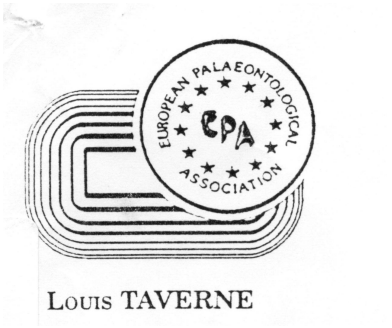

REVISION OF THE GENUS *MARTINICHTHYS*, MARINE FISH (TELESOSTEI, TSELFATIIFORMES) FROM THE LATE CRETACEOUS OF KANSAS (UNITED STATES)

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ABSTRACT – The genus *Martinichthys* belongs to the order Tselfatiiformes and contains two valid species, *M. brevi*s with a short rostrum and *M. ziphoides* with a long rostrum. The species *M. acutus, M. alternatus, M. gracilis, M. intermedius* and *M. latus* are junior synonyms of *M. ziphoides*. The genus is characterized by five autapomorphies: a snout lengthened in a rostrum, a narrow cranial roof, the premaxillae forming a secondary palate and hiding the vomer, the lack of anterior process on the maxilla, and the supraoccipital without a medial crest. Despite its specialized characters, *Martinichthys* also retains some primitive features for the order, such as the presence of an autogenous basisphenoid and the three lingual toothed plates. Within the Tselfatiiformes, *Martinichthys* appears especially close to the genera *Plethodus* and *Thryptodus*.

KEYWORDS: TELEOSTEI, TSELFATIIFORMES, *MARTINICHTHYS*, MARINE LATE CRETACEOUS, KANSAS, OSTEOLOGY.

INTRODUCTION

The genus *Martinichthys* McClung, 1926 was erected for large Teleostei from the Plethodidae family, characterized by a snout elongated forming a rostrum (McClung, 1926). The strong erosion presented by the end and the antero-ventral part of this rostrum, in all known specimens, probably indicates that this fish used it to dig the sea floor in search of preys. *Martinichthys* haunted the waters of Late Cretaceous North American Interior Sea. Its remains have been found in the Niobrara Formation of Kansas (United States) and are thus of a geologic age branching from the Coniacian to the Early Campanian (Schultze et al. 1982). Only skulls, rostra and some vertebrae have been recovered. Almost nothing, then, is known of the postcranial skeleton. Judging by the size of the concerned parts, it can be estimated that the whole specimens were nearing or even were bigger than one meter in length.

The type species of the genus is *Martinichthys brevis* McClung, 1926, whose rostrum is moderately elongated. McClung (1926) also describes a series of other species, where the rostrum elongates in a more marked manner. *Martinichthys ziphoides* (Cope, 1877), M. *acutus* McClung, 1926, *M. alternatus* McClung, 1926, *M. gracilis* McClung, 1926, *M. intermedius* McClung, 1926, and *M. latus* McClung, 1926. These last six species only differ one from the other in minor changes in the shape of their respective rostra (McClung 1926: pl. 1). I have studied the concerned material. These slight morphological differences are due, in my opinion, to individual, sexual, ontogenetic, or erosion variations and do not justify the erection of particular species. I subsequently propose to consider the five long rostrum species erected by McClung as junior synonyms of *Martinichthys ziphoides*, a species clearly distinct from *M. brevis*.

McClung (1926)'s osteologic description remains very superficial and doesn't allow a clear comprehension of *Martinichthys*'s skull, nor does it help envisage the relationships of this fish with other Plethodidae genera. A revision of *Martinichthys* was necessary. This is the aim of the present work which also follows the series of publications that I dedicate to the study of Tselfatiiformes or Bananogmiiformes (Taverne 1975, 1983, 1999 in press a, b), an order of large marine teleostei fish from the Cretaceous to which the Plethodidae family belongs (Patterson 1993: 627; Nelson 1994: 90) et whose shape reminds that of extant Scombridae and Coryphaenidae.

For more information concerning the Tselfatiiformes, as well as the discussion on their systematic position within the Clupeocephala, I recommend Taverne (in press a).

MATERIAL AND METHODS

The material comes from the collections of the Department of Palaeontology, University of Kansas, Lawrence (KUVP) and the American Museum of Natural History of New York (AMNH).

Martinichthys brevis:
KUVP 497 (holotype; 14cm long skull and some vertebrae; Senonian; Smoky Hill Chalk, member of the Niobrara Formation; south side of the Smoky Hill, Gove County, Kansas).
KUVP 40015 (16cm long neurocranium from which the rostrum end is missing, some vertebrae and some bone fragments; Senonian; Niobrara Formation, Gove County, Kansas).

Martinichthys ziphoides:
AMNH 2131 (holotype; 10cm long rostrum; Senonian; Niobrara Formation; Gove County, Kansas).
KUVP 498 (20cm long nearly complete neurocranium and 23 vertebrae; Coniacian; Smoky Hill Chalk, member of Niobrara Formation; ¾ mile from Neuenschwander ranch, Trego County; Kansas).
KUVP 499 (7.3cm long rostrum; holotype of *M. latus*; Coniacian; Smoky Hill Chalk, member of the Niobrara Formation; Martin's Canyon, Gove County, Kansas).
KUVP 500 (4.2cm long rostrum; holotype of *M. alternatus*; Coniacian; Smoky Hill Chalk, member of the Niobrara Formation; 1 ½ mile south of Banner, Trego County, Kansas).
KUVP 501 (5.2cm long rostrum; holotype of *M. intermedius*; Coniacian; Smoky Hill Chalk, member of the Niobrara Formation; 1 ½ mile south of Banner, Trego County, Kansas).
KUVP 502 (2.7cm long rostrum; holotype of *M. acutus*; Coniacian; Smoky Hill Chalk, member of the Niobrara Formation; Martin's Canyon, Gove County, Kansas).
KUVP 503 (2.9cm long rostrum; paratype of *M. acutus*; Coniacian; Smoky Hill Chalk, member of the Niobrara Formation; west side escarpments of sector 3. Trego County, Kansas).
KUVP 504 (5.5cm long rostrum; holotype of *M. gracilis*; Coniacian; Smoky Hill Chalk, member of the Niobrara Formation; Martin's Canyon, Gove County, Kansas).
KUVP 506 (10cm long rostrum; Senonian; Smoky Hill Chalk, member of the Niobrara Formation; West of Kansas).
KUVP 507 (9.5cm long rostrum; Coniacian; Smoky Hill Chalk, member of the Niobrara Formation; 1 ½ mile south of Banner, Trego County, Kansas).

This material has been studied with the use of a stereomicroscope Wild M5, achieved by the author in a clear chamber (camera lucida).

STUDY OF THE MATERIAL

THE SKULL (Fig. 1-9)

The neurocranium is elongated in *Martinichthys brevis* and even more elongated in *M. ziphoides*. In the first, the maximum height of the neurocranium represents 42% of its length, whereas it is no more than 25% in the second. This neurocranium is also laterally compressed. This compression is highly reinforced by the lateral compression that the three discovered skulls have endured during fossilization.

The rostrum, rounded at its proximal end, is formed by the vomeroethmoidian region and by the very large premaxillaries which recover it with a truly ossified capuchon. This rostrum is clearly longer and thinner in *M. ziphoides* than in *M. brevis*. The rostrum length (measured to the distal end of the mesethmoid) equals 158% of its maximum height in *M. brevis* (skull KUVP 497), whereas it is 327% in *M. ziphoides* (skull KUVP 498). The mesethmoid is elongated, thick, very massive and made of a single part, without it being possible to distinguish a dermethmoid and a supraethmoid. It is literally encapsulated in the premaxillaries which nonetheless let a part of it visible laterally and dorsally, but totally recover and hide it ventrally. Laterally, near the posterior edge of the mesethmoid, it can be observed a short and narrow groove used for the articulation of the anteromedial edge of the nasal. The mesethmoid and the premaxillaries are fused together. This fusion is less pronounced in *M. brevis* than in *M. ziphoides*. The sutures are still clearly visible between the two premaxillaries and between these and the mesethmoid on skull KUVP 497 (*M. brevis*), whereas the fusion between the three bones is more advanced in skull 40015 of the same species. In *M. ziphoides*, on the contrary, the two premaxillaries are intimately fused one to the other, without any visible suture persisting between them, and the suture with the mesethmoid is more clearly blurred although still visible in the form of a pad . In the two species, the two premaxillaries join ventrally on the medial skull line, thus forming a kind of false palate covering and entirely hiding the vomer region. More distally on this false palate, the premaxillaries remain separated one from the other by a deep notch. In *M. ziphoides*, the suture between the two premaxillaries at the palate level has completely disappeared, whereas it persists in *M. brevis*. In both species, the ventral face of the premaxillaries is full of small alveoli, traces of the emplacement of the denticles. These alveoli are shaded off by erosion in the anterior part of the rostrum of *M. ziphoides*. On skull KUVP 497 (*M. brevis*) some rare denticles remain on the oral face of the premaxillaries. The external surface of the premaxillaries is ornamented by tiny facets and wrinkles. This ornamentation is more pronounced in *M. brevis* than in *M. ziphoides*. In *M. brevis*, one can observe a pair of lateral ethmoids, just behind the mesethmoid and stuck between the frontals and the parasphenoid. In *M. ziphoides* specimens, the lateral ethmoid region is not preserved.

A large part of the left nasal is present on skull KUVP 497 (*M. brevis*). It is a small bone, wide but not very elongated, flat and which articulates with the frontal lateral edge in a notch situated just above the lateral ethmoid. The nasal is not preserved in *M. ziphoides* specimens.

The skull roof is formed by the frontals, the parietals, the pterotics, the epiotics and the supraoccipital. It is only well preserved in *M. brevis*, whereas only parts of the frontals are visible in *M. ziphoides*. This skull roof is elongated and narrow, even in the parieto-occipital region, and seems to have been relatively flat. However, the lateral crushing endured during fossilization has created an angle between the two frontals and the two parietals which, on skull KUVP497, are pushed on each side in a more oblique plan. In *M. brevis*, the frontals are long, moderately wide, but not a lot more distally than proximally. The distal end of the frontal is situated at the level of the posterior edge of the orbit, just above the sphenotic. A little groove can be observed along the medial part of the frontal lateral edge; it is used to articulate with the supraorbital. The parietals are large, nearly quadrangular, a little longer than wide and in medial contact, thus determining a medioparietal skull. In the middle of the skull roof, the two parietals form a long central depression, bordered on each side by a slightly pronounced crest. The pterotics are elongated but not high. At the level of the junction between the pterotic and the frontal, one can observe, on each side of the skull, a massive sphenotic forming a large lateral postorbital lateral process. The sphenotic is proportionally bigger in *M. ziphoides* than in *M. brevis*. The supraoccipital is small and bears no medial crest. The epiotics are well developed and

form a small protuberance at the back of the neurocranium. A small *dilatator fossa* is drawn across the sphenotic and the pterotic. It is clearly visible on the right side of skull KUVP 497 of *M. brevis*, whereas fossilization has crushed it under the pterotic on the left side. A long articular facet, for the hyomandibular, is visible just below the *dilatator fossa*, along the suture between the pterotic, the prootic and the exoocipital as well as the sphenotic at which level it widens in a clearly visible manner. On skull KUVP 498 (*M. ziphoides*); the fossilization has pushed the pterotic towards the sphenotic, thus hiding the posterior part of the *dilatator fossa* and the hyomandibular articular facet.

The sphenoid bones are large and the orbitosphenoid is even a lot larger than the pleurosphenoid. The orbitosphenoid and the pleurosphenoids ventrally join a dorsomedial aisle of the parasphenoid, thus forming a complete bony interorbital septum. In *M. brevis*, the orbitosphenoid contacts the lateral ethmoids. This doesn't seem to be the case for *M. ziphoides*. Although the lateral ethmoids are not known for the latter, the orbitosphenoid is situated relatively far distally relative to the mesethmoid, which would have prevented any contact with eventual lateral ethmoids. A large foramen, situated between the pleurosphenoid, the orbitosphenoid, the sphenotic and the frontal in *M. brevis*, and between the pleurosphenoid, the orbitosphenoid and the sphenotic in *M. ziphoides*, was used as a passage for the trochlear nerve (IV).The anterior edges of the prootics as well as the parasphenoid ascending processes are broken on skull KUVP 497 (*M. brevis*).

This allows distinguishing a small and massive basisphenoid, articulating with the dorsomedial aisle of the parasphenoid, just at the rear of the pleurosphenoids, and situated at the entrance of the posterior myodome. The parasphenoid ascending processes and the anterior edge of the prootics are preserved on the other skull (KUVP 40015) of *M. brevis*, hiding the basisphenoid. Between the pleurosphenoids, the prootics and the basisphenoid is a large hypophyseal fenestra probably used by the two optic nerves (II) to emerge from the neurocranium. The basisphenoid region is lacking on skull KUVP 498 (*M. ziphoides*). The parasphenoid is long and wide, proportionally longer in *M. ziphoides* than in *M. brevis*.

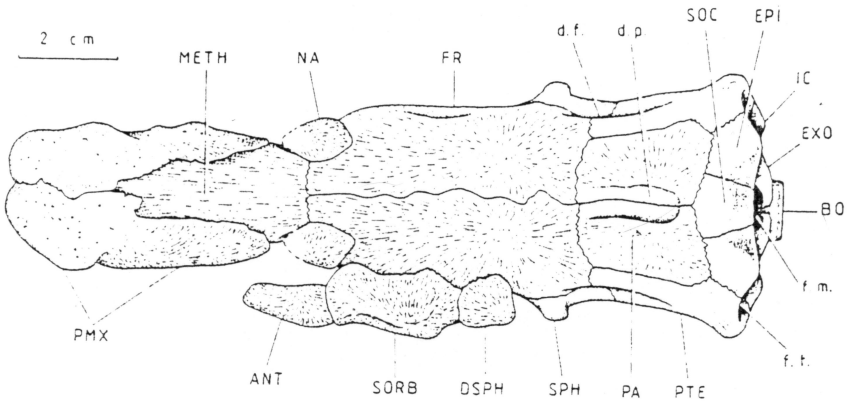

FIGURE 4 - *Martinichthys brevis*. Reconstitution du crâne en vue dorsale d'après l'holotype KUVP N° 497 et l'exemplaire KUVP N° 40015. Même légende qu'aux Figures 1, 2 et **f.m.**: *foramen magnum. Restoration of the skull in dorsal view based on the holotype KUVP N° 497 and the specimen KUVP N° 40015. Same legend as in Figures 1, 2 and* **f.m.**: foramen magnum.

It bears a pair of short ascending processes articulating with the prootics but which climb dorsally to the sphenotics. It has a dorsomedial aisle participating in the interorbital septum. Its ventral face is covered, from the distal end of the bone to the ascending processes region, of small alveoli and wells, traces of denticle implementation of which only a few are preserved. This denticled region is slightly concave, the concavity accentuating distally. The maximal width of the denticled region represents 28% of its length in *M. brevis* (KUVP 497) and 19% in *M. ziphoides* (KUVP 498). One can also observe the foramen of the internal carotid hollowed in the parasphenoid, at the base of the ascending process. Distally, the parasphenoid applies firmly against the

basioccipital, leaving no aperture for an eventual passage of the myodome. There are no observable basipterygoid processes. The angle formed by the denticled region and the distal end of the parasphenoid is small.

The anterior edge of the prootic is well preserved on skull KUVP 40015 (*M. brevis*), thus allowing to observe the trigemino-facial and *pars jugularis* chamber complex. The trigeminal nerve (V) foramen opens between the prootic and the pleurosphenoid. The foramen of *truncus hyoideomandibularis* of the facial nerve *(*VII*)* is situated a lot more distally on the prootic, thus determining a rather long *pars jugularis*. In *M. ziphoides* (KUVP 498), on the contrary, the foramen of the trigeminal nerve (V) is entirely pierced in the prootic and does not contact the pleurosphenoid. The facial nerve (VII) *truncus hyoideomandibularis* foramen opens a little distally to the preceding foramen. The *pars jugularis* is then very short in that case. One can observe on skull KUVP 497 (*M. brevis*), but only on the left side, an opening with regular edges which runs in the prootic, at the limit of the exoccipital and close to the one of the basioccipital. It is probably an auditory fenestra. Such an opening is sometimes found on some Tselfatiiforme

On the other hand, the dermosphenotic doesn't cross over the pterotic, *contra* what is seen in other Tselfatiiformes (pers. obs.). The third and fourth infraorbitals are large and longer than wide. The third is larger than the fourth.

The palato-quadrate arch is nearly entirely preserved on skull KUVP 497 (*M. brevis*). Only the metapterygoid is missing. In *M. ziphoides*, only the autopalatines are known. The autopalatine is a large bone which clings laterally to the rear of the mesethmoid and slides mostly under the premaxillary. The dermopalatine is small, denticled and situated under the proximal part of the entopterygoid. This dermopalatine is not fused to the autopalatine. The ectopterygoid is elongated, sharp proximally, wide distally, whereas the entopterygoid, a little bit longer, remains wide all along. The internal faces of both the

skulls (pers. obs.) and appears in various other Teleostei. The exoccipitals surround the *foramen magnum* and are ventrally hollowed by the vague nerve (X). The intercalars are well developed. The basioccipital is massive, ventromedially hollowed by a short and shallow aortic groove. It forms the neurocranial articular condyle for the first vertebra. This condyle is oval, a lot higher than wide.

The temporal fossae (posttemporals) open on the distal face of the neurocranium, between the epiotic, the pterotic and the intercalar. These fossae are not visible on the lateral face of the skull because they are covered dorsolaterally by the pterotic. The supratemporal (= extrascapular) is not preserved. There is no subtemporal fossa.

Some bones of the right circumorbital series are preserved on skull KUVP 497 (*m. brevis*): the antorbital, the supraorbital, the dermosphenotic and two of the three posterior infraorbitals. The antorbital, the supraorbital and the dermosphenotic articulate together. The antorbital is more elongated than high. The supraorbital is wide and articulates with the frontal. The dermosphenotic is small and also articulates with the frontal.

ectopterygoid and the entopterygoid are nearly totally covered by small alveoli and small holes, traces of where the denticles were planted. The quadrate is well developed, equilateral triangle-shaped, equipped of a large articular condyle for the mandibular and devoid of any differentiated quadratojugal process. The ventral edge of the bone bears a narrow groove used for the articulation with the preopercular.

The upper jaw, as well as the mandibular, is in most part preserved on skull KUVP 497 (*M. brevis*). Besides the premaxillary, each upper hemi-maxillary also comprises a maxillary edging the mouth distally to the premaxillary and only one supramaxillary.

The external surface of these two bones is ornamented by riddles. The maxillary is short, shorter than the premaxillary, and wide. It bears a series of denticles on its internal face, along its ventral edge. Its anterior edge is not blown in an articular condyle; it remains, on the contrary, wide and flat but is hollowed by a narrow vertical groove permitting the articulation with the ventral part of the premaxillary posterior edge. The posterior edge of the maxillary is hollowed by a notch into which articulates the anterior part of the small supramaxillary, as in numerous Tselfatiiformes (pers. obs.). The mandibular is elongated, seems moderately raised, and when one articulates it on the neurocranium *via* the quadrate and the hyomandibular, it can be observed that its proximal end remains slightly behind the rostrum proximal end. The upper edge of the dentary is covered by a series of denticles which, proximally, extends beyond the internal and external faces of the bone. In the symphyseal region, the dentary shows, on its internal face, below the denticled region, a large oblique crest used for the articulation with the homologous bone of the other hemi-mandible. The angular and the retroarticular are totally fused, without any suture remaining between the two bones. The articular is large, massive and autogenous. Its superior edge extends that of the angular and is even visible on the mandible external face. The articular facet for the quadrate is hollowed in the angulo-retroarticular and in the articular. The case of another Tselfatiiforme, *Tselfatia formosa* ARAMBOURG, 1943, shows nonetheless that the retroarticular does not participate in the formation of this facet in fishes of this order (Taverne, in press a: fig. 4B). The angular extends beyond the facet in a strong postarticular ascending process. Some traces of the mandibular sensory canal are observed on the external faces of the dentary and the angular. The canal posterior opening is located on the angular internal face, at the base of the postarticular process.

The bones from the opercular series are poorly known. Parts of the left preopercular, right opercular, right subopercular and four right branchiostegal rays subsist on skull KUVP 497 (*M. brevis*). The preopercular shows a very short ventral branch and a narrow and longer dorsal branch. Traces of the preopercular sensory canal are visible on the bone surface. The preserved part of the opercular is too small to help estimate its shape and size. The subopercular and the branchiostegal rays are wide. The external bone surface of the opercular series is ornamented with riddles.

HYOIDEO-BRANCHIAL SKELETON (Fig. 8b, 10)

Important parts of the hyoidal arch and of the branchial skeleton are preserved on skull KUVP 497 (*M. brevis*).

Two large parts of the right hyomandibular allows reconstructing approximately its shape. It is wide dorsally and extends ventrally in a long and thick bony rod. The *opercularis process* is present but broken and it is thus difficult to estimate its length. Neither the symplectic nor the posterior ceratohyal are known. The anterior ceratohyal is massive, two and a half longer than wide and devoid of beryciforme foramen. The dorsal and ventral hypohyals are well developed. The basihyal is thick, elongated and covered on all its length by a large denticled dermobasihyal with a convex surface.

The three first basibranchials are ossified and covered by a long and wide denticled dermobasibranchial, with a convex surface, and that fossilization has broken into three fragments. A posterior dermobasibranchial, corresponding to the fourth branchial arch, is also present. It is smaller, denticled, with a convex surface, and is not associated with an ossified basibranchial, the basibranchial region of the fourth and fifth arches remaining cartilaginous in Teleostei. The existence of a fourth arch dermobasibranchial is rare within Teleostei and seems to indicate a primitive

state of he branchial skeleton of these fishes, as such a bone is known for some Elopomorpha, some rare Osteoglossomorpha, as well as the Esociformes (Nelson 1968: fig. 5, 8, 1969: fig. 7a, pl. 1, fig. 3, pl. 2, fig. 1, 2, pl. 7, fig. 2).The denticled bony dermal covering of the basihyo-basibranchial region is then performed here by three distinct and articulated plates. The fragments of four right ceratobranchials and one right hypobranchial are also visible in the part of the skull which bears some bits of bone from the opercular series. Two other isolated bones pertain also to branchial complex. They consist of a left epibranchial and a pharyngobranchial. The epibranchial is short, blown at one of its ends, flattened at the other and bears a small aliforme dorsal bony expansion.

The pharyngobranchial is narrow, rather flat and covered by a careen which goes through all its dorsal face, whereas its pharyngeal face is entirely covered by tiny sharp conical denticles. This indicates that this bone is the result of the fusion of a pharyngobranchial and a dermopharyngobranchial. Judging by the size of this bone and its elongation, it is probably the third arch pharyngobranchial.

THE GIRDLES (Fig. 2)

The skull KUVP 497 (*M. brevis*) has preserved its right posttemporal. It is a large bone, long, wide and flat that fossilization has embedded between the supraoccipital and the epiotic. Nothing else is known from the scapular or pelvic girdles.

THE AXIAL SKELETON (Fig. 1, 2)

Some abdominal vertebrae are known for both species of *Martinichthys*. These vertebrae are higher than wide, with lateral faces ornamented by fine horizontal scores and a few very small alveoli. The first vertebra is even narrower than the following ones. The first vertebrae have an oval section and are a lot higher than wide. The following vertebrae acquire a more rounded section. Dorsally, the vertebrae are hollowed by two small facets in which the autogenous neural arches articulate. Ventrolaterally, one observes two other fossae which receive the autogenous haemal arches. At the abdominal level, the haemal arch is represented by a pair of hemapophyses reduced to two small spherical bones. On skull KUVP 497 (*M. brevis*), the first vertebra has remained attached to the basioccipital and still bears its autogenous neural arch. This one is composed of a pair of small bony plates attached to the exoccipitals, on both sides of the *foramen magnum*. This first neural arch is devoid of neurospine. The caudal vertebrae, the ribs, the fishbones, the neural spines, the hemal spines, the urophoric complex and the odd fins are unknown.

DISCUSSION

MARTINICHTHYS AND THE TSELFATIIFORMES

The various cranial bones with denticled regions, full of small alveoli and holes that we find in *Martinichthys* are typical of Tselfatiiformes (Hay 1903: fig. 32, 34, for example; pers. obs.). It is the same for the antorbital, supraorbital and dermosphenotic articulated between them and with the frontal and the pterotic (Loomis 1900: pl. 21, fig. 2; Steward 1900: pl. 64; Hay 1903: fig. 23; Taverne 1999c: fig. 2). The large quadrangular jointing parietals hollowed by a medial depression also constitute a character found in most of the Tselfatiiformes (Loomis 1900: pl. 21, fig. 1; Hay 1903: fig. 27; Taverne 1999c: fig. 2; pers. obs.). The complete bony interorbital septum is another typical trait of this order (Loomis 100: pl. 22, fig. 9; Hay 1903: fig. 28, 30; Taverne 1983: fig. 3, in press b: fig. 4A) even if it can be found in some other Teleostei families. Considered altogether, these characters leave no doubt concerning the membership of *Martinichthys* within the order Tselfatiiformes.

On the other hand, *Martinichthys* represents a valid genus being different from all the other Tselfatiiforme genera through at least five unique characters:

(1) narrow skull roof. In other Tselfatiiformes with a relatively flat skull roof, this one is very wide on all its length (Loomis 1900: pl. 21, fig. 1; Hay 1903: fig. 23, 27; Taverne 1999c: fig. 2).
(2) snout elongating into a rostrum formed by the vomero-mesethmoidial complex, partially covered by the vast premaxillaries more or less fused to it. No other member of Tselfatiiformes shows such a rostrum-ending snout.
(3) oral edges of premaxillaries extending in two bony, denticled, ventral aisles which rejoin on the skull medial line, thus forming a false palate. Such a false palate is unknown in all other Tselfatiiforme genera.
(4) maxillary lacking an anterior condyle. Its anterior edge remains flat but is hollowed by a narrow groove used to articulate with the posteroventral edge of the premaxillary. In most Tselfatiiformes, the premaxillary is proximally thickened to form a large condyle (Loomis 1900: pl. 21, fig. 7a, b; pers. obs.) In some evolved forms, such as *Tselfatia formosa* ARAMBOURG, 1943, the maxillary also looses its condyle and the articulation with the premaxillary must then be formed by a simple contact between the two bones through a ligamentary attach (Taverne 1983: fig. 2)
(5) medial crest lost in supraoccipital, small but present in other genera of the order.

DIAGNOSIS OF GENUS *MARTINICHTHYS* AND ITS TWO SPECIES

The present study allows to propose for *Martinichthys* a new diagnosis more complete than that given by McClung (1926): large Tselfatiiforme; elongated head with a narrow and somewhat flat skull roof; snout elongated into a more or less long rostrum, with rounded extremity, where large premaxillaries cover nearly completely the vomero-mesethmoidial complex and are more or less intimately fused to it; denticled and joined ventral faces of the premaxillaries, forming a false palate hiding the vomer; short and wide maxillary, bearing a denticled region on its internal face, along its ventral edge, and articulating with the premaxillary by a small vertical groove on its anterior edge; one small supramaxillary anteriorly articulating in a notch of the maxillary dorsal edge; big-sized lateral ethmoids; short and wide nasals, articulating with the frontals; large joined quadrangular parietals, hollowed by a medial depression; parasphenoid long and wide, with a concave and denticled ventral face; orbitosphenoid, pleurosphenoids and dorsomedial aisle of the parasphenoid forming an complete interorbital bony septum; orbitosphenoid much larger than pleurosphenoid; autogenous basisphenoid; temporal fossa opening posteriorly between the pterotic, the epiotic and the intercalar and dorsolaterally covered by the pterotic; *dilatator fossa* of small size, hollowed on the pterotic and the sphenotic; proximally wide (on the sphenotic) hyomandibular articular facet going to the limit of the sphenotic, the pterotic, the prootic and the exoccipital; supraoccipital devoid of a medial crest; basioccipital forming, alone, the neucranial condyle for the first vertebra; antorbital, supraorbital, and dermosphenotic articulating between them and with the frontal; autogenous autopalatine, very massive, and partially encapsulated by the premaxillary; small dermopalatine denticled; entopterygoid and ectopterygoid well developed, flat and denticled on all their internal faces; quadrate of equilateral triangle shape; elongated mandible but less long than the rostrum; dentary bearing a vast denticled region extending largely beyond both internal and external faces of the bone; large autogenous articular; fused retroarticular and angular; quadrate articular facet hollowed in the angulo-retroarticular and the articular; posterior opening of the mandibular sensory canal situated on the angular internal face; preopercular with short and wide ventral branch; hyomandibular wide dorsally, with a *opercularis process*, and ventrally elongated in long and thick rod; bony denticled dermal covering of the basihyo-basibranchial region formed by three long and wide plates of convex surface articulating between themselves, the dermobasihyal, the first three arches' dermobasibranchial and the fourth arch's dermobasibranchial; hyoidal bar very massive; narrow and elongated third pharyngobranchial, denticled on all its ventral surface; vertebrae higher than wide, finely

scarred on their lateral faces and dorsally and ventrolaterally hollowed by a pair of alveoli used for the articulation of the autogenous haemal and neural arches; first vertebra shorter than the following ones; first vertebrae with oval section, higher than wide, and following vertebrae with rounded sections; first neural arch devoid of neural spine, contacting the skull on both sides of the *foramen magnum*; first haemal arches reduced to hemapophyses in the form of small bony nodules.

The new diagnose for *M. brevis* becomes: *Martinichthys* with long skull; maximum height of neurocranium equals 2/5th of its length; rostrum high and short, 1½ longer than high; sutures clearly visible between the two premaxillaries and between them and the mesethmoid; orbitosphenoid contacts the massive ethmoid; *pars jugularis* long; trigeminal nerve (V) foramen hollowed between the prootic and the pleurosphenoid.

The amended diagnose for *M. ziphoides* is as follows: *Martinichthys* with a very long skull; maximum height of the neurocranium equals 1/4th of its length; rostrum long and low, 3¼ longer than high; sutures have totally disappeared between the two premaxillaries; orbitosphenoid not contacting the ethmoidal complex; *pars jugularis* short; trigeminal nerve (V) foramen in the prootic, and does not contact the pleurosphenoid.

MARTINICHTHYS WITHIN THE TSELFATIIFORMES

The phylogenetic relationships within the Tselfatiiformes have barely been studied until now. Under these conditions, it is difficult to precise the relations of *Martinichthys* with the other genera of the order.

However, it is clear that this north-American fish belongs to the main group of Tselfatiiformes with relatively flat skull roofs and large parietals, and not to the small group of more evolved forms which, like *Tselfatia formosa* ARAMBOURG, 1943, possess a highly curved skull roof along the medial line (Taverne 1983, in press a, b).

Two specialized characters present in *Martinichthys*, i.e. the large development of the premaxillaries which dorsal aisles recover the mesethmoid, as well as the well marked widening of the lingual denticled plates, favour the close relationship with two other genera of Tselfatiiformes: *Plethodus* DIXON, 1850 and *Thryptodus* LOOMIS, 1900 which also present these two evolved characters (Woodward 1899: pl. 13, fig. 1, 4; Loomis 1900: pl. 21, fig. 1, 3, 4a, b; Taverne in press b: fig. 2A, 5C). Moreover, in these two last genera, the premaxillaries show a horizontal folding of their anterior edge and recover the anterior extremity of the vomer (Loomis 1900: pl. 21, fig. 3; Taverne in press b: fig. 1), which announces the situation observed at this level in *Martinichthys*. However, *Plethodus* and *Thryptodus* differ from *Martinichthys* by the absence of a rostrum and by a branchial skeleton that has already lost the fourth dermobranchial and, in *Plethodus* alone, by the fusion in one denticled lingual plate of the dermobasihyal and the dermobasibranchials of the three first arches (Dixon 1850: pl. 32*, fig. 4; Woodward 1899: pl. 13, fig. 1, 4; Loomis 1900: pl. 21, fig. 4a, b).

On the other hand, the so peculiar rostrum of *Martinichthys* is a specialized character quite remarkable which would make this fish a rather evolved genus within the Tselfatiiformes. This is not the case. The other osteologic characters of the fossil indicate, to the contrary, that this specialization has occurred through a particularly primitive form within this order. Our fish has preserved, in fact, a plesiomorphic state for several characters, at the level of which some, if not most, of the other genera of the group show a more evolved condition:

(a) a denticled dermopalatine is present, independently from the autopalatine. This is the primitive condition in Teleostei. Some Tselfatiiformes loose the dermopalatine and only keep the autopalatine (Taverne 1983: fig. 4);

(b) the ectopterygoid is elongated, flat and completely denticled on its internal face. Again, this is a primitive state for Teleostei. Some Tselfatiiformes loose a part or the totality of the ectopterygoid denticles (Taverne 1983: fig. 4; 1999c: fig. 2);
(c) the basisphenoid is autogenous, which is the case in primitive Teleostei. In most Tselfatiiformes, there is no independent basisphenoid recovered, either this bone disappears, or it fuses with the pleurosphenoids in the interorbital bony septum (pers. obs.);
(d) the supramaxillary is articulated in a notch in the upper edge of the maxillary. In some specialized Tselfatiiformes, this articulation disappears and the supramaxillary simply borders the dorsal edge of the maxillary (Bardack 1965: fig. 2; Taverne 1983: fig. 2, in press b: fig. 3);
(e) the denticled dermal covering of the basihyo-basibranchial region is formed by three large plates, articulating with each other and with the dermobasihyal, the dermobasibranchial of the three first arches and the dermobasibranchial of the fourth arch. It is the situation found in the most archaic Tselfatiiformes (Hay 1903: fig. 21; Nelson 1973: fig. 6D; pers. obs.). In other Tselfatiiformes, there is only two plates found due to the disappearance of the fourth arch dermobasibranchial (Loomis 1900: pl. 21, fig. 4a, b, pl. 22, fig. 4a, b; pers. obs.). In some Tselfatiiformes, the evolution continues until the fusion of the dermobasihyal and the three first arches' dermobasibranchial into a single denticled lingual plate (Woodward 1899: pl. 13, fig. 1, 4, 5, 6; Taverne under press a: fig. 5, in press b: fig. 2, 5C);
(f) the hemapophyses are autogenous, which is the general case in Tselfatiiformes. In some specialized members of the order, the hemapophyses can fuse completely or partially with the corresponding vertebral centra (Taverne 1999, in press a: fig. 7, in press b: fig. 2, 4).

CONCLUSION

Martinichthys is a valid genus of Tselfatiiformes, characterized by at least five unique characters and which comprises two species: *M. brevis* with a short and thick rostrum and *M. ziphoides* with a long and narrow rostrum. The other species described in this genus, *M. acutus, M. alternatus, M. gracilis, M. intermedius* and *M. latus* are junior synonyms of *M. ziphoides*. Despite its characterized traits, *Martinichthys* also retains some primitive characters of the order, such as the presence of an autogenous basisphenoid and three denticled lingual plates. Among the Tselfatiiformes, *Martinichthys* is more particularly close to *Plethodus* and *Thryptodus*.