A Hypomaxillary Bone in *Harengula* (Pisces: Clupeidae)

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THE HERRING GENUS *Harengula* Valenciennes (as herein restricted) contains five bilateral pairs of bones in the upper jaw (Fig. 1*A*). Most other clupeid fishes contain three or four such pairs of bones: premaxillary, maxillary, and one or two supramaxillaries. The extra pair of bones in *Harengula* is here termed the hypomaxillary. The hypomaxillary also occurs in the clupeid genera *Pliosteostoma* Norman and *Pellona* Valenciennes, and its presence has been used to distinguish these two genera from other genera. The presence of the hypomaxillary in *Harengula* and its usefulness as a taxonomic character in separating *Harengula* from other closely related genera previously has been overlooked.

The hypomaxillary previously has been termed "an ossified ligament," "a narrow, toothed bone," and "a bone, bearing teeth lying in the membranous section between the distal end of the premaxillary and the middle of the maxillary." It is desirable to have a specific name for this unique pair of bones, and hypomaxillary is a logical choice. Other similar terms that have restricted meaning or are synonyms of other bones are intermaxillary, inframaxillary, bimaxillary, submaxillary, and surmaxillary.

Four closely related genera are involved in the evaluation of this character: *Harengula* Valenciennes 1847, *Lile* Jordan and Evermann 1896, *Sardinella* Valenciennes 1847, and one whose designation currently is uncertain, but here is referred to as *Clupalosa* Bleeker 1851. (The distinguishing characteristics are listed below.)

The position of the hypomaxillary in *Harengula* is shown in Figure 1*A*. Its posterior end overlaps the maxillary laterally. The hypomaxillary, premaxillary, and maxillary all bear a single row of small pointed teeth. The connective tissue in the space between the hypomaxillary may also bear teeth. The hypomaxillary was ossified in the smallest specimen examined (16 mm S.L.). The presence of the hypomaxillary and the characteristic elongation of the posterior supramaxillary (Fig. 2*A*) in *Harengula* have been verified in the following species:

- *H. clupeola* (Cuvier 1829), St. Lucia, British West Indies, SU35458, and syntype of *H. latulus* Valenciennes, SU32769
- *H. humeralis* (Cuvier 1829), Jamaica, SU5041
- *H. pensacolae* Goode and Bean 1880, Sanibel Island, Florida, SU36092, and Santos, Brazil, SU36065 (as *S. majorina* Storey 1938)
- *H. peruana* Fowler and Bean 1924, many specimens from Peru to Costa Rica in several institutions
- *H. thrissina* Jordan and Gilbert 1882, many specimens from Pacific Mexico in several institutions

	HYPOMAXILLARY	SHAPE OF POSTERIOR SUPRAMAXILLARY	BILOBED FOLD ON CLEITHRUM
Harengula	present	elongated, ventral constriction anterior	present
Lile	absent	elongated, ventral constriction anterior	absent
Sardinella	absent	rounded, ventral constriction vertical to dorsal constriction	present
Clupalosa	absent	elongated, ventral constriction anterior	present

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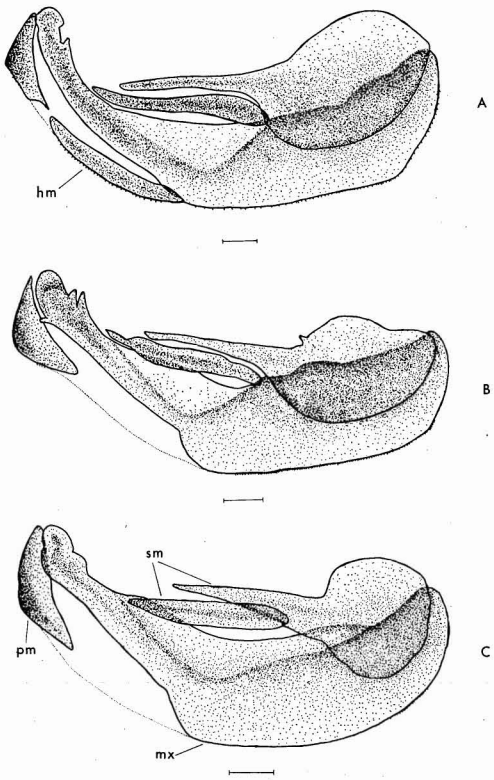

FIG. 1. Upper jaw bones of *Harengula thrissina* (*A*), *Lile stolifera* (*B*), and *Sardinella sindensis* (*C*). Abbrev.: mx, maxillary; pm, premaxillary; sm, supramaxillaries; hm, hypomaxillary. The scale below each is 1 mm.

The presence of the hypomaxillary in the syntype of *Harengula latulus,* the type species of the genus, is considered to restrict the genus *Harengula* to comparable species possessing this structure. The synonymy of *H. latulus,* the probability of the erroneous original locality designation, and the type species designation were detailed by Storey (1938:36–39), who gave evidence that *Harengula* does not occur in the eastern Atlantic. Based on present information, the genus *Harengula* apparently occurs only in the western Atlantic and the eastern Pacific.

Lile lacks the hypomaxillary bones, and the intervening space along the gape between the premaxillary and the maxillary is occupied by unossified connective tissue (Fig. 1*B*). The elongated supramaxillary is shown in Figure 2*B*. These two characters have been verified in *L. stolifera* (Jordan and Gilbert 1881) on specimens from many eastern Pacific localities in the collections of several institutions. *Lile* apparently only occurs in American waters.

Sardinella is similar to *Lile* in lacking hypomaxillaries (Fig. 1*C*). The expanded distal end of the posterior supramaxillary is rounded, with the dorsal constriction about vertical to the ventral constriction (Fig. 2*C*). This has been verified in the following species:

- *S. aurita* Valenciennes 1847, Florinapolis, Brazil, SU53863 and SU51662
- *S. brachysoma* Bleeker 1852, Tai Ping, China, SU25701
- *S. cameronensis* Regan 1917, West Africa, RGMAC 94987
- *S. clupeoides* (Bleeker 1849), Singapore, China, SU33838
- *S. dayi* Regan 1917, Ceylon, SU22866
- *S. eba* (Valenciennes 1847), eastern Atlantic, RGMAC 94994
- *S. fimbriata* (Valenciennes 1847), Manila, Philippines, SU20330
- *S. jussieui* (Lacépède 1803), Manila, Philippines, SU60478
- *S. leiogaster* Valenciennes 1847, Sulu Prov., Philippines, SU28571
- *S. longiceps* Valenciennes 1847, Madras, India, SU35273
- *S. melanura* (Cuvier 1829), Malekula Island, New Hebrides, SU25031
- *S. perforata* (Cantor 1850), Formosa, SU7420
- *S. rouxi* (Poll 1953), West Africa, RGMAC 94999
- *S. sindensis* (Day 1878), Manila, Philippines, SU38369
- *S. sirm* (Walbaum 1792), Apia, Samoa, SU 8984
- *S. zunasi* (Bleeker 1854), Onomichi, Japan, SU20140

Sardinella occurs in the Atlantic and Indian oceans and in the western Pacific, but not in the eastern Pacific.

Because the genus *Harengula* is restricted to species possessing hypomaxillaries, certain Indo-Pacific species, which have usually been placed in *Harengula,* but which lack this pair of bones, are tentatively assigned to the genus *Clupalosa.* They have the posterior pair of supramaxillaries

elongated, with the ventral constriction anterior to the dorsal constriction. Species of this genus that I have examined are:

C. dispilonotus (Bleeker 1852), Philippines, SU33545

C. punctata (Rüppell 1835), Philippines, SU20885; Pelew Islands, SU37332; Ceylon, SU22892; South Andaman Islands, SU 37100; Philippines, SU28556

C. schrammi (Bleeker 1849), Philippines, SU33538

C. tawilis Herre 1927, Philippines, SU28559

Bleeker erected the genus *Clupalosa* for his monotypic new species *C. bulan* from the Java Sea in 1849. *Clupalosa* has subsequently been placed in synonymy of both *Harengula* and *Sardinella.* I have not seen this species, and the type specimens, if extant, should be examined to confirm its relationships. I presume that it is distinct from the hypomaxillary-bearing *Harengula,* because no species of *Harengula* (as restricted) have been observed from the Indo-Pacific. I presume that it is distinct from the genus *Sardinella,* because it was not included in a recent and comprehensive review of the Indo-Pacific species of *Sardinella* by Chan (MS). However, Regan (1917), who said he examined Bleeker's types of *bulan,* placed that species in synonymy of *Sardinella perforata* (Cantor 1850). Subsequent authors have listed *bulan* as a distinct species, notably Fowler (1941). If *Clupalosa* proves to be unavailable for this genus, the following generic names might apply: *Paralosa* Bleeker 1868 (type species *Harengula valenciennesi* Bleeker 1868), *Wilkesina* Fowler and Bean 1923 (type species *Harengula fijiense* Fowler and Bean 1923), *Herklotsichthys* Whitley 1951 for *Herklotsella* Fowler 1933 (type species *Harengula dispilonotus* Bleeker 1852), or *Escualosa* Whitley 1940 (type species *Clupea macrolepis* Steindachner 1879). The status and identity of *Macrura* van Hasselt 1823 is uncertain; it has been proposed for species of this group, but also has been suggested as a synonym of *Hilsa* Regan 1916.

Of the four genera discussed above, I have not examined the following nominal species and am not certain of their generic or specific status:

Harengula callolepis Goode 1880
Sardinella albella (Valenciennes 1847)
Sardinella allecia (Rafinesque 1810)
Sardinella aurovittata (Swainson 1839)
Sardinella caeruleovittata (Richardson 1846)
Sardinella dactylolepis (Whitley 1940)
Sardinella desmaresti (Risso 1826)
Sardinella maderensis (Lowe 1836)
Sardinella nymphea (Richardson 1848)
Sardinella posterus (Whitley 1931)
Lile piquitinga (Schreiner and Miranda Ribeiro 1903)
Lile platana Regan 1917
Harengula abbreviatata Valenciennes 1847
Harengula blackburni (Whitley 1948)
Clupalosa bulan Bleeker 1849
Harengula dollfusi Chabanaud 1933
Harengula hualiensis Chu and Tsai 1958

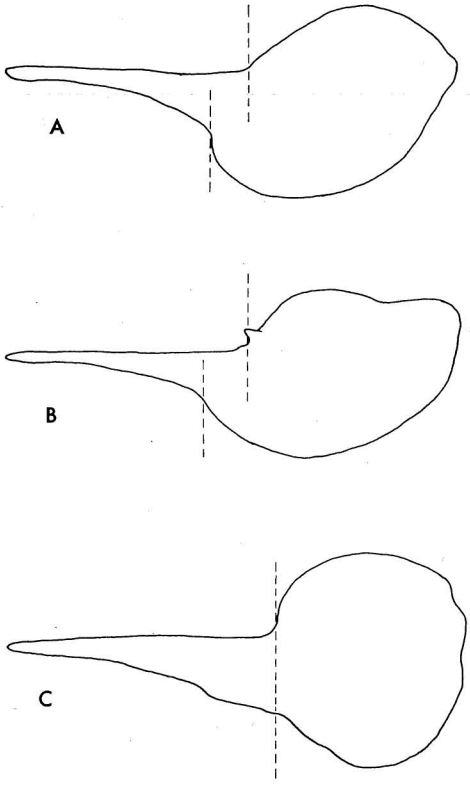

FIG. 2. Posterior supramaxillaries of *Harengula* (*A*), *Lile* (*B*), and *Sardinella* (*C*), showing their characteristic shapes and the relative positions of the dorsal and ventral constrictions.

Harengula konigsbergeri (Weber and de Beaufort 1912)
Clupalosa lippa (Whitley 1931)
Harengula maccullochi Whitley 1931
Harengula macrolepis (Steindachner 1879)
Harengula ovalis (Bennett 1830)
Harengula vittata (Valenciennes 1847)

The last 11 species are Indo-Pacific and may all belong to *Clupalosa.*

I have tabulated 110 nominal species that appear to belong to these four genera, of which only about 43–51 species may be valid. There are many conflicting opinions and uncertainties concerning the synonymies of these nominal species. In listing the species above I have used and attempted to reconcile the works of Chan (MS), Fowler (1941), Herre (1953), Regan (1917), Rivas (1950), and Whitley (1940, 1941, 1948).

The separation of *Harengula* and *Sardinella* was discussed by Chan (MS), who was the first to emphasize the differences in the larger and more posterior of the two supramaxillaries in these two genera. Chan also detailed differences in scale sculpture between these genera and commented upon the two enlarged terminal anal fin rays in *Sardinella.* Whitehead (1962) suggested that *Harengula* might have a greater number of parietal striae than *Sardinella;* but this difference, if valid, is complex, because the number of parietal striae in *Harengula thrissina* progressively increases from about 5 at 50 mm S. L. to about 13 at 130 mm. Chan and previous authors were unaware of the hypomaxillary bones in American species assigned to *Harengula,* however, and considered *Harengula* in its broad sense to include the Indo-Pacific species which lack hypomaxillaries.

The phylogenetic significance of the hypomaxillary and its importance in the classification of the Clupeidae are subject to various interpretations. A thorough knowledge of the morphology of the genera and species of Clupeidae and of the origin and development of this bone will furnish a more definitive answer to these issues.

The hypomaxillary is a specialized structure that must have developed independently in two phyletic lines of the Clupeidae—in the typical herring genus, *Harengula,* and in *Pellona* and *Pliosteostoma* of the group of clupeids with a high number of anal rays and greatly compressed bodies, sometimes referred to as "bloodless clupeids." It probably arose as a permanent splitting off of a portion of the maxillary or premaxillary; it is less probable that its origin was the spontaneous development of a new site of ossification.

In *Aphredoderus* (Percopsiformes) and in certain species of Amblyopsidae (Amblyopsiformes) each premaxillary is divided distally into from 2 to about 7 distinct but closely associated parts of progressively decreasing size (Rosen, 1962). These smaller terminal portions of the premaxillaries were termed segments, and Rosen (1962:23) suggested that these segments produced a flexibility to the upper jaw in full extension of the mouth. This might indicate that these segments were developed in response to a need for additional flexibility, or that, after they had developed, additional flexibility was possible. The clupeid hypomaxillary undoubtedly developed independently from the premaxillary segments of *Aphredoderus* and the amblyopsids, and, if any such functionalism were once a factor in the origin of the hypomaxillary in these clupeids, it has subsequently been lost or occluded.

My studies have led me to believe that, within the two clupeid groups concerned, the hypomaxillary must be significant in indicating a distinct phylogenetic (and taxonomic) difference between the species which have it and those which lack it. Myers (1950) found the hypomaxillary present on one side and absent on the other in a large specimen of *Pellona* and questioned its significance; but in the hundreds of specimens of all species of *Pellona, Pliosteostoma,* and *Harengula* that I have examined, both sides of the upper jaw have hypomaxillaries of similar size.

To stabilize the nomenclature until extant uncertainties are clarified, and because published generic names are available, I have proposed above that the presence of the hypomaxillary be regarded as a criterion of generic distinction, and restriction of the genus *Harengula.*

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REFERENCES

CHAN, W. L. (MS). A systematic revision of the Indo-Pacific fishes of the genus *Sardinella.* Unpublished thesis, Stanford University (1962).

FOWLER, H. W. 1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostarophysi obtained by the United States Bureau of Fisheries steamer "Albatross" in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Bull. U.S. Nat. Mus. No. 100, Vol. 13, 879 p.

HERRE, A. W. 1953. Check list of Philippine fishes. Fish & Wildl. Serv., Res. Rept. 20, 977 p.

MYERS, G. S. 1950. Systematic notes on some Amazonian clupeid fishes of the genus *Ilisha.* Copeia (1):63–64.

REGAN, C. T. 1917. A revision of the clupeid fishes of the genera *Sardinella, Harengula,* &c. Ann. Mag. Nat. Hist., Ser. 8, 19:377–395.

RIVAS, L. R. 1950. A revision of the American clupeid fishes of the genus *Harengula,* with descriptions of four new subspecies. Proc. U.S. Nat. Mus. 100(3263):275–309.

ROSEN, D. E. 1962. Comments on the relationships of the North American cave fishes of the family Amblyopsidae. Amer. Mus. Novitates, No. 2109, 35 p.

STOREY, M. 1938. West Indian clupeid fishes of the genus *Harengula,* with notes on *H. thrissina* from the Pacific coast. Stanford Ichthyol. Bull. 1(1):3–56.

WHITEHEAD, P. J. P. 1962. A review of the Indo-Pacific gizzard shad genera *Nematalosa, Clupanodon* and *Konosirus* (Pisces: Dorosomatidae). Bull. British Mus. (Nat. Hist.) 9(2):89–102.

WHITLEY, G. P. 1940. Illustrations of some Australian fishes. Austr. Zool. 9(4):397–428.

——— 1941. Ichthyological notes and illustrations. Austr. Zool. 10(1):1–50.

——— 1948. New sharks and fishes from Western Australia, Part 4. Austr. Zool. 11 (3):259–276.