

A Systematic Revision of the Indo-Pacific Clupeid Fishes of the Genus *Sardinella* (Family Clupeidae)*

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Introduction

Sardinella, a genus of clupeid fishes, includes a rather large number of circum-tropical species which have often proved to be exasperatingly difficult to distinguish from one another. The differences between most of the species are subtle and almost impossible to express in words with the degree of clarity required to enable workers to recognize easily the species being described. As a result, most investigators, who have usually been working with general collections from local areas, have applied names to the clupeids in their material which are in error as often as not. Furthermore, certain species have been placed in the genus *Sardinella* only to have been removed and replaced again and again. Such uncertainty in the generic allocation of species is clear indication that the generic limits are not satisfactorily drawn. The accumulated confusion is being steadily compounded due to the inadequacy of the existing literature and because most workers do not have the facilities for the detailed investigations and comparisons necessary. It is, therefore, evident that a careful revision of these fishes is very much in order. The present study attempts to contribute to this end by redefining *Sardinella*, and presenting a systematic revision of the Indo-Pacific species of this genus.

The work was carried out at the Hopkins Marine Station and the Division of Systematic Biology of Stanford University, and at the George Vanderbilt Foundation Laboratory and Research Center in Bangkok, Thailand. It has been my good fortune to have available two of the largest ichthyological collections in the world and also two very excellent libraries, those of the Division of Systematic Biology and of the George Vanderbilt Foundation. I owe a debt of gratitude to Dr. George S. MYERS and to Dr. Robert R. ROFEN for entrusting to me the clupeid material of these collections under their care, and for permitting me full use of the libraries.

Although most of the pertinent material has been available in one or the other of these great collections, it has been necessary to seek additional information on the species *S. nymphaea* not represented, and on the type specimens of several forms. I wish to offer my very sincere thanks to a number of generous persons who have aided me in this regard. Mr. N. B. MARSHALL of the British Museum (Natural History) provided me with data on the types of *S. nymphaea*, *S. perforata*, *S. dayi*, *S. zunasi* and *S. sindensis*; and, in addition, he sent me two valuable scales from the type specimen of *S. nymphaea*. Dr. M. BOESEMAN of the Leiden Museum kindly took numerous measurements of Bleeker's type material on my behalf, and also informed me of the results of the designation of the lectotypes of many species of

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Sardinella from Bleeker's collection. Mr. Gilbert P. WHITLEY of the Australian Museum generously sent me many scales and the first branchial arch from one of the paratypes of *Amblygaster posterus* WHITLEY.

Other people, too numerous to mention, have aided me in different ways. However, I do wish to thank Mr. J. B. PHILIPPS of the California Department of Fish and Game, who spent many of his precious hours discussing with me the various problems of scale growth; also Dr. Robert R. ROFEN for frequent advice and a critical reading of the manuscript; and finally Prof. Rolf L. BOLIN, under whose direction the work was done, and who made many valuable suggestions pertinent to the research and its presentation.

Technique of Measuring, Counting and Recording

In order to make it possible for future workers to compare their results with my own, I consider it necessary to explain the manner in which I took measurements and made counts recorded in the present work. Each measurement was taken by means of needle-pointed dividers or vernier calipers and points. All measurements were recorded to the closest 0.1 mm. and the proportions were calculated mathematically. The individual measurements were taken as follows:

Standard length: distance from the tip of snout (most advanced point on median line of upper jaw) to the end of the hypural plate (this point on the base of caudal fin has been taken at the mid-point of the vertical groove formed on the skin when the fin has been bent).

Head length: distance from the tip of snout to the farthest bony point of the suboperculum.

Maxillary: distance from the tip of snout to the farthest point of the posterior edge of the upper jaw (fig. 4: marked by dotted line m).

Orbit: diameter of bony orbit, from the hind end of preorbital to the anterior edge of the postorbital, in a line parallel to the mid-lateral axis of body.

Snout: distance from the tip of snout to the posterior edge of the bony pre-orbital.

Postorbital length: distance from the anterior point of bony postorbital (point used in orbit) to the posterior edge of bony opercle, in a line parallel to the mid-lateral axis of body.

Interorbital width: distance between the dorsal orbital rims measured over the center of the eye.

Width between upper ends of gill openings: measured between the points where the bony opercle joins the body on either side.

Depth at dorsal origin: distance from the insertion of the first dorsal ray to the ventral profile of the body, in a line perpendicular to the mid-lateral axis of the body.

Depth at anal origin: distance from the insertion of the first anal ray to the dorsal profile of the body, in a line perpendicular to the mid-lateral axis of the body.

Least depth of caudal peduncle: distance measured in a line perpendicular to the mid-lateral axis of the body.

Predorsal length: distance from the tip of snout to the insertion of first dorsal ray.

Postdorsal length: distance from the insertion of the first dorsal ray to the uppermost point of the end of the hypural plate (see *standard length*).

Dorsal base: distance from the insertion of the first dorsal ray to the posterior edge of the base of the last ray.

Length of longest dorsal ray: distance measured from the insertion to the tip of that ray, which is usually the fourth or the fifth.

Preanal length: distance from the tip of snout to the insertion of the first anal ray.

Length of third anal ray: distance measured from the insertion to the tip of that ray.

Length of the last branch of the last anal ray: distance measured from the insertion to the tip of the last branch of the last anal ray.

Prepectoral length: distance from the tip of snout to the insertion of the uppermost (first) pectoral ray.

Pectoral length: length of pectoral fin, from the insertion of the uppermost ray to the posterior tip of the pectoral fin.

Preventral length: distance from the tip of snout to the insertion of the first or outer ventral ray.

Ventral length: the length of ventral fin, measured from the insertion of the first ventral ray to the tip of ventral fin.

Length of caudal fin: distance from the mid-base of caudal fin (the end of the hypural plate) to the extreme tip of the lower caudal lobe,

The counts were made as indicated below :

Lateral scales: the number of scales along a lateral series, beginning from the first scale emerging from behind the dermal flap at the cleithrum, and ending with the scale at the end of the hypural plate (scales behind the end of hypural plate have been excluded).

Longitudinal scale rows: number of longitudinal rows of scales, counted along a vertical line from the dorsal origin to the ventral profile of the body. Since the scales are arranged in an imbricated pattern, care must be taken to include all rows, and this is actually accomplished by tracing a slight zigzag line with the needle point.

Predorsal scales: the number of scales forming a longitudinal series in front of the dorsal fin origin on the mid-dorsal ridge. In subgenus *Sardinella*, it is the series of scales immediately to the left side of the mid-dorsal ridge (fig. 1B); in subgenus *Amblygaster*, it is counted on the mid-line (fig. 1A).

Medioventral scutes: (1) preventral scutes: number of scutes from the first one at the isthmus to the most posterior one that touches the vertical of the ventral origin; (2) *postventral scutes*: number of scutes from the one immediately after the last preventral scute, to the last scute which always has its posterior point at, and sometimes overlying, the anal opening.

Gill rakers: the entire first branchial arch is always first completely dissected out; each count includes both full grown and rudimentary gill rakers. In some cases all rakers are counted, in others only those of the lower branch. The dividing line between the rakers of the two branches is readily determined by spreading the limbs of the arch.

Fin rays: every single ray, either simple or branched, is considered as one ray.

In presentation of numerical values based on these measurements and counts, the average value is listed first, followed by the extremes in parentheses.

In listing the material upon which this work is based, specimens have been referred to by museum numbers. Those prefixed by the letters SU are from the collections of the Natural History Museum of Stanford University. Material from the George Vanderbilt Foundation collections are designated by the letters GVF.

The Problem of Generic Delimitation

The genus *Sardinella* has, for more than forty years, invariably been defined and treated according to the principles laid down by REGAN (1917d). In his monograph of the Clupeidae this author distinguished *Sardinella* from the closely related genus *Harengula* primarily by the differences in the scale-groove pattern and in the size of the last two anal rays. These rays he described as enlarged in *Sardinella* and not enlarged in *Harengula*. While the difference in size is recognizable on direct comparison of typical species of both genera, it is not of such magnitude that it can be measured readily, or presented numerically. Since "enlarged" and "not enlarged" are subjective terms, this character is of minor value. The differences noted in the scale-groove patterns appear to be more definite and readily interpreted. According to REGAN's descriptions (which are short and inadequate by modern standards), each scale in *Sardinella* has one continuous transverse groove preceded by a set of interrupted grooves (fig. 3B), whereas in *Harengula* all transverse grooves are continuous (fig. 3F).

If the situation were as simple as REGAN indicated, all would be well. However, there are four species in which scales show groove patterns which differ in various areas along the body. In these forms, REGAN's *Sardinella* scale is often found at Region I (fig. 3A), his *Harengula* scale is prominent at Region III, while at Region II an intermediate type of scale pattern, such as is illustrated in figs. 3C-E, occurs. REGAN evidently did not investigate the characteristics of the scales from all regions in these fishes, but took scale samples from whatever area was convenient, or on

which scales persisted. He made no mention of the intermediate type of scale-groove pattern, although he was familiar with all four species in which it occurs. Had he been aware of the intermediate nature of the scales in Region II, he undoubtedly would have treated these four forms as closely related. Instead he included two of them, *Sardinella brachysoma* and *Harengula hypselosoma* in *Sardinella*, and assigned *Clupea nymphaea* and *Harengula zunasi* to *Harengula*. This treatment is clearly invalid, and the question arises: in which of the two genera should these four forms be placed?

In searching for new methods for differentiating *Sardinella* from *Harengula*, many specimens of numerous species from both Atlantic and the Indo-Pacific have been examined, and a new character that will distinguish the two genera have finally been found. It involves the shape of the expanded portion of the second supramaxillary bone, which forms the posterodorsal part of the movable upper jaw. In *Sardinella* the shape of this bone varies from somewhat rectangular, through almond-shaped, to nearly circular, but in every case the anterior point at the foot of the dorsal crest (d) is almost directly over that of the ventral crest (v; see figs. 4A-D). In *Harengula*, on the other hand, the second supramaxillary bone is somewhat crescentic in shape, and the anterior point at the foot of the dorsal crest (d) is always clearly behind that of the ventral crest (v; see figs. 4E-F).

In all of the "intermediate" species mentioned above, the second supramaxillary is perfectly typical of the normal *Sardinella*, and I have no hesitancy in assigning them to that genus.

It is a well-known fact that during the ontogenetic development of fishes, the scales normally appear first on the posterior part of the body at or near the base of the caudal peduncle, and that from this original locus the squamous area expands as the fish grows. Since it is logical to assume that the phylogenetic development has progressed in the same direction as that which may be observed in ontogeny, the first scales to develop, or those at Region III, may be accepted as the most primitive, and the last ones to form, or those in Region I, as the most advanced. If this is true, the four species with the scale-groove patterns varying along the sides indicate the course of evolution. *Harengula*, with its system of complete grooves on all scales of the body, represents the ancestral type from which *Sardinella*, with its interrupted scale grooves, has evolved.

The shape of the second supramaxillary bone, and the size and degree of branching of the posterior anal rays show, without doubt, that the four species originally described under the names *Sardinella brachysoma*, *Harengula hypselosoma*, *Clupea nymphaea*, and *Harengula Zunasi*, belong to *Sardinella* rather than *Harengula*. However, the fact that only the anterior scales have developed the groove pattern characteristic of *Sardinella*, points to these four species as the most primitive members of their genus; and the fact that their posterior scales are typical of those of *Harengula* indicates that they have evolved from a member of the latter genus or

from a *Harengula*-like ancestor. In this connection it may also be noted that *Harengula* appears to be more primitive than *Sardinella* in regard to the structure of the anal fin. The enlargement and elongation of the posterior anal rays in members of the latter genus is an unusual rather than the common development, and may logically be assumed to represent an advancement from the unspecialized fin of *Harengula*. There seems to be no way to evaluate the different shapes of the second supramaxillary bones in terms of degree of specialization.

Sardinella and *Harengula* may be distinguished from all other genera of Clupeidae by their possession of the following combination of characters: mouth terminal; upper jaw without a distinct median notch; operculum smooth, without radiating grooves; last dorsal ray normal, not prolonged; anal fin comparatively short, of less than 24 rays; ventral fins inserted below dorsal base; predorsal ridge devoid of scutes; a bilobed dermal fold on vertical anterior edge of cleithrum. When a specimen has been determined to belong to this complex, it may be allocated to the proper genus by the characters already outlined and expressed below in the form of a simple key:

- 1a. Expanded portion of second supramaxillary varying from somewhat rectangular (fig. 4A) to almond-shaped (fig. 4B) or nearly circular (fig. 4C), the anterior point at the foot of its dorsal crest situated opposite that of its ventral crest. *Either* all the scales along the mid-lateral body axis marked by a single continuous groove preceded by a set of two to eight interrupted grooves with a wide interspace between the discontinuous portions (fig. 3B), *or* these scales shows varying patterns in different body regions*. Last two anal rays more extensively branched than the anterior ones, and somewhat elongated so that the tip of the anal fin is slightly produced
.....*Sardinella* CUVIER and VALENCIENNES
- 1b. Expanded portion of the second supramaxillary somewhat crescentic in shape (figs. 4E-F), the anterior point at the foot of its dorsal crest situated well behind that of its ventral crest. *All* scales along mid-lateral axis of body with all grooves continuous, none interrupted (fig. 3F). Last two anal rays not more extensively branched near their tips than the others, the posterior ray not prolonged*Harengula* CUVIER and VALENCIENNES

In conclusion of this section it may be well to present a short summary of the value of characters. I consider the shape of the second supramaxillary to be the

* In Region I, each scale patterned as in fig. 3B; in Region II, each scale with one to seven continuous grooves either preceded by, or intermingled with, a set of two to six interrupted grooves whose parts may either be separated by a wide interspace, or may overlap (figs. 3C-E), (when wide interspaces occur between the segments of grooves in scales of Region II, these discontinuous grooves are always followed by more than one continuous groove); in Region III, each scale usually with all grooves continuous, but in some cases, one or two may be discontinuous (figs. 3F-G).

most significant character. It will not only serve to distinguish *Sardinella* from *Harengula*, but its shape is also unique in each of the other clupeid genera that I have examined. It is probable that all of the genera in the family can be recognized on the basis of the morphology of the second supramaxillary and the other parts of the upper jaw.

The scale-groove character is also of extreme significance. REGAN's generic diagnosis is not valid as far as this character is concerned, since he overlooked the intermediate pattern as mentioned previously. However, his monograph (1917d) has contributed much toward our understanding of the Clupeidae and made possible the modern approach toward the taxonomy of the genera. The finding of the intermediate scale-groove pattern indicates the very close relationship of *Sardinella* to, and its derivation from, *Harengula*. With the supporting evidence provided by the shape of the second supramaxillary bone, a logical generic allocation of previously misplaced species is possible.

Systematic Section

Genus SARDINELLA CUVIER & VALENCIENNES

Sardinella CUVIER and VALENCIENNES, 1847: 263 (generic type *Sardinella aurita* CUVIER and VALENCIENNES, 1847: 263, by original designation).

Clupeonia CUVIER and VALENCIENNES, 1847: 345 (generic type *Clupanodon jussieu* LACÉPÈDE, 1803, designated by GILL 1861: 35).

The genus *Sardinella* is a circumtropical group represented in Indo-Pacific waters by fifteen species, one of which is here described as new. According to the existing records, the distribution of these Indo-Pacific forms is restricted to the area between the latitudes of 36°N. and 30°S. and between the meridians of 30°E. and 172°W. longitude. Within this area, the number of species and individuals varies greatly from place to place. This variation is chiefly due to temperature. In general, all species of *Sardinella* are coastal, schooling fishes, most abundant in warmer waters.

The Indo-Pacific representatives of this genus fall into two subgenera *Amblygaster* and *Sardinella*. These are very readily distinguished, one from the other, by marked differences in the arrangement of the scales along the median line anterior to the dorsal fin. There are, in addition, other corroborating features, particularly the degree of compression in the ventral keel and scutes, that give the two groups a very different appearance. In fact they are so distinct that they could, with perfect propriety, be considered as two separate genera. However, since most of the other clupeid genera are in a state of confusion, with uncertain status and unstable generic limits, the time hardly seems ripe to complicate the picture by increasing the number of genera. Therefore, in the present work I have treated the group conservatively as a single genus with two subgenera, *Amblygaster* and *Sardinella*.

Key to the IndoPacific species of SARDINELLA

- 1a. Mediodorsal ridge before dorsal fin covered by *one* longitudinal row of scales (fig. 1A); medioventral ridge only slightly keeled, its acutes not prominent (figs. 2A-B) and without a spiny posterior projection; axillar side of pectoral fin with a blackish streak over the first three or four rays; upper jaw short, its posterior end at most reaching to the front border of eye; expanded portion of second supramaxillary almond-shaped (fig. 4B)Subgenus *Amblygaster* BLEEKER....2
- 1b. Mediodorsal ridge before dorsal fin covered by the adjacent sides of *two* longitudinal rows of scales (fig. 1B); medioventral ridge strongly keeled, with sharp prominent scutes, each having a spiny projection posteriorly (fig. 2C-D); axillar side of pectoral fin pale, without colored streak; upper jaw longer than in *Amblygaster*, its posterior end reaching beyond front border of eye; expanded portion of second supramaxillary varying from somewhat rectangular to circular (figs. 4A, C, D).....Subgenus *Sardinella* CUVIER and VALENCIENNES....4
- 2a. Body with dorsolateral row of 10-20 dark blue, rounded spots; maxillary 2.72 (2.65-2.79) in head, reaching to, or slightly beyond the vertical of the anterior margin of orbit; predorsal length 2.18 (2.12-2.23) in standard length; depth at dorsal origin 4.95 (4.75-5.27) in standard length; gill rakers on lower branch of first arch 40 (38-42)*Sardinella sirm* (WALBAUM)
- 2b. Body without dorsolateral row of dark spots; maxillary 3.27 (2.98-3.34) in head, not reaching the vertical through the anterior margin of orbit; predorsal length 2.00 (1.94-2.05) in standard length; depth at dorsal origin 4.17 (3.71-4.55) in standard length; gill rakers on lower branch of first arch 32 (26-36)3
- 3a. Body moderately heavy, depth at dorsal origin 4.00 (3.71-4.20) in standard length; gill rakers on lower branch of first arch 29 (26-30); predorsal length 2.04 (2.00-2.05) in standard length, so that the dorsal origin is always slightly nearer to tip of snout than to uppermost point of caudal base*Sardinella clupeoides* (BLEEKER)
- 3b. Body slender, elongated, depth at dorsal origin 4.37 (4.18-4.55) in standard length; gill rakers on lower branch of first arch 33 (31-34); predorsal length 1.97 (1.94-1.99), so that the dorsal origin is approximately equidistant between tip of snout and uppermost point of caudal base*Sardinella leiogaster* CUVIER and VALENCIENNES
- 4a. Ventral fin with 9 rays5
- 4b. Ventral fin with 8 rays6
- 5a. Head 3.77 (3.66-3.84) in standard length; diameter of orbit 3.93 (3.53-4.33) in head; postorbital length 2.52 (2.36-2.58) in head; gill rakers on lower branch of first arch 140 (68-166); exposed part of interopercle crescent-shaped (fig. 5A)....*Sardinella aurita* CUVIER and VALENCIENNES
- 5b. Head 3.20 (2.95-3.44) in standard length; diameter of orbit 4.75 (4.12-5.22) in

- head; postorbital length 2.21 (2.20-2.35) in head; gill rakers on lower branch of first arch 210 (145-258); exposed part of interopercle forming approximately a semicircular segment (fig. 5B)...*Sardinella longiceps* CUVIER and VALENCIENNES
- 6a. Tips of caudal lobes blackish (fig. 6A)7
- 6b. Tips of caudal lobes not blackish (fig. 6B)8
- 7a. Gill rakers on lower branch of first arch 40 (37-43)
.....*Sardinella melanura* (CUVIER)
- 7b. Gill rakers on lower branch of first arch 63.....
.....*Sardinella nigricaudata*, new species
- 8a. Groove pattern of scales constant along the mid-lateral axis of body, each scale characterized by one continuous transverse groove preceded by a set of two to seven interrupted grooves with a wide and distinct interspace between the broken ends (fig. 3B).....9
- 8b. Groove pattern of scales varying between different body regions of the same individual as follows: Region I, each scale patterned as in 8a; Region II, each scale with a set of one to seven continuous grooves, either preceded by or intermingled with one to six discontinuous grooves whose parts may either be separated by a wide interspace or may overlap each other (figs. 3C-E); Region III, each scale usually with all grooves continuous, but in some cases one or two grooves may be discontinuous (figs. 3F-G)13
- 9a. Postventral scutes 14-17 (usually 15, rarely 14 or 17); orbit 1.1 (1.0-1.2) in snout; body depth 3.78 (3.22-4.49) in standard length.....10
- 9b. Postventral scutes 11-15 (usually 13, rarely 11 or 15); orbit 0.8 (0.7-1.0) in snout; body length 3.10 (2.78-3.53) in standard length11
- 10a. Gill rakers on lower branch of first arch 52 (47-61)
..... *Sardinella jussieui* (LACÉPÈDE)
- 10b. Gill rakers on lower branch of first arch 64 (58-72) ..*Sardinella sindensis* (DAY)
- 11a. Gill rakers on lower branch of first arch 96 (88-103); body depth 2.82 (2.78-2.85) in standard length*Sardinella dayi* REGAN
- 11b. Gill rakers on lower branch of first arch 67 (49-81); body depth 3.17 (2.83-3.53) in standard length12
- 12a. Gill rakers on lower branch of first arch 72 (69-81); distal end of each body scale greatly produced, fimbriated, and with distinct marginal lines (fig. 7A); depth at dorsal origin 3.26 (2.99-3.53) in standard length
.....*Sardinella fimbriata* (CUVIER and VALENCIENNES)
- 12b. Gill rakers on lower branch of first arch 59 (49-62); distal end of body scale not conspicuously fimbriated, with comparatively indistinct marginal lines (fig. 7B); depth at dorsal origin 3.00 (2.83-3.11) in standard length.....
.....*Sardinella perforata* (CANTOR)
- 13a. Depth at dorsal origin 2.85 (2.64-3.00) in standard length; gill rakers on lower branch of first arch 60 (55-65); free end of scale greatly perforated and with

- distinct marginal lines (fig. 9A).....*Sardinella brachysoma* (BLEEKER)
- 13a. Depth at dorsal origin 3.25 (3.06-3.44) in standard length; gill rakers on lower branch of first arch 52 (48-57) in *S. zunasi* and 69 in *S. nymphaea*14
- 14b. Gill rakers on both branches of first arch 28 (25-31)+52 (48-57); deep bluish brown color on back of alcohol specimens, clearly demarcated from pale color of lower side (in life the color is iridescent blue-green); depth at dorsal origin 3.36 (3.07-3.44) in standard length*Sardinella zunasi* (BLEEKER)
- 14b. Gill rakers on both branches of first arch 41+69; color on back of alcohol specimens not conspicuously demarcated from color of lower side; depth at dorsal origin 3.14*Sardinella nymphaea* (RICHARDSON)

Subgenus *Amblygaster* BLEEKER

Amblygaster is restricted to the Indo-Pacific region. The members of this subgenus range from the Red Sea in the west, along the shores of the Arabian Sea, the Bay of Bengal, the South China Sea and the Pacific Island to Samoa in the east. In the central portion of its range, where the Indo-Australian Archipelago forms a series of stepping stones, it extends as far south as the shores of Queensland, Australia.

Amblygaster comprises three species of relatively great size. These forms are all larger and heavier bodied than any species of the subgenus *Sardinella*. In fact, in overall appearance the members of *Amblygaster* bear less resemblance to the members of the subgenus *Sardinella* than they do to the true sardines (genus *Sardinops*).

Sardinella sirm (WALBAUM)

Figure 13

Clupea sirm WALBAUM, 1792: 38 (original description; type locality: Arabia.—RÜPPELL, 1835: 77, fig. 2.—GÜNTHER, 1868: 425 (part: descriptive material consisted of the type of *S. leiogastroides*, as well as material of *S. sirm* and *S. leiogaster*); 1909: 383.

Sardinella leiogastroides BLEEKER, 1854: 285.

Clupea (Amblygaster) leiogastroides BLEEKER, 1866-72: 102.

Sardinella (Amblygaster) leiogaster BLEEKER, 1866-72: pl. 262, fig. 6.

Clupea (Amblygaster) sirm WEBER and de BEAUFORT, 1913: 62.

Sardinella sirm REGAN, 1917d: 284.—FOWLER, 1928: 31; 1931: 119.—ROXAS, 1934: 272, pl. 2, fig. 4 (scale).—FOWLER, 1935: 90, fig. 10.—ROXAS and MARTIN, 1937: 20.—HERRE and MYERS, 1937: 12.—CHU and TSAI, 1958: 112.

Specimens. A total number of 55 specimens of this species have been examined, and 50 of these have been selected as the basis for the present description. These came from the following localities, and had the indicated size range:

SU-8984: Apia, Samoan Islands, 5 specimens, 158.0-181.0 mm. SU-29009: Lembeh Strait, Celebes, 35 specimens, 21.0-68.0 mm. GVF-422: Lat. 1°02'23"N., Long. 154°47'45"E., Kapingamarangi Atoll, Caroline Islands, 5 specimens, 70.0-73.5 mm. GVF-448:

Lat. 1°05'52"N., Long. 154°46'24"E., Kapingamarangi Atoll, Caroline Islands, 1 specimen, 60.0 mm. GVF-458: Lat. 1°02'18"N., Long. 154°45'08"E., Kapingamarangi Atoll, Caroline Islands, 1 specimen, 59.5 mm. GVF-1475: Lat. 12°33'12"N., Long. 101°16'05"E., Gulf of Thailand, 1 specimen, 143.0 mm. GVF-1541: Cholburi region south to Rayong, Thailand, 2 specimens, 158.0-164.0 mm. GVF-1561: Lat. 12°36'40"N., Long. 100°54'30"E., Sattahip Bay and western end of Rayong Bay east of Goh Samaesan Island, Gulf of Thailand, 5 specimens, 155.0-171.5 mm. GVF-1564: Lat. 12°34'15"N., Long. 101°02'45"E., Rayong Bay west of Goh Samaesan Island, Cholburi Province, Gulf of Thailand, 7 specimens, 117.0-170.0 mm.

Meristic counts. D 18 (17-19); A 18 (16-18); P. 17 (16-17); V. 8. Lateral scales 43 (40-43); longitudinal scale rows 12 (11-12); predorsal scales 14 (13-14). Medioventral scutes 16 (15-16)+15 (14-15). Gill rakers on lower branch of first arch 40 (38-42).

Description. Head 4.00 (3.77-4.21) in standard length. Maxillary 2.72 (2.65-2.79) in head, extending to the vertical of the anterior margin of orbit or slightly beyond; expanded portion of second supramaxillary almond-shaped, about the size of pupil; minute feeble teeth on palatines, pterygoids, and tongue. Snout 3.15 (3.01-3.28) in orbit. Orbit 3.96 (3.86-4.05) in head. Eye very heavily covered by adipose tissue leaving a vertical slit at the pupil. Interorbital width 1.54 (1.44-1.63) in snout, 1.13 (1.06-1.19) in orbit. Width between upper ends of gill openings 3.10 (2.57-3.61) in head. Opercular bones, as well as postorbitals and suborbitals, covered by translucent adipose tissue, under which minute hollow venules present in an inconspicuous radiating pattern.

Body oblong, slightly elongated. Sides slightly compressed; belly weakly keeled medioventrally, with blunt scutes which are not prominent (figs. 2A-B). Depth at dorsal origin 4.95 (4.75-5.27) in standard length; depth at anal origin 6.64 (6.48-6.80) in standard length; least depth of caudal peduncle 2.80 (2.72-2.83) in depth at dorsal origin.

Predorsal length 2.18 (2.12-2.23) in standard length, 1.20 (1.20-1.30) in postdorsal length, so that the dorsal origin is conspicuously nearer to tip of snout than to caudal base; dorsal base 3.75 (3.43-4.07) in predorsal length; length of longest dorsal ray (4th or 5th) 0.91 (0.87-0.95) in dorsal base. Preanal length 1.25 (1.24-1.27) in standard length; length of longest anal ray (3rd or 4th) 2.93 (2.78-3.07) in anal base. Last two anal rays somewhat larger and more extensively branched than preceding rays; the posterior branch of the last one somewhat elongated, so that the extreme end of the fin is slightly produced; the length of this ray 3.05 (2.78-3.31) in anal base. Caudal deeply forked, with pointed upper and lower lobes; its length 4.69 (4.46-4.92) in standard length. Prepectoral length 4.09 (4.00-4.18) in standard length; pectoral length 1.58 (1.54-1.62) in prepectoral length. Ventral inserted below the 6th to 8th dorsal ray; preventral length 2.01 (1.98-2.03) in standard length; ventral length 5.89 (5.71-6.06) in preventral length.

Scales cycloid, thin, deciduous. Predorsal median ridge before dorsal fin covered by a single longitudinal series of scales. Each body scale with one continuous transverse groove posteriorly, preceded by a set of two to five interrupted grooves with a wide, distinct interspace between the discontinuous portions. Posteriorly, such a scales is slightly produced, but not forming a flap, and devoid of perforations or conspicuous marginal lines. Scale sheaths cover the bases of dorsal and anal fins. Caudal with numerous small scales, and an elongated flap-like scale present on each lobe near the fork. An axillar scale present at the ventral fin.

Most of the specimens examined have been preserved in isopropyl alcohol, while some are kept in ethanol. They are dark brownish blue on the back, and silvery on the sides of belly. A row of 10-20 dark blue rounded spots extends along the dorso-lateral part of the body from behind the upper end of gill opening to the caudal peduncle. Tips of jaws dark. The axillar side of the pectoral fin has a dark streak on the anterior two-thirds of the first to fourth or fifth rays. Bases of the first five or six dorsal rays dark. Caudal dusky. Ventral and anal pale or translucent.

Notes. Many systematists have erroneously treated *Sardinella leiogaster* as a synonym of *S. sirm*. *Sardinella leiogaster*, however, has a shorter and smaller maxillary resembling that of *S. clupeioides*, a dorsal origin nearer to the upper end of caudal base than to the tip of snout, a slightly but constantly lower gill-raker count, and a color pattern without the dorsolateral row of dark spots.

Distribution. *Sardinella sirm* occurs along all of the shores of the tropical Indo-Pacific waters. It has been reported from the coasts of the Red Sea, India, Ceylon, Malayan Peninsula, the Gulf of Thailand, Southern China, and Taiwan in the north, to Queensland, Australia, in the south. It occurs as far west as Arabia, and as far east as the Samoan Islands.

Sardinella clupeioides (BLEEKER)

Figure 14

- Amblygaster clupeioides* BLEEKER, 1849: 73 (type locality: Macassar Mare).—MUNRO, 1955: 26, pl. 4, fig. 67.
- Clupea (Amblygaster) clupeioides* BLEEKER, 1866-72: 103, pl. 272, fig. 1.—WEBER, and de BEAUFORT, 1913: 63, fig. 23.
- Clupea clupeioides* GÜNTHER, 1868: 425.
- Sardinella clupeioides* BLEEKER, 1852: 19.—REGAN, 1917d: 385.—FOWLER, 1931: 119; 1941: 619.

Specimens. This description is based on 24 specimens from the localities indicated below:

SU-33828: Singapore market, 3 specimens, 180.0-188.0 mm. SU-38326: Margo-satubig, Luzon, Philippines, 4 specimens, 116.5-132.0 mm. GVF-1541: fish market at Cholburi, collected from east coast of Gulf of Thailand from Cholburi region south to Rayong, Thailand, 2 specimens, 172.0-180.0 mm. GVF-1552: fish market at Chol-

huri, collected in vicinity of Rayong, Rayong Province, Thailand, 3 specimens, 172.0-177.0 mm. GVF-1561: Lat. 12°36'40"N., Long. 100°54'30"E., Gulf of Thailand, 4 specimens, 160.0-166.0 mm. GVF-1565: Lat. 12°30'N.-12°40'N., Long. 100°00'E.-101°25'E., Gulf of Thailand, 4 specimens, 185.0-213.0 mm. GVF-2795: Lat. 11°52'N.-12°14'N., Long. 109°19'E.-109°23'E., South Viet Nam, 4 specimens, 215.0-235.0 mm.

Meristic counts. D 18 (17-18); A 18 (17-18); P 16 (16-17); V. 8. Lateral scales 42 (42-44); longitudinal scale rows 12; predorsal scales 16 (15-16). Medioventral scutes 16 (15-17)+13 (12-13). Gill rakers on lower branch of first arch 29 (26-30).

Description. Head 3.95 (3.80-4.09) in standard length. Maxillary 3.15 (2.98-3.31) in head, not reaching the vertical through the anterior margin of orbit; expanded portion of the second supramaxillary almond-shaped, its area conspicuously less than that of the pupil. Minute feeble teeth present on palatines, pterygoids and tongue. Snout 3.39 (3.21-3.56) in head, 0.96 (0.90-1.02) in orbit. Orbit 3.51 (3.27-3.74) in head. Eye covered very heavily by thick adipose tissue, leaving a vertical slit at the pupil. Interorbital width 1.11 (1.06-1.16) in snout, 1.04 (0.99-1.08) in orbit. Width between upper ends of gill openings 2.34 (2.22-2.46) in head. Opercular bones, as well as postorbitals and suborbitals, covered by translucent dermal tissue, under which minute hollow venules present at the suborbital region in a radiating pattern.

Body oblong, elongated; sides slightly compressed. Belly weakly keeled medioventrally, with blunt scutes which are not prominent (figs. 2A-B). Depth at dorsal origin 4.00 (3.71-4.20), depth at anal origin 6.67 (6.52-6.81), both in standard length; least depth of caudal peduncle 2.91 (2.44-3.38) in depth at dorsal origin.

Predorsal length 2.04 (2.00-2.05) in standard length, so that the dorsal origin is slightly nearer to the tip of snout than to the caudal base; dorsal base 3.66 (3.54-3.78) in predorsal length; length of longest dorsal ray (4th or 5th) 1.16 (1.11-1.21) in dorsal base. Preanal length 1.27 (1.24-1.29) in standard length; anal base 6.01 (5.35-6.66) in preanal length; length of anal ray (3rd or 4th) 3.29 (3.04-3.54) in anal base. Last two anal rays somewhat larger and more extensively branched than preceding rays; the posterior branch of the last one somewhat elongated so that the extreme end of the fin is slightly produced; the length of this terminal ray 2.69 (2.47-2.90) in anal base. Caudal deeply forked with pointed upper and lower lobes; its length 3.10 (3.06-3.24) in standard length. Prepectoral length 4.08 (3.94-4.22) in standard length; length of pectoral 1.59 (1.52-1.66) in prepectoral length. Ventral inserted below the 3rd to 5th dorsal ray; preventral length 1.92 (1.89-1.94) in standard length; ventral length 5.37 (5.18-5.56) in preventral length.

Scales cycloid, thin, deciduous. Predorsal median ridge covered by a single longitudinal series of these scales. Each body scale with one continuous transverse groove posteriorly, preceded by a set of two to six interrupted grooves with a wide distinct interspace between the discontinuous portions. The posterior edge of each scale with a slight projection, but not flap-like, and completely devoid of perforations and marginal lines. Bases of dorsal and anal covered by scale sheaths. Caudal with

numerous small scales, and with an elongated flap-like scale present on each lobe near the fork. An axillar scale present at the ventral fin.

All the specimens available to me have been preserved in isopropyl alcohol. They are dark brownish blue on the back and pale brownish on the sides of belly. A dark bluish brown spot, about size of pupil, present in the supracleithral region at the level of the upper end of gill opening. The external membrane of each scale pocket on the back with a dark brownish blue margin. Bases of the first five dorsal ray dark. Tips of jaws dusky brown. The axillar side of pectoral fin with a dusky streak on the first two to four rays. Caudal dusky brown; ventral and anal pale and translucent.

Notes. This species resembles *Sardinella leiogaster* in having a short maxillary which does not reach to the vertical of the anterior margin of orbit; but it is distinguished from the latter by having a deeper body, by having a lower gill-raker count, and by having a dorsal origin which is slightly closer to the tip of snout than to the upper point of the caudal base. (Compare with *Notes* on *S. sirm*).

Distribution. *Sardinella clupeioides* has been reported from the coasts of the southern and south-eastern parts of the Asian Continent, from the waters of Taiwan, the Philippines, and the East Indies, and from the shores of Queensland, Australia. It has been recorded also from the Red Sea in the west.

Sardinella leiogaster CUVIER and VALENCIENNES

Figure 15

Sardinella leiogaster CUVIER and VALENCIENNES, 1847: 270.

Clupea sirm GÜNTHER, 1868: 425 (part; descriptive material consisted of the type of *S. leiogastroides*, as well as material of *S. sirm* and *S. leiogaster*).

Clupea (Amblygaster) leiogaster BLEEKER, 1866-72: 102 (not the figure).—WEBER, and de BEAUFORT, 1913: 61 (not the color pattern).

Clupea leiogaster KLUNZINGER, 1871: 598.

Specimens. This descriptions is based on 8 specimens from the localities indicated below:

SU-29217: Pelew Island, 1 specimen, 188.0 mm. SU-28572: Culion, Philippines, 5 specimens, 118.0-124.0 mm. SU-33828: Singapore market, Singapore, 2 specimens, 116.7-126.5 mm.

Meristic counts. D 18 (17-18); A 19 (18-21); P 17 (16-17); V 8. Lateral scales 41 (39-41); longitudinal scale rows 12 (11-12); predorsal scales 15 (14-16). Medio-ventral scutes 16 (15-17)+14. Gill rakers on lower branch of first arch 33 (31-34).

Description. Head 3.96 (3.87-4.04) in standard length. Maxillary 3.09 (3.00-3.18) in head, not reaching to the vertical of the anterior margin of the orbit; expanded portion of the second supramaxillary almond-shaped, its area distinctly smaller than that of pupil. Minute feeble teeth present on palatines, pterygoids, and tongue.

Snout 2.98 (2.83-3.13) in head, 0.83 (0.79-0.87) in orbit. Orbit 3.27 (3.58-3.86), post-orbital 2.64 (2.54-2.76), in length of head. Eye heavily covered by adipose tissue, leaving a vertical slit at the pupil. Interorbital width 1.30 (1.23-1.36) in snout, 1.05 (1.00-1.09) in orbit. Width between upper ends of gill openings 2.56 (2.44-2.68) in head. Opercular bones, as well as postorbitals and suborbitals, covered by translucent dermal tissue, under which minute hollow venules spread downwards in a radiating pattern.

Body oblong, elongated; sides slightly compressed. Belly weakly keeled medio-ventrally, with blunt scutes which are not prominent (figs. 2A-B). Depth at dorsal origin 4.37 (4.18-4.55), depth at anal origin 6.35 (6.02-6.70), both in standard length; least depth of caudal peduncle 2.91 (2.70-3.06) in depth at dorsal origin.

Predorsal length 1.97 (1.94-1.99) in standard length, the dorsal origin approximately equidistant between the tip of snout and the upper point of caudal base, or slightly nearer to the latter; base of dorsal 3.86 (3.69-4.03) in predorsal length; length of longest dorsal ray (4th or 5th) 1.09 (1.07-1.14) in length of dorsal base. Preanal length 1.25 (1.23-1.28) in standard length; base of anal 6.30 (5.82-6.77) in preanal length; length of third anal ray 2.47 (2.39-2.55) in anal base. Last two anal rays somewhat larger and more extensively branched than preceding rays; the posterior branch of the last one somewhat elongated so that the extreme of the fin is slightly produced; the length of this terminal ray 2.63 (2.40-2.88) in anal base. Caudal deeply forked (caudal lobes of all specimens have been broken to some extent). Prepectoral length 4.00 (3.91-4.08) in standard length; pectoral length 1.65 (1.63-1.67) in prepectoral length. Ventral inserted below the 5th to 7th dorsal rays; preventral length 1.95 (1.93-1.97) in standard length; ventral length 5.56 (5.52-5.59) in preventral length.

Scales of all specimens have been lost. Scale pockets show that the predorsal median ridge was covered by a single longitudinal row of scales. It is logical to assume that the groove pattern of the lost scales is similar to those of *S. sirm* and *S. clupeoides*, simply on the basis of their close relationship. It should follow also that the distribution and arrangement of scales is similar to that found in these two species.

All of the specimens examined have been preserved in ethyl alcohol. In each the back is greyish blue with a touch of dull brownish hue, while the sides are either silvery or pale brownish. A dark brownish blue spot, about the size of the pupil, present in the supracleithral region at the level of the upper end of gill opening. The external membrane of each scale pocket on the back with a brownish margin. Bases of the first five dorsal rays dark. Tips of jaws brownish. The axillar side of pectoral fin with a dusky streak on the first two to four rays. Caudal dusky brown; ventral and anal pale and translucent.

—to be concluded—