ON THE COMPARATIVE ANATOMY OF ORIENTAL VIVIPARIDAE.

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The members of the family Viviparidae were until recent years known chiefly by their shells, though a few observations on the soft parts had also been made. There are at present no sufficient data on which could be based a comparative study of the anatomy of the various species described. In the last half century various fragmentary accounts of the anatomy of *Vivipara bengalensis* (Lamarck) had been published, but, so far as I know, there was no single Palearctic or Oriental species of Viviparid in which the anatomy in all its details had been completely studied. This gap in our knowledge was first filled in India by the publication in 1921 of a monograph on *Vivipara bengalensis* by Dr. Annandale and Major Sewell.[1] Their observations on certain structures in the mantle edge of this and other species and genera of the family led Dr. Annandale to important and far-reaching conclusions in respect of the sculpture and ornamentation of the shell.

These authors stated in the summary of their account that the anatomy of the Viviparidae, so far as it had been studied, is strikingly uniform in most respects. Their detailed observations were, however, apart from *V bengalensis*, restricted to the structure of the mantle, the brain, and the radula of various species. With a view to examine their statement I undertook, at the suggestion of Dr. Annandale, to make a comparative study of other systems of organs. The material placed at my disposal was all preserved, but I have had opportunities of studying fresh and living specimens of the Burmese genus *Taia* and of *V bengalensis*. A few species from China and Japan were available for comparison in preserved material. A part of the Indian and Chinese material was in a bad state of preservation. Disadvantageous as preserved specimens are for a satisfactory study of the anatomy, I have not hesitated to place together my notes, in the hope that a small attempt in this direction may, at least, be an incentive to an extended and more exhaustive study of the family.

For purposes of comparison structures in which there is appreciable variation have been examined in all the species.

I take this opportunity of expressing my great indebtedness to the late Dr. Annandale for the help received in the preparation of this paper.

The comparative anatomy of the following five genera of Viviparidae was studied in greater or less detail:

Vivipara Montfort.
Taia Annandale.
Dactylochlamys, gen. nov.
Lecythoconcha Annandale.
Margarya Nevill.

[1] Annandale & Sewell, *Rec. Ind. Mus.*, XXII, pp. 215-292, pls. i-iii (1921).

Vivipara Montfort.

I have examined three species of this genus, viz., *Vivipara bengalensis* (Lamarck), *Vivipara dissimilis* (Müller) and *Vivipara quadrata* (Benson). The two former are from India and the last from China. The three species belong to different sections of the genus, namely the Viviparae bengalenses, the Viviparae dissimiles, and the Viviparae angulares. The alimentary organs, the kidney, and the central nervous system are quite uniform and do not show any appreciable variation. Specific differences are found only in the gill-lamellae, in the central nervous system,[1] the male genitalia,[2] and in the number of embryos present in the uterus. The differences in the form of the gill-lamella in the three species are best appreciated by a reference to the figures. In *V bengalensis* the uterus is cramped with numerous fully developed embryos and eggs enclosing small embryos in various stages of development. In *V dissimilis* there are only four to five embryos and about thirty small polygonal eggs in the uterus. The embryonic shells have no bands on them, but bear three rows of chaetae with a few prominent ridges. Some of the secondary ridges on the bodywhorl also bear chaetae. In *V quadrata* the uterus contains two or three relatively large embryos without bands on their shell, and about sixteen eggs. These differences in the three species seem to be constant.

The type-genus *Vivipara*, therefore, has the following anatomical characters:

The margin of the mantle in the adult is moderately thick and bears three short processes corresponding in position with the three rows of chaetae on the embryonic shell. These chaetae usually disappear on the adult shell. The adult shell may or may not bear coloured bands and is usually without ridges or spines of any kind, but a few species are highly sculptured. The head of the animal is small in relation to its size. The gill-lamella is usually broad and has a well-developed blood-vessel on its superior margin. In the central nervous system the cerebral ganglia are better developed than the pleural or the pedal, the pleural ganglia being usually insignificant and placed near the cerebral. The commissures and connectives are relatively short and thin. The uterus usually contains a large number of embryos in various stages of development.

Taia Annandale.

The following five species of the genus were examined:

Taia naticoides f. *intermedia* Annandale.
Taia shanensis (Kobelt).
Taia elitoralis Annandale.
Taia intha Annandale.
Taia crassicallosa Annandale and Rao.

All the five species are from the Shan plateau in Burma.[3]

The genus *Taia* is distinct from *Vivipara* not only in the shell but also in the soft parts. It differs from the latter in the head of the animal

[1] Annandale & Sewell, *op. cit.*, p. 269.
[2] *Id., ibid.*, pp. 232-233.
[3] Annandale, *Rec. Ind. Mus.*, XIV, pp. 123-137, pl. xv-xviii (1918).

being larger, in the relatively narrow marginals of the radula, in the lining of the stomach being transversely folded and often chitinized as two ridges at the junction of the oesophagus and the stomach, in the relatively narrow and tapering gill-lamella, in the greater development

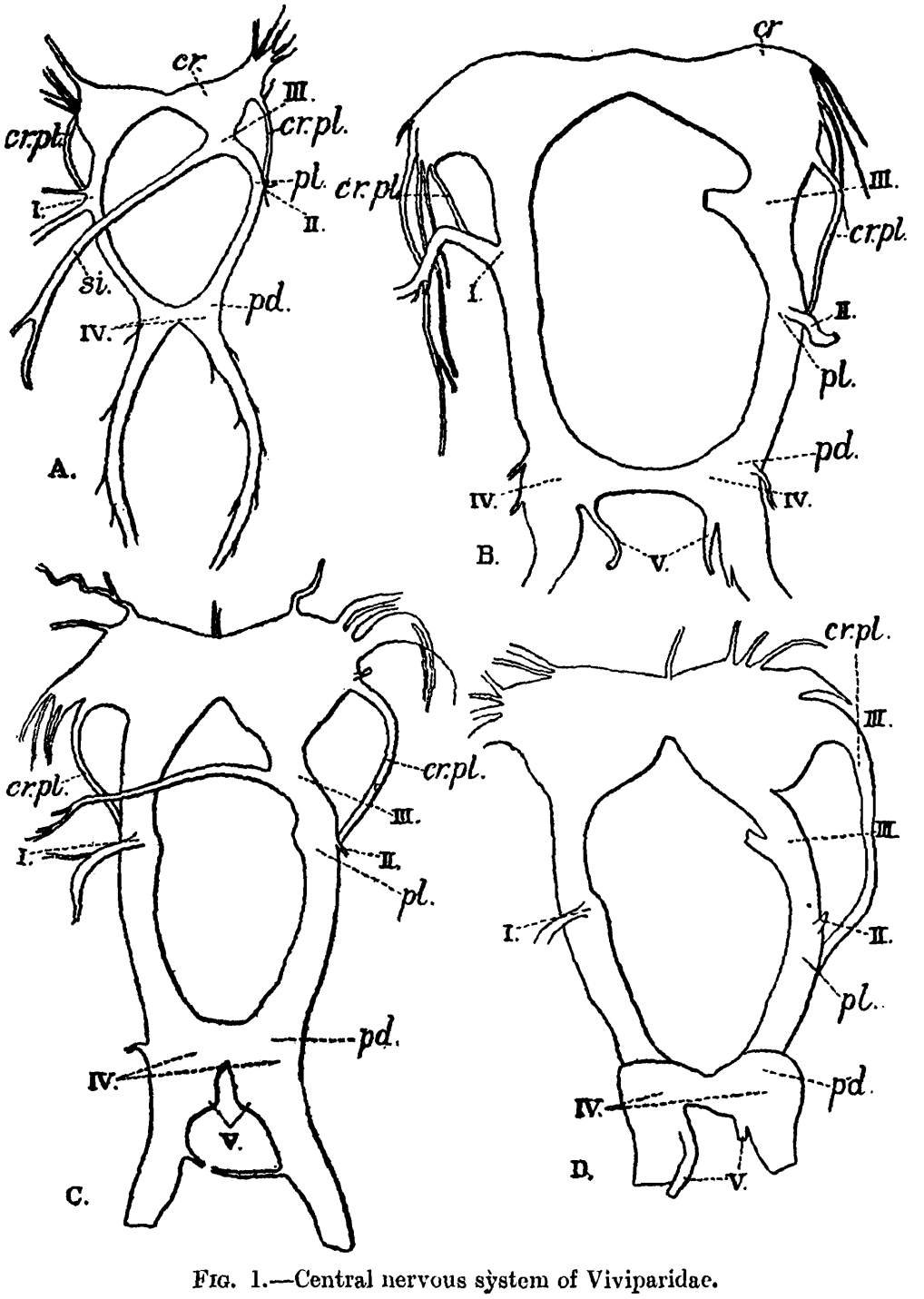

FIG. 1.—Central nervous system of Viviparidae.

A. *Vivipara bengalensis.* C. *Taia shanensis.*
B. *Taia naticoides* f. *intermedia.* D. *Taia intha.*

Cr., cerebral ganglion ; *cr. pl.*, cerebro-pleural commissure ; *pl.*, right pleural ganglion ; *pd.*, pedal ganglion ; *si.*, supra-intestinal nerve ; I. left pleural ganglion ; II., nerve from the right pleural ganglion ; III., ganglion from which the supra-intestinal nerve arises ; IV., portion of pedal ganglion from which the pedal commissure takes its origin ; V., nerve from the posterior side of the pedal ganglion.

of the ganglia and commissures of the brain, and in the much fewer full-grown embryos in the uterus.

Specific differences are found in the gill-lamellae, the stomach and the genitalia. Of these the most reliable are those of the gill-lamella. Other structures such as the radula, the kidney, the heart, and the brain are subject to considerable variability in the individuals of a species. Specific differences have been discussed by Dr. Annandale and myself in a paper on the aquatic Gastropods of the Inlé watershed published immediately before this paper.

Dactylochlamys, gen. nov.

This genus is here proposed for the Assamese and Burmese species *Paludina oxytropis* Benson. It may be defined thus :

The shell is of large size, conical, thin but ornamented with prominent smooth spiral ridges which are concave on the internal surface. The base is somewhat flattened. The umbilicus is broadly rimate with a broad channel descending downwards from it.[1]

The radula and operculum are as in *Vivipara.* The mantle has enlarged and highly vascular finger-shaped processes on the margin.

Type-species.—*Paludina oxytropis* Benson.

Dactylochlamys oxytropis[2] (Benson).

Specimens of this species in the collection are in such a bad state of preservation that the alimentary organs, the kidney, and the genitalia

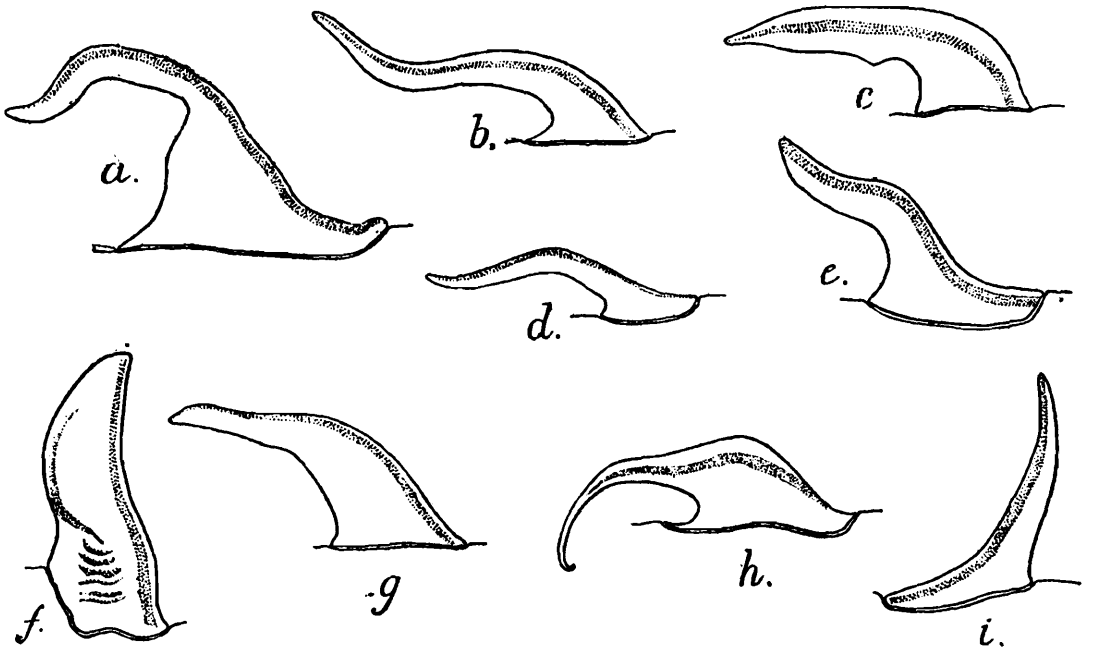

Fig. 2.—Gill-lamellae from the middle region of the ctenidium of Viviparidae.

a. Dactylochlamys oxytropis.
b. Taia crassicallosa.
c. T. shanensis.
d. T. naticoides f. *intermedia.*
e. T. elitoralis.
f. Vivipara bengalensis.
g. V. dissimilis.
h. Taia intha.
i. Vivipara quadrata.

could not be made out.[3] Fresh specimens were, however, dissected by Dr. Annandale who states that there is no material difference in the gross

[1] See Annandale, *Rec. Ind. Mus.*, XXII, pp. 548-550, fig. 3B, pl. iv, figs. 2-5 (1921).

[2] *Paludina oxytropoides* Heude is probably a synonym of this species, at any rate it may be no more than a Chinese race of it. See Heude, *Mem. Hist. Nat. Emp. Chin.*, p. 176, pl. xl, figs. 3, 3a. (Chang-Hai, 1890).

[3] The specimens were hardened in formalin, which, as experience has taught us, should be avoided in the preservation of freshwater molluscs.

internal anatomy of *V bengalensis* and *D. oxytropis*. I have been able to examine the gill-lamellae, the central nervous system, and the uterus of the present species. The gill-lamella approaches that of *V dissimilis* but is distinct in having a broad basal portion, and a long finger-shaped apical half. The brain is very similar to that of the species of *Taia* in the well-developed ganglia and the stout commissures. In the uterus there are about ten relatively small full-grown embryos and an equal or a slightly larger number of eggs with a tough external covering of albuminous material. The embryonic shells bear three rows of chaetae but no bands.[1]

In respect of the gill-lamella and the number of embryos in the uterus the present species may be said to be distinct from those of *Vivipara* or *Taia*.

Lecythoconcha Annandale.

This genus closely resembles *Vivipara* in some features, but has distinctive characters in the mantle, in the gill-lamellae, and in the brain of the animal.

The free-edge of the mantle is greatly thickened, with a strong and conspicuous sphincter muscle along it. The gill-lamella is relatively long and has its superior margin thickened and often thrown into folds. The ganglia and commissures of the brain are strongly developed, much more so than in species of the genera discussed above. There are usually about thirty embryos in the uterus.

I have examined the following three species of the genus, all from outside Indian limits :

Lecythoconcha lecythis (Benson), rice-field phase, from China and Japan.

Lecythoconcha chinensis f. *catayensis* (Heude) from China.

Lecythoconcha sclateri (Frauenfeld) from Japan.

These three species are closely similar in respect of the soft-parts but differ in the form of the gill-lamella and in the number of embryos present.

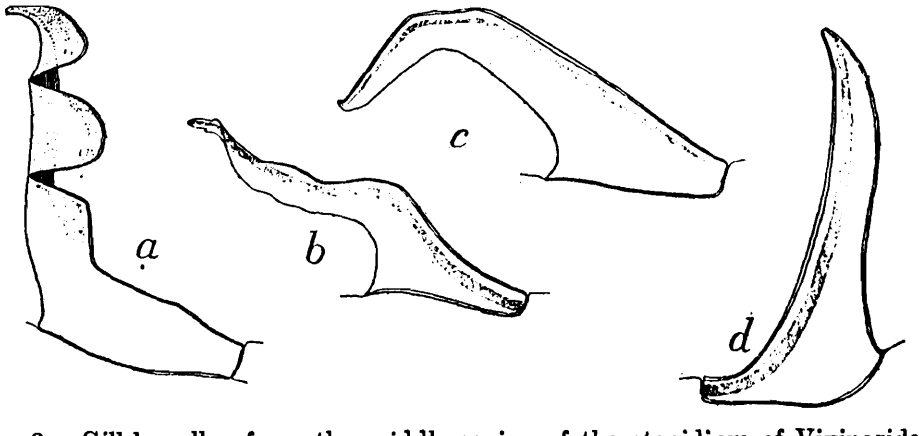

Fig. 3.—Gill-lamellae from the middle region of the ctenidium of Viviparidae.
a. Lecythoconcha lecythis. *b. Lecythoconcha lecythis,* a relatively narrow and less folded type.
c. Lecythoconcha chinensis f. *catayensis.* *d. Margarya melanoides.*

With regard to the latter feature *L. lecythis* and *L. chinensis* f. *catayensis* come very close. They have about thirty more or less equal-sized em-

[1] Dr. Annandale has observed that males of this species are considerably less abundant than females in the Loktak Lake, Manipur valley.

bryos without bands on the shells. In *L. sclateri*, however, there are only five full-grown embryos, which have three rows of chaetae on the shell but no bands. Eggs with undeveloped or partially developed embryos in the uterus are very few and the uterus is often without them.

Margarya Nevill.

The collection contains only one specimen of *Margarya melanoides* Nevill in spirit, which is badly damaged and consequently no observations on the soft parts except the gill-lamella and the brain could be made.[1]

The relationship of the genus to other genera of Viviparidae with regard to the structure of the mantle-edge has been discussed by Annandale in his and Sewell's monograph on *Vivipara bengalensis.*

The head of the animal is small in proportion to its size. The gill-lamella is more or less straight, vertical and narrow, and tapers gradually from the base towards the apex. The superior margin is thickened but never thrown into folds as in *Lecythoconcha.* Heude's figure of the gill-lamella agrees more or less closely in outline with the one figured here, but the natural position of the lamella could not be made out in the specimen examined by me. The ganglia and commissures of the brain are much larger and stouter than in species of *Lecythoconcha.* The form and sculpture of the embryonic shell is quite distinct from those of other genera of Viviparids. The number of embryos found in the uterus is unknown.

Reviewing the family as a whole it is clear that while it stands distinct from the closely allied freshwater families in its viviparity and in the structure of the male organ, the genera are distinguished chiefly by the sculpture of the shell, the variety in which is due to very slight differences in the structure of the mantle-edge. The statement made by Annandale and Sewell as to its anatomical homogeneity is fully justified. There are, however, certain generic characters in the soft parts, though shell-sculpture is the main generic character.

The specific differences are subtle and exist both in the general form of the shell and in the soft parts.

The following synopsis gives the main generic differences in the soft parts of the genera examined.

a. Edge of mantle greatly thickened with a conspicuous sphincter muscle along it. Superior margin of gill-lamella usually thrown into folds — *Lecythoconcha.*

b. Edge of mantle not so thickened and without a conspicuous sphincter. Superior margin of gill-lamella never thrown into folds.

  a. Free part of gill-lamella very long with its superior margin conspicuously thickened — *Margarya.*

  b. Free part of gill-lamella relatively short with superior margin never so conspicuously thickened.

    1. Margin of mantle with enlarged and highly vascular finger-shaped processes. — *Dactylochlamys.*

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[1] Heude, *op. cit.*, pl. xliii, figs. 1 & 2.

2. Margin of mantle with only minute triangular prominences.

1. Full-grown embryos in the uterus never more than four in number. Central nervous system strongly developed. Lining of stomach thrown into folds which are often chitinised and with ridge-like chitinous thickenings at the entrance to the stomach — *Taia.*

2. Full-grown embryos in the uterus, as a rule, more than four. Central nervous system less developed. Lining of stomach without folds or chitinous thickenings — *Vivipara.*

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