

NEW CONCEPTS IN THE EVOLUTION OF THE GADIDAE (VERTEBRATA, PISCES), BASED ON THEIR OTOLITHS

by

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The genera of Gadinae of which fossil otoliths are known are incorporated in a family tree, together with some Ranicepsinae and Lotinae.

From these data it can be concluded that all genera go through a life cycle just like any individual. In the senile stage of each lineage, ontogenetic development (retrograde) is opposite to that of the earlier stages (progressive). In the adult and senile stages a division can occur which differs from cladogenesis and which is called here neogenesis. By means of neogenesis new genera can originate before the ancestral ones become extinct. Each new genus (called neogenus) starts with small individuals in a new life cycle. The term orthogenesis has been replaced by gerontogenesis, because evolution does not follow straight lines, but is subjected to ageing processes. The course of the evolution of the Gadidae has now become predictable to a much greater extent. The ideas introduced here are also significant for genetic, ecological, taxonomic and bio-stratigraphic problems.

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SAMENVATTING

De familie van de kabeljauwen (Gadidae), die in de gematigde tot koude zeeën rond Europa momenteel de meest overheersende groep vissen is en in het Tertiair van het Noordzeebekken ook een belangrijke plaats innam, is met behulp van hun otolieten goed te bestuderen. Het omvangrijke fossiele en recente otolietenmateriaal dat mij ter beschikking stond, heeft het mogelijk gemaakt om een aanzienlijk gedeelte van de stamboom te reconstrueren.

Op grond van otolieten en uitwendige kenmerken kunnen de kabeljauwen in zes subfamilies onderverdeeld worden. Vooral de grootste, die der Gadinae, werd uitvoerig bestudeerd omdat de fossiele otolieten van deze subfamilie op het ogenblik het best bekend zijn.

Een verrassend vast patroon blijkt in de evolutie van deze familie steeds weer op te treden. Elke (evolutie-)lijn (Engels: lineage) doorloopt namelijk vier opeenvolgende fylogenetische stadia. In stadium 1 zijn de otolieten klein en nogal gedrongen. Vervolgens maken de otolieten een snelle groei door, zonder dat de lengte-hoogte (L-H) en lengte-dikte (L-T) verhoudingen merkbaar veranderen (stadium 2). In stadium 3 worden de otolieten niet veel groter meer, maar worden ze relatief slanker en dunner. Het laatste stadium kenmerkt zich doordat de otolieten weer gedrongener en dikker worden; bovendien wijzen de biometrische gegevens erop dat de variatiebreedte in dit stadium waarschijnlijk groter is dan in alle voorgaande stadia. In de loop van dit laatste stadium sterft de lijn uit.

Naast deze fylogenetische ontwikkeling waarop tot nu toe geen uitzonderingen werden gevonden, is ook de ontogenetische ontwikkeling van de otolieten van groot belang. Wanneer van elke soort en van elk fylogenetisch stadium een voldoende groot aantal otolieten gemeten wordt, blijken de grafieken waarin de lengte tegen de hoogte en de lengte tegen de dikte uitgezet worden, als regel geen rechte lijn te volgen; er treedt dus allometrie op. Er kunnen nu twee mogelijkheden gerealiseerd worden. In het ene geval worden de otolieten slanker en dunner naarmate ze groter (en ouder) worden. Dit weerspiegelt zich in een convexe curve welke progressief genoemd wordt (bijv. fig. 4a-b). De andere mogelijkheid is, dat de otolieten alleen in het jeugd stadium geleidelijk slanker en dunner worden en in het volwassen stadium vervolgens steeds gedrongener en dikker worden. Het eerste deel van de curve is dus weer convex, het laatste deel echter concaaf; deze curve wordt retrograad genoemd (bijv. fig. 2a-b). Meestal vormt het concaaf gedeelte het grootste deel van de curve.

Deze ontogenetische curves zijn karakteristiek voor het fylogenetische stadium waarin een lijn zich bevindt. In de fylogenetische stadia 1, 2 en 3 komen steeds progressieve curves voor. In het begin van stadium 4 is de L-H curve progressief en de L-T curve retrograad. Aan het eind van stadium 4 zijn beide curves retrograad.

Door middel van neogenese wordt de continuïteit van de evolutie gegarandeerd. In de fylogenetisch adulte en seniele stadia (stadia 3 en 4) kan er namelijk een splitsing optreden die zich onderscheidt van cladogenese doordat de individuen die zich afsplitsen van de hoofdlijn weer kleine otolieten hebben (welke tot kleine vissen behoord hebben) die het fylogenetische stadium 1 representeren. De nieuwe lijn die aldus ontstaat heeft de mogelijkheid om weer alle volgende stadia te doorlopen.

Uit al deze gegevens kan worden afgeleid, dat alle evolutielijnen (genera, hier "neogenera" genoemd) levenscycli doorlopen net zoals individuen. Een belangrijk verschil kan uiteraard gevonden worden in de tijdsduur van beide cycli. Een levenscyclus van een neogenus omvat bij de kabeljauwen miljoenen tot tientallen miljoenen jaren. De duur van zo'n levenscyclus hangt af van de snelheid waarin de vier stadia worden doorlopen.

De term orthogenese is vervangen door gerontogenese, omdat de evolutie geen rechte lijn volgt maar blijkbaar is onderworpen aan verouderingsprocessen. Het verloop van de evolutie van de kabeljauwen is hiermee veel meer voorspelbaar geworden. De hier geïntroduceerde ideeën over evolutie zullen met behulp van nieuwe vondsten van fossiele kabeljauw-otolieten steeds weer getest kunnen worden. Deze ideeën zijn ook van belang voor genetische, ecologische, taxonomische en biostratigrafische vraagstukken.

INTRODUCTION

The codfishes (Gadidae) form a rather small but very heterogeneous family of bony fishes, which live mainly in temperate seas. Some genera occur in arctic waters (for example *Arctogadus* and *Boreogadus*) and the genus *Merluccius* is cosmopolitan. A single species, *Lota lota* (L.), is adapted to life in fresh water.

Nowadays about 60 to 70 recent species are known to exist, more than 40 of which can be found in the waters around Europe (NW Atlantic, North Sea, Baltic Sea, White Sea, Mediterranean Sea and Black Sea) (Svetovidov, 1973).

It is not surprising that the Gadidae are a relatively small family, since the richness in species in temperate areas is usually much less than that found in the tropics and subtropics (Valentine, 1971, 1973). This is not due to the temperature itself but to the seasonal changes in temperature. In regions with large differences between summer and winter temperatures, considerable demands are made on the living organisms. Fluctuations in the quantities of food are very great. Species have to be flexible in their feeding habits. Many species tend to become habitat generalists. For this reason fewer ecological niches can be established in areas with large seasonal fluctuations than in areas with uniform conditions the year round. In deep oceanic waters where conditions are exceedingly uniform, richness in species is also very high (Valentine, 1971, 1972 and 1973).

Consequently the chance of cladogenesis is much smaller in temperate areas than in the warmer regions or in the deep sea. We can expect therefore only a few bifurcations in the lineages of the codfamily, which facilitates the unravelling of the family tree and the evolution of these fishes.

The codfishes, especially those of the subfamily Gadinae, seem to have had their centre of development in western Europe since they are known from the Upper Cretaceous onwards in this area. It is quite likely that the entire family has a North Atlantic origin. Therefore it is a group of fishes that is easily accessible for an European scientist. Most of the recent species are popular for consumption, so that it is easy to collect large numbers of otolith specimens for

ontogenetic research. Thanks to the generally large quantities of fossil Gadidae otoliths which have been collected, it is also possible to study the ontogenetic development of many fossil species of this family. Another advantage is that otoliths of fishes from this family are usually relatively large, which simplifies the preparation techniques considerably. For the same reason the otoliths can also be measured much more easily with a sliding caliper and the measurements can be reproduced very well in diagrams. This study is restricted mainly to the sub-family of Gadinae because of the fact that fossil remnants of this group (i.e. the otoliths) have been studied more extensively than those of other groups.

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THE DEVELOPMENT OF GADIDAE LINEAGES

All known lineages of the family of Gadidae based on their otoliths show remarkable similarities as far as their trends are concerned. The best examples of a lineage are those of the genera *Colliolus* Gaemers & Schwarzahns and *Trisopterus* Rafinesque, because of all the lineages they are at present the most completely known examples (enclosure 1). The larger part of the lineages of *Gadiculus* Guichenot, *Gadichthys* Gaemers & Schwarzahns, *Neocolliolus* Gaemers and *Micromesistius* Gill is also known. At present only fragments of lineages can be reconstructed for the other genera shown in enclosure 1. When more species of these relatively unknown lineages are found in the future, it will be possible to verify whether my hypothesis concerning the evolution of the Gadidae is correct or not. All available data pertaining to fossil and recent otoliths of Gadidae support my ideas at this moment.

At the beginning of a lineage the species have small otoliths which apparently belong to small fishes (stage 1). After this initial appearance the otoliths increase relatively quickly in size without pronounced changes in the length-height and length-thickness ratios (stage 2). In the subsequent stage the otoliths increase more slowly in size but become relatively more slender and thinner (stage 3). Finally the otoliths again become more compact: once more they are higher and thicker (stage 4), and generally shorter than the otoliths of the preceding stage. In the course of the fourth stage the lineage becomes extinct. All lineages, including their branches, are finite: they always have a distinct begin and a distinct end.

All known lineages follow this scheme and therefore I believe that a rigid law of nature underlies this evolution. Already a long time ago the term "orthogenesis" was introduced by Eimer (1897). In fact a more or less rectilinear

evolution seems to exist if we consider only stages 1 to 3. Nevertheless this term must be rejected for the evolution of the Gadidae otoliths, because stage 4 is a sort of retrograde development (with stages 1, 2, 3, and 4 always phases in the evolutionary development of lineages are meant; thus, the term "stage" is always meant in a phylogenetic sense). The lineages of species with otoliths showing some curvature along the long axis also demonstrate a distinct trend. This curvature always becomes greater as the duration of the lineage increases. Otoliths which are totally flat along the long axis, like *Gadiculus* Guichenot and *Boreogadus* Günther remain so during their entire phylogenetic development.

The development of any lineage shows a striking resemblance to the life cycle of individuals. Consider the otoliths of *Gadus morhua* L. for example: when a codfish is born, it has very small and relatively thick otoliths (ontogenetic equivalent of stage 1). In its youth the otoliths grow very fast and become more slender (equivalent of stage 2); upon reaching its adult stage, it is in the prime of life (equivalent of stage 3). As it grows older the otoliths will become thicker and relatively shorter and more crooked; this is the stage of senile decay (equivalent of stage 4). In comparison with the four phylogenetic stages an otolith of a codfish becomes more slender in its ontogenetic development at an earlier time. This for example is also the case with *Gadus morhua* (see next paragraph). The shift of the slenderness to an earlier ontogenetic stage is in any case not an essential difference between ontogenetic and phylogenetic development, because the point of time upon which the otoliths are most slender is not fixed. Thus we can consider the evolution of a lineage as a life cycle.

A further interesting observation is that the division of a lineage into several branches (cladogenesis) seems to be restricted to stages 3 and 4, but more data will be necessary before we can consider this an established fact. By the term cladogenesis in this publication is meant a "splitting off" of new species from an existing one due to ecological and geographical factors.

ONTOGENETIC DEVELOPMENT IN SUCCESSIVE STAGES

In some species allometric growth of the otoliths is very obvious. Thus the length-height, length-thickness and length-curvature ratios change clearly from juvenile specimens to very aged ones. I noted this phenomenon first in the otoliths of the recent codfish *Gadus morhua* L.; in this species, however, allometric growth is fairly complicated. For a more profound investigation of this phenomenon many otoliths belonging to several fossil and recent species have been measured. The fossil otoliths are from thanatocoenoses. We can consider the otolith material of a species to belong to one population, if all material comes from the same stratigraphical horizon, thus from a short geological space of time. Of course no samples may be used from beds that represent a clear condensed sequence, for in that case material from different periods has been brought together. The basal layer of the Sands of Kallo in the Antwerp region for example is such a condensed sequence and is therefore unsuitable.

For all measured otoliths the maximum length (L), maximum height (H) and maximum thickness (T) were determined; for some species the curvature (C) was also measured (Figs. 1a-b).

The whiting, *Merlangius merlangus* (Linnaeus), shows a peculiar change in the L-H and L-T ratios of the otoliths (Figs. 4a-b). The scatter diagrams show a cloud of points, the spread of which is a measure of the variation; this, of course,

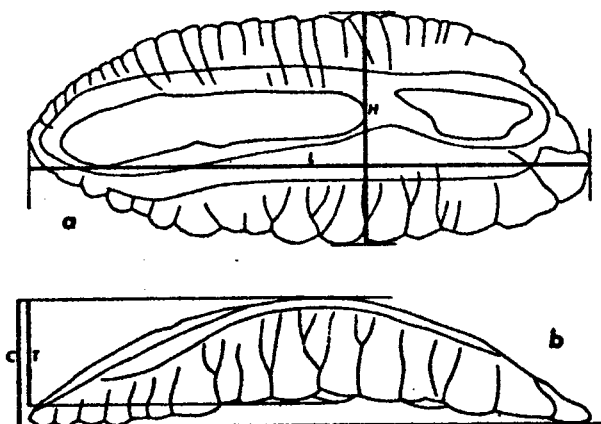


Fig. 1. Defined measurements of a sagitta of *Pollachius virens*.
Magnification 4.5 X.

1a. Maximum length (L) and maximum height (H).

1b. Maximum thickness (T) and curvature (C).

is a character of any ratio diagram. It is possible to draw a line through the mean values of the measurements. For drawing this line it is very important to realize that all curves converge on the zero point of the diagrams. Most investigators forget this when working with dimension ratios. In many cases the zero point is not even given in their diagrams, usually for the simple reason that the juvenile specimens are lacking. Of course I have tried to obtain samples from as many growth stages as possible for all the species studied, but the juvenile otoliths were the most difficult. For several species it was not possible to collect specimens smaller than the minimum length caught by trawlers. Then the zero point is of course even more important. When the variability is great it is also necessary to have many specimens of nearly the same size. Only then the mean curve can be drawn satisfactorily. For these two reasons it is not surprising that so far the lines drawn in ratio diagrams are usually straight. Lines of mean values, if recognizable at all, are very rarely straight in the diagrams that I have prepared. Thus I question the commonly presented rectilinear ontogenetic diagrams where they are based on only a few data.

Returning to the diagrams for the whiting (Figs. 4a-b) an obviously convex curve is seen in the L-H and L-T diagrams. This means that otoliths of juvenile specimens are the shortest and thickest. Gradually the otoliths become relatively longer and thinner as the age of the fishes increases. I call such ontogenetic curves progressive curves. These ontogenetic curves occur in the phylogenetic stages 1, 2 and 3 and the beginning of stage 4. The curvature of the line is greatest in stage 3; the recent whiting is now in this stage, as can be shown by the evolution of the genus *Merlangius* (Enclosure 1). The curves are less convex in stages 1 and 2 and again in the beginning of stage 4. In the latter case this is caused by the transition to the concave curves at the end of stage 4. Excellent examples of the latter curves are the ratio diagrams for *Gadus morhua* Linnaeus (Figs. 2a-b). The beginning of these curves is also convex, but this part is very short in comparison with the rest of the line which is clearly concave. The larger part of the curves, however, is concave, thus the curvature is just the

opposite of that in the most juvenile part of such curves and the curves from earlier representatives of the lineage. I call such curves retrograde curves. Otoliths of rather juvenile specimens which are 8 mm long are much more slender than those of adult ones. Gradually the young slender specimens change into continually thicker and higher otoliths as they grow older. Therefore the most essential feature of these curves is their concavity. If the entire curve was concave it could not approach the zero point of the diagram, which is, as stated above, a typical character of otolith ratio diagrams. For this practical reason it seems highly unlikely that the entire curve is concave. Another explanation might be that the first convex part of the ontogenetic curves is a remnant of earlier phylogenetic stages according to the Biogenetic Law of Haeckel, which says that ontogenetic development is a shortened repetition of phylogeny. Probably both factors act a part in this phenomenon.

In many examples the curves of the L-H and L-T ratios for the same species are the opposite of one another. The diagrams of the L-H ratio for *Gadichthys antwerpiensis* (Gaemers)(Fig. 7a), *Gadichthys benedeni* (Leriche)(Fig. 8a), *Colliolus johannettae* Gaemers (Fig. 10a), *Colliolus schwarzhansi* Gaemers (Fig. 11a)) and the Middle Miocene *Merlangiogadus cognatus* (Koken) is a progressive curve, whereas the diagram of the L-T ratio for these species is retrograde (Figs. 7b, 8b, 10b, 11b). We can assume that all of these species belong to the beginning of stage 4. In the case of *Gadichthys antwerpiensis* and *G. benedeni* this part of stage 4 covers a long period of time, encompassing three species which are distinguishable morphologically. For the other three species mentioned above this part of the life cycle of the lineage was much shorter.

The curves for the haddock, *Melanogrammus aeglefinus* (Linnaeus), which has to be placed in stage 4 (because its direct ancestor *M. conjunctus* Gaemers & Schwarzhans is more slender and of the same size), are weakly s-shaped, with a first convex part and a second concave part; these sections are nearly of the same length. From these ontogenetic curves it can be deduced that *M. aeglefinus* belongs to the end of stage 4. The only difference with other Gadidae (from which it is known that they are in the last part of stage 4) is the proportion of the convex part with respect to that of the concave part. Probably *M. aeglefinus* is not yet so far advanced with the end of stage 4, as *Gadus morhua* for instance.

The diagrams of the L-H ratios for *Trisopterus luscus* (Linnaeus) and *T. minutus* (Linnaeus) seem to consist of straight lines, while the L-T ratios seem to follow a retrograde curve. For both species juvenile material as well as very old otoliths is still too scarce to be sure of these curves. Unfortunately variation is very marked, especially in the adult specimens. Therefore it seems to me that it would be better not to publish these results in diagrams until more measurements are available.

In any case it is a fact that the curve of the L-T ratio is always retrograde sooner than that of the L-H ratio when they are opposite.

Colliolus schwarzhansi has been placed in a side-branch of the lineage *C. parvus* - *C. friedbergi* because the otoliths of this species are clearly flatter than all other *Colliolus* species. This is not evident from the otolith drawings of the enclosure, for here only views of the inner surface are given.

Morphological variation in L-H and L-T ratios is always considerably greater in stage 4, especially when both curves are retrograde. See for example the spread of the cloud of points in the diagram for *Gadus morhua* (Figs. 2a-b). The diagrams for *Pollachius virens* and *P. carbonarius* (Figs. 5a-c) and *Gadicichthys verticalis* (Figs. 9a-b) show by their concavity that these species represent the end of phylogenetic stage 4. It will be interesting to know how great the differences in genetic variation are in comparison with the earlier stages. Possibly the results of such research would provide more information about the process of extinction of the lineages.

The results of the investigation of the ontogenetic development of many Gadidae species in connection with their phylogenetic development lead to the following conclusions.

When both ontogenetic curves of a species are progressive, the species in question is in phylogenetic stage 1, 2 or 3. When the ontogenetic curves of a species are opposites (always the curve of the L-H ratio is progressive and the curve of the L-T ratio is retrograde), the species in question is in the beginning of phylogenetic stage 4. When both ontogenetic curves of a species are retrograde, the species in question is at the end of stage 4.

Progressive and retrograde tendencies in ontogenetic curves are connected with the phylogenetic stage. Therefore phylogenetic development of a lineage in the past and in the future can be predicted approximately, when only the ontogenetic development of one species is known.

THE ORIGIN OF GENERA

The discovery that all genus lineages of Gadidae are finite and rather short living leads to an important problem. How is the continuity of evolution assured ?

The data from the family tree of the codfishes (Enclosure 1) provide an answer to this question. A new genus can arise from the adult stages (stages 3 and 4) of an old genus. Three examples are well-known: *Neocolliolus* arises from *Colliolus*, *Micromesistius* from *Merlangiogadus* and *Gadiculus* from *Gadicichthys*. The differences with respect to cladogenesis are very evident.

In stages 3 and 4 a species can split up into two or more species, while all descendant species remain in the same phylogenetic stage as their immediate ancestor; this is cladogenesis. In Enclosure 1 some divisions are reconstructed which are caused by cladogenesis: *Trisopterus capelanus* (Lacepède), *T. luscus* (Linnaeus) and *T. spectabilis* (Koken) from the succession *T. elegans* - *T. concavus*, and *Colliolus schwarzhansi* and *C. friedbergi* from the succession *C. parvus* - *C. sculptus* - *C. johannettae*. The most conspicuous differences between the new species of the different branches are found in the L-H and L-T ratios which change with time. This is due to the differences in the rate of passing through the following stages of the life cycle of the lineage. It is obvious that the slower the stages of a lineage succeed one another the longer the lineage will exist. Taking this into account we may expect the branch of *Trisopterus capelanus* to have a longer life than that of *T. luscus*. The latter in its turn will live longer than the branch of *T. spectabilis*; this is exactly what is found in the fossil record. The branch of *Colliolus schwarzhansi* potentially also has a longer life than that of *C. fried-*

bergi, but this cannot yet be verified with the help of palaeontological evidence. It is most likely that *C. schwarzhansi* after its appearance in the Middle Miocene North Sea has been driven away from this area. Probably this species has lived along the coasts of the North East Atlantic or in the Mediterranean since the Late Miocene. It is very admissible that *C. friedbergi* and *C. schwarzhansi* became too competitive for one another, when the circumstances changed in the North Sea at the transition of Middle to Late Miocene.

Furthermore a lineage can also become extinct before its senile stage if the environment in which its individuals live changes too much or even ceases to exist, so that the individuals have no chance to adapt themselves to the new circumstances.

A new genus also originates from an older genus by division, but it is always a division into two branches and never more than two. The new genus always starts with stage 1.). This is demonstrated by the fact that the otoliths are small and become larger in the course of time, thus following the sequence of the stages. It is necessary to introduce a new term for this division because it is fundamentally different from cladogenesis. The process of the origin of new genera I call neogenesis - rejuvenation in evolution (from Gr. νεος = young, new, and Gr. γενεσις = origin, creation, birth, descent).

The concept of genus as used here is different from the conventional idea. Therefore I call this sort of genus neogenus, analogous to neogenesis (from Gr. νεος = young, new, and Gr. γενος = genus). The concept of neogenus which is always connected with neogenesis moreover is more clearly circumscribed than the fairly vague term genus.

The resemblance between the life cycle of an individual and the life cycle of a genus becomes even more striking through neogenesis than was shown in the discussion on the development of lineages. A neogenus always starts with small individuals born from an old genus with large individuals. The new generation that originates from fertilized eggs of codfishes also starts with small individuals. An explanation of neogenesis nevertheless is not as easy. We should realize that all comparisons between phylogenetic and ontogenetic development do not have to be valid in total. Neogenesis geologically speaking takes only a very short period of time, but that does not alter the fact that it is a very important event in evolution. The life cycle of a genus seems to be a rather fixed development. Big changes cannot be expected within this development although the increase in size seems to be very spectacular. Cladogenesis is the result of geographical or ecological separation, and causes the diversity and richness in species within a genus, but it does not affect the course of the phylogenetic stages. It seems quite likely that the more fundamental changes take place by means of neogenesis.

All lineages geologically speaking have a relatively short lifetime being of the order of some tens of millions of years. The duration of time of a lineage

) There seems to exist an exception but this is only apparent. The pictured specimen of *Micromesistius tenuis* (Enclosure 1) is an adult otolith, whereas a juvenile otolith of *M. hochti* has been pictured. In the enclosure only drawings of real existing otoliths have been included. I have strived to represent adult specimens as much as possible; in the case of *M. hochti* however it was impossible for lack of adult specimens. The adult specimen of *M. tenuis* is more slender than the juvenile of *M. hochti*, because of the specific places of these species in the respective convex ontogenetic curves.

thus is shorter than is generally accepted now in palaeontology; this can be derived from the fact that it is usual to construct family trees with branches that exist from the first appearance of a family up to and including the total extinction of that group (or up to the present time when such a family still has recent representatives). In such a system of a family tree extinction is seen purely as something negative, namely as the absolute end of existence. In my opinion extinction does not need to be the real end of the evolution of a group of organisms. Thus I believe that there are two sorts of extinction. One is the inevitable result of the course of the evolution, without being the absolute end of the development; this sort of extinction originates from the organisms themselves. The other is yet equally inevitable and is not caused by evolutionary factors in the first instance, but by factors from the surrounding world (ecological factors).

We have to take into account that in the course of a rather long period of time after cladogenesis a marked differentiation can develop between the separate branches. As a result the taxonomist has been inclined to consider each branch to belong to different genera. Such genera however are not of the same order as those which originate by neogenesis, and which are called here neogenera.

REMARKS ON THE EVOLUTION OF THE FAMILY

With the aid of otoliths the family of Gadidae can be divided into six subfamilies.

1. Gadinae. This subfamily includes many recent genera with otoliths that generally have the following basal shape. The outline of the otoliths is more or less elongated with a pointed caudal end and a blunt rostral end. Predorsal and postdorsal angles can be present. *Arctogadus* Drjagin, 1932 is rather aberrant with blunt caudal and rostral ends, which might be the result of later differentiation and not a primary characteristic. Other recent living genera are *Gadus* Linnaeus, 1758, *Eleginus* G. Fisher, 1813, *Theragra* Lucas, 1898, *Pollachius* Nilsson, 1832, *Melanogrammus* Gill, 1863, *Merlangius* Geoffroy-St.Hilaire, 1767, *Microgadus* Gill, 1863, *Micromesistius* Gill, 1864, *Trisopterus* Rafinesque, 1814, *Neocolliolus* Gaemers, 1976, *Gadiculus* Guichenot, 1850, *Gadichthys* Gaemers & Schwarzahns, 1973, and *Boreogadus* Günther, 1862.

2. Merluccinae. The basic shape of the otoliths of this subfamily is a low scalene triangle. Usually there is a clear middorsal angle. The caudal and rostral ends are more or less pointed, but they are not of equal sharpness. The otoliths are flat in comparison with most other otoliths of Gadidae and are only slightly bent along the long axis. Recent living genera are *Merluccius* Rafinesque, 1810 and *Macruronus* Günther, 1873.

3. Lotinae. Otoliths of this subfamily are characterized by a low scalene triangle. The middorsal angle mostly is indistinct. The caudal and rostral ends are rounded or only slightly pointed. The otoliths of the recent species always are clearly bent along the long axis. Some species of *Molva* Lesueur, 1819 develop two dorsal angles in the adult stage, although there is only one middorsal angle in the juvenile stage. Other recent living genera are *Brosme* Oken, 1817 and *Lota* Oken, 1817.

4. Gaidropsarinae. Otoliths of this subfamily are also characterized by a low scalene triangle as basic shape; in comparison with the Merluccinae the otoliths are much smaller with respect to the length of the fishes. The middorsal angle mostly is indistinct. Both ends are more or less pointed. One genus has flat otoliths, the

other two have otoliths that are clearly bent along the long axis. Recent living genera are *Ciliata* Couch, 1832, *Enchelyopus* Bloch & Schneider, 1801, and *Gaidropsarus* Rafinesque, 1810.

5. Phycinae. The otoliths of this subfamily have a shape that closely approximates that of a banana. Height and thickness are usually about the same and the length is much greater than the other dimensions. Moreover the sulcus acusticus consists of an undivided furrow. A separate ostium and cauda cannot be distinguished in contrast to all other subfamilies of Gadidae. Recent living genera are *Phycis* Artedi, 1792, and *Urophycis* Gill, 1864.

6. Ranicepsinae. The otoliths have an egg-shaped, slightly elongated outline without distinct angles. Both ends are bluntly pointed. The caudal end is somewhat more pointed than the rostral end. This subfamily is represented by only one recent living species of the genus *Raniceps* Oken, 1817.

Important differences exist between the above classification and the classification made by biologists which depends on the outward appearance and/or the form of the skeleton. Biologists usually place *Merluccius* in a separate family called Merlucciidae. For various reasons it seems better and more elegant to include this genus in the Gadidae. In the first place the otoliths of the subfamilies of Gadidae show marked differences in shape, so that the shape of the *Merluccius* otoliths is not really aberrant. The otoliths of *Merluccius* resemble those of *Molva*, *Lota* and *Brosme* to a large extent. The three latter genera were grouped in the Lotinae subfamily, together with the Gaidropsarinae, Phycinae and Ranicepsinae by Svetovidov (in Bureau & Monod, 1973); however, such a wide conception of the Lotinae subfamily cannot possibly be based on the otoliths.

In the second place the extinct genus *Palaeogadus*, which very probably is the ancestor of the genus *Molva*, also closely resembles the genus *Merluccius*. In the third place the external shapes of the recent fishes belonging to the genera *Merluccius*, *Molva* and *Lota* have many similarities. For instance the form and size of the fins are much the same. All other Gadidae obviously differ in these characteristics. If *Merluccius* and consequently also *Macruronus* are considered to belong to a separate family Merlucciidae, also the other mentioned subfamilies have to be elevated to families.

How far back in the past are the roots of all subfamilies? It is not easy to answer this question because sufficient data are not yet available. It is to be expected that the roots will extend far back into the past because of the big differences in the shape of the otoliths.

When the photographs and descriptions of the otoliths of the Early Ypresian (earliest Early Eocene) of England, published by Stinton (1965), are studied four subfamilies can easily be distinguished. *Gadophycis ovalis* Stinton can be considered an intermediate form between the recent Phycinae and the primitive Gadinae. The resemblance with the Phycinae is still striking enough to place this species in that subfamily. *Palaeoraniceps upnoriensis* (Stinton) can be recognized immediately as a representative of the Ranicepsinae. This species probably belongs to the lineage of *P. tuberculatus* and *P. regularis*. *Paleogadus pinguis* Stinton undoubtedly belongs to the Merlucciinae. *Protocolliolus eocenicus* (Frost) is a true representative of the Gadinae and belongs to the lineage which precedes that of *Colliolus*. Only the Gaidropsarinae are unknown in the early part of the Paleogene, most probably as a result of the small size of the otoliths. In Neogene deposits they are rather rarely found as well.

Middle Paleocene (Thanetian) deposits contain true Gadinae and Merlucciinae. *Archegadus comptus* Stinton is probably an ancestor of *Gadus* and the closely related genera *Eleginus*, *Theragra* and *Pollachius*. *Palaeogadus trigonus* Stinton is a definite representative of the Merlucciinae. *Proraniceps leiopleurus* Stinton is an ancestor of the *Gadichthys* lineage. Stinton (1965) considers this species to be the joint ancestor of *Raniceps* and *Gadiculus*. In my opinion, however, the wide and distinct collum as well as the thin dorsal and ventral rim, the characteristically sculptured outer surface and the clear symmetrical convexity in the direction of the height point to a much closer relationship with *Gadichthys* (and *Gadiculus*) than with *Raniceps*. Therefore I consider *Proraniceps leiopleurus* as a member of the lineage from which *Gadichthys* originated. Koken (1885) and Leriche (1908) found *Gadidarum balticus* (Koken) in the Paleocene of Denmark and France, respectively. This species is another representative of the Gadinae which probably belongs to the lineage preceding the *Trisopterus* lineage. On the basis of these data it can be concluded that the differentiation among the Gadinae was already considerable in the Paleocene.

Voigt (1926) mentions three species of Gadidae which were found in the Senonian (Late Cretaceous) of Germany: Of these only *Gadidarum erraticus* Voigt is a true representative of the Gadidae, and seems to belong to the Gadinae. *Morrhua anhaltinus* Voigt and *Morrhua* sp. are incorrect identifications because in both cases the ostium is open on the rostral side of the otoliths; these species therefore have been classified as Perciformes.

In view of the above data it appears that many subfamilies have undergone separate development during the entire Tertiary; their joint ancestor must have lived before the Tertiary. It is a pity that the data from the Paleogene and Late Cretaceous in particular are not yet sufficient to be able to trace the roots. Some conclusions, however, can be drawn with the help of otoliths.

The *Ranicepsinae* seem to be the most primitive subfamily of the Gadidae. The otoliths of this group show many similarities with those of the family of *Macruridae*: the outline is compact and does not have distinct angles or straight parts; moreover ostium and cauda are of equal length and have a slightly elongated oval shape. The otoliths of *Gadiculus* and *Gadichthys* have also very primitive features, so that they closely resemble the *Macruridae*. Their outline is somewhat more pronounced than that of the otoliths of *Raniceps*, as demonstrated by the pointed caudal end, blunt dorsal angles and the wide sulcus which is divided into an ostium and a cauda which are nearly equal in length and are filled with slightly elongated oval colliculi. The only distinct differences with respect to the small *Macruridae* of Miocene and Oligocene age (for instance those described by Posthumus, 1923) are the larger size and the shallower sulcus of *Gadiculus* otoliths. In the elongated stages of *Gadichthys*, on the other hand, the cauda is much longer than the ostium. From these data it can be concluded that the *Macruridae* and *Gadidae* are closely related.

The *Phycinae* show a closer relationship with the Gadinae than with the *Merlucciinae*, *Lotinae* and *Gaidropsarinae*. Surely the latter three subfamilies are closely related to one another, while the *Lotinae* and the *Gaidropsarinae* are the most closely related ones of these three subfamilies.

When the known parts of the family tree of the Gadidae are studied, a distinct development in the otoliths can be observed. Younger lineages always have larger otoliths at comparable stages than the ancestral lineages. This tendency is obvious when we compare all known Paleocene and Early Eocene species with the recent species. It is very likely that the outer shape of the fishes has followed the same

evolution as that of the otoliths. To confirm this, I have studied the relationship between the shape of recent fishes and their otoliths for closely related species belonging to the same genus. Thus I found that the otoliths of the relatively slender *Colisa labiosa* indeed are more slender than those of the higher, more compact *Colisa lalia*. Both species belong to the tropical freshwater family Osphromenidae. The otoliths of *Chanda wolffi* likewise are more slender than those of the relatively higher, more compact *Chanda lala*. These two species belong to the tropical family Ambassidae and live in brackish or marine environments.

It is more difficult to correlate the length of fishes with the length of their otoliths. Within a subfamily however, the ratios of these lengths do not seem to be very different. It is of course highly improbable for a small fish to have very large otoliths for spatial reasons. Large fishes theoretically can have small otoliths. Thus it is possible that the ratio of the length of the fish to the length of the otolith will differ to a certain extent for closely related species. Even within a genus different ratios can occur. Therefore this difference sometimes can be used to differentiate between closely related species. See for example *Pollachius virens* and *P. carbonarius* in the systematic descriptions of Gaemers (1976). Nevertheless a general increase in size of the Gadinae in the course of time can be accepted. In the entire animal kingdom this general evolutionary trend of lineages is present and the fossil record has already given us many examples beginning with one-celled animals like Foraminifera up to and including the vertebrates. Because of the increase in size of successive lineages, this trend is also present in the development of a family as a whole.

The increase in size mostly seems to be an inevitable process which always leads to giant forms. The question arises: is there a life cycle for a family as a whole which is comparable with the previously described development of genera? I am inclined to answer this question affirmatively, but more research will be necessary to confirm this. In any case it is clear that there are limits to the size of animals. Any animal with a given structure has a certain maximum size above which it can no longer exist. When an animal species reaches its maximum size, there are only two alternatives: it has to become extinct or to change its structure.

The advantages of an increasing size which apply during younger stages of development become insurmountable disadvantages for a species in the later stages. A stabilization of the size at some point in the evolutionary development does not seem to occur. Moreover the larger a species is the higher it is in the food pyramid. When marked environmental changes occur and the equilibrium of the food pyramid is disturbed, such species are more vulnerable within the entire ecological system than smaller ones; at such times larger species are also threatened by their smaller populations (which can also cause interbreeding) and the smaller number of descendants. Therefore in such cases species can become extinct before they reach full development, that is up to and including the senile stage.

CONSEQUENCES OF THE NEW CONCEPTS

Evolutionary consequences

In broad outline evolution of the Gadidae has now become predictable. With diagrams of length versus height and length versus thickness of otoliths from different ontogenetic stages of a certain species, and/or with the known data of the lineage we can determine the phylogenetic stage of that lineage. Thus we can determine whether a lineage is in the initial stage, youth, prime of life or senile

decay at a certain point of time in the geological history. Missing links can already be reconstructed before they have been discovered. Furthermore the future development of the lineage can now be predicted. Of course some important restrictions must be remembered. The duration of any stage has not been fixed; considerable variations occur. Another unknown factor is the extent of splitting of lineages.

Without saying anything about the exact time of extinction it is possible to indicate the stage for many recent Gadidae: *Gadiculus argenteus* is in stage 1 or 2; *Merlangius merlangus* is in stage 3; *Melanogrammus aeglefinus* is in stage 4; *Gadus morhua*, *Gadichthys thori*, *Trisopterus luscus* and *T. minutus* are already far advanced in stage 4.

Genetic consequences

Although genetic mutations can always take place, evolution of Gadidae seems to follow very distinct and rather narrow paths. By means of neogenesis rapid changes occur. Changes by means of cladogenesis are also relatively rapid. Other changes in the course of the development of lineages are gradual.

The problem of the ageing of a genus is the same as that of the ageing of an individual. Both problems are difficult and are not yet understood, but the fact that ageing occurs in the life cycle of an individual as well as in the evolution of a lineage may possibly throw new light upon this subject.

Taxonomic consequences

Allometric growth causes changes in the proportions of the dimensions giving rise to progressive and retrograde growth curves. Thus the growth curves are specific for a species, not fixed length-height and length-thickness ratios. Moreover, deviations of the mean can be considerable. Therefore earlier identifications of (otolith) species on the grounds of fixed ratios do not need to be correct. By means of growth curves closely related species can be distinguished from one another.

Ecological consequences

Each lineage begins with small individuals which become larger in the course of time. This implies that the successive phylogenetic stages make different ecological demands. It can easily be imagined that a lineage starts lower in the food pyramid than it ends. Thus it is possible and many times even necessary that a small species which is first prey later changes into a larger predator. A small species usually requires other food than a large one. Thus other habits also have to change. On a grand scale this process also takes place in the family as a whole. From this it can be concluded that species have to be very flexible ecologically. Properly speaking this is not astounding, for the development of an individual also undergoes the change from prey to predator during growth. One might consider the individual change even more spectacular than that of a species or genus.

Biostratigraphic consequences

Up to now biostratigraphical correlations and age determinations are made with the help of successive guide fossils which generally do not originate from one another, but accidentally are the most common species. The only water-tight method for correlations and age determinations is the use of successive species of a lineage. Only then we can be sure that no gaps or duplications in the so constructed biostratigraphical system are present. It is self-evident that we need a large number

of lineages for all geological history, since geologically speaking each lineage lives only for a short while. Based on the data of the Gadidae we have to assume periods of some tens of millions of years for their lineages. The rate of development of different animal groups can be very different. Certainly lower and higher values than those given for the family of Gadidae will be encountered in other groups.

The establishment of age determinations with the help of one lineage is never more precise than the "lifetime" of a species. Short well-defined time intervals can be obtained by using short-living lineages or a combination of two or more lineages, for we may assume that the changes within the different lineages usually take place at different points of time. Four examples of better age determinations on the basis of lineages of the Gadidae can be given.

1. The exact stratigraphical position of the Sands of Edegem at Antwerp, Belgium, has long been a problem. With the help of Foraminifera Hooyberghs & de Meuter (1972) placed this formation in the Late Oligocene. Molluscs, shark teeth and otoliths very strongly suggest an age of Miocene. Gaemers (1973) correlated the Sands of Edegem with the deposits of the Lower Hemmoorian (Behrendorf, earliest Middle Miocene) of Northwestern Germany on the grounds of the occurrence of *Gadichthys antwerpiensis* (Gaemers) in both deposits. In the Lower Hemmoorian however, *Colliolus friedbergi* (Chaine & Duvergier) is present, whereas the Sands of Edegem contain the direct ancestor *C. johannettae* Gaemers, which formerly was classified as *C. friedbergi*. With these data it is certain that the Sands of Edegem are older than the Hemmoorian and belong to the Early Miocene.

2. The stratigraphic position of the glauconitic Miocene sands immediately above the Middle Oligocene Boom Clay near Rumst, Reet and Terhagen in Belgium was considered to be the same as that of the Sands of Edegem. The occurrence of *Colliolus friedbergi* in these sands makes this idea impossible. Two possibilities remain: these Miocene sands have to be correlated with the Sands of Kiel (Hooyberghs & de Meuter, 1972) or with the somewhat younger Sands of Antwerp, which are both Middle Miocene.

3. The Sternberger Gestein with a supposed age of Late Oligocene from which Koken (1891) describes diverse otolith species contain among others *Gadichthys spatulatus* (Koken, 1891) (Pl. V, Figs. 3a-b - 5a-b) and *Ctenodentex nobilis miocenicus* (Weiler, 1942). All other Late Oligocene deposits of Northwestern Germany however contain *Gadichthys undosus* Gaemers and *Ctenodentex nobilis* (Koken). *C. nobilis miocenicus* is a descendant of *C. nobilis* and therefore it is sure that the erratic boulders of the "Sternberger Gestein" are younger than the Late Oligocene deposits which are in situ. *Gadichthys spatulatus* is an ancestor of *G. antwerpiensis* and therefore the Sands of Edegem are younger than the "Sternberger Gestein". We can conclude that the "Sternberger Gestein" has an age of latest Late Oligocene or earliest Early Miocene.

4. The Sands of Deurne (Deurnian) can be correlated with the Gramian with the help of the occurrence of *Trisopterus luscus*. Up to now it could not be determined by means of otoliths whether this formation should be correlated with the Langenfeldian or Gramian of Northwestern Germany. The ancestor of *T. luscus* is *T. concavus*, which is found in the Late Miocene deposits of Oploo, which can be correlated with the Langenfeldian.

INDICATIONS OF UNIVERSALITY OF THE NEW CONCEPTS

Nowadays it is fashionable among biologists and many palaeontologists to deny a close connection between ontogeny and phylogeny. This group of scientists readily refers to the Biogenetic Law of Haeckel which has repeatedly been proved to have no universal validity and which at the best is true only roughly in certain cases. Haeckel however, made an expensive mistake in his concepts by supposing that phylogeny determines ontogeny. Phylogeny should be the "causa efficiens" of ontogenetic development. Garstang (1922) and Schindewolf (1929) already suspected with keen insight that this idea was wrong. It is just the opposite: ontogeny is more fundamental than phylogeny and so ontogeny determines phylogeny. In fact we can consider phylogeny to be a chain of numerous successive ontogenetic developments.

Seen from this point of view, there is nothing mystical in the fact that many features of phylogeny are the same as those of ontogeny and that phylogeny has even been subjected to the same processes as ontogeny and has to obey the same laws of nature.

Phenomena of progressive and retrograde development are widespread in the palaeontological record. They are known as anagenesis and katagenesis, respectively. Within lineages of genera anagenesis and subsequent katagenesis occur, for example within Bryozoa (evolution of *Stomatopora* studied by Lang, 1905, see also Swinnerton, 1923, p. 103, fig. 81) and Gastropoda (evolution of *Procerithium*, studied by MacDonald & Trueman, 1921). Within the class of Cephalopoda clear examples of anagenesis and subsequent katagenesis can also be found. First straight shells of the type *Orthoceras* occur; in the course of their evolutionary development these shells curled into increasingly tighter rolls. By the time the ammonites became extinct in the Late Cretaceous many species had again unrolled. These phenomena are best understood when we consider them as ageing processes. Other evolutionary theories provide no explanation at all.

Initially many palaeontologists regarded such developments as ageing processes, but during the past several decades most biologists, including such well-known scientists as Dobzhansky (1955), Rensch (1954, 1959) and Mayr (1966), and many palaeontologists, especially Simpson (1944, 1949 and 1953), have stated that ageing processes do not exist in evolution.

Dobzhansky (1955) presumes along with many others that he has found the proof that evolutionary youth and senescence do not exist in the fact that all species of a large group of animals, for instance the reptiles, do not become extinct simultaneously. According to him it is inconceivable that the origin of all orders occurs in the so-called youth of the reptiles, and not in the so-called maturity of that group when the abundance in number of species and forms is greatest.

To this I would like to offer the following answer. In the first place it is an unallowable generalization to suppose that the phylogenetic ageing of a whole group proceeds at the same rate and also simultaneously. Many palaeontological data, including those in this publication, prove that the rate of evolution is highly variable. This pertains to the animal kingdom as a whole as well as to a relatively small group of closely related organisms like a family. If this rate is very slow or nearly absent, an evolutionary lineage can exist for a long time. Moreover if the size of the individuals of a species of a lineage compared with that of the individuals of the species in the same stage in the preceding lineage has not increased or only slightly, evolution can go on for a long time. Other lineages develop quickly so that they grow old soon and become extinct rapidly. Therefore it is possible that

some species of a group like the reptiles become extinct sooner than others, and those lineages which develop very slowly continue to exist. On the average the reptiles are phylogenetically older than the mammals; this does not alter the fact that some lineages of the reptiles may be younger in the evolutionary and the genetic sense.

Secondly it is not surprising that most of the higher taxonomic units are already established during the youth of a group, whereas only lower taxonomic units originate when such a group is mature. The taxonomic system remains artificial. If we only knew the beginning of a group and not its derivatives which have developed by adaptive radiation, then it is quite likely that we would not try to divide the group into such highly ordered units because the ancestors of all subgroups resembled one another much more than the later descendants.

Undeniably there are many examples of evolution proceeding in certain directions. Such trends were called orthogenesis by Eimer. For many groups of animals the evolutionary development of the lineages does indeed seem to follow a straight line when we consider only a small part of the history of a lineage. Many characteristics change simultaneously and always in the same direction. When we study for example the alveolines, a group of Foraminifera, an increase in the size of the skeletons, indicated mainly by the increasing length, is very obvious; furthermore the mean size of the proloculus increases gradually together with the number of chambers per winding.

Such changes however always undergo accelerations and retardations and therefore orthogenesis is in fact a misleading term, which it is better not to use. I propose the term gerontogenesis (from Gr. γερων, γερωντος = old man, and Gr. γενεσις = origin, creation, birth descent) because it is mainly ageing processes which regulate the development during this part of evolution. Nevertheless these specific trends do exist and cannot be explained by natural selection and changes in environment since they are too similar and too constant. If the milieu should cause such trends, they would be much more capricious and more unequal. The only possibility is that these trends are controlled by the genes, as Goldschmidt (1933, p. 544) already has said: "... orthogenesis is not the result of the action of selection or of a mystical trend, but a necessary consequence on the way in which the genes control orderly development - a way which makes only a few directions available to mutational changes, directions which if once started and not acted upon by counter-selection, will be continued". Only the genes are so stable within hereditary processes that they can cause such slow processes as gerontogenesis. Neither within organisms nor outside organisms is such a remarkably stable mechanism as genetic reproduction known, in spite of the possibility that mutations can occur.

The general pattern of the evolutionary development of lineages, beginning with neogenesis, continued by phylogenetic stages 1 to 4 and ending with extinction however is unchangeable. The different phylogenetic stages always have their own ontogenetic curves. The fourth stage for example always is characterized by the retrograde curve with its concave end; the retrograde curve has never been found in the preceding stages.

Superimposed on the long-term ageing processes are the influences of environment and natural selection which can distort some features of the development of a lineage. Temporarily the individuals can become smaller than their immediate ancestors and descendants of the same lineage when they have had to live in far from favourable circumstances. A good example can be found in the *Gadichthys* lineage (see

Enclosure 1) where the otoliths of *G. benedei* and *G. verticalis* are definitely smaller than those of *G. antwerpiensis* and *G. thori*. Thanks to the year rings which are present in otoliths this can be ascertained without a doubt. *G. miocenicus* possibly takes up an intermediate position in this respect, but the year rings of this species have not yet been studied. The recent *G. thori* lives in fairly deep water (60 - 1.000 m, but preferably 100 - 300 m in depth). *G. antwerpiensis* and its forerunners also must have lived in rather deep water since they are not known from deposits close to the ancient coasts. In contrast otoliths of *G. benedei* and especially *G. verticalis* have been found in large quantities in sediments deposited in shallower water. Probably *Gadichthys* was not able to escape from the Pliocene North Sea which was closed at that time in the South and thus only connected with other seas and oceans in the North between Scotland and Norway. Probably the circumstances in the northern part of the North Sea were even more unfavourable than in the South so that *Gadichthys* was imprisoned and had to find temporarily another environment as suitable as possible in order to be able to survive. Although the otoliths (and consequently also the fishes as a whole) of *Gadichthys* in the Pliocene were smaller than expected on the basis of the ageing processes, the ontogenetic curves of the L-H ratio and L-T ratio were in complete agreement with this theory. It is evident from this that the absolute size is not an entirely reliable factor by which to determine the phylogenetic stage. For this determination it is always necessary to know the ancestors or the ontogenetic curves of the species in question and preferably even both.

One can expect that animal groups, which live in environments that are geographically and ecologically more uniform, undergo such size-reductions much more rarely than animal groups living in more changeable environments. Inhabitants of the sea therefore on an average will undergo less size-reductions in their gerontogenesis than inhabitants of the land. This makes the study of the main lines of evolution of land animals generally more difficult than that of sea animals.

As yet this is the only known aberration within the Gadidae. For many other animal groups however reduction in the size of the individuals is known to have occurred at a time when circumstances were less favourable. It will be clear, I think, that such irregularities will obscure the general trends of evolution. Therefore I believe that a renewed careful study of the well-known and well-documented family trees, whereby the general trends are separated (if possible) from the irregularities caused by environmental changes, will bear much fruit.

Perhaps the origin of new families and higher taxonomic units can be explained by neogenesis on a larger scale than that of genera. It is quite striking that these groups too always start with small individuals.

Finally it is necessary to mention genetics. Nowadays most geneticists believe that genes determine not body parts but developmental processes (Dobzhansky, 1955). If this is true, the ageing processes also have to be governed by genes, for ageing comprises all developmental processes of an individual. Together with Goldschmidt (1933, p. 543) I therefore can conclude: "The nature and the working of the developmental processes of the individual then should, if known, permit us to form certain notions regarding the possibilities of evolutionary changes".

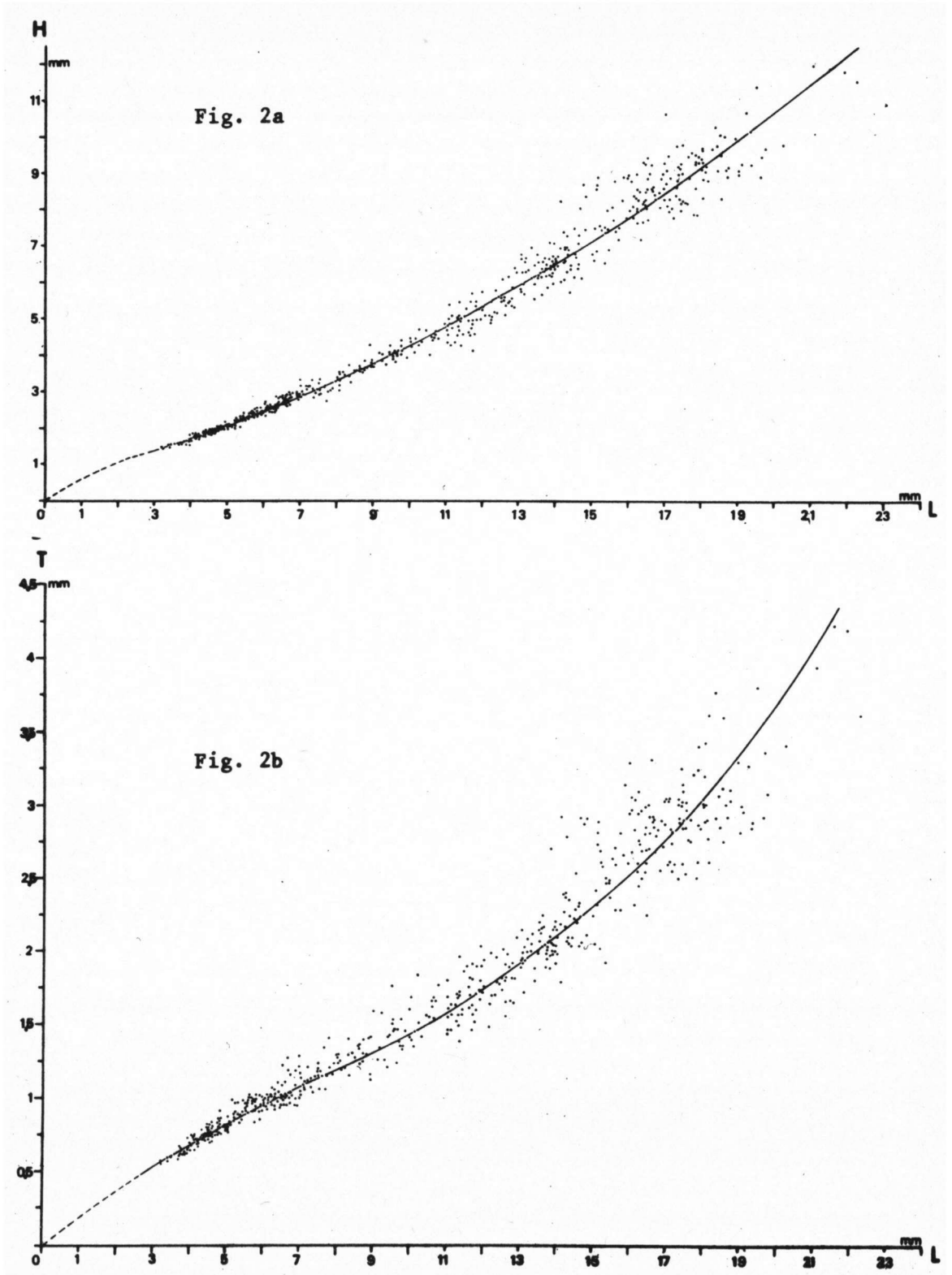


Fig. 2a-b. Sagittas of *Gadus morhua* Linnaeus, 1758. North Sea, Recent.
2a. Relation between length and height.
2b. Relation between length and thickness.

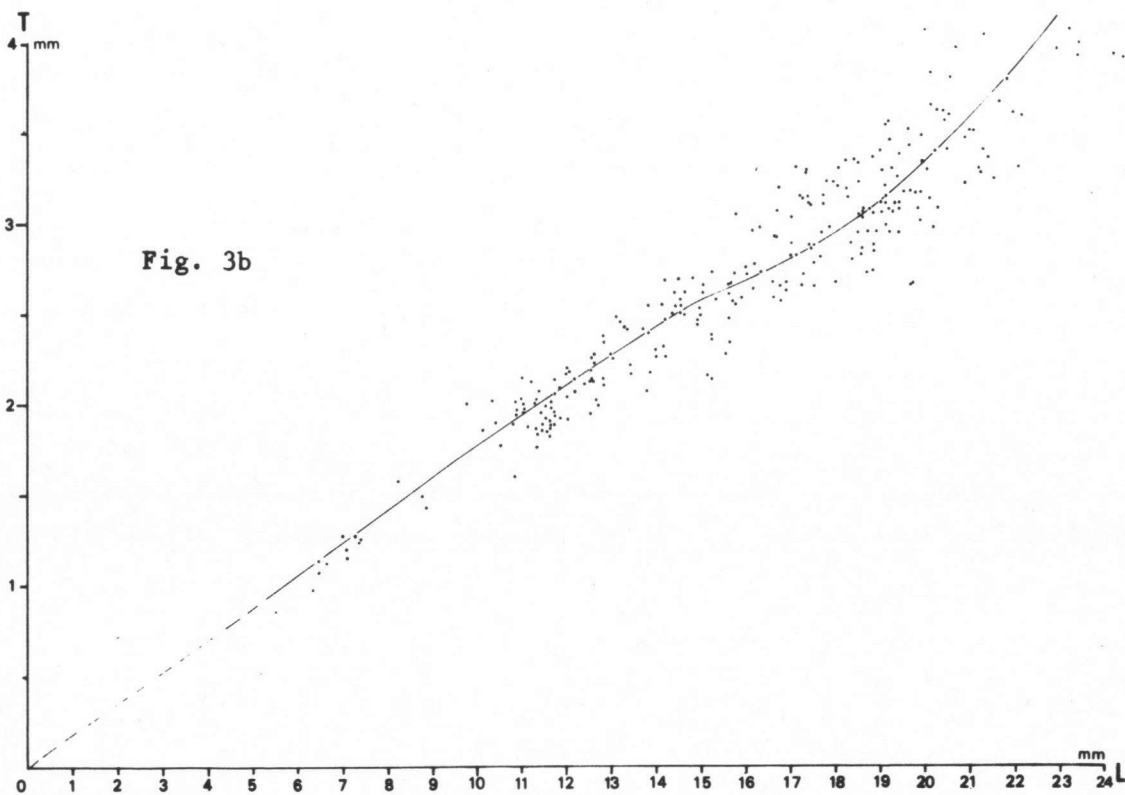
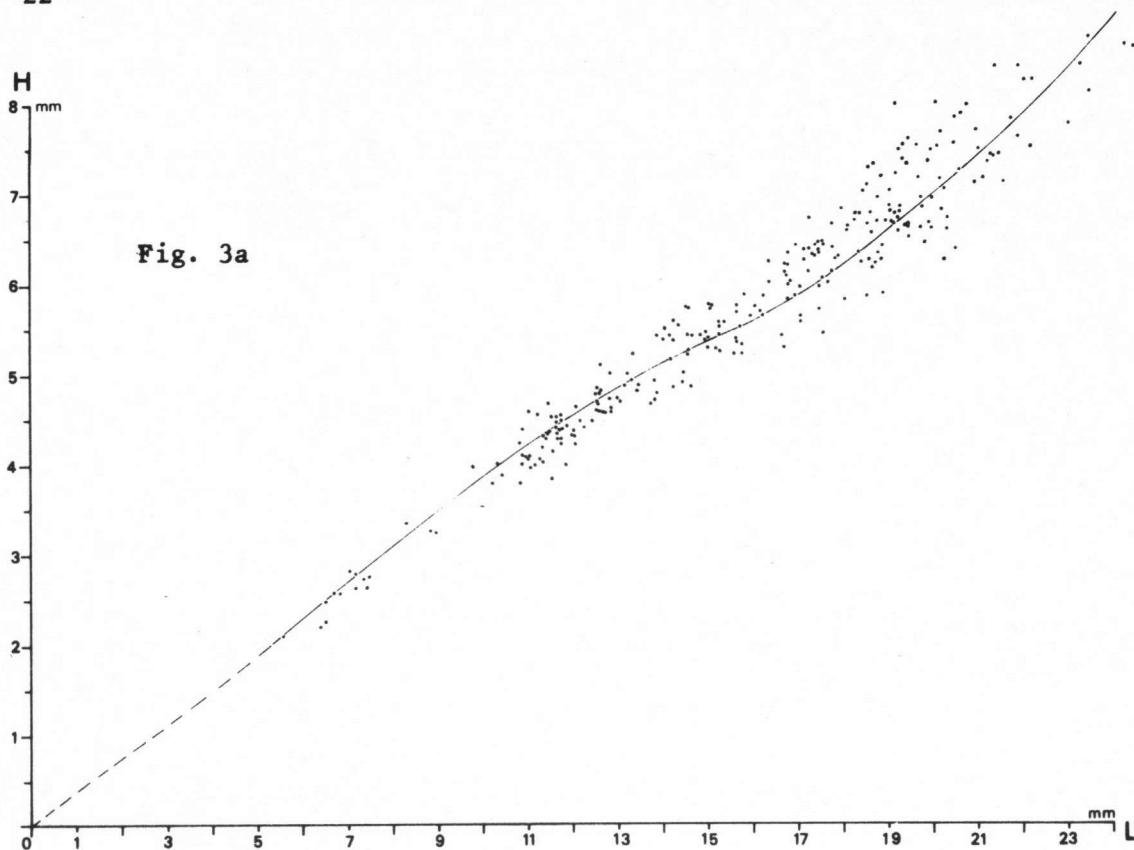


Fig. 3a-b. Sagittas of *Melanogrammus aeglefinus* (Linnaeus, 1758). North Sea, and sea west of Scotland, Recent.
 3a. Relation between length and height.
 3b. Relation between length and thickness.

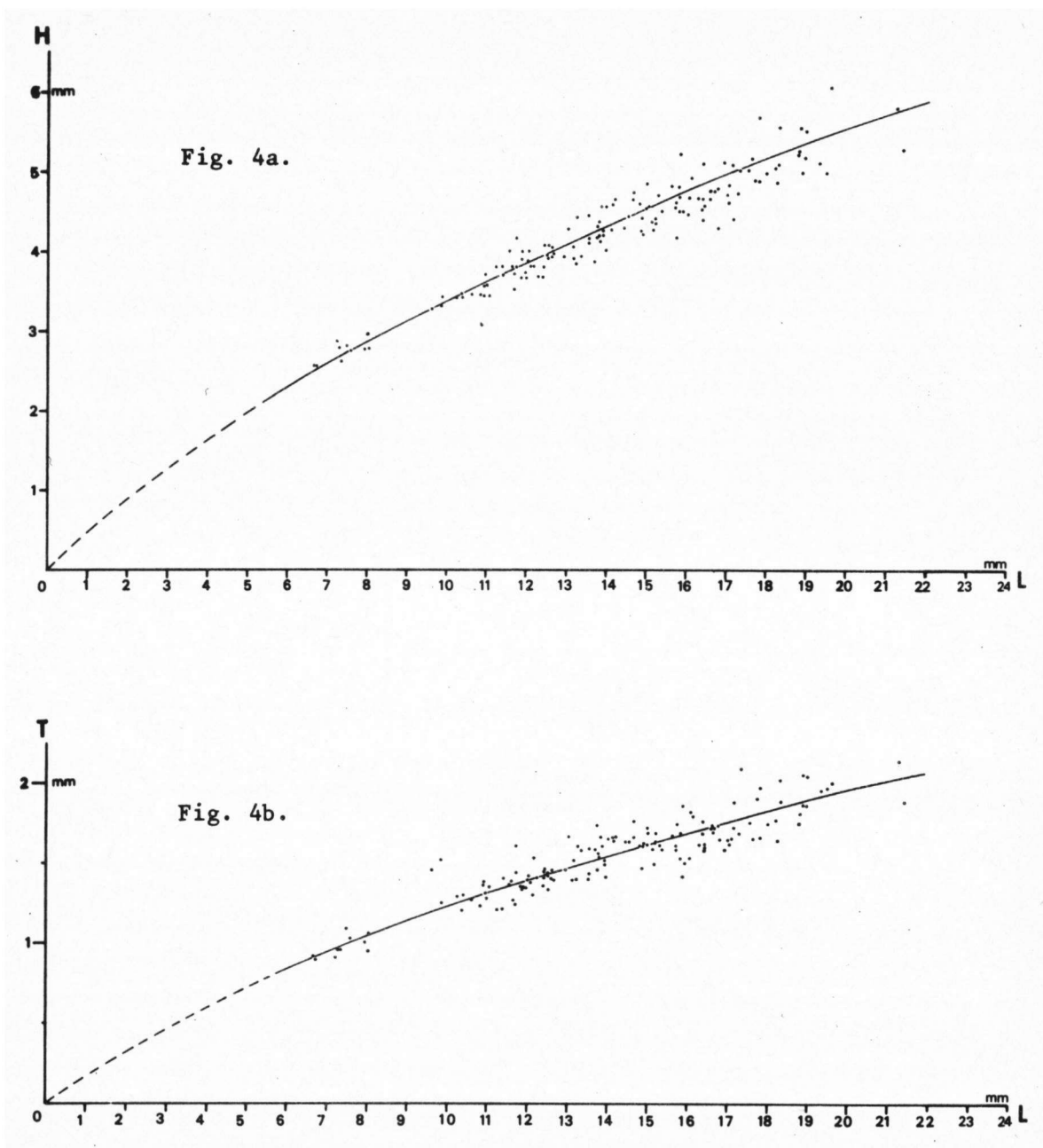


Fig. 4a-b. Sagittas of *Merlangius merlangus* (Linnaeus, 1758). North Sea, Recent
4a. Relation between length and height.
4b. Relation between length and thickness.

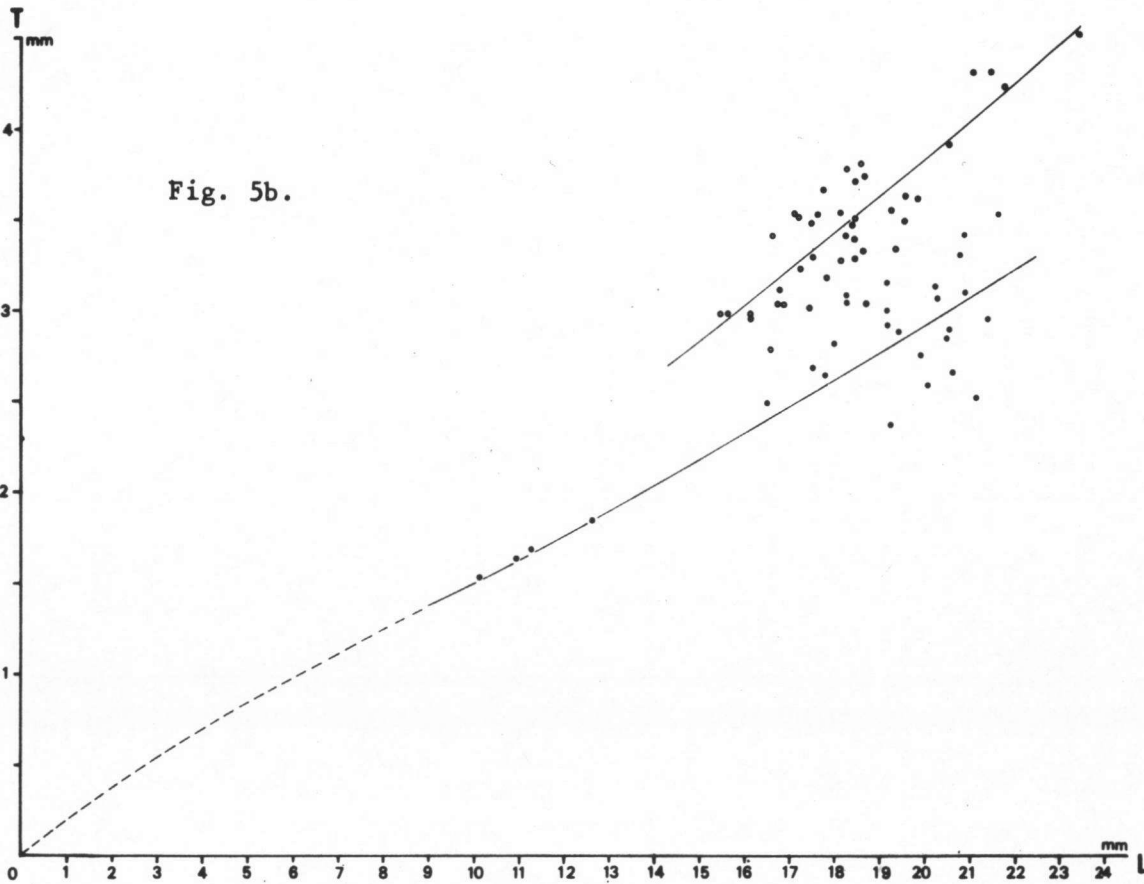
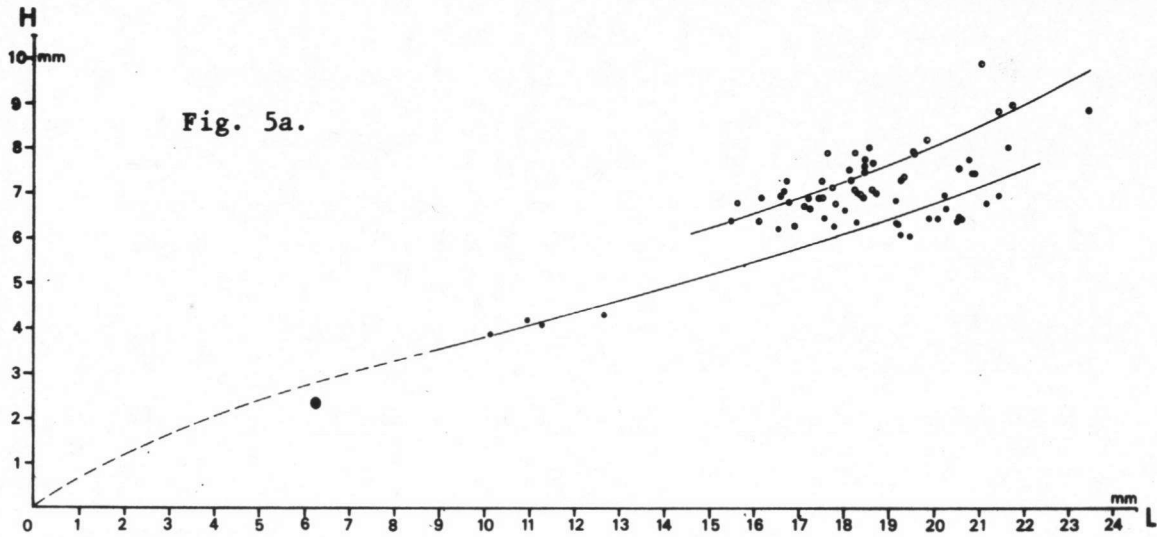
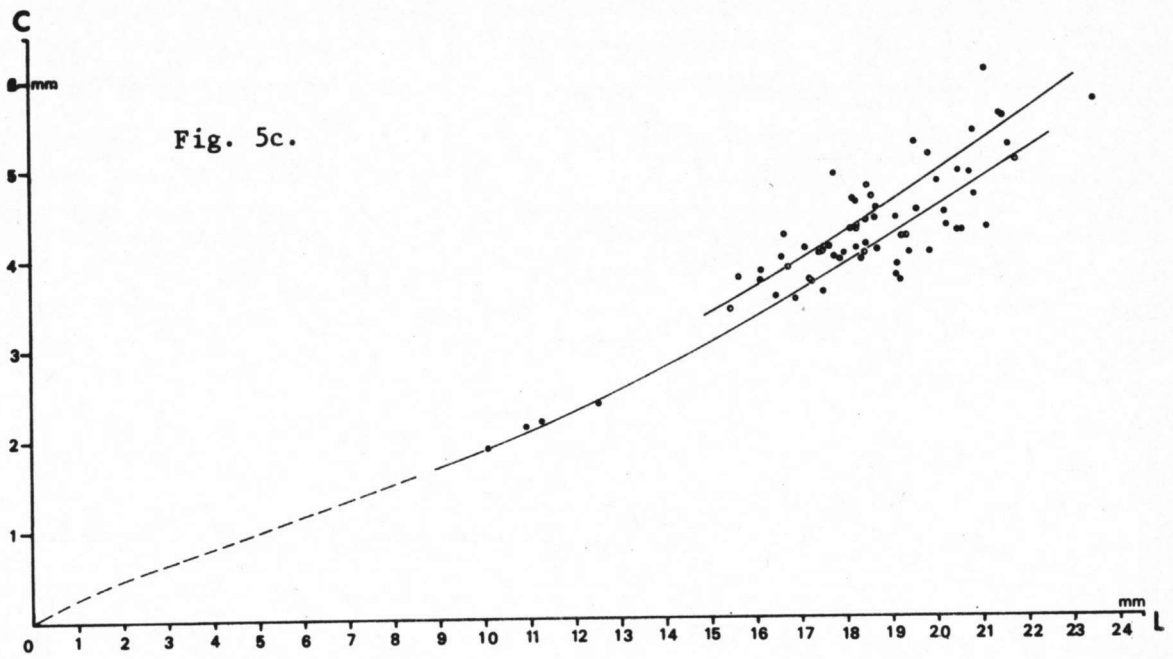


Fig. 5a-c. Sagittas of *Pollachius virens* (Linnaeus, 1758) (open circles) and *P. carbonarius* (Linnaeus, 1758) (black dots). North Sea, Recent.
 5a. Relation between length and height.
 5b. Relation between length and thickness.



5c. Relation between length and curvature.

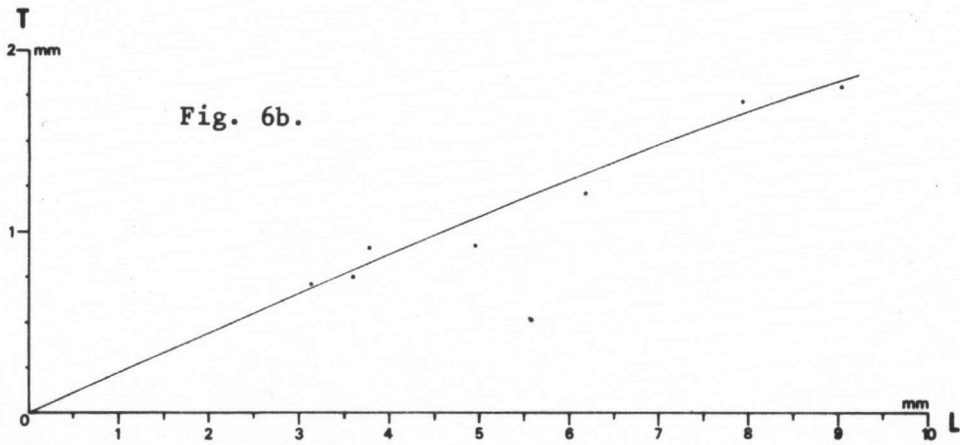
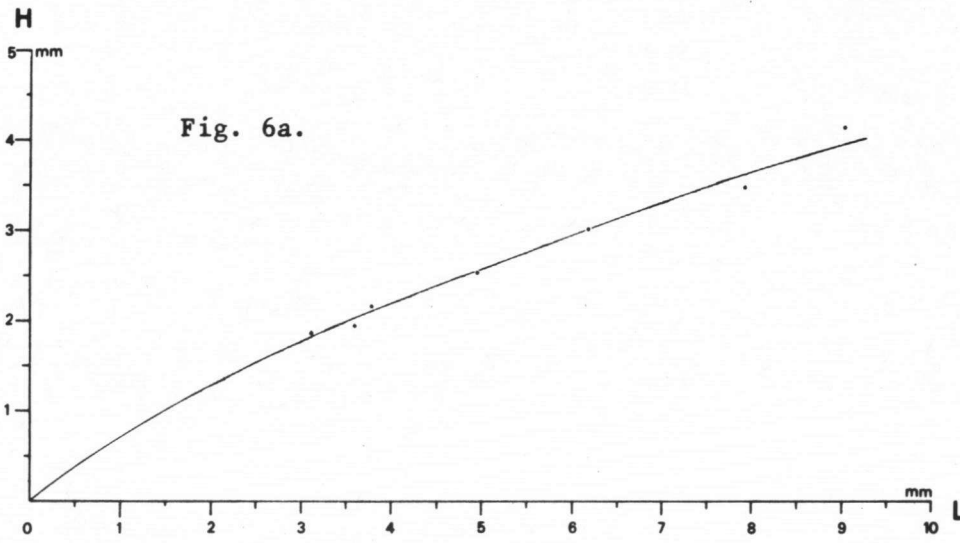


Fig. 6a-b. Sagittas of *Gadichthys undosus* Gaemers, 1973. Neubörnsen, Germany, Late Oligocene.

6a. Relation between length and height.

6b. Relation between length and thickness.

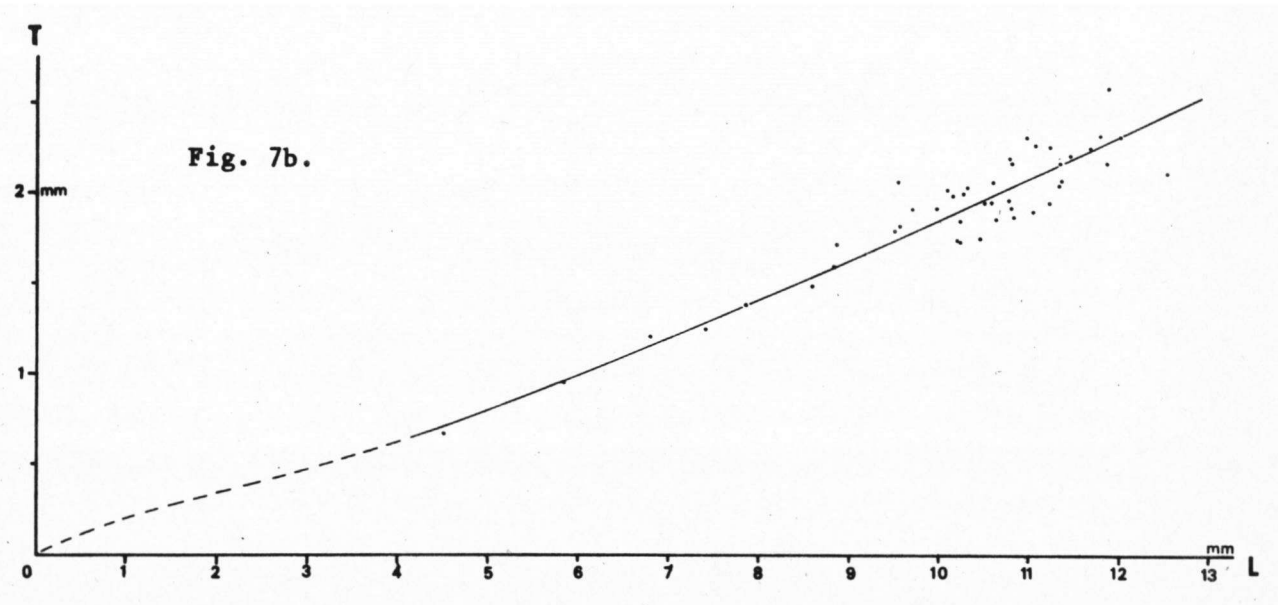
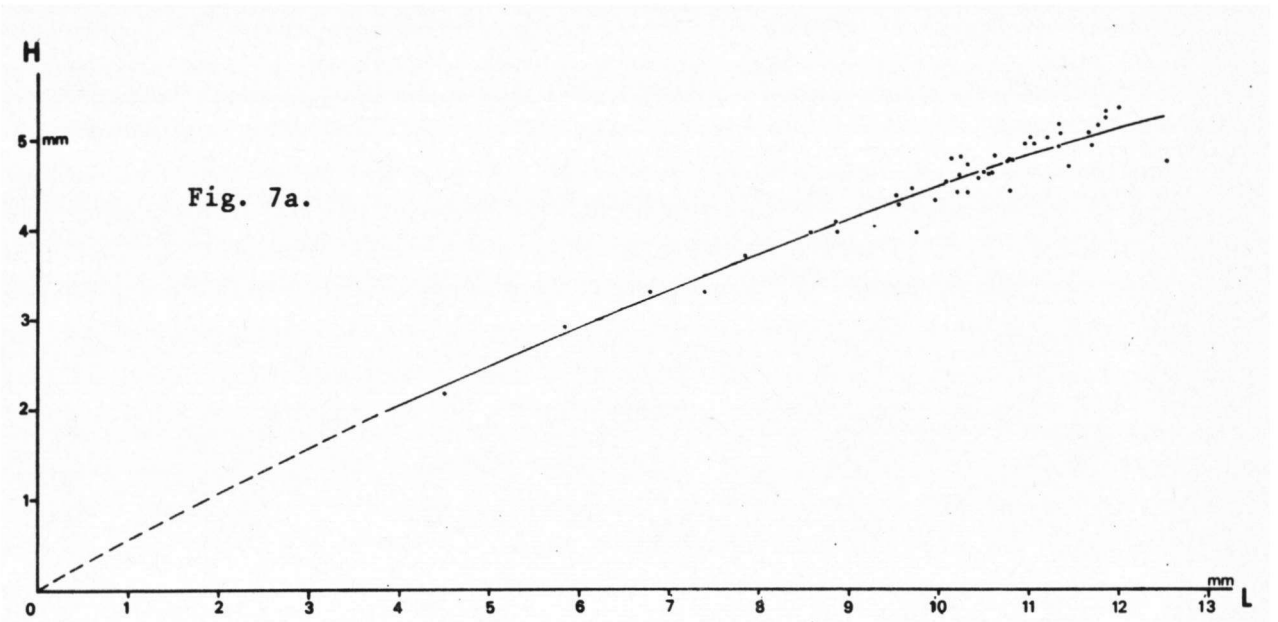


Fig. 7a-b. Sagittas of *Gadichthys antwerpiensis* (Gaemers, 1871). Antwerp, Belgium. Sands of Edegem, Early Miocene.
7a. Relation between length and height.
7b. Relation between length and thickness.

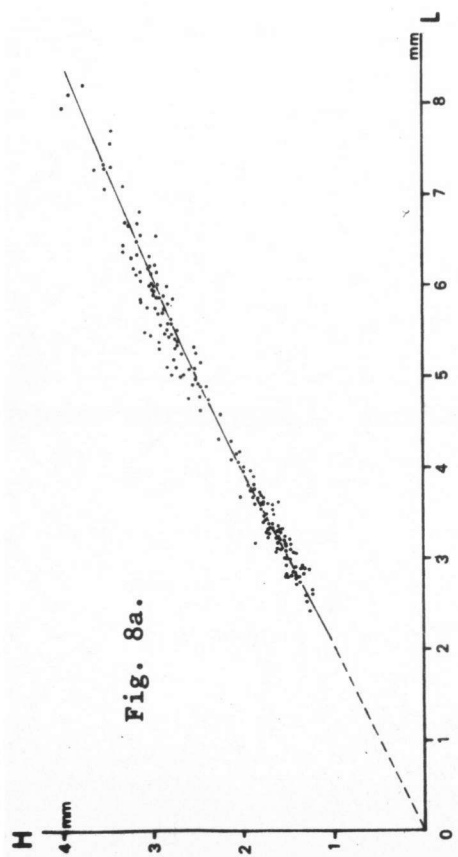


Fig. 8a.

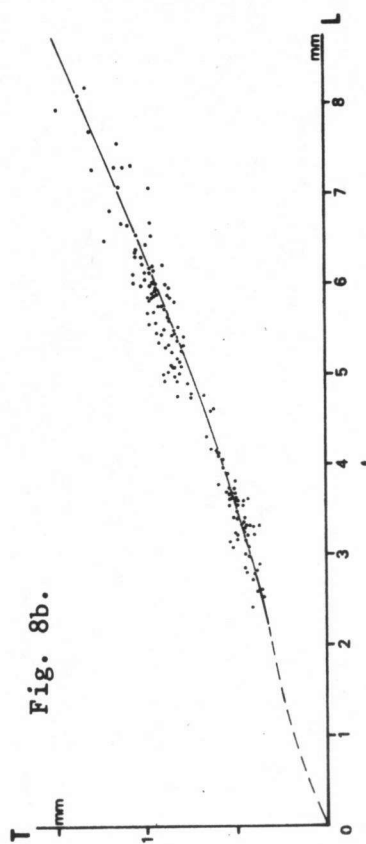


Fig. 8b.

Fig. 8a-b. Sagittas of *Gadichthys benedeni* (Leriche, 1926). Antwerp, Belgium, Sands of Kattendijk, Early Pliocene.
 8a. Relation between length and height.
 8b. Relation between length and thickness.

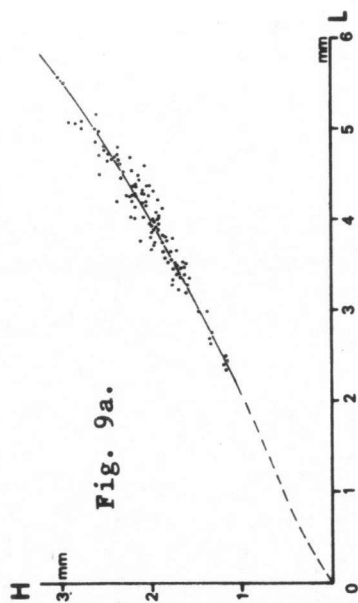


Fig. 9a.

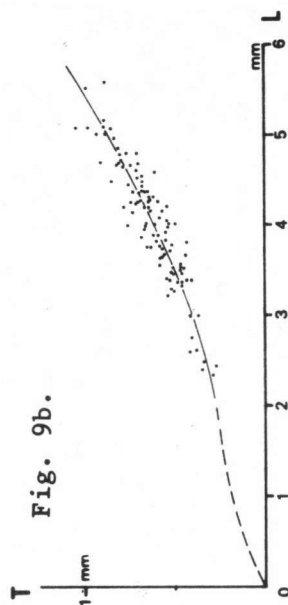


Fig. 9b.

Fig. 9a-b. Sagittas of *Gadichthys verticalis* (Gaemers & Schwarzhans, 1973). Boring Ouwerkerk, the Netherlands, Late Pliocene.
 9a. Relation between length and height.
 9b. Relation between length and thickness.

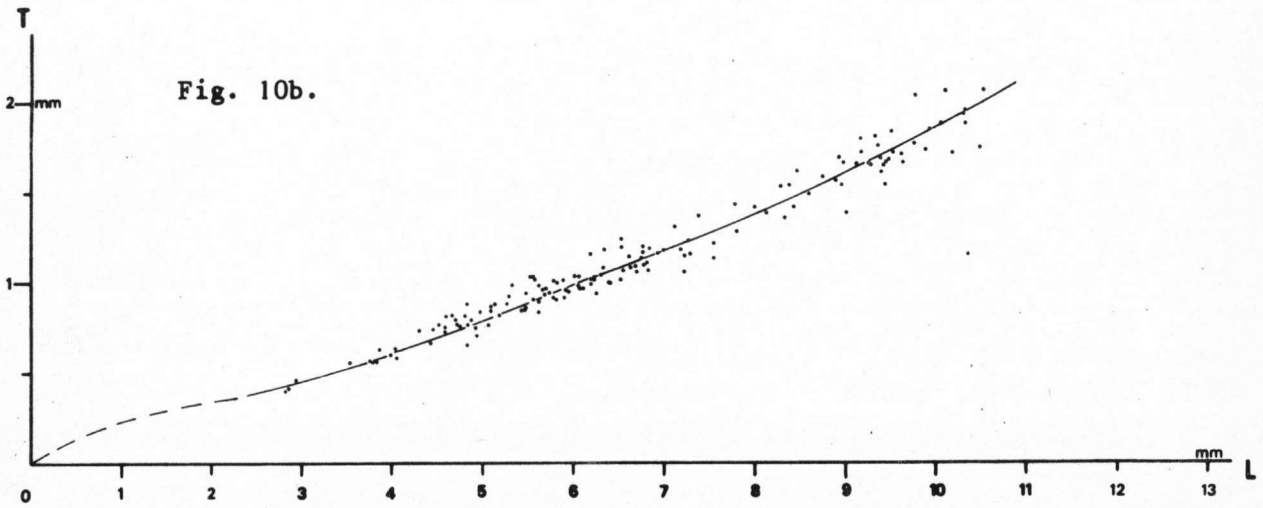
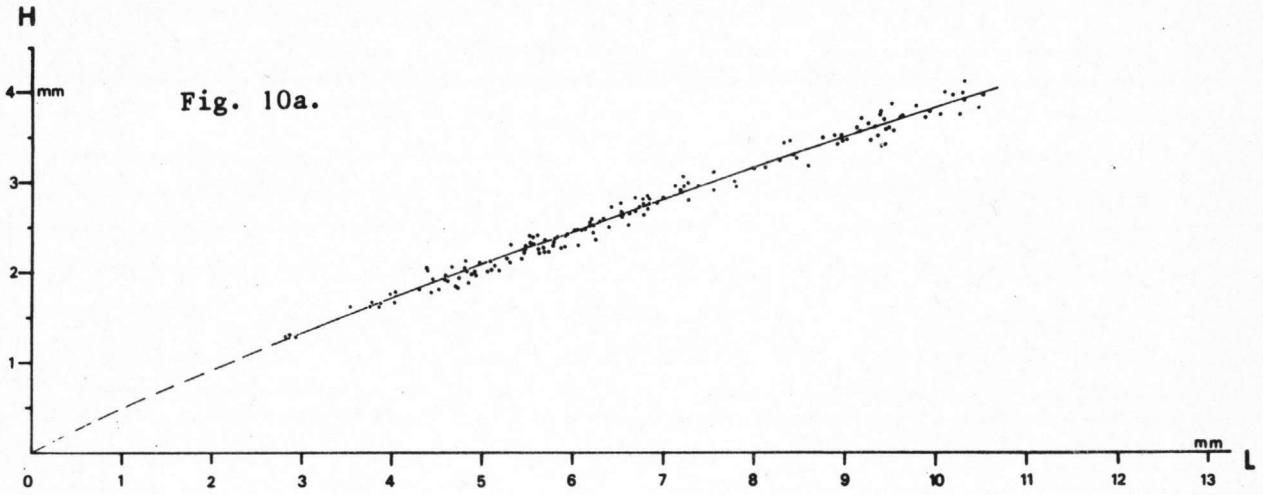


Fig. 10a-b. Sagittas of *Colliolus johannettae* Gaemers. Antwerp, Belgium, Sands of Edegem, Early Miocene.

10a. Relation between length and height.

10b. Relation between length and thickness.

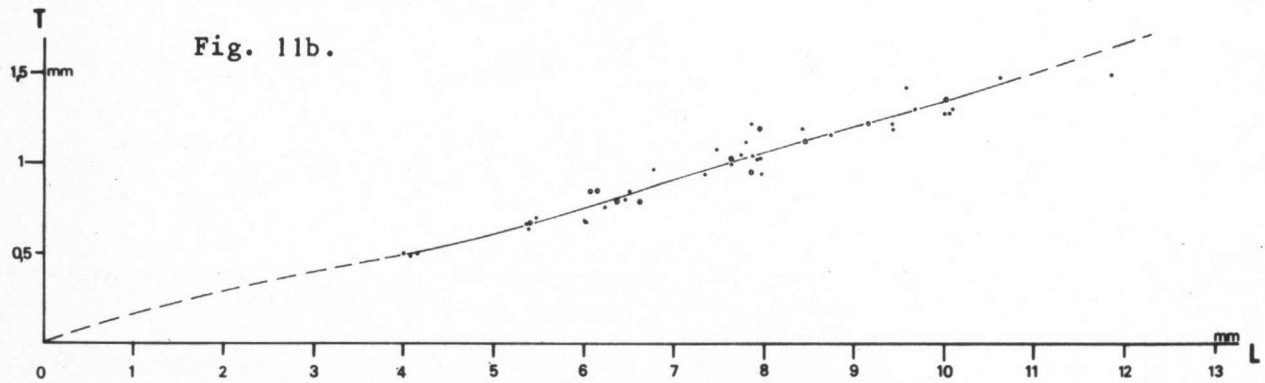
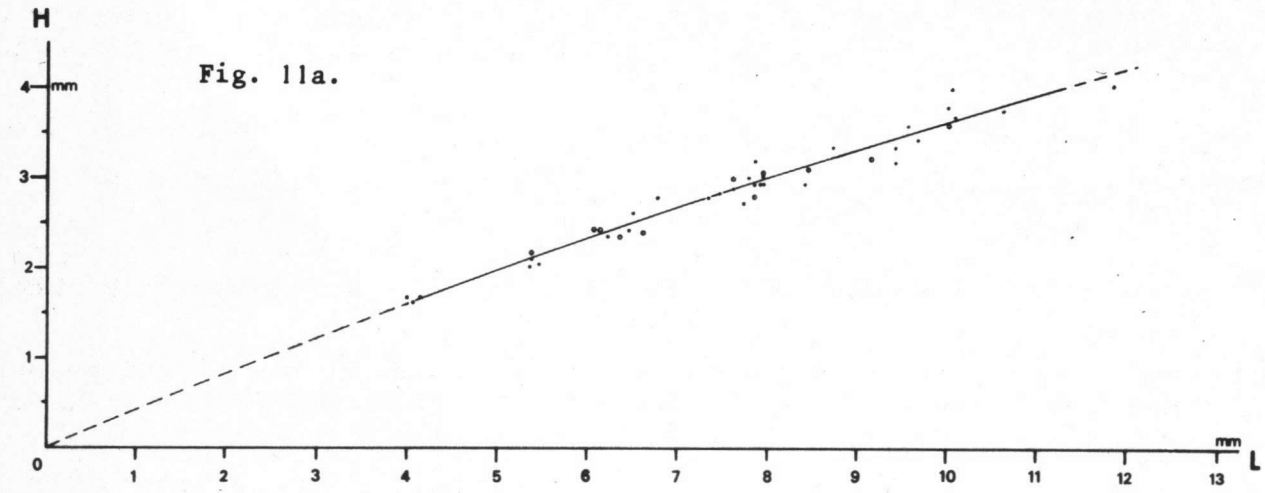
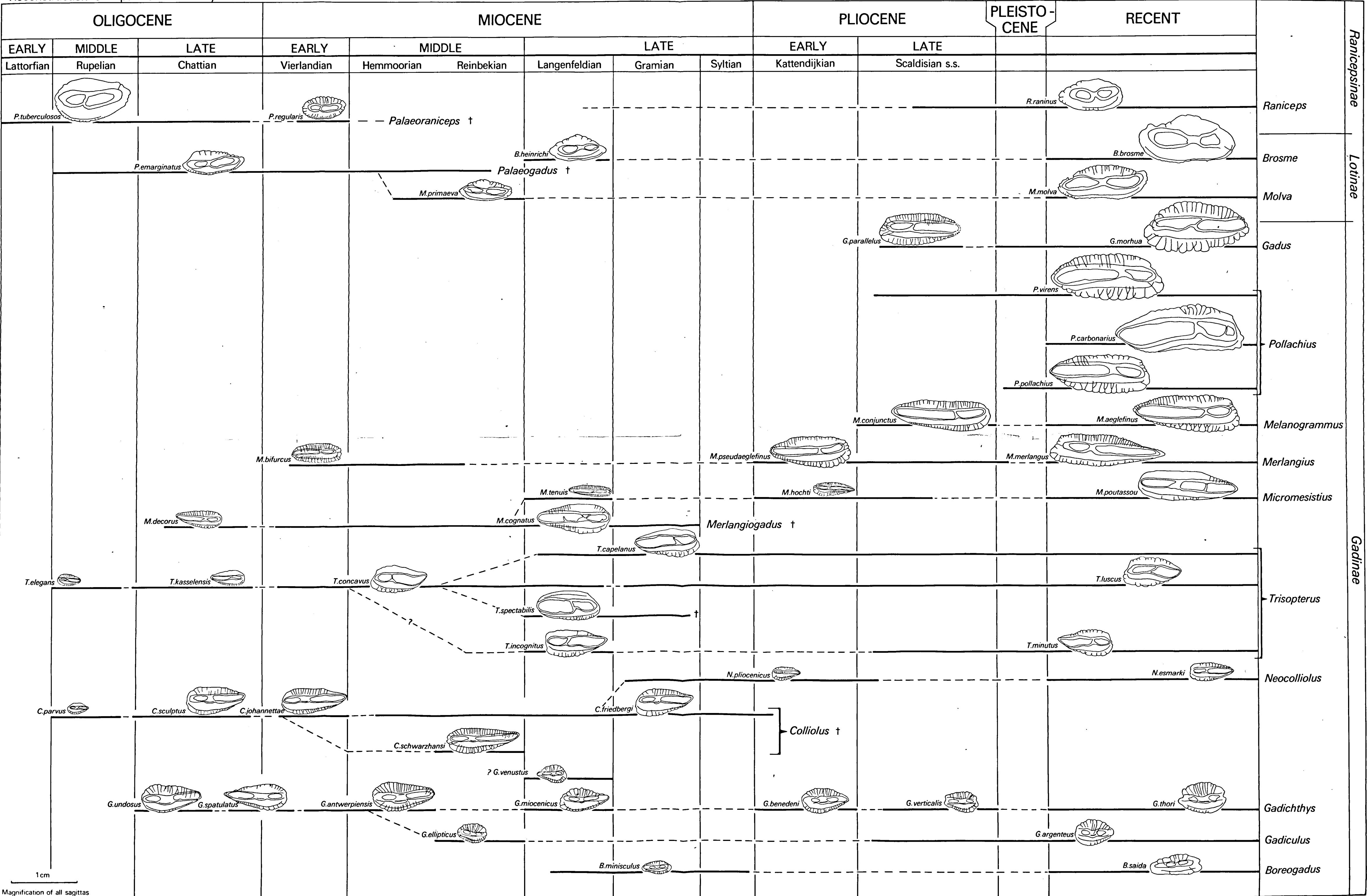


Fig. 11a-b. Sagittas of *Colliolus schwarzhansi* Gaemers. Dingden, Germany. Dingdener Feinsand (in the sense of Janssen, 1967) (black dots) and Dingdener Glimmertone (open circles), Middle Miocene.
 11a. Relation between length and height.
 11b. Relation between length and thickness.

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1cm
Magnification of all sagittas