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Cladistic and Phylogeny of Foraminifera in the Andranomavo Site, Mahajanga Basin, Madagascar

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ABSTRACT

Cladistic or systematic phylogenetic is the theory of clades and cladograms, leading to the reconstruction of kinship relationships between living beings.The principle of the «external group» or «extra-group» is used to root a phylogenetic tree, leading to the cladogram construction of each character. The step length of the character transformation series summary cladogram for Foraminifera Families is equal to 13; it is the shortest tree which represents the phylogenetic hypothesis most acceptable according to the principle of parsimony. The cladistic analysis of character states for each Family confirms their relationships of kinship. Indeed, the hypothetical ancestor of benthic calcareous Foraminifera probably originated from agglutinated calcareous Foraminifera and Foraminifera with hyaline test also come from Foraminifera with agglutinated test.

1. Introduction

The cladistic theory was originally presented in the 1950s by Hennig (1913-1976). Cladistics or phylogenetic systematics is the theory of clades and cladograms, leading to the reconstruction of kinship relationships between living things. The cladogram specifies degree of kinship relationships between the taxa it classifies. A clade (monophyletic group) is a group all of which are more related to each other than to any other group. And in this area, the cladistic study was carried out at the level of the Foraminifera Families found in the Andranomavo site. This work aims to determine the ancestor of benthic Foraminifera through the analysis of their character states. The cladistic principle consists in examining the apomorphic and plesiomorphic characters of the different Families, in explaining the degree of kinship relations for the taxa considered in order to confirm the existence of the common ancestor.

2. General context

Foraminifera have a chronostratigraphic extension ranging from the Early Cambrian to the present day (Bignot, 2001). Foraminifera belong to:

- **Protozoa branch:** for paleontologists, only one type of protist (protozoan) has long been considered to be fossilizable: the Rhizopod, an animal with a soft cytoplasm provided with pseudopods, housed in a solid shell strongly mineralized. In fact, only two large families have been known for a long time: Foraminifera, mostly calcareous, and Radiolaria, all siliceous (Pivetau, 1952).
- **Rhizopod sub-branch:** they are characterized by the fact that they live with pseudopods, expansions of the outer layer of the cytoplasm (ectoplasm) used for locomotion and nutrition.
- **Class of Granulo-reticulosa:** with very fine pseudopodia, in reticulum, running through tiny granules.
    - **1st Order: Athalamia**, naked amoeba.
    - **2nd Order: Thalamia**, with a simple shell, organic or sandy, reproducing only by division.
    - **3rd Order Foraminifera** (Foraminifera), often complex shell, calcareous, chitinous, sandy or siliceous.

No naked Rhizopod is yet known in the fossil state and for paleontologists it is therefore convenient to divide the subphylum into two groups:

- Thecamoebiens, bringing together all the shell forms, almost exclusively freshwater (some fossils);
- Foraminifera, practically all marine, sometimes brackish, some rare living forms adapted to freshwater not being surely known in the fossil state.

3. Materials and Methods

3.1- Rooting and external group

The principle known as the “external group” or “extra-group” is generally used to root a phylogenetic tree, i.e. designated the node corresponding to the root class (containing all the other classes). Any state of character observed outside the internal group is considered plesiomorphic for the internal group. On the contrary, any state specific to taxa of the study group is considered apomorphic. According to the standard parsimony method, the economy of hypothesis affects the number of evolutionary steps. The shortest tree (i.e. the tree with the fewest evolutionary steps) is the tree representing the most acceptable phylogenetic hypothesis. The step count can be influenced by the consideration that one has convergences and / or reversions.

3.2- Construction of the cladogram

The cladogram construction method is based on the state of shared derived characters, also known as synapomorphies. In this, it allows phylogenetic reconstruction within the framework of cladistic theory. Cladistic analysis uses synapomorphy, acquired by an ancestor and inherited by all his descendants, in order to propose clade hypotheses (phenotypic character). Traits can cladistically include morphological knowledge.

After the observation of Foraminifera under a binocular magnifying glass, the determinations of taxa (Families) were made thanks to the characteristic literature of the Upper Jurassic - Lower Cretaceous. The form and the structure of the test make it possible to define a morphological system of Foraminifera (Loeblich and Tappan, 1987). The criterion for determining Foraminifera for the Family is as follows:

- number of chamber,
- chamber arrangement,
- general form,
- wall architecture.

The Andranomavo site has 9 Foraminifera Families. The assignment of character states to taxa is represented in a table called the taxa-character matrix. By convention, for each character:

- the origin is noted ancestor,
- the primitive or plesiomorphic state is noted 0,
- the derivative or apomorphic state is denoted 1,
- the more derivative state is noted 2.

Thus we arrive at the same series of transformation (0, 1, 2, ...) or morphocline (an evolutionary series polarized of such a sequence by morphological characters).

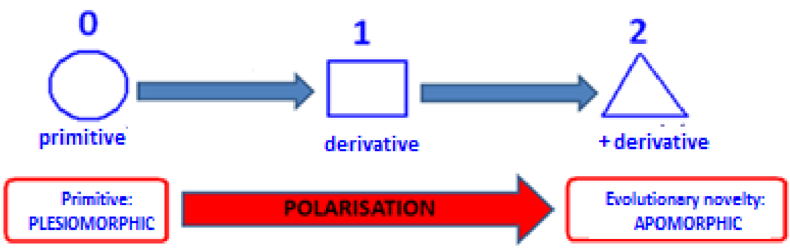


Figure 1 : Morphocline

<u>Taxons:</u> Families

1 ⟶ Textulariidae
2 ⟶ Lituolidae
3 ⟶ Nodosariidae
4 ⟶ Glandulinidae
5 ⟶ Vaginulidae
6 ⟶ Spirillinidae
7 ⟶ Epistomidae
8 ⟶ Polymorphinidae
9 ⟶ Globigerinidae

Characteristics

- **A: chamber number**
  - unilocular → 0
  - bilocular → 1
- **B: chamber arrangement**
  - monoseried → 0
  - biseried → 1
  - triseried and other → 2
- **C : general form**
  - fusiform → 0
  - lenticular → 1
  - flared → 2
  - cylindric → 3
  - trochoid → 4
- **D : wall architecture**
  - monolamellar → 0
  - bilamellar → 1

Cladistic analyses are constructed in using computer programs: PAST software.

4. Results

4.1 Cladogram

The cladogram being the result of a test of character states, it is it which indicates whether a group is monophyletic or paraphyletic. It is therefore important to justify the choice of the character states considered, upstream of the analysis, apomorphic or plesiomorphic.

All the characters at 0 are plesiomorphic and the characters at 1, 2, 3, 4 are apomorphic in the taxa-character matrix table. According to parsimony the principle, the simplest cladogram was chosen (the shortest number of trees), that is to say the minimum of dichotomy because several cladograms are in.

Table 1: Taxa and Characteristic Matrix of Foraminifera

	Characteristic / Taxons	A	B	C	D
0	Extra-group (ancestor)	0	0	0	0
1	Textulariidae	1	1	2	0
2	Lituolidae	1	0	0	0
3	Nodosariidae	1	2	1	0
4	Glandulinidae	1	0	0	0
5	Vaginulinidae	1	2	2	0
6	Sprinilinidae	0	2	3	0
7	Epistomidae	1	2	3	0
8	Polymorphinidae	1	0	0	0
9	Globigerinidae	1	2	4	1

Character A: number of chamber

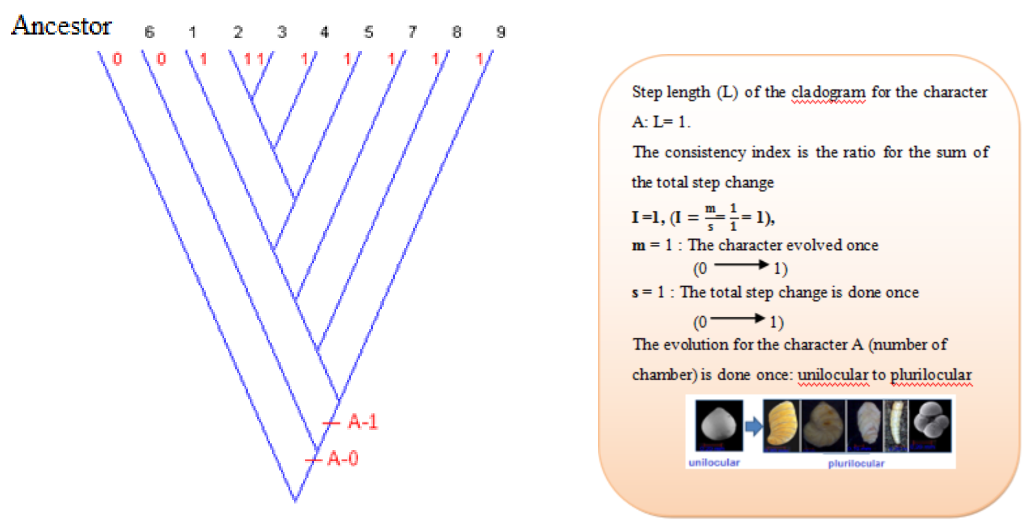
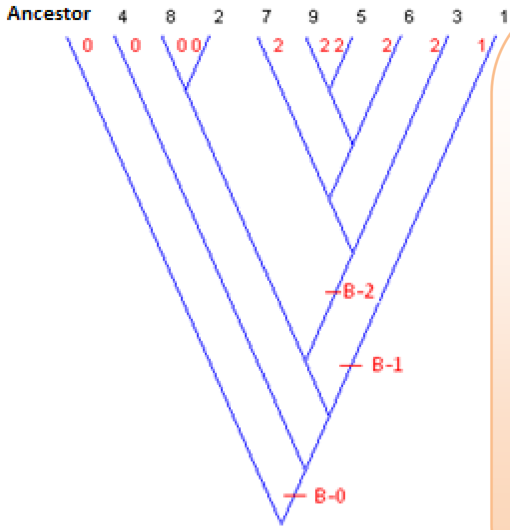


Figure 2: Cladogram for the character A

Character B: chamber arrangement



Step length (L) of the cladogram for the character B: L= 2

I =1, (I = $\frac{m}{s} = \frac{2}{2}$ **= 1)**

m = 2 : The character evolved twice :

(0 ⟶ 1 ⟶ 2)

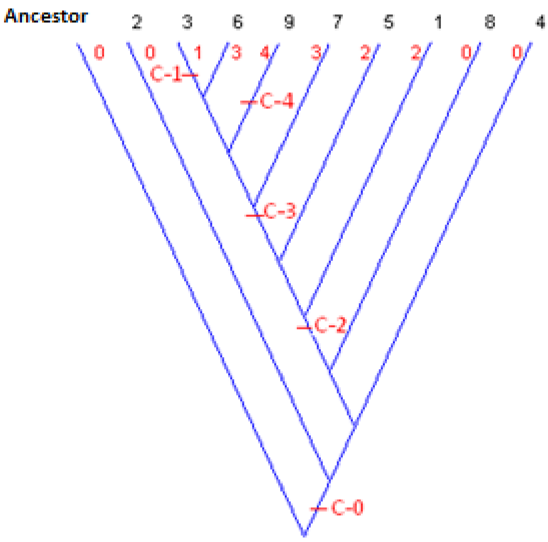
s = 2 : The total step change is done twice

(0 ⟶ 1, 0 ⟶ 2)

The evolution for the character B (chamber arrangement) is done twice : uniseried to biseried, biseried to triseried and in another.

Figure 3: Cladogram for the character B

Character C: general form



Step Length (L) of the cladogram for the character C: L= 4 (Figure 4).

I =1, (I = $\frac{m}{s} = \frac{4}{4}$ **= 1)**

m = 4 : the character evolved forth

(0 ⟶ 1 ⟶ 2 ⟶ 3 ⟶ 4)

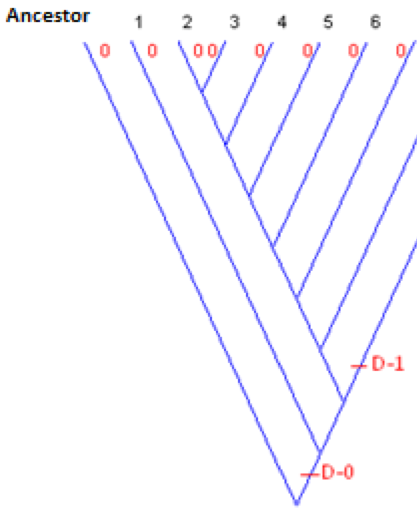
s = 4 : The total step change is done fourth :

(0 ⟶ 2, 0 ⟶ 1, 2 ⟶ 3, 0 ⟶ 4)

The evolution for the character C (general form) is done fourth (fusiform to lenticular, lenticular to flared, flared to cylind

Figure 4: Cladogram for the character C

Character of D: tectum architectural



Step length (L) of the cladogram for the character D:

L= 1

I =1, (I = $\frac{m}{s}$= $\frac{1}{1}$ = 1)

m = 1 : The character evolved once
(0 ⟶ 1)

s = 1: The total step change is done once

(0 ⟶ 1)

The evolution for the character A (tectum architectural) is done once: monolamellar to bilamellar

Figure 5: Cladogram for the character D

The character C is the most evolved character compared to the other characters. The number of cladogram steps for recapitulating the transformations series for the different characters (A, B, C and D) is equal to 13 (the shortest tree). It is the representative of the most acceptable phylogenetic hypothesis according to the parsimony principle. Indeed, the Family of Epistomidae and Globigerinidae are the brother group showing a monophyletic group of higher rank (Figure 6).

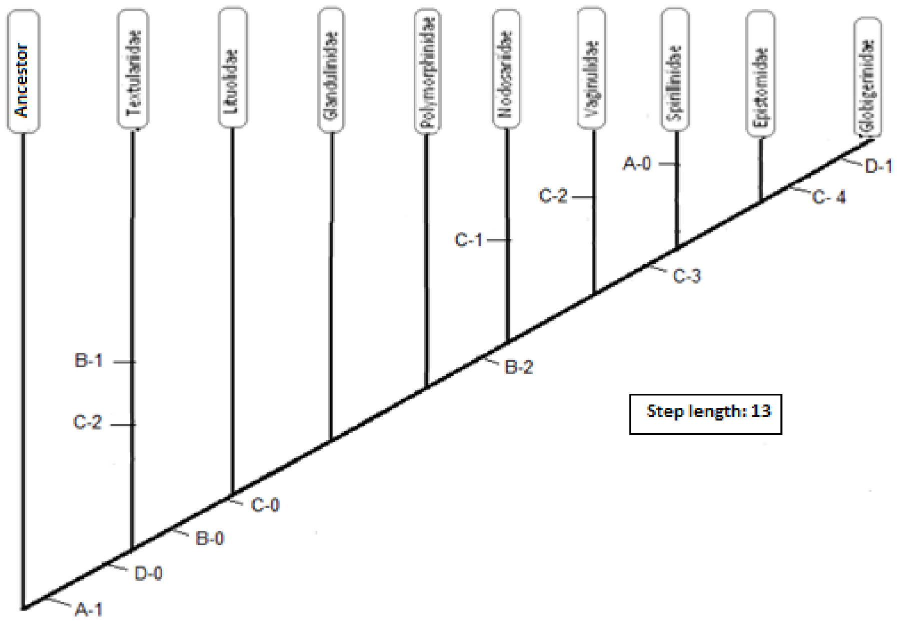


Figure 6: Cladogram of the taxa recapitulation

4.2 Cladistical analysis

Cladistic analysis of the character states for each Foraminifera Family confirms their family relationships (Figure 7).

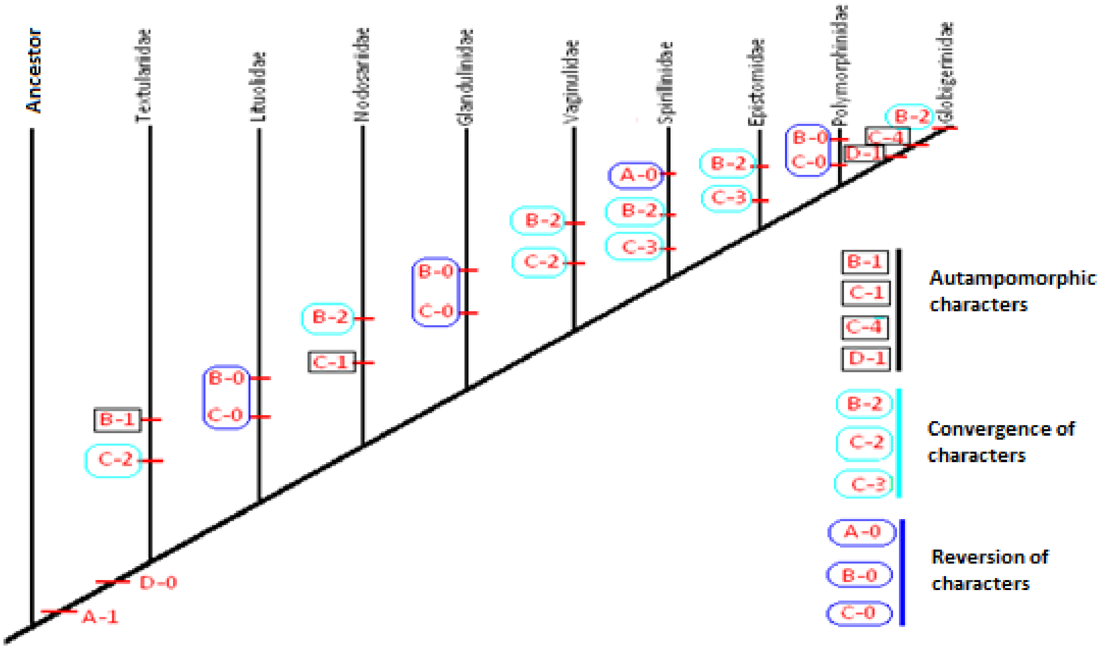


Figure 7 : Cladogram showing descriptions for the characters of Foraminifera families.

5- Discussions

5.1- Autampomorphic characters

Textulariidae (Taxon 1) : one autapomorphic character B-1 : biseried chamber arrangement

Nodosariidae (Taxon 3) : one autapomorphic character C-1 : lenticular general form

Globigerinidae (Taxon 9) : several autapomorphic character : C-4 (trochoid general form),
D-1 (lamellar wall architecture)

The characters B-1, C-1, C-4 and D-1 are autapomorphic characters because they are new characters specific to a taxon.

5.2- Convergence character

Textulariidae (Taxon 1)
Vaginulinidae (Taxon 5)
} a convergence character C-2 (similarity on the general forms for two Families: flared)

Nodosariidae (Taxon 3),
Vaginulinidae (Taxon 5),
Spirillinidae (Taxon 6),
Epistomidae (Taxon 7),
Globigerinidae (Taxon 9)
} a convergence character B-2 (similarity on the chamber arrangement: triseried and other)

Spirillinidae (Taxon 6),
Epistomidae (Taxon 7),
} a convergence character C-3 (similarity on the general forms of two Families: cylindrical)

The characters B-2, C-2, C-3 are convergence characters because they are similarity characters between two different taxa.

5.3- Reversion character

Lituolidae (Taxon 2),
Glandulidae (Taxon 4),
Polymorphinidae (Taxon 8).

} reversion characters: B-0, C-0

The characters B-0, C-0 are reversaion characters, that is to say that after the evolution of these characters in B-1, B-2 and C-1, C-2, C-3, they return to the initial characters.

The initial chamber arrangement for three Families (Lituolidae, Polymorphinidae, Glandulidae) is uniseried (B-0) and after the evolution of these characters into biseried or triseried (B-1, B-2), the chambers arrangement return to the initial (B-0):

B-0 ⇒ B-1, B-2 ⇒ B-0

The initial general forms for the three Families (Lituolidae, Polymorphinidae, Glandulidae) are fusiform (C-0) and after the evolution of these characters into lenticular, flared, cylindrical, trochoid (C-1, C-2, C-3 , C-4), the general forms return to the initial (C-0):

C-0 ⇒ C-1, C-2, C-3, C-4 ⇒ C-0

The characters B-0, C-0 are a reversion character that is to say that after the evolution of these characters in B-1, B-2 and C-1, C-2, C-3, they return to the initial characters.

The initial chamber arrangement for the three Families (Lituolidae, Polymorphinidae, Glandulidae) is uniseried (B-0) and after the evolution of these characters into biseried or triseried (B-1, B-2), the chamber arrangement return to the initial (B-0):

B-0 ⇒ B-1, B-2 ⇒ B-0

The initial general forms for the three Families (Lituolidae, Polymorphinidae, Glandulidae) are fusiform (C-0) and after the evolution of these characters into lenticular, flared, cylindrical, trochoid (C-1, C-2, C-3 , C-4), the general forms return to the initial (C-0):

C-0 ⇒ C-1, C-2, C-3, C-4 ⇒ C-0

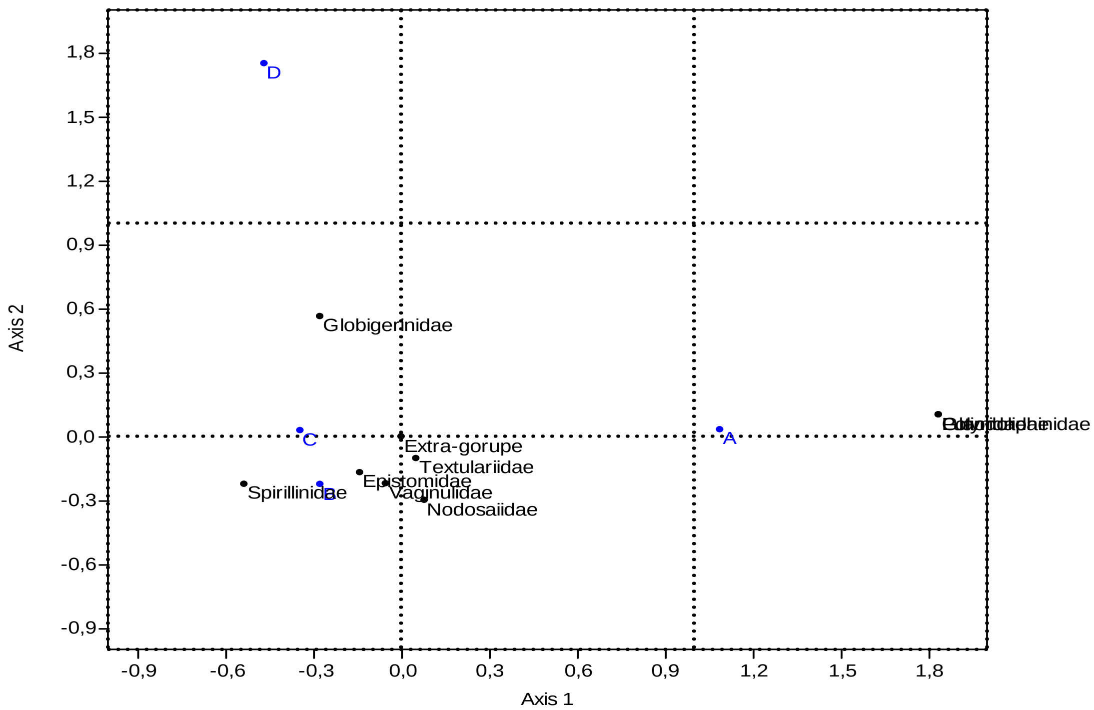


Figure 8 : Correspondence analysis between taxa and character.

5.4 Evolution des taxons

Evolutionary studies have shown that certain character have evolved to transform. By analyzing the length of horizontal branches, this phylogram shows the evolution of taxa (Families) compared to its ancestor (Figure 9).

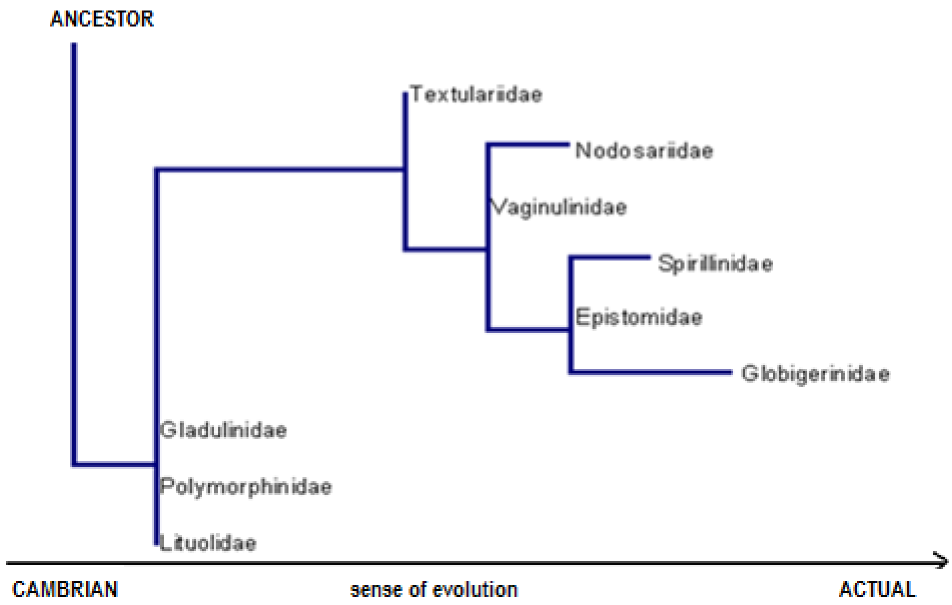


Figure 9: Phylogram of Foraminifera Families

- The Glandulidae, Polymorphinidae, Lituolidae families are less evolved compared to other families (Textulaiidae, Nodosariidae, Vaginulinidae, Spirillinidae, Epistomidae, Globigerinidae) because the branches length is very short and close to the ancestor. Consequently, these families have only character A: character corresponding to the number of chamber ;
- The Textulariidae family is less evolved compared to the Nodosariidae, Vaginulinidae, Spirillinidae, Epistomidae, Globigerinidae families. This Family is characterized by three characters:

- A: character corresponding to the number of chamber;
- B: character designating the chamber arrangement;
- C: character showing general form;

- The Globigerinidae family is the most evolved because it is very far from the ancestor and it has the following characters:

- A: character corresponding to the number of chamber;
- B: character designating the chamber arrangement;
- C: character showing general form;
- D: character indicating the wall architecture.

5.5 Hypothesis for determining the ancestor of benthic Foraminifera

The hypothetical ancestor for the benthic calcareous Foraminifera probably originated from the agglutinated calcareous Foraminifera. Hyaline Foraminifera Test comes from Agglutinate Foraminifera Test. In this case, these two groups present a convergence characteristics on the general form,...
The phylogenetic study of planktonic Foraminifera shows that the planktonic forms probably originate from benthic Foraminifera from which a plankton phase of the cycle would have completely separated at the beginning of Mesozoic times. This scenario is perfectly consistent with the fact that the early Jurassic and basal Cretaceous species are subservient to external platform environments (Caron, 1983).
This hypothesis is confirmed in the classification and biostratigraphy of the main fossil protists because the agglutinating forms existed before the Cambrian (Proterozoic) as well as the calcareous forms were already described in the Cambrian (Anne de Vernal & Leduc, 2000) (Figure 10) .

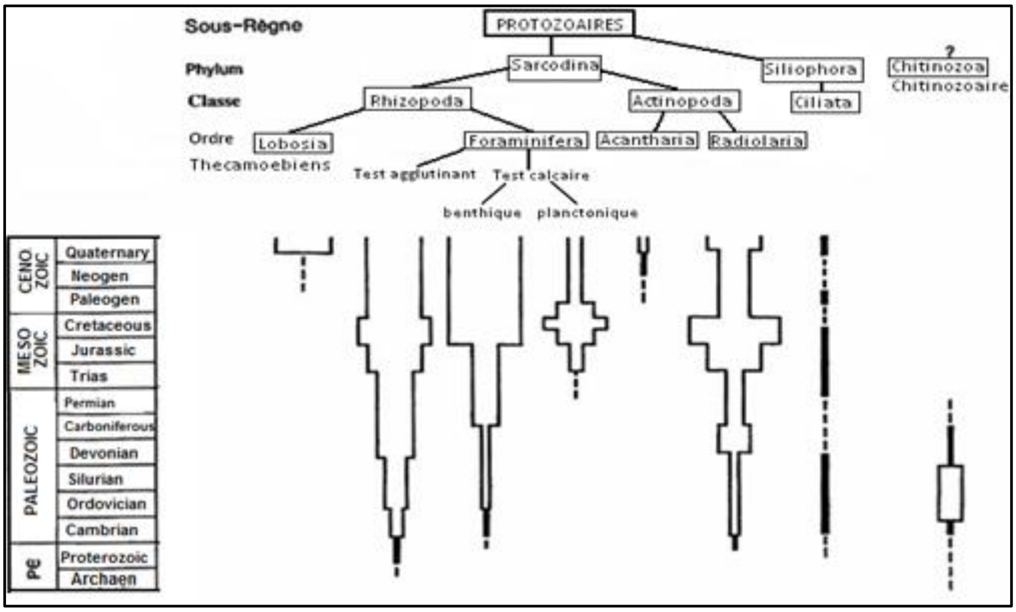


Figure 10 : Diagram illustrating the origin of Foraminifera (Classification and biostratigraphy of the main fossil protists after Anne de Vernal & Julie Leduc, 2000).

Benthic Foraminifera (agglutinated and hyaline) are derived from benthic agglutinated (ancestor) and Planktonic Foraminifera are also derived from benthic Foraminifera (Figure 11)

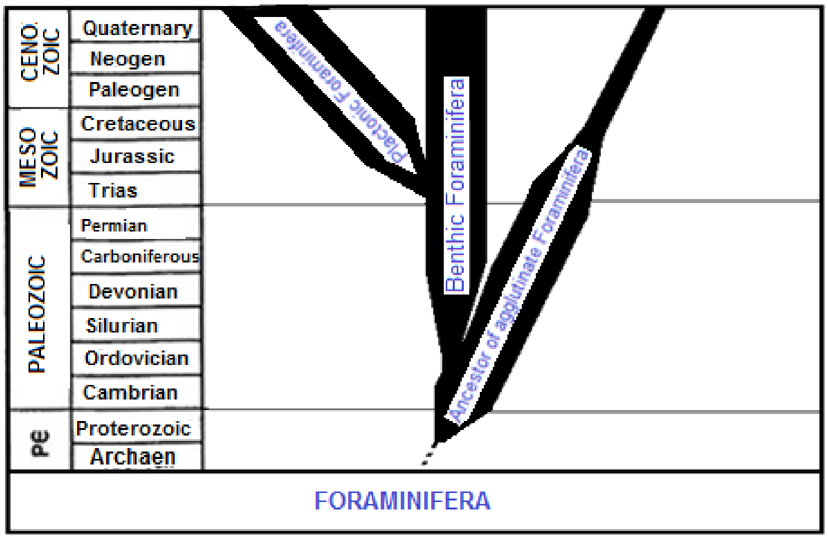


Figure 11: Recapitulation on the determination of the ancestor of benthic Foraminifera (Source: Author)

Conclusion

The cladogram being the result of a test of character states, it is it which indicates whether a group is monophyletic or paraphyletic. The character C is the most evolved character compared to the other characters. The number of cladogram steps for recapitulating the series of transformations for the different characters (A, B, C and D) is equal to 13, it is the shortest tree because it is the representative of the most acceptable phylogenetic hypothesis according to the parsimony principle . Indeed, the families of Epistomidae and Globigerinidae are the brother group showing a monophyletic group. Cladistic analysis of the character states for each Foraminifera family confirms their family relationships between taxa by the presence of convergence, autapomorphic and reversion characters. Analysis of branches length shows that the Globigerinidae family is the most evolved because it is very far from the ancestor. The hypothetical ancestor for the benthic calcareous Foraminifera probably originated from the agglutinated calcareous Foraminifera. Hyaline Foraminifera Test comes from Agglutinate Test Foraminifera. In this case, these two groups present characteristics of convergence especially at the level of the general form.

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