THE HALECOMORPH FISHES
CATURUS AND AMBLYSEMIUS
IN THE LITHOGRAPHIC LIMESTONE
OF SOLNHOFEN (TITHONIAN), BAVARIA

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ABSTRACT
The halecomorph genus Caturus is represented in Solnhofen by the species C. furcatus and the robust form C. giganteus. The anatomy of the skull of C. pachyurus is different from C. furcatus and C. giganteus, but similar to C. bellicianus a species known from Cerin and Solnhofen, originally described as Amblysemius bellicianus. The genus Amblysemius is revived, represented in Solnhofen by the species A. pachyurus and A. bellicianus.

KEY WORDS : PISCES, HALECOMORPHI, CATURUS, AMBLYSEMIUS, TITHONIAN, SOLNHOFEN.

INTRODUCTION
The genus Caturus is known from the Upper Triassic (Austria, Spain) to the lower Cretaceous (Spain). In 1832 Agassiz mentioned, without description, the fish Uraeus pachyurus from Solnhofen. Later Agassiz (1833-1843) described several species of Caturus, including C. furcatus from Solnhofen, Bavaria, and classified U. pachyurus in the genus Caturus. After Agassiz, more species were described from Solnhofen (Münster 1834, 1839, 1842 ; Wagner 1851, 1863 ; Winkler 1862), and from Cerin, dept. Ain, France, by Thiollière & Meyer (1850), Thiollière (1873) and Saint-Seine (1949). Wagner (1851) described Strobilodus a synonym of Caturus, from Solnhofen. Agassiz (1833-1843) very shortly described, without publishing a figure, the genus Amblysemius, the type species A. gracilis, from the Jurassic of Northampton (England). Thiollière (1850-1873) described A. bellicianus from Cerin, later referred to Caturus by Saint-Seine (1949).

In this paper it will be shown that the genus Caturus in Solnhofen can be divided into the genera Caturus (with the species C. furcatus and C. giganteus) and Amblysemius (with the species A. pachyurus [formerly C. pachyurus] and A. bellicianus). This is a preliminary note, a more extensive description and analysis will be published elsewhere. Selected lists of synonyms are presented, containing only the first descriptions of the species and junior synonyms, the citings from Cerin, and publications with more or less complete descriptions and informative figures.
Amblysemius and Caturus are easily recognized by their elongate, fusiform outline, their wide gape, skull roof composed of large frontals and dermopterotics, and small parietals, numerous (20-30) plate-like branchiostegal rays, deeply forked hemiheterocercal tail, powerful dentition and cycloid scales of the amniid type. The vertebral column consists of the species of both genera of 25-30 abdominal vertebrae, 17-19 caudal vertebrae and 11-14 hypurals. Hemichordacentra are usually observed in large individuals only. The vertebrae are disjunctive in the caudal region. The ural neural arches are block-like, which might be considered characteristic of the Caturidae (Patterson 1973, Schaeffer & Patterson 1984).

An other possible synapomorphy is the presence of laterally broadened haemal spines throughout the caudal region. There is no one-to-one relationship between fin rays and hypurals. There are about four epurals.

They show halecomorph characters (Patterson 1973) like a small posterior process fused to the quadrate; the symplectic incorporated in the jaw joint and the dermosphenotic incorporated in the skull roof.

The specimens that have been studied are from the Bayerische Staatsammlung für Paläontologie und Historische Geologie, München (BSP), the Natural History Museum, London (NHM), the Jura-Museum, Eichstätt (JM), the Museum d'Histoire Naturelle de Lyon (MHNL), Teylers, Haarlem, Carnegie Museum, Pittsburg and the Bürgemeister Müller Museum, Solnhofen.

**SYSTEMATIC DESCRIPTION**

Division HALECOSTOMI (sensu Patterson, 1973)
Subdivision HALECOMORPHI (sensu Patterson, 1973)
Family CATURIDAE Owen, 1860
Genus Caturus AGASSIZ, 1834

Emended diagnosis (combination of primitive and derived characters). Elongate, fusiform fishes; snout obtusely pointed; skull roof in a downward angle with the back; caudal peduncle narrow; caudal fin with large symmetrical lobes; dermal bones smooth or sparsely-tuberculated; small parietals and large dermopterotic, dermopterotic with posterior process; rectangular nasals not meeting in the midline, leaving a small part of the ethmoidal region uncovered; antorbital with long premaxillary process reaching from orbit to premaxilla; posttemporal with internal process connected to the intercalar; multiple supraorbitals, usually arranged in several rows, dermosphenotic rectangular and small, incorporated in the skull roof, three infraorbitals, infraorbitals 1 and 2 meeting each other approximately below the orbit, infraorbital 1 bearing a dorsal laminar expansion, infraorbital 2 with a large plate-like portion posterior to the orbit, infraorbital 3 triangular, bordering the orbit posteriorly almost completely; two suborbitals, completely covering the cheek between infraorbitals and preoperculum, the dorsal one more than two times as big as the ventral one; preoperculum long and slender, slightly curved, in its ventral part expanded; operculum roughly triangular, suboperculum deep, smaller than operculum, more or less rectangular, interoperculum small, triangular, situated anteroventrally to the suboperculum; many plate-like branchiostegals, the first two being the largest; maxilla long and slender, in its posterior part expanded dorsally and ventrally, posterior border notched; premaxilla with clear nasal process, sometimes with a foramen for the olfactory nerve; lower jaw with two coronoids; parapneumonic extends beyond the posterior border of the basioccipital, connected with a dorsal process to the intercalar, small basipterygoid process; opisthotic absent; hyomandibular stout, inclined slightly forward; dentition: numerous straight, conical, in large forms laterally compressed teeth on maxilla, premaxilla and dentary, granular teeth on prearticular, two rows of small teeth on coronoids, small, sharply pointed teeth on ectopterygoid, very small granular teeth on entopterygoid and parachonchoid; vomer with marginal teeth; hemichordacentra present in large specimens, small specimens usually with an uncovered notochord; two postcleithra and two postcleithral scales present; endoskeletal shoulder girdle with reduced scapular and coracoid portions; fringing fulcra present on all fins, every fin preceded by a median basal fulcrum.

Type species - Caturus furcatus (AGASSIZ, 1833).

**CATURUS FURCATUS** AGASSIZ : Pl. 1a ; Fig.1

Selected synonymy
1833 - Pachycormus furcatus AGASSIZ, p. 476
1834 - Caturus latus MÜNSTER, p. 539
1839 - ? Caturus ovatus MÜNSTER, p. 679
1839-1843 - Caturus furcatus AGASSIZ, 1843 : vol. 2, pt 2, p. 116 ; 1839 : pl. 66a
1839-1843 - Caturus latus AGASSIZ, 1843 : vol. 2, pt 2, p. 117 ; 1839 : pl. 56
1842 - Caturus obovatus MÜNSTER, p. 42
1842 - Caturus intermedius MÜNSTER, p. 42
1842 - ? Caturus brevicostatus MÜNSTER, p. 42
Figure 1 - Skull of *Caturus furcatus*. Acid preparation, specimen NHM P.37906, Tithonian, Solnhofen. Sutures between opercular bones not determinable. The dermosphenotic is one of bones in the posterodorsal corner of the orbit. IO2 divided in two bones. Crâne de *Caturus furcatus*. Préparation à l’acide, specimen NHM P.37906, Tithonian, Solnhofen. Les sutures entre les os operculaires ne sont pas visibles. Le dermosphenotique est l’un des os dans l’angle posterodorsal de l’orbite. IO2 divisé en deux os.

1862 - *Caturus ferox* WINKLER, p. 57, fig. 10
1863 - *Caturus maximus* AGASSIZ ; Wagner, p. 701
1863 - *Caturus furcatus* AGASSIZ ; Wagner, p. 702
1863 - *Caturus latus* MÜNSTER ; Wagner, p. 702
1863 - *Caturus cyprinoides* WAGNER, p. 702
1863 - *Caturus microchirus* AGASSIZ ; Wagner, p. 703
1863 - *Caturus macrurus* AGASSIZ ; Wagner, p. 706
1863 - *Caturus obovatus* MÜNSTER ; Wagner, p. 707
1863 - *Caturus gracilis* WAGNER, p. 707
1873 - *Caturus furcatus* AGASSIZ ; Thiolière, p. 18 ; pl. 13, fig. 1
1873 - *Caturus latus* MÜNSTER ; Thiolière, p. 18 ; pl. 13, fig. 3
1895 - *Caturus furcatus* AGASSIZ ; Woodward, p. 392
1906 - *Caturus furcatus* AGASSIZ ; Heineke, p. 38; pl. 1 ; pl. 5, fig.1
1949 - *Caturus furcatus* AGASSIZ ; Saint-Seine, p. 165 ; fig. 73, pl. 16, fig. C

**Diagnosis** - Medium-sized caturids, occasionally reaching a standard length of almost 1 m ; numerous infraorbitals arranged in parallel rows ; anterior part of infraorbital 2 extends to halfway below the orbit ; infraorbital 1 long ; supramaxilla extending along approximately 1/3 of the length of the maxilla ; large individuals usually with hemichordacentra ; caudal fin deeply forked. Head length about 28% of SL ; Pectoral fin with 20-25 rays ; Pelvic fin with 7-10 rays ; Dorsal fin at about 54% SL ; 17-20 rays, first three to four rays not transversally segmented and branched ; Anal fin at about 75% SL, 8-10 rays ; Dorsal fin at about 55% SL ; 14-17 rays, the first two to three rays not segmented nor branched ; Anal fin at about 15% SL, 8-10 rays ; Teeth on premaxilla, maxilla and dentary robust, pointed and laterally compressed ; hemichordacentra present ; caudal fin weakly emarginate, less deeply than in *C. furcatus*. Head length 29% of SL ; Pectoral fin with 14-17 rays ; Pelvic fin at about 62% SL, 8-10 rays ; Dorsal fin at about 55% SL ; 14-17 rays, the first two to three rays not segmented nor branched ; Anal fin at about 29% SL ; Pectoral fin with 14-17 rays ; Pelvic fin at about 62% SL, 8-10 rays ; Dorsal fin at about 55% SL ; 14-17 rays, the first two to three rays not segmented nor branched ; Anal fin at about 29% SL.

**CATORUS GIGANTEUS** (WAGNER) : Pl. 1b ; Fig. 2

**Selected synonymy**

1851 - *Strobilodus giganteus* WAGNER, p. 75 ; pl. 2
1863 - *Strobilodus giganteus* WAGNER, p. 674
1881 - ? *Strobilodus giganteus* WAGNER ; Vetter p. 72
1895 - *Caturus (Strobilodus) giganteus* (WAGNER) ; Woodward, p. 346
1992 - *Caturus giganteus* (WAGNER, 1851) ; Lambers, p. 132 ; pl. 16, figs. 22a.b.

**Diagnosis** - Large, robust caturids, reaching a standard length of up to 1 m ; up to seven subcircular supraorbitals ; anterior part of infraorbital 2 extends to almost the level of the anterior border of the orbit, infraorbital 1 small ; supramaxilla relatively long, extending over about half the length of the maxilla (without anterior process) ; teeth on premaxilla, maxilla and dentary robust, pointed and laterally compressed ; hemichordacentra present ; caudal fin weakly emarginate, less deeply than in *C. furcatus*. Head length 29% of SL ; Pectoral fin with 14-17 rays ; Pelvic fin at about 62% SL, 8-10 rays ; Dorsal fin at about 55% SL ; 14-17 rays, the first two to three rays not segmented nor branched ; Anal fin at about 29% SL.
81% SL, 8-11 rays, first two to three not segmented nor branched; Caudal fin 30-33 rays, 11-13 in the epichordal lobe, 18-22 in the hypochordal lobe, first three unsegmented, first 4 unbranched; 26-29 branchiostegal rays.

Species of *Caturus* in Solnhofen - Body outline is a very unreliable character for species distinction in *Caturus* from Solnhofen, because many specimens are deformed due to fossilization. All species distinguished from *C. furcatus* on the ground of body outline only are considered synonyms of *C. furcatus*.

It is not justified to separate *C. giganteus* from *Caturus* as a separate (sub)genus *Strobilodus*. The cranial anatomy of the skull of the type-species *C. furcatus* differs from *C. giganteus* only in the proportions of the infraorbitals and supramaxilla, the build up of the supraorbitals, the dentition, the fin placement and the bifurcation of the caudal fin (see diagnoses). Both species differ from the very similar *C. driani* from Cerin in having a relatively larger dentition, a smaller dorsal fin arising halfway the back (in advance of the middle of the back in *C. driani*), and smaller scales. *C. velifer* is different in having rhomboid scales with a peg-and-socket articulation instead of cycloid scales (Saint-Seine 1949, pers. oberv.).

**AMBLYSEMIUS**

**Diagnosis** - (combination of primitive and derived characters, mainly differences with *Caturus*). Fish of moderate size, SL up to about 30 cm, blunt snout; skull roof and dorsal ridge of trunk almost straight in line; abdomen slightly deepened; deep caudal peduncle; triangular dermosphenotic incorporated in the skull roof; two supraorbitals; infraorbital 1 small and tube-like, large infraorbital 2; small nasal, leaving a large part of the ethmoid region uncovered; jaw joint well behind the orbit; maxilla long and slender, posteriorly curved downward, straight posterior border; dentition: 7-13 large, sharp, anteriorly curved, laterally compressed teeth (at least at the tooth base) in dentary and maxilla, three to four teeth in premaxilla, stouter than the dentary or

![Skull of Amblysemius pachyurus](Image)
maxillary teeth; preoperculum slender and slightly curved, of equal with throughout its length; operculum more or less rectangular, higher than broad; suboperculum smaller, broader than high; hypomandibular stout, inclined steeply forward; serrated appendages present in the pectoral girdle; pelvic fins originating slightly in front or at the level of the origin of the dorsal fin; all fins with basal and fringing fulcra; very small cycloid scales of the amid type, without ganoin.

**Type species** - *Amblysemius pachyurus* (Agassiz 1832).

**Amblysemius pachyurus** (Agassiz) : Pl. 1c, Fig. 3

**Selected synonymy**

1832 - *Uraeus pachyurus* Agassiz, p. 142 (name only).
1842 - *Caturus granulatus* Münster, p. 44.
1863 - *Caturus pachyurus* Agassiz ; Wagner, p. 704.
1863 - *Caturus contractus* Wagner, p. 705.
1863 - *Caturus granulatus* Münster ; Wagner, p. 706.
1895 - *Caturus pachyurus* Agassiz ; Woodward, p. 326.
1907 - *Caturus pachyurus* ; Heineke, p. 36, 38.
1992 - *Amblysemius pachyurus* (Agassiz, 1832) ; Lambers, p. 138 ; pl. 1c, figs. 23, 24.

**Diagnosis** - *Amblysemius* of up to 20 cm SL. Teeth in dentary large, irregular placed, 7-8 in number. Three to four teeth in premaxilla, much larger than the dentary teeth. Skull length 26% SL, Pectoral fin with 15-20 rays, Dorsal fin at about 57% SL, 17-20 rays, first three not segmented, first four not branched, Anal fin at about 75% SL, 13-17 rays, first three segmented nor branched; Pelvic fin about 10 rays, caudal fin 30-31 rays, ten rays in the epichordal lobe, 21-22 rays in the hypochordal lobe, first three unsegmented, about the first five unbranched.

**Species within the genus** - Till now, the only *Amblysemius* other than the type species *A. gracilis* was *A. bellicianus*, so far known from Cerin (Thiolière & Meyer 1850 ; Saint-Seine 1949). It appears that *Caturus pachyurus* can also be assigned to *Amblysemius*. The type specimen of *C. pachyurus* has been lost, which makes recognition of this species difficult, as the original descriptions are insufficient and are not accompanied by any figures. Wagner (1863) considered *C. pachyurus* and *C. granulatus* closely related. The holotype of *C. granulatus* (BSP AS. VII. 1139) resembles the specimens in München labelled *C. pachyurus* in size, body shape of the skull, low number of dentary teeth and very small scales, and in accordance with Woodward (1895) I consider *C. granulatus* a junior synonym (as are probably *C. contractus* and *C. fusiformis*, see Wagner [1863], Woodward [1895]).

*A. pachyurus* and *A. bellicianus* are very similar in skull anatomy (shape of the snout, shape of infraorbital 1, shape of the opercular bones, shape of the maxilla) and relative size of the scales. Well preserved specimens of *Amblysemius pachyurus* (e.g., BSP AS.I.1249, BSP AS.VII.1139 and the acid prepared specimen NHM.P.44900) are smaller than the only well preserved specimens of *A. bellicianus* (BSP.1960.XVIII.50 and
MHNL.15.172, the holotype of *A. bellicianus*). In *A. pachyurus* the teeth in the lower jaw are more slender, irregularly placed and less numerous (maximum of nine in NHM.P.44900 and seven in BSP.AS.VII.1139) than in *A. bellicianus*. In the latter species the teeth are laterally compressed, at least at their bases, regularly placed, without diastemas and more numerous (about 13 in MHNL.15.172 and 11-12 in BSP.1960.XVII.50) Compared to the maxillary teeth, the teeth on the premaxilla of *A. bellicianus* (MHNL.15.172) are not as big as those in *A. pachyurus*. On the basis of these differences, I consider *A. pachyurus* and *A. bellicianus* as two valid species.

*Caturus elongatus* AGASSIZ most probably belongs to the genus *Amblysemius*. Unfortunately the type specimen of this species has been lost. Woodward synonymized *C. elongatus* with *C. pachyurus*. Heineke (1906) synonymized *C. elongatus* with *C. fusiformis*, which is a synonym of *C. pachyurus*. This indicates that this species is very similar to *A. pachyurus*, rather than to *C. furcatus*. But Thiolière's (1873) confusion of *C. elongatus* and *A. bellicianus* is a slight indication (see Saint-Seine 1949) that *C. elongatus* from Bavaria might be the same species as *A. bellicianus* from Cerin. If so, *A. bellicianus* appears to be represented in Bavaria's lithographic limestone by a single specimen (BSP.1960.XVII.50) only. As the identity of *Caturus elongatus* is unknown, I propose to retain the junior species name *A. bellicianus*, which is founded on more or less extensive descriptions and figures (Thiolière 1850, 1873 ; Saint-Seine 1949).

**DISCUSSION**

*C. furcatus* and *C. giganteus*, together with *C. diani* (Saint-Seine 1949) are closely interrelated, forming the genus *Caturus*. *A. pachyurus* and *A. bellicianus* represent the genus *Amblysemius*. *Caturus* and *Amblysemius* differ in the following characters (see generic diagnoses): shape of the snout, the supraorbitals, IO1, the dermosphenotic, the preoperculum, the shape of the operculum and suboperculum, the maxilla, the dentition on premaxilla and dentary, the parasphenoid, inclination of the hyomandibula, the caudal peduncle and the size of the scales.

The differences justify the recognition of two caturid genera in Solnhofen instead of one. Both genera are also known from the lithographic limestone of Cerin, France. At the halecomorph level, using parasemionotids as an outgroup, the follo-wing characters of *Caturus* are derived: supernumerary supraorbitals, very small dermosphenotic, and a preoperculum with an expanded ventral limb and a parasphenoid that extends far posteriorly to the basioccipital. *Amblysemius* uniquely has a tube-like infraorbital 1, the absence of a notch in the maxilla the posterior part of the maxilla being curved downwards, the large premaxillary teeth, the low number of teeth in dentary and maxilla and the very small size of the scales.

**Acknowledgements** - I thank Mr E. Ebbinge and Dr. J. de Vos for giving me the opportunity to study the collection of Teylers Museum, Haarlem. I thank Drs. P. Forey and C. Patterson (NHM, London), Mr. M. Philippe, (Mus. d'Hist. Nat. Lyon), Dr. P. Wellhofer (Bayer. Staatssamml., München), Dr. G. Viohl (Juramuseum, Eichstätt) and Bürgermeister Nürnberg (Bür. Müller Museum, Solnhofen) for allowing me to study specimens in their care. Furthermore I thank Prof. Dr. G.J. Boekschoten, Dr. Y. Chalifa and Dr. S. Wenz for critically reading the manuscript. The photographs were made by T. van der Heide. Drs. A. de Boer checked the English. Financial support for study trips was provided by the Universiteitsfonds of the University of Groningen and the Molengraafffonds. This study is partly financed by the Netherlands Organisation for Scientific Research, project number 751.356.022.

**ABBREVIATIONS**

ANG : angular
AO : antorbital
B : branchial bones
BSP : basisphenoid
Cl : cleithrum
c1 : coronoid teeth
DEN : dentary
DPA : dermopalatine
DPT : dermopterygoid
DSP : dermosphenotic
ENP : entopterygoid
ECP : ectopterygoid
F : frontal
fo : foramen for the olfactory nerve
G : gular plate
Hyo : hyomandibular
IO : infraorbital (1, 2 or 3)
IOP : interoperculum
Le2 : lateral ethmoid
MAX : maxilla
MPT : metapterygoid
np : nasal process
Op : operculum
OSP : orbitosphenoid
P : parietal
PM : premaxilla
PO : preoperculum
ppq : posterior process on the quadrate
PSC : presupraclithrum
PS : parabasal
PT : posttemporal
PtP : posttemporal process
Q : quadrate
R : rostrum
RB : branchiostegal rays
SAN : supranasal
SA : supracleithrum
SM : supramaxilla
SN : suprangular
SOP : suboperculum
S OR : suborbital (1 or 2)
Sp : sphenotic
St : supratemporal
Sy : symplectic
N : nasal

REFERENCES