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REASSESSMENT OF THE MORPHOLOGY OF *SCOMBROCLUPEOIDES SCUTATA* WOODWARD, 1908, A TELEOSTEAN FISH FROM THE EARLY CRETACEOUS OF BAHIA, WITH COMMENTS ON ITS RELATIONSHIPS [1]

(With 10 figures)

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ABSTRACT: *Scombroclupeoides scutata* is a teleostean fish known from the Neocomian (non-marine lowermost Cretaceous) of the Morro do Barro Formation, Almada Basin, State of Bahia. This fish is very scarce in paleontological collections and most of available specimens are poorly preserved. In order to furnish additional morphological data as a framework for evaluating its systematic position, five complete and relatively well preserved specimens from the paleontological collection of the Departamento Nacional de Produção Mineral were studied. The result indicates presence of informative features suggesting that *S. scutata* is more advanced than so-called leptolepids and proleptolepids (*e.g.*, absence of suborbitals, loss of fringing fulcra, reduced number of branchiostegals, absence of preopercular process of hyomandibula, subequal-sized dorsal and ventral hypohyals) and that, on the other hand, indicate putative affinities with primitive euteleostean fishes.

Key words: *Scombroclupeoides*. Euteleostei. Northeastern Brazil. Lower Cretaceous.

RESUMO: Reavaliação da morfologia de *Scombroclupeoides scutata* Woodward, 1908, um teleósteo do Eocretáceo da Bahia, com comentários sobre suas afinidades.

Scombroclupeoides scutata é um peixe teleósteo conhecido do Neocomiano (depósito não marinho do Cretáceo Inferior) da Formação Morro do Barro, Bacia do Almada, Estado da Bahia. Este peixe é raro em coleções paleontológicas e a maior parte dos espécimes disponíveis estão precariamente preservados. Com o intuito de fornecer informações morfológicas para o esclarecimento de sua posição sistemática, foram estudados cinco espécimes completos e relativamente bem preservados pertencentes à coleção paleontológica do Departamento Nacional de Produção Mineral. Os resultados indicam a presença de aspectos anatômicos informativos sugerindo que *S. scutata* é avançado em relação a táxons comumente referidos na literatura com leptolepídeos e proleptolepídeos (*e.g.*, ausência de suborbitais, perda das fulcras em franja, número reduzido de raios branquiostégios, ausência de processo preopercular do hiomandibular, hipiais dorsal e ventral de tamanho aproximado) e que, por outro lado, sugerem putativas afinidades com peixes euteleósteos primitivos.

Palavras-chave: *Scombroclupeoides*. Euteleostei. Nordeste do Brasil. Cretáceo Inferior.

INTRODUCTION

Time after time, Dr. Ignacio Machado Brito realized short trips for practicing field geology and collecting fossil in several localities from the northeastern Brazil, particularly in Bahia, securing his permanent reputation as a leading geologist and paleontologist, and contributing significantly to the development of these sciences in Brazil. Although devoted to fossil invertebrates, he also collected vertebrate remains, mainly fishes. This paper is about a Cretaceous fossil fish coming from the State of Bahia and is dedicated to him.

WOODWARD (1908) described a new species of clupeoid fish from the Lower Cretaceous of Ilhéus, State of Bahia, placing it into the genus *Scombroclupea* Kner, 1863 on the basis of abdominal scutes and thickened scales behind anal fin similar to those associated with finlets in species of *Scombroclupea* [*e.g.*, *S. macrophtalma* (Heckel, 1849) and *S. diminuta* Forey, Yi, Patterson & Davies, 2003]. The species was formally named *Scombroclupea scutata* Woodward, 1908. Later, WOODWARD (1942) erected a new genus for this species, *Scombroclupeoides*, pointing out that differences such as the presence of "expanded ventral ridge-scales, of which seven behind the anal fin are in spaced series" separated it from *Scombroclupea*.

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SCHAEFFER (1947), dealing with Cretaceous fossil fish material from Brazil, described *Leptolepis bahiaensis* Schaeffer, 1947, a poorly known species from the lacustrine fish beds of Ilhas Group, Bahia. Later, PATTERSON (1970) pointed out certain similarities among *Leptolepis bahiaensis*, *Scombroclupeoides scutata*, and *Leptolepis congolensis* Arambourg & Schneegans, 1935. The last one comes from the Neocomian of Coccobeach Series of Angola, West Africa, and was studied by TAVERNE (1975), who pointed out remarkable differences between it and *Leptolepis*. Thus, he erected the new genus *Wenzia* for this species, but since this name is preoccupied, he subsequently replaced it with *Wenzichthys* (TAVERNE, 1976). He also put *Wenzichthys congolensis* in Pattersonellidae, within Argentinoidei. According to Taverne's restoration, the structure of the caudal complex is very different from that of *Leptolepis bahiaensis*.

PATTERSON & ROSEN (1977, p.146) stated that: "*Leptolepis bahiaensis* Schaeffer (1947) is from the Lower Cretaceous (Neocomian) Ilhas Formation of Bahia, Brazil. We have examined the type-material, two fishes on a single slab. This species was briefly discussed by Patterson (1970b, p.289), who noted resemblances between it and *Scombroclupeoides scutata* Woodward, also from the Ilhas Formation of Bahia. Two differences were also mentioned between *L. bahiaensis*, as described by Schaeffer, and the type-material of *S. scutata*: the apparent absence of caudal scutes and epipleural intermusculars in the former. But our examination of *L. bahiaensis* shows that caudal scutes and epipleurals are present, so that the TWO SPECIES ARE PROBABLY SYNONYMOUS" (capitalized letter is mine). They also showed that the fish hitherto was not a clupeoid or leptolepid, but probably a clupeocephalan *incertae sedis* mainly due to the absence of abdominal scutes (mistake of Woodward, displaced opercular bones indeed), presence of epipleural intermuscular bones, and the presence of anterior outgrowth on the first uroneural in the caudal endoskeleton. But they used *Scombroclupeoides bahiaensis* as *nomen superfluum*, ignoring the availability of *S. scutata* Woodward, 1942.

MAISEY (1991), while dealing with *"Leptolepis" diasii* Santos, 1958, from the Araripe Basin stated that *Scombroclupeoides scutata* is separated of "*Leptolepis*" *diasii* by the caudal endoskeleton but he retained "*Leptolepis*" *bahiaensis* (*nomen inquirendum*), expressing his doubt about the proposed synonymy of *Scombroclupeoides scutata* and *Leptolepis bahiaensis* by PATTERSON & ROSEN (1977).

GAYET (1994), agreeing with morphological and phylogenetic data of PATTERSON & ROSEN (1977), suggested that *Scombroclupeoides bahiaensis* (=*S. scutata*) is closely related to the clupeocephalan *Tchernovichthys exspectatum* Gayet, 1994, from the Lower Cretaceous of Israel. Also, she suggested the placement of both species in Clupeomorpha.

While writing an essay on right and supposed fossil clupeomorph fishes from Brazilian strata, I had the opportunity to study some relatively complete specimens deposited in the Paleontological Collection of the Museu de Ciências da Terra, of the Departamento Nacional de Produção Mineral (DNPM). Some features present in these specimens allow me to agree with the synonymy suggested by PATTERSON & ROSEN (1977) but a redescription demonstrated to be necessary.

This paper is a complementary account of the osteology of *Scombroclupeoides scutata* based on material of DNPM. In the discussion, I included comments on certain fossil teleosteans not closely related to *Scombroclupeoides* but traditionally placed into *Leptolepis*-like taxa or even stem group otocephalans (protoclupeomorph fishes *sensu* TAVERNE, 1977).

MATERIAL AND METHODS

The material consists of complete and articulated specimens preserved in dark shale. I have considered the specimens all adults, in spite of their small size, because of the high degree of ossification of the skeleton and branching of fin rays.

The fossils was prepared using steel needles under a binocular microscope. A film of ammonium chloride was applied on surface of the fossils to enhance anatomical details during observations (see FELDMANN, 1989). All drawings were made using a camera lucida attached to a stereomicroscope Nikon SMZ 800. Abbreviations (r) and (l) before abbreviations of skeletal strucutures indicate right and left sides respectively.

Anatomical abbreviations: (a.cer) anterior ceratohyal; (a.smx) anterior supramaxilla; (aa) anguloarticular; (an.pt) anteriormost pterygiophore of the anal fin; (auc) autocentrum; (anto) antorbital; (asph) autosphenotic; (bs) basisphenoid; (ber. fo) beryciform foramen; (brr) branchiostegal rays; (chc) chordacentrum; (cl) cleithrum; (co) coracoid; (d.c) dentigerous cluster;

(d.c.sc) dorsal caudal scute; (d.hy) dorsal hypohyal; (de) dentary; (ecpt) ectopterygoid; (enpt) endopterygoid; (ep) epural; (ep.c) epiphyseal commissural canal; (epl) epipleural intermuscular bone; (epn) epineural intermuscular bone; (ethm.c) ethmoidal commissure; (f.r) fin rays; (fr) frontal; (gr.hyo.art) groove for hyodean artery; (h) hypural; (hm) hyomandibula; (h.arc) haemal arch; (h.sp) haemal spine; (inh) interhaemal bone; (io) infraorbital bone; (iop) interopercle; (k) keel; (lep.n) leptolepid notch; (let) lateral ethmoid; (l.l.c) lateral line canal; (md.c) mandibular sensory canal; (mpt) metapterygoid; (mx) maxilla; (n.arc) neural arch; (n.arc.pu1) neural arch of the first preural centrum; (n.sp), neural spine; (n.sp.pu2) neural spine of second preural centrum; (na) nasal; (not.c) notochordal canal; (op) opercle; (op.pr.hm) opercular process for hyomandibula; (ors) orbitosphenoid; (p. cer) posterior ceratohyal; (p.smx), posterior supramaxilla; (pa) parietal; (pa.b) parietal branch of supraorbital sensory canal; (pal) palatine; (pas) parasphenoid; (pcl) postcleithrum; (p.cr) clustered pigments of chromatophores; (pelv.b) pelvic bone; (pelv.spl) pelvic splint; (ph) parhypural; (pl.r) pleural rib; (pmx) premaxilla; (pop) preopercle; (pr.r) procurrent rays; (ptg) pterygiophore; (ptm) post-temporal; (pto) pterotic; (pts) pterosphenoid; (pu) preural centrum; (qu) quadrate; (rar) retroarticular; (rd) radials; (rode) rostrodermethmoid; (s) sympletic; (sca) scapula; (scl) supracleithrum; (sl.c) "slime" canal; (smx) supramaxilla; (sn) supraneural; (sop) subopercle; (sorb) supraorbital; (sorb.s.c) supraorbital sensory canal; (t.s.c.) temporal sensory canal; (u) ural centrum; (uh) urohyal; (un) uroneural; (v.hy) ventral hypohyal; (v.c.sc) ventral caudal scute.

SYSTEMATIC PALEONTOLOGY

TELEOSTEI Müller, 1844
CLUPEOCEPHALA Patterson & Rosen, 1977
EUTELEOSTEI Greenwood *et al.*, 1967
indetermined family

Scombroclupeoides Woodward, 1942

Diagnosis (amended) – small and slender fish reaching about 120mm total length, recognized by the following combination of features: head length contained of about 24% of maximum body length; cranial roof without ornamentation and lacking fontanelles; sagitate rostrodermethmoid with short ethmoideal commissure; drop-shaped nasal; parasphenoid edentulous and without basipterygoid process; large and arched maxillae weakly ornamented with longitudinal wrinkles and bearing a single row of minute conical teeth along the oral border; two smooth and longitudinally keeled supramaxillae; dentary edentulous with deep slime-canal, leptolepid notch, and coronoid process robust; fusiform antorbital present; one lanceolate supraorbital; suborbitals absent; preopercle triangular with few tubules of the main preopercular sensory canal not reaching its ventral and posterior border; quadrate-mandibular articulation beneath the hinder part of the orbit; dorsal and ventral hypohyals of subequal size; 13 branchiostegal rays; dorsal and pelvic fins in opposition; smooth and cylindrical vertebrae with large notochordal canal and two lateral ridges; pleural ribs moderately robust with longitudinal groove; epineural and epipleural intermuscular bones present; interhaemal bone present; three uroneurals, the first showing an anterior laminar outgrowth and reaching second preural centrum; neural spine and arch of first preural centrum reduced and lanceolate; three epurals; six autogenous hypurals, but diastema absent; parhypural fused with first preural centrum; dorsal and ventral caudal scutes present; fringing fulcra absent on leading border of caudal fin; 19 principal caudal rays. Uniquely derived character: a cluster of teeth on the posterior corner of the maxilla.

Type (and only) species – *Scombroclupea scuttata* Woodward, 1908 (Br.Mus.Nat.Hist., P.10570).

Scombroclupeoides scutata

1908 – *Scombroclupea scutata* Woodward; Woodward: 360, pl.43, figs.3-4.
1942 – *Scombroclupeoides scutata* Woodward; Woodward: p.909.
1947 – *Leptolepis bahiaensis* Schaeffer; Schaeffer: p.13, pl.2, figs.1-2.
1970 – *"Leptolepis" bahiaensis* Schaeffer; Patterson: p.289.
1977 – *Scombroclupeoides bahiaensis* (Schaeffer); Patterson & Rosen: p.146, fig.47.
1991 – *"Leptolepis" bahiaensis* (Schaeffer); Maisey: p.273.
1994 – *Scombroclupeoides bahiaensis* (Schaeffer); Gayet:p.89-90.

Horizon and Locality – Lower Cretaceous (Neocomian) of Almada Basin (Morro do Barro Formation); outcrop yielding dark greenish to

grayish shales in the Ilha de Bacuparytuba [currently Ilha de Bacuparituba in Lagoa Encantada (=Lagoa de Itaipé)], Municipality of Ilhéus, Bahia State (see HARTT, 1870, p.348; ROXO, 1936; NETTO, WANDERLEY FILHO, & FEIJÓ, 1994).

Referred material – DGM-DNPM 455-P (complete fish, total length 49mm); DGM-DNPM 948-P (incomplete specimen lacking caudal fin, estimated total length 62mm); DGM-DNPM 949-P (complete fish; total length 43mm); DGM-DNPM 950-P (almost complete fish lacking caudal fin rays; estimated total length 42mm); DGM-DNPM 951-P (complete fish, total length 58mm).

Meristics – D ii, 10; P 12; V9; A i,8; C x, I, 9, 8, I, x. Vertebrae: 37-38 (19-22 abdominal, 16-17 caudal).

Remarks – The type-specimen (AMNH 10014) of the so-called *Leptolepis bahiaensis* was figured by SCHAEFFER (1947, pl.2), including a photograph and a line drawing. It corresponds to complete but flattened fish with skull badly crushed so that few informative characters are available. All that may be seen of the specimens used in the description is described and figured by him and complemented by PATTERSON (1970). It is not suitable for a detailed analysis. The measurements and proportions of this specimens agree with that of the DNPM material. Both, the AMNH and DNPM materials come from the same locality, that is Ilha de Bacuparituba. It is probable that only part of the material collected in the 1930s and sent to the American Museum of Natural History by the late Director of the Geological Survey of Brazil, Euzebio de Oliveira, was studied by Schaeffer. Other material remained in Brazil, particularly in the DNPM collection. Fortunately, the DNPM specimens are better preserved than that of AMNH and BMNH having many informative characters, therefore they are mainly used in the description. In addition, I have also examined the type-material of *Scombroclupea scutata* (P 10570) housed in the BMNH and, agreeing with PATTERSON & ROSEN (1977), assuming that both species are synonyms.

ANATOMICAL DESCRIPTION

Skull

The skull roof (Figs.1-4) is smooth except for cannulate relief for sensory canals on surface of certain bones. In the snout region there is a reduced and sagitate rostrodermethmoid (Fig.1, 3-4, rode) provided of short lateral process. There is a short ethmoidal commissure (Fig.3, ethm.c) passing through the bone transversally. The nasal (Figs.3, na) is an elongate drop-shaped bone reduced to its neurodermal component. The squarish lateral ethmoid (Fig.4, let) is relatively large and corresponds to a flimsy shield of perichondral bone obliquely placed in the anterior margin of the orbit.

The frontal (Figs.1-4, fr) is the largest bone of the skull roof covering most of the orbit. It is narrow anteriorly and broadens progressively backwards, expanding at the posterior margin of the orbit. No sclerotic bones are preserved inside the orbit. There is a sinuous median contact between the frontals. The supraorbital sensory canal (Fig.2-4, sorb.s.c) runs the frontal in an almost straight bony tube which gives off an atrophic medial tubule posteriorly, interpreted as an epiphyseal commissural canal (Fig.2, ep.c). In the posterior third of frontal, the supraorbital sensory canal gives off a long and sinuous parietal branch (Fig.2, pa.b) running towards the parietal and piercing its anterior half (as in *Elops lacerta* Cuvier & Valenciennes, 1846; see TAVERNE, 1974). A connection between the temporal and supraorbital sensory canals is present as in *Paraclupavus caheni* de Saint-Seine & Casier, 1962 (TAVERNE, 2001). The parietal (Figs.1, 2 and 4, pa) is relatively large and squarish and meets its partner medially. Pit-lines are absent.

The autosphenotic (Fig.4, asph) is a triangular bone sited in the postero-dorsal corner of the orbit. It has a well-developed spine-like process and bears a short oblique articular facet for the hyomandibula. The pterotic (Fig.1,2 and 4, pto) is a roughly trapezoid bone. The temporal sensory canal (Fig.2 and 4, t.s.c) passes through the bone near its lateral border. In the posterior third of the bone there is a short branch followed by an opening for preopercular sensory canal, indicating the division of the temporal sensory canal into its otic and post-otic portions.There is no evidence of a *recessus lateralis* or transverse parietal-pterotic pit-line.

The supraoccipital is not discernible. There are crushed dermal bones in the occiput of most of the specimens interpreted as remains of extrascapula.

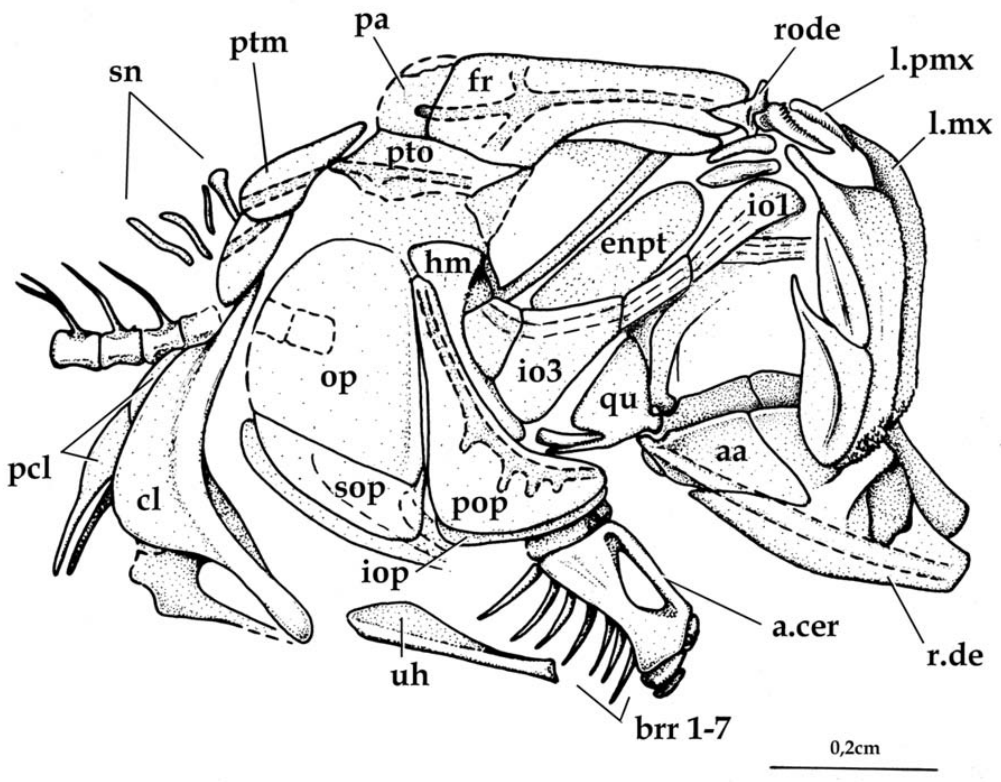

Fig.1- *Scombroclupeoides scutata.* Skull, pectoral girdle, fin rays, and anteriormost vertebral column with associated elements as preserved in DGM-DNPM 949-P.

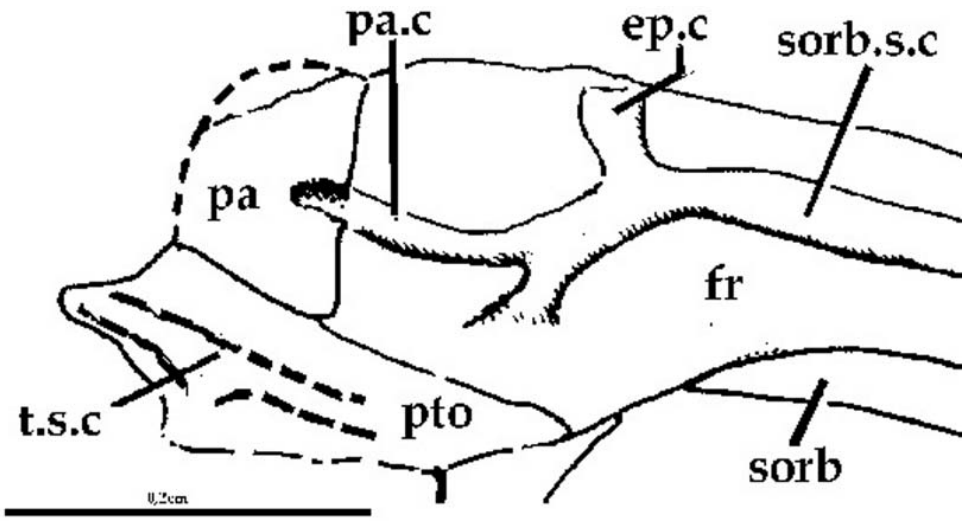

Fig.2- *Scombroclupeoides scutata.* Detail of the skull roof showing pattern of arrangement of sensory canals as preserved in DGM-DNPM 949-P.

Bordering the orbit, there is a ring of circumorbital bones. A long spatulate supraorbital (Figs.2-4, sorb) lies in the anterodorsal part of the orbit. The antorbital (Fig.3, anto) is a large fusiform bone (apparently non-anamestic) bordering the large and trapezoid first infraorbital dorsally (Fig.1, io1). Posteriorly, the first infraorbital (lachrymal) meets the rectangular second infraorbital (Fig.3, io2). The third infraorbital is trapezoidal and is the largest bone of the series, and it is placed on the posteroventral corner of the orbit. It seems to cover partially the quadrate. There is a short and squarish fourth infraorbital bone (Fig.3, io4). The infraorbital sensory canal runs the infraorbital bones through a thin longitudinal tube. Only the first infraorbital gives off short tubules (at least three are visible in DGM-DNPM 951). The other two infraorbitals (fifth and sixth infraorbitals) are poorly preserved in all specimens, but they appear to be small and flimsy plate bones as in *Leptolepides sprattiformis* (Blainville, 1818) (TAVERNE, 1981).

Inside the orbit, a crescent-shaped pterosphenoid is visible in 950-P (Fig.4, pts). Anteriorly, it meets an anvil-shaped orbitosphenoid (Fig.4, ors) which has a slightly oblique crest at its middle point. A shallow cleft for the olfactory nerve is visible in its anterior end. From the basisphenoid (Fig.4, bs) there is only an impression in the rock of a forwardly inclined pedicel placed at the posteroventral corner of the orbit.

The parasphenoid (Fig.3-4, pas) is a long and inclined shaft of bone. It is toothless and lacks a basipterygoid process. Anteriorly, it meets a toothless vomer (Fig.4, vo) at the level of lateral ethmoid.

The premaxilla (Figs.1, 3-4, pmx) is a small triangular bone. It shows a relatively large and round ascending process. The toothed alveolar process is long but does not extend below the maxilla. It bears a row of pointed teeth.

The maxilla (Figs.1-5, mx) is large and moderately arched with a long and simple capitate anterior process. The maxilla is weakly ornamented with longitudinal wrinkles (especially in large specimens) and has a row of minute conical teeth on its oral border finishing in a cluster of conical teeth on its posterior part (Fig.3, d.c). Two supramaxillae overlie a dorsal crest of the maxilla. The anterior supramaxilla (Figs.3-5, a. smx) is a broad spindle-shaped bone. It is partially covered by the large posterior supramaxilla, whose shape resembles a rose thorn. The anterodorsal process of the posterior supramaxilla (Figs.3-5, p.smx) is long and pointed but does not extend forwards to cover the first supramaxilla as in *Clupavus maroccanus* Arambourg, 1968 (TAVERNE, 1977). Both supramaxillae are devoid of ornamentation except for a deep longitudinal keel (Fig.5, k).

The dentary (Figs.1, 3, and 5, de) is short and deep, with well-developed coronoid process (Fig.5, cor.pr), and apparently lacks teeth on the oral border. No pores for mandibular sensory canal are visible on surface. A so-called “slime canal” (probably a fossa to anchor upper jaw ligaments) (Figs.3 and 5, sl.c) forms a deep groove at the midpoint of the oral border of the dentary and a leptolepid notch (Figs.3 and 5, lep.n) is present in front of the coronoid process. The angular is apparently co-ossified with articular forming a large angulo-articular bone (Figs.1, 3, and 5, aa), which shows a deep articular facet for the quadrate. The postarticular process is short and round. No pore is visible on the lateral face of the angulo-articular suggesting a medial opening for the mandibular sensory canal. A comma-like retroarticular (Figs.3 and 5, rar) is present in the posterior corner of the lower jaw immediately beneath the articular facet, but is excluded from the joint surface for the quadrate. The mandibular sensory canal runs throughout the bone in a rectilinear tube near its ventral border (Figs.3 and 5, md.c).

The hyomandibula (Figs.1, 3-4, hm) shows a large and apparently single oblique articular head for the autosphenotic and pterotic. The opercular process is large and rounded. The ventral process is relatively long and there is an anterior flimsy lamina for the trapezoidal metapterygoid (Fig.4, mpt). There is no preopercular process for the hyomandibula as usually found in the so-called leptolepid fishes [*e.g.*, *Leptolepis coryphaenoides* (Bronn, 1830)].

The quadrate (Figs.3-4, qu) is large and slightly curved anteriorly. It has a shallow cleft for the long and pipe-like sympletic (Figs.3-4, s), as well as a long and straight postero-ventral process bordering the anterior part of sympletic ventrally. The articulatory condyle of the quadrate is well-developed. Anteriorly, the quadrate abuts against the boomerang-shaped ectopterygoid (Figs.3-4, ecpt) which projects forwards to meet the toothless and anvil-like palatine (Fig.4, pal). The endopterygoid (Figs.3-4, enpt) forms an ovoid lamina beneath the parasphenoid.

The opercular series is relatively narrow but most of the bones are incompletely preserved in

all specimens. The opercle (Figs.1 and 4, op) is roughly triangular, with its dorsal edge rounded off. There is no crenulation in the posterior border. The subopercle (Fig.1, sop) is falcate and relatively large, with a rounded posteroventral edge and narrow posterodorsal portion; it shows a reduced finger-like process at its anterodorsal corner. The interopercle (Fig.1, iop) is a long triangular bone mostly hidden by the preopercle (Figs.1 and 4, pop). The latter is elongate and roughly L-shaped with a shorter horizontal than vertical limb. The preopercle lacks a posteroventral projection or a notch on its posterior margin. The preopercular sensory canal (Fig.4, pop.s.c) is enclosed in a bony tube close to its anterior margin, giving off at least four short and slightly arched tubules do not reach its ventral or posterior margin.

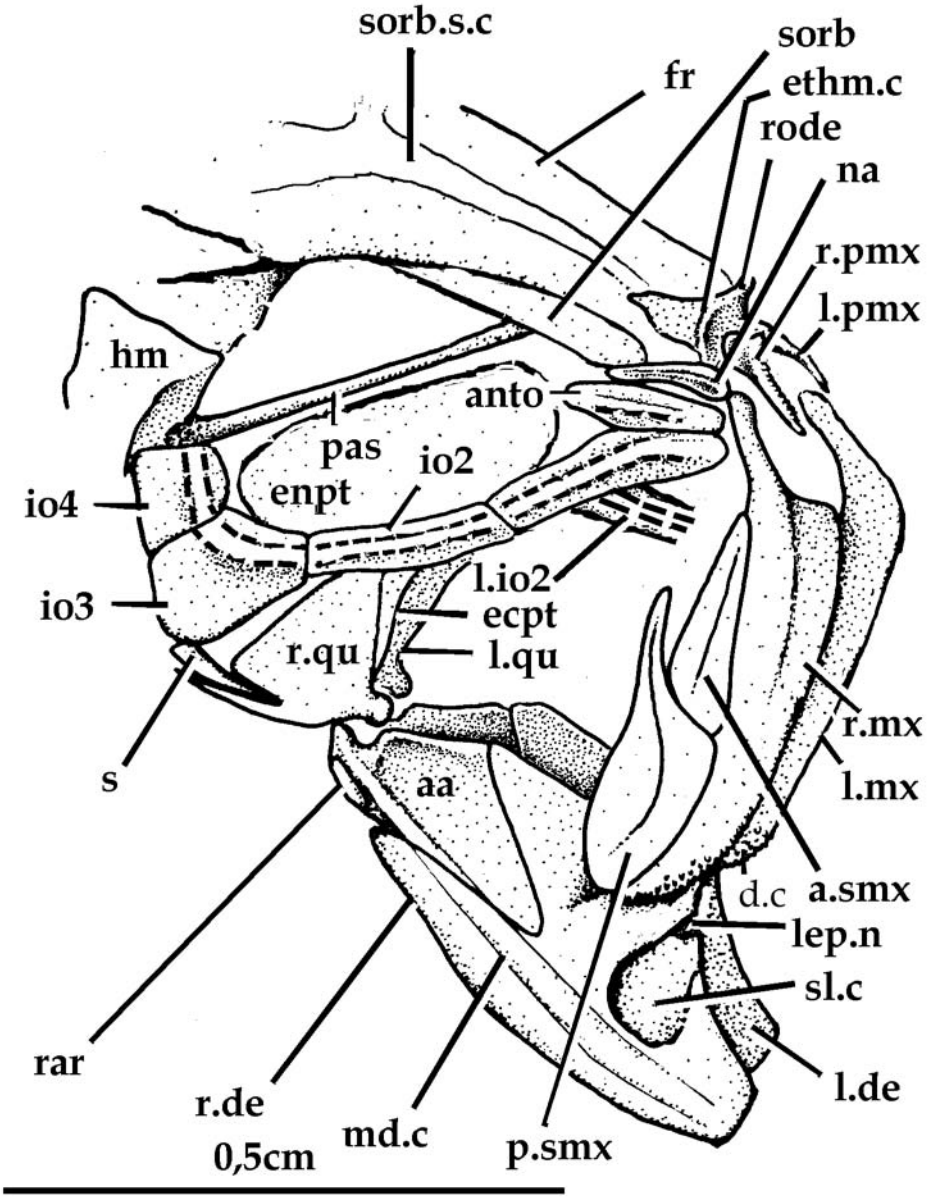

Fig.3- *Scombroclupeoides scutata.* Skull roof, circumorbital bones, upper and lower jaw, and associated strutures as preserved in DGM-DNPM 949-P

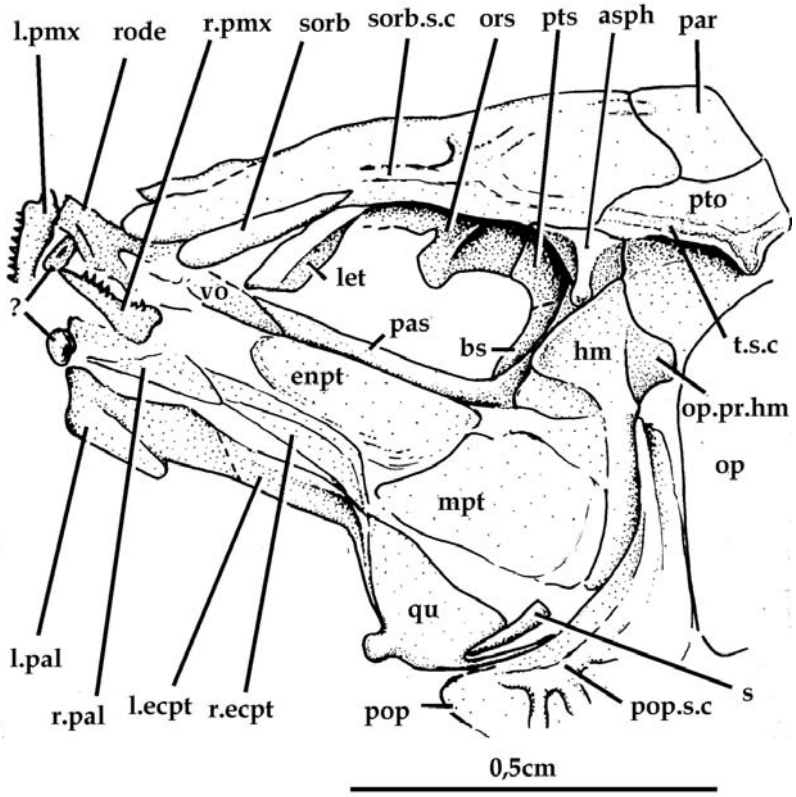

Fig.4. *Scombroclupeoides scutata.* Neurocranium and suspensorium as preserved in DGM-DNPM 950-P.

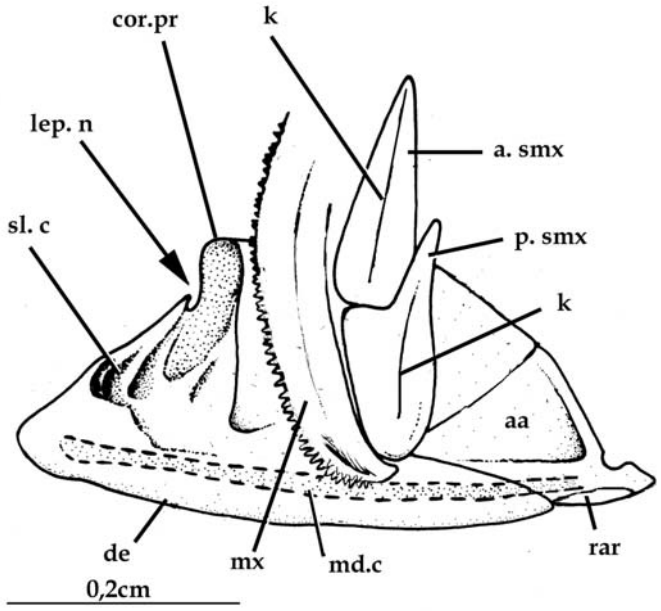

Fig.5- *Scombroclupeoides scutata.* Upper and lower jaw as preserved in DGM-DNPM 950-P.

The dorsal and ventral hypohyals (Fig.6, d.hy and v.hy) are small bones of almost equal size. The ventral hypohyal is the largest and better preserved in the examined specimens. Both seem to have been synchondrally articulated in life with the obtuse anterior surface of the anterior ceratohyal (Figs.1, 3, and 5, a.cer). The latter is a hourglass shaped bone in lateral view and shows a large triangular beryciform foramen (Fig.6, ber.fo) followed by deep groove for the hyodean artery posteriorly (Fig.6, gr.hyo.art). Its ventral margin bears seven to eight slender and acinaciform branchiostegal rays (Figs.1 and 6, brr). The posterior ceratohyal (Figs.1, 3, and 5, p.cer) forms an almost equilateral triangle whose anterior border is truncate. Its anterior half bears a longitudinal short deep groove for the hyoidean artery continuing that from the anterior ceratohyal. The bone supports about five falcate branchiostegal rays, the posteriormost of which are large and falcate. The total number of branchiostegals is low when compared with certain *Leptolepis*-like taxa (*e.g.*, *Proleptolepis elongata* Nybelin, 1974) in which can reach twelve.

The urohyal (Figs.1 and 6, uh) is a long and shallow shafted bone provided of a short capitate anterior end. Other hyobranchial elements are not sufficiently preserved to permit a suitable description. Gular plate is absent.

Pectoral girdle and fin

The posttemporal (Figs.1 and 8, ptm) is only visible laterally. It is well-developed and triangular with a large base bearing an oblique sensory canal. The supracleithrum (Figs.7a and 8, scl) is spatulate and bears the main lateral line sensory canal (Fig.7a and 8, l.l.c) on the superior half of its posterior border.

The cleithrum (Figs.1, 7a, and 8, cl) is large with almost equal dorsal and ventral limbs. At the confluence of both limbs the bone expands posteriorly. The anterior margin of the bone is strengthened by a strongly ossified arch. The dorsal limb ends in a prominent spine for the supracleithrum. The lateral lamina is well developed and bears three scale-like postcleithra (Figs.1 and 7a, pcl) in a series posteriorly. The ventralmost is ovoid with slender and long ventral process, but the other two are falcate.

There are four slender proximal radials (Fig.7a, rd) plus very reduced distal ones, forming a graded series supporting twelve fin rays (Fig.7a, f.r). The anteriormost fin ray shows typically a large proximal end associated with an enlarged propterygium.

The scapula (Fig.7a, sca) is reduced and typically bears an oval scapular foramen. The coracoid (Fig.7a, sca) is short and arched but does not reach the antero-ventral tip of the cleithrum. It is impossible to determine the presence or absence of a mesocoracoid arch due to the poor preservation of the girdle at this level.

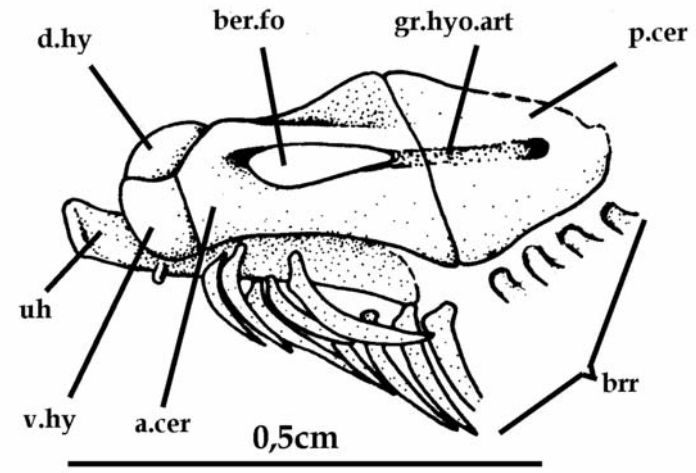

Fig.6- *Scombroclupeoides scutata*. Some hyoidean bones as preserved in DGM-DNPM 949-P.

Pelvic girdle and fin

The pelvic bone (Fig.7b, pelv.b) lies in front of the origin of the dorsal and pelvic fins beginning approximately below the first fin-ray of the dorsal. It is a roughly triangular plate with a well marked ridge running from the anterior tip to its posterolateral corner. It bears a well-developed posterior process medially. There are two minute inner pelvic radials associated with fin rays. There is one splint bone (Fig.7b, pelv.spl) plus nine fin rays, all of which are segmented and branched distally (Fig.7b, f.r). Therefore, it differs from the higher count for the most of the so-called leptolepids (13-14) [*e.g.*, *Leptolepis coryphaenoides* (Bronn, 1830); see NYBELIN, 1974]. The axillary process was not found in any specimen.

Vertebral column and associated bones

The vertebral column is composed of 37-38 vertebrae. The anteriormost ones are slightly displaced from the main body axis in almost all specimens. It is difficult to identify the precise transition from abdominal to caudal vertebrae, but apparently there are 16-17 vertebrae in the caudal region. Each vertebra consists of a smooth holospondylous centrum that is longer than deep, with two lateral longitudinal ridges. Apparently, each centrum is composed by a thin autocentrum (Fig.8, auc) covering a thick chordacentrum (Fig.8, chc). A large notochordal canal (Fig.8, not.c) is visible. Both halves of each neural spine are separated medially in the abdominal vertebrae and fused to each other in the caudal vertebrae (Figs.8-9, n.sp). In the caudal region, neural (Fig.9, n.sp) and hemal spines (Fig.9, h.sp) almost reach the dorsal and ventral borders of the body. The pleural ribs (Fig.8, pl.r) are long and stout with a longitudinal groove. The ribs are attached to large parapohyses and almost reach the ventral edge of the body. A set of short, thin arched intermuscular epineurals (Fig.8, epn) are associated with the abdominal vertebrae. They are almost parallel to the neural spines and each one is apparently attached to the base of the neural arch.

Short and aciform epipleurals (Fig.9, epl) when present (949-P and 455-P) are only visible in the transition from the abdominal to caudal region (preural vertebrae 16-19), and overlie the proximal ends of the rib or the bases of the hemal arches, where they are parallel to the vertebral column.

There are of about twelve long sigmoid and slender supraneurals (Figs.1 and 8, sn) extending from behind the occiput to the first proximal pterygiophore of the dorsal fin. Blackish spots of minute size, apparently representing pigments of chromatophores (Fig.8, p.cr), are visible above the anteriormost supraneurals.

The dorsal fin is short-based and supported by twelve long, triangular proximal pterygiophores. The first dorsal pterygiophore is broad and long and has two anterior projections. The other pterygiophores are narrow and slender. The posteriormost oe is very reduced and triangular. There are 12 fin rays, all segmented and distally branched except for the anteriormost two which are very reduced and unbranched.

The anal fin is small and remote, originating below the twelfth preural vertebra and extending to the ninth. There are eight slender and straight pterygiophores supporting nine fin rays (Fig.9, f.r). The first pterygiophore (Fig.8, an.pt) is long and more obliquely inclined than the others. It contacts the hemal spine of preural vertebra 14. There is a short and slender club-like interhemal bone (Fig. 8, inh) between preural vertebrae13 and 14.

Caudal endoskeleton and fin and squamation

Four preural vertebrae plus two ural centra support the caudal fin. There are six autogenous hypural plates (Fig.10, h). The first and second hypurals are subequal and articulate with each other proximally. Both are attached to the first ural centrum (Fig.10, u1). A large hypural foramen is present between them. A diastema is absent between second and third hypurals. The 3-6 dorsal hypurals gradually decrease in size upwards. The third hypural is the largest and has a long longitudinal crest. The parhypural (Fig.10, ph) is fused to the first preural centrum.

Three uroneurals are present (Fig.10, un), the first one is the largest and stretches forwards reaching the second preural centrum (Fig.10, pu2). A shallow outgrowth is visible on its anterior margin. The neural arch of the first ural centrum seems to be ankylozed with the other neural arch and uroneural complexes. It is tentatively interpreted as a stegural (Fig.10, st?) in spite of the difficult to identify a possible fusion of uroneural with a neural arch in poorly preserved and non three-dimensional fossils.

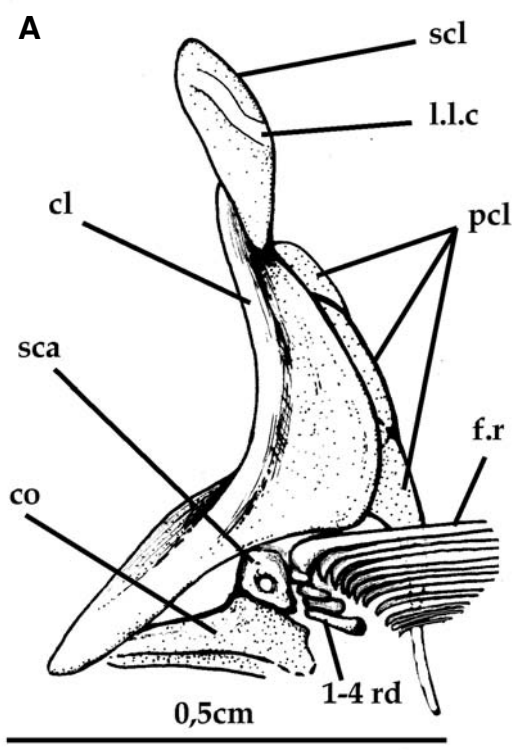

Fig.7- *Scombroclupeoides scutata*. (A) pectoral girdle and fin as preserved in DGM-DNPM 951-P; (B) pelvic bone and fin rays as preserved in DGM-DNPM 951-P.

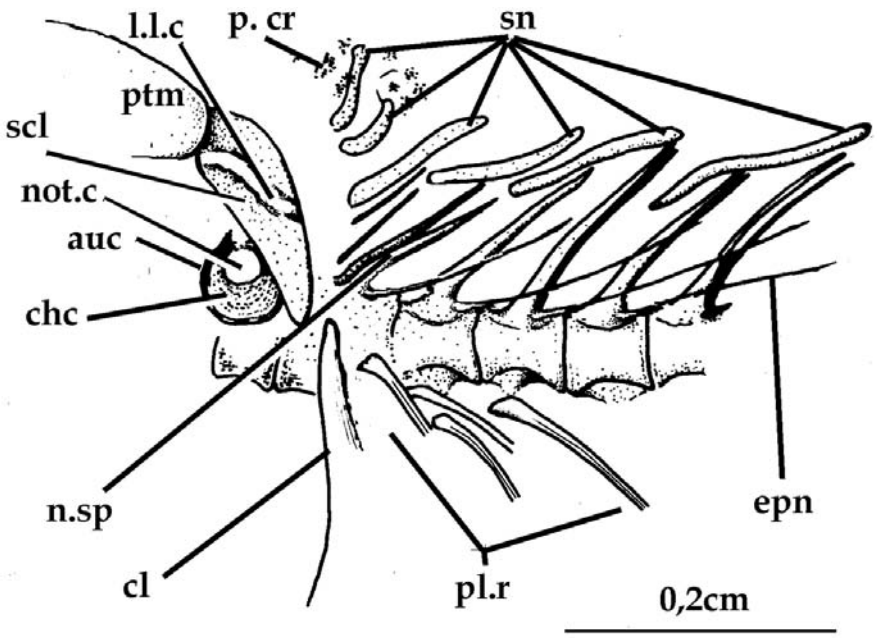

Fig.8- *Scombroclupeoides scutata.* Vertebral column in abdominal region and associated structures as preserved in DGM-DNPM 950-P.

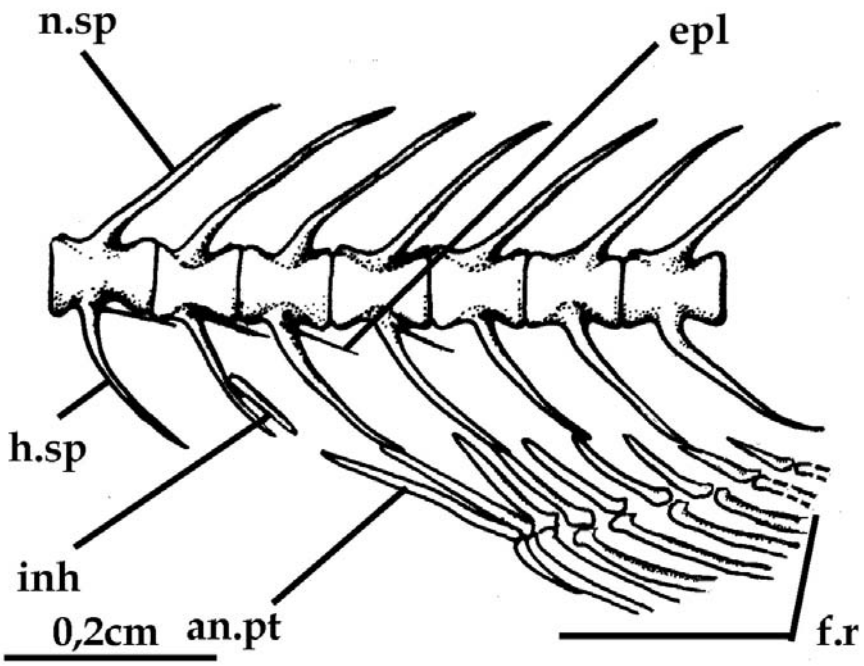

Fig.9- *Scombroclupeoides scutata.* Vertebral column in caudal region and associated bones (including anal pterygiophores), restored based in DGM-DNPM 950-P.

In DGM-DNPM 951-P there is a cleft in the anterior end of the first uroneural resembling the condition of the extant *Elops saurus* Linnaeus, 1766 and in DGM-DNPM 453-P the first uroneural apparently does not reach the second preural centrum. The second uroneural (Fig.10, un 2-3) reaches the posterior end of the second ural centrum while the third (Fig.10, un 2-3) one is more remote originating at the level of the sixth hypural. The fin rays of the upper lobe of the caudal fin extend over 4-6 hypurals. The first preural neural arch and spine (Fig.10, n.arc.pu1) is very reduced. The neural spine of the second preural centrum (Fig.10, n.sp.pu2) is long and slender but it is shorter than other neural spines. There are three elongate and narrow epurals (Fig.10, ep), obliquely and independently positioned above the upturned caudal axis.

There are 19 principal caudal fin rays, 9 segmented and branched fin rays in the dorsal lobe and 8 below. The two innermost principal rays of the dorsal and ventral lobes have expanded bases and partially cover the third and second hypurals respectively. There are 10 procurrent rays in both the dorsal and ventral lobes, and the two posteriormost ones are segmented. There are no fringing fulcra along the leading border of the epaxial and hypaxial lobes, but elongate dorsal (Fig.10, d.c.sc) and ventral caudal scutes (Fig.10, v.c.sc) precede the procurrent caudal rays associated with neural and hemal spines of preural vertebrae 3-5.

Few is known of the squamation. Only faint impressions of oval and imbricate cycloid scales with circuli but without radii are visible in certain parts of best preserved specimens. Along the dorsal and ventral edges of the tail are dark stripes probably representing clustered pigments of chromatophores.

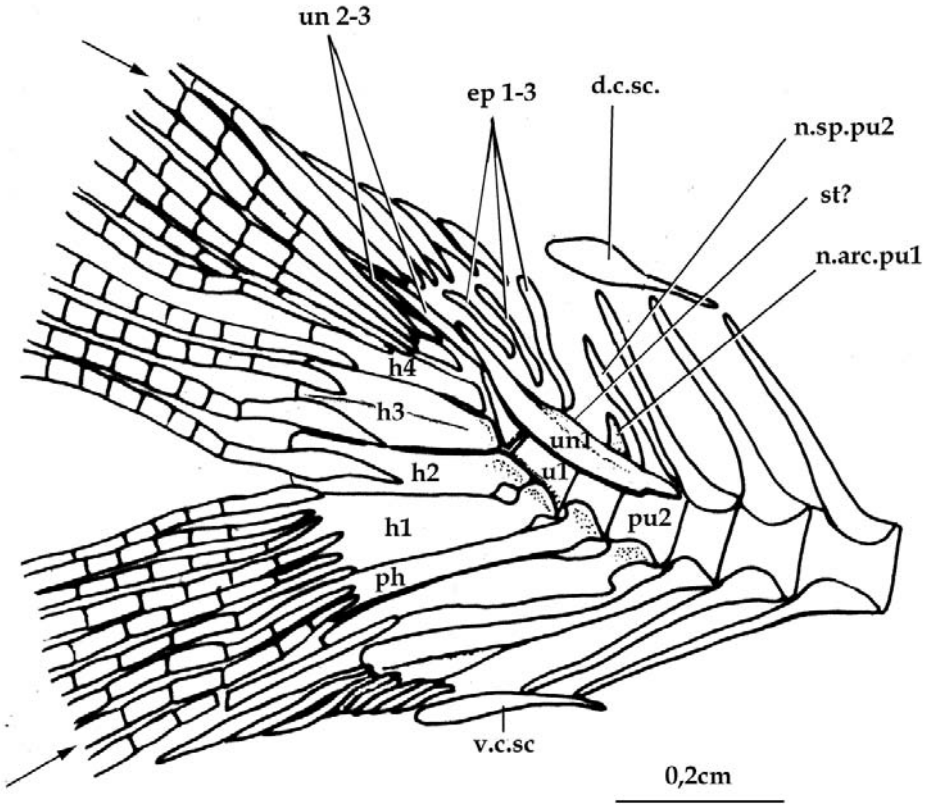

Fig.10- *Scombroclupeoides scutata.* Caudal endoskeleton and fin rays as preserved in DGM-DNPM 949-P. Arrows indicates unbranched principal fin rays.

DISCUSSION AND CONCLUSIONS

Previous descriptions (WOODWARD, 1908; SCHAEFFER, 1947) and interpretations (PATTERSON, 1970; PATTERSON & ROSEN, 1977; MAISEY, 1991; GAYET, 1994) of the anatomy of *S. scutata* have been contradictory. The specimens studied by A.S. Woodward and deposited in the British Museum are the largest, each one reaching about 12cm maximum length, whereas Schaeffer's specimens range from 4.4 to 5.7cm. Comparing the descriptions, is evident that Woodward's specimens are more incomplete. For instance, he noted fewer pectoral fin rays (8 instead of 12). But the count of fin rays and vertebrae show the close similarity among specimens. It is corroborated with the counts of this paper. WOODWARD (1908) and SCHAEFFER (1947) did not observe epipleural bones, or teeth on dermal bones of the upper oral border of the specimens they examined. Although PATTERSON & ROSEN (1977) noted the presence of diastema in the caudal endoskeleton, this is probably due to the fact that the ventral border of the third hypural below the longitudinal keel is frequently damaged or lost in specimens. They also omitted the presence of short neural spine and fused parhypural on the first preural centrum, probably because of the poor preservation of available specimens.

Scombroclupeoides shares with *Leptolepis*-like taxa and remaining teleosts the presence of cycloid scales and principal fin rays of the upper caudal lobe reduced to one simple plus nine branched rays. It is more advanced than *Proleptolepis elongata* and *Leptolepis coryphaenoides* in lacking an enameloid layer on skull bones, loss of the prearticular in the lower jaw, and presence of smooth autocentra weakly constricting the notochord, and first ural centrum bearing two hypurals (see PATTERSON & ROSEN, 1977).

With *Leptolepis coryphaenoides* (see WENZ, 1967; NYBELIN, 1974) it shares three epurals, loss of separate surangular and presence of retroarticular in the corner of lower jaw, lower caudal lobe with one simple and eight branched rays, loss of fringing fulcra on ventral margin of lower lobe of the caudal fin. It shares with osteoglossomorph fishes and clupeocephalans a reduced number of hypurals (less than seven in *Scombroclupeoides*), and caudal axis upturned at level of first preural centrum.

Scombroclupeoides scutata, *Leptolepides sprattiformis* (TAVERNE, 1981; ARRATIA, 1997) and *Tchernovichthys exspectatum* (Gayet, 1994) share many similarities in advance to *Proleptolepis elongata* and pholidophorid fishes. So far as known, in all these taxa the retroarticular is excluded from the articular surface for the quadrate, the angular and articular are co-ossified, there is a reduced number of tubules in the preopercular sensory canal, a preopercular process in the hyomandibula is absent, epipleurals are present, and there is an anterior outgrowth of the uroneural. *Scombroclupeoides* Woodward, 1942 and *Tchernovichthys* Gayet, 1994 share the first pterygiophore of dorsal fin in a single piece and absence of a basipterygoid process. *Leptolepides* Nybelin, 1974 is more primitive than *Scombroclupeoides* and *Tchernovichthys* in having a higher number of hypurals and extension of the first uroneural over the third preural centrum (see TAVERNE, 1981; ARRATIA, 1997, 1999).

ARRATIA (1997) combined *Leptolepides* together with *Orthogonikleithrus* Arratia, 1987 into the family Orthogonikleitridae. Both share an anteriorly expanded supraorbital (not verified in *Scombroclupeoides* or *Tchernovichthys*). She did not discuss the status of *Scombroclupeoides* and *Tchernovichthys*, but they are probably more advanced than Orthogonikleithridae at least by the caudal endoskeleton. *Scombroclupeoides* agrees with *Leptolepides* in retaining a connection between the supraorbital and infraorbital sensory canals.

GAYET (1994) erroneously thought that retroarticular is included in the quadrate-mandibular joint and that a diastema is present in *Scombroclupeoides*. She suggested a close affinitiy between *Tchernovichthys* and *Scombroclupeoides*, based on ankylosis of the neural arch over first ural centrum with other neural arch and uroneural complexes. In addition, she pointed out similarities in the caudal endoskeleton. Curiously, the differences based on caudal skeleton between both taxa stated by M. Gayet simply do not occur. Although both have a caudal endoskeleton without a diastema, dorsal and ventral caudal scutes, and median fin rays of similar size and shape, these features are better interpreted as plesiomorphies.

Tchernovichthys has 11 branchiostegal rays, whereas *Scombroclupeoides* possesses 12. Also, *Scombroclupeoides* has 9 pelvic fin rays whereas *Tchernovichthys* has 6. GAYET (1994) suggested that *Tchernovichthys* is more advanced than *Scombroclupeoides* based on these counts, but such variation is probably unreliable in establishing phylogenetic relationships (McALLISTER, 1968; PATTERSON, 1970). *Scombroclupeoides* differs from *Tchernovichthys* for having a connection between supraorbital and infraorbital canals, short first

preural neural arch, hypural foramen, first preural centrum fused to parhypural, and uroneural not extending forward beyond second preural centrum. On the other hand, the neural arch of the first preural centrum is reduced and lanceolate in *Scombroclupeoides* (not figure by PATTERSON & ROSEN, 1977), and there is an uniquely derived long acessory neural spine between neural spines of preural centra 4-5 in *Tchernovichthys.*

Some features of clupeomorphs and euteleostean fishes are shared by both taxa but a placement of them in Clupeomorpha as claimed by GAYET (1994) is not justified. *Scombroclupeoides* and *Tchernovichthys* lack all synapomorphies of the group as stated by GRANDE (1985), i.e., abdominal scutes, otophysic connection, second hypural fused to first ural centrum (see MAISEY, 1993, for a critical review of synapomorphies proposed by GRANDE, 1985). In addition, the anamestic antorbital claimed by GAYET (1994) to be diagnostic for the group is a widely spread character found in various non-clupeomorph fishes.

A comparison with other fossil euteleosts found in Brazilian Cretaceous strata is inevitable because of general similarities shared. *Santanichthys diasii* (Santos, 1958) is a rare otophysan fish found in Brazilian marine Cretaceous strata, particularly in the calcareous concretions of the Romualdo Member in Santana Formation (Araripe Basin). It is a small-sized fish as *Scombroclupeoides* but it differs from that by several remarkable anatomical features. For instance, *Santanichthys* has skull roof with posterior fontanelle, maxilla with oral border strongly convex and toothless, and Weberian apparatus (SANTOS, 1995; FILLEUL & MAISEY, 2004; FIGUEIREDO & GALLO, 2004). Noteworthy, the caudal skeleton shows a long second ural centrum, fused first preural and ural centra, and, apparently, a pleurostyle (MAISEY, 1991; FILLEUL & MAISEY, 2004; FIGUEIREDO & GALLO, 2004). The arrangement and shape of caudal endoskeleton resembles that of the *Clupavichthys* Gayet, 1989 an otocephalan closely related to the clupavid *Clupavus* Arambourg, 1950, from the Cretaceous of Equatorial Africa (GAYET, 1989), and *Lusitanichthys* Gayet, 1981 from the European Cretaceous (GAYET, 1981).

Finally, *Britoichthys marizalensis* Figueiredo, 2004, a small and slender euteleostean fish from the Lower Cretaceous of the Tucano Basin (Marizal Formation) is separate of *Scombroclupeoides scutata* by having fang-like teeth, dentate and massive dentary, two epurals, neural spine of second preural centrum equal in size to other preural spines, and presence of leaf-like process of first preural neural arch (FIGUEIREDO, 2004).

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