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A NEW SPECIES OF *VINCIGUERRIA*  
(SALMONIFORMES: PHOTICHTHYIDAE)  
FROM THE RED SEA AND GULF OF AQABA,  
WITH COMMENTS ON THE DEPAUPERACY  
OF THE RED SEA MESOPELAGIC FISH FAUNA

ROBERT KARL JOHNSON

ROSS M. FELTES

February 29, 1984

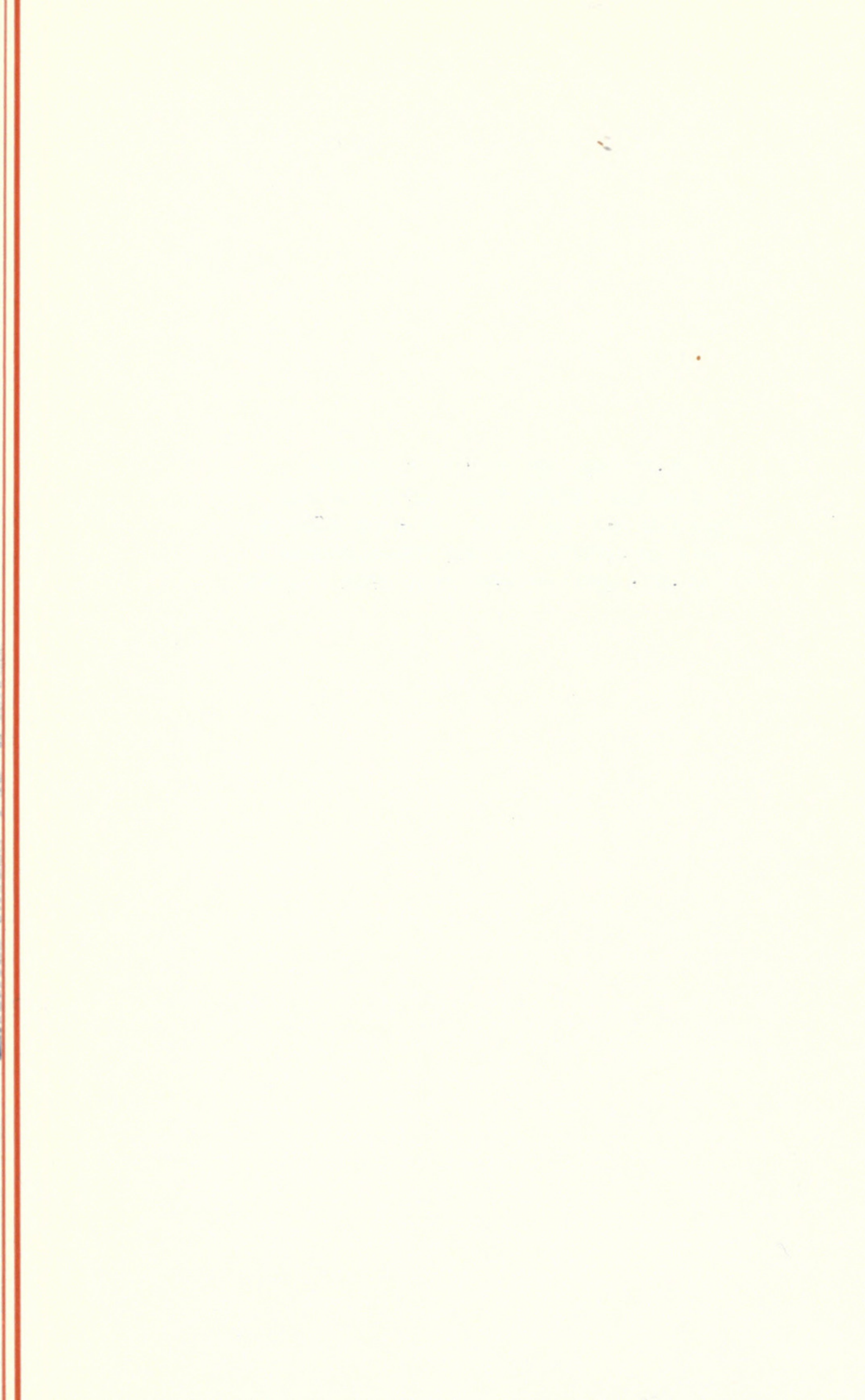
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ROBERT KARL JOHNSON

*Department of Zoology*  
*Field Museum of Natural History*

ROSS M. FELTES

*Museum of Zoology*  
*Ohio State University*

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## CONTENTS

List of Illustrations .....	vi
List of Tables .....	vi
Abstract .....	1
Introduction .....	1
Methods .....	2
Abbreviations and Material Examined .....	2
Counts and Measurements .....	3
Statistical Methods .....	4
Status of the Red Sea Population .....	6
Distinguishing Characters .....	6
Discussion .....	8
Conclusion .....	22
<i>Vinciguerria mabahiss</i> sp. nov. ....	22
Synonymy .....	22
Diagnosis .....	23
Description .....	23
Discussion .....	27
Acknowledgments .....	31
Material Examined .....	31
Literature Cited .....	32



## LIST OF ILLUSTRATIONS

1. Geographic subareas chosen for study of variation within <i>Vinciguerria mabahiss</i> and for purposes of comparison with Red Sea material	5
2. Size of larvae of <i>Vinciguerria</i> species at comparable states of development	9
3. Interorbital width plotted against standard length for species of <i>Vinciguerria</i>	11
4. Head length divided by tail length plotted against standard length for species of <i>Vinciguerria</i>	12
5. Composite index plotted against standard length for 107 specimens of <i>Vinciguerria</i>	13
6. Relative position of 107 specimens of <i>Vinciguerria</i> in the projection of the first two principal components of a 21-morphometric character correlation matrix	15
7. Relative position of 107 specimens of <i>Vinciguerria</i> in the projection of sheared second principal components for morphometric characters against first principal components for meristic characters	17
8. Number of maxillary teeth plotted against standard length for specimens of <i>Vinciguerria</i>	18
9. Composite index plotted against maxillary tooth index for specimens of <i>Vinciguerria</i>	19
10. Total both photophores tallied by total gill raker number for specimens of <i>Vinciguerria</i>	20
11. <i>Vinciguerria mabahiss</i> , holotype, USNM 224860, 30.5 mm SL	21
12. Distribution of <i>Vinciguerria mabahiss</i>	26

## LIST OF TABLES

1. Photophore counts of <i>Vinciguerria</i>	6
2. Total body photophores in <i>Vinciguerria</i>	7
3. Number of vertebrae in <i>Vinciguerria</i>	8
4. Comparison of values for five morphometric characters between North Atlantic and Red Sea specimens of <i>Vinciguerria</i>	14
5. Characters used in principal component analysis of <i>Vinciguerria</i>	16
6. Meristic characters used in principal component analysis of <i>Vinciguerria</i>	16
7. Comparison of characters among larvae of <i>Vinciguerria</i>	22



## ABSTRACT

*Vinciguerria mabahiss* n. sp. is described from 471 (4.5–30.5 mm SL) specimens from the Gulf of Aqaba and northern and central (north of 19°N) Red Sea. *Vinciguerria mabahiss* shares with its close congeners *V. nimbaria* (Jordan and Williams, 1896) and *V. lucetia* Garman (1899) the presence of SO photophores (a pair found just behind the mandibular symphysis), but differs in having only 58 to 63 total body photophores (vs. 64–73) and 37 to 38 vertebrae (vs. 39–44). *Vinciguerria mabahiss* also differs, but not without overlap, in a number of morphometric characters and in having more maxillary teeth at any given size (over an 18- to 31-mm SL range). *Vinciguerria mabahiss* is one of but eight mesopelagic species known from the Red Sea. Limited available evidence suggests that this depauperacy is related to both the Pleistocene history of the Red Sea and to its unique hydrography.

## INTRODUCTION

The photichthyid genus *Vinciguerria* Jordan and Evermann (1896) contains four currently recognized species (Grey, 1964; Gorbunova, 1972). *Vinciguerria attenuata* (Cocco, 1838) and *V. poweriae* (Cocco, 1838) lack symphyseal photophores; *V. lucetia* Garman (1899) and *V. nimbaria* (Jordan and Williams, 1896; in Jordan & Starks, 1896) possess symphyseal photophores. Close morphological similarity and lack of adequate material throughout the warmwater ocean have caused great uncertainty in identification of specimens as *V. lucetia* or *V. nimbaria* from different sites, especially Indian Ocean material (e.g., Brauer, 1906; Ahlstrom & Counts, 1958; Grey, 1964; Silas & George, 1971). Recent work has established with near certainty that *V. lucetia* and *V. nimbaria* are distinct: *V. lucetia* is endemic to the eastern tropical Pacific, whereas *V. nimbaria* is broadly tropical-subtropical and nearly circumglobal in the warmwater ocean (Gorbunova, 1972; Feltes, 1978).

That a *nimbaria*-like form of *Vinciguerria* exists in the Red Sea has been known for some years (Marshall, 1963). This form is one of but eight mesopelagic species thus far reported from the Red Sea. Marshall (1963, p. 187) believed that the Red Sea form was probably distinct from the one taken by Norman (1939) in the Gulf of Oman and Arabian Sea, and the latter in turn he believed to be distinct from *V. nimbaria*. Characters mentioned to support these beliefs included numbers of gill rakers, photophores, and dorsal-fin rays, with the Red Sea form said to have fewer photophores and dorsal-fin rays. Lack of material from throughout the range of *V. nimbaria* and relative lack of Red Sea material precluded Marshall's naming of either the Red Sea or northern Indian Ocean populations. Marshall probably had access only to uncatalogued MANIHINE



Expedition (1950–1951) material, which as reported here, contained a number of larvae but only five juvenile specimens, the largest 19.1 mm in standard length. Subsequent authors (Kotthaus, 1967; Aron & Goodyear, 1969; Botros, 1971) have used the name *V. lucetia* for the Red Sea population. Although this identification was consistent with literature available to these authors, it is not consistent with evidence that *V. lucetia* is endemic to the eastern tropical Pacific (Gorbunova, 1972; Feltes, 1978; Johnson, 1982). New material from the Red Sea and exhaustive study of variation in *V. nimbaria* (much of which will be communicated in a separate and subsequent publication) have provided the resolution that is the basis for this paper.

The first documented record of *Vinciguerria* from the Red Sea is the single 13-mm specimen (METEOR Station 23) reported in Kotthaus (1967). In August, 1968, the Smithsonian Institution and Hebrew University cooperated in a joint research cruise of the Ethiopian trawler MENELIK II to the Gulf of Aqaba and closely adjacent waters of the northern Red Sea (north of 27°38'15"N). A total of 20 trawls was taken with a modified Isaacs-Kidd Midwater Trawl (IKMT). For midwater fishes, reported by Aron & Goodyear (1969), this survey remains the most extensive ever done in the Red Sea. A single species of *Vinciguerria* was taken in 19 of 20 hauls: 245 specimens from the Gulf of Aqaba and 319 specimens from the Red Sea. Recently, through aid of the staff of the British Museum (Natural History), we have had the opportunity to study specimens taken by the MANIHINE Sudanese Red Sea Expedition of 1950–1951 from the northern and central (to 19°45'N) Red Sea. These are certainly the specimens alluded to by Marshall (1963, p. 187). Lastly, two specimens from the central Red Sea (21°21.74'N to 19°02'N) taken by recent German expeditions (Thiel, 1980; Klauswitz, 1980) were kindly made available by the staff of the Forschungsinstitut Senckenberg (Frankfurt). Study of this material and several thousand specimens of *V. nimbaria* and *V. lucetia* from throughout the warmwater ocean has convinced us that Marshall was right, that the Red Sea form is a third distinct species in the "*nimbaria*" group. Documentation of this conclusion and description of the Red Sea form are the purposes of this paper.

## METHODS

### ABBREVIATIONS AND MATERIAL EXAMINED

The following abbreviations are used in reference to material examined:

- BM(NH) British Museum (Natural History), London; material listed by MANIHINE (MH) Sudanese Red Sea Expedition of 1950–1951 station number.
- FMNH Field Museum of Natural History, Chicago; material listed by FMNH catalogue number.
- ISH Institut für Seefischerei, Bundesforschungsanstalt für Fischerei, Hamburg; material listed by ISH catalogue number.
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge; material listed by Richard H. Backus (RHB) station number or by ship, cruise, and station number (AB = R/V ANTON BRUUN).
- SIO Scripps Institution of Oceanography, University of California at San Diego, La Jolla; material listed by SIO catalogue number or by ship,



- cruise, and station number (J = R/V DAVID STARR JORDAN; TC = R/V TOWNSEND CROMWELL).
- SMF    Forschungsinstitut Senckenberg, Frankfurt am Main; material listed by SMF catalogue number.
- UH    Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe; all UH material has been or will be deposited in several permanent institutional collections; material listed by date of capture (year/month/station number) or by ship, cruise, and station number.
- UMML    Rosenstiel School of Marine and Atmospheric Science, University of Miami; material listed by UMML catalogue number.
- USNM    National Museum of Natural History, Smithsonian Institution, Washington, D.C.; material listed by USNM catalogue number, by ACRE (Ocean Acre Expeditions, see Gibbs et al., 1971) cruise and station numbers, or MENELIK II (MNK, see Aron & Goodyear, 1969) station numbers.
- ZIZM    Zoological Institute and Zoological Museum, Hamburg; material listed by METEOR (FS "METEOR") station number.

#### COUNTS AND MEASUREMENTS

Unless specified below, methods of taking counts and measurements follow those given by Hubbs & Lagler (1958, pp. 19–26), Grey (1964, p. 79), and Johnson (1970, pp. 437–438). Measurements were made to 0.1 mm with needlepoint dividers or to 0.01 mm with an ocular micrometer on a Wild M5 microscope. Measurements are expressed as thousandths of the standard length (SL). Counts are given as the range and the mean.

The following symbols are used to designate photophores: SO, a pair found just behind the mandibular symphysis; ORB, photophores situated anterior and posterior (one each) to the eye (on each side); OP, three photophores (on each side) forming a nearly right triangle on the gill covers; BR, photophores on the branchiostegal membranes; IV, from the beginning of the ventral series on the isthmus to the pelvic-fin insertion; VAV, from posterior to the pelvic-fin base to the anal-fin origin; AC, from the last VAV to the end of the series; IC, summation of IV + VAV + AC; OV, the lateral series from the opercular margin to the pelvic-fin insertion; VAL, from the last OV to the end of the series; TOT, summation of IC + OV + VAL.

A total of 22 measurements was taken on each specimen selected for morphometric analysis. Those measurements listed below are either undefined in or taken differently from methods described in Hubbs & Lagler (1958).

Body depth at pectoral insertion = vertical distance between dorsal and ventral body contours taken on a line through base of anteriormost pectoral-fin ray.

Adipose fin: distance to midcaudal ray = distance from posterior intersection of adipose fin with body and base of upper middle caudal-fin ray.

Pectoral to pelvic distance = distance from base to base of anteriormost ray of each fin.

Preanal, prepectoral, and prepelvic distances = distance from tip of snout to base of first (anteriormost) ray in each case.



Anal fin: length of base = distance between bases of anteriormost and posteriormost rays.

Pelvic fin to anal fin distance = distance between bases of anteriormost fin rays in each case.

Length of "tail" = distance from base of anteriormost anal-fin ray to base of upper middle caudal-fin ray.

#### STATISTICAL METHODS

Principal components analysis (PCA) was employed for multivariate comparisons of 107 specimens and was performed separately on meristic and morphometric data. Principal components for meristic data were computed from the correlation matrix. Principal components for morphometric data were computed from the covariance matrix of the log, base 10, transformed data. The methodology described in Humphries et al. (1981) to remove the effect of size from the second principal component (PCII) and subsequent principal components was used for the morphometric data to allow for size-free comparisons of shape among specimens. Procedures of the SAS Institute were employed throughout this analysis (Helwig & Council, 1979; SAS Institute, 1981).

Other statistical techniques were performed using a Hewlett-Packard 9825A calculator and 9827A plotter in the Advanced Technology Laboratories of Field Museum of Natural History (using manufacturer-supplied software). Also used were standard reference works (Sokal & Rohlf, 1969; Tate & Clelland, 1957).

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#### Opposite:

FIG. 1. Geographic subareas chosen for study of variation within *Vinciguerria nimbaria* and for purposes of comparison with Red Sea material. Symbols show actual capture localities for lots of *Vinciguerria* included in this study. Stippled bands denote areas transitional between water mass regions (after Sverdrup et al., 1942). Solid lines (Atlantic only) indicate boundaries between areas recognized as mesopelagic faunal regions by Backus et al., 1977. CNA = subtropical North Atlantic (including Caribbean Sea and Gulf of Mexico); EQA = tropical Atlantic, including Mauritanian Upwelling Region (stations labeled TC1, TC2, and TE are from a 1970 single transect of the R/V ATLANTIS II; data for specimens from these stations are combined with data for CNA [TC1 + TC2] or EQA [TE] specimens except where noted); CSA = subtropical South Atlantic; SIO = equatorial Indian Ocean, south of 10°N; NIO = Arabian Sea; RDS = Red Sea; SCS = South China Sea; PHS = subtropical North Pacific Philippine Sea area; NWG = subtropical North Pacific "Northwest gyre" area (see Barnett, 1975); CNP = subtropical North Pacific Hawaiian area; EPW = tropical Pacific (western area); CEP = tropical Pacific (central area); EEP = tropical Pacific (eastern area); CSP = subtropical South Pacific; LUC = eastern tropical Pacific (material of *V. lucetia*).

Key: ●▲ = localities in central-water-mass regions (*nimbaria* "central" specimens); ○△ = localities in equatorial-water-mass regions (Indian, Pacific), tropical Atlantic, and South China Sea (*nimbaria* "equatorial" specimens; except South China Sea where material is from within region of Western North Pacific Central water, see Sverdrup et al., 1942); ■ = localities in Red Sea; ▣ = localities for *lucetia*.

The distinction between "central" vs. "equatorial" water-mass regions refers to those areas underlain by the principal warmwater (i.e., bounded by the subtropical convergence regions of the North and South) upper water masses as depicted by Sverdrup et al., 1942, p. 740). The term "equatorial" is also applied to Atlantic specimens of *nimbaria* from the Atlantic Tropical and Mauritanian Upwelling Regions of Backus et al. (1977).



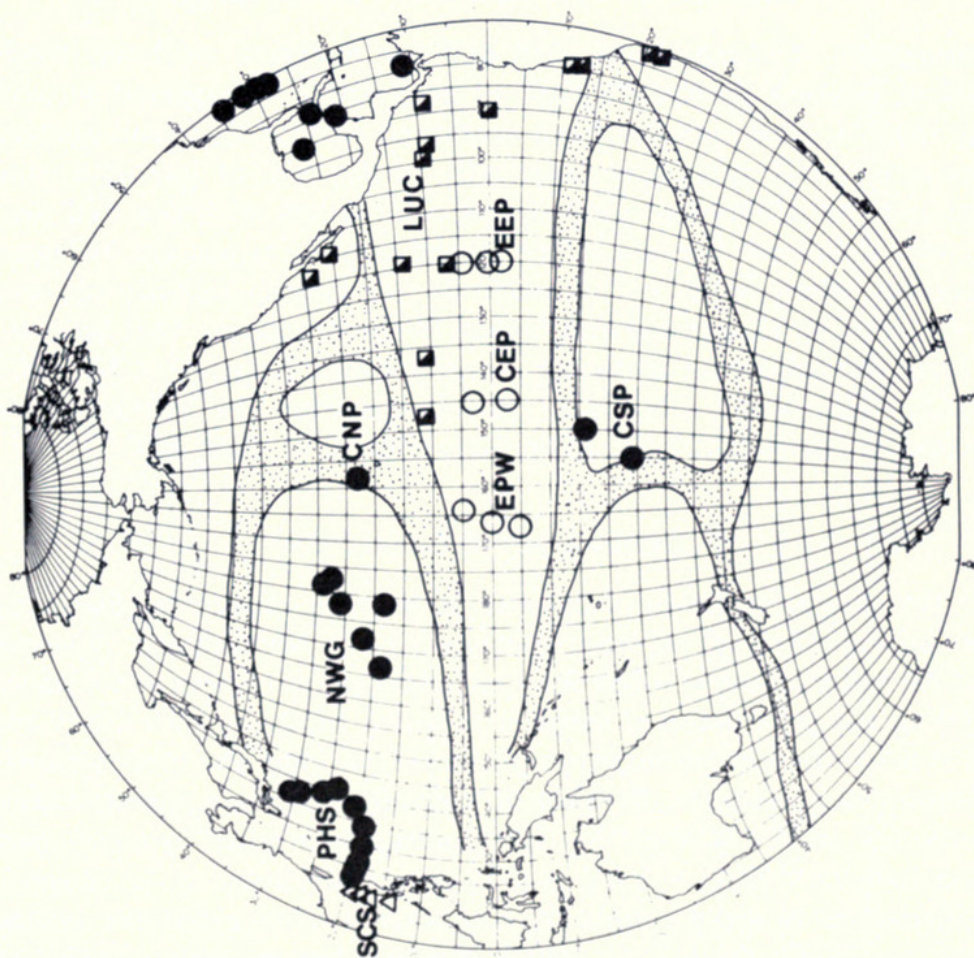
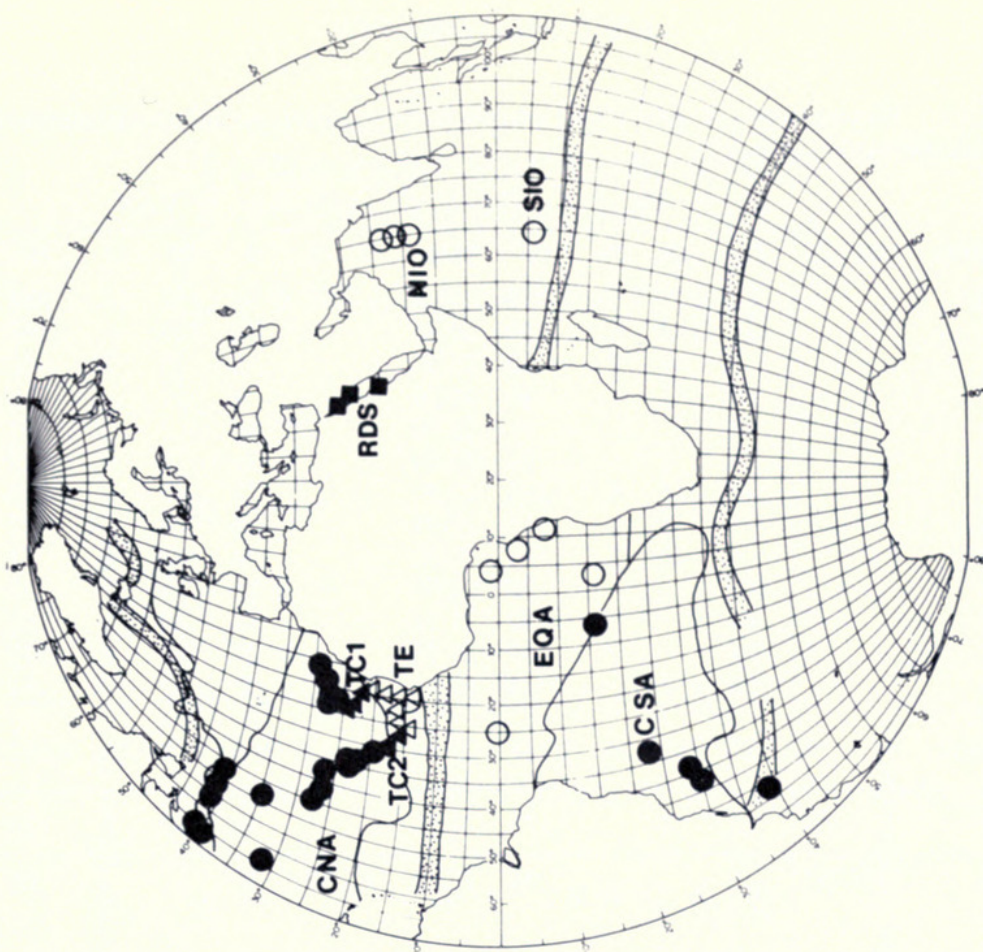




TABLE 1. Photophore (IV and VAV) counts in *Vinciguerria* (subarea abbreviations and locations are given in fig. 1).

Subarea	IV							VAV						
	20	21	22	23	24	N	Mean	7	8	9	10	11	N	Mean
CNA			22	232	5	259	22.93			58	191	10	259	9.81
EQA			11	182	6	199	22.97			36	159	4	199	9.84
CSA			1	49	2	52	23.02			5	45	2	52	9.94
SIO			15	1		16	22.06			4	12		16	9.75
NIO		5	46			51	21.90		2	46	3		51	9.02
SCS		1	21	2		24	22.04			21	3		24	9.13
PHS			34	218	8	260	22.90			77	177	6	260	9.73
NWG			2	8	1	11	22.91			4	6	1	11	9.73
CNP			1	48	2	51	23.02			4	46	1	51	9.94
EPW			20			20	22.00			4	15	1	20	9.85
CEP		3	49			52	21.94			12	40		52	9.77
EEP		5	104			109	21.95			27	75	1	103	9.75
CSP			12	2		14	22.14			7	7		14	9.50
<i>nimbaria</i> subtotal		14	338	742	24	1,118	22.69		2	305	779	26	1,112	9.75
LUC		80	92	3		175	21.56		1	40	135	2	178	9.78
RDS	10	53	1			64	20.86	6	48	10			64	8.06

## STATUS OF THE RED SEA POPULATION

For purposes of comparison with Red Sea material, we have divided our material of *nimbaria* and *lucetia* into 14 geographic areas based on collection locality (fig. 1). Although we have examined several thousand specimens of *nimbaria* and *lucetia*, including (especially in the case of *lucetia*) a substantial number not listed here, for purposes of comparison with the Red Sea population, only data from the specimens whose position is plotted in Figure 1 are used (except where noted). This material was chosen to fully represent the range of variation in *nimbaria* and *lucetia*. In the discussion that follows, specimens from the following areas (fig. 1) are labeled "central": CNA, TC1, TC2, CSA, SCS, PHS, NWG, CNP, CSP. Specimens from the following areas are designated as "equatorial": TE, EQA, SIO, NIO, EPW, CEP, EEP.

## DISTINGUISHING CHARACTERS

Only two characters, both of them serial meristic characters, distinguish the Red Sea specimens from all other specimens of *V. nimbaria* and *V. lucetia*.

*Serial Photophore Counts.*—Red Sea specimens exhibit lower serial photophore counts than any population of *nimbaria* or *lucetia*. Modally, both the IV and VAV (Table 1) series are one photophore (or more) less than the modal count in any other group of specimens. Because of virtually complete correspondence between the OV and IV ( $OV = IV - 10$ ; 13 exceptions noted in 1,118 specimens) and VAL and VAV ( $VAL = VAV + 1$ ; 12 exceptions noted in 1,112 specimens), these differences in serial counts are emphasized when expressed as total body photophores, (TOT; table 2) in which the Red Sea specimens differ without overlap.

*Vertebral Counts.*—Red Sea specimens differ without overlap in having 37 or 38 vertebrae vs. 39 to 44 vertebrae in all other "populations" (table 3).



TABLE 2. Total body photophores (TOT) in *Vinciguerria* (subarea abbreviations and locations are given in fig. 1).

	TOT																	
Subarea	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	N	Mean
CNA										9	37	41	107	48	14		256	69.74
EQA											1	24	87	79	7	1	199	70.35
CSA											1	1	34	12	4		52	70.33
SIO								1	2		10	2					15	67.67
NIO							4	25	16	5	1						51	65.49
SCS							3	3	13	3	4						23	66.35
PHS										3	45	44	115	22	4	2	235	69.54
NWG											2	1	5	3			11	69.82
CNP												4	38	8	1		51	70.12
EPW									3	2	13	1	1				20	67.75
CEP									6	9	32	5					52	67.69
EEP									6	11	45	13					75	67.87
CSP									4	3	6	1					14	67.29
nimbria																		
subtotal							4	29	50	45	197	137	387	172	30	3	1,054	69.25
lucetia*							14	82	324	308	229	189	26	7	1		1,180	67.16
RDS	2	2	17	37	5	1											64	60.69

\* Counts for *V. lucetia* are based on Feltes (1978) and include all specimens counted for that study.



TABLE 3. Number of vertebrae in *Vinciguerria* (subarea abbreviations and locations given in fig. 1).

Subarea	No. of vertebrae								N	Mean
	37	38	39	40	41	42	43	44		
CNA					1	17	5	3	26	42.38
EQA						16	40	2	58	42.76
CSA						8	9		17	42.53
SIO				3	3	2			8	40.88
NIO			2	12	2				16	40.00
SCS			6	5					11	39.45
PHS				3	12	8			23	41.22
CEP			1	23	7				31	40.19
CNP			—	—	6	21	—	—	27	41.78
<i>nimbaria</i> subtotal			9	46	31	72	54	5	217	41.60
<i>lucetia</i> *			21	57	92	29	1		200	40.66
RDS	3	3							6	37.50

\* Counts for *V. lucetia* are based on Feltes (1978) and include all specimens counted for that study.

## DISCUSSION

The problem in interpreting the serial meristic data is one of separating possible ecophenotypic effects from genetic difference. It is well known that, in fishes, lower meristic counts are typically found in populations in areas of warmer water (i.e., warmer water during the breeding season if reproduction is seasonal; for reviews see Barlow, 1961; Fowler, 1970; Johnson & Barnett, 1975). Virtually all of the Red Sea material, much of it larval or early juvenile, was taken by the MENELIK II in August. The Red Sea is nearly isothermal at about 22° C below 200 m, but surface temperatures in the northern Red Sea may exceed 30° C (Botros, 1971, p. 236), although average summer surface temperatures are lower (Siedler, 1969, p. 133). A surface temperature of 30° C exceeds oceanic surface temperatures encountered anywhere else in the combined ranges of *nimbaria* or *lucetia* (Sverdrup et al., 1942).

Eggs and larvae of *lucetia*, and almost certainly of *nimbaria*, occur predominantly in the upper 100 m (Ahlstrom, 1958; Ahlstrom & Counts, 1958; Silas & George, 1971). Most of the smallest larvae taken by MENELIK II, all less than 12 mm SL, accounting for 111 of 564 specimens, were captured at one station (station No. 1946) limited to the upper 100 m. This, combined with the month of capture, makes it conceivable that the distinctness of the Red Sea specimens in serial meristics represents an ecophenotypic effect related to temperature. This possibility seems all the more probable with evidence that, by one plausible index of developmental rate, individuals of the Red Sea population develop more rapidly than individuals in other populations. In *Vinciguerria*, the last four photophores of the VAL series are late forming, usually the left member of a pair appears just before the right, and the number yet to appear can be determined uniquely from exact correspondence (99% of all cases) with photophores in the VAV series (VAL = VAV + 1; see Johnson & Barnett, 1975). A plot of VAL photophores yet to appear vs. standard length (fig. 2) shows that individuals in the Red Sea complete metamorphosis—here defined by attain-



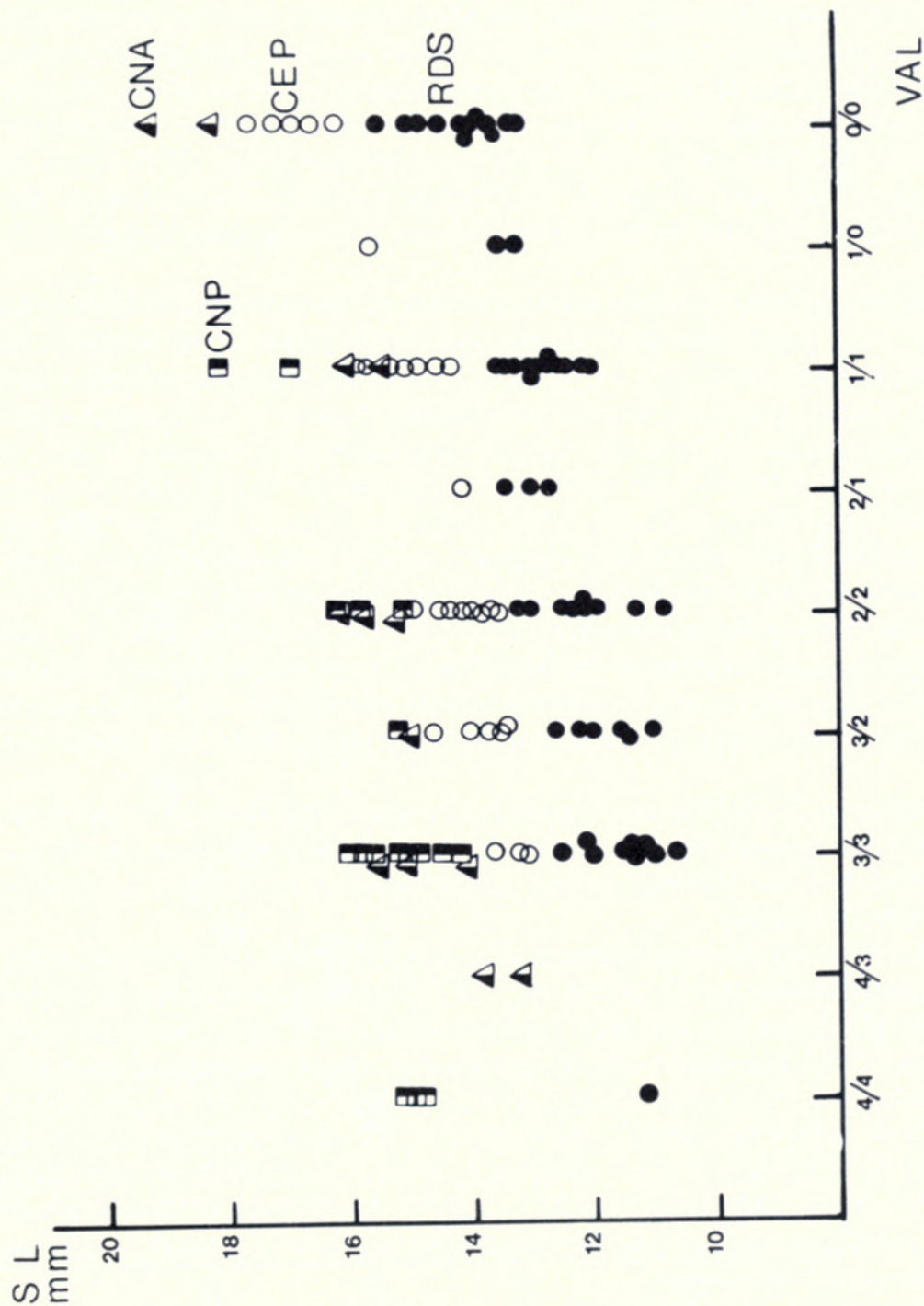


FIG. 2. Size of larvae of *Vinciguerria* species at comparable states of development. Y-axis = standard length in millimeters; X-axis = number of VAL photophores yet to appear (see text for explanation). Selected data points are offset for clarity of presentation.

Key: *Vinciguerria* sp.—● = Red Sea. *Vinciguerria nimbaria*—○ = CEP; ▲ = CNA; ■ = CNP.



ment of a complete photophore set—at a smaller size than individuals from central and equatorial populations of *nimbaria*. Size at metamorphosis may or may not be related to developmental rate in these fishes (comparison of developmental rates between equatorial and central populations of broadly distributed midwater species offers fascinating prospects for further understanding of open ocean biology but remains undone), but these data suggest that the possibility of faster developmental rates, and the presumed concomitant of lower values for serial meristic characters, should not be ignored. Perhaps relevant to this suggestion is the fact that Red Sea individuals as small as 16 mm SL were found packed with eggs. Off Hawaii, *V. nimbaria* does not attain reproductive maturity until a minimum size of 27 mm is achieved (Clarke, 1974). Thus, the Red Sea population may be unique in attaining maturity at a very small size. The comparative study necessary to demonstrate this suggestion remains to be done.

Partly offsetting these concerns is the presence in the MANIHINE Expedition material of very small (less than 12 mm SL) larvae taken in November 1950 ( $N = 3$ ) and January 1951 ( $N = 34$ , 4.5–12.1 mm). This suggests that spawning takes place during summer (August) and winter (January). Year-round reproduction is apparently the rule for *Vinciguerria* (Ahlstrom & Counts, 1958). The values for all characters for the juveniles (maximum size = 19.1 mm SL) in the MANIHINE material agree exactly with values for those in the northern Red Sea and Gulf of Aqaba, which may suggest a lack of seasonal variation in meristic character values for the Red Sea population. Remaining problems include: (1) We know nothing about the actual period of peak spawning, if such a peak occurs; (2) we know nothing of the actual time course of development; (3) the southernmost Red Sea material available is from the vicinity of 19°45'N off the central Sudan coast—there is no material from the far southern Red Sea or Gulf of Aden.

The paragraphs that follow summarize the results of our search for additional evidence for (or against) the distinctness of the Red Sea population. Specimens from the Red Sea are distinctive, but not without overlap, in a number of morphometric characters.

Values for 22 morphometric characters (including SL, see table 5 for a listing) and 10 meristic characters (IV, VAV, AC, OP, VAL, TOT, dorsal-fin rays, anal-fin rays, gill rakers on first gill arch, number of maxillary teeth) were recorded from a total of 107 specimens distributed among the 14 geographic areas (fig. 1) as follows: CNA, 11 (17.9–32.9); TC1 + TC2, 10 (20.7–35.2); TE, 10 (20.0–36.3); EQA, 10 (21.9–36.9); CSA, 10 (21.7–35.5); SIO, 5 (19.0–29.8); NIO, 10 (20.8–31.8); RDS, 11 (17.2–30.5); SCS, 5 (21.7–30.0); SCS, 5 (21.7–30.0); PHS, 5 (18.7–30.5); CNP, 5 (21.8–29.6); CEP, 5 (20.5–35.5); *V. lucetia*, 10 (20.8–31.3). Except where noted, all statements concerning morphometric characters or tooth counts are based on these 107 specimens.

*Interorbital Width.*—The Red Sea form has a broader (fig. 3) interorbital (45–53, median = 47; values are thousandths of the SL) than do the central (36–48, median = 41) or equatorial (36–48, median = 40) populations of *nimbaria* or *lucetia* (35–42, median = 38.5).

*Head Length vs. Tail Length.*—Red Sea specimens tend to have a relatively longer head and shorter tail than specimens from elsewhere. In the listing that follows, values in parentheses are the median. Head length: Red Sea, 279 to 314 (293); central *nimbaria*, 250 to 302 (280); equatorial *nimbaria*, 255 to 290 (271.5);



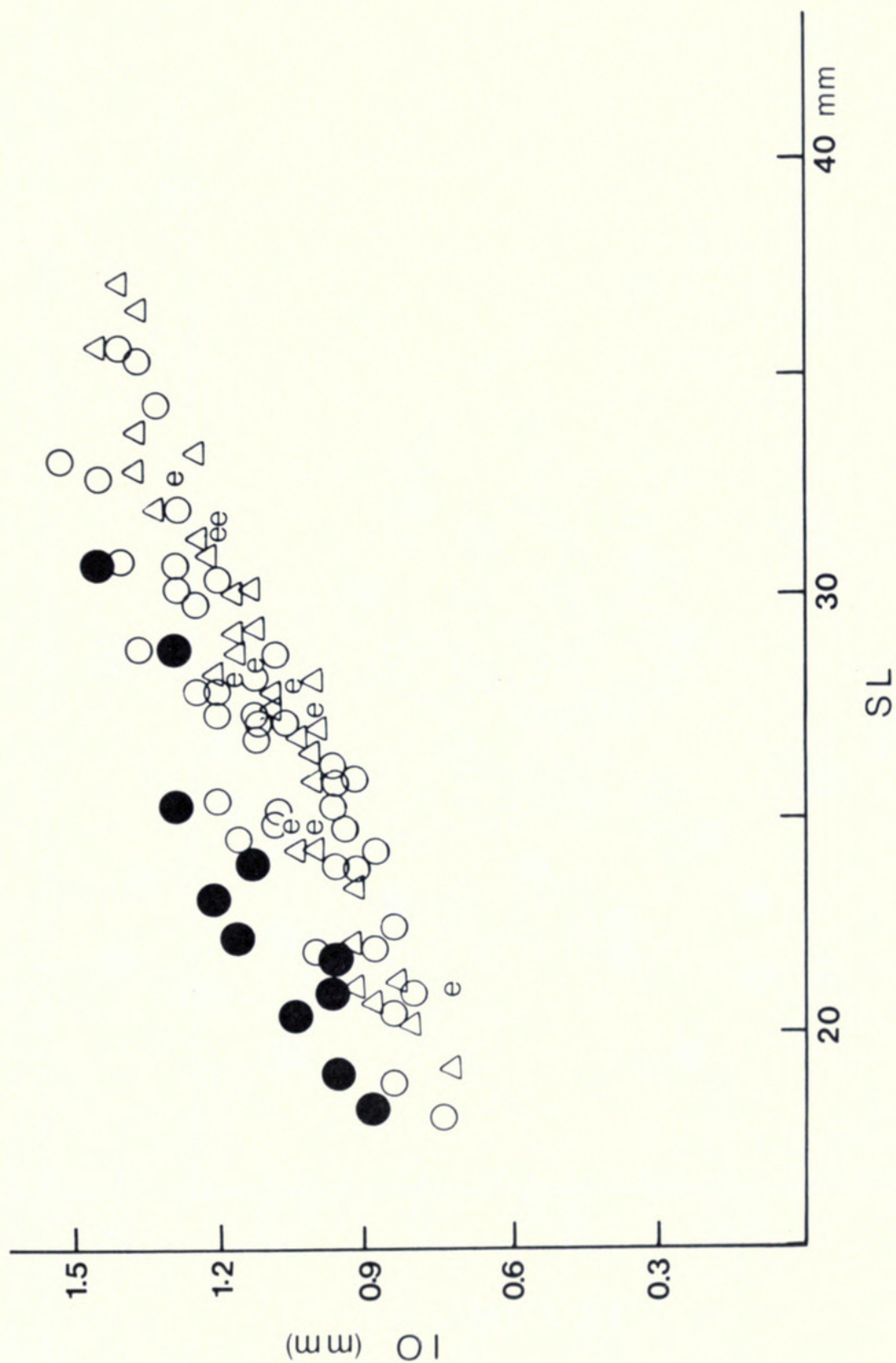


FIG. 3. Interorbital width (IO, in millimeters) plotted against standard length (SL, in millimeters) for species of *Vinciguerria*.

**Key:** ● = Red Sea specimens; ○ = central specimens of *nimbaria* (CNA, CSA, SCS, PHS, CNP); △ = equatorial specimens of *nimbaria* (EQA, SIO, NIO, CEP); e = *Vinciguerria lucetia*.



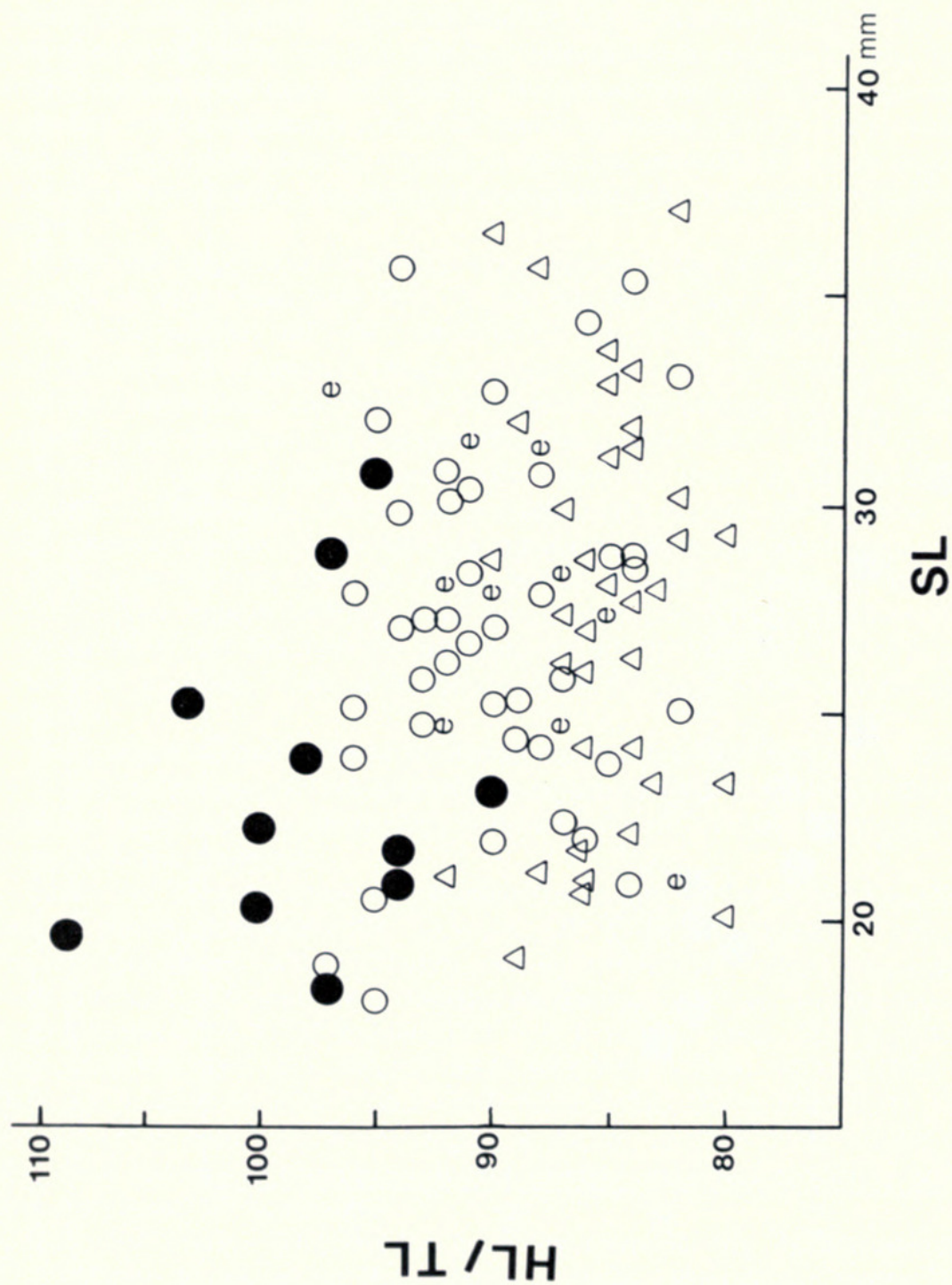


FIG. 4. Head length divided by tail length (y-axis) plotted against standard length (x-axis, in millimeters) for species of *Vinciguerria*.  
**Key:** ● = Red Sea specimens; ○ = central specimens; △ = equatorial specimens (see fig. 3 for listing); e = *Vinciguerria lucetia*.



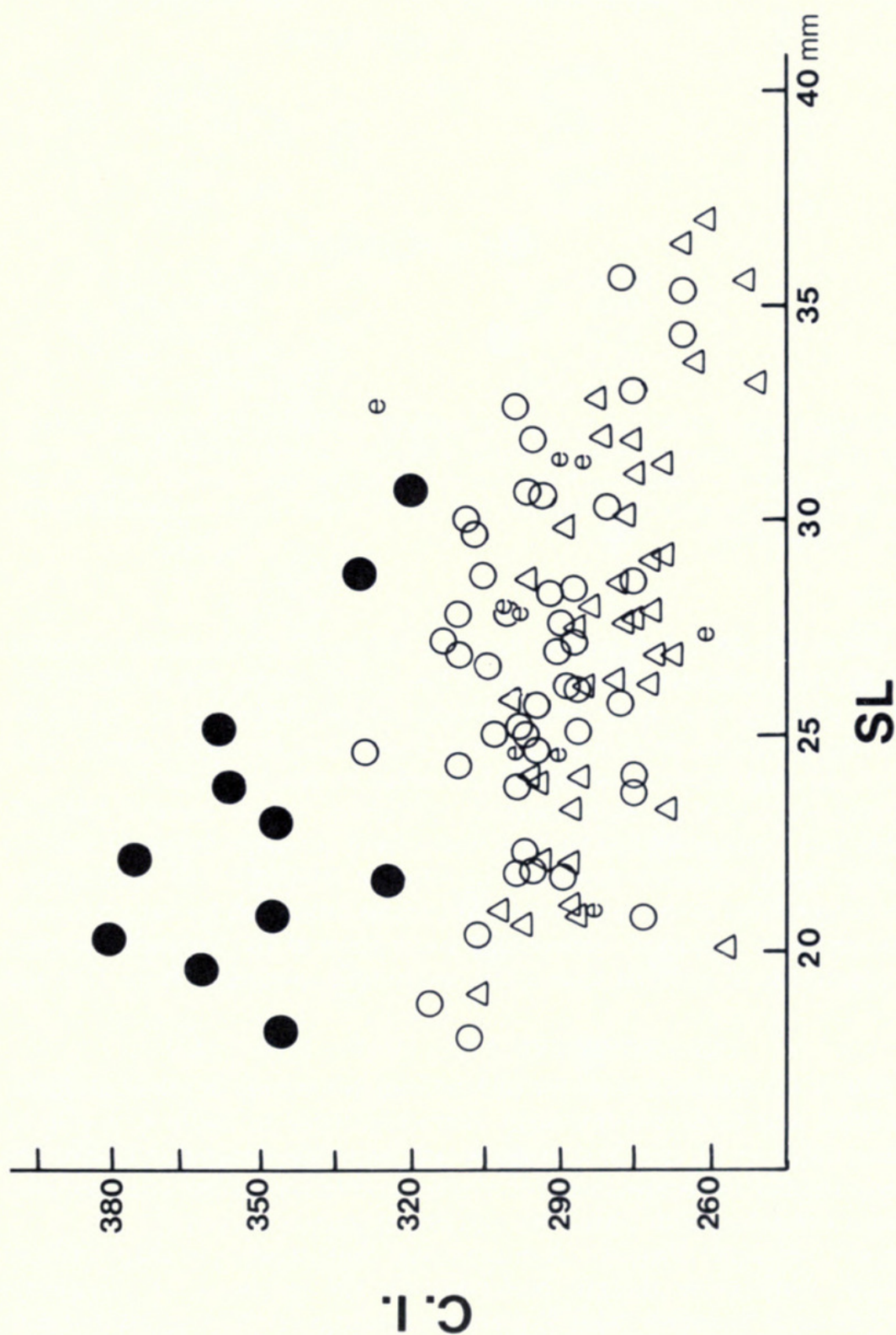


FIG. 5. Composite index (y-axis) plotted against standard length for 107 specimens of *Vinciguerria*. See text for derivation of composite index.  
**Key:** ● = Red Sea specimens; ○ = equatorial specimens (see fig. 3 for listing); △ = *Vinciguerria lucetia*.



TABLE 4. Comparison of values for five morphometric characters between North Atlantic (CNA) and Red Sea (RDS) specimens of *Vinciguerrina*.\*

Character	<i>Vinciguerrina nimbaria</i> from CNA (N = 11)	<i>Vinciguerrina</i> sp. from RDS (N = 11)
A. Range of Values		
SL (mm)	17.9-32.9	17.2-30.5
BDP	186-202	195-219
EYE	63-91	87-107
IO	38-48	45-53
VAF	174-204	142-184
H/T	82-96	90-109
B. Mean $\pm$ 95% Limits		
BDP	191.64 $\pm$ 3.55	207.27 $\pm$ 5.13
EYE	84.09 $\pm$ 2.47	94.27 $\pm$ 3.92
IO	43.91 $\pm$ 2.39	48.36 $\pm$ 1.98
VAF	187.18 $\pm$ 6.07	164.91 $\pm$ 8.33
H/T	90.64 $\pm$ 2.90	97.91 $\pm$ 3.43

SL = Standard length; BDP = body depth at pectoral insertion; EYE = horizontal fleshy diameter of eye; IO = bony interorbital width; VAF = distance from pelvic-fin insertion to anal-fin origin; H/T = head length divided by tail length, expressed as a percentage.

\* Data for specimens from CNA subareas TC1 and TC2 (fig. 1) were excluded from the preparation of this table.

*lucetia*, 279 to 300 (287). Tail length: Red Sea, 282 to 312 (304), central *nimbaria*, 291 to 326 (310); equatorial *nimbaria*, 300 to 331 (318.5); *lucetia*, 304 to 343 (319.5). Thus, in a plot (fig. 4) of head length divided by tail length vs. SL, values for the Red Sea specimens tend to be different from those for all the other "populations," although there is considerable overlap in this character.

*Composite Index*.—Of 22 morphometric characters, values for five (table 4) seemed to best distinguish Red Sea specimens from other specimens of *nimbaria* and *lucetia*. Using methods described in Johnson (1982, p. 110), a composite index was calculated as the sum of standard scores calculated for each character for each specimen (adjusted relative to a mean score of 100 for each character for all specimens of *nimbaria* from CNA, excluding specimens from TC1 and TC2):

$$CI = BDP + EYE + IO - VAF + H/T$$

where BDP is the standard score for each specimen for body depth at pectoral-fin insertion, and so on for the other characters listed in Table 4. A plot of composite index vs. SL (fig. 5) shows virtually complete separation of Red Sea specimens from all other specimens of *nimbaria* and *lucetia* (except one specimen of *nimbaria* from the South China Sea and one specimen of *lucetia*).

*Principal Components Analysis*.—A multivariate consideration of shape utilized a principal components analysis performed on 107 specimens of *Vinciguerrina* using 22 distance measures (table 5). Variable loadings on PCI suggest that both size and shape are represented in this component. The removal of size from PCII (shearing) slightly clarifies the separation of *V. mabahiss* from all other specimens when plotted against PCI (fig. 6). Neither PCIII nor sheared PCIII assists in distinguishing *V. mabahiss*.

Character loadings on sheared PCII reflect shape differences, most notably of the head, as in the interorbital width, eye diameter, and snout length. Other



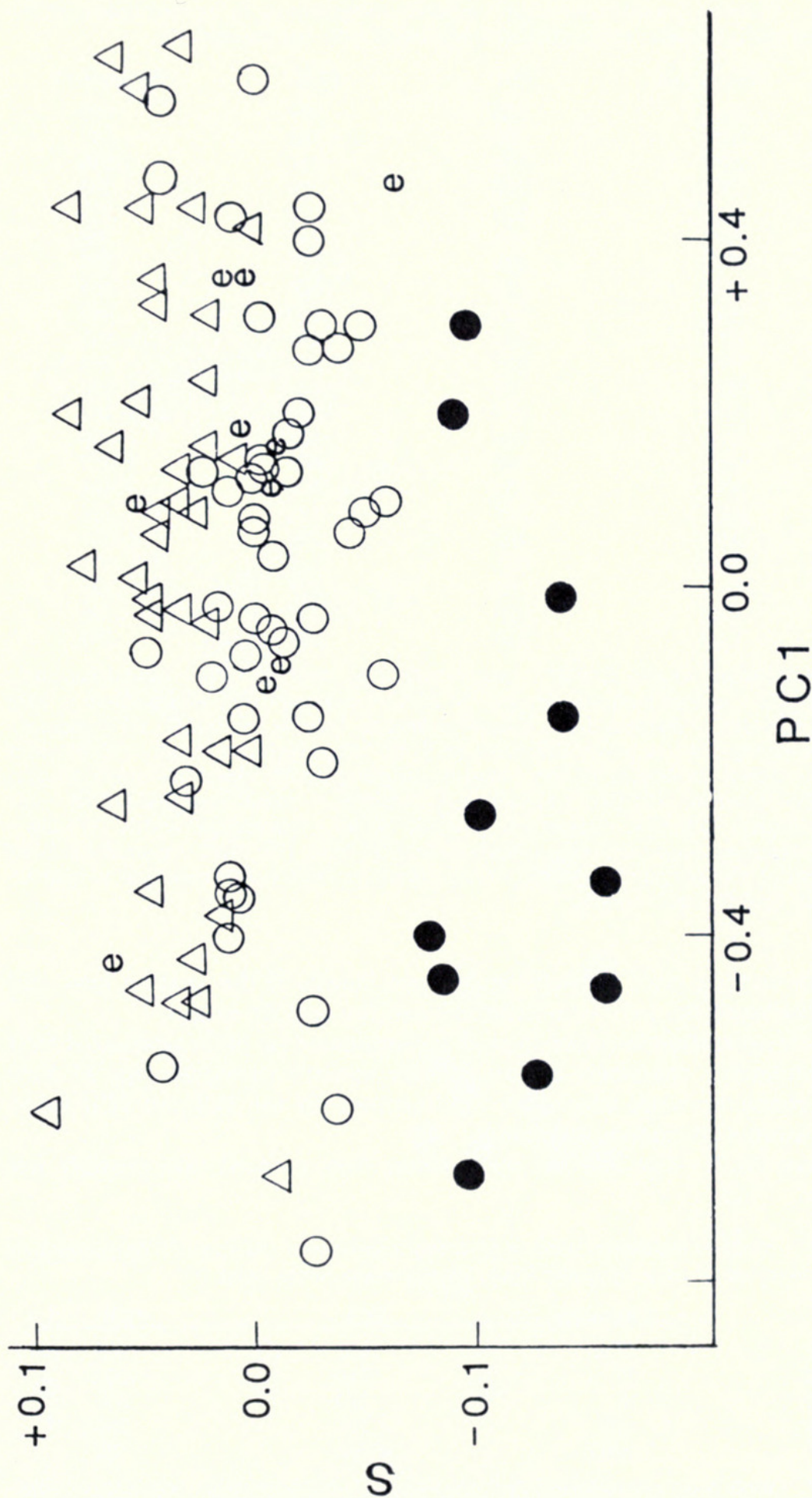


FIG. 6. Relative position of 107 specimens of *Vinciguerria* in the projection of the first two principal components of a 21-morphometric character correlation matrix. The y-axis (S) represents "sheared" value of PCII (see text).

Key: ● = Red Sea specimens; ○ = central specimens; △ = equatorial specimens (see fig. 3 for listing); e = *Vinciguerria lucetia*.



TABLE 5. Characters used in principle component analysis of *Vinciguerria* data with the loadings of each character for principle components I, II, and sheared II.

	Character	PCI	PCII	Sheared II
1	SL	.222	.077	.079
2	BDP	.206	-.160	-.158
3	CPZ	.206	.017	.018
4	CPL	.210	.204	.205
5	ADC	.220	.225	.227
6	DPC	.216	.247	.249
7	PV	.243	-.077	-.075
8	PD	.226	-.070	-.068
9	PA	.223	.000	.002
10	PP	.200	-.195	-.193
11	PV2	.225	-.096	-.094
12	HL	.199	-.160	-.158
13	SNL	.179	-.264	-.262
14	EYE	.186	-.360	-.359
15	UJL	.192	-.080	-.079
16	IO	.200	-.470	-.468
17	DB	.217	.134	.136
18	AB	.202	.296	.297
19	POH	.235	.019	.022
20	LJ	.182	-.127	-.125
21	VAF	.270	.347	.349
22	TAIL	.212	.252	.254

(1) SL = Standard length, (2) BDP = body depth at pectoral, (3) CPZ = caudal peduncle depth, (4) CPL = caudal peduncle length, (5) ADC = distance from adipose base to base of caudal, (6) DPC = distance from dorsal-fin base to base of caudal, (7) PV = distance from pectoral insertion to pelvic insertion; (8, 9, 10, 11) in each case distance from snout to (8) PD = dorsal-fin origin, (9) PA = anal-fin origin, (10) PP = pectoral insertion, (11) PV2 = pelvic insertion; (12) HL = head length, (13) SNL = snout length, (14) EYE = eye diameter (fleshy), (15) UJL = upper jaw length, (16) IO = interorbital width, (17) DB = length of dorsal-fin base, (18) AB = length of anal-fin base, (19) POH = postorbital head length, (20) LJ = lower jaw length, (21) VAF = distance from pelvic insertion to anal-fin origin, (22) TAIL = "tail" length.

characters varying most between groups are length of the anal-fin base and distance between the pelvic-fin insertion and the anal-fin origin.

A greater separation between clusters is represented by plotting sheared PCII for morphometric characters against PCI for meristic characters (fig. 7). Five meristic characters were employed. The loadings for the PCI and PCII based on these counts are shown in Table 6.

*Maxillary Teeth.*—The Red Sea form differs from *nimbaria* (but possibly not

TABLE 6. Meristic characters used in principal component analysis of *Vinciguerria* data with the loadings of each character for principal components I and II.

	Character	PCI	PCII
1	TOT	.637	-.065
2	D	.549	.301
3	A	.363	.531
4	GR	-.316	.592
5	MXT	-.249	.522

(1) TOT = total body photophores (see Methods); (2) D = dorsal-fin rays; (3) A = anal-fin rays; (4) GR = total gill rakers on first gill arch; (5) MXT = teeth on maxilla.



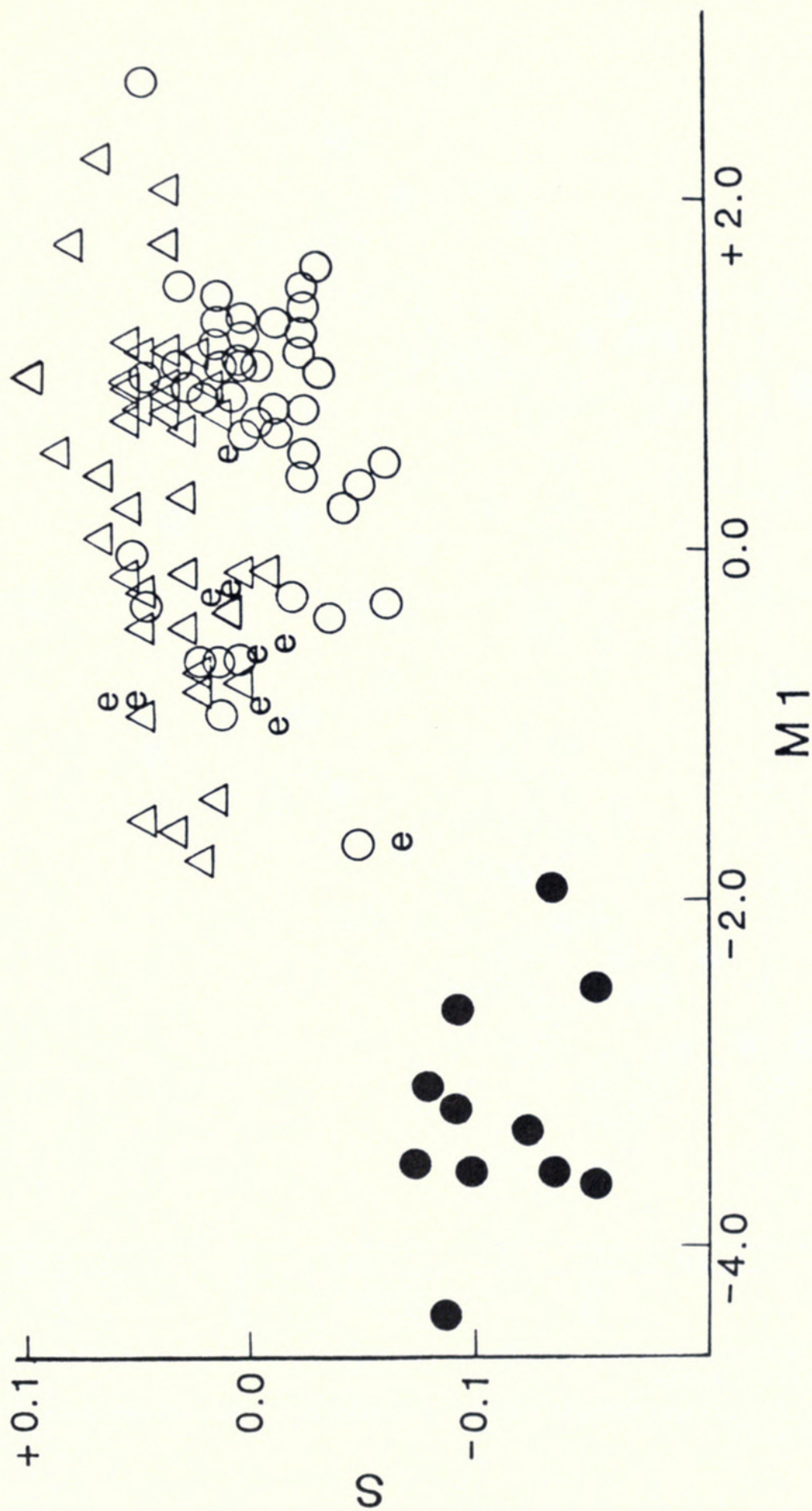


FIG. 7. Relative position of 107 specimens of *Vinciguerria* in the projection of sheared PCII (S) for morphometric characters (table 5) against PCI (M1) for meristic characters (table 6).

**Key:** ● = Red Sea specimens; ○ = central specimens; △ = equatorial specimens (see fig. 3 for listing); e = *Vinciguerria lucetia*.



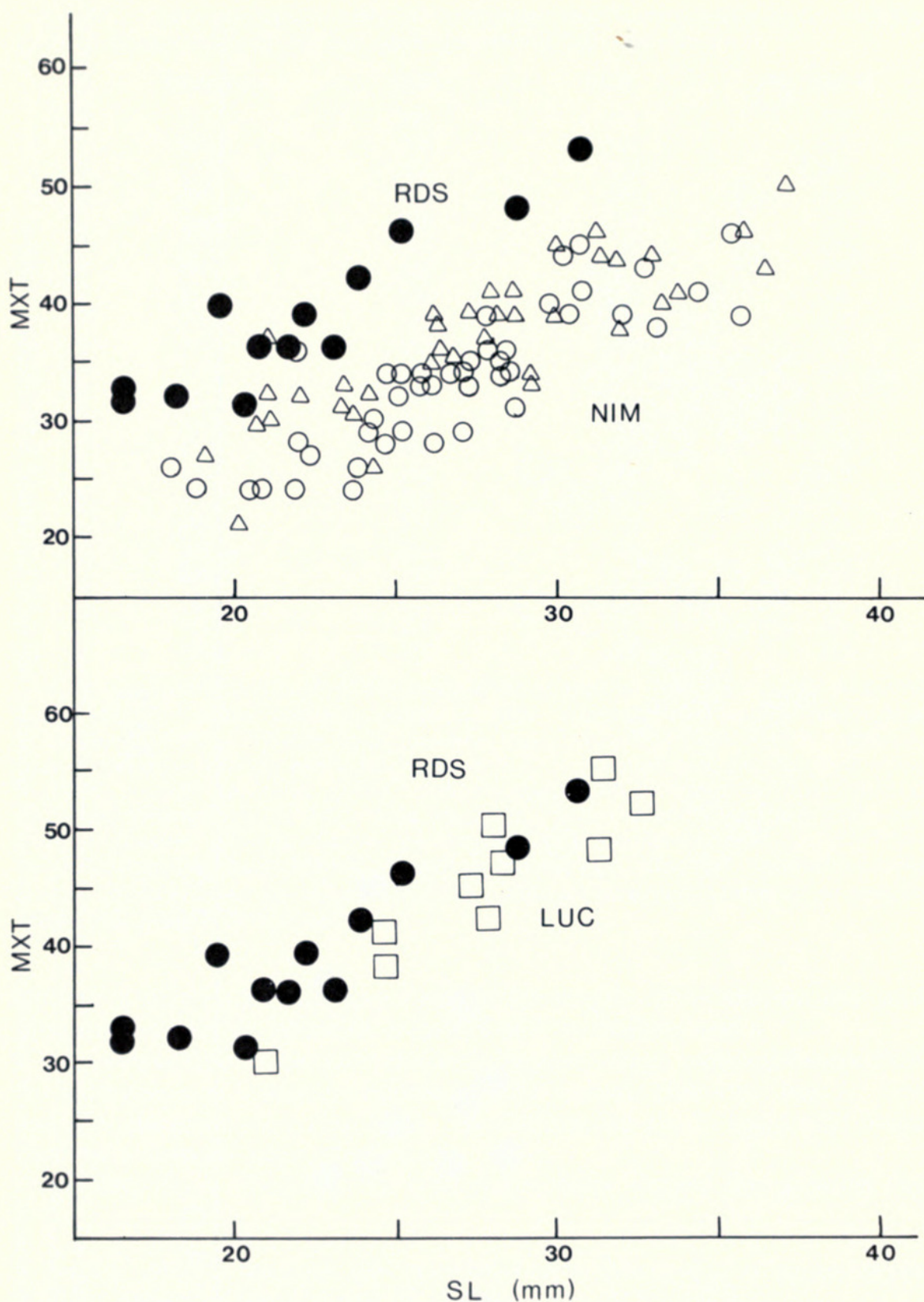


FIG. 8. Number of maxillary teeth (y-axis) plotted against standard length (x-axis) for specimens of *Vinciguerria*.

**Key:** ● = Red Sea specimens; ○ = central specimens; △ = equatorial specimens; □ = *Vinciguerria lucetia*.



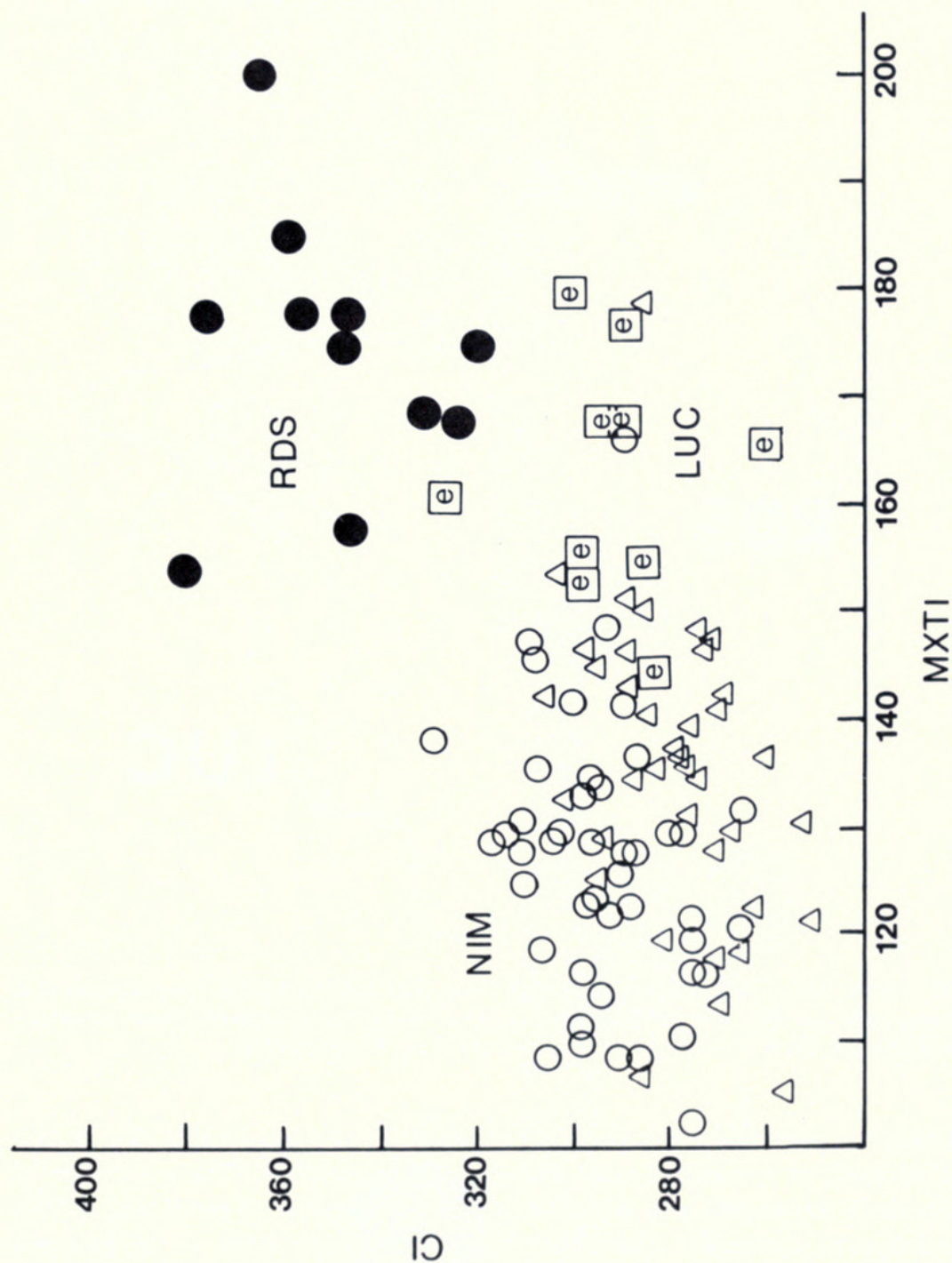


FIG. 9. Composite index (CI, y-axis) plotted against maxillary tooth index (MXTI, x-axis) for specimens of *Vinciguerria*. See text for derivation of each index.

**Key:** ● = Red Sea specimens; ○ = central specimens; △ = equatorial specimens (see fig. 3 for listing); □ e = *Vinciguerria lucetia*.



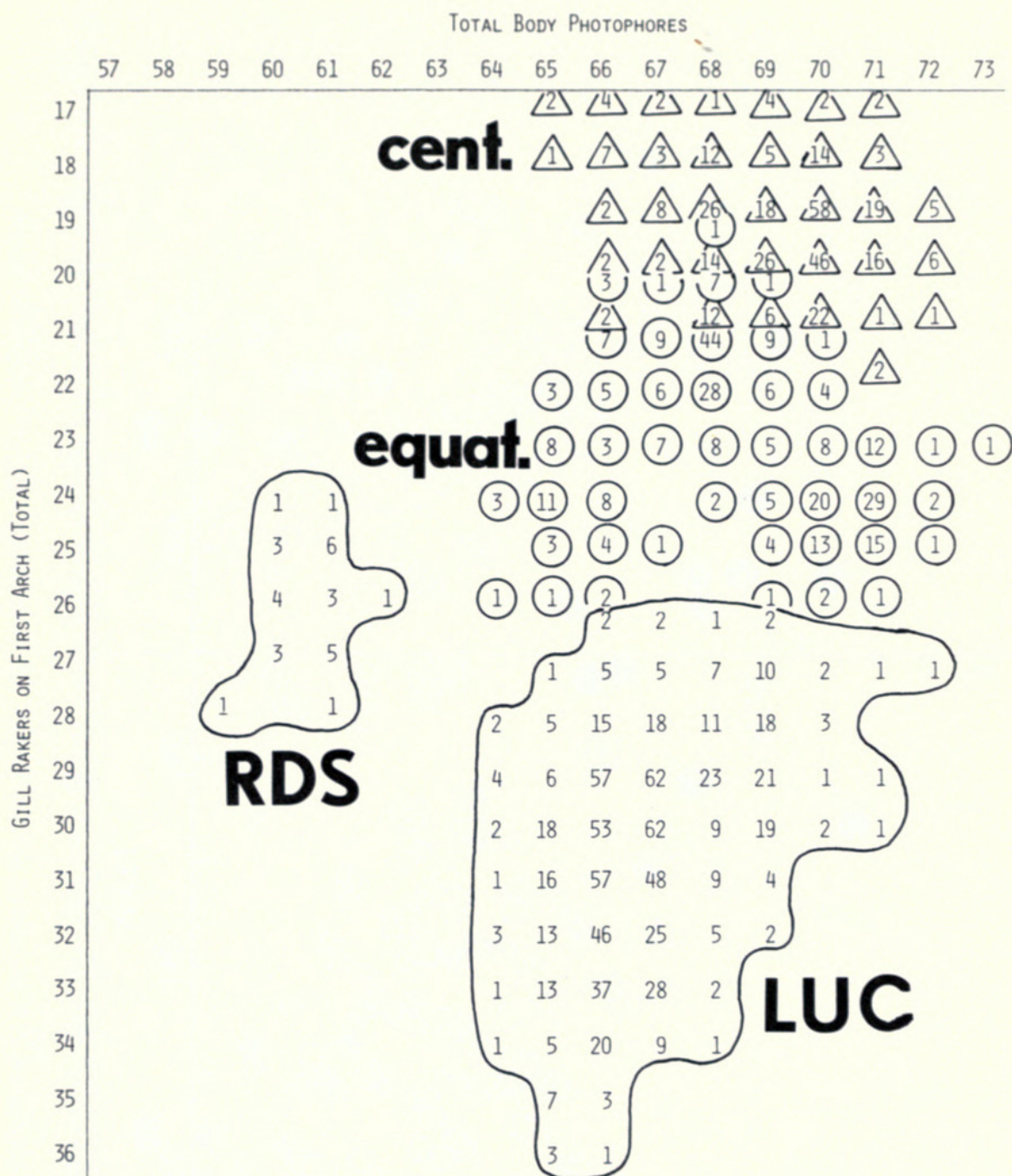


FIG. 10. Total body photophores tallied by total gill raker number for specimens of *Vinciguerria*. Data for Red Sea and *nimbaria* material based on specimens from areas depicted in Figure 1. Data for *Vinciguerria lucetia* based on Feltes (1978).

from *lucetia*) in possessing more maxillary teeth at any given size (fig. 8; the number of teeth is correlated with length of the maxilla). When number of maxillary teeth expressed as a maxillary tooth index ( $[\text{No. of teeth}/\text{SL}] \times 100$ ) is plotted against composite index (fig. 9), complete separation of the Red Sea specimens is achieved. Also achieved is good separation of "central" and "equatorial" specimens of *nimbaria* vs. *V. lucetia*.

*Gill Rakers.*—Gill rakers in *nimbaria* number 17 to 26, and in *lucetia*, 26 to 36. Specimens from the Red Sea are intermediate in gill raker number, 24 to 28, and in that respect differ from both of the other species. In a tally of gill raker number against total body photophores (fig. 10), four groups are identifiable.



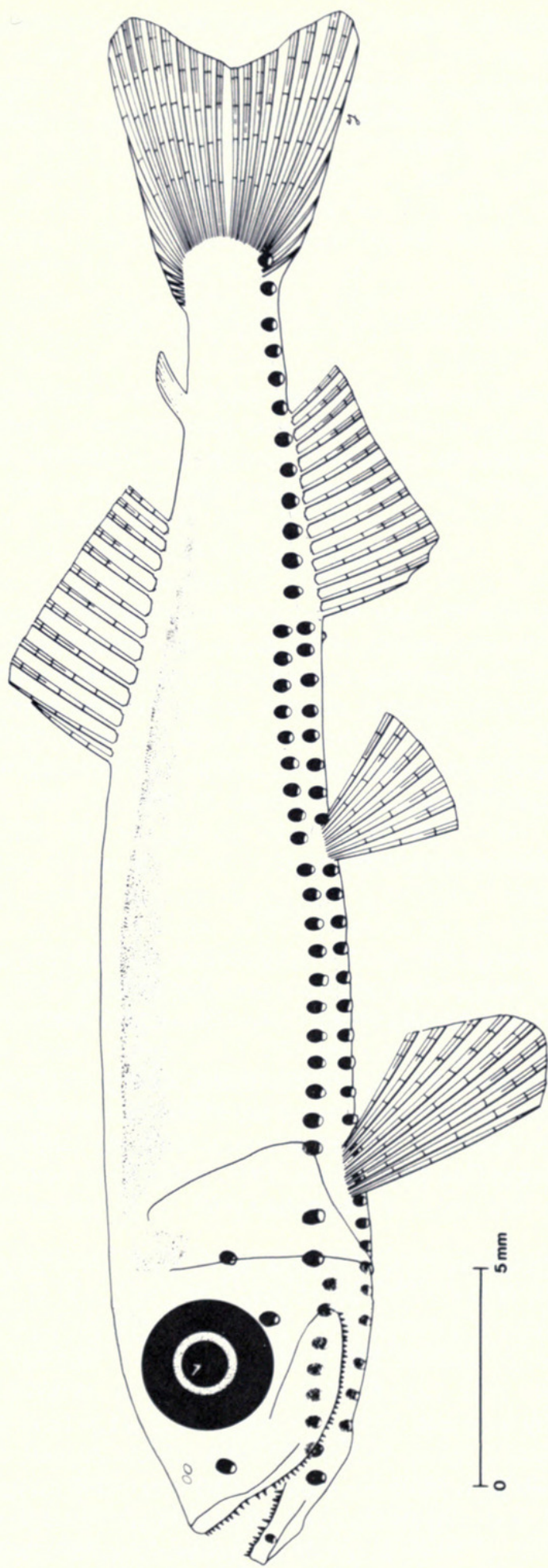


FIG. 11. *Vinciguerria mabahiss*, holotype, USNM 224860, 30.5 mm SL.



TABLE 7. Comparison of characters among larvae of *Vinciguerria*, based on prometa-morphic stage larvae only.

Species	Position of anal-fin origin vs. dorsal-fin ray number	Predorsal distance (as % SL)	Body segment number at dorsal-fin origin
<i>lucetia</i> *	9-10	61.0-66.0	21-22
<i>nimbaria</i> *	10-11	57.0-62.0	19-20
<i>mabahiss</i> (N = 7, 9.3-13.0)	8-9, 9-10	61.7-65.5	19-20

\* Data for *V. lucetia* and *V. nimbaria* are from Gorbunova (1981).

The Red Sea form and *V. lucetia* are distinct from *nimbaria* and from each other. It is also apparent that central vs. equatorial populations of *nimbaria* differ in gill raker number, equatorial specimens having more. This and other distinctions will be the subject of a subsequent paper (Johnson & Feltes, in prep.).

#### CONCLUSION

We conclude that the Red Sea form is distinct among all populations of *nimbaria*, including that population recognized as the distinct species *lucetia*. We believe that taxonomic recognition of the Red Sea population is warranted. We are proposing the name *Vinciguerria mabahiss* for the Red Sea form to honor the work of the MABAHISS or "John Murray" Expedition (1933-1934) to the Red Sea, Gulf of Aden, and Arabian Sea (Sewell, 1935). The 50th anniversary of the departure of that expedition occurred on Sept. 3, 1983.

***Vinciguerria mabahiss* sp. nov.** Figure 11.

#### SYNONYMY

*Vinciguerria* sp., Marshall, 1963, p. 187 (population of *Vinciguerria* in Red Sea said to differ from that in Gulf of Oman and Arabian Sea); 1971, p. 66 (body size and presumably fecundity lower in Red Sea form than in Indian Ocean form).

*Vinciguerria lucetia* (not of Garman, 1899), Kotthaus, 1967, p. 15 (first documented record from Red Sea, 13-mm specimen from METEOR Stn. No. 23, 25°22.6'N, 36°09.4'E); Aron & Goodyear 1969 (first record from the Gulf of Aqaba, also records from adjacent Red Sea); Botros, 1971, Table III (listed among "fishes recovered in the Red Sea"); Klauswitz, 1980, p. 13 (listed, after Aron & Goodyear, 1969).

Holotype: USNM 224860 (ex USNM 224860), MNK 1945, 29°15'20"N, 34°52'30"E; Gulf of Aqaba, 6 ft IKMT; 0-500 m; 10 Aug. 1968, 30.5 mm SL.

Paratypes: BMNH, MH 3, 21°53'N, 37°10'E, Red Sea, 100 fm wire out, N100 B, 29 Nov. 1951, 1 (17.0). BMNH, MH 8, 19°45'N, 37°25'E, Red Sea, 200 fm wire out, N100 B, 16 Jan. 1951, 2 (11.9-19.1). BMNH, MH 11, 19°45'N, 37°25'E; Red Sea, N100 B, 200 fm wire out, N100 B, 16 Jan. 1951, 2 (11.9-19.1). FMNH 94574 from USNM 224860, 1 (25.2). SIO 83-176 from USNM 224860, 1 (28.8). SMF 17682, 21°21.74'-19.02'N, 38°05.32'-06.46'E, Red Sea, 0-500 m, pelagic closing trawl, MESEDA I, F. S. "SONNE," Leg 14.XI.1977, 2 (ca. 14.0-17.5). USNM 203824, MNK 1933, 27°54'00"N, 34°25'30"E, Red Sea, 500 meters wire out



(mwo), 6 ft IKMT, 9 Aug. 1968, 0035–0200 hr, 63 (11.0–19.9). USNM 224856, MNK 1899, 27°46'30"N, 34°19'30"E, Red Sea, 0–1,500 m, 6 ft IKMT, 7 Aug. 1968, 1755–1955 hr, 16 (12.5–18.8). USNM 224857, MNK 1946, 29°19'30"N, 34°53'30"E, Gulf of Aqaba, 0–100 m, 6 ft IKMT, 11 Aug. 1968, 2400–0110 hr, 6 (11.2–23.5). USNM 224858, MNK 1893, 27°44'45"N, 34°22'00"E, Red Sea, 0–1,400 m, 6 ft IKMT, 6 Aug. 1968, 2117–2300 hr, 28 (12.1–21.5). USNM 224859, MNK 1901, 27°50'15"N, 34°21'30"E, Red Sea, 0–1,000 m, 6 ft IKMT, 7 Aug. 1968, 2235–0012 hr, 20 (12.1–20.2). USNM 264320, MNK 1945, Gulf of Aqaba, 29°15'20"N, 34°52'30"E, 0–500 m, 6 ft IKMT, 10 Aug. 1968, 2234–2350 hr, 6 (11.1–23.9). USNM 224861, MNK 1942, 29°06'15"N, 34°48'45"E, Gulf of Aqaba, 0–1,500 m, 10 Aug. 1968, 1410–1650 hr, 1 (13.0). USNM 224862, MNK 1931, 27°47'00"N, 34°20'15"E, Red Sea, 0–1,450 m, 6 ft IKMT, 8 Aug. 1968, 2021–2212 hr, 13 (11.5–19.9). USNM, uncatalogued, MNK 1980, 29°06'20"N, 34°47'05"E, Gulf of Aqaba, 1,450 mwo, 6 ft IKMT, 5 Aug. 1968, 2100–2323 hr, 26 (10.5–20.0). USNM, uncatalogued, MNK 1891, 29°00'00"N, 34°44'40"E, Gulf of Aqaba, 1,000 mwo, 6 ft IKMT, 6 Aug. 1968, 2353–0125 hr, 23 (10.8–20.1). USNM, uncatalogued, MNK 1897, 27°44'45"N, 34°22'00"E, Red Sea, 500 mwo, 6 ft IKMT, 7 Aug. 1968, 0130–0358 hr, 45 (10.1–22.8).

Not designated as paratypes: BMNH, MH 2, 26°16'30"N, 36°38'E, Red Sea, 100 fm wire out, N100 B, 23 Nov. 1950, 2 (6.2–11.2). BMNH, MH 3, 26°16'30"N, 36°38'E, Red Sea, 100 fm wire out, N100 B, 23 Nov. 1950, 2 (5.6–10.5). BMNH, MH 4, 19°45'N, 37°25'E, Red Sea, 100 fm wire out, N100 B, 16 Jan. 1951, 6 (4.5–6.2). BMNH, MH 6, 19°45'N, 37°25'E, Red Sea, 200 fm wire out, N100 B, 16 Jan. 1951, 10 (5.5–11.2). BMNH, MH 8, data as above, 1 (ca. 8.5). BMNH, MH 10, 19°45'N, 37°25'E, Red Sea, 100 fm wire out, N100 B, 16 Jan. 1951, 5 (ca. 5.5–12.0). BMNH, MH 11, data as above, 3 (11.7–12.1). BMNH, MH 12, 19°45'N, 37°25'E, Red Sea, 200 fm wire out, N100 B, 16 Jan. 1951, 4 (8.2–12.0). USNM 203824, data as above, 1 (13.2). USNM 224856, data as above, 14 (12.1–13.0). USNM 224857, data as above, 111 (7.5–13.0). USNM 224858, data as above, 16 (11.2–17.8). USNM 224859, data as above, 3 (11.8–18.9). USNM 264321 from USNM 224860, 5, 3 (12.0–12.2) + 2 (frag.). USNM 224862, data as above, 15 (9.2–13.0), 2 prolarvae, 3 juvenile fragments. USNM, uncatalogued, MNK 1890, data as above, 4 (11.1–12.2). USNM, uncatalogued, MNK 1891, data as above, 8 (9.8–13.8). USNM, uncatalogued, MNK 1897, data as above, 4 (10.6–11.6). ZIZM, ZMH 4855, 25°22.6'N, 36°09.4'E, Red Sea, 0–150 m, Helgoland larval net, METEOR Stn. No. 23, 20 Nov. 1964, 1415–1915 hr (badly damaged), 1 (ca. 13.0).

#### DIAGNOSIS

A species of *Vinciguerria* with symphyseal photophores present, total body photophores 58 to 63, vertebrae 37 to 38, and total gill rakers on first gill arch 24 to 28. These characters distinguish *V. mabahiss* from all other species of *Vinciguerria*. For detailed documentation of these and other characters see preceding pages.

#### DESCRIPTION

Based on a total of 471 (4.5–30.5) specimens, including the holotype (30.5), 255 paratypes (10.1–28.8), and 215 (4.5–18.9) other specimens. In listings below, values in parentheses are those for the holotype.



*Meristic Characters*.—Branchiostegal rays, 12 (12). Gill rakers: first arch, total 24 to 28 (27); first arch, upper limb 7 to 8 (7); first arch, lower limb 17 to 20 (20). Fin rays: dorsal 12 to 14 (13); anal 13 to 14 (14); pectoral 9 to 10 (10); pelvic 7 (7); caudal (principal) 19 (19). Vertebrae 37 to 38 (38).

*Photophores* (where the two sides, left vs. right, differ, either in the extremes or values for the holotype, the count for each side is given, left/right).—IV, 20 to 22 (21). VAV, 7 to 9 (8). AC, 10 to 13 (12/13). IC, 39/40 to 42 (41/42). OV, 10 to 12 (11). VAL, 8 to 10 (9). TOT 58 to 63 (61/62).

*Proportional Dimensions*.—Expressed as thousandths of the SL; based on the holotype (30.5 mm SL) and 10 paratypes (18.1–28.6 mm SL); values given as the range, mean and 95% confidence limits, and values for the holotype (in parentheses). Body depth at pectoral insertion, 195 to 219,  $207 \pm 1.5$  (196). Caudal peduncle: depth, 70 to 80,  $75 \pm 2.0$  (70); length, 138 to 166,  $152 \pm 5.4$  (144). Distance from adipose base to base of upper middle caudal-fin ray, 131 to 152,  $142 \pm 4.8$  (131). Distance from base of last dorsal-fin ray to base of upper middle caudal-fin ray, 228 to 256,  $245 \pm 6.1$  (228). Pectoral-fin insertion to pelvic-fin insertion, 241 to 274,  $255 \pm 6.1$  (262). Distance from snout to: dorsal-fin origin, 601 to 628,  $617 \pm 7.0$  (609); anal-fin origin, 691 to 731,  $712 \pm 8.9$  (718); pectoral-fin insertion, 275 to 304,  $288 \pm 8.0$  (278); pelvic-fin insertion, 529 to 553,  $541 \pm 5.7$  (535). Head length, 279 to 314,  $294 \pm 7.4$  (281). Snout length, 68 to 83,  $75 \pm 3.4$  (73). Eye diameter (fleshy), 87 to 107,  $94 \pm 3.9$  (87). Upper jaw length, 183 to 210,  $199 \pm 6.4$  (189). Interorbital width (bony), 45 to 53,  $48 \pm 2.0$  (47). Length of dorsal-fin base, 156 to 182,  $173 \pm 3.1$  (178). Length of anal-fin base, 133 to 162,  $149 \pm 6.3$  (150). Postorbital head length, 104 to 131,  $113 \pm 5.1$  (108). Lower jaw length, 204 to 238,  $224 \pm 8.0$  (210). Pelvic insertion to anal-fin origin, 142 to 184,  $165 \pm 8.2$  (184). "Tail" length, 282 to 312,  $301 \pm 6.2$  (296). Head length divided by "tail" length, 0.90 to 1.09,  $0.98 \pm 0.03$  (0.95).

*Body*.—Scales, if present, extremely deciduous—no remnants of scales or scale pockets visible in any of the available specimens. Anus immediately in advance of anal-fin origin, between seventh and eighth VAV photophores. Anal-fin base rather short, with origin under posterior one-third of dorsal-fin base. Dorsal-fin origin distinctly behind a vertical through midpoint of standard length. Pelvics abdominal, inserted well in advance of dorsal-fin origin. Pectorals ventrolateral, inserted just behind concave ventroposterior edge of subopercle. Adipose origin directly over or slightly before or behind a vertical through base of last anal-fin ray.

*Head*.—Head relatively massive, depth a little greater than body depth. Eyes large, round. Interorbital area a shallow trough between low lateral ridges on frontals, covered with a very delicate skin. Nostrils close together, directly anterior to dorsal half of pupil.

*Head Photophores*.—Anterior ORB slightly exceeding posterior in diameter. Anterior ORB distinctly dorsad (one or more diameters) to posterior ORB. In left lateral view, anterior ORB at ventroanterior ("eight o'clock") and posterior ORB at ventroposterior ("five o'clock") margins of orbit, respectively. Three OP. The dorsal OP about one-half the diameter of the ventral two OP, and located on a horizontal line through or just below center of pupil. Anterior two OP located on the line of the preopercular portion of the preoperculomandibular laterosensory canal. Posterior OP about three photophore diameters directly posterior to ventroanterior OP. SO present, small, the smallest of all head pho-



tophores. Short, dark, band of pigment extending forward from each SO. BR consistently eight.

*Teeth*.—Teeth present on premaxillae, maxillae, dentaries, vomer, palatines, and gill arch elements. Teeth on premaxillae and maxillae uniserial, teeth on dentary partly biserial. One tooth on each side of vomer. Two to four large teeth (increasing sequentially in size from anterior to posterior) on each palatine. Teeth absent on pterygoids and tongue.

*Gill Chamber*.—Four gill arches, with well-developed slit behind fourth. Lath-like gill rakers on first three arches, only small teeth in patches on fourth.

*Main Photophore Rows*.—As in Figure 9, the IV beginning at a point on the isthmus at or slightly anterior to a vertical through anterior margin of orbit. No accessory body photophores.

*Color*.—Color in alcohol beige to brown with iridescent highlights. Presumed silvery in life. An especially dense band of pigment above horizontal septum, extending from occiput to below adipose fin. Peritoneum black.

*Larvae*.—Most available specimens of *mabahiss* are larvae. All six postembryonic stages (Ahlstrom & Counts, 1958, p. 367) are present in the material. The smallest stage I (larva, prior to photophore formation) specimen is 4.5 mm SL. *Vinciguerria mabahiss* larvae are quite similar in appearance and gross morphology to those of *V. nimbaria* (Silas & George, 1971) and *V. lucetia* (Ahlstrom & Counts, 1958). Three typical pigment spots reported by these authors for *nimbaria* and *lucetia*, respectively, were not seen in *mabahiss*: postpectoral spot, anal spot, and precaudal spot (see listing in Ahlstrom & Counts, 1958, p. 377). The other typical pigment areas listed are present; viz., prepectoral spot, anal-base pigment, caudal spot, and pigment (as one continuous bar rather than divided at caudal fork) at base of upper and lower caudal rays. In the very smallest larvae, only the pigment at the anal base and the base of the middle caudal-fin rays are consistently present (the caudal spot is present in some larvae as small as 6.2 mm SL). The midmetamorphic stage (Ahlstrom & Counts, 1958, p. 367) occurs when specimens are (roughly) 10 to 13 mm in size. Ahlstrom & Counts (1958, p. 371) indicated that standard length "may even diminish" during metamorphosis, depending on the timing of ossification of the vertebral column. While this has not been determined for Red Sea individuals, there are numerous stage II (prometamorphic) individuals in excess of 12.5 mm SL (maximum = 13.2 mm SL), whereas the smallest stage IV (postmetamorphic) individuals are 10 to 11 mm SL (minimum = 10.1). Postmetamorphic individuals of 13.0 mm SL (see fig. 2) are (using the criterion of completion of photophore development) nearly stage V (juvenile). We suspect (but cannot establish with our material) an actual shrinkage of 1 to 2 mm in SL during metamorphosis. Gorbunova (1981) presents a key to the larvae of *Vinciguerria*. Characters used to distinguish larvae (prometamorphic) of *lucetia* from *nimbaria* are listed in Table 7 as are the corresponding values for *mabahiss*. *Vinciguerria mabahiss* agrees with *lucetia* in values for two characters and with *nimbaria* in values for one character (number of somites before dorsal-fin origin). In fact, we suspect that detailed study of larval development in different environments (especially environments differing in productivity) would reveal variation in these characters not seen in the 20 specimens studied by Gorbunova (1981, p. 146).

*Distribution*.—*Vinciguerria mabahiss* is known only from the northern and central Red Sea north of 19°N (fig. 12). No known samples exist from the southern



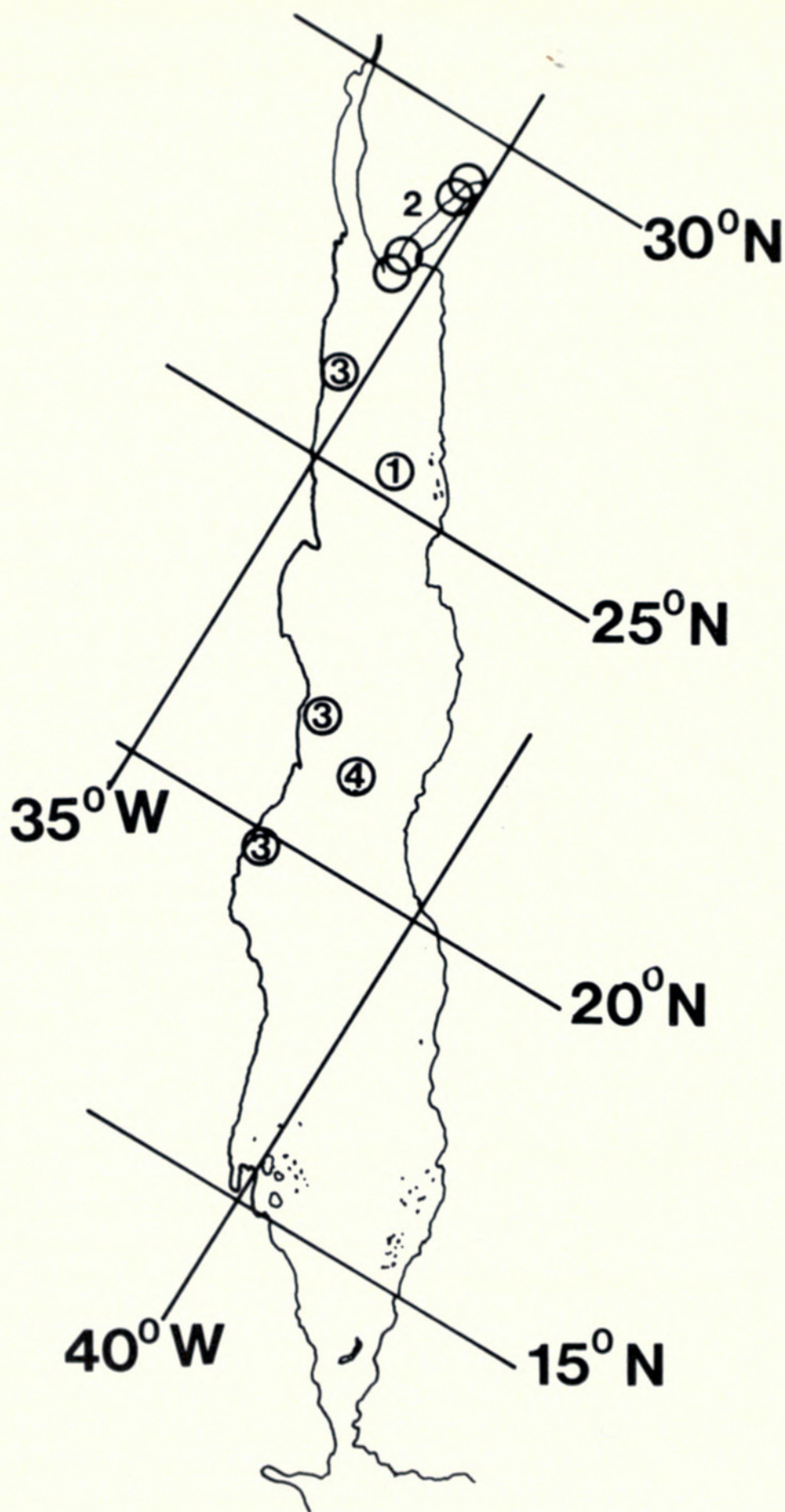


FIG. 12. Distribution of *Vinciguerria mabahiss*. 1 = METEOR (ZIZM) station 23; 2 = MENELIK II (USNM) material (a number of closely adjacent stations not plotted); 3 = MANIHINE (BMNH) Sudanese Red Sea Expedition of 1950-1951 material; 4 = MESEDA I (SMF) Expedition material.



half of the Red Sea. All specimens were taken in open net hauls, with trawl depths to 1,400 m. Numerous specimens and most larvae were taken above 200 m, and many, in the upper 100 m. Marshall (1971, p. 66) states that the Red Sea *Vinciguerria* does exhibit (diel) vertical migration, but gives no documentation.

*Etymology*.—*Vinciguerria mabahiss* is named for the H.E.M.S. MABAHISS, for her captain and crew, for the scientists aboard, for the organizing committee and supporters, and for scientists serving as authors of the 11 volumes (November 1935–May 1967) issued as Scientific Reports of the John Murray Expedition 1933–1934.

## DISCUSSION

### DISTINCTIONS AND DEPAUPERACY OF THE RED SEA MESOPELAGIC FISH FAUNA

*Faunal Uniqueness*.—Only eight mesopelagic species,\* including *Vinciguerria mabahiss*, are known from the Red Sea (Marshall, 1963; Aron & Goodyear, 1969; Botros, 1971; Post & Svoboda, 1980; Klausewitz, 1980). Explanations offered for this depauperacy have involved both the peculiar recent (Pleistocene) history of this basin and its unique hydrography.

The Red Sea is usually considered an appendix of the vast Indo-West Pacific biogeographic province (Briggs, 1974). Near-continuous surface inflow from the Gulf of Aden (Siedler, 1969) should allow substantial recruitment of pelagic organisms and organisms with planktonic larvae, yet a large proportion of widespread species found in the Indian Ocean is absent or only temporarily present in the Red Sea. For other taxa, the number of species represented in the Red Sea is markedly reduced compared with that represented in the Indian Ocean. The total number of fish species for the Indian Ocean is estimated at 2,000; for the Red Sea, 800. Of 270 species of calanoid copepods recorded from the Indian Ocean, 158 occur in the Red Sea. There are 452 species of Indian Ocean dinoflagellates, but only 88 species are known from the Red Sea (Kimor, 1973). About 31% of Indian Ocean euphausiids are present in the Red Sea (Halim, 1969). There seems to be a further reduction in overall diversity to the north (Foin & Ruebush, 1969; Por, 1972; Kimor, 1973).

Both relative depauperacy and endemism are important components of Red Sea distinctiveness. For benthic forms, the percentage of endemics is high: crinoids, 70%; decapod crustaceans, > 30%; hermatypic corals, 25%; cephalopods, ca. 50%; cowries, 15%; neritic hydromedusae, 20%; echinoderms, 15%; coral reef fishes, 10% to 15% (Briggs, 1974; Ekman, 1953; Gohar, 1954; Marshall & Bourne, 1964). Compared with these figures, the number of endemic planktonic forms is much smaller (Halim, 1969), although our knowledge of Red Sea and Indian Ocean plankton remains quite imperfect. Of the eight mesopelagic species (at least two of which, *Maurolicus muelleri* and *Diaphus coeruleus*, are bottom-associated as adults but planktonic as larvae and juveniles), only two, *Astronesthes martensi* and *Vinciguerria mabahiss*, are Red Sea endemics.

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\* The others: *Astronesthes martensi* Klunzinger, 1871; *Benthosema pterota* (Alcock, 1891); *Bregmaceros arabicus* (D'Ancona and Cavinato, 1965); *Diaphus coeruleus* (Klunzinger, 1871); *Lestidiops luetkeni* (Ege, 1933); *Maurolicus muelleri* (Gmelin, 1788); *Stomias affinis* (Gunther, 1887).



In length, breadth, depth, virtual isolation by arid lands, high evaporative water loss with consequent high salinity (increases in north to exceed 40 ‰), northwest to southeast main axis, and considerable north to south extension, the Red Sea is fairly comparable to the Gulf of California. Both contain rich reef-associated shorefish faunas, with moderately high endemism (exceeding 10% in both cases).

The two bodies of water differ most dramatically in that the Gulf of California is broadly open to the eastern Pacific at its southern end, with a "sill" depth of thousands of meters. Thus, the vertical distribution of such properties as temperature, salinity, and dissolved oxygen is typically oceanic for areas south of the "mid-riff" (Sal Si Puedes Sill; Robison, 1972). By contrast, the main channel at the Strait of Bab-el-Mandeb is about 20 km broad and only 300 m deep. Near Great Hannish Island the channel is only 100 m deep.

The Gulf of California midwater fish fauna is comprised of at least 39 species and is a representative, if reduced, eastern tropical Pacific mesopelagic fauna (especially true in the south, markedly less true to the north; see Robison, 1972). The Red Sea mesopelagic fauna contains only eight species, a very small fraction of the 300 deepwater pelagic fish species estimated to exist in the Indian Ocean (Cohen, 1973). It seems likely that the considerably greater isolation of the Red Sea, its geographic position in a highly arid and seasonal climate, its consequent unique hydrography, plus Pleistocene perturbations, have all contributed to the distinctions and depauperacy of the Red Sea mesopelagic fish fauna. We have attempted a summary of these factors in the paragraphs that follow, but note that our knowledge, especially of history, is very incomplete.

**Oceanographic Summary.**—Extending NNW to SSE between 30°N and 12°30'N, the Red Sea is approximately 1,932 km long, with an average breadth of 280 km. The depth averages 700 m away from the reef-bound coast, while depths of over 2,500 m can be found between 22°N and 19°N. The main trough extends to the Sinai Peninsula, which divides the northern part of the sea into the shallow Gulf of Suez and the deep Gulf of Aqaba (Morcos, 1970). The latter reaches 1,830 m in depth (Almogi-Labin, 1982) and is separated from the Red Sea by a sill 256 to 340 m deep. The separation of the Red Sea and the Gulf of Aden may appropriately be placed near Great Hannish Island (13°41'N), where the channel is approximately 100 m deep. From May to September the winds blow from the NNW; from October to April the winds average from the SSE south of 20°N. Seasonal temperature differences may be marked, especially in the north where winter temperatures of 18° C and summer temperatures up to 30° C are experienced (Sverdrup et al., 1942). The deep waters of the Red Sea have higher temperatures (below 200 m, conditions are essentially isothermal at about 22° C) than waters at comparable depths elsewhere in the world oceans, including the Gulf of Aden. The Red Sea is also very salty—the surface salinity increases to the north and may exceed 40 ‰ at the tip of the Sinai Peninsula. Below approximately 200 m and the 22°-C isotherm, the water is nearly isohaline below the 40.5 ‰ isopleth. An intermediate oxygen minimum exists between 300 and 600 m. A core with less than 0.5 ml/L exists at 400 m in the southern Red Sea. In the northern Red Sea the minimums are less extreme, and no sharp O<sub>2</sub> zonation exists in the Gulf of Aqaba (Morcos, 1970; Sverdrup et al., 1942; Thompson, 1939).

Physical exclusion of midwater organisms by extreme conditions of temper-



ature and salinity is the most commonly cited explanation for impoverishment of the Red Sea pelagic fauna (e.g., Kimor, 1973, p. 223). Sewell (1948) argues for actual fatality of some organisms brought (by advection) in contact with the warm salty water, as evidenced by large deposits of pteropods near the sill. No data exist relevant to the possibility of actual intolerance of fishes to Red Sea conditions.

Marshall (1963, pp. 187–188) goes to some length to point out the striking differences at 200 to 400 m on either side of the sill separating the Red Sea and Gulf of Aden (up to a 10°C difference in temperature, up to 4 ‰ difference in salinity). His conclusion: "The greater the physical differences between deeper waters inside and outside a basin with a shallow sill, the more [probable] . . . genetic divergence [between populations inside vs. outside, and] at the same time, [the] fewer [the number of] species able to colonize the extreme environment." Available samples do not permit the rigid testing of this hypothesis, but it is of interest that Marshall's implicit prediction of faster developmental rate as a species-defining character in the case of Red Sea species is corroborated by what we thus far know of *V. mabahiss*.

Historical Summary.—Although the Red Sea basin is relatively young, there is disagreement regarding its exact age and especially the chronicle of its formation. Whitmarsh (1981) and Davies (1969) suggest the first spreading associated with the Red Sea basin began about 25 million years before present (YBP). Others propose establishment earlier in the Tertiary (Laughton, 1966; Bignell, 1978; Garson & Miroslav, 1976). The central trough of the Red Sea was forming during the Miocene (Garson & Miroslav, 1976; Girdler, 1969; Ross & Schlee, 1973). The northern part is geologically oldest. Along the Gulf of Suez, the northern Red Sea was connected to the Mediterranean Sea and was thus part of the Tethys Sea. The Gulf of Aqaba did not fill until late Pliocene or early Pleistocene times (Said, 1969). Late in the Miocene there appears to have been some period of separation of the Red Sea from the Mediterranean (Botros, 1971). The loss of a substantial connection between the Red Sea and the Mediterranean is usually placed in the Pliocene (Botros, 1971; Fox, 1926; Ross & Schlee, 1973; Heybrock, 1965). Marshall (1952) believes the connection was lost in the Miocene, followed by intensive evaporation, hypersaline conditions, and elimination of most of the marine life. Large deposits of evaporites did build up during the Miocene (Girdler, 1969). It has been suggested that, before the closure to the north, the first connection with the Indian Ocean occurred, probably in the Pliocene. The result would have been a mixed Tethys Sea and Indian Ocean fauna. Evidence of Pliocene fauna of the Indian Ocean has been found as far north as the Suez region (Ross & Schlee, 1973). Sewell (1948) cites an argument by Steinitz (1929) that a marine passage between the Red Sea and the Mediterranean Sea existed into the beginning of the Quaternary. It is commonly believed that complete isolation of the Red Sea took place (probably several times) in the Pleistocene due to eustatic fluctuations. Sewell (1948) discusses a lowering of the sea level of 90 to 200 m during the last glacial epoch. He believes in an "almost complete disappearance of the Red Sea as it exists today and its reduction to two small inland lakes that were in all probability hypersaline." Under such changes, he finds it difficult to suppose that any elements of the marine fauna survived and believes that the original Tethys Sea fauna must have disappeared. Similarly, Klausewitz (1974) states the opinion that, at



some point, hypersaline conditions became so extreme that nearly the entire ichthyofauna was lost. Subsequent connections must have allowed only Indian Ocean faunal elements to become established in the Red Sea.

Examination of the microfossils from core samples has produced interpretations of the oceanographic conditions during the Pliocene and Pleistocene. A collection of the microfossil papers shows agreement that fluctuations in several taxonomic groups are attributable to alternating intervals of lowered sea level, isolation from the Indian Ocean, and increased salinity, followed by reestablishment of contact and influx of water from the Indian Ocean (McIntyre, 1969; Goll, 1969; Chen, 1969; Berggren, 1969; Deuser & Degens, 1969; Ku et al., 1969; Berggren & Boersma, 1969). Corresponding oscillations in the sea level have been demonstrated for the Mediterranean (Emiliani & Flint, 1963; Zeuner, 1959). The last glacial period began some 70,000 YBP with associated restricted flow between the Red Sea and the Indian Ocean (Berggren & Boersma, 1969; Ku et al., 1969). The coolest period of the late Pleistocene was 23,000 to 13,000 YBP (Berggren, 1969), with the glacial maximum approximately 18,000 years ago (Emiliani & Flint, 1963; Almogi-Labin, 1982). Four major influxes of Indian Ocean waters are indicated near 11,000 YBP, 20,000 to 25,000 YBP, 40,000 to 45,000 YBP, and a broad period from 65,000 to 200,000 YBP (McIntyre, 1969). Goll (1969) reports that an invasion of Indian Ocean radiolarians took place during the period 9,000 to 12,000 YBP.

At the glacial maximum, the salinity may have exceeded 50 ‰, and temperatures may have been lowered (seasonally) to 14° C (Almogi-Labin, 1982; Reiss et al., 1980; Berggren & Boersma, 1969). Almogi-Labin (1982) and Reiss et al. (1980) agree that there was reduction in species diversity during the glacial periods which may have been partly related to elevated salinity and lowered temperature values; however, in their opinion, changes in these two factors cannot serve as a total explanation for the reduced diversity. This they base partly on the known tolerance of present members of the fauna. They suggest that a greater stratification of the water column existed in glacial times. Pteropod and foraminifera assemblages indicate increased fertility, along with lower oxygen content of the underlying waters during glacial periods.

Por (1972) accepts periods of isolation for the Red Sea but disagrees with Sewell's (1948) contention that the Red Sea basin of glacial periods was occupied by two hypersaline lakes devoid of marine life. To support this he refers to Gohar's (1954) statement that there are no indications of growth discontinuities in the subfossil coral reefs. Varying, but in some cases substantial, amounts of speciation which have taken place in different taxonomic groups, as roughly indexed by levels of endemism, would seem to require a longer period of time and more stable marine conditions than postulated by Sewell (1948). Klauswitz (1980, p. 11) rejects entirely "an abiogenic period during the Pleistocene and a postglacial recolonization of the Red Sea from the Indian Ocean . . ." Although there was potential access from the Indian Ocean during recent interglacial periods, the degree of endemism in certain taxa suggests that some endemic species had earlier origins (early Pleistocene or late Pliocene). As noted above, the mesopelagic fish fauna is depauperate. Klauswitz (1980) comments on the theoretical difficulty deep pelagic and benthic fishes would have crossing the sill between the Red Sea and the Indian Ocean compared with the difficulty littoral species would have. He states this difficulty may have been eased during the interglacial periods when sea levels may have exceeded the present level



by 60 to 80 m or perhaps 200 m, and believes it may have been then that the deep sea fishes entered the Red Sea. In summary, the consensus view is that conditions during Pleistocene isolation events lead to divergence and speciation in some Red Sea populations (Por, 1972; Klausewitz, 1974) plus complete elimination (from the Red Sea) of other organisms. For mesopelagic fishes, the result is a highly impoverished fauna, but (with *Astronesthes martensi* and *Vinciguerria mabahiss*) also a fauna with endemic species and, thereby distinct.

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#### MATERIAL EXAMINED

##### *Vinciguerria nimbaria*

ATLANTIC OCEAN—2,904 specimens (11–58 mm SL) from 91 stations.

CNA—599 specimens (13–58 mm SL) from 40 stations. MCZ, RHB: 1003 (35), 1008 (13), 1013 (20), 1017 (4), 1123 (1), 1124 (2), 1127 (4), 1129 (5), 1289 (36), 1271 (148), 1307 (19), 1312 (129), 1501 (21), 1942 (19), 2022 (13), 2088 (48), 2089 (11), 2090 (7), 2091 (2), 2092 (4), 2093 (5), 2095 (1), 2099 (4), 2100 (4), 2108 (2), 2120 (1); USNM, ACRE: 12-17C (1), 12-18A (2), 12-18B (2), 12-28B (1), 12-36C (1), 12-35C (1), 12-62 (1), 12-81 (1), 12-86 (1).

TC1 and TC2—702 specimens (11–43 mm SL) from 18 stations. MCZ, RHB: 2023 (21), 2024 (22), 2025 (79), 2028 (3), 2029 (34), 2030 (107), 2033 (35), 2034 (173), 2035 (3), 2076 (41), 2077 (43), 2080 (19), 2081 (4), 2082 (19), 2083 (14), 2084 (62), 2085 (83), 2086 (16).

TE—669 specimens (11–44 mm SL) from 23 stations. MCZ, RHB: 2037 (1), 2044 (7), 2047 (3), 2048 (80), 2049 (10), 2050 (6), 2051 (9), 2053 (160), 2054 (35), 2056 (6), 2057 (16), 2058 (49), 2059 (5), 2060 (64), 2062 (4), 2063 (3), 2065 (84).

EQA—825 specimens (14–50 mm SL) from 5 stations. MCZ, RHB: 972 (700), 2276 (24), 2287 (20), 2290 (22); UMML: 21902 (59).

CSA—109 specimens (14–49 mm SL) from 5 stations. ISH: 1419/68 (3), 440/71 (3), 1773/71 (8); MCZ, RHB: 1321 (58), 1436 (39).



INDIAN OCEAN—109 specimens (16–43 mm SL) from 4 stations.

SIO—15 specimens (20–31 mm SL) from 1 station. MCZ: AB VI-340B (15).

NIO—94 specimens (16–43 mm SL) from 3 stations. MCZ: AB VI-328B (15), AB VI-329B (43), AB VI-330 (36). Also examined were 6 lots of ZIZM material from the METEOR (stations 125, 127, 153, 167, 168, 170, 179); unfortunately, the preservative appears to have failed and the specimens are nearly useless.

PACIFIC OCEAN—1,201 specimens (12–38 mm SL) from 61 stations.

SCS—35 specimens (12–38 mm SL) from 6 stations. SIO: 70-341 (4), 70-343 (5), 70-344 (10), 70-345 (5), 70-346 (5), 70-347 (6).

PHS—739 specimens (12–40 mm SL) from 19 stations. SIO: 70-306 (63), 70-308 (6), 70-309 (18), 70-310 (23), 70-311 (29), 70-314 (45), 70-318 (52), 70-326 (7), 70-327 (3), 70-328 (12), 70-329 (12), 70-331 (22), 70-332 (2), 70-333 (11), 70-334 (173), 70-336 (15), 70-337 (6), 70-339 (14), 70-340 (226).

NWG—29 specimens (13–34 mm SL) from 9 stations. SIO: 68-465 (1), 68-472 (1), 68-476 (5), 68-482 (4), 68-483 (10), 68-486 (2), 68-490 (2), 68-492 (2), 68-495 (2).

CNP—69 specimens (14–31 mm SL) from 2 stations. UH: 69-11-5 (49), 69-11-6 (20).

EPW—122 specimens (13–30 mm SL) from 3 stations. SIO: 68-553 (8), 68-534 (63), 68-535 (51).

CEP—102 specimens (13–38 mm SL) from 2 stations. FMNH: 77,100 (52); SIO: TC 69-47 (50).

ECP—79 specimens from 10 stations. SIO: J 60-77 (10), J 60-83 (10), TC 51-51 (10), TC 51-59 (1), TC 51-60 (10), TC 51-63 (10), TC 51-67 (21), TC 51-78 (1), TC 51-81 (2), TC 51-86 (4).

CSP—25 specimens (15–32 mm SL) from 9 stations. SIO: 70-110 (1), 70-118 (1), 72-303 (5), 72-305 (2), 72-308 (1), 72-310 (5), 72-313 (5), 72-317 (2), 73-105 (3).

*Vinciguerria lucetia*

PACIFIC OCEAN—178 specimens from 12 stations.

LUC—SIO: 52-84 (6), 55-237 (20), 60-12 (51), 62-640 (4), 63-836 (5), 65-603 (8), 65-608 (6), 65-611 (1), 65-614 (14), 72-177 (33), 72-180 (20), Krill I, stn. 5 (10).

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