

STUDIES ON NERITIDAE (NERITACEA : PROSOBRANCHIA) FROM PENINSULAR INDIA*

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The present paper is part of a general study which is under way on the life-histories and ecology of Indian Neritidae with a view to gaining knowledge on their speciation and evolution in the major estuaries. Three species of Neritidae, viz., *Dostia crepidularia* Lamarck, *Neritina layardi* Lesson and *Septaria tessellata* (Lamarck) occur together in the fresh water zone (upper reaches) of the Coleroon estuary (lat : 11°25'N, long : 79°48'E) in peninsular India. The present report is on a comparative study of the shell morphology, reproductive anatomy and breeding structure in these three species. These three species are primarily considered because the fresh water fluviatile genus *Septaria* is supposed to have been evolved from the marine *Nerita* through *Dostia* and *Neritina*.

The present study shows that all the three species are reproductively isolated. On the basis of dissimilarities between their breeding structure and further differences in shell morphology, the three species seem to be distinct from each other with no overlapping. Both behavioural and morphological barriers exist to prevent their interbreeding. This is therefore conducive to the conclusion that the three are distinct species. However, the retention of free-swimming veligers in all the three species, in spite of their adaptation to fresh-water, only goes to confirm the mosaic organisation already reported to be characteristic of Neritidae.

The presence of a thick shell and a pelagic dispersal phase in *Dostia* and its wide distribution in the entire length of the estuary, are clear indications of its marine ancestry. In the same token, the retention of free swimming veligers in *Neritina* and *Septaria* in spite of their adaptation to fresh water and their distribution restricted to a very small length of the river in the upper reaches of the estuary show them to be comparatively recent additions to fresh waters. It is thus imperative that *Neritina* and *Septaria* are evolved from *Dostia*. The results of the present study on morphology and breeding show that the three species are distinct and reproductively isolated and no transition or intergradation is to be seen between them. It further reveals that there are more similarities between *Dostia* and *Neritina* on one hand, and between *Dostia* and *Septaria* on the other, while *Septaria* and *Neritina* do not have much in common. In other words, it is implied that both *Neritina* and *Septaria* were probably derived from *Dostia* by divergence rather by transition. To obtain conclusive evidence, a serological assessment of species interrelationship is now under way.

Since neritids are supposed to have had an independent evolution in various rivers, it is suggested that an intensive study of Indian Neritidae by means of collecting critical information at the levels of morphology and ecology, with an emphasis on experimental approach, will help us to throw considerable light on their taxonomic and phylogenetic interrelationships and their speciation in the estuarine environment.

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INTRODUCTION

The marine intertidal gastropod molluscs of the family Neritidae, an annectant group with a mosaic organisation and great adaptability, have very successfully invaded fresh water through the estuaries in the tropics. Though the marine neritids may be considered as monophyletic, the actual entry into and acclimatisation to fresh water, with much parallel evolution, may perhaps be considered only as polyphyletic (Bourne 1908; Purchon 1968), as a result of which their systematics is still in confusion and their interrelationships very unclear. It is also surprising that malacologists have neglected this group for more than 50 years past and this is especially true of the tropical Indo-Pacific forms.

Previous works on neritids of chiefly the Atlantic and Pacific regions are those of Baker (1923), Fabre-Domerque (1924) Risbec (1932), Andrews (1933 *a, b*; 1935 *a, b*; 1936; 1937; 1940 *a, b*), Lewis (1960), D'Asaro (1962), Kolipinski (1964) and Fretter (1965, 1966). The European *Theodoxus fluviatilis* has been the subject of intensive study by Lenssen (1899 *a, b*; 1902), Bondesen (1940), Fretter (1946, 1965), Whitaker (1951), Lumbye (1958), Neumann (1959, 1960*a, b*), Bielawski (1960), Fretter and Graham (1962), and Lafon and Alause (1963). Excepting for Bourne's (1908) classical work relating to the anatomy of *Septaria bougainvillei* from Fiji Islands, we have very meagre knowledge of the Indo-Pacific neritids and the present study is an attempt to fill up this gap. This report discusses briefly the results of a comparative study on shell morphology, reproductive anatomy and breeding structure in the three species of Neritidae occurring in the upper reaches (fresh water zone) of the Coleroon estuary (Fig. 1) in peninsular India. The study was initiated in order to understand the evolutionary trends and resulting speciation in these snails. The three species are primarily considered because it is generally held (Cooke 1959) that the fresh water genus *Septaria* (*Navicella*) has evolved from the marine *Nerita* through forms like *Dostia* and *Neritina*. However, no comprehensive resource material is available thus far on the systematics and biology of the tropical neritids of Indo-Pacific in confirmation of the above. Therefore, the scope of the present work is to re-examine the taxonomic status of neritids by using cytogenetic as well as morphological and ecological data. Collection of such taxonomic and cytogenetical data also provides the means for elucidating the mode of speciation. It is thus hoped that the body of data presented here and discussion made on them will help the investigators to plan further work.

MATERIALS AND METHODS

Fig. 1 is a map of the Vellar and Coleroon estuaries indicating also the place of occurrence of *Dostia crepidularia* Lamarck, *Neritina layardi* Lesson and *Septaria tessellata* (Lamarck), the neritids employed in the present study. Actually *Dostia* is found distributed throughout the estuary but *Neritina* and *Septaria* are restricted in their distribution. All the three species occur together clinging to the bricks, stones and cement slabs only in a particular area near and around the railway and road bridges of the Coleroon river (Fig 1—*J, I*) about 7 miles from its mouth. The salinity in this area during the year ranges from 0.5 to 6 ‰ and the water temperature from 27.5°C to 34.5°C. An increase in the tidal level of

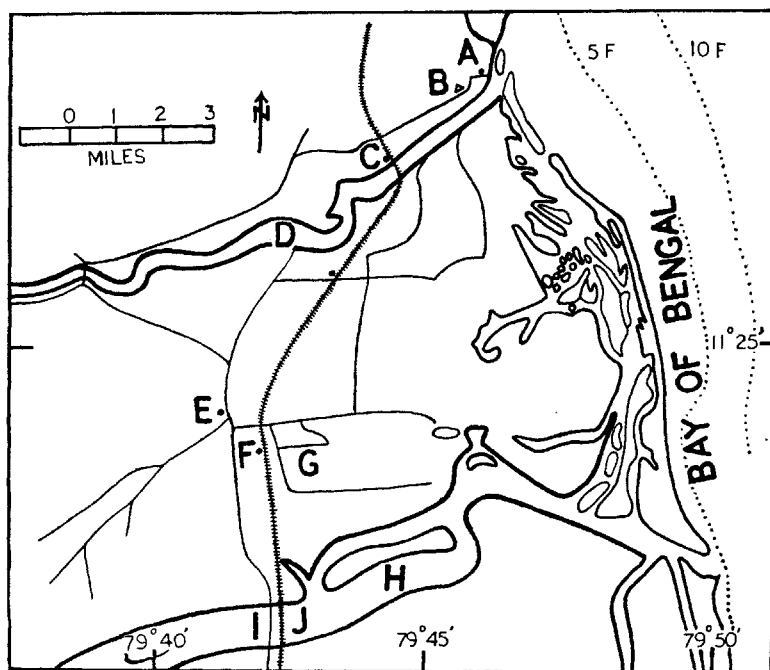


FIG. 1. Map of the Coleroon — Vellar estuaries. A, Marine Biological Station ; B, Portonovo ; C, Portonovo Railway Station ; D, Vellar estuary ; E, Chidambaram ; F, Chidambaram Railway Station ; G, Annamalai University ; H, Coleroon estuary ; I, Collection area near the Road Bridge ; J, Collection area near the Railway Bridge.

about 15-23 cm is also noted during various seasons of the year. *Dostia* and *Septaria* are always seen aggregated in groups at the watermark, intertidally and are collected fairly easily. *Neritina* occurs as solitary forms and never in aggregations. Also, it is always found among stone crevices or algal growths, submerged in water at a depth of 30 cm and more. Only a few of them could be collected at a time.

Dostia has the largest shell, white in colour with black pigments, tessellated, thick, with a high spire and a calcified operculum. The shell of *Neritina* is smaller than *Dostia*, thin, dull olive coloured, with a very expanded wing-like septum and a calcified operculum. *Septaria* has a very thin and more flat tessellated shell, purple in colour with black and white pigments, the body whorl well inflated and the spire reduced to a beak-like projection. Consequent to the great enlargement of the body whorl, the operculum is reduced, horny and has become internal.

The procedures followed were the standard techniques currently used for collection of data on distribution, morphology and general ecology.

OBSERVATIONS

Shell

It may be seen from Table I that the length-width ratios of the shells of all three species range between 1.40 and 1.51, indicating that the length of the shell is almost

TABLE I
Shell characteristics in neritids

Name of species	No. of shells studied	Length (mm)			Width (mm)			Height (mm)			L/W ratio	L/H ratio	W/H ratio
		\bar{X}	S	Se	\bar{X}	S	Se	\bar{X}	S	Se			
<i>Dostia crepidularia</i>													
Female	50	22.28	2.03	0.29	15.06	0.47	0.07	11.56	1.33	0.19	1.48	1.91	1.29
Male	25	18.52	1.65	0.33	12.68	0.67	0.13	9.36	1.02	0.20	1.46	1.98	1.36
<i>Neritina layardi</i>													
Female	50	17.42	1.62	0.23	12.48	0.67	0.09	8.02	0.81	0.11	1.40	2.17	1.56
Male	25	15.72	1.96	0.39	10.96	1.39	0.28	7.36	1.10	0.22	1.43	2.14	1.49
<i>Septaria tessellata</i>													
Female	50	21.62	2.86	0.40	14.54	1.97	0.28	6.00	1.00	0.14	1.49	3.60	2.42
Male	25	15.20	1.69	0.34	10.08	1.21	0.24	4.08	0.75	0.15	1.51	3.73	2.47

\bar{X} = The mean, S = Standard deviation, Se = Standard error of the mean

$1\frac{1}{2}$ times that of the width. Irrespective of sex, this normal pattern in length-width ratio is maintained in all the three species.

However, the height seems to vary in all the three species. In *Dostia* and *Neritina*, the length-height ratio differs from 1.91 to 2.17 and the width-height ratio varies from 1.29 to 1.56. However, it must be noticed that these ratios are the same between the sexes of each species, showing no variation. *Septaria* differs widely from the above two species indicating that the length is $3\frac{1}{2}$ times and the width $2\frac{1}{2}$ times greater than the height in both male and female shells. This difference is, however, due only to the reduction in height of spire in *Septaria* rather than to any increase in the length or width of its shell (Table I).

The present study on the shell characteristics of males and females in the three species shows a definite occurrence of sex dimorphism—the male being smaller than the female. It can be seen from Table II that the dimorphism is highly pronounced in *Septaria* and slightly less in *Dostia*. *Neritina* shows only very slight sex dimorphism. In other words, the males of *Septaria* appear much smaller than the females while the dimorphism is very difficult to be observed by the naked eye in *Neritina*.

TABLE II

Differences between male and female shells in neritids (in mm)

Name of species	Difference in \bar{X} lengths	Difference in \bar{X} widths	Difference in \bar{X} heights
<i>Dostia crepidularia</i>	3.76	2.38	2.30
<i>Neritina layardi</i>	1.70	1.52	0.66
<i>Septaria tessellata</i>	6.42	4.46	1.92

It is worthwhile to point out here that Natarajan (1969) reported the occurrence of sex chromosomes in neritids (Table III). The male is the heterogametic sex and is characterised by an X chromosome in all the three species with a X-O type of sex-determining mechanism. It is very interesting to note that the shells in these three species also show a dimorphism associated with sex (male being smaller than the female), indicating thereby that this character is probably a genetically based one.

Reproductive anatomy

The results of a study of the spermatophores of the three species are given in Table IV. From that it can be seen that the spermatophore of each species is very distinct in size and shape. *Septaria* produces a smooth, very long and rather thick spermatophore compared to that of *Neritina*, in which it is short, thin and spirally ridged. In *Dostia* also the spermatophore is seen to be spirally ridged but appears very thick, and longer than *Neritina*.

TABLE III
Chromosomes of neritids
(Taken from Natarajan 1969)

Name of species	Male		Female		Sex determining mechanism
	2n	n	2n	n	
<i>Dostia crepidularia</i>	22+X	11+X	—	—	XO-XX type
<i>Neritina layardi</i>	—	11+X	—	—	XO-XX type
<i>Septaria tessellata</i>	22+X	11+X	22+X	11+X	XO-XX type

TABLE IV
Spermatophores of neritids

Name of species	No. of spermatophores studied	Length (in mm)			Width (in mm)			L/W ratio	No. of spirals	Maximum no. of spermatophores found in a single female specimen
		\bar{X}	S	Se	\bar{X}	S	Se			
<i>Dostia crepidularia</i>	15	11.72	1.68	0.43	0.56	0.20	0.05	20.93	25	44
<i>Neritina layardi</i>	15	10.69	0.97	0.25	0.33	0.05	0.01	32.40	27	56
<i>Septaria tessellata</i>	15	17.26	2.00	0.51	0.40	0.07	0.02	43.14	—	28

\bar{X} = The mean, S = Standard deviation, Se = Standard error of the mean

The sexes are separate and the female is triaulic in all the three species studied presently. The female reproductive organs in *Dostia*, *Neritina* and *Septaria* closely resemble the general neritid pattern (Andrews 1937). Fig 2A shows the organs of the female reproductive system in *Neritina layardi*. Oviduct (*od*) from the ovary (*ov*) runs anteriorly on the right side of the mantle cavity and gives rise to two branches of which one opens into the posterior region of the pallial oviduct and the other (*cod*) opens to the coelomic cavity. The pallial oviduct is chiefly glandular and is differentiated into an anterior capsule (*cpg*) and a posterior albumen (*ag*) regions. The capsular region of the pallial oviduct opens anteriorly by means of the female opening (*fo*) by the side of the anus (*a*) along the right side of the mantle cavity. To the right anterior side of the capsule gland lies the crystal sac (*csa*). The vagina (*vag*) is separated from the pallial oviduct. It runs ventrally, parallel to the pallial oviduct and the rectum (*r*) along the right side of the mantle cavity. The vagina opens anteriorly by means of vaginal opening (*vo*). Posteriorly, its blind end is dilated to form a storage sac (*sps*) for the spermatophore (*sp*). A small duct known as the vaginal canal (*vac*) arising from the left lateral

side of the vagina forms a junction. There are two ducts arising from this junction, of which one runs anteriorly along the ventral side of the capsule gland and opens (*deo*) halfway down to the right side of the vagina and is called the ductus enigmaticus (*de*). The other continues posteriorly to form the receptaculum seminis (*rcs*) just below the albumen gland. The ductus enigmaticus is dorso-ventrally compressed, broadened posteriorly and narrow anteriorly giving the appearance like a flap. A short and a narrow duct connects the junction ventrally to the right anterior region of the albumen gland.

A comparative study of the female genital organs in *Dostia*, *Neritina* and *Septaria*, however, reveals a few differences as follows :

(i) The relative positions of the vaginal opening (Fig. 2 B-D-1), the female opening (Fig. 2 B-D-2) and the opening of the ductus enigmaticus (Fig. 2 B-D-3) differ in *Neritina layardi* (Fig. 2B), *Dostia crepidularia* (Fig. 2 C) and *Septaria tessellata* (Fig. 2 D).

(ii) A distinct bend is seen in the vaginal tract (near the anterior region) in *Neritina* (Fig. 2 A) and (in the middle region) in *Dostia* but is absent in *Septaria*.

(iii) The receptaculum seminis appears black in *Septaria* whereas it is white in colour in *Dostia* and *Neritina*.

Breeding and development

Table V summarises the behavioural aspects of reproduction observed in the three species. It can be seen clearly that there are very definite behavioural differences in copulation as well as in egg-laying in the three species. However, it may be noted that the time of egg-laying after copulation was the same (two days) in all the three species. So also, the time for fixing the egg capsule to the substratum did not show any change in the three species studied.

Dostia and *Septaria* prefer to fix their egg capsules on the shells of the same and those of other species in addition to fixing them on stones, etc. But this tendency seems to be absent in *Neritina* since their egg capsules are found attached only to the stones and bricks. In the laboratory also, they were always found to attach their egg capsules to the sides of the glass aquarium and stones.

Tables VI-VII summaris all observations on spawning and development. It can be seen from Table VI that, for all the three species, the breeding season is the same extending from March to November. However, it is interesting to note that peak breeding occurs during June to August in *Dostia* and during August to October in *Neritina* whereas *Septaria* shows a rather extended peak from July to October—overlapping both *Dostia* and *Neritina*.

It can be seen from Table VI that ail the three species are highly fecund with the capability of the female of each species to lay during the breeding season thousands of eggs, which, in turn, may contain several thousands of embryos. However, of the three species, *Septaria* appears to be more productive because it has a larger population, and an extended egg-laying season and packs greater number of embryos in its egg capsules. *Dostia* also seems to have an equally high capacity as it occurs in large numbers and is found to be capable of laying almost double the number of egg capsules than that of *Neritina* (Table VI). Thus when we consider

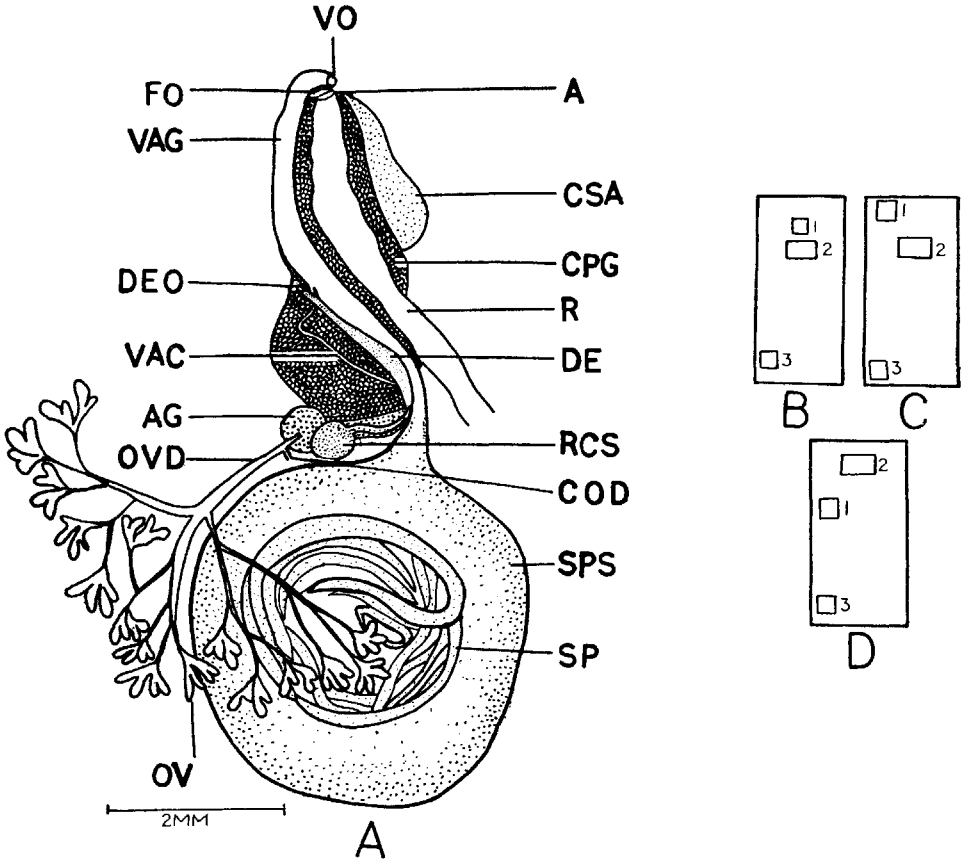


FIG. 2. A, *Neritina layardi*. Dissection of the female reproductive system; B, C, and D, diagrammatic representation showing the relative positions of the vaginal opening, female opening and the opening of the ductus enigmaticus in *Neritina layardi*, *Dostia crepidularia* and *Septaria tessellata* respectively. (A, anus; AG, albumen gland; COD, coelomic duct; CPG, capsule gland; CSA, crystal sac; DE, ductus enigmaticus; DEO, opening of ductus enigmaticus; FO, female opening; OV, ovary; OVD, oviduct; R, rectum; RCS, receptaculum seminis; SP, spermatophore; SPS, spermatophore sac; VAC, vaginal canal; VAG, vagina; VO, vaginal opening); 1, vaginal opening; 2, female opening; 3, opening of ductus enigmaticus.

the total number of embryos produced, *Dostia* and *Septaria* appear to be highly fecund, while the fecundity of *Neritina* seems to be reduced.

The size of the ova is the same in *Neritina* and *Dostia* (142μ) while *Septaria* has a very much reduced size (107μ). Perhaps because of this reduced size, it is capable of packing more embryos in its capsules.

The hatching out time of the embryos from the egg capsules, while being more or less the same (two weeks) in *Dostia* and *Septaria*, takes an extended time (three weeks) in *Neritina*. In all the three species, the hatching out occurs at the veliger stage. Planktonic larval stages were not studied.

TABLE V
Copulatory and egg laying behaviour of neritids

Name of species	Nature of copulation	Time of egg laying after copulation (days)	Time taken for a single egg capsule to be laid (min)	Time taken to fix the capsule on the substratum after its appearance at the pore (sec)	No. of egg capsules laid by a single animal at one time
<i>Dostia crepidularia</i>	Penis introduced 4 to 5 times for a period of 1-5 min with an interval of 15-30 sec, with a vigorous jerking action.	2	6-8	10-15	1-30
<i>Neritina layardi</i>	Penis introduced 2 to 3 times for a period of 1-3 min with an interval of 10-15 sec with slight jerking action	2	5-7	10-15	1-28
<i>Septaria tessellata</i>	Penis introduced 2 to 4 times for a period of 3-4 min with an interval of 1-1½ min with no jerking action.	2	6-12	10-15	1-24

TABLE VI
Breeding and spawning in neritids

Name of species	Breeding season	Peak of the breeding season	Total no. of egg capsules laid by a single animal during a period of 30 days (during peak season)	No. of embryos per egg capsule (Range)	Time taken for hatching out of the egg capsules (days)	Size of the ovum (μ)
<i>Dostia crepidularia</i>	March to November	June, July August	594	52-104	15-16	142
<i>Neritina layardi</i>	March to November	August, September & October	282	64-124	20-22	142
<i>Septaria tessellata</i>	March to November	July to October	254	92-145	14-15	107

It is clear from above that the breeding and development in each species is distinct and different from the other.

TABLE VII
Egg capsules of neritids

Name of species	No. of egg capsules studied	Length (mm)			Width (mm)			L/W ratio
		\bar{X}	S	Se	\bar{X}	S	Se	
<i>Dostia crepidularia</i>	100	1.45	0.057	0.006	1.12	0.063	0.006	1.29
<i>Neritina layardi</i>	75	1.40	0.285	0.033	0.83	0.173	0.020	1.69
<i>Septaria tessellata</i>	75	1.38	0.173	0.020	1.02	0.173	0.020	1.35

\bar{X} = The mean, S = Standard deviation, Se = Standard error of the mean

CONCLUSIONS AND DISCUSSION

Shell

The lengths, widths and heights of the shells of both males and females in all the three species were measured and analysed. Measurements of length and width in both sexes in all the three species show no significant variation but the height seems to vary. A close look at Table I shows that the variation is due only to the height of spire and not due to difference in lengths or widths. It must also be pointed out here that the ratios between male and female shells of the same species are always the same in spite of distinct interspecific variations. It is, therefore, clear that the shell characters are very specific and distinctive for each species with no overlappings or intergradations. Since all the three species occur together in the same environment, perhaps the variation in height is not an environmentally controlled factor but alternatively may be a genetically determined variant fixed by selection. It is true that a very low spire found in *Septaria* may be of definite advantage in a fluvial habit and may help the species for deeper penetration into the rivers.

The present findings on shell size (Table I) showed a definite occurrence of sex dimorphism—the male being smaller than female (Table II) in all the three species. The sexual dimorphism in shell size in Neritidae found in the present study has not been reported so far in literature. This tendency is most pronounced in *Septaria* with *Dostia* coming next while *Neritina* shows only very slight dimorphism.

It is very interesting that this sex dimorphism seen in the shells of three species is found to have a cytogenetic basis too (Natarajan 1969). An XO-XX type of sex determining mechanism of the chromosomes has been reported to occur (Table III) in all the three species presently studied. The male is heterogametic and has a single X chromosome. The occurrence of a cytogenetic basis for sex dimorphism

together with the fact that L/W, L/H and W/H ratios are the same between the sexes in each species with no overlappings, lends further support to the idea that the shell character is most probably genetically determined in each species.

Breeding

The breeding is reported to be of a primitive type in Archaeogastropods (Purchon 1968) including Neritacea. Development is oviparous in all Neritacea and the embryos hatch out as veligers. The exceptions are *Nerita alticola*, (Andrews 1935), *Nerita reticulata*, *Nerita albicilla* (Risbec 1932) and *Neritina (Theodoxus) fluviatilis* of Europe (Bondeson 1940; Fretter and Graham 1962) where it is reported that only one embryo hatches out from each capsule in the crawling stage (Table VIII). We have no information, however, on, the breeding and spawning of the tropical Indo-Pacific forms. Some data collected in the present study are given in Table VI. The breeding, spawning and development of the three species show certain differences. The most obvious differences are in the size of spermatophores, in copulation behaviour, in the peak breeding season, in the size of the ovum and the number of embryos per capsule and in the hatching out time of the embryos. (vide Table VI). However, it must be noted that all three species are highly fecund, each female of each species capable of laying several thousand eggs from which tens of thousands of embryos may hatch out. The great fecundity of the species and the relatively small size of the eggs and veligers indicate that all the three species have long planktotrophic lives in which a large mortality occurs (Thorson 1950). The extent of the development may also be taken to suggest a long planktotrophic life (Struhsaker 1966). The general pattern of development is similar in *Dostia* and *Septaria* wherein the embryos hatch out in about two weeks. In *Neritina* on the other hand, the hatching out time is extended to nearly three weeks.

On the basis of the dissimilarities in their breeding structure, the three species seem to be distinct from each other. There is no evidence for any interbreeding or hybridisation in spite of the fact that the three species occur intermixed in the same place and are in close proximity during the entire breeding period. Both behavioural and morphological barriers exist to prevent their interbreeding. It is therefore obvious that *Dostia*, *Neritina* and *Septaria* are reproductively isolated distinct species.

The retention of a free-swimming larval stage in all the three species, in spite of their successful life in fresh water, indicates the way in which, in the process of adaptation, these species are still retaining a primitive trait. It must be remembered here that Neritacea as a whole is considered as a mosaic group with a combination of advanced characters and some primitive ones (Fretter 1966). Further, the retention of free-swimming larval stages in *Neritina* and *Septaria* together with the fact that their distribution is confined to a relatively short length of the river immediately above the main region of salt water penetration, may be taken as an indication that these two species are comparatively recent additions to fresh water (Purchon 1968).

TABLE VIII
Development in neritids

Name of species	Country	No. of embryos per egg capsule (Range)	Hatching out time	Hatching out stage	Reference
Martine					
<i>Nerita tessellata</i>	Florida, USA Barbados	31-189 —	21 days 14 days	Veligers -do-	D'Asarao 1962 Lewis 1960
<i>N. peloronta</i>	-do-	—	—	-do-	Lewis 1960
<i>N. fulgurans</i>	-do-	—	14 days	-do-	Lewis 1960
	Florida, USA	43-142	36 days	-do-	Kolpinski 1964
<i>N. versicolor</i>	-do-	27-112	—	—	Kolpinski 1964
	Barbados	—	—	Veligers	Lewis 1960
<i>N. alticola</i>	Jamaica	60	—	Juvenile	Andrews 1935
<i>N. reticulata</i>	New Caledonia	3-9	More than 59 days	do-	Risbec 1932
<i>N. albicilla</i>	-do-	150-200	More than 52 days	-do-	Risbec 1932
	India	85-121	—	Veligers	Natarajan 1957
Brackish water					
<i>Neritina fluviatilis</i>	Europe	50-60	—	One crawling stage embryo	Fretter and Graham 1962
	Denmark	50-82	—	-do-	Bondesen 1940
<i>N. virginea</i>	Jamaica	30-90	—	—	Andrews 1935
Fresh water					
<i>Neritina virginea varilisteri</i>	Martinique Islands	50	21-28 days	Veligers	Fabre-Domergue 1924
<i>N. virginea</i>	Jamaica	80-215	—	—	Andrews 1935
<i>N. punctulata</i>	-do-	60-80	—	—	Andrews 1935
<i>N. recivata</i>	Florida, USA	50	21 days	Veligers	Andrews 1935
<i>N. meleagris</i>	Jamaica	16-20	—	—	Andrews 1935
<i>N. fluviatilis</i>	Europe	140-150	—	Juvenile	Fretter and Graham 1962
<i>Dostia crepidularia</i>	Denmark	70-160	—	-do-	Bondesen 1940
<i>Neritina layardi</i>	India	52-104	15-16 days	Veligers	Present study
<i>Septaria tessellata</i>	-do-	64-124	20-22 days	-do-	-do-
	-do-	92-145	14-15 days	-do-	-do-

TABLE IX
Similarities and dissimilarities between Dostia, Neritina and Septaria

Occurrence	<i>Dostia</i>	<i>Neritina</i>	<i>Septaria</i>
	In groups	Solitary	In groups
Tessellated shell	+	—	+
L/H ratio of shell	+	+	—
W/H ratio of shell	+	+	—
Operculum thick, calcified, lunate and paucispiral	+	+	—
Sex dimorphism of shell	+	—	+
Spermatophores	+	+	—
A bend in the vaginal tract	+	+	—
Relationship of the vaginal opening, female opening and the opening of the ductus engimaticus	+	+	—
Colour of the seminal receptacle	+	+	—
Nature of copulation	+	+	—
Total number of egg capsules laid by a single animal during a period of 30 days (during peak season)	—	+	+
Fecundity	+	—	+
Number of embryos per capsule	+	+	—
Time taken for hatching out of the egg capsules	+	—	+
Size of the ovum	+	+	—
Time taken for a single egg capsule to be laid	+	+	—
L/W ratio of egg capsules	+	—	+
Preference for fixing the egg capsules on the shells	+	—	+
+ Similarities — Dissimilarities			

Species interrelationships

That *Dostia* is derived from marine *Nerita* is very clearly indicated by its thick shell, the presence of a pelagic dispersal phase and its wide distribution in the entire estuary. The present study has also indicated that, by the retention of free-swimming veligers and by their confined distribution to a small length of the river, *Neritina* and *Septaria* are comparatively recent additions to the freshwater and, most likely, are evolved from *Dostia*. It is further seen from the present study that *Dostia*, *Neritina* and *Septaria* are reproductively isolated and distinct species and the speciation process thus appears to be complete. The cytological approach, which is fundamental to the study of speciation, has failed to give us a clue as to interrelationships between the three species. However, based on the results of the present study, on morphology and breeding, the similarities and dissimilarities found between the three species are given in Table IX, excluding the common features shared by all the three. According to this, *Dostia* and *Neritina* have eleven features in common while *Dostia* and *Septaria* share seven common features. Between *Neritina* and *Septaria* there is only one. The implication of the findings is thus suggestive by itself. *Septaria* and *Neritina* appear to have evolved separately from *Dostia* by divergence. The earlier assumption (Cooke 1959) was based mainly on the shapes of the shell as an adaptation for invading freshwater, depicting a series of transitional forms from marine *Nerita* towards the limpet shaped *Septaria*. The present

study which reveals that, probably, the shell shape may be a genetically fixed variant rather than one controlled by the environment and the fact that no transition or intergradation is to be seen between the three species, lead us only to the conclusion that *Septaria* and *Neritina* are perhaps derived separately from *Dostia* by divergence rather than through transition. Confirmative and conclusive evidence on this, can however be obtained only by a serological assessment of the three species. Since it is assumed that neritids have had an independent evolution in all rivers of the Indo-Pacific region (Bourne 1908), it is imperative to collect information on them from all the major estuaries in India to throw more light on their systematics, phylogeny, evolutionary trends and the resulting speciation in the estuarine environment.

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REFERENCES

- Andrews, E. A., (1933 a). The storage sac for capsule reinforcement in the Neritidae. *Science.*, **78**, 39-41.
- (1933 b). *Neritina virginea* in the town creek of Montego Bay Jamaica. B. W. I. *Nautilus.*, **47**, 50-51.
- (1935 a). Shell repair by the snail, *Neritina*. *J. exptl. zool.*, **70**, 75-107.
- (1935 b). The egg capsules of certain Neritidae. *J. Morphol.*, **57**, 31-59.
- (1936). Spermatophores of the snail *Neritina reclivata*. *J. Morphol.*, **60**, 191-209.
- (1937). Certain reproductive organs in the Neritidae. *J. Morphol.*, **61**, 525-563.
- (1940 a). The snail *Neritina virginea* in a changing salt pond. *Ecology*, **21**, 335-346.
- *———(1940 b). *Neritina virginea* in Jamaica. *Nautilus*, **54**.
- Baker, H. B. (1923). Notes on the radula of the Neritidae. *Proc. Acad. nat. Sci. Phil.*, **75**, 117-178.
- *———Bielawski, J. (1960). Influence of salinity and oxygen content in the external medium upon the respiration of *Theodoxus*. *Acta. Biol. exp. Vars.* **20**.
- Bondesen, P. (1940). Preliminary investigations into the development of *Neritina fluviatilis*. L. in Brackish and fresh water. *Vidensk. Medd. dansk naturh. Foren.*, **104**, 283-317.
- Bourne, G. C. (1908). Contributions to the morphology of the group Neritacea of Aspidobranch gastropods. Part I. The Neritidae. *Proc. zool. Soc. Lond.*, 810-887.
- Cooke, A. H. (1959). Mollusca. The Cambridge Natural History. Vol. III : pp. 535. Reprint Edition.
- *D'asaro, Charles (1962). Some observations on the development of *Nerita tessellata*. Typed manuscript. Unpublished.
- *Fabre-Domerque (1924). Sur la *Neritina virginea* Linn. Var listeri' Pfeiffer et sur le role des mollusques Gasteropodes dans l'équilibre biologique des aquariums. *Reve Hist. nat. appl.*, **5**, Fretter, V. (1946). The genital ducts of *Theodoxus*, *Lamellaria* and *Trivia*, and a discussion on their evolution in the prosobranchs. *J. mar. biol. Ass. U. K.*, **26**, 312-351.
- (1965). Functional studies of the anatomy of some neritid prosobranchs, *J. Zool.*, **147**, 46-74.

- Fretter, V. (1966). Some observations on neritids, *Malacologia*, **5**, 79-80.
- Fretter, V., and Graham, A. (1962). British Prosobranch Molluscs. Ray Society London, pp. 755.
- Kolipinski, M. C. (1964). The life history, growth and ecology of four intertidal gastropods (genus *Nerita*) of Southeast Florida. Ph. D. Thesis, University of Miami.
- Lafon, C., and Alause, P. (1963). Recherches sur les *Theodoxus fluviatilis*. *Vie Milieu*, **14**, 143-147.
- Lenssen, J. (1899 a). Systeme digestif et systeme genital de la *Neritina fluviatilis*. *Cellule*, **16**, 179-232.
- *———(1899 b). Anatomie de la *Neritina fluviatilis*. *Anat. Anz.*, **16**,
- *———(1902). Systeme nerveux, circulaire respiratoire et excreteur de la *Neritina fluviatilis*. *Cellule*, **20**, 289-331.
- Lewis, J. B. (1960). The fauna of rocky shores of Barbados, West Indies. *Can. J. Zool.*, **38**, 391-435.
- Lumbye, J. (1958). The oxygen consumption of *Theodoxus fluviatilis* (L) and *Potamopyrgus jenkinsi* (Smith) in brackish and fresh water. *Hydrobiologia*, **10**, 245-262.
- Natarajan A. V. (1957). Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. *Proc. Indian Acad. Sci.*, **46**, 170-228.
- Natarajan, R. (1969). Cytological studies of Indian molluscs (Archaeogastropoda: Neritidae) *Malacologia*, **9**, 279-281.
- *Neumann, D., (1959). Variabilitat der Farmuster auf der Schale von *Theodoxus*. *Z. Morph. Okol. Tiere*, **48**,
- (1960 a). Experimentelle untersuchungen des Farbmusters der Schale von *Theodoxus fluviatilis*. *Zool. Anz. Suppl.*, **23**, 152-156.
- (1960 b). Osmotische Resistenz und osmoregulation der *Theodoxus fluviatilis*. *Biol. Zent.*, **79**, 585-606.
- Purchon, (1968). The Biology of the Mollusca. International series of Monographs in pure and applied Biology. Vol. **40**, pp. 560.
- Risbec, J., (1932). Notes sur la ponte et le developement de mollusques gastropodes de Nouvelle-Caledonie. *Bull. Soc. Zool. Fr.*, **57**, 358-374.
- Struhsaker, J. W. (1966). Breeding, Spawning, Spawning periodicity and early development in the Hawaiian *Littorina* : *L. pintado* (Wood), *L. picta* Philippi and *L. scabra* (Linne). *Proc. malac. Soc. Lond.* **37**, 137-166.
- Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25**, 1-45.
- Whitaker, M. B. (1951). On the homologies of oesophageal glands of *Theodoxus fluviatilis* (L.). *Proc. malac. Soc. Lond.*, **29**, 21-34.

*Not seen in original