POPULATION STUDIES ON A POLYMORPHIC PROSOBRANCH SNAIL (*CLITHON* (*PICTONERITINA*) *OUALANIENSIS* LESSON)

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CONTENTS

The prosobranch gastropod *Clithon* (*Pictoneritina*) *oualaniensis* Lesson which is widely spread in the Indo-Pacific region, shows a high degree of variability as regards shell colour and pattern. The present report is based on some 72000 snails collected round the coasts of Ceylon, in Malaya and Singapore, and in Hong Kong; and on some preliminary breeding results (Nugaliyadde, appendix 4).

Clithon has an axial (transverse) pattern which most commonly consists of fine transverse lines (f.t.l.); less often, there are coarse transverse lines (c.t.l.) or more widely spaced patterns such as zebras or tigers (which are rare in Ceylon, but common in the eastern provinces). F.t.l. and, to a lesser extent, c.t.l. are often complicated by the presence of small triangles or tongues the density of which increases with age. Superimposed on the axial is often a spiral pattern which generally consists of three roughly equidistant spirals. The ratio of axial:spiral patterns is about the same over the whole area and about 62:38. The spiral patterns in Ceylon include spiral tongues, ladders and yellow spirals; these are fairly distinct in certain populations, but grade into each other to a varying extent in others. In the eastern provinces, ladders are completely absent, but there are other spiral patterns which may be their equivalents. Between them, these simple axial and spiral patterns account for the great majority of all animals. In addition, there are certain rarer types which are mostly sharply classifiable (dilution, purple-tipped tongues, purple spirals, black and a few others).

Preliminary breeding experiments show that axial as compared with spiral patterns correspond to distinct genotypes, spirals being dominant over axial patterns.

Within the axial patterns, there are numerous intergrades between f.t.l. and c.t.l.; the tongue pattern can vary from absence to a density which covers most of the shell; it is largely an age effect like greying of hair in man. In the same shell, these patterns can change into each other gradually or sometimes abruptly following a temporary cessation of growth (including attempted predation by hermit crabs). They are probably largely, if not entirely, non-genetic in origin; this is compatible with the few breeding data so far available. Zebras and tigers which are almost confined to the eastern provinces are probably genetically distinct separate entities.

Both population studies and breeding experiments make it probable that the spiral group includes a significant element of genetic segregation. Purple spirals are probably due to a single (? recessive) gene, and a simple genetic basis is probable for most or all of the rarer variants.

Within a given province, populations are remarkably uniform. The rarer variants are generally homogeneously distributed within a province (except purple spirals which are much commoner on the east than on the west coast of Ceylon). There is more variance between populations as regards the ratio of axials to spirals, and as regards the various spiral patterns. But the variance between populations, both in space and in time, is not significantly greater than the error variance, and it thus appears that what variance there is lacks permanence; i.e. there is oscillation round essentially stable mean values. There is thus no need to invoke permanent differences in gene frequencies or permanent differences in the environment as between populations.

On the other hand, there are consistent and major differences between provinces, and these must clearly be genetic in nature. They may have arisen during the spread of *Clithon* from its original home which, presumably, has been coastwise and slow. *Clithon* has probably no pelagic larva and, as localities where it can exist are separated by many miles of open coastline where it cannot, its spread must have been at the mercy of rare accidents: these probably convey only a few individuals at a time from one suitable locality to another and thus expose populations to genetic drift (founder effects). As, within provinces, there is little or no evidence for this, it seems most probable that gene frequencies are stabilized by selection, and as long as an allele is not lost altogether, the interplay of selective forces will tend to bring gene frequencies back to normality. Whereas it thus appears probable that the polymorphism of *Clithon* is kept in being by selection, there is no reason to suppose that any particular pattern is better adapted, over the life cycle as a whole, than any other. The whole array of variability may thus be adaptively neutral.

INTRODUCTION

Many years ago, I became interested in some highly variable Middle Devonian snails, the group of *Murchisonia turbinata* Bronn which has been the source of many controversies among systematists. The variation involves the position of the slit band (which may be adjacent to the suture or well above it) and the presence or absence of certain sculptural elements such as a row of nodes or a rounded ridge above or below the slit band. Known under many different names, the various types were eventually combined again as a single species under the new name of *M. Archiaci* by Paeckelmann (1922). It occurred to me (Grüneberg 1927) that the varieties of *M. Archiaci* could be interpreted as the result of segregation and recombination of a few pairs of genes. This Mendelian concept required the existence of two additional phenotypes which were eventually discovered. There was an intriguing group of individuals which started life with the phenotype of one variety but then switched over abruptly to that of another. Such snails evidently had two options, and it was suggested that they might be heterozygotes with a change of dominance during growth. However, with fossil material, the limits of what can be tested are soon reached, and the matter could not be pursued beyond that point.

The situation is more favourable with living species, and there is no shortage of variable gastropods. This paper will deal with an unusually variable prosobranch, *Clithon* (*Pictoneritina*) *oualaniensis* Lesson which is widely spread in brackish water habitats of the Indo-Pacific Region. The variation of its shell pattern will be described in some detail and an attempt will be made to examine its genetic basis and to discover what keeps it in being. This report is mainly based on extensive collections which were made in Hong Kong, Malaya and Singapore and Ceylon between 1971 and 1974. The results of some breeding experiments subsequently carried out by Mr Lionel Nugaliyadde (Peradeniya, Ceylon) are given in appendix 4 and will be referred to in the Discussion.

MATERIAL AND METHODS

My attention was first drawn to *Clithon oualaniensis* by Dr A. G. Searle who, in 1955, sent me from Singapore sample no. 21A (table 8). The species is widely distributed in the Indo-Pacific region. In the older literature, it has often been included in the genera *Neritina* or *Theodoxus*. The following description is taken from van Benthem Jutting (1956) where references to the older literature can also be found.

> Shell small, globular, with low spire. Very prettily coloured with various patterns of dark triangles, zigzag lines, spiral bands, etc. on a yellow, greenish or pink background. Finely sculptured by the growth lines.
>
> Whorls about four, rapidly increasing in size. Suture shallow. Umbilicus closed.
>
> Aperture oblique, semilunar. Columellar side somewhat convex, white, yellow or greyish, porcellaneous, smooth or slightly rugulose. Along the entrance to the aperture the columellar edge is somewhat concave and minutely serrated. Exterior margin of peristome sharp, not reflected.
>
> Operculum semilunar. Exterior surface dark-grey, with lighter nucleus. Finely granular. From the nucleus an oblique groove runs over the surface. On the back of the operculum this groove corresponds with a low ridge. Interior side of operculum with two apophyses, connected by a shelly callus.
>
> Dimensions: height 8–9, width 7–8, height of aperture about 6 mm.

Most of the present animals are smaller than the Indonesian ones described above. Their size and general shape is that of a small pea. The first few whorls are usually eroded, and in practice little more than the body whorl is available for inspection, but in some localities the earlier whorls are better preserved. In old animals, the end of the last whorl may be turned downwards as seen in the conventional orientation of the shell. For the radula of *Clithon* and other *Neritidae* see Baker (1923). This paper will deal with the extraordinary variability of the shell patterns of this species. The more important variants from one locality are shown in plates 1–4. For the present study, the 'provinces' of Hong Kong, of Malaya and Singapore and of Ceylon were chosen (using the word province in a rather more restricted sense than usual). The material is summarized in tables 1 and 8. It amounts to 52457 individuals which have been fully classified, and one very large population from Ceylon, of about 20000 snails, which has been scanned for certain rare variants only. In the above tables, repeated collections in the same locality are shown as 8A, 8B, etc. In some populations, adults (A′, etc.) and juveniles (A″, etc.) were mixed and easily sorted out into distinct sub-populations (particularly in the Trincomalee region, table 1). Details concerning the various localities in which collections were made will be found in appendix 3.

Clithon lives mainly on muddy sand and less commonly on stones or 'eelgrass' (*Halophila ovalis* (R.Br.); family *Hydrocharitacea*) in the upper reaches of the tides in brackish water, generally in sheltered localities near the inlets of lagoons or near mangroves, and often near the mouth of a rivulet. It is not found on open beaches where there is any surf. Some populations are very large and may run into millions, and hundreds of snails may in such places be found on a single square metre. But as suitable habitats are usually very circumscribed and generally separated from each other by long stretches of coastline where *Clithon* cannot exist, the populations are virtually completely isolated from each other. *Clithon* (whose sexes are separate) has probably no free-swimming pelagic larva; the eggs are laid as egg capsules (often attached to the shell of another animal of the same species), and from these capsules miniature snails complete with shells emerge. Hence the spread of the species must depend essentially on accidents such as a journey on a rotting palm frond where such animals are occasionally found. Whereas some populations are abundant, others are small. In Kalpitiya (no. 10), for instance, the population was rather sparse and consisted mainly of big adults with few juveniles; hence it may be in the process of dying out. In Kalutara, south of Colombo, *Clithon* was plentiful not very long ago: in a prolonged search, a few dead shells were found, but despite considerable efforts no living population could be located. We had a similar experience on the east coast of Ceylon at Kallar (south of Batticaloa) where there were many dead shells and a very few living individuals, obviously in poor condition; a local skin diver volunteered the information that, following the building of a new concrete bridge, various animals in the lagoon had become scarce or died out. Again, about 40 km north of Trincomalee, in a lagoon between Kuchchaveli and Tiriyai, only a sprinkling of living *Clithon* was found, not enough to make an attempt at collecting. With the possible exception of Kalpitiya, we thus made our collections where *Clithon* was flourishing at the time.

The collections were made in most instances by scooping up the top layer of the sediment by means of a large plastic scoop and getting rid of finer particles by sifting; the coarser part of the sediment was then sorted on trays and the snails separated from the numerous specimens of *Cerithium* and other molluscs with which they are associated, not to mention their predators such as hermit crabs and *Natica*. This type of collection is not liable to selection. In some instances, hand-picking was resorted to, particularly where the snails were sitting on stones or on 'eelgrass'. Here, there is the danger that the more conspicuous types might be over-represented. However, though the differences in pattern are great when seen under the dissecting microscope, the animals do not look very different in their natural surroundings, and it is believed that hand-picking has not resulted in any appreciable bias.

The animals were killed by boiling and the shells were subsequently dried. Most of the opercula remained in position. After classification, groups of snails were weighed so that the relationship of shell pattern to size could be studied.

In addition to the data of tables 1 and 8, some material from the British Museum (Natural History) has been used, particularly one sample from the Philippines (see appendix 1).

Maps showing the localities of the various collections will be given at the beginning of the major sections. We begin with Ceylon for which the material is most extensive, and because its relatively lower degree of variability is less difficult to unravel.

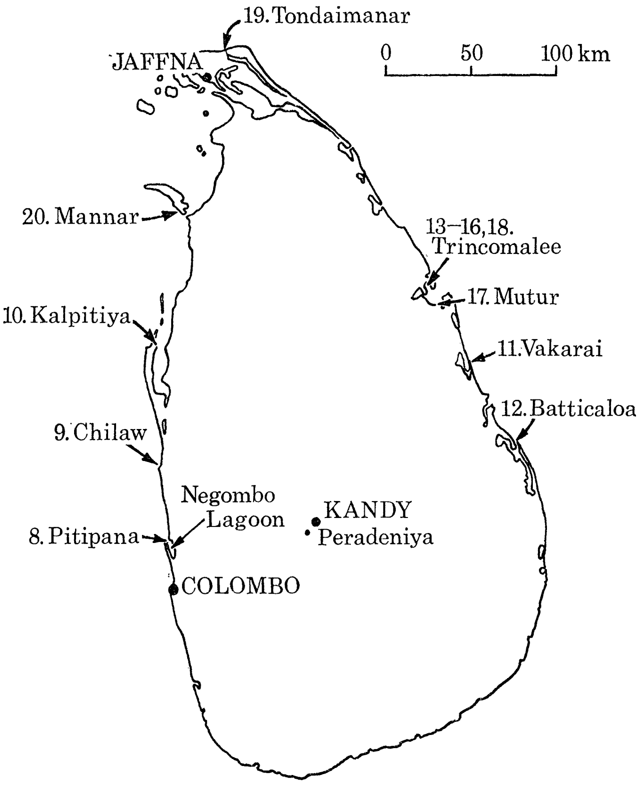


FIGURE 1. Map of Ceylon with the localities in which populations of *Clithon* were collected.

CEYLON

The main localities in Ceylon, or Sri Lanka as it is now officially known, are shown in figure 1 (see also appendix 3). Starting north of Colombo, there are four on the west coast (Pitipana, Chilaw, Kalpitiya and Mannar) and five on the east coast (Tondaimanar, Trincomalee, Mutur, Vakarai and Batticaloa). The deeply indented and sheltered coastline near Trincomalee provided five distinct populations (figure 2), and as in each of these adults could be separated from juveniles, the total number of populations from Ceylon amounts effectively to 18 (table 1), with a total of 29210 fully classified individuals. In some regions there are no coastal roads (between Pottuvil and Hambantota in the southeast, between Puttalam and Jaffna in the northwest, and between Point Pedro and Mullaitivu in the northeast); these stretches have either not been visited, or they have only been reached by stabs from the interior, as in Mannar and Mullaitivu. Otherwise, the whole coastline has been visited though, of course, it has not

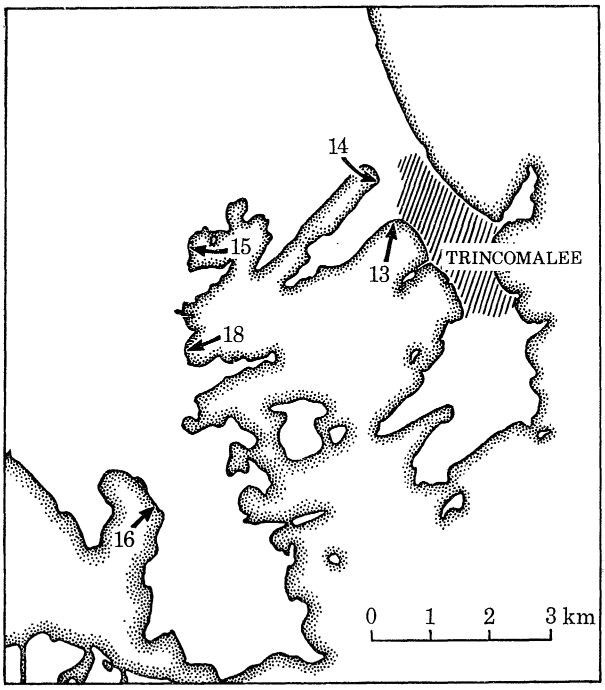


Figure 2. Map of the neighbourhood of Trincomalee. Numbers refer to the populations in table 1. 14, Yard Cove; 15, Cod Bay; 18, China Bay.

Table 1. The *Clithon* populations from Ceylon

		n	mean weight in mg
8	Pitipana, Negombo	1618	170.4
9A	Chilaw	1334	84.0
9B	Chilaw (about 20000)†		
10	Kalpitiya	553	251.8
11	Vakarai	2152	94.6
12	Batticaloa	1751	102.7
13	Trincomalee A′	529	77.7
13	Trincomalee A″	3305	20.5
14	Trincomalee B′	301	249.0
14	Trincomalee B″	807	79.0
15	Trincomalee C′	642	218.3
15	Trincomalee C″	1130	87.5
16	Trincomalee D′	373	151.6
16	Trincomalee D″	2927	53.7
17	Mutur	3258	48.8
18	Trincomalee E	772	98.4
18	Trincomalee E″	3146	27.3
19	Tondaimanar	2083	160.8
20	Mannar	2529	247.0
	total	29210	—

† Only partly classified.

been possible to cover the whole of it equally thoroughly. No populations have been obtained from the south coast between Batticaloa in the east and Colombo in the west, though *Clithon* may well exist in places which we have failed to locate.

The colour patterns of Clithon *from Ceylon*

We shall here give a description of those patterns which are regularly found in Ceylon (for the mechanisms underlying the formation of these patterns see appendix 2). Patterns peculiar to other provinces will be added later. The classification of the *Clithon* patterns presents considerable difficulties. Some are quite distinct and sharply defined so that one is rarely in doubt as to whether a given snail is, for example, a 'purple spiral' or whether it has 'purple-tipped tongues'. Other types are equally characteristic and encountered in every population, such as 'ladders' and 'yellow spirals'. But whereas in some populations these are quite distinct, in others there are varying numbers of intermediates. And some types are connected by so many intergrades that no more than a semi-quantitative classification with arbitrary classes is possible.

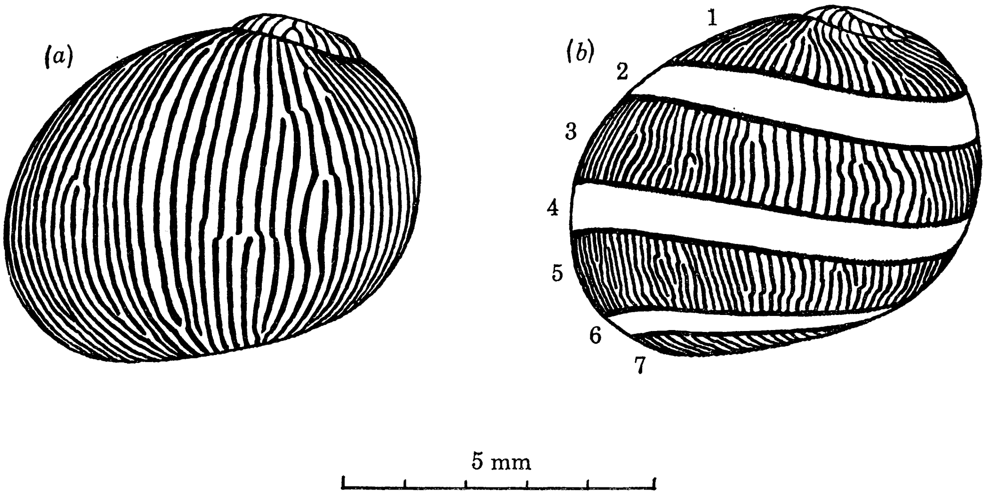


FIGURE 3. *Clithon* with the basic transverse pattern (*a*) and with the fully developed spiral ('ladder') pattern superimposed on it (*b*). Chilaw (9B). All text-figures of *Clithon* are camera lucida drawings.

The snail's shell is an indelible record of the physiological state of the pigment-producing cells of the edge of the mantle, and of any changes which it may have undergone. However, this record is soon hidden again by the further growth of the shell, and in *Clithon* little more than the body whorl is usually visible at any one time. Certain patterns persist essentially unchanged throughout life. Others change gradually with age, or sometimes abruptly as in *Murchisonia*. Such events are informative as they reveal potentialities which would otherwise have remained dormant.

The basic pattern of *Clithon* consists of fine transverse (axial) lines (figure 3*a*). This pattern is often complicated by small triangles or tongues. A spiral pattern may be superimposed on the transverse lines (figure 3*b*). Typically, there are three spirals, and in adult animals deviations from that number are uncommon. Counting from the suture, seven zones may thus be distinguished of which the spirals occupy zones 2, 4 and 6; when fully developed, they interrupt the axial pattern so that the diffuse background colour only is visible; the axial pattern is then confined to zones 1, 3, 5 and 7 (as in figure 3*b*). More often, the spirals merely modify the axial pattern as will be described in more detail below. A distinction must be made between *primary* and *secondary* spirals. Primary spirals arise early in life and have firm outlines; they are the great majority of spirals. Secondary spirals tend to be ghost-like; they certainly overlap normal and possibly also the primary spirals. Before breeding data became available (appendix 4), it was believed that primary spiralization was not an all-or-none character, but rather one limb of a U-shaped distribution with a small contingent of intergrades between axial and spiral phenotypes. It now appears more likely that basically axial and primary spiral patterns are distinct entities, and that the 'intermediates' are in fact secondary spirals which become manifest under certain conditions.

The axial patterns

The basic pattern of the *Clithon* shell consists of black or dark-brown transverse (axial) lines which run roughly (but not exactly) parallel to the lines of accretion and to each other on a diffuse background of orange, yellow, pink, greenish, beige or off-white (figure 3*a*). Individual lines may branch, or be displaced bayonet-fashion, or end abruptly. The pattern is thus reminiscent of finger prints and is probably as uniquely characteristic for each snail. In the majority of snails, the axial pattern consists of fine transverse lines (f.t.l.) like those in figure 21, plate 1, but some individuals have coarse transverse lines (c.t.l.) like those in figure 22, plate 1.

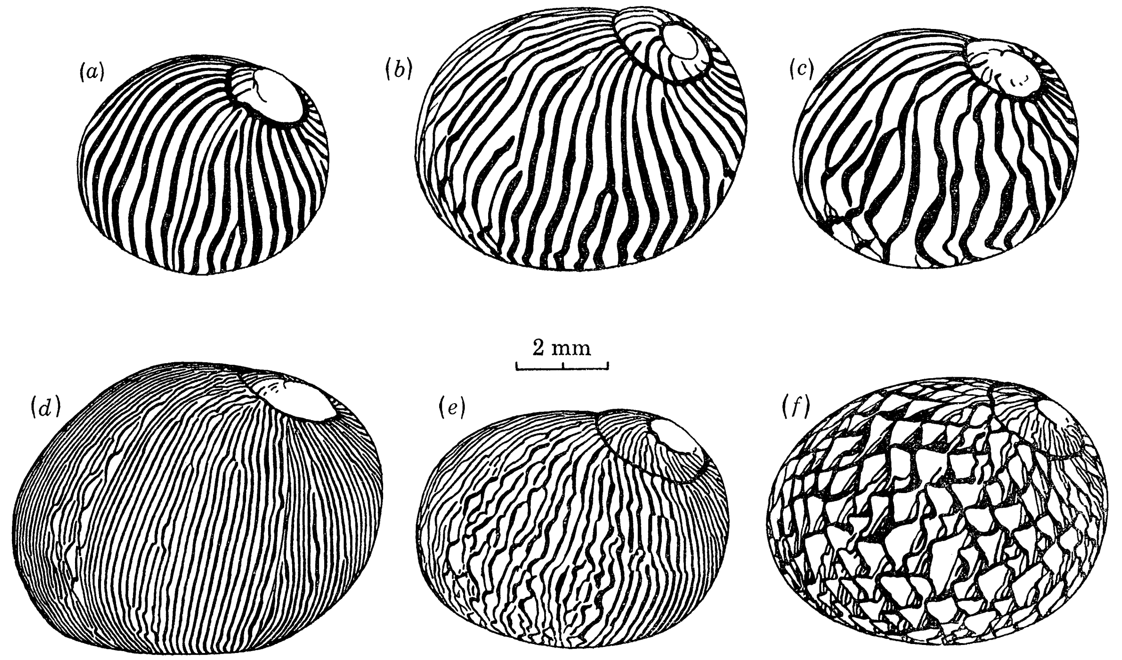


FIGURE 4. Coarse (*a*, *b*, *c*) and fine transverse pattern (*d*, *e*, *f*).
Note the increasing number of tongues from (*d*) to (*e*) and (*f*). Chilaw (9B).

Tongues

The axial pattern is usually complicated to a varying extent by small triangles or better, on account of their rounded contours, by *tongues*. These arise by the bending forward (towards the aperture) and back again of a single transverse line (figure 4*d*, *e*, *f*). Snails with f.t.l. may be completely free of them; commonly, a few are present, particularly near the base where they are not very conspicuous unless the shell is turned over; by degrees, their numbers may increase until they cover almost the whole surface of the shell (figure 25, plate 2). Turning individual shells round, one often notices a tendency for the density of the little tongues to increase towards the aperture, i.e. with increasing age, and indeed the most striking instances of 'many small tongues' occur in the largest individuals. The opposite is the case in c.t.l. where the transverse lines are less close together; they are often gently wavy and form broad but shallow tongues. In Ceylon, at any rate, a sharp distinction between f.t.l. and c.t.l. is often impossible, but the clearest specimens of c.t.l. are nearly always small. These general impressions can be confirmed in a variety of ways.

TABLE 2. RELATION BETWEEN SIZE OF SHELL AND INCIDENCE OF 'MANY SMALL TONGUES' (EXPRESSED AS A PERCENTAGE OF ALL NON-SPIRAL TYPES, EXCLUDING THOSE IN BLACKS): POPULATIONS ARRANGED IN ASCENDING ORDER OF MEAN WEIGHT

		non-spirals		many small tongues	
population	mean weight in mg	*n*	%	*n*	%
Trincomalee A″	20.5	2059	62.30	497	24.14
Trincomalee E″	27.3	1935	61.51	879	45.43
Mutur	48.8	1997	61.30	129	6.46
Trincomalee D″	53.7	1931	65.97	251	13.00
Trincomalee A′	77.7	262	49.53	131	50.00
Trincomalee B″	79.0	483	59.85	176	36.44
Chilaw A	84.0	593	44.45	136	22.93
Trincomalee C″	87.5	689	60.97	209	30.33
Vakarai	94.6	1383	64.27	718	51.92
Trincomalee E′	98.4	431	55.83	245	56.84
Batticaloa	102.7	1076	61.45	141	13.10
Trincomalee D′	151.6	183	49.06	121	66.12
Tondaimanar	160.8	1062	50.98	523	49.25
Pitipana, Negombo	170.4	887	54.82	581	65.50
Trincomalee C′	218.3	351	54.67	175	49.86
Mannar	247.0	1517	59.98	1464	96.51
Trincomalee B′	249.0	179	59.47	74	41.34
Kalpitiya	251.8	328	59.31	314	95.73
total	—	17346	59.38	6764	—

Within populations, the weights of shells with c.t.l., of shells with f.t.l. with few or no tongues, and of f.t.l. with many tongues can be compared with each other. In 15 out of 18 populations, the mean weights increased in that order though not all the individual differences were significant. The same order was also found in a 16th population (Trincomalee E″), but as all the three weights were between 27 and 28 mg, no importance can be attached to that case. In Trincomalee B′, c.t.l. were absent and the other two classes were marginally in the 'wrong' order; as in this old population most snails had evidently reached their final size, the exception is probably spurious. Finally, in Mutur (few or no tongues: 51.0 mg as compared with 49.9 for many tongues), the exception probably has a different reason, as will be discussed below.

Next, if the 18 Ceylon populations are arranged in order of ascending mean weight of shells, i.e. increasing mean age (table 2), the 11 younger populations (20–103 mg) average 33.10 %, the 7 older populations (151–252 mg) 66.33 % of animals with many small tongues (expressed as a percentage of all non-spiral shells; unweighted means). Whereas the general tendency is thus unmistakable, there is considerable scatter round the means, some populations running ahead and others lagging behind. Evidently, factors other than age are also at work. For instance, in Mutur (48.8 mg), the snails with f.t.l. have virtually no tongues at all; but in Trincomalee A″ (20.5 mg), there are definitely more than in Mutur.

Thirdly (table 3), in all five Trincomalee populations, the older age group (A′, B′, etc.) has a higher incidence of many small tongues than the corresponding younger age group (A″, B″, etc.) though in one case (Trincomalee E″) the difference is not very reliable.

Clearly, shells tend to start with c.t.l. and subsequently change to f.t.l., and the number of small tongues tends to increase with age. But not all shells start with c.t.l.; some are f.t.l. from the beginning. Also, some c.t.l. retain the coarse pattern beyond the normal time. Finally, in extreme old age, animals with many small tongues may revert to a state with extremely fine transverse lines (often faintly purplish) and no tongues at all (particularly in Trincomalee C′). There is thus no reason to assume that these patterns are genetically distinct however strikingly they may differ phenotypically.

TABLE 3. THE MAIN NON-SPIRAL VARIANTS IN CEYLON. 1, FINE TRANSVERSE LINES WITH FEW OR NO TONGUES; 2, FINE TRANSVERSE LINES WITH MANY TONGUES; 3, COARSE TRANSVERSE LINES; 4, TOTAL OF COLUMNS 1, 2 AND 3: THE TABLE DOES NOT INCLUDE BLACK SHELLS

	1		2		3		4	
	n	%	*n*	%	*n*	%	*n*	%
8	235	14.52	581	35.91	71	4.39	887	54.82
9A	336	25.19	136	10.19	121	9.07	595†	44.60‡
10	9	1.63	314	56.78	5	0.90	328	59.31
11	604	28.07	718	33.36	61	2.83	1383	64.27
12	898	51.28	141	8.05	37	2.11	1076	61.45
13′	126	23.82	131	24.76	5	0.95	262	49.53
13″	1436	43.45	497	15.04	126	3.81	2059	62.30
14′	105	34.88	74	24.58	—	—	179	59.47
14″	259	32.09	176	21.81	48	5.95	483	59.85
15′	173	26.95	175	27.26	3	0.47	351	54.67
15″	378	33.45	209	18.50	102	9.03	689	60.97
16′	54	14.48	121	32.44	8	2.14	183	49.06
16″	1599	54.63	251	8.58	81	2.77	1931	65.97
17	1661	50.98	129	3.96	207	6.35	1997	61.30
18′	181	23.45	245	31.74	5	0.65	431	55.83
18″	912	28.99	879	27.96	144	4.58	1935	61.51
19	518	24.87	523	25.11	21	1.01	1062	50.98
20	37	1.46	1464	57.93	16	0.63	1517	59.98
total	9521	32.60	6764	23.16	1061	3.63	17348	59.39

† This total also includes one individual with giant tongues and one with dilution.

‡ This population includes an additional 141 (or 10.57%) non-spirals with change of pattern during growth which do not occur in columns 1–4.

Changes of pattern during growth

If further proof for the above statement were needed, it would be provided by changes of pattern of the *Murchisonia* type. These can come about in at least two different ways.

Hermit crabs attack *Clithon* by first cutting off the free edge of the aperture down to the level of the operculum, but they do not always succeed in prising the operculum open. Often, they give up their attempt, and the snail lays down a new shell which is easily recognized by its irregular juncture with the old shell and by the fact that its outer surface is stepped down to correspond with the inner surface of the old shell (figure 7). The new shell formed following attempted predation often shows an abrupt change of pattern, such as from c.t.l. to f.t.l. or vice versa, and particularly there is often a veritable outbreak of many small tongues following on f.t.l. Depending on the local abundance of hermit crabs, such shells are rare in some and common in other populations; particularly large numbers were found in Chilaw.

The second mode, also very common in Chilaw (figure 5), is not visibly connected with predation. During an interruption of growth for whatever reasons, the physiological state of the mantle's edge may change and lead to an abrupt change of pattern. Such interruptions of growth are often recognizable by a fine groove following exactly the lines of accretion as if it had been impressed in wax by a nail. Sometimes, pattern changes are not accompanied by structural signs of interrupted growth.

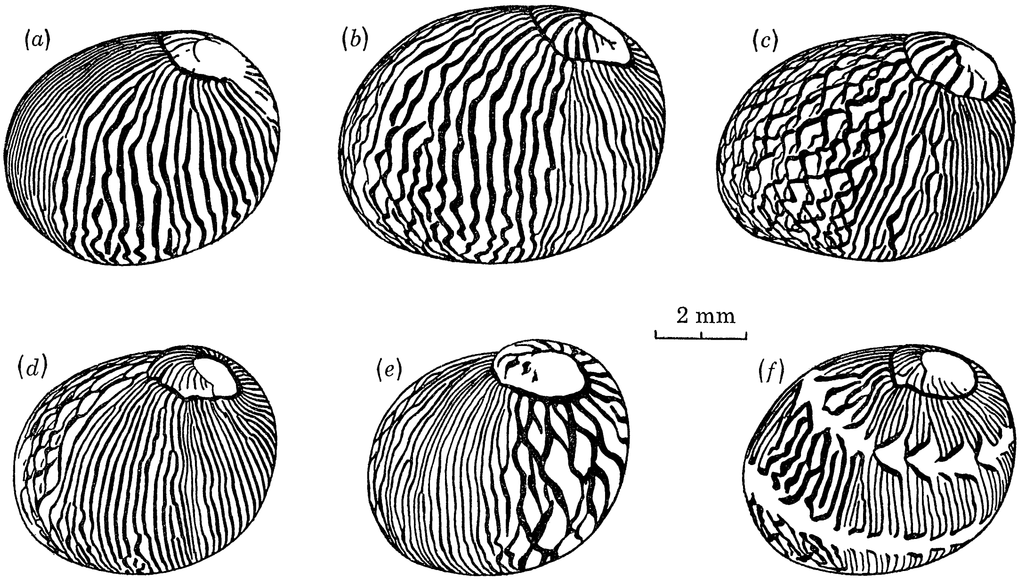


FIGURE 5. Change of pattern. In (*a*), the coarse pattern is followed by fine transverse lines, in (*b*) the opposite is happening. In (*c*) and (*d*), fine transverse lines are followed by many small tongues; note that in (*c*), the snail started with coarse but continued with fine transverse lines, there thus being two changes of pattern. In (*f*), the change from fine to coarse transverse lines does not involve the spiral pattern which continues unchanged. Chilaw (9B).

The situation as regards small tongues can be compared with the greying of human hair which does not happen with the same speed in all people, and in some it makes little progress. Also, there are genes for premature greying. A young human population of, say, the age range of 25–30 years, will fall rather sharply into two classes, grey and not-grey, and this will generally behave like a single-gene difference. When an ageing population is similarly classified, all intergrades between grey and not-grey will be found, and the group of premature greying can no longer be picked out by inspection.

Small tongues which increase with age are generally derived from f.t.l.; but they may also be derived from c.t.l. which is a juvenile feature. This is largely so in the Mutur population which is young (48.8 mg). The small tongues in that population are, in a way, a counterpart of premature greying in man.

Secondary spiralization

Whereas primary spirals arise early in life and are well-defined patterns, secondary spiralization happens at a later stage and generally leads to somewhat ill-defined spirals. They were first noticed in f.t.l. shells with small tongues: as these increase in numbers, they are often not distributed at random over the shell, but tend to favour zones 2, 4, 6 and particularly zone 6. In this way, rather vague spirals become visible first by their paler colour and eventually the tongues in these zones tend to become larger than those in between (figure 6). Many of these secondary spirals are quite obvious to the naked eye, but are less easily seen under the dissecting microscope or in drawings. By stages, situations are reached where one can be in doubt as to whether a weak spiral tendency is present or not; this may even happen when tongues are numerous.

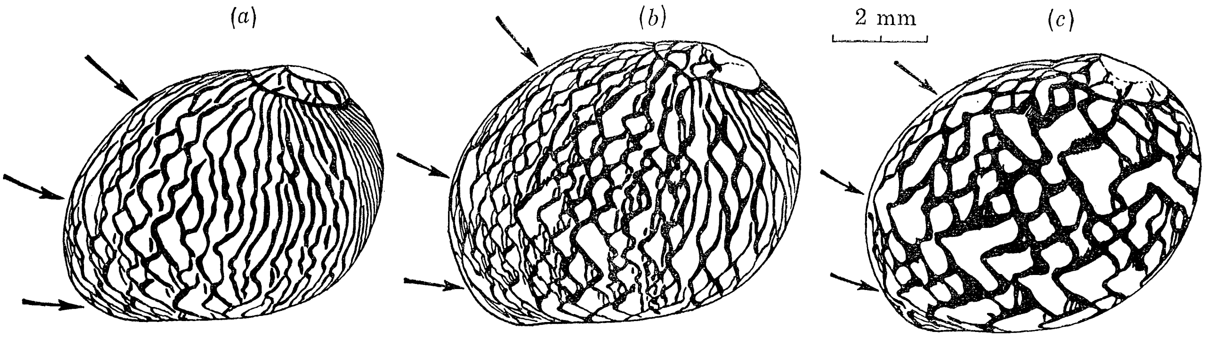


FIGURE 6. Secondary spiralization made manifest by the background pattern of small tongues. The secondary spirals are far more conspicuous to the naked eye than in drawings and their position is here indicated by arrows. Chilaw (9B).

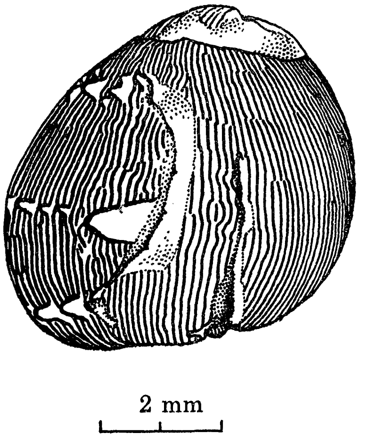


FIGURE 7. Transition from transverse basic pattern to primary spirals following attempted predation, a very rare event. Chilaw (9B).

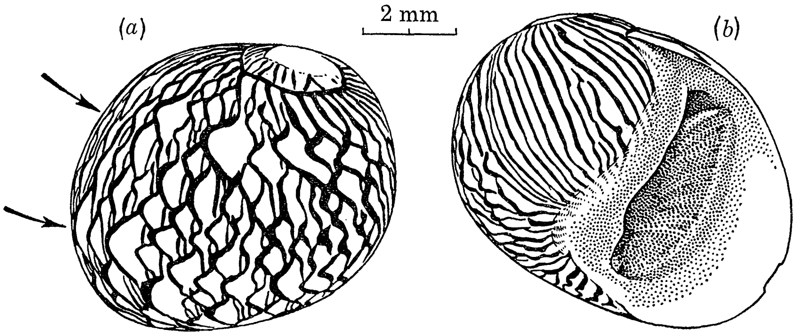


FIGURE 8. Transition ('spontaneous') from fine transverse lines without manifest spiralization to many small tongues with secondary spirals. Chilaw (9B).

In old populations with many small tongues, secondary spiralization can dominate the picture. An extreme case is the Kalpitiya population where, in a total of 332 'non-spiral' shells, at least 238 show secondary spirals. Indeed, the question must be asked whether latent spiral tendencies are present in all our snails. I strongly suspect that this is so. It would appear that the small tongues act like iron filings which make the lines of force of a magnet visible. The relationship between small tongues and secondary spirals is demonstrated rather strikingly in figure 8 where a snail which started without any manifest spiral tendencies suddenly switched over to small tongues complete with secondary spirals.

Primary spirals can generally be recognized as such by their firm outlines even if they appear late in life, as in the rare case of figure 7 where this has happened as the result of attempted predation. One is thus rarely in any real doubt in separating secondary spirals made visible by small tongues from primary ones. But there are certain populations (such as Vakarai) where apparently some secondary spirals begin to consolidate themselves by the running together of small tongues into continuous spirals. Hence occasional errors of classification may well occur. But their number is probably too small to matter in practice and in any case they are confined to a few ageing populations.

As they cannot be enumerated accurately and are, in any case, a secondary phenomenon correlated with age, secondary spirals have been ignored: f.t.l., regardless of the number of small tongues, and regardless of whether they are accompanied by secondary spirals or not, have simply been treated as f.t.l.

It is conceivable that secondary spirals may occur in the absence of 'many small tongues'. In a subsequent section, certain abortive cases of 'spiral tongues' will be described which do not seem to occur in small juveniles and which may be secondary spirals. A decision will require breeding tests which are not yet available.

The incidence of the non-spiral group

Pooling f.t.l. and c.t.l. regardless of tongues and secondary spiralization, the average incidence of snails with these axial patterns only, in the 18 Ceylon populations and sub-populations (table 2) is 59.38 %. The fluctuations round this mean are too great to be accounted for by errors of sampling ($\chi^2_{17} = 82.4$ and $P < 10^{-10}$). They can also not be explained in terms of the small uncertainties as to where to draw the line between spirals and non-spirals (see below). Part, at least, of the variance must thus be regarded as genuine deviations from the overall mean.

An analysis of variance may be based on the material from the Trincomalee region which was collected in five distinct localities; in each of these, adult and juvenile sub-populations could easily be separated from each other. These 10 sub-populations yield 9 degrees of freedom; one of these represents the comparison between adults and juveniles from the same localities (variance within populations), four represent the variance between populations from different localities, and the remaining four are used for the estimation of the error, as follows.

	d.f.	mean square	variance ratio
within populations	1	0.015677	7.50
between populations	4	0.000504	—
error	4	0.002089	—

The between populations variance is smaller than the mean square of the error; it thus requires no additional explanation. The within populations variability (i.e. that between juveniles and adults) gives a variance ratio of 7.50 and thus does not quite reach the 5 % point for 1 and 4 degrees of freedom (which is 7.71). There are two other reasons why it is probably to be regarded as accidental. The decrease of non-spirals from 63.06 to 55.07 % from juveniles to adults in the Trincomalee region is not borne out by the data of table 2 as a whole; the incidence of the non-spiral patterns does not seem to change with age. Moreover, it is difficult to imagine what could make variations within populations greater than those between them, except, of course, that a comparison between A′ and A″ automatically involves an age and hence a seasonal difference which is not always so in inter-population comparisons.

We thus reach the conclusion that, for the parameter under discussion, neither inter- nor intra-population variance significantly exceeds the error variance. There is thus no reason to look for systematic genetical or stable environmental differences between populations to account for the fluctuations round the general mean. What we observe is essentially error variance, and the whole gamut of Ceylon populations may be regarded as a single super-population in so far as the ratio of spirals to non-spirals is concerned.

The situation may be compared with the surface of the sea which is at any one moment in some places above, in others below the mean level. However, the amplitude of the waves in space is the same as that in a single locality in time. Through all these ups and downs, the mean sea level remains the same.

Primary spirals

In 15 out of 18 populations from Ceylon, non-spirals are heavier than spirals; the mean difference amounts to 6.7 % and is clearly significant.

With few exceptions, primary spirals are easily recognizable by the clear definition and firmness of the spiral pattern. In certain populations (such as Mutur), primary spirals fall almost without intergrades into three categories, 'spiral tongues', 'ladders' and 'yellow spirals', and it is only among the spiral tongues that doubts as to the delimitation of primary spirals occasionally arise. In most populations, there are more intergrades between the three categories, and an extreme case is the Mannar population; this consists almost entirely of very large snails and includes more than 300 primary spirals which have so far defied all attempts at classification: they certainly do not fit into the simple Mutur trinity, and probably no Ceylon population is quite free of such individuals. On the other hand, all three types occur in many typical specimens in all populations from Ceylon, including Mannar, and they thus represent undoubted realities which cannot be ignored.

Spiral tongues

These consist of sequences of tongues in zones 2, 4, 6 (figure 30, plate 3 and others). Often, the tips of the tongues are picked out in brilliant red or purple (see below under Purple-tipped tongues). Most spiral tongues are fully developed in small juveniles, and they tend to go on essentially unchanged for a long time. But sometimes the tongues eventually run together and form continuous spirals (figure 9). This may happen once and for all. More often, the snail teeters on the brink and sequences of spiral tongues alternate irregularly with bits of continuous spirals. A spiral pattern once formed in a young animal rarely disappears again (figure 10). But in old age, a snail which started with continuous spirals may switch over to spiral tongues and these sometimes peter out more or less completely. It is thus clear that spirals proper and spiral tongues are mutually interchangeable though most animals most of the time tend to be one or the other.

Spiral tongues which have arisen early in life are always clearly primary spirals. The situation is sometimes less clear with a minority of spiral tongues which arise later in life (figure 11). In such animals, an essentially transverse (axial) pattern gradually takes on a wavy course; in positions 2, 4, 6 the lines bend forward first slightly and gradually more deeply until the tongues so formed touch each other; indeed, they may become purple-tipped. It is not difficult to assemble a sequence of animals which, step by step, show a seemingly continuous gradation of stages from essentially axial to clearly spiral patterns, as in figure 11. Indeed, it was this kind of montage which suggested to me in the first place that axial and spiral patterns might be merely the extremes of an essentially continuous U-shaped distribution. This may still be true. On the other hand, it is conceivable that such spirals which arise late in life are the result of secondary spiralization (in the absence of 'many small tongues'), some phenotypic overlaps with primary spirals notwithstanding. As already indicated above, a decision between these two possibilities cannot be made except by breeding tests.

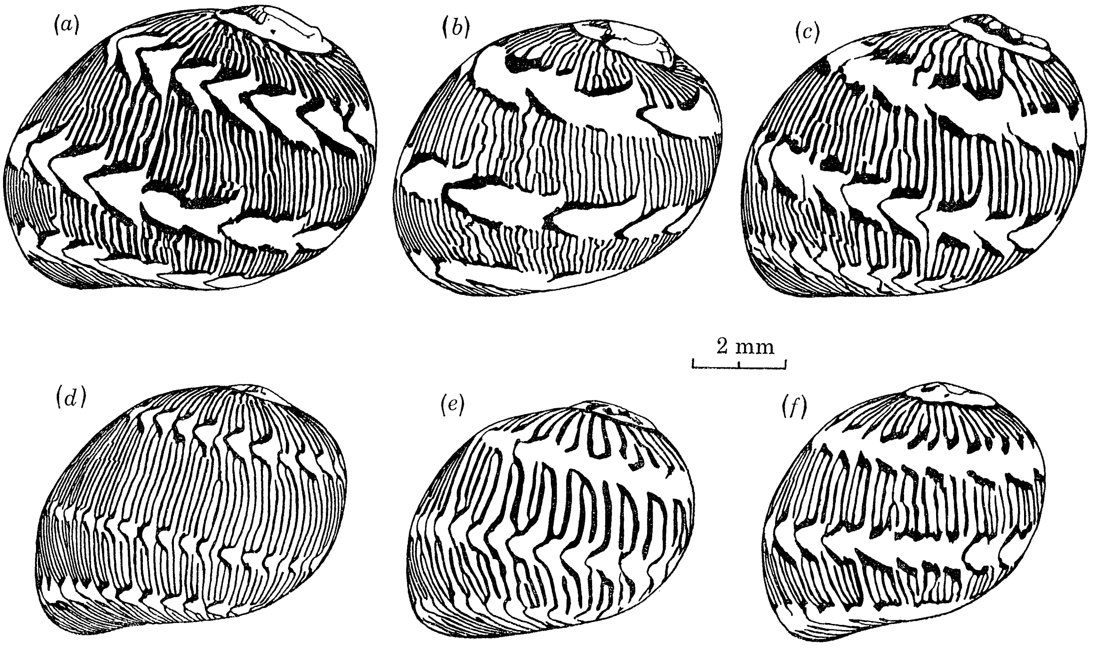


FIGURE 9. Spiral tongues (*a*, *d*) and transition to spirals. Chilaw (9B).

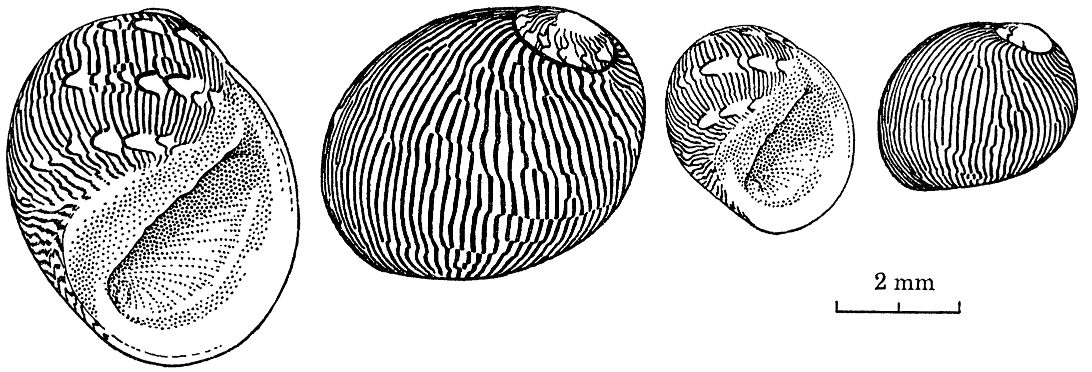


FIGURE 10. 'Spontaneous' transition from spiral tongues to absence of manifest spirals. Population 5 (JV 919 766, N.T., Hong Kong).

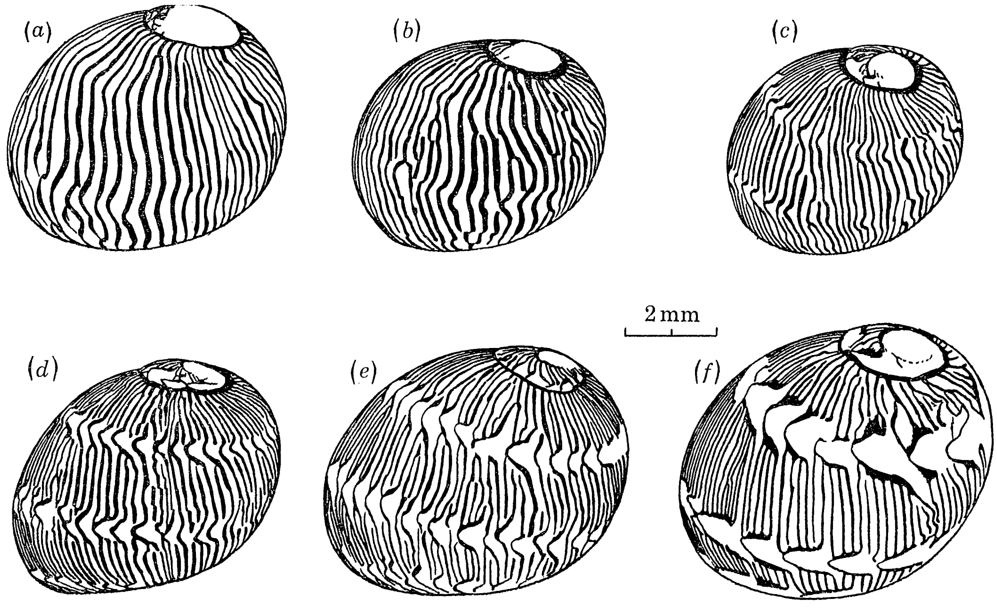


FIGURE 11. Transition from transverse pattern to spiral tongues. Chilaw (9B).

Ladders

Among the spirals proper, 'ladders' form a rather well-defined group. The pattern is generally fully developed in small juveniles. The continuous spirals in zones 2, 4, 6 are typically remarkably regular and sharply outlined by black seams; these form the uprights of two ladders in positions 3 and 5 which are connected by rungs (i.e. the transverse pattern) in an orderly fashion (zones 1 and 7 have of course a single upright only, see figure 3*b* and figure 12*a*). Precision and tidiness is the hallmark of ladders. Usually there is no background pattern of small tongues to disturb the regularity of the rungs. The uprights vary in width; often they are fairly wide bands, sometimes they are thin and occasionally absent. This also tends to happen in very old individuals (figure 12*c*) and may herald the gradual disappearance of the spiral pattern. The background coloration of ladders is usually beige, but yellow or orange is sometimes encountered. Next to these 'perfect' ladders (column 4 in table 4), there are some with irregularities of the uprights which in places may become wavy indicating an imminent transition to tongues; a few tongues may cross one or the other of the spirals and these tongues may be purple-tipped (p.t.t., see below); these marginally abnormal ladders (figure 12*b*; column 3, table 4) are followed by true intermediates (column 2) leading to spiral tongues (column 1) from which they differ by the possession of pieces of spirals lined by uprights which alternate irregularly with spiral tongues. For the whole of the Ceylon material, the frequencies of these groups are as follows

'perfect' ladders	4.46 %
marginally abnormal ladders	2.58 %
intermediates	5.73 %
total	12.77 %

Ladders, perfect or nearly so, are thus commoner than true intermediates, but there are some exceptional populations as will be discussed in a later section.

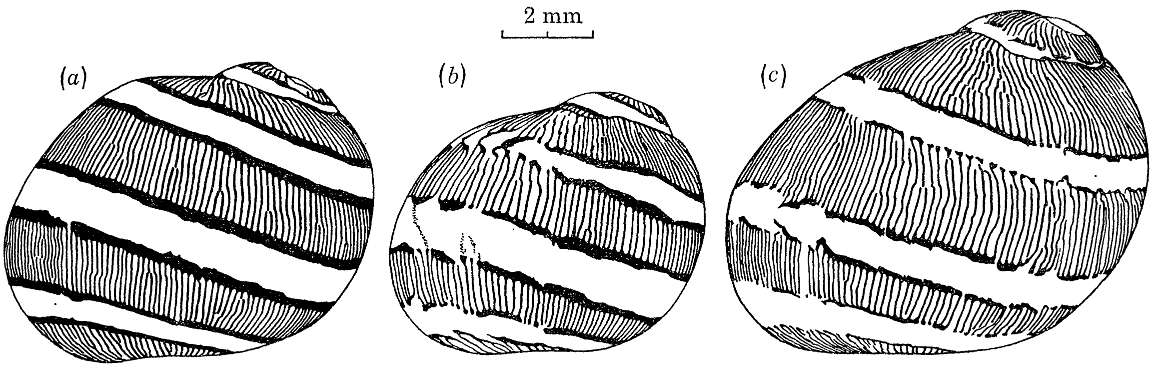


FIGURE 12. Ladders. (*a*), A 'perfect' ladder; (*b*) a ladder with some irregularities like beginning transition to spiral tongues; (*c*) an old specimen in which the uprights are gradually disappearing. Chilaw (9B).

Yellow spirals

The background coloration of this group is yellow at first, but gradually becomes paler. Whereas the pattern of ladders tends to be almost diagrammatically tidy, that of yellow spirals (figure 13) is usually messy or even blotchy; the transverse lines in zones 1, 3, 5 are usually coarse and irregular; the black pigment is often smudgy and sometimes runs together so that occasionally the zones 1, 3, 5 are almost solidly black in places. Unlike ladders in which the 7 spiral zones are generally complete in small juveniles, yellow spirals often start as solidly yellow shells with only a narrow zone of black spikes near the suture. Zones 3 and 5 are often formed much later (figure 13*a* and *b*), usually abruptly as a band which is first narrow and gradually widens. The general untidiness of zones 1, 3, 5 is often enhanced by the existence of a background pattern of small tongues which is generally absent in ladders. Zone 1 in yellow spirals is often deeply serrated and forms a star-shaped collar round the suture (figure 13*d*, *e* and *f*). More often than not, uprights are missing altogether in yellow spirals (figure 13*e* and *f*); where present they are generally irregular and weakly developed.

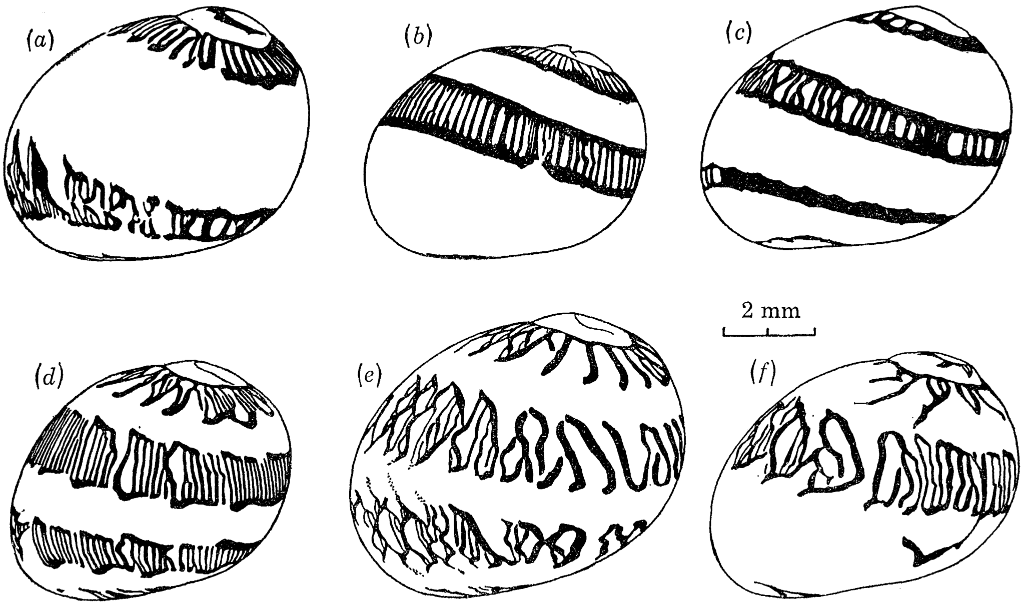


FIGURE 13. Yellow spirals. In (*a*) zone 3 and in (*b*) zone 5 have not yet made their appearance. Chilaw (9B).

Most Ceylon populations include individuals which are intermediate between yellow spirals and ladders, usually of a uniform nature. Less commonly, individuals which started as ladders turn into yellow spirals (particularly in the Tondaimanar population; see also figure 14). The opposite type of change is less common, but the Mutur population (in which the two types are virtually distinct) includes one such case. The separation of yellow spirals from spiral tongues is even less satisfactory in view of many intergrades. None the less, the intergrades between spiral tongues, ladders and yellow spirals cannot obliterate the fact that there is an underlying biological reality in these distinctions, just as in the case of non-spiral and spiral snails, occasional intergrades notwithstanding.

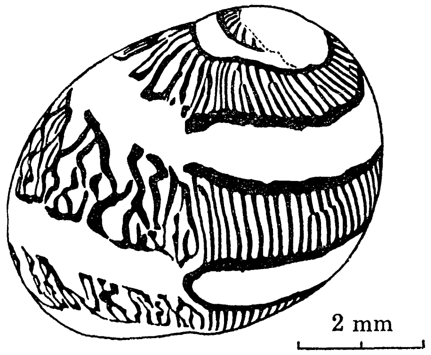


FIGURE 14. Transition from ladder to yellow spiral. In this case there seems to have been a 'spontaneous' cessation of growth as indicated by a fine groove which follows the lines of accretion. The closing of the middle spiral and the beginning of the irregular rungs precede the actual cessation of growth by a little. The change in the physiology of the mantle's edge and the interruption of growth may thus have had a common cause. Chilaw (9B).

The incidence of the spiral variants

The incidence of the primary spirals (except purple spirals and those in blacks, see below) in the 18 populations from Ceylon is given in table 4. Heterogeneity between populations is obvious beyond the need of tests. The uncertainties as to classification discussed in the preceding sections have undoubtedly contributed to this situation. But it is clear that the major part of the heterogeneity is due to other causes.

The category which is best defined is that of ladders, both 'perfect' and with marginal anomalies. If these two classes (columns 3 and 4, table 4) are combined, the resulting group is not liable to any serious errors of classification; its remaining heterogeneity must thus be due to other causes. In certain populations (17, 18″, 15′, 13″, 13′), there is a heavy preponderance of 'good' ladders over the intermediates whereas in others (9A, 10, 8, 16″) the situation is reversed. This ratio (columns (3+4)/column 5) is also not very sensitive to misclassifications. It may be regarded as a measure of developmental stability which increases with the pure ladder phenotype. An analysis of variance for ladders of the Trincomalee region is given separately for all ladders (column 5) and for columns (3+4)/5.

	d.f.	column 5 mean square	columns (3+4)/5 mean square
within populations	1	0.001327	0.012960
between populations	4	0.002942	0.045063
error	4	0.000677	0.016079

Table 4. The main spiral variants in Ceylon. 1, Spiral tongues; 2, intermediates between spiral tongues and ladders; 3, marginally abnormal ladders; 4, 'perfect' ladders; 5, sum of $2+3+4$; 6, yellow spirals; 7, sum of $1+5+6$

		1		2		3		4		5		6		7	
	total	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
8	1618	263	16.25	145	8.96	40	2.47	59	3.65	240	14.83	210	12.98	713	44.07
9A	1334	169	12.67	211	15.82	27	2.02	59	4.42	297	22.26	113	8.47	579	43.40
10	553	80	14.47	33	5.97	13	2.35	4	0.72	50	9.04	91	16.46	221	39.96
11	2152	189	8.78	75	3.49	99	4.60	96	4.46	270	12.55	236	10.97	695	32.30
12	1751	81	4.63	87	4.97	83	4.74	165	9.42	335	19.13	184	10.51	600	34.27
13′	529	90	17.01	10	1.89	27	5.10	35	6.62	72	13.61	77	14.56	239	45.18
13″	3305	310	9.38	47	1.42	96	2.90	220	6.66	363	10.98	454	13.74	1127	34.10
14′	301	22	7.31	22	7.31	4	1.33	20	6.64	46	15.28	46	15.28	114	37.87
14″	807	76	9.42	12	1.49	20	2.48	13	1.61	45	5.58	179	22.18	300	37.17
15′	642	94	14.64	10	1.56	28	4.36	43	6.70	81	12.62	83	12.93	258	40.19
15″	1130	104	9.20	17	1.50	46	4.07	32	2.83	95	8.41	197	17.43	396	35.04
16′	373	38	10.19	29	7.77	21	5.63	17	4.56	67	17.96	75	20.11	180	48.26
16″	2927	233	7.96	323	11.04	90	3.07	180	6.15	593	20.26	105	3.59	931	31.81
17	3258	259	7.95	36	1.10	6	0.18	330	10.13	372	11.42	500	15.35	1131	34.71
18′	772	87	11.27	29	3.76	16	2.07	26	3.37	71	9.20	140	18.13	298	38.60
18″	3146	320	10.17	30	0.95	54	1.72	212	6.74	296	9.41	482	15.32	1098	34.90
19	2083	123	5.90	95	4.56	43	2.06	96	4.61	234	11.23	602	28.90	959	46.04
20†	2529	249	9.85	93	3.68	42	1.66	66	2.61	201	7.95	247	9.77	697	27.56
total	29210	2787	9.54	1304	4.46	755	2.58	1673	5.73	3728	12.76	4021	13.77	10536	36.07

† Sample 20 (Mannar) includes 314 individuals with unclassified spirals which appear in the total, but not in columns 1–7.

It is obvious that, for ladders as a group, neither variance ratio comes anywhere near the 5 % point of significance. The situation is similar for the ratio of 'good'/all ladders. It is not surprising that an analysis of variance for the two other primary spirals, spiral tongues and yellow spirals, yields a similar result, as follows

	d.f.	spiral tongues mean square	yellow spirals mean square
within populations	1	0.001960	0.000813
between populations	4	0.000908	0.001369
error	4	0.000623	0.004166

The conclusion thus seems justified that there is no reason to incriminate stable local differences to account for the inter-population differences observed. As in the case of the spiral versus the non-spiral classes, there is no evidence that anything but 'error' variance is at work, whatever that may mean in physiological terms.

Purple-tipped tongues (*p.t.t.*)

As already mentioned, the tips of spiral tongues in zones 2, 4, 6 are often picked out in bright red or purple (figure 30*b*, *c*, plate 3) as may also happen in ladders and yellow spirals in places where tongues are present. P.t.t. can also be classified easily in blacks and in purple spirals. Except occasionally in old animals, p.t.t. presents no difficulties in classification. Expressed as a percentage of all primary spirals (including purple spirals), the mean incidence in the 18 Ceylon populations and sub-populations (table 5) is 19.67 %. Though there is some evidence

Table 5. Purple-tipped tongues (p.t.t.), expressed as a percentage of all snails with primary spirals, including purple spirals

	primary spirals	p.t.t., *n*	p.t.t. (%)
Pitipana, Negombo	720	148	20.56
Chilaw	582	107	18.38
Kalpitiya	221	58	26.24
Vakarai	744	177	23.79
Batticaloa	651	109	16.74
Trincomalee A′	262	61	23.28
Trincomalee A″	1212	227	18.73
Trincomalee B′	120	19	15.83
Trincomalee B″	312	81	25.96
Trincomalee C′	274	51	18.61
Trincomalee C″	431	71	16.47
Trincomalee D′	188	32	17.02
Trincomalee D″	993	200	20.14
Mutur	1219	230	18.87
Trincomalee E′	326	64	19.63
Trincomalee E″	1172	208	17.75
Tondaimanar	1003	199	19.84
Mannar	1010	208	20.59
total	11440	2250	19.67

of heterogeneity ($\chi^2_{17} = 29.28$; $P = 0.03$), it appears to be slight in extent. This is confirmed by an analysis of variance of the 10 Trincomalee populations and sub-populations, as follows

	d.f.	mean square
within populations	1	0.000220
between populations	4	0.000492
error	4	0.001724

The error variance thus exceeds both the within and the between populations variance. Hence again, for p.t.t., the whole of the Ceylon material may be regarded as a single homogeneous super-population.

Purple spirals

This characteristic variant is generally classifiable sharply and probably conditioned by a single gene. Typically, zones 1 and 5 are solidly covered by deep purple (figures 33 and 35*d*, plate 4; figure 15*a*, *d*, *f*). Often, the continuity of the purple is interrupted by roundish holes through which the underlying background colour is visible (e.g., figure 15*e*), and sometimes there are so many such holes as to give the purple ribbon a speckled appearance. The nature of these holes is revealed particularly in individuals from Trincomalee D (population 16) in which the purple spirals are often reduced to a greater or lesser extent; they may be interrupted or come to an end prematurely, either abruptly or gradually, and the ribbon in zone 5 may be narrowed down to a mere pencil-line. So one can often see what is hidden underneath the purple bands: in zones 1 and 5, there are often (but not always) corresponding ribbons of small tongues (figure 15*g*–*i*); and the holes correspond to tongues which have not been filled in. Not rarely, the purple is narrower than the zones of small tongues so that the tongues peep out from under the margin in the form of 'clubs' (figure 15*c*, *i*); in such cases, the distinction from shells with primary spiralization (figure 15*d*) may become difficult.

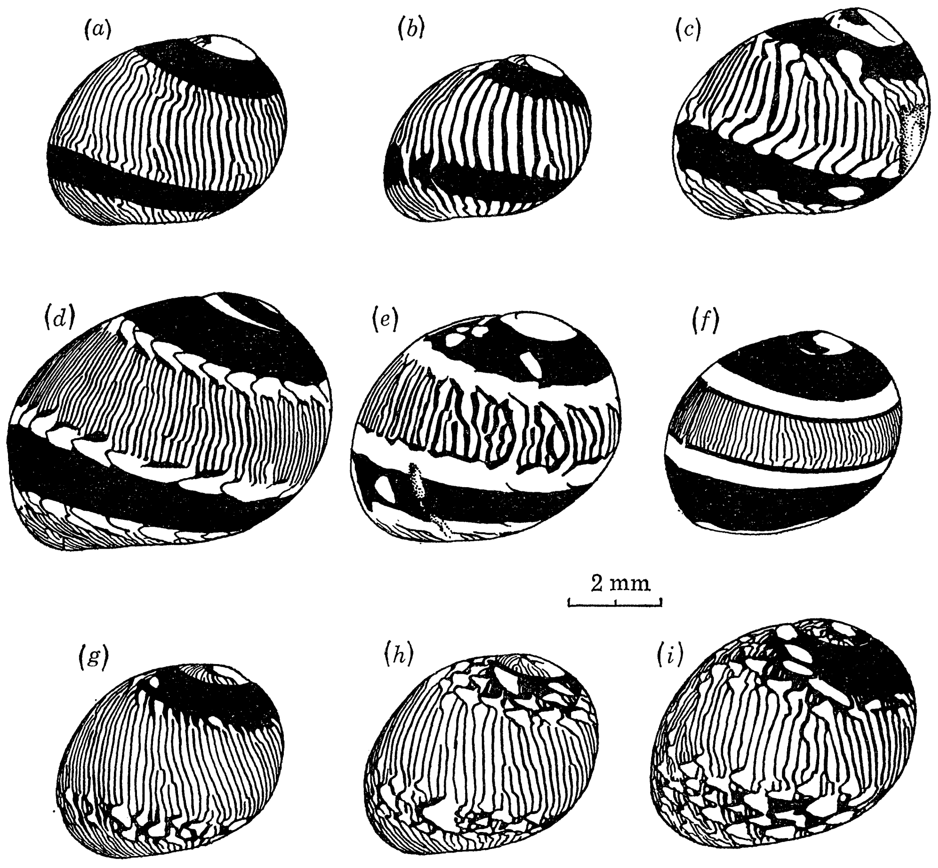


FIGURE 15. Purple spirals. (*a*) Associated with f.t.l.; (*b*) with c.t.l.; (*c*) with 'clubs' adjacent to the purple ribbons; (*d*) with spiral tongues and p.t.t.; (*e*) with yellow spiral; and (*f*) with ladder. (*a–c*), (*e*) and (*f*) from Mutur (population 17), (*d*) from Batticaloa (population 12). (*g–i*) individuals from Trincomalee D (population 16) in which reduction of the purple reveals the underlying zones of little tongues.

Purple spirals may be combined with fine or coarse transverse lines and among the spirals with spiral tongues (with or without p.t.t.), with yellow spirals and with ladders (figure 15*a–f*). This is in agreement with expectation for a single gene for this variant. Enumeration of these types from the east coast of Ceylon gives the following picture (figures in brackets refer to p.t.t.)

purple spirals with non-spiral variants	435
purple spirals with spiral tongues	28 (16)
purple spirals with yellow spirals	23
purple spirals with ladders	23 (5)
total	509

There is a considerable excess of non-spirals and a corresponding deficiency of primary spirals. As the distinction between non-spiral variants with 'clubs' and spiral tongues is not always sharp, let us confine ourselves to yellow spirals and ladders; taken together, these amount to 46/509 or 9.04 %; in the absence of purple spirals (table 4), they total 26.54 %. There is thus a striking interaction between purple spirals and primary spiralization. As described above, the majority of purple spirals sit on ribbons of small tongues in zones 1 and 5; if these ribbons are formed at the expense of primary spiralization in zones 2, 4, 6, this would account for the interaction just described. As purple spirals can occur in the absence of the ribbons of small tongues in zones 1 and 5, the latter are evidently secondary: they cannot be the physiological cause for the formation of the purple spirals.

Table 6. Purple spirals on the east and west coast of Ceylon

			purple spirals	
		total	*n*	%
East coast	Vakarai	2151	42	1.95
	Batticaloa	1751	39	2.23
	Trincomalee A	3834	89	2.32
	Trincomalee B	1108	16	1.44
	Trincomalee C	1772	46	2.60
	Trincomalee D	3300	69	2.09
	Mutur	3258	80	2.46
	Trincomalee E	3918	88	2.25
	Tondaimanar	2083	40	1.92
	total	23176	509	2.20
West coast	Pitipana, Negombo	1618	0	—
	Chilaw A	1334	0	—
	Chilaw B	~ 20000	3	0.015
	Kalpitiya	553	0	—
	Mannar	2529	1	0.040
	total	26034	4	0.015

The incidence of purple spirals differs greatly as between the east and west coasts of Ceylon; these are given separately in table 6. The difference is beyond the need of significance tests. The east coast populations are homogeneous ($\chi^2_8 = 12.92$; $P = 0.11$). So are those on the west coast, where three individuals were found in a total of about 20000 from Chilaw B, and another specimen in the remaining 6034 snails.

The purple spirals from Trincomalee D″ include one with an additional ribbon in zone 3. If purple spirals is due to a single semi-dominant gene, the gene frequency would be $q = 0.0111$, and in a sample of 509 individuals, 2.856 homozygotes would be expected. If this were the whole information available, the snail with three purple spirals might well be suspected of being the homozygote. However, this can scarcely be so, as no similar animal has been found among over 1000 purple spirals from Malaya–Singapore and from Hong Kong.

Black

The black colour (figure 34, plate 4) is brought about by close spacing of the transverse pattern so that eventually the background colour almost disappears, except where it is uncovered in tongues. The closer the spacing of the transverse lines, the narrower the tongues become; indeed, in some shells, they are almost dagger-like. Some shells are solidly black, others have many small tongues (sometimes with secondary spiralization) and a few are primary spirals (sometimes with p.t.t.). The closeness of the spacing of the transverse pattern varies, and in a minority (probably less than 10 %), classification is somewhat subjective. The incidence in the Ceylon populations is given in table 7. It is clearly not homogeneous ($\chi^2_{12} = 114.6$; $P < 10^{-10}$). The main sources of heterogeneity are Trincomalee D and Mannar in which blacks are either very rare or absent. If these two populations are omitted, there are 356 blacks in a total of 23381 animals, or 1.52 %, and this group is no longer seriously heterogeneous ($\chi^2_{10} = 20.14$; $P \approx 0.03$).

Table 7. Incidence of black in *Clithon* from Ceylon

		black			
	total	Non-spiral	spiral	total	%
Pitipana, Negombo	1618	10	7	17	1.05
Chilaw A	1334	16	3	19	1.42
Kalpitiya	553	4	0	4	0.72
Vakarai	2152	25	7	32	1.49
Batticaloa	1751	24	12	36	2.06
Trincomalee A	3834	39	19	58	1.51
Trincomalee B	1108	14	4	18	1.62
Trincomalee C	1772	27	5	32	1.81
Trincomalee D	3300	5	1	6	0.18
Mutur	3258	42	8	50	1.53
Trincomalee E	3918	54	14	68	1.74
Tondaimanar	2083	18	4	22	1.06
Mannar	2529	0	0	0	0.00
total	29210	278	84	362	1.239

In what way do the Trincomalee D and Mannar populations differ from the rest? It can hardly be a coincidence that these two populations are the only ones in which the snails were living and feeding on 'eelgrass'. It is not yet known whether the scarcity of blacks is a result of selection or whether on an eelgrass diet many potential blacks overlap normal.

The nature of the shell pigments of *Clithon* is unknown. It is uncertain whether black and purple are chemically distinct, or whether they are the same substance in different concentrations or dispersions, or whether perhaps purple is a precursor substance to black. The reduction of black in Trincomalee D and Mannar, and the anomalies of the purple spirals in Trincomalee D mentioned in the preceding section could thus have a common cause. Unfortunately, the matter cannot be decided by reference to the only other 'eelgrass' population, Mannar. But a single purple spiral has been found in that locality; its phenotype was essentially normal and thus gives no information either way.

Black may be conditioned by a single gene, but as the classification is not quite sharp, alternative interpretations are by no means ruled out.

Rare variants

The variants described above occur in all *Clithon* populations in Ceylon. A few rarities will be briefly mentioned here; their significance will be discussed in a later section.

A general dilution of the line pattern is common in the eastern provinces where it will be dealt with in more detail. A single individual of 'little tongues, yellow' and typical in every respect was found in Pitipana, Negombo (8D). In the same sample and in Chilaw (9A), a single transparent and honey-coloured shell each was found (an intermediate between spiral tongues and ladders and a c.t.l., respectively). The affiliations of six 'pale' yellow spirals from Tondaimanar are uncertain.

The tongues in *Clithon* from Ceylon are generally small. As will be described below, in the other provinces variants with more widely spaced transverse patterns ('zebra' and 'tiger') are common, along with their equivalents among the tongues ('large' and 'giant' tongues). In the large sample from Chilaw (9B), there are 43 zebras and 21 large tongues among about 20000 individuals, or about 1:500 and 1:1000 respectively; no tigers were encountered, but there was a single juvenile shell with giant tongues and p.t.t. in Chilaw (9A).

A search for rare variants (including purple spirals) was the rationale for collecting the monster sample 9B.

Summary of the Ceylon populations

As explained in some detail in preceding sections, the classification of the *Clithon* variants from Ceylon, with the exception of purple spirals, p.t.t., dilution and perhaps black, is subject to errors whose magnitude differs from case to case. Little weight can be attached to the distinction between f.t.l. and c.t.l., and within the spiral group there are also numerous intermediates. Summing over the whole 18 populations and sub-populations, the following mean values are obtained; exceptions are the values for zebras and large tongues which are based on the large Chilaw population (9B) only.

f.t.l.	55.75 %	
c.t.l.	3.63	
zebra	0.22	
large tongues	0.11	
	59.87	(including 141 non-spirals with change of pattern from Chilaw)
spiral tongues	9.54	
ladders	12.76	
yellow spirals	13.77	
	37.14	(including 314 unclassified primary spirals from Mannar. 19.67 % of this group are p.t.t.)
dilution	0.01	
purple spirals	1.75	
black	1.24	
	3.00	(2.20 and 0.015 % purple spirals on east and west coast, respectively)

Comparing the populations with each other, there are two major differences. Purple spirals are strikingly more common on the east than on the west coast of Ceylon. However, there is no evidence for heterogeneity either between the 14 east coast or between the four west coast populations. The regional differentiation as regards purple spirals is thus completely tidy and orderly. In the case of black, two populations stand out from the rest. In this instance, there is evidence that ecological factors (eelgrass) may be involved. The remaining 16 populations again show little sign of heterogeneity.

The axial (non-spiral) patterns in Ceylon are overshadowed by f.t.l. As this cannot be separated sharply from c.t.l., and as the remainder is a small minority, it is convenient to pool all these phenotypes. Inter-population differences as to the incidence of small tongues can also be disregarded as they are largely age effects. The essential unity of the group is strikingly illustrated by the ease with which one type of pattern can change into another in one and the same individual. Treating all axial patterns (other than those in purple spirals and blacks) as one group, their overall incidence is just under 60 %. This does not change with age, but the dispersion round the mean is too great to be accounted for in terms of sampling errors or in terms of the small uncertainty inherent in separating spirals from non-spirals. An analysis of variance based on the 10 populations and sub-populations from Trincomalee shows that neither the intra-population variance (i.e. that between adults and juveniles from the same locality) nor the inter-population variance (i.e. that between different localities) significantly exceeds the error variance. It follows that the whole of the variance can be regarded as the result of transient changes without permanence either in space or in time.

What is true for the axial group of course equally applies to the spiral types as a group, as between them these two categories account for 97 % of the whole material.

Despite many overlaps, spiral tongues, ladders and yellow spirals are characteristic phenotypes which are common in all populations from Ceylon. As, in some populations at least, they can easily be separated from each other, they are clearly biological realities. In this respect they are quite unlike, say, the symmetrical 'Dutch' spotting type in the mouse: spotting in the mouse (and distinct from that in rabbit and rat) is essentially irregular, and a symmetrically marked animal is a rarity. The three spiral types here distinguished are common everywhere and hence evidently represent physiologically probable states (though the degree of that probability varies as between populations). An analysis of variance analogous to that in the axial patterns reveals a similar situation, i.e. the variance for these three phenotypes is essentially an 'error' variance.

Finally, the purple-tipped tongues (p.t.t.) which are common in spiral tongues and less often encountered in the other spiral types, occur with about the same frequency in all the populations which have been sampled.

Looking at the populations as a whole, there is a surprising uniformity. One population is very much like another, and with the exception of purple spirals in east and west, almost the only major differences between populations involve age and hence the mean incidence of 'many small tongues'. Field work gradually becomes tedious, and one starts to long for something really different for a change.

MALAYA–SINGAPORE AND HONG KONG

The *Clithon* populations from Malaya and Singapore and from Hong Kong differ strikingly from those in Ceylon. The two eastern provinces have so much in common that it will be convenient to consider them together. The localities where collections were made are shown in figures 16 and 17. The material is summarized in table 8. The snails from the eastern provinces are smaller than those from Ceylon (table 2). Whether this difference is significant or not, it probably does not appreciably affect the main topics of this investigation.

It is obvious by inspection that the snails from the eastern provinces are more variable and more colourful than those from Ceylon. In the eastern snails there are many widely spaced transverse patterns which are almost absent in Ceylon, and in these the orange or yellow background dominates the general appearance of the shells. Secondly, whereas in Ceylon the line pattern is nearly always a sombre dark-brown or black, in the eastern provinces various shades of purple are common, some of them quite bright. To illustrate the general appearance of these shells, colour photos of individuals from Singapore (21A) are given in plates 1–4. They are

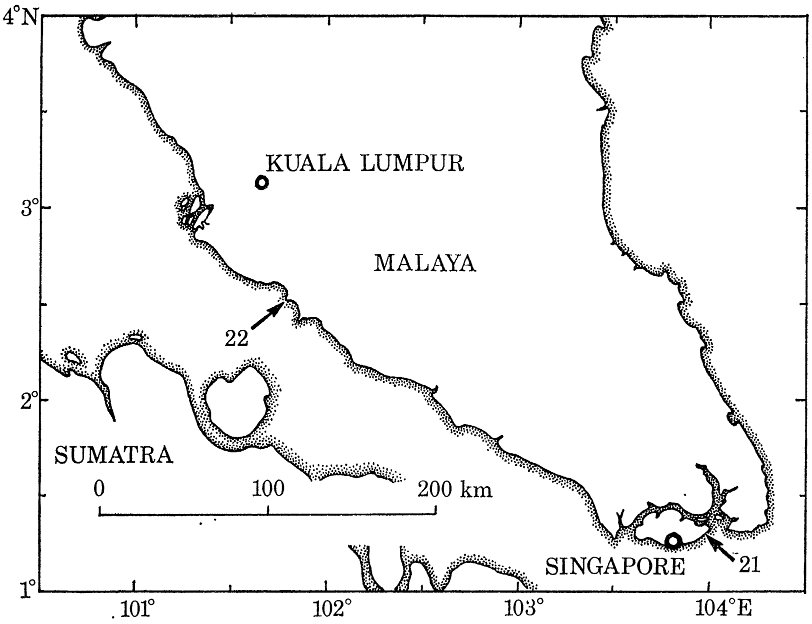


FIGURE 16. Map of the southern part of Malaya and of Singapore. The location of Mata Ikan, Singapore (21) and of Port Dickson, Malaya (22) is indicated.

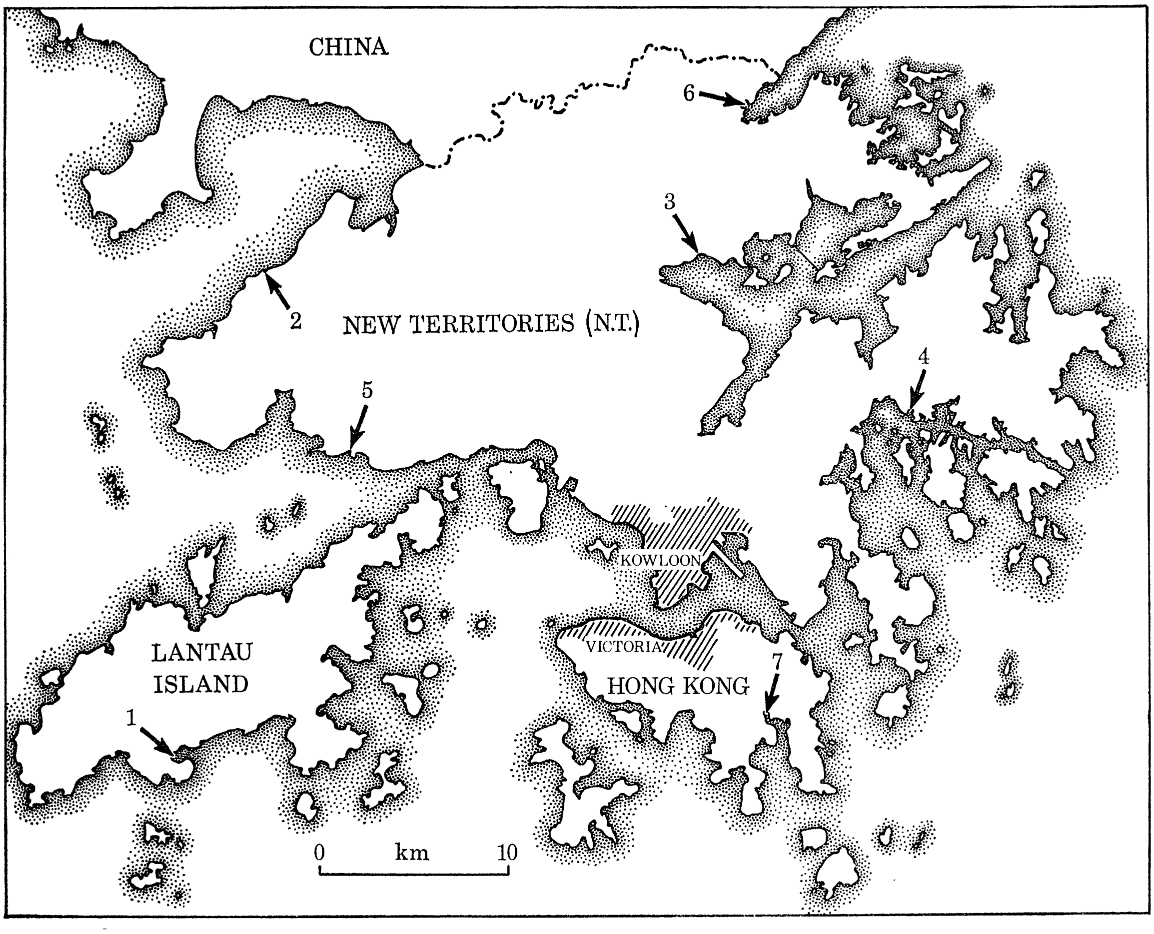


FIGURE 17. Map of Hong Kong. The localities in which the various populations were collected are indicated as follows. 1, Shui Hau; 2, Ngau Hom Sha, Deep Bay; 3, Ha Hang, Tai Po Market, Tolo Harbour; 4, Tai Mong Tsai, Sai Kung; 5, JV 919 766; 6, Lap Wo Tsuen, Starling Inlet; and 7, Tai Tam Bay.

Table 8. The *Clithon* populations from Malaya–Singapore and from Hong Kong

	n	weight in mg
21A Mata Ikan, Singapore	270	43.7
21B Mata Ikan, Singapore	2022	116.9
22A Port Dickson, Malaya	2255	41.7
22B Port Dickson, Malaya	1786	74.5
22C Port Dickson, Malaya	5962	40.2
sub-total	12295	—
1 Shui Hau, Lantau Island, H.K.	1148	25.8
2 Ngau Hom Sha, Deep Bay, N.T.†	1213	84.1
3 Ha Hang, Tai Po Market, Tolo Harbour, N.T.	1795	41.5
4 Tai Mong Tsai, Sai Kung, N.T.	1239	76.3
5 JV 919 766, N.T.	2436	36.5
6 Lap Wo Tsuen, Starling Inlet, N.T.	1173	63.3
7′ Tai Tam Bay, Hong Kong Island	1526	75.9
7″ Tai Tam Bay, Hong Kong Island	424	13.2
sub-total	10954	—

† N.T., New Territories, Hong Kong.

shown in groups of six which might appear extravagant. However, it is difficult in any other way to demonstrate the essential uniformity of some and the wide range of variability in other categories. The eastern populations are not only more colourful, but also more variable within themselves. In the non-spiral group, this is due to the presence of widely spaced patterns in addition to the closely spaced ones, and to the presence of large and giant tongues in addition to small ones; there is also the new category of dilution. Among the primary spirals, there are two types which are rare or absent in Ceylon (black-and-white spirals and narrow spirals); and the yellow spirals as a group present a much tidier pattern. On the other hand, ladders which are so typical and ubiquitous in Ceylon are completely absent. It will be convenient to introduce first the new non-spiral and then the new spiral types as these two major divisions are presented in turn.

The axial patterns

The incidence of the non-spiral (axial) patterns in the two eastern provinces is given in table 9, and a comparison between all three provinces in an abbreviated form in table 10. Having regard to the fact that in roughly 1–2 % of the snails the distinction between non-spirals and spirals is somewhat subjective, there cannot be any doubt that the ratio of the two is substantially the same throughout, i.e. about 62:38.

The non-spiral group in Malaya–Singapore and in Hong Kong differs from that in Ceylon in that it includes many widely spaced patterns like zebras, tigers, and large and giant tongues. In this shift from closely to more widely spaced patterns, f.t.l. is the sole loser. The coarser type of pattern (c.t.l.) which in Ceylon occurs mainly in juveniles and is difficult to separate from f.t.l., tends to persist into adult life and there is less overlapping.

Table 9. The non-spiral (axial) variants in Malaya–Singapore and in Hong Kong

		f.t.l.		c.t.l.		zebra		tiger		large and giant tongues		total axial patterns	
	total	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
21A	270	57	21.11	31	11.48	1	0.37	27	10.00	40	14.81	156	57.78
21B	2022	649	32.10	36	1.78	1	0.05	160	7.91	129	6.38	975	48.22
22A	2255	621	27.54	121	5.37	5	0.22	157	6.96	259	11.49	1163	51.57
22B	1786	528	29.56	36	2.02	7	0.39	155	8.68	153	8.57	879	49.22
22C	5962	1637	27.46	347	5.82	19	0.32	465	7.80	477	8.00	2945	49.40
total	12295	3492	28.40	571	4.64	33	0.27	964	7.84	1058	8.61	6118	49.76
1	1148	199	17.33	68	5.92	24	2.09	181	15.77	81	7.06	553	48.17
2	1213	270	22.26	59	4.86	10	0.82	190	15.66	118	9.73	647	53.34
3	1795	296	16.49	149	8.30	85	4.74	153	8.52	106	5.90	789	43.96
4	1239	257	20.74	73	5.89	4	0.32	195	15.74	85	6.86	614	49.56
5	2436	414	17.00	101	4.15	57	2.34	368	15.11	220	9.03	1160	47.62
6	1173	266	22.67	68	5.80	14	1.19	145	12.36	46	3.92	539	45.95
7′	1526	378	24.77	93	6.09	18	1.18	241	15.79	133	8.72	863	56.55
7″	424	80	18.87	27	6.37	—	—	50	11.79	31	7.31	188	44.34
total	10954	2160	19.72	638	5.82	212	1.94	1523	13.90	820	7.49	5353	48.87

Table 10. Axial and spiral patterns in the three provinces (except those in dilution, purple spirals, black, pink and purple)

	axial		spiral		
	n	%	*n*	%	total
Ceylon	17489	61.72	10850	38.28	28339
Malaya–Singapore	6118	63.16	3568	36.84	9686
Hong Kong	5353	61.22	3391	38.78	8744
total	28960	61.92	17809	38.08	46769

Zebras and tigers

The widely-spaced transverse patterns include 'zebras' (which rarely also occur in Ceylon) and 'tigers'. As the name suggests, zebras (figure 23*e*, plate 1) have alternating stripes of black and white which are wider than those in the coarse transverse pattern (figure 22, plate 1); the separation between the two categories is, however, not quite sharp. The relative areas covered by black and white respectively are roughly the same in both, zebras having fewer but wider stripes. The stripes of zebras are usually essentially transverse, but curvatures (similar to those in figure 11*a* and *b*) sometimes suggest an underlying spiral tendency. As they cannot be separated satisfactorily on the basis of this criterion, all zebras have been treated as non-spiral. The intervals between the black stripes of zebras are generally white (for some more details see appendix 2). Sometimes, the diffuse orange or yellow colour underneath the 'whitewash' begins to show through; tigers by contrast, lack 'whitewash' between successive stripes.

In both eastern provinces, tigers (figure 23*a–d*, *f*, plate 1) are much commoner than zebras, and their separation from each other is rarely in doubt. In typical tigers, the number of transverse stripes is smaller than that in zebras, the stripes themselves are much thinner, and the intervening spaces typically orange or yellow; in old individuals, they take on a olive-greenish tinge. The majority of tigers have a simple transverse pattern, but by imperceptible degrees, curvatures in these lines reveal underlying spiral tendencies which, however, generally do not lead to the formation of proper spiral tongues; however, in a minority of specimens, the tips of the curvatures in zones 2, 4, 6 become purple-tipped (p.t.t.) which leaves no doubt as to their true nature. Although it is thus clear that spiral and non-spiral forms are present among the tigers, their separation is not practicable and tigers have thus been treated as non-spiral throughout. This introduces a small (but, it is hoped, constant) error into the estimates of the incidence of non-spirals, as mentioned in a previous section. The p.t.t. of tigers will be treated below, together with that feature in other categories. When the number of transverse lines is very low and their course correspondingly less well controlled, the separation from 'giant tongues' occasionally becomes difficult; while there are thus probably some intergrades between these two classes, their number is small as compared with the named types.

Large and giant tongues

Whereas 'large' and 'giant' tongues are very rare in Ceylon, they are common in the eastern provinces (figures 26–28, plate 2). These two categories cannot be sharply separated from each other and have thus been pooled. Their separation from the 'small' tongues (figure 25, plate 2) is usually fairly easy though intergrades occasionally occur. Large tongues often and giant tongues regularly originate directly at the suture and with a wide sweep may cover a large part and sometimes the whole circumference of a whorl. In the presence of large tongues, spiral tendencies like those in spiral tongues are often more difficult to recognize, and this adds another uncertainty to the delineation of the spiral group which is not present in Ceylon. However, it is much the same in Malaya–Singapore and in Hong Kong, and whereas it presumably leads to some underestimation of the incidence of spirals, the error is probably small compared with the size of the group as a whole.

The incidence of the non-spiral group

The incidence of the main non-spiral types is summarized in table 9. The chief difference between Ceylon and the eastern provinces is the prevalence of the widely spaced patterns in the latter. The shift in that direction is less in Malaya–Singapore than in Hong Kong. The incidence of zebras and tigers combined is 8.11 and 15.84 % respectively, and a similar though smaller difference is already present in the coarse transverse lines (c.t.l.). For f.t.l. the situation is of course reversed (28.40 and 19.72 % respectively). The incidence of tigers in Malaya–Singapore shows no signs of heterogeneity ($\chi^2_4 = 5.341$; $P \approx 0.25$), but that in Hong Kong is clearly heterogeneous ($\chi^2_7 = 55.545$; $P \approx 10^{-9}$). This is entirely due to the Ha Hang population (no. 3) in which difficulties in classifying the widely spaced patterns were immediately noticed; that population has the lowest incidence of tigers, but the highest of both c.t.l. and zebras. If that population is omitted, the incidence of tigers in the remainder is 14.97 % and no longer heterogeneous ($\chi^2_6 = 10.277$; $P = 0.12$). Whereas both provinces may thus be regarded as homogeneous as to tigers, their means differ highly significantly from each other.

The other variants in table 9 cluster less closely round the respective means within provinces; the inter-population differences thus cannot be accounted for by sampling errors alone. Inconsistencies of classification in these less well-defined variants no doubt make a contribution, but this is not sufficient in itself to account for the whole of the heterogeneity. As in the case of the Ceylon populations discussed above, there seems to be some heaving up and down round essentially stable mean values. The overall picture is, however, clear – substantial uniformity within provinces, but major differences between provinces. Those between Ceylon and the eastern provinces are immediately obvious on inspection, those between Malaya–Singapore and Hong Kong obtrude themselves while one is collecting, particularly the high incidence of tigers in Hong Kong.

Primary spirals

As already mentioned, the overall incidence of primary spirals in Malaya–Singapore and in Hong Kong is substantially the same as that in Ceylon. There are, however, considerable differences in the types of spirals encountered. Ladders which are so characteristic in Ceylon are completely absent. Yellow spirals are present regularly (figure 31*a*, *c*, *d*, *e*: figure 32*a–e*, plate 3), but the transverse pattern is generally more orderly than that of Ceylon yellow spirals. Spiral tongues of many kinds are also regularly present (figures 29 and 30, plate 3), often with purple-tipped tongues (p.t.t.), as in figure 30*b* and *c*, plate 3.

There is, however, a twin pair of spiral types with occurs in all populations of the eastern provinces examined and which is rare or absent in Ceylon. What appears to be the more basic form may be called 'black-and-white spirals' (figure 18). These are similar to yellow spirals in that the transverse pattern in zones 1 and 5 appears with considerable delay and the latter sometimes not at all. However, whereas in yellow spirals the zones 2, 4, 6 are of a transparent yellow or orange colour, they are in the present form solidly covered by whitewash (see appendix 2) so that the overall appearance of the shells is that indicated by their name. There are occasional intergrades. For instance, the shell in figure 31*b*, plate 3, has so little whitewash that the underlying yellow shows through; similarly, in figure 18*a*, *b*, zones 5 and 7, respectively, are not covered by white. However, the separation of black-and-white spirals from yellow spirals is generally fairly sharp. As indicated in figure 18, there are all intergrades between

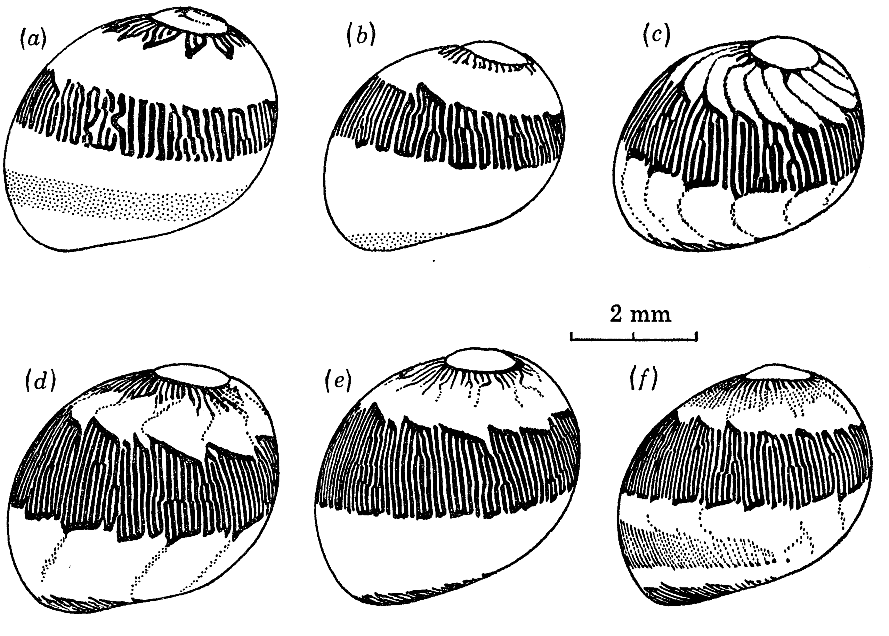


FIGURE 18. Black-and-white spirals. The overall appearance of the shells is black and white, except in the finely stippled zones 5 and 7 in (*a*) and (*b*) respectively in which the underlying transparent yellow of the shell shows through the whitewash. In (*f*), a separate zone 5 makes its appearance by the break-up of the white band which represent the zones 4, 5, 6. This band is still solidly white in the other shells except in (*a*) where a future separation is foreshadowed by the semi-transparent yellowish zone in the position of 5. Port Dickson, Malaya (22C).

continuous spirals and spiral tongues, and the latter often show in a rather spectacular manner p.t.t. on their white background.

The other category is 'narrow spirals' (figure 30*f* and 31*f*, plate 3), again covering the whole range from spiral tongues to continuous spirals with all intergrades. It is not certain whether some of these shells are narrow spirals from the onset. Many of them clearly arise from black-and-white spirals by the break-up of the white band representing zones 4 + 5 + 6. In the case of the animals shown in figure 18*a*, *f*, zone 4 would have remained fairly wide, and the animals would scarcely have been included among narrow spirals. But in the two shells shown in figure 19 which started as black-and-whites, the break-up of the lower white band leads to narrow spirals 4 and 6. In these and similar cases, the spirals often correspond in width accurately to the 'chalk-line' (appendix 2) which in some animals occupies the middle of zones 2, 4 and 6, and particularly of zone 4. The separation of narrow spirals from ordinary spiral tongues is not always sharp and occasional mis-classifications are unavoidable. But the reality of the category as such is not in doubt. On the other hand, this does not seem to be so in Ceylon. The width of zones 2, 4, 6 is of course variable, and in the large numbers examined, occasional specimens may have overlapped the range of narrow spirals in the eastern provinces. They did not impress themselves as a separate category, however, and they were certainly very rare. To avoid being dogmatic, we have above referred to their incidence in Ceylon as 'rare or absent'. No attempt has been made to isolate these extreme variants as a separate class.

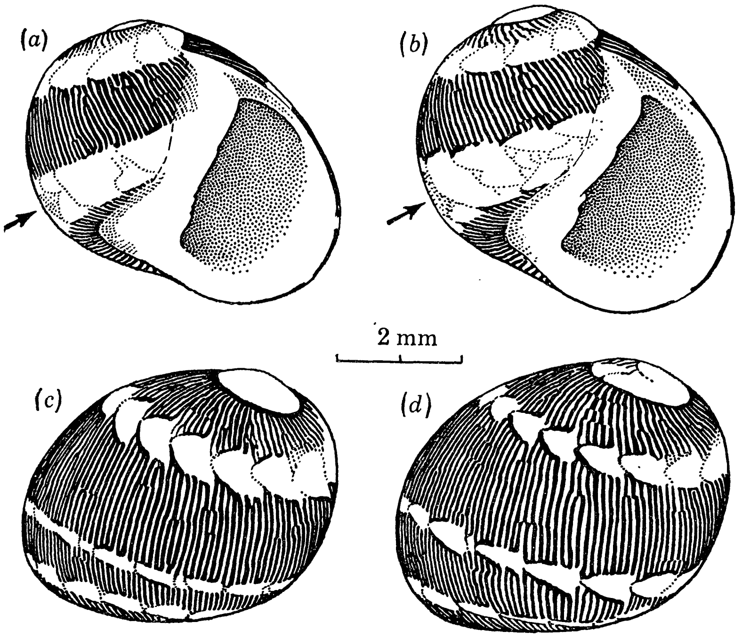


FIGURE 19. Transition from black-and-white spirals to narrow spirals at the points indicated by arrows. The actual break-up is usually preceded by the formation of tongues (often in several rows) which are visible structurally, but not pigmented. Port Dickson, Malaya (22C).

The incidence of the spiral variants

The incidence of the spiral variants discussed in the preceding section is summarized in table 11. The frequency of black-and-white spirals is given in column 3 and that of narrow spirals in column 4. As many, if not most narrow spirals are ontogenetically derived from black-and-white ones, and as the two cannot be sharply separated from each other, the sum of these

TABLE 11. THE MAIN SPIRAL VARIANTS IN MALAYA–SINGAPORE AND IN HONG KONG (1, SPIRAL TONGUES; 2, YELLOW SPIRALS; 3, BLACK-AND-WHITE SPIRALS; 4, NARROW SPIRALS; 5, 3 AND 4 COMBINED.)

		1		2		3		4		5		
	total	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	total %
21A	270	44	16.29	18	6.67	1	0.37	1	0.37	2	0.74	
21B	2022	460	22.75	155	7.67	12	0.59	35	1.73	47	2.32	
22A	2255	360	15.97	149	6.61	27	1.20	65	2.88	92	4.08	
22B	1786	384	21.50	139	7.78	15	0.84	36	2.02	51	2.86	
22C	5962	900	15.10	494	8.29	87	1.46	186	3.12	273	4.58	
total	12295	2148	17.47	955	7.77	142	1.15	323	2.63	465	3.78	29.12
1	1148	189	16.46	81	7.06	40	3.48	14	1.22	54	4.70	
2	1213	286	23.58	33	2.72	39	3.22	8	0.66	47	3.88	
3	1795	363	20.21	97	5.40	59	3.29	31	1.73	90	5.02	
4	1239	269	21.71	65	5.25	36	2.91	10	0.81	46	3.72	
5	2436	518	21.27	207	8.50	65	2.67	17	0.70	82	3.37	
6	1173	290	24.72	29	2.47	32	2.73	16	1.36	48	4.09	
7′	1526	341	22.34	56	3.67	40	2.62	12	0.79	52	3.41	
7″	424	113	26.65	22	5.19	9	2.12	4	0.94	13	3.06	
total	10954	2369	21.63	590	5.39	320	2.92	112	1.02	432	3.94	30.96

two classes is given in column 5. That sum is clearly about the same in Malaya–Singapore and in Hong Kong, the joint percentage being 3.86. But, though the separation is not sharp, in the hands of a single observer a tolerably consistent if arbitrary classification is possible, and this reveals a peculiar situation. Comparing columns 3 and 4, it is obvious that in Malaya–Singapore narrow spirals consistently predominate (ignoring 21A with only one of each), but that in all 8 Hong Kong populations the situation is reversed, with black-and-white ones being much the commoner. The differences between the two provinces are so massive and consistent that they cannot possibly be accounted for in terms of mis-classification. Once again, there is homogeneity within, but heterogeneity between provinces. Of course, it is unknown why transition from black-and-white to narrow spirals is so much commoner in Malaya–Singapore than in Hong Kong.

TABLE 12. COMPARISON BETWEEN THE PRIMARY SPIRAL TYPES IN THE THREE PROVINCES

	spiral tongues	ladders	yellow spirals	black-and-white and narrow spirals	total
Ceylon	9.60	12.78	13.74	—	36.12
Malaya–Singapore	17.47	—	7.77	3.78	29.02
Hong Kong	21.63	—	5.39	3.94	30.96

The spiral tongues in the eastern provinces differ from those in Ceylon mainly by the fact that they include many large-tongued specimens (e.g. figure 29*a–e* and figure 30*b*, plate 3) which are virtually absent in Ceylon. Spiral tongues are commoner in Hong Kong than in Malaya–Singapore (21.63 compared with 17.47 %). The situation is reversed for yellow spirals (5.39 compared with 7.77 %). In some populations (notably 21A, 3 and 5), the majority of these animals show continuous spirals, but in other populations (particularly in 22A, B and C and in 2, 4, 6 and 7) many or most are more nearly spiral tongues.

A comparison between the primary spirals in the three provinces is made in table 12, which is based on tables 4 and 11. In Ceylon, ladders and yellow spirals considerably overlap spiral tongues, and the same applies to yellow spirals in the eastern provinces. A better classification would perhaps reduce the differences between populations both as regards spiral tongues and as regards yellow spirals. The following differences between provinces are firmly established.

(1) Ladders are confined to Ceylon.
(2) Black-and-white and narrow spirals are (? very nearly) confined to eastern provinces.
(3) The ratio black-and-white/narrow spirals differs greatly as between Malaya–Singapore and Hong Kong.
(4) The yellow spirals in Ceylon are much untidier than those in the eastern provinces.

Is there a relation between ladders in Ceylon and black-and-white and narrow spirals in the eastern provinces? The two have one feature in common: the almost complete absence of background patterns of small tongues and the resulting tidiness of the transverse pattern. The suspicion arises that these mutually exclusive phenotypes may in fact be equivalent to each other. If the zones 2, 4, 6 in narrow spirals were a little wider and flanked by uprights, perfectly creditable ladders would result; but black-and-white spirals resemble yellow spirals in the way zones 3 and 5 tend to arise rather later. Hence judgment had better be suspended for the time being.

Purple-tipped tongues

Both in Ceylon and in the eastern provinces, the tips of spiral tongues are often vividly red or purple. This is in contrast to overall purple patterns which are common in the eastern region, but absent in Ceylon. P.t.t. is commoner in Hong Kong than in Malaya–Singapore (24.29 as compared with 17.04 %; table 13). A similar and indeed proportionately greater difference is

TABLE 13. PURPLE-TIPPED TONGUES (P.T.T.) IN SPIRALS, IN TIGERS AND IN LITTLE TONGUES, YELLOW

The significance tests at the bottom of the table refer to the totals of Malaya–Singapore compared with those of Hong Kong

		p.t.t.			p.t.t.		little tongues yellow	p.t.t.	
	spirals	*n*	%	tigers	*n*	%		*n*	%
21A	89	16	17.98	27	—		11	—	
21B	864	169	19.56	160	2		145	—	
22A	850	151	17.76	157	2		133	2	
22B	763	148	19.40	155	3		97	2	
22C	2453	371	15.12	465	11		335	3	
total	5019	855	17.04	964	18	1.87	721	7	0.97
1	419	87	20.76	181	8		49	1	
2	446	94	21.08	190	11		39	2	
3	732	222	30.33	153	8		61	2	
4	460	115	25.00	195	17		49	1	
5	978	214	21.88	369	17		88	2	
6	476	136	28.57	145	6		38	2	
7′	535	124	23.18	241	6		53	1	
7″	178	34	19.10	50	1		19	—	
total	4224	1026	24.29	1524	74	4.86	396	11	2.78
χ_1^2			74.48			15.453			5.259
P			$< 10^{-10}$			$< 10^{-4}$			0.022

found in p.t.t. of tigers and of little tongues, yellow, two variants which have otherwise been treated as 'non-spiral' (tables 9, 14). The incidence of p.t.t. in Ceylon is intermediate between that in the two eastern provinces. However, it differs from both of them significantly ($\chi_1^2 = 15.8$ and 40.6 for Malaya–Singapore and Hong Kong respectively). Although the absolute differences between the three values are not great (17.04, 19.67 and 24.29 %), they cannot be explained in terms of mis-classification and hence must be regarded as real.

TABLE 14. DILUTION: INCIDENCE IN MALAYA–SINGAPORE AND IN HONG KONG

	f.t.l. and c.t.l.	little tongues yellow	large and giant tongues	primary spirals	total	
					n	%
21A	—	11	—	—	11	4.07
21B	—	141	—	4	145	7.17
22A	3	114	6	11	134	5.94
22B	—	88	4	5	97	5.43
22C	13	264	20	51	348	5.84
total	16	618	30	71	735	5.98
1	—	35	14	6	55	4.79
2	—	39	—	—	39	3.22
3	—	46	12	3	61	3.40
4	—	49	—	—	49	3.95
5	18	70	17	1	106	4.35
6	—	38	—	—	38	3.24
7′	—	43	8	2	53	3.47
7″	—	16	3	—	19	4.48
total	18	336	54	12	420	3.83

Dilution

The first sample of *Clithon* to be examined (21A, Mata Ikan, Singapore) included a homogeneous and very characteristic group of snails which was given the name of 'little tongues, yellow' (figure 24, plate 1). The same phenotype has been found in all eastern populations since examined, and as it presented no difficulties in classification, it was at first regarded as a separate entity *sui generis*. As will be described presently, this phenotype is due to dilution of the melano-pigment (see appendix 2), and that dilution may also be associated with other patterns.

Rather rarely, dilute forms of f.t.l. or c.t.l. with few or no tongues are encountered; these are usually somewhat transparent and honey-coloured or orange in appearance. By far the commonest type is 'little tongues, yellow' which are yellow or orange at first, but gradually assume an olive-greenish hue like large tigers as they become larger and opaque. The dark line pattern almost disappears except where it is normally heaviest, i.e. near the tips of the tongues. Most individuals have many small tongues whose tips are outlined in white on the inside and in black on the outside (i.e. towards the aperture; see also appendix 2 and figure 20*e*). Sometimes the whole area of the small tongues is filled with white leuco-pigment so that the overall impression is that of a yellow or greenish snail dappled with white triangles. The black line round the tip of the tongues may disappear more or less completely so that the tongues are recognizable as white outlines only; this is indeed the case with most of the rest of the transverse pattern which is mainly of the fine (f.t.l.), but sometimes of the coarse (c.t.l.) variety. Some dilutes have large rather than small tongues and occasionally giant tongues or something close to the tiger pattern. Secondary spiralization occurs in a minority of 'little tongues, yellow', sometimes with p.t.t.: this may be an exception to the rule that p.t.t. is generally confined to primary spirals.

Primary spiralization nearly always occurs in the form of spiral tongues; these are usually quite narrow and often form ribbons of 2–3 minute tongues abreast rather than a single line; also, zone 5 tends to be filled in with small tongues. P.t.t. is sometimes encountered. Primary spirals usually have very little melano-pigment and the spiral tongues are often strikingly revealed in leuco-pigment. The incidence of dilution in relation to the other patterns is shown in table 14. Two facts stand out. Primary spirals which normally account for about 38 % are reduced to about 7 % in the aggregate of the two provinces. On the other hand, the background pattern of small tongues is greatly increased. Combining the data for Malaya–Singapore and Hong Kong for ordinary f.t.l., 3473/5652 or 61.45 % show many small tongues; among the dilutes, the ratio is 954/984 or 96.95 %. The net result is the great preponderance of 'little tongues, yellow' among the dilutes.

The incidence of dilutes in the two eastern provinces is given in table 14. There is no sign of heterogeneity in either province (Malaya–Singapore: $\chi^2_4 = 7.520$; $P = 0.11$; and Hong Kong: $\chi^2_7 = 9.294$; $P = 0.31$), but the two provinces differ highly significantly from each other (5.98 % compared with 3.83 %, with $\chi^2_1 = 52.8$). By contrast, dilution is very rare in Ceylon (see under Rare variants above).

Classification of dilution is generally easy, and as it occurs in company with most, if not all other patterns, it may be due to a single gene. The phenotype closest to it is pink (see below).

Purple spirals

In essentials, the purple spirals from the eastern provinces (figures 33 and 35*d*, plate 4) are similar to those from Ceylon. There is a similar tongue pattern underneath the purple, but in keeping with the generally wider spacing of patterns, the tongues tend to be so large that they usually project beyond the purple zones (see, for example, figure 33*e*, plate 4); this creates so many difficulties in identifying primary spirals (figures 33*a*, *b* and *d*) that attempts at a finer classification had to be given up. It is, however, beyond doubt that purple spirals can occur in company with all the other patterns. Completely typical specimens have been found of combinations with f.t.l., with c.t.l., with zebra and tiger patterns, with large tongues and with dilution (little tongues, yellow); similarly, among primary spirals, with spiral tongues (with or without p.t.t.), with yellow spirals and with narrow spirals (figure 33*b*, plate 4); in black-and-white spirals where zones 4 + 5 + 6 are completely covered by leuco-pigment (see appendix 2), the purple ribbon in position 5 is absent. Purple spirals have also been seen on a black background where they are rather inconspicuous, and on a pink background; they can also be associated with generalized purple, regardless of whether this is bright or very dark in hue, as in figure 35*d*, plate 4. There is thus clearly a *prima facie* case that purple spirals are conditioned by a single gene.

Table 15. Purple spirals, and purple spirals, yellow: incidence in the three provinces

		purple spirals		purple spirals, yellow	
	total	*n*	%	*n*	%
Ceylon, west coast	26034†	4	0.015	0	0
Ceylon, east coast	23176	509	2.20	0	0
Malaya–Singapore	12295	505	4.11	117	0.95
Hong Kong	10954	500	4.56	11	0.10

† Includes an estimated 20000 individuals from Chilaw (9B).

It should be mentioned that in Hong Kong, but not in Malaya–Singapore, the purple zones are often diluted to a tobacco-brown, a variant which could perhaps be enumerated separately.

In addition, there occurs in Malaya–Singapore and in Hong Kong a category of 'purple spirals, yellow' which presents difficulties of classification and which, for that reason, has been kept separately. Typically, the same deep purple bands in zones 1 and 5 are present on a pure yellow background. But the band in zone 5 is often reduced and interrupted; it may be represented by only one or two short regions and, presumably, it may be absent altogether. When this happens, the band in zone 1 also tends to be reduced, and as pigmentation generally persists longest (or starts earliest) in the neighbourhood of the suture, gradual transitions to phenotypes like that in figure 32*d*, plate 3, are encountered. In this paper, no shell has been regarded as belonging to this class unless a typical deep purple band is present in zone 1 and at least one region in zone 5 is similarly pigmented. (Note: the shell in figure 33*d*, plate 4, is not a 'purple spiral, yellow' as it has a pigmented ribbon in zone 3; it represents a combination of purple spiral with yellow spiral as in figure 32*a* and *b*, plate 3).

The incidence of purple spirals and of purple spirals, yellow, is given, in a condensed form, in table 15. The incidence of purple spirals in Malaya–Singapore and in Hong Kong is about the same ($\chi^2_1 = 2.927$); the combined incidence of 4.32 % is just about twice that on the east coast of Ceylon. Homogeneity tests are as follows

	χ^2	d.f.
Ceylon, east coast	12.920	8
Malaya–Singapore	2.450	4
Hong Kong	17.353	7
total	32.723	19

The value of χ^2_{19} with $P \approx 0.025$ suggests a mild degree of heterogeneity; the culprit is Hong Kong. However, in the large samples on which this paper is based, degrees of heterogeneity reach the level of statistical significance which are generally ignored in samples of more modest size.

Purple spirals, yellow are completely absent in Ceylon; they occur rarely (about 1:1000) in

TABLE 16. BLACK IN MALAYA–SINGAPORE AND IN HONG KONG

		black		black	
	total	n	%	non-spiral	spiral
21A	270	15	5.56	12	3
21B	2022	87	4.30	79	8
22A	2255	145	6.43	133	12
22B	1786	89	4.98	78	11
22C	5962	332	5.57	242	90
total	12295	668	5.43	544	124
1	1148	73	6.36	64	9
2	1213	67	5.52	58	9
3	1795	139	7.75	120	19
4	1239	85	6.86	83	2
5	2436	102	4.19	87	15
6	1173	51	4.35	50	1
7′	1526	70	4.59	65	5
7″	424	26	6.13	26	0
total	10954	613	5.60	553	60

Hong Kong, but reach nearly 1 % in Malaya–Singapore (all differences being highly significant). The relation between purple spirals, yellow and ordinary purple spirals remains somewhat problematical, not to mention other possibilities, such as the yellow juveniles (table 16).

Black

Black is about equally common in Malaya–Singapore and in Hong Kong (5.43 and 5.60 % respectively, table 16). Its incidence is thus much higher than in Ceylon (1.24 %, table 7). In Malaya–Singapore there is little evidence for heterogeneity between populations ($\chi^2_4 = 9.760$; $P = 0.045$), but the Hong Kong data are clearly not homogeneous ($\chi^2_7 = 38.4$; $P < 10^{-5}$); omitting the most divergent population (no. 3), the remainder is still heterogeneous ($\chi^2_6 = 18.634$; $P = 0.005$). Whereas in Ceylon there was evidence that heterogeneity between populations had something to do with the eelgrass habitat, no obvious ecological factor can be incriminated in Hong Kong.

Throughout, blacks include an excess of non-spirals as compared with the overall incidence of about 62 %; the excess is least in Ceylon and greatest in Hong Kong (table 17). It is not clear whether this is due to 'factor interaction' or to mis-classification: perhaps some black spiral types have not been recognized as such.

TABLE 17. INCIDENCE OF NON-SPIRAL TYPES AMONG BLACKS

		non-spiral	
	total	*n*	%
Ceylon	362	278	76.80
Malaya–Singapore	668	544	81.44
Hong Kong	613	553	90.21

Pink

A small group of shells from Hong Kong province (table 18) appears pinkish to the naked eye, partly on account of the diffuse background colour of these rather transparent shells and partly on account of a dilution of the line pattern which tends to be reddish or purplish. Various patterns from f.t.l. to spiral tongues have been encountered, with f.t.l. with many small tongues predominating. Classification is not sharp, and the group has been treated as a separate category with some hesitation.

TABLE 18. PINK AND 'YELLOW JUVENILES' FROM HONG KONG

	pink				yellow juveniles	
	non-spiral	spiral	total	%	total	%
1	2	—	2	0.17	23	2.00
2	3	—	3	0.25	—	—
3	35	9	44	2.45	21	1.17
4	20	3	23	1.86	3	0.24
5	23	6	29	1.19	39	1.60
6	27	3†	30	2.56	6	0.51
7′	12	4	16	1.05	2	0.13
7″	4	3	7	1.65	4	0.94
total	126	28	154	1.41	98‡	0.89

† One of these is a purple spiral.

‡ A similar group of 101 'yellow juveniles' from Malaya–Singapore has not been tabulated separately.

'Yellow juveniles'

This small but heterogeneous group is confined to the eastern provinces. Typically, the shell is transparent yellow with a little dark pigment in the neighbourhood of the suture (figure 32*d*, plate 3). Such a snail might later have become a yellow spiral by forming spirals in zones 3 and 5; or it might have become a purple spiral, yellow, by forming a wider deep purple zone 1 and eventually a narrower such zone 5. Alternatively, giant tongues might have been formed from the pigmented collar round the suture. It is thus impossible to classify such individuals as either spiral or non-spiral. Nor is it certain that all such snails would eventually have revealed their true nature. However, the absence of 'yellow juveniles' from population 21B, the only really large-sized population from the eastern provinces, indicates that most of these animals are, in fact, juveniles.

But some animals included in this class are not yellow. As will be discussed in more detail in appendix 2, deposition of black pigment depends on the previous formation of a white substance. In 'yellow juveniles' proper, no white – and hence no black – is formed except near the suture, and as a result, the transparent yellow background colour dominates the picture. But black is never formed on top of white, and hence it is not deposited unless the formation of white has come to an end. Occasionally, the white material is formed without intermission, and the shell is covered by a continuous opaque 'whitewash' with no black pattern except, perhaps, near the suture.

The incidence of yellow juveniles in Hong Kong province is given in table 18. Considering that the group is heterogeneous and that its manifestation involves an age element, it is not surprising that its incidence as between populations is also heterogeneous. The same applies to a similar group of 101 individuals from Malaya–Singapore: it has already been mentioned that in the large-sized Mata Ikan population (21B), the phenotype is not represented.

TABLE 19. THE INCIDENCE OF 'PURPLE' IN MALAYA–SINGAPORE AND IN HONG KONG

	non-spiral	spiral	total	%
21A	—	10	10	3.70
21B	15	54	69	3.41
22A	1	78	79	3.50
22B	2	59	61	3.42
22C	72	192	264	4.43
sub-total	90	393	483	3.93
1	32	36	68	5.92
2	20	23	43	3.54
3	37	41	78	4.35
4	10	22	32	2.58
5	48	47	95	3.90
6	38	35	73	6.22
7′	3	20	23	1.51
7″	5	10	15	3.54
sub-total	193	234	427	3.90

Purple

As a separate entity, purple is essentially confined to the eastern provinces. Vague purple tinges sometimes occur in Ceylon, but not a single shell has been found in that province which could be described as a proper purple: in Tondaimanar (no. 19) where the earlier whorls tend to be well preserved, they often have a purplish hue which darkens with age; a purplish blush also sometimes re-appears in adults following insults by crabs; similarly, a vague purplish tinge is occasionally seen in old individuals with very fine transverse lines. Hence purple may become detectable where the total amount of pigment is small, and perhaps the pattern of *Clithon* behaves like a dinner jacket which is also not truly black, but a very intense red (or green). But this suggestion is not borne out by little tongues, yellow in which pigment is greatly reduced without becoming purple in appearance, except in p.t.t. (table 13). It should indeed be emphasized that purple has nothing to do with p.t.t.; it affects the pattern as a whole whereas p.t.t. is confined to the tips of spiral tongues, and purples with or without p.t.t. can usually be distinguished. It is only as part of purple spirals, in zones 2–4, that this colour occurs in Ceylon.

By contrast, bright purples (brighter even than those in figure 35, plate 4) are regularly found in all eastern populations examined; and time and again one hopefully starts to sort them out as a separate category. Alas, these hopes are always disappointed as there are all intergrades between vivid purples verging on lilac down to shells where the distinction between dark purple and blackish-brown becomes first difficult and in the end impossible. The dividing line between purples and non-purples is thus highly subjective and probably not consistent from day to day, and the data of table 19 are given here mainly for sake of completeness.

In the Malaya–Singapore province, there is a heavy preponderance of spirals among the purples; in Hong Kong, this is much less so. The reality of this inter-province difference is beyond doubt.

The purple category is probably heterogeneous. It includes a rather rare type in which a deep purple forms a continuous and opaque layer (like that in zones 1 and 5 in purple spirals) with roundish windows (tongues) through which the transparent yellow of the shell underneath is strikingly revealed. Sometimes such windows are so large and the intervening purple correspondingly so narrow that the distinction from giant tongues becomes problematical (as in figure 27*b* and 28*e*, plate 2). There are also intergrades between a solid sheet of purple and closely spaced transverse lines (as in figure 26*c*, plate 2), as also happens in purple spirals.

Discussion

At long last, we are in a position to give a general conspectus of the *Clithon* variants in all three provinces. The first two panels of table 20 include the axial and the spiral patterns, respectively, except those in the variants of the third panel. The ratio of axial:spiral patterns is essentially the same in all three provinces (table 10) and amounts to about 62:38. In Ceylon, they include between them as many as 97 % of the total, in the eastern provinces a little less than 80 %. The variants in the third panel have widely different ratios of axial:spiral patterns and will be discussed later.

We now have to examine the relation between the axial and the spiral patterns. Although most animals clearly belong to one or the other, there are a few borderline cases. In principle, two genetic mechanisms can give rise to such a situation.

(1) Axial and spiral phenotypes are not distinct genetically, but are the extremes of a continuous U-shaped distribution which corresponds to a single genotype, and the axial and spiral phenes are the states of greatest physiological stability. In such a situation, there is no parent–offspring correlation, and the array of populations round the coast of Ceylon, etc., is automatically stable genetically though, of course, subject to the influences of the environment.

No stabilizing forces (such as selection) are required to maintain this state of affairs, and the populations are not subject to genetic drift (founder effects) however small the inoculum. The situation is thus analogous to the behaviour of minor variants in inbred strains of mice (for a summary see Grüneberg 1963); and as sub-lines of inbred strains tend to drift apart genetically as the result of mutations, so differences between provinces are likely to arise.

(2) Axial and spiral phenotypes correspond to distinct genotypes. In the simplest (monofactorial) case, *AA* may be axial and *AA** and *A*A** spiral. If so, *AA* may sometimes show secondary spiralization (in the absence of small tongues), and these abortive spirals would not be intermediates in the strict sense. Alternatively, if *AA* and *AA** are axial and *A*A** spiral, occasional *A*A** snails may come close to overlapping the axial phenotype, and such animals would be real intermediates between presence and absence of primary spiralization. Another possibility is that abortive spirals are confined to occasional *AA** heterozygotes, not to mention multiple alleles or bi- and multi-factorial situations. In all these instances, there will be parent–offspring correlation. Hence an array of populations will not be automatically stable genetically. If stability is actually encountered, stabilizing forces (such as selection) must be at work, and founder effects are to be expected if the number of pioneers is small.

TABLE 20. THE VARIANTS OF *CLITHON* IN THE THREE PROVINCES

(Explanation in the text. In Hong Kong, some putative double recessives have been counted twice; hence the total exceeds 100.)

	Ceylon	Malaya–Singapore	Hong Kong
fine transverse lines (f.t.l.)	55.75	28.40	19.72
coarse transverse lines (c.t.l.)	3.63	4.64	5.82
zebra	0.22	0.27	1.94
tiger	—	7.84	13.90
large and giant tongues	0.11	8.61	7.49
sub-total, axial patterns	59.87†	49.76	48.87
spiral tongues	9.54	17.47	21.63
ladders	12.76	—	—
black-and-white spirals	—	1.15	2.92
narrow spirals	—	2.63	1.02
yellow spirals	13.77	7.77	5.39
sub-total, spiral patterns	37.14†	29.02	30.96
dilution	0.01	5.98	3.83
purple spirals	(1.75)‡	4.11	4.56
purple spirals, yellow	—	0.95	0.10
black	1.24	5.43	5.60
pink	—	—	1.41
purple	—	3.93	3.90
yellow juveniles	—	0.82	0.89
sub-total, remainder	3.00	21.22	20.29
grand total	100.01	100.00	100.12
p.t.t. in primary spirals§	19.67	17.04	24.29
p.t.t. in tigers	—	1.87	4.86
p.t.t. in dilutes	—	0.97	2.78

† For fuller explanation see under Summary of the Ceylon populations above, p. 408.

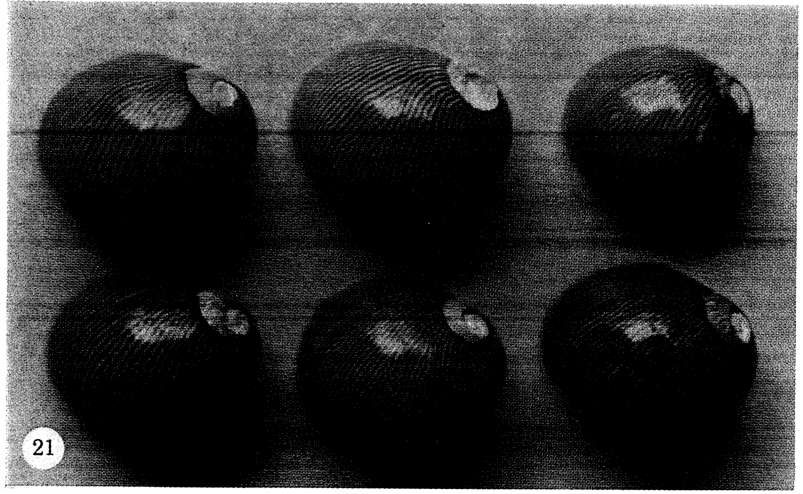
‡ 2.20% and 0.015%, respectively, on east and west coast.

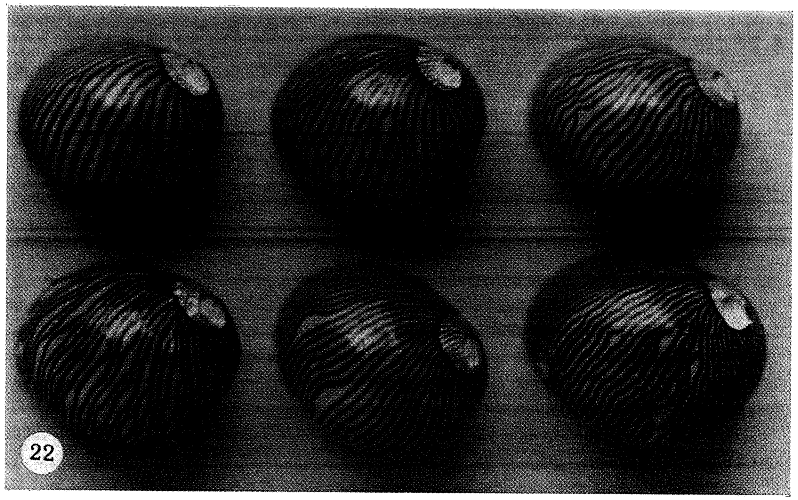
§ As a percentage of all primary spirals (including purple spirals); of all tigers; and of all dilutes, respectively.

EXPLANATION OF PLATES 1–4

The first 15 photographs include 90 individuals or just one third of the total population 21A from Mata Ikan, Singapore. The six snails on each photograph are referred to as follows:

a b c
d e f





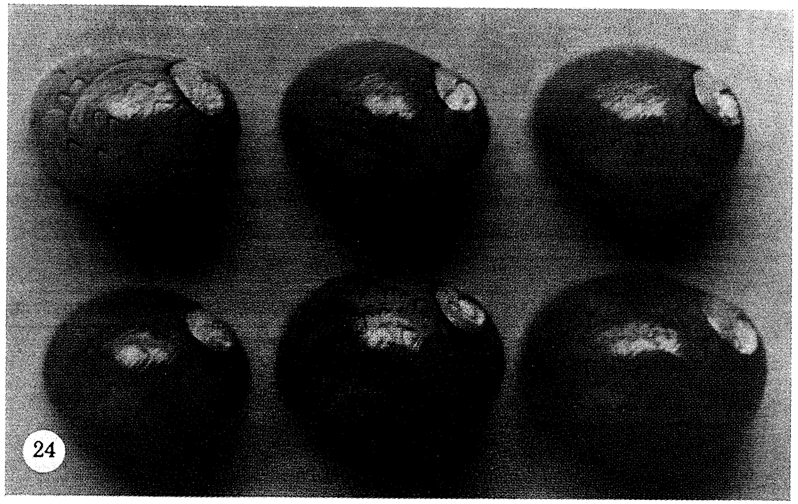


FIGURE 21. Fine transverse lines (f.t.l.).
FIGURE 23. a–d, f: tiger; e: zebra.

FIGURE 22. Coarse transverse lines (c.t.l.).
FIGURE 24. Little tongues, yellow.

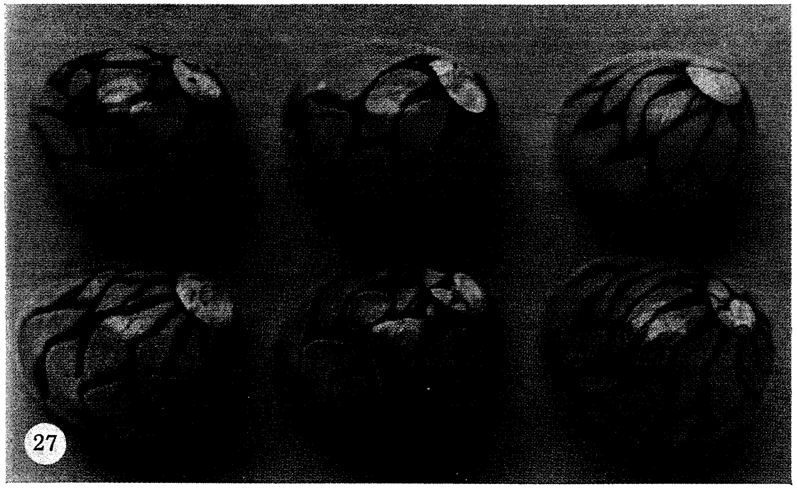


FIGURE 25. Many small tongues.
FIGURE 27. Large and giant tongues.

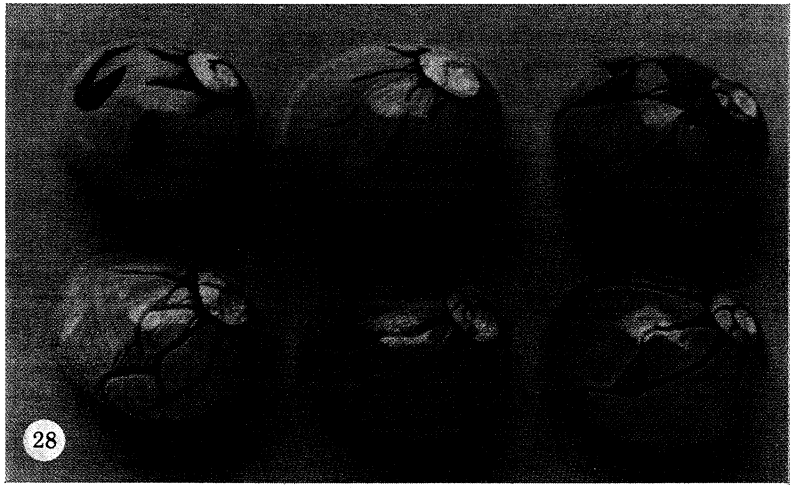


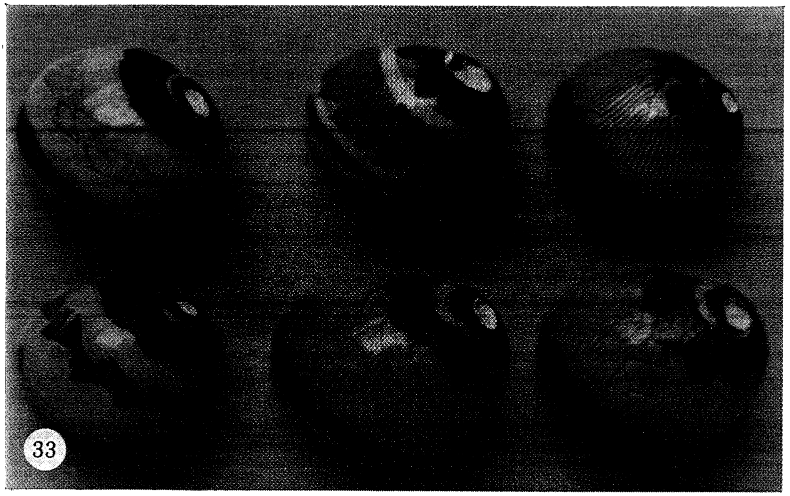
FIGURE 26. Large and giant tongues.
FIGURE 28. Large and giant tongues.

FIGURE 29. a, c–f: spiral tongues; b: large tongues, spiralization dubious.

FIGURE 31. a and c: yellow spirals (transitional to spiral tongues); d and e: yellow spirals; b: black-and-white spiral; f: narrow spiral.

FIGURE 30. Spiral tongues; b and c: purple-tipped tongues (p.t.t.); f: narrow spiral tongues.

FIGURE 32. a–c, e and f: yellow spirals; d: juvenile form of either yellow spiral or giant tongues.



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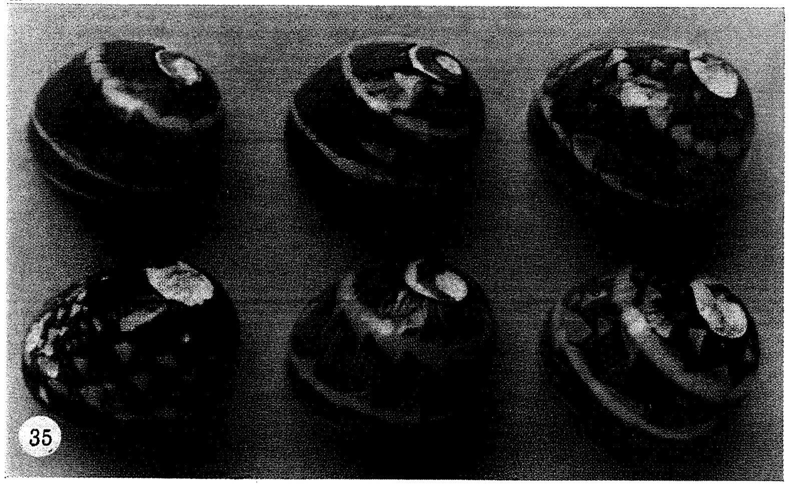

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FIGURE 33. Purple spirals.

FIGURE 35. a–c, e and f: purple (note the chalk lines in most of the spirals); d: a purple spiral on a very dark purple background.

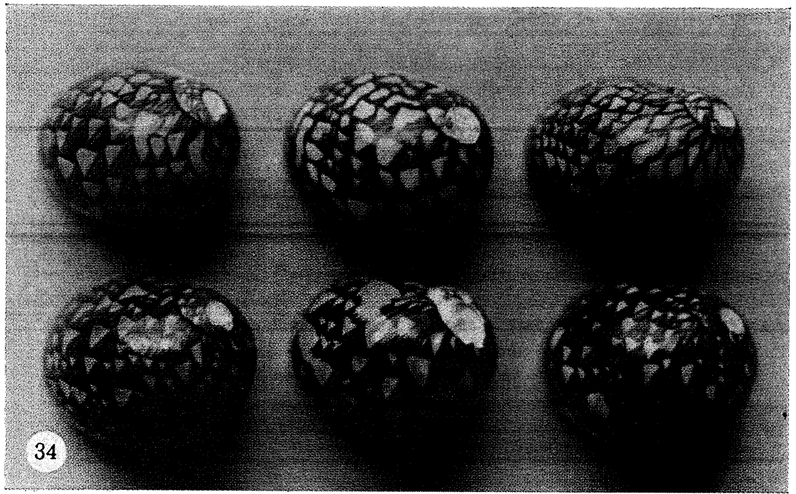

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FIGURE 34. Black.

FIGURE 36. Group of *Clithon* shells from Tai Po Marshes, Tolo Harbour, N.T., Hong Kong, a locality not mentioned elsewhere in this paper. It illustrates the appearance of an unsorted sample.

As the distinction between (1) and (2) hinges on whether or not there is parent–offspring correlation as regards axial and spiral patterns, controlled breeding experiments are essential. It is fortunate that pioneer studies by Mr Lionel Nugaliyadde (see appendix 4) are sufficient to decide the issue. As a preliminary to more detailed genetical studies, it was necessary to discover the conditions under which *Clithon* can be maintained and bred in the laboratory. The number of aquaria available was limited, and it seemed in any case more promising to try larger units and hence less uniform conditions first. To have a reasonable density of snails in the aquaria, groups of juveniles with axial patterns were introduced into some and groups of juveniles with spiral patterns into other containers (all from Pitipana, Negombo). The snails grew up with little mortality and eventually produced the following offspring.

parents	offspring	
	axial	spiral
axial	115	0
spiral	12	95

There is thus a clear parent–offspring correlation which shows that there is genetic segregation, with presence of spirals dominant over their absence. The data are, however, probably biased and hence not suitable for a test of a single-gene hypothesis, as the parents were selected for clear manifestation of axial and spiral phenotypes respectively, and hence presumably (or possibly) include an excess of homozygotes.

As (1) is thus ruled out, it becomes necessary to discover the mechanism(s) which keeps the ratio of axial to spiral patterns so remarkably uniform over the whole area sampled. It was reported earlier that snails with axial patterns are, on an average, about 6.7 % heavier than snails with spiral patterns. It is conceivable that this indicates quicker growth, and hence that axials reach sexual maturity a little earlier and thus have an advantage over the spirals. If this should be true, one would have to postulate the existence of another selective process acting in the opposite direction without which no equilibrium could exist. As shown in appendix 1, the ratio of axials to spirals can be different from that encountered in the present study. Needless to say, no claim is made that earlier sexual maturity of axials is a selective mechanism actually at work. But it may serve as a model.

As discussed earlier on, in Ceylon and elsewhere habitats in which *Clithon* can exist are separated by long stretches of coastline where it can not. The methods of dispersal are such that presumably it has to rely on rare accidents which will involve but a few individuals at a time. It is thus the classical situation in which founder effects will make themselves felt if the pioneers are drawn from a segregating population. As the ratio of axials/spirals is not very far from equality, the risk of losing one allele altogether may not be very great, and as long as both are represented in the founder population, the proper ratio will presumably re-establish itself in the end as the result of the interplay of selective forces.

In the axial group, changes of pattern with age or after a temporary cessation of growth (including the effects of attempted predation) make it clear that, in Ceylon at any rate, a given individual is often capable of switching from c.t.l. to f.t.l. or vice versa and that there may be a gradual or rapid increase of the density of the tongue pattern, and sometimes back again. Studies of the shell patterns thus do not suggest that these phenotypes correspond to the segregation of genes. It remains uncertain whether the few widely spaced patterns in Ceylon are part of the f.t.l.–c.t.l. sequence. In the eastern provinces where zebras and tigers are common, they are generally easily classifiable and may well be distinct genetic entities, but breeding tests will be required to settle the point.

Having regard to the fact that breeding data from Ceylon (table 21, appendix 4) are derived from mass matings, that they are not yet extensive and that classification was not carried out at standardized ages, they are in general agreement with the suggestion that variation within the axial group is essentially non-genetic in nature. There is perhaps a slight suggestion of parent–offspring correlations, but more extensive data from single paired matings would be required to show whether there is, in addition, a genetic component in the axial group.

The situation is rather less clear in the spiral patterns. In the Mutur population, spiral tongues, ladders and yellow spirals can be separated from each other with little difficulty, and if no other populations had been examined, there would have been a strong *prima facie* case for genetic segregation. But in other populations intergrades are common, and there are many transitions in time in individual snails. Evidently, once a decision in favour of spirality has been made, many snails are capable of following any of these courses and indeed not rarely 'change their minds' as time goes on. But population studies, in themselves, cannot tell us whether this applies to all snails, or perhaps only to certain heterozygotes, etc. Similarly, in the eastern provinces, though there are many intergrades between spiral tongues and yellow spirals, other types (black-and-white spirals, narrow spirals) stand out rather distinctly and suggest the segregation of individual genes.

The breeding data of spirals (table 22, appendix 4) are less subject to age effects, and though they are not numerous, they suggest parent–offspring correlations. In experiment 5*a*, the parent group with spiral tongues produced 47 offspring of the same pattern and only 6 ladders; in experiment 7 where the parents are ladders, the situation is reversed (2 spiral tongues and 6 ladders). Both population studies and mass matings thus indicate that the spiral group includes an element of genetic segregation. Controlled breeding experiments with single paired matings (also from the eastern provinces) will, however, be required to sort out what may well prove to be a complicated genetic situation.

The variants in the third panel of table 20 (except the yellow juveniles) have one feature in common. Whereas in their absence there are about 38 % primary spirals, in their presence the incidence of spirals is as follows.

	primary spirals (%)
dilution	7.2
purple spirals (east coast of Ceylon)	9.0
black (Ceylon)	23.2
black (Malaya–Singapore)	18.6
black (Hong Kong)	9.8
pink	18.2
purple (Malaya–Singapore)	81.4
purple (Hong Kong)	54.8

Primary spiralization is thus generally reduced except in purple where it is strikingly increased. All these variants differ in their incidence from province to province, but are homogeneously distributed within provinces (except purple spirals and black in Ceylon).

A mass mating of purple spirals from Trincomalee A produced 8 young of the same phenotype

(Nugaliyadde, appendix 4). Purple spirals is thus presumably conditioned by a single gene. If dominant, almost all purple spirals would be heterozygotes, and a 3:1 ratio would be expected; the observed ratio of 8:0 does not rule this out ($P = 0.10$), but it is more likely that the gene for purple spirals is recessive; if so, its frequency in Malaya–Singapore and Hong Kong would be about 0.21, on the east coast of Ceylon 0.15 and on the west coast 0.012.

No breeding data are available yet for the other variants, but some of them are likely to have a simple genetic basis. In order of probability, this would apply to purple-tipped tongues (p.t.t.), dilution, tiger and black all of which, with the exception of black, are homogeneously distributed within provinces, but show considerable differences in incidence as between provinces. These differences may have arisen during the spread of *Clithon* from its original home which, it may be presumed, will have been coastwise and slow. If so, an orderly progression along the coastline may be expected such that *Clithon* from the Gulf of Siam would be intermediate between the populations from Hong Kong and Malaya–Singapore, etc.

As remarked above, purple spirals show a marked deficiency of primary spiralization. Now, the purple ribbons of these snails tend to sit on ribbons of small tongues (figure 15*g*–*i*). Let us consider snails with both primary spiralization and purple spirals. If the spirals which are normally present in zones 2 and 4 are, in these animals, shifted to positions 1 and 5, respectively, the primary spiralization would no longer be recognizable as such and the animals would be mis-classified as axials. But they should breed as spirals.

There is no *prima facie* case that snails with dilution, purple spirals, black or pink differ systematically in weight from their respective populations. This is so whether the variants are considered individually, or jointly as a group. On the other hand, in the case of purple, in 12/13 populations the purples are lighter, and only once are they marginally heavier. Now, as axials are generally heavier than spirals, the presence of many spirals among the purples would, in itself, tend to reduce the mean weight of that group. However, the average reduction in weight of purples is 11.4 % and thus greater than would be expected. But, as there is a considerable scatter of values, the excess over expectation may well be spurious. With the probable exception of purple spirals, and possibly of black (where mis-classification might be responsible), the nature of the 'interaction' with primary spiralization thus remains obscure.

We now have to compare the behaviour of *Clithon* with that of other polymorphic snails. Most other neritine snails are tropical animals except the genus *Theodoxus* which is found in the temperate zone. It includes the variable species *Theodoxus fluviatilis* L. whose shell patterns have been studied by Becker (1949) and more recently by Neumann (1959*a*, *b*). These consist of three elements which can occur in combination, a synchronous transverse pattern, a longitudinal drop pattern, and a spiral pattern with seven zones, but otherwise quite different from that in *Clithon*. Abrupt changes from the transverse to the drop pattern or vice versa are found in shells collected in the wild, often following a temporary cessation of growth. Evidently, one and the same genotype can manifest itself in different ways, presumably depending on the environment. By rearing young snails in the laboratory, Neumann succeeded in identifying some of these factors by the abrupt change of pattern which, in certain instances, follows transfer from one environment to another. The most important factor was the Ca/Mg ratio whereas changes in the anionic composition, or the degree of salinity as such, proved ineffective; temperature had little and speed of growth or a change of food no effect. The situation as regards the transverse and drop patterns is thus similar to that in the axial patterns of *Clithon* (though Neumann suspects that an element of genetic segregation might also be involved), and similar environmental factors may be operative in *Clithon*, such as ionic changes during the monsoons, etc. As in *Clithon*, the presence or absence of the spiral pattern in *Th. fluviatilis* corresponds to genetic segregation as shown by wide differences between wild populations and partly by some breeding experiments in the laboratory (which have not been published in detail).

Among land snails, the striking genetic polymorphism of *Cepaea nemoralis* (L.) and related species has long attracted the interest of geneticists. Variable features include shell colour (yellow, pink, brown), the presence or absence of spiral bands (the full complement is 12345, another common variant 00300, and there are many others due to fusions or reductions of bands), brown rather than colourless lip of the shell and others. The few references given here (Cain & Currey 1963; Cain, King & Sheppard 1960; Cain & Sheppard 1954, 1957; Cain, Sheppard & King 1968; Cook 1967; Jones 1973; Lamotte 1951) are merely to serve as an introduction to a field which in several aspects is still rather controversial. As shown by numerous breeding experiments, much of the variation of *Cepaea* is the result of the segregation of a few pairs of genes (or multiple alleles) with major effects. A highly characteristic feature of *Cepaea* is the fact that individual colonies which are sometimes not far apart may differ greatly in gene frequencies, and these differences appear to be stable in time. Similar differences differentiate larger areas which include many colonies, and again these area effects appear to be stable.

There is no unanimity as to the factors which have brought about this situation and which keep it in being. Natural selection by predators (such as thrushes) in conjunction with ecological conditions is favoured by some authors, as well as other mechanisms of selection. Others, working in different localities, have either denied selectionist interpretations altogether or at any rate have tried to relegate them to minor roles, and in turn have advocated other mechanisms, such as mutation or migration, or they have regarded the vast and stable inter-population variance of *Cepaea* as random.

The situation is similar in principle in the land snails of the genus *Partula* in the Pacific (Crampton 1932; Murray & Clarke 1966). Considerable genetic polymorphism again involves presence or absence of spiralization, background coloration and, on this occasion, also dextrality as opposed to sinistrality. There are great differences in gene frequencies from population to population which appear to be stable, and hence there are the same problems as to origin and maintenance of these systems as in *Cepaea.*

In striking contrast to *Theodoxus*, *Cepaea* and *Partula*, in *Clithon* the incidence of variants within provinces is remarkably uniform. But major genetic differences separate provinces or sub-provinces (such as the east and west coasts of Ceylon) from each other. There is thus no need to invoke stable environmental or genetic differences within provinces. There are merely ups and downs round essentially stable mean values. But the stability of such means in space and time cannot be accounted for in terms of Hardy–Weinberg equilibria. It can hardly be explained without recourse to stabilizing selection. Selective forces are required to bring the ratio of phenes back to the common mean, not least following the changes of gene frequencies which inevitably happen when new populations are established from small groups of founder individuals derived from segregating populations.

It is an altogether different question whether selection necessarily leads to increased fitness all round. An accelerated rate of development may confer an advantage on one allele as compared with another. But there is no reason to suppose that the faster allele has necessarily greater survival value in other respects. Indeed, the very opposite could be the case, and greater speed might be balanced by reduced fitness elsewhere in the life cycle. Although it appears that the polymorphism of *Clithon* is maintained by an interplay of selective forces, this presumably is the result of a balance between advantages and disadvantages and hence a compromise.

Finally, there are the changes in pattern of the *Murchisonia* type which intrigued me so much back in the 1920s. These were originally interpreted as heterozygotes in which first one and subsequently the other allele manifested itself (Grüneberg 1927). At the time this interpretation was purely intuitive, but it has since been vindicated in *Cepaea nemoralis* where many heterozygotes for shell colour behave in a similar way (Cain *et al.* 1960). On the other hand, abrupt changes in the pattern of *Theodoxus fluviatilis* have been induced experimentally by specific management of the environment (Neumann 1959*a*). These two situations may not be mutually exclusive. It could well be that heterozygotes respond more readily to changes of the environment than homozygotes, and this could be one of the reasons why certain fraternities in Neumann's experiments proved to be refractory to treatments which were effective in others. As a phenomenon, a change of phenotype is merely an expression of a change in physiological conditions. It thus cannot discriminate between situations in which this is a property of heterozygotes or of homozygotes.

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APPENDIX 1. A *CLITHON* POPULATION FROM THE PHILIPPINES

The collections of the British Museum (Natural History) include a rather unusual sample of our animal ('*Neritina ualanensis*' from the Philippines, this being the sole reference to locality of collection). There are 900 adults (mean weight 129.1 mg) in seven boxes; these are labelled at the bottom in an unknown hand as Mut.Dirempta, Mut.Frondicincta, Mut.Conferta, Mut.Polydelta and Mut.Parcipicta. Assuming this to be an unselected population, it has been reclassified as follows:

f.t.l. and c.t.l. (nearly all f.t.l.; 2 purple)	297	
tiger	62	
large and giant tongues	3	
sub-total	362	40.22 %
spiral tongues	307	
spiral tongues, p.t.t.	206	
spiral tongues, purple	23	
spiral tongues, purple, p.t.t.	1	
'pale' yellow spiral	1	
sub-total	538	59.78 %

There are thus many more primary spirals than in the present material, and even the figure of nearly 60 % is almost certainly an underestimate. With few exceptions, the 297 f.t.l. and c.t.l. shells show small tongues, but generally not in large numbers. In at least half of them, these are arranged sparsely in zones 2, 4, 6 (and sometimes not in all three of them); there are all intergrades between individuals in which spiral tendencies are just detectable and others which are almost certainly primary spirals. Indeed, it seems that in this population the distinction between primary and secondary spirals breaks down. Apparently, there has been a general shift towards spirals, and in the process small tongues (which are not very numerous and thus would normally mainly be randomly distributed) tend to occupy zones 2, 4, 6. The incidence of p.t.t. (38.5 %) is also much higher than in Ceylon and the eastern provinces (where it ranges from 17 to 24 %). As in the main material, purples show an excess of spiralized forms. None of the putative morphs is present, with the possible exception of two tigers which (??) show a hint of purple spirals. The 'pale' yellow spiral resembles certain variants from Tondaimanar (population 19). The wide divergence of this sample from the main material underlines the desirability of examining populations from other localities. It remains, however, possible that this population was, in fact, selected for the more conspicuous spiral phenotypes.

APPENDIX 2. NOTES ON THE FORMATION OF THE *CLITHON* SHELL PATTERNS

Although the chemical nature of the shell pigments of *Clithon* is unknown, certain regularities can be deduced from visual observations of the shell patterns under the dissecting microscope.

As in other gastropods, shell pigmentation is confined to the surface and situated immediately under the periostracum which is essentially smooth and transparent, except for very fine lines of accretion and a delicate surface pattern somewhat reminiscent of a textile structure; this only becomes noticeable at higher magnifications and will be disregarded in this context. The colour of the shell in young animals is a diffuse yellow which may shade into orange or pink. As the animals grow, the shell becomes thicker and less transparent and the colour gradually turns into a faint olive or occasionally dove-grey; this is particularly noticeable where much of the diffuse background is exposed to view, as in tigers, large and giant tongues, and in little tongues, yellow. In most other types, much of the diffuse background is hidden from view by a line pattern of black, dark-brown or purple 'melano-pigment' which is superimposed on it. In addition, there is an opaque white 'leuco-pigment' which may conceal much of the diffuse yellow background, and which is probably identical with Helmcke's (1935) shell granules ('Schalengranula').

There is a close relation between melano-pigment and leuco-pigment which is seen most easily in patterns which have little of both of them, such as the tiger pattern (figure 20*c*; see also figure 23, plate 1). Periodically as the shell grows, a fine line of leuco-pigment is laid down on the yellow background; following on the deposition of the leuco-pigment, there is a brief interval during which the yellow background once again becomes visible as a narrow zone. Next, melano-pigment is laid down in accurate alignment with the leuco-pigment, and never is melano-pigment deposited except where leuco-pigment was laid down a moment before. Exactly the same sequence of events happens everywhere. In fine transverse lines (f.t.l.), the same sequence occurs at narrow intervals (figure 20*a*), and the overall effect of yellow background, leuco- and melano-pigment as perceived by the naked eye gives the shell a biscuit or mud colour. By contrast in c.t.l. and particularly in zebras, the deposition of leuco-pigment continues for longer periods and is then followed by a heavier zone of melano-pigment (figure 20*b*); little of background colour thus remains visible, and the overall colour of such shells is essentially black-and-white. One gets the impression that there is some relation between the amount of leuco-pigment and that of melano-pigment formed. This is seen, for example, near the tips of tongues. Tongues are formed (figure 20*d*) when leuco-pigment is not laid down as a strip, but locally thickens to form a spindle-shaped swelling, a tongue-like projection or even a dagger-like narrow triangle (as sometimes in very dark blacks). Near the tip of the tongues, where they are backed by the deepest layer of leuco-pigment, the deposition of melano-pigment is also heaviest. (It should be mentioned that by no means all tongues are solidly filled by leuco-pigment: sometimes the leuco-pigment is mainly at the edge and in the middle the diffuse background may show through to a greater or lesser extent.) A relation between the two kinds of pigment is also seen in little tongues, yellow. In this condition (figure 20*e*; see also figure 24, plate 1), both pigments are reduced in quantity; over much of the pattern, the threshold for the formation of melano-pigment is evidently not reached so that one can see the white in the absence of black pigment; the threshold is crossed mainly near the tips of the tongues where both are formed in greater quantity. Yet another situation is shown in the yellow spiral of figure 32*a*, plate 3. Normally in zones 1, 3, 5, there is an alternation of leuco- and melano-pigments just as in the absence of spiral patterns; but in the individual shown in the figure, there has anomalously been the continuous deposition of leuco-pigment in part of zone 3. It is apparent that melano-pigment cannot be laid down on top of leuco-pigment – it has to wait until the white matter comes to an end. In the snail under discussion, when the continuous ribbon of leuco-pigment eventually did come to an end, a large quantity of melano-pigment had accumulated to be laid down as a massive blob.

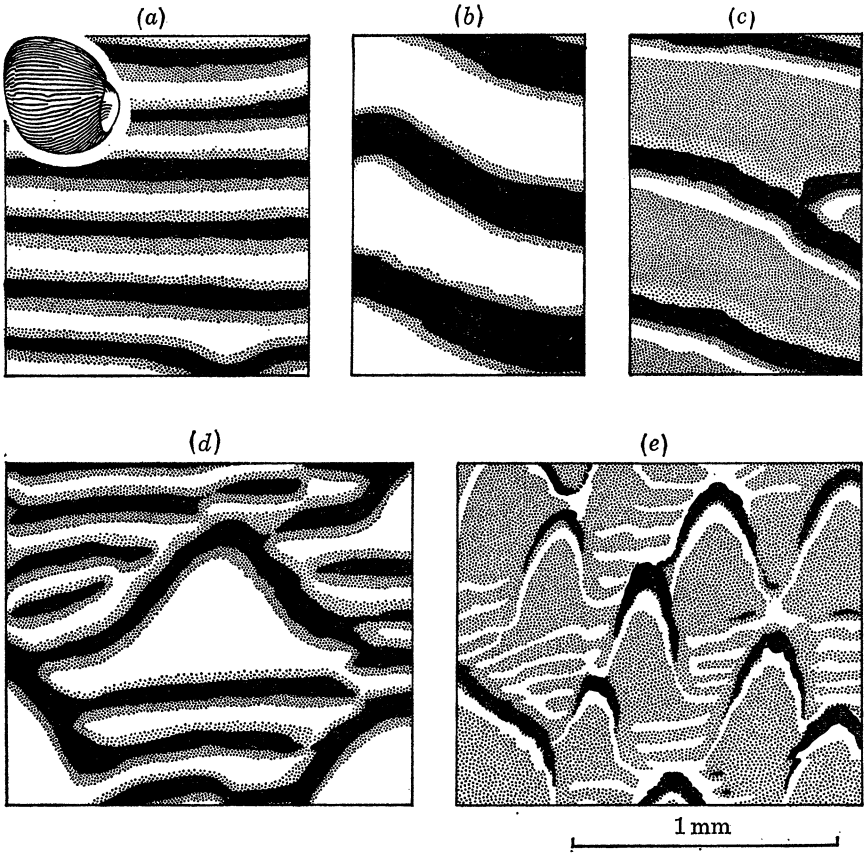

FIGURE 20. The deposition of melano-pigment (black) and of leuco-pigment (white) on the transparent yellow background of the shell (stippled). As indicated by the snail in the top left hand corner, accretion is taking place in the direction from the bottom upwards. (*a*) Fine transverse lines (f.t.l.); (*b*) coarse transverse lines (c.t.l.); (*c*) tiger; (*d*) a tongue in f.t.l.; (*e*) little tongues, yellow. All specimens from population 21A (Mata Ikan, Singapore).

Visual observation thus leaves no doubt that the pattern of melano-pigment is conditioned by that of leuco-pigment. Once an element of the leuco-pigment has been formed and temporarily completed, melano-pigment is laid down closely adjacent to it. The deposition of melano-pigment is carried out by melanocytes at the edge of the mantle. In places where not too much pigment is laid down, it can indeed be seen that melano-pigment is deposited in narrow strips which accurately follow the lines of accretion, and regardless of the overall shape and direction of the pigmented line so formed. It is evident that melanocytes are activated as they are being approached by leuco-pigment, but switched off again as soon as the leuco-pigment actually reaches them.

How, then, is the leuco-pigment pattern produced? Let us suppose that, in zones 2, 4, 6, the cells which produce that substance were permanently switched on. The result would be a continuous white spiral without any transverse bars of melano-pigment (which is not formed as long as leuco-genesis continues without interruption); this happens, for example, in black-and-white spirals (figure 18*a*, *b*); as soon as leuco-genesis becomes intermittent, spiral tongues begin to replace the continuous spirals (*c*, *d*), and eventually rapid alternation of leuco- and melano-phase leads to intercalation of zone 5 in *f* (see also figure 19). Continuous or intermittent leuco-genesis on a narrow front is indeed the basis of narrow spirals or spiral tongues, respectively. Narrow 'chalk-lines' are particularly common in purples (figures 29*f*, plate 3; figure 35*a–c*, *e*, *f*, plate 4). They are also often found in ladders in which they occupy the middle on zones 2, 4, 6 only with transparent yellow seams visible on either side, and similarly sometimes in yellow spirals.

Conversely, if leuco-genesis is switched off, so is melano-genesis. The result may be a uniformly yellow shell (figure 32*d*, plate 3) or usually, following the switching on of leuco-genesis in zones 1, 3, 5, the result is a yellow spiral. The zones 2, 4, 6 exhibit their transparent yellow background colour because, in the absence of leuco-pigment, melano-pigment also is not formed.

The apparent simplicity of this situation is, however, complicated by the fact that the lines of leuco-pigment, though they are more or less axial in their general arrangement, do not run parallel to the lines of accretion and thus to the mantle's edge. As long as the parent cells of the leuco-pigment have not yet been identified, speculations concerning the mechanism underlying the leuco-pattern will hardly be profitable.

Appendix 3. Notes on the localities where the material was collected

Ceylon

8. *Pitipana*, *Negombo* (8A: 58 snails collected in November 1971 by Miss Y. R. Rafael (Colombo); 8B: 150 snails collected in July 1973; and 8C: 663 on 8 April 1973 by L. Nugaliyadde; 8D: 747 animals on 11 December 1973 by the author). In the grounds of the Brackish Water Fisheries Research Station, near the entrance to the Negombo Lagoon. Sandy mud, with much *Cerithium* and debris of various molluscs, some of them large. *Clithon* not very plentiful.
9. *Chilaw* (9A: 1334 snails on 12 December 1973; 9B: about 20000 on 5/6 January 1974). On the west side of the river-like outlet of Chilaw Lake, about halfway between the bridge and Chilaw Point. Fine sandy mud, with many large *Cerithium*, often with barnacles attached. The 9B sample collected with the help of numerous children. Very large population. Main predators are hermit crabs.

10. *Kalpitiya* (13 December 1973). Near the mouth of Puttalam Lake, facing east. Close to the jetty of a small establishment of the Ceylon Navy. Stony beach with numerous large living *Cerithium* and dead shells of other molluscs, many of them large *Murex*, etc. Main sediment more sandy than muddy. *Clithon* sitting on stones, in the sand, but also on rotting palm fronds, etc. Sparse population, largely hand-picked.
11. *Vakarai* (27 January 1974). West side of Upaar Lagoon, opposite the bar between northern and southern spit at entrance to the lagoon and about 0.4 km ($\frac{1}{4}$ mile) north of Vakarai Rest House. Muddy sand with little *Cerithium*, but other large turriform gastropods, oyster shells, barnacles and occasional small *Natica*; sediment also contains some small twigs and black decayed leaves. Population very localized but plentiful. *Natica* an important predator here.
12. *Batticaloa* (28 January 1974). Near entrance to the lagoon close to the lighthouse. Fairly dense population, associated with countless medium-sized *Cerithium* and other gastropods and many bivalves, many of them alive. Sediment more sandy than muddy. No signs of *Natica* predation.
13. *Trincomalee* A (10 February 1974). Inner Harbour. Near the Orr's Hill Road northeast of the Welcombe Hotel. Stony beach with gravel and small pebbles. Numerous bivalves and gastropods (rather few *Cerithium*; empty shells of large *Murex* and many other gastropods). *Clithon* plentiful.
14. *Trincomalee* B (11 February 1974). Eastern corner of Yard Cove close to road from Dambulla. Very shallow bay, much less stony and more muddy than *Trincomalee* A, full of many gastropods (including many large *Cerithium*) and bivalves. Main pedators seem to be large crabs which try to crack *Clithon* right across; no evidence of predation by small hermit crabs or by *Natica*.
15. *Trincomalee* C (13 February 1974). Cod Bay, next to road (culvert $\frac{80}{4}$) and railway, opposite Mangrove Island. Thin layer of coarse sand over thick layer of blackish mud and sand. Plentiful population associated with numerous *Cerithium*, etc.
16. *Trincomalee* D (13 February 1974). Near Road A15, about 0.4 km ($\frac{1}{4}$ mile) south of China Bay Airforce Station, on the west side of the peninsula, i.e. in a northeastern outpocketing of Tambalagam Bay. A plentiful population nearly all on eelgrass on somewhat swampy ground. Few *Cerithium*. Snails easily obtained by hand-picking.
17. *Mutur* (14 February 1974). Description supplied by L.N. and G.A. About 200 yards north of launch jetty. 'Marshy land, grassy, short grassy seaweed towards water. Blackish muddy shore, fine sand beneath the thin layer of mud. Almost no dead shells. *Cerithium* widely spread, but not a very thick population. Still stagnant water, almost no current, but tide rose quite quickly within the 45 min during which the collection was made.' The snails could be separated from the fine-grained sediment almost completely by sifting so that a virtually pure sample was obtained by that simple method. Collected by L. Nugaliyadde and G. Abeyasekera.
18. *Trincomalee* E (15 February 1974). China Bay, by milestone 78, near the south side of the jetty. Mainly small stones and very coarse sand (very similar to Trincomalee A). Little *Cerithium*. Population plentiful (collection took only 15 min). In a sample of 100 dead *Clithon* shells, 40 had been predated by *Natica*, 20 probably by hermit crabs of various sizes, and 40 showed no obvious signs of predation.
19. *Tondaimanar* (10 March 1974). Location about 9° 49′ N, 80° $7\frac{1}{2}'$ E, roughly 13 km (8 miles)

west of Point Pedro. East side of inlet to lagoon, about 150 m from the bar. Coarse sand with many small stones, with very little mud. Locality small and circumscribed, but *Clithon* population fairly numerous. On the west side of the inlet to the lagoon, only a few dead shells were found.

20. *Mannar* (20A: 377 animals collected by Dr A. Gunatilaka (Peradeniya) on 17 February 1974; 20B: 2150 snails collected by author on 12 March 1974). Next to railway bridge situated roughly 0.4 km ($\frac{1}{4}$ mile) southeast of Mannar Railway Station. Snails hand-picked from eelgrass which grows on rich, black, oozy, squelchy mud in a locality not far from small mangroves. Biotop most similar to that in Trincomalee D. Plentiful population of large *Clithon*.

Malaya–Singapore

21. *Mata Ikan, Singapore* (21A collected by Dr A. G. Searle on 23 January 1955; 21B collected by Professor Shou-Hwa Chuang (Singapore) on 11 April 1973). For 21A, all snails collected from within 40 9 in^2 quadrats thrown at random within area of medium density (approximately half-way between upper and lower limits). Random samples also taken from seaward and landward edge of distribution area (not by quadrats but by clearing larger areas of all snails enclosed in them). On muddy sand. (The above refers to a larger collection than the 270 individuals sent to me. H.G.)
22. *Port Dickson, Malaya* (collections made by Dr Yong Hoi-Sen (Kuala Lumpur) on 10 October 1971, on 8 March 1972 and in October 1972 respectively). Blue Lagoon Mangrove, Port Dickson. 'These snails were collected in a relatively very small area, roughly 10 ft × 10 ft near the mangrove. The animals do not sit on the roots of mangrove trees but are buried under sandy-clay. During low tide they surface and move around...the collection was by no means exhaustive'.

Hong Kong

1. *Shui Hau, Lantau Island* (6 November 1973). Moderately muddy sand at head of bay near mouth of a freshwater rivulet. *Clithon* all small and associated with other small molluscs, notably *Cerithium*.
2. *Ngau Hom Sha, Deep Bay*, N.T., H.K. (8 November 1973). A rich mud on open though sheltered beach, close to shore. *Clithon* large and associated with numerous large *Cerithium*, about 2.5 cm (1 in) long. From the large size of both, it is obvious that the oozy mud is rich in nutrients.
3. *Ha Hang*, near Tai Po Market, Tolo Harbour, N.T., H.K. (14 November 1973). Contaminated beach, muddy but full of stones, broken glass, tannery debris, etc. *Clithon* in vast numbers associated with many small molluscs, notably *Cerithium*. Many broken shells of *Clithon* (? predation).
4. Near *Tai Mong Tsai*, Sai Kung, N.T., H.K. (16 November 1973). Inlet next to jetty. Rather sparse population on compacted mud with many stones. Roughly $\frac{1}{4}$ of the sample hand-picked and thus possibly somewhat selected for conspicuousness. (Note added 3 days later: following sorting, it becomes clear that the population is less sparse than appeared at first. Hence the hand-picked shells are a much smaller fraction and the possibility of selection, for practical purposes, may be discounted.)

5. Map reference JV 919 766 (Map of Hong Kong and New Territories 1:100000, published by D. Survey, Ministry of Defence, U.K., 1970). Near Brothers Point, N.W. of Tai Lam Chung Marine Police Base, N.T., H.K. (collected by Miss Fung Lin-Foon, Hong Kong, on 20 November 1973). *Clithon* plentiful on muddy sediment near freshwater rivulet; accompanied by many medium-sized *Cerithium* and other turriform gastropods.
6. *Lap Wo Tsuen*, Starling Inlet, N.T., H.K. (21 November 1973). Collected near mouth of rivulet near mangrove swamp. Fairly hard muddy sand. *Clithon* not very plentiful. Under the surface sediment with *Clithon* very stony ground. Associated with many *Cerithium*, some of them large.
7. *Tai Tam Bay*, Hong Kong Island (collected by Dr Brian Morton (Hong Kong) in October 1972). Head of bay, on muddy sand. Unselected sample from which adult and juvenile sub-populations could easily be separated.

Appendix 4. Laboratory experiments with *Clithon*

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At the suggestion of Professor Grüneberg, studies were initiated in December 1973 with a view to breeding *Clithon* in the laboratory. This has now been successful. But as several ancillary investigations are not yet complete and as a systematic breeding programme has barely been started, it seems advisable to postpone full publication until more data are available. I shall here merely report the results of some preliminary experiments which, however, help in the interpretation of the population data which form the main part of this paper.

The pilot studies designed to develop breeding methods for *Clithon* in the laboratory were carried out in large aquaria which required the use of groups of animals (rather than paired matings) for a suitable population density. The snails were introduced into the tanks as juveniles of less than 5 mm in diameter which had presumably not yet reached sexual maturity. The animals were collected in Pitipana, Negombo, and each parental group included typical specimens of a single phenotype only, except in experiment 6, table 22. Table 21 includes groups with axial and table 22 groups with spiral patterns. In addition, a group of snails with purple spirals from Trincomalee A has produced 8 offspring, all of them purple spirals. The data

Table 21. Offspring of mass matings of snails with axial patterns

experiment	parents	f.t.l.	c.t.l.	many small tongues	total
1*a*	f.t.l.	3	0	0	3
1*b*	f.t.l.	13	2	3	18
2*a*	f.t.l.	26	1	5	32
sub-total	f.t.l.	42	3	8	53
3*a*	c.t.l.	17	4	0	21
4*a*	many small tongues	11	12	18	41
total		70	19	26	115

of tables 21 and 22 show that axial and spiral patterns are genetically distinct. And the breeding behaviour of purple spirals strongly suggests a simple genetic basis.

TABLE 22. OFFSPRING OF MASS MATINGS OF SNAILS WITH SPIRAL PATTERNS

experiment	parents	many small tongues	spiral tongues	spiral tongues + small tongues	ladders	ladders + small tongues	total
5*a*	spiral tongues	0	40	7	6	0	53
6	spirals	12	17	11	1	5	46
7	ladders	0	2	0	4	2	8

Note: experiment 6 included among the parents various kinds of spirals. It was set up in December 1974 and the offspring first classified in May 1975. By July 1975, five of the offspring with many small tongues (which had by then reached a diameter of about 5 mm) had developed spiral tongues whereas the remaining seven animals were unchanged.

Note added in proof 25 *March* 1976. Since this manuscript was completed, additional collections of *Clithon* have been made in India during the period from December 1975 to February 1976. These throw fresh light on the situation reported in this paper and will be submitted to the Society in due course.

The colour plates in this issue were printed by Henry Ling Ltd, The Dorset Press, Dorchester, Dorset.


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FIGURE 21. Fine transverse lines (f.t.l.).
FIGURE 23. a–d, f: tiger; e: zebra.


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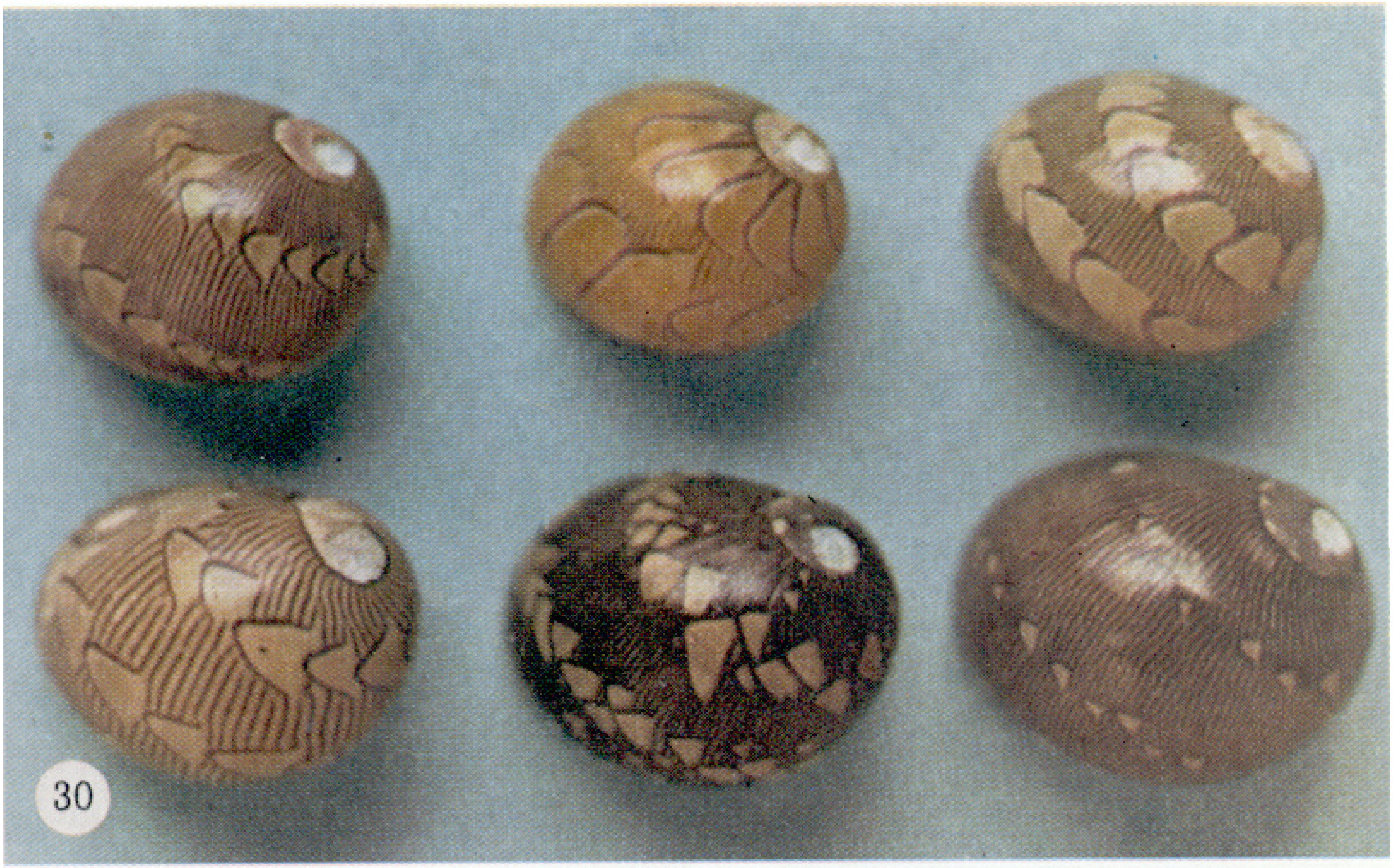
FIGURE 22. Coarse transverse lines (c.t.l.).
FIGURE 24. Little tongues, yellow.

FIGURE 25. Many small tongues.
FIGURE 27. Large and giant tongues.

FIGURE 26. Large and giant tongues.
FIGURE 28. Large and giant tongues.

FIGURE 29. a, c–f: spiral tongues; b: large tongues, spiralization dubious.

FIGURE 31. a and c: yellow spirals (transitional to spiral tongues); d and e: yellow spirals; b: black-and-white spiral; f: narrow spiral.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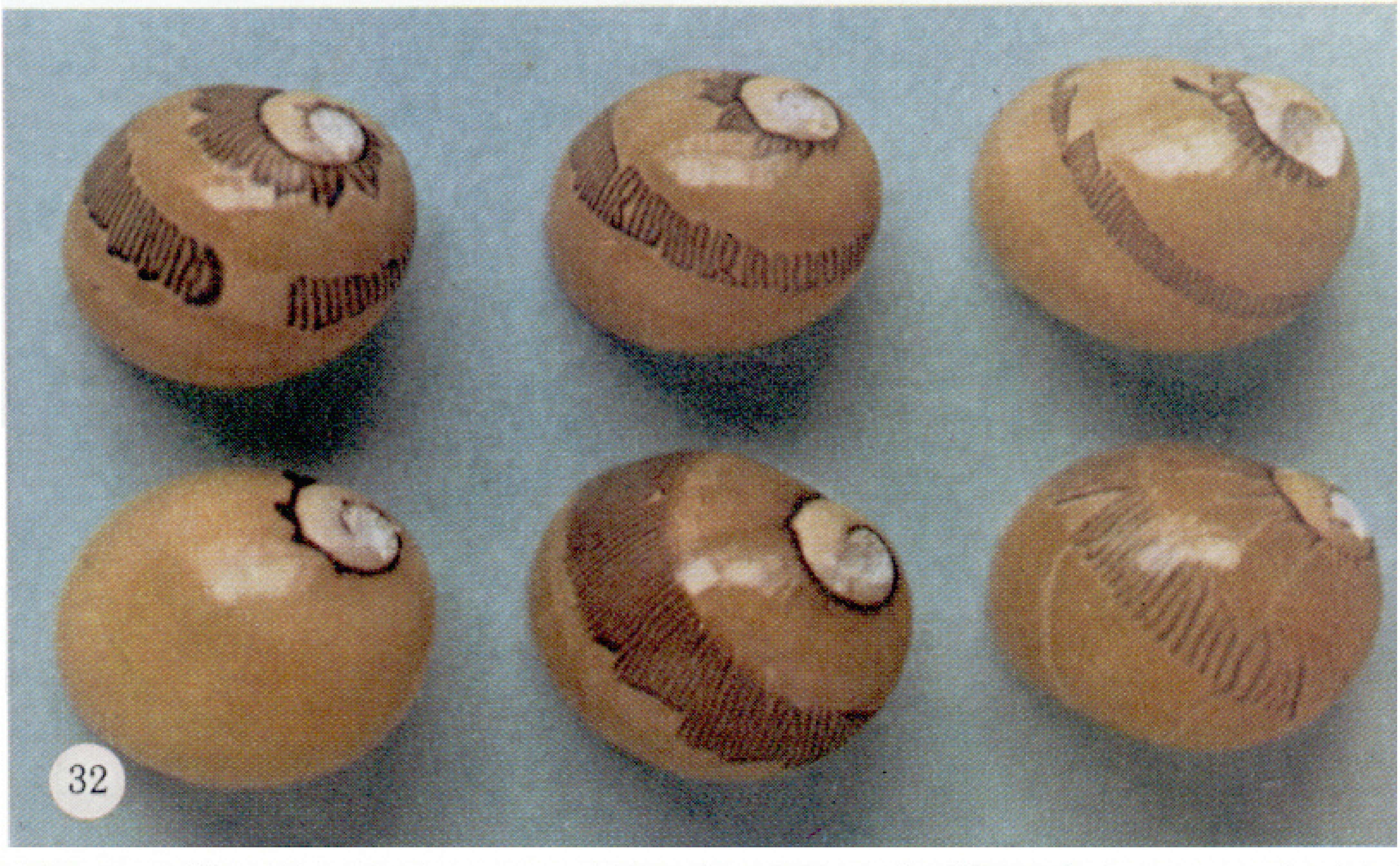
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FIGURE 30. Spiral tongues; b and c: purple-tipped tongues (p.t.t.); f: narrow spiral tongues.

FIGURE 32. a–c, e and f: yellow spirals; d: juvenile form of either yellow spiral or giant tongues.

FIGURE 33. Purple spirals.

FIGURE 35. a–c, e and f: purple (note the chalk lines in most of the spirals); d: a purple spiral on a very dark purple background.

FIGURE 34. Black.

FIGURE 36. Group of *Clithon* shells from Tai Po Marshes, Tolo Harbour, N.T., Hong Kong, a locality not mentioned elsewhere in this paper. It illustrates the appearance of an unsorted sample.