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“Odd partnership”, a particular size relation between close species of larger foraminifera, with an emendation of an outstandingly odd partner, *Glomalveolina delicatissima* (Smout, 1954), Middle Eocene

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Key words: Larger foraminifera, alveolinids, functional morphology, shell size, embryo size, dimorphism, stereotypy, global community maturation (GCM), life strategy

ABSTRACT

“Odd partnerships” are introduced here and defined by an association of two sympatric species exhibiting a structurally identical or (beyond stereotypy) similar adult shell architecture but distinguished by striking size differences. The latter are expressed by foraminifera in the proloculus, in the adult test or in both at the same time. Odd partners share their habitat and therefore often their taphocoenoses. Shallow environments produce odd associations more frequently than deeper ones. In Earth History, odd partnerships appear in a stage of global community maturation (GCM) when generic dominance of the K-strategists is reached and specific diversification starts. Adult shell sizes reflect growth strategies and duration of life of a generation within the life cycle of a foraminifer. Megalosphere size differences may reflect differences in growth rates. The size difference in odd partnerships may be interpreted as a response to seasonality in tropical, oligotrophic environments modifying the life history of the K-strategists in order to push the carrying capacity to a level never to be reached by one partner alone.

RESUME

«Odd partnership», c'est-à-dire le terme «alliance disparate» est introduit ici pour désigner la cohabitation frappante de deux ou plusieurs espèces de taille différente qui ont cependant une architecture identique ou, au-delà d'une simple stéréotypie, très voisine témoignant de leur proximité phylogénétique. Chez les foraminifères benthiques, cette disparité s'exprime dans la taille inégale soit du proloculus soit de la taille de la coquille adulte. Les partenaires inégaux se partagent leur habitat, et par conséquent souvent aussi leur taphocoenoses. L'alliance disparate est plus fréquente dans les zones néritiques qu'en profondeur. Dans le cours de l'Histoire de la Terre, les partenaires inégaux apparaissent dans un cycle de maturation communautaire global (GCM) au moment où un nombre restreint de genres commencent à dominer les associations de stratégies K et à diversifier leurs espèces en rameaux phylétiques parallèles. Chez les foraminifères vivant en de telles alliances la différence de taille des coquilles adultes reflète des stratégies de croissance et une durée de vie différentes, une différence de taille de la mégalosphère peut indiquer une différence du taux d'accroissement du volume par pas de croissance. Tenant compte des périodes de reproduction déphasées observées dans des alliances disparates vivant aujourd'hui, celles-ci sont interprétées comme un moyen de mieux utiliser les ressources temporairement disponibles dans le cycle saisonnier d'un environnement oligotrophe tropical favorisant des stratégies K.

Introduction

The size of an organism as compared to the sizes of its fellow organisms within the same community has autecological meanings in many ways: an elephant has other relationships with its ambient environment than a mouse living in the same area. Extreme size differences such as the one between elephant and mouse often reflect extremely loose, if ever very indirect relationships between such mismatching partners in the same community. Comparing an elephant with a mouse, of course, involves not only the difference in adult size but also all the other particularities distinguishing a proboscidean from a rodent. Therefore, in this case, the autecological role of the respective sizes will be difficult to isolate and to identify.

Larger foraminifera, their fossil record and their extant dis-

tribution, provide numerous examples of species coexisting in space and time, exhibiting identical shell architecture and similar shell shapes but differing, almost exclusively, by their size ranges. The latter seem to be the only morphological element reflecting divergent autecological functions. Larger foraminifera therefore represent a particularly favourable field to explore the role of organism size in ecosystems and their evolution in time. Moreover, they may shed some light on the significance of the size difference in adult shells of different generations within the same species (dimorphism). Hallock (1985) has produced a plausible explanation why the semelparous (i.e. reproducing once in their life-time) larger foraminifera are large: growth to large size involving a com-

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paratively long ontogenesis would be of considerable advantage under conditions of environmental stability and limited food resources, i. e. under conditions enforcing so-called K-strategies of life. With this term, ecologists designate a type of life strategy adapted to constant or at least predictable carrying capacities of the ambient environment in contrast to the more opportunistic r-strategy taking advantage of resources available only during short and unpredictable periods of time (Hottinger 1996). However, since closely related species of strikingly different sizes may share their habitat, the explanation for large sizes in foraminifers will have to be differentiated and refined.

The present, preliminary paper, far from offering beyond some hypotheses any definite conclusion, introduces the term "odd partnership" as a label for size differences other than dimorphism between specimens with identical or closely similar architecture, in order to trigger a discussion on this subject. A particularly striking example of an odd pair was observed in Eocene alveolinid assemblages corresponding to the culmination point of global community maturation in the Middle Lutetian. The odd partner was identified as *Alveolina delicatissima* Smout, 1954. This name, based on a poor type description and supported by a single picture of a non-centered, oblique section, needs an emendation (given as annex to this paper) if the name is to be used in a context beyond regional, Near-Eastern biostratigraphy.

Characteristics of odd partnerships

Don Quijote and Sancho Pansa in Cervantes' famous novel may symbolize an "odd partnership" of two human beings living together through their common adventures. Don Quijote, of high stature, is the more differentiated and more vulnerable person, Sancho, small and corpulent, is less exposed to the complications of life. From this, we will call the larger, by its size and duration of lifetime more exposed partner "Don" for Don Quijote, the smaller one "San" for Sancho Pansa. Beyond simple Don - San pairs, odd partnerships may be characterized by several and diverse Don partners and usually few, much more uniform San partners.

Taxonomic "closeness" of odd partners

In thin sections of cemented limestones rich in larger foraminifera we often observe the coexistence of large- and small-sized shells exhibiting identical or almost identical structural features in their adult shell architecture. The similarity of their architecture reflects their mutual closeness in the taxonomic system: most of them will have to be classified as different species within the same genus, some of them may be attributed to different sister genera belonging to the same subfamily.

The history of generic classification of Eocene alveolinids may illustrate the situation: Reichel (1937) proposed the subgenus *Glomalveolina* for alveolinids with a reduced or absent dimorphism in the early growth stages characterized by strep-

tospiral test coiling in both generations in contrast to *Alveolina* s. str. which is planispirally coiled from the start of megalospheric growth. The adult architecture is characterized by planispiral-involute chamber arrangement, a subdivision of the chamber by septula alternating in position from one chamber to the next, by the presence of pre- and post-septal passages and by a double row of apertures alternating in position in subsequent transverse shell planes. This diagnosis for the genus *Alveolina* s.l. is in contrast to Cretaceous or Late Tertiary genera (Reichel, 1937; Caus, 1981). Hottinger (1960 b) demonstrated the diachronous and diaphyletic nature of the subgeneric limit and showed, in 1963, the separating architectural trait to be dependent on a threshold value of the megalosphere diameter (0.11 mm in Eocene alveolinids). A similar threshold value in elongation was found to trigger the appearance of supplementary, tubiform passages in the bipolar columella of elongate alveolinids. This character defines an other subgeneric name, *Eoalveolinella*, introduced by Silvestri in 1928 but afterwards never used again. Megalosphere diameter and elongation rates during growth are specific characters used to differentiate biostratigraphically successive species of a phyletic line as interpreted by Hottinger (1960 a,b). Finally, Loeblich and Tappan (1987) elevated *Glomalveolina* to generic rank with the argument that taxa of subgeneric rank would not have any use in foraminiferal systematics by lack of a clear concept differentiating the generic from a subgeneric level. Thus, "closeness" in architectural traits can not be defined without ambiguity by taxonomic relationships, i.e. by common names on a particular level of the hierarchy of systematics, but has to be discussed case by case.

Considering the geological history of the alveolinids from Middle Cretaceous to Recent, the generic identity based on the identical distribution pattern of the apertures on the apertural face (and its consequences for the architecture) in Eocene alveolinids indicates that the "closeness" of the Eocene odd partners is not simply due to stereotype response to an environmental situation but that they represent separate offsprings from the same phylogenetic root (called progenitor by Kauffman and Harries 1996) in the Late Paleocene (Thanetian) time period. The alveolinid stereotype, a planispiral-involute shell tending to become fusiform at large sizes, with a subdivision of the chambers into long, tubiform chamberlets in parallel rows, is a generalized response of a porcelaneous foraminiferal shell derived from a pseudonummuloculinid ancestor with a streptospiral shell and a low, basal slit as aperture (Hottinger et al. 1989). The pseudonummuloculinid adaptation to a K-strategy corresponds to an increase in size, and must thereby respond to the often conflicting requirements of metabolism, growth, motility, symbiosis and successful reproduction: the fusiform shell with its supplementary apertures at the poles including polar torsion is a stereotypic device to shorten the spiral ways of intracellular communication in the equator to about a tenth of its length in polar direction (Hottinger 1978). This stereotypic feature appears in many unrelated forms, also in fusulinids (Leppig 1995).

Thus, true odd partners have more in common than their stereotype response to environment: they should be derived from a common ancestor and therefore have a similar genome. Proof for common ancestry can be derived only from a comprehensive overview of the systematic sector to which the odd partners are assigned, including its historical background. In alveolinids, common ancestry is reflected by the disposition pattern of the apertures on the apertural face with all its consequences for the shell architecture (Caus, 1981).

Morphological differences between odd partners

While the architectural traits of odd partners are close or identical, as discussed above, other morphological elements may be different beyond their discrepancy in size. Such elements are linked to size, usually at threshold values, differing in value and broadness from genus to genus (Hottinger, 1963). Thus, the smaller megalospheres of the San partners often are undifferentiated and followed by nepionic stages with a simplified nepionic structure lacking for instance an endoskeleton while the Don partners possess an embryonic apparatus in the megalospheric generation with an architecture of its own (orbitoidiforms, orbitolitids, advanced soritids etc.) followed immediately by the full structural differentiation of the adult.

Considering shell shapes in the adult and their progressive change in time, such as the index of elongation in alveolinids or fusulinids, we find the San partner less or at most equally far advanced as its Don associate. Often, the shape indices of the San partner are similar when the microspheric Don partner is compared at a growth stage matching the adult size of the San partner (Pl. 1, figs. 10–16, 17). This means that the mode of nepionic growth in odd partners may be similar when starting with comparable proloculus sizes.

Common occurrence of odd partners

The example of odd partnership in alveolinids as registered by the association of *Alveolina* and *Glomalveolina* in taphocoenoses over a long period of Global Community Maturation (GCM, Hottinger 1997), demonstrates that the ranges of the two partners are largely overlapping but do not perfectly match in the various ecological gradients nor in geological time. The latter mismatch might be due to artificial limits between phenotypes substituting each other in time within a phylum. The mismatch in the ecological gradients are documented by facies types characterized by the exclusive presence of either the San or the Don partner (Hottinger, 1960 a, pl.II a,b). Exclusive San partner assemblages indicate “marginal” environmental conditions produced either by stress at the poles of an ecological gradient or by a very short period of community maturation. The imperfect match of the ecological ranges in odd partnerships demonstrates a differentiated respective relationship to their ambient environment and is important to understand the phenomenon of odd associations (see discussion below).

Examples of odd partnerships

Early Jurassic

San partner: *Lituosepta recoarensis* Cati (Hottinger, 1967, p.34, text fig. 16). Megalosphere 0,08–0,10 mm in diameter, simple, bilocular embryo (dyad), followed by about 13 spiral chambers lacking an endoskeleton. Microspheric adult up to 2,5 mm large.

Don partner: *Orbitopsella praecursor* (Gümbel) (Hottinger, 1967, p.40, text fig. 20). Embryonic apparatus (sphaeroconch) 0,3–0,8mm; first chambers following the embryo with endoskeleton. Microspheric adults reaching 40 mm in diameter.

Common features: Exoskeleton consisting of simple beams, no rafters, endoskeleton formed by radial pillars alternating in radial position in neighbouring stolon planes.

Common occurrence: Aguelmane el Agzigza, Middle Atlas, Morocco.

Late Jurassic

San partner: *Pseudospirocyclina mauretana* Hottinger (1967, p. 73 pl. 18, fig. 13–20). Bilocular (?) embryo, proloculus 0,08–0,12 mm, about 6 nepionic chambers lacking an endoskeleton. Microspheric specimens not found.

Don partner: *Anchispirocyclina lusitanica lusitanica* (Egger) (Hottinger 1967, p.74, pl. 13, fig. 6–8). Sphaeroconch 0,18–0,24 mm, early chambers with endoskeletal pillars.

Common features: Exoskeleton a polygonal, subepidermal network. Endoskeleton consisting of radial pillars in alternating position.

Common occurrence: Eastern flank of Kerker mountain, Eastern Morocco.

San partner: *Streptocyclamina muluchensis* Hottinger (1967, p. 62, pl.11, fig. 29–42). Megalosphere 0,08–0,13 mm, at least 6 nepionic chambers lacking an endoskeleton, microspheric adults reaching 1,9mm.

Don partner: *Anchispirocyclina lusitanica minor* Hottinger (1967, p.76, pl. 13, fig. 1–5). Sphaeroconch about 0,3 mm followed by early spiral chambers with pillars. Microspheric specimens reach 4 mm in diameter.

Common features: Polygonal network as exoskeleton, radial pillars in alternating position as endoskeleton. We do not know if the earliest microspheric chambers in the Don partner are streptospiral as in the San partner, or planispiral. In the latter case, the two partners would have a different phyletic origin and merely reflect stereotypy.

Common occurrence: Bou Haidour, Hassi Ouenzga, Eastern Morocco.

San partner: *Alveosepta personata* (Tobler) (Hottinger, 1967, p. 80, pl. 15, fig. 1–8, pl. 16, fig. 10–19). Simple megalosphere 0.10–0.22 mm, microspheric forms 2 mm in diameter.

Don partner: *Alveosepta powersi* (Redmond) (Hottinger, 1967, p. 81, pl. 17, fig. 1–16; pl. 18, fig. 1–12). Spheroconch 0.14–0.2 mm, endoskeletal structures appearing after about the tenth nepionic instar. Microspheric specimens reach 3 mm in diameter.

Common features: Exoskeleton a polygonal subepidermal network extending on the septal face. The alveoles on the septal face are transformed by resorption into irregular multiple foramina. Main apertures in a single row at the base of the apertural face. The beams of the exoskeleton are transformed into irregular median partitions in the chamber, incomplete in the San partner and complete in the Don partner where they take over endoskeletal function.

Common occurrence: Bou Blah, Eastern Morocco, Kimmeridgian.

Cretaceous

San partner: *Cuneolina pavonia* d'Orbigny (1846, p. 253, pl. 21, fig. 50–52). Megalosphere about 0.08 mm, embryonic architecture to be cleared in detail. No annular chambers. Microspheric generation unknown.

Don partner: *Dicyclina simplex* Cherchi and Schroeder (1990, p. 331, fig. 1–4) Embryonal apparatus with exoskeleton, 0.3–0.4 mm large, followed by annular chambers. Microspheric generation unknown.

Common features: Biserial arrangement of broadened chambers subdivided by radial septula in continuation from one chamber to the next one. Exoskeleton a polygonal network, the beams fusing with the septula. One row of apertures at the base of the apertural face.

Common occurrence: Ile Madame, South-Western France, Cenomanian.

In this case there might be an exceptional second San partner, *Cuneolina conica* d'Orbigny, awaiting redescription. Similar odd pairs of *Cuneolina* and *Dicyclina* are observed in Late Cretaceous (Santonian) shallow water deposits (e.g. Montsech, Southern Pyrenees or Marseille, Southern France).

Paleogene

San partner: *Orbitolites minimus* Henson (Hottinger et al. 1964, p. 640, pl. IV, fig. 2e,f). Embryonic apparatus of similar size as in *O. complanatus*, presumably the Don partner, but very few stolon planes throughout ontogeny producing a comparatively small, paper-thin disc of very low chamber cavity volume.

Don partner: *Orbitolites complanatus* Lamarck (Lehmann, 1961, p. 618, text fig. 18). Embryonic apparatus about 0.2–0.5 mm, many stolon planes from the start in the megalosperic ontogenesis.

Common traits: Apertures with oblique, layerwise alternating in direction, spirally overcrossing stolon axes. Embryonic apparatus characterized by complex flexostyle structures constricting the megalosphere in axial direction. The San partner in this case is characterized mainly by its much smaller proto-plast volume.

Common occurrence: Numerous localities in Spain, the Adriatic Platform and Iran, in strata of Cuisian to Lutetian age. The species *minimus* needs revision and its Don partner reidentification; most occurrences are not analysed in detail because of the difficulties of suitable preparation of the thin shells. However, the odd association is easy to recognize even from fragmented specimens in thin sections.

Alveolina and *Glomalveolina*: in shallow water the two odd partners dominate a series of communities succeeding each other through the Paleocene to Middle Eocene global community maturation (GCM) cycle without interruption. The last, comparatively small representatives exhibiting the *Alveolina* architecture in the Late Eocene, *Glomalveolina ungaroi* Bassi (Barbin 1986, Bassi and Broglio 1999), may represent a belated San partner surviving its Don partner under the “adverse” ecological conditions which have exterminated also the very large nummulites. An example of the odd partnership in a fully mature GCM phase is given in the annex of this paper: *Alveolina munieri* Hottinger and *Glomalveolina delicatissima* (Smout).

Dictyoconoides and *Lockhartia*: The successive species of these two genera follow the GCM cycle extending from Late Paleocene to Middle Eocene. The species have to be revised however one by one. Their interpretation as odd pairs is tentative because it is not clear whether the eventual Don partner *Dictyoconoides*, characterized by multiple spirals and by a large adult shell size, is a separate taxon with megalosheric and microspheric forms or the microspheric generation of particular *Lockhartia* species with a simple spiral. There are, however, microspheric forms with simple spirals in the species *Lockhartia tipperi* (Earliest Eocene), while Smout (1954, see also van Rijsinge 1930) indicates a nucleoconch of 0.16 mm in *Dictyoconoides cooki*, presumably representing the megalosheric generation, without documenting it with a good photograph. So far, I have not been able to find *Dictyoconoides* megalospheres in my material. Similar problems arise with *Kathina* and *Dictyokathina*, another rotaliid odd pair from Paleocene shallow deposits of the Near and Middle East.

Nummulitids: Odd partnerships in this exceptionally diverse group of larger foraminifera await investigation. In the Paris basin, representing a marginal faunal province with reduced diversity, we find *N. variolarius* as a San partner of *N. laevigatus* in the Middle Eocene (Blondeau 1972). In less marginal faunal provinces with a higher diversity of Don partners, the San partners may have been overlooked among the numerous megalosheric specimens difficult to prepare and to identify when poorly ornamented (striate small species such as *N. parvulus* Douvillé from Biron, South-Western France). When the diversity starts decreasing again in the Late Eocene

and Early Oligocene, the parallel lineages of reticulate *N. fabianii*-*N. fichteli* and the striate *N. incrassatus*-*N. vascus* may not represent odd partners but coexisting phyla of different grades of organisation: reticulate "ornamentation" in the *N. fabianii* - *N. fichteli* lineage in my view reflects a particular pattern of the disposition of sutural canals and therefore is a true structural particularity meriting separate taxonomic designation at least on the generic level.

In orbitoidiform and orthophragminiform foraminifera I am not aware of any true odd partnership. Co-occurrent pairs with conspicuous size differences such as *Hellenocyclina* with *Lepidorbitoides* or *Linderina* with *Lepidocyclina* are structurally too divergent by their respective presence or absence of lateral chamberlets in order to fulfil the requirements of odd pairs. Their similarity is restricted to the stereotype reflecting radial growth which seems to be independent of shell size since even very small benthics may exhibit the same trait.

Odd pairs in recent foraminifera

The most striking odd pair observed in recent biota is represented by *Sorites orbiculus* and *Amphisorus hemprichii*, two porcelainous discoïdal soritids characterized by overcrossed stolon systems and simple, septular chamber partitions. The latter are in opposite position in *Sorites* and in alternating position in *Amphisorus* (Lehmann 1961, Hottinger 1978, Hottinger et al. 1994). In contrast to alveolinids (Reichel 1947), the different disposition of the septula is not considered as reflecting a separate phylogenetic origin because the pattern of the apertural disposition according to cross-wise oblique stolon axes (Hottinger 1978) is the same in both partners. *Sorites* species have a small megalosphere with a flexostyle followed by spiral nepionic chambers. *Amphisorus* species exhibit a much larger megalosphere with a loose flexostyle followed by an even larger deuteroconch called forecourt by Lehmann 1961. The two partners share their habitat on *Halophila* leaves. Their basic life strategy is very similar: there is an endosymbiosis with dinoflagellate algae including light regulation devices in order to avoid photoinhibition by an active change of place of the symbionts within the shell through the lacunar system of the host cell (Leutenegger, 1977). The light regulation device enforces an epiphytic habitat on a dark substrate in areas where light reflecting coral sands are deposited. Microspheric specimens have brood chambers for the protection of offspring in both partners. However, there seems to be a delay of the reproduction period: during the seasonal cycle the Don partner *Amphisorus* reproduces in the period of maximum algal bloom in April–May (Zohary et al. 1980) while the San partner *Sorites* reproduces some weeks earlier. This delay corresponds to the lower volume accretion rates in soritid nepionts as compared to the larger ones in *Amphisorus* nepionts accelerating radial growth. It is not known if there is a difference in diet or in the mode of reproduction cyclicity.

The archaiasinids constitute the Caribbean ecological equivalent to the Indopacific soritines. Among them, we ob-

serve the odd pair *Archaias angulatus* - *Androsina lucasi* (Levy 1977, Crapon-Crapona 1985). Their megalospheric embryo is almost equal in size but their chamber volume at comparable growth stages differs considerably, exhibiting relationships corresponding to the observations in the odd pair *Orbitolites complanatus* - *O. minimus*. The architecture in *Archaias* and *Androsina* follows identical patterns in both partners: radial stolon axes alternating from one stolon plane to the next in radial position. The free pillars constituting the endoskeleton follow this pattern. There are no subepidermal partitions of any kind. The planispiral-involute chamber arrangement tends to become peneropliform in the adult. Levy (1994) reported particularly shallow areas of distribution where the San partner alone is present. As expected, and in parallel to Eocene alveolinids, the San partner adapts to areas where, under conditions of seasonal change in environmental conditions, the stress is higher than in somewhat deeper environments.

In the lower part of the photic zone of indo-pacific warm waters we observe the cohabitation of San partner *Heterostegina operculinoides* (spiral architecture) with either *Heterocyclina tuberculata* in the faunal province of the Western Indian Ocean or with *Cyclocypeus carpenteri* in the central Indopacific realm, as Don partner with cyclical growth. The three genera involved have a similar, basically nummulitic architecture with secondary septa produced by radial folds of the septal flap. Their detailed systematic relationships (Hottinger 1977) need additional investigation.

On the Maledivan Islands bearing the faunas of the Central Indopacific, *Alveolinella quoyi* and *Borelis schlumbergeri* live together in partially overlapping areas (Hottinger 1980). Again, the San partner *Borelis* has a somewhat shallower depth range than the Don partner. In the marginal Red Sea province, the San partner lives alone in the corresponding, depth-delimited environments and exhibits an unusual intraspecific variability in its elongation index (Hottinger et al. 1994). On Mauritius, we find *Borelis schlumbergeri* together with *B. pulchra*, two small species with San characters lacking a Don partner. The same situation is found in the Caribbean. Further investigations on their respective phylogeny and their paleobiogeography are necessary to understand the significance of this particular, "2-San" composition of the Mauritian and Caribbean alveolinid faunas.

Discussion

Considering the examples given above, we observe odd pairs with differences of megalosphere size ranging from insignificant to at least three orders of magnitude in volume. Where the megalospheres are of comparable size, the volume of the subsequent chambers differs notably and indicates different growth rates reflecting different metabolic rates. Minor structural differences, and in particular the architecture in a megalospheric apparatus, may be linked to absolute size as demonstrated within the phylogeny of Eocene alveolinids (Hottinger 1963).

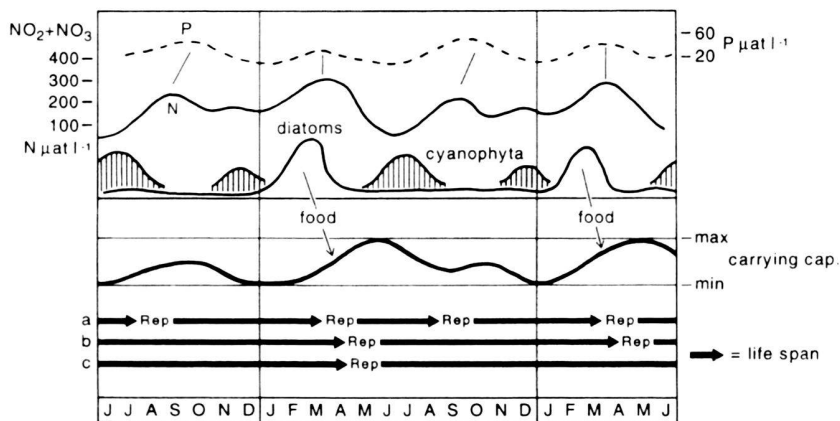


Fig. 1. Seasonal change in an oligotrophic, tropical, shallow environment as observed in the Gulf of Aqaba, Red Sea (Reiss and Hottinger 1984). Schematic, monthly over two years. The nutrient concentration in the free water column governs the growth of the diatoms, food for the foraminiferan populations. This resource constitutes also the limiting condition of the carrying capacity of the benthic realm in the photic zone. The difference between the algal blooms in spring and autumn as well as the relations between nitrate and phosphate concentrations are not fully understood at present. During the "dead" periods of the year, when the scarceness of the phytoplankton admits a deep penetration of light into the sea ("blue desert" conditions), the cyanophytes will grow in the deep water. They are the only organisms which have access to molecular nitrogen to feed their protein synthesis and will provide the deeper waters with new nitrates after the demise of their populations.

In the benthic consumer populations, reproduction (Rep) will take place immediately prior to the availability of vegetal food. Life time will correspond to the periodicity of this resource according to the different strategies a–c which are available either to odd partners or to different generations of the same species. a: populations controlled by coordinated reproduction cycles taking advantage from autumn and spring blooms. b: coordinated reproduction once a year during the main algal bloom. c: perennial populations controlled by the minimum carrying capacity during the "dead" seasons.

The most complete evolutionary sequence of odd partners in geological time known so far, the parallelism of *Alveolina* sstr. and *Glomalveolina*, teaches us that odd pairs develop in a GCM period when the phase of generic dominance is reached and specific diversification starts. This is when dimorphism in dominant species starts to be distinctive in adult shells.

Sofar, odd partners have been found mainly among foraminiferal K-strategists (Hottinger 1997) in the upper photic zone. In these shallow environments, seasonality has its heaviest impact on ecologic conditions. Whether odd partners may be recognized among the numerous and diversified smaller benthics below the photic zone remains at present an open question.

Pécheux (1995) has shown the growth rates (conceived as volume accretion rates per instar) to depend on the total volume of the previously formed protoplast at least during the early growth stages.

Reiss and Hottinger (1984, fig. G 34) review the arguments to interpret alternating chamber arrangement as a device to diminish growth rates under the geometric constraints for accretion rates under conditions of radial growth. Thus, we may link size and architecture of the foraminiferal shell to growth and growth rates in the time gradient.

Growth rates may be linked with reproduction strategy. Zohari et al. (1980) show the growth of *Amphisorus hemprichii* to be linked to the seasonal cycle in the Gulf of Aqaba. The coordination of growth and reproduction with the seasonal cycle obviously represents a strategy to use the highest level of food resources during the spring season for the most active period of protoplasm synthesis during the nepionic growth stages following reproduction. Consequently, differences in size as observed in odd partners are presumed to reflect differences in growth strategy coordinated with the seasonal cycle.

Levy (1994) describes a differentiation of the habitat of *Androsina lucasi* versus *Archaias angulatus* in Florida. As mentioned briefly above, the San partner *A. lucasi* inhabits almost exclusively the restricted, near-shore environments characterized by strong variations of salinity (1.7–5.5‰) during the seasonal cycle while the euhaline outer lagoon with salinity changes between 3.5–4.2‰ is dominated by the Don partner *A. angulatus*. The salinity dependence of the extant benthic foraminifera is characterized by threshold values at about 4.5‰ towards the hypersaline realm and by maybe more diversified values around 2.0–2.8‰ towards the brackish realm. In seasons of extreme salinity reaching or surpassing the threshold values, growth, reproduction or even the life of particular species may be hampered or suppressed. Under these conditions, the species may have to adapt and coordinate their way of life in respect to growth, life-time and reproduction to the period of euhaline conditions within the seasonal cycle. Similar effects may be produced by any kind of resources limiting the carrying capacity and in particular by the seasonal input of nutrients into an oligotrophic environment as observed in the Gulf of Aqaba.

Thus, in odd pairs, the size difference in the embryo may reflect different nepionic growth rates and the size difference of the adult different life-times. Their coexistence may reflect different life strategies permitting, by their combination, a better use of the seasonal resources in their common habitat (Fig. 1). Dimorphism in adult shells of different generations in a reproduction cycle is expected to mean the same kind of differentiation of life strategy, not in equilibrated competition between two closely related species, but within a single species.

Conclusions

1. In larger foraminifera, we observe often two, sometimes more than two, beyond stereotypy taxonomically closely related species occurring in common, undisturbed taphocoenoses or sharing today a habitat. Their respective ranges in the ecological gradient or in geologic time overlaps largely without being a perfect match. Such particular associations are called here “odd partners”. Inspired by Cervantes’ novel *Don Quijote*, the small sized partners are called San (for Sancho Pansa), the larger sized ones Don (for Don Quijote).
2. Odd partnerships develop in phases of global community maturation (GCM) cycles when generic dominance permits specific diversification.
3. Odd partnerships may be reflected by a striking difference in embryo size and embryo architecture, by the size difference of adult shells (in the respective generation) or, commonly, by both characters together.
4. In accordance with today’s knowledge on the biology of extant larger foraminifera, the size difference in the adult is interpreted as reflecting different life-times in relation to seasonal cycles. The size difference in the megalospheric proloculus indicates different nepionic growth rates, higher in the Don and lower in the San partners.
5. The San partner seems to be more tolerant to periodical environmental stress than the Don partner, since San partners may occur alone in shallower environments or marginal basins, as expected when considering the shorter life-times and the lower growth rates in the San partner.
6. The odd partnership is interpreted as a particular adaptation to seasonal change in the environment. It is designed for both partners to profit optimally from the periodical change of the carrying capacity. Dimorphism in the adult shell may reflect similar strategies distributed between the generations of the same species. Adult dimorphism in the Don partner and the absence of adult dimorphism in the San partner may, by combination, produce a threefold strategy within the same habitat under the same seasonal constraints.

Annex: Emendation of *Glomalveolina delicatissima* (Smout, 1954), Alveolinidae, Middle Eocene.
(Pl. 1, fig.12–16)

1954 *Alveolina delicatissima* Smout, A.H., p. 83, pl. 14, fig. 13.

1960 *Alveolina* cf. *boscii* (Defr. in Bronn). Hottinger, L. p. 151, pl. 10, fig. 21

1999 *Glomalveolina delicatissima* (Smout). Bassi and Broglio, p. 230, figs. 6 a–d.

Emended diagnosis:

Tiny alveolinids reaching about 3 mm length and 0.5–0.8 mm in thickness, with pointed poles. 7–8 chambers per whorl in adult growth stages. Sutures straight or maybe slightly curved, flush, no polar torsion. Centered axial sections show a strep-

tospiral nepionic stage forming a glomerulus of 3 whorls around a spherical proloculus of about 0.03 mm in diameter. During the 4th whorl, the axis of coiling stabilizes. Axial growth is accelerated after the second regular, planispiral volution for 5–7 whorls producing a bipolar columella with the polar thickening of the basal layer. Poles remain pointed throughout ontogeny, even in the adult whorls where the rates of elongation are gradually reduced. Index of elongation about 5 in growth stages corresponding to 0.5 mm equatorial diameter, reaching 6 in more complete adult specimens. There are 28 chamberlets per mm axial chamber length in growth stages corresponding to 0.5 mm equatorial diameter. No dimorphism recognized.

The regularly coiled volutions of *Glomalveolina delicatissima* exhibit the architectural traits of Eocene alveolinids, i.e. chamberlets in alternating position from one chamber to the next, in correspondance to the alternating disposition of the foramina on the apertural face and to the presence of a post septal passage in addition to the preseptal one. The presence of streptospiral nepionic shell whorls corresponding to the small proloculus size together with the adult architectural traits typical for *Alveolina* sstr. obliges to place the species *delicatissima* as emended here into the genus *Glomalveolina* as defined by Loeblich and Tappan 1987.

Remarks: As Smout (1954) correctly stated, *G. delicatissima* is by far the smallest and most delicate elongated alveolinid known in the Middle Eocene. Insofar, its identification with the single oblique section published by Smout is unambiguous. Bassi and Broglio (1999) have refigured Smout’s holotype and some additional oblique sections deposited in the British Museum (Natural History) in London. *Alveolina boscii* Defr. from the lower Middle Eocene of the Paris Basin is definitely larger and shorter, with an elongation index reaching 4 at most.

The present emendation is based on numerous free specimens from Avesa, Northern Italy, level 10 as noted by Hottinger 1960, p. 210, fig. 109 and 110. They occur in a yellowish bed of volcanic ash where the rich foraminiferal fauna is often decalcified. They have to be washed out of the encasing sediment with great care because the tufts, by taking up water, tend to swell and to destroy the delicate microfossils. Thin sections have to be prepared with oil instead of water. Therefore, many free specimens at our disposal have lost their last two or three, adult whorls and may appear a little smaller than Smout’s specimen. In 1960, I have mistaken them for inner whorls of the larger species present in the association: *Alveolina munieri* Hottinger.

G. delicatissima has also been found in Egypt, below the Gizeh pyramids, in a faunal association with specimens of *A. elliptica* group to be described in detail elsewhere. According to the nummulites of *N. gizehensis* group and many other foraminiferans associated with the *G. delicatissima* level, and in accordance with the age of the type level in Qatar, the range of the emended species may be defined as Lower to lower part of Middle Lutetian (Middle Eocene), zone of *Alveolina munieri*.

Barbin (1986) and some other authors before him observed similar, delicate and elongate alveolinids in the Late Eocene (Priabonian). Bassi and Broglio (1999) describe a centered section from the Colli Berici, Northern Italy, exhibiting a comparatively large, 0.05–0.06 mm wide proloculus followed by a reduced glomerulus. This is their main argument to designate these Late Eocene forms with a particular specific name, *Glo-malveolina ungaroi*. The replacement of *G. delicatissima* by the obviously closely related *G. ungaroi* must take place in the uppermost Lutetian or in the lower Bartonian.

G. delicatissima and *A. munieri* from the same Middle Eocene bed in Avesa are figured on Pl. 1 at the same enlargement to demonstrate a typical odd pair of very elongate alveolinids. The two species are associated, however, to a third one of much lower frequency, *Alveolina* cf. *elliptica nutalli* Checchia-Rispoli.

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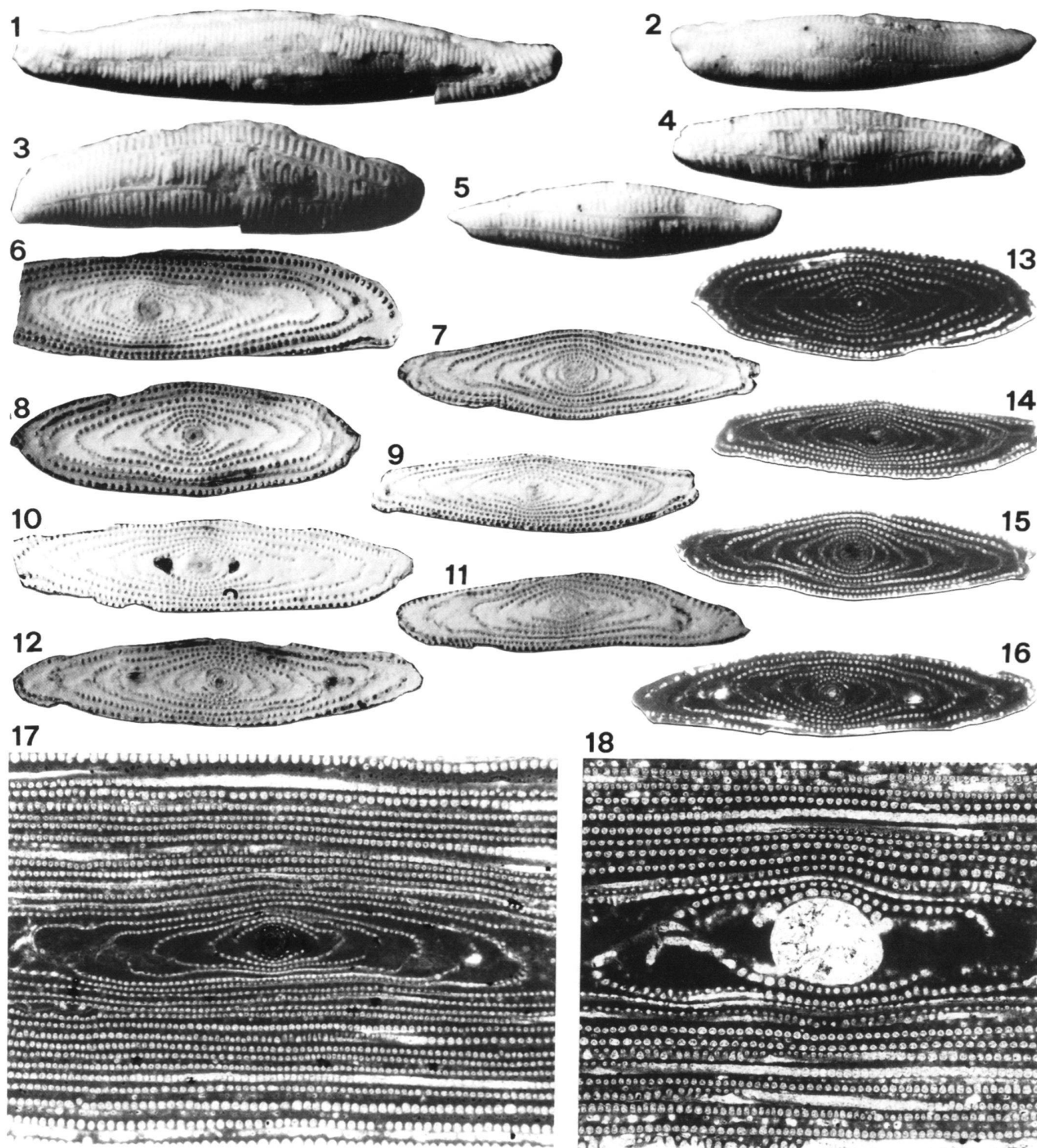


Plate 1. Odd partners in the association of alveolinids from Avesa section, level 10, Northern Italy, Alveolina munieri Zone, Middle Lutetian, Middle Eocene. Enlargement $\times 20$.

1-16: San partner: *Glomalveolina delicatissima* (Smout, 1954). 1-5: external views of free specimens, note the pointed poles. NHMB C 37875-37879. 6-11: axial sections as seen in incident light. NHMB C 37880-37886. 13-16: axial sections of some same specimens in transmitted light.

17-18: Don partner: *Alveolina munieri* Hottinger, 1960. Axial sections, transmitted light. 17: Microspheric generation, equatorial zone of the shell. Note the similarity of the shell outline in the inner whorls at similar equatorial diameter with the one of *G. delicatissima*. NHMB C 37887. 18: Megalospheric generation. Note the size difference of the respective megalospheres in the odd partners. NHMB C 37888.

