Typological versus morphometric separation of orthophragminid species in single samples – a case study from Horsarrieu (upper Ypresian, SW Aquitaine, France)

Séparation typologique et morphométrique des espèces d’Orthophragmines dans des échantillons isolés – application à un échantillon provenant de Horsarrieu (Yprésien supérieur, Sud-Ouest de l’Aquitaine, France)

György Lessa,*, Lajos Ó. Kovácsb

a University of Miskolc, Department of Geology and Mineral Resources, 3515, Miskolc-Egyetemváros, Hungary
b Hungarian Office for Mining and Geology, Columbus u. 17-23, 1145, Budapest, Hungary

Abstract

Thirteen different orthophragminid taxa could be separated typologically from a single sample collected by C.W. Drooger from the late Ypresian of Horsarrieu, marnière Sourbet (SW France). Drooger doubted the existence of many co-occurring evolutionary lineages of larger foraminifera in the Eocene suggesting that this may be an artifact of the typological species concept widely used by the Paleogene larger foraminiferal experts. It is shown here that typologically determined taxa can be separated as well with the morphometric method, recommended by Drooger. This proves also the validity of the concept of simultaneous evolutionary lineages. It has been found that the typological method is preferable when separating different taxa in single samples, but in some cases, the independence of quantitatively close populations can only be proved biometrically. At the same time, the morphometric method is more advantageous in characterizing the evolution within particular evolutionary lineages because it gives much more reliable stratigraphical results. The 13 orthophragminid taxa from Horsarrieu are systematically described. A new species, Orbitoclypeus droogeri nov. sp., and two new chronosubspecies, O. furcatus palaeofurcatus and Asterocyclina stella praestella are introduced.

© 2008 Elsevier Masson SAS. All rights reserved.

Résumé

Treize taxons d’Orthophragmines ont été identifiés selon leur typologie sur un seul échantillon prélevé par C.W. Drooger dans la marnière Sourbet située à Horsarrieu (Sud-Ouest de la France) et daté de l’Yprésien supérieur. Drooger met en doute la coexistence d’un grand nombre de lignées évolutives de grands foraminifères du Paléogène, pensant à un artéfact lié au concept d’espèces typologiques largement appliqué par les experts des grands foraminifères de l’Éocène. Dans cet article, il est démontré que des taxons déterminés selon leur typologie pouvaient également être séparés par leur morphométrie, méthode recommandée par C.W. Drooger. Cela confirme la coexistence de différentes lignées évolutives. Il apparaît qu’une séparation typologique des différents taxons d’échantillons isolés est préférable, mais que dans certains cas, l’indépendance de populations quantitativement proches peut être prouvée uniquement par la biométrie. Par ailleurs, la morphométrie est plus adaptée à la caractérisation de l’évolution au sein de lignées particulières, car elle permet un meilleur contrôle des résultats stratigraphiques. Les 13 taxons d’Orthophragmines sont systématiquement décrits. Une nouvelle espèce, Orbitoclypeus droogeri nov. sp., et deux nouvelles sous-espèces chronologiques, O. furcatus palaeofurcatus et Asterocyclina stella praestella sont introduites.

© 2008 Elsevier Masson SAS. All rights reserved.

Keywords: Lower Eocene; Foraminifera; Discocyclinidae; Orbitoclypeidae; Biometry; France

Mots clés : Éocène inférieur ; Foraminifères ; Discocyclinidae ; Orbitoclypeidae ; Biométrie ; France

* Corresponding author.
E-mail address: foldgy@uni-miskolc.hu (G. Less).

doi:10.1016/j.revmic.2008.10.001
1. Introduction

All the three major groups of Eocene larger foraminifera (Nummulitidae: Hottinger, 1977; Schaub, 1981; Alveolinidae: Hottinger, 1960; Drobne, 1977; Discocyclinidae and Orbitoclypeidae united under the informal collective name of orthophragmines: Less, 1987, 1998) are characterized by a considerable number of co-occurring evolutionary lineages. This is in sharp contrast with the behavior of both the Late Cretaceous and Oligo-Miocene forms (Drooger, 1993). In the opinion of the “Utrecht School” (Khan and Drooger, 1971) this controversy may be not real and appears only due to the different taxonomical concepts, since the evolutionary lineages of the Eocene forms are determined typologically, while those of the Late Cretaceous and Oligo-Miocene forms are separated on a morphometric basis.

Concerning the orthophragmines, Drooger (1993: pp. 171–172, 174) writes:

“Less (1987) … had evidently a wider [than that of the Utrecht School] species concept [of the orthophragmines] because, if their [the Utrecht School’s] numerical data per sample showed no clear discontinuity, they treated such observations as representing a single population or species. Less’ determinations cannot be evaluated in this respect because his numerical data are rather generalized, neither tabulated nor presented graphically. His introduction of a large number of 0–1 discriminations for the establishing of species (groups) evidently leads to frequent recognition of many species per sample. For instance, his locality Horsarrieu in southern France contains as many as eight species of Discocyclina based on a total of 25 specimens, and in addition two species of Nemkovella on six specimens and another two of Orbitoclypeus on seven individuals. With such a species variation at one locality, I start to feel uneasy, fearing that the species concept is too narrowly typological rather than populational. . . I am quite willing to believe that it is possible that the procedure of Fermont (1982) led to undue lumping of unrelated forms. On the other hand, however, the splitting that Less is showing is primarily based on his firm belief in the important role of the discriminating qualitative parameters, but it is not convincing from the morphometric point of view. Although there is no proof, one starts to suspect that at least part of Less’ species (groups) could well be members or variants in otherwise homogeneous populations . . . the morphometric methods of the Utrecht School seem to lead to the conclusion that development courses of the Orthophragminae were random. There may be a chance of arriving at greater clarity if the classification methods of Less can be confirmed and re-shaped from a better documented investigation of populational variation”.

Based on a large number of specimens, the aim of this paper is to check whether the empirically recognized and typologically identified orthophragminid populations (referring to different evolutionary lineages, each corresponding to different species in our interpretation) can, or cannot, be discriminated by the morphometric method. The term “typological determination” is used in this paper in Drooger’s (1993) interpretation. It includes not only the identification of each specimen with a certain taxon but also the preceding procedure characterized by Drooger (1993: pp. 27) as “the intuitive appraisal of differences recognized by the specialist on the basis of his ‘experience’”, i.e. the entire process of empirical pattern recognition. Thus, the crucial difference between the typological and morphometric approaches in Drooger’s (1993) interpretation is the manner of generating populations: empirical or numerical. The way of giving an appropriate name is of secondary interest in this respect, since at the end of the morphometric procedure also, a Linnean name is given to each population (Drooger, 1993: pp. 31–32).

In 1988, C.W. Drooger collected a sample from Horsarrieu (Fig. 1), marnière Sourbet (Fr. 2358, in the collection of the Department of Micropaleontology, Rijksuniversiteit, Utrecht) to assess the validity of the multitude of species in one single sample. The locality of this sample is the same as for sample HX in Less (1987) and sample HORSA in Less and Ó. Kovács (1996) and in Less (1998), but Drooger’s sample (marked by HORSX in the last two papers cited above) represents the topmost part of the marl-pit because at that time it was already abandoned and mostly flooded (C.W. Drooger, personal communication).
The senior author studied the orthophragmines of this sample both typologically and morphometrically. Almost 80% of the 400 randomly picked specimens could be split into two halves along the equatorial plane by pliers (Less, 1981) and then stained by pink chemical ink. Two hundred and eighty-eight well-preserved specimens of the A-generation and eight of the B-generation could be determined typologically on the species level. In 205 of the A-forms, it was possible to execute all the necessary measurements and counts (see in detail below). Based on an agreement with C.W. Drooger, one-half of each of these latter specimens was sent back to Utrecht, the other halves are deposited in the Eocene collection of the Geological Institute of Hungary in Budapest.

2. Investigation methods

2.1. Selection of specimens

Almost all the important features for determining orthophragmines have to be studied in their equatorial section (Less, 1987, 1993), which has to be prepared first. Thus, the specimens to be split have to be selected beforehand, by their exterior. As discussed by Less (1987: pp. 70–71), the presence/absence of ribs is the only external feature that has a determining role, but only at the species level. Otherwise, there exists some kind of correlation between the exterior and the interior characters of orthophragminid taxa, but it is by far not straightforward because the external variability of most of the species is rather wide. The correlation is quite strong in ribbed forms and much less significant when the test’s surface is unribbed.

Therefore, we executed the random picking of specimens separately for the unribbed and the ribbed forms. Since unribbed forms are much more diverse, we picked 300 unribbed and 100 ribbed specimens for splitting. We managed to split into two halves, 241 unribbed and 76 ribbed specimens. Of these, 225 unribbed and 71 ribbed forms could be determined on the species level. Seven unribbed (3.1%) and one ribbed specimens (1.4%) were found to be micro-spheric. In 161 unribbed and 44 ribbed specimens, we were able to apply all the necessary measurements and counts (see below).

2.2. The typological determination of orthophragminid taxa

Orthophragmines (Fig. 2) are three-layered orbitalid larger foraminifera of the late Paleocene and Eocene with two well-developed lateral layers symmetrical to the central equatorial one and with almost rectangular equatorial chamberlets. The name “orthophragmines” is an informal collective term comprising two independent families, Discocyclinidae and Orbitoclypellidae, that can be distinguished unambiguously only by their completely different microspheric juvenaria observable in the equatorial section. More details about their architecture are given in Less (1987, 1993), Ferrandez-Cañadell and Serra-Kiel (1992) and Ferrández-Cañadell (1998). Both families are found in two biogeographical provinces, in America and in the Tethys, having developed almost separately from each other. The way of determining Tethyan orthophragminid taxa is described in detail by Less (1987, 1993). Fig. 3 summarizes the discriminative qualitative features for separating the four different Tethyan orthophragminid genera. In practice, Asterocyclina is easily identifiable also in the equatorial section by its star-shaped equatorial annuli with mostly five rays.

Within these genera, particular species are distinguished by the combination of some clearly qualitative features, such as the external shape (ribbed or unribbed), the type of rosette (the network of pyles and lateral chamberlets on the test’s lateral surface), the type of adauxiliary chamberlets and the shape of equatorial annuli and also of some primarily quantitative features – that are in fact evaluated qualitatively and, therefore, recognizable immediately by the expert – such as the shape and dimension of the A-form embryon and the shape and width of equatorial chamberlets. All these features are immediately synthesized by an experienced human eye on each specimen (pattern recognition) and identified with a certain type (described in the literature), whose image is stored in the brain of an expert on a given group. In fact, this process, termed here typological determination, is an intuitive synthesis in which pattern recognition and typological identification are practically combined for an experienced specialist.

Some of these typologically determinable species rapidly follow each other in stratigraphical order (e.g. D. pseudouaugustae with a multilepidine embryon is followed by D. fortisi with a centrelipidine one), but much more often their specific features are rather stable. At the same time, one can observe a gradual (uni-directional in the long term but fluctuating in the short term) change (mostly increase in size or in number) of some morphological elements of these qualitatively stable species throughout their long stratigraphical range. Such species are interpreted as evolutionary lineages whose development can efficiently be used for stratigraphical purposes. Therefore, this evolution has to be characterized as precisely as possible.
Recently, there has been a general agreement among larger foraminiferal experts working on different groups on the existence of long-lived evolutionary lineages but two methods exist for characterizing their evolution. The Basel School (Hottinger, 1960, 1977; Drobne, 1977; Schaub, 1981) uses a typological approach and characterizes the course of the evolution by a succession of typical forms each including the holotype and also the population from the type locality. Hence, these types (interpreted as distinct species) serve as central, favored moments of the development of the given evolutionary lineage and the related populations from other sites are grouped around them. In contrast, the morphometric Utrecht School (as summarized in Drooger, 1993) does not characterize the evolution with the help of “central moments” but subdivides it by artificial limits using a well-measurable, rapidly evolving parameter of the lineage.

We think that the typological distinction of successive taxa, being very close to each other within the evolutionary lineages, may be rather subjective, and therefore, may allow misdeterminations among closely related taxa that, in turn, can cause mistakes in the age-determinations. Unfortunately, these errors are hard to recognize and rectify subsequently. A second disadvantage of the typological discrimination of successive evolutionary stages is that they cannot be recognized immediately by the human brain (unlike different evolutionary lineages, see above). Therefore, in this case, the typological approach is not a reflection of the immediate pattern recognition but rather translates somehow a complicated procedure of comparisons, at the end of which the result is very often just a name, the validity of which is hard to control.

Therefore, in order to eliminate these pitfalls, in the case of orthophragmines, Less (1987, 1993, 1998) has chosen the morphometric method of the Utrecht School. If successive evolutionary stages are delimited based on biometrical values – that are certainly artificial due to the gradual nature of the evolution – their determination becomes much more reliable because it is supported by statistically evaluated measurements.
that can be easily summarized in simple tables. In the practice of orthophragmines, species-names are used for typologically recognizable entities. These species, which in most cases correspond to evolutionary lineages, are subdivided into artificial chronospecies that are defined by biometric limits of the populational means of the outer cross diameter of the second chamber of the A-form embryo in equatorial section (\(d\)). This quantitative feature has been chosen among several other quantitative parameters because it was proven to be the most easily and objectively measurable one and because it reflects the fastest and least variable evolutionary progress (Less, 1998).

Other parameters are also very useful because they may support the determination of subspecies in intermediary cases, and also because they are of much help to the less experienced researchers in determining the actual population at species level. In this paper, they are used for the morphometric separation of populations in the Horsfair sample.

The nine parameters measured (in micrometers) and counted on the equatorial section of A-forms are as follows (Fig. 4):

- \(p\) and \(P_2\): outer width and height of the protoconch;
- \(d\) and \(D_2\): outer width and height of the deuteroconch;
- \(a\): distance from the bottom of the deuteroconch to the bottom of the protoconch upwards (in Fig. 4, \(a\) is negative);
- \(N\): number of adauxiliary chamberlets (Fig. 4, \(N = 15\));
- \(H\): average height of adauxiliary chamberlets;
- \(w\): average width of equatorial chamberlets;
- \(n\): number of equatorial annuli (in the first 500 \(\mu m\) from the embryo’s rim (in Fig. 4, \(n = 6.6\)).

For a biometrical characterization of populations, 10 quantitative parameters are used; six parameters (\(p, d, N, H, w\) and \(n\)) are measured or counted directly, while four others are calculated as follows:

- \(Z\): evolutionary index of the embryon (Less, 1992).
  \[Z = 100(0.5 + (P_2 + 2a)(D_2 - P_2 - 2a + abs(P_2 + 2a)))\]
- \(W\): average width of the adauxiliary chamberlets (in micrometers).
  \[W = (D_2/c)((d + H)^2 + (D_2 + H)^2)/2)^{1/2}/(N + 1),\]
  where \(c = D_2 - a\) if \(a < 0\), otherwise \(c = D_2\);
- \(F\): isometry index of adauxiliary chamberlets.
  \[F = 100H/H + W;\]
- \(G\): isometry index of equatorial chamberlets.
  \[G = 100[(500 - H)(n - 1)]/[((500 - H)(n - 1) + w].\]

2.3. Morphometric separation of populations

As it is discussed above, both qualitative and quantitative features play a role in determining orthophragmines. Since in this group A-forms are usually the majority, quantitative analysis is exclusively based on them and therefore, the different juvenaria of the B-forms (separating Discocyclinidae from Orbitoclypeiidae) are not used. In order to avoid Drooger’s (1993: pp. 171) criticism, that Less (1987) worked with too many discriminative parameters of yes/no character, with as a result the very numerous taxa present in any single sample, only the presence/absence of the two most important and unambiguous characters are used here for the primary group segregation. These are as follows:

- the presence or absence of the annular stolon of the equatorial chamberlets (Fig. 3). This separates the two Tethyan genera of Discocyclinidae from one another, namely Nemkovella, bearing only radial stolons, from Discocyclina, possessing also proximal annular ones. The Tethyan genera of Orbitoclypeiidae (Orbitoclypeus and Asterocyclina) do not have annular stolons, except for the first few annuli embracing the embryo. Therefore, they are also placed into the group without annular stolons. There are two ways to establish this feature in a split equatorial section. If the equatorial chamberlets are filled with micrite or glauconite, the annular stolon can be observed directly in the equatorial section (stained by pink chemical ink). In the case of shells which are empty or infilled with limonite, the shape of the chamberlets is rectangular in Discocyclina and slightly hexagonal in the other three genera;
- the presence or absence of ribbing on the surface of the test. By the former nomenclature of orthophragmines, this feature separated the unribbed Discocyclina from Asterocyclina and Aktinocyclina, both with ribs (Douvillé, 1922; Schweighauser, 1953; Neumann, 1958; Kecskeméti, 1959 and others). Although this is no longer applicable for generic determination because Discocyclina, Nemkovella and Orbitoclypeus have both ribbed and unribbed species (Less, 1987; Ferrández-Cañaddel, 1997), it still remains a useful character because Asterocyclina is always ribbed. Moreover, this
feature is unambiguously recognizable without any major preparation.

Nine \((p, d, Z, N, H, W, F, n \text{ and } G)\) out of the 10 quantitative parameters (see above) were chosen for morphometric separation. Parameter \(w\) was not taken into consideration because its discriminative power is considerably lower than that of the other parameters. \(p, d, N, H, W\) and \(n\) were logarithmically transformed, since their distribution in particular populations is closer to the lognormal than to the normal.

Since there are several closely related taxa in the Hor Sarrieu sample, two different methods, an analytical and a synthetic one, have been tested in order to validate the typological separation. In the first method, the specimens are selected into ever fewer groups through successive bivariate plots constructed for different parameters, until the previously determined typological taxa are reached and eventually validated. Although this method provides spectacular results, it requires a lot of time and the presentation is also rather lengthy.

In the synthetic method of cluster analysis, all the nine quantitative parameters (see above) are simultaneously considered, first with both qualitative parameters, then with only one of them each time and finally without any of them, in order to study the influence of the qualitative parameters on the resolution power of the separation. These qualitative parameters are treated as binary: 0 when absent and 1 when present. In this paper, one of the most widely employed and simplest varieties of cluster analysis is used: the similarity measure is Euclidean distance; the variables are rescaled into the range of 0 to 1; and the agglomeration schedule is the between-group average linkage (Norušis, 1993: pp. 267–277). The obtained dendrograms, although they are less immediate than the bivariate plots, show at once the number of the obtained groups, the agglomeration schedule is the between-group average linkage.

3. Typological determination of taxa in the Horsarrieu sample

Two hundred and five specimens of A-forms (used for both the typological and morphometrical studies) could be empirically grouped into 13 species belonging to four genera of two families. For a better comparison the equatorial sections of A-forms of these 13 species are shown in Plates 1–3 with the same magnification. The typological determination at species level can be described by the procedure below (in fact, it is a recognition process based upon the synthetic skills of the human brain):

(A) ribs on the surface:
   (a) ribbed forms (steps B–C) – 44 specimens,
   (b) unribbed forms (steps D–H) – 161 specimens;
(B) ribbed forms in equatorial section:
   (a) sharp, stellate annuli, five to six rays, small nephro- to semi-isolepidine embryon \(A.\ stella\) (Gümbel) (Plate 2, Figs. 6 and 7) – eight specimens,
   (b) gently undulated annuli, seven to nine waves, larger eu- and excenitrepidine embryon (ribbed \(O.\ trabayensis\), step C) – 36 specimens;
(C) ribbed \(O.\ trabayensis\) in equatorial section:
   (a) smaller, mostly eulepidine embryon, smaller equatorial chamberlets
   \(O.\ furcatus\) (Rütiimeyer) (Plate 3, Figs. 7–9) – 11 specimens,
   (b) larger, mostly excenitrepidine embryon, larger equatorial chamberlets.
   \(O.\ munieri\) (Schlumberger) (Plate 3, Figs. 5 and 6) – 25 specimens;
(D) unribbed forms in equatorial section:
   (a) rectangular equatorial chamberlets with annular stolons (genus \(D.\) – 71 specimens,
   (b) slightly hexagonal equatorial chamberlets without annular stolons (steps F–H) – 90 specimens;
(E) \(D.\) in equatorial section:
   (a) small semi-isolepidine embryon, very few adauxiliary chamberlets with arcuate outer wall, small equatorial chamberlets.
   \(D.\ trabayensis\) Neumann (Plate 1, Fig. 11) – one specimen,
   (b) small, mostly semi-isolepidine embryon, few adauxiliary chamberlets with straight outer wall, small equatorial chamberlets.
   \(D.\ archiaci\) Schlumberger (Plate 1, Figs. 1 and 2) – 71 specimens,
   (c) moderately small, mostly semi-nephrolepidine embryon, average in number adauxiliary and medium-sized equatorial chamberlets.
   \(D.\ dispansa\) (Sowerby) (Plate 1, Figs. 6 and 7) – seven specimens,
   (d) moderately large, mostly tryblolepidine embryon, numerous adauxiliary and large equatorial chamberlets.
   \(D.\ archiaci\) (Schlumberger) (Plate 1, Figs. 1 and 2) – 13 specimens,
   (e) large centrielepide embryon, many adauxiliary and large equatorial chamberlets.
   \(D.\ fortisi\) (d’Archiac) (Plate 1, Figs. 3–5) – 21 specimens;
(F) embryon of the forms with equatorial chamberlets without annular stolons:
   (a) nephro- and semi-isolepidine embryon (genus \(N.\) – 31 specimens,
   (b) Eu- or centrielepide embryon (unribbed \(O.\), step H) – 59 specimens;
(G) \(N.\) in equatorial section:
   (a) larger, mostly nephrolepidine embryon, more numerous adauxiliary and larger equatorial chamberlets.
   \(N.\ evae\) (Less) (Plate 2, Figs. 2 and 3) – 20 specimens,

Sections équatoriales d’Orthophragmines provenant de Horsarrieu (France), marnière Sourbet, limite des zones SBZ 10/11, Yprésien supérieur.


N. strophiolata (Gümbel) (Plate 2, Figs. 4 and 5) – 10 specimens,
(c) very small, semi-isolepidine embryo, very few adaxiliary and smaller equatorial chamberlets.

N. bodrakensis (Less) (Plate 2, Figs. 8 and 9) – two specimens;
(H) unribbed Orbitocyclus in equatorial section:
(a) small, mostly eulepidine embryo, few adaxiliary and small equatorial chamberlets.
O. douvillei (Schlumberger) (Plate 3, Figs. 10–12) – 33 specimens,
(b) large centralepidine embryo, numerous adaxiliary and large equatorial chamberlets.

O. droegeri nov. sp. (Plate 3, Figs. 1–4) – 26 specimens.

4. Morphometric separation of taxa in the Horsarrieu sample

4.1. Separation with bivariate plots

Step 1: segregation of the ribbed and unribbed forms (as step A in the typological separation).
Step 2: the distribution of ribbed forms on the Z–d bivariate plot (Fig. 5) confirms the typological separation into

Sections équatoriales d’Orthophragmines provenant de Horsarrieu (France), marnière Sourbet, limite des zones SBZ 10/11, Yprésien supérieur.
three taxa (*A. stella*, *O. furcatus* and *O. munieri*). None of them has annular stolons.

Step 3: segregation of the unribbed forms into two by the presence or absence of annular stolons of the equatorial chamberlets. *Discocyclina* belong to the first group while *Nemkovella* and the unribbed *Orbitoclypeus* to the second one (as step D in the typological separation).

Step 4: separation of *Discocyclina* into a group with large embryo (*D. fortisi* and *D. archiaci*) and into another one with small or medium size embryo (*D. dispensa*, *D. augustae* and *D. trabayensis*) by the Z–d bivariate plot (Fig. 6).

Step 5: segregation of the two taxa of *Discocyclina* with large embryo (*D. fortisi* and *D. archiaci*) by the d–n (Fig. 7) and d–G (Fig. 8) bivariate plots. This was more or less visible in Fig. 6, too.

Step 6: isolation of *D. dispensa* from the group formed by *D. augustae* and *D. trabayensis* by the d–F (Fig. 9) and d–H (Fig. 10) bivariate plots. In this sample these latter two taxa cannot be separated biometrically. Typologically they differ from one another in the character of the adauxiliary chamberlets (“archiaci” versus “varians” type with straight versus arcuate outer wall).

Step 7: returning to the group of *Nemkovella* and unribbed *Orbitoclypeus*, three groups can be recognized on the Z–d bivariate plot (Fig. 11). The one with large d values corresponds to *O. droogeri* nov. sp. The middle group represents three taxa, whereas *N. bodrakensis* is alone in the cluster with small d values.

Step 8: the remaining three taxa (*O. douvillei*, *N. evae* and *N. strophiolata*) are well segregated from each other on the enlarged Z–d bivariate plot (Fig. 12).

Following this procedure, 12 groups have been unambiguously distinguished. They correspond to the determined taxa except one group, in which there are two taxa (*D. augustae* and *D. trabayensis*) that are separable by using another qualitative feature of yes/no character.

4.2. Separation by cluster-analysis

Four different cluster-dendrograms have been obtained with the method described earlier. The nine selected quantitative
parameters (Z, F, G and the logarithmically transformed $p$, $d$, $N$, $H$, $W$ and $n$) are used in all of them.

In constructing Fig. 13, the two qualitative features (the presence/absence of ribs and the presence/absence of annular stolons of the equatorial chamberlets) have been used as well. The 205 specimens are grouped into 12 clusters clearly corresponding to the 12 typologically separated species. Only $D. \text{trabayensis}$ could not be isolated from $D. \text{augustae}$, just as in the case of the bivariate plots. Altogether, five of the 205 specimens (2.4%) fell into an inadequate cluster.

In constructing Fig. 14, none of the qualitative parameters were used. Even in this dendrogram that eliminates all subjectivity, 10 clusters have been obtained. Eight of them correspond to separate species ($D. \text{fortisi}$, $D. \text{archiaci}$, $D. \text{augustae}$, $D. \text{dispansa}$, $N. \text{eva}$, $N. \text{bodrakensis}$, $O. \text{droogeri}$ and $O. \text{munieri}$), while the other two are constituted by a pair of species each ($O. \text{douvillei}$ with $O. \text{furcatus}$ and $A. \text{stella}$ with $N. \text{strophiolata}$). $D. \text{trabayensis}$ falls into this last combined cluster. Altogether, 12 specimens (5.9%) fell into an inadequate cluster. This dendrogram shows that even without being aware of anything of the qualitative features of orthophragmines, at least 10 different taxa can be distinguished in the Horsarrieu sample.
The combined use of qualitative and quantitative parameters elaborated by Less (1987, 1993) is suitable for distinguishing parallel lineages but (since there are always specimens falling into an inadequate cluster) cannot take the lead over the empirical discrimination. Moreover, the latter requires much less time. The morphometric separation of lineages can be misleading if the system used for their discrimination is inadequate, since different species can be erroneously identified with each other. Therefore, the use of discriminating qualitative parameters (of yes/no character) must not be given up.

However, in some other aspects, the morphometric method is more advantageous (provided an adequate system of parameters is defined):

- it can validate the typological separation (although, it cannot disprove it);
- it assures a much more reliable identification of particular taxa from different localities (especially, if they are determined by different authors);
- by choosing a fairly evolutive quantitative parameter, it can be much more objectively used in determining the evolutionary degree of particular populations within their own evolutionary lineages (determined beforehand typologically). This is crucial in age-determination.

So, it is concluded that use of both the typological and morphometric methods can be verified. Their advantages and disadvantages are compared in Fig. 15.

6. Systematic description

In this chapter, taxa from the sample studied from Horsarieu are described at subspecies level (whenever possible), with emended diagnosis based on the population mean of the inner cross diameter of the deuteroconch (d) by using values defined in Less (1998) (instead of D, the mean deuteroconch medium diameter in Less, 1987).

In the zonal distribution by Less (1998), this assemblage falls to the boundary of orthophragminid zones OZ 6 and OZ 7 (it contains D. archiaci archiaci marking OZ 6 together with D. fortisi simferopolensis marking OZ 7) corresponding to the transition of the lower and middle Cuisian substages (SBZ 10/11 shallow benthic zone boundary) used in the larger foraminiferal stratigraphy by Serra-Kiel et al. (1998) or to the upper Ypresian in terms of the standard stratigraphical subdivisions.

New taxa are described in detail. In characterizing their internal morphology, the same types of embryos, of adauxiliary chamberlets and of the growth pattern (g.p.) of equatorial chamberlets are used as in Less (1987, 1993). For other taxa, only the necessary bibliography is cited, sometimes with some additional remarks due to the changes in their extent and/or nomenclature as compared with Less (1987).

Statistical data of quantitative parameters (for the 205 specimens studied in detail in this paper) per population are summarized in Fig. 16, including the number of specimens, the

Dendrogramme de 205 spécimens d’orthophragmines d’Horsarrieu. Utilisation de neuf paramètres quantitatifs et de deux paramètres qualitatifs. Les spécimens tombant dans un groupe inadapté sont déplacés vers la gauche. Voir également les explications dans le texte.
Fig. 14. Dendrogram of 205 orthophragminid specimens from Horsarrieu. No qualitative parameters are used. Specimens falling into an inadequate cluster are shifted to the left. Same abbreviations for species as in Fig. 13. See also explanation in the text.

Dendrogramme de 205 spécimens d’orthophragmines d’Horsarrieu. Aucun paramètre qualitatif n’a été utilisé. Les spécimens tombant dans un groupe inadapté sont déplacés vers la gauche. Les abréviations des espèces sont les mêmes que dans la Fig. 13. Voir également les explications dans le texte.
Fig. 15. Comparison of the typological and morphometric approaches from different aspects.

Comparaison, selon différents aspects, des approches typologiques et morphométriques.

<table>
<thead>
<tr>
<th>Method of taxon-determination</th>
<th>Typology</th>
<th>Morphometry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recognition (synthesis by human brain)</td>
<td>Comparison of numerical parameters (analysis)</td>
<td></td>
</tr>
<tr>
<td>Taxonomical concept</td>
<td>Central grouping (around the type)</td>
<td>Putting in between limits</td>
</tr>
<tr>
<td>Disadvantage</td>
<td>Possible oversplitting</td>
<td>Possible over lumping</td>
</tr>
<tr>
<td>Requirement of time</td>
<td>Little</td>
<td>Great</td>
</tr>
<tr>
<td>Separation of parallel lineages</td>
<td>Mostly successful</td>
<td>Easily can be lumped</td>
</tr>
<tr>
<td>Separation of successive taxa within particular lineages</td>
<td>Subjective</td>
<td>Objective</td>
</tr>
<tr>
<td>Documentation</td>
<td>Photo</td>
<td>Photo and statistical data</td>
</tr>
<tr>
<td>Communication between researchers</td>
<td>Subjective, a lot of pitfalls</td>
<td>Tends to be objective, fewer errors</td>
</tr>
<tr>
<td>Subsequent correction</td>
<td>Difficult</td>
<td>Easy</td>
</tr>
<tr>
<td>Preferential applications</td>
<td>Complex geometry</td>
<td>Simple geometry</td>
</tr>
<tr>
<td></td>
<td>Few specimens</td>
<td>Many specimens</td>
</tr>
<tr>
<td></td>
<td>Separation of parallel lineages</td>
<td>Orientation within particular lineages</td>
</tr>
</tbody>
</table>

Fig. 16. Statistical data for orthophragminid populations from Horsarrieu. For details on the abbreviations of parameters see text. s.e.: standard error. A.: Asterocyclina, D.: Discocyclina, N.: Nemkovella, O.: Orbitoclypeus.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of specimens</th>
<th>Embryon</th>
<th>Adaxial chamberlets</th>
<th>Equatorial chamberlets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>protocolch</td>
<td>deuterococh</td>
<td>embracement</td>
</tr>
<tr>
<td>D. archiaci</td>
<td>13</td>
<td>210.8 ± 11.3</td>
<td>160 – 310</td>
<td>431.5 ± 16.7</td>
</tr>
<tr>
<td>D. fortisi</td>
<td>21</td>
<td>560.5 ± 29.6</td>
<td>320 – 820</td>
<td>939.5 ± 43.3</td>
</tr>
<tr>
<td>D. dispansa</td>
<td>7</td>
<td>118.6 ± 5.4</td>
<td>105 – 140</td>
<td>214.3 ± 5.4</td>
</tr>
<tr>
<td>D. angustae</td>
<td>29</td>
<td>85.9 ± 2.4</td>
<td>70 – 118</td>
<td>129.5 ± 3.2</td>
</tr>
<tr>
<td>D. trubayensis</td>
<td>1</td>
<td>72.0</td>
<td></td>
<td>116.1</td>
</tr>
<tr>
<td>N. evae</td>
<td>19</td>
<td>159.3 ± 4.6</td>
<td>133 – 206</td>
<td>234.6 ± 5.6</td>
</tr>
<tr>
<td>N. strophiolata</td>
<td>10</td>
<td>86.9 ± 2.7</td>
<td>69 – 99</td>
<td>131.0 ± 3.6</td>
</tr>
<tr>
<td>N. bodrakensis</td>
<td>2</td>
<td>57.0</td>
<td>53 – 61</td>
<td>80.0</td>
</tr>
<tr>
<td>A. stella</td>
<td>8</td>
<td>85.5 ± 2.5</td>
<td>76 – 99</td>
<td>123.8 ± 2.8</td>
</tr>
<tr>
<td>O. droogeri</td>
<td>26</td>
<td>543.3 ± 18.7</td>
<td>390 – 750</td>
<td>896.0 ± 26.9</td>
</tr>
<tr>
<td>O. mutieri</td>
<td>25</td>
<td>213.6 ± 6.7</td>
<td>150 – 290</td>
<td>394.4 ± 9.8</td>
</tr>
<tr>
<td>O. furcatus</td>
<td>11</td>
<td>106.9 ± 4.2</td>
<td>72 – 126</td>
<td>192.5 ± 6.0</td>
</tr>
<tr>
<td>O. douvillei</td>
<td>33</td>
<td>98.8 ± 2.1</td>
<td>80 – 137</td>
<td>184.2 ± 2.7</td>
</tr>
</tbody>
</table>

Données statistiques des populations d’orthophragmines d’Horsarrieu. Se référer au texte pour le détail des abréviations des paramètres, s.e.: écart-type.
is synonymized with *D. archiaci* archiaci pp. 82.

Figured specimens (marked by E.) are deposited in the Eocene collection of the Geological Institute of Hungary in Budapest.

Class FORAMINIFERIDA Eichwald, 1830.
Order ROTALIACEA Ehrenberg, 1839.
Family DISCOCYCLINIDAE Galloway, 1928.

**Genus Discocyclina** Gümbel, 1870.

*D. archiaci archiaci* (Schlumberger, 1903).

**Plate 1, Figs. 1 and 2.**
1903. *Orthophragmina archiaci* nov. sp. (partim) – Schlumberger, pp. 277, Pl. 8, Figs. 5, 11 (non Pl. 8, Fig. 7, Text-Fig. C = *O. schopeni* crimensis).

1987. *D. archiaci archiaci* (Schlumberger) – Less, pp. 132–133, Pl. 1, Fig. 13, Pl. 2, Figs. 1, 2, 6, 9–11, Pl. 3, Figs. 1–6, 8–11, Text-Fig. 26d (with synonymy).

1987. *D. weijdeni* nov. sp. – Less, pp. 139–140, Pl. 5, Fig. 11, Pl. 6, Figs. 1–3, Text-Fig. 26l.

1992. *D. archiaci archiaci* (Schlumberger) – Ferrandez-Cañadell and Serra-Kiel: Pl. 1, Figs. 1–8, Pl. 2, Figs. 1–8, Pl. 3, Figs. 1–8, Pl. 4, Figs. 4–8, Pl. 5, Figs. 1, 3, 4, 6–8, Pl. 6, Figs. 1–6, Pl. 7, Figs. 1, 2, 4, 5, Pl. 8, Figs. 1–4.

2002. *D. archiaci archiaci* (Schlumberger) – Özcan et al., pp. 293, Figs. 8i, 9 (partim).

2007b. *D. weijdeni* Less – Özcan et al., pp. 301, Fig. 8n.

**Emended diagnosis:** *D. archiaci* populations with *d* mean ranging from 390 to 600 μm.

**Remarks:** formerly (Less, 1987) *D. weijdeni* of Horsarrieu was distinguished from *D. archiaci* by its narrower and more elongated equatorial chamberlets. However, this feature can very easily be caused by the greater water depth in our locality (as compared to other classical upper Ypresian localities like Gan, Bos d’Arros, Campo, etc.) that is supported also by the multitude of orthophragminid taxa and by the poor nummulitid fauna (*Nummulites* aff. *irregularis* and *N. praeculci*, based on Schaub, 1981). Elongation of chambers with increasing water depth is a well-known phenomenon at operculinid forms, too (Hottinger, 1977; Drooger, 1993). Therefore, here *D. weijdeni* is synonymized with *D. archiaci archiaci*.


**Plate 1, Figs. 3–5.**
1987. *D. fortisi* (d’Archiac) *simferopolensis* nov. sp. – Less, pp. 146–147, Pl. 7, Figs. 10–14, Pl. 8, Figs. 1–4, Text-Figs. 26t–u (with synonymy).


**Emended diagnosis:** *D. fortisi* populations with *d* mean ranging from 850 to 1100 μm.

**Remarks:** according to Less (1987, 1998), the *D. fortisi* lineage can be subdivided into *D. fortisi fortisi* and *D. fortisi simferopolensis* that are separated by the biometrical limit of *d* mean equals to 850 μm and characterize the OZ six and seven zones (corresponding to the early and middle part of the late Ypresian, respectively) of Less (1998). Özcan (2002) could follow the evolution of the *D. fortisi* in Çayraz and Yeşilyurt (Haymana-Polatlı Basin, central Anatolia) further to the latest Ypresian and to the early Lutetian (*OZ* 8a–9) and described a new taxon, *D. fortisi cairazensis* with *d* mean exceeding 1100 μm thus; the diagnosis of *D. fortisi simferopolensis* had to be modified as it is delimited above.


**Plate 1, Figs. 6 and 7.**
1987. *D. dispansa* (Sowerby) *taurica* nov. sp. – Less, pp. 159–160, Pl. 12, Figs. 1–6, Text-Fig. 27m.

1987. *D. aaroni* nov. sp. *chalossensis* nov. sp. – Less, pp. 174, Pl. 18, Fig. 6–9, Text-Fig. 28b.

2002. *‘dispansa’* (Sowerby) *taurica* Less – Özcan, pp. 81, Pl. 2, Figs. 4–6, Text-Fig. 3E.

**Emended diagnosis:** *D. dispansa* populations with *d* mean ranging from 160 to 230 μm.

**Remarks:** the Horsarrieu forms are described in Less (1987) as *D. aaroni chalossensis* based on two specimens only. The diagnostic feature of *D. aaroni* is its “varians” type adauxiliary chamberlets (with arcuate outer walls) that distinguishes it from *D. dispansa* with “archiaci” type adauxiliary chamberlets (with straight outer walls). In our sample some additional specimens were found. Among these forms, both types occur as well as their transitional ones. Also, in the upper part of the *Nummulites distans* beds of the Crimean Simferopolitan stage (population DF in Less, 1987, sample CRIDU in Less and Ö. Kovács, 1996 and Less, 1998) these forms can be found together with very similar quantitative parameters (Less, 1987: Table 11). Therefore, here *D. aaroni chalossensis* is synonymized with *D. dispansa taurica*.


**Plate 1, Figs. 8–10.**
1987. *D. augustae* Weijden *sourbetensis* nov. sp. – Less, pp. 152–153, Pl. 9, Figs. 7, 9–12, Pl. 10, Fig. 1, Pl. 17, Fig. 4, Text-Fig. 27f.

1987. *D. dispansa* (Sowerby) *ganensis* nov. sp. – Less, pp. 158–159, Pl. 11, Figs. 10–13, Text-Figs. 27l, 28a.


?2002. *D. augustae* Van der Weijden *sourbetensis* Less – Özcan, pp. 80, Pl. 1, Figs. 11, 12, Pl. 2, Figs. 1–3, Text-Fig. 3C.

2003. *D. augustae* Van der Weijden *sourbetensis* Less – Çolakoğlu and Özcan, pp. 52, Pl. 1, Figs. 6–11, Text-Fig. 3B.

**Emended diagnosis:** D. augustae populations with $d_{\text{mean}}$ less than 145 $\mu$m.

**Remarks:** since Less (1987), the early representatives of both the D. augustae and D. dispensa-lineages from Gamarde, Gan-Berdoulou, Bos d’Arros, Horsarrieu (SW France) and the Haymana-Polatlı and Safranbolu Basins of Turkey ( Özcan, 2002; Çolakoğlu and Özcan, 2003; Özcan et al., 2007b) have been investigated. These two lineages are very similar in their qualitative features. Their evolution is parallel, in terms of quantitative parameters, D. augustae repeats the evolution of D. dispensa but with a four to six million years delay (Less and Ö. Kovács, 1996). From its quantitative parameters it became clear that the forms described as D. dispensa ganensis from Gan-Tuilerie rather belong to the D. augustae-lineage, therefore, they are put in synonymy here with D. augustae sourbetensis.

Plate 1, Fig. 11.

1955. D. trabayensis nov. sp. – Neumann, pp. 130, Pl. 6, Figs. 2–4, Pl. 7, Figs. 2, 3.

1959. D. concentrica nov. sp. – Kecskeméti, pp. 45–47, Pl. 2, Figs. 6, 7, 9, Text-Fig. 10(?)

1987. D. trabayensis trabayensis Neumann – Less, pp. 171, Pl. 17, Figs. 1–3, 5–9, 13, Text-Fig. 27 (with synonymy).

1987. D. trabayensis Neumann concentrica Kecskeméti – Less, pp. 172, Pl. 17, Figs. 10–12, Pl. 18, Figs. 1, 2, Text-Fig. 27 (with synonymy).

2002. D. trabayensis trabayensis Neumann – Özcan, pp. 79–80, Pl. 1, Figs. 8–10, Text-Fig. 3D.

**Emended diagnosis:** D. trabayensis populations with $d_{\text{mean}}$ less than 125 $\mu$m.

**Remarks:** based on additional data on the middle Eocene representatives of D. trabayensis from Gibret and Biarritz, rocher de Peyreblanque (both France), it became clear that two subspecies (D. t. trabayensis and D. t. concentrica) of the lineage distinguished earlier by Less (1987) widely overlap stratigraphically. Therefore, here they are united under the name of D. trabayensis trabayensis. This implies that the evolution of this lineage is extremely slow during the late Ypresian and almost the entire middle Eocene where it is very rare as well. However, in the late Bartonian and Priabonian, its evolution considerably accelerated; at the same time, it became much more frequent as well (Less, 1999; Özcan et al., 2007a).


Plate 2, Figs. 1–3.

1987. N. evae nov. sp. – Less, pp. 184, 186–187, Pl. 23, Figs. 1–7, 9–12, Pl. 24, Figs. 1–4, Text-Fig. 29a (with synonymy).

2002. N. evae Less – Özcan, pp. 84, Pl. 1, Fig. 3, Text-Fig. 3B.

2003. N. evae Less – Çolakoğlu and Özcan, pp. 54, Text-Fig. 3A.

2003. N. strophiolata (Gümbel) fermonti Less (partim) – Çolakoğlu and Özcan, pp. 54, Pl. 1, Figs. 2–4, Text-Fig. 3A (specimens from sample SAK 24).


**Remarks:** formerly (Less, 1987, 1998; Less and Ö. Kovács, 1996) we believed that the evolution of N. evae is very slow, and therefore, it could not be subdivided into chronosubspecies. Later ( Özcan et al., 2007b) it appeared that the early and middle Lutetian representatives of the lineage have much larger embryon than that of the Ypresian forms. Thus, recently two chronosubspecies, the Ypresian N. evae evae and the early-middle Lutetian N. evae karitensis (introduced in Özcan et al., 2007b), subdivided by the biometric limit of $d_{\text{mean}}$ equals to 260 $\mu$m, are distinguished.

Plate 2, Figs. 4 and 5.

1987. N. fermonti nov. sp. – Less, pp. 187–188, Pl. 23, Fig. 8, Pl. 24, Figs. 5, 6, Text-Fig. 29b.

2002. N. strophiolata (Gümbel) fermonti Less – Özcan, pp. 84, Pl. 1, Figs. 1, 2, 4–7, Text-Fig. 3A.

2003. N. strophiolata (Gümbel) fermonti Less (partim) – Çolakoğlu and Özcan, pp. 54, Pl. 1, Figs. 1, 5, Text-Fig. 3A (specimens from sample SAK 25).

2007b. N. strophiolata (Gümbel) fermonti Less – Özcan et al., pp. 302, Figs. 12b–d, 13 (partim).

**Emended diagnosis:** N. strophiolata populations with $d_{\text{mean}}$ less than 150 $\mu$m.

**Remarks:** analyzing our quantitative data on late Ypresian and early Lutetian Nemkovella, it appeared (Less and Ö. Kovács, 1996) that the forms described as “fermonti” much rather belong to the N. strophiolata-lineage than those called “bodrakensis”. Horsarrieu is one of the oldest occurrences of the N. strophiolata lineage along with Çayraz ( Özcan, 2002) and Kiriklar ( Özcan et al., 2007b). Nemkovella from the early/late Ypresian boundary from Sakarya (Haymana-Polatlı Basin, Çolakoğlu and Özcan, 2003) represent probably the segregation of N. strophiolata from N. evae, therefore it is difficult to attribute these forms to either of them.

Plate 2, Figs. 8 and 9.

1987. N. strophiolata (Gümbel) bodrakensis nov. ssp. – Less, pp. 189, Pl. 24, Figs. 7–12, Text-Figs. 29c–e.

**Emended diagnosis:** small-sized, flattened forms. The extremely small embryon is mostly semi-isolepidine. The adaxial chambers are of the “varians” type, very low in numbers, relatively wide but very low. The equatorial chamberlets are medium wide but very low. The growth pattern of the annuli is of the “strophiolata” type.

**Remarks:** the poor quality of figuration of this taxon is caused by its preservation and rare occurrence in the sample studied. N. bodrakensis is very rare in the Mediterranean upper
Ypresian and lower Lutetian but it is easily distinguished due to its minute internal morphology from the contemporaneous *N. evae evae* and *N. strophiolata fermoni* not only in Horsarriu but also in Saint-Barthélémy. See also the remarks to *N. strophiolata fermoni*.

Family ORBITOCLYPEIDAE Brönnimann, 1946.

Genus *Asterocyclina* Gümbel, 1870.

*A. stella* (Gümbel, 1861) *praestella* nov. ssp.

*Plate 2*, Figs. 6 and 7.


1982. *A. taramellii* (Munier-Chalmas) – Fermont, pp. 131–132, Table 3 (partim), Pl. 4, Figs. 1–6, Pl. 11, Figs. 1–3.

1987. *A. stella* (Gümbel) *taramellii* (Munier-Chalmas) (partim) – Less, pp. 230–231, Pl. 36, Figs. 8–13 (non Pl. 36, Fig. 7 and Pl. 42, Fig. 10).

2003. *A. stella* (Gümbel) – Çolakoğlu and Özcan, pp. 58, Pl. 3, Fig. 9.

**Etymology:** it indicates that this subspecies is ancient as compared to the nominate subspecies of the lineage.

**Holotype:** specimen E. 9232, *Plate 2*, Fig. 6.

**Depository:** Geological Institute of Hungary, Budapest.

**Type locality:** Horsarriu (Landes, SW Aquitaine, France), topmost part of marneir Sourbet.

**Type level:** Upper Ypresian, boundary of the OZ 6 and OZ 7 orthophragminid and of the SBZ 10 and 11 shallow benthic biozones.

**Diagnosis:** *A. stella* populations with *d* *mean* less than 150 μm.

**Description:** external morphology: small (1–2 mm) more or less inflate asteroidal forms with five or rarely with six strong rays, with “marthae” type rosette and with no interray areas. The size ratio of forms “A” and “B” is not yet.

For internal morphology see *Fig. 17*.

**Remarks:** Less (1987) described all Ypresian and Lutetian *Asterocyclina* with small (*d* *mean* less than 200 μm) embryo and with no “stellate” type adauxiliary chamberlets under the name of *A. stella taramellii*. Later, Less (1993) separated these forms from the *A. stella*-lineage as *A. taramellii*. Unfortunately, the equatorial section of topotypical “taramellii” from the middle Ilerdian of Spilecco is known only from the bibliography (Schlumberger, 1904: *Plate 6*, Fig. 51 and Neumann, 1958: *Plate 28*, *Fig. 9*, *Pl. 29*, *Fig. 1*, all figuring the same specimen). Numerous specimens of *Asterocyclina* from the middle part of the lower Ypresian of Aurignac (*Plate 2*, Figs. 10 and 11, sample AUR91, in *Less, 1998*), corresponding to the passage of bed j – Marbres de Mancioux à Mélóbésiées – and bed k – Marnes à Asterodiscus et Xanthopsis – in Tambareau and Villatte (1977) were studied; however, that helped a lot in distinguishing *A. taramellii* (characteristic for the early Ypresian) from the early members of the *A. stella* lineage from the upper Ypresian and lower Lutetian.

The main difference between them is in the shape of the cycles especially in the first annuli: while *A. stella praestella* (and also the following members of the lineage) has strong rays passing rather sharply into the interray area already in the very early annuli, these passages are rather gradual at *A. taramellii* and also their rays are much less definite, especially in the first annuli. In other words, the first five to 10 annuli of *A. taramellii* are rather undulating, whereas in the case of *A. stella*, they are much more asteroidal. The above mentioned figures of the topotypical Spilecco “taramellii” show rather undulating first cycles; therefore, this name had to be reserved for the lower Ypresian forms and, consequently, the upper Ypresian and lower Lutetian representatives of the *A. stella* lineage needed a new name. Probably, its the earliest occurrence that is recorded by Çolakoğlu and Özcan (2003) from the lower/upper Ypresian boundary beds from Sakarya (Central Turkey).

The upper biometrical limit of the former *A. stella taramellii* (in *Less, 1987*) is also modified in the definition of *A. stella praestella* nov. ssp., in order to follow Fermont’s (1982) distinction between his *A. taramellii* (=*A. stella praestella* here) and *A. stella* (=*A. stella stella* according to *Less, 1998*) from Israel.

**Comparison:** *A. stella praestella* can be confused only with other members of the genus bearing similarly small embryo. The distinction from *A. taramellii* is given above. The other similar form, *A. stellata adourensis* (with practically the same stratigraphic range), has “stellate” type adauxiliary chamberlets. However, sometimes (especially in the lower and middle Cuisian) the type of these chamberlets is not too definite, e.g. in Gan-Tuilerie (France), we can find both types and their transitions as well (Brolsma, 1973; Ferràndez i Cañadell, 1999). In this case, the distinction of the two species is rather artificial: here we deal rather with one single population but in the “moment” of separation of the two species.

**Range:** the late Ypresian and early Lutetian OZ 5–8b orthophragminid and SBZ 10–13 shallow benthic biozones.

SW Aquitaine (Horsarriu, Gan, Saint-Barthélémy), Crimea (the upper part of the Nummulites distans zone of the Simfer-
Genus *Orbitoclypeus* Silvestri, 1907.

*O. droogeri* nov. sp.

**Plate 3, Figs. 1–4.**

**Etymology:** in honor of Cornelis W. Drooger, the outstanding researcher of orbitoidal foraminifera who initiated this study.

**Holotype:** specimen E. 9219, *Plate 3, Fig. 1.*

**Depository:** Geological Institute of Hungary, Budapest.

**Type locality:** Horsarrieu (Landes, SW Aquitaine, France), topmost part of marnière Sourbet.

**Type level:** Upper Ypresian, boundary of the OZ 6 and OZ 7 orthophragminid and of the SBZ 10 and 11 shallow benthic biozones.

**Diagnosis:** medium-sized, moderately inflate forms with “chudeaui” type rosette. The embryon is centrilepidine, the two chambers are very large. The “varians” type adauxiliary chamberlets are numerous, very wide and moderately high as well as the equatorial chamberlets. The annuli are circular, their growth pattern is of “varians” type.

**Description:** external morphology: usually medium-sized (3 to 6 mm), moderately inflate forms without a distinct umbo. The rosette is of the “chudeaui” type. The granules are coarse (80 to 120 µm in diameter), somewhat bigger in the center than in the periphery. Each granule is surrounded by five to eight lateral chamberlets whose size is smaller than that of the granules.

**Remarks:** no *Orbitoclypeus* with such large embryon has been known yet, that is why this new species is established. Its closest ancestor might be *O. multiplicatus* known from the lower Ypresian of Spilecco (Northern Italy) and Turkey (*Less et al., 2007*). However, the size of the embryon of this form (*d* mean is about 350–500 µm) seems to too small for inferring a direct evolution towards *O. droogeri.* Unfortunately, we could not find microspheric specimens that could prove the generic identity of *O. droogeri.*

We have no knowledge of any descendant of *O. droogeri* that bears far the largest embryon of its genus.

**Comparison:** this species can be confused only with some *Discocyclina* (*D. fortisi simferopolensis*, *D. pulcra pulcra*, *D. spliti spliti*, *D. pratti minor*) having similar-sized centrilepidine embryon. Therefore, the recognition of the presence or lack of the annular stolons of the equatorial chamberlets is crucial in distinguishing *O. droogeri* from the above-mentioned taxa of *Discocyclina.***

In this respect, it is interesting to compare *D. fortisi simferopolensis* and *O. droogeri* that occur together in our sample. In *Fig. 19*, we have plotted the average width of the adauxiliary chamberlets (*W*) against the average shape of the equatorial chamberlets (*G*) for all specimens of the two taxa. *Fig. 19* clearly shows that the two taxa form two different clusters even not taking into account by their different stolon system of the equatorial chamberlets. Also on the dendrogram of *Fig. 14* (in whose construction we did not use the presence/lack of annular stolons) they are separated into two different clusters.

**Range:** it is known so far only from the upper Ypresian beds of the type level in Horsarrieu.

*O. munieri munieri* (*Schlumberger, 1904*).

**Plate 3, Figs. 5 and 6.**

1904. *Orthophragmina munieri* nov. sp. – Schlumberger, pp. 125, Pl. 3, Fig. 12.

**Fig. 19.** Distribution of specimens belonging to *Discocyclina fortisi simferopolensis* and *Orbitoclypeus droogeri* on the *W–G* bivariate plot.

Répartition des spécimens appartenant à *Discocyclina fortisi simferopolensis* et *Orbitoclypeus droogeri* dans un diagramme *W–G.*
and O. bayani (Munier-Chalmas) (partim) – Less, pp. 203–205, Pl. 27, Figs. 5, 6.

2007b. O. munieri munieri (Schlumberger) – Özcan et al., pp. 309–310, Figs. 13 (partim), 141 p. (with synonymy).

Remarks: these forms were described in Less (1987) as O. bayani. However, a relatively abundant material from Spilecco (Northern Italy, the type locality of O. bayani) and from Turkey (Özcan et al., 2007b) demonstrated that O. munieri and O. bayani correspond to two different taxa (Less, 1998) and evolutionary lineages. O. munieri is described in detail in Özcan et al. (2007b) and is subdivided into two chronospecies, O. munieri munieri, with d_{mean} above 220 µm, and O. munieri ponticus (described in Less et al., 2007), below this limit, at about the boundary of the OZ 3/4 orthophragminid zones by Less (1998). We assume that O. munieri with d_{mean} between 220 and 300 µm is characteristic for the late early Ypresian and represents an intermediate chronosubspecies between O. munieri ponticus and the topotypical O. munieri munieri with d_{mean} above 300 µm from the Marne à Xanthopsis in Sainte-Colombe, close to Horsarrieu and representing the same lithostratigraphic unit. Such populations with reasonable number of specimens, however, are not yet recorded.

O. furcatus (Rüttimeyer, 1850) palaeofurcatus nov. ssp.
Plate 3, Figs. 7–9.

Etymology: it marks that this subspecies is the most ancient one of its lineage known so far.

Holotype: specimen E. 9225, Plate 3, Fig. 7.

Depository: Geological Institute of Hungary, Budapest.

Type locality: Horsarrieu (Landes, SW Aquitaine, France), topmost part of marnière Sourbet.

Type level: Upper Ypresian, boundary of the OZ 6 and OZ 7 orthophragminid and of the SBZ 10 and 11 shallow benthic biozones.

Diagnosis: O. furcatus populations with d_{mean} less than 200 µm.

Description: external morphology: small and medium-sized (3 to 6 mm), flattened forms with seven to nine relatively thick ribs that bifurcate at the edges. “Marthae” type rosette.

For internal morphology see Fig. 20.

Remarks: according to Less (1987) the O. furcatus lineage starts only in the late Lutetian and it is subdivided into two evolutionary stages, namely “rovasendai” and “furcatus” (this latter name is corrected here to “furcatus” in agreement with the gender of the genus). Since then we have found more primitive forms of the lineage in stratigraphically much lower strata. The population from the lower Lutetian beds of Gibret, église (Orbitoclypeus furcatus nov. ssp. Gibret) will be described later with the diagnosis of d_{mean} between 200 and 270 µm (Less, 1998) while the even less advanced Horsarrieu population belongs to the new subspecies described here.

Comparison: among the ribbed Orbitoclypeus only the most primitive members of the O. munieri-lineage (O. munieri ponticus, described in Less et al., 2007) possesses similar type and similar-sized embryo as O. furcatus palaeofurcatus. Concerning their quantitative parameters, they cannot be distinguished from each other in practice. However, the bifurcation of O. munieri ponticus is less regular and also their annuli are less regularly undulated. Due to the difference in stratigraphical level, the accompanying fauna is totally different.

Range: as yet, Horsarrieu is the oldest known occurrence of the lineage. Consequently, O. furcatus palaeofurcatus may extend from about the beginning of the late Ypresian up to about the end of this stage.

O. douvillei douvillei (Schlumberger, 2003).
Plate 3, Figs. 10–13.

1903. Orthophragmina douvillei nov. sp. – Schlumberger, pp. 283–284, Pl. 9, Figs. 21, 22(7), 23, 24.

1987. Orbitoclypeus douvillei (Schlumberger) (partim) – Less, pp. 205–206, Pl. 27, Figs. 7–9, Text-Figs. 30i, j (non k).

1987. Orbitoclypeus varians (Kaufmann) horsarrieuensis nov. ssp. – Less, pp. 209, Pl. 28, Figs. 9–12, Text-Fig. 30m.

1999. Orbitoclypeus douvillei (Schlumberger) – Ferrandez i Cañadell, pp. 82–84, 88, Pl. 1, Figs. 5–8, Pl. 2, Figs. 5–8, Pl. 5, Figs. 2, 3, 6, Pl. 7, Figs. 1–8, Pl. 9, Figs. 5–8, Pl. 12, Figs. 1–8, Pl. 16, Figs. 3, 6–8.

2002. Orbitoclypeus douvillei douvillei (Schlumberger) – Özcan, pp. 84–85, Pl. 2, Figs. 10–12, Pl. 3, Fig. 6, Text-Fig. 4B (partim).

2003. Orbitoclypeus douvillei douvillei (Schlumberger) – Çolakoğlu and Özcan, pp. 56, Pl. 3, Fig. 11.

2007b. Orbitoclypeus douvillei douvillei (Schlumberger) – Özcan et al., pp. 305, Figs. 12k–r, 13 (partim).

Emended diagnosis: O. douvillei populations with d_{mean} less than 200 µm.

Remarks: having examined more material from the lower Lutetian deposits of Gibret, église (France) it became clear that O. douvillei and O. chudeaui described in Less (1987) as separate species constitute in fact one single evolutionary lineage, and therefore, they have been united into
O. douvillei by Less (1993, 1998). The upper Ypresian representatives of this rapidly evolving lineage characterized by $d_{\text{mean}}$ less than 260 $\mu$m by Less (1998) are recently subdivided into two by Özcan (2002) using the limit of $d_{\text{mean}}$ equals to 200 $\mu$m. The name of O. douvillei douvillei is preserved for populations with $d_{\text{mean}}$ less than 200 $\mu$m, because in its type locality, Bos d’Arros (France), $d_{\text{mean}}$ is 161 $\mu$m according to Less (1998) and 185–190 $\mu$m based on Ferrandez i Cañadell (1999). For latest Ypresian populations with $d_{\text{mean}}$ ranging from 200 to 260 $\mu$m Özcan (2002) introduced a new name, O. douvillei yesilyurtenensis.

Having compared O. varians horsarrieiensis from Horsarrieu described in Less (1987) (named O. marthaes horsarrieiensis in Less, 1993) with O. douvillei douvillei from the sample analyzed in this paper, they proved to be very similar and, therefore, the name of “horsarrieiensis” is abandoned here. We have found only four specimens of these latter forms from sample HORDSA (HX in Less, 1987) whose surface was not very well preserved, and probably therefore, their type of rosette was incorrectly determined.

Acknowledgements

This paper is a contribution to the I.G.C.P. projects No. 286 (“Early Paleogene Benthos”) and 393 (“Neritic events at the Middle-Upper Eocene boundary”) and it was partly funded by the National Scientific Research Fund of Hungary (OTKA, Grants, No. T 16863, 32370 and K 60645). We are especially grateful to Cornelis W. Drooger (Utrecht) and Lukas Hottinger (Basel, special thanks also for reviewing and improving the terminology used both in English and French) whose ideas about the two (typological versus morphometric) methods inspired us to write this paper. Many thanks are due to Yvette Tambareau (Toulouse) for sending comparative early Asterocyclina from Aurignac (S France), to Ercan Özcan (Antalya, then Istanbul) for the possibility to study Turkish materials and for consultations, to Maria and Stephen Szabó (London) for linguistic improvements of the English text, to Helène Pauwels (Orléans) and Gábor Csillag (Budapest) for the French translation and to the workers in the Department of Micropaleontology at the State University of Utrecht who kindly assisted in studying the material in their collection. The very useful remarks of Johannes S. Pignatti (Rome, special thanks for additional linguistic corrections) and Carles Ferrandez-Cañadell (Barcelona) helped a lot in improving this paper.

References

Ferrandez-i Cañadell, C., 1999. Morfoestructura i paleobiologia dels ortofragminids de la mesogea (Discocyclinidae i Orbitoclypeidae, Foraminifera) [Morphostructure and paleobiology of Mesogean orthophragminids (Discocyclinidae and Orbitoclypeidae, Foraminifera), Institut d’Estudis Catalans, Secció de Ciències i Tecnologia, Arxius de les seccions de ciències 121, 1–339 (in Catalan with English summary)].
Less, Gy., Özcan, E., Báldi-Beke, M., Kollányi, K., 2007. Thanetian and early Paleogene larger foraminiferal assemblages of the Western Tethys (Turkey, Italy and Bulgaria) and their Revised Taxonomy and Biostratigraphy. Rivista Italiana di Paleontologia e Stratigrafia 113, 419–448.
Neumann, M., 1955. Étude des Orthophragmines contenues dans les marnes à Xanthopsis dufourii (Lutétien inf.) de la Chalosse de Montfort (Landes).


