OSTEOLOGY AND RELATIONSHIPS OF THE GENUS *SPANIODON* (TELEOSTEI, SALMONIFORMES) FROM THE SANTONIAN (UPPER CRETACEOUS) OF LEBANON

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ABSTRACT. The genus *Spaniodon* is decribed in detail. Contrary to previous authors, we have only recognized two species, *S. elongatus* and *S. latus. Spaniodon* shows the synapomorphies of clupeocephalans, protacanthopterygians and salmoniforms. Its relationships among salmoniforms are still undecided, although it could be closely related to the Osmeroidei. The main character that supports this grouping is the dermal part of the mesethmoid formed by the partial fusion of a pair of lateral dermethmoids, whereas the rostral is absent. These conclusions are also supported by a global phylogenetic study of the teleosts.

KEY WORDS: Teleostei, Salmoniformes, *Spaniodon*, Lebanon, Upper Santonian.

THE genus *Spaniodon* was erected by Pictet (1850, pp. 33–36) for a small marine teleost fish recovered from Upper Santonian localities at Sahel Alma, Lebanon. This fish displays very well-developed caniniform teeth, and larger specimens reach 250 mm in total length. It was a predatory fish and its abdominal cavity often contains the remains of other, almost complete, small fishes.

Originally, Pictet (1850) divided *Spaniodon* into two different species, *S. blondeli* Pictet, 1850, the type species, being characterised by a moderately elongated head and body, and *S. elongatus* Pictet, 1850, the head of which is longer and the body more elongated in shape.

Pictet and Humbert (1866, pp. 86–87) included a third species from Sahel Alma: *S. brevis* Pictet and Humbert, 1866, previously described by Agassiz (1844) as *Clupea lata*. This species is mostly characterized by a deeper head and a shorter body. Woodward (1901, pp. 53) renamed it *Spaniodon latus* (Agassiz, 1844).

A fourth species, *S. simus* Cope 1878, from the Niobrara formation (Upper Turonian–Lower Campanian) of Yankton, South Dakota (USA) was subsequently described (Cope, 1878, p. 69; Hay 1903, pp. 47–48). We have studied this material, which appears to be identical to *S. latus*. The only difference proposed by Hay (1903, p. 47) to separate this form from *S. latus* is the number of vertebrae (45 against the 50 vertebrae counted by Woodward, 1901, p. 53, for *S. latus*). However, Hay (1903, p. 47) did not take into consideration either the ural centrum 2 or the vertebrae hidden behind the opercular series and the scapular girdle. In fact, both forms have the same number of vertebrae. In addition, the provenance of the specimens was also erroneous as they come from Sahel Alma instead of South Dakota, as has been demonstrated by an analysis of the matrix and a study of the foraminifera (Bardack 1967). We consider here that *S. simus* is a junior synonym of *S. latus*.

Subsequently, Davis (1887, pp. 586–596) described two more new species and a new related genus from the same locality: *S. electus* Davis, 1887, *S. hakelansis* Davis, 1887 and *Lewissia ovalis* Davis, 1887. A few years later Woodward (1901, pp. 48, 53) showed that *S. electus* was a synonym of *S. blondeli* and *L. ovalis* a synonym of *S. latus*. He also demonstrated (p. 274) that *S. hakelensis* should not be included in the genus *Spaniodon* since it was a gonorhynchid. Finally, Woodward (1901, p. 54) showed that *S. lepturus* von der Marck, 1894, from the Upper Cretaceous of Wesphalia, was clearly not related to the genus *Spaniodon*.

S. blondeli and *S. latus* are the only remaining problematical species. The original descriptions of these two species are based on a very small number of specimens but the difference between them seems clear.

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The former shows a moderately deep body, the body height being equal to one-sixth of the total length, and has 50 vertebrae. The latter displays a head which is as deep as it is long, the length of which is equal to one-quarter of the total length, and less than 50 vertebrae (Agassiz 1844; Pictet 1850; Pictet and Humbert 1866). However, the collections of the Museum national d'Histoire naturelle, Paris, contain dozens of specimens of *Spaniodon* and one can find all the intermediates between these two forms. The deeper splanchnocranium in *S. latus* is essentially a result of a dislocation of the suspensorium and a ventral displacement of the opercular bones, pectoral girdle, and branchiostegals. Otherwise, the shape of the cranial bones is identical in both species, within the range of intraspecific variation. In addition to the deep and short proportions of *S. latus*, the ribs are straighter than those of *S. blondeli*. This may not be an artefact of preservation and could be a result of feeding or reproductive rhythm of these fishes. All intermediates between the straightest and the most curved are found. There is also a difference in the number of vertebrae among specimens (50–58), again without any gap in the distribution. Such a disparity is unusual but not exceptional. It has been noticed in extant species such as the herring. In conclusion, we think that *S. blondeli* and *S. latus* are merely extreme forms of the intraspecific variability of only one species, which should be called *Spaniodon latus* on the basis of priority. We use this name herein.

The relationships of the genus *Spaniodon* are still unresolved. Pictet (1850, p. 33) considered it to be a halecoid, close to the genus *Eurypholis*. Pictet and Humbert (1866, p. 58) maintained that it is a halecoid but their conception of the group was quite different, the suborder also including clupeiforms, one elopomorph and one ichthyodectiform. Davis (1887, p. 555) followed his predecessors and classified *Spaniodon* in the family Halecidae, which contains both clupeids and salmonids. On the other hand, Woodward (1901, p. 8), Hay (1903, p. 47) and Frickinger (1991, p. 508) preferred to regard *Spaniodon* as an elopid. Lastly, Jordan (1905, p. 43) erected a new family, Spaniodontidae, which was supposedly closely related to elopids. He included in it the genera *Thrissopater* Gunther, 1872, *Sardinius* von der Marck, 1868, *Notelops* Woodward, 1901, and *Rhacolepis* Agassiz, 1841. Subsequent studies have shown that *Notelops* and *Rhacolepis* are pachyrhizodontids (Forey 1977) and that *Sardinius* is related to myctophiforms (Goody 1969). *Spaniodon* is not related to these two orders as we show herein. As for *Thrissopater*, this taxon has never been studied in detail and its relationship with *Spaniodon* is not supported.

In fact, the descriptions of Agassiz (1844), Pictet (1850), Pictet and Humbert (1866), Cope (1878), Davis (1887), Woodward (1901) and Hay (1903) are very superficial. The revision made by Forey (1971) in his PhD thesis on the basis of 20 specimens in the collections of The Natural History Museum, London, has never been published. Consequently, the endocranium and the caudal skeleton of *Spaniodon* are almost unknown and there is no morphological data available to assign *Spaniodon* to any teleost group.

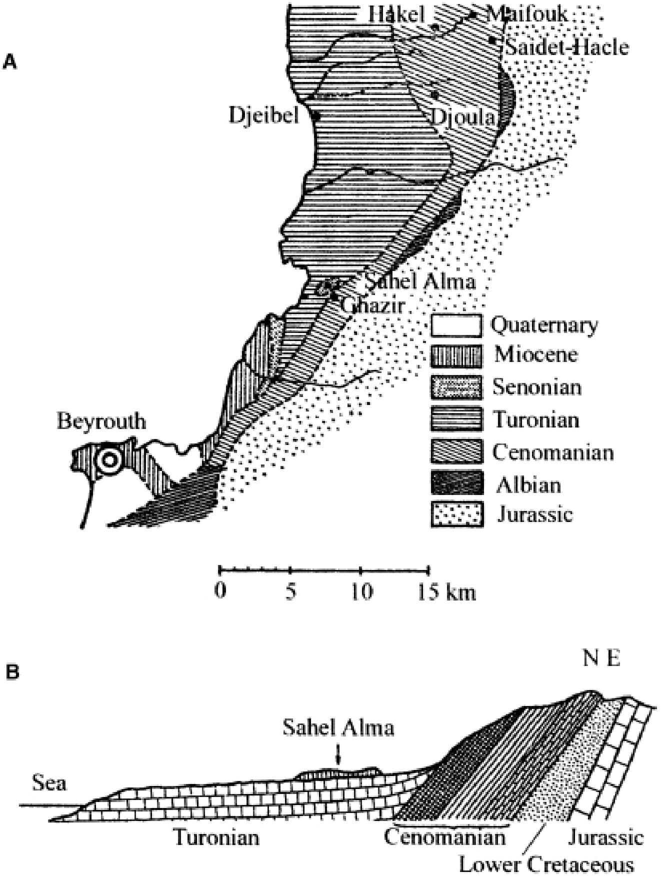
Spaniodon is described in detail in this paper and its systematic position is discussed.

GEOLOGICAL BACKGROUND

Lebanese localities are known for their rich fossil content, especially a few fish beds which have provided some of the best preserved fish and crustacean fossils to date. *Spaniodon* was collected from one of these fish beds, known as Sahel Alma (Text-fig. 1A). Sahel Alma was described by Ejel and Dubertret (1966) as 'a small patch of Senonian chalk, plotted on the surface of the Turonian' (Text-fig. 1B) in relation to the very small size of the bed. The precise age of this chalk was discussed by Zumoffen (1926), Roger (1946), Ejel and Dubertret (1966), and Schram (1999). All authors agree that Sahel Alma is Senonian, but the most precise study was performed by Ejel and Dubertret (1966) who analysed the foraminiferans of the sediment and concluded it is late Santonian. Sahel Alma is consequently younger than other Lebanese localities famous for their fish fossils, such as Haqel and Hadjoula, which are of Cenomanian age.

MATERIAL AND METHODS

The material is housed at the Museum national d'Histoire naturelle, Paris (MNHP), the American Museum of Natural History, New York (AMNH), and the Museum d'Histoire naturelle, Genève (MHNG).



TEXT-FIG. 1. A, geological map of Lebanon, modified after Roger (1946). B, cross-section of Sahel Alma area, modified after Roger (1946).

Specimens were studied using a Wild M5 binocular and a camera lucida. The drawings were made by the senior author. The specimens examined are listed below.

Spaniodon latus (=*S. blondeli*, *S. simus*). MHNG V-622, 623, 627 (syntypes of *S. blondeli*); AMNH 2508, 2509 (cotypes of *S. simus*); MNHN 1872-cat. 9, 1871-11; MNHN 1939-7-14, 25, 38, 44d, 44g, 46, 54, 62, 64, 69, 84, 111, 122, 124, 133, 164–166, 168, 169, 173, 174d, 174g, 178d, 184, 186d, 186g, 187, 188, 189d, 189g, 193, 195d, 195g, 198, 199, 201, 202; MNHN 1946-18-1, 52, 89, 118, 119, 123, 130, 130d, 137, 152d, 152g, 153, 161, 167, 168, 223, 228, 874, 911, 1078, 1224d, 1224g, 1231–1233, 1235, 1236, 1238, 1244, 1245g, 1250, 1257, 1259, 1271, 1273, 1275, 1277, 1279, 1280, 1282, 1286, 1292, 1293, 1300, 1309, 1317, 1319, 1329, 1350–1352, 1355, 1357, 1358, 1360, 1364, 1371, 1378; MNHN SHA 3156, 3164, 3172, 3173, 3195, 3199.

Spaniodon elongatus. MHNG V-621, 629 (syntypes), 630, 730a, 730b, 731, 732a, 732b, 1256; MNHN 1939-7-23, 43, 72, 74, 118, 158, 159, 160d, 160g, 161, 171, 175d, 175g, 185g, 200; MNHN 1946-1-21, 49, 125d, 125g, 134–136, 138, 144g, 162, 162d, 937, 942, 1076, 1079, 1080, 1081g, 1228, 1229, 1234, 1248, 1251, 1252, 1255, 1256, 1258, 1261, 1263d, 1263g, 1264, 1270, 1272, 1276, 1283, 1301, 1307, 1315, 1322, 1328, 1330, 1331, 1335, 1336, 1347, 1373, 1386; MNHN SHA 3242, 3255, 3259, 3262, 3282.

SYSTEMATIC PALAEONTOLOGY

Division TELEOSTEI *sensu* Patterson and Rosen, 1977
Order SALMONIFORMES *sensu* Johnson and Patterson, 1996

Genus SPANIODON Pictet, 1850

Type species. Spaniodon latus (Agassiz, 1844) p. II, p. 118, pl. 61.

Diagnosis. Salmoniform with a razor-shaped body; dermal part of the mesethmoid formed by partly fused laterodermethmoids; edentulous vomer; reduced orbitosphenoid; reduced pleurosphenoids; basisphenoid present; small parietals separated by the supraoccipital; no median crest of the supraoccipital; dilatator fossa large but not deep; temporal fossa open dorsally; reduced supratemporal; thin and edentulous parasphenoid without basipterygoid process; articulation between neurocranium and vertebra formed by basioccipital and exoccipitals; premaxillae bearing a small ascending process and two caniniform teeth; edentulous maxilla with a rounded extremity articulating with the palatine and the internal side of the premaxilla; no supramaxilla; oral edge of the dentary bearing three teeth; well-developed coronoid process; hammer-shaped and edentulous palatine; edentulous endopterygoid and ectopterygoid; reduced antorbital bone; well-developed supraorbital bone; five infraorbitals; infraorbitals 1 and 2 hypertrophied and in contact with the maxilla; reduced ventral branch of the preopercular; 15 branchiostegal rays; triangular posttemporal; only one postcleithrum; 15–18 rays at the pectoral fin; 10–12 rays forming the pelvic fin; 17–19 rays at the dorsal fin; dorsal fin situated in the middle of the body; first dorsal pterygiophore branched; anal fin posteriorly placed and composed of 16–18 rays; 50–58 vertebrae; vertebrae with ridges and crests; vertebral arches narrow except for the last; autogenous arches in the abdominal region, fused in the caudal region apart from the last haemal arches; expanded last neural and haemal spines form a keel; numerous supraneurals, the first three being larger; unramified epineurals, epipleurals, and epicentrals; neural spine of preural centrum 2 almost complete; PU1, U1, and U2 unfused; two small epurals; autogenous parhypural; five hypurals, the third being greatly enlarged; three uroneurals, the third being small; presence of a stegural; second uroneural overlapping the first; caudal scute present in both lobes; 19 principal rays; base of the inner fin rays expanded; cycloid scales with numerous circuli but without radii.

Spaniodon latus (Agassiz, 1844)

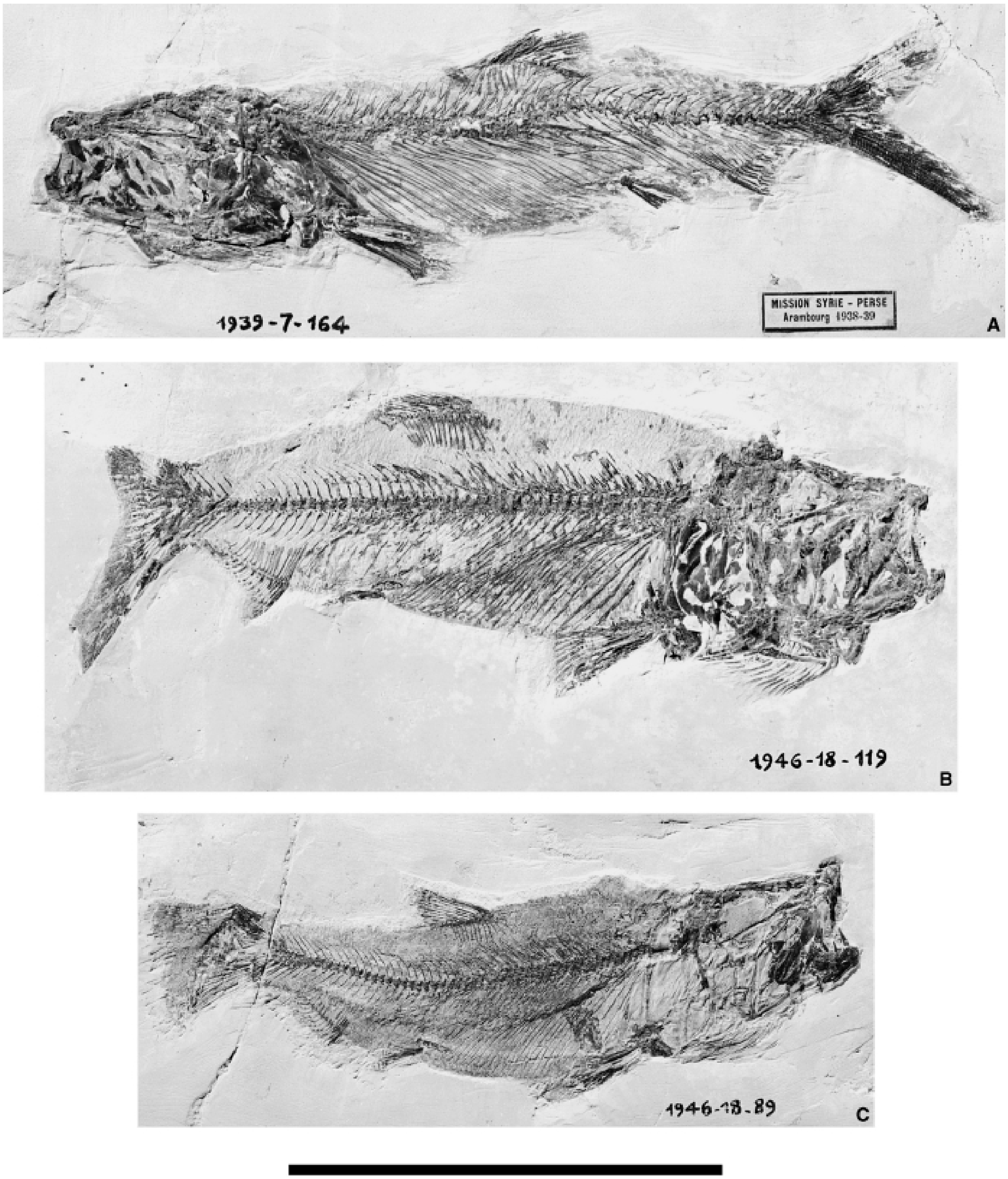
Text-figures 2, 4–9A, 10A, 11

1844 *Clupea lata* Agassiz, p. 118, pl. 61.
1850 *Spaniodon blondelii* Pictet, p. 34, pl. 5, figs 2–4.
1850 *Clupea lata* Agassiz, p. 37.
1866 *Spaniodon brevis* Pictet and Humbert, p. 86, pl. 12, figs 3–4.
1878 *Spaniodon simus* Cope, p. 67.
1887 *Spaniodon blondelii* Pictet, p. 587, pl. 34, fig. 3.
1887 *Spaniodon electus* Davis, p. 589, pl. 34, fig. 3.
1887 *Lewisia ovalis* Davis, p. 593, pl. 33, fig. 6.
1899 *Lewisia ovalis* Davis; Woodward, p. 319.
1899 *Spaniodon brevis* Davis; Woodward, p. 319.
1901 *Spaniodon blondeli* Pictet; Woodward, p. 48, fig. 4.
1901 *Spaniodon latus* (Agassiz); Woodward, p. 53.
1901 *Spaniodon simus* Cope; Woodward, p. 53.
1903 *Spaniodon simus* Cope; Hay, p. 47, pl. 4, figs 1–2.

Type. MHNG V-622, 623, 627 (Agassiz, 1844, p. 118, pl. 61).

Type locality and age. Sahel Alma, Lebanon; Late Santonian.

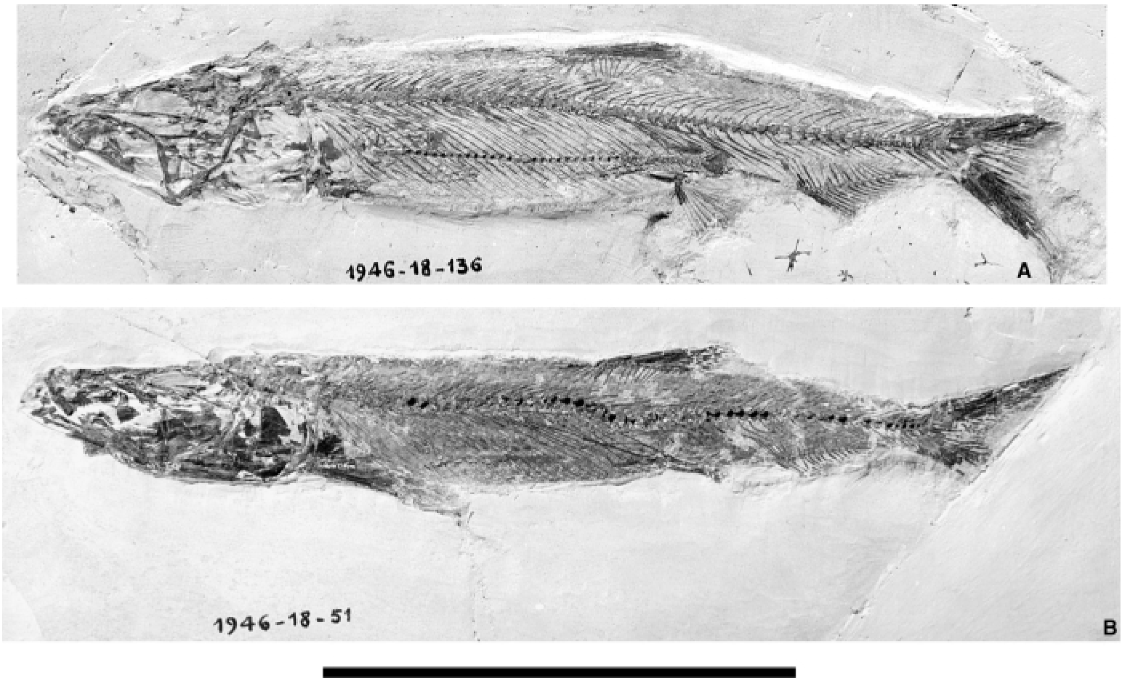
Diagnosis. Head height equals 0·7–0·9 head length and 0·2–0·3 standard length; quadrate-lower jaw articulation situated below the posterior part of the orbit, 50–58 vertebrae.



TEXT-FIG. 2. *Spaniodon latus* (Agassiz, 1844). A, specimen MNHN 1939-7-164, elongated body specimen (previously *S. blondeli*). B, specimen MNHN 1946-18-119, short body specimen. C, specimen MNHN 1946-18-89, intermediate body length. Scale bar represents 100 mm.

Description

In order to make a quick comparison, the proportions of three specimens of *Spaniodon* are given in Table 1, an *S. latus* with an elongated shape (previously *S. blondeli*), an *S. latus* with a short body, and an *S. elongatus* (Text-figs 2–3).



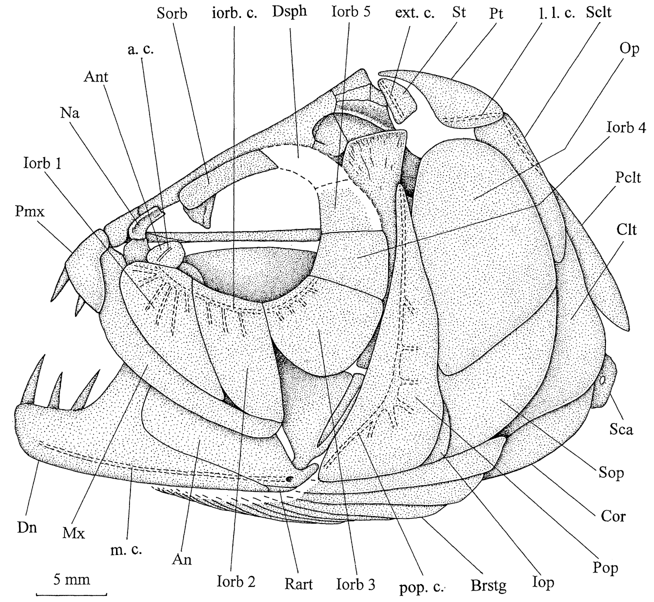
TEXT-FIG. 3. *Spaniodon elongatus* Pictet, 1850. A, specimen MNHN 1946-18-136. B, specimen MNHN 1946-18-51. Scale bar represents 100 mm.

TABLE 1. Size and proportions in *Spaniodon*.

	Spaniodon latus MNHN 1939-7-164 (elongated body)	*Spaniodon latus* MNHN 1946-18-119 (short body)	*Spaniodon elongatus* MNHN 1939-7-158
Standard length (st. l.)	153 mm	145 mm	145 mm
Head length (opercular included)	35·9% st. 1.	35·2% st. 1	33·5% st. 1.
Head height	22·2% st. 1.	31·0% st. 1.	11·6% st. 1.
Body height	21·9% st. 1.	32·4% st. 1.	17·7% st. 1.
Predorsal length	55·6% st. 1.	62·1% st. 1.	58·5% st. 1.
Prepelvic length	75·2% st. 1.	74·5% st. 1.	72·6% st. 1.
Preanal length	87·6% st. 1.	86·9% st. 1.	86·0% st. 1.
Caudal peduncle length	7·2% st. 1.	10·3% st. 1.	5·2% st. 1.
Length of the caudal fin ventral lobe	22·9% st. 1.	24·1% st. 1.	20·7% st. 1.

Both species of *Spaniodon* had a very thin body, razor-shaped like Notopteridae or Schilbeidae. This is very easy to see on specimen MNHNP 1946-1-937 where the pectoral girdle is observable from the ventral side. The ventral branches of the cleithra and the hypocoracoids of both sides are joined to each other.

Skull (Text-figs 4–7). The mesethmoid is small, posteriorly flat, and develops two small lateral processes anteriorly. The suture with the frontals is serrated. A small notch in the anterior edge of the mesethmoid is visible. The posterior region of the bone is divided into two lateral elements. The anterior notch and the posterior suture are almost joined so that the bone is fused only in a very small area. We interpret this situation as the result of the fusion of the two laterodermethmoids. There is no supraethmoid. The vomer is present as an edentulous stick articulated with the ventral



TEXT-FIG. 4. *Spaniodon latus* (Agassiz, 1844); skull in lateral view. Restoration from specimens MNHN 1939-7-14, 69, 133, 164, 166, 174g, 186d, 188, 195g and 1946-18-130, 137, 153, 1244, 1259, 1271, 1352, 1378.

surface of the mesethmoid. It is posteriorly thin and becomes thick towards the anterior, a condition interpreted as the fusion with a small hypoethmoid. The lateral ethmoids are well developed and lie far posteriorly, edging the anterior part of the orbit. In some specimen, they are in contact with the parasphenoid. They are never in contact with the mesethmoid and this suggests that there was a space filled with cartilage between these three bones. The nasals are small, forming a groove that is externally curved in the anterior part, and lie on both sides of the mesethmoid.

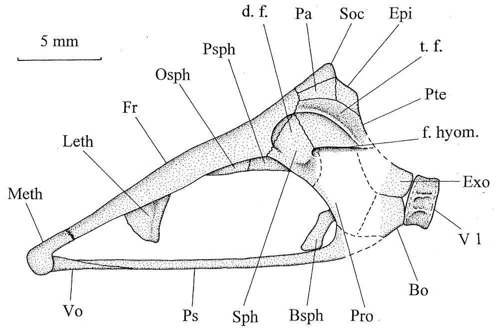
Much of the dermal roof is formed by the frontals, which are long and narrow. The parietals are small and separated from each other by the supraoccipital. The skull is clearly lateroparietal. However, Forey (1971) pointed out a specimen in The Natural History Museum, London, (P.4782) that shows parietals joining in their anterior part. This situation remains exceptional. The supraoccipital displays a median creast. The epiotics are visible posterior to the parietals. The braincase is bordered laterally by the sphenotics and pterotics. The *S. latus* specimen MNHNP 1939-7-14 is particularly well preserved in this region. One can see that these bones are high, the postorbital process of the sphenotic is weakly developed, and a large dilatator fossa is present just above the articular fossa for the hyomandibular. Above the dilatator fossa, the pterotic presents a long, narrow, dorsally open, temporal fossa reaching the posterior limit of the frontals. Imperfectly preserved supraorbital and otic sensory canals are visible on the frontals and the pterotics in some specimens. These two canals are linked together.

In some specimens, a small, almost oval supratemporal, bearing the extrascapular sensory commissure, is observable posterior to the epiotic. This bone lies laterally and does not reach the median part of the skull.

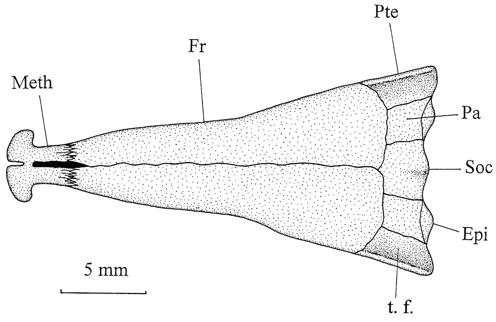
The orbitosphenoid and the pleurosphenoid are poorly developed. The basisphenoid is small but complete with the belophragm and the meningosts. The parasphenoid is long, very narrow, edentulous, and shows a moderately high ascending process and no basipterygoid process.

The anterior edge of the prootic is visible in very few specimens but nothing is known about the pars jugularis or the trigeminofacial chamber. The presence of an intercalar is undecided. A few specimens show preserved basioccipital and exoccipitals in contact with the first vertebra. These three bones participate equally in the formation of the occipital condyle.

The jaws are well developed. The premaxilla is large and bears a short, wide ascending process. The oral edge bears two large teeth. The maxilla is long and edentulous. Its anterior extremity, partly hidden by the premaxilla, forms a sharp angle with the oral part of the bone and forms a condyle that articulates with the lateral process of the mesethmoid and the palatine. The lower jaw is composed of a dentary, an angulo-articular and a retroarticular. The presence of a corono-meckelian bone is undecided. The oral edge of the dentary bears three caniniform teeth in its



TEXT-FIG. 5. *Spaniodon latus* (Agassiz, 1844); restoration of the neurocranium in lateral view based on specimens MNHN 1939-7-14, 69, 133, 164, 166, 174g, 186d, 188, 195g and 1946-18-130, 137, 153, 1244, 1259, 1271, 1352, 1378.



TEXT-FIG. 6. *Spaniodon latus* (Agassiz, 1844); restoration of the neurocranium in dorsal view based on specimens MNHN 1939-7-14, 166, 169 and 946-18-1280, 1286.

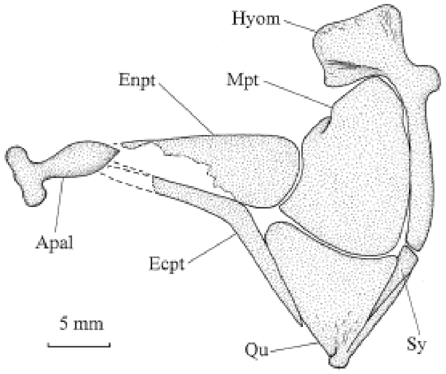
anterior part, the second one being the smallest. In its posterior part, the oral edge of the dentary is much deeper, forming with the angulo-articular a well-developed coronoid process. Only the angulo-articular is involved in the articulation with the quadrate, from which the very small retroarticular is excluded. Although poorly preserved, the path of the mandibular sensory canal on the dentary and the angulo-articular can be distinguished. The posterior opening of this canal is situated on the external side of the lower jaw, ventral to the small postarticular process of the angulo-articular. The lower-jaw-quadrate articulation is situated below the posterior part of the orbit in *S. latus*.

Eight bones are present around the orbit: the antorbital, five infraorbitals, the dermosphenotic, and the supraorbital. The antorbital is small, more or less oval, and bears the antorbital sensory commissure. The first two infraorbitals are large, hooked-shaped, and their ventral edge lies against the maxilla. The size of the three posterior infraorbitals decreases towards the posterior. Posteriorly, these bones reach the anterior edge of the preopercle. The second and third infraorbitals are in contact dorsally but remain clearly separated ventrally, revealing the quadrate. The antorbital and supraorbital bones are separated from each other. The infraorbital sensory canal passes through the five infraorbitals and the dermosphenotic, sending off lateral tubules in the three posterior infraorbitals.

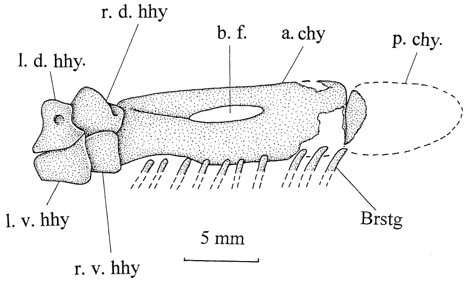
The autopalatine is a massive bone, hammer-shaped, the head of which articulates with the lateral process of the mesethmoid and with the maxilla. There is no dermopalatine. The ectopterygoid is long, narrow and curved (Text-fig. 7). The entopterygoid is wider but also shorter than the ectopterygoid, these two bones being edentulous. The metapterygoid is a large bone showing a small notch in its dorsal edge. The quadrate does not show any peculiar features; it is triangular, shows a quadrato-jugal process that supports the symplectic, and bears the jaw articulation ventrally.

The preopercular is almost triangular and divided into a long dorsal branch and a short ventral branch. The posterior edge of the bone shows a small notch. The preopercular sensory canal sends off numerous short tubules. The interopercular is present but often covered by the preopercular. The opercular and the subopercular are well developed. The subopercular develops a small antero-dorsal process that extends up to the anterior margin of the opercular. Fifteen to 16 branchiostegals are present. The anteriormost ones are short and thin but the others become larger posteriorly. The last three branchiostegals are long and wide. All branchiostegals articulate with the anterior and posterior ceratohyals, but never with the ventral hypohyal.

The visceral skeleton (Text-figs 8–9). The hyomandibula is larger dorsally and shows only one head articulating with the neurocranium. The opercular process is short but present. Ventrally, the hyomandibula is stretched into a long, thin



TEXT-FIG. 7. *Spaniodon latus* (Agassiz, 1844); part of the suspensorium of specimen MNHN 1939-7-133 in left lateral view.



TEXT-FIG. 8. *Spaniodon latus* (Agassiz, 1844); right hyoid bar and anterior part of the left one of specimen MNHN 1946-18-223.

rod. The ossified wing that is often present in teleosts on the anterior edge of the bone is absent in *Spaniodon*. The symplectic is an elongated bone; no interhyal has been seen. The hyoid bar is composed of a dorsal hypohyal, a ventral hypohyal, an anterior ceratohyal, and a posterior ceratohyal. The anterior ceratohyal is, classically, the larger bone and shows a vast beryciform foramen. The urohyal is a very thin rod that becomes wider posteriorly.

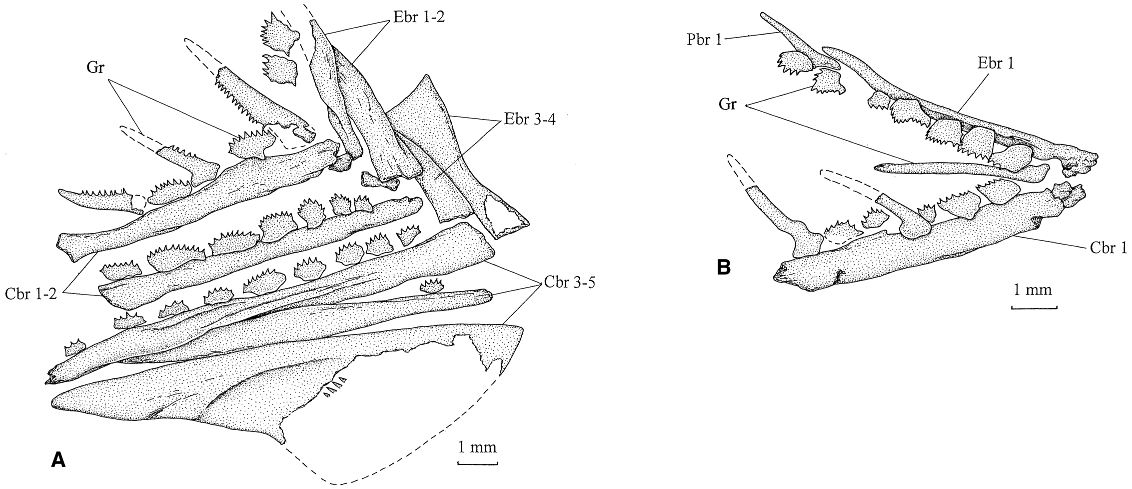
Some specimens, especially *S. latus* specimen MNHNP 1946-1-223, show a very well-preserved branchial skeleton. The basihyal is well ossified. It is a long bone entirely situated in front of the ceratohyals. No dermobasihyal can be seen. The two first basibranchials are ossified. The possible presence of a third and fourth basibranchial remains undecided. The first gill arch is classically composed of a hypobranchial, a ceratobranchial, an epibranchial, and a pharyngobranchial. The three following arches seem to be composed of the same bones but poor preservation obscures the pharyngobranchial. The epibranchial of the fourth arch is wider in its antero-dorsal part. The fifth arch displays only a triangular ceratobranchial, in the middle of which a few denticles are visible. The first four arches bear wide, short, denticle-bearing gill rakers. On the first arch, some elongated gill rakers alternate with the short ones. These long gill rakers bear denticles on one of their edges in *S. latus*.

Girdles (Text-fig. 4). The pectoral girdle is complete. The posttemporal is wide and develops an antero-dorsal process that leans against the neurocranium. The supracleithrum is a large bone. The sensory canal of the lateral line passes through the posttemporal and supracleithrum. The cleithrum is divided into two equally long dorsal and ventral branches. The base of the dorsal wing is especially wide. There is a large postcleithrum. The hypercoracoid is small and pierced by a vascular foramen. The hypocoracoid is large and as long as the ventral branch of the cleithrum.

The pectoral fin is long and composed of 15–18 rays in both species. The first ray, which is also the largest, is segmented and pointed. The following rays are segmented and branched. In some specimens of *S. latus* (especially MNHN 1939-7-1749), a small unpaired bone precedes the first ray.

The pelvic girdle is abdominal. The pelvic bones are small, pointed anteriorly and widen posteriorly. Poor preservation prevents observation of the radials. Ten to 12 rays can be counted; all are segmented and branched except for the first, which is segmented but unbranched. The pelvic fins originate behind the level of the anterior part of the dorsal fin, i.e. from vertebrae 33–36.

Axial skeleton (Text-fig. 10). The axial skeleton presents 50–58 vertebrae, including the two urals, most commonly 54–55, 18–19 of which are caudals. The first vertebra is shorter than those that follow and is taller than long.



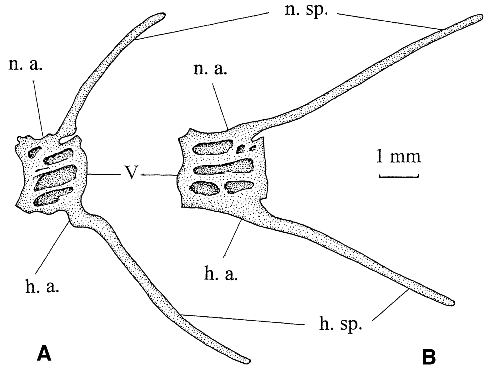
TEXT-FIG. 9. A, *Spaniodon latus* (Agassiz, 1844); part of the branchial skeleton of specimen MNHN 1946-18-223. B, *Spaniodon elongatus* Pictet, 1850; first gill arch of specimen MNHN SHA 3262.

Abdominal centra are also deeper than long by contrast to the caudal centra, which are much longer. The vertebrae are ornamented with ridges separated from each other by long crests. Neural and haemal arches are narrow, autogenous in the abdominal region, but fused to their respective centra in the tail except for the last haemal arches. In the abdominal region, neural spines are bifid and each haemal arch is composed of two haemapophyses that support long narrow ribs that reach the extremity of the situs viscerum ventrally. The first haemapophyses are short but they become progressively longer along the abdominal cavity. The three or four last abdominal vertebrae show short haemal spines associated with the last, very shortened ribs. Short, thin supraneurals, associated with the neural spines, are present in front of the dorsal fin. The first three supraneurals are larger than those that follow, which are reduced to thin rods. Epineurals are present along the abdominal region up to the beginning of the caudal region. Long epicentrals are associated with the first abdominal vertebrae. Posteriorly, epipleurals that are shorter than epicentrals are present in the abdominal region and in the anterior part of the caudal region. All the intermuscular bones are free and unramified.

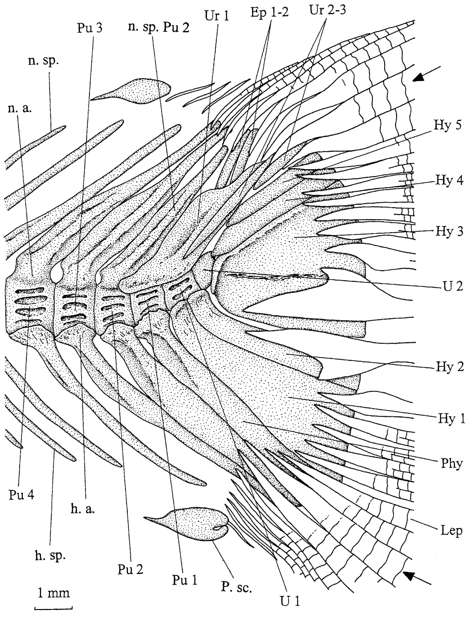
Dorsal and anal fin. The dorsal fin is small, originating in the midpart of the body and showing a similar number of rays in both species; i.e. 17–19 supported by 16–17 pterygiophores. The first ray is very short, pointed and unsegmented. The second ray is slightly longer, pointed, and either segmented or not depending on the specimens. The third ray is clearly longer and segmented but remains unbranched. All subsequent rays are segmented and branched. The last ray is doubled. The first pterygiophore is ramified into three branches.

The anal fin is small in both species, less deep than the dorsal one, and situated far to the posterior. The number of rays is similar to that of the dorsal; i.e. 16–18 rays supported by 15–16 pterygiophores. The first three rays show the same morphology as those of the dorsal fin. The following rays are segmented and branched. The last ray is doubled. The pterygiophores prolong the haemal spines, except in a few instances, because they are more numerous than the corresponding haemal spines. The first anal pterygiophore prolongs the first long haemal spine.

Caudal skeleton (Text-fig. 11). The last vertebrae are reduced in size. The preural centrum 1, and ural centra 1 and 2 are generally autogenous. Some specimens show a slight suture between the preural centrum 1 and ural centrum 1. The ural centrum 2 is greatly reduced. The upward flexure of the caudal skeleton is visible from the preural centrum 1. The last two neural arches are fused to their respective centrum, whereas the last haemal arches are autogenous. Depending on the specimen, the last three or four haemal spines are greatly expanded. The last neural spine is associated with the preural centrum 2. It is well developed, although slightly shorter than those preceding it. The preural centrum 1 and the ural centrum 1 lack neural ossifications. The last haemal spine and the parhypural are notably larger than the preceding haemal spines. Three unfused uroneurals can be seen. The first uroneural is greatly expanded antero-dorsally and forms a stegural with its fellow. Anteriorly, it reaches the preural vertebra 2. The second uroneural is long, thin and completely overlaps the posterior edge of the stegural. The third uroneural



TEXT-FIG. 10. A, *Spaniodon latus* (Agassiz, 1844); caudal vertebra of specimen MNHN 1939-7-186g. B, *Spaniodon elongatus* Pictet, 1850; caudal vertebra of specimen MNHN 1946-18-136.

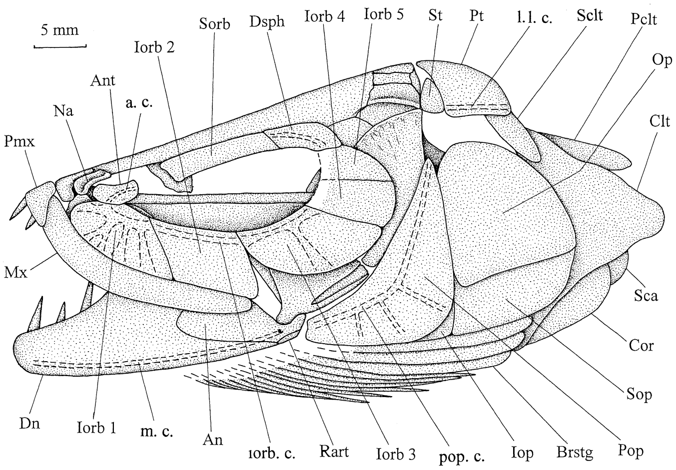


TEXT-FIG. 11. *Spaniodon latus* (Agassiz, 1844); restoration of the caudal skeleton based on specimens MNHN 1939-7-46, 54, 164, 166, 174g and 1946-18-130, 130g, 153, 911, 1238; the two arrows indicate the principal rays of each lobe.

is very small and lies far to the posterior, in between the bases of the caudal fin rays. Two small epurals can be counted, the bases of which are covered by the stegural. There are five unfused hypurals, which are visible on some well-preserved specimens in the MNHN. Hypurals 1 and 2 are articulated with the first ural centrum. The first hypural is large, whereas the second is narrow. The third hypural is notably enlarged and articulates with the second ural centrum. This very large bone is quite often split; it could be interpreted as two different hypurals but is, no doubt, an artefact of fossilization. There is no diastema between the second and third hypurals. A fourth and a fifth hypural are present; they remain narrow. There are no urodermals. The caudal skeleton is limited dorsally and ventrally by a precaudal scute.

The caudal fin is divided into two lobes comprising 19 principal rays, 17 of which are branched. The ventral lobe is longer than the dorsal one. The rays present a sinusoidal, not a step-like, segmentation. The bases of the two innermost rays are considerably expanded, leaf-like and bear a small process. Procurrent rays, most of them segmented, are present in both lobes.

Scales are badly preserved and frequently lacking. They are large, cycloid and show numerous circuli, but no radii.



TEXT-FIG. 12. *Spaniodon elongatus* Pictet, 1850; restoration of the skull in lateral view based on specimens MNHN 1939-7-158, 160d, 1946-18-1248, 1251, 1258, 1263d, 1283, 1307, 1331, 1332, and SHA 3255.

Spaniodon elongatus Pictet, 1850

Text-figures 3, 9B, 10B, 12–13

1850	*Spaniodon elongatus* Pictet, p. 35, pl. 6, figs 1–2.
1866	*Spaniodon elongatus* Pictet, p. 85, pl. 12, figs 1–2.
1877	*Spaniodon elongatus* Davis, p. 588.
1901	*Spaniodon elongatus* Pictet; Woodward, p. 51, pl. 7, fig. 3.

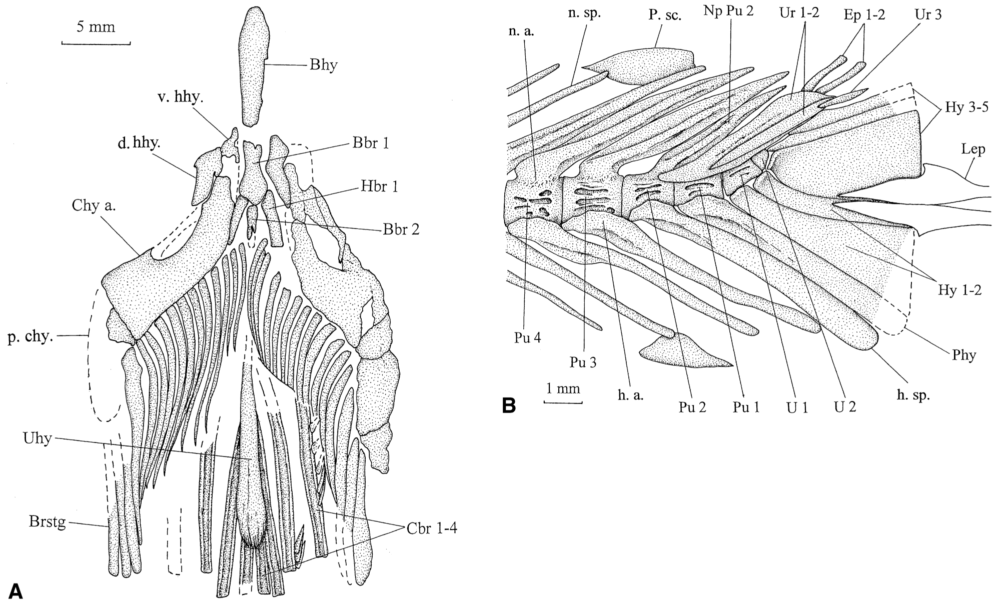
Type. MHNG V-621, 629 (Pictet, 1850, p. 35, pl. 7, figs 1–2).

Type locality and age. Sahel Alma, Lebanon; Late Santonian.

Diagnosis. Head height equals 0·5–0·6 head length and 0·17–0·18 standard length, quadrate-lower jaw articulation situated below the posterior part of the orbit, 56–58 vertebrae.

Description

Spaniodon elongatus mostly displays the same features as *Spaniodon latus*, but differs in proportions. The skulls in *S. latus* and *S. elongatus* are very similar. The only difference is in the shape of the bones since the head of *S. elongatus* is notably less deep and longer (Text-fig. 12). These differences are very clear when the length of the jaws and the width of the opercular bones are considered. In *S. latus*, the neurocranium is proportionally smaller compared to the splanchnocranium than in *S. elongatus*. In the *S. elongatus* specimen MNHN SHA 3255, the mesethmoid is clearly visible. The bone displays a notch in its anterior edge and its posterior region is divided into two lateral elements. The lower-jaw-quadrate articulation is situated below the middle of the orbit in *S. elongatus* whereas it is situated below the posterior part of the orbit in *S. latus*. The dermosphenotic is only visible in *S. elongatus* specimen MNHNP 1946-1-1263d. It is a large elongated bone articulating with a well-developed supraorbital. The bones of the opercular series are less deep and more elongated in *S. elongatus* than in *S. latus*. *S. elongatus* specimen MNHNP 1946-1-937 shows a very well preserved branchial skeleton (Text-fig. 13A). The gill rakers are longer in *S. elongatus* than in *S. latus* but do not bear any denticles. The base of the dorsal branch of the cleithrum is especially wide in *Spaniodon* and this is even more conspicuous in *S. elongatus* than in *S. latus*. The pelvic fins originate posterior to the level of the anterior part of the dorsal fin, from vertebrae 34–37. In *S. elongatus*, 56–58 vertebrae are present, 17–18 of which are caudals. All centra, especially those of the caudals, are proportionally more elongated in *S. elongatus* than in *S. latus*. Both species present the same ossifications of the

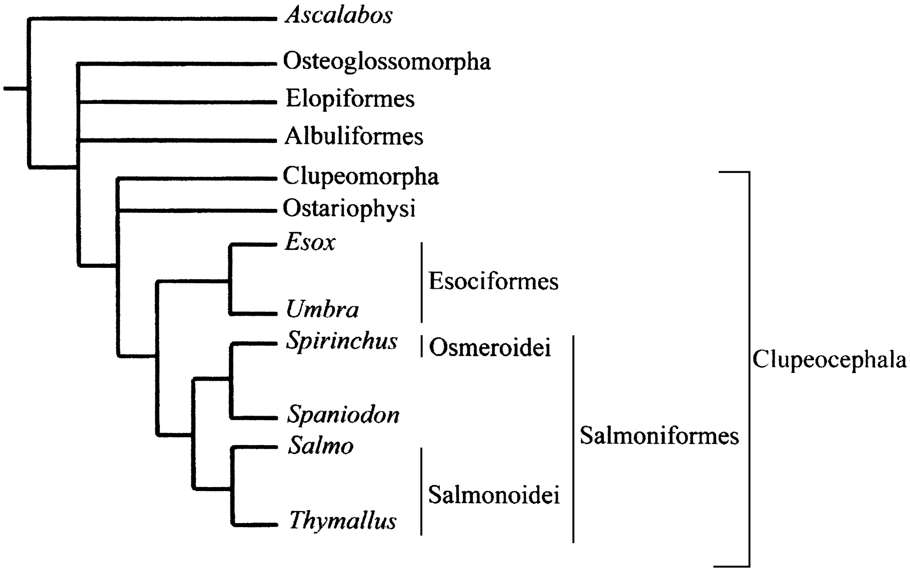


TEXT-FIG. 13. A, *Spaniodon elongatus* Pictet, 1850; branchial skeleton in ventral view of specimen MNHN 1946-18-937. B, *Spaniodon elongatus* Pictet, 1850; restoration of the caudal skeleton based on specimens MNHN 1939-7-159, 161 and 1946-18-135, 1331.

caudal skeleton. However, the caudal skeleton of *S. elongatus* is narrower and the third hypural is narrower than in *S. latus* (Text-fig. 13B).

DISCUSSION

Since it was first erected, *Spaniodon* has been classified within many different teleost groups. The complete description provided herein should help not only to understand *Spaniodon* relationships better but also the phylogeny of the Teleostei generally. Fossil taxa, thanks to their peculiar combination of characters, are of primary importance in a phylogenetic analysis and we hope that *Spaniodon* will be included in future matrices involving teleosts. The Teleostei is the most species-rich and diversified group of vertebrates, with about 24,000 species (Nelson, 1994). The first modern definition of this assemblage and the classification of the main teleost groups were given by Patterson (1968) and Patterson and Rosen (1977), who proposed the presence of uroneurals as the most convincing characters supporting teleostean monophyly. The inclusion of some fossil groups is still unclear, but in the most restricted sense, the Teleostei is also defined by the presence of a diural caudal skeleton. Although Patterson and Rosen's (1977) phylogeny is by far the most cited, there is no real agreement about the ingroup relationships. The relative positions of the major lineages (elopomorphs, osteoglossomorphs, clupeomorphs, ostariophysans, euteleosts) are still very controversial (Text-fig. 14). Arratia (1997, 1999) suggested that elopomorphs are the most basal extant teleosts, by contrast to Patterson and Rosen (1977) who believed osteoglossomorphs to be more basal. Ostariophysans are now often proposed as the clupeomorph sister-group (Lê *et al.*, 1993; Lecointre and Nelson 1996; Arratia 1997), whereas they were previously thought to be the most basal euteleostean group (Patterson and Rosen 1977). Johnson and Patterson (1996) also proposed a new definition of the Euteleostei excluding the Ostariophysi. The consensus of these different views is an almost unresolved cladogram, and the only group that seems to remain supported in all hypotheses is the Clupeocephala (Clupeomorpha + Ostariophysi + remaining teleosts) although the relationships within this group are still not fully understood. Furthermore, all of these earlier proposed phylogenies among teleosts were based on *a priori* assumptions about the monophyly of the studied groups. This approach has been



TEXT-FIG. 14. Consensus tree of 70 equiparsimonious topologies (306 steps, CI: 0·35, RI: 0·59). This is a simplified tree taken from the one obtained by Filleul (2001) based on a matrix of 28 taxa and 95 characters. In all the topologies obtained, *Spirinchus* and *Spaniodon* are sister-taxa, which is consistent with our conclusion and fits the hypothesis that *Spaniodon* is closely related to the Osmeroidei.

criticized by Filleul (2000, 2001) and Filleul and Lavoué (2001). For instance, Johnson and Patterson (1996) performed a parsimony analysis of the Eutelostei, based on a very comprehensive morphological study, but the monophyly of the assemblage was accepted *a priori* although no consensus could be reached on this question. By following that course, possible relationships of some euteleosts with other teleostean groups were excluded. This is a very common approach, and the monophyly of many groups is suspect because it is never really tested. Filleul (2000, 2001) performed a phylogenetic analysis of all major teleostean groups, including many fossil taxa (including *Spaniodon*), to test the monophyly of currently accepted groups, especially elopomorphs (Text-fig. 14). The result shows how the phylogeny of the Teleostei remains a complex issue, as most of the usually accepted groups were not recovered by global parsimony analysis. Once again, however, the Clupeocephala was one of the only well-defined and supported groups, while the monophyly of the Elopomorpha was not confirmed. Relationships of *Spaniodon* are, therefore, extremely difficult to establish within such an unstable framework.

Spaniodon possesses the following derived features: (1) the retroarticular is excluded from the articulation with the quadrate; (2) the flexion of the axial skeleton begins from the first preural centrum; (3) there is no neural spine above U1; (4) the neural arch of U1 is absent; (5) there are two anteriormost uroneurals; (6) the first uroneural is modified; and (7) there are five hypurals. All of these characters show that it belongs to the Clupeocephala (Patterson 1977, p. 631; Patterson and Rosen 1977, p. 130; Taverne 1989, pp. 99–100; 2000, pp. 16–20; Arratia 1997, pp. 153–154) and is not closely related to the most basal teleostean clades like the Osteoglossomorpha or the Elopomorpha. Consequently, its inclusion in the Elopidae (Woodward 1901; Hay 1903; Frickinger 1991) was a mistake.

Spaniodon is more derived than the Crossognathiformes, the most basal clupeocephalan group (Taverne 1989), in having (8) a reduced supratemporal that does not meet its fellow in the midline. It is also more derived than the Tselfatiiformes, another group of plesiomorphous clupeocephalans, owing to the presence of (9) a fused angular and articular, and (10) the posterior opening of the mandibular canal situated on the external part of the jaw. It is also clear that *Spaniodon* lacks any synapomorphy of the Clupeomorpha (Grande 1985) or the Ostariophysi (Fink and Fink 1996), and that it is a euteleost because of the presence of (11) supraneurals with morphotype 2 (Johnson and Patterson 1996); (12) a stegural formed by an anterodorsal ossification of the first uroneural (Johnson and Patterson 1996, pp. 286–287; Arratia 1997, p. 155); (13) the parhypural unfused laterally to its autocentrum (Arratia 1997, p. 155); and (14) the lost of the neural spine of PU1 (Arratia 1997, p. 155). Moreover, the maxilla lining the mouth margin, the absence of the anterior process on the maxilla and the articular process on the premaxilla, the abdominal position of the pelvic girdle, the large number of supraneurals, the lack of spines on dorsal, pelvic, and anal fins, the presence of an unfused preural centrum 1 and ural centra 1 and 2, the presence of three unfused uroneurals, 19 caudal fin rays, and cycloid scales support the assumption that *Spaniodon* is a relatively primitive clupeocephalan, and that it does not belong to the Ctenosquamata. It does not exhibit any synapomorphy of the Esociformes (Wilson and Veilleux 1982; Johnson and Patterson 1996), Stomiiformes (Fink and Weitzman 1982; Harold and Weitzman 1996) or Aulopiformes (Goody 1969; Rosen 1973; Baldwin and Johnson 1996). Consequently, *Spaniodon* is not a halecid, an aulopiform group, as has previously been proposed (Pictet 1850; Pictet and Humbert 1866; Davis 1887).

By contrast, *Spaniodon* is less problematic to classify among protacanthopterygians since it shows synapomorphies of the Salmoniformes (Johnson and Patterson 1996) such as: (15) a separation between the dermal and endochondral part of the mesethmoid; (16) the dorsally open temporal fossa; (17) the last neural and haemal spines forming a keel; (18) the second uroneural overlapping the stegural instead of being posterior to it; (19) scales without radii.

Among salmoniforms, the Salmonoidei is characterized, among other synapomorphies, by the presence of a series of small adjacent supratemporals, forming an extrascapular commissure, and extending across the entire width of the cranial roof (Berg 1940; Devillers 1958; Norden 1961). Neither this character nor those proposed by Sanford (1990) and Johnson and Patterson (1996) are present in *Spaniodon*. However, (20) the dermal part of the mesethmoid of *Spaniodon* is formed by the partial fusion of a pair of laterodermethmoids, whereas the rostral is absent. This is a derived character of the Osmeroidei (Chapman 1941, fig. 3; 1944, fig. 1; Weitzman 1967, fig. 1) and we here propose that *Spaniodon* is a potential member of this group. All known Osmeroidei, however, share many derived features that are lacking in *Spaniodon*, such as the loss of the orbitosphenoid and the basisphenoid, the reduction of the articular, the loss of the postcleithra, and the fusion of the preural centrum 1 with the ural centrum 1 (Johnson and Patterson 1996). Therefore, we cannot ensure that *Spaniodon* belong to this group, although it seems to be the most probable hypothesis. It could be the sister group of all other Osmeroidei, but this needs to be tested in a complete phylogenetic analysis of the Salmoniformes, which was not the purpose of the present paper. We conclude here that *Spaniodon* is, no doubt, a salmoniform but its relationships among salmoniforms are still to be determined.

PHYLOGENETIC ANALYSIS

The simplified consensus tree presented here is based on a more comprehensive global phylogenetic analysis of the basal teleosts performed elsewhere (Filleul 2001). The osmerid *Spirinchus* was coded to test the possible relationships of *Spaniodon* with this group, and these two taxa appear as sister-taxa in all the topologies obtained and thus in the strict consensus tree presented. Characteristics of the tree are given in Text-figure 14. However, the taxonomic sampling just allows us to propose that *Spaniodon* is a salmoniform and is possibly related to the Osmeroidei. The main aim of this analysis was to classify *Spaniodon* among teleosts, and a cladistic analysis including more salmoniform taxa will hopefully resolve the relationships of *Spaniodon* among the Salmoniformes.

The phylogeny of basal teleosts is still very controversial and has been a source of major debate in ichthyology for the last three decades. *Spaniodon* has been assigned to many different groups since the genus was created because of its peculiar combination of characters. We predict that major changes in the phylogeny of the Teleostei are to come, since most of the clades usually accepted have rarely been tested in a global phylogenetic analysis of the teleost fishes. This is also suggested by the polytomy obtained in the consensus tree presented here, and discussed in Filleul (2001). *Spaniodon* is certainly one of the fossil taxa that should be included in future phylogenetic studies in order to understand better the phylogeny of the Teleostei as a whole.

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APPENDIX

Abbreviations used in figures. An, angular; Ant, antorbital; Apal, autopalatine; a.c., antorbital sensory commissure; a. and p. chy., anterior and posterior ceratohyal; Bbr 1–2, basibranchials 1–2; Bhy, basihyal; Bo, basioccipital; Brstg, branchiostegals; Bsph, basisphenoid; b. f., beryciform foramen; C, centrum; Cbr 1–5, first five ceratobranchials; Clt, cleithrum; Cor, coracoid; Dn, dentary; Dsph, dermosphenotic; d. f., dilatator fossa; d. and v. hh, dorsal and ventral hypohyals; Ebr 1–4, first four epibranchials; Ect, ectopterygoid; Ent, entopterygoid; Ep 1–2, epurals 1–2; Epi, epiotic; Exo, exooccipital; ext. c., extrascapular sensory commissure; f. hyom., fossa for the hyomandibula; Fr, frontal; Gr, gill rakers; Hy 1–5, hypural 1–5; h. a., haemal arch; h. sp., haemal spine; Iop, interopercular; Iorb 1–5, infraorbitals 1–5; iorb. C. infraorbital sensory canal; Lep, lepidotrichia; Leth, lateral ethmoid; l. l. c., lateral line sensory canal; m. c., mandibular sensory canal; Meth, mesethmoid; Mpt, metapterygoid; Mx, maxilla; Na, nasal; n. a., neural arch; n. sp., neural spine; Op, opercular; Osph, orbitosphenoid; Pa, parietal; Pbr 1, first pharyngobranchial; Pclt, postcleithrum; Phy, parhypural; Pmx, premaxilla; Pop, Preopercular; pop. C., preopercular sensory canal; Pro, proötic; Ps, parasphenoid; Psph, pterosphnoid; Pt, posttemporal; Pte, pterotic; Pu 1–4, preural vertebrae 1–4; P. sc., precaudal scute; Rart, retroarticular; r. and l. d. hhy, right and left dorsal hypohyals; Qu, quadrate; Sca, scapula; Soc, supraoccipital; Sop, subopercular; Sorb, supraorbital; St, supratemporal; Sclt, supracleithrum; Sph, sphenotic; Sy, symplectic; t. f., temporal fossa; U 1–2, ural vertebrae 1–2; Uhy, urohyal; Ur 1–3, uroneurals; V 1, first vertebra; Vo, vomer; v. r. and l. v. hhy, right and left ventral hypohyals.