Analysis of test ontogenesis (ATO) in small foraminifera: implications from *Pseudonodosinella*

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ABSTRACT

Foraminifera perfectly preserve shell (test) ontogenesis, which is genetically controlled and influenced by environmental factors. Analysis of foraminiferal test ontogenesis (ATO) suffers from the lack of a universal time (stage) reference scheme applied to fossil forms. The question is how to refer shape changes to ontogenetic stages. Different methods of ATO have been investigated and focused on ontogeny of individual chambers in multilocular tests instead of gross cumulative tests. It can be concluded that chamber number reference system is not suitable for ontogenetic analysis because chamber reference numbers are time- and stage-dependant. In specific cases, if chamber numbers are required, "backward" numbering is recommended. The study based on the chamber number reference system with "backward" numbering has shown that relative size of two final chambers may serve as a good tool for taxonomic identification. **Relative size reference system** applied to foraminiferal chambers seems to express ontogenetic trends better than other schemes because it is time- and stage- independent and therefore it is preferred for the analysis of test ontogenesis. *Pseudonodosinella* (*"Reophax"*) as the most simple uniserial foraminifer has been analysed and revealed different types of ontogenetic chamber allometries. Some forms reveal simple allometry, which is very close to isometry. Another quite characteristic allometry is termed here as **multiphasic isometry**, when at certain chamber size (critical stage) isometrically growing chambers switch to another isometric mode of growth. This case study also indicates that Albian *P. troyeri* (Tappan, 1960) and *Pseudonodosinella* sp. 3 are indistinguishable in all ontogenetic trends. Both taxa may represent two varieties (?ecophenotypes) of the same species. Thus, it is proposed to move *Pseudonodosinella* sp. 3 to *P. troyeri* as a variety of this species named *Pseudonodosinella troyeri* var. *scabra* var.n.

INTRODUCTION

"The form of an organism is determined by its rate of growth in various directions" (Thomson, 1942). We also deal with growth and form by studying the foraminifera. The foraminiferal multilocular shells (tests), built by addition of successive newly formed chambers to the already existing structure, provide a full ontogenetic record of its form (Scott, 1974). The overall shape of the foraminiferal test depends to a large extent on chamber arrangement during its ontogeny. The arrangement, size, proportions, expansion rate of chambers among other features (test composition, aperture type, ornamentation etc.) give qualitative and quantitative basis of a taxon and set its intraspecific as well as ecophenotypic variability. All these structural traits are usually described and graphically presented to give "an impression" of how a species looks, or how it varies. Nonetheless, qualitative description is not precise enough to express size and proportions of shells. In order to quantify these features, a biometric approach can be applied.

Unfortunately, in the history of research on the foraminiferal shell, biometry has usually played an insignificant role (Scott, 1974). Studies of gross shell form using two or three dimensions have shown to be not very informative and strongly size-dependant. Measurements are strongly affected by the ultimate growth stage and polymorphism of shells. It is well known that gross shell size and shape change during ontogenesis. One can try to remove the effects of the ontogenetic development (Gould, 1970; Gradstein, 1974). But the other way is to use ontogenesis as a dynamic trait, which is likely to be species specific. It seems to be an easy task for foraminifera, but reality shows many limitations. First of all, the literature on foraminiferal test architecture describes the structural features in diverse ways and at different levels of accuracy (Hottinger, 1978). A further problem concerns presenting ontogenetic data without direct time control and clear ontogenetic stage control.

Most studies in ontogenetic test trends focused on planktonic and larger foraminifera (e.g., see Scott, 1974 for an overview). This study goes back to basics, discussing methods of presenting morphometric data and focusing on the most simple foraminiferal architecture – uniserial rectilinear forms represented by agglutinated foraminifers of the genus *Pseudonodosinella*.

According to Simpson *et al.* (1963), there are three quantitative aspects of growth in which we are interested. The first is concerned with change over time in some dimensions of an animal. The second problem of growth is that of the relative sizes of two dimensions. Time can be eliminated from this relation, because it is assumed to be the same for both measurements (e.g., length and width). The third aspect of growth is concerned with changes of shape (Simpson *et al.*, 1963). All three problems are addressed in this paper, but the second one is emphasised because "by measuring the growth dimensions of chambers during ontogeny one can gain an important insight into the genetic changes that are taking place during evolutionary change" (Olsson, 1972).

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Specific aims are focused on (1) quantitative examination of *Pseudonodosinella* species to determine whether proposed "qualitative" taxa are distinct enough to be named as individual species; (2) testing different methods of ontogenetic analyses; (3) preliminary investigations of different modes of growth in a very simple rectilinear chamber arrangement (isometry vs. allometry of growth).

MATERIAL

Ninety-one specimens of *Pseudonodosinella* were analysed from the Lower Albian to the lower part of Upper Albian of Lower Saxony (the Kirchrode II borehole). All specimens were numbered and fixed in two Plummer-cells with 60 squares (e.g. 1\12 means the cell no. 1 and a cell square no. 12). The material is curated in the *Geoscientific collections* of the *Bundesanstalt für Geowissenschaften und Rohstoffe* (Hanover, Germany). Previously, most of the specimens were identified as *Reophax minutus* (Tappan). Recently, this deep-water agglutinated foraminiferal taxon has been revised by Geroch & Kaminski (1995) and assigned to *P. troyeri* (Tappan) or *P. parvula* (Huss).

TAXONOMIC (QUALITATIVE) NOTES

Genus ***Pseudonodosinella*** Saidova

According to Loeblich & Tappan (1987), *Pseudonodosinella* differs from *Reophax* in having strongly overlapping chambers, multilayered wall, and typical thickening of the wall of the produced terminal face.

Pseudonodosinella parvula (Huss, 1966)

Plate 1, Figs 1-3, 6, 7

Reophax parvulus Huss, 1966, p. 21, pl. 1, figs. 26-30.
Reophax minuta Tappan. –Bartenstein & Bettenstaedt, 1962, p. 282, pl. 39, fig. 16.
Pseudonodosinella parvula (Huss, 1966). –Geroch & Kaminski, 1995, p. 118-119, pl. 2, figs. 1-20; textfig. 2 (species emendation).

Description. Test free, tapered, and rectilinear with uniserial chambers. Megalospheric forms usually have 3-4 chambers and nearly parallel periphery. Microspheric individuals are constructed from 4-6 (up to 7) chambers. Early chambers are subspherical, later chambers become higher (more elongated). All chambers are usually compressed. Sutures horizontal and depressed. Multiple-layered thin wall agglutinated from fine quartz and calcareous grains, smoothly finished. Aperture is terminal on an indistinct short and broad neck.

Remarks. *P. parvula* differs from *Pseudonodosinella troyeri* in polymineral composition of test (visible in transmitted light under high magnification), in having more elongated final 1-3 chambers, and lacking a distinct terminal neck and. Some specimens of *P. parvula* show less elongated chamber that resembles *P. troyeri.* It differs from *Reophax helveticus* in having more globular chambers. The specimen illustrated by Bartenstein & Bettenstaedt (1962) reveals a slightly higher, more elongated last chamber.

Range & Occurrence. Rare to frequent throughout the Kirchrode II borehole (Albian). Recorded from the Barremian to Middle Albian of NW Germany (Bartenstein & Bettenstaedt, 1962), Upper Cretaceous of the Carpathians (Huss, 1966; Geroch & Kaminski, 1995).

Pseudonodosinella troyeri (Tappan, 1960)

Plate 1, Figs 4, 8-14

Reophax troyeri Tappan, 1960, p. 291, pl. 1, figs. 10-12. –Tappan, 1962, p. 153, pl. 30, figs. 11-13.
Reophax minutus Tappan. –Ten Dam, 1950, p. 6, pl. 1, fig. 3. –Bartenstein & Bettenstaedt, 1962, p. 282, pl. 39, fig. 1. –Fuchs & Stradner, 1967, p. 262, pl. 1, fig. 7, non 9. –Geroch & Nowak, 1984, pl. 1, fig. 9.
Pseudonodosinella troyeri (Tappan, 1960). –Geroch & Kaminski, 1995, p. 118, pl. 1, figs. 1, 2, 4-17, Textfig. 2 (with refs.).
Scherochorella minuta (Tappan). –Szarek *et al.*, 2000, p. 453, pl. 1, fig. 13.

Description. Test free, tapered, rectilinear or slightly arched. Megalospheric forms have fewer chambers (3-4) including large proloculus and successive chambers. Microspheric forms usually have 4-6 (up to 8) rapidly enlarging chambers. Sutures are very distinct, horizontal, and depressed. Chambers are subspherical, inflated, gradually enlarging with growth. They are wider than high at early stage to slightly higher than wide in the late stage. The wall is thin, roughly finished consisting of fine to medium size quartz grains. Chambers are nearly always compressed. Periphery is distinctly lobulate. Terminal aperture is located on a neck surrounded by the typical thickening of the wall. The neck varies from short (low) and broad to distinct, high, and slightly pointed.

Remarks. This species has been usually assigned to *Reophax minutus* Tappan or recently to *Scherochorella minuta* (Tappan) (Szarek *et al.*, 2000). Geroch & Kaminski (1995) revised the Lower Cretaceous specimens and placed in *Pseudonodosinella troyeri* (Tappan, 1960). This paper adopts this view. Original *Scherochorella minuta* (Tappan) has much lower chambers, no lobulate periphery, and no apertural neck. Type specimens figured by Geroch & Kaminski (1995) reveal noticeably more chambers (up to 11) than the maximal number of chambers (up to 8) in *P. troyeri* analysed here. The specimens studied here have much closer affinity to original *P. troyeri,* but on average show less distinct apertural necks. Nevertheless, the whole variability of necks is very gradual. Specimens with longer necks tend to have finer wall and to be more frequent in the Upper Albian of Kirchrode I borehole (based on the collection prepared by A. Thies; not analysed here). *P. troyeri* differs from *P. parvula* in having lower, nearly spherical chambers and a terminal neck, as well as in a different wall texture (slightly coarser fraction composed of exclusively quartz grains).

Range & Occurrence. Frequent in the Middle and Upper Albian; rare in the Lower Albian of the Lower Saxony Basin (Kirchrode II). It is a very cosmopolitan species recorded from the Lower Cretaceous of NW Europe (e.g., Ten Dam, 1950; Bartenstein & Bettenstaedt, 1962), the Outer Carpathians (Geroch & Nowak, 1984; Geroch & Kaminski, 1995), the Arctic slope of Alaska (Tappan, 1962) (Geroch & Kaminski, 1995).

Pseudonodosinella sp. 3 (compare taxonomic conclusions)

Plate 1, Figs 5, 15-17

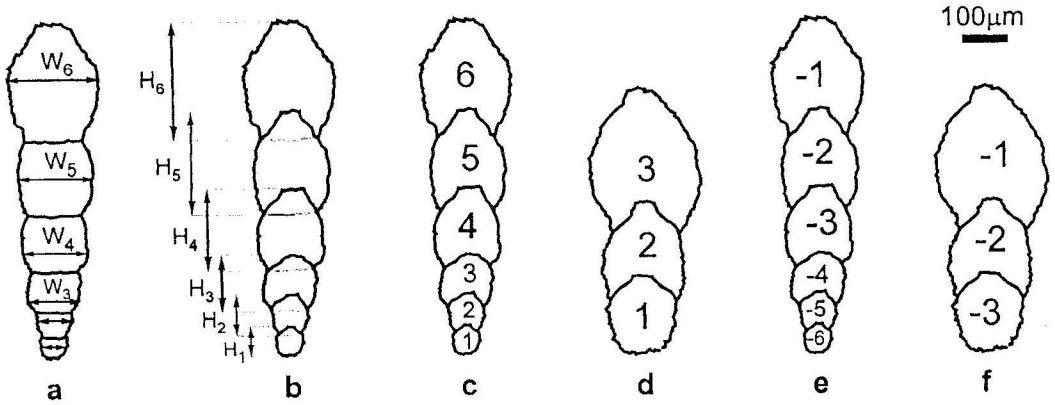

Figure 1. Methods of measurements and numbering of chambers depicted on outlines of two *Pseudonodosinella troyeri* specimens; (a-c, e) microspheric form; (d, f) megalospheric form. W – chamber widths; H – chamber heights; (c, d) "classical" chamber numbering; (e, f) "backward" chamber numbering.

Reophax sp. –Herrero & Haynes, 1997, pl. 1, fig. 18.

Description. Test is free, tapered and, rectilinear. Megalospheric forms have a large proloculus and on average fewer gradually enlarging chambers (3-5). Microspheric forms usually contain 4-6 (infrequently up to 9) rapidly enlarging chambers. Chambers are inflated, subspherical, gradually enlarging with growth, wider than high at early stage to slightly higher than wide in the late ontogenetic stage. Sutures are horizontal and depressed, often obscured by coarse grains. The wall is medium thick, multilayered, roughly finished consisting of coarse to medium size quartz grains. Chambers are not compressed with some exceptions for terminal chambers. Periphery is lobulate. Indistinct thickening of the wall surrounds the terminal aperture. There is no clear apertural neck.

Remarks. This species can be distinguished from *P. troyeri* by much coarser grains, very rough wall surface, usually not depressed chambers, and the lack of a distinct apertural neck.

Range & Occurrence. This taxon has been frequently found in the Lower Albian, but rarely in the Middle and lower part of the Upper Albian of Kirchrode II (Lower Saxony). It probably occurs in other parts of the epicontinental European basin (e.g., the Albian Gault at Ford, UK – in the Hollis and Neaverson Collection revised by Herrero & Haynes, 1997)

METHODS

Specimens covering the whole spectrum of intrageneric variability of *Pseudonodosinella* were selected. Manual measurements were done using an optical microscale built into the Zeiss stereomicroscope Stemi 2000-C. Every successive chamber (height and width) of all specimens was measured and measurements entered in an Excel worksheet. The maximum width and height of every successive chamber has been measured (Fig. 1a). Heights have been measured in transmitted light in order to see overlapped parts of chambers The chamber height is defined here as a distance from a suture to the aperture measured perpendicularly to the growth (elongation) axes (Fig. 1b). Chambers were numbered using two schemes, which are described in the next chapter (Fig. 1c-f). Simple methods of bivariate statistics have been applied (described below) using Excel 2000 'chart trendlines' employing various types of regression lines (usually linear and exponential). These lines are a graphical representations of the trend of data in a series calculated by the least squares fit through points by using various equations (linear or exponential). For exponential trendlines, Excel uses a transformed regression model. Trendline reliability is presented as a R-squared value, which is not adjusted.

We have to be aware that regression analysis is not well suited to variables dependent on growth time because it assumes the presence of an independent and a dependent variable (Gradstein, 1974). On the other hand, "in morphology, the observation of a particular regression on another is useful in making inferences about the growth relations of these organs" (Simpson *et al.*, 1963). In order to avoid time/stage-dependent problems, we don't analyse cumulative variables, such as additive growth of chambers. Instead of measuring gross shell values, we can focus on separate chambers and their dimensions. The regression analysis seems to be appropriate for such measurements. Moreover, this method is well accessible and seems to be good enough to present general trends within scatter fields.

How to refer to growth of foraminiferal tests? The question is how to describe an ontogenetic stage in multilocular foraminifera? An analysis of test ontogenesis, as ontogenesis itself, has to be referred to the time scale. The absolute time of chamber accretion (ontogenesis) can only be controlled in cultures. Another way is to use relative timing represented by events recorded in accretive shells, i.e., discrete growth steps (chambers) in this case. In fossil material one can assume that equality in chamber number indicates similarity in ontogenetic stage, which may be erroneous if the taxon is polymorphic (Scott, 1974). Unfortunately, this is probably the case for most foraminifers. Different methods are tested and described below.

RESULTS

"Classical" chamber numbering. The most natural method is to number successive chambers from the proloculus towards the final chamber (e.g., Gradstein, 1974 – fig. 8; Hilbrecht, 1995). This seems to be very logical because numbers mimic growth steps (stages)

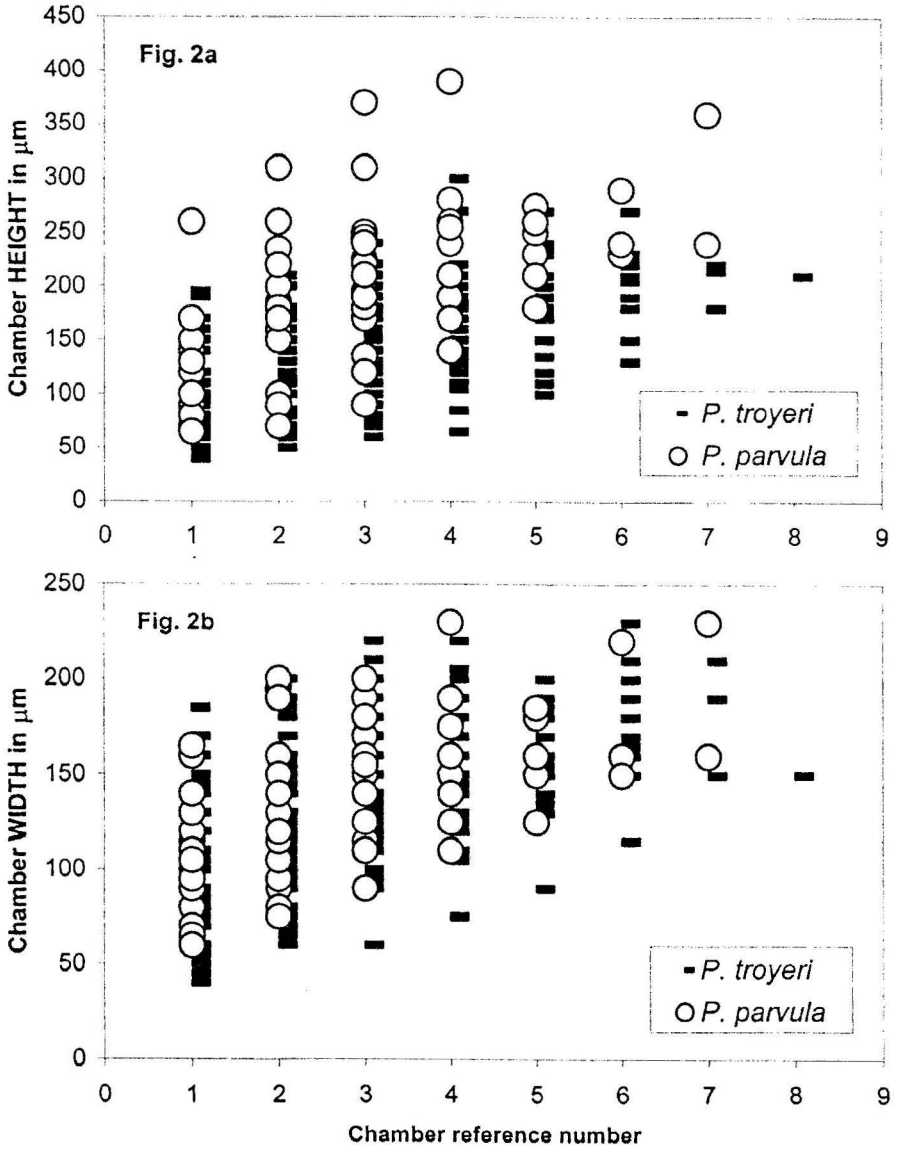

Figure 2. Chamber heights (a) and chamber widths (b) plotted against "classical" chamber numbering in *Pseudonodosinella troyeri* vs. *Pseudonodosinella parvula*.

during ontogeny (Fig. 1a-d). Chamber reference numbers are usually presented against chamber dimensions (width, height, diameter etc.). Figure 2 presents such relationships between chamber heights (Fig. 2a) and chamber widths (Fig. 2b) plotted against chamber numbers for two investigated taxa, i.e., *P. troyeri* and *P. parvula*. Both scatters show that measurements representing the taxa distinctly overlap each other. Chamber heights of *P. parvula* reveal single points, which plot above values for *P. troyeri*. All points are spread around large overlapping clusters, which do not show any linear trends.

"Backward"-chamber numbering. Another numbering system would consider a "backward" counting of chambers from the youngest (final) chamber to the oldest one (proloculus) (Fig. 1e, f). This way a terminal chamber is set as a reference chamber no. "-1". Actually, foraminifers do not grow backwards, thus, for convenience, negative value for every number is preferred (Fig. 1e, f). Negative values are also useful for straightforward recognition of two different numbering schemes. This approach is presented on Fig. 3a where chamber numbers are plotted against heights of chambers. It can be seen that scatters of two species highly overlap again. Exponential trendlines show slight differences, but their coefficients (R^2) are very low (see Fig. 3a, b). On average, specimens of *P. parvula* show higher chambers described with the same chamber number than specimens of *P.* sp. 3 and *P. troyeri*. Variability of last chambers is very high, which is obvious from the wide range of data (Fig. 3a, b – chambers no. "-1"). Chamber widths vs. chamber numbers plotted for two species reveal no clear pattern. Both scatters overlap each other. Plots for other pairs of taxa are not presented because they show the same fully overlapping patterns.

On the other hand, the ratios between heights and widths (H/W) of every chamber plotted against chamber reference numbers indicate (Table 1) that last three chambers of *P. parvula* on average show higher values (means 1.57, 1.51, and 1.22 for chambers "-1", "-

Table 1. Descriptive statistics of chamber height/width ratios (H/W) for last three chambers in *Pseudonodosinella parvula*, *Pseudonodosinella troyeri* and *Pseudonodosinella* sp. 3.

TAXA	*P. parvula*	*P. troyeri*	*P.* sp. 3	*P. parvula*	*P. troyeri*	*P.* sp. 3	*P. parvula*	*P. troyeri*	*P.* sp. 3
CHAMBER ref. number	-1	-1	-1	-2	-2	-2	-3	-3	-3
Mean H/W	**1.573**	**1.096**	**1.133**	**1.508**	**1.070**	**1.034**	**1.217**	**1.026**	**0.927**
Standard Error	0.062	0.024	0.056	0.059	0.019	0.048	0.036	0.020	0.044
Median	1.500	1.105	1.167	1.500	1.063	1.000	1.235	1.000	0.887
Standard Deviation	0.271	0.174	0.216	0.258	0.134	0.186	0.146	0.138	0.166
Sample Variance	0.074	0.030	0.047	0.067	0.018	0.035	0.021	0.019	0.028
Kurtosis	0.101	-0.022	-0.109	-0.340	-0.820	-1.181	-0.014	0.292	-1.581
Skewness	0.591	-0.252	-0.558	-0.172	0.232	0.235	0.255	0.346	0.253
Range	1.039	0.750	0.762	0.970	0.507	0.567	0.568	0.667	0.488
Maximum	**2.214**	**1.438**	**1.429**	**2.000**	**1.357**	**1.353**	**1.520**	**1.417**	**1.188**
Minimum	**1.175**	**0.688**	**0.667**	**1.030**	**0.850**	**0.786**	**0.952**	**0.750**	**0.700**
Sum	29.879	56.970	16.998	28.648	55.628	15.503	20.687	51.311	12.979
Count	19	52	15	19	52	15	17	50	14
Confidence Level (95.0%)	0.131	0.049	0.119	0.124	0.037	0.103	0.075	0.039	0.096

2", "-3" respectively) than last three chambers of *P.* sp. 3 (means 1.13, 1.03 and 0.93 respectively). Furthermore, the last two chambers of *P. parvula* on average show higher values (means 1.57 and 1.51) than the last two chambers of *P. troyeri* (means 1.09 and 1.05). The ranges of these ratios for the last two chambers just partly overlap (Fig. 4b). In contrast, scatter plots of *P.* sp. 3 and *P. troyeri* completely overlap, showing no distinct pattern for H/W ratio against chamber reference numbers. Differences between mean values for last three chambers are also not distinctive (Table 1).

Relative size change. Another way of presenting growth patterns is to depict two dimensions, which change during ontogenesis. Such relationships between two scalar values of every successive foraminiferal chamber give an example. For instance, chamber heights plotted against chamber widths represent successive chambers, which do not need reference numbers any more. Various analyses of shape and size in bivariate data are summarised by Scott (1974).

Chamber widths vs. heights can be plotted in this case. All three taxa show scatters, plotting along exponential lines (Fig. 5a-c). All analysed specimens (their chambers) of *Pseudonodosinella* sp. 3 give a trendline with a high correlation index (R^2=0.91). Exponential regression of those values for *P. troyeri* shows slightly lower correlation (R^2=0.84). Chambers of *P. parvula* have revealed the lowest coefficient (R^2=0.73). All three scatters are also presented on the same plot, which graphically shows differences and similarities of the analysed taxa (Fig. 6). The exponential equations of trendlines for investigated taxa are compared below:

Pseudonodosinella sp. 3: $y=28.51e^{0.0103x}$
Pseudonodosinella troyeri: $y=38.66e^{0.009x}$
Pseudonodosinella parvula: $y=52.04e^{0.0085x}$

Trendlines of *Pseudonodosinella* sp. 3 and *P. troyeri* are placed very close to each other. Furthermore, both groups of the data-points closely overlap. Widths and heights values of *P. parvula* chambers show another pattern. In comparison to two other taxa, most of the points are shifted towards higher chambers (larger values of chamber heights). The trendline plotted for chambers of *P. parvula* is also shifted, consequently that is expressed by the highest parameter (a=52.04) in the equation (Fig. 6).

There is another way of studying ontogenetic changes of chamber proportions by plotting individual chamber relative size lines separately for every specimen. This way the true ontogenetic relationships can be investigated. Averaged relationships based on more than one specimen may obscure real growth patterns. Figures 7a and 7b show such lines plotted for two specimens of *Pseudonodosinella* sp. 3. Best fits for proportions of chambers for both individuals are represented by two separated nearly linear trends broken around the width approximating 150 μm value. It seems that both specimens reveal two different 'linear' (isometric) stages of growth separated by a threshold value related to the certain size, i.e. the width of chambers at about 150 μm (Fig. 7a, b). Eight selected specimens of the same taxon presented on multiple plots show a similar pattern, no matter whether they are micro- or megalospheric (Fig. 7c, d).

REMARKS ON PRESERVATION

Shape and size of foraminiferal chambers may be altered after death. Agglutinated tests are especially at risk. Tests of *Pseudonodosinella* (*Reophax*) are often depressed. Originally, their tests were constructed from fine sand grains glued by organic cement (see Bender, 1995). Such an organic wall is more or less flexible, thus, it collapses just after death or during compaction processes. This is the case with the most of the studied material. It seems that our specimens show tendency of having more collapsed (depressed) chambers strongly related to the thickness of the wall and the size fraction of grains in the wall. These rela-

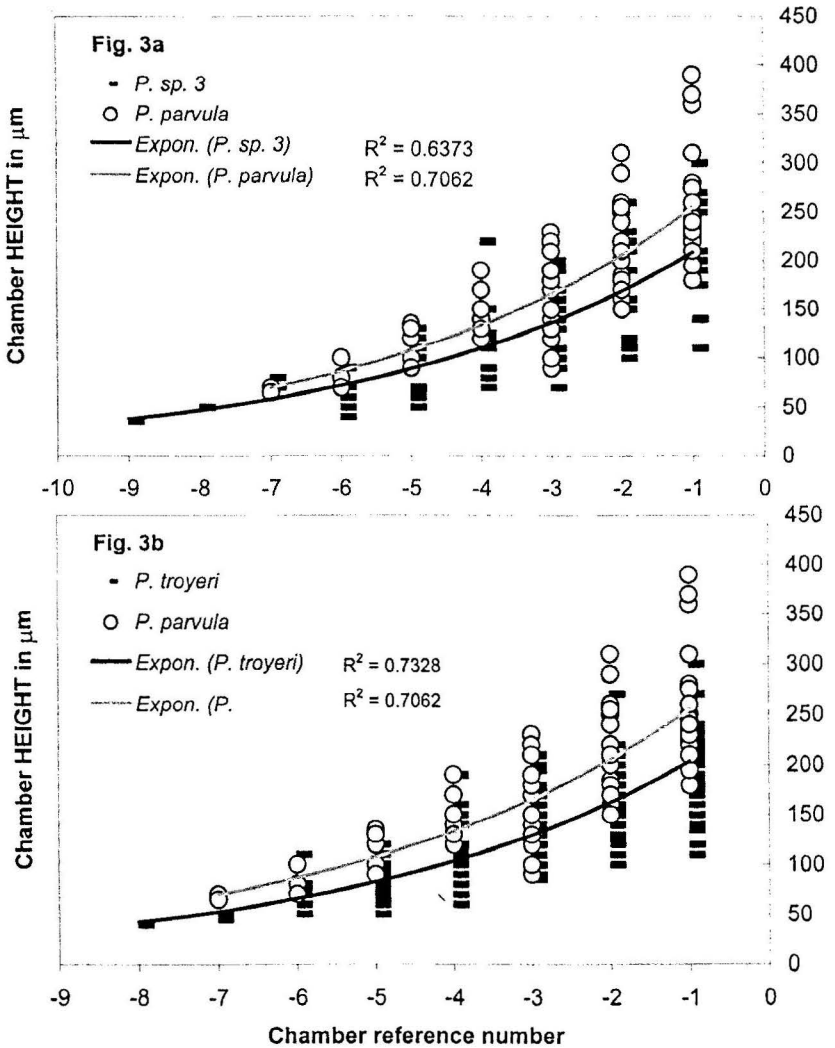

Figure 3. Chamber heights plotted vs. "backward" chamber numbering; (a) *Pseudonodosinella* sp. 3 and *Pseudonodosinella parvula*; (b) *Pseudonodosinella troyeri* and *Pseudonodosinella parvula*.

Table 2. Comparison of wall textural relationships in *Pseudonodosinella parvula*; *Pseudonodosinella troyeri* and *Pseudonodosinella* sp. 3.

Taxon	Grains	Wall	Depressed early chambers	Depressed late chambers
Pseudonodosinella sp. 3	coarse	thick	never	rarely
Pseudonodosinella troyeri	intermediate/fine	thin	always	nearly always
Pseudonodosinella parvula	fine	very thin	always	always

tionships are described in the taxonomic notes and summarised in Table 2.

Depressed chambers definitely alter measured dimensions. A diameter of a globular chamber may theoretically increase up to 157% (this value comes from theoretical squashing of a circle and equals a half of its periphery). Chamber heights change as well that depends on a shape of the chamber. In general, this chamber transformation depends on the thickness of the wall, as well as shape, and size of the chamber. For instance, it is often observed that larger final chambers of an individual are often distinctly squashed in comparison to smaller early chambers. It is closely related to the ratio between thickness of the wall and size of the chamber. These relationships may partly obscure our results. It would be possible to correct measured values by certain factors depending on several parameters, but it needs extra studies that are beyond the scope of this research.

It should be noted that specimens representing species (*P. troyeri* and *P. parvula*) with fine-grained wall and usually depressed chambers have revealed the lowest correlation coefficients (Fig. 5). *Pseudonodosinella* sp. 3 with coarse grained thick walls and rigid chambers shows the best correlation (Fig. 5a). It could be speculated that a higher variability of chamber measurements may be partly connected with different patterns of collapse of original chambers.

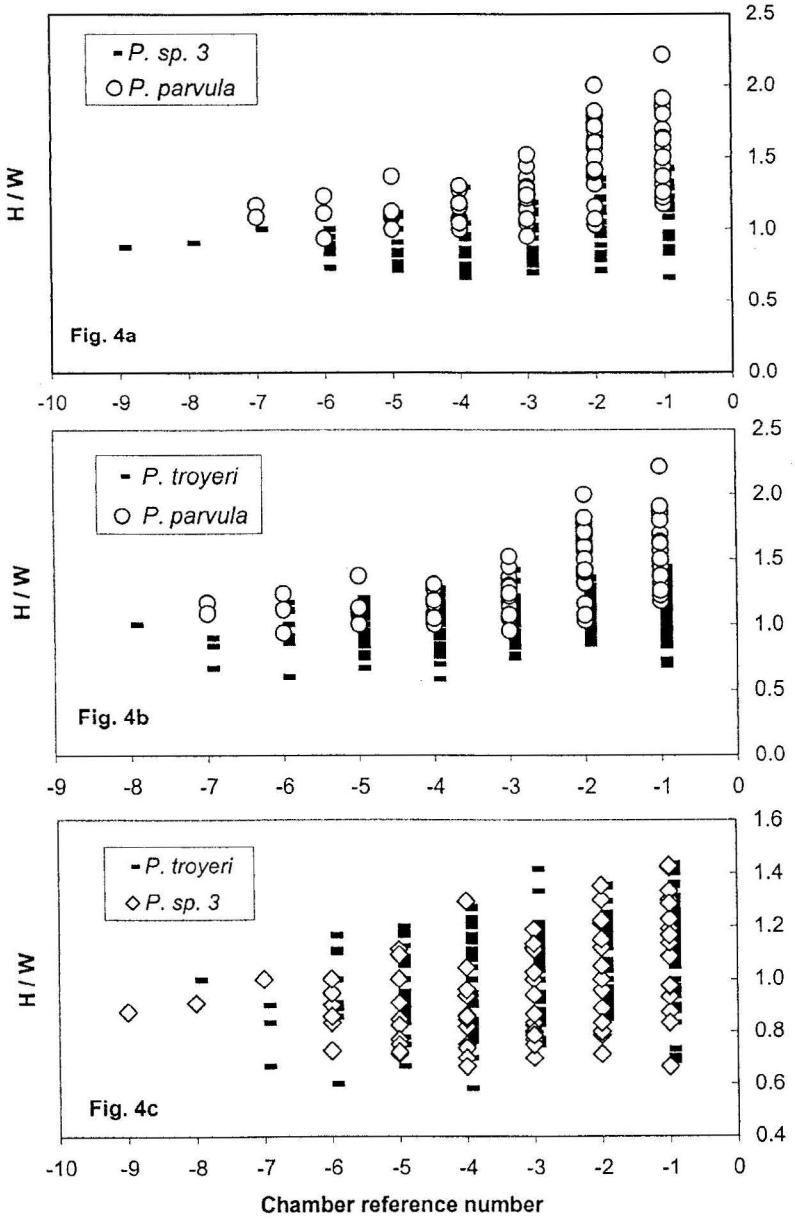

Figure 4. Chamber height/width ratios (H/W) plotted against "backward" chamber numbering: (a) *Pseudonodosinella* sp. 3 and *P. parvula*; (b) *Pseudonodosinella troyeri* and *Pseudonodosinella parvula*; (c) *Pseudonodosinella troyeri* and *Pseudonodosinella* sp. 3.

DISCUSSION

Chamber number reference system. The number of chambers is thought to correspond to the age of a specimen, at least to represent growth steps (Gradstein, 1974). Nevertheless, we should be cautious, because foraminifera are polymorphic, which is well visible in variety of prolocular dimensions within the same population. It is especially obvious in benthic foraminifera, which are usually bimorphic (microspheric and megalospheric), but also show clear variability of proloculi within the same generation.

All plots that refer to numbers of chambers do not reveal clear trends and data points are spread around large clusters (Figs. 2-4). Thus, results are usually very difficult to interpret, because "ontogenetic growth lines" of individual specimens are usually distinctly shifted. If a proloculus is referred as a "chamber no. 1", it does not help to identify following growth stages. For instance, chamber no. 3 may represent a terminal chamber in most investigated megalospheric forms. The same chamber number in microspheric forms refers to the chamber often representing the "juvenile stage". In order to avoid such problems, another rule has been proposed here, i.e., "backwards" counting of chambers (Figs. 3-4). "Backward" numbering has appeared to be more applicable because biomorphism and general polymorphism of early foraminiferal chambers can be neglected. Nevertheless, this scheme would be perfect for tests with identical terminal chambers. This may be true for some matured forms, but may be very misleading for juveniles or overgrown forms, which are quite frequent in every assemblage. Another important thing is that chamber numbers as integers are correlated with rational numbers (scalar values), which is not very correct. Therefore, this method is not promising, but may be useful in specific cases.

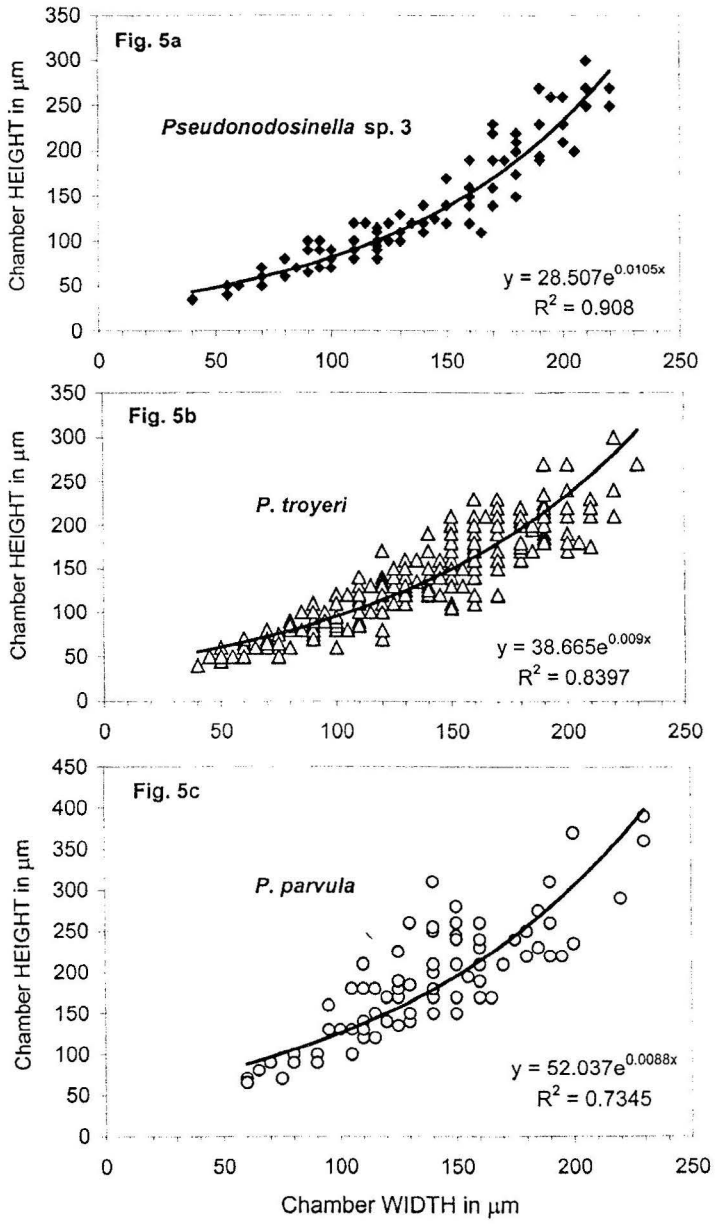

Figure 5. Chamber heights plotted against widths with exponential trendlines for (a) *Pseudonodosinella* sp. 3; (b) *Pseudonodosinella troyeri*; (c) *Pseudonodosinella parvula*.

This part of the study based on the chamber number reference system has shown that quantitative analyses of last two (or three) final (ultimate, penultimate) chambers may serve as a good tool for identification of difficult taxa. This may also be the case for other foraminiferal taxa. However, one should be very careful with terminal chambers, which are often very different from others, and often do not fit to the trend in the whole shell. For instance, some species of planktonic foraminifera often develop abnormal terminal chambers, such as sac-like chambers or kummerform chambers (with reduced size) (Hecht & Savin, 1972). It is suggested that abnormal terminal foraminiferal chambers (e.g., saclike or kummerform) are formed during an early phase of reproduction process in planktonic foraminifera. (e.g., Bé *et al.*, 1983). Abnormal final chambers have also been recognised in various benthic foraminifers (Tyszka, unpublished). Such final abnormal chambers should be eliminated from ontogenetic analyses (e.g., Olsson, 1972; Gradstein, 1974).

Relative size reference system. Size-reference approach gives a reasonable alternative. This system is based on measurements in two dimensions. This way time is eliminated from this relation, because it is assumed to be the same for both measurements (Simpson *et al.*, 1963). Changes of various morphological traits in large coiled foraminifera are often referred to the revolution angle partly depending on an ontogenetic stage (e.g., Hottinger, 1960; Hohenegger *et al.*, 2000). Growth changes of planktonic foraminifers have also been referred to degrees of whorl (Olsson, 1972). This approach cannot be applied for rectilinear (uncoiled) forms. Moreover, it does not define ontogenetic stages in polymorphic foraminifera. The problem is actually very similar to that one of the chamber numbering scheme. It means the same volution number and/or the identical angles

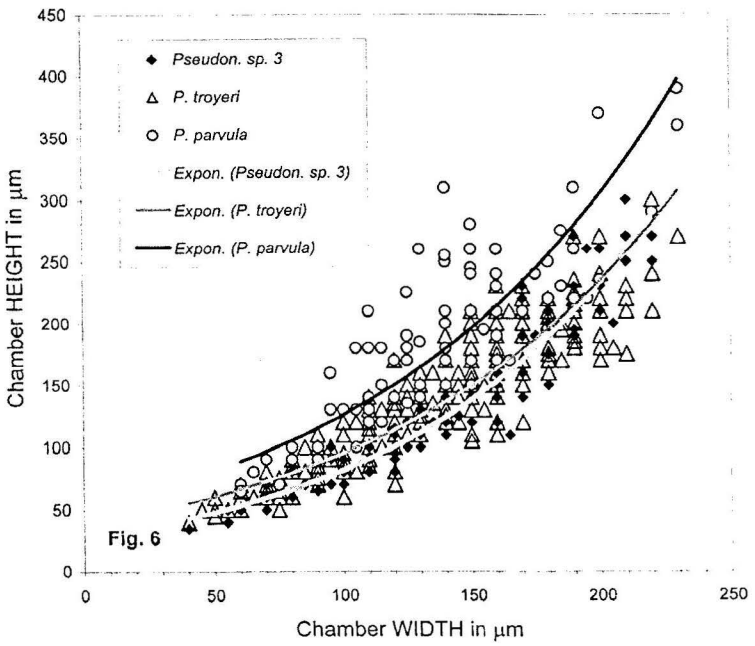

Figure 6. Chamber heights plotted against widths with exponential trendlines for all three taxa, i.e. *Pseudonodosinella* sp. 3; *Pseudonodosinella troyeri*; *Pseudonodosinella parvula* (see Fig. 5a-c for details).

of whorl are often not adequate for comparison of two specimens. Measurements of parameters related to the whole (gross) test yield the same problem. More appropriate is to refer to values, which are not dependent on overall test size. Therefore, chamber width vs. height scheme seems to be well suited for analyses of foramininiferal tests ontogenesis. Other stage-independent measures can also be used, such as overlap values, apertural neck size, chamber volumes etc.

It should also be noted that application of this relative size reference system reveals that microspheric and megalospheric forms of the same species follow the same chamber relative growth line. Departures from a principle may probably be attributed to susceptibility of chamber morphology to external (environmental) factors.

Allometry of foraminiferal shells vs. allometry of chambers. The concept of allometry was first introduced by Huxley & Teissier (1936). Allometry is defined as change of shape with increase or decrease in size (Gould, 1977). It focuses on the different ratios of growth between two parts of the body or between one part and the whole organism. There are two basic types of growth, i.e., **isometric** growth where the relationship between characters is defined by a straight line (shape is stable through ontogeny) and **allometric** growth, if the relationship between characters is defined by a curve (shape changes with changing size).

Ghose (1970) noted that accretive shell growth of foraminifers is not applicable for the allometric formula. This seems to be true for gross shell analysis. Our *Pseudonodosinella* gives the best example because the cumulative growth of the whole test is strongly allometric. Addition of every chamber changes the ratio between non-cumulative widths and cumulative heights of the whole test. This allometry is extremely difficult to study because it depends on polymorphism (including bimorphism) and an ontogenetic stage of a specimen. There is no simple way to compare whole, cumulative, accretive changes of gross foraminiferal tests without time or ontogenetic stage control. We should agree with Scott (1974) that the question really concerns the form of the relationship between the sizes of successive chambers. Actually, all chambers are treated here as separated units with focus on changes in their shape through the ontogeny.

Actually, first sight interpretation of the relative growth of *Pseudonodosinella* sp. 3 suggests simple allometry described by an exponential equation. Therefore, the height of chambers seems to grow faster than the width of the same chambers. It means that chambers get more elongated when added. However, individual relative chamber growth lines reveal that this "exponential" interpretation is just an approximation based on averaged series of chambers from various specimens (Fig. 5a). This method does not yield clear information on a specimen itself and the position in a succession of chambers. Individual chamber growth lines based on individual specimens give more precise information on variability of growth.

Surprisingly, the individual chamber growth lines for most of *Pseudonodosinella* sp. 3 specimens are not exponential any more, but can be defined by two straight lines with different slope parameters. Simple isometry is broken around a certain size range, i.e., the width (chamber diameter) at around 150 µm. This pattern of "broken isometry" resembles multiphasic allometry, when overall course is divided into several phases within which the slope is nearly constant in the logarithmic scale. Therefore, our "broken isometry" can be analogically termed as **multiphasic isometry**, which represents a special kind of allometry. This is still allometry (sensu Gould, 1977) because shape changes with increasing chamber size. Actually, in this case, this is biphasic isometry, i.e., at the first phase chambers grow nearly without changing shapes, then in the second stage they switch to another shape that is unchanged with further growth.

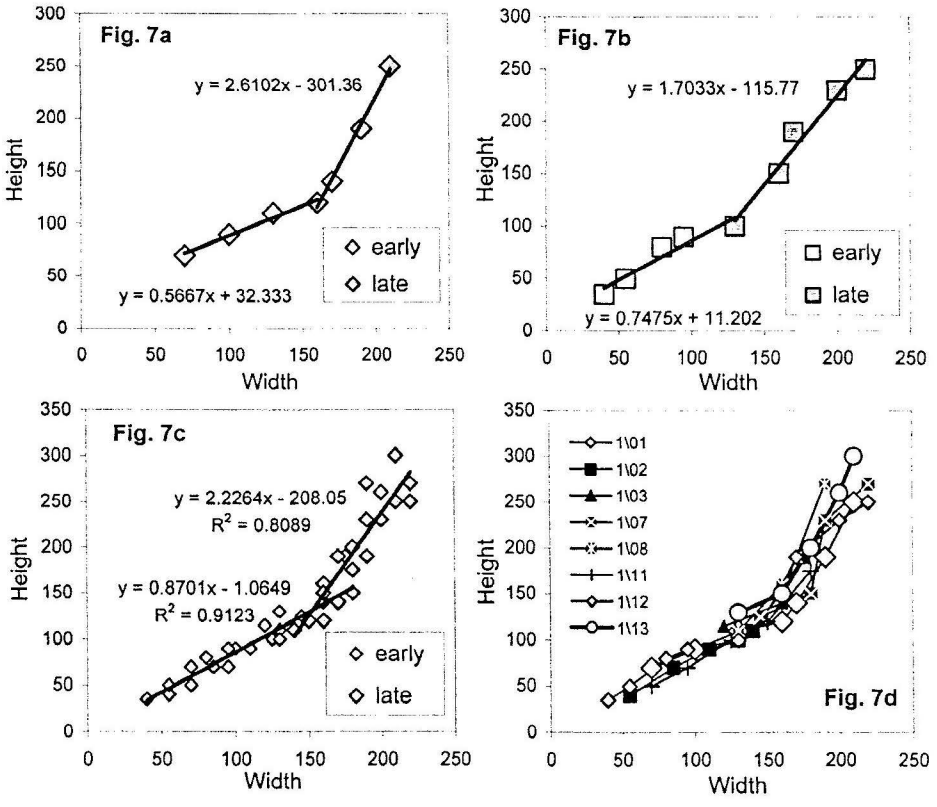

Figure 7. (a,b) Individual relative growth of chambers in single *Pseudonodosinella* sp. 3 specimens; (a) specimen 1\01; specimen (b) 1\12 (see late 1 fig. 5). (c) Averaged trends of relative growth of chambers in eight *Pseudonodosinella* sp. 3 specimens; 'early' and 'late' ontogenetic stages are separated. (d) Individual relative growth trajectories of eight specimens; all measurements in μm

This individual relative growth of the studied specimens can be defined by two straight lines, which have different parameters. The analysed individuals of *Pseudonodosinella* sp. 3 grew nearly isometrically with a slope parameter fairly below 1.0 at an early ontogenetic stage and switched to another isometric trend with slope parameters well above 2.0 (Fig. 7a-d). This allometric switchover usually took place at a certain size range. This probably happened at a ***critical stage in development*** (sensu Simpson *et al.*, 1960) for this species. Simpson *et al.*, 1960 defined this critical stage describing different deviations from simple allometry. Such critical stages (phase transitions) during ontogeny were also identified in planktonic foraminifera. They correlate much better with size than a specific number of chambers (Brummer *et al.*, 1986; Signes *et al.*, 1993).

There is a long discussion on isometry and allometry of planktonic foraminifera shells. Olsson (1971, 1972) has shown allometric growth relationships of chamber dimensions as a fundamental characteristic of the species. His growth curves also show some deviations from simple allometry. In contrast, Malmgren & Kennett (1976) concluded that planktonic foraminifers grow isometrically. On the other hand, Brummer *et al.* (1986) documented drastic morphological changes between consecutive size-dependent stages in ontogeny of planktonic foraminifers. Signes *et al.* (1993) supported this assumption that those drastic morphological changes in planktonic foraminifera may be viewed as a constructional bridge between juvenile and adult architecture. Therefore, "the neanic stage of Brummer (1986)" marks the transition from a set of 'juvenile' parameters to 'adult' ones while maintaining exponential growth per chamber increment" Signes *et al.* (1993). These changes happen during the critical stage that resembles our broken-isometry pattern in selected *Pseudonodosinella*. Some specimens investigated here more or less deviate from biphasic isometry showing a simple allometric pattern, which is very close to simple isometry.

Control on growth and morphology. It has already been noticed above that bimorphic generations of the same species seem follow the same relative chamber growth line. However, megalospheric and microspheric forms may live under different conditions (for instance, associated with seasons). These conditions are likely to control morphogenesis of foraminifers. "Within genetically determined limits, growth is controlled by such factors as nutrient supply, temperature and salinity" (Masters, 1977). These are probably not the only controlling factors. However, food availability seems to be the most important one as was already suggested by Rhumbler (1909) who found varying chamber ratios of benthic foraminifers and ascribed them to fluctuations in the food supply (after Berger, 1969). This statement cannot be directly tested on the fossil material. However, Holbourn *et al.* (2001) report fossil example of two ecophenotypes of a calcareous foraminifer *Osangularia schloenbachi* (Reuss). Specimens from the Albian black shale show much larger, broader and more inflated chambers in contrast to narrow crescentic chambers of specimens above the black shale. It could be speculated that the trophic regime was responsible for different chamber

size and shapes. It seems to be clear that future research on Recent foraminifers focusing on culture studies may help to understand genetic and external controls on size and shape relationships in the ontogeny of the foraminifera.

TAXONOMIC CONCLUSIONS

Analysis of test ontogenesis indicates that *P. parvula* is a distinct taxon separated from *Pseudonodosinella troyeri* and *Pseudonodosinella* sp. 3. By contrast, *P. troyeri* and *Pseudonodosinella* sp. 3 have revealed very similar ontogenetic patterns, therefore, they cannot be distinguished based on biometric features. The only difference is the composition of their walls, i.e., coarser grains of *Pseudonodosinella* sp. 3 and associated rough wall surface and resistance to chamber compression. These features intergrade between both taxa and are not sufficiently distinct according to taxonomic judgement to be classified as clear species-specific traits. It is very likely that both taxa represent two varieties (?ecophenotypes) of the same species. Thus, it is proposed to move *Pseudonodosinella* sp. 3 to *P. troyeri* as a variety of this species named *Pseudonodosinella troyeri* var. *scabra*.

Pseudonodosinella troyeri (Tappan) **var. *scabra*** var.n.

Plate 1, Figs 15-17.

Reophax sp. –Herrero & Haynes, 1997, pl. 1, fig. 18.
Pseudonodosinella sp. 3. –this study

Etymology. The Latin word *scabra* means rough and refers to the wall texture of the foraminifer.
Description. See above.

Pseudonodosinella troyeri (Tappan) **var. *troyeri***

Plate 1, Figs 7-14.

Pseudonodosinella troyeri (Tappan, 1960). –this study.
Description. See above.

Remarks. When a subspecific taxon, such as 'variety' (*varietas*) is named, another subspecific taxon of the same rank is automatically created that repeats the name of the species.

GENERAL CONCLUSIONS

The study based on the chamber number reference system with "backward" numbering has shown that quantitative analyses (proportions) of two (or three) final chambers may serve as a good tool for taxonomic identification. Specimens with abnormal final chambers are eliminated from analyses. Except for this conclusion above, the chamber number reference system is not suitable for ontogenetic analysis because chamber numbers are time- and stage-dependant. In specific cases, if chamber numbers are necessary, "backward" numbering is suggested (compare Figs. 1-4).

A relative size reference system applied to foraminiferal chambers, instead of whole tests, seems to express ontogenetic trends better than other systems. This system is time- and stage- independent and therefore is preferred for the analysis of test ontogenesis (see Figs. 5, 6).

The investigated taxa of *Pseudonodosinella* have revealed different types of ontogenetic chamber allometries. In general, there is a tendency to increase heights of chambers distinctly faster than widths (diameters of chambers in cross-sections). It varies from simple allometry, which is very close to isometry. Another quite characteristic allometry is termed here **multiphasic isometry**, when at certain chamber size (critical stage) isometrically growing chambers switch to another isometric mode of growth. This individual relative growth line is defined by two straight lines, which have different parameters (Fig. 7a,b).

It seems to be clear that chamber growth lines depend on intrinsic (genetic algorithms), as well as external (environmental) factors. Morphogenetic reaction norms of foraminifers across a range of environmental conditions may be very variable. Some taxa may have very strict "morphogenetic algorithms"; others may be very susceptible to environmental conditions.

ATO can help identify dimorphism (e.g., as two erroneously described species), verify qualitative identifications, as well as predict test ontogenesis in phylogenetic development or intraspecific variability. It may serve as a tool for studying foraminiferal life history strategies.

It is necessary to stress that taphonomic processes may alter size relationships. Depressed chambers of agglutinated foraminifers are especially affected. The investigated specimens of *Pseudonodosinella* show that larger final chambers of an individual are often distinctly squashed in comparison to smaller early chambers. This pattern is closely related to the ratio between the thickness of the wall and the size of the chamber.

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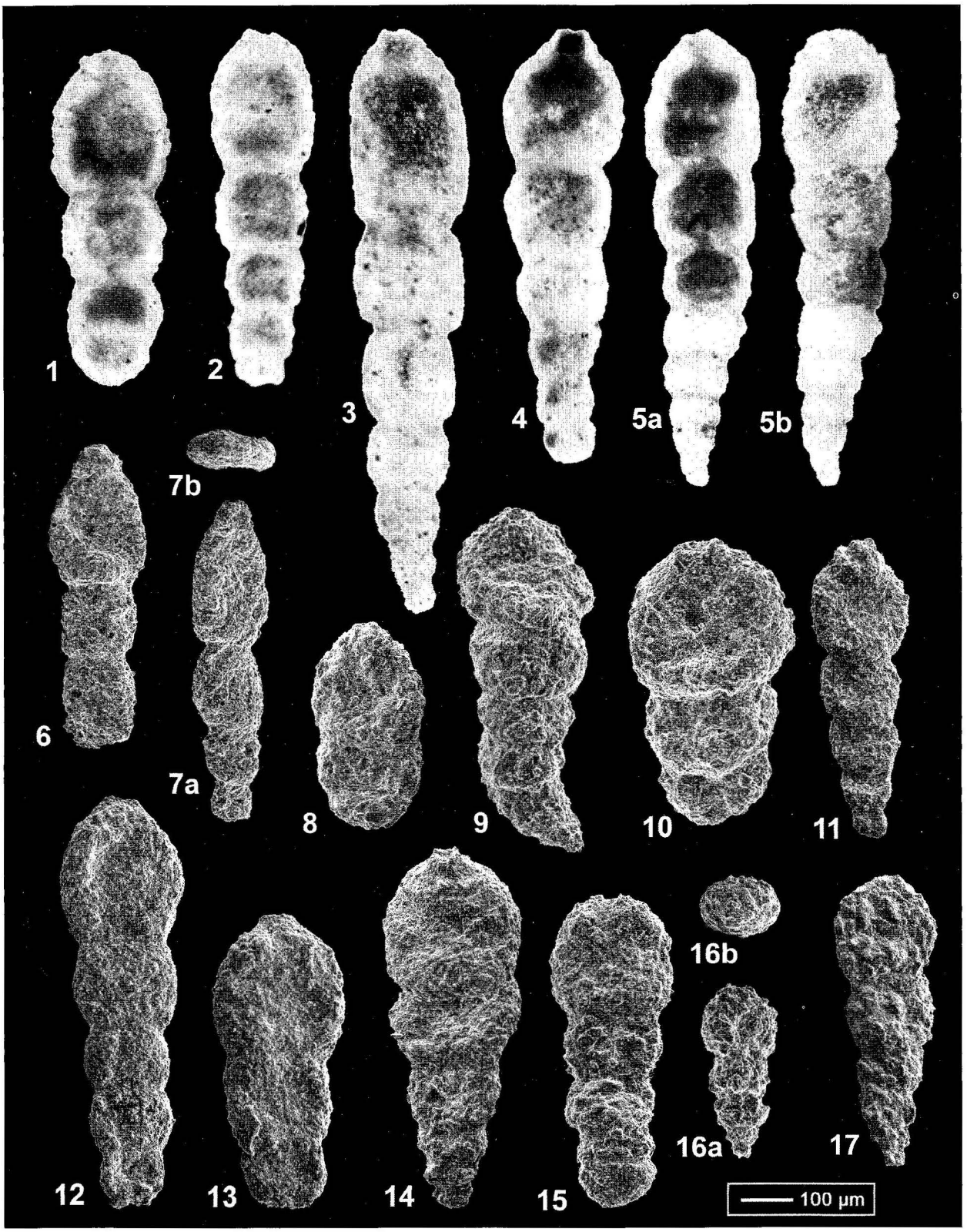
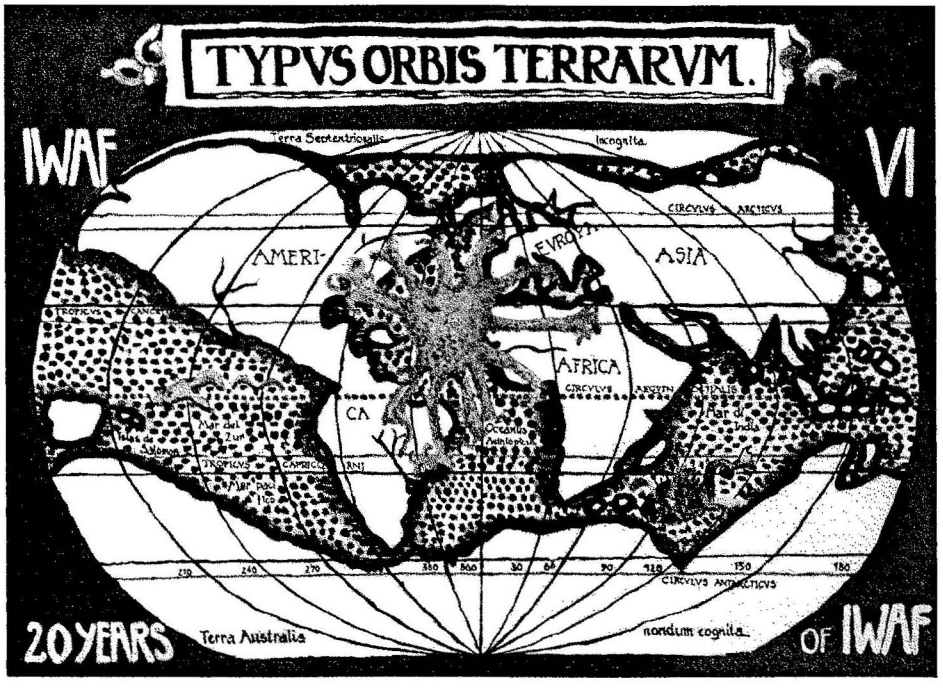


Plate 1. 1-3. *Pseudonodosinella parvula* (Huss, 1966): (1) sample Ki II–265.23-35 m [specimen 1\07]; (2) Ki II–185.55-70 m [1\35]; (3) Ki II–265.23-35 m [1\06]; **4.** *Pseudonodosinella troyeri* (Tappan, 1960), Ki II–181.72-85m [1\53]. **5.** *Reophax* sp. 3, Ki II–263.18-30 m [1\12]; (5a) the same wet and (5b) dry specimen; (1-5) in reflected light. **6,7.** *Pseudonodosinella parvula*, Ki II–264.10-22m; **8-14.** *Pseudonodosinella troyeri*: (8) Ki II–277.15-25 m; (9, 10) Ki II–260.27-37 m; (11) 269.25-40 m; (12, 13) Ki II–192.13-25 m; (14) Ki II–192.13-25 m. (9, 10) Ki II–260.27-37 m; (11) 269.25-40 m; (12, 13) Ki II–192.13-25 m; (14) Ki II–192.13-25 m. **15-17.** *Reophax* sp. 3, (15) Ki II–269.25-40 m; (16, 17) Ki II–264.10-22 m (see Taxonomic conclusions); (6-17) SEM photographs.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IWAF
VI
Terra Septentrionalis
Incognita
CIRCVLVS ARCTICVS
AMERI-
EVROPA
ASIA
AFRICA
CIRCVLVS
Mar de India
TROPICVS
CAPRICOR
Terra Australis
nondum cognita
CIRCVLVS ANTARCTICVS
20 YEARS
OF IWAF

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