

# Phylogenetical relationships and palaeozoogeography of the marine Cretaceous Tselfatiiformes (Teleostei, Clupeocephala)

by

Louis TAVERNE (1) & Mireille GAYET (2)

**ABSTRACT.** - The order Tselfatiiformes comprises three families, the Protobramidae (three genera and four species), the Eoplethodidae (one genus and one species) and the Plethodidae (seventeen genera and twenty-seven species). Although very specialised, the Protobramidae are the most primitive family within the order. Eoplethodidae, only known by the caudal skeleton, are less evolved than the Plethodidae. Within the Plethodidae, *Paranogmius*, the only one keeping a subtemporal fossa, is the most plesiomorphic genus. A more apomorphic clade unites together *Bananogmius*, *Niobrara*, *Syntegmodus* and *Luxilites*. Another clade still more apomorphic joins *Martinichthys*, *Pseudothryptodus*, *Thryptodus* and *Plethodus*. *Pseudanogmius*, *Pentanogmius*, *Zanclites* and *Bachea* are successively more and more specialised genera. *Enischnorhynchus*, *Tselfatia* and *Dixonanogmius*, with their skull roof strongly curved in cross-section, represent the most advanced clade. *Moorevillia*, characterised by its latero-parietal skull, could not be classified unambiguously within the family. The relative positions of the Tselfatiiformes and the Pachyrhizodontoidei within the Clupeocephala are discussed. The latter are considered to be more primitive than the former. The paleozoogeography of the Tselfatiiformes is also considered. They appear in the Eurafrikan Mesogea during the Albian and expand there during the Cenomanian and Turonian. During the same period, they get across the Proto-Atlantic Ocean and colonize the north of South America, the Gulf of Mexico, Central America and the North American seaway. During the Coniacian and Santonian, they are abundant in North America but seem to be absent from the Eurafrikan Mesogea. A few species subsist in the Gulf of Mexico and in Egypt during the Campanian. The Tselfatiiformes disappear after the Campanian.

**RÉSUMÉ.** - Relations phylogénétiques et paléozoogéographie des Tselfatiiformes marins du Crétacé.

L'ordre des Tselfatiiformes comprend trois familles, les Protobramidae (trois genres et quatre espèces), les Eoplethodidae (un seul genre et une seule espèce) et les Plethodidae (dix-sept genres et vingt-sept espèces). Quoique très spécialisée, la famille des Protobramidae est la plus primitive de l'ordre. Les Eoplethodidae, connus uniquement par le squelette caudal, sont moins évolués que les Plethodidae. Au sein des Plethodidae, *Paranogmius*, le seul qui garde une fosse subtemporale, est le genre le plus plésiomorphe. Un clade plus apomorphe réunit *Bananogmius*, *Niobrara*, *Syntegmodus* et *Luxilites*. Un autre clade encore plus apomorphe lie *Martinichthys*, *Pseudothryptodus*, *Thryptodus* et *Plethodus*. *Pseudanogmius*, *Pentanogmius*, *Zanclites* et *Bachea* sont successivement de plus en plus spécialisés. *Enischnorhynchus*, *Tselfatia* et *Dixonanogmius*, avec leur toit crânien très incurvé en coupe transversale, représentent le clade le plus avancé. *Moorevillia*, caractérisé par son crâne latéro-pariétal, ne peut être situé dans la famille sans ambiguïté. Les positions relatives des Tselfatiiformes et des Pachyrhizodontoidei au sein des Clupeocephala sont discutées. Les seconds sont considérés comme plus primitifs que les premiers. La paléozoogéographie des Tselfatiiformes est aussi envisagée. Ils apparaissent dans la Mésogée eurafrikanne à l'Albien et s'y développent durant le Cénomanien et le Turonien. À la même période, ils franchissent le Proto-Atlantique et colonisent le nord de l'Amérique du Sud, le Golfe du Mexique, l'Amérique Centrale et la mer intérieure nord-américaine. Au Coniacien et au Santonien, ils sont très abondants en Amérique du Nord mais semblent absents dans la Mésogée eurafrikanne. Quelques espèces subsistent dans le Golfe du Mexique et en Égypte au Campanien. Les Tselfatiiformes disparaissent après le Campanien.

Key words. - Teleostei - Tselfatiiformes - Marine Cretaceous - Osteology - Phylogeny - Palaeozoogeography.

The Tselfatiiformes (= Bananogmiiformes, the 'banana-fishes' of the English-speaking paleoichthyologists) are one of the most important radiations of marine Cretaceous teleosts. They were thought for long to be part of the Osteoglossomorpha, the Elopomorpha or of some other orders (for a review, see Taverne, 2000a). Recent cladistic studies on their osteological characters make it clear now that they are primitive Clupeocephala, which represent a plesiomorphic sister-group of a clade including the Otocephala (Clu-

peomorpha and Ostariophysii) and the Euteleostei (Taverne, 2000a; Cavin, 2001; Taverne and Gayet, 2004).

The Tselfatiiformes comprise three families, the Protobramidae (three genera, four species), the Eoplethodidae (one monospecific genus) and the Plethodidae (seventeen genera, twenty-seven species). Protobramidae are small deep-bodied fishes, with long dorsal and anal fins and a forked caudal fin. Primitively, the pectoral fins are inserted low on the flanks but become high in *Protobrama*. The pelvic girdle is

(1) Université Libre de Bruxelles, Faculté des Sciences, Département de Biologie des Organismes, Unité de Morphologie fonctionnelle (C.P. 160/11), Avenue F.D. Roosevelt 50, B-1050 Bruxelles, BELGIQUE. [Louis.Taverne@iph.fgov.be].

(2) 18 rue Vauban, F-69006 Lyon, FRANCE. [Gayet.Mireille@free.fr]

thoracic in *Abisaadichthys* or lost in *Protobrama* and *Eusebichthys*. The monogeneric Eoplethodidae, only known by the caudal skeleton, are moderately large teleosts. Plethodidae look like the modern Scombridae, Thunnidae and Coryphaenidae. They are large fishes, some of them reaching a length of two or three metres. The body is laterally compressed, more or less elongated in some, deep in others. The pectoral fins are inserted high on the flanks. The long and high dorsal fin arises close to the head and extends along most of the back. The ventral fins are abdominal. The caudal fin is deeply forked.

The Tselfatiiformes appear in the uppermost part (Albian) of the Lower Cretaceous and become extinct a few million years before the end (Campanian) of the Upper Cretaceous (Patterson, 1993). Their fossil remains were found in Europe, the Near East, North and Central America, northern South America, and North Africa.

Some authors think that the Plethodidae is the only valid family within the order and placed the Bananogmiidae, the Niobraridae, the Thryptodontidae, the Tselfatiidae and the Protobramidae in synonymy with it (Patterson, 1993). Others consider the Tselfatiidae as a second valid family (Nelson, 1994). That was also Taverne's opinion for long (Taverne, 1975, 1983) but recent studies of plethodid material (Taverne, 1999a, 2000a-d, 2001a-c, 2002a, 2002b, 2003, 2004) convince us that *Tselfatia* belongs to the Plethodidae and does not need a special family status, in spite of its numerous autapomorphies.

On the other hand, we think that *Eoplethodus*, recently described from the Lower Cretaceous of France (Chanet, 1997; Taverne, 2000d), deserves a peculiar family status, the Eoplethodidae, because of its caudal skeleton much more primitive than in all plethodid genera.

Concerning the Protobramidae, Taverne and Gayet (2004) present convincing evidence that they should be included in the Tselfatiiformes as a third valid family, quite different from the Plethodidae, contra Patterson (1993) who has united the two families into one and contra Cavin (2001) who has gathered the Protobramidae, the Araripichthyidae and the Ferrifronsidae into a new suborder Protobramoidei not allied to the Tselfatiiformes.

The present article summarizes briefly the osteological data from the numerous papers we have previously written on the Tselfatiiformes (Taverne, 1975, 1983, 1999a, 2000a-d, 2001a-c, 2002a, 2002b, 2003, 2004; Taverne and Gayet, 2004) and is dealing with their phylogeny, relationships and paleozoogeography.

## MATERIAL

As interpreted in this paper, the Tselfatiiformes comprise three families, twenty-one genera and thirty-two species:

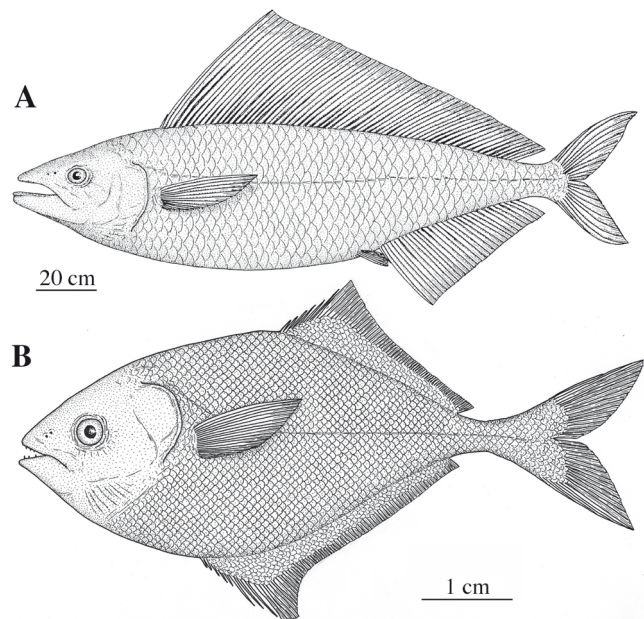


Figure 1. - Reconstruction of the plethodid *Pentanogmius evolutus* (Cope, 1877) (A) and of the protobramid *Protobrama avus* Woodward, 1932 (B).

Family Protobramidae Le Danois & Le Danois (Lower Cenomanian, Lebanon), 1964. *Protobrama* Woodward, 1942 (see Taverne and Gayet, 2004), *P. avus* Woodward, 1942, *P. woodwardi* Taverne & Gayet, 2004; *Eusebichthys* Taverne & Gayet, 2004, *E. byblosi* Taverne & Gayet, 2004; *Abisaadichthys* Taverne & Gayet, 2004, *A. libanicus* Taverne & Gayet, 2004.

Family Eoplethodidae nov. (monogeneric, same diagnosis as *Eoplethodus*, cf. Taverne, 2000d). *Eoplethodus* Taverne, 2000, *E. chaneti* Taverne, 2000 (Lower Albian, France) (cf. Taverne, 2000d).

Family Plethodidae Loomis, 1900. *Plethodus* Dixon, 1850 (cf. Taverne, 2000c), *P. expansus* Dixon, 1850 [type-species] (Upper Albian to Turonian, England), *P. rotundus* (Loomis, 1900) (Coniacian/Santonian, Kansas); *Thryptodus* Loomis, 1900 (cf. Taverne, 2000c, 2003), *T. zitteli* Loomis, 1900 (Upper Cenomanian to Lower Campanian, Kansas, Texas, Alabama); *Pseudothryptodus* Loomis, 1900 (cf. Taverne, 2003), *P. intermedius* Loomis, 1900 (Coniacian/Santonian, Kansas); *Syntegmodus* Loomis, 1900 (cf. Taverne, 2001c), *S. altus* Loomis, 1900 (Coniacian/Santonian, Kansas); *Niobrara* Jordan, 1924 (cf. Taverne, 2001a), *N. encarsia* Jordan, 1924 (Coniacian/Santonian, Kansas); *Zanclites* Jordan, 1924 (cf. Taverne, 1999), *Z. xenurus* Jordan, 1924 (Coniacian/Santonian, Kansas); *Luxilites* Jordan, 1924 (cf. Taverne, 2002a), *L. striolatus* Jordan, 1924 (Coniacian/Santonian, Kansas); *Martinichthys* McClung, 1926 (cf. Taverne, 2000b), *M. brevis* McClung, 1926 [type-species] (Upper

Coniacian, Kansas), *M. ziphioides* (Cope, 1877) (Upper Coniacian, Kansas); *Paranogmius* Weiler, 1935 (cf. Taverne, 2003), *P. doederleini* Weiler, 1935 (Lower Cenomanian, Egypt, Libya); *Bananogmius* Whitley, 1940 (cf. Taverne, 2001b), *B. aratus* (Cope, 1877) [type-species] (Coniacian/Santonian, Kansas), *B. favirostris* (Cope, 1877) (Coniacian/Santonian, Kansas), *B. ornatus* (Woodward, 1923) (Upper Cenomanian, England), *B. ellisensis* Fielitz & Shimada, 1999 (Middle Turonian, Kansas); *Tselfatia* Arambourg, 1943 (cf. Taverne, 1975, 1983, 2000a), *T. formosa* Arambourg, 1943 (Upper Cenomanian/Lower Turonian, Morocco, Italy, Croatia, Germany, Mexico; Coniacian/Santonian, Texas); *Enischnorhynchus* Bardack, 1965, *E. dallasensis* Bardack, 1965 (Upper Santonian, Texas); *Moorevillia* Applegate, 1970, *M. hardi* Applegate, 1970 (Lower Campanian, Alabama); *Bachea* Paramo-Fonseca, 1997, *B. huilensis* Paramo-Fonseca, 1997 (Upper Turonian, Colombia); *Dixonanogmius* Taverne, 2000, *D. oblongus* (Dixon, 1850) [type-species] (Upper Cenomanian, England); *D. dalmatia* (Bardack & Teller-Marshall, 1980) (Cenomanian/Turonian, Croatia), *D. sp.* Taverne, 2000 (Coniacian/Santonian, Kansas); *Pentanogmius* Taverne, 2000 (cf. Taverne, 2004), *P. pentagon* (Woodward, 1899) [type-species] (Upper Cenomanian, England), *P. evolutus* (Cope, 1877) (Coniacian/Santonian, Kansas, South Dakota) (Fig.1). *P. furcata* (Fritsch,

1878) (Turonian, Czechia), *P. crieleyi* (Applegate, 1970) (Lower Campanian, Alabama); *Pseudanogmius* Taverne, 2002, *P. maiseyi* Taverne, 2002 (Coniacian/Santonian, Kansas).

At least four other Tselfatiiformes will be added to the list in the future. The first is the *Plethodus* (?) sp. mentioned by Stromer and Weiler (1930) in the Campanian of southern Egypt on the basis of some very small dentigerous bony fragments. Those remains are too partial to allow a generic determination but they certainly belong to a plethodid fish. The second is the figured but very poorly described plethodid from the Coniacian of Manitoba (Canada) referred to *Ananogmius* sp. (Bardack, 1968). The third is the still undescribed large plethodid from the Cenomanian of Venezuela (Moody and Maisey, 1994). The fourth is a newly discovered but still unpublished long-snouted species from Kansas that seems intermediate between *Thryptodus* and *Martinichthys* (K. Shimada, *in litt.* 20 Dec. 2002).

### A SHORT ACCOUNT ON THE TSELFATIIFORM OSTEOLGY

The osteological data mentioned hereafter derive from Bardack (1965), Applegate (1970), Taverne (1975, 1983, 1999a, 2000a-d, 2001a-c, 2002a, 2002b, 2003, 2004), Bardack and Teller-Marshall (1980), Paramo-Fonseca (1997), Fielitz and Shimada (1999) and Taverne and Gayet (2004).

#### Plethodid and eoplethodid skeleton (Figs 2-4, 10)

The dermal bones of the plethodid skull are often thick and ornamented. The mesethmoid is well developed, comprising a dermal rostral (= dermethmoid) and sometimes a small endochondral supraethmoid. The nasals are often large and articulated with the frontals and the mesethmoid. The large parietals meet on the midline,

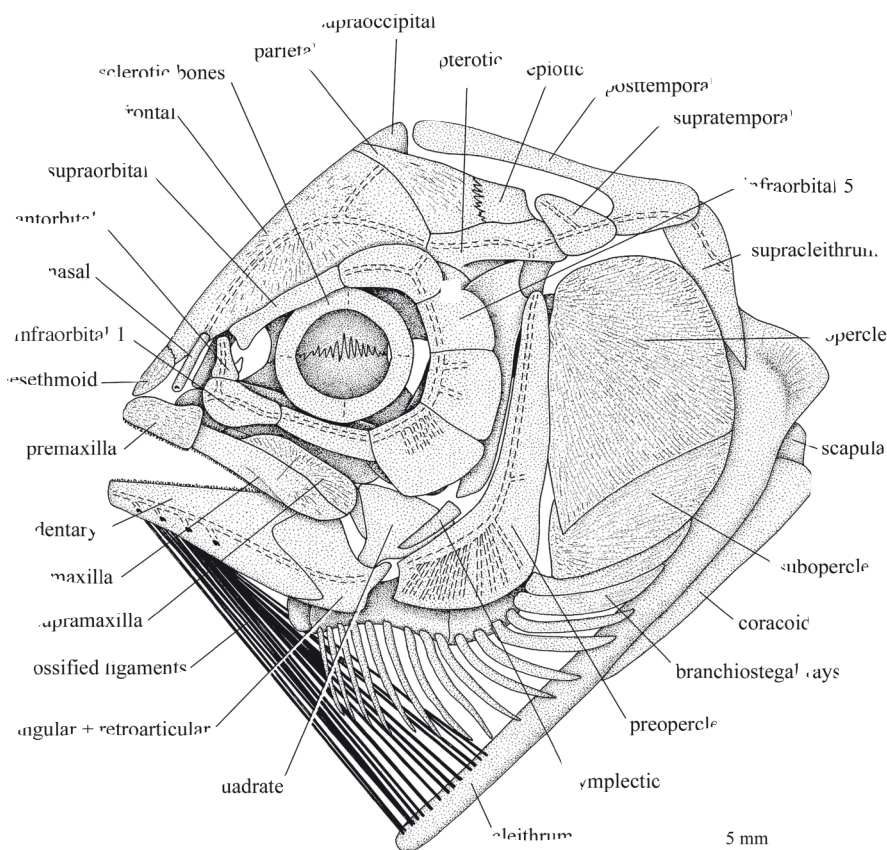


Figure 2. - Reconstruction of the skull and pectoral girdle of *Tselfatia formosa* Arambourg, 1943 in left lateral view (modified and compiled from Taverne, 1983: fig. 2, and 2000a: fig. 3. [Reconstruction du crâne et de la ceinture pectorale de *Tselfatia formosa* en vue latérale gauche (modifié d'après Taverne, 1983 : fig. 2, et 2000a : fig.3.)



except in one genus, *Moorevillia*. The posttemporal fossa is roofed and opens in the rear of the neurocranium between the pterotic, the epiotic and the intercalar. The supratemporal is small and does not join its fellow in the midline. The orbitosphenoid, the pterosphenoids and the parasphenoid form a complete osseous interorbital septum. The basisphenoid is severely reduced and hidden in the myodome. The eye is surrounded by a complete ring of eight bones, the antorbital, five infraorbitals, the dermosphenotic and the supraorbital. The posterior infraorbitals are large. The antorbital, supraorbital and dermosphenotic are ankylosed together and articulated with the frontal border. The jaws are toothed and bear patches of minute recurved conical teeth. The palato-lingual bite is well developed and consists also of toothed patches on the vomer, the parasphenoid, the dermopalatine, the endopterygoid, the ectopterygoid, the dermobasihyal, the dermobasibranchials and the posterior dermopharyngobranchials. Such a dentition allowed the Plethodidae to be predators of molluscs, crustaceans and small fishes. The dentigerous bones and especially those of the palato-lingual bite are pierced by very small pits open under the teeth and passing deeply down into the osseous mass. The maxilla enters into the gape of the mouth. There is only one supramaxilla, the posterior one. The angular and retroarticular are generally fused but the articular remains autogenous. When unfused, the retroarticular is excluded from the articulation facet for the quadrate. The mandibular sensory canal opens posteriorly on the medial side of the angular. The opercle, subopercle, preopercle, interopercle and branchiostegal rays are well developed.

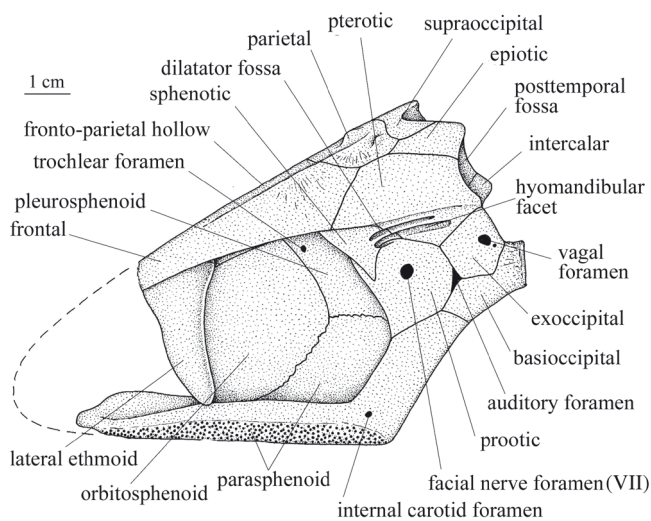


Figure 3. - Reconstruction of the neurocranium of *Syntegmodus altus* Loomis, 1900 in left lateral view (based on the neotype Amer. Mus. Nat. Hist. 2112, completed after Loomis, 1900 for the lateral ethmoid). [Reconstruction du neurocrâne de *Syntegmodus altus* Loomis, 1900 en vue latérale gauche (fondée sur le néotype Amer. Mus. Nat. Hist. 2112, complété d'après Loomis, 1900 pour l'éthmoïde latéral.)]

The posterior ceratobranchials are toothless (only known in *Pentanogmius evolutus*).

The cleithrum consists of a short dorsal branch and a very long obliquely oriented ventral one. The pectoral fins are inserted high on the flanks. Ossified ligaments connect the mandibular symphysis region to the cleithra.

The neural and haemal spines are not fused with the vertebrae but are simply set in deep dorsal and ventral pits of the centra (= gomphosis). In the caudal vertebrae the arches often extend on the lateral faces of the centra. Supraneurals are lost. Epicentrals and epineurals are present but only in the abdominal part of the body. There are no epipleurals, except in *Zanclites* which shows peculiar enlarged ones (Taverne, 1999a).

The dorsal and anal fins are large. Most rays are branched but generally not segmented. The dorsal and anal pterygiophores are often expanded distally by lateral processes.

The caudal skeleton and its evolution within Eoplethodidae and Plethodidae has been thoroughly described in Taverne (2000d) and will be only very briefly recalled here (Figs 4, 10). There is a large hypural plate resulting from the fusion of the first four hypurals (Fig. 4). The ural centra are reduced and joined together in a small terminal vertebra which is fused to the hypural plate. There is no neural arch on the preural centrum 1 and the terminal vertebra. The preural centrum 1 is reduced and the parhypural is missing. There are neither epurals nor uroneurals. *Eoplethodus*, which displays a parhypural, three epurals and a paired stegural, is the only exception (Fig. 10, characters A; Taverne, 2000d).

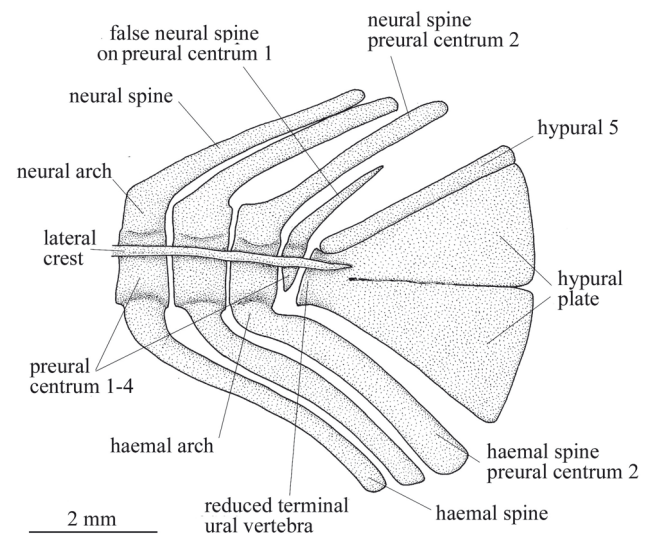


Figure 4. - Reconstruction of the caudal skeleton of *Tselfatia formosa* Arambourg, 1943 (modified from Taverne, 1975: fig. 3, and 1983: fig. 5). [Reconstruction du squelette caudal de *Tselfatia formosa* Arambourg, 1943 (modifié d'après Taverne, 1975 : fig. 3, et 1983 : fig. 5).]

The caudal fin exhibits 19 principal rays of which 17 are branched.

The scales are cycloid.

### Protobramid skeleton

The dermal bones of the skull are thinner than in plethodids but also ornamented. The mesethmoid is devoid of an endochondral ossified element. The skull is medio-parietal. The temporal fossa is dorsally bordered by the parietal. The supratemporal is reduced. The orbitosphenoid and pterosphenoids are small and there is no osseous interorbital septum. The basisphenoid is normally developed. The parasphenoid and the bones of the palato-quadratic arch are toothless except the entopterygoid. The infraorbitals are large in *Eusebichthys* and *Abisaadichthys* but fragmented in a series of numerous small bones in *Protobrama*. There is no supraorbital. The jaws are feebly toothed or toothless. The maxilla, never toothed, is bordering the upper jaw. There is no supramaxilla. An autogenous retroarticular exists in *Abisaadichthys* but this bone is fused to the angular in *Eusebichthys* and *Protobrama* as in the Plethodidae.

The ventral branch of the cleithrum is short and the pectoral fins are inserted low on the flanks in *Abisaadichthys* and *Eusebichthys*, unlike *Protobrama* which exhibits a long oblique ventral branch of the cleithrum and the pectoral fins high on the flanks as in plethodid fishes. A thoracic pelvic girdle is preserved in *Abisaadichthys*. The pelvic girdle is lost in *Eusebichthys* and *Protobrama*.

The neural and haemal arches are articulated with the corresponding vertebrae all along the axial skeleton (= gomphosis). Supraneurals are numerous. The ribs are generally fused with the haemapophyses. Epineurals are present but osseous epicentrals and epipleurals are lost.

The dorsal and anal fins are long and their rays pointed or branched but not segmented. The first anal pterygiophores are very elongated, obliquely and backwards oriented, joined together and resting against the first long haemal spines forwards bent.

Hypurals 3 and 4 are fused together in a hypural plate. Hypural 6 is lost and sometimes also hypural 5. There are no free epurals but ural centrum 1 bears a neural spine probably resulting from the capture of an epural. *Abissadichthys* exhibits an autogenous ural centrum 2, three uroneurals and 19 principal caudal rays. Ural centrum 2 is fused to the hypural plate, there is only one uroneural and the number of principal caudal rays increases in *Eusebichthys* and *Protobrama*. The segmentation of the caudal rays regresses in these two genera.

The scales are covering the basis of the unpaired fins.

## OSTEOLOGICAL EVOLUTION WITHIN EOPLETHODIIDAE AND PLETHODIDAE

The protobramid specimens preserved in the fossil record are sufficiently complete to allow an easy reconstruction of the phylogeny within the family (Taverne and Gayet, 2004). The situation is not so easy with regard to the Eoplethodidae and the Plethodidae. The genera presently included in these two families are all clearly defined by one or more peculiar characters. However many genera within them remain very poorly known. The skull or even fragments of the skull are often the only preserved parts, the trunk and caudal skeleton being lost. So many important anatomical informations are missing. Such a situation makes it difficult to establish unambiguously the phylogeny of these fishes. Fortunately, the evolution of a few characters within these two families allows to clear up the problem and to range accurately the genera according to these informations. The characters are:

### The skull roof

Most plethodids have a transversally broadened neurocranium with a flat or slightly curved skull roof in cross-section. This is the plesiomorphic condition found in *Bananogmius*, *Luxilites*, *Niobrara*, *Syntegmodus*, *Thryptodus*, *Martinichthys*, *Zanclites*, *Moorevillia*, *Pentanogmius*, *Paranogmius* and *Pseudanogmius* (Fig. 5A). *Bachea* exhibits a more curved cranial vault in cross section (Fig. 5B), and this curvature is still many more important in *Enischnorhynchus*, *Tselfatia* and *Dixonanogmius* (Fig. 5C).

### The parietals

Generally the parietals are large, more or less quadrangular and broadly joined along the midline (Fig. 6A). *Bachea*, *Bananogmius*, *Enischnorhynchus*, *Luxilites*, *Martinichthys*, *Niobrara*, *Paranogmius*, *Pentanogmius*, *Pseudanogmius*, *Syntegmodus*, *Thryptodus* and *Zanclites* share such a primi-

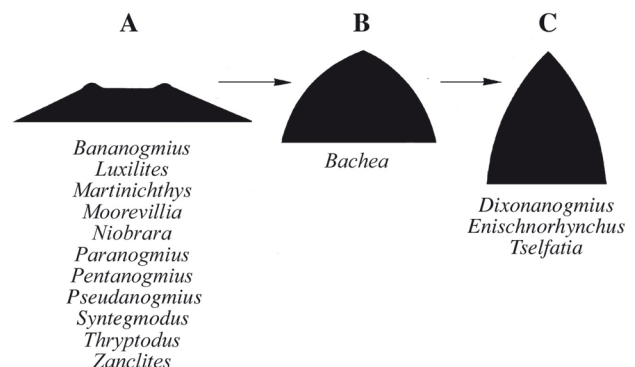


Figure 5. - Diagram showing the evolution of the skull roof in cross-section within Tselfatiiformes. [Diagramme montrant l'évolution en coupe du sommet du crâne chez les Tselfatiiformes.]

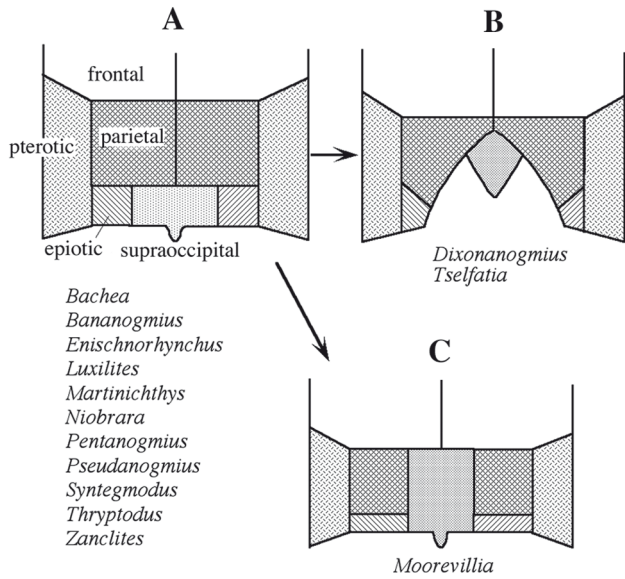


Figure 6. - Diagram showing the evolution of the parietals within Tselfatiiformes. [Diagramme montrant l'évolution des pariétaux chez les Tselfatiiformes.]

tive pattern. In *Tselfatia* and *Dixonanogmius*, the parietals are broader than long and very narrow at their meeting point in the midline (Fig. 6B). In *Moorevillia*, the parietals are smaller and separated by the supraoccipital (Fig. 6C).

**The lateral ethmoid**

Primitively the lateral ethmoid is a large bone reaching the frontal and the parasphenoid in plethodid fishes. This is the case in *Bananogmius*, *Martinichthys*, *Paranogmius*, *Pseudanogmius*, *Syntegmodus* and *Thryptodus*. The lateral ethmoid becomes smaller and often loses its contact with the parasphenoid in *Bachea*, *Dixonanogmius*, *Enischnorhynchus*, *Pentanogmius* and *Tselfatia*.

**The maxilla/supramaxilla articulation**

Plethodidae possess only one supramaxilla, the posterior one. In primitive plethodids, such as *Bananogmius*, *Martinichthys* and *Thryptodus*, the supramaxilla is short and articulates in a deep notch of the posterior part of the maxillar dorsal border (Fig. 7A). This is the plesiomorphic state in Plethodidae. More evolved plethodids, such as *Bachea* and *Pentanogmius*, show a more derived condition in which the

supramaxilla still articulates in the notch but presents also a sharp extension anterior to this notch (Fig. 7B). In highly specialised plethodids, such as *Dixonanogmius*, *Enischnorhynchus* and *Tselfatia*, there is no more notch on the maxillar dorsal border and the supramaxilla simply lies on the maxilla (Fig. 7C). This is the apomorphic state in Plethodidae.

It is noteworthy that the plesiomorphic state of this character within plethodids apparently corresponds to a specialised condition within the teleosts and the apomorphic state to a return to a teleostean more primitive pattern. There is a possible explanation of such a situation. In primitive plethodids, the anterior supramaxilla is probably completely fused with the dorsal border of the maxilla, forming so the notch into which the posterior supramaxilla is fitted. In more advanced plethodids, the supramaxillar component of the maxillar dorsal border is gradually thinning and so the notch is progressively lost, the posterior supramaxilla then lying again on a more or less rectilinear dorsal border of the maxilla as normally in teleosts.

**The preopercle**

Primitive plethodid fishes, like *Bananogmius*, *Luxilites*, *Niobrara* and *Paranogmius*, have a broad preopercle with the dorsal and ventral limbs well developed and of approximately the same length (Fig. 8A). In more specialised genera, such as *Bachea*, *Dixonanogmius*, *Enischnorhynchus*, *Martinichthys*, *Pentanogmius*, *Thryptodus* and *Tselfatia*, the

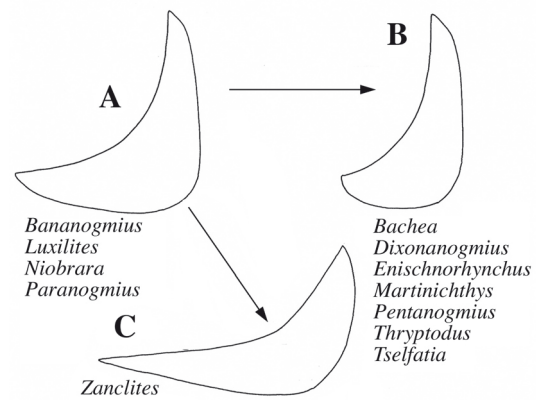


Figure 8. - Diagram showing the evolution of the preopercle within Tselfatiiformes. [Diagramme montrant l'évolution du pré-opercule chez les Tselfatiiformes.]

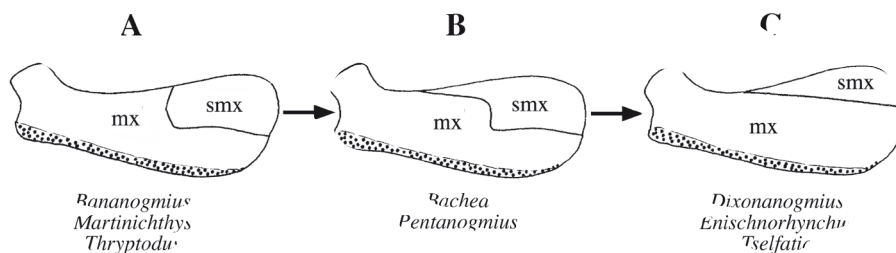


Figure 7. - Diagram showing the evolution of the supramaxilla/maxilla articulation within Tselfatiiformes. [Diagramme montrant l'évolution de l'articulation supra-maxillaire/maxillaire chez les Tselfatiiformes.]



ventral limb of the preopercle is shortened (Fig. 8B). *Zanclites* is the only genus with the ventral limb of the preopercle markedly longer than the dorsal one (Fig. 8C).

**The subtemporal fossa**

*Paranogmius* still exhibits a large and deep subtemporal fossa. All the other plethodid genera in which the neurocranial floor is known (*Bananogmius*, *Martinichthys*, *Niobrara*, *Pentanogmius*, *Pseudanogmius* and *Thryptodus*) have already lost this teleostean primitive structure.

**The lower dental plate**

Primitively the lower dental plate of the Plethodidae consists of three articulated bones, the dermobasihyal, the fused dermobasibranchials of the three first branchial arches and the dermobasibranchial of the fourth arch. This plesiomorphic condition occurs in *Bananogmius* and *Martinichthys* (Taverne, 2000b, 2001b). A dermobasibranchial of the fourth arch rarely occurs within teleosts but is probably the teleostean primitive condition since such a bone is known in some Elopomorpha, Osteoglossomorpha and Esociformes (Nelson, 1968, 1969). *Thryptodus*, *Pseudothryptodus* and *Pentanogmius* have already lost the dermobasibranchial of the fourth arch and only the two remaining bones make up the lower dental plate (Taverne, 2003, 2004). *Dixonanogmius*, *Plethodus*, *Tselfatia* and perhaps *Bachea* exhibit a more apomorphic pattern in which the dermobasihyal and the dermobasibranchials of the three first arches are fused in a single lower dental plate (Dixon, 1850; Woodward, 1899; Taverne, 2000a-c). This character seems independently acquired in *Plethodus* on the one hand and in *Dixonanogmius* and *Tselfatia* on the other hand.

**The pelvic girdle and fins**

*Bananogmius* and *Niobrara* possess the pelvic girdle and fins normally developed with a length corresponding to about fourteen or fifteen vertebrae (Woodward, 1923; Taverne, 2001a, 2001b). *Pentanogmius* shows a slightly reduced pelvic girdle with a length of eleven vertebrae (Taverne, 2004). In *Dixonanogmius*, *Enischnorhynchus*, *Tselfatia* and *Zanclites* the pelvic girdle becomes really tiny compared to the size of the fishes (Bardack, 1965; Patterson, 1967b; Bardack and Teller-Marshall, 1980; Taverne, 1983, 1999a). Its length corresponds only to five to seven vertebrae.

**The haemaxanal complex**

Blot (1968) has defined the haemaxanal complex as the relationships between the anal fin and the axial skeleton. He distinguished three major patterns of haemaxanal complex within teleosts. *Bananogmius*, *Niobrara* and *Pentanogmius* show the type 1, the more primitive one, in which the first anal pterygiophores are obliquely ranged in the direct pro-

longation of the first haemal spine (Fig. 9, type 1; Blot, 1968). *Dixonanogmius*, *Tselfatia* and *Zanclites* offer the more apomorphic type 3 with the first anal pterygiophores bent backward and forming an angle with the first haemal spine (Fig. 9, type 3; Blot, 1968).

In Taverne (2004) *Pentanogmius evolutus* is described as having a type 3 of haemaxanal complex. Taverne's assertion is based on a specimen (NHMP.9202, Natural History Museum, London), in which only the first anal pterygiophore is preserved, showing a backward orientation. A photograph of another specimen of *P. evolutus* (FHSMVP-2117, Sternberg Museum of Natural History, Fort Hays, Kansas) recently received by one of us (L. T.) shows a complete anal fin. The haemaxanal complex clearly is of type 1. The backward bend of the first anal pterygiophore in the London specimen is thus the result of a post mortem shifting and does not reflect the real anatomy of the fish.

**The caudal skeleton (Figs 4, 10)**

As already seen, Eoplethodidae and Plethodidae exhibit a specialised caudal skeleton. The ural centra are fused together into a small terminal vertebra united to a large hypural plate. The plate is consisting of the fused first four hypurals. The most primitive pattern is found in *Eoplethodus* (Fig. 10, characters A; Taverne, 2000d) with a reduced preural neural spine 2, three epurals, well developed preural haemal arch 1 and parhypural, one pair of short stegurals and two autogenous hypurals above the hypural plate. *Eoplethodus* also shows on the parhypural an enlarged hypurapophysis articulated in a notch on the rear of the preural haemal arch 2. In *Bananogmius* and *Niobrara* (Fig. 10, characters B; Taverne, 2001a, 2001b), the epurals and the parhypural are lost, the two autogenous hypurals are preserved, there is a full preural neural spine 2, probably as the result of the capture of the first epural, the stegurals are complete-

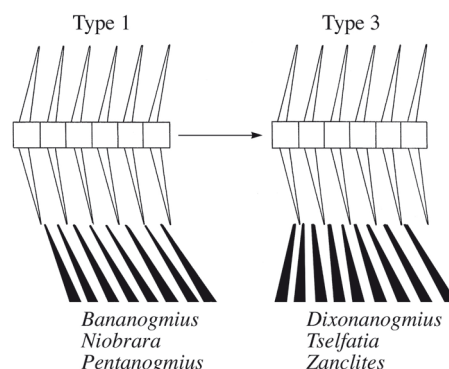
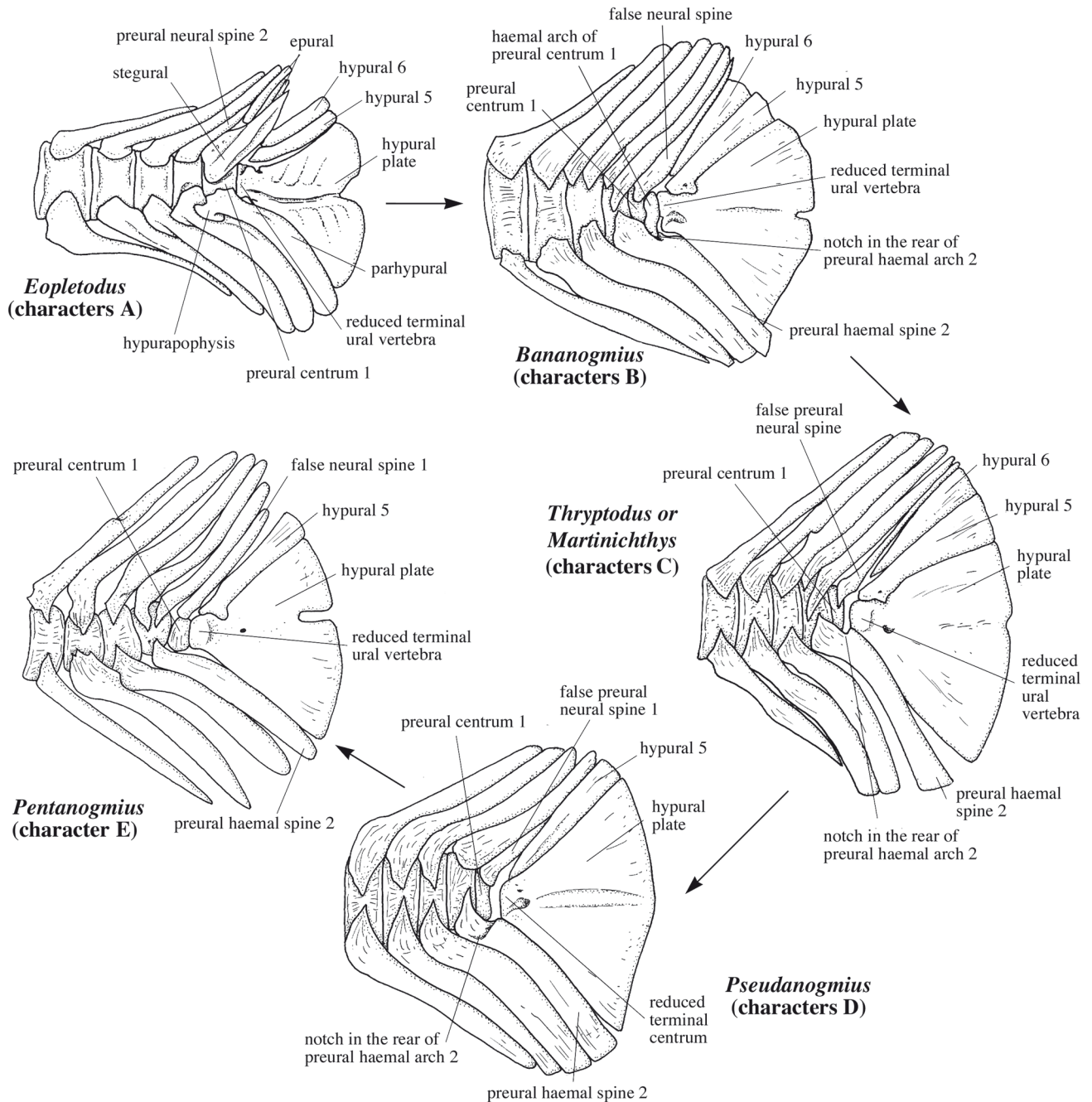


Figure 9. - Diagram showing the evolution of the haemaxanal complex (= relationships between the first anal pterygiophores [in black] and the haemal spines [in white]) within *Tselfatiiformes*. [Diagramme montrant l'évolution du complexe hémamaxanal (= relations entre les premiers ptérygophores anaux [en noir] et les hémépines [en blanc]) chez les *Tselfatiiformes*.]

ly fused together and get narrower, forming a false full preural neural spine 1, and the preural haemal arch 1 is strongly reduced but still articulated in the posterior notch of the preural haemal arch 2. More specialised plethodids completely lose the preural haemal arch 1. Some of them (probably *Martinichthys* and *Thryptodus*) keep the two autogenous hypurals and the posterior notch in the preural haemal arch 2 (Fig. 10, characters C; Taverne, 2000a). Only one

autogenous hypural remains in a few genera, such as *Tselfatia*, *Dixonanogmius*, *Zanclites*, *Pseudanogmius* and *Pentanogmius* (Figs 4, 10, characters D, E; Bardack and Teller-Marshall, 1980; Taverne, 1983, 1999a, 2002b, 2004). *Pseudanogmius* still keeps the notch of the preural haemal arch 2 (Fig. 10, characters D; Taverne, 2002b). The notch is lost in the four other genera (Figs 4, 10, character E; Taverne, 1999a, 2004).





## DISCUSSION AND CONCLUSIONS

**The phylogeny of the Tselfatiiformes (Fig. 11)**

Tselfatiiform fishes possess all the derived features of the basal Clupeocephala (Patterson, 1977; Patterson and Rosen, 1977; Lauder and Liem, 1983; Taverne, 1989; Arratia, 1997, 1999) except two, the articular fused with the angular (condition of the articular only known in Plethodidae) and the posterior opening of the mandibular sensory canal on the external side of the angular (Taverne, 2000a). Furthermore they are characterised by the following apomorphies:

(1) All along the axial skeleton, the neural and haemal arches are articulated by gomphosis on the corresponding centra (Taverne, 2000a; Taverne and Gayet, 2004).

(2) The body is more or less deep and compressed.

(3) There is no anterior supramaxilla (Fig. 2; Taverne and Gayet, 2004).

(4) The postcleithra are lost (Fig. 2; Taverne and Gayet, 2004).

(5) The dorsal and anal fins are very long, reaching the caudal peduncle (Fig. 1).

(6) The dorsal and anal rays, pointed or branched, are not segmented (Fig. 1).

(7) Ossified epipleurals are missing (Patterson, 1967a; Taverne, 2001a, b, 2004; Taverne and Gayet, 2004). This character is a reversal from an apomorphic pattern to a more plesiomorphic one. Indeed there are already an extensive serie of epipleurals within the Elopiformes, a teleost order quite more primitive than the Tselfatiiformes (Taverne, 1974; Patterson and Johnson, 1995).

(8) Hypurals 3 and 4 are fused in a hypural plate (Fig. 4; Taverne and Gayet, 2004).

Some of these specialised characters occur in other teleo-

stean lineages but never them all at the same time. Apomorphies (7) and (8) are uncommon and apomorphies (1) and (6) really exceptional.

Protobramidae offer several other derived characters (Taverne and Gayet, 2004) that distinguish them from the other Tselfatiiformes:

(9) The endochondral part of the mesethmoid is not ossified.

(10) The temporal fossa is dorsally bordered by the parietal.

(11) The maxilla is toothless.

(12) The posterior supramaxilla is lost.

(13) The bones of the palato-quadratic arch are toothless except the endopterygoid.

(14) The parasphenoid is toothless.

(15) The supraorbital is lost.

(16) The ribs are generally fused with the haemapophyses.

(17) Some haemal spines present an anterior winglike widening, forming a medio-ventral vertebral septum.

(18) Epicentrals are lost.

(19) The haemaxanal complex shows a highly specialised pattern with the first anal pterygiophores elongated, backward bent, joined together and resting against the first long haemal spines forward slanted.

(20) Epurals are lost.

(21) Ural centrum 1 bears a neural spine, probably resulting from the capture of one epural.

(22) Hypural 6 is lost.

(23) The bases of the dorsal, anal and caudal fins are covered with scales.

The phylogeny within the Protobramidae is explained in details by Taverne and Gayet (2004) and thus shall not be

Figure 10. - Evolution of the caudal skeleton within Tselfatiiformes. **Characters A:** All the neural and haemal arches autogenous; fully developed preural centrum 1; ural centra reduced and fused in a small terminal vertebra; hypurals 1 to 4 fused in a large hypural plate; hypurals 5 and 6 autogenous; terminal vertebra and hypural plate fused; preural neural spine 2 reduced; no preural neural spine 1; three epurals with the two last reduced; one pair of stegurals and no other uroneurals; preural haemal arch 1 and parhypural fully developed; enlarged button like hypurapophysis on parhypural articulated in a notch in the rear of the preural haemal arch 2; a deep groove on hypural plate. **Characters B:** Preural centrum 1 reduced; preural haemal arch 1 reduced; parhypural lost; notch of preural haemal arch 2 preserved; preural neural spine 2 complete by probable capture of epural 1; epurals 2 and 3 lost; stegurals fused and getting narrower, forming a false preural neural spine 1; hypural 6 preserved. **Characters C:** Reduced preural haemal arch 1 lost; notch of preural haemal arch 2 preserved; hypural 6 preserved. **Characters D:** Hypural 6 lost; notch of preural haemal arch 2 preserved. **Character E:** Notch of preural haemal arch 2 lost. (*Eoplethodus* modified from Taverne, 2000d: fig. 1; *Bananogmius* modified from Taverne, 2001b: fig. 8; *Thryptodus* or *Martinichthys* modified from Taverne, 2000a: fig. 2; *Pseudanogmius* modified from Taverne, 2002b: fig. 7; *Pentanogmius* modified from Taverne, 2004: fig. 14). [Évolution du squelette caudal chez les Tselfatiiformes. **Caractères A :** Tous les arcs neuraux et hémaux autogènes ; centre préural 1 complètement développés ; centres uraux réduits et fusionnés en une petite vertèbre terminale ; hypurales 1 à 4 fusionnés en une grande plaque hypurale ; hypurales 5 et 6 autogènes ; vertèbre terminale et plaque hypurale fusionnées ; neurépine préurale 2 réduite ; pas de neurépine préurale 1 ; trois épuraux avec les deux derniers réduits ; une paire de stéguraux et pas d'autres uroneurals ; arc hémal préural 1 et parhypural complètement développés ; grande hypurapophyse en forme de bouton sur le parhypural et articulée dans un creux à l'arrière de l'arc hémal préural 2 ; profonde gouttière sur la plaque hypurale. **Caractères B :** Centre préural 1 réduit ; arc hémal préural 1 réduit ; parhypural perdu ; creux de l'arc hémal préural 2 conservé ; neurépine préurale 2 complète par capture probable de l'épural 1 ; épuraux 2 et 3 perdus ; stéguraux fusionnés et devenant plus étroits, formant une fausse neurépine préurale 1 ; hypural 6 conservé. **Caractères C :** Arc hémal préural 1 perdu ; creux de l'arc hémal préural 2 conservé ; hypural 6 conservé. **Caractères D :** Hypural 6 perdu ; creux de l'arc hémal préural 2 conservé. **Caractère E :** Creux de l'arc hémal préural 2 perdu. (*Eoplethodus* modifié d'après Taverne, 2000d : fig. 1 ; *Bananogmius* modifié d'après Taverne, 2001b : fig. 8 ; *Thryptodus* ou *Martinichthys* modifié d'après Taverne, 2000a : fig. 2 ; *Pseudanogmius* modifié d'après Taverne, 2002b : fig. 7 ; *Pentanogmius* modifié d'après Taverne, 2004 : fig. 14).]

TSELFATIIFORMES

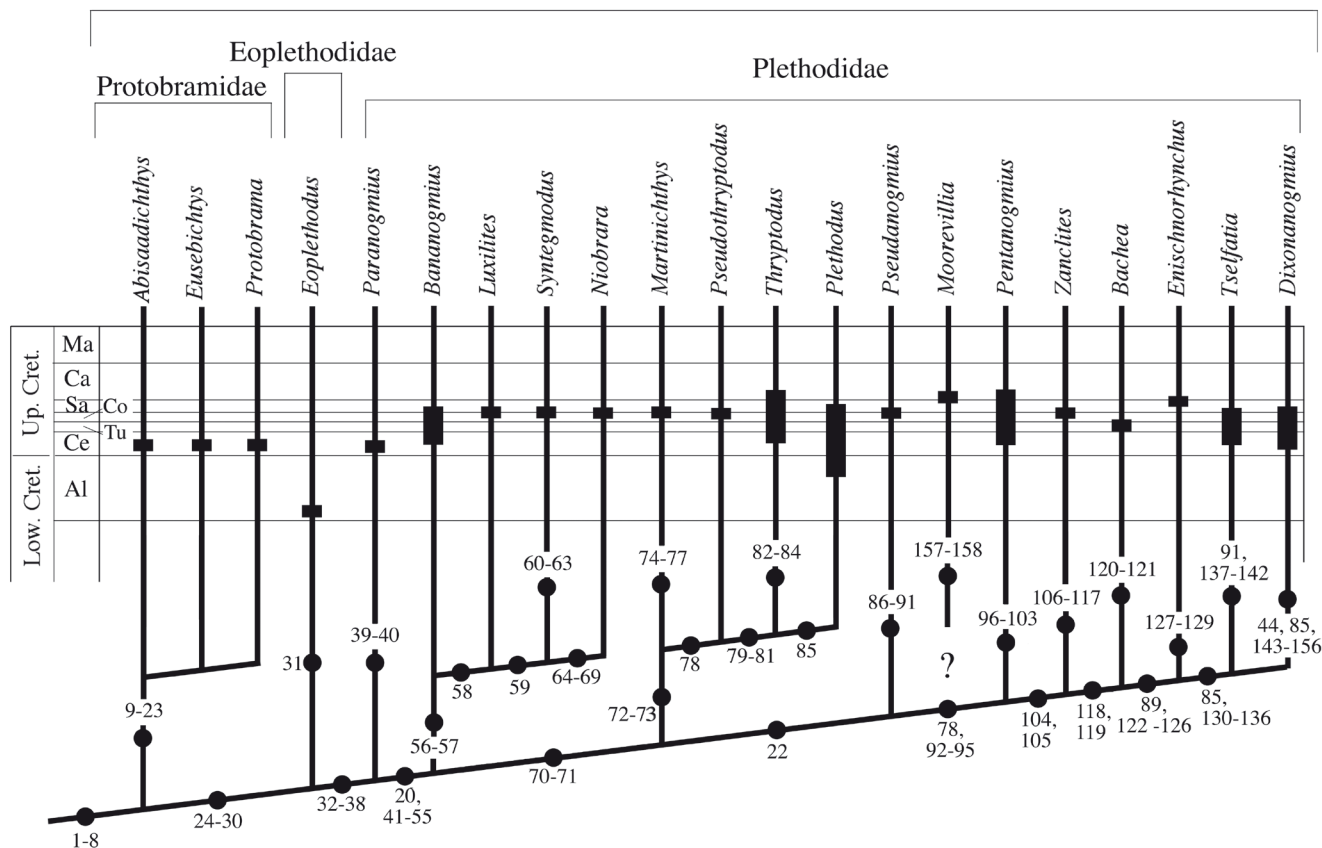


Figure 11. - The phylogeny and stratigraphic distribution of the Tselfatiiformes. The numbers refer to the characters in the text. Geological abbreviations: Low. Cret.: Lower Cretaceous; Up. Cret.: Upper Cretaceous; Al: Albian; Ce: Cenomanian; Tu: Turonian; Co: Coniacian; Sa: Santonian; Ca: Campanian; Ma: Maastrichtian. [*Phylogénie et distribution stratigraphique des Tselfatiiformes. Les nombres se rapportent aux caractères discutés dans le texte.*]

developed here.

Eoplethodidae and Plethodidae share other apomorphies not present in Protobramidae:

(24) The ural centra are greatly reduced and fused in a small terminal vertebra (Figs 4, 10).

(25) There is no neural arches on the preural centrum 1 and the terminal ural vertebra (cf. Fig. 10, characters A; Taverne, 2000d).

(26) The first four hypurals are fused into a large hypural plate which is joined to the terminal vertebra (Fig. 4). A deep horizontal groove is dividing the plate into a dorsal and a ventral part (Fig. 10, characters A; Taverne, 2000d). This division is also marked by a large notch in the posterior edge of the plate.

(27) The neural spine of the preural centrum 2 is short (Fig. 10, characters A; Taverne, 2000d).

(28) Three epurals are present but the second and the third one are reduced (Fig. 10, characters A; Taverne, 2000d).

(29) The stegural is articulated in a facet on the lateral side of the preural vertebra 1 and does not extend beyond this centrum (Fig. 10, characters A; Taverne, 2000d).

(30) Other uroneurals are lost (Fig. 10, characters A; Taverne, 2000d).

Some of these specialised characters could be present in other teleostean families but never them all together.

The caudal skeleton is the only part preserved in *Eoplethodus*. So the Eoplethodidae and their single genus could be characterised by only a caudal apomorphy:

(31) The hypurapophysis of the parhypural is greatly enlarged, forming a sort of bulky button which is articulated in a notch on the rear of the haemal arch of the preural centrum 2 (Fig. 10, characters A; Taverne, 2000d).

The genera of the more apomorphous family Plethodidae share some other derived characters:

(32) The jaws, the palate and the lingual plate are covered with patches of small teeth (Fig. 3; Taverne, 2001b).

(33) The toothed bones are pierced by numerous small

pits (Taverne, 2000a).

(34) The orbitosphenoid, pleurosphenoids and parasphenoid form a complete osseous interorbital septum (Figs 2, 3).

(35) The antorbital, supraorbital and dermosphenotic are articulated together and with the frontal border (Taverne, 1999, 2000b, 2001b, 2003, 2004).

(36) The cleithrum has a very long and obliquely oriented ventral branch (Fig. 2; Taverne, 1983, 2002a).

(37) The pectoral fin is inserted high on the flank (Fig. 1; Taverne, 1983, 1999, 2001a, b).

Characters (36) and (37) are linked. Indeed, the pectoral fin is inserted at the level where the dorsal and ventral branches of the cleithrum meet. In that way, if the cleithral ventral branch grows longer and is obliquely oriented, the pectoral fin becomes positioned higher on the flank than with a short and horizontally oriented cleithral ventral branch. Those two characters also exist in *Protobrama* but not in the two more primitive protobramid genera *Eusebichthys* and *Abisaadichthys* which display a short ventral branch of the cleithrum and the pectoral fins inserted low on the flanks.

(38) The groove on the hypural plate is greatly reduced or totally missing (Fig. 10, characters B; Taverne, 2001b).

Characters (32) to (37) were perhaps already present in *Eoplethodus*. But the corresponding parts of the skeleton in *Eoplethodus* are not preserved.

*Paranogmius* is the only plethodid keeping the subtemporal fossa, an archaic teleost feature, and seems therefore the most primitive of them all (Taverne, 2003). It offers at least two autapomorphies:

(39) The vomer is 'T'-shaped, with a very broad anterior edge and a long and thin body (*ibid.*).

(40) The toothed patches on the vomer and the parasphenoid are in continuity and possess a convex surface in cross-section (*ibid.*). These toothed patches are flat or concave in the other genera.

Other plethodids share numerous more derived characters:

(41) The nasal is large and articulated with the frontal and the mesethmoid (Taverne, 2003, 2004).

(42) The subtemporal fossa is lost (Fig. 3; Taverne, 2000b, 2001a, 2001c, 2002b, 2003, 2004).

(43) There is only one supramaxilla which articulates in a deep notch of the dorsal border of the maxilla (Fig. 7A; Taverne, 2000b, 2001b, 2003, 2004).

(44) The angular and retroarticular are fused together while the articular remains autogenous (Nelson, 1973a; Taverne, 2000a, 2000b, 2002a, 2003, 2004). Such a character also exists in *Protobrama* and *Eusebichthys* but not in *Abisaadichthys*, the less specialised protobramid genus,

which exhibits an autogenous retroarticular.

This character (44) also exists within the Elopomorpha (Nelson, 1973b; Forey, 1973; Taverne, 1974, 1999a; Nybelin, 1976, 1982; Arratia, 1997) although the articular could partially fuse with the two other bones in some rare and generally old specimens (Arratia, 1987; 1997). Fused angulo-retroarticular and a free articular are also known in some recent Osteoglossomorpha, the genus *Gymnarchus* (Nelson, 1973b; Taverne, 1972) and old specimens of *Hiodon* (Nelson, 1973b; Hilton, 2002, 2003). Young specimens of *Hiodon* possess an autogenous retroarticular (Taverne, 1977; Arratia, 1997; Hilton, 2002). Other members of this super-order show another pattern for these three bones. In the Pachyrhizodontoidae, a primitive group of Clupeocephala, the angular and retroarticular never fuse. Cavin (2001) codes the pachyrhizodontoids as having the angular and articular fused (his character 37[2]), and presents as a second derived state the case of *Notelops* (Forey, 1977) in which the articular is autogenous (his character 37[3]). In contrast, we interpret an autogenous articular as the plesiomorphic pattern within these fishes, the Notelopidae being more primitive for many characters than the Pachyrhizodontidae. Besides, the articular is unknown in the pachyrhizontid genera *Platinx*, *Greenwoodella*, *Elopopsis* and *Tingitanichthys*, and some species of *Pachyrhizodus* still possess an articular partially free from the angular (Taverne, 1987). More apomorphic Clupeocephala always offer fused angular and articular (Nelson, 1973b). However, within the Clupeomorpha, the Denticipitioidae could present both conditions depending on specimens, either a fused angulo-articular (Greenwood, 1968) or an autogenous articular (Arratia, 1997).

(45) The supraneurals are missing (Taverne, 1983, 2001a, 2001b, 2004).

(46) The dorsal fin extends from near the head to near the root of the tail (Fig. 1; Taverne, 1983, 1999, 2001a, 2001b, 2004).

These two characters (45) and (46) are probably linked. Indeed, there is no longer place left for the supraneurals when the dorsal fin arises close to or above the head.

(47) Most of the dorsal and anal pterygiophores possess an enlarged distal portion (Taverne, 1975, 1999, 2001b, 2002b, 2004).

(48) The epineurals are present only in the abdominal region of the body (Patterson, 1967a; Taverne, 2001a, 2001b, 2004). This character is a reversal from an apomorphic pattern to a more plesiomorphic one. Indeed there is already an extensive series of epineurals covering most of the abdominal and caudal regions within the primitive teleostean order Elopiformes (Taverne, 1974; Patterson and Johnson, 1995).

(49) There are ossified ligaments connecting the mandibular symphysis to the cleithra (Bardack and Teller-Marshall, 1980; Taverne, 1983, 1999, 2001a, 2002a, 2004; Paramo-



Fonseca, 1997; Fielitz and Shimada, 1999). Fielitz and Shimada (1999) interpret them as the mineralized protractor hyoidei muscles.

(20) The epurals are lost (Fig. 4). The reduction of the two posterior epurals in *Eoplethodus* [character (28)] foreshadows the loss of the epurals in Plethodidae. Protobramiidae also exhibit that character but independently acquired.

(50) There is a full neural spine on the preural centrum 2, probably resulting from the capture of the first epural (Figs 4, 10, characters B, C, D, E; Taverne, 1999, 2000a, 2000d, 2001a, 2001b, 2002b, 2004).

(51) The preural centrum 1 is reduced (*ibid.*).

(52) The haemal arch of the preural centrum 1 is greatly reduced but still articulated in the posterior notch of the preceding haemal arch (*ibid.*).

(53) The parhypural is lost (*ibid.*).

(54) The stegurals get narrower and are fused together to form a false preural neural spine 1 which is articulated with the corresponding vertebral centrum (*ibid.*).

(55) The caudal fin rays, branched or pointed, are not segmented.

The presence of characters (41), (43) to (49) and (55) is possible in *Eoplethodus* and *Paranogmius* and therefore could perhaps be also valid for all the members of the families Eoplethodidae and Plethodidae. The characters (50) to (54) perhaps already exist in *Paranogmius*. But once again the corresponding osteological structures are not preserved in those two genera.

Within the Plethodidae more advanced than *Paranogmius*, the less apomorphic clade consists of the four genera *Bananogmius*, *Luxilites*, *Syntegmodus* and *Niobrara*. Taverne (2001a, 2001c, 2002a) explained in detail the reasons of such a linkage. They still retain a preopercle with two well developed branches, an unreduced pelvic girdle, the haemaxanal complex of type 1 and a small haemal arch on the preural centrum 1. They are characterised by two apomorphies:

(56) The antorbital has a long and sharp postero-ventral process (Taverne, 2001a, 2001b).

(57) The ectopterygoid becomes toothless (Taverne, 2001b, 2002a).

*Bananogmius* is the less specialised of these four primitive genera. *Luxilites* differs from it by only one derived feature also shared by *Syntegmodus* and *Niobrara*:

(58) The dorsal part of the pterotic is enlarged, giving a triangular shape to the skull roof, with an occipital region markedly broader than the frontal one (Taverne, 2001c, 2002a).

*Syntegmodus* and *Niobrara* share another derived feature:

(59) The pterotic and the parietal have a reduced contact

because the frontal posterior portion is slipping backwards along the parietal anterior border (*ibid.*).

Besides, *Syntegmodus* offers some autapomorphies:

(60) The big lateral ethmoid is narrow but particularly high (Fig. 3).

(61) The orbitosphenoid is very large (Fig. 3; Taverne, 2001c).

(62) The posterior part of the parasphenoid medio-dorsal crest is particularly enlarged, giving rise to a very high inter-orbital osseous septum (*ibid.*).

Characters (60), (61) and (62) are probably linked.

(63) The postorbital process is reduced and the sphenotic is completely covered by the frontal and the pterotic in dorsal view (*ibid.*).

*Niobrara*, the most specialised genus within the clade, is characterised by other advanced features:

(64) The backward slip of the frontal along the parietal border [character (59)] is so important that the pterotic becomes posteriorly located respect to the parietal (Taverne, 2001a).

(65) There is a triangular fronto-parietal hollow on the skull roof (*ibid.*).

(66) The *dilatator fossa* migrates from the pterotic ventral wall to its dorsal one, and so becomes visible on the skull roof (*ibid.*).

(67) The dorsal part of the hypercleithrum is enlarged (Taverne, 2001a).

(68) The dorsal branch of the cleithrum is very short but also very broad and articulates with the expanded portion of the hypercleithrum (*ibid.*).

Characters (67) and (68) are probably linked.

(69) The lateral surface of most abdominal vertebrae are ornamented by two or three strong ridges (Taverne, 2001a), and not by numerous small narrow ridges as generally in other Tselfatiiformes and in many primitive teleosts.

Plethodids more evolved than *Bananogmius*, *Luxilites*, *Syntegmodus* and *Niobrara* share at least two new apomorphies:

(70) The ventral branch of the preopercle becomes notably shorter than the dorsal one (Fig. 2; Bardack, 1965; Taverne, 1983, 2000b, 2000c, 2003, 2004).

(71) The reduced haemal arch of the preural centrum 1 totally disappears but the posterior notch on the haemal arch of the preural centrum 2 is preserved (Fig. 10, characters C, D; Taverne, 2000a, 2000d, 2002b).

The paleontological collections of the University of Kansas contain a few isolated and well preserved plethodid caudal skeletons from the *Niobrara* Formation which have already lost the haemal arch of the preural centrum 1 but still

display two autogenous hypurals above the hypural plate (Taverne, 2000a, 2000d). These isolated caudal remains almost certainly belong to *Martinichthys* and *Thryptodus*, two closely related genera (Taverne, 2003) abundantly represented in the Niobrara Formation but of which no tail has never been discovered in connection. The caudal skeletons of all other evolved plethodid genera from the Niobrara Formation are known and exhibit a more advanced pattern in which there is only one autogenous hypural above the hypural plate, the sixth hypural being already lost.

Taverne (2000b, 2003) has shown that, within those plethodids more specialised than *Bananogmius* and its three fellows, the four genera *Martinichthys*, *Pseudothryptodus*, *Thryptodus* and *Plethodus* are forming a clade. They share two noteworthy apomorphies:

(72) The premaxillae are enlarged and articulated, ankylosed or totally fused together, covering a great part or totally the mesethmoid and the anterior border of the vomer (Taverne, 2000b, 2000c, 2003).

(73) The lingual tooth plate is greatly broadened, becoming more or less oval or round (Taverne, 2000b, 2000c, 2003).

*Martinichthys* shows a few autapomorphies:

(74) The snout is greatly elongated, forming a strong rostrum (Taverne, 2000b).

(75) The enlarged premaxillae join not only dorsally over the mesethmoid but also ventrally, forming a false palate which covers entirely the vomer and partially the autopalatines (*ibid.*).

(76) The autopalatine is a very large bone, not fused with the dermopalatine (*ibid.*).

(77) There is no maxillar anterior articular condyle. Unlike other plethodids, the maxillar anterior border is broad, flat and bears a narrow vertical groove allowing the articulation with the premaxillar posterior border (*ibid.*).

*Pseudothryptodus*, *Thryptodus* and *Plethodus* share another advanced feature:

(78) In the dentigerous lingual plate, the dermobasibranchial of the fourth branchial arch is lost. The dermobasihyal and the fused dermobasibranchials of the three first arches remain the two only components of the lingual plate (Taverne, 2000c, 2003).

*Thryptodus* and *Plethodus* offer some more specialised characters:

(79) The snout is short, very broad and very bulky (Taverne, 2000c, 2003).

(80) The parasphenoid tooth plate is greatly broadened and becomes oval or rounded (Woodward, 1899; Taverne, 2000c, 2003).

(81) The lingual tooth plate becomes perfectly rounded (Woodward, 1899; Taverne, 2000c, 2003).

*Thryptodus* exhibits a few more autapomorphies:

(82) The nasals are considerably enlarged and articulate with the premaxillae and the frontals (Taverne, 2003).

(83) The vomer is toothless and very broad (*ibid.*).

(84) The preopercle and opercle are small compared to the skull size (*ibid.*).

Characters (82), (83) and (84) are perhaps also present in *Pseudothryptodus* and *Plethodus* but the corresponding parts of the skeleton are missing in those two genera.

The vomer of *Martinichthys*, completely covered by the premaxillae, is very likely toothless but certainly not broadened. Character (84) perhaps also occurs in *Martinichthys* but the opercular bones are too partially preserved in that genus to be sure (Taverne, 2000b).

*Plethodus* differs from *Thryptodus* by one new derived feature:

(85) The dermobasihyal and the dermobasibranchial of the first three branchial arches are fused together in a single lower dental plate (Woodward, 1899; Taverne, 2000c).

More evolved plethodids share a new apomorphy:

(22) The sixth hypural is lost (Figs 4, 10, characters D, E; Taverne, 1999, 2000d, 2002b, 2004). This character, independently acquired, also occurs in Protobramidae.

*Pseudanogmius*, which still retains a large lateral ethmoid and the posterior notch in the haemal arch of the preural centrum 2, seems to be the less apomorphic genus of the group and offers a few autapomorphies:

(86) The long and toothed vomer is considerably narrower than the parasphenoid (Taverne, 2002b).

(87) The posterior part of the vomer is wedged in between ventro-posterior processes of the lateral ethmoids (*ibid.*).

(88) The toothed portion of the parasphenoid exhibits a very peculiar relief (*ibid.*).

(89) The epiotic and the supraoccipital do not meet, the parietal lying between them (*ibid.*).

The derived character (89) occurs several times within plethodids. It is known in one species of the genus *Bananogmius*, *B. favirostris* (Taverne, 2001b) and also in the three genera with a very curved skull roof in cross section, *Enischnorhynchus*, *Tselfatia* and *Dixonanogmius* (Fig. 2; Bardack, 1965; Taverne, 2000a, 2000c).

(90) The first caudal vertebrae possess on each side a small lateral process (Taverne, 2002b).

(91) The neural spine of the preural centrum 1 is reduced (*ibid.*).

More apomorphic plethodids offer new derived characters:

(92) The lateral ethmoid is more or less reduced, frequently losing its contact with the parasphenoid (Bardack,

1965; Taverne, 1983, 2000c, 2004).

(93) The supramaxilla articulates in a notch of the dorsal border of the maxilla but also shows an anterior sharp extension in front of the notch (Fig. 7B; Paramo-Fonseca, 1997; Taverne, 2004).

(78) The lower dental plate comprizes only the dermobasihyal and the fused dermobasibranchial of the three first branchial arches, the dermobasibranchial of the fourth arch being lost (Taverne, 2000a, 2000c, 2004). This character, already met in *Pseudothyrtodus*, *Thryrtodus* and *Plethodus*, is here independently acquired.

Characters (78) and (93) perhaps already exist in *Pseudanogmius*, but the corresponding skeletal structures are not preserved in this genus.

(94) The pelvic girdle is slightly reduced, its length corresponding to eleven vertebrae in *Pentanogmius* versus fourteen to fifteen vertebrae in more primitive genera such as *Bananogmius* and *Niobrara* (Taverne, 2004). The pelvic girdle is not preserved in the *Thryrtodus* group and in *Pseudanogmius*. So it is possible that a moderate shortening of the pelvic girdle [character (94)] occurs sooner in the plethodid evolution.

(95) The posterior notch of the haemal arch of the preural centrum 2 is lost (Figs 4, 10, characters E; Taverne, 2004).

*Pentanogmius*, essentially known by the species *P. evolutus* and *P. crieleyi*, offers a few autapomorphies:

(96) The orbitosphenoid is reduced and the interorbital osseous septum incomplete (Taverne, 2004).

(97) The fifth infraorbital is greatly reduced (*ibid.*).

(98) The dentary tooth patch is broad, covering the upper part of the inside of the bone and protruding on the outside in a sort of osseous plate (*ibid.*).

(99) There are only 7 to 9 branchiostegal rays (*ibid.*). Other plethodids generally exhibit 12 to 16 branchiostegal rays.

(100) The dermobasihyal is pentagon-shaped (*ibid.*).

(101) The coracoid is small and short (*ibid.*).

(102) The number of vertebrae greatly increases, reaching 81 (*ibid.*). Other plethodids possess between sixty and seventy vertebrae.

(103) There are some dorsal scutes (*ibid.*).

*Zanclites* and the more apomorphic genera share two derived features:

(104) The haemaxanal complex is of type 3 (Fig. 9; Blot, 1968).

(105) The pelvic girdle is extremely reduced, not exceeding a length of five to seven vertebrae (Bardack, 1965; Bardack and Teller-Marshall, 1980; Taverne, 1983, 1999).

*Zanclites* offers numerous autapomorphies:

(106) The supraorbital is very long and articulated not only with the frontal but also with the pterotic (Taverne, 1999).

(107) The *dilatator fossa* is located on the dorsal wall of the pterotic as in *Niobrara* but is here very weakly developed (*ibid.*).

(108) The quadrate is reduced and elongated (*ibid.*).

(109) The toothless ectopterygoid is rodlike (*ibid.*).

(110) The ectopterygoid anterior tip is swollen and meets a dorsal process of the endopterygoid, forming a strong cup-like structure that was probably supporting a big palatine (*ibid.*).

(111) The ventral branch of the preopercle is greatly elongated (*ibid.*).

(112) The supratemporal and the posttemporal are articulated together (*ibid.*).

(113) The haemal arches of the abdominal vertebrae are partially or totally fused with the corresponding centra (*ibid.*).

(114) There are small scalelike epipleurals at the end of the abdominal region of the body and at the beginning of the caudal one (*ibid.*).

(115) The anal pterygiophores possess expanded tips which are articulated together (*ibid.*).

(116) The neural spine of the preural centrum 1 is fused to the corresponding centrum (*ibid.*).

(117) The fifth hypural is greatly reduced (*ibid.*).

*Bachea* and the more apomorphic genera share two new advanced characters:

(118) The skull roof is more curved in cross section than in all the previous genera (Fig. 5B; Paramo-Fonseca, 1997).

(119) The angular and retroarticular are unfused [*Bachea* and *Enischnorhynchus*] (Bardack, 1965; Paramo-Fonseca, 1997) or only partially fused [*Tselfatia*] (Taverne, 2000a).

*Bachea* exhibits at least two autapomorphies:

(120) The fifth infraorbital is greatly enlarged (Paramo-Fonseca, 1997).

(121) There are two well developed scalelike postcleithra (*ibid.*). These bones are unknown in other plethodid fishes.

*Enischnorhynchus*, *Tselfatia* and *Dixonanogmius* share a few more derived features:

(122) The skull roof is very strongly curved in cross section (Fig. 5C). That is an accentuation of character (118) shown in *Bachea*.

(123) The tooth patches on the premaxilla, the maxilla and the dentary are very narrow (Bardack, 1965; Taverne, 1983, 2000a, 2000c).

(124) The notch in the dorsal border of the maxilla is lost and the supramaxilla simply lies on the maxilla (Fig. 7C;



Bardack, 1965; Taverne, 1983, 2000c).

(89) The epiotic and the supraoccipital are separated by the parietal (Fig. 2; Bardack, 1965; Taverne, 2000a, 2000c) as in *Pseudanogmius* and *Bananogmius favirostris*, a character considered here as independently acquired.

(125) The ventral branch of the hyomandibula is especially long (Bardack, 1965, Taverne, 1983, 2000c).

(126) The posttemporal develops a well marked dorsal branch (Bardack, 1965; Bardack and Teller-Marshall, 1980; Taverne, 1983, 2000a).

*Enischnorhynchus* presents at least three autapomorphies:

(127) The ectopterygoid is narrow and shortened (Bardack, 1965).

(128) The metapterygoid is greatly enlarged, separating the quadrate from the hyomandibular, and extending dorso-medially along the anterior border of the hyomandibular (*ibid.*).

(129) The subopercle is enlarged (*ibid.*).

*Tselfatia* and *Dixonanogmius* possess several more apomorphic characters:

(130) The skull is particularly high at the occipital level (Fig. 2; Bardack and Teller-Marshall, 1980; Taverne, 1983, 2000c).

(131) The parietals are broader than long and very narrow where they meet in the midline of the skull roof (Fig. 6B; Taverne, 2000a, 2000c).

(132) The nasal is reduced and no more ankylosed with the frontal and the mesethmoid (Taverne, 1983).

Character (132) perhaps already exists in *Zanclites*, *Bachea* and *Enischnorhynchus*, three genera in which the nasal is not known.

(133) The antorbital is no more articulated with the supraorbital (*ibid.*).

(134) The posttemporal dorsal branch is greatly elongated (Bardack and Teller-Marshall, 1980; Taverne, 1983, 2000a).

(85) The dermobasihyal and the dermobasibranchial of the three first branchial arches are fused into a single lower dental plate (Dixon, 1850; Taverne, 2000a, 2000c) as in *Plethodus*. This character is considered as homoplastic in the two lineages.

(135) The first large dorsal and anal fin rays are segmented and bear a row of pseudo-fulcræ all along their anterior border (Taverne, 2000a, c).

(136) The dorsal and ventral parts of the hypural plate are not completely fused and the suture line remains clearly visible (Fig. 4; Bardack and Teller-Marshall, 1980; Taverne, 1983).

*Tselfatia* is characterised by a few autapomorphies:

(137) The *dilatator fossa* is reduced to a small and short groove on the pterotic (Fig. 2; Taverne, 1983).

(138) The palatine is toothless (*ibid.*).

Character (138) perhaps also exists in *Enischnorhynchus* and in *Dixonanogmius*, two genera in which the palatine is not known.

(139) The neural and haemal arches are partially or totally fused with the corresponding centra (Taverne, 2000a).

(140) The tips of the dorsal and anal pterygiophores are expanded in large semi-circular plates (Taverne, 1975).

(141) In Eurafrikan populations from the Cenomanian/Turonian, the last caudal vertebrae develop winglike lateral processes in young specimens. The processes fuse into a long continuous prominent lateral keel in old specimens (Fig. 4; Taverne, 1983). In the younger North American population from the Coniacian/Santonian, there are rounded lateral projections on most of the caudal vertebrae but not on those directly preceding the tail (Bardack and Teller-Marshall, 1980). It is thus possible that those specimens from Texas belong to another species than *T. formosa* (see also Maisch and Lehmann, 2000).

(91) The neural spine of the preural centrum 1 is reduced (Fig. 4; Bardack and Teller-Marshall, 1980; Taverne, 1983). This character, already met in *Pseudanogmius*, is thought here as being independently acquired.

(142) The scales possess a pectinated posterior border (Arambourg, 1954).

*Dixonanogmius* exhibit numerous autapomorphies:

(143) The mesethmoid is long and narrow (Taverne, 2000c).

(144) The mesethmoid and the vomer are partially fused (*ibid.*).

(145) The lateral ethmoid does not ossify or is weakly ossified (*ibid.*).

(146) A crest on the pterotic is supporting the supratemporal (*ibid.*).

(147) The premaxillaries are greatly reduced and fused together in a small cuplike bone covering the mesethmoid anterior tip (*ibid.*).

(148) The maxilla does not possess an articular condyle and is simply in contact with the premaxilla (*ibid.*).

(149) There is an osseous wing on the anterior part of the maxillar dorsal border. That allows a slipping of the first infraorbital over the maxilla when the mouth is closed (*ibid.*).

(150) The supramaxilla is reduced (*ibid.*).

(151) The lower jaw is high and short (*ibid.*).

(44) The angular and retroarticular are fused once again (*ibid.*) as in the primitive *Tselfatiiformes*.

(152) On the hyomandibula, the *processus opercularis* is strongly reduced (*ibid.*).

(85) The single lower dental plate is broadened and ovoid (Dixon, 1850; Taverne, 2000c) as in *Plethodus*. This character is considered here as independently acquired.

(153) The urohyal is extremely enlarged and triangular (*ibid.*).

(154) The pectoral fin is so highly located on the flank that it is inserted above the axial skeleton level (Bardack and Teller-Marshall, 1980).

(155) The body is very deep (*ibid.*).

(156) The neural spines of the preural centra 1 and 2 are lost (*ibid.*).

Characters (154) to (156) are only known in *D. dalmatia*.

Many important osteological data concerning *Moorevillia* are lacking. So the phylogenetic position of these flat skull genus within the family remains unclear. *Moorevillia* has no subtemporal fossa (Applegate, 1970) and thus is more evolved than *Paranogmius*. The toothed pterygoids and the small premaxillae (*ibid.*) exclude any closeness with both the *Bananogmius* and the *Thryptodus* groups. The supramaxilla articulates in a notch of the maxillar dorsal border and there is no extension of the supramaxilla in front of the notch (*ibid.*). Such a feature places *Moorevillia* in a more plesiomorphic position than *Pentanogmius*, *Bachea*, *Enischnorhynchus*, *Tselfatia* and *Dixonanogmius*. Nothing else can be said about its relationships within the Plethodidae. *Moorevillia* shows two autapomorphies:

(157) The parietals are separated by the supraoccipital (Fig. 6C; Applegate, 1970).

(158) The premaxillary toothed patch is reduced to a single row of small conical teeth (*ibid.*).

As we have just seen above, the osteological differences between the plethodid genera are numerous. However, in our mind, they are not important enough to justify their splitting into more than one family. Thus, we suggest to include all those genera, in the single family Plethodidae and to consider the *Bananogmiidae*, the *Niobrariidae*, the *Thryptodontidae* and the *Tselfatiidae* as junior synonyms of the former as Patterson (1993) did.

### The position of the Tselfatiiformes within the Clupeocephala

Taverne (2000a) and Cavin (2001) agree that the Tselfatiiformes are primitive Clupeocephala, both authors basing their analysis only on the Plethodidae at that time. However Taverne (2000a) considers the Tselfatiiformes as more apomorphic than the Pachyrhizodontoidei, whereas Cavin (2001) treats them as more plesiomorphic than the latter. Taverne's conclusion is essentially based on two osteological features. The Pachyrhizodontoidei possess fully developed supratemporals generally meeting in the midline of the skull (Bartholomai, 1969; Forey, 1977; Taverne, 1994; Cavin, 2001) and

their paired branchial toothed plates are not fused with the corresponding branchial bones (Forey, 1977). That is also the plesiomorphic condition within teleosts. On the contrary, the Tselfatiiformes and the more apomorphic Clupeocephala exhibit a more derived pattern with reduced supratemporals and the paired branchial toothed plates fused to the branchial bones. Concerning the first character, the Stephanoberyciformes are the only clupeocephalan exception. Many of them possess enlarged supratemporals meeting on the midline and articulating with the frontals (Johnson and Patterson, 1993). However, that is not the preservation of the plesiomorphic teleost condition but an autapomorphy of those fishes linked with their strongly reduced parietals, their broad extrascapular sensory commissure and their large epiphyseal mucous cavity (*ibid.*).

Cavin (2001) does not consider those two characters but his interpretation rests on eighteen other features which lead from the node separating the Tselfatiiformes and the more apomorphic Clupeocephala to the Pachyrhizodontoidei at the level of the genus *Platinx*, that is to say successively his characters 4[1], 10[1], 18[1], 24[1], 37[2], 38[1], 50[0], 23[1], 27[1], 29[0], 2[0], 3[1], 12[0], 40[0], 24[0], 63[1], 64[2] and 67[0] (Cavin, 2001). From this list, characters 10[1], 18[1], 37[2], 27[1], 29[0], 2[0], 40[0], 63[1], 64[2] and 67[0] are said to be homoplasies and thus bring no real information about the relationships between the two teleost lineages. Characters 24[1] and 24[0] are not informative regarding this problem as the second one counterbalances the first. The six remaining characters (4[1], 38[1], 50[0], 23[1], 3[1] and 12[0]) deserve a more detailed analysis.

### The parietal commissure (Cavin's character 4)

Cavin codes the Pachyrhizodontoidei as having no parietal portion of the supraorbital sensory canal (4[1]). Indeed the parietal commissure seems very often missing in these fishes (Bartholomai, 1969; Forey, 1977; Taverne, 1994; Cavin, 2001) but not always. The pachyrhizodontid genera *Platinx*, *Greenwoodella* and *Tingitanichthys* possess such a commissure and, in *Greenwoodella*, the commissure even enters the parietal bone (Taverne, 1980, 1991, 1996). The supraorbital sensory canal and its branches are difficult to see on the thick bones of the plethodid skull roof. That probably explains why a commissure reaching the parietal border is only known in young specimens of *Tselfatia* (Taverne, 2000a). *Protobrama* also exhibits a parietal commissure (Taverne and Gayet, 2004). Thus we find no real differences between the Pachyrhizodontoidei and the Tselfatiiformes concerning the parietal commissure since such a structure is present in some members of both groups. Besides, the loss of the parietal commissure is a highly homoplastic character which is only playing a very minor role in the teleostean phylogeny. Within the primitive teleost super-orders Elopomorpha and Osteoglossomorpha for instance such a loss

appears several times. The Elopiformes still possess a well developed commissure running on the frontal and the parietal (Forey, 1973; Taverne, 1974) but the commissure is severely shortened in the Albuliformes (Forey, 1973), not enclosed in bones in the Notacanthiformes (McDowell, 1973) and completely lost in the Anguilliformes (Trewavas, 1932; Gosline, 1951; Robins and Robins, 1967; Castle, 1972; McCosker, 1977). The Hiodontiformes exhibit a highly primitive pattern in which the supraorbital sensory canal is ending on the parietal and has no contact with the otic (= postorbital) canal (Gaudant, 1968: fig. 5; Greenwood, 1970; Taverne, 1977; Hilton, 2002, 2003). More evolved osteoglossomorph groups as the Osteoglossiformes, the Mormyroidae or the Notopteroidei have lost the parietal commissure (Taverne, 1972, 1977, 1978; Hilton, 2003). On the other hand, a branch of the supraorbital canal entering the parietal is preserved in some teleosts more evolved than the Pachyrhizodontoidei and the Tselfatiiformes. That is the case in some primitive Clupeocephala (Forey, 1975), in some basal Clupeomorpha (Patterson, 1967b, 1970; Chang and Grande, 1997), in some archaic Ostariophysi (Gayet, 1981; Patterson, 1984; Taverne, 1995), in a few modern Characiformes (Weitzman, 1962; Roberts, 1969) and in many Beryciformes (Patterson, 1964, 1967c; Kotlyar, 1992).

*The posterior opening of the mandibular sensory canal (Cavin's character 38)*

Cavin describes the Pachyrhizodontoidei as having the posterior opening of the mandibular sensory canal located on the lateral wall of the angular (38[1]) and considers as a reversal to the plesiomorphic condition the location on the medial wall (38[0]) found in *Notelops* (Forey, 1977). The situation is not so clear. The pachyrhizodontid genus *Goulmimichthys* effectively shows the apomorphic stage of the character (Cavin, 2001). However, in addition to *Notelops*, some species of the pachyrhizodontid genus *Pachyrhizodus* also exhibit the posterior opening of the mandibular canal on the medial wall of the angular (Nelson, 1973b; Taverne, 1987). Besides, in *Rhacolepis*, the mandibular canal opens by three pores on the lateral surface of the angular but probably also by one pore on the inner surface of the bone (Forey, 1977). The location of this opening is unknown in the pachyrhizodontid genera *Platinx*, *Elopopsis*, *Greenwoodella* and *Tingitanichthys*. We could therefore not conclude that the Pachyrhizodontoidei are differing from the Tselfatiiformes concerning this feature as some of the former and all of the latter share the primitive pattern with the opening in the internal wall of the lower jaw.

*The hypurapophysis (Cavin's character 50)*

Cavin includes the Pachyrhizodontoidei in a large group of teleosts in which the hypurapophysis is lost. According to

this, he presents the Pachyrhizodontoidei as devoid of hypurapophysis on the parhypural (50[0]) and the presence of an hypurapophysis (50[1]) in the pachyrhizodontid genera *Rhacolepis*, *Pachyrhizodus* and *Goulmimichthys* as a reversal to a more plesiomorphic pattern. An hypurapophysis being a plesiomorphic character in basal teleosts, we consider its presence as the primitive condition within the Pachyrhizodontoidei and its lack as the derived one. Within tselfatiiform fishes, the Protobramidae are devoid of a hypurapophysis on the parhypural and the Plethodidae have lost both the parhypural and its hypurapophysis. But *Eoplethodus*, which retains the parhypural, exhibits on the contrary an enlarged button-like hypurapophysis. So, we could think that there was no difference between the Tselfatiiformes and the Pachyrhizodontoidei on that level and that the presence of an hypurapophysis is the primitive condition in both lineages.

*The antorbital (Cavin's character 23)*

The loss of the antorbital (23[1]) and the joining between the elongated supraorbital and the first infraorbital are two of the pachyrhizodontoid most prominent autapomorphies. The antorbital is well developed (23[0]) in the Plethodidae. The presence of an antorbital is possible but not certain in the protobramid primitive genus *Abisaadichthys* (Taverne and Gayet, 2004). This character does not give any information about the relationships between the two lineages.

*The pterotic posterior spine (Cavin's character 3)*

Some Pachyrhizodontidae but not all exhibit a small posterior spine on the pterotic (3[1]). Such a spine does not exist (3[0]) in the Tselfatiiformes, in the pachyrhizodontoid family Notelopidae and in the pachyrhizodontid genera *Pachyrhizodus* and *Greenwoodella*. Once again, we could not reach any conclusion about the respective phylogenetic positions of the two groups with this feature.

*The subepiotic fossa (Cavin's character 12)*

Neither the Pachyrhizodontoidei nor the Tselfatiiformes possess a subepiotic fossa (12[0]). There is thus no difference between the two lineages on that level.

It is now obvious that none of these six characters really testifies in favour of a more apomorphic phylogenetic position for the Pachyrhizodontoidei than for the Tselfatiiformes. On the other hand, the two characters put forward by Taverne are still valid. Thus, we maintain Taverne's first conclusion that within the Clupeocephala the Pachyrhizodontoidei are the direct plesiomorphic sister-group of a clade uniting the Tselfatiiformes, and the more apomorphic Otocephala and Euteleostei (Taverne, 2000a).



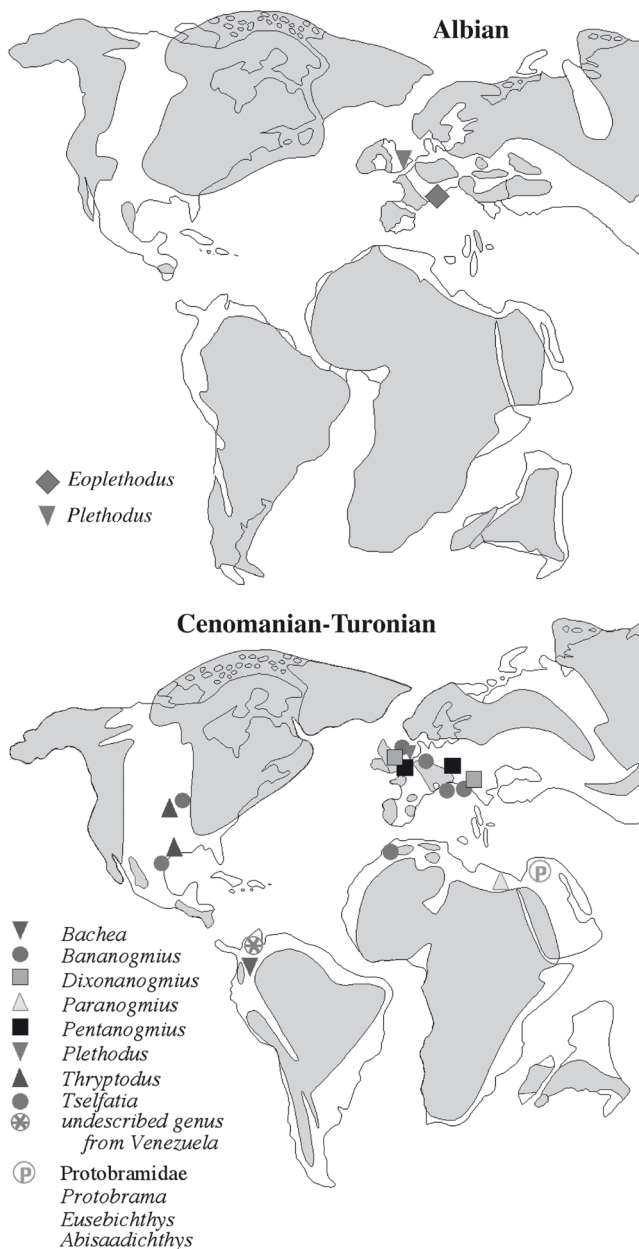


Figure 12. - The Tselfatiiform geographic distribution during the Albian, the Cenomanian/Turonian. The emerged lands are in grey (map modified from Smith *et al.*, 1994). [Distribution géographique des Tselfatiiformes pendant l'Albien, le Cénomaniien et le Turonien. Les terres émergées sont grisées (carte modifiée d'après Smith *et al.*, 1994).]

### The paleozoogeography of the Tselfatiiformes

During the Albian [112 Ma - 97 Ma] (Fig. 12)

The Tselfatiiformes make their first appearance in the fossil record during the Albian in Europe, and more precisely in a Tethyan northern branch crossing France, the southeastern region of England and reaching the North Sea (Tyson and Funnell, 1987). Two genera are known: *Eoplethodus* with *E. chaneti* from the Lower Albian of Haute-Provence (Cha-

net, 1997; Taverne, 2000d), and *Plethodus* with *P. expansus* from the Upper Albian of Kent (Woodward, 1899; Taverne, 2000c).

During the Cenomanian and Turonian [97 Ma - 88.5 Ma] (Fig. 12)

During the marine Cenomanian-Turonian transgression the Plethodidae successfully continue their spread in the Eurafrikan province of the Tethys Ocean realm. *Plethodus expansus* persists in England throughout this period (Taverne, 2000c). As early as the Lower Cenomanian, the family is present in the most eastern part of the Eurafrikan Mesogea, Egypt and Libya, with the gigantic *Paranogmius* and its only species *P. doederleini* (Quaas, 1902; Weiler, 1935; Stromer, 1936; Taverne, 2003). Three new genera appear in England during the Upper Cenomanian, *Bananogmius* with *B. ornatus* (Woodward, 1923), *Dixonanogmius* with *D. oblongus* (Woodward, 1899; Taverne, 2000c) and *Pentanogmius* with *P. pentagon* (Woodward, 1899; Taverne, 2000c, 2004). Another genus, *Tselfatia*, also appears during the same period with the widespread species *T. formosa* from the Upper Cenomanian and Lower Turonian of Morocco, Italy, Croatia and Germany (Arambourg, 1954; Sorbini, 1976; Bardack and Teller-Marshall, 1980; Taverne, 1983; Maisch and Lehmann, 2000). A second species of *Dixonanogmius*, *D. dalmatia*, and a second species of *Pentanogmius*, *P. furcata*, are respectively known from the Cenomano-Turonian boundary in Croatia (Bardack and Teller-Marshall, 1980) and from the Turonian of Czechia (Fritsch, 1878).

During the Lower Cenomanian the Near East endemic tselfatiiform family Protobramidae expands in Lebanon with three genera, *Protobrama*, *Eusebichthys* and *Abisaadichthys*, and four species, *P. avus*, *P. woodwardi*, *E. byblosi* and *A. libanicus*. No other geographic and stratigraphic occurrence of that family is known.

The Plethodidae also start their westward dispersal during the Cenomanian, getting across the Central Proto-Atlantic Ocean to reach the Caribbean Sea, the Gulf of Mexico, South and Central America and the large and shallow Upper Cretaceous epicontinental seaway then bisecting North America into two land masses. The clockwise gyres that affected the ocean drift currents in the Proto-Atlantic at that time certainly helped the spread of the plethodids from the Eurafrikan Tethys to the South American coast and the Gulf of Mexico. Two plethodids have been discovered in the northern part of South America, an undescribed Cenomanian species from Venezuela (Moody and Maisey, 1994) and the monospecific Upper Turonian genus *Bachea*, with *B. huilensis* from Colombia (Paramo-Fonseca, 1997). On the other hand, *Thryptodus*, with its single species *T. zitteli*, is known in the Upper Cenomanian of Texas (unpubl. inf., K. Shimada, *in litt.*, 20 Dec. 2002) and of Kansas (Shimada and Schu-

macher, 2003), whereas *Bananogmius*, a genus already met in Europe, is also present with a second species, *B. ellisensis* from the Middle Turonian of Kansas (Fielitz and Shimada, 1999). *Tselfatia*, a genus also known from the Cenomano-Turonian of the Eurafrikan Mesogea, occurs in the Turonian of Northeastern Mexico (Blanco-Pinon *et al.*, 2002). These authors do not determine specifically the fish but their description completely fits the one of *T. formosa* (Arambourg, 1954; Taverne, 1975, 1983, 2000a; Bardack and Teller-

er-Marshall, 1980; Maisch and Lehmann, 2000).

*During the Coniacian and the Santonian [88.5 Ma - 83 Ma] (Fig. 13)*

No plethodid has ever been discovered in the Coniacian and Santonian deposits from the Eurafrikan Tethyan realm and from the South American coast. But well dated and ichthyologically documented Coniacio-Santonian deposits in that area are rather rare. On the other hand, the family becomes highly diversified in the North American seaway during that geological period, reaching a region as northern as the Manitoba (Canada) where an unidentified plethodid has been reported from Coniacian sediments (Bardack, 1968). Many new endemic and generally monospecific genera known in the Kansas deposits, and especially in the Smoky Hill Member of the Niobrara Formation, appear during this period, *Pseudothryptodus* with *P. intermedius*, *Syntegmodus* with *S. altus*, *Niobrara* with *N. encarsia*, *Zanclites* with *Z. xenurus*, *Martinichthys* with *M. brevis* and *M. ziphioides*, *Pseudanogmius* with *P. maiseyi* (Loomis, 1900; Jordan, 1924; McClung, 1926; Everhart, 2001; Taverne, 2002b) and the newly discovered but still undescribed long-snouted genus allied to *Thryptodus* and *Martinichthys* (K. Shimada, *in litt.* 2002). The already met species *Thryptodus zitteli* is also present in the Coniacian and Santonian of Kansas (Loomis, 1900), as well as an unnamed species of *Dixonanogmius* (Taverne, 2000c), a second species of *Plethodus*, *P. rotundus* (Loomis, 1900; Taverne, 2000c), and two new species of *Bananogmius*, *B. aratus* and *B. favirostris* (Hay, 1903; Taverne, 2001b). A third species of *Pentanogmius*, *P. evolutus*, also exists in Kansas and in South Dakota during the same geological period (Taverne, 2004). *Tselfatia formosa* apparently is the only Cenomano-Turonian species of Eurafrikan origin surviving during the Coniacian/Santonian times in North America and more precisely in Texas (Bardack and Teller-Marshall, 1980). Another American endemic genus, *Enischnorhynchus* with the single species *E. dallasensis*, is reported from the Upper Santonian of Texas (Bardack, 1965).

*During the Campanian [83 Ma - 74 Ma] (Fig. 13)*

Contrasting with their high diversity during the Coniacian/Santonian period, few Plethodidae survive during the Campanian. We know only the undetermined species from the Campanian of southern Egypt (Stromer and Weiler, 1930) and three other fishes, all from the Lower Campanian of Alabama, not in the North American seaway but on the Gulf of Mexico sea front: the endemic genus *Moorevillia* with the single species *M. hardi*, *Pentanogmius crieleyi*, the youngest species within the genus, and *Thryptodus zitteli*, already living in North America since the Upper Cenomanian (Applegate, 1970). No plethodid has ever been mentioned in the Maastrichtian.

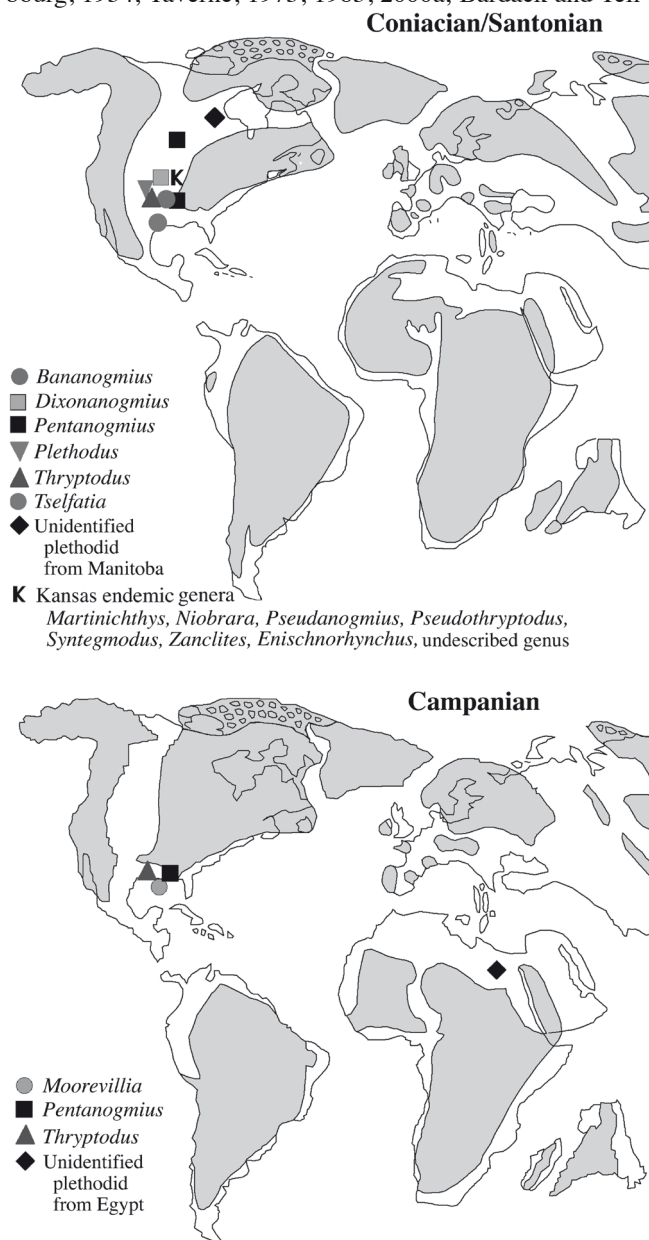


Figure 13. - The tselfatiiform geographic distribution during the Coniacian/Santonian and the Campanian. The emerged lands are in grey (map modified from Smith *et al.*, 1994). [Distribution géographique des Tselfatiiformes pendant le Coniacien, le Santonien et le Campanien. Les terres émergées sont grisées (carte modifiée d'après Smith *et al.*, 1994).]

*Palaeozoogeographical conclusions*

Eoplethodidae and Plethodidae appear in Europe during the Albian, but the primitive Eoplethodidae a few million years sooner (Lower Albian, France) than the more apomorphic Plethodidae (Upper Albian, England). Eoplethodidae and their single genus *Eoplethodus* are known only in Europe and in Albian time, whereas the Plethodidae exhibit a more important geographic expansion (Europe, North Africa, North and Central America, northern South America) and chronological duration (Upper Albian to Campanian). Protobramidae occur only in Lebanon during a short geological period in the Lower Cenomanian. The Tselfatiiformes fail to expand in the Australasian Ocean realm, unlike the Pachyrhizodontoidei and the Ichthyodectiformes well represented in Cretaceous Australian marine deposits (Bartholomai, 1969; Lees and Bartholomai, 1987).

The Tselfatiiformes seem to vanish after the Campanian and thus before the North American seaway begins to regress and about 12 million years before the catastrophic mass extinction at the Cretaceous/Tertiary boundary. The Tselfatiiformes have had so a life time duration of about 35 million years.

Within the Plethodidae, only one genus, *Paranogmius*, is endemic in the Eurafrikan Tethys. Some Upper Albian to Lower Turonian plethodids from the Eurafrikan Tethyan realm are congeneric, and even conspecific in one case, with some Turonian to Lower Campanian plethodids from Central and North America. The five concerned genera are *Plethodus*, *Bananogmius*, *Tselfatia*, *Dixonanogmius* and *Pentanogmius*. Ten endemic plethodid genera, *Pseudothryptodus*, *Syntegmodus*, *Niobrara*, *Zanclites*, *Luxilites*, *Martinichthys*, *Enischnorhynchus*, *Moorevillia*, *Pseudanogmius* and the still undescribed genus closely related to *Thryptodus* and *Martinichthys*, exist in North America. Only one endemic plethodid genus, *Bachea*, is known in South America.

*Tselfatia formosa* is the only species of Cenomano-Turonian Eurafrikan origin which succeeds to reach Central America during the Turonian and to survive in North America during the Senonian.

*Thryptodus zitteli*, known in North America from the Upper Cenomanian to the Lower Campanian, and *Plethodus expansus*, present in England from the Upper Albian to the Turonian, are the two more long-living species of all the Tselfatiiformes with a life time duration of about 15 million years.

The Campanian plethodid from Egypt poses a problem as to the survival of the Tselfatiiformes in the Eurafrikan Tethys after the Turonian since they are apparently absent there during the Coniacian and Santonian. Two hypotheses are possible. Either one or a few plethodids not yet discovered in the fossil record were effectively present there during that geological period, or some Campanian North American plethodids undertook an eastern trip from the Gulf of Mexico

across the Proto-Atlantic to reach the Eurafrikan Tethys.

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