



Ontogeny and phylogeny in temnospondyls: a new method of analysis

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A new method has been devised to compare the ontogeny and phylogeny of some of the better documented tetrapods from the Stephanian to the Trias. This approach is based on global parsimony analysis of several temnospondyl amphibians, in which some ontogenetic sequences have been highlighted. Forty-one homologous morphoanatomical character states have been separated into larval, juvenile and adult stages of each of six tetrapod species. The taxonomic congruence (TC) approach involves comparing trees based on larval, juvenile and adult character states. These so-called 'ontotrees' are not congruent, either in their topologies or in the distribution of the character states. The total evidence (TE) approach involves a combined analysis of all the character states observed in the various growth stages of the taxa, and is secondarily used in order to test this taxonomic incongruence. In this case, the TE result corroborates the TC analysis: the TE tree is robust and reveals a few homoplasies which cause the taxonomic incongruence. This is interpreted as either the result of heterochronic events in temnospondyl evolution, or as the product of inaccurate identification of larval and metamorphic fossil forms.

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ADDITIONAL KEY WORDS:—taxonomic congruence – total evidence – growth stages – heterochrony – larval identification.

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INTRODUCTION

Comparative ontogeny is a long-established field, dating back to von Baer's (1828) *Entwicklungsgeschichte der Thiere*, Agassiz's recapitulation (1833–1843), and Haeckel's (1866) comparison of vertebrate embryonic developments, in support of his biogenetic dictum: “ontogeny recapitulates phylogeny” (Richardson, 1998). Nowadays, the use of comparative ontogeny is relatively widespread in palaeontology. There is not space here to provide a complete bibliography.

Cladistic analysis, when it involves comparative ontogeny, is commonly based on larval, juvenile and adult character states. These character states are either included in the same combined tree, or in separate (and therefore comparable) trees (one tree per growth stage).

Practitioners of the first approach include ichthyologists (larval, juvenile, and adult combined character states; Johnson, 1983a, b; Houde, 1983; Pietsch, 1983; de Sylva, 1983, botanists (sporophyte and gametophyte combined character states; Pryer, Smith & Skog, 1995), and entomologists (Grandcolas, pers. comm.), all frequently having non-homologous (*sensu* Rieppel, 1988) character states through complete and well documented developments at their disposal. In recent years a combined analysis has been recently tested on tyrannosaurid dinosaurs (Carr, 1998).

The second approach has been used only by neontologists (such as Fuiman, 1983; Leis, 1983). As far back as 1943, Hennig described the problem of different putative phylogenies between larval and adult *Drosophilae*. Grandjean (1947, 1957) also encountered the same problem with larval and nymphal Acaridae when proposing his ‘Évolution selon l'âge’ theory. In this paper I attempt to apply such a method to fossils by testing the taxonomic congruence (TC) and total evidence (TE) approaches (Kluge, 1989). It is the first time that both have been used to compare different growth stages.

MATERIAL

Temnospondyls

Amphibians show a very broad range of forms and developmental patterns. They are the only tetrapods which undergo metamorphosis. This has been observed in numerous living amphibians (Keller, 1946), but not, however, in all the fossil groups: metamorphosis remains unproven in some Palaeozoic amphibians (Boy, 1974; Steyer, 1996a; Schoch, in press a). An aquatic herbivorous larva or tadpole does not necessarily metamorphose into a terrestrial carnivorous adult. For instance, the facultative paedomorphosis of several non-metamorphosed species of the living *Ambystoma* (Keller, 1946) has been known for more than a century (Gould, 1977).

Such a retention process has also been recognized in the developments of several Palaeozoic ‘amphibians’ (de Ricqlès, 1975, 1979; Steyer, 1996b).

The six taxa selected for this analysis are temnospondyls, which represent useful fossil ‘amphibians’ for testing (*sensu* Popper, 1972) hypotheses (such as morphometric analyses: Orlov, 1991; Steyer, 1996a). They were chosen because well preserved larval, juvenile and adult specimens were available. These six genera are among the best known temnospondyls. The cladistic analysis features the following as an ingroup:

Acanthostomatops Kuhn, 1961, from the Lower Permian of Germany, belonging to the monophyletic (Schoch, 1997) ornamented-skulled Zatrachydidae.

Apateon von Meyer, 1844 from the Rotliegend (Upper Carboniferous?-Lower Permian) of Central Europe, which belongs to the small-sized Branchiosauridae family.

Cheliderpeton Fritsch, 1877 from the Lower Permian of Czech Republic, Germany and France (Steyer, 1996a), belonging to semirostral-longirostral forms of Archegosauridae *sensu* Boy 1993.

Onchiodon Geinitz, 1861, from the Lower Permian of Czech Republic, Germany and France (Werneburg, 1997), which represents the Eryopidae here.

Parotosuchus Ochev & Shishkin, 1968 (in Kalandadze *et al.*, 1968) from the Trias of Australia, Europe, Russia, and Africa, belonging to the widespread and large-sized ‘Capitosauridae’ (or Mastodontosauridae).

The basal genus *Dendrerpeton* Owen, 1853, from the Upper Carboniferous of Ireland and Nova Scotia (Canada), has been chosen as outgroup and represents the monotypic (Milner, 1980) Dendrerpetontidae. The genus corresponds to the most primitive temnospondyl with well documented ontogeny.

Recognition of the growth stages

The study initially concerned itself with the identification of growth stages. A standardized system of dividing developmental sequences into homologous stages was used to compare homologous morphological characters through development. Some authors (Hennig, 1966; Schoch, 1998) have considered this division as artificial (“There is no general rule for determining what constitutes a stage”, Hennig, 1966: 33). Nevertheless, as Naef wrote in 1931 “we comprehend ontogenesis by fixing a series of momentary pictures or stages [. . .]. In practice we select as many as seem necessary for understanding the process”.

For lissamphibians, numerous methods have been used to assist in the recognition of the growth stages, including morphometrics (growth rates of Beebe, 1980), skeletochronology (lines of arrested growth of Francillon-Viellot *et al.*, 1990), and morpho-anatomy (belly pattern of Hagström, 1973).

In *Triturus helveticus* (Salamandridae) for instance, there is a general agreement that the larval stage commences after eclosion and/or first food capture, the juvenile with the appearance of the limbs, and the adult with disappearance of the gills and appearance of functional gonads (sexual maturity) (Gipouloux & Chambolle, 1995; Steyer, pers. obs.). These useful anatomical character states are very rarely found in fossils, except in cases where soft tissue have been preserved (Spinar, 1972; Boy, 1974; Heyler, 1994).

Three developmental stages have been recognized in the temnospondyl genera:

larval (which includes the 'metamorphic stage' *sensu* Boy, 1989), juvenile (which includes the 'immature' stage *sensu* Warren & Hutchinson, 1988), and adult. The aim of this paper is not to redescribe all complete developmental sequences with the growth stages of the taxa being used, as these have already been defined.

The character states of the growth stages include the following: ossification degree (Boy, 1974; Heyler, 1994; Milner & Sequeira, 1994; Schoch, 1992; Warren & Schroeder, 1995), presence/absence of the cerato- or hyo-branchial skeleton (Boy, 1974, 1990; Heyler, 1994; Warren & Hutchinson, 1988; Werneburg, 1998), connection of the skull bones (Boy, 1974, 1989, 1990, 1993; Carroll, 1967; Heyler, 1994; Warren & Hutchinson, 1988; Werneburg, 1993), sculpturing stage (Boy, 1974, 1990; Carroll, 1967; Schoch, 1992), size and shape of marginal teeth (Boy, 1990), presence of bone apophysis (such as transversal process on vertebrae or uncinated process on ribs, Werneburg & Steyer, 1999, 2000), number of dermic growth lines (Werneburg & Steyer, 1999, 2000), and number of line of arrested growth (Laurin *et al.*, 1999). Size has not been taken into account.

METHODS

Cladistic analysis of fossil vertebrates commonly requires adult specimens, which are often considered morphologically static. However, a taxon represents a dynamic unity (i.e. a holomorph) which is entirely comprised within its own development (Danser, 1950; Hennig, 1966). Therefore, in this study, the parsimony analyses have been tested not only on adult taxa, but also on larval and juvenile stages. Hennig86 version 1.5. (Farris, 1988), the branch and bound option of which searches exhaustively for the most parsimonious tree, was chosen to perform each analysis.

Forty-one morpho-anatomical homologous characters were examined on most complete larval, juvenile and adult specimens (Appendix 1), with many data obtained from the literature and personal observations (Appendix 2). Three matrices were produced, one for each growth stage (Appendix 3). Whatever the stage, the same morphological characters are featured in the analysis and all of them have the same weight. Each character state was differentiated from others at the same growth stage. The same character state was coded differently according to growth stage. For instance, the posterior position of the orbits (character 2, Appendix 1) is coded as '2' in the juvenile forms (where an intermediate central position has been highlighted), and as '1' in the adult ones (the state '0' corresponds to an anterior position in both stages).

After obtaining the most parsimonious tree for each growth stage, these so-called 'ontotrees' are initially compared (taxonomic congruence *sensu* Kluge, 1989) and then combined together (total evidence *sensu* Kluge, 1989). Comparison of the 'ontotrees', as well as distribution of the character states in the combined analysis are discussed in the following section (see below).

The differentiation of characters is based on outgroup analysis (i.e. comparative anatomy criteria); based on ontogenetic criteria it would produce a circular reasoning. Ontogeny has indeed already been included in the analysis, either by comparison or combination of ontotrees.

The body size of these 'amphibians' was not taken into account in character differentiation, because of its large variability according to various parameters. In

lissamphians, the metamorphosed adult of *Alytes obstetricans* (Discoglossidae, Anura) is smaller (20 mm, 720 mg) than the tadpole (44 mm, 800–900 mg) (Bounhiol, 1995). In a wider sense, establishing absolute size is not necessarily a significant reason to divide the ontogenetic series into stages, for several reasons: (i) size is not necessarily increasing during development, (ii) if size is really increasing during development, different growth rates (iso- or allometric growths) between several taxa (Bystrow, 1935) could imply problems in the homology of the growth stages.

RESULTS

Taxonomic congruence

Whatever the treatment of the multistate characters (additive or not), one most parsimonious tree has been obtained for each growth stage: larval (Fig. 1), juvenile (Fig. 2) and adult (Fig. 3). Comparison of 'ontotrees' is therefore possible. These three trees are surprisingly different (i.e. incongruent).

Figure 3 shows the inter-relationships of adult specimens of the selected temnospondyls, in which *Parotosuchus* is closely related to *Cheliderpeton*. This group is included in the clade (((*Parotosuchus*, *Cheliderpeton*), *Onchiodon*), *Acanthostomatops*), rooted with the unsolved stem node comprising the outgroup *Dendrerpeton* and *Apateon*. This result is compatible neither with that of Schoch (1997:237), in which Dissorophoidea (i.e. Branchiosauridae and Dissorophidae) are closely linked to Zatrachydidae, nor with that of Milner (1990:324–327), in which Branchiosauridae are more closely related to Eryopidae. However this result is partly congruent with that of Yates and Warren (2000:84), in which Zatrachydidae are closely linked to Eryopidae.

The pre-adult (larval and juvenile) trees also show incongruent topologies. The distribution of the character states is also different for each growth stage. Results gained by the applied method for each growth stage do not agree. In the larval (Fig. 1) and adult trees (Fig. 3), *Apateon* appears to be a basal genus, and forms (along with *Dendrerpeton*) the basal polytomy of the trees. In the juvenile tree (Fig. 2), this taxon forms, with *Parotosuchus*, a robust clade which is supported by five synapomorphies (node 2).

In these three stages (larval, juvenile, and adult), the ingroup taxa form a clade. But the configuration of this clade drastically changes through ontogeny: it is composed of two sister groups, (*Onchiodon*, *Acanthostomatops*) and (*Cheliderpeton*, *Parotosuchus*) in the larval tree, ((*Apateon*, *Parotosuchus*) and (*Cheliderpeton*, (*Acanthostomatops*, *Onchiodon*))) in the juvenile tree. However, it forms a Hennigian comb in the adult tree. In the juvenile tree, *Parotosuchus* seems to be (with *Apateon*) the most basal taxon of the ingroup, while it represents the most derived one in both the larval and adult trees.

The total evidence approach

A combined analysis was devised to test the taxonomic incongruence of the ontotrees, including all larval, juvenile and adult character states per the 'total evidence' (TE) approach (*sensu* Kluge, 1989). This global parsimony analysis is based

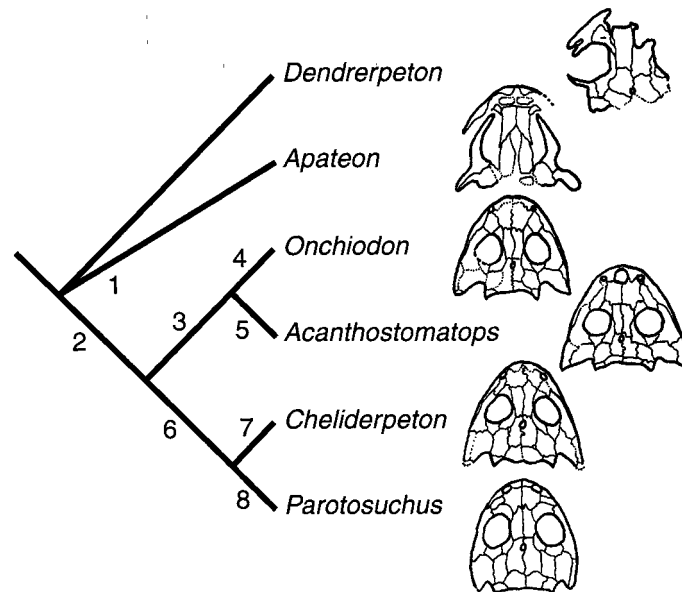


Figure 1. Larval tree of six temnospondyls. The most parsimonious cladogram ('branch and bound', Hennig86 version 1.5) of the larval forms. The treatment of the multistate characters (additive or not) does not influence the result. Consistency index (CI)=0.86, Retention index (RI)=0.71, Number of steps (L)=60. Skull size not to scale. *Dendrerpeton* as preserved, according to Carroll (1967:122); see text.

Node 1. Autapomorphies of *Apateon*: median position of a large pineal foramen along the interparietal suture. Convergences: large parabolic skull roof, squared supratemporal, small and medial alary process on premaxilla, absence of prefrontal-postfrontal suture.

Node 2. Synapomorphies of the clade ((*Onchiodon*, *Acanthostomatops*), (*Cheliderpeton*, *Parotosuchus*)): very opened otic notches, large orbits, small and pointed tabular, presence of the squamosal-tabular contact, triangular postorbital, no bone process on the quadratojugal, lacrimal in contact with orbit, anterior position of the pineal foramen on the interparietal suture. Convergence: squared supratemporal, small alary process on premaxilla.

Node 3. Synapomorphies of the clade (*Onchiodon*, *Acanthostomatops*): small septomaxilla, not well developed nasolacrimal dermo-sensory canal, marginal tooth with broad base, few denticles on parasphenoid, denticles on vomer, on ectopterygoid, and on pterygoid, elongated palatine, large dorsal part of the ilium. Convergences: parabolic skull roof, no internasal vacuity.

Node 4. Autapomorphies of *Onchiodon*: large orbits, elongated prefrontal, denticles on palatine, dorso-ventrally deep mandible with a coronoid apophysis and an elongated antero-external part of the surangular. Convergence: broad anterior part of the nasal.

Node 5. Autapomorphies of *Acanthostomatops*: large dorsal part of septomaxilla, posterior internasal vacuity, nasolacrimal dermo-sensory canals, numerous denticles on parasphenoid, choana not oval, anterior premaxilla-maxilla suture relative to the choana, square interclavicle. Convergences: presence of the squamosal-tabular contact, middle-sized prefrontal, cultriform process with broad extremities, broad palatine.

Node 6. Synapomorphies of (*Cheliderpeton*, *Parotosuchus*): anterior orbits, elongated supratemporal, squared postparietal, lacrimal in contact with neither orbits nor nostrils.

Node 7. Autapomorphies of *Cheliderpeton*: dermo-sensory canals shallow depressed (behind orbits), rhombic interclavicle. Convergences: parabolic outline of the skull roof, medial alary process on the premaxilla, no internasal vacuity.

Node 8. Autapomorphies of *Parotosuchus*: large tabular, large and subrectangular postorbital, small Meckelian fenestra. Convergences: contact between squamosal and tabular, no contact between prefrontal and postfrontal, broad anterior part of the nasal, cultriform process with broad extremities, broad palatal. Reversion: no alary process on premaxilla.

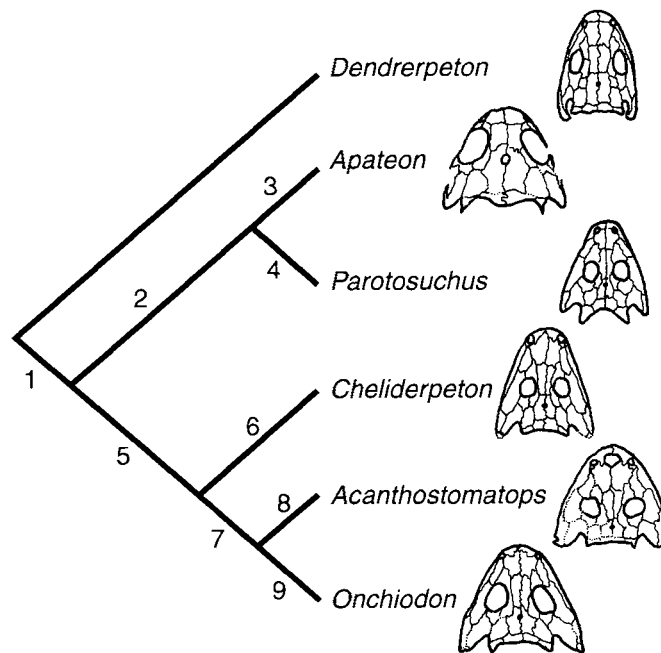


Figure 2. Juvenile tree of six temnospondyls. The most parsimonious cladogram ('branch and bound', Hennig86 version 1.5) of the juvenile forms. The treatment of the multistate characters (additive or not) does not influence the result. CI=0.77, RI=0.50, L=62. Skull size not to scale.

Node 1. Synapomorphies of the clade ((*Apateon*, *Parotosuchus*), (*Cheliderpeton*, (*Acanthostomatops*, (*Onchiodon*)))): parabolic outline of the skull roof, large otic notches.

Node 2. Synapomorphies of the clade (*Apateon*, *Parotosuchus*): large-sized and elongated tabular, no contact between prefrontal and postfrontal, denticles on vomer and on palatine. Convergences: large postorbital.

Node 3. Autapomorphies of *Apateon*: broad anterior part of the nasal, large pineal foramen, anterior premaxilla-maxilla suture relative to the choana, hooked palatine, rhombic interclavicle. Convergences: large orbits, denticles on pterygoid.

Node 4. Autapomorphies of *Parotosuchus*: relatively developed antero-external part of the surangular. Convergences: triangular skull roof, narrow otic notches, contact squamosal-tabular, elongated prefrontal, lacrimal in contact with neither nostrils nor orbits, marginal tooth with broad base, few denticles on ectopterygoid, interpterygoid fenestra not broad, narrow choana, broad extremities of the cultriform process.

Node 5. Synapomorphies of the clade (*Cheliderpeton*, (*Acanthostomatops*, *Onchiodon*)): small alary process, small septomaxilla, dermo-sensory canals shallow depressed. Convergences: central orbits, elongated prefrontal, lacrimal in contact with neither nostrils nor orbits.

Node 6. Autapomorphies of *Cheliderpeton*: relatively elongated supratemporal, median pineal foramen relative to the interparietal suture, denticles on the parasphenoid, dorso-ventrally deep mandible, developed coronoid apophysis. Convergences: triangular outline of the skull roof, elongated alary process, large septomaxilla, broad based marginal tooth, few denticles on ectopterygoid, denticles on pterygoid, interpterygoid fenestra not broad, narrow choana, cultriform process with broad extremities, rhombic interclavicle.

Node 7. Synapomorphies of the clade (*Acanthostomatops*, *Onchiodon*): pointed tabular, medial alary process along premaxilla, large postparietal, dermo-sensory canals well developed.

Node 8. Autapomorphies of *Acanthostomatops*: posterior position of the orbits, at least one process of the quadratojugal, internasal vacuity in posterior position, contact of the lacrimal with orbits, squared interclavicle, constricted dorsal part of the ilium. Convergences: narrow otic notches, contact between squamosal and tabular, elongated alary process, large septomaxilla, large postorbital.

Node 9. Convergences of *Onchiodon*: large orbit, broad based marginal tooth.

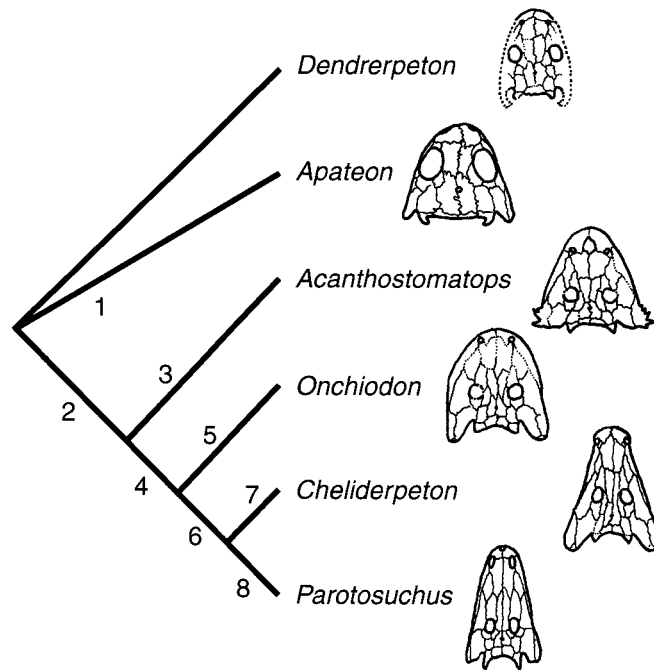


Figure 3. Adult tree of six temnospondyls. The most parsimonious cladogram ('branch and bound', Hennig86 version 1.5) of the adult forms. The treatment of the multistate characters (additive or not) does not influence the result. CI=0.65, RI=0.38, L=89. Skull size not to scale.

Node 1. Autapomorphies of *Apateon*: large otic notches, large orbit, large pineal foramen, straight posterior extremity of the cultriform process, medio-anterior premaxilla-maxilla suture relative to the choana, narrow and hooked palatine. Convergences: parabolic skull roof, large and hooked tabular, small septomaxilla, no contact between prefrontal and postfrontal, triangular postorbital, very large postparietal, few denticles on vomer, no denticles on palatine, ectopterygoid, and on pterygoid, elongated interpterygoid fenestra, mandible not dorso-ventrally deep, elongated antero-external part of the surangular, rounded scapulocoracoid, large dorsal part of the ilium.

Node 2. Synapomorphies of the clade (*Acanthostomatops*, (*Onchiodon*, (*Cheliderpeton*, (*Parotosuchus*)))): narrow otic notches, central orbit, broad anterior part of the nasal, lacrimal in contact with orbits, rounded choana, no coronoid apophysis. Convergence: small septomaxilla.

Node 3. Autapomorphies of *Acanthostomatops*: bone process on the quadratojugal and on angular, internasal vacuity in posterior position, numerous denticles on parasphenoid. Convergences: parabolic outline of the skull roof, pointed tabular, contact between squamosal and tabular, triangular postorbital, very large postparietal, broad posterior extremity of the cultriform process, not dorso-ventrally deep mandible, large dorsal part of the ilium.

Node 4. Synapomorphies of the clade (*Onchiodon*, (*Cheliderpeton*, (*Parotosuchus*)))): nasal elongated, lacrimal in contact with neither nostrils nor orbits, median pineal foramen relative to the interparietal suture, oval interpterygoid fenestra, rhombic interclavicle.

Node 5. Autapomorphies of *Onchiodon*: middle sized tabular, middle sized alary process, large postparietal, marginal tooth with broad base and convex sides. Convergences: parabolic outline of the skull roof, triangular postorbital, no denticles on vomer, few denticles on palatine, very broad posterior extremity of the cultriform process.

Node 6. Synapomorphies of the clade (*Cheliderpeton*, *Parotosuchus*): elongated skull roof, large prefrontal, elongated choana, relatively elongated palatine, rhombic interclavicle. Convergence: elongate interpterygoid fenestra.

Node 7. Autapomorphies of *Cheliderpeton*: concave outline of the skull roof, narrow supratemporal, small alary process, relatively broad extremities of the cultriform process. Convergences: pointed tabular, bean-rounded scapulocoracoid, enlarge dorsal part of the ilium. Reversion: hamate process of the coronoid apophysis.

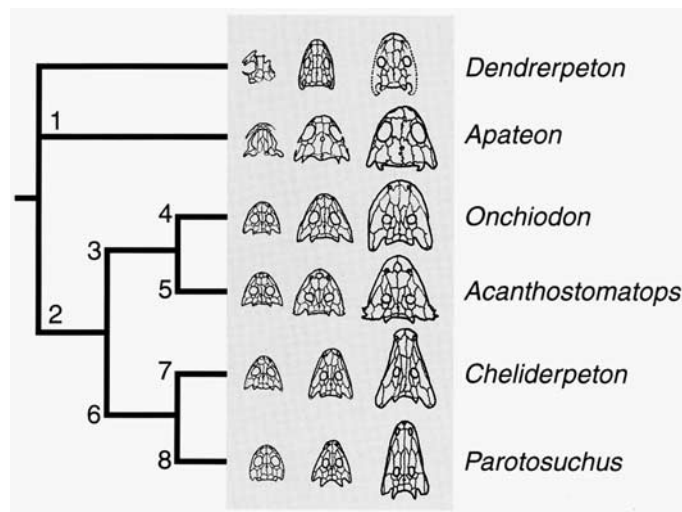


Figure 4. Combined tree of six temnospondyls, integrating all the growth stages of all the studied taxa. The most parsimonious cladogram ('branch and bound', Hennig86 version 1.5) obtained by the total evidence approach (Kluge, 1989). The treatment of the multistate characters (additive or not) does not influence the result. CI=0.73, RI=0.44, L=216. Skull size not to scale.

Node 1. Autapomorphies of *Apateon*: very large pineal foramen and large orbits.

Node 2. Synapomorphies of the clade ((*Onchiodon*, *Acanthostomatops*), (*Cheliderpeton*, *Parotosuchus*)): contact of the lacrimal at best with orbits, non anterior pineal foramen along the interparietal suture, presence of an alary process.

Node 3. Synapomorphies of (*Onchiodon*, *Acanthostomatops*): rounded choana and at least one broad extremity of the cultriform process of the parasphenoid.

Node 4. Autapomorphies of *Onchiodon*: rounded interclavicle.

Node 5. Autapomorphies of *Acanthostomatops*: posterior internasal vacuity, bone process on quadratojugal.

Node 6. Synapomorphies of (*Cheliderpeton*, *Parotosuchus*): very long postorbital, antero-posteriorly elongated skull.

Node 8. Autapomorphies of *Parotosuchus*: anterior internasal vacuity.

on a combined matrix of six taxa and 123 character states (= 41 character states per three different growth stages). Whatever the treatment of the multistate characters (whether additive or not), all having the same weight, one most parsimonious combined tree was obtained (Fig. 4).

Surprisingly, the combined tree has the same topology as the larval one (Fig. 1), but a different character state distribution. The ingroup is composed of the clade ((*Onchiodon*, *Acanthostomatops*), (*Cheliderpeton*, *Parotosuchus*)) and it is rooted on the stem polytomy represented by the outgroup *Dendrerpeton* and *Apateon*.

This result corroborates the distributions of the character states in the first analysis: the TE tree is robust (Consistency Index=0.72) and reveals a few homoplasies

Node 8. Autapomorphies of *Parotosaurus*: anterior internasal vacuity, presence of dermo-sensory canals, marginal tooth with narrow base and relatively convex sides, well-developed Meckelian fenestra. Convergences: large and pointed tabular, contact between squamosal and tabular, no contact between prefrontal and postfrontal, subrectangular postorbital, denticles on vomer, palatine, ectopterygoid, and pterygoid (?), not dorso-ventrally deep mandible, elongated antero-external part of the surangular. Reversions: otic notches almost closed, no septomaxilla.

which correspond to polymorphic character states found in the different ontotrees.

A (very) large postparietal (character 16, Appendix 1) represents a convergence between *Apateon* and *Acanthostomatops* (nodes 1 and 5, Fig. 4). *Acanthostomatops* also shows a convergence with *Parotosuchus* (contact between squamosal and tabular, nodes 5 and 8, Fig. 4; character 7, Appendix 1), while *Parotosuchus* shows a convergence with *Apateon* (absence of contact between prefrontal and postfrontal, nodes 8 and 1, Fig. 4; character 12, Appendix 1). Moreover, both reversals occur in *Acanthostomatops* (an anterior pineal foramen along the interparietal suture, node 5, Fig. 4; character 20, Appendix 1) and in *Parotosuchus* (disappearance of the alary process, node 8, Fig. 4; character 8, Appendix 1). These homoplastic characters—relative size of the postparietal, contact between prefrontal and postfrontal, contact between squamosal and tabular, position of the pineal foramen along the interparietal suture, presence of the alary process, added to the position of the putative dermo-sensory canals and the shape of the nasal—are also those which cause incongruent topologies of the compared ontotrees (Figs 1–3).

DISCUSSION

The polymorphic character states which cause taxonomic incongruence of the ontotrees correspond to the few homoplastic ones found in the combined tree. These character states could be interpreted either as developmental heterochronies, or as a re-evaluation of the systematic identification of larval specimens.

Developmental heterochronies

The ontogenetic patterns of the species used in this analysis have already been described by many authors (Appendix 2), especially those concerning the development of the skull (compared with Urodeles, see Schoch, 1998, in press b). The morphology of the skull bones, fused with others or formed at different growth steps during osteogenesis, implies differing polarizations and character states. These ossifications, when compared with others and according to the distribution of the character states at nodes, could be interpreted as heterochronies.

Heterochronic events have already been chronicled in the development of the temnospondyl skull (Schoch, 1995; Steyer, 1996b). Here, comparison of the ontotrees could reveal some heterochronies. For instance, *Acanthostomatops* is not basal on the larval tree (Fig. 1, node 5), and is in a crown position on the juvenile one (Fig. 2, node 8). In the adult stage, however, *Acanthostomatops* ‘becomes comparatively more primitive’, its adult form belonging to the basal branch of the in group (Fig. 3, node 3). Acceleration (i.e. hyperadult shape with adult size: a peramorphosis, *sensu* McNamara, 1986) or shift of the ossification process to earlier ontogenetic stages could therefore occur in dermal bones such as the quadratojugal and the angular, all showing more developed apophysis (autapomorphies of the adult form, Fig. 3, node 3). At the same time, a striking retention of some primitive characters (paedomorphosis, *sensu* McNamara, 1986), such as a parabolic outline of the skull roof (convergence in Fig. 3, node 3; synapomorphy in Fig. 2, node 1) or contact

between squamosal and tabular (convergences from larval to adult stage of *Acanthostomatops*), are observed in the adult stage.

Comparison of the ontotrees is therefore useful for detecting possible heterochronies.

Problem in systematic identification of larval forms

Another hypothesis, which may account for these taxonomic incongruences, is a possible erroneous identification of the larvae. In many cases, the younger an individual is, the less differentiated are its morpho-anatomical characters, and the more difficult its systematic assignment. It is clear that a larval individual does not represent a small-scale model of the adult one. Identification of both larval and metamorphic temnospondyls is questionable. A degree of ossification or a stage of sculpturing (both *sensu* Schoch, 1992) of fossilized bones, such as the honeycombed sculpture of *Melanerpeton* (Branchiosauridae) (Werneburg, 1988), are not significant indicators of metamorphosis (Schoch, in press a). Other metamorphic criteria could be involved. For instance, sclerotic rings could be retained in adult terrestrial temnospondyls (such as *Cheliderpeton*, Werneburg & Steyer, 2000). They do not necessarily imply adaptation to water, and their disappearance during development is not proof of metamorphosis.

Larval assignment of an extinct amphibian and its species identification are therefore questionable if morpho-anatomical, palaeoecological and taphonomical data have not been taken into account. For example, the presence of larvae and adults in the same geological layers is insufficient evidence for an attribution to the same species (Bechly *et al.*, 1998). In other words, small preserved specimens associated with larger ones are not necessarily younger forms of the same taxa (Heyler, 1994).

This is the case with the larval *Dendrerpeton* used in this analysis (Fig. 1): it was first identified (Carroll, 1967) as the smallest *Dendrerpeton* in a series of about one hundred specimens from a unique assemblage (Joggins Formation, Carboniferous of Nova Scotia). It was recently re-interpreted as an adult indeterminate microsaur (Milner, 1996) according to its striated sculpturing stage and position of the tabular (laterally to both parietal and postorbital).

CONCLUSION

Cladistic analysis is a powerful tool for testing different scenarios. Cladograms have already been incorporated into working hypotheses when developing the biochronological (Martinez, 1997) or palaeoecological (Nel, 1997) implications of new findings. In this paper, the TC approach has been used to compare trees based on larval, juvenile or adult morpho-anatomical character states. These 'ontotrees' are not congruent either in topology or in character state distribution. The TE approach has been used to compile the data and to test the taxonomic incongruence of the ontotrees. The result corroborates the first analysis: the unique combined tree is robust and shows a few homoplasies. These homoplasies correspond to the polymorphic character states which cause the incongruence of the ontotrees, and

have been interpreted either as heterochronic events or problems in systematic identification of larval forms. Finally, these polymorphic characters—relative size of the postparietal, contact between prefrontal and postfrontal, contact between squamosal and tabular, position of the pineal foramen along the interparietal suture, presence of the alary process, position of the putative dermo-sensory canals, and shape of the nasal—should be treated with caution in the future diagnosis of temnospondyls, whatever the growth stage.

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REFERENCES

- Agassiz L. 1833–1843.** *Recherches sur les Poissons fossiles*. I introduction, questions générales (340 pp.), II Ganoides (650 pp.), III Placoides (400 pp.), IV Cténoïdes (300 pp.), V Cycloïdes (270 pp.). Ed. Neufchatel: Petitpierre.
- Baer KE. von. 1828.** *Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion*. Königsberg: Bornträger.
- Bechly G, Nel A, Martinez-Delclos X, Fleck G. 1998.** Four new Dragonflies from the Upper Jurassic of Germany and the Lower Cretaceous of Mongolia (Anisoptera: Hemeroscopidae, Sonidae and Proterogomphidae Fam. Nov.). *Odonatologica* **27(2)**: 149–187.
- Beebe TJC. 1980.** Amphibian growth rates. *British Journal of Herpetology* **6**: 107.
- Bounhiol JJ. 1995.** La croissance du têtard et du jeune adulte. In: Grasse PP, ed. *Traité de Zoologie. Anatomie, Systématique, Biologie. Amphibiens*. Paris: Masson, Tome XIV, Fasc. IA, 1085–1100.
- Boy JA. 1974.** Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon-Trias). *Paläontologische Zeitschrift* **48(3/4)**: 236–268.
- Boy JA. 1986.** Studien über die Branchiosauridae (Amphibia: Temnospondyli) 1. Neue und wenig bekannte Arten aus dem mitteleuropäischen Rotliegenden (?oberstes Karbon bis unteres Perm). *Paläontologische Zeitschrift* **60**: 131–166.
- Boy JA. 1989.** *Acanthostomatops* and the Zatrachydidae. *Acta Musei Reginaehradecensis S.A.: Scientiae Naturales* **22**: 139.
- Boy JA. 1990.** Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon–Perm) 3. *Onchiodon*. *Paläontologische Zeitschrift* **64(3.4)**: 107–132.
- Boy JA. 1993.** Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon–Perm) 4. *Cheliderpeton latirostre*. *Paläontologische Zeitschrift* **67**: 123–143.
- Bystrow AP. 1935.** Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. I – Mitteilung: Schädel der Stegocephalen. *Acta Zoologica* **16**: 64–141.
- Carr TD. 1998.** Tyrannosaurid (Dinosauria, Theropoda) craniofacial ontogeny: comparative parsimony analysis of ontogenetic characters. *Journal of Vertebrate Paleontology* **18(3)**: 31.
- Carroll RL. 1967.** Labyrinthodonts from the Joggins Formation. *Journal of Paleontology* **41(1)**: 111–142.

- Damiani RJ, Warren A. 1997.** Re-interpretation of *Parotosuchus wadei* Cosgriff, a Capitosaurid from the Triassic Narrabeen Group at Gosford, New South Wales, with comments on its growth stage. *Alcheringa* **21**: 281–289.
- Danser BH. 1950.** A theory of systematics. *Bibliotheca Biotheoretica* **4**: 117–180.
- Farris JS. 1988.** *Hennig86 version 1.5*. Privately published: Port Jefferson, New York.
- Francillon-Viellot H, Arntzen JW, Géraudie J. 1990.** Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): a skeletochronological comparison. *Journal of Herpetology* **24**: 13–22.
- Fritsch A. 1877.** Über die Wilbeltierfauna in der Vorzeit Böhmens. *Sitzungsberichte der königlich böhmischen Gesellschaft der Wissenschaften*. In: Fritsch A, ed. *Fauna der Gaskhole und der Kalksteine der Permformation Böhmens*. Prague, 18.
- Fritsch A. 1885.** *Fauna der Gaskhole und der Kalksteine der Permformation Böhmens. Band II Heft I (Dendroperonidae. Archegosauridae, Chauliodontia, Melosauridae)*. Prague; Brenntegasse.
- Fuiman LA. 1983.** Ostariophys: development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, eds. *Ontogeny and systematics of Fishes*. Lawrence: Allen Press, 126–138.
- Geinitz HB. 1861.** *Dyas oder Zeichsteinformation und das Rotliegende*. Dresden.
- Gipouloux JD, Chambole P. 1995.** Les formes larvaires et leur métamorphose. In: Grassé PP, ed. *Traité de Zoologie. Anatomie, Systématique, Biologie* **14**(1A): 871–896.
- Gould SJ. 1977.** *Ontogeny and Phylogeny*. Cambridge, MA: Harvard University Press.
- Grandjean F. 1947.** Sur la distinction de deux sortes de temps en biologie évolutive et sur l'attribution d'une phylogenèse particulière à chaque état statique de l'ontogénèse. *Comptes Rendus de l'Académie des Sciences* **225**(15): 612–615.
- Grandjean F. 1957.** L'évolution selon l'âge. *Archives des Sciences de Genève* **10**: 477–526.
- Haeckel E. 1866.** *Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*. Berlin: Reimer.
- Hagström T. 1973.** Identification of newt specimens (Urodela, Triturus) by recording the belly pattern and a description of photographic equipment for such registration. *British Journal of Herpetology* **4**: 321–326.
- Hennig W. 1943.** Ein Beitrag zum Problem der "Beziehungen zwischen Larven- und Imaginalsystematik". *Arbeiten über morphologische taxonomische Entomologie* **10**: 138–140.
- Hennig W. 1966.** *Phylogenetic Systematics*. Chicago: University of Illinois Press.
- Heyler D. 1994.** Les Branchiosaures stéphaniens et permien de Montceau-les-Mines et des autres bassins du Massif Central. In: Comité des travaux historiques et scientifiques, ed. *Quand le Massif Central était sous l'équateur*, 227–247. Paris.
- Houde ED. 1983.** Bregmacerotidae: Development and Relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, eds. *Ontogeny and Systematics of Fishes*. Lawrence: Allen Press, 300–308.
- Johnson RK. 1983a.** Scopelarchidae: Development and Relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, eds. *Ontogeny and Systematics of Fishes*. Lawrence: Allen Press, 245–250.
- Johnson RK. 1983b.** Evermannellidae: Development and Relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, eds. *Ontogeny and Systematics of Fishes*. Lawrence: Allen Press, 250–254.
- Kalandadze NN, Ochev VG, Tatarinov LP, Chudinov PK, Shishkin MA. 1968.** Katalog permiskikh i triasovykh tetrapod SSSR In: Akademiya Nauk SSSR, ed. *Verkhnepaleozoyskiye i mesozoskiye zemnovodnyye i presmykayushchiyesya SSSR* (Upper Paleozoic and Mesozoic amphibians and reptiles of the USSR). Otdeleniye Obshehey Biologii, 72–91.
- Keller R. 1946.** Morphogenetische Untersuchungen am Skelett von *Siredon mexicanus* SHAW mit besonderer Berücksichtigung des Ossifikationsmodus beim neotenen Axolotl. *Revue Suisse de Zoologie* **53**: 329–426.
- Kluge AG. 1989.** A concern for evidence and a phylogenetic hypothesis of relationships among Epicrates (Boidea: Serpentes). *Systematic Zoology* **38**(1): 7–25.
- Kuhn O. 1961.** *Die Familien der rezenten und fossilen Amphibien und Reptilien*. Bamberg: Meisenbach.
- Laurin M, Steyer JS, de Ricqlès A. 1999.** Histological evidence for the conquest of land and returns to the aquatic environment among early stegocephalians. In: Hoch E, ed. *Secondary Adaptation to Life in Water*. Copenhagen: Geologisk Museum Press.
- Leis JM. 1983.** Tetraodontoidae: Development. In: Moser HG, Richards WJ, Cohen DM, Fahay

- MP, Kendall AW, Richardson SL, *Ontogeny and Systematics of Fishes*. Lawrence: Allen Press, 447–450.
- McNamara KJ. 1986.** A guide to nomenclature of heterochrony. *Journal of Paleontology* **60**: 4–13.
- Martinez JN. 1997.** Biochronogrammes: un usage plus rationnel de la méthode biochronologique des lignées évolutives. *Geobios* **20**(mem. sp.): 347–355.
- Meyer H. von. 1844.** Briefliche Mittheilung an Prof F. Bronn. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie, und Petrefaktenkunde* **1844**: 336–337.
- Milner AR. 1980.** The temnospondyl amphibian *Dendroperpeton* from the Upper Carboniferous of Ireland. *Paleontology* **23**(1): 125–141.
- Milner AR. 1990.** The radiation of Temnospondyl amphibians. In: Taylor PD, Larwood GP, eds. *Major evolutionary radiations*. Oxford: Clarendon Press, Systematics Association Special Volume 42, 321–349.
- Milner AR. 1996.** A revision of the temnospondyl amphibians from the Upper Carboniferous of Joggins, Nova Scotia. 81–103. In: Milner AR, ed. *Studies on Carboniferous and Permian vertebrates. Special Papers in Palaeontology* **52**: 1–148.
- Milner AR, Sequeira SEK. 1994.** The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84**: 331–361.
- Naef A. 1931.** Phylogenie der Tiere. In: von Baur G, Hartmann WA, eds. *Handbuch der Vererbungswissenschaft* III, 1.
- Nel A. 1997.** The probabilistic inference of unknown data in phylogenetic analysis. In: Grandcolas P, ed. *The origin of biodiversity in insects: phylogenetic test of evolutionary scenarios*. Paris: Mémoires du Muséum national d'Histoire naturelle, 305–327.
- Orloy AN. 1991.** A mathematical method of studying vertebrates. *Paleontological Journal* **1990**(2): 113–118.
- Owen R. 1853.** Notes on the above-described fossil remains. *Quarterly Journal of the Geological Society of London* **9**: 66–67.
- Pietsch TW. 1983.** Lophiiformes: Development and Relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, eds. *Ontogeny and Systematics of Fishes*. Lawrence: Allen Press, 320–325.
- Popper KR. 1972.** *Objective knowledge: an evolutionary approach*. Oxford: Clarendon Press.
- Pryer KM, Smith AR, Skog JE. 1995.** Phylogenetic relationships of extant ferns based on evidence from morphology and *rbcL* sequences. *American Fern Journal* **85**(4): 205–282.
- Richardson M. 1998.** Une fraude en embryologie. *Pour la Science* **247**(4): 10–12.
- Ricqlès A de. 1975.** Quelques remarques paléo-histologiques sur le problème de la néoténie chez les stégocéphales. In: Centre National de la Recherche Scientifique, ed. *Problèmes actuels en Paléontologie – Evolution des Vertébrés*. Paris: Colloque International CNRS, 4–9 juin 1973, 351–363.
- Ricqlès A de. 1979.** Relations entre structures histologiques, ontogénèses, stratégies démographiques et modalités évolutives: le cas des Reptiles Captorhinomorphes et Stegocéphales temnospondyles. *Comptes Rendus de l'Académie des Sciences* **288D**: 1147–1150.
- Rieppel OC. 1988.** *Fundamentals of Comparative Biology*. Basel: Birkhäuser.
- Schoch RR. 1992.** Comparative ontogeny of Early Permian Branchiosaurid Amphibians from Southwestern Germany. Developmental stages. *Paleontographica* **222A**: 43–83.
- Schoch RR. 1995.** Heterochrony in the development of the amphibian head. In: McNamara KJ, ed. *Evolving change and heterochrony*. Chichester: Wiley.
- Schoch RR. 1997.** Cranial anatomy of the Permian temnospondyl amphibian *Zatrachys serratus* COPE 1878, and the phylogenetic position of the Zatrachyidae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **206**(2): 223–248.
- Schoch RR. 1998.** Homology of cranial ossifications in urodeles: Significance of developmental data for fossil basal tetrapods. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1998**(1): 1–25.
- Schoch RR. in press a.** Can metamorphosis be recognized in Palaeozoic amphibians? Implications on the transition from water to land. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*.
- Schoch RR. in press b.** Patterns of skeleton formation in urodeles and temnospondyls. 1. Cranial ossification in *Apateon* and *Ranodon*. *Zoological Journal of the Linnean Society*.
- Spinar ZV. 1972.** *Tertiary frogs from Central Europe*. Prague: Czechoslovak Academy of Sciences.
- Steen MC. 1937.** On *Acanthostoma vorax* CREDNER. *Proceedings of the Zoological Society of London* **107B**: 491–500.
- Steyer JS. 1996a.** Une nouvelle espèce de *Cheliderpeton* (Amphibia, Temnospondyli) du Permien inférieur de Buxières-les-Mines (Allier, France). Position phylétique et relations ontogénie-phylogénie des eryopoides. Unpublished DEA report, University of Montpellier 2.

- Steyer JS. 1996b.** Readaptation to the aquatic environment and developmental heterochronies in the eryopoids (Amphibia, Temnospondyli). In: Mazin JM, Vignaud P, Buffrenil de V, eds. *Secondary Adaptation to Life in Water*. Poitiers: Poitiers University Press, 82–83.
- Sylva de DP. 1983.** Sphyraenoidei: Development and Relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, eds. *Ontogeny and systematics of Fishes*. Lawrence: Allen Press, 534–540.
- Warren AA, Hutchinson MN. 1988.** A new capitosaurid (amphibian) from the Early Triassic of Queensland, and the ontogeny of the capitosaurid skull. *Paleontology* **31**(3): 857–876.
- Warren AA, Schroeder N. 1995.** Changes in the capitosaur skull with growth: an extension of the growth series of *Parotosuchus aliciae* (Amphibia, Temnospondyli) with comments on the otic area of capitosaurids. *Alcheringa* **19**: 41–46.
- Welles SP, Cosgriff JW. 1965.** A revision of the labyrinthodont family Capitosauridae and a redescription of *Parotosaurus peabodyi* n. sp. from the Moenkopi Formation of Northern Arizona. *University of California Publications in Geological Sciences* **54**: 1–61.
- Werneburg R. 1988.** Die Stegocephalen der Goldlauterer Schichten (Unterrotliegendes, Unterperm). Teil III: *Apateon kontheri* n.sp., *Melanerpeton eisfeldi* n. sp. des Thüringer Waldes und andere. *Freiberger Forschungshefte* **C427**: 19–29.
- Werneburg R. 1993.** *Onchiodon* (Eryopidae, Amphibia) aus dem Rotliegendes des Innersudetischen Beckens (Böhmen). *Paläontologische Zeitschrift* **67**(3/4): 343–355.
- Werneburg R. 1997.** Der Eryopide *Onchiodon* (Amphibia) aus dem Rotliegendes des Beckens von Autun (Frankreich). *Freiberger Forschungshefte, Heft 4. Paläontologie, Stratigraphie, Fazies* **C466**: 167–181.
- Werneburg R. 1998.** Ein larvaler *Acanthostomatops* (Zatrachydidae, Amphibia) aus der Niederhäslich-Formation (Unter-Perm) des Döhlen-Beckens. *Veröffentlichungen Museum für Naturkunde Chemnitz* **21**: 49–52.
- Werneburg R, Steyer JS. 1999.** Redescription of the holotype of *Actinodon frossardi* Gaudry, 1866 (Amphibia, Temnospondyli) from the Lower Permian of the Autun basin (France). *Geobios* **32**(4): 599–607.
- Werneburg R, Steyer JS. 2000.** Redescription of *Cheliderpeton vranyi* Fritsch, 1877 (Amphibia, Temnospondyli) from the Lower Permian of Czech Republic. *Paläontologische Zeitschrift*, in press.
- Yates AM, Warren AA. 2000.** The phylogeny of the ‘higher’ temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* **128**: 77–121.

APPENDIX 1: CHARACTERS USED IN FORMULATION OF THE DATA MATRICES

Character coded 0, 1, etc. Polarity based on outgroup criteria.

0. Outline of the skull roof:
 - rounded (0), parabolic (1) in larvae,
 - rounded (0), parabolic (1), triangular (2) in juveniles,
 - rounded (0), parabolic (1), elongated (2), concave (3) in adults.
1. Relative otic notches size:
 - non formed (0), very opened (1) in larvae
 - almost closed (0), narrow (1), large (opening > 33% of the skull table width; 2) in juveniles and adults.
2. Orbit position on the skull roof:
 - non-totally closed (0), anterior (1) in larvae,
 - anterior (0), central (1), posterior (2) in juveniles,
 - anterior (0) posterior (1) in adults.
3. Relative orbit size:
 - opened orbits (0), large (>25% of the skull length; 1) in larvae,
 - large (0), small (20–25% of the skull length; 1) in juveniles
 - very small (<20% of the skull length; 0), large (1) in adults.

4. Supratemporal shape:
enlarged (length/width < 1; 0), squared (1), elongated (length/width = 1.4–2.5; 2) in larvae,
enlarged to squared (0), elongated to narrow (1) in juveniles,
enlarged to elongated (0), narrow (length/width > 2.5; 1) in adults
5. Relative size of the tabular:
tabular non-differentiated (0), small (10% of the skull length; 1), large (20% of the
skull length; 2) in larvae,
small (0), large (1) in juveniles,
small (0), middle (1), large (2) in adults
6. Shape of the tabular:
tabular non differentiated (0), pointed (1) in larvae,
squared (0), pointed (1), elongated (2) in juveniles,
rounded (0), pointed (1), elongated or hooked (2) in adults.
7. Contact between squamosal and tabular:
tabular not differentiated (0), no (1), yes (2) in larvae,
no (0) yes (1) in juveniles and adults.
8. Relative size of the alary process:
no alary process (0), small (10% of the skull length; 1) in larvae,
no alary process (0), small (1), long (16–20% of the skull length; 2) in juveniles and adults.
9. Position of the alary process along premaxilla: external (0), medial (1) in larvae, juveniles and
adults
10. Relative size of the septomaxilla:
no septomaxilla (0), small (1), large (>15% of the skull length; 2) in larvae and juveniles,
no septomaxilla (0), small (1) in adults.
11. Relative size of the prefrontal:
small or wide (0), elongated (>25% of the skull length; 1) in larvae, juveniles and adults.
12. Contact between prefrontal and postfrontal: short to middle (0), absent (1) in larvae, juveniles and
adults.
13. Relative shape of the postorbital:
non formed (0), triangular (1), subrectangular (2) in larvae,
elongated (0), large (1) in juveniles,
elongated (0), subrectangular (1), triangular (2) in adults.
14. Presence/absence of bone process of the quadratojugal:
non formed (0), absent (1) in larvae,
absent (0), at least one process (1) in juveniles and adults.
15. Internasal vacuity:
nasal not sutured (0), no vacuity (1), in posterior position (2) in larvae,
no vacuity (0), in posterior position (1) in juveniles,
no vacuity (0), in anterior position (1), in posterior position (2) in adults.
16. Relative shape of the postparietal:
large or non differentiated (0), squared (width/length = 1:1) in larvae,
(sub-)squared (0), large (1) in juveniles,
sub-squared (0), large (1), very large (width/length > 2.5; 2) in adults.
17. Dermo-sensory canals:
absent (0), shallow depression (1), present (2) in larvae, juveniles,
absent (0), present (1) in adults.
18. nasal shape:
entirely broad (0), anterior part only broad (1) in larvae,
anterior part only broad (0), entirely broad (1) in juveniles,
squared (0), with a broad anterior part (1), elongated (2) in adults.
19. Contact of the lacrimal:
lacrimal not formed (0), contact with orbits (1), contact with neither nostrils nor orbits (2) in larvae,
contact with orbits and nostrils (0), with orbits (1), with neither nostrils nor orbits (2) in juveniles
and adults.

20. Position of the pineal foramen along the interparietal suture:
posterior (0), median (1), anterior in larvae,
anterior (0), median (1) in juveniles and adults
21. Relative size of the pineal foramen:
small (0), large (at least 18% of the interparietal length; 1) in larvae, juveniles and adults.
22. Relative shape of the marginal tooth:
narrow base (0), broad base (1) in larvae and juveniles.
broad base and straight sides (0), narrow base and relatively convex sides (1), very
broad base and convex sides (2) in adults.
23. Denticles on the parasphenoid:
absent (0), few (1), numerous (2) in larvae,
absent (0), presence (1) in juveniles,
absent or few (0), numerous (1) in adults.
- 24, 25. Denticles on the vomer, on the palatine (respectively):
absent (0), presence (1) in larvae and juveniles,
numerous (0), absent or few (1) in adults.
26. Denticles on the ectopterygoid:
absent or non-differentiated (0), (very) few (1) in larvae and juveniles,
numerous (0), absent or a few present (1) in adults.
27. Denticles on the pterygoid:
absent (0), present (1) in larvae and juveniles,
numerous (0), absent or a few present (1) in adults.
28. Shape of the interpterygoid fenestra:
broad (0) or not (1) in larvae and juveniles,
very broad (0), oval (1), elongated (2) in adults.
29. Shape of the choana:
rounded or oval (0), non-oval (1) in larvae,
oval (0), (very) narrow (1) in juveniles,
oval (0), rounded (1), elongated (2) in adults.
30. Shape of the cultriform process of the parasphenoid:
broad posterior extremity (0), broad extremities (1) in larvae,
straight (0), broad extremities (1) in juveniles,
narrow (0), straight posterior extremity (1), relatively broad extremities? (2), (very)
broad posterior extremity (3) in adults.
31. Position of the premaxilla-maxilla suture relative to the choana:
medio-anterior (0), anterior (1) in larvae and juveniles,
very anterior (0), medio-anterior (1) in adults.
32. Shape of the palatine:
non differentiated (0), elongated (1), broad (2) in larvae,
elongated (0), hooked (1) in juveniles,
short and broad (0), relatively elongated (1), narrow and hooked (2) in adults.
33. Shape of the mandible: not dorsoventrally deep (0), dorsoventrally deep (1) in larvae, juveniles
and adults.
34. Presence of the coronoid apophysis:
hamate (i.e. prearticular) process (0), developed coronoid apophysis (1) in larvae and juveniles,
(well) developed (0) or not (1) in adults.
35. Antero-external part of the surangular:
relatively developed (maximum 10% of the mandible length; 0), very elongated (at least 18% of
the mandible length; 1) in larvae,
relatively developed (1) or not (0) in juveniles,
not or relatively developed (0), elongated (1) in adults.

36. Bone process on angular: absent (0), presence (1) in larvae, juveniles and adults.
37. Meckelian fenestra:
poorly developed (0), small sized (1) in larvae,
absent or small (0), well developed (1) in juveniles and adults.
38. Shape of the interclavicle:
rounded to oval (0), squared (1), elongated or rhombic (2) in larvae and juveniles,
pear-shaped (0), rounded (1), rhombic (2) in adults.
39. Scapulocoracoid:
bean-shaped (0) in larvae and juveniles
pear-shaped (0), bean-rounded (1) in adults.
40. Dorsal part of the ilium:
not ossified (0), enlarged (1) in larvae
very large (0), constricted (1) in juveniles,
straight and narrow (0), (very) enlarged (1) in adults.

APPENDIX 2: BIBLIOGRAPHIC REFERENCES

	Skull roof	Palate
<i>Acanthostomatops</i>	Boy, 1989:137	Boy, 1989:141
<i>Cheliderpeton</i>	Boy, 1993:127; Werneburg & Steyer, 2000	Boy, 1993:131; Steyer, 1996a:5–6
<i>Onchiodon</i>	Boy, 1990:292–293; Werneburg, 1993: 346–348	Boy, 1990:297
<i>Dendrerpeton</i>	Milner, 1980:131; Carroll, 1967:122	Milner, 1980:132
<i>Apateon</i>	Schoch, 1992	Schoch, 1992
<i>Parotosuchus</i>	Damiani & Warren, 1997:286	Damiani & Warren, 1997:284; Welles & Cosgriff, 1965:50–87 Warren & Hutchinson, 1988:865–870
	Interclavicle	Mandible
<i>Acanthostomatops</i>	Boy, 1989:145	Boy, 1989:142
<i>Cheliderpeton</i>	Boy, 1993:134; Werneburg & Steyer, 2000	Boy, 1993:133; Fritsch, 1885:Pl.56; Steyer, 1996a:6
<i>Onchiodon</i>	Boy, 1990:300; Werneburg, 1993:346–348	Boy, 1990:298; Werneburg & Steyer, 1999
<i>Dendrerpeton</i>	Milner, 1980:133	Milner, 1980:128; Carroll, 1967:114–123
<i>Apateon</i>	Schoch, 1992:79	Boy, 1986:155
<i>Parotosuchus</i>	Damiani & Warren, 1997:284	Damiani & Warren, 1997:284; Welles & Cosgriff, 1965:117
	Warren & Hutchinson, 1988:867	Warren & Hutchinson, 1988:866–871
	Ilium	Marginal tooth
<i>Acanthostomatops</i>	Boy, 1989:145	Boy, 1989:141–142
<i>Cheliderpeton</i>	Fritsch, 1885:pl.54; Werneburg & Steyer, 2000	Boy, 1993:131–133; Fritsch, 1885:22; Steyer, 1996a:6
<i>Onchiodon</i>	Boy, 1990:301	Boy, 1990:289
<i>Dendrerpeton</i>	Carroll, 1967:132	Milner, 1980:132
<i>Apateon</i>	Schoch, 1992:64	Schoch, 1992:65
<i>Parotosuchus</i>		Warren & Hutchinson, 1988:866
	Scapulocoracoid	
<i>Acanthostomatops</i>	Steen, 1937:497	
<i>Cheliderpeton</i>	Fritsch, 1885:Pl.56; Steyer, 1996a:6	
<i>Onchiodon</i>	Boy, 1990:299	
<i>Dendrerpeton</i>	Carroll, 1967:124	
<i>Apateon</i>	Schoch, 1992:64	
<i>Parotosuchus</i>	Welles & Cosgriff, 1965:122 Warren & Hutchinson, 1988:867	

APPENDIX 3: DATA MATRICES USED IN THE CONSTRUCTION OF THE CLADOGRAMS

The data matrix used in the construction of the combined tree (total evidence, see text) corresponds to a end-to-end combination of these three matrices.

Characters	01234	56789	11111	11111	22222	22222	33333	33333	4
Larval			01234	56789	01234	56789	01234	56789	0
<i>Acanthostomatops</i>	11011	11210	20011	20301	20121	01101	112???	???1?	1
<i>Cheliderpeton</i>	11112	11111	00011	11102	20???	?????	?????	???2?	?
<i>Onchiodon</i>	11011	11110	11011	10211	20111	11100	00111	10000	1
<i>Dendrerpeton</i>	00000	000??	?000?	?00?0	00???	?????	?????	?????	?
<i>Apateon</i>	10001	00011	00100	00000	11000	00000	000??	???00	0
<i>Parotosuchus</i>	01112	2120-	00121	11012	20?00	00000	10200	001??	?
Juvenile									
<i>Acanthostomatops</i>	11210	01121	21011	11201	00???	?????	?????	???10	1
<i>Cheliderpeton</i>	22111	00020	21000	00102	10110	01111	10011	0002?	?
<i>Onchiodon</i>	12100	01011	11000	01202	001??	?????	?????	???0?	?
<i>Dendrerpeton</i>	00010	0000-	01000	00000	00???	?????	?????	?????	?
<i>Apateon</i>	12000	1200-	00110	00010	01001	10100	011??	???20	0
<i>Parotosuchus</i>	21110	1210-	01110	00002	00101	11011	10000	10000	?
Adult									
<i>Acanthostomatops</i>	11100	0110-	10021	22011	00010	00001	30001	010??	1
<i>Cheliderpeton</i>	31101	01010	11000	00022	100??	???22	20110	00?21	1
<i>Onchiodon</i>	11100	10020	10020	01022	10201	10011	30011	?0?10	0
<i>Dendrerpeton</i>	00000	0000-	00000	00000	00000	00000	00010	00000	0
<i>Apateon</i>	12010	2200-	10110	02000	01001	11120	11200	10?01	1
<i>Parotosuchus</i>	20100	2210-	01110	10122	10101	11122	00101	10120	0