

HETEROCHRONY WITHIN AMBLYPTERIDAE (ACTINOPTERYGII; PERMO-CARBONIFEROUS) ?

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Abstract : Certain morphological traits of the Amblypteridae, i.e. *Amblypterus* and *Paramblypterus*, suggest local heterochronic processes by paedomorphosis. Since data on the ontogenetic stages of an ancestral paramblypterid species are not available, *Elonichthys palatinus*, a fairly basal actinopterygian species, is used as a model for the potential ancestral ontogeny to polarize patterns of heterochrony in the Amblypteridae. Presumably, ornamentation and shape of the skull, squamation, and growth of the opercular series of *Paramblypterus* and/or *Amblypterus* were affected by processes related to heterochrony.

Key words: lower actinopterygians, Permo-carboniferous, heterochrony, paedomorphosis, skull, squamation, opercular series

Hétérochronie chez les Amblypteridae (Actinopterygii, Permo-Carbonifère) ?

Résumé - Certains traits morphologiques des Amblypteridae, i.e. *Amblypterus* et *Paramblypterus*, suggèrent une hétérochronie correspondant à une paedomorphose. Les différentes étapes ontogénétiques des Paramblypteridae basaux n'étant pas connues, une espèce d'actinoptérygien basal, *Elonichthys palatinus*, est utilisée comme modèle pour reconstruire un ancêtre potentiel afin d'établir les formes d'hétérochronie chez les Amblypteridae.

Vraisemblablement, l'ornementation et la forme du toit crânien, la squamation, et la croissance de la série operculaire de *Paramblypterus* et/ou d'*Amblypterus* sont affectées par des processus conditionnés par l'hétérochronie.

Mots-clés : Actinoptérygiens basaux, Permo-Carbonifère, hétérochronie, paedomorphose, toit crânien, squamation, série operculaire.

INTRODUCTION

Studies of the Amblypteridae are connected with research on paleoecosystems of lakes from the Lower Permian of Central Europe (e.g., Boy, 1994, 1998, in press; Boy *et al.* 1994; Clausing & Boy, 2000). Objectives are the reconstruction of environmental conditions, paleocommunities, and food chains. The members of the family Amblypteridae, *Paramblypterus duvernoyi*, *P. gelberti*, *P. decorus*, and *Amblypterus latus*, have been (re)described recently (Dietze, 1998, 1999, 2000). Their morphology and intra-specific variation has been examined in detail and were the basis for three-dimensional models of the skull

and the body. One objective of the restoration in three dimensions was to gain a certain understanding of the biology of *Paramblypterus duvernoyi* and its relatives. The likely diet and food uptake, and the likely locomotor capabilities of *Paramblypterus* have been dealt with earlier (Dietze, 2001). In the following, I will point out heterochronic processes that probably affected the morphology of the skull, ornamentation of the skull bones, growth of the opercular series, and the serration of the scales.

Heterochrony is the change in the relative time of appearance or rate of development of a character during phylogeny and is considered part of evolutionary mechanisms (e.g., Gould, 1977; Alberch *et al.*,

1979; Alberch & Alberch, 1981; Hall, 1984; McNamara, 1986). During ontogeny, the development or onset of growth of certain structures may be accelerated or slowed down in relation to the ancestral state, which is called peramorphosis and paedomorphosis, respectively (Gould, 1977; Alberch *et al.*, 1979; McNamara, 1986).

Paedomorphosis refers to the retention of ancestral juvenile characters in the descendant adult phase by either progenesis, neoteny, or post-displacement. Progenesis corresponds to precocious sexual maturation, neoteny to reduced rate of morphological development, and post-displacement to delayed onset of growth (Gould, 1977; Alberch *et al.*, 1979; McNamara, 1986). Neoteny, progenesis, and post-displacement can affect only certain structures or major entities of the organism. This is referred to as local or global changes, respectively (McKinney & McNamara, 1991).

Morphological changes related to heterochrony have been described for many recent vertebrate taxa, such as cichlid (Mayer, 1987) and characid (Fink, 1989) fishes, salamanders (Gould, 1977; Alberch & Alberch, 1981), snakes (Irish, 1989), and rodents (Hafner & Hafner, 1984). In fossil vertebrate species, heterochrony is difficult to identify, since more often than not, ontogenetic stages of a possible ancestor are not available. Still, features related to heterochrony could be postulated for a variety of taxa, such as diploans (Bemis, 1984), certain dissorophoid amphibians (Boy, 1993, 1995; Schoch, 1995), dinosaurs (Long & McNamara, 1995), and deer (Gould, 1974).

Certain morphological traits of the Amblypteridae suggest local heterochronic processes by paedomorphosis.

MATERIAL AND METHODS

Material of the Amblypteridae, i. e. the genera *Paramblypterus* Sauvage, 1888 and *Amblypterus* Agassiz, 1833, examined here, is from Late Carboniferous to Early Permian lacustrine deposits from the Saar-Nahe Basin of Germany (e.g., Boy, 1976, 1994; Dietze 1999, 2000) and from the Commentry Basin of France (Blot, 1966; Poplin 1994). The type species of *Paramblypterus* is *Paramblypterus decorus* (Egerton, 1850) designated by Blot (1966). Other species

included in this genus are *Paramblypterus duvernoyi* (Agassiz, 1833), *Paramblypterus gelberti* (Goldfuss, 1847), and *Paramblypterus rohani* (Heckel, 1861). The remaining nominal species in the genus (*P. caudatus*, *P. luridus*, *P. obliquus*, *P. reussi*, *P. comblei*, and *P. gaudryi*) either represent junior synonyms, or are known too poorly to allow for a comparison (Dietze, 2000). *Amblypterus*, the other genus of the Amblypteridae, contains only one species, *Amblypterus latus* Agassiz 1833.

In the course of this study, 413 specimens of *Paramblypterus duvernoyi* (Agassiz, 1833) with a size range of 19 - 220 mm, 106 specimens of *Paramblypterus gelberti* (Goldfuss, 1847) with a size range of 35.5 - 151 mm, 83 specimens of *Paramblypterus decorus* (Egerton, 1850) with a size range of 66 - 245 mm, and 73 specimens of *Amblypterus latus* with a size range of 34 - 128 mm were examined, thus representing the most comprehensively examined family of basal fossil actinopterygians to date. Intra-specific variation concerning the dermohyal, «suborbital», rostral, parietal and extrascapular bones of these species have been described earlier (Dietze 1999, 2000). For a complete list of catalogue numbers see Dietze (2000).

Specimens from the Saar-Nahe Basin and the Commentry Basin are preserved as compressions flattened during fossilization either articulated or disarticulated. Bones of articulated specimens usually are somewhat spread out around the midline of the body by post-mortem bursting, thus preventing bones from being distorted. Surface structure, such as sculpturing of the skull roofing bones and scales, is present on many specimens. A Wild M8 microscope equipped with a *camera lucida* was used to draw the specimens. Drawings of the best preserved specimens were used for three-dimensional restoration. These drawings were transferred onto thin paper which was melted on thin plates of bees' wax. These paper and wax «bones» of the skull and palate were then cut out and assembled in a three-dimensional model. The paper was used as control as not to exceed the degree of bending and to avoid too much distortion of the wax and paper bones. Reconstruction of the postcranial part was undertaken in similar fashion and, including the restored fins, fit onto the reconstructed skull and photographed. Trunk length was measured from the posterior margin of the

supracleithrum to the centre of the caudal fin. To establish D-values (Schmidt-Kittler, 1984, 1986), drawings of the scales and opercular bones were digitised in AUTOCAD 12 and areas and circumference were calculated. D-values can be used to distinguish shapes by comparing them to the area of a circle with the same circumference (L) as the object in question (Schmidt-Kittler, 1984, 1986). D is a descriptive parameter and equals the area of the according circle divided by the area of the shape (F) :

$$D = \frac{L^2}{4 \pi \cdot F}$$

Objects with an area similar to that of a circle yield D-values close to 1, whereas more complex shapes have higher D-values.

Areas and circumference of subopercular and opercular bones calculated in AUTOCAD 12 were also entered into a two-sample analysis. In order to compensate for the size of the specimens, this value was divided by the standard length of the individual specimen.

Paramblypterus differs from *Amblypterus* by the following characters: «nasal» split up secondarily. Dermohyal not present as a single ossification. More than two «suborbitals». Seven to nine branchiostegal rays. Gap between opercular series and skull roofing bones absent. Duplication of the extrascapular series present. Scales serrated weakly, with little ornamentation.

Paramblypterus decorus is characterized by the following combination of characters: all bones of the skull ornamented densely. Parietal process absent. Rostral flaring anteriorly. Almost equal sized dermosphenotic 1 and supratemporal. Sturdy sclerotic bones present. Six to nine «suborbital» bones. Maxillary plate of medium depth. Premaxilla contacts lacrimal ventrally. Seven to ten dermohyal bones. Dermosphenotic 1 contacts «nasal 1». Jugal 2 contacts «spiracular». «Spiracular» angular. Nine branchiostegal rays. Postcleithral region variable; up to three enlarged scales ventral to postcleithrum. Forty-six or forty-seven scale rows along lateral line. Scales serrated weakly.

Paramblypterus duvernoyi is characterized by the following combination of characters: distinct ornamentation of parietals, postparietals, extrascapulars, posttemporals, dermosphenotics, supratemporals and supracleithra. Parietals with variable lateral process. One or two medial extrascapular(s). Additional lateral extrascapulars contact opercle. Rostral tapering anteriorly. Sclerotic bones absent. Six «suborbital» bones. Maxillary plate deep. One or two dermohyal bones. «Spiracular» rounded. Opercular and subopercular areas and D-values different from those of *P. gelberti*. Eight branchiostegal rays. D-values of scales 1.4 to 2.0. Area of serrated scales narrowing towards anal fin. Forty-two ± two scale rows along lateral line.

Paramblypterus gelberti is characterized by the following combination of characters: little ornamentation of parietals, postparietals, extrascapulars, posttemporals, dermosphenotics, supratemporals and supracleithra. Parietals with lateral process. One or two medial extrascapular(s). Additional lateral extrascapulars do not contact opercle. Rostral tapering anteriorly. Sclerotic bones absent. Five «suborbital» bones. Maxillary plate deep. One to three dermohyal bones. «Spiracular» rounded. Eight branchiostegal rays. D-values of scales higher than 2.0. Forty-two ± two scale rows along lateral line. Area of serrated scales on body not tapering towards anal fin. Ornamentation of scales fairly prominent.

The genus *Amblypterus*, and its only species *Amblypterus latus*, are characterized by the following combination of characters: distinct ornamentation of parietals, postparietals, extrascapulars, posttemporals, dermosphenotics, and supratemporals. No parietal process. Single pair of lateral extrascapulars. Rostral probably tapering anteriorly (Gardiner, 1963). Delicate sclerotic bones present. «Nasal» present as single ossification. «Nasal» borders the orbit anteriorly. Supratemporal more than two times longer than dermosphenotic 1. Dermosphenotic 1 and dermosphenotic 2 contact «nasal». Single dermohyal. Two «suborbitals». Maxillary plate deep. Ten branchiostegal rays. Postcleithrum absent. Posterior edges of scales straight, bearing concentric striae. Forty ± two scale rows along lateral line.

Institutional abbreviations

GPIM, Geologisch-Paläontologisches Institut Mainz; **MB**, Museum für Naturkunde der Humboldt-Universität, Berlin; **MNHN**, Muséum national d'Histoire Naturelle, Paris; **NHM/LfN-PWL**, Landessammlung für Naturkunde Rheinland-Pfalz, Naturhistorisches Museum Mainz; **SMF**, Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt/Main. See Dietze (2000) for a complete list of material examined.

Anatomical abbreviations

a.no, anterior nostril; **ac.Op**, accessory opercle; **Ang**, angular; **Br.r**, branchiostegal rays; **Cl**, cleithrum; **Cor**, coronoid; **D**, dentary; **Dhy**, dermohyal; **Dph (1-2)**, dermosphenotic (1-2); **Hym**, hyomandibula; **inf.s.c**, infraorbital sensory canal; **Ju 1-2**, jugal 1-2; **l.Exc (1-2)**, lateral extrascapular (1-2); **l.Gu**, lateral gular; **La**, lacrimal; **m.Exc**, medial extrascapular; **m.Gu**, median gular; **Mx**, maxilla; «**Na**», «nasal»; «**Na 1-2**», secondarily split up «nasal»; **Op**, opercle; **Pa**, parietal; **Pcl**, postcleithrum; **Pmx**, premaxilla; **p.no**, posterior nostril; **Pop**, preopercle; **Ppa**, postparietal; **Proc.op**, processus opercularis; «**Pspi**», «postspiracular»; **Ptt**, posttemporal; **Qj**, quadratojugal; **Ro**, rostral; **Sa**, surangular; «**Sbo**», «suborbital»; **Scl**, supracleithrum; **Sop**, subopercle; **sorb.s.c**, supraorbital sensory canal; «**Spi**», «spiracular»; **S.r**, sclerotic ring elements; **St**, supratemporal; **st.s.c**, supratemporal sensory canal.

Terminology

Terminology follows Arratia & Schultze (1991) and Arratia & Cloutier (1996). Other terminologies set off by quotation marks, except for the «nasal», refer to terms commonly used in previous works (e.g., Blot, 1966; Heyler, 1969) on paramblypterid fishes. Different terminologies are currently being used for dermal cranial bones (e.g., Arratia & Cloutier, 1996: based on homologization; Poplin & Lund, 1997: traditional nomenclature). For bone terminology adopted herein differing from common usage see Dietze (2000).

Remarks

Data on *E. palatinus* was kindly provided by T. Schindler. His research was part of a doctoral dissertation carried out at the Johannes-Gutenberg-Universität, Mainz, the results of which have not been published yet. Specimens are deposited in the collection of the Geologisch-Paläontologisches Institut, Johannes-Gutenberg-Universität, Mainz.

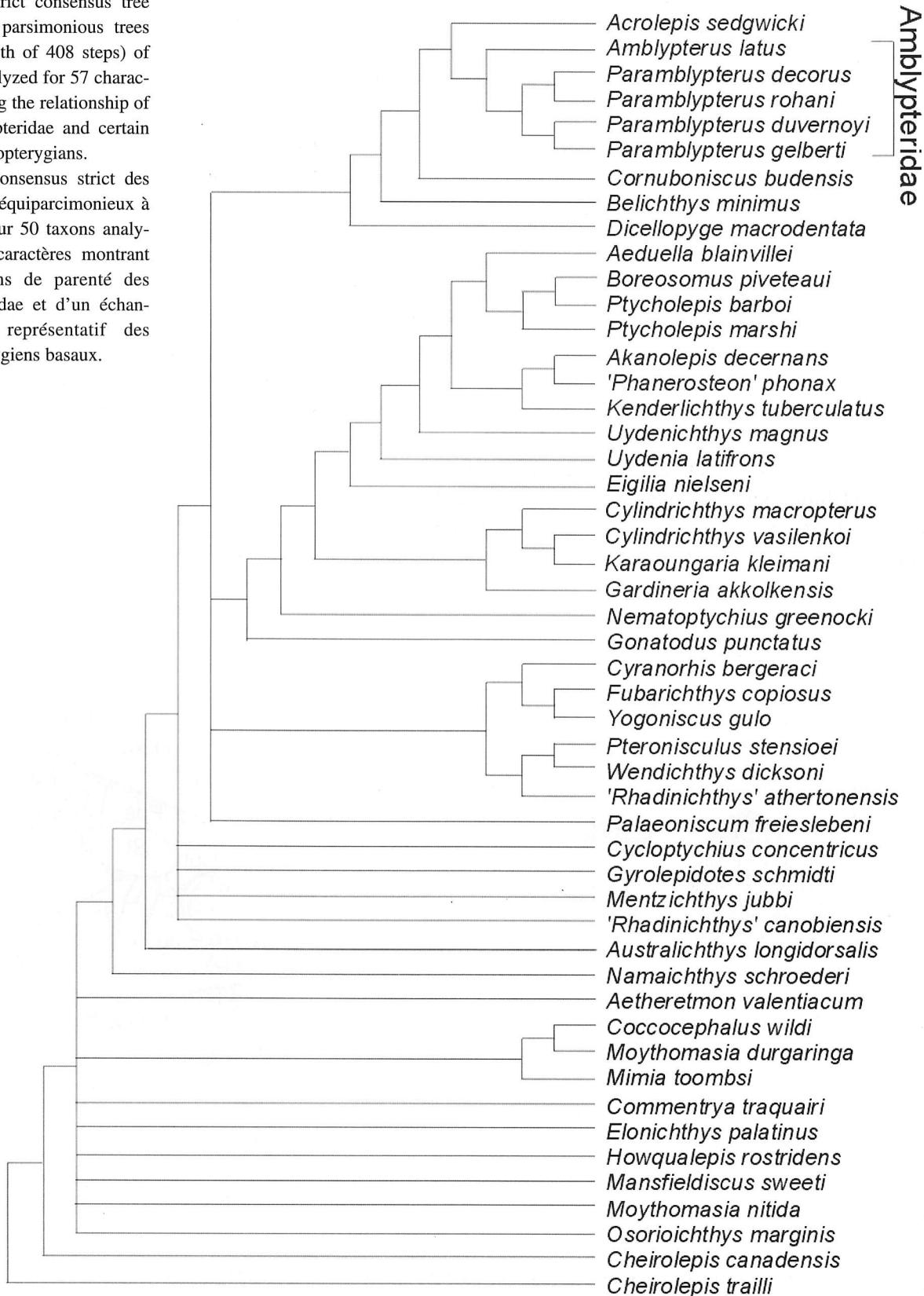
FEATURES INDICATING HETEROCHRONY

Fifty taxa of basal actinopterygians were analysed using PAUP version 3.1.1 (Swofford, 1993). The distribution of 48 cranial and 9 postcranial characters was determined. All characters were run unordered with delayed transformation (DELTRAN) as character optimisation. A heuristic search was carried out using the branch-swapping algorithm. *Cheirolepis trailli* (Pearson, 1982), a primitive actinopterygian, was used as outgroup. PAUP resulted in 330 most parsimonious trees with each having a tree length of 408. The strict consensus tree is illustrated in figure 1. Each parsimonious tree has a consistency index (CI) of 0.24, and a retention index (RI) of 0.57. Apparently, the low consistency index is related to a high degree of homoplasy among lower actinopterygians.

All 330 most parsimonious trees resulted in a monophyletic group containing [*Amblypteridae* + *Acrolepis sedwicki*) + *Cornuboniscus budensis*) + *Belichthys minimus*) + *Dicellogype macrodentata*]. This group formed a polychotomy with three other monophyletic groups in the strict consensus tree (fig. 1). The Amblypteridae were resolved completely with (*P. decorus* + *P. rohani*) being the sister group of (*P. duvernoyi* + *P. gelberti*), and *Paramblypterus* being the sister taxon of *Amblypterus*. Even though several polychotomies are present in the strict consensus tree (fig. 1), the position of the Amblypteridae is unambiguous for the taxa that have been analysed. Various analyses were run with reduced data sets (see Dietze, 2000) excluding taxa with many uncertainties, and/or accelerated transformation (ACCTRAN) as character state optimisation. All analyses resulted in the same topology concerning the Amblypteridae.

Fig. 1 : Strict consensus tree (330 most parsimonious trees with a length of 408 steps) of 50 taxa analyzed for 57 characters showing the relationship of the Amblypteridae and certain lower actinopterygians.

Arbre de consensus strict des 330 arbres équiparcimonieux à 408 pas pour 50 taxons analysés et 57 caractères montrant les relations de parenté des Amblypteridae et d'un échantillonnage représentatif des Actinoptérygiens basaux.



Since data on ontogenetic stages of an ancestral species are not available, *Elonichthys palatinus* (fig. 2B) is used as an outgroup to polarize patterns of heterochrony in the Amblypteridae. The position of *E. palatinus* in the strict consensus tree indicates that it is a basal actinopterygian species with many plesiomorphic characters. Moreover, it is more or less the only basal fossil actinopterygian for which ontogenetic data is available. As in most osteichthyans, ornamentation of the skull and of the scales, as well as serration of the scales increases during ontogeny in *E. palatinus* (T. Schindler, unpublished data 1998). The snout of *E. palatinus* is bluntly rounded in juvenile specimens, whereas it is drawn out into a blunt rostrum in adults (T. Schindler, unpublished data 1998). According to the ontogeny of *E. palatinus*, it is likely that the ancestor of the Amblypteridae started out with little serration and ornamentation of the scales and little skull ornamentation, both of which increased during ontogeny, and a rounded snout which subsequently grew more pointed during ontogeny.

The skull

Most basal fossil actinopterygians, such as *Mimia* (Gardiner, 1984), *Osorioichthys* (Taverne, 1997), or *Cyranorhis* (Lund & Poplin, 1997), have a drawn out snout, but *Amblypterus latus*, *Paramblypterus duvernoyi*, and *P. gelberti* (Dietze, 1999, 2000) have a bluntly rounded snout in adults (figs. 2A, 3). It is possible that the skulls of these species resemble a juvenile condition which might be related to paedomorphosis. In contrast, the skulls of adult specimens of *P. decorus* are not affected by paedomorphosis. According to the relationships of the Amblypteridae (Dietze, 2000), paedomorphosis regarding the skull must have arisen at least twice, i.e. on the branch leading to *A. latus* and on the branch leading to *P. duvernoyi* and *P. gelberti* (fig. 3).

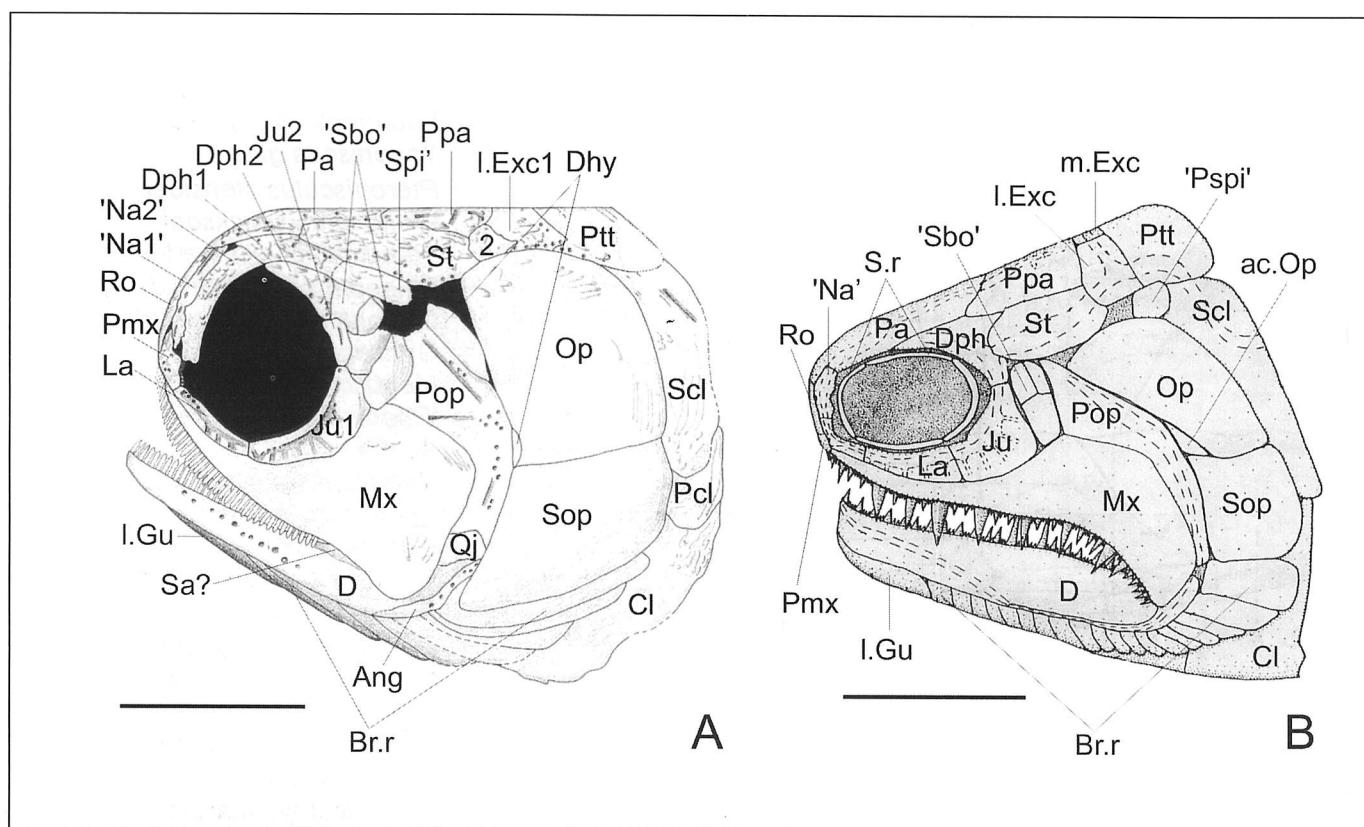


Fig. 2 : A. *Paramblypterus duvernoyi*, restoration of the skull (GPIM-M5819 & GPIM-M4939), lateral view, scale bar = 10 mm (after Dietze, 1999). B. *Elonichthys palatinus*, lateral view (modified after Schindler, 1993); scale bar = 5 mm.

A. *Paramblypterus duvernoyi*, reconstitution du crâne (GPIM-M5819 & GPIM-M4939), en vue latérale, barre d'échelle = 10 mm (d'après Dietze, 1999). B. *Elonichthys palatinus*, en vue latérale (modifié d'après Schindler, 1993), barre d'échelle = 5 mm.

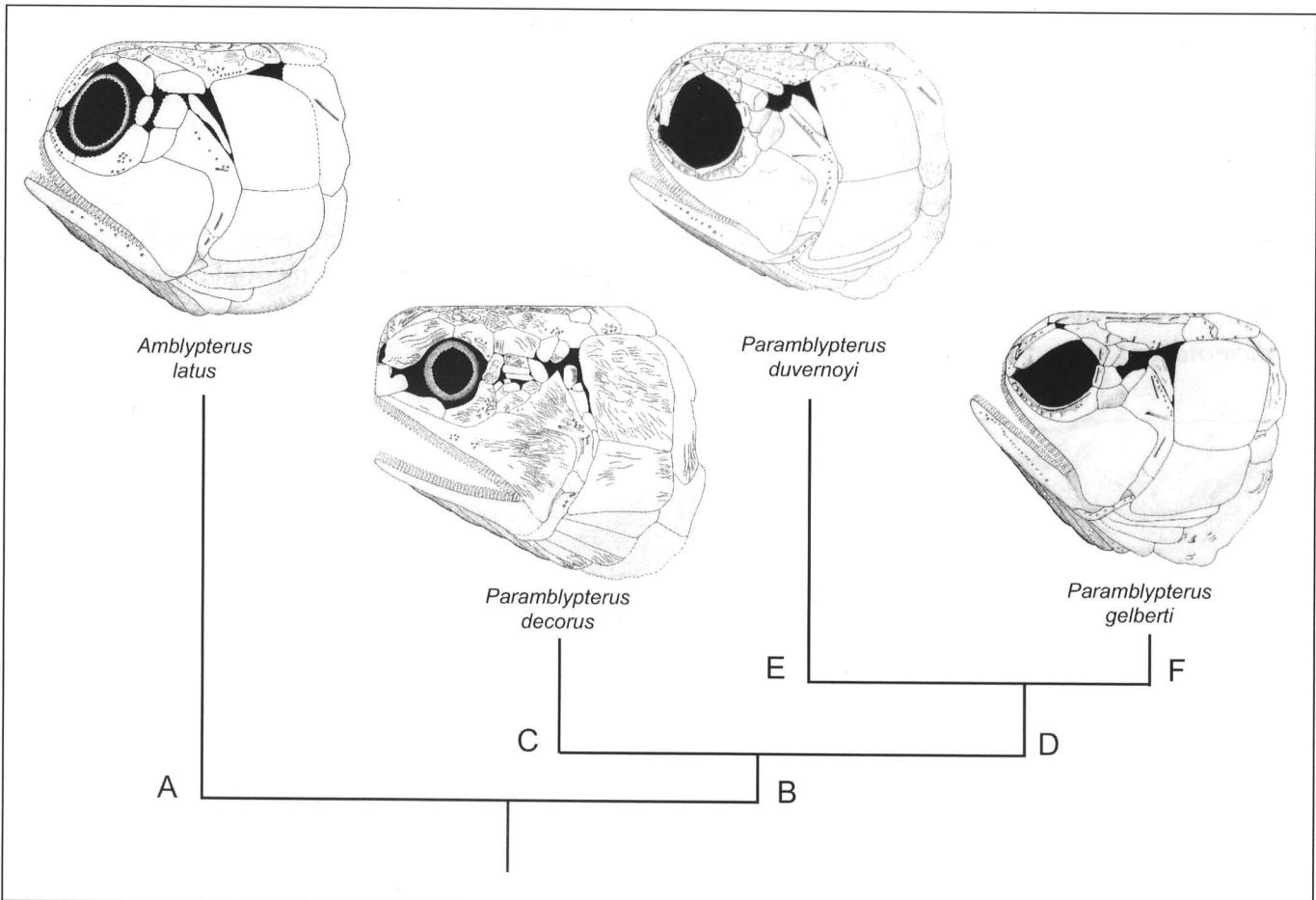


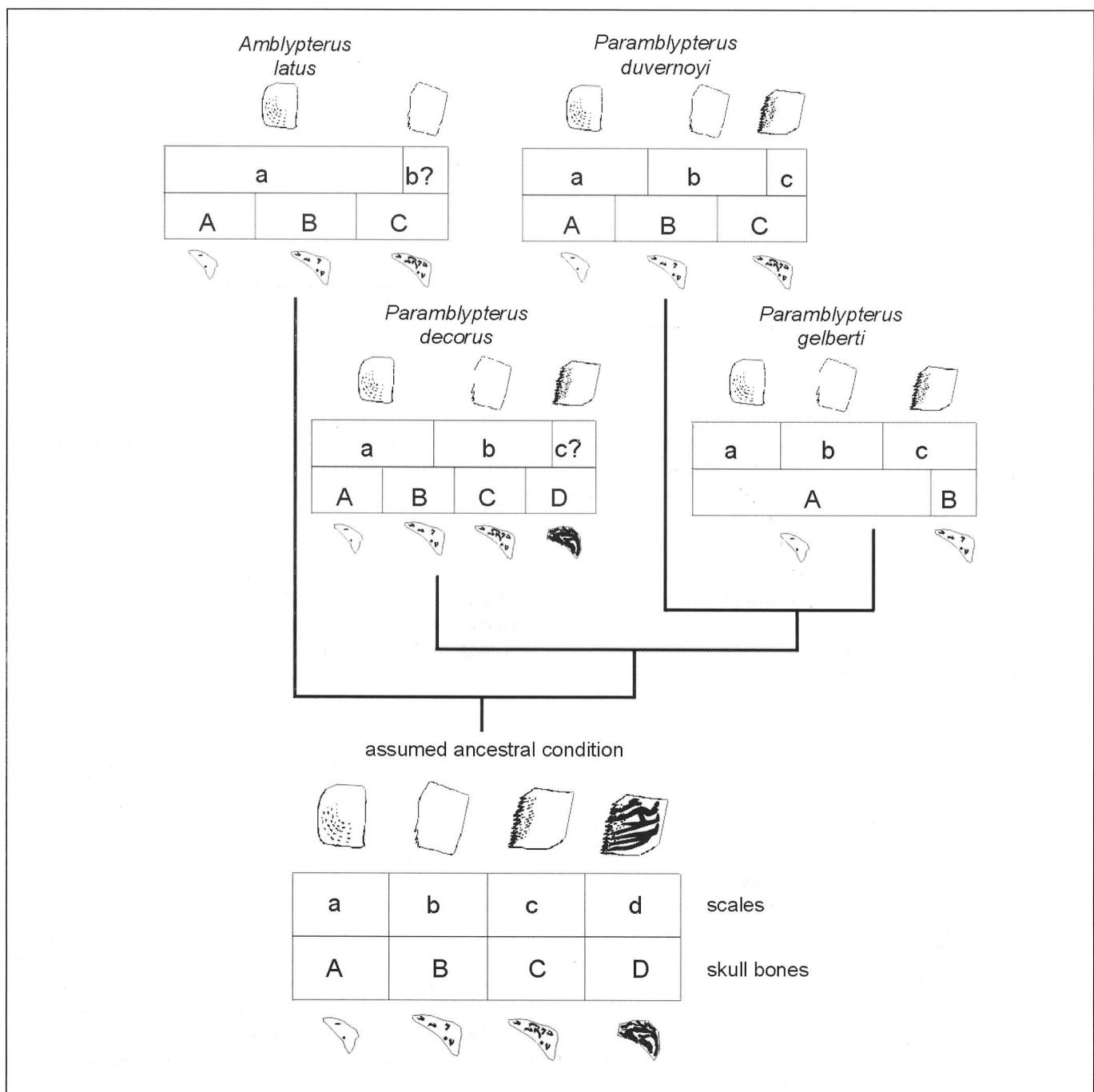
Fig. 3 : Skull morphology of the Amblypteridae according to Dietze (1999, 2000), left to right: *Amblypterus latus* (SMF75P & MB.f.3809b), *Paramblypterus decorus* (MNHN1962-1), *Paramblypterus duvernoyi* (GPIM-M5819 & GPIM-M4939), *Paramblypterus gelberti* (GPIM-M2248). Hypothesis of phylogenetic relationships of *Amblypterus* and *Paramblypterus* from Dietze (2000), based on the distribution of 57 characters among 50 species of lower actinopterygians. Node A: supratemporal more than two times longer than dermosphenotic 1, dermosphenotic 1 contacts «nasal», dermosphenotic 2 contacts «nasal», jugal 2 does not contact «spiracular», «suborbitals» contact jugal 2, gap between opercular series and skull roofing bones present, postcleithrum absent, posterior edges of scales straight. Node B: additional lateral extrascapular do not contact opercle, ventral protuberance of supratemporal absent, three to six «suborbitals», «nasal» split up secondarily, nine or eight branchiostegal rays, dermohyal not single. Node C: postparietal does not contact lateral extrascapular 1, anterior third of supratemporal contacts parietal, «spiracular» angular, maxillary plate of medium depth, ventral margin of maxilla straight. Node D: parietal processus present, supratemporal longer than dermosphenotic 1, dermosphenotic 2 does not contact «spiracular», dermosphenotic 2 contacts «suborbitals», jugal 1 contacts «suborbitals» posterodorsally, jugal 2 does not contact «spiracular», sclerotic ring absent. Node E: additional lateral extrascapulars contact opercle. Node F: supratemporal does not contact opercle, little skull ornamentation.

Morphologie du toit crânien des Amblypteridae d'après Dietze (1999, 2000), de gauche à droite: *Amblypterus latus* (SMF75P & MBf3809b), *Paramblypterus decorus* (MNHN 1962-1), *Paramblypterus duvernoyi* (GPIM-M5819 & GPIM-M4939), *Paramblypterus gelberti* (GPIM-M2248). Hypothèse des relations phylogénétiques d'*Amblypterus* et de *Paramblypterus* d'après Dietze (2000) basée sur la distribution de 57 caractères parmi 50 espèces d'actinoptérygiens basaux. Noeud A: supratemporal deux fois plus long que dermosphénétique 1, dermosphénétique 1 en contact avec le «nasal», dermosphénétique 2 en contact avec le «nasal», jugal 2 sans contact avec le «spiraculaire», «supraorbitaux» en contact avec le jugal 2, espace entre la série operculaire et les os du toit crânien, postcleithrum absent, écailles avec un bord postérieur droit. Noeud B: extrascapulaire latéral additionnel sans contact avec l'opercule, absence de protubérance ventrale sur le supratemporal, trois à six «sous-orbitaux», division secondaire du «nasal», huit ou neuf rayons branchiostèges, dermohyal non unique. Noeud C: postparietal sans contact avec l'extrascapulaire latéral 1, tiers antérieur du supratemporal en contact avec le pariétal, «spiraculaire» anguleux, plaque du maxillaire présentant une hauteur moyenne, maxillaire présentant une marge ventrale droite. Noeud D: présence du processus pariétal, supratemporal plus long que le dermosphénétique 1, dermosphénétique 2 sans contact avec le «spiraculaire», dermosphénétique 2 en contact avec les «sous-orbitaux», jugal 1 en contact avec les «sous-orbitaux» postéro-dorsalement, jugal 2 sans contact avec le «spiraculaire», absence des anneaux sclérotiques. Noeud E: extrascapulaires latéraux additionnels en contact avec l'opercule. Noeud F: supratemporal sans contact avec l'opercule, faible ornementation du toit crânien.

Ornamentation of skull bones

Skull bones of *Paramblypterus decorus* are ornamented as densely as in adult specimens of *Elonichthys palatinus*, but bear less ornamentation in specimens of *A. latus* and *P. duvernoyi*, the bones of which are ornamented moderately. Little ornamentation is present on the bones of the skull of *P. gelberti* (Dietze, 1999), which is even less than in *A. latus* and *P. duvernoyi*. Ornamentation of the skull bones

increases during ontogeny in all species to various degrees. However, ornamentation in *P. duvernoyi* and *A. latus* does not reach the level of density which is present in *P. decorus*. Skull bones of juvenile specimens of *P. gelberti* are more or less smooth with the degree of ornamentation hardly increasing during ontogeny. According to the distribution of this feature, it occurred twice within the Amblypteridae, on the branch that characterizes *P. duvernoyi* and *P. gelberti*, and on the branch characterizing *A. latus* (fig. 4).



Opercular series

Paramblypterus gelberti and *P. duvernoyi* vary from one another in the growth and shape of the subopercle and the opercle. In specimens smaller than 100 mm trunk length, opercle and subopercle of *P. gelberti* are larger than in *P. duvernoyi* (Dietze, 1999: figs. 16, 17). A statistical two sample analysis of subopercular and opercular bones of *P. gelberti* and *P. duvernoyi* showed that these differ significantly ($p < 0.001$). Distinction between pairs of means was greatest, when areas of opercle (fig. 5A) or subopercle (fig. 5B) were divided by their circumference and trunk length of the specimen. The growth of the opercular bones of *P. gelberti* is different from *P. duvernoyi*: either the growth of the opercle is delayed in *P. gelberti* or accelerated in *P. duvernoyi*. However, ontogenetic data on the development of the opercular series of *E. palatinus* are not available as yet and therefore could not be compared with the data of *P. duvernoyi* and *P. gelberti* to determine polarity.

← Fig. 4

Features of heterochrony of the Amblypteridae in comparison to a potential ancestor which is reconstructed from features present in the plesiomorphic species *Elonichthys palatinus*: serration and ornamentation of the scales (upper row), and ornamentation of the skull bones, e.g., dermosphenotic 2 (lower row); lower case letters represent morphological stages of the scales (smooth, with concentric striae-serrated-serrated along entire posterior margin-serrated and ornamented), upper case letters represent morphological stages regarding the ornamentation of skull bones (scarce-little-moderate-dense), all of which are present in the ancestral condition during the ontogenetic development. Missing morphological stages in the individual species indicate heterochronic processes.

Comparaison entre les caractères d'hétérochronie des Amblypteridae et un ancêtre potentiel reconstitué d'après des caractères présents chez l'espèce plésiomorphe *Elonichthys palatinus*: dentelure et ornementation des écailles (rangée supérieure) et ornementation des os du toit crânien, e.g. dermosphénotique 2 (rangée inférieure); les lettres minuscules représentent les stades morphologiques des écailles (lisses, avec stries concentriques, dentelées, dentelées le long du bord postérieur, dentelées et ornemées), les lettres majuscules représentent les stades morphologiques selon l'ornementation des os du crâne (rare, faible, modérée, dense). Tous ces états sont présents durant le développement ontogénique de la condition ancestrale. Les stades morphologiques manquants chez certaines espèces indiquent un phénomène d'hétérochronie.

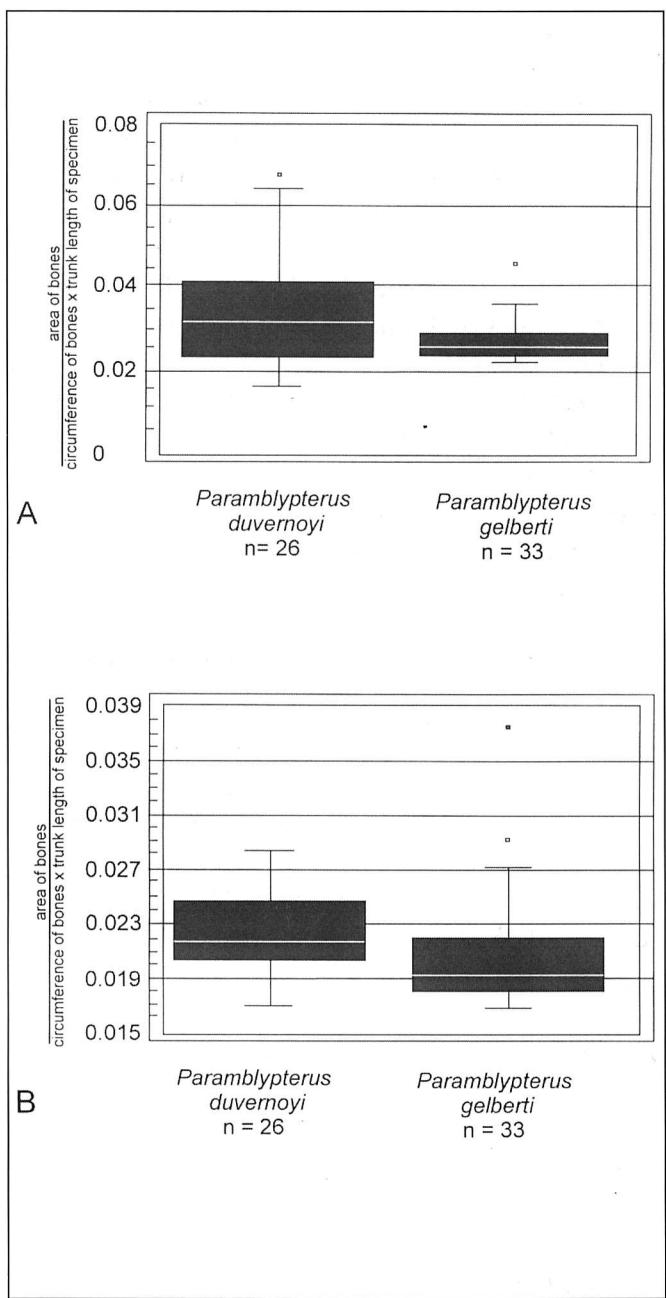


Fig. 5

Box and whisker plot of area of bones divided by their circumference and trunk length of specimen of *Paramblypterus duvernoyi* and *P. gelberti*. The Box-and-Whisker Plot displays a plot of paired differences, which are divided into four areas of equal frequency (quartiles). Tiny squares correspond to outliers (extreme individual values). **A.** Opercular bones (OP). **B.** Subopercular bones (SOP). Les distributions ‘box and whisker’ correspondent à la surface des os divisée par leur circonférence et la longueur du tronc pour *Paramblypterus duvernoyi* et *P. gelberti*. Les quartiles (i. e. aire de distribution équivalentes) sont représentés sur le graphique. Les petits carrés correspondent aux ‘outliers’, individus isolés. **A.** Os operculaires (OP). **B.** Os sous-operculaires (SOP).

Squamation

The scales of *A. latus* are completely smooth, bear concentric striae only, and are not serrated (fig. 6). The scales of *P. decorus* bear little ornamentation and are weakly serrated (fig. 6). Serration and ornamentation of the scales of *P. duvernoyi* (fig. 6) is similar to *P. decorus* and is less than in *P. gelberti* (fig. 6). Scales of *A. latus* remain smooth and without serration throughout ontogeny. In small specimens of *P. duvernoyi*, the area on the body bearing serrated scales is larger than in adult ones. Ornamentation and serration is less than in equal sized specimens of *P. gelberti*. Whether this applies to specimens of *P. decorus* as well is difficult to evaluate, since the posterior edges of the scales are broken in most of the specimens.

According to the degree of serration, scales of *P.*

duvernoyi and *P. decorus* have D-values between 1.4 and 2.0, whereas scales of *P. gelberti* have D-values higher than 2.0. In *P. duvernoyi* (fig. 7), the portion of the body bearing serrated scales decreases in area during ontogeny so that serrated scales are confined to the area immediately posterior to the skull, whereas the degree of serration stays the same in specimens of *P. gelberti* (fig. 8). It appears that the development of the serration and ornamentation of scales of *P. duvernoyi* and *P. gelberti*, or as a matter of fact of all species of the Amblypteridae described herein, are affected by paedomorphosis. Even though scales of *P. gelberti* are more serrated than scales of *P. duvernoyi*, serration is less than in *E. palatinus*. Since scales of *P. gelberti* are more serrated and bear more ridges than the other species of the Amblypteridae, paedomorphic characteristics of the squamation must have evolved separately in all four species (fig. 3).

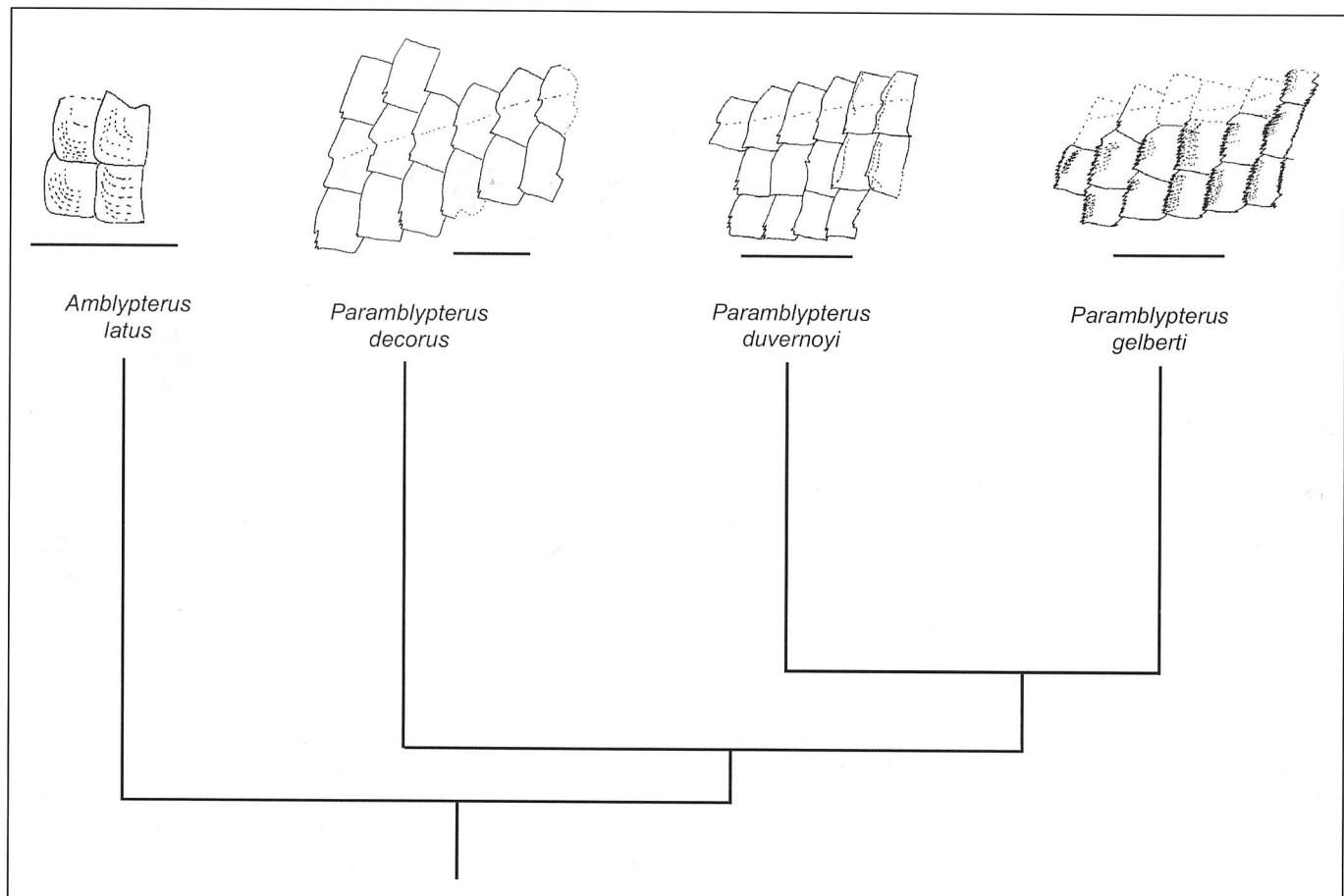


Fig. 6. : Detail of squamation, left to right: *Amblypterus latus*, *Paramblypterus decorus*, *Paramblypterus duvernoyi*, *Paramblypterus gelberti*. Scale bar = 5 mm (from Dietze, 2000).

Détail de la squamation, de gauche à droite: *Amblypterus latus*, *Paramblypterus decorus*, *Paramblypterus duvernoyi*, *Paramblypterus gelberti*. Barre d'échelle = 5 mm (d'après Dietze, 2000).

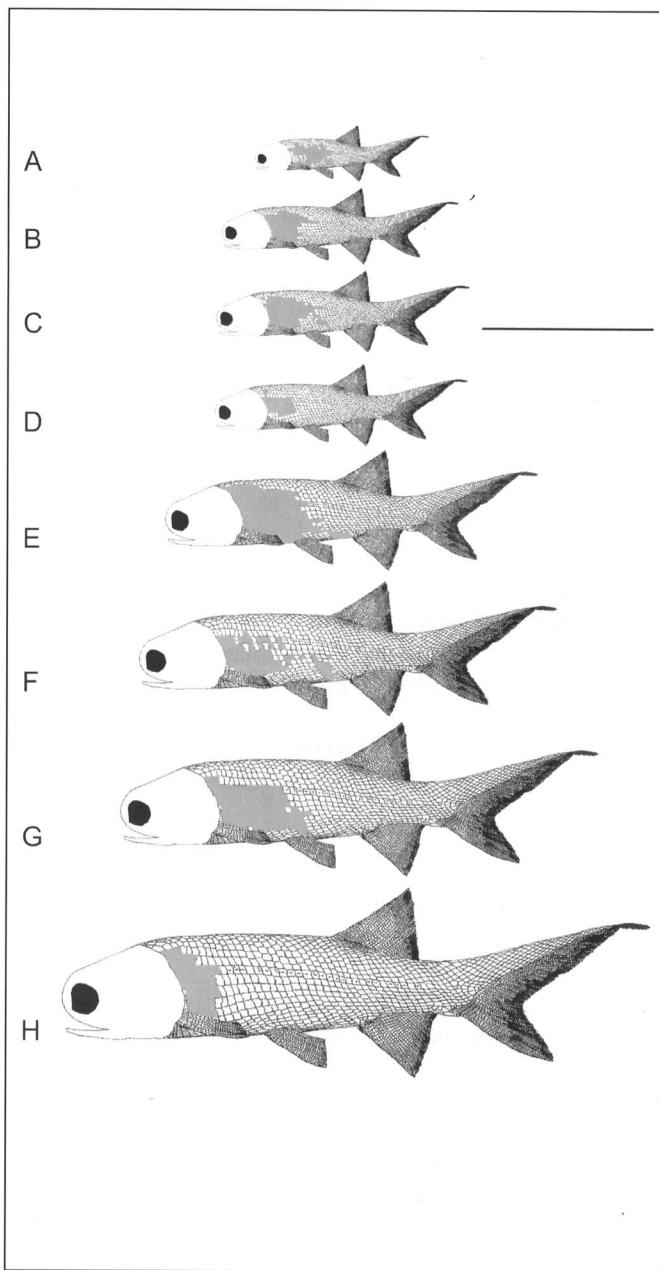


Fig. 7

Paramblypterus duvernoyi, shaded area corresponds to serrated scales on specimens, trunk length of specimens in parentheses. **A.** GPIM-M5816 (55 mm). **B.** NHM/LfN-PWL1985/4 (75 mm). **C.** GPIM-M5817 (80 mm). **D.** GPIM-M5822 (80 mm). **E.** GPIM-M5811 (118 mm). **F.** GPIM-M5814 (132 mm). **G.** GPIM-M5815 (151 mm). **H.** GPIM-M5835 (186 mm). Body depth and caudal peduncle not to scale. Scale bar = 100 mm.

Paramblypterus duvernoyi, la surface ombrée correspond aux écaillles dentelées, la longueur du tronc des spécimens étant entre parenthèses. **A.** GPIM-M5816 (55 mm). **B.** NHM/LfN-PWL1985/4 (75 mm). **C.** GPIM-M5817 (80 mm). **D.** GPIM-M5822 (80 mm). **E.** GPIM-M5811 (118 mm). **F.** GPIM-M5814 (132 mm). **G.** GPIM-M5815 (151 mm). **H.** GPIM-M5835 (186 mm). Hauteur du corps et pédoncule caudal non à l'échelle. Barre d'échelle = 100 mm.

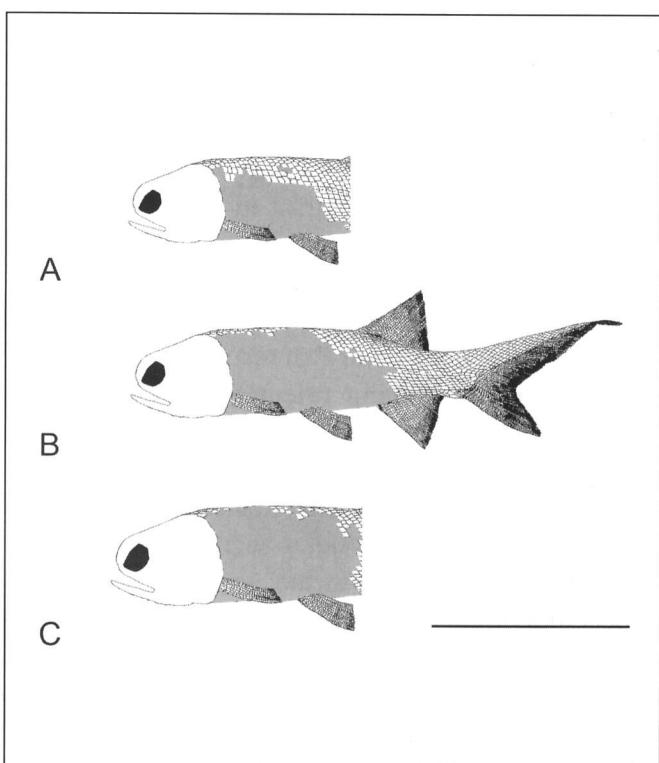


Fig. 8.

Paramblypterus gelberti, shaded area corresponds to serrated scales on specimens, trunk length of specimens in parentheses. **A.** GPIM-M2272 (129 mm). **B.** GPIM-M5834 (136 mm). **C.** GPIM-M2315 (150 mm). Body depth and caudal peduncle not to scale. Scale bar = 100 mm. Scale growth in *Paramblypterus* is allometric (Dietze 1999, 2000). Thus, trunk length of broken specimens can be estimated according to the size of their scales.

Paramblypterus gelberti, la surface ombrée correspond aux écaillles dentelées, la longueur du tronc des spécimens étant entre parenthèses. **A.** GPIM-M2272 (129 mm). **B.** GPIM-M5834 (136 mm). **C.** GPIM-M2315 (150 mm). La taille des spécimens incomplets a été estimée d'après leurs séries de croissance (Dietze 1999). Hauteur du corps et pédoncule caudal non à l'échelle. Barre d'échelle = 100 mm. La croissance des écaillles chez *Paramblypterus* est allométrique (Dietze 1999, 2000). Ainsi, la longueur des spécimens cassés peut être estimée grâce à la taille de leurs écailles.

CONCLUSIONS

In comparison with the ontogenetic sequence of *Elonichthys palatinus* as outgroup, certain features of the Amblypteridae suggest heterochronic processes of paedomorphosis. In contrast to the common pattern among lower actinopterygians, i.e. a blunt snout, *Paramblypterus duvernoyi*, *P. gelberti*, and *Amblypterus latus* have a more rounded snout. Retaining a rounded snout in the adult fish results in a short gape with the mouth opening oriented further anteriad. This is advantageous for suction feeding (Liem, 1993) and could represent an adaptation for feeding. Unlike the squamation in most osteichthyans, serration of the scales appears not to increase during ontogeny, but to be reduced in the Amblypteridae. This affects individual scales or the area on the body bearing serrated scales. Moreover, various degrees of reduction of the ornamentation of the skull bones, dense – moderate – little, can be observed within the Amblypteridae. Data on opercular and subopercular bones of *P. duvernoyi* and *P. gelberti* indicate either a delayed growth in the latter, or an accelerated growth in the former. However, more information on the growth of opercular bones of an ancestral species would be needed to further corroborate this observation.

ACKNOWLEDGEMENTS

My foremost thanks go to Jürgen Boy for valuable comments and discussion. I am indebted to Peter Bartsch for revising an earlier version of the manuscript. Helpful criticism was given by Lance Grande and Hans-Peter Schultze. I am grateful to Gloria Arratia, William E. Bemis, Peter Forey, and Richard Lund for discussion and constructive suggestions. For access to specimens and loans I thank Peter Forey (London), Gloria Arratia and Hans-Peter Schultze (Berlin), Daniel Goujet, Cécile Poplin, and Sylvie Wenz (Paris), the Saarbergwerke Museum (Saarbrücken), Herbert Lutz (Mainz), Martin Sander (Bonn), Dieter Schweiss (Bad-Dürkheim), Günther Plodowski (Frankfurt), Jean-Claude Gall and Rosemaire Buntz (Strasbourg), Thomas Brachert, Markus Forst, Ulrich Heidtke, Manfred Keller, Klaus and Regine Krätschmer, Markus Poschmann, Frank San-

zenbacher, Thomas Schindler, Arnulf and Harald Stapf, and Klaus Weiss. I thank Gaël Clement and Arnaud Filleul for French translations, Regina Kraus for assisting me with the drawings, Karl Schuchmann for preparatory assistance, and Manfred Schmicking for photographs. Moreover, I thank Dragana Bjekovic, Michael Fastnacht, Eberhard Frey, Jürgen Hämmeler, Oliver Hampe, Michael Morlo, Volker Sigwarth, and Günther Witrock. Funds were provided by the Deutsche Forschungsgemeinschaft (Bo 553-9), and a grant of the Landesgraduiertenförderung of Rheinland-Pfalz.

REFERENCES

- AGASSIZ, L. 1833. Recherches sur les poissons fossiles. Vol. 2: 336 pp. Published by the author, printed by Petitpierre. Neuchâtel.
- ALBERCH, P. & ALBERCH, J. 1981. Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical salamander, *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). *Journal of Morphology*, **167**: 249-264.
- ALBERCH P.; GOULD, S. J.; OSTER, G. F. & WAKE, D. B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology*, **5**(3): 296-317.
- ARRATIA, G. & CLOUTIER, R. 1996. Reassessment of the morphology of *Cheirolepis canadensis* (Actinopterygii); pp. 165-197. In SCHULTZE, H.-P. & CLOUTIER, R. (eds.) *Devonian Fishes and Plants of Miguasha, Quebec*. Verlag Dr. Pfeil, München.
- ARRATIA, G. & SCHULTZE, H.-P. 1991. Palatoquadrate and its ossifications: Development and homology within Osteichthyans. *Journal of Morphology*, **208**: 1-81.
- BEMIS, W. E. 1984. Paedomorphosis and the evolution of the Dipnoi. *Paleobiology*, **10**(3): 293-307.
- BLOT, J. 1966. Étude des Palaeonisciformes du Bassin Houiller de Commentry (Allier, France), 99 pp. Cahiers de Paléontologie, CNRS Paris.
- BOY, J. A. 1976. Überblick über die Fauna des saarpfälzischen Rotliegenden (Unter-Perm). *Mainzer geowissenschaftliche Mitteilungen*, **16**: 13-85.
- _____. 1993. Synopsis of the tetrapods from the Rotliegend (Lower Permian) in the Saar-Nahe Basin (SW-Germany); pp. 159-169. In HEIDTKE, U. (ed.) *New research on Permo-Carboniferous Faunas*. Pollichia Buch 29, Bad Dürkheim.
- _____. 1994. Seien der Rotliegend-Zeit – Ein Lebensraum vor rund 300 Millionen Jahren in der Pfalz, pp. 107-116. In V. KOENIGSWALD, W. & MEYER, W. (eds.) *Erdgeschichte im Rheinland*. Verlag Dr. Pfeil, München.
- _____. 1995. Über die Micromelerpetontidae (Amphibia: Temnospondyli). 1. Morphologie und Paläoökologie des *Micromelerpeton credneri* (Unter-Perm; SW-Deutschland). *Paläontologische Zeitschrift* **69**(3/4): 429-457.
- _____. 1998. Möglichkeiten und Grenzen einer Ökosystem-Rekonstruktion am Beispiel des spätpaläozoischen lakustrinen

- Paläo-Ökosystems. 1. Theoretische und methodische Grundlagen. *Paläontologische Zeitschrift*, **72**: 207-240.
- _____. In press. Rekonstruktion von Nahrungsnetzen im permokarbonen lakustrinen Paläo-Ökosystem. *Courier Forschungsinstitut Senckenberg*.
- BOY, J. A.; CLAUSING, A.; MARTENS, T.; SCHINDLER, T. & SCHMIDT, D. 1994. Rotliegend-Paläoökologie. 181 pp. Unpublished report for the Deutsche Forschungsgemeinschaft (DFG), Johannes-Gutenberg University, Mainz.
- CLAUSING, A. & BOY, J. A. 2000. Lamination and primary production in fossil lakes: relationship to paleoclimate in the Carboniferous-Permian transition; pp. 5-16. In HART, M. B. (ed.) *Climates: Past and Present. Special Publications*. Geological Society, London.
- DIETZE, K. 1998. Skull morphology, intra-specific variation, and a reevaluation of amblypterid-paramblypterid fishes (Actinopterygii, Lower Permian). Doctoral dissertation, Johannes-Gutenberg-Universität, Mainz, 155 pp.
- _____. 1999. *Paramblypterus duvernoyi* (Actinopterygii): Skull morphology and intra-specific variation, and its implications for the systematics of paramblypterid fishes. *Journal of Vertebrate Paleontology*, **19**: 247-262.
- _____. 2000. A revision of paramblypterid and amblypterid actinopterygians from Upper Carboniferous to Lower Permian lacustrine deposits of Central Europe. *Palaeontology*, **43** (5): 927-966.
- _____. 2001. Biological aspects of an interesting fossil fish: *Paramblypterus duvernoyi* (Amblypteridae, Actinopterygii). *Mitteilungen des Museums für Naturkunde Berlin, Geowissenschaftliche Reihe*, **4**: 121-138.
- FINK, W. L. 1989. Ontogeny and phylogeny of shape and diet in the South American fishes called Piranhas. *Geobios, mémoire spécial*, **12**: 167-172.
- GARDINER, B. G. 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum of Natural History (Geology)* **37**: 173-428.
- GOULD, S. J. 1974. The origin and function of «bizarre» structures: antler size and skull size in the «Irish Elk», *Megaloceros giganteus*. *Evolution*, **28**: 191-220.
- _____. 1977. Ontogeny and Phylogeny. 501 pp. Belknap, Cambridge.
- HAFNER, M. S. & HAFNER, J. C. 1984. Brain size, adaptation and heterochrony in geomyoid rodents. *Evolution*, **38**(5): 1088-1098.
- HALL, B. K. 1984. Developmental processes underlying heterochrony as an evolutionary mechanism. *Canadian Journal of Zoology*, **62**: 1-7.
- HEYLER, D. 1969. Vertébrés de l'Autunien de France. 225 pp. Cahiers de Paléontologie. CNRS Éd., Paris.
- IRISH, F. J. 1989. The role of heterochrony in the origin of a novel bauplan: evolution of the ophidian skull. *Geobios, Mémoire Spécial*, **12**: 167-172.
- LIEM, K. F. 1993. Ecomorphology of the teleostean skull; pp. 422-452. In HANKEN, J. & HALL, B. K. (eds). *The Skull*, Vol. 3. The University of Chicago Press, Chicago and London.
- LONG, J. A. & MCNAMARA, K. J. 1995. Heterochrony in dinosaur evolution; pp. 151-168. In MCNAMARA, K. J. (ed.). *Evolutionary Change and Heterochrony*. John Wiley & Sons, New York.
- LUND, R. & POPLIN, C. 1997. The rhadinichthyids (paleoniscoid actinopterygians) from the Bear Gulch Limestone of Montana (USA, Lower Carboniferous). *Journal of Vertebrate Paleontology*, **17**: 466-486.
- MAYER, A. 1987. Phenotypic plasticity and heterochrony in *Cichlosoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution*, **41**(6): 1357-1369.
- MCKINNEY, M. L. & MCNAMARA, K. J. 1991. *Heterochrony: the Evolution of Ontogeny*. 437 pp. Plenum Press, New York and London.
- MCNAMARA, K. J. 1986. A guide to the nomenclature of heterochrony. *Journal of Paleontology*, **60**(1): 4-13.
- PEARSON, D. M. 1982. Primitive bony fishes, with especial reference to *Cheirolepis* and paleonisciform actinopterygians. *Zoological Journal of the Linnean Society*, **74**: 35-67.
- POPLIN, C. 1994. Montceau-les-Mines, Bassin Intramontagneux Carbonifère et Permien de France. Reconstitution, Comparaison avec l'Euramérique; pp. 289-328. In POPLIN, C. & HEYLER, D. (eds.) *Quand le Massif Central était sous l'Équateur: Un écosystème carbonifère à Montceau-les-Mines*. Mémoires de la Section des Sciences 12. CTHS, Paris.
- POPLIN, C. & LUND, R. 1997. Evolution of the premaxillary in the primitive fossil actinopterygians. *Geodiversitas*, **19**(3): 557-565.
- SAUVAGE, H. E. 1888. Faunes ichthyologique et entomologique. Études sur le terrain houiller de Commentry. *Bulletin de la Société de l'Industrie minérale, Théolier, St. Etienne*, **3**(1): 39-120.
- SCHMIDT-KITTNER, N. 1984. Pattern analysis of occlusal surfaces in hypodont herbivores and its bearing on morpho-functional studies. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, **87**: 453-480.
- _____. 1986. Evaluation of occlusal patterns of hypodont rodent dentition by shape parameters. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **173**: 75-98.
- SCHINDLER, T. 1993. «*Elonichthys palatinus* n. sp.», a new species of actinopterygians from the Lower Permian of the Saar-Nahe-Basin (SW-Germany); pp. 67-81. In HEIDTKE, U. (ed.) *New research on Permo-Carboniferous Faunas*. Pollichia Buch 29, Bad Dürkheim.
- SCHOCH, R. 1995. Heterochrony in the development of the amphibian head; pp. 107-124. In MCNAMARA, K. J. (ed.) *Evolutionary Change and Heterochrony*. John Wiley & Sons, New York.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.1.1. Illinois Natural History Survey, Champaign, Illinois.
- TAVERNE, L. 1997. *Osorioichthys marginis*, «Paléonisciforme» du Famennien de Belgique, et la phylogénie des Actinopterygiens dévoniens (Pisces). *Bulletin de l'Institut Royal des sciences naturelles de Belgique, Sciences de la Terre*, **67**: 57-78.