On the presence of the osteoglossid fish genus *Scleropages* (Teleostei, Osteoglossiformes) in the continental Paleocene of Hainin (Mons Basin, Belgium)

Louis Taverne [1], **Dirk Nolf** [2] **& Annelise Folie** [2]

[1] **Université Libre de Bruxelles (U. L. B.), Faculté des Sciences, Département de Biologie des Organismes, Unité de Morphologie fonctionnelle (C. P. 160/11), avenue F. D. Roosevelt 50, B-1050 Brussels, Belgium**
[2] **Royal Institute of Natural Sciences of Belgium, Department of Paleontology, Section of Vertebrate Paleontology, Vautier street 29, B-1000 Brussels, Belgium**

Corresponding author : Louis Taverne, e-mail : louis.taverne@gmail.com

ABSTRACT. Some bony remains, otoliths and squamules belonging to the osteoglossid genus *Scleropages* are described from the continental Paleocene of Hainin (Mons Basin, Belgium). The hypotheses to explain the occurrence of such a freshwater fish in Europe at that time are discussed.

KEY WORDS : Teleostei, Osteoglossidae, *Scleropages*, fossil remains, continental Paleocene, Belgium.

RÉSUMÉ. Quelques restes osseux, des otolithes et des squamules appartenant à l'ostéoglossidé *Scleropages* sont décrits dans le Paléocène continental de Hainin (Bassin de Mons, Belgique). Les hypothèses expliquant la présence de ce poisson dulçaquicole en Europe à cette époque sont discutées.

MOTS-CLÉS : Teleostei, Osteoglossidae, *Scleropages*, restes fossiles, Paléocène continental, Belgique.

INTRODUCTION

Continental deposits of Paleocene age, overlying the marine Calcaire de Mons (Danian), were described by RUTOT (1886) from the railway section at Hainin, about 13km West of Mons. In 1970, a test hole (HA 1) was drilled (at x = 107.250, y = 124.890) by the Geological Laboratory of the "Faculté Polytechnique de Mons" at the municipal football field of Hainin, about 600m North of the railway section, with the aim to realize a complete section through the lacustrine continental deposits (observed between 8.5m and 38.4m depth). Another test hole, HA 2 (at x = 107.045, y = 124.990) was drilled, some 250m North West of HA 1, with the intention to explore the underlying marine Danian deposits (GODFRIAUX & ROBASZYNSKI, 1974).

According to STEURBAUT (1998 : 144-145), the concerned "continental Montian" deposits, now called Hainin Formation, represents the lowstand systems tract of sequence TP 1.4, which corresponds to the oldest Seelandian of Europe (about 60 million years old).

Sediments from the HA 1 hole provided the oldest mammal teeth from the European Cenozoic (GODFRIAUX & THALER, 1972; VIANEY-LIAUD, 1979; SUDRE & RUSSEL, 1982; CROCHET & SIGÉ, 1983; SIGÉ & MARANDAT, 1997). This fauna has been chosen as reference-level MP1-5 of the mammalian biochronological scale for the European Paleogene (SCHMIDT-KITTLER, 1987; AGUILAR et al., 1997). The "Montian" fauna of Hainin also contains fossil amphibians (GROESSENS-VAN DYCK, 1981), turtles (GROESSENS-VAN DYCK, 1984; SCHLEICH et al., 1988), crocodiles (GROESSENS-VAN DYCK, 1986), lizards (FOLIE et al., 2005) and many fish remains. Additional fossils were obtained in 1974, from a hole with a diameter of 1m, known as "Puits Hainin", located at 25m North of the mentioned exploration drilling. This hole was burrowed till a depth of 25m and provided the bulk of the now available Hainin fossils.

In 1994, MAGIONCALDA published additional data on three new boreholes made at Hainin in 1986 and located in the area immediately East of the HA 1 hole. He mentioned otoliths of osmerids (?), *Thaumaturus* Reuss, 1844, percoids, umbrids and esocids, based on otolith identification by Nolf. The list of Magioncalda does not mention osteoglossids, because his work did not considered the "Puits Hainin", from where a small sample examined by Nolf about 20 years ago yielded osteoglossid otoliths, identified in the collection as *Scleropages* Günther, 1864 but never published until now.

Osteoglossiformes are one order of the primitive teleostean super-order Osteoglossomorpha, commonly known as the "bony tongue" fishes by reason of their peculiar bite between parasphenoid, pterygoid bones, dermobasihyal and dermobasibranchials. Osteoglossiformes are heavily ossified teleosts, with a medio-parietal skull, very large posterior infraorbitals, a more or less prognathous lower jaw, and generally large acute teeth on both jaws and a reduced or lost subopercle (TAVERNE, 1977; 1978). Their scales frequently offer a reticular pattern formed by small bony plates, the squamules, separated from each other by very narrow grooves and resting on the basal cal-

cified collagenous layer of the scale (GAYET & MEUNIER, 1983; MEUNIER, 1984).

Osteoglossiformes appear in the fossil record as soon as the Early Cretaceous with species such *Laelichthys ancestralis* Silva-Santos, 1985 from Brazil, *Chanopsis lombardi* Casier, 1961 from the Democratic Republic of Congo and *Nieerkunia liae* Su, 1992 and *Xixiaichthys tongxinensis* Zhang, 2004 both from the South East of China. Most fossil and all Recent Osteoglossiformes are freshwater fishes but there are also a few fossil marine species in the Paleocene and Eocene of Europe, North America, Central Asia and Africa. "Genus Osteoglossidarum" *tavernei* Nolf & Stringer, 1996 from the Maastrichtian of Mississipi is the first known marine occurrence for the order. Recent freshwater Osteoglossiformes generally tolerate brackish waters and sometimes enter in marine waters near the estuaries.

The fossil record of the suborder Osteoglossoidei shows a worldwide distribution, essentially because of the wide expansion of marine species during the Lower Paleogene. Recent species offer a remarkable example of Gondwanan distribution with *Osteoglossum* Cuvier, 1829 and *Arapaima* Müller, 1843 in tropical South America, *Heterotis* Rüppel, 1829 and *Pantodon* Peters, 1877 in Africa and *Scleropages* in Australia, New Guinea and Southeastern Asia. Such a Gondwanan distribution already occurs for the oldest osteoglossoid species in the continental Lower Cretaceous deposits.

Recent Osteoglossoidei are moderately large fishes with the exception of the small *Pantodon* reaching only a few centimetres. *Arapaima*, the giant of the group, grows to about 3 or 4 metres in length. Those Recent genera are grouped in three families, Osteoglossidae with *Osteoglossum* and *Scleropages*, Arapaimidae (= Heterotidae) with *Heterotis* and *Arapaima* and Pantodontidae for the sole *Pantodon* (Taverne, 1979). Some consider Arapaimidae as a simple subfamily of Osteoglossidae and also include in this family the fossil subfamily Phareodontinae (NELSON, 2006 : 104-106).

In the present paper, we describe fossil fish remains belonging to *Scleropages* from the continental Paleocene of Hainin in the Mons Basin (Belgium) and we discuss the occurrence of such an osteoglossid genus in those geological layers of that Belgian locality.

The present day distribution of *Scleropages* is restricted to Southeastern Asia, Australia and New Guinea, with a total of six species : *Scleropages formosus* (Müller & Schlegel, 1844) or Asian arowana (Fig. 1) from Indonesia, Malaysia, Thailand and Cambodia, *Scleropages leichardti* Günther, 1864 or spotted barramundi from Eastern Australia, *Scleropages jardinii* (Saville-Kent, 1892) or northern barramundi from Southern New Guinea and Northern Australia, *Scleropages aureus* Pouyaud et al., 2003 from the Siak river in Sumatra, *Scleropages legendrei* Pouyaud et al., 2003 from West Borneo and *Scleropages macrocephalus* Pouyaud et al., 2003 from Borneo too (POUYAUD et al., 2003). *Scleropages* is known as a fossil in the Neogene of Queensland, Australia (HILLS, 1943) and in the Eocene of Sumatra where it is contemporaneous with *Musperia radiata* (Heer, 1874), another fossil osteoglossid from Sumatra (SANDERS, 1934; TAVERNE, 1979). "Genus Osteoglossidarum" *deccanensis* Rana, 1988 and "genus Osteoglossidarum" *intertraptus* Rana, 1988, both from the Maastrichtian "Deccan Intertrappean Beds" of India (RANA, 1988), can also confidently be attributed to *Scleropages* or to a closely related genus and provides the oldest fossil record of the taxon. KUMAR et al. (2005) further mention the presence of an osteoglossid skull, *Taverneichthys bikanericus* Kumar et al., 2005, that seems close to *Osteoglossum* and *Scleropages,* in the continental Paleocene of Rajasthan, India.

Recent Osteoglossiformes no more exist in Europe today but *Scleropages* is not the unique fossil osteoglossiform fish on that continent. However, most other European fossil Osteoglossiformes are marine teleosts. They include *Brychaetus muelleri* Woodward, 1901, "genus Osteoglossidarum" *rhomboidalis* (Stinton, 1977) and "genus Arapaimidarum" *acutangulus* (Stinton, 1977), all three from the Lower or Middle Eocene of the southern North Sea Basin, *Monopteros gigas* Volta, 1796, *Thrissopterus catullii* Heckel, 1856 and *Foreyichthys bolcensis*, Taverne 1979, all three from the lowermost Lutetian of Monte Bolca, and four still unpublished new osteoglossoid genera in the Eocene of Denmark (BONDE, 1966, 1987, in press; TAVERNE, 1998).
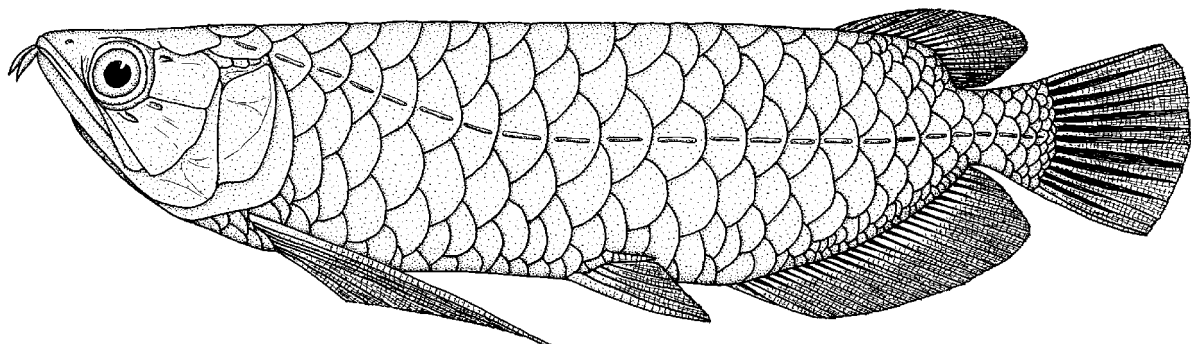

Fig. 1. – *Scleropages formosus* (Müller & Schlegel, 1844) from Southeast Asia (modified from TAVERNE, 1977 : fig. 70). This species can grow to about 90cm in length.

MATERIALS AND METHODS

IRSNB P 8238 : A right premaxilla, Hainin, at 17-17.7m depth (level R1).

IRSNB P 8239 : An incomplete right maxilla, Hainin, at 17-17.7m depth (level R1).

IRSNB P 8240 : A fragment of a right entopterygoid, Hainin, at 13.7-14m depth (level N2).

IRSNB P 8241 : A fragment of a left palato-ectopterygoid, Hainin, at 13.3-13.7m depth (level N1).

IRSNB P 8242 : An abdominal vertebra, Hainin, at 14-14.6m depth (level O1).

IRSNB P 8243 : A left saccular otolith, Hainin, precise depth unknown, and a fragmentary saccular otolith, Hainin, at 17-17.7m depth (level R1).

IRSNB P 8244-8251 : Squamules, Hainin, at 13.3-13.m (level N1), 13.7-14m (level N2), 16-16.6m (level Q1), 16.6-17m (level Q2), 17-17.7m (level R1) and 17.7-18m depth (level R2).

Levels N1, N2 and O1 are grey clays with calcareous concretions broken by peaty ruptures, while levels Q1, Q2, R1 and R2 are rough tufaceous grey marls (GODFRI-AUX & ROBASZYNSKI, 1974).

The material has been studied with a Wild M5 stereo-microscope supplied with a camera lucida used for the drawings.

PALEONTOLOGICAL STUDY

Division **TELEOSTEI** Müller, 1846

Super-order **OSTEOGLOSSOMORPHA** Greenwood et al., 1966

Order **OSTEOGLOSSIFORMES** Regan, 1909

Suborder **OSTEOGLOSSOIDEI** Regan, 1909

Family **Osteoglossidae** Bonaparte, 1832

Genus **Scleropages** Günther, 1864

Species **Scleropages** sp.

Bony remains (Figs 2 ; 3)

The preserved right premaxilla (Fig. 2, B1-3) is complete. It is a robust bone, triangular in shape. The oral border bears ten teeth most of which visible only by their roots. Those teeth are large, laterally compressed and closely arranged side by side except the first one which seems to be the larger of the series and which is slightly separated from the other teeth. The second tooth stands in a more inner position than the other teeth. The base of the two partially preserved teeth is covered with bone. The symphyseal ascending process is reduced to a small bony knob. A small hollow is located on the symphyseal border of the bone, just before and below the ascending process. A deep longitudinal groove for the articulation with the maxilla is visible in a median position on the inner side of the bone.

Only the middle portion of a right maxilla (Fig. 2, A1-4) is preserved. The oral border carries the roots of ten teeth. The dorsal rim of the bone forms a small crest.

A fragment of a right entopterygoid (Fig. 3, A1, 2), representing its postero-dorsal part, is preserved. A short but deep vertical groove is visible at the raised top of the external face of the bone. On the internal face, at a short distance from the dorsal margin of the bone, there is a longitudinally disposed single row of large, conical, pointed teeth of whose the most posterior are the largest. Below that row of large teeth, the surface of the bone is covered with much smaller teeth irregularly ranged.

A middle portion of a left palato-ectopterygoid (Fig. 3, C1, 2) is also preserved. The external face of the bone bears an osseous horizontal crest close to its ventral border. The internal face is covered by numerous very small teeth, irregularly disposed. The teeth of the ventral margin are conical and a little larger than the others.

Only one abdominal vertebra (Fig. 2, C1, 2) is known. It bears on its left side a long, large and obliquely oriented haemapophysis (= parapophysis). The right haemapophysis is lost. Only the base of the broad neural arch is preserved. Both the lateral faces of the centrum and the haemapophysis are deeply sculptured by crests and holes.

The saccular otolith is large and robust, with a strongly prominent rostrum and a well marked angle in the central portion of the ventral rim. Although the dorsal rim is somewhat corroded, the lacking part does not substantially alter the shape of the otolith. The anterior part of this rim is somewhat concave. The outer face is very slightly convex, nearly flat. Its surface is smooth, but shows some fine concentric growth lines, especially near the ventral rim. The greatest thickness of the otolith is located in its posterior portion. The inner face is clearly convex, especially in the dorso-ventral direction. The sulcus, entirely located in the upper half of the outer face, is not divided in an ostial and a caudal part, and is completely filled with colliculum which shows a rough surface, which strongly contrasts with the very smooth surface of the ventral area. The ventral rim shows a sharp profile, which becomes gradually smoother towards the posterior rim. This rim shows an angulous profile at the junction with the inner face, but a smooth transition to the outer face.
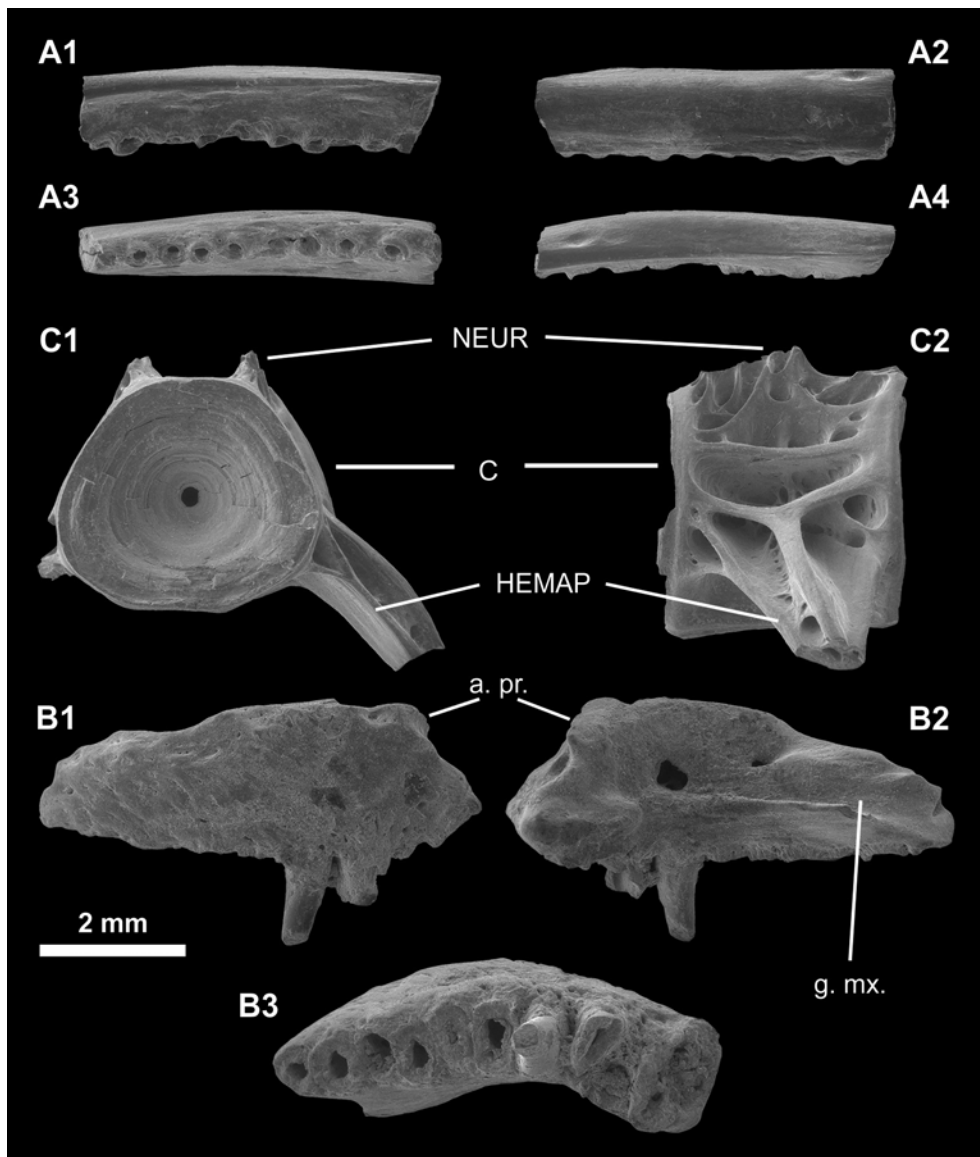
Fig. 2. – *Scleropages* sp. from the Paleocene of Hainin. (A) Fragment of a right maxilla (IRSNB P 8239) in internal (A1), external (A2), ventral (A3) and dorsal view (A4). (B) Right premaxilla (IRSNB P 8238) in external (B1), internal (B2) and oral view (B3). (C) Abdominal vertebra (IRSNB P 8242) in anterior (C1) and left lateral view (C2). Legend : **C** : vertebral centrum; **HEMAP** : haemapophysis (= parapophysis); **NEUR** : neural arch; **a. pr.** : symphyseal ascending process of the premaxilla; **g. mx.** : groove on the inner face of the premaxilla for the articulation of the maxilla.

Scales (Fig. 5)

Numerous small quadrangular, rhombic and polygonal squamules have been found at Hainin. The lower face of each squamule is concave, with the margin raised in the form of a ridge, and thus is looking like an opened box. The internal face generally is smooth but in some squamules a few large widely spaced tubercules are present. The apex of those internal tubercules sometimes is perforated by a minute hole. The external face of the squamules is flat and always ornamented with granular tubercules. Those tubercules are very small and more or less arranged in irregular concentric rows on the squamules from the anterior field of the scale. The tubercules are much larger and irregularly ranged on the squamules from the posterior field of the scale. Circuli and radii do not exist.

DISCUSSION

The discovery of squamules ornate with granulations in the Hainin continental Paleocene deposits attests the presence there of a fossil osteoglossoid fish. The African osteoglossomorph family Mormyridae also possesses scales with squamules but their ornamentation is formed by normal circuli and not by granulations as in Osteoglossoidei.
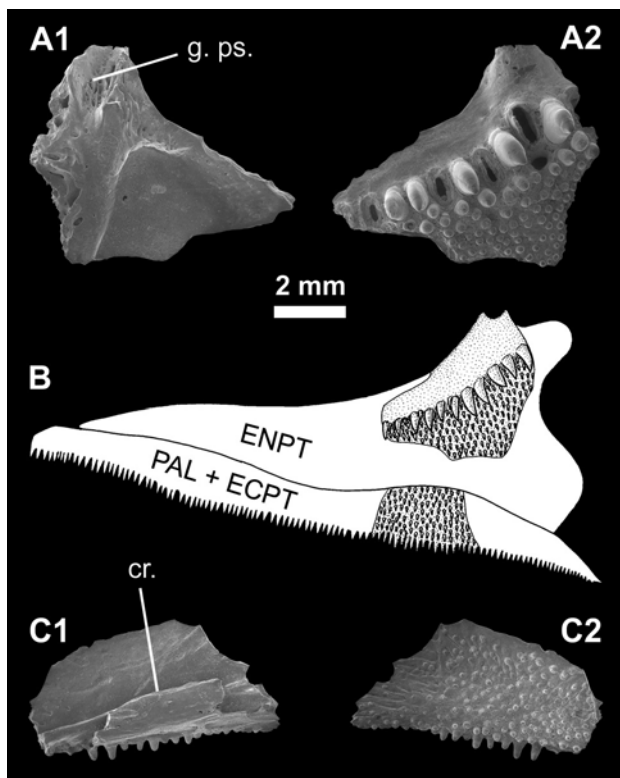

Fig. 3. – *Scleropages* sp. from the Paleocene of Hainin. (A) Fragment of a right entopterygoid (IRSNB P 8240) in external (A1) and internal view (A2). (B) Schematic drawing of the right entopterygoid and palato-ectopterygoid of *Scleropages* in internal view to show the location of the Hainin pterygoid fragments (IRSNB P 8241). (C) Fragment of a left ectopterygoid in external (C1) and internal view (C2). Legend : **cr.** : crest on the external face of the ectopterygoid; **g. ps.** : groove on the external face of the entopterygoid to receive the basipterygoid process of the parasphenoid.
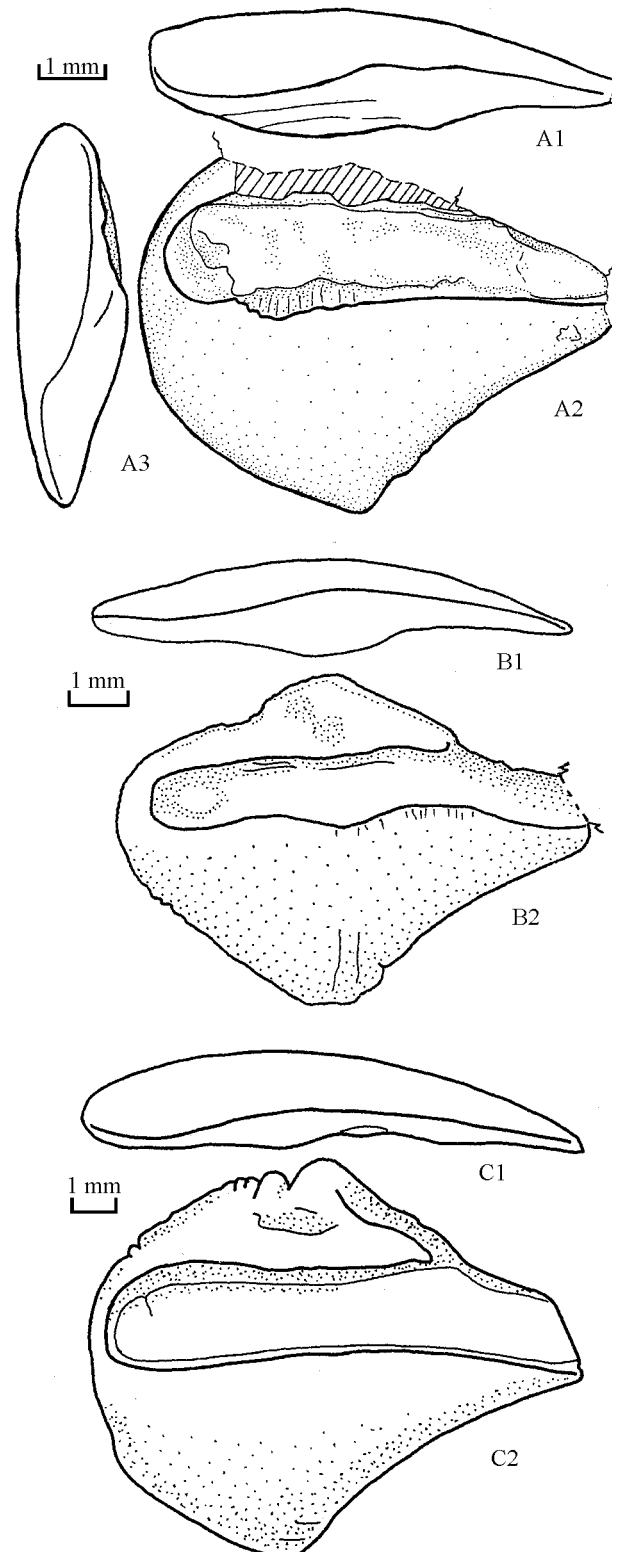

Fig. 4. – (A) Left sagitta (IRSNB P 8243) of the *Scleropages* sp. from the Paleocene of Hainin, in dorsal (A1), profile (A2) and external view (A3). (B) Left sagitta of *Scleropages formosus* (Müller & Schlegel, 1844) in external view (modified from Taverne, 1977 : fig. 81). (C) Left sagitta of *Scleropages leichardti* Günther, 1864 in external view (modified from Nolf, 1993 : Fig. 4A).
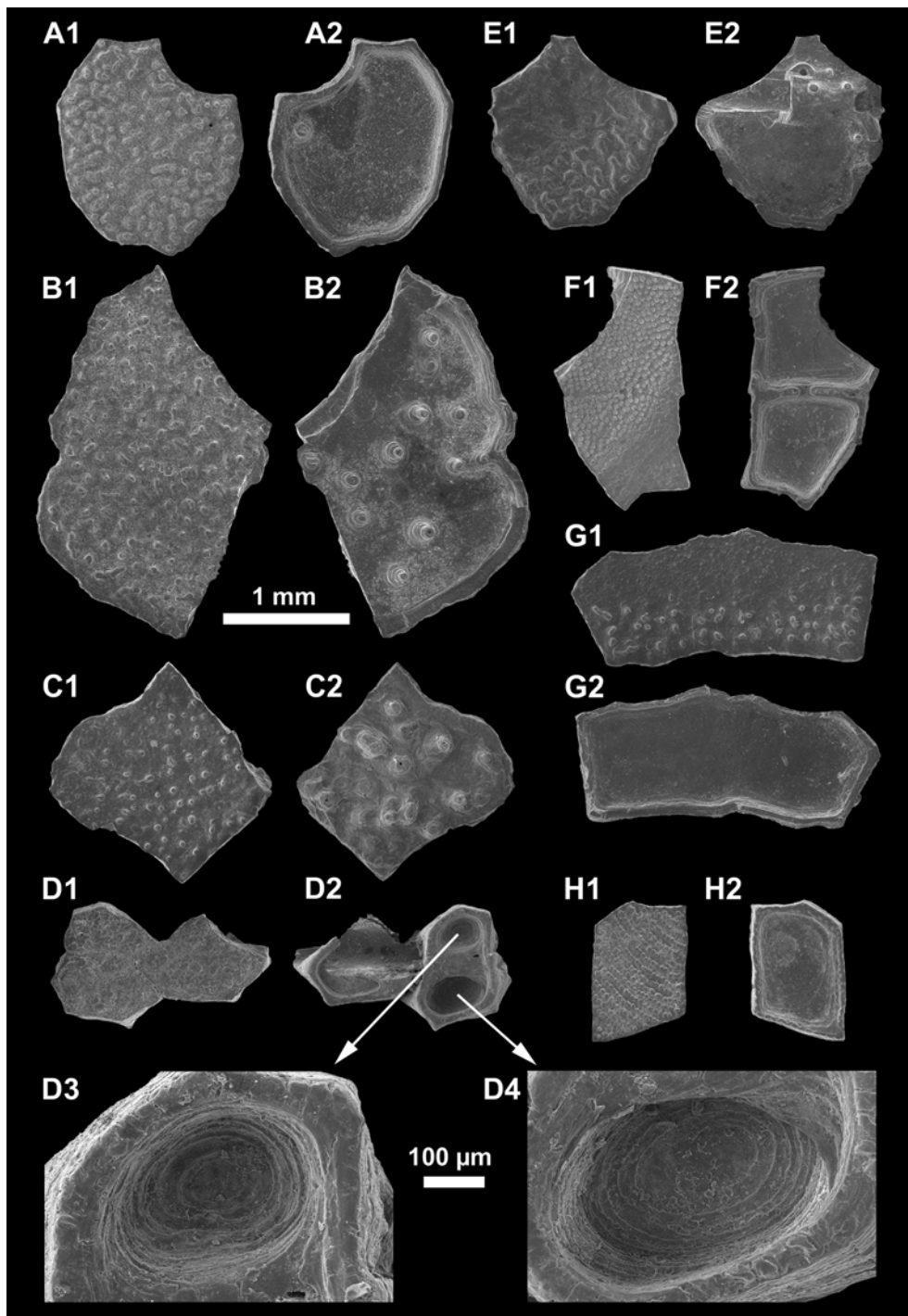
Fig. 5. – *Scleropages* sp. from the Paleocene of Hainin. Squamules (IRSNB P 8244-8251) of the posterior field of the scale in external (A1, B1, C1, E1, G1) and internal view (A2, B2, C2, E2, G2). Three united squamules from the lateral field in external (D1) and internal view (D2), with enlargement of (D2) in (D3) and (D4). Two united squamules of the anterior field of the scale in external (F1) and internal view (F2). A squamule of the anterior field of the scale in external (H1) and internal view.

A deep groove is present at the top of the external face of the entopterygoid in the Hainin fossil fish. Such a groove is a unique autapomorphy of the osteoglossoid families Osteoglossidae, Arapaimidae and Pantodontidae (TAVERNE, 1977 : Figs 53, 54, 82, 83, 107, 134; 1978 : Figs 40, 41). No other teleost offers such a specialized structure. That groove receives the paired basipterygoid

process of the parasphenoid (BRIDGE, 1895 : pl. 22, fig. 4) which is firmly fixed there by an elongated anterior process of the hyomandibula, except in *Pantodon* where that hyomandibular process is missing. That very peculiar structure allows a supplementary articulation between the neurocranium and the hyopalatine arch that strengthens the palato-lingual bite in those fishes.

The pattern of the dentition on the inner face of the entopterygoid, with one dorsal row of large teeth and a ventral area with much smaller and irregularly arranged teeth, agrees with a belonging to Osteoglossidae (Taverne, 1977 : Figs 54, 83) but not to Arapaimidae and Pantodontinae. Indeed, there are only some large teeth on the upper part of the entopterygoid in *Heterotis* and *Pantodon* (Taverne, 1977 : Fig. 107, 1978 : Fig. 41) and very small denticles on practically the whole inner surface of the bone in *Arapaima* (Taverne, 1977 : Fig. 134).

Fossil and Recent Osteoglossidae offer premaxillae with a well developed symphyseal ascending process (Taverne, 1977 : Figs 42, 47, 49, 1978 : Figs 2, 7, 20; Gayet, 1991 : Fig. 7a; Li, 1996 : Fig. 3; Li et al., 1997 : Figs 3, 8). In *Scleropages* however, this symphyseal process is very short (Taverne, 1977 : Fig. 71). The premaxilla of the Hainin osteoglossid, with its very short symphyseal process, completely looks like the corresponding bone of *Scleropages* and more particularly to the one of the Recent Asian *Scleropages formosus* which also possesses ten or eleven premaxillar teeth. In the Recent *Scleropages leichardti* from Australia, there are only three to five teeth on the premaxilla.

The identification of the Hainin fossil fish with the genus *Scleropages* is further confirmed by its saccular otoliths that look very much like those of *Scleropages leichardti* (Nolf, 1993 : fig. 4A). It differs only from them by a wider sulcus and a thicker posterior portion. Otoliths of *Sleropages formosus* (Fig. 4B2) are more elongate and have a narrower sulcus.

The *Scleropages* from Hainin is neither the first mentioned, nor the oldest Osteoglossidae present in the European continental deposits. A fragment of a toothed jaw bone and some squamules of an undetermined osteoglossid have already been described in the continental Campanian (Late Cretaceous) of Champ-Garimond, in southern France (Sigé et al., 1997). This French fossil may also belong to the genus *Scleropages*, but those remains are too fragmentary for decisive conclusions.

The occurrence of *Scleropages*, a freshwater genus actually living in Southeast Asia and Oceania, in the continental Paleocene of Belgium and perhaps already in the continental Campanian of France, can be explained by two different ways.

In the first hypothesis, the osteoglossoid distribution is considered as worldwide since the origin of the suborder during the Cretaceous thanks to the tolerance of those fishes for brackish and even marine waters. The present day distribution (see map in Berra, 2001 : 53), which suggests an ancient "Gondwana pattern", is then viewed as a fallacious picture. In that case, the European fossil *Scleropages* simply is a relic of that old cosmopolite distribution.

Another interpretation of the osteoglossoid geographic distribution is possible. Indeed, the Lower Cretaceous osteoglossoids only are known in Gondwanan regions. It is during the Upper Cretaceous that a few Osteoglossoidei appear for the first time in continental deposits of the northern continents. At that time, only one species is known in Europe, the undetermined Campanien osteoglossid of Champ-Garimont, and two species are

reported in the western part of North America, the osteoglossid *Cretophareodus alberticus* Li, 1996 from the Campanian of Alberta, and the osteoglossoid incertae sedis *Chandlerichthys strickeri* Grande, 1986 from the Cenomanian of Alaska. A real worldwide distribution of the Osteoglossoidei only occurs during the Lower Tertiary and is principally due to the numerous marine species then present in the oceans. The disappearance of all those marine Paleogene osteoglossoids, of *Scleropages* in Europe, and of *Phareodus acutus* Leidy, 1873 and *Phareodus testis* (Cope, 1877) in North America after the Eocene has brought back the dispersal of the suborder to Gondwanan frontiers as in the Lower Cretaceous.

That second hypothesis puts a question about the European fossil *Scleropages*. How this freshwater genus has succeeded to reach Europe?

An Indian origin is questionable. During the Upper Cretaceous and the Lower Tertiary, India still was isolated in the ocean and separated from Western Europe by all the length of the Mesogea, a too long marine distance to pass over for a freshwater fish.

A connection between North America and Europe is possible via Greenland and Britain during practically all the Cretaceous times. The marine expanses between those areas during that geological period are not very wide and we know that Osteoglossidae are able to tolerate brackish and even marine waters. However, the two Upper Cretaceous osteoglossoid species are located westward to the large Cretaceous epicontinental seaway then bisecting North America into two land masses. To go over such a wide marine expanse is practically impossible for freshwater teleosts and moreover no freshwater osteoglossoid has ever been found located eastward to that sea in North America during the Cretaceous. Thus, a North American origin for the European *Scleropages* also is improbable.

A connection between North Africa and Europe during the Cretaceous is possible via the Iberian and/or the Apulian platforms and the surrounding islands. The marine expanses between those emerged territories at that time were not very wide. We know also that the occurrence of Osteoglossidae in Africa is attested as soon as the Early Cretaceous with *Chanopsis lombardi* from the Valanginian-Barremian (Cahen et al., 1959), a geological period during which South-America and Africa were still connected. Other fossil Osteoglossiformes are known in Africa during the Cretaceous but they are younger : the arapaimid *Paradercetis kipalaensis* Casier, 1965 and the kipalaichtyid *Kipalaichthys sekirksyi* Casier, 1965, both from the Cenomanian of the Democratic Republic of Congo (Taverne, 1976). In addition to that it is obvious that the Recent South-American *Osteoglossum* and the Southeast Asian and Oceanian *Scleropages* are very close relatives, sharing an almost similar osteology and differing only by a few details (Taverne, 1977). Even if no fossil remains of *Sleropages* were found until now in Africa, the actual Gondwanan distribution of those two freshwater genera implicates that an *Osteoglossum-Scleropages*-like osteoglossid was present in Africa in the earliest period of the Cretaceous, before a too important break up of Gondwana. An African origin for the European fossil *Scleropages* is thus the most probable hypothesis.

REFERENCES

AGUILAR JP, LEGENDRE S & MICHAUX J (1997). Actes du Congrès Biochrom '97. Mém. Trav. Ecole Prat. Hautes Etudes, Inst. de Montpellier, 21 : 1-818.

BERRA T (2001). Freshwater fish distribution. Acad. Press, San Diego, San Francisco, New York : 604 p.

BONDE N (1966). The fishes of the Mo-clay Formation (Lower Eocene). A short review. Saertr. Meddel. Dansk Geol. Forening., 16 : 198-202.

BONDE N (1987). Moler – its origin and its fossils especially fishes. Skam. Skarreh. Molerv. a/s : 1-53.

BONDE N (in press). Osteoglossomorphs of the marine Lower Eocene of Denmark. In : LONGBOTTOM A, RICHTER M & CAVIN L (eds), Fishes and the Break-up of Pangea, Geol. Soc., London, Spec. Publ.

BRIDGE TW (1895). On certain features of the skull of *Osteoglossum formosum*. Proc. Zool. Soc. London, 20 : 302-310.

CAHEN L, FERRAND J, HAARSMA MJF, LEPERSONNE J & VERBEEK T (1959). Description du sondage de Samba. Ann. Mus. Roy. Congo Belge, sér. in-8, Sci. Géol. : 1-210.

CROCHET JY & SIGÉ B (1983). Les mammifères montiens de Hainin (Paléocène moyen De Belgique. Part III : Marsupiaux. Palaeovertebrata, 13 : 51-64.

FOLIE A, SIGÉ B & SMITH T (2005). A new scincomorph lizard from the Palaeocene of Belgium and the origin of Scincoidea in Europe. Naturwissensch., 92(11) : 542-546.

GAYET M (1991). "Holostean" and teleostean fish of Bolivia. In : SUAREZ-SORUCO R (ed), Fosiles y facies de Bolivia – Vol. 1. Vertebrados, Rev. Tecn. YPFB, 12(3-4) : 453-493.

GAYET M & MEUNIER FJ (1983). Ecailles actuelles et fossiles d'Ostéoglossiformes (Pisces, Teleostei). C. R. Acad. Sc. Paris, sér. 2, 297 : 867-870.

GODFRIAUX I & ROBASZYNSKI F (1974). Le Montien continental et le Dano-Montien marin des sondages de Hainin (Hainaut, Belgique). Ann. Soc. Géol. Belg., 97 : 185-200.

GODFRIAUX I & THALER L (1972). Note sur la découverte de dents de mammifères dans le Montien Continental du Hainaut (Belgique). Acad. Roy. Belg., Bull. Cl. Sci., 5e sér., 58 : 536-541.

GROESSENS-VAN DYCK MC (1981). Etude des amphibiens du Montien continental de Hainin. Bull. Soc. Belg. Géol., 90 : 87-101.

GROESSENS-VAN DYCK MC (1984). Les tortues du Paléocène continental de Hainin et Vianalmont (Belgique). Stud. Geol. Salmantic., Vol. Esp. 1, Stud. Palaeochelon., 1, Edic. Univ. Salamanca : 133-139.

GROESSENS-VAN DYCK MC (1986). Les crocodiliens du gisement "montien" continental De Hainin (Hainaut, Belgique) et leur environnement faunique. Ann. Soc. Roy. Zool. Belg., 116 : 55-60.

HILLS ES (1943). Tertiary fresh-water fishes and crocodilian remains from Gladstone and Duaringa, Queensland. Mem. Queensl. Mus., 12(2) : 96-100.

KUMAR K, RANA RS & PALIWAL S (2005). Osteoglossid and lepidosteid fish remains From the Paleocene Palana Formation, Rajasthan, India. Paleontol., 48(6) : 1187-1209. implications. Cretaceous Res, 12 : 93-114.

LI GQ (1996). A new species of Late Cretaceous osteoglossid (Teleostei) from the Oldman Formation of Alberta, Canada, and its phylogenetic relationships. In : ARRATIA G & VIOHL G (eds), Mesozoic Fishes – Systematics and Paleoecology, Verl. Dr. F. Pfeil, München : 285-298.

LI GQ, GRANDE L & WILSON MVH (1997). The species of +*Phareodus* (Teleostei, Osteoglossidae) from the Eocene of North America and their phylogenetic relationships. J. Vert. Paleont., 17(3) : 487-505.

MAGIONCALDA R (1994). Studio stratigrafico di alcuni sondaggi dell'area di Hainin (Belgio) biostratigrafia, paleoecologia, paleogeografia. Thesa di Laurea : 158 p.

MEUNIER FJ (1984). Structure et minéralisation des écailles de quelques Osteoglossidae (Osteichthiens, Téléostéens). Ann. Sci. Nat. Zool., 13e sér., 6 : 111-124.

NELSON JS (2006). Fishes of the World. Fourth Edition. Wiley J. & Sons edit., New York : 601 p.

NOLF D (1993). A survey of perciform otoliths and their interest for phylogenetic analysis, with an iconographical synopsis of Percoidei. Bull. Mar. Sci., 52(1) : 220-239.

POUYAUD L, SUDARTO & TEUGELS GG (2003). The different colour varieties of the Asian arowana *Scleropages formosus* (Osteoglossidae) are distinct species : morphologic and genetic evidences. Cybium, 27(4) : 287-305.

RANA RS (1988). Freshwater fish otoliths from the Deccan Trap associated sedimentary (Cretaceous-Tertiary transition) beds of Rangapur, Hyderabad District, Andra Pradesh, India. Geobios, 21(4) : 465-493.

RUTOT A (1886). La tranchée de Hainin. Bull. Mus. Roy. Hist. nat. Belg., 4 : 61-74.

SANDERS M (1934). Die fossilen Fische der Alttertiären Süsswasserablagerungen aus Mittel-Sumatra. Verhandel. Geol.-Mijnbouwk. Genootsch. Nederl. Kolon., Geol. Ser., 11(1) : 1-144.

SCHLEICH HH, KASTLE W & GROESSENS-VAN DYCK MC (1988). Paläogene Eischalenreste von Hainin (Belgien). Paläont. Z., 62(1/2) : 133-146.

SCHMIDT-KITTLER N (1987). European reference levels and correlation tables. Münch. Geowissensch. Abh., A, 10 : 15-31.

SIGÉ B & MARANDAT B (1997). Apport à la faune du Paléocène inférieur d'Europe : un Plésiadapiforme du Montien de Hainin (Belgique). In : AGUILAR JP, LEGENDRE S & MICHAUX J (eds), Actes du Congrès Biochrom '97, Mém. Trav. Inst. Montpellier, Ec. Prat. H. Et., Sci. Vie Terre : 679-686.

SIGÉ B, BUSCALONI AD, DUFFAUD S, GAYET M, ROTH B, RAGE JC & SANZ JL (1997). Etat des données sur le gisement crétacé supérieur continental de Champ-Garimond (Gard, Sud de la France). Münch. Geowiss. Abh., A, 34 : 111-130.

STEURBAUT E (1998). High-resolution holostratigraphy of Middle Paleocene to Early Eocene strata in Belgium and adjacent areas. Palaeontogr., A, 247 : 91-156.

SUDRE J & RUSSEL DE (1982). Les Mammifères Montiens de Hainin (Paléocène moyen de Belgique). Part II : Les Condylarthres. Palaeovertebr., 12 : 173-184.

TAVERNE L (1976). Les téléostéens fossiles du Crétacé moyen de Kipala (Kwango, Zaïre). Ann. Mus. Roy. Afr. Centr., sér. in-8, Sci. Géol., 79 : 1-50.

TAVERNE L (1977). Ostéologie, phylogénèse et systématique des téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes. Première partie. Ostéologie des genres *Hiodon*, *Eohiodon*, *Lycoptera*, *Osteoglossum*, *Scleropages*, *Heterotis* et *Arapaima*. Acad. Roy. Belg., Mém. Cl. Sci., coll. in-8, 2e sér., 42(3) : 1-235.

TAVERNE L (1978). Ostéologie, phylogénèse et systématique des téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes. Deuxième partie. Ostéologie des genres *Phareodus*, *Phareoides*, *Brychaetus*, *Musperia*, *Pantodon*, *Singida*, *Notopterus*, *Xenomystus* et *Papyrocranus*. Acad. Roy. Belg., Mém. Cl. Sci., coll. in-8, 2e sér., 42(6) : 1-213.

TAVERNE L (1979). Ostéologie, phylogénèse et systématique des téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes. Troisième partie. Evolution des structures ostéologiques et conclusions générales relatives à la phylogénèse et à la systématique du super-ordre. Addendum. Acad. Roy. Belg., Mém. Cl. Sci., coll. in-8, 2e sér., 43(3) :1-168.

TAVERNE L (1998). Les ostéoglossomorphes marins de l'Éocène du Monte Bolca (Italie) : *Monopteros* Volta, 1796, *Thrissop-*

terus Heckel, 1856 et *Foreyichthys* Taverne, 1979. Considérations sur la phylogénie des téléostéens ostéoglossomorphes. In : Studi e Ricerche sui giacimenti terziari di Bolca. VII. Miscellanea Paleontologica, Mus. Civ. St. Nat. Verona : 67-158.

Vianey-Liaud M (1979). Les Mammifères montiens de Hainin (Paléocène moyen de Belgique). Part. I : Multituberculés. Palaeovertebr., 9 : 117-131.