AQUATIC MOLLUSCS OF THE INLE LAKE AND CONNECTED WATERS.

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(Plates X—XIX.)

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INTRODUCTION.

The following paper is based on the collection of Mollusca made in the Inlé Lake and the surrounding district by Dr. F. H. Gravely and myself in February and March, 1917.

The district is one of great interest to students of the freshwater Mollusca because it is one of those in which the fauna, apparently isolated for a long period, has proved extraordinarily plastic, with the result that large numbers of peculiar forms have been evolved. It is not necessary here to describe its physical characters as this has already been done in the Introduction to the volume, but there are a few points that it is of importance to remember. In the first place, the Inlé Lake, which lies on the Shan Plateau at an altitude of 3,000 feet above sea-level, occupies a basin that it has dissolved for itself out of limestone. Its water, therefore, contains abundant salts of lime

and also of magnesium. Though now shrunken and shallow, the lake is the last relic of a once extensive lake-system and was at a period geologically not remote both larger and much deeper than it is at the present day. The water of its central region is remarkably clear and its bottom covered with a peculiar semi-liquid mud formed of calcareous particles and fragments of decayed vegetable refuse. Round the margin there is a curious rim of floating islands composed of dead and living plants, and the formation of peat is proceeding with great activity. The water of the marginal zone is, therefore, much contaminated. Considerable differences exist in the fauna of the two regions. Certain peculiarities can also be observed in that of the intermediate zone between the two. As there are no rocks or stones in the lake rupicolous molluscs are absent.

Many of the specimens from the lake were obtained by dredging, others by the careful examination of masses of weeds. We also searched several of the small streams that flow into the lake, as well as the larger streams and swamps of the He-Ho plain, which lies a few miles to the south-west at an altitude about 800 feet higher. Further, we obtained good series of fossil and subfossil shells from several deposits both in this plain and in the Hsing-Dawng valley some five miles north-east of the lake.

So far as I am aware, no molluscs have been recorded from the Inlé Lake, but several of the species common to it and neighbouring waters have been described by Theobald,[1] by Nevill,[2] by von Martens,[3] by Kobelt[4] or by Pilsbry,[5] from the Northern Shan States and Upper Burma. The species described by Theobald have been admirably figured in Theobald and Hanley's *Conchologia Indica* (1876). I have found the references to literature in Mr. H. B. Preston's volume on the freshwater Mollusca (1915) in the *Fauna of British India* series of great value, though they are far from complete. I have to thank my friends Mr. E. Vredenburg of the Geological Survey of India and Mr. Stanley Kemp of my own department for going through certain parts of the proofs of this paper and making valuable suggestions.

Part I.—SYSTEMATIC.

Gastropoda.

Order **PULMONATA.**

Family SUCCINEIDAE.

Genus **Succinea,** Draparnaud.

It is only by some stretching of terms that a species of *Succinea* can be dealt with in a paper exclusively on aquatic molluscs, for there

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[1] *Journ. As. Soc. Bengal* (2), XXXIV, pp. 273-279 (1865).
[2] *Journ. As. Soc. Bengal* (2), XLVI, pp. 14-41 (1877).
[3] *Wiegm. Arch. Naturg.*, LXV (1), pp. 30-48 (1899).
[4] *Paludinen* in Martini and Chemnitz's *Conch. Cab.* (ed. Küster), (1909).
[5] *Proc. Ac. Nat. Sci. Philadelphia*, pp. 188-190 (1901).

is no reason to think that this species differs from its congeners in habits. It lives at the edge of water and can doubtless swim attached shell-downwards to the surface film, but does not lead a true aquatic life. My reason for referring to it here is the remarkable resemblance between its shell and that of a *Limnaea* to be discussed later (p. 109).

Succinea indica, Pfeiffer.

Plate x, figs. 10, 11 ; plate xi, figs. 5, 6.

1876. *Succinea indica*, Hanley and Theobald, *Conch. Ind.*, pl. lxvii, figs. 1 & 4.
1914. *Succinea indica*, Gude, *Faun. Brit. Ind., Moll.* 11, p. 447.

Living specimens were found at the edge of the Inlé Lake at Thalé-u on the eastern shore and in the swamp at the northern end. Subfossil shells occur in considerable numbers in the superficial deposits on the He-Ho river just above its gorge.

Shells from the Inlé Lake (fig. 10, pl. x) agree as regards outline and general appearance with Theobald and Hanley's figures, but are rather smaller (14 mm. long) and of a darker colour. The animal is that of a normal *Succinea*. I figure the jaw and a central and a lateral tooth from the radula (pl. xi, figs. 5, 6). Subfossil shells from the He-Ho river (pl. x, fig. 11) are thicker and have the growth-lines so coarse that the surface approaches that of *S. plicata*, Blanford, in sculpture. They do not differ otherwise from living shells.

The species is essentially a Himalayan one, hitherto known from Kumaon and Kashmir. Gude (*op. cit.*, 1914) doubts the identity of Egyptian shells assigned to it by Jickeli.

Family LIMNAEIDAE.

Genus **Limnaea,**[1] Lamarck.

The genus is cosmopolitan and capable of living in conditions generally unfavourable to molluscs, for example at great altitudes and in great depths. Its shell is remarkably plastic and varies in size, shape, thickness and colour with changes in the environment. This character of plasticity is admirably illustrated by the forms found living and fossil in the Inlé and He-Ho basins. I have been able to recognize only three species among the living forms, but one of these has several fossil and subfossil phases. I have also to refer briefly to a fourth (fossil) species represented in our collection by two imperfect shells.

The three living species fall into two well marked groups and in one of these a remarkable series of shells can be arranged, linking together two living species unlike in shell-characters by means of several apparently extinct phases. The third living species has two distinct phases, each of which lives in a different kind of habitat.

[1] I take this opportunity to state that the species from Japan described by Preston (*Ann. Mag. Nat. Hist.*, (8) XVII, p. 160, pl. ix, fig. 6, 1916) under the name *Lithotis japonica* is not related to the Indian species of *Lithotis* and does not belong to the Succineidae. The radula is that of a *Limnaea*. The shell is like that of *L. brevispira*, von Martens.

A noteworthy feature of the Shan *Limnaeae* is their small size. We saw no shell more than 12 mm. long.

Limnaea andersoniana, Nevill.

Plate x, figs. 1, 2.

1877. *Limnaea andersoniana*, Nevill, *Journ. As. Soc. Bengal*, (2) XLVI, p. 26.
1881. *Limnaea andersoniana, id., ibid.*, L (2), p. 142, pl. v, fig. 9.

"Shell small, horny brown, imperforate, globose, spire short; whorls four to five, last whorl large, ovate; columella remarkably thick and reflected, straight, without any twist; aperture subovate, anteriorly rather wide.

This small species, well characterized by its remarkable columella, is unlike any Indian species; the figure that it most resembles in 'Kuster's Monog.' is var. of *L. peregra*, pl. 3, figs. 17, 18; there is no shell like it figured in the 'Conch. Iconica'; probably *L. andersoniana* will prove to be a common species throughout S. China." (*Nevill*).

The species was originally described from Yunnan. It was also recorded by its author from the Shan States, but there is no reference to it in Preston's volume in the official *Fauna of British India* (1915). The shell, as Nevill notes, resembles that of *L. pervia*, von Martens, a common Chinese and Japanese species, but differs in its very coarse columellar callus; his statement that the columella is absolutely straight is not substantiated by either his figure or his type-specimen. The animal has a peculiar leaden grey colour, which extends almost uniformly over all the exposed parts except the sole of the foot, this being pale. The jaw and radula are of normal type. The lateral teeth are bicuspid and one of the cusps is very long and slender.

Both in the Chinese collection obtained by the late Dr. J. Anderson and examined by Nevill and in our own, shells of two forms are present. I have no information about the habitat of the Chinese molluscs except that they were taken at an altitude of about 4,000 feet. In the Inlé basin, however, the two forms of shell represent two distinct phases of the species, each associated with a definite type of habitat. In one phase (pl. x, fig. 1) the shell is relatively broad and, though by no means large, is considerably larger than in the other, attaining a length of 12 mm. Nevill selected a shell of this phase as the type of the species and figured it in 1881. Shells of the other, narrower phase (pl. x, fig. 2) do not exceed 9 mm. in length. They are duller and greener in colour and perhaps a little thicker. The larger, broader form of shell is found in ponds and marshes amidst dense aquatic vegetation; we took a single dead shell floating on the surface of the water at the edge of the Inlé Lake. The smaller form was observed in considerable abundance in a small slow-moving stream with a muddy bottom and devoid of vegetation at Fort Stedman (*ca.* 3,000 feet). We also collected a few shells in small streams at Thamakan (Hsamönghkam) about 1000 feet higher.

[**Limnaea bowelli,** Preston.]

Plate x, fig. 4.

1909. *Limnaea bowelli*, Preston, *Rec. Ind. Mus.* III, p. 115, figs. 1, 2.

This species is known only from very high altitudes (13,000 to 14,000 feet) in Tibet, where it lives in small streams.

Preston describes the shell as follows :—

"Shell rimate, acuminately ovate, rather solid, polished, shining, pale yellowish horn colour; whorls 4, shouldered above, marked with rather coarse lines of growth: sutures deeply impressed; columella obliquely and diffused above into a thick callus which joins the upper margin of the peristome; peristome simple; aperture ovately, inversely auriform."

He also refers, on the authority of the Rev. E. W. Bowell, to the peculiar form of the upper jaw, the central part of which is produced into a blunt beak-like projection, and to the *Planorbis*-like appearance of the radula. Mr. Bowell even suggested the erection of a new genus on account of the former character.

I mention *L. bowelli* here because we found in the Inlé and He-Ho basins a series of fossil and recent shells that differed considerably in different deposits and zones but formed a very regular gradation between a shell that resembled that of *L. bowelli* in certain characters but differed from it considerably in others, and one that had little outward resemblance to it. The only living phase in this series, moreover, though far removed from the Tibetan form in shell-characters, proved on comparison to be identical with it in buccal armature. *L. bowelli* is probably itself a modified form, living as it does at an almost unique altitude, but it is, to say the least, highly probable that still further links might be found between it and the various phases I have here grouped together under the name *L. shanensis*.

Limnaea shanensis, sp. nov.

Plate x, figs. 5, 8; plate xi, figs. 2, 3.

The shell in all the phases of this species is much narrower than in *L. bowelli*, the aperture is less patent, the peristome projects less, the spire consists of two instead of three whorls, the whorls are not at all flattened above and the suture is more sinuous and more oblique. These characters become intensified with the gradual evolution of what appears to be a true lacustrine deep-water type, but certain features are always retained, *viz.*, the complete aperture, the imperforate but rimate condition of the shell, the short, rather blunt spire, impressed suture, ovate form, coarsely developed growth-lines and small size. More important than any of these is the structure of the jaw and radula in the only living phase. Each phase, of which I can distinguish four, is or was associated with a definite type of environment. I will refer to them alphabetically and describe them *seriatim*. The complete gradation is better shown on plate x than can be described in words.

Type-specimen (phase A). No. M. 11059/2, Zoological Survey of India (*Ind. Mus.*).

Phase A.

In this phase the shell is nearer that of *L. bowelli* than any other, but there are distinct and constant features in the much narrower form, more oblique suture, longer and narrower aperture, etc. The shell is fairly thick and its growth-lines are very coarse. It is of approximately

the same size as the type of *L. bowelli*. The following are the measurements of a specimen :—

	mm.
Length	9
Greatest breadth	6·5
Length of aperture	6·25
Greatest breadth of aperture	3·75

The shell occurs abundantly in the friable clay of the He-Ho lake-deposit at an altitude of about 3,600 feet. The specimens are well preserved so far as form is concerned, but difficult to extract in a perfect condition owing to their fragility. They have evidently sunk to the bottom of an open lake and there been buried in very fine mud. This phase is, therefore, the most ancient with which we are acquainted as well as the nearest to the Tibetan species. It is very constant.

Phase B.

The shell is still narrower than in phase A and the aperture, which is of about the same length, is constricted posteriorly. The suture is still more oblique and the apical whorl is reduced in size. The shell is rather thick and has still coarser growth-lines. There is no great divergence in size from the former phase. The measurements of shells are as follows :—

	mm.	mm.	mm.
Length	10	9	8·5
Greatest breadth	6	5·75	5
Length of aperture	6·5	6	5·75
Greatest breadth of aperture	3·75	3·5	3

Shells are abundant in the superficial deposit on the banks of the He-Ho river just before it plunges down towards the Inlé plain, about a mile to a mile and a half east of the point where the types of phase A were discovered and at a slightly lower altitude. It is probable that the deposits represent the debris at the edge of a marsh or lake. The shells are sometimes slightly waterworn and as a rule more or less broken. I class them as subfossil. They also are constant.

Phase C.

This is the only phase I have seen in a living condition. The shell is thin and fragile but of a rather dark brown colour. It is a little narrower and more acuminate than that of phase B and has the apical whorl still smaller, but the suture is not quite so sinuous and the aperture is not so contracted posteriorly. The growth-lines are conspicuous but not so coarse. The rimation, though quite distinct, is less strong. The shell is rather larger ; the following are measurements of two specimens :—

	mm.	mm.
Length	10·25	8
Greatest breadth	6	4·25
Length of aperture	7	5
Greatest breadth of aperture	4	2·25

We found a small but constant series of living specimens near the shore-line of the marginal zone of the Inlé Lake at Fort Stedman. They were living amidst much decaying vegetation matter in conditions which favoured the formation of peat.

Phase D.

The shell is thicker than that of phase C and has coarser growth-lines. The sutures are sinuous but not very oblique and the whorls of the spire swollen. The apical whorl is very small and almost globular. The body-whorl is contracted and the whole shell is narrow. The aperture is also narrow but less contracted posteriorly than in phase B. The columellar callus is less well developed than in the other phases. The size is much reduced, as the following measurements will show :—

	mm.
Length	6·5
Greatest breadth	2·75
Length of aperture	4·5
Greatest breadth of aperture	2

I only know this phase from two dead shells dredged from the bottom in about 7 feet of water in the central region of the Inlé Lake. There is no doubt that the animal lived approximately in the place where the shells were found, for one of the specimens has been perforated (see figure) and must have sunk at once into the bottom of the lake. The phase is of great interest in that, while clearly a member of the same series as the other phases, it leads on towards the next species, which I have called, for other reasons, *L. mimetica*.

Considering all these phases together we may be sure of the following facts :—

(*i*) They may be regarded conventionally as the links in a chain of evolution in which the tendency is towards a narrowing of the shell and of its aperture and a reduction of the spire.

(*ii*) Evolution has affected the buccal armature less than it has affected the shell and though there is a distinct break in shell-form between phase C and the Tibetan species with which I have associated the phases, the radula and jaw are practically identical.

I will discuss the significance of these facts when dealing with variation among the shells of the Inlé and He-Ho basins (*v.* p. 151).

Limnaea mimetica, sp. nov.

Plate x, figs. 9, 9*a* ; plate xi, fig. 4.

The shell is very small and delicate, transparent, colourless or tinged with yellow, imperforate, rimate, narrow, subcylindrical. It has the lines of growth well marked but not coarse. The spire, which is set on the body-whorl at a slight angle, is blunt and short, but so obliquely spiral that it appears twice as long in the dorsal as it does in the

ventral aspect ; in the latter it occupies only one tenth of the length of the shell. It consists of two whorls, which are neither shouldered nor markedly tumid. The suture is not or hardly impressed. The body-whorl is ovate, elongate and narrow ; its lateral outlines do not project far beyond those of the base of the spire ; its anterior internal margin is broadly rounded, its anterior outer margin angulate and a little produced. The aperture is almost straight, narrow, elongate and practically lanceolate in outline. Posteriorly it tapers gradually to a fine point and in front it is angulate externally. The peristome is simple, the rimate margin of the orifice distinct but delicate. The columella is almost concealed ; it is nearly straight and slopes forwards and outwards. Its callus is feebly developed.

The animal is that of a typical *Limnaea*. The foot is very extensible but can be retracted well within the shell. The tentacles are short. The whole external surface is white or greyish, with black eyes and an effusion of black pigment on the dorsal surface of the body and on the mantle. The specimens examined are sexually mature. A figure of the genital system, dissected out and drawn for me by Dr. Baini Prashad of the Bengal Fishery Department, is reproduced on p. 175 of this paper. It seems quite normal, but all the parts are slender as compared with those of European and American species. The spermathecal duct is long and the penis-sheath stout.

The jaw resembles that of *L. bowelli*, but is much less produced. The radula (pl. xi, fig. 4) is also similar, but the cusps of the lateral teeth are more nearly equal and equidistant and the marginal teeth (except at the extreme edge) have four instead of three cusps.

	mm.
Length of shell	6
Greatest breadth of shell	2·5
Length of aperture	4·25
Greatest breadth of aperture	2

Type-specimen. No. M. 11271/2, Zoological Survey of India (*Ind. Mus.*).

The species is probably but the final stage in a line of evolution similar to that of the phases of *L. shanensis* (pl. x, figs. 4–8). It may be no more than an extremely degenerate phase of *L. acuminata*,[1] Linn.

L. mimetica lives amidst dense growing vegetation both in the intermediate zone and the central region of the Inlé Lake, but probably avoids the extreme edge. It is not uncommon but nowhere abundant. Individuals from the intermediate zone have both shell and soft-parts darker than those from the open lake.

In general appearance the shell bears a very striking resemblance to that of *Succinea indica*, a mollusc not uncommon at the edge of the Inlé Lake, but one that does not live submerged. The shell of this semi-terrestrial species differs from that of the *Limnaea* in its much

[1] The upper jaw of *L. acuminata* is not produced in front, but the radula is very like that of *L. mimetica*. I am not convinced that the shape of the jaw is constant. Moreover, the radular teeth are subject to minor variations in shape.

arge size, darker colour, less extreme fragility, non-rimate character and non-angulate anterior margin. How close the resemblance is in other respects is shown clearly by figs. 9–11 on plate x.

It is difficult to see how this resemblance can be anything but fortuitous. It can be of no protective value to animals that never meet, have entirely different habits and probably different enemies. It cannot be due to convergence, to use the term in its technical sense, because of the difference in habits. It is well that attention should be called to apparently fortuitous resemblances of the kind, for they are apt to be ignored by students of mimicry—a series of phenomena as to the meaning and causation of which I must confess myself, after nearly twenty years' experience of tropical nature, in an agnostic frame of mind.

Limnaea ? prox. **ovalis,** Gray.

Plate x, fig. 3.

I am unable to assign two fossil specimens from the old lake-deposit in the He-Ho plain to any described species but think it probable that they represent one allied to *L. ovalis* (pl. x, fig. 3). They are not unlike some dwarfed shells of *L. ovalis* from pools of brackish water in Orissa, but differ in the almost complete bilateral symmetry of the body-whorl and in the very long aperture. With such imperfect material it is best not to give the form a name.

Genus **Planorbis,** Geoffroy.

Living specimens of five species of this genus were found in the Inlé Lake, while the shells of a sixth are not uncommon in the superficial deposits of the He-Ho plain. These six species fall into three of the subgenera or groups into which the genus has been divided, *viz.*, *Planorbis, s.s.; Gyraulus,* and *Segmentina.* They may be distributed into these groups as follows :—*Planorbis exustus* to *Planorbis s.s.*, *P. saigonensis* (subfossil), *P. velifer*, sp. nov. and possibly *P. trochoideus*, which lacks the characteristic internal partitions of the shell of *Segmentina*, to *Gyraulus; P. calathus* and *P. caenosus* to *Segmentina.*

Planorbis exustus, Desh.

Plate xi, figs. 1, 1*a*.

1834. *Planorbis exustus*, Deshayes, *Belang. Voy. Ind. Orient., Zool.*, p. 417, pl. i, figs. 11-13.
1836. *Planorbis Indicus*, Benson, *Journ. As. Soc. Bengal*, V, p. 743.

The shell of this species seems to differ from *P. coromandelicus*, of which I have examined specimens from Bangalore, in its less inflated whorls, darker and duller colour and in the fact that the angle at the lower end of the mouth is less produced. Shells from the Kashmir lakes, from a small pond of slightly brackish water on Barkuda Island in the Chilka Lake, from the marginal zone of the Inlé Lake and from ponds and swamps at Yawnghwe and on the He-Ho plain are closely similar ; except that the Kashmir examples are a little smaller. Speci-

mens from the Talé Sap in Peninsular Siam differ very little. The species, therefore, seems to be a remarkably constant one, neither plastic nor variable. It is common in the more swampy parts, close inshore, of the marginal zone of the Inlé Lake and in all ponds, etc., in the district. It is found in similar situations in Bengal and Siam and it does not appear to be anywhere a true lacustrine mollusc.

I figure the shell of a very young individual, which puzzled me greatly until I had seen a series.

Planorbis saigonensis (?), Crosse & Fischer.

Plate xi, fig. 12.

1909. *Planorbis saigonensis*, Germain, *Rec. Ind. Mus.*, III p. 117.
1915. *Planorbis* (*Gyraulus*) *compressus*, Preston, *Faun. Brit. Ind., Freshw. Moll.* p. 118.

Germain has discussed the synonymy of this species in the paper cited. I assign to it with some doubt a number of subfossil shells from the banks of the He-Ho stream. They seem to be intermediate between *P. saigonensis* and *P. convexiusculus*, which is perhaps no more than a variety, but in none of them is the aperture definitely lunate. In some a faint peripheral ridge can be detected, while in others there is no trace thereof. The largest shell is only 5 mm. in greatest diameter.

The species is widely distributed in Mesopotamia, Afghanistan, India, Indo-China, China, Japan and the Malay Region.

Planorbis velifer, sp. nov.

Plate xi, figs. 7—11.

Shell minute, delicate, transparent, colourless or faintly tinted with yellow, with very fine close-set regular transverse striae, with $3\frac{1}{2}$ whorls, slightly depressed above in the centre, with the upper surface very slightly convex and the suture impressed, with the periphery angulate and as a rule faintly carinate, with the centre of the lower surface moderately depressed and with this surface otherwise almost flat ; aperture large, broad, moderately oblique, its lower margin slightly concave, its upper margin moderately convex ; the edge of the lip sharply defined without thickening ; no internal callus. Maximum diameter 4 mm., minimum diameter 3·5 mm., height 1·75 mm.

Type-specimen. M. 11288/2 Zoological Survey of India (*Ind. Mus.*).

var. **ciliata,** nov.

This variety only differs from the typical form in having a variable number (usually five or six) of spiral ridges on both surfaces. These ridges are formed entirely of very minute epidermal cilia closely pressed together. They are often obsolete.

The two forms of shell fade gradually one into the other. Both exhibit considerable variation in the size and obliquity of the aperture

and in the degree of depression of the whole shell. In both there is usually a curious protruding veil-like structure running along the peripheral carination or angle. This " velum " is rarely altogether absent, but I believe it to be of parasitic origin. The presence of a similar structure on the shells of *P. saigonensis* is perhaps indicated in Clessin's[1] figure of the upper surface of the shell of *P. compressus*. In well-preserved specimens it has a gelatinous appearance and is full of bacteria.

The species (both varieties) is common in all parts of the Inlé Lake among dense masses of living weed.

Possibly *P. velifer* should be regarded simply as a lacustrine phase of *P. saigonensis*. Its shell closely resembles subfossil specimens from He-Ho, except that it is considerably smaller, has the sculpture finer and more regular and appears to be thinner. The subfossil shells are naturally more opaque than living ones.

Planorbis trochoideus, Benson.

1836. *Planorbis trochoideus*, Benson, *op. cit.*, p. 742.
1876. *Planorbis trochoideus*, Hanley and Theobald, *Conch. Ind.*, pl. xxix, figs. 4-6.

This species occurs commonly with *P. velifer* in both the central region and the marginal zone of the Inlé Lake. It is also found in the fossil lake-deposit of the He-Ho plain. Shells from the lake agree well with Hanley and Theobald's figures. The largest are about 3 mm. in maximum diameter. They are diaphanous but tinted with yellow. I can find no trace of internal partitions such as exist in *P. calathus* and *P. caenosus*.

The species has hitherto been found only in the neighbourhood of Calcutta.

Planorbis calathus, Benson.

1850. *Planorbis Calathus*, Benson, *Ann. Mag. Nat. Hist.*, (2) V, p. 348.
1876. *Planorbis calathus*, Hanley and Theobald, *op. cit.*, pl. xxix, figs. 1-3.

P. calathus is common in the Inlé Lake with the two preceding species. The specimens are very small, not exceeding 3 mm. in maximum diameter. Some are colourless, while others are distinctly brownish, but all are transparent.

The species has a wide distribution in northern India (mainly in the Himalayas) and Ceylon ; it is also recorded from Siam.

Planorbis caenosus, Benson.

1850. *Planorbis caenosus*, Benson, *op. cit.*, p. 349.
1876. *Planorbis caenosus*, Hanley and Theobald, *op. cit.*, pl. xxix, figs. 7-9.

We found two very small specimens, only 2 mm. in maximum diameter, in the marginal zone of the Inlé Lake off Fort Stedman. They are fully adult, as one of them contains eggs in the ovary. In spite of their small size the shells agree well with Hanley and Theobald's

[1] Clessin, " Limnaeiden " in Martini and Chemnitz's *Conch. Cab.* (*ed.* Küster), p. 191, pl. xvii, fig. 10 (1886).

figures. They are transparent and of a faint yellowish colour. Possibly they represent a dwarfed race of the species.

P. caenosus has been found in Ceylon as well as in Northern India.

Order **PECTINIBRANCHIATA.**

Suborder **Taenioglossa.**

Family MELANIIDAE.

Genus **Melania,** Lamarck.

1915. *Tiara*, Preston, *op. cit.*, p. 10.

The species found living in the Inlé Lake and its basin belong to two groups or subgenera, *Striatella*, Brot and *Melanoides*, H. and A. Adams. The former is represented by the widely distributed and plastic *M. tuberculata*, while we have of the latter *M. terebra* and a race of *M. baccata*. A single shell of a form of *M. variabilis*, which also belongs to this group, was found in a cave-deposit at Hsin-Dawng. The only one of all these species that lives in the lake is M. *tuberculata*.

Melania tuberculata (Müller).

Plate xii, figs. 1, 2.

1874. *Melania tuberculata*, Brot, *Melaniaceen* in Martini and Chemnitz's *Conch. Cab.* (ed. Küster), p. 247, pl. xxvi, figs. 11-11*h*.

This is the most widely distributed species in the genus, ranging as it does from the southern and eastern shores of the Mediterranean, through Africa and Asia to China and North Australia. The shell is very plastic in certain characters, notably in size, but also to a lesser degree in shape and sculpture. I have before me a large series from many localities in India and the neighbouring countries and also from Mesopotamia, Palestine and China. Numerous varieties have been described, but our collection seems to prove that as a rule the differences are directly due to differences in environment rather than to locality. The tubercles on specimens from southern Asia are, however, often less strongly developed than in those from Palestine. I will discuss certain aspects of the plasticity of this mollusc in dealing with the variation and evolution of the Inlé shells. Here it will be sufficient to say that the shells, both living and subfossil, from the Inlé and He-Ho basins fall into three phases :—(1) normal living shells of rather dark colouration, of moderate size, not exceeding 25 mm. in length ; (2) subfossil shells which were apparently also of dark colour, but are much larger (reaching at least 35 mm. in length) and rather broader in the basal whorl ; and (3) subfossil shells of very small size with the suture much impressed. These do not exceed 16 mm. in length.

The first group still lives both in the central region of the Inlé Lake and in the middle of the Yawnghwe river, while shells of the other two occur at different points in the superficial calcareous and peaty

deposits on the He-Ho plain. Each of these phases was constant in the locality or precise deposit in which it was found.

Melania terebra, Benson.

Plate xii, fig. 9.

1836. *Melania Terebra,* Benson, *op. cit.,* p. 747.
1876. *Melania terebra,* Hanley and Theobald, *op. cit.,* pl. lxxi, figs. 8, 9.

A few living shells were found in the Yawnghwe river with *M. tuberculata.* They agree well with Hanley and Theobald's figures. The species is known from Sylhet and north-eastern Assam.

Melania baccata (Gould).

Plate xii, figs. 3, 3*a*, 4—7.

1915. *Tiara* (*Melanoides*) *baccata,* Preston, *op. cit.,* p. 26.

Melania baccata is a species, or possibly a group of species, that seems to have become differentiated on the Shan Plateau and in Upper Burma into a large number of well-defined races. To what extent all these races are constant we do not yet know, but the only one found living or subfossil in the Inlé and He-Ho basins, though it varies somewhat in sculpture and is plastic in size, is, nevertheless, remarkably constant in the shape of the shell, in which it differs from any form as yet described. I have thought it best, in view of our ignorance of the anatomy and our scanty knowledge of the distribution of the various "varieties," to call this form a subspecies, by which I mean a local race.

subsp. **elongata,** nov.

In shape the shell is long, narrow and tapering. When complete it has 11 or 12 whorls, but the first two are usually eroded. The aperture is very narrow and nearly oval; the lip is considerably produced forwards and the columella is less bent than in most forms of the species. The sculpture is always well developed; on the last three whorls there are usually three spiral rows of tubercles joined together by ridges in such a way as to form a very regular reticulation. On the body-whorl the uppermost row of tubercles is situated close to the upper edge. There are three well-developed simple or superficially somewhat undulated ridges beneath the lowest row. Sometimes, however, there are only two rows of tubercles on this and the preceding whorl. The shell is thin; the epidermis is dark-brown or dull olivaceous-green; internally the surface is white and somewhat opalescent, as a rule with several deep-brown spiral bands.

At least two phases of this race can be distinguished:—(*a*) With a very large shell, when complete nearly 80 mm. long and 26 mm. in greatest breadth, and (*b*) with a much smaller shell not exceeding 50 mm. in length and 17 mm. in breadth. Of the first phase we found only a few specimens, all living in a swamp on the He-Ho plain. The second phase is abundant in the Yawnghwe river in a living condition and is also common subfossil in peaty and calcareous deposits on the He-Ho plain.

The type-specimen of the race (belonging to the large form) is No. M. 11155/2 in the collection of the Zoological Survey of India.

Genus **Paludomus,** Swainson.

This genus is represented in our collection by two small shells only. They were found near the town of Yawnghwe. The genus, though occasionally found in still water, is usually an inhabitant of small streams and never lacustrine.

Paludomus ornata, Benson.

1856. *Paludomus ornata,* Benson, *Ann. Mag. Nat. Hist.,* (2) XVII, p. 496.
1876. *Paludomus ornata,* Hanley and Theobald, *op. cit.,* pl. cviii, fig. 8.

The two shells of this species in our collection are very small, the larger being only 15 mm. in length. They are covered with a thin but somewhat dense layer of calcareous matter, which partly conceals the parallel grooves running round the top of the whorls, and gives the shell a dull appearance. When this calcareous matter is removed, however, the natural colouration and sculpture of the surface appear uninjured.

The shells were found living on a muddy bottom in a small runnel of clear water by the roadside some two miles east of Yawnghwe.

The species was described from Upper Burma, but occurs also in Pegu and in the valley of the Brahmaputra.

Family HYDROBIIDAE.

1915. Paludestrinidae, Preston,[1] *op. cit.,* p. 67.

A large proportion of the members of this family are lacustrine and it is therefore not surprising that several species are common in the Inlé Lake. In Indo-China and China a number of peculiar genera have been evolved, but most of these seem to be peculiar to swift-running water, a type of environment of which we had little experience in the Shan States. None of the Indo-Chinese genera, perhaps for this reason, were found in the Inlé basin. With one exception, the six species of the family that we found belong to the peculiar genus *Hydrobioides,* Nevill. This genus was erected, as a subgenus of *Bithynia,* to include two species, one of which (*H. turrita,* Blanford) we found in a subfossil condition on the He-Ho plain, while the other, the position of which is still doubtful and which has not yet received a name, was from Kach. The named form was described from the Irrawaddi system and is still only known from empty shells, but four other species were found living in the Inlé basin and it has been possible to give a description of the operculum, the radula and the external anatomy of three.

The only other species of the family is assigned provisionally to the genus *Amnicola,* from the typical forms of which, however, it differs in its calcareous operculum.

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[1] Preston's removal of *Bithinella* (*op. cit.,* p. 66) from the family and its inclusion as a subgenus in *Cremnoconchus* (fam. Littorinidae) is not explained.

Genus **Hydrobioides**, Nevill.

1884. *Hydrobioides* (subgenus of *Bithynia*), Nevill, *Hand List Moll. Ind. Mus.* II, p. 42.

The shell is thick, of moderately small or minute size, imperforate, of somewhat variable shape but not definitely neritiform. The aperture is large, ovoid or subtriangular. There is a very stout columellar callus, which is in continuation at both ends with a thickening of the outer lip. The lip is often fortified also by a strong ridge or varix that runs across the outer surface of the shell a short distance from the margin.

The operculum is calcified and thick but often surrounded by a membranous margin. The nucleus is almost central and surrounded by numerous well-defined concentric striae.

The soft-parts, externally at any rate, closely resemble those of *Bithynia*, the penis in particular being bifid. Both of its branches are well-developed. There is a deep but narrow transverse groove on the sole of the foot parallel to and close behind the anterior margin.

The radula is like that of *Bithynia*.

Type-species. Bithynia (?) *turrita*, Blanford.

The genus is closely allied to *Bithynia*, of which it might, but for the inconvenience of multiplying subgeneric names, rank as a subgenus. Of the five species assigned to it, one approaches the stouter and shorter forms of *Bithynia* such as *B. orcula*, one is elongate, while the other three agree in general appearance with more normal species of *Bithynia* such as *B. tentaculata*. The most characteristic feature is the peculiar armature of the mouth of the shell.

The shells may be distinguished as follows :—

I. Shell more or less elongate, with the spire in the same axis as the body-whorl.
  A. A ridge or varix running across the outer aspect of the body-whorl ... ... *H. nassa.*
  B. No varix.
    1. Shell at least 6 mm. long.
      (*a*) Shell twice as long as broad ... *H. turrita.*
      (*b*) Shell much less than twice as long as broad ... ... *H. avarix.*
    2. Shell not more than 3 mm. long ... *H. nana.*

II. Shell globose, with the spire short, directed backwards and outwards ... ... *H. physcus.*

Hydrobioides turrita (Blanford).

1869. *Fairbankia ?* (an *Bithynia ?*) *turrita*, Blanford, *Proc. Zool. Soc. London*, p. 446.
1881. *Bithinea* (*?*) *turrita*, Nevill, *Journ. As. Soc. Bengal*, L (2), p. 157, pl. vi, fig. 15.
1884. *Bithinea* (*Hydrobioides*) *turrita*, Nevill, *op. cit.*, II, p. 42.

Blanford describes the shell as follows :—

"Testa subperforata, turrita, solidula, fulva, glabra, nitidula. Spira elongata-conica, sutura impressa. Anfr. 7, convexi, ultimus antice subascendens, subtus rotundatus. Apertura ovata, postice vix angulata, varice externo mediocri instructa; peristoma undique expansiusculum, marginibus callo junctis, externo leviter arcuato, columellari obliquo, antic ecum basali subangulatum juncto. Operc. ? Long. 6¼ diam. 3 mm.; aperturae long. 2½, lat. 1¾ mm."

Nothing is known of the operculum or of the soft parts, but the shell is so like that of the species here described as *Hydrobioides avarix* that they must be congeneric.

The species was described from Kyoukpong on the Irrawaddi. Several subfossil shells were found on the banks of the He-Ho stream.

Hydrobioides nassa (Theobald).

Plate xiii, figs. 1—7 ; plate xiv, figs. 4, 4*a*.

1865. *Bithinia nassa*, Theobald, *Journ. As. Soc. Bengal*, XXXIV (2), p. 275.
1870. *Bithinia nassa*, *id.*, *ibid.*, XXXIX (2), p. 402, pl. xviii, fig. 8.
1876. *Bithynia nassa*, Hanley and Theobald, *op. cit.*, pl. xxxvii, figs. 8, 9.

Theobald describes the shell as follows :—

"Testâ elongatâ, turbinatâ, politâ, diaphanâ, solidusculâ. Labio expansiusculo, plicâ callosâ externâ munitâ. Anfractibus quinque. 0·45 0·25."

I figure the radular teeth and external male organ on pl. xiv. Both branches of the latter are well-developed and, from the point at which the organ bifurcates to their tips, are about equal in length. The inner branch is somewhat expanded distally, but flattened at the apex. The outer branch tapers gradually to a point. The whole organ is practically smooth. A band of dark pigment runs along the middle of the upper surface of the outer branch and of the basal undivided part.

The expanded foot is tongue-shaped and truncate in front, with the anterior angles slightly produced. The proboscis is moderately stout ; not distinctly notched in front ; it extends beyond the anterior margin of the foot. The antennae are filiform and when fully expanded longer than the shell. They are, however, highly contractile and one is often (temporarily) more extended than the other. The foot, the base of the tentacles and the edge of the mantle are dull yellow ; the proboscis is black with gold specks, becoming paler distally ; the tentacles (except at the base, where they are pale) are greenish and speckled.

The operculum is narrowly ovoid, pointed and a little produced posteriorly ; the marginal membraneous part is narrow ; there is a well-marked depression in the centre of the external surface : although the striae are concentric on the peripheral part of the surface, there is a distinct spiral in this depressed region ; a low but broad ridge runs along the internal margin. The whole operculum is whitish and transparent.

The shell, though not markedly variable in any one habitat, exhibits considerable plasticity and it is possible to recognize at least four races or phases among the living and fossil specimens we obtained.

Theobald's types, of which there are several in the collection of the Indian Museum, came from a locality situated at a considerable distance north-east of the Inlé basin. The form common in ponds in that basin does not, however, differ in any important character from these specimens. All that can be said is that the shells are as a rule a little smaller and a little more conoidal. I think it best, therefore, not to distinguish this form by name and will refer to it as the *forma typica*. The most interesting feature in which the four races

differ from one another is the structure and position of the ridge that runs, nearer or further from the aperture, across the outer aspect of the body-whorl.

forma typica.

The shell exhibits some variation, and possibly some local plasticity in size and shape. The spire is, however, in all cases sharply pointed, unless eroded, and the colour dull. The condition of the ridges at or near the mouth is fairly constant, the varix being separated from the lip, to which it runs nearly parallel, by a broad groove. This groove is, however, somewhat variable in breadth. There is no trace of an intermediate ridge.

Individuals of this type are abundant in ponds round Yawnghwe, always living amongst dense weeds. They are also to be found, with the race *lacustris*, at the edge of the Inlé Lake, but never in the central region.

Type-specimen. M. 2237/2, Zoological Survey of India (*Ind. Mus.*) (Theobald Coll.).

subspecies **lacustris,** nov.

This race differs from the *forma typica* in its narrower, more pointed and more brightly coloured shell and in the structure of the varix and lip. It also attains a larger size and the microscopic sculpture of the surface of the shell is usually more strongly developed. In both these latter characters, however, it is somewhat variable. Well-developed shells are as much as 10·5 mm. long by 6·5 mm. broad. Microscopic longitudinal striae run, close together, along all the whorls and the shell is sometimes minutely decussated; obscure spiral ridges are also sometimes to be detected, while opaque, almost flat longitudinal ribs can be seen on the body-whorl of some individuals. In fully developed shells the edge of the aperture is always widely separated from the varix, which does not run parallel to it but rather across the arc it forms. The distance apart of the two ridges is variable. The intermediate space, moreover, is not a groove but distinctly convex; strong transverse striae and often one or more incompletely developed transverse ridges occur on it.

The largest and most brightly coloured shells of this race are found in the least congested part of the intermediate zone of the lake. They are of a pale amber-yellow colour. In the central region shells do not as a rule exceed 9·5 mm. in length and, when free from minute algae, are of a pale cream tint. These shells also tend to have the spire narrower and more sharply pointed. In all parts of the lake this mollusc is found amongst dense growing weeds.

Type-specimen. M. 11135/2, Zoological Survey of India (*Ind. Mus.*).

subspecies **rivulicola,** nov.

The shells of this form are much thinner than those of the others assigned to the species. They are of a dull green colour and have the longitudinal striae well-developed. The spire tapers less regularly than in the *forma typica*, the whorls are more swollen individually and

the suture more impressed. The varix is very low and the thickening of the margin of the aperture comparatively slight ; the relation between the varix and the edge of the shell is similar to that noticed in the *forma typica.*

We found a few specimens of this race among weeds in the back-waters of small streams at Thamakan, which lies some 1000—1200 feet higher than the Inlé Lake.

Type-specimen. M. 11139/2, Zoological Survey of India (*Ind. Mus.*).

subspecies **distoma,** nov.

The shell is small and compact, not exceeding 8 mm. in length and 5 mm. in greatest breadth. The longitudinal striae are often well-developed, but the surface has a smooth appearance. The varix, which is prominent, is situated very close to the edge of the shell.

Shells of this race are abundant in a fossil and subfossil condition on the He-Ho plain in all the deposits that we examined. It must be regarded as the most primitive in the series of forms to be included under the name *Hydrobioides nassa.*

Type-specimen. M. 11140/2, Zoological Survey of India (*Ind. Mus.*).

Hydrobioides avarix, sp. nov.

Plate xiv, figs. 1, 2, 2*a*, 2*b*, 2*c*.

In this species the shell, though the peristome is thickened, entirely lacks a varix on the body-whorl. I can find no trace of a ridge. Otherwise the shell closely resembles that of *H. nassa distoma.* It is small (not longer than 7 mm. and broader than 3·5 mm.), moderately thick, with longitudinal striae, of a dark olivaceous colour. I have examined the animals of several individuals. The females agree precisely with those of the typical form of *H. nassa* in external anatomy. I have found only one male. Its external male organ only differs from that of *H. nassa typica* in that the internal branch is much shorter. This, however, may be due to immaturity or contraction. The radula closely resembles that of *H. nassa* (see figures), except that the outer lateral tooth is slightly broader and the marginal tooth a little shorter.

Measurements of shells.

	mm.	mm.	mm.
Length of shell	7	6·5	6·25
Greatest breadth	4	4·75	4
Length of aperture	3·5	3	2·5
Greatest breadth of aperture	2·5	2·25	2

The operculum is a little broader than that of *H. nassa* and less clearly spiral in the centre ; it lacks the membranous margin.

Most of our specimens have the tip of the shell eroded.

This species was found in great abundance among weeds (*Hydrilla*) in a stream of slightly warm water flowing out of a spring about a mile from the edge of the Inlé Lake near Fort Stedman. I have discovered in the collection of the Indian Museum some shells from Moulmein in

Tenasserim which belong to the same species. They are labelled "*Bithynia subnassa*, Nevill." This is apparently a *nomen nudum*. They only differ from the Shan types in being slightly larger, the largest being about 9 mm. long.

Type-specimens. M. 11127-9/2, Zoological Survey of India (*Ind. Mus.*). From near Fort Stedman.

Hydrobioides nana, sp. nov.

Plate xiv, fig. 3.

Shell conoidal, moderately elongate, thick, transparent, brownish, with the spire darker than the body-whorl, smooth and polished on the surface, narrowly umbilicate, with the spire straight, blunt; with 4 whorls; whorls swollen, suture somewhat impressed; aperture large, ovate, oblique, bluntly pointed posteriorly; peristome thickened, continuous; no varix on the body-whorl.

Measurements of specimen.

	mm.
Length of shell	2·75
Breadth of shell	1·75
Length of aperture	1·25

The operculum is ovoid, thick, whitish, translucent, with the central area marked off by a distinct external ovoid ridge in the adult, with very numerous fine concentric striae.

From young shells of *H. nassa* those of this species can be recognized by their more swollen whorls, less pointed aperture and umbilicate condition, and especially by the structure of the operculum, which in young *nassa* is distinctly spiral.

We found about half a dozen specimens of this species at the edge of the Inlé Lake at Fort Stedman and in a small pool in the marsh at the northern end of the lake. I have been unable to examine the anatomy.

Type-specimen. M. 11289/2, Zoological Survey of India (*Ind. Mus.*).

Hydrobioides physcus, sp. nov.

Plate xiii, figs. 8, 8*a*, 9; plate xiv, figs. 5, 5*a*.

Shell thick, translucent, white or pale yellow, globose, subneritiform, sub-umbilicate, with the spire short, pointed, directed obliquely backwards; suture not strongly impressed; $4\frac{1}{2}$ whorls, the body-whorl relatively very large and swollen. Aperture patent, oblique, almost as broad as long, with the outer lip slightly produced outwards, not much thickened, as a rule brownish; columellar callus very broad, longitudinally striate, strongly convex. The first $3\frac{1}{2}$ whorls rounded; basal whorl with a strong but blunt ridge running round its dorsal aspect a short distance below the suture and as a rule broken up more or less distinctly by longitudinal grooves; other almost obsolete spiral ridges sometimes to be detected running parallel to it on the central

part of the whorl. The whole shell ornamented with coarse, more or less sinuous longitudinal striae. The varix, which is not well-defined, running a short distance above the lip, but not precisely parallel to it, on the central part of the whorl.

Measurements of shells.

	mm.	mm.	mm.
Total length	6·5	7	6·5
Greatest breadth	6·25	6·25	6·25
Length of aperture	3·25	4	3·75
Greatest breadth of aperture	2·5	3	3

The radular teeth and external male organ are figured on pl. XIV The latter differs considerably from that of *P. nassa*. The inner branch is much longer, distinctly annulated and not at all expanded at the tip; the outer branch is irregularly annulated and narrowed abruptly a short distance before its apex, which is blunt.

The foot is quadrangular, expanded in front, truncated behind, with a slight median posterior notch. The outline of the posterior extremity is, however, subject to considerable variation. The outline of the anterior margin is sinuous. The proboscis is stout and short and notched in front, it does not extend quite so far forward as the anterior margin of the foot. The tentacles are slender and tapering, not quite as long as the shell when fully extended. All the soft parts extruded from the shell are bright olivaceous, speckled with golden green.

The operculum is broadly ovoid, bluntly pointed posteriorly; the central part is thick and almost porcelainous, but translucent; the membranous marginal border is rather broader externally than internally. The outer surface is flat with a small depression round the nucleus, which is less clearly spiral than in *H. nassa*. There is a strong semi-circular ridge running round the outer margin of the thickened region on the inner surface.

Type-specimen. M. 11113/2, Zoological Survey of India (*Ind. Mus.*).

This species is extremely abundant in all parts of the Inlé Lake and also in swamps at He-Ho. It is found in much smaller numbers in ponds near Yawnghwe. I can discern no constant difference between shells from different localities or types of habitat, except that those from He-Ho are slightly smaller than those from the Inlé Lake.

Genus **Amnicola,** Gould & Haldeman.

I assign provisionally to this genus a species which apparently differs from the American forms in having a testaceous operculum.

Amnicola alticola, sp. nov.

Plate xiv, figs. 6, 6*a*.

Shell ovately fusiform, moderately elongate, minute, thin, transparent, chestnut-brown, sculptured with very minute longitudinal striae set close together, otherwise smooth, strongly opalescent internally,

with the whorls swollen in both planes and the suture impressed, narrowly umbilicate; aperture large, broadly sub-oval, rounded both in front and behind, strongly rimate and projecting; lip thin, sharp; columella arched.

Measurements of specimen.

	mm.
Length of shell	3
Breadth of shell	2
Length of aperture	1·5
Greatest breadth of aperture	1

The operculum is ovoid, pointed posteriorly, broadly rounded or sub-truncate anteriorly; it is thick but hyaline; 4 whorls can be distinguished on it; the outer surface is nearly flat; numerous spiral striae run round its periphery; the inner surface, which has a peripheral ridge, is strongly convex. Towards the periphery the suture becomes merely a ridge on the inner surface.

Type-specimen. No. M. 11110/2, Zoological Survey of India (*Ind. Mus.*).

The species is probably allied to *A. cincta*, Gould, from Tenasserim, but differs in that the body-whorl of the shell is not subcarinate. From *A. parvula* (Hutton) the shell may be at once distinguished by the broader whorls of its spire. Moreover, *A. parvula* is stated to have a horny operculum.

This species is not uncommon in the Inlé Lake, in which it occurs both in the central region and the marginal zone, always among living weeds. We found several subfossil shells on the banks of the He-Ho stream. They did not differ from fresh specimens.

Family VIVIPARIDAE.

Genus **Vivipara,** Lamarck.

It is a remarkable fact that only a single specimen that can be assigned to any normal species of this almost universally distributed genus was found in the course of our tour in the Southern Shan States.

Vivipara lecythis (Benson).

1836. *Paludina Lecythis*, Benson, *op. cit.*, p. 745.
1876. *Paludina lecythis*, Hanley and Theobald, *op. cit.*, pl. lxxvi, fig. 6.
1909. *Vivipara lecythis*, Kobelt, *Paludinen* in Martin and Chemnitz, *Conch. Cab.*, p. 148, pl. 30, figs. 1, 2.

Specimens of this species from different localities differ considerably, but as we obtained only a single broken shell in the Inlé Lake, it is impossible to describe the local race it probably represents.

The shell was found floating on the surface of the water in the marginal zone close to the western shore of the lake.

Genus **Taia,** gen. nov.

I have thought it necessary to give a new generic name to a group of Viviparidae that seems to be peculiar to the Shan Plateau and Upper

Burma. The shells of these remarkable species exhibit affinities both with *Vivipara* (*s.s.*) and with *Margarya*, Nevill; they also have some resemblance to those of *Tulotoma*, Haldeman.

The genus may be defined concisely as follows :—

Shell conical-ovate, conoidal or conical, varying greatly in thickness but never excessively thick and often quite thin, with coarse longitudinal striae and strong spiral ridges usually of a granular, nodular or squamous structure ; at least three such ridges present on the basal whorl ; whorls 7 to 8 ; spire well-developed, often produced but never cylindrical ; aperture of shell sub-triangular, often contracted above ; *columellar callus very broad and thick, extending over the umbilicus in the form of a convex ridge or flat plate ;* operculum nearly as large as aperture of shell, horny, pyriform, concave on the external surface, and with a strong ridge along the inner margin, with the muscular scar relatively large but not very thick, with at any rate the outer margin membranous. Radular teeth elongate, with the terminal denticulation strong, with a well-developed lamellar process on the tip of the central and lateral teeth. Anatomy of the soft parts as in *Vivipara.*

Type-species : *Vivipara naticoides.* Theobald.

I assign to this new genus eleven species from the Shan Plateau ; also *Vivipara noetlingi*, Kobelt, from the Lower Chindwin district of Upper Burma and an undescribed species from Ava on the Irrawaddi which I only know from a single broken shell. Of the Shan species six are extinct.

In describing a new genus and so many species I have followed the course that seemed most convenient. In the first draft of this paper I adopted a trinomial or rather quadrinomial system, but not only did I find myself constantly tripping over the names, but in several instances could not be quite sure to which species to assign a subspecies. Moreover, between the different sets of specimens that I had proposed to regard as representing distinct races or varieties I found constant differences in the form of operculum and in the proportions of the radular teeth, in all instances in which it was possible to examine these structures.

The development of the columellar callus, which sometimes extends from the aperture across the whole of the lower surface of the inner part of the body-whorl, is the most constant feature of the genus, and distinguishes it from *Margarya* and also from *Tulotoma.* This constitutes a resemblance to the Chinese genus *Rivularia*, Heude, but in other respects the structure and form are very different. From *Tulotoma*, *Taia* is also differentiated by the structure of the prominences on the chief spiral ridge of the body-whorl. My friend Mr. G. H. Tipper of the Geological Survey of India has been kind enough to cut sections of shells of *Margarya melanioides*, *Tulotoma magnifica*[1] and *Taia lacustris* for me. In transverse sections of the *Tulotoma* shell, the prominences on the chief ridge of the body-whorl appear to be com-

[1] For figures of this shell, which is apparently somewhat variable, see Küster's Monograph of Paludina, etc., in *Chemnitz's Conch. Cab.*, p. 23, pl. v, figs. 3-6 (1852), *T. magnifica* lives on stones in the Alabama river. It is the only known living species of its genus.

posed of convex, concentric layers of shell-substance. The layers are often oblique, but not so oblique that the layer is directed outwards or forwards on the shell. In similar sections of the shell of *Margarya* and *Taia* the layers of shell-substance are nearly straight, and project outwards and forwards in the form of well-defined lamellae. In a longitudinal section the appearance of the layers would be hardly different in *Tulotoma*, but in the other two shells they would be convex and more or less concentric. This is evident from the fact that the prominences in the American shell are arched both longitudinally and transversely, whereas in the Asiatic shells their convexity is longitudinal; horizontally they project almost flat.

Key to the Shan Species of Taia.

A. Shell somewhat globosely conoidal.
  1. Shell almost subumbilicate, with the spiral ridges always present but never strongly developed and never regularly tubercular or squamous ... *T. theobaldi.*
  2. Shell entirely non-umbilicate, with some or all of the ridges distinctly tubercular if at all well defined, sometimes almost absent.
    (*a*) Shell obese, thick, with the microscopic sculpture on the apical whorls resembling a web of fine cloth, with the spiral sculpture granular or tubercular ... ... *T. obesa.*
    (*b*) The microscopic sculpture of the apical whorls less well developed; shell as a rule longer and less obese.
      (i) Spiral sculpture extremely variable; a regular series of subspiniform scales never present on body-whorl ... *T. naticoides.*
      (ii) Spiral sculpture much more constant, granular or tubercular, sometimes with a regular series of subspiniform scales on the body-whorl .... *T. intermedia.*

B. Shell elongate-conoidal.
  1. Elongation of shell moderate; shell thin; a regular series of subspiniform scales present on the body-whorl ... ... *T. shanensis.*
  2. Elongation of shell considerable, suture extremely oblique above body-whorl; scale-like projections on body-whorl, if developed, never spiniform.
    (i) Shell large (length 45-60 mm.), extremely elongate ... ... *T. cylindrica.*
    (ii) Shell smaller (length 35-37 mm.), less elongate ... ... *T. lacustris.*

C. Shell conical.
  1. A regular series of subspiniform or spiniform scales never produced on the shell ... ... *T. analoga.*
  2. A more or less regular series of spiniform or subspiniform scales present on the body-whorl.
    (i) Scales on body-whorl spiniform, regular; shell not exceeding 32 mm. in length, narrowly conical, constant ... ... *T. intha.*
    (ii) Scales on body-whorl subspiniform, less regular; shell at least 35 mm. in length, less narrowly conical, variable in size, shape and sculpture.
      (*a*) Scales on body-whorl irregular; shell at least 45 mm. in length, thick ... *T. conica.*
      (*b*) Scales on body-whorl more prominent and less irregular; shell as a rule less than 40 mm. long, thinner ... *T. elitoralis.*

Taia theobaldi (Kobelt).

Plate xv, fig. 18; plate xvi, fig. 1;
plate xviii, fig. 15-17.

1909. *Vivipara* (*naticoides* var. ?) *theobaldi*, Kobelt, *Paludinen* in Martin and Chemnitz's *Conch. Cab.* (ed. Küster), p. 151, pl. xxx, figs. 10, 11.

Kobelt describes this species as follows :—

"Testa exumbilicata, ovato-conica, tenuis, haud nitens, unicolor fusco-olivacea vel sub-nigricans subtiliter striatula, plerumque limo ferrugineo adhaerente induta, apice nigricante. Spira conica, apice acuto, sutura parum impressa. Anfractus 7, superi convexi, inferi supra planati et angulati, carinis spiralibus plus minusve distinctis 3 cincti, ultimus acute carinatus, carina versus aperturam distinctiore et subtuberculata, utrinque convexus, carinulis tribus superioribus, prima et secunda magis approximatis, duabus inferis minoribus cinctus, antice descendens, basi irregulariter costato-sulcatus, spirae altitudinem superans. Apertura parum obliqua, basi recendens, ovata, supra acutiuscula, faucibus coerulescentibus, vix fasciatis; peristoma callo anguste nigro-marginato continuum, margine externo vix incrassato, extus ad carinam angulato, columellari calloso, distincte duplici sed parum incrassato, albo, nigro-marginato.
Alt. 31·5, diam. 24, alt. apert. obl. 17, diam. 12 mm."

I figure the radular teeth and operculum on pl. XVIII, figs. 16, 17. The former are of a dark brown colour.

The species on the whole is a constant one, but somewhat variable in colour—partly owing to the fact that there is often a deposit of some kind on the surface, and partly because the dark spiral bands may be either present or absent. It is as a general rule smaller than *T. naticoides*. The whorls are more separate and more swollen. The spiral sculpture is never very prominent, and never includes well-defined nodules, granules or scales. Two of the spiral ridges of the body-whorl are usually more prominent than the others. An interesting feature of the shell is that the columellar callus is not so well-developed as in the other species of the genus, and the shell in consequence is almost subumbilicate. The callus, however, has exactly the same general structure as in *T naticoides* and its allies.

We found *T theobaldi* living in abundance in small streams devoid of vegetation both in the Inlé plain and near Kalaw, 2,000 feet higher. It is also common at the latter locality in a subfossil state in the soil, and we obtained single specimens both from the superficial deposits of the He-Ho plain and from the caves at Hsin-Dwang.

Taia naticoides (Theobald).

Plate xv, figs. 16, 17; plate xvi, figs. 3-6;
plate xviii, figs. 1-3.

1865. *Paludina naticordes*, Theobald, *op. cit.*, p. 274, pl. ix, figs. 1-3.
1876. *Vivipara Shanensis*, *id.*, *Cat. Land Fresh W. Shells, Brit. Ind. Moll.*, p. 14.
1876. *Paludina naticoides*, Hanley and Theobald, *op. cit.*, pl. lxxvi, figs. 1, & 4.
1884. *Paludina naticoides*, Nevill, *op. cit.*, p. 25.
1899. *Vivipara naticoides* (with var. *obsolescens*[1]), von Martens, *Wiegm. Arch. Naturg.* LXV(1), p. 35, pl. iv, figs. 4, 5.
1909. *Vivipara naticoides*, Kobelt, *op. cit.*, p. 149, pl. xxx, figs. 4-9.
1915. *Vivipara naticoides*, Preston, *op. cit.*, p. 85.

Kobelt gives the following Latin diagnosis of the species :—

Testa exumbilicata, ovato-acuta, solida, crassa, parum nitida, undique oblique costellato-striata, costellis confertis, regularibus, sculptura spirali obsoletissima, olivaceo

[1] Founded on an immature shell.

viridis, fasciis latis castaneis 2 in anfractibus superis, 3 in ultimo ornata. Spira conica apice acuto, nigrofusco; sutura distincta pallidius marginata, interdum subirregulariter impressa. Anfractus 7 regulariter accrescentes, supri convexi, laeves, inferi ad suturam planati et cingulis spiralibus parum prominentibus distantibus varie cingulati, ultimus interdum subrotundatus, interdum distincte angulatus, postice spirae altitudinem superans, antice vix descendens. Apertura obliqua, irregulariter ovata, faucibus fuscescentibus fasciis translucentibus; peristoma callo crasso fuscescente continuum, margine externo recto vel (? in spec. adultioribus) leviter expanso, columellari usque ultra basin valde calloso, incrassato, dilatato, interdum saturate fusco, appresso, umbilicum omnino claudente.

Alt. 32, diam. max. 21·5, alt. apert obl. 18, diam. cum perist. 16 mm.

The operculum and radular teeth are figured on pl. XVIII, figs. 1, 2. The teeth are rather paler in colour than those of *T theobaldi.*

All authors who have referred to and figured the shell have recognized its variability. Theobald in his original description named two varieties (*fasciata* and *carinata*), while Nevill gave the typical form the name var. *concolor.* These varieties, however, as their authors recognized, have no constant character and are linked together by intermediate phases. They represent no more than individual variation, and shells belonging to all of them, and to intermediate phases, occur together under identical conditions. The species also exhibits a certain racial variation correlated with environment. Theobald's specimens, of which some are preserved in the Indian Museum, were from the Upper Salween in the eastern part of the Shan States. Unfortunately we have no information as to the type of environment in which they were found. They are of relatively small size, and of somewhat elongate form, though the body-whorl is usually globose or sub-globose. We found in small sluggish streams on the He-Ho plain a very similar race, exhibiting almost the same variation in shell-characters, but including individuals of somewhat larger size. In ponds and swamps in the Inlé basin there lives a slightly different race, with the shell of somewhat smaller size, a little more globose and never with the sculpture so well-developed as in the var. *carinata.* The differences in both races are beyond the range of exact statistics or of mensuration, depending as they do mainly on differences in outline and details of the prominences on the shell and of colouration. I will, however, discuss them as precisely as possible later (p. 160).

The form that I have described in this paper as *Taia intermedia* (p. 128) is hardly more than a standardized type of *T naticoides* var. *carinata,* but the fact that it is standardized is of great interest and seems to warrant its reception of a differential name. I have already alluded to the awkwardness inherent in a trinomial nomenclature when large numbers of allied forms have to be considered, and here the difficulty is increased because *intermedia* is to all appearance a fairly constant form derived from and but little differentiated from a most variable species. To adopt for it Theobald's name *carinata* might be legitimate on purely technical grounds, but this would conceal its true relation to *T naticoides.* Moreover, its identity with the var. *carinata* of that species, though closely approximate, is not absolute (see figs. 3-6, pl. xvi).

The only locality records for *T naticoides*, apart from Theobald's, are Kobelt's :—Meungyaw in Upper Burma and Lashio in the Northern Shan States.

Taia intermedia, sp. nov.

Plate xv, fig. 13 ; plate xvi, figs. 7-9.

I describe this form, as I have already explained, as a distinct species purely as a matter of convenience in nomenclature, for it certainly does not appear to be more than a fixed race of the inconstant species *T naticoides*. It will be sufficient, therefore, to note the differences that distinguish it.

The shell is always a little more conical than that of *T naticoides* and has the sculpture of the spiral ridges definitely nodular, but the nodules are small. The main ridge of the body-whorl is not as a rule strongly developed, but in some shells has a scaly character. Occasionally definite squamous projections are present on this ridge, but they are never spiniform and rarely arranged in a regular series. The first four whorls of the spire are smooth, but there are at least two nodular ridges on the fifth whorl. The aperture of the shell, though somewhat variable, is relatively small and narrow.

Measurements.

	mm.	mm.	mm.	mm.
Total length	37	34	33	32
Greatest breadth	23	22	25	20
Length of spire (on dorsal surface) ...	17	14	14	15
Length of aperture	15	13	15	14
Greatest breadth of aperture ...	12	10	11	10

Type-specimen. M. 11030/2, Zoological Survey of India (*Ind. Mus.*).

Shells are common in a subfossil condition in all the superficial deposits of the He-Ho plain, but the species appears to be extinct.

Taia obesa sp. nov.

Plate xv, fig. 19 ; plate xvi, fig. 2.

This species is distinguished from *T. naticoides* mainly by its very thick shell and more globose form. The two basal whorls are considerably swollen, and the outline of the whole shell is less broken. The ventral surface of the basal whorl is considerably swollen. The aperture is very broadly ovoid, sub-angulate posteriorly and rounded anteriorly. The columellar callus is broad, rather flat and very irregularly grooved in a longitudinal direction.

Microscopic transverse striae are abundant and well-developed on the protoconch, forming with the longitudinal striae a well-defined pattern like that of the web of fine cloth. The first five whorls are otherwise smooth. There are either two or three well-defined low spiral ridges on the sixth whorl, on which the microscopic pattern is continued. The ridges are undulate on the surface. On the upper part of the body-whorl there are two ridges that have a marked granular character. The third ridge is more prominent and occasionally exhibits a certain squamosity. Below it there are three lower undulate

ridges. The longitudinal striae are coarser and more irregular on this whorl and have sometimes almost the character of low ridges.

Measurements of shells.

	mm.	mm.
Total length	40	35
Greatest breadth	30	26
Length of spire (on dorsal surface)	17	15
Length of aperture	20	18
Breadth of aperture	14	13

Type-specimen. M. 11037/2, Zoological Survey of India (*Ind. Mus.*). A cotype in the collection of the Geological Survey of India.

Four shells of this species, two of which are immature, were found in the cave-deposits of the Hsin-Dawng valley in red soil.

Taia shanensis (Kobelt).

Plate xv, figs. 14, 15; plate xvi, fig. 10; plate xviii, figs. 4-6.

1909. *Vivipara shanensis*, Kobelt (*nec* Theobald), *op. cit.*, p. 411, pl. lxxvii, figs. 4, 5.
1915. *Vivipara shanensis*, Preston, *op. cit.*, p. 93.

There has been some confusion about the specific name *shanensis*. It was first introduced into literature by Theobald in his "Catalogue" (1876) as an absolute synonym of *naticoides*, a name which he had himself used in 1865 for the species here called *Taia naticoides*. He proposed the change of name under the impression that *naticoides* was preoccupied in *Paludina*.[1] Kobelt, however, in 1909, under a misapprehension, revived the name *shanensis*, which had been dropped by Nevill and other Indian authors, but applied it to a different species. He did this, apparently, because he found in Moellendorff's collection specimens of this species labelled "*shanensis*" and stated to have come from the "Gebiet der Shan in Hinterindien," and because he was unaware that the types of *Paludina naticoides*, which was described as from the "Upper Salween," also came from the Shan States. He therefore concluded that the form *shanensis* was at least a "sehr gute Lokalform."

His Latin diagnosis is as follows:—

"Testa exumbilicata, ovato-conica, solida, crassa, oblique striata, in aufractibus inferis spiraliter et peculiariter costata, costis nodosis, nitida, virescenti-fusca, subunicolor vel subnigro trifasciata. Spira elata, apice acuto, nigro; sutura distincta, inter anfractus inferos subirregularis, impressa. Anfractus 7, superi 3 lentissime accrescentes laeves, conulum regularem formentes, superi subscalati, liris spiralibus rudibus tribus primum laevibus, dein tuberculatis, sculpti; ultimus postice fere 3 5 altitudinis aequans, liris tuberculiferis vel sereibus tuberculorum obliquis 4-5 majoribus nonnullisque minoribus cinctus, serie quarta peripherica peculiariter squamosa, aperturam versus supra sub-declivis, subangulatus, ad angulum productus, vix descendens. Apertura irregulariter ovalis, supra accuminata, basi valde recendens, intus concolor vel fasciata; peristoma callo anguste nigro-marginato continuum, margine externo tenui, acuto, ad

[1] Strictly speaking he was correct in this view, for Férussac's *Paludina naticoides*, now placed in the Hydrobiidae, has long priority.

peripheriam subangulato, margine columellari calloso; dilatato fusco, nigromarginato, processum semilunarem, umbilicum omnino occludeatem emittente.
Alt. 30, lat. max. 24, alt. apert. obl. 18, diam. 14-15 mm."

The teeth, figured on plate XVIII, fig. 6, are almost black.

The species is a fairly constant one, exhibiting considerable individual variation in shell-colour in respect to the presence or absence of dark spiral bands, but not in sculpture or, except sexually, in form of shell. The shell figured by Kobelt is that of a female; those figured on pl. XV of this paper belong to both sexes. The species seems to be closely related to *T lacustris*, but the shell is larger, thinner and less produced and its sculpture more regular.

T shanensis lives in great abundance in the marginal zone of the Inlé Lake, especially towards the shore, where the formation of floating islands and of peat is proceeding with the greatest vigour. The food consists largely of a somewhat massive alga of the family Rivulariaceae that contains a considerable proportion of calcareous matter. It is perhaps in correlation with this fact that the radular teeth are thicker and darker than those of the other species examined.

Taia cylindrica, sp. nov.

Plate xv, fig. 9; plate xvii, fig. 2.

The shell is thick, of large size, elongate, with the first five whorls sharply conical, and the two basal whorls subcylindrical, there being 7 whorls in all. The basal whorl is remarkably oblique. The first four whorls form a regular, moderately broad cone. The fifth whorl is considerably broader than the fourth, but its outlines are hardly convex. It is nearly as long on the dorsal surface as the third and fourth whorls together. The sixth whorl is again considerably broader than the fifth, and about twice as long; its outlines are a little more convex. In dorsal view the body-whorl is not much broader than the sixth, but more than twice as long. This is owing largely to the abrupt change in the spiral of the suture. In the first four whorls, which may be taken to represent the protoconch, the suture is very regular and not at all impressed; the fifth whorl is, however, shouldered. Above the sixth whorl the suture becomes impressed, and the upper surface of the whorl is sub-angular. Above the seventh it is also impressed, but considerably more so on the outer part of the shell than on the inner part of the ventral surface. The body-whorl is not shouldered above, and is no broader above than the sixth whorl. The ventral surface of the sixth whorl is considerably swollen. The aperture is broadly ovoid, hardly angulate posteriorly, broadly rounded anteriorly and very oblique both transversely and in its longitudinal plane. The outer lip is slightly produced outwards and downwards. The callus is broad, not so prominent as in some species, irregularly grooved longitudinally.

The first five whorls are almost smooth to the naked eye, but bear numerous longitudinal and spiral microscopic striae. On the fifth whorl traces of a double ridge can be detected in well-preserved specimens. The sixth whorl bears four spiral ridges, one of which is situated at

the lower edge of the whorl. All the ridges are more or less granular. This is the case to a greater extent in the two median ridges. The microscopic sculpture is much as in the upper whorls. There are three irregular ridges on the upper part of the body-whorl, often tending to split up transversely and always irregularly nodular. The longitudinal striae on this part of the shell are much coarser and more irregular, and the transverse striae much less apparent. The fourth spiral ridge on the body-whorl consist mainly of a row of low squamous projections, which are not at all spiniform. Below it there are three or four irregular ridges, nodular, sub-nodular or undulate on the surface.

Measurements of shells.

	mm.	mm.
Total length	50	45
Greatest breadth (without projections)	27	28
Length of spire (on dorsal surface)	25	25
Length of aperture	22	21
Breadth of aperture	16	16

I have given the measurements of the two most perfect adult shells we obtained, the first of which I have selected as the type-specimen; but most of our specimens are broken, and some must have attained a considerably larger size.

Type-specimen. M. 11028/2, Zoological Survey of India (*Ind. Mus.*).

We obtained over twenty more or less complete specimens in the cave-deposits in which the type of *Taia obesa* was also found, in the Hsin-Dawng valley a few miles east of the town of Yawnghwe.

Taia lacustris, sp. nov.

Plate xv, figs. 10, 11; plate xvii, fig. 1; plate xviii, figs. 7-9.

The shell of this species resembles that of *T cylindrica* but is considerably smaller, less elongate and less oblique in the body-whorl. Its sculpture is more prominent, and at the same time less definitely nodular. There are two obtuse spiral ridges on the fourth whorl and four on the fifth. The projections on the chief ridge of the body-whorl are irregular and have a less definitely squamous character. The aperture is relatively smaller and less oblique in its longitudinal and transverse axes. The columellar callus is even broader and distinctly more prominent. It retains a fine oily lustre even in the fossil shell.

Measurements of shells.

	mm.	mm.
Total length	37	35
Greatest breadth (without projections)	24	23
Length of spire (on dorsal surface)	20	20
Length of aperture	14	14
Breadth of aperture	10	11

The shell sometimes retains a trace of colour. It does not seem to have been banded.

Type-specimen. M. 11029/2, Zoological Survey of India (*Ind. Mus.*).

We found a large series of well-preserved shells of this species in a lacustrine deposit at the eastern end of the He-Ho plain. It occurs in the superficial deposits of the same plain, but is there scarce.

Our specimens are fairly uniform in structure and shape, though the details of the sculpture vary slightly. The change in the direction of the suture above the body-whorl is not so marked in all specimens as in the one figured, which is perhaps the best preserved in the series.

The lacustrine deposit in which the shells were found is at least 20 feet deep, and is divided horizontally a few feet above its apparent base by a layer of peat only a few inches thick. The shells were found both above and below this layer, in very fine friable grey clay.

Taia analoga, sp. nov.

Plate xv, figs. 6, 7, 12 ; plate xvii, figs. 3, 4.

The shell is rather narrowly conical, sharply pointed at the apex, moderately thick, entirely non-umbilicate. It has seven complete whorls in addition to a minute vestigial apical whorl or half whorl. The protoconch closely resembles that of *T intha* but is perhaps a little broader at the base. Indeed, the whole shell is very similar, differences being its greater thickness, rather broader base, larger size, broader columellar callus, broader aperture ; its less regular sculpture and greater variability in size and shape. In this variability it exactly resembles *T conica* and *T elitoralis*, to which I regard it as the He-Ho analogue. The main difference between it and the shells of *T conica*, *T elitoralis* and *T intha* lies, however, in the fact that the third (or fourth) spiral ridge of the body-whorl never has a regular series of spiniform projections. This ridge, indeed, is sometimes but little more developed than the two immediately above it. It is more or less squamous and sometimes bears irregular projections of a half scaly, half nodular character. In one of the specimens figured on plate XVII, the spire is not in the same straight line as the body-whorl, but this is evidently no more than an individual abnormality.

Measurements of shells.

	mm.	mm.	mm.
Total length	43	37	35
Greatest breadth	27	24	19
Length of spire (on dorsal surface) ...	20	18	18
Length of aperture	16	15	14
Breadth of aperture	12	12	10

Type-specimen. M. 11069/2, Zoological Survey of India (*Ind. Mus.*).

We found four shells of this species on the He-Ho plain in superficial deposits. They are all filled with peaty substance. I class the form as subfossil, but it may have considerable antiquity. As it occurred in much smaller numbers than the other forms associated with it, it may not have lived in precisely the same habitat as *T intermedia*.

Taia conica, sp. nov.

Plate xv, fig. 8; plate xvii, fig. 8.

The shell is thick, of moderate size, conical in outline, sharply pointed apically. There are seven complete whorls and a rudiment of an eighth. The protoconch (apart from the rudimentary apical whorl) consists of four whorls, of which the first three have together a pyramidical outline. They are all very small. The fourth whorl is considerably broader, but not very much deeper than the third, and the four together are only a little longer than the fifth, while the five are not much longer than the sixth, and the six a little shorter than the seventh or body-whorl. The suture is not deeply depressed; on the spire it runs almost transversely across the shell, but above the body-whorl assumes a marked outward and downward obliquity. None of the whorls are swollen. The spire as a whole is conical, the body-whorl, as seen from below, truncate-ovoid, the broader and rounded end being situated anteriorly. The aperture is oblique, broad and patent, subtriangular but with all the angles rounded. The lip is a little expanded outwards and forwards and joins the columellar callus at the posterior end of the aperture. The callus is very broad and almost smooth.

The whorls of the protochonch are somewhat worn, though not at all eroded, in my specimens. Traces can still be seen under the microscope of a pair of spiral ridges. These ridges grow stronger on the fourth whorl and gradually assume a coarsely granular structure. On the fifth whorl they are still stronger, and a third ridge begins to arise below them round the base of the whorl. On the sixth whorl they remain much as on the fifth, but the new ridge becomes stronger and more tubercular, while a fourth, which has from its commencement an irregularly tubercular structure, appears at the base of the whorl and soon grows stronger than any of the others; on the ventral surface of the shell its projections assume a distinctly squamous appearance. It is this ridge that becomes the chief ridge of the body-whorl, on which the upper of the two primitive ridges grows obsolete and disappears. On the chief ridge of the body-whorl a series of strong but not exactly spinous scale-like projections appear. They are truncate apically and strongly concave outwardly. Below the chief ridge two others and finally traces of a third make their appearance. These three ridges are undulate or irregularly serrate on the surface.

As the shell is only known as a fossil, nothing can be said about its natural colouration. It is actually yellowish white, stained with red. It retains a certain degree of translucency.

Measurements of type-specimen.

	mm.
Total length	46
Greatest breadth (without projections)	27
Length of spire (on dorsal surface)	18
Length of aperture	21
Breadth of aperture	16

Type-specimen. M. 11018/2, Zoological Survey of India (*Ind. Mus.*) : a co-type in the collection of the Geological Survey of India.

I have examined 9 specimens. They were found in cave-deposits on the eastern slope of the Hsin-Dawng valley. Some of the specimens, including the one selected as type and figured on plate XV, are in a very perfect condition.

Taia elitoralis, sp. nov.

Plate xv, figs. 4, 5 ; plate xvii, figs. 5, 6 ;
plate xviii, figs. 13, 14.

In this living species the shell is considerably thinner and as a rule smaller than in *T. conica,* apparently more variable in shape and more regular in sculpture. At any rate in the male shell the spire is relatively narrower and more elongate, but there is considerable individual and sexual variation in this respect. The suture is a little more impressed and not so oblique above the body-whorl. The whorls of the protoconch are still smaller but relatively broader. The ornamentation has essentially the same pattern but the squamous processes on the body-whorl are more numerous, more prominent and more spiniform.

Measurements of shells.

	mm.	mm.	mm.	mm.
Total length	39	46	35	36
Greatest breadth (without projections)	24	24	22	23
Length of spire (on dorsal surface) ...	19	25	17	18
Length of aperture	16	20	18	17
Breadth of aperture	11	16	14	13

The epidermis is thin. When not stained by the growth of minute algae it is brown on the three last whorls, and practically colourless on the protoconch. It becomes gradually darker towards the anterior end of the shell. The shell-substance is white and translucent, except in the protoconch, in which it is bluish-grey and opaque. There are no dark spiral bands. The interior of the shell is lustrous and has a strong white opalescence.

The operculum is dark brown, broadly ovoid, somewhat sinuous on the outer margin, and a little produced posteriorly, though the apex is blunt. The inner margin is strongly convex. The external surface is concave, the false nucleus excentric and situated near the outer margin ; the lines of growth are strongly marked. The internal surface is convex, its muscular scar relatively large, and of a broadly ovoid shape, approaching the outer surface of the operculum for a considerable distance. The inner margin is membranous.

The external soft parts are precisely like those of *Vivipara*. The radular teeth are elongate, those of the marginal and outer lateral rows particularly so, and all have a rather pale brown colour. The central teeth are short and broad, truncate and very slightly emarginate above, with the sides slightly sinuous; the lamellar projection of the edge is broad, shallow and nearly symmetrical; it has five small denticulations on either side. The lateral teeth are stout, considerably longer than the central teeth and produced vertically into a fine process at the inner basal angle. Their lamellar process is broad, and has three or four stout denticulations on either side of it. The teeth of the two outer rows are sub-equal and much longer than those of the inner lateral row. The inner marginal teeth are narrow and produced triangularly at the base; the lamellar projection points slightly inward but is submedian; it is small and the denticulations are rather feeble. The outer marginal teeth are similar in form but slightly broader. Their denticulations are slender and rather long in the middle of the edge, becoming gradually shorter on either side.

Type-specimen. M. 11012/2, Zoological Survey of India (*Ind. Mus.*).

Habitat. This species lives in the Inlé Lake. It is not found in the middle of the lake, though it avoids water fouled with decaying vegetation, but inhabits the outer edge of the marginal zone (*i.e.*, the intermediate zone of the lake), concealing itself amongst dense vegetation. Individuals occasionally stray through the ring of floating islands that surround the lake. We found a few shells in a pool in the swamp at the northern end, and even in the canal at Yawnghwe. The species is much less abundant than either *T intha* or *T shanensis*. We obtained only 12 specimens.

Taia intha, sp. nov.

Plate xv, figs. 1-3; plate xvii, fig. 7;
plate xviii, figs. 10-12.

The shell is fairly thin, of relatively small size, narrowly and regularly conical, with the spire produced and tapering and the apex sharply pointed; it is not at all umbilicate. When complete it has eight whorls, but the apical whorl is minute and often disappears in adult shells. It is, therefore, best ignored in reference to them. I will describe the embryonic shell presently. In that of the adult the first two whorls (apart from the vestigial apical whorl) are minute, rounded and smooth; the third whorl, though still very small, is as long as the first and second together; the fourth is twice as broad as the third and as long as the second and third together. These four whorls in a sense represent the protoconch, though they do not represent the complete embryonic shell. Below the fourth there is a slight change in the direction of the spiral often accompanied by a constriction of the shell. The upper part of the fifth whorl is very little broader than the base of the fourth, and it does not increase much in breadth towards its own base. The sixth whorl is much broader and deeper, and increases gradually on to the seventh or

body-whorl, which is obliquely transverse and usually shorter than the spire. Except the smaller whorls of the protoconch none of the whorls are swollen or shouldered. The suture is not impressed except above the fifth and seventh whorls and there only slightly. The aperture is broadly ovoid, oblique, of moderate size, hardly angulate posteriorly, broadly rounded anteriorly. The columella is strongly arched, the columellar callus broad, smooth, and polished. The outer lip is thin.

The spiral sculpture commences on the third complete whorl, on the dorsal surface of which a faint groove appears. As this groove curves round the shell its margin becomes gradually raised until it assumes the appearance of a pair of smooth highly convex ridges. The double ridge thus formed proceeds on to the fourth whorl, becoming gradually stronger and assuming a granular structure. On the sixth whorl it becomes regularly tubercular and a single ridge appears below it at the base of the whorl near the inner edge of the dorsal surface. Almost from its point of origin this new ridge has a squamous appearance, and bears small, not at all granular projections. On the body-whorl the primitive paired ridge persists, but its tubercles become irregular and more or less confluent. The ridge that appeared on the sixth whorl also persists and grows stronger, its projections taking the form of short spiniform processes, blunt at the tip and concave outwards and forwards. Below this ridge there are two and a half or three others, all of which are rather feebly developed and undulate rather than tubercular.

Measurements of shells (in millimetres).

Total length	31	31	32	31
Greatest breadth (without projections)	20	18	20	20
Length of spire (on dorsal surface) ...	16	17	15	15
Length of aperture	15	12	15	14
Breadth of aperture	10	9	11	10

The colour of the external surface of the shell is very pale olivaceous green tinged with ferruginous brown. The protoconch is brownish or colourless ; the fifth and sixth whorls are paler than the body-whorl but the colour is shaded gradually. The spiral ridges are a little darker than the rest of the surface, but there are no definite dark spiral bands. The shell substance is whitish and translucent, except in the protoconch, in which it is bluish-grey. The inner surface is whitish, tinged with brown, but with opaque white bands corresponding in position with the spiral ridges. This surface is lustrous and has a milky opalescence. The columellar callus is brown externally and white internally, very highly polished.

The embryonic shell, removed from the parent at full time, consists of six whorls, but the apical whorl, which often disappears in the adult shell, is minute. The external colour is very pale green with several light brown spiral bands. The shape is sub-conical, but the main axis is oblique and the part surrounding the aperture somewhat produced. The first five whorls have a different character from the sixth, in which there is an abrupt change of direction in the spiral. The minute apical whorl is smooth ; on the second whorl a rather

obscure, broad spiral ridge appears; on the third this grows stronger while on the fourth it becomes double; on the fifth whorl there are three ridges of this kind, and on the sixth, which represents the upper part of the fifth whorl in the adult shell, there are five. On this whorl the two upper ridges become definitely nodular.

The operculum of *T intha* closely resembles that of *T elitoralis*, but is thinner and less produced posteriorly. The radular teeth are of a bright golden colour. They differ from those of *T. elitoralis* mainly in proportions; a characteristic feature that both have in common is the coarseness of the lateral denticulation of the central tooth. The differences are that the upper margin of the central teeth is convex, the teeth of the inner lateral row are rather larger, only a little longer than the central teeth, and distinctly shorter than the marginal teeth.

Type-specimen. M. 11004/2, Zoological Survey of India (*Ind. Mus.*).

Habitat, etc.—This species only lives in the central region of the Inlé Lake, where it is extremely abundant. It crawls slowly on the bottom, on weeds and on posts, but is very sluggish, and often remains for days without moving. Its food consists of minute algae of a very soft consistency.

As I have examined many hundreds of specimens of this remarkable species I am able to speak with confidence of its constancy. There is very little sexual variation in the shell and I did not always find it possible to distinguish males from females by the shell alone. The only characters in which individual variation was found were the development of the spiniform processes, the number of spiral ridges, the degree of attenuation of the spire, and changes in the direction of the spiral. In all these points, moreover, the shells that exhibited variation were what a lepidopterologist would call aberrations. Shells occur occasionally, but very rarely, in which the spiniform processes are developed on the basal ridge of the penultimate whorl as well as on the body-whorl. A shell of this kind is figured on pl. XV, fig. 2. Shells in which there are three instead of two tubercular ridges above the main ridge of the body-whorl are less rare, and others in which the spire is considerably more attenuated than usual are still more common, while shells in which there is an abrupt change in the spiral at more than one point are not uncommon. In no case, however, is the abnormality at all extreme. Towards the edge of the lake shells are a little larger than those out in the middle, but the average difference in length is not more than 2 mm. The larger shells, moreover, sometimes have the sculpture slightly less regular and the body-whorl broader. There is, however, no transition to *T elitoralis*.

Family AMPULLARIIDAE.

1915. *Pilidae*, Preston, *op. cit.*, p. 96.

Genus **Ampullaria**, Lamarck.

1911. *Pachylabra*, Kobelt, in Martini and Chemnitz's *Conch. Cab.* (ed. Küster), I, pt. II *Ampullaria*, p. 44.
1915. *Pila*, Preston, *op. cit.*, p. 96.

Kobelt has shown that the American species to which the name *Ampullaria* belongs in a restricted sense differ from those of Africa and

Asia in having a horny operculum. He, therefore, calls the latter *Pachylabra*, Swainson. Preston calls them *Pila*, Bolten. I am not convinced, however, that the generic division is necessary, and in the case of generic names I am not in favour of disinterring those which have long been buried and forgotten, even if this be done with due rites and in accordance with law.

Only a single species of *Ampullaria* was found in the Inlé basin and none were obtained, either recent or fossil, on the He-Ho plain.

Ampullaria winkleyi, Pilsbry.

Plate xii, fig. 10.

1901. *Ampullaria Winkleyi*, Pilsbry, *Proc. Ac. Nat. Sci., Philadelphia*, LIII p. 189, pl. v, figs. 2, 3.
1915. *Pila winkleyi*, Preston, *op. cit.*, p. 103.

This species is somewhat plastic. In specimens from streams running out of hot springs on the western side of the lake, the shells are not longer than 45 mm. and have the mouth narrow, while those from flooded rice-fields in the same district reach 65 mm. and have the mouth somewhat broader, though a little narrower than in Pilsbry's figure. The latter specimens are also paler in colour. Specimens from the edge of the Inlé Lake and from the Yawnghwe river are intermediate. Probably the most characteristic and the most constant feature of the species is the concentric sculpture of the columellar side of the scar of the operculum. This is constant in a large series and differentiates the operculum from those of *A. conica*, Gray and *A. compacta*, Reeve, in both of which the sculpture is irregular and without definite pattern.

As in many other species, the resting-stages in growth are often marked by distinct ridges on the shell, and in some specimens from two to four distinct regions can be distinguished on the body-whorl in this way. In the specimen figured on pl. X there are four regions of the kind and the last one is much paler in colour than the remainder of the shell.

The species was described from Henzada, Pegu. According to Pilsbry it is somewhat allied to *A. begini*, Morlet, a species distributed through the whole of Cambodia and on the lower Mekong.

Pelecypoda.

Order **TETRABRANCHIA.**

Family UNIONIDAE.

Genus **Physunio,** Simpson.

1900. *Physunio*, Simpson, *Proc. U. S. Nat. Mus.*, 22, p. 830.

Two species from the Inlé basin that represent this genus both belong to the section *Physunio*, s.s.

Physunio micropteroides, sp. nov.

Plate xix, figs. 1-3.

Shell inequilateral, suboval, elongate, thin, with a broad low blunt wing on the dorsal margin, rounded anteriorly, subtruncate and often a little produced posteriorly, with a pair of low diverging ridges (obsolete in old shells) proceeding backwards and downwards from the umbo, with coarse irregular transverse striae on the surface, slightly inflated; the umbo rounded, not at all prominent; epidermis dark brown, with obscure concentric transverse dark or black lines; nacre rather dull, of a livid bluish tint; lateral tooth long, thin, nearly straight, on right valve trifid almost from its point of origin, on left valve simple, its hinge-margin obscurely corrugated; pseudo-cardinal teeth on both the valves very short, curved, prominent, rounded ventrally, the left tooth with the edge produced triangularly and somewhat retroverted; edge smooth on both teeth.

Measurements of shells (in millimetres).

	Type.		
Length of shell	58	55	55
Greatest depth of shell	37	36	37
Thickness of shell	15	16	15

Type-specimen. M. 11048/2, Zoological Survey of India (*Ind. Mus.*).

Habitat.—Sluggish streams on the Yawnghwe plain, in dense mud in about 3 feet of water.

This species is very closely allied to *Physunio micropterus* (Morelet), with shells of which from Cambodia I have compared my specimens. It differs, however, in the form of the hinge, in its even less produced wing, in its less prominent umbo and darker colouration.

I hope that Dr. Ekendranath Ghosh will shortly publish a general account of the anatomy of this and the succeeding species.[1] Mr. Baini Prashad has given me a paper for this volume on the glochidia and marsupium of both.

The glochidium is parasitic on the fins of the small loaches *Nemachilus brevis*, Boulenger and *N. brunneanus*, mihi.

Physunio ferrugineus, sp. nov.

Plate xix, figs. 4-9.

This species is allied to the last one, but larger, with a thinner shell, with the wing better developed, with the diverging longitudinal ridges stronger, with the striae on the external surface finer and more regular, with the epidermis of a rich iron-brown (sometimes with darker concentric lines), with the nacre paler, with the lateral teeth more prominent and the pseudo-cardinal teeth of a different shape (see figures). In general appearance the young shell resembles *P. semialatus*.[2]

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[1] In *Rec. Ind. Mus.*, XV (1918). The paper is now in press.

[2] Deshayes and Jullien, *Nouvelles Archives du Museum*, X, p. 123, pl. vi, fig. 1, 2, *Bulletin*, 1874.

Fig 1

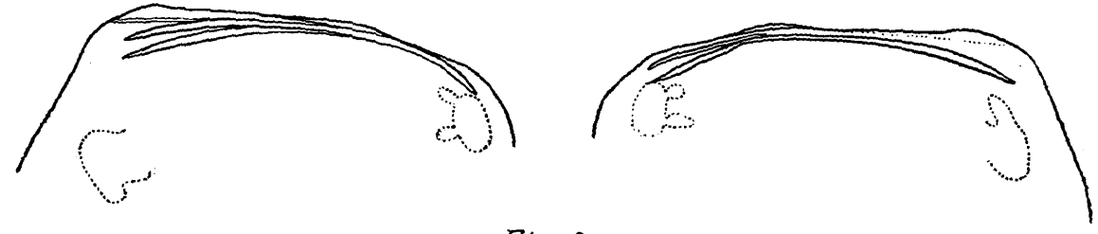

Fig. 2.

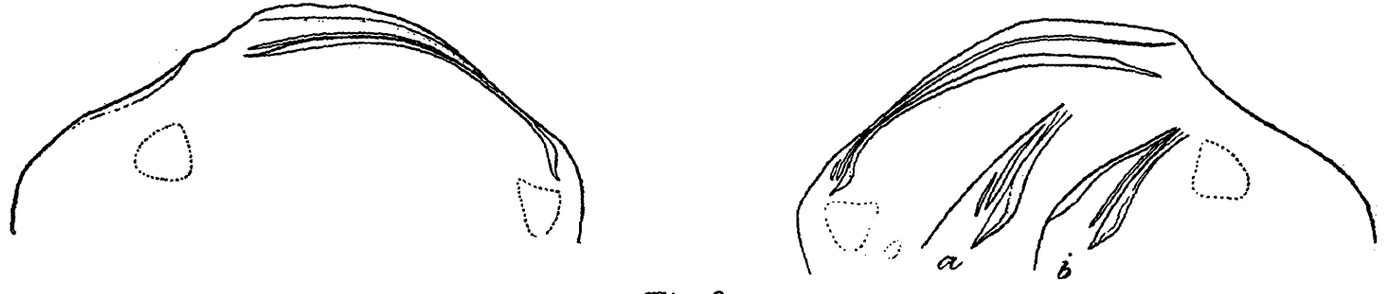

Fig. 3.

FIGS. 1-3.—Hinges of shells of *Physunio.*

FIG. 1. *Physunio micropteroides.* Type-specimen from the Yawnghwe river. *a*=pseudocardinal teeth enlarged.

FIG. 2. *Physunio micropterus.* Shell from Cambodia for comparison.

FIG. 3. *Physunio ferrugineus.* Type-specimen from the Inlé Lake. *a*=pseudocardinal teeth of same specimen enlarged : *b*=same teeth of another specimen also enlarged.

The shape is variable (see figures). I figure on pl. XIX a series showing different growth-stages as well as variation in old shells.

Measurements of shells (in millimetres).

	Type.		
Length of shell	71	73	70
Greatest depth of shell	47	49	50
Thickness of shell	18	18	20

Type-specimen. M. 11290/2, Zoological Survey of India (*Ind. Mus.*).

Habitat.—This mollusc is very abundant in the semi-liquid mud at the bottom of the central region of the Inlé Lake in water from 7 to 12 feet deep. Its position of rest in the mud is with the longer axis vertically upright and the valves buried nearly as far as the posterior end of the wing. It progresses through the mud by thrusting out the foot downwards and forwards. This forces the whole animal in the opposite direction and at the same time presses the dorsal edge of the valves downwards. The foot is then withdrawn and the shell regains its vertical attitude a little in advance of its former position. The foot is thrust out again and the movement repeated. The result is that the mollusc progresses with a see-saw motion, dorsal edge in front, the wing assisting greatly in overcoming friction by acting as a kind of ploughshare. The posterior end of the valves is often covered with a massive brown alga of the family Rivulariaceae.

The glochidium is parasitic on the fins of *Barilius auropurpureus, mihi.*

Suborder **Conchacea.**

Family CYRENIDAE.

Genus **Corbicula,** Mergerle.

Corbicula noetlingi, v. Martens.

Plate xix, fig. 12.

1899. *Corbicula Noetlingi,* von Martens, op. cit., p. 47, pl. iv, figs. 7-9.

Shells from the Inlé and He-Ho basins differ from those figured by von Martens in being somewhat longer. There is, however, some individual variation in this respect, and probably greater plasticity. Shells from Thamakan (alt. 4,000 feet) approach the typical form in shape more nearly than do those from the Inlé basin.

Measurements of shells (in millimetres).

Specimen A is from Thamakan, specimen B from the Yawi ghwo river, while specimen C was found subfossil in the superficial deposits of the He-Ho plain; specimems D and E, an adult and a young shell, are recent and from the same locality as C.

	A.	B.	C.	D.	E.
Length of shell	21·75	21	22·25	29·5	14·5
Height of shell	18·25	18·5	20·5	26·25	11·25
Transverse diameter ...	11·75	11·5	14	16·5	8·25

No species of *Corbicula* was found in the Inlé Lake, but C. *noetlingi* is abundant in ponds, marshes and slow streams in its basin and also in similar situations at He-Ho and Thamakan. Even the thinnest-shelled forms of the genus would sink in the semi-liquid mud of the lake.

The species was described from the Northern Shan States.

Pisidium casertanum (Poli).

Plate xix, figs. 13, 14.

? 1878. *Pisidium hydaspicola*, Theobald, *Journ. As. Soc. Bengal*, XLVII, p. 147.
1900. *Pisidium* (*Fluminina*) *dubium*, Lindholm in Korotneff's *Wiss. Ergebn. Zool. Exp. Baikal-See*, IV (Moll.), p. 85, pl. ii, figs. 45, 46.
1913. *Pisidium casertanum*, Woodward, *Cat. Brit. Pis.*, p. 31, pls. i, figs. 3-6, iii, fig. 3, xiii-xviii.
? 1915. *Pisidium hydaspicola*, Preston, *op. cit.*, p. 225, fig. 27.
1916. *Pisidium casertanum*, Annandale, *Mem. As. Soc. Bengal*, VI, pl. i, p. 53, pl. iii, fig. 14.

Specimens from the Inlé Lake and the He-Ho plain are so like those from Japan, examined by Woodward, in structure and appearance that they must be assigned to the same species. Their shells differ from those from Lake Biwa in being as a rule still smaller, in being subtruncate posteriorly and in having the umbo more prominent. In outline they closely resemble Lindholm's figure of his *P. dubium* from Lake Baikal, but the shell is smaller, evidently thinner and more transparent and the external striae closer, finer and more regular. A specimen from the He-Ho stream is more globose than those from the Inlé Lake and a little broader.

The following measurements (in millimetres) are those (A) of the He-Ho shell, (B) and (C) of shells from the lake.

	A.	B.	C.
Length	3·75	3·5	2·75
Height	3·0	3·0	2·25
Transverse diameter	2·25	1·75	1·05
Height to length	1 : 1·18	1 : 1·16	1 : 1·22
Transverse diameter to height	1 : 1·33	1 : 1·7	1 : 1·8
Transverse diameter to length	1 : 1·66	1 : 2·0	1 : 2·2

The specimen from the He-Ho was found in a crevice in the bark of a tree-trunk submerged at the edge of the stream in a kind of small backwater. In the soft mud of the central region of the Inlé Lake the species is not uncommon. In shells from this mud the posterior extremity is coated with a reddish substance precisely as in Japanese deep-water specimens. There is no deposit of the kind on the He-Ho shell.

P. casertanum is widely distributed in Europe. In Asia it has been reported only from Lake Baikal in Siberia (2-3 fathoms) and from deep water (17-30 fathoms) in Lake Biwa in Japan. It seems to me by no means improbable that *P. atkinsonianum*, Theob., which is not uncommon in small pools in streamlets in the Eastern Himalayas at altitudes between 5,000 and 10,000 feet, is merely a dwarfed form of the species, and I am very doubtful whether *P. hydaspicola*, Theob., from Kashmir is specifically distinct.

PART II.—PALAEONTOLOGICAL.

The deposits in the Inlé and He-Ho basins from which fossil and subfossil shells were obtained are of three classes: (1) cave-deposits, (2) lake-deposits and (3) superficial deposits on the banks of streams and in dried-up marshes.

CAVE-DEPOSITS.

The cave-deposits were discovered in two small limestone caves on the eastern slope of the valley of the Hsin-Dawng stream some three miles east of the town of Yawnghwe. They are at a height of three to five hundred feet above the level of the Inlé Lake and in what was probably the basin of a small but deep subsidiary lake that dried up at a period long before the He-Ho lake disappeared. Unfortunately there are no precise data for fixing the age of the deposits, but it seems legitimate at any rate to class the animal remains as fossil. These remains were in or upon the surface of banks of red soil, the depth of which was not ascertained. They consisted (apart from teeth of the Thamin, *Cervus eldi*—probably those of a single individual) of shells of *Taia* and *Melania*, those of the former genus being abundant but the latter represented by a single specimen. In other words, the smaller molluscs such as the Limnaeidae and Hydrobiidae that are likely to have existed in the fauna are entirely absent, while the larger shells of more expanded form are well represented. This is probably due to the fact that shells of *Taia* when dry and full of air or gas float readily on the surface of water,[1] while those of molluscs of smaller size or more contracted shape such as *Planorbis* or *Hydrobioides* as a rule sink. If this theory be correct the shells must have floated on the surface of a lake or pool until they were stranded at the base of limestone rocks and there been buried. Their unworn condition proves that they have not been carried by running water.

The remains from these cave deposits represent the following species:—

Mammalia.	Mollusca.
Cervus eldi.	*Melania variabilis.*
	Taia obesa.
	Taia cylindrica.
	Taia conica.

These remains must have been contemporaneous, but it is by no means improbable that the molluscs lived in different types of environment and were brought together in the manner indicated. The deer and the *Melania* survive, the species of *Taia* are all extinct.

LAKE-DEPOSIT.

At the north-east corner of the He-Ho basin there is, between two limestone spurs, a small plain through which the He-Ho river has cut for itself a narrow but rather deep bed. On the north side of this bed

[1] This was observed both in the Inlé Lake and in the He-Ho streams.

a deposit of about 20 feet deep is exposed. It consists for the most part of grey clay of great friability and composed of very minute particles mixed with fragments of vegetable origin. This clay seems to be precisely similar to that now being deposited in the open parts of the Inlé Lake and we may take it that the deposit is of true lacustrine origin. There is evidence, however, that conditions did not remain uniform throughout the period of its deposition, for there exists, about 5 feet above the base of the exposure, a layer of black peaty substance not more than six inches deep. This layer must have been formed in conditions different to those in which the friable clay was laid down and points to a brief interruption in the formation of the deposit. The whole exposure, nevertheless, is full of shells and no difference can be detected between those above and those below the peaty layer. The shells found in this deposit were :—

Limnaea, sp. ? nov.
Limnaea shanensis.
Planorbis trochoideus.
Hydrobioides nassa distoma.
Taia lacustris.

The most abundant form was the *Taia*. Though in a rather brittle condition and often broken, none of the shells were at all waterworn. No other animal remains were observed. I think that the shells should be regarded as fossil. The *Hydrobioides*, the *Taia* and possibly one of the *Limnaeae* are extinct.

SUPERFICIAL DEPOSITS.

The superficial deposits of the He-Ho basin are of two kinds. Firstly we have masses of exposed and usually broken shells lying on the banks of the He-Ho river in sheltered places. The largest of these is on the northern bank just above the point at which the stream plunges downwards through a narrow gorge into the Inlé plain. This deposit is situated a mile to a mile and a half east of the lacustrine deposit exposure already described and lies at an altitude of about 3,600 feet, *i.e.*, about 600 feet higher than the Inlé Lake. To judge from the molluscs represented in it, it is mainly a marginal deposit formed at the edge of the old He-Ho lake. This is indicated in particular by the abundance of shells of *Succinea*. Some of the shells are, however, slightly waterworn.

The species are :—

Succinea indica.
Limnaea shanensis.
Planorbis saigonensis.
Melania baccata elongata.
Hydrobioides turrita.
Hydrobioides nassa distoma.
Amnicola alticola.
Taia theobaldi.
Taia intermedia.
Taia lacustris.
Corbicula noetlingi.

No other animal remains were found, except a few land shells, which may have been quite recent. They include a *Plectopylis* still living in the He-Ho gorge. Probably all the shells should be regarded as subfossil. They include only two apparently extinct species, namely *Taia lacustris* and *T intermedia*. The race *distoma* of *Hydrobioides nassa* is also extinct.

The other kind of superficial deposit in the He-Ho basin is of a peaty or calcareous nature, the calcareous parts taking the form of narrow ridges of tufa in the masses of peat. No difference could be detected between the species from the tufa and those from the peat, but there is evidence that the shells had in some instances been carried about for short distances by the streams whose beds are represented by calcareous ridges,[1] and it is probable that all are not precisely of the same age. Specimens of *Melania baccata* and of *Planorbis exustus* in some cases retain their epidermis, which has entirely disappeared from the other shells. The fresher specimens were as a rule found embedded in tufa. The species are :—

Planorbis exustus.
Melania tuberculata.
Melania baccata elongata.
Hydrobioides nassa distoma.
Taia intermedia.
Taia lacustris.
Taia analoga.
Corbicula noetlingi.

These species and races, with the exception of *Taia intermedia*, *T lacustris* and *T analoga*, still survive. The shells are probably not all contemporaneous but the deposits as a whole evidently represent the last stages of the old He-Ho lake, when it had already become a mere swamp and parts of its bed were practically dry, with small streams winding through them. I class the shells as subfossil.

In this section of the paper mention should also be made of the extinct phase of *Limnaea shanensis* dredged from the bottom of the Inlé Lake. It was the only fossil or subfossil shell found in this position.

PART III.—GEOGRAPHICAL.

I. LIVING MOLLUSCA.

In considering the geographical relationships of the fauna of the Inlé Lake it is necessary to consider also those of the non-lacustrine aquatic fauna of connected waters. In the following list I have included the names of all the species and races of Mollusca found in streams, pools and marshes in both the Inlé and the He-Ho basins, as well as those of the species and races that live in the lake. The fossil and subfossil forms of the district I will consider separately.

Gastropoda.

Succinea indica.
Limnaea andersoniana.
Limnaea shanensis.
Limnaea mimetica.
Planorbis exustus.
Planorbis velifer.
Planorbis trochoideus.
Planorbis calathus.
Planorbis caenosus.
Melania tuberculata.
Melania terebra.
Melania baccata elongata.
Paludomus ornata.
Hydrobioides nassa.
Hydrobioides nassa lacustris.
Hydrobioides physcus.
Hydrobioides avarix.
Hydrobioides nana.
Amnicola alticola.
Vivipara lecythis.
Taia naticoides.
Taia theobaldi.
Taia shanensis.
Taia elitoralis.
Taia intha.
Ampullaria winkleyi.

[1] See the Introduction to this volume, p. 5.

Pelecypoda.

Physunio micropteroides.
Physunio ferrugineus.
Corbicula noetlingi.
Pisidium casertanum.

In this list of 30 species and races we have the names of 13 genera. Of these, 10 are of wide distribution, one distinctly Indo-Chinese, and 2 peculiar to Burma.

The widely distributed genera have, as genera, little geographical interest. The characteristic Indo-Chinese genus (*Physunio*) is, however, interesting because it represents a real element in the fauna of the Shan Plateau. This genus, of which one species (*P. velaris*, Sow.) has penetrated as far west as Assam, and another to Sumatra, is found mainly in Cambodia, Cochin China and Siam. The Inlé species belong to a Siamese-Cambodian section of the genus, while the Assamese form represents a section of wider range.

The endemic Burmese genus *Hydrobioides* bears in some respects the same relation to the widely distributed *Bithynia* as *Taia* does to the still more widely distributed *Vivipara*. Both genera have probably originated on the Shan Plateau, but have spread sparsely beyond its borders.

Of the 30 names on the list 28 are those of the *formae typicae* of their species, while 2 are those of races or subspecies. Of the 28, 16 (more than half) are those of species endemic or practically endemic on the Shan Plateau, while 7 (one quarter) are those of species only known from the Inlé basin. It is clear, therefore, that a well-marked endemic Shan element is present among the aquatic Mollusca of the district. It is represented by 17 out of 30 species and races, *i.e.*, by over 50 per cent. of the whole.

No other geographical element is so conspicuous. One Western Chinese species (*Limnaea andersoniana*) has been found, while only two (*Paludomus ornatus* and *Ampullaria winkleyi*) apart from endemic Shan forms are exclusively Burmese or Burmese and Assamese, and one (*Vivipara lecythis*) Assamese, Burmese and Western Chinese. These four species (a little less than one-seventh of the species represented in the fauna) may be considered to compose together a Far Eastern element.

Two species (*Melania tuberculata* and *Planorbis exustus*) are widely distributed in the Oriental region and *M. tuberculata* ranges far beyond the limits even of that region. It is probable that three other species (*Planorbis calathus*, *P. caenosus* and *P. trochoideus*) have also a wide Oriental distribution, but their minute size has caused them to escape the notice of collectors, and the records of their occurrence are few and scattered.

Evidence of the existence of a Palaearctic element, though not very definite, is not altogether lacking. *Pisidium casertanum* has hitherto been found only in the Palaearctic Region, and the form that lives in the Inlé Lake closely resembles those only known hitherto from the eastern part of the Region, from Lake Baikal and Japan. The existence of a species allied to the Tibetan *Limnaea bowelli* on the Shan Plateau points in the same direction.

No exclusively Indian species is on the list, but *Melania terebra* has been known hitherto only from Assam, and *Succinea indica* from the Himalayas.

The living molluscan fauna of the Inlé and He-Ho basins is, therefore, to a considerable extent endemic, so far as species are concerned. A Far Eastern element, represented by one genus and by about one-seventh of the species, is also apparent. A certain proportion of the species, as well as the great majority of the genera, are of wide geographical range, while two of the species are Palaearctic or have strong Palaearctic affinities. Most of the characteristic genera of Indo-China (*e.g.*, *Lacunopsis*, *Julliena*, etc.) are, however, absent and the Palaearctic forms are both Eastern. It seems by no means improbable, therefore, that the Far Eastern element has immigrated on to the plateau from the north-west, but the importance of the absence of such genera as *Lacunopsis* and *Julliena* is somewhat decreased by the fact that they are mainly fluviatile, whereas the fauna with which we are dealing is predominantly lacustrine. The Palaearctic forms, moreover, may have been introduced by migratory water-birds such as ducks, and have been able to survive owing to the comparatively low temperature of the plateau. We know that one of them has been established in the neighbourhood for a considerable period.

2. FOSSIL AND SUBFOSSIL MOLLUSCA.

I have already discussed the different deposits in the Inlé and the He-Ho basins from which shells of aquatic Mollusca have been obtained. Here it is only necessary to consider the shells in two categories, those of fossil and of subfossil forms. The distinction is of course conventional.

The fossil forms were found in two beds, in cave-deposits near Yawnghwe in a basin probably at one time subsidiary to the Inlé basin, and in an old lake-deposit in the He-Ho plain. In these two beds the following species and subspecies occur :—

Limnaea, ? sp. nov.
Limnaea shanensis.
Planorbis trochoideus.
Melania variabilis.
Hydrobioides nassa distoma.
Taia theobaldi.
Taia obesa.
Taia conica.
Taia cylindrica.
Taia lacustris.

Of these 10 forms, 6 (5 species and 1 subspecies) are apparently extinct and have not been found elsewhere. Moreover, of the four surviving species only *Planorbis conoideus* and *Taia theobaldi* survive in identical form, the shells of *Limnaea shanensis* and the *Melania* (which we did not find living in either basin) being slightly different from those of living individuals.

The subfossil shells were taken in superficial deposits on the He-Ho plain. The following is a list of the species and subspecies :—

Succinea indica.
Limnaea shanensis.
Planorbis exustus.
Planorbis saigonensis.
Planorbis trochoideus.
Melania tuberculata.
Melania baccata elongata.
Hydrobioides turrita.
Hydrobioides nassa distoma.
Amnicola alticola.
Taia intermedia.
Taia theobaldi.
Taia analoga.
Corbicula noetlingi.

Most of these shells are specifically identical with those now found living in the Inlé basin and only two species (*T analoga* and *T intermedia*) are apparently extinct. *Hydrobioides turrita*, originally described from the Irrawaddi, was not found living in the district, while the race of *Planorbis saigonensis* that survives in the Inlé Lake has changed so considerably that it has to be described as a new species. The shells of *Succinea*, *Limnaea* and *Hydrobioides* from these deposits also differ, but in a less degree, from those of the living forms.

The extinct forms have not been found elsewhere. Among the living forms there is less apparent trace of the Far Eastern element noted among the living mollusca of the district, but the endemic element is as clearly marked, represented by the same genera (*Hydrobioides* and *Taia*) and by 7 species and subspecies out of 14. We have, however, in these fossil and subfossil forms a much less complete record of the fauna than in the case of the living Mollusca.

3. CONCLUSIONS.

The geographical conclusions to be drawn from a study of the living and extinct aquatic mollusca of the district, so far as the latter are known, are as follows :—

The fauna of the Inlé basin has been isolated for a considerable period from that of districts outside the limits of the Shan plateau, but not sufficiently long for the evolution of highly specialized genera. Some of the living molluscs may possibly be descended from forms more peculiar than themselves that inhabited large lakes now no longer existing, but the ancestors of the majority probably came from the east of the Shan States, *i.e.*, the country now watered by the Mekong and the Upper Salween. We know very little about the aquatic molluscs of other parts of the Shan Plateau or of the Upper Salween, but, except in so far as purely lacustrine species are concerned, there is no reason to think that there is any great divergence in different parts of the plateau. The small Palaearctic element may have been introduced by the agency of water-birds, which migrate annually from higher latitudes.

PART IV.—PLASTICITY AND EVOLUTION.

We have now considered the molluscan fauna, living and extinct, of the Inlé Lake and the neighbouring waters from a geographical, a palaeontological and a taxonomic point of view ; there remains to discuss it in reference to its variability, plasticity and evolution. To do this it will be necessary to recapitulate the information available as to each genus and species, searching out parallel instances where possible, and then to summarize the whole.

PULMONATA.

The genus *Limnaea* provides us with interesting evidence as to the course evolution has taken, and is taking, on the Shan Plateau so far as

the shell-form of aquatic Gastropods is concerned. The three species now living in the Inlé Basin belong to two groups, that of *L. pervia* and that of *L. bowelli*. These groups are separated not only by the form and structure of the shell but also by those of the buccal armature. To the first group belongs *L. andersoniana*, while the group of *L. bowelli* is represented by *L. shanensis* and *L. mimetica*.

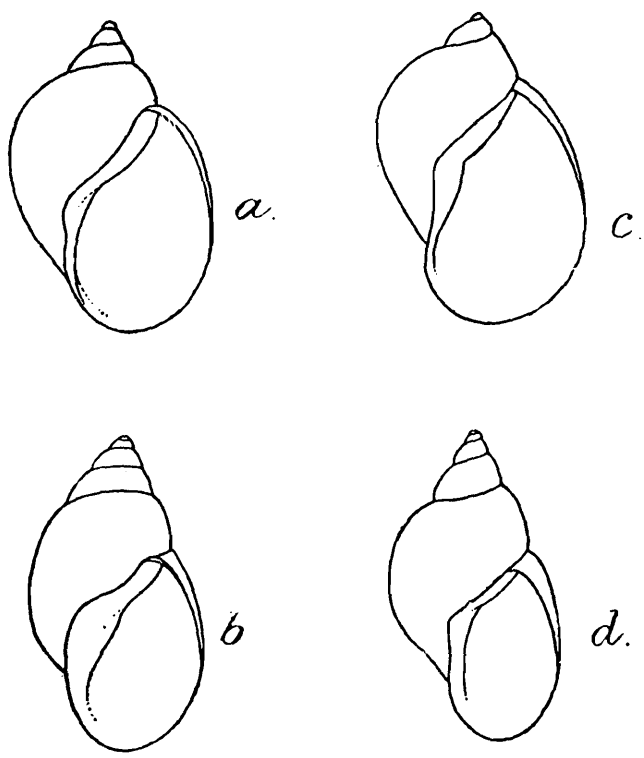

FIG. 4.—Shells of *Limnaea* illustrating differences between pond and stream forms.

a. Pond form of *L. andersoniana* from a pond near Yawnghwe.

b. Stream form of the same species from a small stream at Fort Stedman.

c. *L. ovata* from Germany.

d. *L. peregra* from Germany.

The figures are not drawn to scale. Figs. C and D are after Thiele.

Two phases of *L. andersoniana* are found both in the Inlé basin and in Yunnan. In the Shan States at any rate, one of these phases lives in ponds, while the other has been found only in a small stream. Moreover, the differences between the shells of the two phases are precisely comparable to those between the European *L. ovata* and *L. peregra*, forms still accepted by German conchologists[1] as distinct species, although it has been shown that it is possible to transform the direct offspring of one into the other by transferring the eggs of *L. ovata* into running water, or those of *L. peregra* into still water.[2] In both cases

[1] Thiele states that both forms are found in still and slow-running water, but it is not improbable that the form of the shell becomes fixed at an early age and that a later transference would not alter it. See Thiele, "Mollusca" in Brauer's *Süsswasserfauna Deutschlands*, XIX, pp. 6, 7 (1909).

[2] See Cooke in the volume (III) on Mollusca, etc. in the *Cambridge Natural History*, p. 93 (1895). I have not been able to refer to Hazay's work on the subject.

the chief differences between the shells are that that of the still-water form is considerably broader and has a more patent aperture and a shorter spire than that of the running-water form.

The other two Inlé species of *Limnaea* (*L. shanensis* and *L. mimetica*) are proved to be related to *L. bowelli* rather by the structure of their jaws and radulae than by any very close resemblance in the shell. The peculiarities of the buccal armature of *L. bowelli* are so great that it has been proposed to erect a new genus for its reception. The similarity in this respect between *L. bowelli* and the only living phase of *L. shanensis* is so close as to amount to a practical identity. We know of four phases of *L. shanensis*, three of which are fossil or subfossil, while one survives in the lake. Information is available as to the habitat in which each phase lives or lived. The shell in the four phases represents a gradual and almost even series from a form of normal shape, not very far removed from that of *L. bowelli*, but narrower and with a smaller spire. This phase lived in an open but rather shallow lake at an altitude of about 3,800 feet. The next phase, which is distinctly narrower and has the spire rather more reduced, lived in the same neighbourhood and at the same altitude, but in conditions that were rather paludine than lacustrine. The third phase, which still lives in the Inlé Lake at an altitude 800 feet lower, inhabits the marginal zone amidst decaying vegetation. While going further in the direction of narrowness and reduction of the spire, the shell differs from all the other phases in its thinness. The fourth phase lived in the open part of the Inlé Lake, possibly at a time when the water was very much deeper than it is now. The shell is in all respects, except that it is rather thick,[1] that of a typical deep-water form of the genus, and is by no means remote, so far as shape is concerned, from *L. mimetica*, the only species that now lives in the central region of the Inlé Lake.

In every particular, including thinness and paleness of shell and lack of pigment in the soft parts, *L. mimetica* is a typical deep-water form, although it survives in water that is nowhere more than 12 feet deep. Its actual descent from the extinct deep-water phase of *L. shanensis* is negatived by the divergence in the structure of the radula and columella; the differences are greater than those between that phase and *L. bowelli*. *L. mimetica* and the extinct Inlé form have, however, at any rate followed a similar course in the line of descent. The shells in both cases are greatly reduced in size; the spire is relatively small; the whole shell is narrow, and the aperture, though by no means expanded, is relatively of great size. The differences between the shell of these two forms on the one hand and that of the Tibetan *L. bowelli* on the other are strictly comparable to those between *L. abyssicola* and *L. foreli* of the deeper parts of the Swiss Lakes and the common European

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[1] It has struck me as not improbable that dead shells in strongly calcareous water may grow thicker by the equal deposition on their surface of salts of lime. Geologists whom I have consulted on the subject are not agreed as to the possibility of this but one distinguished member of the Geological Survey of India tells me that he believes that it frequently occurs.

The position of the shells of phase D on or near the surface of the mud is difficult to account for if they lived at a period previous to the filling in of the lake. There is no evidence that the water-level has sunk to any great extent.

shallow-water *L. auricularia*, from which, according to Forel,[1] the deep-water "species" are derived.

The cases of *L. shanensis* and *L. mimetica* are not altogether parallel to that of *L. andersoniana*, for we have not here a difference induced in the shell by a change from still to running or running to still water, but rather, at any rate in *L. shanensis*, an apparently gradual evolution, the physical changes in environment connected with which are complex and therefore obscure. I have already pointed out that phase D of *L. shanensis* and also *L. mimetica* have a considerable resemblance in shell-form to the deep-water Swiss species or varieties *L. foreli* and *L. abyssicola*. Swiss conchologists agree with Forel that these deep-water Limnaeae are derived from the common shallow-water *L. auricularia*, a species of which the geographical range extends as far south and east as the great plateau just north of the Himalayas and even into Kashmir. There is in the collection of the Indian Museum a fine series of shells of this species from various localities on the Pamirs. I have found among these shells numerous specimens of a phase that is abundant in small streams at high altitudes in Central Asia. Like the typical form of the species, it has an expanded mouth to the shell, but this feature is not nearly so pronounced as in the *forma typica*. The shell is small compared with that of the *forma typica*, although somewhat larger than that of *L. bowelli*, with which I propose to compare it as being also a running-water form from high altitudes on an Asiatic plateau. *L. auricularia* is a very plastic species and a large number of varieties have received names; I select one (var. *andersoni*, Clessin [2]) which seems to bear much the same superficial relationship to the Pamir form as phase A of *L. shanensis* does to *L. bowelli*. It was found in the Gulf of Bothnia in salt or brackish water and differs from the Pamir phase in that the shell is considerably narrower and its mouth less patent. I have arranged outline figures of the Pamir race, of the variety *andersoni* and of *L. foreli* side by side with those of *L. bowelli* and phases A and D of *L. shanensis*. It is easy to see how closely parallel the differences and resemblances are. In all cases the lowest figure is much more highly magnified than the other two.

L. mimetica, so far at any rate as the shell is concerned, seems to bear much the same relationship to the *forma typica* of the common Indian *L. acuminata*, Lamarck, an extremely plastic species, as phase D does to *L. bowelli*, and among the varieties of *L. acuminata* it would be possible to select at least as complete a series of intermediate forms as in the case of *L. auricularia* and *L. foreli*. Extreme types of shell in

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[1] *Le Léman*, III, p. 102 (1906). See also Clessin, *Malakoz. Blatt.* XXIV, pp. 171-177. pl. iii, figs. 1-4, 8-9. More recently Roszkowski (*Zool. Anz.* XL, p. 375) has demonstrated that the genitalia of *L. foreli* agree with those of *L. ovata* rather than those of *L. auricularia*. The bearing of this fact on the present inquiry is rendered less evident by the existence of many phases intermediate between *L. ovata* and *L. auricularia* so far as their shells are concerned. Indeed, Bollinger apparently claims to have found a complete series of shells linking the two together. It may be, therefore, that the true specific distinctions are anatomical and not conchological. In any case the facts as represented by Roszkowski—I have been unable to consult Bollinger's work—have a distinct bearing on my remarks in the next paragraph.

[2] Clessin, *Malakoz. Blatt.* XXV, p. 73, pl. iii, fig. 8 (1878).

L. acuminata[1] appear to bear the same relationship to one another as do *L. peregra* and *L. ovata*, but in this species the differences are not correlated with life in still or running water. I have recently examined

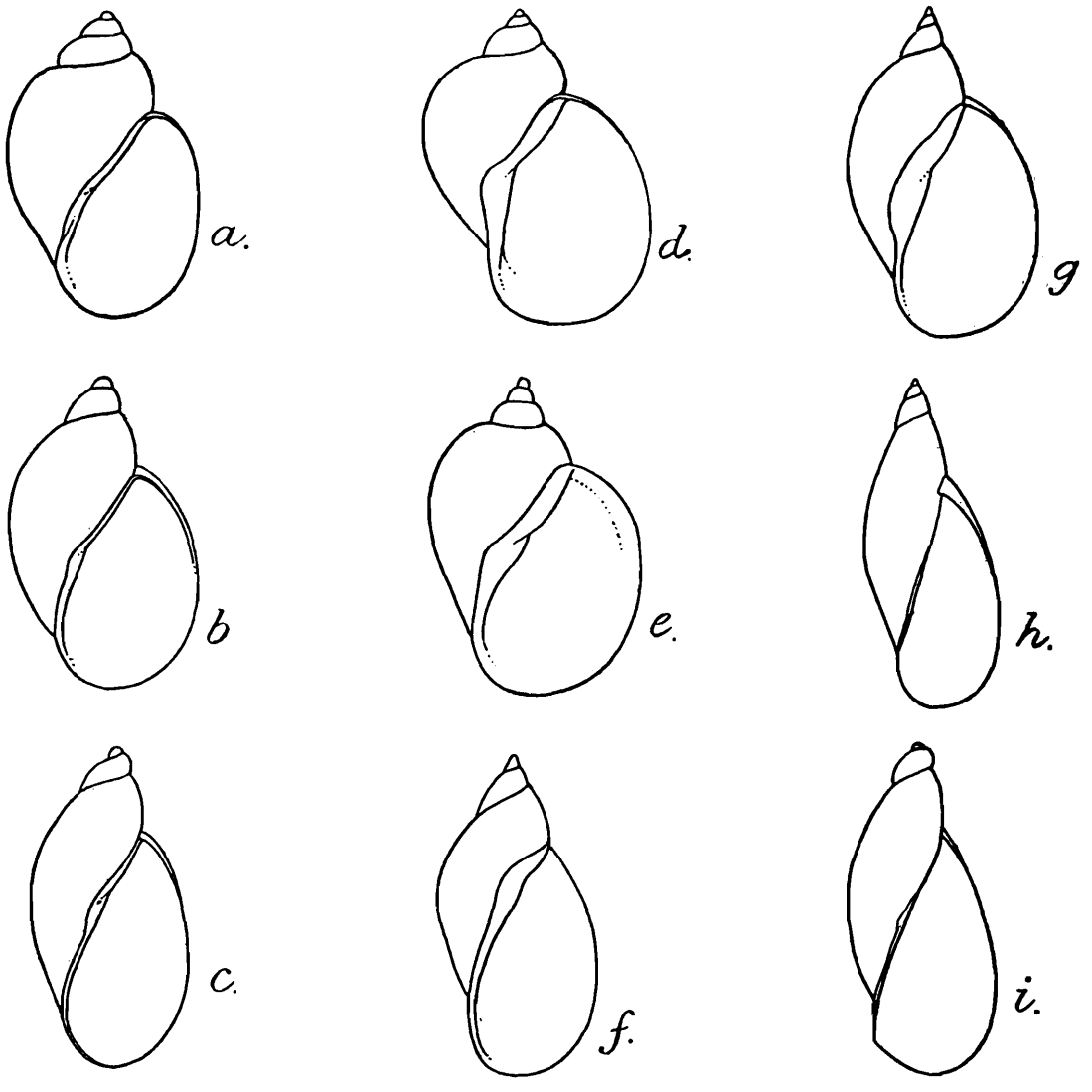

FIG. 5.—Shells of *Limnaea* illustrating the evolution of deep-water forms.

a. Type-specimen of *L. bowelli* from Tibet.
b. Living form (phase C of *L. shanensis*) from the Inlé Lake.
c. Fossil form (phase D of the same species) from the bottom of the Inlé Lake.
d. *L. auricularia*. Form from small streams on the Pamirs.
e. *L. auricularia* var. *andersoni* from the Gulf of Bothnia.
f. *L. foreli* from the depths of the Lake of Geneva.
g. *L. acuminata*. Typical form from Calcutta.
h. Narrow form (?) of the same species from near Khulna in the Gangetic Delta.
i. Type-specimen of *L. mimetica* from the Inlé Lake.

The figures are not drawn to scale. Figs. E and F are after Clessin.

shells of the narrowest type known to me—narrower even than the var. *gracilior*, Marts.—both from the river Ganges and from the

[1] Dr. N. N. Marshall has recently sent me specimens of a small form of *L. acuminata* from Rangoon. For good figures of the varieties of this species see von Martens, *Mitth. Conch.* I, p. 75, pl. xiv (1886).

tank in the Museum compound in Calcutta. The form may, indeed, represent a distinct species, but it is in any case closely allied. The different phases of *L. shanensis* probably resemble those of *L. acuminata*, assuming the narrow form to be specifically identical, in this respect, and there is no more reason to be certain that one is directly descended from the other, than there would be reason to claim that the Baltic race of *L. auricularia* was directly descended from the Pamir race, or the deep-water Swiss forms from the Baltic race. It is convenient to arrange the shells in a regular series, but it is not improbable that they represent divergent lines from a common type, rather than a single line of descent undergoing progressive modification. They may, therefore, be called links in a chain of evolution only in quite a general sense. Details of these instances of plasticity in *Limnaea* are different in the different cases, but they have one important point in common. They provide little evidence of individual variation. The individuals of each species found in the same environment as a rule resemble one another closely, but those from different environments differ.

These facts, observed under natural conditions, receive considerable additional interest from the experiments made by Semper,[1] by de Varigny,[2] by Whitfield[3] and by Roszkowski[4] in aquaria. The investigations of Semper and deVarigny were carried out independently and mainly with the object of discovering the results of confinement on *Limnaea*. Both experimentors agree that if individuals of this genus are kept in small masses of water, the shells of their young, bred in captivity, are dwarfed and more or less altered in shape. They found, moreover, that the effect was cumulative from generation to generation. The chief point in which they differed was that of the agency that produced these changes, but it seems not improbable that the most important factor in all cases was the products of metabolism, which contaminated the water and did not diffuse equally through the whole of an aquarium even when the individuals on which the experiment was being made were confined merely by means of a piece of muslin covering the end of an open tube. This factor was, therefore, essentially a chemical change in the water. For our purpose it is not necessary to follow these interesting experiments further. An excellent summary is given by Vernon in his "*Variation in Animals and Plants*" (London : 1903).

Whitfield, apparently by accident, obtained additional evidence of the dwarfing and distorting of the shells of *Limnaea* through succeeding generations in captivity. He discovered that confinement in an aquarium resulted, after three generations, "in the production of a monoecious animal from a dioecious one of the most perfect kind. Also in changing the specific characters, as far as the form of the shell can be considered, to such an extent that when shown to a good working conchologist (Dr. James Lewis) he gave it as his opinion that they could have no specific relations to each other."

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[1] *Arb. a. d. Zool. Inst. in Wurzburg*, I, p. 137 (1874).
[2] *Journ. de l'Anat. et de la Physiol.*, p. 147 (1894).
[3] *Bull. Amer. Mus. Nat. Hist.*, I, p. 29 (1882).
[4] *Zool. Anz.* XL, p. 375 (1912).

Roszkowski reared in captivity eggs of *L. profunda*, which he regards as synonymous with *L. foreli*, from deep water. He found that after nine months the shells of the young molluscs showed an extraordinary resemblance to those of the shallow-water form *L. palustris*, Müller.

The only other genus of true aquatic pulmonates represented in the Inlé basin is *Planorbis*, the shell of which is apparently less plastic than that of *Limnaea*. Possibly the flattened spiral form offers less opportunity for variation. Be that as it may, the species of the genus that occurs in the Inlé Lake fall into two categories. We have on the one hand the widely distributed, comparatively large and thick-shelled species *P. exustus* (belonging to the group or subgenus *Planorbis*, *s.s.*) the geographical range of which is very great and the variation and plasticity small. On the other hand we have a number of minute thin-shelled forms of the groups or sub-genera *Gyraulus* and *Segmentina*, most of which have also a wide distribution, while their variation, though by no means extreme, is in some respects less restricted. *P. exustus* need not concern us further in this connection as it is in no sense a variable form. The smaller species (*P. calathus*, *P. caenosus*, *P. velifer*, and *P. trochoideus*) are not, however, altogether devoid of interest. With the exception of *P. velifer*, which is only known as yet from the Inlé Lake, all these species have in the lake even smaller and thinner shells than they do in other localities. Their shells, moreover, are almost or completely devoid of colouring matter, while the pigmentation of their soft parts is also reduced. We have a few specimens of *P. trochoideus* from a lacustrine deposit in the He-Ho plain ; so far as can be ascertained, they did not differ when living from living individuals in the existing lake.

P. velifer is interesting for two reasons. In the first place it is little more than a highly specialized, dwarfed race of a widely distributed form (*P. convexiusculus*), which in its turn is possibly no more than a variety of *P. compressus* or *saigonensis*, a species of still wider distribution. Shells intermediate between *P. convexiusculus* and *P. saigonensis* occur in the superficial deposits of the He-Ho plain and only differ from the typical Indian form of the latter species in being rather smaller and in having the peculiar structure of the aperture that distinguish the form from *P. saigonensis*, a little less strongly developed. From these shells those of living individuals of *P. velifer* differ in their smaller size, still less developed aperture, thinness and transparency. Individuals from the middle of the lake are absolutely colourless, while those from the margin have a faint yellowish tint.

There is very little variation in the shape of these living shells, but their ornamentation is by no means constant. In some examples there are a number of curious spiral ridges on both surfaces of the shell. Examined under a fairly high power of the microscope these ridges are seen to be entirely epidermal, and to consist of closely adpressed cilia or minute horny processes. The rows of these processes vary in number and degree of development ; sometimes they are quite absent, though at least traces can usually be detected by careful examination. Variation in this respect is entirely individual and occurs both among the colourless shells from the centre of the lake and among the tinted shells

from the marginal zone. Its explanation can hardly be the same as that which would apply to the gradual change in the shape of the shell illustrated by the various phases of *Limnaea shanensis*. In the one case we are dealing with mere individual variability, on the other with true plasticity.

PROSOBRANCHIATA.

Of the Pectinibranchiate genera that are found in the Inlé basin there is nothing particular to be said about *Amnicola*, the single species of which seems to be very constant, while in *Vivipara* and *Ampullaria* the material available so far as the Shan States are concerned does not suffice for serious study. I shall have to notice a peculiarity of certain shells of *Ampullaria*, but will do so in discussing those of *Hydrobioides* in the final part of this section of my paper. In *Hydrobioides*, however, in *Melania*, and above all in *Taia* the variation observed is of a very remarkable character.

The only species of *Melania* found in the Inlé Lake is *M. tuberculata*. The shell of this species, which has an extremely wide range in Africa and Asia, is very plastic as regards its size and sculpture, though variation in shape is less common or at any rate less marked. In the Inlé Lake and also in the Yawnghwe river the shells (fig. 6*a*) are of a rather small size, not exceeding 25 mm. in length. They are of dark colour and have the tubercular sculpture characteristic of the species well-marked. In a ridge of recent tufa on the He-Ho plain we found a number of shells of much larger size, from 38 mm. to 40 mm. long (fig. 6*b*). They retain remains of the epidermis, which appears to have been dark, and their sculpture is less strongly developed. On another ridge on the same plain, however, we found shells (fig. 6*c*) not more than 16 mm. long with the sculpture very strongly developed and with the suture more impressed than usual. Unfortunately we have no information as to the differences in environment correlated with this difference in size and form of shell.

At first sight it is remarkable that in this species shells from the central region of the lake, where the water is extremely clear and where vegetation is rather abundant, differ in no respect from those taken in the muddy streams that traverse the Yawnghwe plain, but in both types of environment the animal lives almost buried in very soft mud. Moreover, there is evidence that the factor or factors which most strongly influence plasticity in this species are not always those that are most conspicuous or most readily ascertained. For the sake of clarity in discussing the facts known to me I will confine my statement on this species to forms that I have been able to investigate in the field myself. I have collected specimens chiefly in four districts, *viz.*, the lake of Tiberias in Palestine, the Gangetic Delta, the shores of the Chilka Lake on the east coast of India, and Yawnghwe State. The normal form of the species, that is to say, the one that approximately strikes the mean between extremes, chances also to be the *forma typica*, which was described from the coast of Madras. In this form (fig. 6*a*) the size is moderate, the length being from 25 to 30 mm., the spire tapers gradually, the colour is brown or dull green with more

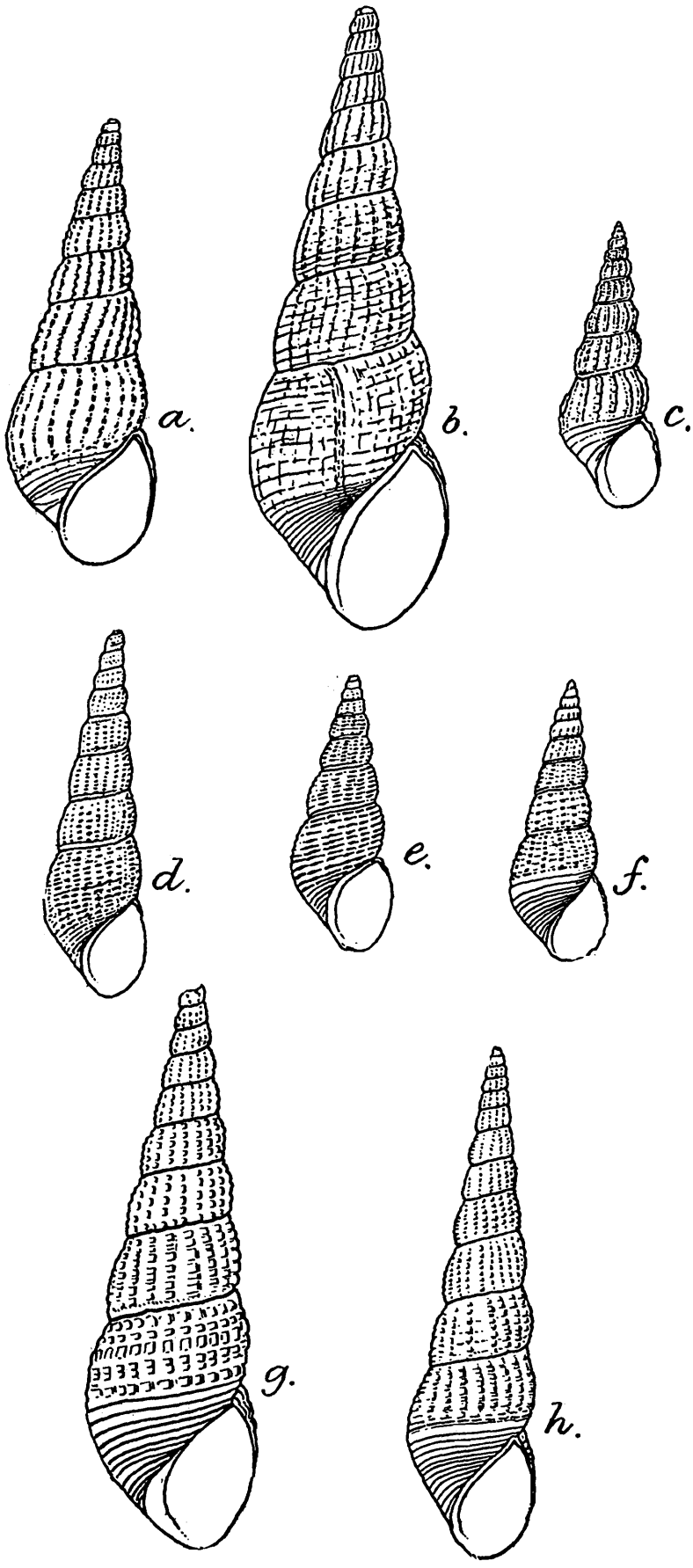

Fig. 6.—Shells of *Melania tuberculata* from different localities and types of environment.

a. Typical form from Inlé Lake. × 2.
b. Large form from a superficial deposit on the He-Ho plain.
c. Small form from another superficial deposit on the same plain.
d. Slightly dwarfed form from a pond in the Museum garden in Calcutta.
e. Dwarfed form from a small basin in a fern-house in the same garden.
f. Dwarfed form from a pool of brackish water at Port Canning in the Gangetic Delta.
g. and *h.* Large varieties from the Lake of Tiberias in Palestine.

or less evident reddish markings, and the sculpture consists of by no means prominent granules or tubercles arranged more or less definitely in longitudinal and spiral lines. Shells from some ponds in Calcutta agree well with those of the *forma typica*. In the pond, however, in the Museum compound—it is about 150 yards square and from 12 to 20 feet deep in the middle and has a fairly, but not a very abundant vegetation of entirely sub-aquatic plants—a distinct dwarfing is noticeable, shells (fig. 6*d*) rarely, if ever, exceeding 23 mm. in length ; the sculpture is also as a rule somewhat obliterated and the shell rather narrow. The only reason I can give for the dwarfing of the shells from this pond—a feature which is also noticeable in *M. variabilis* and in *Vivipara bengalensis*—is extreme overcrowding. Individuals of these three species abound to such an extent that we find it impossible to grow any kind of water-lily, because the snails congregate in such large numbers on the stems of young leaves shooting up from the bottom that they bear them down and prevent them reaching the surface of the water. In the same compound there is a small fern-house, thatched with an open layer of straw on wire-netting, but not enclosed with glass. In this fern-house there is an oval concrete basin 5 feet long by 4 feet broad by 1 ft. 4 inches deep. It is supplied with filtered water by a tap and is never entirely stagnant for long, as it overflows in wet weather and the gardeners are apt, contrary to municipal regulations, to leave the tap running. There is, moreover, in it a fairly dense growth of *Vallisnieria spiralis*. Some years ago one or two plants of the water hyacinth were introduced into the basin, and apparently brought with them, probably from a pond in Calcutta, the eggs or young of *M. tuberculata*. The molluscs (fig. 6*e*) have flourished so far as numbers are concerned, and must have gone through several generations. None of the shells are longer than 17 mm., and the shape is broader and shorter than that of individuals from ponds. Similar peculiarities are to be noted in shells from pools and canals of brackish water in both the Gangetic Delta and Orissa, except that the shell (fig. 6*f*) is a little more elongate.

Individual variability is not usually characteristic of *Melania tuberculata*, but in the Lake of Tiberias, and apparently also in other parts of Palestine, two varieties (fig. 6*g*, *h*) occur. Both have the sculpture well developed and both are of relatively large size. In one, however, the shell is rather smaller and distinctly narrower than in the other. (There is some doubt as to the proper name to be applied to the narrower form.) The interesting points, however, about these two forms from Palestine are (1) that they are found together under identical conditions and (2) that even though they live in water of very abnormal chemical composition they are not dwarfed, but rather above the average size.

All these facts about *M. tuberculata* are illustrated in the outlines of shells reproduced in text-figure 6.

Two other species of the genus *Melania* are found in the Yawnghwe river, *viz.*, *M. terebra* and *M. baccata*. There is very little difference between the shells of the former species from this stream and specimens from Cachar, the original locality. Our series is not a large one and does not exhibit any marked individual variation.

M. baccata is a species or a group of species that raises great difficulties in nomenclature owing to the variability and plastic character of the shell. It is found chiefly in the Shan Plateau, but in different parts thereof a number of local races seem to have become differentiated. All the shells, both recent and fossil, that we obtained in the two basins belong in a sense to a single race for which it has been necessary to find a new name. In reference to the elongation of the shell I have called it "subspecies *elongata*." But this race has at least two, if not three, phases, and shells from the same environment exhibit considerable individual variation in sculpture. The shells of the different phases do not differ in shape, but those from streams both in the Inlé and the He-Ho plains are very considerably smaller than those from a swamp in the latter. Subfossil shells from both peaty and calcareous deposits on the He-Ho plain seem to have the sculpture rather more sharply developed than those from streams, with which they agree in size. In a large series of living specimens from the Yawnghwe river the majority have three well-developed spiral ridges with series of tubercles on the last two whorls, but in a small proportion of specimens there are only two ridges of the kind. No actually intermediate individuals were found, but in one or two shells the uppermost of the simple ridges below the series of tubercles on the body-whorl has a slightly tubercular character. The same variation occurs among subfossil shells. Further information is necessary before we can discuss in detail the meaning of the differences in this species. I figure in outline a specimen of a shell from the Northern Shan States side by side with one of the smaller phase of the sub-species *elongata* for comparison.

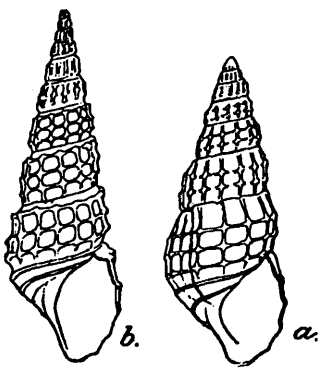

Fig. 7.—Shells of *Melania baccata* ($\times \frac{2}{3}$).
a. Shell from Hsipaw in the Northern Shan States.
b. Shell of small phase of var. *elongata* from the Yawnghwe river.

I have recognized the genus *Hydrobioides* as consisting of five species, one of which is very unlike the others in appearance. This species (*H. physcus*) departs widely in form of the shell from the type usual in *Bithynia*, the genus from which *Hydrobioides* is derived, and is not plastic. Specimens from a swamp near He-Ho hardly differ from those taken in the central region of the Inlé Lake except in being a little smaller. This species is only known from the two basins. Three other species of more normal shape are also, so far as we know, neither variable nor plastic.

It is otherwise, however, with the remaining species of the genus—*H. nassa*, which has a wide range in the Shan States and departs much less far from *Bithynia* than does *H. physcus*, but further than *H. avarix*, the species to which it is most closely related. *H. nassa* was originally described from a locality that lies some considerable distance east or north-east of the Inlé Lake, but is common all over Yawnghwe and the neighbouring states. There are cotypes of the species in the collection of the Indian Museum. They differ very slightly from the

form that now lives in ponds and swamps both in the Inlé and the He-Ho basins, but have the spire constantly a little more elongate and slender. Unfortunately we have no information as to the type of habitat in which they were found. Both in them and in the Inlé pond-form the most important of the specific characters is well marked. The character is—not only is the whole margin of the aperture thickened but on the outer part of the shell there is also a thick ridge or varix running almost parallel to the thickened margin across the body-whorl. In the type-specimens and in those of the Inlé pond-form the ridge lies very near, but distinctly separated from the rim of the aperture. In the Inlé Lake another race is predominant. The shell attains a larger size, is usually of a brighter and yellower colour, is invariably narrower and more elongate, and has the varix separated from the lip by a considerably greater though very variable space. When the shell is fully developed the ridge no longer lies parallel to the rim of the aperture but has a much less marked downward convexity. To this form I have given the name *lacustris*, regarding it as a race or subspecies of *H. nassa*. I cannot find any anatomical difference between it and the latter. A third race is found in fair abundance in small streams at Thamakan some distance west of He-Ho. This locality lies about 400 feet higher than He-Ho, and 1200 feet higher than the Inlé Lake. For the Thamakan race I have proposed the subspecific name *rivulicola*. The shell agrees with the typical form in its general structure, but is distinctly thinner and more conoidal; in size it slightly exceeds it. Yet a fourth race (subspecies *distoma*) occurs, or rather occurred, in the Inlé district. It is found both fossil and subfossil in the different deposits of the He-Ho plain. The shell is small, thick, and moderately elongate, but its chief character lies in the very close proximity of the varix to the rim of the aperture. So close, indeed, do they lie that the two thickenings form together little more than a single ridge divided transversely by a narrow groove.

In this species, therefore, and in its ally *H. avarix* we have a most interesting series illustrating the gradual accentuating of a generic character. In *H. avarix* the actual rim of the mouth of the shell is thickened, but there is no varix. In the fossil and subfossil race of *H. nassa* the varix is beginning to be differentiated from the thickened rim of the aperture, in the Thamakan race the process has been carried further, in the typical form of the species further still, while in the lacustrine form the two ridges have little connection.

In the Inlé Lake the local phase of the typical form of the species and the lacustrine race occur together in the marginal zone, in which conditions are not very different from those to be found in a large pond full of vegetation such as the former usually effects, but in the open central region only the lacustrine race occurs. This race grows to a larger size in the intermediate zone of the lake than it does in the centre of the central region or in the marginal zone, but I have not been able to find any other difference in shells from different parts of the lake, except that examples from clear water are usually more transparent than those from places where it is at all turbid or discoloured. It is difficult, moreover, to be sure that the latter peculiarity is not

due to the absence or presence of minute algae on the surface of the shell.

In the genera we have as yet considered it has been possible, at any rate in the more conspicuous cases, to trace some one line of evolution, but we have now to consider a genus in which matters are more complicated, namely the genus *Taia*. In some respects *Taia* is comparable to *Hydrobioides*, having originated, probably on the Shan Plateau, from a genus with a simple, almost smooth shell, but possessing itself a shell with pronounced and peculiar sculpture. The genus from which it is derived is the almost universally distributed *Vivipara*. As we shall see presently, this genus has undergone a very similar but quite independent course of evolution in other parts of the world also. I have thought it most convenient to recognize no less than eleven species of *Taia* among the living and extinct forms of the Inlé, He-Ho and Hsin-Dawng basins, but some of them are closely allied and might doubtless be regarded from a purely taxonomic point of view as races (subspecies) or varieties, rather than distinct species. These forms, whatever we may call them, do not follow a single line of evolution but diverge from one ancestral type in different directions. The ancestral type is represented by a species (*T theobaldi*) that still survives but is known also in a fossil state. The relationship of the other ten forms to this species and to one another is shown in a diagrammatic fashion in the figure on the opposite page. Two other species, one of which is still unnamed and very imperfectly known, are found in different parts of the Irrawaddi system. The possible place of one of these (*T noetlingi*) is shown in the diagram, but it may have been derived from an unknown form analogous to *T intermedia*, or direct from *T naticoides*.

T theobaldi, if it stood alone, might be accepted as a somewhat abnormal type of the genus *Vivipara* comparable to *V quadrata* (Benson) from China, but it is distinguished from all the species of that genus *sensu stricto* by the structure of the columellar callus, and from most of the species by the spiral ridges on its shell. These are the two chief generic characters of *Taia ;* they are less strongly developed in *T theobaldi* than in other forms. *T theobaldi* has a wide range in the Southern Shan States, and was originally described from "Burma." It is an inhabitant of small streams, and single shells have been found both in the cave deposits of the Hsin-Dawng valley and in the superficial deposits of the He-Ho basin.

From a geographical and biological point of view the species of *Taia* that occur on the Shan Plateau fall into four groups. Firstly we have two non-lacustrine species, *T. theobaldi* and *T naticoides*, that have a wide or fairly wide range on the plateau, if not beyond its limits. Then we have three little groups of lacustrine species each of which is, or was, peculiar to a single lake—one to the old He-Ho lake, one to the smaller but probably still older Hsin-Dawng lake, and a third to the existing Inlé Lake. All these lakes must have in a sense belonged to the same lake-system, but probably intermigration of the fauna had many obstacles.

The two surviving widely distributed, non-lacustrine species are certainly among the most primitive in the genus ; to one of them (*T*

theobaldi) I have already referred as representing the ancestral type. I have also referred to the fact that in it the generic characters are less

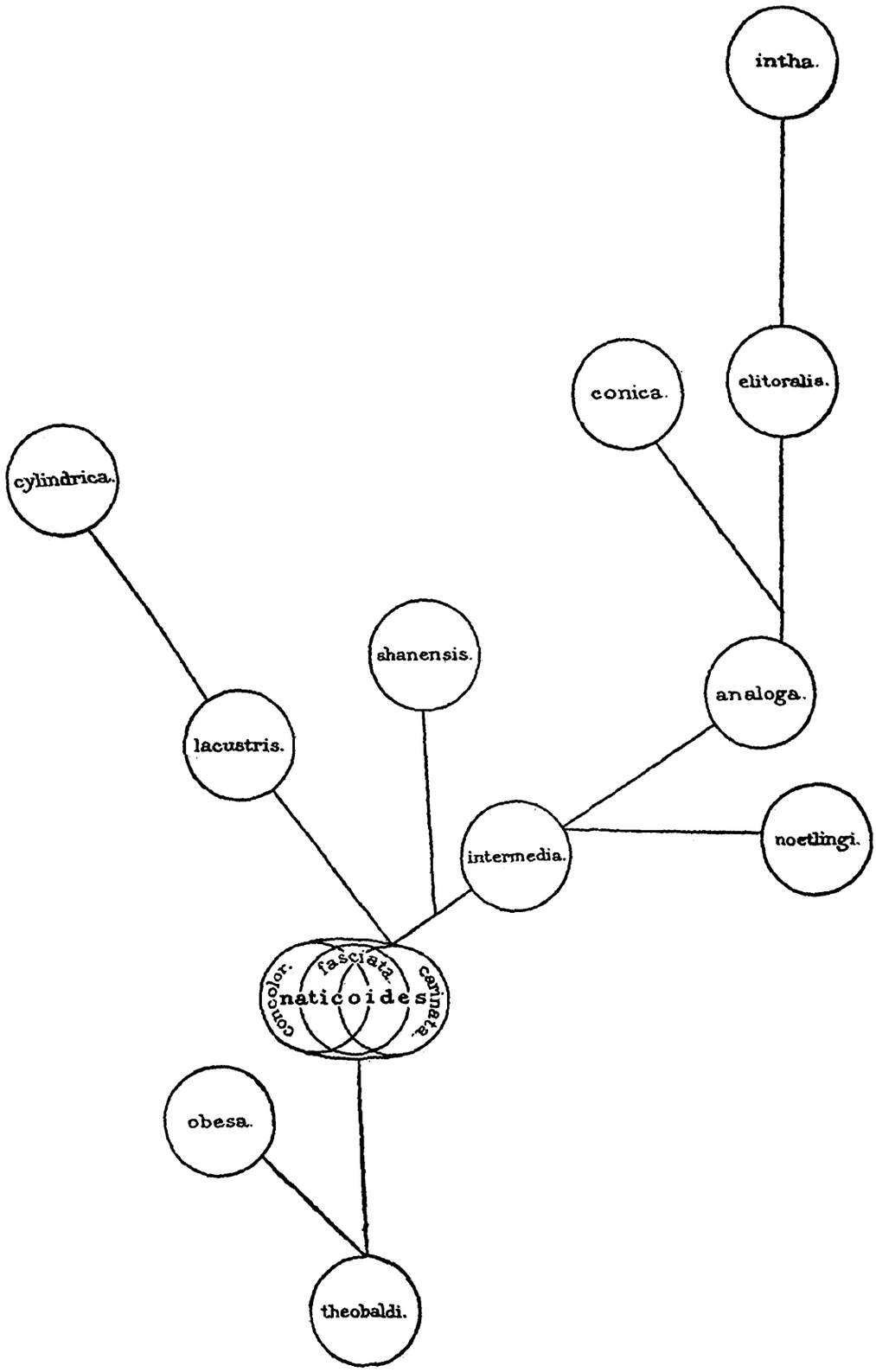

Fig. 8. Diagram showing the relations of the different described species of *Taia*.

marked than in the other species, the spiral ridges on its shell being less strongly developed and its columellar callus less expanded.

T theobaldi is a fairly constant form. Shells from 3,000 feet do not differ, except in such accidental characters as being more free from a coating of calcareous deposit, from shells from 5,000 feet, nor do those from ancient deposits differ from those found with the animal alive. The fact that shells from Kalaw are coated in the manner indicated while those from Yawnghwe are nearly clean proves in itself that the two lots were living under different conditions ; that they closely resemble one another proves that the shell of the species is not plastic. In some at any rate of the streams in which it occurs *T theobaldi* is subjected to the influence of frost. It is not always easy to distinguish single shells of *T theobaldi* from selected shells of the other non-lacustrine species (*T naticoides*), though their radular teeth differ considerably in proportions ; but *T naticoides*, which lives in swamps, pools and the back-waters of larger streams, never so far as we know at very high altitudes, is an extraordinarily variable species in respect not only to shell-sculpture, but also to colouration and to shell-form. Theobald in his original description recognized three " varieties," which he named " the typical form," var. *fasciata* and var. *carinata*, but he acknowledged that it was not possible to draw an exact line between them. The shell of his typical form (afterwards named var. *concolor* by Nevill) was almost smooth, while those of the varieties *fasciata* and *carinata* had spiral ridges developed in different degrees. So far as these characters are concerned, Theobald's observations are fully borne out by my own, but a large series of specimens does not support his assumption that differences in colouration and shape of shell are always correlated with differences in shell-sculpture. The more highly ornamented shells are often more conical than others, but beyond this I cannot go. The differences that do exist are entirely individual and in a single handful of shells from a single pool one may find specimens that are nearly smooth, specimens in which the sculpture is highly developed, and all intermediate phases. As I will show presently the proportionate number of individuals that can be assigned approximately to one variety or another differs in different localities.

In describing the three varieties Theobald, probably with a limited number of shells before him, gave due attention to colouration, shape and sculpture. His specimens were apparently all from the Upper Salween, several hundred miles from the localities in which we collected. I have taken at random one hundred shells from a series collected in a sluggish stream on the He-Ho plain. Of these nine have no definite spiral ridges, but none are absolutely smooth (see figs. 3, 4, pl. xvi). All these shells without spiral ridges are distinctly banded in colouration. I found fifteen shells that could be definitely assigned to the var. *carinata* so far as shape and sculpture were concerned, but unbanded, while the remaining seventy-six shells formed an unbroken series between *carinata* and *fasciata* in shell-form and sculpture, but were all banded. The nine banded, comparatively smooth shells were all of a somewhat globose type, on an average distinctly less conical than the carinate examples, but no difference of a kind that could be measured or accurately estimated in any other way was observed. The average size of fully adult shells in this series (length 35-38 mm.) is greater than was probably the case

among the shells included in Theobald's series, but it is evident from his description and figures that he did not examine adult shells only.

We may legitimately conclude from this statement that Theobald and I are dealing with the same species, but that races from different localities differ considerably in details of variation. I have not been able to find a single specimen from He-Ho in which the shell is absolutely smooth, or in which even approximate smoothness is correlated with absence of spiral bands. But Nevill called the typical smooth form from Theobald's series " var. *concolor*."

There is, therefore, evidence that details of variation differ in different localities. This is further proved by an examination of a series from Yawnghwe, 800 feet below the He-Ho plain. This series was taken in a large pond and a canal. In fifty specimens, twenty-nine are unbanded and carinate, fifteen banded and carinate, two smooth and banded, two smooth and unbanded. These results may be expressed in a table of percentages.

Locality.	Smooth and unbanded.	Smooth and banded.	Carinate and unbanded.	Carinate and banded.
He-Ho	*None*	9	15	76
Yawnghwe	8	4	58	30

In addition to this difference in individual variation between the shells from the two localities (and also from two types of environment) there is a distinct racial difference in structure. The shells of the Yawnghwe race are all thinner than those of the He-Ho race. They are smaller, fully adult shells being from 30 mm. to 32 mm. long. When bands are present they are rarely so dark, and it is often difficult to say whether they are present or absent, so faint may the bands be. Moreover, the shells are constantly a little more globose (*cf.* figs. 17, 16, pl. xv, and figs. 3, 4, pl. xvii), the smooth examples are smoother, and the carinate ones never quite so nodular. Finally the chief ridge of the body-whorl is often more distinctly squamous than it ever is in the He-Ho race, thus affording some approach to *T shanensis*. The radulae of the two races are very similar, but the teeth of the Yawnghwe race are paler in colour and probably less stout than those of the He-Ho race.

We have no evidence of the existence of this variable and plastic species in a fossil state, but to it all except one of the lacustrine forms of the three basins can be traced directly. The exception is *T obesa*, with which I shall deal when discussing the Hsing-Dawng group, but the He-Ho species must be discussed first because they are less highly specialized than those of the other two lakes. It is with the more highly specialized individuals of *T. naticoides* that all the lacustrine species must be associated. Indeed, it is not always easy to distinguish between the more strongly carinate shells of the former and the typical shells of *T. intermedia*, the simplest of the He-Ho forms.

In *T intermedia* the shell, however, is constantly more tubercular and a little more globose than *T. naticoides*, and no even approximately smooth specimens are found. There is considerable variation both in

the details of shell-sculpture and in shell-form, while in a few individuals a distinct series of squamous projections occur on the body-whorl; but the variability is small as compared with that of *T naticoides*. The species is, therefore, no more than an extension in one direction of the carinate type of *T naticoides*. It apparently lived in a swampy marginal zone which gradually encroached upon the open water of the old lake.

Two other species, both more remote from *T naticoides*, also lived in this lake. They belonged respectively to the conical and the elongate-conoidal types that we shall find also in the other two lakes. The conical type is represented by a somewhat variable species of which only a few shells were obtained. They were found in the same deposits as *T. intermedia*, but need not necessarily have lived in precisely the same conditions. On account of their resemblance in shell-form to species that live or lived in the Inlé and Hsin-Dawng Lakes I have called them *T analoga*. The corresponding Inlé species lives in the outer parts of the central region. The shell of *T analoga* has the spiral ridges well developed, and the chief ridge of the body-whorl sometimes bears a series of definite projections, but these projections are not spiniform, and are not arranged in a regular series. The shell is very like that of *T noetlingi* (Kobelt) from the Lower Chindwin, but we have no particulars as to the habitat of that species. The third He-Ho species is distinctly conoidal though elongate. We know that it lived in the open parts of the lake, and persisted without change for a considerable period. It is chiefly interesting on account of its relationship to one of the Hsin-Dawng species, *T cylindrica*. It was constant in shell-form and not very variable in sculpture.

All the He-Ho shells are thicker than those from the Inlé Lake, but thinner than those from Hsin-Dawng. In the Hsin-Dawng valley we found, in cave deposits, the shells of four quite distinct species of the genus. One of these, represented by a single shell, is *T theobaldi*; the other three belong to the same three types as those from the He-Ho deposits, *viz.*, the conoidal, the elongate-conoidal and the conical, but all are more highly specialized, larger and considerably thicker. The representative of the conoidal type is *T obesa*, a shell that seems to come from the common stock of *T theobaldi* and *T naticoides* but has the spiral sculpture better developed than that of the former and is more globose than either. I have been able to examine only four specimens of this species, but it does not seem to be variable. The elongate-conoidal shell (*T cylindrica*) is a very remarkable one, allied to *T lacustris* from the He-Ho deposits, but both more elongate and with the chief spiral ridge of the body-whorl distinctly squamous though without spiniform projections. We collected a good series, which is constant. The conical shell (*T conica*) from this basin differs from *T. analoga*, apart from its greater size and thickness, mainly in the more elaborate nature of its spiral sculpture and especially in the possession of a regular series of subspiniform projections on the body-whorl. Our series is not a large one but the specimens in it are uniform.

More information is available about the three species of *Taia* that still live in the Inlé Lake than about those that formerly lived at He-Ho

and Hsin-Dawng, because it has been possible to examine them in a living condition. The three species are *T intha*, *T elitoralis* and *T shanensis*. The first two of these have a conical shell, while that of *T shanensis* is elongate-conoidal, but not so elongate as those of *T lacustris* and *T. cylindrica*. All the shells are thin or moderately thin and all have a regular series of well-developed spiniform or subspiniform squamous processes on the chief spiral ridge of the body-whorl. *T. intha* and *T. shanensis* are constant species, while *T elitoralis* is a variable one.

T intha lives only in those parts of the lake in which the water is clear and transparent. It has the most elaborately sculptured shell of any of the species in the genus, and it varies as little as any. Shells from the less congested parts of the outer edge of the marginal zone are slightly larger on an average, a little broader than and not quite so constant or so regular in sculpture and in shape as those of individuals that live in the middle of the lake. Even the former, however, show no real approximation to the shell of *T. elitoralis*. This species, which is found living only in the intermediate zone of the lake amidst dense aquatic vegetation, is much scarcer than *T intha*. It is also very much more variable both in shape and size, and has the sculpture decidedly less regular. Some shells are much more elongate than others. On the whole the species is nearest to the fossil *T conica* from Hsin-Dawng, but it is nearer to *T intha* than it is to *T shanensis*.

T. shanensis does not reach so large a size as *T elitoralis*, but is more constant both in this respect and also in shell-form. It is indeed a fairly constant species, although it lives in conditions very different from those in which *T intha* is found. It inhabits the comparatively foul water of the marginal zone among floating islands, where circumstances are favourable for the formation of peat. It is at least as closely related to *T naticoides* as to any other species.

We have thus three species of *Taia* from each of the three lakes, for there is every reason to suspect that the few shells of *T theobaldi* that have been found at He-Ho and Hsin-Dawng are adventitious so far as their position is concerned. From the He-Ho lake we have *T intermedia*, *T. lacustris* and *T analoga*; from Hsin-Dawng *T obesa*, *T cylindrica* and *T conica*; from the Inlé Lake *T elitoralis*, *T. intha* and *T shanensis*. Each of the nine species is either conical, globosely conoidal or elongate-conoidal in shell-form. To the first group belong *T analoga*, *T. conica*, *T. elitoralis* and *T. intha*; to the second *T lacustris*, *T cylindrica* and, less definitely, *T shanensis*, while in the third *T obesa* and *T. intermedia* find a place. In the Inlé Lake at any rate, the conical type of shell is definitely associated with true lacustrine conditions, and this was probably the case also in the other two lakes; whereas the globosely conoidal type is or was to be found rather in the swampy marginal zone. The elongate-conoidal forms seem to have been strictly lacustrine, but *T shanensis*, which is intermediate between the globosely conoidal and the elongate-conoidal, is practically paludine in habits. The non-lacustrine species (*T theobaldi* and *T naticoides*) may be classified among the globosely conoidal forms. As all the conical shells are also elongate, elongation of the shell in *Taia*, therefore,

seems, in this district at any rate, to be associated with life in an open lake.

In order to avoid confusion I have confined the foregoing statement about *Taia* to species from the Shan Plateau, with a passing reference to those found in other parts of Burma. Before proceeding, however, to consider variation in the bivalve shells of the lake and its vicinity it will be convenient to discuss briefly certain cases from other countries parallel at any rate to some extent to that of the Shan *Taiae*. The most important cases are those of *Margarya* in Yunnan and of a remarkable series of *Vivipara* described from Tertiary deposits in Austria.

Margarya is a genus of Viviparidae known only from Western China. All the forms as yet discovered have been assigned by conchologists to a single species, *M. melanioides*, Nevill; but eight or nine varieties have been described. Some of these are apparently constant and at least as distinct from the typical form as *T theobaldi* or *T shanensis* is from *T obesa*. The shells resemble those of the species of *Taia* in sculpture, but are much thicker and larger and have not the expanded columeller callus characteristic of my genus. I have examined a large series of fresh and subfossil specimens from Tali-Fu in Yunnan, the type-locality. They include representatives of three of the varieties (*carinata*, Neumayr, *rotundata*, Neumayr, and *francheti*, Mabille) as well as of the typical form, of which we have the type-specimens. Individuals intermediate between the typical form and *carinata* are common, but I can find none between the latter and *rotundata* or between *rotundata* and *francheti*, which I am inclined to regard as distinct species. I have not seen the forms called var. *Monodi*, var. *Mansuyi*, and var. *obsoleta* by Dautzenberg and Fischer,[1] but they also seem likely to be specifically distinct. Among the eight or nine forms there are two groups, in one of which the spire is moderately elongate and more or less conical, while in the other it is greatly produced and almost cylindrical. In both groups we find a transition from almost smooth shells to shells ornamented much as in *T elitoralis*. We find none, however, that have the sculpture so regular as in *T intha*, and none in which the shell is so globose as in *T obesa* or even *T naticoides*.

Unfortunately we know very little about the types of environment in which these forms live or lived. Dautzenberg and Fischer[1] say :—

"La forme typique du *Margarya melanioides* et les variétés *Delavayi* et *Monodi* sont représentées dans les récoltes de *M. Mansuy* par des exemplaires provenant du gisement quaternaire du déversoir du lac de Yunnan-Sen, á Koui-An.

La var. *Mansuy* est plus abondante que les autres formes : M. Mansuy en a récolté des spécimens actuels (fig. 2) dans les lacs de la Chaussée, à Mong-Tsé ; il l'a trouvée également dans les gisements quaternaires de Tong-Hai (fig. 3), jusqu'à 50 mèters d'altitude au-dessus du niveau du lac actuel, et dans le quaternaire de Mong-Tsé, près le ville (fig. 4)

La var. *obsoleta* n'a été recueillie que dans les gisements quaternaires des lacs de la Chaussée, plaine de Mong-Tsé (fig. 5) et de Tong-Hai.

Les var. *Francheti*, Mab. et *tropidophora*, Mab. n'ont pas été rapportées par M. Mansuy."

Thus some of the forms are apparently extinct. Mr. J. Coggin Brown of the Geological Survey of India, who collected a large series of shells

[1] *Journ. Conch.* (Paris) LIII, pp. 420-425, figs. 1-5.

in Yunnan, is of the opinion that environment and shell-type are correlated in a general way, but no precise information is available to him.

The case of the Austrian Viviparidae is an even more remarkable one and perhaps in some points more closely parallel to that of the Shan *Taiae*. Neumayr and Paul[1] have discussed it in considerable detail, both from a palaeontological and from a strictly geological point of view, in their treatise on the *Congeria* and *Paludina* Beds of Slavonia. They recognize no less than thirty-nine species, which Neumayr assigns to the subgenus *Tulotoma* of the genus *Vivipara*. The shells of the different species vary greatly in both shape and sculpture and provide a complete transition from normal smooth forms to forms in which the sculpture approaches that of the more highly specialized varieties or species of *Margarya* and *Taia* and agrees very closely with that of the North American living genus or subgenus *Tulotoma*, but apparently there is no excessive individual variation within the limits of each species. All these forms come from Tertiary deposits and have long been extinct, but the racial variation was progressive in time as well as in structure and the smooth shells are older than the highly sculptured ones. About these Viviparidae Neumayr (*op. cit.*) writes as follows :—

"Wie mein Freund Paul im geologischen Theile nachgewiesen hat, sind in den von uns untersuchten Gegenden von Westslavonien die glatten *Viviparen* mit äusserst geringer Ausnahme auf die unteren, die mit ausgesprochenen Kielen und Knoten versehenen Formen vollständig auf die mittleren und oberen Paludinenschichten beschränkt. In der mittleren und oberen Abtheilung konnten zahlreiche Horizonte unterschieden und auf grössere Erstreckung nachgewiesen werden und in Folge dessen konnten die rein morphologisch aufgestellten Formenreihen der gekielten und geknoteten *Viviparen* sofort der geologischen Controle unterworfen werden. Für die unteren Paludinenschichten konnte eine Gliederung noch nicht durchgeführt werden, und es fehlt daher für die glatten, wie für die nicht von uns selbst gesammelten Formen der Nachweis für die Concordanz der chronologischen und morphologischen Reihe."

It is of course impossible to say precisely in what environment the different species flourished, but it is clear from Paul's sections in the geological part of the treatise on these Slavonian beds, that the molluscs all lived in a country similar in some respects to the Shan Plateau and that some of them were certainly lacustrine. Bourguignat[2] says of part of the country in which they were probably evolved :—

"Il a dû y avoir, à cette époque reculée, dans cette partie de la vallée de la Cettina, une vaste dépression remplie d'eau salée, qui, peu à peu, par des causes qui me sont inconnues, sont devenues saumâtres, pour finir par être entièrement douces."

The interest of these two cases so far as our present purpose is concerned lies in the fact that they prove that *Vivipara*, from which *Margarya* and *Tulotoma* are certainly derived, has, in widely separated districts, and in peculiar circumstances, developed a similar tendency to become extremely plastic and to elaborate the sculpture of its shell in spiral series of nodules. What the circumstances probably were will be considered later. A few other, less striking perhaps but none the less interesting instances of the same kind may be cited more briefly.

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[1] *Abh. K. K. Geol. Reichsanstalt*, VII, pp. 1-105, pls. iv-vi (1875). See also Penecke on the Slavonian Paludina Beds in Mojsisovics and Neumayr, *Beitr. Palaeontologie Ost.-Ungarns*, IV, pp. 15-44, pl. ix (6) (1886). I have to thank Mr. G. de P. Cotter of the Geological Survey of India for these references.

[2] *Et. Fossiles tert. & quatern. de la Vallée de la Cettina*, p. 2 (Saint-Germain : 1880).

In the lakes and rivers of Eastern China many species or races of *Vivipara* occur in which the shells are ornamented with spiral ridges of a more or less marked character but are much smaller and thinner than those of *Margarya*. Figures of these forms will be found in Kobelt's monograph and in Heude's[1] account of the molluscs of the Yang-tse. I have recently observed *V lapillorum* (Heude), a member of this group, in natural conditions in the Tai-Hu (Great Lake) in the Kiangsu province of China. It lives chiefly on stones near the edge of the lake, in very muddy water and in a district in which limestone is abundant. It is a variable species and apparently not found together with any closely allied form.

Single species of the genus with similarly but even more strongly sculptured shells have been described from several other eastern lakes and lacustrine districts, *e.g.*, *V grossicosta*, von Martens[2] from Lake Singkarah in Sumatra, *V persculpta*, P. & E. Sarasin,[3] from Lake Posso in Celebes and *V oxytropis* (Benson)[4] from Manipur in Assam, the basin of a lake which has shrunk in recent ages to small dimensions.

Moreover, Neumayr's *Viviparae* from Slavonia, though the most complete series as yet known, are by no means the only forms of a similar nature that have been described from Tertiary beds in Eastern Europe. The first instance of the kind to be discussed was that of certain forms from the island of Cos to which Edward Forbes[5] drew attention in 1847.

PELECYPODA.

We may consider the three genera of Pelecypoda that occur in the Inlé basin together. They are *Physunio* of the family Unionidae, *Corbicula* and *Pisidium* of the family Cyrenidae. *Corbicula* is the only one of these represented, so far as we know, in the deposits of the district and it is only found in quite superficial deposits.

Two species of *Physunio* are found living in the district, one (*P. ferrugineus*) in the open parts of the lake, the other (*P. micropteroides*) in the streams that run into it. A feature of the genus is the production of a triangular " wing " on the dorsal surface ; as I have shown above, this wing is used by the lake-form in ploughing its way through semi-liquid mud. The structure exhibits, in this and other species, a great difference in shape and relative size at different periods of growth, being much smaller in very young and very old shells than it is in those which are just attaining maturity. Otherwise, *P. ferrugineus* shows only slight variations in outline and proportion and in the structure of the

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[1] Heude, *Mem. Nat. Hist. Emp. Chinois* I, pl. xl (1880-1890).

[2] v. Martens in Weber's *Zool. Ergebn. Niederl. Ost.-Ind.* IV, p. 25, pl. ii (1897).

[3] P. and E. Sarasin, *Sussw.-Moll. Celebes*, p. 62, pl. x (1898).

[4] Benson, *Journ. As. Soc. Bengal* V, p. 745 (1836). He does not state the precise locality of his specimens, but the Indian Museum possesses others collected in Manipur by Godwin-Austen.

Forbes, *Edinb. Phil. Journ.* XLII, p. 271, pl. ii (1847). See also Newton, who gives other references : *Proc. Mal. Soc London* IX, p. 363 (1911). In the Tertiary beds of Eastern Europe other families of molluscs, especially the Neritidae and the Hydrobiidae, exhibit a similar evolution, while in the recent fauna of the Yang-tse, which possesses a remarkable resemblance to the later Tertiary freshwater faunas of Eastern Europe, peculiar shells occur in the Hydrobiidae in many respects analogous to those of the Tertiary *Viviparae* or of the living *Taiae*.

hinges of the shell, and these variations seem to be entirely individual. The Yawnghwe river-species differs from the lake-form in its smaller. thicker and higher shell and also in the very feeble development of the wing. Possibly this last character is correlated with life in much stiffer mud. This species is not a variable one.

The only *Corbicula* found in the Inlé basin is *C. noetlingi*, a form that has a wide range in the Shan States. Von Martens refers to a small variety which has a certain difference in outline from the typical form, but we did not find this variety in the Inlé and He-Ho basins. The species lives in streams and does not enter the lake. Subfossil shells do not differ constantly from living ones and there is no very definite racial difference between shells from altitudes varying from 3,000 to 4,500 feet, but the local phase has probably developed into a distinct race. I have refrained from giving it a name and from discussing it in detail because great confusion exists as to both the nomenclature and the specific limits of the eastern *Corbiculae*.

Pisidium casertanum is perhaps the most interesting bivalve mollusc found in the district, as it is a characteristic Palaearctic form. Specimens from the lake do not exhibit any great individual variation. The species is an extraordinarily plastic one, with a very wide geographical range. The limits of its variation have been discussed in great detail by B. B. Woodward[1] in his catalogue of the British species of the genus. He says :—

> "In external conformation this is a most variable species and may at times, especially when dwarfed, resemble forms of *P. pusillum* .... *P. personatum*.... and even *P. nitidum*.
>
> "There is one well marked form, a lake or still water form, which almost amounts to a variety. In this the shell is rounder than the type, and more compressed ..... whilst the hinge being narrower and lighter is less arcuate and the flexure less pronounced."

In three localities in Eastern Asia a form has been found that resembles "this lake or still water form," *viz.*, in Lake Biwa in Japan, in Lake Baikal in Siberia, and in the Inlé Lake on the Shan Plateau. I have not seen shells from Lake Baikal, but those from the Inlé Lake resemble Lindholm's figure[2] very closely. The Japanese shell, which is a little wider than Inlé specimens, has been examined by Woodward,[3] who remarks that it was "rather more oval than usual," *i.e.*, in the still water form. A single shell from a stream on the He-Ho plain is much more inflated than those from the lakes and approaches the Himalayan *P. atkinsonianum*,[4] which is also found in streams.

CONCLUSIONS.

This is not a general treatise on variation or evolution, but merely an attempt to demonstrate so far as demonstration is possible, and with as little reference to contentious works as may be, certain phenomena

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[1] *Catalogue of the British Species of Pisidium in the Collection of the British Museum*, pp. 31-44, pls. i, figs. 3-6 ; iii, fig. 3 ; xiii-xviii (London : 1913).

[2] Lindholm in Korotneff's *Wiss. Ergebn. Zool. Exp. Baikal-See*, IV (Moll.), p. 85, pl. ii, figs. 45, 46.

[3] See Preston, *Ann. Mag. Nat. Hist.* (8), XVII, p. 162 (1916).

[4] See Preston, *Faun. Brit. Ind. Moll.*, p. 226, fig. 29 (1915).

manifested by the aquatic molluscs of a single district. Parallel cases have been cited for comparison, not to support any one theory.

Four facts stand out prominent in reference to these Mollusca :—

(1) That racial plasticity is a more common phenomenon among them than extreme individual variability, and that the two are not necessarily correlated.

(2) That both plasticity and individual variability are specific characters ; they may be almost absent for the time being in a stable species, but may be either acquired or lost in the course of evolution.

(3) That in very few instances is it possible to detect any advantage that the race can have gained by its plasticity.

(4) That the moulding forces, or the causes of plasticity, of greatest influence are not the same in all species, and that apparently slight differences in environment are sometimes of greater practical moment than changes which seem to be much greater.

I will deal with each of these points in some detail.

(1)

In most of the aquatic molluscs of the Inlé district, individuals from the same environment are very like one another. The main exceptions are *Planorbis velifer* (of which two distinct varieties live together), *Melania baccata*, *Taia naticoides* and *Taia elitoralis*.

The case of *Taia naticoides* is a remarkable one, for the species is both variable and plastic. Individuals from any one environment differ greatly from one another, falling roughly into three groups, the limits of which are, however, undefined. At the same time races from different types of environment differ from one another, while retaining their individual variability in slightly modified ways. It is, however, to the most extreme variety of the species (*carinata*, Theobald) that all the more highly modified forms of the genus are most closely related. Indeed, one of these forms (*intermedia*) is little more than a fixed race of this variety. *T intermedia* is not, however, precisely speaking, a mutation in the sense in which the term is used by most biologists, because it is not descended, so far as can be seen from the evidence available, from a single individual or group of individuals that have departed suddenly from the normal type of the species. *T naticoides* has a fairly wide distribution, and the variety *carinata* always occurs with the typical form. Moreover the transition between the two forms is quite gradual.

The circumstances of *T elitoralis* are different in that it is only known from a single locality and a single type of environment, but it also seems to have given rise to a constant species very like itself, namely, *T intha*, which is at once the most highly specialized form and one of the most constant forms in the genus.

On the other hand *Taia theobaldi*, probably the parent form of all these species, is a constant species. So also, in a sense, is *Hydrobioides nassa*, which has produced four races, each fairly constant in its own type of environment. Further, *H. nassa* is derived from another constant

form, *H. avarix*, in which its most striking peculiarity (the varix) is absent.

(2)

In species such as *Planorbis exustus* neither individuals nor local communities as a rule differ much one from another. A deficiency—it is not of course an entire absence—in variation of all kinds is also well exemplified in *Taia theobaldi* and *Hydrobioides avarix*. Yet these two constant forms have both given rise to species that are both variable individually and plastic: to *T naticoides*, in which both individual variation and plasticity are extreme, in the one case, to *H. nassa*, in which plasticity is more marked than individual variability, in the other. *Limnaea shanensis*, on the other hand, has proved itself plastic without exhibiting individual variability; we only know it as a plastic species because of the discovery of shells of extinct phases: each phase was constant in its proper environment. *Taia intha*, a highly specialized form descended from ancestors that were both plastic and variable individually, has become in its own proper habitat a constant species and has apparently lost plasticity. That *Limnaea mimetica* has done so is proved by its continued existence as a modified form in conditions totally different from those with which its modification must be correlated; for its resemblance to deep-water forms is not merely superficial as in some of the instances cited on p. 174, but so detailed as to be almost beyond dispute.[1] Further, it is even possible that plasticity once lost may in certain circumstances be regained. This is, however, more difficult to demonstrate. The He-Ho living phase of *T naticoides* may conceivably be descended direct from *T intermedia* and represent a reversion to the variability of the ancestral form, but it seems on the whole more probable that *T naticoides*, even after giving rise to *T intermedia*, persisted in the neighbourhood unchanged, in a different environment from its daughter form.

(3)

The species or groups of species that have exhibited greatest plasticity are *Limnaea andersoniana*, *L. shanensis*, *Melania tuberculata*, *Hydrobioides avarix* and *nassa*, and the species of *Taia*.

On general grounds it is clear that two types of aquatic environment are the most favourable, at any rate in tropical and subtropical climates, for the type of plasticity that results in the evolution of peculiar species and genera. They are small mountain streams and large lakes. This is the case not only with molluscs but also with other groups of animals. Many of the most highly modified Indian genera of fish and of aquatic molluscs, as well as the most peculiar species of Batrachian and insect larvae, live in small streams in the hills, *e.g.*, *Pseudecheneis* of the family Siluridae among the fish; the almost neritiform *Stomatodon* of the family Melaniidae among the molluscs; and the tadpoles of such frogs and

[1] Compare the blind prawn *Typhocaris galilea*, which has all the characters of an underground animal but now lives in an open fountain in which it has probably been isolated by an earthquake. See Annandale and Kemp, *Journ. As. Soc. Bengal*, IX (*n. s.*), p. 245 (1913).

toads as *Rana afghana*,[1] *Bufo penangensis*[2] and *Megalophrys montana*.[3] On the other hand, in countries in which large lakes exist many of the most highly specialized genera are found only in them, *e.g.*, the peculiar Mollusca of Lake Tanganyika in Central Africa, of Lake Tali Fu in Western China and of the deeper lakes of Celebes, or the peculiar prawns and crabs of Tanganyika, or even the peculiar fish of the Inlé Lake. We may assume therefore that in hill streams and large lakes there are certain factors that encourage extreme plasticity; but they cannot be the same in both instances.

In most of the highly modified genera and species that inhabit hill streams, the modifications in structure have a definite function in enabling the animal to cling tightly to rocks or other solid bodies in rapid-running water. But this is not the case with most modified organisms from large lakes.

It is possible[4] that in *Limnaea*, a pulmonate mollusc that has no gills or other special organ by means of which oxygen can be absorbed direct from the water, it may be advantageous in deep water or in water highly charged with vegetable matter to have a relatively large aperture to the shell; for this enables a large surface of skin to be extruded and it is probable that oxygen, in conditions in which the animal cannot rise to the surface, must be absorbed through the skin. If, however, this is the case, it is probable that the benefit is to a large extent fortuitous, for we have no evidence whatsoever that the modification has been produced through any kind of selection of individuals; it rather seems to be the result of the direct influence of physical or chemical forces working suddenly or gradually on a plastic organism, as is suggested by the series of shells figured on plate X, figs. 5-8, as well as by the experiments cited above. Further, the deep-water forms of the genus resemble the young of shallow-water forms in the shape as well as the size of the shell. They are essentially forms which retain when adult the external characters of immaturity.

As I have already pointed out it is not uncommon in *Ampullaria* for ridges to be produced on the surface of the body-whorl owing to the resumption of growth after a period of rest. There is every reason to think that the varix of *H. nassa* has a similar origin, but whereas in *Ampullaria* the lip of the shell is thin and therefore the ridge representing it is low, in *H. nassa* the lip and the ridge representing it are thick. Our visit to the Inlé Lake was made in early spring, at a time when many hibernating animals were just beginning to awake from their winter sleep. I noticed that large numbers of young individuals of *H. nassa* of from 2 to 3 mm. long had at this season a very thick lip, but that in others only slightly longer or even a little shorter, the thickening had disappeared and the lip was thin and sharp. It seems probable, therefore, that the marginal thickening can be absorbed in the course of growth. The retention of the varix in adult shells would seem to indicate merely that at a certain period of growth the animal

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[1] Annandale, *Rec. Ind. Mus.*, VIII, p. 9 (1912).
[2] Flower, *Proc. Zool. Soc. London*, (1899), p. 908.
[3] Annandale, *Mem. As. Soc. Bengal*, VI, p. 155 (1917).
[4] Pelseneer, *Arch. de Biol.* XIV, p. 379 (1895).

loses the power of absorbing the ridge left when the shell grows beyond the old lip. All this is in favour of the view that the varix is a vestigial structure, vestigial that is to say so far as the individual and not the race is concerned. It may otherwise be considered as a sign of the approach of senescence or at any rate of full maturity, for when the old lip ceases to be absorbed the animal has not the power to grow very much larger.

It is difficult to see in what way differences of size in the shells of *Melania* or of shape and sculpture in those of *Taia* could be of any benefit to the race either directly or indirectly. The shells in the latter genus are as a rule so thin and fragile, even when highly decorated, that they could not protect the animal from powerful enemies of any kind. Neither could the knobs and scales on their surface protect them from parasites. *T. intha* at any rate, the species which I have been able to observe most closely in natural conditions, seems to be a peculiarly sluggish and unprotected animal, and to be altogether devoid of enemies except leeches of the genus *Glossosiphonia*, which make their way in through the mouth of the shell and are not deterred from doing so by the sculpture round the aperture or on the surface.

(4)

We have seen that in *Limnaea* the cause of change in the shape of the shell is, in some species, the change from running to still water or conversely, and that this change acts directly on the young individual. In other species of the same genus, however, other forces come into play and the case becomes much more complicated. Indeed, almost all that can be said with certainty is that the shells of individuals living in water of peculiar chemical composition, as all the Inlé species do, are usually dwarfed, and that individuals living in deep water are still more strongly dwarfed and very narrow and have the mouth of the shell very long and the spire short, and that these are essentially immature characters.

In *Melania tuberculata* overcrowding, especially in a small space, and also undue salinity of the water in some cases, produces dwarfing, but in the Lake of Tiberias, where the water is distinctly saline, the shells are large and well-developed.

We know that *Hydrobioides nassa distoma* survived for a considerable period both in lacustrine and paludine conditions without change, although the species, probably under slightly different conditions, has developed a distinct race in the central region of the Inlé Lake, and the race *distoma* has become extinct.

Some of the different races of *Taia* that have become so far differentiated as to be regarded conventionally as distinct species, have been produced, so far as we can see, in circumstances that differ little, and the same thing has apparently occurred in *Margarya* in Yunnan. in the Tertiary Viviparidae of Slavonia and in other widely scattered instances.

It follows almost as a corollary that similar modifications may be brought about in very different biological circumstances. This is clearly shown by the resemblance between the shells of *Succinea indica* and *Limnaea mimetica*; but it must be noted that only the *Limnaea* can

be considered to be a highly modified form. The *Succinea* is a normal form of its genus.

The smaller mollusca of the Inlé Lake, especially those belonging to the genera *Limnaea*, *Planorbis* and *Pisidium*, would undoubtedly be taken for deep-water forms by a conchologist accustomed to the deep-water molluscs of the Swiss Lakes.[1] Their minuteness, their fragility, the lack of pigment in both shell and soft parts, and, in the *Limnaea*, the extremely long mouth of the shell and the rudimentary but relatively narrow shape of the spire, are all features characteristic of deep water. The Inlé Lake was once very much deeper than it is now and *Limnaea mimetica* is probably a deep-water form that has survived from the period when that was the case, but two of the three species of *Planorbis* that are now found in the central region of the lake are also found, with some of the same characters, in waters that can never have been deep and never even have formed part of a lake-system. The *Pisidium* is no smaller or more fragile than the form (*P. atkinsonianum*) common in small streams in the Himalayas. Indeed, it is very like this form, except that the shell is less swollen, a feature in which it also differs from the phase found in streams on the He-Ho plain.

Moreover, smallness, fragility and colourlessness of shell in the case of bivalve molluscs are often associated with life in soft mud in shallow water in very different biological conditions. This is so not only with *P. atkinsonianum* in small mountain streams, but also with *Corbicula tenuistriata* [2] in the Whangpoo River near Shanghai, and with species of a number of different families in the brackish water of the Chilka Lake.[3]

In the life of these bivalve molluscs there is a common biological feature in that they live in soft mud, and the modification of the shell may be of practical utility to the individual and the race. In the bionomics of *Taia*, *Margarya* and the Slavonian Viviparidae also it is not improbable there is or was some common feature, but there is no evidence that it was of biological importance and, if it existed, it is, with our present knowledge, obscure. In any case the circumstances of their life-history cannot have been by any means identical. All that can be said is that in each case the peculiar forms with highly sculptured shells seem to have been evolved in a region of great lakes, in which an abundance of soluble mineral salts was present and in which the climate was temperate rather than tropical, warm rather than cold. Apparently also the water did not possess any marked power of erosion of the shell, which would have destroyed the sculpture and rendered its perfection impossible.

From the facts stated and the inferences already drawn it seems very doubtful whether the peculiar modifications of the shell observed in so many of the aquatic molluscs of the Inlé Lake can have any bearing on the more highly specialized modern theories of evolution, which, even if sound in certain instances, are perhaps of less general application than their rival exponents are willing to admit. None of

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[1] See Zschokke, *Die Tiefseefauna der Seen Mitteleuropas*, pp. 155, 164 (1911).
[2] Annandale, *Mem. As. Soc. Bengal*, VI, pt. i, p. 67 (1916).
[3] Annandale and Kemp, *Mem. Ind. Mus.*, V, p. 341 (1916).

these theories have been put forward with the same wealth of natural illustration that Darwin gathered together in his *Origin of Species*, and it is just as important that observations should be continued in the field on as large a scale as possible, and without reference to any one preconceived theory, as that experiments should be conducted in the laboratory or garden-plot with a theory to support. I do not think that any single formula can express, much less explain, evolution.

I am of the opinion that the Inlé shells illustrate two different and possibly somewhat exceptional lines along which evolution may proceed.

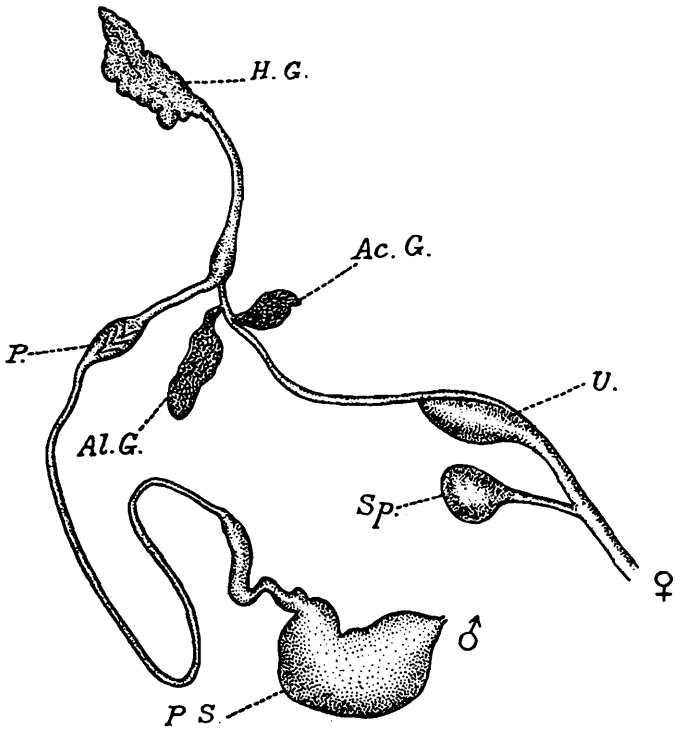

Fig. 9.—Genitalia of *Limnaea mimetica*.

Ac. g.—accessory gland. *Al. g.*—albumen gland. *H. G.*—hermaphrodite gland. *P.*—prostate. *P. S.*—penis-sheath. *Sp.*—spermatheca. *U.*—uterus.

We know that in some forms of *Limnaea* the plasticity is of the young individual, and that modification can be produced and reproduced in either direction from one generation to another. Probably, however, even in comparatively simple shells such as those of *Limnaea*, a time would come, if the environment were constantly changed in one direction, at which plasticity disappeared. This is indicated by Whitfield's observation that individuals of this genus if kept in captivity for several generations lost their monoecious structure and became dioecious. He was of the opinion, that this was directly due to abortion of that part of the shell in which certain of the sexual organs were normally lodged. It follows, therefore, that in suggesting that altered environment may finally result in a modification of the race rather than of individuals, one is not necessarily expressing heretical views as to the inheritance of acquired characters—a series of phenomena, or supposed phenomena, which it seems to be quite impossible either to prove or definitely to disprove. If the organs of one sex in a monoecious animal can disappear after several generations as a direct result of a change of conditions on the shape of inanni-

mate parts, there can be no difficulty in claiming that change of conditions may ultimately affect the gonads in such a way that a new race or species is evolved, for either the animal must become parthenogenetic or else new combinations in the germ-plasm must be liable to occur. The precise meaning of Whitfield's statement is, however, obscure, and it cannot be applied to *Limnaea mimetica*, in which the genitalia are quite normal and as usual hermaphrodite. I reproduce a figure (fig. 9) prepared for me by Mr. Baini Prashad to illustrate this point.

It does not seem to be possible to explain the extraordinary development of the forms of *Taia* in the same way as that of the genera already discussed. The history of the genus as we know it may be summarized as follows :—*Taia theobaldi*, a constant species, lived and lives in running water in mountainous districts. It gave rise, how we do not know, to *T naticoides*, an extremely variable species that lives in ponds and marshes and the backwaters of streams. Some individuals of *T naticoides* closely resemble the parent form, while others depart from it widely and represent a much higher degree of specialization. From this extreme form of *T naticoides* some ten or eleven other forms have been derived, mostly if not solely in large lakes. Evolution, therefore, seems to have taken place in this genus along somewhat peculiar lines, but the highly specialized sculpture of the shell can hardly have been more than a by-product of evolution.[1] Dendy and Nicholson[2] have recently shown that certain sponge-spicules of somewhat elaborate outline owe their peculiar shape to the mechanical forces produced by the flow of water through the sponge. Dendy has also pointed out, however, that advantage is taken of the modifications thus produced, should they chance to be useful. The cases are o course analogous, not homologous, for the forces, be they chemical or purely physical, to which a free-living mollusc is subjected in still water cannot be the same as those that have moulded the spicules into shape ; and even the analogy must not be pressed too far, for we have evidence in *Taia naticoides* that at any rate the rudiments of the peculiar sculpture of the shell may appear without the application of any well-defined physical or chemical force. The resemblance consists in this—that in both cases highly peculiar and elaborate forms have been produced in the inanimate parts of living organisms without any apparent utility in the first instance, but capable of utilization and as it were of standardization. In the life-history of *Taia* there seems to have been no economic need for the application of these peculiarities, but they have become standardized by what seems to have been a racial (or possibly a germinal) as distinct from an individual selection ; *Taia intermedia* affords no evidence of the survival of the fittest individuals but suggests rather that all the individuals born in a certain locality and type of environment were formed in accordance with a certain pattern that already existed, with others, in the reproductive potentialities—the phrase is purposely vague—of *T naticoides*, its immediate ancestor.

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[1] Dendy, *Journ. Quekett Micr. Club* (2), XIII, p. 38 (1916).

[2] Dendy, *ibid.*, XIII, pp. 1-16 (1917) ; Dendy and Nicholson, *Proc. Roy. Soc.*, London (B), LXXXIX, pp. 573-587.

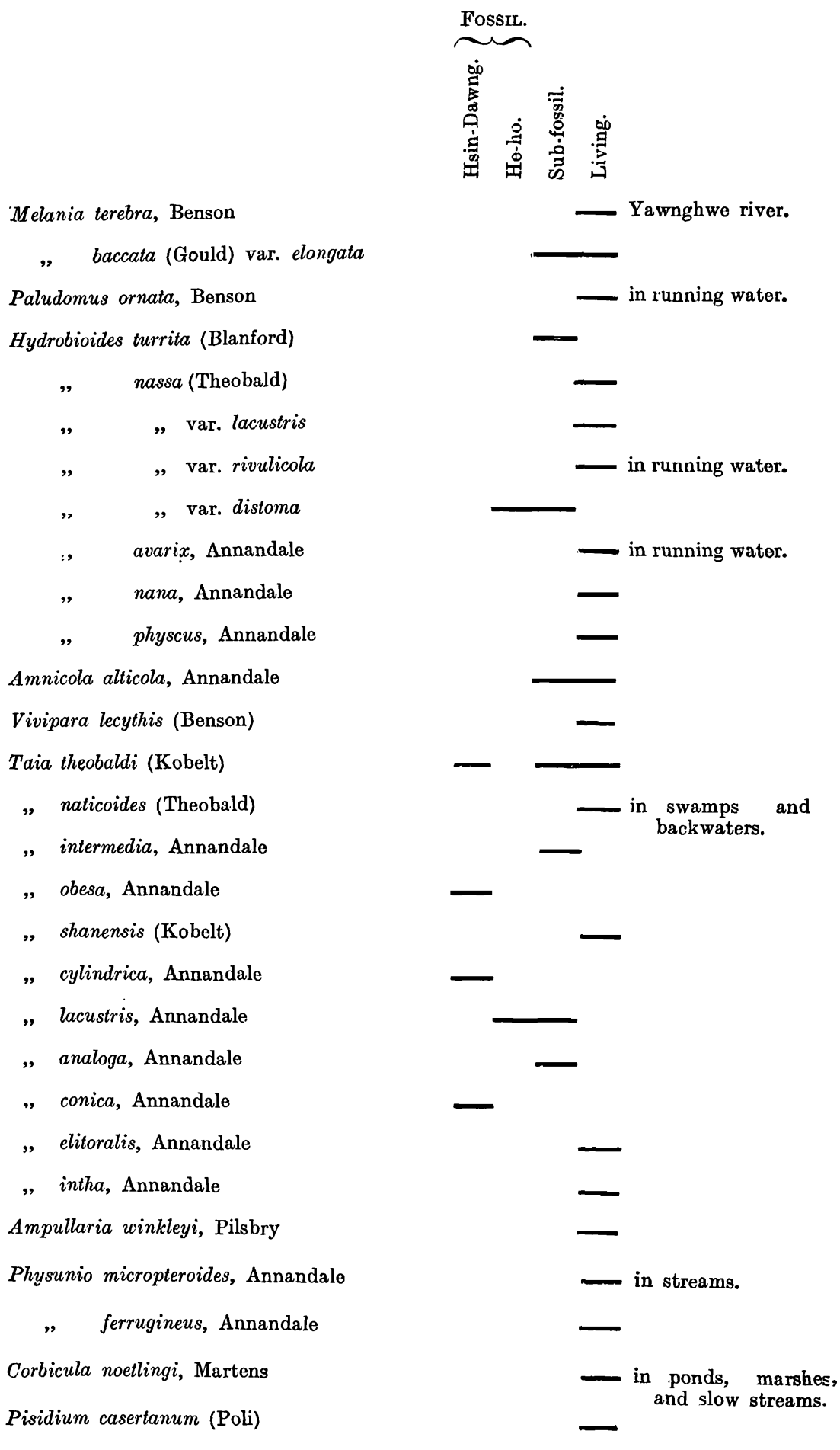
The knobs, ridges and spines on the shell of *Taia intha*, the culminating species of the genus, seem to be of no use to the animal, which is a sluggish creature, quite incapable, so far as it is possible to judge, of aesthetic perception of its own beauty. Its shell has reached perfection in calm and undisturbed surroundings, which place no bar in the path of eccentricity. The sculpture seems to have made its appearance in a primitive form in *T theobaldi* in circumstances that forbade its full development, and to have had a cumulative development in proportion as the surroundings became more and more peaceful and settled. Lack of enemies, abundance of food, absence of aquatic currents, abundance of free oxygen, an equable temperature without frost, absence of free acid and erosive algae have all combined to give an inherent tendency full play, probably not through the elimination of individuals in which this tendency was feeble so much as through its strengthening in all individuals.

The Inlé Lake, or rather the system as a shrunken relic of which it persists, was, on a comparatively small scale, one of those districts, such as Lake Tanganyika or the lake country of Celebes, in which phenomena of the kind have been manifested to an exceptional degree.

List of species giving approximate age, etc.

	Fossil.			
	Hsin-Dawng.	He-ho.	Sub-fossil.	Living.
Succinea indica, Pfeiffer			—	—
Limnaea andersoniana, Nevill				— in streams and ponds.
„ *shanensis*, Annandale, A		—		
„ „ , B			—	
„ „ , C				—
„ „ , D				?
„ *mimetica*, Annandale				—
„ ? prox. *ovalis* Gray		—		
Planorbis exustus, Deshayes				—
„ *saigonensis*, Crosse and Fischer			—	
„ *velifer*, Annandale			—	—
„ „ var. *ciliata*				—
„ *trochoideus*, Benson		—		—
„ *calathus*, Benson				—
„ *caenosus*, Benson				—
Melania tuberculata (Müller)			—	—

List of species giving approximate age, etc.—contd.



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NOTE ON THE PALAEONTOLOGY OF THE INLE MOLLUSCA.

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The shells occurring in various geological formations have been classified, by Dr. Annandale, according to their relative antiquity, as sub-fossil and fossil. How far these two groups correspond with the two divisions generally recognised by geologists in the Quaternary era, the " Pleistocene " and the " Holocene " (or " sub-recent " or " recent ") cannot at present be definitely settled.

In Europe and in many other temperate regions, the termination of the Glacial Period forms a convenient datum line for separating the two divisions. In India, the study of the corresponding formations has not yet progressed far enough to correlate them in detail with the sequence of local physical changes.

Nevertheless, the shells which Dr. Annandale has classified as " sub-fossil " may confidently be regarded as " holocene " or " sub-recent," but it would be difficult at present to say for certain whether those described as " fossil " should be ascribed to an earlier phase of the " holocene," or else regarded as frankly pleistocene, though the latter alternative is more probable.

Considering the great plasticity of some of the forms above described, length of time need not represent a factor of primary importance in the evolution of the extinct and living mutations or species under consideration. Their transformations seem directly connected with the changes in physical geography of the Shan plateau, and, without precise information as to the geological dates of the physiographical evolution of that region, we are unable to fix the exact period of the correlated biological changes.