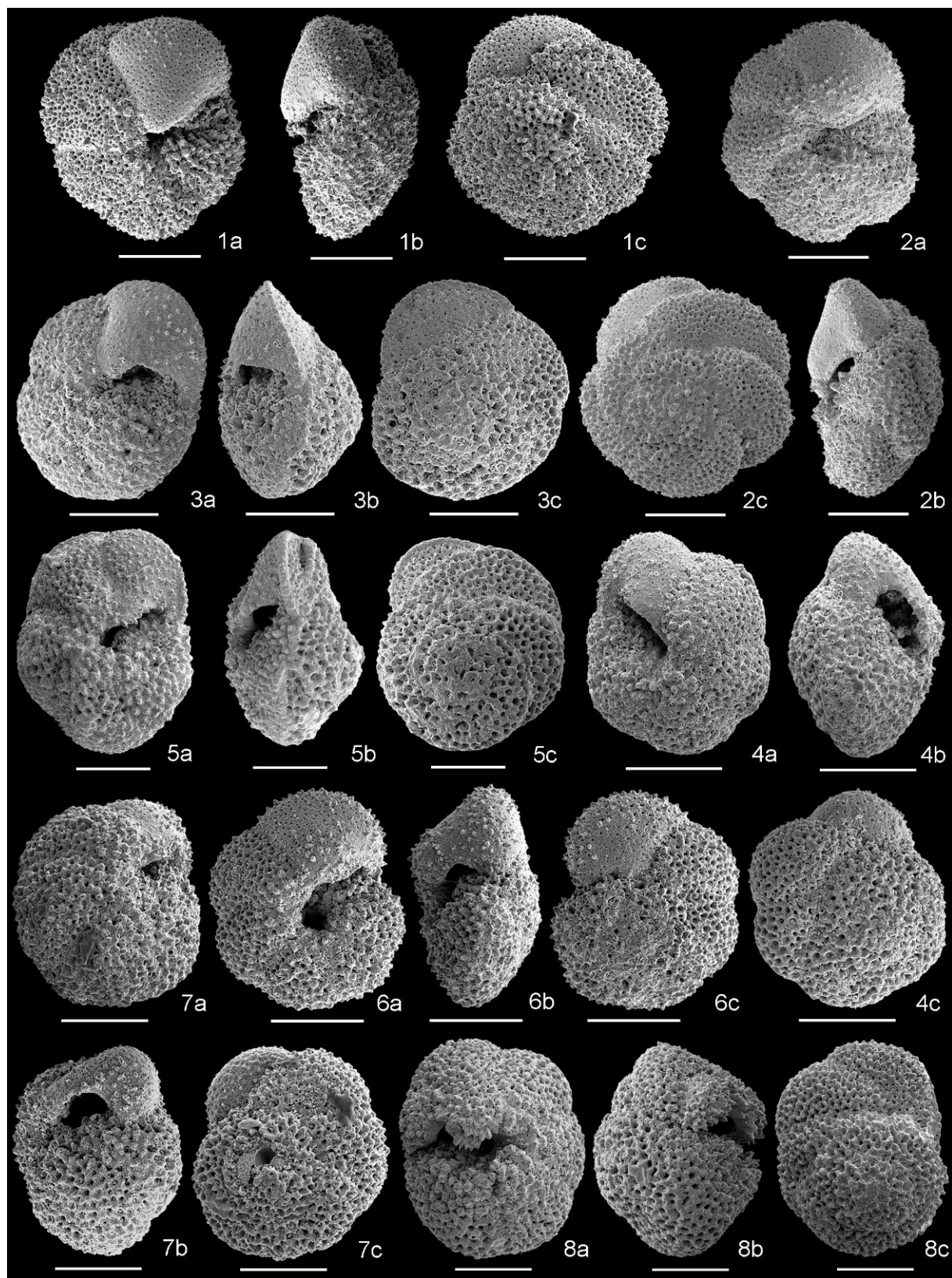


FIGURE 4. *Igorina* species analyzed in parsimony analysis. 1 *Igorina pusilla*, sample 198-1209B-24H-CC, 3–4 cm. 2 *Igorina pusilla*, sample 198-1209B-24H-7, 41–42 cm. 3 *Igorina laevigata*, sample 198-1209B-23H-3, 111–112 cm. 4 *Igorina convexa*, sample 198-1209B-23H-3, 91–92 cm. 5 *Igorina laevigata*, sample 143-865B-14H-4, 47–49 cm. 6 *Igorina trichotrocha*, sample 198-1209B-24-CC, 3–4 cm. 7 *Igorina tadjikistanensis*, sample 198-1209B-22H-4, 101–102 cm. 8 *Igorina tadjikistanensis*, sample 198-1209B-23H-1, 3–4 cm. Scale bar = 100 μ m.

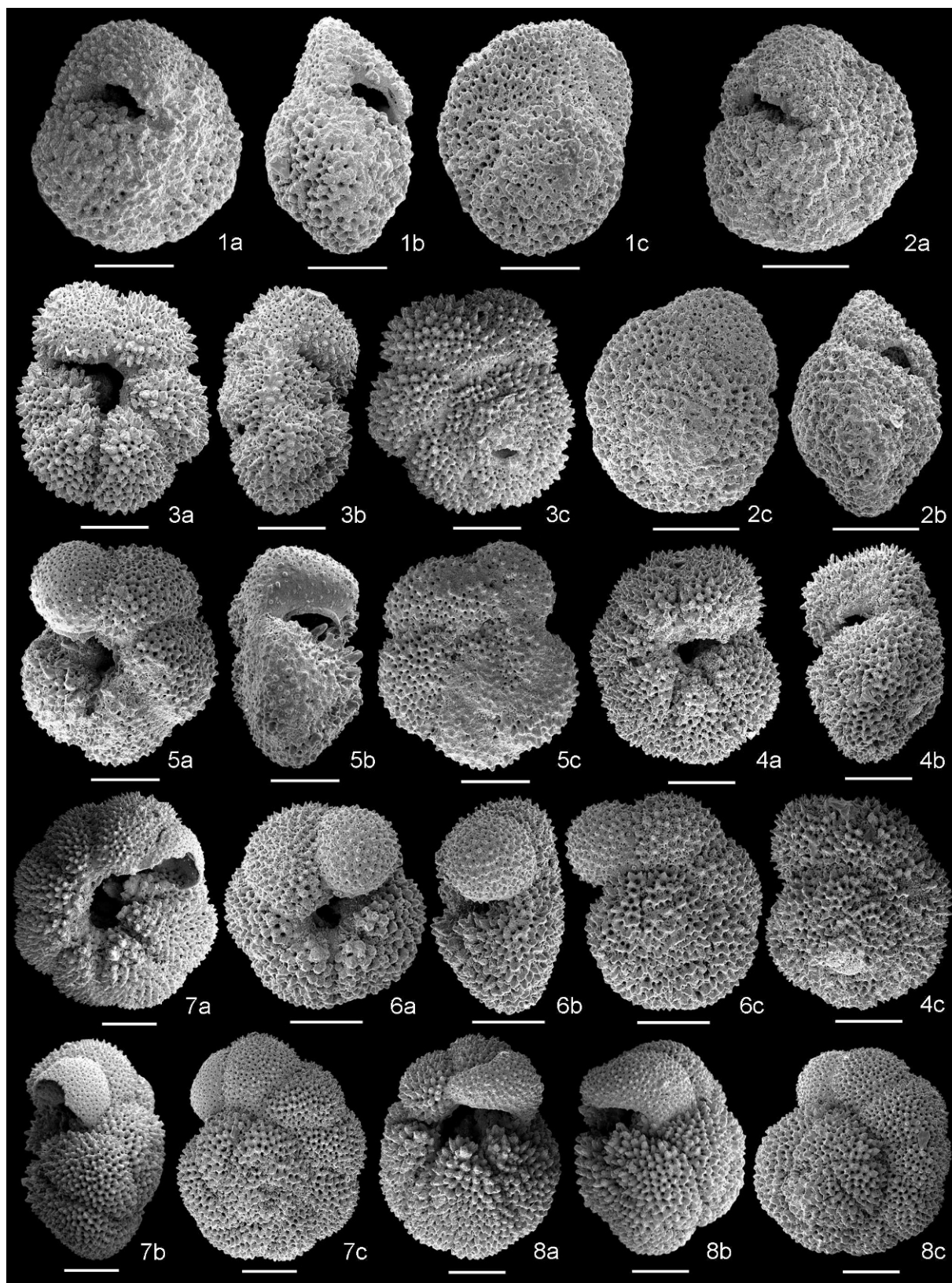


FIGURE 5. *Igorina* species analyzed in parsimony analysis. 1 *Igorina albeardi*, sample 143-865B-14H-4, 47–49 cm. 2 *Igorina albeardi*, sample 198-1209B-23H-3, 111–112 cm. 3 *Igorina lodoensis*, sample 143-865B-11H-4, 48–50 cm. 4 *Igorina broedermanni*, sample 143-865B-7H-3, 130–132 cm. 5 *Igorina lodoensis*, sample 15-152-3-5, 21–23 cm. 6 *Igorina broedermanni*, sample 143-865B-7H-3, 130–132 cm. 7 *Igorina anapetes*, sample 143-865B-8H-2, 130–132 cm. 8 *Igorina anapetes*, sample 143-865B-8H-2, 130–132 cm. Scale bar = 100µm.

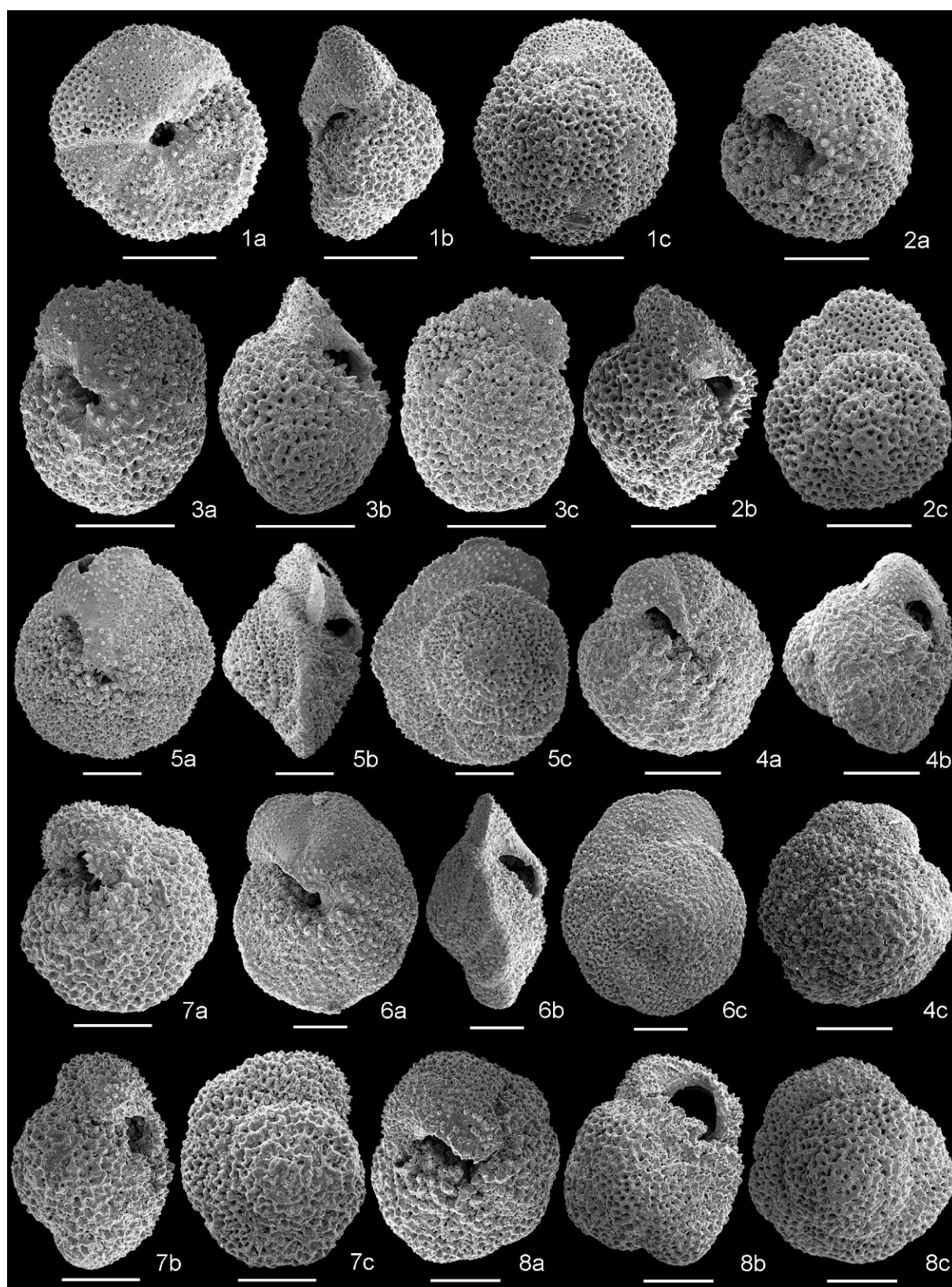


FIGURE 6. Morphotypes of *Igorina* observed in the studied assemblages and analyzed separately in parsimony analysis. **1** *Igorina* morphotype A, sample 198-1209B-24H-7, 41–42 cm. **2** *Igorina* morphotype B, sample 198-1209B-23H-2, 81–82 cm. **3** *Igorina* morphotype B, sample 198-1209B-22H-4, 101–102 cm. **4** *Igorina* morphotype C, sample 198-1209B-22H-6, 1–2 cm. **5** *Igorina* morphotype D, sample 198-1209B-23H-7, 11–12 cm. **6** *Igorina* morphotype D, sample 198-1209B-23H-7, 31–32 cm. **7** *Igorina* morphotype E sample 198-1209B-22H-5, 101–102 cm. **8** *Igorina* morphotype F, sample 198-1209B-22H-CC, 3–4 cm. Scale bar = 100 μ m.

TABLE 1. Description of the most important morphocharacters in the species of *Igorina*.

Characters	Shape of test	Wall texture	Periphery	Number of whorls	Number of chambers in last whorl		Shape of chambers	Shape of suture on spiral side	Keel
					umbilical	spiral			
<i>Igorina pusilla</i>	biconvex	encrusted	subacute	2½	6	5–6	crescentic	strongly curved	no
<i>Igorina laevigata</i>	biconvex	encrusted	subacute	2½	6	5–6	crescentic	strongly curved	yes
<i>Igorina albeari</i>	biconvex	encrusted	subacute	3	7–9	7–9	petaloid	strongly curved	Thin keel on last chamber
<i>Igorina trichotrocha</i>	planconvex	encrusted	subacute to subangular	2½	6–7	6½	petaloid to subcrescentic	slightly curved-straight radial	no
<i>Igorina tadjikistanensis</i>	biconvex	encrusted	subangular to subrounded	2½–3	6–9	7–9	subcrescentic	curved	no
<i>Igorina convexa</i>	biconvex	encrusted	subacute	2½	6	6	subcrescentic	slightly curved	no
<i>Igorina lodoensis</i>	biconvex	no crust	subangular	2½	6	6	subglobular to trapezoidal	curved	no
<i>Igorina broedermanni</i>	biconvex	no crust	subangular to subrounded	3	6–7	6–7	trapezoidal	slightly curved	no
<i>Igorina anapetes</i>	planconvex	no crust	subangular to subrounded	3	8–9	8–9	trapezoidal	slightly curved-straight radial	no
<i>Igorina</i> morphotype A	biconvex	encrusted	subacute	3	6	6–7	crescentic	strongly curved	no
<i>Igorina</i> morphotype B	biconvex	encrusted	subacute	3	7–9	7–9	petaloid	strongly curved	Thin keel on last chamber
<i>Igorina</i> morphotype C	biconvex	encrusted	subacute to subrounded	3	8–9	8–9	petaloid	strongly curved	no
<i>Igorina</i> morphotype D	biconvex	encrusted	subacute	2½	9	9–10	crescentic	strongly curved	yes
<i>Igorina</i> morphotype E	biconvex	encrusted	subrounded to subangular	3	7–9	7–9	petaloid	strongly curved	no
<i>Igorina</i> morphotype F	biconvex	encrusted	subrounded to subangular	3	9–10	9–10	petaloid	strongly curved	no

important Paleocene planktic foraminiferal species is known.

In our analysis, all characters were assumed to be equally weighted and morphological characters were treated as unordered (non-additive) in order to avoid *a priori* assumptions on character importance. For instance, the different types of wall textures were assumed to be equally weighted compared to the other characters. Since this study is the first to quantitatively analyze phylogenetically relevant characters among *Igorina* species, we consider this approach as the most objective and, at the same time, the most useful starting framework for future researches. The stratigraphic character was treated as ordered (additive). Taxa containing multiple states for a character were treated as polymorphic for that state.

The character states matrix (Appendix 1) has been processed with the software PAUP* vers. 4.01 (Swofford, 2002). Character state polarity has been determined including three taxa as outgroup (see below). Each analysis performed 1000 random addition sequence heuristic search replicates, with maxtree limit set at 50000. Nodal support was calculated performing 1000 bootstrap analyses (Felsenstein, 1985) to the data matrix, following the same procedure used in the heuristic search.

MORPHOMETRIC CHARACTERS

To perform the parsimony analysis, we inserted in the matrix (Appendix 1) nine character states based on

morphologic measurements (Fig. 9). Some of these character states are given by ratio based on morphological measurements such as maximum height and length of the first and penultimate chambers in umbilical view, and penultimate chambers in spiral view. The measurements were performed on 25 specimens for each taxon analyzed. We then calculated the mean value for each morphological character (Table 2).

To find character states, morphologic characters were subdivided by examining the means of each species and dividing the values into two classes based on natural breaks. Natural breaks were placed at gaps, evident variation, or slope changes within the distribution. Subsequently, we statistically analyzed the validity of the groups forming the character states. To verify if morphometric data taken from the population have a normal distribution, we analyzed them with the Shapiro-Wilk test and Kolmogorov-Smirnov (Hammer and Harper, 2006). Because data forming the groups did not exhibit normal distribution, the data were statistically analyzed with the Mann-Whitney U test, which does not assume normal distribution. The Mann-Whitney U test is a nonparametric method used to determine whether the median measurements of the two populations are equal (Hammer and Harper, 2006). All statistical calculations were performed with the STATSOFT STATISTICA 7 computer package. Once the statistical validity of the morphometric data was verified, the analyzed groups were separated into character states (Table 3).

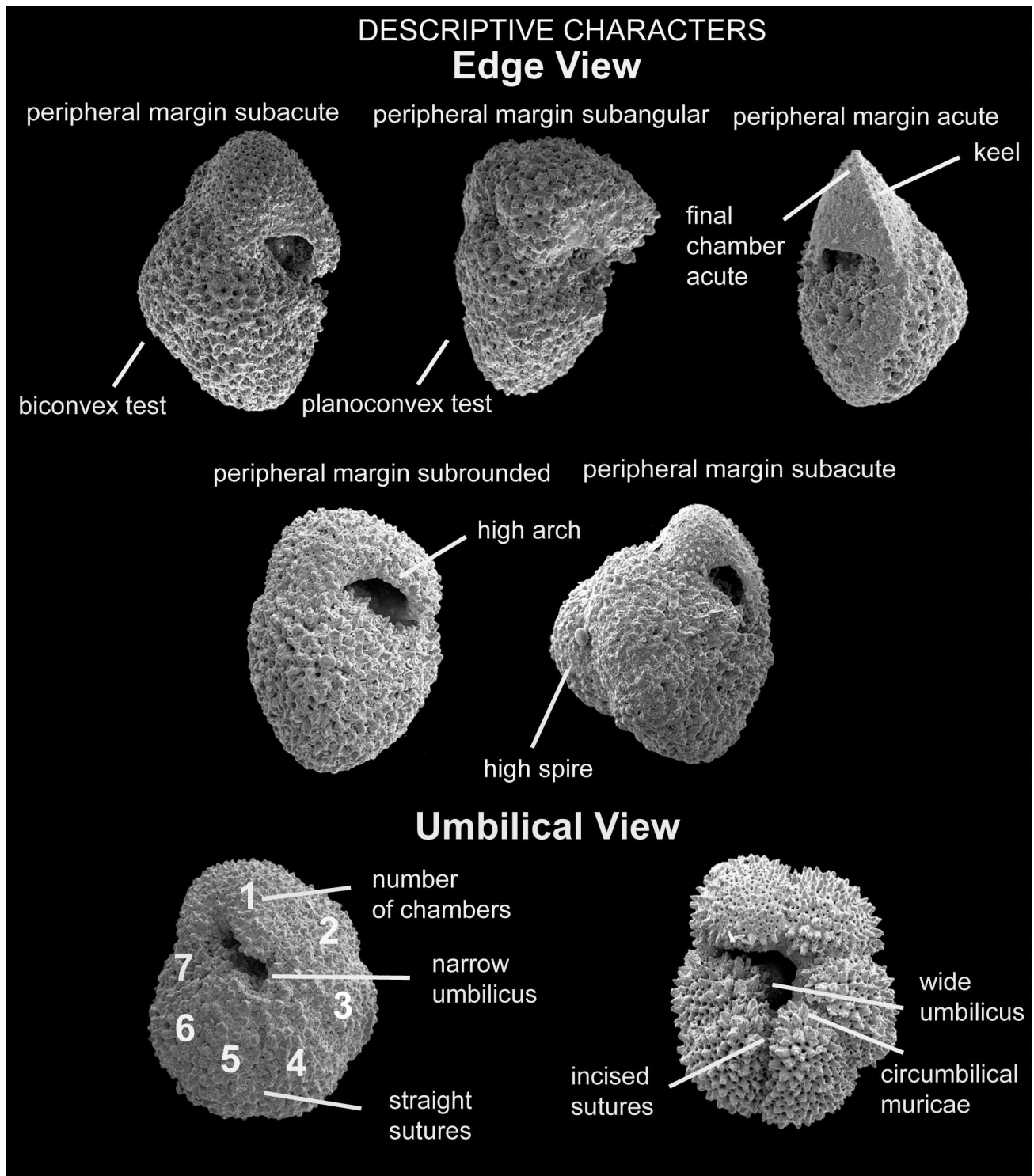


FIGURE 7. Descriptive characters observed in edge and umbilical views.

Outgroups

As the origin and the ancestor taxon of the igorinids is still uncertain, in our analysis we considered three species as possible ancestors. *Premurica uncinata* (Bolli 1957) has been included in the outgroup to analyze the likely phylogenetic derivation of *Igorina* in agreement with previous interpre-

tations (Pearson, 1993; Olsson and Hemleben, 1996; Olsson and others, 1999). In preliminary investigations, we also included *P. inconstans* as an outgroup since it displays character state combinations similar to *Igorina*. The results of these tests clearly showed the *Igorina* group always related to *P. uncinata*. We therefore consider the inclusion of *P. inconstans* not phylogenetically informative for our

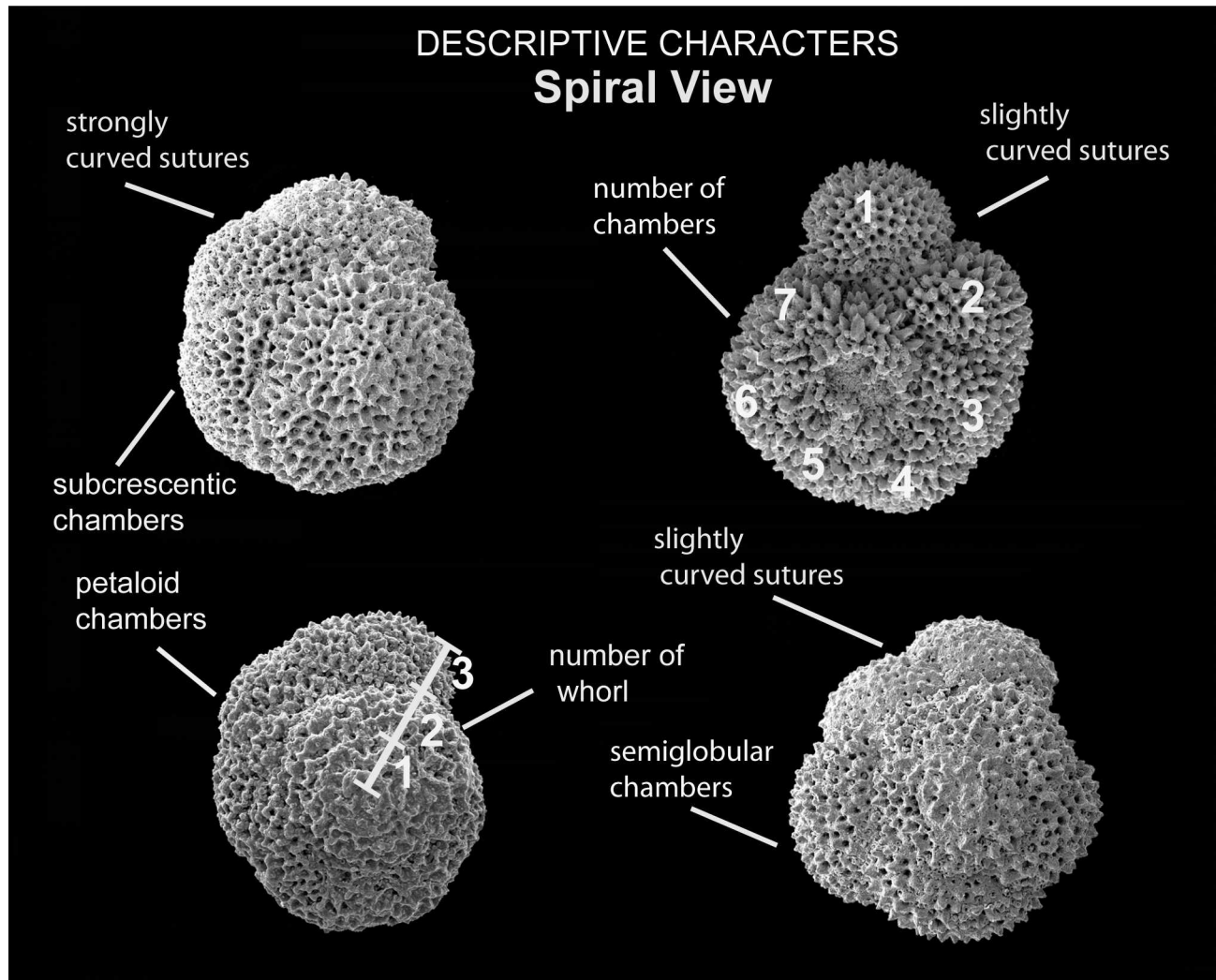


FIGURE 8. Descriptive characters observed in spiral view.

study. *Eoglobigerina spiralis* (Bolli 1957) was selected because it was considered the direct ancestor of *Morozovella pusilla* (= *Igorina pusilla*) by some authors (Bolli, 1957; Berggren, 1977; Blow, 1979), and on the basis of the previous cladistic analysis on Paleocene trochospiral planktic foraminifera performed by Berggren and Norris (1997), that showed it to be the ancestor of the muricate taxa lineage. We observed several specimens strictly resembling *E. spiralis* but possessing a nonspinose wall. In agreement with Olsson and others (1999), we included these forms in *E. spiralis*. The possibility that we are dealing with two different species cannot be excluded, so further detailed studies are needed. In this paper, both morphotypes were included in *E. spiralis*. Accordingly, we considered the character of its wall as uncertain due to polymorphism (see Appendix 2). A third species, *Parasubbotina varianta* (Subbotina 1953), was included as a “remote” outgroup not closely related to the igorinids. The inclusion of this taxon allows the analysis to bypass the uncertainties in the character-state polarity present in *Eoglobigerina spiralis* (discussed previously).

Ingroup

Nine species of *Igorina* have been included in the ingroup: *I. pusilla* (Bolli 1957), *I. trichotrocha* (Loeblich and Tappan 1957), *I. tadjikistanensis* (Bykova 1953), *I. albeari* (Cushman and Bermúdez 1949), *I. laevigata* (Bolli 1957), *I. convexa* (Subbotina 1953), *I. lodoensis* (Mallory 1959), *I. broedermanni* (Cushman and Bermúdez 1949), and *I. anapetes* (Blow 1979). In addition, the coded morphotypes related to *Igorina*, which show consistent morphological and wall texture features, were analyzed separately as morphotypes A–F to determine their ancestor-descendant relationships and to evaluate their validity as discrete species (Fig. 6).

RESULTS

EVOLUTIONARY HISTORY THROUGH PARSIMONY ANALYSIS

Our parsimony analysis found 68 most-parsimonious trees (MPTs) of 153 steps each, with Consistency and Retention Indices (CI and RI) of 0.6863 and 0.6690,

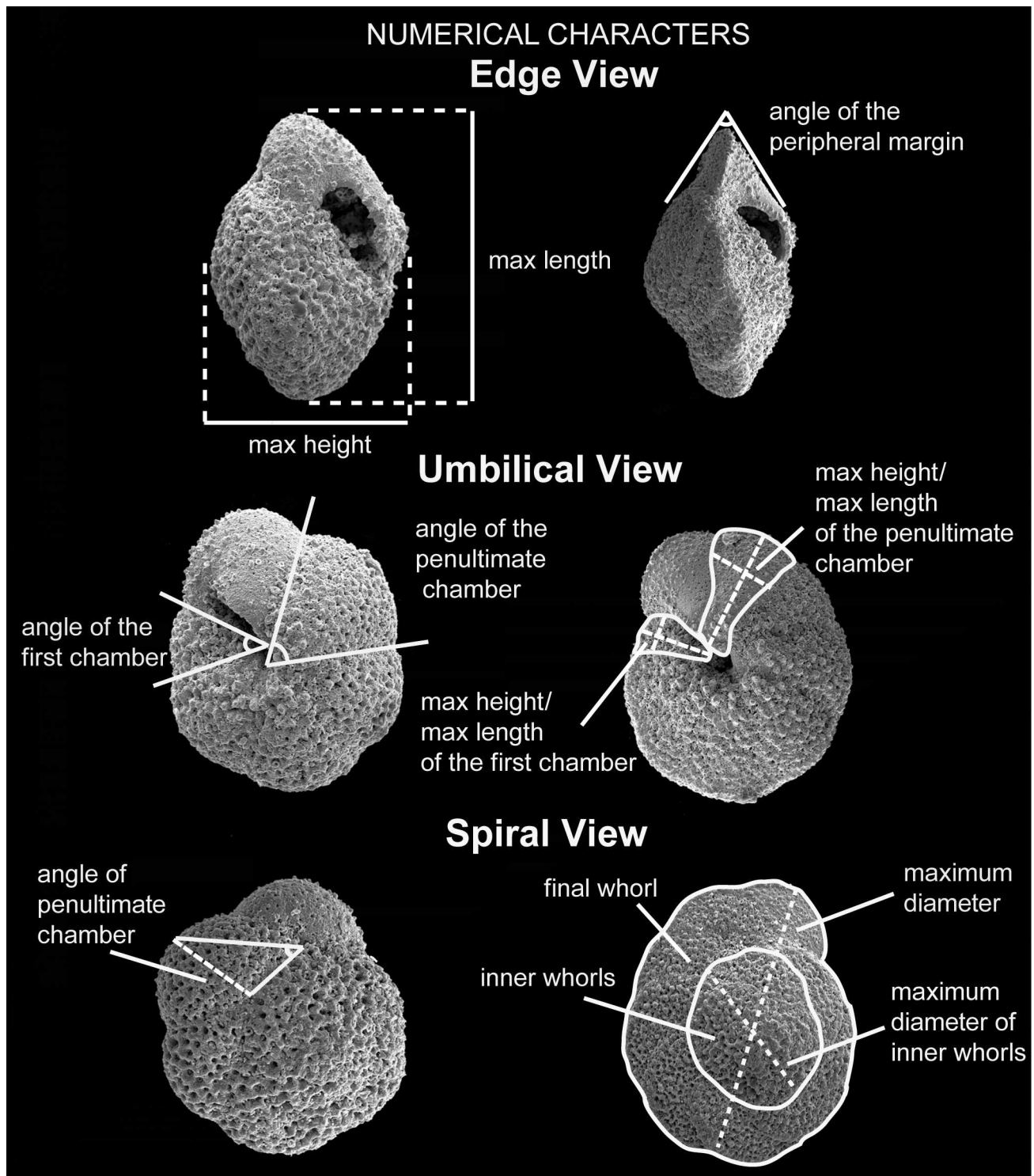


FIGURE 9. Numerical characters measured on edge, umbilical, and spiral views.

respectively. The Strict Consensus tree of the MPTs, shown in Figure 10, identifies only those nodes shared by all alternative MPTs (Smith, 1994).

Our first analysis suggests that the igorinids derived directly from *Praemurica uncinata*, which agrees with Pearson (1993) and Olsson and others (1999). On the other hand, our phylogenetic analysis had results different from

those obtained through the analysis with parsimony by Berggren and Norris (1997, fig. 10) that showed the igorinids to be closely related to *Eoglobigerina spiralis*. Although the phylogenetic relationships among the Paleocene species of *Igorina* are not well resolved in the comprehensive tree, within the ingroup it is possible to identify a clade constituted by the upper Paleocene–Eocene

TABLE 2. Means of the morphometric measurements of the studied taxa (see Appendix 2 for description of characters).

Character	23	24	25	26	27	28	29	30	31
Mean									
<i>Parasubbotina varianta</i>	124.44	64.64	74.70	55.60	2.48	0.93	0.87	0.67	1.61
<i>Eoglobigerina spiralis</i>	120.94	48.68	63.96	46.92	1.88	1.10	0.91	0.58	1.54
<i>Praemurica uncinata</i>	120.40	48.90	60.78	53.00	2.67	1.07	0.98	0.80	1.66
<i>Igorina pusilla</i>	100.20	41.08	58.50	40.60	1.67	1.20	1.03	0.54	1.57
<i>Igorina trichotrocha</i>	106.05	32.65	47.63	41.42	1.89	1.64	1.17	0.62	1.75
<i>Igorina tadjikistanensis</i>	106.10	30.90	45.06	37.30	1.73	1.84	1.21	0.51	1.32
<i>Igorina convexa</i>	109.58	33.06	52.09	37.14	1.63	1.57	1.07	0.49	1.38
<i>Igorina laevigata</i>	73.78	33.23	56.40	35.32	1.82	1.51	1.05	0.41	1.73
<i>Igorina albeari</i>	91.51	27.10	37.39	32.89	1.77	1.65	1.39	0.48	1.52
<i>Igorina lodoensis</i>	102.06	35.20	61.40	47.10	1.81	1.40	0.98	0.60	1.58
<i>Igorina broedermanni</i>	105.82	37.02	49.32	47.92	1.85	1.40	1.11	0.66	1.43
<i>Igorina anapetes</i>	114.10	30.40	37.78	46.50	1.78	1.80	1.34	0.77	1.35
<i>Igorina</i> morphotype A	87.70	49.56	61.62	36.95	1.67	1.15	0.97	0.44	1.69
<i>Igorina</i> morphotype B	92.42	35.78	48.16	36.42	1.69	1.49	1.22	0.46	1.35
<i>Igorina</i> morphotype C	102.16	29.76	45.94	33.84	1.46	1.51	1.24	0.43	1.14
<i>Igorina</i> morphotype D	74.36	25.24	33.20	34.86	1.78	1.87	1.49	0.40	1.73
<i>Igorina</i> morphotype E	98.43	31.12	39.63	37.26	1.71	1.66	1.22	0.53	1.47
<i>Igorina</i> morphotype F	109.96	35.62	46.50	37.86	1.57	1.34	1.19	0.47	1.22

taxa *Igorina lodoensis*, *I. broedermanni*, and *I. anapetes*. Our analysis suggests that *I. lodoensis* is not a descendant of *I. tadjikistanensis* (as proposed by Berggren and others, 2006) because this clade is clearly separate from the other Paleocene igorinids (Fig. 10). Moreover, our analysis provides evidence that the clade formed by *I. lodoensis*, *I. broedermanni*, and *I. anapetes* (here called “*I. broedermanni*

lineage/plexus”) is more closely related to *I. pusilla* and clearly belongs to a different lineage. These results could imply that the upper Paleocene-Eocene taxa evolved directly from *I. pusilla*, but we consider that unlikely, as *I. pusilla* was extinct well before the representatives of the *I. broedermanni* lineage appeared.

To better understand which phyletic lineages the *broedermanni* plexus is most related, and to define the taxonomic position of the other Paleocene species of *Igorina*, we performed an additional parsimony analysis that included a few key species of *Acarinina*. This genus is characterized by its medium-sized trochospiral and muricate test without muricocarina. It was chosen because previous authors (Bolli, 1957; Berggren and Norris, 1997) regarded it as the ancestor of *Igorina*. Therefore, we have included within the ingroup the five principal species of acarininids commonly occurring in the Paleocene (Fig. 11): *A. strabocella* (Loeblich and Tappan 1957), *A. nitida* (Martin, 1943), *A. mckannai* (White 1928), *A. subsphaerica* (Subbotina 1947), and *A. soldadoensis* (Brönnimann 1952).

In the second parsimony analysis we measured the morphologic variation of 25 specimens for each species of *Acarinina* and included these data with the previous measurements of *Igorina* to redefine the numerical characters based on statistical parameters (Table 4). Subsequently, we statistically tested the new groups by adding the morphometric data of the *Acarinina* species to verify the validity in the division of character states. We found that the morphometric parameters of the *Acarinina* species fall within the division of the character states shown in Table 3.

The second analysis produced 89 MPTs of 187 steps, with a CI of 0.6631 and a RI of 0.7110. The robustness of the nodes was evaluated by the statistical method of bootstrapping. The strict consensus tree obtained with this analysis is shown in Figure 12. We found relatively strong bootstrap support for the node that links *I. lodoensis* with *I. broedermanni*, and that which links *I. anapetes* (a = 66%; Fig. 12) and *I. broedermanni* with *I. anapetes* (b = 77%, Fig. 12). The knot that ties the outgroup *Praemurica uncinata* to the ingroup of Paleocene *Igorina* species is also relatively good (c = 54%, Fig. 12).

TABLE 3. Separation of morphometric characters in character states based on statistical analysis with Mann-Whitney U test.

Character range	Mann-Whitney U test
23 -Angle of peripheral margin (0) ≥ 100.20 (1) < 100.20	p<0.001
24 -Angle of the first chamber in umbilical view (0) ≥ 41.08 (1) < 41.08	p<0.001
25 -Angle of the penultimate chamber in umbilical view (0) ≥ 56.4 (1) < 56.4	p<0.001
26 -Angle of the penultimate chamber in spiral view (0) ≥ 40.6 (1) < 40.6	p<0.001
27 -Maximum diameter/inner whorls diameter ratio (0) ≥ 1.81 (1) < 1.81	p<0.001
28 -maximum height/maximum length ratio of the first chamber in umbilical side (0) ≤ 1.34 (1) > 1.34	p<0.001
29 -Maximum height/maximum length ratio of the penultimate chamber in umbilical side (0) ≤ 0.98 (1) > 0.98	p<0.001
30 -Maximum height/maximum length ratio of the penultimate chamber in spiral side (0) ≥ 0.51 (1) < 0.51	p<0.001
31 -Maximum diameter/Width (0) ≥ 1.52 (1) < 1.52	p<0.001

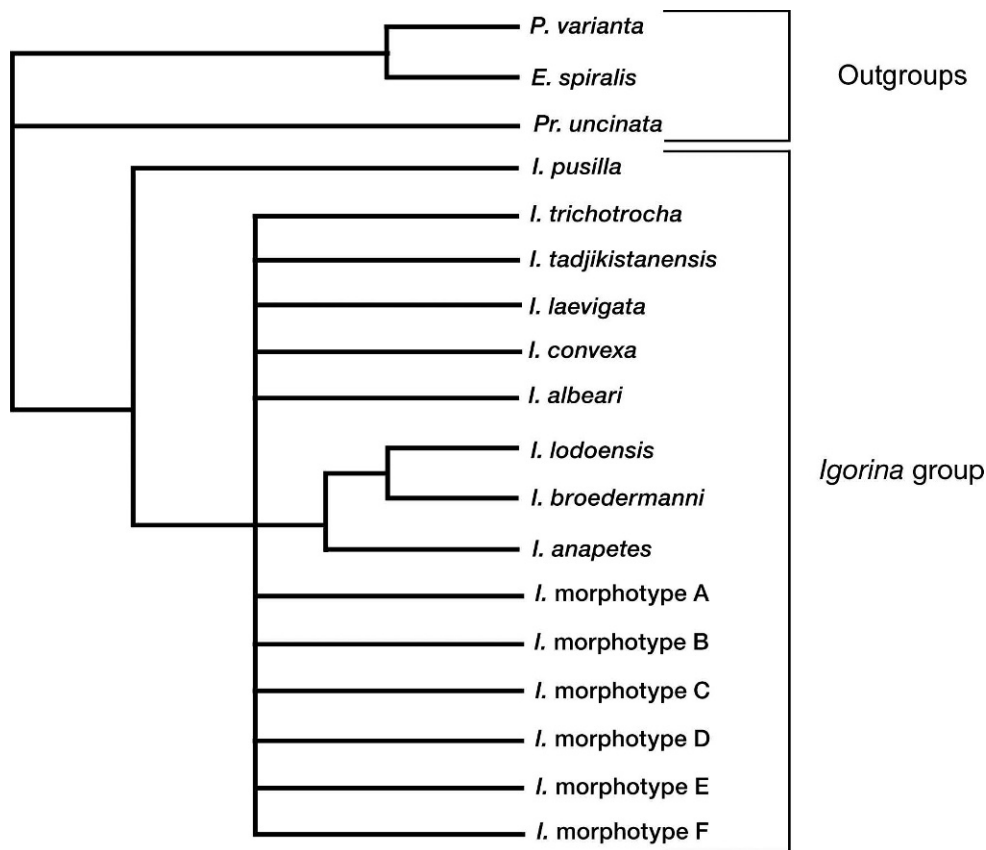


FIGURE 10. The strict consensus of 68 most parsimonious trees. The ingroup is formed by species of *Igorina*. The group of *I. broedermanni*, composed by *I. lodoensis*, *I. broedermanni*, and *I. anapetes*, forms a single clade with respect to the other igorinids.

One of the most parsimonious trees that well explains the relationships among the species of *Igorina* is shown in Figure 13. The results show that the Paleocene *Igorina* group descends directly from *I. pusilla*, which is in agreement with the biostratigraphic data (Bolli, 1957; Berggren and Norris, 1997; Olsson and others, 1999). *Igorina pusilla* is characterized by its small, symmetrically biconvex, compressed test with subacute axial periphery, and strongly curved sutures on the spiral side. *Igorina* morphotype A (which may be transitional between *I. pusilla* and the keeled forms) evolved from *I. pusilla* (a on Fig. 13). *Igorina* morphotype A is characterized by strongly curved sutures and an almost flat umbilical side sometimes with a slight keel on the last chamber. Most likely, *I. convexa* evolved from *Igorina* morphotype A and is ancestral to *I. tadjikistanensis* and *I. trichotrocha* (b on Fig. 13).

The clade with the keeled forms includes *I. laevigata* and *Igorina* morphotype D (c on Fig. 13). *Igorina* morphotype D differs from *I. laevigata* in having more chambers in the final whorl and it is likely a morphologic variant of *I. laevigata*. *Igorina albeari* appears related to forms with a high trochospire and a slight keel on the last chamber of the final whorl (*Igorina* morphotype B), and to forms showing a large number of chambers as *Igorina* morphotype E (d on Fig. 13). The inferred relationship of *Igorina* morphotype B with *I. albeari* is supported by their similarities in chamber shape, strongly curved (backward)

sutures, and peripheral margin passing from markedly rounded to subacute-acute in the last chamber. *Igorina* morphotype E is characterized by having a very variable peripheral margin ranging from subrounded to subangular, and a high number of chambers in the final whorl that tend to be arranged in a lower plane with respect to the elevated inner spire, and gives rise to forms (e on Fig. 13) having a high trochospire, an almost flat umbilical side, and a subangular peripheral margin (*Igorina* morphotype C). *Igorina* morphotype F apparently correlates with *Igorina* morphotype C and exhibits a high spire and a peripheral margin similar to *I. albeari*.

Igorina broedermanni, which occurs in the upper part of the Zone P5, is characterized by an increase in chamber number and the development of curved sutures on the spiral side. The analysis shows that the *broedermanni* group is more similar to the *mckannai-soldadoensis* group, as both are characterized by evolute coiling and a wide umbilicus (f on Fig. 13). Although the most parsimonious interpretation of the character conditions among the second ingroup (including the *Acarinina* species) places the *I. broedermanni* group closer to *A. soldadoensis* than to the *A. subsphaerica*–*A. mckannai* group, we recognize that this result may be an artifact of taxon sampling among the *Acarinina* species that may change with the inclusion of additional taxa (i.e., *A. esnehenensis*). Pending more detailed investigation of the relationships among the *Acarinina* group, it is likely that *I.*

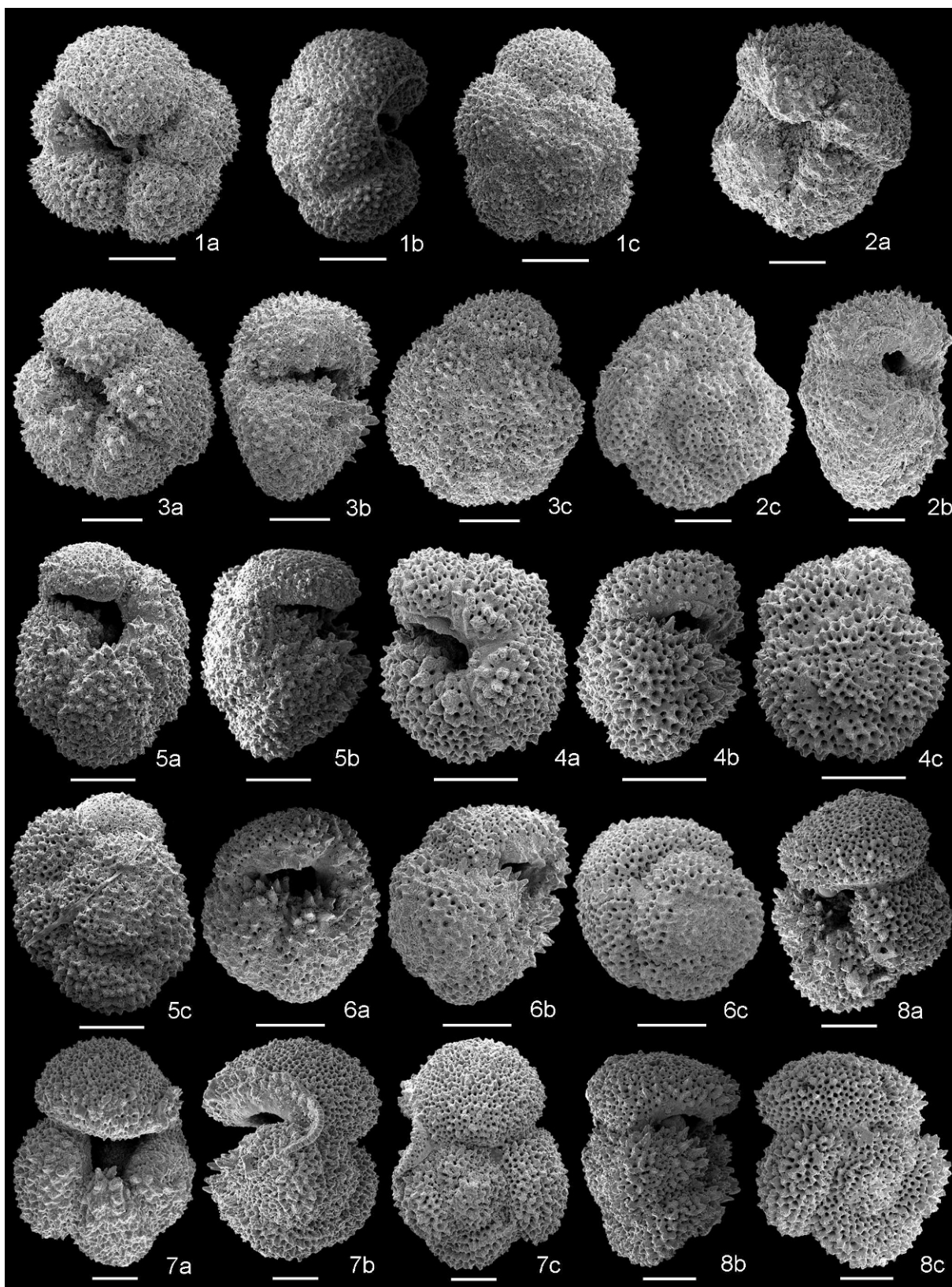


FIGURE 11. Species of the genus *Acarinina*. 1 *A. strabocella*, sample 198-1209B-25H-1, 140–141 cm. 2, 3 *A. nitida*: 2, sample 198-1209B-23H-1, 22–23 cm; 3, sample 198-1209B-23H-2, 21–22 cm. 4, 5 *A. mckannai*: 4, sample 198-1209B-23H-1, 82–83 cm; 5, sample 198-1209B-23H-3, 123–124 cm. 6 *A. subsphaerica*, sample 198-1209B-23H-5, 21–22 cm. 7, 8 *A. soldadoensis*: 7, sample 143-865B-12H-1, 130–132 cm; 8, sample 143-865B-12H-1, 130–132 cm. Scale bar = 100 μ m.

TABLE 4. Means of the morphometric measurements including the species of *Acarinina* (see Appendix 2 for description of characters).

Character	23	24	25	26	27	28	29	30	31
Mean									
<i>Parasubbotina varianta</i>	124.44	64.64	74.70	55.60	2.48	0.93	0.87	0.67	1.61
<i>Eoglobigerina spiralis</i>	120.94	48.68	63.96	46.92	1.88	1.10	0.91	0.58	1.54
<i>Praemurica uncinata</i>	120.40	48.90	60.78	53.00	2.67	1.07	0.98	0.80	1.66
<i>Igorina pusilla</i>	100.20	41.08	58.50	40.60	1.67	1.20	1.03	0.54	1.57
<i>Igorina trichotrocha</i>	106.05	32.65	47.63	41.42	1.89	1.64	1.17	0.62	1.75
<i>Igorina tadjikistanensis</i>	106.10	30.90	45.06	37.30	1.73	1.84	1.21	0.51	1.32
<i>Igorina convexa</i>	109.58	33.06	52.09	37.14	1.63	1.57	1.07	0.49	1.38
<i>Igorina laevigata</i>	73.78	33.23	56.40	35.32	1.82	1.51	1.05	0.41	1.73
<i>Igorina albeardi</i>	91.51	27.10	37.39	32.89	1.77	1.65	1.39	0.48	1.52
<i>Igorina lodoensis</i>	102.06	35.20	61.40	47.10	1.81	1.40	0.98	0.60	1.58
<i>Igorina broedermanni</i>	105.82	37.02	49.32	47.92	1.85	1.40	1.11	0.66	1.43
<i>Igorina anapetes</i>	114.10	30.40	37.78	46.50	1.78	1.80	1.34	0.77	1.35
<i>Igorina</i> morphotype A	87.70	49.56	61.62	36.95	1.67	1.15	0.97	0.44	1.69
<i>Igorina</i> morphotype B	92.42	35.78	48.16	36.42	1.69	1.49	1.22	0.46	1.35
<i>Igorina</i> morphotype C	102.16	29.76	45.94	33.84	1.46	1.51	1.24	0.43	1.14
<i>Igorina</i> morphotype D	74.36	25.24	33.20	34.86	1.78	1.87	1.49	0.40	1.73
<i>Igorina</i> morphotype E	98.43	31.12	39.63	37.26	1.71	1.66	1.22	0.53	1.47
<i>Igorina</i> morphotype F	109.96	35.62	46.50	37.86	1.57	1.34	1.19	0.47	1.22
<i>Acarinina strabocella</i>	123.60	46.02	67.06	46.61	1.83	1.14	0.93	0.58	1.33
<i>Acarinina nitida</i>	119.80	49.26	80.69	44.55	1.85	1.20	0.85	0.55	1.34
<i>Acarinina subsphaerica</i>	125.94	57.40	61.18	46.23	1.51	1.03	0.94	0.51	1.04
<i>Acarinina mckannai</i>	124.73	42.16	56.67	37.38	1.78	1.17	0.97	0.51	1.32
<i>Acarinina soldadoensis</i>	124.50	54.84	69.56	46.32	2.13	0.97	0.80	0.56	1.42

lodoensis, which is distinguished by its biconvex and lobulate test, evolved from either *A. soldadoensis* or *A. mckannai* approximately at the P4c/P5 zonal boundary in the upper Paleocene.

Our cladistic analysis also suggests that the *Acarinina* group derives from the cancellate *Eoglobigerina spiralis*, which agrees with the analytical results of Berggren and Norris (1997), who also reported occurrences of specimens

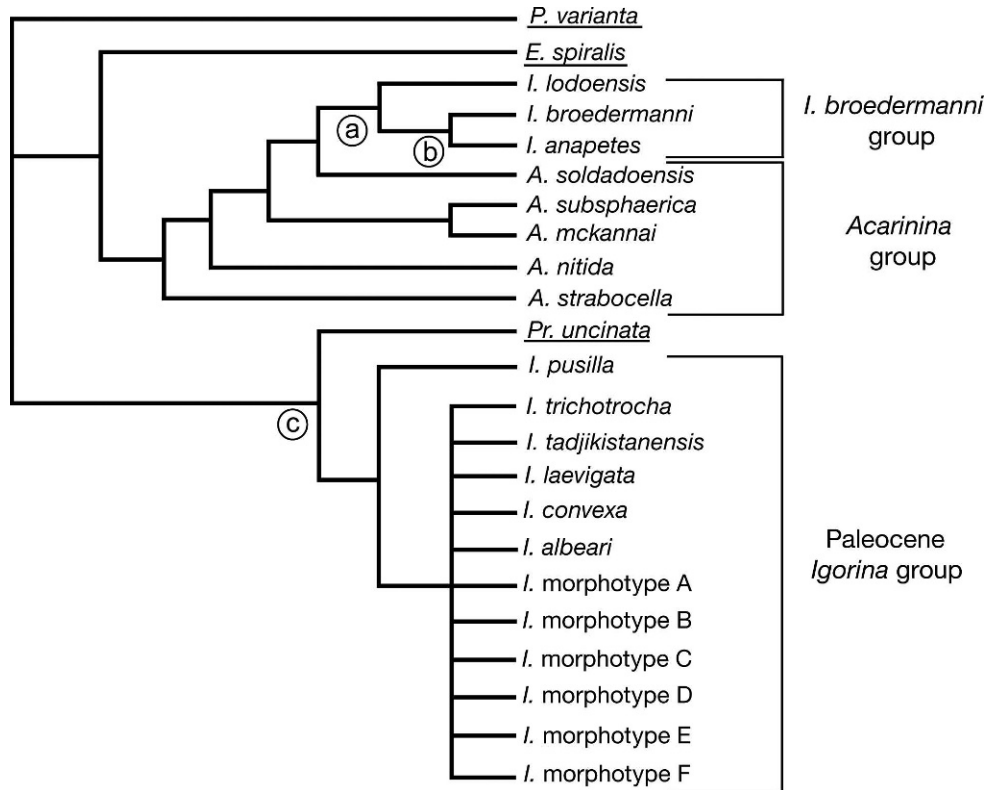


FIGURE 12. Strict consensus tree obtained including the main species of Paleocene *Acarinina*. The *broedermanni* group is more closely related to *Acarinina* rather than to *Igorina*. Letters indicate percentage of occurrence of the node under the bootstrapping test (see further explanation in the text). Outgroups are underlined.

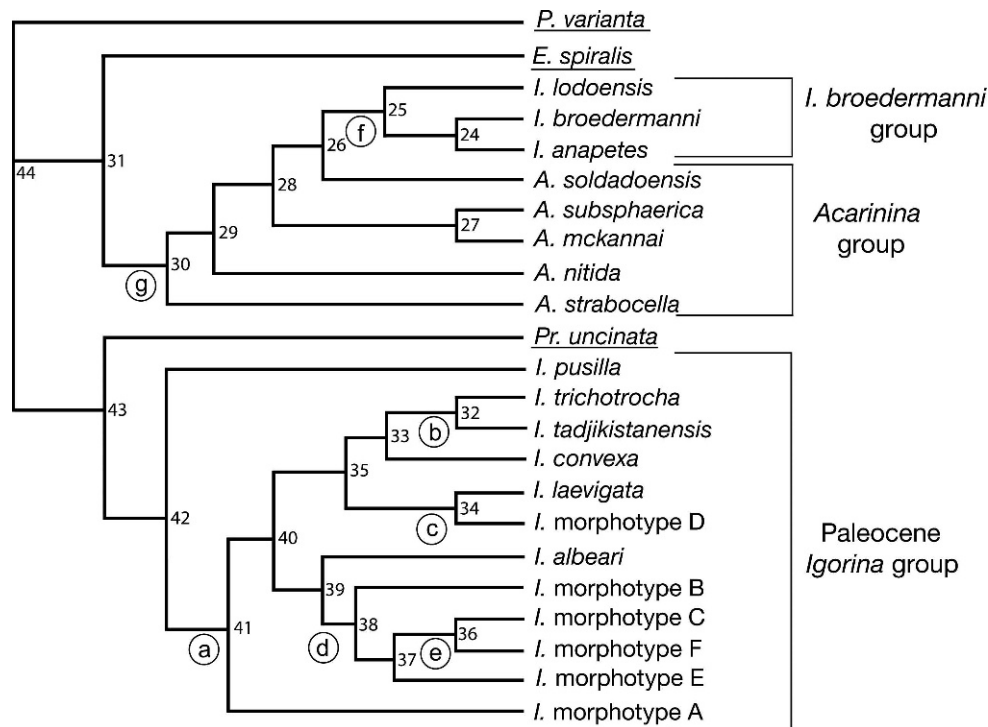


FIGURE 13. One of the 89 parsimonious trees obtained after the inclusion of *Acarinina* in the phylogenetic analysis. Outgroups are underlined. The letters in the circle indicates the main evolutionary steps on cladogram (see further explanation in the text). The numbers represent the node and relative character state changes. All characters states supporting the node under Deltran optimisation. Unambiguous apomorphies are listed in parentheses. Node 44 → *P. varianta*: 8.1, 22(0); Node 44 → Node 31: 20(1), 21(1); Node 31 → *E. spiralis*: 9(0); Node 31 → Node 30: 1(1), 12(1), 14(1), 31(1), 32(1); Node 30 → Node 29: 32(3); Node 29 → Node 28: 13(1); Node 28 → Node 26: 32(5); Node 26 → Node 25: 1 (0), 14(0), 24(1), 28(1), 32(6); Node 25 → *I. lodoensis*: 4.0, 20(0), 31(0); Node 25 → Node 24: 15(1), 16.3, 18.0, 25(1), 29(1); Node 24 → *I. anapetes*: 3.0, 10(2), 17(2), 27(1), 32(7); Node 26 → *A. soldadoensis*: 8(1); Node 28 → Node 27: 27(1); Node 27 → *A. subsphaerica*: 7.1, 9(0), 19(1); Node 27 → *A. mckannai*: 8(1), 26(1); Node 29 → *A. nitida*: 9(0), 20(0); Node 44 → Node 43: 1(0), 16(0), 18(0); Node 43 → *Pr. uncinata*: 3(0), 4.0, 8.1; Node 43 → Node 42: 2(1), 4.1, 9(0), 27(1), 32(1); Node 42 → *I. pusilla*: 15(1), 29.1; Node 42 → Node 41: 23(1), 26(1), 30(1), 32(2); Node 41 → Node 40: 24(1), 25(1), 28(1), 29.1; Node 35 → Node 33: 23(0); Node 33 → Node 32: 16.1, 19.1, 30(0); Node 32 → *I. trichotrocha*: 3(0), 18(1), 26(0), 27(0); Node 32 → *I. tadjikistanensis*: 4.02, 8.1, 11(1), 31.1; Node 33 → *I. convexa*: 31.1; Node 35 → Node 34: 5(1), 6(2), 15.1, 19.1; Node 34 → *I. laevigata*: 25(0), 27(0); Node 34 → *I. morphotype D*: 10(12), 16.2, 17(12), 21(1); Node 40 → Node 39: 10(2), 16.2, 17(2), 20.1; Node 39 → Node 38: 8(1), 31(1); 32(3); Node 38 → *I. morphotype B*: 6(1); 7.1, 32(4); Node 38 → Node 37: 21(1), 22(2); Node 37 → Node 36: 7.1, 23(0); Node 36 → *I. morphotype C*: 15.1; Node 37 → *I. morphotype E*: 4.02, 15.1, 30(0); Node 36 → *I. morphotype F*: 4.02, 19(1), 28(0); Node 41 → *I. morphotype A*: 20.1.

possessing a nonspinose wall. Our analysis also shows that *A. strabocella*, the first representative of the genus *Acarinina*, characterized by weakly developed muricae, evolved from *Eoglobigerina spiralis* (g on Fig. 13). In addition, the group of quadrate acarininids (*A. nitida*) and the group of round acarininids (*A. mckannai* and *A. soldadoensis*) evolved from *A. strabocella*. Finally, *A. subsphaerica*, characterized by its high trochospire, evolved from *A. nitida* by developing rounded chambers, and subsequently evolved into *A. mckannai*.

ZONAL BIOEVENTS AND BIOSTRATIGRAPHIC IMPLICATIONS

The application of planktic foraminiferal Paleocene biostratigraphy was introduced in the 1950s for petroleum exploration, in particular in the northern Caucasus, Crimea, and other sites in the southwestern region of the former Soviet Union (i.e., Subbotina, 1953; Alimarina, 1963 and references therein). Other independent biozonal schemes were developed and applied in western countries based on materials from the Caribbean Sea (Brönnimann, 1952; Bolli, 1957 modified in 1966), the Gulf and Atlantic coasts of the United States (Loeblich and Tappan, 1957),

and in the Tethys (i.e., Luterbacher, 1964). Blow (1969) assigned a numerical notation to the nominal biozones using the prefix P (for Paleocene) followed by a progressive number. Since then, the biostratigraphic database has rapidly increased, especially after the initiation of the Deep Sea Drilling Project (DSDP) in 1968. Both the DSDP and its successor, the Ocean Drilling Project (ODP) recovered continuous sedimentary successions with well-preserved specimens that allowed improved definition of the boundaries between biozones and development of a biostratigraphic scheme on a global scale (Blow, 1979; Berggren and others, 1995). The latest biostratigraphic scheme is that of Berggren and Pearson (2005), in which the tropical-subtropical zonation comprises seven biozones (P0–P5) and eight subzones in the Paleocene and 16 biozones in the Eocene (E1–E16), each subdivision defined by the lowest or highest occurrences of marker species.

Since the first biostratigraphic studies, the mid-Paleocene interval corresponded to the important step in the evolutionary history of planktic foraminifera in which the rapid spread of muricate taxa is manifested in the appearance of the genera *Morozovella*, *Igorina*, and *Acarinina*. In early schemes (Bolli, 1957, modified in

1966), this interval included two biozones, namely the *Globorotalia pusilla pusilla* Zone and the *Globorotalia pseudomenardii* Zone, each based on the first occurrences of the two nominal taxa (now *Igorina pusilla* and *Globanomalina pseudomenardii*, respectively). Berggren and others (1985) and Toumarkine and Luterbacher (1985) first subdivided the *Globorotalia pusilla pusilla* Zone (= P3 of Blow, 1969) into two subzones (P3a and P3b) based on the supposed earlier appearance of *Morozovella angulata* with respect to *I. pusilla*. Successive studies of well-preserved specimens from deep-sea cores, however, demonstrated that these two taxa appeared contemporaneously. Subsequently, Berggren and others (1995) and Berggren and Pearson (2005) equated the base of Subzone P3b to the lowest occurrence of *I. albeari*, a taxon that had not been used as a marker species in the previous biostratigraphic schemes (Bolli, 1957, 1966; Premoli Silva and Bolli, 1973; Berggren and Miller, 1988). Arenillas and Molina (1997) subdivided Zone P3 into three subzones that in stratigraphic order are the *Morozovella angulata*, *Morozovella crosswicksensis*, and *Igorina albeari* subzones, based on including the lowest occurrence of *M. crosswicksensis* (Olsson, 1960), which was later shown to be a junior synonym of *M. occlusa* (Loeblich and Tappan, 1957) by Olsson and others (1999) and Sprong and others (2009). According to our study we can confirm that the appearances of *I. pusilla* and *M. angulata* are coeval and define the base of Subzone P3a (Fig. 14).

A major problem in defining the boundary between Subzones P3a and P3b is the concept of the marker species *I. albeari* that, as mentioned above, may have been interpreted differently by the various authors (i.e., Olsson and others 1999; Sprong and others 2009). In our opinion, lumping *I. laevigata* with *I. albeari* is not correct and should be rejected; furthermore, *I. albeari* should not include specimens with five chambers in the final whorl, which instead fall within the variability of *I. laevigata*.

Although most authors have continued to lump the *I. laevigata* morphotaxon with *I. albeari*, thereby confusing the definition of the zonal boundaries, we observed that *I. laevigata* appears earlier than *I. albeari*. Consequently, we redefine Subzone P3b as the interval from the lowest appearance of *I. laevigata* to the lowest appearance of *G. pseudomenardii* (= base of Zone P4), whereas *I. albeari* appears in the mid-upper part of Subzone P3b.

Berggren and others (1995) subdivided Zone P4 into three subzones of very uneven duration: Subzone 4a is extremely short and was redefined by Berggren and others (2000) as the interval ranging from the lowest occurrence of *G. pseudomenardii* to the highest occurrence of *Parasubbotina variospira* instead of *Acarinina subsphaerica*; Subzone P4c is well defined by the lowest occurrence of *A. soldadoensis*, whereas the long Subzone P4b is intermediate between the top of Subzone P4a and the bottom of Subzone P4c.

In the present study, we apply the tropical-subtropical zonation proposed by Berggren and Pearson (2005) for the Paleocene and Eocene interval, except for their redefinition of Subzone P3b (see above). However, we have updated the stratigraphic ranges of igorinid species (Fig. 14) according to our current and prior observations (Petrizzo, 2005, 2007;

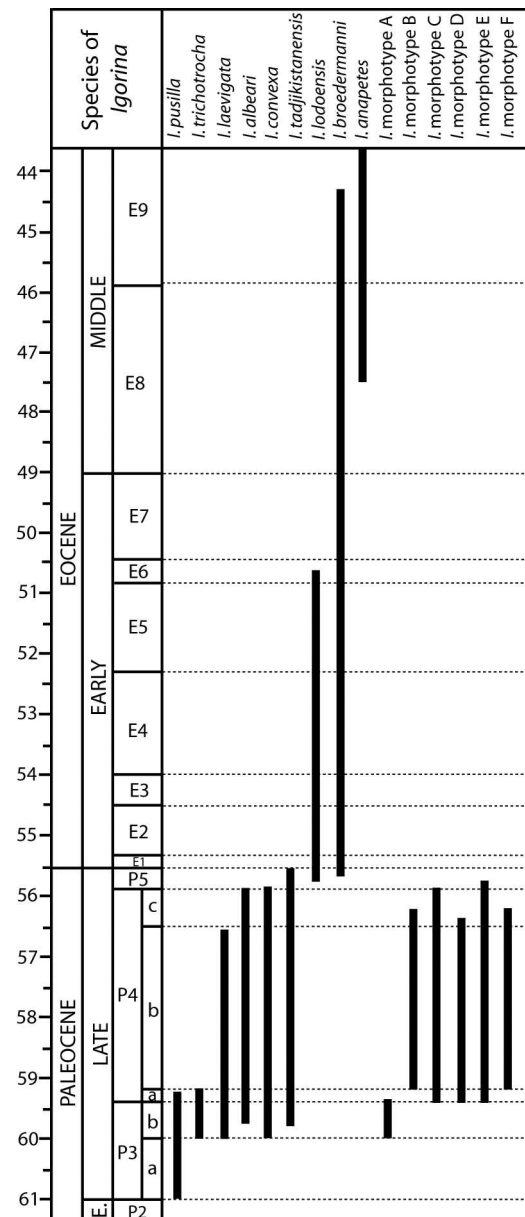


FIGURE 14. Stratigraphic distribution of species of *Igorina* modified after Olsson and others (1999), and Pearson and others (2006).

Petrizzo and others, 2005, 2008), even though they agree largely with those in Berggren and Norris (1997), Olsson and others (1999), and Berggren and others (2006).

SUMMARY AND CONCLUSIONS

The reconstructed phylogenetic relationships illustrated in Figure 15 provide insight into the evolutionary history of the genus *Igorina*. Our analysis confirms that *I. pusilla* is the first representative of the *Igorina* lineage and that it evolved from praemuricate forms of the *uncinata* plexus at the base of Subzone P3a (Olsson and others, 1999) upon acquiring a thicker layer of pustules that covers the praemuricate wall of the inner spire and by developing conical to elongate-ovate chambers.

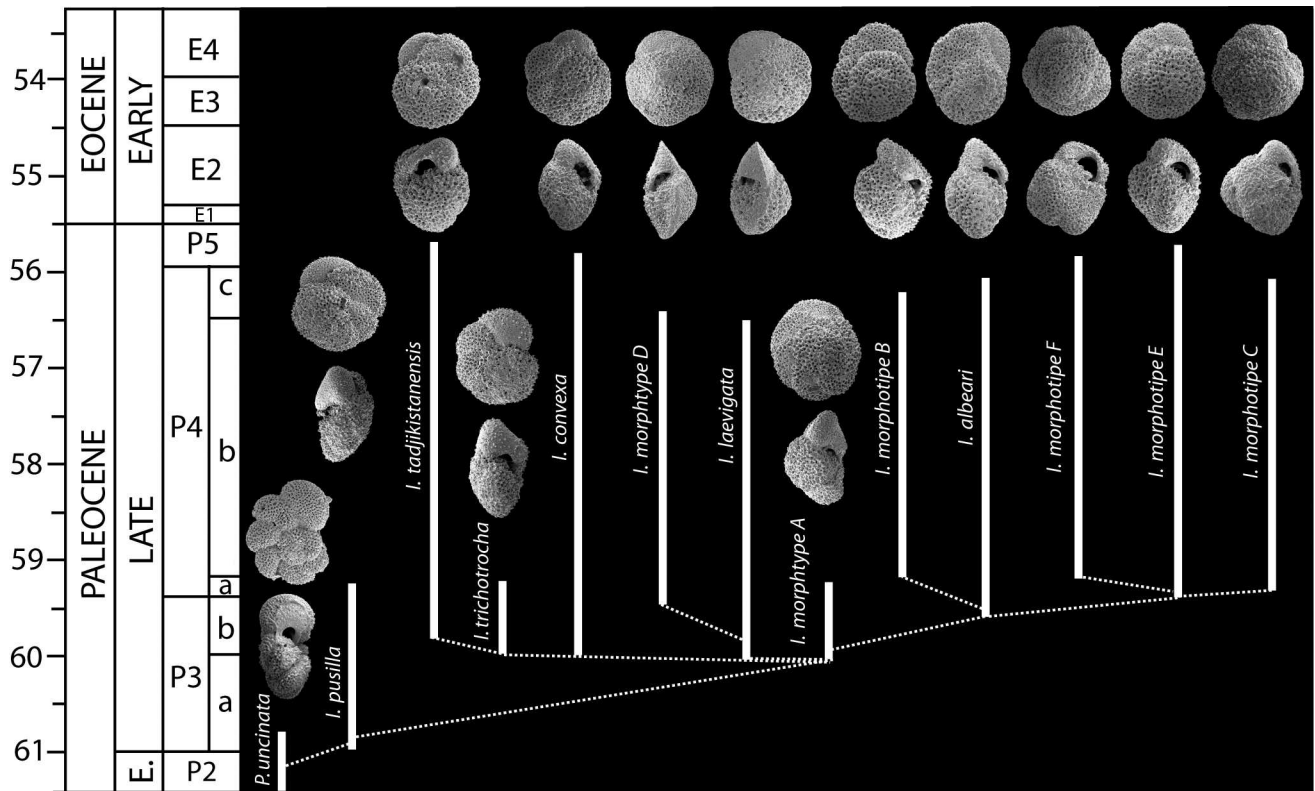


FIGURE 15. Phylogenetic reconstruction of the genus *Igorina* based on stratigraphic data and parsimony analysis. See explanation in the text.

In agreement with the results obtained from our parsimony analysis, we suggest that *I. laevigata* and *I. albeari* both derived from a common ancestor, here identified as *Igorina* morphotype A, and evolved into two independent phyletic lineages. Our observations reveal that the first occurrence of *I. laevigata* predates the appearance of *I. albeari* and, as mentioned above, is used here to denote the base of Subzone P3b. Moreover, *I. laevigata* disappears within Subzone P4b, whereas *I. albeari* disappears at the P4c/P5 boundary.

Igorina morphotype A appears at the top of Subzone P3a and represents a transitional form from *I. pusilla* and the “keeled” taxa (*I. laevigata* and *I. albeari*). Specimens closely resembling *Igorina* morphotype A have been regarded as primitive forms of *I. albeari* by Sprong and others (2009). *Igorina* morphotype A, formally described as *I. praecarinata*, is here regarded as a new species (see Systematic Taxonomy section, Fig. 16).

In our sample from the Pacific Ocean (Holes 1209B and 865B), we have observed keeled forms characterized by a large number of chambers. These forms, named *Igorina* morphotype D, appear in Subzone P4a, having evolved from *I. laevigata*. Similar forms with 7–8 chambers in the final whorl have been illustrated by Blow (1979, pl. 93, figs. 1, 4). Based on our results and observations, we include *Igorina* morphotype D within the morphologic variability of *I. laevigata*.

Igorina convexa, which appears in Subzone P3b, is characterized by its symmetrically biconvex test and it evolved from *Igorina* morphotype A (= *I. praecarinata* n. sp.) by developing less-elongate chambers. In our samples,

I. convexa disappears at the P4c/P5 boundary. *Igorina trichotrocha*, the most enigmatic taxon assigned to the genus *Igorina* (Olsson and others, 1999), also correlates with the *convexa* plexus.

Olsson and others (1999) believed that *I. tadjikistanensis* evolved from *I. pusilla* in the middle to upper part of Subzone P3b, then disappears within Zone P5. Conversely, our cladistic analysis suggests that *I. tadjikistanensis* evolved from *I. convexa* in the middle part of Subzone P3b. Throughout its stratigraphic range *I. tadjikistanensis* tends to increase the number of chambers (8–9) in its outer whorl, even though in our material we noticed some morphotypes with 6 chambers in the final whorl. Moreover, some morphotypes of *I. tadjikistanensis* in Zone P4 display a higher trochospire.

In the residues of Zone P4 from Hole 1209B, we have noticed some igorinids that are different from the usually observed taxa. These specimens are of medium size and display a larger number of chambers (9–10) in the last whorl, which has a rounded peripheral margin. High-spined specimens are also very frequent, appearing in Zone P4 and displaying a various combinations of features used to identify them as *Igorina* morphotypes B, C, E, and F.

According to our analysis, *Igorina* morphotype B, characterized by a thick biconvex test and fine keel on the last chamber, evolved from *I. albeari* and is considered here to fall within the variability of *I. albeari*. This morphotype of *I. albeari* was previously reported and illustrated by Berggren and Norris (1997, pl. 9, fig. 19) from ODP Hole 758A. *Igorina* morphotype C is similar to *Igorina* morphotype E in having a high number of chambers in the final

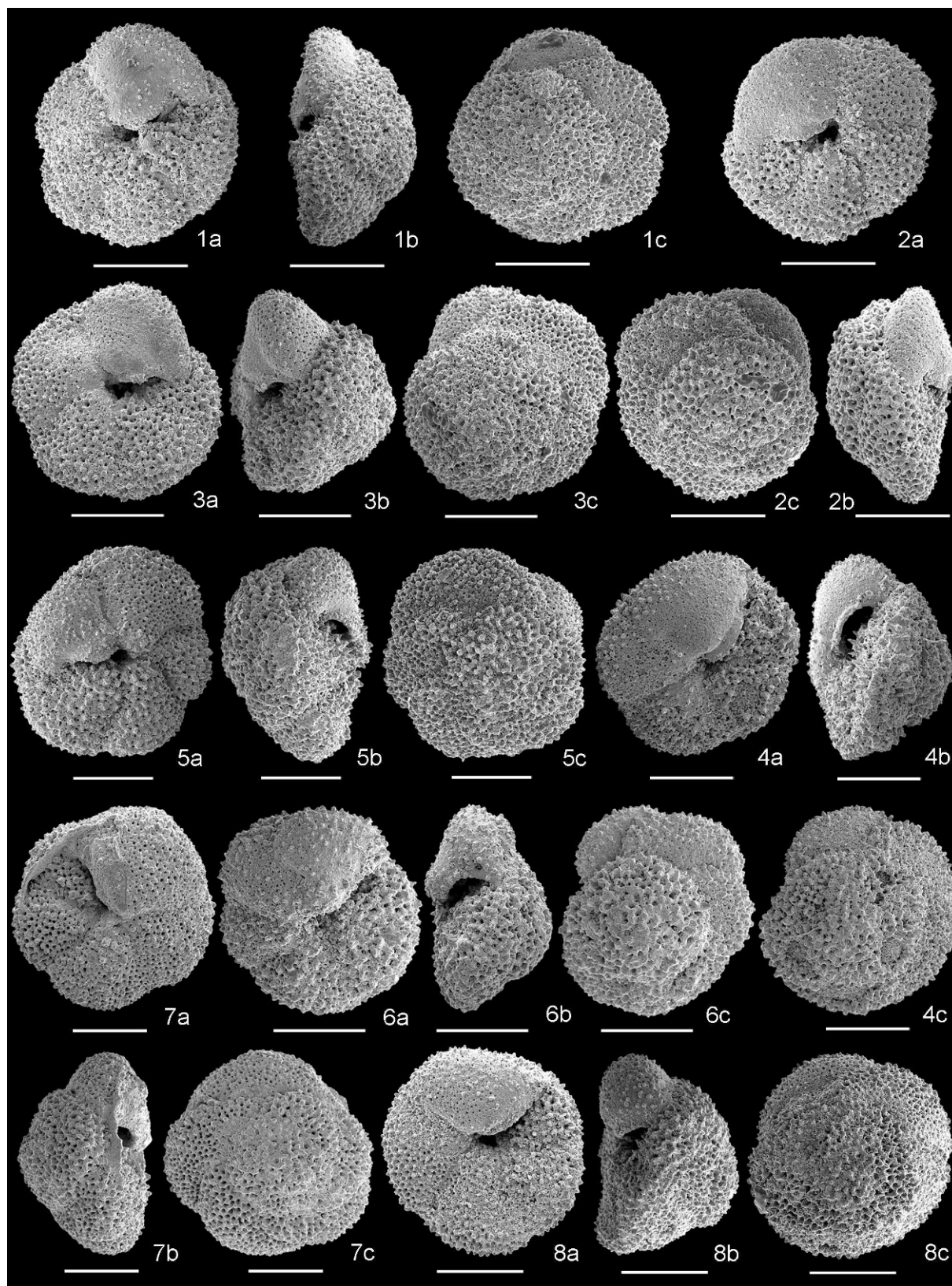


FIGURE 16. *Igorina praecarinata*, n. sp. (= *Igorina* morphotype A); scale bar = 100 μ m: 1–3 Primary types: 1, holotype (Micro-Unimi no. 1977), from 198-1209B-24H-7, 41–42 cm; 2, paratype 1 (Micro-Unimi no. 1978), from 198-1209B-24H-7, 41–42 cm; 3, paratype 2 (Micro-Unimi no. 1979), from 198-1209B-24H-7, 41–42 cm. 4–8 Secondary types: 4, from 198-1209B 24H-6, 21–22 cm; 5, from 198-1209B-24H-7, 41–42 cm; 6, from 198-1209B-24H-6, 21–22 cm; 7, from 198-1209B-24H-7, 41–42 cm; 8, from 198-1209B-24H-7, 41–42 cm.

whorl, but it is distinguished by its very high trochospire, almost flat umbilical side, and subangular peripheral margin. *Igorina* morphotype F is very close to *Igorina* morphotype C but differs by its irregular, more-convex umbilical side. These three morphotypes (C, E, F) are closely related to each other as well as to the *I. albeari* group, from which they descend and appear in Subzones P4a and P4b (Fig. 14). To accommodate these three morphotypes, a new species, *Igorina paraspiralis*, is erected here based on their consistent occurrences and distinctive features (see Systematic Taxonomy section, Fig. 17).

The topmost part of the Paleocene (Zone P5) is marked by the appearance of *I. lodoensis*. Blow (1979) suggested that *I. lodoensis* evolved from the *convexa* plexus in the upper Paleocene. Berggren and others (2006), considering *I. convexa* and *I. tadjikistanensis* synonyms, indicated that *I. lodoensis* is probably a direct descendant of *I. tadjikistanensis*. *Igorina lodoensis* develops a more-planoconvex test, more-lobulate chambers, and straighter sutures compared to *I. tadjikistanensis*. In our parsimony analysis, *I. lodoensis* evolved from *Acarinina*, not *Igorina*. Another species occurring in the terminal part of Zone P5 is *I. broedermanni*, which Blow (1979) suggested as having evolved gradually from *I. lodoensis* in lower Eocene Zone P8. However, we agree with Berggren and others (2006) that transitional forms between these two species already appear within (former) Zone P5. The last descendant of the *broedermanni* lineage is *I. anapetes*, which evolves from *I. broedermanni* by increasing the number of chambers in the final whorl and developing an increasingly larger umbilicus and evolute spire. *Igorina anapetes* disappears in the middle Eocene (Zone E9). Consequently, our phylogenetic analysis suggests that the genus *Igorina* is actually a polyphyletic group with the Eocene forms having evolved from a different ancestor than that of the Paleocene forms.

Finally, in order to verify the results of the cladistic analysis, we have performed a preliminary SEM analysis on the wall structure of the Paleocene specimens of *Igorina*. The Paleocene representatives of *Igorina* appear more incrustated and the pustules are short, whereas *I. lodoensis* and the other Eocene taxa are not incrustated and have pustules more similar to muricae (Fig. 18). Moreover, in Paleocene *Igorina*, the ridges among pores appear thicker and more robust with respect to those observed in the *broedermanni* plexus. However, further detailed studies of the wall texture of these taxa are needed to determine the real ancestor and taxonomic position of the *broedermanni* plexus.

SYSTEMATIC TAXONOMY

Igorina trichotrocha (Loeblich and Tappan, 1957)

Fig. 4.6

Globorotalia trichotrocha Loeblich and Tappan in Loeblich and Tappan, 1957, p. 195, pl. 50, figs. 5a–c.

Globorotalia trichotrocha Loeblich and Tappan in Olsson, 1960, p. 49, pl. 10, figs. 1–3.

?*Acarinina* aff. *trichotrocha* (Loeblich and Tappan) in Shutskaya, 1970, p. 118–120, pl. 20, figs. 3a–c.

Acarinina trichotrocha (Loeblich and Tappan) in Shutskaya, 1970, p. 118–120, pl. 24, figs. 6a–c.

Igorina “trichotrocha” (Loeblich and Tappan) in Berggren and Norris, 1997, p. 62, pl. 9, figs. 3–4, 7.

Igorina trichotrocha (Loeblich and Tappan) in Berggren and others, 2000, p. 12, pl. 3, fig. 20.

Occurrence. Zones P3b–P4a.

Geographic distribution. This species has been recorded at low and mid-latitudes and is present in (sub)tropical assemblages from the Atlantic and Pacific Oceans.

Dimensions of holotype. Diameter = 0.15 mm, thickness 0.8 mm.

Description. Test small, trochospiral, planoconvex, spiral side flat, umbilical side markedly convex tending to conical; equatorial outline subcircular, moderately lobate; periphery subangular to subacute; 2½–3 whorls; 6½ chambers in the last whorl, initially petaloid, then becoming subcrescentic (nearly equal breadth and height in holotype) in last three, on spiral side slightly inflated, on umbilical side triangular with slightly inflated surface; sutures on spiral side distinct, initially slightly depressed, curved obliquely backwards becoming straight radial and depressed in the last chambers, on umbilical side slightly to moderately depressed, straight and radial; umbilicus small and deep; aperture a very small umbilical-extraumbilical slit; test surface pustulose throughout, early spire more prominently pustulose with a slightly developed crust passing to very short irregular ridges overall poorly developed, last two chambers somewhat smoother, covered by single sparse pustules, umbilical side covered by single pustules more prominent around umbilical area.

Remarks. The taxonomic status of the species *trichotrocha* has been uncertain for some time. Loeblich and Tappan (1957) originally included this species in *Globorotalia* and successively in *Acarinina* (Loeblich and Tappan 1970). Pearson (1993) included *I. trichotrocha* in the “muricate biconvex muricates and related forms” plexus. Berggren and Norris (1997) assigned it with caution to *Igorina*, but Berggren and others (2000, pl. 3, fig. 20) firmly assigned it to the genus.

Berggren (communication, 2009) suspected that the holotype of *I. trichotrocha* was planoconvex benthic foraminifera. However, we found forms in Hole 1209B that correspond to the original description of this species; therefore, we retain valid the status of this taxon, which is distinguished by its small size, planoconvex test, and essentially straight radial sutures in the final chambers on the spiral side.

Blow (1979) considered one of the paratypes of *I. trichotrocha* (Loeblich and Tappan 1957, pl. 50, fig. 5a–c) to belong to his new taxon, *Morozovella finchi*. Berggren and Norris (1997) agreed with Blow’s opinion but considered *M. finchi* a junior synonym of *M. edgari*.

This form probably evolved from *I. convexa* in upper Paleocene Subzone P3b by developing a planoconvex test and a subangular peripheral margin.

Igorina praecarinata Soldan, Petrizzo, Premoli Silva and Cau, n. sp.

Figs. 16.1 (holotype), 16.2 (paratype 1), 16.3 (paratype 2), 16.4–16.8

Globorotalia (*Acarinina*) sp. in Blow, 1979, pl. 87, fig. 9.

Globorotalia (*Acarinina*) *convexa convexa* Subbotina in Blow, 1979, pl. 88, fig. 3.

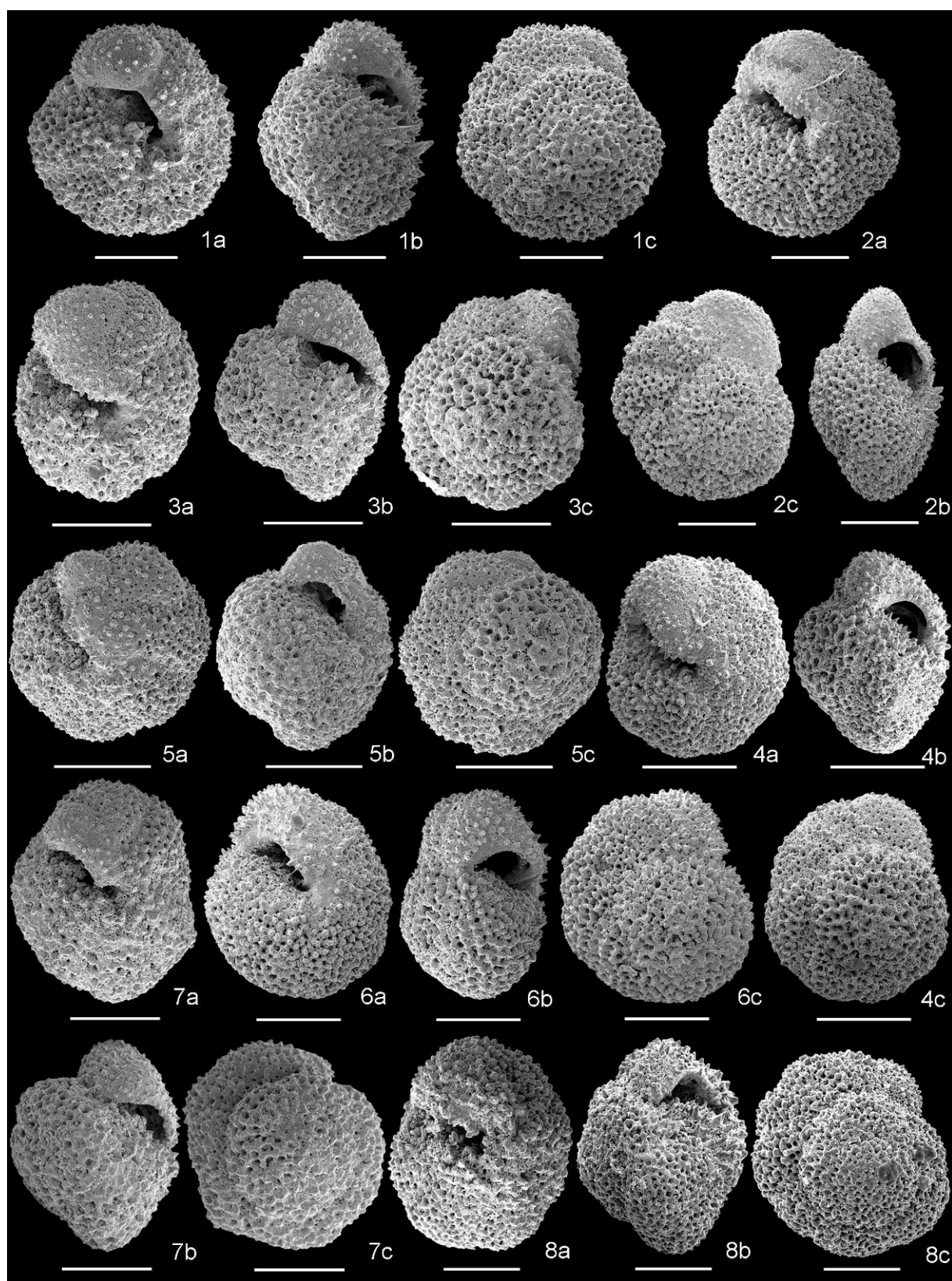


FIGURE 17. *Igorina paraspiralis*, n. sp. (= *Igorina* morphotypes C, E, and F). Scale bar = 100 μ m. 1–3 Primary types: 1, holotype (Micro-Unimi no. 1980), from 198-1209B-22H-4, 101–102 cm; 2, paratype 1 (Micro-Unimi no. 1981), from 198-1209B-22H-4, 101–102 cm; 3, paratype 2 (Micro-Unimi no. 1982), from 198-1209B-22H-4, 101–102 cm. 4–8 Secondary types: 4, from 198-1209B-22H-4, 101–102 cm; 5, from 198-1209B-23H-1, 103–104 cm; 6, from 198-1209B-22H-6, 21–22 cm; 7, from 198-1209B-22H-6, 1–2 cm. 8, from 198-1209B-23H-3, 91–92 cm.

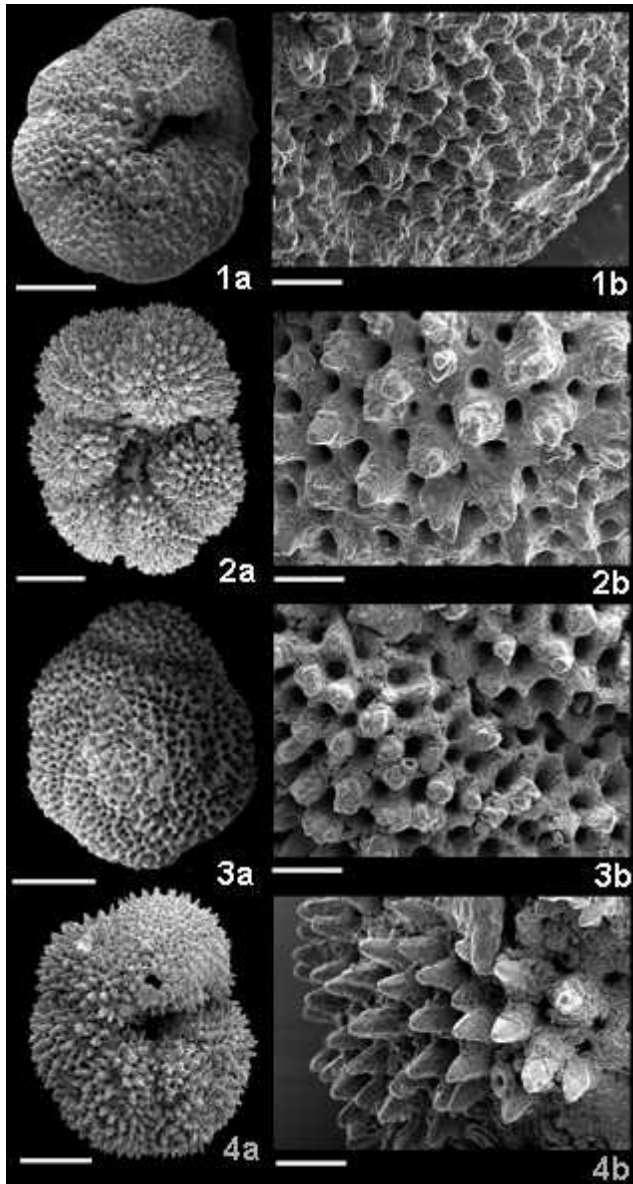


FIGURE 18. 1 *I. laevigata*, from 143-865B-13H-2, 50–52 cm. 2 *I. lodoensis*, from 143-865B-11H-4, 48–50 cm. 3 *I. tadjikistanensis*, from sample 143-865B-14H-4, 47–49 cm. 4 *I. broedermanni*, from 143-865B-7H-3, 130–132 cm. The test surfaces of Paleocene species of *Igorina* (1b and 3b) are more encrusted than the Eocene species (2b and 4b). Subparallel ridges between pores only occur in Paleocene species whereas only Eocene forms have muricae on the umbilical side. Scale bar = 100 μ m for 1a, 2a, 3a, and 4a; scale bar = 20 μ m for 1b, 2b, 3b, and 4b.

Igorina albeari (Cushman and Bermúdez) in Olsson and others, 1999, p. 69, pl. 56, figs. 13–16.

Igorina pusilla (Bolli) in Sprong and others, 2009, p. 70, fig. 4, 4a–c, 5a–c.

Igorina albeari (Cushman and Bermúdez) in Sprong and others, 2009, p. 70, fig. 4, 7a–c.

Derivation of name. Refers to the absence of a keel on the peripheral margin.

Material. Holotype (Micro-Unimi no. 1977); paratypes 1 and 2 (Micro-Unimi no. 1978 and 1979, respectively) deposited in the Micropaleontological Collection, Univer-

sità degli Studi di Milano, Dipartimento di Scienze della Terra “A. Desio”, Italy.

Occurrence. Zones P3b–P4a (basal part).

Geographic distribution. This species has been recorded at low and mid latitudes and it is present in (sub)tropical fossil assemblages from the Atlantic and Pacific oceans.

Dimensions of holotype. Diameter = 0.22 mm; thickness = 0.13 mm.

Description. Test moderately to strongly biconvex, periphery essentially circular, peripheral margin subacute, surface texture pustulose; umbilical side very flat with 5–6 triangular chambers, intercameral sutures straight, weakly incised, umbilicus small, round and narrow; spiral side with 6–7 crescentic chambers in last whorl, intercameral sutures strongly recurved; aperture an interiomarginal, umbilical-extraumbilical, low arch extending nearly to the periphery.

Remarks. *Igorina praecarinata* is considered here as an intermediate form between *I. pusilla* and the keeled taxa (*I. laevigata* with well-developed keel and *I. albeari* sometimes with a slight keel on the last chamber). This form has never been described by previous authors because it has often been reported as *I. pusilla* or *I. albeari* (Sprong and others, 2009) or it was interpreted as a primitive (early) form of *Igorina albeari* (Olsson and others, 1999; Sprong and others, 2009). Nevertheless, *I. praecarinata* can be distinguished from other igorinids, particularly *I. pusilla* and *I. albeari*, by its very flat umbilical side and in the marked compression of the chambers. Blow (1979) illustrated in edge view a specimen from Zone P3 that he assigned to *Globorotalia (Acarinina) convexa convexa*. The peripheral margin of this form is very similar to that of *I. praecarinata* and probably should be included in this taxon. Generally, *I. praecarinata* lacks the carina, but in some specimens show a slight keel on the last chamber. In Hole 1209B (Subzone P3b), we have found several specimens characterized by a high spire (Fig. 16.8). In these morphotaxa, the umbilical side is very flat and never displays a keel on the last chamber. *Igorina praecarinata* descended from *I. pusilla*, and according to our analysis it evolved into *I. laevigata* and *I. albeari* in Subzone P3b.

Distinguishing features. *Igorina praecarinata* is distinguished from *I. pusilla* in having a more acute peripheral margin. It differs from *I. laevigata* in the absence of a well-developed keel and from *I. albeari* in possessing a much flatter umbilical side and fewer chambers in the last whorl.

Igorina paraspiralis Soldan, Petrizzo, Premoli Silva and Cau, n. sp.

Figs. 17.1 (holotype), 17.2 (paratype 1), 17.3 (paratype 2), 17.4–17.8

Globorotalia (Acarinina) convexa cf. *convexa* (Subbotina) in Blow, 1979, pl. 100, figs. 1, 2, 4.

Globorotalia (Acarinina) convexa convexa (Subbotina) in Blow, 1979, pl. 100, figs. 5–9.

Igorina pusilla (Bolli) in Olsson and others, 1999, p. 70, pl. 57, figs. 6–8.

Igorina pusilla “high trochospire” (Bolli) in Petrizzo, 2005, p. 29, pl. 4, figs. 6a–c, 9a–c.

Derivation of name. Refers to the variable height of the spire.

Material. Holotype (Micro-Unimi no. 1980); paratypes 1 and 2 (Micro-Unimi no. 1981 and 1982, respectively) deposited in the Micropaleontological Collection, Univer-

sità degli Studi di Milano, Dipartimento di Scienze della Terra "A. Desio", Italy.

Occurrence. Zones P4a–P5 (basal part).

Geographic distribution. This species has been recorded at low and mid latitudes and it is present in (sub)tropical assemblages from the Atlantic and Pacific Oceans.

Dimensions of holotype. Diameter = 0.26 mm, thickness = 0.19 mm.

Description. Test small to medium sized, subcircular to circular, almost compact outline, asymmetrically biconvex with a moderate to very prominent high spire and slightly convex umbilical side; peripheral margin ranging from broadly rounded to slightly subangular, surface texture pustulose; umbilical side with 9–10 essentially equidimensional triangular chambers, sutures straight radial, umbilicus small, narrow, and deep; spiral side with three whorls tightly coiled with 7–8 (rarely 9–10) chambers in the final whorl, increasing very slowly in the size as added, sutures strongly recurved and weakly incised; aperture an interiomarginal, umbilical-extraumbilical, moderately high arch extending nearly to the periphery.

Remarks. In our samples this taxon is abundant in Zone P4 (sub)tropical assemblages of Pacific Ocean (Holes 1209B and 865B). Generally, this species is characterized by having a moderately to strongly biconvex test and a circular profile. Typical forms of *Igorina paraspiralis* n. sp. have been reported and illustrated by Blow (1979) in Zone P5 from the Atlantic province. However, we have observed this species to have a wide range of morphologic variation. Some specimens are characterized by a trochospire that projects up to 2/3 the total length of the entire shell. A similar morphotype was illustrated by Olsson and others (1999) from the Vincentown Formation (Glendola Well, New Jersey). Moreover, in Subzone P4b assemblages, we have observed rare morphotypes that display a thicker test with a shorter but wider spire and with a broadly arched aperture on the last chamber. The latter forms usually display 8–9 (rarely 10) chambers of almost equal size in the last whorl. *Igorina paraspiralis* is distinguished from all the other igorinids by the large number of chambers visible on its spiral side. Our phylogenetic analysis suggests that this form probably evolved from *I. albeardi* in Subzone P4a. Its highest occurrence is in the lower part of Zone P5.

Distinguishing features. *Igorina paraspiralis* is distinguished from *I. albeardi* in having a more-subrounded peripheral margin and lack a carinate last chamber.

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APPENDIX 1

Data matrix used for cladistic analysis. This table can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2011008.

APPENDIX 2

Description of characters. This glossary can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2011008.