

Determination of Upper Triassic and Lower Jurassic *Ichthyolarias* using morphogenetic programs

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ABSTRACT: Species of the genus *Ichthyolaria* from the Upper Triassic and Lower Jurassic are investigated and described. First the morphology of each chamber, rib and the keel surrounding the test are transferred to geometrical functions reducing complete test morphology to a small set of parameters. Then dependencies of each parameter on growth are modelled by geometrical functions representing the morphogenetic programs. Parameters of these growth independent functions are used as characters in classification analyses based on clustering and ordination methods. Groups demonstrating homogeneity in characters can now be interpreted as biological species using the criterion of cohesion in morphogenetic programs. Classification of *Ichthyolarias* results in 10 species, where one of lowermost Jurassic age (*Ichthyolaria gigantea*) and two of Triassic age (*I. serotriadica*, *I. parvolimbata*) are new. Evolutionary tendencies and phylogenetic relationships are proven using multivariate discriminant analyses.

INTRODUCTION

Representatives of the genus *Ichthyolaria* are characterized by polythalamous tests showing a uniserial arrangement of inverse chevron-shaped chambers, similar to that of the genus *Fron-dicularia*. The wall structure is hyaline, finely perforate and, in contrast to *Fron-dicularia*, nonlamellar, as found in most Permian and older Mesozoic lagenids. Tests are flat and ornamented on both sides with longitudinal ribs. A keel surrounds the test margins except for the apertural region. The first appearance of *Ichthyolaria* is during the Upper Permian, the last in the basal Toarcian (Lower Jurassic).

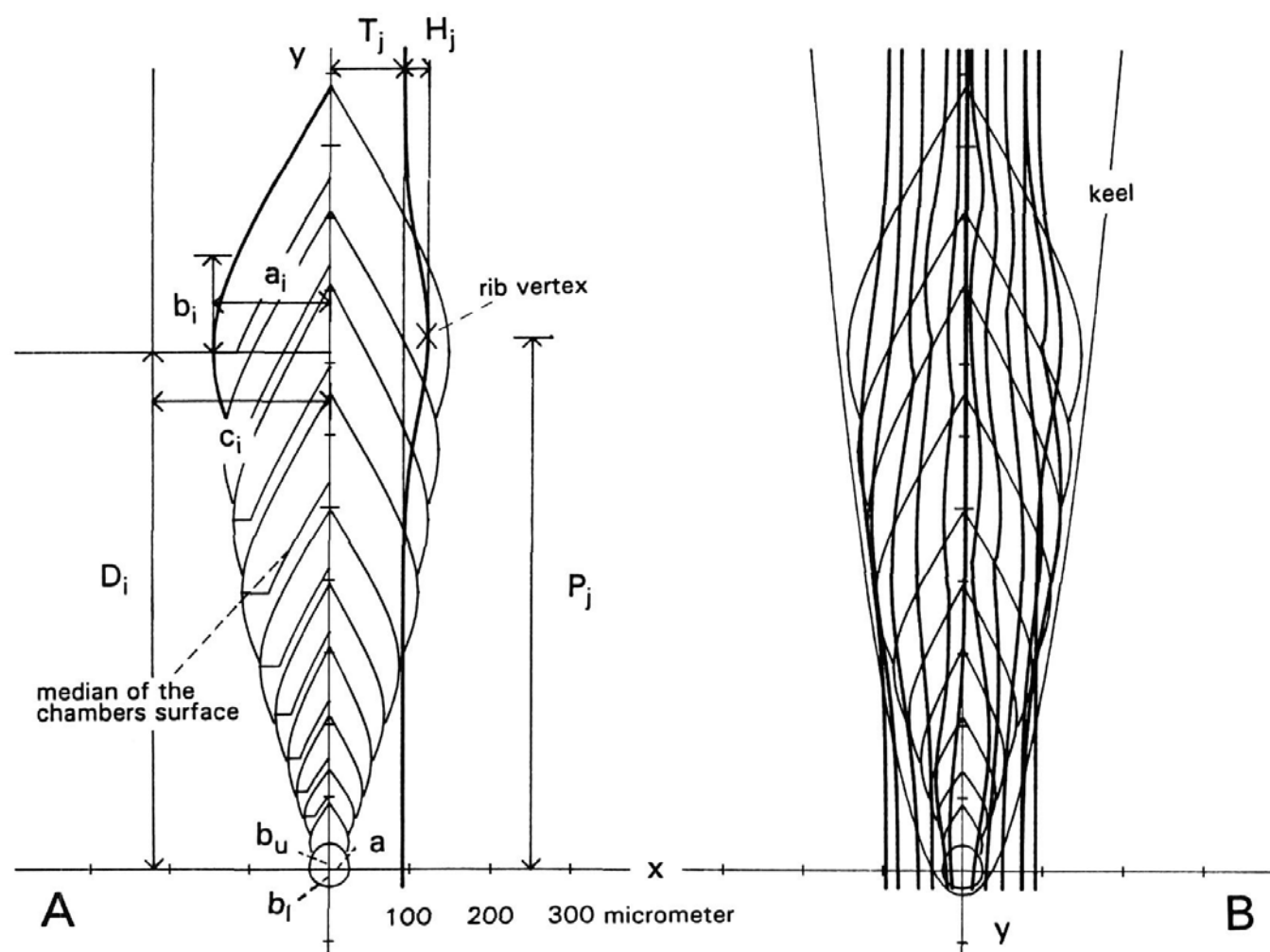
Many species have been erected since the first description of Liassic "Fron-dicularias" (d'Orbigny 1849), especially by Terquem (1858, 1866) and his successors in the late 19th and first half of the 20th century. These species are all founded on an extreme typological concept, without regard to continuous morphological variation. Wedekind (1937) introduced the genus *Ichthyolaria* separating Lower Jurassic from Middle Jurassic to Recent "Fron-dicularias," with the only difference being a temporal gap in the uppermost Lower Lias. Sellier de Civrieux and Dessauvagie (1965) and Gerke (1967) recognized the different wall structures within the Lagenina, allowing Norling (1966, 1968) to extend the diagnosis of the genus *Ichthyolaria* based on nonlamellar wall structures.

Berthelin (1879) detected morphological transformation within the Liassic *Ichthyolarias*, but a stratigraphical interpretation was not given. Well-founded investigations on the temporal successions of different *Ichthyolaria* forms were done contemporaneously by Barnard (1957) and Norvang (1957), yielding similar results but different interpretations. While Norvang, adhering to a typological species concept, introduced the new genus *Span-delina* in ignorance of Wedekind's work, Barnard noticed the morphological homogeneity of the Liassic forms, manifested in an extreme variability combined with a more or less gradual temporal change. Since morphological homogeneity suggests only one species, Barnard regarded the whole group as a plexus, taxonomically expressed in a single species named *Fron-dicularia sulcata*.

Since most specialists in Liassic foraminifers ignored Barnard's revolutionary ideas, continuing to use a typological species concept, the number of defined species increased further (Ruget 1967; Ruget and Sigal 1970). Difficulties arose in the differentiation and interpretation of species, especially since individual growth was neglected. Thus, growth dependent characters (e.g. the number of ribs) often used in the determination of *Ichthyolaria* species led to the description of growth stages as different species.

To avoid growth dependent characters in species determination, a species concept has been developed founded on homogeneities in morphogenetic programs (Hohenegger 1980, 1992). Since the criterion of homogeneity is used, this species definition can be regarded as similar to Templeton's (1989) "cohesion concept," which explains character homogeneities created by population genetic and demographic mechanisms. The concept of homogeneities in morphogenetic programs was exemplified through Jurassic *Ichthyolarias* (Hohenegger 1980, 1981, 1987). In a first step, all characters concerning chamber form and the form of ribs and keels are transformed to geometrical functions. Thereafter, chamber arrangement and the position of the ribs during growth are expressed by mathematical functions representing a model for the latent morphogenetic programs. These enable complete geometrical reconstructions of each test, including its ornamentation (Hohenegger 1987). Thus, homogeneities in parameters of these mathematical functions may be equivalent to homogeneities within morphogenetic programs and can be used for species determination.

Using multivariate classification algorithms, Barnard's *Ichthyolaria sulcata* plexus could be differentiated into four groups, each homogeneous in their morphogenetic programs, and thus were interpreted as different species (Hohenegger 1980, 1981). Their stratigraphical usefulness was strengthened, and different evolutionary models could be demonstrated (Hohenegger 1989). The oldest form (*I. densicostata*), restricted to the Hettangian, is replaced in the Sinemurian by *I. sulcata*, showing quite different tests with the development of fewer, but coarser, ribs. During Upper Sinemurian a gradual change towards the smooth *I. terquemi* is visible, but *I. sulcata* persists until the



TEXT-FIGURE 1

A. Morphometric parameters of chamber contour and rib form. B. Geometric test construction and rib pattern of individual in plate 1, figure 8.

beginning of the Lower Toarcian, both forms possibly occupying different ecological niches. Independently from these trends, a much smaller form with fine ribs (*I. squamosa*) evolved during the late Sinemurian, but also became extinct with all other *Ichthyolaria* species at the beginning of the Lower Toarcian (Riegraf 1985; Copestake and Johnson 1989). These trends were confirmed by investigations of Ruget (1985) based on a quite different species concept and therefore using different names.

The same uncertainties as in Liassic forms are present in descriptions of Permian and Triassic *Ichthyolarias* despite a much smaller number of publications. Permian (Gerke 1961) and Middle Triassic (Heath and Apthorpe 1986) *Ichthyolarias* differ to a high degree from Liassic forms. Therefore, new names were correctly introduced. On the contrary, Upper Triassic *Ichthyolarias* are very similar to Liassic species. This resulted in two types of species descriptions. One uses species names identical to the Liassic forms, reducing the stratigraphical value of the latter (Strong 1984). The other concept insists on the typological species, leading to new species and subspecies (Kristan-Tollmann 1964).

Thus, it seems quite necessary to investigate the Triassic *Ichthyolarias*, applying the same concept of homogeneities within morphogenetic programs as used for Liassic representatives. Many samples from the uppermost Triassic (Rhaetian sensu Krystyn 1990) were investigated, thus species determination using multivariate classification analyses based on rich material is possible.

LOCATION AND STRATIGRAPHIC POSITION

Through its entire stratigraphic range, the genus *Ichthyolaria* was ecologically restricted to open marine conditions. It can be found in Upper Triassic marine basins developed in front of and behind carbonate platforms (Dachstein limestones).

The Koessen beds of the northern calcareous Alps are sediments deposited in an epicontinental sea, running from the west to the east and delimited to the south by carbonate platforms. Transgression of the Koessen Sea began in Upper Norian and was followed in the Rhaetian by a deepening and development of intraplatform basins. During the Rhaetian stage an exchange with the open Tethyan Sea was possible, resulting in higher

microfaunal diversity than in the Upper Norian. At the end of the Rhaetian a strong regression took place, which characterizes the Triassic-Jurassic boundary (Golebiowski 1990b).

The type section of the Koessen beds was reinvestigated by Urlichs (1972) in the Weißloferbach near Kössen (Tyrol, Austria). Urlichs (1972) and Mostler et al. (1978) described ostracodes, conodonts and pollen, evaluating their stratigraphical importance. Ichthyolarias were found in 19 samples from the type locality, all restricted to the Rhaetian part of the section (Eiberg member sensu Golebiowski 1990a, *Choristoceras marshi* zone). The stratigraphically older part (Hochalm member sensu Golebiowski 1990a, section C of Urlichs 1972) is distinguished by a foraminiferal fauna showing low diversity, dominated by a coarse-ribbed *Nodosaria* and lack of Ichthyolarias.

The transition from the Triassic Koessen beds to the basal Lias (Lias-Basiskalke sensu Fabricius 1966) can be found in various localities of the northern calcareous Alps (Golebiowski 1990b). Just above the Triassic-Jurassic boundary (Tiefengraben member part A, Golebiowski 1990b), as exposed in the "Kendelbach" and "Vorderer Ampelsbach" sections, the marls contain a restricted foraminiferal fauna in which *Trochammina alpina* Kristan-Tollmann dominates. Other foraminifers (e.g. *Trocholina*) seem to be allochthonous, originating from older carbonate platform regions. Large Ichthyolarias, however, never found in platform regions, seem to be autochthonous and are restricted to these marls.

The main open marine facies of the Tethyan Sea, developed in the Norian as Hallstatt limestones and Pedata beds, is located south of the carbonate platforms (Mostler 1986). A change in sedimentation during the basal Rhaetian resulted in a sequence of marls and limestones, called the "Zlambach beds" (Matzner 1986; Krystyn 1987, 1990). Their microfauna is characterized by various groups, such as foraminifers (Kristan-Tollmann 1964; Tollmann and Kristan-Tollmann 1970), ostracodes (e.g. Bolz 1971) and nannofossils (e.g. Janofske 1987). They are all distinguished by high diversities manifesting open marine conditions.

The transition from Hallstatt limestones to Zlambach marls was investigated at the Steinbergkogel near Hallstatt, Upper Austria, (Hohenegger 1974) close to the type locality of the Norian (Krystyn et al. 1971). Ichthyolarias are found there in marls intercalated with gray limestones.

A 60m large section of Zlambach beds was investigated by Hohenegger and Piller (1977) in the Roßmoosgraben east of Bad Goisern, Upper Austria. Starting with nodular limestones of Lower Rhaetian age (*Vandaites stuerzenbaumi* zone sensu Krystyn 1987) the transition to gray marls representing the main part of the section is continuous. The uppermost part of the marls (*Choristoceras marshi* zone) is characterized by a dominance of dark clays with a lack of limestones, indicating a more or less anoxic milieu. With the exception of the nodular limestones, all marls and clays contain a large number of Ichthyolarias.

Lowermost Jurassic Ichthyolarias were investigated to demonstrate the differences to the Triassic forms on the one hand and to strengthen the distinctions between the Hettangian and Sinemurian representatives on the other. Three localities were chosen. The basal Hettangian of the quarry Hagnach, Lustenau,

northeast of Tübingen (Germany), containing Ichthyolarias consists of 2.5m thick marls just above the basal "Psilodenbank" (Schwarzer Jura alpha₁). Upper Hettangian specimens originate from the Xeuilley quarry south of Nancy, Lorraine, France. A third sample, which may demonstrate the differences between *I. densicostata* and *I. sulcata*, stems from the micropaleontological collection of the Stuttgarter Museum für Naturkunde. The age of the sample is Lower Sinemurian (Betzgenreith near Göppingen, Germany; Schwarzer Jura alpha₃), obtained from the Feifel collection.

The investigated material is deposited in the Institut für Paläontologie, Universität Wien, collection number P 4301.

MEASUREMENTS AND STATISTICAL INVESTIGATIONS

Each specimen was treated with carbon tetrachloride to reveal the inner test structures and then photographed using a transmitted light microscope (Leitz Orthoplan). Afterwards the test surfaces were photographed with a scanning electron microscope (Stereoscan 600). Measurements of chamber forms, ornamentation and forms of the keels were performed by digitizing all the characters based on the photographs, allowing a totally geometrical reconstruction of tests in two-dimensional space (text-fig. 1). Thickness of tests and height of ribs were measured directly on coated specimens using a microscope with incident light (Leitz Orthoplan) and focusing on a number of succeeding points (distances 100µm; see text-fig. 2).

Geometrical functions were calculated for the contour of chambers, the progress of ribs and the form of the keels, using HP-Basic programs written by the author. Programs were also written to evaluate statistically the parameters of growth functions representing the morphogenetic programs.

Multivariate classification and discriminant analyses were carried out using the program package SPSS on the mainframe computer (IBM 3090 400-E) of the Vienna University. Prior to classification processes, all characters had been standardized in a special form, which incorporates the information contained in the form of univariate frequency distributions (Hohenegger 1986). For this task special programs were written in Microsoft Basic for personal computers and in Fortran 77 for mainframes (Hohenegger and Tatzreiter 1992).

MORPHOMETRICS

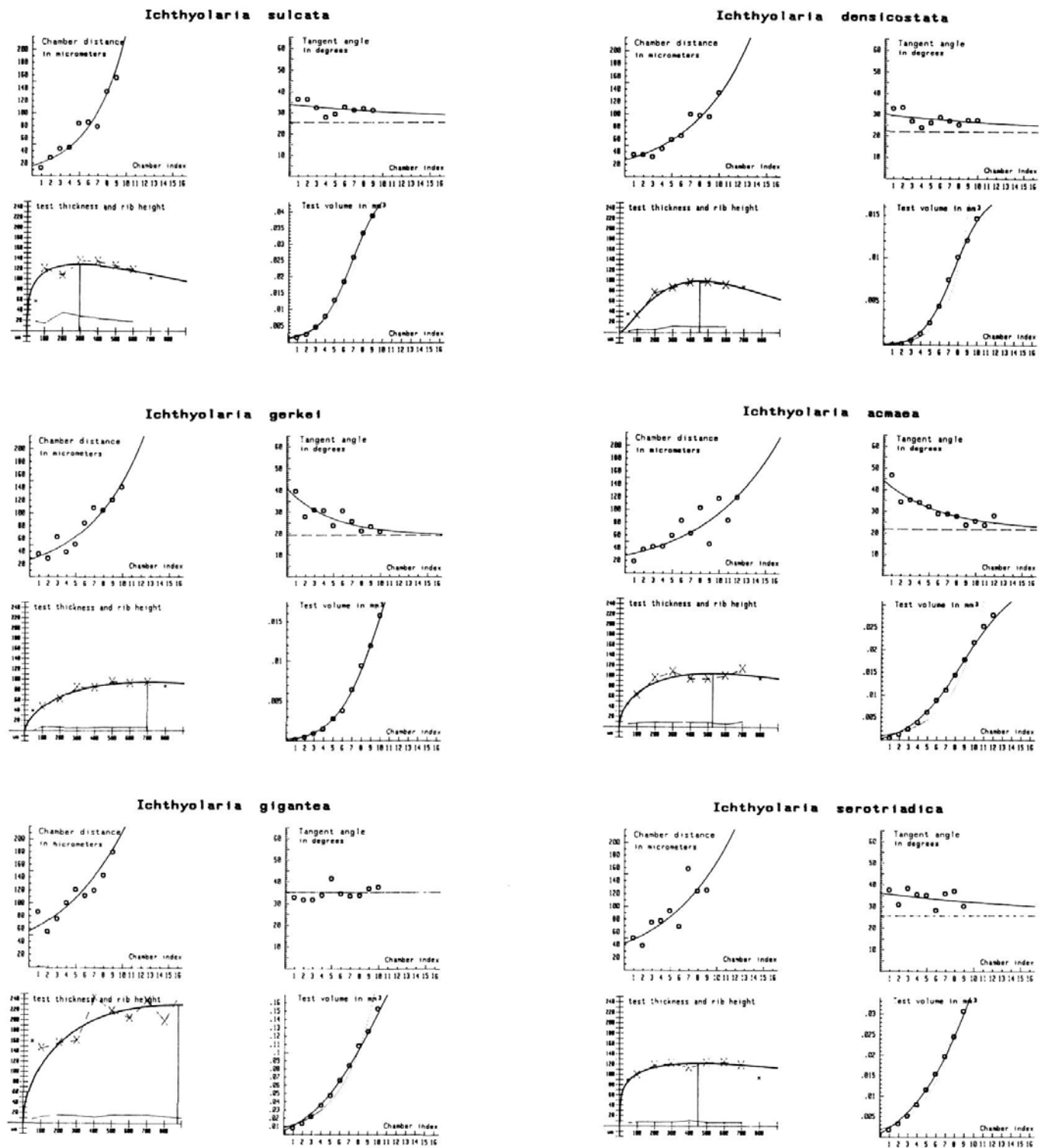
All morphological characters of *Ichthyolaria* tests are transferable to geometrical functions that can reproduce the morphology of the outer test using only a few parameters (Hohenegger 1980, 1981, 1987).

The proloculus can be modelled by two cups of ellipsoidal form, which are compounded at their borders. The halves differ in only one parameter. If the common center of the half-ellipsoids is regarded as the origin of a three-dimensional coordinate system (x-coordinate = width, y-coordinate = length, z-coordinate = thickness), wherein the *Ichthyolaria* test is represented in geometrical functions, the proloculus can be modelled by Equation 1 (l = lower cup, u = upper cup; text-fig. 1):

$$f_l(x, y, z): b_l^2 c^2 x^2 + a^2 c^2 y^2 + a^2 b_l^2 z^2 = a^2 b_l^2 c^2, -b_l \leq y \leq 0 \quad (1a)$$

$$f_u(x, y, z): b_u^2 c^2 x^2 + a^2 c^2 y^2 + a^2 b_u^2 z^2 = a^2 b_u^2 c^2, 0 \leq y \leq b_u \quad (1b)$$

Mathematical models of the other chambers are more difficult, but are prone to simplification from the flatness of the tests



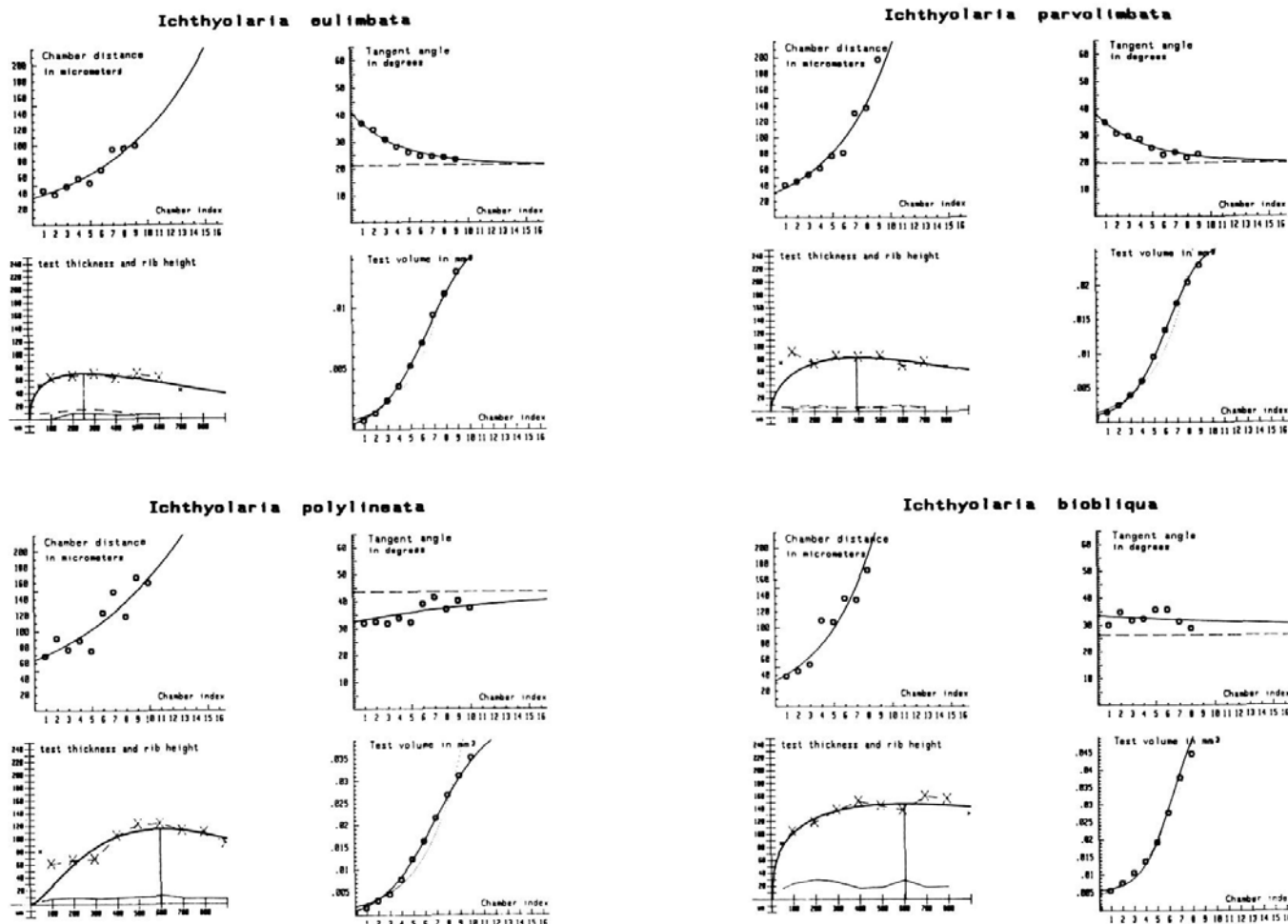
TEXT-FIGURE 2a

Functions representing morphogenetic programs of test construction. The dotted line in the graph of volume growth indicates exponential growth. Representatives for the different species as figured in plates 1-3. *Ichthyolaria sulcata*: plate 1, figure 1; *Ichthyolaria densicostata*: plate 1, figure 8; *Ichthyolaria gerkei*: plate 2, figure 10; *Ichthyolaria acmaea*: plate 1, figure 13; *Ichthyolaria gigantea*: plate 1, figure 15; *Ichthyolaria serotriadica*: plate 3, figure 9.

(Hohenegger 1987). Each chamber's contour can be described by two hyperbolas linearly translated from the origin of the coordinate system (text-fig. 1):

$$f(x, y): b^2(x \pm c)^2 - a^2(y - D)^2 = a^2b^2 \quad (2)$$

Since only parts of the hyperbolas' arcs are used, function 2 must be modified, introducing i as the chamber index and $s_{i,i-1}$



TEXT-FIGURE 2b

Functions representing morphogenetic programs of test construction. The dotted line in the graph of volume growth indicates exponential growth. Representatives for the different species as figured in plates 1-3. *Ichthyolaria eulimbata*: plate 3, figure 3; *Ichthyolaria parvolimbata*: plate 3, figure 4; *Ichthyolaria polylineata*: plate 3, figure 6; *Ichthyolaria biobliqua*: plate 3, figure 14

as the x-coordinate of the point of intersection between two succeeding chambers (text-fig. 1):

$$y = f(x) = D_i - (b_i/a_i)[(x + c_i)^2 - a_i^2]^{1/2}, \quad -(c_i - a_i) \leq x \leq -s_{i,i-1}$$

$$y = f(x) = D_i - (b_i/a_i)[(x - c_i)^2 - a_i^2]^{1/2}, \quad s_{i,i-1} \leq x \leq c_i - a_i$$

$$y = f(x) = D_i + (b_i/a_i)[(x + c_i)^2 - a_i^2]^{1/2}, \quad -(c_i - a_i) \leq x \leq 0$$

$$y = f(x) = D_i + (b_i/a_i)[(x - c_i)^2 - a_i^2]^{1/2}, \quad 0 \leq x \leq c_i - a_i$$

The parameter $s_{1,0}$ is defined as the point of intersection between both hyperbolas' arcs, modelling the first chamber and the function that represents the section of the proloculus with the x-y plane:

$$f_u(x, y) = b_u^2 x^2 + a^2 y^2 = a^2 b_u^2, \quad 0 \leq y \leq b_u$$

Neglecting the deviation from ideal geometrical functions in the foraminal and apertural regions, each chamber form can be modelled again by the use of ellipses within the y-z plane (Hohenegger 1987, pl. 2, fig. 1), retaining this geometrical form in all sections parallel to this plane. Since the height of all ellipses remains nearly constant up to the marginal region of the chamber, which is situated at the hyperbolas' vertices, chamber form can be described by a continuous sequence of ellipses. The

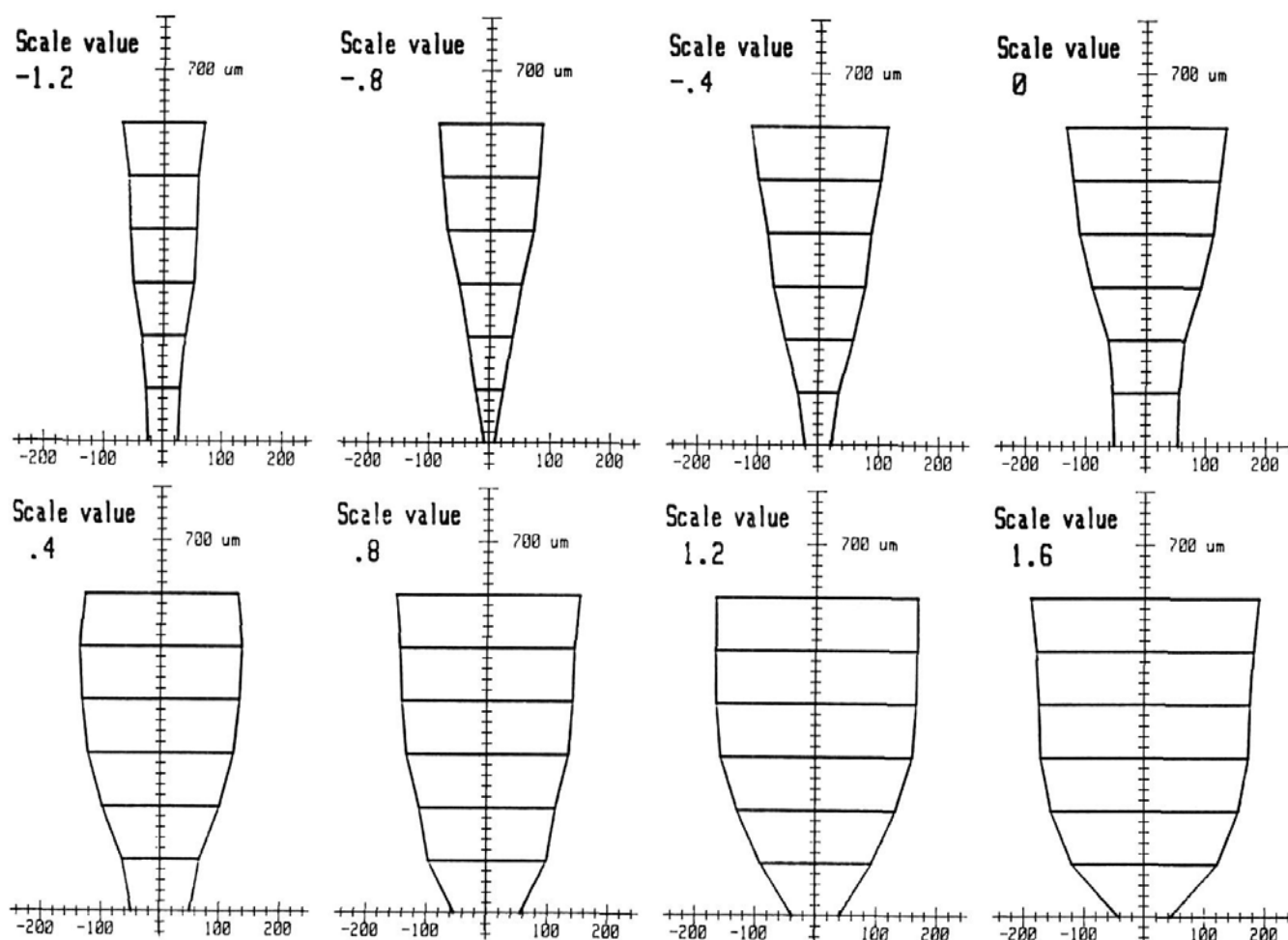
centers of these ellipses follow a function within the x-y plane, which is similar to the hyperbolas describing the chamber contours (text-fig. 1). This will be labelled as the "median of the chambers surface."

If it is assumed that all *Ichthyolaria*s possess pure nonlamellar walls, each chamber will be marked by a deepening of sutures, resulting from the arched chambers surface. This, however, can only be seen in the final chambers of large tests, when they become smaller than the preceding ones. Thus, most of the *Ichthyolaria*s filled these deepenings with supplementary wall material, resulting in a flat test surface (Hohenegger 1987, pl. 2, fig. 1).

The test surface is covered by longitudinal ribs. The course of a rib can be modelled by the following function within the x-y plane (text-fig. 1):

$$x = f(y) = H e^{-W^2(y-P)^2} + T, \quad y \in \mathbb{R} \quad (3)$$

If j is introduced as an index for rib number, whereby ribs situated to the left of the axis of symmetry have negative values, then T_j characterizes the minimal distance of the j th rib to this axis. Parameter H_j determines the height of the bell-shaped



TEXT-FIGURE 3
Representation of test width belonging to selected scale values.

function 3. Thus, the maximal deviation from the median axis of rib j , introduced as a new parameter, Max_j , will result from the sum of parameters T_j and H_j . The vertex position of function 3 along the y-axis is determined by parameter P_j . Investigations on Liassic Ichthyolarias (Hohenegger 1987) demonstrated the coincidence of the rib vertex positions with the "median of the chambers surface" (text-fig. 1). This may be a vestige of the ancestral program of rib development. In the case of costated *Nodosarias*, which may be the ancestors of the genus *Ichthyolaria*, all ribs show a bend in the middle of the chambers, caused by their arched surfaces. The flat surfaces of *Ichthyolaria* tests, on the contrary, do not require arched ribs, but this program seems to be preserved rudimentarily. The last parameter (W_j) of the bell-shaped function 3 determines its width and therefore characterizes the gradation of divergence and/or convergence of ribs. In the case of larger tests, rib forms are characterized by a set of functions 3, which differ in parameters W , P and H .

The height of ribs varies from the center to the lateral margins. In Liassic representatives, a minor decrease in rib height starting from the median axis can be observed, but some Triassic specimens show a development of strong marginal ribs. In most cases, rib height seems to be constant during growth (text-fig. 2).

All Ichthyolarias possess a keel derived from the most lateral ribs. It differs from the other ribs in height. The keel's contour can be modeled in the initial part of the test by the power function (text-fig. 1)

$$y = f(x) = ux^w + v, \quad x \in \mathbf{R} \quad (4)$$

This function describing the form of keels changes in the later part of the tests, following the chamber's contours (Hohenegger 1987). Thus, the form of the keels depends strongly on test growth.

MORPHOGENETIC PROGRAMS

Each parameter value of functions 2-4 changes during growth of the tests, but in a very regular manner. This is transferable again into mathematical functions. The new parameters of these growth functions may represent the latent morphogenetic program.

First, chamber position along the y-axis, expressed by parameter D_i of function 2, is determined. Differences of positions between succeeding chambers are used as the dependent variable; therefore, an ontogenetic change of these parameters can be

expressed by a simple exponential function (text-fig. 2)

$$D_i - D_{i-1} = f(i) = p_1 p_2^i, \quad i \in N_0^+ \quad (5)$$

Parameter p_1 indicates the distance of the first chamber's hyperbolas from the origin situated in the proloculus center. The rate of growth is expressed by parameter p_2 . Deviations of empirical values from this function are minimal in most Triassic and Liassic forms, with the exception of some specimens of the Koessen beds. This homogeneous group is characterized by remarkable deviations from the ideal growth function, which may be regarded as typical and useful for species interpretation. Both parameters of function 5 were used in succeeding classification analyses, introduced in a verbal form as "initial chamber distance" (p_1) and "growth rate of chamber distance" (p_2).

The angle between hyperbola tangents situated at the point of intersection with the y-axis is highly variable, but is useful for species determination. This character changes again during growth (text-fig. 2), a fact that was neglected in earlier investigations, where a constancy in chamber form within one individual was postulated (Hohenegger 1980, 1981, 1987). More precise investigations made it necessary to take into account a dependency of chamber angles from the chamber index i in the form of

$$\alpha_i = f(i) = p_3 \exp(p_4 i) - p_5/p_6, \quad i \in N_0^+ \quad (6)$$

The four parameters of function 6 are biologically not as interpretable as the parameters of function 5. Thus, a transformation of these parameters, which produces more illustrative attributes, seems useful. These new characters are named

1) "initial chamber angle," represented by the value of function 6 at $i = 0$ (proloculus),

2) the "growth rate of the chamber angle" ($\exp(p_4)$) and

3) the "limit of the chamber angle" ($-p_5/p_6$).

Since tests possessing few chambers make difficult the precise estimation of parameters p_3 to p_6 using statistical methods, an additional character, "mean chamber angle," with a weighting of values α_i by $D_i - D_{i-1}$ was introduced, facilitating comparison with earlier descriptions of *Ichthyolarias* (Hohenegger 1980, 1981, 1987).

Thickness of tests also changes with growth in a remarkable manner. Earlier investigations on Liassic *Ichthyolarias* demonstrated a trend characterized by a strong increase in the initial part of the test and a constant thickness during later growth. Some Triassic representatives deviate from this pattern, and therefore more detailed investigation was necessary. The general growth form of test thickness can be described now as follows: after an initial increase, a maximum chamber thickness is achieved, which is always followed by a slow decrease (text-fig. 2). Since the test surfaces are flat and not complicated by suture deepenings, this progress can be modelled by a continuous function:

$$d_i = f(y) = p_6 y^{p_7} \exp(p_8 y), \quad y \in \mathbf{R} \quad (7)$$

In the case of growth escalation, a second function of the same form as function 7 with differing parameter values allows the description of test thickness.

A biological interpretation of parameters p_6 to p_8 is again difficult. Thus, more comprehensive parameters derived from function 7 are used in classification analyses for determination of individual test thickness. These are the position and intensity of the extreme, called "maximum test thickness" and "position of maximum test thickness" (text-fig. 2).

One of the most important characters is represented by the test volume, which in the case of *Ichthyolarias* can be deduced easily from geometrical functions describing chamber form. Growth of test volume can be equated with protoplasmatic growth, therefore this part of the morphogenetic programs is most important for biological interpretations of organisms. Volume growth can be modelled for *Ichthyolarias* using the following function for restricted growth (text-fig. 2):

$$V_i = f(i) = p_9 + \frac{p_{10} - p_9}{1 + p_{11} \exp[-p_{12}(p_{10} - p_9)i]}, \quad i \in N_0^+ \quad (8)$$

While parameter p_9 represents the proloculus volume ($i = 0$), parameter p_{10} designates the upper limit of volume growth. This upper limit cannot actually be reached by the test, since the differences in growth functions between chamber distances and the volume cause smaller chambers to sever from the preceding ones in the final part of the test (Hohenegger 1980, 1981). Thus, most parameters of formula 8 are not comprehensive, with the exception of parameter p_9 , which will be used as the character "initial test volume" in the following classifications. Therefore, more biologically interpretable characters derived from formula 8 are used. The character "volume with maximum growth rate" can be calculated by

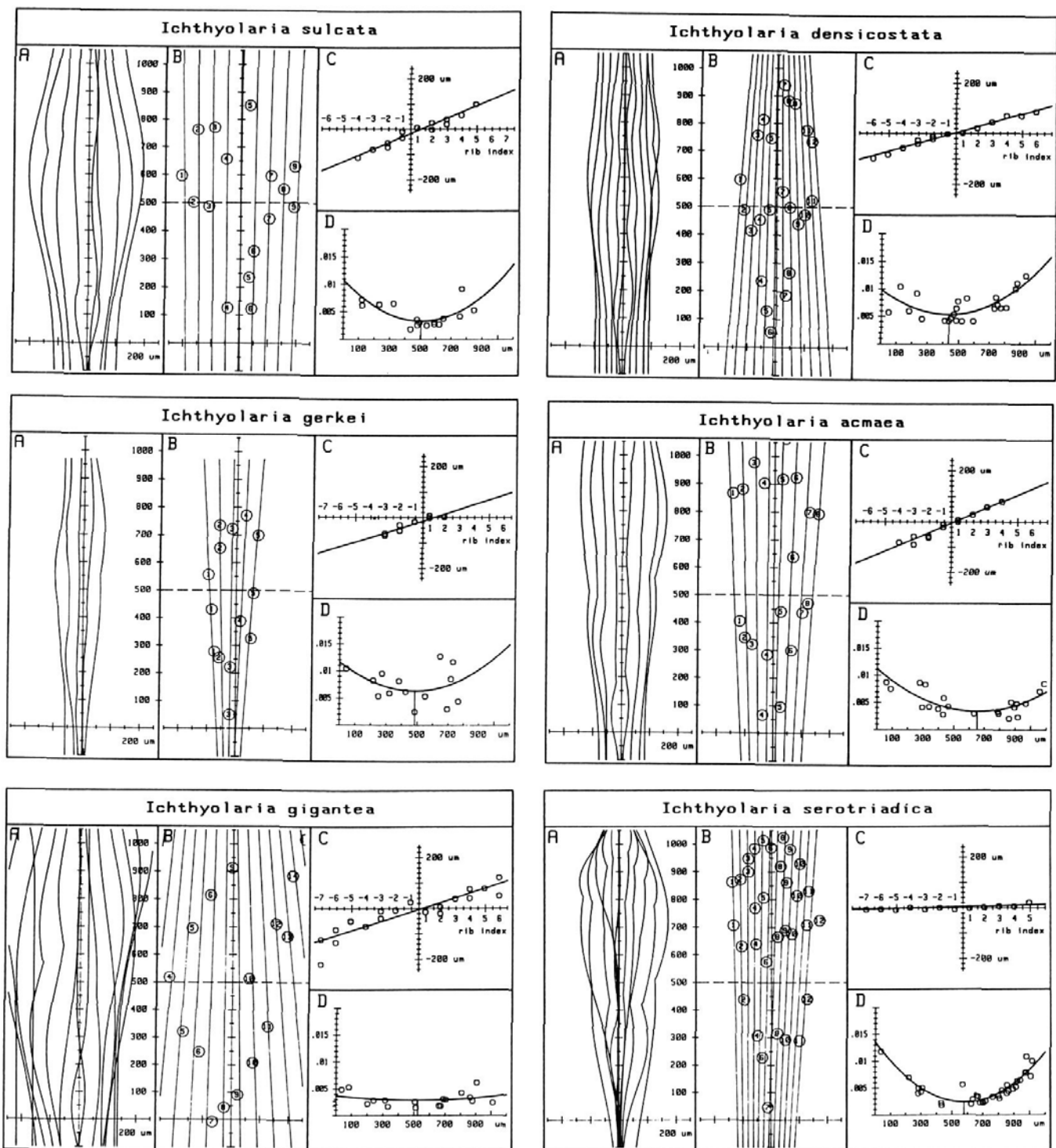
$$(p_9 + p_{10})/2$$

and is combined with the index i of the "chamber with maximum growth rate." All tests exceed that index by one or two chambers only, so both characters are important for the comparison of individuals (Hohenegger 1980, 1987). The last character describing growth of test volume is the "test volume growth rate," as derived from formula 8 (see Batschelet 1971, p. 298).

Although the entire test of each *Ichthyolaria* specimen is geometrically constructable using formulas 5-8, the chamber width, an important and instructive character, which will cause the form of the test during growth, is suppressed in classification analyses. This character is deducible for each chamber from formula 2 by

$$K_i = f(i) = 2(c_i - a_i), \quad i \in N_0^+$$

The change of chamber width during growth can be derived in a complex manner, as described above. A further attempt was made to find a single parameter characterizing growth. This method was developed by the author not only for quantitative but also qualitative growth-dependent characters (for a detailed description, see Hohenegger and Tatzreiter 1992). In a first step, the variable (K_i) must be combined with a character representing growth (D_i). Afterwards the independent growth variable is

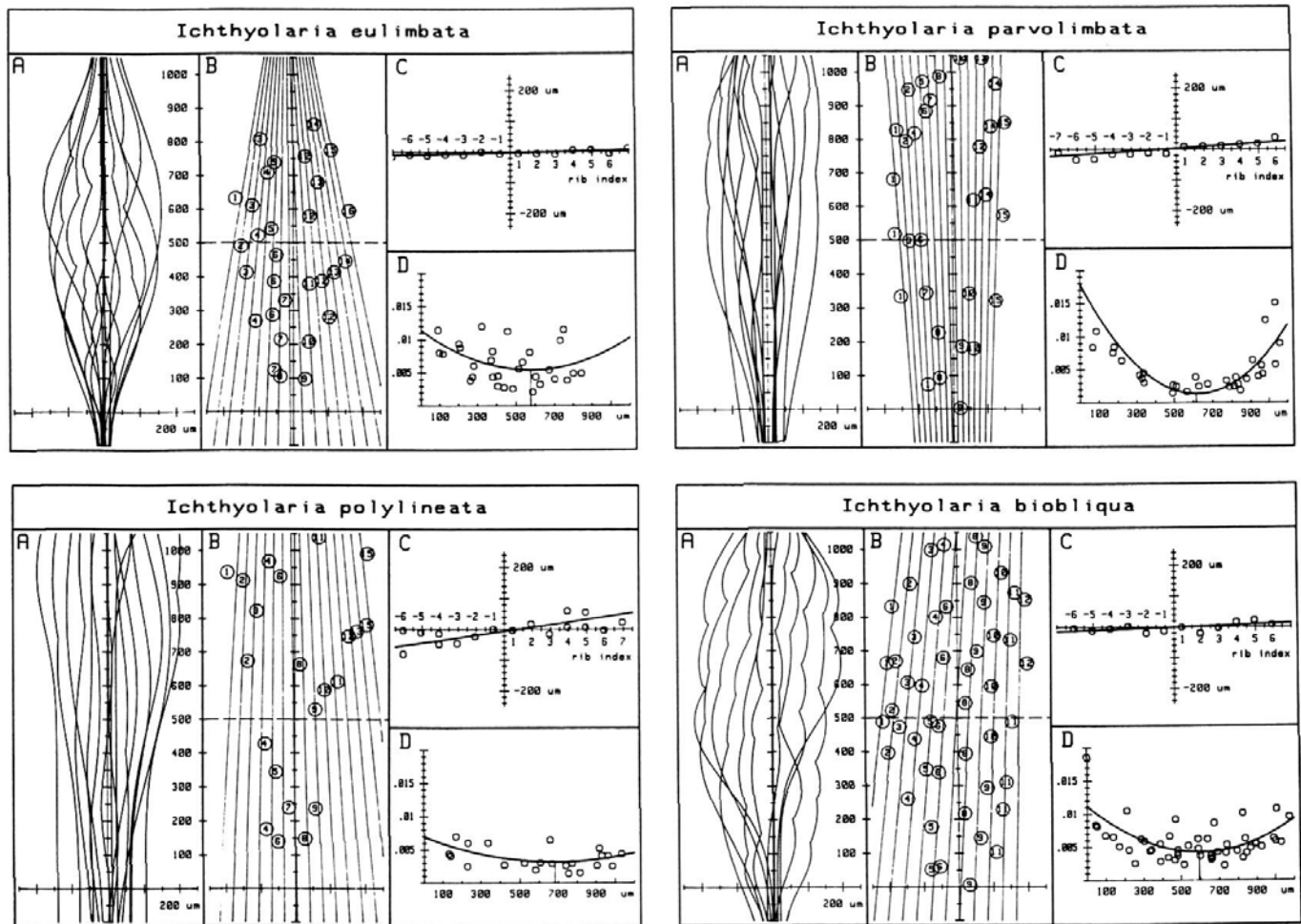


TEXT-FIGURE 4a

Morphogenetic programs of rib construction. A. Rib pattern. B. Position of rib vertices (parameters S_{ij}) and their statistical model using a bundle of linear functions. C. Connections between minimal rib distances (parameters T_{ij}) in form of linear functions. D. Parabolic functions modelling dependencies of rib width (parameters W_{ij}) from test length. Same representative individuals as in text-figure 2.

artificially divided into intervals, which remain constant for all objects. Theoretical values for the dependent variable at distinct interval boundaries are defined by the use of linear functions between both empirical values enclosing a boundary with their independent variables. In the case of Ichthyolarias, the intervals

chosen were 100 μ m, starting with the center of the proloculus (0 μ m) and ending with 600 μ m. Each interval boundary is now used as an independent variable, and the estimated values of the dependent variable belonging to the boundaries can be compared between the objects. In a second step, the multidimen-



TEXT-FIGURE 4b

Morphogenetic programs of rib construction. A. Rib pattern. B. Position of rib vertices (parameters S_{ij}) and their statistical model using a bundle of linear functions. C. Connections between minimal rib distances (parameters T_{ij}) in form of linear functions. D. Parabolic functions modelling dependencies of rib width (parameters W_{ij}) from test length. Same representative individuals as in text-figure 2.

sional character space (7 dimensions in the case of *Ichthyolaria* width) is reduced to fewer dimensions using multidimensional scaling (Torgerson 1952). The reduction of *Ichthyolaria* width to one dimension seems optimal with a stress of 0.084 (compare Kruskal 1964). Some selected scale values and test widths belonging to these are represented in text-figure 3 to facilitate the transition from scales to forms. This character is named "scaled test width." A character "proloculus width" (parameter a of function 1) is additionally introduced to strengthen the differences between sexual and asexual generations, expressed in most foraminiferids by differing proloculus sizes.

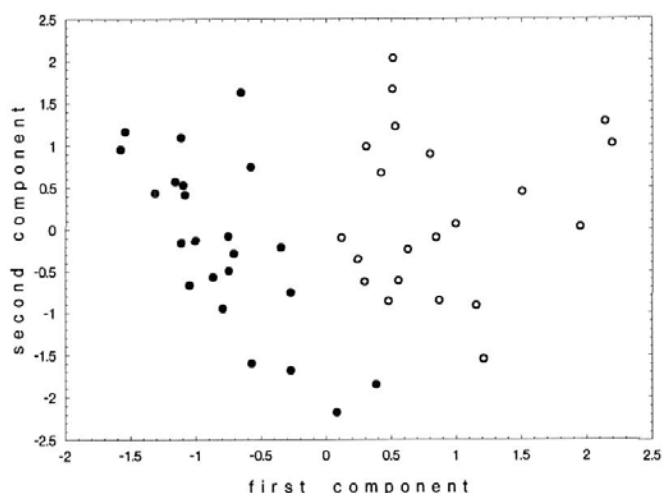
Ribbing of *Ichthyolaria*s is characterized by morphogenetic programs that are in strong connection to programs describing test growth. In the case of Liassic representatives, the form of a single rib can be interpreted geometrically by one or two functions of form 3 (Hohenegger 1980, 1981, 1987). Triassic specimens, on the contrary, show more complicated ribs, which can be modelled only by a series of functions 3 with changing parameter values H , P and W (text-fig. 4A). By functions only those parts with maximum deviation from the axis of symmetry are expressed (Hohenegger 1987).

The minimum distance of a rib to the y-axis—parameter T of function 4—remains constant for all functions describing one rib, with the exception of final test parts, where chambers become smaller than the preceding ones (Hohenegger 1987). A larger number of ribs will be developed during test growth, depending on the character test width. Connections between lateral ribs can be expressed by the formula

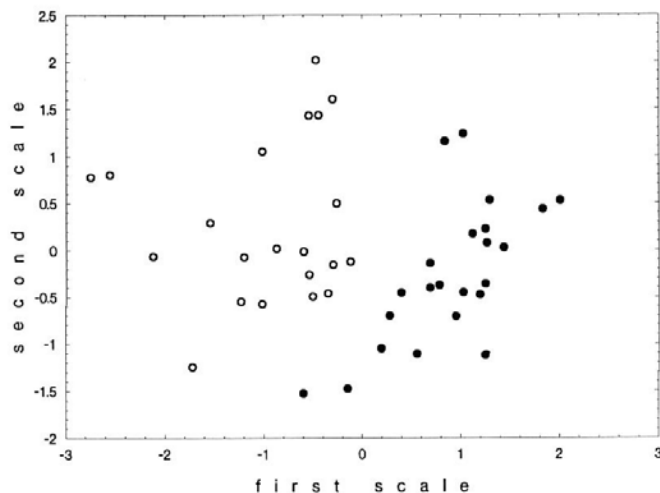
$$T_j = f(j) = p_{13} + p_{14}j, \quad j \in \mathbb{N}_0 \quad (9)$$

This function is characteristic of many specimens (text-fig. 4C), but often rib patterns differ in the left and right half of the test. In this case, the connections of parameters T_j must be modelled by two functions of type 9. But for classification analyses, only one function 9 including all ribs of an individual was calculated. Thereafter, information was reduced to the character "minimum distance of ribs" (parameter p_{14})

The bell-shaped function 3 is characterized additionally by the vertex position. In the case of a series of functions 3 describing the form of a single rib, an index t is introduced indicating a series of functions starting with the partial function next to the



TEXT-FIGURE 5
Ordination of Liassic *Ichthyolarias* by principal component scores. Empty symbols = *Ichthyolaria sulcata*, filled symbols = *Ichthyolaria densicostata*.



TEXT-FIGURE 6
Ordination of Liassic *Ichthyolarias* based on simple standardized characters by metric multidimensional scaling. Signatures as in text-figure 5.

proloculus. Vertex positions are indicated in the x-y- coordinate system by

$$S_{ij}[\text{Max}_{ij}, P_{ij}]$$

The positions of vertices during the progress of a single rib can be modelled by a simple linear function, with the exception of the final parts of large tests, as described above. Thus, the coordinates of all ribs' vertices are represented by a bundle of linear functions (text-fig. 4B), and lateral connections between them can be expressed by the equation

$$\text{Max}_{ij} = f(j, y) = p_{15} + p_{16}j + p_{17}y + p_{18}jy, j \in \mathbb{N}_0, y \in \mathbb{R} \quad (10)$$

Parameter p_{15} determines the initial position of function 10 and will not be used in further classification analyses. Parameter p_{16} , which designates the distance between consecutive ribs at $y = 0$, is more important for the pattern of ribbing. Since these linear functions either converge or diverge, a modified character derived from parameter p_{16} is introduced. The "maximum distance of ribs" is determined by the distance between contiguous functions at $y = 500\mu\text{m}$ (text-fig. 4B). The last parameters of function 10 characterize the intensity of convergence or divergence of linear functions describing the vertex positions of ribs. Parameter p_{17} designates the mode of rib courses in the axis of symmetry (divergence or convergence), and p_{18} determines the further progress (negative values = progressing convergence; positive values = progressing divergence). Both parameters are used as characters in classification analyses, named "increase of rib vertices" and "vergence of rib vertices." Differences in rib pattern between the right and left side of an *Ichthyolaria* test are expressed in parameter p_{17} and were used in further classifications as an additional character named "difference in the median increase of rib vertices."

The exact positions of the coordinates of vertices S_{ij} result from the points of intersection between linear functions of equation 10 and the "median of the chambers surface," as described in the morphometric chapter. Since each chamber's median intersects the linear functions 10, the question arises about the

realization of vertices. This depends on the distance between neighboring ribs, as has been demonstrated in detail for Liassic representatives by Hohenegger (1987). The more complex ribbing of Triassic forms requires further study.

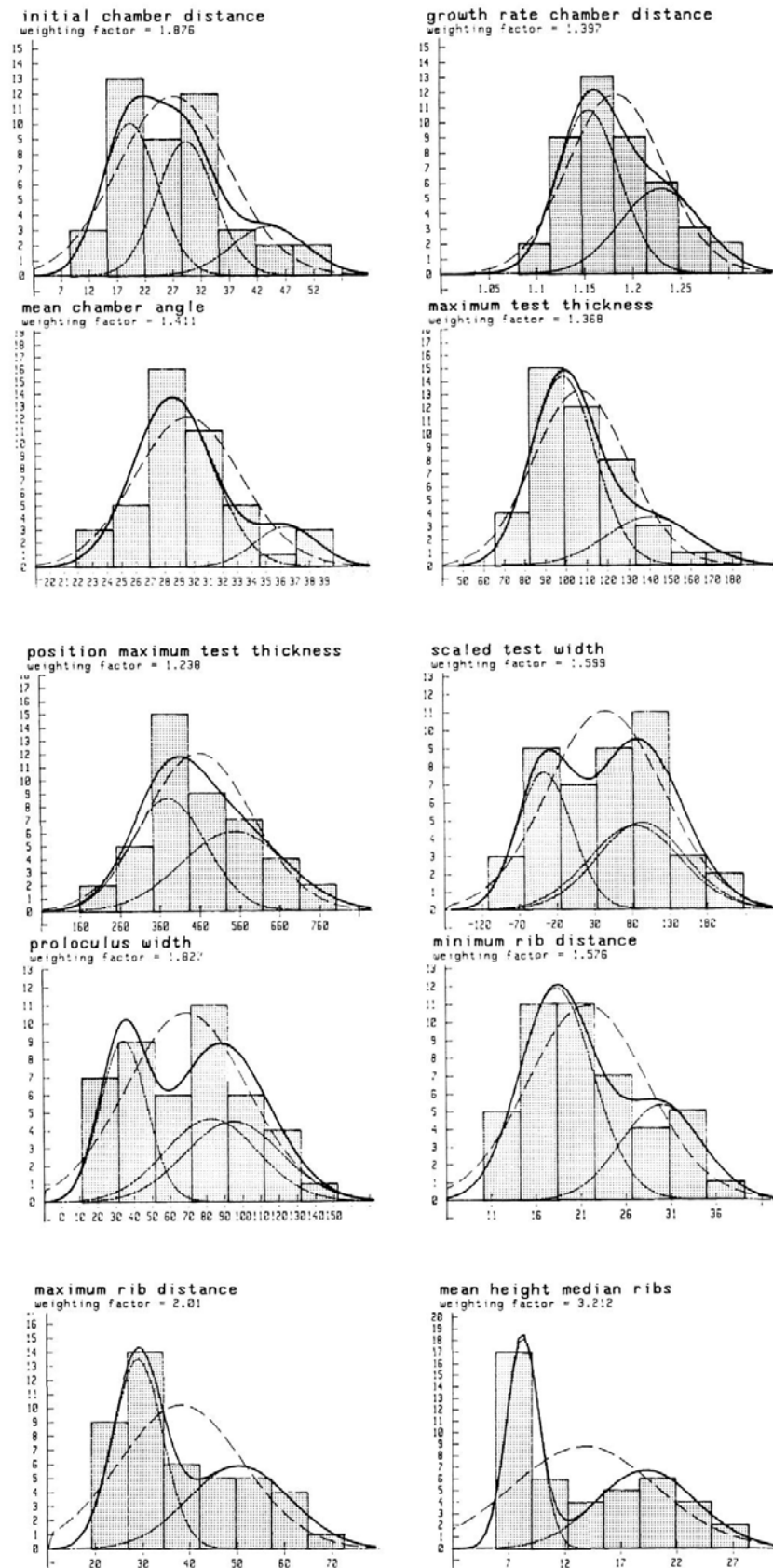
Dependencies of the last parameter of function 3 with growth remained unclear (Hohenegger 1980, 1987) until elucidation of a series of functions describing a single rib within the Triassic representatives. Thus, growth changes of parameters W can be modelled by

$$W_{ij} = f(y) = p_{19} + p_{20}y + p_{21}y^2, y \in \mathbb{R} \quad (11)$$

This parabolic function (text-fig. 4D) is characterized by a minimum value. Low values of W designate a minor bending of rib progress, larger values a stronger one. Thus, the partial functions of a single rib can be characterized as follows: in the initial part of the test a strong bending of ribs is detectable, which is followed by a weaker one. The final part of larger tests again shows a stronger bending of ribs. Since the parameters of function 11 are again not instructive, the following characters are introduced for classification purposes:

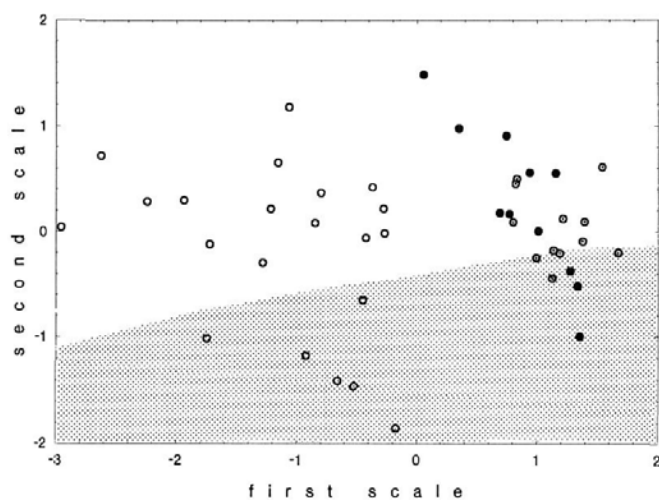
- 1) "minimum of rib width," which can be derived from function 11,
- 2) "position of the minimum of rib width" along the y-axis and, finally,
- 3) "difference to the extreme at a distance of $\pm 300\mu\text{m}$ length."

The height of ribs is the last character describing rib form. Rib height remains invariant during growth, as demonstrated in the morphometric chapter (text-fig. 2). Thus, the mean of measured heights of a single rib can be used as the growth independent variable. Since the heights between neighboring ribs differ, the mean of the median and the marginal rib heights were introduced as characters for classification, named "mean height of median ribs" and "mean height of marginal ribs."



TEXT-FIGURE 7

Decomposition of frequency distributions into normal components. Broken line = normal distribution, thick line = compounded distribution.



TEXT-FIGURE 8

Ordination of Liassic Ichthyolarias based on weighted standardized characters by metric multidimensional scaling. Empty symbols = *Ichthyolaria sulcata*, filled symbols = *I. densicostata* from Upper Hettangian, dotted symbols = *I. densicostata* from Lower Hettangian; dashed area indicates microspheric generations.

The growth of the keel is described in the morphometric chapter. A mathematical treatment, which is also valid for Triassic representatives, can be found in Hohenegger (1987). Since keel growth depends strongly on test form, as demonstrated in detail by Hohenegger (1987), this character is neglected in the following classification procedures.

CLASSIFICATION

Classification is understood in the following as the process of grouping objects into classes that are homogeneous in one or a set of characters. The results of classifications, named classification systems, are natural by definition, if all classes are differentiated through inhomogeneities in the same set of characters used for the classification processes. A classification that is based on growth dependent characters often results in natural classes representing only growth stages. These insufficiencies may be surmounted using parameters of the morphogenetic programs as characters. All classes of the resulting class system are then homogeneous in their morphogenetic programs and thus can be defined as different species according to the cohesion concept (Templeton 1989).

Since all morphogenetic program parameters of Ichthyolarias are metric, classification algorithms based on metric similarity or dissimilarity measures can be used to objectify the classification processes. But different parts of the morphogenetic program, e.g. test thickness, volume growth or rib height, are characterized by varying numbers of parameters leading in the following classification to an intrinsic weighting of program portions (Hohenegger 1982, 1986). Thus, an a priori weighting of characters according to their discriminatory power seems necessary, but all methods hitherto developed can be used only after the erection of class systems falling into the category of discriminant analyses. Therefore, a reduction of the morphogenetic program parameters is exemplified with respect to two propositions. First, all morphogenetic partitions must be represented and, second, the characters representing them must be

independent to a high degree. In this case, a factor analysis with maximum likelihood extraction (Lawley 1940, Dillon and Goldstein 1984) and Eqimax rotation (Harman 1976) was performed on the morphogenetic program parameters of Triassic representatives. The factor loading matrix indicates that within 11 factors explaining 75% of the total variance, few variables are loaded by a common factor, indicating the high independence of morphometric parameters. With the exception of the first factor, out of each factor one variable with highest loading was chosen. The following characters are then used in the classification algorithms:

	Factor number	Explained variance
Initial chamber distance	4	9.2%
Growth rate of chamber distance	3	8.4%
Mean chamber angle	7	5.0%
Maximum test thickness	6	2.5%
Position of maximum test thickness	5	3.6%
Scaled test width	10	3.4%
Proloculus width	2	11.2%
Minimum distance of ribs	8	5.6%
Maximum distance of ribs	11	2.5%
Mean height of median ribs	1	18.2%
Mean height of lateral ribs	1	18.2%

These are less than half of all morphogenetic parameters used in the description part.

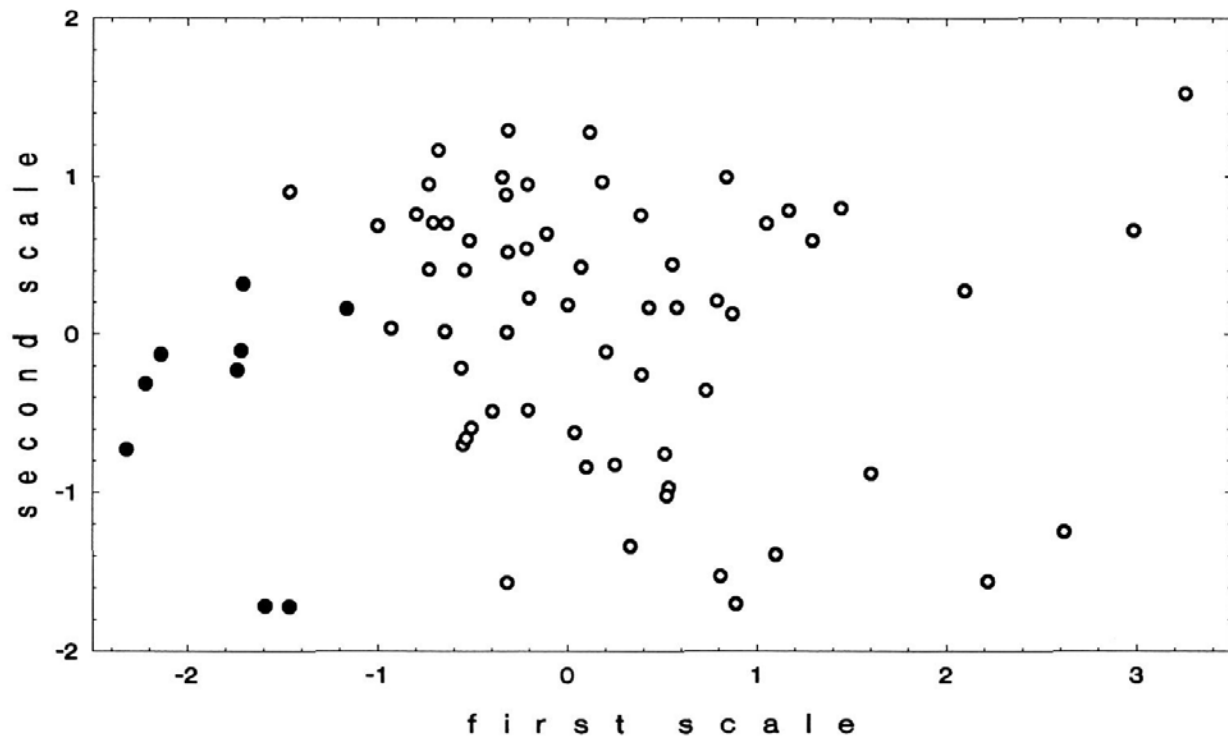
Liassic Ichthyolarias

Several classification methods are used on Liassic Ichthyolarias to demonstrate the advantages or disadvantages incorporated in the underlying theoretical models. Since lateral ribs in Liassic Ichthyolarias do not differ in height from the median ribs, only the height of median ribs is used in classification analyses, reducing the number of characters to 10.

Automatic classification of the Liassic forms must result in four homogeneous groups, as previously described (Hohenegger 1980, 1981), representing two species (*I. densicostata* and *I. sulcata*) each consisting of two generations (megalospheric and micropospheric). Standardized Euclidean distance between individuals was used as a multivariate dissimilarity measure prohibiting weighting effects through scale differences. Ward's method was chosen as an agglomerative hierarchical cluster method producing distinct classes based on a minimum variance criterion (Ward 1963; Orloci 1967). The reallocation algorithm (McQueen 1967), creating distinct, nonhierarchical and non-overlapping classes, was performed to control the results of Ward's procedure.

Ordination methods reduce the multidimensional character space to a lower dimension. Firstly, principal component analysis was performed (Hotelling 1936; Jöreskog et al. 1976; Reyment et al. 1984), which creates orthogonal axes in the direction of maximum multivariate variance. Since the first three axes explain 77% of total variance, the position of objects within this three-dimensional component space seems optimal (text-fig. 5). A transformation of character values to logarithms preceding principal component analyses leading to the extraction of growth components (Jolicoeur 1963) seems unnecessary since the morphogenetic parameters are growth independent by definition.

Secondly, the metrical form of multidimensional scaling (Torgerson 1952) based on distance matrices, often called "principal



TEXT-FIGURE 9

Ordination of slender Triassic Ichthyolarias based on weighted standardized characters by metric multidimensional scaling. Empty symbols = megalosperic generation, filled symbols = microsperic generation.

coordinate analysis" (Gower 1966; Reyment et al. 1984; Reyment 1991; Sneath and Sokal 1973), was performed. This reduction can be qualified by a stress parameter (Kruskal 1964) relating the distances between objects of the original character space to the distances of the reduced coordinate space (text-fig. 6).

Both clustering methods produce classes that do not correspond to the four biologically induced phenotypes (text-figs. 5, 6). Reducing the original character space to two dimensions, not only the configuration of individuals in principal component analysis (61% explained total variance) by their component scores but also their disposition within two orthogonal axes in multidimensional scaling (stress = 0.171), demonstrates homogeneous distributions prohibiting an objective grouping based on dispersion inhomogeneities (text-figs. 5, 6).

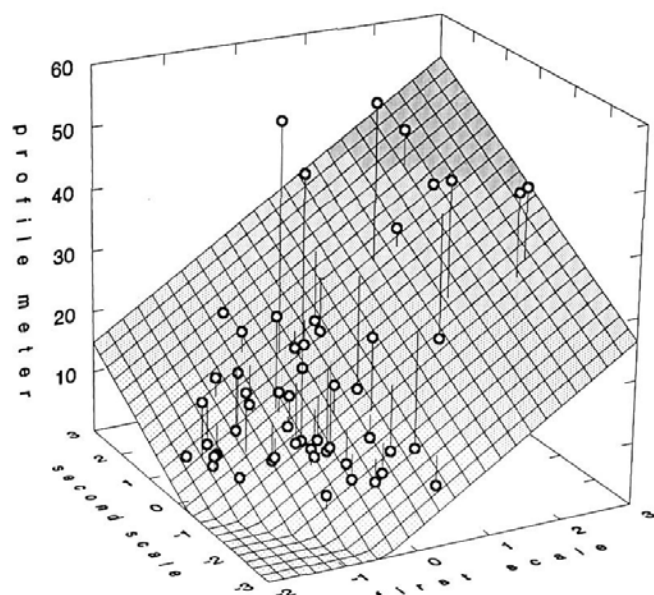
These insufficiencies are caused by simple standardization of characters, creating scale free parameters, but suppressing the additional information gained in the form of univariate character distributions (Hohenegger 1982). Therefore, an objective a priori weighting of standardized characters was performed, which is based on decomposing the characters' frequency distributions into normal components and then relating the sum of component variances to total variance (weighting factor b of Hohenegger 1986; Hohenegger and Tatzreiter 1992).

In Liassic Ichthyolarias, these weighting factors may demonstrate the discriminatory power of characters (text-fig. 7). The variable "mean height of median ribs" (weight 3.21) seems to be most essential in differentiating phenotypes, followed by the attribute "maximum distance of ribs," indicating with a weight

of 2.01 a doubled importance in comparison to normally distributed characters (weight 1.00). Further characters useful for discrimination are the "initial chamber distance" (1.87) and "proloculus width" (1.83), separating the megalosperic and microsperic generations, while the variables "growth rate of chamber distance" (1.40) and "position of maximum test thickness" (1.22) seem to be of least importance.

Both cluster analyses (Ward's method and reallocation) using weighted standardized data result in two groups, being easily interpreted as two species, *I. densicostata* and *I. sulcata*. The differentiation of generations within both species seems difficult. Ward's algorithm resulted in a more detailed class system than the reallocation algorithm. All individuals of *I. sulcata* except one are grouped correctly into their appropriate generations, characterized by proloculus size. Individuals of *I. densicostata*, on the contrary, lack this clear differentiation, which is possibly caused by their origination from two samples of different age and ecology.

This supposition is confirmed through the results of metric multidimensional scaling, where the reduction of the character space to two dimensions seems optimal (stress = 0.121). Inhomogeneities characterize the dispersion of individuals, demonstrating three homogeneous classes (text-fig. 8). The *I. sulcata* group, divided into two classes, shows a larger dispersion within the first axes than *I. densicostata*, indicating larger morphological plasticity. Within the dispersion of *I. sulcata* a further inhomogeneity separates the megalosperic and microsperic generations along the second axes. Note that the misclassification of one microsperic individual in Ward's



TEXT-FIGURE 10

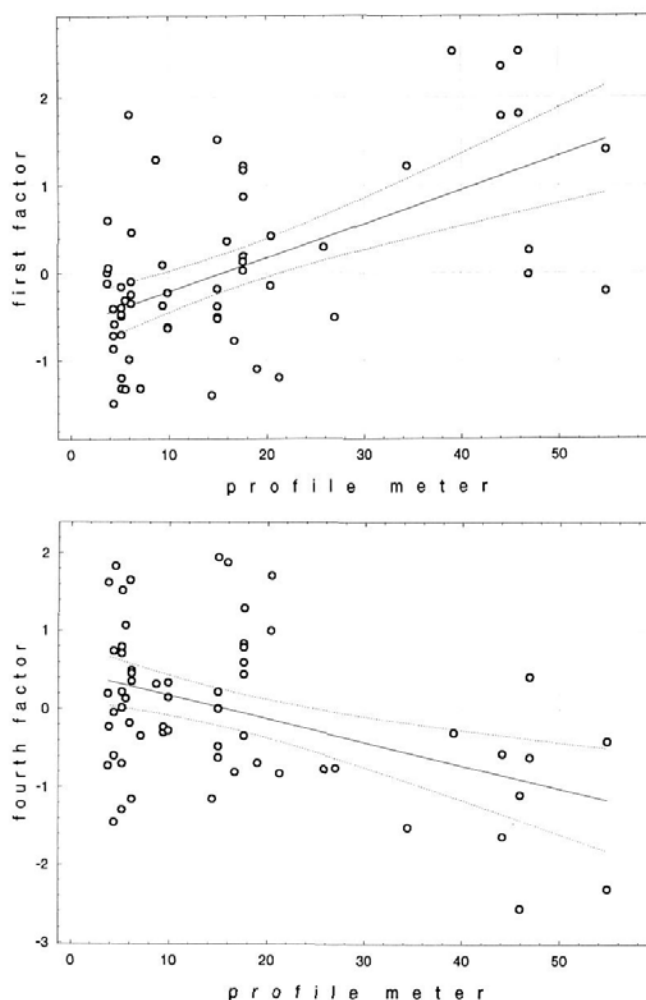
Dependency of *Ichthyolaria gerkei* from geological age in the Roßmoos-graben section using linear regression plane.

method can now be interpreted. If this outlier is grouped within the microspheric generation, its total variance will be raised to a higher degree than the variance of the megalospheric generation including the outlier. Only microspheric individuals of *I. sulcata* resemble *I. terquemi* of Middle Liassic age in rib reduction.

Homogeneity and indistinctness of *I. densicostata* as demonstrated in the results of cluster analysis are confirmed by metric multidimensional scaling. A separation of the Lower Hettangian forms from Upper Hettangian representatives, however, yields a similar gap and separation of generations compared to *I. sulcata* in the younger group (text-fig. 8). The older Hettangian forms situated in multidimensional scaling between both generations of the younger Hettangian individuals are characterized by slender tests starting with a small proloculus. A differentiation into generations is not observed. Phenotypic differences between the two samples can be interpreted as either ecologically or phylogenetically induced. An argument for the latter is the exclusive occurrence of slender forms in the lowermost Hettangian of the Alpine Lias (Restental, Lower Austria, R. Golebiowsky, pers. comm.).

Triassic *Ichthyolarias*

The results and interpretability of classes in Liassic *Ichthyolarias* confirm the utility of metric multidimensional scaling and are supported by Ward's cluster method for classifying Triassic forms. Triassic representatives demonstrate, in contrast to Liassic individuals, larger varieties of morphotypes. This large number of morphotypes and the high number of individuals require a four-dimensional coordinate space using multidimensional scaling to obtain a useful representation of connections between individuals. Such a large dimensionality prevents easy identification of inhomogeneities in dispersion. Therefore, firstly, only Ward's clustering was performed. The standardized weighting of characters including the variable "mean height of



TEXT-FIGURE 11

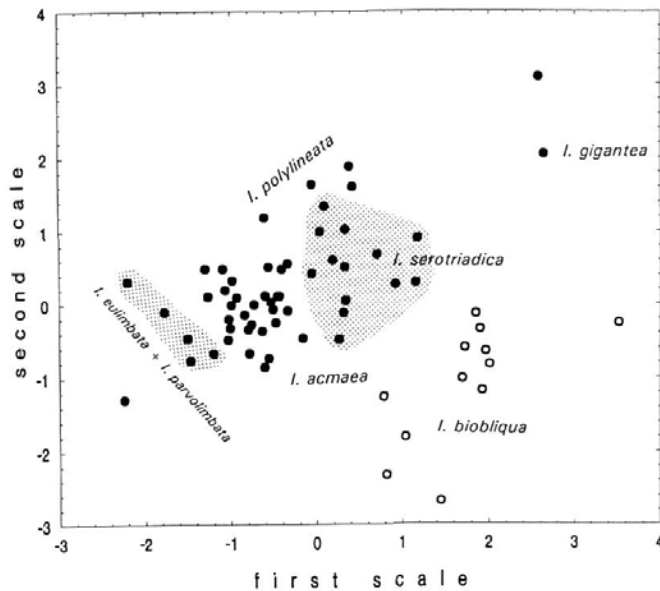
Dependency of *Ichthyolaria gerkei*, represented by factor scores, from profile meters using linear regressions.

lateral ribs" resulted in an ordering of characters quite different from that of the Liassic forms. Most important for classification is the character "scaled test width" (weight 2.94), followed by "position of maximum test thickness" (weight 2.14), "mean chamber angle" (weight 1.83) and "growth rate of chamber distance" (weight 1.61). The character "maximum test thickness" (weight 1.10) is less important in discriminating Triassic forms.

Ward's clustering algorithm resulted in a clear separation of two classes, one demonstrating much higher homogeneity than the other. In the following both classes were investigated separately using classification and ordination algorithms.

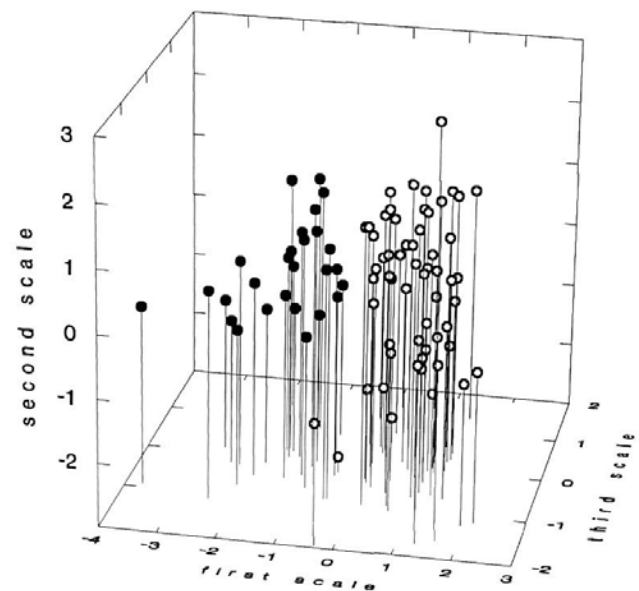
First Group

All 62 tests of this group demonstrating homogeneity in the total of morphogenetic variables are characterized by regular ribbing that is similar to the ribbing of the Liassic forms. They originate from the Rhaetian fore reef basins, with the exception of three individuals (two belonging to the Triassic/Jurassic boundary and one to the Koessen beds). Standardized weighting of characters preceding classification resulted in a high weight for



TEXT-FIGURE 12

Ordination of Triassic Ichthyolarias except slender forms based on weighted standardized characters by metric multidimensional scaling.



TEXT-FIGURE 13

Ordination of Triassic Ichthyolarias from the *sulcata* group based on weighted standardized characters by metric multidimensional scaling. Empty symbols = *Ichthyolaria gerkei*, filled symbols = *Ichthyolaria acmaea*.

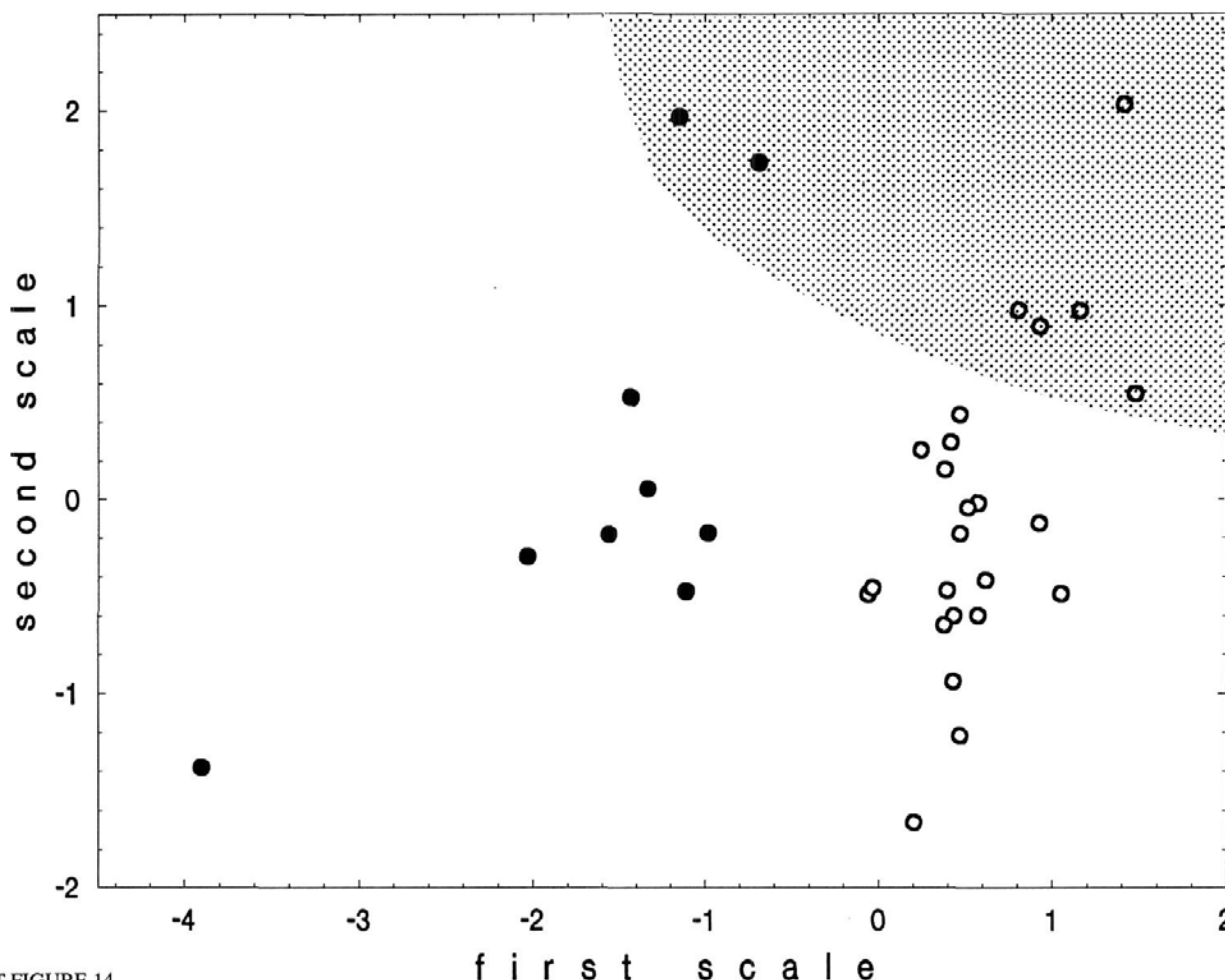
variables "position of maximum test thickness" (weight 2.04), "scaled test width" (weight 1.97) and "initial chamber distance" (weight 1.90). Characters "maximum test thickness" (weight 1.31) and "growth rate of chambers distance" (weight 1.09) seems to possess the lowest discrimination power.

Two analyses of metric multidimensional scaling based on the one hand on simple standardized data (stress = 0.221) and on the other on weighted standardized data (stress = 0.235) were performed, reducing the character space to two axes. The two analyses yielded similar results with approximately identical positions of individuals in coordinate space. The coincidence of the ordinations in combination with the high common variance of Ward's algorithms confirms the indivisibility of this group, based on the obvious morphogenetic homogeneity (text-fig. 9). An exclusion of characters determining generation differences raises the degree of homogeneity.

A time factor using profile meters of a standard section (Hohenegger and Piller 1977) was introduced to prove the dependency of morphogenetic variability on geological age. Therefore, only individuals from the Roßmoosgraben were investigated. Twenty-three additional individuals could be classified excluding both parameters characterizing rib distances. The weighting of characters is changed to a lesser degree compared to the weighting of the total group 1 ("position of maximum test thickness" = 2.15, "proloculus width" = 2.06, "initial chamber distance" = 1.84). A two-dimensional reduction of character space by metric multidimensional scaling (stress = 0.161) again yields homogeneous dispersions, but a small inhomogeneity allowing a distinction into two groups is visible. Just as in Ward's classification, a further distinction in two generations is possible, which is obliterated, however, through the large variability of that group through time.

Time dependency was proven in a three-dimensional space, where x- and y-axes are the coordinates of multidimensional scaling and the z-axis represents the profile meters of the Roßmoosgraben section. If no connection exists between principal coordinates and time, independence will result in a horizontal regression plane created by linear smoothing. Dependence of one coordinate from time is characterized by an inclined plane. In the case of Roßmoosgraben Ichthyolarias the inclination of the regression plane is directed in both coordinates (text-fig. 10), indicating a statistically significant dependence of both multidimensional scales on time. Principal component analysis was performed to strengthen the relationships between morphogenetical parameters and time. The first four principal components were extracted, explaining 77% of total variance. Thereafter, component scores were related to time using linear regression analysis. Significant regression was observed for the first and fourth components (text-fig. 11). The first component is loaded positively by the characters "scaled test width," "maximum test thickness" and "mean height of median ribs" and to a lesser degree by both variables related to rib distances. This means that during time these characters change by increasing values. The fourth component is loaded only by the parameter "position of maximum test thickness" and shows negative correlation to profile meters, indicating a dislocation of that position towards the proloculus.

Thus, a change in morphology during the Rhaetian of the Zlambach beds is confirmed for this group. Despite the erection of numerous species by Kristan-Tollmann (1964), this more or less homogeneous group must be regarded as a single discontinuously evolving species, denominated as *Ichthyolaria gerkei* (Kristan-Tollmann 1964), which is clearly separated morphologically into an older and a younger group.



TEXT-FIGURE 14

Ordination of regular ribbed Ichthyolarias from the Kössen beds based on weighted standardized characters by metric multidimensional scaling. Empty symbols = *Ichthyolaria acmaea*, filled symbols = *I. serotriadica*; dashed area indicates microspheric generations.

Second group

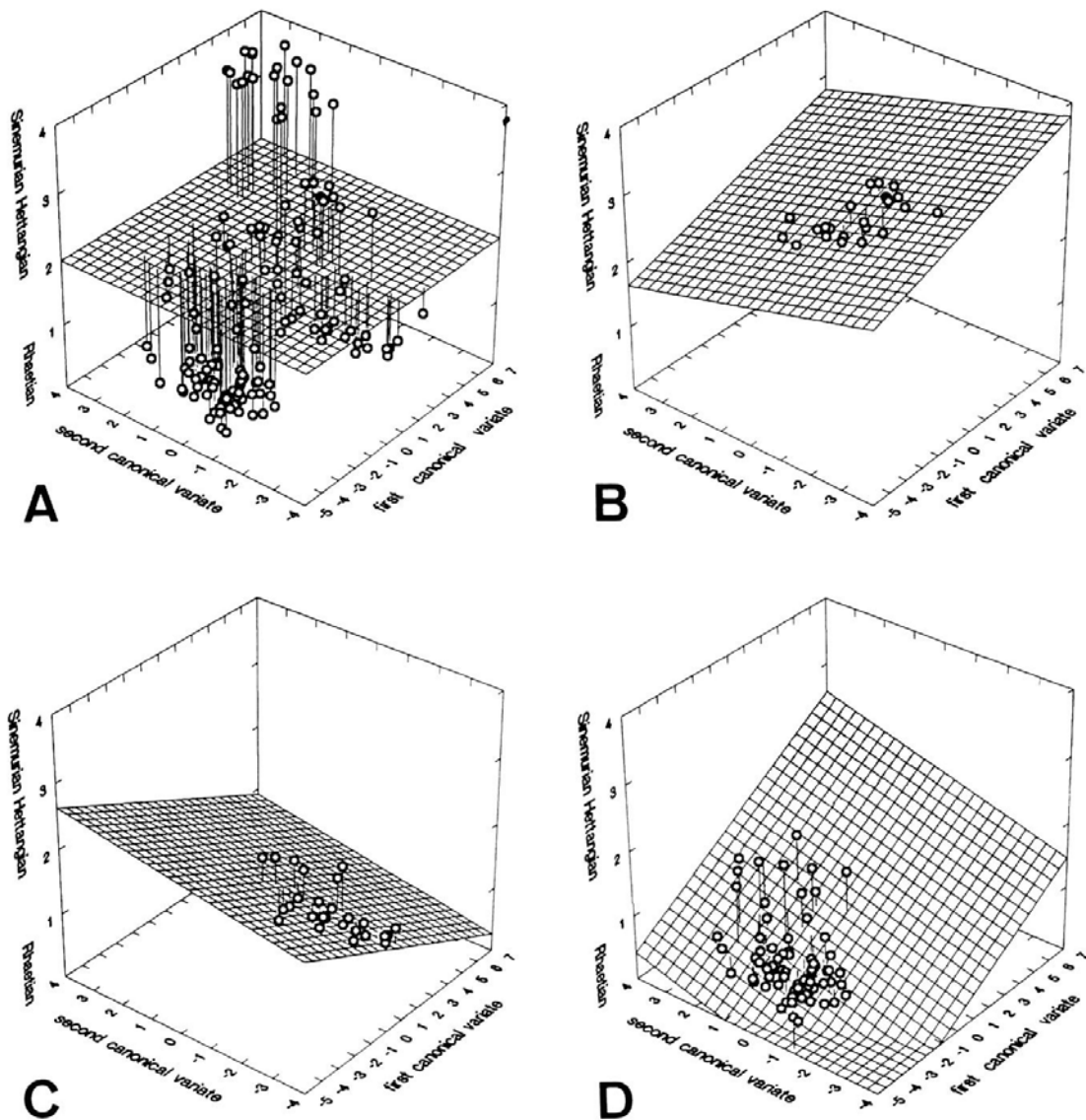
Representatives of that group showing high variability as expressed in Ward's algorithm can be found in both Zlambach and Koessen beds. Standardized weighting results in high weights for characters "mean chamber angle" (2.03), "growth rate of chamber distance" (1.91) and "scaled test width" (1.80). Three distinct classes are separated objectively by Ward's algorithm and subjectively by dispersion gaps represented in three-dimensional space resulting from multidimensional scaling (stress = 0.117). A very small class is extracted only by Ward's Clustering but incorporates typical and distinct forms.

In multidimensional scaling (text-fig. 12), one class is separated by a distinct gap from the others. Members of this group are distinguished by large and thick tests, showing irregular growth and strong diverging ribs, which are often bent during their courses. They are restricted to Zlambach beds and denominated *Ichthyolaria biobliqua* (Kristan-Tollmann 1964).

Members of the second class originating from Koessen beds are similar in regular ribbing to Liassic forms and *I. gerkei*, but demonstrate in contrast to the Triassic species thicker tests in combination with a more irregular growth. The differences from *I. gerkei* are proven by classification and ordination methods.

Weighted standardization results in high weights for the characters "position of maximum test thickness" (2.25), "scaled test width" (1.94) and "growth rate of chamber distance" (1.76). Multidimensional scaling (three dimensions, stress = 0.124) clearly separates the Koessen forms from *I. gerkei* (text-fig. 13), and even both individuals from the Triassic/Jurassic boundary, formerly placed in *I. gerkei*, are now included in the Koessen class. Therefore, this morphogenetically and phenotypically homogeneous group must be regarded as a distinct species, which is similar to *I. acmaea* as described from the Upper Triassic of Alaska by Tappan (1951).

The third class, situated in multidimensional scaling exactly between *I. biobliqua* and *I. acmaea*, can be partitioned into two groups. The larger portion incorporates tests from the Koessen beds, which are similar to *I. acmaea*. Differentiation from *I. acmaea* is again confirmed by classification and ordination methods. The characters "proloculus width" (weight = 2.11), "maximum of rib distances" (1.99), "maximum test thickness" (1.93) and "mean height of lateral ribs" (1.69) are emphasized in multivariate classification using weighted standardized variables. In multidimensional scaling, the reduction to two axes is optimal (stress = 0.125), which resulted in four homogeneous groups separated by clear gaps. Similar to the Liassic forms



TEXT-FIGURE 15

Dependencies of *sulcata* group species from geological age using discriminant analysis. A. Position of individuals by their discriminant scores in age; the horizontal plane indicates Triassic-Jurassic boundary. B. Evolution of *Ichthyolaria densicostata* as demonstrated by regression plane. C. Evolution of *Ichthyolaria acmaea* as demonstrated by regression plane. D. Evolution of *Ichthyolaria gerkei* as demonstrated by regression plane.

described above, these classes can be interpreted as two species, each incorporating megalospheric and microspheric generations (text-fig. 14). Since there are significant differences between *I. acmaea* and the contemporaneous group, the latter is regarded as a distinct species denominated as *Ichthyolaria serotriadica*, n. sp.

The smaller portion of the third class incorporates only four individuals, which are similar to *I. biobliqua*, but differ from the latter through flat tests showing a dense and fine ribbing. These forms, denominated *Fronicularia polylineata* by Kristan-Tollmann (1964), are again restricted to Zlambach beds.

Tests with strong lateral ribs showing regular growth are partitioned into two groups. One, *Ichthyolaria eulimbata*

Kristan-Tollmann (1964), is distinguished by tests of extreme flatness, strong lateral costae and low median ribs converging to the median axes. The other is characterized by thicker tests, smaller marginal costae and median ribs situated parallel to the median axis. This species, denominated as *Ichthyolaria parvolimbata*, n. sp., can be found in both Koessen and Zlambach beds.

Two outliers are detected using multidimensional scaling ordination (text-fig. 12), being quite different from all species described. A taxonomic approach seems unnecessary for one of these, since it is represented by a single specimen. The other individual, distinguished by the largest and thickest test within all *Ichthyolaria*s hitherto described, originates from the lowermost Alpine Lias. It is found together with other specimens, but

TABLE 1

Morphologic characters (means and standard deviations; $n = 23$, except as specified) for *I. sulcata* and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. acmaea</i>	<i>I. gerkei</i>	<i>I. densicostata</i>
Chamber distance growth	1.18	0.050	>	>	=
Angle growth	0.93	0.048	=	=	=
Angle limit	27.1	14.99	=	=	=
Angle mean	30.7	2.86	>	>	=
Thickness maximum	120	23.0	=	>	>
Position thickness	444	96.9	=	<	=
Volume growth maximum	187	89.8	=	=	=
Volume growth	1.79	0.353	>	>	=
Scaled width	91	57.4	>	>	>
Rib distance minimum	27.1	5.3	>	>	>
Rib distance maximum	48.0	10.0	>	>	>
Rib vertex increase	1.5	15.8	=	=	=
Rib vertex difference	—	—			
Rib vertex vergence	-1.1	18.6	=	<	=
Rib width minimum	411	85	=	<	=
Position rib width	543	176	=	=	=
Difference 300µm rib width	230	332	=	=	=
Rib height median	19.5	4.17	>	>	>
Rib height lateral	14.6	3.21	>	>	>
Megalospheric ($n = 17$)					
Chamber distance initial	35.0	8.76	=	=	=
Angle initial	35.8	4.84	=	=	=
Volume initial	7.23	4.01	=	=	=
Position volume	6.5	1.7	=	<	=
Proloculus width	102	17.0	>	>	>
Microspheric ($n = 6$)					
Chamber distance initial	15.6	9.24	<	=	=
Angle initial	46.7	13.44	=	=	=
Volume initial	0.69	1.11	=	=	=
Position volume	11.2	2.9	=	<	=
Proloculus width	35	19.9	=	=	=

they could not be measured in all characters necessary for the detection of morphogenetic program parameters. Thus, the denomination of this group as *Ichthyolaria gigantea*, n. sp., seems to be justified.

TAXONOMY

All morphogenetic parameters described in the chapter on morphogenetic programs are included in species description and differentiation. Parametric statistics can be used, since in all species the characters are metric and normally distributed except one ("difference in rib vergence"). Differences in single characters between species and generations were tested using variance analyses in combination with the Student-Newman-Keuls procedure, which distinguishes the differences between pairs of groups. In addition to verbal description and differential diagnoses as a help for the identification of new individuals without using extensive measurements, a table is presented for each species containing character means and standard deviations in combination with statistically significant differences from related species. All scale units except derived characters and angles are expressed in micrometers. In comparison of species to related forms, the symbols must be interpreted as:

> ... significantly higher (larger) than ...
 < ... significantly lower (smaller) than ...
 = ... no significant differences at the 5% level.

Classification analyses resulted in a partition of Triassic and Liassic *Ichthyolaria* species into three groups. The first species group is characterized by regular ribbing and test growth. According to Barnard (1957) it should be called the *sulcata* group. Its temporal distribution is from the Norian to lowest Upper Lias. The second group is distinguished by irregular ribbing and test formation, and the third can be characterized by high marginal ribs. The last species groups of *Ichthyolarias* are restricted to the Upper Triassic.

Sulcata group

Ichthyolaria sulcata (Bornemann)

Plate 1, figures 1-5

- Fronicularia sulcata*, m. – BORNEMANN 1854, p. 37, pl. 3, figs. 22a-c.
Fronicularia dubia, m. – BORNEMANN 1854, p. 37, pl. 3, figs. 23a-c.
Fronicularia pulchra Terquem. – TERQUEM 1858, p. 32, pl. 1, figs. 10a-c. – TERQUEM 1866, p. 481, pl. 19, fig. 16. – BURBACH 1886, p. 51, pl. 2, figs. 45-46.
Fronicularia Baueri, n. sp. – BURBACH 1886, p. 52, pl. 2, figs. 48-52.
Fronicularia sulcata Bornemann – FRANKE 1936, p. 71, pl. 7, fig. 8. – BARTENSTEIN and BRAND 1937, p. 158, pl. 4, fig. 50. – MACFADYEN 1941, p. 58, fig. 4, pl. 4, figs. 60a-b. – BARNARD 1957, p. 174, pl. 1, forms E, F, G, H; pl. 2, figs. 8-14, 22. – RUGET 1967, p. 25, pl. 2, figs. 25-29; pl. 3, figs. 1-16.
Fronicularia interrupta-costata, n. sp. – FRANKE 1936, p. 72, fig. 1.
Fronicularia dubia Bornemann – FRANKE 1936, p. 72, pl. 7, fig. 6. – BARTENSTEIN and BRAND 1937, p. 158, pl. 3, fig. 41; pl. 5, figs. 41a-b; pl. 6, fig. 25. – RUGET 1967, p. 27, pl. 4, figs. 10-11, 13-18, 20-25.
Fronicularia bicostata d'Orbigny – BARTENSTEIN and BRAND 1937, p. 158, pl. 2B, fig. 23; pl. 3, fig. 35. – RUGET 1967, p. 23, pl. 1, figs. 1-32.
Fronicularia baueri Burbach – BARTENSTEIN and BRAND 1937, p. 158, pl. 3, fig. 36.
[non] *Spandelina bicostata* (d'Orbigny) subsp. *sulcata* (Bornemann) – NORVANG 1957, p. 341, figs. 56-59.
Spandelina bicostata (d'Orbigny) subsp. *dubia* (Bornemann) – NORVANG 1957, p. 344, fig. 65.
Spandelina bicostata (d'Orbigny) subsp. *baueri* (Burbach) – NORVANG 1957, p. 346, fig. 66.
Spandelina bicostata (d'Orbigny) subsp. *bicostata* (d'Orbigny) – NORVANG 1957, p. 347, figs. 62-63.
Spandelina bicostata (d'Orbigny) subsp. *terquemi* (d'Orbigny) – NORVANG 1957, p. 349, fig. 69.
Fronicularia quadricosta Terquem – BIZON 1960, p. 14, pl. 3, fig. 4, pl. 4, fig. 13.
Ichthyolaria dubia (Bornemann) – SELLIER DE CIVRIEUX and DESSAUVAGIE 1965, p. 72, pl. 22, figs. 1a-d, 2a-f. – NORLING 1966, p. 13, pl. 1, figs. 4-6.
Ichthyolaria baueri (Burbach) – NORLING 1966, p. 14, pl. 2, figs. 1-2.
Ichthyolaria sulcata (Bornemann) – NORLING 1966, p. 15, pl. 2, figs. 3-4. – RUGET 1985, pl. 14, figs. 2-11; pl. 15, figs. 7, 10, 11; pl. 16, figs. 2-13; pl. 17, figs. 1-11; pl. 18, figs. 2-7; pl. 27, fig. 11; pl. 28, figs. 1-3, 5-11, 19; pl. 29, figs. 2, 9; pl. 39, fig. 5; pl. 47, figs. 3, 5, 6, 8, 9, 13-15.
Fronicularia laneuevillensis, n. sp. – RUGET 1967, p. 25, pl. 2, figs. 7-24.
Fronicularia rugosa Crick et Sherborn – RUGET 1967, p. 27, pl. 3, figs. 17-20.
Fronicularia sp. nov. (ex gr. *sulcata*) – RUGET 1967, p. 27, pl. 4, figs. 1-9, 19, 21, 26.
Ichthyolaria sulcata (Bornemann) – HOHENEGGER 1981, p. 99, pls. 1-3, figs. 4-6, 9-10; pl. 4, figs. 4-6, 9-10; pl. 5, figs. 4-10; pl. 6, figs. 1-2. – RIEGRAF 1985, p. 149, pl. 8, fig. 27. – HOHENEGGER 1987, pl. 1, fig. 1; pl. 3, figs. 1, 3, 4, 7, 8.
Ichthyolaria bicostata (d'Orbigny) – RUGET 1985, pl. 15, figs. 1-6, 8-14; pl. 27, figs. 1, 5, 9; pl. 28, figs. 4, 15; pl. 29, figs. 1, 6-8, 14; pl. 48, figs. 6-13.

Ichthyolaria bicostata terquemi (d'Orbigny) – RUGET 1985, pl. 27, fig. 6; pl. 29, fig. 12.

Fronicularia terquemi subsp. B – COPESTAKE and JOHNSON 1989, p. 174, pl. 6.2.3, figs. 4-5.

Fronicularia terquemi sulcata Bornemann – COPESTAKE and JOHNSON 1989, pl. 6.2.3, figs. 8-15.

Material examined: Twenty-three specimens from Betzgenreith near Göppingen, Schwarzer Jura α_3 .

Distribution: Lias, Sinemurian to lower Toarcian.

Description: This species is distinguished by broad, large and thick tests demonstrating regular growth and showing obtuse chamber angles. Ornamentation is characterized by strong, high and coarse ribs, running nearly parallel to the median axes. A well-developed keel surrounds the tests laterally except in the apertural region. Generation differences are additionally expressed in microspheric generations by lower but coarser ribs, leading to the succeeding species *Ichthyolaria terquemi* (d'Orbigny) of Middle Liassic age. Measurements are presented in table 1.

Comparison: Closest connections exist to the temporal precursor *I. densicostata*, which differs in flat tests covered by low and dense ribs. Both Triassic forms, *I. gerkei* and *I. acmaea*, differ from *I. sulcata* in lower heights and lesser distances of ribs. Whereas *I. gerkei* is additionally differentiated by slender tests and the position of maximum thickness near the aperture, *I. acmaea* is distinguished by an irregular mode of test growth. In all the other species keels are not as well developed as in *I. sulcata*. See table 1.

Ichthyolaria densicostata Hohenegger

Plate 1, figures 6-10

Fronicularia sulcata plexus – BARNARD 1957, pl. 1, forms A, A', B, C, D, C', D; pl. 2, figs. 1-7.

Ichthyolaria densicostata, n. sp. – HOHENEGGER 1981, figs. 5A, 6A; pl. 1, figs. 1-8. – HOHENEGGER 1987, pl. 1, fig. 3; pl. 3, fig. 2.

Ichthyolaria bicostata (d'Orbigny) – RUGET 1985, pl. 3, figs. 1, 5, 12, 13; pl. 4, figs. 3, 5-7, 9.

Ichthyolaria sulcata (Bornemann) – RUGET 1985, pl. 3, figs. 2-4, 6-8, 11; pl. 4, figs. 10.

Ichthyolaria sulcata (Bornemann), forme *muelensis* (Ruguet et Sigal) – RUGET 1985, pl. 3, figs. 9, 10; pl. 4, fig. 11; pl. 47, fig. 1.

Fronicularia terquemi subsp. A Barnard – COPESTAKE and JOHNSON 1989, pl. 6.2.3, fig. 3.

Fronicularia terquemi sulcata Bornemann – COPESTAKE and JOHNSON 1989, pl. 6.2.3, fig. 6.

Material examined: Fifteen specimens from Hägnach, Schwarzer Jura α_1 , *planorbis* zone; 9 specimens from Xeulley, *angulata* zone.

Distribution: Lias, Hettangian.

Description: Tests of this species are flat, showing regular growth, and are covered by narrow and dense ribs, running more or less parallel to the median axis. Chamber angles are as obtuse as in *I. sulcata*, and the keel is less developed. Differences in generations are expressed only in proloculus size. The stratigraphically older forms are distinguished by slender tests, starting with small megalospheric proloculi, which are a little bit larger than proloculi of Upper Hettangian microspheres. Measurements are presented in table 2.

TABLE 2

Morphologic characters (means and standard deviations; n = 24, except as specified) for *I. densicostata* and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. acmaea</i>	<i>I. gerkei</i>	<i>I. sulcata</i>
Chamber distance growth	1.18	0.046	>	>	=
Angle growth	0.93	0.116	>	>	=
Angle limit	37.8	29.98	>	>	=
Angle mean	29.0	4.20	=	>	=
Thickness maximum	96	11.5	<	=	<
Position thickness	473	170.8	=	<	=
Volume growth maximum	102	55.5	=	=	=
Volume growth	1.81	0.369	>	>	=
Scaled width	-4	62.3	<	>	<
Rib distance minimum	16.4	2.6	<	=	<
Rib distance maximum	28.3	4.6	<	<	<
Rib vertex increase	3.2	12.1	=	=	=
Rib vertex difference	—	—	—	—	—
Rib vertex vergence	-6.8	9.8	=	<	=
Rib width minimum	464	130	>	=	=
Position rib width	454	147	=	=	=
Difference 300µm rib width	223	263	=	=	=
Rib height median	8.2	1.04	=	=	<
Rib height lateral	6.0	0.79	=	=	<
Megalospheric (n = 8)					
Chamber distance initial	29.6	9.24	=	=	=
Angle initial	34.7	7.94	=	=	=
Volume initial	5.79	4.95	=	=	=
Position volume	5.2	2.4	=	<	=
Proloculus width	87	28.0	=	=	<
Microspheric (n = 3)					
Chamber distance initial	14.5	5.13	<	=	=
Angle initial	40.7	16.72	=	=	=
Volume initial	0.17	0.02	=	=	=
Position volume	9.7	2.2	=	<	=
Proloculus width	25	3.5	=	=	=

Comparison: Both Triassic forms of the *sulcata* group show coarser and higher ribs in combination with thicker tests. *I. gerkei* differs additionally through the position of maximum test thickness lying near the aperture, and the divergence of ribs caused by test form. *I. acmaea* is distinguished by much broader tests in combination with an irregular test growth. See table 2.

Ichthyolaria gerkei (Kristan-Tollmann)

Plate 2, figures 1-16

Fronicularia gerkei, n. sp. – KRISTAN-TOLLMANN 1964, p. 144, pl. 30, figs. 19-21.

Fronicularia frankei Brand – KRISTAN-TOLLMANN 1964, p. 145, pl. 30, figs. 22-23.

Fronicularia bicostata d'Orbigny subsp. *intercosta* n. ssp. – KRISTAN-TOLLMANN 1964, p. 151, pl. 33, figs. 12-13.

Material examined: Five specimens from Steinbergkogel near Hallstatt, *stuerzenbaumi* zone; 74 specimens from Roßmoosgraben near Bad Goisern, Rhaetian; 1 specimen from Weißloferbach near Koessen, *marshi* zone.

TABLE 3

Morphologic characters (means and standard deviations; $n = 80$, except as specified) for *I. gerkei* and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. acmaea</i>	<i>I. densicostata</i>	<i>I. sulcata</i>
Chamber distance growth	1.15	0.031	>	<	<
Angle growth	0.88	0.072	=	<	=
Angle limit	22.6	13.85	=	<	=
Angle mean	26.4	2.59	<	<	<
Thickness maximum	103	16.3	<	=	<
Position thickness	736	218.7	>	>	>
Volume growth maximum	188	144.9	=	=	=
Volume growth	1.59	0.228	=	<	<
Scaled width	-71	30.7	<	<	<
Rib distance minimum	18.0	5.9	=	=	<
Rib distance maximum	35.7	9.8	=	>	<
Rib vertex increase	7.8	21.6	=	=	=
Rib vertex difference	—	—			
Rib vertex vergence	13.5	18.9	>	>	>
Rib width minimum	473	128	>	=	>
Position rib width	567	178	=	=	=
Difference 300µm rib width	220	220	=	=	=
Rib height median	8.0	3.41	=	=	<
Rib height lateral	5.8	2.54	=	=	<
Megalospheric ($n = 71$)					
Chamber distance initial	31.3	6.07	=	=	=
Angle initial	35.4	8.54	=	=	=
Volume initial	3.50	1.94	=	=	=
Position volume	10.6	2.52	>	>	>
Proloculus width	74	14.4	=	=	<
Microspheric ($n = 9$)					
Chamber distance initial	14.7	2.17	<	=	=
Angle initial	49.1	2.16	=	=	=
Volume initial	0.03	0.01	=	=	=
Position volume	16.5	3.28	>	>	>
Proloculus width	17	1.16	=	=	=

Distribution: Rhaetian.

Description: This species shows slender tests with regular growth but slowly increasing thickness. Acute chamber angles are characteristic. The tests are covered by regular, diverging ribs of medium height and medium distances. A narrow keel is developed. Similar to *I. sulcata*, generation differences are expressed by the reduction of ribs especially in microspheric generations, often leading to smooth tests. Transformation during geological time is detectable by the strengthening of ribs in combination with the appearance of larger tests in the Upper Rhaetian. Measurements are presented in table 3.

Comparison: Tests of the contemporaneous species *I. acmaea*, possessing more obtuse chamber angles, differ in being broader and thicker than *I. gerkei*, additionally showing a slightly irregular test growth and rapid increase in thickness. The ribs of *I. acmaea* do not diverge to the same degree as in *I. gerkei*. Differences of the latter species to Liassic forms can be read in the appropriate descriptions. See table 3.

TABLE 4

Morphologic characters (means and standard deviations; $n = 27$, except as specified) for *I. acmaea* and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. gerkei</i>	<i>I. densicostata</i>	<i>I. sulcata</i>
Chamber distance growth	1.13	0.039	<	<	<
Angle growth	0.87	0.062	=	<	=
Angle limit	23.6	13.76	=	<	=
Angle mean	28.0	2.27	>	=	<
Thickness maximum	113	16.3	>	>	=
Position thickness	403	178.9	<	=	=
Volume growth maximum	149	97.2	=	=	=
Volume growth	1.52	0.145	=	<	<
Scaled width	33	48.2	>	>	<
Rib distance minimum	20.6	4.1	=	>	<
Rib distance maximum	36.5	5.3	=	>	<
Rib vertex increase	9.6	17.1	=	=	=
Rib vertex difference	—	—			
Rib vertex vergence	1.5	15.0	<	=	=
Rib width minimum	394	103	<	<	=
Position rib width	513	179	=	=	=
Difference 300µm rib width	212	153	=	=	=
Rib height median	8.1	1.37	=	=	<
Rib height lateral	6.0	1.12	=	=	<
Megalospheric ($n = 22$)					
Chamber distance initial	31.4	5.21	=	=	=
Angle initial	36.6	6.52	=	=	=
Volume initial	4.72	3.47	=	=	=
Position volume	7.2	2.4	<	=	=
Proloculus width	78	22.8	=	=	<
Microspheric ($n = 5$)					
Chamber distance initial	21.9	4.73	>	>	>
Angle initial	45.9	4.18	=	=	=
Volume initial	0.50	0.05	=	=	=
Position volume	8.9	2.3	<	=	=
Proloculus width	35	11.9	=	=	=

Ichthyolaria acmaea (Tappan)

Plate 1, figures 11-14

Fronicularia acmaea Tappan, n. sp. — TAPPAN 1951, p. 13, pl. 4, figs. 1-3.

Ichthyolaria squamosa (Terquem and Berthelin) — STRONG 1984, p. 22, pl. 3, figs. 56-57; pl. 8, fig. 185; pl. 9, figs. 186-187.

Ichthyolaria sulcata Bornemann — STRONG 1984, p. 23, pl. 3, figs. 58-62; pl. 9, figs. 188-197.

Ichthyolaria terquemi d'Orbigny — STRONG 1984, p. 23, pl. 3, figs. 63-64; pl. 9, fig. 198.

Material examined: Twenty-three specimens from Weißloferbach near Koessen, *marshi* zone; 4 specimens from Vorderer Ampelsbach, Triassic-Liassic boundary section.

Distribution: Norian to ?Lowermost Lias (Hettangian).

Description: Broad tests are constructed by a rectilinear series of inverse chevron-shaped chambers. Their growth is slightly irregular. Maximum test width and thickness are reached by a rapid increase. Well-developed ribs of medium height and distances, initiated near the median axis, diverge in the initial part of the tests, later running parallel to this axis. A narrow keel

is developed. In addition to the smaller proloculus sizes, microspheric generations differ from the megalospheric in the development of slender tests, which are covered by coarser ribs. The lowermost Jurassic forms, represented only by megalospheric tests, differ from the Triassic antecedents in the development of large tests, showing more regular ribbing. Measurements are presented in table 4.

Comparison: Within the *sulcata* group this species is characterized by irregularities in test growth rate. *I. gerkei* differs in possessing slender tests, acute chamber angles and diverging ribs. The Liassic *I. densicostata* is distinguished by flat tests covered with narrow and dense ribs. *I. sulcata*, on the contrary, shows much broader tests with obtuse chamber angles and the development of high and coarse ribs. See table 4.

***Ichthyolaria gigantea* Hohenegger, n. sp.**

Plate 1, figure 15

Material examined: Three specimens from Kendelbachgraben, Triassic-Liassic boundary section.

Distribution: Lowermost Lias, Hettangian.

Type locality: Kendelbachgraben, Salzburg, Austria.

Type sample: 85/5/16 (collection of R. Golebiowski).

Type level: Boundary marls, lowermost Lias, Hettangian.

Type specimens: Holotype, plate 1, figure 15, P4301/208, Institut für Paläontologie, Universität Wien.

Description: This species is distinguished by very large, broad and thick tests, built by a rectilinear series of inverse chevron-shaped chambers. Their growth is regular, and chamber angles are obtuse to a high degree. Strong ribs running more or less parallel to the median axis cover the test surfaces. A well-developed keel surrounds the tests except in the apertural region. All specimens investigated seem to belong to the megalospheric generation, which has developed a large proloculus. Measurements are presented in table 5.

Comparison: This species is the largest within the *Ichthyolarias*, differing from all Triassic and Liassic species in test dimensions. The most similar is *I. sulcata*, which differs in addition to size in coarser and higher ribs. See table 5.

***Ichthyolarias* with high marginal ribs**

***Ichthyolaria serotriadica* Hohenegger, n. sp.**

Plate 3, figures 8-10

Material examined: Nine specimens from Weißloferbach near Koessen, upper *marshi* zone.

Distribution: Upper Rhaetian.

Type locality: Weißloferbach near Koessen, Tyrol, Austria.

Type sample: D9 (Urlichs 1972).

Type level: Koessen beds, Upper Rhaetian, *marshi* zone.

Type specimens: Holotype, plate 3, figure 9, P4301/173; illustrated paratypes, plate 3, figure 8, P4301/167, and figure 10, P4301/171; Institut für Paläontologie, Universität Wien.

TABLE 5

Morphologic characters for the holotype of *I. gigantea*, n. sp., and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. Significant differences means out of $\mu \pm 2\sigma$. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Value	<i>I. acmaea</i>	<i>I. gerkei</i>	<i>I. densicostata</i>	<i>I. sulcata</i>
Chamber distance growth	1.14	=	=	=	=
Angle growth	1.10	>	>	=	>
Angle limit	—				
Angle mean	35.9	>	>	=	=
Thickness maximum	230	>	>	>	>
Position thickness	882	>	=	>	>
Volume growth maximum	1448	>	>	>	>
Volume growth	1.31	=	=	=	=
Scaled width	212	>	>	>	>
Rib distance minimum	18.6	=	=	=	=
Rib distance maximum	47.6	=	=	>	=
Rib vertex increase	-7.0	=	=	=	=
Rib vertex difference	—				
Rib vertex vergence	-20.1	=	=	=	=
Rib width minimum	281	=	=	=	=
Position rib width	525	=	=	=	=
Difference 300µm rib width	29	=	=	=	=
Rib height median	14.5	>	>	>	=
Rib height lateral	10.9	>	>	>	=
Megalospheric					
Chamber distance initial	56.2	>	>	>	>
Angle initial	32.3	=	=	=	=
Volume initial	36.25	>	>	>	>
Position volume	9.8	=	=	=	=
Proloculus width	162	>	>	>	>

Description: This species is distinguished by thick tests, built by a series of inverse chevron-shaped chambers with obtuse chamber angles. The ribs are of medium height and distance in comparison to other species. Lateral ribs are pronounced. Since all ribs begin close to the median axis, these marginal ribs start at the beginning of the proloculus, tracing the contour of tests to a lesser degree. Beyond differences in proloculus sizes both generations are separated by the development of low median ribs in microspheres. Measurements are presented in table 6.

Comparison: Differences from the similar species *I. acmaea* are expressed by thicker tests, more obtuse chamber angles and the development of higher marginal ribs in *I. serotriadica*. *I. polylineata* is distinct from the new species in constructing flat tests and in the lack of pronounced lateral ribs. *I. parvolimbata* shows more regular test growth and again flat tests in comparison to *I. serotriadica*. See table 6.

***Ichthyolaria parvolimbata* Hohenegger, n. sp.**

Plate 1, figures 4, 5

Material examined: Two specimens from Roßmoosgraben, Rhaetian; 2 specimens from Weißloferbach, Upper Rhaetian, *marshi* zone.

Distribution: Rhaetian.

TABLE 6

Morphologic characters (means and standard deviations; $n = 9$, except as specified) for *I. serotriadica*, n. sp., and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. acmaea</i>	<i>I. polylineata</i>	<i>I. parvolimbata</i>
Chamber distance growth	1.15	0.035	=	=	=
Angle growth	0.89	0.036	=	=	=
Angle limit	27.9	2.50	=	<	=
Angle mean	37.4	3.34	>	=	>
Thickness maximum	142	16.5	>	>	>
Position thickness	393	147.7	=	=	=
Volume growth maximum	253	10.7	=	=	=
Volume growth	1.50	0.165	=	=	=
Scaled width	75	53.7	=	=	=
Rib distance minimum	1.5	0.8	<	=	=
Rib distance maximum	37.2	10.9	=	=	=
Rib vertex increase	-8.0	26.0	=	=	=
Rib vertex difference	2.7	8.8	=	=	=
Rib vertex vergence	17.0	15.8	>	>	=
Rib width minimum	302	76	<	<	=
Position rib width	501	146	=	=	=
Difference 300µm rib width	260	121	=	=	=
Rib height median	6.4	2.36	=	=	=
Rib height lateral	8.1	4.53	>	=	>
Megalospheric ($n = 7$)					
Chamber distance initial	35.9	7.36	=	<	=
Angle initial	45.2	9.36	>	>	=
Volume initial	8.31	2.13	>	=	>
Position volume	8.0	2.3	=	=	=
Proloculus width	100	10.5	>	=	>
Microspheric ($n = 2$)					
Chamber distance initial	13.6	4.93	<	=	=
Angle initial	55.4	13.63	=	=	=
Volume initial	0.39	0.11	=	=	=
Position volume	12.2	0.9	=	=	=
Proloculus width	32	5.7	=	=	=

Type locality: Roßmoosgraben near Bad Goisern, Upper Austria.

Type sample: RM 76/97 (Hohenegger and Piller 1977).

Type level: Zlambach beds, Upper Rhaetian, *marshi* zone.

Type specimens: Holotype, plate 4, figure 4, P4301/53; paratype, plate 4, figure 5, P4301/122; Institut für Paläontologie, Universität Wien.

Description: Tests of this species, constructed by a series of inverse chevron-shaped chambers, are distinguished by an extreme regular growth. All ribs are low in comparison to other *Ichthyolarias*; both marginal costae, beginning at the proloculus, are more pronounced than the median ribs running more or less parallel to the central axis. These median ribs often disappear, leading to smooth parts in the center of tests. Measurements are presented in table 7.

Comparison: *I. eulimbata*, in contrast to the new form, possesses extremely flat tests, more pronounced marginal costae

TABLE 7

Morphologic characters (means and standard deviations; $n = 4$) for *I. parvolimbata*, n. sp., and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. eulimbata</i>	<i>I. serotriadica</i>
Angle growth	0.79	0.057	=	=
Angle limit	22.3	1.34	=	=
Angle mean	29.6	3.53	=	<
Thickness maximum	91	5.9	=	<
Position thickness	345	94.7	=	=
Volume growth maximum	121	38.4	=	=
Volume growth	1.72	0.130	=	=
Scaled width	92	40.5	=	=
Rib distance minimum	2.4	1.35	=	=
Rib distance maximum	26.8	6.38	=	=
Rib vertex increase	-3.3	26.0	=	=
Rib vertex difference	—	—	=	=
Rib vertex vergence	10.1	3.7	>	=
Rib width minimum	334	191	=	=
Position rib width	501	99	=	=
Difference 300µm rib width	342	65	=	=
Rib height median	3.6	1.59	=	=
Rib height lateral	4.8	1.55	<	<
Megalospheric				
Chamber distance initial	31.8	8.71	=	=
Angle initial	46.0	12.00	=	=
Volume initial	4.65	2.58	<	<
Position volume	6.4	0.5	=	=
Proloculus width	85	24.8	<	<

and strong bending of median ribs. *I. serotriadica* is much thicker and distinguished by a more irregular ribbing and test growth. See table 7.

Ichthyolaria eulimbata (Kristan-Tollmann)

Plate 3, figures 1-3

Fronicularia eulimbata, n. sp. — KRISTAN-TOLLMANN 1964, p. 149, pl. 32, figs. 13-14.

Material examined: Four specimens from Roßmoosgraben, Zlambach beds, Rhaetian.

Distribution: Rhaetian.

Description: Flat tests with two thick and high marginal ribs combined with a strong peripheral keel characterize this species. Median ribs are poorly developed, with an extreme bend towards the median axis. Measurements are presented in table 8.

Comparison: The similar species *I. parvolimbata* is characterized by thicker tests, low marginal costae and median ribs parallel to the central axis. See table 8.

Ichthyolarias with irregular test growth and rib courses

Ichthyolaria polylineata (Kristan-Tollmann)

Plate 3, figures 6, 7

TABLE 8

Morphologic characters (means and standard deviations; $n = 4$) for *I. eulimbata* and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. parvolimbata</i>
Chamber distance growth	1.14	0.027	=
Angle growth	0.77	0.078	=
Angle limit	23.3	1.60	=
Angle mean	29.5	2.77	=
Thickness maximum	65	16.4	=
Position thickness	276	45.9	=
Volume growth maximum	78	25.4	=
Volume growth	1.79	0.204	=
Scaled width	83	60.3	=
Rib distance minimum	1.9	0.8	=
Rib distance maximum	21.1	10.5	=
Rib vertex increase	8.1	31.8	=
Rib vertex difference	—	—	—
Rib vertex vergence	-26.6	32.2	<
Rib width minimum	508	102	=
Position rib width	397	173	=
Difference 300µm rib width	772	686	=
Rib height median	6.0	0.32	=
Rib height lateral	11.8	4.98	>
Megalospheric			
Chamber distance initial	33.6	1.84	=
Angle initial	39.7	2.09	=
Volume initial	8.30	4.04	>
Position volume	5.7	1.0	=
Proloculus width	103	19.2	>

Fronidularia polylineata, n. sp. — KRISTAN-TOLLMANN 1964, p. 152, pl. 33, figs. 14-15.

Material examined: Four specimens from Roßmoosgraben, Zlambach beds, Rhaetian.

Distribution: Rhaetian.

Description: In contrast to the *sulcata* group, this species is distinguished by flat tests with an irregular growth pattern. Chamber angles are obtuse; ornamentation is distinguished by narrow, dense ribs showing numerous bendings within their courses and a weak keel. Measurements are presented in table 9.

Comparison: Distinctness from *I. acmaea* is caused by obtuse chamber angles and dense ribbing. Closest connections are to *I. biobliqua*, which is distinguished by larger and thicker tests, showing quite stronger and coarser ribs. See table 9.

Ichthyolaria biobliqua (Kristan-Tollmann)

Plate 3, figures 11-14

Fronidularia biobliqua, n. sp. — KRISTAN-TOLLMANN 1964, p. 153, pl. 34, fig. 1.

Material examined: Sixteen specimens from Roßmoosgraben, Zlambach beds, Rhaetian.

Distribution: Rhaetian.

Description: Large and thick tests caused by an irregular growth characterize this species. Chamber angles are obtuse in compar-

TABLE 9

Morphologic characters (means and standard deviations; $n = 4$) for *I. polylineata* and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. biobliqua</i>	<i>I. serotriadica</i>	<i>I. acmaea</i>
Chamber distance growth	1.07	0.024	<	=	=
Angle growth	0.83	0.297	=	=	=
Angle limit	56.3	29.43	>	>	>
Angle mean	35.4	1.44	=	=	>
Thickness maximum	105	8.3	=	<	=
Position thickness	438	150.0	=	=	=
Volume growth maximum	130	80.4	=	=	=
Volume growth	1.58	0.077	<	=	=
Scaled width	43	27.5	<	=	=
Rib distance minimum	6.5	3.8	=	=	<
Rib distance maximum	28.4	4.2	=	=	=
Rib vertex increase	-9.9	25.9	=	=	=
Rib vertex difference	5.8	6.69	>	=	=
Rib vertex vergence	-0.8	15.5	=	<	=
Rib width minimum	445	185	=	>	>
Position rib width	560	107	=	=	=
Difference 300µm rib width	132	64	=	=	=
Rib height median	10.3	2.23	=	=	=
Rib height lateral	7.9	1.74	=	=	=
Megalospheric					
Chamber distance initial	59.1	4.42	>	>	>
Angle initial	26.7	8.83	<	<	=
Volume initial	8.88	5.92	=	=	>
Position volume	5.6	1.3	=	=	=
Proloculus width	101	34.1	=	=	=

ison to other *Ichthyolarias*. The strong and coarse ribs show irregular courses characterized by numerous strong bends. Some specimens demonstrate a strong linear divergence of ribs. Generation differences are expressed only in proloculus sizes. Measurements are presented in table 10.

Comparison: The only species similar to *I. biobliqua* is *I. polylineata*, distinguished by flat tests and dense, narrow ribs. See table 10.

PHYLOGENETIC AND ECOLOGICAL IMPLICATIONS

Ichthyolarias from the Rhaetian are exemplified by high morphological diversity in contrast to Liassic forms. All Triassic species except *I. parvolimbata* and *I. gerkei* occurring in both Koesen and Zlambach beds are restricted to either epicontinental marine basins (*I. serotriadica*, *I. acmaea*) or fore reef basins (*I. eulimbata*, *I. polylineata*, *I. biobliqua*). *I. biobliqua*, frequent within the Zlambach beds, allowing ecological interpretation, is restricted to the lower Zlambach beds. In these parts a high proportion of limestones intercalated by marls in combination with large numbers of sessile foraminifers indicates unstable conditions induced by water currents near the sediment surface (Weiland 1991). The younger parts of Zlambach beds, distinguished by a dominance of black shales indicating high organic content which points to anoxic conditions, lack this characteristic species.

Representatives of the *sulcata* group, however, can be found in all Rhaetian open marine sediments. Differing distribution patterns of *I. acmaea*, restricted to Koessen beds, and *I. gerkei*, dominating in Zlambach beds, are obvious. Thus, differences between both contemporaneous Rhaetian species, separated in habitat only by carbonate reefs and platforms of 20 km maximum diameter, are stronger than differences between all Lower Liassic species.

Evolutionary trends and phylogenetic relationships between species of the *sulcata* group are suggested using discriminant analyses (24 characters, canonical variate extraction; e.g. Rao 1952; Reymont et al. 1984) between the megalospheric generations. Differences in morphogenetic programs expressed by Mahalanobis distances (Mahalanobis 1936), again using megalospheres, but dividing *I. gerkei*, *I. acmaea* and *I. densicostata* into stratigraphically older and younger groups as inferred by classification analyses, can be represented in three-dimensional space, where the x-y plane is stretched by both first canonical variates, and time is depicted in the third dimension (text-fig. 15).

The megalospheres of *I. acmaea* demonstrate closest connections between Rhaetian and lowermost Liassic specimens of the same species (Mahalanobis distance = 2.16), supporting proposed trends. Similar relations exist between the lowermost Liassic individuals of *I. acmaea* and Upper Rhaetian *I. gerkei* (Mahalanobis distance = 2.93) and respectively younger Hettangian *I. densicostata* (Mahalanobis distance = 2.53).

The differences between *I. densicostata* megalospheres which are distinct in geological age is also expressed in the relationships to other species. While the younger Hettangian forms are most similar to *I. acmaea* (Mahalanobis distance = 2.53), the lower Hettangian forms possessing slender tests are morphologically more similar to Lower Rhaetian *I. gerkei* (Mahalanobis distance = 3.10), followed by the Rhaetian *I. acmaea* (3.30).

Relationships between the gradually evolving *I. gerkei* and the other species seem to be more complex. The strongest morphogenetic similarities exist between Upper Rhaetian *I. gerkei* megalospheres and lowermost Liassic *I. acmaea* (Mahalanobis

TABLE 10

Morphologic characters (means and standard deviations; n = 16, except as specified) for *I. biobliqua* and comparisons to related forms. All scale units except derived characters and angles are expressed in micrometers. >, significantly higher (larger) than; <, significantly lower (smaller) than; =, no significant differences at the 5% level.

	Mean	S.D.	<i>I. polylineata</i>
Chamber distance growth	1.30	0.075	>
Angle growth	0.87	0.066	=
Angle limit	28.0	4.66	<
Angle mean	35.1	4.62	=
Thickness maximum	107	24.7	=
Position thickness	326	137.3	=
Volume growth maximum	189	110.1	=
Volume growth	2.23	0.433	>
Scaled width	133	71.4	>
Rib distance minimum	2.0	2.2	=
Rib distance maximum	42.1	6.0	=
Rib vertex increase	-16.7	34.3	=
Rib vertex difference	-71.1	67.3	<
Rib vertex vergence	1.4	17.3	=
Rib width minimum	468	70	=
Position rib width	509	111	=
Difference 300µm rib width	447	468	=
Rib height median	14.0	3.50	=
Rib height lateral	10.6	2.69	=
Megalospheric (n = 13)			
Chamber distance initial	28.6	5.13	<
Angle initial	40.9	5.40	>
Volume initial	7.59	2.34	=
Position volume	5.3	1.4	=
Proloculus width	98	18.4	=
Microspheric (n = 3)			
Chamber distance initial	14.0	0.96	
Angle initial	50.8	6.01	
Volume initial	0.73	0.48	
Position volume	6.9	0.7	
Proloculus width	36	14.0	

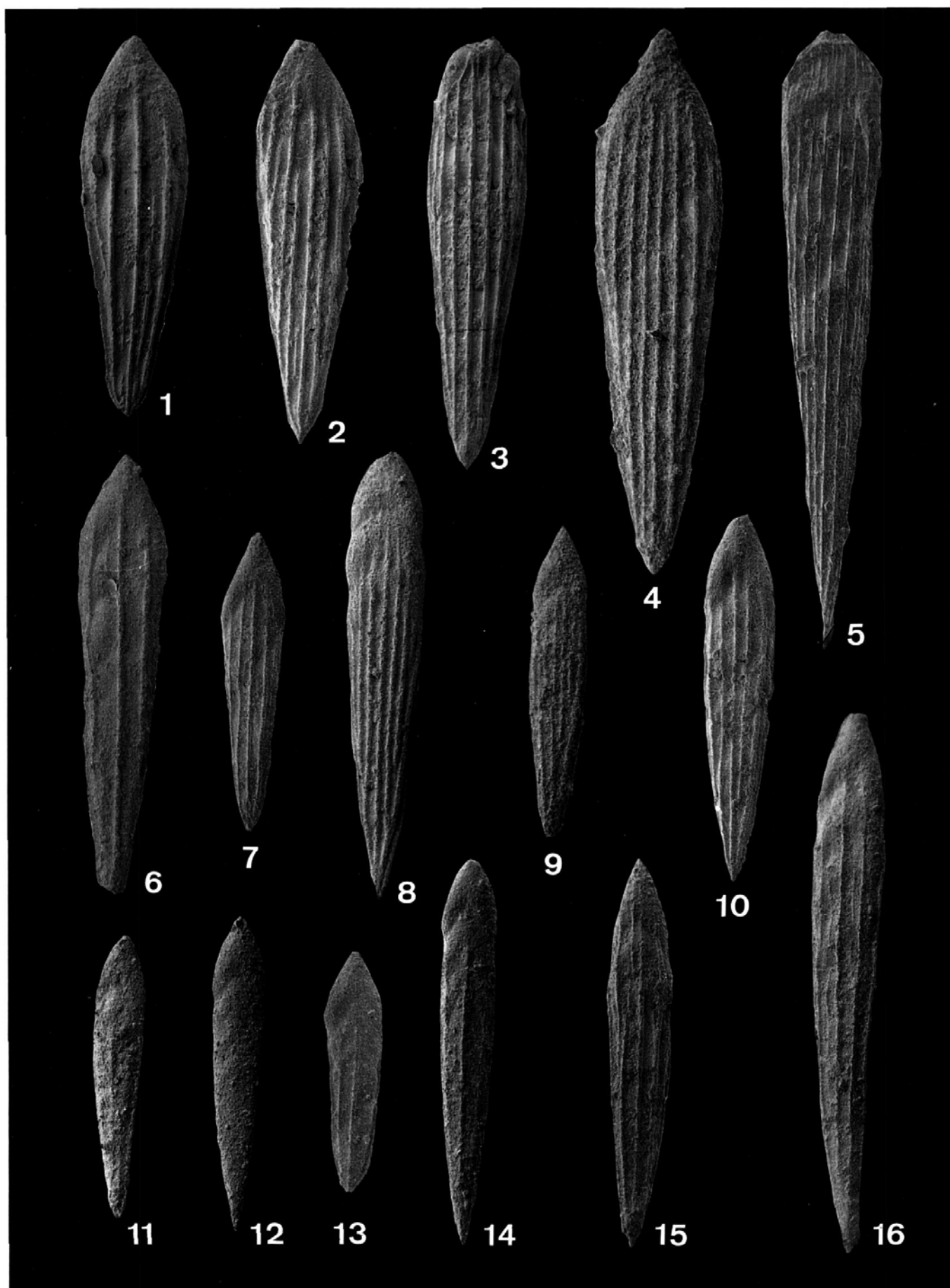
distance = 2.92), followed by weaker relationships to Lower Hettangian *I. densicostata* (Mahalanobis distance = 3.73).

I. sulcata megalospheres are more distinct morphogenetically from the other species. Smaller similarities exist to lowermost

PLATE 1

Magnification 60×.

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|---|---|
| <p>1-4 <i>Ichthyolaria sulcata</i> (Bornemann): megalospheric generation. 1. P4301/229. 2. P4301/233, showing denser ribbing. 3. P4301/224. 4. P4301/221, a "bicosata" form. Betzgenreith, Sinemurian.</p> <p>5 <i>Ichthyolaria sulcata</i> (Bornemann): microspheric generation, P4301/228, leading as a typical "bicosata" form to <i>Ichthyolaria terquemii</i>; Betzgenreith, Sinemurian.</p> <p>6-10 <i>Ichthyolaria densicostata</i> Hohenegger: megalospheric generation. 6-8. P4301/188, P4301/186, P4301/183; Hagnach, Lower Hettangian. 9, 10. P4301/198, P4301/196; Xeuilly, Upper Hettangian.</p> | <p>11 <i>Ichthyolaria acmaea</i> (Tappan): microspheric generation; P4301/137, Weißloferbach B165; Rhaetian.</p> <p>12-14 <i>Ichthyolaria acmaea</i> (Tappan): megalospheric generation. 12. P4301/123, Weißloferbach B151. 13. P4301/126, Weißloferbach B151, Rhaetian. 14. P4301/203, Vorderer Ampelsbach, Triassic/Jurassic boundary.</p> <p>15 <i>Ichthyolaria gigantea</i>, n. sp.; P4301/208, Kendelbachgraben, basal Hettangian.</p> |
|---|---|



Liassic *I. acmaea* (Mahalanobis distance = 6.43), but it is similarly distant not only from Upper Rhaetian *I. gerkei* (Mahalanobis distance = 6.72) but also from Upper Hettangian *I. densicostata* (Mahalanobis distance = 9.41).

This results in phylogenetic interpretations supported through discriminant analyses on morphogenetic program parameters, excluding the characters which differentiate megalos- and microspheric generations (text-fig. 15). In the Rhaetian marine basins both *I. acmaea*, distinguished by irregular growth, and *I. gerkei*, demonstrating slender tests, evolve toward larger size and regular ribbing, thus showing similar trends. Especially *I. acmaea*, which became extinct just above Triassic/Jurassic boundary, resembles the middle and upper Hettangian forms. This clear pattern is broken by the occurrence of lower Hettangian *I. densicostata* differing in their possession of slender tests from older and younger forms, and resembling Upper Rhaetian *I. gerkei* in test formation. Therefore, phylogenetic relationships between Upper Triassic and Lower Liassic species are not clear. More or less gradual transformations, as occurred in both Triassic species during the Rhaetian, cannot be detected.

ACKNOWLEDGMENTS

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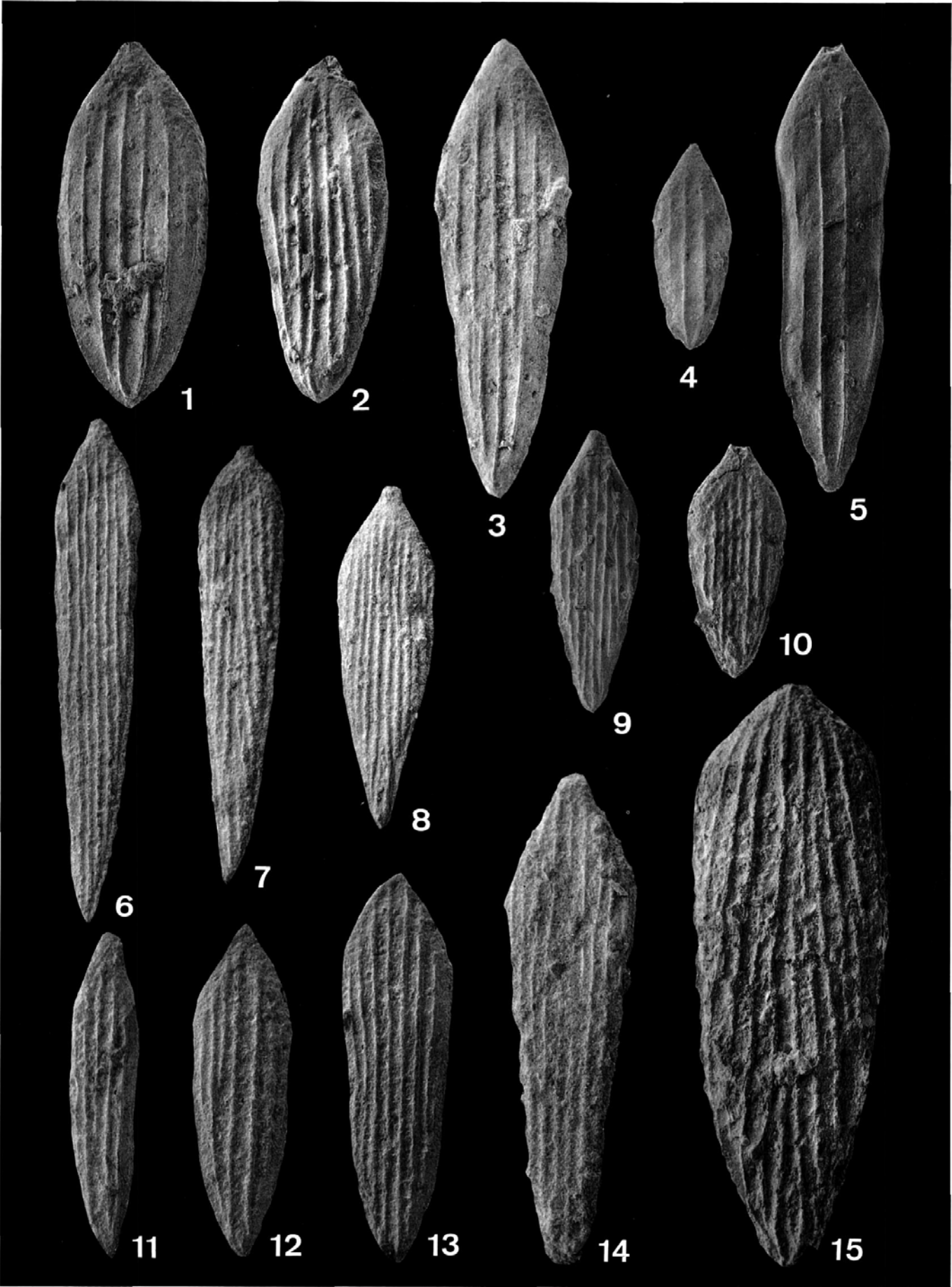
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PLATE 2

Ichthyolaria gerkei (Kristan-Tollman). All specimens from Roßmoosgraben, Rhaetian. Magnification 60X.

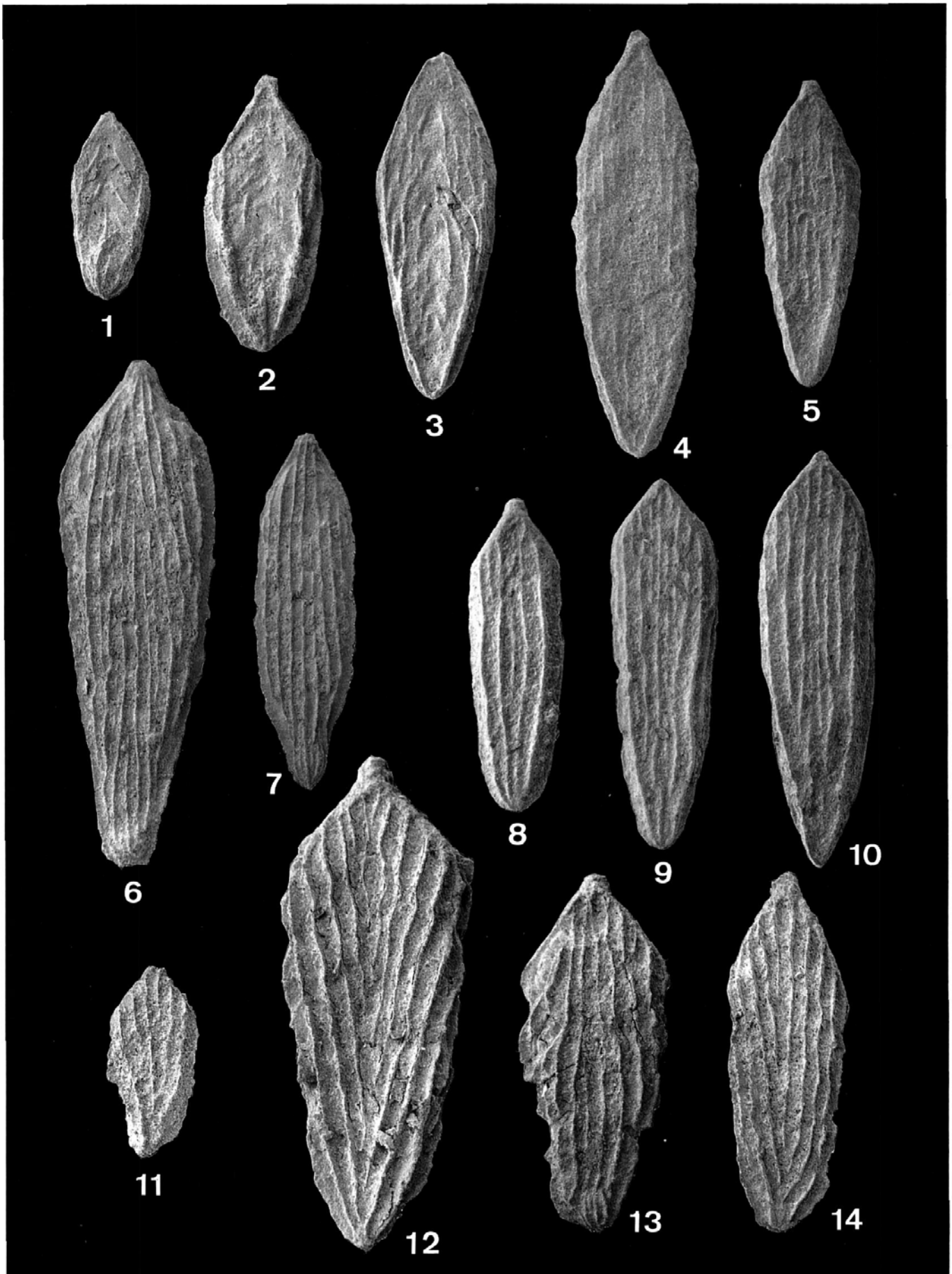
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| <p>1-4 Megalospheric generations from the Upper Rhaetian showing many regular ribs. 1. P4301/118, RM 76/145. 2. P4301/65, RM 76/171. 3. P4301/120, RM 76/146. 4. P4301/59, RM 76/141.</p> <p>5 Microspheric generation of regular ribbed form, P4301/61, RM 76/147.</p> | <p>6-16 Various typical <i>gerkei</i> forms showing intermediate ribs and rib reduction. 6. P4301/7, RM 76/33. 7. P4301/64, RM 76/147. 8. P4301/9, RM 76/34, microspheric form. 9. P4301/99, RM 76/30. 10. P4301/11, RM 76/34. 11. P4301/26, RM 76/75. 12. P4301/28, RM 76/75, microspheric form. 13. P4301/52, RM 76/95. 14. P4301/49, RM 76/92, microspheric form. 15. P4301/31, RM 76/75. 16. P4301/38, RM 76/79.</p> |
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PLATE 3
Magnification 60×

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| <p>1-3 <i>Ichthyolaria eulimbata</i> (Kristan-Tollmann): megalospheric generation. 1. P4301/32, RM 76/75. 2. P4301/72, RM 76/13. 3. P4301/56, RM 76/122. Roßmoosgraben, Rhaetian.</p> <p>4, 5 <i>Ichthyolaria parvolimbata</i>, n. sp.: megalospheric generation. 4. P4301/53, RM 76/97; Roßmoosgraben. 5. P4301/122, B145; Weißloferbach, Rhaetian.</p> <p>6, 7 <i>Ichthyolaria polylineata</i> (Kristan-Tollmann): megalospheric generation. 6. P4301/6, RM 76/33. 7. P4301/117, RM 76/145. Roßmoosgraben, Rhaetian.</p> | <p>8, 9 <i>Ichthyolaria serotriadica</i>, n. sp.: megalospheric generation. 8. P4301/167, D7. 9. P4301/173, D9. Weißloferbach, Rhaetian.</p> <p>10 <i>Ichthyolaria serotriadica</i>, n. sp.: microspheric generation; P4301/171, D7; Weißloferbach, Rhaetian.</p> <p>11 <i>Ichthyolaria biobliqua</i> (Kristan Tollmann): microspheric generation; P4301/80, RM 76/13; Roßmoosgraben, Rhaetian.</p> <p>12-14 <i>Ichthyolaria biobliqua</i> (Kristan-Tollmann): megalospheric generation. 12. P4301/57, RM 76/139. 13. P4301/78, RM 76/13. 14. P4301/82, RM 76/13. Roßmoosgraben, Rhaetian.</p> |
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