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A Review of the fossil Caudata of Europe

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With 2 tables

Summary

A taxonomic and stratigraphic review of European fossil Caudata is given. Their earliest record (*Marmorerpeton*, Middle Jurassic) is, at the same time, the oldest known tailed amphibian. Two families have Mesozoic-Tertiary occurrence. Some Tertiary representatives (e.g. Cryptobranchidae, some Salamandridae) have been largely distributed in Eurasia; however, due to climatic deterioration in the early Pleistocene they disappeared from Europe. Contemporary European Caudata appeared as early as in the late Oligocene and, except for *Mertensiella* and *Pleurodeles*, they regained their original distribution after the Pleistocene glaciations.

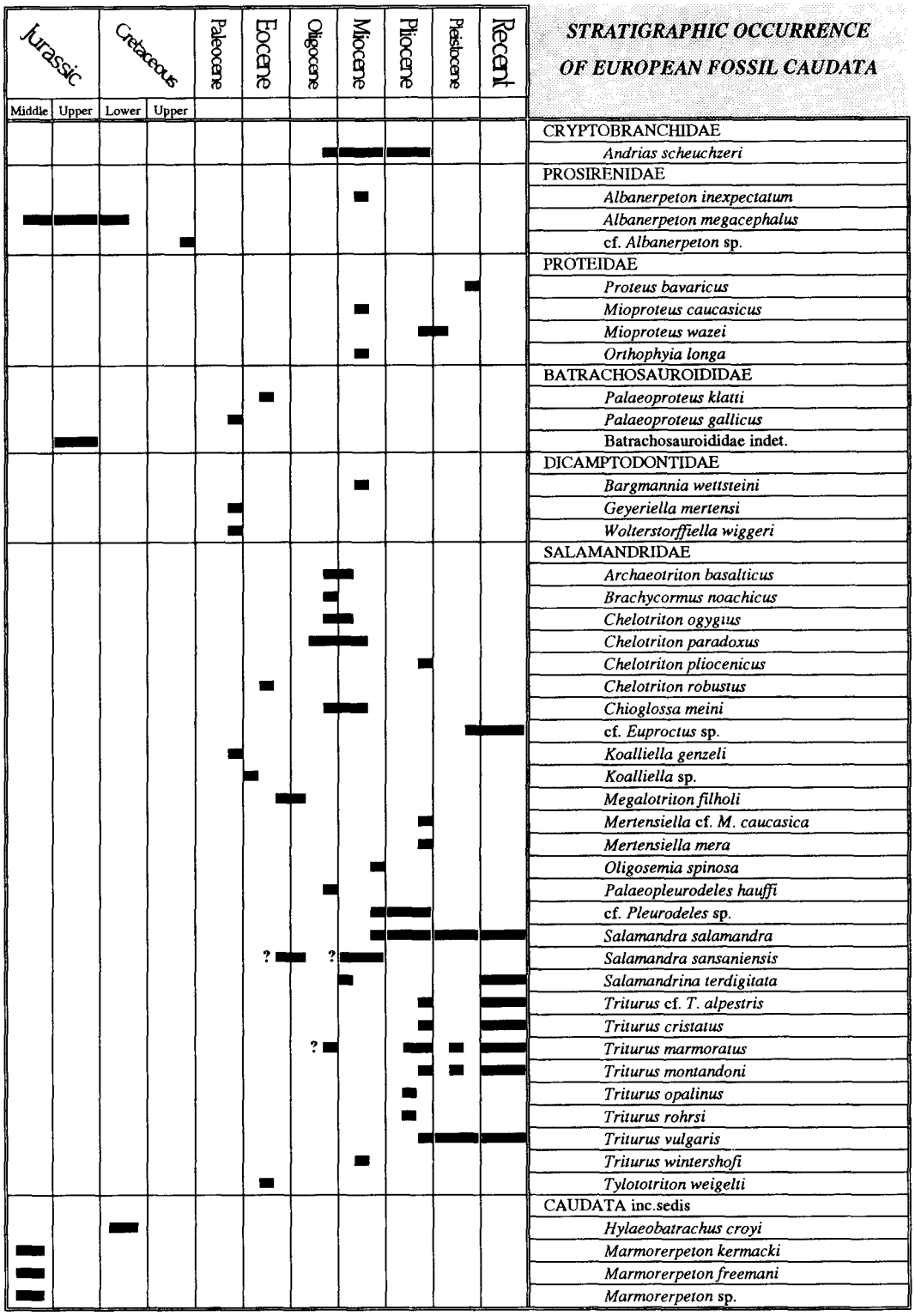
Zusammenfassung

Es wird ein taxonomischer und stratigraphischer Überblick über die fossilen Caudata gegeben. Der früheste Nachweis (*Marmorerpeton*, mittleres Jura) ist gleichzeitig der älteste bekannte Schwanzlurch. Zwei Familien haben ein mesozoisch-tertiäres Auftreten. Einige Tertiärvertreter (z.B. die Cryptobranchidae und einige Salamandridae) waren weit in Eurasien verbreitet, verschwanden aber während der pleistozänen Klimaverschlechterung aus Europa. Rezente europäische Schwanzlurche erschienen bereits im späten Oligozän und konnten, mit Ausnahme von *Mertensiella* und *Pleurodeles*, ihre ursprünglichen Areale nach dem Ende der pleistozänen Vereisungen wieder rückbesiedeln.

The European fossil tailed amphibians can be traced back to the Middle Jurassic (Upper Bathonian; see Tab.1). The earliest record is represented by *Marmorerpeton* EVANS, MILNER & MUSSET, 1988. At the same time, this is the earliest known unequivocal record of the Caudata in the world. It should be noted that *Marmorerpeton*, though being the earliest known tailed amphibian, was already diversified into at least three distinct species (EVANS et al. 1988).

Hylaeobatrachus croyi is another early tailed amphibian, found in the Lower Cretaceous (Wealdian) deposits of Belgium. Because of its obviously neotenic nature (suggested by presence of five ossified branchial arches) its taxonomic status remains obscured, as it is the case with *Marmorerpeton*.

Albanerpeton is classified either as belonging to the Prosirenidae or as a member of its own family Albanerpetontidae. Its stratigraphic occurrence is extensive. Although *A. inexpectatum* was found in the Miocene (France), *A. megacephalus* was reported already from the Bajocian (Middle Jurassic, Aveyron, S France). Thus, *A. megacephalus* belongs to the earliest Caudata, too. This species can be traced up to the Neocomian (Lower Cretaceous) of Spain; however, an undetermined *Albanerpeton* was recently reported also from the Maastrichtian (Upper Cretaceous) of Spain (ASTIBIA et al. 1991). It is worthy to note that a single atlas from the Bajocian of Aveyron (see above) de-



STRATIGRAPHIC OCCURRENCE OF EUROPEAN FOSSIL CAUDATA

- CRYPTOBRANCHIDAE
  - *Andrias scheuchzeri*
- PROSIRENIDAE
  - *Albanerpeton inexpectatum*
  - *Albanerpeton megacephalus*
  - cf. *Albanerpeton* sp.
- PROTEIDAE
  - *Proteus bavaricus*
  - *Mioproteus caucasicus*
  - *Mioproteus wazei*
  - *Orthophyia longa*
- BATRACHOSAUROIDIDAE
  - *Palaeoproteus klatti*
  - *Palaeoproteus gallicus*
  - Batrachosauroididae indet.
- DICAMPTODONTIDAE
  - *Bargmannia wettsteini*
  - *Geyeriella mertensi*
  - *Wolterstorffiella wiggeri*
- SALAMANDRIDAE
  - *Archaeotriton basalticus*
  - *Brachycormus noachicus*
  - *Chelotriton ogygius*
  - *Chelotriton paradoxus*
  - *Chelotriton pliocenicus*
  - *Chelotriton robustus*
  - *Chioglossa meini*
  - cf. *Euproctus* sp.
  - *Koalliella genzeli*
  - *Koalliella* sp.
  - *Megalotriton filholi*
  - *Mertensiella* cf. *M. caucasica*
  - *Mertensiella mera*
  - *Oligosemia spinosa*
  - *Palaeopleurodeles hauffi*
  - cf. *Pleurodeles* sp.
  - *Salamandra salamandra*
  - *Salamandra sansaniensis*
  - *Salamandrina terdigitata*
  - *Triturus* cf. *T. alpestris*
  - *Triturus cristatus*
  - *Triturus marmoratus*
  - *Triturus montandoni*
  - *Triturus opalinus*
  - *Triturus rohrsi*
  - *Triturus vulgaris*
  - *Triturus wintershofi*
  - *Tylototriton weigelti*
- CAUDATA inc.sedis
  - *Hylaeobatrachus croyi*
  - *Marmorerpeton kermacki*
  - *Marmorerpeton freemani*
  - *Marmorerpeton* sp.

scribed by SEIFFERT (1969) and referred to *Albanerpeton* by ESTES & HOFFSTETTER (1976) is so aberrant from all other Caudata that FOX & NAYLOR (1982) even suggested that it might represent a distinct order of Amphibia. However, the available information on its morphology is insufficient for determining its relationships (MILNER 1988); for the time being it is maintained within the Caudata. Recently, EVANS & MILNER (1991) and ENSOM et al. (1991) mentioned undetermined *Albanerpeton* from the Middle and Upper Jurassic of England. Jurassic findings of this amphibian were also reported from Portugal (KÜHNE 1968). It can be supposed that if the determination is correct, then *Albanerpeton* was persisting in Europe from the Jurassic until the Miocene, and further findings linking both species can be expected.

Although *Palaeoproteus* was reported from the Palaeogene (Paleocene of Cernay, France and Eocene of Geiseltal, Germany), the recent record of an undetermined representative of the family Batrachosauroididae from the Upper Jurassic of England (ENSOM et al. 1991) is astonishing and indicates another group of Caudata that survived from the Mesozoic until Tertiary.

Besides Mesozoic (*Marmorerpeton*) and Mesozoic-Tertiary lineages (Prosirenidae, Batrachosauroididae), all other known European fossil Caudata are recorded from the Tertiary and later periods. Remarkable is *Andrias*, the largest tailed amphibian (length up to 135 cm), the earliest record of which is from the Upper Oligocene of Rott (Germany). Osteological comparison of fossil and recent forms (WESTPHAL 1958, BÖTTCHER 1987) revealed that there are no significant differences between them; the same holds true for both fossil and contemporary forms from Asia and North America. Since the earliest records of Cryptobranchidae are from the Paleocene of Asia (CKHIKVADZE 1982) and North America (NAYLOR 1981), and because of the presence of cryptobranchids in Japan (separated from the continental Asia in the Pliocene or early Pleistocene), one may suppose that the European findings are only a part of a formerly large and continuous distribution area of a single species. This is also supported by findings from central Asia (*A. karelcapeki* and *Zaissanurus beliajevae* are synonyms of *A. scheuchzeri*; see BÖTTCHER 1987). Low geographic and stratigraphic variation of *A. scheuchzeri* suggests that it is a morphologically very conservative species which disappeared from Europe due to the climatic deterioration in the early Pleistocene (BÖTTCHER 1987, fig.15).

Fossil Dicamptodontidae are known both from North America and Europe; today, they are extinct in Europe. *Geyeriella* and *Bargmannia* are closely related and their affinities to the Dicamptodontidae seem to be beyond any doubt. This is not the case with *Wolterstorffiella* the assignment of which to Dicamptodontidae remains doubtful (ESTES 1981: 49).

Some Salamandridae have a similar distributional history as *Andrias*. Besides *Koalliella* which is the earliest European representative of this family, recorded from the Upper Paleocene of Cernay, France and Lower Eocene of Dormaal, Belgium (ESTES, HECHT & HOFFSTETTER 1967, GODINOT et al. 1978), there are three genera closely related with each other, namely *Brachycormus*, *Chelotriton* and *Tylototriton*. They inhabited Europe, undoubtedly as a part of larger distribution area, until the late Pliocene and then they withdrew to south-east Asia, surviving there only by the latter genus. *Palaeopleurodeles* and *Pleurodeles* are representatives of a lineage which was closely related to the *Brachycormus* / *Chelotriton* / *Tylototriton* lineage. Although *Palaeopleurodeles* was recorded already from the Oligocene, its probable descendant *Pleurodeles* was able to survive in Europe until today, in spite of the Pleistocene climatic changes. However, it was not able to regain the original distribution of its ancestor.

< Tab. 1. Stratigraphic occurence of European fossil Caudata.
Stratigraphisches Vorkommen der fossilen Salamander Europas.

Salamandrid genera that are living in Europe today are evidenced with certainty in this area as early as in the Miocene (except for *Euproctus*; see SANCHÍZ 1977). This early origin implies that they had to survive Pleistocene glaciations either in Mediterranian refugia from which they expanded again in Holocene times (not in the case of *Mertensiella* which remained restricted to Caucasus, and *Pleurodeles*; see above) or, as suggested by Pleistocene records of Caudata in Poland (MŁYNARSKI & SZYNDLAR 1989), the distribution of Caudata could fluctuate in close correlation with changes in the extent of continental glaciation. The Tertiary-Holocene occurrence may be exemplified in *Salamandra* which is recorded (though with certain doubts) as early as in the Upper

CRYPTOBRANCHIDAE FITZINGER, 1826
- ***Andrias*** TSCHUDI, 1837
  - ***Andrias scheuchzeri*** (HOLL, 1831)

PROSIRENIDAE ESTES, 1969
- ***Albanerpeton*** ESTES & HOFFSTETTER, 1976
  - ***Albanerpeton inexpectatum*** ESTES & HOFFSTETTER, 1976
  - ***Albanerpeton megacephalus*** (COSTA, 1864)

PROTEIDAE HOGG, 1838
- ***Proteus*** LAURENTI, 1768
  - ***Proteus bavaricus*** BRUNNER, 1956
- ***Mioproteus*** ESTES & DAREVSKY, 1978
  - ***Mioproteus caucasicus*** ESTES & DAREVSKY, 1978
  - ***Mioproteus wazei*** ESTES, 1984
- ***Orthophyia*** V. MEYER, 1845
  - ***Orthophyia longa*** V. MEYER, 1845

BATRACHOSAUROIDIDAE AUFFENBERG, 1956
- ***Palaeoproteus*** HERRE, 1935
  - ***Palaeoproteus klatti*** HERRE, 1935
  - ***Palaeoproteus gallicus*** ESTES, HECHT & HOFFSTETTER, 1967
- **Batrachosauroididae indet.**

DICAMPTODONTIDAE (TIHEN, 1958)
- ***Bargmannia*** HERRE, 1955
  - ***Bargmannia wettsteini*** HERRE, 1955
- ***Geyeriella*** HERRE, 1950
  - ***Geyeriella mertensi*** HERRE, 1950
- ***Wolterstorffiella*** HERRE, 1950
  - ***Wolterstorffiella wiggeri*** HERRE, 1950

SALAMANDRIDAE GRAY, 1825
- ***Archaeotriton*** V. MEYER, 1860
  - ***Archaeotriton basalticus*** (V. MEYER, 1859)
- ***Brachycormus*** V. MEYER, 1860
  - ***Brachycormus noachicus*** (GOLDFUSS, 1831)
- ***Chelotriton*** POMEL, 1853
  - ***Chelotriton ogygius*** (GOLDFUSS, 1831)
  - ***Chelotriton paradoxus*** POMEL, 1853
  - ***Chelotriton pliocenicus*** BAILON, 1989
  - ***Chelotriton robustus*** WESTPHAL, 1980
- ***Chioglossa*** BOCAGE, 1864
  - ***Chioglossa meini*** ESTES & HOFFSTETTER, 1976
- ***Euproctus*** GENÉ, 1838
  - cf. ***Euproctus* sp.**
- ***Koalliella*** HERRE, 1950
  - ***Koalliella genzeli*** HERRE, 1950
  - ***Koalliella* sp.**
- ***Megalotriton*** ZITTEL, 1890
  - ***Megalotriton filholi*** ZITTEL, 1890
- ***Mertensiella*** WOLTERSTORFF, 1925
  - ***Mertensiella* cf. *M. caucasica***
  - ***Mertensiella mera*** HODROVÁ, 1984
- ***Oligosemia*** NAVÁS, 1922
  - ***Oligosemia spinosa*** NAVÁS, 1922
- ***Palaeopleurodeles*** HERRE, 1941
  - ***Palaeopleurodeles hauffi*** HERRE, 1941
- ***Pleurodeles*** MICHAHELLES, 1830
  - cf. ***Pleurodeles* sp.**
- ***Salamandra*** LAURENTI, 1768
  - ***Salamandra salamandra*** (LINNAEUS, 1758)
  - ***Salamandra sansaniensis*** LARTET, 1851
- ***Salamandrina*** FITZINGER, 1826
  - ***Salamandrina terdigitata*** (LACÉPEDE, 1788)
- ***Triturus*** RAFINESQUE, 1815
  - ***Triturus* cf. *T. alpestris***
  - ***Triturus cristatus*** (LAURENTI, 1768)
  - ***Triturus marmoratus*** (LATREILLE, 1800)
  - ***Triturus montandoni*** (BOULENGER, 1880)
  - ***Triturus opalinus*** (V. MEYER, 1851)
  - ***Triturus rohrsi*** HERRE, 1955
  - ***Triturus vulgaris*** (LINNAEUS, 1758)
  - ***Triturus wintershofi*** LUNAU, 1950
- ***Tylototriton*** ANDERSON, 1871
  - ***Tylototriton weigelti*** HERRE, 1935

CAUDATA inc. sedis
- ***Hylaeobatrachus*** DOLLO, 1884
  - ***Hylaeobatrachus croyi*** DOLLO, 1884
- ***Marmorerpeton*** EVANS, MILNER & MUSSETT, 1988
  - ***Marmorerpeton kermacki*** EVANS, MILNER & MUSSETT, 1988
  - ***Marmorerpeton freemani*** EVANS, MILNER & MUSSETT, 1988
  - ***Marmorerpeton* sp.**

Tab. 2. Systematic review of European fossil caudata.
Systematische Übersicht der fossilen Salamander Europas.

Eocene or Lower Oligocene. The phylogenetic continuity of *S. sansaniensis* and *S. salamandra* is very probable. A similar case is the Proteidae, which are well documented by *Mioproteus* from the Miocene through the uppermost Lower Pleistocene (MŁYNARSKI & SZYNDLAR 1989); *Proteus* seems to be the contemporary survivor of this lineage. The number of *Triturus* species will probably be reduced in the future because *T. opalinus*, *T. rohrsi* and *T. wintershofi* are either larvae or insufficiently preserved specimens. The same holds true for some other salamandrids (e.g. *Oligosemia* which is probably a synonym of *T. marmoratus*; ESTES 1981: 84).

It can be summarized that at present, 45 species or distinct but specifically undetermined forms belonging to at least 26 genera (tab. 2) of tailed amphibians are known as fossils in Europe. At least 4 of them, belonging to 2 genera (including the earliest ones), can be categorized only as family incertae sedis. Only two families of the European Caudata have Cretaceous-Tertiary occurrence (Prosirenidae, Batrachosauroididae). The Tertiary European Caudata were partly affected by climatic changes at the beginning of the Pleistocene (their contemporary distribution in north Africa - south Iberian Peninsula or south-east Asia indicates their original ecological requirements), but some of them were considerably resistant to Pleistocene glaciations.

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