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Sedenhorstia dayi (Hay), a New Elopoid from the Cenomanian of Hajula in the Lebanon

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INTRODUCTION

During a revision of Woodward's (1901) family Enchodontidae it was found necessary to examine representatives contained within his family Scopelidae. One of the genera considered was a little-known genus, *Sedenhorstia*, represented by three species occurring in different localities—Sendenhorst in Westphalia and both Hakel and Hajula in the Lebanon. The genus was originally named *Microcoelia* by Marck (1863, p. 48) when he described the type species from the upper Senonian (Campanian) of Sendenhorst, *Microcoelia granulata*. White and Moy-Thomas (1941, p. 396) pointed out that this generic name was preoccupied, and they erected the new name *Sedenhorstia*.

Woodward (1901, p. 252) considered this genus to be a scopeloid related to *Sardinioides* Marck, and erected a new species, *Microcoelia libanica*, to accompany the type. Woodward's species is from the middle Cenomanian of Hakel in the Lebanon. (The allotting of a middle Cenomanian age to the Lebanese deposits of both Hakel and Hajula is in accordance with the findings of Patterson, 1967, p. 72). A third species, *Microcoelia dayi*, was later erected by Hay (1903, p. 430) to cover several specimens from the middle Cenomanian of Hajula, Lebanon. Apart from the change in generic name by White and Moy-Thomas (1941),

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no further mention of the genus, or any of the species, occurs in the literature. This genus on further study was seen to have no direct relationships with either the Enchodontidae or the Scopelidae, but is in fact a representative of the Elopiformes. Consequently two specimens were prepared in acetic acid by the transfer method (see Toombs and Rixon, 1950), and a closer study was made. The following descriptions and figures are the result. As in all flattened specimens, the head region is somewhat difficult to interpret, but the superficial bones become visible after preparation. The neurocranium remains for the most part undescribed except for some of the roofing bones.

Sedenhorstia can be compared with the recent genera *Elops* and *Megalops*, and it is readily seen that only minor differences exist. Sufficient grounds are found, however, to warrant the erection of a new family, Sedenhorstiidae, within the suborder Elopoidei. According to Greenwood *et alii* (1966), this suborder is contained within the order Elopiformes which in turn is contained in the superorder Elopomorpha.

The specimens utilized in the descriptions are found in the collections of the British Museum (Natural History) and the American Museum of Natural History. For permission to work on these collections I extend my thanks to Dr. Errol I. White and Dr. Bobb Schaeffer, respectively. Also thanks are due to Dr. Colin Patterson and Dr. P. Humphry Greenwood of the British Museum, and to Dr. Brian G. Gardiner of Queen Elizabeth College (London University) for much useful information and advice.

ABBREVIATIONS USED IN FIGURES

ac.r, procurrent accessory rays of the upper caudal lobe
ant, antorbital
art, articular
b.f., basal fulcral scale
bs, basisphenoid
den, dentary
d.f., dilatator fossa
enp, endopterygoid
ep.f.r, uppermost epaxial principal fin ray
ep 1, ep 2, ep 3, first, second, and third epural bones
fr, frontal
fr.f, fringing fulcral scales
h.mx, head of the maxilla
h.s, haemal spine
hy 1, hy 6, first and sixth hypural bones
inf 3, inf 5, third and fifth infraorbital bones
iop, interoperculum
la, lacrimal

l.e, lateral ethmoid
 md.s.c, openings for the mandibular sensory canal
 mpt, metapterygoid
 mx, maxilla
 na, nasal
 n.a.pu 1, neural arch of the first preural vertebra
 n.s., neural spine
 op, operculum
 ors, orbitosphenoid
 ph, parhypural
 pls, pleurosphenoid
 pm, premaxilla
 pop, preoperculum
 pop.s.c, openings for the preopercular sensory canal
 p.r. 1, first pelvic fin ray
 p.s, pelvic splint bone
 pt, posttemporal
 p.t.f, posttemporal fossa
 pu 1, pu 4, first and fourth preural vertebrae
 q, quadrate
 ro, rostral
 r.n.s.pu 2, reduced neural spine of the second preural vertebra
 smx 1, anterior supramaxilla
 smx 2, posterior supramaxilla
 so, supraorbital
 sop, suboperculum
 sop.s, anterodorsal spine on the suboperculum
 spo, sphenotic
 st, supratemporal
 sym, symplectic
 u 1, u 2, first and second ural vertebrae
 ur 1, ur 2, ur 3, first, second, and third uroneurals

ABBREVIATIONS OF INSTITUTIONS

A.M.N.H., the American Museum of Natural History
 B.M.N.H., British Museum (Natural History)

SYSTEMATIC DESCRIPTION

ORDER ELOPIFORMES

SUBORDER ELOPOIDEI

SEDENHORSTIIDAE, NEW FAMILY

DIAGNOSIS: Elopoidei in which epaxial region of caudal fin supports fringing fin fulcra. Basal fulcral scales present both above and below caudal peduncle. Pelvic fins abdominal, with an asymmetrically placed

pelvic splint bone basally. Row of middorsal, hook-shaped ossifications between occiput and origin of dorsal fin.

GENUS *SEDENHORSTIA* WHITE AND MOY-THOMAS, 1941

DIAGNOSIS: As for family, only genus.

Sedenhorstia dayi (Hay), 1903

DIAGNOSIS: *Sedenhorstia* of standard length not exceeding 75 mm. Greatest depth of body just exceeds length of head which is contained somewhat more than three times in standard length. Dorsal fin situated in mid-back region consisting of 23 rays, first five spinous. Anal fin more remote in position, with 22 rays, first four spinous. Pectoral fin low on flank, with 13 rays. Pelvic inserted below origin of dorsal, with approximately nine rays. Vertebrae 49 in number, of which 25 are caudal.

HOLOTYPE: A.M.N.H. No. 3692, a complete but flattened fish from the middle Cenomanian of Hajula, Lebanon.

MATERIAL: B.M.N.H. No. P. 13886; A.M.N.H. Nos. 3692, 3677, 3798, 3803, 3816. All these specimens are from Hajula in the Lebanon. The American Museum specimens are those that were studied by Hay (1903, pp. 430-432, pl. 31, fig. 3, pl. 34, fig. 1).

DESCRIPTION

NEUROCRANIUM: The neurocranium is not well shown in any of the specimens examined. The head is somewhat deepened, but the neurocranium has remained shallow. The parasphenoid, visible below the orbit, is straight and narrow. The skull roof is curved, sloping antero-ventrally, and the greatest depth of the neurocranium is at the occiput. The frontals occupy most of the skull roof, reaching back as far as the mid-region of the cranial cavity itself. The frontal is curved above the upper margin of the orbit and extends onto the dorsal surface of the sphenotic. The parietal is large and appears to meet its partner in the midline. The parietal contacts the pterotic laterally in the roof of the posttemporal fossa, and the epiotic posteriorly on the medial wall of the posttemporal fossa. The roof of the fossa is excavated slightly along its posterior edge. The epiotic, posteromedial to the posttemporal fossa, is thickened to provide the articulatory region for the dorsal limb of the posttemporal. Covering part of the opening of the posttemporal fossa is a thin slip of bone which appears to be canal bearing. This slip of bone is in the correct position to be a supratemporal. It is drawn out posteriorly where it housed the anteriormost portion of the lateral-line sensory canal. The supraoccipital is small and has a rounded, poste-

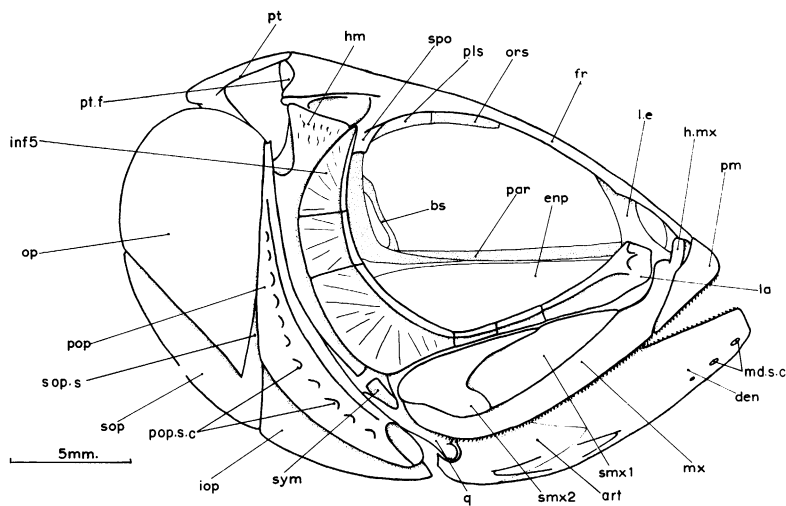


FIG. 1. *Sedenhorstia dayi*, reconstruction of the skull in lateral view.

riorly directed crest. The supraoccipital hardly appears on the skull roof, being represented by merely a transverse strip of bone on the extreme occipital border. The pterotic forms the posterolateral border of the skull roof, meeting the sphenotic anteriorly in the dilatator fossa. This fossa is an excavation of the dorsolateral part of the pterotic and sphenotic. Below the dilatator fossa the hyomandibular facet is present as a groove on the sphenotic and pterotic. Below the hyomandibular facet and behind the head of the hyomandibular, part of the exoccipital is visible with an intercalar adhering to it posteriorly. The exoccipital does not enter into the occipital condyle but appears as a thickened area above the condyle. The suture between the basioccipital and exoccipital is clearly visible lateral to the condyle.

The anterior region of the neurocranium is difficult to interpret. The mesethmoid is short and broad, with prominent anterolateral extensions. The frontal touches the rear edge of the mesethmoid, and the nasal bone is represented by a flat, crushed slip of bone lying on the dorsal surface of both frontal and mesethmoid. The long, straight parasphenoid meets the vomer anteriorly in advance of the lateral ethmoid. The vomer is fused to the under surface of the mesethmoid and is produced into lateral wings. The facet formed between the mesethmoid wing and the vomerine wing provides a facet for the reception of the articular head of the maxilla. The lateral ethmoid is attached to the dorsal surface of

the parasphenoid and possibly the palatine, delimiting the anterior border of the orbit. The lateral ethmoid touches the palatine medial to the maxillary process of the palatine.

Within the orbit the pleurosphenoid joins the sphenotic laterally, and anteriorly meets the large median orbitosphenoid. The vertical suture between the pleurosphenoid and the orbitosphenoid is clearly visible, and the orbitosphenoid is situated in the mid-region of the orbit. The impression of a prominent basisphenoid pedicel is seen in the postero-ventral region of the orbit.

CIRCUMORBITALS: The circumorbital bones are shown in lateral view in the reconstructed skull (fig. 1). An infraorbital series of bones surrounds much of the orbit. At the anterior end of the orbit is a small antorbital almost vertical in position and slightly curved. The antorbital extends ventrally from the frontal over the anterior part of the lateral ethmoid, in contact with the lacrimal. The lacrimal is the enlarged anterior member of the infraorbital series. The succeeding two infraorbital bones are elongated and shallow, lying beneath the orbit and above the dermal upper jaw. Three expanded infraorbitals occur posterior to the orbit, covering the cheek region. These expanded infraorbitals have a slight ornamentation of raised ridges. The orbital edge of each of the infraorbitals bears a groove roofed by a projecting flange for the infraorbital sensory canal. The last infraorbital is reduced in width dorsally where it rests on top of the sphenotic.

HYOPALATINE BONES: The hyopalatine apparatus is difficult to distinguish because of the overlying circumorbital bones and dermal upper jaw. The hyomandibular is long and narrow, with an expanded head region. The head is elongated anteroposteriorly and inclined antero-ventrally, fitting into the hyomandibular facet on the pterotic and sphenotic. A lateral crest is present on the posterior edge of the hyomandibular. In the dorsal region this crest is produced backward into a small pointed projection, on a level with the opercular condyle. The hyomandibular tapers ventrally as does the lateral crest. The quadrate is a prominent, large, well-ossified bone inclined anteroventrally. It is triangular and has a stout, transversely orientated condyle below the hind end of the orbit. The posterior edge of the quadrate is thickened where the ventral edge of the preoperculum rests against it. The posterodorsal edge of the quadrate is deeply indented, and within the indentation the long stout symplectic bone is visible connecting the hyomandibular to the quadrate. The ectopterygoid and the palatine form, together, a long, curved strut which is extensively toothed. Anteriorly the palatine is supported dorsomedially by the lateral ethmoid and anteromedially fuses with the

vomer. The maxillary process of the palatine is excavated somewhat to associate with a corresponding process from the maxilla.

DERMAL UPPER JAW: The dermal upper jaw is shown in lateral view in the reconstructed skull (fig. 1). The premaxilla is small, forming only a minor part of the oral border, and extending for a short distance beneath the anterior region of the maxilla. There is no ascending process on the premaxilla, and the premaxillae meet anteriorly in the midline. (A vague articular process may, however, be present laterally, associated with a facet on the anterior edge of the maxillary head.) The oral edge of the premaxilla bears a single row of small, acutely pointed teeth.

The maxilla enters the gape behind the premaxilla and is long and stout, the head region lying above the premaxilla and curving in toward the midline. Medially the maxilla bears a prominent projection associated with the maxillary process of the palatine. The head of the maxilla in front of the maxillary process is elongate, narrow, and slightly expanded terminally where it is associated with the mesethmoid and vomer. The maxillary tooth row is continuous with that on the premaxilla. The extreme posterior end of the maxilla lies lateral to the quadrate. The dorsal edge of the maxilla is thinner and supports two enormous supramaxillae. The posterior supramaxilla is the larger and extends forward above the posterodorsal part of the anterior supramaxilla. This antero-dorsal projection is in the form of a thickened rib extending back onto the face of the main part of the bone. The anterior supramaxilla is more ovoid and pointed anteriorly.

MANDIBLE: The mandible is partially shown in lateral view in the reconstructed skull (fig. 1). It is elongate and somewhat deepened. The posterior edge of the dentary is indented, and this indentation is occluded by the anterior region of the articular. Lateroventrally, within the dentary, is a tube that opens to the exterior through several large pores (for the mandibular sensory canal). Toward the posterior part of the dentary the tube opens into a groove which is continued on the articular. The dentary bears prominent teeth on its oral edge; all are similar to those on the premaxilla and maxilla in shape and size. The articular facet is well developed, with a short retroarticular process behind it. The posterior edge of the articular rises steeply from the facet to touch the dentary where it forms the coronoid process. A tube within the articular passes through the retroarticular process and runs beneath the facet to open into a groove on the ventrolateral region of the articular (for the mandibular sensory canal).

OPERCULAR BONES: The opercular bones are shown in lateral view in the reconstructed skull (fig. 1). The preoperculum is deepened, but nar-

row dorsally. It rests against the posterior face of the hyomandibular crest and against the posterior edge of the quadrate. Ventrally the preoperculum curves forward to follow the hind margin of the hyomandibular and quadrate. The anterior edge of the preoperculum is slightly thickened, but the more posterior region is thinner. The preopercular sensory canal appears to have passed within the thickened anterior region; the tube that contained it opening anteroventrally on the extremity of the preoperculum just posterior to the retroarticular process. The outer face of the preoperculum has small excavations along its length which may represent openings through which branches of the preopercular sensory canal passed posteriorly.

The operculum is large, considerably deeper than it is long, and has the opercular facet near the upper limit of the anterior edge. The anterior edge of the operculum is straight and thickened. The ventral edge is obliquely inclined, whereas the posterior margin is rounded.

The dorsal edge of the suboperculum lies medial to the ventral edge of the operculum. The anterior edge of the suboperculum is extended into a short, dorsally projecting spine, clearly visible medial to the anterior edge of the operculum. The ventral edge is smoothly rounded.

The interoperculum is long and projects slightly below the preoperculum.

PECTORAL GIRDLE AND FIN: The pectoral girdle is poorly preserved in all specimens. The posttemporal bone has a large, flattened dorsal limb articulating with the epiotic region of the neurocranium, and a narrower ventral limb associated with the neurocranium more ventrally. The junction of the two limbs is expanded and flattened into a small vertical plate onto which the head of the supracleithrum is attached. The supracleithrum is long, narrow, and associated ventrally with the lateral face of the upper part of the cleithrum. The cleithrum is a large sigmoid bone curving anteriorly and ventrally. The anterior edge of the cleithrum is medially inclined, and the lateral face is expanded above the insertion of the pectoral fin. This expanded region supports a narrow postcleithral element, which extends ventrally medial to the pectoral fin.

The endoskeletal girdle is attached to the internal face of the cleithrum low down on the flank. The outlines of the girdle are indistinct, but the coracoid is produced posteriorly below the fin insertion, and anteriorly toward the tip of the cleithrum. The articular edge of the scapulocoracoid is horizontal; thus the pectoral fin is inserted extremely low down on the body.

The pectoral fin is composed of 12 or 13 stout, branched, and segmented rays.

PELVIC GIRDLE AND FIN: The pelvic fin is abdominal, positioned below the origin of the dorsal fin. The pelvic bones are prominent, well ossified, triangular in shape, and fused to one another posteriorly in the mid-ventral line. The fin consists of eight or nine branched, segmented rays and a small, asymmetrically placed, pelvic splint bone (that of *Elops* is shown in fig. 8), which is unbranched and spinous in character.

VERTEBRAL COLUMN: The vertebral column is shown in lateral view in the restoration of the whole skeleton (fig. 3). It consists of 49 vertebrae (excluding the ural vertebrae, but including all the preural vertebrae), of which 25 are caudal. The centra are short, deeper than they are long, and not mesially constricted. The lateral region of each centrum is ornamented with several longitudinal ridges with intervening lateral fossae. All, except the first two preural vertebrae, have the neural arches drawn out into elongated, backwardly curved neural spines. The neural spines of the anterior region of the column are longer and finer than those posteriorly and are separated into lateral halves. The neural arches form separate ossifications to the centra. Nevertheless they are closely connected to them. The precaudal vertebrae bear small, insignificant, transverse processes anteroventrally, and these support pleural ribs. The ribs are long and flattened and very prominent, curving posteriorly and ventrally around the body cavity. On the first two or three caudal vertebrae the haemal arches gradually lengthen, but a true haemal spine does not occur until the fourth caudal vertebra. Shortened pleural ribs are still associated with the anteriormost three caudal vertebrae. Epineurals and epipleurals are associated with the first 33 vertebrae.

MEDIAN FINS AND TAIL: The median fins are shown in the restoration of the whole skeleton (fig. 3). The dorsal fin has some 23 rays. The first six gradually lengthen, so that the sixth ray is the longest in the dorsal fin. The first four rays are unbranched and unsegmented, being spinous in form. These are not true fin spines, because of their double nature. The fifth and sixth rays are also unbranched but are clearly segmented. The remaining rays are all branched and segmented and decrease in length gradually to the sixteenth ray; the remaining eight rays are of approximately equal length, all relatively short. The dorsal fin rays are supported on elongate, narrow, proximal radials. The two anteriormost proximal radials are fused together to give a single expanded radial element projecting anteriorly, and this supports the first four fin rays. Medial radial elements are present as small slips of bone lying obliquely between the bases of adjacent fin rays. These elements are not visible between the anteriormost fin rays which are crowded together.

Anterior to the first radial element and behind the occipital region of

the skull, a further series of accessory radial elements (interneurals) are present. These accessory radials are similar to the dorsal fin radials but are noticeably more curved and more deeply embedded within the body. At least 18 accessory radial elements are present. The first of the series is expanded and associated with the neural spine of the first vertebra.

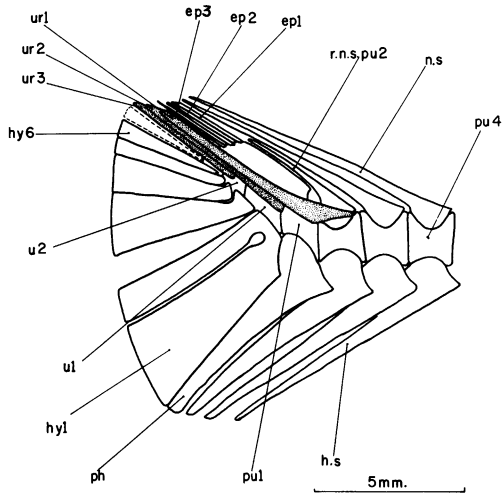


FIG. 2. *Sedenhorstia dayi*, caudal fin skeleton in lateral view.

A further series of structures are present in the midline of the dorsal part of the body, anterior to the dorsal fin. These are numerous small, hook-shaped ossifications, not arranged in a truly uniform sequence. The ossicles are found beneath the body surface, the typical body scaling being produced beyond and above them. Anteriorly the ossifications sink deeper into the body behind the occipital region of the skull. Posteriorly the ossicles extend to the origin of the dorsal fin, and the last ossicle is very similar in form to the first fin ray.

The anal fin has approximately 22 rays, and these gradually increase in size so that the fifth or sixth ray is the longest. The anteriormost fin rays are spinous and unsegmented. The remainder of the rays are branched and segmented, and the general shape of the fin is like that of the dorsal. The proximal radial elements are long, straight, and unexpanded.

The caudal fin skeleton is shown in lateral view in figure 2. It is made up of seven vertebrae in all, of which five are preural and two ural. The fifth preural vertebra supports accessory rays on its haemal spine, but

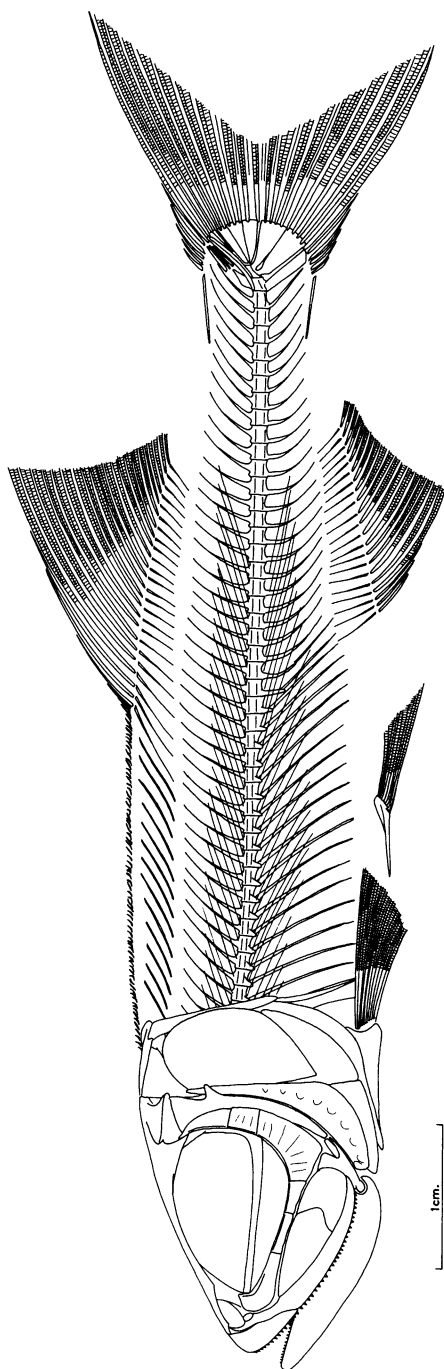


FIG. 3. *Sedenhorstia dayi*, reconstruction, scales omitted.

not on its neural. The remaining four preural vertebrae bear expanded, flattened, haemal spines which extend posteroventrally. The most prominent haemal spine is that on the first preural vertebra, and it is termed the parhypural. Preural vertebra 3 bears a normal, backwardly projecting neural spine with a slight anterior expansion. Preural vertebra 2 has a reduced neural spine, whereas preural vertebra 1 simply bears an enlarged neural arch. The first preural centrum is inclined posterodorsally, and this inclination is continued by the ural vertebrae. The first ural bears hypurals 1 and 2. These hypurals are fused only basally. Hypural 1 is the larger of the two, with an anterior expansion overlapping part of the parhypural. The third hypural articulates with both of the ural vertebrae at the junction between the centra. Ural vertebra 2 is smaller than the first and appears to support at least three hypurals. The dorso-lateral surfaces of preurals 1 and 2 and the ural vertebrae are covered by uroneural elements. The uroneurals extend posterodorsally as narrow thickened struts. Three uroneurals are present, uroneural 1 arising in connection basally with preural vertebra 1 and 2, and uroneural 2 in association with the first ural vertebra. The third uroneural is shorter than the preceding ones and attached posteriorly to the second uroneural. Three narrow epural elements are present in advance of the upper region of uroneural 1, and are associated basally with the expanded neural process of preural vertebra 1.

Nineteen principal caudal fin rays are present, of which 17 are branched. In front of the anteriormost epaxial principal ray are two series of smaller epaxial rays (fig. 9A). The anterior series correspond to the normal accessory fin rays and are supported by neural spines. The posterior series are inserted on the leading edge of the uppermost principal ray. These latter elements are fringing fulcra and probably form from the subdivision of the leading principal ray. The fringing fulcra and the accessory rays are unbranched. There are three fringing fulcra and 10 accessory rays epaxially, all being unsegmented, and simply 10 or 11 accessory rays hypaxially, but the first two accessories are segmented. Anterior to the accessory rays a large, flattened, basal, fulcral scale is present both above and below the peduncle.

SCALES: The entire body is covered with a uniform coat of small cycloid scales. These scales are absent from the operculum and are undifferentiated along the lateral line.

DISCUSSION

The genus *Sedenhorstia* was placed by Woodward (1901, p. 252) and

Hay (1903, p. 431) in the scopeloid (myctophoid) group along with *Sardinioides*, *Acrognathus*, and *Nematonotus*. Such an association has little justification. The following characters, taken together, completely separate *Sedenhorstia* from the scopeloid complex: (1) the nature of the jaws, with a small premaxilla and an enormous maxilla forming almost the entire oral border of the upper jaw; (2) the considerable posterior expansion of the last three infraorbitals behind the orbit; (3) the large number of accessory radials between the occiput and the origin of the dorsal fin; (4) the nature of the median fins, in which the anteriormost rays are unsegmented and spinous; (5) the nature of the caudal fin skeleton, with two free ural vertebrae and no stegural component; and (6) the presence of fringing fin fulcra on the epaxial region of the caudal fin.

These features, as well as separating *Sedenhorstia* from the scopeloids, are just the characters that are found in representatives of the order Elopiformes (*sensu* Greenwood *et al.*, 1966). Thus the most useful comparison would seem to be between *Sedenhorstia* on the one hand and *Elops* and *Megalops* on the other.

The one feature that would indisputably connect *Sedenhorstia* with the elopiforms is the presence of a rostral commissure running within a rostral element; however, it is impossible to interpret this region in the imperfectly preserved and flattened material.

The premaxilla of *Sedenhorstia* is small and simple, without an ascending process, but with what may be a small articular process abutting against the anterior edge of the maxilla. Allis (1909, p. 25) doubted the presence of an articular process in *Elops*, and on examination this conclusion would appear to be correct. The presence in the fossil may be an artifact of preservation. If this slight discrepancy be set aside, the premaxilla of *Sedenhorstia* is very similar to that of *Elops* (fig. 6) and that of *Megalops* (fig. 5).

The maxilla in *Sedenhorstia* is a prominent bone, forming almost all the oral border of the mouth and supporting a single row of small, acutely pointed teeth, as in *Elopopsis microdon* Arambourg (1954, p. 64). Most of the remaining elopoid genera have minute teeth arranged in bands in a brushlike form on the premaxilla and maxilla. The maxilla extends posteriorly to cover the lateral face of the quadrate and supports two large supramaxillae.

An interesting feature arose from the transfer preparation of a second specimen, B.M.N.H. No. P.9983 (fig. 4). This specimen is the head and anterior part of the body of a form that at first sight appeared to be *Sedenhorstia dayi*. There is a difference, however, concerning the angle of the jaw when it is compared with the holotype of *Sedenhorstia dayi*. The

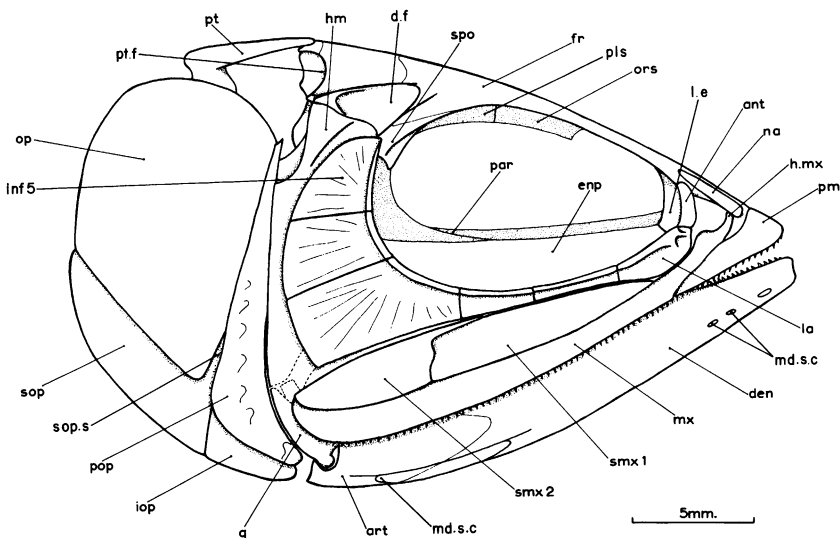


FIG. 4. *Sedenhorstia orientalis*, reconstruction of the skull in lateral view.

maxilla of the latter is markedly curved and somewhat shortened, resembling that of *Megalops*. Correlated with this feature is the position of the mandibular articulation which lies beneath the orbit. In B.M.N.H. No. P.9983 the maxilla is longer and straighter, as is the mandible, thus resembling *Elops* more closely. Again the correlation with the somewhat longer jaw is that the mandibular articulation lies almost below the occipital region, well behind the orbit. Although this would appear to be the only difference, it is sufficient to warrant the erection of a new species.

***Sedenhorstia orientalis*, new species**

DIAGNOSIS: *Sedenhorstia* of estimated standard length 80 mm. Mandibular articulation situated almost vertically below occiput. Mandible almost five times as deep as long. Length of mandible considerably in excess of maximum depth of head at occiput.

The foregoing features contrast with those of *Sedenhorstia dayi* in which the mandibular articulation lies below the orbit, the mandible is just more than three times as long as deep, and the length of the mandible is considerably less than the maximum depth of the head.

HOLOTYPE: B.M.N.H. No. P.9983, from the middle Cenomanian of Hajula, Lebanon.

The maxillary head is similar in both fossil and recent forms, being extended and narrowed anteriorly. Behind the head the medial part of the maxilla bears a prominent knob associated with a slight projection from the palatine. In this factor the elopoids differ from the more advanced Protacanthopterygii (*sensu* Greenwood *et al.*, 1966), which possess a maxillary process from the palatine fitting into a facet on the maxilla. This point was discussed by Gosline, Marshall, and Mead (1966, p. 2, fig. 1). The maxillary head is slightly thinner and more attenuated in *Sedenhorstia* than in *Megalops*.

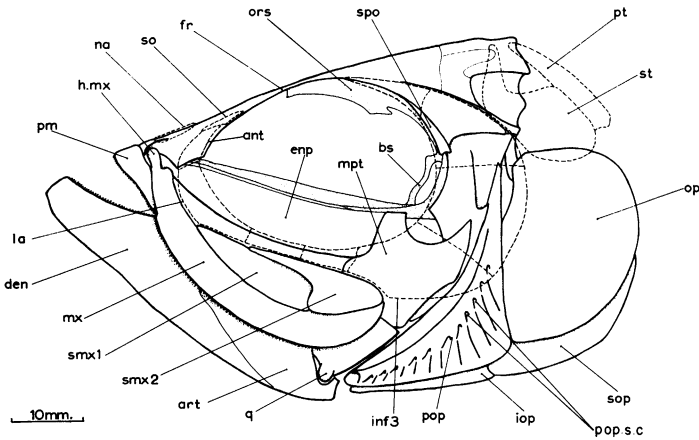


FIG. 5. *Megalops cyprinoides*, skull in lateral view.

Within the orbit both orbitosphenoid and basisphenoid are present, and the parasphenoid remains narrow in both fossil and recent forms.

Sedenhorstia has a neurocranium like that of *Elops*. (It is to be remembered that *Megalops* is rather specialized in this respect, with the posterior region much deepened and the posttemporal fossae confluent above the cranial cavity; Ridewood, 1904). In all three genera the posttemporal fossa is roofed, but the nature of the parietals in *Sedenhorstia* could not be ascertained. The occipital is formed solely of basioccipital in all three forms, and the exoccipitals are thickened above the condyle.

The hyomandibular in all three has a single elongated head composed of dense bone, with a slightly pitted external aspect. On the lateral face of the hyomandibular, lateral to the opercular process, there is a small, posterolaterally projecting spine abutting against the anterior edge of the preoperculum. The same structure is also present in both the *Ctenothris-*

siformes and the basal Myctophiformes, and represents the uppermost limit of the crest on the posterolateral edge of the hyomandibular against which the preoperculum rests.

An antorbital is present as a small slip of bone associated with the anterodorsal part of the lacrimal and is clearly seen in *Sedenhorstia orientalis*. An antorbital is also present in both *Elops* and *Megalops*. Unfortunately,

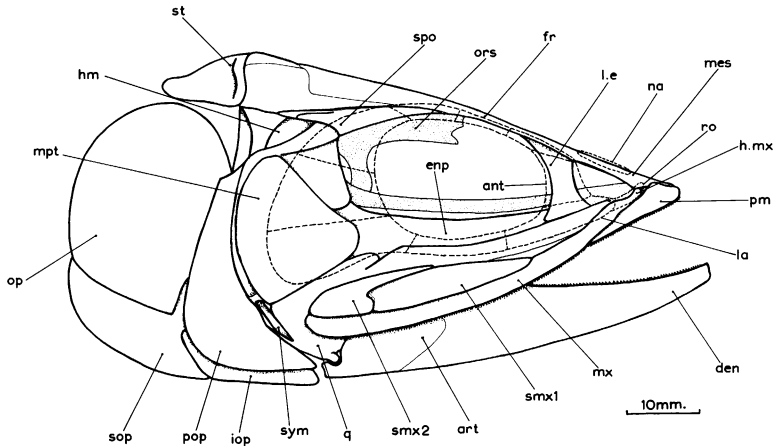


FIG. 6. *Elops machnata*, skull in lateral view.

no traces of supraorbital bones were found in *Sedenhorstia*, although several are present in *Elops* and a single one in *Megalops*. All three genera have an enlarged lacrimal, with the succeeding two infraorbitals narrowed below the orbit. Posterior to the orbit the last three infraorbitals are expanded to cover virtually all of the cheek region. In *Megalops* this backward extension covers much of the preoperculum, but in *Sedenhorstia* and *Elops* the expansions do not quite reach the preoperculum. The expanded infraorbitals of *Sedenhorstia* are ornamented with irregular radiating ridges, a feature not seen in either of the recent genera.

The preoperculum is similar in form in all three, and in the recent genera the sensory canal opens onto the surface through a series of small semilunar openings along the length of the bone (those of *Megalops* being far more evident than they are in *Elops*.) In *Sedenhorstia* there is some evidence of such openings, but they are fewer. In the recent forms the leading edge of the preoperculum is slightly convex in the region of the junction between hyomandibular and quadrate. This slight expansion marks the point of insertion of parts of the adductor mandibulae

muscle. That this expansion is not evident in *Sedenhorstia* does not mean that the musculature was not attached here (Gardiner, 1967, has considered this feature in the evolution of the actinopterygian preoperculum and its ultimate association with the jaw musculature).

The structure of the median fins is alike in *Elops* and *Sedenhorstia*, with the anterior rays spinous in form and gradually lengthening to attain a maximum length at about the sixth ray. The first four rays are unsegmented and spinous but are composed basally of ray-halves. Marshall (1962, p. 257) has described all stages in the transition from typical, segmented, and branched soft rays to the true fin spines in the notacanth group. Both Marshall (1962) and Greenwood *et alii* (1966, p. 355) have allied the notacanth with the elopiforms in the superorder Elopomorpha. Patterson (1964, p. 454) put forward a possible reason for the origin of fin spines. He maintained that the more rapid movement and maneuverability associated with the teleost grade have imposed greater stresses on the median fins, which may in part be counteracted by the strengthening of the leading edges of the fins with spinous elements. The first three or four spinous rays are associated with a single radial element, whereas the remainder of the rays exhibit the more typical teleost condition, with one radial element to each ray. Accessory radials (interneurals) are present in advance of the origin of the dorsal fin. In both *Elops* and *Sedenhorstia* these accessory radials are somewhat more curved and situated deeper in the dorsal myoseptum than the true dorsal fin radials. In this respect the elopiforms approach the condition in the Salmonidae which have as many as 12 accessory radials (Norden, 1961, p. 710). Also, Norden (1961, p. 707) noticed that the neural spines lying before and below the dorsal fin in *Thymallus* consist of separate lateral elements, as is the case in *Sedenhorstia*. In *Sedenhorstia dayi* (B.M.N.H. No. P.47513) the first two of these accessory radials are expanded, the first being closely associated with the neural spine of the first vertebra. Rosen (1964, p. 253) noticed this feature in the myctophiforms *Myctophum* and *Synodus*.

The pectoral fins in all three genera are situated low down on the flanks. Both *Elops* and *Megalops* have a mesocoracoid arch, but this cannot be ascertained in the fossil. The fins themselves, in the recent genera, have a small, asymmetrically placed, rudimentary spine at the base of the first fin ray, but this is absent from *Sedenhorstia*. All three genera have abdominal pelvic fins, and those of *Elops* and *Sedenhorstia* possess an asymmetrically placed, pelvic "splint-bone." Gosline (1961, p. 18) has considered this structure in a number of lower teleostean fishes, and Patterson (1964, p. 445) has listed the genera of recent and fossil teleosts

that possess such a pelvic splint. The spine of *Sedenhorstia* is identical to that of *Elops* (fig. 8). No functional significance or evidence of relationship can be attached to this structure. Patterson (1964, p. 445) suggested that the spines are primitive features retained in certain primitive or generalized groups.

The caudal fin skeleton is very similar in the three genera. The fins of both *Elops* (fig. 7) and *Sedenhorstia* (fig. 2) are supported on seven

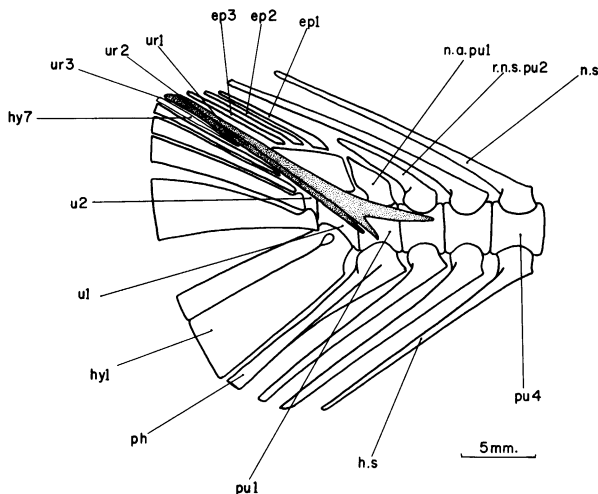


FIG. 7. *Elops saurus*, caudal fin skeleton in lateral view.

vertebrae, five of which are preural and two ural. Two differences are visible, one of them merely seeming to be trivial in that the first uroneural of *Elops* has a forked basal region whereas *Sedenhorstia* has not. The second difference concerns the neural arch and spine elements. Both appear to have a reduced neural spine on preural vertebra 2, but the spine itself may not strictly be reduced in length; it may be that the spines of the preceding preural vertebrae (3, 4, and 5) are elongated and produced back above that of the second to support the accessory epaxial rays. In *Elops* preural vertebra 1 has no neural spine, only an expanded neural arch, and in advance of the first uroneural there is a small anterior expansion. This small ossification is shown by Nybelin (1963) in *Elops saurus*, and by Norden (1961, pl. 15, fig. D) in *Elops affinis*. This expansion may represent the neural arch of the first ural vertebra. In *Sedenhorstia* there is no distinction between these two ossifications, there being simply a single large ossification associated with the dorsal surface

of preural vertebra 1 and the leading edge of the first uroneural. The epural elements in *Elops* are associated with the dorsal edge of the expansion on the first uroneural, and in *Sedenhorstia* with the single ossification. According to Monod (in press), the stegural of the Salmoniformes is formed from the incorporation of the neural arch of the first preural vertebra with the first uroneural. It seems possible that the neural arch of ural vertebra 1 enters into the composition of the stegural; if so, then the forerunner of a stegural component may be present in *Sedenhorstia*.

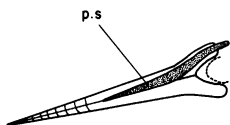


FIG. 8. *Elops saurus*, first pelvic fin ray in anterior view, showing the pelvic splint bone at the base of the dorsal half of the ray. After Patterson (1964).

Fringing fin fulcra are present on the uppermost epaxial principal fin ray of both *Sedenhorstia* (fig. 9A, B) and *Megalops* (fig. 9C, D). Fringing fin fulcra were recognized in *Megalops* by Regan (1910, p. 356). The fringing fin fulcra in *Sedenhorstia dayi* (B.M.N.H. No. P.47513, fig. 9A) are three in number. In the holotype of *Sedenhorstia libanica* (fig. 9B) there are five such fulcra. These fringing fulcra would appear to have been formed by the segmentation and delamination of the uppermost principal caudal fin ray, well shown in the holotype of *Sedenhorstia dayi*, A.M.N.H. No. 3692. In front of the fringing fulcra, true accessory fin rays are found in both genera, these rays representing the remains of the old epaxial rays.

An enlarged basal fulcral scale occurs both above and below the caudal peduncle anterior to the accessory fin rays in both *Sedenhorstia* and *Elops*, but not in *Megalops*. These basal fulcra, as is the pelvic splint, are primitive characters inherited from some halecostome ancestor and are retained only in some generalized forms, such as Elopiformes, Ctenothrissiformes, and some basal Myctophiformes.

The many features shared by *Sedenhorstia* and the recent elopoids are sufficient to warrant their inclusion in the same suborder, the Elopoidei. The familial designation for *Sedenhorstia* is more difficult. One character that may set it apart from the other elopoids is the presence of peculiar, middorsal, hooklike ossifications between the occiput and the dorsal fin (fig. 3). Hay (1903, p. 431) in reference to these ossifications said: ". . . they have the appearance of narrow folds or ridges, which are directed upward and backward, each ending in a point. What the relation of these crimpings is to the median row of scales has not been determined." From the specimens that the present author has examined it is clear

that these ossicles have no relation to the dermal scales that lie above them. The ossicles are within the body and probably lie in the dorsal myoseptum. Anteriorly the median ossicles are associated with the expanded first accessory radial, which in turn appears to touch the first

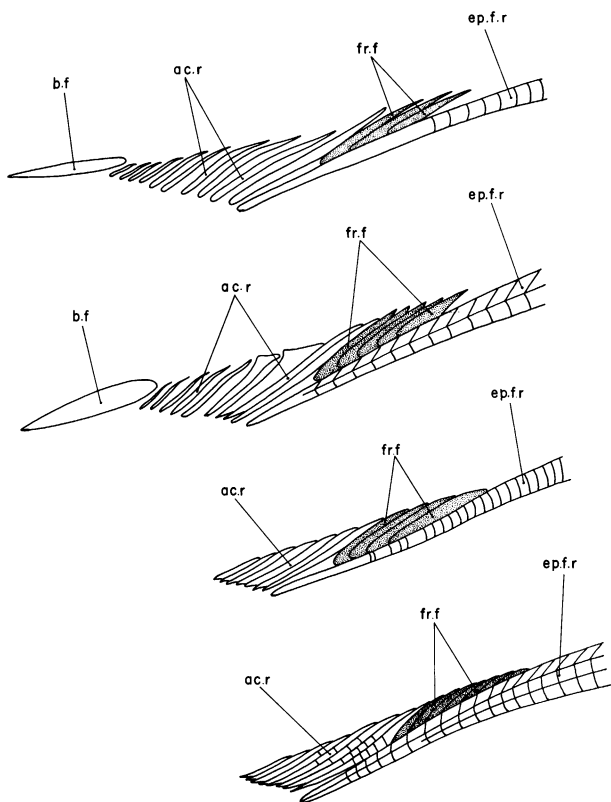


FIG. 9. Fringing fin fulcrum on the uppermost principal caudal fin ray. A. *Sedenhorstia dayi*. B. *Sedenhorstia libanica*. C. *Megalops atlanticus*. After Regan (1910). D. *Megalops cyprinoides*. After Regan (1910).

neural spine. The row of ossicles extends back to the origin of the dorsal fin, where they merge almost imperceptibly with the first rays of the fin. Possibly these ossicles represent the median basal fulcrum (ridge scales) of the halecostomes, but they are internal, whereas fulcrum would be superficial in position. Dissection of the middorsal region of *Elops* revealed a median dorsal ligament similar to that in other teleosts, but this ligament in *Elops* appears to be either calcified or ossified along some

part of its length. The ossifications in *Sedenhorstia* may represent points within a dorsal ligament, but it is impossible to say why it should ossify in such a peculiar manner. This factor, together with the others given in the description of *Sedenhorstia*, is sufficient to warrant the erection of a new family, Sedenhorstiidae.

Certain other fossil genera can now be reassessed. Firstly, the genus *Dactylopogon* Marck, 1868, was placed by Woodward (1901, p. 248) in the family Scopelidae along with *Sedenhorstia*. This genus is from the same locality as the type species of *Sedenhorstia*, that is, Sedenhorst. An examination of Marck's (1868) material established that this genus is, like *Sedenhorstia*, an elopiform. It more closely approaches the recent elopoids in the greater length of the vertebral column (*Elops*, 60–80 vertebrae; *Dactylopogon*, 70 vertebrae). Several of the other acknowledged elopiform genera (e.g., *Elopopsis* Heckel, *Osmeroides* Marck, *Notelops* Agassiz, and *Spaniodon* Pictet) all appear to be good elopoids in that they possess the following features: (1) gradually lengthening spinous rays at the front of both the dorsal and anal fins; (2) fulcral scales at the base of the caudal fin; (3) small toothed premaxilla without an ascending process; (4) a large maxilla supporting two large supramaxillae and an extensive row of teeth; (5) a radiating ornamentation on the expanded posterior infra-orbitals; (6) accessory radial elements in great abundance; and (7) individual vertebral elements with several lateral fossae and intervening bars. This last feature is not strictly diagnostic for the elopoids, but, as Schaeffer (1947, p. 15) pointed out, the typical elopoid vertebra has an unconstricted centrum with two or three lateral bars.

CONCLUSION

The foregoing description and discussion show that the genus *Sedenhorstia* is clearly an elopoid little different from the present-day *Elops* and *Megalops*. It is generally accepted that the Elopoidei represent the most primitive of living teleosts, with the included genera retaining the greatest number of halecostome characters. *Sedenhorstia* illustrates that the elopoids have remained unchanged since the Middle Cenomanian. Nybelin (1963) has described an elopid caudal fin skeleton from the Late Jurassic which again is little different from the recent *Elops*. Thus it seems probable that the elopiform lineage was in existence throughout the Upper Jurassic and Lower Cretaceous, and possibly even the earlier part of the Jurassic. In all this time no structural advance has been made, the genera remaining on an equivalent primitive level within the teleosts. As Greenwood *et alii* (1966, p. 355) stated, "the Elopiformes with their sum

of morphological characters present a picture of primitiveness . . . once the elopiform level of organization was reached, the group entered an evolutionary cul de sac."

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