

A REVISION OF THE RECENT
ROUND HERRINGS
(PISCES: DUSSUMIERIIDAE)

BY

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SYNOPSIS

The recent round herrings, the Dussumeriidae, are here maintained as a family distinct from the Clupeidae or true herrings. Two subfamilies are recognized, the Dussumeriinae containing the genera *Dussumieria* and *Etrumeus*; and the Spratelloidinae, which is further split into the tribes Spratelloidini and Ehiravini. The former contains the genera *Spratelloides* and *Jemkinsia*, and the latter *Ehirava*, *Gilchristella* and *Sawagella*.

In those genera with a wide distribution (e.g. *Dussumieria*, *Etrumeus*, *Spratelloides*), morphometric and meristic data, from samples covering the entire geographical range, indicate that many former species are no more than geographical variants, or in some cases subspecies. Ten species are recognized, and these are described and figured. Keys are given for all taxa.

The systematics and phylogeny of the Dussumeriidae are examined in the light of certain hitherto neglected characters, principally the development of abdominal and pelvic scutes, the formation of the posterior cranial fontanelles, the shape of the cleithral outline of the gill opening, the shape of the bones in the opercular series, and the number and shape of the supra-maxillary bones. It is concluded that the Dussumeriidae are modern representatives of a primitive non-scuted clupeid.

INTRODUCTION

THE Dussumeriidae, or round herrings, are small clupeid fishes fairly widely distributed in tropical and temperate seas, mainly in the Indo-Pacific region. They are usually separated from the Clupeidae by their absence of abdominal scutes, thus having rounded rather than keeled bellies. Jordan & Gilbert (1883), Günther (1868), and Weber & de Beaufort (1913), among earlier writers, placed the round herrings as a subfamily of the Clupeidae, but nowadays they are usually given family status (e.g. since Jordan, 1925). Svetovidov (1952) however retained them in a subfamily of the Clupeidae, but the absence of scutes in all but one species of round herring is here considered evidence that the evolution of this group predated the evolution of the scuted clupeid groups.

The most recent revision of the family was that of Bertin (1943), who recognized eight genera containing recent species within two subfamilies, the Dussumeriinae and the Spratelloidinae. I have here rejected three of these genera (*Montalbania*, *Perkinsia* and *Halecula*) but have accepted two others (*Ehirava* and *Jenkinsia*). Comparatively little systematic work has been published recently on the group, being for the most part descriptions of species and some notes on bionomics. Chapman (1948) published a useful description of the osteology of the round herrings, comparing them with the clupeids, but considered only a single genus, *Etrumeus*. Ridewood (1904) had earlier compared the skull of *Dussumieria* with certain clupeoids, but scarcely any work has been done on the osteology of the spratelloidine round herrings (except caudal anatomy by Hollister, 1936).

The recent discovery of abdominal scutes in a round herring (Whitehead, 1962a) raises the problem of the relationship of the Dussumeriidae to the Clupeidae; it has also thrown more light on the division between the Spratelloidinae and the Dussumeriinae. I have found here that, although the Spratelloidinae approach the Clupeidae in many respects, and especially in the form of the pelvic scute, those species which most closely approach the Clupeidae are at the same time those which also most closely resemble the Dussumeriinae in other characters. On the other hand, in certain characters the division between the Spratelloidinae and the Dussumeriinae is as marked as is the division between either and the Clupeidae. But

the presence or absence of scutes seems to me to be of such fundamental importance that the round herrings should be separated from the clupeids at family level.

Although Gosline (1951) drew attention to the Ruling of the International Commission for Zoological Nomenclature concerning the use of the generic name *Stolephorus*, it is worth repeating that, under Opinion 93, the genotype of *Stolephorus* Lacépède is *S. commersonianus*¹ Lacépède, by description and figure an undeniable anchovy, so that *Spratelloides* Bleeker must replace *Stolephorus* as a round herring genus, and the round herrings are the Dussumieriidae, not the Stolephoridae, as Fowler (1941, 1958), Smith (1955), and others have termed them. The error arose through an inadequate description by Houttuyn of a fish later included by Lacépède in his engraulid genus *Stolephorus*; this is discussed further on p. 340.

This revision is based on collections in the British Museum (Natural History) and on material lent or donated by other institutions, for which I would like to thank particularly, Dr. R. Rosenblatt of the Scripps Institute of Oceanography; Professor C. R. Robbins of the Institute of Marine Studies, University of Miami; Professor J. L. B. Smith of Rhodes University; Mr. A. Ben-Tuvia, of the Sea Fisheries Research Station, Haifa; Dr. L. Woods of the Chicago Natural History Museum; Dr. M. Blanc of the Museum Nationale d'Histoire Naturelle, Paris; Dr. J. Nielsen, Universitetets Museum, Copenhagen, and Dr. H. Steinitz of the Hebrew University, Jerusalem.

Family DUSSUMIERIIDAE

Diagnosis

Clupeoid fishes usually with elongate, fusiform bodies and rounded bellies (body more compressed in the tribe Ehiravini). One or two abdominal scutes associated with the pelvic fin; pre- or post-pelvic scutes entirely absent except for the former in one instance (*Gilchristella aestuarius*); neither the pelvic scutes nor, where present, the pre-pelvic scutes are keeled.

Anal fin normally equal to or shorter than dorsal, exceptionally longer. Pelvics slightly in front, below or a little behind dorsal. Pectorals set low on body. Anal always behind dorsal.

Mouth terminal, lower jaw more or less projecting. Premaxilla small, edentulous or with a single series of small conical teeth which are often deciduous. Small, conical and sometimes deciduous teeth on dentary, along lower edge of maxilla, on glossohyal, suprabasal (where present), mesopterygoids and palatine. A well-developed posterior supra-maxilla overlapping distal tip of maxilla and produced anteriorly into a pointed shaft; a second, plate-like supra-maxilla sometimes present, lying between the shaft and the upper edge of the maxilla.

Hyomandibular with two separate cranial heads articulating with both sphenotic and pterotic; ceratohyal with or without indented ventral edge. Branchiostegal rays from six to twenty.

Pseudobranchiae well-developed; gill membranes separate, free from isthmus; gillrakers fine and slender but rarely more than about forty. Pyloric caecae numerous. Adipose tissue often entirely covering eye.

¹ A cheironym which should be rejected in favour of the name actually used by Lacépède, *commersonii*.

Sensory canals of head well-developed, with superficial ramifications extending on to pre-operculum, sub-orbitals, operculum, and sometimes on to maxilla, part of articular, and sub-operculum.

Scales cycloid, covering entire body except head, often highly deciduous; elongate axillary scales in angle of pectoral and pelvic fins and elongate scales on upper and lower lobes of caudal. Vertebrae 30-56.

The Dussumieriidae are small, often brilliantly silvery fishes chiefly found in the Indo-Pacific region between latitudes 40° N. and 40° S., but with a few species along the Pacific and Atlantic coasts of North America. They are found in coastal regions and in estuarine and tidal lagoons and, although rarely exploited by any large fishery, they are acceptable in some places as food fishes when caught in sufficient number. One of the three fishes constituting the "Iwashi" fishery of Japan, is the round herring, *Etrumeus*.

The Dussumieriidae fall into two very distinct groups, the Dussumieriinae, larger fishes with more branchiostegal rays (14-19); and the Spratelloidinae, comprising species which rarely exceed 110 mm. and have 6-7 branchiostegal rays. The former subfamily appears to be the more primitive, while the latter approaches the Clupeidae so nearly in certain cases (e.g. *Gilchristella aestuarius*), that it would be tempting to place the Spratelloidinae with the clupeids were it not for the closely related but more typical spratelloidines, such as *Spratelloides gracilis*.

- | | | |
|-----|---|------------------------|
| I. | Branchiostegal rays 14-19; adult size 150-350 mm.; pelvic scute w-shaped; no posterior cranial fontanelles in adults; ceratohyal not excavated ventrally; dorsal rays 16-21 | <i>Dussumieriinae</i> |
| II. | Branchiostegal rays 6-7; adult size 50-110 mm.; pelvic scute often with ascending process; a pair of posterior cranial fontanelles in adults of most species; ceratohyal excavated ventrally; dorsal rays 11-16 | <i>Spratelloidinae</i> |

Subfamily DUSSUMIERIINAE

Diagnosis

Dussumieriid fishes, with 14-19 branchiostegal rays, the first seven to nine attached to the ceratohyal whose ventral edge is not excavated. Premaxilla toothed, teeth not deciduous; maxilla with a narrow posterior supra-maxilla whose depth is about half that of the maxilla at its widest point; a second, anterior supra-maxilla present in some cases. Ventral scutes absent except for a modified w-shaped scute surrounding the base of the pelvic fins and sometimes a second triangular, plate-like scute immediately behind the pelvics.

No posterior cranial fontanelles in adults, this portion of the head forming a shallow, triangular depression. Posterior margin of pre-operculum not vertical but inclined forwards; ventral margin of operculum not horizontal but rising posteriorly.

A small, usually little developed, fleshy eminence on the postero-ventral angle of the cleithrum. Inter-operculum barely exposed in lateral view.

Dorsal rays 16-21; anal 9-19. Transverse scales on body 11-15. Vertebrae 52-56.

Adult size 150–350 mm.

Two genera, *Dussumieria* and *Etrumeus*.

- A. Pelvic fins under dorsal base; two supra-maxillae present; anal rays 14–19; exposed portion of sub-operculum sub-rectangular *Dussumieria*
 B. Pelvic fins behind dorsal base; a single supra-maxilla; anal 9–13; exposed portion of sub-operculum triangular *Etrumeus*

Etrumeus and *Dussumieria* are obviously closely related, but Fowler (1958) used the differences in pelvic position, number of anal rays, and presence or absence of a second supra-maxilla to erect a tribal division in the Dussumieriinae. This does not seem justified and the differences between these two genera are small compared with those used here to split the Spratelloidinae into two tribes (p. 329).

Genus *DUSSUMIERIA* Valenciennes

Dussumieria Valenciennes, 1847, *Hist. Nat. Poiss.*, 20 : 467 (Type: *Dussumieria acuta* Valenc.).
Montalbiana Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 7. (Type: *Etrumeus* (*Montalbiana*) *albulina* Fowler, 1934.)

Body elongate, more or less compressed. Snout pointed, jaws equal. Two supra-maxillae, each about half the length of the maxilla (Text-fig. 28). Proximal half of maxilla thickened along its dorsal edge, distal half flat, tip of maxilla rounded, almost entire ventral edge bearing small conical teeth. Premaxillae toothed. A single w-shaped scute surrounding base of pelvic fins. Dorsal rays 17–21, anal rays 14–19, 20–34 gillrakers on lower part of first gill arch. Branchiostegals 14–20. Vertebrae 54–56. Anal well behind the dorsal, whose origin is a little nearer the caudal base than the tip of the snout. Pelvic origin below middle of dorsal fin. A slight fleshy eminence on the angle of the posterior margin of the cleithrum (cleithral flap), not so developed as in *Spratelloides*, but more developed than that of *Etrumeus* (see Text-fig. 30b). Gill filaments of first arch shortened to accommodate this eminence. Ventral margin of operculum nearer to horizontal than in *Etrumeus* (Text-fig. 30b).

A single species recognized here, *D. acuta*.

This genus is entirely Indo-Pacific in its natural distribution, but since the opening of the Suez Canal there have been several records of *Dussumieria*, and especially the Erythrean form, being caught in the eastern Mediterranean (Lissner, 1949, and Ben-Tuvia, 1953). I have examined twenty such specimens and they have the high gillraker count typical of the Red Sea population (Text-fig. 3). The Red Sea form evidently is not so closely adapted to hot, hypersaline conditions that it cannot survive elsewhere. On the other hand it has been able to survive passage through the even more saline Bitter Lakes. It will be interesting to see whether the Mediterranean population will now lose the rather distinctive characters of the Red Sea form.

Dussumieria acuta Valenciennes

(Text-fig. 5)

- Dussumieria acuta* Valenciennes, 1847, *Hist. Poiss. Nat.*, **20** : 467, pl. 606 (Type locality : Bombay, Coromandel); Cantor, 1849, *J. Asiat. Soc. Beng.*, **18** : 1268; Day, 1865, *Fishes of Malabar* : 226; Kner, 1865, *Reise Novarra, Fische* : 330; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 466; Bleeker, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 94, pl. 271, fig. 1; Day, 1878, *Fishes of India*, pt. 4 : 647, pl. 166, fig. 4; Weber and Beaufort, 1913, *Fishes Indo-Aust. Arch.*, **2** : 21, fig. 13; Fowler, 1928, *Mem. Bernice P. Bishop Mus.*, **10** : 30; Roxas, 1934, *Philipp. J. Sci.*, **55** : 251, pl. 1, fig. 5; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 570; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 3, figs. 1 (scale) and 2; Liang, 1948, *Quart. J. Taiwan Mus.*, **1** : 2; Monroe, 1955, *Marine and freshwater fish. Ceylon* : 28; Fowler and Steinitz, 1956, *Bull. Res. Council. Israel*, **5 B** (3-4) : 261.
- Dussumieria elopsooides* Bleeker, 1849, *Verh. Bat. Gen.*, **22** : 12; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 466.
- Dussumieria hasselti* Bleeker, 1850, *Natuurk. Tijdschr. Ned. Ind.*, **1** : 422; *Idem*, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 95, pl. 271, fig. 2; Day, 1878, *Fishes of India*, pt. 4 : 647, pl. 166, fig. 5; Weber and Beaufort, 1913, *Fish. Indo-Aust. Arch.*, **2** : 23; Roxas, 1934, *Philipp. J. Sci.*, **55** : 250; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 572; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 6, fig. 2; Schultz and Wellander, 1953, *Bull. U.S. nat. Mus.*, No. 202 : 25; Monroe, 1955, *Marine and freshwater fish, Ceylon* : 28; Fourmanoir, 1961, *Mem. Inst. sci. Madagascar*, (F) **4** : 84, fig. 1.
- Dussumieria productissima* Chabanaud, 1933, *Bull. Inst. océanogr. Monaco*, No. 627 : 4, figs. 3-6; *Idem*, 1933, *Bull. Soc. zool. France*, **58** : 289; Gravel and Chabanaud, 1937, *Mém. Inst. égypt. (Égypte)*, **35** : 3, fig. 3; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 570; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 6; Ben-Tuvia, 1953, *Bull. Sea Fish. Res. Stat., (Israel)*, No. 8 : 6, fig. 1.
- Etrumeus (Montalbana) albulina* Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 244, fig. 7; *Idem*, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 574, fig. 14.
- Montalbiana albulina* Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 8.

Notes on Synonymy

The most important references are cited here; full synonymies are given by Fowler (1941) under *D. acuta*, *D. productissima*, and *D. hasselti*.

Fowler (1941), Bertin (1943) and Herre (1953) amongst others, have all included *Dussumieria elopsooides* Bleeker in the synonymy of *D. acuta* Valenciennes, recognizing two further species, *D. hasselti* Bleeker, which extends to the eastern limits of the range of this genus (China), and *D. productissima* Chabanaud from the extreme western fringe (Gulf and Isthmus of Suez). Günther (1868) had, however, placed *D. hasselti* in synonymy with *D. elopsooides*. Examination of the holotypes of the last two species has revealed no possible basis for specific distinction on preserved characters (see Table I). At the same time, the specimens in this museum labelled *D. acuta* and *D. elopsooides* (*sensu* Günther) both show a parallel variation in several characters which can clearly be correlated with geographical distribution. Specimens from the intermediate part of the range of these two species could be assigned to either species, and in fact Bertin (1943) stated that all but two of Valenciennes types of *D. acuta* should be referred to *D. hasselti*.¹

¹ I have examined these specimens through the courtesy of Dr. M. Blanc of the Museum Nationale d'Histoire Naturelle, Paris, and wish to thank him for allowing me to borrow them.

Unfortunately Valenciennes did not state the number of scales in lateral series in his *D. acuta*, and neither did Chabanaud for *D. productissima*. The scales in *Dussumieria* are highly deciduous; amongst 29 specimens of *D. acuta* in this museum, there is only one in which a scale count can even be estimated. In this case 36 scales are actually present, but at least 12 scales, more likely 15, are missing but fairly well represented by scale pockets. This would place the fish in the range of *D. elopsoides* (i.e. 52–56 scales; cf. 42–44 reported for *D. acuta*). In the majority of descriptions it is rarely stated whether the scale count is an actual one based on the specimens examined, or whether it merely follows previous descriptions. An exception is Blegvad (1944), who counted 42–44 scales in specimens from the Gulf of Iran and assigned them to *D. acuta*; I have examined these fishes, but all traces of even the scale pockets are now obliterated.

It seems therefore that scale counts are an unreliable character for separating *D. acuta* from *D. elopsoides*. Delsman (1925) came to the same conclusion and found little difference in vertebral counts in a specimen each of *D. acuta* and *D.*

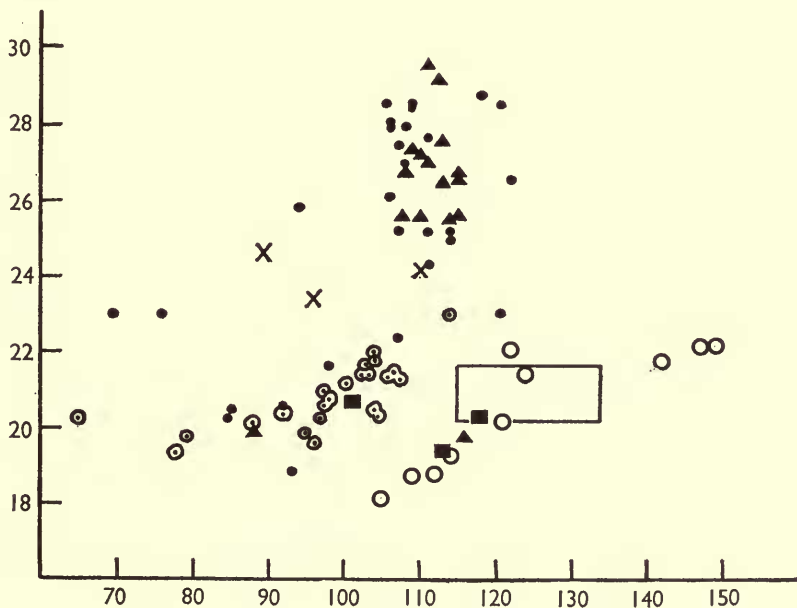


FIG. 1.

Dussumieria acuta. Body depth expressed as a percentage of standard length (ordinate) plotted against standard length in mm. (abscissa) for various populations. Based on specimens (see list of Study Material) labelled or recorded under the following names:

- D. acuta*
- × Iranian Gulf specimens collected by Blegvad (1944).
 - Gulf of Aden specimens
 - (in rectangle, five Taiwan specimens, based on Liang, 1948).
- D. elopsoides*
- All others.
 - Hong Kong and China specimens.
 - ▲ All others.
- D. productissima*
- Specimens from Haifa (eastern Mediterranean).

hasselti (55 and 54 respectively). He also mentions a slight difference in dorsal position, but I have not found this. The weight of other evidence (snout length, body depth, gillraker and dorsal fin ray counts) strongly suggests that the number of scales conforms to the general geographical trends shared by both *D. acuta* and *D. elopsooides*. On the basis of the four characters mentioned, it is impossible to recognize *D. elopsooides* as a separate species; the evidence for this is presented below under each heading.

(a) *Body Depth*

The measurements plotted in Text-fig. 1 (as percentages of standard length) refer to specimens of *Dussumieria* covering almost the entire geographical range of the genus. The Aden specimens (open circles) suggest positive allometry with standard length, and this may explain some of the lower figures for the fishes labelled *D. acuta* (black dots). The scatter-diagram shows clearly that size for size, the specimens of *D. elopsooides* (triangles) cannot be distinguished from *D. acuta* in this character, except in a few cases; three of these are from China (black squares), one is from Amboina, and one bears no locality label. In addition, measurements for five fishes from the Pescadores Islands, Taiwan (*D. acuta* of Liang, 1948) have been placed within a rectangle. The result is a striking similarity between the far-eastern specimens (*D. elopsooides*) and the Gulf of Aden specimens, with the Mediterranean specimens (encircled dots) also giving low values.

I conclude that body depth cannot be used to separate *D. elopsooides* from *D. acuta* and that in general the lowest values are found in both the eastern and the western populations, with higher values in intermediate areas. The two specimens recorded (as *D. hasselti*) by Schultz & Wellander (1953) from Batavia appear to be much more slender than any I have measured, having a body depth of only 15% of standard length. In addition, these authors count 61 scale pockets. Unfortunately the fishes were rather damaged, so it would be unwise to include these figures until more specimens can be examined.

(b) *Snout Length*

Although the snout comprises only 8–10% of standard length and variations in its length are barely perceptible, nonetheless, when plotted in a series of histograms for various populations (Text-fig. 2) the results are very suggestive of a cline which may reverse direction after reaching a minimum value in the Indian Ocean. Thus the highest figures are those for specimens from the Gulf of Aden, from the eastern Mediterranean (derivatives of a Red Sea population) and from China; the lowest are those from the coasts of India. The samples are small, but the overall picture deserves attention because of its almost perfect correspondence with the situation found in gillraker counts (Text-fig. 3).

In Text-fig. 2 specimens from each locality have been separated into the species under which they were recorded or labelled. The result shows clearly that in areas where both *D. acuta* and *D. elopsooides* are represented, there is nothing to distinguish the two, and that *D. elopsooides* from China, and *D. productissima* from the Mediterranean merely continue the trends already shown by the other populations. Snout

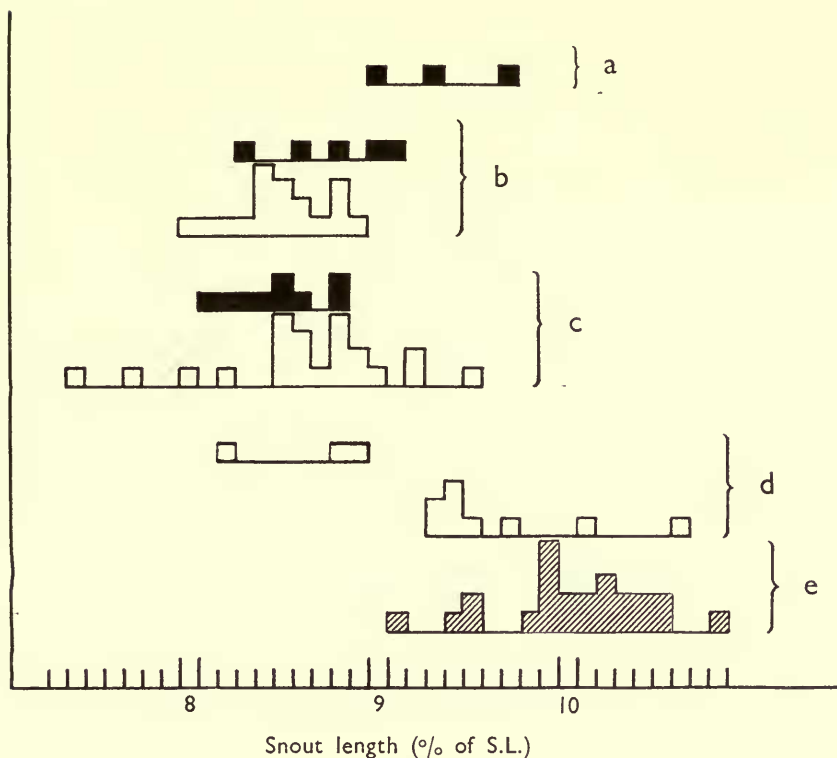


FIG. 2.

Dussumieria acuta. Snout length (expressed as a percentage of standard length) in various populations, showing relative frequency in each group. Based on specimens (see list of Study Material) which have been labelled or recorded under the following names:

White *D. acuta*, Black *D. elopsoides*, Hatched *D. productissima*.

- a. Hong Kong, Foochow, Amoy.
- b. Siam, Amboina, Java, Madura, Sumatra, Borneo, Andamans, Singapore.
- c. Malabar, Calicut, Bombay, Madras, Coromandel.
- d. Gulf of Iran (upper), Gulf of Aden (lower).
- e. Haifa (eastern Mediterranean).

length cannot serve as a basis for distinguishing the species when specimens from the entire range are considered.

(c) Gillrakers

Gillraker frequency counts are presented similarly in Text-fig. 3. These counts were made on the lower part of the first arch only, and included in the count was the occasional raker lying exactly in the angle of the arch. Counts for the Mediterranean specimens lie in the lower part of the range cited by Chabanaud (1933) for *D. productissima*. It is possible that, like other meristic characters, gillrakers are susceptible to exogenous factors (especially temperature), and that a higher count may

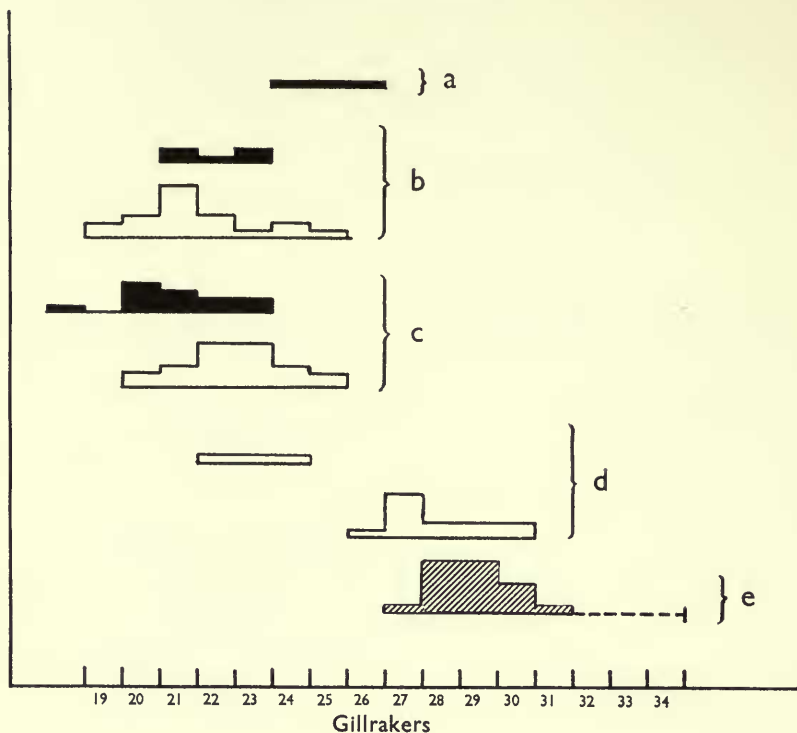


FIG. 3.

Dussumieria acuta. Gillraker count frequencies (lower half of first arch only) in various populations. Based on specimens (see list of Study Material) which have been labelled or recorded under the following names :

White *D. acuta*, Black *D. elopsoides*, Hatched *D. productissima*.

- a. Hong Kong, Foochow, Amoy.
- b. Siam, Amboina, Java, Madura, Sumatra, Borneo, Andamans, Singapore.
- c. Malabar, Calicut, Bombay, Madras, Coromandel.
- d. Gulf of Iran (upper), Gulf of Aden (lower).
- e. Haifa—eastern Mediterranean (broken line includes range given by Chabanaud (1933) for 16 specimens from the Gulf and Isthmus of Suez).

occur in Red Sea populations ; this is, however, the reverse of the usual direction in temperature-influenced meristic variations.

As in snout length and body depth, there is a hint that the general west to east trend of decreasing gillrakers is reversed, so that the China specimens again approach the western population in numbers.

The Gulf of Aden specimens (Text-fig. 3d—lower histogram) effectively bridge the gap between "*D. productissima*" (*sensu* Chabanaud) and the remaining populations of *D. acuta*. The sample from the Gulf of Iran (d—upper histogram) only contained three fishes, but a larger sample might well provide a more effective bridge linking the Gulf of Aden population with that of the Indian Ocean. But for the Gulf of Aden specimens, there would be good reason to suppose the Red Sea

D. productissima a distinct species. If a subspecies were considered, then the Gulf of Aden fishes should be included also, but I do not think such a subspecies could be maintained once adequate collections have been made in the western Indian Ocean.

(d) *Dorsal Rays*

The first simple ray of both dorsal and anal fins is easily missed, being small, often minute. For this reason simple and branched rays in both fins have been counted separately, and only the latter plotted in Text-fig. 4. Here the trend, if such there is, appears to be reversed, highest values occurring in Indian Ocean populations, and lowest values at the extremities of the geographical range. But variations in both dorsal and anal rays are very small, and the graph probably shows no more than that once again no distinction can be made between *D. acuta* and *D. elopsoides*.

I have been unable to find other characters on which populations of *Dussumieria* can be distinguished. The shape of the exposed portion of the suboperculum varies somewhat, from a rectangle with an obliquely truncated posterior margin, to a more triangular area with a rather rounded margin (as in *Etrumeus*), but such differences appear to be individual variants. Similarly, the area and shape of the palatopterygoid toothpad also shows some variation, and the size and number of jaw teeth varies. Nor can any distinction be made on the sculpture patterns on the wedge-shaped fronto-parietal surface, the shape of the operculum, or in any body proportions.

Thus the only difference remaining between the three recognized species is in numbers of scales in lateral series, a badly recorded and uncertain character. From the evidence presented on other characters it seems unlikely that scale numbers would in fact show the clear-cut differences suggested by previous descriptions. Therefore, I do not think that three separate species of *Dussumieria* can be maintained, the populations from one area merging imperceptibly with those of the next. There are more grounds for considering the Red Sea population a distinct subspecies, but here again no definite limits can be drawn between the Red Sea specimens and those for example from the Gulf of Aden. If the Red Sea form is to be separated, so also should the far eastern populations, but the latter could only be defined in terms which could include the Red Sea fishes, which would surely be an unrealistic use of the concept of subspecies. It seems preferable therefore, to leave all in one rather variable species, *D. acuta*, until much more work has been done.

Several authors have noted the similarity between specimens of *Dussumieria* from the extreme eastern and western limits of its range. Bertin (1943) suggested "segregation centrifuge". Certainly there is no hydrological similarity between the two areas, so that exogenous factors cannot be held entirely responsible for the reversal in the east-west trend in certain characters.

Finally, mention must be made of *Etrumeus (Montalbania) albulina* Fowler, which is here placed in the synonymy of *D. acuta*. Bertin (1943) raised this form to generic status, apparently believing it to be intermediate between *Dussumieria* and *Etrumeus*, but nearer to the former than the latter. From Fowler's description and figure however, it is clear that this form cannot be referred to *Etrumeus*. Thus the almost

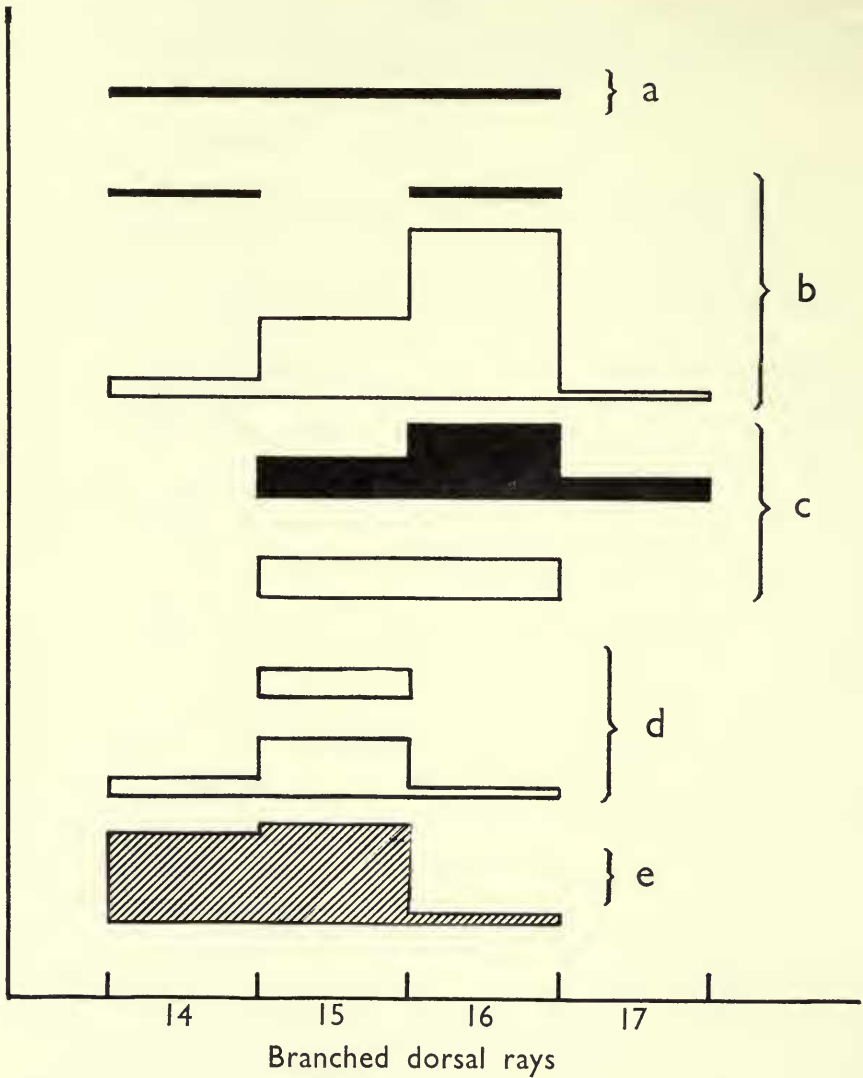


FIG. 4.

Dussumieria acuta. Dorsal finray count frequencies (branched rays only) in various populations, showing relative frequency in each group. Based on specimens (see list of Study Material) which have been labelled or recorded under the following names:

White *D. acuta*, Black *D. elopsoides*, Hatched *D. productissima*.

- a. Hong Kong, Foochow, Amoy.
- b. Siam, Amboina, Java, Madura, Sumatra, Borneo, Andamans, Singapore.
- c. Malabar, Calicut, Bombay, Madras, Coromandel.
- d. Gulf of Iran (upper), Gulf of Aden (lower).
- e. Haifa (eastern Mediterranean).

horizontal border of the operculum, and the shape of the sub-operculum are characteristic of *Dussumieria* (see Text-fig. 30a and b). In no case has a specimen of *Etrumeus* been found with 11 branched anal rays (7-8, Text-fig. 6) or 25 gillrakers (27-36, see Text-fig. 8) or a body depth exceeding 21% of standard length (Text-fig. 9), whereas these are all within the normal range of *Dussumieria*. Bertin (*loc. cit.*) stresses the rather advanced dorsal origin in his *Montalbiana albulina*, but this may be an error; it is not apparent in Fowler's figure. *M. albulina* should therefore be included in *D. acuta*.

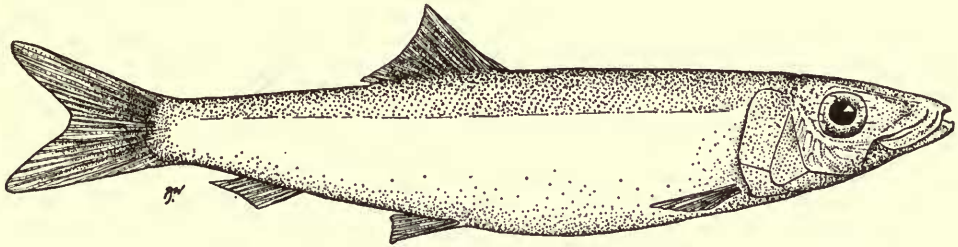


FIG. 5.

Dussumieria acuta (from a specimen 148 mm. standard length, Gulf of Aden. Scales omitted).

DESCRIPTION: Based on the holotypes of *D. elopsoides* (124 mm.) and *D. hasselti* (134 mm.); eight fishes, 112-117 mm. standard length from Calicut, S. Malabar; and six fishes, 121-148 mm. standard length from Shihr and Burum, Gulf of Aden. In addition, meristic counts and proportions of snout and body depth for all specimens listed under Study Material have been used (including sixteen syntypes of *D. acuta*).

In percentages of standard length: body depth 18.2-29.6 (Text-fig. 1), head length 25.7-29.4, snout length 7.4-10.6 (Text-fig. 2), eye diameter 5.3-6.3, post-orbital distance 9.2-10.1, inter-orbital width 5.6-5.8, maxilla length 8.4-9.3, lower jaw length 12.3-12.4, pectoral length 15.8-16.2, pelvic length 8.6-8.9, pre-dorsal distance 53.0-59.0, pre-pelvic distance 60.0-65.5, pre-anal distance 79.0-81.5 (84.5 in one instance).

Body moderately compressed, more or less rounded ventrally, its depth less or equal to head length. Snout pointed, larger than eye diameter. Lower jaw projects beyond upper. Maxilla shorter than snout, not quite reaching anterior eye border; two supra-maxillae, the posterior about half width of maxilla, not expanded posteriorly. Curved, conical teeth on premaxilla, maxilla (anterior two thirds) and dentary. Post-orbital about equal to snout length. Dorsal origin nearer to caudal base than to snout tip. Pelvic origin below middle or anterior half of dorsal fin, nearer to caudal base than to pectorals.

Dorsal iv 14-17 (Text-fig. 4), pectoral i 11-14, pelvic i 7, anal iii 11-13.

Gillrakers on lower part of first arch 18-34 (Text-fig. 3), longest raker 3.4-3.5% in standard length.

Scales in lateral series 42-56, transverse 11-12.

Vertebrae 53 (1 fish), 54 (4), 55 (1), 56 (4) (ten fishes from Singapore).

Branchiostegal rays 14-16.

SYNTYPES. Coast of Coromandel (India). Paris Museum, No. 3697, 3694 and 3217.

COLOUR IN ALCOHOL. Dorsal surfaces brown, sides yellow-brown or silver. Tip of snout strongly pigmented. Sometimes a dusky line from operculum to caudal base. Fins pale, but first pectoral ray and tips of caudal dusky.

MAXIMUM SIZE. 216 mm. (Day).

DISTRIBUTION. Red Sea, Madagascar to northern part of Indian Ocean, Indo-Malayan Archipelago and northwards to Hong Kong.

The presence of *D. acuta* in the Mediterranean was first noted by Lissner (1949), and later Ben-Tuvia (1953) stated that these round herrings were common along the shores of Israel and were caught by trawl or purse seine. It will be interesting to see whether the change in environment will produce any corresponding departure from the Red Sea form. Fowler & Steinitz (1955) placed Lissner's five fishes in *D. acuta* (rather than *D. productissima*, as Ben-Tuvia had done for his own specimens), but it is not clear from the text whether this determination was based solely on an approximate scale count, or whether gillrakers, etc. were also considered.

ETRUMEUS Bleeker

Etrumeus Bleeker, 1853, *Verh. Bat. Gen.*, 25 : 48 (Type : *Clupea micropus* Schlegel).

Perkinsia Eigenmann, 1891, *Amer. Nat. Philad.*, 25 : 153 (Type : *Perkinsia othonops* Eigenmann).

Halecula Jordan, 1925, *Stanford Univ. Publ. Biol. Sci.*, 4 : 41 (Type : *Halecula acuminata* Jordan).

Parahalecula Fowler, 1958, *Notul. Naturae, Philad.*, No. 310 : 5. (*Halecula* Jordan, 1925, pre-occupied).

For notes on this synonymy, see under species.

DESCRIPTION. Body elongate, almost round, scarcely compressed. Snout pointed, jaws equal or lower projecting slightly. A single supra-maxilla, about half length of maxilla, tapering uniformly to point anteriorly and about a quarter as deep as maxilla (Text-fig. 28). Maxilla thickened along whole dorsal edge and bearing a branched sensory canal. Small conical teeth along almost entire ventral edge of maxilla. Premaxilla toothed. A w-shaped scute surrounding base of pelvic fins and a smaller, triangular scute immediately behind this. Dorsal 17-22, anal 10-11, 26-39 gillrakers on lower part of first arch. Branchiostegal rays 14-15. Vertebrae 48-56. Anal well behind dorsal, whose origin is a little nearer to snout than to caudal base. Pelvic origin behind dorsal fin. Very small or no fleshy eminence at postero-ventral angle of gill opening (Text-fig. 30a). Ventral margin of operculum rises at steep angle ; exposed portion of suboperculum triangular.

There are five principal populations of *Etrumeus* in temperate seas : North American Atlantic and North American Pacific coasts, the coasts of Japan, of South Africa and of southern Australia. In addition there appears to be a population in the Red Sea, members of which have now colonized parts of the eastern Mediterranean ; another population in the region of the Galapagos Islands ; and a population near Hawaii. This distribution will be discussed later.

Etrumeus teres (DeKay)

(Text-fig. II)

- Alosa teres* De Kay, 1842, *Nat. Hist. New York*, pt. 4—*Fishes*: 262, pl. 40, fig. 128 (type locality New York region).
- Clupea micropus* Schlegel, 1846, *Faun. Japon. Poiss.*, pts. 10–14: 236, pl. 107, fig. 2 (type locality, southeast coast of Japan).
- Etrumeus micropus* Bleeker, 1853, *Verh. Bat. Gen.*, 25 : 48 ; *Idem, op. cit.*, 26 : 5 ; Günther, 1868, *Cat. Fish. Brit. Mus.*, 7 : 467 ; Jordan and Evermann, 1905, *Bull. U.S. Fish Comm.*, 23 (1) : 58 ; Jordan and Herre, 1906, *Proc. U.S. nat. Mus.*, 31 : 628 ; Gilchrist and Thompson, 1917, *Ann. Durban Mus.*, 1 (4) : 295 ; Barnard, 1925, *Ann. S. Afr. Mus.*, 21 (1) : 108 ; Fowler, 1928, *Mem. Bernice P. Bishop Mus.*, 10 : 29 ; *Idem*, 1934, *Proc. Acad. nat. Sci. Philad.*, 86 : 410 ; *Idem*, 1941, *Bull. U.S. nat. Mus.*, No. 100: 576 ; Chapman, 1948, *Proc. Calif. Acad. Sci.*, 26 (2) : 25, figs. 1–3, 7–10, 12–13, 15, 17–18 ; Svetovidov, 1952, *Tabl. Anal. Faune U.R.S.S. N.S. No. 48*, 2 (1) : 102 ; Smith, 1955, *Ann. Mag. nat. Hist.*, (12) 8 : 307 ; Fowler and Steinitz, 1956, *Bull. Res. Council. Israel*, 5 B (3–4) : 261 ; Matsubara and Iwai, 1959, *Fishes. biol. Res. Jap. Antarct. res. Exped.*, No. 9.
- Harengula teres* Girard, 1859, *Proc. Acad. nat. Sci. Philad.*, 2 : 158.
- Dussumieria teres* Brevoort, 1856, in Perry, *Narrative of the U.S. Exped. to Japan : Washington*, 2 : 279 ; Gill, 1861, *Proc. Acad. nat. Sci. Philad.*, 12 : 21.
- Etrumeus teres* Günther, 1868, *Cat. Fish. Brit. Mus.*, 7 : 467 ; Jordan and Gilbert, 1882, *Bull. U.S. nat. Mus. Wash.*, 16 : 263.
- Etrumeus jacksoniensis* Macleay, 1879, *Proc. Linn. Soc. N.S.W.*, 3 : 36, pl. 4, fig. 1 ; Ogilby, 1886, *Cat. Fishes New South Wales* : 56 ; McCulloch, 1914, *Rec. W. Aust. Mus.*, 1 : 211, pl. 29 ; Waite, 1921, *Rec. S. Aust. Mus.*, 2 (1) : 36, fig. 51 ; Blackburn, 1941, *Bull. Coun. sci. industr. Res. Aust.*, No. 138 : 64.
- Etrumeus sadina* Jordan and Evermann, 1896, *Bull. U.S. nat. Mus. Wash.*, No. 47 : 420 ; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 9, fig. 4.
- Etrumeus acuminatus* Gilbert, 1891, *Proc. U.S. nat. Mus. Wash.*, 13 : 56.
- Jenkinsia acuminata* Jordan and Evermann, 1896, *Bull. U.S. nat. Mus. Wash.*, No. 47 : 419.
- Perkinsia othonops* Eigenmann, 1891, *Amer. Nat. Philad.*, 25 : 153 ; Jordan and Evermann, 1896, *Bull. U.S. nat. Mus. Wash.*, No. 47 : 420 ; Breder, 1928, *Bull. Bingham. oceanogr. Coll. N.Y.*, 2 (2) : 5, figs. 2–4 ; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 13.
- Halecula acuminata* Jordan, 1925, *Stanford Univ. Publ. Biol. Sci.*, 4 : 41 ; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 24.
- Parahalecula acuminata* Fowler, 1958, *Notul. Naturae, Philad.*, No. 310 : 5.
- Stolephorus delicatulus* Seale, 1940, *Reps. Allan Hancock Pacific Exped.* 1932–38, 9 : 3.
- Etrumeus othonops* Phillips, 1961, *Calif. Fish Game*, 37 : 512.

Notes on Synonymy

Bertin (1943) gave *Clupea sadina* Mitchill 1814 as the earliest name for this species, but in fact he cited a paper published in 1815 ; it was first used by Mitchill in 1814 in a short paper entitled " Report in part of Samuel L. Mitchill, M.D., Professor of Natural History, &c., on the fishes of New York " (pp. i–x, 1–30). Described by Bashford Dean as " one of the rarest of American contributions to ichthyology ", it was reprinted in 1898 by Theodore Gill. In his first description of *Clupea sadina*, Mitchill follows a colour description with " scales fall off very readily ; body has a taper, slender, and very delicate appearance. Abdomen not at all serrated, but quite smooth . . . ". Although this description fits a species of *Etrumeus*, Mitchill enlarged on it in a paper read within the space of a year (8th December,

1814) and published in 1815, and while this second description of *Clupea sadina* does not contradict the first in any way, it adds details which cannot be reconciled with a species of *Etrumeus*. Thus he places *Clupea sadina*, the "New York Shadine", under a subheading "Bellies carinated without serrae" and says that "On account of the even connection of the false ribs, the belly is not at all serrated, but quite smooth." More important are the discrepancies in meristic counts, and especially that for branchiostegal rays; he counts 7 rays, as against 14 or 15 in *Etrumeus*. He records 9 pelvic rays (normally 8 in *Etrumeus*), and 15 anal rays (never more than 11 counting the minute first, unbranched ray). He also states that the mouth is wide and toothless and mentions "a small smutty spot behind the gill-cover". Finally, he states that there is "A semitransparent space in front of the eyes from side to side."

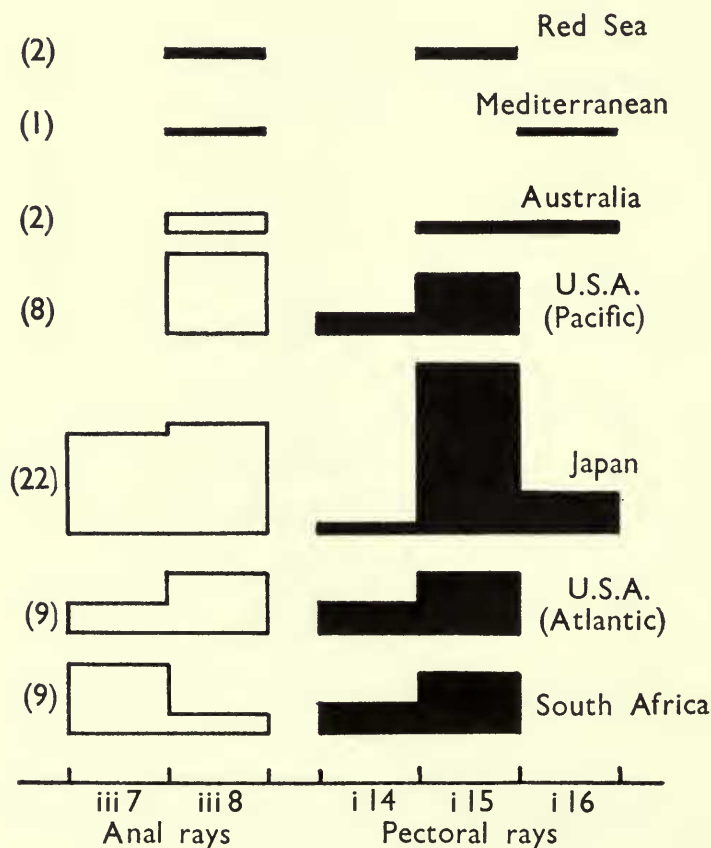


FIG. 6.

Anal (white) and pectoral (black) finray count frequencies in seven different populations of *Etrumeus*. Branched rays only. Number in sample placed in parentheses.

Elsewhere (Whitehead, in press) I have dealt more fully with this problem and have shown that *Clupea sadina* Mitchill need not become a *nomen dubium*, because the second description strongly suggests that Mitchill was describing a species of *Sardinella* and nothing in the first description contradicts this. There is also good reason to believe that both descriptions were based on the same specimen or specimens. DeKay's description of *Etrumeus teres* on the other hand leaves no doubt that it is a species of *Etrumeus*.

Perkinsia othonops (American Pacific) is placed in the synonymy because the corselet of scales surrounding the pectoral fin base, a supposed generic character, is in fact found in large specimens of *Etrumeus*.

Etrumeus (*Montalbania*) *albulina* Fowler has here been synonymized with *Dussumieria acuta* (see p. 312). The advanced pelvic base and the shape of the suboperculum exclude it from *Etrumeus*, and numbers of gillrakers and anal rays are those of *Dussumieria*.

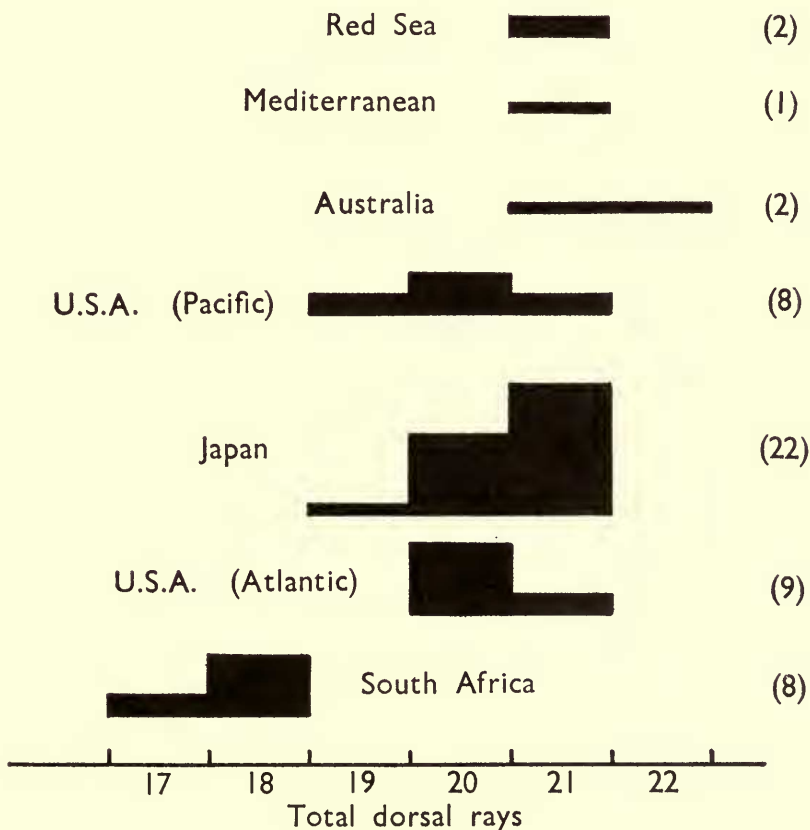


FIG. 7.

Dorsal finray frequencies (branched and unbranched combined) in specimens of *Etrumeus* from seven different populations. Number in sample placed in parentheses.

Halecula acuminata is placed in the synonymy since it was based on juvenile specimens of *E. acuminatus* (Hubbs, *in litt.*).

(a) *Meristic Differences*

Variations in anal finray counts (Text-fig. 6) are small (7 or 8 branched rays and always 3 simple rays, the first very small and easily missed). Pectoral finray numbers also vary little, and in my material only the Australian, Mediterranean, and Japanese specimens occasionally have 16 branched rays, the remainder 14 or 15 (Text-fig. 6). Differences in dorsal rays are more marked. Normally there are 4 simple rays (occasionally 5), the first very small, but sometimes the last of the simple rays is branched, although recognizable by its length. In dorsal ray numbers one population, that of South Africa, can be separated immediately because of its low count, but the remainder overlap and cannot be separated from each other (Text-fig. 7). Pelvic counts are always 7.

In numbers of gillrakers there is also some variation. The Australian and American Pacific specimens have low counts, the South African are intermediate, and the Japanese, Mediterranean and American Atlantic have high counts (Text-fig. 8.) Again there is considerable overlap between the regions.

(b) *Morphometric Differences*

The most obvious proportional difference found between the samples is that of body depth (Text-fig. 9). Again the Japanese and the American Atlantic specimens resemble each other, and are more slender than the rest. But although insufficient numbers have been measured, Text-fig. 10 strongly suggests that body depth shows positive allometry with standard length. Thus the Japanese form may well be deeper-bodied in larger fishes, as is suggested by the two large Japanese specimens examined (126 and 136 mm.). Certainly the American Atlantic and the American Pacific specimens can be distinguished on this character, but the remainder, and probably also the Japanese specimens, are very similar.

A second morphometric difference is found in the positions of the dorsal, pelvic and anal fins. In the American Pacific specimens these fins are all set slightly further from the snout than in the fishes from the American Atlantic (see Table II). The remaining differences are small and would probably disappear in larger samples.

If the American Atlantic population is taken as the starting point, then the American Pacific fishes can be distinguished by their deeper bodies and fewer gillrakers (27-33; cf. 34-36). The South African population can be separated from all others by its lower dorsal count (17-18 total rays; cf. 19-22). The Japanese population, however, cannot, on the basis of my material, be adequately separated from the American Atlantic population, and the two Australian specimens are in all characters within the range of the American Pacific population.

The distribution of *Etrumeus* is difficult to explain in zoogeographical terms. In some ways it resembles that of *Sardinops* in the Southern Hemisphere, but so far no specimens have been recorded from South American localities; the Galapagos population may represent a southern American form, pushed northwards by the

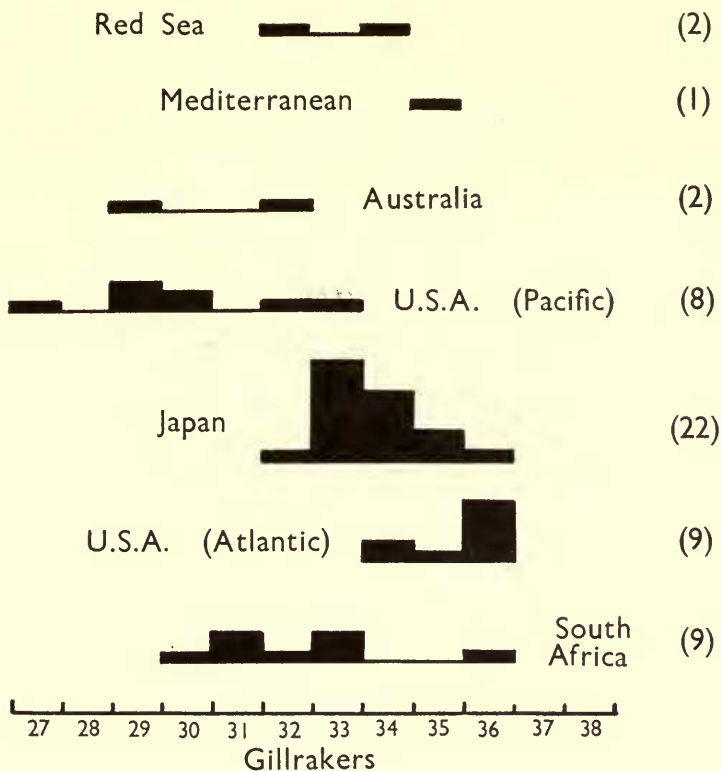


FIG. 8.

Range and frequency in numbers of gillrakers in seven different populations of *Etrumeus*. Number in sample placed in parentheses.

cold Peruvian current. I have not been able to examine specimens from the Galapagos Islands, and cannot relate them to any of the other forms examined here. Possibly the Hawaiian population represents a link between the former and the Japanese population; Jordan & Evermann (1905) stated that their Hawaiian specimens were indistinguishable from the Japanese form.

The isolated Red Sea population is even more difficult to explain. The two Eilat specimens, and the single fish from the eastern Mediterranean, certainly do not belong to the South African population, their nearest neighbours; they appear to be most closely related to the Japanese fishes. This seems to provide further evidence that meristic characters may coincide in populations which are not closely related geographically. It is certainly strange that a species which elsewhere appears to be limited to between the (approximately) 12° and 20° C. isotherms should appear in the Red Sea, and equally remarkable that it should, under these conditions, show so little divergence from other populations.

The isolation of each of these populations is probably complete and it would be expected that each would have diverged at least slightly. It is possible therefore

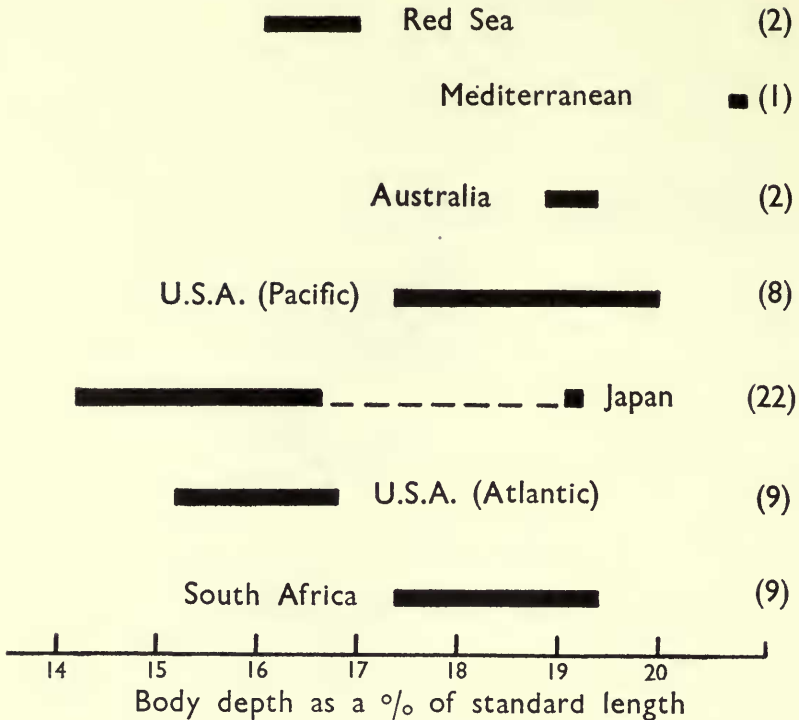


FIG. 9.

Range of variation in body depth (expressed as a percentage of standard length) in seven populations of *Etrumeus*. Number in sample placed in parentheses.

that, since variation is principally restricted to a few meristic characters, similarities have occurred between otherwise well isolated populations purely as a result of parallel evolution. Thus the similarities between the two population pairs cited above may be to a large extent coincidental. This in some ways resembles the case of *Dussumieria* discussed earlier, where morphological similarities contradict probable geographical relationships. But whereas in *Dussumieria* there is a series of both geographical and morphological intermediates, in *Etrumeus* the populations are well isolated.

The genus *Etrumeus* is at present under revision by Prof. Carl L. Hubbs and Mr. Robert Wisner, and I have therefore made no attempt to interpret the present data. I have here followed the example of the last reviewer (Bertin) and have placed all the forms in a single species, rather than create new taxa on the basis of my material alone.

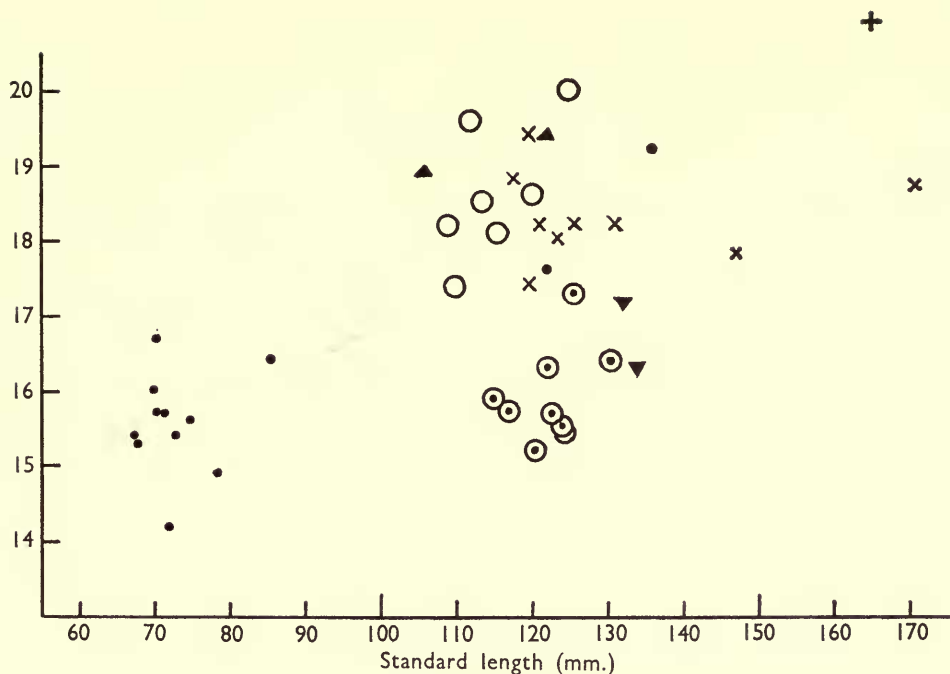


FIG. 10.

Body depth expressed as a percentage of standard length (ordinate) plotted against standard length (abscissa) for specimens of *Etrumeus* from seven different populations.

- Japan and Hong Kong.
- American Atlantic.
- American Pacific.
- × South Africa.
- ▲ Australia.
- + Mediterranean.
- ▼ Eilat (Red Sea).

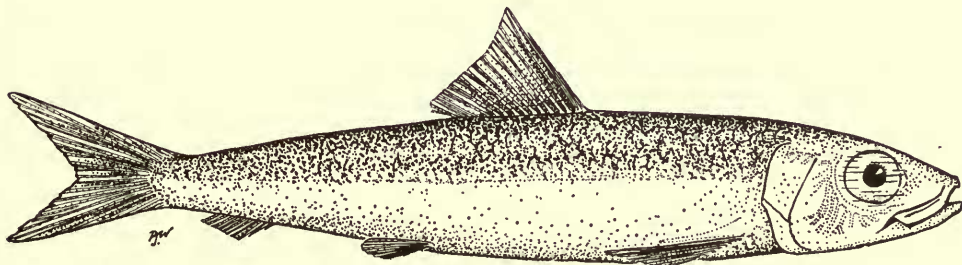


FIG. 11.

Etrumeus teres. From a specimen 150 mm. S.L., ex Woods Hole, Mass. Scales omitted.

Etrumeus teres (DeKay)

(Text-fig. 11)

DESCRIPTION. Based on twelve Japanese specimens (67.5–85.5 mm. standard length); nine fishes from South Africa (117.5–166.0 mm.); two fishes from Australia (105.5–122.0 mm.); nine American Atlantic fishes (115.0–130.2 mm.); seven American Pacific fishes (110.0–125.0 mm.); one Mediterranean fish (165.0 mm.); the type of *Perkinsia othonops* (265.0 mm.); and two Red Sea fishes (133.2 and 134.0 mm.). Specimens listed in Study Material (p. 374).

In percentages of standard length: body depth 14.6–21.2 (Text-figs. 9 and 10), head length 23.2–29.2, snout length 6.9–8.8, eye diameter 7.0–9.8, post-orbital distance 7.9–10.6, maxilla length 8.7–9.7, pectoral length 14.7–17.4, pelvic length 7.6–10.2, pre-dorsal distance 44.0–48.4 (also 49.4 and 50.0), pre-pelvic distance 62.0–70.0, pre-anal distance 82.0–88.0.

Body rounded, little compressed, its depth less than head length. Snout pointed, more or less equal to eye diameter. Lower jaw usually projects beyond upper. Maxilla longer than snout, reaching vertical with anterior border of pupil. A single supra-maxilla, not expanded posteriorly. Conical pointed teeth on pre-maxilla, maxilla and dentary. Post-orbital exceeds snout length. Dorsal origin nearer to snout than to caudal base. Pelvic origin behind dorsal base, nearer to caudal base than to pectorals. Anal origin further from that of pelvics than from anal base.

Dorsal iii–v, usually iv, 14–18, pectoral i 14–16, pelvic i 7, anal iii 7–8 (Text-figs. 6 and 7).

Gillrakers on lower part of first arch 27–36 (Text-fig. 8).

Scales in lateral series 50–56, transverse 13–14 (after Bertin).

Vertebrae 48–56 (Hubbs, *in. litt.*).

Branchiostegal rays 14–15.

COLOUR IN ALCOHOL. Dorsal surfaces light or dark brown, sides silver, the two meeting at a fairly well-defined midlateral line. Tip of snout strongly pigmented. Fins hyaline.

MAXIMUM SIZE. At least 260 mm.

DISTRIBUTION. Seven probably discrete populations: American Atlantic coast (Cape Cod to Gulf of Mexico); American Pacific coast (Gulf of California and north of Los Angeles area—see Phillips, 1951); eastern coast of South Africa (Natal, Zululand); southern coasts of Australia (New South Wales, Victoria, St. Vincent's Gulf, and Albany in Western Australia—see Blackburn, 1941); coasts of Japan (Nagasaki, Wakanoura, Misaki, Aomora, Tokyo); Galapagos Islands (see Seale, 1940); and the eastern Mediterranean (? migrants from the Red Sea), and Red Sea (Eilat) (Fowler & Steinitz, 1956).

Subfamily SPRATELLOIDINAE

Diagnosis

Dussumieriid fishes with 6–7 branchiostegal rays, the first three to five attached to the cerato-hyal, which is excavated ventrally (Text-fig. 29). Premaxilla sometimes toothed; maxilla with a broadly expanded posterior supra-maxilla, often as

deep as the maxilla at its widest point ; an anterior supra-maxilla sometimes present. Abdominal scutes represented by either a w-shaped plate surrounding pelvic base (*Spratelloides*, *Jenkinsia*) or a horse-shoe-shaped plate with ascending spines (tribe Ehiravini) (Text-fig. 26) ; exceptionally a series of 6-9 such plates between pectoral and pelvic fins (*Gilchristella aestuarius*), all with ascending spines but never keeled ventrally (Text-fig. 27).

Posterior fontanelles present, but decreasing in extent with size of fish, and in some species (*Ehirava malabaricus*) absent entirely in large fishes. Posterior margin of pre-operculum more or less vertical. Posterior margin of operculum excavated, ventral margin horizontal or slightly inclined. A small, fleshy eminence at postero-ventral angle of gill opening, prominent in some genera. Lower edge of inter-operculum exposed in lateral view. Sub-operculum rectangular.

Dorsal rays 11-16 ; anal 9-20. Transverse scales on body 7-10. Vertebrae 30-46.

Adult size 50-110 mm.

Five genera are recognized here, *Ehirava*, *Gilchristella*, *Sauvagella*, *Spratelloides* and *Jenkinsia*. The first three differ so much from the other two that I have thought it advisable to split the *Spratelloidinae* into two tribes.

- A. Pelvic scute with an ascending, pointed spine ; a single supra-maxilla ; premaxilla toothed ; pelvic fins under anterior half of dorsal or in advance of first dorsal ray ; fleshy eminence at postero-ventral angle of gill opening little developed ; posterior fontanelles broadly divided anteriorly by wedge of bone Ehiravini
- B. Pelvic scute w-shaped as in *Dussumieriinae*, without ascending spine ; one or two supra-maxillae ; pre-maxilla normally edentulous ; pelvic fins under middle, or second half of dorsal ; fleshy eminence at postero-ventral angle of gill opening usually well developed ; posterior fontanelles narrowly divided anteriorly in most species *Spratelloidini*

Notes on Tribe Ehiravini

In his review of the round herrings, Bertin (1943) recognized two genera from southern Africa and Madagascar which differed from *Spratelloides* in having the pelvic base in advance of the dorsal origin, not under the dorsal. The first, *Gilchristella* Fowler, contained *G. aestuarius* Fowler, and also Sauvage's *Spratelloides madagascariensis*, into which Bertin had earlier placed his two subspecies of *Sauvagella madagascariensis* (*longianalis* and *breviodorsalis*, Bertin, 1940). The second genus, the monotypic *Sauvagella* Bertin, was further distinguished by possession of a split anal, the last two anal rays being distinctly separated from the rest of the fin (confirmed in alizarin preparations, Bertin, 1943). Bertin (1943) felt it possible that *Sauvagella bianalis* might be merely a mutant form of *Gilchristella madagascariensis*, the two differing little except in the form of the anal fin.

Later, Angel, Bertin & Guibé (1946) proposed the *nomen novum* *Spratellomorpha* to replace *Sauvagella* of Bertin, 1943 (not of Bertin, 1940, which was now included in *Gilchristella*). This is discussed under the synonymy of *Sauvagella*.

These three South African and Malagasi species could be placed in a single genus but for the discovery that *G. aestuarius*, alone of the whole *Dussumieriidae*, possesses ventral scutes (Whitehead, 1962a). While the split anal fin of *S. bianalis* could

perhaps be considered a chance mutation, the possession of abdominal scutes cannot be lightly dismissed in view of the importance of scutes in the phylogeny of the group as a whole. I have found these scutes in two specimens of *G. aestuarius* from Durban, and also in seven further specimens from various South African localities (see under species description).

Although *G. aestuarius* is thus unique, and shows supra-limital variation (in the sense of Myers, 1960) in this one character, otherwise it closely resembles its non-scuted geographical relatives. Therefore, I do not think *G. aestuarius* should be separated from the South African species at higher than generic level. Nor does it seem that *G. aestuarius* is the sole representative of an ancient line deriving from earlier clupeids. It belongs to a group in which at least one other clupeid character is also found, the divided anal fin of *S. bianalis* (i.e. in the clupeid genus *Corica*). It would appear therefore that the Ehiravini share certain potential genetic patterns characteristic of the clupeids, but that these have shown only a partial development in some species but not at all in others. The Ehiravini may thus be derived from forms which lay close to the split between the round herrings and the true herrings.

The South African group, although all more closely allied to *Spratelloides* than to any other dussumierid genus, differ from the latter in six important characters.

- i. Pelvic scute with lateral spines (Text-fig. 26).
- ii. A single supra-maxilla.
- iii. Advanced pelvics.
- iv. Fleshy eminence on postero-ventral angle of cleithrum little developed.
- v. A toothed premaxilla.
- vi. Posterior fontanelles broadly divided by wedge of bone anteriorly, in front of which is a triangular depression (Text-fig. 32a).

These characters are also shared by *Spratelloides malabaricus* from the Malabar coast of India, which should therefore be included with the South African species. *S. malabaricus* is at the same time identical to *Ehirava fluviatilis* Deraniyagala. Deraniyagala (1929) proposed a new family, the Ehiravidae, on the strength of this one species, distinguishing it from the Dussumeriidae by the possession of only one supra-maxilla; he considered *Ehirava* intermediate between *Spratelloides* and *Dussumieria*. Since its description, *Ehirava* has been mentioned only once (Monroe, 1955). Since *S. malabaricus* cannot be retained in *Spratelloides*, the genus *Ehirava* is available for it. At the same time I have been unable to find any but very small differences between *S. malabaricus* and the Malagasi species *Gilchristella madagasca-riensis*. The latter should therefore be placed in *Ehirava* also, but it can be separated from the Indian form at species level, at least on the available material; the greatest difference is in scale numbers, but this may well prove dependent on locality when a larger sample is examined.

The tribe Ehiravini thus contains three genera and five species.

Tribe EHIRAVINI

Diagnosis

Members of the subfamily Spratelloidinae which possess only a single supra-maxilla and a toothed premaxilla. Eminence on postero-ventral angle of cleithrum

poorly developed and similar to that found in *Etrumeus* or *Dussumieria*. Pelvic scute horse-shoe-shaped, with pointed, ascending spines. Pelvic origin just behind, below, or just in front of dorsal origin. Posterior fontanelles broadly separated at anterior end by wedge of bone (frontals), in front of which is shallow triangular depression.

DISTRIBUTION. Eastern coast of South Africa, coast of Madagascar, and the western coast of India.

KEY TO GENERA

- A. Additional scutes absent between pectoral and pelvic fins
 i. Anal fin entire, last two rays not separate *Ehirava*
 ii. Last two anal rays separate from rest of fin *Sauvagella*
 B. Six to nine abdominal scutes between pectoral and pelvic fins ; anal fin entire
Gilchristella

Ehirava Deraniyagala

Ehirava Deraniyagala, 1929, *Spolia Zeylan*, 15 : 34, pl. 14 (type *E. fluviatilis* Deraniyagala = *Spratelloides malabaricus* Day).

Sauvagella Bertin (*part.*), 1940 (*Sauvagella madagascariensis*, i.e. *S. m. longianalis* and *S. m. brevidorsalis*, but non *S. m. bianalis*), *Bull. Mus. Hist. nat. Paris*, (2) 12 : 300 (type *Spratelloides madagascariensis* Sauvage *ex* Madagascar) ;

DESCRIPTION. Body elongate, more compressed than in *Spratelloides*, snout pointed, lower jaw projecting. Posterior supra-maxilla present, as deep as maxilla, anterior absent ; maxilla toothed, with anteriorly indented lower border (Text-fig. 28f). Premaxilla toothed. Small fleshy eminence on postero-ventral angle of cleithrum (cleithral flap), not more prominent than in *Dussumieria* (Text-fig. 30b). Posterior border of operculum slightly indented, but not to the extent found in *Spratelloides* ; junction between operculum and sub-operculum not horizontal (as in *Spratelloides*, Text-fig. 30c), but inclined (as in *Dussumieria*, Text-fig. 30b).

A single (pelvic) scute with ascending spines (Text-fig. 26). Pelvic origin just behind or in front of dorsal origin. Branchiostegal rays 6. Scales not strongly deciduous.

Two species recognized, but more material may merge the differences shown here.

- a. Snout equal to or smaller than eye ; pelvic origin below first dorsal or slightly behind ; scales 35-38 *E. malabaricus*
 b. Snout a little greater than eye ; pelvic origin in front of first dorsal ray ; scales 43-48
E. madagascariensis

Ehirava malabaricus (Day)

(Text-fig. 12)

Spratelloides malabaricus Day, 1873, *Proc. zool. Soc. Lond.*, 240 ; *Idem*, 1878, *The Fishes of India* : 648, pl. 161, fig. 5 (Type locality : Malabar, India) ; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 17.

Ehirava fluviatilis Deraniyagala, 1929, *Spolia Zeylan*, 15 : 35, pl. 14 (Type locality : Ceylon) ; Monroe, 1955, *Marine and freshwater fish. Ceylon* : 28.

Note on Synonymy

The five specimens of *S. malabaricus* in the Museum are identical to the type and paratypes of *E. fluviatilis* in both meristic characters and proportional measurements.

Pellonulops Smith, purported to be based on *Spratelloides madagascariensis* Sauvage, is not placed in the synonymy because the genus is clearly based in fact on a clupeid, not a dussumieriid. Thus Smith (1949) described both pre- and post-pelvic scutes, and the presence of the latter eliminates the chance that his specimens were *Gilchristella aestuarius*.

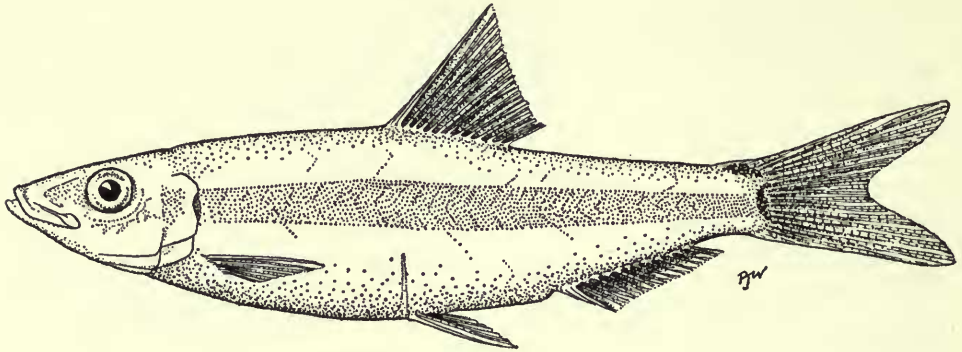


FIG. 12.

Ehirava malabaricus. From a specimen 58 mm. standard length, Canara. Scales omitted.

DESCRIPTION. Based on the type and seven of the larger paratypes of *E. fluviatilis* from Kehelvatta, Ceylon (35.1–48.6 mm. standard length) and five specimens of *S. malabaricus* from Malabar (40.5–56.2 mm.).

In percentages of standard length: body depth 15.4–22.4, head length 22.4–26.7, snout length (5.7 one fish) 6.6–8.2, eye diameter 6.8–8.5, post-orbital distance 7.9–9.8, maxilla length 8.7–9.9, pectoral length 13.9–16.3, pelvic length 11.3–12.5, pre-dorsal distance 50.0–52.2, pre-pelvic distance 49.1–52.5 (53.4), pre-anal distance 72.0–76.5 (80.0).

Body fairly strongly compressed; especially in larger fishes, depth less than head length. Snout pointed, equal or a little smaller than eye. Jaws unequal, lower projecting. Maxilla longer than snout, almost reaching vertical with anterior rim of pupil, with excavated lower edge anteriorly (Text-fig. 28f). One supra-maxilla only, expanded posteriorly as in *Spratelloides*. Maxilla with a single row of conical teeth along lower edge. Pre-maxilla also with conical pointed teeth in a single series.

Dorsal origin mid-way between snout and caudal base. Pelvic origin below first dorsal ray or just behind, a little nearer anal origin than to pectoral base. Anal origin almost equidistant between that of pelvics and caudal base.

Dorsal iii 11–12, pectoral i 10–12, pelvic i 7, anal ii–iii 12–15 (total 14–18).

Scales in lateral series 35–38, 9 transverse.

Branchiostegal rays 6.

HOLOTYPE. Kehelvatta, Ceylon. B.M. (N.H.) 1929.7.1.1.

COLOUR IN ALCOHOL. A uniform light brown with in some specimens a faint silvery midlateral stripe not quite as broad as eye. A short oblique line of dark pigment on lower half of caudal base and another, almost horizontal, line along upper edge of caudal base. In smaller specimens, bases of dorsal and anal fins pigmented.

SIZE. Largest specimen examined 56.2 mm. standard length.

ALLOMETRY. Apart from the eye (negative) there is no evidence from the specimens measured that any other body part shows allometry with standard length.

DISTRIBUTION. Ceylon and Malabar coast of India.

Ehirava madagascariensis (Sauvage)

Spratelloides madagascariensis Sauvage, 1883, *Bull. Soc. philom., Paris* (7) 7 : 160 ; *Idem*, 1891, *Hist. Nat. Madagascar, Poiss.* : 496, pl. 48, fig. 2.

Sauvagella madagascariensis longianalis and *S. m. brevidorsalis* Bertin, 1940, *Bull. Mus. Hist. nat., Paris* (2) 12 : 300.

Gilchristella madagascariensis Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 21 ; Angel, Bertin and Guibé, 1946, *Bull. Mus. Hist. nat., Paris* (2) 18 : 473-4.

DESCRIPTION. Based on a specimen, 40.0 mm. standard length *ex* Madagascar (paratype of *Spratelloides madagascariensis*) ; and eleven other fishes, 41.0-52.5 mm. from Buffalo river, Cape Province (S. Africa).

In percentages of standard length : body depth 16.0-22.8, head length 25.0-28.2, snout length 7.3-7.8, eye diameter 7.3-8.5, post-orbital (8.2) 10.6-11.9, maxilla length 8.7-9.0, pre-dorsal distance 50.3-56.0, pre-pelvic distance 50.0-54.9, pre-anal distance 66.8-72.5.

Body compressed, depth less than head length. Snout pointed, usually a little greater than eye diameter. Jaws subequal, lower projecting. Maxilla longer than snout, reaching vertical through anterior border of pupil. Maxilla shape as in *Gilchristella*. A single supra-maxilla.

Dorsal origin slightly nearer caudal base than snout. Pelvic origin in front of dorsal, about equidistant between snout and caudal base, nearer anal base than pectoral base. Anal nearer pelvic base than caudal base.

Dorsal iv 10-11, pectoral i 9, pelvic i 7, anal iii 14-17, gillrakers 40-56 (lower numbers mainly in the smaller specimens and vice versa).

Scales in lateral series 43-48, transverse 8.

TYPE. Madagascar. Paris Museum No. 3794.

COLOUR IN ALCOHOL. Uniform grey-brown. A faint silvery mid-lateral stripe. Two pigmented lines at base of caudal, as in *Sauvagella bianalis*.

SIZE. 60 mm. (Bertin, 1943).

DISTRIBUTION. Madagascar and Buffalo river, King Williamstown (Cape Province).

GILCHRISTELLA Fowler

Gilchristella Fowler, 1935, *Proc. Acad. nat. Sci. Philad.*, 87 : 365, fig. 4 (Genotype : *Spratelloides aestuarius* Gilchrist from Swartkops river).

DESCRIPTION. Body compressed, more so than in *Ehirava*, its depth almost equal to head length. Snout pointed, lower jaw projecting. Anterior supra-maxilla

absent; posterior supra-maxilla expanded posteriorly to almost depth of maxilla, anterior shaft-like. Maxilla toothed along lower edge; pre-maxilla toothed. Small fleshy eminence on postero-ventral angle of cleithrum scarcely as developed even as in *Ehirava* (i.e. nearer to the *Etrumeus* than to the *Dussumieria* condition). Posterior border of operculum slightly indented, as in *Ehirava*; junction between operculum and suboperculum not horizontal but oblique, more steeply inclined than in *Ehirava* and thus resembling that of *Etrumeus* (Text-fig. 30a).

Pelvic scute with thin, pointed ascending arms. Between pectoral and pelvic bases, a series of six to nine similar scutes (Text-fig. 27).

Dorsal origin a little further from snout than caudal base; pelvic origin below first dorsal ray or in front, equidistant between snout and caudal base. Branchiostegal rays 6-7. Scales moderately deciduous.

A single species recognized here.

Gilchristella aestuarius (Gilchrist)

(Text-fig. 13)

Spratelloides aestuarius Gilchrist, 1914, *Mar. Biol. Rep. S. Afr.*, No. 1: 55 (Type material from: Swartkops river, Port Elizabeth); Regan, 1916, *Ann. Durban Mus.*, 1: 167; Gilchrist and Thompson, 1917, *Ann. Durban Mus.*, 1 (pt. 4): 296; Barnard, 1925, *Ann. S. Afr. Mus.*, 21 (pt. 1): 109.

Gilchristella aestuarius Fowler, 1935, *Proc. Acad. nat. Sci. Philad.*, 87: 365, fig. 4; Bertin, 1943 *Bull. Inst. océanogr. Monaco*, No. 853: 21.

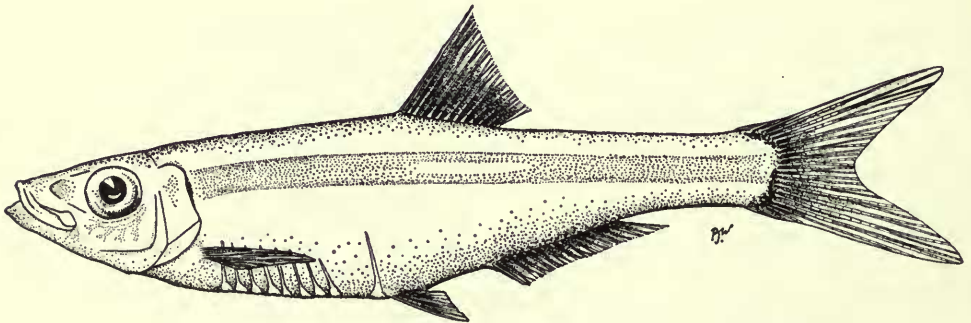


FIG. 13.

Gilchristella aestuarius. From a specimen 60 mm. standard length, Durban. Scales omitted.

DESCRIPTION. Based on two fishes 51.0 and 53.0 mm. standard length from Durban, and seven fishes 35.9-51.5 mm. from other South African localities (East London, Knysa, St. Lucia, Keimouth, Milnerton and the type locality Swartkops river—on loan from Professor J. L. B. Smith).

In percentages of standard length: body depth (17.5 one fish) 19.2-24.5, head length 25.2-27.5, snout length 6.3-7.5 (8.1), eye diameter 6.8-8.1, post-orbital 8.1-9.5, maxilla length 10.2, pectoral length 14.2, pelvic length 11.7, pre-dorsal distance 52.5-57.7, pre-pelvic distance 50.0-54.4, pre-anal distance 66.7-70.0.

Body strongly compressed, especially in larger fishes, its depth just less than head length. Snout pointed, usually a little less than eye diameter. Jaws sub-equal, lower projecting slightly. Maxilla longer than snout, reaching vertical through anterior border of pupil, anterior excavation not as pronounced as in *Ehirava* (see Text-fig. 28f). One supra-maxilla only, shape and proportions as in *Ehirava*. Maxilla and premaxilla with single row of conical teeth.

Dorsal origin a little further from snout than caudal base. Pelvic origin below first dorsal ray or more usually in front, equidistant between snout and caudal base or a little nearer the latter, and nearer to anal than to pectoral base. Anal origin nearer that of pelvics than to caudal base. Six to nine pre-pelvic scutes.

Dorsal iii 11-12, pectoral i 10-11, pelvic i 7, anal iii 17 (total 20).

Scales in lateral series 40, transverse 9-10 (Bertin, 1943).

Branchiostegal rays 6-7, gillrakers on lower part of first arch 39-45; inner series on first two arches absent, and lower part of inner series on third arch also absent.

TYPES. Swartkops river, near Port Elizabeth. South African Museum. (Nos. 10822-4).

COLOUR IN ALCOHOL. A uniform light brown with a faint midlateral silvery band. Individual bases of dorsal and anal rays pigmented (black). Two short dark pigment lines at base of anal, one almost horizontal along upper border, the other oblique on lower border.

SIZE. Largest fish examined 53.5 mm. Barnard (1925) gives maximum size 70 mm.

ALLOMETRY. No indication except with eye measurement (negative allometry with standard length).

DISTRIBUTION. Estuaries and lagoons of the eastern coast of South Africa.

SAUVAGELLA Bertin

Sauvagella (*part.*) Bertin, 1940 (*Sauvagella madagascariensis bianalis* only), *Bull. Mus. Hist. nat.*

Paris (2) 12: 300; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 22.

Spratellomorpha Bertin, 1946, in Angel, Bertin and Guibé, 1946, *Bull. Mus. Hist. nat. Paris* (2)

18: 473-4 (type *Sauvagella madagascariensis bianalis* Bertin *ex* Madagascar).

Note on Synonymy

Spratellomorpha was proposed (Angel, Bertin & Guibé, 1946) as a *nomen novum* in order to overcome the confusion arising from the splitting of *Spratelloides madagascariensis* into three subspecies (Bertin, 1940), first placed all together in the genus *Sauvagella* and later separated, two being united and placed in *Gilchristella*. Because of this the meaning of *Sauvagella* became obscured. However, as a result of placing *G. madagascariensis* (in the sense of Bertin, 1943) in *Ehirava*, there is no reason why *Sauvagella* cannot again be applied to *bianalis*; thus *Sauvagella* Bertin, 1940 and *Sauvagella* Bertin, 1943 both included *bianalis*, the latter description being the more definitive since the two other subspecies had by that time been transferred to *Gilchristella*.

DESCRIPTION. Body elongate, compressed, as in *Gilchristella*. Snout pointed, lower jaw projecting. Anterior supra-maxilla absent; posterior supra-maxilla

expanded posteriorly to almost maxilla depth, anterior shaft-like. Pre-maxilla and maxilla with a single row of conical teeth. Fleshy eminence on postero-ventral angle of cleithrum very small, similar to that in *Etrumeus* (Text-fig. 30a). Posterior border of operculum slightly excavated; junction between operculum and sub-operculum not as steeply inclined as in *Gilchristella* but resembling that in *Ehirava* and thus *Dussumieria* (Text-fig. 30b).

Pelvic scute with thin, pointed ascending arms. No abdominal scutes.

Dorsal origin further from snout than caudal base. Pelvic origin in front of dorsal.

Branchiostegal rays 6.

A single species.

Sauvagella bianalis Bertin

(Text-fig. 14)

Sauvagella madagascariensis bianalis Bertin, 1940, *Bull. Mus. Hist. nat. Paris*, (2) 12 : 300.

Sauvagella bianalis Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 22, fig. 8.

Spratellomorpha bianalis Bertin, 1946, in Angel, Bertin and Guibé, 1946, *Bull. Mus. Hist. nat. Paris* (2) 18 : 473-4.

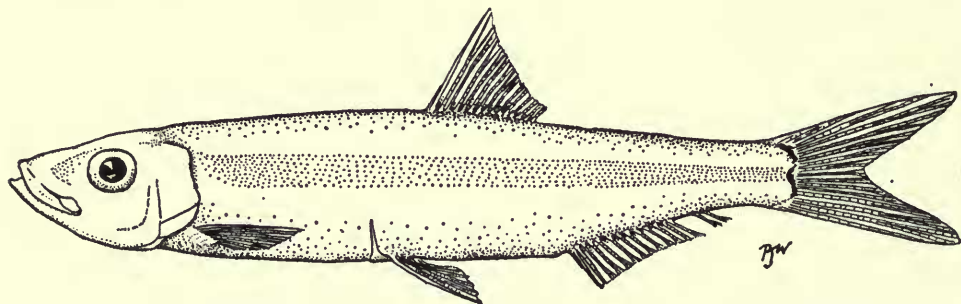


FIG. 14.

Sauvagella bianalis. From a specimen 47 mm. standard length, Madagascar (syntype, Paris Museum No. A 5174). Scales omitted.

DESCRIPTION. Based on four fishes, 44.0-45.5 mm., *ex* Madagascar (types of *Sauvagella bianalis*).

In percentages of standard length : body depth 17.1-18.0, head length 25.2-26.5, snout length 6.9-7.1, eye diameter 7.2-7.8, post-orbital 8.4-8.6, maxilla length 9.7-10.0, pre-dorsal distance 53.4-56.5 (62.8 one fish), pre-pelvic distance 49.4-52.2, pre-anal distance 69.0-72.5.

Body compressed, but body depth less than head length. Snout pointed, a little less than eye diameter. Jaws subequal, lower projecting slightly. Maxilla longer than snout, reaching vertical through anterior border of pupil. Maxilla as in *Gilchristella*. A single supra-maxilla.

Dorsal origin a little nearer caudal base than snout. Pelvic origin in front of dorsal, nearer to anal base than to pectoral base. Anal origin nearer that of pelvics than to caudal.

Dorsal iii 12-13, pectoral i 12, pelvic i 7, anal iii 11-12 + 2.

Last two rays of anal fin separated from others by a gap equal to three rays. After examining an alizarin stained specimen, Bertin (1943, p. 23) stated that the gap between the two parts of the fin is due, not to a complete separation of the two, but the fact that "*l'actiniophore du premier rayon de l'anale postérieure est trois plus allongé, dans sa partie horizontale, que les autres actiniophores.*"

Scales in lateral series 42-45, transverse 8-9. Vertebrae 45-46 (16-17 caudal) (after Bertin).

SYNTYPES. Madagascar. Paris Museum No. A.5174.

COLOUR IN ALCOHOL. A uniform grey-brown. A faint silvery midlateral stripe. Caudal base with two dark pigmented lines, as in *Gilchristella aestuarius*.

SIZE. 60 mm. (Bertin, 1943).

ALLOMETRY. Except in eye size (negative) no allometry found in other body parts with standard length.

DISTRIBUTION. Madagascar.

Tribe SPRATELLOIDINI

Diagnosis

Members of the subfamily Spratelloidinae which possess a w-shaped pelvic scute (Text-fig. 25), two supra-maxillae (except in *Jenkinsia*), well-developed posterior fontanelles usually narrowly divided anteriorly, and pelvic fins below the middle of the dorsal.

DISTRIBUTION. Ranging from Japan and Australia to the Red Sea and South Africa, with a genus in the Caribbean area (Venezuela to Bermuda).

Two genera :

- A. Two supra-maxillae; premaxilla edentulous; cleithral flap well developed; posterior border of suboperculum evenly rounded; posterior fontanelles always narrowly divided anteriorly; Indo-pacific region *Spratelloides*
- B. A single supra-maxilla; premaxillary teeth sometimes present; cleithral flap little developed; posterior and ventral margins of suboperculum meeting at well-defined angle; posterior fontanelles sometimes broadly divided anteriorly; Caribbean region *Jenkinsia*

In many ways *Jenkinsia* stands between *Spratelloides* and the genera of the Ehiravini, but the evolution of the spined pelvic scute seems to be such an important step taken by the Ehiravini in the direction of the Clupeidae that *Jenkinsia* must be placed closer to *Spratelloides*. In addition, within the genus *Jenkinsia*, one species differs from *Spratelloides* principally in lacking the anterior supra-maxilla, whereas the other species is much nearer the Ehiravini, possessing premaxillary teeth, and a formation of the posterior fontanelles which differs from that in *Spratelloides*. This is further discussed under the generic descriptions.

Bertin (1943) included the Caribbean species in *Spratelloides*, but the two are well separated by the characters listed in the key above, geographical isolation reinforcing this distinction.

SPRATELLOIDES Bleeker

Spratelloides Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 29 (type *Clupea argyrotaeniata* Bleeker = *Clupea gracilis* Schlegel).

Stolephorus (non Lacépède) Fowler, 1941, *Bull. U.S. nat. Mus.*, **13** (No. 100) : 561.

Note on Synonymy

Some recent authors have substituted *Stolephorus* for Bleeker's *Spratelloides*, but this is quite wrong and is discussed fully after the synonymy for *Spratelloides gracilis*.

DESCRIPTION. Body elongate, slightly compressed, rounded ventrally; snout pointed, jaws equal or lower very slightly projecting. Two supramaxillae, the second (posterior) bone paddle-shaped with a slender anterior shaft; maxilla toothed, with evenly rounded lower border (Text-fig. 28). Pre-maxilla edentulous. Fleshy eminence on postero-ventral angle of cleithrum (cleithral flap) well-developed, indented anteriorly (Text-fig. 30c), gill filaments of first arch also indented to accommodate cleithral flap. Posterior border of operculum strongly indented, more so than in *Ehirava*. Junction between operculum and sub-operculum horizontal, the latter bone subrectangular, its posterior margin rounded. Interoperculum exposed and three or four branchiostegal rays visible externally. Posterior border of pre-operculum vertical. Posterior border of gill opening s-shaped.

Two posterior fontanelles with a narrow median division (see Text-figs. 31 and 32).

A single, w-shaped pelvic scute. No abdominal scutes. Dorsal equidistant between snout and caudal base or a little nearer snout. Pelvic origin below mid-dorsal or below second half of dorsal.

Two species of *Spratelloides* recognized here, each with a subspecies.

- | | | |
|----|---|-----------------------|
| a. | A bright and prominent silver mid-lateral band; total anal rays 11-14; scales in lateral series 41-49 | <i>S. gracilis</i> |
| b. | No silver band, but whole lower flank silver; total anal rays 9-11; scales in lateral series 32-46 | <i>S. delicatulus</i> |

These two species also differ in body depth, head length, post-orbital distance and pectoral length.

Spratelloides gracilis (Schlegel)

(Text-fig. 18)

Clupea gracilis Schlegel, 1846, *Faun. Japon. Poiss.*, pts. 10-14 : 238, pl. 108, fig. 2 (type locality : southeast coasts of Nagasaki).

Clupea argyrotaeniata Bleeker, 1849, *Journ. Ind. Arch.*, **3** : 72 (type locality : Macassar, south-west Celebes).

Spratelloides argyrotaenia Bleeker, 1851, *Natuurk. Tijdschr. Ned. Ind.*, **2** : 214; *Idem*, 1852, *Verh. Bat. Gen.*, *Batavia*, **24** : 29; *Idem*, 1852, *Natuurk. Tijdschr. Ned. Ind.*, **3** : 775; Schultz and Wellander, 1953, *Bull. U.S. nat. Mus.*, **1** (202) : 23-24 (*S. argyrotaeniata*).

Spratelloides gracilis Bleeker, 1853, *Verh. Bat. Gen.*, *Batavia*, **25** : 18; *Idem*, 1892, **6** : 96, pl. (8) 266, fig. 2; Günther, 1868, *Cat. Fishes Brit. Mus.*, **6** : 465 (type of *Clupea argyrotaenia*); Klunzinger, 1871, *Verh. zool.-bot. Ges. Wien*, **21** : 601; Weber and Beaufort, 1913, *Fishes Indo-Aust. Arch.*, **2** : 20, fig. 12; Hardenburg, 1933, *Treubia*, **14** (2) : 215; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 15-16.

- Stolephorus japonicus* (non Lacépède) Jordan and Seale, 1905, *Proc. U.S. nat. Mus.*, **28** : 770; Jordan and Herre, 1906, *Proc. U.S. nat. Mus.*, **31** : 629; Fowler, 1928, *Mem. Bernice P. Bishop Mus.*, **10** : 30; Herre, 1936, *Field Mus. nat. Hist. Zool.*, **21** : 33; Fowler, 1941, *Bull. U.S. nat. Mus.*, **13** (100) : 567 (full synonymy); *Idem*, 1956, *Fishes of the Red Sea and Southern Arabia, Jerusalem*, p. 61, fig. 23.
- Stolephorus gracilis* Evermann and Seale, 1907, *Bull. Bur. Fisher.*, **26** : 53; Whitley, 1953, *Aust. Zool.*, **11** : 332.
- Spratelloides japonicus* Mori, 1928, *Journ. Pan Pacific Res. Inst.*, **3** : 3; Tanaka, 1933, *Jap. Fish. Life Colours*, No. 47; Marshall, 1952, *Bull. Brit. Mus. nat. Hist. (Zool.)*, **1** : 22; Schultz and Wellander, 1953, *Bull. U.S. nat. Mus.*, No. 202 : 24; Morrow, 1954, *Ann. Mag. nat. Hist.*, (12) **7** : 804; Okada, 1955, *Fishes of Japan, Tokyo*: 41; Monroe, 1955, *Marine and freshwater fish. Ceylon* : 28; Jones, 1961, *J. Mar. Biol. Assn. India*, **2** (2), 267-8.
- Spratelloides atrofasciatus* Schultz, 1943, *Bull. U.S. nat. Mus.*, No. 180 : 8, fig. 1; Schultz and Wellander, 1953, *op. cit.* No. 202 : 27, fig. 7.

Note on Synonymy

Only the most important references prior to 1940 are cited here; full synonymies are given by Fowler (1941) under *Stolephorus japonicus*.

The synonymy reveals two main issues. The first is whether the Japanese and other far eastern populations should be separated from those of the Red Sea, Indian Ocean and Indo-Malayan Archipelago. Marshall (1952) showed that his (admittedly few) specimens of *S. gracilis* from the Red Sea had lower pectoral and anal counts than did specimens from Japan (the type locality of Schlegel's *Clupea gracilis*). Schultz & Wellander (1953) were however more emphatic, stating that *gracilis*, as understood by Bertin (1943) and Weber & de Beaufort (1913), actually represented "at least two species"—the "*japonicus*" of Houttuyn, and Bleekers "*argyrotaenia*"—and their finray, scale and gillraker counts seemed to support their conclusion. Counts made on specimens in the British Museum, and supplemented by those of Schultz & Wellander (*loc. cit.*) are given in Text-figs. 15-17. Certainly the counts are higher in the Japanese specimens, but not only do the counts from the extreme boundaries of the geographical range overlap (i.e. Red Sea and Japan), but the specimens of intermediate provenance (i.e. from the Indo-Malayan Archipelago) show intermediate values.

The situation is similar to that found in the Museum specimens of *Dussumieria* (see p. 312) and the same conclusion must be drawn. The populations of *S. gracilis* from any one region cannot be distinguished sufficiently clearly to merit specific distinction. The fact that in numbers of dorsal, pectoral and anal rays and in gillrakers there appears to be the same gradual shift to higher numbers as one proceeds eastwards suggests that this is merely a phenotypic response to some environmental factor, possibly temperature (but cf. *Dussumieria*, p. 316).

A second eastern population which has been separated from *S. gracilis* is *S. atrofasciatus* Schultz, 1943, described from Samoa and distinguished from *S. gracilis* by its lower gillraker and scale counts (Schultz, & Wellander, 1953). In numbers of dorsal, anal and pectoral rays it overlaps *S. gracilis*, but in gillrakers it is rather lower (19-23 on the lower part of the first arch; cf. 26 given as the lowest for *S. argyrotaeniata* by Schultz & Wellander (*loc. cit.*)). This, and its geographical isolation from other populations, suggests that separation from *S. gracilis* would be

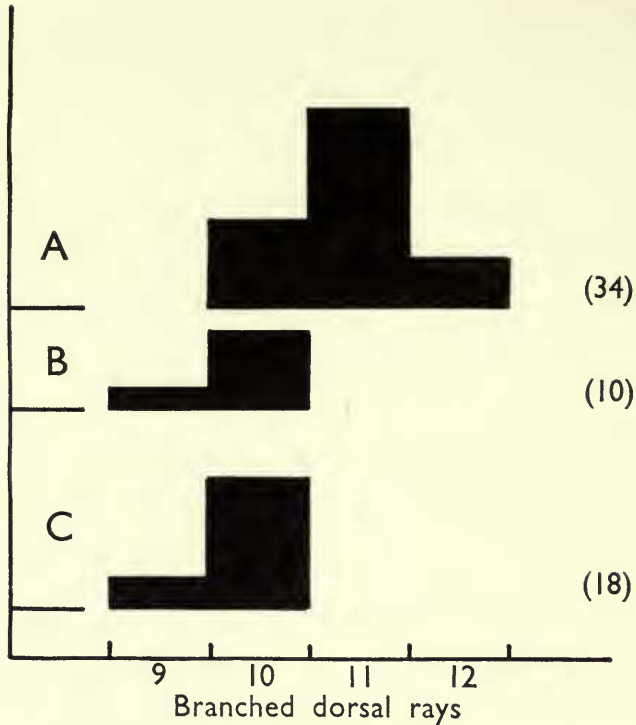


FIG. 15.

Spratelloides gracilis, branched dorsal rays. Dorsal finray frequencies in populations from:

- A. Japan and Formosa.
- B. Indo-Malayan archipelago and Philippines.
- C. Red Sea.

Based on specimens in the British Museum and supplemented by figures from Schultz and Wellander (1953). Numbers in sample placed in parentheses.

justified. But since only a single character is involved (i.e. gillrakers), and since in this character as well as in other meristic counts *S. atrofasciatus* consistently lies at the lower end of the range for *S. gracilis*, there seems good reason to suppose that it represents another ecophenotypic variation of *S. gracilis*. Therefore, I do not believe the Samoan population differs specifically from *S. gracilis*, and I have here given *S. atrofasciatus* subspecific status only in order to emphasize its place amongst the forms included in *S. gracilis*.

The second issue raised by the synonymy is the question of the use of *Stolephorus* Lacépède for a genus of round herring, and the citing of *Atherina japonica* Houttuyn as the genotype of *Stolephorus*.

Some confusion has occurred over the application of the specific name "*japonica*" Houttuyn to a species of *Spratelloides*. Houttuyn (1782) gave a poor description of a Japanese fish, *Atherina japonica*, and Lacépède (1803) placed this fish, together

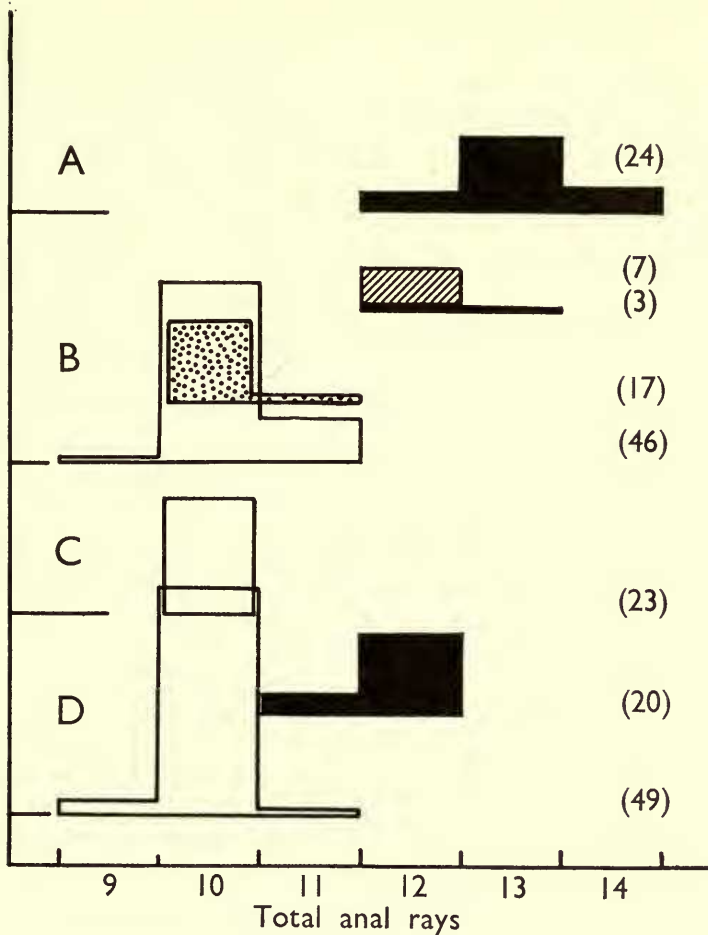


FIG. 16.

Anal finray frequencies in populations of *Spratelloides* from :

- A. Japan and Formosa.
- B. Indo-Malayan archipelago, Philippines and Australia.
- C. Seychelles and Maldives.
- D. Red Sea and Gulf of Aden.

Black *S. gracilis*, White *S. delicatulus*, Hatched *S. argyrotaenia*, Stippled *S. g. robustus* (Australia).

Based on specimens in the British Museum and supplemented by figures from Schultz & Wellander (1953). Numbers in each sample placed in parentheses. N.B.—Both branched and simple rays included in counts.

with an anchovy described but not named by Commerson, in his genus *Stolephorus*. The generic description and figure were evidently based on the latter species, *S. commersonii*, and Opinion 93 given by the International Commission for Zoological Nomenclature directed that *S. commersonianus* (i.e. *S. commersonii*—see footnote,

p. 309) should be the designated genotype of *Stolephorus* and not *Atherina japonica* (Jordan & Gilbert (1883, p. 272) had unfortunately designated the latter previously). The confusion is aggravated because some authors have ignored Opinion 93 and continue to call the round herring genus *Stolephorus* rather than *Spratelloides* (e.g. Fowler, 1941 and 1958, Smith, 1955). At the same time the European anchovy

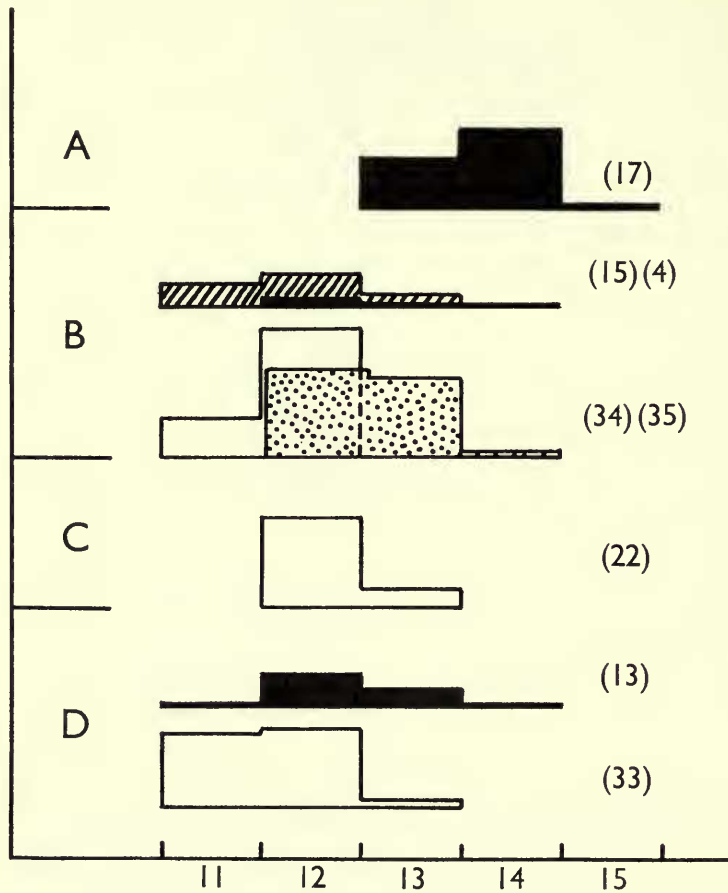


FIG. 17.

Pectoral finray frequencies in populations of *Spratelloides* from :

- A. Japan and Formosa.
- B. Indo-Malayan archipelago and Philippines.
- C. The Seychelles and Maldives.
- D. Red Sea.

Black *S. gracilis*, White *S. delicatulus*, Hatched *S. argyrotaenia*, Stippled *S. robustus* (Australia). Based on specimens in the British Museum and supplemented by figures from Schultz & Wellander (1953). Numbers in each sample placed in parentheses. The first, unbranched ray included in the counts.

(*Engraulis encrasicolus*) has sometimes been placed in *Stolephorus* (Poll, 1947); its very close Japanese relative is the *Engraulis japonicus* of Schlegel. Thus in Fowler (*loc. cit.*) *Atherina japonica* Houttuyn is cited as the type both of a dussumieriid and an engraulid species. *Stolephorus* should in fact refer only to those Indo-Pacific engraulids which have at least some abdominal scutes (cf. the *encrasicolus* forms which do not, and which should be placed in *Engraulis* Cuvier), normal pectoral rays (cf. the species referred to *Setipinna*), and a maxilla not extending beyond the gill opening (cf. *Thrissocles*). *Stolephorus* is generally a synonym for those Indo-Pacific anchovies otherwise placed in *Anchoviella* Fowler.

If Houttuyn's fish is assumed not to be an *Engraulis*, then *E. japonicus* Schlegel is perfectly correct for the Japanese *encrasicolus*-type anchovy. This assumption is based on the supposition that Houttuyn was familiar with the European *E. encrasicolus* and could have located the similar Japanese form in the *Systema Naturae* (to which he refers in his description). Also, of the three possible Japanese fishes with broad silvery lateral stripes (a character stressed by Houttuyn) only the round herring has 8 pelvic rays, the scuted anchovy and non-scuted (*encrasicolus*-type) anchovy each having only seven. Again, placing his fish in Linnaeus' *Atherina*, Houttuyn may have counted (but not recorded) six branchiostegal rays, which also accords with a spratelloidine. In addition, Houttuyn described a fish with 14 pectoral rays. In 24 specimens of *Spratelloides* from Japan, I counted 14 rays in 5 fishes, 13 rays in 15 fishes, and 12 rays in 4 fishes (see Text-fig. 17). Five specimens of *Engraulis* from Japan had 16-18 rays, but in seven specimens of *Stolephorus* from China there were 13 rays. The rays are however, extremely difficult to count in the smaller dussumieriids and perhaps too much reliance should not be placed on Houttuyn's count.

The remaining details of Houttuyn's description could fit all three Japanese fishes (mouth toothless, head scaleless), but the dorsal count of 5 is surely a mistake. He mentions size—4 inches—but says "*Ook heb ik 'er een van drie Duimen*" (which suggests that Jordan & Evermann (1917) were perhaps wrong in thinking that the fish was described from rough notes or memory).

To resolve the matter, two courses are open. Either *japonica* Houttuyn 1782 is considered a *nomen dubium*, there being no type specimen nor adequate description; or one of the three Japanese species with a broad silvery lateral stripe is accepted as Houttuyn's fish. I favour the first course, for although Houttuyn's description probably fits a dussumieriid fish of the genus *Spratelloides* better than it does an anchovy, there is no further evidence that can be produced which will confirm the identity of this fish. *Spratelloides japonica* Houttuyn should therefore be suppressed in favour of *S. gracilis* (Schlegel) as the first recognizable description of this species. Application has been made to the International Commission for Zoological Nomenclature to this effect.

DESCRIPTION. Based on nineteen fishes, 59.0-93.0 mm. standard length, including the lectotype (a specimen 66.7 mm. S.L. believed by Günther (1868) to be Bleeker's type from the East Indian Archipelago), and from Japan (15) and Formosa (3). In addition, all other specimens listed under Study Material (p. 375) used for meristic counts.



FIG. 18.

Spratelloides gracilis. From a specimen 90 mm. standard length, Wakanoura, Japan. Scales omitted.

In percentages of standard length : body depth (under dorsal origin) 13.2–17.3, head length¹ 22.0–24.5, snout length 6.9–8.2 ; eye diameter 5.3–6.3, post-orbital distance² 7.4–8.5, maxilla length 8.1–9.0, pectoral length 11.6–12.2, pelvic length 9.4–9.8, pre-dorsal distance 47.0–50.0 (one fish 52.3), pre-pelvic distance 53.5–58.7, pre-anal distance 79.0–84.7.

Body slightly compressed, its depth less than head length. Snout pointed, a little larger than eye diameter. Maxilla longer than snout, passing front border of eye but not reaching pupil. Post-orbital a little larger than snout length. Dorsal origin equidistant, or usually just nearer snout than caudal base. Pelvic origin under middle or second half of dorsal, a little nearer to caudal base than to snout.

Dorsal ii 9–12 (see Text-fig. 15), pectoral i 10–15 (see Text-fig. 17), pelvic i 7, anal 11–14, of which ii or iii are branched (see Text-fig. 16).

Gillrakers 20–37 on the lower part of the first arch (including one at angle) and 7–12 above angle.

Scales in lateral series 41–49 (based partly on Schultz & Wellander (*loc. cit.*) and Bertin, 1943) ; 8–9 transverse rows.

Vertebrae 46 (3 specimens, Bertin (*loc. cit.*)).

TYPE. East Indian Archipelago. Lectotype, B.M. (N.H.), 1867.11.28.17.

COLOUR IN ALCOHOL. Upper and lower surfaces brown, divided by a broad lateral silver stripe, whose greatest width just exceeds eye diameter ; in some specimens the lateral band is dark brown or black, much darker along its upper margin ; and in all Japanese specimens examined the silvery stripe is outlined above by a thin, dark brown line. In some specimens a dark brown or black line dorsally from nape to caudal. Glandular scales on caudal not, or but faintly pigmented (cf. *S. delicatulus*).

DISTRIBUTION. Indo-Pacific region, from Red Sea to Japan ; southwards along African coast to Pemba (Morrow, 1954) ; in Pacific, southwards to Samoa ; Indian Ocean, Ceylon and Laccadive Sea (Jones, 1961).

¹ The longest measurement, i.e. premaxillary symphysis to posterior border of operculum *below* the indentation in the latter characteristic of *Spratelloides*. The measurement is thus not along a horizontal line.

² The shortest distance, i.e. from posterior eye border to centre of indentation in operculum.

Two subspecies recognized here.

- a. Gillrakers on lower part of first arch 24-37; scales in lateral series 44-49; total anal rays 11-14; Indo-Pacific region excluding Samoa . *Spratelloides gracilis gracilis*
 b. Gillrakers on lower part of first arch 19-23; scales in lateral series 41-42; total anal rays 10-11; restricted to Samoa *Spratelloides gracilis atrofasciatus*

Spratelloides gracilis gracilis Schlegel

Spratelloides gracilis Schlegel, 1846, *Faun. Japon. Poiss.*, pts. 10-14; 238, pl. 108, fig. 2 (for full synonymy, see under species).

DESCRIPTION AND DIAGNOSIS. Distinguished from the Samoan subspecies by a higher gillraker count (24-37) and more scales in lateral series (44-49). Dorsal ii 9-12, pectoral i 10-14, pelvic i 7, anal 11-14 (including ii or usually iii simple rays).

DISTRIBUTION. As for species, but not found in Samoa.

TYPE. *S. gracilis* Schlegel.

Spratelloides gracilis atrofasciatus Schultz

Spratelloides atrofasciatus Schultz, 1943, *Bull. U.S. nat. Mus.*, No. 180: 8, fig. 1; *Idem*, 1953, *op. cit.*, No. 202: 24.

DESCRIPTION AND DIAGNOSIS. A Samoan population distinguished from *S. g. gracilis* by its lower gillraker count (19-23) and fewer scales in lateral series (41-42). Dorsal ii 9-10, pectoral i 10-11, pelvic i 7, anal 10-11 (including ii or usually iii simple rays). Description based on Schultz.

DISTRIBUTION. Samoa only.

TYPE. *S. atrofasciatus* Schultz.

Spratelloides delicatulus (Bennett)

(Text-fig. 19)

Clupea delicatula Bennett, 1831, *Proc. zool. Soc. London*, 1: 168 (Type locality: Mauritius).

Clupea macassariensis, Bleeker, 1849, *Journ Indian Arch.*, 3: 72.

Clupeoides macassariensis Bleeker, 1851, *Natuurk. Tijdschr. Ned. Ind.*, 2: 214; *Idem*, 1852, *Verh.*

Bat. Gen., Batavia, 24: 17; *Idem*, 1852, *Natuurk. Tijdschr. Ned. Ind.*, 3: 772.

Alausa alburnus, Kner, 1867, *Sitzb. K. Akad. Wiss. Wien*, 54: 387, pl. 1, fig. 16.

Spratelloides alburnus Günther, 1868, *Cat. Fishes Brit. Mus.*, 7: 464.

Stolephorus alburnus Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100: 565.

Spratelloides delicatulus Günther, 1868, *Cat. Fishes Brit. Mus.*, 7: 464; Bleeker, 1872, *Atlas*.

Ichth. Ind. Néerland., 6: 96, pl. 264, fig. 3; Günther, 1910, *J. Mus. Goddefroy, Hamburg*, 6:

383; Weber and Beaufort, 1913, *Fishes Indo-Aust. Arch.*, 2: 20; Gilchrist and Thompson,

1917, *Ann. Durban Mus.*, 1: 296; Barnard, 1925, *Ann. S. Afr. Mus.*, 21 (1): 110; Harden-

berg, 1933, *Treubia*, 14 (2): 216; Roxas, 1934, *Philipp. J. Sci.*, 55: 249; Bertin, 1943, *Bull.*

Inst. océanogr. Monaco, No. 853: 18; Marshall, 1950, *Bull. Raffles Mus.*, No. 22: 168; *Idem*,

1952, *Bull. Brit. Mus. nat. Hist. (Zool.)*, 1: 222; Schultz and Wellander, 1953, *Bull. U.S.*

nat. Mus., No. 202: 26; Morrow, 1954, *Ann. Mag. nat. Hist.*, (12) 7: 804; Randall, 1955,

Atoll Res. Bull., No. 47: 6; Fowler and Steinitz, 1956, *Bull. Res. Council Israel*, 5, 13 (3-4):

262; Rofen, 1958, *Nat. Hist. Rennell Is., Brit. Solomon Is.*, 1, *Copenhagen*: 151; Jones,

1960, *J. Mar. biol. Ass. India*, 2 (1): 103; *Idem*, 1961, *op. cit.*, 2 (2): 267.

Stolephorus delicatulus Jordan and Seale, 1906, *Bull. Bur. Fisher.*, **25** : 186 ; Evermann and Seale, 1906, *Bull. Bur. Fisher.*, **26** : 53 ; Fowler, 1928, *Mem. Bernice P. Bishop. Mus.*, **10** : 29 ; Whitley, 1929, *Proc. Linn. Soc. N.S.W.*, **54** : 92 ; Herre, 1936, *Field Mus. nat. Hist. Zool.*, **21** : 32 ; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 562 ; Smith, 1955, *Ann. Mag. nat. Hist.*, (12) **8** : 307.

Spratelloides robustus Ogilby, 1897, *Proc. Linn. Soc. N.S.W.*, **22** : 64 (Type locality : coast of New South Wales) ; Bertin, 1943, *Bull. Inst. océanog. Monaco*, No. 853 : 16.

Stolephorus robustus Waite, 1904, *Mem. New South Wales Nat. Club*, No. 2 : 12 ; McCulloch, 1920, *Rec. Austral. Mus.*, **13** (2) : 42, pl. 11, fig. 1 ; McCulloch and Whitley, 1925, *Mem. Queensland Mus.*, 8 (2) : 131 ; McCulloch, 1927, *Fishes of New South Wales*, ed. 2 : 16, pl. 4, fig. 51a ; Blackburn, 1941, *Bull. Counc. sci. ind. Res. Aust.*, No. 138 : 59.

A fuller synonymy is given by Fowler (1941) under *Stolephorus delicatulus*, *S. robustus* and *S. alburnus*.

Notes on Synonymy

The problem of *Stolephorus* has already been discussed. *Spratelloides alburnus* (Kner), erroneously described from "Valparaiso, Chile"—in fact from Samoa—is almost certainly *S. delicatulus*, which has been recorded from the Marshall Is. and may well occur to the south (Schultz & Wellander, 1953). Bertin (1943) reached the same conclusion.

The only major change from previous synonymies is the inclusion of *S. robustus*. In proportional measurements and in all meristic counts except scales, the specimens of *S. robustus* in the Museum (all from New South Wales) fall within the ranges of *S. delicatulus* (see Table III), and I have been unable to find any colour differences. Unfortunately insufficient specimens of either species have had a full series of scales, and the descriptions of Fowler (1941), Bertin (1943) and Schultz & Wellander (1953) vary somewhat (respectively 32–36, 35–38, 40–42 in lateral series for *S. robustus*, and 36–40, 43–45, 45–46 for *S. delicatulus*). All are agreed however that the New South Wales population has the lower count, and on this basis I believe that it should be considered a subspecies of *S. delicatulus*. There is also a tendency for the New South Wales population to have a slightly longer pelvic fin (Table III) and slightly more rays in the pectoral (Text-fig. 17) but the differences are small.

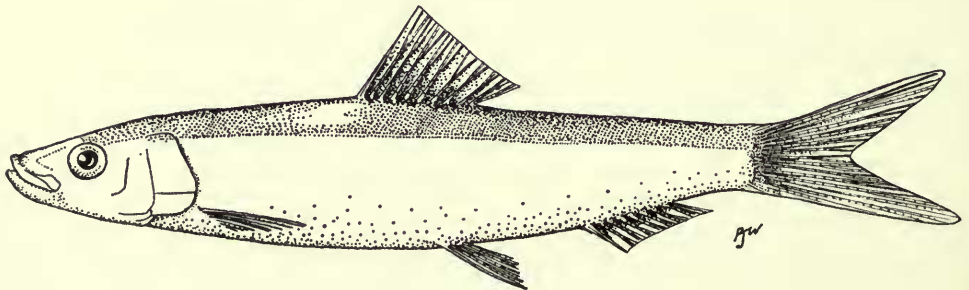


FIG. 19.

Spratelloides delicatulus. From a specimen 69 mm. standard length, Hasler Collection (locality not stated). Scales omitted.

DESCRIPTION. Based on thirteen fishes (*S. delicatulus*), 39.0–52.0 mm. standard length from the Maldives, Thousand Is., Bonham Is., and the Seychelles; and ten fishes (*S. robustus*) 50.3–71.0 mm. standard length from the coast of New South Wales. Additional meristic counts made on other specimens listed under Study Material (p. 376). Single measurements outside normal range are placed in parenthesis.

In percentages of standard length: body depth (16.7) 17.9–21.0, head length¹ 24.0–28.2, snout length 6.6–7.7, eye diameter 6.5–7.7, post-orbital distance 8.8–10.3, maxilla length 8.4–9.6, pectoral length (11.9) 14.0–15.8, pelvic length 9.2–12.8, pre-dorsal distance 45.6–49.2, pre-pelvic distance (50.5) 53.0–57.5, pre-anal distance (75.0) 76.2–83.5.

Body slightly compressed, rounder than in *S. gracilis*, its depth less than head length. Snout pointed, a little larger than eye diameter. Maxilla longer than snout, reaching almost to pupil of eye. Post-orbital a little longer than snout. Dorsal origin equidistant, or usually nearer snout than caudal base. Pelvic origin under mid-dorsal or under second half of dorsal, a little nearer to caudal base than to snout.

Dorsal ii 9–11, pectoral i 10–13 (see Text-fig. 17), pelvic i 7, anal 9–11 of which ii or iii are branched (see Text-fig. 16).

Gillrakers 26–33 on the lower part of the first arch (including one at angle), 9–11 on upper part.

Scales in lateral series 32–46, 7–9 transverse.

Vertebrae 42–44 (Bertin, 1943).

TYPE. Mauritius.

COLOUR IN ALCOHOL. Upper surfaces grey-blue or brown, sides and ventral surfaces white or silvery, the two areas meeting at an abrupt line dorso-laterally. Top of head, tip of snout, lower jaw and tongue dark brown and a small black spot in front of eye. Two black streaks along glandular scales on each lobe of caudal.

DISTRIBUTION. Eastern coast of Africa, from Natal, northwards to Gulf of Aden and Red Sea; India, East Indies, Philippines, Cocos-Keeling Is., Hawaii; New South Wales, Queensland, Tasmania. *S. delicatulus* apparently does not penetrate as far north as *S. gracilis*, but reaches further south (i.e. to Australia).

Two subspecies recognized here.

- a. Scales in lateral series 36–46; pelvic fins 9.2–11.5 % of standard length; pectoral finrays i 10–12; Indo-Pacific region excluding Australia

Spratelloides delicatulus delicatulus

- b. Scales in lateral series 32–42; pelvic fins 11.1–12.8% of standard length; pectoral finrays i 11–13; confined to Australian coasts

Spratelloides delicatulus robustus

Spratelloides delicatulus delicatulus Bennett

Spratelloides delicatulus Bennett, 1831, *Proc. Comm. zool. Soc. London*, 1: 168 (for full synonymy, see species).

¹ Measurements as in *S. gracilis*, footnote, p. 344.

DESCRIPTION AND DIAGNOSIS. Distinguished from the Australian subspecies by its greater number of scales in lateral series, although authors are not agreed on the precise range in this character (see p. 346). It also has slightly shorter pelvic fins (9.2–11.5% of standard length) and fewer pectoral rays (i 10–12).

DISTRIBUTION. As for species but excluding the coasts of Australia.

TYPE. *Spratelloides delicatulus* (Bennett.)

Spratelloides delicatulus robustus Ogilby

Spratelloides robustus Ogilby, 1897, *Proc. Linn. Soc. N.S.W.*, 22 : 64 (see under species for full synonymy).

DESCRIPTION AND DIAGNOSIS. An Australian population differing from *S. d. delicatulus* in having fewer scales in lateral series (32–42), slightly longer pelvic fins (11.1–12.8% of standard length), and slightly more rays in the pectoral (i 11–13).

DISTRIBUTION. Queensland, New South Wales, Victoria, Tasmania (after Fowler, 1941).

TYPE. Coast of New South Wales, Australia. Australian Museum, Sydney, No. I. 3668.

JENKINSIA Jordan & Everman

Jenkinsia Jordan and Evermann, 1896, *Bull. U.S. nat. Mus.*, 50 : 418 (genotype *Dussumieria stolifera* Jordan and Gilbert).

DESCRIPTION. Body elongate, slightly compressed, rounded ventrally; snout pointed, jaws equal or lower slightly projecting. A single (posterior) supra-maxilla, paddle-shaped with a slender anterior shaft; maxilla toothed. Premaxilla with or without a single series of fine conical teeth. Little or no development of fleshy eminence (cleithral flap) at postero-ventral angle of gill-opening. Posterior border of operculum strongly indented, more so than in *Ehirava*. Sub-operculum rectangular, posterior border not rounded but forming a well-defined and slightly obtuse angle. Inter-operculum exposed and three or four branchiostegal rays visible externally. Posterior border of pre-operculum vertical.

A pair of posterior fontanelles becoming reduced in size in adults. Anterior frontal fontanelle present in smaller fishes, sometimes in adults.

A single w-shaped pelvic scute. No abdominal scutes. Dorsal a little nearer snout than caudal base. Pelvic origin below mid-dorsal.

A bright silvery midlateral stripe along flanks.

The Species of Jenkinsia

Authors have recognized variations in finray and gillraker counts amongst specimens of *Jenkinsia* from different parts of the Caribbean region, and several species have been based on these. But Parr (1930), Beebe & Tee-Van (1933) and Longley & Hildebrand (1941) all believed that the overlap between finray counts in such populations was too great for any one population to be separated at specific level.

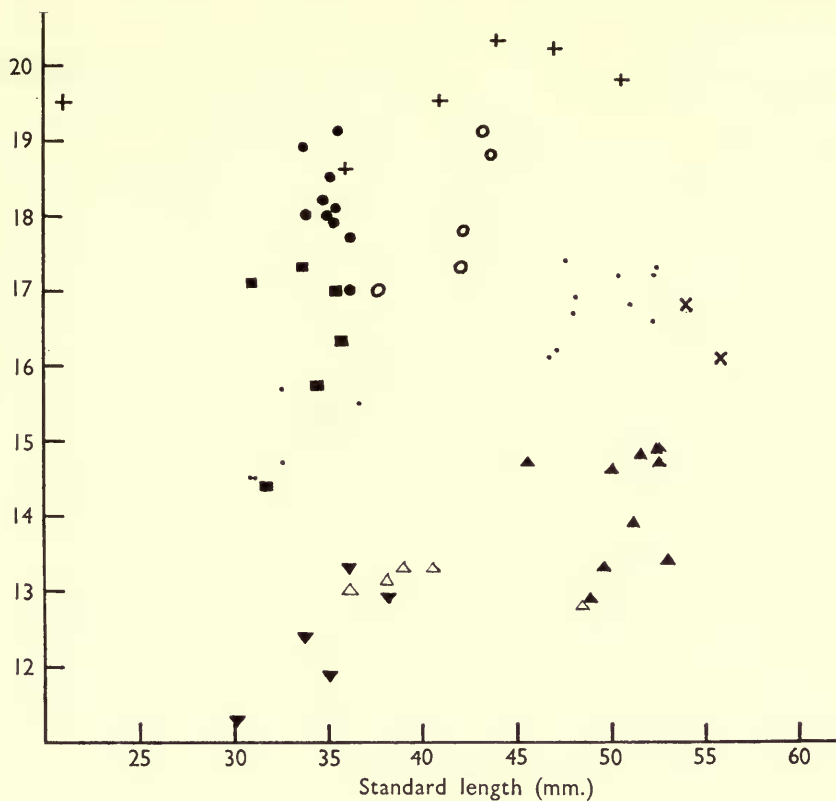


FIG. 20.

Body depth expressed as percentage of standard length (ordinate) plotted against standard length (abscissa) in various populations of *Jenkinisia*.

J. lamprotaenia

- × Jamaica (types of *J. lamprotaenia*).
- Cat Cay, Bahamas.
- Key West (types of *Dussumieria stolifera*).
- St. John, Virgin Islands.
- + Venezuela (figures from Martin, 1955).

J. majua

- ▲ Campeche Banks.
- △ Swan Island.
- ▼ Gun Cay, Bahamas.

I have found however, that the populations in this region can be split into two natural groups on the basis of two correlated non-meristic characters. The first is the presence or absence of teeth on the premaxilla; the second is in the form of the frontal bones at the anterior end of the posterior fontanelles. In the group lacking premaxillary teeth the fontanelles are very narrowly divided even at their anterior end (and this is especially the case in juveniles), and in front of these two fontanelles

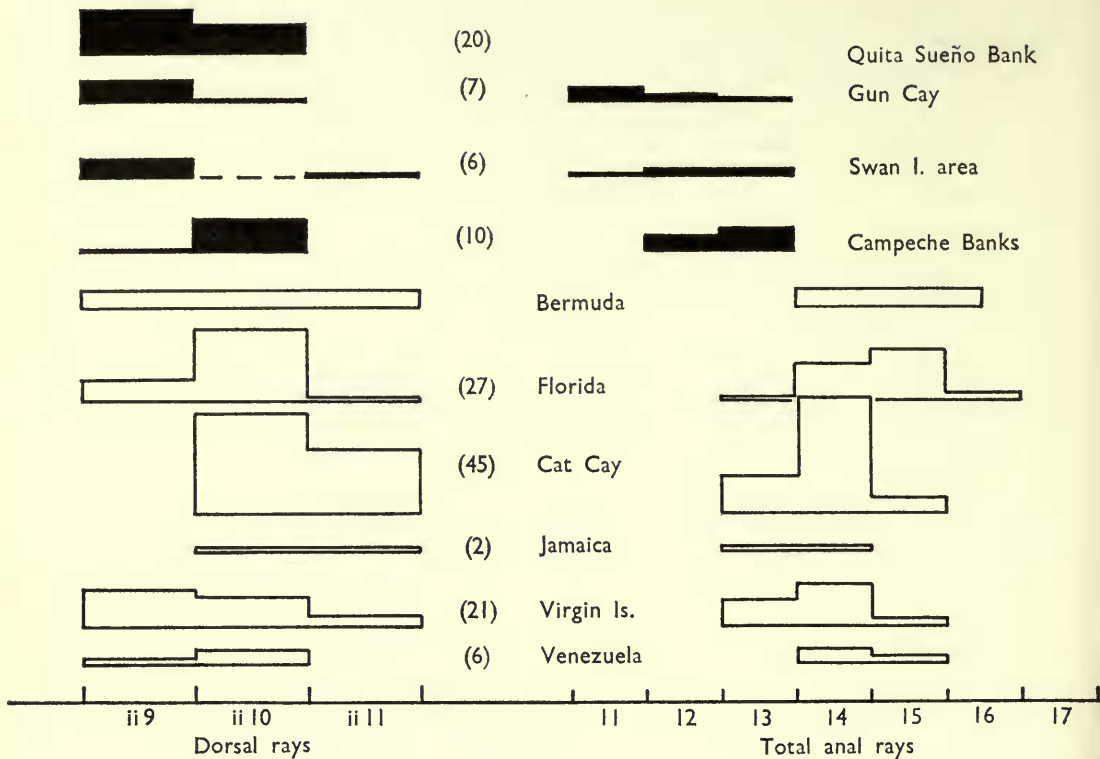


FIG. 21.

Dorsal and anal finray count frequencies in populations of *Jenkinsia*.

Black, *J. majua*; White, *J. lamprotaenia*.

Numbers in sample placed in parentheses. Range only for Bermuda specimens (based on published records—see text).

the part of the head immediately behind the junction of the two inner arms of the transverse frontal sensory canal is domed or flat (again, especially in juveniles) (Text-fig. 32b). In the other group however, the posterior fontanelles are divided anteriorly by a broad wedge, and within this wedge is a triangular depression in which lies a median branch of the post-frontal canal (Text-fig. 32a).

There is also a difference in the size of the fish at which the frontals start to extend posteriorly to close the fontanelles. In the first group this occurs at a larger size than in the second, and in this the former resemble *Spratelloides*, while the second group resemble rather the genera of the Ehiravini.

These two differences are important because they also help to separate the Ehiravini from *Spratelloides*. But for the geographical isolation of *Jenkinsia*, a direct evolution of the Ehiravini from those members of *Jenkinsia* which have premaxillary teeth and a wedge of bone separating the posterior fontanelles would

seem clear. As it is, *Jenkinsia* may have become isolated at a time when *Spratelloides* had only just begun to diverge (through loss of premaxillary teeth, development of the cleithral flap and retention of the second supra-maxilla).

A third character which can be correlated with the tooth and fontanelle characters is the higher number of rays in the anal fin in those fishes with a toothed premaxillary. In addition these fishes also tend to be deeper bodied (Text-fig. 20) although body depth shows positive allometry with standard length and the difference is difficult to define when all size groups are considered.

A final difference between populations of *Jenkinsia* involves gillraker numbers. This is here interpreted as a subspecific character.

- a. Premaxilla toothed ; posterior fontanelles divided anteriorly by wedge of bone, with triangular depression in front ; anal rays 13-16 ; body deeper, its depth usually over 15% of standard length *J. lamprotaenia*
- b. Premaxilla edentulous ; posterior fontanelles narrowly divided anteriorly, area in front domed, becoming flat in adults ; anal rays 11-13 ; body more slender, its depth usually under 15% of standard length *J. majua* sp. nov.

The geographical distribution of these two species overlaps in the Bahamas (where I have examined specimens of the first from Cat Cay, and of the second from the nearby Gun Cay) and in the Gulf of Campeche. Further distributional records are required, but on the basis of the present specimens, *J. lamprotaenia* seems to occur mainly along the outer boundary of the area (i.e. Bermuda, the islands of the West Indies and Antilles, Venezuela), while *J. majua* appears to be a more western species (Gulf of Campeche, Swan Island, British Honduras).

Jenkinsia lamprotaenia (Gosse)

(Text-fig. 23)

Clupea lamprotaenia Gosse, 1851, *Naturalist's Sojourn in Jamaica* : 291, pl. 1, fig. 2 (Type locality : Jamaica).

(*Spratelloides*) *lamprotaenia* Günther, 1868, *Cat. Fish Brit. Mus.*, 7 : 465.

Dussumieria stolidifera Jordan and Gilbert, 1884, *Proc. U.S. nat. Mus.*, 7 : 25 (Type locality : Key West, Florida).

Jenkinsia stolidifera Jordan and Evermann, 1896, *Bull. U.S. nat. Mus.*, No. 47 (pt. 1) : 418 ; Fowler, 1930, *Proc. biol. Soc. Wash.*, 43 : 145.

Jenkinsia lamprotaenia Jordan and Evermann, 1896, *Bull. U.S. nat. Mus.*, No. 47 : 419 ; Parr, 1930, *Bull. Bingham oceanogr. Coll.*, 3 (4) : 3 ; Beebe and Tee-Van, 1928, *Zoologica*, 10 (1) : 43 ; *Idem*, 1933, *Zoologica*, 13 (7) : 136 ; Longley and Hildebrand, 1941, *Pap. Dep. mar. Biol. Carnegie*, 34 (No. 535) : 12 ; Fowler, 1944, *Monagr. Acad. nat. Sci. Philad.*, No. 6 : 123 ; Martin, 1955, *Mem. Soc. Cienc. nat. La Salle*, 15 : 185.

Stolephorus viridis Bean, 1912, *Proc. biol. Soc. Wash.*, 25 : 122 (Type locality : Bermuda).

Jenkinsia bermudana Rivas, 1946, *Smithson. Misc. Coll.*, 106 (14) : 2, fig. 1, pl. 1 (Type locality : Bermuda).

Jenkinsia viridis Collette, 1962, *Copeia*, No. 3 : 659.

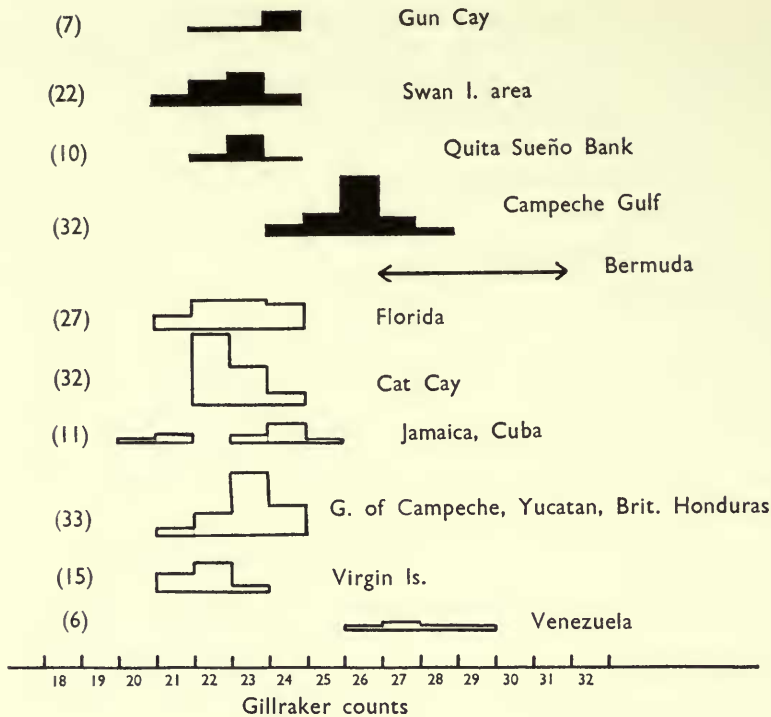


FIG. 22.

Gillraker count frequencies in populations of *Jenkinsia*.

Black, *J. majua*; White, *J. lamprotaenia*.

Numbers in sample placed in parentheses. Rakers counted on lower part of first arch, including one at angle when present.

Note on Synonymy

As already outlined under the generic notes, two principal non-meristic characters are here used to define the species. I have examined the types of *Clupea lamprotaenia* and *Dussumieria stolifera*, and in both cases premaxillary teeth are present, and the posterior fontanelles are divided anteriorly by a wedge of bone, in front of which is a triangular depression. I have also examined specimens from Cat Cay (Bahamas), St. John (Virgin Islands), Monroe County (Florida), the Cayman Islands, Cuba, British Honduras, and the Gulf of Campeche, and these agree with the types. Recently Collette (1962) has re-examined Bean's four type specimens of *Stolephorus viridis* and has shown that in fact two species are represented. The first species, which has a gillraker count of 37 and 39, he believes to be the only Bermuda species; the second, represented by two rather damaged specimens with gillraker counts of 30 and 32, he places with *J. lamprotaenia* and, since there is no other evidence of this species in Bermuda, believes the specimens to have been included in error. He places *J. bermudana* Rivas in the synonymy of *J. viridis*, and informs me (*in litt.*) that the types of both these two species have premaxillary

teeth. Since the presence of premaxillary teeth is so exactly correlated with the fontanelle character there seems little reason to separate the Bermuda species from *J. lamprotaenia* at specific level; I agree however that the specimens with low gill-raker counts from Bermuda may well have come from another locality.

The pre-maxillary teeth are usually obvious and I have seen them in the smallest specimen available, a fish of only 18 mm. Although the teeth may be deciduous, the complete series rarely occurring, some can always be found.

On the basis of published descriptions, the fishes from Bermuda and from Venezuela can clearly be distinguished on gillraker counts (see Text-fig. 22), both having similar and much higher counts than the rest. In numbers of dorsal and anal rays however, there is no evidence (Text-fig. 21) that any one population of *J. lamprotaenia* differs significantly from the rest, although no fishes with only 11 dorsal rays have been recorded from Jamaica or Cat Cay. The latter two populations also agree in being more slender (Text-fig. 20—small dots and crosses) but more specimens are required before they can be positively separated from the Florida and other populations. In turn, the Florida fishes have slightly larger eyes (9.1–11.5% of standard length in the size group 31–36 mm.; compared with 7.7–8.9 in specimens from Jamaica and Cat Cay of 31–55 mm.), but fishes from the Virgin Islands are intermediate and closely resemble the Jamaica specimens (8.5–9.0% in fishes of 37–43 mm.).

Thus on the basis of the present collections there is reason to believe that only the Bermuda and Venezuela populations have diverged sufficiently to be recognized as a distinct subspecies.

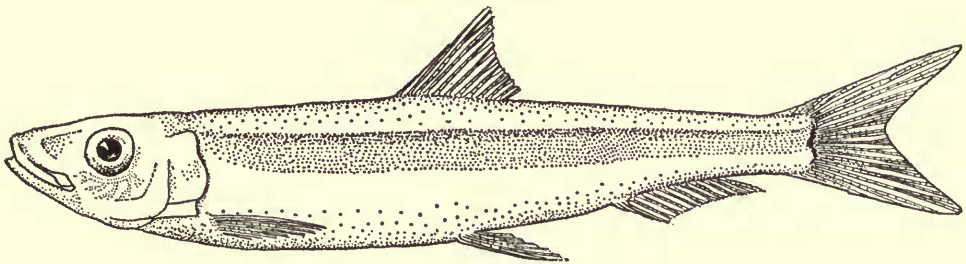


FIG. 23.

Jenkinsia lamprotaenia. From a specimen 51 mm. standard length, Cat Cay, Bahamas. Scales omitted.

DESCRIPTION. Based on the types of *Clupea lamprotaenia* (54.0 and 55.8 mm.) from Jamaica, ten fishes (46.7–52.4 mm.) from Cat Cay (Bahamas), five of the types of *Dussumieria stolidifera* (31.0–35.7 mm.) from Key West (Florida), ten fishes (33.9–36.2 mm.) from Monroe County (Florida), and five fishes (37.7–43.3 mm.) from St. John (Virgin Islands). Meristic counts include 101 specimens (see Text-figs. 20–22).

In percentages of standard length: body depth 14.4–19.1, head length¹ 23.5–28.7, snout length 7.3–9.1, eye diameter 7.7–11.5, post-orbital distance 7.9–9.6, pectoral

¹ Measured to indentation of posterior margin of operculum, i.e. a horizontal measurement; cf. *Spratelloides*, p. 344.

length 12·8–16·8, pelvic length 10·7–13·9, pre-dorsal distance 44·8–50·1, pre-pelvic distance 52·2–58·5, pre-anal distance 71·0–82·0.

Body moderately compressed, its depth much less than head length. Snout pointed, equal to eye (except in Florida and Virgin Islands specimens). Maxilla reaching beyond front border of eye, but not to pupil. Post-orbital equal or larger than snout, larger than eye (except in Florida and Virgin Islands specimens).

Posterior fontanelles broadly separated by wedge of bone (frontals) anteriorly, as shown in Text-fig. 32a. A shallow triangular depression in front of fontanelles containing a branched posterior portion of the transverse frontal sensory canal.

Premaxilla with a single series of conical pointed teeth, often deciduous. Dorsal origin a little nearer snout than caudal base or equidistant. Pelvic origin under middle of dorsal, nearer to caudal base than to snout. Anal origin equidistant between pelvic origin and caudal base.

Dorsal ii 9–11, pectoral i 11–13, pelvic i 7, anal ii–iii 10–13 (total 13–16).

Gillrakers 20–31 on the lower part of the anterior arch (including one at angle).

Scales in lateral series approximately 35–40.

Vertebrae 38 (in a type specimen of *Dussumieria stolifera*).

SYNTYPES. Jamaica. B.M. (N.H.), 1962.7.19.3–4.

COLOUR IN ALCOHOL. Back and sides light brown, with a double line of melanophores down back and extending forwards along frontals to premaxillary symphysis. A broad silvery band along flanks, almost as wide as eye diameter. Lower flanks and belly light brown or cream. Pigment at base of caudal fin.

DISTRIBUTION. Bermuda, Bahamas, Florida; Cuba, Jamaica to Puerto Rico and Virgin Islands; Gulf of Campeche and British Honduras; Venezuela (see Martin, 1955).

Two subspecies are described here, the Bermuda and Venezuela fishes being separated from the rest by their high gillraker count. Although the latter two populations are also well separated geographically from each other (as in the case of the Red Sea and China populations of *Dussumieria*), they both differ so sharply from the remainder that I am forced to recognize them as distinct; future work may well show differences between the two.

Jenkinsia lamprotaenia lamprotaenia (Gosse)

Clupea lamprotaenia Gosse, 1851, *Naturalists Sojourn in Jamaica*: 291, pl. 1, fig. 2 (Type locality: Jamaica). (For remainder of synonymy, see under species for *Dussumieria stolifera* and *Jenkinsia lamprotaenia*).

DIAGNOSIS. Distinguished from Bermuda and Venezuela populations by its lower gillraker count (20–24) as shown in Text-fig. 22.

TYPE. *J. lamprotaenia* (Gosse), Jamaica (syntypes in Brit. Mus. (Nat. Hist.)).

Jenkinsia lamprotaenia viridis (Bean)

Stolephorus viridis Bean, 1912, *Proc. biol. Soc. Wash.*, 25: 122 (Type locality: Bermuda).

Jenkinsia lamprotaenia Hollister, 1936, *Zoologica*, 21 (4): 276, figs. 40–44 (Caudal skeleton).

Jenkinsia bermudana Rivas, 1946, *Smithson. Misc. Coll.*, 106 (14): 2, fig. 1, pl. 1 (Type locality: Bermuda).

DIAGNOSIS. Distinguished from above by its higher gillraker count (26-31) as shown in Text-fig. 23.

TYPE. *Stolephorus viridis* Bean, Bermuda (U.S.N.M. 74084).

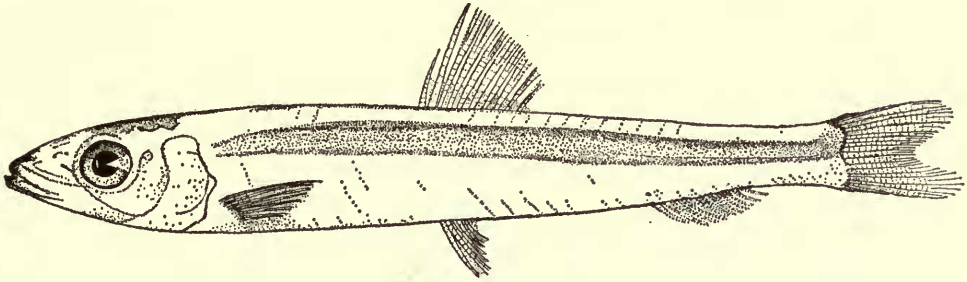


FIG. 24.

Jenkinsia majua sp. nov. Holotype, 53.8 mm. standard length.
(Drawn by Miss Carolyn Reusch.)

Jenkinsia majua sp. nov.

(Text-fig. 24)

DESCRIPTION. Based on the type and seventeen other fishes (45.7-53.8 mm.) from Arcas Cay, Campeche Bank, six fishes (29.3, 36.1-48.4 mm.) from Swan Island, and five fishes (30.1-38.2 mm.) from Gun Cay, Bahamas.

In percentages of standard length: body depth (10.6) 11.3-14.9, head length 20.5-24.4, snout length (6.6) 7.1-8.3, eye diameter 5.3-7.6, post-orbital distance 7.2-9.2, pectoral length 10.3-12.3, pelvic length 8.4-11.8, pre-dorsal distance 45.5-51.0, pre-pelvic distance 49.0-57.5, pre-anal distance 73.0-81.3.

Body moderately compressed, its depth much less than head length. Snout pointed, greater than eye diameter. Maxilla reaching to just beyond anterior eye border, but not to pupil. Post-orbital roughly equal to snout length.

Posterior fontanelles narrowly divided by arm of supra-occipital; a small wedge of bone only between anterior ends of fontanelles (see Text-fig. 32b); frontals domed or flat in front of fontanelles.

Pre-maxillary teeth either absent, or so deciduous that none have been found.

Dorsal origin a little nearer snout than caudal base or just equidistant. Pelvic origin below middle of dorsal, nearer to caudal base than to snout, and nearer anal origin than pectoral base. Anal origin equidistant between pelvic origin and caudal base.

Dorsal ii 9-11, pectoral i 11-12, pelvic i 7, anal ii-iii 9-11 (total 11-13).

Gillrakers 21-28 on lower part of anterior arch (including one at angle when present).

Scales in lateral series approximately 35-40.

COLOUR IN ALCOHOL. Uniform light brown with broad lateral silvery streak a little narrower than eye. Two lines of melanophores down back. Base of caudal pigmented.

DISTRIBUTION. Gulf of Campeche ; Swan Island and Gun Cay (Bahamas) ; and NW. coast of Caribbean Sea.

I would like to record here my gratitude to Dr. Loren P. Woods of the Chicago Natural History Museum for his generosity in allowing me to describe this new species after he had himself begun a preliminary description, and also for so willingly making his material available to me. I have retained the specific name *majua* chosen by him, which is the Cuban name for *Jenkinsia* spp.

Specimens of *J. majua* from Gun Cay and from localities in the Caribbean have a lower gillraker count than do those from the type locality, Campeche Bank (see Text-fig. 22). The difference is one of modal numbers, but the overlap between the two groups is slight, three specimens from Campeche Bank having a low count. The Campeche population seems to be sufficiently isolated from the rest (at least as far as the available material can indicate) for this difference to be given sub-specific rank. No other differences have been found.

- a. Gillrakers on lower part of anterior arch 24-28, mode 26 . . . *J. majua majua*
 b. Gillrakers on lower part of anterior arch 21-24, mode 23 . . . *J. majua woodsi*

Jenkinsia majua majua

Distinguished by a slightly higher range and modal gillraker count. Apparently confined to the Gulf of Campeche and an area to the north of Yucatan.

TYPE. *J. majua* (see list of Study Material).

Jenkinsia majua woodsi subsp. nov.

Distinguished from the above by a slightly lower range and modal gillraker count. Distributed in the Bahamas (Gun Cay), and the N.W. coast of the Caribbean (British Honduras, Swan I., Quita Sueño and Serrano Cays).

Named for Dr. Loren P. Woods.

HOLOTYPE AND PARATYPES. See list of Study Material.

SYSTEMATIC CHARACTERS

In the following section are discussed certain dussumieriid features which are of value in defining subfamilies, tribes, genera and species. Some, such as scutes, have not been utilized before ; others have either been missed or have received passing mention only.

Scutes

Although the round herrings generally lack scutes, all possess in one form or another a single scute lying immediately in front of the pelvic fin. This scute was figured by Chapman (1948) for *Etrumeus*. It is essentially similar to the w-shaped scute shown here for *Spratelloides delicatulus* (Text-fig. 25) and it is found also in *Dussumieria* and in all members of the tribe Spratelloidini. Chapman (*loc. cit.*) shows a second, triangular scute just between the pelvic fin bases in *Etrumeus* ;

I have not found this in *Dussumieria* nor in the Spratelloidini. The anterior scute has been referred to as a "modified" scute (Chapman *loc. cit.*, Whitehead 1962a), but this may imply an erroneous direction to scute evolution (see p. 367 below).

A second type of pelvic scute is found in the Ehiravini. This scute more closely resembles the typical clupeid scute, having lateral ascending arms rising just in front of the pelvic fins, but the central portion of the scute is rounded, not keeled (Text-fig. 26). The ascending arms are very thin, and will conform to the body contours in wrinkled specimens. This pelvic scute was noticed by Bertin (1943) in *Gilchristella* and *Sauvagella* and figured in the latter, but he referred to it as "l'écaille verticale qui précède cette nagoire". The arms of the scute lie below the scales and appear to be embedded in the skin.

In *Gilchristella aestuarius* alone there are also six to nine similarly spined, but slightly shorter scutes lying between the pectoral and pelvic fin bases (Text-fig. 27). All the specimens examined lacked a scute immediately in front of the pelvic scute. In no case were post-pelvic scutes present. These abdominal scutes are also rounded ventrally, not keeled. They are again very thin and are easily overlooked unless the specimen is stripped of scales and thoroughly dried.

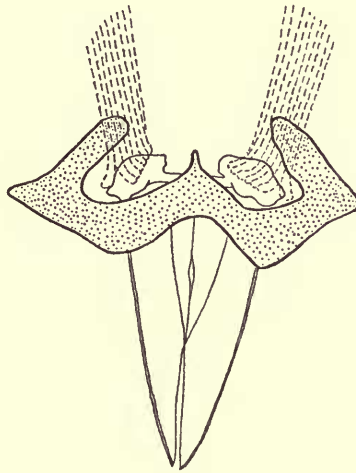


FIG. 25.

The w-shaped pelvic scute (stippled) in *Spratelloides delicatulus*. Ventral view, pelvic finrays shown by broken lines.

Previous records of abdominal scutes in the round herrings have all proved erroneous. Thus Fowler (1941) was correct to presume that the 9 pre-pelvic and 7 post-pelvic scutes shown by Sauvage (1891) for *Gilchristella madagascariensis* were an artist's error: the entire figure is a poor one and there are no such scutes in the types (see Bertin, 1943). The "hard sharp keel on the thoracic region in front of the pectorals" described by Barnard (1925) for *G. aestuarius* is not due to scutes,

but is the sharp keel formed by the ventrally apposed edges of the two coracoids ; it occurs in other species also. The scuted *Pellonulops* Smith was almost certainly based on a clupeid.

Taken in conjunction with other characters (especially numbers of branchiostegal rays) the "modified" w-shaped pelvic scute may perhaps be the primitive form from which fully scuted species have arisen. To some extent the variation in scute development in the round herrings resembles that of the anchovies, where, however, ventral scutes are more common. In the most widespread (and perhaps most

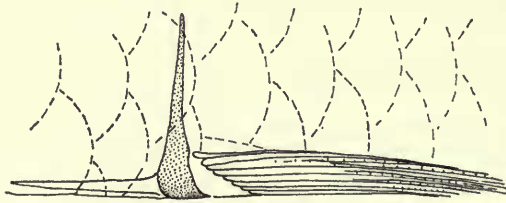


FIG. 26.

Left pelvic scute in *Ehirava malabaricus* (stippled) showing ascending lateral arm.

primitive) anchovy, *Engraulis encrasicolus* (and its allied forms in Australia, America and Japan) there is a single pelvic scute only, which is of the spined, *S. malabaricus* type. This is the case also in all the American anchovies. Of the more specialized anchovies of the Indo-Pacific region, species of *Stolephorus* have up to six or seven keeled scutes, each with a backwardly directed spine between the pectoral and pelvic bases ; *Thrissocles baelama* has both pre- and post-pelvic scutes ; and other species of *Thrissocles*, as well as *Setipinna*, have in addition a few scutes in front of the pectorals also. In the Clupeidae scutes always appear to be present both in front of and behind the pelvic fins. Engraulidae and Clupeidae both have the spined pelvic scute and it seems clear that the evolution of this pelvic scute preceded the evolution of the other abdominal scutes. The pelvic scute may perhaps be the most important functionally, possibly lending support to the pelvic fin ; thus in specimens from all three families I have found a small ligament arising from a point about half way along the posterior edge of the spine of the pelvic scute. This ligament is attached near the base of the outer (or upper) half of the first pelvic ray. It does not occur in those round herrings which have a w-shaped pelvic scute. The

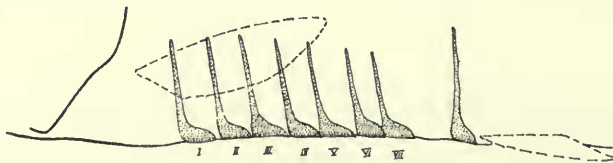


FIG. 27.

Pelvic, and seven pre-pelvic scutes (stippled) in *Gilchristella aestuarius*. Left lateral view. Pectoral and pelvic fins indicated by broken lines.

presence of the ligament suggests that the spined scute plays some role in the movements of the pelvic fins. The abdominal scutes, however, may have had a very different evolutionary history, although closely resembling the pelvic scute in their modern form.

Mention should be made of Chapman's (1944) belief that the abdominal scutes in the Engraulidae are derived from the ventral myorhabdoi (which occur from anus to caudal base in engraulids; and occur anterior to the anus but not behind it in clupeids). This author argued that the possession of ventral scutes is a primitive character in the clupeids "because of the theoretical necessity of the possession of ventral myorhabdoi by antecedent clupeoids"; he notes the absence of these myorhabdoi in the Dussumieriidae (i.e. in *Etrumeus*). Ontogenetic studies might support this view, but such a direction to scute evolution contradicts the evidence of several other characters, and especially that of branchiostegal ray number.

Upper and Lower Jaws

The lower jaw in the Dussumieriidae very closely resembles the lower jaw of the Clupeidae and there appear to be no consistent differences which could serve to separate the two on this character. It is worth noting that the lower jaw in the cretaceous *Clupavus* (i.e. *C. neocomiensis* (Bassani) figured by Arambourg, 1954) is also identical to the normal clupeid condition.

The upper jaw elements, although very similar in the two families, are generally narrower in the round herrings. In the Dussumieriinae in particular, the posterior supra-maxilla is not more than half as deep as the maxilla and in *Etrumeus* it is only about a quarter as deep (see Text-fig. 28d and e). In the Spratelloidinae the posterior supra-maxilla is more paddle-shaped, the expanded portion being equal to or a little deeper than the deepest part of the maxilla, but it is still a narrower bone than in the clupeids, being at least five times as long as deep (see Text-fig. 28a, b and f and compare with a fairly typical clupeid, *Harengula ovalis*, Text-fig. 28c).

A second, anterior supra-maxilla is present in some round herrings but not in others. In the Dussumieriinae, *Dussumieria* has a second supra-maxilla, but *Etrumeus* does not; in the Spratelloidinae this bone is present in *Spratelloides gracilis* and *S. delicatulus*, but is absent in the Ehiravini as well as in *Jenkinsia*. The importance of this little bone in the phylogeny of the group is questionable, but it is worth noting that amongst the Spratelloidinae it is consistently absent in the species with spined pelvic scutes, but present in fishes with w-shaped pelvic scutes (except *Jenkinsia*). When present, the second supra-maxilla is a thin and plate-like bone lying just below the anterior shaft of the first supra-maxilla. Its shape is somewhat variable.

The lower edge of the maxilla is in most dussumieriids fairly evenly rounded but in *E. malabaricus* it is excavated anteriorly as in some clupeids. The lower edge bears a single row of fine teeth along most of its length.

The premaxilla is a short and rather narrow bone in the Dussumieriidae. It bears teeth in both *Etrumeus* and *Dussumieria* but of the Spratelloidinae only *Jenkinsia lamprotaenia* and members of the Ehiravini have toothed premaxillae (species again

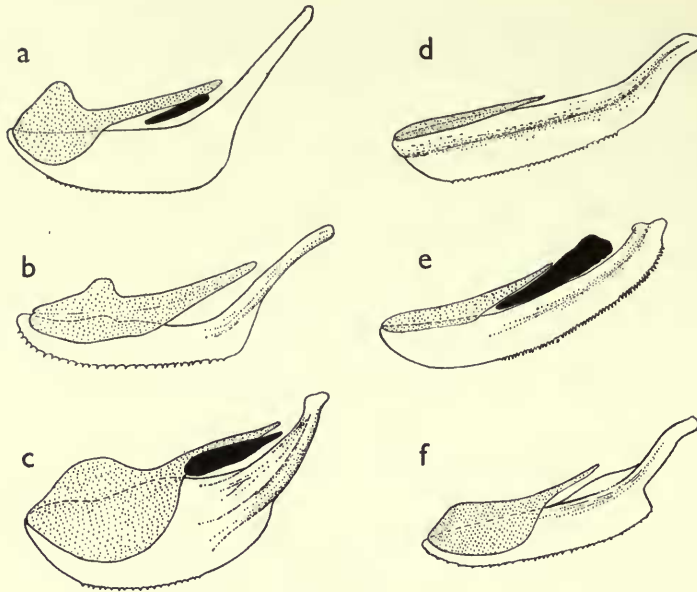


FIG. 28.

Upper jaw elements in species of round herring. Maxilla, plain; 1st (anterior) supra-maxilla, black; 2nd (posterior) supra-maxilla, stippled.

- a. *Spratelloides delicatulus* 41 mm.
- b. *Jenkinsia lamprotaenia* 34 mm.
- c. *Harengula ovalis* 112 mm. (Clupeidae).
- d. *Etrumeus teres* 88 mm.
- e. *Dussumieria acuta* 100 mm.
- f. *Ehirava malabaricus* 58 mm.

which lack a second supra-maxilla). The premaxillary teeth and the anterior supra-maxilla are probably primitive characters whose independent loss in some genera but not others is to be expected.

Branchiostegal Rays

A principle division between the Spratelloidinae and the Dussumieriinae can be made on numbers of branchiostegal rays (6-7 in the former, 14-20 in the latter). In both groups the rays are borne on the epi- and the ceratohyal. In the Spratelloidinae the ceratohyal is excavated ventrally at the head of each ray, as is the case in some (if not all) Clupeids (see Chapman *loc. cit.*), but in both *Etrumeus* and *Dussumieria* the lower edge of the ceratohyal is smooth (Text-fig. 29a-d). The individual rays, and especially the posterior ones, are broader in the Spratelloidinae than in the Dussumieriinae.

There seems little doubt that generally speaking, reduction in the number of branchiostegal rays in the clupeoid fishes has been a progressive evolutionary trend. It is therefore tempting to consider all other differences between the Dussumieriinae

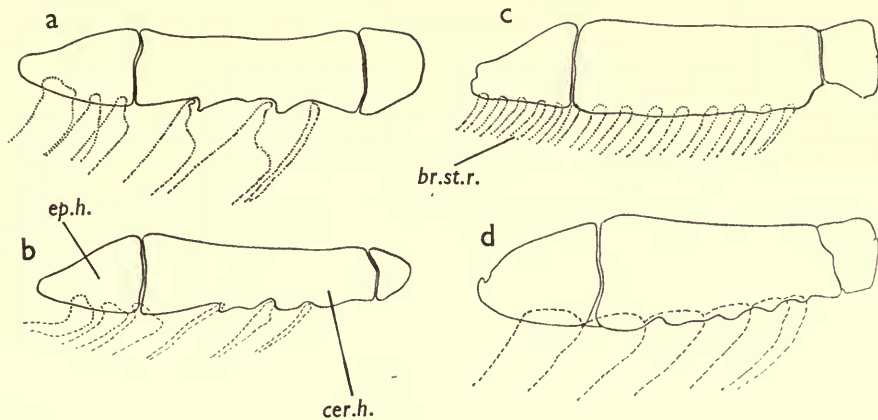


FIG. 29.

Hyoid bones and attachment of branchiostegal rays in species of round herring.

- a. *Spratelloides delicatulus* 41 mm.
 b. *Jenkinsia lamprotaenia* 34 mm.
 c. *Dussumieria acuta* 100 mm.
 d. *Gilchristella aestuarius* 53 mm.
 ep.h. epihyal.
 cer.h. ceratohyal.
 br.st.r. branchiostegal rays.

and the *Spratelloidinae* as evidence of the primitiveness of the former, especially where a series (such as the development of the "cleithral flap") is concerned. Certainly the evidence of branchiostegal ray numbers suggests the direction of scute evolution, from a simple w-shaped pelvic scute to the spined scute and thus to the fully keeled scutes of the *Clupeidae*.

Shape of Gill Opening and Bones of Opercular Series

In the series *Etrumeus-Dussumieria-Spratelloides* there is a steady development of a flap of skin on the postero-ventral angle of the cleithrum (the cleithral flap) as shown in Text-fig. 30a-c. In *Etrumeus* the posterior angle of the gill opening is an approximate right-angle and there is usually no flap of skin. In *Dussumieria* the posterior angle is more acute and individuals show varying degrees of development of the flap. These two genera also differ in the posterior outline of the gill opening, from almost straight and vertical in *Etrumeus*, to curved in *Dussumieria*. In *Spratelloides* the flap of skin is raised markedly above the ventral line of the gill opening and is indented anteriorly, while the posterior outline of the gill opening is rather irregularly shaped, conforming to the indentation in the posterior margin of the operculum, especially in juvenile fishes.

It is rather difficult to see what function the "cleithral flap" serves. Where it is well developed, the ventral outline of the inter- and sub-opercular bones and the branchiostegal rays is indented; obviously, in order to seal the gill opening, one development necessitates the other, but it is difficult to determine which developed

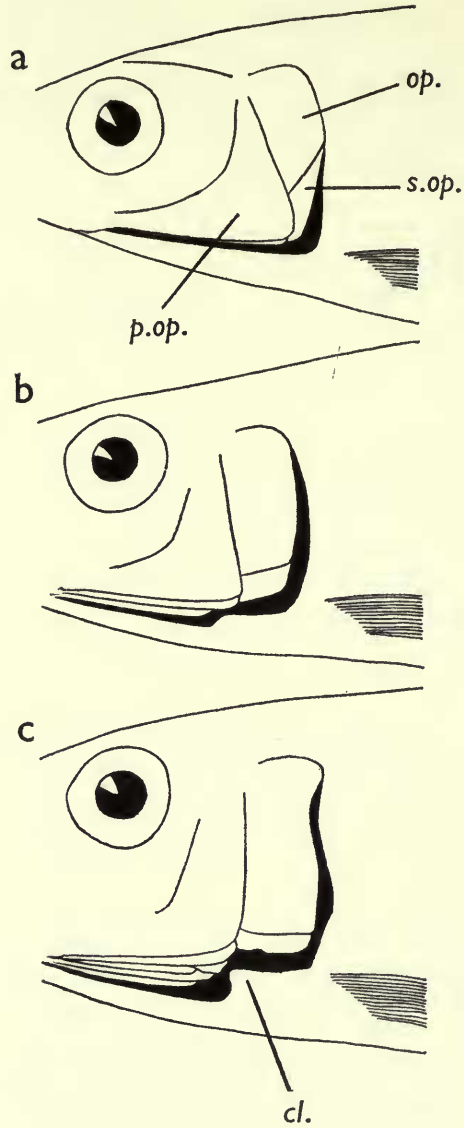


FIG. 30.

The shape of the posterior outline of the gill opening, and of the bones of the opercular series in the species of round herring. Gill cover slightly raised.

- a. *Etrumeus teres*.
- b. *Dussumieria acuta*.
- c. *Spratelloides delicatulus*.
- op. operculum.
- s.op. sub-operculum.
- p.op. pre-operculum.
- cl. "cleithral flap".

first. In *Etrumeus* the interoperculum and branchiostegal rays are barely visible from the outside ; in *Dussumieria* they are more obvious, at least one branchiostegal ray being visible ; in *Spratelloides* three or more branchiostegal rays can be seen, and the penultimate ray is expanded posteriorly. In addition, in *Spratelloides* the gill filaments of the first arch are indented round the cleithral flap.

In members of the tribe Ehiravini and in species of *Jenkinsia* the cleithral flap is very poorly developed, usually approximating to a condition intermediate between *Etrumeus* and *Dussumieria*. This is perhaps surprising since the Ehiravini are in other characters closer to *Spratelloides*. The shape of the operculum and suboperculum in the Ehiravini are also of the dussumieriine type, the angle between these two bones rising posteriorly, and not lying horizontally as in *Spratelloides*. The cleithral flap is well-developed in the clupeid genera *Harengula* and *Sardinella* among others and this is a further reason for expecting it to be large in the Ehiravini. As suggested later (p. 368), the Ehiravini must be considered a group which, although in several ways nearer to the Clupeidae than are the Spratelloidini, have none the less retained some primitive features reminiscent of the Dussumieriinae.

As in the development of the cleithral flap, so in the shape of the operculum and suboperculum a progressive change occurs between *Etrumeus* and *Spratelloides*, with *Dussumieria* occupying an intermediate position. The most obvious trend is in the angle of the line formed between the operculum and suboperculum. In *Etrumeus* (Text-fig. 30a) the lower edge of the operculum rises at a steep angle which, if projected, would meet the dorsal body profile some distance before the dorsal fin. The suboperculum is thus roughly triangular (with its apex pointing forwards). In *Dussumieria* (Text-fig. 30b) the lower opercular margin is nearer the horizontal and the suboperculum more rectangular. This trend is continued in *Spratelloides*, with a horizontal opercular margin and rectangular suboperculum (Text-fig. 30c).

Together with this change is a progressive deepening of the operculum, and its anterior border (i.e. junction with the preoperculum) becomes more vertical. The ascending limb of the preoperculum thus becomes more upright.

To some extent the *Etrumeus* condition can be equated with that found in the engraulids, and the *Spratelloides* condition to that found in the Clupeids. The resemblance is even more marked when the posterior margin of the operculum is also considered, for in *Harengula* at least, there is a tendency for the upper part of the margin to be excavated, with a corresponding bulge in the posterior gill opening profile. In *Spratelloides*, and especially in juveniles, this excavation of the operculum is most marked, but it does not occur in *Dussumieria* or *Etrumeus*.

Other Features of the Skull

The skull of *Dussumieria acuta* was described and figured by Ridewood (1904), who compared it with several other clupeoids. Chapman (1948) compared the osteology of *Etrumeus teres* with that of the clupeid *Sardinops caerulea* and found six principal differences, which were however shared with the Engraulidae. Some of these differences disappear if the Spratelloidinae are included (numerous branchiostegal rays, smooth lower edge of ceratohyal and lack of ventral scutes). Again, while *S. caerulea* has a single articular head to the hyomandibular, the Dussumieriidae

cannot be absolutely separated from the Clupeidae on this character since in *Alosa finta* at least there are two articular facets (Ridewood, *loc. cit.*, fig. 124).

A major difference between the Dussumieriinae and the Spratelloidinae is the retention in adults of the latter of a pair of fontanelles immediately in front of the supra-occipital. These have been referred to here as the posterior fontanelles, and are shown in Text-figs. 31 and 32. They are bounded anteriorly and laterally by the frontals, and are divided in the midline by a narrow median extension of the supra-occipital, which also forms the posterior margin of the fontanelles.

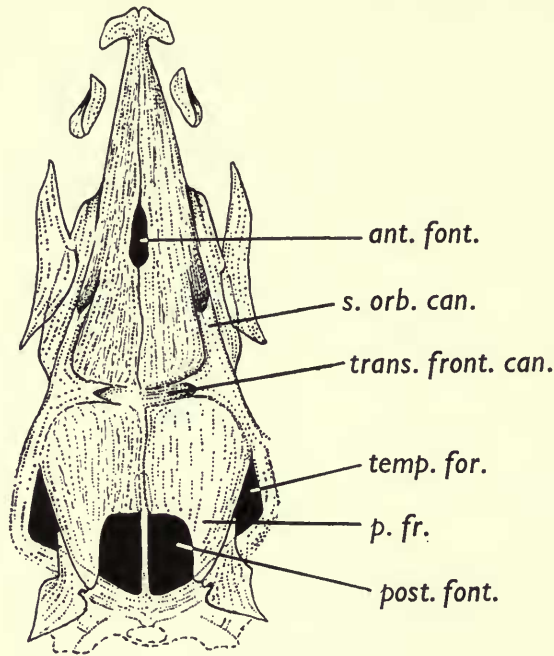


FIG. 31.

Spratelloides delicatulus, dorsal view of cranium showing the anterior and posterior fontanelles and the temporal foramen. From an alizarin stained specimen of 40 mm.

- ant. font.* anterior fontanelle.
s. orb. can. supra-orbital canal.
trans. front. can. transverse frontal canal.
temp. for. temporal foramen.
p. fr. posterior extension of the frontals.
post. font. posterior fontanelle.

No such fontanelles are present in the adults of *Dussumieria* or *Etrumeus*, but in a juvenile of *Dussumieria* of 49 mm. the fontanelles were present and together comprised an area equal to the pupil of the eye.

As has already been pointed out (see p. 349) the form of the fontanelles and of the posterior part of the two frontals is different in the two species of *Jenkinsia*, one resembling the condition found in *Spratelloides* and the other that in the Ehiravini.

Thus in *J. majua* and in species of *Spratelloides*, the posterior median portion of the frontals, while forming a small wedge between the two fontanelles, is not depressed into a shallow triangular hollow, but in juveniles is domed.

In both types of fontanelle formation, the length of the fontanelles decreases with the size of the fish, but more so in *J. lamprotaenia* and the Ehiravini. In large specimens of *Ehirava malabaricus* (of about 60 mm.) the fontanelles are barely apparent. This suggests that the second type of fontanelle formation (i.e. those which are broadly divided anteriorly) is the more primitive of the two. In this respect *J. lamprotaenia* and the Ehiravini show greater affinities with the Dussumieriinae than do species of *Spratelloides* or *J. majua*.

In both the Spratelloidinae and the Dussumieriinae there is a transverse commissure linking the supra-orbital sensory canals a little behind the centre of the orbits (see Text-fig. 32). This has been referred to here as the transverse frontal canal

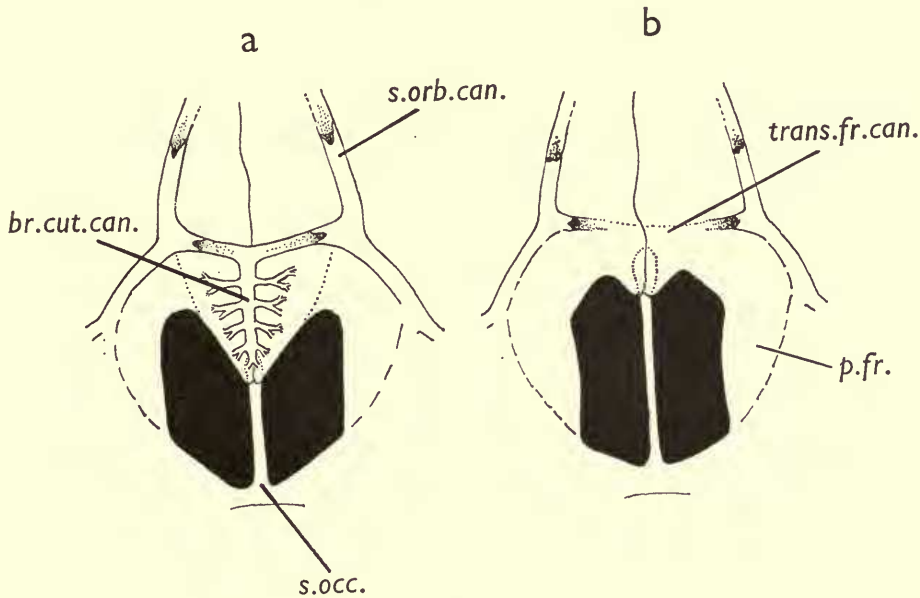


FIG. 32.

Two types of posterior fontanelle (black) found in members of the Spratelloidinae. Dorsal view of head with skin removed to expose fontanelles.

a. *Jenkinisia lamprotaenia* (at 35 mm.) showing large wedge of bone (part of frontals) dividing anterior part of fontanelles. Within the depressed area of this wedge lies a branched, cutaneous sensory canal.

b. *Jenkinisia majua* (at 40 mm.) showing posterior fontanelles only narrowly divided and with no cutaneous sensory canal.

s. orb. can. supra-orbital canal.

p. fr. posterior extension of the frontals.

trans. fr. can. transverse frontal canal.

s. occ. supra-occipital.

br. cut. can. branched cutaneous canal lying in triangular depression.

(the epiphysial canal of Weitzman, 1962). The central part of this canal is cutaneous and not roofed over with bone. Extending posteriorly from this canal there is, in certain dussumieriids, a branched cutaneous canal which reaches to the apex of the triangular depression mentioned earlier. This is found in the Dussumieriinae, in the Ehiravini, and in *Jenkinsia lamprotaenia*, i.e. in those fishes which have a pronounced triangular depression behind the transverse frontal canal. In *J. lamprotaenia* and the Ehiravini this triangular depression is most marked; it also closely resembles the condition found in juvenile *D. acuta*. In adult dussumieriines the triangular depression reaches to the posterior border of the skull, the fontanelles having been occluded by posterior growth of the frontals.

Although the posterior branch leading from the transverse frontal canal appears to be usually absent in those fishes in which the triangular depression is either poorly developed or absent, there is a small canal in large specimens of *Spratelloides*. The triangular depression and its relationship to the cephalic canals was recently mentioned by Gunter & Demoran (1961) in dealing with the Gulf Menhaden (*Brevoortia patronus*); they comment on the absence in the literature of any description of this part of the cephalic sensory system, and they refer to it as the "cephalic spongy sensory area".

The lateral edges of the triangular depression are usually well-defined. In some dorosomatids and clupeids these lateral edges are wedge-shaped and bear a few or many longitudinal striae (see Whitehead, 1962b) but this is only faintly apparent in the dussumieriids (i.e. in *Dussumieria*).

SPECIATION IN THE DUSSUMIERIIDAE

The round herrings are an old group, with a lineage extending back at least to Cretaceous times (if *Clupavus* is to be accepted as a dussumieriid). It is not surprising therefore to find a number of fairly well defined genera which can be clearly separated on osteological grounds. But intrageneric variation is usually small and I have here recognized one or at most two species only per genus, although in some cases the species can then be subdivided into subspecies. The situation is however, one in which the museum worker must decide in a rather arbitrary manner where the boundary between species and subspecies and demes should lie.

If subspecies are defined as geographically isolated members of an interbreeding population which differ consistently in at least one character from the rest of the population, then there is a case for subdividing the forms of *Dussumieria*. But, as already pointed out, the geographically and morphologically intermediate forms so effectively bridge the gap between the extremes that no practical boundaries can be drawn. There is thus reason to suppose that populations of *D. acuta* in China and the Red Sea are reproductively linked, however tenuous that link may be.

In the case of forms which are distinct from each other but whose geographical ranges overlap (e.g. in the two species of *Spratelloides* or *Jenkinsia*) there seems good reason to believe the two forms to be separate species. But where the geographical ranges do not overlap (as in *Etrumeus*) it would seem that the probable value (or weight) of each particular morphological character must be assessed. Thus in *Etrumeus* the differences between populations are small and are of the same order

as those found in populations of *Dussumieria*. In only a single case (the South African population of *Etrumeus*) is there a clear-cut difference. But since this rests solely on a single dorsal ray, it would be unrealistic to consider this of specific value in view of the degree of variation in the rest of the genus.

Since there is as yet no generally applicable criterion of a bio-species other than that it is reproductively isolated from its nearest relatives, the conclusions reached in the museum must contain an element of guesswork. Thus the present classification provides a framework, the details of which will no doubt be altered as larger collections become available.

ORIGIN AND RELATIONSHIPS OF THE ROUND HERRINGS

In attempting to work out a probable phylogeny of the Dussumieriidae and their relationship to the Clupeidae, it is possible to suggest morphological series for several characters. The most obvious and perhaps most reliable trend is the reduction in numbers of branchiostegal rays, with the Dussumieriinae the most primitive and the Spratelloidinae the most advanced. If this is accepted, then it is difficult not to correlate with it scute development, the w-shaped pelvic scute being the most primitive, and the scutes of *Gilchristella aestuarius* being the most advanced form in the Dussumieriidae as a whole. From *G. aestuarius* a fully scuted and keeled clupeid is a logical development. In the shape of the gill opening, the development of the cleithral flap, and the shape of the bones in the opercular series, there is a good transition from *Etrumeus*, through *Dussumieria* to *Spratelloides* (see Text-fig. 30a, b, c), and since these trends also coincide with those of branchiostegal rays and scutes, it would seem at first sight as if the Ehiravini need only be added to the series to make a perfect development through to the Clupeidae. But although the Ehiravini complete the trend in scute development (and compression of the body), and in addition complete also the trends for advance of the pelvics and increase in length of anal, yet in other respects they more closely resemble the Dussumieriinae. Thus the cleithral flap is small, the suboperculum is more nearly triangular, the lower edge of the operculum is less horizontal and the premaxillae bear teeth. But if scute development is a progressive trend, then the place of the Ehiravini seems to be between the Spratelloidinae and the Clupeidae.

Also anomalous in some respects is *Jenkinsia*. Whereas *J. majua* could be placed with *Spratelloides* but for the absence of an anterior supra-maxilla, *J. lamprotaenia* shares with the Ehiravini a toothed premaxilla and a similar shape and development of the posterior fontanelles. Both species however lack the large cleithral flap of *Spratelloides* and thus resemble the Ehiravini. Most likely *Jenkinsia* represents a form which existed before both *Spratelloides* and the Ehiravini diverged fully. Because of its isolation, *Jenkinsia* may still retain early characters which have become lost or modified in *Spratelloides* and the Ehiravini.

The scutes of *G. aestuarius* and the split anal of *S. bianalis* foreshadow trends which become more fully elaborated in the clupeids. In the Ehiravini they probably represent tentative developments which have no adaptive value but which have remained and indicate the type of experiment prevalent amongst ancestors of the modern Clupeidae.

If the phylogeny of the Dussumieriidae and the Clupeidae were to be represented diagrammatically, it would probably be correct in a general way to show the Clupeidae branching from near the split between the Ehiravini and the Spratelloidini, and the latter diverging initially from the Dussumieriinae (Text-fig. 33). Since all these forms have a lower jaw so very different from the long jaw of the Engraulidae (and in addition lack the prominent mesethmoid typical of the anchovies), it seems

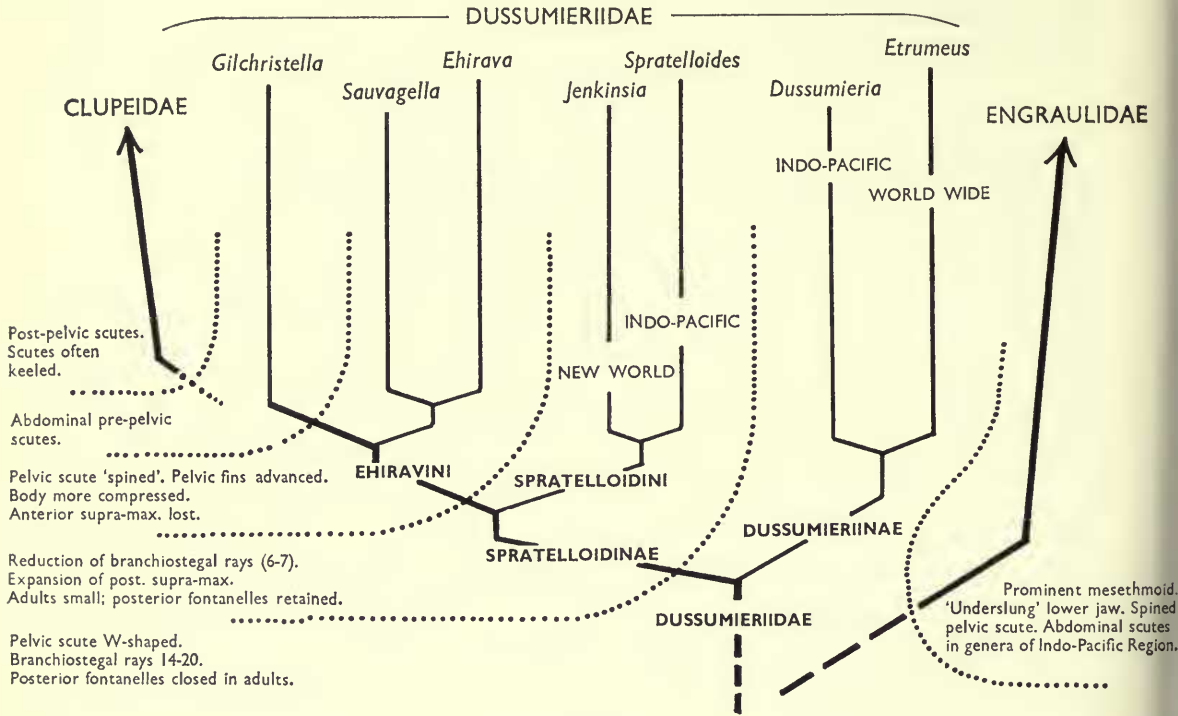


FIG. 33.

A possible phylogeny for the round herrings, indicating stages in the development of certain clupeid-like characters. For further explanation, see text.

reasonable to suggest that, not only did the Engraulidae diverge from the main stem (primitive round herrings) before the Clupeidae did, but that in the Engraulidae the initial trend at least was one of scute development, not degeneration (cf. Jordan & Seale, 1926). Against the proposition that the Engraulidae evolved from a scuted clupeid-like ancestor is the high number of branchiostegal rays in the Engraulidae and the other osteological resemblances which Chapman (1948) found between the anchovies and the Dussumieriinae.

Jordan & Seale (1926) thought an independent development of scutes in both anchovies and herrings unlikely. But in *Engraulis encrasicolus* there is a single pelvic scute only, of the spined type, and as the Ehiravini show, a fully scuted form can be derived from this. Early engraulids may have had a w-shaped pelvic scute,

although it is possible that in the Dussumieriinae and Spratelloidini this type of scute is a degeneration from the spined scute. This possibility, and the implication that the Spratelloidini might have branched off from the Dussumieriinae *after* the Ehiravini had also diverged from the Dussumieriinae, would help to explain the similarities shown by the Ehiravini to the Dussumieriinae rather than to the Spratelloidini. But it also implies the independent reduction of branchiostegal rays in both Ehiravini and Spratelloidini and the parallel evolution of other similarities between these two tribes (small adult size, retention of post-frontal fontanelles, broad posterior supra-maxilla). It seems more likely that the w-shaped pelvic scute marks a step in the evolution of scutes, not a modification, but that it is no longer found in the Engraulidae.

Two further aspects of scute evolution must be mentioned. A striking feature in the present study has been the very constant presence of the pelvic scute, not only in the Dussumieriidae, but in otherwise non-scuted engraulid genera (i.e. in *Engraulis*), as well as in the clupeids. There remains the possibility that this scute has evolved from the pelvic splint bones which are found in some fishes (see Gosline, 1961). Such an evolution demands the expansion of the base of the splint to form either a w-shaped plate or an ascending arm, and at the same time the degeneration of the splint itself (which normally extends along the outer face of the first pelvic ray). Such a development is at least a possibility since splint bones are not present in the Dussumieriidae, Clupeidae or Engraulidae, but occur in certain other lower teleosts (*Tarpon*, *Chanos*, *Salmo*—see Gosline, 1961).

The second aspect of scute evolution is the question whether scutes could have evolved quite simply from the median series of abdominal scales without the prior evolution of the pelvic scute. Thus in *Denticeps clupeoides*, the only extant member of the family Denticipitidae (Clausen, 1959), pre- and post-pelvic abdominal scutes are present, but there are no pelvic scutes comparable to the pelvic scutes of the clupeids, engraulids or dussumieriids. However, the scutes in *Denticeps* are clearly the median series of scales which have become sharply folded in the midline and have developed posterior spines. In appearance they strongly resemble the spiny scutes of the engraulids (e.g. *Stolephorus*) but they differ in one important respect: they have no ascending arms, but are rounded laterally like a scale. The presence of ascending arms in the three clupeoid families discussed here and the constancy of the pelvic scute, seem to indicate that the evolution of the clupeoid scutes was in some manner linked to the evolution of the pelvic scute, and that the evolution of the scutes in *Denticeps* has followed a rather different course; it may be significant that the latter has no pelvic splint bones.

The fossil evidence throws a certain amount of light on the problem, but branchiostegal counts have never been certain and the descriptions are not always adequate to decide whether a dussumieriine or a spratelloidine is involved.

The earliest record of a round herring is probably *Clupavus neocomiensis* (Bassani). Arambourg (1954) placed specimens from the Cretaceous of Morocco in the Dussumieriidae because of their absence of scutes. His figures of the head (figs. 14 and 16) very much resemble *Etrumeus*, especially in the shape of the opercular series, but vertebral numbers (39 or 40) are more those of a modern spratelloidine. Un-

fortunately exact branchiostegal counts were not possible, but there were probably not more than twelve.

The importance of *Clupavus* lies in the links which Arambourg (1950 and 1954) believed that it showed with the primitive actinopterygians (palaeoniscids, holosteans and halecostomes). These were principally in the large parietals, which meet in the midline, and the presence of a pair of posteriorly directed canals branching from the supra-orbital canals and converging across the posterior parts of the frontals (but not meeting each other). But from the position and size of the large parietals, it is tempting to suppose that they are, at least in part, the posterior fontanelles typically found in small round herrings. This would explain the rather abrupt termination of the frontal sensory canal at the border between the frontals and the parietals. In the specimen figured by Arambourg (1954, fig. 15 and pl. 3, fig. 4) much of the median part of both parietals is missing, as also is an area between the anterior ends of the frontals. The latter almost exactly corresponds in shape and position to the normal anterior fontanelle of round herrings. *Clupavus neocomiensis*, as Arambourg recognized, is in many respects very clupeid-like, and such large parietals meeting in the midline seem unlikely. In the round herrings the parietals are fairly small and are well separated (see Text-fig. 31).

With regard to the sensory canal system, in the modern round herrings there is no frontal branch similar to that found in *Clupavus*. However, Arambourg (1950 and 1954) was mistaken in believing that *Clupavus* is unique amongst the teleosts in possessing such a frontal branch. While it may well be absent in the higher teleosts, it is certainly present in the characid genus *Brycon* (the parietal canal in Weitzman, 1962), and Dr. P. H. Greenwood has shown me a short but well-formed canal in the problematical *Denticeps*.

Arambourg (1954) also makes the important observation that differentiation within the clupeoid fishes was well-established by the beginning of the Cretaceous and he mentions the coexistence amongst others of *Parachanos*, *Clupavus* and *Diplomystus*. Presumably the Engraulidae had evolved by this time.

In Text-fig. 33 is shown a possible phylogeny of the round herrings with indications of the points at which particular characters first appear. As discussed above, the Ehiravini are difficult to place in any such scheme because they share characters both with the Spratelloidini and with the Dussumieriinae as well as with the Clupeidae. Thus the diagram presents one of several possible schemes, but the one which appears to involve the least number of contradictions. Whatever scheme is adopted, the independent loss of one or more characters in genera which are not closely related must be assumed.

It is also important to decide which features are primitive and which specialized. Thus *Dussumieria* differs from *Etrumeus* in having two supra-maxillae and more advanced pelvics, but *Etrumeus* only is represented in the fossil record (see Bertin, 1943, Arambourg, 1945). On the other hand, *Leptolepis* as well as the more primitive isospondyls such as *Elops* or *Albula*, all have rather advanced pelvics and two supra-maxillae (except *Albula* with one). Thus *Dussumieria* may in fact be the more primitive of the two. Unfortunately other fossil genera referred to the Dussumieriidae (*Lygisma*, *Quaesita* and *Sternbergia*) are either inadequately described or too

poorly preserved to be of any value in determining which characters are more primitive. But if the Dussumieriinae as a whole are considered more ancient than the Spratelloidinae, then the following characters must be considered primitive: pre-maxillary teeth, two supra-maxillae (the posterior rather narrow), a small cleithral flap, pelvics set below or perhaps in front of the dorsal (the evidence here is however equivocal), post-frontal fontanelles not retained in the adult (but present possibly in *Clupavus*), suboperculum triangular, scutes absent or represented only by a w-shaped pelvic scute, anal fin fairly short.

The possibility that primitive forms were scuted has been discussed on pp. 356-359. This depends largely on whether the ventral myorhabdoi are in fact homologous with the ventral scutes. Although such an interpretation would certainly explain the resemblance shown by the Ehiravini to the Dussumieriinae, it would presuppose the independent degeneration of the pelvic spined scute to a w-shaped scute in the Spratelloidinae as well as the Dussumieriinae, and would involve several other parallel specializations or losses, as already mentioned. It seems more likely on present evidence that the round herrings are modern representatives of an early non-scuted herring.

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STUDY MATERIAL

The first name is that which is used in this paper ; the second (in parenthesis), that under which the specimens have been labelled hitherto.

Dussumieria acuta

(*D. acuta*)

6 fishes, 121-148 mm., Shihr & Burum, Gulf of Aden (1962.3.26.211-216¹).

(*D. acuta*)

5 fishes, 105-114 mm., Mukalla, Gulf of Aden (1962.3.26.217-221).

14 fishes, 105-120 mm., Singapore (1935.4.12.3-12).

1 fish, 114 mm., Andamans (1889.2.1.2047).

1 fish, 122 mm., Bombay (1889.2.1.2037).

¹ British Museum registration numbers unless stated otherwise.

(D. acuta)-contd.

- 4 fishes, 93-141 mm., Madras (1889.2.1.2042-5).
- 1 fish, 118 mm., Borneo (1868.1.28.81).
- 1 fish, 98 mm., Port Blair (1889.2.1.2046).
- 1 fish, 94 mm., locality unknown (1860.3.19.956).
- 2 fishes, 106-107 mm., Djambi, Sumatra (1934.8.18.12.13).
- 3 fishes, 69-84 mm., Malabar (1889.2.1.2039-41).
- 5 fishes, 82-119 mm., Batavia (1934.8.18.17-19).
- 5 fishes, 92-100 mm., Panci Sumatra (1934.8.18.14-16).
- 5 fishes, 89-100 mm., Batavia (1934.8.18.20-22).
- 5 fishes, 64-114 mm., Haifa, Israel (1962.6.13.4-8).
- 1 fish, 48 mm., Malabar (1889.2.1.2049).
- 20 fishes, 77-107 mm., Haifa, Israel (Sea Fisheries Research Station (Israel) collection).

(D. elopsoides)

- HOLOTYPE, 124 mm., Madura (1867.11.28.17).
- 1 fish, 116 mm., Zool. Soc. Coll. (1852.9.13).
- 1 fish, 88 mm., Amboina (1858.4.21.360).
- 2 fishes, 114-115 mm., Siam (1920.7.13.4-5).
- 1 fish, 101 mm., Amoy, China (1860.7.20.88).
- 12 fishes, 107-115 mm., Calicut (1935.9.20.1-8).
- 1 fish, 118 mm., Foochow (1936.10.7.21).
- 1 fish, 113 mm., Hong Kong (1939.3.23.5).

(D. hasselti)

- HOLOTYPE, 134 mm., Java 1867.11.28.21).
- 3 fishes, 85-88 mm., Coromandel (types of *D. acuta*, Paris Museum, No. 3694).
- 9 fishes, 68-120 mm., Malabar (types of *D. acuta*, Paris Museum, No. 3217).
- 4 fishes, 112-131 mm., Coromandel (types of *D. acuta*, Paris Museum, No. 3697).
- 3 fishes, 89-110 mm., Persian Gulf (coll. Blegvad. Univ. Zool. Mus., Denmark, No. CN 5-7).

Etrumeus teres*(E. teres)*

- 9 fishes, 115-130 mm., Woods Hole, U.S.A. (1934.11.30.1-9).
- 1 fish, 120 mm. approx. (*skeleton*), Woods Hole, U.S.A. (1934.11.30.10).

(E. micropus)

- 87 fishes, 67-78 mm., Nagasaki (1923.2.26.73-82).
- 1 fish, 136 mm., Kobe, Japan (1907.12.23.91).
- 1 fish, 85 mm., Hong Kong (1939.3.23.6).
- 1 fish, 126 mm., Japan (1867.11.28.265).
- 1 fish, 165 mm., Haifa (Sea Fish. Res. Sta. (Israel) collection).
- 8 fishes, 117-149 mm., Natal (1903.2.6.11-17).
- 2 fishes, 133-134 mm., Eilat, Red Sea (Sea Fish. Res. Sta. (Israel) collection).

(E. jacksoniensis)

- 2 fishes, 105-122 mm., Botany Bay (1897.10.27.49-50).

(E. acuminatus)

- 1 fish (HOLOTYPE of *Perkinsia othonops*), 265 mm., California (1891.5.19.210).
- 7 fishes, 109-125 mm., California (1962.6.13.9-15).
- 1 fish, 120 mm. approx. (*skeleton*), California (1962.6.13.16).

Ehirava malabaricus*(E. fluviatilis)*

- 1 fish (HOLOTYPE of *E. fluviatilis*), 48 mm., Ceylon (1929.7.1.1).
 13 fishes, 30-46 mm., Ceylon (1929.7.1.2-9).

(Spratelloides malabaricus)

- 4 fishes, 46-56 mm., Canara (1889.2.1.2052-5).
 1 fish, 40 mm., Malabar (1889.2.1.2048).
 1 fish, 53 mm. (*skeleton*), Malabar (1889.2.1.2050).

Ehirava madagascariensis

- 1 fish (TYPE of *Spratelloides madagascariensis*), 40 mm., Madagascar. (On loan from Paris Museum, No. 3794).
 10 fishes, 41.0-52.5 mm., Buffalo river, Cape Province (1878.1.22.33-43).
 1 fish, 52 mm., Buffalo river, Cape Province (1878.1.22.25).

Gilchristella aestuarius*(Spratelloides aestuarius)*

- 1 fish, 51 mm., Durban (1915.7.6.3).
 1 fish, 53 mm., Durban (1919.9.12.3).
 1 fish, 53 mm., Milnerton lagoon, S. Africa.¹
 1 fish, 45 mm., Knyssa, S. Africa.¹
 1 fish, 40 mm., St. Lucia, S. Africa.¹
 1 fish, 35 mm., Swartkops river, S. Africa.¹
 2 fishes, 42-44 mm., East London, S. Africa (1962.6.13.2 and 3).²
 1 fish, 39 mm., Kei mouth, S. Africa (1962.6.13.1).²
 1 fish, 58 mm., Buffalo river, Cape Province (1878.1.22.24).

(Spratelloides sp.)

- 4 fishes, 37-41 mm., Swartkops river, S. Africa (1905.1.7.1-4).

(Clupea sagax)

- 3 fishes, 28-45 mm., Swartkops river, S. Africa (1898.12.17.9-11).

Sauvagella bianalis*(Spratellomorpha bianalis)*

- 5 fishes, 44-45 mm., Madagascar (TYPES of *Sauvagella bianalis* Bertin, Paris Museum, No. A 5174).

Spratelloides gracilis gracilis*(Spratelloides gracilis)*

- 1 fish (TYPE of *Clupea argyrotaenia* Bleeker), 66 mm., E. Ind. Arch. (1867.11.28.17).
 3 fishes, 68-72 mm., Japan (4.46.8134).
 4 fishes, 66-79 mm., Goto I., Japan (1907.12.23.96-9).
 Many fishes, 52-83 mm., Nagasaki (1923.2.26.31-40).
 Many fishes, 88-93 mm., Wakanoura, Japan (1923.2.26.41-50).
 3 fishes, 56-66 mm., Formosa (1934.8.18.1-3).
 2 fishes, 45-47 mm., Ghardaqa, Red Sea (1935.9.30.10-11).
 Many fishes, post-larvae to 37 mm., Senafir, Gulf Aqaba (1951.1.16.36-60).
 3 fishes, 47-48 mm., Sumatra (1934.8.18.9-11).

¹ On loan from Prof. J. L. B. Smith.² Donated by Prof. J. L. B. Smith.

Spratelloides delicatulus delicatulus*(Spratelloides delicatulus)*

- 5 fishes, 53–70 mm., Hasler collection (1855.9.19.1153–58).
 1 fish, 51 mm., Bonham I. (1874.11.19.65).
 1 fish, 65 mm., purchd. of Dr. Bleeker (1869.11.28.34).
 1 fish, 77 mm., Australia (1851.2.20.14).
 1 fish, 28 mm., Kosi Bay, Zululand (1906.11.19.27).
 29 fishes, 37–44 mm., Seychelles (1927.4.14.13–22).
 5 fishes, 50–53 mm., Thousand Is. (1934.8.18.4–8).
 15 fishes, 28–35 mm., Sulu Prov., Philippines (1933.3.11.25–34).
 10 fishes, 21–49 mm., Firaun I., Gulf of Aqaba (1951.1.16.14–23).
 12 fishes, 42–47 mm., Senafir, Gulf of Aqaba (1951.1.16.24–35).
 22 fishes, 27–35 mm., Cocos-Keeling (1949.1.29.5–26).
 16 fishes, 16–45 mm., Marsa Halaib, Red Sea (1960.3.15.16–31).
 8 fishes, 36–39 mm., Kad Eidwid reefs, Red Sea (1960.3.15.33–39).
 2 fishes, 49–52 mm., G'an, Maldives (1962.1.22.2–3).
 16 fishes, 39–42 mm., Gulf of Aden (1962.6.19.1–16).
 1 fish, 40 mm., alizarin preparation, Marsa Halaib, Red Sea (1960.3.15.32).

Spratelloides delicatulus robustus*(Spratelloides robustus)*

- 5 fishes, 33–68 mm., Port Jackson (1897.10.27.43–47).
 81 fishes, 46–74 mm., coast of N.S.W. (1924.4.30.1–10).

Jenkinsia lamprotaenia lamprotaenia*(Dussumieria stolidifera)*

- SYNTYPES, 15 fishes, 30–36 mm., Key West, Florida (1884.7.7.47–56).

(Jenkinsia lamprotaenia)

- SYNTYPES,¹ 2 fishes, 53–56 mm., Jamaica (1962.7.19.3–4).

(Dussumieria lamprotaenia)

- 5 fishes, 19–22 mm., Cayman Island (1939.5.12.6–9).

(Jenkinsia lamprotaenia)

- 52 fishes, 48–53 mm., Cat Cay, Bahamas (1962.7.21.1–50; *ex*² U.M.M.L. 2317).
 15 fishes, 25–36 mm., Cat Cay, Bahamas (1962.7.21.101–115; *ex*² U.M.M.L. 5066).
 25 fishes, 25–30 mm., St. John, Virgin Islands (1962.7.21.121–145; *ex*² U.M.M.L. 5280).
 5 fishes, 38–44 mm., St. John, Virgin Islands (1962.7.21.116–120; *ex*² U.M.M.L. 5278).
 50 fishes, 33–38 mm., Monroe County, Florida (1962.7.21.51–100; *ex*² U.M.M.L. 6742).
 19 fishes, 39–59 mm., Caribbean (20° 12' N; 91° 59' W) (1962.8.1.1–19; *ex*³ C.N.H.M. 66009).
 6 fishes, 33–39 mm., Tom Owen Cay, British Honduras (1962.8.1.20–25; *ex*³ C.N.H.M. 50028).
 22 fishes, 33–45 mm., Belize, British Honduras (1962.8.1.26–47; *ex*³ C.N.H.M. 9831).
 25 fishes, 24–32 mm., Golfo Batabano, Cuba (1962.8.1.48–72; *ex*³ C.N.H.M. 61363).
 8 fishes, 42–46 mm., off Dry Tortugas (1962.8.1.73–80; *ex*³ C.N.H.M. 61365).
 21 fishes, 23–40 mm., Serrana Rock, Caribbean (1962.8.1.81–101; *ex*³ C.N.H.M. 66012).
 6 fishes, 23–51 mm., Alacran Rock, Gulf of Campeche (1962.8.1.102–107; *ex*³ C.N.H.M. 66010).
 19 fishes, 27–45 mm., Alacran Rock, Gulf of Campeche (1962.8.1.108–126; *ex*³ C.N.H.M. 61366).

¹ Stated by Günther (1868) to be two typical specimens from Gosse's collection.

² Donated by Prof. C. Robins from the collections of the University of Miami Marine Laboratory.

³ Donated by Dr. Loren Woods from the collections of the Chicago Natural History Museum.

Jenkinsia majua majua

- 1 fish, HOLOTYPE, 53.8 mm., Arcas Cay, Campeche Bank (U.S. Nat. Mus., No. 197412).
52 fishes, 25-53 mm., PARATYPES, Arcas Cay, Campeche Bank (Chicago Nat. Hist. Mus. No. 61362).
20 fishes, 45-55 mm., PARATYPES, Arcas Cay, Campeche Bank (1962.8.1.152-171; *ex*⁴ C.N.H.M., No. 66007).
2 fishes, 54 mm., PARATYPES (alizarin) Arcas Cay, Campeche Bank (Chicago Nat. Hist. Mus. No. 66008).
10 fishes, 46-54 mm., PARATYPES, Campeche Banks (1962.7.21.146-155).
25 fishes, 40-44 mm., PARATYPES, Arcas Cay, Campeche Bank (1962.8.1.127-151; *ex*⁴ C.N.H.M. 46265).

Jenkinsia majua woodsi

- 1 fish, 48 mm., HOLOTYPE, Nr. Quita Sueno Bank, Caribbean (U.S. Nat. Mus. No. 197413; *ex*⁴ C.N.H.M., No. 66011).
16 fishes, 40-46 mm., PARATYPES, Nr. Quita Sueno Bank, Caribbean (1962.8.1.173-188; *ex*⁴ C.N.H.M. 66011).
10 fishes, 36-46 mm., PARATYPES, Nr. Quita Sueno Bank, Caribbean (C.N.H.M. 66011).
25 fishes, 31-43 mm., PARATYPES, Nr. Swan I., Caribbean (U.S. Nat. Mus. No. 197413; *ex*⁴ C.N.H.M., No. 66013).
6 fishes, 29-48 mm., PARATYPES, Swan I., Caribbean (1962.7.21.181-186; *ex*⁴ C.N.H.M.—no number).
25 fishes, 28-39 mm., PARATYPES, Gun Cay, Bahamas (1962.7.21.156-180; *ex*⁴ U.M.M.L., No. 2102).

⁴ Donated by Dr. Loren Woods from the collections of the Chicago Natural History Museum.

TABLE I.—*A Comparison of Proportional and other Measurements of the Holotypes of
Dussumieria hasselti and D. elopsoides*

	<i>D. hasselti</i>	<i>D. elopsoides</i>
Standard length	134.0 mm.	124.0 mm.
In % of S.L.		
Body depth	20.9	20.8
Head length	26.4	26.9
Snout length	9.0	8.8
Eye diameter	6.7	7.1
Post-orbital	10.1	9.2
Inter-orbital	5.8	5.6
(above eye centre)		
Snout to maxillary tip	8.9	8.7
Lower jaw length	12.3	12.4
Operculum height	11.2	11.3
Peduncle depth	8.2	8.8
Pre-dorsal distance	59.0	55.0
Pre-pelvic distance	65.0	64.5
Longest gillraker on 1st arch	3.4	3.5
<hr/>		
Gillraker count	22	23
Dorsal rays : simple	iv	iv
branched	16	17
Anal rays : simple	iii	iii
branched	13	13
Branchiostegal rays	17	15

TABLE II.—*Proportional Measurements, Expressed as Percentages of Standard Length, for Specimens of Etrumeus from Five Regions*

	N. American Atlantic	Japan and Hong Kong	N. American Pacific	Australia	Natal, P. Elizabeth (South Africa)
Number of fishes . . .	9	12	8	2	9
Standard lengths . . .	115.0-130.2	67.5-85.5 (136.0)*	110.0-125.0 (265.0)†	105.5-122.0	117.5-166.0
In % of S.L.					
Body depth . . .	15.2-16.8	14.2-16.7 (19.2)	17.4-21.2	18.9-19.4	17.4-19.4
Head length . . .	26.2-27.5	24.2-29.2	25.2-27.0	25.4-25.7	24.2-28.2
Snout length . . .	7.2-8.4	(6.9) 7.5-8.8	7.2-8.2	7.0-7.6	7.4-8.4 (9.4)
Eye diameter . . .	7.0-7.8	(7.5) 8.9-9.8	7.0-8.6	8.3	7.8-9.0
Post-orbital distance . . .	8.9-9.8	8.3-9.6	9.2-10.6	8.4-8.6	8.4-9.1
Maxilla length . . .	8.9-9.4	9.5-9.7	8.9-9.7	—	8.7-9.2
Pectoral length . . .	14.8-15.1	14.9-16.0	14.7-16.2	—	15.6-17.4
Pelvic length . . .	8.9-9.7	8.8-9.4	7.6-8.2	—	8.2-10.2
Pre-dorsal distance . . .	44.2-45.5	44.0-48.0	47.0-48.4 (50.0)†	46.4	45.0-47.9 (49.4)
Pre-pelvic distance . . .	62.3-64.0	62.0-68.4	66.1-69.5	66.5	66.2-68.5 (70.0)
Pre-anal distance . . .	82.0-84.0	82.9-88.8	85.4-86.0	85.5	83.0-87.0
Gillrakers . . .	34-36	32-36	27-33	29-32	30-33 (36)
Dorsal rays . . .	iv 16-17	iii-iv 16-18	iv 15-17	iv 17-18	iii-iv 14-15
Pectoral rays . . .	i 14-15	i 14-16	i 14-15	i 15-16	i 14-15
Anal rays . . .	iii 7-8	iii 7-8	iii 8	iii 8	iii 7-8

* Single measurements outside normal range placed in parentheses.

† Type of *Perkinsia othonops*.

TABLE III.—*Proportional Measurements, Expressed as Percentages of Standard Length for Specimens of Spratelloides delicatulus from Australia (S. d. robustus) compared with Specimens from the Indo-Malayan Archipelago and the Seychelles (S. d. delicatulus)*

	Australia <i>S. d. robustus</i>	Other areas <i>S. d. delicatulus</i>
Number of specimens	10	13
Standard lengths	50.3-71.0	39.0-52.0
In % of S.L.		
Body depth	18.2-21.0	(16.7)* 17.9-20.5
Head length	25.2-28.2	24.0-26.7
Snout	7.2-7.7	6.6-7.4
Eye diameter	6.5-7.7	6.5-7.7
Post-orbital distance	9.3-10.3	8.8-10.1
Maxilla length	9.2-9.6	8.4-9.5
Pectoral length	14.2-15.8	(11.9) 14.0-15.0
Pelvic length	11.1-12.8	9.2-11.5
Pre-dorsal distance	46.3-48.0 (49.1)*	46.5-47.1 (49.2)
Pre-pelvic distance	(50.5) 53.0-57.5	53.2-56.0
Pre-anal distance	76.2-83.5	(75.0) 79.2-82.0
Dorsal rays	ii 10-11	ii 9-11
Pectoral rays	i 11-12	i 10-12
Anal rays	ii-iii 7-9	ii-iii 7-9

* Single measurements outside normal range placed in parentheses.

