

HERMAPHRODITISM IN A TELEOST, *POLYNEMUS*
HEPTADACTYLUS CUV. AND VAL.*

P. V. KAGWADE

Central Marine Fisheries Research Institute; Sub-station, Bombay-1

INTRODUCTION

In fishes reproduction is normally sexual by fertilization of male and female reproductive elements borne by individuals of the two separate sexes. However, certain reproductive specializations, viz. gynogenesis, parthenogenesis and hermaphroditism are at times met with. Gynogenesis is observed in *Mollienesia formosa* (Hubbs and Hubbs, 1932, 1946) which exclusively occurs as females, wherein during reproduction the sperms of a related species only stimulate the eggs but do not contribute to any genetic material and the resulting offspring are all females. Gynogenesis has also been observed in a cyprinid fish *Carassius auratus gibelio* (Lieder, 1955). Parthenogenesis or development of eggs without fertilization is very rare. Hermaphroditism, a condition in which both the male and female gametes are produced by the same individual, is very common in the lower animals but rare among the higher vertebrates. In teleosts it occurs either teratologically or normally or by the reversal of sex. Herrings, cods, mackerels, sardines and some of the Pleuronectidae exhibit teratological hermaphroditism. Some of the eels, symbranchids and members belonging to the families Maenidae, Sparidae and Serranidae are normally hermaphrodites. A few members of these three families are subjected to sex reversal. Based on the nature of the ovotestis with respect to the maturing of the gametes, hermaphroditism can be classified into different groups. An ovotestis is said to be gonochoritic when only one of its sexes functions at a time depending on whether it is protandric or proterogynous. Self-fertilization is out of question here. D' Ancona (1945) has observed in *Sparus auralies* protandry where the male germ cells mature earlier than those of the female and in *Diplodus* spp. and other sparids, the presence of both testicular and ovarian parts in the same gonad, but only one of them attaining maturity. This condition presents a transition from hermaphroditism and is considered primitive to gonochorism.

In synchronous hermaphroditic serranids both sperms and ova in an ovotestis develop and become active simultaneously. Under such condition, if there are no physiological and genetic barriers, self-fertilization is a possibility. In fact self-fertilization has been experimentally proved by Clark (1959) in *Serranellus*

* This paper formed part of the thesis for the award of the Ph.D. degree of the Bombay University.

subligarius and by Reinboth (1962) and Salekhova (1963) in *Serranus scriba*. All these three workers have observed that the spawning by two or more individual fishes is likely to bring about cross fertilization.

The collected specimens of the newly discovered *Rivulus marmoratus* along the Florida east coast by Harrington (1961, 1963) were all hermaphrodites and were found to be the progeny of self-fertilization. Amongst the members of the subfamily Serraninae from Bermuda, Smith (1959) observed synchronous hermaphroditism in *Hypoplectrus unicolor*, *Prionodes phoebe*, *P. tigrinus* and *P. tabacarius*. Ovotestes similar in general structure to those of the monoecious percoids have been recorded by Mead (1960) in ten species of the order Inioi.

Another form of functional hermaphroditism is sex reversal. Essenberg (1926) has studied the sex reversal in *Xiphophorus helleri*, Liu (1944) in *Monopterus javanensis*, Zei (1949) in *Maena smaris*, *M. cruselis* and *Pagellus erythrinus*, Lavenda (1949) in *Centropristes striatus* and Smith (*loc. cit.*) in *Epinephelus guttatus*, *E. striatus*, *Mycteroperca bonaci*, *M. tigris*, *M. fulcata*, *M. venerosa*, *Cephalopholis fulvus*, *Petrometopon cruentatus*, *Alphestes afer* and *Promicrops itaiara*. Liu and Ku (1951) have described in detail the histological changes taking place in the gonad of *Monopterus* during sex transformation. In all the species cited where there is sex reversal they are proterogynous, the female sex appearing in smaller ones at a younger age and male sex in larger ones at an older age. The individuals first behave as females and later on as males with a phase of intersex in between. In general, size dimorphism between the sexes in a dioecious species may as well hint the possibility of hermaphroditism in these species.

Teratological hermaphroditism has been met with in a few Indian fishes. Chacko and Krishnamurthy (1949) have recorded this condition in *Hilsa ilisha*, Sathyanesan and Rajan (1953) in *Cirrhina reba*, Sathyanesan (1957) in *Barbus stigma*, Prabhu and Raja (1959) in *Rastrelliger canagurta*, Raju (1960) in *Katsuwonus pelamis*, Raja (1963) in *Sardinella longiceps* and Patnaik (1967) in *Eleutheronema tetradactylum*. The present author (Nayak, 1959) has earlier reported the occurrence of hermaphroditism in *Polynemus heptadactylus* and the present paper deals in detail with the nature of hermaphroditism in this species.

OBSERVATIONS ON THE OVOTESTES

The samples of *P. heptadactylus* were collected from the landings of trawl nets operated by the bull trawlers belonging to the New India Fisheries Co. Ltd., Bombay and of the bag nets of the local fishermen at two major fish landing centres of Bombay, namely, Sassoon Docks and Versova. During the period of 13 months, from October 1958 to October 1959, 858 specimens were studied. The terms 'males' and 'females' in the text refer to the unisexual individuals. The ovarian part of the ovotestis was closely studied and compared with the gonad of the females. Based

on the external morphological characters of the ovotestis and the microscopic structure of the ova along with their diameters, the following maturity key, which is similar to that of the female, was prepared.

Immature - I: Ovotestis small, thread-like, colourless; ova invisible to the naked eye, under microscope yolkless and transparent with a single nucleus in the centre, measuring up to 0.16 mm in diameter.

Immature - II: Ovotestis slightly thicker, less than half the length of the body-cavity, colourless; ova invisible to the naked eye, transparent with a nucleus in the centre, ranging between 0.17 mm and 0.32 mm in diameter.

Maturing - III: Ovotestis occupying nearly half the length of the body-cavity; yellow in appearance due to the deposition of yolk in the ova; ova visible to the naked eye, firmly held by interstitial tissue, getting opaque, ranging from 0.33 mm to 0.48 mm in diameter.

Maturing - IV: Ovotestis more than half the length of the body-cavity; ova opaque, completely filled with yolk and with a transparent periphery, measuring from 0.49 mm to 0.56 mm in diameter.

Maturing - V: Ovotestis completely filling the body-cavity; ova opaque, fully laden with yolk, some getting translucent with many small oil globules and measuring from 0.57 mm to 0.64 mm in diameter.

Maturing - VI: Ovotestis completely filling the body-cavity, somewhat creamish in colour; ova transparent with oil globules ranging from one to many in yellow transparent background; when only one, oil globule ranges from 0.2 mm to 0.3 mm in diameter; ova ranging from 0.65 mm to 1.04 mm in diameter.

Spent - VII: Ovotestis shrunken, flaccid and reddish in colour; innumerable small immature ova with a few large degenerating residual ones.

The above seven maturity stages correspond to the standard maturity stages for fishes adopted by the International Council of the Exploration of the Seas (Wood, 1930).

Maturity stages for the testicular part of the ovotestis could not be determined since the different stages were not distinct from one another. The histological studies of the micro-sections of the ovotestis stained with Delafield's hematoxylin and eosin not only further helped to confirm the histological and cytological changes taking place in the immature, maturing and spent stages in the ovarian part of the ovotestis but also the condition of the testicular part in different stages.

There are no external characters by which hermaphrodites could be distinguished from the unisexual individuals. The paired elongated ovotestes, suspended by the mesenteries, lie side by side with the air bladder above and the intestine below.

Anteriorly, they extend up to the anterior end of the cardiac stomach and posteriorly into the coelom beyond the anal opening. The two ovotestes may be of the same length or the left one slightly longer than the right. In a pair of ovotestes the testicular parts face each other and run from one end to the other. The extent of the development of the testicular part may vary from fish to fish, but it is the ovarian part which always occupies a comparatively larger portion. In an immature ovotestis preserved in 5% formalin, the testicular portion can easily be separated from the ovarian portion.

The cross section of the ovary (Pl. I, Fig. 1) of a female *P. heptadactylus* shows an outer fibrous connective tissue layer. The oocytes in their various developmental stages are seen in the ovigerous lamellae. The testis (Pl. I, Fig. 2) of a male is also covered by a fibrous layer and is seen filled with a number of seminiferous tubules in which the male elements at various stages of spermatogenesis are seen. When fully mature, sperms with long tails aggregate and form a number of bundles.

An ovotestis has a common fibrous layer surrounding both male and female parts. An immature ovotestis (Pl. I, Fig. 3, 4) shows a slender septum separating the testicular and ovarian parts. The ovarian part has its ovarian lamellae all around containing the developing oocytes. In the testicular part, on the other hand, the development of the male sexual elements appears to begin first in the region of the septum separating it from the ovarian part and then gradually progressing towards the opposite periphery.

In a maturing ovotestis (Pl. II, Fig. 5) the ovarian lamellae completely fill the lumen in the centre. Most of the ova are large and filled with yolk. In the testicular part the development of the seminiferous tubules is complete, attaining the form of a normal testis of an unisexual individual. The seminiferous tubules are all full with male sexual elements in their different developmental stages.

The spent hermaphrodite (Pl. II, Fig. 6) has a number of small immature ova along with a few large degenerating and resorbing residual ones in the ovarian part. The testicular part at this stage does not have the dense appearance of the maturing stage, but it is thin with loosely scattered male sexual elements in their developmental stages. This may be due to the shedding of the sperms along with the ova.

Finally in the recovering hermaphrodite (Pl. II, Fig. 7) the ovarian part with the few residual ova is seen to develop once again and the testicular part, in contrast to the earlier spent conditions, is observed to contain some sperm bundles.

HERMAPHRODITE AND UNISEXUAL INDIVIDUALS IN THE SAMPLES

Hermaphrodites formed nearly 17% of the 858 *P. heptadactylus* examined during the 13-month period. The monthly percentages of hermaphrodites in the samples varied from 2 to 45 (Table 1), often being above 10%.

Like females the hermaphrodites in the immature stage II and spent stage VII appeared in the samples all round the year (Table 2). Amongst the maturing stages III, IV and V, stage IV appeared very often and the other two only occasionally. The only ripe mature individual obtained was in November 1958.

TABLE 1. *Monthly percentage of hermaphrodite individuals of P. heptadactylus in the catch.*

Month	No. of fish examined		Hermaphrodites	
			No.	%.
October	1958	163	3	2
November	"	131	25	19
December	"	65	4	6
January	1959	50	8	16
February	"	55	9	16
March	"	52	15	29
April	"	53	10	19
May	"	51	17	33
June	"	49	11	22
July	"	26	2	8
August	"	52	5	10
September	"	62	14	23
October	"	49	22	45

TABLE 2. *Monthly percentage distribution of different stages of maturity in hermaphrodite individuals of P. heptadactylus.*

Months	I	II	III	IV	V	VI	VII
October 1958	—	67	33	—	—	—	—
November	12	64	—	—	4	4	16
December	—	75	—	—	—	—	25
January 1959	13	62	—	12	—	—	13
February	33	34	—	11	11	—	11
March	—	13	—	—	—	—	87
April	—	20	—	20	—	—	60
May	—	23	—	12	—	—	65
June	—	82	—	—	—	—	18
July	—	—	—	—	—	—	100
August	—	80	—	—	—	—	20
September	4	—	—	43	—	—	57
October	4	50	—	—	5	—	41

Table 3 for the different maturity stages at 15 mm length intervals shows that only immature hermaphrodites appeared in the samples up to the length of 113 mm. In the subsequent length of 128 mm, the maturing members in stage V and the spent

TABLE 3. *Percentage of hermaphrodite individuals of P. heptadactylus in different stages of maturity at 15 mm length interval.*

Size group (Mid point) (in mm)	Maturity stages						
	I	II	III	IV	V	VI	VII
98	67	33	—	—	—	—	—
113	17	83	—	—	—	—	—
128	36	50	—	—	7	—	7
143	—	76	—	—	3	—	21
158	—	35	3	8	—	3	51
173	—	28	—	16	—	—	56
188	—	6	—	13	6	—	75
203	—	—	—	25	—	—	75

TABLE 4. *Monthly percentage of unisexual female and hermaphrodite individuals of P. heptadactylus during the period October 1958 to October 1959.*

Months	O	N	D	J	F	M	A	M	J	J	A	S	O	
Unisexual female (%)	..	97	73	90	76	81	70	78	41	70	92	89	75	53
Hermaphrodite (%)		3	27	10	24	19	30	22	59	30	8	11	25	47

TABLE 5. *Monthly percentage of unisexual male and hermaphrodite individual of P. heptadactylus during the period October 1958 to October, 1959.*

Months	O	N	D	J	F	M	A	M	J	J	A	S	O	
Unisexual male (%)		93	60	86	67	44	12	44	56	52	33	62	26	8
Hermaphrodite (%)		7	40	14	33	56	88	56	44	48	67	38	74	92

ones in stage VII contributed 7% each to the sample. Beyond this the percentage of spent individuals increased with the size. Most of the stage II specimens in higher lengths were spent recovering ones. It is of interest to note that the longest hermaphrodite recorded here was 207 mm in furcal length, the length which is very near to the largest male that measured 210 mm.

Table 4 shows that females predominated hermaphrodites during all the months excepting in May when the latter (59%) surpassed the former (41%). In the rest of the months the percentages of the hermaphrodites ranged between 3 and 47. In contrast to this, the males (Table 5) predominated over hermaphrodites only in certain months.

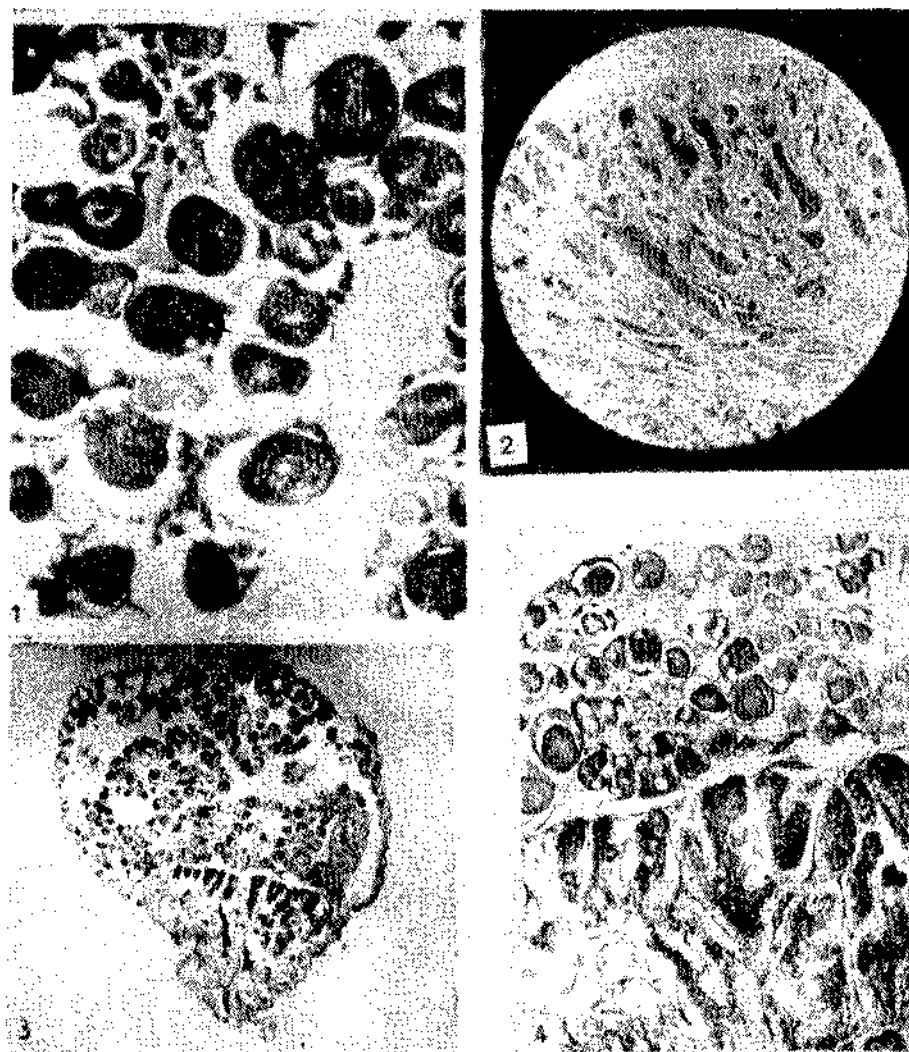


FIG. 1. 1. T. S. of ovary in unisexual female *Polynemus heptadactylus*. $\times 40$.
2. T. S. of testis in unisexual male. $\times 29$. 3. T. S. of ovotestis in
immature hermaphrodite individual. $\times 36$. 4. T. S. of
ovotestis in immature hermaphrodite
individual. $\times 96$.

Facing p. 192

DISCUSSION

The high percentage in which the hermaphrodites in *P. heptadactylus* occurred in most of the months, explains a normal, but not a teratological phenomenon. The simultaneous development of both the sex elements in hermaphrodites and also the appearance of spent individuals wherein both ova and sperms were shed, proves that this species is a synchronous hermaphrodite and not a gonochoritic one. Further the high percentage in which the hermaphrodites occurred, sometimes surpassing even the males in number, leads one to believe that they are functional.

Hermaphrodites almost equal the males in numerical abundance in the samples examined; they also appear to grow to more or less the same maximum size, as shown by the largest individuals met with. Hence a doubt arises whether these hermaphrodites can make up for the wide range in the sex-ratio between the males and females as noticed in the samples by undertaking the role of males.

The ova diameter studies showed that the growth of ova in different maturity stages was identical in both hermaphrodites and females. Since both the ovarian and testicular parts in an ovotestis become spent at the same time and the hermaphrodites could be considered as functional for the above-mentioned reasons, there may be a possibility of self-fertilization in *P. heptadactylus*. The fishes which have been proved to self-fertilize experimentally, have shown in natural conditions a tendency for cross-fertilization. Experiments on this aspect on *P. heptadactylus* may be useful.

Though hermaphrodites, like males, have not been obtained in the higher size-groups the fact that they are encountered from the smallest size when the sexes can be differentiated, to the largest size, along with the males and females rules out the possibility of sex reversal in this species. In the cases, where sex reversal is known, the individuals up to a certain age and length function as one sex, after which they change to opposite sex with a short period of intersex in between.

According to Witschi (1932), as mentioned by D' Ancona (*loc. cit.*) and Liu and Ku (*loc. cit.*), sex differentiation has a double origin, cortex derived from the peritoneal wall giving rise to ova and medulla from the internal blastema giving rise to spermatozoa by the respective female and male inducing factors. D'Ancona states that the somatic substratum of the gonad has a simple origin from the peritoneal wall. He has observed spatial separation of the ovarian and testicular parts in a number of teleosts and believed that the somatic tissue of the gonad which is chemo-differentiated into different regions by the male and female inducing substances, produces sexually different male and female germ cells in the corresponding regions. Essenberg (*loc. cit.*) has found that during sex reversal in *Xiphophorus helleri*, the epithelium of the ovarian cavity gives rise to oocytes first and spermatocytes later.

In Witschi's view the sexually indifferent primordial germ cells are first in the peripheral cortex; if they remain there they develop into ova and if they migrate to the central medulla they develop into spermatozoa. In *P. heptadactylus* the ovarian part occupies a greater area and the ovarian lamellae with oocytes are seen all around whereas the testicular part occupies comparatively a smaller area and the spermatoocytes in it begin to develop from the septum separating it from the ovarian part and proceed further to the periphery. Here the cortex and the medullary portions cannot be identified. The development of sex elements in *P. heptadactylus* appears to be from the somatic substratum as observed by Essenberg (*loc. cit.*), D'Ancona (*loc. cit.*) and Liu and Ku (*loc. cit.*) in other forms.

Liu (*loc. cit.*) has found *Monopterus javanensis* changing with regularity from female to male and considered it to be a developmental gonochorism rather than a hereditary gonochorism, the hermaphroditic condition being merely in time during the short period of sex transformation. He has further stated that in the evolutionary stages this species having a developmental gonochorism, bridges the gap between the functional hermaphroditism as in *Serranus cabrilla* and rudimentary hermaphroditism as in *Lamia nigrofasciata*. *P. heptadactylus* like any other teleost, is highly evolved, but, it however retains a primitive characteristic of hermaphroditism. Since the representatives do not appear to be teratological but regular and functional, they may be significant in maintaining the equilibrium in sex-ratio to help in balancing its population.

It would be very interesting to know whether the progeny of hermaphrodite *P. heptadactylus* would be hermaphrodite or unisexual individuals. If these hermaphrodites are not breeding amongst themselves alone but also with other unisexual individuals, the degree of heterozygosity may be very high to enable them to adopt to the environmental variables. The breeding study on these hermaphrodites would be very useful.

In this connection it is worth mentioning the work of Kallman and Harrington (1964) on the transplantation test on *Rivulus marmoratus*. They have been able to discover from their experiments that all these self-fertilizing hermaphrodites possess identical genotypes and are homozygous. Transplantation test is another aspect of the study to know the homozygosity or heterozygosity of hermaphrodite *P. heptadactylus*.

SUMMARY

P. heptadactylus is normally dioecious, but sometimes monocious with a pair of ovotestes. The narrower testicular parts face each other on the inner side and the larger ovarian parts lie on the outer side of the ovotestes.

Hermaphrodites are about the same proportion as the males and they also grow to about the same maximum size as the males. The hermaphroditic gonads are often mistaken to be ovaries due to the development to a greater extent of the

ovarian part with similar maturity stages of ova. The regular appearance of hermaphrodites in high percentages in the commercial catches throughout the year suggests that this phenomenon is normal and not teratological.

The micro-sections showing the simultaneous development and liberation of both the sex elements in an ovotestis, indicate that this species is a synchronous hermaphrodite. Instances of hermaphrodites very often surpassing even the males in number are suggestive of their being functional and this may help in balancing the populations of the two sexes. Since the ovarian and testicular parts become spent at the same time, there is a possibility of self-fertilization in this fish.

There is no sex reversal in this species because hermaphrodites appear from the smallest size when the sexes can be differentiated till the largest size along with the unisexual individuals. In sex reversal generally, an individual functions as one sex up to a certain length and age and thereafter as its opposite sex.

In an ovotestis the cortical and medullary portions cannot be differentiated. The development of the sex elements appear to be from the somatic substratum.

Polynemids are highly evolved teleosts, but *P. heptadactylus* has, however, retained a primitive trait of hermaphroditism.

ACKNOWLEDGEMENTS

It gives me great pleasure to express my gratitude to Dr. D. V. Bal, former Director, Institute of Science, Bombay, for kindly agreeing to be my guide and to Dr. S. Jones, Director, Central Marine Fisheries Research Institute, Mandapam Camp, for kindly drawing my attention to some references which have been subsequently incorporated in this paper. I am thankful to Shri. K. Virabhadra Rao for critically going through the manuscript and offering suggestions in the preparation of this paper.

REFERENCES

- CHACKO, P.I. AND B. KRISHNAMURTHY. 1949. Hermaphroditism in the Indian shad, *Hilsa ilisha* (Ham). *Proc. 36th Indian Sci. Cong.*, Abst: 167
- CLARK, E. 1959. Functional hermaphroditism and self fertilization in a serranid fish. *Science*, 129: 215-216.
- D'ANCONA, U. 1945. Sexual differentiation of the gonad and sexualization of the germ cells in teleosts. *Nature*, 156: 603.
- ESSENBERG, J.M. 1926. Complete sex-reversal in the viviparous teleost *Xiphophorus helleri*. *Biol. Bull.*, 51: 98-111.

- HARRINGTON, R.W. JR. 1961. Oviparous hermaphroditic fish with internal self-fertilization. *Science*, 134 (3492): 1749-1750.
- HARRINGTON, R.W. JR. 1963. Twenty-four-hour rhythms of internal self-fertilization and of oviposition by hermaphrodites of *Rivulus marmoratus*. *Physiol. zool.*, 36: 325-341.
- HUBBS, C.L. AND L.C. HUBBS. 1932. Apparent parthenogenesis in nature, in a form of fish of hybrid origin. *Science*, 76: 628-630.
- HUBBS, C.L. AND L.C. HUBBS. 1946. Breeding experiments with the invariably female, strictly matroclinous fish, *Mollienixea formosa*. *Genetics*, 31: 218.
- KALLMAN, K.D. AND R.W. HARRINGTON, JR. 1964. Evidence for the existence of homozygous clones in the self-fertilizing hermaphroditic teleost *Rivulus marmoratus* (Poey). *Biol. Bull.*, 126 (1): 101-114.
- LAVANDA, N. 1949. Sexual differences and normal proterogynous hermaphroditism in the Atlantic sea bass, *Centropristes striatus*. *Copeia*, No. 3: 185-194.
- LEIDER, U. 1955. Mannchenmangel und natürliche Parthenogenese bei der Silberkarausche *Carassius auratus gibelio* (Vertebrata, Pisces). *Naturwiss.*, 42: 590.
- LIU, C.K. 1944. Rudimentary hermaphroditism in the symbranchoid eel, *Monopterus javanensis*. *Sinensia*, 15: 1-8.
- LIU, C.K. AND KU. 1951. Histological changes in the gonad of *Monopterus* during sex transformation. *Sinensia*, 2: 85-109.
- MEAD, G.W. 1960. Hermaphroditism in archibenthic and pelagic fishes of the order Iniomi. *Deep Sea Res.*, 6: 234-235.
- NAYAK, P.D. 1959. Occurrence of hermaphroditism in *Polynemus heptadactylus* Cuv. & Val. *J. Mar. biol. Ass. India*, 1 (2): 257-259.
- PATNAIK, S. 1967. Hermaphroditism in the Indian salmon *Eleutheronema tetradactylum* (Shaw). *Curr. Sci.*, 36 (19): 525.
- PRABHU, M.S. AND B.T. ANTONY RAJA. 1959. An instance of hermaphroditism in the Indian mackerel, *Rastrelliger canagurta* (Cuvier). *Curr. Sci.*, 28 (2): 73-74.
- RAJA, B.T. ANTONY 1963. An instance of hermaphroditism in the Indian oil sardine, *Sardinella longiceps* (Cuv. & Val.). *J. Mar. biol. Ass. India*, 5 (1): 148-150.
- RAJU, G. 1960. A case of hermaphroditism and some other gonadal abnormalities in the skipjack *Katsuwonus pelamis* (Linnaeus). *J. Mar. biol. Ass. India*, 2 (1): 95-102.
- REINBOTH, R. 1962. Morphologische und funktionelle zweigeschlechtlichkeit bei marinen Teleostiern (Serranidae, Sparidae, Centranchidae, Labridae). *Zool. Jahrb. Physiol.*, 69: 405-480.
- SALEKHOVA, I.P. 1963. On self-fertilization and development of self-fertilized eggs of *Serranus scriba* (L.). *Voprosy ichtyologii*, 3: 275-287.
- SATHYANESAN, A.G. 1957. Occurrence of oocyte in adult testis of the fish *Barbus stigma* (Cuv. & Val.). *Sci. & Cult.*, 23: 203.

- SATHYANESAN, A.G. AND K.R. RAJAN. 1953. Hermaphroditism in *Cirrhitina reba* (Ham). *Proc. 40th Indian Sci. Cong.*, Abst: 208.
- SMITH, C.L. 1959. Hermaphroditism in some serranid fishes from Bermuda. *Pap. Mich. Acad. Sci.*, 44: 111-119.
- WITSCHI, E. 1932. Sex deviations, inversions and parabiosis. In *Sex and internal secretions*. Edgar Allen (ed.), 5: 160-245. Baltimore.
- WOOD, H. 1930. Scottish herring shoals-prespawning and spawning movements. *Scotland Fish Bd Sci. Invest.*, No. 1: 1-71.
- ZEI, M. 1949. Typical sex-reversal in teleosts. *Proc. zool. Soc. Lond.*, 119: 917-920.
- ZEI, M. 1951. Jadranske Girice (Maenidae) Monografska studija (Monograph of the Adriatic species of *Maenidae*) Slovenska Akademija Znanosti in Umetnosti, Academia Scientiarum et Artium Slovenica. Razred za Prirodoslovne in Medicinske Vede Classis IV: *Historia Naturalis et Medicina, Institut Zoologije, Ljubljana*: 1-127.