

Considerations about the Late Cretaceous genus *Chirocentrites* and erection of the new genus *Heckelichthys* (Teleostei, Ichthyodectiformes) - A new visit inside the ichthyodectid phylogeny

by Louis TAVERNE

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Abstract

The author describes briefly the osteology of the three valid species of the Late Cretaceous genus *Chirocentrites*. He shows that only the type species, *C. coroninii*, belongs to this genus. He creates the new genus *Heckelichthys* for the two other species, *C. microdon* and *C. vexillifer*, with the latter as type species. The phylogeny of the Ichthyodectidae is studied. The systematic position of *Chirocentrites* and *Heckelichthys* is specified.

Keywords: Teleostei, Ichthyodectidae, Late Cretaceous, *Chirocentrites*, *Heckelichthys* gen. nov., osteology, phylogeny.

Résumé

L'auteur décrit brièvement l'ostéologie des trois espèces valides du genre *Chirocentrites* d'âge Crétacé Supérieur. Il montre que seule l'espèce-type, *C. coroninii*, appartient à ce genre. Il crée le nouveau genre *Heckelichthys* pour les deux autres espèces, *C. microdon* et *C. vexillifer*, avec cette dernière comme espèce-type. La phylogénie des Ichthyodectidae est étudiée. La position systématique de *Chirocentrites* et d'*Heckelichthys* est précisée.

Mots-clefs: Teleostei, Ichthyodectidae, Crétacé Supérieur, *Chirocentrites*, *Heckelichthys* gen. nov., ostéologie, phylogénie.

Introduction

The fossil marine teleost family Ichthyodectidae ranges in age from the Late Jurassic (Oxfordian) to the Late

Cretaceous (Maastrichtian)⁽¹⁾, presenting an almost worldwide distribution. Their representatives were long-bodied, with a dorsal fin shifted backward to near the tail, opposite to the anal fin, and with a protruded lower jaw, which led to their nickname of “bull-dog” fishes (Fig. 1). These fishes, the size of which ranged from a few centimetres to almost six meters, were among the major predators within the Cretaceous marine fish communities, as shown by their frequently enlarged dentition. In the floor of the nasal fossa they possess a very peculiar endochondral bone, the latero-basal ethmoid (= ethmopalatine), not present in other teleosts, except in their osteoglossomorph close allies, the Osteoglossidae, Notopteridae and Mormyridae (TAVERNE, 1974: fig. 1, 1975b: fig. 1).

Fifteen genera are currently recognized within the Ichthyodectidae: *Saurocephalus* HARLAN, 1824, *Saurodon* HAYS, 1830, *Thrissops* AGASSIZ, 1833, *Cladocycilus* AGASSIZ, 1841 (= *Chiromystus* COPE, 1885, *Proportheus* JAEKEL, 1909, *Ennelichthys* JORDAN, 1921, *Itaparica* SILVA SANTOS, 1986), *Chirocentrites* HECKEL, 1849, *Spathodactylus* PICTET, 1858, *Ichthyodectes* COPE, 1870, *Xiphactinus* LEIDY, 1870 (= *Portheus* COPE, 1871), *Gillicus* HAY, 1898, *Eubiodectes* HAY, 1903, *Coyoo* LEES & BARTHOLOMAL, 1987, *Prosaurodon* STEWART, 1999, *Faugichthys* TAVERNE & CHANET, 2000, *Vallecillichthys* BLANCO

(1) *Gillicus*, recently found in the Lower Maastrichtian of southwest Japan (TANIMOTO & KIKYO, 2001) and *Saurodon* of the Campano-Maastrichtian of Nardò, southern Italy (TAVERNE & BRONZI, 1999) are the youngest Ichthyodectidae known to date. *Portheus dunedinensis* CHAPMAN, 1935, described from the Paleocene of New Zealand, does not seem to be an ichthyodectid. Its lower jaw is elongated, not protruded and articulated with the quadrate far behind the orbit level (CHAPMAN, 1935: fig. 1). Its shape does not correspond to an ichthyodectid lower jaw.

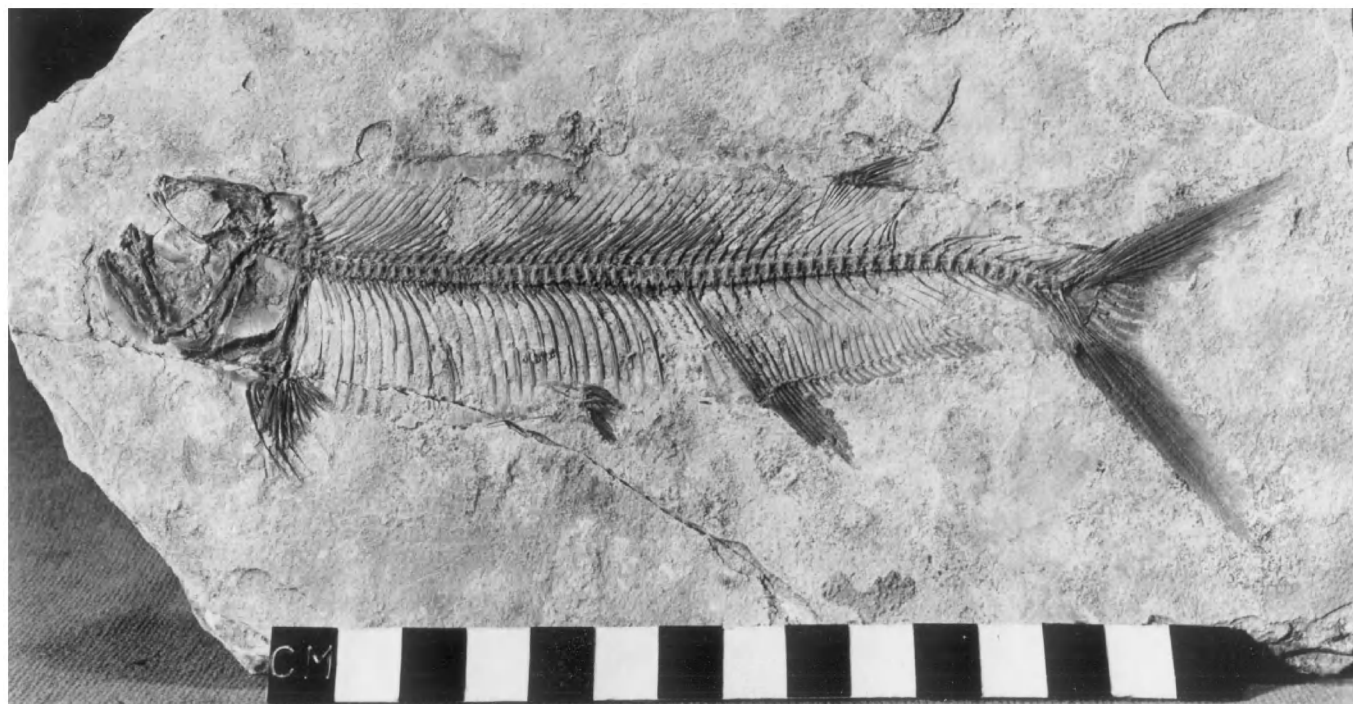


Fig. 1 – *Thrissops subovatus* VON MÜNSTER in AGASSIZ, 1844 from the Kimmeridgian (Upper Jurassic) of Bavaria. Specimen N° 1905 85 12 of the Royal Scottish Museum of Edinburgh (courtesy of the Roy. Scot. Mus. Edinb.).

& CAVIN, 2003 and *Unamichthys* ALVARADO-ORTEGA, 2004. A sixteenth genus will be erected soon by CAVIN & FOREY (in press) for the species *Ichthyodectes bardacki* CAVIN, 1997 from the Turonian of Morocco. I am personally studying new ichthyodectid genera from the Santonian of Italy and from the Aptian/Albian of West Africa. Moreover, some formerly synonymised genera are actually under revision and could be restored (P. M. BRITO, pers. com., Dec. 2007). So it is sure that the generic list of the family will be lengthened in the next future. All the ichthyodectid taxa mentioned above are of Cretaceous age, except for the Late Jurassic *Thrissops*.

The genera *Prymnetes* COPE, 1871 from the Cretaceous of Mexico, *Mesochupea* PING & YEN, 1933 from the Lower Cretaceous of China and *Chuhsiungichthys* LEW, 1974 from the Lower Cretaceous of China and Japan could be three other candidates to be included within the family Ichthyodectidae. However, their skeletons remain too poorly known to be sure of such a relationship (CHANG, 1963; BARDACK, 1965; YABUMOTO, 1994).

A few recent authors divide the classical Ichthyodectidae in several distinct families, the Unamichthyidae, the Cladocyclidae, the Saurodontidae and the Ichthyodectidae *sensu stricto* (MAISEY, 1991, among others). But some of these new families are established on a very weak basis. For instance, the only autapomorphy proposed by MAISEY (1991: 207)

for “his” Cladocyclidae (*Cladocyclus*, *Chiromystus* and *Chirocentrites*) is “supraoccipital crest overhangs occiput”. But such a situation already exists in the primitive *Thrissops* (TAVERNE, 1977: fig. 5-9) and *Unamichthys* (ALVARADO-ORTEGA, 2004: fig. 4) as well as in the advanced *Vallecillichthys* (BLANCO-PINÓN & ALVARADO-ORTEGA, 2007: fig. 3-5). As for the Unamichthyidae, they are based only on the primitive characters of *Unamichthys* (ALVARADO-ORTEGA, 2004: 803). In such conditions, it is possible to establish a particular family for practically each ichthyodectid genus.

That is why other paleontologists refuse this point of view, arguing that the osteology of the Ichthyodectidae *sensu lato* is sufficiently homogenous to range all the genera in a single family, with only a subfamilial rank for the Saurodontinae and Ichthyodectinae (TAVERNE & CHANET, 2000). That is the option followed here.

The aim of the present paper is to verify the homogeneity of one of these ichthyodectid genera, *Chirocentrites* HECKEL, 1849, by comparing briefly the skulls of the different species ranged within the genus, and to study its relationships with the other members of the family. HECKEL (1849: 17) established this genus for three new fossil fish species that he described shortly: *Chirocentrites coroninii* HECKEL, 1849, the type species, from the Cenomanian of Gorizia (north-eastern Italy, near the Slovenian border), *Chirocentrites gracilis* HECKEL, 1849 from the Cenomanian of Volzhji-Grad

(near Comen, Slovenia) and *Chirocentrites microdon* HECKEL, 1849 from the Turonian of Hvar (Lesina) island (Croatia). Shortly afterwards, HECKEL (1850: 203-213, pl. 13-17) gave a more detailed description of these three species, completed with a series of figures. Unfortunately, HECKEL's studies were essentially morphometric and devoid of a real osteological approach as demanded by modern paleoichthyological research. So the cranial skeleton of those fishes remains poorly understood till today and their caudal skeleton is completely unknown. The holotype and only complete specimen of *Ch. coroninii* ever found, as well as the holotype of *Ch. microdon*, were never restudied after HECKEL's works.

Six years later, HECKEL (1856: 245-248, pl. 2) described and figured a fourth species, *Chirocentrites vexillifer* HECKEL, 1856, from the Cenomanian of Slovenia, which he attributed to the genus. He already introduced this name one year before (HECKEL, 1855: 166), but without any description or figure (*nomen nudum*). Today, *Ch. vexillifer* is the best known of all the *Chirocentrites* species since the osteological revision made by TAVERNE (1986) and the only of which the caudal skeleton has been illustrated.

Later on, during the XIXth and XXth centuries, many other paleontologists described fossil fish fragments from Cretaceous beds in Europe and North Africa and ranged them in these four species or in new species synonymised since then with the four former ones (KNER, 1867; BASSANI, 1879, 1882; D'ERASMO, 1922, 1946; ARAMBOURG, 1954; SORBINI, 1976, etc.). These scientists generally considered *Chirocentrites* as a junior synonym of *Thrissops* AGASSIZ, 1833 and, consequently, assigned the four species to the latter. But, NYBELIN (1964) and TAVERNE (1977) showed that *Thrissops* must be restricted to Jurassic species only, and that the Cretaceous species previously referred to this genus belonged to other genera, among which *Chirocentrites*. So the valid generic status of *Chirocentrites* was restored (TAVERNE, 1986).

WEILER (1922, 1961) described incomplete ichthyodectid remains from the Aptian/Albian of Equatorial Guinea and Gabon and named them *Chirocentrites guinensis* WEILER, 1922. Nevertheless nothing in his descriptions and figures reminds of any previously known species of the genus. WEILER's specimens are characterised by big teeth with an enlarged basis, not present in any other known ichthyodectid fish (WEILER, 1961: fig. 1). MAISEY (1991: 196) suggested that this species should be referred to *Cladoclychus*, another ichthyodectid genus from the Aptian/Albian of Brazil and Italia and from the Cenomanian of Morocco.

"*Ch. guinensis* surely belongs to another genus than *Chirocentrites* but more and better-preserved material is necessary to allow a generic valuable determination.

The ichthyodectid fish body from the Albian of Pietraroia (southern Italy) studied by D'ERASMO (1915: 97-100, fig. 34-36, pl. 13, fig. 2) and referred by him to *Ch. coroninii* belongs probably also to the genus *Cladoclychus* (SIGNORE *et al.*, 2005, 2006).

Recently, CAVIN & FOREY (in press) re-examined the holotype of *Ch. gracilis*. They concluded that this species does not differ from *Ch. coroninii* and put the former in synonymy with the latter.

Spathodactylus PICTET, 1858 from the Lower Cretaceous of Les Hivernanches (Voirons), Haute-Savoie, France, is a monospecific genus known by a single badly preserved specimen of about 70 cm length. TAVERNE (1986) placed it in synonymy with *Chirocentrites* on the basis of data outlined by BARDACK (1965). That's why in some recent papers (BLANCO-PINÓN & ALVARADO-ORTEGA, 2007: 457) *Spathodactylus neocomiensis* PICTET, 1858 is cited as *Chirocentrites neocomiensis*. However, the latter possesses middle sized teeth, a dentary with a very low symphyseal border, a preopercle with a long and thin dorsal branch and a short and broad ventral branch, a lower jaw moderately prognathous and hypertrophied ventral fins reaching the anal fin (PICTET, 1858: pl. 1). It is clear that *S. neocomiensis* strongly differs from all the species ranged in *Chirocentrites*, as we shall see in the descriptions hereafter, and does not belong to this last genus. *Spathodactylus* surely is an ichthyodectid, but a revision of the holotype will be necessary for a better understanding of this taxon.

So, actually there are only three valid species in *Chirocentrites*: *Ch. coroninii*, *Ch. microdon* and *Ch. vexillifer*, and the genus is confined to the Late Cretaceous (Cenomanian and Turonian). *Ch. coroninii* is the largest of the three. Its holotype has a total length of about 70 cm. *Ch. microdon* is a little smaller with a maximum total length of about 50 cm, while, *Ch. vexillifer* is the smallest, with a total length not exceeding 25 cm.

I have personally studied in the past the specimens of *Ch. vexillifer* in the collections of the Muséum national d'Histoire naturelle de Paris (ARAMBOURG, 1954: 46) and of the Museo Civico di Storia Naturale di Verona (SORBINI, 1976: 486, erroneously determined as *Ch. microdon*). The brief descriptions of *Ch. coroninii* and *Ch. microdon* are based on the data and figures of HECKEL (1850), BASSANI (1882) and D'ERASMO (1922, 1946).

Systematic paleontology

Division Teleostei MÜLLER, 1846

Super-order Osteoglossomorpha

GREENWOOD *et al.*, 1966

Order Ichthyodectiformes BARBACK & SPRINKLE, 1969

Suborder Ichthyodectoidei ROMER, 1966

Family Ichthyodectidae CROOK, 1892

Genus *Chirocentrites* HECKEL, 1849

Type species: Chirocentrites coroninii HECKEL, 1849

***Chirocentrites coroninii* HECKEL, 1849**

Figs 2-3

The skull (Fig. 2)

The holotype of *Ch. coroninii* seems to be lost.

Fortunately, we know today very well the ichthyodectid cranial osteology (BARDACK, 1965; BARDACK & SPRINKLE, 1969; PATTERSON & ROSEN, 1977; TAVERNE, 1977, 1986; CAVIN & FOREY, in press) and the drawings of HECKEL (1850: pls 13 and 14) are precise enough to allow a good understanding of the skull and the body of this fossil fish.

The skull is short. Its depth in the occipital region is equal to 85 % of its length, opercle included, and the head length to 18 % of the standard length (SL = 60 cm). The head depth at the level of the orbit is almost the same as at the occipital level. The frontal profile is slightly convex. The neurocranium is very small in comparison with the whole skull.

The mesethmoid is slightly convex in side view. The frontal is small, not longer than the pterotic. The epiotic is large, as long as the supraoccipital and ending

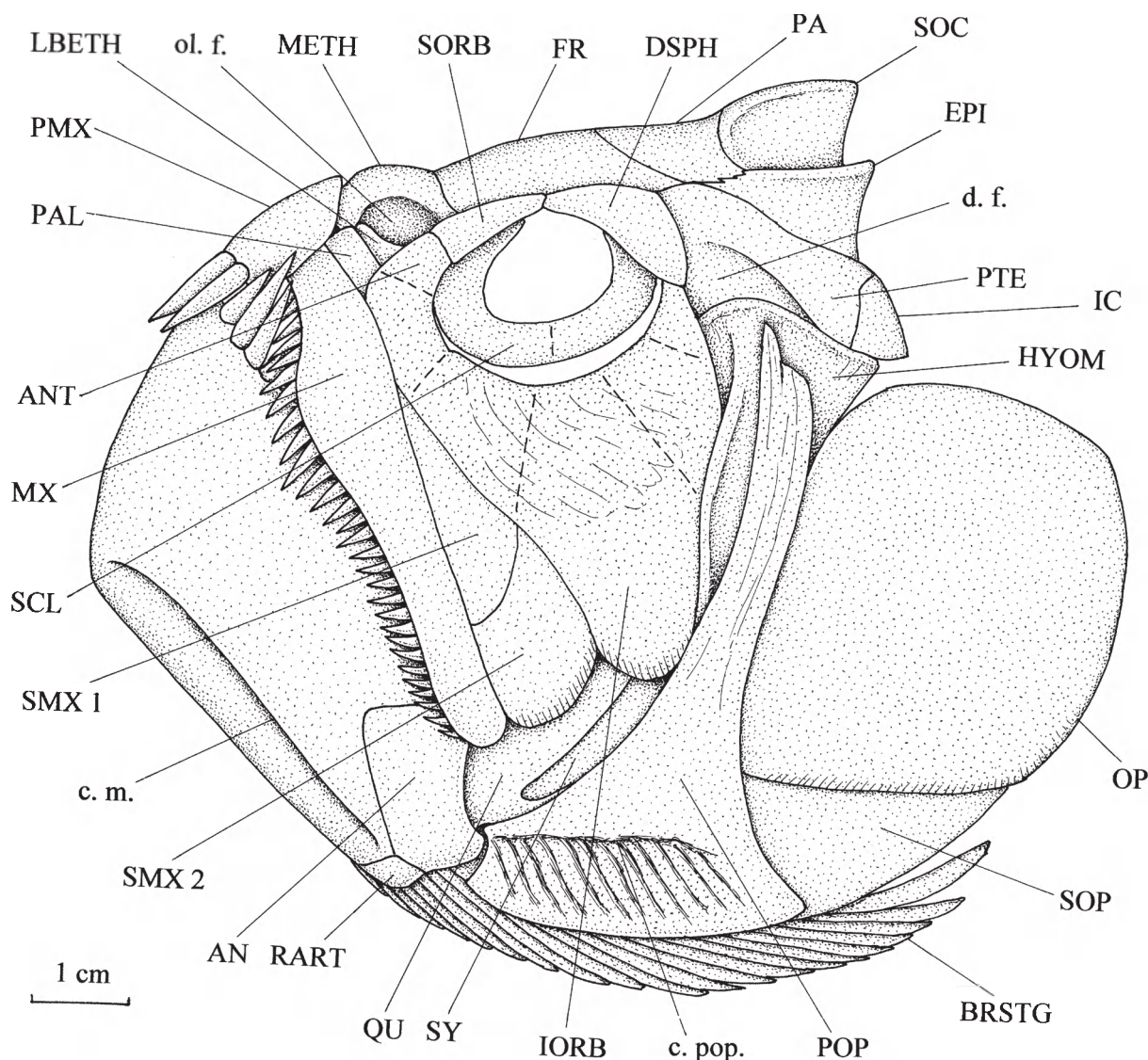


Fig. 2 – *Chirocentrites coroninii* HECKEL, 1849. Reconstruction of the skull in left lateral view based on the holotype (modified from HECKEL, 1850: pl. 13, pl. 14, fig. 1).

anteriorly at the same level with this last bone. The epiotic dorsal border forms a crest. The supraoccipital crest is well developed but rather short and does not overhang the occiput posteriorly. The *dilatator fossa* is well developed.

The upper jaw is formed by the premaxilla, maxilla and two supramaxillae. The premaxilla is higher than long. It bears two long fang-like teeth, which are anteriorly directed. The maxilla is long, not very high, rather straight and deeper anteriorly than posteriorly, except at the junction which the premaxilla where the maxillary oral border is curved inward to produce a notch between the two bones. This notch receives anterior fangs of the lower jaw. The maxilla bears a row of about 28 strong teeth, which are shorter than the two premaxillary fangs. The lower jaw is really huge, high and short, with an extremely deep symphysis and a mouth cleft strongly inclined upward. The quadrate-mandibular articulation lies at the level of the first half of the orbit. The oral border of the dentary bears a row of big teeth. The first three ones are fang-like and visible externally when the mouth is close. They insert in a notch formed by the posterior border of the premaxilla and the oral border of the maxilla. A small retroarticular is seen under the postarticular process of the angular, in a position excluding its participation to the articular fossa for the quadrate. The mandibular sensory canal is located in a long groove near the ventral border of the dentary.

The orbit is located very high on the skull and is completely surrounded by the orbital bones. The supraorbital and dermosphenotic meet each other. It is not possible to count the other orbital bones. The presence of an antorbital and five infraorbitals, as in almost all ichthyodectid fishes, is very probable. The postero-ventral infraorbital, probably the third one, is

large and extended ventrally. It covers the cheek and touches the preopercle at its mid-height. The sclerotic bone is broad.

The preopercle is elongate dorso-ventrally. Its vertical limb is long and rather thin. The ventral branch is very short but broad and bears a dozen of grooves emerging from the preopercular sensory canal. This ventral limb extends posteriorly and forms a triangular pointed process covering the anterior part of the subopercle. The interopercle is not known. The opercle is large but its ventral border does not reach the level of the preopercular ventral border. The subopercle is well developed. There are about 20 branchiostegal rays.

The posterior margin of the second supramaxilla and the ventral margins of the largest infraorbital and of the opercle are fringed.

The body (Fig. 3)

The body is elongated. In the holotype, the maximum depth, just behind the head, is equal to 21 % SL, the prepelvic length to 48 % SL, the predorsal length to 80 % SL and the preanal length to 65 % SL. The number of vertebrae is 61-64, with 33-37 abdominal and 27-28 caudal. In the holotype, there are 30 pairs of long ribs, the first one attached to the fourth vertebra. The first pectoral ray is enlarged, segmented and pointed, as in many ichthyodectid fishes, but presents no particular structure. The dorsal fin comprises 12 to 15 rays, the first five being unbranched. This fin is low and lies far back on the body. Its origin is located at the level of the 46th vertebra. The anal fin is falcate and counts 34 to 37 rays, the first four or five being unbranched. Its origin lies under the 37th vertebra. The caudal skeleton is unknown, but HECKEL's drawing (1950: pl. 13) clearly shows five long uroneurals covering the lateral faces of the last vertebrae.

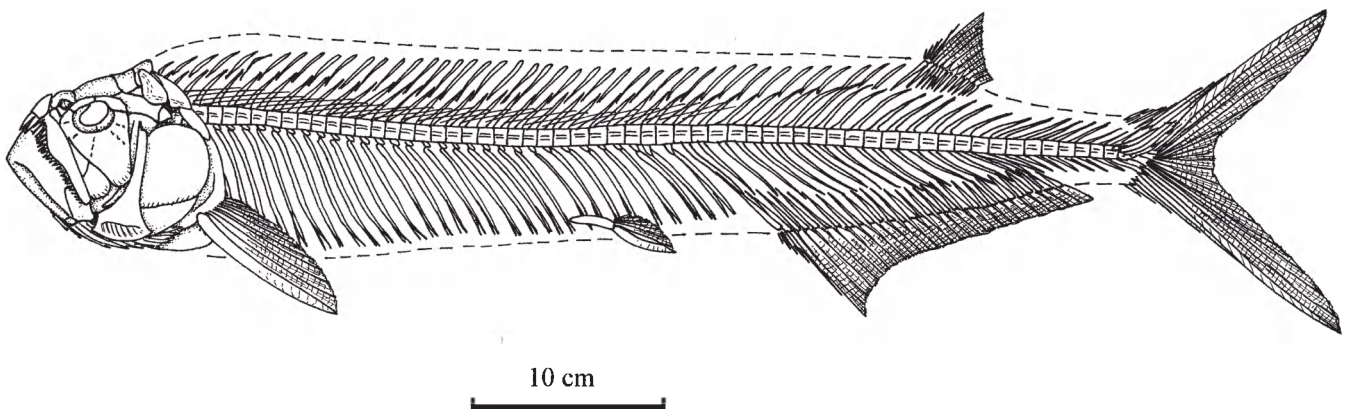


Fig. 3 – *Chirocentrites coroninii* HECKEL, 1849. Reconstruction of the complete fish based on the holotype (modified from HECKEL, 1850: pl. 13).

Chirocentrites microdon HECKEL, 1849

Figs 4-5

The skull (Fig. 4)

The neurocranium of the holotype is severely badly damaged and practically nothing can be said about it. It is broken in several fragments and some small parts are missing (HECKEL, 1850: pl. 16). Only a part of the suspensorium is useful for a description. D'ERASMO (1946: 46-47) briefly described a better preserved braincase but, unfortunately, he did not figure it. BASSANI (1882: 208-210) gave a few interesting morphometric data on two rather complete specimens.

The skull is much longer than high, with a head depth equal to 75 % of its length and a head length to 18 % SL, opercle included. The neurocranium is rather large with a frontal profile slightly concave. The skull roof comprises the usual bones, among which the frontal, the parietal, the supraoccipital, the epiotic and the pterotic, but, further details are not given, neither by HECKEL (1850) nor by D'ERASMO (1946).

Both jaws bear numerous small teeth, however those of the premaxilla and of the dentary are larger than those of the maxilla. The premaxilla is slightly curved.

The lower jaw is short and prognathous. The symphysis is not very deep. The mouth cleft is moderately inclined upward. The mandibulo-quadrato articulation is located before the orbit level. The retroarticular is unknown. The mandibular sensory canal is not enclosed in a gutter.

The orbit is completely surrounded by the ring of the orbital bones. The number of infraorbitals is unknown. The largest infraorbital (probably the second one as in *Ch. vexillifer*) covers the cheek and shows a few long tubules issued from the orbital sensory canal. This bone is lengthened antero-ventrally in a long and sharp process, which runs along the preopercle and reaches the anterior extremity of its ventral limb.

The vertical branch of the preopercle is short and rather thin. On the contrary, its ventral branch is broad, very long and supports a few secondary tubules from the preopercular sensory canal. This preopercular ventral

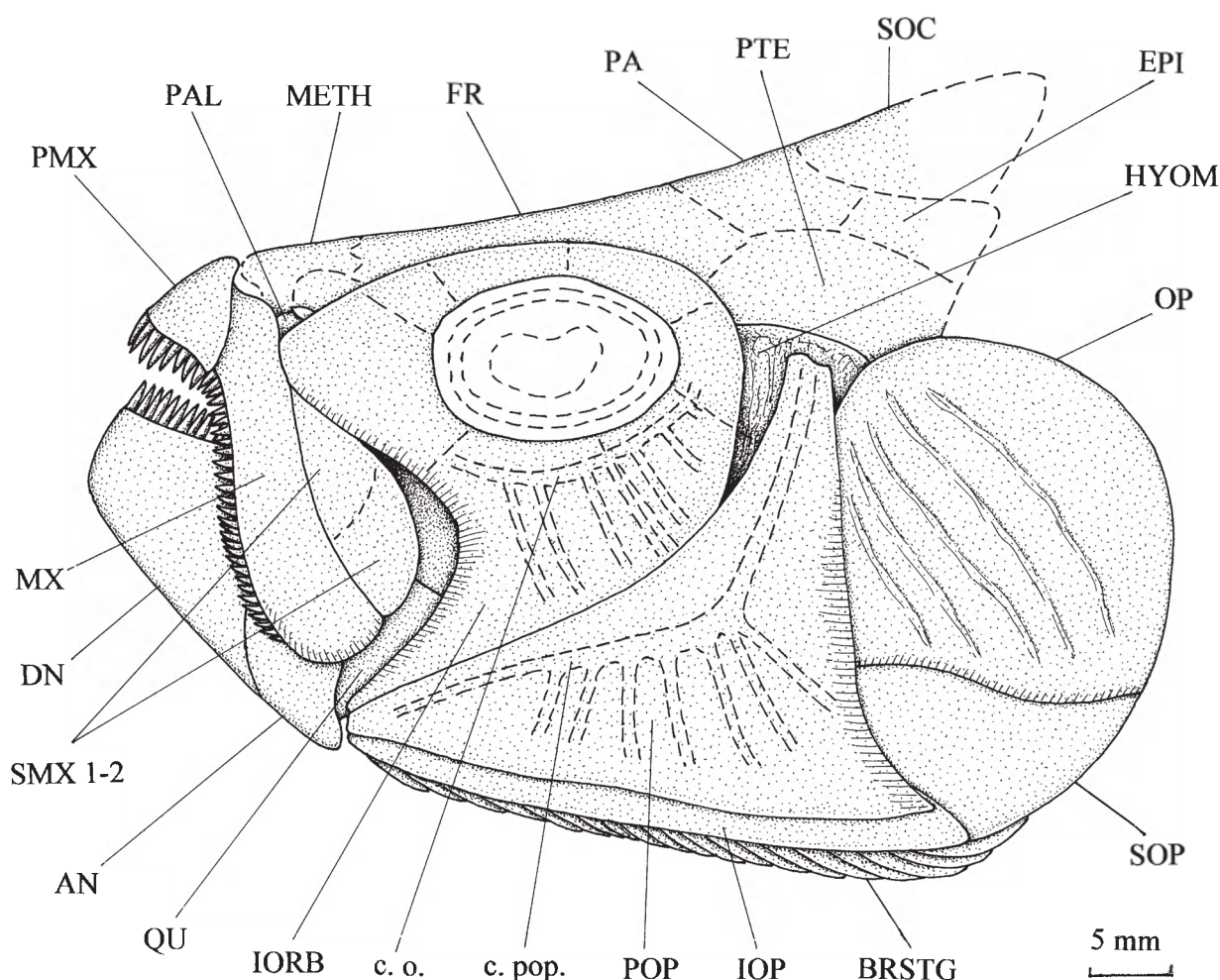


Fig. 4 – *Chirocentrites microdon* HECKEL, 1849. Reconstruction of the skull in left lateral view based on the holotype (modified from HECKEL, 1850: pl. 17, fig. a, b).

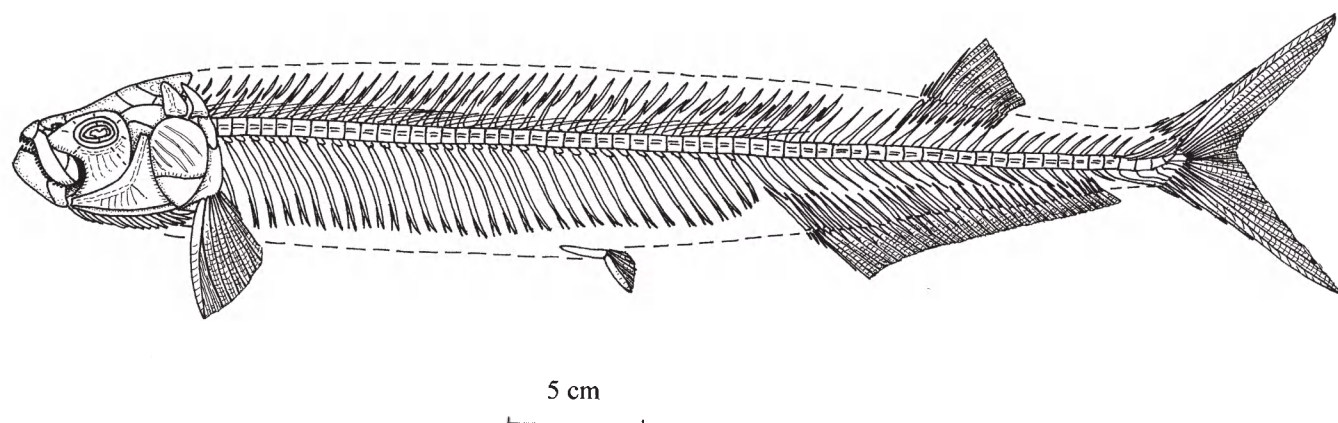


Fig. 5 – *Chirocentrites microdon* HECKEL, 1849. Reconstruction of the complete fish based on the holotype (modified from HECKEL, 1850: pl. 17, fig. g).

branch exhibits a pointed posterior process covering partly the subopercle. The opercle is of moderate size. Its ventral border is located at the preopercular mid-height level. The subopercle is well developed. The interopercle is as long as the preopercular ventral limb. There are 20 pairs of branchiostegal rays.

The posterior border of the maxilla and preopercle and the ventral border of the first infraorbitals and of the opercle are fringed.

The body (Fig. 5)

The body is elongated, with 61–62 vertebrae of which 34 are abdominal and 27–28 caudal. There are 32 pairs of ribs. The body depth is equal to 17 % SL, the prepelvic length to 47 % SL, the predorsal length to 77 % SL and the preanal length to 62 % SL.

The first pectoral ray is very enlarged, with a broad, segmented and sharp first branch and several other thin and divided branches (HECKEL, 1850: pl. 17, fig. a). The dorsal fin is low and contains 14 rays, the first four being unbranched. The anal fin shows 37 rays, the first four being unbranched.

Chirocentrites vexillifer HECKEL, 1856

Figs 6–7

The skull (Fig. 6)

The head is rather long. Its depth in the occipital region is equal to 78 % of its length but is distinctly less at the orbit level. The head length is about 20 % SL, opercle comprised. The frontal profile is slightly concave. The neurocranium is rather large in comparison with the

whole skull size.

The skull roof shows the classic ichthyodectid architecture. The parietal exhibits a small median groove. The supraoccipital crest is large, not involving the parietal, extended posteriorly and clearly overhanging the occiput. The epiotic also forms a crest on its dorsal border. Anteriorly, the epiotic does not reach the level of the supraoccipital origin. The *dilatator fossa* is not visible.

Both jaws are toothless or bear a row of small teeth. The premaxilla is small with a little dorsal process. The maxilla is slightly curved and a little broader anteriorly than posteriorly. The lower jaw is prognathous, rather short and the mouth cleft is strongly oblique. The articulation with the quadrate is located before the orbit level. The symphyseal border of the dentary is moderately deep. The mandibular sensory canal is running all along the dentary and the angular but is not enclosed in a groove. The retroarticular is unknown.

The number of infraorbitals is reduced to four. The second one is the largest; it extends antero-ventrally, covering the cheek and reaching the anterior border of the preopercular ventral branch. Other ichthyodectid fishes possess five infraorbitals and it is the third one which is the most expanded and which covers the cheek. However, some specimens of *Cladocycclus* also exhibit four infraorbitals (PATTERSON & ROSEN, 1977: fig. 2; MAISEY, 1991: fig. p. 198) but, in this case, it is also the third one, which is the largest. The sclerotic bone is very thin.

The preopercle reveals a short, slender and sharp vertical branch and a very long and broad ventral limb on which the preopercular sensory canal displays

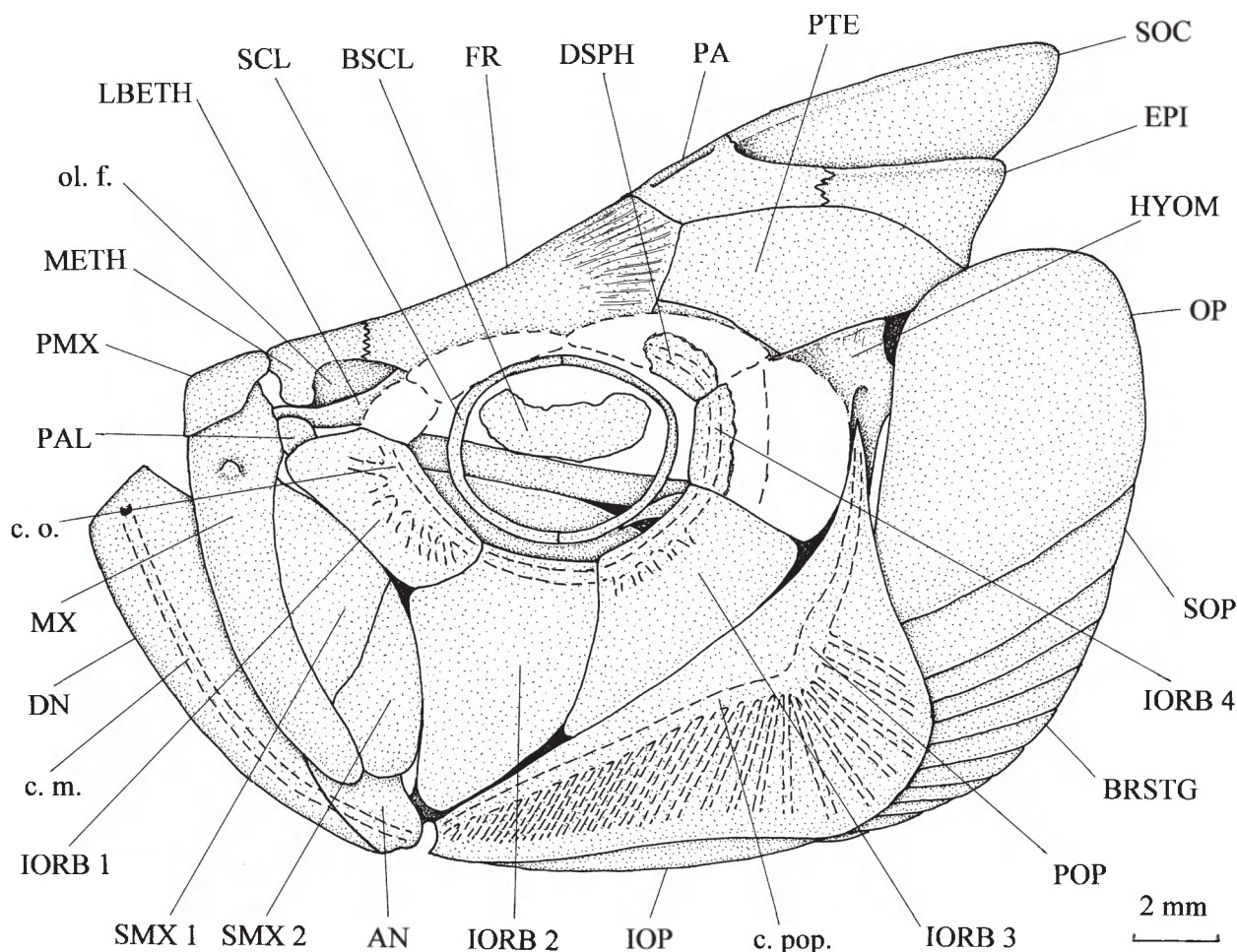


Fig. 6 – *Chirocentrites vexillifer* HECKEL, 1856. Reconstruction of the skull in left lateral view (modified from TAVERNE, 1986: fig. 2). The scale refers to the specimen T. 213 from the Mus. nat. Hist. nat. Paris.

numerous thin secondary tubules. Posteriorly, the ventral branch developed a rounded process covering the anterior part of the subopercle and of the last branchiostegal rays. The interopercle is as long as the preopercular ventral limb. The opercle and subopercle are rather small. The opercular lower border is lying at mid-height of the preopercle. The last branchiostegal rays are located behind the preopercle and just below the subopercle.

For a more detailed description of this skull see TAVERNE (1986).

The body (Fig. 7)

Ch. vexillifer is an elongated fish with a body depth of 16 to 17 % SL. The prepelvic length is equal to about 55 % SL, the predorsal length to about 70 % SL and the preanal length to about 65 % SL.

There are 62 vertebrae, of which 36 abdominal and 26 caudal, and 34 pairs of ribs. The first pectoral ray is broad, unbranched, unsegmented and there is a characteristic paddle-like widening in its distal part.

The dorsal fin is very high, higher than the anal one, and comprises 18 rays, the first four being unbranched. Its origin is located at the level of the 42^d or 43^d vertebra. There are 33 to 36 rays in the anal fin with at least the first two unbranched. Its origin lies at the level of the 39th or 40th vertebra.

The caudal skeleton is shown in TAVERNE (1986: fig. 5). There is no free epural but the first preural centrum bears a complete neural spine.

Discussion

Comparison between the three species

When comparing the cranial skeleton of the two best known species, *Ch. coroninii* and *Ch. vexillifer*, we observe that they completely differ from each other, not only in the general shape of the skull but also in the particular shape of almost all the head bones, as shown in Table 1.

It is clear that the differences between the two

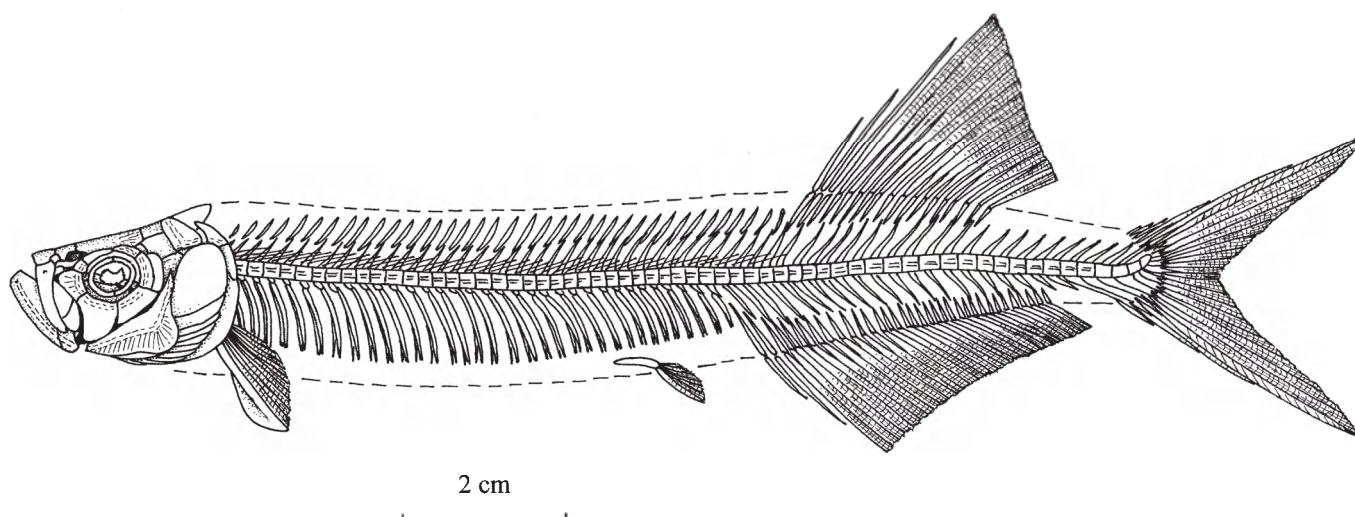


Fig. 7 – *Chirocentrites vexillifer* HECKEL, 1856. Reconstruction of the complete fish (modified from TAVERNE, 1986: fig. 1). The scale refers to the specimen T. 213 from the Mus. nat. Hist. nat. Paris.

species are too numerous and too important to maintain their placement in a same genus. Since *Ch. coroninii* is the type species of *Chirocentrites*, it is necessary to establish a new genus for *Ch. vexillifer*.

A comparison between *Ch. microdon* and the two other species reveals the same differences with *Ch. coroninii* but, on the contrary, close affinities with *Ch. vexillifer*. Indeed both species exhibit a rather elongate head, a slightly concave frontal profile, small teeth when the jaws are toothed, a slightly curved maxilla,

a short lower jaw with a moderately deep symphyseal border, a mandibulo-quadrato articulation placed before the orbit level and a rather small opercle. They also share two unique characters within the Ichthyodectidae. The ventral branch of the preopercle is much longer than the dorsal limb, whereas the other members of this family possess a preopercular ventral limb shorter and often much shorter than the dorsal branch. The largest infraorbital extends antero-ventrally as far as to reach the anterior extremity of the long preopercular ventral

Skull features	<i>Ch. coroninii</i>	<i>Ch. vexillifer</i>
Skull	short	elongated
Frontal profile	slightly convex	slightly concave
Braincase	small	large
Supraoccipital crest	short	long
Premaxillary teeth	large fangs	small or lost
Maxillary teeth	large	small or lost
Dentary teeth	anterior fang-sized, posterior large	small or lost
Lower jaw	huge	normal
Symphysis	very deep	moderately deep
Lower jaw/quadrato	beneath the first half of the orbit	before the orbit
Mandibular sensory canal	in a groove	not in a groove
Orbit	near the top of the skull	at mid-height of the skull
Preopercular ventral limb	short	very elongated
Sclerotic ring bones	broad	thin
Largest infraorbital reaching preopercle	at mid-height	at anterior end of ventral limb

Table 1 – Differences between the cranial skeletons of *Chirocentrites coroninii* and *Ch. vexillifer*.

limb. That is a completely unusual situation within Ichthyodectidae. Normally the largest infraorbital contacts the preopercle at the level of its vertical branch.

Ch. microdon and *Ch. vexillifer* clearly belong to the same genus, which is different from the true *Chirocentrites*.

Emended diagnosis of Chirocentrites HECKEL, 1849

The emended diagnosis of *Chirocentrites* is: Ichthyodectid of median size (up to 70 cm of maximum total length). Head short, its depth equal to 85 % of its length. Small neurocranium. Frontal profile slightly convex. Short supraoccipital crest not overhanging the occiput. Epitotic ending anteriorly at the same level with the supraoccipital. Jaws with large teeth. Two fang-like teeth on the premaxilla. First three teeth of the dentary fang-like and located in a notch between the premaxilla and the maxilla. Maxilla straight with a deepening at the first third of the oral border. Huge lower jaw, with a very deep symphyseal border. Mouth cleft strongly inclined upward. Lower jaw articulated with the quadrate at the level of the first half of the orbit. Mandibular sensory canal located in a groove on the dentary. The largest infraorbital contacted the preopercle at its mid-height. Preopercle with a short and broad ventral branch and a long and thin dorsal branch. Preopercular ventral branch with a pointed posterior process. Opercle large. Body elongated, with 61-64 vertebrae (33-37 abdominal and 27-28 caudal). Dorsal fin with 12 to 15 rays. Anal fin with 34 to 37 rays.

Erection and diagnosis of Heckelichthys gen. nov.

The new genus *Heckelichthys* is erected here to contain the two species *Chirocentrites microdon* and *Ch. vexillifer*. This last species, more completely known than *Ch. microdon*, is chosen as the type species of this new genus.

The diagnosis of *Heckelichthys* is as follows: ichthyodectid of small to median size (25 to 50 cm of total length). Head elongated, its depth equal to 75-78 % of its length. Large neurocranium. Frontal profile slightly concave. Long supraoccipital crest overhanging the occiput. Epitotic not reaching anteriorly the level of the origin of supraoccipital. Jaws with small teeth or toothless. Maxilla slightly curved. Short lower jaw, with a moderately deep symphyseal border. Lower jaw articulated with the quadrate before the orbit level. Mandibular sensory canal not located in a groove. The largest infraorbital covering the cheek and extending antero-ventrally to reach the anterior extremity of the preopercle. Ventral branch of the preopercle longer

than the dorsal branch. Dorsal branch of the preopercle thin. Opercle small to moderate sized, with its lower border terminating far from the preopercular ventral border. Body elongated with 61 to 62 vertebrae (34 to 36 abdominal and 26 to 28 caudal). Dorsal fin with 14 to 18 rays. Anal fin with 33 to 37 rays. A complete neural spine on the first preural vertebra.

The two species *H. microdon* and *H. vexillifer* are easily separable from each other. In *H. microdon* small teeth are present, the largest infraorbital exhibits a long and sharp antero-ventral expansion, the preopercle shows only a few secondary sensory tubules, the subopercle is normally developed, the branchiostegal rays lie under the preopercle, interopercle and subopercle, and the dorsal is low, with 14 rays. On the other hand, in *H. vexillifer* sometimes teeth are absent, the largest infraorbital offers a rounded antero-ventral expansion, the secondary sensory tubules on the preopercle are numerous, the subopercle is reduced, the last branchiostegal rays are located behind the preopercle, and the dorsal fin is very deep, with 18 rays. Moreover, *H. vexillifer* also possesses slightly longer maxilla and lower jaw than *H. microdon*.

Chirocentrites and Heckelichthys in the ichthyodectid phylogeny (Fig. 8)

A few authors have already studied the ichthyodectid phylogeny, some during the precladistic years (DE SAINT-SEINE, 1949; BARDACK, 1965), others with a cladistic method (TAVERNE, 1986; MAISEY, 1991; STEWART, 1999; TAVERNE & CHANET, 2000; ALVARADO-ORTEGA, 2004; BLANCO-PINÓN & ALVARADO-ORTEGA, 2007; CAVIN & FOREY, in press). Some divergences occur in the proposed phylogenetic trees. It is true that a cladogram concerning fossil fishes is only the translation of our osteological knowledge of these fossil taxa at a given moment and of our understanding of their evolution. New discoveries sometimes lead to change of point of view. The phylogeny proposed hereafter is based upon my most recent observations on the Ichthyodectidae and includes both the revised *Chirocentrites* and the new *Heckelichthys*.

If we chose the Upper Jurassic ichthyodectiform *Allothrissops* NYBELIN, 1964 (suborder Allothrissopoidei, family Allothrissopidae) as outgroup, we see that the Upper Jurassic *Thrissops*, the most primitive ichthyodectid genus, exhibits many new specialized characters (NYBELIN, 1964; TAVERNE, 1977; PATTERSON & ROSEN, 1977; CAVIN & FOREY, in press).

- (1) The head is higher and shorter.
- (2) The lower jaw is prognathous.

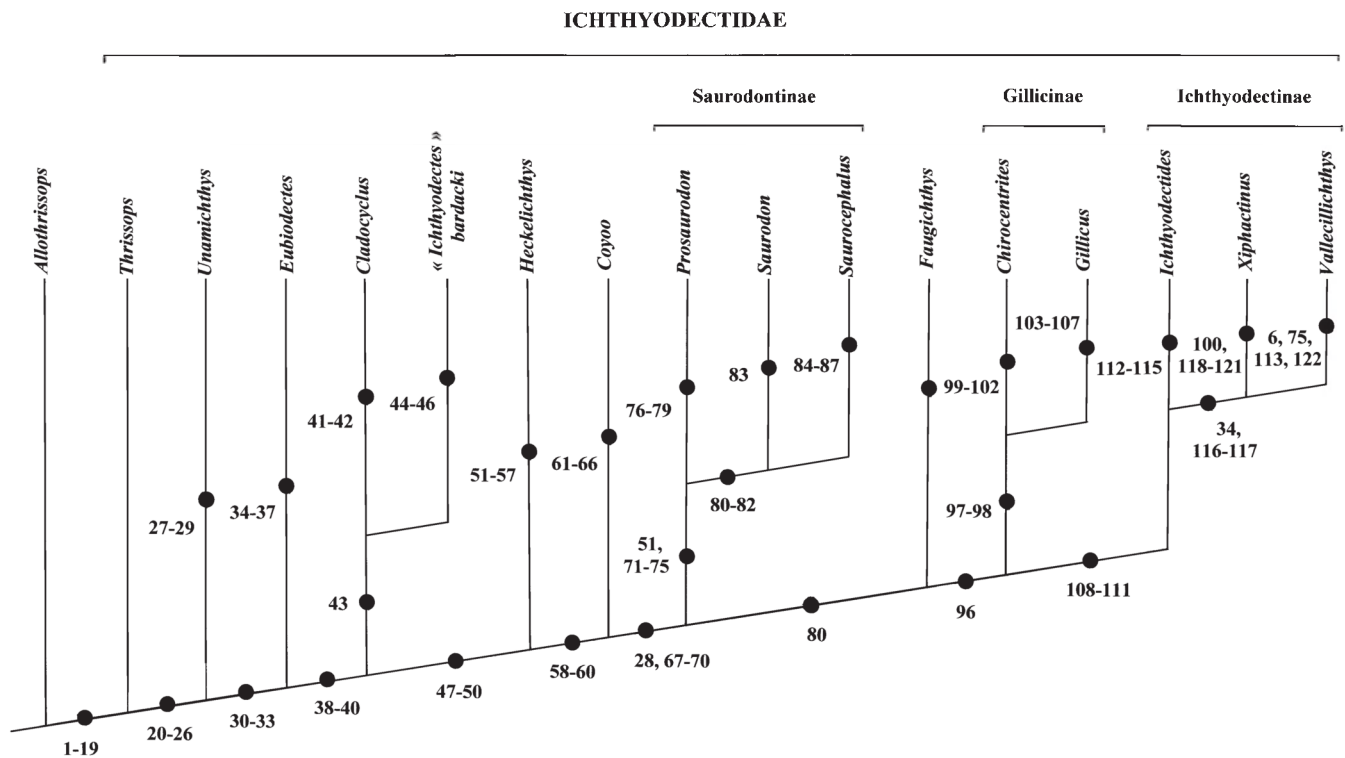


Fig. 8 – Phylogeny of the Ichthyodectidae. The numbers refers to the characters discussed in the text.

- (3) The latero-basal ethmoid (= ethmopalatine) is well developed and ossified.
 - (4) The long antero-ventral process of the lateral ethmoid is lost. Characters (3) and (4) are linked. The latero-basal ethmoid takes partially the place of this process in the Ichthyodectidae.
 - (5) There is a basal sclerotic bone in addition to the sclerotic ring.
 - (6) The supraoccipital crest is large, triangular and overhangs the occiput.
 - (7) The parietals are displaced forward above the posterior margin of the orbit.
 - (8) The epiotic (= epioccipital) is larger and develops a crest along its dorsal border.
 - (9) The enlarged intercalar is a part of the neurocranial hyomandibular facet and of the margin of the posttemporal fossa. It forms an osseous bridge with the prootic over the subtemporal fossa and encloses a small portion of the jugular vein.
 - (10) The antorbital is larger.
 - (11) The third infraorbital is considerably wider. It covers the cheek and reaches the preopercle.
 - (12) The jaws bear large teeth.
 - (13) The premaxilla shortens.
 - (14) The lower jaw is no more leptolepid-shaped and the fossae on the external face of the dentary are lost.
 - (15) The coronoid process on the dentary is located near the posterior end of the lower jaw.
 - (16) The preopercular ventral branch is shorter.
 - (17) The ventral preopercular process of the hyomandibula is lost. A small process exists in a *Thrissops* sp. from the Kimmeridgian of England (CAVIN & FOREY, in press).
 - (18) The first pectoral and ventral rays are moderately enlarged and sabre-shaped.
 - (19) The *radii* are numerous on all the surface of the scales (SCHULTZE, 1966: fig. 2a, b; TAVERNE, 1977: fig. 16). In *Allothrissops*, the *radii* are uncommon (SCHULTZE, 1966: fig. 17).
- Within the family, *Thrissops* is defined by its plesiomorphies rather than by real autapomorphies.
- Unamichthys* shares with the remaining ichthyodectid genera some new advanced characters (ALVARADO-ORTEGA, 2004).
- (20) The anterior end of the maxilla is distinctly broader, allowing a stronger articulation with the premaxilla.
 - (21) The symphyseal border of the dentary is deeper.
 - (22) The angular participates in the articular fossa for the quadrate. This bone is not a component of the fossa in *Allothrissops* (PATTERSON & ROSEN, 1977: 101). The situation in *Thrissops* is unknown.
 - (23) The anterior process of the first dorsal pterygiophore is lost.

- (24) There are only five pairs of uroneurals *versus* six in *Thrissops* (TAVERNE, 1977: fig. 14; PATTERSON & ROSEN, 1977: fig. 14) and six or seven in *Allothrissops* (TAVERNE, 1975a: fig. 14, 15; PATTERSON & ROSEN, 1977: fig. 17, 18). However *Cladocycilus*, a genus more evolved than *Unamichthys*, still retains six uroneurals (ibid., 1977: fig. 19). But its caudal skeleton is known in only one specimen. So that could be due to an exceptional individual variation.
- (25) The first uroneural does not get ahead of the third preural vertebra *versus* the fourth in *Thrissops*.
- (26) The urodermals are lost.

Unamichthys presents three autapomorphies.

- (27) There are some areas with overlapping teeth in the tooth row on the maxilla and the dentary.
- (28) The retroarticular is excluded from the articular facet for the quadrate. This character also exists in the most advanced Ichthyodectidae. In *Thrissops* (CAVIN & FOREY, in press) and *Allothrissops* (PATTERSON & ROSEN, 1977: fig. 8A) the retroarticular is part of the facet. That is also the case in the more advanced *Cladocycilus* (ibid., 1977: fig. 8B, C). On the other hand the retroarticular is not known in *Eubiodectes*, *Heckelichthys*, *Coyoo* and *Faugichthys*. So another interpretation of this character is possible. Instead of being an autapomorphy of the primitive *Unamichthys* that rises again in the most evolved ichthyodectid genera, it could be an apomorphy of all the Ichthyodectidae more specialized than *Thrissops* (ALVARADO-ORTEGA, 2004: 809). The case of *Cladocycilus* could be then an autapomorphic reversal to the plesiomorphic situation existing in *Allothrissops* and *Thrissops*.
- (29) The number of vertebrae increases till 78 to 80. There are only 53 to 63 vertebrae in *Allothrissops* and *Thrissops*. Such a considerable increasing of the number of centra also occurs, but independently acquired, in the most advanced ichthyodectids (*Saurodon*, *Xiphactinus*, *Ichthyodectes* and *Vallecillichthys*).

Eubiodectes (PATTERSON & ROSEN, 1977; CAVIN & FOREY, in press) and more apomorphous genera show new specialized characters.

- (30) The parietals fuse in a median bone.
- (31) The first pectoral ray is still widened, becoming more than two times broader than the second ray.
- (32) There are only two epurals instead of three in *Allothrissops*, *Thrissops* and *Unamichthys*.

- (33) The articular heads of the first and second hypurals are seated in two deep sockets in the ventral face of the first ural vertebra. In *Allothrissops* and *Thrissops* there are only two shallow fossae (CAVIN & FOREY, in press). The situation of *Unamichthys* is unknown (ALVARADO-ORTEGA, 2004: 806).

Eubiodectes is characterized by at least four autapomorphies.

- (34) The latero-basal ethmoid is reduced to its ventral articular part and does not reach the frontal dorsally.
- (35) The epurals are shortened. They are long in *Thrissops*, *Unamichthys* and in the more advanced *Cladocycilus* (TAVERNE, 1977: fig. 15; PATTERSON & ROSEN, 1977: fig. 13, 19; ALVARADO-ORTEGA, 2004: fig. 7).
- (36) The second hypural is very slender.
- (37) The ventral lobe of the caudal fin is much longer than the dorsal one.

Cladocycilus (PATTERSON & ROSEN, 1977; MAISEY, 1991; CASTRO LEAL & BRITO, 2004; FOREY & CAVIN, 2007) and more advanced Ichthyodectidae exhibit new apomorphies.

- (38) The articular head of the palatine is modified into a flat disk articulated ventrally with the maxilla and dorsally with the latero-basal ethmoid (SIGNORE *et al.*, 2006: fig. 2; pers. observ.). In *Thrissops*, *Unamichthys* and *Eubiodectes* the palatine head is not disk-like but rather irregular in shape. Its dorsal articular facet for the latero-basal ethmoid is located more anteriorly than its ventral facet for the maxilla (Fig. 9; TAVERNE, 1977: fig. 6-8; ALVARADO-ORTEGA, 2004: fig. 3B; CAVIN & FOREY, in press: fig. 6, 11, 32).
- (39) There is only one epural.
- (40) The scales possess *radii* only on their anterior field and *punctae* appear on the circuli in the posterior half (JORDAN & BRANNER, 1908: fig. 19). In *Thrissops* and the most primitive genera, the *radii* extend on the whole scale and the *punctae* are restricted to the centre (SCHULTZE, 1966: fig. 2a, b; TAVERNE, 1977: fig. 16).

Cladocycilus shows at least two autapomorphies.

- (41) There is a fenestra between the mesethmoid and the two frontals.
- (42) The ventral part of the latero-basal ethmoid considerably widens and extends below the lateral ethmoid (PATTERSON & ROSEN, 1977: fig. 6A; FOREY & CAVIN, 2007: fig. 4).

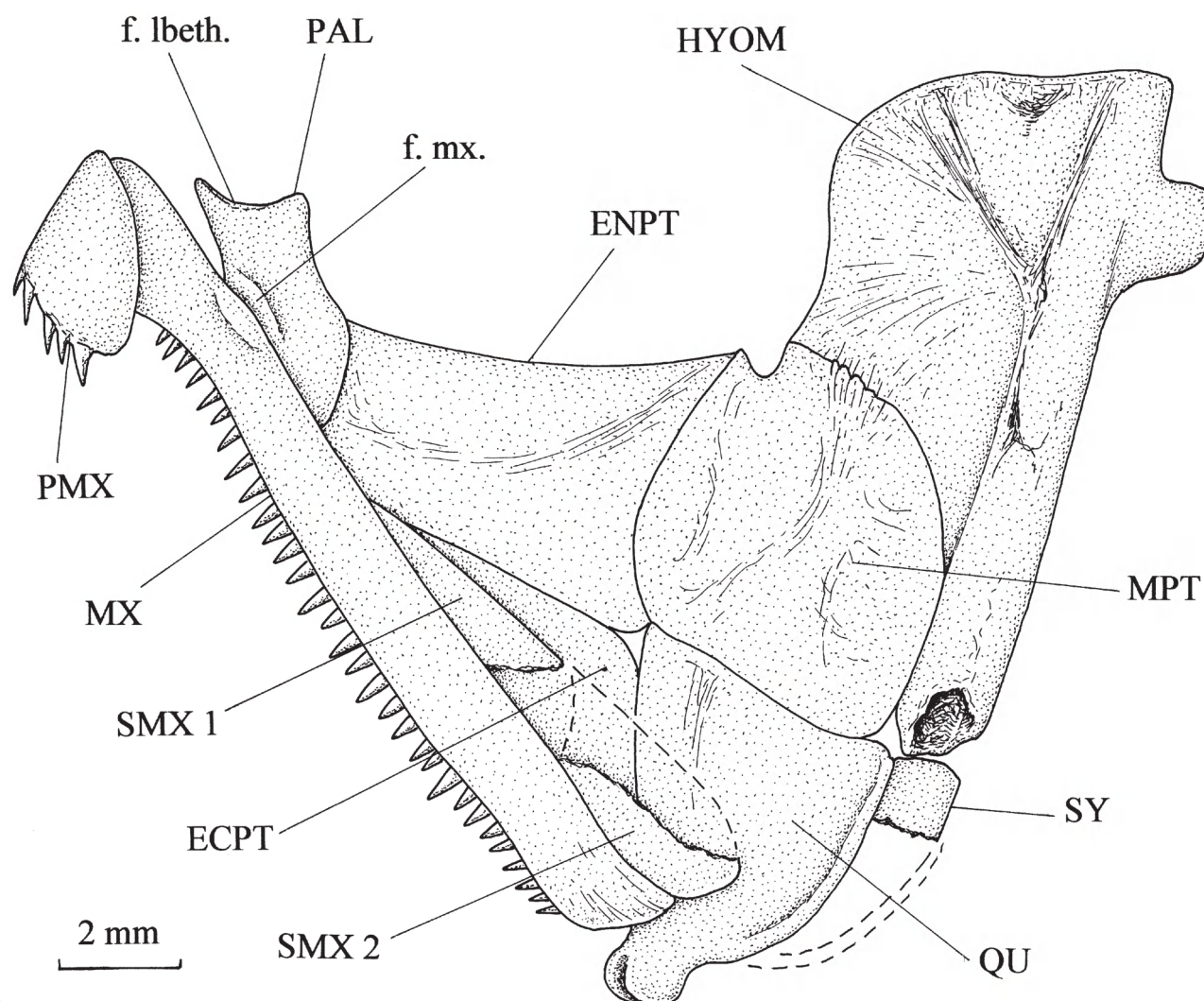


Fig. 9 – *Thrissops subovatus* VON MÜNSTER in AGASSIZ, 1844. The suspensorium of the specimen N° 1905 85 12 (Roy. Scott. Mus. Edinb.) showing the irregular shape of the palatine head and the anterior position of the articular facet for the latero-basal ethmoid in relation to the position of the articular facet for the maxilla.

A few badly preserved specimens of “*Ichthyodectes*” *bardacki* CAVIN, 1997 are known from the Turonian of Morocco (CAVIN, 1997a, b). It does not belong to the genus *Ichthyodectes* and a new generic taxon will be erected soon for this species (CAVIN & FOREY, in press). It shows a flat disk-like head on the palatine (character 38) and is thus more advanced than *Eubiodectes*. Its preopercle possesses a ventral limb shorter than the dorsal one but as long as in *Unamichthys*, *Eubiodectes* or *Cladocycilus*. It is thus less specialized than *Coyoo* and more apomorphous ichthyodectid genera (character 60: important shortening of the preopercular ventral branch). It exhibits a small neural arch but no neural spine on the first preural vertebra and is thus plesiomorphic in regard to *Heckelichthys* (character 49: full neural spine on the first preural centrum). Those characters place “*Ichthyodectes*” *bardacki* at the same level as *Cladocycilus* in my cladogram. Unfortunately

the epurals and the scales of “*I.*” *bardacki* are not known and a comparison with the situation in *Cladocycilus* for those two anatomical data is thus not possible. Both fishes seem closely related and even share at least one particular derived character.

(43) The posttemporal is huge and deeper than long (SILVA SANTOS, 1950: pl. 3, fig. 1; CAVIN & FOREY, in press: fig. 22A).

However, “*I.*” *bardacki* presents enough autapomorphies to allow its differentiation from *Cladocycilus*.

(44) The teeth on the dentary are small *versus* large in *Cladocycilus* (PATTERSON & ROSEN, 1977: fig. 1-3, 8C).

(45) The supratemporal is elongated and ovoid *versus* triangular in *Cladocycilus* (ibid., 1977: fig. 1).

(46) The opercle is large but also very elongated *versus*

large and deeper than long in *Cladocycilus* (ibid., 1977: fig. 1-3).

Heckelichthys (TAVERNE, 1986; this paper) and more specialized ichthyodectids share four more advanced characters.

- (47) The pit-lines on the parietal disappear.
- (48) The articular head of the palatine is still disk-like but grows thicker and is hammer-shaped.
- (49) The first preural vertebra bears a complete neural spine.
- (50) There is no free epural. Characters (49) and (50) probably are linked. Indeed the full neural spine on the first preural centrum probably results from the capture of the last epural by the neural arch of this vertebra.

Heckelichthys possesses a few autapomorphies.

- (51) The skull is elongated.
- (52) The frontal profile is slightly concave
- (53) The teeth are minute or completely lost.
- (54) The articulation between the lower jaw and the quadrate is located before the orbital level.
- (55) The preopercular ventral branch is longer than the dorsal one which is short and narrow.
- (56) The opercle is small or moderately sized.
- (57) The largest infraorbital (which is the second one in *H. vexillifer* and perhaps also in *H. microdon*) extends antero-ventrally and reaches the anterior extremity of the elongated ventral limb of the preopercle.

Coyoo (LEES & BARTHOLOMAI, 1987) and the remaining members of the family present three new apomorphies.

- (58) The supraoccipital crest is still very large but it does no more overhang the occiput.
- (59) The premaxillary deepens; it is rhomboid or ellipsoid in shape and develops small to large antero-ventrally directed fangs.
- (60) The broad preopercular ventral arm considerably shortens.

Coyoo exhibits a few autapomorphies.

- (61) The frontal bears a prominent sagittal ridge and a triangular shelf midway along its lateral margin.
- (62) The subepiotic fossa is greatly enlarged and deepened.
- (63) The intercalar is hypertrophied.
- (64) The entopterygoid becomes narrower.
- (65) The dorsal limb of the preopercle strongly widens in its superior extremity, becoming nearly as broad

as the ventral part of the bone.

- (66) The opercle is huge and the subopercle is not visible or lost.

The subfamily Saurodontinae includes three ichthyodectid genera, *Prosaurodon*, *Saurocephalus* and *Saurodon*. They share some new apomorphies with the more advanced Ichthyodectidae.

- (67) The anterior extremity of the maxilla considerably deepens and becomes by far the broader part of the bone (STEWART, 1900: pl. 48, fig. 1a, b, pl. 55, pl. 56, fig. 1; BARDACK, 1965: fig. 9, 16; BLANCO-PINÓN & ALVARADO-ORTEGA, 2007: fig. 3; among others). This character is still more developed in the Saurodontinae than in other advanced ichthyodectid fishes.
- (68) The parietal is more or less involved in the beginning of the supraoccipital crest.
- (69) The otic part of the parasphenoid lengthens and reaches almost or completely the posterior end of the braincase (BARDACK, 1965: fig. 6, 14, 17; BARDACK & SPRINKLE, 1969: 3).
- (28) The retroarticular is excluded from the articular fossa for the quadrate (NELSON, 1973: fig. 3A, B, C, 6A; among others). We have already met this character in *Unamichthys* (see my previous comments).
- (70) There are only seven hypurals. This number occurs in *Saurodon* (TAVERNE, 1997: fig. 5), *Xiphactinus*, *Ichthyodectes* and *Gillicus* (CAVENDER, 1966: fig. 1). *Allothrissops* and *Cladocycilus* still possess eight hypurals (TAVERNE, 1975a: fig. 14; PATTERSON & ROSEN, 1977: fig. 17-19). The number of hypurals is unknown in *Heckelichthys* and *Coyoo*. So it is possible that this reduction appears sooner in the ichthyodectid evolution.

The Saurodontinae (STEWART, 1900; LOOMIS, 1900; BARDACK & SPRINKLE, 1969; TAVERNE, 1997; TAVERNE & BRONZI, 1999; STEWART, 1999) are characterized by some autapomorphies.

- (51) The skull is low and elongated, a character that also exists in *Heckelichthys* but independently acquired. This cranial shape induces a moderate lengthening of the preopercular lower limb in some species (BARDACK & SPRINKLE, 1969: fig. 5; STEWART, 1999: fig. 5, 6) but not in all (TAVERNE & BRONZI, 1999: fig. 3).
- (71) The mesethmoid is very large.
- (72) The nasal fossa is flattened.
- (73) The lower jaw is much longer than the upper one.
- (74) There is an untoothed predentary before the

dentary.

- (75) The body is much elongated and there is a considerable increasing in the number of vertebrae (between 99 to 119 in *Saurodon*). No complete axial skeleton is known in *Prosaurodon* and *Saurocephalus*. However their long and low skull suggests that they were also long-bodied fishes. An increasing in the number of vertebrae also occurs in *Unamichthys* (character 29) but its body is not particularly elongated (ALVARADO-ORTEGA, 2004: fig. 1).

Prosaurodon presents a few autapomorphies.

- (76) The prementary is in shape of a right triangle, which forms a marked angle with the oral border of the dentary.
- (77) The first supramaxilla is huge and deeper than the second one.
- (78) The second supramaxilla is very short and its anterior ventral arm extends farther forward than its dorsal arm.
- (79) The small anterior teeth of the dentary are inclined slightly backward, whereas the posterior teeth are a little bigger and inclined forward.

Saurocephalus and *Saurodon* differ from *Prosaurodon* by several new apomorphies.

- (80) The dorsal part of the supraoccipital lengthens and narrows (BARDACK & SPRINKLE, 1969: fig. 2). *Prosaurodon* keeps a short and broad supraoccipital (STEWART, 1999: fig. 7).
- (81) The dorsal part of the epiotic narrows but does not reach anteriorly the same level with the supraoccipital (BARDACK & SPRINKLE, 1969: fig. 2). In *Prosaurodon* the epiotic is short and wide (STEWART, 1999: fig. 7).
- (82) There is a notch beneath the teeth on the internal face of both jaws.

Saurodon is characterized by one autapomorphy.

- (83) The prementary is in shape of a long isosceles triangle (STEWART, 1900: pl. 55, 56, fig. 1; BARDACK & SPRINKLE, 1969: fig. 5).

Saurocephalus differs from *Saurodon* by at least four autapomorphies.

- (84) The prementary is in shape of a short equilateral triangle (LOOMIS, 1900: pl. 45, fig. 4; BARDACK & SPRINKLE, 1969: fig. 1A).
- (85) The prementary and the dentaries are articulated by four pairs of raised facets (ibid., 1969: fig. 1B, C).
- (86) The two dentaries are articulated together at the

symphysis by a series of short prongs and shallow grooves (ibid., 1969: fig. 1C).

- (87) The notches beneath the teeth become deeper and form foramina within the bone (LOOMIS, 1900: pl. 25, fig. 2, 3).

Faugichthys is known by only one partial braincase from the Albien of France (TAVERNE & CHANET, 2000). So its systematic position within the family is difficult to establish because many important osteological data are missing. However, it seems clear that *Faugichthys* shares at least one apomorphy with more specialized Ichthyodectidae.

- (80) The dorsal part of the supraoccipital lengthens and narrows (ibid., 2000: fig. 1). Two Saurodontinae, *Saurodon* and *Saurocephalus*, also exhibit this character but independently acquired since it does not exist in their plesiomorphic sister-taxon *Prosaurodon*.

Faugichthys is easily defined by its numerous autapomorphies.

- (88) The parietal is hypertrophied and elongated enough to reach the ethmoid region and to separate the two frontals.
- (89) The orbitosphenoid reaches the lateral ethmoid.
- (90) The basisphenoid is enlarged, located beneath the pleurosphenoids and separated from the prootics.
- (91) The sphenotic is completely hidden by the frontal in dorsal view.
- (92) The subtemporal fossa is lost.
- (93) The subepiotic fossa is lost.
- (94) The intercalar is reduced and does not participate in the articular fossa for the hyomandibula.
- (95) The basioccipital is strongly backward protruded.

The remaining ichthyodectid genera offer one more advanced character.

- (96) The dorsal part of the epiotic narrows and lengthens to almost the same level with the anterior end of the supraoccipital (BARDACK, 1965: fig. 5, 15, 18). *Faugichthys* still possesses a short and broad epiotic (TAVERNE & CHANET, 2000: fig. 1). *Saurodon* and *Saurocephalus* also present a narrowing of the epiotic (character 78) independently acquired. But in this case the bone does not extend anteriorly almost as far as the supraoccipital.

Chirocentrites and *Gillicus* share two apomorphic characters.

- (97) The lower jaw is huge, with an exceptional

deepening of the symphysis and a mandibular sensory canal buried in a long groove (Fig. 2; STEWART, 1900: pl. 52, fig. 4, 5; BARDACK, 1965: fig. 20; CAVIN & FOREY, in press: fig. 24C, 25B).

- (98) The supraoccipital crest is well developed but shortened (Fig. 2; STEWART, 1900: pl. 52, fig. 1; BARDACK, 1965: fig. 17; CAVIN & FOREY, in press: fig. 24C, 25b).

I propose herewith the erection of a new subfamily Gillicinae to group these two genera with the characters (97) and (98) as definition.

Chirocentrites (this paper) offers a few autapomorphies.

- (99) The braincase is particularly small in comparison of the full skull.
 (100) Each premaxilla bears two long fangs antero-ventrally directed.
 (101) The first teeth on the dentary are large and fang-

like.

- (102) The most anterior part of the maxillary oral border curves inward so as to form with the premaxilla a notch in which the anterior fangs of the lower jaw are fitted.

Gillicus (Fig. 10; BARDACK, 1965; CAVIN & FOREY, in press) is characterized by other autapomorphies.

- (103) The maxilla is sabre-shaped, with the anterior end forming a marked angle with the oral part.
 (104) The two supramaxillae are enormous, much deeper than the maxilla.
 (105) The teeth on both jaws are minute.
 (106) The orbital and otic parts of the parasphenoid form a marked angle.
 (107) The preopercle shows a considerably widened dorsal branch.

The three last genera, *Ichthyodectes*, *Xiphactinus* and *Vallecillichthys*, form the subfamily Ichthyodectinae.

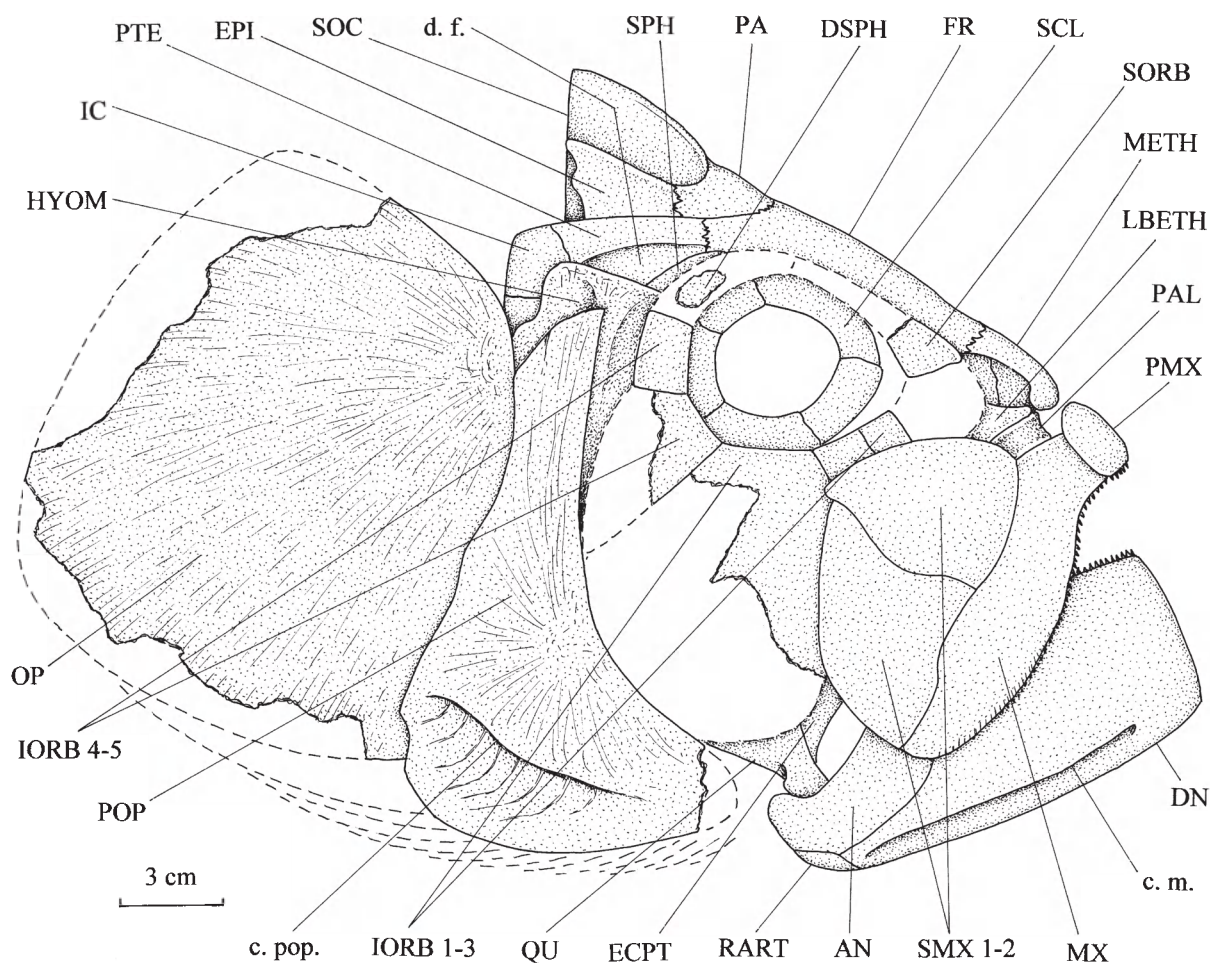


Fig. 10 – *Gillicus arcuatus* (COPE, 1875). Reconstruction of the skull in right lateral view based on a photo of a well preserved skull from the Niobrara Formation (Santonian), Kansas. The rear of the braincase is completed from BARDACK (1965: fig. 17) and the opercular series is added from STEWART (1900: pl. 53).

They share four apomorphies (STEWART, 1900; BARDACK, 1965; BLANCO-PINÓN & ALVARADO-ORTEGA, 2007).

- (108) The neurocranial hyomandibular facet is parallel to the orbital part of the parasphenoid.
- (109) The articular condyle of the quadrate presents an anterior laterally directed projection (STEWART, 1999: fig. 10E, F).
- (110) There is a slight increasing of the number of vertebrae. *Ichthyodectes* counts 68 to 72 centra versus 61-64 in *Chirocentrites* and 69 in *Gillicus*.
- (111) The anal fin is reduced. There are 10-11 rays in *Ichthyodectes*, 14 rays in *Xiphactinus* and 11-13 rays in *Vallecillichthys*. More primitive ichthyodectids generally possess between 30 and 40 rays in the anal fin.

Ichthyodectes offers a few autapomorphies (BARDACK, 1965).

- (112) Seen along the cranial dorsal profile, the parietal forms a marked angle with the frontals.
- (113) The premaxilla bears moderately big fangs.
- (114) The maxilla and the dentary possess rather small teeth.
- (115) The dorsal fin is very short with only 10 rays. The other Ichthyodectidae have more than 10 dorsal rays.

Xiphactinus and *Vallecillichthys* differ from *Ichthyodectes* by at least three more advanced characters.

- (34) The latero-basal ethmoid is reduced to its ventral articular part and does not reach the frontal dorsally (BARDACK, 1965: fig. 6; BLANCO-PINÓN & ALVARADO-ORTEGA, 2007: fig. 3). The bone keeps its dorsal part in *Ichthyodectes* and reaches the frontal (BARDACK, 1965: fig. 14). We have already met this character (34), independently acquired, in *Eubiodectes* where it is still more pronounced (CAVIN & FOREY, in press: fig. 6A, B, C).
- (116) The second supramaxilla is strongly reduced and becomes much shorter than the first one.
- (117) The body lengthens and there is a new increasing in the number of vertebrae, with 85 to 90 centra in *Xiphactinus*.

Xiphactinus shows several autapomorphies (STEWART, 1900; BARDACK, 1965).

- (100) Each premaxilla bears two (sometimes more) long fangs antero-ventrally directed. This character, independently acquired, is also known

in *Chirocentrites*. However, the fangs on the premaxilla could be still larger in *Xiphactinus* than in *Chirocentrites*.

- (118) The anterior teeth on the dentary are fang-shaped whereas the posterior teeth are small.
- (119) The hammer-shaped articular head of the palatine becomes huge and deeper than long.
- (120) The entopterygoid is very reduced.
- (121) The metapterygoid reaches the palatine. Characters (120) and (121) seem to be linked.

Vallecillichthys presents some derived characters (BLANCO & CAVIN, 2003; BLANCO-PINÓN & ALVARADO-ORTEGA, 2007), which differ from *Xiphactinus*.

- (75) The body is still more elongated and there is a new increasing in the number of vertebrae till at least 100 in *Vallecillichthys*. This homoplastic character is shared by *Saurodon* and probably the two other Saurodontinae.
- (6) The supraoccipital crest lengthens and overhangs again the occiput as in the primitive Ichthyodectidae.
- (113) The premaxilla bears moderately sized fangs as in *Ichthyodectes*.
- (122) The dorsal branch of the preopercle becomes narrower.

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List of abbreviations used in the text-figures

AN: angular
 ANT: antorbital
 BRSTG: branchiostegal ray
 BSCL: basal sclerotic bone
 DN: dentary
 DSPH: dermosphenotic
 ECPT: ectopterygoid
 ENPT: entopterygoid (mesopterygoid)
 EPI: epiotic (epioccipital)
 FR: frontal
 HYOM: hyomandibula
 IC: intercalar
 IOP: interopercle
 IORB 1-5: infraorbitals 1 to 5
 LBETH: latero-basal ethmoid (ethmopalatine)
 METH: mesethmoid

MPT: metapterygoid
 MX: maxilla
 OP: opercle
 PA: parietal
 PAL: palatine
 PMX: premaxilla
 POP: preopercle
 PTE: pterotic
 QU: quadrate
 RART: retroarticular
 SCL: sclerotic bone
 SMX 1-2: anterior and posterior supramaxillae
 SOC: supraoccipital
 SOP: subopercle
 SORB: supraorbital
 SPH: sphenotic
 SY: symplectic
 c. m.: mandibular sensory canal
 c. pop.: preopercular sensory canal
 d. f.: *dilatator fossa*
 f. lbeth.: articular facet of the palatine for the latero-basal ethmoid
 f. mx.: articular facet of the palatine for the maxilla
 of. f.: olfactory (nasal) fossa

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