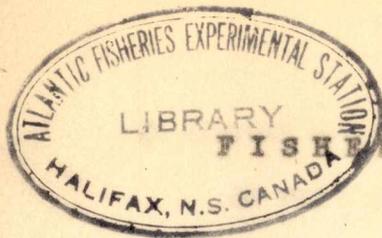


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THE ANATOMY OF THE NORTH AMERICAN PILCHARD AND ITS  
BEARING ON THE GENERIC RELATIONSHIPS AND  
NOMENCLATURE

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INTRODUCTION

The pilchard or sardine of the Pacific coast of North America is known commercially under two names which are generally interchangeable. In California where both mature and immature fish are caught both terms, "California sardine" and "pilchard" are used for the species, the latter term generally referring to the adult. On the North Pacific coast where the adults alone are taken in commercial hauls, the name "pilchard" is universally used. To avoid any confusion and in order to distinguish this species from the European species, Sardina pilchardus, the term "North American pilchard" is used in this paper.

A few years ago the question was raised as to whether the pilchard of North America could be rightly considered as occupying the same genus as that occupied by the pilchards of the North Atlantic. In fact Hubbs (1929), in separating these two species generically expresses doubt as to their having an immediate common origin.

Accordingly the present work was undertaken with the purpose in view of comparing the two types of pilchards anatomically in some detail, noting similarities and differences, and considering the bearing of these on the question of generic nomenclature.

For the greater part of the work the various points of anatomy were determined on four pilchards taken in Barkley sound on the west coast of Vancouver island. The body (standard) lengths of these ranged from 218 to 260 millimetres. These specimens were compared with four European pilchards from Plymouth which had standard lengths of about 210 millimetres.

I here take the opportunity of thanking Dr. C. McLean Fraser of the University of British Columbia, and Dr. W.A. Clemens and Dr. J.L. Hart of the Pacific Biological Station to whom I am indebted for assistance and references.

## HISTORY OF THE NOMENCLATURE

The generic and specific nomenclature of the North American sardine or pilchard has been long disputed. The history of the nomenclature of the species is briefly as follows:-

The pilchard was first recorded from the Californian coast by Girard in 1854 and described under the name of Meletta caerulea. Later, 1862, Gill redescribed the same species as Alausa californica and noted its possible position in the genus Clupea.

Jordan and Gilbert 1881, list the pilchard as Clupea sajax, (Jenyns, 1842), evidently considering it to be the same as the Chilean sardine, yet a few years later Jordan and Evermann changed the specific name to caerulea (Girard). In 1896 the same authors changed the generic name to Clupanodon LaCepede, Jordan and Gilbert having previously (1883) referred the European pilchard to this genus.

It may be mentioned here that none of these generic names are in order -- Clupanodon is reserved for a Chinese genus of fishes, while Meletta and Alausa are synonyms for Spratella and Alosa respectively.

Regan's 1916 contribution has more bearing on the present nomenclature of the North American pilchard. In his paper on the Clupeinae he refers the pilchards of the Pacific to the European genus Sardina Antipa, 1906. Shortly after Regan had done so Jordan synonymised Sardina Antipa with Sardinia Poey, 1858. This synonymy was not generally recognised.

Finally, Hubbs (1929) proposes to divorce the two types of pilchards generically. Thus he retains Sardina for the European pilchard and supplies a new genus, Sardinops, for the North American and related species. At present the validity of Sardinops as a separate genus is questionable.

DIAGNOSES OF THE GENERA

The diagnosis of Sardina as given by Regan to include both forms of pilchards is as follows:-

*Sardina Antipa*, 1906

"Elongate, moderately compressed; abdomen not sharp-edged. Mouth moderate, the maxillary not extending beyond the middle of the eye; lower jaw not prominent; upper without or with slight median notch; teeth minute or absent, none on vomer. Eye with well-developed adipose lids. Operculum with grooves radiating towards suboperculum. Dorsal fin of 16 to 20 rays, highest anteriorly, in the middle of the length of the fish, its origin nearer to end of snout than to base of caudal; a scaly sheath at base extending to tip of last ray. Anal of 16 to 20 rays, low, depressible in a scaly sheath; two last rays enlarged. Caudal forked; on each side enlarged scales on the inner edge of the scaly part of each lobe. Pectorals scaly at base; pelvics 8-rayed, inserted below middle or posterior part of dorsal. About 54 scales in a longitudinal and 10 to 14 in a transverse series; ventral scutes keeled but not projecting beyond the edges of the groove in which they lie. Vertebrae 50 to 53."

The diagnosis of Sardinops which includes the Pacific type of pilchard only, is given by Hubbs as follows:-

*Sardinops* Hubbs, 1929

Type-species, Meletta caerulea Girard, 1854

"Clupeidae with the upper jaw not noticeably notched on the mid-line; the gill rakers of the upper limb folded over those of the lower limb, which

become markedly and progressively shortened towards the angle; carina of glossohyal not denticulate; no bilobed dermal flap on the shoulder-girdle; opercle with strong and markedly oblique ridges; preopercular edge strongly sloping; interopercle widely exposed behind preopercle; scale-rows regularly spaced, the lateral scales all with subequal exposed areas; radii on the scales nearly vertical, and paired on each side of median line; keels on ventral scutes weak; last two rays of dorsal and anal fins somewhat enlarged; a row of dark spots typically developed on upper sides behind head."

EXTERNAL FEATURES -- North American pilchard

HEAD:

The head is green-blue dorsally, brown and silver on the sides and silver below and comprises about twenty-four per cent of the body length of the adult fish. The dorsal surface and sides are covered by a tough dermal layer which is marked by arborescent mucous canals.

The eyes are moderately large and are provided with a well-developed adipose eye-lid. The external nares are supero-lateral, nearer the snout than the eye, and double on each side. The anterior set is smaller and provided with a flap-like valve.

The opercle has four to six strongly marked ridges extending obliquely from the preopercle to the subopercle below. The posterior margin of the opercle is noticeably sloping; the posterior edge of the preopercle is strongly so. The interopercle is considerably exposed below the preopercle.

The upper jaw is not noticeably notched on the mid-line; the lower jaw is dark in colour and the tip projects but slightly beyond the upper jaw. The posterior edge of the maxilla is below the middle or anterior part of the eye.

BODY:

The body is moderately compressed, rounded dorsally and weakly keeled on the mid-ventral line. The colour is dark blue on the upper parts and silvery with metallic lustre below. Laterally, extending backwards from the head there is generally one series of large dark spots in the same level as the eye and sometimes a lesser series below this level. This feature is not

characteristic of the individual however for in a small portion of the species it is lacking altogether. In all the specimens so far examined there is a small dark spot at the base of each scale on the dorsal surface, making in all about five series of dots on each side of the mid-dorsal line.

The scales are thin, transparent, cycloid, and deciduous. They are arranged in regular rows and become markedly smaller towards the base of the caudal fin. There are fifty-three to fifty-four rows in a longitudinal series and ten to fourteen in a transverse. Scales on the mid-line below the dorsal fin have about one-fifth of their total area exposed. The margin of the exposed area is fimbriate, that of the covered portion is regular. The circuli on these scales are parallel but not concentric; the radii are slightly bowed, paired on each side of the median line and nearly vertical when the scale is in position.

The scales on the dorsal surface are smaller than the lateral scales and more or less circular; the circuli are concentric or nearly so; the radii extend out radially from the centre. Otherwise the scales are similar to those of the sides.

Around the shoulders there is a frill of scales which is covered by a dermal flap marked by the arborescent mucous canals.

The mid-ventral line is provided with a series of keeled scales extending from the insertion of the pectorals to the insertion of the ventral fins and from behind the ventrals to the vent. There are about eighteen before and fourteen behind the ventrals; those behind the ventrals become markedly smaller towards the vent.

The keel scales are composed of three parts. The two outer parts are similar being wide at the base and extending well up the side of the

fish by a strong spine-like projection. The median portion is very slightly keeled, bluntly pointed anteriorly but more expanded posteriorly. From the posterior end there are projecting one median and two outer, minute spines.

The dorsal fin is inserted nearer to the snout than to the base of the caudal fin. It is highest anteriorly and has seventeen or eighteen fin rays. The first two or three rays are soft yet unbranched; the rest of the rays are branched. The last two rays are not noticeably enlarged but there is a scaly sheath at the base of the fin which extends to the tips of these rays.

The anal fin has sixteen to eighteen rays; the last two rays are decidedly enlarged and longer. The whole fin has a scaly sheath at the base.

The caudal fin is deeply forked and has twenty-four to twenty-six rays. On each side of the inner edge of the scaly part of each lobe of the caudal fin there is an enlarged modified scale.

The pectoral fins are inserted below the angle of the subopercle; they are scaly at the base and have sixteen to eighteen dermal rays.

The ventral fins are eight-rayed and are inserted below the middle or posterior part of the dorsal.

EXTERNAL FEATURES -- European pilchard

HEAD:

The head comprises twenty-two to twenty-three per cent of the body length and resembles that of the North American pilchard in colouring, arborescent markings, and eye with adipose lid. The opercle has, like that of the other species, four to six ridges, but these differ in being more nearly vertical. Likewise the posterior margins of the preopercle and opercle are more nearly vertical. The interopercle is exposed below the preopercle to less than half the extent it is in the North American species.

The upper jaw is not noticeably notched on the mid-line; and the tip of the lower jaw projects slightly beyond the snout. The maxillary extends back to a point below the anterior half of the eye which is slightly anterior to the point reached by the maxillary of the North American pilchard.

BODY:

The body is like that of the North American pilchard in general colour and shape. The large dark spots on the sides common to the North American species are generally lacking but according to Couch (1835), and Regan (1916), these may be present but not to any great extent. The dark spots at the base of the scales on the back are lacking on the specimens examined.

The scale arrangement is markedly different to that of the North American pilchard. Here the scales are alternately larger and smaller so that the larger scales almost completely cover the smaller scales immediately posterior. This arrangement gives an apparent number of thirty large scales in a longitudinal series whereas the true number of scales is about the same as that of the other pilchard -- fifty-three to fifty-four. There are ten to

fourteen scales in a transverse series.

It may be pointed out here that this peculiar scale arrangement, although characteristic of the species, is not typical for every individual of the species. According to Day (1887), and Bateson (1890, 1894), a small proportion of the European pilchards are in part scaled like the pilchards of the Pacific.

The scales below the dorsal fin on the mid-line are approximately the same as those of the North American pilchard as to the nature of the circuli and the shape. The larger scales are considerably, and the smaller slightly larger than the scales of the North American species from the same body region. The radii are slightly more bowed than in the scales of the other species but are paired on each side of the median line and are nearly vertical when the scale is in position.

The scales of the back are alternately larger and smaller. Those anterior to the dorsal fin are of the same shape as the scales of the sides; those posterior to the dorsal are ovulate. In all of these as in scales from the same position on the North American sardine, the circuli are concentric and the radii radiate from the centre.

The frill of scales and the dermal flap about the shoulders are the same in both species.

The keel scales are similar in number to those of the North American pilchard. The outer parts are similar in design in both sardines except that the spine-like projections are not so strong in the European species. The median part is similar in both when viewed from above, but on the under surface the European sardine has a pronounced keel on the posterior half of the scute.

The dorsal and pectoral fins are in the same relative positions in the two pilchards; the dorsal has seventeen or eighteen fin rays and the pectoral sixteen to eighteen rays. The anal and ventral fins are farther forward in the European sardine but the number of rays for each fin is the same in the two species. The European pilchard has the last two rays of the anal fin enlarged as in the North American species. The scaly sheaths at the base of all the fins except the ventrals are present in both species. The caudal fin is similar in both, even to the two enlarged scales on each side of the fin.

SKELETAL SYSTEM -- North American pilchard

CRANIUM:

The occipital region is composed of four bones; the supra-occipital, the paired exoccipitals, and the basioccipital. The supraoccipital is exposed dorsally in an elevated, triangular portion which separates the parietals and extends a short distance between the frontals. It is marked by a pronounced median ridge and two transverse ridges paired on each side of the median ridge. The median ridge continues down the posterior surface of the supraoccipital to the magnum foramen. The exoccipitals are joined below the supraoccipital to form the dorsal and lateral boundaries of the magnum foramen. The basioccipital bounding the foramen ventrally is a long centrum-shaped bone. The posterior surface of the basioccipital is enlarged and concave and articulates with the first vertebra. The ventral surface is provided with two thin plates which are fitted to similar plates of the parasphenoid to form the eye-muscle canal.

In the region of each auditory capsule there are five bones. The sphenotic is anterior and dorsal; it has a stout lateral process which marks the posterior boundary of the orbit of the eye, and is partially covered by a lateral extension of the frontal. The prootic is ventral to the sphenotic and the prootics of each side are joined ventrally to form the base of the cranium. The pterotic marks the posterior limits of the capsule. It is characterized by a long spine-like process with which one branch of the post-temporal bone articulates. The opisthotic is ventral to the pterotic and external to the exoccipital. It is a small bone and has a short posterior projection. The epiotic is between the supraoccipital and the pterotic and extends backwards to a blunt point.

The anterior part of the brain case is completed by the basisphenoid and the paired alisphenoids. The basisphenoid is a small Y-shaped bone forming part of the boundary of the optic foramen. It extends ventrally by the base of the "Y" and is joined by cartilage to the parasphenoid. The alisphenoids are larger bones dorsal to the foramen; and are joined suturely to the fused orbitosphenoids.

The orbitosphenoid consists of two fused bones; a wide portion bounds the optic foramen anteriorly and a thinner portion extends forward to the prefrontal to separate the orbits of the eyes.

The parasphenoid is a long unpaired bone extending from the vomer to behind the basioccipital. The posterior portion is split into two thin non-divergent processes. Below the basioccipital the parasphenoid is trough-shaped and with that bone it forms the eye-muscle canal which is open in front and behind.

The paired frontals and parietals comprise the dorsal surface of the skull. The frontals are large bones extending from the mesethmoid in front to the supraoccipital behind. They are narrow and pointed anteriorly but are expanded posteriorly. The posterior portion is forked to allow for the superior-temporal fossae. The surface of the frontals is marked by delicate longitudinal ridges. The parietals are small and are situated behind the median extensions of the frontals. They are separated from each other by the supraoccipital, possess short ridges on the surface, and mark the anterior limits of the epiotic fossae.

The bones of the ethmoid region are the paired prefrontals, the mesethmoid and vomer. The prefrontals mark the anterior boundaries of the orbits.

They are each provided with two lateral processes; the larger slopes downwards and backwards around the orbital space; the other, smaller and more ventral, slopes downwards and forwards around the nasal space. The mesethmoid is median, anterior to the frontals; it gives off two thin plates posteriorly which extend for a considerable distance below the frontals. Anteriorly it joins the rostral cartilage. The vomer is a narrow bone forming the roof of the mouth below the mesethmoid. It curls over the rostral cartilage anteriorly and extends backwards in a groove in the parasphenoid to behind the prefrontals. The anterior part of the mesethmoid gives off two bony processes, one to each side, with which the premaxillae articulate. The nasals are joined to the anterior part of the mesethmoid behind the premaxillae; they are small flat bones slightly expanded anteriorly.

Around the orbit of the eye are several scale-like bones; the large preorbital, the supraorbital and four or more suborbitals.

#### SUSPENSORIUM:

The suspensorium of each side contains two bones, the hyomandibular and the symplectic. The hyomandibular is a large bone articulating with the sphenotic and the pterotic. On the posterior margin some distance from the point of articulation with the bones of the auditory capsule the hyomandibular sends off a short rounded process which is the point of articulation of the opercle. Ventrally the hyomandibular extends by a narrow process between the preopercle and the quadrate. The symplectic is a short rod-like bone connected to the ventral extension of the hyomandibular by cartilage; its ventral extremity fits into a slight notch in the quadrate.

JAWS:

The bones of the upper jaw are paired, and toothless. The premaxillae are most anterior; they are small flat bones meeting in the median line to form the tip of the snout. At the point of articulation with the mesethmoid the premaxillae are somewhat thickened. The maxillae are larger bones; they articulate with the lateral processes of the mesethmoid and extend back to below the orbit of the eye. Above the maxilla and attached to it are the first and second admaxillaries. The second admaxillary partially overlaps the posterior portion of the maxilla.

Five pairs of replacing bones form the roof and sides of the buccal cavity within. These are for each side: the palatine, a thin bone forming the roof anteriorly, and extending from the anterior end of the vomer to the mesopterygoid and pterygoid; the pterygoid, extending along the side from the palatine to the quadrate; the mesopterygoid forming the roof posterior to the palatine and bounded behind by a horizontal process from the metapterygoid; the metapterygoid, forming the upper portion of the side posteriorly and touching the hyomandibular; the quadrate, below the metapterygoid and partly separated from that bone by an oval fenestra. The preopercle is attached to the posterior margin of the quadrate where there is a slight thickening of the bone; the ventral end of this thickened portion of the quadrate articulates with the articular of the lower jaw.

The bones of the lower jaw are paired and toothless. The dentary is anterior, large, and deeply notched to receive a thin process from the articular. The articular is smaller, thin anteriorly but thickened posteriorly so that the thickened portion resembles a "Y". The posterior projection articulates with the quadrate. The angular is a small inconspicuous bone below the region of articulation of the articular.

OPERCULUM:

The operculum consists of four bones: the preopercle, the interopercle, opercle and subopercle. The preopercle is roughly crescentic in shape, slightly thickened along the concave margin and attached to the quadrate at the lower end of this thickened portion. The interopercle is below the preopercle and more than half covered by it and is attached at its anterior end to the articular of the mandible. The opercle is the largest of the four bones; it is widest dorsally and articulates with the hyomandibular by a concave disc situated about a third of the distance down the anterior margin. On the external surface of the opercle are four to six strong, slightly curved ridges which radiate from the region of articulation to the whole extent of the ventral margin. The subopercle is a small flat bone below the opercle and is attached to that bone at its ventral margin. A short process from the subopercle extends up the anterior margin of the opercle.

HYOID ARCH AND ASSOCIATED BONES:

The hyoid arch is joined to the cartilage between the hyomandibular and symplectic by a small pad-like bone, the interhyal. The arch contains three bones: the epihyal, ceratohyal, and double basihyal. The epihyal is flat, triangular, and joins the interhyal at the apex and the ceratohyal at the base. The ceratohyal is long and flat and bears near its ventral margin, three or four perforations into which the branchiostegal rays are hooked. The basihyal is small, double, and is anterior to the ceratohyal.

Attached to the hyoid arch are certain investing bones. The glossohyal is supported by the basihyals; it is a small, keeled, toothless bone supporting the tongue. The branchiostegals are attached to the ceratohyal and the epihyal.

They are sword-shaped bones increasing in length and width posteriorly in the series. There are six, seven, or eight, as the case may be, in the series; the first three or four hook into the holes in the ceratohyal; the rest of the rays are attached to the flat surface of the ceratohyal and epihyal, and to the interopercle by the branchiostegal membrane.

The urohyal forms the isthmus of the throat; it is a sabre-shaped bone, attached to the basihyal anteriorly and by cartilage to the pectoral girdle posteriorly.

#### BRANCHIAL ARCHES:

There are five branchial arches diminishing in size from in front backwards. The first three arches are complete, consisting of four segments; the hypobranchial and ceratobranchial form the lower limb of the arch; the epibranchial and superior pharyngeal form the upper limb. In the fourth arch the hypobranchial is small and the superior pharyngeal is unossified. The epibranchial has strong teeth along posterior margin and bears dorsally a large plate-like bone, the superior epibranchial. The fifth arch contains a single bone, the inferior pharyngeal (ceratobranchial) which bears teeth along its posterior margin. The epibranchials of the first three arches bear single posterior projections which extend over the superior pharyngeals of the arches immediately behind.

The hypobranchials of the arches of the two sides are connected by an unpaired basibranchial which is in five segments, one segment to each arch. The first segment is joined to the glossohyal; the last two segments are not ossified. The last segment extends beyond the fifth arch in a cartilaginous plate.

The superior pharyngeals of the first arch are connected to the parasphenoid by a small bone, the suspensory pharyngeal.

Each branchial arch bears a single row of long gill rakers on its dorsal surface and a double row of gill filaments on the ventral surface. In the adult fish there are about ninety rakers on the lower limb of the first arch and about fifty on the upper limb. In the first arch the rakers of the upper limb fold over the rakers of the lower of which a number (about ten) become markedly shortened at the angle.

Each gill raker bears a row of minute processes on each side; these are about half as long as the raker is wide, and are spaced about three to the distance of their length. Each process consists of a flask-shaped stalk with a fimbriated leaf-like terminal element.

#### VERTEBRAL COLUMN:

Generally there are twenty abdominal and thirty-one caudal vertebrae exclusive of the hypural bone. Each abdominal vertebra, with the exception of the first, consists of a centrum, shaped like an hour-glass, concave at the anterior and posterior surfaces; parapophyses on each side of the centrum ventrally; long pleurals or ribs, extending ventrally to lie under the processes from the keel scales and attached to the parapophyses; shorter epipleurals attached to the parapophyses above the pleurals; adpleurals or extracostal bones joined horizontally to the sides of the centrum; neurapophyses which are joined dorsally to form the neural arch and continue in the neural spine; zygapophyses projecting forwards from the base of the neurapophyses and connecting them with the neurapophyses of the vertebra in front; epineurals at the base of the neurapophyses.

The first abdominal vertebra or atlas possesses only the neurapophyses and epipleurals; the first few neural spines are split at the ends.

The epipleurals, adpleurals and epineurals are absent in the posterior caudal vertebrae: the pleurals become modified to form the haemapophyses. The haemapophyses of the first few caudal vertebrae are connected ventrally by a transverse bar which is gradually replaced by the haemal spine. The parapophyses remain, but in the posterior vertebrae they become similar in shape to the zygapophyses and touch the haemapophyses of the vertebrae in front.

In addition to these bones connected to the vertebrae, there are certain numerous small bones situated in the myosepta; a sheath of fine bones is attached to the epiotic and extends backwards in a fold of the intermuscular septum; below and above the adpleurals is a series of thin intermuscular bones which are forked at the anterior end. These bones become widened to form a sheath over the caudal plate.

#### APPENDICULAR SKELETON:

The pectoral girdle is suspended from the skull by the post-temporal. The girdle has the usual number of parts; the post-temporal is flat and forked at one end to articulate with the epiotic by one fork and the pterotic process by the other; the supraclavicle is a scale-like bone joining the post-temporal with the clavicle below by extending along the outer surface of each. The postclavicle is in two parts, the upper part is attached to the outer surface of the clavicle and the lower part extends to a point behind the insertion of the pectoral fins. The dorsal part of the clavicle is narrow and sharp-edged posteriorly; the ventral part is bent to the horizontal plane and the edge is

rolled inwards; at the angle of the bend there is a short process with an expanded end. The clavicles of each side lock anteriorly by means of two or three short processes.

The ventral and inner part of the girdle is formed by three bones; the hypocoracoid is flat, with a rounded margin anteriorly and pointed behind and joins its fellow of the other side to form a keel ventrally; the mesacoracoid is above the hypocoracoid and anterior to the glenoid facet; the hypercoracoid is small, posterior to the mesacoracoid and dorsal to the glenoid facet.

The pectoral rays are segmented and split lengthwise; they are connected to the girdle by four rod-like actinosts and a number of small pad-like actinosts over which the bent ends of the two halves of each ray fit.

The pelvic plate consists of a single flat bone, pointed anteriorly, thickened and expanded posteriorly: the pelvic rays are similar in form to the pectoral rays and are attached to the plate by two or three small actinosts.

The rays of the dorsal fin are individually supported by the interneural spines and two actinosts. Smaller interneural spines extend from the head to behind the dorsal fin.

The rays of the anal fin are similarly supported by haemal spines and actinosts, the first spine being the largest of the series.

The hypural plate supports the caudal fin. It is formed by the haemal and neural spines of the last two vertebrae and the spines associated with the hypural bone. The spines from the last vertebra support the outer rays of the fin but they are not greatly modified and do not enter into the composition of the plate proper. The neural spine of the last vertebra may bear a small accessory spine in front.

The hypural bone and the spines attached to it form a solid plate in the following manner: the hypural is actually a modified vertebrae presenting an upturned end posteriorly which represents the ossified tip of the notochord; the neural spine from the hypural lies over the upturned tip and bears an accessory spine anteriorly; the haemal spine is double, plate-like, and forms a great portion of the caudal plate. The lower portion of the haemal spine from the hypural bears a thin horizontal ridge which serves to support the basal segment of the two median caudal rays. Along the tip of the hypural, posterior to the neural spine, are two small bones which evidently represent the neural spines of unformed vertebrae. Below one of these spines there is a double haemal spine, smaller than that of the hypural but similarly modified; the haemal spine below the last neural spine is small and not so well developed.

The rays of the caudal fin with the exception of the two median ones are similar to those of the dorsal or pectoral fin. In the two median rays the basal segments are enlarged on each side into paddle-shaped pieces which extend over the caudal plate.

SKELETAL SYSTEM -- European pilchard

The skeleton of the European pilchard is mainly similar to that of the North American pilchard: in the region of the skull the carina of the glossohyal, the vomer, and the palatines bear no teeth; the ceratobranchials of the fourth branchial arch, and the inferior pharyngeals bear strong spine-like teeth. The chief differences are found in the shape of the four opercular bones; the preopercle is not crescent-shape but more L-shaped along its posterior margin thus causing the interopercle to be more than two-thirds covered; the opercle is as wide at its ventral edge as it is at the articular facet, the ridges are very slightly curved but otherwise the same as those of the other pilchard; the subopercle is slightly wider than that of the North American species because of the expanded ventral margin of the opercle; the interopercle is slightly less expanded posteriorly and the margin is more curved so that the posterior extremity is ventral instead of dorsal as in the North American pilchard.

Another difference is found in the nature of the gill rakers; here the rakers are slightly shorter and less numerous -- there being about seventy-five on the lower limb of the first arch. Only one or two rakers are shortened at the angle and the rakers of the upper limb lie along those of the lower limb but do not overlap them.

This feature is perhaps due to the shorter rakers and a slightly deeper mouth for if the two limbs are pressed closer together artificially the gill rakers overlap as in the North American pilchard.

The minute processes on the gill rakers are, in the specimens examined, similar in shape to those of the North American pilchard, and of about the same length and spacing. This is contrary to the findings of Bigelow as

reported by Hubbs (1929) who states that the processes are short, spine-like, and slightly bent. This type of process is found on the gill rakers of the herring, Clupea pallasii, but so far has not been discovered by an examination of several specimens of each type of sardine.

The vertebral column, the girdles and the hypural plates are similar in both species. There are generally fifty-one vertebrae in each species, but specimens with one vertebra more or less than this number are found.

## MUSCULATURE

The muscle system may be conveniently separated into the following:-

1. Muscles of the trunk, the great longitudinal muscles.
2. Muscles of the head region.
3. Muscles of the dorsal fin.
4. Muscles of the anal fin.
5. Muscles of the pectoral fin.
6. Muscles of the pelvic fin.
7. Muscles of the caudal fin.

### MUSCLES OF THE TRUNK, THE LONGITUDINAL MUSCLES:

This group of muscles forms the major mass of muscle substance on each side of the body of the sardine. There are three sets of muscles in this group; dorsally there are the supracarinales; laterally are the great lateral muscles proper, and ventrally there are the infracarinales.

#### The great lateral muscles proper

These are the largest muscles in the fish and extend from the base of the skull to a tendon at the base of the caudal fin on each side of the fish. The entire muscle layer is divided into segments or myomeres, each myomere corresponding with a vertebra below. The myomeres are separated from one another by thin septa, the myocommata. The shape of the myomeres is complex being somewhat of the form of the letter "W" but so arranged that one myomere overlaps in the central portion the myomere directly behind it, but is in turn overlapped at the angles by the same myomere. This overlapping becomes more noticeable in the caudal myomeres where the central portions become semi-conical.

The great lateral muscle consists of a superficial division and a deep division. The superficial division or musculus lateralis superficialis, is separated from the deep divisions by a thin septum, and is itself divided by

a much less noticeable septum into an epaxial, and a hypaxial division. This muscle extends over only part of the deeper muscle, is dark brown in colour, and is separated from the dermis by a layer of fat. The deep division or *musculus lateralis profundis*, has an epaxial and hypaxial division, extends over the whole side and is salmon pink to white in colour. These muscles are the chief swimming muscles, their purpose being to bend the body laterally.

The dorsal longitudinal muscles, the *supracarinales*

These muscles are paired on each side of the mid-dorsal line, well developed, and enclosed in heavy connective sheaths. The myomeres are spirally arranged. There are two divisions to this group; the anterior one is the *protractor dorsalis*, the posterior, the *retractor dorsalis*.

The *protractor dorsalis* is attached by a sheet-like tendon or fascia to the shoulder girdle and occipital bones. It is inserted at the base of the first ray of the dorsal fin, and also along the full length of the median septum by slips from the myomeres. This muscle draws the dorsal fin forward and flexes the body dorsally.

The *retractor dorsalis* is not so well developed as the *protractor*. It is inserted at the base of the last ray of the dorsal fin and is attached posteriorly, by a broad tendon, to the connective tissue around the neural spines of the caudal region. This muscle serves to move the dorsal fin backwards and co-operates with the *protractor* to flex the body. Both of these muscles are cylindrical in form.

The ventral longitudinal muscles, the *infracarinales*

These muscles are paired on each side of the midventral line. They are well developed, cylindrical, and enclosed for the most part in a distinct sheath. There are three divisions to this muscle; the anterior division is

the protractor ischii, the mid division is the retractor ischii or protractor analis, the posterior division is the retractor analis.

The protractor ischii originates in a flat tendon mass which is attached to the ventral edge of the hypocoracoid and to the septa of the lateral muscles of this region. It is inserted posteriorly into the antero-ventral border of the ischial or pelvic plate and into a tendon connected with the retractor ischii. This muscle acting alone serves to draw forward the pelvic girdle.

The retractor ischii arises from the posterior border of the ischium as well as from the tendon from the protractor ischii. It passes around the anal opening and has its insertion at the base of the first interhaemal spine. Acting alone or with the protractor ischii it protracts the anal fin. Acting with the retractor analis, it retracts the pelvic fin.

The retractor analis is quite slender. It is inserted at the base of the last interhaemal spine and originates from the ends of the haemal spines of the caudal plate. This muscle co-operates with the other muscles to flex the body ventrally or acts alone to draw the anal fin backward.

#### MUSCLES OF THE HEAD:

The dorsal head muscles may be divided into a superficial set and a deep set.

Of the superficial set the adductor mandibulae is by far the most noticeable. This muscle forms the "cheek" of the pilchard and has a cephalic and a mandibular division. The cephalic division originates partly from each of the following: the anterior border of the preopercle, the surface of the quadrate, the metapterygoid, the hyomandibular, and the connective tissues around the levator arcus palatini. At the place of convergence of this fan-

shaped muscle a tendon arises which goes out to the angle of the jaw. The mandibular portion originates from the tendon over the quadrate bone and is inserted into the inner surface of the mandible. Both of these muscles serve to close the mouth.

The levator arcus palatini fills the space immediately posterior to the eyeball. It originates from the sphenotic and passes underneath the cephalic division of the adductor mandibulae to its point of insertion on the superior portion of the hyomandibular and the superior margin of the metapterygoid.

The dilator operculi is small and is situated immediately behind the levator arcus palatini. It originates from the pterotic and sphenotic and passes backward and downward to a little knob where the opercle articulates with the hyomandibular. The muscle is attached by a strong tendon to the upper margin of the opercle, thus causing the opercle to spread outwards when the muscle contracts.

The levator operculi originates from the posterior border of the pterotic and spreads forward to be inserted in the upper posterior margin of the opercle. Contraction of this muscle elevates the operculum.

There are two deep dorsal head muscles, one concerned with the opercle and the other with the palatine arch. The first of these, the adductor operculi, originates on the ventral surface of the pterotic under the point of origin of the levator operculi. It is inserted into the inner surface of the opercle and opposes the dilator operculi in action.

The second of these, the adductor arcus palatini, originates from the outer surface of the orbitosphenoid and is inserted by a broad attachment into the metapterygoid and mesopterygoid.

### The muscles of the eye

The six characteristic eye muscles appear in the sardine, well developed. The superior and inferior oblique muscles are attached to the margin of the cornea of the eyeball and pass forward to be attached near the anterior end of the interorbital septum. The superior oblique is directly above the inferior oblique. The superior rectus and the inferior rectus muscles are attached to the eye near the place of attachment of the superior and inferior obliques respectively. The external or anterior rectus and the internal or posterior rectus are attached at the other two quadrants of the eyeball. These four muscles pass backwards in close proximity to each other in an "eye muscle canal" to their origin at the base of the skull.

There are in addition to these muscles many which are much less noticeable. These are the branchial arch, and mandibular and hyoid arch muscles which aid in respiration.

### MUSCLES OF THE DORSAL FIN:

The muscles of the dorsal fin are all slip-like in form, one slip being present for each ray.

The superficial muscle is the inclinator dorsalis which is paired to each side of the fin. This muscle is composed of nineteen small slips each of which takes its origin in a fascia which is attached to the skin. This muscle bends the fin to the side.

Below the inclinator are the slips of the erector dorsalis and the depressor dorsalis, alternating with each other and one of each lying between two interneural spines. The erector is the more anterior of the set of two. The erector dorsalis slips originate from the interneural spines and the fasciae between the slips of the two types of muscles. It is inserted on the "toe" of

the foot-shaped ending of the dermal fin ray. The depressor originates similarly and is inserted on the "heel" of the basal portion of the ray.

#### THE MUSCLES OF THE ANAL FIN:

The muscles of this fin are on the same plan as those of the dorsal fin and are; the inclinor analis, the erector analis, and the depressor analis. There are also slight muscle fibres between the dermal fin rays constituting the interfilamenti analis.

#### THE MUSCLES OF THE PECTORAL FIN:

The muscles of the pectoral girdle are: the abductor pectoralis superficialis, the abductor pectoralis profundus, the adductor pectoralis superficialis, the adductor pectoralis profundus, the extensor pectoralis, and the interfilamenti pectoralis. Of these the interfilamenti, extensor, and abductor superficialis are first exposed.

The interfilamenti pectoralis consists of a group of muscle fibre extending from ray to ray near their bases.

The abductor superficialis has its origin along the anterior ventral border of the coracoid as far back as the base of the fin. Anteriorly some of the tendons from this muscle join with those of the protractor ischii. The muscle is inserted by a series of tendinous slips to the tips of the processes of the ventral, or external half rays of the fin, in such a way that contraction of the muscle bends the fins downward and forward.

The extensor takes its origin from the ventral portion of the clavicle, under the anterior margin of the abductor superficialis and is inserted into the base of the first fin ray. This muscle serves to spread the fin in the

horizontal plane.

The abductor pectoralis profundus lies beneath the superficialis. It originates from the ventral portion of the coracoid and is inserted by a series of tendon slips, into the inner margins of the basal processes of the ventral halves of the fin rays. This muscle pulls the fin downwards.

The adductor pectoralis superficialis and profundus both lie in the angle between the clavicle and the coracoid and are both inserted into the dorsal or internal half rays. They both serve to press the fin against the sides of the body. The superficialis arises from the posterior ventral surface of the coracoid and from the mesacoracoid. The profundus arises from the most ventral portion of the clavicle and from the dorsal margin of the coracoid.

#### MUSCLES OF THE PELVIC FIN:

The abductor ventralis superficialis is the most median of the muscles of the pelvic fin and has its origin on the ventral border of the anterior portion of the pelvic plate. It is also connected with the tendon between the protractor ischii and the retractor ischii. It is inserted into the tips of the ventral halves of the rays of the fin.

The abductor profundus lies next to this. It takes its origin from the ventral surface of the pelvic plate and is inserted into the ventral halves of the rays. Both these muscles tend to move the fin downward, away from the body; and to proximate the fin rays.

The adductor profundus is a large muscle lateral to the abductors. It arises from the dorsal surface of the pelvic plate and is inserted into the median borders of the dorsal halves of the rays.

The adductor superficialis is dorsal to all of these muscles, and has its origin on the dorsal surface of the pelvic plate and its insertions into

the dorsal halves of the rays of the fin. The adductor group accomplish the spreading of the rays of the pelvic fin, as well as rotating the fin in towards the body.

#### MUSCLES OF THE CAUDAL FIN:

The only superficial muscles here are the interfilamenti caudalis which are muscle fibres running obliquely between the central fin rays. .

After the tendons of the lateral muscles have been removed the deep caudal muscles are exposed. The adductor caudalis ventralis is roughly triangular in shape. It arises from the dorsal margin and the surface of the lowest hypural bones and is inserted into the more dorsal caudal fin rays. This muscle flexes the dorsal lobe of the fin.

The flexor caudalis dorsalis superior, and inferior both flex the tail for swimming and steering. The superior originates in the median septum over the neural spines near the caudal end, and is inserted on the sides of the most dorsal fin rays. The origin of the inferior is from the margin of the hypural plate and the insertion is only the slightly more median rays of the dorsal lobe.

The flexor caudalis ventralis arises from the bases of the haemal spines and extends backward to its insertion on the sides of the rays of the ventral lobe. It has an inferior and superior division.

The above account applies in general to the musculature of the European pilchard. It is quite possible that a similar type of musculature applies in general to all the members of the sub-family Clupeinae.

### DIGESTIVE SYSTEM

The pharynx has two pouches or pockets dorsally and is connected with the so-called stomach by a short oesophagus; the stomach is Y-shaped, the lower branch being connected with the duodenum; the median caecum, which forms the base of the "Y", is connected with the swim bladder by the pneumatic duct which passes forwards and upwards from the end of the caecum to the swim bladder. The duodenum is of slightly larger diameter than the rest of the intestine, is separated from the lower limb of the stomach by a slight constriction, and bears the numerous pyloric caeca. The duodenum is folded upon itself and then passes backwards to the vent by the straight tubular intestine.

In the vicinity of the duodenum are the gall bladder, liver, spleen and pancreas; the liver is right and left lobed, the left lobe being larger, and covering the duodenum and pyloric caeca; the gall bladder is in the right lobe of the liver, is fairly large, globular, and empties into the duodenum by means of a short cystic duct; the pancreas is found in the mesentery of the fold of the duodenum; the spleen is brown, long, narrow and three ridged, and is situated immediately dorsal to the intestine below the median caecum.

The swim bladder is well developed and besides possessing a pneumatic duct it opens upon the vent by a posterior duct. Anteriorly the air bladder passes into the neck region where it first narrows and then dilates to form a bulb from which the diverticula pass forward to rest against the auditory fenestrae.

The digestive system of the European pilchard is in general similar to that of the North American pilchard as described. Pyloric caeca were not counted but should the number be slightly different for the two species any such difference is not of generic importance.

### URINO-GENITAL SYSTEM

The kidney of both sardines is of the usual Clupeoid type; it is an unpaired, brown, glandular mass extending the length of the body cavity immediately ventral to the vertebral column, and empties into the vent by a mesonephric duct.

The gonads are paired and are supported in the body cavity by the dorsal mesentery; the gonoduct from each gonad passes backwards to a common duct which opens upon the vent. The ovaries are torpedo-shaped and are of a semi-granular consistency in an immature female. In the mature female the ova can be seen in the ovary. The testes are knife-shaped and are of a more even texture.

The pelagic ova may be mentioned here. The ova of the European pilchard as described by Cunningham (1896), have a reticulated yolk, a single oil globule and a great space between the yolk and the egg membrane. Regan (1916), and Barnard (1925), describe a similar type of egg for the pilchards of the southern hemisphere, S. neopilchardus and Sardina sajax, which are closely related to the North American pilchard.

## BLOOD-VASCULAR SYSTEM

Due to the difficulties presented by non-injected material the vascular system is here merely outlined in gross aspect. It is not to be expected that any great differences should occur in this for the system is similar for all the Clupeoid fish.

### HEART:

The heart is situated in the pericardial cavity between the two halves of the pectoral arch and ventral to the oesophagus. It is enclosed within the pericardium and consists of three chambers; the sinus venosus is dorsal and posterior, and receives the two ducti Cuvieri; the auricle is thin-walled, anterior and dorsal, and is connected with the sinus venosus by the sinu-auricular opening; the ventricle is ventral and posterior, thick-walled and muscular and connected with the auricle. Anteriorly the ventricle opens into the bulbous aorta which is a thickened portion of the ventral aorta.

### ARTERIES:

From the bulbous aorta the ventral aorta extends anteriorly to give off the pairs of afferent branchial arteries. There are four such paired arteries. The fourth and the third branches arise from a common stem; the second branchial arises separately; and the first set is formed by the bifurcation of the ventral aorta.

The afferent arteries are joined by capillaries to the efferent branchial branches. The efferent branchial arches come together dorsally to form a ring from which the external carotids are given off anteriorly and the dorsal aorta posteriorly. The dorsal aorta passes back to the caudal region close

under the vertebrae, enclosed by the haemal arches for part of the distance. In its anterior portion the dorsal aorta gives off arteries which supply the viscera of the body.

VEINS:

Three sets of veins empty into the sinus venosus. The first of these is the set which supplies the pectoral girdle and the ventral abdominal wall.

The second of these are the hepatic veins which connect by sinusoids with the hepatic portal system which gathers the blood from the viscera.

The third set are the two stout Cuvierian ducts which receive the jugular veins from each side of the head region, the genital veins and the posterior cardinal veins.

The jugular veins are enlarged and bulbous before they join the ducti Cuvieri; the genital veins enter ventral to the jugulars. The right posterior cardinal only is well developed and extends the whole length of the kidney, imbedded therein. It receives at its posterior end the caudal vein which lies below the dorsal aorta enclosed within the haemal arches.

## NERVOUS SYSTEM

The nervous system is presented only in gross aspect; it is similar for both species.

### BRAIN AND CRANIAL NERVES:

The prosencephalon is divided into the usual divisions of telencephalon and diencephalon. The telencephalon is divided into two fairly small cerebral hemispheres or corpora striata posteriorly and into two smaller olfactory lobes anteriorly. The olfactory lobes each give off an olfactory nerve which is about two centimetres long and ends on the inner surface of the nasal capsules.

The diencephalon is not well developed and is covered dorsally by the optic lobes. Its position is marked however by the pineal body which rises on its dorsal surface and projects between the optic lobes and over the telencephalon to a slight extent. Ventrally the diencephalon gives rise to two kidney-shaped bodies, the lobi inferiores and between these are situated the hypophysis anteriorly and the saccus vasculosus posteriorly. These bodies are both roughly spheroid and are easily detached. From the antero-ventral margin of the diencephalon the second cranial or optic nerves are given off. They are very large and thick and do not merge to form an optic chiasma, but out directly, the right nerve crossing over the left to go to the left eye and the left nerve to the right eye.

The mesencephalon is well developed into two large optic lobes, and is curiously bent upon itself, due to the extensive growth forward. The mid-brain gives rise to the third cranial or oculomotor nerve on its extreme posterior dorsal surface.

The rhombencephalon has the usual divisions into metencephalon and myelencephalon. The metencephalon or cerebellum is pronounced but small. It lies above the medulla oblongata and is slightly wedge-shaped.

The myelencephalon or medulla oblongata extends from the posterior margin of the mid-brain to merge posteriorly into the spinal cord. It gives rise to the rest of the cranial nerves. The sixth cranial or abducens arises from the ventral surface of the medulla; all the others have lateral origins.

#### AXIAL NERVOUS SYSTEM:

The spinal nerve cord is enclosed by the neural spines. It is exposed between the spines and in these regions it gives off the dorsal and ventral roots of the body nerves.

#### SENSE ORGANS:

The inner ear consists of a rather large system of semicircular canals, utricle, and saccule, which contain the endolymph. This whole system is surrounded by the perilymph contained in the bony auditory capsule. The perilymph is separated by a membrane from the brain and has a fenestra in the posterior otic bones.

The saccule contains the large otolith, the saggitta; the utricle contains two smaller otoliths. The saggittae of the two sardines are similar and can hardly be distinguished, the one from the other.

The anterior chamber of the eye is very shallow so that the cornea lies close against the lens. The lens is spherical, very hard, and cannot be altered in shape. There is found in the posterior chamber of the eye the falciform process of the choroid which joins with the slender campanuli Halleri and serves to adjust the focal length for the sight of objects.

### SUMMARY AND CONCLUSIONS

The European and North American pilchards when compared anatomically present the following differences:-

- (1) The size and arrangement of the scales is different for the type of each species.
- (2) The series of dark body spots is usually present in the North American and generally lacking in the European species; the series of smaller spots at the base of the dorsal scales is present only in the North American pilchard.
- (3) The keel scales differ in shape and in the prominence of the ventral keel.
- (4) The opercular bones are different in shape.
- (5) The gill rakers of the first branchial arch differ in each type as to numbers and to length; in the North American pilchard the shortening of the rakers at the angle is more noticeable and the rakers of the upper limb fold over those of the lower.

The two types of pilchards present the following similarities:-

- (1) Each has approximately the same number of vertebrae.
- (2) The same type of ridges on the opercle.
- (3) The same type of caudal scales.
- (4) The same type of gill raker processes.
- (5) The absence of vomerine and palatine teeth.

The remaining similarities are mainly characteristic of the sub-family.

The genera of the sub-family Clupeinae are closely related, particularly those that were formerly considered as occupying the genus Clupea, and in order to separate the various groups generically it is necessary to resort mainly to superficial differences. However, with respect to this fact, and in view of the differences and similarities presented by the two species in question, it is difficult to consider the two types of pilchards as occupying separate genera. Two of the differences noted, the spotting and the scale arrangement, are intergrading; the slight difference in shape of the keel scales and opercular bones does not exclude the possibility that the two species were derived from the same ancestral type.

The only difference that could possibly be considered as of generic importance is the peculiar overlapping of the gill rakers found in one type but not in the other. This feature taken alone would serve to separate the North American pilchard from the European pilchard but would not separate the latter from the members of the genus Clupea. However since both types of pilchards have similar gill raker processes it is quite probable that the overlapping arrangements of the rakers as found in the North American pilchard, is a modified form of the arrangement found in the European pilchard.

Two other points show the close relationship between the two pilchards. It is difficult to conceive how two peculiarities such as the opercular striations and the caudal scales arose in both types of pilchards if the types did not have an immediate common origin. To this argument is added the fact that the respective pilchards have similar habits and the same type of pelagic ova.

The relationship of the North American pilchard, (Sardina caerulea) to the pilchards of Australia, Japan, Chile, and South Africa, is as yet not fully known. Further investigation is necessary in order to decide whether these are

separate species, sub-species, or geographical populations. If the latter possibility should be the case the North American pilchard becomes Sardina sajax, (Jenyns).

A list of the possible species of the genus Sardina frequenting the Pacific and South Atlantic oceans is given below:-

Sardina sajax (Jenyns), 1842. Chilean.

Sardina caerulea (Girard), 1854. North American.

Sardina melanosticta (Temminck and Schlegel), 1846. Japanese.

Sardina ocellata (Pappe), 1853. South African.

Sardina neopilchardus (Steindachner), 1853. Australian.

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